**Explaining ecological shifts: The roles of temperature and primary production in the long-term dynamics of benthic faunal composition**

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**Abstract**

Predicting the ecological consequences of environmental change requires that we can identify the drivers of long-term ecological variation. Biological assemblages can exhibit abrupt deviations from temporal trends, potentially resulting in irreversible shifts in species composition over short periods of time. Such dynamics are hypothesised to occur as gradual forcing eventually causes biological thresholds to be crossed, but could also be explained by biota simply tracking abrupt changes to their environment. Here, we modelled temporal variation in a North Sea benthic faunal assemblage over a 40-year period (1972–2012) to test for changes to temporal trends of biota and determine whether they could be explained by underlying patterns in sea temperature and primary production. These extrinsic factors were postulated to influence community dynamics through their roles in determining and sustaining the metabolic demands of organisms, respectively. A subset of mainly large and long-lived taxa (those loaded on the first principal component of taxa densities) exhibited two significant changes to their temporal trends, which culminated in a shift in assemblage composition. These changes were explained by an increase in pelagic primary production, and hence detrital food input to the seabed, but were unrelated to variation in sea temperature. A second subset of mainly small and short-lived taxa (those loaded on the second principal component) did not experience any significant changes to their temporal trends, as enhanced pelagic primary production appeared to mitigate the impact of warming on these organisms. Our results suggest that abrupt ecological shifts can occur as biota track underlying variation in extrinsic factors, in this case primary production. Changes to the structure of ecosystems may therefore be predictable based on environmental change projections.

**Introduction**

Biodiversity is rapidly changing in an era of human dominance over the natural world (Steffen et al. 2007; Dornelas et al. 2014; McGill et al. 2015), putting species under increased risk of extinction and altering the functioning of ecosystems (Cardinale et al. 2012, Naeem et al. 2012; Dirzo et al. 2014). Predicting the impacts of environmental change requires that we identify the drivers of ecological variation. To this end, experiments are vital in demonstrating the effects of extrinsic factors (Hairston 1989; Stenseth et al. 2002). However, long-term monitoring is also required to track temporal variability in natural biological assemblages and determine whether potential drivers can explain the observed patterns (Dauvin 2010; Magurran et al. 2010). One pattern to recently emerge from long-term ecological datasets is the occurrence of abrupt deviations from temporal trends (e.g. Spencer et al. 2012); potentially resulting in irreversible shifts in species composition and functioning over short periods of time. The drivers of such community dynamics are not well understood. A common hypothesis is that abrupt ecological changes represent non-linear responses to gradual forcing, as biological thresholds are eventually crossed (Scheffer et al. 2001; Möllmann et al. 2015). An alternative explanation is that biota are tracking similar underlying patterns in extrinsic factors (Scheffer et al. 2001; Lees et al. 2006).

In attempting to understand the drivers of variation in species composition, a logical approach is to focus on the factors that are expected to exert the greatest ecological impacts. One of the most pertinent aspects of modern environmental change in this regard is the rise in global surface temperature associated with enhanced ‘greenhouse gas’ emissions (Hansen et al. 2006; Cook et al. 2013; Karl et al. 2015). Recent climate change has already had impacts on biological assemblages (Walther et al. 2002; Hoegh-Guldberg & Bruno 2010), and with global warming set to continue, severe impacts on biodiversity are predicted in the future (Bellard et al. 2012). Various other environmental changes are set to occur as a result of greenhouse gas emissions, including alterations to primary productivity (Chavez et al. 2011; Blanchard et al. 2012). Experiments indicate that such changes are likely to have their own ecological impacts (e.g. Walker et al. 2006; Wimp et al. 2010; Witt et al. 2011), but may also interact to exacerbate or ameliorate effects on biota (e.g. O’Connor et al. 2009; Castro et al. 2010; Hale et al. 2011).

Disentangling the roles of multiple extrinsic factors is one of the biggest challenges faced by those tasked with predicting the ecological impacts of environmental change (Stenseth et al. 2002). Selecting the appropriate analyses to achieve this goal is aided by consideration for the mechanisms through which potential drivers are expected to act (and interact). Increasing primary production is likely to lead to greater food availability for consumers, which can fuel population growth (Silby & Hone 2002). Small increases in temperature, on the other hand, can substantially increase metabolic rate and, thus, food requirements (Gillooly et al. 2001; Brown et al. 2004). Temperature and primary production may therefore drive community dynamics via their roles in determining and sustaining the metabolic demands of organisms, respectively. Moreover, it is plausible that these factors will interact in their effects on consumers, and that interactions will be either positive or negative. For example, a species may only decline in density in response to warming if there are insufficient food resources available to sustain the associated increase in its metabolic demand (i.e. a negative interaction); or a species that responds positively to warming might require that there are plentiful food resources to fuel population growth (i.e. a positive interaction). These interactions could exacerbate or mitigate changes to the temporal trends of consumers. For example, if temperature and primary production increase simultaneously, then a positive interaction could induce an abrupt shift in species composition, whereas a negative interaction could act to prevent such a shift from occurring.

Here, we study the existence and causes of changes to temporal trends in a North Sea benthic faunal assemblage using a 40-year time series. Specifically, our aims are to determine 1) whether changes to temporal trends occur, and 2) whether these changes are explained by underlying variation in sea surface temperature (SST) and pelagic primary production (hence detrital food input to the seabed); or whether other mechanisms, such as different extrinsic drivers or the crossing of biological thresholds, are implied. The North Sea experienced abrupt increases in SST and pelagic primary production in the late 1980s (Reid et al. 2001; Reid & Edwards 2001; Beaugrand 2004), with cold winters occurring both before (in the late 1970s; Reid & Edwards 2001) and, to a lesser degree, after this period (in the mid-1990s; Kröncke et al. 2013). The North Sea over the last 40 years is therefore an ideal ecosystem within which to address these questions. We test for the above postulated interactions between extrinsic factors in our analyses. We also test whether these factors interact with season, as the effect of changing food input may differ between the period following summer growth and the period after winter die-offs, and this effect may in turn depend on whether the system is subjected to warm summers, cold winters, or mild conditions in either season.

**Material and methods**

**Benthic community time series**

Dove Station M1 sits under 55 m of water in predominantly sandy sediment, 10.5 km east of the Northumberland coast in NE England (55° 04ʹ N, 01° 20ʹ W). Strong tidal currents cause turbulent mixing in the area surrounding Station M1, thus preventing seasonal stratification of the water column and maintaining oxygenic conditions at the seabed (Evans 1985). The station is located away from local river discharges and outside the main grounds of a *Nephrops* trawl fishery. Temporal patterns in the benthos at Station M1 do not appear to be influenced by the level of fishing activity in the local area (Frid et al. 1999).

Macroinfauna have been sampled biannually at M1 in March/April (spring) and September/October (autumn) since September 1972. Data are missing only for the springs of 1998 and 2004 and the autumns of 1987 and 1991, as weather conditions and/or operational constraints prevented sampling on these occasions. Samples were collected using van Veen grabs (0.1 m2), sieved over 0.5 mm mesh and fixed with 4% buffered formalin. Retained fauna were identified to the lowest possible taxonomic level and enumerated. Sampling methods are described in detail in Buchanan & Warwick (1974). Since 1980 a total of 5 grabs have been collected on each sampling occasion; however, sampling effort ranged from 10 to 20 grabs up to this point. As the original raw data are no longer available for the early years of the time series, we use all available data from autumn 1972 to autumn 2012. The removal of rare taxa from the dataset (see below) will reduce any effect that temporal variation in sampling effort may have on our results.

**Time series of potential extrinsic drivers**

*Pelagic primary production*

Pelagic primary production in the area of the study site (standard area C2, central-western North Sea; see [https://www.sahfos.ac.uk/data/our-data](https://www.sahfos.ac.uk/data/our-data/)) was indexed using the phytoplankton colour index (PCI) (Reid et al. 1998; Johns 2015). PCI is based on the ‘greenness’ recorded on the silk of the continuous plankton recorder. The scale by which greenness is measured is calibrated using acetone-based measures of phytoplankton biomass. As the sedimentation of organic matter increases with increasing pelagic primary production (Suess 1980), PCI can be used as a proxy for detrital input to the seabed (e.g. Buchanan 1993; Frid et al. 2009a,b). Moreover, as the turbulent conditions in the area of the study site cause high turbidity (Buchanan et al. 1978), which severely limits the light available to phytobenthic organisms (at > 50m in the North Sea, light intensity is 0–1% of that recorded in surface water; see Riegman et al. 1990), it also follows that detrital input constitutes at least the vast majority of food supply to benthic fauna at the study site.

We took the mean PCI over 12-month periods starting at two different points in the annual cycle (January-December and July-June) to create estimates of detrital input that could be matched to the macroinfaunal assemblage sampled in the spring and autumn of each year (for full explanation, see ‘Data analysis’). The mean of these data over the preceding 5 years was also used to indicate the amount of detritus that had been made available to the benthos over a longer temporal scale (see ‘Data analysis’).

## *Sea surface temperature*

## Sea surface temperature (SST) records were obtained from three sampling stations located on the northeast coast of England, in Blyth (55° 8ʹ N, 1° 32ʹ W), Redcar (54° 38ʹ N, 1° 5ʹ W) and Scarborough (54° 17' N, 0° 22' W). The data were downloaded from the Coastal Temperature Network maintained by CEFAS (see stations 1–3 at [www.cefas.co.uk/cefas-data-hub/sea-temperature-and-salinity-trends/station-positions-and-data-index](https://www.cefas.co.uk/cefas-data-hub/sea-temperature-and-salinity-trends/station-positions-and-data-index/)). Currents that carry cool water from the Atlantic into the northern North Sea flow down the northeast coast of the Great Britain toward Flamborough Head (Lee & Ramster 1981), passing over each of these stations and Dove Station M1. The temperature records at all three stations are therefore considered here to be indicative of the hydrothermal conditions experienced at the study site. As the water column at the study site is well mixed, variation in SST is a reasonable proxy for variation in temperature at the seabed.

## None of the individual SST datasets formed complete time series over the entire study period. Monthly means were therefore averaged across all stations for which there were available data. Aggregate figures for December, January and February were then averaged to give a value for mean winter temperature each year. Likewise, figures for June, July and August were averaged to give mean summer temperatures. This produced a complete time series for winter and summer temperatures over the entire study period. These data were then standardised to temperature anomalies (i.e. standard deviations from the season-specific mean) to indicate temperature variability relative to the average conditions in the relevant season.

## Data analysis

## At each sampling occasion, taxa abundances were mean-averaged across all replicate samples and standardised to the number of individuals per square metre. Taxa that occurred at a density of ≥ 10 individuals per square metrein any year of the time series (in spring or autumn) were retained in the community dataset. Taxa that only ever occurred at densities of less than 10 individuals per square metre (one individual per grab) were excluded, as their abundances will not have been reliably estimated. Using this approach, over 98% of total abundance was represented in each year of the analysed dataset.

Principal components (PCs) were used to describe the main patterns of temporal variation in faunal composition (see Jolliffe 2002). PCs were derived from the correlation matrix of transformed taxa abundances, to prevent numerically dominant taxa from masking temporal variation in the densities of less abundant taxa. When community data were missing (i.e. benthic samples were not collected), PCs were estimated by taking the mean of the PC scores of the preceding and following years for the appropriate season. For this analysis we considered only PCs 1 and 2, which accounted for 16% and 9% of variation, respectively. All other PCs accounted for ≤ 6% of variation.

Generalized Additive Mixed Models (GAMMs; Wood 2006, section 6.6) were used to model temporal variation in PCs 1 and 2. In GAMMs, part of the linear predictor is specified in terms of ‘smoothed’ covariates, with the shape of the trend estimated via penalised regression splines (Lin & Zhang 1999). Here, time (i.e. the year of the time series; + 0.25 for spring samples and + 0.75 for autumn samples) was treated as a smoothed covariate to avoid making assumptions about the particular form of the relationship between PCs and time. The initial additive mixed model took the form:

where is the value of the *j*th principal component () at time *i*, is the smoothed time function, is the season in which sampling was conducted (spring *vs.* autumn) and is a residual error, assumed to be normally distributed with zero mean and temporal autocorrelation described by a first-order continuous-time autoregressive (CAR(1)) model (Pinheiro & Bates 2000, section 5.3). GAMMs were fitted using the **mgcv** package in R (version 3.2.2; R Development Core Team). Smoothing was performed using restricted maximum-likelihood (REML) estimation (Harville 1977), which is preferable to other smoothing parameters as it tends to avoid severe ‘undersmoothing’ (Wood 2015).

To test for changes to the temporal trends of PCs 1 and 2, 95% confidence intervals for second derivatives (i.e. significant changes to the rate of change) were estimated by simulation following a modified version of the method in Orr et al. (2015) for confidence intervals on first derivatives (described below). For high-dimensional data, such as the dataset used in this study, the first principal component is expected to show a trend (i.e. a significant first derivative) even where each component is simply a random walk (Bookstein 2013). We therefore focus only on changes to the temporal trend, as the trend itself is of little interest when investigating the causes of ecological change.

Random samples were drawn from the posterior distribution of smoothed time coefficients and multiplied by the linear predictor matrix to simulate the temporal trend. Second derivatives were estimated numerically by finite differences (Davis and Polonsky, 1965, section 25.3.23) with increments of years around each point on a grid of 200 equally-spaced time points. Simultaneous 95% confidence intervals for these second derivatives were obtained from the 0.025- and 0.975-quantiles of 10,000 such simulations. Fitted values of PCs 1 and 2 were plotted against time, and periods during which the second derivative was significantly positive were highlighted in red, whereas periods during which the second derivative was significantly negative were highlighted in blue. With principal components the sign is arbitrary, but once the sign is fixed, this also fixes the definitions of positive and negative second derivatives.

To investigate the drivers of community dynamics, the initial models for PCs 1 and 2 were modified to include pelagic primary production and standardised SST as (non-smoothed) covariates. The maximum life-span and body length of taxa loaded on PCs 1 and 2 (the top ten positively-loaded taxa and top ten negatively-loaded taxa) were compiled to determine the temporal scales over which phytoplankton biomass would be integrated when matched to each principal component of taxa densities. Small and short-lived opportunistic taxa are likely to respond to short-term fluctuations in primary production through rapid reproduction and recruitment (Gooday et al. 1990), whereas large and long-lived taxa, whose population growth rates are highly influenced by adult survival (Stearns 1992), are likely to respond to variation in primary production over longer temporal scales. When longevity was unknown, we assumed that body size alone was indicative of whether a taxon’s population dynamics are likely to be driven mainly by short-term recruitment (i.e. small-bodied) or long-term adult survival (i.e. large bodied). The feeding modes of taxa loaded on PCs 1 and 2 were also compiled to assess whether community variation in relation to food input and/or temperature was reflected in the trophic ecology of the species involved. Species traits information was taken from Marine Species Identification Portal (<http://species-identification.org/>) and MarLIN’s biological trait catalogue (<http://www.marlin.ac.uk/biotic/biotic.php>), with additional literature review and expert consultation used to corroborate and fill in gaps in information.

PC 1 was loaded mainly with large and long-lived organisms, with the majority of taxa for which longevity is known having a maximum lifespan of 5 or more years (see ‘First principal component’in ‘Results’ and Table 1). To approximate a timescale over which detrital input is likely to influence the survival of these taxa, faunal data were matched to phytoplankton biomass data that were averaged over the preceding 5 years, with a 3-month time-lag to allow time for phytoplankton in suspension toward the end of this period to settle on the seabed and be made available to the benthos (e.g. fauna sampled in spring 1980 was matched to mean phytoplankton biomass from January 1975 to December 1979). As PC 2 was loaded mainly with small and short-lived taxa, the majority of which have a lifespan of 1-3 years (see ‘Second principal component’ in ‘Results’ and Table 2), faunal data were matched to phytoplankton biomass data averaged over a 12-month period. Given that the densities of these taxa will be highly dependent on recruitment, the time lag for this PC was extended to 9 months to allow more time for individuals recruited within the 12-month period to reach the size necessary to be retained on the 0.5 mm mesh (e.g. fauna sampled in autumn 1980 was matched to mean phytoplankton biomass from January 1979 to December 1979). For both PCs, the assemblages sampled in spring and autumn were matched to the standardised SST of the previous winter and the previous summer, respectively.

As it was postulated *a priori* that the effects of temperature and primary production might interact in their effects on biota, and that their effects may differ with respect to season, these terms were added into the initial model as a three-way interaction with the season term:

where is an estimate of pelagic primary production in the area of the study site (and a proxy for detrital input to the seabed) and is standardised sea surface temperature.

Wald-like tests (implemented using the anova.gam function) were used to approximate the statistical significance of each model term, conditional on the smoothing parameter estimates (Wood 2013). The resulting *p*-values are better justified than those derived from multi-model comparisons and have close to the correct distribution under the null, providing that the smoothing parameters are not poorly identified (Wood 2015). All non-significant interactions were removed from the models to reduce model complexity and free up degrees of freedom. Terms were considered to be statistically significant at *p* < 0.05.

Final models, with all statistically significant terms retained within the linear predictor matrix, were then tested for significant second derivatives in the smoothed time term in the same way as described above for the initial models. Fitted values of PCs 1 and 2 were plotted against time, with significantly positive and negative second derivatives highlighted in red and blue, respectively. If significant second derivatives identified in the initial models were not identified in the final models, then it was inferred that there was no reason to postulate additional mechanisms (e.g. extrinsic factors not included in the model or the crossing of biological thresholds) to explain changes to the temporal trend observed in the initial model.

**Results**

**First principal component**

The taxa with the top ten most positive and top ten most negative loadings on PC 1 consisted of representatives from eight phyla in total: seven phyla were among taxa with the most positive loadings and four were among taxa with the most negative loadings (Table 1). Many of these taxa were large and long-lived compared to those loaded on PC 2: nine out of twenty could reach a body length of over 100 mm and a further three could reach over 40 mm; five out of the eight taxa for which longevity information was available have a maximum lifespan of five or more years (Table 1). Deposit feeders, suspension feeders and predators were approximately equally represented among these taxa; however, predators were relatively common among positively-loaded taxa whereas deposit feeders and suspension feeders were relatively common among negatively-loaded taxa (Table 1). Over the time series as a whole, the taxa with the top ten most positive and top ten most negative loadings on PC 1 together made up 5% of total abundance.

The densities of taxa loaded on PC 1 varied significantly over time (Table 3). In the initial model (the model containing only the (smoothed) time and season terms as explanatory variables) the temporal trend for PC 1 was positive at the onset of the time series and experienced a significant positive second derivative (i.e. a positive change to the rate of change) from 1987 to 1989, followed by a significant negative second derivative from 1993 to 1997 (Fig. 1a, solid line). These changes to the temporal trend culminated in a compositional shift from negatively-loaded to positively-loaded taxa (see Table 1). No further significant second derivatives occurred (Fig. 1a, solid line).

Temporal variation in the densities of taxa loaded on PC 1 was not significantly related to standardised SST, but was significantly related to pelagic primary production (PCI)\*Season (Table 3). The relationship with pelagic primary production (averaged over the preceding 5 years) was positive in both seasons, but the slope was steeper in autumn (Fig. 2, solid line) than in spring (Fig. 2, dashed line). In other words, taxa with positive loadings tended to increase in density when pelagic primary production was high, and taxa with negative loadings tended to increase in density when pelagic primary production was low, but the increase was greater following the summer growth period than following winter die-off.

The densities of taxa loaded on PC 1 closely tracked variation in pelagic primary production (averaged over the preceding 5 years) from the mid-1980s to the mid-1990s (Fig. 3a,c), which was the period during which both significant second derivatives occurred (Fig. 1a, solid line). In the final model (which included PCI\*Season along with the (smoothed) time term) there were no significant second derivatives and the temporal trend was consistently positive and linear (Fig. 1a, dashed line), indicating that underlying variation in pelagic primary production explained the changes to the temporal trend of taxa loaded on PC 1.

**Second principal component**

For PC 2, the top ten taxa with positive loadings and top ten taxa with negative loadings together consisted mainly of annelids (11) and molluscs (6) (Table 2). Three other phyla each had one representative (Table 2). In contrast to PC 1, the taxa loaded on PC 2 were mainly small and short-lived: eight could reach over 40 mm, of which only two could reach over 100 mm; eleven out of the seventeen taxa for which longevity information was available have a maximum lifespan of 1–3 years (Table 2). Deposit feeders were generally dominant among the top taxa loaded on PC 2; however positively-loaded taxa had a relatively high representation of suspension feeders, whereas negatively-loaded taxa had an additional predator and a parasite (Table 2). Over the time series as a whole, the taxa with the top ten most positive and top ten most negative loadings on PC 2 together made up 18% of total abundance.

The densities of taxa loaded on PC 2 varied significantly over time (Table 3). The temporal trend for PC 2 was initially slightly positive and gradually became more negative (Fig. 1b), resulting in a long-term increase in the densities of negatively-loaded taxa and decrease in the densities of positively-loaded taxa (see Table 2). There were, however, no significant second derivatives (i.e. no changes to the temporal trend) in the initial model (the model containing only the (smoothed) time and season terms as explanatory variables; Fig. 1b, solid line).

Seasonal variation in the densities of taxa loaded on PC 2 was significant and marked (Table 3; Fig. 3b), with positively-loaded taxa experiencing a relative increase in autumn and negatively-loaded taxa experiencing a relative increase in spring. PC 2 varied significantly in relation to a negative interaction between pelagic primary production (averaged over 12 months) and standardised SST (PCI\*SST; Table 3). Warming was associated with an increase in the densities of positively-loaded taxa and a decrease in the densities of negatively-loaded taxa; however, this effect became weaker as the level of pelagic primary production increased (Fig. 4).

Both pelagic primary production (averaged over 12 months) and standardised SST abruptly increased in the mid-late 1980s (Fig. 3d,e). However, the combined effect of these drivers on the densities of taxa loaded on PC 2 appears to have been small, as the (smoothed) time effect was similar in models with and without their inclusion (Fig. 1b).

**Discussion**

While abrupt shifts in ecosystems are now well-documented (see Möllmann et al. 2015), their causes are poorly understood. The main aim of this study was to test for changes to the temporal trends of biota in a natural ecosystem and determine whether they could be explained by underlying patterns in primary production and temperature. Changes to the temporal trend were identified for a subset of a benthic faunal assemblage (the taxa loaded on the first principal component) and resulted in a shift in species composition. These changes were explained by variation in pelagic primary production and, hence, detrital food input to the seabed. In contrast, taxa loaded on the second principal component of the assemblage did not experience any significant alterations to their temporal trend, but did show significant long-term change in relation to pelagic primary production and SST.

The onset of the shift in the taxa loaded on PC 1 occurred during a prolonged positive phase of the North Atlantic Oscillation Index (NAOI), during which Atlantic inflow, SST and pelagic primary production all increased in the North Sea (Beaugrand 2004). Various other biological components abruptly changed in their composition during this period, from phytoplankton (Reid et al. 1998) through to zooplankton (Beaugrand et al. 2002) and fish (Reid et al 2001; Beaugrand et al. 2003). The present study may therefore reveal within the benthic component of the ecosystem a signal of a multi-trophic level, multi-component regime shift in the North Sea (see Beaugrand 2004). Indeed, an increase in the prevalence of predators (i.e. taxa positively-loaded on PC 1; Table 1) suggests that the benthic system itself may have underwent a shift in trophic structure under increased food input. While this trophic shift may not be reflected in the benthic assemblage as a whole (see Clare et al. 2015), the large size and thus presumably high biomass of taxa loaded on PC 1 means that changes to their densities could disproportionately affect ecosystem functioning (Garnier et al. 2004). Previous studies have reported local alterations to the composition and trophic structure (an increase in the prevalence of predators) of the North Sea benthos during the same period, and have attributed their results to climate variability (e.g. Kröncke et al. 1998; Kröncke 2011; Kröncke et al. 2013). Analyses conducted here build on these findings by explicitly demonstrating changes to the temporal trends of biota and providing some indication of the relative importance of different extrinsic factors in driving their dynamics.

The apparent role of pelagic primary production in inducing the compositional shift is consistent with other studies that show detrital input to be an important driver of faunal assemblages (Moore et al. 2004), including those focused on the benthos (e.g. Levinton & Kelaher 2004; Ruhl & Smith 2004; Walther & Whiles 2011; Weigel et al. 2015). Previous analyses of the dataset used in this study suggest that the seabed was a food-limited environment prior to the increase in pelagic primary production in the mid-late 1980s (Buchanan 1993; Frid et al. 1996). As such, the taxa that subsequently increased in density (those positively-loaded on PC 1) may have been able to utilise the enhanced food input to increase survival and/or reproduction (Silby & Hone 2002), whereas the taxa that decreased in density may have a relatively high ability to meet their nutritional demands in a food-limited environment and therefore gained a competitive advantage when detrital input was low (see Ruhl & Smith 2004). That the relationship between PC 1 and pelagic primary production was more positive in autumn than in spring (Fig. 2) suggests that the effect of changes to detrital input is weakened over winter, possibly because species that are abundant under a particular level of detrital input experience a degree of density-dependent mortality during this period of the year.

The mechanism underlying temporal variation in taxa loaded on PC 2 appears to be different to that underlying variation in taxa loaded on PC 1, with a negative interaction between pelagic primary production (averaged over 12 months) and SST suggesting that an increase in food input mitigated the effect of warming on these organisms. Experiments have shown that metabolism and consumption increase in animals when they are subjected to higher temperatures (O’Connor et al. 2009; Carr & Bruno 2013; Seifert et al. 2014). It therefore follows that species densities may only be affected by warming when there are insufficient food resources available to sustain the associated increase in metabolic demand, as suggested by the results of our study. Another experiment found that the impact of warming on consumption rate was greater for a small species than for a large species of the same family and functional group (Lang et al. 2012), reflecting a greater effect of temperature on the metabolism of smaller organisms. This may explain why the mainly small taxa loaded on PC 2 experienced relatively little long-term variation as both pelagic primary production and SST increased (i.e. the enhanced detrital food input compensated for the elevated metabolism), whereas the mainly large taxa loaded on PC 1 were affected only by pelagic primary production and experienced a shift in species composition when the ecosystem became warmer and more productive.

A high sensitivity of taxa loaded on PC 2 to environmental fluctuations is possibly reflected by their prominent seasonal variability. Some of the earliest analyses of the dataset used in this study reported that small, abundant species exhibited a marked seasonal cycle of summer population growth followed by winter die-off (Buchanan et al. 1978; Buchanan et al. 1986; Buchanan 1993; Frid et al. 1996), probably due to seasonal variation in temperature and/or detrital input. Moreover, at different points during the first two decades of the time series, some of these populations (including taxa positively-loaded on PC 2, e.g. *Pholoe inornata* and *Levinsenia gracilis*) appeared to be affected by year-to-year variation in SST and/or pelagic primary production (Buchanan et al. 1978; Buchanan et al. 1986; Buchanan 1993; Frid et al. 1996). These effects were mainly apparent in spring, possibly pointing to the importance of temperature and food input in determining winter survival. However, when the North Sea became warmer and more productive later in the time series, the apparent effect of these extrinsic drivers on the spring assemblage largely disappeared (Frid et al. 2009a). The novel analyses presented here suggest that a single mechanism, i.e. a mitigating effect of high primary productivity on the ecological impacts of changing SST, may explain these previous observations.

As with any observational study conducted on a small spatial scale, the broad-scale applicability of our findings needs to be examined carefully. It is reassuring in this regard that the ecological shift identified here was apparently driven by an extrinsic factor that changed throughout the North Sea (Beaugrand 2004), and that benthic communities at distant sites experienced simultaneous changes in species composition, e.g. off of Norderney, Germany (Kröncke et al. 1998, 2013). Interestingly, a further climate-driven reorganisation of the benthos off of Norderney occurred around 2001 (Dippner et al. 2010, 2014), which was not observed in our analyses. This might be explained by the stations off of Norderney lying closer to the northern Boreal–southern Lusitanian biogeographical boundary (Forbes 1858), where conditions may be more conducive to temperature-induced ecological shifts. That said, a previous analysis of the dataset studied here does suggest a change to the benthic assemblage off of Northumberland around the turn of the millennium (Frid et al. 2009a), which may have gone undetected in the present study due to the temporal community variation not captured by our analyses. Either way, the large geographic scale over which the ecological shift identified here appears to have occurred suggests that our results provide a broad, if not comprehensive, insight into the dynamics of benthic assemblages.

While correlative analyses such as the one conducted for this study cannot demonstrate causality, the results leave no reason to postulate alternative explanations for the observed community dynamics. The results are also consistent with theory and experimental findings, which gives us reason to be confident that the inferred mechanisms are indeed valid. Pelagic primary production is under climatic influence (Behrenfield et al. 2006; Boyce et al. 2010; Blanchard et al. 2012) and is therefore likely to be affected by ongoing climate change. Future changes to North Sea pelagic primary production will allow us to scrutinize its apparent influence over the large and long-lived taxa studied here (i.e. those loaded on PC 1) and determine whether our interpretation remains tenable. Likewise, if our interpretation is valid, then any future reductions in pelagic primary production should make the small and short-lived taxa (i.e. those loaded on PC 2) more responsive to temperature variation. Being able to explain long-term patterns in biological assemblages using proposed drivers is essential if we are to predict the impacts of future environmental change. The results of this study suggest that abrupt ecological shifts may, at least in some cases, be foreseeable based on projected changes to extrinsic factors.

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**Tables and table legends**

**Table 1.** The top ten taxa with positive loadings (above dashed line) and the top ten taxa with negative loadings (below dashed line) on the first principal component of the macroinfaunal assemblage at Dove Station M1 from 1972 to 2012. Phyla are in brackets. The maximum body length and maximum lifespan of each taxon are shown, along with the mean values (± standard error) across positively- and negatively-loaded taxa. In cases where maximum lengths of taxa were reported as a range, we used the midpoint when calculating the overall mean and standard error. Feeding modes are shown: Dep = deposit feeder, Sus = suspension feeder, Pre = predator.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Taxon | PC loading | Max length (mm) | Max lifespan (years) | Feeding mode |
| *Arctica islandica* (Mollusca) | 0.160 | 120 | 500 | Sus |
| *Saccoglossus horsti* (Hemichordata) | 0.157 | 200 | - | Dep/Sus |
| *Parexogone* *hebes* (Annelida) | 0.156 | 10 | 2 | Pre |
| *Cerebratulus* spp. (Nemertea) | 0.153 | 100–1000 | - | Pre |
| *Glyphohesione klatti* (Annelida) | 0.150 | 13 | 5 | Pre |
| *Tubulanus polymorphus* (Nemertea) | 0.149 | 750 | - | Pre |
| *Trichobranchus* spp. (Annelida) | 0.139 | 20–35 | - | Dep |
| *Araphura brevimanus* (Arthropoda) | 0.126 | 3 | 1 | Dep |
| *Golfingia* spp. (Sipuncula) | 0.126 | 100–300 | - | Dep |
| Platyhelminthes | 0.126 | 1–600 | - | Pre |
| *Laonome kroyeri* (Annelida) | -0.096 | 50 | - | Sus |
| *Lucinoma borealis* (Mollusca) | -0.097 | 40 | - | Sus |
| *Cerianthus lloydii* (Cnidaria) | -0.098 | 150 | 20 | Pre |
| *Polycirrus medusa* (Annelida) | -0.098 | 70 | 10 | Dep |
| *Glossobalanus marginatus* (Hemichordata) | -0.099 | 80 | - | Dep/Sus |
| Phyllodocidae (Annelida) | -0.103 | 10–500 | - | Pre |
| *Kellia suborbicularis* (Mollusca) | -0.120 | 10 | - | Sus |
| *Sphaerodoropsis minuta* (Annelida) | -0.120 | 6 | - | Dep |
| *Chaetozone caputesocis* (Annelida) | -0.121 | 17 | 3 | Dep/Sus |
| *Magelona* spp. (Annelida) | -0.135 | 40–170 | 5 | Dep/Sus |
| Mean (± SE) | | 148 (± 44) | 68 (± 62) |  |

**Table 2.** The top ten taxa with positive loadings (above dashed line) and the top ten taxa with negative loadings (below dashed line) on the second principal component of the macroinfaunal assemblage at Dove Station M1 from 1972 to 2012. Phyla are in brackets. Maximum body length and maximum lifespan of each taxon are shown, along with the mean values (± standard error) across positively- and negatively-loaded taxa. In cases where maximum lengths of taxa were reported as a range, we used the midpoint when calculating the overall mean and standard error. Feeding modes are shown: Dep = deposit feeder, Sus = suspension feeder, Pre = predator, Par = parasite.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Taxon | PC loading | Max length (mm) | Max lifespan (years) | Feeding  Mode |
| *Pholoe inornata* (Annelida) | 0.172 | 8 | 4 | Pre |
| *Spiophanes bombyx* (Annelida) | 0.162 | 60 | 2 | Dep/Sus |
| *Phoronis muelleri* (Phoronida) | 0.159 | 120 | 1 | Sus |
| *Ophelina acuminata* (Annelida) | 0.159 | 60 | 3 | Dep |
| *Gattyana cirrhosa* (Annelida) | 0.158 | 50 | 4 | Pre |
| *Phaxas pellucidus* (Mollusca) | 0.156 | 40 | - | Sus |
| *Levinsenia gracilis* (Annelida) | 0.156 | 25 | 2 | Dep |
| *Ampharete* spp. (Annelida) | 0.155 | 12–50 | 3–5 | Dep/Sus |
| *Acanthocardia echinata* (Mollusca) | 0.147 | 75 | 20 | Sus |
| *Poecilochaetus serpens* (Annelida) | 0.142 | 55 | 2 | Dep/Sus |
| *Thracia phaseolina* (Mollusca) | -0.056 | 38 | 10 | Sus |
| *Laonice* spp. (Annelida) | -0.058 | 60–120 | 1–3 | Dep |
| *Pseudocuma longicorne* (Arthropoda) | -0.058 | 4 | 2 | Dep/Sus |
| *Ophiura* spp. (Echinodermata) | -0.059 | 8–35 | 3–6 | Pre |
| *Retusa umbilicata* (Mollusca) | -0.070 | 4 | 2 | Pre |
| *Thyasira biplicata* (Mollusca) | -0.070 | 8 | 3 | Dep/Sus |
| *Ophelina cylindricaudata* (Annelida) | -0.078 | 19 | 3 | Dep |
| *Paramphinome jeffreysii* (Annelida) | -0.086 | 15 | 1 | Pre |
| *Aphelochaeta* spp. (Annelida) | -0.091 | 10–15 | - | Dep |
| *Vitreolina philippi* (Mollusca) | -0.096 | 8 | - | Par |
| Mean (± SE) | | 37 (± 7) | 4 (± 1) |  |

**Table 3.** Generalized additive mixed model (GAMM) output showing variation in the first two principal components (PCs 1 & 2) of macroinfaunal taxa densities at Dove Station M1 from 1972 to 2012. Relationships between the PCs and pelagic primary production (PCI; averaged over the preceding 5 years (with a 3-month time-lag) for PC 1 and over 12 months (with a 9-month time-lag) for PC 2), standardised sea surface temperature (SST; standard deviations from the seasonal mean) and season (i.e. spring *vs*. autumn) are shown. All possible two-way and three-way interactions were tested. Non-significant interactions were removed. Significant *p*-values (< 0.05) are in bold.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | PC 1 | |  |  | PC 2 | |
| Source | d.f. | *F* | *p* |  | d.f. | *F* | *p* |
| (Smoothed) Time | 1 | 57.83 | **< 0.0001** |  | 1 | 4.27 | **0.0469** |
| PCI | 1 | 16.49 | **0.0001** |  | 1 | 0.85 | 0.3590 |
| SST | 1 | 1.85 | 0.1775 |  | 1 | 6.99 | **0.0100** |
| Season | 1 | 25.98 | **< 0.0001** |  | 1 | 198.17 | **< 0.0001** |
| PCI\*SST | - | - | **-** |  | 1 | 4.77 | **0.0322** |
| PCI\*Season | 1 | 35.72 | **< 0.0001** |  | - | - | - |
| SST\*Season | - | - | **-** |  | - | - | - |
| PCI\*SST\*Season | - | - | **-** |  | - | - | - |

**Figures and figure legends**

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**Fig. 1.** Variation in (A) the first principal component and (B) the second principal component of taxa densities within the macroinfaunal assemblage at Dove Station M1 over (smoothed) time. Solid lines represent the relationships in the initial models (including only (smoothed) time and season terms) and the dashed lines represents the relationships in the final models, which included extrinsic drivers (i.e. pelagic primary production (PCI) and standardised sea surface temperature (SST; standard deviations from the seasonal mean)) that were significantly related (*p* < 0.05) to the principal components (including any significant interactions among extrinsic drivers and season) as terms in the linear predictor matrix. Periods during which second derivatives were significantly positive (i.e. changing toward positive PC scores; assessed with respect to 95% confidence intervals) are highlighted in red. Periods during which second derivatives were significantly negative (i.e. changing toward negative PC scores; assessed with respect to 95% confidence intervals) are highlighted in blue.



**Fig. 2.** Variation in the first principal component (PC 1) of macroinfaunal taxa densities at Dove station M1 from 1972 to 2012 in relation to pelagic primary production (Phytoplankton Colour Index; averaged over the preceding 5 years (with a 3-month time-lag)). Points for spring are hollow (dashed line) and points for autumn are solid (solid line).

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**Fig. 3.** Temporal variation in: (A) the first principal component and (B) the second principal component of macroinfaunal taxa densities at Dove Station M1; (C) pelagic primary production (Phytoplankton Colour Index) averaged over the preceding 5 years; (D) pelagic primary production averaged over 12 months; and (E) standardised sea surface temperature (SST anomalies; standard deviations from the seasonal mean). For (C), pelagic primary production was lagged by 3 months from the end of the 5-year period to the points marked on the graph. For (D), pelagic primary production was lagged by 9 months from the end of the 12 month period to the points marked on the graph.



**Fig. 4.** Variation in the second principal component (PC 2) of macroinfaunal taxa densities at Dove Station M1 from 1972 to 2012 in relation to pelagic primary production (Phytoplankton Colour Index; averaged over 12 months (with a 9-month time-lag)) and standardised sea surface temperature (SST anomalies; standard deviations from the seasonal mean). The 3D surface is based on the predicted values from a model containing each term and their interaction. ‘Season’ was set to “spring”. The points represent the actual observations and the lines connecting the points to the 3D surface represent the residuals.