Species Composition, Diversity, Biomass and Production of the Benthic Invertebrate Community of the North Sea.

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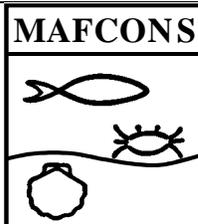
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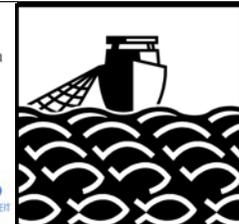
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SPECIES COMPOSITION, DIVERSITY, BIOMASS AND PRODUCTION OF THE BENTHIC INVERTEBRATE COMMUNITY OF THE NORTH SEA

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SUMMARY

Sampling of the epibenthic invertebrate community was undertaken using a 2m beam trawl at stations sampled for fish by the IBTS and DBTS. Epibenthic sample data obtained using a beam trawl is subject to the same catchabilty issues that affect the sampling of fish in trawl-based groundfish surveys. However, unlike the fish, data were not available for the epibenthic community to allow estimation of catchability coefficients for all species sampled. Organisms taken in the samples were identified to species, measured and weighed. This allowed size-based approaches to be applied to the resulting abundance at size data to provide estimates of the productivity of the epibenthic community at each sampling location. The same three indices were applied to the total epibenthic species abundance data, Hill's N_0 (species richness), N_1 (exponential of Shannon-Weiner Index) and N_2 (reciprocal of Simpson's Index), as were applied to the fish survey data.

The spatial distributions of individual species tended to be relatively restricted, with different species responding differently to different environmental parameters (water depth, bottom water temperature, bottom water salinity and sediment particle size). Cluster analysis of the species composition data suggested two main epibenthic invertebrate communities; a northern and a southern community. These different communities existed in significantly different environmental conditions. Species richness and diversity was higher in the northern community than in the southern community and strong latitudinal and longitudinal trends were observed in all three indices. Unimodal relationships between species richness and diversity and water depth and bottom water temperature and salinity were indicated, but no effect of sediment particle size was observed. Species richness estimates for each ICES rectangle were significantly influenced by sampling effort. The same was true for the two diversity metrics, but the effect was much weaker.

Total epibenthic biomass varied considerably across the North Sea, but tended to be lower where sediment particle size was less than 200µm. Because of this lower biomass, overall productivity tended to be lower in the muddier habitats. P/B ratios, and hence overall productivity, was also significantly positively related to bottom water temperature, which was not surprising given that temperature is one of the terms in the models used to estimate productivity. Because of the link between water depth and water temperature, epibenthic productivity and P/B ratios were also related to depth. All three species richness and diversity indices tended to be negatively related to epibenthic P/B ratio. When different weight classes of epibenthic invertebrates were examined, considerable variation in the spatial patterns of biomass, production and P/B ratio were evident between different sized epibenthic invertebrates. The biomass and production of larger epibenthic invertebrates was least in the southern North Sea.

Infaunal invertebrates were sampled using a Van Veen grab and the community described was that consisting of organisms retained within a 1mm mesh sieve. The same models used to estimate productivity in the epibenthic community were applied to the infaunal abundance data, but for the infauna, size structuring was limited to estimates of mean individual biomass of each species retained in sieves of 4mm, 2mm and 1mm mesh size. All individuals retained in the sieves were identified to one of 73 different taxon groups.

Because taxon groups consisted of more than one species, distributions of the key taxon groups tended to be more widely dispersed than the individual epibenthic species. Nevertheless, some concentration of some taxon groups in limited regions of the North Sea was apparent. The highest overall abundance and biomass of infaunal invertebrates were observed in the southern North Sea. Cluster analysis of the taxon group composition again revealed two distinct communities occupying the northern and southern North Sea. Taxon group richness and diversity tended to be higher in the northern North Sea. Infaunal productivity tended to be highest in the southern North Sea, but with some isolated hotspots of productivity located in the northern North Sea.

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1. THE EPIBENTHIC INVERTEBRATE COMMUNITY

1.1.   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 section of the report is to present the findings of the epibenthic surveys that have been undertaken in the North Sea since the Biodiversity project as part of the SEERAD funded MF0753 and EC funded 5th framework projects "Managing Fisheries to Conserve Groundfish and Benthic Invertebrate Species Diversity" (MAFCONS). This project has extended the sampling protocol to include infaunal benthic communities (see Section 2) and to link characteristics of the benthic invertebrate communities to demersal fish diversity (Greenstreet et al 2007a) and to levels of ecological disturbance associated with the North Sea demersal fishing industry (Greenstreet et al 2007b). 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.

1.1.1.   Catchability issues

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 by Greenstreet et al

(2007a), 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. Infact 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).

1.1.2. Sampling effort issues

As discussed by Greenstreet et al (2007a), 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.

1.1.3. 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 (Cushman *et al.*, 1978; Wildish & Peer, 1981; Crisp, 1984; Morin *et al.*, 1987). None of these methods are practical when trying to quantify secondary production at the community level. During this 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. 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.

1.2.   METHODS

1.2.1. Data set

One beam trawl tow was taken at each 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 1.2.1.1). 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 Callaway et al 2007 for further details of trawling procedure).
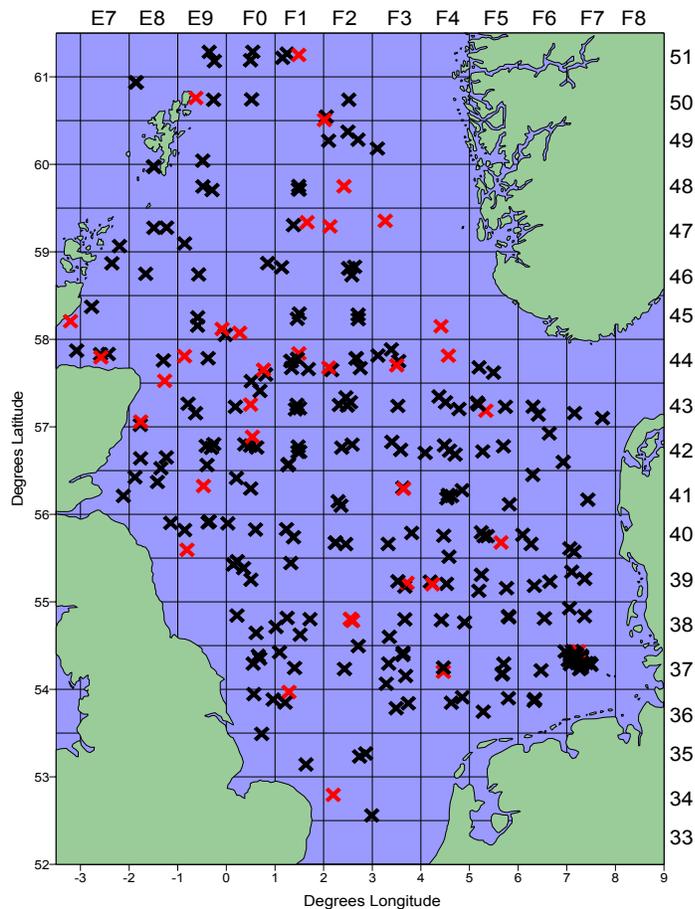
Figure 1.2.1.1. All 283 stations sampled for epifauna with a 2-metre beam trawl during the 2003 and 2004 surveys. Red symbols represent those stations that did not fit within the criteria set for tows standardised on swept area (see Section 1.2.3). N.B. The cluster of samples taken in ICES rectangle 37F7 represent the small-scale study undertaken by the Senckenburg Institute.

1.2.2. 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.

1.2.3. 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 1.2.3.1). The full database was then interrogated to extract all 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 1.2.3.2). 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 1.2.3.3). This standardization process resulted in approximately 12% of the 2metre beam trawl tows being identified as non-standard samples (Figure 1.2.1.1).

Statistic	2m Beam trawl (m^2)
Number trawls	173
Mean	551.2746
Standard Deviation	149.1461
Lower 5% range point	302.174
Upper 5% range point	798.750

Table 1.2.3.1 Trawl swept-area statistics for 2metre beam trawl samples with actual trawl distance recorded (using Scanmar) and with tow durations of between 4.5 and 7.5 minutes.

Statistic	2m Beam trawl (m^2)
Number trawls	273
Mean	518.3796
Standard Deviation	143.0754
Lower 5% range point	314.361
Upper 5% range point	777.802

Table 1.2.3.2. Trawl swept-area statistics for all trawl samples with swept-areas falling between the lower and upper 95% cut-off points indicated in Table 1.2.3.1.

Statistic	2m Beam trawl (m^2)
Number trawls	247
Mean	512.702
Standard Deviation	114.2544
Lower 5% range point	341.901
Upper 5% range point	706.053

Table 1.2.3.3. Trawl swept-area statistics for all "standard" 2metre beam trawl samples (excludes trawl samples outside the lower and upper 95% cut-off points indicated in Table 1.2.3.2.).

1.2.4. 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 2 metre 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 2metre beam trawl dataset was explored.

1.2.5. 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* 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.

1.2.6. 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*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).

1.2.7. 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 expH´, where H´ is the Shannon-Wiener index of diversity); and Hill's N_2 (an index of diversity influenced by dominance defined as 1/D, where D is Simpson's index of diversity). Hill's N_1 is computed as:

$$N_1 = e^{-\sum_{s=1}^{S} p_s * Ln(p_s)}$$

1.2.6.1.1

and Hill's N_2 is computed as:

$$N_2 = 1 \bigg/ \sum_{s=1}^{S} p_s^2$$

1.2.6.2.2

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 N_0) was broken down to all species (including presence/absence data) and non-colonial species, whilst Hill's N_1 and N_2 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).

1.2.8. 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 α diversity started to be confounded by the inclusion of elements of β diversity. Because of their more sedentary nature compared with fish, it was thought that the inclusion of β diversity into estimates of epibenthic α diversity would occur at considerably smaller 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 to this 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.

1.2.9. Secondary production

All productivity analysis was carried on density data (N.m^{-2} and kg.m^{-2}). As secondary production from these surveys was 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 this project was 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.

1.2.9.1. *Edgar's Empirical Model*

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

$$LogP = -1.99 + (0.78LogB) + (0.68LogT)$$ 1.2.9.1.1

is based on the relationship between daily production, mean individual body mass and water temperature, where *P* is the daily production (µg.day^{-1}), *B* is the mean individual ash-free dry mass (µg) 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).

1.2.9.2. *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 weight at length 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 circumstances a mean body mass was assumed, derived from the total sample weight and sampled number of the species in question.

1.2.9.3. *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.

1.2.9.4. *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 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.

1.2.9.5. *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).

1.2.9.6. *Total Daily Commmunity 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.

1.3. RESULTS

1.3.1. 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 1.3.1.1.). 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).

| Taxon | Catching efficiency in Box A | | Catching efficiency in Box N | |
	Abundance (%)	Biomass (%)	Abundance (%)	Biomass (%)
Corystes cassivelaunus	64[1]	55 ± 5	-	-
*Liocarcinus holsatus**	18 ± 5	20 ± 10	9 ± 2	9 ± 3
Pagurus bernhardus	-	-	51[2] ± 1	64 ± 8
*Crangon allmanni**	56 ± 4	58 ± 4	26 ± 8	27 ± 7

Crangon crangon	43 ± 6	40 ± 6	31 ± 7	28 ± 5
Processa spp.	72^2 ± 8	83 ± 24	-	-
Asterias rubens	42 ± 7	46 ± 8	46 ± 6	53 ± 7
Astropecten irregularis	34 ± 9	34 ± 9	35 ± 10	37 ± 12
Nucula nitidosa	19^2 ± 19	11 ± 16	-	-
Branchiostoma lanceolata	-	-	0^2 ± 0	0 ± 0
All taxa	44 ± 5	32 ± 8	36 ± 4	45 ± 9

*Indicates significant differences between sites (see Reiss *et al.*, 2006).
[1]Based on one replicate only; [2]Based on two replicates only.

Table 1.3.1.1. 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 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 1.3.1.1). In order to assign catching efficiencies to the entire 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 1.3.1.1.) it would be very difficult to group unrepresented species based on 'like' species covered in Table 1.3.1.1, 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 dataset by the catching efficiency of the entire catch (e.g. 'All taxa' in Table 1.3.1.1.) 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.
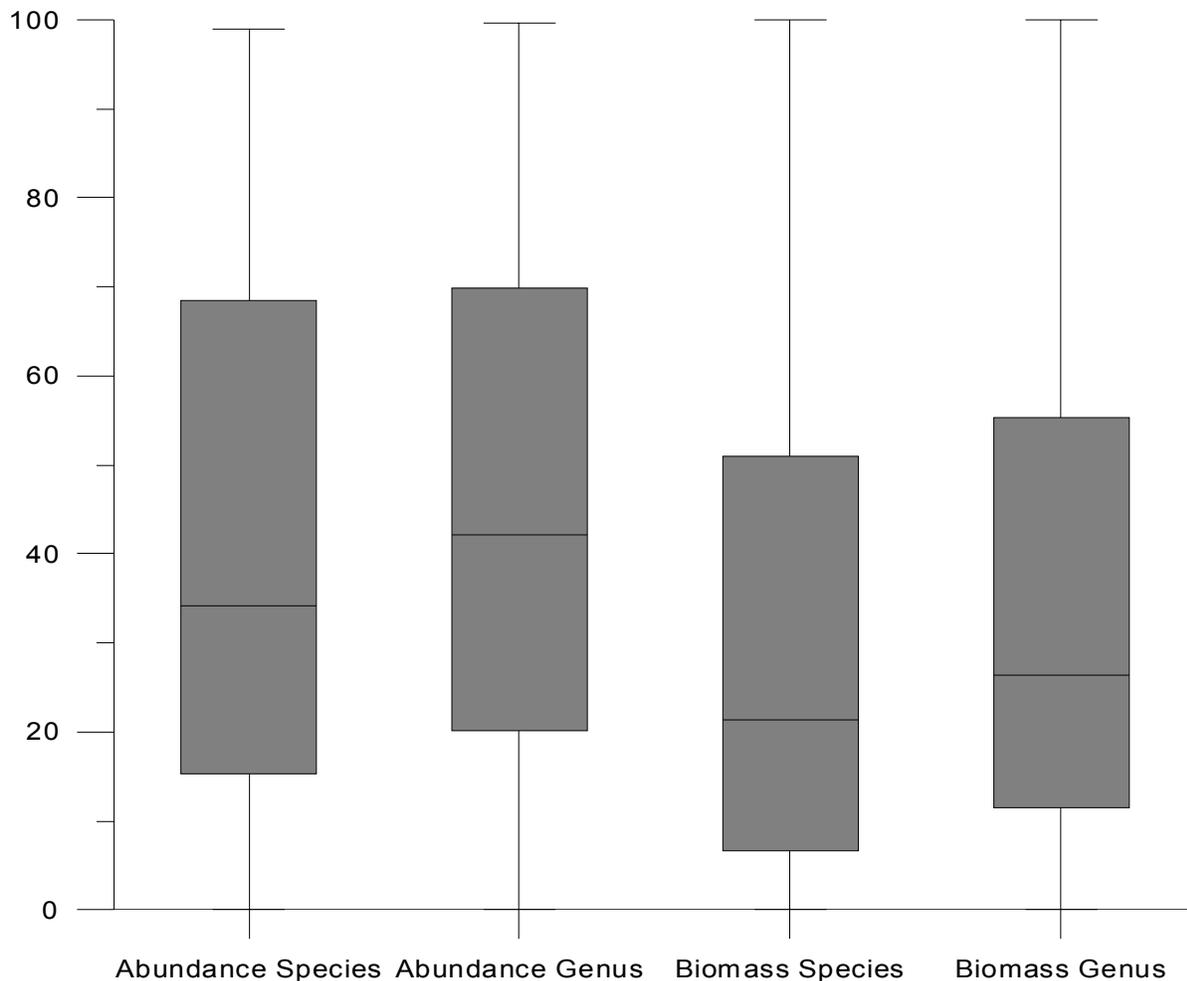
Figure 1.3.1.1. Box whisker plots of the percentage contribution to total station abundance and biomass by the species (and genera of those species) for which catching efficiency was given in Reiss *et al.* (2006). The grey box represents 75% of the data; the black line within the box represents the median of the data and the whiskers outside of the box, the range of the data.

1.3.2. 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 1.3.2.1 (based on numerical abundance) and Figure 1.3.2.2 (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 others, 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 1.3.2.3 to 1.3.2.10).
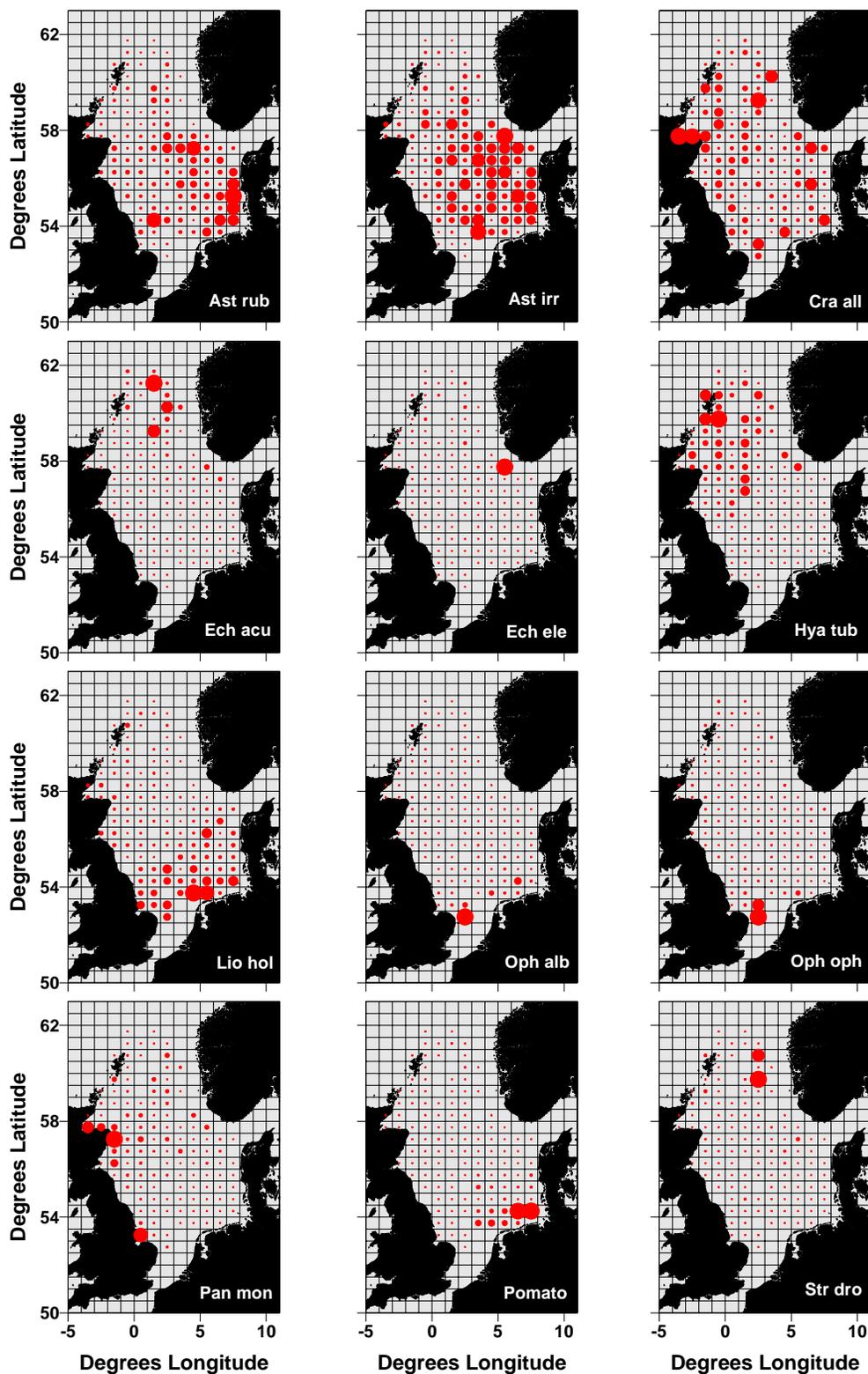
Figure 1.3.2.1. Spatial variation in the density (nos.m^{-2}) of the 12 most abundant epibenthic invertebrates based on abundance. Ast rub: *Asterias rubens*; Ast irr: *Astropecten irregularis*; Cra all: *Crangon allmanni*; Ech acu: *Echinus acutus*; Ech ele: *Echinus elegans*; Hya tub: *Hyalinoecia tubicola*; Lio hol: *Liocarcinus holsatus*; Oph alb: *Ophiura albida*; Oph oph: *Ophiura ophiura*; Pan mon: *Pandalus montagui*; Pomato: *Pomatoschistus*; Str dro: *Strongylocentrotus droebachiensis*.
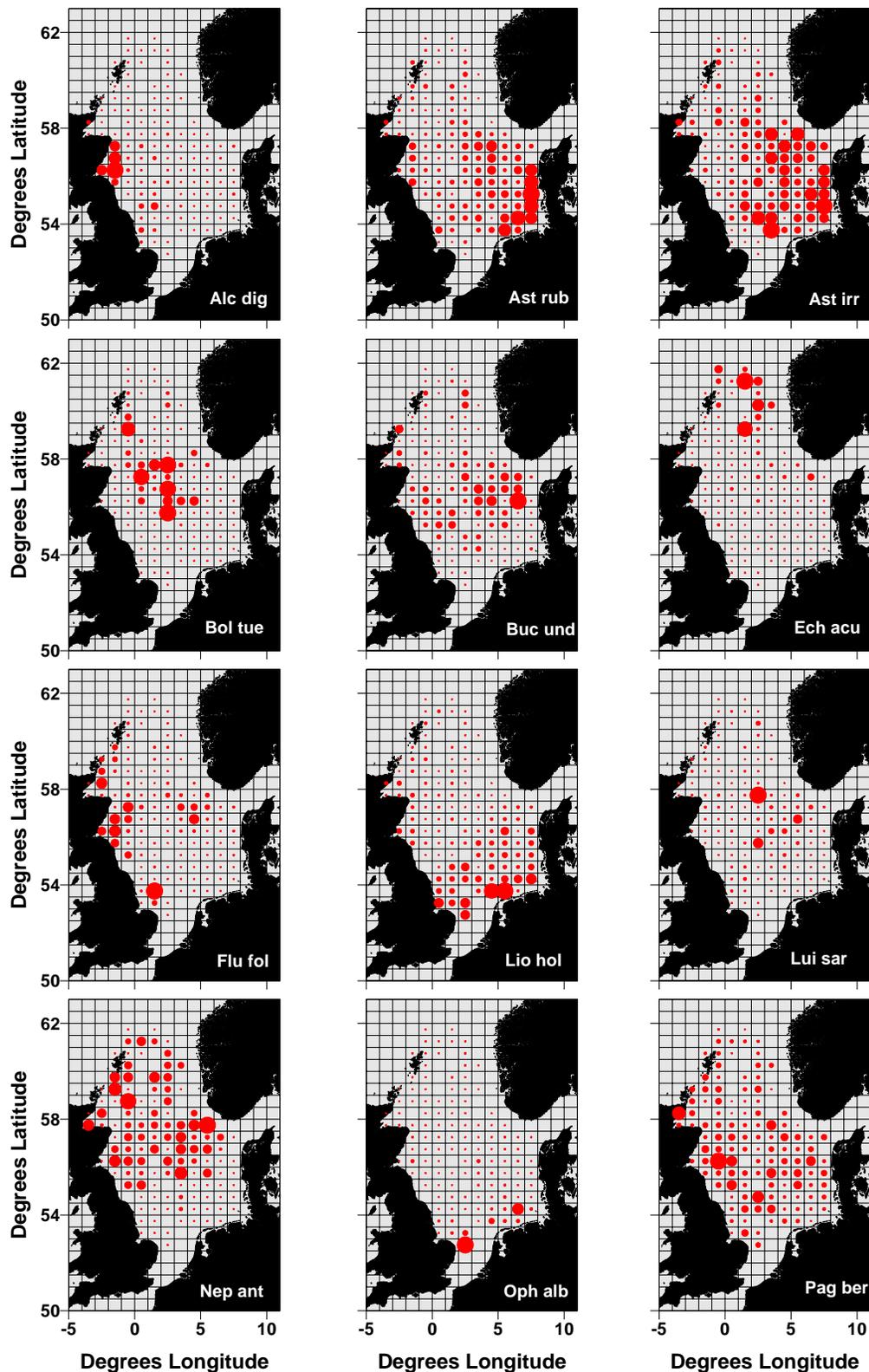
Figure 1.3.2.2. Spatial variation in the density (g.m^{-2}) of the 12 most abundant epibenthic invertebrates based on biomass. Alc dig: *Alcyonium digitatum*; Ast rub: *Asterias rubens*; Ast irr: *Astropecten irregularis*; Bol tue: *Bolocera tuediae*; Buc und: *Buccinum undatum*; Ech acu: *Echinus acutus*; Flu fol: *Flustra foliacea*; Lio hol: *Liocarcinus holsatus*; Lui sar: *Luidia sarsi*; Nep ant: *Neptunea antique*; Oph alb: *Ophiura albida*, Pag ber: *Pagurus bernhardus*.
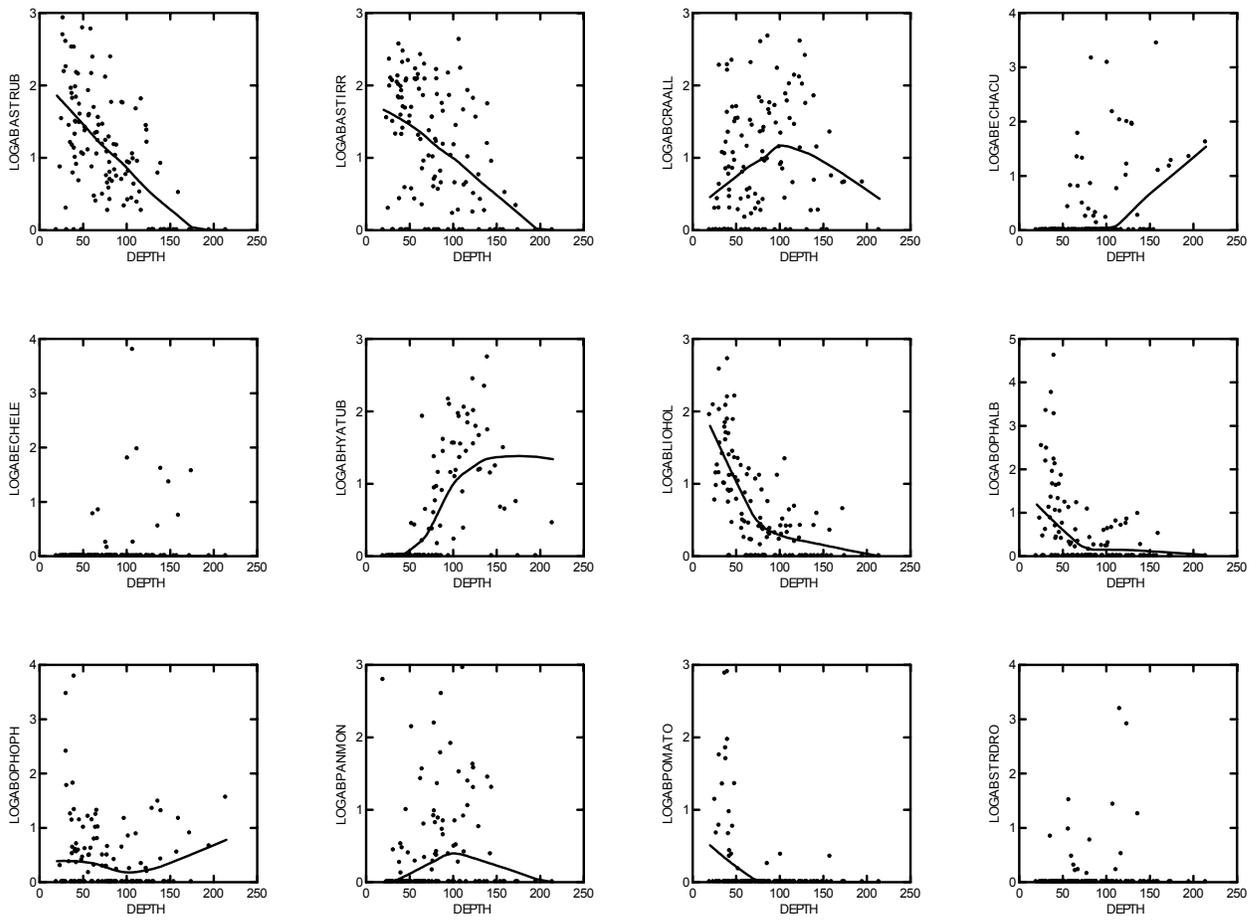
Figure 1.3.2.3. Effect of water depth on the density of the 12 key epibenthic invertebrates based on their numerical abundance (n.m^{-2}). Data are fitted by a Lowess curve.
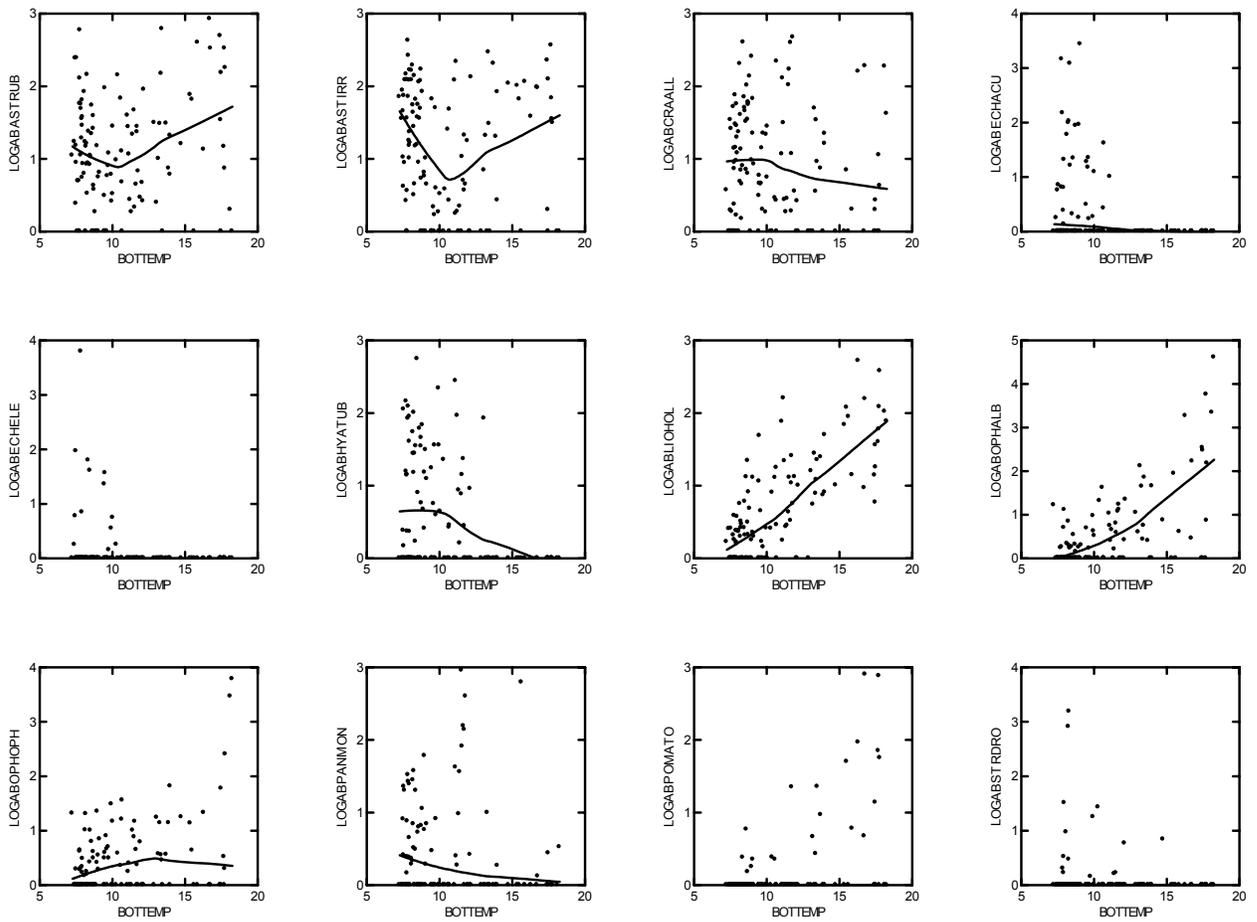
Figure 1.3.2.4. Effect of bottom water temperature on the density of the 12 key epibenthic invertebrates based on their numerical abundance (n.m^{-2}). Data are fitted by a Lowess curve.
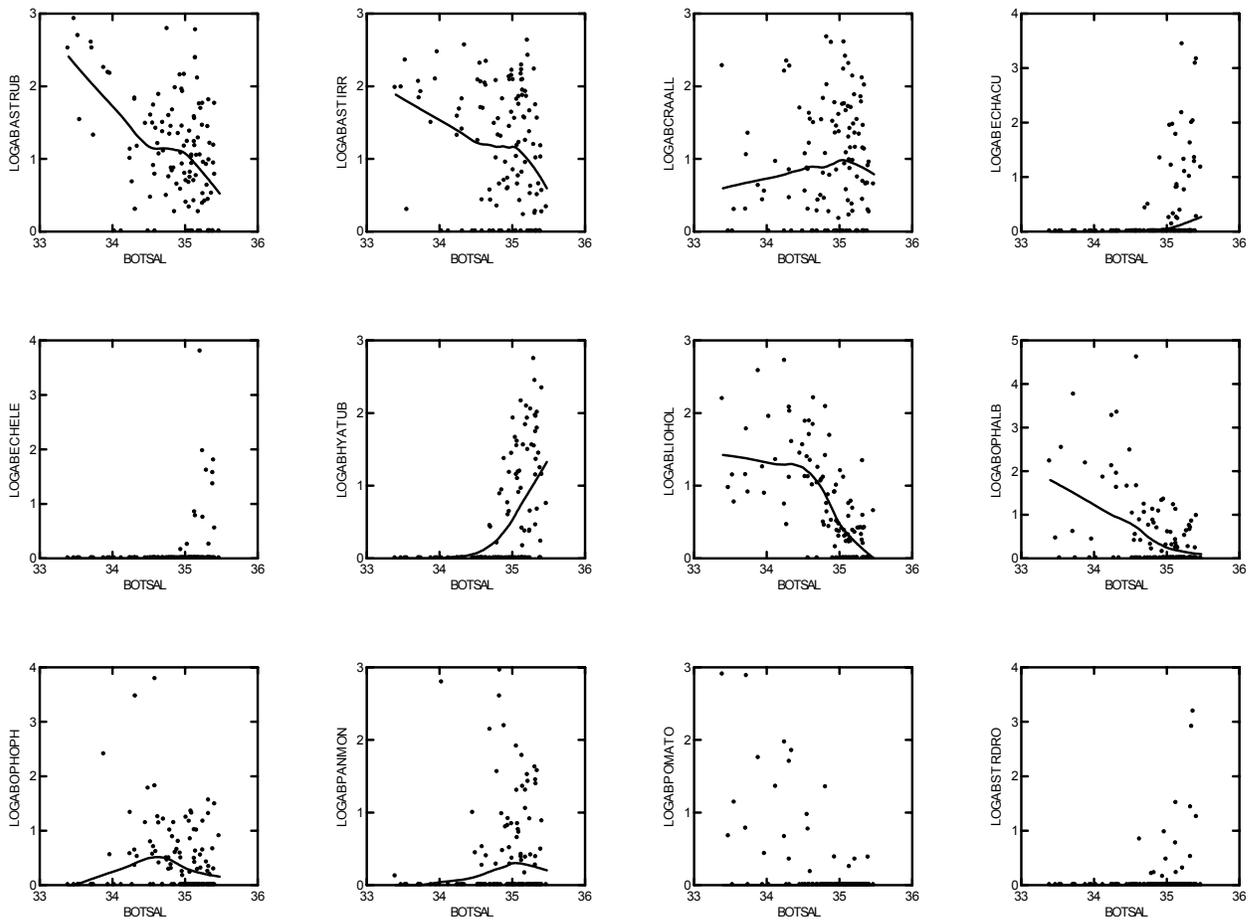
Figure 1.3.2.5. Effect of bottom water salinity on the density of the 12 key epibenthic invertebrates based on their numerical abundance (n.m^{-2}). Data are fitted by a Lowess curve.
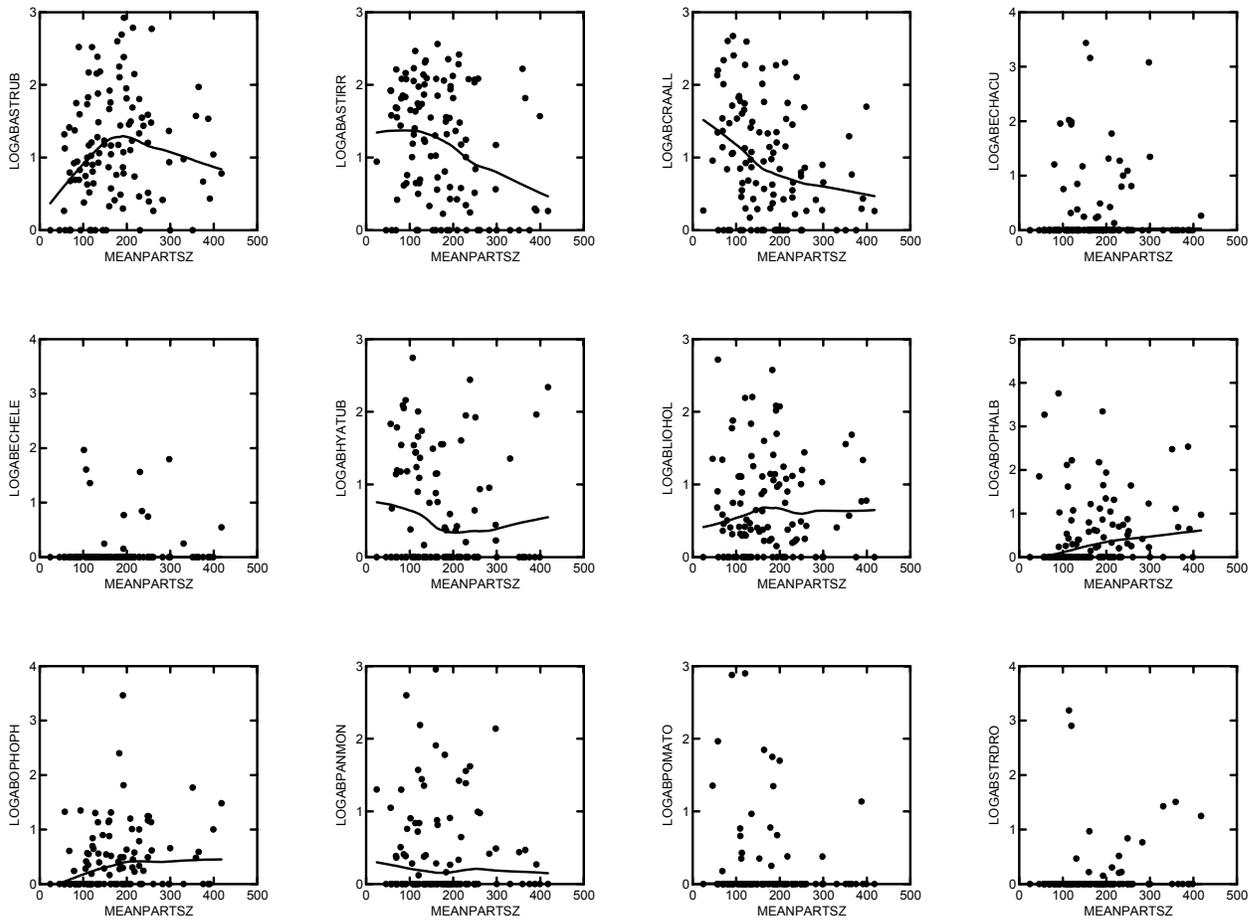
Figure 1.3.2.6. Effect of sediment mean particle size on the density of the 12 key epibenthic invertebrates based on their numerical abundance (n.m^{-2}). Data are fitted by a Lowess curve.
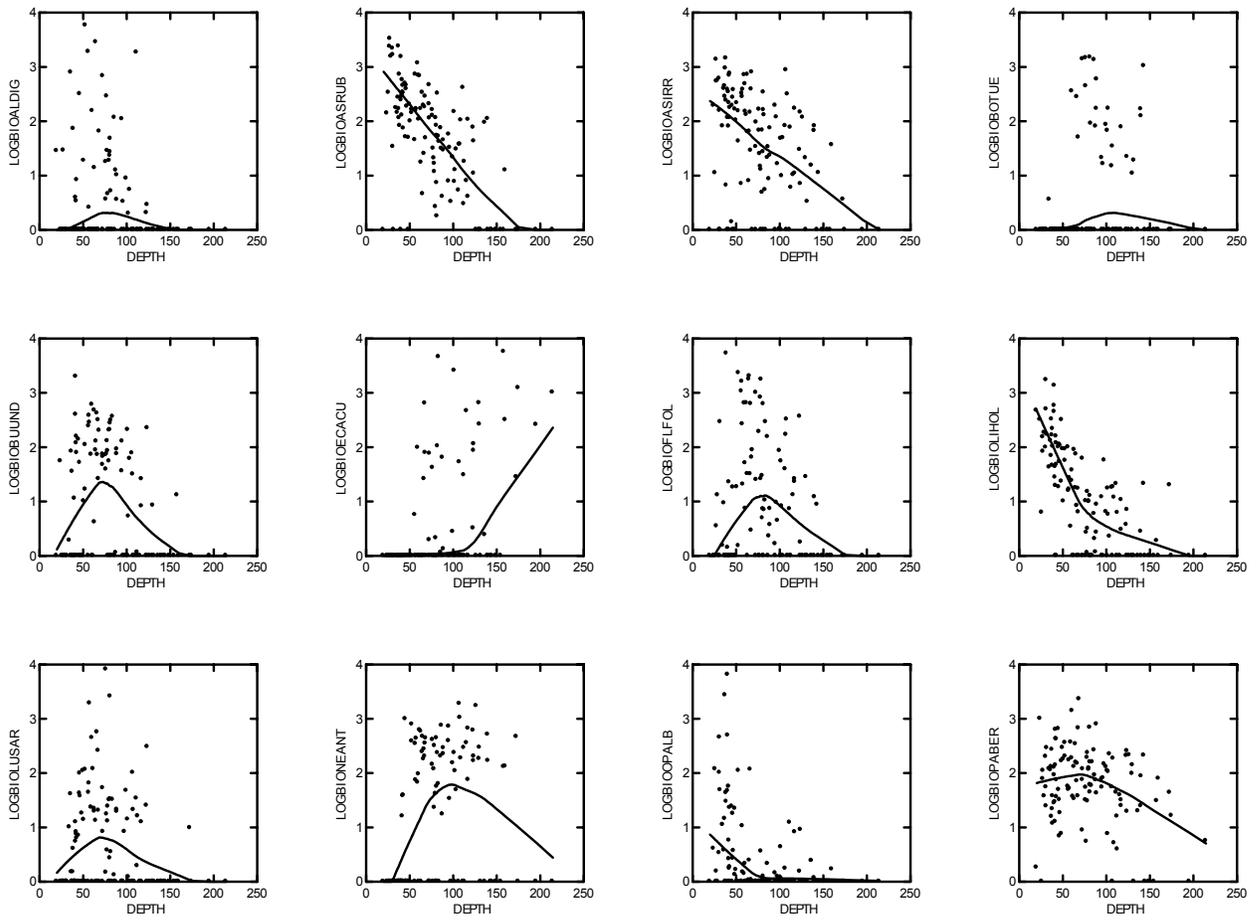
Figure 1.3.2.7. Effect of water depth on the density of the 12 key epibenthic invertebrates based on biomass (g.m^{-2}). Data are fitted by a Lowess curve.
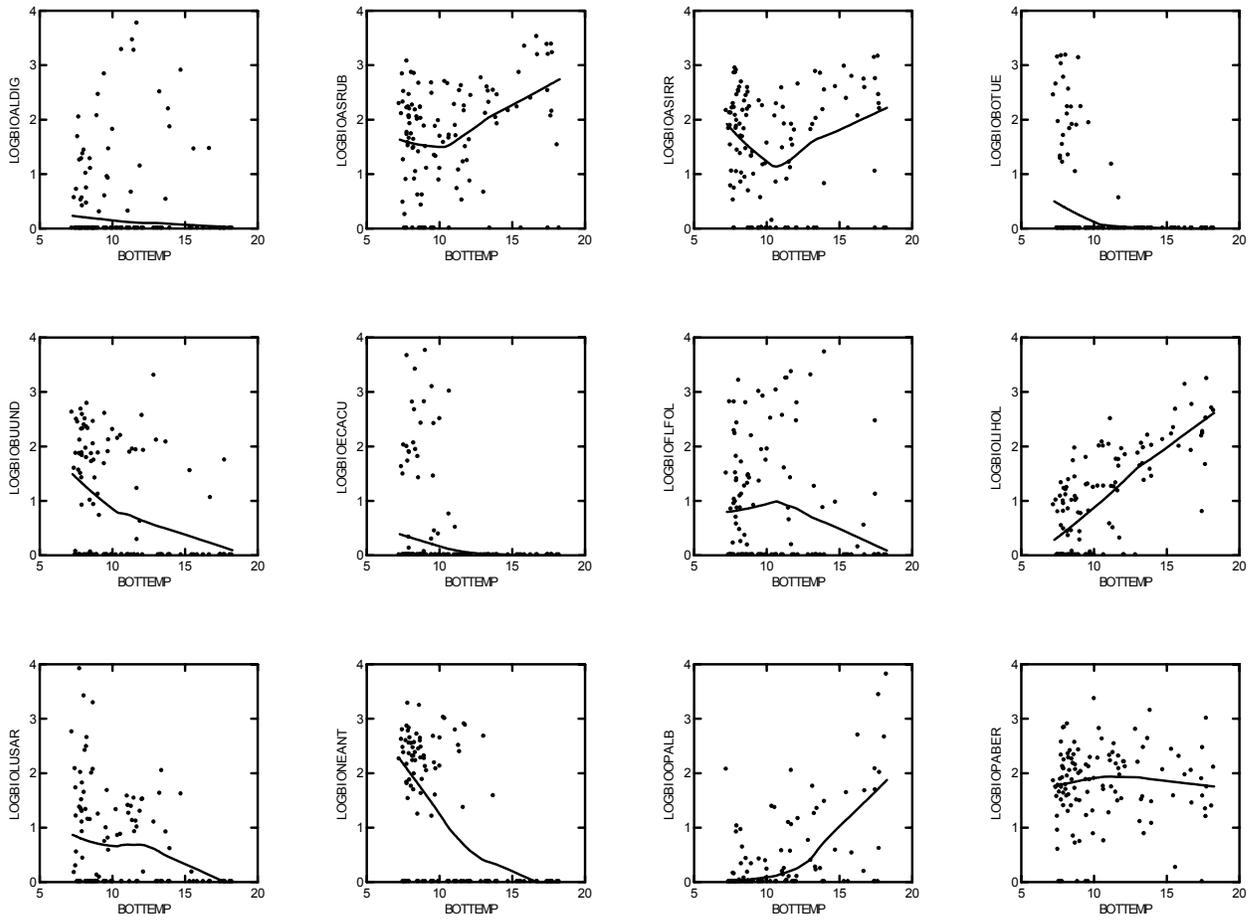
Figure 1.3.2.8. Effect of bottom water temperature on the density of the 12 key epibenthic invertebrates based on their biomass (g.m^{-2}). Data are fitted by a Lowess curve.
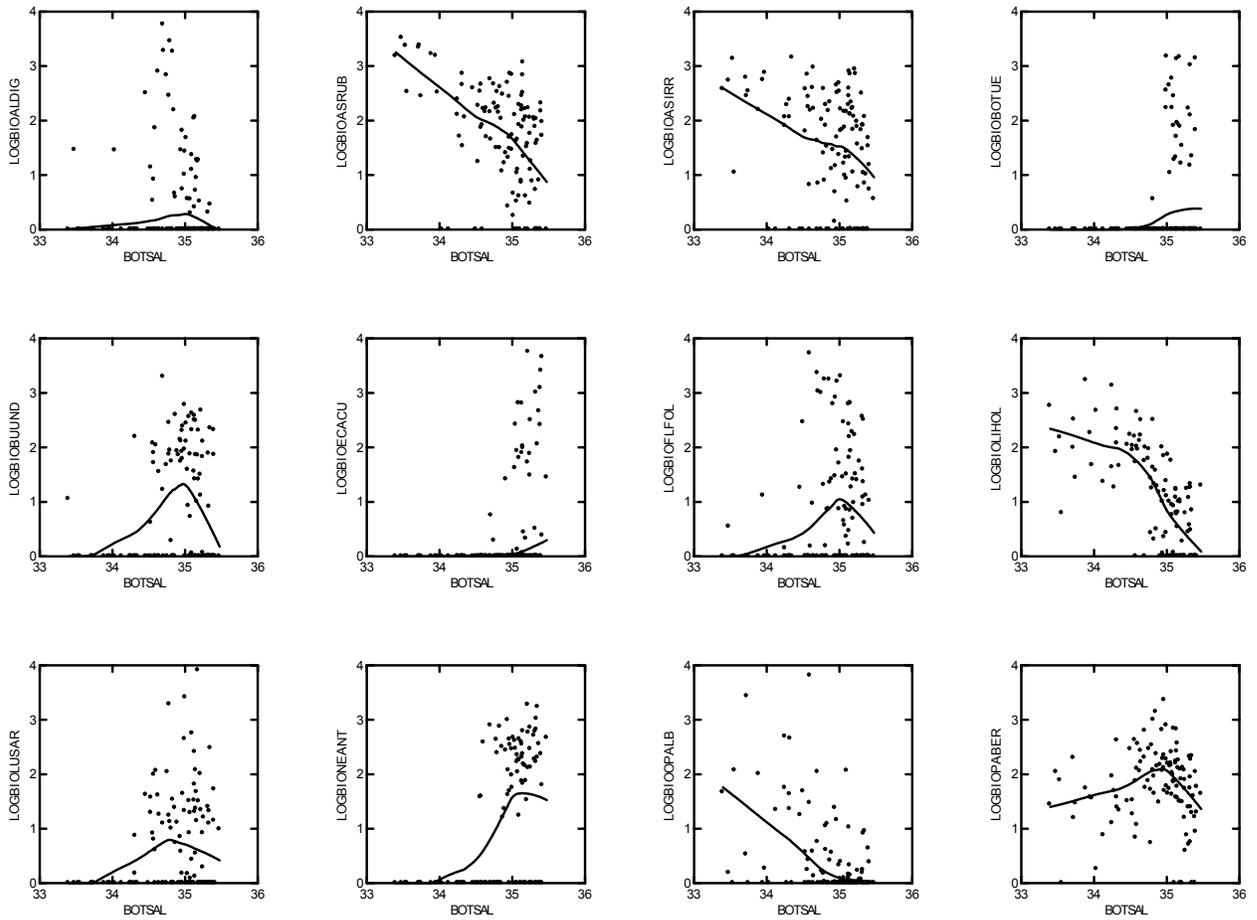
Figure 1.3.2.9. Effect of bottom water salinity on the density of the 12 key epibenthic invertebrates based on their biomass (g.m^{-2}). Data are fitted by a Lowess curve.
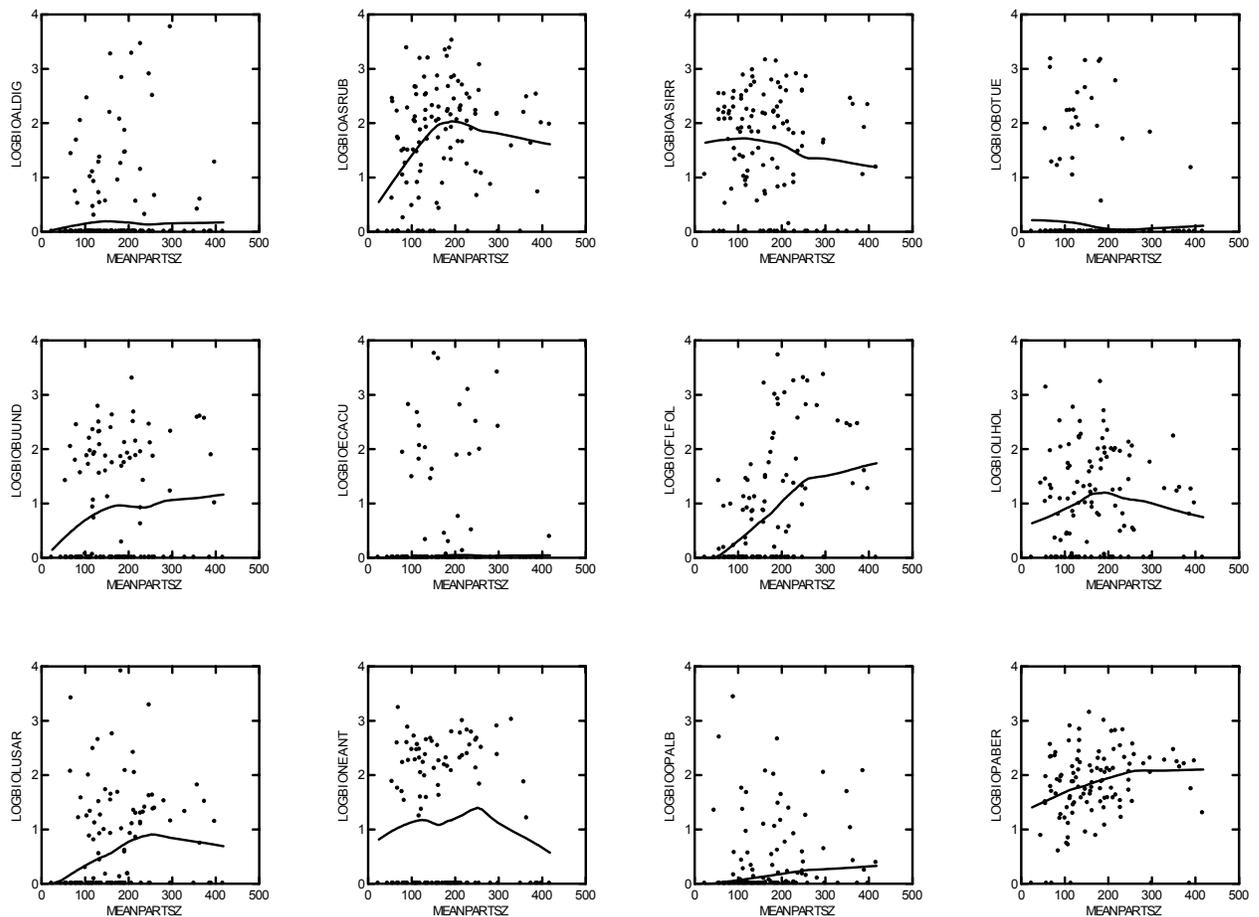
Figure 1.3.2.10. Effect of sediment mean particle size on the density of the 12 key epibenthic invertebrates based on their biomass (g.m^{-2}). Data are fitted by a Lowess curve.

1.3.3. 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 1.3.3.1. 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 1.3.3.2). Furthermore, these community composition cluster maps for the epibenthic assemblage bore a marked resemblance to similar maps produced for the groundfish assemblage (Greenstreet et al 2007a).
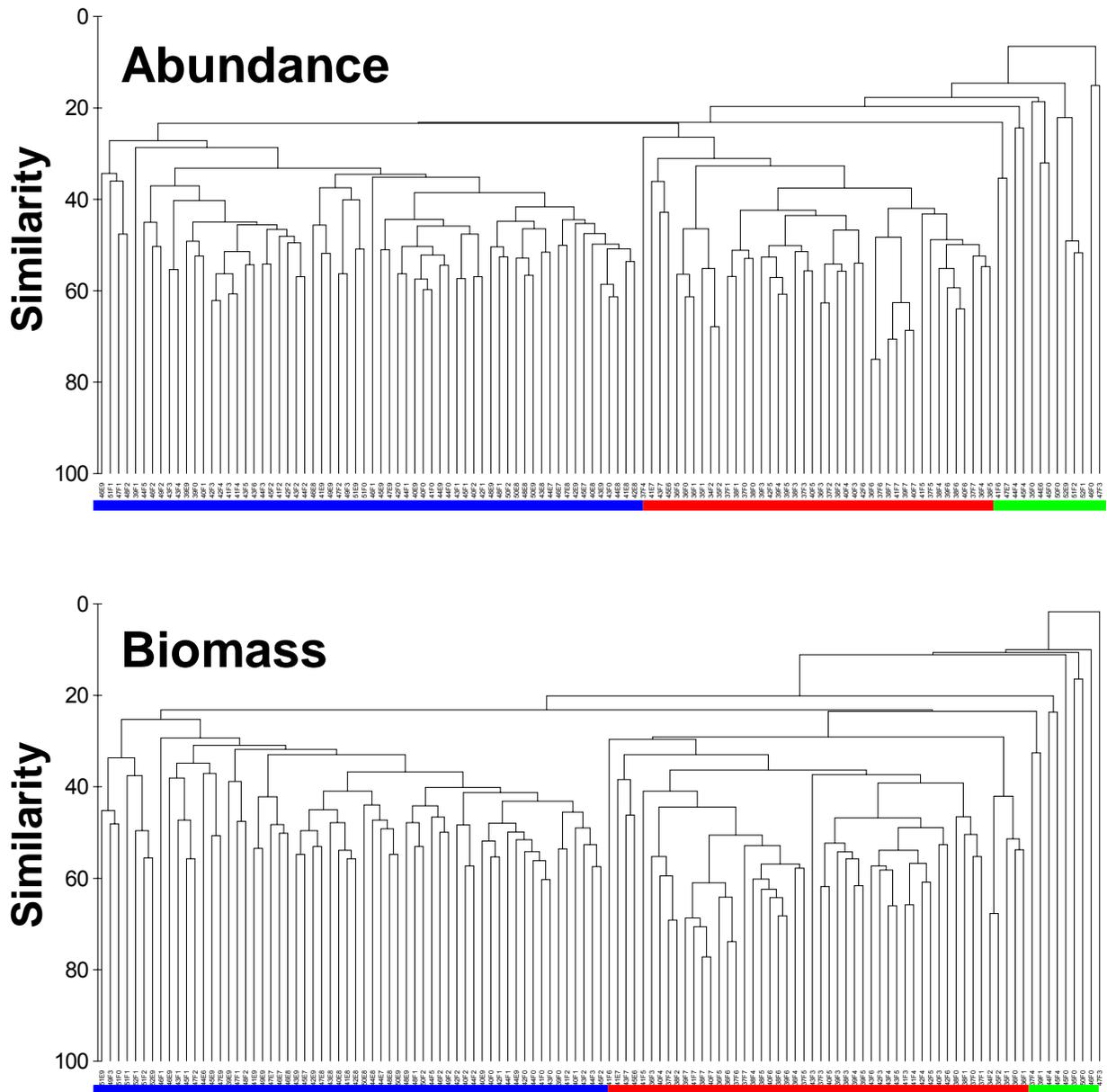
Figure 1.3.3.1. Group average cluster dendograms of epibenthic invertebrate density data based on mean abundance (n.m^{-2}) and biomass (g.m^{-2}) densities in each ICES rectangle. Colour coding links to Figure 1.3.3.2.
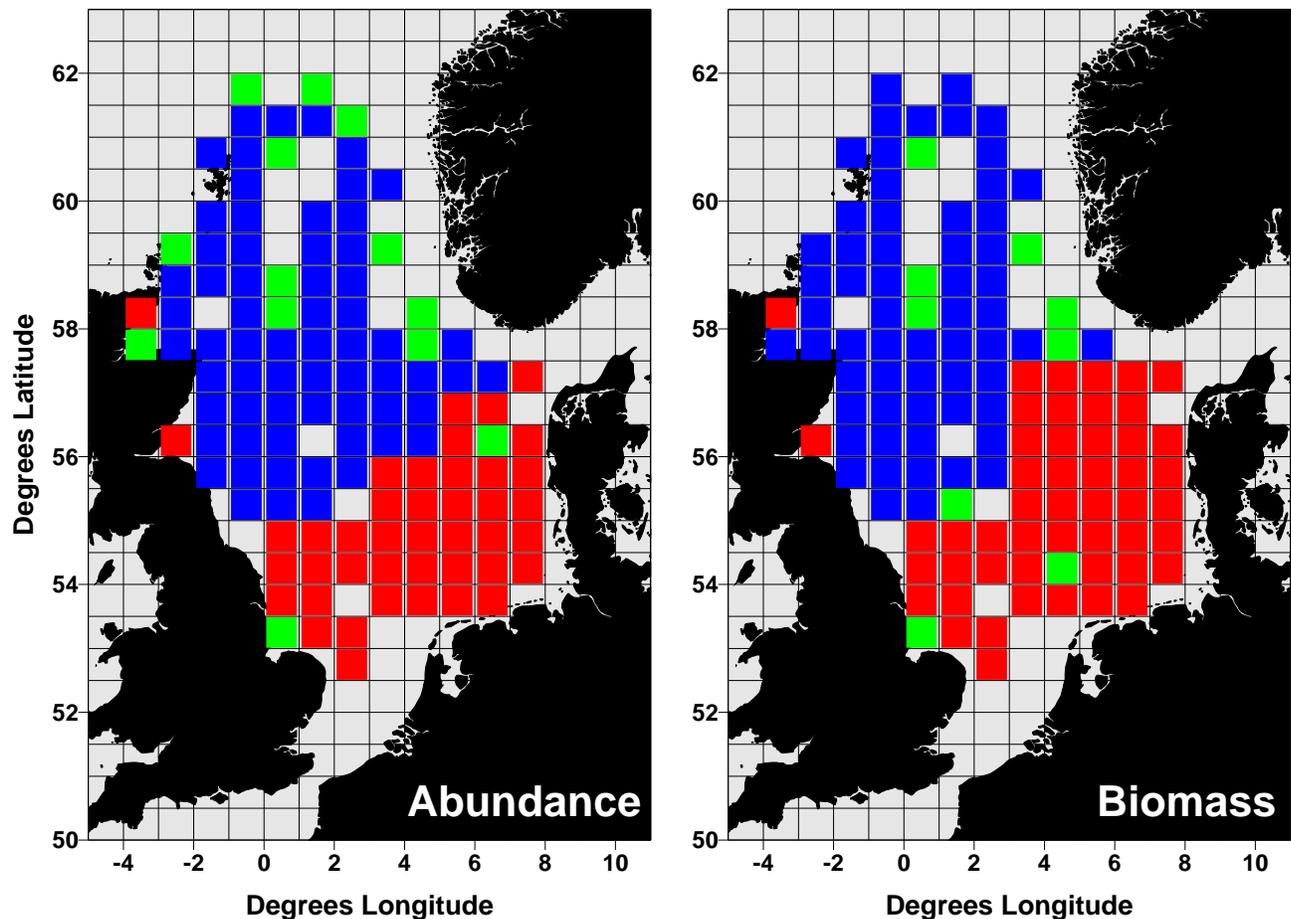
Figure 1.3.3.2. Spatial distributions of the clusters defined in Figure based upon mean abundance (n.m^{-2}) and biomass (g.m^{-2}) densities in each ICES rectangle. Colour coding links to Figure 1.3.3.1.

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 1.3.3.3 for clusters based on numerical abundance data and Figure 1.3.3.4 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.
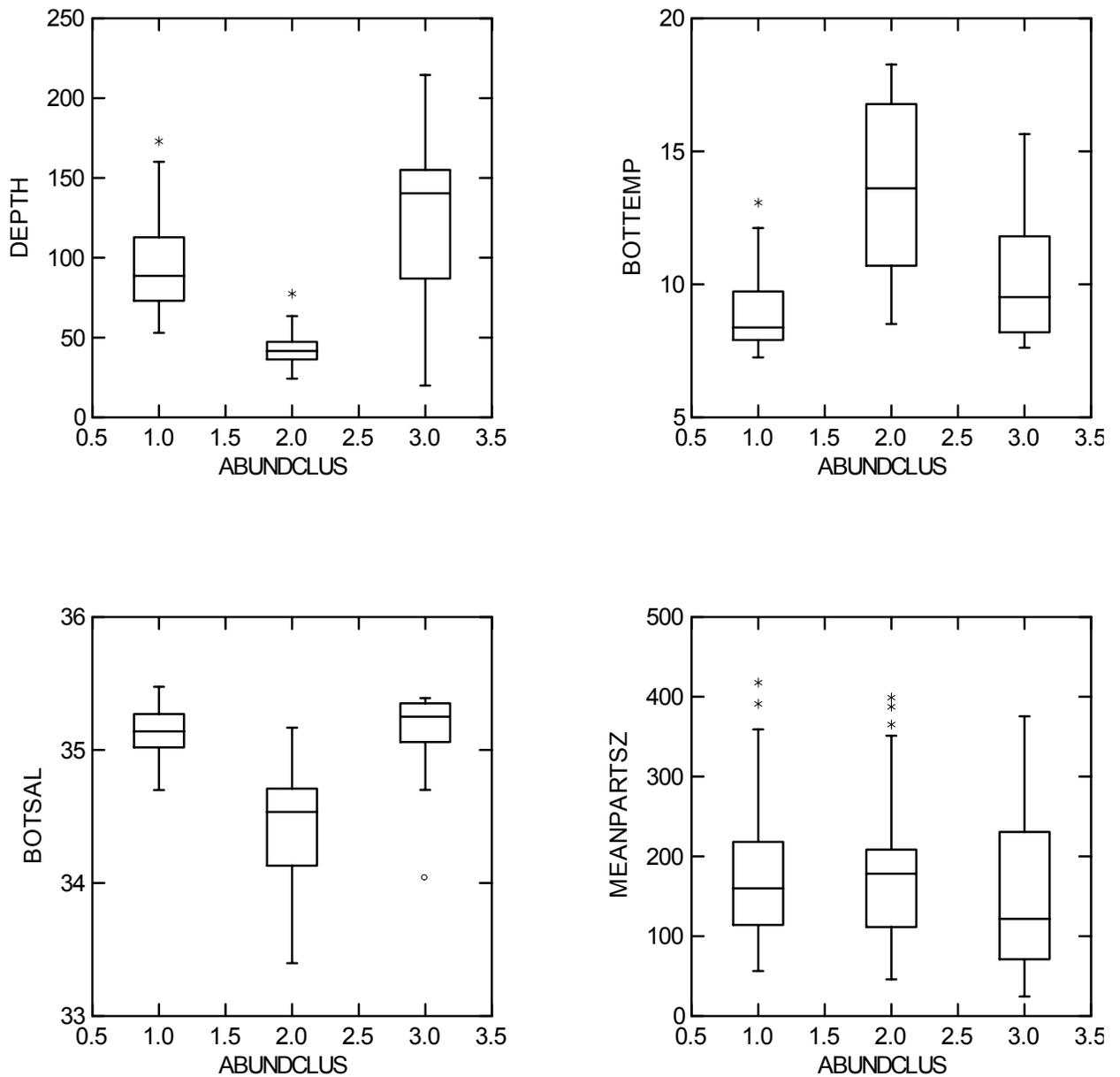
Figure 1.3.3.3. Box plots showing the range in water depth, bottom temperature, bottom salinity and mean sediment particle size associated with each epibenthic community type cluster based on numerical abundance identified in Figures 1.3.3.1 and 1.3.3.2.
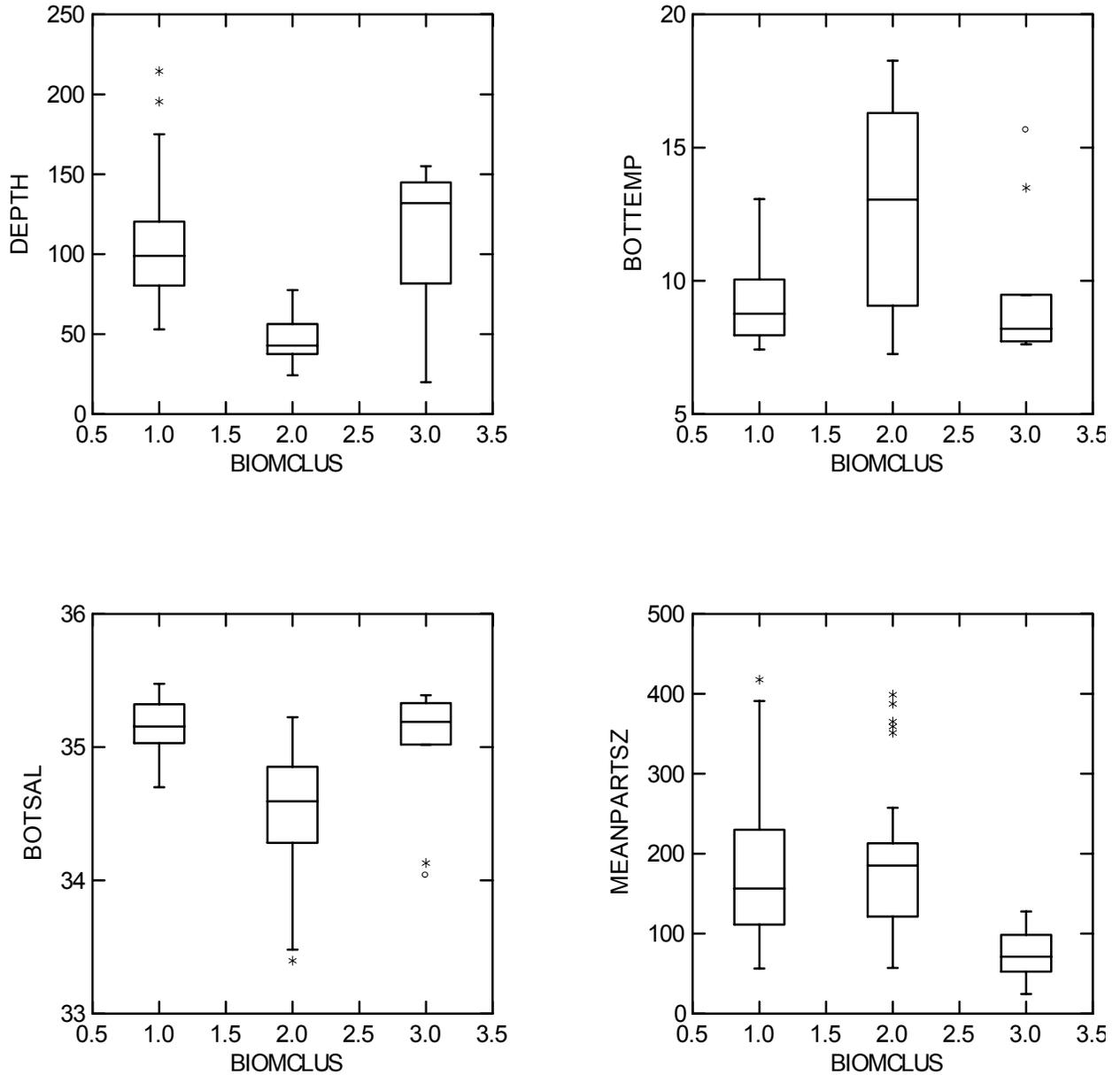
Figure 1.3.3.4. Box plots showing the range in water depth, bottom temperature, bottom salinity and mean sediment particle size associated with each epibenthic community type cluster based on biomass identified in Figures 1.3.3.1 and 1.3.3.2.

1.3.4. 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 1.3.4.1). 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 1.3.4.2 to 1.3.4.5). Species

diversity (Hill's N1 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 1.3.4.6 and 1.3.4.7). 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 1.3.4.6 and 1.3.4.7). The effects of water depth, bottom water temperature and salinity, and mean sediment particle size are shown in Figures 1.3.4.8 to 1.3.4.11 for metrics based on numerical abundance and in Figures 1.3.4.12 to 1.3.4.15 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.
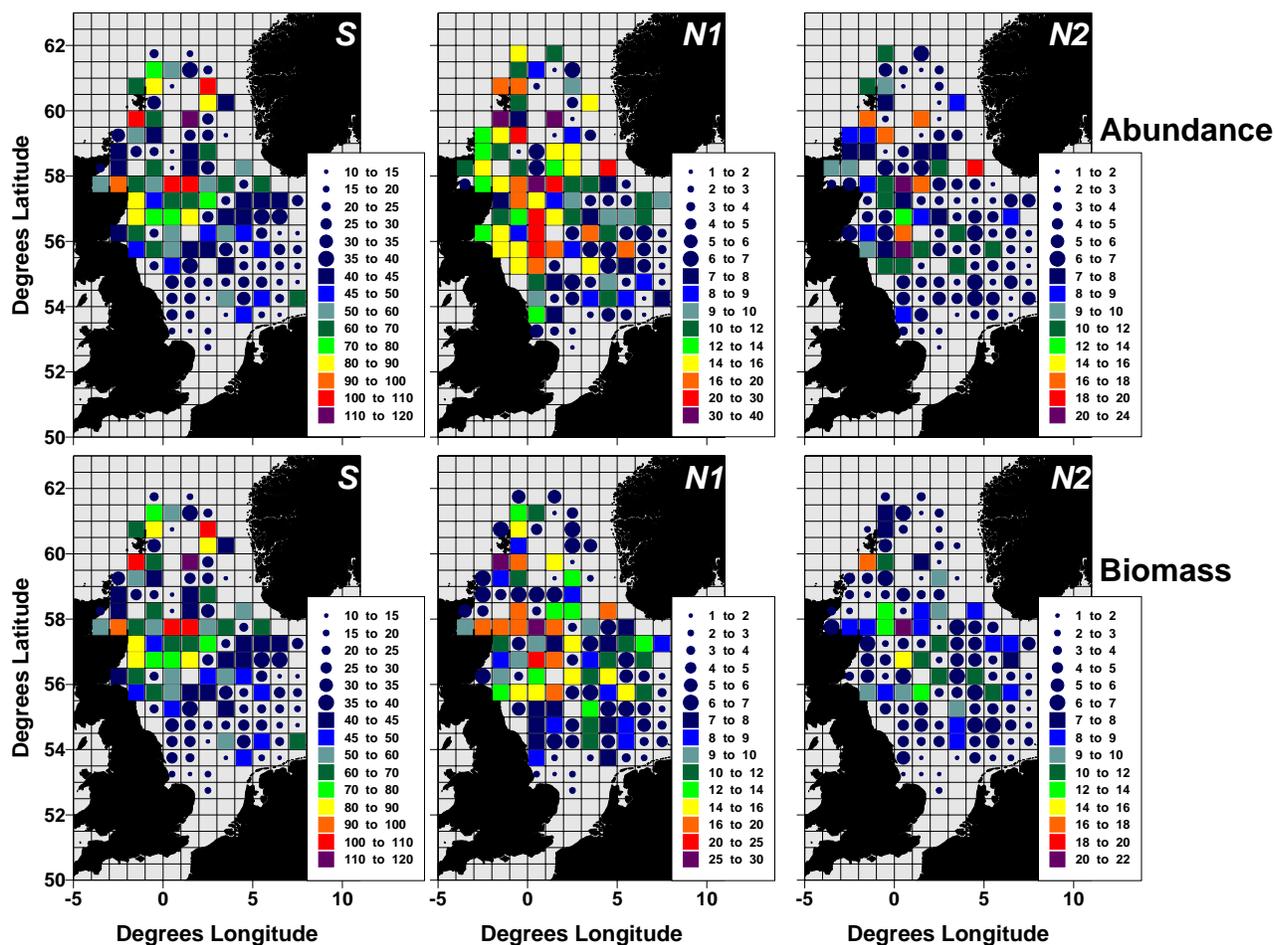
Figure 1.3.4.1. Spatial variation in species richness (S) and Hills N1 and N2 calculated on mean sample abundance and biomass data in each ICES statistical rectangle.
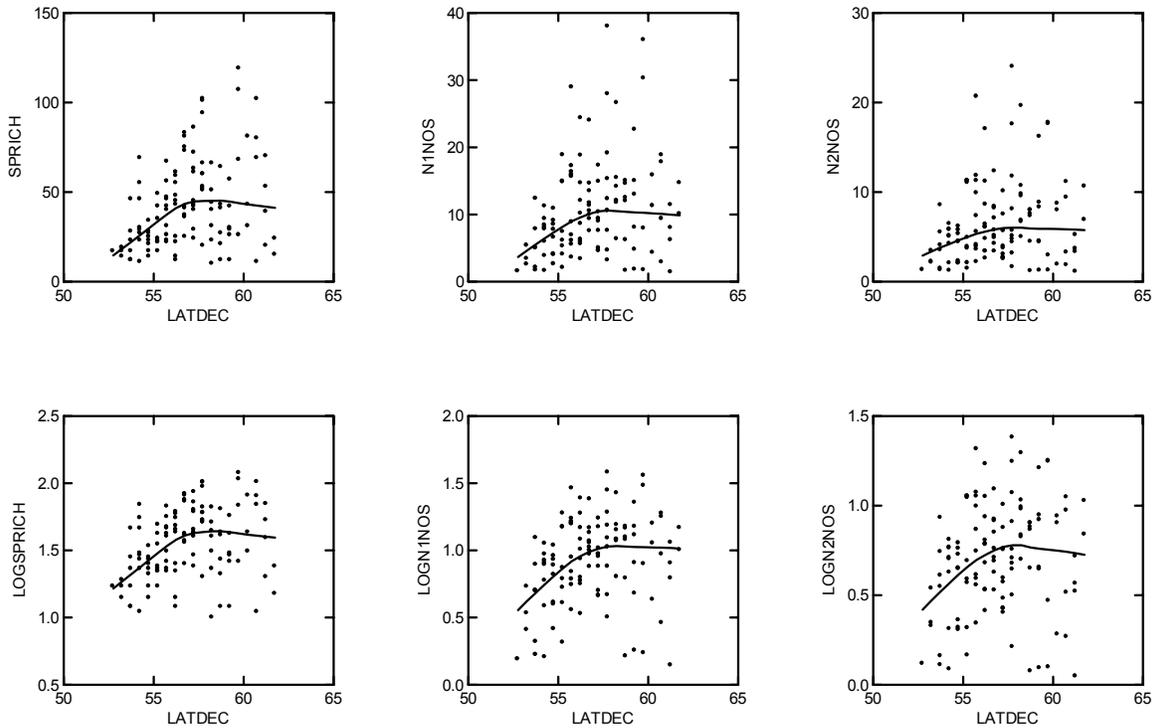
Figure 1.3.4.2. Variation in species richness, N_1, N_2, Log of species richness, log of N_1 and Log of N_2 based on numerical density data with latitude. Lowess smooth fitted to data.
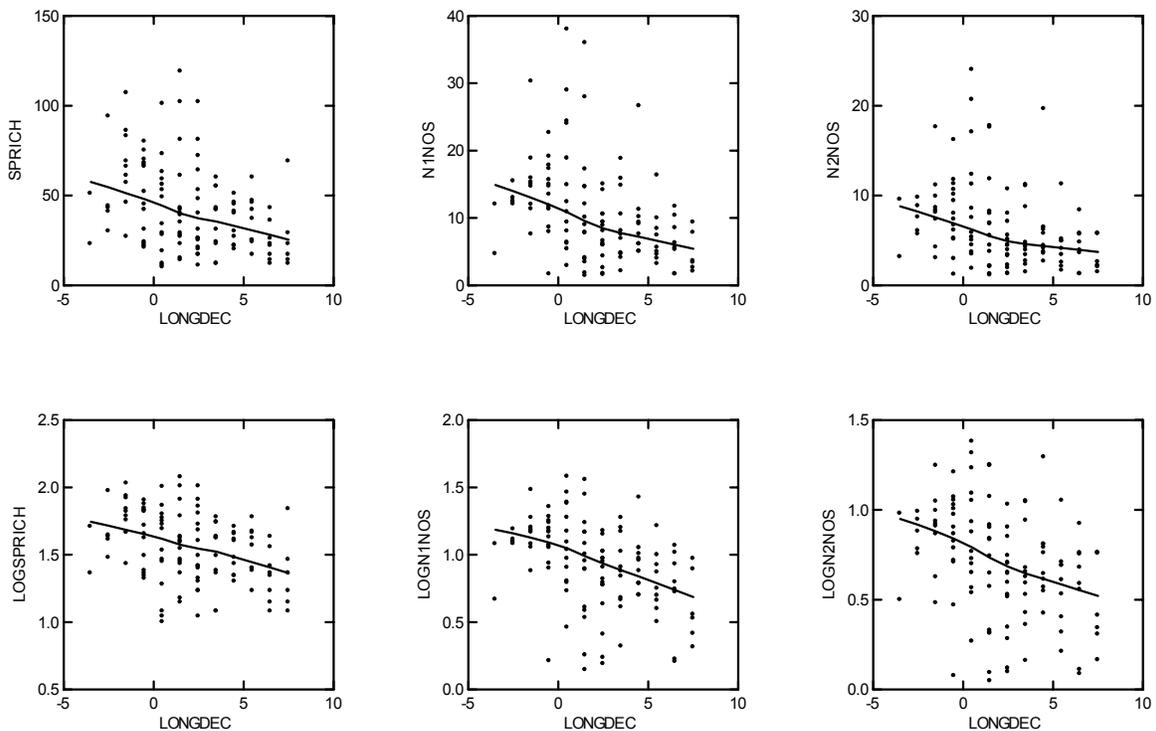
Figure 1.3.4.3. Variation in species richness, N_1, N_2, Log of species richness, log of N_1 and Log of N_2 based on numerical density data with longitude. Lowess smooth fitted to data.
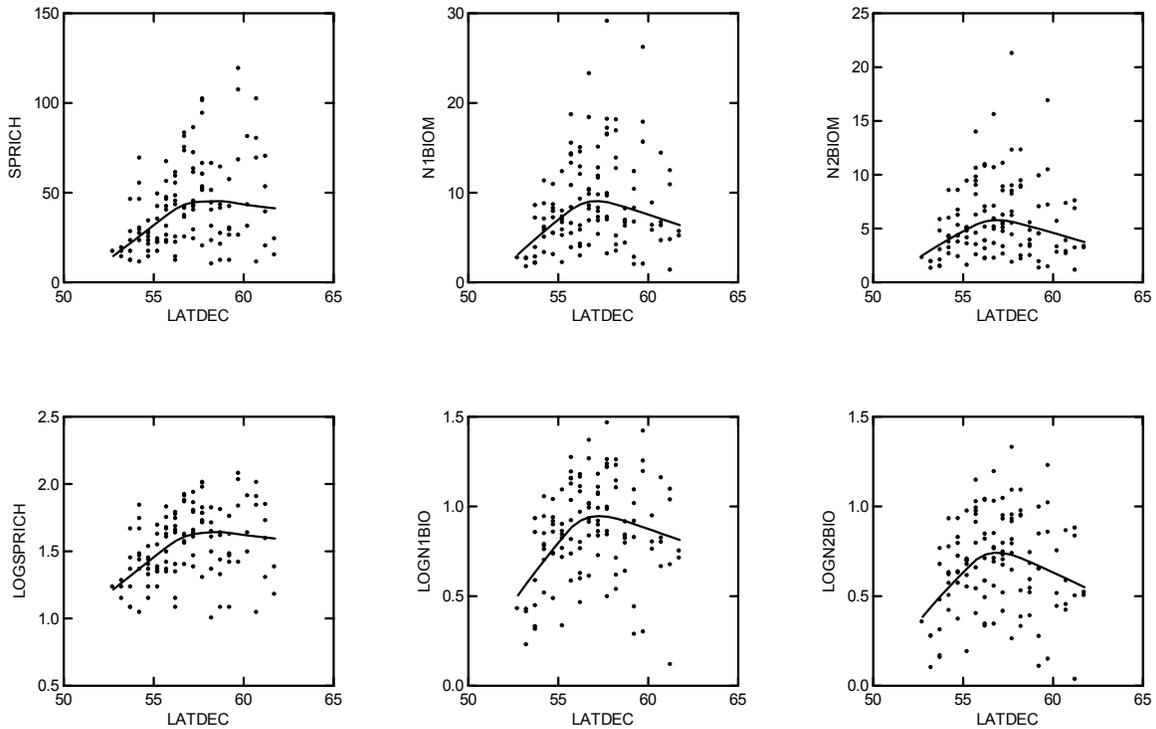
Figure 1.3.4.4. Variation in species richness, N_1, N_2, Log of species richness, log of N_1 and Log of N_2 based on biomass density data with latitude. Lowess smooth fitted to data.
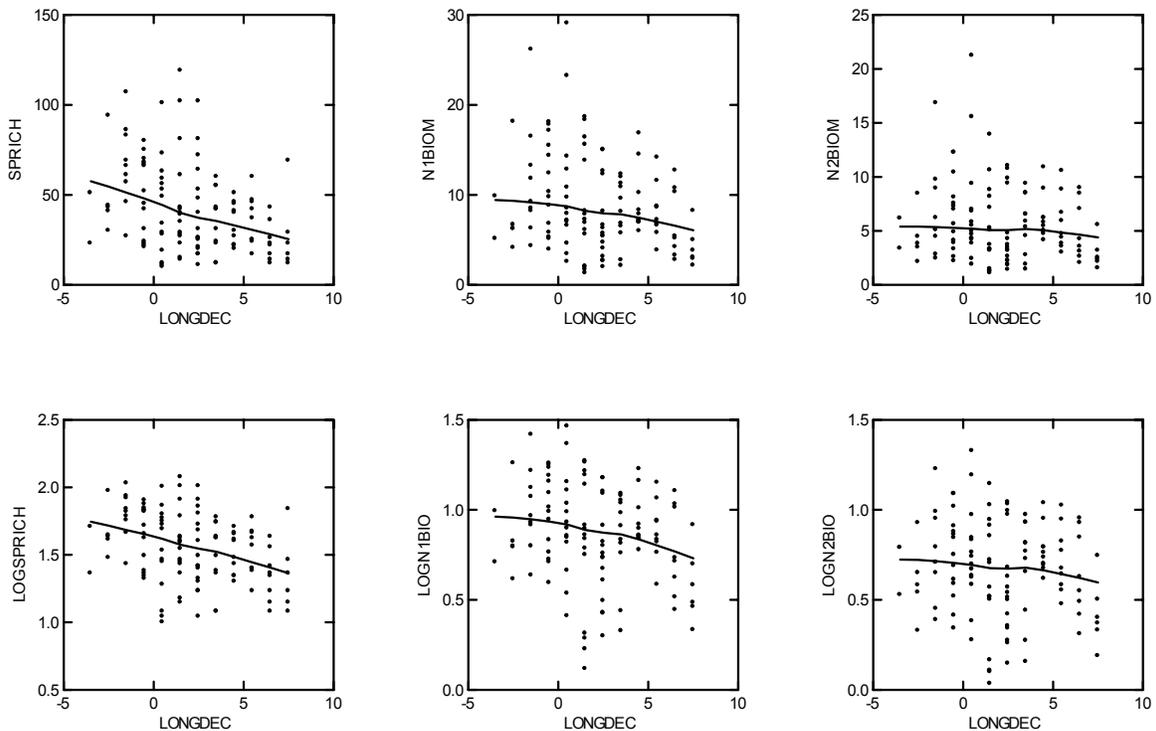
Figure 1.3.4.5. Variation in species richness, N_1, N_2, Log of species richness, log of N_1 and Log of N_2 based on biomass density data with longitude. Lowess smooth fitted to data.
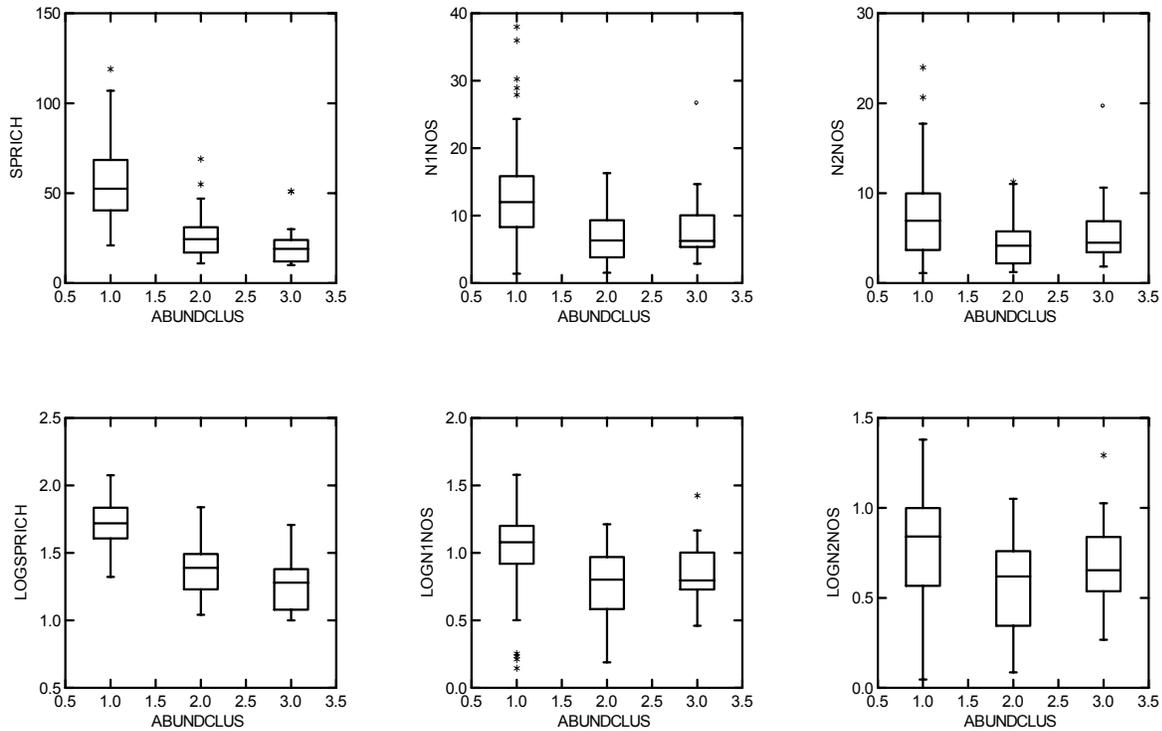
Figure 1.3.4.6. Box plots showing the range in species richness, N_1, N_2, Log of species richness, log of N_1 and Log of N_2 associated with each epibenthic community type cluster based on numerical abundance identified in Figures 1.3.3.1 and 1.3.3.2.
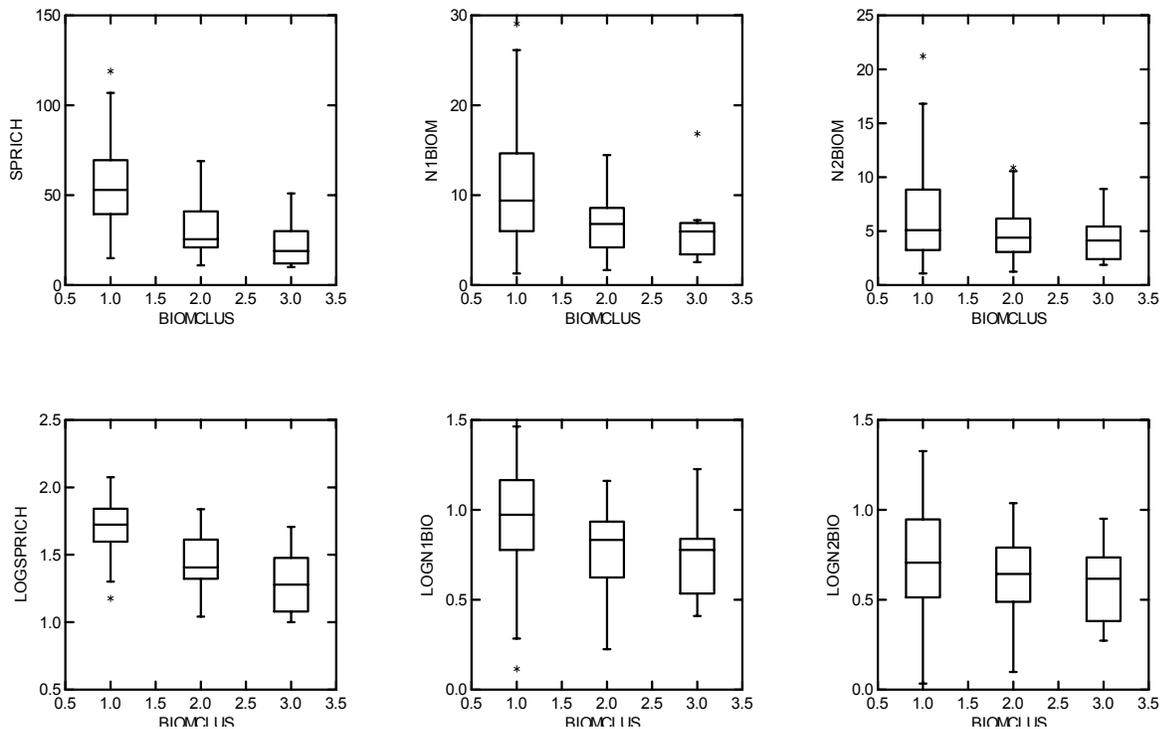
Figure 1.3.4.7. Box plots showing the range in species richness, N_1, N_2, Log of species richness, log of N_1 and Log of N_2 associated with each epibenthic community type cluster based on biomass identified in Figures 1.3.3.1 and 1.3.3.2.
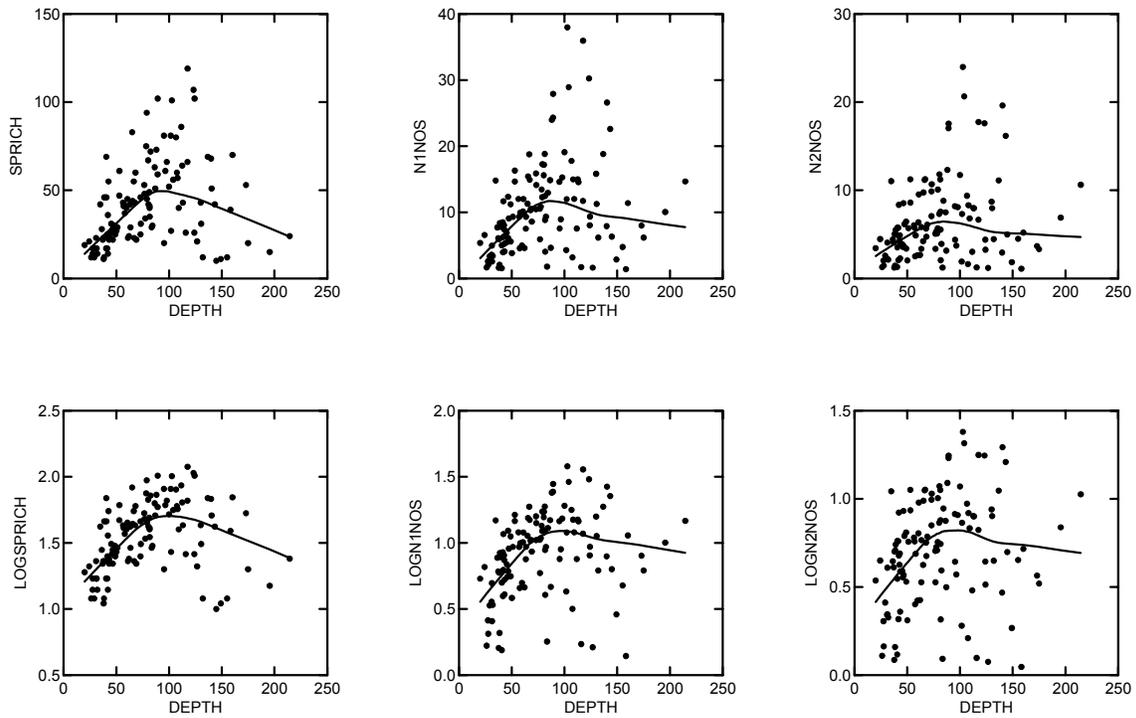
Figure 1.4.3.8. Relationships between species richness, N_1, N_2, Log of species richness, log of N_1 and Log of N_2 based on numerical abundance and water depth.
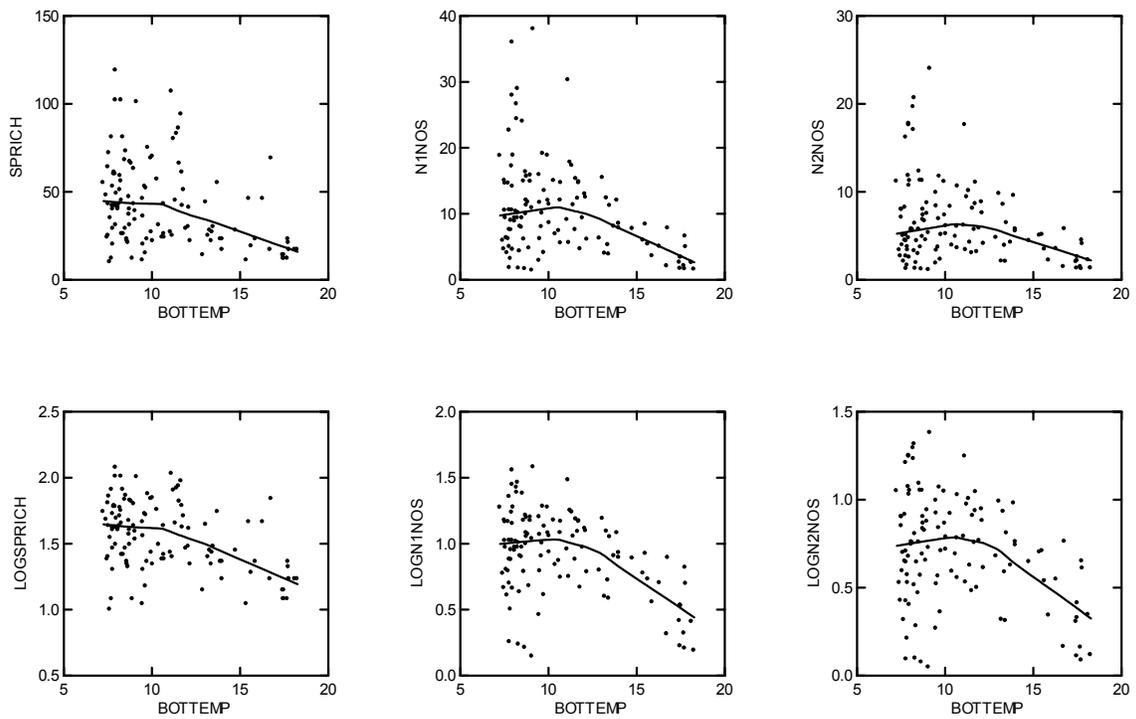
Figure 1.4.3.9. Relationships between species richness, N_1, N_2, Log of species richness, log of N_1 and Log of N_2 based on numerical abundance and bottom water temperature.
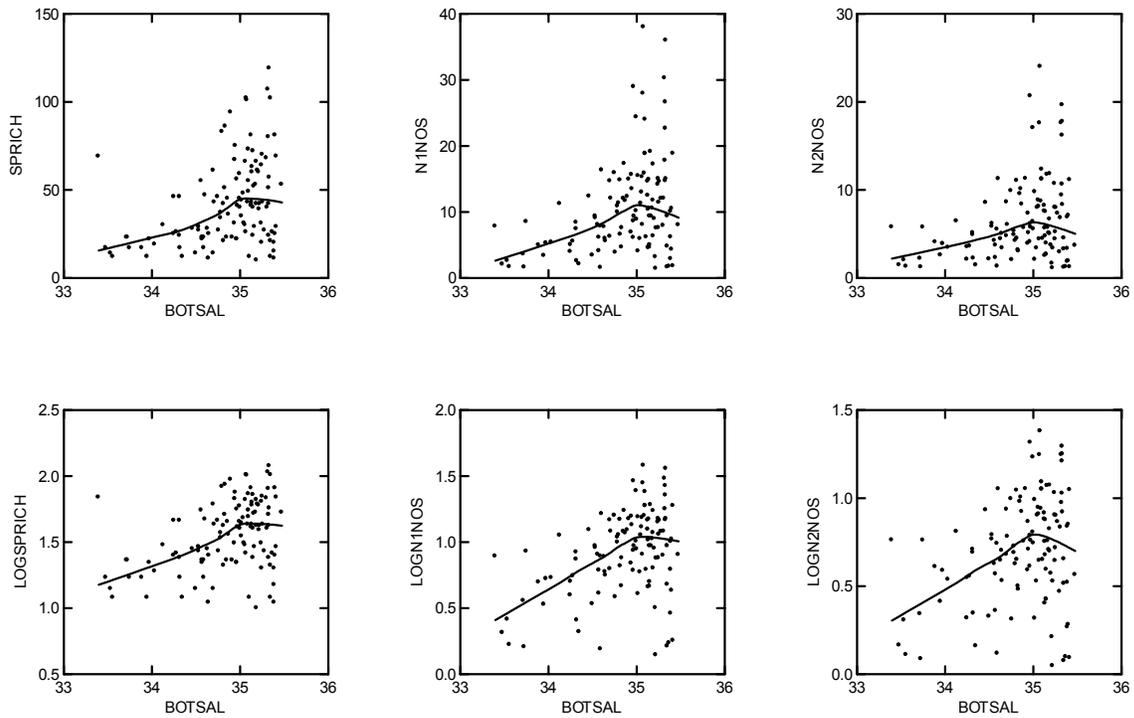
Figure 1.4.3.10. Relationships between species richness, N_1, N_2, Log of species richness, log of N_1 and Log of N_2 based on numerical abundance and bottom water salinity.
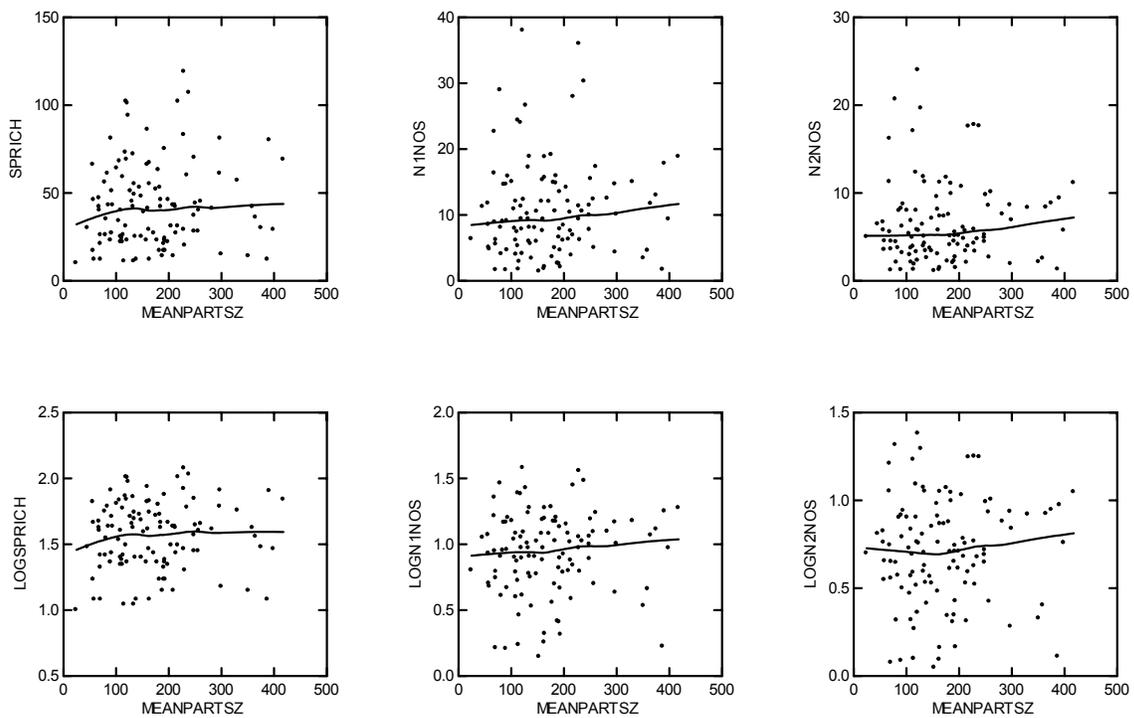
Figure 1.4.3.11. Relationships between species richness, N_1, N_2, Log of species richness, log of N_1 and Log of N_2 based on numerical abundance and sediment mean particle size.
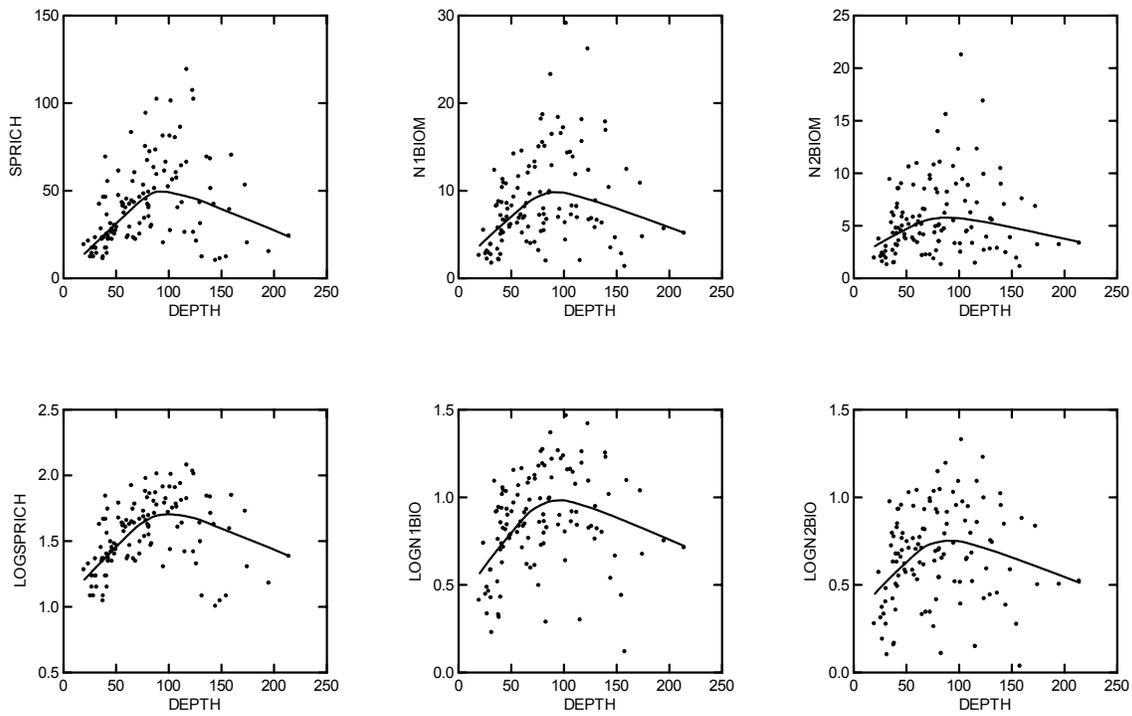
Figure 1.4.3.12. Relationships between species richness, N_1, N_2, Log of species richness, log of N_1 and Log of N_2 based on biomass and water depth.
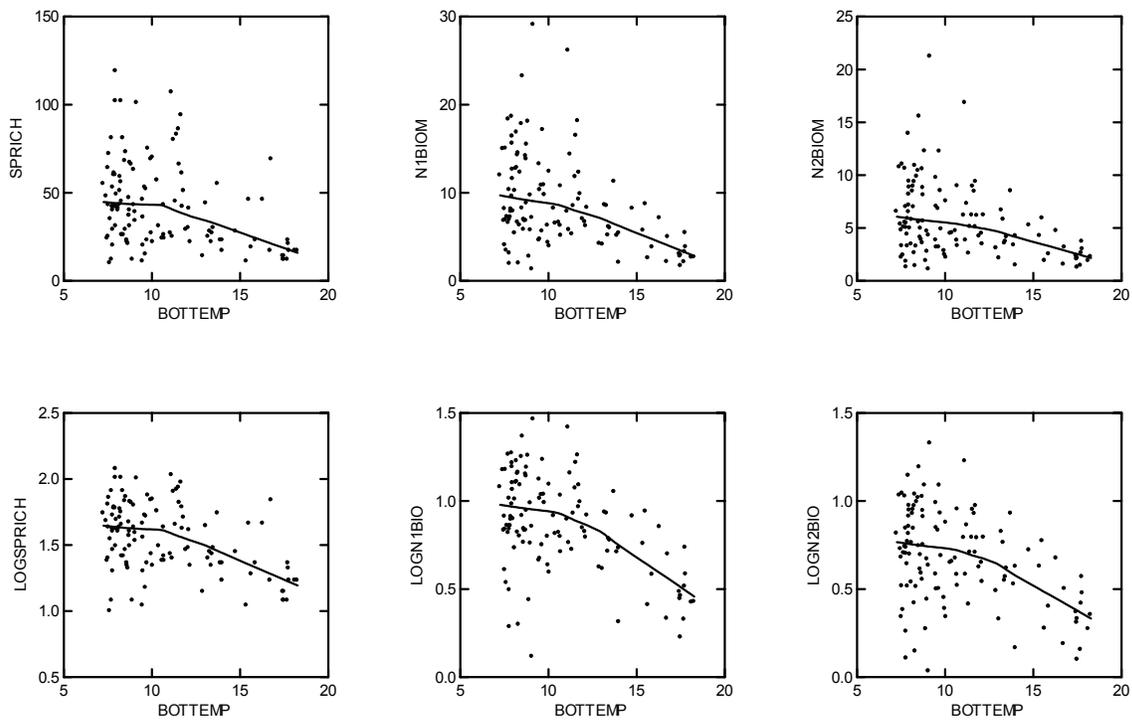
Figure 1.4.3.13. Relationships between species richness, N_1, N_2, Log of species richness, log of N_1 and Log of N_2 based on biomass and bottom water temperature.
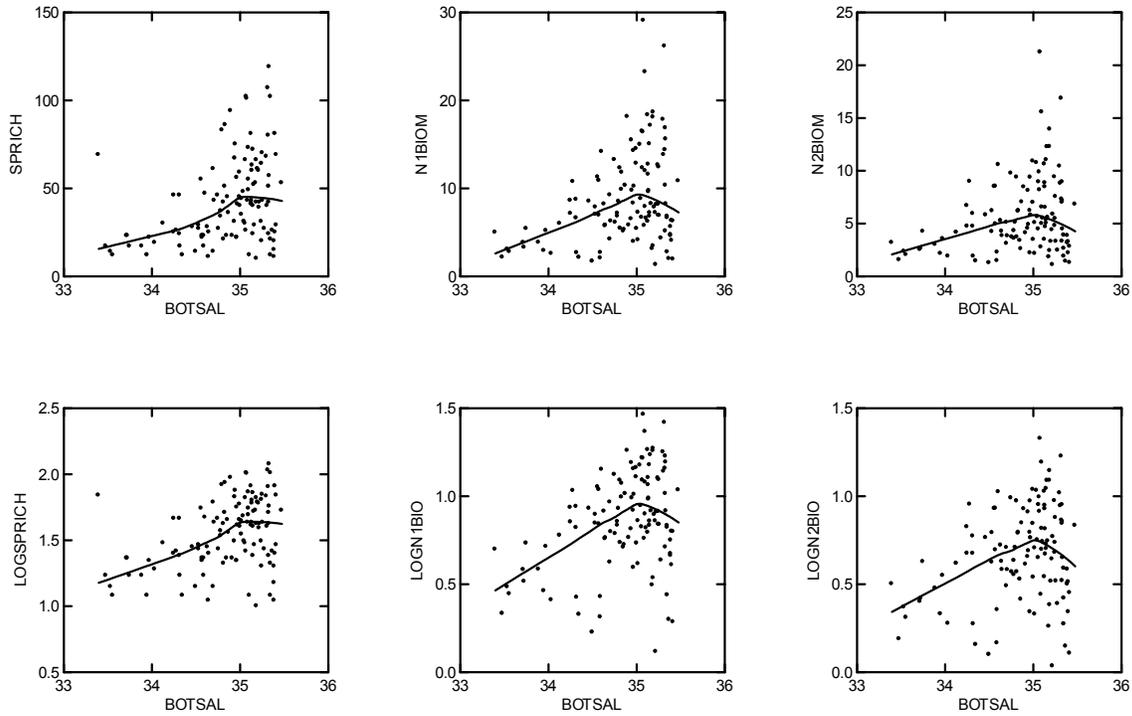
Figure 1.4.3.14. Relationships between species richness, N_1, N_2, Log of species richness, log of N_1 and Log of N_2 based on biomass and bottom water salinity.
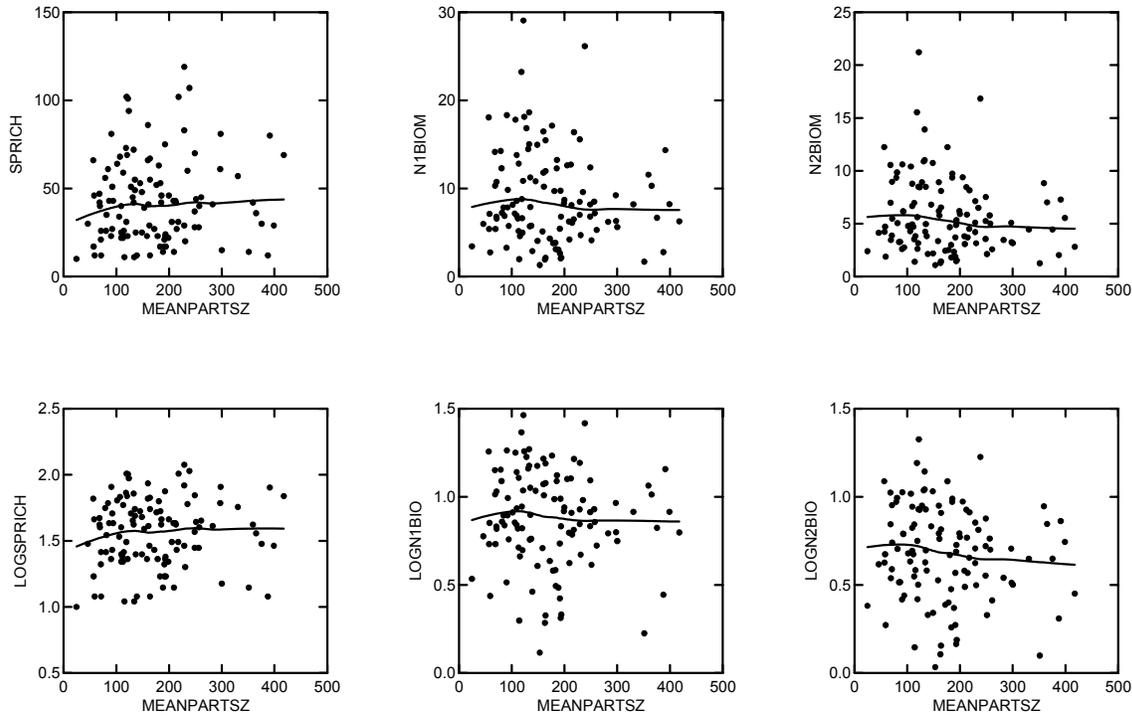
Figure 1.4.3.15. Relationships between species richness, N_1, N_2, Log of species richness, log of N_1 and Log of N_2 based on biomass and sediment mean particle size.

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 1.4.3.16). When all the data were included a major outlier with considerable leverage had a large influence on the fitted relationship (Figure 1.4.3.16A). This was the rectangle that was intensively sampled by the German partner (Figure 1.2.1.1). This rectangle stood out as having relatively high species richness, surrounded by rectangles with among the lowest species richness recorded (Figure 1.3.4.1). It would seem that this rectangle was over-sampled with respect to species richness, such that the count of species became "saturated" (see Greenstreet et al 2007a; 2007c)). 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 1.4.3.16B). 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 1.4.3.1). Examination of Figure 1.4.3.1 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.
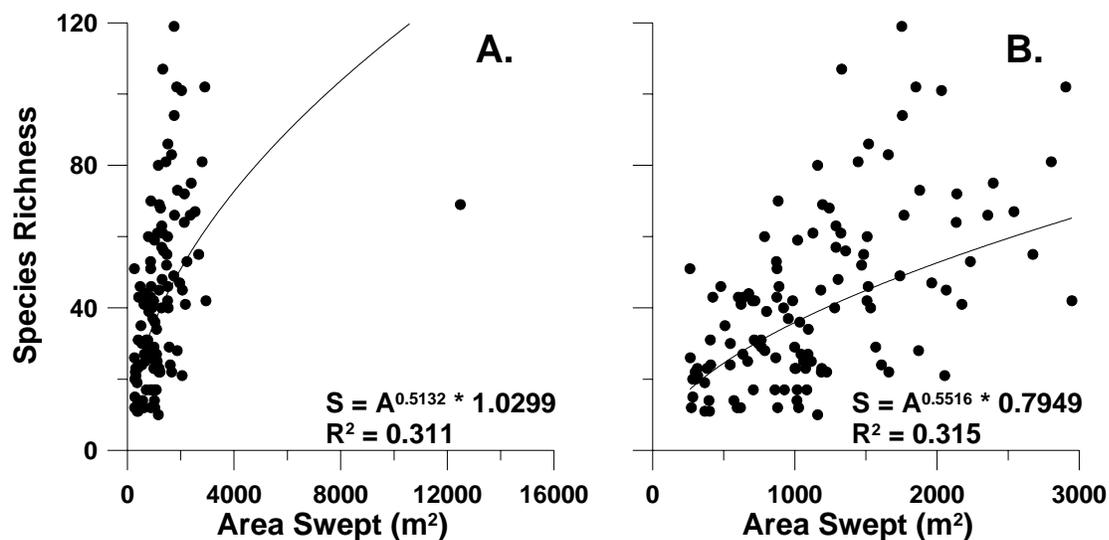
Figure 1.4.3.16. Relationships between the species richness estimates for each ICES rectangle and the area swept by the 2m beam trawl. Plot A shows the relationship calculated for all rectangles sampled. Plot B shows the same data, but excluding the rectangle intensively sampled by the German partner.

Metric	Intercept	Slope	P	R^2
Numerical N_1	-4.695	5.073	0.029	0.040
Numerical N_2			Not Significant	
Log Numerical N_1	0.231	0.230	0.027	0.041
Log Numerical N_2			Not Significant	
Biomass N_1	-10.994	6.571	0.000	0.124
Biomass N_2	-5.558	3.726	0.001	0.089
Log Biomass N_1	-0.113	0.325	0.000	0.110
Log Biomass N_2	-0.160	2.77	0.001	0.083

Table 1.4.3.1. 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.

1.3.5. Productivity

Total epibenthic invertebrate biomass and production varied considerably across the North Sea (Figure 1.3.5.1), with no clear geographic trends (Figure 1.3.5.2, Table 1.3.5.1). 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 1.3.5.3, Table 1.3.5.1). Because of this, productivity also tended to decrease in the muddier parts of the North Sea, but P/B ratios were also lower (Figure 1.3.5.3, Table 1.3.5.1). However, productivity was also significantly influenced by bottom water temperature (Figure 1.3.5.3, Table 1.3.5.1). 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 1.3.5.3, Table 1.3.5.1). 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 1.3.5.3, Table 1.3.5.1). 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 1.3.5.3, Table 1.3.5.1).
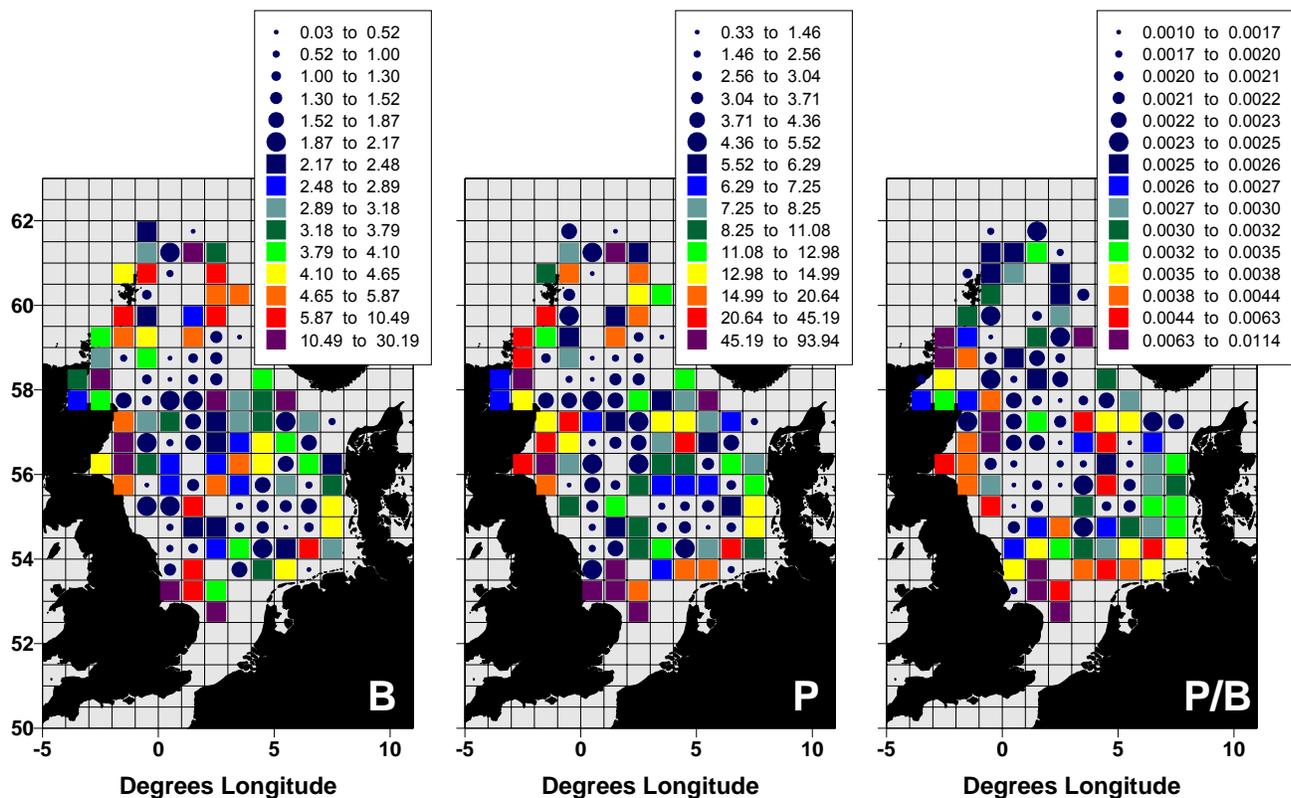
Figure 1.3.5.1. Plots of the spatial distribution of total epibenthic invertebrate biomass (g.m^{-2}) (B), secondary production (mg.m^{-2}.d^{-1}) (P), and the production/biomass ratio (P/B).
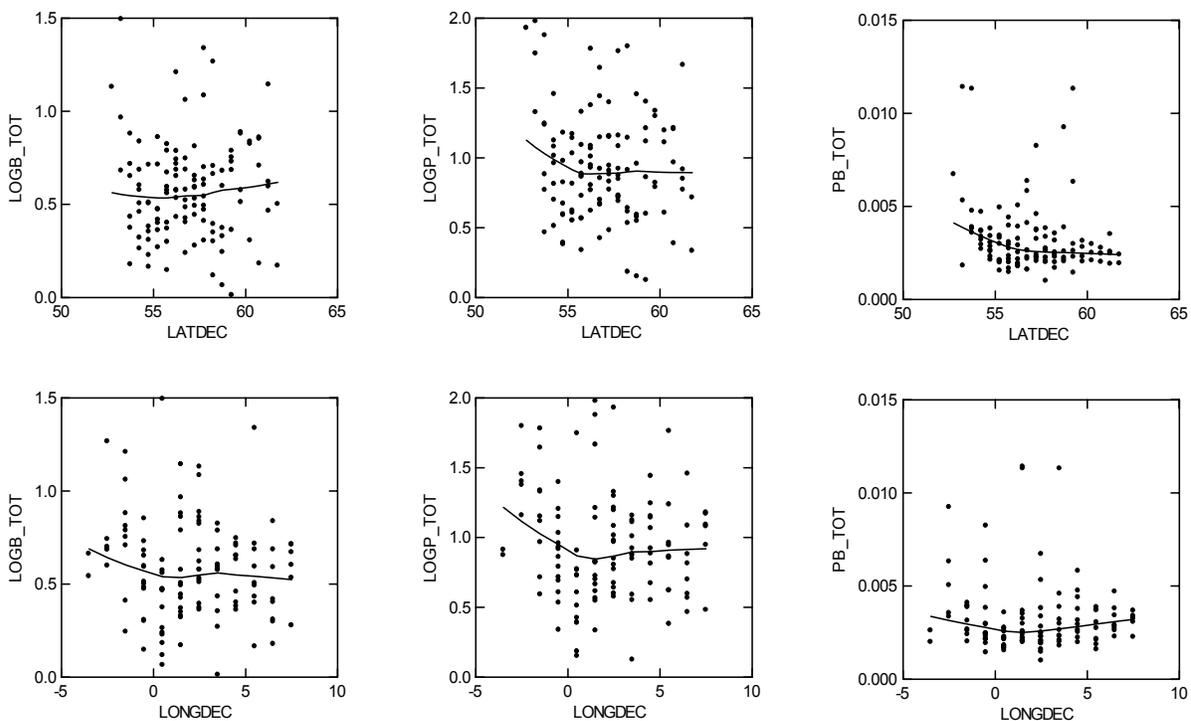
Figure 1.3.5.2. Relationships between Log biomass (B) (g.m^{-2}), Log production (P) (mg.m^{-2}.d^{-1}) and the production-biomass ratio (PB) and latitude and longitude

	Biomass	Production	P/B ratio
Latitude	0.944	0.151	0.017*
Longitude	0.249	0.268	0.492
Water depth	0.228	0.007**	0.028*
Bottom water temperature	0.084	0.000***	0.000***
Bottom water salinity	0.781	0.109	0.057
Sediment mean particle size	0.013*	0.001***	0.019*

Table 1.3.5.1. 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 1.3.5.3. 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 relationship run contra to current general dogma, that increased biodiversity leads to raised productivity (Emmerson & Huxham 2002; Tilmanet al 2001; 2002;Worm & Duffy 2003).
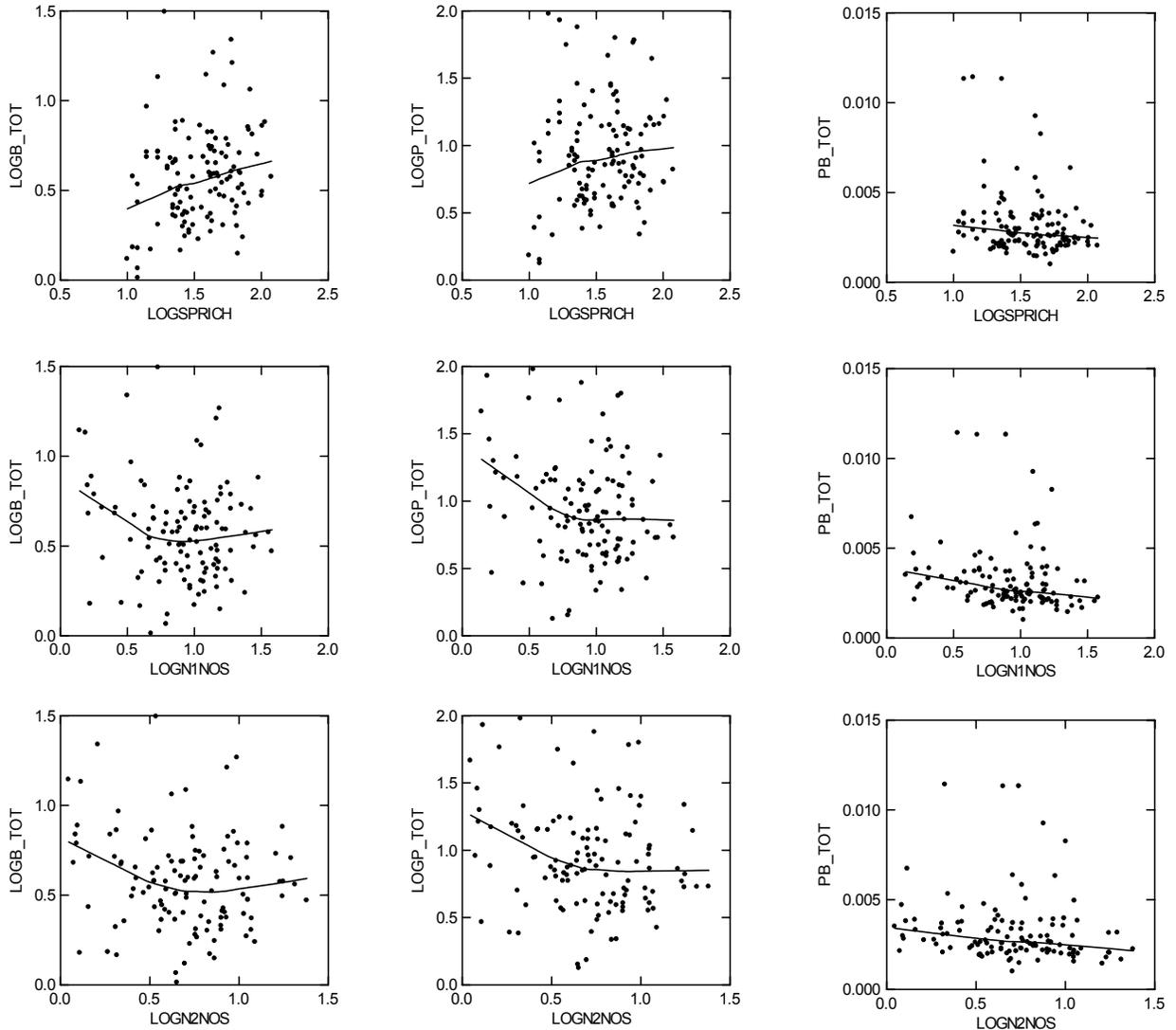
Figure 1.3.5.4. Relationships between Log biomass (B) (g.m^{-2}), Log production (P) (mg.m^{-2}.d^{-1}) and the species richness and diversity of the epibenthic invertebrate community.

Figures 1.3.5.5 to 1.3.5.7 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.
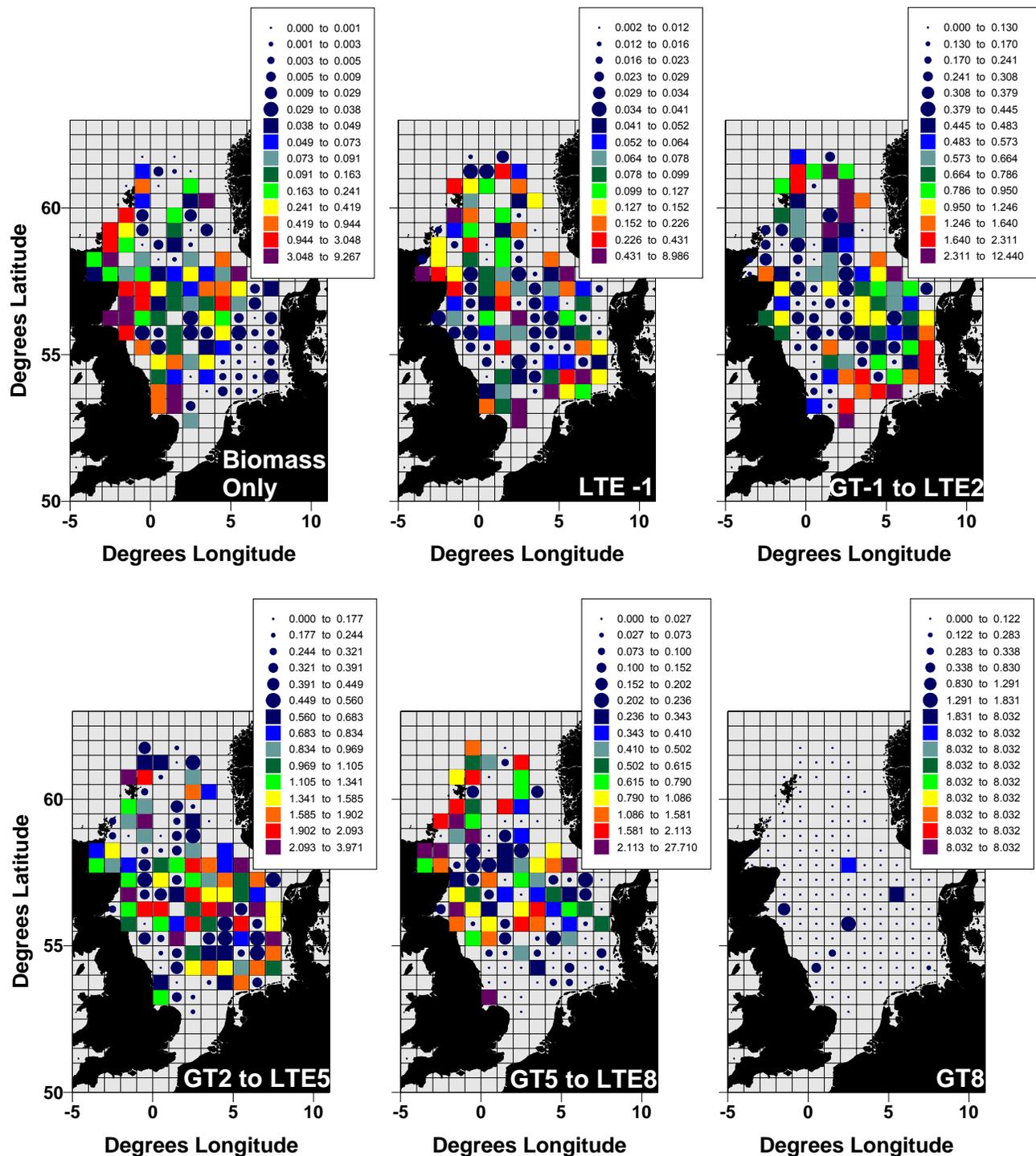
Figure 1.3.5.5. Plots of the spatial distribution of total epibenthic invertebrate biomass (g.m^{-2}) assigned to six different types or weight ranges of organism. Biomass Only: invertebrates that could not be individually counted or weighed; LTE-1: individual invertebrates of Log$_2$ body mass less 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 5; GT8: individual invertebrates with Log$_2$ body mass greater than 8.
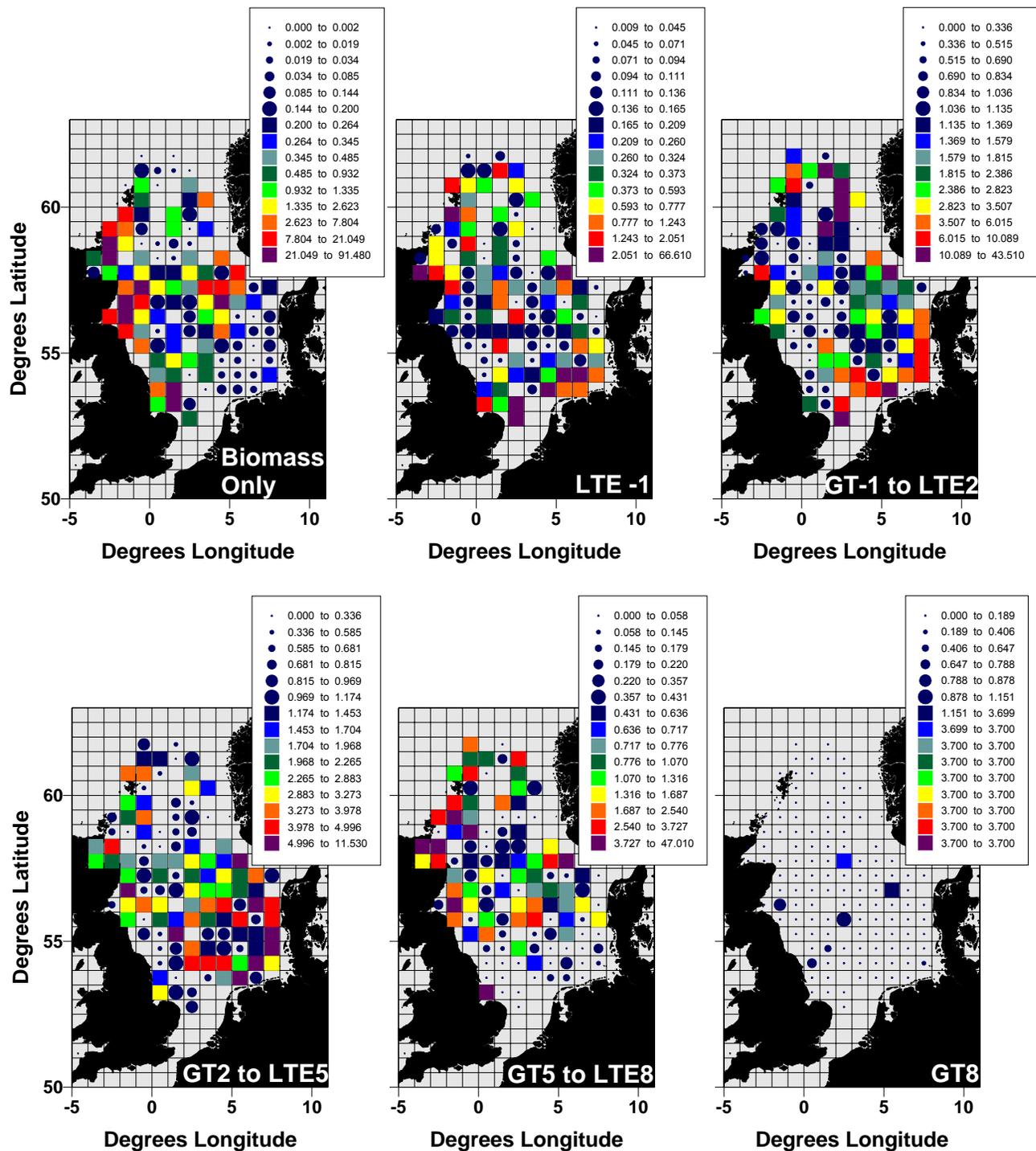
Figure 1.3.5.6. Plots of the spatial distribution of total epibenthic invertebrate production (mg.m^{-2}.d^{-1}) assigned to six different types or weight ranges of organism. Biomass Only: invertebrates that could not be individually counted or weighed; LTE-1: individual invertebrates of Log$_2$ body 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 5; GT8: individual invertebrates with Log$_2$ body mass greater than 8.
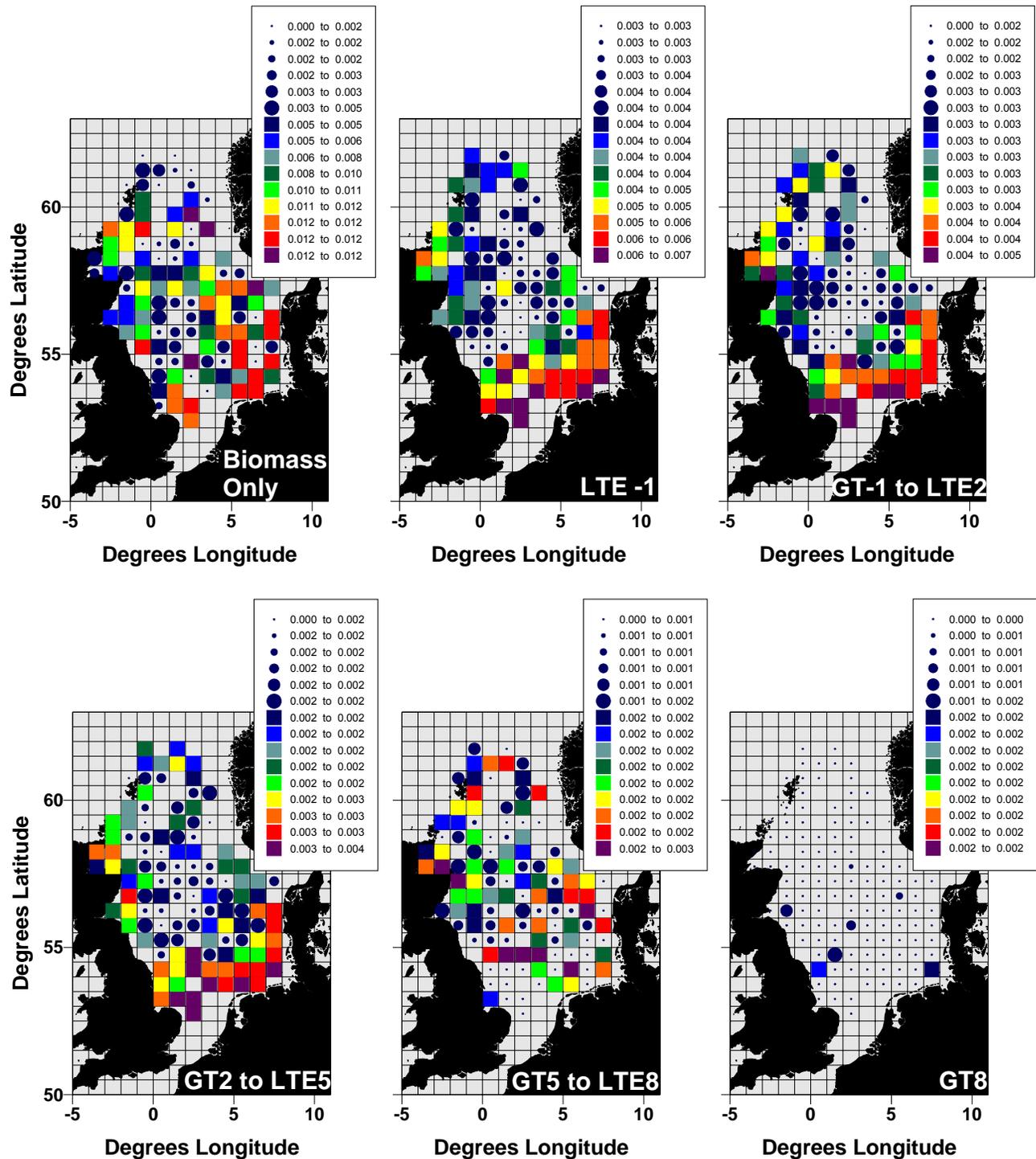
Figure 1.3.5.7. Plots of the spatial distribution of total epibenthic invertebrate production/biomass ratio assigned to six different types or weight ranges of organism. Biomass Only: invertebrates that could not be individually counted or weighed; LTE-1: individual invertebrates of Log_2 body mass less 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 5; GT8: individual invertebrates with Log_2 body mass greater than 8.

2. THE INFAUNAL INVERTEBRATE COMMUNITY

2.1. INTRODUCTION

The infauna (endofauna) are the component of the benthic invertebrate community that spend the majority of their lifecycle living within 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 (for examples see Basford *et al.*, 1990; Duineveld *et al.*, 1991; Heip & Craeymeersch, 1995; Kroncke, 1995; Kunitzer *et al.*, 1992). Based on the findings of these studies, the major factors affecting the distribution of infaunal invertebrate communities within the North Sea are sediment composition, depth, food availability and water temperature. This leads, at the coarsest level, to a division of northern taxa that extend south to the northern margins of the Dogger Bank; and southern taxa that extend north to the 100m depth contour. There is an area of overlap and variability around the 70m depth contour in the central North Sea. Temporal variability at smaller scales has been attributed to a number of potential driving factors including eutrophication and temperature effects (particularly in the shallower areas of the North Sea), fisheries disturbance and localised changes in availability of food resources (see reviews in Clark & Frid, 2001; Kroncke & Bergfeld, 2001).

It was considered essential to include the infaunal community in the sampling of the benthic community because of its contribution to secondary production available to the rest of the demersal community (larger epifaunal invertebrates and the invertebrate feeding demersal fish). Infaunal production is calculated here and used in tests of Huston's model linking both diversity of demersal fish and the larger epifaunal invertebrate assemblages to secondary production and fisheries disturbance (Greenstreet et al 2007d). At the same time some broad descriptions of distributions of key taxa and diversity and composition of these are described in terms of the North Sea system.

2.1.1. The community described

In attempting to describe the infaunal 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. This is not the absolute infaunal community, but that which has been sampled by the gear and retained in the handling process. As discussed in Annexes 4 and 5, no sampling gear ever samples all the individuals present. However, infauna are sampled using a Van Veen grab and this can be described as a quantitative sampler for those infaunal animals that live within the depth range that it samples. We acknowledge that certain animals living below the depth of sediment sampled (some of high biomass and thus high contribution to production) will not be sampled well by this sampling apparatus. Also, those highly mobile animals living in contact with the seafloor (hyperbenthos) will also be poorly represented because they can move out of the way of the grab before it makes contact. The community described is a macrofaunal assemblage of animals large enough to be retained in a 1mm sieve.

2.1.2. 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 require 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 (Cushman *et al.*, 1978; Wildish & Peer, 1981; Crisp, 1984; Morin *et al.*, 1987). None of these methods are practical when trying to quantify secondary production at the community level. In this project, assessments of the secondary production from the infaunal and epifaunal benthos at between 100 and 150 stations per year over two years have been undertaken.

Over the last 20 years, efforts have turned towards parameterising empirical models that can be used to estimate secondary production (for review see 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. A detailed review of the empirical models that have been developed is given in Section 1.

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 infaunal data have been size structured to reduce the variability around the mean individual weight per taxon using a stacked sieve method (see Edgar, 1990a) and error associated with individual taxa relationships is reduced when applied to the entire community (Brey, 2002; Edgar, 1990b). In this project we examined the methods available for estimating secondary productivity from the infauna. The infauna include both colonial and individual based populations of animals. Due to this it was necessary to combine two methods, one based on biomass (for colonial animals), and one based on average mean weight per sieve size class.

2.2. METHODS

2.2.1. Data set

Five 0.1 m^2 Van Veen grabs were taken at each station sampled, close to the track of the main demersal fish-sampling trawl. Overall 1250 Van Veen grab samples were taken across the North Sea, from 250 stations (120 in 2003 and 130 in 2004) but it was only possible to process the samples from 200 of these stations (105 in 2003, 95 in 2004; red stations in Figure 2.2.1.1.). Sampling was undertaken between July and September in each year. Bottom water temperature data, necessary for the production calculations, were recorded using a CTD at the time of sampling.
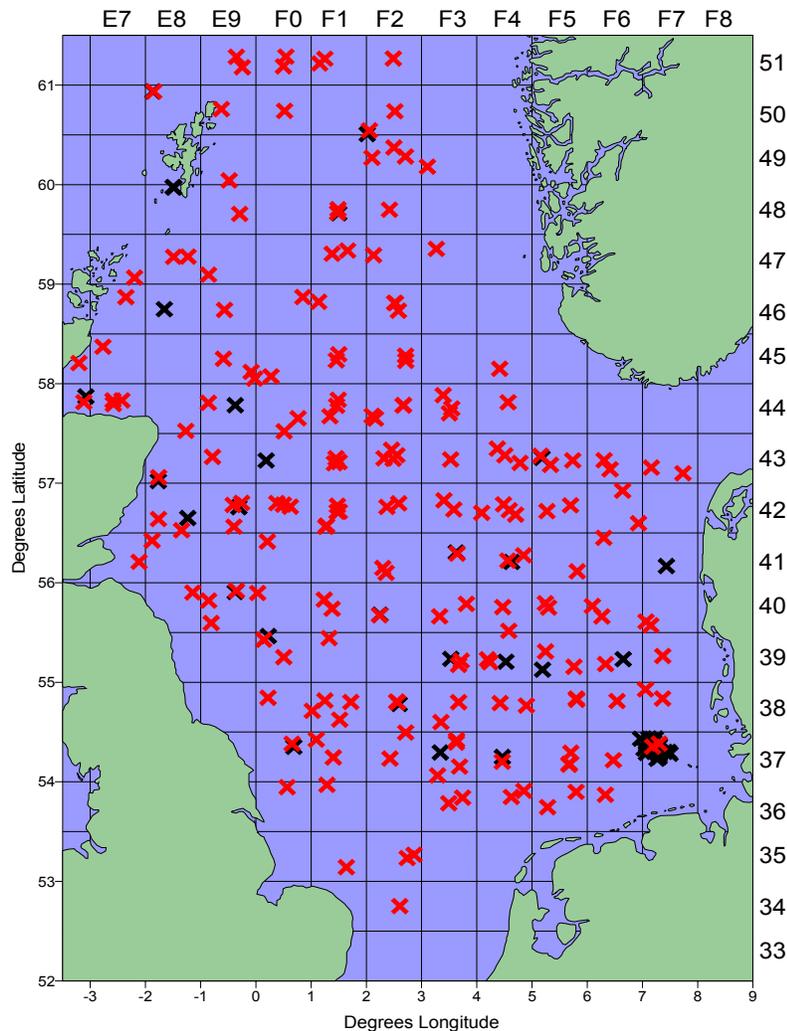
Figure 2.2.1.1. All 250 stations sampled for infauna with Van Veen grabs (5 taken at each station) during the 2003 and 2004 surveys. Red stations indicate the 200 stations it was possible to process and analyse in this report.

2.2.1.1. *Sample Treatment.*

Infaunal samples were washed through a stack of sieves (0.5mm, 1mm, 2mm and 4mm) and all material preserved before processing in the laboratory. Total abundance and total biomass of animals in the 1-4mm sieves were recorded for animals sorted to one of 73 possible taxon groups (Appendix 1). The criteria used to determine the taxon groups were; (1) The ease to separate out animals into these groups during the sorting process (i.e. no requirement for use of keys; obvious at first sight); (2) the likelihood of the groups within Phyla having different morphologies and different behaviours in the sieving process. Samples were also identified and enumerated at the species level (where possible) but the species level data are not considered further here. A detailed description of the sample processing is given in the methods manual (Callaway 2007).

2.2.1.2.   *Data Standardisation*

It was assumed that catchability of the gear was consistent for the assemblage found within the depth range sampled by the Van Veen grab. However, it is acknowledged that depth range sampled varies dependent on sediment type of the sample location. Those species living outside of the sampled depth range are not covered in this assemblage and it is accepted that this will have implications for total biomass, productivity and diversity of the communities described. We also recognise that the volume of sediment sampled by each individual grab varied around a mean of 10 litres. Unfortunately it was not possible to standardise abundance and biomass data to account for this variation in volume sampled, because several sets of stations did not have a recorded volume per sample.

For all taxon groups where all or a high percentage of records had no abundance value, abundance data were converted to presence/absence codes and could not be used for abundance weighted analyses. These taxon groups included: Bryozoa, Foraminifera, Hexacorallia, Hydrozoa, Octocorallia and Porifera.

2.2.2. Distribution of total 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 numbers per m^2 by working up the individual $0.1m^2$ grab sample data to numbers per metre squared and then calculating the mean of all five grab samples per station. 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 average density and biomass (*N* and *B* per m^2) calculated for each ICES rectangle using all stations sampled in a particular rectangle. Distributions of the 12 dominant taxa based on total abundance across the survey (none-colonial taxon groups), and the 12 dominant taxa based on biomass (including colonial taxon groups) were plotted for the combined surveys.

2.2.3. Distribution of communities based on relative abundance of taxon groups (community composition)

Firstly, taxon groups were standardised within Phyla to exclude multiple taxonomic levels that could potentially cover the same animals. Inclusion of multiple taxonomic level groups could obscure true variation in community composition. The common taxonomic level varied between Phyla; in some cases all data were recorded at the Phyla level, but in most cases data were organised at the Order or Class level (See 'Community Analysis Group' list in Appendix 1). In order to enable full analysis where only presence/absence data were available, the fauna were subdivided into two groups – all infauna (including colonial species – presence/absence analysis) and non-colonial taxa only (where taxon abundance (N. m^2) for each station was used as the basic input data). A Bray-Curtis similarity matrix comparing the similarity between the infauna community taxon compositions 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 ICES rectangles with similar taxon compositions. All abundance data were root transformed to down-weight the effect of the most abundant taxa on the Bray-Curtis similarity indices. All analyses were performed using the *PRIMER©* software (Clarke & Warwick 2001).

2.2.4. Distribution of taxon group diversity

2.2.4.1. *Diversity Metrics*

Species (taxon group here) 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 (e.g. Southwood, 1978): Hill's N_0, total number of species (species richness); Hill's N_1, an index the number of species present, defined as the exponential of H', where H' is the Shannon-Wiener diversity index; and Hill's N_2 an index that is predominantly influenced by the abundance of the dominant species defined as the reciprocal of D, where D is Simpson's dominance index. Hill's N_1 is therefore computed as:

$$N_1 = e^{-\sum\limits_{s=1}^{S} p_s * Ln(p_s)}$$

2.2.4.1.1

and Hill's N_2 as:

$$N_2 = 1 \Big/ \sum\limits_{s=1}^{S} p_s^{\,2}$$

2.2.4.2.2

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.

Taxon group richness (Hill's N_0) was calculated using all taxa, whilst Hill's N_1 and N_2 indices were calculated using only the non-colonial taxon group data, as they require the individual taxon abundance values. Groupings of data were standardised to the same taxon level within Phyla as described in section 2.2.4 (see PRIMER Group list in Appendix 1). All diversity metrics were determined using the *PRIMER©* software package (Clarke & Warwick 2001).

2.2.5. Secondary production

Total community production per day (g AFDM per m^2) was estimated using an empirical model based on the relationship between daily production, mean individual body mass and water temperature following the method of Edgar (1990a). As secondary production from the benthic 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 this project was interested in spatial patterns at the scale of the North Sea, where variation in bottom temperature was considerable, it was considered imperative that temperature be taken into account. It should be noted, however, that given that the benthic survey data were collected during the summer months, biomasses and associated productions are likely to be at the peak of annual cycles.

2.2.5.1. *Edgar's (1990) Model*

Edgar's (1990) model for benthic infauna invertebrate secondary production relates production to both organism dry-weight biomass and water temperature as:

$$LogP = -2.46 + 0.79 LogB + 1.05 LogT$$

2.2.5.1.1

where P is the daily production (μgAFDM.day^{-1}), B is the mean individual ash free dry body mass (μgAFDM) and T is the bottom water temperature (ºC). Edgar's model was developed using a dataset of actual data for all of these parameters from studies of 41 macrobenthic species in environments that covered the temperature range found in the benthic surveys (6-18.5ºC). On examining this relationship, Edgar found that models for mollusca and crustacea separated from other infauna and other epifauna. Thus all the taxa in the infaunal database were assigned to one of these four groups before the empirical relationships for each one were applied (Infauna group relationship given in equation 2.2.5.1.). If some of the taxon groups were known to include both epifaunal and infaunal species, it was assumed that, as these data were collected with an infaunal sampler, the infaunal species within that taxon group would be prevalent. If there were no infaunal species known within a taxon group, this was assigned as epifaunal ('Edgar Group' in Appendix 1).

2.2.5.1.1. 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) has a table of wet mass to ash free dry mass (WM>AFDM) conversion factors for invertebrates and fish 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 taxon group in the infaunal 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).

2.2.5.2.   *Production Analysis Steps*

2.2.5.2.1. Taxa with total abundance and biomass data

For Edgar's model both 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. This was calculated for each taxon group within the individual sieve sizes of each replicate sample. 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 taxon was calculated by multiplying individual daily production per sieve size class by the total number of individuals within that sieve size and then summing all production across sieve sizes.

2.2.5.2.2. Taxa with only biomass data

For a number (or all) of the records for some taxon groups, 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 but no abundance data were given, it was still possible to assign total production using production-biomass (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 production. Three different steps were followed to assign P/B ratios to taxa with only biomass

data. Firstly, where a P/B ratio was available for that taxon group within the same sieve size based on survey data, this was used. Secondly, where no P/B ratio for the specific taxon group was available, but there were data for other taxa within the same Phylum, a Phyla level P/B ratio specific to the sieve size was assigned. Finally, where no P/B ratios were available for a Phylum (e.g. Bryozoa), the average of all P/B ratios from within the same sample and sieve size was assigned.

2.2.5.2.3. Taxa with only presence/absence data

It was not possible to estimate production attributable to these taxa because there was no measurement of individual weight or total biomass.

2.2.5.3. *Total Daily Community Production*

Once total daily production had been calculated for each taxon group within a sieve fraction following the methods described above, total community production was calculated by summing across all taxa within a sample. Station specific production was calculated for the individual survey years by calculating the mean production per station across the five replicate grab samples. ICES rectangle level data were then produced by averaging stations within individual rectangles across the two years sampled.

2.3. RESULTS

2.3.1. Distribution of abundance and biomass

From the 200 stations sampled and processed over the two years of surveys, a total of 73 taxon groups were recorded from the Van Veen grab samples covering 23 different Phyla (Appendix 1). Of these 73 taxon groups, the 12 dominant taxa based on abundance (none-colonial taxa only) made up 85% of the total abundance across the whole survey, whilst the 12 dominant taxa based on biomass made up 88% of the total biomass across the whole survey. Spatial variation in mean total density is shown in Figure 2.3.1.1 and whilst highest abundances are mainly located in the southern North Sea, distribution of high biomass areas is more variable. The spatial distributions of the key taxon groups based on abundance and biomass (Figures 2.3.1.2 and 2.3.1.3) illustrate a number of different patterns in terms of dominance. Some taxa were particularly dominant in small areas and rare elsewhere (e.g. Phoronida and Echinoidea) whilst others were more dominant in a particular area of the North Sea (e.g. Scaphopoda, Echinoida and Nematoda in the northern North Sea and Pelecypoda, Asteroidea and Ophiuroidea in the southern North Sea) and some were fairly ubiquitous in their distributions (e.g. the Polychaete groups). Examination of the influence of environmental factors on these distributions is not implicitly undertaken here. However, given the well described differences in terms of depth, temperature and hydrography in the southern and northern North Sea, it is clear that some of these taxon groups may be more sensitive to these drivers than others.
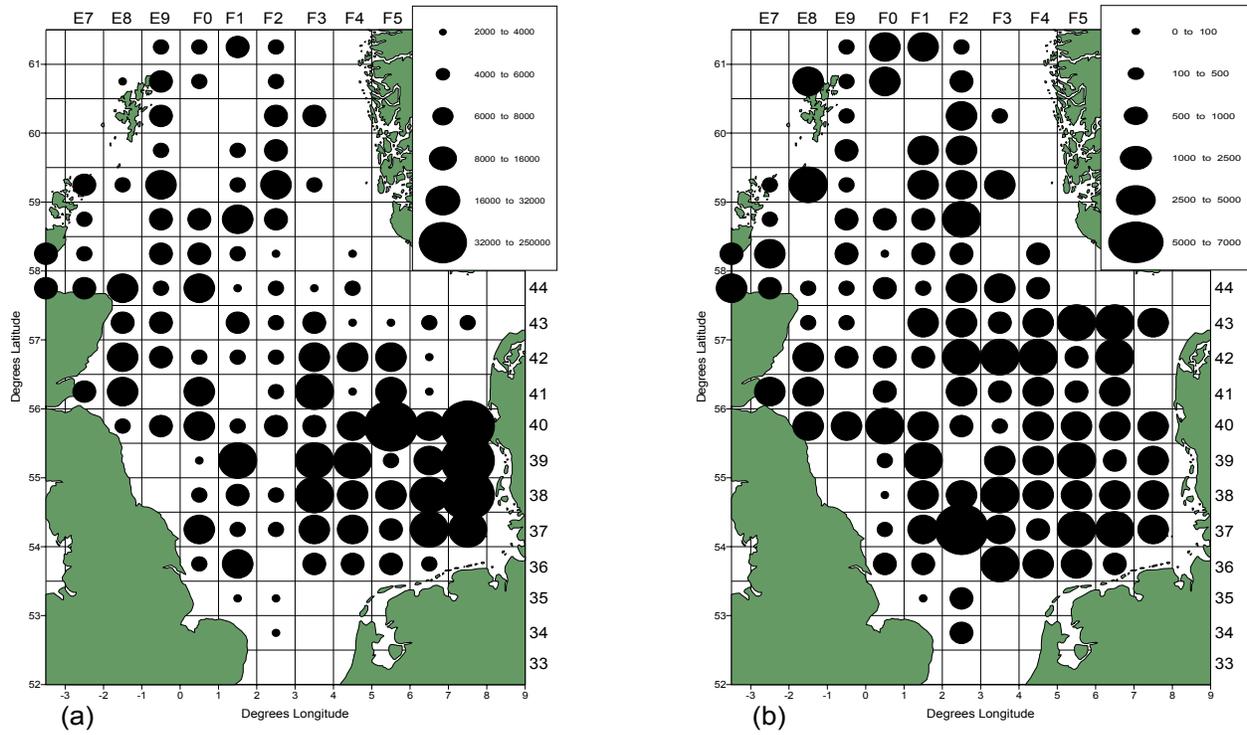
Figure 2.3.1.1. Spatial variation in mean density of the infaunal community based on (a) abundance (N. m^{-2}) (none-colonial taxa only) and (b) biomass (g wet weight. m^{-2}) (all taxa).
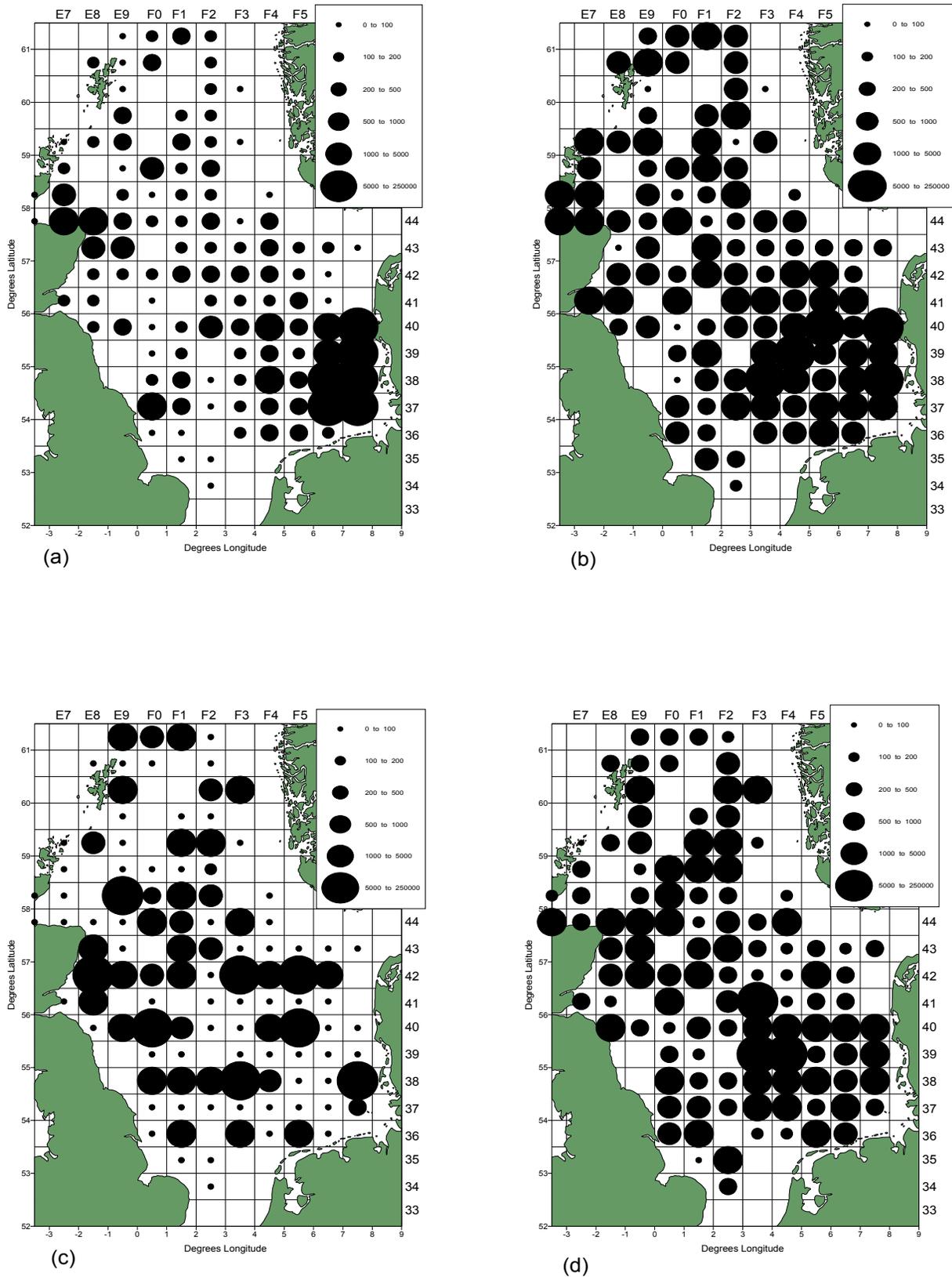
Figure 2.3.1.2. Spatial variation in mean density (N. m^{-2}) of the dominant taxon groups based on abundance: (a) Phoronida, (b) Polychaeta sedentaria, (c) Polychaeta, (d) Spatangoida.
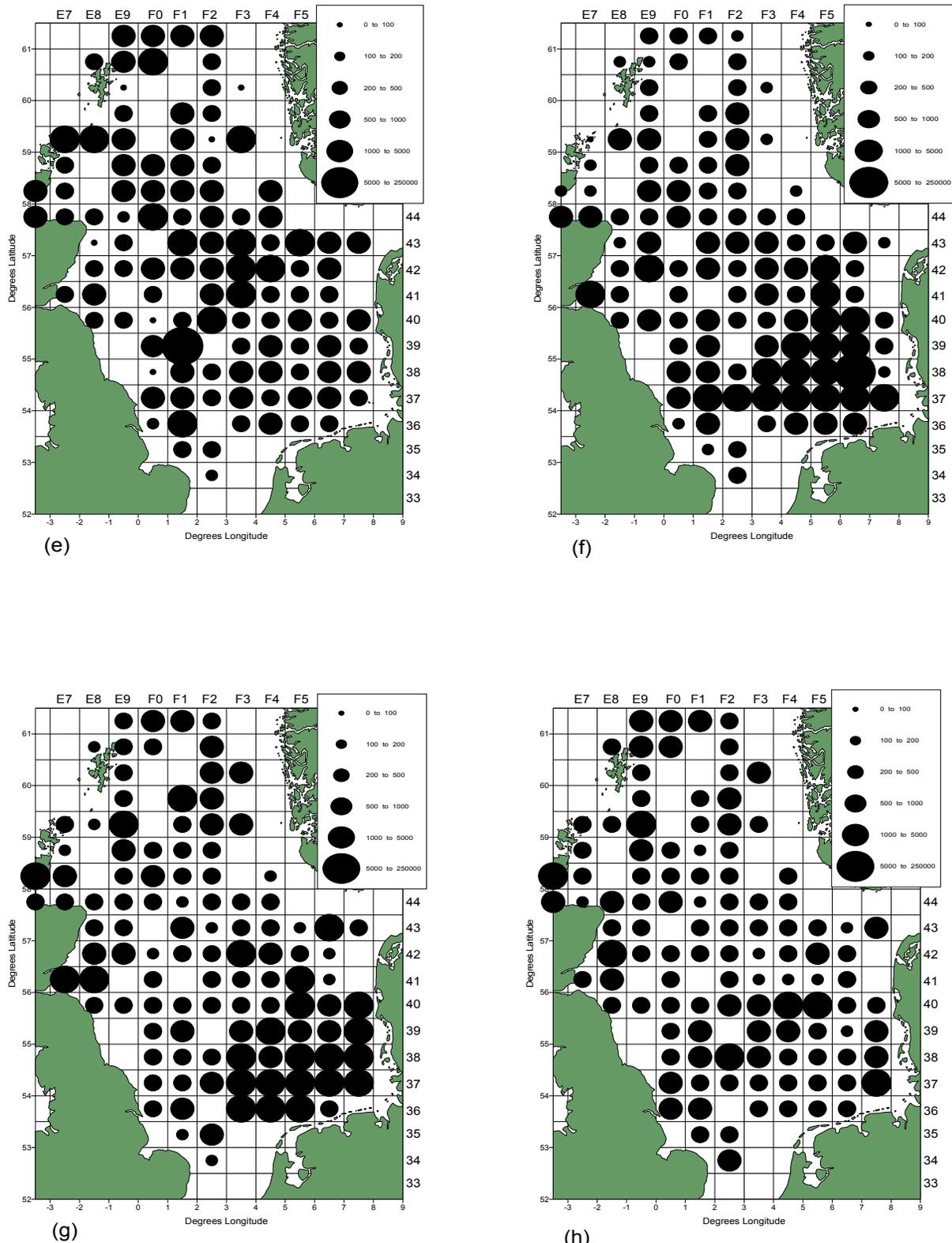
Figure 2.3.1.2 continued. Spatial variation in mean density (N. m m^{-2}) of the dominant taxon groups based on abundance: (e) Polychaeta errantia, (f) Ophiuroidea, (g) Pelecypoda, (h) Amphipoda.
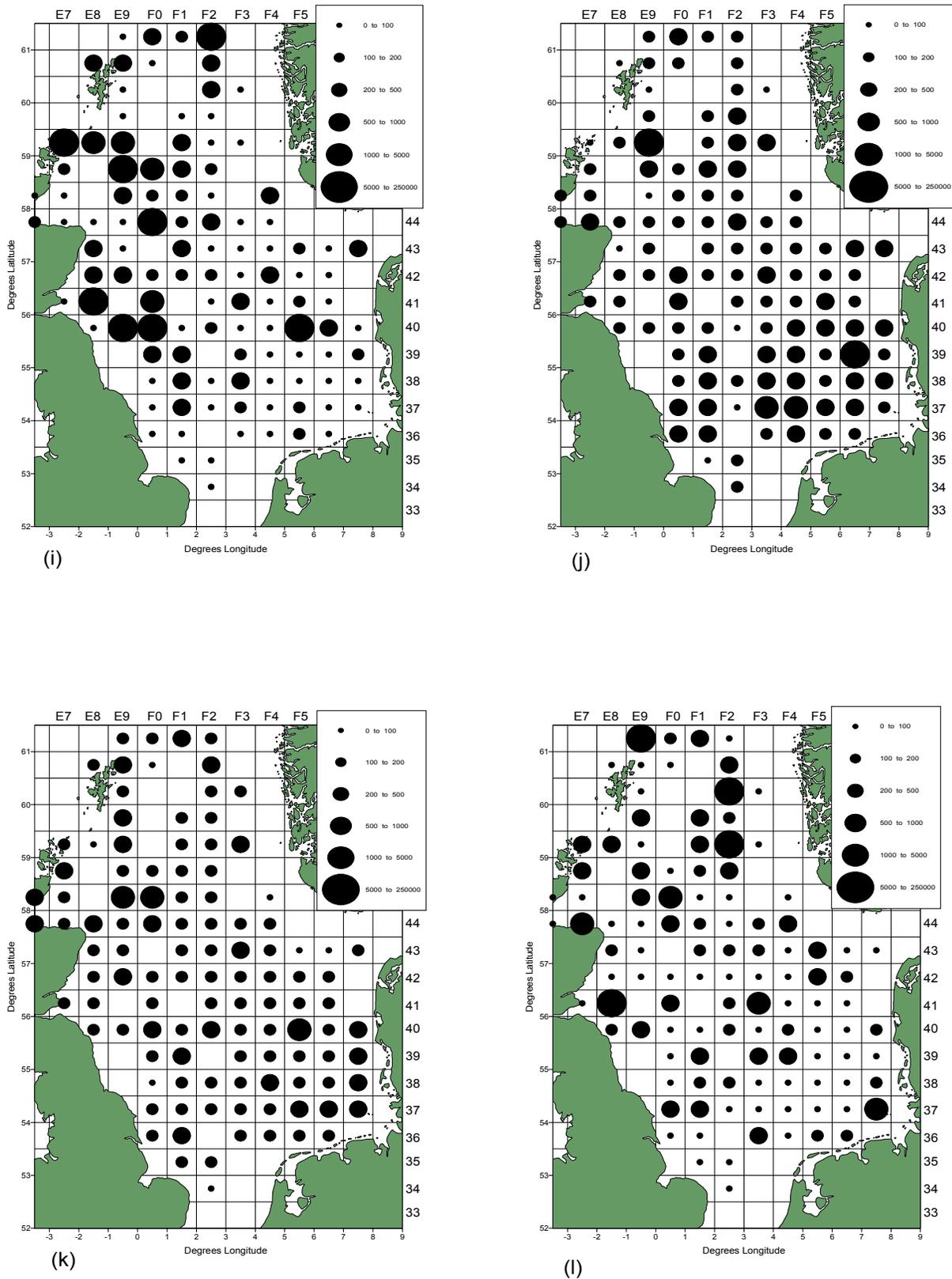
Figure 2.3.1.2 continued. Spatial variation in mean density (N. m^{-2}) of the dominant taxon groups based on abundance: (i) Nematoda, (j) Gastropoda, (k) Cumacea, (l) Echinoida.
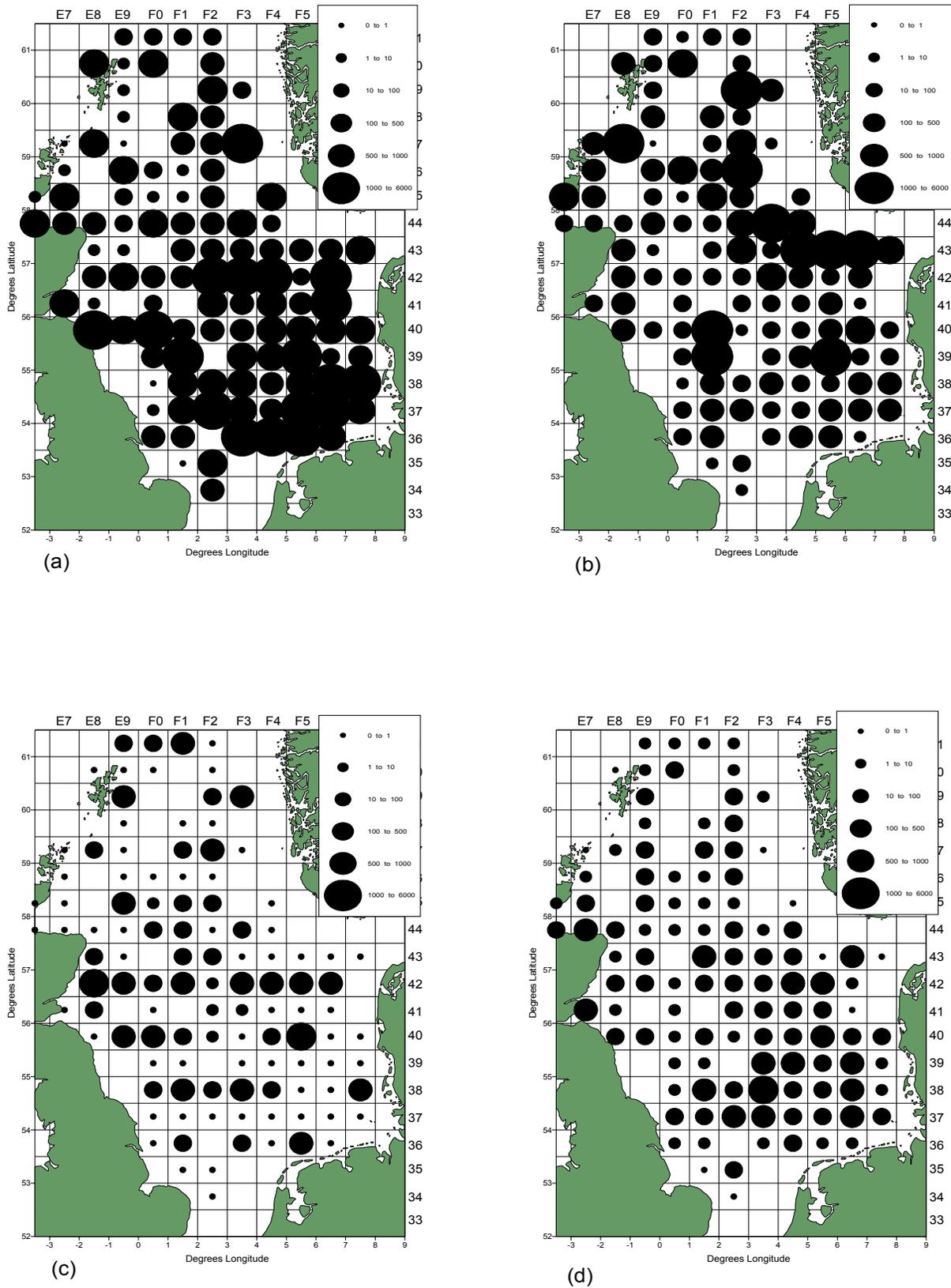
Figure 2.3.1.3. Spatial variation in mean density (g WW. m^{-2}) of the dominant taxon groups based on biomass: (a) Spatangoida, (b) Pelecypoda, (c) Polychaeta, (d) Ophiuroidea.
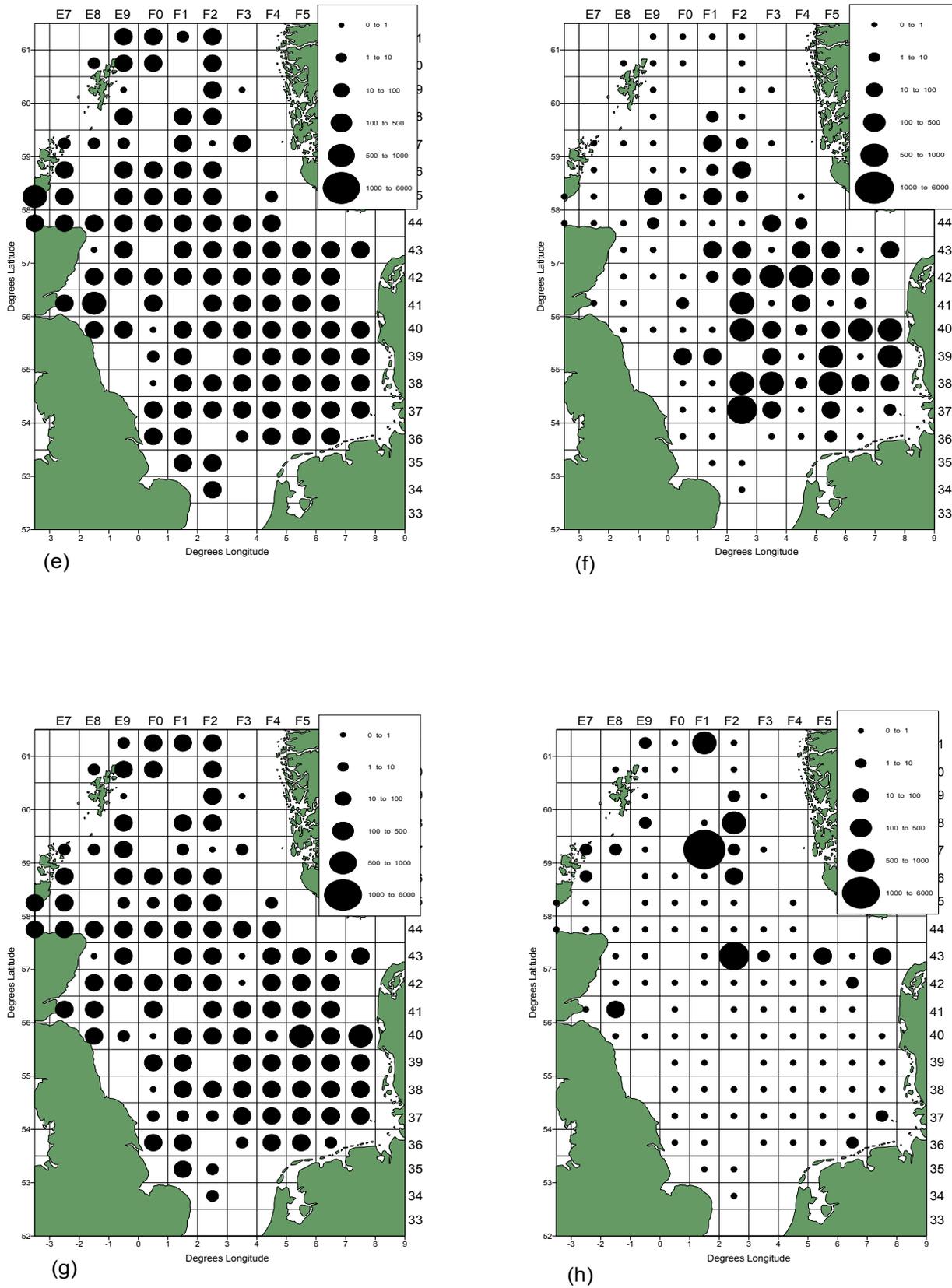
Figure 2.3.1.3 continued. Spatial variation in mean density (g WW. m^{-2}) of the dominant taxon groups based on biomass: (e) Polychaeta errantia, (f) Asteroidea, (g) Polychaeta sedentaria, (h) Echinoida.
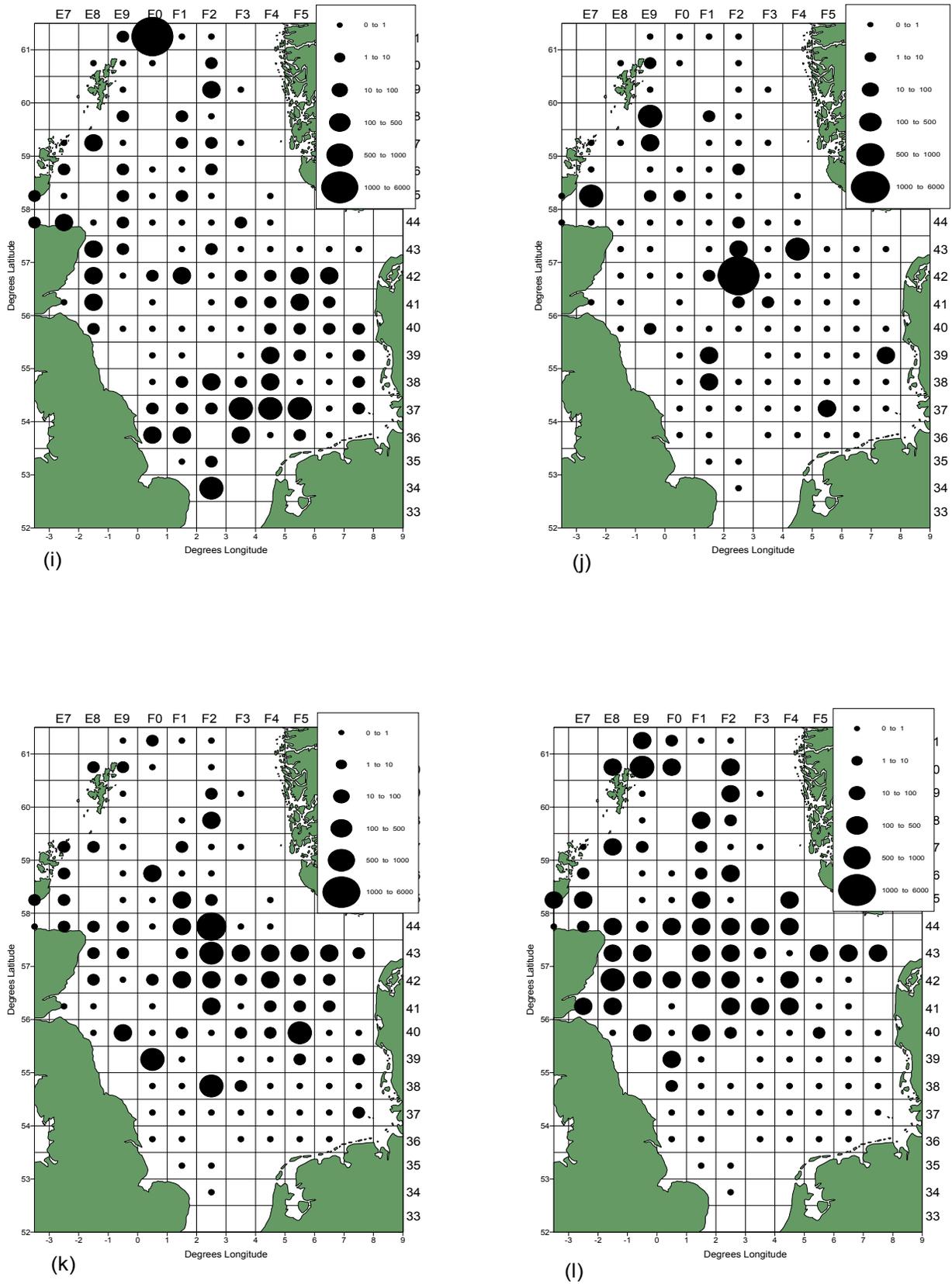
Figure 2.3.1.3 continued. Spatial variation in mean density (g WW. m^{-2}) of the dominant taxon groups based on biomass: (i) Decapoda, (j) Echinoidea, (k) Actinaria, (l) Scaphopoda.

2.3.2. Community structure based on relative abundance of taxon groups

Following hierarchical cluster analysis of the stations based on the Bray Curtis similarity in taxon group composition, two main clusters were identified in the infaunal community data that had over 65% similarity between rectangles within them (Figure 2.3.2.1. red and blue clusters). These clusters were identified independent of whether the analysis included just the abundance-weighted taxon data or the presence/absence data of all species including colonials. Infact the inclusion of colonial species appeared to have little effect in altering the clustering of contagious stations to that already shown by the abundance-weighted data (Figures 2.3.2.1. ands 2.3.2.2.). Broad distributions appeared to be show clear resemblance to the major patterns observed for both the epibenthic and demersal fish communities (Section 1 and Greenstreet et al 2007a). The outlier stations (all labeled as one cluster for convenience here in green), were found mainly around the edges of the survey area, which could reflect increased heterogeneity of environmental variables in these areas, but could equally be an artifact edge effect on the analysis. The distributions do suggest areas of increased heterogeneity in the south- and central-west North Sea and the eastern and northeastern North Sea.
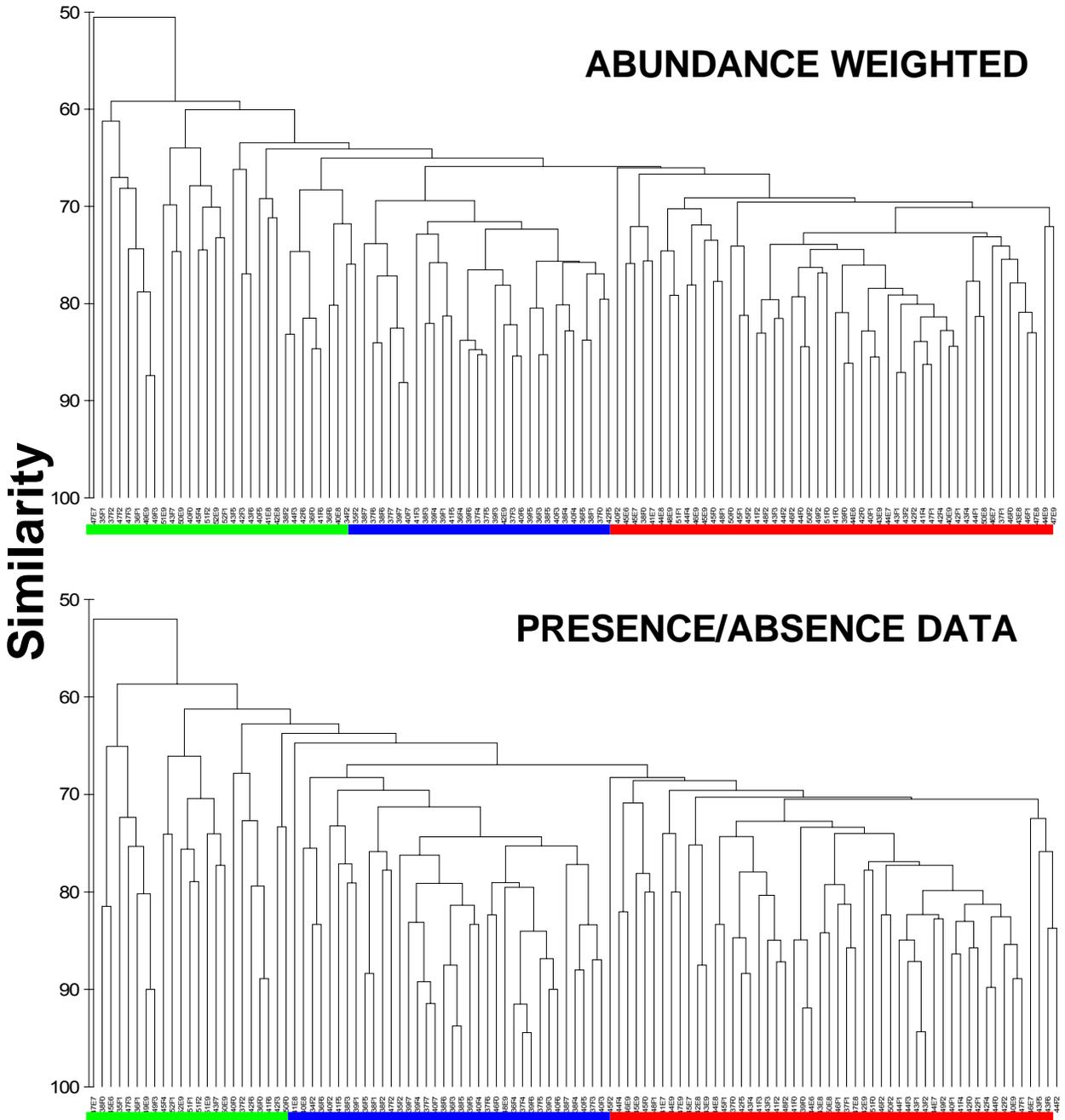
Figure 2.3.2.1. Group average cluster dendograms of the similarity of relative infaunal taxon group densities based on mean abundance (N. m^{-2}) and presence-absence data for each ICES rectangle. Colour coding links to Figure 2.3.2.2.
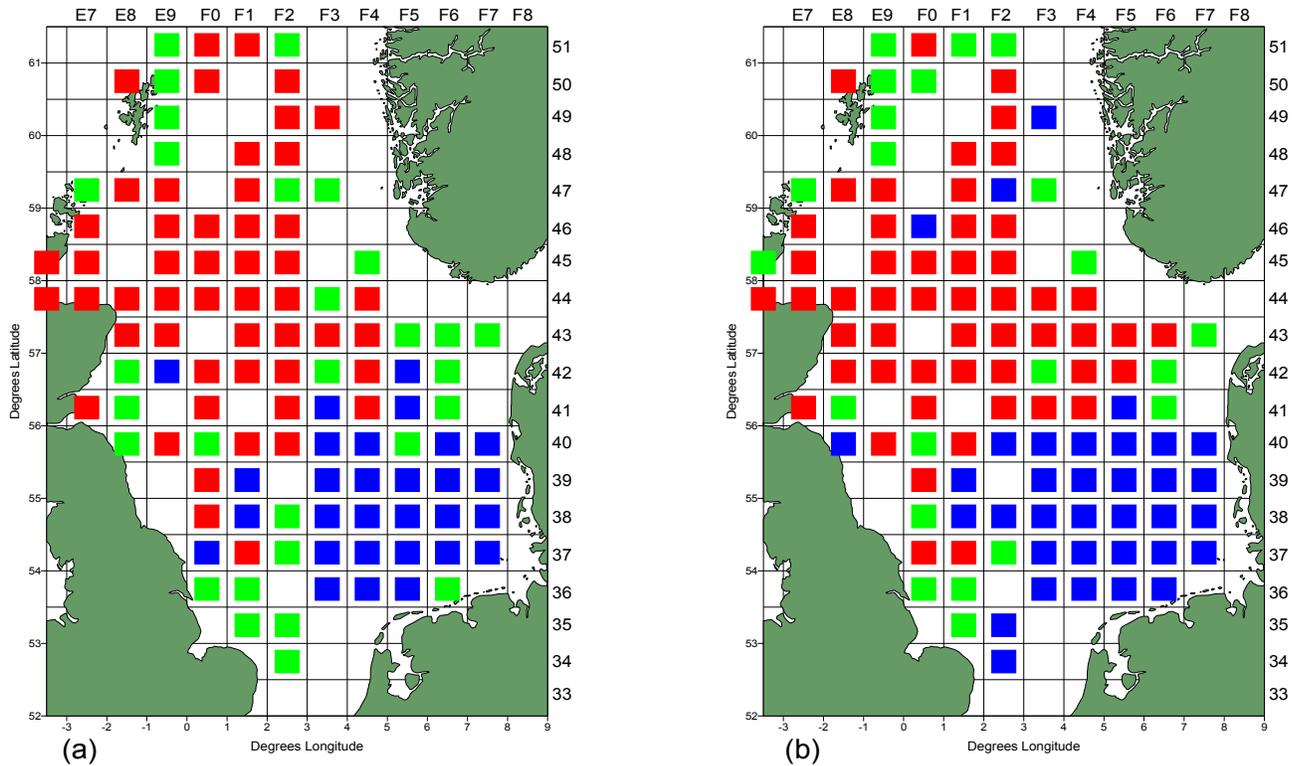
Figure 2.3.2.2. Spatial distributions of the clusters defined in Figure 2.3.2.1. based upon (a) mean abundance (N. m^{-2}) and (b) presence-absence data for each ICES rectangle. Colour coding links to Figure 2.3.2.1

2.3.3. Taxon group diversity

Infaunal taxon group richness varied from 8 to 32 taxa found from a potential pool of 49 taxon groups. Even at this coarse taxonomic level, where most taxon groups were not resolved further than Order or even Class and Phyla, there is some evidence of higher richness in taxonomic groups in the northern North Sea which corresponds with the overall patterns found for epibenthos in Section 1 (Figure 2.3.3.1 (a)). For non-colonial fauna, Hill's diversity indices N1 and N2 were also calculated, taking into account the effect of individual abundance in addition to the number of species. The general trend of higher diversity in the northern North Sea is confirmed, but both indices also indicate some relatively diverse areas in the central North Sea (Figure 2.3.3.1 (b) and (c)).
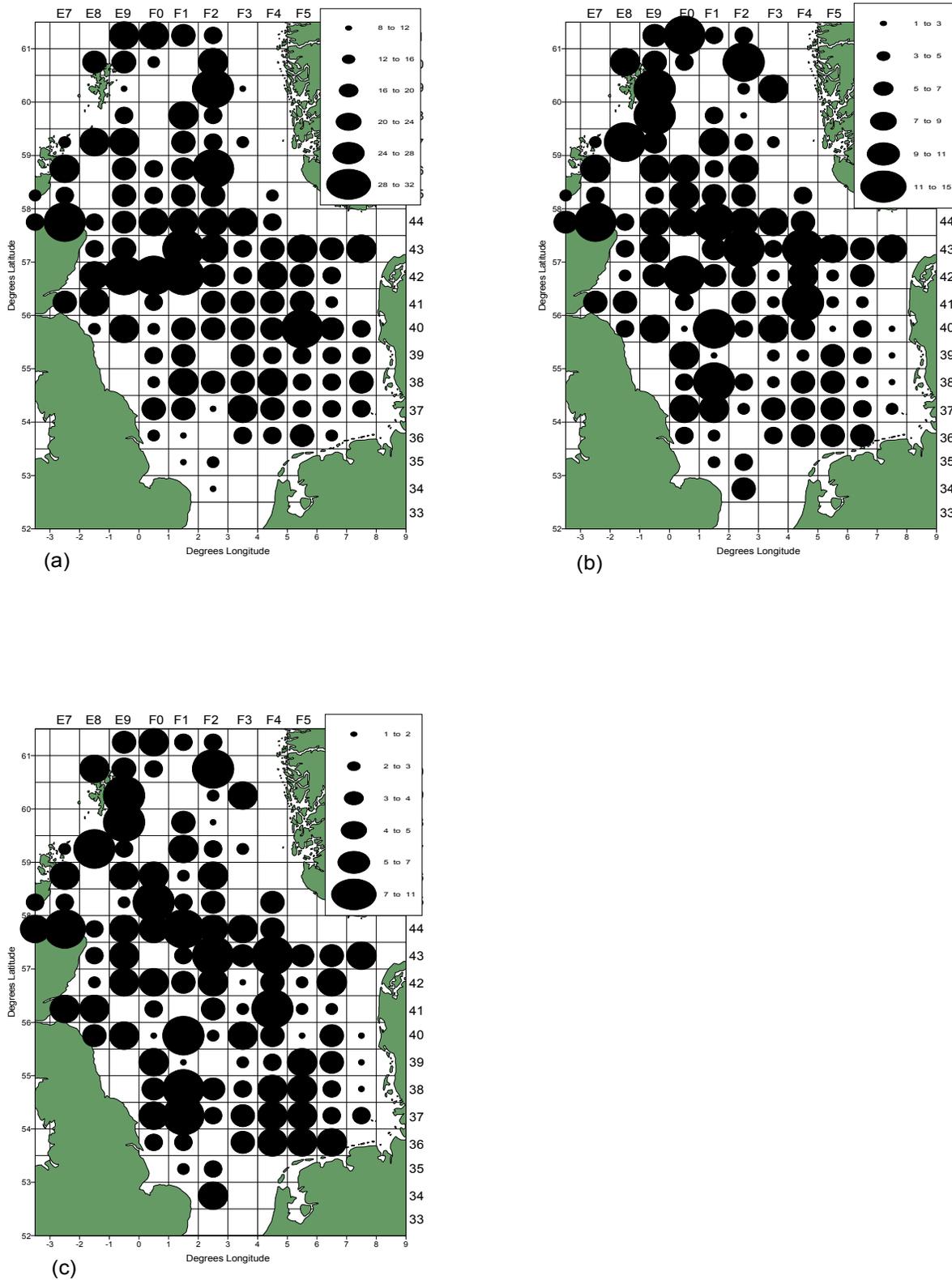
Figure 2.3.3.1. Spatial distributions of (a) species richness based on all taxa and Hill's (b) N1 and (c) N2 calculated on mean abundance (N. m^{-2}) for each ICES rectangle.

2.3.4. Distribution of secondary production

Total infaunal community production was highest in the southern North Sea but there were also a number of smaller separate areas with comparable levels of production (Figure 2.3.4.1.). Animals found in the 4mm sieve fraction of the samples were found to contribute the most to overall production even though the smaller animals had much higher P/B ratios. In these cases the greater biomass of the larger animals outweighs the higher metabolic rates of the smaller animals in terms of actual daily production rates.

Figure 2.3.4.1. Spatial variation in daily production (g AFDM m^{-2} day^{-1}) of (a) the whole infaunal community, (b) the infauna retained in a 1mm sieve, (c) 2mm sieve and (d) 4mm sieve.

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4. APPENDIX 1

List of Taxon groups found from 200 stations sampled for infauna in the North Sea in 2003 and 2004

Taxon Group	Phylum	Class	Community analysis group	Brey AFDW conversion group	Edgar productivity group
Hirudinea	Annelida	Hirudinea	Hirudinea	Annelida	Infauna
Oligochaeta	Annelida	Oligochaeta	Oligochaeta	Oligochaeta	Infauna
Polychaeta	Annelida	Polychaeta	Polychaeta	Annelida	Infauna
Polychaeta errantia	Annelida	Polychaeta	Polychaeta	Polychaeta errantia	Infauna
Polychaeta sedentaria	Annelida	Polychaeta	Polychaeta	Polychaeta sedentaria	Infauna
Insecta	Arthropoda	Insecta	!!EXCLUDE	Crustacea	Crustacea
Brachiopoda	Brachiopoda		Brachiopoda	Cnidaria	Infauna
Bryozoa	Bryozoa		Bryozoa	Bryozoa	Epifauna
Chaetognatha	Chaetognatha		Chaetognatha	Chaetognatha	Epifauna
Prostigmata	Chelicerata	Arachnida	Prostigmata	Crustacea	Crustacea
Ascidia	Chordata	Ascidiacea	Enterogona	Ascidiae	Epifauna
Tunicata	Chordata	Ascidiacea	Tunicata	Ascidiae	Epifauna
Osteichthyes	Chordata	Osteichthyes	Osteichthyes	Demersal Fish	Epifauna
Osteichthyes demersal	Chordata	Osteichthyes	Osteichthyes	Demersal Fish	Epifauna
Cephalochordata	Chordata		Cephalochordata	Ascidiae	Infauna
Tunicata	Chordata		Tunicata	Ascidiae	Epifauna
Hexacorallia	Cnidaria	Hexacorallia	Hexacorallia	Actinaria	Infauna
Actiniaria	Cnidaria	Hexacorallia	Hexacorallia	Actinaria	Infauna
Octocorallia	Cnidaria	Octocorallia	Octocorallia	Actinaria	Infauna
Pennatulidae	Cnidaria	Octocorallia	Octocorallia	Actinaria	Infauna
Cnidaria	Cnidaria		!!EXCLUDE	Actinaria	Infauna
Anthozoa	Cnidaria		!!EXCLUDE	Actinaria	Infauna
Hydrozoa	Cnidaria		Hydrozoa	Bryozoa	Epifauna
Cirripedia	Crustacea	Cirripedia	Cirripedia	Cirripedia	Crustacea
Amphipoda	Crustacea	Eumalacostraca	Amphipoda	Amphipoda	Crustacea
Caprellidae	Crustacea	Eumalacostraca	Amphipoda	Amphipoda	Crustacea
Cumacea	Crustacea	Eumalacostraca	Cumacea	Cumacea	Crustacea
Decapoda	Crustacea	Eumalacostraca	Decapoda	Decapoda	Crustacea
Pleocyemata	Crustacea	Eumalacostraca	Decapoda	Decapoda	Crustacea
Caridea	Crustacea	Eumalacostraca	Decapoda	Decapoda	Crustacea
Euphausiacea	Crustacea	Eumalacostraca	Euphausiacea	Euphausiacea	Crustacea
Isopoda	Crustacea	Eumalacostraca	Isopoda	Isopoda	Crustacea
Mysidacea	Crustacea	Eumalacostraca	Mysidacea	Crustacea	Crustacea
Tanaidacea	Crustacea	Eumalacostraca	Tanaidacea	Crustacea	Crustacea
Malacostraca	Crustacea	Malacostraca	!!EXCLUDE	Crustacea	Crustacea
Leptostraca	Crustacea	Malacostraca	Leptostraca	Crustacea	Crustacea
Copepoda	Crustacea	Maxillopoda	Copepoda	Crustacea	Crustacea
Harpacticoida	Crustacea	Maxillopoda	Copepoda	Crustacea	Crustacea
Ostracoda	Crustacea	Ostracoda	Ostracoda	Crustacea	Crustacea
Pycnogonida	Crustacea	Pycnogonida	Pycnogonida	Crustacea	Crustacea
Crustacea	Crustacea		!!EXCLUDE	Crustacea	Crustacea

Taxon Group	Phylum	Class	Community analysis group	Brey AFDW conversion group	Edgar productivity group
Ctenophora	Ctenophora		Ctenophora	Bryozoa	Epifauna
Asteroidea	Echinodermata	Asteroidea	Asteroidea	Asteroidea	Epifauna
Echinoidea	Echinodermata	Echinoidea	!!EXCLUDE	Echinoidea	Infauna
Echinoida	Echinodermata	Echinoidea	Echinoida	Echinoidea	Epifauna
Spatangoida	Echinodermata	Echinoidea	Spatangoida	Echinoidea	Infauna
Holothurioidea	Echinodermata	Holothurioidea	Holothurioidea	Holothuroidea	Infauna
Ophiuroidea	Echinodermata	Ophiuroidea	Ophiuroidea	Ophiuroidea	Infauna
Echinodermata	Echinodermata		!!EXCLUDE	Echinodermata	Infauna
Echiura	Echiura		Echiura	Priapulida	Infauna
Entoprocta	Entoprocta		Entoprocta	Bryozoa	Epifauna
Foraminifera	Foraminifera		Foraminifera	Bryozoa	Epifauna
Caudofoveata	Mollusca	Caudofoveata	Caudofoveata	Nudibranchia	Mollusca
Gastropoda	Mollusca	Gastropoda	Gastropoda	Gastropoda	Mollusca
Opisthobranchia	Mollusca	Opisthobranchia	Opisthobranchia	Nudibranchia	Mollusca
Nudibranchia	Mollusca	Opisthobranchia	Opisthobranchia	Nudibranchia	Mollusca
Pelecypoda	Mollusca	Pelecypoda	Pelecypoda	Bivalvia	Mollusca
Polyplacophora	Mollusca	Polyplacophora	Polyplacophora	Mollusca	Mollusca
Neoloricata	Mollusca	Polyplacophora	Polyplacophora	Mollusca	Mollusca
Scaphopoda	Mollusca	Scaphopoda	Scaphopoda	Gastropoda	Mollusca
Solenogastres	Mollusca	Solenogastres	Solenogastres	Nudibranchia	Mollusca
Mollusca	Mollusca		!!EXCLUDE	Mollusca	Mollusca
Nematoda	Nematoda		Nematoda	Annelida	Infauna
Cerebratulidae	Nemertea	Anopla	Nemertea	Nemertea	Infauna
Nemertea	Nemertea		Nemertea	Nemertea	Infauna
Phoronida	Phoronida		Phoronida	Oligochaeta	Infauna
Platyhelminthes	Platyhelminthes		Platyhelminthes	Nemertea	Infauna
Pogonophora	Pogonophora		Pogonophora	Oligochaeta	Infauna
Porifera	Porifera		Porifera	Porifera	Epifauna
Priapulida	Priapulida		Priapulida	Priapulida	Infauna
Sipuncula	Sipuncula		Sipuncula	Sipunculida	Infauna
Epifauna			!!EXCLUDE	Other Organic Matter	Epifauna
Other Organic Matter			!!EXCLUDE	Other Organic Matter	Infauna