

Not to be cited without prior reference to and permission from the author.

Species Composition, Diversity, Biomass and Production of the Demersal Fish Community of the North Sea.

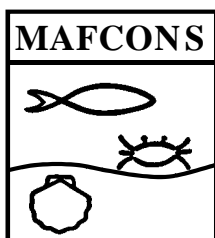


Simon Greenstreet¹, Helen Fraser¹, Gerjan Piet⁴, Leonie Robinson¹, Ruth Callaway²,
Henning Reiss³, Siegfried Ehrich⁷, Ingrid Kröncke³, Johan Craeymeersch⁴, John
Lancaster², Liz Jorgensen⁶ and Annelies Goffin⁵

1: Fisheries Research Services, Marine Laboratory, Aberdeen, Scotland. 2: University, of Wales Swansea, Swansea, Wales. 3: Forschungsinstitut Senckenberg, Wilhelmshaven, Germany. 4: The Netherlands Institute for Fisheries Research, IJmuiden, Netherlands. 5: University of Ghent, Ghent, Belgium. 6: Institute of Marine Research, Tromsø, Norway. 7: Institute for Sea Fisheries, Hamburg, Germany

Greenstreet@marlab.ac.uk

Dr S.P.R. Greenstreet, Fisheries Research Services, Marine Laboratory, PO Box 101, Victoria Road, Aberdeen, AB11 9DB, Scotland



PRIFYSGOL CYMRU ABERTAWE
UNIVERSITY OF WALES SWANSEA



ANIMAL SCIENCES GROUP
WAGENINGEN



FISHERIES RESEARCH SERVICES

HAVFORSKNINGSINSTITUTTET
INSTITUTE OF MARINE RESEARCH

senckenberg
forschungsinstitut und naturmuseum



Marine Biologie
Vakgroep Biologie



Not to be quoted without prior reference to the authors

© Crown Copyright 2007

Fisheries Research Services Collaborative Report No. 07/07

**SPECIES COMPOSITION, DIVERSITY, BIOMASS AND PRODUCTION OF THE
DEMERSAL FISH COMMUNITY OF THE NORTH SEA**

Simon Greenstreet, Helen Fraser, Gerjan Piet, Leonie Robinson, Ruth Callaway,
Henning Reiss, Siegfried Ehrich, Ingrid Kröncke, Johan Craeymeersch,
John Lancaster, Liz Jorgensen and Annelies Goffin

April 2007

Fisheries Research Services
Marine Laboratory
375 Victoria Road
Aberdeen AB11 9DB

SUMMARY

Problems with the use of diversity indices as indicators of the “health” of fish communities are discussed and particular problems related to sampling effort requirements and catchability in the trawl gears used are identified. Two quarter three (Q3) groundfish survey data sets were analysed, the ICES International Bottom Trawl Survey (IBTS), which uses a GOV otter trawl, and the Dutch Beam Trawl Survey (DBTS). Trawl sample statistics were examined to select a sub-set of “standardised” samples from each data set.

A method for estimating catchability at length for each species sampled in the GOV otter trawl IBTS is described. IBTS densities at age of the assessed species are related to the densities derived from the stock assessments. Comparisons of catch rates in the IBTS and DBTS between non-assessed and assessed species are then used to estimate catchabilities at age/length for all other species. Catchability of different species in the GOV trawl varied markedly. For some species and size classes, such as large cod and small whiting, almost all fish in the path of the trawl were caught. For others, flatfish such as plaice and thickback sole, or small benthic fish such as dragonets for example, the proportion of fish in the path of the GOV trawl that was actually caught was very low. Application of the catchability coefficients to the IBTS data suggested that the total biomass of the demersal fish community varied between 3 and 7 million tonnes, with peak biomass occurring in 1999 and 2000. Trends in the population biomass varied markedly between species, as did their spatial distributions.

Cluster analysis of the survey species abundance data suggested the presence of three or four distinct community types across the North Sea. Rectangles in each community with the highest levels of sampling were selected to assess the levels of sampling effort required to determine accurate estimates of species richness and species diversity. Three indices were applied to the survey abundance data, Hill's N_0 (species richness), N_1 (exponential of Shannon-Weiner Index) and N_2 (reciprocal of Simpson's Index). For both the IBTS and the DBTS data sets, it was necessary to aggregate approximately 20 trawl samples in order to arrive at richness and diversity statistics that were representative of the actual diversity in the area sampled. However, the need to aggregate samples in space runs the risk of confounding α (point) and β (transect) diversity. The fact that the similarity of the fish community occupying pairs of ICES rectangles decreased linearly with increasing distance between the rectangles suggested that this risk was real. Further analysis suggested that where the aggregation of 20 IBTS trawls could be achieved within a search radius of less than 50km, then the estimate of diversity produced consisted entirely of α diversity, but where the search radius exceeded 50km, the resulting diversity estimates included an increasing component of β diversity.

Spatial variation in species richness was similar for both the IBTS and DBTS data sets. However, the two data sets suggested very different spatial patterns of Hill's N_1 and N_2 species diversity, suggesting that these two indices were strongly affected by the variable catchability of different species in otter and beam trawls. Application of the catchability coefficients to the IBTS abundance data produced a third very different pattern of spatial variation in species diversity, one that was now explicable on the basis of environmental variation. Based on the data raised to account for catchability, species diversity was highest in the shallower, hydrographically mixed, more productive southern North Sea. Furthermore, while variation in N_1 and N_2 were strongly positively correlated, variation between species richness and both the species diversity indices was negatively correlated.

Species richness of the fished component of the demersal fish community (\log_2 weight classes 8 and above) was highest in the northern North Sea. Species diversity was also highest in this

region when catchability in the GOV was accounted for. However, when based on the raw abundance data, diversity appeared highest in the southeastern North Sea, again stressing the importance of considering catchability in the sampling gear. Similar spatial community composition clustering was observed for the fished component of the demersal fish assemblage, as when the entire community was considered.

A method for estimating growth productivity of the fish assemblage from the species abundance at length data provided by the groundfish surveys, based on the von Bertalanffy growth function and weight at length relationships, is presented. A linear regression method for estimating the required parameter values for each species sampled in the surveys is described. As with diversity, accounting for species- and size-related catchability in the GOV trawl profoundly affected the resulting maps of spatial variation in biomass density, production density and production:biomass (P/B) ratios. Spatial patterns of productivity and P/B ratio differed between different weight-class components of the demersal fish assemblage. Productivity in the prey-fish component of the assemblage (Log_2 weight-classes 3 and 4) was highest in the northern North Sea.

TABLE OF CONTENTS

1.	Introduction	1
1.1.	Current issues with the use of diversity metrics in management	1
1.1.1.	Sampling effort issues	4
1.1.2.	Catchability issues	5
1.2.	Productivity	6
2.	Methods	7
2.1.	Data sets	7
2.1.1.	ICES Q3 IBTS	7
2.1.2.	Q3 DBTS	7
2.2.	Sample standardization	8
2.3.	Estimation of catchability coefficients (q)	9
2.3.1.	Determining fish density in trawl samples	9
2.3.2.	Determining numbers and biomass of fish in the North Sea based on the IBTS	13
2.3.3.	Correcting for difference in area covered by the IBTS and stock assessments	14
2.3.4.	Correcting for differences in the timing of the IBTS and stock assessments	17
2.3.5.	Comparing IBTS and assessment ICES area IV numbers at age to estimate q	17
2.3.6.	Conversion of q at age to q at length	19
2.3.7.	Determining q for non-assessed species	20
2.4.	Diversity metrics and data analysis	22
2.4.1.	Diversity metrics	22
2.4.2.	Assessing the level of sample aggregation required	23
2.5.	Estimating productivity of the demersal fish community	24
2.5.1.	Derivation of an index of productivity	24
2.5.2.	Determining productivity index parameter values for each species	25
3.	Results	27
3.1.	Catchability: correcting the IBTS view to see the real world	27
3.1.1.	Catchability (q) at length for the assessed species	27
3.1.2.	Catchability (q) at length for the non-assessed species	30
3.1.3.	Estimate of total demersal fish biomass	37
3.2.	Assessment of the level of sample aggregation required to measure diversity	42
3.2.1.	Spatial patterns in demersal fish species composition	42
3.2.2.	Sample aggregation analysis	44
3.2.2.1.	IBTS: sampling restricted to focal rectangles	44
3.2.2.2.	IBTS: sampling restricted to focal rectangles and immediate neighbours	49
3.2.2.3.	DBTS: sampling restricted to focal rectangles	54
3.2.2.4.	Confounding α diversity and β diversity	59
3.3.	Spatial variation in the diversity of the demersal fish community	62
3.3.1.	Based on the raw survey data	62
3.3.2.	Based on the raised IBTS GOV data taking account of catchability	65
3.3.2.1.	The “entire” demersal fish community	65
3.3.2.2.	Sub-sets of the demersal fish community	70
3.4.	Spatial variation in the productivity of the demersal fish community	74
3.4.1.	The entire demersal fish community	74
3.4.2.	Sub-sets of the demersal fish community	76
4.	References	88
5.	Appendix 1.	i
6.	Appendix 2	vii

1. INTRODUCTION

Previous analyses of groundfish survey data suggest that fishing has affected the species diversity of the demersal fish community (Greenstreet and Hall 1996; Greenstreet *et al.* 1999; Greenstreet and Rogers 2006; Rogers and Ellis 2000; Piet and Jennings 2005). Given the commitment to (a) conserve and (b) restore biodiversity explicit in the Convention on Biological Diversity (CBD) and Annex V of the OSPAR convention, Ecological Quality Objectives (EcoQOs) for EcoQ Issue 5, Fish Communities, are likely to include objectives such as “prevent further decline in groundfish species diversity” or “restore groundfish diversity to a specified level” (e.g. ICES 2006). Such management initiatives will need to be based on specific metrics, or indicators, of species diversity.

1.1. Current Issues with the use of Diversity Metrics in Management

The move towards an “ecosystem approach to management” in the North Sea has generally stimulated a plethora of studies to investigate and develop potential “indicators” of “ecosystem health” (Frid 2003). Many different metrics or indices that numerically describe multi-species aspects of community composition and structure have been proposed and applied to biological data (Southwood 1978; Washington 1984; Magurran 1988). Many have been applied to marine community data (Clarke and Warwick 1994), including data gathered in the North Sea (Jennings and Reynolds 2000). These include variation in populations of indicator species (Bustos-Baez and Frid 2003), change in species composition, species diversity indices (Greenstreet and Hall 1996; Greenstreet *et al.* 1999), taxonomic diversity (Clarke and Warwick 1998; Hall and Greenstreet 1998; Rogers *et al.* 1999), calculation of community averaged life history traits (Jennings *et al.* 1998; Jennings *et al.* 1999), determination of community size-spectra or size composition (Rice and Gislason 1996; Hall and Greenstreet 1996), estimation of community trophic structure (Jennings *et al.* 2002), and so on. In 2001, the ICES Working Group on “The Ecosystem Effects of Fishing Activities” (WGEKO) proposed a set of criteria by which to judge these various indicators (Table 1.1.1). After evaluation according to these criteria, ICES considered metrics based on the mean size of fish, the proportion of large fish, and the ultimate body size of fish in the community, to be the most appropriate indicators of the impact of fishing on fish communities. The Advisory Committee on Ecosystems advised accordingly (ICES 2001), and to date, these are the only elements of Ecological Quality for fish and benthic assemblages listed in Bergen Ministerial Declaration at the 5th North Sea Ministerial Meeting.

Criterion	Property
a	Relatively easy to understand by non-scientists and those who will decide on their use
b	Sensitive to a manageable human activity
c	Relatively tightly linked in time to that activity
d	Easily and accurately measured, with a low error rate
e	Responsive primarily to a human activity, with low responsiveness to other causes of change
f	Measurable over a large proportion of the area to which the EcoQ metric is to apply
g	Based on an existing body or time-series of data to allow a realistic setting of objectives

Table 1.1.1: ICES criteria for a “good” Ecological Quality Objective metric.

The application of these criteria to identify the most useful indicators puts great emphasis on identifying metrics that are easy to understand and use, and which have a tight functional relationship with the activity of concern. Metrics selected in this way instil confidence that the activity of concern has actually caused any observed changes in the metric, and that reduction in activity levels will bring about a change in the metric towards some desired value – the EcoQO. From a management perspective, such tight linkage between the activity and metric performance is highly advantageous, and as such, it is easy to understand the appeal of metrics of fish size. Fishing is a size selective activity - mesh size regulations as well as market forces ensure this - so there is a tight conceptual, and easily comprehensible, link between the performance of size-based indicators and variation in the level of fishing. They therefore score highly with regard to criteria b, c, and e (Table 1.1.1). The concept of “size” is easily understood and fish length is easily and accurately measured and recorded with little need for specialist knowledge or training. These indicators therefore also score highly against criteria a and d (Table 1.1.1). Finally, groundfish surveys covering the entire North Sea have been carried out routinely over several decades and the numbers of individuals of given size of all species in each catch is the basic data recorded. So size based metrics also score highly on the remaining two criteria, f and g (Table 1.1.1). However, metrics of fish size in the assemblage provide no explicit information about change in the biodiversity of the fish assemblage. They cannot therefore help managers to set biodiversity objectives or identify appropriate measures to achieve these.

Addressing the impact of fishing on marine biodiversity requires the application of biodiversity indicators. However, biodiversity is a far more complex concept than fish length. Numerous definitions of biodiversity exist in the literature, but it is generally assumed to be synonymous with the “variety of life”, and to consider such variety at several levels: variety within a species, variety between species and variety between communities of organisms in different habitats or ecosystems (Gaston 1996). Consequently, it is unlikely that any single metric will ever be developed that adequately conveys information regarding the “variety of life” across all levels simultaneously (Gaston 1996). Such an index is therefore bound to fail several of the criteria listed in Table 1.1.1. Since the early 1980s the number of “biodiversity” publications has increased massively (Haila and Kouki 1994; Harper and Hawksworth 1994), and invariably these studies have quantified only a single dimension of biodiversity, i.e. genetic diversity within species (Mallet 1996), or species diversity within communities (Gaston 1996). Of the various components of biodiversity, the diversity of species has received by far the most attention to date, having a research history that long predates the coining of the term biodiversity (see references in Greenstreet 2007a).

However, the concept of species diversity when considered in isolation, is itself not a simple one (Hurlbert 1971), consisting as it does of two components, the number of species in a community, and the evenness of the distribution of all individuals between the constituent species of the community. A variety of different indices of species diversity have been proposed and used (Magurran 1988), and these tend to lie along a continuum from indices of purely species richness to indices of purely species evenness (Hill 1973). No one index therefore conveys all the information that might be required, and the majority of indices, those lying between the extremes of this continuum, convey some information about both aspects of species diversity, although the degree of sensitivity of particular indices to either species richness or species evenness is often ill defined (but see Hill 1973). Consequently, species diversity indices were considered to score poorly with respect to criterion a (Table 1.1.1). In reporting metrics of species diversity, it has often been suggested that at least two should be used so as to adequately represent these two quite different aspects of species diversity, giving rise to the notion of using a “suite” of indices or “composite” indices (e.g. Fulton *et al.*, 2005; Buckland *et al.*, 2005; Wilsey *et al.*, 2005). Most studies reporting changes in fish species diversity in the North Sea have, at the very least, reported variation in two of the first three Hills’ metrics, N_0 , N_1 , and N_2 (e.g. Greenstreet and Hall, 1996; Greenstreet *et al.*, 1999a; Piet and Jennings, 2005).

Species diversity indices require the numbers of individuals belonging to different species to be recorded, information that is routinely recorded on groundfish surveys. Such surveys covering the whole North Sea, and many other marine regions, have been carried out for decades, thus species diversity indices score well under criteria f and g (Table 1.1.1). However, derivation of species diversity indices requires a level of taxonomic expertise (individuals have to be identified to species) and so they are less easily measured and are potentially more prone to error, impairing their score with respect to criterion d (Table 1.1.1).

Early studies related temporal trends in fish species diversity to temporal trends in fishing effort (Greenstreet and Hall 1996; Rogers *et al.* 1998; Greenstreet *et al.* 1999; Rogers *et al.* 1999; Rogers and Ellis 2000). Such correlative studies could not unequivocally link changes in diversity to changes in fishing effort, and so failed to establish direct cause and effect. Used in this way, species diversity indices score poorly under criteria b, c, and e (Table 1.1.1). Further studies have redressed these shortcomings to some extent. Jennings *et al.* (1998) hypothesized that species with *k*-strategist type life-history characteristics, i.e. slow growth rates, large ultimate body-size, large size and late age at maturity, would be less capable of sustaining the additional mortality inflicted by fishing than species with the opposite, *r*-strategist type, life-history characteristics. Jennings *et al.* (1999) then demonstrated that in an area of the northern North Sea where fishing had steadily increased in intensity, the groundfish assemblage had indeed become increasingly dominated by fish with *r*-strategist type life-history characteristics. This supported the earlier contention that the changes in the species composition of the groundfish assemblage in this part of the North Sea, which resulted in the reduction in species diversity (Greenstreet & Hall 1996; Greenstreet *et al.* 1999), had indeed been caused by the increase in fishing disturbance in the area. Through a combination of temporal and spatial analysis, Greenstreet and Rogers (2006), provide further compelling evidence that long-term declines in species richness, diversity and evenness in heavily fished ICES rectangles in the north-western North Sea were caused by the fishing activity there.

Despite the evidence confirming the link between declines in species diversity and fishing activity in the northwestern North Sea, the precise functional relationship between fishing disturbance and species diversity remains unclear. Fishing activity over recent decades in the

southern North Sea, and around the southern coasts of England, has also increased, but here the species diversity of coastal demersal fish assemblages has increased (Rogers and Ellis 2000; Piet and Jennings 2005). These seemingly contradictory results imply that increased fishing disturbance can result in both increased and decreased species diversity. This apparent dichotomy has been interpreted as suggesting that species diversity indicators perform weakly against criteria a, b, c, and e (Table 1.1.1). But rather than being a failure of the indices and an indictment of the usefulness of the concept of species diversity from a management framework perspective, this interpretation highlights the current lack of understanding of the mechanisms that control species diversity. Huston's (1994) Dynamic Equilibrium Model predicts that, dependent upon local productivity, positive and negative relationships between species diversity and disturbance are both possible. Where productivity is high, diversity should increase as disturbance levels rise, while in areas of low productivity, increased disturbance should bring about a reduction in species diversity. Primary productivity in the central and southern North Sea tends to be higher than in more northern areas (Reid *et al.* 1990; Joint and Pomroy 1993), so these apparently opposing results actually tend to support Huston's model. Put within a proper theoretical framework, these results suggest that species diversity indices have just as strong a theoretical basis as size-based indicators.

Two further issues that currently compromise the apparent usefulness of diversity indices with respect to the criteria listed in table 1.1.1 are addressed explicitly in this report. These are the issues of sample size dependence and sampler catchability bias, both of which directly affect diversity index values and therefore can potentially influence interpretation of the results of any analysis.

1.1.1. Sampling effort issues

The ability of different diversity indices actually to detect environmental and anthropogenic impact on communities has frequently been questioned (e.g. Robinson and Sandgren, 1984; Chadwick and Canton, 1984). In many instances, problems have arisen through a failure to appreciate the influence of sampling effort on index performance, insufficient effort being made therefore to assess *a priori* the level of sampling effort required, and consequential inadequate sample sizes (Soetaert and Heip, 1990). The issue is most clearly exemplified by Island Biogeography theory wherein it is amply demonstrated that species richness (Hill's N_0) increases as a power function of the area sampled $S=cA^z$ where S is the species richness count and A the area sampled, c is a constant and z the exponent of the sampled area (MacArthur and Wilson, 1967; Rosenzweig, 1995). The implication here is that one can never obtain a true estimate of the actual species richness of a community until the entire area has been sampled; estimates of species richness will continually increase as an ever increasing area is sampled.

Traditional sampling theory is based on the underlying premise that each "sample" mean provides an estimate of the "population" mean. This is clearly not the case in this instance. No single (reasonably sized) sample can possibly estimate the species richness of the sampled community; community species richness will always be higher than the sample species count. Calculating the mean species richness value for a number of samples of the community is therefore also a worthless exercise, since the mean value determined for several single samples still remains the estimate of species richness for an area sampled by a single sample, and therefore is just as poor an indicator of the actual species richness of the community as would be obtained from any single sample individually (e.g. Colwell *et al.*, 2004). To estimate species richness of a community, successive samples need to be aggregated, such that one can track both the increase in the number of species contained in all the samples combined, as

well as the increase in the total combined area sampled. In this way, through linear regression of $\log A$ on $\log S$, it is possible to obtain estimates of c and z and so parameterise the above relationship to determine an estimate of species richness in the community. Such an approach has for example been adopted to estimate total species richness of a variety of different plant and animal taxa in many different regions of the world (see examples in Rosenzweig, 1995), but this approach has not to date been applied to the analysis to groundfish survey data. Because all species diversity indices are sensitive to a greater or lesser extent to increase in the number of species contained in a sample, they will all tend to behave in the same way; that is as the area sampled increases, so the index value will have a tendency to increase. However, as indices become more sensitive to the evenness of the distribution of individuals between species, and less sensitive to increase in the number of species (i.e. with increase in suffix number in Hill's notation), they become less affected by variation in species number associated with variable sampling effort (Soetaert and Heip, 1990).

In any analysis of species diversity data, a 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. Greenstreet and Hall (1996) carried out this preliminary analysis and determined that in order to represent the "true" diversity of the groundfish community of the northwestern North Sea, a minimum of five one-hour (48ft Aberdeen) trawl samples needed to be combined. They decided that such a level of sampling was adequate for Hills N_1 and N_2 indices, but was still inadequate for Hill's N_0 (species richness count). In subsequent studies (Greenstreet *et al.*, 1999; Greenstreet and Rogers 2006) all "treatment" cells have included the aggregation of many more than five one-hour trawl samples, ensuring that the index values, including the index of species richness, were as representative of actual community values as possible, and as a consequence, these studies have been able to demonstrate trends in diversity associated with variation in fishing impact. Other studies have examined trends in diversity estimated as the mean of single haul samples (e.g. Piet and Jennings, 2005). In the case of the ICES International Bottom Trawl Survey (IBTS), these samples consist of single half-hour trawls, one tenth of the sampling effort deemed necessary in the analysis of the Scottish AGFS data, the Scottish precursor to participation in the co-ordinated quarter 3 IBTS. Not surprisingly therefore, these studies have failed to demonstrate fishing effects on fish species diversity. Failure to standardise analytical methodology with respect to the application of species diversity indices to groundfish survey species abundance data has resulted in these inconsistent results, making interpretation difficult and contributing to the general confusion regarding the value of such indices as indicators of fish community health.

1.1.2. Catchability issues

The MAFCONS project has attempted to identify the processes that control the composition and structure of fish communities so as to provide a theoretical basis to relating specific changes in the species diversity of the groundfish community to particular fishing disturbance regimes. Any such theoretical model will tend to predict the "actual" species diversity of the community concerned. Research surveys provide estimates of the abundance of each species sampled at any particular location. However, 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 fish of different species and size in any given fishing gear vary considerably. Many factors can be involved. The vertical distribution of many species varies with time of day and this can affect the availability of fish to demersal trawl gears (Michalsen *et al* 1996; Casey and Myers 1998;

Korsbrekke and Nakken 1999; Benoît and Swain 2003). Fish of different species behave very differently ahead of the trawl gear. Some may be herded into the path of the net by the action of the otter doors and trawl sweeps stirring up a sediment cloud (Main and Sangster 1981; Bublitz 1995; Ramm and Xiao 1995; Somerton 2004), others may show net avoidance behaviour (Main and Sangster 1981). Variation in swimming endurance can also strongly influence which individuals fall back into the net (Wardle 1989; Winger *et al* 1999). Similarly, the catchability of particular species and sizes of fish can vary considerably in different types of fishing gear, dependent upon the characteristics of the gear. Several factors influence the catch efficiency and selective properties of trawl gears, such as sweep length (Engås and Godø 1989), mesh size (Suuronen and Millar 1992), net spread (Rose and Nunnallee 1998; von Szalay and Somerton 2005), trawl speed (Somerton and Weinberg 2001; Weinberg *et al* 2002) and the size and type of trawl groundgear (Main and Sangster 1981; Engås and Godø 1989; Walsh 1992). Consequently, all trawl surveys provide gear-biased perceptions of the actual abundance of different species and size-class at any particular location. In order to estimate actual species densities at each location, survey trawl catch density estimates need to be converted to estimates of actual absolute density by taking into account the catchability of the fish involved in the particular gear employed (Harley and Myers, 2001).

Several studies have attempted to estimate total biomass of the fish community of the North Sea by scaling survey catch rate data to biomass estimates of the main commercial species determined from MSVPA (Daan, 1990; Sparholt, 1990). However, none of these studies made any attempt to distribute the biomass estimates obtained across the North Sea. These previous studies also only considered total biomass and total catch rates; no attempt was made to consider the biomass and catch rates of different age and size classes of each species. Given the importance of size structure in aquatic food-web (Duplisea *et al.*, 1997; Jennings *et al.*, 2002), and the importance placed on fish size in assessing the impact of fishing on fish communities (ICES, 2001) this short-coming was also addressed in the approach adopted here.

In this study we analyse ICES International Bottom Trawl Survey (IBTS) quarter 3 (Q3) data, the Dutch Beam Trawl Survey (DBTS) Q3 data and ICES stock assessment data to model the catchability of each 1cm size class of demersal fish caught in the IBTS. We then use the derived catchability coefficients to estimate the biomass of each species present in each ICES rectangle. Summing across rectangles we present annual variation in the total biomass of key demersal fish species and of the entire fish community.

1.2. Productivity

Many of the fish present in the demersal fish community are piscivorous to a variable degree (Daan 1989; Hislop *et al.* 1991; Hislop 1997; Greenstreet *et al.* 1997; 1998; Temming *et al* 2004). In order to take account of all the potential sources of productivity in the food resources utilized by the full demersal fish community, estimates of the productivity of the fish prey components were required. Here we develop and apply an index of fish productivity based on the von Bertalanffy growth curve function that can be calculated from the numbers at length data for each species provided by the groundfish survey data.

2. METHODS

2.1. Data Sets

For the purposes of this study, only data covering the time period 1998 to 2004 were analysed because prior to this, not all participating countries used the same Grande Overture Vertical (GOV) trawl gear, and tow durations also varied. After 1998 trawl gear and duration was standardised across the entire survey, producing the most spatially consistent dataset with which to estimate spatial variation in fish abundance. Two primary survey data sets were used in this analysis; the ICES International Bottom Trawl Survey (IBTS) covering the period 1998 to 2004 and the Dutch Beam Trawl Survey (DBTS). To estimate catchability of the GOV, information on the actual abundance of fish was required. For the commercial species, estimates of total number of fish at age in the North Sea were taken from the VPA results provided by the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK) (ICES 2005).

2.1.1. ICES Q3 IBTS

The IBTS is an internationally coordinated survey which covers the whole of the North Sea and takes place in the 3rd quarter of the year (Q3) between July and October. The survey design is based on ICES statistical rectangles (one degree longitude x 0.5 degree latitude). Each rectangle is usually fished by ships of two different countries using a GOV trawl, resulting in at least two hauls per rectangle in most rectangles in most years. Additional GOV trawls that were not reported to ICES, but which were undertaken when the vessels involved were carrying out the Q3 surveys (according to IBTS protocols) were also included in our analysis (ICES 2006b). Raw catch data were 'cleaned' using the methods described in Daan (2001). Numbers at length of all species considered to be members of the "Demersal Fish Community" (Appendix 1) caught in each trawl sample were quantified, together with information on location, distance towed, and area swept by the gear. Otoliths are collected from the assessed species (haddock *Melanogrammus aeglefinus*, whiting *Merlangius merlangus*, cod *Gadus morhua*, Norway pout *Trisopterus esmarkii* and plaice *Pleuronectes platessa*) to determine age at length keys. These are used at ICES to convert numbers at length to number at age in each tow.

2.1.2. Q3 DBTS

The DBTS was initiated in 1985 to estimate the abundance of the dominant age groups of plaice and sole including pre-recruits. Initially the survey was only carried out in the south-eastern North Sea but from 1996 onwards it was expanded to cover the western, central and part of the northern North Sea. The survey is conducted in the 3rd quarter and uses a pair of 8m-Beam Trawls (8BT). The survey was designed to take between one and three hauls per ICES rectangle in the area previously covered by the original survey and one haul per ICES rectangle in the expanded area (ICES, 2006c). The stations are allocated over the fishable area of each rectangle on a "pseudo-random" basis and no attempt is made to return to the same tow positions each year. Towing speed is 4 knots for a tow-duration of 30 minutes and fishing occurs during daylight only. Again, number at length of each species in each catch are quantified and information on location, distance towed, and area swept by the gear recorded. Number at age data were available for all species for which otoliths were collected, mainly plaice and sole (*Solea vulgaris*).

2.2. Sample Standardization

The Q3 IBTS and DBTS databases for the seven year period 1998 to 2004 contained data for 2076 and 1064 hauls respectively. Despite fairly rigid protocols being laid down for each survey, the trawl samples contained in each were not fully standardized. Although most trawls were of the standard 30min duration, this was not the case for all samples. Furthermore, although a set trawl speed is defined, the distance trawled within the stipulated 30min showed substantial variation. Because of the sensitivity of diversity metrics to variation in sampling effort, it was deemed necessary to define the “standard sample” and only to include those trawl samples that met this definition in further analyses. 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.

Although the standard trawl duration was set at 30min, hauls upto ± 5 min of this were common. In addition because tow speed clearly varied, as did door and wing spread, the area swept by a standard 30min tow varied considerably. Thus as a first step, the area swept by trawl samples of between 27min and 33min was examined and the upper and lower 5% extreme cut-off points identified (Table 2.2.1). This was done only for trawls where the tow distance was actually recorded, although trawls where wing spread was estimated (see section 2.3.1) were included in this analysis. Wing-spread rather than door-spread values were used to estimate swept area because most of the rare species likely to be most affected by sampling variation in any analysis of diversity are unlikely to be herded into the path of the net by the action of the doors and sweeps.

The full databases were then interrogated to extract all IBTS and DBTS trawls falling between the upper and lower 5% swept area cut-off points. This extraction included data for 2008 IBTS and 1041 DBTS trawl samples (Table 2.2.2). 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 2.2.3). This standardization process resulted in approximately 8% of the IBTS and DBTS trawls being excluded from subsequent analysis.

Statistic	Q3 IBTS GOV (m ²)	Q3 DBTS 8mBT (m ²)
Number trawls	1063	134
Mean	65833.5	31106.6
Standard Deviation	11787.0	1956.2
Lower 5% range point	42731.1	27272.6
Upper 5% range point	108564.6	58379.1

Table 2.2.1: Trawl swept-area (net) statistics for IBTS and DBTS trawls samples with actual trawl distance recorded and with tow durations of between 27min and 33min.

Statistic	Q3 IBTS GOV (m ²)	Q3 DBTS 8mBT (m ²)
Number trawls	2008	1041
Mean	65611.5	31131.9
Standard Deviation	8466.1	459.8
Lower 5% range point	49017.8	30230.8
Upper 5% range point	82205.1	32033.1

Table 2.2.2: Trawl swept-area (net) statistics for all IBTS and DBTS trawl samples with swept-areas (net) falling between the lower and upper 95% cut-off points indicated in Table 2.2.1.

Statistic	Q3 IBTS GOV (m ²)	Q3 DBTS 8mBT (m ²)
Number trawls	1909	974
Mean	66154.2	31137.1
Standard Deviation	7490.2	103.5
Lower 5% range point	51473.4	30934.2
Upper 5% range point	80834.9	31339.97

Table 2.2.3: Trawl swept-area (net) statistics for “standard” IBTS and DBTS trawl samples (i.e. excluding trawl samples outside the lower and upper 95% cut-off points indicated in Table 2.2.2).

2.3. Estimation of Catchability Coefficients (q)

The catchability coefficient, q , of a fishing gear determines what fraction of the actual number of a given class of fish (e.g. of species s and size class l , or species s and age class a) in the path of the trawl ($N_{s,l}$ or $N_{s,a}$) actually gets caught ($C_{s,l}$ or $C_{s,a}$), thus (e.g. King 1995);

$$C_{s,l} = q * N_{s,l} \quad \text{or} \quad C_{s,a} = q * N_{s,a} \quad 2.3.1.$$

With no knowledge of the actual numbers of fish present at each trawl location, it is not possible to estimate q for each trawl sample individually. However, average q can be estimated across the whole North Sea if the numbers of fish estimated to be present in the North Sea from the IBTS trawl survey data can be compared with a second estimate of the abundance of fish in the entire area. Such estimates are provided by the ICES VPA stock assessment process (e.g. ICES 2005), but only for the assessed species. Within the demersal fish community, and considering only those species occurring frequently in IBTS samples, these included haddock, whiting, cod, Norway pout and plaice. Thus the first step to estimating q is to estimate the numbers of fish (of species s and age a) based on the IBTS data. This was done by estimating the density of fish in the trawled area of each ICES rectangle, multiplying this by the area of each rectangle to obtain an estimate of the numbers of fish in the rectangle, then summing these values over all rectangles covered by the survey to estimate fish numbers in the whole area surveyed.

2.3.1. Determining Fish Density in Trawl Samples

To calculate fish density at each trawl sample location, estimates of the area sampled by the fishing gear were required. Gear geometry information i.e. door-spread, and wing-spread (Figure 2.3.1.1) are recorded in the IBTS database, but these fields were not always completed. To estimate values for these missing data, Scottish net geometry data from 1998, 2001-2004 were analysed to examine the relationships between door-spread and depth and between wing-spread and depth. Data from all five years were combined and a regression analysis performed on the combined data (Figure 2.3.1.2). For hauls where net geometry data was

missing, mean door-spread (DS) and wing-spread (WS) values could then be estimated from the depth (D) recorded at the station by:

$$DS = 33.251 * \log D + 15.744 \quad 2.3.1.1$$

and;

$$WS = 6.8515 * \log D + 5.8931 \quad 2.3.1.2$$

In some instances, the distance towed (DT) during a trawl was not recorded and could not be determined directly because shoot and haul positions were not both recorded. To fill in these missing values, the average distance towed by each of the different research vessels during a 30 minute tow was determined (Figure 3.2.1.3.) and divided by 30 to obtain vessel-specific estimates the distance trawled per minute of towing for each of the research vessels involved in the survey. Missing trawl distance values were then estimated by multiplying the recorded trawl durations by these vessel-specific trawl-distance per minute values. Once these gaps in the database had been filled, two measures of the area swept by the trawl gear were determined, the area swept between the otter doors A_{DS} (m^2) and the area swept between the wings of the net A_{WS} (m^2), by:

$$A_{DS} = DS * DT \quad 2.3.1.3$$

and;

$$A_{WS} = WS * DT \quad 2.3.1.4$$

Knowing the area swept by the gear, two estimates of the density of fish of species s and age class a ($FD_{s,a}$, numbers. m^{-2}) could then be determined for each trawl sample. The first ($FD_{s,a,g}$), based on the area swept by the entire gear including the otter doors and sweeps, was considered to be most appropriate for species that are herded into the path of the net by the action on the seabed of these parts of the gear stirring up a sediment cloud, and was therefore used for haddock and whiting (Main and Sangster 1981; Wardle 1983; Sangster and Breen 1998; Breen *et al* 2004),

$$FD_{s,a,g} = \frac{C_{s,a}}{A_{DS}} \quad 2.3.1.5$$

and the second ($FD_{s,a,n}$) based on the area swept by the net alone, considered to be most appropriate for species not prone to the herding action of the door and sweeps,

$$FD_{s,a,n} = \frac{C_{s,a}}{A_{WS}} \quad 2.3.1.6$$

where $C_{s,a}$ is the number of fish (of species s and age class a) caught in the trawl sample. In most years each ICES statistical rectangle was fished more than once. The mean density of fish calculated over all trawls carried out in each rectangle in each year provided the required estimates of the density of fish in each ICES rectangle ($FD_{rect,s,a,g}$ or $FD_{rect,s,a,n}$). However, abundance data are rarely normally distributed and are frequently characterised by many low values and a few relatively high values. Under such circumstances arithmetic means of the sample densities provide a biased estimator of the “population” mean density (Sokal and Rohlf 1981). For all age classes of each species in each year, the arithmetic mean density in each rectangle was plotted on the x axis against the variance on the y axis. Invariably the fitted slopes obtained were close to 1.0, indicating the need to use the geometric mean of the sample densities as a less biased estimator of the “population” mean density of fish in each rectangle (Sokal and Rohlf 1981).

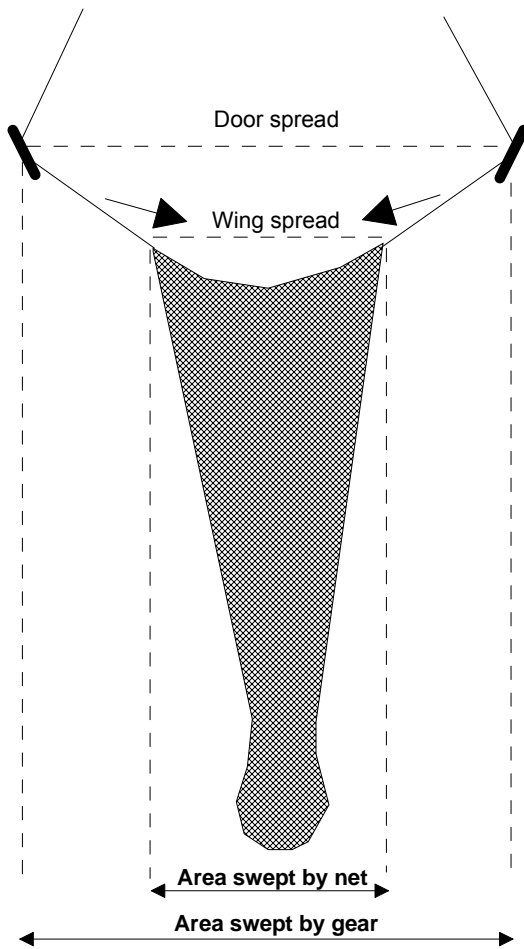


Figure 2.3.1.1: Schematic drawing of a fishing net illustrating the terms “wing-spread” and “door-spread”. Arrows indicate the possible herding effect of the otterboards and sweeps.

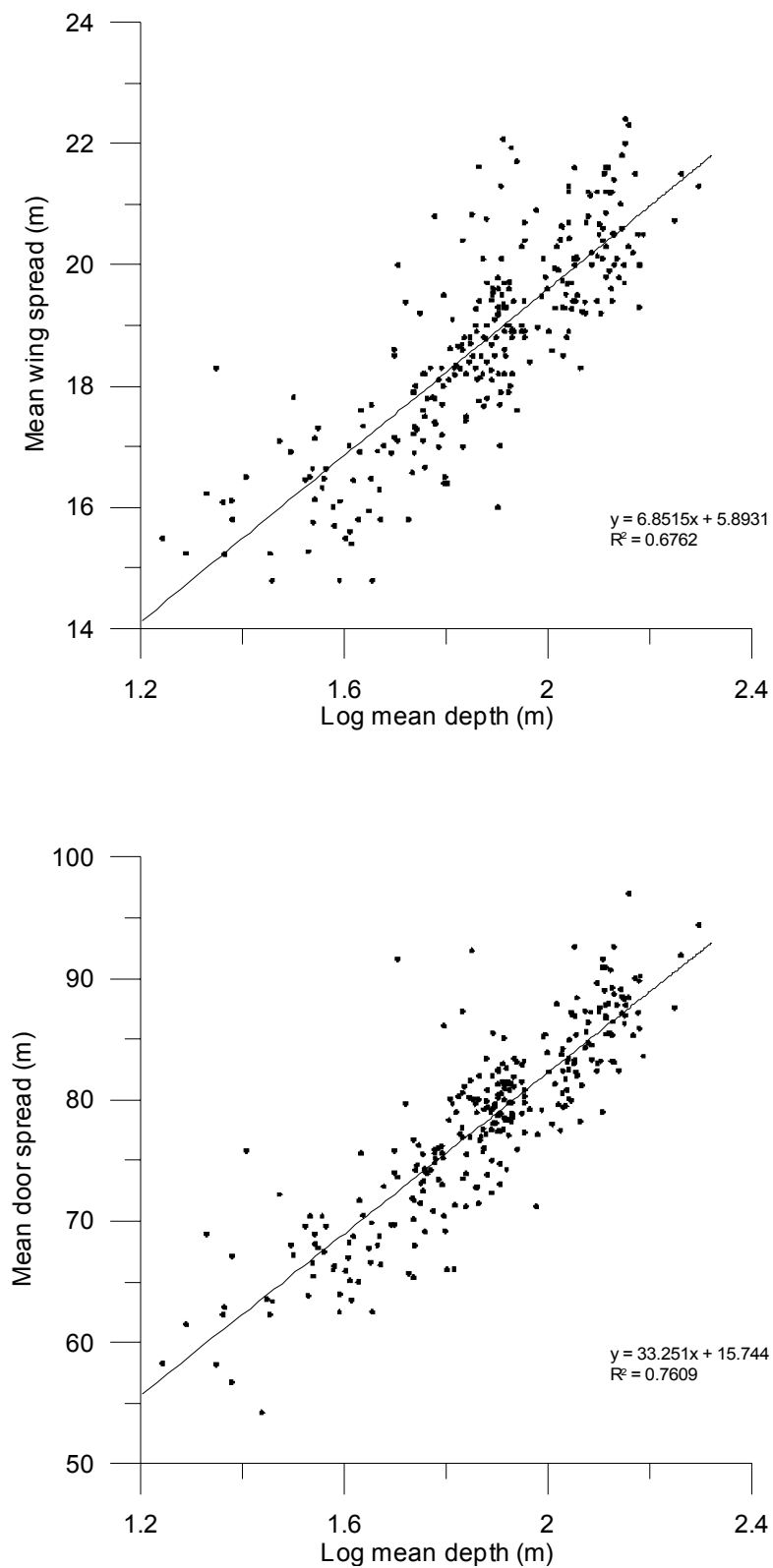


Figure 2.3.1.2: Relationship between mean wing and door-spread and log depth using SCANMAR© data collected on the Scottish 3rd Quarter IBTS.

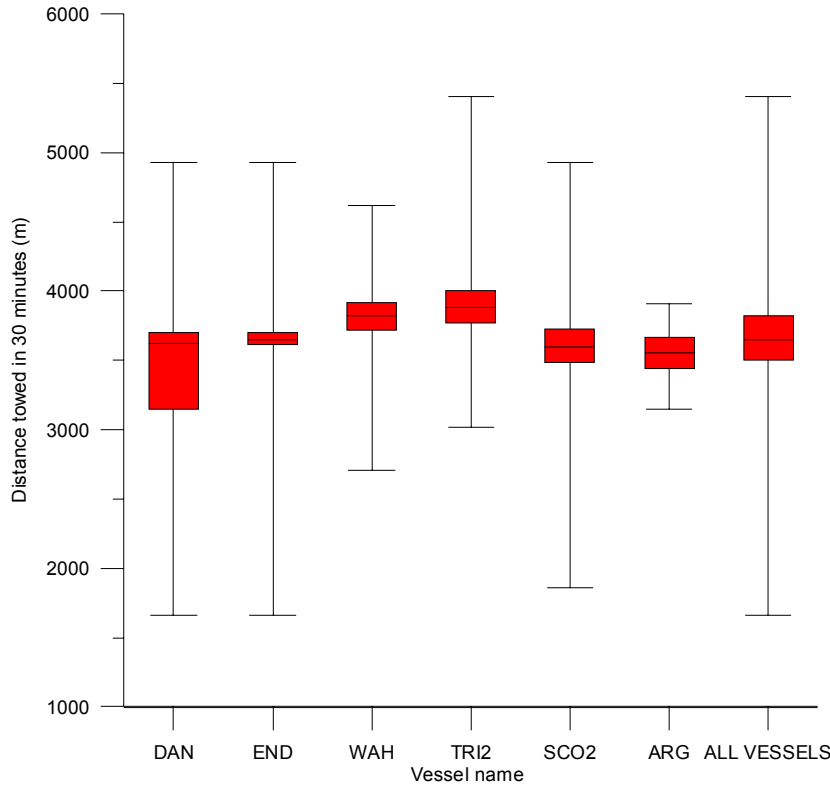


Figure 3.2.1.3: Box-whisker plot of the average distance towed in a 30 minute tow by each vessel: Dana (DAN, Denmark), Endeavour (END, England), Walter Herwig (WAH, Germany), Tridens (TRI2, Netherlands), Scotia (SCO2, Scotland), Argos (ARG, Sweden). Filled blocks indicate 50% data range, bars show extreme data range and medians are indicated by horizontal line. ANOVA $P < 0.05$.

2.3.2. Determining numbers and biomass of fish in the North Sea based on the IBTS

The number of fish (of species s and age a) in each rectangle ($N_{rect,s,a}$) is then estimated by multiplying the appropriate estimate of the density of fish in the rectangle ($FD_{rect,s,a,g}$ or $FD_{rect,s,a,n}$) by the area of each rectangle (A_{rect}), thus:

$$N_{rect,s,a} = FD_{rect,s,a,g} * A_{rect} \quad 2.3.2.1$$

or;

$$N_{rect,s,a} = FD_{rect,s,a,n} * A_{rect} \quad 2.3.2.2$$

However, the area of an ICES rectangle is not constant. While the height of each rectangle, delineated by 0.5° latitude (≈ 30 NM or approximately 55.6 Km), remains constant, rectangle width, delineated by 1.0° longitude decreases with increasing latitude. The area (Km^2) of each ICES rectangle (A_{rect}) is therefore given by:

$$A_{rect} = 30 * 60 * \cos(Lat_{rect}) * 1.853^2 = 6080.4342 * \cos(Lat_{rect}) \quad 2.3.2.3$$

where Lat_{rect} is the latitude of the rectangle mid-point. Furthermore, rectangles around the edges of the North Sea containing coastline did not consist entirely of “sea-area”. Thus, the area of each ICES rectangle was further modified by multiplying by the proportion consisting of “sea-area” (pS_{rect}). The number of fish (of species s and age class a) in the area covered by the IBTS ($N_{surv,s,a}$) was then determined by summing over all rectangles covered by the survey ($surv$), thus:

$$N_{surv,s,a} = \sum_{rect=1}^{surv} FD_{rect,s,a,g} * 6080.4342 * \cos(Lat_{rect}) * pS_{rect} \quad 2.3.2.4$$

or;

$$N_{surv,s,a} = \sum_{rect=1}^{surv} FD_{rect,s,a,n} * 6080.4342 * \cos(Lat_{rect}) * pS_{rect} \quad 2.3.2.5$$

dependent on which fish density estimate was used.

Where necessary, these numbers of fish (by species, size class, and area or sub-area) could be converted to biomass by application of the appropriate weight at length relationships, given as:

$$W = aL^b \quad 2.3.2.6$$

where W is the weight of a fish of given length (L) and a and b are species specific parameters. These parameter values for each species sampled in the IBTS and DBTS were obtained from Coull *et al* (1991), unpublished data collected by FRS, CEFAS and RIVO, or from FishBase (<http://www.FishBase.org>). Numbers at length data from the IBTS were converted to numbers at age data using age-length keys determined for each survey.

In each year, there were at least two ICES rectangles within the area normally covered by the IBTS where no fishing took place. For these missing rectangles, IBTS numbers and biomass estimates were “filled in” by interpolation based on the mean of the IBTS numbers and biomass estimates in surrounding ICES rectangles.

2.3.3. Correcting for difference in area covered by the IBTS and stock assessments

ICES area IV covers the whole of the North Sea and is shown in Figure 2.3.3.1. The shaded portion represents the area covered by the IBTS survey over the time period 1998 to 2004; areas in white were not covered by the IBTS during this time period. As fishing did not take place in all statistical rectangles within ICES areas IV, a raising factor RF was used to multiply estimates of the numbers of fish (of species s and age class a) determined for the area covered by the IBTS to make these estimates equivalent to the numbers expected had all of area IV been surveyed, thus;

$$RF = \frac{A_{ICESarealIV}}{A_{surv}} \quad 2.3.3.1$$

where $A_{ICESarealIV}$ is the area of area IV in Km^2 and A_{surv} is the area covered by the IBTS survey in Km^2 . To take account of the fact that fish were not evenly distributed across the North Sea, raising factors were determined and applied independently for each of five sub-areas shown in Figure 2.3.3.1. The raising factors obtained for each sub-area of the North Sea are given in Table 2.3.3.1.

Species Composition, Diversity, Biomass and Production of the Demersal Fish Community of
the North Sea

Area	ICES area Km ²	IBTS area Km ²	Raising factor
IVa1	133,049	100,900	1.317
IVa2	131,294	85,069	1.543
IVb1	125,519	121,142	1.036
IVb2	151,764	143,427	1.058
IVc	66,572	46,655	1.427

Table 2.3.3.1: Total area of each of the five sub-areas that make up the whole North Sea (whole ICES area IV) and the area included within the IBTS coverage over the period 1998 to 2004. Raising factors to 'raise' the area covered by the IBTS to the entire ICES area IV are given for each sub-area.

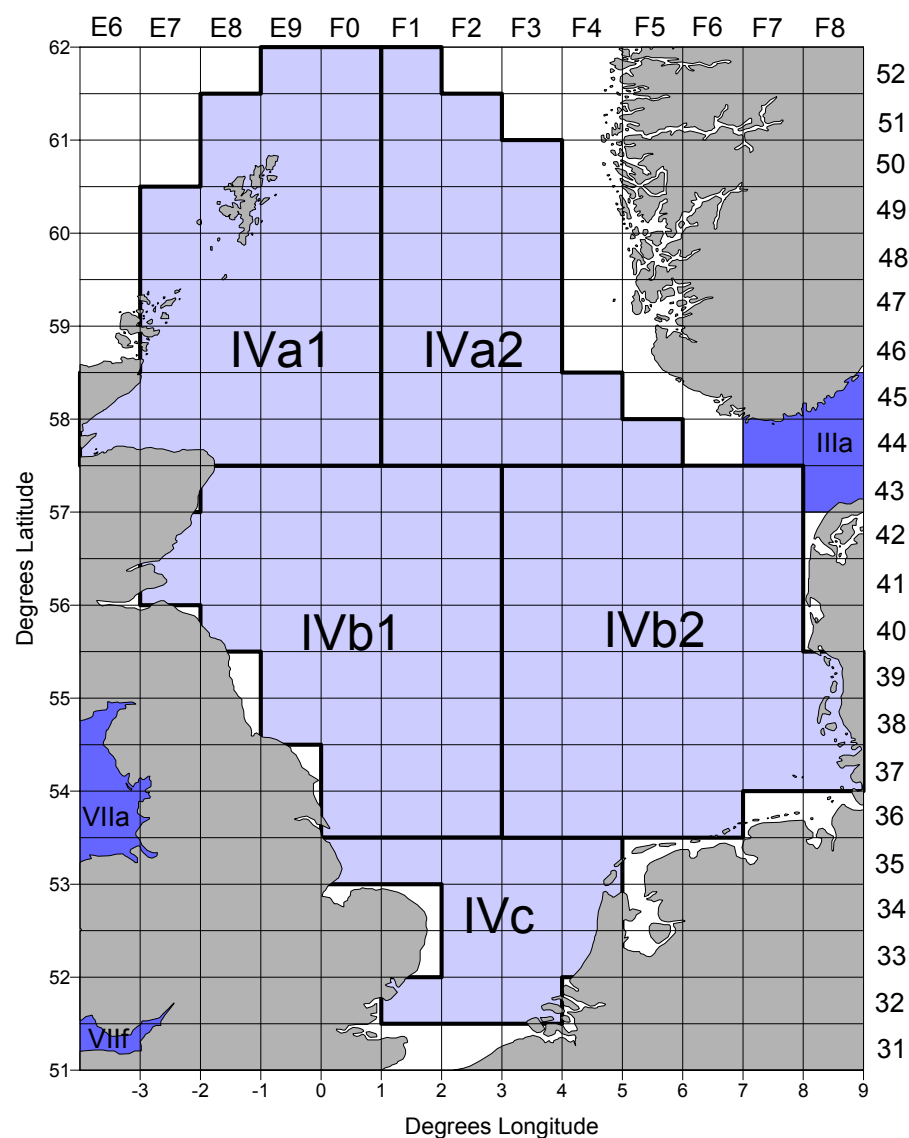


Figure 2.3.3.1: Areas shaded light blue are parts of ICES area IV which are included in the IBTS study area. White areas are part of ICES area IV which are not included in the IBTS study area. The IBTS area has been divided in to five parts IVa1, IVa2, IVb1, IVb2, IVc.

Assessments are carried out for five demersal species that are regularly caught in the IBTS survey (haddock, whiting, cod, Norway pout and plaice). However, the assessments for each of these species are made for different geographic areas. In order to compare the IBTS derived estimates of the numbers at age of each species with the assessed stock numbers at age for each species, the proportion that ICES area IV made up of the total area included in each stock assessment was calculated (Table 2.3.3.2). The assessment estimates of numbers at age of each species were then multiplied by this correction factor to provide equivalent estimates of the numbers at age of each species in ICES area IV only. This assumes that the density of fish was the same on average in ICES area IV and other ICES areas that made up each stock assessment area. This assumption was verified by examining landings data to check whether estimates of the numbers of fish in ICES area IV, based on the assessments, would have altered radically had the stocks been allocated between ICES area IV and outside ICES area IV *pro rata* on the basis of landings rather than area. Essentially both methods arrived at similar allocations.

Species	ICES area covered in VPA assessment	Proportion of total area
Haddock	IIIa	0.091
	IV	0.909
Whiting	IV	0.921
	VIIId	0.086
Cod	IIIa	0.084
	IV	0.843
	VIIId	0.072
Norway pout	IIIa	0.091
	IV	0.909
Plaice	IV	1

Table 2.3.3.2: ICES areas included in the assessment of each VPA species and the proportion of the total assessed area which they represent.

2.3.4. Correcting for differences in the timing of the IBTS and stock assessments

The stock assessments provide estimates of the numbers at age of the assessed species on the 1st January in each year (ICES, 2005) and assume that the catch at age is known without error. The Q3 IBTS data were collected in July to September. Over the intervening period, mortality would have reduced the numbers of fish actually present in the North Sea. In order to compare the two abundance estimates so as to estimate q , this reduction in the actual number of fish in the sea needs to be taken into account. Fortunately, estimates of both fishing (f) and natural mortality (m) for each age class of each of the assessed species are also provided by the assessment reports (ICES 2005). Thus the number of fish (by species s and age a) present in Q3 ($N_{Q3,s,a}$) can be calculated from the numbers present on 1st January ($N_{Jan1,s,a}$) and the combined mortality rate $z_{s,a}$ (where $z_{s,a}=f_{s,a}+m_{s,a}$). These are annual mortality rates, so z must be multiplied by p , the length of the intervening period as a proportion of a year (assuming that on average 9 months pass between 1st January and the time of the Q3 surveys, $p=0.75$), thus:

$$N_{Q3,s,a} = N_{Jan1,s,a} * e^{(-p*z_{s,a})} \quad 2.3.4.1$$

Numbers of 0 group haddock are available in the stock assessment as of 1st July. The above equation was applied to the numbers of 0 group haddock using $p=0.25$ to give the number of 0 group haddock in the middle of Q3. The stock assessment for Norway pout was available for Q3 so no mortality was applied to the number at age estimates of this species.

2.3.5. Comparing IBTS and assessment ICES area IV numbers at age to estimate q

Having corrected both the IBTS derived and assessment derived estimates of the numbers of fish (by species s and age a) to the same area and time, ICES area IV and Q3, these two values can be substituted into equation 2.3.1, and rearranged to solve for q , thus:

$$q_{s,a} = \frac{N_{surv,s,a}}{N_{Q3,s,a}} \quad 2.3.5.1$$

Generally, we expect $q < 1$, indicating that the fishing gear only catches a fraction of the fish in the path of the trawl. The converse, $q > 1$, indicates that the gear catches more fish than are actually in the path of the trawl, implying an “attraction” process drawing fish into the path of the trawl. Figure 2.3.5.1 demonstrates the bias involved if arithmetic means were used to estimate fish density in each ICES rectangle rather than geometric means. Arithmetic means produced

estimates of q that equalled or exceeded 1.0 for some age classes of whiting. When the more appropriate geometric means were used instead, this problem was resolved.

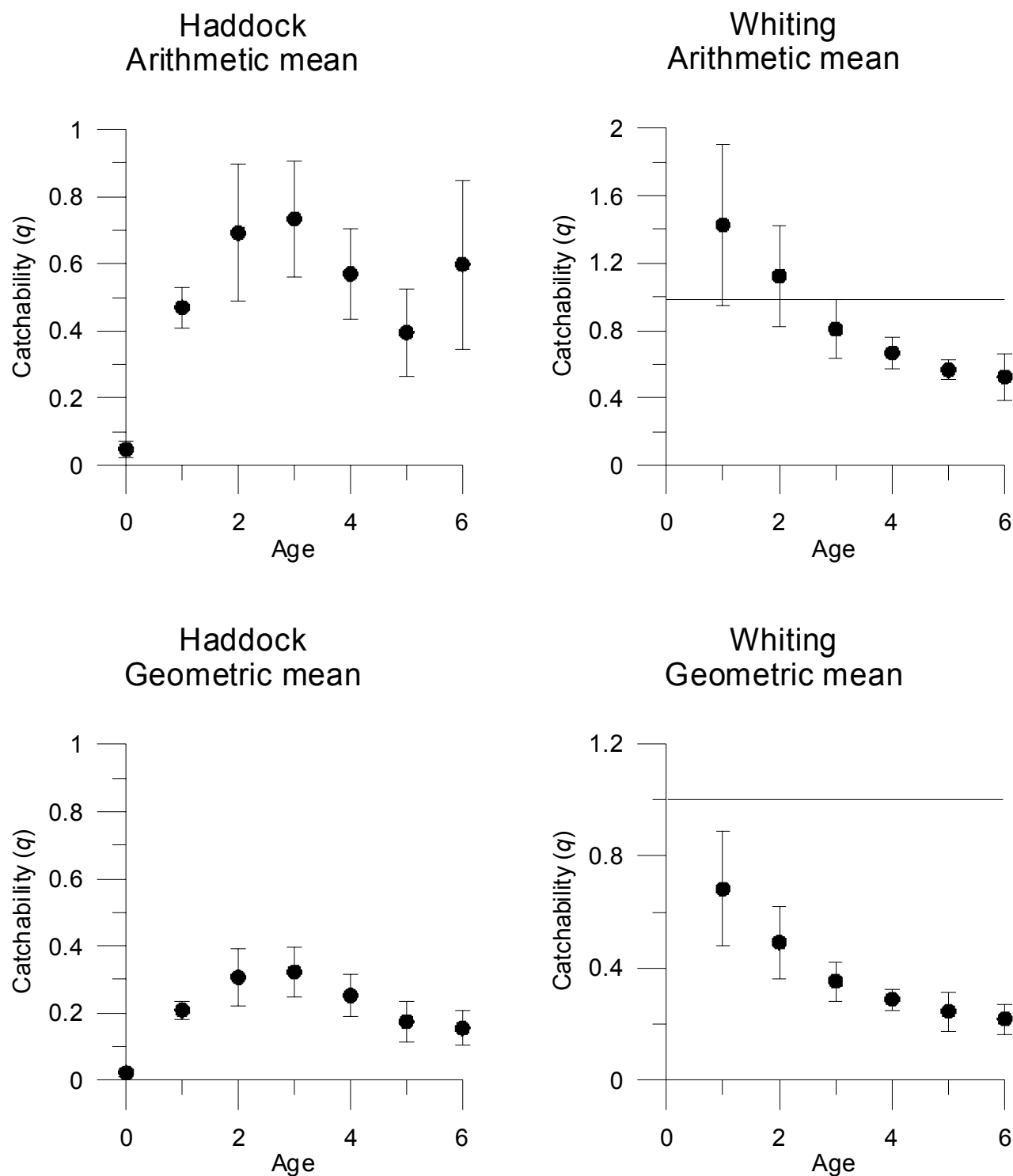


Figure 2.3.5.1: Comparison of catchability at age of haddock and whiting determined using arithmetic means and geometric means to estimate fish density in each ICES rectangle.

2.3.6. Conversion of q at age to q at length

Because the survey data are length based, estimates of q at age for each species needed to be converted to q at length in order to fit relationships that enable q to be estimated for each 1cm length class for each species. For the five assessed species, q for each age class was converted to q at mean length at age through the application of appropriate length at age keys (Figure 2.3.6.1).

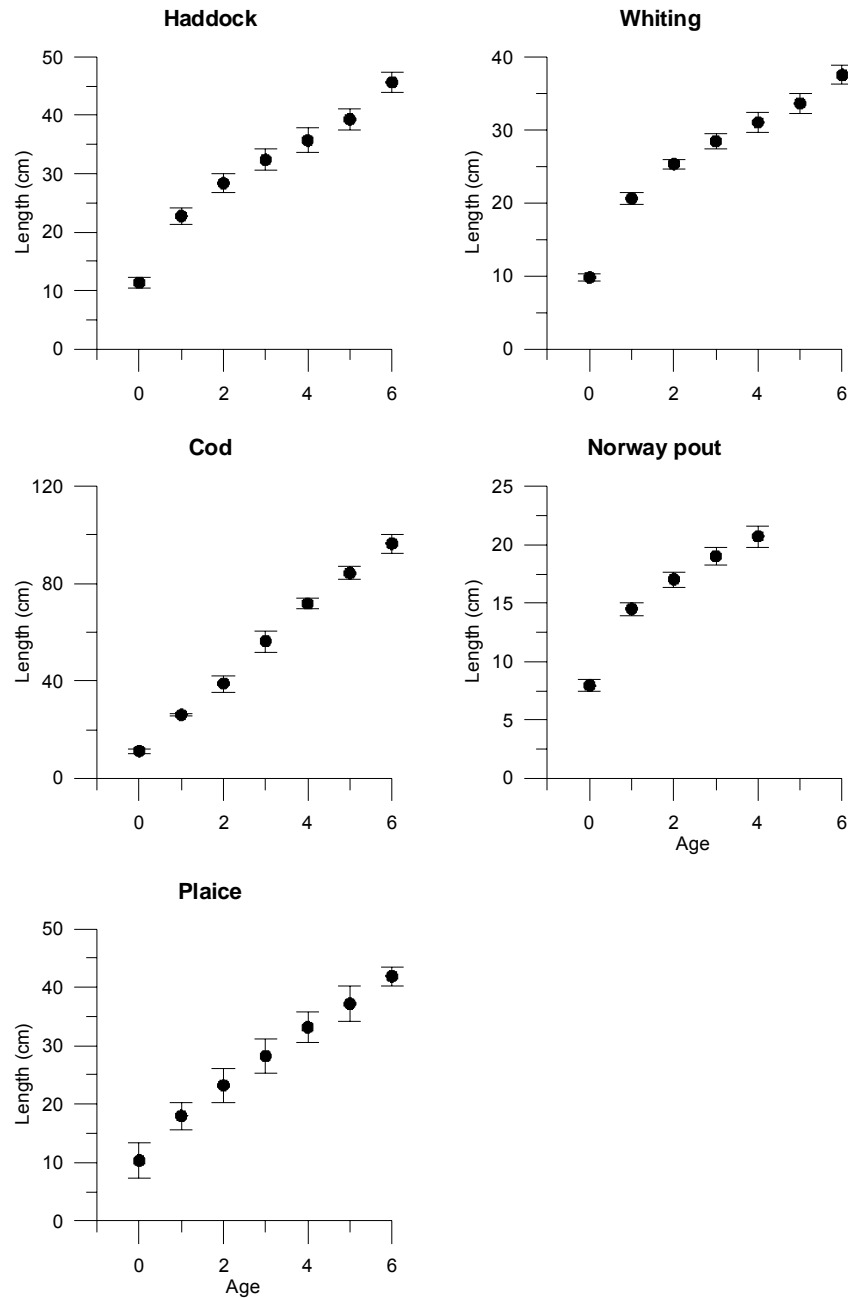


Figure 2.3.6.1: Mean (± 1 SD) length at age relationships for haddock, whiting, cod, Norway pout, and plaice over the period 1998 to 2004.

2.3.7. Determining q for non-assessed species

The IBTS Q3 survey caught 95 different demersal species during the time period 1998 to 2004. Catchability values could only be estimated directly for 5 of the species routinely caught. In order to calculate a total biomass of all the demersal fish in the North Sea, catchabilities for all demersal species both assessed and non-assessed need to be established. To establish q at length for additional species, catch ratios between the GOV and 8-metre Beam Trawl (8BT) were examined. In order to find GOV trawls which were carried out at the same time and in the same area as an 8BT, each statistical rectangle was divided in to 9 'mini' rectangles (Figure 2.3.7.1).

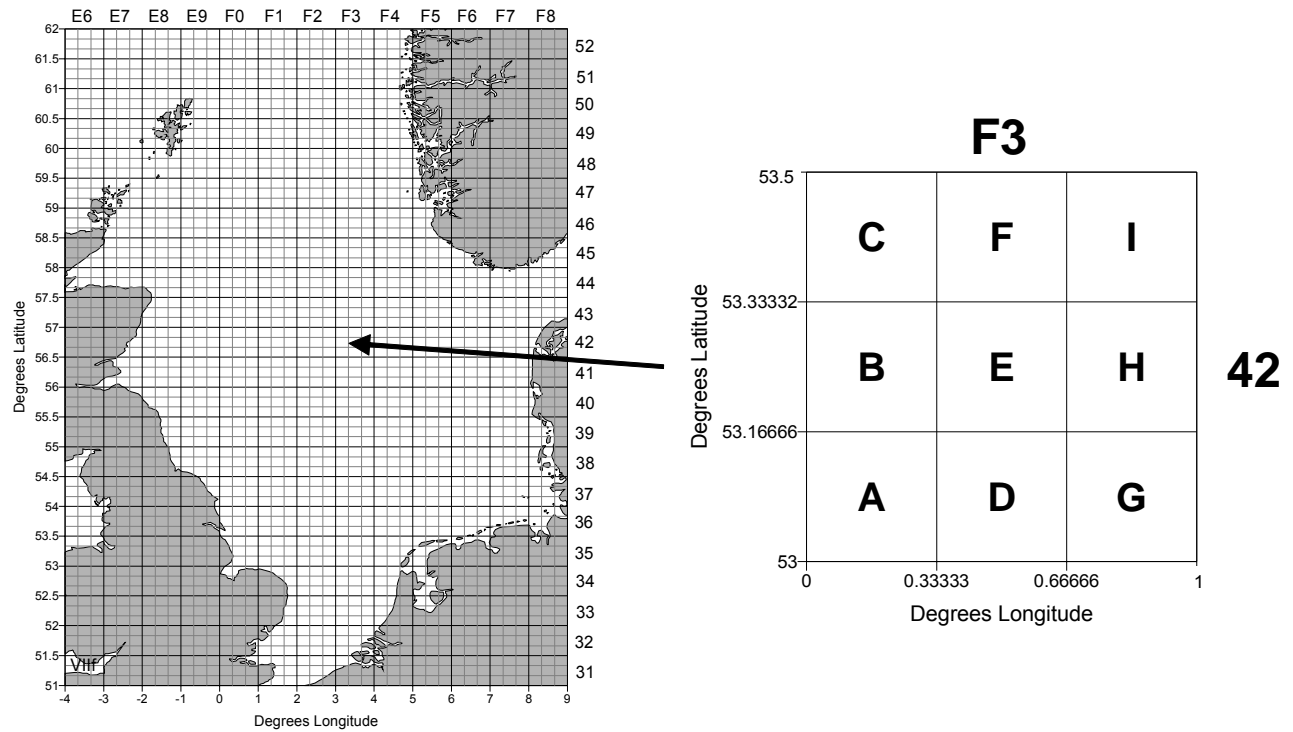


Figure 2.3.7.1: Statistical rectangles were divided in to 9 'mini' rectangles.

If a valid GOV and 8BT haul were located within the same mini statistical rectangle in the same year they were considered a 'paired haul'. All fish were assigned to a 5cm length class l and the density of each species s at each length class l in both the GOV ($FD_{GOV,s,l}$) and 8BT ($FD_{8BT,s,l}$) samples were determined. Catch ratios ($CR_{s,l}$) were then calculated:

$$CR_{s,l} = \text{Log} \left(\frac{FD_{GOV,s,l}}{FD_{8BT,s,l}} \right) \quad 2.3.7.1$$

If the catch ratio was greater than zero then more fish were caught in the GOV, if catch ratio was less than zero then more fish were caught in the 8BT. In some cases a species/length class combination was represented in the GOV or 8BT but not in the other gear, i.e. a positive/zero "paired haul" (caught in the GOV but not in the 8BT) or a zero/positive "paired haul" (not caught in the GOV but caught in the 8BT). Catch ratios could only be used to estimate q for any given species and length class combination where positive/positive "paired haul" data were available, i.e. where both the GOV and the 8BT hauls contained fish of the

same species and length class. Mean catch ratios for each species and length class were determined by summing the estimates for each of the individual “paired haul” samples (n), and dividing by N , the total number of positive/positive “paired hauls” where the focal species and length class combination was sampled by both gears:

$$\overline{CR}_{s,l} = \frac{\sum_{n=1}^N \text{Log} \left(\frac{FD_{GOV,n,s,l}}{FD_{8BT,n,s,l}} \right)}{N} \quad 2.3.7.2$$

For the vast majority of the non-assessed species and length-class combinations where valid mean catch ratios could be determined, these ratios were negative. Two of the assessed species, plaice and cod, also had negative catch ratios across their entire length ranges. Catchability ($q_{s,l}$) of each length class (l) of each non-assessed species (s) with valid mean catch ratio data ($\overline{CR}_{s,l}$) could then be determined knowing the mean catch ratios ($\overline{CR}_{PLA,l}$ and $\overline{CR}_{COD,l}$) and catchabilities ($q_{PLA,l}$ and $q_{COD,l}$) at the same length class of both cod and plaice respectively using the following equation:

$$q_{s,l} = \frac{\left(\left(\frac{10^{\overline{CR}_{s,l}}}{10^{\overline{CR}_{PLA,l}}} * q_{PLA,l} \right) + \left(\frac{10^{\overline{CR}_{s,l}}}{10^{\overline{CR}_{COD,l}}} * q_{COD,l} \right) \right)}{2} \quad 2.3.7.3$$

Non-assessed species with positive catch ratios over the majority of sizes classes for which there was data available (poor cod (*Trisopterus minutus*), bib (*Trisopterus luscus*) and saithe (*Pollachius virens*)) were treated differently and this is discussed in the results section.

For a number of species and size class combinations that featured in the mini-rectangle “paired haul” data set, only zero/positive or positive/zero “paired haul” data were available. For these species therefore, it was not possible to determine valid catch ratios, so their catchability in the GOV trawl could not be estimated using the approach outlined above. However, even under these circumstances, Odds Ratios could be calculated. Odds Ratios (O) were therefore calculated for all species (s) and 5cm length-classes (l) for which any mini statistical rectangle data were available:

$$O_{s,l} = \frac{(p_{1,s,l} * q_2)}{(p_2 * q_{1,s,l})} \quad 2.3.7.4$$

where $p_{1,s,l}$ is the proportion of the total catch of species s and length class l taken by both gears over all N mini-rectangle samples that was taken in the GOV samples ($C_{GOVs,l}$):

$$p_{1,s,l} = \frac{\sum_{n=1}^N C_{GOVn,s,l}}{\sum_{n=1}^N C_{GOVn,s,l} + C_{8BTn,s,l}} \quad 2.3.7.5$$

$q_{1,s,l}$ is the proportion of the total catch of species s and length class l taken by both gears over all N mini-rectangle samples that was taken in the 8BT samples ($C_{8BT,s,l}$):

$$q_{1,s,l} = \frac{\sum_{n=1}^N C_{8BTn,s,l}}{\sum_{n=1}^N C_{GOVn,s,l} + C_{8BTn,s,l}} \quad 2.3.7.6$$

p_2 was the proportion of the total area swept by both gears combined over all N mini-rectangle samples that was swept by the GOV (SA_{GOV}):

$$p_2 = \frac{\sum_{n=1}^N SA_{GOV,n}}{\sum_{n=1}^N SA_{GOV,n} + SA_{8BT,n}} \quad 2.3.7.7$$

q_2 was the proportion of the total area swept by both gears combined over all N mini-rectangle samples that was swept by the 8BT (SA_{8BT}):

$$q_2 = \frac{\sum_{n=1}^N SA_{8BT,n}}{\sum_{n=1}^N SA_{GOV,n} + SA_{8BT,n}} \quad 2.3.7.8$$

For each species and length-class the Log Odds Ratio (Log O) was calculated only where there was a positive p_1 and q_1 . If p_1 or $q_1 = 0$ for a species/length-class combination then the data were excluded as Log O could not be calculated on either zero or infinity values:

$$Log O_{s,l} = Log \left[\frac{(p_{1,s,l} * q_2)}{(p_2 * q_{1,s,l})} \right] \quad 2.3.7.9$$

Logarithms to the base 10 of the Odds Ratio were taken so that the positive values indicate species/length-class combinations of fish taken preferentially by the GOV and negative values indicate species/length class combinations taken preferentially by the 8BT. The numerical value of the log transformed index indicates orders of magnitude differences in the relative catchability of the two gears, thus $Log_{10} O = 1$ and $Log_{10} O = 2$ values indicate the situation where the catchability of a particular length-class is 10 times and 100 times higher in the GOV than in the 8BT respectively while values of -1 and -2 indicate the reverse situation. For every species and length-class where Log O could be calculated and estimates of q could be determined from the catch ratio analysis, (i.e. all the species/length class combinations with positive/positive mini-rectangle “paired haul” data), Log O was plotted against q for each species and length-class combination. This relationship was then used to determine q at length for those species and length class combinations where valid catch ratio values could not be determined and for which only Odds Ratio data were available.

It was not possible to determine either valid catch ratios or Odds Ratios for many of the rarest species sampled in the IBTS survey. Catchability in the GOV trawl for the various length classes of these species was estimated by dividing these 51 species into four groups based on their body morphology; roundfish, flatfish, elasmobranchs (skates and rays) and elasmobranchs (dogfish). The 39 non-assessed species which had q values for every 1cm length-class were also divided in to the same four groups. The average q at length of the non-assessed species in each of the four groups was then calculated. The average q at every 1cm length class of the appropriate group was then given to each of the 51 non-assessed species for which there was no catch ratio or Odds Ratio data.

2.4. Diversity Metrics and Data Analysis

2.4.1. Diversity metrics

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 (e.g. Southwood, 1978). Species richness (S) was simply the count of all species encountered in a sample, a metric that is strongly influenced by sampling effort variation (also equivalent to Hill's N_0). We also apply two indices of species diversity; Hill's (1973) N_1 and N_2 . Hill's N_1 is the exponential of the Shannon-Weiner index, computed as:

$$N_1 = e^{-\sum_{s=1}^S p_s \cdot \ln(p_s)} \quad 2.4.1.1$$

and Hill's N_2 is the reciprocal of Simpson's index, computed as:

$$N_2 = \frac{1}{\sum_{s=1}^S p_s^2} \quad 2.4.1.2$$

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. All diversity metrics were determined using the *PRIMER*® software package (Clarke and Warwick 2001).

2.4.2. Assessing the level of sample aggregation required

Previous studies of groundfish species diversity in the northwestern North Sea have considered the level of trawl sample aggregation required to produce metric values that were representative of the actual community sampled, rather than simply reflecting the limitation of each individual sample (Greenstreet and Hall 1996; Greenstreet *et al* 1999; Greenstreet and Rogers 2006). A total of five hours of trawling was deemed to be the minimum requirement with respect to N_1 and N_2 applied to Aberdeen 48ft trawl samples. This would suggest that at least 10 IBTS or DBTS trawls would need to be aggregated to produce a single "reliable" diversity sample, and the level of aggregation necessary is likely to be even higher for the analysis of species richness. None of the data sets currently available achieve this level of sampling effort (10 samples per ICES rectangle per year), so aggregation in either time or space is inevitable. If considering temporal trends, samples need to be aggregated in space and conversely if considering spatial effects, samples need to be aggregated in time (Greenstreet and Rogers 2006). Since the tests of Huston's (1994) Dynamic Equilibrium Model conceived and executed in Greenstreet *et al* (2007b) essentially consider spatial variation in species diversity, calculation of useful diversity metrics for each ICES rectangle therefore requires samples to be aggregated in time, potentially pooling all the data collected in each ICES rectangle over the full seven year period, 1998 to 2004.

The level of sample aggregation required was assessed for both surveys by analyzing data from selected ICES rectangles where the number of samples available over the full time period was relatively high. We were also concerned that we assessed this over the full range of different community types present in the North Sea. So as the first step to selecting rectangles for this assessment, a cluster analysis was performed to assign each ICES rectangle to a particular community type. Bray-Curtis similarity matrices comparing the similarity between the fish community species composition present in all pairs of ICES rectangle were constructed from each of the surveys after first pooling all the sample data collected for each ICES rectangle. Abundance data were first root-root transformed to down-weight the effect of the most abundant species on the Bray-Curtis similarity indices. The Bray-Curtis similarity matrices were then subjected to hierarchical group-average clustering to identify the groups of ICES rectangles with

fish communities of similar species composition. These analyses were also performed using the *PRIMER*© software (Clarke and Warwick 2001).

2.5. Estimating Productivity of the Demersal Fish Community

2.5.1. Derivation of an index of productivity

The von Bertalanffy growth curve (vBGC) function

$$L_{t,s} = L_{\infty,s} \left(1 - e^{-K_s(t-t_0)}\right) \quad 2.5.1.1$$

has been widely used to describe how fish length increases over time (where $L_{t,s}$ is the length at time t of a fish of species s , and $L_{\infty,s}$ and K_s are two species specific parameters, the ultimate body length that fish of species s will reach and the speed at which these fish grow to this length. Similarly, the weight of fish of any particular length and species is generally well described by the weight at length (WaL) relationship

$$W_{t,s} = c_s \cdot L_{t,s}^{b_s} \quad 2.5.1.2$$

where $W_{t,s}$ is the body mass of a fish at time t of species s when the fish has length $L_{t,s}$ and c_s and b_s are constants specific to each species. Thus for a fish of any given species and length at time t , the daily increase in length can be determined through differentiation of the vBGC, thus:

$$\frac{dL_{t,s}}{dt} = K_s (L_{\infty,s} - L_{t,s}) \quad 2.5.1.3$$

Further, the daily increase in weight associated with this daily increase in length can be determined through differentiation of the WaL relationship, so:

$$\frac{dW_{t,s}}{dL_{t,s}} = c_s \cdot b_s \cdot L_{t,s}^{b_s-1} \quad 2.5.1.4$$

Since weight is a function of length and length is a function of time,

$$\frac{dW_{t,s}}{dt} = \frac{dW_{t,s}}{dL_{t,s}} \cdot \frac{dL_{t,s}}{dt} = c_s \cdot b_s \cdot L_{t,s}^{b_s-1} \cdot K_s (L_{\infty,s} - L_{t,s}) \quad 2.5.1.5$$

Since K_s is in units of years, to get daily increases in weight K_s must be divided by 365. To convert these to specific daily growth rates (SGR) as a percentage of body weight for a fish of species s at time t , fish weight at that moment in time (equation 2) is used as the denominator, thus;

$$SGR_{t,s} = \frac{c_s \cdot b_s \cdot L_{t,s}^{b_s-1} \cdot \frac{K_s}{365} (L_{\infty,s} - L_{t,s})}{c_s \cdot L_{t,s}^{b_s}} \cdot 100$$

$$SGR_{t,s} = b_s \cdot L_{t,s}^{-1} \cdot \frac{K_s}{365} (L_{\infty,s} - L_{t,s}) \cdot 100 \quad 2.5.1.6$$

Thus, for each fish of any given species and length in any sample, the specific daily growth rate can be determined provided three species-specific parameters are known; b_s , one of the two WaL constants, and $L_{\infty,s}$ and K_s , the vBGC function parameters. Determining the specific growth productivity (SGP) index for the whole assemblage is then simply a summing procedure for all species and individuals:

$$SGP_t = \frac{\sum_{s=1}^S \sum_{i=1}^{N_s} c_s \cdot b_s \cdot L_{t,s}^{b_s-1} \cdot \frac{K_s}{365} (L_{\infty,s} - L_{t,s})}{\sum_{s=1}^S \sum_{i=1}^{N_s} c_s \cdot L_{t,s}^{b_s}} \cdot 100 \quad 2.5.1.7$$

2.5.2. Determining productivity index parameter values for each species

Groundfish in the North Sea have been sampled over several decades and WaL relationships have been determined for all species caught in the various surveys (e.g. Coull *et al* 1989; FRS unpublished data; RIVO unpublished data; CEFAS unpublished data). Values for c_s and b_s for all 123 groundfish species recorded in the Scottish August Groundfish (1925-1996), ICES International Bottom Trawl (1998-2004), and Dutch Beam Trawl (1998-2004) Surveys, along with the source, are given in Appendix 3. After reviewing studies of fish growth available for the North Sea region, Jennings *et al* (1998; 1999) could find reliable vBGC parameter values for 33 species (see Appendix 3). Although these 33 species account for over 90% of the individual fish caught in most trawl samples included in these three surveys, in order to determine an SGP index that is inclusive of the entire demersal fish community, vBGC parameters for the remaining 90 species are ideally required.

Interrogation of the web-based *FishBase* database provided data on the largest individual ever recorded (L_{max}) of each of the 123 North Sea groundfish species recorded in the three surveys (Appendix 3). A close and highly significant correlation between $L_{max,s}$ and $L_{\infty,s}$ was obtained (after first log-transforming each variable to standardise the variance) for the 33 species where North Sea derived vBGC parameters were provided by the two Jennings *et al* (1998; 1999) studies (Figure 2.5.2.1A). vBGC parameter values were also available in *Fishbase* for a further 35 groundfish, albeit derived from growth studies carried out in regions close to, but outside the North Sea (e.g. the northeast Atlantic, Barents Sea, Bay of Biscay and western Mediterranean Sea). These parameter values are also listed in Appendix 3. The regression relationship shown in Figure 2.5.2.1A was used to predict $L_{\infty,s}$ from $L_{max,s}$ for these additional 35 species and the predicted $L_{\infty,s}$ values were compared with the actual $L_{\infty,s}$ values obtained *FishBase* (Figure 2.5.2.1B). This analysis, particularly the high R^2 value of 0.95 indicated in Figure 2.5.2.1B, suggests two things. Firstly, $L_{max,s}$ values derived from *FishBase* for each species provide reliable predictors of $L_{\infty,s}$. Secondly, $L_{\infty,s}$ parameter values obtained from *FishBase* for the additional 35 species that derived from growth studies carried out outside the North Sea appear to be just as reliable as the parameter values provided by Jennings *et al* (1998; 1999) derived from studies carried out within the North Sea area. Consequently, a final linear regression model to predict $L_{\infty,s}$ from $L_{max,s}$ was determined combining the two sets of data (Figure 2.5.2.1C). Appendix 3 gives $L_{\infty,s}$ values for each species and indicates whether the parameter value was provided by Jennings *et al* (1998; 1999), from *FishBase*, or estimated from the regression model shown in Figure 2.5.2.1C.

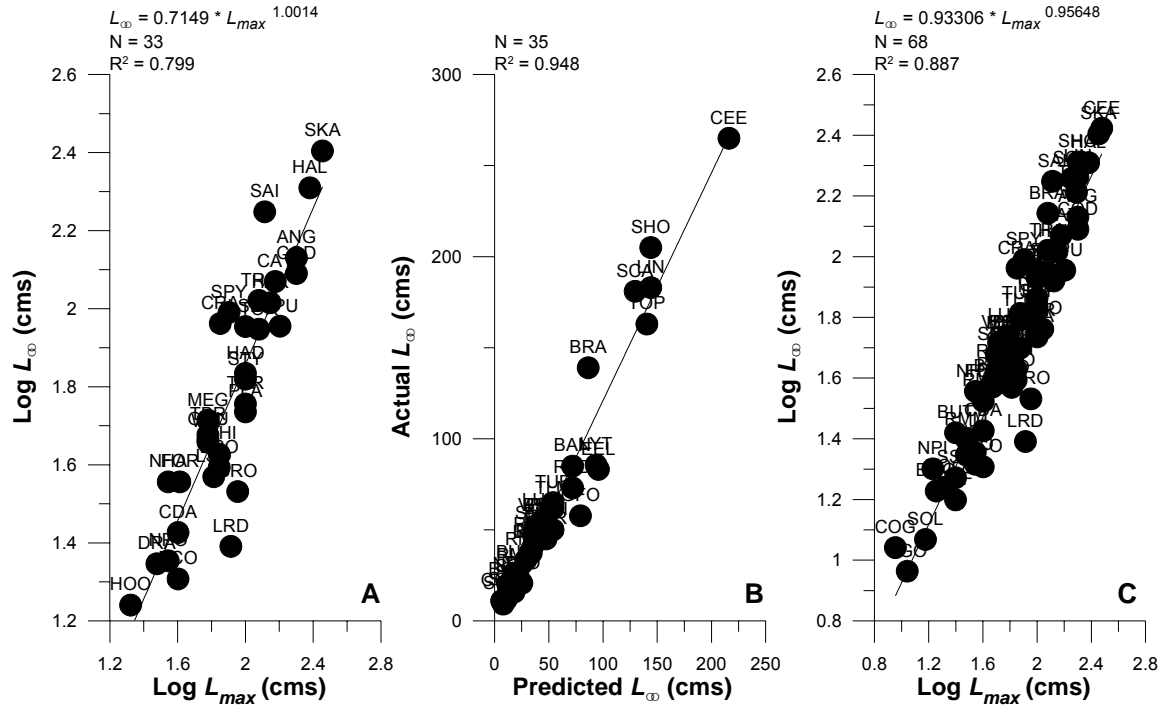


Figure 2.5.2.1: (A) Relationship between L_{max} and the von Bertalanffy growth curve parameter L_{∞} for 33 species for which L_{∞} values were obtained from Jennings *et al* (1998; 1999) based on growth studies performed within the North Sea region. (B) Comparison of actual L_{∞} values for 35 species for which L_{∞} values were obtained from *FishBase* based on studies performed outside the North Sea region with predicted L_{∞} values derived from L_{max} using the regression model obtained in panel A. (C) Final regression model to predict L_{∞} from L_{max} based on all 68 species for which vBGC parameter data were available. Data points are labelled with three letter species codes (see Appendix 2).

Estimates of K_s were obtained for each of the 123 North Sea groundfish species following a similar procedure. For the 33 species where values of K_s were provided following review of growth studies carried out in the North Sea region by Jennings *et al* (1998; 1999), K_s was significantly correlated with $L_{\infty,s}$ (Figure 2.5.2.2A). The regression model obtained was used to predict K_s from $L_{\infty,s}$ for the 35 additional species for which K_s parameter values had been obtained from *FishBase*, derived from growth studies undertaken outside the North Sea region (Figure 2.5.2.2B). As previously, the resulting significant correlation suggests that K_s can be reliably predicted from $L_{\infty,s}$ and that estimates of K_s determined from growth studies performed outside the North Sea region are as reliable as parameter values derived from growth studies carried out within the region. The two data sets were therefore combined and a final regression analysis performed to derive the optimum model to predict K_s from $L_{\infty,s}$ (Figure 2.5.2.2C). Finally, Appendix 3 also gives K values for each species and indicates whether the parameter value was provided by Jennings *et al* (1998; 1999), from *FishBase*, or estimated from the regression model shown in Figure 2.5.2.2C. It is obvious that, for the 55 species where K was estimated using the regression model in Figure 2.5.2.2C, K is clearly directly linked to L_{∞} . However, both Figures 2.5.2.2A and 2.5.2.2B suggest that these two parameters are far from independent anyway. It should also be emphasised that these 55 species represent the rarest species in the North Sea and individuals belonging to these species rarely accounted for more than 1% of the total number of fish caught in any single trawl sample in the three survey data sets examined.

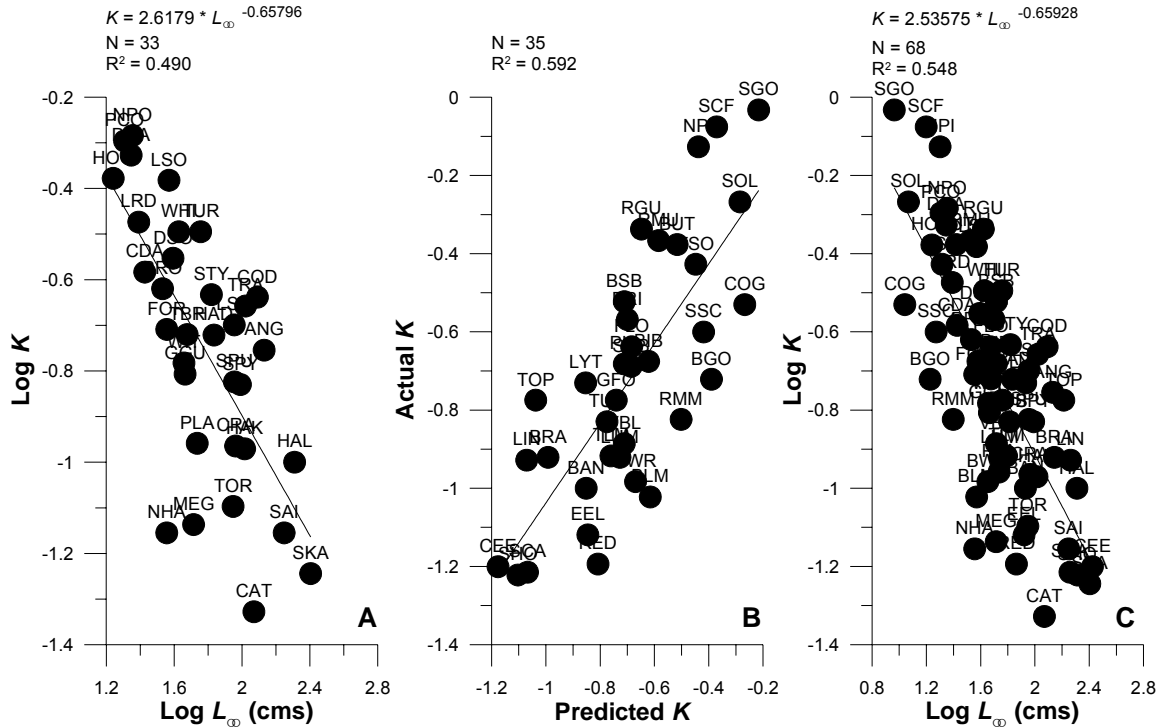


Figure 2.5.2.2: (A) Relationship between the two von Bertalanffy growth curve parameters L_{∞} and K , for 33 species for which values were obtained from Jennings *et al* (1998; 1999) based on growth studies performed within the North Sea region. (B) Comparison of actual K values for 35 species for which K values were obtained from *FishBase* based on studies performed outside the North Sea region with predicted K values derived from L_{∞} using the regression model obtained in panel A. (C) Final regression model to predict K from L_{∞} based on all 68 species for which vBGC parameter data were available. Data points are labelled with three letter species codes (see Appendix 2).

3. RESULTS

3.1. Catchability: Correcting the IBTS View to see the Real World

3.1.1. Catchability (q) at length for the assessed species

Table 3.1.1.1 gives the numbers of each age class of each species in the North Sea in each year based on the IBTS density data ($N_{surv} * RF$, equations 2.3.2.4/5 and 2.3.3.1) and the stock assessments after correction to account for mortality between January 1st and the time of the surveys and to reduce the stock assessment areas to just the North Sea (see Table 2.3.3.1). Catchability (q) in the GOV trawl used in the IBTS was then calculated for each age class of each of the five assessed species (equation 2.3.5.1) and, knowing the length at age of each species (see Figure 2.3.6.1), converted to catchability at length (Figure 3.1.1.1). The manner in which catchability (q) varied with increase in length differed markedly between the five assessed species requiring different approaches to relationship fitting. In some cases more than one relationship was used.

For haddock, a polynomial relationship was used to calculate q at length. For Norway pout and plaice, q for young/small fish differed markedly from the older/larger fish, so no trend in q

Species Composition, Diversity, Biomass and Production of the Demersal Fish Community of the North Sea

with increase in length could be determined for the smaller fish of these two species. All Norway pout ≤ 11 cm were therefore assigned the same value of q , equal to the mean for all 0 group Norway pout, and all plaice ≤ 21 cm were assigned the same value of q , equal to the mean value for 1 group plaice. For older plaice, q decreased linearly with length, providing a linear regression equation with which to estimate q for any plaice > 21 cm. No such trend was apparent for Norway pout, so all pout ≥ 12 cm were assigned a value of q , equal to the mean for all Norway pout aged 1+. For cod, q increased with length at age and a polynomial relationship was used to estimate q for any length of cod. For all age classes of whiting, q decreased with increasing length and a linear relationship provided the best fit to the data. The stock assessments provide no information for 0 group whiting abundance, so it was not possible to determine directly estimates for q for whiting smaller than 21cm. All whiting ≤ 21 cm were given a q of 0.62.

Year	Age	Haddock		Whiting		Cod		Norway pout		Plaice	
		IBTS	VPA	IBTS	VPA	IBTS	VPA	IBTS	VPA	IBTS	VPA
1998	0	92,474	5,102,051	1,250,936	-	141,496	-	3,889,628	56,332,548	0	-
	1	85,395	355,556	167,508	424,612	2,510	51,797	986,593	7,854,669	8,558	449,969
	2	54,738	153,389	66,660	138,518	38,934	117,279	931,532	3,599,640	113,321	901,985
	3	16,400	42,288	21,747	91,673	2,392	10,416	14,520	99,081	5,711	118,804
	4	13,313	82,954	12,698	48,145	856	3,613	3,818	31,815	4,939	65,840
	5	935	3,637	4,539	21,220	535	1,500	-	-	233	17,834
1999	6+	518	2,829	1,894	7,694	297	487	-	-	164	23,924
	0	2,350,247	61,138,492	800,955	-	10,475	-	8,000,374	138,964,284	27	-
	1	58,547	302,806	344,835	633,178	15,153	87,811	2,904,187	10,901,637	10,150	718,891
	2	31,096	94,117	76,731	172,890	1,665	16,061	271,987	1,088,982	18,464	338,744
	3	15,962	50,156	23,054	58,655	7,947	17,881	143,135	474,498	56,780	546,767
	4	3,954	15,491	10,520	37,764	494	2,182	2,527	20,907	2,399	43,462
2000	5	3,169	38,855	4,251	19,233	190	837	-	-	274	25,427
	6+	452	1,972	1,765	11,948	85	452	-	-	201	19,409
	0	403,296	12,311,741	772,830	-	5,023	-	1,825,235	50,188,617	-	-
	1	868,985	3,610,901	404,843	704,522	20,249	166,813	8,442,521	27,136,377	-	847,372
	2	14,883	100,761	153,097	259,311	5,379	22,695	370,031	1,470,762	-	488,665
	3	6,369	25,926	27,262	64,296	385	3,581	14,088	53,631	-	226,878
2001	4	3,356	17,925	5,510	20,568	1,118	3,451	6,635	84,537	-	285,527
	5	1,258	10,222	2,605	13,159	153	478	-	-	-	20,525
	6+	972	9,909	1,955	10,226	226	278	-	-	-	62,420
	0	6,306	1,276,188	867,147	-	3,461	-	2,194,977	43,975,602	328	-
	1	118,753	682,764	366,010	548,696	6,881	40,310	1,406,950	9,807,201	7,829	540,600
	2	411,694	1,552,586	143,690	335,295	12,626	56,515	1,067,815	3,024,243	15,546	402,150
2002	3	9,498	36,091	42,435	124,001	1,998	5,783	34,716	63,630	10,165	192,025
	4	2,085	8,999	8,121	25,516	280	854	3,985	20,907	7,260	97,554
	5	1,135	6,623	1,728	6,379	358	828	-	-	7,618	107,218
	6+	911	11,417	2,800	8,781	305	184	-	-	893	25,812
	0	39,036	2,156,959	89,726	-	208	-	3,067,451	31,191,426	251	-
	1	16,156	74,726	352,307	452,471	19,554	92,300	837,623	8,245,539	2,206	1,606,306
2003	2	72,423	254,319	103,539	261,843	5,177	16,635	115,593	1,771,641	39,108	270,580
	3	204,510	808,713	51,891	164,227	3,180	14,484	76,813	445,410	1,991	165,667
	4	3,416	10,864	14,243	59,907	983	1,735	295	16,362	2,802	79,940
	5	852	4,619	2,277	11,430	203	282	-	-	316	40,609
	6+	1,050	6,459	1,177	6,036	121	352	-	-	321	57,324
	0	31,427	1,750,613	135,198	-	3,007	-	1,390,213	14,354,928	695	-
2004	1	22,753	124,481	123,939	121,327	3,167	39,670	1,235,155	6,046,668	8,216	421,025
	2	11,483	27,097	133,667	182,208	4,728	34,974	281,295	1,292,598	35,203	755,483
	3	70,246	162,077	59,429	136,734	1,317	4,742	17,039	149,076	14,919	125,497
	4	143,194	473,710	28,260	80,889	984	5,027	9,285	79,083	5,509	68,756
	5	954	5,426	6,927	31,677	477	372	-	-	1,270	36,513
	6+	736	4,501	1,873	8,811	366	117	-	-	1,325	43,696
2005	0	40,747	1,780,612	382,294	-	4,238	-	949,700	17,161,011	-	-
	1	21,367	100,862	75,946	96,189	7,467	-	753,660	2,886,984	-	1,024,232
	2	15,637	46,620	18,858	51,461	3,264	-	189,381	1,120,797	-	210,664
	3	4,782	13,457	31,197	96,955	2,273	-	16,691	171,801	-	382,501
	4	34,393	110,310	22,934	75,655	478	-	0	30,906	-	67,428
	5	78,604	344,657	17,066	43,369	325	-	-	-	-	33,722
2006	6+	651	3,853	4,853	22,458	175	-	-	-	-	41,958

Figure 3.1.1.1: Number at age ($\times 10^3$) of each species estimated in the North Sea based on the IBTS GOV density data (corrected to account for the fact that not all of ICES area IV was included in the surveyed area) and ICES 2005, VPA stock assessments (corrected to reduce all stock assessment areas to just the area of ICES area IV and to adjust for the difference in timing between the assessment data, January 1st and the timing of the survey in quarter 3).

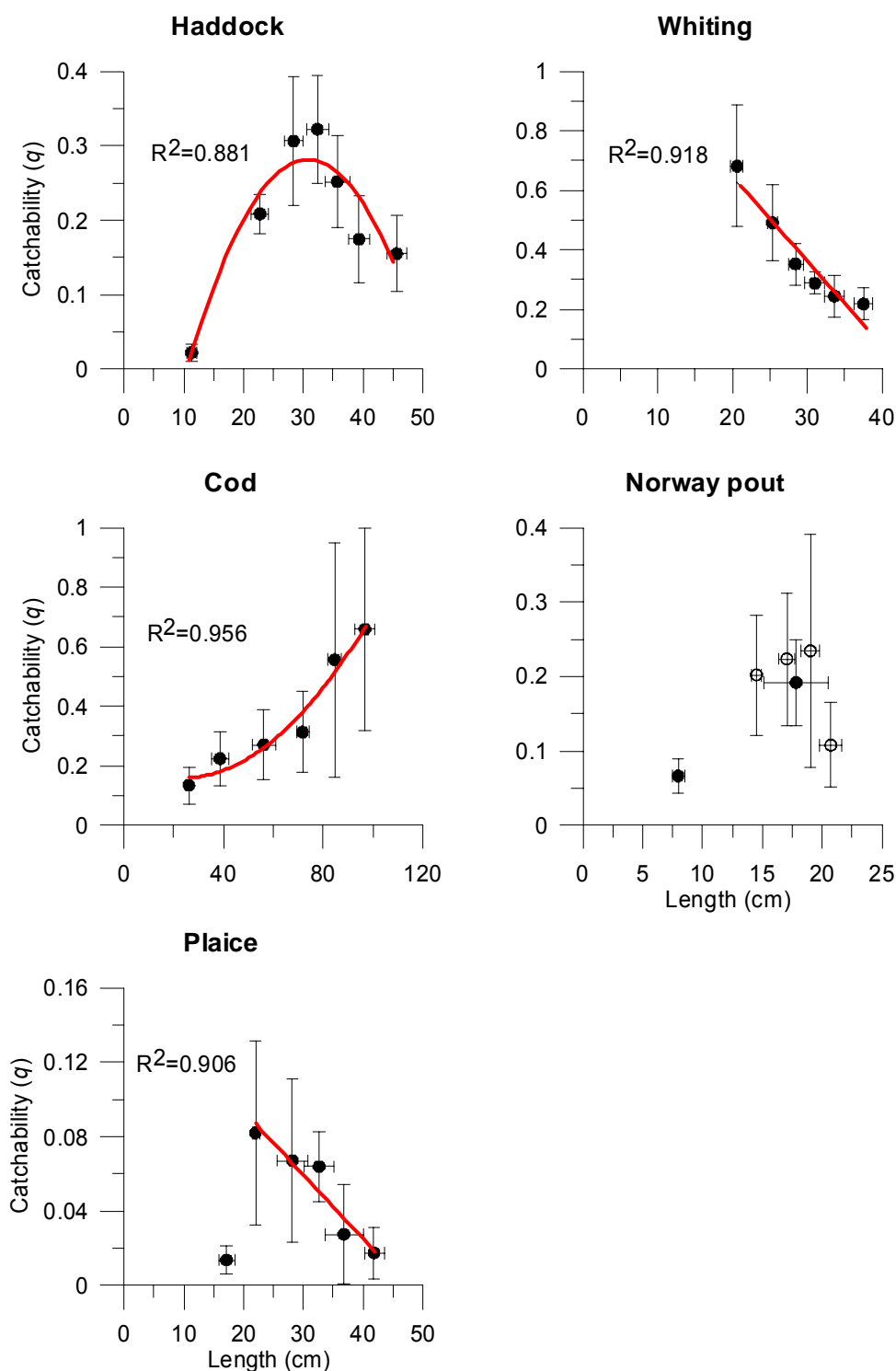


Figure 3.1.1.1: Catchability (q) at length for haddock, whiting, cod, Norway pout and plaice. Vertical bars show SDs for estimates of q derived for each species in each year. Horizontal bars show SDs for length determined from variation in length at age between years. For Norway pout, the filled datum shows the q value applied to all fish ≥ 12 cm, since no significant length-related trend in q was apparent for fish of 12cm and larger. The filled datum for fish ≤ 11 cm shows the q value applied to all fish below this size.

3.1.2. Catchability (q) at length for the non-assessed species

Table 3.1.2.1 gives the catch ratio (CR) data for each 5cm length class of the assessed species along with CR data for a further 21 species for which positive/positive “paired haul” data were available so allowing valid CR values to be determined. The CR data for bib, poor cod and saithe are also shown. Application of equation 2.3.7.3 provided estimates of q for each of the additional species/5cm length class combinations where CR data were available (Table 3.1.2.2). Best fit curves were plotted to these data to explore the relationship between q and length for each species. These relationships were used to provide estimates of q for each 1cm length class of each species. For many species sufficient data were available to allow curve fitting. In all instances a polynomial function provided the best fit. To estimate q at each 1cm length class for these species, the polynomial expression was used over the length range over which CR data were available. Where it was necessary to extrapolate beyond the data range, a constant q equal to the q obtained at the extreme of the data range was assumed. Figure 3.1.2.1 shows examples of the application of this approach used to estimate q at each 1cm length for common dab (panel a) and grey gurnard (panel b). This approach was adopted for all species in Tables 3.1.2.1 and 3.1.2.2 where three or more CR derived q values were available. For species where only two CR values were available to provide estimates of q in a 5cm length class an alternative approach was adopted. If the CR trends between the two length classes for which data were available for the non-assessed species in question were in the same direction as the trends between the same length classes for both plaice and cod, then a linear relationship between q and length between the two length ranges with CR data was assumed. If extrapolation beyond these length classes was necessary, q was again assumed to remain constant and equal to the value obtained at the extreme ranges of the data (e.g. bullrout in Figure 3.1.2.1). If, on the other hand, the CR trends between the two length ranges for the non-assessed species in question differed from the trends observed for either cod or plaice, then a constant q , equal to the average of the two q values derived from the application of equation 2.3.7.3 to the CR data, across all 1cm length classes of the non-assessed species was assumed (e.g. solenette in Figure 3.1.2.1). Appendix 1 gives the resulting “rules” used to provide estimates of q for each 1cm length class of the 21 non-assessed species listed in Tables 3.1.2.1 and 3.1.2.2 where q was estimated from the CR data.

Species Composition, Diversity, Biomass and Production of the Demersal Fish Community of the North Sea

Species	Length Class (cm)												
	0-4.9	5-9.9	10-14.9	15-19.9	20-24.9	25-29.9	30-34.9	35-39.9	40-44.9	45-49.9	50-54.9	55-59.9	60-64.9
HAD		1.20	1.08	1.08	1.00	0.98	0.90	0.64	0.61	-0.40			
WHI		0.92	0.67	0.70	0.91	0.98	0.91	0.36	-0.67				
COD		-0.41	-0.54		-0.07	-0.12	-0.05	-0.22	-0.21	-0.41	-0.72	-0.88	
NPO		1.21	1.55	1.49									
PLA		-0.84	-1.71	-1.29	-1.01	-0.81	-0.70	-0.60	-0.60	-0.56			
ANG						-0.50	-0.52	-0.58	-0.51	-0.19	-0.11		
BRO				-0.90	-0.64	0.20							
CDA		-0.73	-0.38	-0.01	0.22	0.14	-0.37						
DRA			-0.65	-0.73	-0.60								
DSO				-0.77	-1.09	-0.84							
FLO					0.38	-0.26	-0.10	-0.61					
FOR			-1.28	-0.49	-0.67	-0.96							
GGU		-1.03	-0.43	-0.13	0.25	0.42	0.45	-0.06					
HAK						-0.60	-0.36						
HOO		-0.83	-1.09	-1.06									
LRD		-0.30	-0.42	-0.27	-0.17	-0.09	-0.30						
LSD					-0.08				-1.16		-1.16		-0.55
LSO			-0.63	-0.26	-0.16	-0.15	-0.29	-0.28					
MEG						-0.67	-0.60						
RMU		0.08	-0.22	-0.13	0.14	0.07							
SCF		-1.51	-1.87	-0.97									
SOL		-1.18	-1.35										
STY		-0.64	-1.13	-0.92	-0.91	-0.87	-0.79	-0.60	-0.64	-0.48	-0.33		
TUB					-0.40	-0.51	-0.03	-0.29					
WEE		-0.45	-0.25	-0.77									
WIT					-0.68	-0.83	-0.84	-0.60	-0.66				
BIB		-1.45	0.45	-0.08	-0.01								
PCO		0.98	0.65	0.22	-0.15								
SAI									0.54	0.19	-0.09	0.31	

Table 3.1.2.1: Table showing the catch ratios for every 5cm length class of the 5 assessed species: haddock (HAD), whiting (WHI), cod (COD), Norway pout (NPO) and plaice (PLA). The catch ratio's for every 5cm length class of the 21-non assessed species for which there was catch ratio data available are also shown: angler (ANG), bull-rout (BRO), common dab (CDA), dragonet (DRA), Dover sole (DSO), flounder (FLO), four-bearded rockling (FOR), grey gurnard (GGU), hake (HAK), hooknose (HOO), long rough dab (LRD), lesser spotted dogfish (LSD), lemon sole (LSO), megrim (MEG), striped red mullet (RMU), scaldfish (SCF), solenette (SOL), starry ray (STY), tub gurnard (TUB), weever (WEE) and witch (WIT). The catch ratios are also shown for bib (BIB), poor cod (PCO) and saithe (SAI).

Species Composition, Diversity, Biomass and Production of the Demersal Fish Community of
the North Sea

Species	Length Class (cm)									
	0-4.9	5-9.9	10-14.9	15-19.9	20-24.9	25-29.9	30-34.9	35-39.9	40-44.9	45-49.9
ANG					0.12	0.11	0.07	0.06	0.06	0.20
BRO					0.52					
CDA		0.05	0.26		0.88	0.46	0.10			
DRA			0.14		0.13					
DSO					0.04	0.05				
FLO					1.00	0.18	0.18	0.05		
FOR			0.03		0.11	0.04				
GGU		0.02	0.23		0.94	0.87	0.64	0.19		
HAK						0.08	0.10			
HOO		0.04	0.05							
LRD		0.13	0.24		0.36	0.27	0.11			
LSD					0.44				0.01	
LSO			0.15		0.36	0.23	0.12	0.11		
MEG						0.07	0.06			
RMU		0.30	0.38		0.73	0.39				
SCF		0.01	0.01							
SOL		0.02	0.03							
STY		0.06	0.05		0.06	0.04	0.04	0.05	0.05	0.10
TUB					0.21	0.10	0.21	0.11		
WEE		0.09	0.35							
WIT					0.11	0.05	0.03	0.05	0.04	

Table 3.1.2.2: Table showing q at each 5cm length class for the 21 non-assessed species (not including plaice and cod therefore) calculated using equation 2.3.7.3. For species codes, see legend to Table 3.1.2.1.

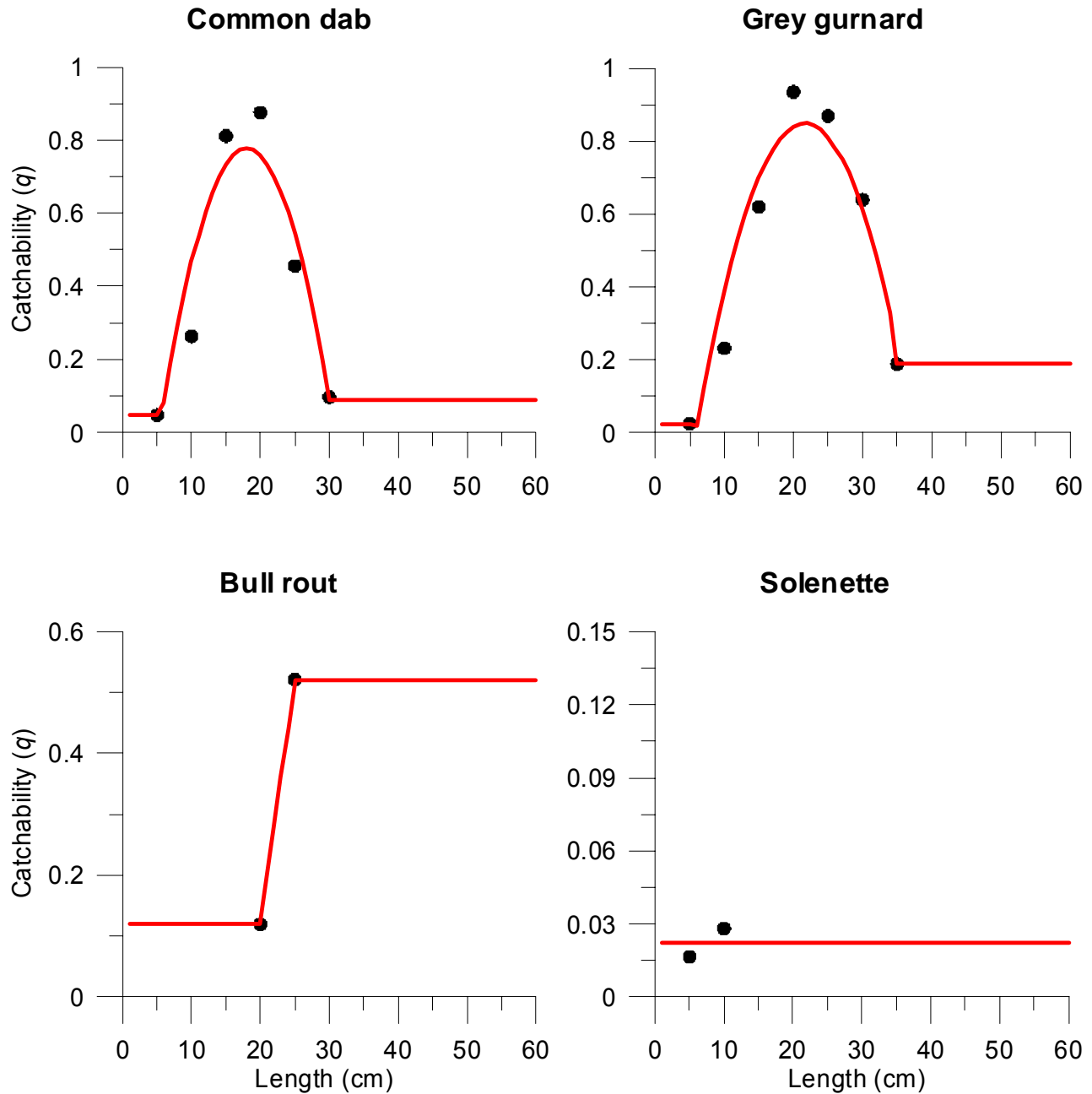


Figure 3.1.2.1: Catchability (q) at length for common dab, grey gurnard, bull rout and solenette based on the relationship between catch ratio and q at length of cod and plaice and the catch ratio of each of the non-assessed species.

The log Odds Ratio was plotted against q for each of the 21 non assessed species for which a value for q at length was calculated using the relationship between CR and q at length of cod and plaice and the CR at length of the non-assessed species. Figure 3.1.2.2 shows the relationship between the log Odds Ratio and q . This relationship was then used to estimate q at length for an additional 15 species for which log Odds Ratio values could be calculated, but for which CR values could not be determined. Figure 3.1.2.3 shows the catchability at length for four species for which only log Odds Ratio data were available. Catchability at length was

calculated using the relationship between q and $\text{Log } O$ shown in Figure 3.1.2.2, then fitting a relationship between the data points. Where there were only 2 data points the average q was used (Figure 3.1.2.3, ling and thickback sole).

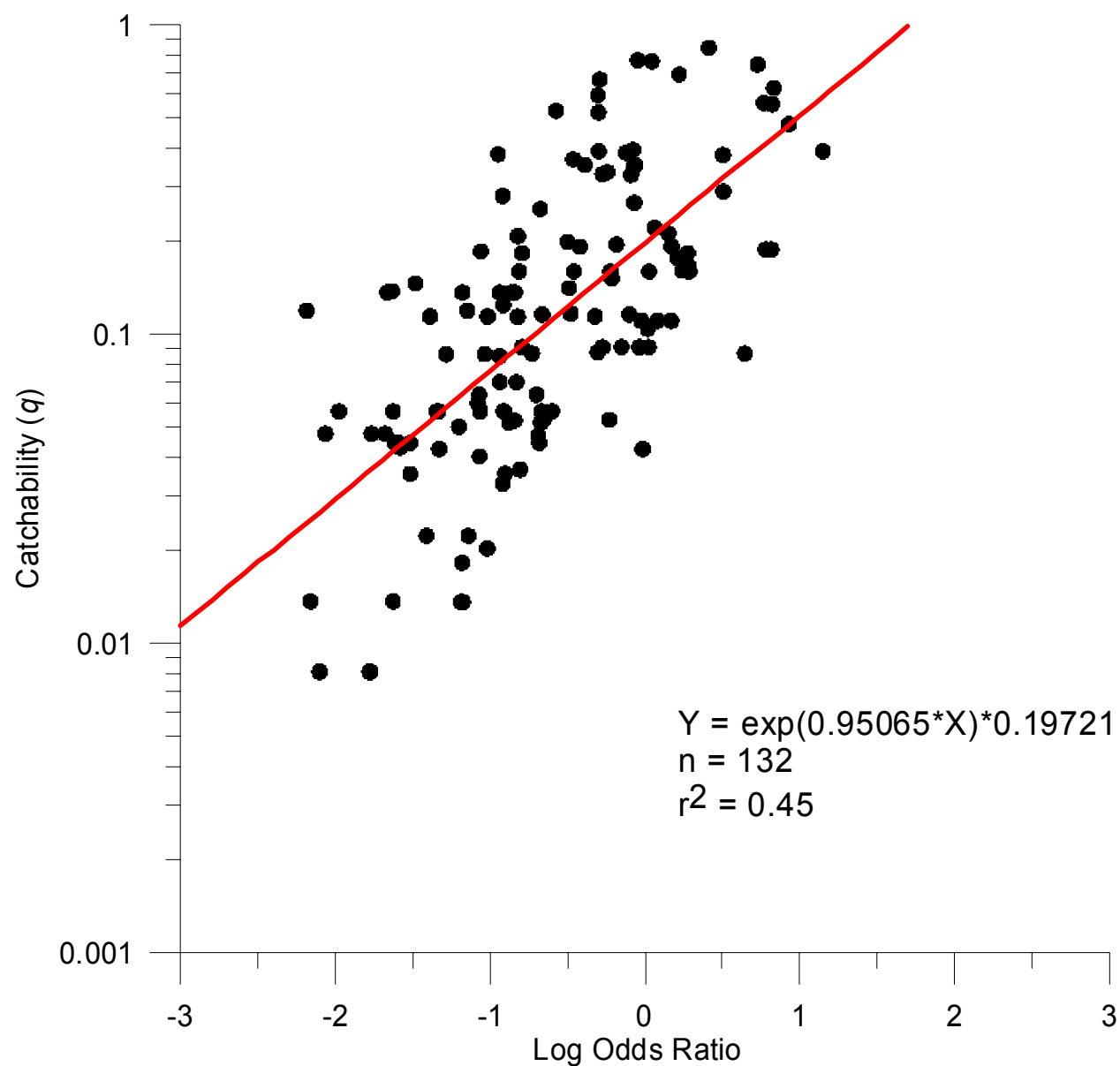


Figure 3.1.2.2: The relationship between the log odds ratio and q for each length-class of the 21 non-assessed species.

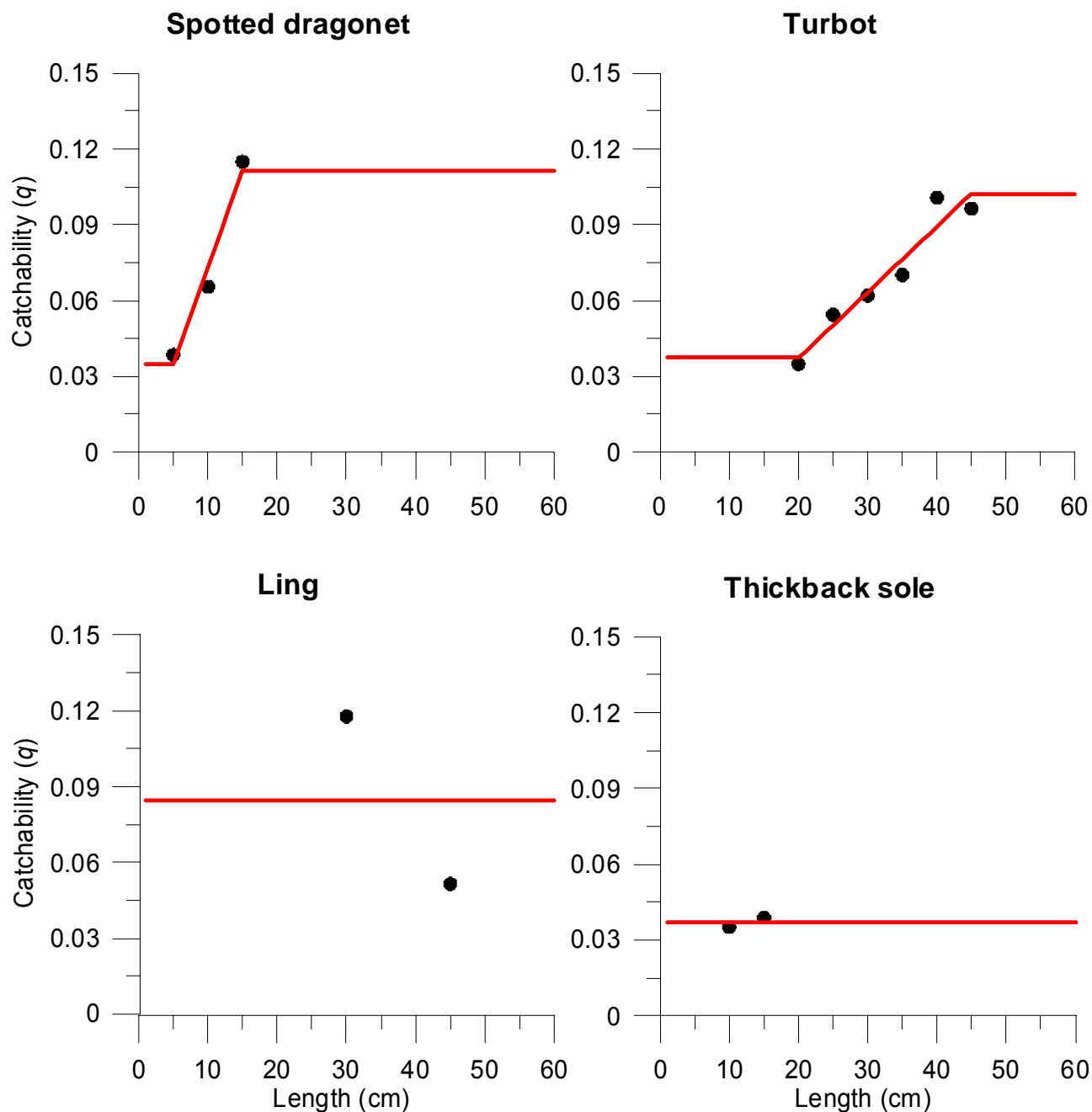


Figure 3.1.2.3: Catchability (q) at length for spotted dragonet, turbot, ling and thickback sole calculated using the relationship between the log odds ratio of the above 4 species and the relationship between the log odds ratio and q of the 12 non-assessed species.

Norway pout (NPO) was caught much more effectively in the GOV than in the 8BT, having high positive catch ratio's over all length classes (Table 3.1.2.1). Despite this, q for all lengths of Norway pout was actually relatively low ($q = 0.06$ to 0.19 ; Figure 3.1.1.1). The more pelagic nature of this species probably results in many individuals passing above the GOV headline, so while the GOV may not be a particularly good sampler of Norway pout, the 8BT is even worse. In previous studies poor cod (PCO, *Trisopterus minutus*) and bib (BIB, *Trisopterus luscus*) have

been placed in the same catchability group as Norway pout (Yang 1982; Sparholt 1990) on the basis of the physical and presumed behavioural similarities between these two species. However, examination of the catch ratio at length signatures of poor cod and bib suggests that, unlike Norway pout, they became increasingly better caught by the 8BT, compared with the GOV, as they increased in length (Table 3.1.2.1). This corresponds with what is known about the biology of poor cod and bib which suggest that they become increasingly benthic in nature with increasing age and length (FishBase, <http://www.FishBase.org>). However, it is not clear that their catchability in the GOV would necessarily increase as a result of this. Being small and close to the seabed, it is possible that poor cod and bib may pass below the ground-gear of the GOV trawl. So, despite the clear differences in the catch ratio at length signatures of Norway pout, poor cod and bib, we have simply followed previous convention and given poor cod and bib the same catchability at length as Norway pout.

Saithe (SAI, *Pollachius virens*) were not caught in significant numbers in the GOV survey to be treated the same way as the other assessed species. Generally only large saithe were caught and catch ratio data were therefore only available for the larger 5cm size classes (Table 3.1.2.1). At this size range there was no obvious correspondence between the variation in catch ratios with length for saithe and the other gadoid species. Consequently saithe q at length was given the average q at length of the three assessed gadoids; haddock, whiting and cod.

Application of the processes described above provided estimates of q for each 1cm length class of 44 species, including the 5 assessed species. However it was not possible to determine either valid catch ratios or Odds Ratios for many of the rarest species sampled in the IBTS survey. The 39 non-assessed species were divided into four groups based on their body morphology; round-fish, flatfish, elasmobranchs (skates and rays) and elasmobranchs (dogfish). The average q at length of fish in each group was then determined (Figure 3.1.2.4). The 51 demersal species for which catch ratio or Odds Ratio data were available were then assigned to the same four groups and assumed to have the group average q at length for each 1cm size class. This final step provided an estimate of q for every 1cm length class of every demersal fish species sampled by the GOV. For each species and length class, the steps by which q was estimated is summarised in Appendix 1.

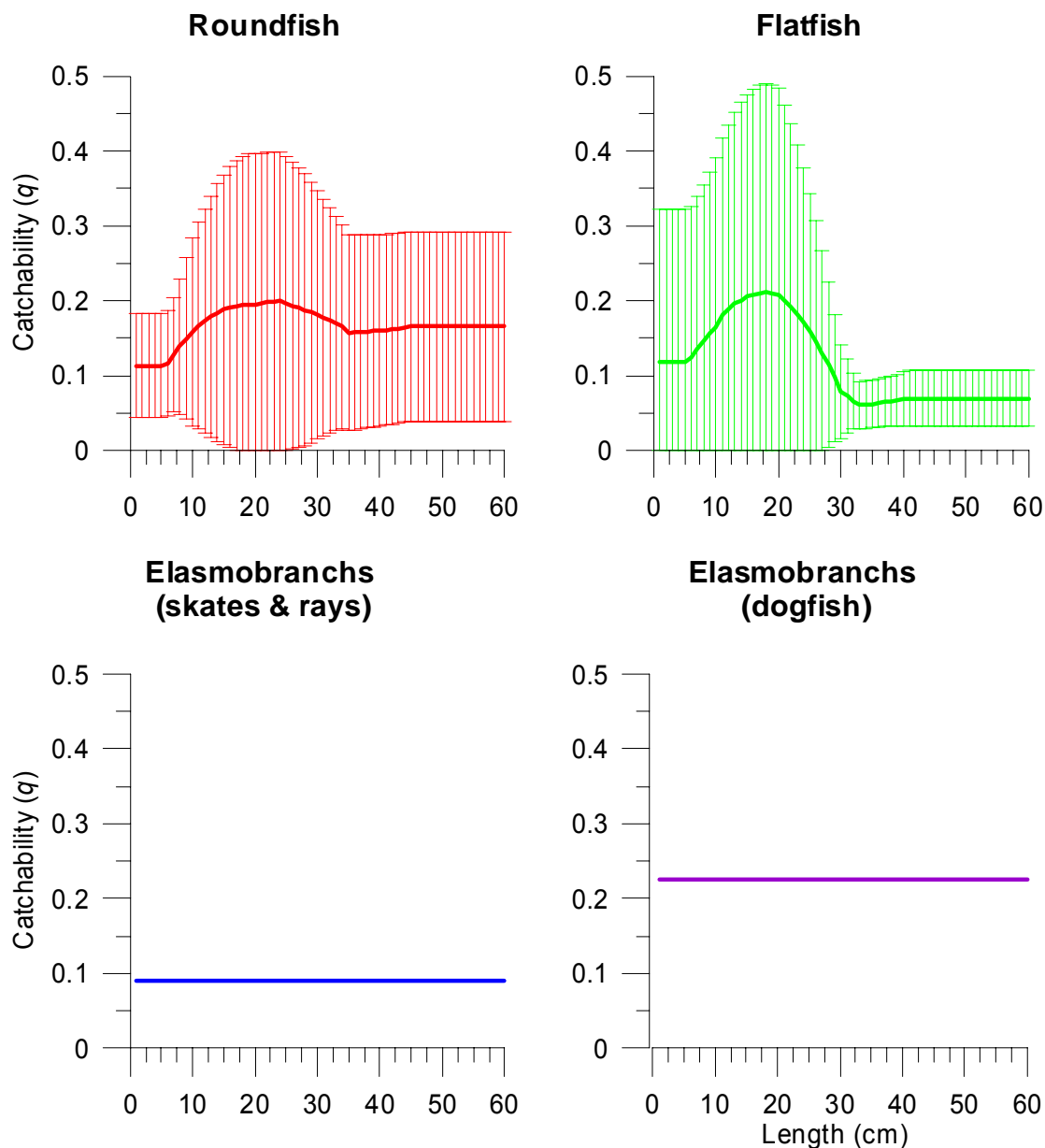


Figure 3.1.2.4: Average q at length of the four groups of fish a) roundfish, b) flatfish, c) skates and rays and d) dogfish.

3.1.3. Estimate of total demersal fish biomass

The total biomass of individual demersal fish species in the North Sea was calculated by raising the catches of each species in the IBTS 3rd Quarter GOV survey by the appropriate catchability value and area raising factors to give the total biomass of that species in the whole of area IV. Variation in the total raised biomass of nine key demersal fish species in the North Sea over the period 1998 to 2004 is illustrated in Figure 3.1.3.1. Haddock biomass increased sharply to a maximum of 3 million tonnes in 1999, decreasing to a low of 450,000 tonnes in 2004. The biomass of both whiting and Norway pout increased until 2000 then decreased to their lowest biomass in 2004. The total biomass of cod, plaice and grey gurnard decreased over the time

period analysed. Lemon sole, common dab and long rough dab biomass remained relatively constant over the seven years.

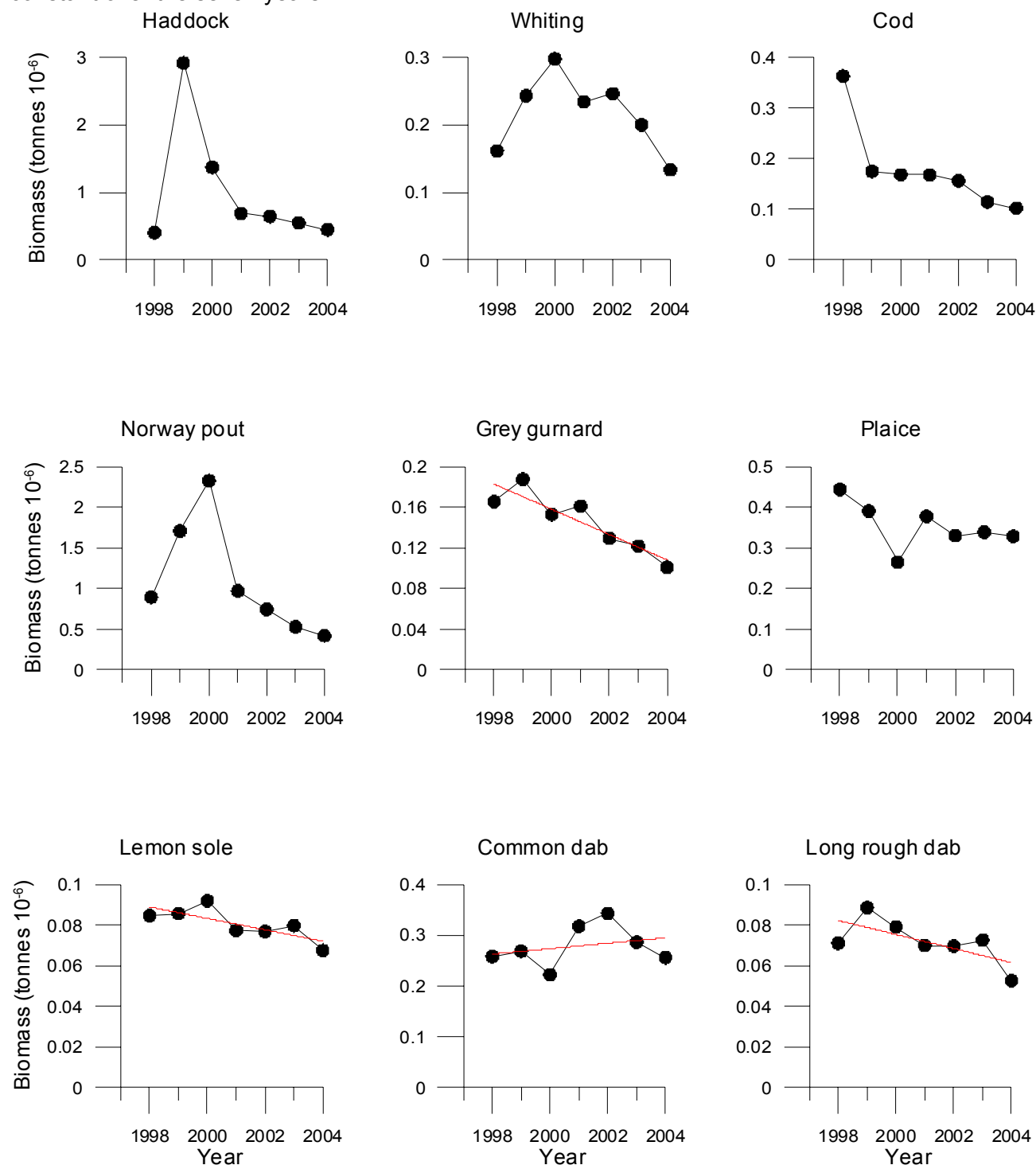


Figure 3.1.3.1: Changes in the total raised biomass of nine key demersal fish species in the North Sea, 1998 to 2004.

Total demersal fish biomass in the North Sea increased from almost 4 million tonnes in 1998 to a maximum of just over 7 million tonnes in 2000 (Figure 3.1.3.2). The biomass of fish less than 10cm increased to a maximum of just over 1.6 million tonnes in 1999. This peak in total fish biomass and biomass of fish less than 10cm is reflected in the peak in biomass of haddock in 1999 (Figure 3.1.3.1). The following year these fish had grown to larger than 10cm in length, accounting for the increase in biomass of fish greater than 10cm in 2000. Since 2000 the total biomass of fish in the North Sea had decreased to a low of 3 million tonnes in 2004. These changes are mirrored by the change in biomass of fish greater than 10cm. The biomass of fish less than 10cm remained relatively constant at around ¼ million tonnes apart from the peak of 1.6 million tonnes in 1999.

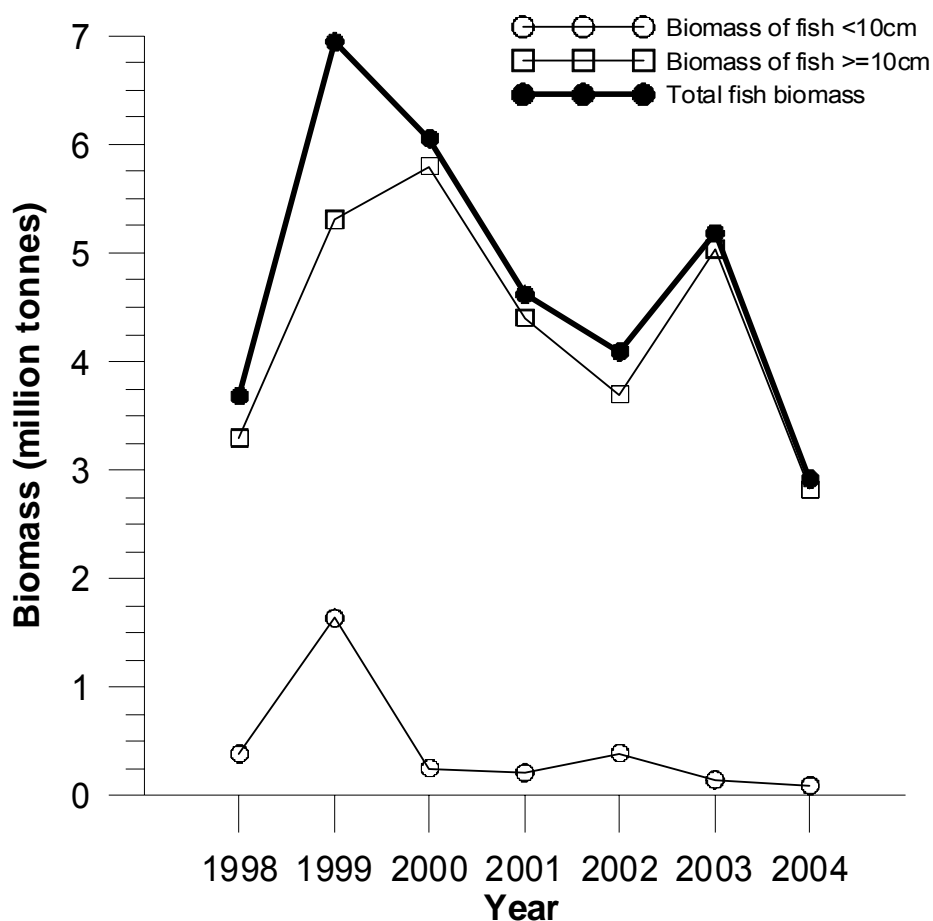


Figure 3.1.3.2: Total demersal fish biomass in the North Sea 1998 to 2004. Open circles represent the total demersal biomass of fish <10cm, open squares represent total demersal biomass of all fish ≥10cm, filled circles represent total demersal fish biomass.

Spatial variation in the average density of nine key demersal species across the North Sea over the period 1998 to 2004 is shown in Figure 3.1.3.3. Haddock were mainly confined to the northern North Sea. Whiting were widely spread across the study area with the highest densities occurring off the east coast of England. Cod were also widespread at low densities with the highest densities found in the eastern North Sea off the southern coast of Norway. The highest densities of Norway pout were found mainly in the north-western North Sea. Grey gurnard were widely distributed at low densities with the highest densities occurring in the

central North Sea. Plaice were mainly confined to the central and southern North Sea. Lemon sole were found mainly in the northwestern North Sea, with the highest densities located around the Shetland Isles. Common dab were found mainly in the central, southern and south-eastern North Sea with the highest densities occurring off the coasts of Denmark and The Netherlands. The highest densities of long rough dab were found in the central North Sea and northern North Sea.

Species Composition, Diversity, Biomass and Production of the Demersal Fish Community of the North Sea

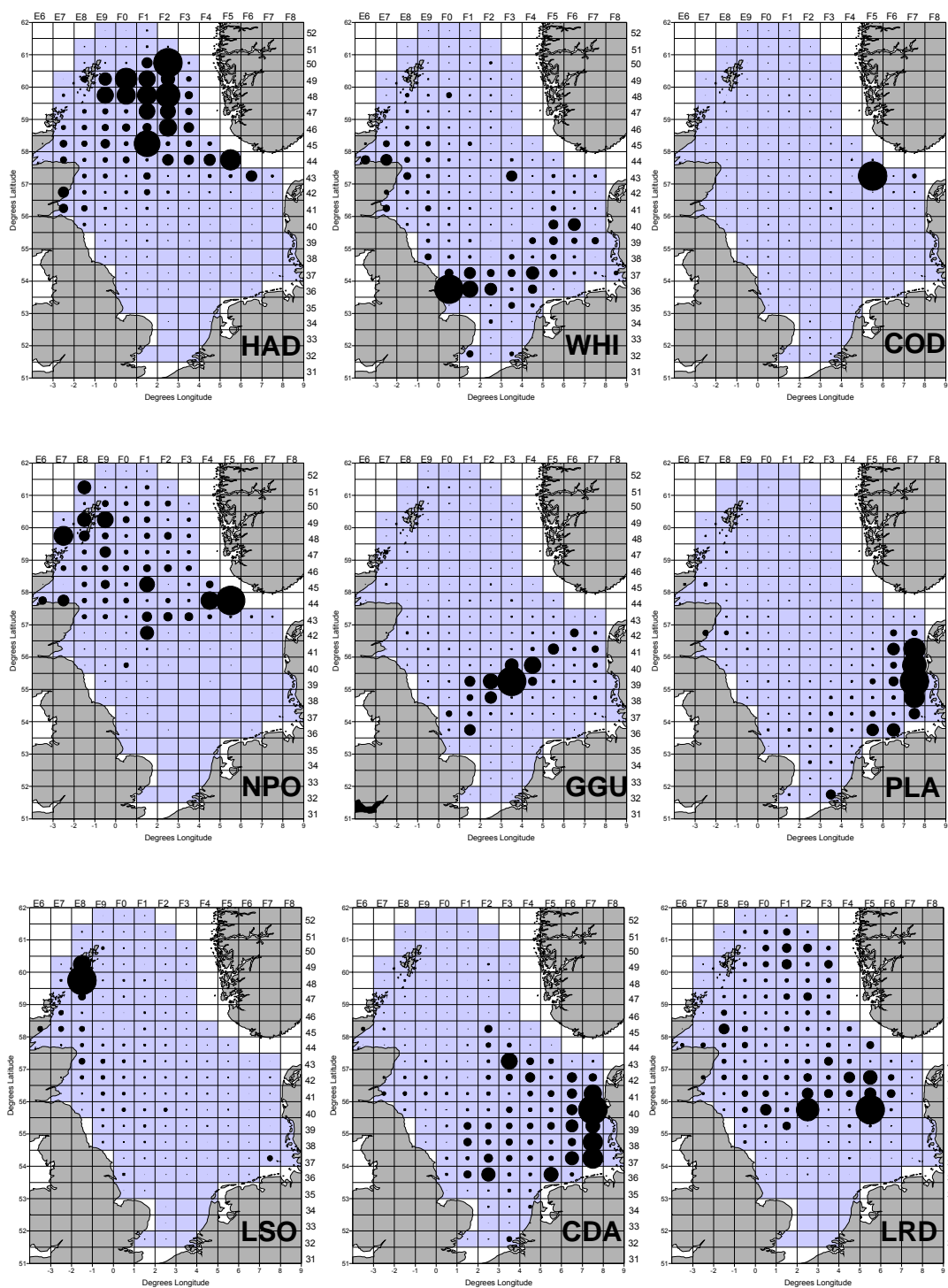


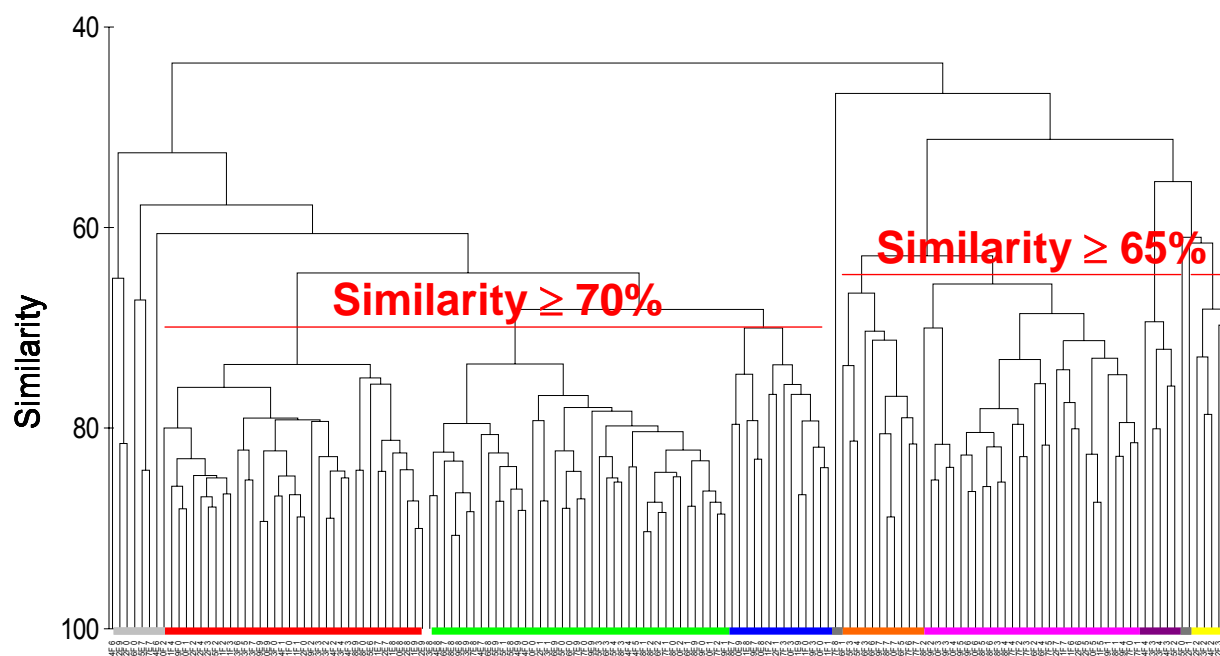
Figure 3.1.3.3: Average density (number fish per m²) of haddock (HAD, max density 0.75), whiting (WHI, max density 0.07), cod (COD, max density 0.07), Norway pout (NPO, max density 2.25), grey gurnard (GGU, max density 0.04), plaice (PLA, max density 0.06), lemon sole (LSO, max density 0.02), common dab (CDA, max density 0.10) and long rough dab (LRD, max density 0.03) in each statistical rectangle in the North Sea over the period 1998 to 2004.

3.2. Assessment of the Level of Sample Aggregation Required to Measure Diversity

3.2.1. Spatial patterns in demersal fish species composition

Results of the cluster analysis performed on both the IBTS and DBTS data sets, after pooling all data collected between 1998 and 2004 for each ICES rectangle, are shown in Figure 3.2.1.1. When the clusters to which each ICES rectangle had been assigned by the cluster analysis were mapped, similar spatial mosaics of variation in the demersal fish community were revealed for both data sets, despite the different sampling gears having very different catchabilities for round and flatfish species (Figure 3.2.1.2). The numbers of trawl samples available for each ICES rectangle and the rectangles selected for sample aggregation analysis are also indicated. Focal rectangles were selected on basis of their having a large number of trawl samples available for analysis and, as far as possible, for being surrounded by neighbouring rectangles that had also been assigned to the same fish community type.

GOV data: all years combined



8BT data: all years combined

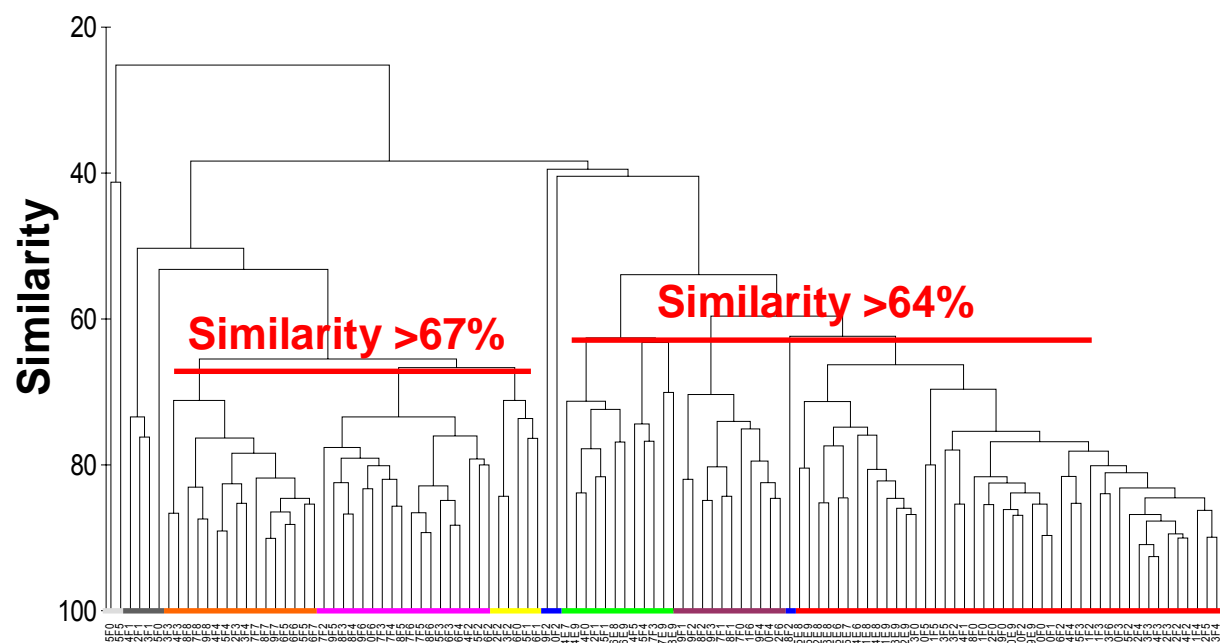


Figure 3.2.1.1: Hierarchical group group-averaging cluster dendograms analysis of Bray-Curtis similarity matrices constructed for both the IBTS (GOV) and DBTS (8BT) data sets. Colour coding defines the clusters to which each ICES rectangle has been assigned and this coding carries through to Figure 3.2.1.2.

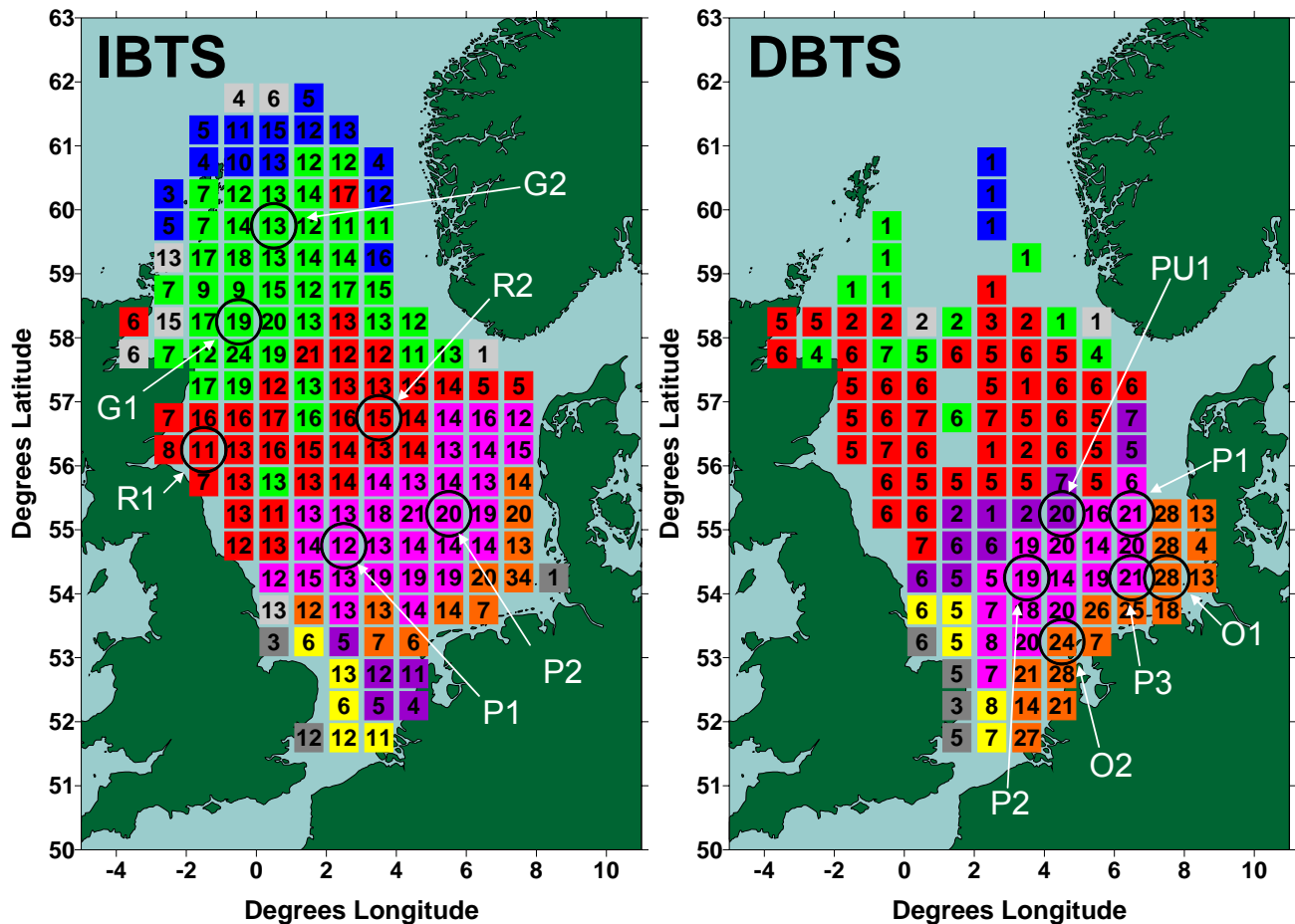


Figure 3.2.1.2: Spatial variation in demersal fish community “types”. Each ICES rectangle is colour coded according to the cluster it was assigned to by the cluster analysis illustrated in Figure 3.2.1.1. The number of trawl samples available for analysis for each survey in each ICES rectangle are indicated along with the focal rectangles selected for sample aggregation analysis.

3.2.2. Sample aggregation analysis

3.2.2.1. IBTS: sampling restricted to focal rectangles

The order in which samples are aggregated affects the shape of the species area relationship (SAR), depending on whether the first sample in the accumulation order happens to be relatively species rich or relatively species poor compared with the remaining samples. To counter this samples were selected at random (without replacement) from the available sample pool for each focal rectangle and this process was repeated ten times so that the order of aggregation was randomized. After the addition of each new sample, the aggregated area-swept and aggregated species richness was noted and plotted. Power functions were then fitted to the combined data for all ten randomizations (Figure 3.2.2.1.1). The SARs obtained when extrapolated to the scale of the ICES rectangle suggest an unrealistically high number of species for three of the focal rectangles (Figure 3.2.2.1.2); clearly indicating the dangers involved with such extrapolation (see also section 3.2.2.2). However, when these

SARs are examined in detail at the small local scale, it becomes clear that the species richness ranking order of the six focal rectangles does not become fully established until 0.4 km² has been sampled, equivalent to combining at least 7 GOV trawl samples (Figure 3.2.2.1.2).

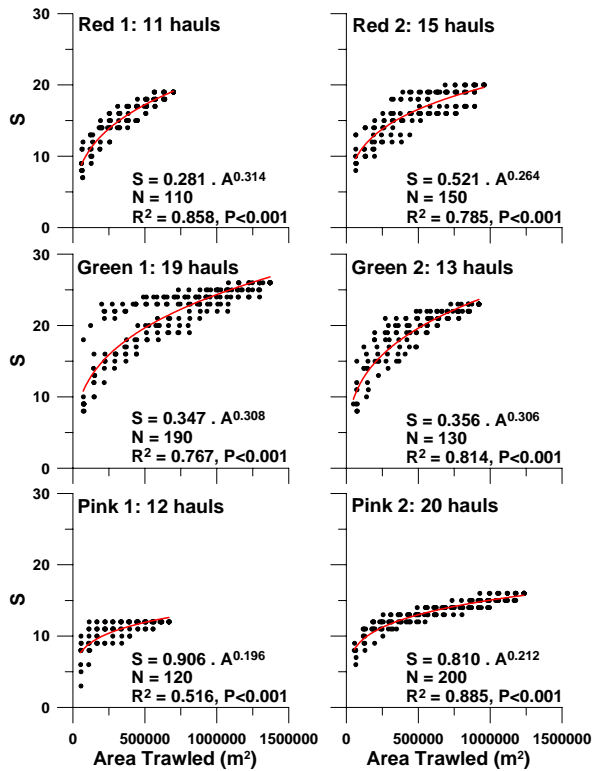


Figure 3.2.2.1.1: Species area curves (SARs) for the six focal rectangles shown in figure 3.2.1.2 illustrating the effects of trawl sample aggregation on the area sampled and the number of species recorded.

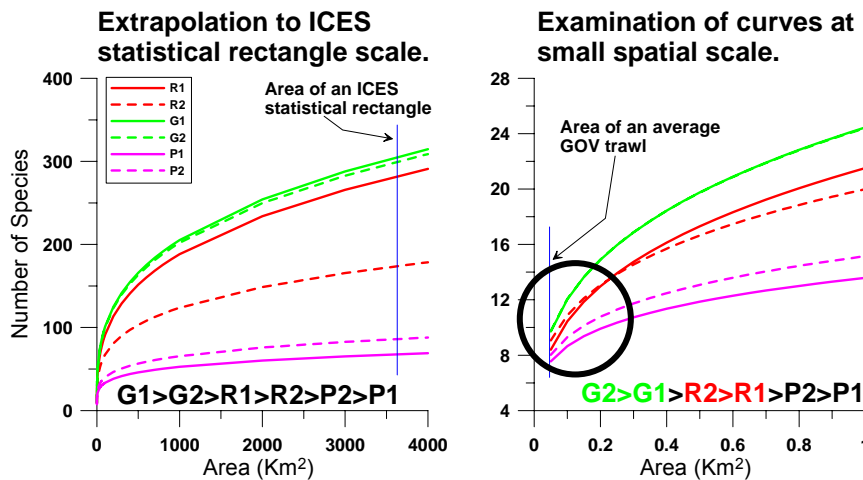


Figure 3.2.2.1.2: Evaluation of the SARs shown in figure 3.2.2.1.1 at both ICES rectangle scale, illustrating the dangers involved in extrapolating SARs to the rectangle scale, and at fine spatial scale, illustrating failure to rank the species richness of the six focal rectangles correctly until at least 0.4km² has been sampled.

The same approach was adopted with the two diversity indices, Hill's N_1 and N_2 (Figure 3.2.2.1.3). The shape of the data clouds differ from those for species richness (Hill's N_0) because N_1 and N_2 take account of both aspects of species diversity, richness and evenness. With species richness, it is possible that the first sample in the accumulation order might be particularly species rich or particularly species poor, thereby causing the observed spread of data at the left of the data clouds (Figure 3.2.2.1.1). But it is also inevitable that as the combined area sampled increases, new species will be added to the aggregated total, no matter how high the initial start point, hence the characteristic shape of the data clouds in Figure 3.2.2.1.1. Stochastic variation in the species richness of the first samples aggregated affects N_1 and N_2 in similar fashion, thereby accounting for the increasing asymptotic curves that best fit the data in the majority of cases (Figure 3.2.2.1.3). However, the degree of evenness may also vary in a stochastic manner, so that the first samples in an aggregation order might be characterized by relatively low levels of dominance (unusually low abundance of the normally dominant species), or high evenness (higher than usual abundance of some of the less common species), resulting in unusually high N_1 and N_2 values. Further accumulation of additional samples may then result in reduced aggregated evenness, as samples characterized by more normal levels of dominance are included, causing the aggregated N_1 and N_2 values to fall. This gives rise to the characteristic funnel shaped data clouds prevalent in Figure 3.2.2.1.3. Finally, Figure 3.2.2.1.4 shows the results of the same randomized aggregation analysis as presented in Figure 3.2.2.1.3, but now the x axis shows the number of trawl samples aggregated. The data suggest that a minimum of 10 GOV trawls need to be aggregated before reliable measures of N_1 and N_2 are obtained. However, the level of aggregation at which stabilization of the metric values occurred appeared dependent on the number of trawl samples available. For example in focal rectangle Red 1, N_1 and N_2 stabilized at 8 trawls aggregated, but only 11 trawls were available. Whereas in Focal rectangle Pink 2, where 20 trawl samples were available, stabilization of N_1 and N_2 occurred at 14 trawls aggregated. The possibility that the number of trawl samples available may be affecting the interpretation of this randomization analysis is addressed in section 3.2.2.2.

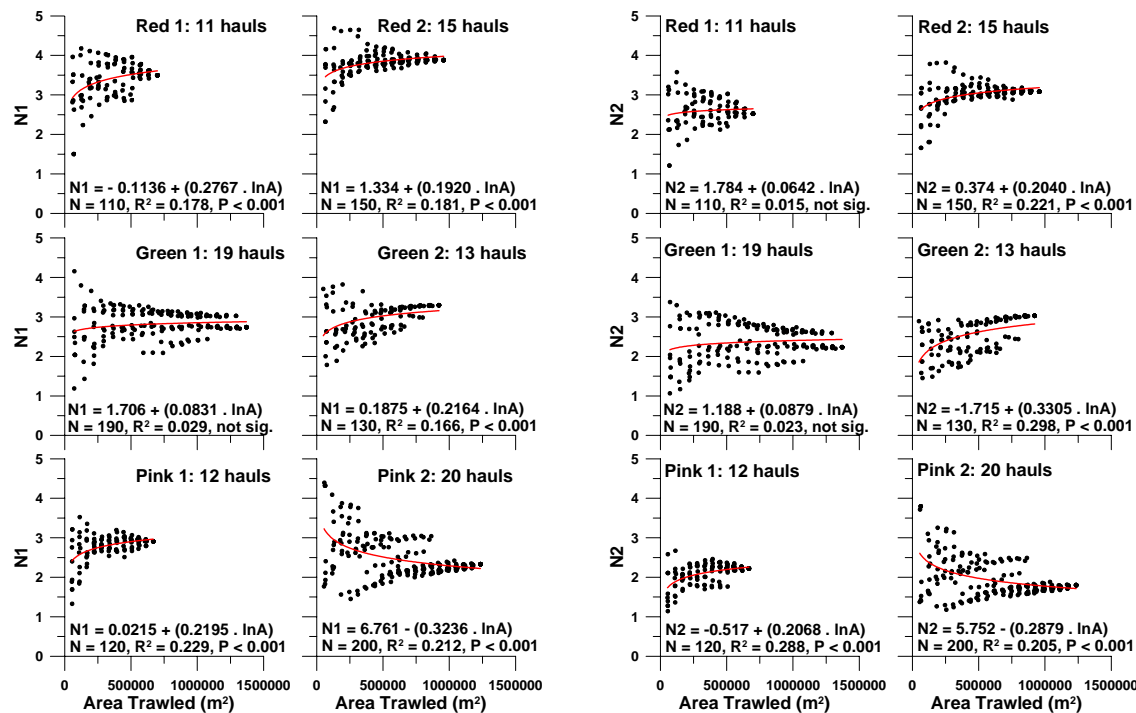


Figure 3.2.2.1.3: Effects of increasing the area sampled on measures of N_1 and N_2 calculated for the demersal fish community of each of the six focal ICES rectangles.

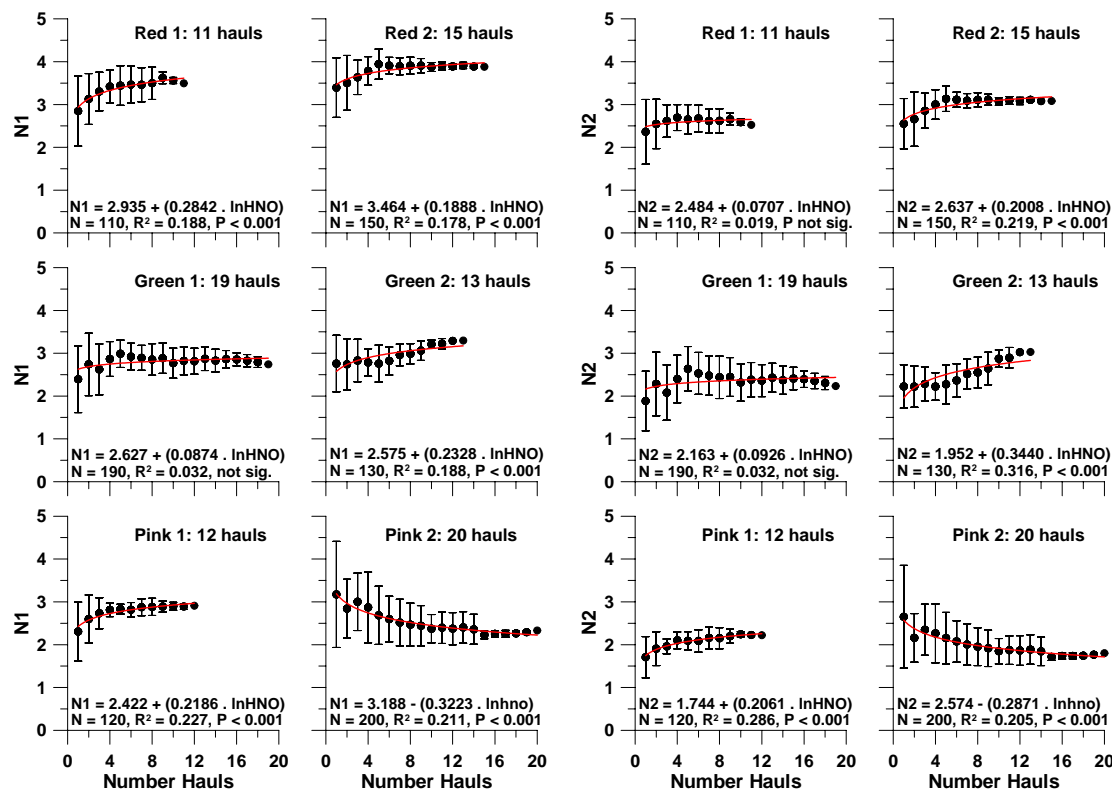


Figure 3.2.2.1.4: Effects of increasing the number of trawls samples aggregated on measures of N_1 and N_2 calculated for the demersal fish community of each of the six focal ICES rectangles.

The performance of the three metrics at different levels of trawl sample aggregation was examined by comparing the rank ordering of the six focal rectangles according to each metric based on one trawl sample, two samples combined, three samples combined, and so on. This was done for all ten randomizations at each aggregation level, and the number of randomizations where the rank order was the same as the rank order obtained when all samples available were aggregated was scored (Figure 3.2.2.1.5). This test suggested that diversity analyses based on individual “samples” consisting of fewer than 12 GOV trawls samples combined would be extremely unreliable. Any concerns raised by these results are further enhanced when one considers that one of the principal reasons why the scores improve at aggregation levels of greater than 11, is that the number of focal rectangles available in the ranking process starts to decline. Rectangle Red 1, for example, only had 11 trawl samples available, so at aggregation levels of 12 or more, only 5 rectangles remained to be ranked, thereby reducing the chances of getting the order “wrong”. However, this test is exceptionally strict, the slightest error in the ranking order gives a “no” score, no matter how well the remainder of the rectangles were ranked. An alternative performance analysis was therefore carried out. For each of the six rectangles, the values determined for each metric at each aggregation level (as the y variable) were compared with the values obtained for each metric when all trawls samples available (as the x variable). Pearson’s correlation analysis was then used to assess how well the metrics calculated at each aggregation level agreed with the overall metric value for each of the six rectangles. Pearson’s correlation coefficients approaching a value of 1 indicated good metric performance, while scores near zero indicated a poor performance. Negative coefficients imply a reversal of the correct ranking order. Since 10 randomizations were carried out for each aggregation level, ten separate correlation coefficients were obtained allowing a mean and standard deviation correlation coefficient to be determined for each metric at each aggregation level (Figure 3.2.2.1.6). These data suggest that for each of the two diversity indices, at least ten trawl samples needed to be aggregated, while species richness appeared to perform slightly better, requiring the aggregation of a minimum of seven GOV trawls samples. This does not mean that measures of species richness based on as few as seven GOV trawl samples provide accurate estimates of the actual species richness of the community at a particular location. Rather it suggests that measures of species richness based on seven or more samples are sufficient to compare species richness between different locations.

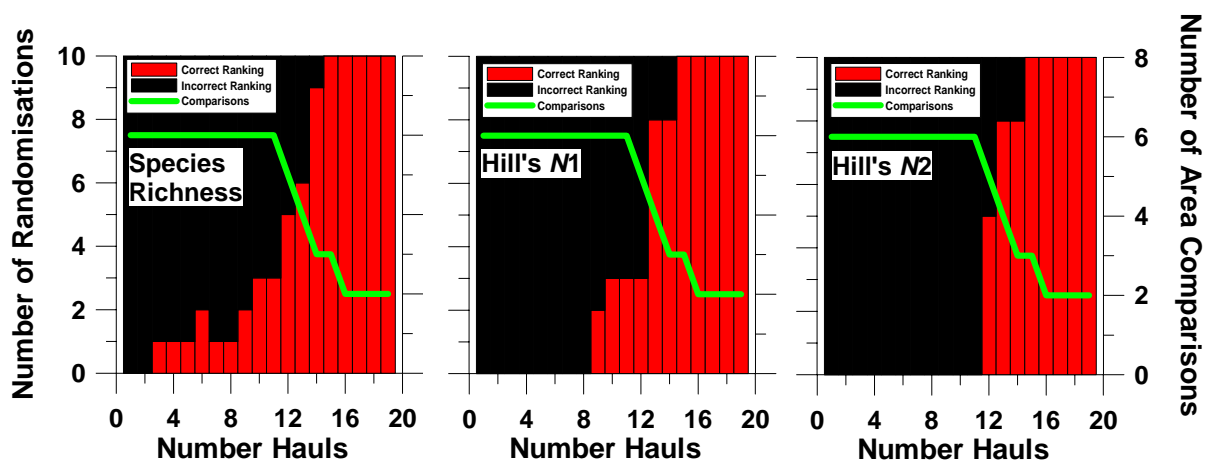


Figure 3.2.2.1.5: Plots showing the number of randomizations that ranked the six focal rectangles in the correct order with increasing number of trawl samples aggregated. The number of rectangles available to be ranked at each aggregation level is also indicated.

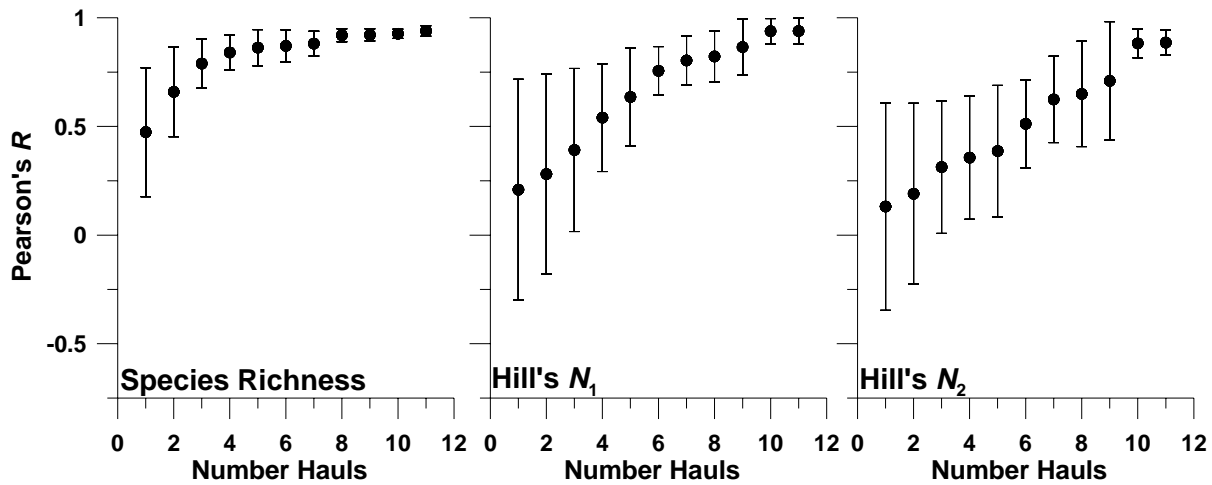


Figure 3.2.2.1.6: Mean (± 1 S.D.) Pearson correlation coefficient scores for different aggregation levels of each diversity metric.

3.2.2.2. IBTS: sampling restricted to focal rectangles and immediate neighbours

To address concerns that the number of trawl samples available for analysis in each focal rectangle may have influenced our conclusions regarding the number of trawl samples required to be aggregated to obtain reliable species diversity metrics, the analyses described above were repeated, but now allowing samples to be included not only from the focal rectangle, but also from its nearest neighbouring rectangles. Focal rectangle Red 1 and its neighbours still contained the smallest number of trawl samples available, but this was now increased from 11 to 91.

The species area relationships obtained for each focal rectangle and its neighbours are shown in Figure 3.2.2.2.1. All the fitted SARs still showed a strong positive gradient, despite the aggregation of 90 trawl samples. Comparison of the SARs at increasing spatial scale suggest that the correct species richness ranking of the six rectangles may not be achieved until 60 km² have been sampled. Extrapolation of these SARs to the scale of the ICES rectangle suggested rectangle species richness counts of similar magnitude as the previous analysis, and just as unrealistically high (Figure 3.2.2.2.2). However, closer examination of Figure 3.2.2.2.1 presents an explanation. Compared with Figure 3.2.2.1.1 in the previous section, the goodness of fit of the fitted power functions is less good. At the high end of the area trawled, the data points show a strong tendency to fall below the fitted line, and for four of the rectangles, the residuals show a significant negative downward trend at high areas sampled (Figure 3.2.2.2.3). This suggests that species saturation has occurred. Although the data fit the traditional species-area power function well, the size of the North Sea regional fish species pool is insufficient to supply all the species that the species area curves imply should be present at the local ICES rectangle scale.

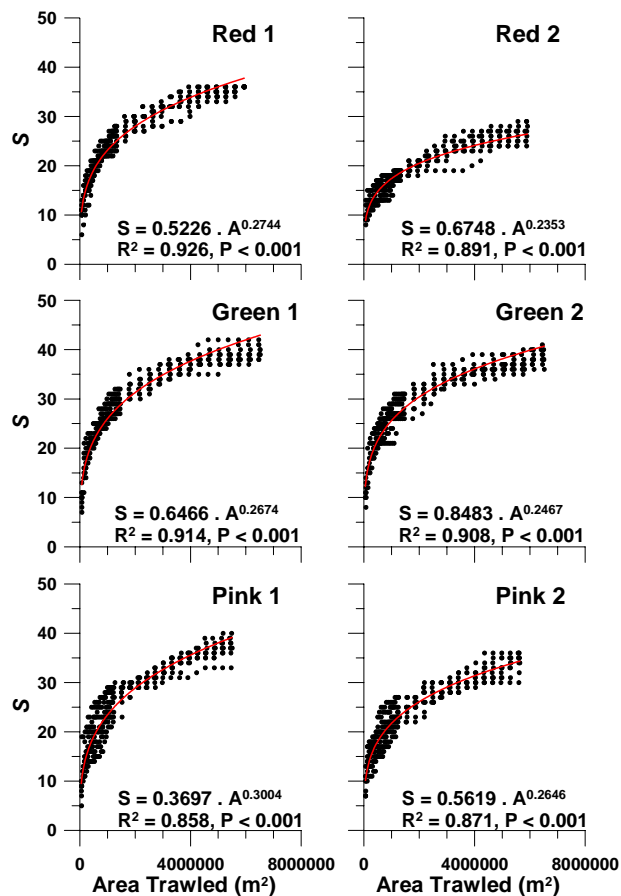


Figure 3.2.2.2.1: Species area curves (SARs) for the six focal rectangles shown in figure 3.2.1.2, and their immediate neighbours, illustrating the effects of trawl sample aggregation on the area sampled and the number of species recorded.

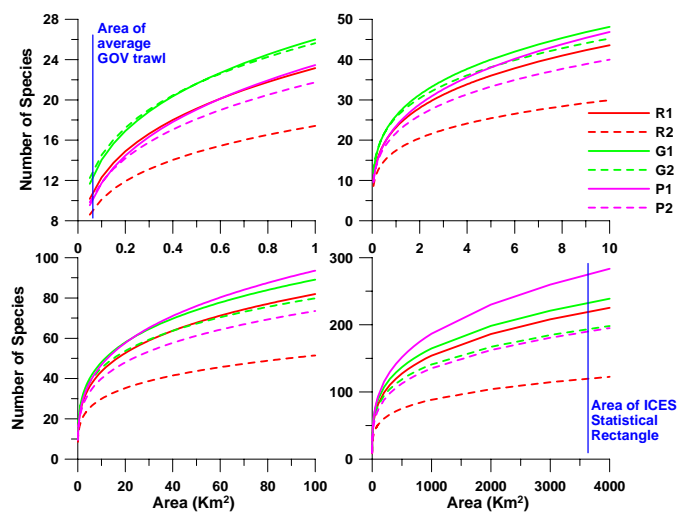


Figure 3.2.2.2.2: Evaluation of the SARs shown in figure 3.2.2.2.1 at ICES rectangle scale, illustrating the dangers involved in extrapolating SARs to the rectangle scale, and at finer spatial scales, illustrating failure to rank the species richness of the six focal rectangles correctly until at least 60km² has been sampled.

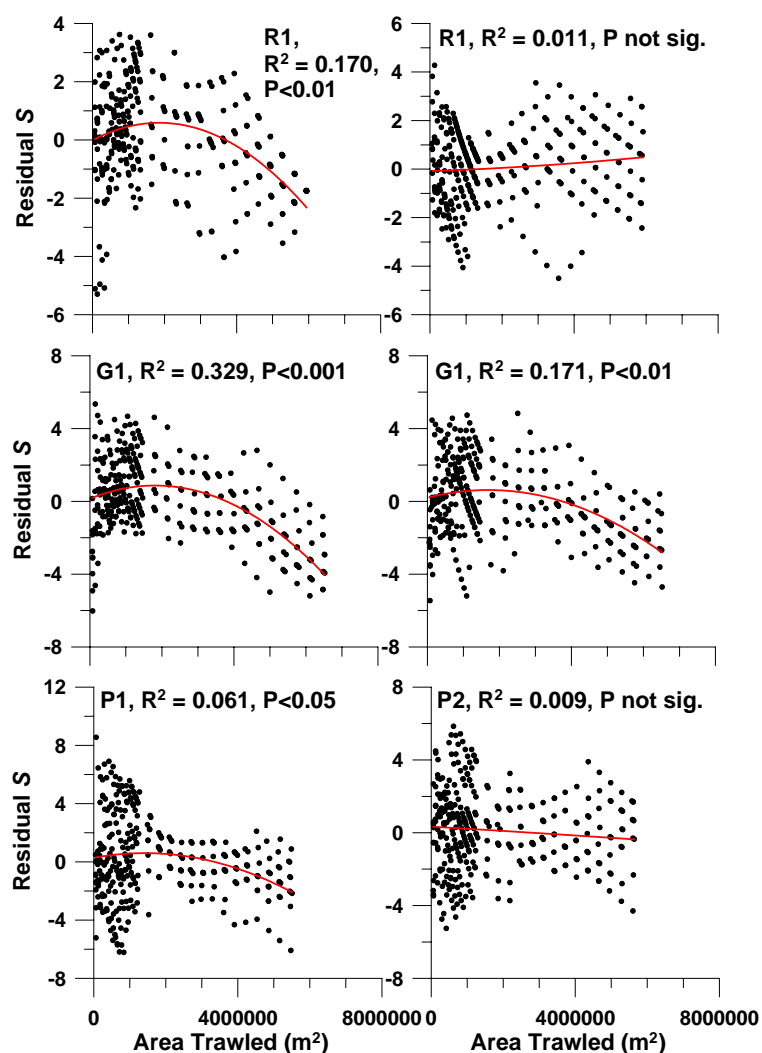


Figure 3.2.2.2.3: Plots of variation in the residuals from the SARs shown in figure 3.2.2.2.1 with increasing area sampled.

The effects of increasing the area sampled, and of increasing the number of hauls aggregated, on Hills N_1 and N_2 are shown in Figures 3.2.2.2.4 and 3.2.2.2.5 respectively. The performance of both metrics was similar, with the data suggesting that an area of approaching 2Km^2 needed to be sampled, or approximately 20 hauls aggregated, before the metric values stabilized and became reliable. Some variation between areas was again apparent.

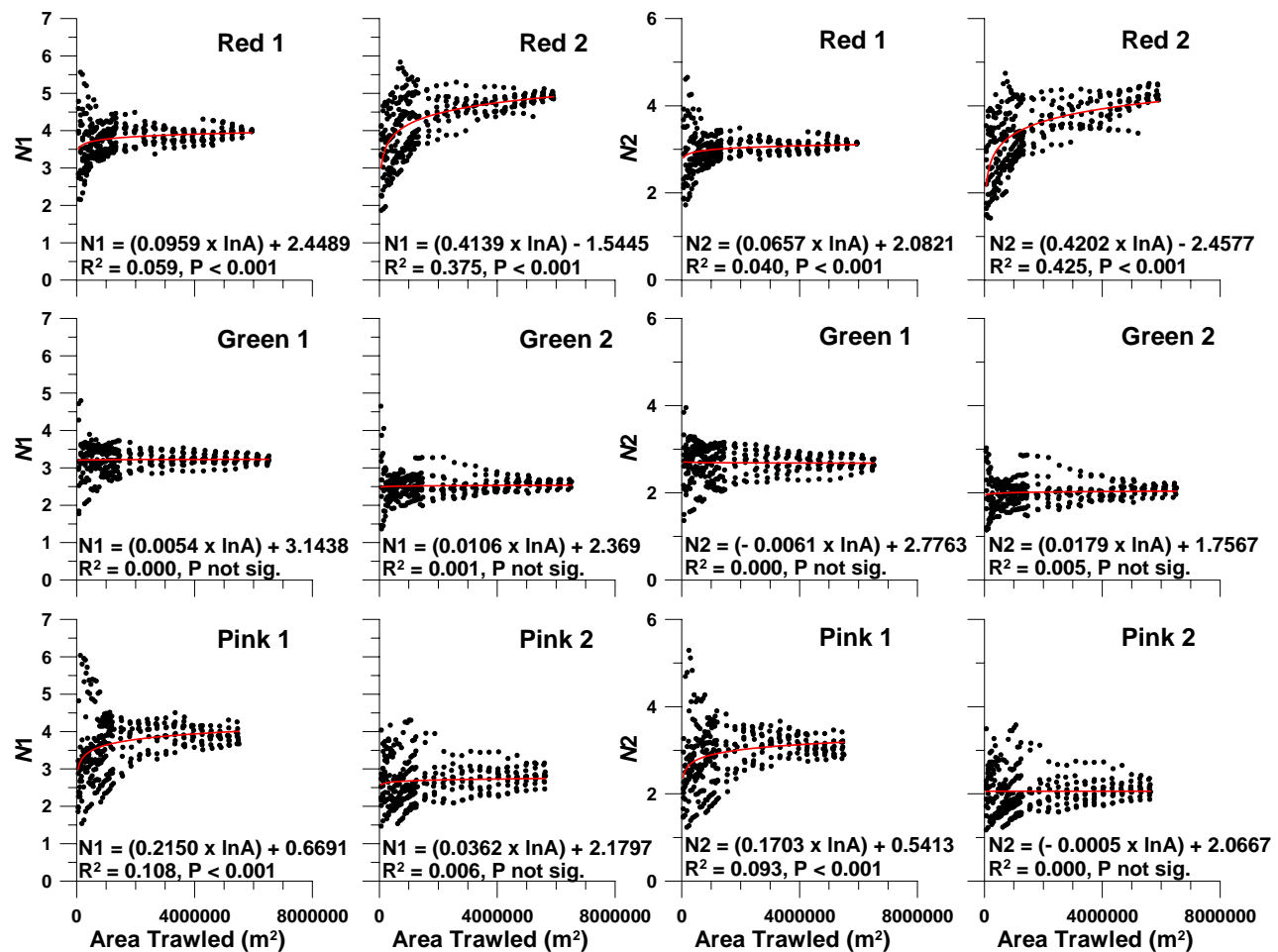


Figure 3.2.2.2.4: Effects of increasing the area sampled on measures of N_1 and N_2 calculated for the demersal fish community of each of the six focal ICES rectangles and their immediate neighbours.

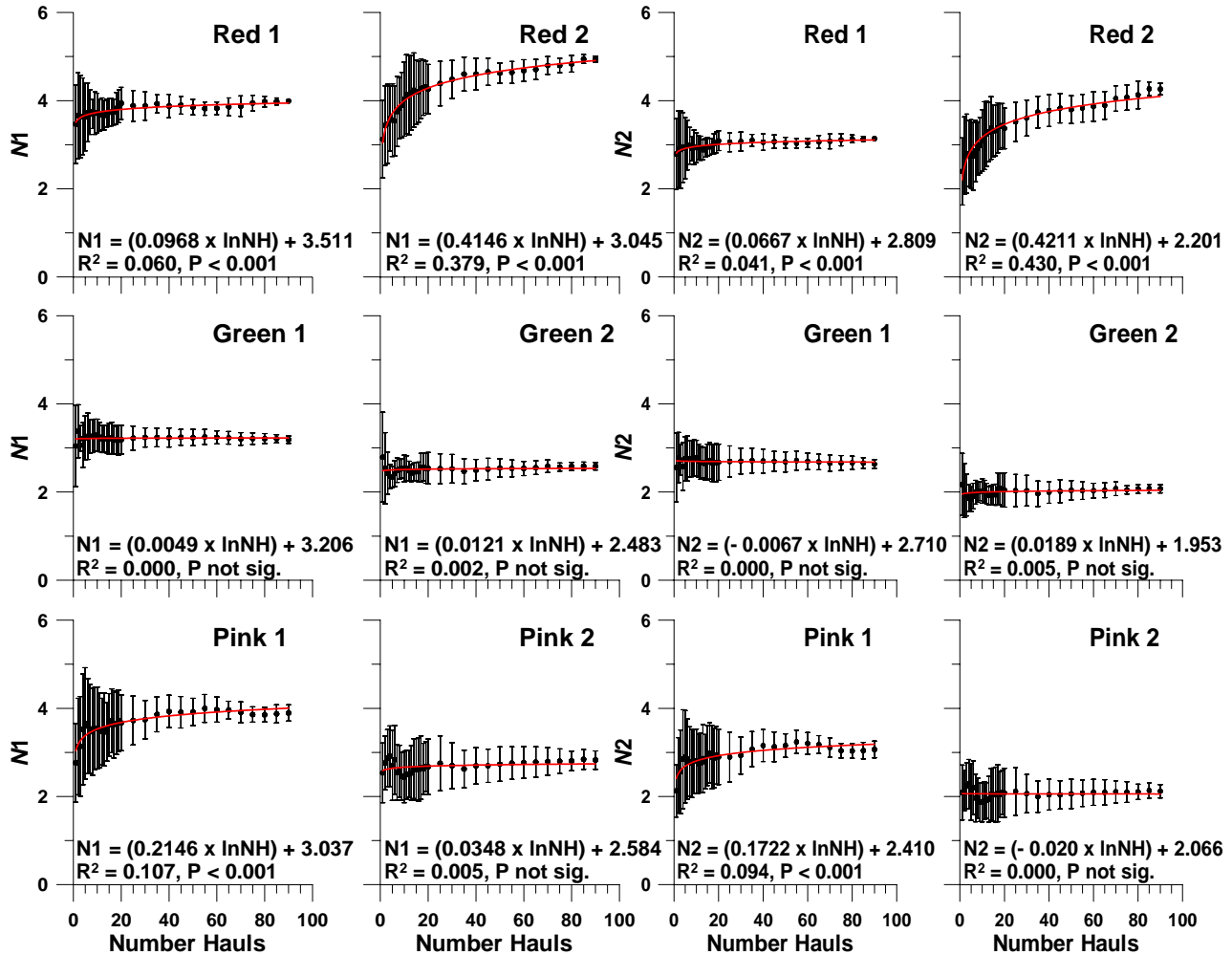


Figure 3.2.2.5: Effects of increasing the number of trawls samples aggregated on measures of N_1 and N_2 calculated for the demersal fish community of each of the six focal ICES rectangles and their immediate neighbours.

The performance of all three metrics was assessed using the Pearson's correlation technique. This suggested that it was necessary to aggregate a minimum of 15 to 20 hauls before reliable metric values were obtained, and that variation in the correlation coefficients was relatively high until up to 30 GOV samples had been aggregated (Figure 3.2.2.2.6.). This analysis would tend to suggest that, when concentrating only on the focal rectangles themselves, the limitation to the number of trawl samples available for aggregation in the randomization process did indeed affect our assessment of the aggregation level required. However, even this analysis, where the "search area" for samples has been extended to include the rectangles surrounding each focal rectangle, is not without its inherent drawbacks. These are discussed in Section 3.2.2.4.

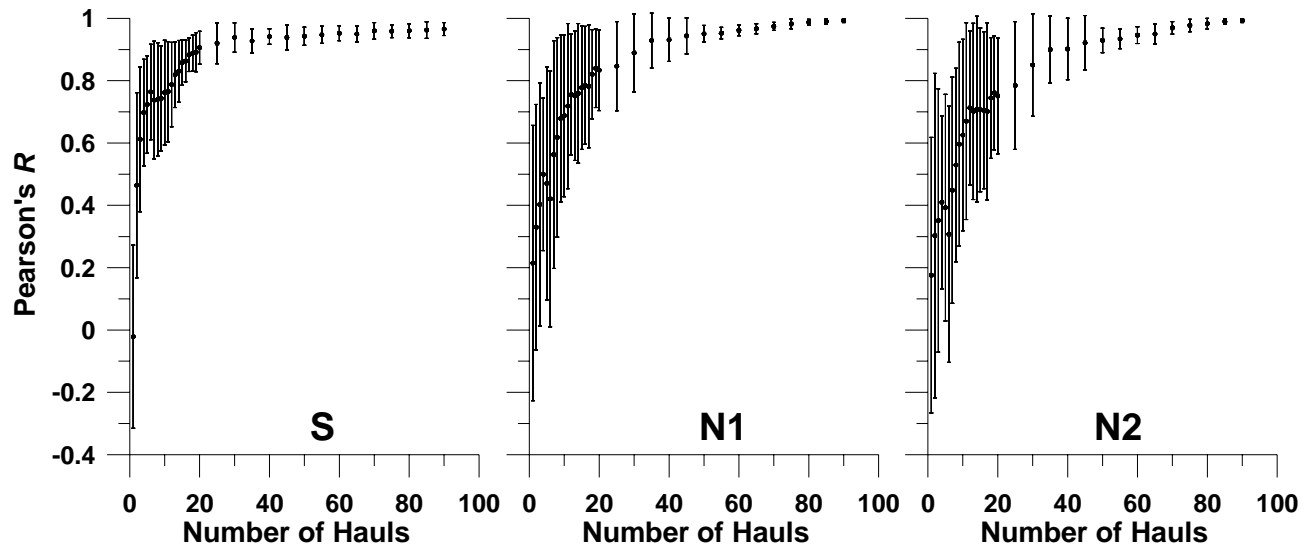


Figure 3.2.2.2.6: Mean (± 1 S.D.) Pearson correlation coefficient scores for different aggregation levels of each diversity metric.

3.2.2.3. DBTS: sampling restricted to focal rectangles

As the area sampled increased with increase in the level of sample aggregation, species richness in combined DBTS 8m beam trawl samples also increased following traditional power function SARs for each of the six focal rectangles (Figure 3.2.2.3.1). Examination of these SARs at various spatial scales revealed similar results to the GOV IBTS data (Figure 3.2.2.3.2). Once again extrapolation to the ICES rectangle scale suggests rectangle level species richness in some rectangles far in excess of anything possible given the known North Sea species pool (Yang 1982). While at smaller spatial scale, the trajectories of the six different power functions suggest that not until 6km^2 had been sampled, would the species richness ranking of the six rectangles be established.

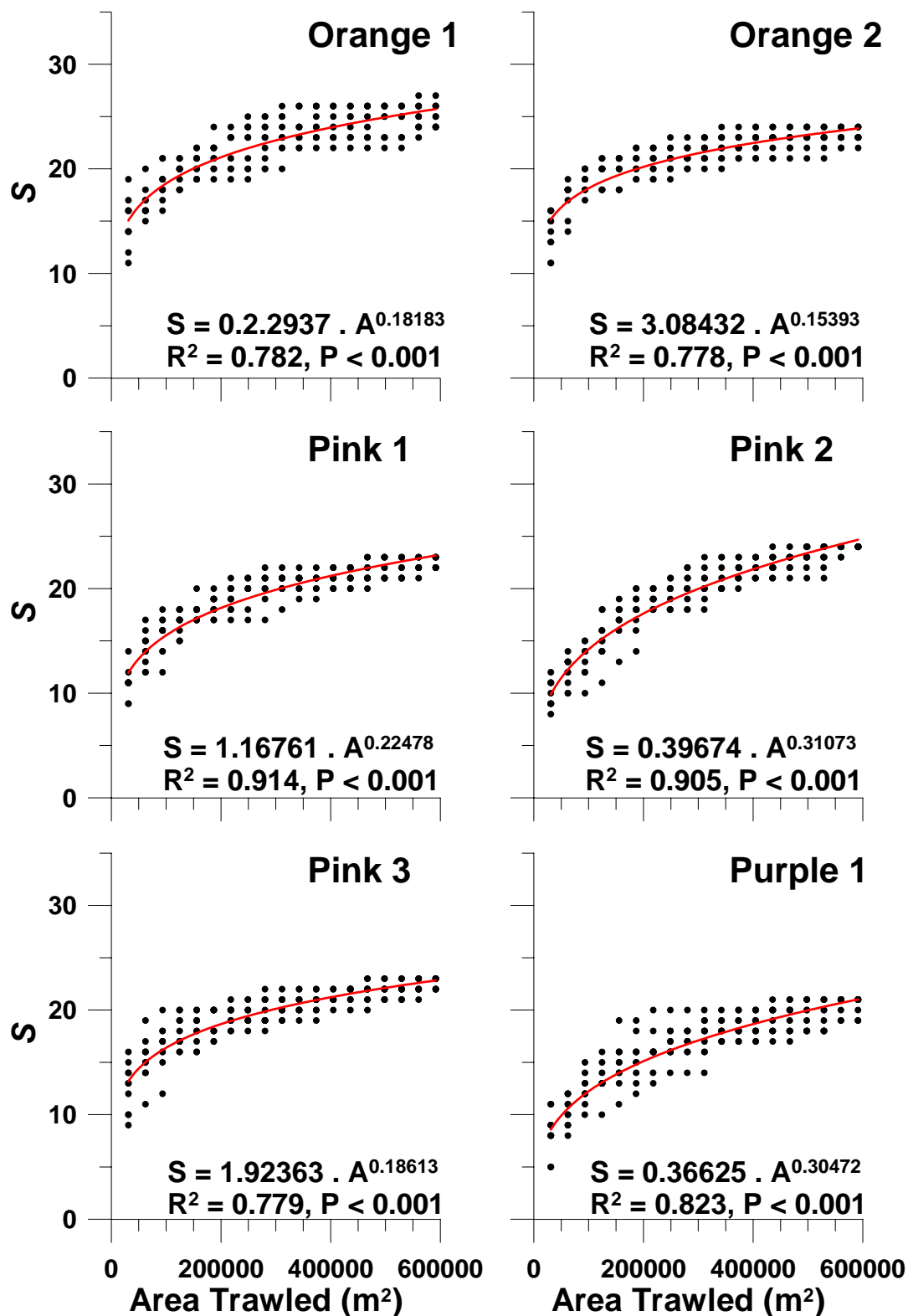


Figure 3.2.2.3.1: Species area curves (SARs) for the six focal rectangles shown in figure 3.2.1.2, illustrating the effects of 8BT sample aggregation on the area sampled and the number of species recorded.

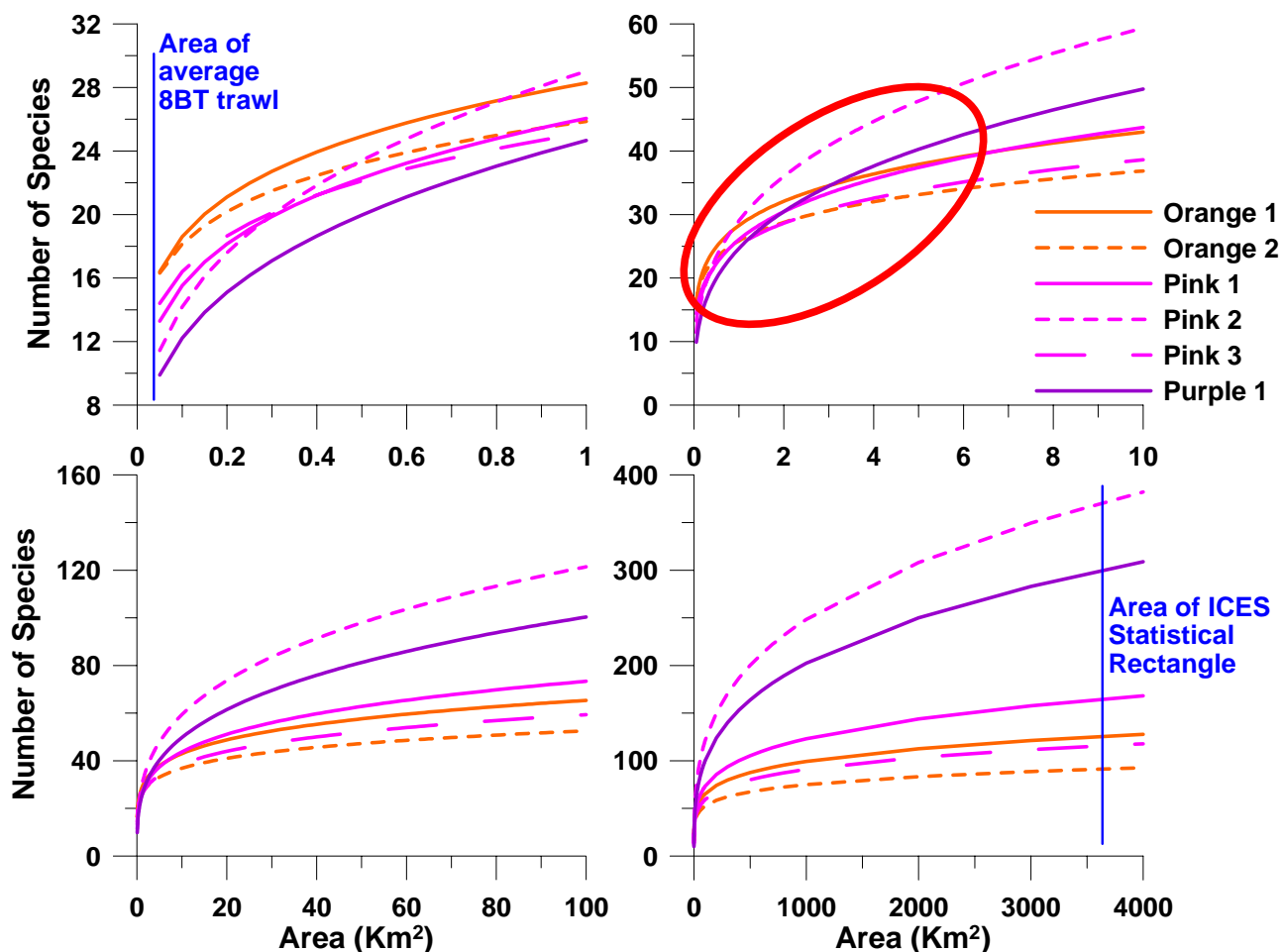


Figure 3.2.2.3.2: Evaluation of the SARs shown in figure 3.2.2.3.1 at ICES rectangle scale, illustrating the dangers involved in extrapolating SARs to the rectangle scale, and at finer spatial scales, illustrating failure to rank the species richness of the six focal rectangles correctly until at least 6km² has been sampled.

The effects of increasing the area sampled, and of increasing the number of hauls aggregated, on Hills N_1 and N_2 are shown in Figures 3.2.2.3.3 and 3.2.2.3.4 respectively. The performance of both metrics was similar, with the data suggesting that an area of between 0.3Km² and 0.4Km² needed to be sampled, or approximately 12 to 15 hauls aggregated, before the metric values stabilized and became reliable. Some variation between areas was again apparent.

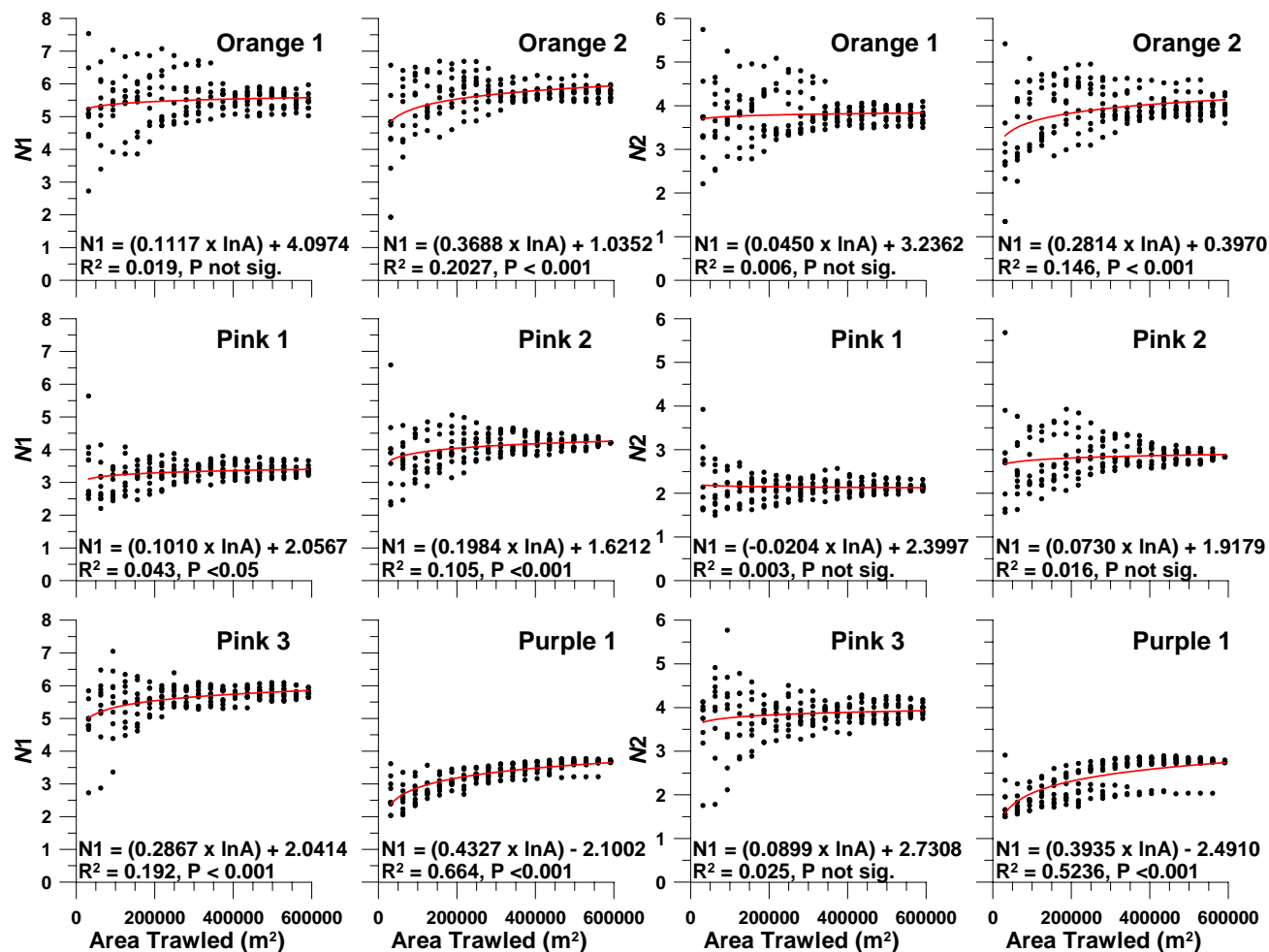


Figure 3.2.2.3.3: Effects of increasing the area sampled on measures of N_1 and N_2 calculated for the demersal fish community of each of the six focal ICES rectangles.

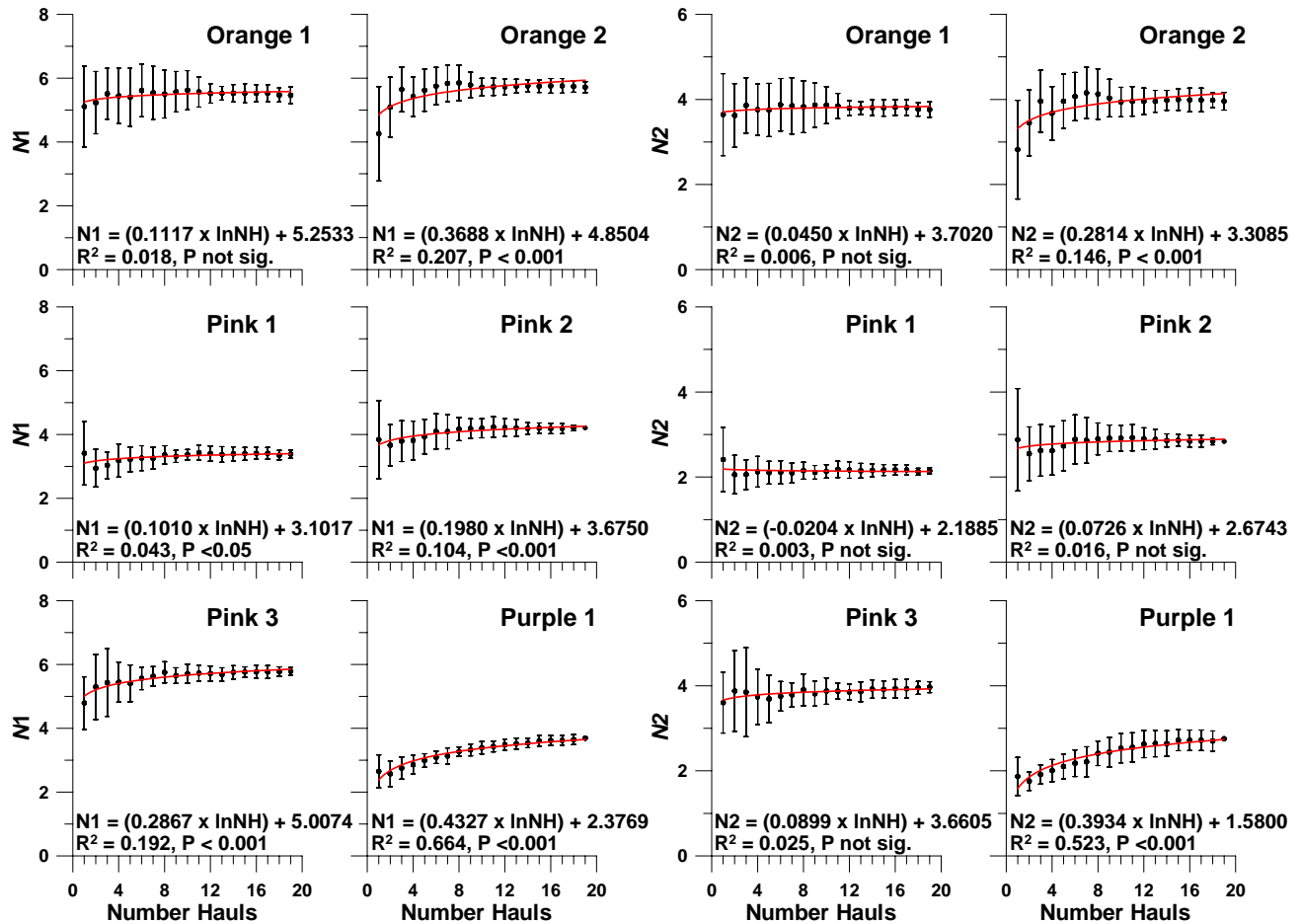


Figure 3.2.2.3.4: Effects of increasing the number of trawls samples aggregated on measures of N_1 and N_2 calculated for the demersal fish community of each of the six focal ICES rectangles.

Once again the Pearson's correlation analysis was used to examine the performance of the three metrics with increase in aggregation level (Figure 3.2.2.3.5). This analysis suggested that the two diversity indices, Hills N_1 and N_2 , were performing well, correlation coefficients were close to 1.0 and the standard deviations were small, at aggregation levels of 15 8BT samples. However, even at the maximum level of aggregation possible with the numbers of trawl samples available in the focal rectangles, performance of Hill's N_0 (the species richness count) was still poor. Indeed the negative correlations coefficients imply that at low aggregation levels, the species richness rankings were reversed. The reasons for this are apparent in Figure 3.2.2.3.2 where it is obvious that at small spatial scales, the trajectories of the six SARs switch around to a considerable extent.

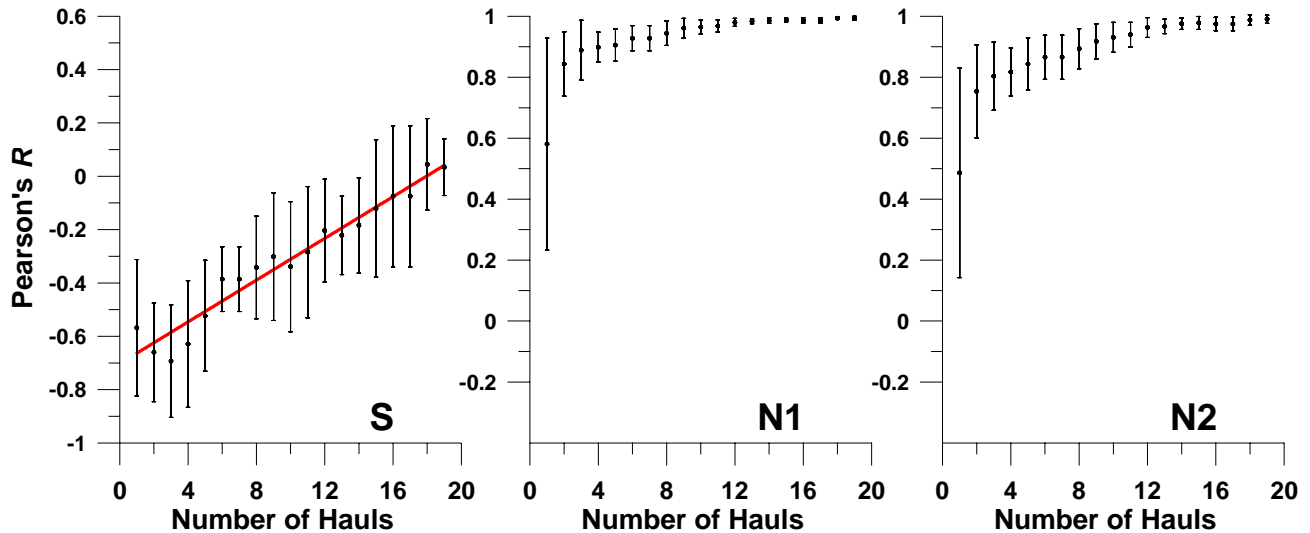


Figure 3.2.2.3.5: Mean (± 1 S.D.) Pearson correlation coefficient scores for different aggregation levels of each diversity metric.

3.2.2.4. Confounding α diversity and β diversity

To test Huston's DEM (see Greenstreet *et al* 2007b), point estimates of species diversity representative of the diversity in each ICES rectangle were required. But if large numbers of trawls samples need to be aggregated to provide reliable point estimates of species diversity (known as α diversity), inevitably requiring these samples to have been collected over a relatively large area, then there is a significant risk of incorporating aspects of β diversity into the estimate (the increase in diversity as one moves in space, thereby incorporating additional habitat types and their associated fauna). With the randomization process used here, such a situation would introduce variability into the estimate of species diversity, leading to the aggregation level required to stabilize the diversity metrics being over-estimated. This is a real risk in the North Sea situation where the Bray-Curtis similarity between the fish communities occupying pairs of ICES rectangles decreases as a linear function of geographical distance between the rectangles, an observation noted for both the IBTS (Figure 3.2.2.4.1) and the DBTS (Figure 3.2.2.4.2) data sets. Similar effects of geographic distance on community similarity have been noted elsewhere. For example, as the distance between sites classified as belonging to the same land system increased, so the vascular plant and invertebrate species assemblages occupying the sites became more different (Oliver *et al* 2004).

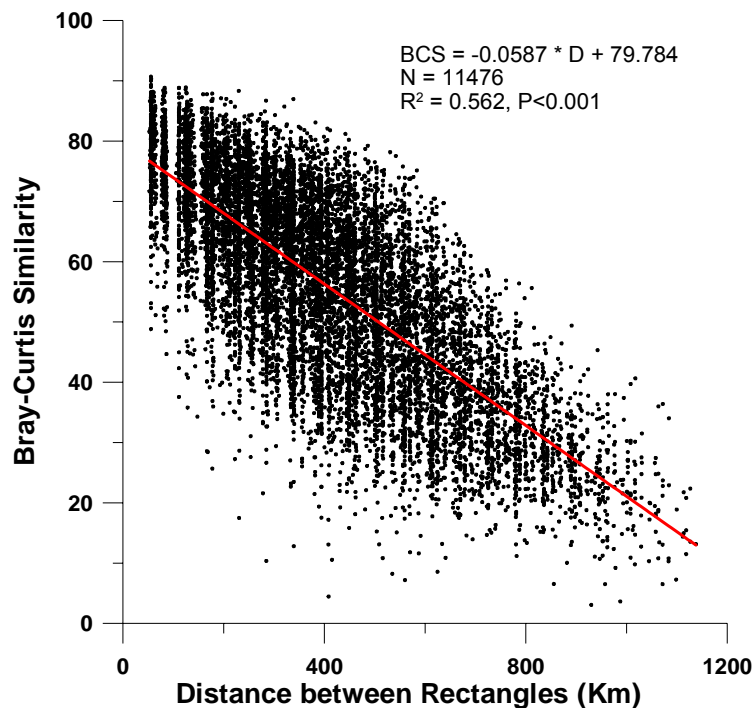


Figure 3.2.2.4.1: Relationship between the geographical distance between pairs of ICES rectangles and the Bray-Curtis measure of the similarity of the fish communities present in each rectangle as determined by the IBTS data set.

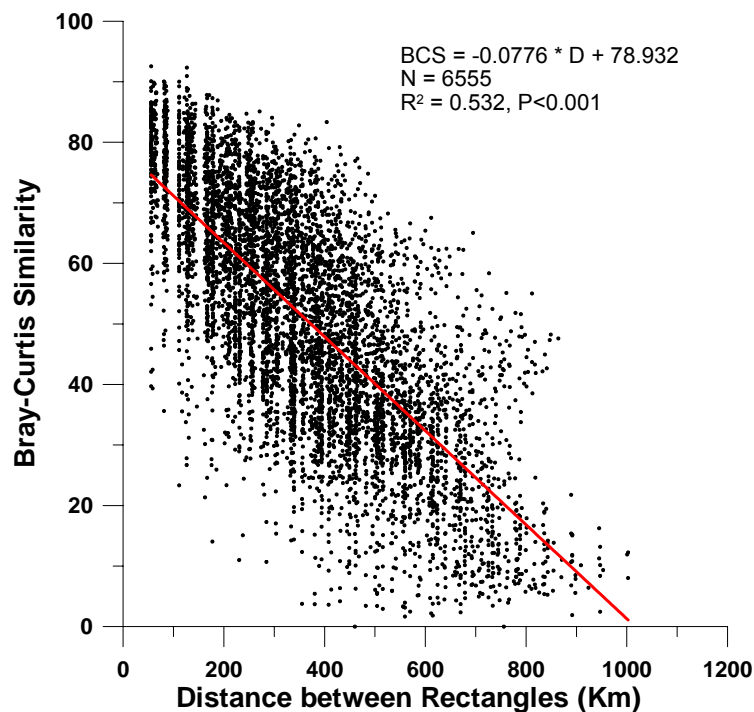


Figure 3.2.2.4.2: Relationship between the geographical distance between pairs of ICES rectangles and the Bray-Curtis measure of the similarity of the fish communities present in each rectangle as determined by the DBTS data set.

The data analysed in the preceding sections suggests that approximately 20 GOV or 8BT samples need to be aggregated in order to obtain estimates of species richness and species diversity that are representative of the actual community being sampled. The degree of aggregation required raises the real concern that in order to acquire this number of samples, the search radius around each focal location would be so large that there was an appreciable risk of the α diversity estimates obtained being inflated by the inclusion of elements of β diversity. This was examined by using the centre point positions of each ICES rectangle as the focal location and aggregating the species abundance data for twenty closest sample stations. Species richness and Hill's N_1 and N_2 were then determined for each aggregated sample, and the influence of search radius size on metric values investigated. Figure 3.2.2.4.3 shows lowess smoothers fitted to the data for species richness for both the IBTS GOV and DBTS 8BT data sets. The effect of search radius on species richness is particularly obvious in the IBTS GOV sample data. Here for search radii up to 50km in size, no effect on species richness is apparent. With further increase in search radius, a positive linear effect on species richness is apparent. We interpret this as indicating that where the search radius is 50Km or less in size, the species richness estimates obtained are pure α diversity, but further increase in search radius results in a steady increase in the contribution of β diversity to the species richness estimate, such that at search radii of around 90Km, about 24% (8/33) of the species richness estimate has been contributed by β diversity. The effect is less obvious in the DBTS 8BT data, but here again an upward kick in the lowess smoother occurs at a search radius of 50Km, although a more obvious change in trajectory occurs at 75Km.

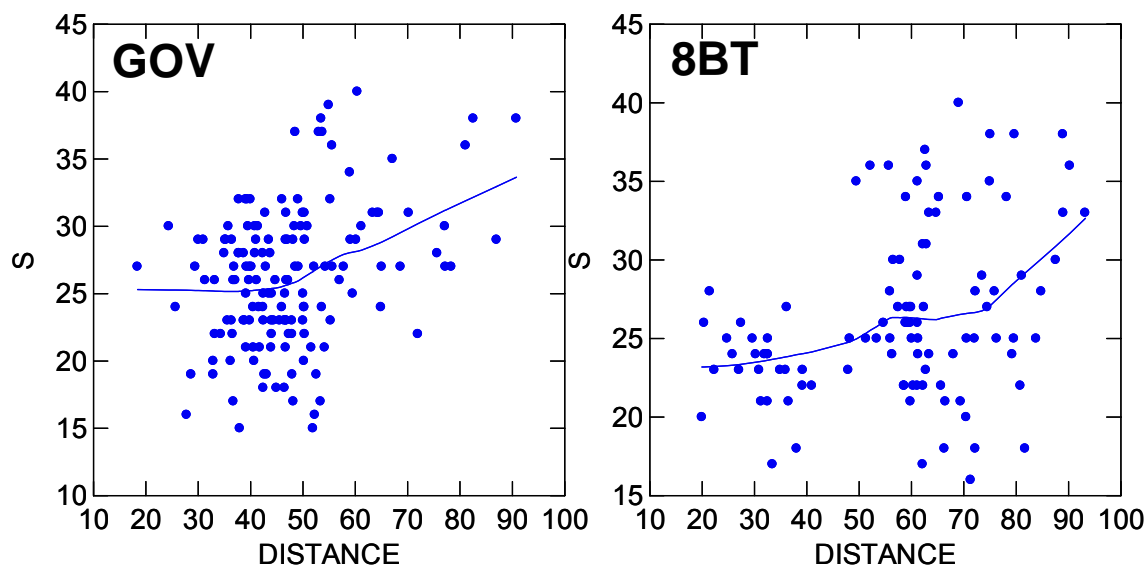


Figure 3.2.2.4.3: Lowess smoothers fitted to ICES rectangle species richness estimates based on 20 aggregated samples and the size of the search radius around each rectangle central point focal location required to acquire the necessary 20 samples.

Figure 3.2.2.4.4. examines the effect of search radius on all three metrics calculated for each of the two surveys. Here polynomial functions provide a significant fit to the species richness data, confirming the increasing contribution of β diversity at search radius distances greater than 50Km. Two straight line fits are also applied to the GOV data, the first for search radii up to 50Km in length and the second for search radii greater than 50Km in length. These two straight

lines almost exactly over lay the polynomial fit and therefore provide just as good a fit to the data as the polynomial expression. The upward sloping line for search radii greater than 50Km is itself statistically significant with $R^2=0.321$, $N=56$, $P<0.02$. For the IBTS GOV data, search radius had no discernable affect on either of the two species diversity indices, suggesting that as species were added through the incorporation of β diversity, the impact of this on the overall distribution of individuals was undetectable; the added species must therefore have been rare (low abundance) compared with the species already present in the aggregated sample. Both Hill's N_1 and N_2 calculated for the DBTS 8BT data were significantly related to the size of the search radius.

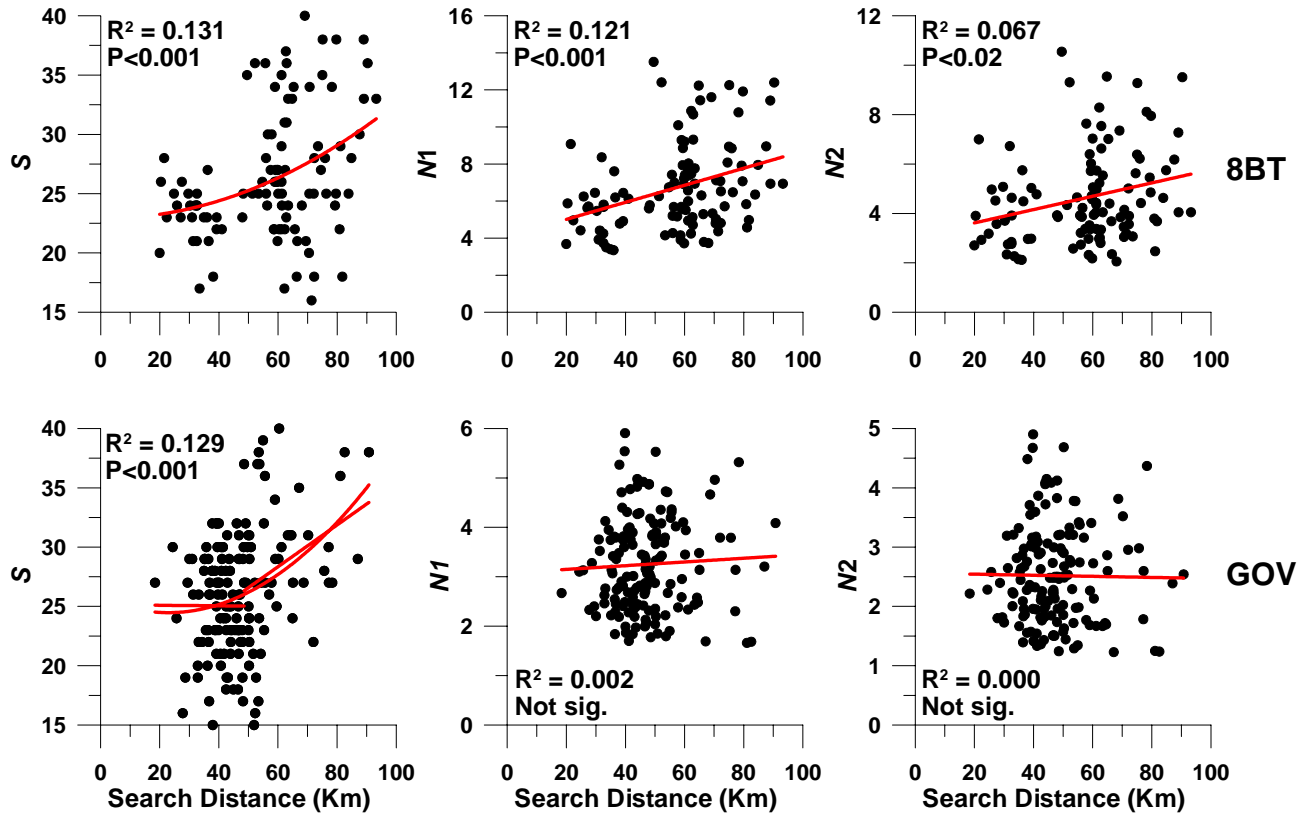


Figure 3.2.2.4.4: Examination of the effect of the size of the search radius around each rectangle central point focal location required to acquire the necessary 20 samples on the estimates of species richness and species diversity derived from aggregating 20 samples for each of the two surveys, the IBTS (GOV) and the DBTS (8BT).

3.3. Spatial Variation in the Diversity of the Demersal Fish Community

3.3.1. Based on the raw survey data

Here we examine the patterns of species richness and species diversity determined from each of the two surveys. Rectangles where the search distance required to acquire 20 samples exceeded 95k were excluded from the analysis. The pattern of spatial variation in species richness across the North Sea was similar for both surveys (Figure 3.3.1.1). But this was not the case for the two diversity indices. For both Hills N_1 and N_2 the impression gained as to how species diversity varied across the North Sea was entirely dependent on which survey data set was used (Figures 3.3.1.2 and 3.3.1.3). Examination of the correlation between the three

metrics revealed quite different patterns for the two surveys. In both cases Hill's N_1 and N_2 were significantly positively correlated, while both Hill's N_1 and N_2 were positively correlated with species richness in the DBTS data set, and negatively correlated in the IBTS data set (Figure 3.3.1.4).

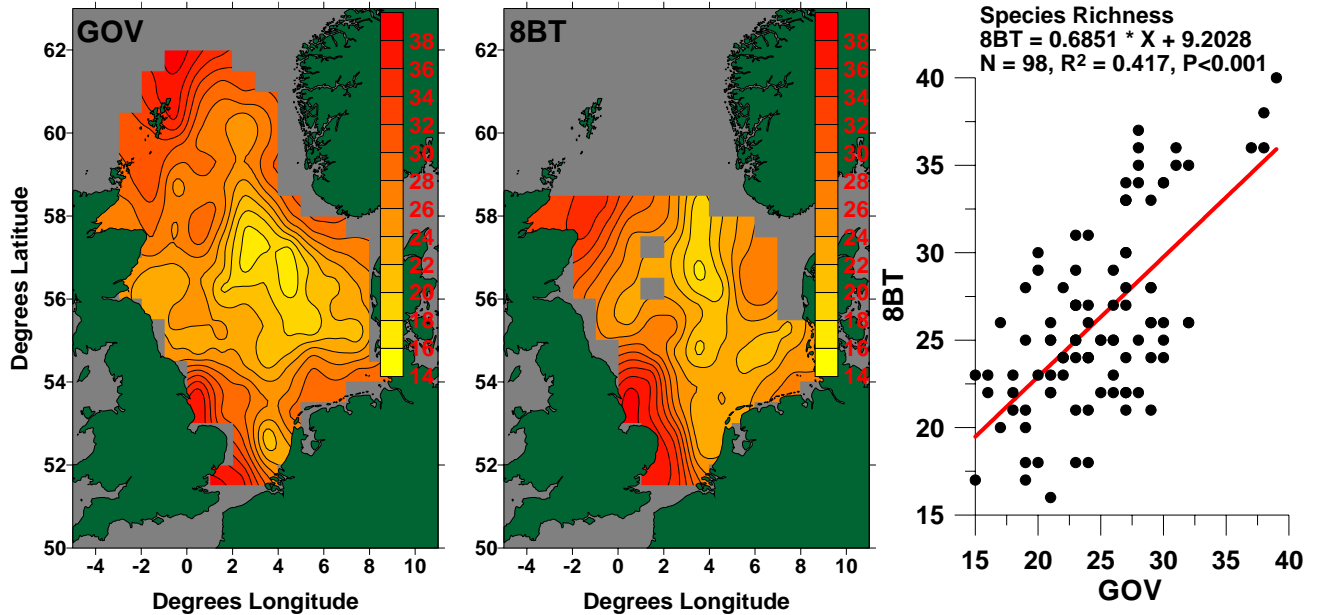


Figure 3.3.1.1: Spatial variation in species richness across the North Sea based on the IBTS (GOV) and DBTS (8BT) survey data sets. Scatterplot shows correlation between the two data sets.

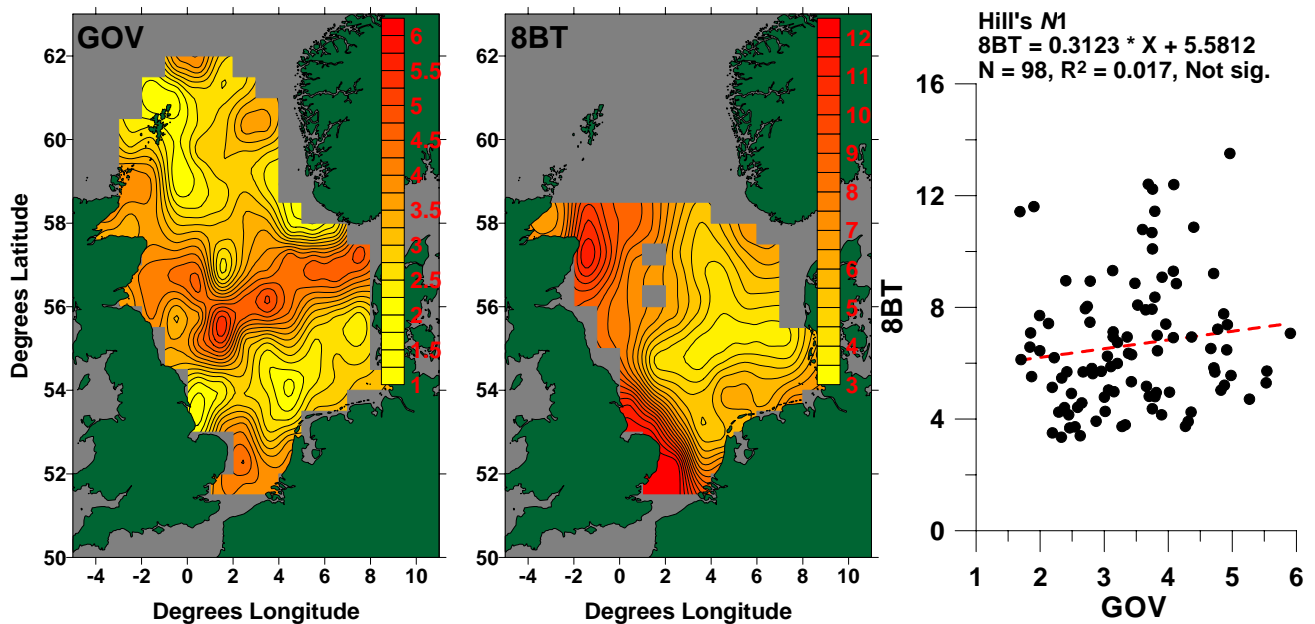


Figure 3.3.1.2: Spatial variation in Hill's N_1 across the North Sea based on the IBTS (GOV) and DBTS (8BT) survey data sets. Scatterplot shows correlation between the two data sets.

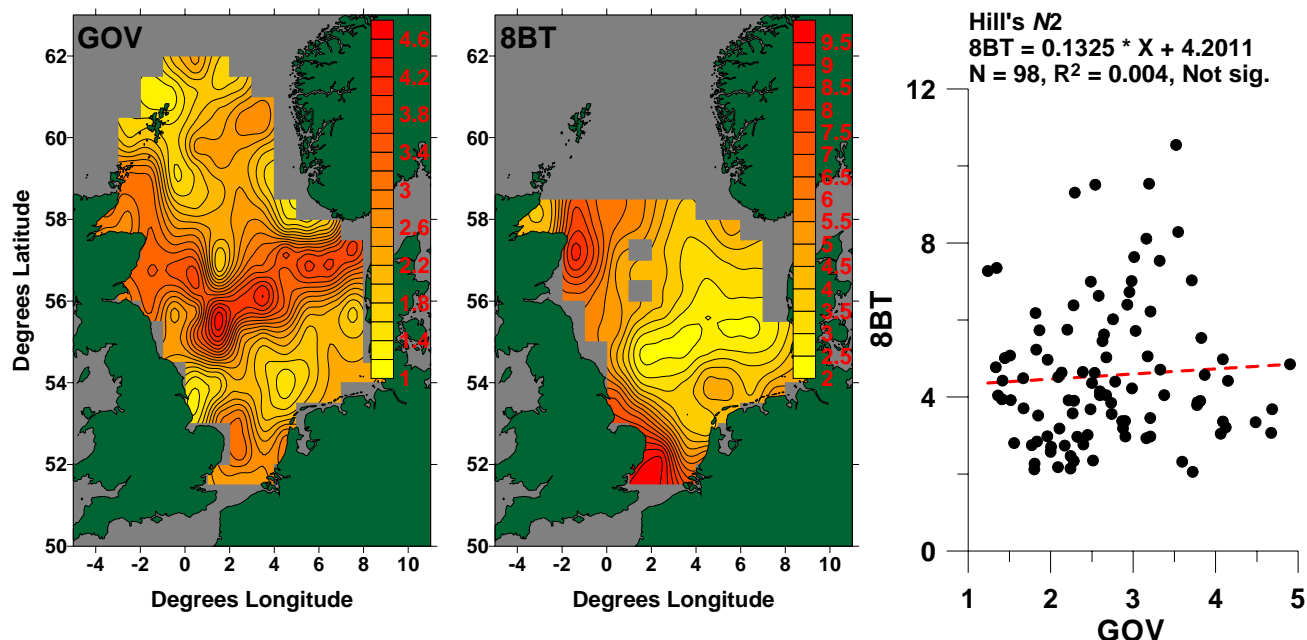


Figure 3.3.1.3: Spatial variation in Hill's N_2 across the North Sea based on the IBTS (GOV) and DBTS (8BT) survey data sets. Scatterplot shows correlation between the two data sets.

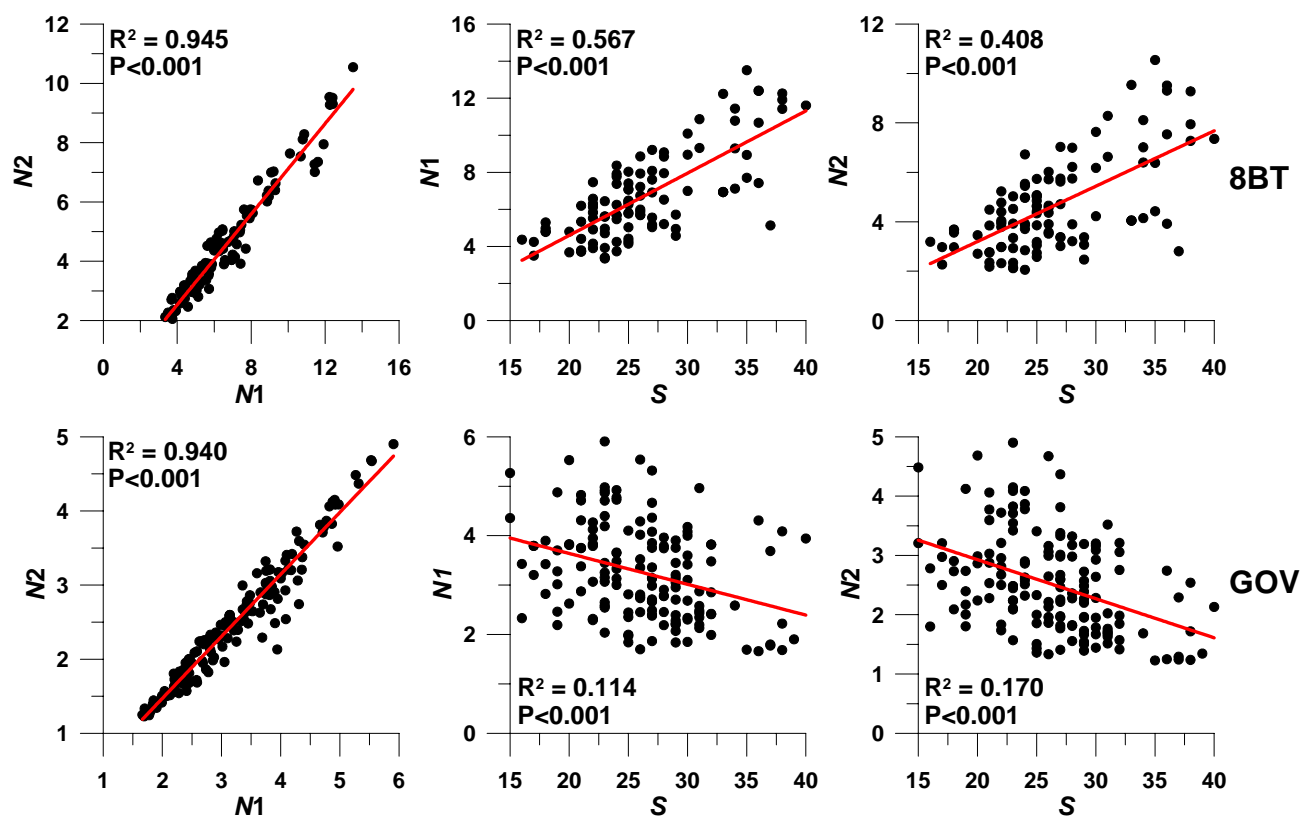


Figure 3.3.1.4: Inter-correlations between the species richness and species diversity metrics calculated for both survey data sets, the IBTS (GOV) and DBTS (8BT).

3.3.2. Based on the raised IBTS GOV data taking account of catchability

The first point to realize here is that when considering the entire community in this section, we mainly focus on spatial variation in Hill's N_1 and N_2 . There is no disputing that the catchability issue is of relevance with regard to species richness, it is simply that we cannot address this issue as yet. To apply the q coefficients to the IBTS GOV catch data, one needs to have caught something in the first place. Species not recorded in a GOV sample, i.e. zero value catch, will still have a zero score when multiplied by q . Thus the GOV species richness patterns shown in section 3.3.1 are unaffected by taking account of catchability. Taking account of catchability as described in section 3.1 only affects the relative abundance of the species actually sampled, so only influences our interpretation of the Hill's N_1 and N_2 data.

Secondly, we need to recall that in the estimation of catchability coefficients, geometric means densities were calculated, and it was these densities over all rectangles that were raised to the area sampled to determine IBTS biomass estimates for comparison with estimates derived from the assessments. Simply applying the catchability coefficients to the catch totals of each species at length over all 20 aggregated haul samples in each rectangle would therefore not be appropriate. This would be tantamount to treating these data as arithmetic mean densities, and would consequently have introduced bias such that the raised abundance of abundant and patchily distributed species would have been over-estimated. To examine the effects of gear catchability on diversity estimates therefore, geometric means of the density of each species at length were calculated. These geometric means were then multiplied by the area swept by all twenty hauls in each rectangle to provide unbiased estimates of the aggregate raised catches. However, this then introduced the possibility that it was the use of these geometric mean densities that were the cause of any difference between the resulting diversity maps. This possibility was explored by determining geometric mean densities based on the raw uncorrected (for catchability) catch data at length for each of the 20 trawl samples in each rectangle, and then applying identical analytical procedures.

3.3.2.1. The “entire” demersal fish community

Taking account of catchability has a profound effect on our understanding of the factors that influencing the species diversity of the demersal fish assemblage. When based on the raw survey data no easily comprehensible pattern emerges. When based on the raised GOV data, after taking catchability into account, it becomes obvious that species diversity is highest in the shallower, hydrographically mixed, more productive region in the southern North Sea (Figures 3.3.2.1.1 and 3.3.2.1.2). This difference was entirely driven by taking species catchability at length in the GOV into account, rather than by the use of geometric mean densities. Whilst the use of geometric means certainly affected diversity estimates, their use had no fundamental effect on the pattern of spatial variation in species diversity across the North Sea. Figure 3.3.2.1.3 explores the relationships between the three diversity and richness metrics. Comparison with Figure 3.3.1.4 indicates that correcting for catchability had little effect on these relationships.

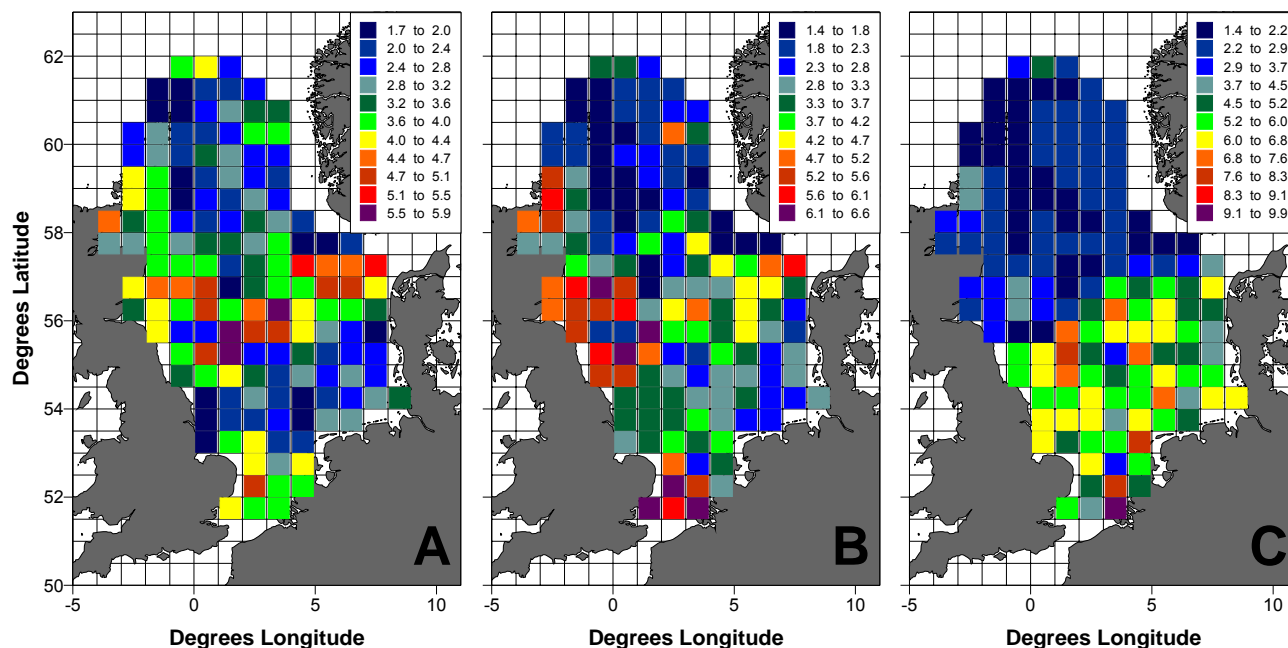


Figure 3.3.2.1.1: The effects of taking catchability into account on spatial variation in Hills N_1 based on the IBTS GOV data set. A: Aggregated species totals across all 20 hauls in each rectangle. B: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raw uncorrected (for catchability) trawl densities. C: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raised corrected (for catchability) trawl densities.

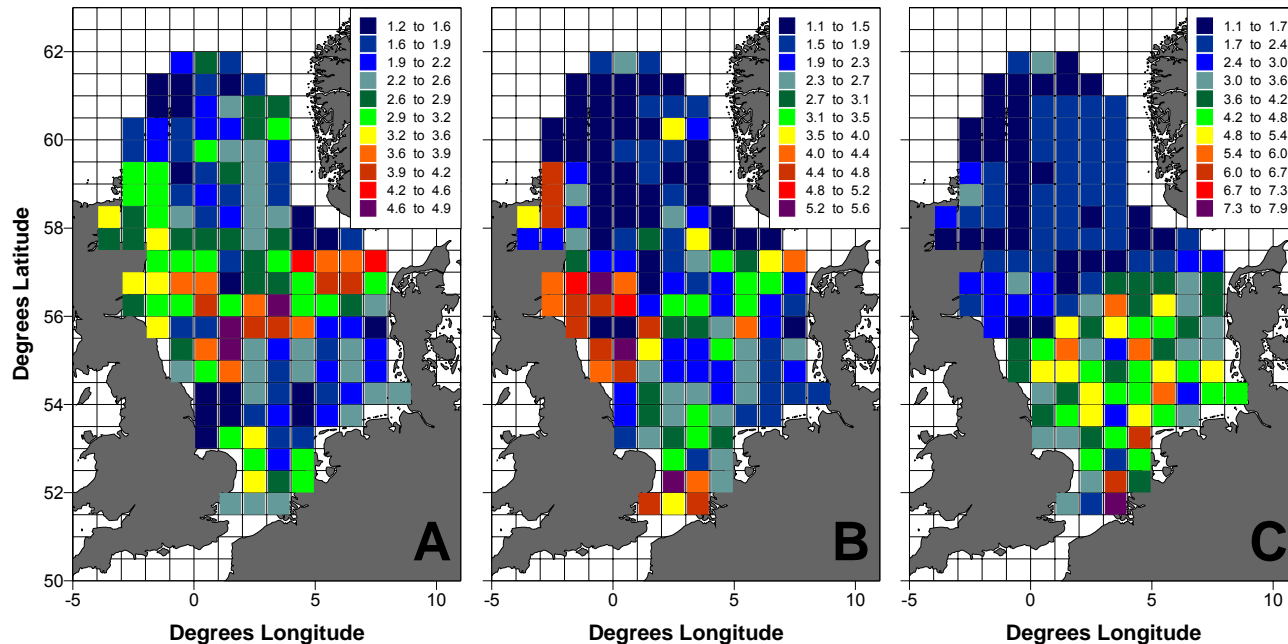


Figure 3.3.2.1.2: The effects of taking catchability into account on spatial variation in Hills N_2 based on the IBTS GOV data set. A: Aggregated species totals across all 20 hauls in each rectangle. B: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raw uncorrected (for catchability) trawl densities. C: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raised corrected (for catchability) trawl densities.

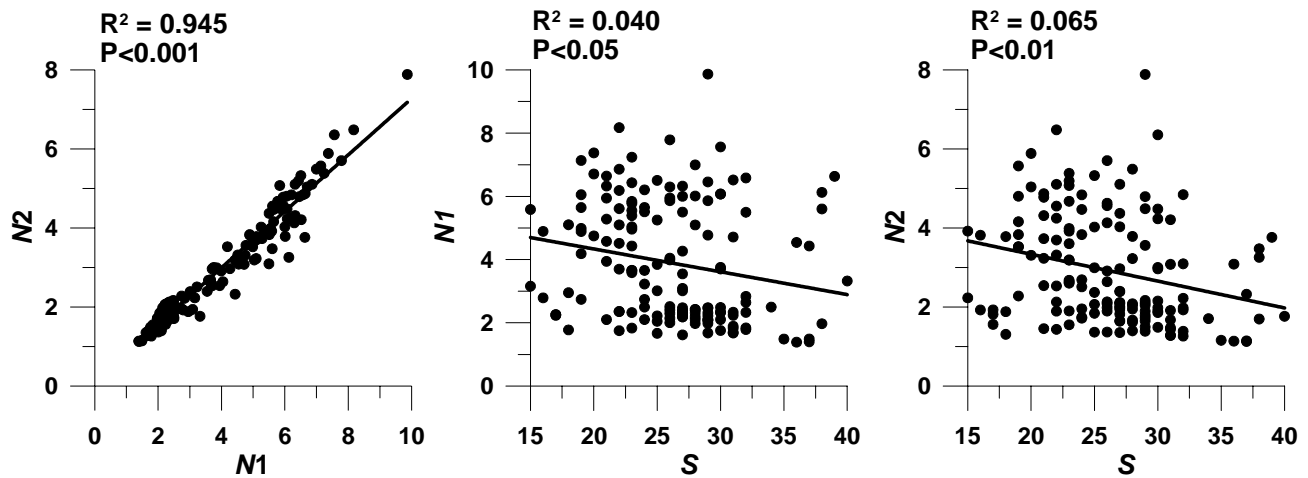


Figure 3.3.2.1.3: Intercorrelations between the species richness and the species diversity metric calculated on the geometric mean densities calculated across all 20 hauls in each rectangle on the raised corrected (for catchability) trawl densities.

Cluster analysis of the raised, sample effort standardised, GOV data set suggested more pronounced clustering, with three clearly defined clusters at a similarity of 60% (Figure 3.3.2.1.4). When the spatial locations of these clusters was mapped, a highly distinctive pattern emerged (Figure 3.3.2.1.5), that closely matched the spatial patterns in species diversity. Spatial variation in species composition clustering was relatively robust to species and length based variation in catchability in the GOV trawl. One obvious effect was the disappearance of the fourth blue cluster when catchability was taken into account. Rectangles assigned to this cluster based on the raw uncorrected data were distributed between the two neighbouring green and red clusters. The use of geometric mean densities or aggregated sums of the raw data had no effect on the spatial distribution of community composition clusters at all. Figure 3.3.2.1.6 shows the effect of taking into account species- and length-related catchability in the GOV research trawl relationship on the relationships between Hill's N_1 and N_2 and depth. When variation in catchability was ignored no significant relationship was detected. When catchability is included, the relationships between the two diversity indices and depth are highly significant. This figure also shows the colour coding related to the species composition clusters.

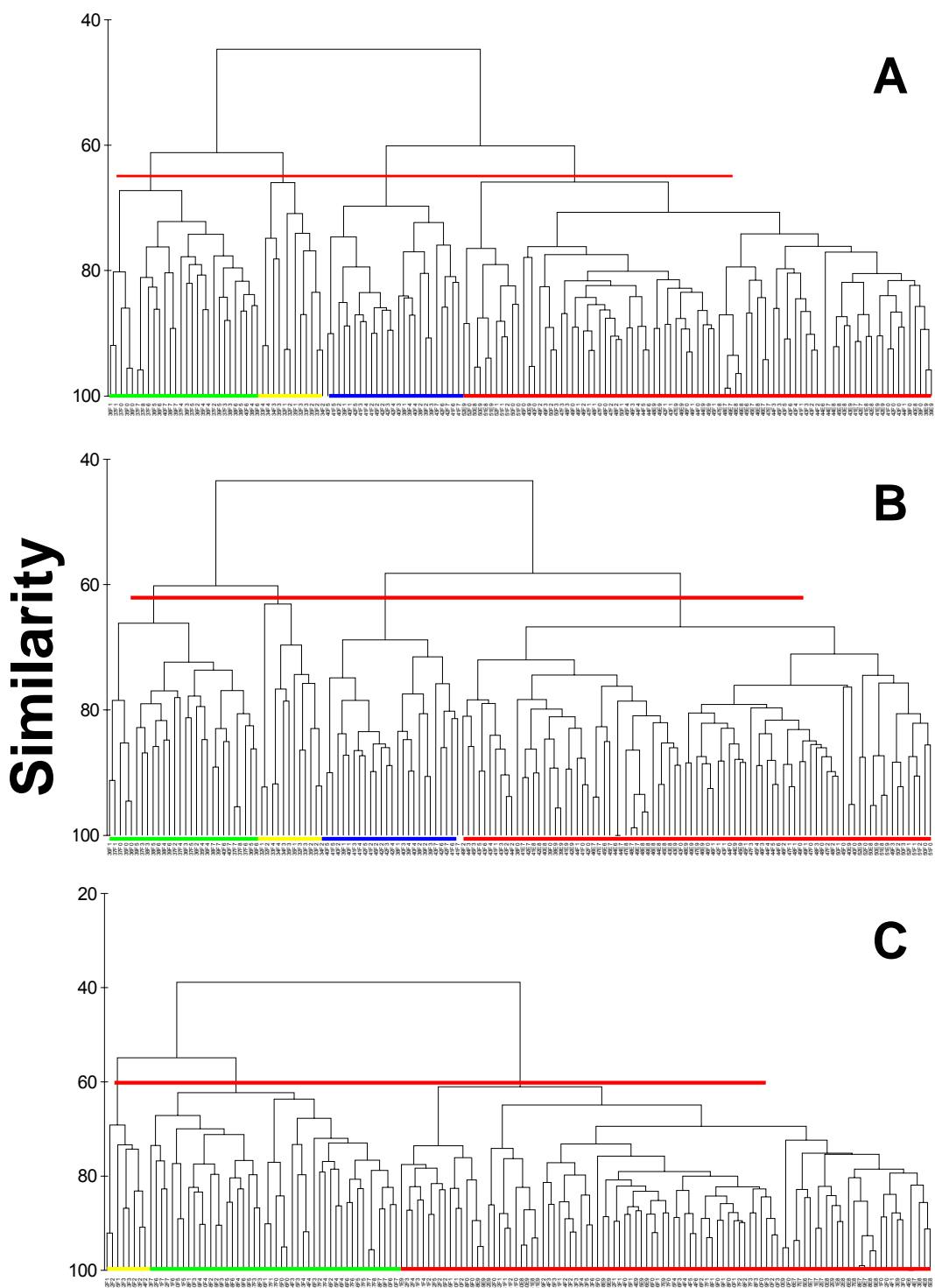


Figure 3.3.2.1.4: Cluster analysis dendrogram of the IBTS GOV data, standardised to equal sampling effort in each rectangle (20 trawl samples). A: Aggregated species totals across all 20 hauls in each rectangle. B: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raw uncorrected (for catchability) trawl densities. C: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raised corrected (for catchability) trawl densities.

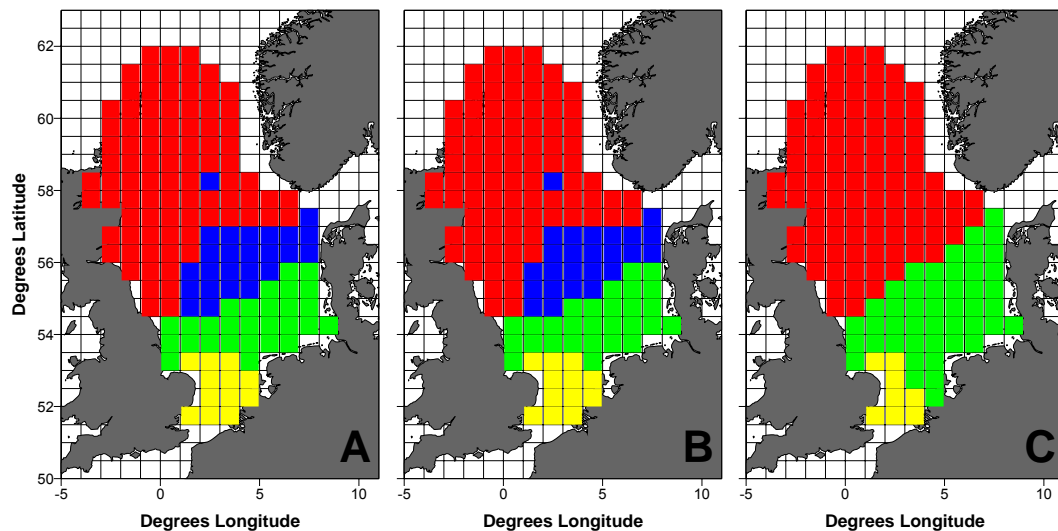


Figure 3.3.2.1.5: Spatial plots of the demersal fish community composition clusters shown in figure 3.3.2.1.3. A: Aggregated species totals across all 20 hauls in each rectangle. B: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raw uncorrected (for catchability) trawl densities. C: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raised corrected (for catchability) trawl densities.

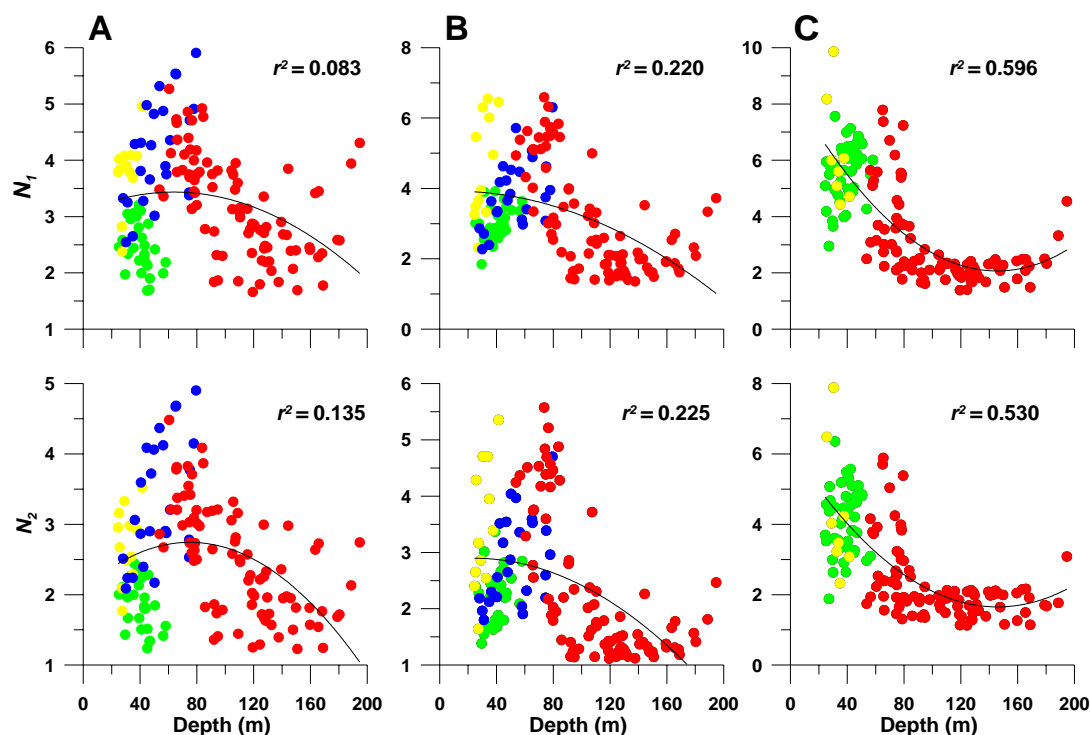


Figure 3.3.2.1.6: Relationship between Hill's N_1 and N_2 and depth illustrating the effect on this relationship when the trawl abundance data are raised to take account of species- and size-related variation in catchability. Data point colour coding corresponds to the cluster identity indicated in Figures 3.3.2.1.4 and 3.3.2.1.5. A: Aggregated species totals across all 20 hauls in each rectangle. B: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raw uncorrected (for catchability) trawl densities. C: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raised corrected (for catchability) trawl densities.

3.3.2.2. *Sub-sets of the demersal fish community*

In this section we determine spatial variation in species richness and species diversity for various size-class sub-sets required either for specific tests of Huston's DEM, or for development of an alternative ecological model linking fishing disturbance to species diversity consequences (Greenstreet *et al* 2007b).

Fishing is a size-based activity because of market forces (larger fish are more valuable) and regulation (it is illegal to land fish below a certain length). For most species targeted specifically in the North Sea, the legal landing size is in the region of 25cm to 30cm. For most species, this equates to a fish of approximately 256g in weight (Log_2 weight class 8). Thus the deliberately fished fraction of the demersal fish community of the North Sea consists of fish in Log_2 weight classes 8 and higher. Figure 3.3.2.2.1 shows spatial variation in the species richness and species diversity of fish belonging to this weight category, comparing the spatial pattern when Hill's N_1 and N_2 are computed on the raw abundance data (as aggregated summed catches or geometric mean densities over all 20 hauls) and on the geometric mean raised density data taking account of species- and size-related variation in catchability. Taking account of catchability tended to reverse the spatial diversity patterns, with diversity highest in the deeper water in the northern North Sea. When diversity is calculated on the raw data, hotspots of diversity are suggested around the southern and eastern periphery of the North Sea, along with a hotspot in the extreme northwest. Based on either the raw or raised abundance data, Hills N_1 and N_2 plots for fish in the fished weight classes (Figure 3.3.2.2.1) show different spatial patterns of species diversity from plots made for the entire demersal fish assemblage (Figures 3.3.2.1.1 and 3.3.2.1.2.). When based on the raised data, spatial distributions of species diversity for the whole community and for the fished weight classes only were almost reversed (Figure 3.3.2.2.2). However, this was not the case with respect to species richness. Plots of species richness for the whole demersal fish community and only the fished weight classes subset showed strong spatial similarity (Figures 3.3.1.1 and 3.3.2.2.1) and were positively correlated (Figure 3.3.2.2.2). Species richness in the fished weight classes sub-set of the demersal fish community was closely related to species richness in the entire demersal fish assemblage. A linear regression fitted to the data ($S_{W\text{Log}_2 8+} = 0.45526S_{\text{Whole}} + 2.9019$) suggested species richness in the fished weight classes was approximately half the species richness of the entire assemblage, and this fraction was relatively constant across the entire range of species richness (Figure 3.3.2.2.2).

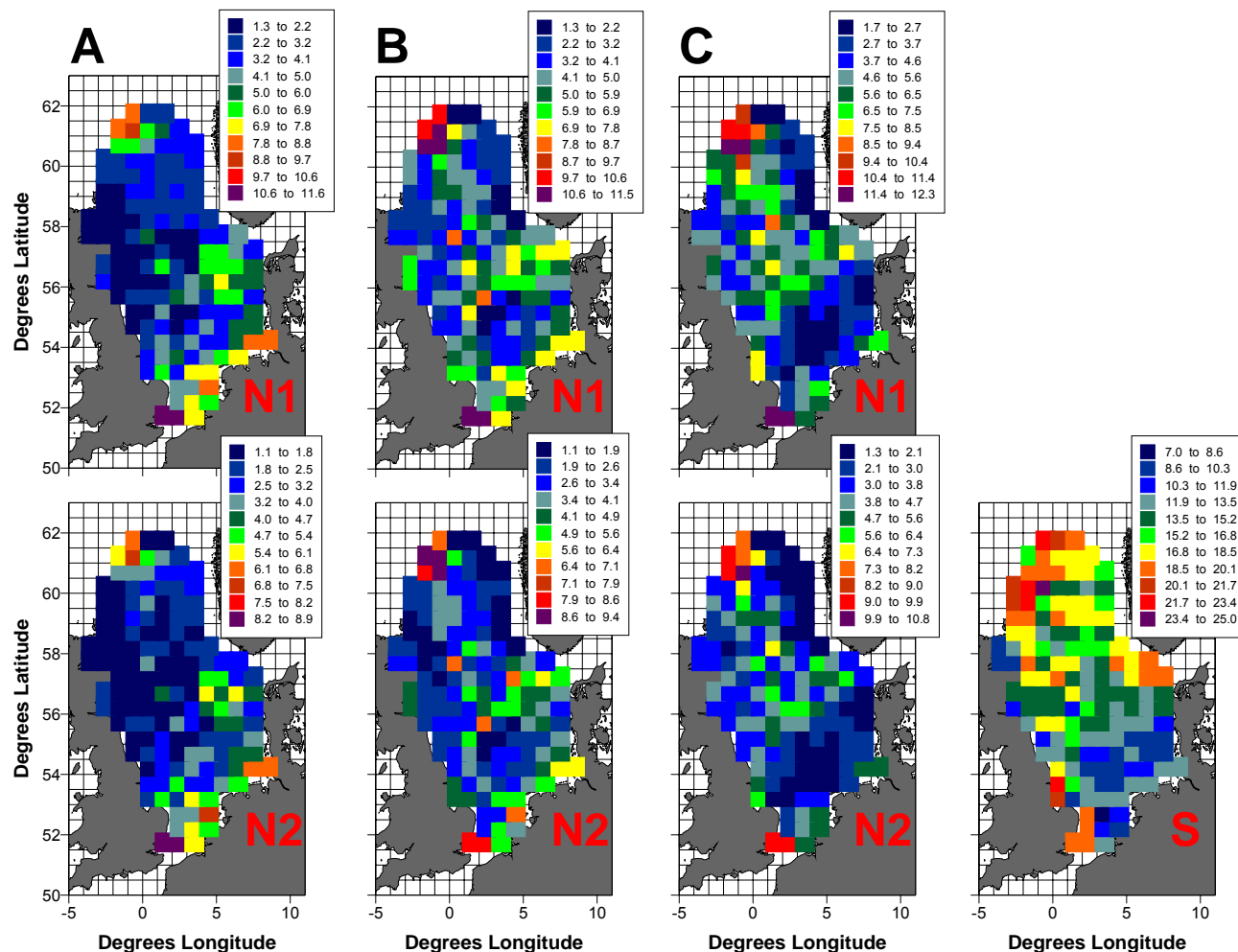


Figure 3.3.2.2.1: Spatial variation in the species richness (S) and species diversity (Hill's N1 and N2) of North Sea demersal fish belonging to the fished weight classes, Log₂ weight classes 8 and higher. A: Aggregated species totals across all 20 hauls in each rectangle. B: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raw uncorrected (for catchability) trawl densities. C: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raised corrected (for catchability) trawl densities.

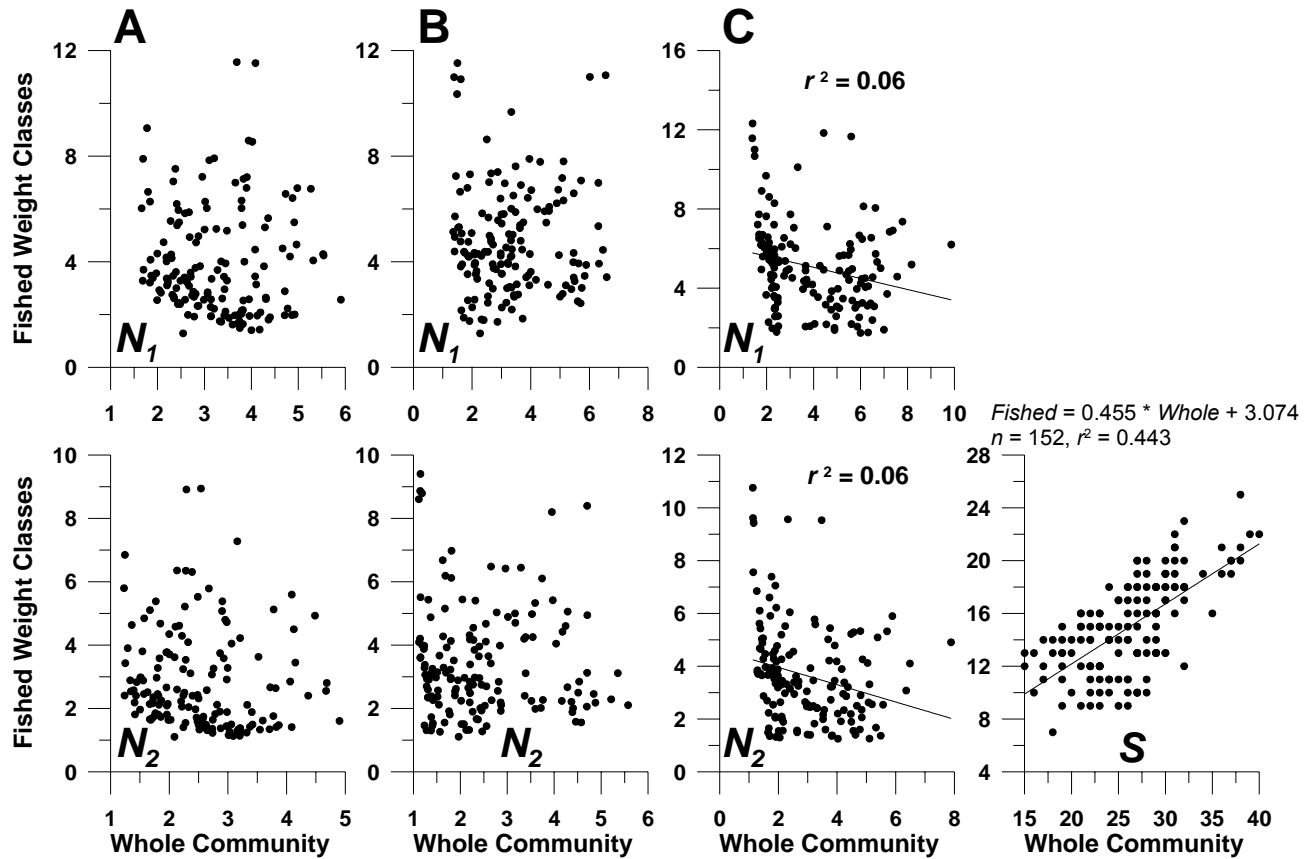


Figure 3.3.2.2.2: Relationships between ICES Rectangle species richness S and Hill's N_1 and N_2 species diversity indices calculated for the whole demersal fish community and a sub-set of the community consisting only of individuals belonging to the fished weight classes, Log₂ weight classes 8 and higher. A: Aggregated species totals across all 20 hauls in each rectangle. B: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raw uncorrected (for catchability) trawl densities. C: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raised corrected (for catchability) trawl densities.

Cluster analysis was carried out on abundance data of only the fished weight classes. Raising to account for catchability had very little effect on the characteristics of the dendrograms (Figure 3.3.2.2.3), and spatial plots of the clusters detected at a similarity of 50% revealed almost identical boundary locations between different community types (Figure 3.3.2.2.4). Furthermore, the community cluster maps determined for the fish weight classes only bore a strong resemblance to the maps plotted for the whole demersal fish community (Figures 3.2.1.2 and 3.3.2.1.4).

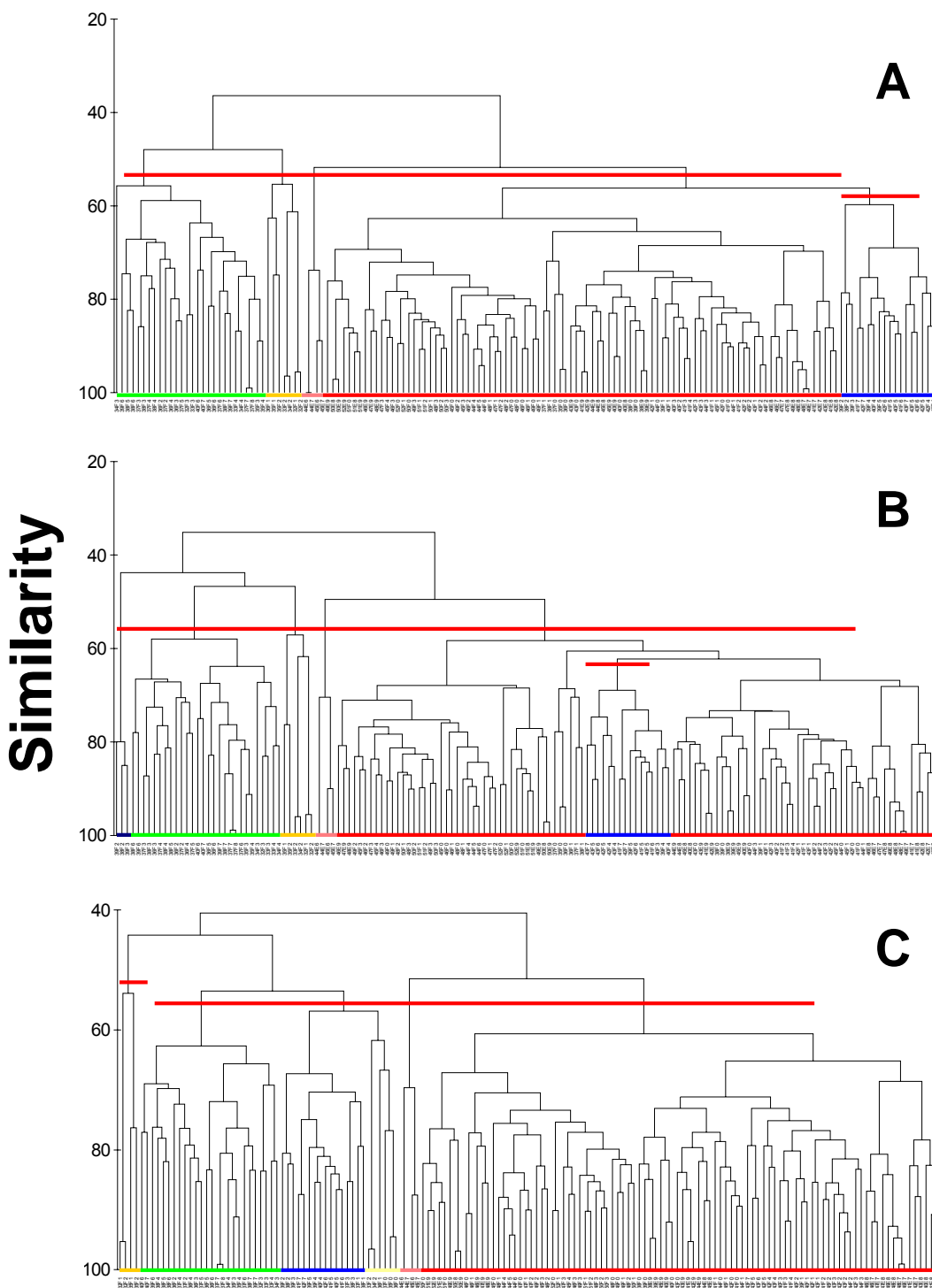


Figure 3.3.2.2.3: Dendrograms showing the results of group-average cluster analysis performed on Bray-Curtis similarity matrices constructed on root-root transformed IBTS GOV abundance data for fish in Log₂ weight classes 8 and above. A: Aggregated species totals across all 20 hauls in each rectangle. B: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raw uncorrected (for catchability) trawl densities. C: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raised corrected (for catchability) trawl densities.

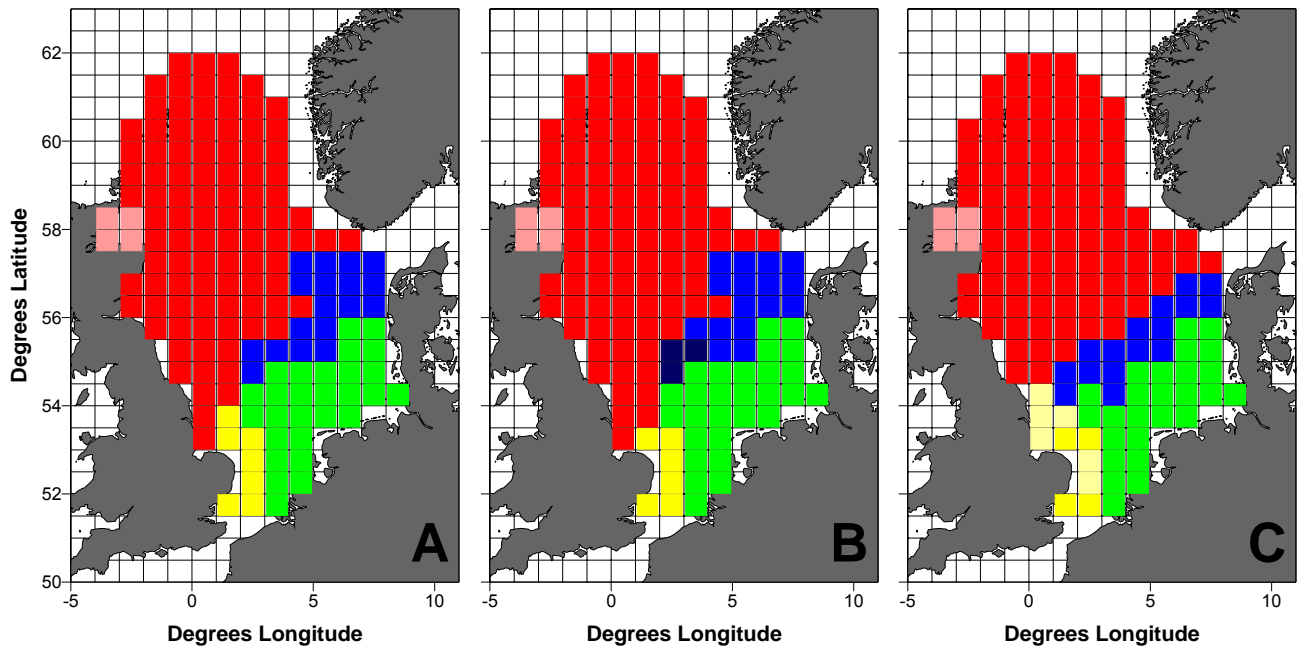


Figure 3.3.2.2.4: Spatial plots of the Fish community composition clusters indicated in Figure 3.3.2.2.4 for fish of \log_2 weight classes 8 and larger. A: Aggregated species totals across all 20 hauls in each rectangle. B: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raw uncorrected (for catchability) trawl densities. C: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raised corrected (for catchability) trawl densities.

3.4. Spatial Variation in the Productivity of the Demersal Fish Community

In this section we determine spatial variation in productivity of the demersal fish community for various size class sub-sets that are either required for specific tests of Huston's DEM, or for development of an alternative ecological model linking fishing disturbance to species diversity consequences (Greenstreet *et al* 2007b).

3.4.1. The entire demersal fish community

Accounting for species-and size-related variation in catchability in the GOV trawl greatly affected interpretation of spatial variation in biomass, absolute growth production and production per unit biomass (Figure 3.4.1.1). Examination of the raw data, based either on arithmetic mean densities or geometric mean densities, suggested that both biomass and production were highest down the western side of the North Sea and across the northern North Sea, whilst production per unit biomass was more evenly distributed with the lowest values observed in the central North Sea. When catchability was taken into account, both production and biomass are highest in the northern North Sea, whilst the effect on production per unit biomass was even more profound with a clear division between the northern and southern North Sea now apparent.

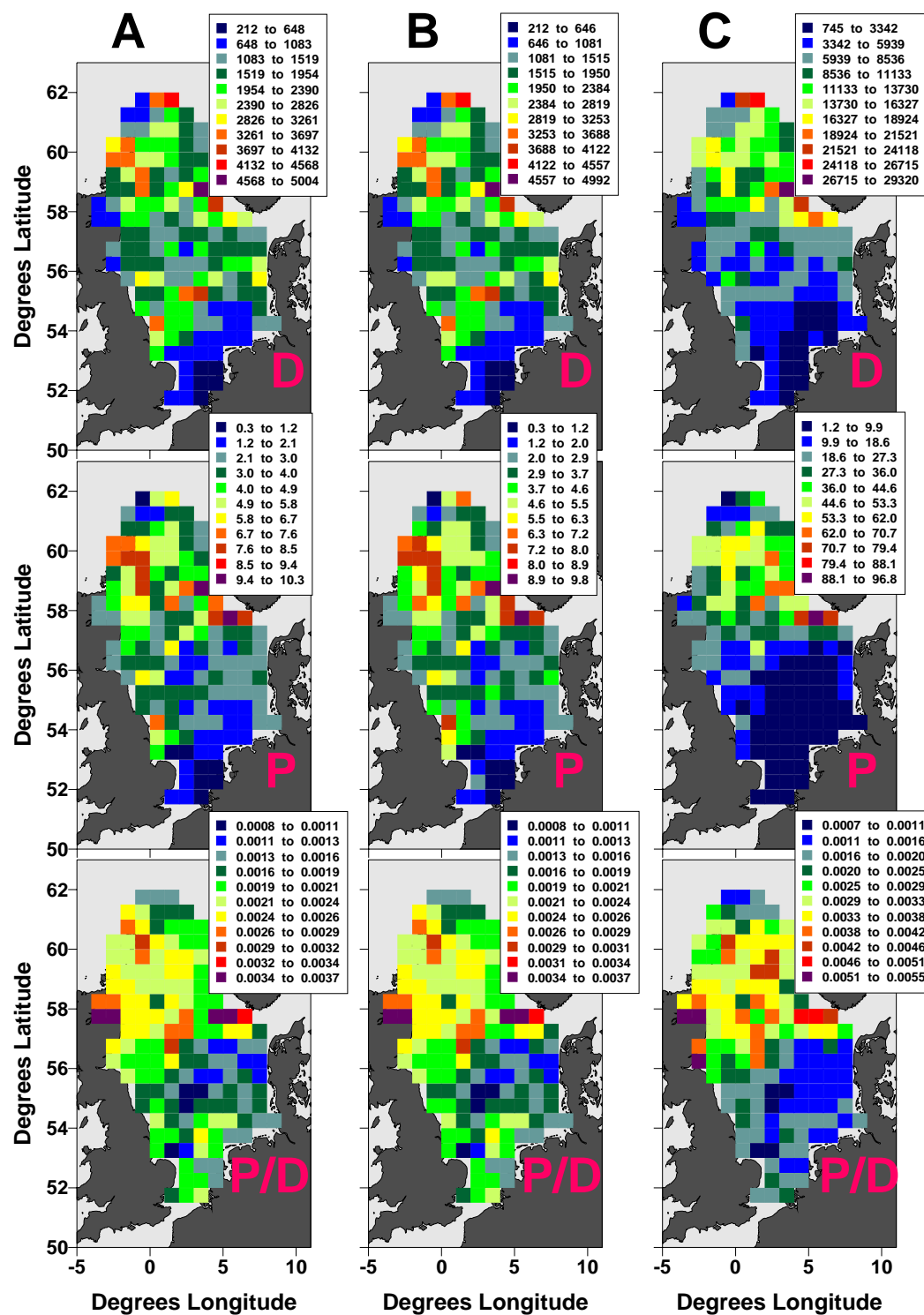


Figure 3.4.1.1: Spatial variation in the biomass density (D, Kg.Km⁻²), growth production (P, Kg.Km⁻².d⁻¹), and production per unit biomass (P/D) of the demersal fish community. A: Based on arithmetic mean densities calculated across all 20 hauls in each rectangle on the raw uncorrected (for catchability) trawl densities. B: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raw uncorrected (for catchability) trawl densities. C: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raised corrected (for catchability) trawl densities.

3.4.2. Sub-sets of the demersal fish community

In size structured modelling (Greenstreet *et al* 2007b) and for specific tests of the Dynamic Equilibrium Model, estimates of the productivity of particular size strata within the fish community will be required. As a preliminary analysis we examined the extent to which productivity of the various weight classes co-varied across the North Sea. Cluster analysis, based on group average clustering of Bray-Curtis similarity matrices, and examination of Pearson Correlation matrices revealed that the patterns of spatial variation for some weight classes were similar, while others differed, suggesting that the 15 weight classes could be grouped into six groups. Within groups each constituent weight classes showed similar patterns of spatial variation, while between groups, different patterns of spatial variation tended to be evident. Spatial variation in the biomass, productivity and production/biomass ratios of each of these weight-class groups, based on arithmetic mean densities, are shown in Figures 3.4.2.1 to 3.4.2.3 respectively. Figures 3.4.2.4 to 3.4.2.6 show the same parameters for each weight-class, but based on geometric mean densities, and finally, Figures 3.4.2.7 to 3.4.2.9 show the same parameters for each weight-class, but based on geometric mean densities raised to take account of catchability.

Species Composition, Diversity, Biomass and Production of the Demersal Fish Community of the North Sea

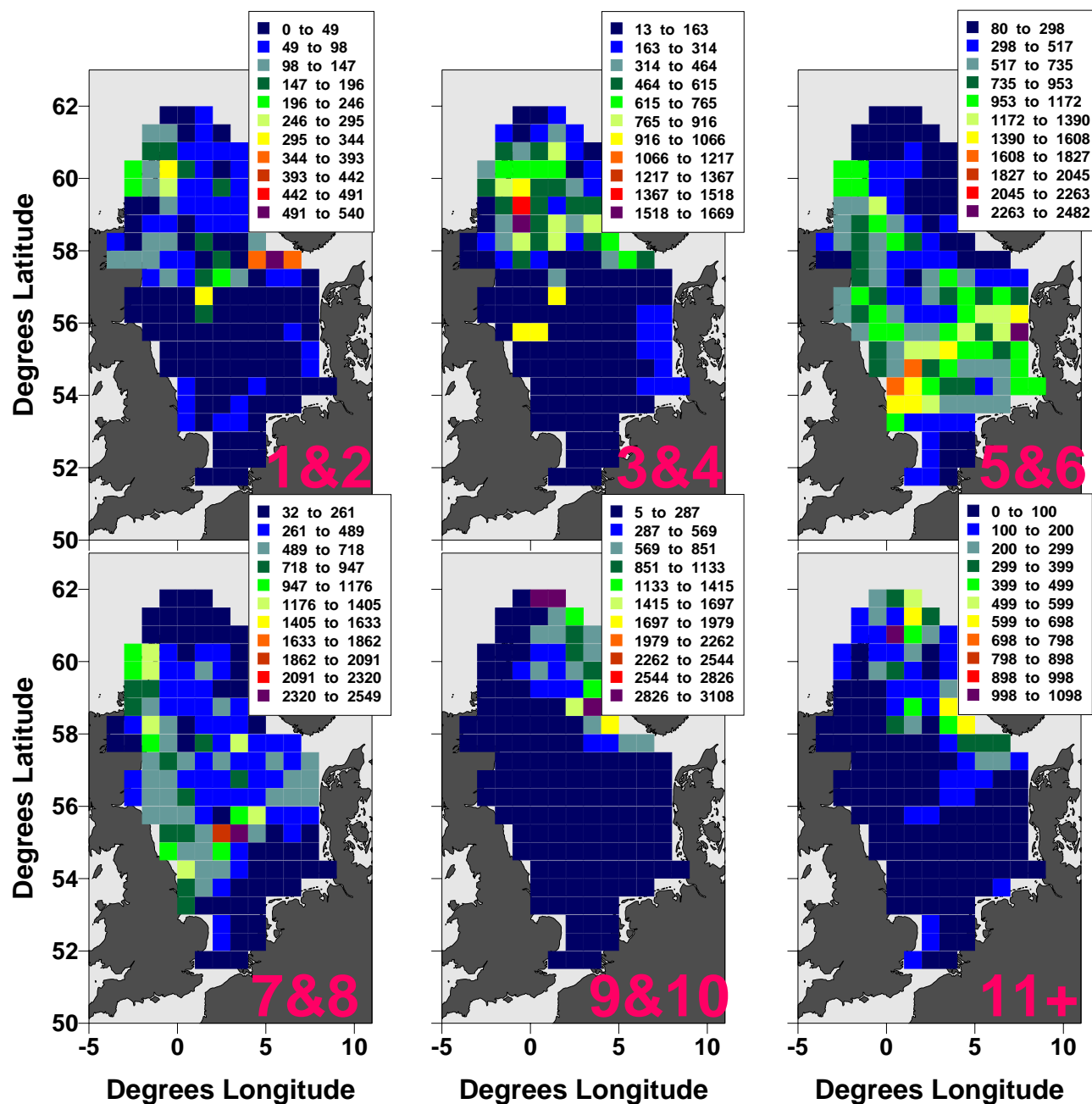


Figure 3.4.2.1: Spatial variation in the biomass density (kg.km⁻²) of demersal fish in six groups of individual Log₂ weight classes based on the raw arithmetic mean densities over 20 GOV trawl samples in each ICES rectangle.

Species Composition, Diversity, Biomass and Production of the Demersal Fish Community of the North Sea

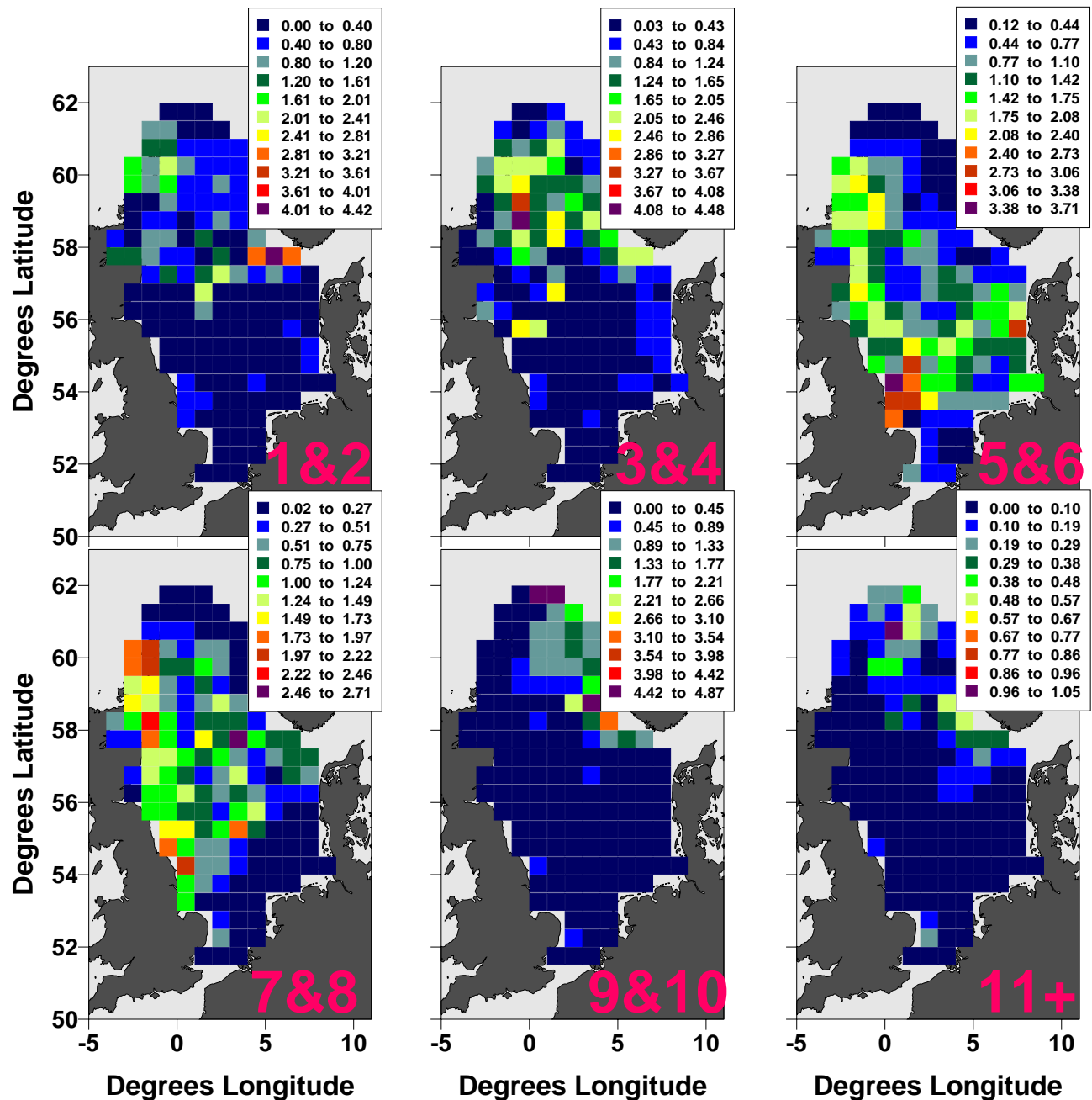


Figure 3.4.2.2: Spatial variation in the daily production density (kg.km⁻².d⁻¹) of demersal fish in six groups of individual Log₂ weight classes based on the raw arithmetic mean densities over 20 GOV trawl samples in each ICES rectangle.

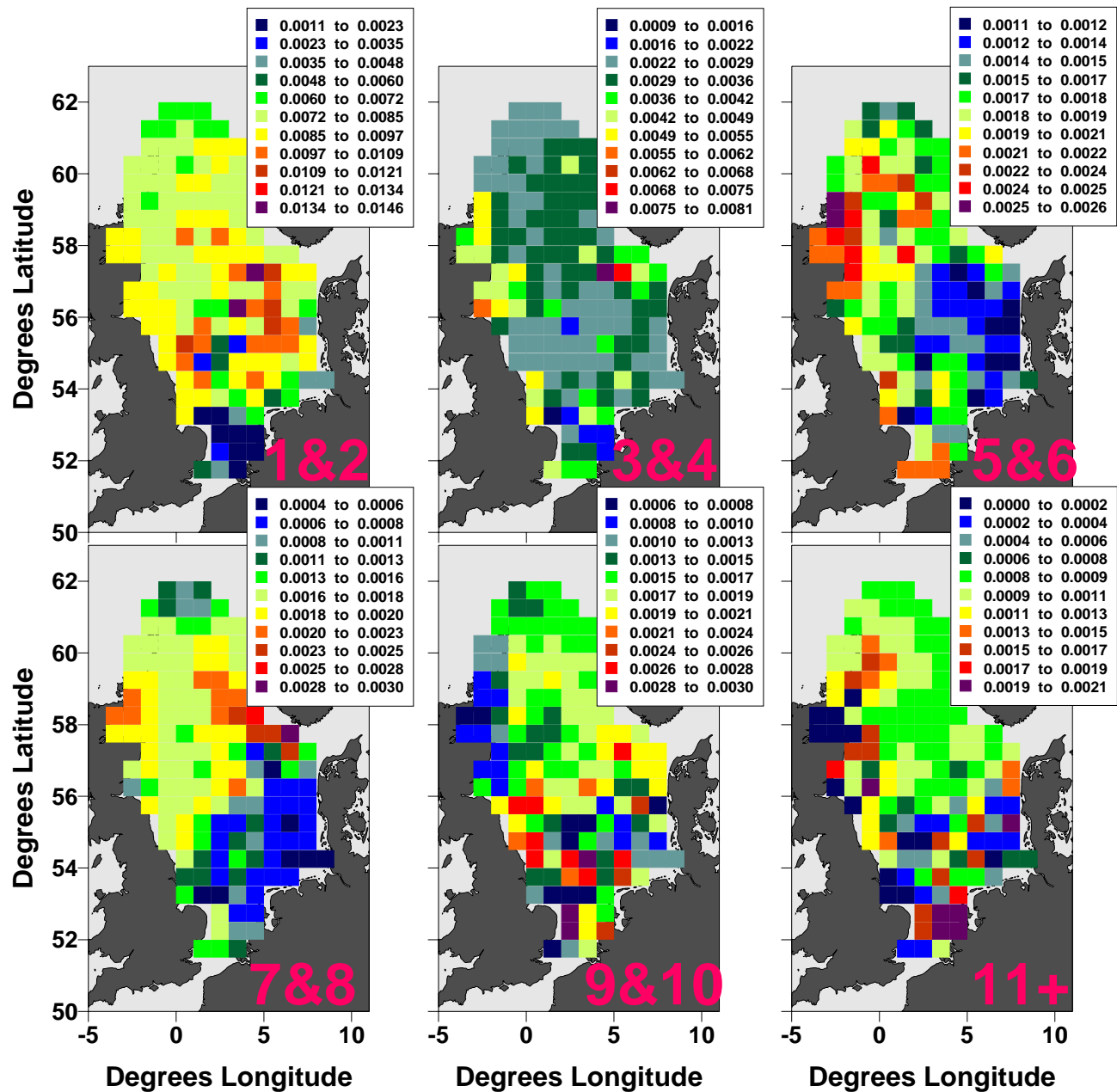


Figure 3.4.2.3: Spatial variation in the daily production:biomass ratio of demersal fish in six groups of individual Log_2 weight classes based on the raw arithmetic mean densities over 20 GOV trawl samples in each ICES rectangle.

Species Composition, Diversity, Biomass and Production of the Demersal Fish Community of the North Sea

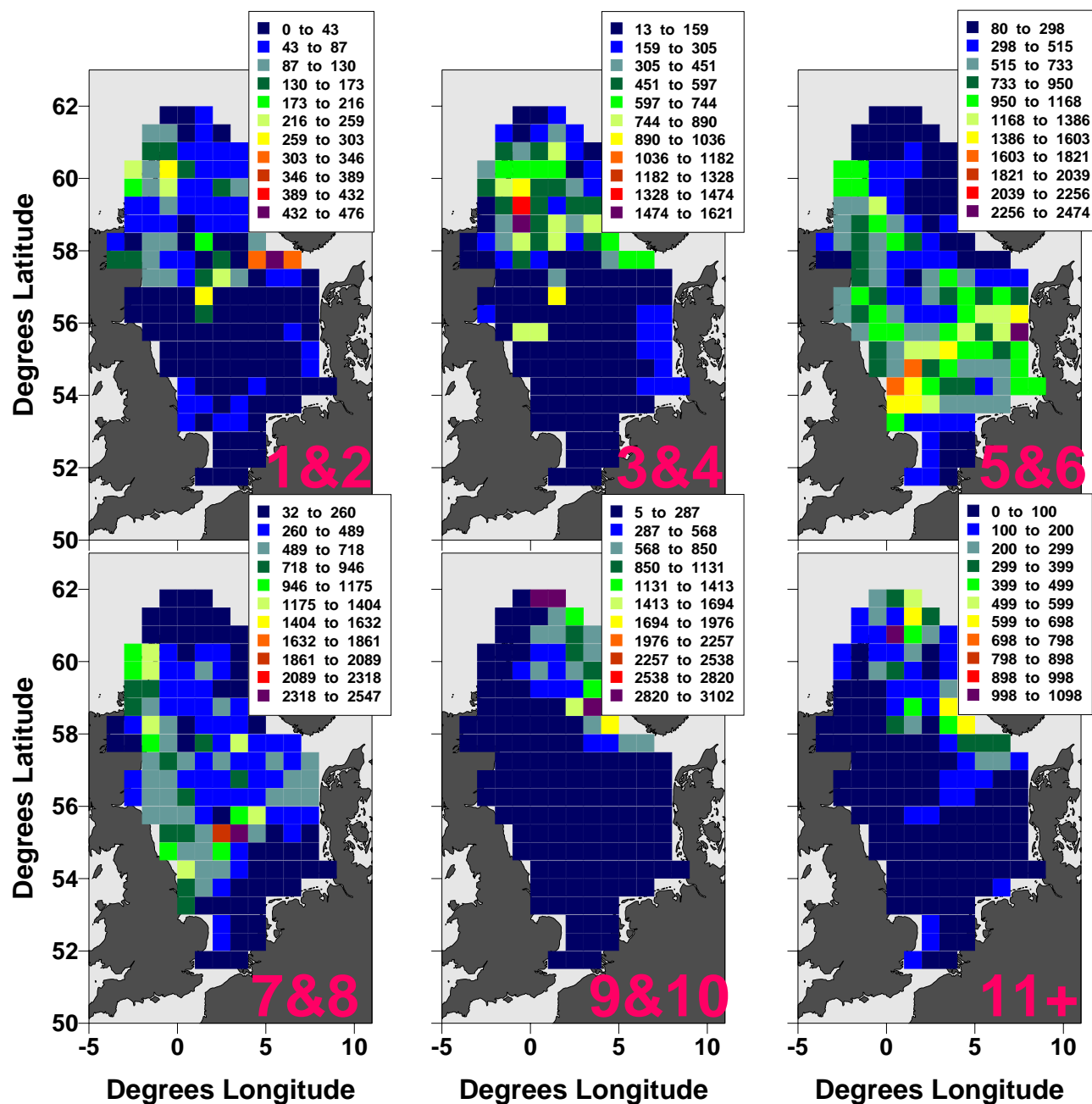


Figure 3.4.2.4: Spatial variation in the biomass density (kg.km⁻²) of demersal fish in six groups of individual Log₂ weight classes based on the raw geometric mean densities over 20 GOV trawl samples in each ICES rectangle.

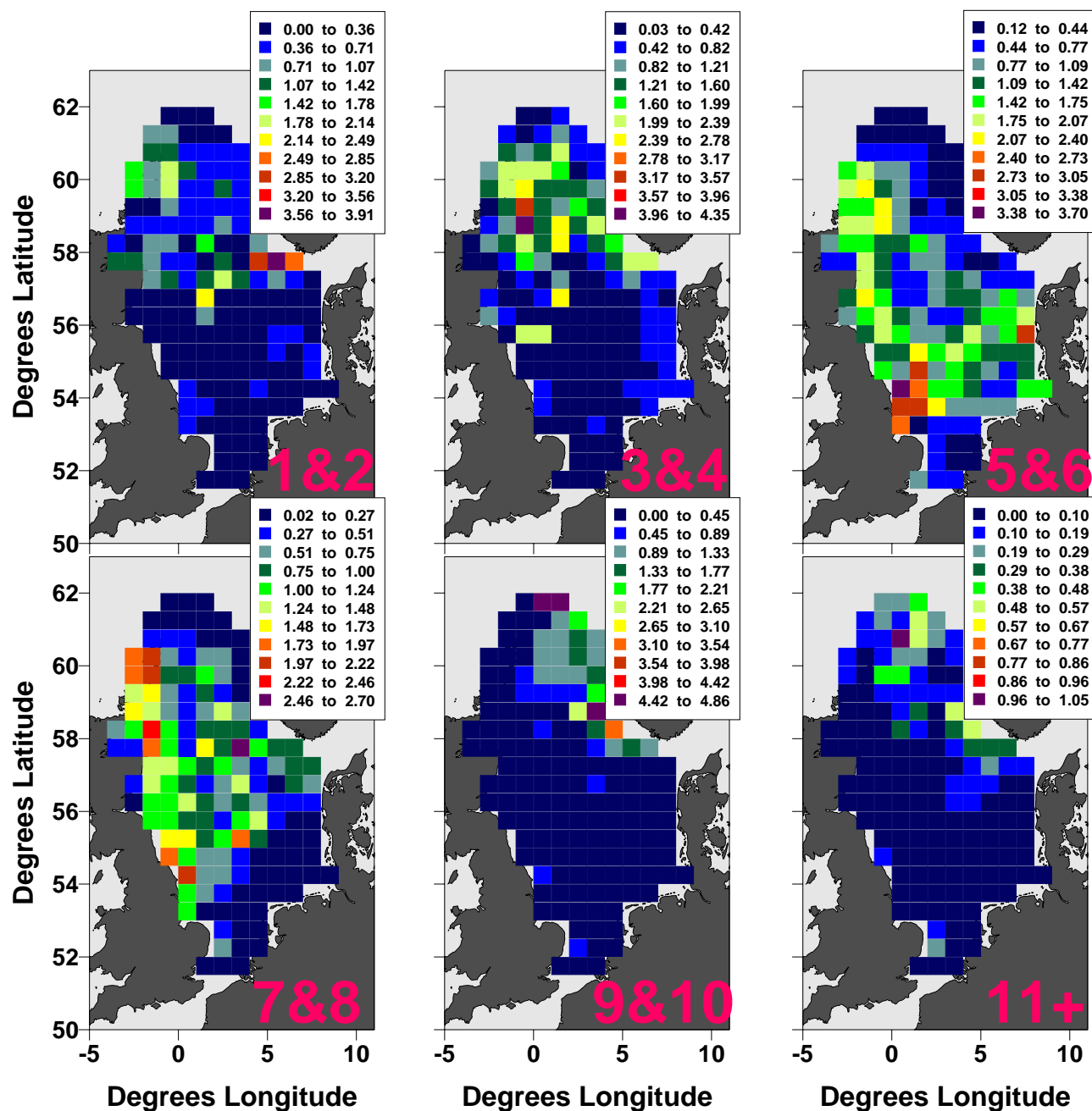


Figure 3.4.2.5: Spatial variation in the daily production density (kg.km⁻².d⁻¹) of demersal fish in six groups of individual Log₂ weight classes based on the raw geometric mean densities over 20 GOV trawl samples in each ICES rectangle.

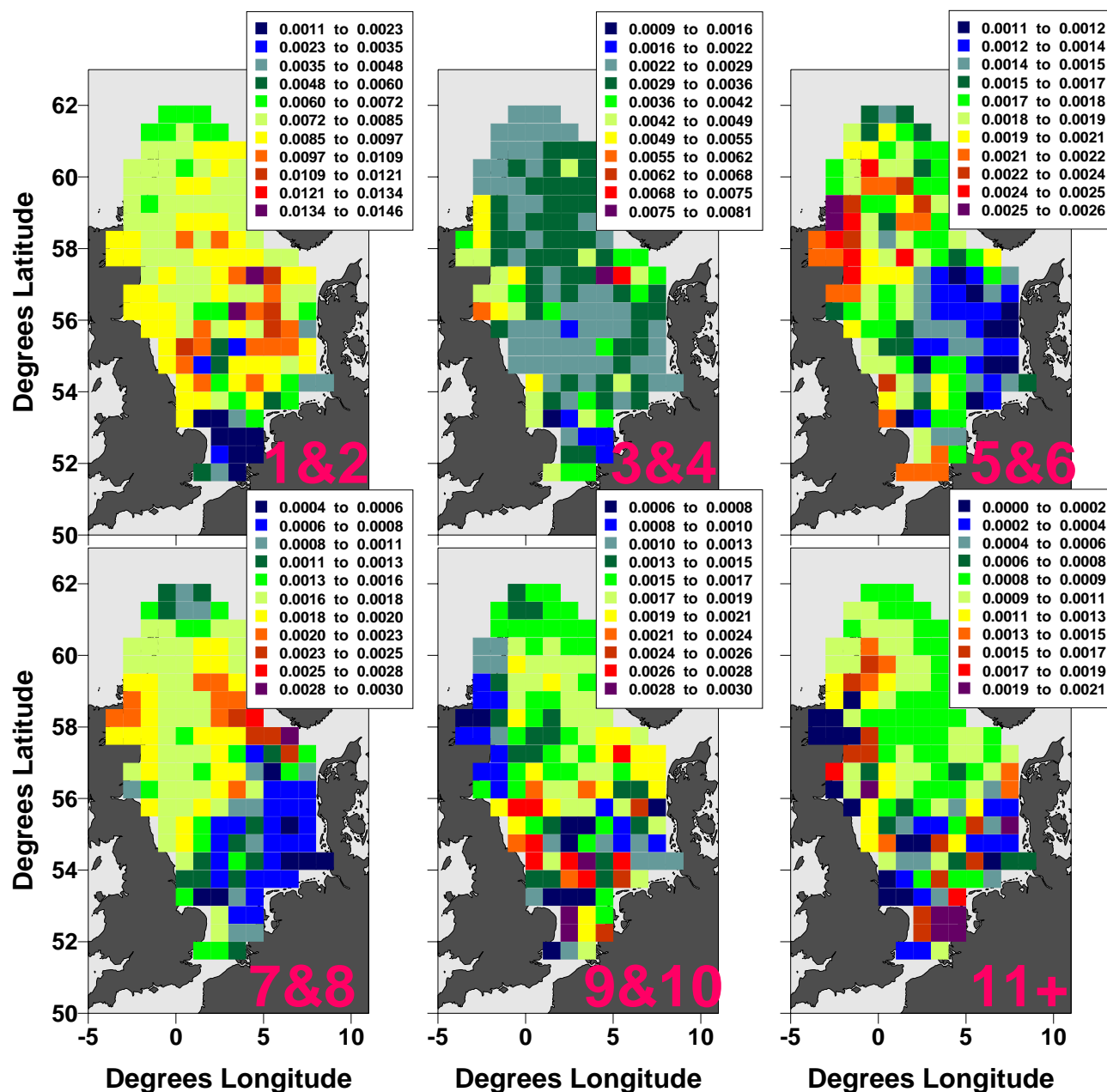


Figure 3.4.2.6: Spatial variation in the daily production:biomass ratio of demersal fish in six groups of individual Log_2 weight classes based on the raw geometric mean densities over 20 GOV trawl samples in each ICES rectangle.

Species Composition, Diversity, Biomass and Production of the Demersal Fish Community of the North Sea

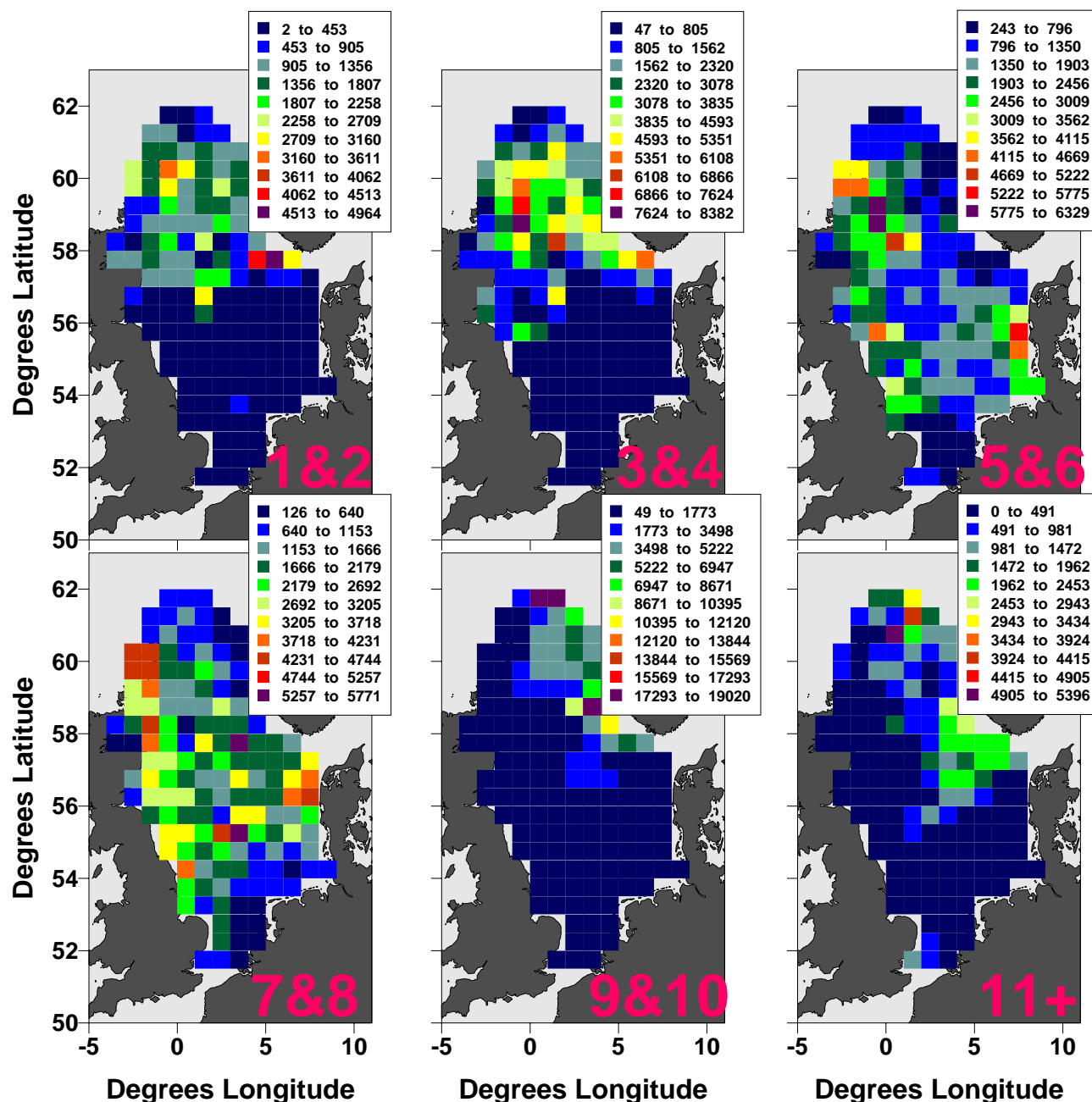


Figure 3.4.2.7: Spatial variation in the biomass density (kg.km^{-2}) of demersal fish in six groups of individual Log_2 weight classes based on the geometric mean densities raised to take account of species and length based variation in catchability over 20 GOV trawl samples in each ICES rectangle.

Species Composition, Diversity, Biomass and Production of the Demersal Fish Community of the North Sea

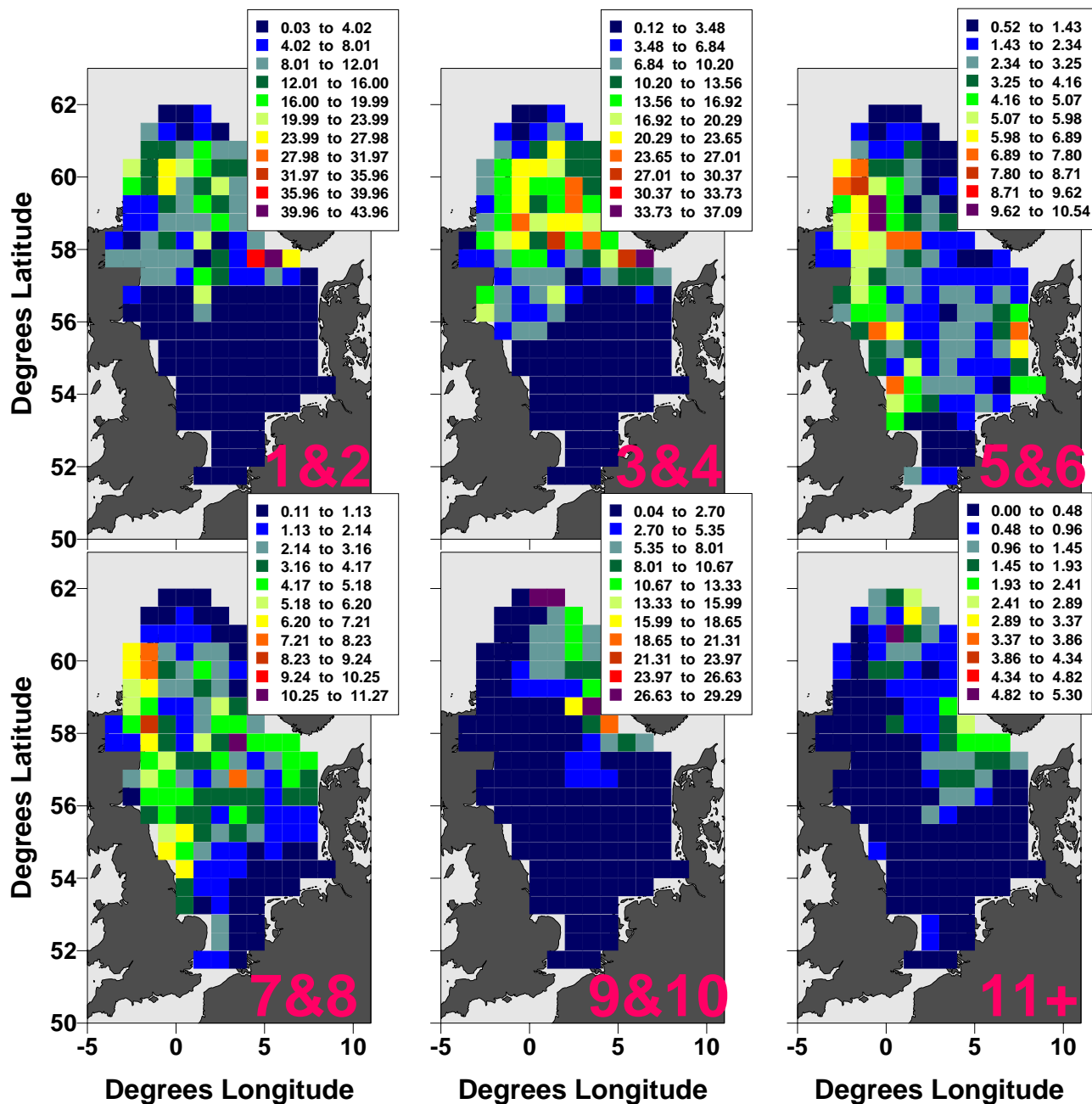


Figure 3.4.2.8: Spatial variation in the daily production density (kg.km⁻².d⁻¹) of demersal fish in six groups of individual Log₂ weight classes based on the geometric mean densities raised to take account of species and length based variation in catchability over 20 GOV trawl samples in each ICES rectangle.

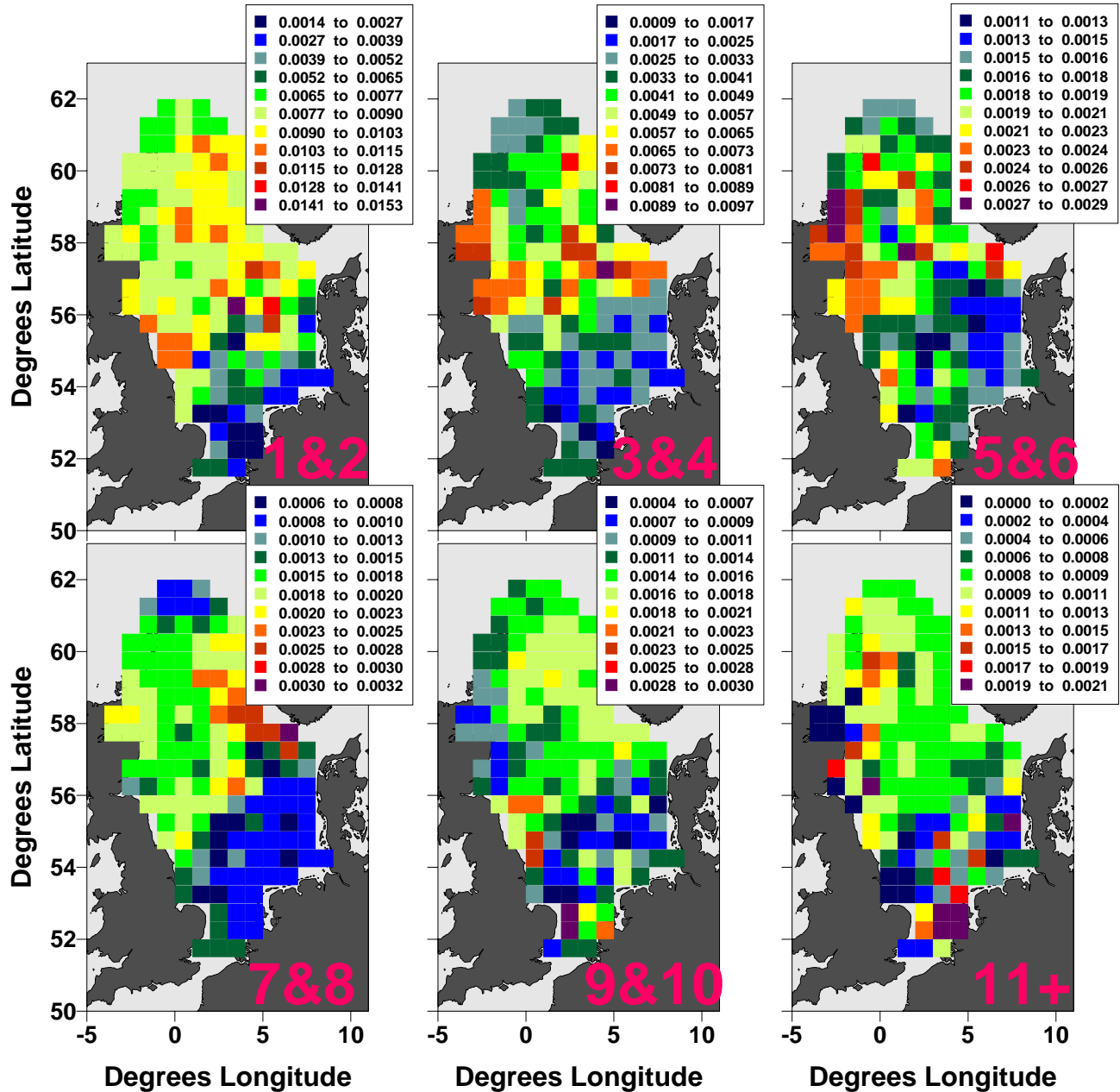


Figure 3.4.2.9: Spatial variation in the daily production:biomass ratio of demersal fish in six groups of individual Log_2 weight classes based on the geometric mean densities raised to take account of species and length based variation in catchability over 20 GOV trawl samples in each ICES rectangle.

Many of the fish over 256g in weight are piscivorous in as much as up to 50% (by weight) , or more, of the prey they consume consists of fish. Generally these prey fish are small, being of between 8 and 31g in weight (Log_2 weight classes 3 and 4) (Hislop *et al* 1997; Greenstreet *et al* 1998). In a DEM situation, variation in the productivity of fish in these weight classes may influence the relationship between fishing disturbance and the diversity of fish in the fished weight classes component of the community. Spatial variation in biomass, absolute growth production, and production per unit biomass of these “prey-fish” weight classes are therefore shown in Figure 3.4.2.10., with these parameters calculated on raw arithmetic mean densities,

raw geometric mean densities, and geometric mean densities raised to take account of species- and size-related variation catchability in the GOV trawl. The spatial patterns were relatively unaffected by taking catchability into account, but the absolute estimates of biomass and production were raised by an order of magnitude. Biomass and production of fish in Log_2 weight classes 3 and 4 was almost entirely restricted to the northern North Sea. P/B ratios were highest along the Scottish east coast and close to the Norwegian deeps.

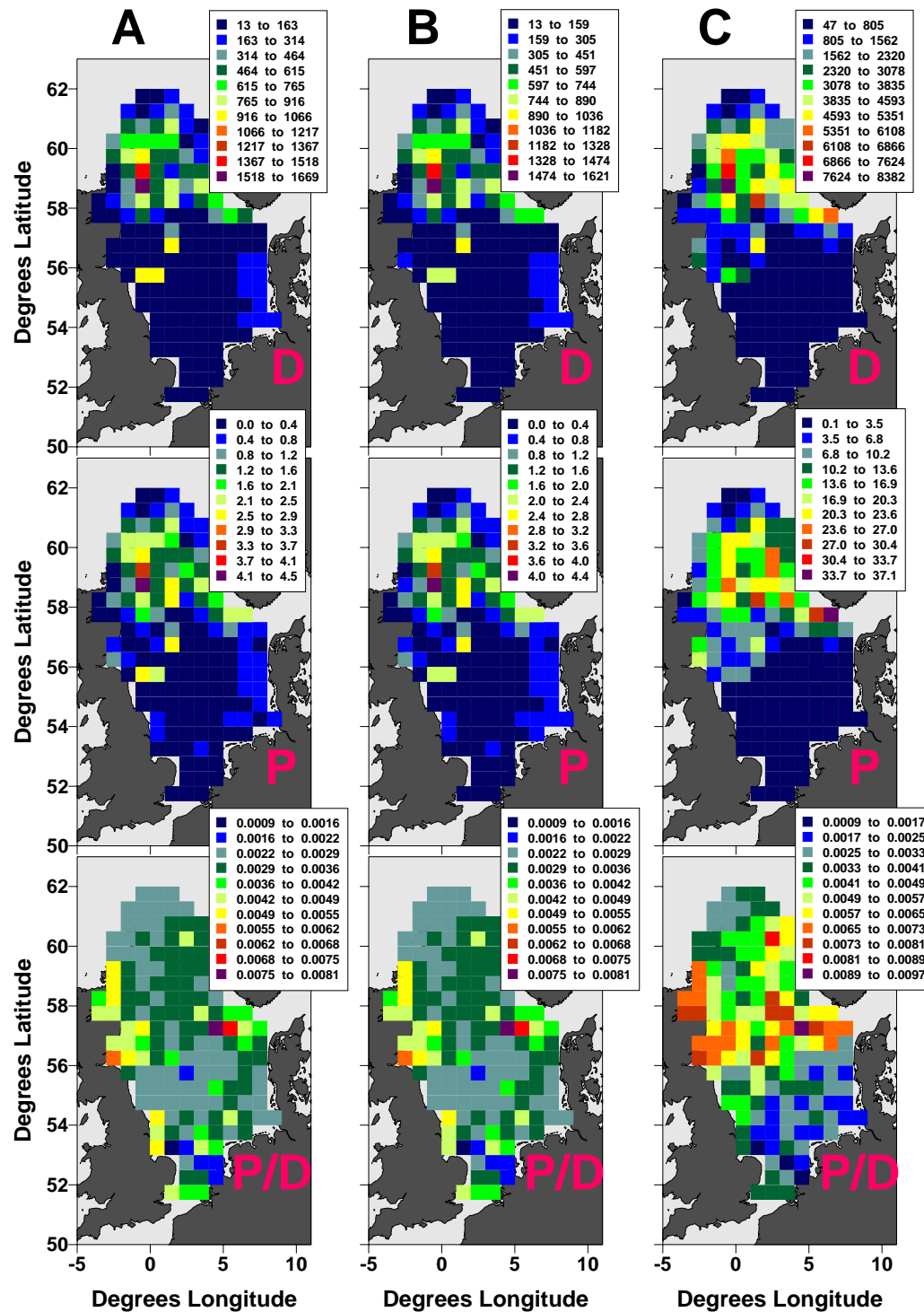


Figure 3.4.2.10: Spatial variation in the biomass density (D, Kg.Km^{-2}), growth production (P, $\text{Kg.Km}^{-2}.\text{d}^{-1}$), and production per unit biomass (P/D) of demersal fish in the “prey-fish” weight range, Log_2 weight classes 3 and 4. A: Based on arithmetic mean densities calculated across all 20 hauls in each rectangle on the raw uncorrected (for catchability) trawl densities. B: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raw uncorrected (for catchability) trawl densities. C: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raised corrected (for catchability) trawl densities.

4. REFERENCES

- Benoit, H. P. & Swain, D. P. Standardizing the southern Gulf of St. Lawrence bottom-trawl survey time series: Adjusting for changes in research vessel, gear and survey protocol. 2003. Canadian Technical Report of Fisheries and Aquatic Sciences.
- Breen, M., Dyson, J., O'Neil, F. G., Jones, E. G. & Haigh, M. (2004) Swimming endurance of haddock (*Melanogrammus aeglefinus* L.) at prolonged and sustained swimming speeds, and its role in their capture by tower fishing gears. *ICES Journal of Marine Science*, **61**, 1071-1079.
- Bublitz, M. Mesh size and shape: Reducing the Capture of Undersized Fish. Solving Bycatch: Considerations for Today and Tomorrow. Alaska Sea Grant Collective Report 96-03. 1995. University of Alaska, Fairbanks.
- Buckland, S. T., Magurran, A. E., Green, R. E. & Fewster, R. M. (2005) Monitoring changes in biodiversity through composite indices. *Philosophical transactions of the Royal Society B*, **360**, 243-254.
- Bustos-Baez, S. & Frid, C. L. J. (2003) Using indicator species to assess the state of macrobenthic communities. *Hydrobiologia*, **496**, 299-309.
- Casey, J. M. & Myers, R. A. (1998) Diel variation in trawl catchability: Is it clear as day and night? *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 2329-2340.
- Chadwick, J. W. & Canton, S. P. (1984) Inadequacy of diversity indices in discerning metal mine drainage effects on a stream invertebrate community. *Water, Air and Soil Pollution*, **22**, 217-223.
- Clarke, K. R. & Warwick, R. M. (1994) Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Natural Environmental Research Council, Plymouth, U.K.
- Clarke, K. R. & Warwick, R. M. (2001) Change in Marine Communities: an Approach to Statistical Analysis and Interpretation. 2nd Edition. PRIMER-E, Plymouth, UK.
- Clarke, K. R. & Warwick, R. M. (1998) A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology*, **35**, 523-531.
- Colwell, R. K., Mao, C. X. & Chank, J. (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, **85**, 2717-2727.
- Colwell, R. K., Rahbek, C. & Gotelli, N. J. (2004) Mid-domain effect: what have we learned? *American Naturalist*, **163**, E1-E23.
- Coull, K. A., Jermyn, A. S., Newton, A. W., Henderson, G. I. & Hall, W. B. (1989) Length/weight relationships for 88 species of fish encountered in the North East Atlantic. *Scottish Fisheries Research Report*, **43**, 1-81.
- Daan, N. (1989) Database report of the stomach sampling project 1981. *ICES Cooperative Research Report*, **164**, 1-144.

Daan, N. (2001) A spatial and temporal diversity index taking into account species rarity, with an application to the North Sea fish community. *ICES Paper*, **ICES CM 2001/T:04**.

Daan, N., Bromley, P. J., Hislop, J. R. G. & Nielsen, N. A. (1990) Ecology of North Sea fish. *Netherlands Journal of Sea Research*, **26**, 343-386.

Duplisea, D. E., Kerr, S. R. & Dickie, L. M. (1997) Demersal fish biomass size spectra on the Scotian Shelf, Canada: species replacement at the shelfwide scale. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 1725-1735.

Engas, A. & Godo, O. R. (1989) The effect of different sweep lengths on the length composition of bottom-sampling trawl catches. *Journal du Conseil International pour l'Exploration de la Mer*, **45**, 263-268.

Frid, C. L. J. (2003) Managing the health of the seafloor. *Frontiers in Ecology and the Environment*, **1**, 429-436.

Fulton, E. A., Smith, A. D. M. & Punt, A. E. (2005) Which ecological indicators can robustly detect effects of fishing. *ICES Journal of Marine Science*, **62**, 540-551.

Gaston, K. J. (1996) Species richness: measure and measurement. *Biodiversity: A Biology of Numbers and Difference* (ed K. J. Gaston), pp. 77-113. Blackwell Science, Oxford, U.K.

Gaston, K. J. (1996) What is biodiversity. *Biodiversity: A Biology of Numbers and Difference* (ed K. J. Gaston), pp. 1-9. Blackwell Science, Oxford, U.K.

Greenstreet, S. P. R., Bryant, A. D., Broekhuizen, N., Hall, S. J. & Heath, M. R. (1997) Seasonal variation in the consumption of food by fish in the North Sea and implications for foodweb dynamics. *ICES Journal of Marine Science*, **54**, 243-266.

Greenstreet, S. P. R. & Hall, S. J. (1996) Fishing and the ground-fish assemblage structure in the north-western North Sea: an analysis of long-term and spatial trends. *Journal of Animal Ecology*, **65**, 577-598.

Greenstreet, S. P. R., McMillan, J. A. & Armstrong, F. (1998) Seasonal variation in the importance of pelagic fish in the diet of piscivorous fish in the Moray Firth, NE Scotland: a response to variation in prey abundance? *ICES Journal of Marine Science*, **55**, 121-133.

Greenstreet, S. P. R. & Rogers, S. I. (2006) Indicators of the health of the fish community of the North Sea: identifying reference levels for an Ecosystem Approach to Management. *ICES Journal of Marine Science*, **63**, 573-593.

Greenstreet, S. P. R., Spence, F. E. & McMillan, J. A. (1999) Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. V. Changes in structure of the North Sea groundfish assemblage between 1925 and 1996. *Fisheries Research*, **40**, 153-183.

Greenstreet, S. P. R., Spence, F. E., Shanks, A. M. & McMillan, J. A. (1999) Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. II.

Trends in fishing effort in the North Sea by U.K. registered vessels landing in Scotland. *Fisheries Research*, **40**, 107-124.

Greenstreet, S. P. R., Tuck, I. D., Grewar, G. N., Armstrong, E., Reid, D. G. & Wright, P. J. (1997) An assessment of the acoustic survey technique, RoxAnn, as a means of mapping seabed habitat. *ICES Journal of Marine Science*, **54**, 939-959.

Haila, Y. & Kouki, J. (1994) The phenomenon of biodiversity in conservation biology. *Annals Zoologica Fennici*, **31**, 5-18.

Hall, S. J. & Greenstreet, S. P. R. (1996) Diversity, abundance and body size: relationships in the North Sea fish fauna. *Nature*, **383**, 133.

Hall, S. J. & Greenstreet, S. P. R. (1998) Taxonomic distinctness and diversity measures: responses in marine fish communities. *Marine Ecology Progress Series*, **166**, 227-229.

Harley, S. J. & Myers, R. A. (2001) Hierarchical Bayesian models of length-specific catchability of research trawl surveys. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 1569-1584.

Harper, J. L. & Hawksworth, D. L. (1994) Biodiversity: measurement and estimation: preface. *Philosophical Transactions of the Royal society of London B*, **345**, 5-12.

Hill, M. O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology*, **54**, 427-432.

Hislop, J., Bromley, P. J., Daan, N., Gislason, H., Heesen, H. J. L., Robb, A. P., Skagen, D., Sparholt, H. & Temming, A. (1997) Database Report of the Stomach Sampling Project, 1991. *ICES Cooperative Research Report*, **219**, 1-421.

Hislop, J. R. G. (1997) Database report of the stomach sampling project 1991. *ICES Cooperative Research Report*, **219**, 1-422.

Hislop, J. R. G., Robb, A. P., Bell, M. A. & Armstrong, D. W. (1991) The diet and food consumption of whiting (*Merlangius merlangus*) in the North Sea. *ICES Journal of Marine Science*, **48**, 139-156.

Hurlbert, S. H. (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, **52**, 577-586.

Huston, M. A. (1994) Biological Diversity: The Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge.

ICES (2001) Report of the ICES Advisory Committee on Ecosystems. *ICES Cooperative Research Report*, **249**.

ICES (2005) Report of the ICES advisory committee on fishery management, advisory committee on the marine environment and advisory committee on ecosystems.

ICES (2006) Report of the International Bottom Trawl Survey Working Group (IBTSWG), 27-31 March 2006, Lysekil, Sweden. *ICES CM 2006, RMC:03, Ref ACFM*, 298pp.

ICES (2006) Report of the Study Group on Multispecies Assessments in the North Sea (SGMSNS). 20-25 February 2006, ICES Headquarters Copenhagen. *ICES CM 2006*, **RMC:02**, 75pp.

ICES (2006) Report of the Working Group on Beam Trawl Surveys (WGBEAM), 16-19 May 2006, Hamburg, Germany. *ICES CM 2006*, **LRC:11**, 104pp.

ICES (2006) Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK), 5-14 September 2006, ICES Headquarters. **ACFM:35**, 1160pp.

ICES (2005) Report on the Assessment of the Demersal Stocks in the North Sea and Skagerrak, 7-16 September 2004, Bergen, Norway. *ICES CM 2005*, **ACFM:07**, 783pp.

ICES (2006) Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK), 6-15 September 2005, ICES Headquarters Copenhagen. *ICES CM 2006*, **ACFM:09**, 958pp.

Jennings, S., Alvsvåg, J., Cotter, A. J., Ehrich, S., Greenstreet, S. P. R., JarreTeichmann, A., Mergardt, N., Rijnsdorp A.D. & Smedstad, O. (1999) Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. III. International fishing effort in the North Sea: an analysis of spatial and temporal trends. *Fisheries Research*, **40**, 125-134.

Jennings, S., Greenstreet, S. P. R., Hill, L., Piet, G. J., Pinnegar, J. & Warr, K. J. (2002) Long-term trends in the trophic structure of the North Sea fish community: evidence from stable isotope analysis, size-spectra and community metrics. *Marine Biology*, **141**, 1085-1097.

Jennings, S., Greenstreet, S. P. R. & Reynolds, J. (1999) Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology*, **68**, 617-627.

Jennings, S., Lancaster, J., Woolmer, A. & Cotter, J. (1999) Distribution, diversity and abundance of epibenthic fauna in the North Sea. *Journal of the Marine Biological Association of the United Kingdom*, **79**, 385-399.

Jennings, S., Pinnegar, J. K., Polunin, N. V. C. & Warr, K. J. (2002) Linking size-based and trophic analyses of benthic community structure. *Marine Ecology Progress Series*, **226**, 77-85.

Jennings, S. & Reynolds, J. D. (2000) Impacts of fishing on diversity: from pattern to process. In *Effects of Fishing on Non-Target Species and Habitats: Biological, Conservation and Socio-economic Issues*. (eds M. J. M.J. Kaiser & B. de Groot), pp. 235-250. Blackwell Science, Oxford, U.K.

Jennings, S., Reynolds, J. D. & Mills, S. C. (1998) Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society of London*, **265**, 1-7.

Jennings, S., Warr, K. J. & Mackinson, S. (2002) Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs. *Marine Ecology Progress Series*, **240**, 11-20.

- Jennings, S., Nicholson, M. D., Dinmore, T. A. & Lancaster, J. E. (2002) Effects of chronic trawling disturbance on the production of infaunal communities. *Marine Ecology Progress Series*, **243**, 251-260.
- Jennings, S., Pinnegar, J. K., Polunin, N. V. C. & Warr, K. J. (2002) Linking size-based and trophic analyses of benthic community structure. *Marine Ecology Progress Series*, **226**, 77-85.
- Jennings, S., Warr, K. J. & Mackinson, S. (2002) Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs. *Marine Ecology Progress Series*, **240**, 11-20.
- Jennings, S., Greenstreet, S. P. R. & Reynolds, J. (1999) Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology*, **68**, 617-627.
- Jennings, S., Greenstreet, S. P. R., Hill, L., Piet, G. J., Pinnegar, J. K. & Warr, K. J. (2002) Long-term trends in the trophic structure of the North Sea fish community: evidence from stable isotope analysis, size spectra and community metrics. *Marine Biology*, **141**, 1085-1097.
- Joint, I. & Pomroy, A. (1993) Phytoplankton biomass and production in the southern North Sea. *Marine Ecology Progress Series*, **99**, 169-182.
- King, M. (1995) Fisheries Biology, Assessment and Management. Blackwell Science, Oxford, UK.
- Korsbrekke, K. & Nakken, O. (1999) Length and species-dependent diurnal variation of catch rates in the Norwegian Barents Sea bottom-trawl surveys. *ICES Journal of Marine Science*, **56**, 284-291.
- MacArthur, R. H. & Wilson, E. O. (1967) The Theory of Island Biogeography. Princeton University Press, Princeton and Oxford.
- Magurran, A. E. (1988) Ecological Diversity and Its Measurement. Chapman and Hall, London.
- Main, J. & Sangster, G. I. (1981) A study of the fish capture process in a bottom trawl by direct observations from a towed underwater vehicle. *Scottish fisheries research report, 1981*. Department of Agriculture and Fisheries for Scotland, Aberdeen, UK.
- Main, J. & Sangster, G. I. (1981) A study of the sand clouds produced by trawl boards and their possible effect on fish capture. *Scottish fisheries research report, 1981*. Department of Agriculture and Fisheries for Scotland, Aberdeen, UK.
- Mallet, J. (1996) The genetics of biological diversity: from varieties to species. *Biodiversity: A Biology of Numbers and Difference* (ed K. J. Gaston), pp. 13-53. Blackwell Science, Oxford, U.K.
- Michalsen, K., Godoe, O. R. & Fernoe, A. (1996) Diel variation in the catchability of gadoids and its influence on the reliability of abundance indices. *ICES Journal of Marine Science*, **53**, 389-395.

- Piet, G. J. & Jennings, S. (2005) Response of potential fish community indicators to fishing. *ICES Journal of Marine Science*, **62**, 214-225.
- Ramm, D. C. & Xiao, Y. (1995) Herding of groundfish and effective path-width of trawls. *Fisheries Research*, **24**, 243-259.
- Reid, P. C., Lancelot, C., Gieskes, W. W. C., Hagmeier, E. & Weichart, G. (1990) Phytoplankton of the North Sea and its dynamics: a review. *Netherlands Journal of Sea Research*, **26**, 295-331.
- Rice J. & Gislason, H. (1996) Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. *ICES Journal of Marine Science*, **53**, 1214-1225.
- Robinson, J. V. & Sandgren, C. D. (1984) An experimental evaluation of diversity indices as environmental discriminators. *Hydrobiologia*, **108**, 187-196.
- Rogers, S. I., Clarke, K. R. & Reynolds, J. D. (1999) The taxonomic distinctness of coastal bottom-dwelling fish communities of the Northeast Atlantic. *Journal of Animal Ecology*, **68**, 769-782.
- Rogers, S. I. & Ellis, J. R. (2000) Changes in the demersal fish assemblages of British coastal waters during the 20th century. *ICES Journal of Marine Science*, **57**, 866-881.
- Rogers, S. I., Maxwell, D., Rijnsdorp, A. D., Damm, U. & Vanhee, W. (1999) Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. IV. Can comparisons of species diversity be used to assess human impacts on demersal fish faunas? *Fisheries Research*, **40**, 135-152.
- Rogers, S. I., Rijnsdorp, A. D., Damm, U. & Vanhee, W. (1998) Demersal fish populations in the coastal waters of the UK and continental NW Europe from beam trawl survey data collected from 1990-1995. *Journal of Sea Research*, **39**, 79-102.
- Rose, C. S. & Nunnallee, E. P. (1998) A study of changes in groundfish trawl catching efficiency due to differences in operating width, and measures to reduce width variation. *Fisheries Research*, **36**.
- Rosenzweig, M. L. (1995) Species Diversity in Space and Time. Cambridge University Press, Cambridge.
- Sangster, G. I. & Breen, M. (1998) Gear performance and catch comparison trials between a single trawl and a twin rigged gear. *Fisheries Research*, **36**, 15-26.
- Soetaert, K. & Heip, C. (1990) Sample-size dependence of diversity indices and the determination of sufficient sample size in a high-diversity deep-sea environment. *Marine Ecology Progress Series*, **59**, 305-307.
- Sokal, R. R. & Rohlf, F.J. (1981) Biometry. Freeman, New York.

- Somerton, D. (2004) Do Pacific cod (*Gadus macrocephalus*) and walleye pollock (*Theragra chalcogramma*) lack a herding response to the doors, bridles, and mudclouds of survey trawls? *ICES Journal of Marine Science*, **61**, 1186-1189.
- Somerton, D. A. & Weinberg, K. L. (2001) The affect of speed through the water on footrope contact of a survey trawl. *Fisheries Research* , **53**, 17-24.
- Southwood, T. R. E. (1978) Ecological Methods: with Particular Reference to the Study of Insect Populations. Chapman and Hall, London.
- Sparholt, H. (1990) An estimate of the total biomass of fish in the North Sea. *Journal du Conseil International pour l'Exploration de la Mer*, **46**, 200-210.
- Suuronen, P. & Millar, R. B. (1992) Size selectivity of diamond and square mesh codends in pelagic herring trawls: Only small herring will notice the difference. *Canadian Journal of Fisheries and Aquatic Sciences* , **49**, 2104-2117.
- Temming, A., Gotz, S., Mergardt, N. & Ehrich, S. (2004) Predation of whiting and haddock on sandeel: aggregative response, competition and diel periodicity. *Journal of Fish Biology*, **64**, 1351-1372.
- Von Szalay, P. G. & Somerton, D. A. (2005) The effect of net spread on the capture efficiency of a demersal survey trawl used in the eastern Bering Sea. *Fisheries Research* , **74**, 86-95.
- Walsh, S. J. (1992) Size-dependent selection at the footgear of a groundfish survey trawl. *North American Journal of Fisheries Management* , **12**, 625-633.
- Wardle, C. S. (1983) Fish reactions to towed fishing gears. (eds A. G. MacDonald & I. G. Priede).
- Wardle, C. S. (1989) Understanding fish behaviour can lead to more selective fishing gears. *The Proceedings of the World Symposium on Fishing Gear and Fishing Vessel Design*. (eds S. G. For & J. Huntington), Marine Institute, St. Johns, Newfoundland, Canada.
- Washington, H. G. (1984) Diversity, biotic and similarity indices: a review with special relevance to aquatic ecosystems. *Water Research*, **18**, 653-694.
- Weinberg, K. L., Somerton, D. A. & Munro, P. T. (2002) The effect of trawl speed on the footrope capture efficiency of a survey trawl. *Fisheries Research* , **58**, 303-313.
- Wilsey, B. J., Chalcraft, D. R., Bowles, C. M. & Willig, M. R. (2005) Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. *Ecology*, **86**, 1178-1184.
- Winger, P. D., He, P. & Walsh, S. J. (1999) Swimming endurance of American plaice (*Hippoglossoides platessoides*) and its role in fish capture. *ICES Journal of Marine Science* , **56**, 252-265.
- Yang, J. (1982) The dominant fish fauna in the North Sea and its determination. *Journal of Fish Biology*, **20**, 635-643.

Yang, J. (1982) An estimate of the fish biomass in the North Sea. *Journal du Conseil International pour l'Exploration de la Mer*, **40**, 161-172.

5. APPENDIX 1

Table 5.1: Table showing all the fish species caught in both the 3rd Quarter IBTS 1998 to 2004 and the 8m Beam Trawl survey from the same period. The table shows whether a species was considered demersal or pelagic. Only demersal species were included in this analysis. The table also shows how the catchability of each of the 95 demersal species caught in the GOV was derived, whether it was derived using the VPA assessment (Assessed), using the catch ratio information from the mini statistical rectangles (Catch ratio), using the Odds ratio (Odds ratio), the average q at length of either the round-fish, flatfish, skates & rays or dogfish groups (Average) or whether it was derived some other way (Other). The relationship used in order to calculate the catchability at length for each of the 95 demersal fish species caught in the 3rd quarter IBTS, 1998 to 2004 is also shown.

Species code	Scientific Name	Common Name	Demersal/Pelagic	Catchability estimation method	Catchability at length	
					Size (cm)	Relationship (Y=)
ANG	<i>Lophius piscatorius</i>	Angler	Demersal	Catch ratio	≤25 26-44 ≥45	0.114175 $1.18892 - 0.06886 * L + 0.00103L^2$ 0.18552
BAN	<i>Lophius budegassa</i>	Black bellied angler	Demersal	Average		Roundfish average
BFI	<i>Capros aper</i>	Boarfish	Demersal	Average		Roundfish average
BIB	<i>Trisopterus luscus</i>	Bib	Demersal	Other	≤11 ≥12	0.00662 0.19186
BLI	<i>Molva dypterygia</i>	Blue ling	Demersal	Average		Roundfish average
BLM	<i>Helicolenus dactylopterus</i>	Bluemouth	Demersal	Average		Roundfish average
BMD	<i>Galeus melastomus</i>	Black mouthed dogfish	Demersal	Average		Dogfish average
BRI	<i>Scophthalmus rhombus</i>	Brill	Demersal	Odds ratio	≤25 26-39 ≥40	0.05721 $0.064507 - 0.04050 * L + 0.00067L^2$ 0.12605
BRO	<i>Myoxocephalus scorpius</i>	Bull rout	Demersal	Catch ratio	≤20 21-24 ≥25	0.0119327 $0.08036 * L - 1.48785$ 0.521122
BSB	<i>Spondylusoma cantharus</i>	Black sea bream	Demersal	Average		Roundfish average
BUT	<i>Pholis gunnellus</i>	Butterfish	Demersal	Average		Roundfish average
CAT	<i>Anarhichas lupus</i>	Catfish	Demersal	Odds ratio	all	0.137233
CDA	<i>Limanda limanda</i>	Common dab	Demersal	Catch ratio	≤6 6-29 ≥30	0.046903 $-0.78944 + 0.17388 * L - 0.00482L^2$ 0.08671
CEE	<i>Conger conger</i>	Conger eel	Demersal	Average		Roundfish average

CGO	<i>Crystallogobius linearis</i>	Crystal goby	Demersal	Average		Roundfish average
CHI	<i>Chimaera monstrosa</i>	Rabbit ratfish	Demersal	Average		Roundfish average
COD	<i>Gadus morhua</i>	Cod	Demersal	Assessed	≤26 26-96 ≥97	0.15963 $0.20935 - 0.00434 * L + 0.00009L^2$ 0.66822
COG	<i>Pomatoschistus microps</i>	Common goby	Demersal	Average		Roundfish average
CRA	<i>Leucoraja naevus</i>	Cuckoo ray	Demersal	Odds ratio	all	0.06147
DRA	<i>Callionymus lyra</i>	Dragonet	Demersal	Catch ratio	all	0.13650
DSO	<i>Solea vulgaris</i>	Dover sole	Demersal	Catch ratio	≤20 21-23 ≥25	0.04253 $0.00105 * L + 0.02162$ 0.03657
EEE	<i>Lycodes esmarkii</i>	Esmark's eelpout	Demersal	Average		Roundfish average
EEL	<i>Anguilla anguilla</i>	European eel	Demersal	Average		Roundfish average
FIR	<i>Ciliata mustela</i>	Five-bearded rockling	Demersal	Average		Roundfish average
FLO	<i>Platichthys flesus</i>	Flounder	Demersal	Catch ratio	≤20 21-32 ≥33	0.78097 $-0.05693 * L + 1.91951$ 0.05298
FOR	<i>Enchelyopus cimbrius</i>	Four-bearded rockling	Demersal	Catch ratio	≤10 11-24 ≥25	0.03298 $-0.34995 + 0.05352 * L - 0.00152L^2$ 0.03647
GFO	<i>Phycis blennoides</i>	Greater forkbeard	Demersal	Average		Roundfish average
GGU	<i>Eutrigla gurnardus</i>	Grey gurnard	Demersal	Catch ratio	≤5 6-34 ≥35	0.02377 $-0.74300 + 0.14729 * L - 0.00340L^2$ 0.18799
GOM	<i>Liza aurata</i>	Golden grey mullet	Demersal	Average		Roundfish average
GPI	<i>Syngnathus acus</i>	Great pipefish	Demersal	Average		Roundfish average
GRM	<i>Mugil cephalus</i>	Flathead (Grey) mullet	Demersal	Average		Roundfish average
GWE	<i>Trachinus draco</i>	Greater weever	Demersal	Average		Roundfish average
HAD	<i>Melanogrammus aeglefinus</i>	Haddock	Demersal	Assessed	≤11 12-45 ≥46	0.0116121 $-0.3704530 + 0.04227 * L - 0.00068L^2$ 0.123268
HAG	<i>Myxine glutinosa</i>	Hagfish	Demersal	Odds ratio	≤20 21-39	0.06196 $0.26274 - 0.01577 * L + 0.00028L^2$

					≥40	0.067205
HAK	<i>Merluccius merluccius</i>	Hake	Demersal	Catch ratio	all	0.0909
HAL	<i>Hippoglossus hippoglossus</i>	Halibut	Demersal	Average		Flatfish average
HOO	<i>Agonus cataphractus</i>	Hooknose	Demersal	Catch ratio	all	0.0445
ISC	<i>Arnoglossus imperialis</i>	Imperial scaldfish	Demersal	Average		Flatfish average
LIN	<i>Molva molva</i>	Ling	Demersal	Odds ratio	all	0.104976
LNS	<i>Raja oxyrhynchus</i>	Long nosed skate	Demersal	Average		Skate average
LRD	<i>Hippoglossoides platessoides</i>	Long rough dab	Demersal	Catch ratio	≤5 6-29 ≥30	0.11348 -0.15522 + 0.06276 * L - 0.00180L ² 0.104245
LSD	<i>Scyliorhinus canicula</i>	Lesser spotted dogfish	Demersal	Catch ratio	all	0.225
LSO	<i>Microstomus kitt</i>	Lemon sole	Demersal	Catch ratio	≤10 11-32 ≥33	0.14605 -0.10831 + 0.04620 * L - 0.00119L ² 0.11569
LUM	<i>Cyclopterus lumpus</i>	Lumpsucker	Demersal	Odds ratio	all	0.122018
LYT	<i>Pollachius pollachius</i>	Pollack	Demersal	Average		Roundfish average
MEG	<i>Lepidorhombus whiffiagonis</i>	Megrim	Demersal	Catch ratio	all	0.0638
MSC	<i>Triglops murrayi</i>	Moustache sculpin	Demersal	Average		Roundfish average
MSS	<i>Liparis montagui</i>	Montagu's sea snail	Demersal	Average		Roundfish average
NHA	<i>Sebastes viviparus</i>	Norway haddock	Demersal	Average		Roundfish average
NPI	<i>Syngnathus rostellatus</i>	Nilsson's pipefish	Demersal	Average		Roundfish average
NPO	<i>Trisopterus esmarki</i>	Norway pout	Demersal	Assessed	≤11 ≥12	0.066204 0.191855
NTO	<i>Phrynorhombus norvegicus</i>	Norwegian topknot	Demersal	Odds ratio	all	0.05862
PBU	<i>Stichaeidae</i>	Pricklebacks unidentified	Demersal	Average		Roundfish average
PCO	<i>Trisopterus minutus</i>	Poor cod	Demersal	Other	≤11 ≥12	0.066204 0.191855
PEF	<i>Echiodon drummondi</i>	Pearlfish	Demersal	Average		Roundfish average
PLA	<i>Pleuronectes platessa</i>	Plaice	Demersal	Assessed	≤17 18-21 22-41 ≥42	0.013702 0.087079 -0.00344 * L + 0.16280 0.01825
RDR	<i>Callionymus reticulatus</i>	Reticulated dragonet	Demersal	Odds ratio	all	0.033498

RED	<i>Sebastes marinus</i>	Redfish (marinus)	Demersal	Average		Roundfish average
RGU	<i>Aspitrigla cuculus</i>	Red gurnard	Demersal	Average		Roundfish average
RLA	<i>Lampetra fluviatilis</i>	European river lamprey	Demersal	Average		Roundfish average
RMM	<i>Mullus barbatus</i>	Red mullet	Demersal	Average		Roundfish average
RMU	<i>Mullus surmuletus</i>	Striped red mullet	Demersal	Catch ratio	≤6 7-24 ≥25	0.302699 $-0.15257 + 0.09263 * L - 0.002738L^2$ 0.390786
SAI	<i>Pollachius virens</i>	Saithe	Demersal	Other		Average q at length of haddock, whiting and cod
SAR	<i>Leucoraja circularis</i>	Sandy ray	Demersal	Average		Skate average
SCA	<i>Anarhichas minor</i>	Spotted catfish	Demersal	Average		Roundfish average
SCF	<i>Arnoglossus laterna</i>	Scaldfish	Demersal	Catch ratio	all	0.0081
SDR	<i>Callionymus maculatus</i>	Spotted dragonet	Demersal	Odds ratio	≤5 6-14 ≥15	0.05129 $0.008886 * L + 0.002980$ 0.139888
SGO	<i>Pomatoschistus minutus</i>	Sand goby	Demersal	Odds ratio	all	0.133303
SHO	<i>Mustelus mustelus</i>	Smooth hound	Demersal	Average		Dogfish average
SKA	<i>Dipturus batis</i>	Skate	Demersal	Average		Skate average
SLA	<i>Petromyzon marinus</i>	Sea Lamprey	Demersal	Average		Roundfish average
SNB	<i>Lumpenus lampretaeformis</i>	Snake blenny	Demersal	Odds ratio	all	0.188895
SOL	<i>Buglossidium luteum</i>	Solenette	Demersal	Catch ratio	all	0.0223
SPB	<i>Leptoclinus maculatus</i>	Spotted snake blenny	Demersal	Average		Roundfish average
SPI	<i>Entelurus aequoraeus</i>	Snake pipefish	Demersal	Average		Roundfish average
SPU	<i>Squalus acanthias</i>	Spurdog	Demersal	Average		Dogfish average
SPY	<i>Raja montagui</i>	Spotted ray	Demersal	Odds ratio	all	0.1526
SRA	<i>Raja fullonica</i>	Shagreen ray	Demersal	Average		Skate Average
SSC	<i>Taurulus bubalis</i>	Sea scorpion	Demersal	Average		Roundfish average
SSH	<i>Mustelus asterias</i>	Starry smooth hound	Demersal	Average		Dogfish average
SSN	<i>Liparis liparis</i>	Sea snail	Demersal	Odds ratio	all	0.159476
STY	<i>Raja radiata</i>	Starry ray	Demersal	Catch ratio	all	0.0564
TBR	<i>Gaidropsarus vulgaris</i>	Three-bearded rockling	Demersal	Average		Roundfish average
TOP	<i>Galeorhinus galeus</i>	Tope	Demersal	Average		Roundfish average
TOR	<i>Brosme brosme</i>	Torsk	Demersal	Average		Roundfish average
TPK	<i>Zeugopterus punctatus</i>	Topknot	Demersal	Average		Flatfish average

TRA	<i>Raja clavata</i>	Thornback ray	Demersal	Average		Skate average
TSO	<i>Microchirus variegatus</i>	Thickback sole	Demersal	Odds ratio	all	0.049504
TUB	<i>Trigla lucerna</i>	Tub gurnard	Demersal	Catch ratio	≤20 21-34 ≥35	0.207872 -0.003724 * L + 0.26021 0.1107
TUR	<i>Scophthalmus maximus</i>	Turbot	Demersal	Odds ratio	≤20 21-44 ≥43	0.04691 0.00303 * L - 0.010431 0.119081
VBE	<i>Etmopterus spinax</i>	Velvet belly	Demersal	Average		Roundfish average
VEE	<i>Lycodes vahlII</i>	Vahl's eelpout	Demersal	Average		Roundfish average
WEE	<i>Echiichthys vipera</i>	Lesser weever	Demersal	Catch ratio	≤5 6-9 ≥10	0.08993 0.05261 * L - 0.17315 0.35302
WHI	<i>Merlangius merlangus</i>	Whiting	Demersal	Assessed	≤21 20-37 ≥38	0.616878 -0.028159 * L + 1.208229 0.138165
WIT	<i>Glyptocephalus cynoglossus</i>	Witch	Demersal	Catch ratio	≤20 21-38 ≥39	0.110196 0.471011 - 0.02627 * L + 0.0003948L ² 0.051816
APO	<i>Leptagonus decagonus</i>	Atlantic poacher	Demersal	n/a	n/a	Not caught in GOV
BGO	<i>Gobius niger</i>	Black goby	Demersal	n/a	n/a	Not caught in GOV
BRA	<i>Raja brachyura</i>	Blond ray	Demersal	n/a	n/a	Not caught in GOV
CSB	<i>Sparus pagrus</i>	Couch's sea bream	Demersal	n/a	n/a	Not caught in GOV
FGO	<i>Lesueurigobius friesii</i>	Fries's goby	Demersal	n/a	n/a	Not caught in GOV
LBA	<i>Notolepis rissoi</i>	Lesser barracudina	Demersal	n/a	n/a	Not caught in GOV
NRO	<i>Ciliata septentrionalis</i>	Northern rockling	Demersal	n/a	n/a	Not caught in GOV
PGO	<i>Pomatoschistus pictus</i>	Painted goby	Demersal	n/a	n/a	Not caught in GOV
PLO	<i>Pomatoschistus lozanoi</i>	Lozano's goby	Demersal	n/a	n/a	Not caught in GOV
YBL	<i>Chirolophis ascanii</i>	Yarrell's blenny	Demersal	n/a	n/a	Not caught in GOV
ANC	<i>Engraulis encrasicolus</i>	Anchovy	Pelagic	n/a	n/a	n/a
ARU	<i>Argentinidae</i>	Argentines	Pelagic	n/a	n/a	n/a
ASH	<i>Alosa alosa</i>	Allis shad	Pelagic	n/a	n/a	n/a
BAS	<i>Dicentrarchus labrax</i>	Bass	Pelagic	n/a	n/a	n/a
BWH	<i>Micromesistius poutassou</i>	Blue whiting	Pelagic	n/a	n/a	n/a

CBS	<i>Hyperoplus immaculatus</i>	Corbin's sandeel	Pelagic	n/a	n/a	n/a
CSA	<i>Ammodytes tobianus</i>	Common sandeel	Pelagic	n/a	n/a	n/a
FST	<i>Spinachia spinachia</i>	Fifteen spined stickleback	Pelagic	n/a	n/a	n/a
GAR	<i>Argentina silus</i>	Greater argentine	Pelagic	n/a	n/a	n/a
GRF	<i>Belone belone</i>	Garfish	Pelagic	n/a	n/a	n/a
GSA	<i>Hyperoplus lanceolatus</i>	Greater sandeel	Pelagic	n/a	n/a	n/a
HER	<i>Clupea harengus</i>	Herring	Pelagic	n/a	n/a	n/a
HMA	<i>Trachurus trachurus</i>	Horse mackerel	Pelagic	n/a	n/a	n/a
JDO	<i>Zeus faber</i>	John dory	Pelagic	n/a	n/a	n/a
LAR	<i>Argentina sphyraena</i>	Lesser argentine	Pelagic	n/a	n/a	n/a
MAC	<i>Scomber scombrus</i>	Mackerel	Pelagic	n/a	n/a	n/a
PEA	<i>Maurollicus muelleri</i>	Pearlside	Pelagic	n/a	n/a	n/a
PIL	<i>Sardina pilchardus</i>	Pilchard	Pelagic	n/a	n/a	n/a
RSA	<i>Ammodytes marinus</i>	Raitt's sandeel	Pelagic	n/a	n/a	n/a
SAL	<i>Salmo salar</i>	Salmon	Pelagic	n/a	n/a	n/a
SJD	<i>Zenopsis conchifera</i>	Silvery John Dory	Pelagic	n/a	n/a	n/a
SPO	<i>Gadiculus argenteus</i>	Silvery pout	Pelagic	n/a	n/a	n/a
SPR	<i>Sprattus sprattus</i>	Sprat	Pelagic	n/a	n/a	n/a
SSA	<i>Gymnammodytes semisquamatus</i>	Smooth sandeel	Pelagic	n/a	n/a	n/a
SUN	<i>Ammodytes sp.</i>	Sandeel unidentified	Pelagic	n/a	n/a	n/a
TRO	<i>Salmo trutta</i>	Trout	Pelagic	n/a	n/a	n/a
TST	<i>Gasterosteus aculeatus</i>	Three-spined stickleback	Pelagic	n/a	n/a	n/a
TWS	<i>Alosa fallax</i>	Twaite shad	Pelagic	n/a	n/a	n/a

6. APPENDIX 2

Table 6.1: von Bertalanffy growth curve and weight at length relationship parameters for each of the species sampled by either the GOV or the 8BT survey trawl gears in the IBTS and DBTS respectively. Source¹ and Source² indicate the the source of these parameter values respectively. For each species, the scientific name, British common name and three letter codes by which they are on occasion referred to are provided.

Scientific name	Common name	Code	L _{max}	L _∞	k	Source ¹	a	b	Source ²
<i>Agonus cataphractus</i>	Hooknose	HOO	21	17.4	0.419	Jennings <i>et al</i> 1998; 1999	0.02300	2.7478	FRS
<i>Amblyraja radiata</i>	Starry ray	STY	100	66.0	0.233	Jennings <i>et al</i> 1998; 1999	0.04938	2.8454	FRS
<i>Anarhichas lupus</i>	Catfish	CAT	150	117.4	0.047	Jennings <i>et al</i> 1998; 1999	0.00873	3.0323	FRS
<i>Anarhichas minor</i>	Spotted catfish	SCA	180	181.0	0.061	FishBase	0.00170	3.3990	FishBase
<i>Anguilla anguilla</i>	European eel	EEL	133	83.2	0.076	FishBase	0.00140	3.0600	RIVO
<i>Aphia minuta</i>	Transparent goby	TGO	8	5.4	2.230	FishBase	0.01000	2.9400	RIVO
<i>Argyrosomus regius</i>	Meagre	MEA	230	210.0	0.089	FishBase	0.02000	2.7700	RIVO
<i>Arnoglossus imperialis</i>	Imperial scaldfish	ISC	25	20.3	0.349	Modelled	0.00450	3.1700	FishBase
<i>Arnoglossus laterna</i>	Scaldfish	SCF	25	15.8	0.840	FishBase	0.00240	3.3890	FRS
<i>Aspitrigla cuculus</i>	Red gurnard	RGU	50	41.7	0.460	FishBase	0.00460	3.2171	FRS
<i>Brosme brosme</i>	Torsk	TOR	120	88.6	0.080	Jennings <i>et al</i> 1998; 1999	0.00949	3.0538	FRS
<i>Buglossidium luteum</i>	Solenette	SOL	15	11.7	0.540	FishBase	0.01520	2.9066	FRS
<i>Callionymus lyra</i>	Dragonet	DRA	30	22.2	0.471	Jennings <i>et al</i> 1998; 1999	0.00220	2.5907	FRS
<i>Callionymus maculatus</i>	Spotted dragonet	SDR	16	13.2	0.462	Modelled	0.01620	2.5781	FRS
<i>Callionymus reticulatus</i>	Reticulated dragonet	RDR	11	9.3	0.585	Modelled	0.01620	2.5781	FRS
<i>Capros aper</i>	Boarfish	BFI	30	24.1	0.311	Modelled	0.01440	3.0578	FRS
<i>Chelidonichthys lastoviza</i>	Streaked gurnard	SGU	40	39.5	0.580	FishBase	0.00490	3.0390	FishBase
<i>Chelon labrosus</i>	Thick-lipped mullet	TLM	75	61.8	0.121	FishBase	0.01080	2.9480	FishBase
<i>Chimaera monstrosa</i>	Rabbit ratfish	CHI	150	112.5	0.113	Modelled	0.00039	3.3664	FRS
<i>Chirolophis ascanii</i>	Yarrell's blenny	YBL	25	20.3	0.349	Modelled	0.04170	2.2532	FRS
<i>Ciliata mustela</i>	Five-bearded rockling	FIR	25	20.3	0.349	Modelled	0.00270	3.1921	FRS
<i>Ciliata septentrionalis</i>	Northern rockling	NRO	20	16.4	0.401	Modelled	0.01280	3.0864	FRS
<i>Conger conger</i>	Conger eel	CEE	300	265.0	0.063	FishBase	0.00018	3.5622	FRS
<i>Crystallogobius linearis</i>	Crystal goby	CGO	5	4.4	0.962	Modelled	0.01000	2.9400	RIVO
<i>Cyclopterus lumpus</i>	Lumpsucker	LUM	60	55.0	0.120	FishBase	0.05780	2.9498	FRS
<i>Dasyatis pastinaca</i>	Sting ray	STR	60	46.9	0.201	Modelled	0.00113	3.9924	FRS

<i>Diplecogaster bimaculata</i>	Two-spotted clingfish	TCL	6	5.2	0.857	Modelled	0.01960	2.9055	FRS
<i>Dipturus batis</i>	Skate	SKA	285	253.7	0.057	Jennings <i>et al</i> 1998; 1999	0.00678	2.9772	FRS
<i>Dipturus oxyrhynchus</i>	Longnose skate	LNS	150	112.5	0.113	Modelled	0.01460	2.9795	FishBase
<i>Echiichthys vipera</i>	Lesser weever	WEE	15	12.4	0.481	Modelled	0.00180	3.4099	FRS
<i>Echiodon drummondii</i>	Pearlfish	PEF	30	24.1	0.311	Modelled	0.00906	2.3352	FRS
<i>Enchelyopus cimbrius</i>	Four-bearded rockling	FOR	41	36.0	0.196	Jennings <i>et al</i> 1998; 1999	0.00270	3.1921	FRS
<i>Entelurus aequoraeus</i>	Snake pipefish	SPI	60	46.9	0.201	Modelled	0.00020	3.0000	FishBase
<i>Etmopterus spinax</i>	Velvet belly	VBE	60	46.9	0.201	Modelled	0.03042	2.4545	FRS
<i>Eutrigla gurnardus</i>	Grey gurnard	GGU	60	46.2	0.156	Jennings <i>et al</i> 1998; 1999	0.00819	3.0150	FRS
<i>Gadus morhua</i>	Cod	COD	200	123.1	0.230	Jennings <i>et al</i> 1998; 1999	0.00506	3.1921	FRS
<i>Gaidropsarus vulgaris</i>	Three-bearded rockling	TBR	60	47.5	0.191	Jennings <i>et al</i> 1998; 1999	0.01010	2.9807	FRS
<i>Galeorhinus galeus</i>	Tope	TOP	195	163.0	0.168	FishBase	0.00036	3.6291	FRS
<i>Galeus melastomus</i>	Black mouthed dogfish	BMD	90	69.0	0.155	Modelled	0.00276	3.0293	FRS
<i>Gasterosteus aculeatus</i>	Three spined stickleback	TST	11	6.9	1.790	FishBase	0.00940	3.0000	FishBase
<i>Glyptocephalus cynoglossus</i>	Witch	WIT	60	45.5	0.165	Jennings <i>et al</i> 1998; 1999	0.00229	3.2910	FRS
<i>Gobius niger</i>	Black goby	BGO	18	16.9	0.190	FishBase	0.01600	2.8900	FRS
<i>Helicolenus dactylopterus</i>	Bluemouth	BLM	47	37.2	0.095	FishBase	0.01970	2.9542	FRS
<i>Hippoglossoides platessoides</i>	Long rough dab	LRD	82	24.6	0.336	Jennings <i>et al</i> 1998; 1999	0.00440	3.2039	FRS
<i>Hippoglossus hippoglossus</i>	Halibut	HAL	240	204.0	0.100	Jennings <i>et al</i> 1998; 1999	0.00562	3.1655	FRS
<i>Icelus bicornis</i>	Twohorn sculpin	TSC	16	13.0	0.468	Modelled	0.01440	2.9279	FRS
<i>Labrus bergylta</i>	Ballan wrasse	BWR	66	45.0	0.104	FishBase	0.01622	3.0248	FRS
<i>Lampetra fluviatilis</i>	European river lamprey	RLA	50	39.4	0.225	Modelled	0.00190	3.0000	FRS
<i>Lepidorhombus whiffiagonis</i>	Megrim	MEG	60	51.8	0.073	Jennings <i>et al</i> 1998; 1999	0.01136	2.8433	FRS
<i>Leptagonus decagonus</i>	Atlantic poacher	APO	21	17.2	0.389	Modelled	0.00350	3.0000	FishBase
<i>Leptoclinus maculatus</i>	Spotted snake blenny	SPB	20	16.4	0.401	Modelled	0.00910	2.3352	FRS
<i>Lesueurigobius friesii</i>	Fries's goby	FGO	13	10.9	0.527	Modelled	0.02120	2.6264	FRS
<i>Lesueurigobius suerii</i>	Le sueur's goby	LSG	5	4.4	0.962	Modelled	0.01000	2.9400	RIVO
<i>Leucoraja circularis</i>	Sandy ray	SAR	120	90.9	0.130	Modelled	0.00312	3.1467	FRS
<i>Leucoraja fullonica</i>	Shagreen ray	SRA	120	90.9	0.130	Modelled	0.00165	3.2576	FRS
<i>Leucoraja naevus</i>	Cuckoo ray	CRA	71	91.6	0.109	Jennings <i>et al</i> 1998;	0.10602	2.2820	FRS

						1999			
<i>Limanda limanda</i>	Common dab	CDA	40	26.7	0.261	Jennings <i>et al</i> 1998; 1999	0.00724	3.1216	FRS
<i>Liparis liparis</i>	Sea snail	SSN	15	12.4	0.481	Modelled	0.01960	2.9055	FRS
<i>Liparis montagui</i>	Montagu's sea snail	MSS	12	10.1	0.554	Modelled	0.01960	2.9055	FRS
<i>Liza aurita</i>	Golden grey mullet	GOM	59	54.1	0.199	FishBase	0.01090	2.5376	FishBase
<i>Lophius budegassa</i>	Black bellied angler	BAN	100	85.0	0.100	FishBase	0.02124	2.9198	FRS
<i>Lophius piscatorius</i>	Angler	ANG	200	135.0	0.176	Jennings <i>et al</i> 1998; 1999	0.02964	2.8392	FRS
<i>Lumpenus lampretaeformis</i>	Snake blenny	SNB	50	47.6	0.205	FishBase	0.00910	2.3352	FRS
<i>Lycenchelys sarsi</i>	Sar's wolf eel	LSA	20	16.4	0.401	Modelled	0.00010	4.0957	FRS
<i>Lycodes esmarkii</i>	Esmark's eelpout	EEE	75	58.0	0.174	Modelled	0.00010	4.0957	FRS
<i>Lycodes vahlii</i>	Vahl's eelpout	VEE	52	40.9	0.220	Modelled	0.04170	2.2532	FRS
<i>Melanogrammus aeglefinus</i>	Haddock	HAD	100	68.3	0.190	Jennings <i>et al</i> 1998; 1999	0.00840	3.0328	FRS
<i>Merlangius merlangus</i>	Whiting	WHI	70	42.4	0.320	Jennings <i>et al</i> 1998; 1999	0.00612	3.0856	FRS
<i>Merluccius merluccius</i>	Hake	HAK	140	103.6	0.107	Jennings <i>et al</i> 1998; 1999	0.00840	2.9343	FRS
<i>Microchirus variegatus</i>	Thickback sole	TSO	35	20.7	0.374	FishBase	0.00890	3.0790	FRS
<i>Microstomus kitt</i>	Lemon sole	LSO	65	37.1	0.415	Jennings <i>et al</i> 1998; 1999	0.00851	3.0660	FRS
<i>Molva dypterygia</i>	Blue Ling	BLI	155	134.0	0.142	FishBase	0.00190	3.1490	FishBase
<i>Molva molva</i>	Ling	LIN	200	183.0	0.118	FishBase	0.00610	2.9951	FRS
<i>Mugil cephalus</i>	Flathead (grey) mullet	GRM	120	105.0	0.110	FishBase	0.01480	2.9030	FishBase
<i>Mullus barbatus</i>	Red mullet	RMU	40	33.4	0.430	FishBase	0.00475	3.3242	FRS
<i>Mullus surmuletus</i>	Striped red mullet	RMM	30	25.0	0.150	FishBase	0.00440	3.3510	FishBase
<i>Mustelus asterias</i>	Starry smooth hound	SSH	140	105.4	0.118	Modelled	0.00202	3.1174	FRS
<i>Mustelus mustelus</i>	Smooth hound	SHO	200	205.0	0.060	FishBase	0.00620	2.7580	FRS
<i>Myoxocephalus scorpius</i>	Bull rout	BRO	90	34.0	0.240	Jennings <i>et al</i> 1998; 1999	0.01310	3.1110	FRS
<i>Myxine glutinosa</i>	Hagfish	HAG	80	61.7	0.167	Modelled	0.00030	3.4046	FRS
<i>Pagellus acarne</i>	Spanish Sea Bream	SSB	36	32.0	0.240	FishBase	0.01000	3.2100	RIVO
<i>Pagrus pagrus</i>	Couch's sea bream	CSB	91	64.5	0.142	FishBase	0.01350	3.0370	FishBase
<i>Pegusa lascaris</i>	Sand sole	SSO	40	28.7	0.379	FishBase	0.00690	3.1170	FishBase
<i>Petromyzon marinus</i>	Sea Lamprey	SLA	120	90.9	0.130	Modelled	0.00033	3.4045	FRS
<i>Pholis gunnellus</i>	Butterfish	BUT	25	26.3	0.420	FishBase	0.00430	3.0180	FRS
<i>Phycis blennoides</i>	Greater forkbeard	GFO	110	57.7	0.168	FishBase	0.00565	3.1048	FRS
<i>Platichthys flesus</i>	Flounder	FLO	60	47.3	0.230	FishBase	0.00940	3.0996	FRS

<i>Pleuronectes platessa</i>	Plaice	PLA	100	54.4	0.110	Jennings <i>et al</i> 1998; 1999	0.00911	3.0430	FRS
<i>Pollachius pollachius</i>	Pollack	LYT	130	85.6	0.186	FishBase	0.00798	3.0526	FRS
<i>Pollachius virens</i>	Saithe	SAI	130	177.1	0.070	Jennings <i>et al</i> 1998; 1999	0.00831	3.0115	FRS
<i>Pomatoschistus lozanoi</i>	Lozano's goby	PLO	8	8.6	0.890	FishBase	0.01689	2.8132	FRS
<i>Pomatoschistus microps</i>	Common goby	COG	9	11.0	0.295	FishBase	0.01000	2.9400	RIVO
<i>Pomatoschistus minutus</i>	Sand goby	SGO	11	9.2	0.928	FishBase	0.02118	2.6264	FRS
<i>Pomatoschistus pictus</i>	Painted goby	PGO	6	5.2	0.857	Modelled	0.01260	3.0000	FishBase
<i>Psetta maxima</i>	Turbot	TUR	100	57.0	0.320	Jennings <i>et al</i> 1998; 1999	0.02012	3.0243	FRS
<i>Raja brachyura</i>	Blond ray	BRA	120	139.0	0.120	FishBase	0.00990	3.2051	FRS
<i>Raja clavata</i>	Thornback ray	TRA	120	105.0	0.220	Jennings <i>et al</i> 1998; 1999	0.00279	3.2163	FRS
<i>Raja montagui</i>	Spotted ray	SPY	80	97.8	0.148	Jennings <i>et al</i> 1998; 1999	0.01378	2.8017	FRS
<i>Raniceps raninus</i>	Tadpole fish	TFI	28	22.2	0.328	Modelled	0.00620	3.2670	FishBase
<i>Scophthalmus rhombus</i>	Brill	BRI	75	50.0	0.270	FishBase	0.01166	3.0849	FRS
<i>Scyliorhinus canicula</i>	Lesser spotted dogfish	LSD	100	90.0	0.200	Jennings <i>et al</i> 1998; 1999	0.00156	3.2072	FRS
<i>Scyliorhinus stellaris</i>	Nurse hound	NHO	170	126.9	0.104	Modelled	0.00493	2.9550	FRS
<i>Sebastes marinus</i>	Redfish (marinus)	RED	100	73.0	0.064	FishBase	0.01710	2.9499	FRS
<i>Sebastes viviparus</i>	Norway haddock	NHA	35	36.0	0.070	Jennings <i>et al</i> 1998; 1999	0.01380	3.0726	FRS
<i>Solea vulgaris</i>	Dover sole	DSO	70	39.2	0.280	Jennings <i>et al</i> 1998; 1999	0.00494	3.2284	FRS
<i>Spinachia spinachia</i>	Fifteen spined stickleback	FST	22	17.3	1.780	FishBase	0.00210	3.0000	FishBase
<i>Spondylusoma cantharus</i>	Black sea bream	BSB	60	52.0	0.300	FishBase	0.02214	2.9163	FRS
<i>Squalus acanthias</i>	Spurdog	SPU	160	90.2	0.150	Jennings <i>et al</i> 1998; 1999	0.00180	3.1782	FRS
<i>Stichaeidae</i>	Unidentified Pricklebacks	PBU	37	29.5	0.272	Average of SNB and YBL	0.02530	2.2682	FRS
<i>Syngnathus acus</i>	Greater pipefish	GPI	50	39.4	0.225	Modelled	0.00006	3.5270	FRS
<i>Syngnathus rostellatus</i>	Nilsson's pipefish	NPI	17	20.0	0.747	FishBase	0.00010	3.5300	RIVO
<i>Taurulus bubalis</i>	Sea scorpion	SSC	25	18.7	0.251	FishBase	0.01310	3.1110	FRS
<i>Trachinus draco</i>	Greater weever	GWE	53	41.6	0.217	Modelled	0.00162	3.4323	FRS
<i>Trigla lucerna</i>	Tub gurnard	TUB	75	65.0	0.148	FishBase	0.01230	2.9329	FRS
<i>Trigla lyra</i>	Piper gurnard	PIP	60	52.0	0.208	FishBase	0.01070	2.8850	FishBase
<i>Triglops murrayi</i>	Moustache sculpin	MSC	20	16.4	0.401	Modelled	0.01569	2.7447	FRS
<i>Trisopterus esmarki</i>	Norway pout	NPO	35	22.6	0.520	Jennings <i>et al</i> 1998; 1999	0.00441	3.2130	FRS

						1999			
<i>Trisopterus luscus</i>	Bib	BIB	46	38.0	0.211	FishBase	0.01198	3.0484	FRS
<i>Trisopterus minutus</i>	Poor cod	PCO	40	20.3	0.506	Jennings <i>et al</i> 1998; 1999	0.00680	3.1277	FRS
<i>Zeugopterus norvegicus</i>	Norwegian topknot	NTO	12	10.1	0.554	Modelled	0.02000	2.9050	FishBase
<i>Zeugopterus punctatus</i>	Topknot	TPK	25	20.3	0.349	Modelled	0.01446	3.1479	FRS
<i>Zoarces viviparus</i>	Viviparous blenny	VBL	52	52.0	0.130	FishBase	0.04170	2.2532	FRS