5.3 Relations and interactions between environmental factors and biotic properties

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5.3.1 Introduction

This section examines in more detail the relationships between the biological and environmental data and highlights any differences between 1986 and 2000. The best way to express these relationships is identified. This work is designed to complement and extend the findings of Sections 5.1 and 5.4. Heip *et al*. (1992) performed a similar assessment of the relationship between biomass, density, diversity, and individual weight with abiotic variables for the NSBS 1986 dataset. The present analyses include the samples both from 1986 and 2000. Also, additional environmental variables, not available to Heip *et al*. (1992), were available (e.g. tidal stress, stratification; see Table 5.3.1).

This is a unique opportunity to search for trends on the scale of the whole North Sea, which measures 1000 by 600 km. Such a large-scale comparison of abiotic variables with the benthic fauna is rare. In the following account, a number of macro-ecological hypotheses are tested, including the relation between latitude and diversity, and temperature and individual weight. The outcome is summarized in a schematic overview to facilitate the communication of findings to a wider readership. The NSBP 2000 survey extended the geographical scope of the 1986 survey by including data for the eastern English Channel. Though a component of the greater North Sea as defined by OSPAR and the EU, the predominantly coarse substrata of the Channel provide a notable contrast to the generally finer sediments to the north.

5.3.2 Methodology

As a first step, the non-parametric Kendall's tau correlation between all biotic and abiotic variables was calculated. Next, a principal components analysis (PCA) was performed to visualize the multivariate relations between the abiotic variables. For the 1986 and 2000 datasets, separate correlation analyses and PCA were conducted. The communities identified by Künitzer *et al*. (1992) for the 1986 stations, and in this report (Section 5.1) for the 2000 samples, were superimposed on the PCA plots to facilitate interpretation of the outcome.

Table 5.3.1. Overview of the environmental and biological variables in the dataset.

VARIABLE	1986	2000	VARIABLE	1986	2000
latitude	x	x	average salinity June	x	x
longitude	x	x	mode mm	–	x
depth	x	x	d10 mm	–	x
tidal stress	x	x	d50 mm	x	x
peak wave stress	x	x	d90 mm	–	x
stratification	x	x	ratio d10/d90	–	x
chla water	x	x	gravel %	–	x
chla bottom	x	–	sand %	–	x
pigment total	x	–	mud %	x	x
protein	x	–	ES(50)	x	x
Org. C %	x	–	density	x	x
average temperature February	x	x	biomass	x	x
average temperature June	x	x	individual weight	x	x
average salinity February	x	x			

Based on the outcome of correlation and PCA analyses, a subset of the most influential environmental variables was identified and relationships with biotic variables expressed as a

series of scatterplots. The first group of plots expresses relationships for the 1986 and 2000 datasets and include trend lines to aid interpretation. Because of their often distinctive character, samples from the eastern English Channel were identified separately and were not used in the construction of the linear trend line. The second group of plots allowed a comparison of the relation between the biotic and abiotic variables for 1986 and 2000. Variables that were the most strongly correlated with density, biomass, and diversity were determined from a combination of correlation analysis, PCA, and scatterplots. Because such a large ecological dataset was available, several macro-ecological hypotheses could be tested.

5.3.3 Results

5.3.3.1 Correlation 1986

Spatial relationships

There is a north–south decrease in the average winter bottom temperature and depth (see Figures 4.1.2 and 4.1.3), because both variables are negatively correlated with latitude (latitude–depth: r = 0.55; latitude–av. temp. feb86: r = 0.71). In the east–west direction, the peak wave stress increases towards the east (longitude–peak wave stress: r = 0.57). Winter and summer salinity decreases eastwards towards the Baltic (longitude–salinity feb86/jun86: r = −0.75 and −0.80). The density, biomass, individual weight, and ES(50) show no correlation with longitude or latitude.

Abiotic variables

At greater depth, the winter temperature was higher (r = 0.67), because shallow locations are less buffered for atmospheric temperature fluctuations. The temperature and salinity values are highly intercorrelated (r = 0.38–0.81). Overall, and as expected given the nature of the data, the sediment variables show a high correlation with each other. The percentage of sand and percentage of mud have the highest correlation (r = −0.92) and percentage of sand vs. d50 (r = −0.60), respectively. The water column chlorophyll *a*, the sediment chlorophyll *a*, total pigments, proteins, and organic carbon percentages show a very low correlation with each other and the other abiotic and biotic variables. Also, peak and tidal stress are totally unrelated according to the correlation analysis.

Relationships of abiotic and biotic variables

Diversity expressed as ES(50) correlates moderately with depth (r = 0.42) and temperatures (temp. February: 0.41; temp. June: r = −0.43). Other correlations between biotic and abiotic variables are low.

5.3.3.2 Correlation 2000

The tidal stress increases southwards (latitude–tidal stress: r = −0.46). As in 1986, the temperature and salinity values (from the same Pohlmann model) are highly intercorrelated. All sedimentological variables are highly correlated with each other and the average temperature in February (r = 0.45–0.63). Overall, the correlations between biotic and abiotic variables are very low.

5.3.3.3 Ordination

The PCA was performed on the abiotic variables per sample. Plots of the sample locations in the ordination space were colour-coded relative to the assigned community (Künitzer *et al.*, 1992; Section 5.1). By doing so, we could determine whether the abiotic clustering of the samples coincided with the biotic clustering of communities from the species abundance matrix. Overall, the communities occupied relatively well-defined regions in the PCA plots (see Figures 5.3.1 and 5.3.2).

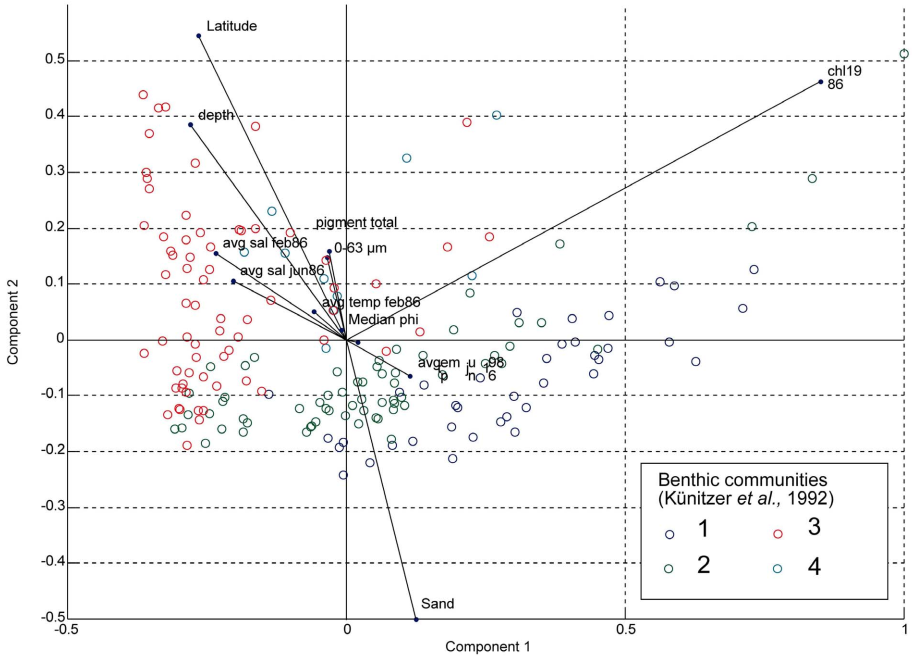

Figure 5.3.1. Principal components analysis of the NSBS 1986 samples (PC1 vs. PC2), colour-coded according to the benthic communities encountered (Künitzer *et al.*, 1992). Vectors indicate the orientation of the environmental variables in relation to the first two PCA components.

This illustrates that the communities can be separated largely according to the abiotic variables. The major separation in communities is perpendicular to the variables latitude, depth, and sand. Thus, for example, community 1 is generally found in sediments with a high percentage of sand in shallower waters and at lower latitudes. The first PCA component (PC1) is positively correlated with surface chlorophyll *a* and negatively with depth and latitude (Figures 5.3.1 and 5.3.2). PC2 is positively correlated with latitude and depth (Figure 5.3.1), and negatively with sand. PC3 is positively correlated with sand and latitude (Figure 5.3.2). Chlorophyll *a* shows no relation with any other variable. The variables latitude, depth, and percentage of sand are very similar in orientation, which illustrates their strong relationship. Thus, as expected, depth changes with latitude, and lower depths are associated with sediments having a higher percentage of sand. The total amount of pigment is highly correlated with the percentage of mud. The salinities in June and February are highly correlated and inversely related to the temperature in June.

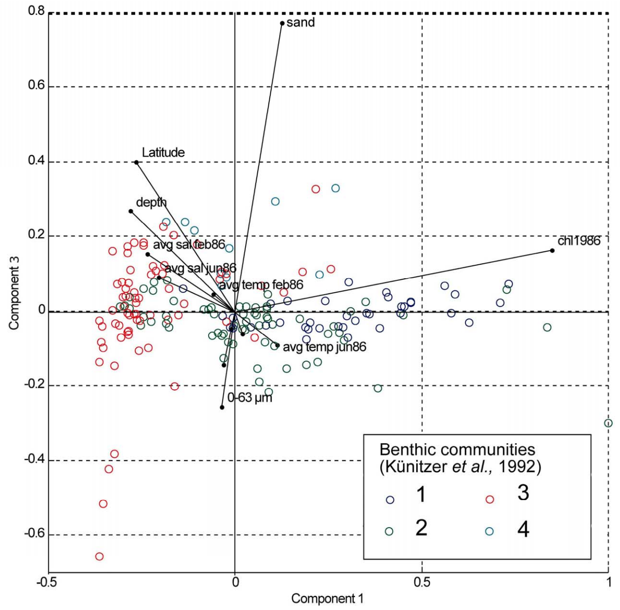

Figure 5.3.2. Principal components analysis of the NSBS 1986 samples (PC1 vs. PC3), colour-coded according to the benthic communities encountered (Künitzer *et al.*, 1992). Vectors indicate the orientation of the environmental variables in relation to the first and third PCA component.

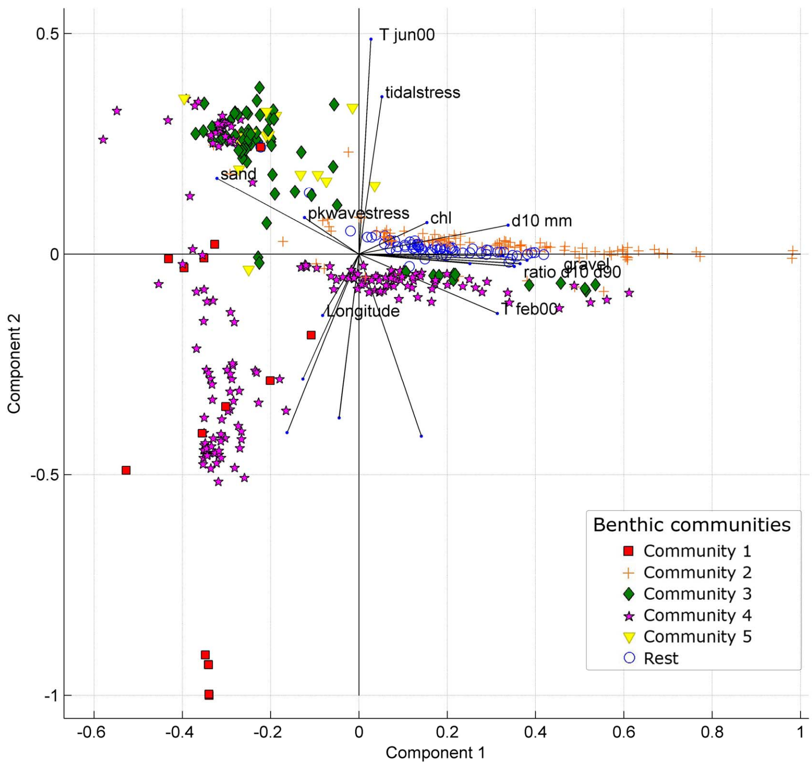

Figure 5.3.3. Principal components analysis of the NSBP 2000 samples (PC1 vs. PC2), colour-coded according to the benthic communities encountered in Section 5.1 (i.e. Community 1 = Cluster group A; Community 5 = Cluster group E; Rest = Group F and "x" samples). Vectors indicate the orientation of the environmental variables in relation to the first two PCA components.

In the PCA plots of the NSBP 2000 samples (Figure 5.3.3 and Figure 5.3.4), the spatial distinction between communities (Section 5.1) is also evident, though there is greater overlap than for the 1986 data. Thus, it is not possible to discriminate accurately between communities according to the available abiotic variables, but patterns can be identified. PC1 is positively

related with most sediment variables, the temperature in February, and the surface chlorophyll *a*, and negatively correlated with the percentage of sand. As expected, all sediment variables are linearly related. PC2 is positively related with the temperature in June and tidal stress, and negatively with the depth, latitude, and salinity in June. As in the 1986 samples, the depth increases with latitude over the North Sea basin. Finally, PC3 is positively related to longitude and chlorophyll *a*, and negatively with tidal stress and mud. The chlorophyll *a* increases eastwards, while the tidal stress, mud, and depth appear to increase westwards, according to the PCA output.

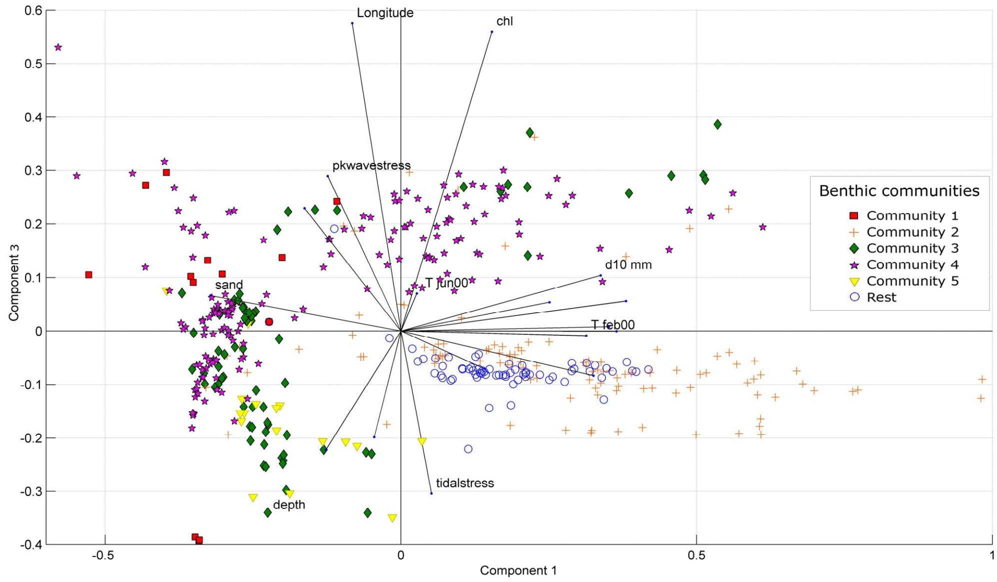

Figure 5.3.4. Principal components analysis of the NSBP 2000 samples (PC1 vs. PC3), colour-coded according to the benthic communities encountered (Section 5.1). Vectors indicate the orientation of the environmental variables in relation to the first and third PCA component.

5.3.3.4 Scatterplots

All abiotic variables were plotted against all biotic variables. For brevity, only a selection – principally those showing the strongest relationships – are presented here.

Diversity ES(50)

The Channel is clearly more diverse than other sites at low latitude (Dutch and Belgian coasts). The ES(50) rises almost linearly with latitude (Figure 5.3.5), if Channel samples are excluded from the trend line. The highest ES(50) values, however, are found on the German continental shelf. The trend of increasing ES(50) with latitude is similar in 1986 and 2000 (Figure 5.3.6). Heip *et al.* (1992) observed that, for the 1986 samples, diversity showed a trend with latitude, and the northern North Sea was more diverse. An effect of longitude and depth was observed by Heip *et al.* (1992), but not found for the combined 1986/2000 dataset in the present analysis.

Overall, there is a trend ($r^2 = 0.211$) of increasing ES(50) with increasing salinity in June (Figure 5.3.7). The lowest salinities are found in the Skagerrak where the ES(50) is intermediate. The lowest ES(50) values are found at a salinity of 34–34.5 psu. From this point, the ES(50) rises with rising salinity values. The ES(50) decreases almost linearly with the average temperature in June (Figure 5.3.8; $r^2 = 0.234$). The Channel has a much higher diversity relative to regions with similar temperatures. The 1986 and 2000 datasets show a similar trend of decreasing ES(50) with average temperature in June (Figure 5.3.9). However, the average temperature in June 2000 was significantly higher than in 1986 for each station (paired *t*-test; $p < 0.001$). The average temperature in 2000 was, on average, 1.07°C (stdev.

0.42) higher than in 1986. There is a positive relationship between stratification and ES(50) (not shown; $r^2 = 0.213$). The central part of the North Sea above 54° latitude is fully stratified and more diverse. The Channel is slightly more diverse and exhibits no to very little stratification. At low median grain sizes (median grain size <1000 µm), a range of diversities are encountered (Figure 5.3.10). Coarser samples, especially along the southeast English coast and the Channel show a much higher minimum and average ES(50). The coarsest (gravelly) Channel samples have a minimum ES(50) of 20 species.

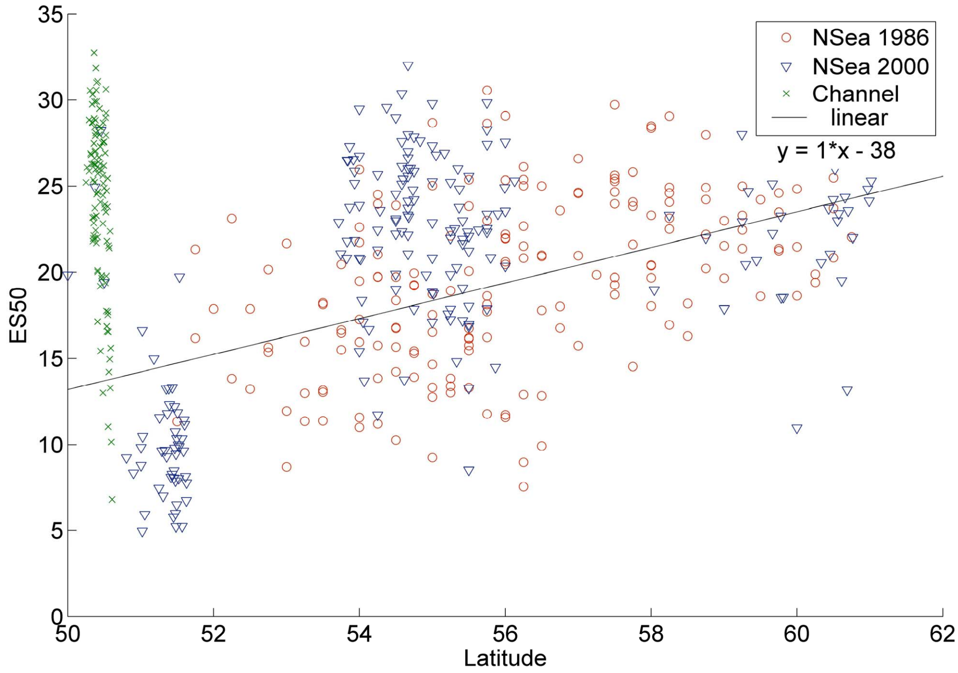

Figure 5.3.5. Scatterplot of the expected number of species for 50 individuals (ES(50)) vs. latitude for the 1986 and 2000 samples. The trendline $r^2 = 0.228$, excluding the Channel data.

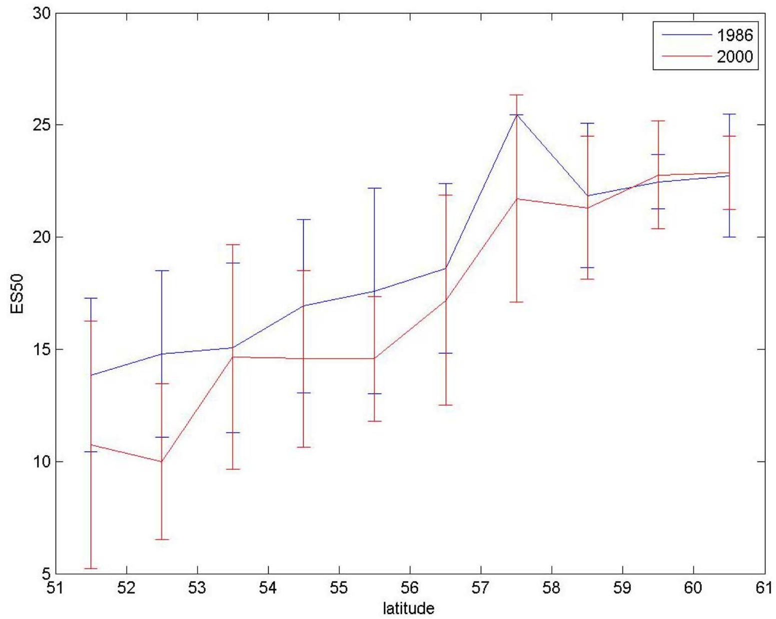

Figure 5.3.6. Plot of the average ES(50) for each degree of latitude. The error bars indicate the variance.

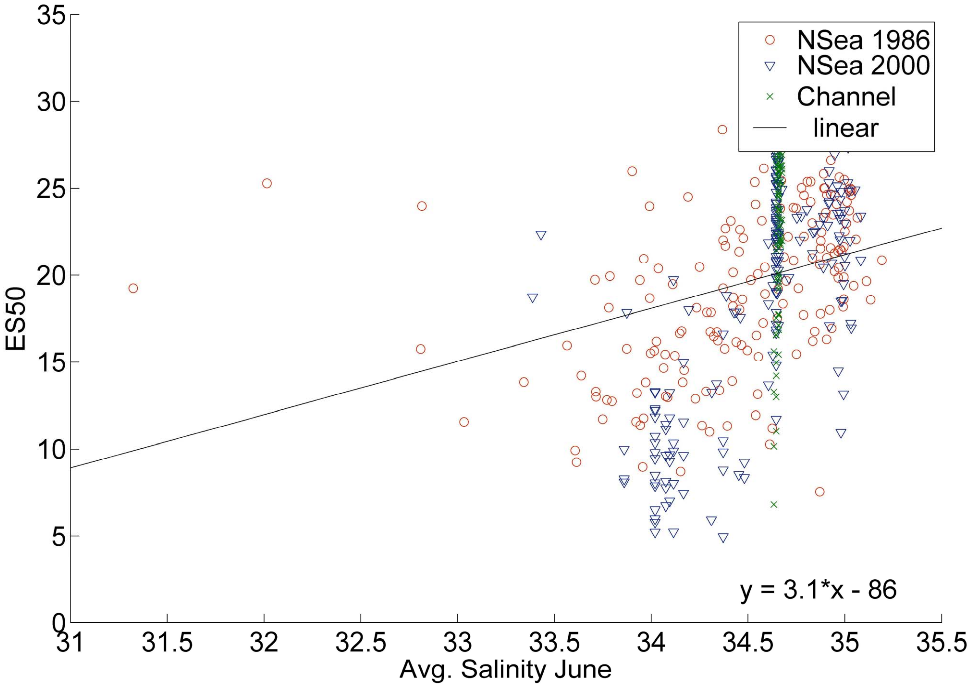

Figure 5.3.7. Scatterplot of the expected number of species for 50 individuals (ES(50)) vs. the average salinity in June for the 1986 and 2000 samples. The trendline r² = 0.211, excluding the Channel data.

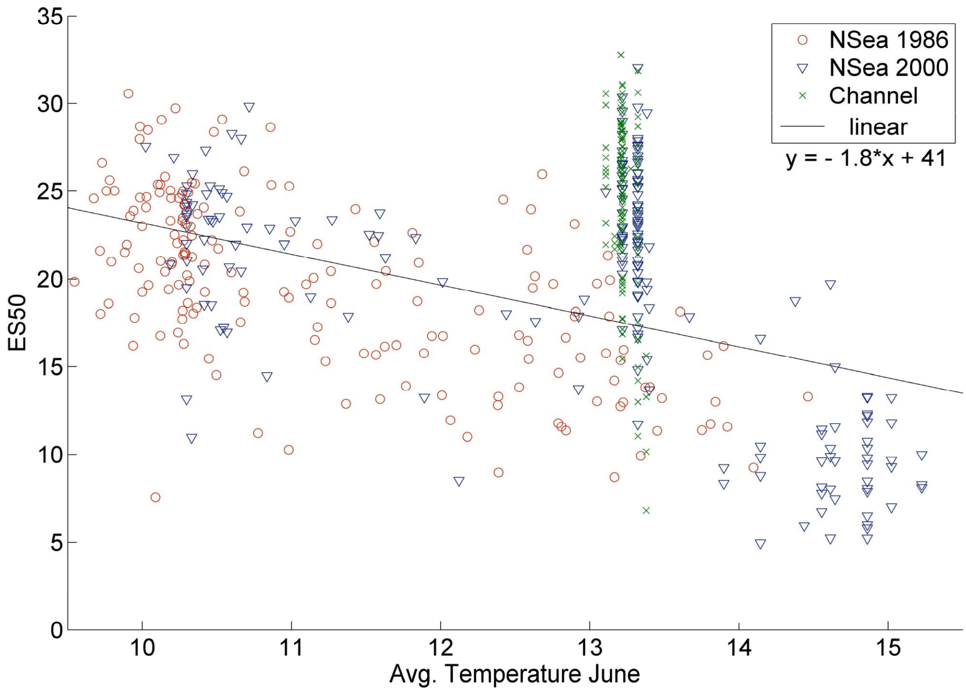

Figure 5.3.8. Scatterplot of the expected number of species for 50 individuals (ES(50)) vs. the average temperature in June for the 1986 and 2000 samples. The trendline r² = 0.234, excluding the Channel data.

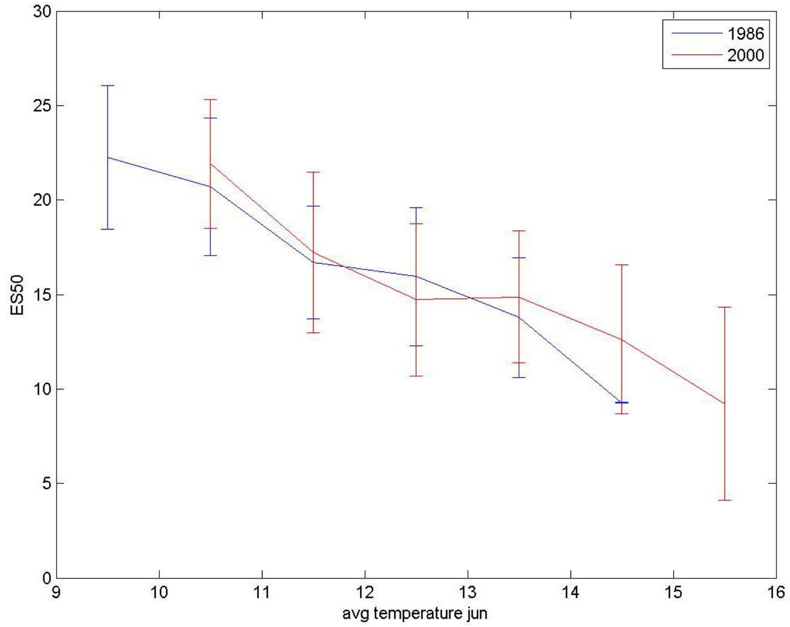

Figure 5.3.9. Plot of the average ES(50) for the average temperature in June. The error bars indicate the variance.

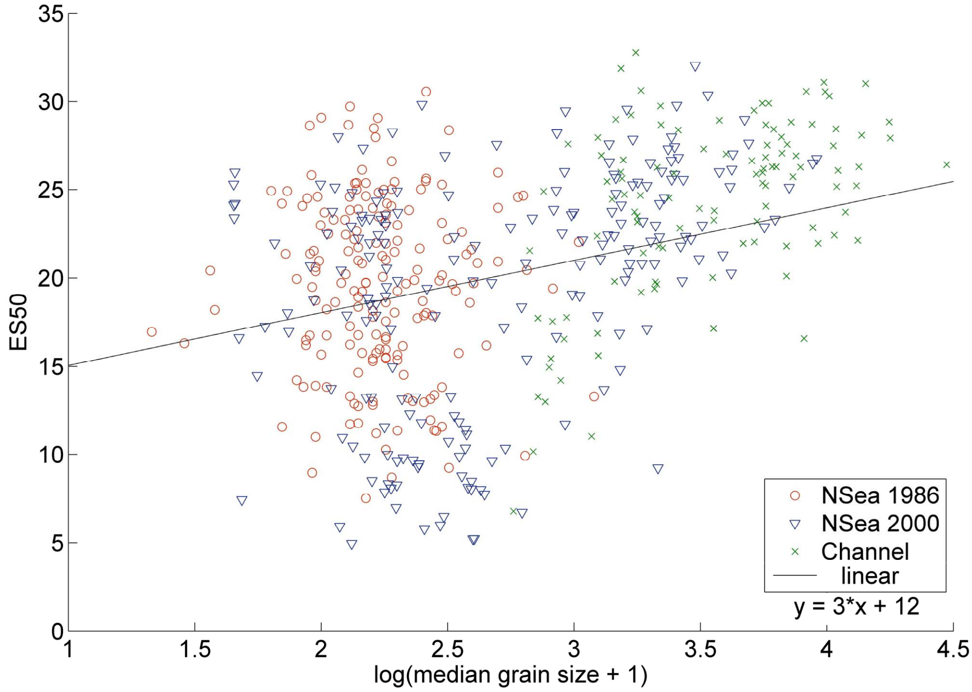

Figure 5.3.10. Scatterplot of the expected number of species for 50 individuals (ES(50)) vs. the median grain size (d50) for the 1986 and 2000 samples, excluding the Channel data.

Density

The logarithm of densities shows an almost linear relationship with latitude (Figure 5.3.11). However, samples with the highest densities were found in the Belgian part of the North Sea at low latitude (around 51.5°N). Samples close to the French coast (Calais–Dunkerque) have a low density. The samples in the Channel have a high density. The maximum and minimum densities were observed at shallow depths (not shown). At and above 50 m depth, the

minimum density is 200 ind. m^{-2}. At low median grain sizes (mud–sand), a range of densities are encountered (not shown). Coarser samples, especially gravelly substrata in the Channel, show a much higher average density. The coarsest Channel samples have a minimum density of 200 individuals. Density is negatively correlated with tidal stress (Figure 5.3.12). High levels of tidal stress are found near Dunkerque–Calais and in the Belgian part of the North Sea.

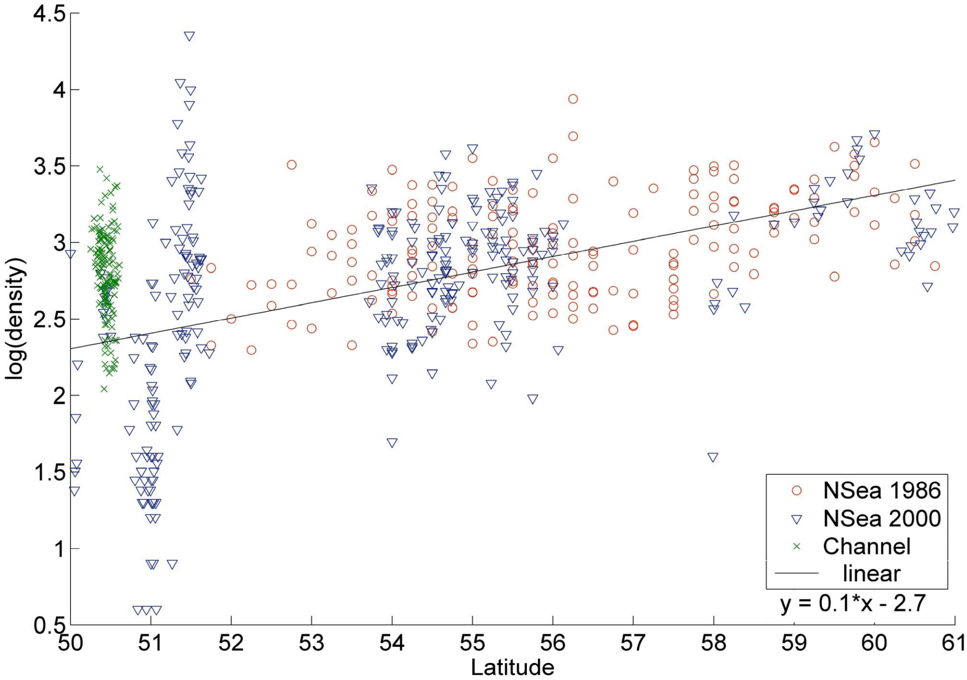

Figure 5.3.11. Scatterplot of the log(density) vs. the latitude for the 1986 and 2000 samples. The trendline r^2 = 0.246, excluding the Channel data.

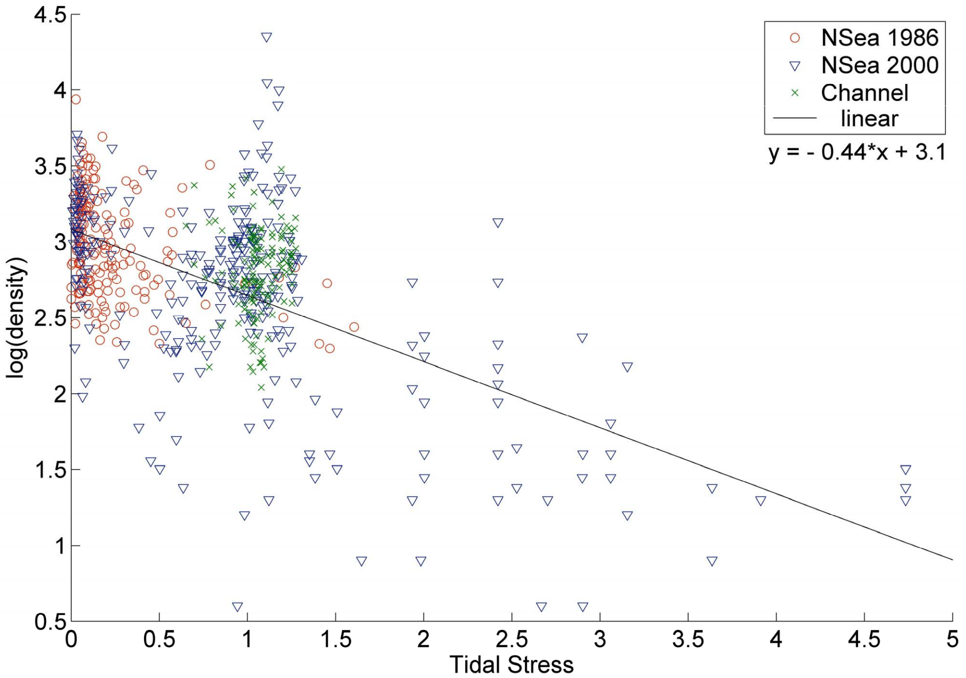

Figure 5.3.12. Scatterplot of the log(density) vs. the tidal stress for the 1986 and 2000 samples. The trendline r^2 = 0.360, excluding the Channel data.

Biomass

No clear trend with latitude was observed at low latitudes in or close to the Channel (Figure 5.3.13). Above 52°, the logarithm of the biomass decreases linearly with latitude. Below 52°, biomass was low close to Dunkerque–Calais and variable in the Belgian part of the North Sea.

The matching stations of the 1986 and 2000 datasets do show a relation with latitude (Figure 5.3.14), because the biomass decreases farther north. This can be explained by the exclusion of the Channel data and stations close to Dunkerque–Calais, because they were not sampled in 1986. The median grain size (not shown) shows the same pattern as for ES(50): at low median grain size (d50) both very high and very low biomasses occur. Above a median grain size of 5000 µm, the minimum biomass is about 0.1 g m^{-2}.

The logarithm of the biomass decreases almost linearly with the average temperature in February (Figure 5.3.15). Contrary to expectation, there is no relationship between benthic biomass and surface water chlorophyll *a* content (Figure 5.3.16). The latter data were derived from the HAMSOM model (Section 3.1.3). Bottom chlorophyll was only available for the 1986 samples and did show a relationship with benthic biomass (Heip *et al.*, 1992). The samples from 1986 and 2000 differed significantly, but identical trends were observed (Figure 5.3.17). The surface chlorophyll in 2000 was significantly higher than in 1986 for each station (paired *t*-test; p <0.001). The chlorophyll was, on average, 89.96 µg l^{-1} (s.d. 43.72) higher than in 1986.

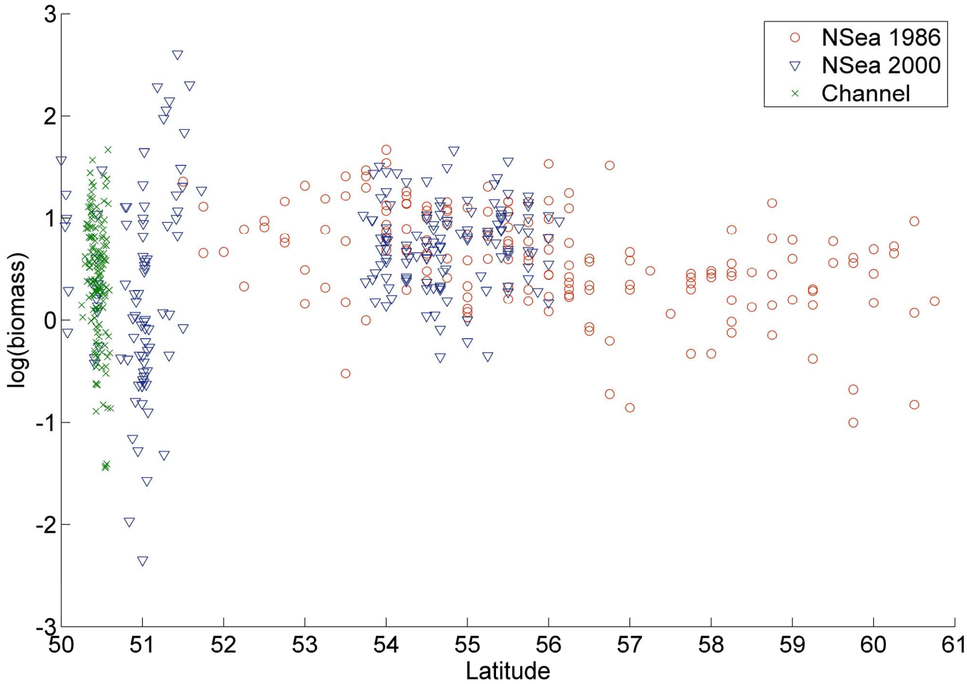

Figure 5.3.13. Scatterplot of the log(biomass) vs. the latitude for the 1986 and 2000 samples.

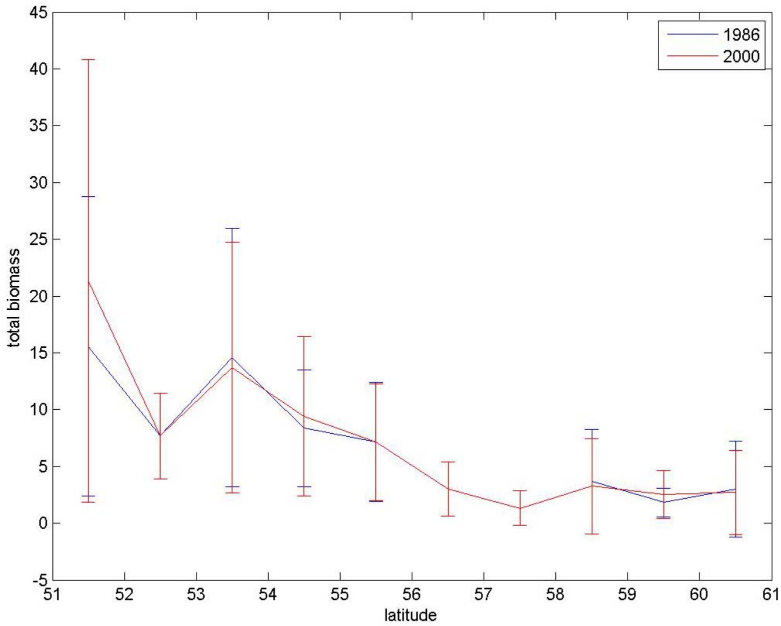

Figure 5.3.14. Plot of the average of the total biomass for each degree of latitude. The error bars indicate the variance.

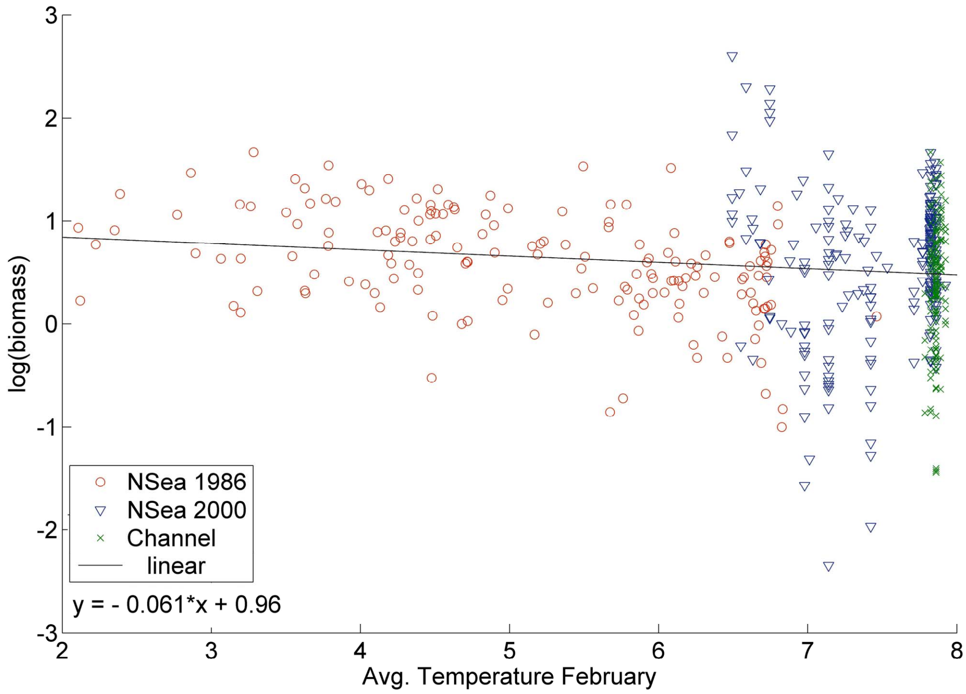

Figure 5.3.15. Scatterplot of the log(biomass) vs. the average temperature in February for the 1986 and 2000 samples.

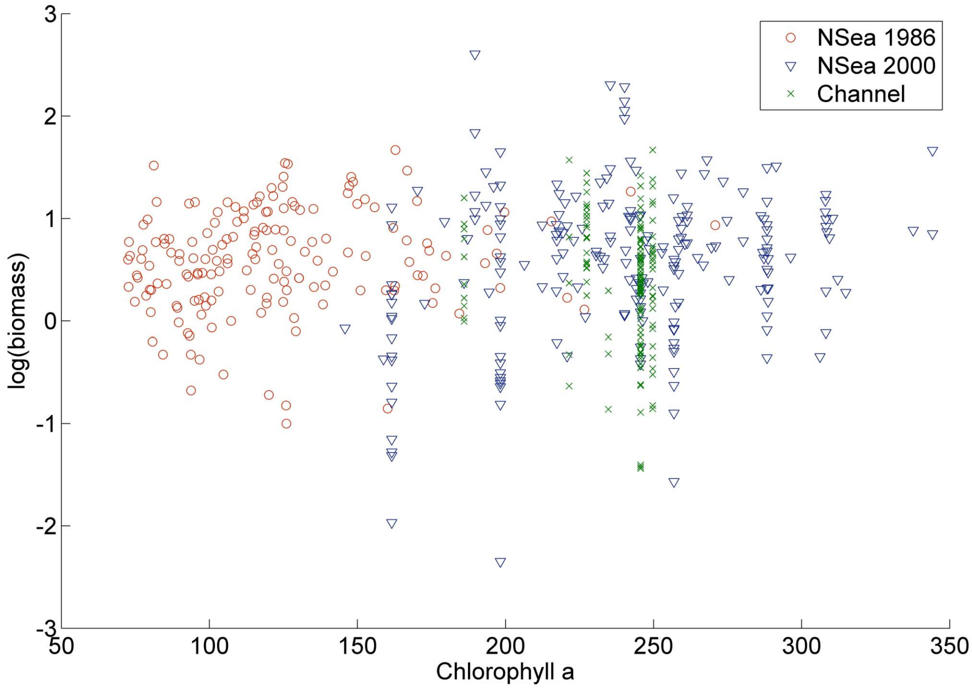

Figure 5.3.16. Scatterplot of the log(biomass) vs. the surface-water chlorophyll *a* for the 1986 and 2000 samples.

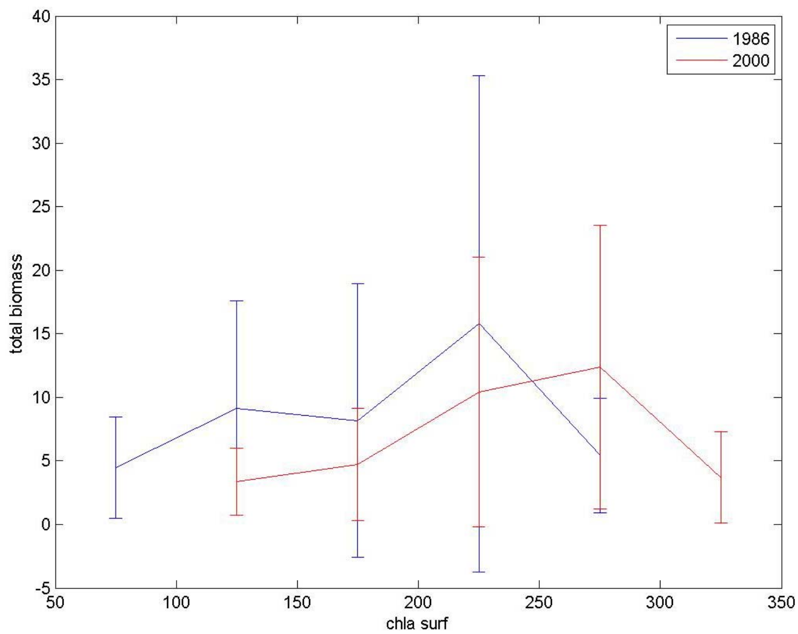

Figure 5.3.17. Plot of the average of the total biomass against the surface-water chlorophyll *a*. The error bars indicate the variance.

Individual Weight (IW)

The log(individual weight) (IW) shows a clear negative trend with latitude (Figure 5.3.18; r^2 = 0.283). The Channel samples have an IW below the trend line. In the reduced dataset with only the matching 1986/2000 samples, the pattern is clearer (Figure 5.3.19). The log IW shows a clear decreasing trend with depth (Figure 5.3.20; r^2 = 0.198). The Channel data also

follow this trend. The log(IW) shows a decreasing trend with the average salinity in June (not shown), while it increases with the temperature in June (Figure 5.3.21). It was also observed that log(IW) decreases linearly with stratification (Figure 5.3.22).

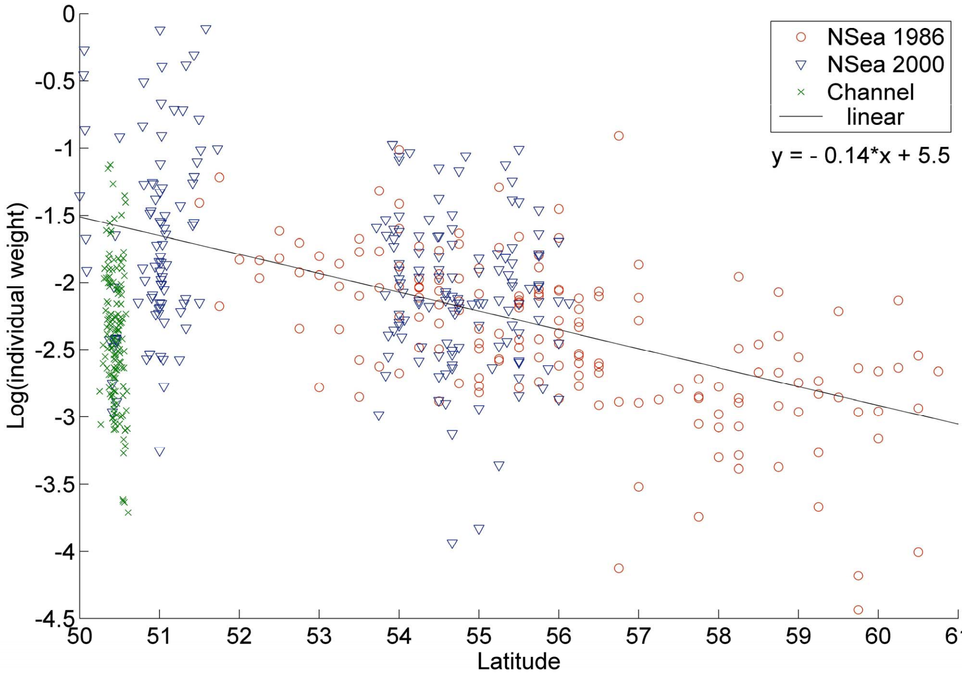

Figure 5.3.18. Scatterplot of the log(IW) vs. the latitude for the 1986 and 2000 samples. The trendline r² = 0.283, excluding the Channel data.

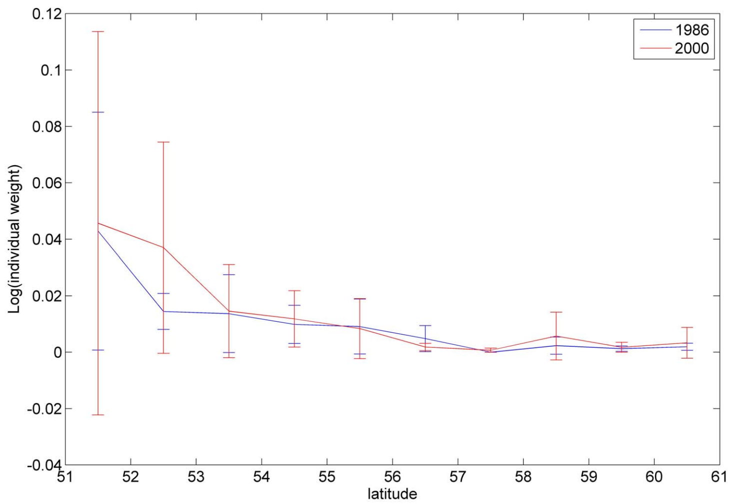

Figure 5.3.19. Plot of the average individual weight for each degree of latitude. The error bars indicate the variance.

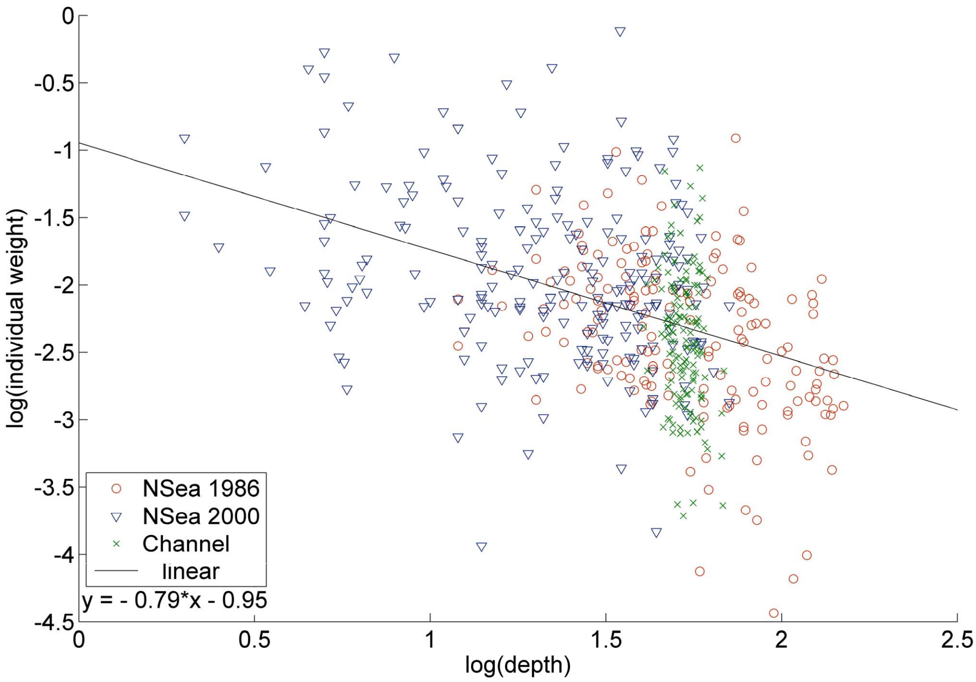

Figure 5.3.20. Scatterplot of the log(IW) vs. depth (m) for the 1986 and 2000 samples. The trendline $r^2 = 0.198$, excluding the Channel data.

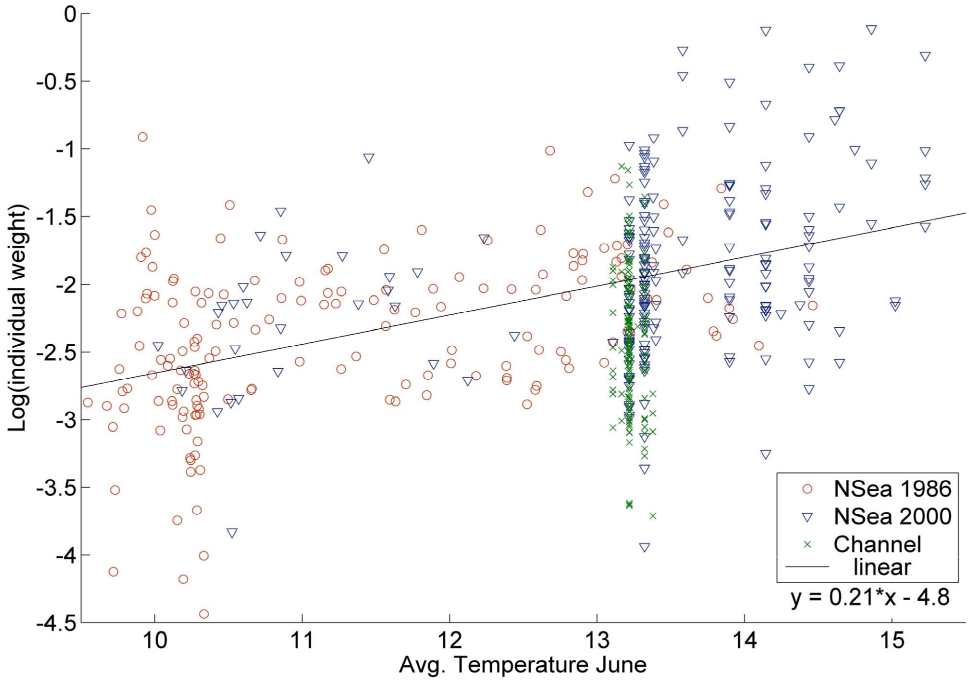

Figure 5.3.21. Scatterplot of the log(IW) vs. the average temperature in June for the 1986 and 2000 samples. The trendline $r^2 = 0.253$, excluding the Channel data.

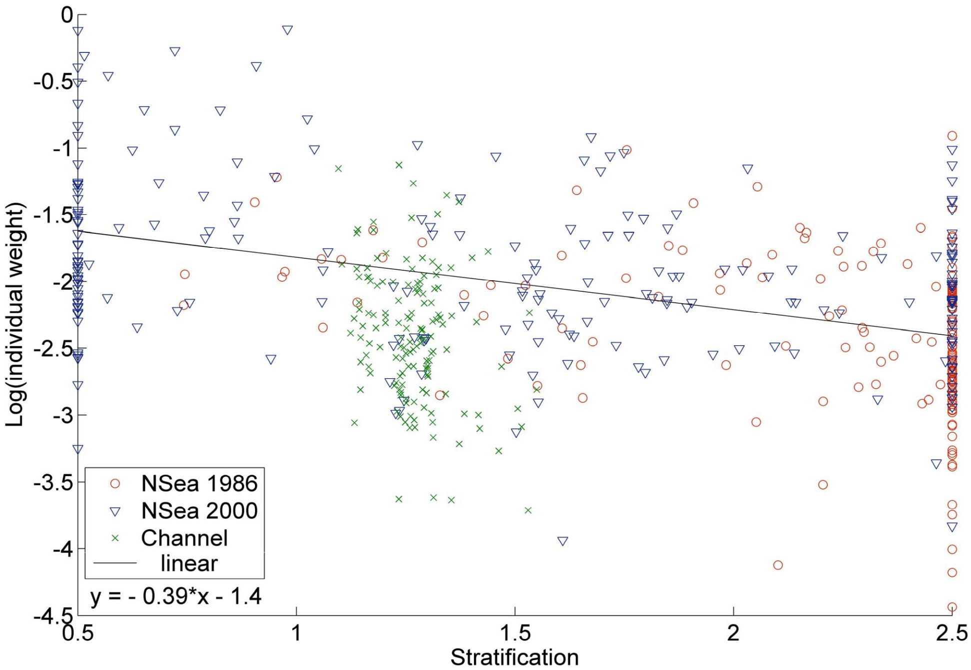

Figure 5.3.22. Scatterplot of the log(individual weight) vs. the stratification for the 1986 and 2000 samples.

5.3.4 Discussion

The comparison of biotic and abiotic variables showed that large-scale patterns exist and that a major part of the variance in the biotic variables can be explained by the abiotic variables. Although significant linear correlations with several variables were identified, it is generally not possible to determine their relative importance as causal influences because there is clearly scope for interaction among the variables, which is illustrated in the outcome of multivariate analyses (Figures 5.3.1–5.3.4). Overall, however, the outcomes of statistical analyses in this account advanced our insight into the mechanisms by which abiotic factors can influence the distribution of macrobenthic communities and species.

Correlation analysis provided an initial insight into the relationship between biotic and abiotic variables. The correlation coefficients were low overall, although some strong correlations were expected. The combined effect of interaction between environmental variables and the likelihood that the benthos was responding to multiple influences, therefore, complicated the search for cause–effect relationships. The PCA outputs identified related groups of variables, which was useful in selecting from the extensive list of available measures. By superimposing the outcome of earlier cluster analyses of the benthos data onto PCA plots of the environmental variables, useful insights were gained into the nature of the “realized niches” of the North Sea benthic communities.

Correlation and PCA analyses also highlighted differences between the 1986 and 2000 datasets, which were largely attributable to survey design and geographical scope. The 1986 dataset was derived from an evenly spaced sampling grid, while the 2000 dataset was highly clustered, with many more stations in the southern North Sea. Also, the 2000 survey extended into the eastern English Channel. The use of a reduced dataset, including only matched stations (see Section 5.2), was important in illustrating similarity in trends between the two sampling occasions.

Table 5.3.2. Strongest relationships observed between the biotic and abiotic variables in the NSBP dataset.

	ES(50)	DENSITY	BIOMASS	IW
latitude	+	+	–	–
depth	+			–
tidal stress		–		
chla water	–			
average temperature June	–			+
average temperature February			–	
average salinity June	+			–
stratification	+			

+ = positive relation; – = negative relation.

Based on abiotic variables, the eastern English Channel clearly represented a different biotope, and this was evidenced by the discrete cluster that the stations occupied in several of the scatterplots. It is also evident that the Channel is more biodiverse than the rest of the North Sea. This can be ascribed to the coarser (gravelly) nature of the substrata here and also along parts of the southeast English coast which, combined with the interstitial sandy sediments, present a more complex habitat for colonization by an array of benthic species. This is in contrast to the predominantly soft sediments at the majority of stations in the North Sea, and explains why the trend lines for correlations between biotic and abiotic variables are generally higher after exclusion of the Channel samples.

Environmental variables

Most environmental variables are expected to interact: e.g. lower winter temperatures are expected in shallower areas, and these often have a different sediment composition, typically under the influence of stronger tidal currents and wave action. So, if a relationship between diversity and depth is observed, it is not necessarily clear which is the causative variable, if indeed a single cause is to be expected. It is essential, therefore, to explore interrelationships between the abiotic variables to help distinguish between correlative and causative influences on benthic communities.

Three types of environmental variables were identified by Austin *et al.* (1984): resource gradients are composed of matter and energy consumed (nutrients, water, and food); direct gradients have physiological importance (temperature, pH); while indirect gradients have no direct physiological relevance (slope, depth). Most variables in the present dataset represent indirect gradients (sediment type, currents, depth, and stratification). Indirect variables usually replace a combination of different resource and direct gradient variables in a simple way (Guisan *et al.*, 1999). For instance, depth (an indirect variable) is related to a number of resource and direct gradients (i.e. temperature, chlorophyll). The strongest relationships between biological and environmental variables are summarized in Table 5.3.2.

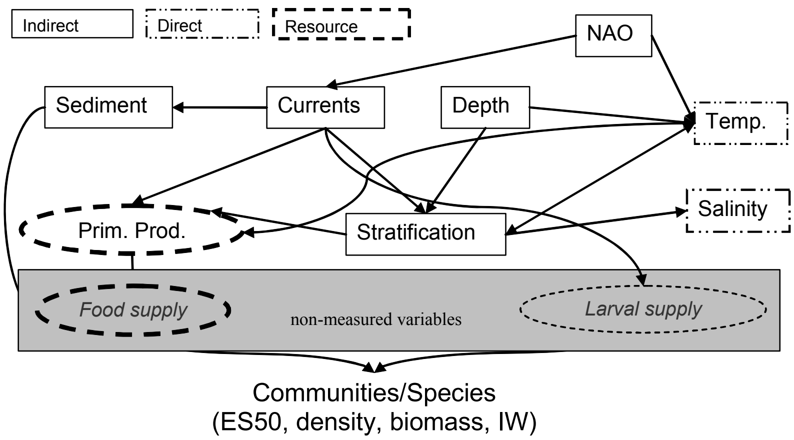

Figure 5.3.23. Simplified scheme of the expected relationships between the measured biotic and abiotic variables in the NSBP dataset. NAO = North Atlantic Oscillation; IW = individual weight (biomass/density). Food supply and larval supply were not measured in the NSBP dataset. The type of each variable is indicated: direct/indirect or resource gradient (*sensu* Austin *et al.*, 1984).

A conceptual model to represent the inferred relationships between the abiotic and biotic variables in the NSBP dataset is shown in Figure 5.3.23. For the NSBP dataset, the only resource gradient measured was chlorophyll *a*. Temperature and salinity influence the physiology and thus are direct gradients. Temperature determines the metabolism of macrobenthic animals. The other variables (sediment, currents, depth, and stratification) are indirect gradients. In predictive modelling studies, these indirect variables are often used because they are relatively easy to measure and, therefore, are widely available. However, only locally valid empirical models can be constructed with indirect variables (Guisan and Zimmerman, 2000).

The presence and biological properties of species/communities are dependent on the advection of food (Kröncke and Bergfeld, 2003) and the supply of larvae. The food supply is determined by how much of the primary production products reach the benthos. This downwards transport is governed mainly by currents/stratification. We expect primary production to be related to currents, stratification, and temperature in the NSBP dataset. Heip *et al.* (1992) hypothesized that the impact of stratification and current patterns on food input to the benthos might be one of the most important factors explaining large-scale patterns.

The North Atlantic Oscillation (NAO) is one of the most important drivers of climate fluctuations in the North Atlantic realm. The NAO index indicates the difference in atmospheric pressure between the Icelandic Low and the Azores High. The NAO controls the strength of westerly winds and storm tracks across the North Atlantic and surrounding continents and has a period of 7.3–8 years (Rogers, 1984). Persistently strong westerlies over middle latitudes in the Northeast Atlantic cause an increased transport of warm air and moisture into northern Europe, which results in milder winters as opposed to the more continental climate during low NAO periods (Gröger and Rumohr, 2006). Typically, positive NAO values will be associated with mild winters and reduced water column stratification. Macrofauna communities are severely affected by cold winters, with shallow stations affected the most (Reiss *et al.*, 2006).

The NAO index correlates with zooplankton, primary production, and macrobenthic abundances (Hagberg and Tunberg, 2000). In the western Baltic, Gröger and Rumohr (2006) observed that species richness was influenced positively by the winter NAO index and negatively by salinity (with a lag of four years for the salinity). Internal growth lines in shells of three suspension-feeding bivalves were correlated with monthly values of the NAO index, phytocolour, temperature, and wind (Witbaard *et al.*, 2005). Kröncke *et al.* (1998) found a strong positive relationship between abundance, species number, and (less clear) biomass in

the second quarter of the year and the NAO index. The mediator between the NAO and the benthos is probably the sea surface temperature (SST) in late winter and early spring (Kröncke *et al.*, 1998). Unfortunately, the NSBP dataset is not a time-series; therefore, the temporal relationships with NAO and temperature could not be tested.

Hagberg *et al.* (2003) found a relationship between macrobenthic communities and depth. Production–biomass ratios were negatively related to water depth and positively related to water temperature. Also, depth influences stratification, as shallow areas are rarely stratified, because mixing between all water depths can take place.

Tidal or wind-driven currents are known to influence food transport and availability (Herman *et al*., 1999) and larval supply. However, microscale current measurements are rarely available in macrobenthic studies. In the NSBP dataset, the modelled bottom current (HAMSOM, Section 3.1.3) was available. Grain size is an important predictor of community type (van Hoey *et al.*, 2004) and species (Willems *et al.*, in press). Sediment distribution is determined by (a) the sediment source; (b) interactions between sediment particles; (c) hydrodynamic regime; (d) biological effects (Snelgrove and Butman, 1994). The sediment composition is in dynamic equilibrium with the bottom current regime. Regions with strong tidal currents tend to have coarser sediment, because finer particles do not settle. Similarly, larval transport and deposition and particulate flux are also governed by the benthic boundary-layer flow. Fine (muddy) sediments generally have higher levels of microbial abundance because they are typically encountered in more depositional environments, as well as providing a larger surface area for colonization (Snelgrove and Butman, 1994). Thus, sediment grain size can be used as a proxy for the strength of tidal currents or food supply.

Relation between biotic and abiotic variables

Abiotic variables and diversity (ES(50))

The diversity, expressed as expected number of species ES(50), increased with depth, salinity in June, and stratification. ES(50) decreased with chlorophyll *a* at the surface and the temperature in June. The analyses support the hypothesis of Heip *et al.* (1992) that the impact of stratification on food input to the benthos is one of the most important factors explaining large-scale patterns. In the NSBS 1986 dataset used by Heip *et al.* (1992), measures of stratification were not available. Heip *et al.* (1992) also identified a relationship between sediment type and diversity. However, depth and median grain size are positively related. At great depths and high median grain sizes, the diversity is high; at low depths and low grain sizes, there is a wide range of diversity. Deeper and coarser stations are thus more similar and exhibit a narrower range of diversity. Salinity had a large impact on diversity in the western Baltic according to Gröger and Rumohr, (2006). Kröncke *et al.* (1998) found a strong relationship between diversity and the sea surface temperature in late winter and early spring (Kröncke *et al.*, 1998). In the NSBP dataset, a negative relation of ES(50) with bottom summer temperature was found.

Latitudinal gradient and diversity

A regional decrease of biodiversity with increasing latitude has been observed in numerous studies across a range of biota and is one of the keystone observations of macro-ecology (Hillebrand, 2004). Although this pattern is observed frequently, there is a lack of consensus on the primary cause because several environmental variables are correlated with latitude. This was also evident in the analyses of NSBP data. In the present dataset, there is a latitudinal gradient of 11° (50–61°) representing a length of 1200 km (Figure 5.3.24). In addition to diversity, the relation between latitude, density, and biomass was also explored.

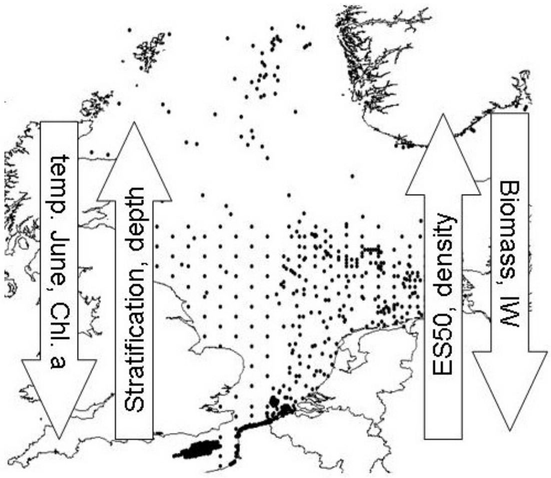

Figure 5.3.24. Schematic overview of the abiotic and biotic gradients. The arrows point in the direction of the highest values for the variables.

It was possible to test the global hypothesis of decreasing biodiversity with latitude at the regional level of the entire North Sea. For the combined dataset (1986/2000), there was an increase of diversity with latitude ($r^2 = 0.228$). For the 1986 and 2000 samples separately (Figure 5.3.6), the pattern was similar. This is contrary to the global pattern of increasing biodiversity towards the equator (Hillebrand, 2004). The northern North Sea was more diverse. However, the diversity gradient in the North Sea can be regarded as, at most, regional in scale, and the global diversity gradient in the macrobenthos remains to be explored. Most biotic variables correlate well with latitude. Density increased positively with latitude ($r^2 = 0.246$), while IW decreased with latitude ($r^2 = 0.283$).

Only biomass is less well correlated, mainly at low latitudes (Dutch and Belgian coasts). From a multiple regression analysis of the NSBS 1986 data, Heip *et al.* (1992) found that the log(biomass) was significantly related to latitude, chlorophyll *a* in sediment, and log(% mud). Latitude always accounted for the largest part of the variance. On the Norwegian shelf, species richness was highly variable (35–148 species), but showed no evidence of a relationship with latitude or other environmental variables (Ellingsen and Gray, 2002). Although latitude is clearly not a physical variable, it can be regarded as a “summarizing gradient”, because a number of variables are correlated with it. For example, stratification and depth increase northwards, while the summer temperature in June increases southwards. Latitude explained more variation than depth for biomass, density, and IW.

Biomass vs. water temperature

Temperature is one of the primary factors influencing metabolic rate of ectotherms; it also varies significantly over time and across microhabitats (Helmuth *et al.*, 2002). At low temperatures, metabolism, and thus respiration, is reduced, which (to a degree) can be beneficial to an organism in saving energy and increasing tolerance to lower oxygen levels. Biomass increased with decreasing winter temperatures in February. The summer temperature showed no clear relationship with biomass. Chapelle and Peck (2004) stated that size optima change with water temperature. In colder water, the metabolism is expected to decrease, which results in a lower food requirement, but also there is less food uptake (Chapelle and Peck, 2004). The balance between metabolism and uptake is important, but is not known for the studied species. Sebens (2002) stated that, with limited prey, the net result is that periods of lower temperature are energetically costly. For the NSBP dataset, the opposite seems to be true, as colder regions have higher biomass.

Abiotic variables and individual weight

Which abiotic variables correlate with average IW (community biomass divided by density)? For example, in a stable environment with lower temperature, one might expect a lower metabolism and a reduced oxygen demand and, thus, an individual may grow larger. On the other hand, the food supply might be limiting in colder environments.

IW decreased with depth, latitude, stratification, and salinity in June, and it increased with temperature in June. The resulting north–south pattern in IW is a result of the biomass decreasing moderately with latitude (Figure 5.3.13) and log(density) increasing with latitude (slope = 0.1; Figure 5.3.11). The factors that increase IW (depth, latitude, stratification, and salinity) are all correlated and have a north–south gradient. This prevents us from disentangling the causal relationships with IW. The decrease of mean individual weight with latitude was also observed for the NSBS 1986 dataset by Heip *et al.* (1992).

Benthic biomass and surface chlorophyll *a*

Generally, one might expect high surface chlorophyll levels to be linked with high benthic biomass. However, several processes govern the transfer of primary production products to the seabed. Stratification can keep the food particles locked in the upper water layers, where they are constantly recycled. High water depths increase the sinking time and may cause the quality of the food input to the seabed to be lowered as the particles are consumed through microbial action during descent. Finally, water currents can divert the surface production leading to, for example, localized sinks of settled products away from the majority of organisms. In the present study, surface chlorophyll *a* levels from a model (ECOHAM1, Section 3.1.3) were compared with benthic biomass for the same location. Additionally, the relationship of chlorophyll *a* with density, diversity, and individual weight was also explored.

Contrary to expectation, no relationship between surface chlorophyll *a* and benthic biomass was found for the combined 1986/2000 dataset. The chlorophyll *a* level, however, was derived from a model and not from actual measurements. For the NSBS 1986 samples, Heip *et al.* (1992) found a relationship between sediment chlorophyll *a* and benthic biomass. However, no relationship was found between the sediment chlorophyll *a* content and the surface chlorophyll *a*. The coupling of surface and benthic chlorophyll *a* levels is complex and is determined by a number of factors (including water depth and stratification). Neither was a relationship found between chlorophyll *a* and density, diversity, or individual weight. The hypothesis of a link, therefore, was not supported by the available data.

5.3.5 Conclusions

Larger scale patterns exist in the structure (diversity and density) and functional attributes (biomass and mean individual weight) of the macrobenthos in the North Sea. The spatial trends could often be linked with one or more environmental variables. The variables measured were sometimes highly correlated, and the outputs from multivariate (PCA) analyses for 1986 and 2000, overlain with the main community types, were helpful in niche characterization. It was difficult to compare the 1986 and 2000 surveys in their entirety because the sampling grids differed significantly, but analysis of the reduced datasets based on matching stations revealed that, overall, the relationships between biotic and abiotic variables were similar for both years. Samples collected from the eastern English Channel and parts of the English east coast in 2000 were distinctive both in terms of the (coarser) substratum type and the benthic fauna. Most of the variation in biological properties of the North Sea benthos can be explained by the environmental variables. The diversity increased with increasing latitude, contrary to the general hypothesis. The biomass increased with decreasing winter temperatures in February. No relationship between surface chlorophyll *a* and biomass was found.

However, viewed on a global scale, it is possible that the observed relationships between the biotic and abiotic variables are only valid within the relatively limited geographical extent of the North Sea. A number of the relationships could therefore be correlative rather than causative. No resource gradient variables were available for the NSBP dataset, except surface chlorophyll *a*. However, the latter showed no relationship with the benthic biological variables. The other variables could be classified as having direct (e.g. temperature) or indirect (e.g. depth) physiological relevance (Austin *et al.*, 1984). Herman *et al.* (1999) state that food may be the most limiting factor over large spatial scales. In the NSBP dataset, environmental variables had to be used as proxies for food and larval availability. Human impacts were not considered in this analysis, but are also expected to play a role.

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