Spatial and inter-decadal variability in plankton abundance and composition in the Northwest Atlantic (1958–2006)

ERICA J. H. HEAD [1]* AND PIERRE PEPIN [2]

[1]FISHERIES AND OCEANS CANADA, BEDFORD INSTITUTE OF OCEANOGRAPHY, PO BOX 1006, DARTMOUTH, NS, CANADA B2Y 4A2 AND [2]FISHERIES AND OCEANS CANADA, NORTHWEST ATLANTIC FISHERIES CENTRE, PO BOX 5667, ST JOHN'S, NL, CANADA A1C 5X1

*CORRESPONDING AUTHOR: erica.head@dfo-mpo.gc.ca

The results of Continuous Plankton Recorder sampling in the NW Atlantic between 1958 and 2006 are presented for 11 plankton taxa in eight shelf and deep ocean regions. For shelf regions, phytoplankton abundances increased in the early 1990s, mainly in winter, as the contribution of Arctic-derived freshwater to the Newfoundland (NLS) and Scotian shelves (SS) increased. Farther east, in the sub-polar gyre, phytoplankton levels increased with rising temperatures during the 1990s and 2000s. In both areas, the changes can be explained by increased stratification. The increased influx of arctic water to the NLS in the 1990s was also probably directly responsible for the increased abundances of two arctic *Calanus* species (*C. glacialis* and *C. hyperboreus*) and indirectly responsible for the decreased abundance of *Calanus* I–IV (mainly *C. finmarchicus*), perhaps via changes in food composition. On the SS the arctic *Calanus* species increased in abundance in the 2000s, likely as the result of increased transport from the Arctic via the Gulf of St Lawrence. In the deep ocean, plankton seasonal cycles changed little over the decades and increasing phytoplankton levels in the 2000s were accompanied by increases in zooplankton abundance, suggesting bottom-up control. In shelf regions, phytoplankton increases in the 1990s were in winter and *Calanus* I–IV appeared earlier in spring than in previous decades. Zooplankton levels generally did not change overall however, perhaps because the species examined were mainly inactive during winter.

KEYWORDS: Phytoplankton; zooplankton; inter-decadal change; Northwest Atlantic

INTRODUCTION

Over the last decade, there has been a proliferation of studies using the long-term data set collected by the Continuous Plankton Recorder (CPR) survey in the North Atlantic, operated by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS, e.g. Edwards *et al.*, 2001; Beaugrand *et al.*, 2002, 2009; Barton *et al.*, 2003, 2009; Beaugrand, 2003; Greene *et al.*, 2003; Leterme *et al.*, 2005; Head and Sameoto, 2007). Most have been concerned with large-scale changes in the abundance, distribution and/or diversity of a variety phytoplankton and zooplankton taxa and their links to changes in physical forcing (e.g. Richardson and Schoeman, 2004; Beaugrand, 2009; Beaugrand *et al.*,

2009) and/or the effects of fisheries (e.g. Beaugrand *et al.*, 2003, 2008; Frank *et al.*, 2005). In addition, most have been in the Northeast Atlantic and adjacent areas, where coverage has been good since 1958. There have been fewer studies in the Northwest Atlantic, where CPR sampling is mainly along one route between Iceland and New England (Fig. 1). Parts of this route have been sampled since 1957, although coverage was poor during some decades (Fig. 2).

Previous CPR studies in the NW Atlantic have generally focused on the continental shelf and Gulf of Maine, where a dramatic increase in phytoplankton abundance occurred in the early 1990s (Sameoto, 2001), which was attributed to increased stratification resulting from increased freshwater content at the surface (Johns *et al.*, 2003; Head and Sameoto, 2007). The freshwater increase is thought to have been caused by a greater contribution of arctic water to the southerly flowing on-shelf currents from the Arctic down to the Gulf of Maine (Loder *et al.*, 1998). The increased contribution of arctic water also led to increased abundances of two arctic *Calanus* species (*C. hyperboreus* and *C. glacialis*) on the Newfoundland (NLS) and Scotian shelves (SS) during the 1990s (Head and Sameoto, 2007).

The increases in phytoplankton levels in the Gulf of Maine in the 1990s were in late autumn/winter and were accompanied by increases in the abundance of several small copepod species and young-stage *Calanus* and a decrease in the abundance of late-stage *Calanus finmarchicus* (Greene and Pershing, 2000; Pershing *et al.*, 2005). On the SS and NLS, the increases in phytoplankton abundance were in late winter or early spring and were accompanied by increases in the levels of *Oithona* spp. and *Centropages* spp., and decreases in the abundance of young and late-stage *C. finmarchicus* (Head and Sameoto, 2007). The changes for the small copepods in the 1990s in the Gulf of Maine were explained in terms of bottom-up control (Pershing *et al.*, 2005). The changes in abundance of late-stage *C. finmarchicus* were attributed to changes in the supply of overwintered individuals in the Gulf of Maine (Greene and Pershing, 2000), and to increased levels of predation by small pelagic fish on the Eastern Scotian Shelf (ESS) (Frank *et al.*, 2005).

Attempts to relate changes in the plankton on the NW Atlantic continental shelves to climate, as manifested by the phase of the North Atlantic Oscillation (NAO), have met with only limited success (Greene and Pershing, 2000; Conversi *et al.*, 2001). The NAO switched from a mainly negative mode in the 1960s to
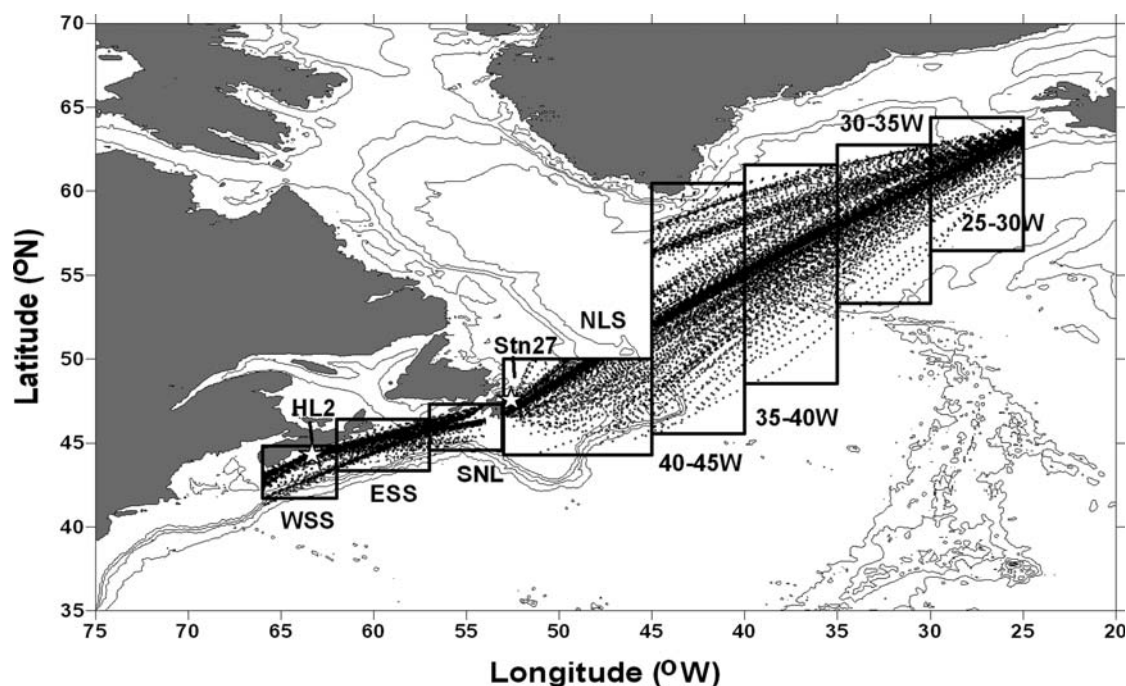
Fig. 1. Positions where individual CPR samples were collected between 1957 and 2006 and of the Atlantic Zone Monitoring Zone Programme time series stations HL2 and Stn 27, and boxes for which sea-surface temperatures were averaged. The bathymetry is represented by the 200, 1000, 2000 and 3000 m contours. The shelf regions are the Western Scotian Shelf (WSS), the Eastern Scotian Shelf (ESS), the South Newfoundland Shelf (SNL) and the Newfoundland Shelf (NLS). The regions east of the shelf are defined by their longitudinal limits (e.g. 40–45°W is bounded by 40°W and 45°W).
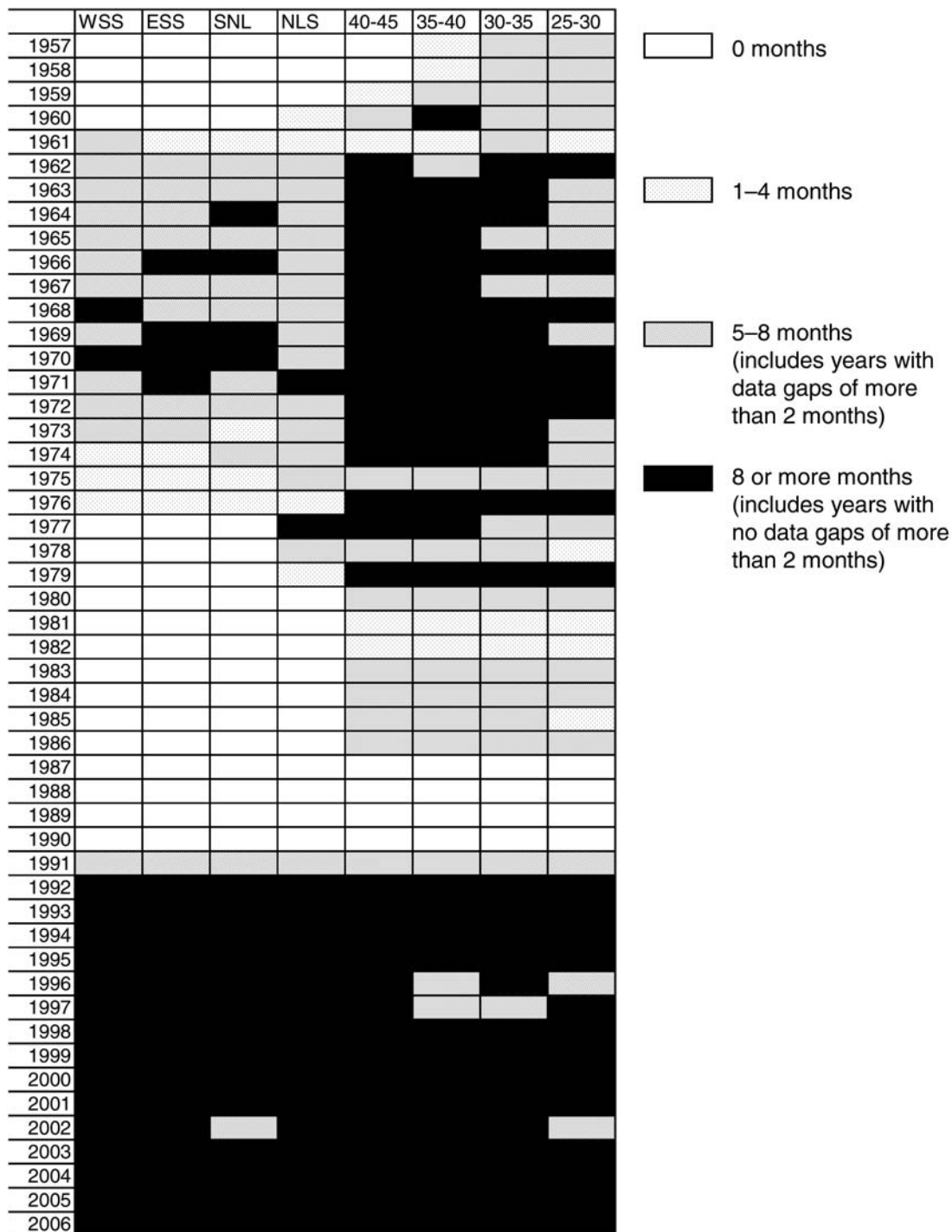
Fig. 2. Number of months sampled by the CPR in each year between 1957 and 2006 in eight regions of the NW Atlantic along the Z and E lines. The regions are as named in Fig. 1.

a mainly positive mode in the 1980s and over this period the abundance of *C. finmarchicus* increased in the Gulf of Maine (Greene and Pershing, 2000) and the two were correlated with a 4-year time lag (Conversi *et al.*, 2001) until 1989 when the relationship broke down (Greene *et al.*, 2003). *Calanus finmarchicus* abundance and the NAO were not related on the SS or NLS over the 1962 to 2003 period (Head and Sameoto, 2007), nor

were they related between the early 1960s and 2000s in the Irminger Sea region of the NW Atlantic sub-polar gyre (Heath *et al.*, 2008).

Head and Sameoto (Head and Sameoto, 2007) previously reported on the abundances of 3 CPR phytoplankton taxa and 10 zooplankton taxa on the Canadian continental shelf between 1962 and 2003. This paper will update that information to 2006 as temperatures continued an upward trend that started in the early 1990s. In addition, this paper will extend the spatial coverage to the deep waters of the NW Atlantic sub-polar gyre between Flemish Cap and Iceland. Most of the CPR taxa featured here are the same as those in Head and Sameoto (Head and Sameoto, 2007), namely, diatoms, dinoflagellates, the phytoplankton colour index (PCI), *Calanus* I–IV, *C. finmarchicus* V–VI, *C. glacialis*, *C. hyperboreus* and euphausiids. We also include an index of small copepods (*Para-Pseudocalanus* spp.), a genus of pteropod (*Limacina* spp.) and a taxon representing all foraminifera. The latter two groups are included because while ocean acidification has been identified as a threat to calcifying organisms in many regions of the world's oceans (Fabry *et al.*, 2008), it is especially imminent in cold waters such as the Arctic (Yamamoto-Kawai *et al.*, 2009) and its outflows (Azetsu-Scott *et al.*, 2010).

The objectives of this paper are: (i) to confirm previous suggestions and/or provide new insights as to the mechanisms that have led to the inter-decadal changes in plankton abundances and seasonal cycles on the Canadian continental shelf that were previously reported, or that became evident with the addition of more data from the early 2000s; (ii) to present data on the inter-decadal changes in plankton abundance and seasonal cycles in the NW Atlantic sub-polar gyre and the Irminger Sea in the same format as those on the shelves and to provide interpretations for these changes; (iii) to investigate trophic interactions between pairs of zooplankton grazers and their phytoplankton prey in shelf and deep ocean ecosystems; and (iv) to set a baseline for the abundance of acid-susceptible planktonic organisms in the NW Atlantic against which effects of ocean acidification can be judged in the future.

DATA SOURCES AND DATA ANALYSIS

CPR plankton data

The details of CPR sample collection and analysis have been reported elsewhere (Richardson *et al.*, 2006). Data on the eleven CPR categories referred to above were provided by SAHFOS under a Joint Project Agreement with Fisheries and Oceans Canada for the SAHFOS "Z" and "E" lines. The categories "diatoms" and "dinoflagellates" represent the sum of abundances of all diatom and dinoflagellate species identified in each sample. The PCI gives a semi-quantitative estimate of total phytoplankton biomass. It is determined by laying the CPR silk against a white background and by assigning each sample a colour category, by reference to a standard colour chart (Colebrook, 1960). The PCI includes contributions from both large and small phytoplankton species (Batten *et al.*, 2003). There are four categories of *Calanus* corresponding to stages V and VI of *C. finmarchicus* and *C. glacialis*, and stages III–VI of *C. hyperboreus*, while *Calanus* I–IV includes stages I–IV of *C. finmarchicus* and *C. glacialis* and stages I–II of *C. hyperboreus* (A.W.G. John, SAHFOS, personal communication). The CPR category *Para-Pseudocalanus* spp., which "includes *Paracalanus* spp., adults of *Pseudocalanus* spp. (the latter identifiable to genus but not species) and any unidentifiable small copepods (<2 mm)" (Richardson *et al.*, 2006), is used here as a general index of small copepods. Abundances are numbers per sample, which represent $\sim 3\,m^3$ and were log $(N + 1)$ transformed before further calculations were done; PCI data were not transformed in this way.

The CPR tracks were divided longitudinally into eight regions (Fig. 1). Samples collected south of the continental shelf regions were excluded, as were samples collected north of 50°N in the NLS region. There is always a trade-off when examining CPR data as to how much spatial resolution can be achieved without creating numerous data gaps. In this work, the choice as to how to divide the study area was mainly on the basis of the regional hydrography and bathymetry. The SS is strongly influenced by the outflow from the Gulf of St Lawrence (Loder *et al.*, 1998), through Cabot Strait, but the influx of slope water into central regions and plankton distributions warrant division into western and eastern regions. Farther east, the inshore branch of the Labrador Current has a strong influence on both the NLS and South Newfoundland Shelf (SNL), but while the NLS region is also influenced by the offshore branch of the Labrador Current beyond the shelf-break, the SNL is not, which is why these two regions were separated. The deep ocean regions farther east were divided at 5° longitudinal intervals, although all four regions were generally within the sub-polar gyre, the westernmost covering the central gyre and the three easternmost regions representing different portions of the Irminger Sea.

All data collected between 1958 and 2006 were included. Although the CPR survey attempts to collect

data once per month per year, very often there was no sampling in several months of a given year. As well, between 1977 and 1990, there was no sampling on most of the continental shelf and between 1987 and 1990 there was no sampling anywhere (Fig. 2).

All calculations were made using regionally averaged data. Regional monthly average abundances were calculated by averaging the log-transformed data for all samples collected within each region for individual months of individual years. Decadal monthly average abundances were then calculated by averaging these monthly averages over all years within each decade. Here the term decade is use loosely. The 1960s included data from 1958 to 1969, the 1970s included data from 1970 to 1979, the 1980s included data from 1980 to 1986, the 1990s included data from 1990 to 1999 and the 2000s included data from 2000 to 2006. Decadal annual average abundances were calculated for each region by averaging decadal monthly averages.

In order to decide whether differences in decadal annual average abundances were actually significant, estimates of the errors associated with them were required. Ideally, comparisons would have been made using decadal average annual abundances calculated from values for individual years, and their associated variance. Frequently, however, data were only available for a few months of the year, so that reliable average annual values could not be calculated (Fig. 2). Thus, we decided to make estimates of the errors for the decadal annual average abundances based on the years and decades for which data coverage was relatively good. To do this, we first calculated annual averages for individual years that included at least 8 months of data, with data gaps of no more than 2 months, using linear interpolation to fill in for missing months. Next, we calculated decadal annual averages and associated standard deviations using values for the individual years, but only for decades for which five or more individual annual average values were available. Data coverage was adequate for these calculations in all regions for the 1990s and 2000s, in nearly all deep water regions for the 1960s and 1970s and in no region in the 1980s (Fig. 2). From these decadal annual averages and standard deviations, we calculated coefficients of variation (CV), which we applied to the decadal annual averages that had been calculated from the monthly decadal averages, i.e. the values derived using all data. When no CV was available for a particular decade in a given region, the highest CV value found in any other decade in that region was used. We consider this provides a conservative estimate of the underlying uncertainty of the average abundance on a decadal time scale because it errs towards greater variance.

Table I: Longitudinal and latitudinal limits of the regions over which sea-surface temperature data were averaged

Region	Southern limit (°N)	Northern limit (°N)	Western limit (°W)	Eastern limit (°W)
WSS	41.70	44.82	66.00	62.00
ESS	43.34	46.43	62.00	57.00
SNL	44.58	47.30	57.00	53.06
NLS	44.28	50.00	53.00	45.00
40–45°W	45.55	60.47	45.00	40.00
35–40°W	48.53	61.58	40.00	35.00
30–35°W	53.32	62.76	35.00	30.00
25–30°W	56.45	64.39	30.00	25.00

WSS, Western Scotian Shelf; ESS, Eastern Scotian Shelf; SNL, South Newfoundland Shelf; NLS, Newfoundland Shelf.

Sea-surface temperature data

Sea-surface temperatures (SSTs) were taken from UK Met Office Hadley Centre's sea ice and SST data set, HadISST1. The data are provided with $1° \times 1°$ resolution (Rayner *et al.*, 2003). Regional monthly averages were calculated for boxes that covered the eight regions of the Z and E CPR lines for the years between 1960 and 2006. Annual averages were calculated from these (Fig. 1). The latitudinal and longitudinal limits of each box were defined by the limits of the CPR data (Table I).

Stratification anomalies

For the SS, stratification was calculated as the density (sigma-t) difference between 0 and 50 m. The density differences were calculated for monthly mean density profiles for sub-areas of the SS obtained from the DFO climate database held at the Bedford Institute of Oceanography. Long-term monthly mean density gradients for 1971–2000 were estimated, which were subtracted from the individual monthly values to obtain monthly anomalies. Annual anomalies for the entire shelf were estimated by averaging all available monthly anomalies within a calendar year using an area-weighted combination of sub-areas. Stratification anomalies were also calculated in a similar way for a single site, Stn 27 on the NLS (Fig. 1).

RESULTS

Inter-decadal changes in three phytoplankton taxa

Decadal annual averages for all three indices of phytoplankton abundance (diatoms, dinoflagellates and PCI) were generally higher for shelf than for the deep ocean

regions (Fig. 3). Regional and inter-decadal differences were judged to be significant when there was no overlap of the error estimates (Supplementary Data, Table S1). The shelf/deep ocean differences were not generally significant for diatoms and the PCI in the 1960s and 1970s, but generally were after the 1990s. Dinoflagellate abundances were, however, significantly higher in shelf regions in all decades.

Diatom abundances decreased significantly on the ESS and SNL between the 1960s and 1970s, and increased significantly in those areas and on the Western Scotian Shelf (WSS) between the 1970s and the 1990s (Fig. 3, Supplementary Data, Table S1). Diatom levels in the 2000s were similar to those in the 1990s on the SS and SNL, and on the NLS they rose to be significantly higher than those of the 1960s and 1970s. None of the inter-decadal changes in the deep ocean were significant.

The abundance of dinoflagellates and the PCI did not change significantly between the 1960s and 1970s in any of the shelf regions, but levels of both increased significantly in all four shelf regions between the 1970s and 1990s, remaining unchanged in the 2000s (Fig. 3, Supplementary Data, Table S1). In the deep ocean, there were no significant changes over the decades, except that in the 40−45°W region dinoflagellate abundance was higher in the 2000s than in all previous decades except the 1960s, and in the 30−35°W region

the PCI was higher in the 1990s and 2000s than in previous decades.

For three representative regions (Fig. 4), the maximum abundance of diatoms and the maximum value of the PCI occurred earliest in the year in the southwest (WSS, March or April), at an intermediate date in a mid-latitude region (NLS, April or May) and latest in the northeast (30−35°W, May or June). Over the decades, the increases in diatom abundance and the PCI in the 1990s were mostly in the winter months (January−March) on the continental shelf. In the deep ocean, diatoms and the PCI started increasing earlier in the year in the 2000s than in previous decades. On the continental shelf, dinoflagellates were most abundant in summer (WSS) or autumn (NLS) prior to the 1990s. During and after the 1990s, however, dinoflagellate abundances were also relatively high earlier in the year, and on the NLS, they remained high year-round. In the deep ocean, the seasonal cycle of dinoflagellate abundance was similar to those of the other groups before the 2000s, but peak abundance appeared earlier in the 1990s and 2000s than in previous decades.

Inter-decadal changes in four *Calanus* taxa

The abundance of *Calanus* I−IV on the NLS in the 1960s was significantly higher than in any other region in any decade (Fig. 5, Supplementary Data, Table S2). The value in the 1970s was still relatively high on the NLS, but not significantly different from other decades, or from some of the decadal averages in other regions and decades. Otherwise, abundances were fairly similar in all regions for all decades, except for slight increases in regions east of 35°W in the 2000s, the only significant one being in the 30−35°W region. In all decades, the seasonal cycle of *Calanus* I−IV had broad abundance peaks during early to mid-summer on the WSS and during mid- to late summer in the 30−35°W sub-polar gyre region (Fig. 6). In both of these regions, higher levels occurred earlier in the year in the 1990s and 2000s on the WSS and in the 2000s in the 30−35°W sub-polar gyre region. On the NLS in the 1960s and 1970s, there were broad peaks of *Calanus* I−IV abundance from mid-summer through to winter. The pattern was similar in the 1990s and 2000s, but peak abundances were lower.

The abundance of *Calanus finmarchicus* V−VI on the WSS and ESS and the SNL showed the same low−high−low−high patterns over the decades (Fig. 5, Supplementary Data, Table S2), but the only significant differences were those on the ESS between the 1970s and 1990s and between the 1990s and the 2000s. Abundances on the NLS showed a downward trend
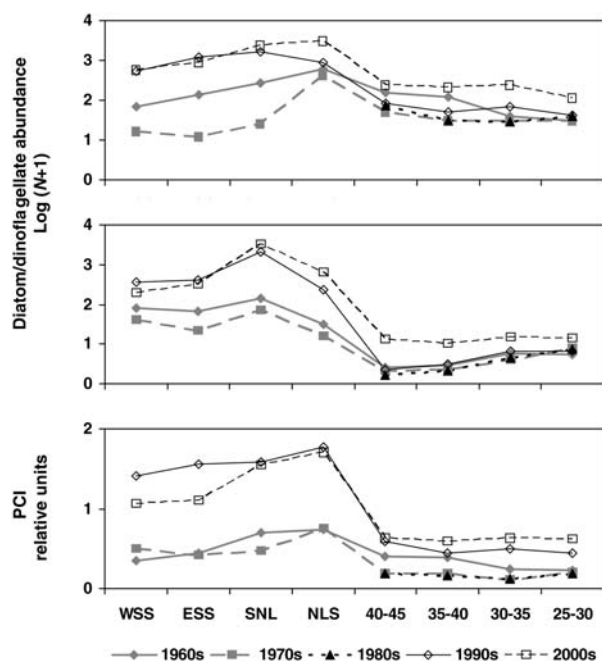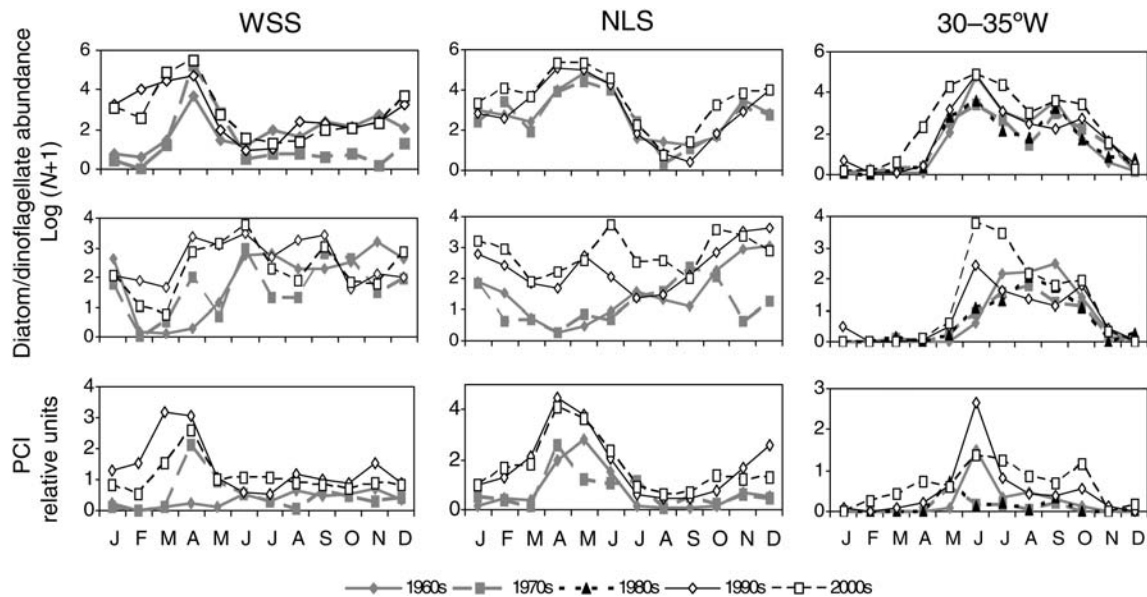

Fig. 3. Decadal annual average abundances of diatoms (top panel) and dinoflagellates (middle panel) and the phytoplankton colour index (PCI, bottom panel) in eight regions of the Northwest Atlantic.

Fig. 4. Seasonal cycles, by decade, of the abundance of diatoms (top row) and dinoflagellates (middle row) and the PCI (bottom row) in three regions of the Z and E CPR lines across the Northwest Atlantic.

over the decades, but no significant differences. There were no inter-decadal changes in abundance of *C. finmarchicus* V–VI in the sub-polar gyre. The seasonal cycle of *Calanus finmarchicus* V–VI abundance on the WSS was inconsistent over the decades (Fig. 6). On the NLS, there appeared to be two broad peaks in abundance separated by months of consistently low abundance in August and January. In the 30–35°W sub-polar gyre region, the seasonal cycle also appeared to show two peaks, which were compressed to cover a shorter period of the year, so that abundances were very low during winter, and dipped in July and August.

Calanus glacialis V–VI abundance was significantly higher on the NLS than in any other region in every decade (Fig. 5, Supplementary Data, Table S2) and significantly higher there in the 1990s and 2000s than in the earlier decades. Abundances increased in the 1990s and/or 2000s in other shelf regions, but differences were not generally significant, due to high variability. East of 40°W abundances were always extremely low, too low to merit the detailed examination of seasonal cycles. On the WSS and NLS, *C. glacialis* V–VI was only found during the first half of the year (Fig. 6).

Calanus hyperboreus III–VI abundance was higher on the NLS Shelf than in any other region in every decade (Fig. 5, Supplementary Data, Table S2) and these inter-regional differences were generally significant, except that the abundance on the NLS was not different from that in the adjacent deep ocean region (40–45°W) in the 1990s, nor from that on the ESS in the 2000s. The inter-annual variability in all regions was such that the

only significant intra-regional difference between decades was on the ESS, where the abundance in the 2000s was higher than in the 1960s and 1970s. In all decades, *C. hyperboreus* III–VI was present for only 2 or 3 months (April–June) on the WSS and NLS (Fig. 6), as was the case for all regions west of 45°W: farther east, it was only seen in May.

Inter-decadal changes in other zooplankton taxa

Euphausiid abundance was generally highest in the deep ocean between 35 and 45°W and lowest on the SNL (Fig. 7, Supplementary Data, Table S3). On the WSS, abundances in the 1960s and 1970s were not significantly different from each other, but both were significantly higher than values in the 1990s and 2000s. In the other shelf regions, abundances were higher in the 1970s than in other decades, but not significantly so. There were no significant differences between decadal annual average abundances in the deep ocean, except in the 40–45°W region, where the abundance in the 2000s was lower than in the 1970s.

Small copepods, as manifested by the CPR taxon "*Para-Pseudocalanus*", were significantly more abundant on the SS and SNL than in the deep ocean, with the NLS showing an intermediate abundance, which was generally significantly different from shelf and deep ocean regions (Fig. 7, Supplementary Data, Table S3). Inter-decadal changes in abundance were not significant for shelf regions, but farther east decadal annual average
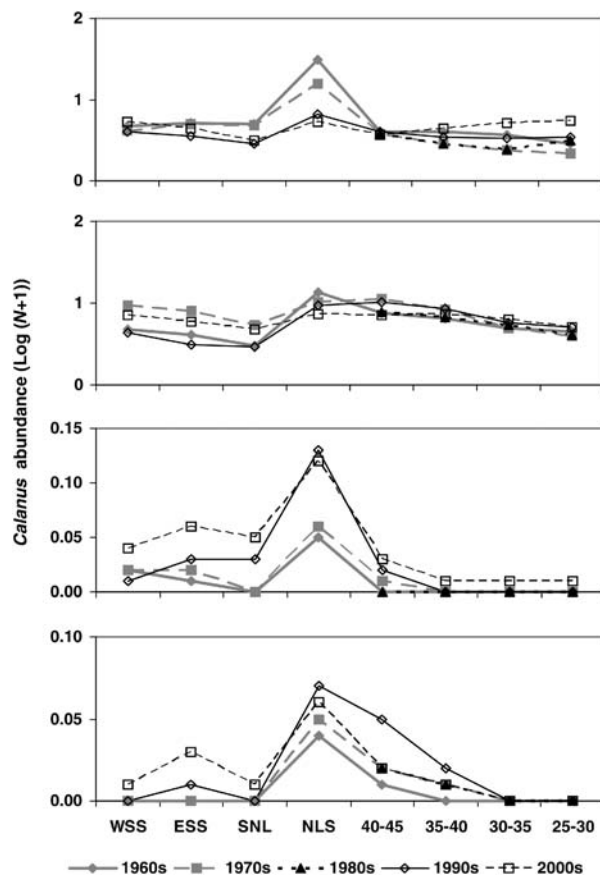
Fig. 5. Decadal annual average abundances of *Calanus* I–IV (top panel), *C. finmarchicus* V–VI (second panel), *C. glacialis* (third panel) and *C. hyperboreus* (bottom panel) in eight regions of the Northwest Atlantic.

abundances were generally significantly higher in the 2000s than in the 1960s, 1970s and 1980s. In shelf regions, there were no pronounced seasonal cycles of abundance for small copepods and in deep ocean regions seasonal cycles were similar to those for phytoplankton abundance (i.e. elevated between May and November) with no changes over the decades (data not shown).

Identification and enumeration of foraminifera only started at SAHFOS in 1993 and thereafter foraminifera were more abundant in the deep ocean than in shelf regions (Fig. 7, Supplementary Data, Table S3), with inter-regional differences significant only between the SNL region and regions between 30 and 40°W. No inter-decadal changes were significant. In shelf regions, there were no pronounced seasonal cycles, and in the deep ocean regions, seasonal cycles more-or-less followed the phytoplankton abundance cycles with no changes between decades (data not shown).

Decadal annual average abundances for the sum of all *Limacina* species were generally very variable and regional differences were generally not significant

(Fig. 7, Supplementary Data, Table S3). The only significant inter-decadal changes were the increases in abundance that occurred on the NLS between the 1970s and 1990s and in the 35–40°W region between the 1980s and 1990s.

Relationships between potential predator/prey groups

Relationships between decadal annual average abundances of zooplankton grazers and potential phytoplankton prey were examined using linear regression analysis (Table II). In shelf regions, there were few significant correlations (12.5% of pairs), which were all negative and were between either *Calanus* I–IV or euphausiids and one or more of the phytoplankton indices. In deep ocean regions east of 40°W, there was a higher proportion of significant correlations (29%), which were all positive and were between *Calanus* I–IV, *C. finmarchicus* V–VI and/or small copepods and one of the phytoplankton indices.

Inter-decadal changes in sea-surface temperature and stratification and relationships with plankton abundance

Decadal average SSTs were coolest in the 1970s on the NLS and warmest in the 2000s on the WSS (Fig. 8). The 1960s were relatively cool on the WSS and relatively warm in the deep ocean regions (sub-polar gyre). All regions were warmest in the 2000s. Linear regression analysis showed that there were more significant relationships between the phytoplankton indices and SST than between zooplankton taxa and SST (Table III); most were in the deep ocean and all were positive.

Stratification data were only available for the SS and the NLS (Stn 27). Inter-annual variability was high, but over the decades both time series showed increasing trends between the 1960s and 1990s, and lower levels in 2000–2006 (Fig. 9). Decadal annual average PCI values were significantly positively correlated with those for the stratification anomalies on the WSS ($R^2 = 0.98$, $P < 0.05$), ESS ($R^2 = 0.91$, $P < 0.05$) and NLS ($R^2 = 0.92$, $P < 0.05$), but diatom and dinoflagellate abundance and stratification were not significantly related in any of the three regions.

DISCUSSION

Phytoplankton taxa

There have been several studies examining the changes in abundance of phytoplankton indices as measured by CPR sampling in the Northwest Atlantic, or regions
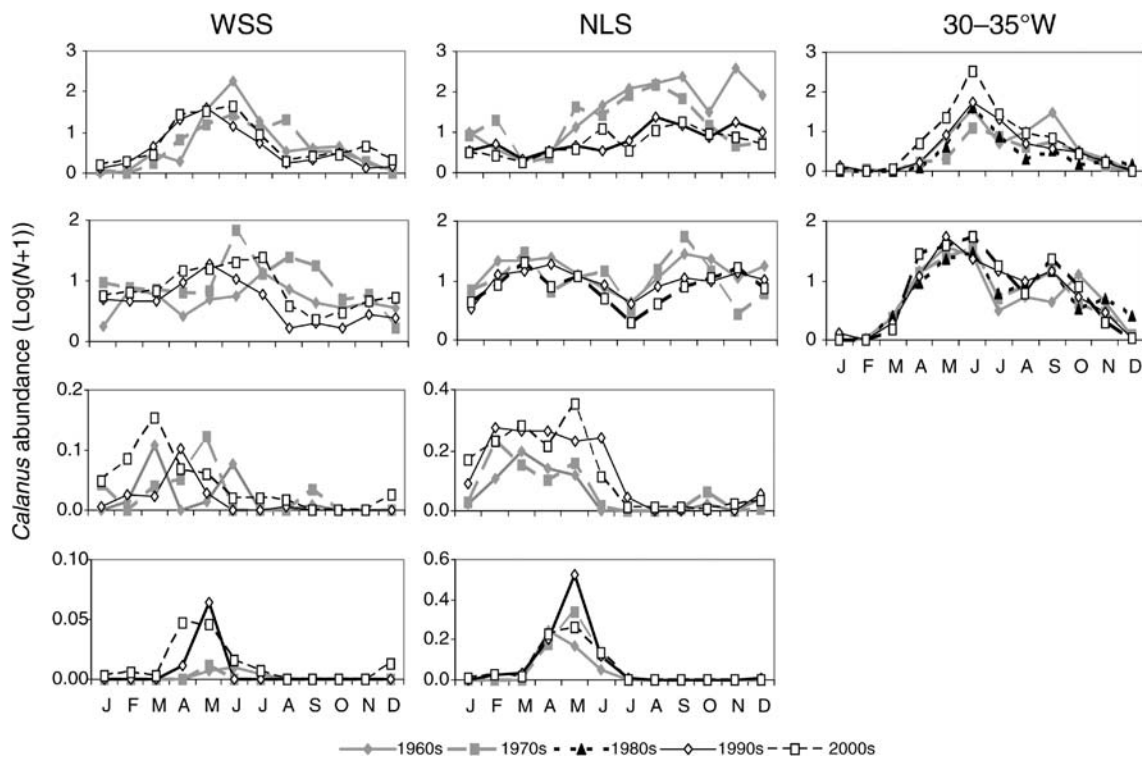
Fig. 6. Seasonal cycles, by decade, of the abundances of *Calanus* I–IV (top row), *C. finmarchicus* V–VI (second row), *C. glacialis* (third row) and *C. hyperboreus* (bottom row) in three regions of the CPR Z and E lines in the Northwest Atlantic.

thereof, but none have used data extending into the mid-2000s, and the areas over which plankton abundances were spatially averaged were somewhat different from the ones used here. Barton *et al.* (Barton *et al.*, 2003) averaged values of the PCI over the SAHFOS standard areas to examine trends throughout the North Atlantic, while Leterme *et al.* (Leterme *et al.*, 2005) used data aggregated over somewhat larger areas to examine trends in the PCI and the abundances of diatoms and dinoflagellates, again over the entire North Atlantic. Neither study actually showed the spatial distributions of phytoplankton abundance, which are shown here (Fig. 3). The results presented here are largely consistent with those of Barton *et al.* (Barton *et al.*, 2003) and Leterme *et al.* (Leterme *et al.*, 2005), except that by extending the time series to 2006, it was possible to observe the effects of a noticeable temperature increase between the 1990s and 2000s (Fig. 8), which were generally most marked in deep ocean regions (Table III, Figs 3 and 7).

On the SS average temperatures and salinities were both higher in 2000–2006 than in the 1990s, and although the average stratification anomaly was lower (Fig. 9), it was still higher than it had been in the 1960s and 1970s. On the NLS, average temperatures and salinities were also higher in the 2000–2006 than in the

1990s, and stratification also decreased, but only very slightly. Head and Sameoto (Head and Sameoto, 2007) found that the annual average PCI on the SS and NLS was correlated with the annual stratification index. Here, on a decadal time scale, PCI was again significantly correlated with stratification. The inter-decadal changes in PCI occurred mainly during the winter months (Fig. 4), when increased stratification would be expected to enhance phytoplankton growth, by reducing vertical mixing and hence light limitation (e.g. Doney, 2006). Ji *et al.* (Ji *et al.*, 2007) found that between 1998 and 2006, the timing of the bloom on the WSS was related to an index of sea-surface salinity nearby in the eastern Gulf of Maine, with earlier blooms in low salinity years. This is consistent with our results, because salinity contributed more than temperature to stratification throughout the 1990s and 2000s (B. Petrie, BIO, personal communication).

Diatom abundances on the WSS and ESS increased in winter in the 1990s in the same way as did the PCI, but decadal annual average abundances were not significantly correlated with stratification anomalies; nor were they on the NLS. Nevertheless, annual stratification anomalies on the SS and the NLS were lower in the 1960s and 1970s than in the 1990s and 2000s, as was diatom abundance, and the increases in diatom
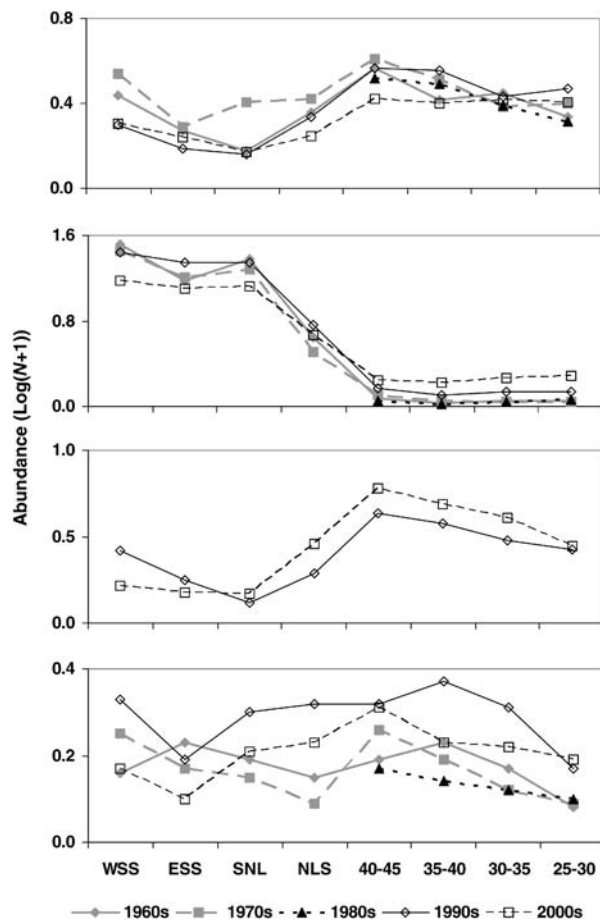
Fig. 7. Deacadal annual average abundances of euphausiids (top panel), small copepods (second panel), foraminifera (third panel) and *Limacina* spp. (bottom panel) in the NW Atlantic.

abundance were mainly at the time of year when increased stratification should promote higher growth rates (i.e. winter/spring). Annual average phytoplankton abundances reflect processes that occur during all seasons, but while increased stratification in winter/spring may increase growth rates then, and make for earlier blooms, thereafter it reduces nutrient supply from depth, leading to lower growth rates, especially for large phytoplankton, such as diatoms, which cannot compete effectively for scarce nutrients. Since the PCI is an index that reflects the abundance of both small and large phytoplankton (Batten *et al.*, 2003), the former which can compete better for nutrients than diatoms in summer when nutrient levels are low, it is perhaps reasonable that its decadal annual average should be more closely related to the decadal annual stratification anomaly than was that of diatom abundance.

Dinoflagellates, despite their large size, can compete for nutrients in well-stratified waters by swimming to the depth of the nitracline at night to absorb nutrients, returning to the surface layers to grow during the day. For this reason, they are generally abundant in summer and early autumn. On the SS, the increase in abundance in the 1990s/2000s was most obvious in May (Fig. 4), as the spring bloom was ending. On the NLS, dinoflagellate abundance increased most during the first half of the year in the 1990s/2000s (Fig. 4) and this was also the case on the SNL (data not shown). In all four shelf regions, the increases in dinoflagellate abundance were consistent with increased stratification.

In all four deep ocean regions, there were slight, albeit statistically insignificant, increases in abundance

Table II: *Results of linear correlation analysis of the decadal average abundances of zooplankton grazers versus those of their phytoplankton prey*

| Region	WSS	ESS	SNL	NLS	40–45°W	35–40°W	30–35°W	25–30°W
Diatoms as prey								
Calanus I–IV		−0.93*				0.94**	0.81*	0.88*
C. finmarchicus V–VI							0.79*	
Euphausiids	−0.99**			−0.94*				
Smcopes.							0.99**	0.96**
Dinoflagellates as prey								
Calanus I–IV							0.91*	
C. finmarchicus V–VI								
Euphausiids	−0.93*							
Smcopes.						0.90*	0.93**	
PCI as prey								
Calanus I–IV			−0.94*			0.89*		0.78*
C. finmarchicus V–VI							0.78*	
Euphausiids		−0.94*						
Smcopes.							0.88*	0.94**

Values are R^2, with the sign indicating the sign of the relationship. Levels of significance are *$P < 0.05$, **$P < 0.01$.
Smcopes. stands for small copepods (the CPR category *Para-Pseudocalanus* spp.).

of both diatoms and dinoflagellates in the 2000s over previous decades, and in the PCI in three regions, which were matched by increases in temperature (Figs 3 and 8, Supplementary Data, Table S1), with decadal average annual temperatures significantly correlated with the phytoplankton indices in 41% of the cases (Table III). Harrison and Li (Harrison and Li, 2007) concluded that between 1994 and 2005, stratification increased in the northwest arm of the sub-polar gyre (i.e. the central Labrador Sea) and they also found that light was more important than nutrients in regulating phytoplankton growth for most of the year, with nitrate becoming limiting only in late summer. Also, using weekly estimates of chlorophyll concentration derived from remote sensing, Head *et al.* (Head *et al.*, 2010) found that spring blooms in the central Labrador Sea started progressively earlier as late winter/early spring temperatures increased between 1998 and 2006, which they also attributed to earlier/increased stratification. This may also have been occurring in the deep ocean regions sampled by the CPR. Unlike the more southerly shelf regions (e.g. the SS), however, increased stratification did not lead to winter blooms, because of low ambient light levels at these latitudes.

Calanus taxa

The abundance of *Calanus* I−IV was quite stable over the decades on the SS (Fig. 5, Supplementary Data, Table S1). What did change, however, was the timing of
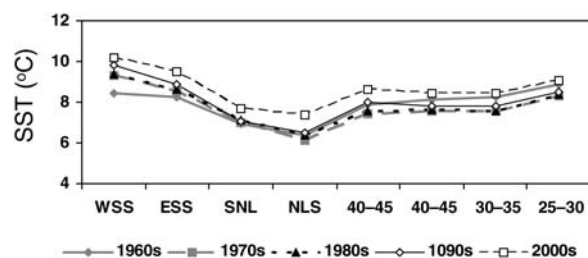
**Fig. 8.** Decadal annual average sea-surface temperatures (SSTs) in the NW Atlantic.

the appearance of the young stages. Bi-weekly net sampling at the fixed station HL2 (Fig. 1) in the Canadian Atlantic Zone Monitoring Programme (AZMP, Therriault *et al.*, 1998) has shown that between 1999 and 2006 young-stage *C. finmarchicus* appeared at HL2, on average, in April and disappeared by August, similar to CPR results for the WSS in the 1990s and 2000s. AZMP sampling has also shown, however, that *C. finmarchicus* young stages appeared earlier when late winter temperatures were warm, and/or when the spring bloom was early (Head and Pepin, 2008). Consistent with these observations, high abundances of the CPR category *Calanus* I−IV occurred earlier in the year in the 1990s and 2000s (Fig. 6), decades when average annual (and winter) temperatures were higher (Fig. 8) and spring blooms were earlier (Fig. 4), than in the 1960s and 1970s. The earlier emergence of young stages did not, however, lead to increased annual average abundances of *Calanus* I−IV or *C. finmarchicus* V−VI.

On the NLS, *Calanus* I−IV were significantly more abundant in the 1960s than in either the 1990s or 2000s, with intermediate values in the 1970s (Fig. 5, Supplementary Data, Table S2). At Stn 27, outside St John's harbour (Fig. 1), net sampling has shown that young-stage *C. finmarchicus* have a prolonged presence in the surface layers, from May to January (Head and Pepin, 2008; Head *et al.*, 2010) and this is also apparent in the CPR data (Fig. 6). The peak in *Calanus* I−IV abundance occurs much later on the NLS than on the SS, probably because of the relatively low temperature there, which delays reproduction (Melle and Skjoldal, 1998) and reduces growth and development rates (Campbell *et al.*, 2001). In contrast to the SS, the peak in *Calanus* I−IV abundance on the NLS is later than the peaks in diatom abundance and the PCI, as is also seen via AZMP sampling at Stn 27 (Head *et al.*, 2010). Similar to the SS, however, warmer conditions and earlier blooms promote the earlier appearance of young-stage *C. finmarchicus* at Stn 27 (Head and Pepin, 2008; Head *et al.*, 2010), which is not apparent in the CPR data, probably due to inadequate temporal resolution.

Table III: Results of linear regression analysis of decadal average plankton abundances versus those of sea-surface temperatures

Region	WSS	ESS	SNL	NLS	40–45°W	35–40°W	30–35°W	25–30°W
Diatoms				0.99**		0.99**		
Dinoflagellates					0.82*	0.81*		
PCI					0.82*	0.83*		
Calanus I−IV						0.94**	0.92*	
Euphausiids				0.92*				
Smcopes.								

Values are R^2, with the sign indicating the sign of the relationship. Levels of significance are *$P < 0.05$, **$P < 0.01$.
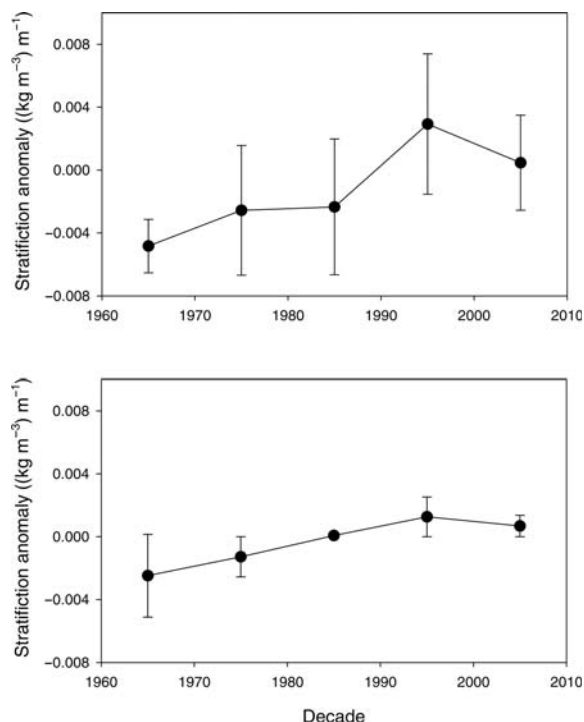
Fig. 9. Decadal average annual stratification anomalies for the Scotian Shelf (upper panel) and at Stn 27 (Newfoundland Shelf) (lower panel) relative to the 1971–2000 averages.

The decrease in *Calanus* I–IV abundance that occurred on the NLS was the most notable change seen for this taxon anywhere, and merits discussion. One possibility is that it was caused by changes in the food supply (i.e. the phytoplankton). The increases in diatoms and the PCI occurred in February–May, when young *Calanus* stages were only starting to appear, but dinoflagellate levels increased during most months, with *Ceratium arcticum* in particular becoming much more abundant in autumn and winter (Johns *et al.*, 2003). Some *Ceratium* species are unpalatable to *C. finmarchicus* (Teegarden *et al.*, 2001), and if the dinoflagellate species that became more abundant during summer in the 1990s were also unsuitable, then decreasing *Calanus* I–IV abundance might have been linked to an increasing proportion of poor quality items in the food. Despite the changes in food conditions, however, the decadal average abundance for *C. finmarchicus* V–VI did not change. This population is probably re-stocked by individuals overwintering in the adjacent slope waters in spring (Head and Pepin, 2007), and by advection in spring and summer (e.g. in the Labrador Current), which might make it less susceptible to changes in local feeding conditions.

In the deep ocean, as represented by the 30–35°W region, the decadal average abundance of *Calanus* I–IV

increased in the 2000s as temperatures and phytoplankton levels increased (Fig. 5, Tables II and III) and, as on the SS, the seasonal cycle of abundance in the 2000s and the spring bloom both appeared to show advances in timing (Figs 4 and 6). These observations are consistent with those of Head *et al.* (Head *et al.*, 2010) in the Labrador Sea, who found that between 1998 and 2006, as temperatures warmed and spring blooms started progressively earlier, *C. finmarchicus* populations sampled in late May were more developed each year. Decadal average abundances of *C. finmarchicus* V–VI in the deep ocean were generally similar to or higher than those on the continental shelf, and did not change over the decades (Fig. 5, Supplementary Data, Table S2); neither did the seasonal cycle of abundance (Fig. 6).

Calanus glacialis and *C. hyperboreus* are slow growing arctic species, which have multi-year life-cycles, with overwintering occurring in one of any of the CIV–CVI stages for the former and CIII–CVI stages for the latter (Conover, 1988). In the central and southern Labrador Sea, *C. glacialis* is restricted to the shelves, the regions most influenced by arctic outflow (Head *et al.*, 2003). *Calanus hyperboreus* is also most concentrated over the shelves, but is also found in low numbers in the central basin in spring. Bi-monthly net sampling at Stn 27 between 1999 and 2006 shows that the arctic species were generally dominant during March to May, when young-stage *C. finmarchicus* were not very abundant so that averaged over the entire year, young-stage *C. hyperboreus* and *C. glacialis* comprised only ∼20% of all of the CPR *Calanus* I–IV category. Similarly, regular net sampling at HL2 shows that over the 1999–2006 period, the young stages of the two arctic species made up only ∼10% of the *Calanus* I–IV category on an annual basis. Thus, all previous discussions that assume that the CPR category *Calanus* I–IV is equivalent to *C. finmarchicus* I–IV are valid.

Late stages of *C. glacialis* (V–VI) and *C. hyperboreus* (III–VI) were only encountered in CPR samples from the SS and NLS during part of the year, and this was also the case for young and late stages for net samples collected at Stn 27 and HL2, where sampling is over the entire water column (Head and Pepin, unpublished results). Thus, the arctic populations in these regions are transients, and must be replenished every year. Reproductive females are more than 1 year old, so that their original source populations may be quite remote, but any late-stage individuals arriving on the shelves in late winter/spring must have spent the previous winter in deep water areas that are relatively close. For the NLS, such areas are probably located to the north on the Labrador Shelf (e.g. in the saddles or Labrador fjords) or the slope waters adjacent to the shelf. The

increased proportion of arctic water on the NLS in the 1990s thus led to a greater influx of arctic organisms. For the SS, the source of overwintering arctic *Calanus* is the Gulf of St Lawrence, via Cabot Strait and the Nova Scotia Current (Sameoto and Herman, 1992; Head *et al.*, 1999). Relatively high concentrations (10 000–35 000 ind. m^{-2}) of *C. hyperboreus* (mainly CIVs and CVs) were found at overwintering depths of 200–400 m in Cabot Strait in autumn between 2003 and 2007 (Head, unpublished results). Plourde *et al.* (Plourde *et al.*, 2003) found lower concentrations (<8000 ind. m^{-2}) in the lower St Lawrence Estuary and concluded that the population there could not be self-sustaining, but must rely on being replenished periodically by an influx of water and organisms from the Labrador Shelf via the Strait of Belle Isle. This influx of water varies in magnitude from year-to-year and was higher during the early 2000s than during the last half of the 1990s (Galbraith, 2006; Galbraith *et al.*, 2009), consistent with the observation that the arctic species became more abundant on the SS in the 2000s than they had been in the 1990s. There is also influx of water into the Cabot Strait region from along the shelf-break to the south via the Laurentian Channel (Loder *et al.*, 1998), but concentrations of *C. hyperboreus* in the slope waters upstream of the mouth of the Laurentian Channel (off St Pierre Bank) in autumn 2003 and 2006 were <300 ind. m^{-2} in the 0–1000 m depth range, whereas downstream (off Banquereau Bank) they were >7 000 ind. m^{-2} (Head, unpublished results), suggesting that Cabot Strait is a source to the slope waters, rather than the reverse so that the increased abundance of arctic *Calanus* on the SS in the 2000s was probably linked to increased advection from the Labrador Shelf via the Gulf of St Lawrence.

Other zooplankton taxa

Euphausiid concentrations were generally higher in the deep ocean than in shelf regions, except on the WSS, where concentrations were relatively high in the 1960s and 1970s (Fig. 7). While decadal changes were generally not significant (Supplementary Data, Table S3), the decrease on the WSS between the 1970s and 1990s was, and it may have had an impact on at least one commercial fish species. There were less euphausiids in the diet of pollock on the SS in the 1990s than in the 1960s, and the fish were in poorer condition and less abundant (Carruthers *et al.*, 2005).

Foraminifera were generally more abundant in the deep ocean than on the SS and the SNL, whereas small copepods showed the opposite pattern (Fig. 7). Abundances were intermediate for both in the NLS region, which covers deep water and shelf areas. In the deep ocean, the seasonal cycles of all three taxa followed those of the phytoplankton, which was not the case in shelf regions. *Limacina* spp. showed no affinity with deep water or shelf regions and there were no obvious changes in abundance over time.

Relationships between plankton taxa and with sea-surface temperature and stratification

Positive relationships between the abundance of predators (grazers) and prey (phytoplankton) are indicative of food limitation of the predators (i.e. bottom-up control). Such relationships are more likely where food (phytoplankton) levels are low, which is consistent with the observation that significant positive correlations were observed between the abundances of *Calanus* I–IV, *C. finmarchicus* V–VI and small copepods and one, or more, of the three phytoplankton groups in deep ocean regions, but not in shelf regions (Table II). The possibility of food limitation of young *Calanus* I–IV is supported by the suggestion that *C. finmarchicus* nauplii are severely food-limited in the Irminger Sea (Heath *et al.*, 2008) and food limitation of the other taxa seems plausible. In fact, these three taxa tended to show positive relationships with all three phytoplankton indices, although correlations were generally not significant. The abundance of foraminifera also increased with the increase in phytoplankton levels from the 1990s to the 2000s. The genus most often found in the CPR samples was *Globigerina* (M. Edwards, SAHFOS, personal communication) and the species was most probably *G. bulloides* (Schiebel *et al.*, 1997; Darling and Wade, 2008), which is an herbivore that increases its growth rate in response to increasing phytoplankton production (Schiebel *et al.*, 2001). Thus, the abundance of the CPR category "foraminifera" seems to be regulated by bottom-up control in the NW Atlantic. The influence of increasing temperature on zooplankton abundance, via a direct effect on growth rates, cannot be assessed here, because phytoplankton levels also generally increased with increasing temperature (Table III).

Negative correlations between abundances of predator and prey are indicative of top-down control (i.e. of grazers controlling the abundance of the phytoplankton) as has been postulated by Frank *et al.* (Frank *et al.*, 2005) for the ESS. Here, however, significant negative relationships over the decades were relatively rare, occurring only in shelf regions and only for *Calanus* I–IV and euphausiids. Whether these relationships are indicative of top-down control is debatable, since in only one region (the WSS) did any of the zooplankton

1645

taxa (euphausiids) actually change significantly in abundance over the decades, and euphausiids only represent a small proportion of the grazer biomass on the continental shelves. Furthermore, here and elsewhere, the increases in phytoplankton concentrations on the NW Atlantic shelf and in the Gulf of Maine in the 1990s have been attributed to increased stratification (Johns *et al.*, 2003; Head and Sameoto, 2007; Ji *et al.*, 2007; Greene *et al.*, 2008). If the latter is the correct interpretation, then the negative relationships between the abundances of zooplankton and phytoplankton abundance are not the result of the release of grazer control, but rather are reflections of the characteristics a new, alternative, ecosystem state; one with higher annual phytoplankton levels and (slightly) lower annual abundances for some zooplankton taxa. Reduced euphausiid abundance in this new state may be related to increased predation by the high abundance of small pelagic fish, but between 2000 and 2006 the abundance of *C. finmarchicus* V–VI on the ESS was closer to the high level of the 1970s than to the low level of the 1990s, whereas the abundance of small pelagic fish was equally high in the 1990s and 2000s (N. Shackell, BIO, personal communication), suggesting that its abundance is not closely related to this predation pressure.

Abundance, production and trophic interactions

One question that arises from these observations is the degree to which changes in phytoplankton abundance reflect changes in primary production, and specifically "new" production, i.e. the portion fuelled by nitrate from depth that is available for transfer up the food chain. Increased stratification reduces vertical mixing in the water column and increases phytoplankton growth rates in areas where and when the mixed layer depth generally exceeds the critical depth (Doney, 2006). On the other hand, when the nutrients in the near-surface layers have been used up, increased stratification reduces new production. In the NW Atlantic, nutrient levels are near zero in the near-surface waters in shelf regions for most of the summer (Pepin *et al.*, 2008; Harrison *et al.*, 2009), while in the Labrador Sea (sub-polar gyre) they become limiting for only a relatively short period of the year (Harrison and Li, 2007). In addition, sub-surface nutrient concentrations on the SS decreased slightly between the 1960s and the 1990s (P. Yeats, BIO, personal communication), whereas they increased slightly between 1990 and 2006 in the Labrador Sea (Harrison and Li, 2007). Thus, it seems that while increases in phytoplankton abundance on the shelf were probably not associated with increases in

new production, in the sub-polar gyre, they probably were. As well, however, for the shelf regions, the proliferation of diatoms during winter in the 1990s and 2000s may have been the result not only of higher growth rates, but also of low grazing rates, since zooplankton are not very abundant in winter (Pepin *et al.*, 2008; Harrison *et al.*, 2009), the inference being that this winter production mostly sank out as the bloom ended. For the deep ocean regions, on the other hand, enhanced growth in the 2000s occurred during the "normal" phytoplankton and zooplankton growth season. Several zooplankton groups/species would have been ready to take advantage of the seasonal increase in phytoplankton production, and did apparently increase their productivity.

SUMMARY AND CONCLUSIONS

For shelf regions, the addition of data from 2004–2006 to that reported previously (Head and Sameoto, 2007) supports the idea that increased arctic freshwater outflow in the early 1990s led to the most significant changes in their ecosystems, at least at the level of the plankton. Primarily, it caused increased stratification, which led to higher annual phytoplankton abundances and earlier blooms, the latter which led to an advance in the seasonal cycle of *C. finmarchicus* on the SS. In contrast, similar changes in stratification and phytoplankton abundance and seasonal cycles on the NLS apparently led to lower *C. finmarchicus* productivity, perhaps because of changes in phytoplankton (food) composition. The increased arctic inflow also brought an influx of arctic species, notably *C. glacialis* and *C. hyperboreus*, which were transported directly to the NLS, but indirectly (via the Gulf of St Lawrence) to the SS.

For the deep ocean regions, decadal average abundances of the individual planktonic taxa were similar everywhere, except that the arctic *Calanus* species were confined to the more western regions. The most important influence seems to have been the steady increase in temperature that occurred through the 1990s and 2000s. This seems to have contributed to increased stratification, stimulating phytoplankton production, especially during the early part of the growth season, and to have led, directly or indirectly, via its influence on the phytoplankton, to increased production for some zooplankton taxa.

Finally, there have, as yet, been no discernable changes in the abundance of the acid-sensitive taxa *Limacina* spp., organisms with aragonite shells, which are equally abundant in shelf and deep ocean regions, or foraminifera, organisms with calcite shells, which are

found mainly in the sub-polar gyre, although there has been a detectable decrease in the pH in the NW Atlantic sub-polar gyre (Labrador Sea, Azetsu-Scott *et al.*, 2010). The abundances reported here should therefore be regarded as baselines against which effects of ocean acidification can be judged in future.

SUPPLEMENTARY DATA

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

ACKNOWLEDGEMENTS

FUNDING

REFERENCES

Azetsu-Scott, K., Clarke, A., Falkner, K. *et al.* (2010) Calcium Carbonate Saturation States in the waters of the Canadian Arctic Archipelago and the Labrador Sea: Corrosive Arctic outflows to the North Atlantic. *J. Geophys. Res.* (under review).

Barton, A. D., Greene, C. H., Monger, B. C. *et al.* (2003) The Continuous Plankton Recorder survey and the North Atlantic Oscillation: interannual to multidecadal-scale patterns of phytoplankton variability in the North Atlantic Ocean. *Prog. Oceanogr.*, **58**, 337–358.

Batten, S. D., Walne, A. W., Edwards, M. *et al.* (2003) Phytoplankton biomass from continuous plankton recorder data: an assessment of the phytoplankton colour index. *J. Plankton Res.*, **7**, 697–702.

Beaugrand, G. (2003) Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. *Fish. Oceanogr.*, **12**, 270–283.

Beaugrand, G. (2009) Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. *Deep-Sea Res. II*, **56**, 656–673.

Beaugrand, G., Reid, P. C., Ibañez, F. *et al.* (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, **296**, 1692–1694.

Beaugrand, G., Brander, K. M., Lindley, J. A. *et al.* (2003) Plankton effect on cod recruitment in the North Sea. *Nature*, **426**, 661–664.

Beaugrand, G., Edwards, M., Brander, K. *et al.* (2008) Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecol. Lett.*, **11**, 1157–1168.

Beaugrand, G., Luczak, C. and Edwards, M. (2009) Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Global Change Biol.*, **15**, 1790–1803.

Colebrook, J. M. (1960) Continuous plankton records: methods of analysis, 1950–59. *Bull. Mar. Biol.*, **5**, 51–64.

Campbell, R. G., Wagner, M. M., Teegarden, G. J. *et al.* (2001) Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. *Mar. Ecol. Prog. Ser.*, **221**, 161–183.

Carruthers, E. H., Neilson, J. D., Waters, C. *et al.* (2005) Long-term changes in the feeding of *Pollachius virens* on the Scotian Shelf; responses to a dynamic ecosystem. *J. Fish Biol.*, **66**, 327–347.

Conover, R. J. (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the Northern Hemisphere. *Hydrobiologia*, **167/168**, 127–142.

Conversi, A., Piontkovski, S. and Hameed, S. (2001) Seasonal and interannual dynamics of *Calanus finmarchicus* in the Gulf of Maine (Northeastern US shelf) with reference to the North Atlantic Oscillation. *Deep-Sea Res. II*, **48**, 519–530.

Darling, K. F. and Wade, C. M. (2008) The genetic diversity of planktic foraminifera and the global distribution of ribosomal RNO genotypes. *Mar. Micropaleontol.*, **67**, 216–238.

Doney, S. C. (2006) Plankton in a warmer world. *Nature*, **444**, 695–696.

Edwards, M., Reid, P. and Planque, B. (2001) Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960–1995). *ICES J. Mar. Sci.*, **58**, 39–49.

Fabry, V. J., Seibel, B. A., Feely, R. A. *et al.* (2008) Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES J. Mar. Sci.*, **65**, 414–432.

Frank, K. T., Petrie, B., Choi, J. S. *et al.* (2005) Trophic cascades in a formerly cod-dominated ecosystem. *Science*, **308**, 1621–1623.

Galbraith, P. S. (2006) Winter water masses in the Gulf of St. Lawrence. *J. Geophys. Res.*, **111**, C06022. doi:10.1029/2005JC003159

Galbraith, P. S., Pettipas, R. G., Chassé, J. *et al.* (2009) Physical Oceanographic Conditions in the Gulf of St. Lawrence in 2008. CSAS, Res. Doc. 2009/014. Available at: http://www.dfo-mpo.gc.ca/csas/.

Greene, C. H. and Pershing, A. (2000) The response of *Calanus finmarchicus* populations to climate variability in the Northwest Atlantic: basin-wide forcing associated with the North Atlantic Oscillation. *ICES J. Mar. Sci.*, **57**, 1536–1544.

Greene, C. H., Pershing, A. J., Conversi, A. *et al.* (2003) Trans-Atlantic responses of *Calanus finmarchicus* populations to basin-scale forcing associated with the North Atlantic Oscillation. *Prog Oceanogr.*, **58**, 310–312.

Greene, C. H., Pershing, A. J., Cronin, T. M. *et al.* (2008) Arctic climate change and its impacts on the ecology of the North Atlantic. *Ecology*, **89**(suppl.), S24–S38.

Harrison, W. G. and Li, W. K. W. (2007) Phytoplankton growth and regulation in the Labrador Sea: light and nutrient limitation. *J. Northw. Atl. Fish. Sci.*, **39**, 71–82.

Harrison, W. G., Johnson, C., Head, E. *et al.* (2009) Optical, chemical, and biological oceanographic conditions in the Maritimes Regions in 2008. CSAS, Res. Doc. 2009/054. Available at: http://www.dfo-mpo.gc.ca/csas/.

Head, E. J. H. and Pepin, P. (2007) Variations in overwintering depth distributions of *Calanus finmarchicus* in the slope waters of the NW Atlantic continental shelf and the Labrador Sea. *J. Northw. Atl. Fish. Sci.*, **39**, 49–69.

Head, E. J. H. and Sameoto, D. D. (2007) Inter-decadal variability in zooplankton and phytoplankton abundance on the Newfoundland and Scotian shelves. *Deep-Sea Res. II*, **54**, 2686–2701.

Head, E. J. H. and Pepin, P. (2008) Seasonal cycles of *Calanus finmarchicus* abundance at fixed time-series stations on the Scotian and Newfoundland shelves (1999–2006). *AZMP Bull.*, **7**, 17–20. Available at: http://www.meds-sdmm.dfo-mpo.gc.ca/zmp/main_zmp_e.html.

Head, E. J. H., Harris, L. R. and Petrie, B. (1999) Distribution of *Calanus* spp. on and around the Nova Scotia Shelf in April: evidence for an offshore source of *Calanus finmarchicus* to the central and western regions. *Can. J. Fish. Aquat. Sci.*, **56**, 2463–2476.

Head, E. J. H., Harris, L. R. and Yashayaev, I. (2003) Distributions of *Calanus* spp. and other mesozooplankton in the Labrador Sea in relation to hydrography in spring and summer (1995–2000). *Prog. Oceanogr.*, **59**, 1–30.

Head, E. J. H., Melle, W., Pepin, P. *et al.* (2010) On the ecology of *Calanus finmarchicus* in the sub-arctic North Atlantic: a comparison of population dynamics and environmental conditions in areas of the Labrador Sea-Labrador/Newfoundland shelf and Norwegian Sea Atlantic and Coastal waters. *Prog. Oceanogr.* (in press).

Heath, M. R., Rasmussen, J., Ahmed, Y. *et al.* (2008) Spatial demography of *Calanus finmarchicus* in the Irminger Sea. *Prog. Oceanogr.*, **76**, 39–88.

Ji, R., Davis, C. S., Chen, C. *et al.* (2007) Influence of ocean freshening on shelf phytoplankton dynamics. *Geophys. Res. Lett.*, **34**, L24607. doi:10.1029/2007GL032010

Johns, D. G., Edwards, M., Richardson, A. *et al.* (2003) Increased blooms of a dinoflagellate in the NW Atlantic. *Mar. Ecol. Prog. Ser.*, **265**, 283–287.

Leterme, S. C., Edwards, M., Seuront, L. *et al.* (2005) Decadal basin-scale changes in diatoms, dinoflagellates, and phytoplankton color across the North Atlantic. *Limnol. Oceanogr.*, **50**, 1244–1253.

Loder, J. W., Petrie, B. and Gawarkiewicz, G. (1998) The coastal ocean off northeastern North America: a large-scale view. In Robinson, A. R. and Brink, K. H. (eds), *The Sea*. Vol. 11. Wiley and Sons, New York, NY, pp. 105–133.

Melle, W. and Skjoldal, H. R. (1998) Reproduction and development of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in the Barents Sea. *Mar. Ecol. Prog. Ser.*, **169**, 211–228.

Pepin, P., Maillet, G. L., Fraser, S. *et al.* (2008) Biological and chemical oceanographic conditions on the Newfoundland and Labrador Shelf during 2007. CSAS, Res. Doc. 2008/034. Available at: http://www.dfo-mpo.gc.ca/csas/.

Pershing, A. J., Greene, C. H., Jossi, J. W. *et al.* (2005) Interdecadal variability in the Gulf of Maine zooplankton community, with potential impacts on fish recruitment. *ICES J. Mar. Sci.*, **62**, 1511–1523.

Plourde, S., Joly, P., Runge, J. A. *et al.* (2003) Life cycle of *Calanus hyperboreus* in the lower St. Lawrence Estuary and its relationship to local environmental conditions. *Mar. Ecol. Prog. Ser.*, **255**, 219–233.

Rayner, N. A., Parker, D. E., Horton, E. B. *et al.* (2003) Global analyses of sea surface temperature, sea ice, and marine air temperature since the late nineteenth century. *J. Geophys. Res.*, **108**, doi:10.1029/2002JD002670.

Richardson, A. J. and Schoeman, D. S. (2004) Climate impact on plankton ecosystems in the Northeast Atlantic. *Science*, **305**, 1609–1612.

Richardson, A. J., Walne, A. W., John, A. W. G. *et al.* (2006) Using continuous plankton recorder data. *Prog. Oceanogr.*, **68**, 27–74.

Sameoto, D. (2001) Decadal changes in phytoplankton color index and selected calanoid copepods in continuous plankton recorder data from the Scotian Shelf. *Can. J. Fish. Aquat. Sci.*, **58**, 749–761.

Sameoto, D. D. and Herman, A. W. (1992) Effect of the outflow from the Gulf of St. Lawrenceon on Nova Scotia shelf zooplankton. *Can. J. Fish. Aquat. Sci.*, **49**, 857–869.

Schiebel, R., Bijma, J. and Hemleben, C. (1997) Population dynamics of the planktic foraminifer *Globigerina bulloides* from the eastern North Atlantic. *Deep-Sea Res. I*, **44**, 1701–1713.

Schiebel, R., Waniek, J., Bork, M. *et al.* (2001) Planktic foraminiferal production stimulated by chlorophyll redistribution and entrainment of nutrients. *Deep-Sea Res. I*, **48**, 721–740.

Teegarden, G. J., Campbell, R. G. and Durbin, E. (2001) Zooplankton feeding behavior and particle selection in natural plankton assemblages containing toxic *Alexandrium* spp. *Mar. Ecol. Prog. Ser.*, **218**, 213–226.

Therriault, J.-C., Petrie, B., Pepin, P. *et al.* (1998) Proposal for a Northwest Atlantic Zonal Monitoring Program. *Can. Tech. Rep. Hydrogr. Ocean Sci.*, **194**, vii+57.

Yamamoto-Kawai, M., McLaughlin, F. A., Carmack, E. C. *et al.* (2009) Aragonite undersaturation in the Arctic Ocean: effects of ocean acidification and sea ice melt. *Science*, **326**, 1098–1100.