10. Annex 5 - Species Composition, Diversity, Biomass and Production of the Epibenthic Invertebrate Community

10.1. Introduction

The epibenthos are the component of the benthic invertebrate community that spend the majority of their lifecycle living in close association with the surface of the seafloor. They form a major component of the North Sea fauna and previous studies of these animals have described the distribution of a number of characteristics of the community, such as species diversity and species relative abundance, with interpretations of the physical and biological factors affecting their distribution (Basford et al., 1989; Frauenheim et al., 1989; Rees et al., 1999). Based on the findings of these studies, the major factors affecting the distribution of epifaunal invertebrate communities within the North Sea are depth, sediment composition, water temperature and hydrography. This leads, at the coarsest level, to a division of northern and southern epifaunal communities split at the 70m-depth contour. However, the interpretation of these studies at a North Sea scale is restricted, as the sampling methods and analyses employed originally were not consistent amongst surveys and conclusions were often based on a limited number of samples.

The EC project FAIR (project CT 95-0817) (Jennings et al., 1999) developed a standardised epibenthic sampling methodology that could be used onboard routine groundfish surveys, such as the quarterly International Bottom Trawl Surveys (IBTS) coordinated through the International Council for Exploration of the Seas (ICES). This would enable minimisation of funding required to undertake regular North Sea scale epibenthic surveys. Using the standardised methodology developed from this, a subsequent EC project, Biodiversity (project 98/021), undertook the first North Sea wide survey during the 3rd quarter IBTS survey in 1999 and repeated this with five participating nations in 2000. The results of these surveys have now been published (Zühlke, 2001; Zühlke et al., 2001; Callaway et al. 2002) and information is given on distribution patterns, diversity and community structure at the scale of the ICES rectangle. Initial interpretations of the environmental factors affecting these patterns confirm the findings of the earlier studies, emphasising the importance of hydrography, sediment type and temperature. Three major boundaries between community types were noted, following the 50m, 100m and 200m depth contours (Zühlke, 2001).

The purpose of this chapter of the report is to present the findings of the epibenthic surveys that have been undertaken since the Biodiversity project as part of the EC 5th framework project Managing Fisheries to Conserve Groundfish and Benthic Invertebrate Species Diversity (MAFCONS). This project has extended the sampling protocol to include infaunal benthic communities (Chapter 11) and to link characteristics of the benthic invertebrate communities to demersal fish diversity (Chapter 9) and to levels of ecological disturbance associated with the North Sea demersal fishing industry (Chapters 2 and 8). As part of this development, methods for estimating secondary production from the size-structured epibenthic community have also been explored, as this is an important link to the overlying demersal fish community.

10.1.1. Catchability issues

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In attempting to describe the epifaunal community in terms of its composition, diversity, and productivity, it is important to take account of the restrictions that the sampling procedure has on the community being represented. The impressions of the epibenthic community gained from the analysis of our sample data is not that of the actual epifaunal community present at each sampled location, but that rather it is a view of the community biased by the differential selectivity of the sampling gear for each species present at each location. As discussed in Chapter 9, no trawl gear ever samples all the individuals present in the path of the net. Trawling is a selective process because the catch rates of different species in any given fishing gear vary considerably, both between species and between size classes of the same species. Many factors can be involved. Although many of the epibenthic species sampled are less motile than the fish species sampled in the fish surveys, it is likely that a proportion of the more mobile species can move out of the way of the gear. Also, some of the species live partially submerged in the sediment during certain times of the day and these too may not be sampled well by a towed trawling gear. In fact it is likely that catchability of the epibenthic community in the 2-metre beam trawl varies as a result of a number of factors including motility, size and living position on/within the seafloor. Because there have been few large-scale epibenthic surveys to date, there is little information available to account for catchability issues. Based on the findings of a recent study, we have examined this issue and discuss the implications of the results on epifaunal community analyses (Reiss et al 2006).

10.1.2. Sampling effort issues

As discussed previously in Section 9.1.1.1., any analyses involving species diversity, must take account of the influence of sampling effort on index performance. Previous explorations of variation in species diversity of macrofaunal invertebrates have tried to standardise for sampling effort effects on diversity indices, by calculating diversity based on an arithmetic mean of a number of iterations of the indices for a given abundance of animals randomly selected from the sample (Heip et al., 1992). However, these methods do not account for the inherent influence of abundance on the indices and the fact that both this and species number will continue to increase up to a given sampled area (Colwell & Coddington 1994; Connor et al 2000; Gotelli & Colwell 2001; van Gemerden et al 2005). Preliminary analysis of the relationship between index value and variation in sampling effort is a critical first step to determine at what sampling effort level index values stabilize, and thus begin to represent the true community diversity rather than just being a consequence of the level of sampling effort. Previous attempts to determine the number of 2-metre beam trawl samples required to represent community diversity of an ICES rectangle suggest that not only do you need greater than 5 replicate tows, but that the number of tows required varies depending on: the index of diversity used (i.e. species number Vs. indices of dominance and evenness), species group considered (i.e. sessile vs. free-living epifauna) and the geographical area studied (Biodiversity report; Henning; Daan & Ehrich?). These relationships are revisited here with the additional data collected in the MAFCONS surveys.

10.1.3. Productivity

Traditional methods for calculating secondary production from the benthos have been applied to single animals or populations based on the change in body mass or growth over time. However, the methods used to calculate this generally involve the destruction of samples and requires intensive sampling of the same population to account for changes over time. Methods include those based on cohort analysis, size class based methods and the relationship between productivity and mortality
None of these methods are practical when trying to quantify secondary production at the community level. During the MAFCONS project, assessment of spatial variation in secondary production from the infaunal and epifaunal benthos at between 100 and 150 stations per year over two years has been undertaken.

Over the last 20 years, efforts have turned towards parameterising empirical models that can be used to estimate secondary production (Brey, 2002). These models describe the relationships between easily measured parameters such as biomass, individual body mass and water temperature with production (P) or the production/biomass (P/B) ratio for individual populations. Empirical relationships between these parameters are calculated using the combined published results of the traditional studies as described above. It is then possible to predict P or the P/B ratio for new sampled populations just using data for the easily measured parameters such as biomass and temperature. All of these approaches depend more or less directly on the negative exponential relationship between metabolic rate and body mass (Peters 1983).

The earliest empirical models related the P/B ratio to one parameter. For example, the P/B ratio was related to lifespan by Robertson (1979), to adult body mass (at maturity) by Banse & Mosher (1980) and to mean individual body mass by Schwinghamer et al. (1986). Two-parameter models were published by Brey (1990) (P vs. biomass and mean individual body mass) and by Edgar (1990a) (P vs. mean individual body mass and bottom water temperature). Even more complex three-parameter models were published by Morin & Bourassa (1992), who related production of stream benthos to biomass, mean body mass and annual mean water temperature; Plante and Downing (1989), who related production of lake benthos to biomass, maximum body mass, and surface water temperature, and; Tumbiolo & Downing (1994), who related production of marine benthos to biomass, maximum body mass, surface water temperature and water depth. More recent models have generally all included environmental parameters (usually water temperature and sometimes depth) in recognition of the influence of these on growth rates and thus also productivity. Brey et al. (1996) and Brey (1999) unified all previous habitat-specific approaches into one large model for macrofaunal benthos in general. In Brey et al. (1996) "Artificial Neural Networks" were trained to estimate P/B from body mass, taxon, mode of living, water temperature and water depth and it is suggested that this approach performs slightly better than the usual multiple linear models. The latest models are available on a website maintained by Brey (2002). Here the relationships are updated regularly to include any new field studies of direct measurements of population production and P/B ratios, thus increasing the number of studies that the empirical model is based on.

In all cases, models are based on data for individual species populations. Thus production is calculated for each species making up a community and all species totals are then summed to give total community production. Where species level data do not exist, the variability around mean individual weight will be likely to increase as taxonomic resolution decreases and this may affect the validity of using the empirical models that include mean individual weight as a parameter. However, here the epibenthic data have been size structured to reduce the variability around the mean individual weight per species. When carrying out routine, large-scale surveys such as those undertaken in this project, it may not be feasible to work up the data to species level (particularly for the infaunal samples – see Chapter 11). In this project we examined the methods available for estimating secondary productivity from the epifauna. The epifauna include both colonial and individual based populations of animals. Due to this it was necessary to combine a number of methods, some based on biomass, some based on size-classed individuals grouped based on their individual weights and some based on average mean weight.
10.2. Methods

10.2.1. Data set

One beam trawl tow was taken at each MAFCONS station sampled, close to the track of the main demersal fish-sampling trawl. Overall 283 2-metre beam trawl samples were taken across the North Sea, 134 in 2003 and 149 in 2004 (Figure 10.2.1.1). Sampling was undertaken between July and September in each year. All samples were taken with a 2-m beam trawl constructed from galvanised steel, fitted with a 20mm mesh (10mm knot to knot) and a liner of 4mm knotless mesh (2mm ‘knot to knot’) (a detailed description of the specifications can be found in Jennings et al., 1999). The beam trawl was shot with a warp length of approximately three times water depth and towed at between 1-1.5 knots for 5 minutes. Where possible, a Scanmar© depth unit (which shows when the trawl reaches and leaves the seabed) was attached to allow accurate timing of the duration of beam trawl fishing (see Chapter 6 for further details of trawling procedure).

Figure 10.2.1.1. All 283 stations sampled for epifauna with a 2-metre beam trawl during the 2003 and 2004 MAFCONS surveys. Red symbols represent those stations that did not fit within the criteria set for tows standardised on swept area (see Section 10.2.3). N.B. The cluster of samples taken in ICES rectangle 37F7 represent the small-scale study undertaken by the Senckenburg Institute.
10.2.2. Sample treatment

Samples were washed through a 5mm and 2mm sieve (internal mesh size) and epibenthic invertebrates and fish separated from the remains. For those animals retained in the 5mm sieve the majority of species were identified, measured and weighed (blotted wet weight) onboard. Sessile animals were recorded as present or absent with a total weight given where possible. Weights were taken using a seagoing marine scale (Pols) with an accuracy of 0.01g. For those species that were either too small to be accurately weighed onboard, or too difficult to identify without a microscope, specimens were preserved in 4% buffered formaldehyde and returned to the laboratory. Species identification was based on Haywood & Ryland (1990), a number of specialised identification keys, and a digital identification key (SID) developed under EC FAIR project CT 95-0817 (see Appendix 3 in Annex 1: Methods Manual). Specimens that individual partners had found difficult to identify were examined at a workshop held six months after the surveys at the Senckenburg Institute, Germany. All names were standardised to the nomenclature of Howson & Picton (1999) and where more recent changes in nomenclature have occurred, or new species found, a record was made. All specimens in the 5mm-sieve fraction were identified to the lowest taxonomic level. Demersal fish caught in the 2m-beam trawl samples are not considered further in this report.

10.2.3. Defining “Standard Samples”

Despite fairly rigid protocols being laid down for each survey, the trawl samples contained were not fully standardized. Trawls were expected to be over 5min, because the actual trawl duration was taken as the time between the trawl starting to tow on the seafloor and the time when the trawl had lifted off the seafloor (this could be several minutes after the 5min timed tow). However, some trawls were greater than 2min over the standardised tow time. Maximum tow duration in the database was 9min. For some reason three tow were less than 5min duration, with the minimum duration recorded being 3min. Average tow duration of all tows of 5min duration and less than 9min duration was 5.41min. Furthermore, although a set trawl speed was defined, the distance trawled within the stipulated time showed substantial variation that could be explained by both variable trawl duration and speed. Because of the sensitivity of diversity metrics to variation in sampling effort, it was necessary to define the “standard sample” so that in examination of residual variance in our diversity analyses we could determine whether significant outliers were non-standard tows or not. With respect to diversity indices, the area sampled is the critical aspect, thus ultimately our objective was to standardise the trawl samples with respect to area swept.

As a first step, the area swept by trawl samples of between 4.5min and 7.5min were examined for all samples where a Scanmar© had been used (allowing for accurate calculation of trawl duration) and the upper and lower 5% extreme cut-off points identified (Table 10.2.3.1). The full database was then interrogated to extract all MAFCONS trawls falling between the upper and lower 5% swept area cut-off points and those that had not been included in the first step added back into this dataset. This extraction then included data for 273 2metre beam trawl samples (Table 10.2.3.2). Once again the upper and lower 5% cut-off points were identified and trawl samples with swept areas either larger or smaller than these cut-off points were excluded to leave the final selection of “standardised samples” (Table 10.2.3.3). This standardization process resulted in approximately 12% of the MAFCONS 2metre beam trawl tows being identified as non-standard samples (Figure 10.2.1.1).

<table>
<thead>
<tr>
<th>Statistic</th>
<th>MAFCONS 2m Beam trawl (m²)</th>
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<tbody>
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</tbody>
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<table>
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<tr>
<th>Statistic</th>
<th>MAFCONS 2m Beam trawl (m²)</th>
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</thead>
<tbody>
<tr>
<td>Number trawls</td>
<td>273</td>
</tr>
<tr>
<td>Mean</td>
<td>518.3796</td>
</tr>
<tr>
<td>Standard Deviation</td>
<td>143.0754</td>
</tr>
<tr>
<td>Lower 5% range point</td>
<td>314.361</td>
</tr>
<tr>
<td>Upper 5% range point</td>
<td>777.802</td>
</tr>
</tbody>
</table>

Table 10.2.3.2. Trawl swept-area statistics for all MAFCONS trawl samples with swept-areas falling between the lower and upper 95% cut-off points indicated in Table 10.2.3.1.

<table>
<thead>
<tr>
<th>Statistic</th>
<th>MAFCONS 2m Beam trawl (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number trawls</td>
<td>247</td>
</tr>
<tr>
<td>Mean</td>
<td>512.702</td>
</tr>
<tr>
<td>Standard Deviation</td>
<td>114.2544</td>
</tr>
<tr>
<td>Lower 5% range point</td>
<td>341.901</td>
</tr>
<tr>
<td>Upper 5% range point</td>
<td>706.053</td>
</tr>
</tbody>
</table>

Table 10.2.3.3. Trawl swept-area statistics for all “standard” MAFCONS 2metre beam trawl samples (excludes trawl samples outside the lower and upper 95% cut-off points indicated in Table 10.2.3.2.).

### 10.2.4. Catchability of the gear

Catchability of the gear affects interpretation of all analyses because it has a direct effect on both the number of species caught, and the number and biomass of individuals caught of each species. Ideally all catch data should be raised to account for catchability. However, in order to calculate catchability it is necessary to compare abundances reported by the survey gear with a reliable independent estimate of the total abundances of the species caught. There are no independent estimates of the abundance of any epifauna species for the North Sea currently available (other than some estimates for a small number of commercial shellfish stocks - see references in Reiss et al., 2006). Previous studies have compared either: the catch from the 2metre beam trawl with other samplers, such as the 3 metre beam trawl and the anchor dredge, or the catchability of the 2metre beam trawl as a function of the total catch of a number of beam trawls towed directly after each other (Reiss et al., 2006). Clearly these results do not give an absolute catchability value, and those species not sampled by any of the gears examined will not be covered at all, but they do provide interesting results in terms of the magnitude of underestimation encountered and how this varies between different taxa and different habitats. Reiss et al. (2006) calculated catching efficiency for all taxa combined and the individual invertebrate taxa that had at least 10 individuals in the first trawl, by comparing the values for the first of three beam trawls towed directly behind each other.
with the total values for all three combined. In this study the potential to apply catchabilities determined by Reiss et al. (2006) to the MAFCONS 2metre beam trawl dataset was explored.

10.2.5. **Distribution of abundance and biomass**

For each station, total abundance \((N)\) (not including colonial species) and total biomass \((B)\) (including all species except a small number of encrusting species that could not be weighed) were standardised to densities per m\(^2\) by dividing the biota totals by the station specific swept area. Swept area was itself calculated by multiplying the total track fished by the width of the beam trawl (two metres). Univariate indices of total abundance and total biomass were calculated for each station as point estimates for each year. Both years were subsequently combined and mean density \((N\text{ per m}^2)\) and biomass calculated for each ICES rectangle using all tows taken in a particular rectangle. Distributions of the 12 dominant species based on total abundance across the survey area (none-colonial species only), and the 12 dominant species based on total biomass across the survey area (including colonial species) were plotted for each year.

10.2.6. **Distribution of communities based on relative abundance of species (community composition)**

In order to enable full analysis where only presence/absence data were available, the fauna were subdivided into two groups – all epifauna (including colonial species – presence/absence analysis) and non-colonial species only (where species abundance \((N\text{ m}^{-2})\) for each station was used as the basic input data). Initially, the Bray-Curtis similarity in species composition between stations was explored separately for each of the two surveys (2003 & 2004). Subsequently, a Bray-Curtis similarity matrix comparing the similarity between the epifauna community species composition present in all pairs of ICES rectangle, was constructed for the combined surveys after first pooling the entire sample data collected for each ICES rectangle. The Bray-Curtis similarity matrices were then subjected to hierarchical group-average clustering to identify the groups of stations within years and ICES rectangles overall with similar species compositions. Species characteristic of these individual community clusters were extracted using the SIMPER routine in PRIMER. This examines the percentage contribution of each species to the similarity within the characteristic community group and between different groups. The term ‘characteristic community’ is used here to depict a group of stations with similar epibenthic species composition and does not imply any particular ecological interactions. All abundance data were root-root transformed to down-weight the effect of the most abundant species on the Bray-Curtis similarity indices. All analyses were performed using the **PRIMER**© software (Clarke & Warwick 2001).

10.2.7. **Distribution of species diversity**

Species diversity conceptually consists of two different aspects of species relative abundance; the actual number of species included in any particular sample, and the evenness of the distribution of individuals between the species encountered. Here we use three different metrics each differing in the extent to which they are influenced by one or other of these two aspects of species diversity (Southwood, 1978): Hill’s \(N_0\) (the total number of species, or species richness); Hill’s \(N_1\) (an index of diversity influenced by species richness defined as \(\exp(H')\), where \(H'\) is the Shannon-Wiener index
of diversity); and Hill’s N₂ (an index of diversity influenced by dominance defined as 1/D, where D is Simpson’s index of diversity). Hill’s N₁ is computed as:

\[ N_1 = e^{-\sum_{s=1}^{S} p_s \cdot \ln(p_s)} \]

and Hill’s N₂ is computed as:

\[ N_2 = \frac{1}{\sum_{s=1}^{S} p_s^2} \]

where \( p_s \) is the proportion of the total number of individuals contained in the sample in question contributed by each of the S species recorded in the sample (Magurran, 1988). \( N_1 \) is more sensitive to the number of species recorded in the sample, where as \( N_2 \) is more sensitive to the evenness of the distribution of individuals between species. Species richness (Hill’s N₀) was broken down to all species (including presence/absence data) and non-colonial species, whilst Hill’s N₁ and N₂ were calculated using only the non-colonial species data, as they require the individual species abundance values. All diversity metrics were determined using the PRIMER© software package (Clarke & Warwick 2001).

### 10.2.8. Assessing the level of sample aggregation required

Unlike the fish assemblage, for which the full 3rd quarter ICES IBTS data set covering a seven year period could be accessed, the number of epibenthic invertebrate samples available for analysis was extremely limited. Analysis of the fish data suggested that at a search radius exceeding 50km, estimates of \( \alpha \) diversity started to be confounded by the inclusion of elements of \( \beta \) diversity. Because of their more sedentary nature compared with fish, it was thought that the inclusion of \( \beta \) diversity into estimates of epibenthic \( \alpha \) diversity would occur at considerably range than this. Thus, the data for formal evaluation of the levels of sample aggregation required to properly assess epibenthic species richness and diversity were simply not available for the MAFCONS study alone. This would require considerably more data than was available to the MAFCONS study alone. Incorporation of the datasets collected as part of the earlier Biodiversity projects would certainly help in this respect, and such analyses may be possible in the future. However, considering the data requirements necessary to assess adequate sampling effort for the fish assemblage, we feel that this would still fall short of what was really necessary. Proper assessment of epibenthic invertebrate assemblage still requires the collection of additional data.

For the purposes of this study therefore, we simply aggregated all the epibenthic invertebrate samples available from each of the two years sampling combined and calculated all our statistics for each ICES rectangle. The total area sampled in each rectangle was determined and the effect of sampling effort on all statistic values was assessed. Where significant effects were observed, the values calculated for each ICES rectangle for the statistic in question could then be corrected for variation in sampling effort.

### 10.2.9. Secondary production

All productivity analysis was carried on density data (N.m⁻² and kg.m⁻²). As secondary production from the MAFCONS surveys is based on data only collected at one time of year, it was not possible to use any of the empirical models that also take annual variation in biomass and temperature into
account. Jennings et al. (2001) published an empirical relationship between P:B and individual weight but this did not take into account the additional variability associated with temperature and as the MAFCONS project is interested in spatial patterns at the scale of the North Sea, where variation in bottom temperature is considerable, it was considered imperative that temperature be taken into account.

10.2.9.1.  Edgar’s empirical model

Edgar’s (1990a) empirical model for epifauna, given by:

\[
\log P = -1.99 + (0.78 \log B) + (0.68 \log T)
\]

is based on the relationship between daily production, mean individual body mass and water temperature, where \( P \) is the daily production (\( \mu g \text{day}^{-1} \)), \( B \) is the mean individual ash-free dry mass (\( \mu g \)) and \( T \) is the bottom water temperature (ºC). The model was developed using a dataset of actual data for all of these parameters from studies of 41 individual species. On examining this relationship, Edgar found that models for mollusca and crustacea separated from other infauna and other epifauna (epifauna equation given above). Thus all the taxa in the epifaunal databases were assigned to any of these four groups before the empirical relationships for each one was applied. For the epifaunal dataset, the data were per species so it was possible to assign these to either epifauna or infauna directly based on knowledge of the living habit of the specific species. If an animal is both epifaunal and infaunal, it was assigned to the living habit for which it was known to spend over 50% of its time (see Appendix 1).

10.2.9.2.  Applying Edgar’s model to species with size structured data

For the majority of species sampled it was possible to individually weigh and measure all individuals. Based on this, a length frequency was constructed for each species in each sample and length: weight relationships determined and used to calculate mean individual weight per size class (see Appendix 2). Mean individual wet weight in grams was then converted to ash free dry weight (AFDM) in micrograms (Brey, 2002 - see below). Daily production per species was then calculated using mean individual weight and water temperatures recorded on the environmental data sheets at each station. Total daily production per species was calculated by multiplying daily production per mean weight class by the total number of individuals in that weight class and then summing across all size classes within a sample. In some instances size structure data were missing and under these circumstance a mean body mass was assumed, derived from the total sample weight and sampled number of the species in question.

10.2.9.3.  Applying Edgar’s model to species without size structured data but with abundance and biomass

For a number of species no individual length and weight data were available, but total abundance and total biomass were and these were used to calculate an individual mean weight. Although this is not as accurate as using individual weights per size category, it is more accurate than using published P:B ratios which only tend to be available for very low taxonomic resolution groups (e.g. Class or Phyla). For each sample, total biomass per species was converted to ash free dry mass (AFDM) using published conversion factors (Brey, 2002 - see below) and the mean individual weight per species calculated using the total number of individuals and total biomass (AFDM).
Daily production was then calculated using mean individual weight and water temperatures taken from the environmental data recorded at each station. Total daily production per species was calculated by multiplying daily production per mean weight class by the total number of individuals.

10.2.9.4. Applying Edgar’s model to species with only biomass data

For Edgar’s model either size structured data or at least the total number of individuals and total ash free dry mass (biomass) are required to calculate the mean individual weight required by the empirical relationship. For a number of taxa in the epifaunal database there were no biomass data as the animal encountered was encrusting and thus it could not be weighed. In these cases no production could be calculated. More commonly however, biomass data were available but abundance data were not. This occurred either because animals were colonial (and thus it was not possible to count the number of individuals), or where individual animals were fragmented. In these cases it was not possible to account for production directly by applying Edgar’s model. However, where biomass data were available it was still possible to assign total production using P/B ratios. A P/B ratio was assigned to the taxon group following the steps described below and then biomass multiplied by the ratio to give total daily production.

Three different steps were followed to assign P/B ratios to species with only biomass data. Firstly, where a P/B ratio was available for that species based on survey level data at the level of the Phyla this was used. Secondly, where no P/B ratios were available from the survey, but were available in the literature these were assigned. Finally, where no P/B ratios were available for a group (e.g. Bryozoa), the P/B ratio provided by Brey (2002) of 0.012 for miscellaneous benthic invertebrates was applied.

10.2.9.5. Converting wet mass to ash free dry mass

Using Edgar’s method, all wet mass (WM) biomass values need to be converted to ash free dry mass (AFDM). Brey (2002) gives a table of WM>AFDM conversion factors for invertebrates at the level of taxonomic resolution for which there are sufficient data to assign a value. All conversion factors are based on calculations of the difference between wet mass and ash free dry mass for a number of examples for each group (a full reference list can be obtained from the author). Each species in the epifaunal database was assigned to a corresponding Brey group, but where no corresponding link to a Brey group was available; a number of steps were followed. If no alternative source of conversion factor was available, but it was agreed that a taxon resembled a group with a Brey conversion factor, based on its behaviour in the ashing and drying procedure, this alternative group’s conversion factor was used. For ‘Other organic matter’, where fragments of biomass were found in a sample but it was not possible to assign them to any taxonomic group, the WM>AFDM conversion was a mean of the Mollusca, Echinodermata, Annelida and Crustacea values (see Appendix 1 for assigned Brey groups).

10.2.9.6. Total daily community production

Once total daily production had been calculated for each species within a sample following the methods described above, total community production was calculated by summing across all species within a sample.
10.3. Results

10.3.1. Catchability

The findings of Reiss et al. (2006) suggest high variability in catching efficiency of a standard 2 metre beam trawl between species and even within species between different areas. Even between two species of the same genera, *Crangon allmanni* and *Crangon crangon*, there was over ten percent difference in catching efficiency at the Box A study site (Table 10.3.1.1.). Between 70% and 76% of the total species caught were caught by the first trawl in Box A and between 54% and 84% in Box N. Box N had a more coarse sandy substratum in comparison to the muddy sand substrate found in Box A. It is suggested that the lower catching efficiency of some of the species described for Box N was due to the lower penetration depth of the gear in coarser sediments (Reiss et al., 2006).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Catching efficiency in Box A</th>
<th>Catching efficiency in Box N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Abundance (%)</td>
<td>Biomass (%)</td>
</tr>
<tr>
<td><em>Corystes cassivelaunus</em></td>
<td>64†</td>
<td>55 ± 5</td>
</tr>
<tr>
<td><em>Liocarcinus holsatus</em></td>
<td>18 ± 5</td>
<td>20 ± 10</td>
</tr>
<tr>
<td><em>Pagurus bernhardus</em></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Crangon allmanni</em></td>
<td>56 ± 4</td>
<td>58 ± 4</td>
</tr>
<tr>
<td><em>Crangon crangon</em></td>
<td>43 ± 6</td>
<td>40 ± 6</td>
</tr>
<tr>
<td><em>Processa</em> spp.</td>
<td>72‡ ± 8</td>
<td>83 ± 24</td>
</tr>
<tr>
<td><em>Asterias rubens</em></td>
<td>42 ± 7</td>
<td>46 ± 8</td>
</tr>
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<td><em>Astropecten irregularis</em></td>
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</tr>
<tr>
<td><em>Nucula nitidosa</em></td>
<td>19§ ± 19</td>
<td>11 ± 16</td>
</tr>
<tr>
<td><em>Branchiostoma lanceolata</em></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>All taxa</td>
<td>44 ± 5</td>
<td>32 ± 8</td>
</tr>
</tbody>
</table>

*Indicates significant differences between sites (see Reiss et al., 2006).
†Based on one replicate only; ‡Based on two replicates only.

Table 10.3.1.1. Mean catching efficiency (± s.d.) of the 2-m beam trawl at the two study sites (Box A and Box N) as taken from Reiss et al. (2006).

On examination of the MAFCONS 2metre beam trawl dataset it was found that the ten species covered by Reiss et al. (2006) contributed on average 42% (mean ± 31% s.d.) of the total abundance and 34% (mean ± 33% s.d.) of the total biomass found at each station. When this was expanded to all species within the genera covered by Reiss et al. (2006), the mean contribution to total abundance only increased to 45% and the mean contribution to total biomass to 37%. Although the contribution of these 10 species to the total community abundance and biomass was relatively high on average, variation, in terms of both abundance and biomass, around these means was considerable. Furthermore, when considering each individual sample, total abundance or biomass attributable to these 10 species ranged from 0% to 98.9% and 0-100% respectively (Figure 10.3.1.1). In order to assign catching efficiencies to the entire MAFCONS species list based on the limited data available from Reiss et al. (2006), it would be necessary to make a number of major assumptions. Even if any species whose genus is represented by one or more of the 10 species covered, was assigned the raising factor of the corresponding species, most of the species in the dataset would still need to be assigned catchabilities with little or no information. Given the high variability in catching efficiencies between species within the same taxonomic group (e.g. decapods in Table 10.3.1.1.) it
would be very difficult to group unrepresented species based on ‘like’ species covered in Table 10.3.1.1, particularly as the findings of Reiss et al. (2006) suggest that catchability varies based on a number of characteristics of the species including size, living position, motility and behaviour. If, however, all species whose genus was not represented were assigned a raising factor based on a mean catching efficiency, whilst those represented in Reiss et al. (2006) were assigned their species-specific raising factors, the relative contributions of species to the community (which drives species diversity and community composition analyses), would be biased by the variation in contribution of the represented species in the samples taken. However, simply raising the entire MAFCONS dataset by the catching efficiency of the entire catch (e.g. ‘All taxa’ in Table 10.3.1.1.) has its own limitations. It would provide an interesting comparison in terms of the overall difference in abundance and biomass, but would not reflect any of the changes in species diversity and community composition that result from the real variation in catchability of the different species. Because of these limitations, the effects of catchability in the 2m beam trawl on estimates of epibenthic invertebrate abundance/biomass, diversity and community composition could not be examined with the data available to the MAFCON project. Further catchability studies for 2 metre beam trawls, following the design of Reiss et al. (2006), are required so that this important issue can be properly examined in the future.

Figure 10.3.1.1. Box whisker plots of the percentage contribution to total station abundance and biomass by the species (and genera of those species) for which catching efficiency was given in Reiss et al. (2006). The grey box represents
75% of the data; the black line within the box represents the median of the data and the whiskers outside of the box, the range of the data.

10.3.2. **Abundance and Distribution**

The majority of epibenthic taxa were relatively scarce. In total, 209,545 individual epibenthic organisms were sampled, not including the colonial taxa, and altogether 621,549g of material was processed. These epibenthic animals belonged to a total of 591 individual taxonomic classifications (species or higher level) identified over the course of the project. Of this large number of different taxa, 12 key species that dominated the epibenthic fauna on the basis of numerical abundance made up 58% of the total number of individual animals sampled, while the 12 key species that dominated the epibenthos on the basis of biomass constituted 43% of all the material processed. Spatial variation in the mean density of these key epibenthic taxa are shown in Figure 10.3.2.1 (based on numerical abundance) and Figure 10.3.2.2 (based on biomass). Variation in 2m beam trawl sampling effort between ICES rectangle had no significant impact on these abundance or biomass estimates. Each species had quite distinctive distributions, however density was calculated, with clear regions where densities were high and, in most instances, large areas where they were either scarce or absent. At this stage only preliminary examination of the environmental factors influencing the distributions of different epibenthic taxa have been carried out. However, it is quite clear that water depth, bottom water temperature, bottom water salinity, and mean sediment particle size all play a role in influencing the spatial distributions of these epibenthic invertebrates. Some of these factors were more important than other, seabed water temperature and water depth compared with sediment mean particle size for example, and it is also apparent that each species responded most to different environmental variables (Figures 10.3.2.3 to 10.3.2.10).
Figure 10.3.2.1. Spatial variation in the density (nos.m$^{-2}$) of the 12 most abundant epibenthic invertebrates based on abundance. Ast rub: Asterias rubens; Ast irr: Astropecten irregularis; Cra all: Crangon allmanni; Ech acu: Echinus acutus; Ech ele: Echinus elegans; Hya tub: Hyalinoecia tubicola; Lio hol: Liocarcinus holsatus; Oph alb: Ophiura albida; Oph oph: Ophiura ophiura; Pan mon: Pandalus montagui; Pomato: Pomatoschistus; Str dro: Strongylocentrotus droebachiensis.
Figure 10.3.2.2. Spatial variation in the density (g.m$^{-2}$) of the 12 most abundant epibenthic invertebrates based on biomass. Alc dig: Alcyonium digitatum; Ast rub: Asterias rubens; Ast irr: Astropecten irregularis; Bol tue: Bolocera tuediae; Buc und: Buccinum undatum; Ech acu: Echinus acutus; Flu fol: Flustra foliacea; Lio hol: Liocarcinus holsatus; Lui sar: Luidia sarsi; Nep ant: Neptunea antique; Oph alb: Ophiura albida, Pag ber: Pagurus bernhardus.
Figure 10.3.2.3. Effect of water depth on the density of the 12 key epibenthic invertebrates based on their numerical abundance (n.m\(^{-2}\)). Data are fitted by a Lowess curve.
Figure 10.3.2.4. Effect of bottom water temperature on the density of the 12 key epibenthic invertebrates based on their numerical abundance (n.m\(^{-2}\)). Data are fitted by a Lowess curve.
Figure 10.3.2.5. Effect of bottom water salinity on the density of the 12 key epibenthic invertebrates based on their numerical abundance (n.m⁻²). Data are fitted by a Lowess curve.
Figure 10.3.2.6. Effect of sediment mean particle size on the density of the 12 key epibenthic invertebrates based on their numerical abundance (n.m⁻²). Data are fitted by a Lowess curve.
Figure 10.3.2.7. Effect of water depth on the density of the 12 key epibenthic invertebrates based on biomass (g.m⁻²). Data are fitted by a Lowess curve.
Figure 10.3.2.8. Effect of bottom water temperature on the density of the 12 key epibenthic invertebrates based on their biomass (g.m⁻²). Data are fitted by a Lowess curve.
Figure 10.3.2.9. Effect of bottom water salinity on the density of the 12 key epibenthic invertebrates based on their biomass (g.m$^{-2}$). Data are fitted by a Lowess curve.
Figure 10.3.2.10. Effect of sediment mean particle size on the density of the 12 key epibenthic invertebrates based on their biomass (g.m\textsuperscript{-2}). Data are fitted by a Lowess curve.

### 10.3.3. Community Species Composition

Group average cluster analysis of Bray-Curtis similarity matrices calculated for both the mean numerical density and mean biomass density of epibenthic invertebrates in each ICE rectangle produced the dendograms shown in Figure 10.3.3.1. Essentially the species composition of the epibenthic invertebrate community was highly variable and similarity between ICES rectangles was relatively low. Nevertheless, two main clusters were apparent for both the numerical based and biomass based density data. For convenience, all outlier rectangles were grouped together into a third small cluster. Mapping of the three clusters revealed highly contagious cluster distributions with similar spatial patterns for both the numerical and biomass density data (Figure 10.3.3.2). Furthermore, these community composition cluster maps for the epibenthic assemblage bore a marked resemblance to similar maps produced for the groundfish assemblage (Chapter 9).
Figure 10.3.3.1. Group average cluster dendograms of epibenthic invertebrate density data based on mean abundance (n.m⁻²) and biomass (g.m⁻²) densities in each ICES rectangle. Colour coding links to Figure 10.3.3.2.
Given the apparent effects of environmental conditions in determining the distributions of individual epibenthic species, the influence of water depth, seabed water temperature and salinity, and sediment mean particle size on whole epibenthic community composition was examined. The distributions of each environmental variable for ICES rectangles assigned to each of the three epibenthic invertebrate communities are indicated in the box plots in Figure 10.3.3.3 for clusters based on numerical abundance data and Figure 10.3.3.4 for cluster based on biomass data. Water temperature and seabed water temperature and salinity varied significantly (ANOVA P<0.001 in each case) between rectangles assigned to the red and blue epibenthos community clusters (the southeastern and northwestern North Sea blocks), with identical results for both the numerical and abundance based clusters. The same three environmental parameters varied significantly between rectangles assigned to the outlier cluster (green) and red cluster rectangles (southeastern North Sea) (ANOVA P<0.01 in all cases), but no significant difference between these environmental variable was detected between green (outlier) and blue (northwestern North Sea) cluster rectangles. No significant difference in mean sediment particle size was observed between rectangle assigned to the three community type clusters when the clustering was based on the numerical density data. However, when clustering was based on the biomass density data, rectangles in the outlier cluster (green) differed significantly from rectangles assigned to each of the other two community type clusters. It would appear that mean sediment particle size was important in influencing the species composition of the epibenthic community in the outlier rectangles.
Figure 10.3.3.3. Box plots showing the range in water depth, bottom temperature, bottom salinity and mean sediment particle size associated with each epibenthic community type cluster based on numerical abundance identified in Figures 10.3.3.1 and 10.3.3.2.
Figure 10.3.3.4. Box plots showing the range in water depth, bottom temperature, bottom salinity and mean sediment particle size associated with each epibenthic community type cluster based on biomass identified in Figures 10.3.3.1 and 10.3.3.2.

10.3.4. Community Species Richness and Species Diversity

Epibenthic species richness and species diversity varied markedly between ICES rectangles. There was however a tendency both richness and diversity to be higher in the northwestern North Sea than in the southeastern North Sea (Figure 10.3.4.1). Plots of species richness and Hill’s $N_1$ and $N_2$, based on either numerical abundance or biomass, against both latitude and longitude confirmed the geographic trends across the North Sea (Figures 10.3.4.2 to 10.3.4.5). Species diversity (Hill’s $N_1$...
and N2) of the epibenthic community in ICES rectangles assigned to the blue community type cluster (northwestern North Sea) was significantly higher than in rectangles assigned to the red cluster (southeastern North Sea) for diversity metrics based on both abundance and biomass (ANOVA P<0.01 in all cases, Figures 10.3.4.6 and 10.3.4.7). Species richness in the blue cluster rectangles (northwestern North Sea) was significantly higher than in rectangles assigned to each of the other two clusters (ANOVA P<0.001 in both cases, Figures 10.3.4.6 and 10.3.4.7). The effects of water depth, bottom water temperature and salinity, and mean sediment particle size are shown in Figures 10.3.4.8 to 10.3.4.11 for metrics based on numerical abundance and in Figures 10.3.4.12 to 10.3.4.15 for metrics based on biomass. Effects of water depth and bottom water temperature and salinity are suggested, but in each case the relationships are curvilinear or unimodal. Mean sediment particle size had no appreciable effect on epibenthic species richness of diversity.

Figure 10.3.4.1. Spatial variation in species richness (S) and Hills N1 and N2 calculated on mean sample abundance and biomass data in each ICES statistical rectangle.
Figure 10.3.4.2. Variation in species richness, $N_1$, $N_2$, Log of species richness, log of $N_1$ and Log of $N_2$ based on numerical density data with latitude. Lowess smooth fitted to data.

Figure 10.3.4.3. Variation in species richness, $N_1$, $N_2$, Log of species richness, log of $N_1$ and Log of $N_2$ based on numerical density data with longitude. Lowess smooth fitted to data.
Figure 10.3.4.4. Variation in species richness, $N_1$, $N_2$, Log of species richness, log of $N_1$ and Log of $N_2$ based on biomass density data with latitude. Lowess smooth fitted to data.

Figure 10.3.4.5. Variation in species richness, $N_1$, $N_2$, Log of species richness, log of $N_1$ and Log of $N_2$ based on biomass density data with longitude. Lowess smooth fitted to data.
Figure 10.3.4.6. Box plots showing the range in species richness, $N_1$, $N_2$, Log of species richness, log of $N_1$ and Log of $N_2$ associated with each epibenthic community type cluster based on numerical abundance identified in Figures 10.3.3.1 and 10.3.3.2.

Figure 10.3.4.7. Box plots showing the range in species richness, $N_1$, $N_2$, Log of species richness, log of $N_1$ and Log of $N_2$ associated with each epibenthic community type cluster based on biomass identified in Figures 10.3.3.1 and 10.3.3.2.
Figure 10.4.3.8. Relationships between species richness, $N_1$, $N_2$, Log of species richness, log of $N_1$ and Log of $N_2$ based on numerical abundance and water depth.

Figure 10.4.3.9. Relationships between species richness, $N_1$, $N_2$, Log of species richness, log of $N_1$ and Log of $N_2$ based on numerical abundance and bottom water temperature.
Figure 10.4.3.10. Relationships between species richness, $N_1$, $N_2$, Log of species richness, log of $N_1$ and Log of $N_2$ based on numerical abundance and bottom water salinity.

Figure 10.4.3.11. Relationships between species richness, $N_1$, $N_2$, Log of species richness, log of $N_1$ and Log of $N_2$ based on numerical abundance and sediment mean particle size.
Figure 10.4.3.12. Relationships between species richness, $N_1$, $N_2$, Log of species richness, log of $N_1$ and Log of $N_2$ based on biomass and water depth.

Figure 10.4.3.13. Relationships between species richness, $N_1$, $N_2$, Log of species richness, log of $N_1$ and Log of $N_2$ based on biomass and bottom water temperature.
Figure 10.4.3.14. Relationships between species richness, $N_1$, $N_2$, Log of species richness, log of $N_1$ and Log of $N_2$ based on biomass and bottom water salinity.

Figure 10.4.3.15. Relationships between species richness, $N_1$, $N_2$, Log of species richness, log of $N_1$ and Log of $N_2$ based on biomass and sediment mean particle size.
Species richness estimates for each ICES rectangle were significantly affected by variation in sampling effort with the traditional species-area log-log power function providing the best fit to the data (Figure 10.4.3.16). When all the data were included a major outlier with considerable leverage had a large influence on the fitted relationship (Figure 10.4.3.16A). This was the rectangle that was intensively sampled by the German partner (Figure 10.2.1.1). This rectangle stood out as having relatively high species richness, surrounded by rectangle with among the lowest species richness recorded (Figure 10.3.4.1). It would seem that this rectangle was over-sampled with respect to species richness, such that the count of species became “saturated” (see Chapters 7 and 9). Continued sampling therefore added new species at a rate much lower than predicted by the species area power function. Exclusion of this rectangle from the whole North Sea analysis resulted in a power function that provided a better fit to the majority of the data (Figure 10.4.3.16B). Both Hill’s $N_1$ and $N_2$, based on numerical abundance or biomass, log-transformed or not, tended also to be significantly correlated with variation in the area sampled in each ICES rectangle, but in these cases the amount of variance explained by the fitted functions was considerably lower (Table 10.4.3.1). Examination of Figure 10.4.3.1 shows that Hill’s $N_1$ and $N_2$ values in the intensively sampled rectangle were not markedly dissimilar to values recorded in neighbouring rectangles.

![Figure 10.4.3.16. Relationships between the species richness estimates for each ICES rectangle and the area swept by the 2m beam trawl. Plot A shows the relationship calculated for all rectangles sampled. Plot B shows the same data, but excluding the rectangle intensively sampled by the German partner.](image)

<table>
<thead>
<tr>
<th>Metric</th>
<th>Intercept</th>
<th>Slope</th>
<th>P</th>
<th>$R^2$</th>
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<tbody>
<tr>
<td>Numerical $N_1$</td>
<td>-4.695</td>
<td>5.073</td>
<td>0.029</td>
<td>0.040</td>
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<td>Numerical $N_2$</td>
<td>Not Significant</td>
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<td></td>
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</tr>
<tr>
<td>Log Numerical $N_1$</td>
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<td>0.230</td>
<td>0.027</td>
<td>0.041</td>
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<tr>
<td>Log Numerical $N_2$</td>
<td>Not Significant</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass $N_1$</td>
<td>-10.994</td>
<td>6.571</td>
<td>0.000</td>
<td>0.124</td>
</tr>
<tr>
<td>Biomass $N_2$</td>
<td>-5.558</td>
<td>3.726</td>
<td>0.001</td>
<td>0.089</td>
</tr>
<tr>
<td>Log Biomass $N_1$</td>
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<td>0.325</td>
<td>0.000</td>
<td>0.110</td>
</tr>
<tr>
<td>Log Biomass $N_2$</td>
<td>-0.160</td>
<td>2.77</td>
<td>0.001</td>
<td>0.083</td>
</tr>
</tbody>
</table>

Table 10.4.3.1. Parameter values obtained from the log-log power function fits to variation in Hill’s $N_1$ and $N_2$ with variation in the area sampled in each ICES rectangle.
10.3.5. Productivity

Total epibenthic invertebrate biomass and production varied considerably across the North Sea (Figure 10.3.5.1), with no clear geographic trends (Figure 10.3.5.2, Table 10.3.5.1). Variation in biomass appeared unrelated to depth, bottom water temperature or salinity, but biomass tended to be lower in regions of mean sediment particle size of less than 200microns (Figure 10.3.5.3, Table 10.3.5.1). Because of this, productivity also tended to decrease in the muddier parts of the North Sea, but P/B ratios were also lower (Figure 10.3.5.3, Table 10.3.5.1). However, productivity was also significantly influenced by bottom water temperature (Figure 10.3.5.3, Table 10.3.5.1). This was not surprising given the fact that water temperature was one of the terms influencing secondary production, effectively resulting in higher production-biomass ratios in regions of water warmer. This was confirmed by the significant relationship between water temperature and P/B ratios (Figure 10.3.5.3, Table 10.3.5.1). Both productivity and P/B ratio were significantly correlated with water depth, but this was almost certainly due to the fact that the shallower water was also the warmest (Figure 10.3.5.3, Table 10.3.5.1). Shallow, warmer water tends to be located in the southern North Sea in the summer period, so P/B ratios were also highest in southern latitudes (Figure 10.3.5.3, Table 10.3.5.1).

Figure 10.3.5.1. Plots of the spatial distribution of total epibenthic invertebrate biomass (g.m⁻²) (B), secondary production (mg.m⁻².d⁻¹) (P), and the production/biomass ratio (P/B).
Figure 10.3.5.2. Relationships between Log biomass (B) (g.m\(^{-2}\)), Log production (P) (mg.m\(^{-2}.d^{-1}\)) and the production-biomass ratio (PB) and latitude and longitude

<table>
<thead>
<tr>
<th></th>
<th>Biomass</th>
<th>Production</th>
<th>P/B ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude</td>
<td>0.944</td>
<td>0.151</td>
<td>0.017*</td>
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<tr>
<td>Longitude</td>
<td>0.249</td>
<td>0.268</td>
<td>0.492</td>
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<tr>
<td>Water depth</td>
<td>0.228</td>
<td>0.007**</td>
<td>0.028*</td>
</tr>
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<td>Bottom water temperature</td>
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<td>0.000***</td>
<td>0.000***</td>
</tr>
<tr>
<td>Bottom water salinity</td>
<td>0.781</td>
<td>0.109</td>
<td>0.057</td>
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<tr>
<td>Sediment mean particle size</td>
<td>0.013*</td>
<td>0.001***</td>
<td>0.019*</td>
</tr>
</tbody>
</table>

Table 10.3.5.1. Correlation probabilities between Log biomass (B) (g.m\(^{-2}\)), Log production (P) (mg.m\(^{-2}.d^{-1}\)) and the production-biomass ratio (PB) and latitude, longitude, water depth (m), mean particle size, and bottom water temperature (ºC) and salinity.
Figure 10.3.5.3. Relationships between Log biomass (B) (g.m⁻²), Log production (P) (mg.m⁻².d⁻¹) and the production-biomass ratio (PB) and water depth (m), mean particle size, and bottom water temperature (°C) and salinity.

The relationships between species richness and diversity and biomass, productivity and productivity-biomass ratios were examined. Species richness was positively related with both biomass and productivity. However, such relationships are common and are invariably due to the increased probability of sampling rarer species when abundance/biomass is higher generally (Guo & Berry 1998; Gaston & Matter 2002). More interestingly though, the P/B ratio was negatively associated with species richness (R=-0.23, P<0.05). Productivity was negatively related to both
Hill’s $N_1$ and $N_2$ ($R=-0.21$, $P<0.05$ and $R=-0.22$, $P<0.05$ respectively) and the P/B ration was also negatively related to Hill’s $N_1$ ($R=0.21$, $P<0.05$). These relationships run contra to current general dogma, that increased biodiversity leads to raised productivity (Emmerson & Huxham 2002; Tilman et al 2001, 2002; Worm & Duffy 2003).

Figure 10.3.5.4. Relationships between Log biomass (B) (g.m$^{-2}$), Log production (P) (mg.m$^{-2}$.d$^{-1}$) and the species richness and diversity of the epibenthic invertebrate community.

Figures 10.3.5.5 to 10.3.5.7 show the spatial distributions in biomass, productivity and the productivity-biomass ratio respectively for colonial epibenthic organisms and five Log2 size groups of individual invertebrate animals. These data may be required for specific tests of Huston’s dynamic equilibrium model, and are not examined exhaustively here. There was an indication that the biomass and productivity of larger epibenthic invertebrates was lower in the southern North Sea.
Figure 10.3.5.5. Plots of the spatial distribution of total epibenthic invertebrate biomass (g.m⁻²) assigned to six different types or weight ranges of organism. Biomass Only: invertebrates that could not be individually counted or weighed; LTE-1: individual invertebrates of Log₂ body mass less than or equal to -1; GT-1 to LTE2: individual invertebrates with Log₂ body mass greater than -1 and less than or equal to 2; GT2 to LTE5: individual invertebrates with Log₂ body mass greater than 2 and less than or equal to 5; GT5 to LTE8: individual invertebrates with Log₂ body mass greater than 5 and less than or equal to 5; GT8: individual invertebrates with Log₂ body mass greater than 8.
Figure 10.3.5.6. Plots of the spatial distribution of total epibenthic invertebrate production (mg.m\(^{-2}\).d\(^{-1}\)) assigned to six different types or weight ranges of organism. Biomass Only: invertebrates that could not be individually counted or weighed; LTE-1: individual invertebrates of Log\(_2\) body mass less than or equal to -1; GT-1 to LTE2: individual invertebrates with Log\(_2\) body mass greater than -1 and less than or equal to 2; GT2 to LTE5: individual invertebrates with Log\(_2\) body mass greater than 2 and less than or equal to 5; GT5 to LTE8: individual invertebrates with Log\(_2\) body mass greater than 5 and less than or equal to 8; GT8: individual invertebrates with Log\(_2\) body mass greater than 8.
Figure 10.3.5.7. Plots of the spatial distribution of total epibenthic invertebrate production/biomass ratio assigned to six different types or weight ranges of organism. Biomass Only: invertebrates that could not be individually counted or weighed; LTE-1: individual invertebrates of Log₂ body mass less than or equal to -1; GT-1 to LTE2: individual invertebrates with Log₂ body mass greater than -1 and less than or equal to 2; GT2 to LTE5: individual invertebrates with Log₂ body mass greater than 2 and less than or equal to 5; GT5 to LTE8: individual invertebrates with Log₂ body mass greater than 5 and less than or equal to 5; GT8: individual invertebrates with Log₂ body mass greater than 8.
10.4. References


