



Climate effects and benthic–pelagic coupling in the North Sea

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ABSTRACT: The North Sea is one of the most biologically productive ecosystems in the world and supports important fisheries. Climate-induced changes occurred in the pelagic ecosystems of the North Sea during the 1980s. These changes, which have been observed from phytoplankton to fish and among permanent (holoplankton) and temporary (meroplankton) plankton species, have resulted in alterations in plankton community composition and seasonality. Until now, the effects of climate-driven changes on biological linkages between pelagic and benthic ecosystems have not been examined. The present study indicates that changes in benthic organisms could have a profound effect on the trophodynamics of the pelagos. We demonstrate this by analyses of a long-term time series of North Sea plankton and sea surface temperature data. We discover that pronounced changes in the North Sea meroplankton, mainly related to an increased abundance and spatial distribution of the larvae of a benthic echinoderm, *Echinocardium cordatum*, result primarily from a stepwise increase in sea temperature after 1987 that has caused warmer conditions to occur earlier in the year than previously. Key stages of reproduction in *E. cordatum*, gametogenesis and spawning, appear to be influenced by winter and spring sea temperature and their larval development is affected by the quantity and quality of their phytoplankton food. Our analyses suggest that a new thermal regime in the North Sea in winter and spring may have benefited reproduction and survival in this benthic species. As a result, *E. cordatum* may be altering the trophodynamics of the summer pelagic ecosystem through competition between its larvae and holozooplankton taxa.

KEY WORDS: Benthic–pelagic coupling · Global warming · *Echinocardium* · North Sea · Plankton · Temperature

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INTRODUCTION

Large-scale changes have occurred in the abundance, distribution and seasonal cycles of plankton in the North Sea in recent years that are apparently climate driven (Beaugrand et al. 2002, 2003, Edwards & Richardson 2004). In particular, there has been an increase in the abundance of the merozooplankton (larval planktonic stages) and decrease in the abundance of the holozooplankton (Lindley & Batten 2002). Most of these changes have been detected in the North Sea using samples collected by the Continuous Plankton Recorder (CPR)

survey (see Fig. 2) (Warner & Hays 1994). For example, Table 1 shows the changes in echinoderm larvae (merozooplankton, larval planktonic stages) and copepods (holozooplankton) from 1949 to 2002. Measurements of Phytoplankton Colour Index (a measure of phytoplankton chlorophyll) derived from the CPR survey (Batten et al. 2003a, Raitsos et al. 2005) have also increased over the whole North Sea since 1987 and chlorophyll levels are now also higher throughout the year (Edwards et al. 2001). All these changes in the plankton have had significant implications for ecosystem structure, including commercial fisheries (Beaugrand et al. 2003).

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Table 1. Echinoderm larvae and copepods in the North Sea. Data are means (\pm SD) of annual total values in the Continuous Plankton Recorder (CPR) database for copepods and echinoderm larvae for five 5 yr periods within the area 51 to 61°N, 3°W to 11°E, from 1949 (first year for which data were available for echinoderms) to 2002

	Echinoderm larvae	Copepods
1949–1953	247.3 (57.9)	1231.4 (120.2)
1965–1969	174.5 (46.0)	646.6 (77.6)
1981–1985	220.1 (169.4)	534.5 (220.2)
1988–1992	268.4 (79.7)	629.0 (71.6)
1998–2002	620.2 (87.6)	457.6 (19.2)

Notable among the changes in the North Sea meroplankton taxa are increases in the relative and absolute abundance of the larvae of benthic echinoderms (Lindley & Batten 2002) and an advance by 47 d, over 45 yr, in their timing of peak occurrence; this represents the largest phenological change detected in the plankton of this region so far (Greve et al. 2001, Edwards & Richardson 2004). To determine which echinoderm species are involved in the increase in the meroplankton we sampled echinoderm larvae at the time of their peak abundance in June and July 2004 from CPR tow-routes between 53 and 58°N, and 0 and 7°E (Kirby & Lindley 2005). Genetic analysis revealed that larvae of *Echinocardium cordatum* (Fig. 1), a burrowing psammivorous spatangoid, were overwhelmingly dominant in these samples (Kirby & Lindley 2005). *E. cordatum* was also the dominant species of echinoderm larvae in the North Sea plankton from 1949 to 1951 (Rees 1954). Although we cannot rule out changes in echinoderm community composition, changes in the meroplankton between the period 1949 to 1951 and the year 2004 therefore appear to be due to a substantial increase in the larvae of an established species.

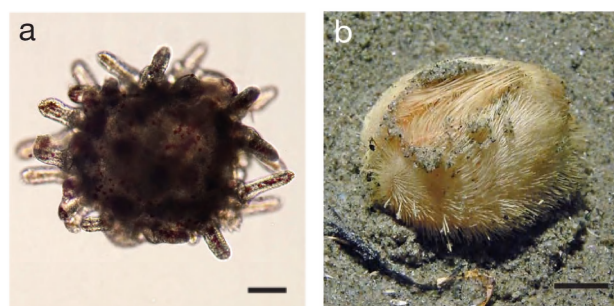


Fig. 1. *Echinocardium cordatum*. (a) Post-larval stage, which has increased in abundance in North Sea Continuous Plankton Recorder (CPR) samples. Scale bar = 0.1 mm. (b) Adult on sediment surface. Raised sediment around its base is formed as the animal burrows to 10–15 cm depth, where it normally lives (image © Kåre Telnes, www.seawater.no). Scale bar = 1 cm

The greater abundance of *Echinocardium cordatum* larvae in the North Sea plankton could result from enhanced individual fecundity, more adults reproducing or improved larval survival. Temperature, through its influence on physiological processes, has the potential to affect all these life-history stages (Rumrill 1990, Sheader 1996, Fischer et al. 2003, Nunes & Jangoux 2004). The abundance of phytoplankton food will also affect the development of planktonic *E. cordatum* larvae (Feneaux et al. 1994) and sedimented phytoplankton is likely to influence recruitment and growth of the benthic adults (Ólafsson et al. 1994, Millar & Emlet 1999, Nunes & Jangoux 2004). We have therefore examined whether long-term temporal and spatial changes in temperature in the North Sea, and changes in the abundance of phytoplankton food, might explain changes in the abundance of *E. cordatum* larvae in the plankton.

MATERIALS AND METHODS

Sampling of North Sea plankton by the CPR. Plankton data for the North Sea from 1949 to 2003 were collected by the CPR survey (Warner & Hays 1994) (Fig. 2); this data is available upon request from the Sir Alister Hardy Foundation for Ocean Science (www.sahfos.ac.uk) that runs the CPR survey. The CPR is an upper layer plankton sampler towed behind merchant ships on regular routes. Seawater enters the machine through a front aperture and the plankton are retained on a moving band of silk gauze of mesh size 280 μ m that is slowly wound into a tank of formalin (Batten et al. 2003b). In the laboratory the gauze is cut into sections (a CPR sample), each representing the plankton from 3 m³ of water taken during 10 nautical miles (18 km) of tow at an average depth of 7 m, and up to 450 taxa are identified and enumerated visually (Richardson et al. 2006) or by using molecular genetic



Fig. 2. Continuous Plankton Recorder (CPR) tow-routes and sampling (black dots) in the North Sea between 1946 and 2002

methods (Kirby & Lindley 2005). The survey has operated in the North Sea and North Atlantic on a routine monthly basis since 1946 and is the largest marine biological time series in the world; data on echinoderm larvae in the North Sea were first recorded in 1949.

Examination of long-term biological change. Long-term change in the echinoderm larvae and the Phytoplankton Colour Index of North Sea CPR samples were examined by spatialised standardised principal component analysis (PCA). The Phytoplankton Colour Index of each CPR sample is an index of the amount of chlorophyll that is routinely assessed subjectively by comparison of the silk sample to a colour chart (Batten et al. 2003a). This Phytoplankton Colour Index is correlated with fluorimeter and satellite measures of chlorophyll (Batten et al. 2003a, Raitsos et al. 2005). The PCA analyses were applied on a matrix of 154 geographical squares (latitudes from 50.5 to 60.5° N and from 3.5° W to 9.5° E) \times 54 yr (1949 to 2002). Eigenvectors and principal components were calculated from a correlation matrix of 154 \times 154 geographical squares. This analysis allows spatial and temporal changes to be taken into account in a single procedure. Maps of eigenvectors show where the main patterns of temporal variability (represented by principal components) occur. Such analyses have been described in Beaugrand et al. (2001) and are identical to the analysis performed on sea level pressure to identify the main pattern of climatological variability (Hurrell & van Loon 1997).

Examination of long-term changes in sea surface temperature (SST). Temperature data for the North Sea were obtained from the COADS 1-degree enhanced dataset provided by the comprehensive NOAA-CIRES Climate Diagnostics Center database (Boulder, Colorado, USA) (Woodruff et al. 1998). The data were analysed by standardised PCA. Therefore, the dispersion matrix *S* was a correlation matrix. The same equations were used to calculate eigenvectors and principal components. This analysis was performed on the matrix 57 yr (1946 to 2002) \times 12 mo to identify months for which the year-to-year signal was strongest. The method used here was similar to that previously applied in Beaugrand et al. (2003). A discontinuity analysis called split moving-window boundary analysis (Webster 1973) was applied to detect rapid changes, which are persistent in time series. The principle of this method is simple and can be summarised in 4 steps: (1) a period of even-numbered size is introduced at the beginning of the time series; (2) this period is divided into 2 windows (here a window of 8 yr, which was chosen after examination of the autocorrelation function); (3) an association coefficient (here the Euclidean distance) is used to evaluate the differences between both time periods; and (4) the window is then moved from year to year, repeating

steps 2 and 3 until the end of the time series is reached. The probability of change was estimated by using a Multiple Response Permutation Procedure (Mielke et al. 1981). To determine if the SST or thermal characteristics of the North Sea have changed temporally, we calculated the number of days needed to reach a range of SSTs between 4 and 16°C over the period 1946 to 2002; these temperatures were chosen as they are the minimum and maximum North Sea SST for winter and spring. We used a standardised PCA to examine spatial change in North Sea SST; this was performed on the matrix 1° (lat./long.) grid \times number of days from the beginning of the year needed to reach a given temperature over 57 yr (1946 to 2002).

Examination of the relationship between biological and physical change. The Pearson linear correlation coefficient was used to assess the relationships between long-term changes in the zooplankton and the hydro-climatic environment. Probabilities of significance (*p*) of coefficients of correlation were calculated, taking into consideration the temporal autocorrelation. A Box-Jenkins (Box & Jenkins 1976) 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. Series were detrended by the use of Singular Spectrum Analysis (Vautard & Ghil 1992). The method uses a principal component analysis performed on an autocovariance matrix (also called a Toeplitz matrix) to decompose a time series into a succession of signals of decreasing variance (Beaugrand & Reid 2003). The long-term trend of each time series was first assessed by using both the eigenvectors and principal components representing the low-frequency variability; the detrended time series were then calculated by subtracting from each original time series its respective long-term trend.

RESULTS

Pronounced increase in winter and spring SST in the North Sea after 1987

A PCA performed on long-term monthly SST for the North Sea indicated that pronounced changes in temperature had occurred in the late 1980s mainly for the months January to May, when the SST is close to the sea bottom temperature in most continental shelf waters (from January to May the eigenvector values varied between 0.626 and 0.915 and from June to December the eigenvector values were between 0.08 and 0.52) (Fig. 3). A discontinuity analysis indicated that a marked stepwise increase in North Sea SST (*p* < 0.001) occurred after 1987 (Fig. 3).

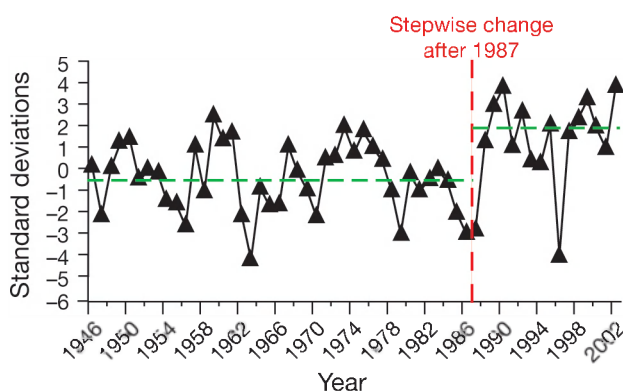


Fig. 3. Variation in North Sea sea surface temperature (SST), expressed as standard deviations from mean North Sea SST (black triangles) for 1946 to 2002. Vertical dashed line = step change in 1987, as determined by discontinuity analysis. Horizontal dashed lines = means for the 2 periods, which were -0.538 SD (1946 to 1987) and $+1.9530$ SD (1988 to 2002)

Positive covariation between changes in echinoderm larvae and SST

Long-term changes in echinoderm larvae show an increase in abundance for most parts of the North Sea, but particularly in the central and northern regions (Fig. 4a). Correlations calculated between SST (in winter and spring, January to May) and the abundance of echinoderm larvae (original time series, Fig. 4b; detrended time series, Fig. 4c) indicated the existence of a significant link between these 2 variables (original data $r = 0.50$, $p < 0.004$; detrended data $r = 0.40$, $p < 0.001$). After removal of the long-term trend the residuals revealed high year-to-year variability between the 2 time series and an immediate response of larval numbers to temperature.

Appearance of warmer conditions earlier in the year in the North Sea

Gametogenesis in *Echinocardium cordatum* commences when sea temperature exceeds 6°C (Nunes & Jangoux 2004). Fig. 5a shows that any given temperature within the range 4 and 16°C now appears earlier in the year especially for winter and spring temperatures. A correlation analysis indicated that the increase in abundance of echinoderm larvae is positively correlated with an increase in the number of days above 6°C ($r = 0.70$, $p < 0.001$; probability adjusted for temporal autocorrelation). Fig. 5b shows the average North Sea SST from January to March for 2 time periods, 1946 to 1987 and 1988 to 2002, which reveals that a larger area of the North Sea is now warmer at this time of year. The mean numbers of echinoderm larvae per sample for these 2 periods were 252.2 ± 132.2 (1949 to 1987) and 403.6 ± 203.4 (1988 to

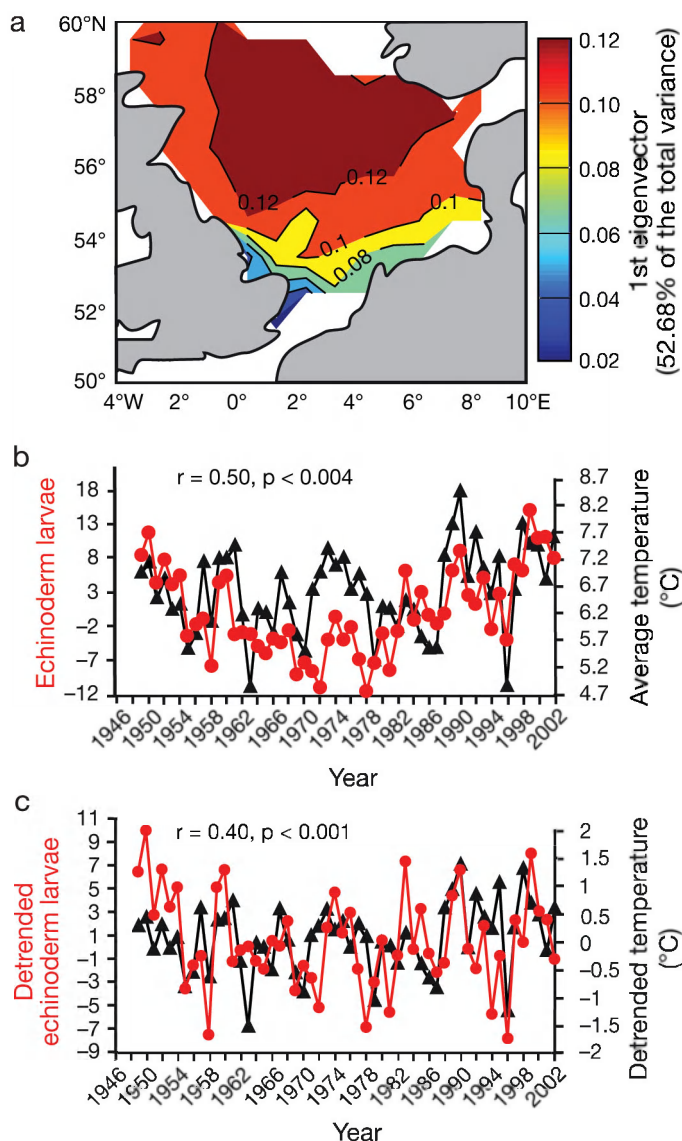


Fig. 4. *Echinocardium cordatum*. Spatial correlations between larval abundance ($\log_{10}(x+1)$ transformed) and sea surface temperature (SST) in the North Sea for period 1949 to 2002. (a) Long-term spatial changes in the first eigenvector of larval abundance in the North Sea. (b) Average SST from January to May of each year (\blacktriangle) and first principal component of matrix $54 \text{ yr} \times 12 \text{ mo}$ larval abundance (\bullet). (c) Detrended time series of temperature (\blacktriangle) and first principal component of larval abundance (\bullet)

2002). A PCA on the matrix $1^{\circ} \text{ grid} \times \text{number of days}$ needed to reach a given temperature over 57 yr (1946 to 2002) confirmed there has been a reduction in the number of squares with temperatures less than 7°C after the mid-1980s (the first principal component explained 58.95% of the variance). There was a highly significant positive correlation between this reduction and increased larval echinoderm abundance ($r = 0.59$, $p < 0.001$; probability adjusted for temporal autocorrelation).

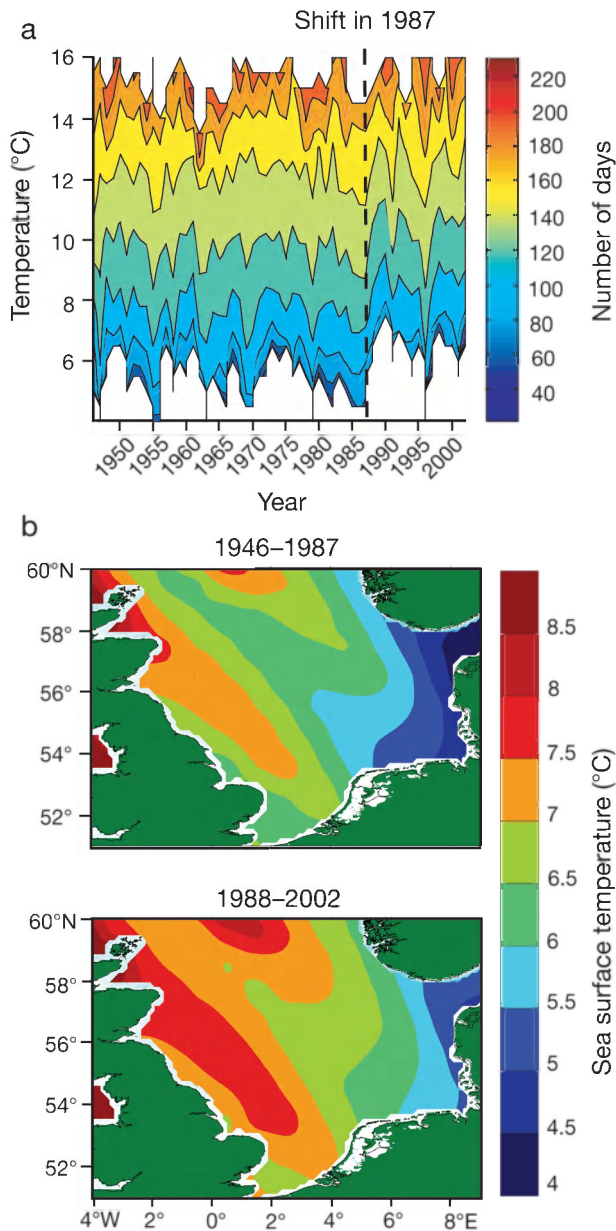


Fig. 5. Changes in sea surface temperature (SST) in the North Sea. (a) Three-dimensional plot of number of days required to reach certain SST in the North Sea each year, showing pronounced shift (dashed line) after 1987. (b) Change in winter (January to March) SST for 2 periods, 1946–1987 and 1988–2002, revealing warmer conditions in winter in recent years

Correlation between spatial distribution of echinoderms and increasing SST

Fig. 6a,b shows the change in the abundance of echinoderm larvae between the 2 periods 1949 to 1987 and 1988 to 2002. They reveal a pronounced northward expansion of echinoderm larvae; this is particularly evident when the difference between these 2

periods is examined (Fig. 6c). Spatial correlations provide evidence that the increase in larvae to the north has been influenced by the increase in SST (Fig. 6d).

Long-term changes in phytoplankton and echinoderm larvae

Food availability influences echinoderm larval development and survival (Feneaux et al. 1994). Fig. 7a shows the long-term changes in the Phytoplankton Colour Index and in echinoderm larval abundance in the North Sea for the period 1958 to 2002. Correlation analysis between Phytoplankton Colour Index and the abundance of echinoderm larvae indicated there is no significant correlation between the variables over the whole of the North Sea ($r = 0.31$, $p = 0.331$; probability adjusted for temporal autocorrelation). However, local correlation analysis indicates a stronger positive relationship between changes in the Phytoplankton Colour Index and echinoderm larvae in the northern North Sea (Fig. 7b), where the change in abundance of echinoderm larvae is the greatest (Fig. 6c).

DISCUSSION

The recent dominance of the larvae of benthic echinoderms in the plankton in summer (Lindley & Batten 2002) represents a major change in the balance between the meroplankton and the holoplankton and is indicative of a shift in resource partitioning between the benthos and pelagos. The abundance of adult *Echinocardium cordatum* is influenced by temperature (Moore 1936, Beukema 1985) and our analyses also suggest that sea temperature has an important influence on the numbers of *E. cordatum* larvae in the plankton. Discontinuity analysis indicates that a step-wise change towards a warmer thermal regime occurred in the North Sea after 1987. The strong contemporaneous link between winter and spring North Sea SST and the abundance of echinoderm larvae in the summer is notable (for example, the cold winter of 1996, which was a year with a negative North Atlantic Oscillation, led to reduced larval abundance in the summer of the same year [Fig. 4b,c]).

Echinocardium cordatum requires 3 yr to reach maturity in the North Sea (Buchanan 1966) and may live for more than 10 yr, although cold winters can cause high mortality (Beukema 1985). Gametogenesis in adult *E. cordatum* is initiated towards the end of winter, when North Sea winter temperature exceeds 6°C (Nunes & Jangoux 2004). We have shown that winter temperatures colder than the 6°C lower threshold for the initiation of gametogenesis (Nunes & Jan-

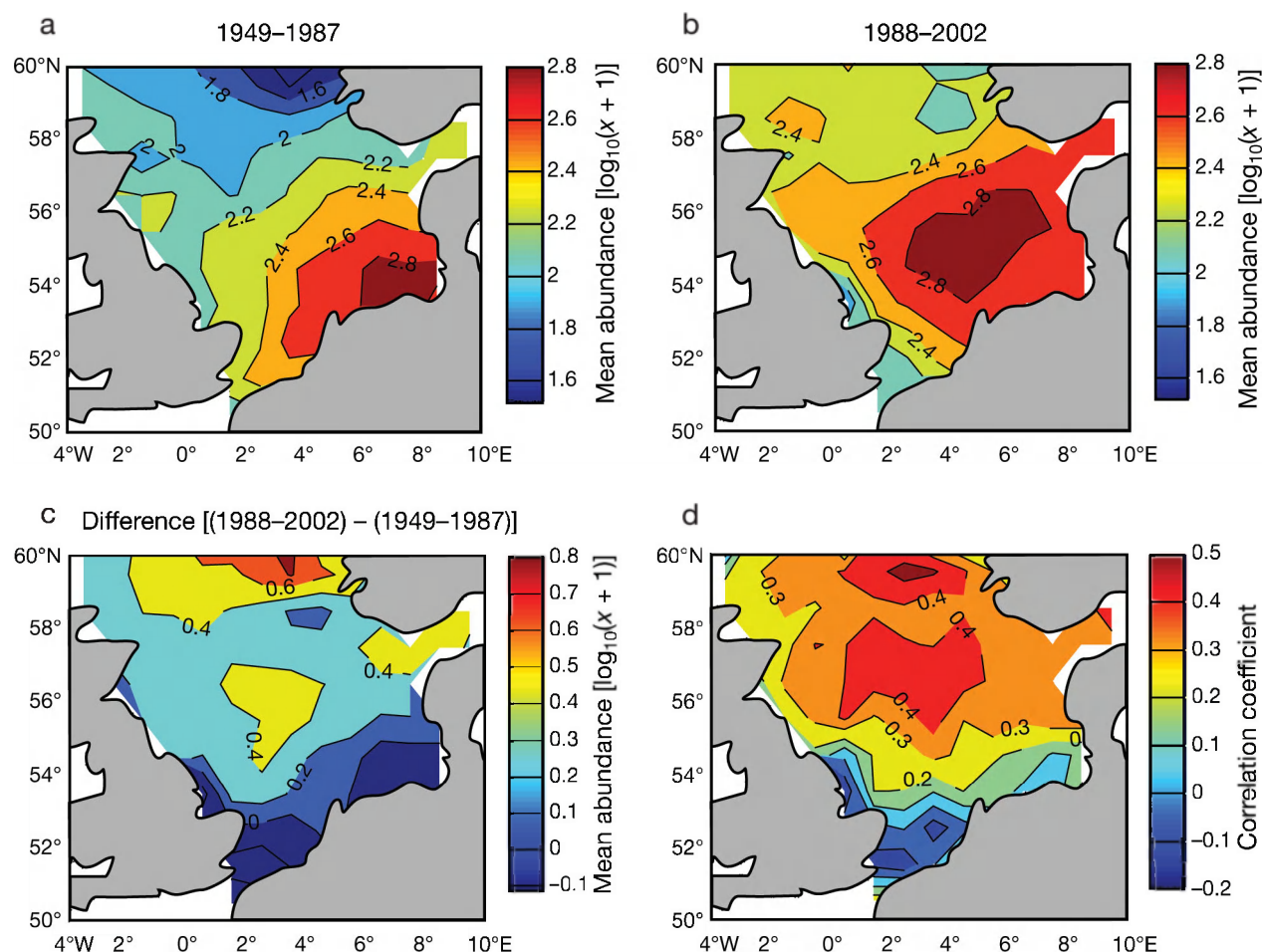


Fig. 6. *Echinocardium cordatum*. Spatial variation in larvae abundance and the correlation with sea surface temperature (SST) in the North Sea. (a) Abundance between 1949 and 1987; (b) abundance between 1988 and 2002; (c) difference in abundance between the 2 periods 1949–1987 and 1988–2002, showing change in abundance to be greatest in northern North Sea; (d) correlation between abundance of echinoderm larvae and SST between 1949 and 2002

goux 2004) have been less frequent since 1987 and that the spatial extent of regions in the North Sea in winter above the threshold temperature have also increased. In poikilotherms, temperature can also affect egg size and number, which are phenotypically plastic traits; warmer temperatures during gametogenesis are associated typically with smaller eggs and larger clutch sizes (Sheader 1996, Fischer et al. 2003). In all these ways therefore, warmer winter temperatures in the North Sea after 1987 may influence both the number of adult *E. cordatum* that are reproducing in any year and their individual fecundity. Since spawning in *E. cordatum* may also be influenced by temperature, in this case the achievement of a threshold temperature between 10 and 13°C (Nunes & Jangoux 2004), higher spring temperatures earlier in the year in the North Sea might also explain the phenological shift recorded in peak larval echinoderm abundance (Edwards & Richardson 2004).

In marine invertebrates with planktonic larvae, sea temperature during the larval stage can also influence larval survival, and hence abundance, by reducing the time spent in the plankton, which is a period of high mortality (Rumrill 1990). Growth and development of the planktonic larvae of benthic echinoderms is also affected by the abundance and quality of their phytoplankton food (Feneaux et al. 1994). We found a relationship with larval echinoderm abundance and the CPR Phytoplankton Colour Index in the northern North Sea, where phytoplankton biomass and chlorophyll is the lowest historically (Colebrook & Robinson 1965). Together with the phenological changes in the North Sea among phytoplankton and grazing holozooplankton that has created a mismatch in the food chain (Edwards & Richardson 2004), changes in phytoplankton in the northern North Sea may help support the increase in abundance of *Echinocardium cordatum* in this region.

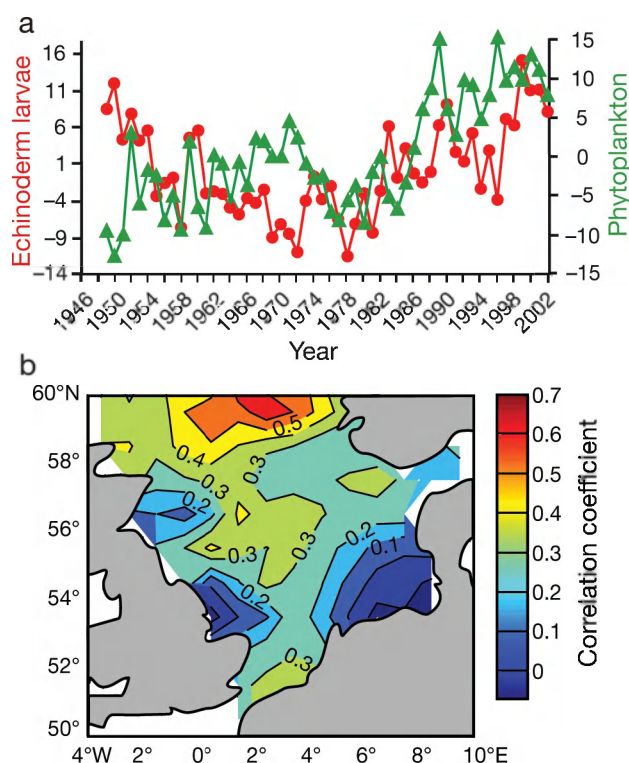


Fig. 7. Long-term changes in *Echinocardium cordatum* larval abundance and Phytoplankton Colour Index in the North Sea for period 1958 to 2002. (a) First principal component of changes in larval abundance (●) and first principal component of changes in the Phytoplankton Colour Index (▲). (b) Spatial variation in the correlation between larval abundance and Phytoplankton Colour Index showing greatest correlation in the northern North Sea, where the change in larval abundance is also greatest (see Fig. 6c)

Increased larval abundance may improve recruitment (Ólafsson et al. 1994, Millar & Emlet 1999) and warmer winters after 1987 may reduce adult mortality (Moore 1936, Beukema 1985). In this way, warmer conditions in the North Sea after 1987, together with increased phytoplankton, may act synergistically to increase the reproductive output, population density and habitat range of *Echinocardium cordatum* year after year. The large increase in echinoderm larvae between 1998 and 2002 is entirely consistent with our hypothesis that temperature influences larval abundance, since 1998 was the warmest year since the beginning of instrumental records (see Intergovernmental Panel on Climate Change WGI 2001; their Fig. 5). The rise in abundance of the merozooplankton (Lindley & Batten 2002), which comprises predominantly *E. cordatum* larvae (Kirby & Lindley 2005), may therefore reflect the synergy we propose. This may also explain observations from recent benthic surveys (Anonymous 2004) that indicate *E. cordatum* has increased in density and extended its

range, particularly in the shallow waters of the German Bight, the coldest area of the North Sea in winter (Lee & Ramster 1981).

It is hypothesised that the ecological regime shift that occurred in the North Sea plankton during the 1980s is related to changes in hydro-climatic forcing (Beaugrand 2004). This present study found an immediate response of echinoderm larval abundance to winter and spring sea surface temperature and a stepwise warming in North Sea surface temperature after 1987, particularly in winter and spring. Together, they suggest that climate changes are the most likely cause of the increase in echinoderm larval abundance and spatial distribution in the North Sea. The resulting increase in echinoderm larvae could now act to reinforce the new ecological regime by competitive exclusion of other holozooplanktonic taxa during spring and summer, such as copepods whose abundance has declined at this time of year.

This North Sea study, which shows the impact of climate on the biological linkages between different ecosystem components, highlights the importance of understanding the interrelated biological changes that will occur if forecasts of global climate change are realised. Our results also clearly suggest new areas of research. Experimental investigation of the effect of temperature on the biology of *Echinocardium cordatum* would test our hypothesis of the influence of the regime shift, which is currently based upon data from observational studies. Laboratory experiments investigating competition between *E. cordatum* larvae and holozooplankton for phytoplankton food would test our hypothesis regarding the impact of *E. cordatum* larvae on plankton trophodynamics.

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