

## **Changes in environmental conditions and the population dynamics of *Calanus finmarchicus* in the Labrador Sea (1990-2006)**

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### **Abstract**

A suite of physical, chemical and biological variables are measured at stations along a section across the Labrador Sea between southern Labrador and southern Greenland once a year by scientists from the Bedford Institute of Oceanography. Satellite images of sea surface temperature and chlorophyll provide extended coverage over space and time. From 1990 until 2006 near-surface temperatures increased by about 1°C. Over the same period nitrate concentrations in the central basin increased, while silicate concentrations decreased. Total inorganic carbon concentrations, measured since the mid-1990s, increased and pH decreased. The phytoplankton community appeared to respond to these changes with an overall increase in spring/summer chlorophyll concentrations, but with changes in size/species composition. The zooplankton community did not show large changes in biomass or community composition. On the other hand, for *Calanus finmarchicus*, which dominates the zooplankton biomass in the central basin, the timing of the appearance of young copepodites was apparently linked to temperature and the timing of the spring bloom. Warmer conditions in late winter were associated with earlier blooms and a higher abundance of young stage *C. finmarchicus* in late spring. Whether the observed environmental trends are the result of global warming or are part of a normal climatic cycle is unclear. Climate model predictions for the Labrador Sea region are for air and sea temperatures to rise. If this occurs, we expect to see changes in the population dynamics of this most importance component of the zooplankton community.

### **Introduction**

The Labrador Sea is an area where global warming is likely to have important effects in future decades and centuries. Model predictions include warming and freshening of the surface layers (Rahmstorf and Ganopolski 1999, ICPP 2001) and increased acidification due to increased uptake of carbon dioxide (Orr et al. 2005). The Labrador Sea is an important site for deep convection, which provides a pathway for the transport of atmospheric gases, such as oxygen and carbon dioxide, and biogenic carbon (dissolved and particulate organic carbon) from the surface to intermediate depths (Azetsu-Scott and Yeats 2007). Model predictions suggest reduction of deep convection will result from the surface freshening (Clark et al. 2002), reducing the capacity of the area to take up the ever increasing levels of atmospheric carbon dioxide caused by the combustion of fossils fuels.

Since 1990, scientists from the Bedford Institute of Oceanography have carried out annual spring or early summer occupations of a hydrographic section across the Labrador Sea between Hamilton Bank (on the Labrador Shelf) and Cape Desolation on the Greenland Shelf (Fig. 1). Temperature, salinity and a suite of chemical variables including nutrients and dissolved inorganic carbon are measured on these surveys. Since 1995 measurements of biological variables such as dissolved and particulate organic carbon, phytoplankton, bacteria and zooplankton have been included. In this paper we will present a summary of observations made during these surveys for a period over which temperatures have been increasing and the depth of winter convection has generally been relatively shallow. These conditions serve as an *in situ* experimental scenario for us to investigate the future potential effects of global warming. In particular, we will show trends in composition of the plankton community, spring bloom dynamics and in the timing of reproduction of *Calanus finmarchicus*, and will discuss the implications of our observations for the Labrador Sea ecosystem.

## Materials and Methods

### Hydrographic and water sampling and related sample analysis

Hydrographic profiles (T and S) were recorded and water samples were collected at all sampling stations, using a CTD probe and Niskin bottles mounted on the CTD rosette. Chlorophyll and nutrient concentrations were determined using methods described by Head et al. (2000) and pH was estimated from measurements of total inorganic carbon and total alkalinity (DOE 1994). Samples for flow cytometric analyses of phytoplankton and bacteria were preserved in 1% paraformaldehyde and stored in cryovials at -80°C prior to analyses, which were according to the methods of Li and Dickie (2001). Detailed analysis of pigment composition was carried out for surface samples by high performance liquid chromatography according to the method described by Head and Horne (1993). Fucoxanthin and peridinin were used as diagnostics markers for microplankton groups (e.g. diatoms, dinoflagellates, *Phaeocystis*) and ratios of these to chlorophyll a from literature values were used to calculate their contribution to the chlorophyll a in the samples (Uitz et al. 2006). Similarly, 19'-hexanoyoxyfucoxanthin, 19'-butanoyloxyfucoxanthin and alloxanthin were used as markers for nanoplankton groups (e.g. nanoflagellates, coccolithophores, cryptophytes), while zeaxanthin and chlorophyll b were used as markers for picoplankton (e.g. prasinophytes).

### Zooplankton sampling and sample analysis

During annual cruises zooplankton samples were collected at between 11 and 29 stations of the AR7W line. Zooplankton were collected between 100 m and the surface using vertical ring net hauls fitted with a 200 µm mesh, using a set up such that the net only collected plankton during its ascent. Samples were preserved in 2% formalin. At least 100 individual *Calanus* from each tow were identified to the level of species and stage. Dry weights for the *Calanus* species and other zooplankton groups were determined as described by Head et al. (2003). Abundances for *C. finmarchicus*, by stage, were averaged over stations in each of five zones along the line, which were defined on the basis of zooplankton community composition (Head et al. 2003). These corresponded geographically to the Labrador Shelf, Labrador Slope, Central Labrador Sea, Eastern Labrador Sea and Greenland Shelf, although the positions of the boundaries between adjacent zones varied from year to year.

### Sea-surface temperature and chlorophyll measurements from other data sources

Remote sensing allowed for measurements of sea surface temperature and chlorophyll concentration at times of year outside the cruise sampling periods. Images of sea-surface temperature for the Labrador Sea region from AVHR satellites were obtained from the Dept. of Fisheries and Oceans website ([http://www.mar.dfo-mpo.gc.ca/science/ocean/ias/seawifs/seawifs\\_1.html](http://www.mar.dfo-mpo.gc.ca/science/ocean/ias/seawifs/seawifs_1.html)). Sea-surface temperature

anomalies for the entire AR7W line for January 1989 to December 2006 were calculated based on data obtained from the HadISST data base (Hadley Centre, UK). Sea surface temperatures and chlorophyll concentrations were obtained for “boxes” representative of the zones over which *C. finmarchicus* data were averaged, using a combination of Reynolds/NCEP data (from <http://poet.jpl.nasa.gov/>), which combines *in situ* and AVHR satellite observations for temperature, and SeaWiFS satellite data for chlorophyll concentration (Level 3 data from <ftp://oceans.gsfc.nasa.gov/SeaWiFS/Mapped/8Day/CHLO/>). Data for the Labrador Shelf, Central Labrador Sea and eastern Labrador Sea were averaged first over the boxes (Fig. 1), then over 7 (temperature) or 8 day (chlorophyll) intervals for individual years.

## Results

Temperatures were colder on the Labrador and Greenland shelves than they were in the central Labrador Sea, in late May in both 1998 and 2006, but the areas covered by cold water (pink) or ice (white, Labrador Shelf) were more extensive in 1998 than in 2006 (Fig. 2). Sea-surface temperature anomalies along the AR7W line showed a warming trend between 1990 and 2006 and 0-50 m temperatures measured during occupations and averaged over stations in different regions, followed the upward trends found in the SST data (Fig. 3). Total inorganic carbon levels in the newly ventilated Labrador Sea water (depth range 100-500 m) increased between 1996 and 2006, while the pH decreased by ~0.04 units (Fig. 4). Silicate concentrations decreased from west to east and decreased over time in all regions (Fig. 5). Nitrate concentrations were higher in the central and slope water regions than on the shelves. They increased over time in the deep waters and decreased on the Greenland Shelf, while showing no significant change on the Labrador Shelf.

Integrated chlorophyll concentrations (0-100m) either decreased (Labrador Shelf) or increased (Labrador Basin, Greenland Shelf) between 1994 and 2006, but none of the trends was statistically significant (Fig. 6). Integrated bacterial abundance showed parallel trends and the increase over time on the Greenland Shelf was significant ( $p = 0.05$ ). Integrated picoplankton abundance increased slightly on the Labrador Shelf and nanoplankton abundances decreased on the shelf and in the central basin, while other trends were slight. The fraction of chlorophyll a that could be accounted for by pigments corresponding to microplankton (diatoms, dinoflagellates, *Phaeocystis*) decreased over time both on the Labrador Shelf and in the central basin, while the contribution of nanoplankton (coccolithophores, nanoflagellates) rose in both regions and the concentration of picoplankton (prasinophytes) increased on the Labrador Shelf (Fig. 7).

Annual average sea-surface temperatures for the satellite boxes corresponding to the zooplankton community areas increased over time in all areas, but the variability was high and the trend was insignificant in the Eastern Labrador Sea (Fig. 8). Sea-surface chlorophyll concentrations in the Central Labrador Sea box, averaged for bimonthly intervals and then from April to August each year (1998-2006) showed a significant ( $p = 0.053$ ) increase over time, but there were no significant trends on the Labrador Shelf or in the Eastern Labrador Sea. The day of year when the sea surface chlorophyll concentration reached  $1 \text{ mg m}^{-3}$ , used as an index of the start of the spring bloom, decreased over time, although the only significant trend was in the Eastern Labrador Sea.

Total zooplankton dry weight biomass showed no trends over time in any of the three sampling areas when all sampling years were included, and this was true for each of the three *Calanus* species that dominated the biomass (Fig. 9). When data from May alone was used there were still no significant trends for total biomass or for any of the *Calanus* species.

Seasonal cycles of *Calanus finmarchicus* abundance by stage were derived by averaging copepodite stage abundances over stations within zones for each year and then over 2 week periods for different years (Fig. 10). *C. finmarchicus* were much more abundant in the Eastern Labrador Sea than elsewhere and young stages (CI-III) were dominant in late May. In the other areas females were dominant in late May and there were relatively few young stages. In order to examine trends over time in the timing of reproduction/recruitment, a “population development index” (the sum of CI-CIII x 100/Total abundance) was calculated for late May cruises. The population development index (PDI) in late May decreased over time on the Labrador Shelf and in the Eastern Labrador Sea and increased in the Central Labrador Sea, although the trends were not significant anywhere (Fig. 11). Late winter-spring (early March – late May) SSTs increased in all regions over time, as did the annual temperatures (Figs. 3 and 8), although the increase was more variable and the trend, less significant in the Eastern Labrador Sea. Plots of PDI versus March-May SST showed a positive relationship in the Central Labrador Sea, a negative relationship in the Eastern Labrador Sea and a positive relationship on the Labrador Shelf, if one anomalous data point was omitted (Fig. 12). Plots of PDI versus bloom start date showed a significant negative relationship in the Central Labrador Sea ( $p = 0.002$ ) and no relationship on the Labrador Shelf or in the Eastern Labrador Sea. Plots of bloom start date versus Mar-May SST showed negative relationships in all areas, but only on the Labrador Shelf was the relationship significant ( $p = 0.01$ ).

## Discussion

All measures of temperature along the AR7W line and in the zooplankton community areas showed increases in the near-surface layers over the 1990-2006 or 1995-2006 periods (Figs. 2, 3 and 8). The cold temperatures in the early 1990s were the result of severe winters and convection to depths of 2 km, which filled the Central basin with cold water. Since then, winter convection depths have been shallower (500-1000 m) and there has been a greater input of Atlantic Water into the central basin, via the Irminger Current and thus less influence of Arctic Water input from the North (Hendry et al. 2008). Total inorganic carbon concentrations have been increasing in the surface layers due to increasing levels of carbon dioxide in the atmosphere and vertical mixing has led to transport to greater depths (Azetsu-Scott and Yeats, 2007). This has been accompanied by a measurable degree of acidification, which, if it continues, may have important effects on calcifying organisms (Orr et al. 2005).

The changes in the relative inputs of the different water masses have led to changes in silicate and nitrate concentrations in the sub-surface layers in the central basin (Fig. 5), because Atlantic Water has a higher nitrate concentration, but lower silicate concentration, than Arctic Water (Bauch et al. 1995). The expected impact on the phytoplankton community in the central Labrador Sea basin is for a decreased contribution of diatoms, since silicate levels here are depleted to limiting levels in summer (Harrison and Li 2008), but an increase in the concentration of phytoplankton overall, due to increasing nitrate levels. There is evidence that both of these predictions have been fulfilled: sea surface chlorophyll concentrations, averaged over the growth season, increased from 1998 to 2006 (Fig. 8) and the abundance of large cells decreased, as did the contribution of large microplankton, relative to smaller forms, to the total phytoplankton chlorophyll concentration (Fig. 7). On the Labrador and Greenland shelves, absolute concentrations of silicate and nitrate both decreased, but the ratio of nitrate to silicate increased to more-or-less the same extent as it did in the central Labrador Sea (data not shown), indicating an increased contribution of Atlantic Water. For the Labrador Shelf nitrate, not silicate, reaches concentrations limiting for phytoplankton growth in summer (Harrison and Li 2008). Thus, the prediction for an increasing contribution of Atlantic Water should be for increasing phytoplankton

growth, which is manifested in increasing average concentrations of sea surface chlorophyll during the growth season (Fig. 8), but no great depletion in diatom levels, which is supported by the upward trend in large cell abundance, but not by the diagnostic pigment data (Fig. 7). *In situ* measurements of changes in bacterial abundance, which parallel those in phytoplankton abundance, suggest that bacterial growth is more linked to its resource supply (dissolved organic material released by phytoplankton), than to temperature (Li et al. 2006).

As well as trends in phytoplankton abundance and community structure there were also trends in the timing of the start of the spring bloom, here defined as when the sea surface chlorophyll concentration reached  $1 \text{ mg m}^{-3}$  (Fig. 8). The trend was significant in the Eastern Labrador Sea, weakly so in the Central Labrador Sea and not significant on the Labrador Shelf. One suggestion is that blooms occur earlier when thermal stratification occurs earlier, *i.e.* when late winter/spring temperatures are higher. There were negative relationships in all areas between bloom start dates and March-May SSTs, but correlations were not significant, except on the Labrador Shelf, where stratification derives mainly from ice melting upstream farther north and not from surface warming (Fig. 12).

The zooplankton biomass was dominated by *Calanus finmarchicus* in the Central Labrador Sea and the Eastern Labrador Sea, but on the Labrador Shelf the Arctic copepods *Calanus glacialis* and *Calanus hyperboreus* made important contributions (Fig. 9). There were no significant trends over time in total zooplankton biomass, nor in those of any of the individual *Calanus* species, when all cruises were included. Observations made during different 2 week sampling periods were, however, made at different stages of the growth season for *C. finmarchicus* (Fig. 10), which suggested that the inclusion of all years in the time series trend analysis was inappropriate. Sampling was in late May in 6 years, but even when only these data were included in the analysis, the only observable trends were slight increases for *C. finmarchicus* biomass on the Labrador Shelf and for the non-*Calanus* biomass in the Central and Eastern Labrador Sea areas and none of these trends was significant ( $r^2 \leq 0.41$ ,  $p \geq 0.17$ ). In late May *C. finmarchicus* biomass and *C. hyperboreus* biomass were positively correlated in the Central Labrador Sea ( $p = 0.04$ ) and negatively correlated in the Eastern Labrador Sea ( $p = 0.05$ ), which suggests that the two share a common springtime source in the Central Labrador Sea, but different sources in the Eastern Labrador Sea.

On the Scotian and Newfoundland shelves the population dynamics of *C. finmarchicus* are influenced by both the spring bloom dynamics and temperature, such that either populations have a larger proportion of later stage copepodites at a fixed time of year (Head et al. 2005) or that young stages appear earlier at time series stations (Head and Pepin 2008) when late winter/spring temperatures are higher and when the spring bloom develops earlier. In order to examine trends in the timing of appearance of young stages, we calculated a “population development index” (PDI) for *C. finmarchicus* populations for late May, which we defined as the sum of the abundances of young (CI-III) stages divided by the total *C. finmarchicus* abundance, expressed as a percentage. The PDI showed a positive trend over time in the Central Labrador Sea (Fig. 11), which was expected since late winter/spring SSTs were increasing and blooms were starting earlier over time (Fig. 8). In fact, the relationship between PDI and bloom start date was highly significant, although the relationship between PDI and temperature was not (Fig. 12). On the Labrador Shelf, exclusion of one anomalous data point would have led to a positive trend in PDI with time and a positive relationship with temperature, but there was no relationship with bloom start date. In the Eastern Labrador Sea, there was a negative trend in PDI over time. This may have been because here the population was already well developed by late May; the PDI is only an appropriate index when young stages are starting to appear and when population size is increasing.

## Summary and conclusions

From 1995 to 2006 the Labrador Sea region was affected by increasing atmospheric temperatures, reduced convection and changes in advective inputs. In the central basin these changes led to increasing water temperatures and increasing phytoplankton (chlorophyll) concentrations, with decreasing concentrations of large cells, and earlier spring blooms. These changes in themselves suggest a possible reduction in the flux of particulate organic carbon to the deep ocean, and hence possibly a reduced capacity of the Labrador Sea to take up anthropogenically produced carbon dioxide. Acidification may also pose problems. Calcifying plankton presently account for a high proportion of the particulate sedimenting carbon flux, but it is not known whether actual growth of these organisms would be affected by higher carbon dioxide partial pressures (Iglesias-Rodriguez et al. 2008). Total zooplankton biomass, by contrast, was not greatly affected by the changing conditions, although there was a trend over time towards earlier reproduction and/or population development for *Calanus finmarchicus*, the dominant zooplankton species. These recent trends in the Labrador Sea may only be temporary, but they suggest how global warming may affect the lower trophic levels in the future. On the Greenland and Labrador shelves *C. finmarchicus* eggs and nauplii are important food items for larval groundfish, and copepodite and adult stages are consumed by small pelagic fish. If the seasonal cycles of these predators do not change to accommodate those occurring for *C. finmarchicus*, these higher trophic levels may suffer, with possible consequent impacts on fisheries and higher trophic levels such as birds and mammals.

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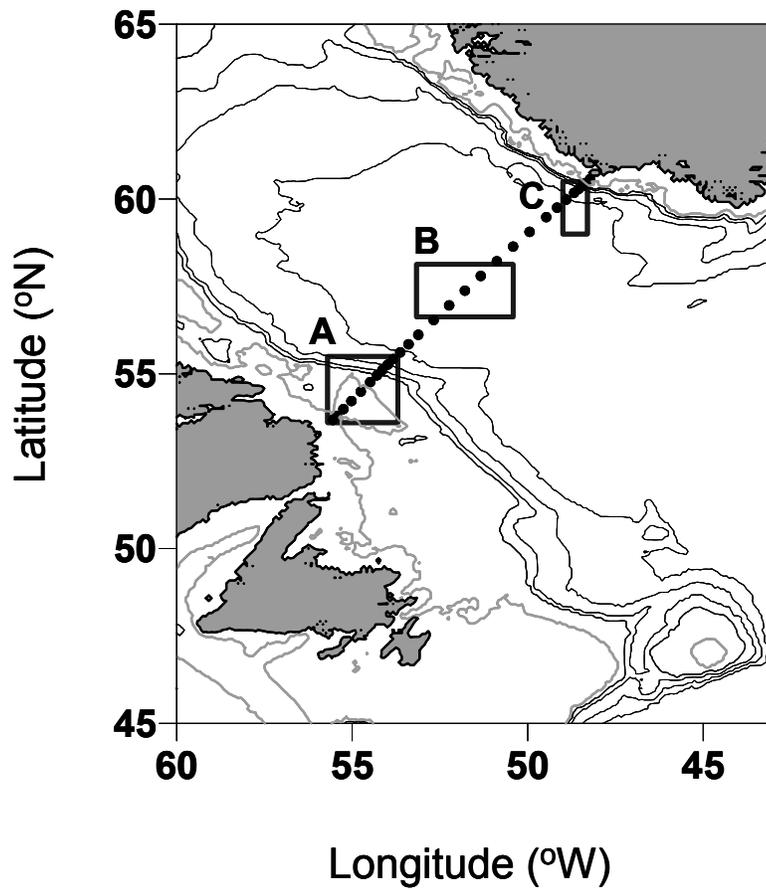


Fig. 1. The Labrador Sea showing the stations of the AR7W line and the boxes delineating the areas over which sea-surface temperature and chlorophyll measurements were made to represent (A) the Labrador Shelf, (B) the Central Labrador Sea and (C) the Eastern Labrador Sea. Bathymetry is shown by the 200 m (grey), the 1000, 2000 and 3000 m (black) contours.

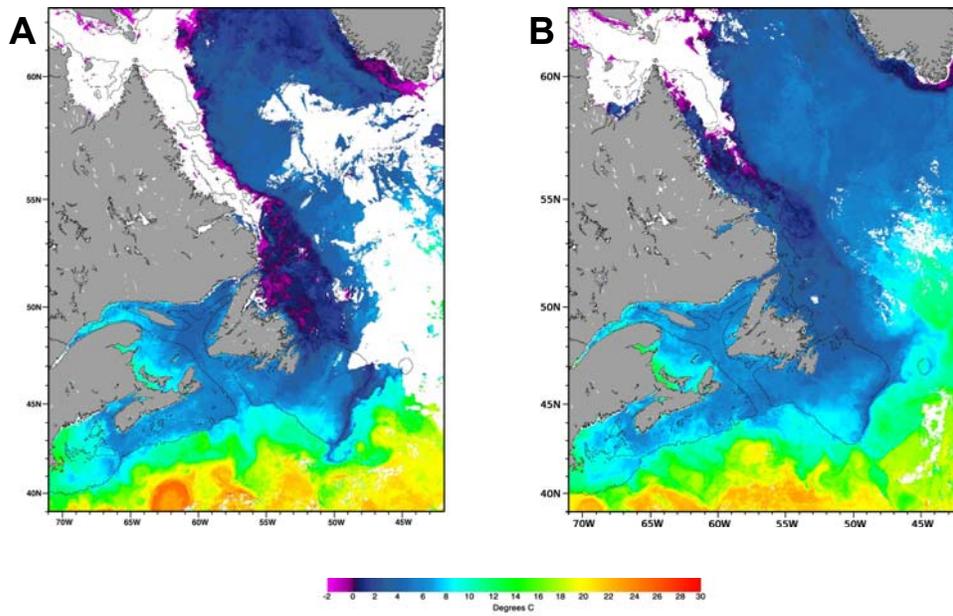


Fig. 2. AVHR satellite images of sea-surface temperature in the Labrador May 16-31 in (A) 1998 and (B) 2006. The white area on the Labrador Shelf corresponds to the area covered by ice.

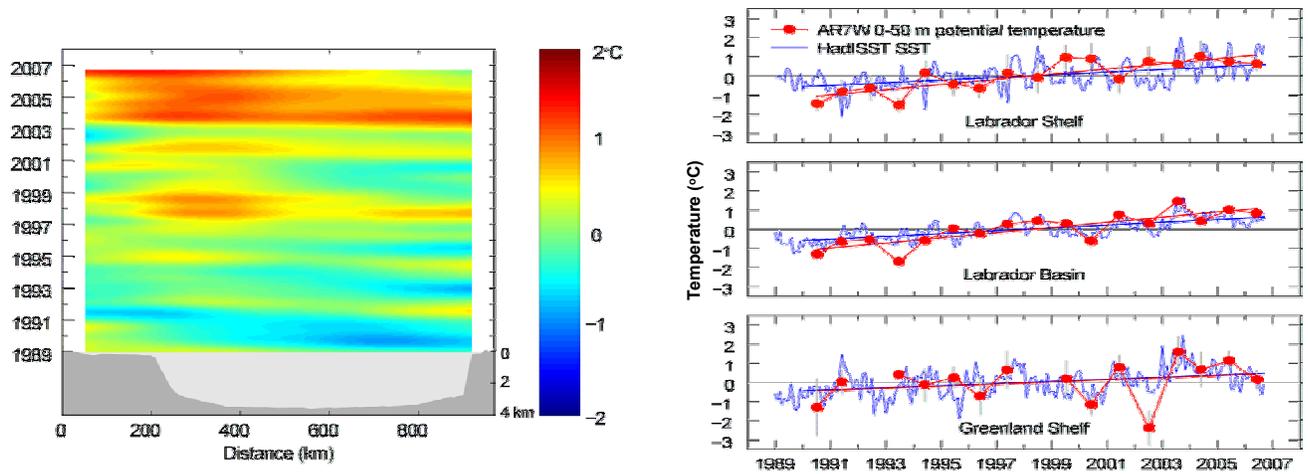


Fig. 3. Trends in temperature anomalies along the AR7W line. (A) SST anomalies relative to 1971-2000 for January 1989 to October 2006 from low-pass filtered monthly HadISST data. AR7W line bathymetry is shown at the bottom. (B) Time series of deseasoned 0-50 m AR7W potential temperature for 1990-2006 spring and early-summer occupations. HadISST SST monthly anomalies from 1989-2006 relative to 1990-2006 means are also shown. Trend lines are based on 1990-2006 data

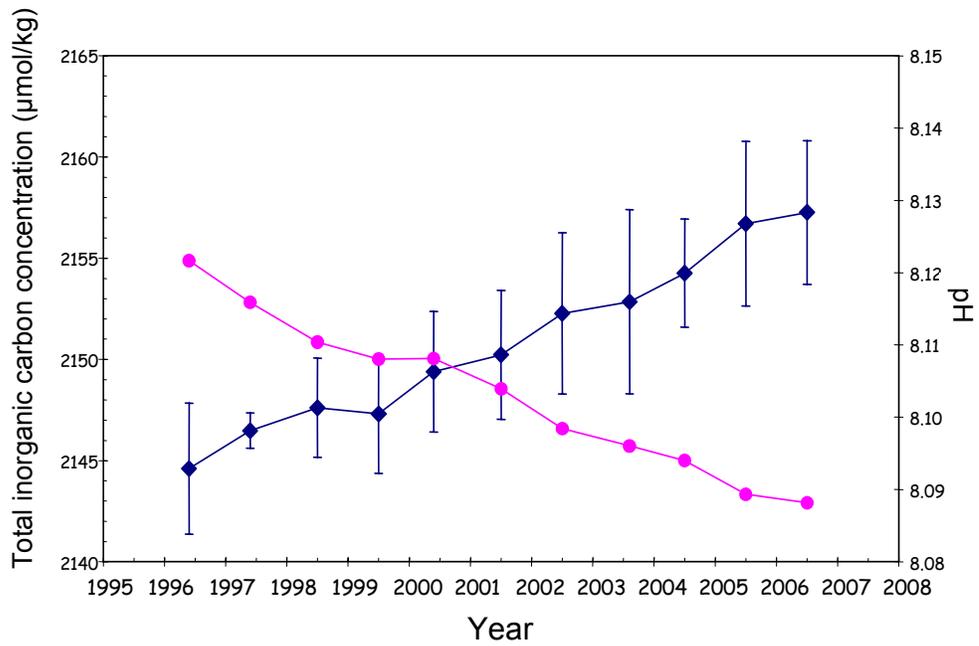


Fig. 4. Time series of total inorganic carbon concentration (blue) and corresponding estimate of pH (pink) in the newly ventilated (100-500 m) Labrador Sea Water derived from annual cruises 1996-2006.

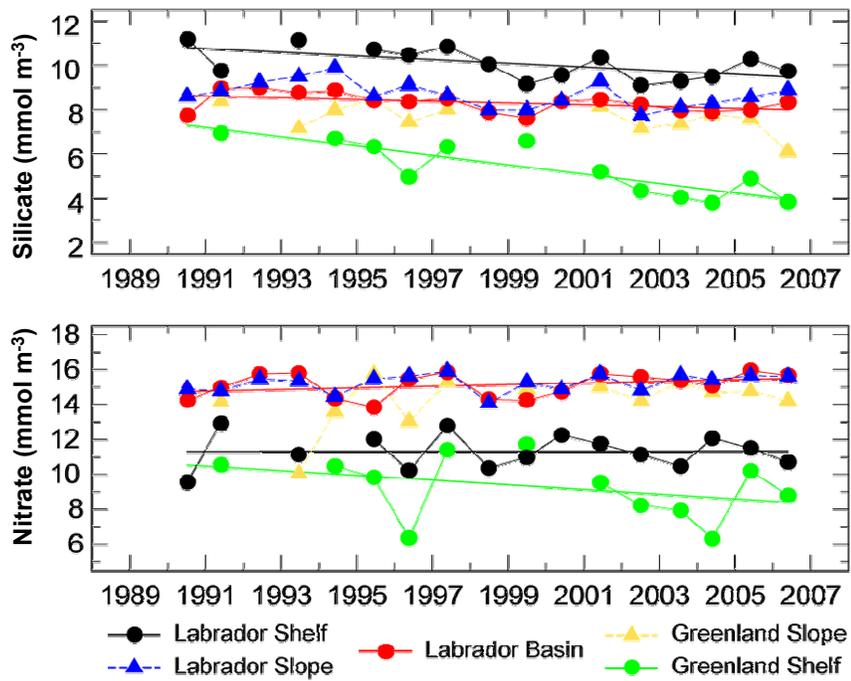


Fig. 5. Trends in silicate and nitrate concentrations (averages for 60-200 m, or 60-bottom for shelves) averaged over stations in different areas of the AR7W line.

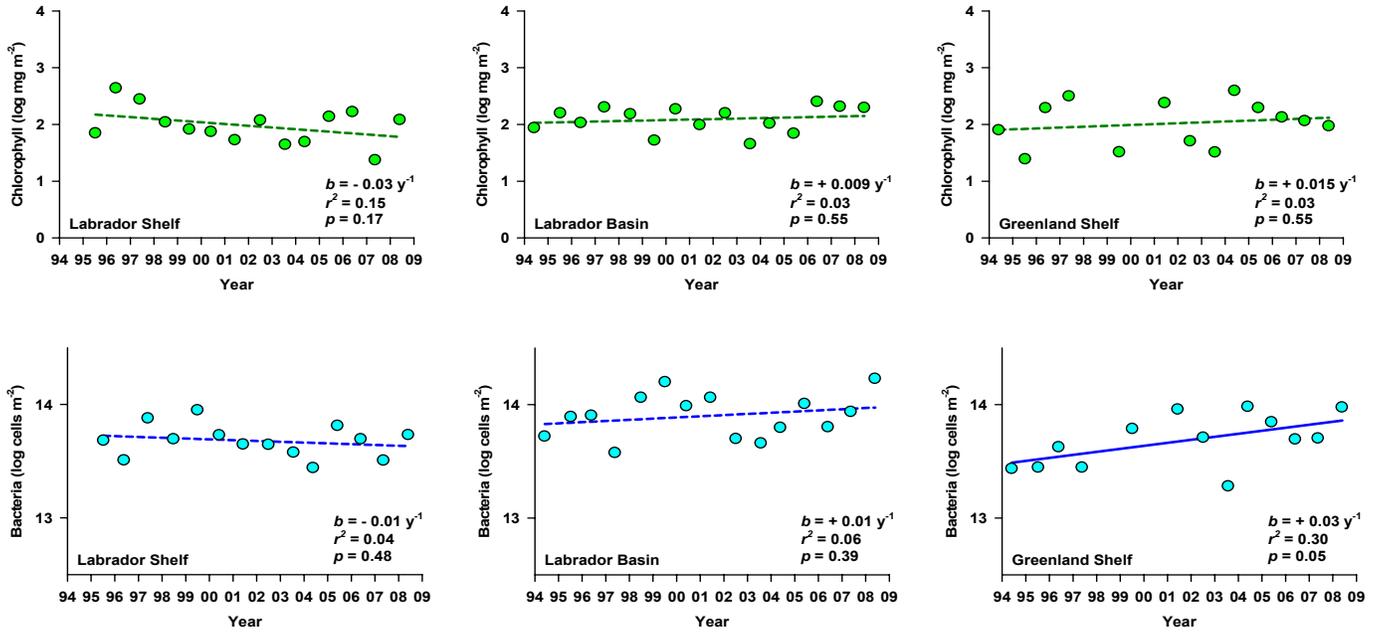


Fig. 6. Trends in integrated chlorophyll concentration and bacterial abundance (0-100 m) on the Labrador Shelf, in the central Labrador Sea Basin and on the Greenland Shelf measured during cruises in May, June or July between 1994 and 2008.

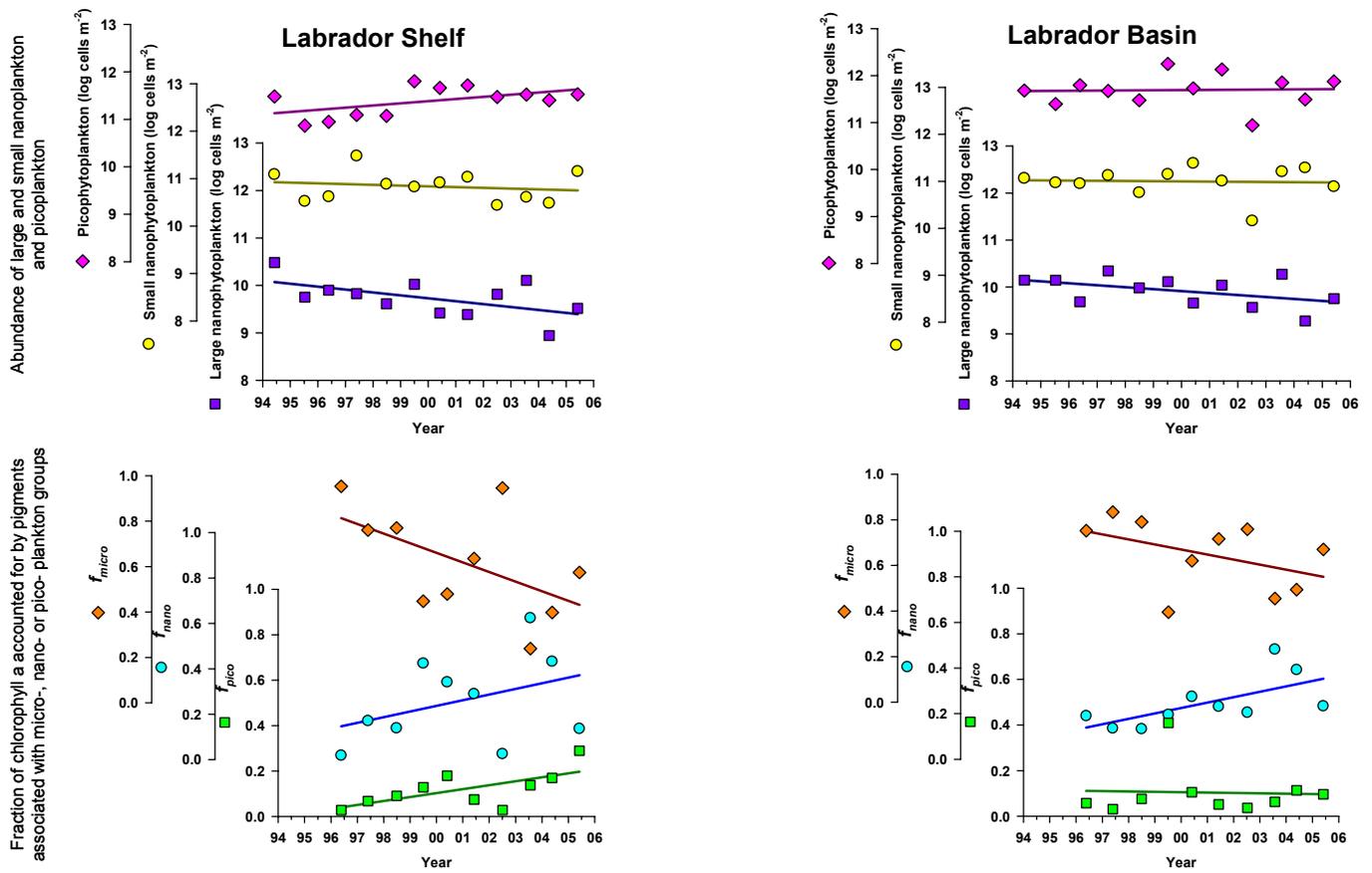


Fig. 7. Trends in abundance of phytoplankton groups differentiated by size (upper row) or pigment composition (lower row) from 1994 to 2006.

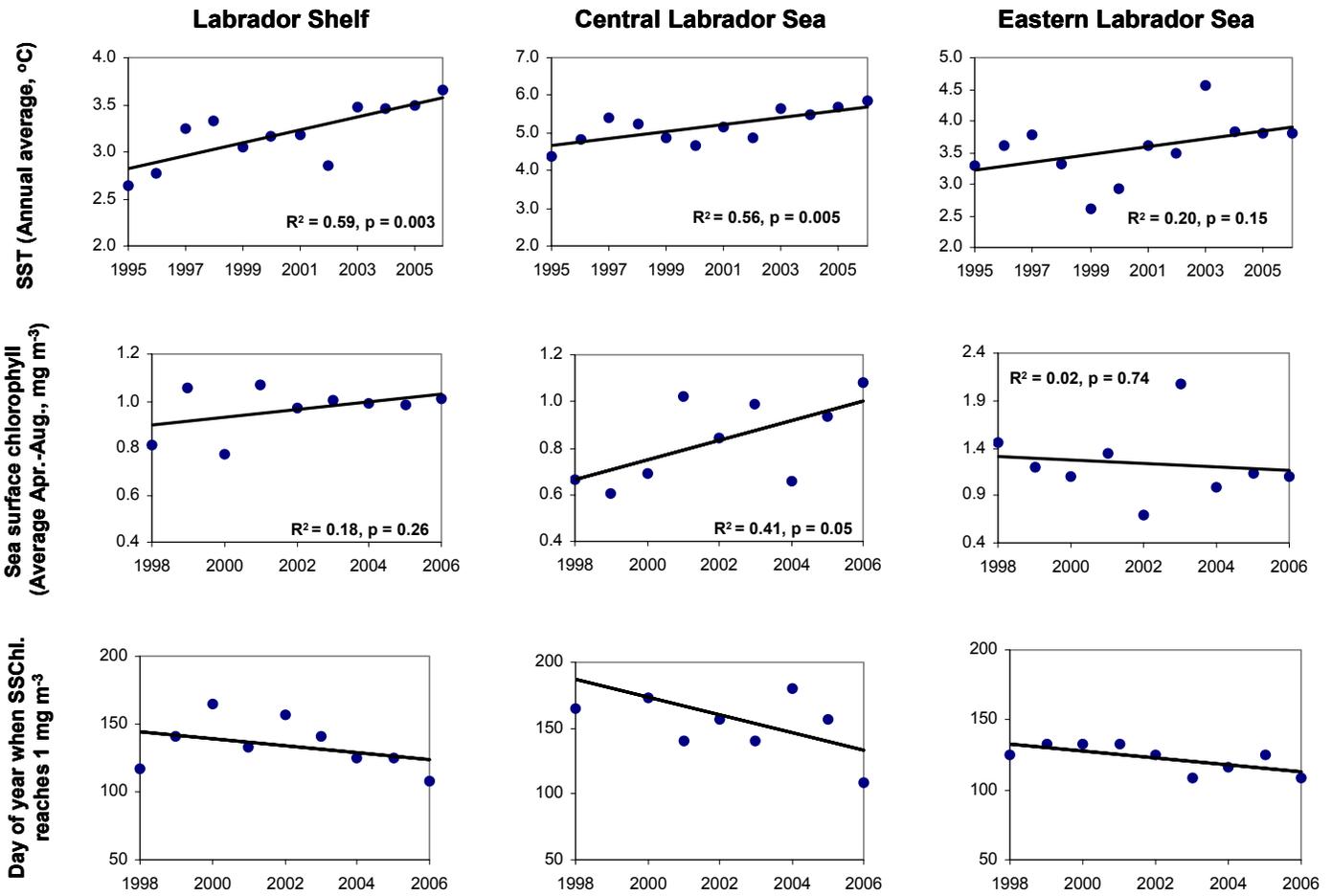


Fig. 8. Trends in annual average SSTs (1995-2006) and April-August sea surface chlorophyll concentrations (1998-2006) and in bloom start dates (i.e. year day when sea surface chlorophyll reaches 1 mg m<sup>-3</sup>) for the satellite boxes on the AR7W line

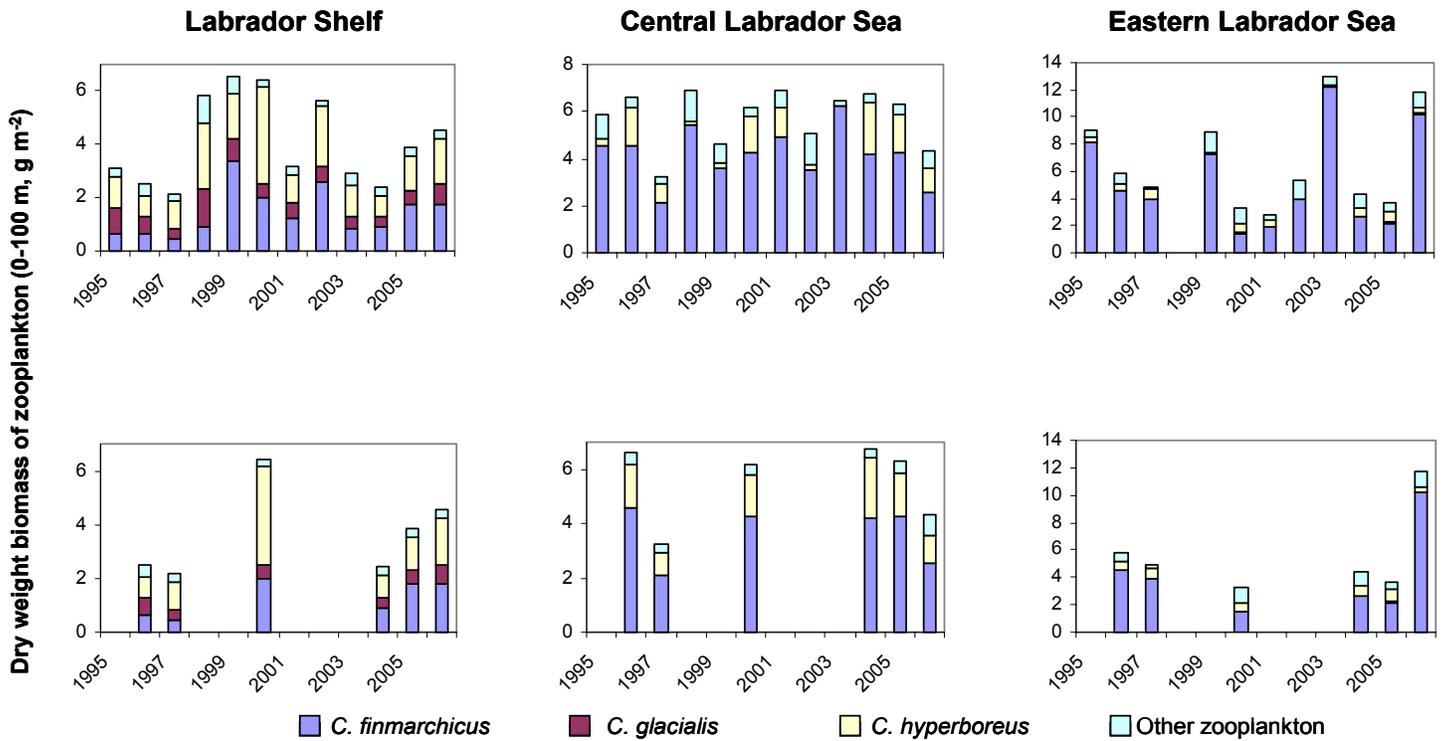


Fig. 9. Trends in zooplankton dry weight biomass (1995-2006). Data were averaged over stations within zones for 6 cruises in late May (1996, 1997, 2000, 2004, 2005, 2006), one in early June (2001), one in late June (1998), 3 in early July (1995, 1999, 2002), one in late July (2003). The upper panel shows data from all sampling years, the lower panel shows data for years when sampling was in late May.

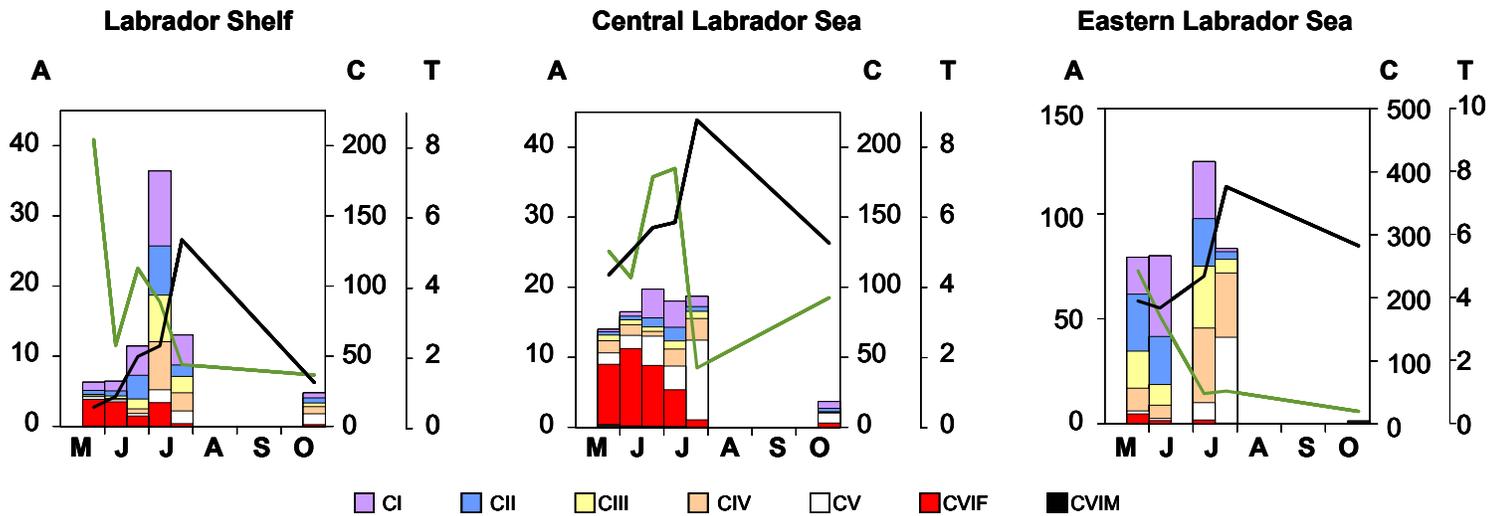


Fig. 10. Average abundances of *Calanus finmarchicus* by stage in the 0-100 m depth range on cruises between 1995 and 2006. (A) *C. finmarchicus* abundance (stacked bars, 1000s m<sup>-2</sup>), (C) integrated chlorophyll concentration (0-100 m, green line, mg m<sup>-3</sup>), (T) temperature (0-20 m average, black line, °C). Data were averaged for 2-week periods over stations within zones from 6 cruises in late May (1996, 1997, 2000, 2004, 2005, 2006), one in early June (2001), one in late June (1998), 3 in early July (1995, 1999, 2002), one in late July (2003) and one in late October (1996).

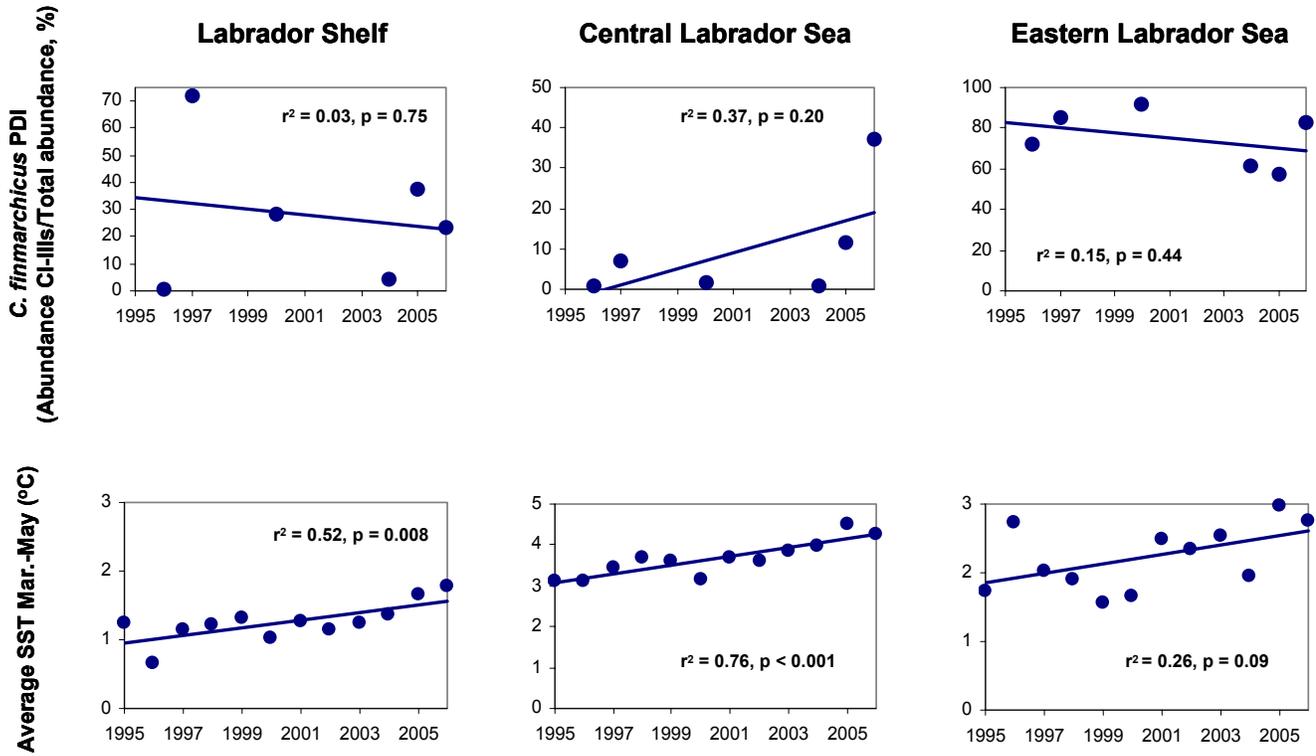


Fig. 11. Trends in the *C. finmarchicus* population development index (PDI) in late May and in SST temperatures for March-May (1995-2006).

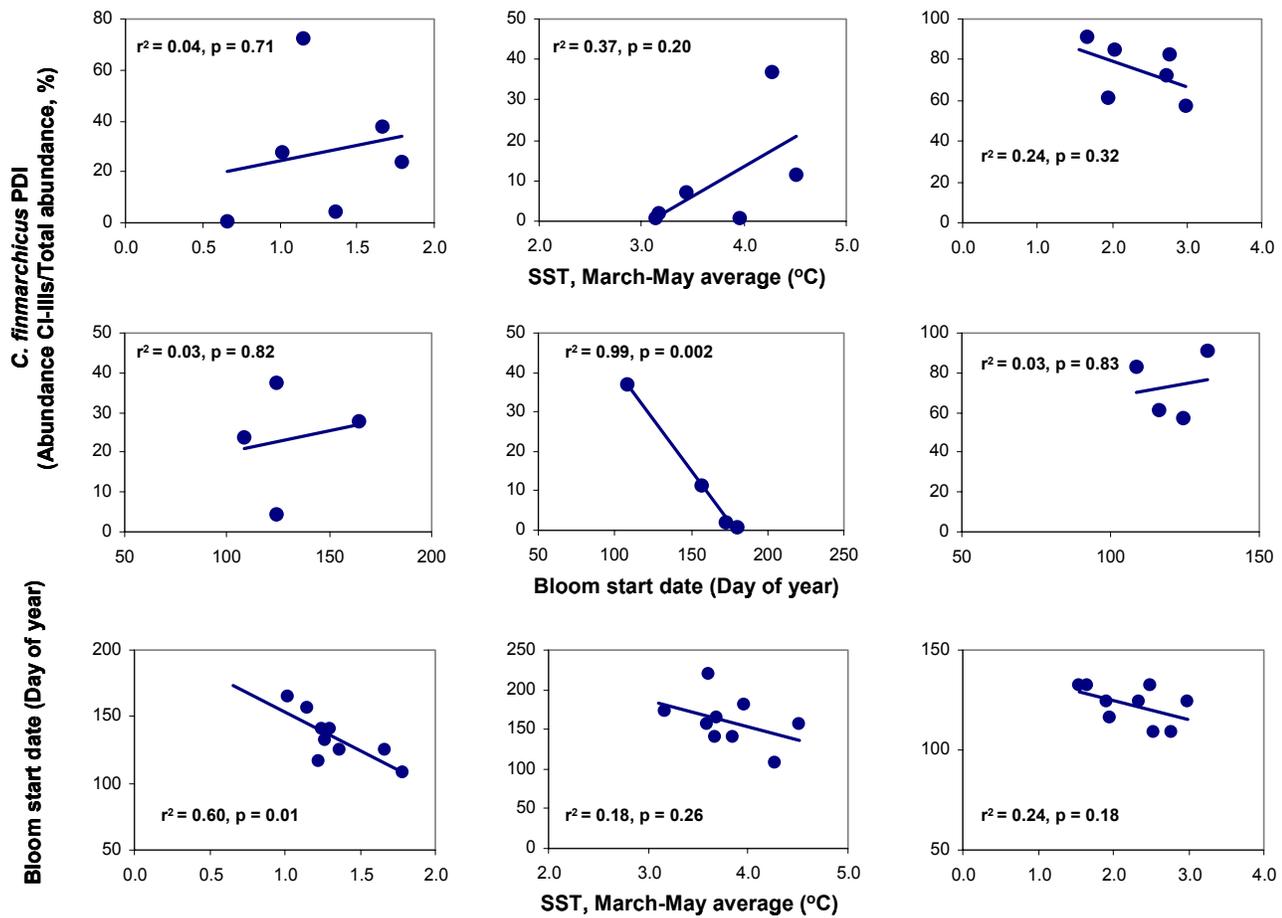


Fig. 12. Plots of *C. finmarchicus* population development index (PDI) in late May versus March-May average SST (upper panel, 1996-2006), of *C. finmarchicus* PDI versus bloom start date (middle panel, 2000-2006) and of bloom start date versus March-May SST (lower panel).