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# Climate-induced effects on the meroplankton and the benthic-pelagic ecology of the North Sea

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## *Abstract*

Analyses of long-term time series of North Sea plankton and sea surface temperature (SST) data reveal that the annual planktonic larval abundance of three benthic phyla, Echinodermata, Arthropoda, and Mollusca, responds positively and immediately to SST. Long-term outcomes for the planktonic abundance of these three phyla are different, however. The planktonic larvae of echinoderms and decapod crustaceans have increased in abundance from 1958 to 2005, and especially since the mid-1980s, as North Sea SST has increased. In contrast, the abundance of bivalve mollusc larvae has declined, despite the positive year-to-year relationship between temperature and bivalve larval abundance continuing to hold. We argue that the changes in meroplankton abundance, coincident with increased phytoplankton and declining holoplankton, reflect the synchronous effect of rising SST and related changes in the pelagic community on the reproduction and recruitment of many benthic marine invertebrates. Under this scenario, the long-term decline in bivalve mollusc larvae will reflect increased predation on the settled larvae and adults by benthic decapods. These alterations in the zooplankton may therefore describe an ecosystem-wide restructuring of North Sea trophic interactions.

Ocean warming over short timescales can bring about comprehensive changes in benthic communities (Schiel et al. 2004). There are few time series that contain data on a sufficient range of taxa to enable complex ecological climate-induced changes to be investigated at a community scale over the long term, however. The Continuous Plankton Recorder (CPR) survey (Batten et al. 2003) records up to 450 planktonic taxa routinely (Richardson et al. 2006) and maintains a long-term time series of North Atlantic and North Sea plankton community data that extends over 70 yr and is continuous in the North Sea since 1948. Samples of the North Sea plankton collected by the CPR survey on a monthly basis from 1958 to the present day reveal an increase in abundance of the meroplankton (the planktonic life history stages of benthic species) and a concordant decline in abundance of holoplankton taxa over this period (Lindley and Batten 2002). In particular, the larvae of benthic echinoderms, notably those of *Echinocardium cordatum*, now dominate numerically the North Sea plankton community in the summer (Kirby et al. 2007). The timing of peak occurrence of echinoderm larvae

has also changed, advancing by 47 d over the same period (Edwards and Richardson 2004). Like other changes that have been reported in the distributions, abundances, and seasonal cycles of the North Sea and Atlantic plankton (Edwards et al. 2002), the changes in echinoderm larvae appear to be climate driven (Kirby et al. 2007).

Although the larvae of benthic echinoderms have shown the greatest numerical increase and the largest seasonal advance among the plankton of the North Sea, changes in other meroplankton have also been observed (Lindley and Batten 2002). The other dominant meroplankton in CPR samples are the larvae of benthic decapods, bivalves, cirripedes, and ectoprocts (cyphonautes larvae) (=bryozoa). Although the greatest increase in North Sea sea surface temperature (SST) has occurred in the winter and spring months, SST is now higher throughout the year (Kirby et al. 2007). Fecundity in poikilotherms, egg size, and number of eggs are phenotypically plastic traits influenced by temperature; warmer temperatures during gametogenesis are usually associated with smaller eggs and larger clutch sizes (Fischer et al. 2003); in marine organisms this phenomenon is often represented by latitudinal clines or depth variation in reproductive output (Ramirez-Llodra 2002). In this way, increases in SST (sea bottom temperatures are close to SST in most continental shelf waters for much of the year) could influence reproductive output in a wide variety of organisms with similar life history strategies.

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Meroplankton abundance is also influenced by SST during the planktonic phase. Warmer SST will shorten larval development times (Hoegh-Guldberg and Pearse 1995), thereby increasing larval survival when food is not limiting (Reitzel et al. 2004). The availability of phytoplankton food during the planktonic stage will therefore also have an effect on larval survival. Increases in the North Sea Phytoplankton Colour Index (PCI; a measure of phytoplankton chlorophyll) derived from the CPR survey (Raitsos et al. 2005) show that chlorophyll levels have increased over the whole North Sea region since the mid-1980s and are now also higher throughout the year (Edwards et al. 2001). Coincident changes in temperature and phytoplankton in the North Sea could thus act in concert to increase meroplankton abundance.

It is known that climate change can uncouple trophic interactions in aquatic ecosystems with severe consequences for resource flow (Winder and Schindler 2004). In continental shelf seas, changes in meroplankton abundance may affect the trophodynamics of the spring and summer plankton and, if their recruitment also improves, may have an effect on benthic community ecology to intimately link the benthic and pelagic environments. Here, we provide the first comprehensive study of the changes recorded by the CPR in five meroplankton phyla in the North Sea between 1958 and 2005 and contrast them with alterations in temperature and food availability. Our analyses indicate a community-wide response to hydroclimatic change, from the benthos to the pelagos.

## Methods

*Sampling of the North Sea plankton by the CPR*—Plankton community data for the North Sea were obtained from the CPR survey (Batten et al. 2003; Richardson et al. 2006). The CPR survey has operated in the North Sea on a routine monthly basis since 1946 and is the largest marine biological time series in the world. In this study we used plankton data from the period 1958–2005, which represents the date from which all the taxa in this study have been recorded routinely to current analyses; these data are available from the Sir Alister Hardy Foundation for Ocean Science ([www.sahfos.ac.uk](http://www.sahfos.ac.uk)) that runs the CPR survey. This present study focuses upon the meroplankton and the phytoplankton, the former comprising the larvae of echinoderms, decapods, bivalves, cirripedes, and ectopods. The CPR is an upper-layer plankton sampler towed behind merchant ships on regular routes. Seawater enters the CPR through a front aperture and the plankton is retained on a moving band of silk gauze of mesh size 270  $\mu\text{m}$  that is slowly wound into a tank of formalin (Batten et al. 2003). In the laboratory the silk gauze is cut into sections (a CPR sample), each representing the plankton from 3  $\text{m}^3$  of water taken during 10 nautical miles (18 km) of tow at an average depth of 7 m. Up to 450 taxa are identified and enumerated either visually or using molecular genetic methods.

*Identification of North Sea meroplankton in CPR samples*—Difficulties associated with the visual identification of many taxa, or practicalities associated with pure logistics, mean that the meroplankton are identified to a

lesser resolution than the holoplankton in CPR samples. Although a recent genetic analysis indicated that the predominant echinoderm larvae in CPR samples from the North Sea are those of *E. cordatum* (Kirby et al. 2007), echinoderm larvae counted in CPR samples represent the pluteus larvae of several species of ophiuroids and echinoids. Decapod larvae also comprise all the developmental stages of the different decapod species that are retained on the silk. Similarly, no distinction is made among different bivalve, cyphonautes, or cirripede larvae.

*Analysis of North Sea phytoplankton in CPR samples*—The CPR dataset for North Sea phytoplankton comprises 86 diatom taxa (Bacillariophyceae) and 90 dinoflagellate taxa (Dinophyceae), which are identified variously to species, genus, or higher taxonomic levels (Richardson et al. 2006). In addition to determining diatom and dinoflagellate diversity, the greenness of each sample is also compared to a color chart to determine its PCI (Raitsos et al. 2005). The PCI provides an estimate of the amount of chlorophyll in each sample because it estimates the greenness derived from both trapped cells and more fragile phytoplankton taxa that burst upon impact. The PCI correlates well with both fluorimeter and satellite measures of chlorophyll (Raitsos et al. 2005). To be sure that changes in the PCI do not reflect wind-driven resuspension of benthic material as a result of changes in wind strength and direction over the North Sea, we examined the long-term abundance of the benthic diatom *Paralia sulcata* in the CPR samples.

*North Sea SST data*—Temperature data for the North Sea were calculated from the Comprehensive Ocean-Atmosphere Data Set (COADS) 1-degree enhanced dataset provided by the comprehensive National Oceanic and Atmospheric Administration-Cooperative Institute for Research in Environmental Sciences (NOAA-CIRES) Climate Diagnostics Center Database (Woodruff et al. 1998).

*Statistical analyses*—We performed similar statistical analyses to those of Kirby et al. (2007), with three modifications. In this study we considered annual SST in three dimensions within the same analysis: time (months)  $\times$  time (years)  $\times$  space; we used only plankton data from 1958 to 2005; and finally, we reassessed (i.e., smoothed) the original SST and plankton time series to remove part of the unexplained variance. The statistical methods may be summarized briefly as follows:

*Spatialized standardized principal component analysis*—Spatialized standardized principal component analyses (PCAs) were performed on a two-dimensional matrix of 154 geographical squares (latitudes from 50.5° to 60°N and from 3.5°W to 9.5°E)  $\times$  (12 months  $\times$  48 yr [1958–2005]) with the double objective of identifying major long-term monthly changes (examination of principal components) and locating their geographical variation (mapping of eigenvectors). Further information on the technique can be found in Beaugrand (2003).

*Correlation analysis*—Probabilities of significance ( $p$ ) of coefficients of correlation were calculated taking into

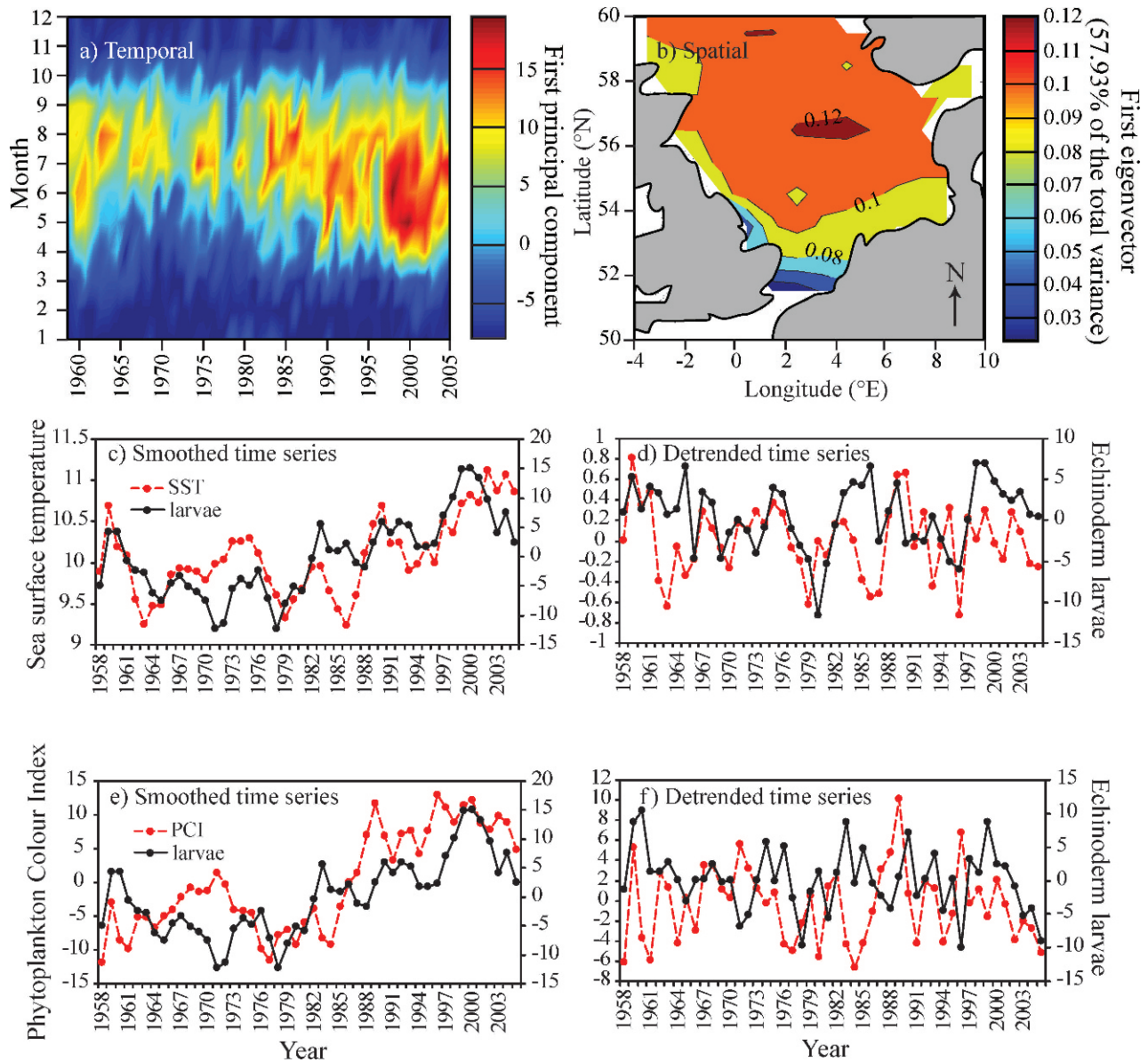


Fig. 1. Temporal and spatial changes in echinoderm larval abundance ( $\log_{10}(x + 1)$ ) and correlations between larval abundance, SST, and the PCI in the North Sea for the period 1958–2005. (a) Three-dimensional plot of temporal changes in the first principal component of echinoderm larval abundance in North Sea CPR samples. (b) Spatial changes in the first eigenvector of larval abundance obtained from a PCA performed on the two-dimensional matrix of 154 geographical squares (latitudes from 50.5° to 60°N and from 3.5°W to 9.5°E)  $\times$  (12 months  $\times$  48 yr [1958–2005]). (c) Smoothed time series of the first principal component of echinoderm larval abundance and SST. (d) Detrended time series of the first principal component of echinoderm larval abundance and temperature. (e) Smoothed time series of the first principal components of echinoderm larval abundance and the PCI. (f) Detrended time series of the first principal components of echinoderm larval abundance and the PCI.

consideration the temporal autocorrelation. A Box-Jenkins autocorrelation function modified by Chatfield (1996) was used to assess the temporal dependence of years and a Chelton (1984) formula was applied to adjust the degrees of freedom.

*Temporal decomposition of time series*—All series were decomposed by the use of singular spectrum analysis (Vautard et al. 2002). The method uses a PCA performed on an autocovariance matrix (also called a Toeplitz matrix)

to divide a time series into a succession of signals of decreasing variance (Beaugrand and Reid 2003). The long-term trend of each time series was first assessed by using both the eigenvectors and the principal components representing the low-frequency variability. Reassessment (i.e., smoothing) of the original time series was accomplished by using the first five principal components and eigenvectors, which removed part of the unexplained variance. Detrended time series were calculated by subtracting the original time series by their respective long-term trends.

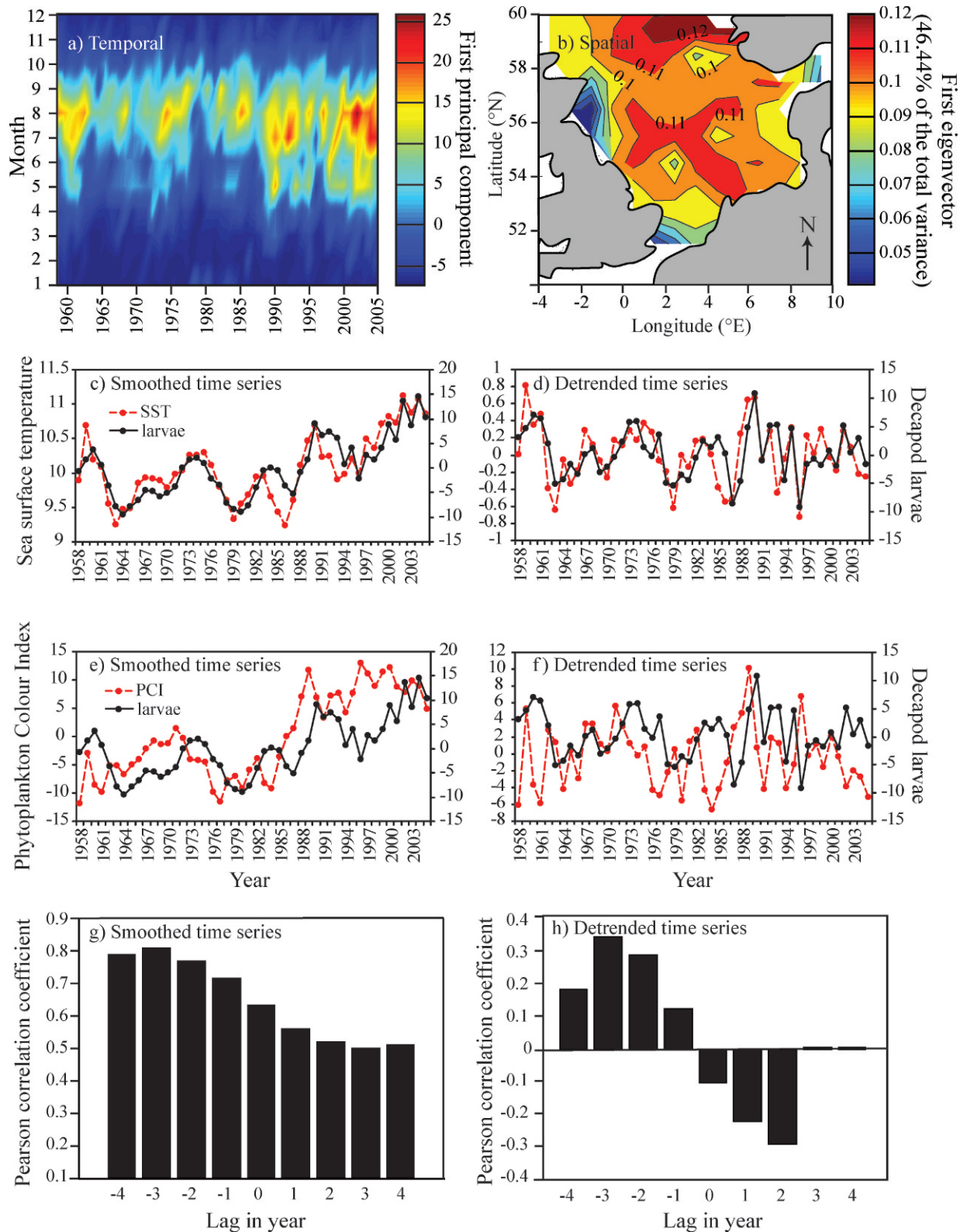


Fig. 2. Temporal and spatial changes in decapod larval abundance ( $\log_{10}(x + 1)$ ) and correlations between larval abundance, SST, and the PCI in the North Sea for the period 1958–2005. (a) Three-dimensional plot of temporal changes in the first principal component of decapod larval abundance in North Sea CPR samples. (b) Spatial changes in the first eigenvector of larval abundance obtained from a PCA performed on the two-dimensional matrix of 154 geographical squares (latitudes from 50.5° to 60°N and from 3.5°W to 9.5°E)  $\times$  (12 months  $\times$  48 yr [1958–2005]). (c) Smoothed time series of the first principal component of decapod larval abundance and SST. (d) Detrended time series of the first principal component of decapod larval abundance and temperature. (e) Smoothed time series of the first

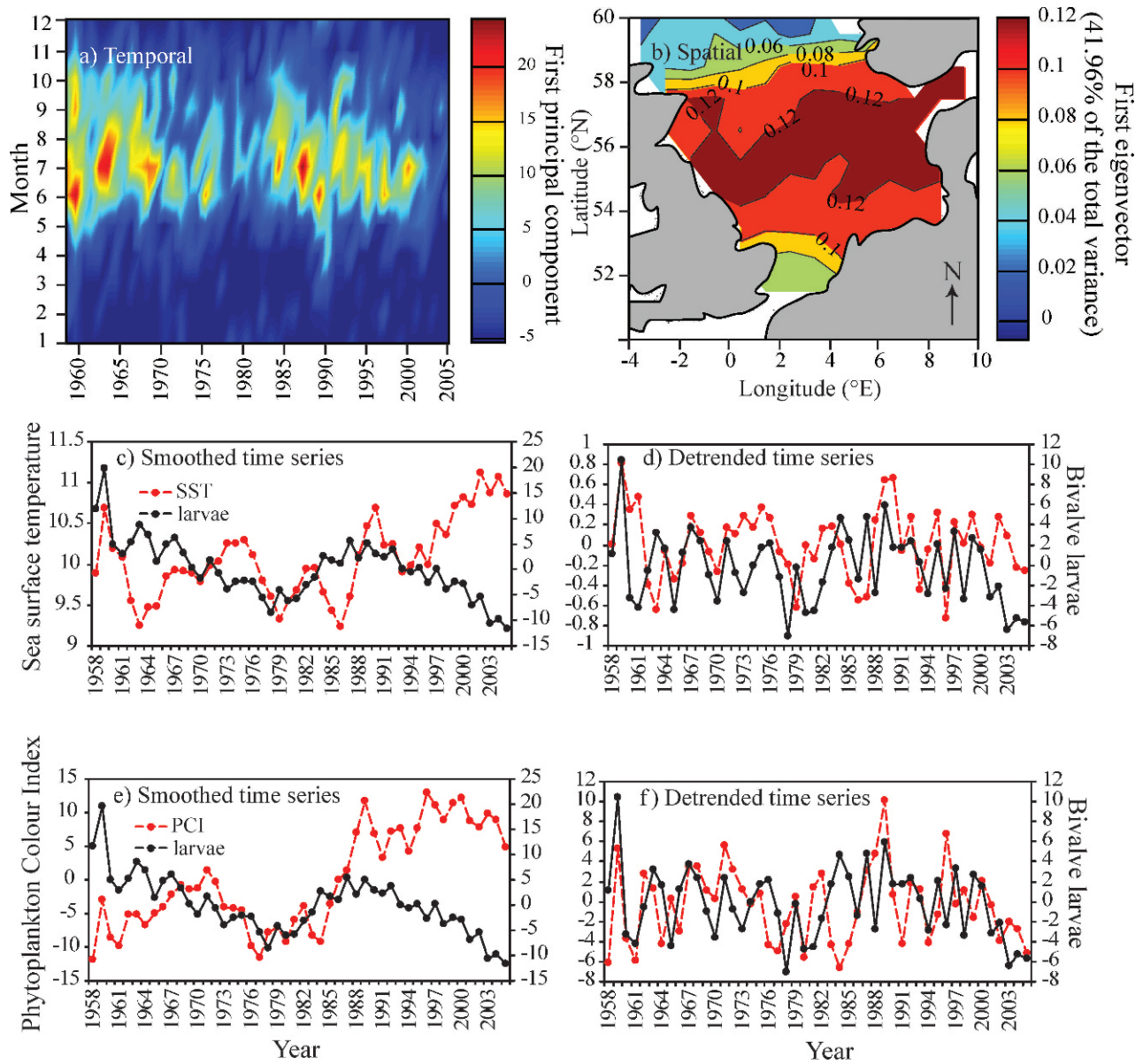


Fig. 3. Temporal and spatial changes in bivalve larval abundance ( $\log_{10}(x + 1)$ ) and correlations between larval abundance, SST, and the PCI in the North Sea for the period 1958–2005. (a) Three-dimensional plot of temporal changes in the first principal component of bivalve larval abundance in North Sea CPR samples. (b) Spatial changes in the first eigenvector of larval abundance obtained from a PCA performed on the two-dimensional matrix of 154 geographical squares (latitudes from 50.5° to 60°N and from 3.5°W to 9.5°E)  $\times$  (12 months  $\times$  48 yr [1958–2005]). (c) Smoothed time series of the first principal component of bivalve larval abundance and SST. (d) Detrended time series of the first principal component of bivalve larval abundance and temperature. (e) Smoothed time series of the first principal components of bivalve larval abundance and the PCI. (f) Detrended time series of the first principal components of bivalve larval abundance and the PCI.

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principal components of decapod larval abundance and the PCI. (f) Detrended time series of the first principal components of decapod larval abundance and the PCI. (g) Cross-correlation, smoothed time series, between temporal changes in decapods and the PCI. (h) Cross-correlation, detrended time series, between temporal changes in decapods and the PCI. A negative lag of 1 yr means that a change in PCI leads to a change in decapods the following year.

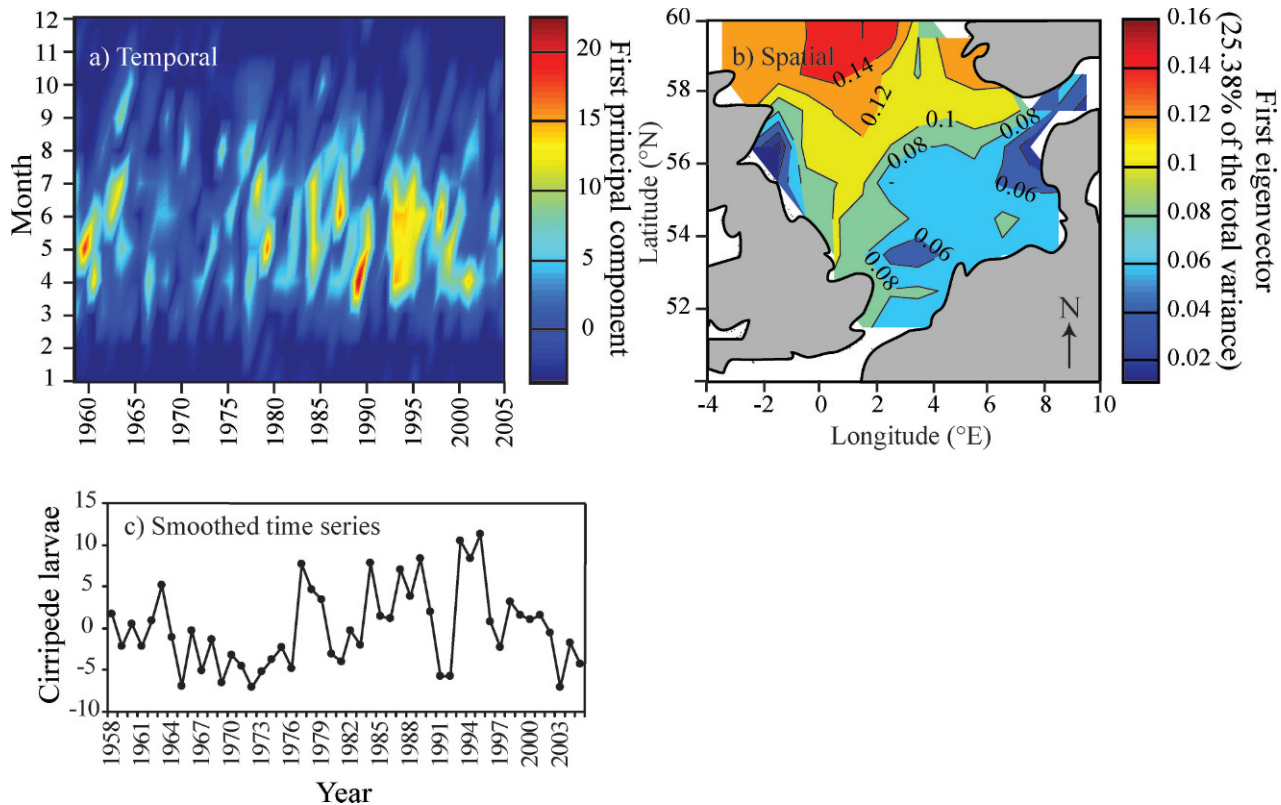


Fig. 4. Temporal and spatial changes in cirripede larval abundance ( $\log_{10}(x + 1)$ ) and correlations between larval abundance, SST, and the PCI in the North Sea for the period 1958–2005. (a) Three-dimensional plot of temporal changes in the first principal component of cirripede larval abundance in North Sea CPR samples. (b) Long-term spatial changes in the first eigenvector of abundance of cirripede larvae in the North Sea. (c) First principal component of cirripede larval abundance.

## Results

*Long-term changes in North Sea echinoderm larvae, SST, and phytoplankton*—Long-term monthly changes in echinoderm larvae show a marked increase in abundance after the mid-1980s and particularly after the mid-1990s (Fig. 1a). Although echinoderm larvae increased in abundance throughout most parts of the North Sea, the greatest increases occurred in the central and northern regions (Fig. 1b). Correlations calculated between SST and the abundance of echinoderm larvae show the existence of a significant link between these two variables (smoothed time series,  $r = 0.65$ ,  $p = 0.04$ , Fig. 1c; detrended time series,  $r = 0.41$ ,  $p = 0.0034$ , Fig. 1d). After removal of the long-term trend, the residuals revealed high year-to-year variability between the two time series and an immediate response of larval numbers to temperature. There is also a significant positive relationship between the abundance of echinoderm larvae and the PCI (smoothed time series  $r = 0.65$ ,  $p = 0.03$ , Fig. 1e), which only holds when long-term changes are considered (detrended time series  $r = -0.09$ ,  $p = 0.53$ , Fig. 1f).

*Long-term changes in North Sea decapod larvae, SST, and phytoplankton*—Figure 2a shows that decapod larvae have increased in abundance since the mid-1980s in CPR samples and now also appear earlier in the year, showing

the same trend as that seen in echinoderm larvae. Also as in echinoderm larvae, the long-term changes in decapod larval abundance are greatest in the central and northern North Sea (Fig. 2b). There is a very strong positive relationship between SST and the abundance of decapod larvae (smoothed time series,  $r = 0.86$ ,  $p < 0.0001$ , Fig. 2c), showing the existence of a significant link between these two variables. After removal of the long-term trend, the residuals revealed high year-to-year variability between the two time series and an immediate response of decapod larval numbers to temperature (detrended time series,  $r = 0.61$ ,  $p < 0.0001$ , Fig. 2d). There is also a significant positive relationship between the abundance of decapod larvae and the PCI with a time lag of 3 yr (smoothed time series,  $r$  3 yr = 0.82,  $p = 0.01$ , Fig. 2e,g; detrended time series,  $r$  3 yr = 0.36,  $p = 0.02$ , Fig. 2f,h).

*Long-term changes in North Sea bivalve larvae, SST, and phytoplankton*—Long-term monthly changes in bivalve larvae reveal a general decline in abundance in CPR samples from 1958 to 2005 with two periods, from the late 1970s to the early 1980s and from 2000 to the present day, of particularly low abundance (Fig. 3a). Figure 3b shows that the greatest changes in abundance of bivalve larvae are in the central North Sea. Correlations calculated between the abundance of bivalve larvae and SST did not reveal any relationship between long-term changes in SST and larval

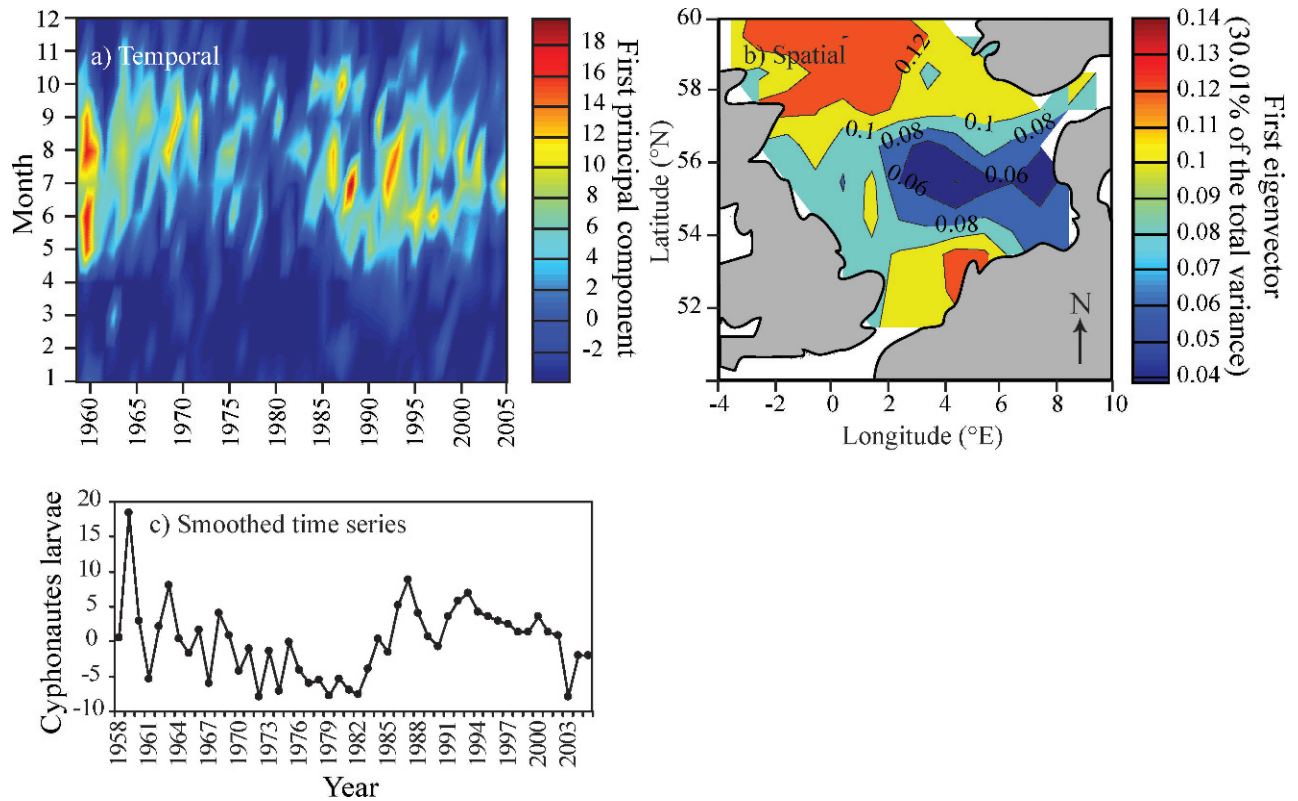


Fig. 5. Temporal and spatial changes in cyphonautes larval abundance ( $\log_{10}(x + 1)$ ) and correlations between larval abundance, SST, and the PCI in the North Sea for the period 1958–2005. (a) Three-dimensional plot of temporal changes in the first principal component of cyphonautes larval abundance in North Sea CPR samples. (b) Long-term spatial changes in the first eigenvector of abundance of cyphonautes larvae in the North Sea. (c) First principal component of cyphonautes larval abundance.

abundance (smoothed time series,  $r = -0.27$ ,  $p = 0.33$ , Fig. 3c). However, after removal of the long-term trends there is a clear positive relationship between SST and bivalve larval abundance, with an immediate response of larval numbers to temperature (detrended time series,  $r = 0.31$ ,  $p = 0.02$ , Fig. 3d). There was no evidence of a correlation between long-term changes in the PCI and bivalve larval abundance (smoothed time series,  $r = -0.23$ ,  $p = 0.55$ , Fig. 3e). However, the detrended time series indicated a positive relationship exists between chlorophyll and larval abundance (detrended time series,  $r = 0.31$ ,  $p = 0.03$ , Fig. 3f).

*Long-term changes in North Sea cirripede and cyphonautes larvae*—There were no clear patterns in the long-term abundance of cirripede (Fig. 4a,c) or cyphonautes larvae (Fig. 5a,c), which occur in relatively low numbers in CPR samples and seem to vary sporadically throughout the time series. Cirripede and cyphonautes also show quite different spatial patterns of abundance from the larvae of echinoderms, decapods, and bivalves (Figs. 4b, 5b).

*Long-term changes in North Sea phytoplankton*—Long-term monthly changes show that chlorophyll levels in the North Sea recorded by the CPR PCI have increased from the mid-1980s to 2005 (Fig. 6a). The PCI is now also higher

throughout the summer months. Long-term changes show that the increase in the PCI is most pronounced in the central and eastern North Sea, with additional increases in the northern North Sea and the coastal areas bordering the Netherlands (Fig. 6b).

Neither the long-term monthly abundance of diatoms nor that of dinoflagellates in North Sea CPR samples appears to increase after the mid-1980s (Fig. 6c,d, respectively). The main diatom bloom occurs in the spring, with a smaller subsequent bloom in late summer and early autumn (Fig. 6c). However, during the 1960s and from 2000 to 2005, diatoms also appear throughout the summer months. The peak time of dinoflagellate abundance is in the summer (Fig. 6d) and its timing of occurrence has advanced throughout the time series so that this group now appears earlier in the year (Edwards and Richardson 2004). The duration of the dinoflagellate bloom also now appears to be shorter (Fig. 6d). There were no long-term relationships between changes in the PCI and diatom abundance (smoothed time series,  $r = 0.24$ ,  $p = 0.57$ , Fig. 6e; detrended time series,  $r = 0.03$ ,  $p = 0.81$ , Fig. 6f) or dinoflagellate abundance (smoothed time series,  $r = 0.08$ ,  $p = 0.77$ , Fig. 6g; detrended data,  $r = 0.02$ ,  $p = 0.88$ , Fig. 6h). There was also no long-term relationship between the abundance of the benthic diatom *P. sulcata* and the PCI ( $r = 0.19$ ,  $p = 0.63$ ).



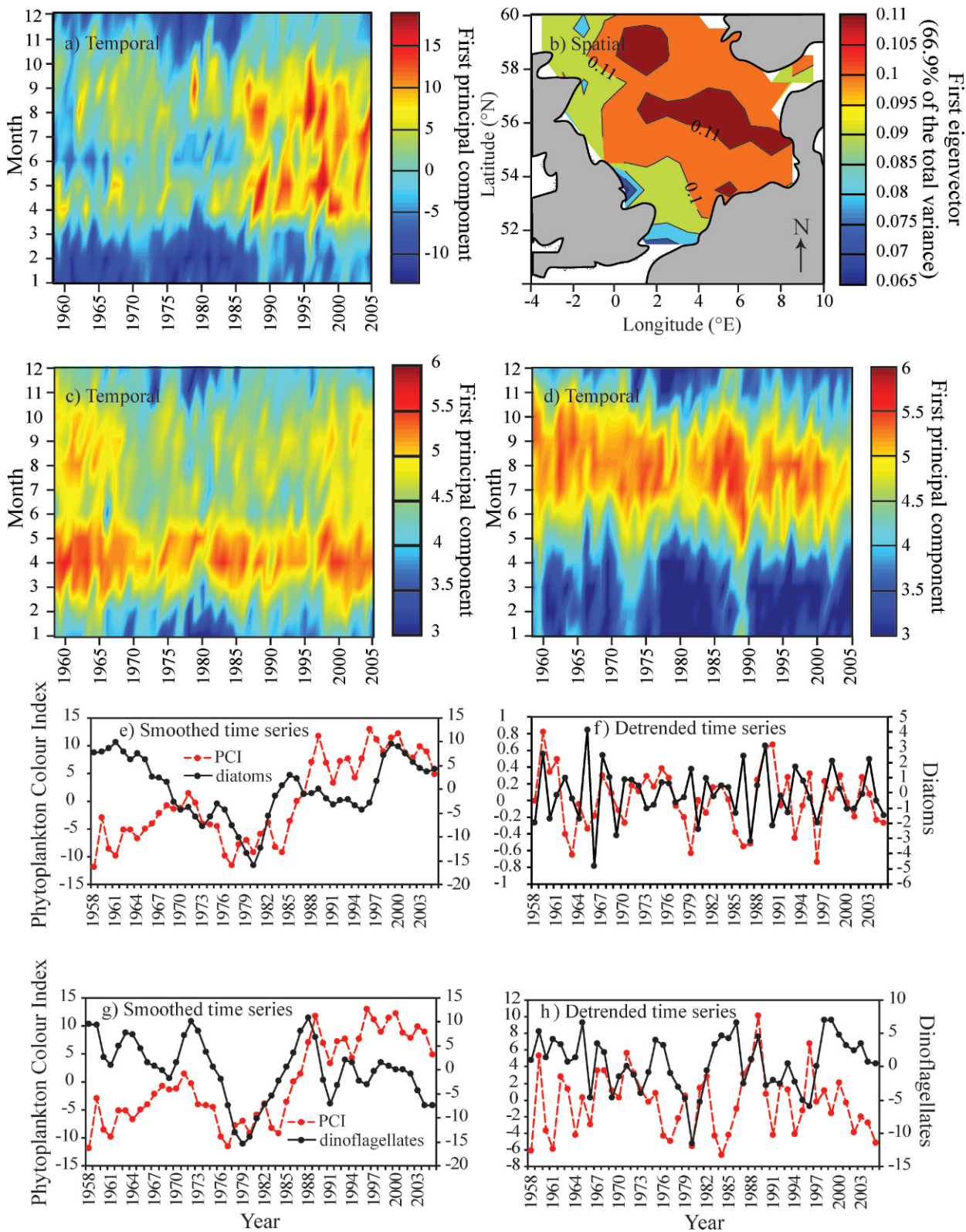


Fig. 6. Temporal and spatial changes in the PCI ( $\log_{10}(x + 1)$ ) and correlations with diatom and dinoflagellate abundance ( $\log_{10}(x + 1)$ ) in the North Sea for the period 1958–2005. (a) Three-dimensional plot of temporal changes in the first principal component of the PCI in North Sea CPR samples. (b) Spatial changes in the first eigenvector of the PCI obtained from a PCA performed on the two-dimensional matrix of 154 geographical squares (latitudes from 50.5° to 60°N and from 3.5°W to 9.5°E)  $\times$  (12 months  $\times$  48 yr [1958–2005]). (c) Three-dimensional plot of temporal changes in the first principal component of diatom abundance. (d) Three-dimensional plot of temporal changes in the first principal component of dinoflagellate abundance. (e) Smoothed time series of the first principal

## Discussion

Warmer SSTs in the North Sea correlate with the larval production of three benthic phyla that have the same life history strategies. Analyses of long-term time series of the North Sea meroplankton have revealed positive correlations between North Sea SST and the planktonic larval abundance of Echinodermata (ophiuroids and echinoids), Arthropoda (decapods), and Mollusca (bivalves). Long-term trends in the larval abundance of these three phyla are quite different, however. Although there has been a coincident increase in the abundance of echinoderms and decapods (Figs. 1d, 2d) in the North Sea meroplankton, especially from the mid-1980s to 2005, the abundance of bivalve larvae has declined over this period (Fig. 3d).

In addition to clear relationships between temperature and larval abundance of echinoderms, decapods, and bivalves, we also found significant positive relationships between the North Sea PCI and the abundance of echinoderm, decapod, and bivalve larvae. The changes in the North Sea meroplankton consequently extend a major regime shift that has occurred in the North Sea phytoplankton and holoplankton (Beaugrand 2004) to include changes in the biology of benthic species (Kröncke et al. 1998; Warwick et al. 2002). The boundaries of the regions of greatest change in meroplankton abundance and the PCI follow approximately the mixed stratified environment of the North Sea (Pingree and Griffiths 1978); the greatest changes in abundance are in the deeper regions characterized by stratification in summer.

It should be noted that there are limitations to the CPR data, because of the method of plankton sampling (Batten et al. 2003), that will affect the changes in the plankton we have described. As with all plankton sampling devices, the aperture of the CPR and the mesh size, which is large for meroplankton and phytoplankton, influence the diversity of organisms sampled (Richardson et al. 2006). Because the mesh size and methods of analysis have remained constant throughout the survey, the sampled taxa must nevertheless be considered to be consistent. The CPR also samples nearshore taxa poorly because it is not deployed until the towing vessel is in a suitable water depth. The temporal changes in the plankton we have reported could, of course, also reflect changes in the relative depth distribution of different taxa, because the CPR samples at a fixed depth. However, we are unaware of any reports of temperature influencing the vertical distribution of meroplankton in the North Sea on either an annual or a long-term basis.

In a recent paper, Kirby et al. (2007) demonstrated a significant positive relationship between warmer North Sea winter SSTs and an increased abundance of echinoderm larvae in the summer plankton, predominantly those of *E. cordatum*. During winter, the SST is close to the sea bottom temperature in the North Sea, and Kirby et al. (2007)

suggested that warmer winter sea temperatures had affected gametogenesis in this echinoderm and that warmer spring temperatures had also influenced the timing of spawning. In a similar way, warmer sea temperatures could influence gametogenesis in decapods and bivalves to explain the positive relationships we found between SST and meroplankton abundance.

The planktonic larval stage is a time of high mortality for all benthic species (Rumrill 1990), and so meroplankton abundance in CPR samples will also increase if larval survival improves. Warmer temperatures, within the thermal niche limits of a species, can improve larval survival by speeding development and shortening the time spent in the plankton (Hoegh-Guldberg and Pearse 1995). In bivalves, increases in temperature shorten the duration of the larval phase more than do increases in food availability (Mackie 1984). Milder winters also improve the survival of benthic stages (Zeiss and Kröncke 1997), particularly in nearshore regions (Reiss et al. 2006). A larger benthic community will further improve reproductive output because of the density-dependent effect on fertilization rates (Levitan et al. 1992). Observations from recent North Sea benthic surveys also indicate a wider spatial distribution of the echinoderm *E. cordatum*, particularly in the northern North Sea (Rees et al. 2007).

Despite the positive relationship between the abundance of bivalve larvae and SST (Fig. 3d) the long-term decline in abundance of bivalve larvae reveals that not all taxa benefit from the new North Sea hydroclimatic regime. Bivalve recruitment in the North Sea is affected deleteriously by benthic decapod predation on the newly settled larvae (Phillipart et al. 2003). The dominant decapod taxa in North Sea CPR samples are Polybiinae, *Upogebia deltaura*, *Callinassa subterranea*, and *Cancer pagurus* (Rees 1955; Lindley et al. 1993). Fisheries data show that landings of the predatory decapods (*Pandalus* and *Nephrops*; ICES 2006) and *Cancer* (Heath 2005) have increased markedly in the North Sea. Rees et al. (2007) also noted increases in *U. deltaura* and *C. subterranea* in parts of the North Sea. The declining abundance of bivalve larvae in the North Sea may therefore represent a dwindling adult population because of poor recruitment year on year caused by increased decapod predation (Cardoso et al. 2007).

Food availability and food quality are also important factors affecting growth and survivorship in the plankton (Reitzel et al. 2004). The PCI in the North Sea shows an increase in primary production after the mid-1980s. Neither diatoms nor dinoflagellates, which are of poor nutritional quality for developing planktonic larvae (Sterner and Hessen 1994), could explain the change in the PCI (Fig. 6e–h). Other photosynthetic eukaryotes that contribute to the PCI, but which cannot be identified, with the exception of *Phaeocystis* sp. (Gieskes et al. 2007), must account for the observed changes. The increase in the PCI

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components of diatom abundance and the PCI. (f) Detrended time series of the first principal components of diatom abundance and the PCI. (g) Smoothed time series of the first principal components of dinoflagellate abundance and the PCI. (h) Detrended time series of the first principal components of dinoflagellate abundance and the PCI.

therefore not only represents increased primary production but may also reflect an increase in the abundance of phytoplankton of a better nutritional quality; this may also offset greater energetic costs to the larvae because of the influence of warmer temperatures on metabolic rates.

Greater phytoplankton abundance has also been accompanied by phenological changes in the plankton that may increase food availability for the meroplankton by reducing competition with holoplankton taxa (Heath 2005). The time of spawning of many benthic species is influenced by temperature (Orton 1920). As a result of warmer SST, many meroplankton taxa now occur earlier in the year (Edwards and Richardson 2004). Conversely, holoplankton taxa such as copepods, whose life cycles may be more sensitive to photoperiod (Speirs et al. 2005), have not shown a similar advance in their seasonality (Edwards and Richardson 2004) and have also declined in abundance (Reid et al. 2003).

The benthic recruitment of newly settled larvae is also affected by food supply, in this case sedimented phytoplankton (Olafsson et al. 1994). In the North Sea, sedimented phytoplankton can represent over two thirds of the annual organic input to the benthos (Graf et al. 1983). Higher summer phytoplankton levels, reduced grazing pressure in the summer plankton because of the long-term decline in holoplankton abundance (Beaugrand 2004), and high autumn sedimentation rates in the North Sea (Smetacek 1980) improve food supply to the North Sea benthos. Greater year-round export of phytoplankton to the benthos benefits the growth of adult stages of psammivorous detritivores such as *E. cordatum* (Nunes and Jangoux 2004) and many benthic bivalves (Morton 1983). Previous studies have shown that sediment chlorophyll *a* content influences total benthic biomass and the biomass of most North Sea macroinvertebrates positively (Heip et al. 1992).

The differences in the relationships between the PCI and the larval abundance of each benthic taxon may simply reflect the interaction between phytoplankton and the biology of each group. The existence of a clear 3-yr time lag in the correlation between the PCI and decapod larval abundance indicates the importance of phytoplankton only during the larval stage. In this case, the 3-yr time lag represents the time taken for the dominant Brachyuran year classes to reach maturity and spawn (Tallack 2002). Likewise, the different relationships we observed between the PCI and the larval abundance of other taxa are likely to represent the importance of phytoplankton throughout their life cycles reducing the strength of any signal during the larval stage.

Our analysis of a long-term plankton community dataset shows that although larval production of benthic organisms with similar life histories may respond similarly to ocean warming, the interactions among species may bring about quite different outcomes. For example, after the North Sea regime shift and since the beginning of the 1990s, although the positive year-to-year relationship between temperature and bivalve larval abundance continues to hold, a negative relationship between the two long-term trends appears that is likely to be related to an increase in decapod predation. The changes in the North Sea meroplankton may signal ecosystem-wide changes in nutrient cycling through changes

in benthic–pelagic coupling (Marcus and Boero 1998). Analysis of surveys of the North Sea macrobenthos collected prior to 1986 has revealed a significant decreasing trend in the macrobenthic biomass with latitude (Heip et al. 1992). Since 1986, warmer temperatures and increased phytoplankton may have influenced these latitudinal gradients. Likewise, changes in the relative abundances of the adult benthic stages, because of improved recruitment, may be restructuring the benthic community through competition, predation, and disturbance (Ebert 1983; Connell 1985; Roughgarden et al. 1985). Continued long-term monitoring of the North Sea may therefore provide insights into the effect of climate on uncoupling the trophic linkages between species and systems.

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