Managing Fisheries to Conserve North Sea Groundfish and Benthic Invertebrate Species Diversity

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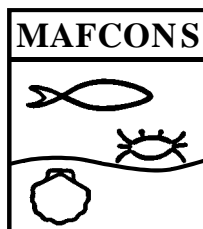Dr S.P.R. Greenstreet, Fisheries Research Services, Marine Laboratory, PO Box 101, Victoria Road, Aberdeen, AB11 9DB, Scotland

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SUMMARY

Section 1: Introduction to the MAFCONS Project

Concerns over man's impact on the environment and ecosystems of the world have resulted in a shift in emphasis in the management of marine natural resources. Consequently, an ecosystem approach to management (EAM) is in the process of being developed and implemented for the North Sea. Several political drivers, such as the Conventions on Biological Diversity (CBD) and Protection of the Marine Environment of the North East Atlantic (OSPAR), as well as the emerging European Union Marine Strategy Directive, require the conservation and restoration of biodiversity to be priority objectives for managers.

Even at the start of the 20th century, one million tonnes of fish were landed from the North Sea per year. This increased to a peak of around 3.5mt in the 1970's, since when landings have declined. Given an estimated fish standing crop biomass of 10mt in the North Sea, these landings figures represent 10% to 35% of standing crop biomass. Further, considering that these landings data exclude fish caught and discarded or landed illegally, it seems likely that, at its peak, fishing may have removed as much as 50% to 60% of fish standing crop biomass each year. The North Sea may be the most heavily impacted by fishing of any marine region in the world.

Many studies have examined the impact of fishing on fish and benthic invertebrate communities. These data suggest that in both communities the species considered to be most vulnerable to fishing, because of their life-history, size, ecology, or physical characteristics, have decreased in abundance, while species considered to be more resilient have increased. In general, these changes have tended to result in reduced species richness and diversity.

However, not all the evidence indicates a consistently negative relationship between fishing activity and species diversity. Some studies suggest that in the southern North Sea, fish species diversity may have increased as a result of fishing activity. This leads to the possibility that fishing might cause fish species diversity to decline in the northern North Sea and to increase in the southern North Sea. Huston's Dynamic Equilibrium Model (DEM) predicts that in more productive environments increased disturbance should stimulate an increase in species diversity, but where productivity is low, a similar change in disturbance should cause diversity to decrease. Primary production in the shallow mixed southern North Sea is higher than in the deeper stratified northern North Sea. Thus these apparently contradictory trends in fish species diversity in different parts of the North Sea may in fact comply with the DEM.

This presents the possibility that the DEM could provide a theoretical basis allowing the ecological consequences, in terms of changes in species diversity, of specific fisheries regimes to be estimated prior to the implementation of whatever management options might be under consideration.

Section 2: Tests of Huston's (1994) Dynamic Equilibrium Model

Three explicit tests of the DEM were carried out. The first test used species diversity of the whole groundfish assemblage, production of the entire benthic invertebrate community, and fishing disturbance calculated assuming the entire assemblage was impacted. The second test took account of the size selectivity involved in the fisheries operating in the North Sea, thus it considered the species diversity of the size classes of fish subject to fishing exploitation. These

fish tend to be piscivorous, so productivity in the prey fish size classes provided the test production parameter. Fishing disturbance parameter values were also calculated only on that component of the assemblage specifically targeted by fisheries. The third test considered the diversity of epifaunal benthic invertebrates, the production of infaunal benthic invertebrates, and the disturbance (mortality) imposed on epibenthic invertebrates by fishing activity. In each of these tests the data failed to support hypotheses derived from the DEM. Thus the DEM is unlikely to provide a reliable basis for scientific advice in support of an EAM attempting to meet biodiversity objectives for the North Sea.

Section 3: The Management Protocol

The failure of the DEM to provide the theoretical basis for predicting the biodiversity consequences of specific fisheries management scenarios does not necessarily preclude the use of the proposed management protocol. However, it does mean that an alternative theoretical species diversity – fishing disturbance model is required. However, the usefulness of the management protocol is also seriously impaired by the difficulties associated with the continued use of "catch limitation" as the principal management regime. For all but the targeted species, determining appropriate indicators of fishing disturbance requires a modelling approach based on metrics that quantify the perturbation activity itself, such as fishing effort statistics. In order to predict the biodiversity consequences of specific sets of Total Allowable Catches (TACs), this would involve predicting the likely fishing effort patterns associated with each set of TACs. This remains problematic.

The principle underlying the original management protocol was that the spatial distribution of fishing effort could be manipulated by judicious setting of TACs so that the detrimental effects of fishing on species diversity could be minimised. Such manipulation of fishing activity can be achieved explicitly through the use of Marine Protected Areas (MPAs) in which fishing activity is regulated explicitly.

The benthic invertebrate and fish abundance data collected during the course of the project provide an invaluable source of information for identifying areas of particular ecological importance, and can therefore be used to specify the location of MPAs aimed at specific ecosystem objectives. The international landings and fishing effort databases allow the economic consequences (loss of potential fish landings) associated with specific closed areas to be estimated, and knowledge of catch per unit effort (CPUE) in areas outside MPAs allows estimates to be made of the "displaced fishing effort" that would be required to make up these landings in other parts of the North Sea. The fishing effort – ecological disturbance models developed during the project can then be applied to provide estimates of the ecological consequences of this displaced fishing effort. Thus the databases generated and the models developed over the course of the project allow the ecological consequences of specific MPA proposals to be assessed.

This approach was adopted to assess two potential MPA scenarios; closing 7.7% of the North Sea to safeguard the most important areas for groundfish species diversity and closing 7.3% of the North Sea to reduce the impact of fishing on benthic invertebrate communities. The analysis suggested that closing nearly 8% of the North Sea to protect groundfish species diversity would result in an overall increase in fishing effort across the North Sea. Consequently, the impact of fishing on benthic invertebrates would in all likelihood increase. Closing over 7% of the North Sea specifically to reduce the impact of fishing on the benthic invertebrate community actually resulted in a reduction of benthic mortality of only 1.7% to

3.8%. In both cases much of the benefit gained from the introduction of MPAs was negated by the displacement of fishing effort into the remainder of the North Sea.

This preliminary assessment of the use of MPAs to achieve global scale objectives for an EAM in the North Sea suggests that in the absence of simultaneous reductions in TACs, the introduction of MPAs is unlikely to achieve significant ecosystem gains. When TACs were reduced by the amount of landings normally taken from within the closed area, then closure of 7.3% of the North Sea to reduce the impact of fishing on benthic invertebrates resulted in a reduction of benthic mortality of between 16.2% and 17.4%.

Section 4: Alternative Theoretical Model

An EAM based on a structured indicator framework, such as the Pressure-State-Response (PSR) framework, will require the mechanistic linkages between the various indicators to be well understood. The DEM, for example, could have supplied the theoretical linkage between indicators of fishing pressure and indicators of the state of the system such as diversity indices. However, failure of the DEM means that the mechanistic link between fishing activity and species diversity remains poorly understood, making it difficult to address biodiversity objectives in an EAM using an indicator based management framework. Given the political importance placed on biodiversity, the need to develop theoretical models linking fishing to changes in species diversity remains paramount.

The DEM is a model that describes the diversity of **species** as a function of variation in productivity and disturbance. However, in communities consisting of species characterised by non-deterministic growth, such as marine fish and benthic invertebrate communities, the concept of the **species** as the "functional unit" makes less sense than it does for communities composed of species displaying deterministic patterns of growth. In non-deterministic growth assemblages the "functional unit" is better defined by body size. Consequently marine and aquatic communities have often been described by "biomass-abundance spectra". The shape of such spectra has been shown to be influenced by variation in fishing pressure applied to the communities concerned.

Furthermore, models such as the DEM assume Lokta-Voltera type population dynamics. Therefore a fundamental assumption of such models is that the potential for population growth is directly proportional to the abundance of mature individuals in the population. For many fish and benthic species this assumption is inappropriate. These species display what has been termed "storage" and "lottery" type population dynamics. For each individual in the population, fecundity is a function of body-mass, and since in non-deterministic growth organisms, body mass continues to increase, so *per capita* fecundity continues to increase with increasing age. Thus while mortality might reduce population size, the survivors continue to grow and increase their individual fecundity. As a result, population growth potential is maintained ("stored"), or even increased, despite the diminishing number of mature individuals. The "lottery" aspect covers the stochastic nature of the situation whereby numerous environmental factors combine to alter substantially the survival probabilities of the recruits produced. Thus when conditions are favourable, even low numbers of spawners can produce exceptionally large recruit cohorts.

Both these factors explain why the DEM fails to predict variation in fish and benthic communities in the North Sea. An alternative size-structured species diversity model is outlined. This model takes account of the ontogenetic changes that occur as individuals of each species continue to grow and it allows "storage" and "lottery" effects to be modelled explicitly.

An analysis is carried out that demonstrates significant effects of fishing on the species per individual relationships for different size classes. This confirms that a size-structured species diversity model should provide useful insight for scientists advising an EAM addressing biodiversity issues.

Section 5: Important Issues

In any indicator based framework for an EAM, access to appropriate data that adequately quantifies the "pressure" on the system is essential. Currently in the single species based management of individual fish stocks, considerable resources are expended in obtaining adequate data to quantify "pressure". A similar expenditure of resources will be required to gather this essential information in the broader-scoped EAM. Access to appropriate fishing effort data is therefore essential in this respect. Currently such data are not readily available, a situation that, if continued, will seriously impede the development and implementation of an EAM.

Estimating the abundance of organisms present at a location at any one time is fundamental to understanding all ecological processes. It is critical to understanding food web structure and tropho-dynamics and to the estimation of actual species diversity in time and space. No fish or benthic sampler currently employed samples all individuals in the sampled area, neither is the fraction of animals sampled constant. Catchability in any sampler is affected by a variety of complex factors giving rise to considerable variability between species and between different size classes of any particular species. This seriously affects the resulting estimates of abundance. Consequently the advice provided by scientists supporting an EAM, based on these abundance estimates, may be flawed. Research to investigate catchability in the major marine sampling systems used by scientists in the North Sea must therefore be a high priority.

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1. INTRODUCTION TO THE MAFCONS PROJECT

1.1. Policy Drivers Underpinning the Need to Consider the Conservation and Restoration of Biodiversity in an "Ecosystem Approach to Management"

Recent years have witnessed a shift in emphasis in the underlying objectives of fisheries management in the North Sea. Whilst the need to conserve individual stocks at sustainable and economically viable levels is still clearly a major priority, managers are now being asked to adopt a broader ecosystem approach to managing fisheries. The political impetus behind this change in attitude has largely been provided by the "North Sea Ministerial Conferences", five of which, along with a further two "Intermediate Ministerial Meetings", have occurred over the period 1982 to 2002. Initially attention was directed towards more fully implementing the Oslo and Paris Conventions to reduce pollution in the North Sea, but by the late 1980s the focus was starting to shift towards more ecological issues. The first North Sea "Quality Status Report" (QSR), produced as part of the preparatory documentation for the London Conference in 1987, highlighted shortcomings in the available data and indicated the need to enhance scientific knowledge and understanding of the North Sea environment. As a result, the North Sea Task Force (NSTF) was established and tasked with examining the effects of all human activities on the North Sea environment and ecosystem. At the subsequent Ministerial Conference, held at The Hague in 1990, attention was directed for the first time towards the protection of species and habitats, and to the impact of fishing activities on the broader North Sea ecosystem.

A major factor explaining this shift in focus was the imminent United Nations Conference on Environment and Development (UNCED), the "Earth Summit", held at Rio de Janeiro in June 1992. At Rio all countries with a stake in the management and exploitation of the marine fish resources of the North Sea (the EC, individual EC member states and Norway) were signatories to two documents with the potential to be hugely influential with respect to the future development of fisheries management practice. These were the "Convention on Biological Diversity" (CBD) and Chapter 17 of "Agenda 21" ("Protection of the Oceans, all Kinds of Seas, including Enclosed and Semi-Enclosed Areas, and the Protection, Rational Use and Development of Their Living Resources"). The CBD bound signatory governments to the conservation of biological diversity, requiring them to ensure that biological resources were exploited in a sustainable manner that would not lead to the long-term decline of biological diversity. The CBD also required governments to monitor activities likely to have an adverse impact on biological diversity, to take measures to reduce such effects and, where possible, to restore degraded ecosystems. Agenda 21 Chapter 17 identified several major problems associated with the exploitation of marine natural resources by commercial fisheries. By signing Agenda 21, states committed themselves to, among other things, the conservation and sustainable use of marine living resources, the protection and restoration of endangered marine species, and the preservation of rare and fragile ecosystems and habitats, and other ecologically sensitive areas. Shortly after the Rio Earth Summit, at the first of the Intermediate Ministerial Meeting in Copenhagen in 1993, ministers accepted that, as a general goal, fisheries management should safeguard the North Sea ecosystem as a whole.

Another significant event also occurred in 1992, the signing in Paris of the Oslo/Paris (OSPAR) Convention for the Protection of the Marine Environment of the North-East Atlantic. Initially this convention simply combined the two original Oslo and Paris Commissions in the original four annexes. However, OSPAR was always intended to be more than this and, in July 1998, a fifth annex on the "Protection and Conservation of the Ecosystems and Biological Diversity of the Maritime Area" was added. The language of Annex V bears close comparison with the wording

used in the CBD. Article 2, for example, requires contracting parties to "take the necessary measures to protect and conserve the ecosystems and biological diversity of the maritime area, and to restore, where practicable, marine areas which have been adversely affected". Articles 2 and 3 also require that human activities likely to have a detrimental impact on marine ecosystems should be controlled. Appendix 3 of Annex V sets out criteria by which to identify potentially detrimental human activities. These include the intensity and duration of the activity under consideration, the actual and potential adverse effects of the activity on species, communities, habitats and ecological processes, and the irreversibility, or durability of these effects. Fishing activities in the North Sea clearly meet these criteria. Fishing occurs over almost all of the North Sea (Jennings *et al* 1999), it is intensive and many areas are repeatedly disturbed (Rijnsdorp *et al* 1998), and it takes place almost continuously (Greenstreet *et al*. 1999a). Actual adverse effects at the species, community, habitat and ecological process level have all been demonstrated, and in at least some instances, these effects, if not irreversible, have been shown to be long-lived (Collie *et al* 1997; Greenstreet & Rogers 2006; Kaiser *et al* 2006).

Ministers attending the fourth North Sea Ministerial Conference at Esbjerg in 1995 realised that all matters relating to the protection of the marine environment and ecosystem of the North Sea could potentially be addressed through OSPAR. To initiate this process an Intermediate Ministerial Meeting was convened in Bergen in 1997. The Bergen Ministerial Declaration stated that an "ecosystem approach" should be adopted towards the management of fisheries in the North Sea. The ministers declared that fisheries, conservation and environmental management measures should be integrated, thereby bringing environmental objectives into fisheries policies. Furthermore, the ministers introduced some guiding principles to underpin the development of this new approach to management, principal among which was the requirement that this should involve a multi-species approach, i.e. taking into account interactions between different components of the food web, and other important ecosystem interactions. In keeping with their commitments to the CBD, Agenda 21, and OSPAR, the ministers stated that exploitation of the natural resources of the North Sea should be consistent with the conservation of biodiversity and the sustainable use of its components. Implicitly, if not explicitly therefore, the ecosystem approach to management of fisheries in the North Sea is required to ensure that biodiversity is conserved, and where there may be evidence of loss of biodiversity, remedial action should be taken to restore biodiversity.

The emerging EU Marine Strategy, "Towards a strategy to protect and conserve the marine environment" (Brussels, 02.10.2002 COM(2002) 539 final), now states such objectives explicitly. This document identifies two overarching objectives with implications for biodiversity. First the strategy requires managers to "protect and where possible, restore the function and structure of marine ecosystems in order to achieve and maintain good environmental status of these ecosystems", which includes halting the decline of biodiversity by 2010 and by 2012. Secondly, the document requires managers to set up a network of marine and coastal protected areas; to "control the use of marine services (including fisheries) that have or may have a negative impact on the status of the marine environment". This includes a recommendation to implement the FAO Code of Conduct for Responsible Fisheries as soon as possible.

1.2. Evidence that fishing has affected the biodiversity of fish and benthic invertebrate communities

1.2.1. Trends in fishing pressure

Many studies examining the impacts of fishing on fish and benthic invertebrate communities in the North Sea have focused on the analysis of temporal trends, and this is particularly true in respect of fish communities. The logic underpinning such an approach is founded on the fact that fishing disturbance of marine ecosystems is believed to have increased more or less continuously throughout the course of the last century, the period for which almost all the data available to assess the impact on marine ecosystems are available. Here we examine the evidence to support this contention, and assess how large a perturbation to the marine ecosystem of the North Sea fishing represents.

Landings increased steadily over most of the 20th century (Figure 1.2.1.1, Daan *et al* 1990). However, two points emerge from the examination of these data. Firstly, even at the start of the century, the removal of fish biomass stood at around one million tonnes each year. Few fish and benthic invertebrate survey data are available to examine the impact of fishing prior to this period, so that it is important to realise that, even at the start of the longest time-series studies available (e.g. Rijnsdorp *et al* 1996; Greenstreet *et al* 1999a; Rogers and Ellis 2000), the marine ecosystem of the North Sea was already under pressure from fishing activity. Secondly, following a relatively steady increase in landings over the first 60 years of the century, annual fish landings increased markedly during the 1960s to peak at around 3.5 million tonnes per year by the late 1970s. Most of the coordinated groundfish surveys in the North Sea started during the 1970s and few of the published long-term times series analyses for the North Sea include data from before this period (e.g. Corten and van de Kamp 1996; Heessen and Daan 1996; Rogers and Millner 1996; Piet & Jennings 2005). One might conclude therefore that time-series analyses of the ICES coordinated IBTS data published in recent years have actually covered a period when fishing pressure on the North Sea has been reducing.
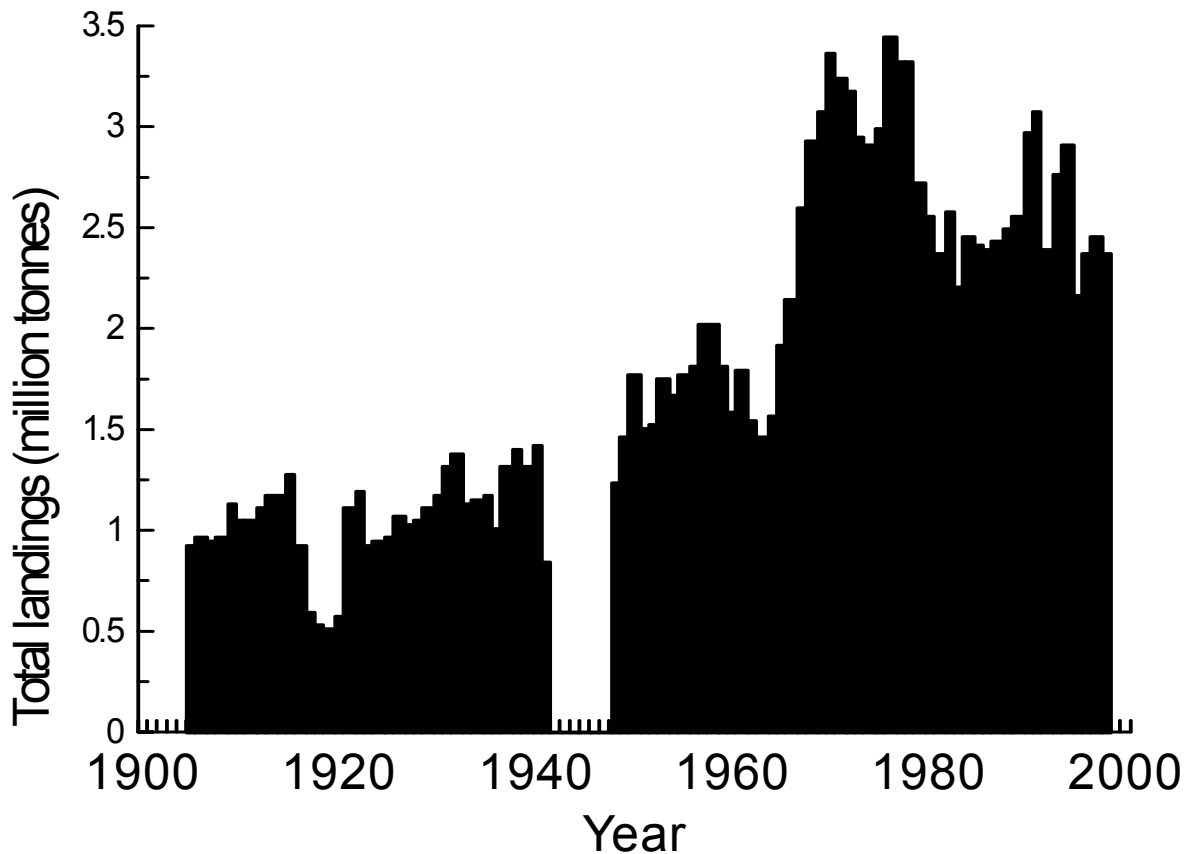
Figure 1.2.1.1: Trends in landings of fish taken from the North Sea over the course of the 20th century.

Estimates of the total biomass of fish in the North Sea during the 1980s indicated values that varied around a mean of approximately ten million tonnes (Yang 1982; Sparholt 1990; Daan *et al* 1990). Annual landings at this time represented approximately 25% of the total fish standing crop biomass. However, landings data do not portray the full impact of fishing on fish communities since they take no account of the biomass of fish (and of benthos) caught by the gear, but not landed. Stock assessment data suggests that the biomass of haddock and whiting caught and discarded each year represents at least 50% of the biomass that is actually landed, and at times considerably more (Figure 1.2.1.2; Stratoudakis *et al* 1998; 1999). Studies of the Dutch beam-trawling fleet suggest that discarded plaice amounted to 49% of the total plaice catch (Van Beek *et al* 1990). But even studies such as these do not reveal the full story as many non-targeted fish are also caught and discarded by both the gadoid otter trawl and flatfish beam-trawl fleets in the North Sea. Discarding rates in the beam trawl plaice and sole fisheries suggest that the total biomass of fish caught may be as much as five or six times the biomass landed (Garthe and Damm 1997; Lindeboom and de Groot 1998). Frid *et al* (2000) suggest that such discarding rates would amount to 200,000t of fish being discarded each year by the beam-trawl fleets alone, while Garthe *et al* (1996) estimated that in 1992, discards exceeded 561,000t, representing at least 25% of the biomass of fish landed. These studies suggest considerable variation in the estimation of the amount of fish discarded each year, but it would not be unreasonable to conclude that the quantity is substantial, at least equivalent to somewhere in the range 30% to 100% of the biomass landed. Official landings data also do not

include illegally landed fish, although in recent years, efforts have been made to take account of these in estimating total fishing mortality for stock assessment purposes (ICES 2005).
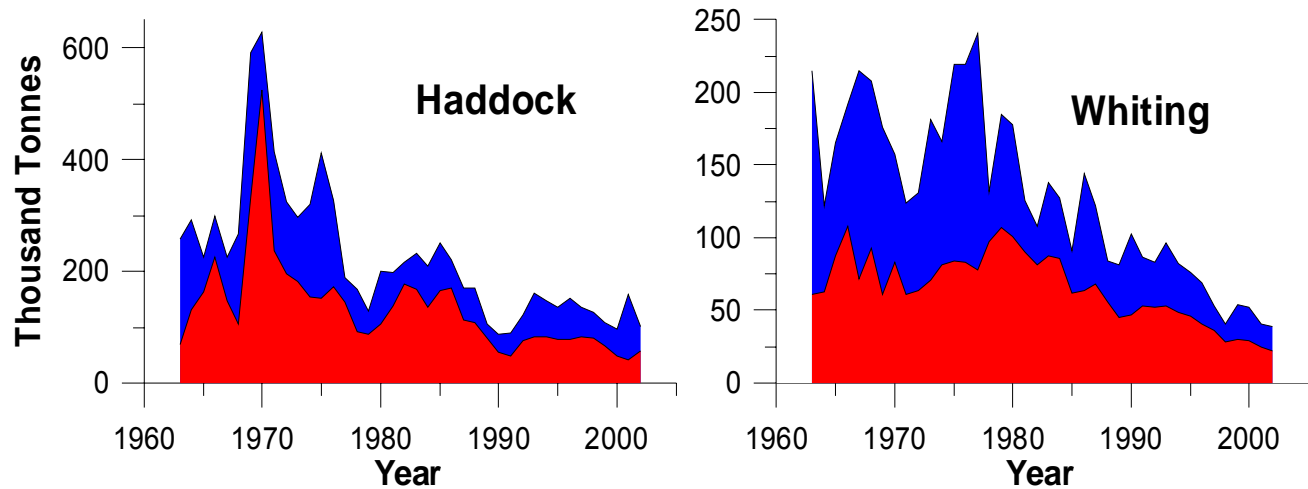
Figure 1.2.1.2: Trends in landings (red fill) and discarding (blue fill) of haddock and whiting (data from ICES 2005).

Taking account of the additional removals associated with discarding and illegal landing suggests that perhaps as much as 50% of the fish standing crop biomass in the North Sea may have been removed each year as a result of fishing activity. How serious a perturbation to the marine ecosystem of the North Sea might this represent? Globally 35% of the world's fish catch is taken from non-tropical continental shelf seas, such as the North Sea, yet such seas represent only 5% of the worlds total ocean surface area. This makes non-tropical continental shelf seas the most heavily fished marine regions in the world (Pauly and Christensen 1995). Pauly and Christensen (1995) estimate that it requires 36% of the all the primary productivity occurring in non-continental shelf seas simply to support the biomass of fish removed by fisheries, and this is bound to have serious consequences for the marine ecosystems in these regions (Beddington 1995). Of the world's continental shelf seas, losses to fishing mortality compared with natural mortality are among the highest in the North Sea (Figure 1.2.1.3; Bax 1991), making the North Sea ecosystem perhaps the most heavily impacted by fishing of any marine ecosystem in the world.

North Sea

Catch

Predation

Georges Bank

Catch

Predation

E. Berring Sea

Catch

Predation

Barents Sea
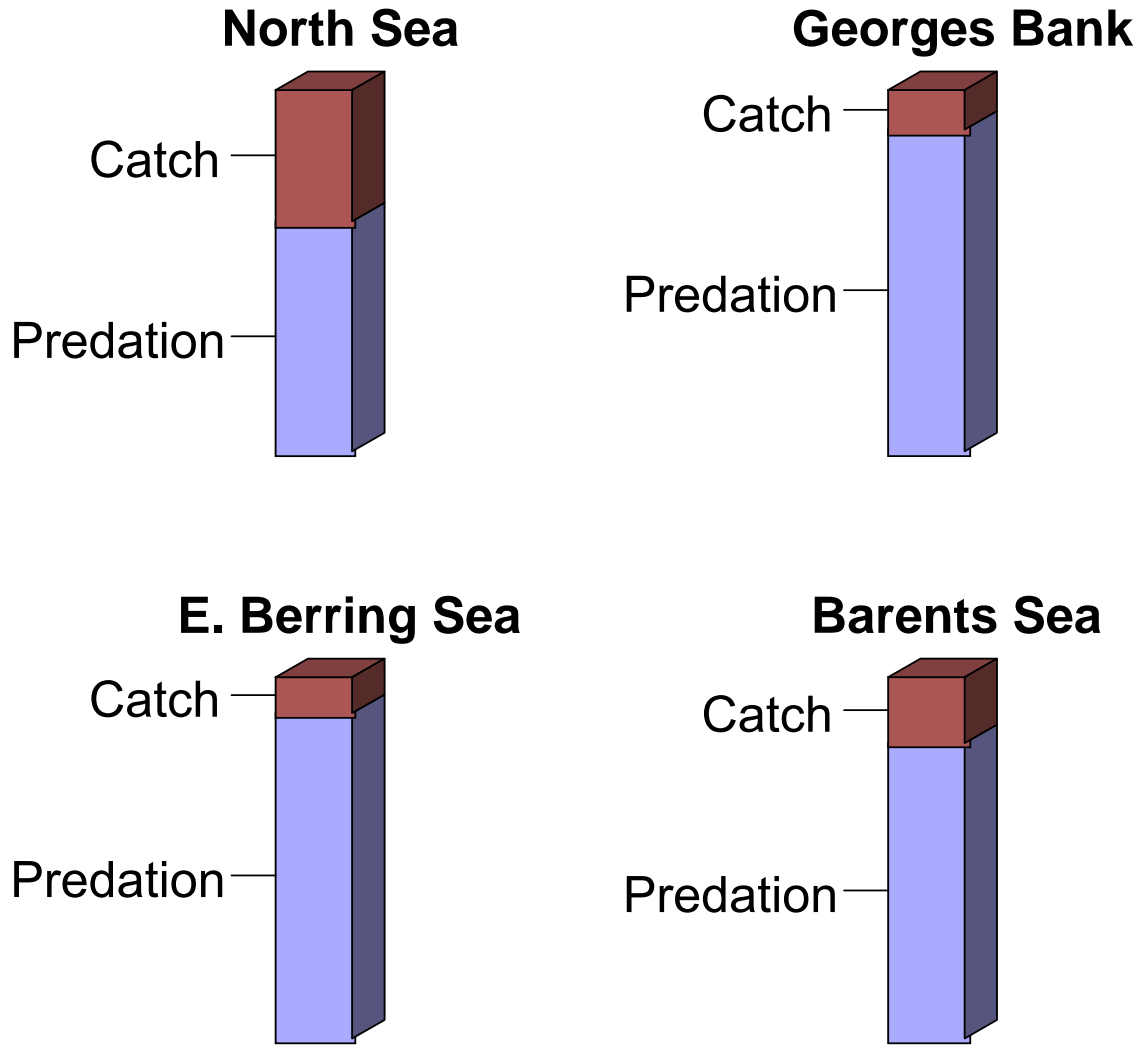
Catch

Predation

Figure 1.2.1.3: Comparison of catch and predation mortality of fish in four continental shelf seas.

1.2.2. Effects on the diversity of benthic invertebrate communities

There have been few long-term, large-scale studies of the effects of fishing on benthic invertebrate communities. The principal reason for this is the scarcity of appropriate data due to the logistical difficulties of setting up the necessary sampling programmes and the costs involved in post-survey sample analysis. Whilst continuous long-term benthic data sets are relatively scarce, a few studies have examined local scale surveys repeated in a few areas with relatively long intervals between the surveys. In many instances species considered to be vulnerable to fishing pressure have declined in abundance, so that communities contain fewer low productivity slow reproducing species and become increasingly dominated by high productivity opportunistic species (Gilkensen *et al*. 1998; Schroeder and Knust 1999). Increased fishing activity in the intervening period between the surveys has been cited as a possible cause of these changes (Reisen and Reise 1982; Schroeder and Knust 1999). However, whilst long-term changes in the benthic invertebrate community may very well be a fishing effect, an environmental influence cannot entirely be discounted (Engel and Kvitek 1998; Kröncke 1990; 1992; Kaiser *et al* 2000; Bergman and van Santbrink 2000; Frid and Clark 2000;

Kröncke and Bergfield 2001). One study involving long-term monitoring (since 1971) of the benthos compared the communities in two sites, one inside a *Nephrops* fishing ground where annual fishing frequencies may have exceeded 10 times per year and the second site outside the main fishing area. The communities at both sites changed in response to changing environmental conditions (increased organic input), but at the heavily fished site, this relationship broke down during the period when fishing disturbance was highest. Individual taxa were categorised *a priori* as vulnerable to fishing (likely to decrease in abundance), or resilient to fishing (likely to increase in abundance). At the site outside the main fishing ground no consistent trends in abundance were detected. At the heavily fished site however, while no significant trends in the abundance of vulnerable species was observed, resilient species showed increased abundance over time. Such increases in abundance can result in increased dominance, leading to lower species diversity. In this study, the taxa predicted to increase in abundance in response to fishing disturbance dominated the community when fishing activity was greatest (Frid *et al* 1999; Frid and Clark 2000).

Most studies investigating the effects of fishing on benthic invertebrate communities have compared communities in un-fished control areas with the community remaining in experimentally fished areas, or they have compared the community present in an area both before and after experimental fishing (Jennings & Reynolds 2000). A variety of characteristics combine to determine the vulnerability of different benthic taxa to fishing activity, including life-history, size, ecology, physical characteristics, habitat preference, depth in the sediment, etc (Rumohr and Krost 1991; Bergman and Hup 1992; Engel and Kvitek 1998; Collie *et al* 2000; Bergman and van Santbrink 2000; Piet *et al* 2000; Eno *et al* 2001; Johnson 2002; Duplisea *et al* 2002; Kaiser *et al* 2006). It has also been suggested that species with a strong scavenging tendency may benefit directly from fishing activity by exploiting damaged organisms left in the paths of towed gears (Ramsay *et al* 1998; Groenewold and Fonds 2000). Many of the experimental studies investigating the effects of fishing on benthic invertebrate communities have demonstrated either a reduction in the abundance, or the extirpation, of species deemed to be vulnerable, and in some cases species considered to be resilient have increased in abundance (e.g. Reisen & Reise 1982; Langton and Robinson 1990; Bergman & Hup 1992; Hill *et al* 1996; Tuck *et al* 1998; Frid *et al* 1999; Bergman 2000; Bergman and Moore 2001a; 2001b). Such changes in population abundance have tended to result in reduced species richness and diversity (e.g. Kaiser and Spencer 1996; Collie *et al* 1997; Tuck *et al* 1998). An alternative experimental design compares the composition of benthic invertebrate communities in areas that differ in the levels of fishing pressure imposed upon them. In one such study off the southwest coast of England, benthic communities were compared in areas where the use of towed fishing gears was restricted to varying degrees because of interference with the use of more traditional static gears. In the two areas where the use of towed gears was most restricted (in one of which towed gear use was completely abolished), both the biomass and species richness of benthic epifauna showed a significant increase (Blyth *et al* 2004). In recent meta-analyses of large numbers of such studies, Collie *et al* (2000) showed that in general, fishing reduced species richness by 27% across all studies of all gears affecting a variety of different types of communities in different habitats, with the greatest impacts being observed on mud and gravel habitats. Kaiser's *et al* (2006) analysis indicated, however, that the greatest effect on benthic invertebrate species richness occurred on muddy-sand habitats, although they go on to say that in many cases the spatial scales of these studies may not have been adequate to show the full effect of fishing on species richness and diversity.

Several studies examining spatial variation in benthic invertebrate communities across the North Sea have noted that communities in areas that are heavily fished appear to be dominated by

opportunistic and scavenging species that are resilient to, or which may benefit from fishing damage (Künitzer 1990; Dewarumez *et al* 1992; Rees *et al* 1999; Frid *et al* 2000; Rumohr and Kujawski 2000; Callaway *et al* 2002; Hinz *et al* 2004). Several of these studies speculated that the presence of large numbers of scavenging and opportunistic species and the low abundance of large, sedentary species was a result of fishing impact (e.g. Rumohr and Kujawski 2000; Callaway *et al* 2002). Such speculation is supported by studies elsewhere. Blanchard *et al* (2004) showed that species diversity, richness and evenness of the benthic mega-fauna along the Bay of Biscay coast of France were lowest, and the abundance of vulnerable species was least, in areas where fishing effort was highest. Likewise, Collie *et al* (1997) noted that biomass, species richness and species diversity of benthic megafaunal communities were all highest on the least fished parts of the Georges Bank.

As with terrestrial systems (e.g. MacArthur and MacArthur 1961; Pianka 1966; 1967; Recher 1969; Rosenzweig & Winakur 1969; Kotler & Brown 1988), the diversity of benthic invertebrate communities is closely linked to the structural complexity of the habitat (Jennings & Kaiser, 1998; Thrush *et al*. 2001). All towed fishing gears affect the seabed, digging in, turning over and resuspending fine sediments and removing larger cobbles and boulders (Churchill 1989; Krost *et al* 1990; Messieh *et al* 1991; Riemann and Hoffmann 1991; Schwinghamer *et al* 1996). The net result of these processes is to reduce the structural complexity of the benthic habitat (Schwinghamer *et al* 1996), so reducing the potential for fished areas to support diverse benthic invertebrate communities. The structural complexity of the benthic environment is further enhanced by biogenic structuring organisms. Sedentary species such as hard or soft corals, anemones, hydroids, and sponges attach to the physical substrate and grow out into the water column to filter feed. Other organisms such as polychaetes, bivalves, and shrimps and prawns tunnel into the sediment forming burrows and tunnels, adding to the complexity of the sediment structure. Such biogenic structuring organisms provide attachment surfaces, stabilise sediments, ameliorate the sediment by irrigation or fertilization, extend the oxygen supply into deeper layers, change hydrodynamic properties or provide refuge from predation (Fager 1964; Featherstone & Risk 1977; Woodin 1978; Dean 1981; Crowder & Cooper 1982; Eckman 1983; Reise 1983; Gallagher *et al*. 1983; Lubchenco 1983; Jones & Jago 1993; Forster & Graf 1995; Lackschwitz & Reise 1998; Bartol *et al*. 1999; Qian *et al*. 1999; Ragnarsson & Raffaelli 1999; Friedrichs *et al*. 2000; Pederson & Peterson 2002; Callaway 2003), all of which provides opportunities for other benthic invertebrate and fish species to colonise the area thereby increasing diversity (Kohn 1967; 1968; Pringle 1990; Thrush *et al*. 2001). The use of towed fishing gears in an area can almost entirely denude it of these biogenic organisms (Auster *et al* 1996; Collie *et al* 1997; Watling and Norse 1998). The loss of these biogenic structuring species in itself reduces benthic invertebrate diversity, but the total impact is further exaggerated by the additional loss of species associated with the structures that they provided (Mayer *et al*., 1991; Dayton *et al*., 1995; Jennings & Kaiser, 1998; Thrush *et al*., 1998; Talman *et al*. 2004).

1.2.3. Effects on the diversity of fish communities

Around the world there is considerable evidence that fishing has a negative impact on species richness and diversity of fish assemblages. On coral reef systems, for example, species richness tends to be negatively correlated with fishing intensity (Jennings *et al* 1995; Jennings and Polunin 1997), and in comparisons between fished and unfished (e.g. marine reserves) areas, species richness and diversity is consistently higher in the latter (Samoilys 1988; Roberts and Polunin 1991; 1993; Watson and Ormond 1994; Jennings *et al* 1995; Jennings *et al* 1996; Jennings and Polunin 1997). In many marine continental shelf regions, regular surveys of the

demersal fish assemblage are undertaken to support stock assessment and management processes, with in many cases, time series extending back over several decades (e.g. Overholtz and Tyler 1985; Gabriel 1992; Heessen 1996; Heessen and Daan 1996). The data collected on these surveys, numbers of each species in the catch, normally by length class, are exactly the data required to examine long-term changes in the structure and composition of the groundfish community (e.g. Magnussen 2002; Jouffre & Inejih 2005; Mueter and Megrey 2005; Erzini *et al* 2005; Yemane *et al* 2005; Blanchard *et al* 2005; Duplisea 2005; Stobberup *et al* 2005; Bundy *et al* 2005). The availability of such data have allowed long-term trends in the species diversity of the demersal fish community in the North Sea to be examined to an extent that simply has not been possible for the benthic invertebrate communities.

The situation is clearest for the northern North Sea, where the longest data time series of both groundfish survey data and fishing effort statistics have been available for analysis. Two studies have examined trends in groundfish species diversity in either three or four regions of the North Sea. The first of these studies compared data collected annually over the period 1980 to 1993 with seven years of data collected across the period 1929 to 1956 in three regions of the northwestern North Sea and in all three regions Hill's (1973) N_1 index of species diversity tended to be lower in the later period than in the earlier (Greenstreet and Hall 1996). This result was corroborated through comparison of *k*-dominance curves (Platt *et al* 1993) constructed for each area. These indicated increased dominance (= reduced diversity) in all three regions during the later period (Greenstreet and Hall 1996). In the second study the full data set was available for analysis, spanning the period 1925 to 1996, and data were also available for a fourth region in the central North Sea. Significant negative trends in both Hill's N_1 and N_2 were observed in the same three regions in the northwestern North Sea (Figure 1.2.3.1) and again *k*-dominance curve analyses indicated corresponding increases in dominance in all three areas (Greenstreet *et al* 1999b). In the fourth area in the central North Sea, no trends in either species diversity or dominance were detected (Greenstreet *et al* 1999b). In a related study, long-term trends in taxonomic distinctness and diversity were found to closely follow trends in Hill's N_1 and N_2 (Hall and Greenstreet 1998). The implication of this is that, as species diversity declined over time, taxonomic diversity also declined, suggesting an overall long-term reduction in genetic diversity within the groundfish community, another of the three main components of biodiversity (Gaston 1996).
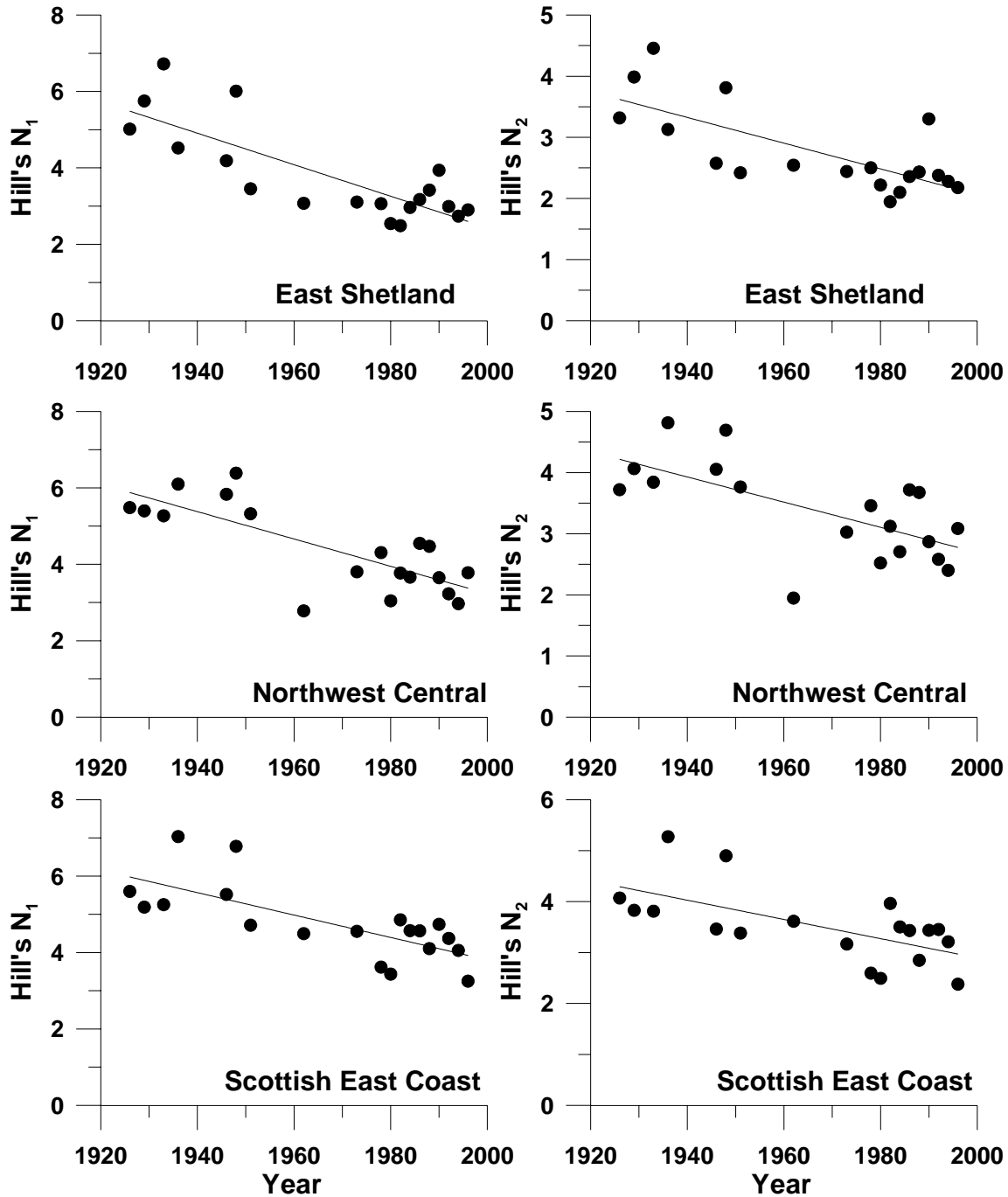
Figure 1.2.3.1: Long-term trends in Hill's N_1 and N_2 indices of demersal fish species diversity in three regions of the northwestern North Sea (from Greenstreet *et al* 1999b). See Greenstreet and Hall (1996) for map showing the precise location and boundaries of the three regions.

Fishing effort data by UK registered fishing vessels landing in Scotland were available for the four regions covered by these studies for the period 1960 to 1994 (Greenstreet *et al* 1999a; Greenstreet *et al* 2006). For the three regions in the northwestern North Sea these vessels Fishing effort increased by a factor of 2 to 3 in two of the three areas in the northwestern North Sea where negative trends in groundfish species diversity had been detected, but in the third

area total fishing effort showed a significant decline in terms of total hours fishing. However, the principal fishing gear used in this area had traditionally been Seine nets. Over the period for which data were available Seine fishing activity declined markedly as fishermen converted to otter trawling. Thus otter trawling activity increased in this third area following a trend similar to those observed in the other two areas. Overall total fishing effort was considerably higher in the third area and, despite the decreasing trend in total effort, the annual number of hours fishing in this area remained the highest of the three at the end of the time series. Thus fishing activity levels in this third area were considerably higher, and had been at high levels for a much longer period of time, than in the other two regions. Consequently, both studies concluded that fishing had had a negative effect on species diversity on the three regions in the northwestern North Sea (Greenstreet and Hall 1996; Greenstreet *et al* 1999b). In the forth region in the central North Sea where no temporal trends in diversity or dominance were observed, fishing activity by UK vessels landing in Scotland was considerably lower, and only a weak increasing trend was detected (Greenstreet *et al* 1999b).

Although indicative of a negative effect of fishing on demersal fish species diversity, these correlative type studies do not definitively confirm cause and effect. The two variables, fishing effort and species diversity, could be auto-correlated, both responding to a third (perhaps environmental) factor. Neither is the directionality of any relationship explicitly identified. However unlikely or implausible, these studies cannot rule out the possibility that the observed decline in groundfish species diversity has in some way improved the situation for fishing, and so stimulated increased fishing activity. Both studies showed that, along with the declines in species diversity in the three regions of the northwestern North Sea, marked changes in species composition of the groundfish assemblage occurred over time (Greenstreet and Hall 1996; Greenstreet *et al* 1999b). Life-history theory suggests that fish species with particular life-history characteristics, such as slow growth, large ultimate body size, late age/large size at maturity, and low fecundity should be the most vulnerable to increased mortality rates caused by fishing (Jennings *et al* 1998). Thus if fishing caused the observed changes in species composition in the demersal fish communities occupying the three northwestern North Sea regions, which resulted in long-term declines in groundfish species diversity, then species with these life-history characteristics should have been the ones to decline in relative abundance, while species with the opposite life-history characteristics should have increased in abundance. This hypothesis was subsequently tested by determining average life history characteristic values for the entire demersal fish community, and examining trends in these values over time. In an area where fishing activity has increased threefold over the period 1960 to 1994, the average ultimate length, age at maturity and length at maturity have all shown long-term declines, while the average growth rate has increased (Jennings *et al* 1999). This result provided strong support that it was indeed the increase in fishing activity in this area that caused the changes in demersal fish species composition, resulting in reduced species diversity.

The causal relationship between fishing activity and groundfish species diversity in the northwestern North Sea has been further established in a recent study that combined spatial and temporal analyses (Greenstreet and Rogers 2006). Groundfish survey data were analysed for 75 ICES statistical rectangles assigned to one of three fishing effort categories; low (<5,000h.y^{-1}), medium (5,000h.y^{-1} to 20,000h.y^{-1}) and high (>20,000h.y^{-1}). Five indices of species richness and species diversity were determined. Long-term trends in index values in rectangles assigned to each of the three effort treatments followed predictions based on a fishing effect. No significant trends were observed in rectangles assigned to the low effort category, while trends in the medium and high effort categories were all significant and

negative. Furthermore, slopes for each of the metric trends were steeper for rectangles assigned to the high effort category compared with medium effort rectangles.
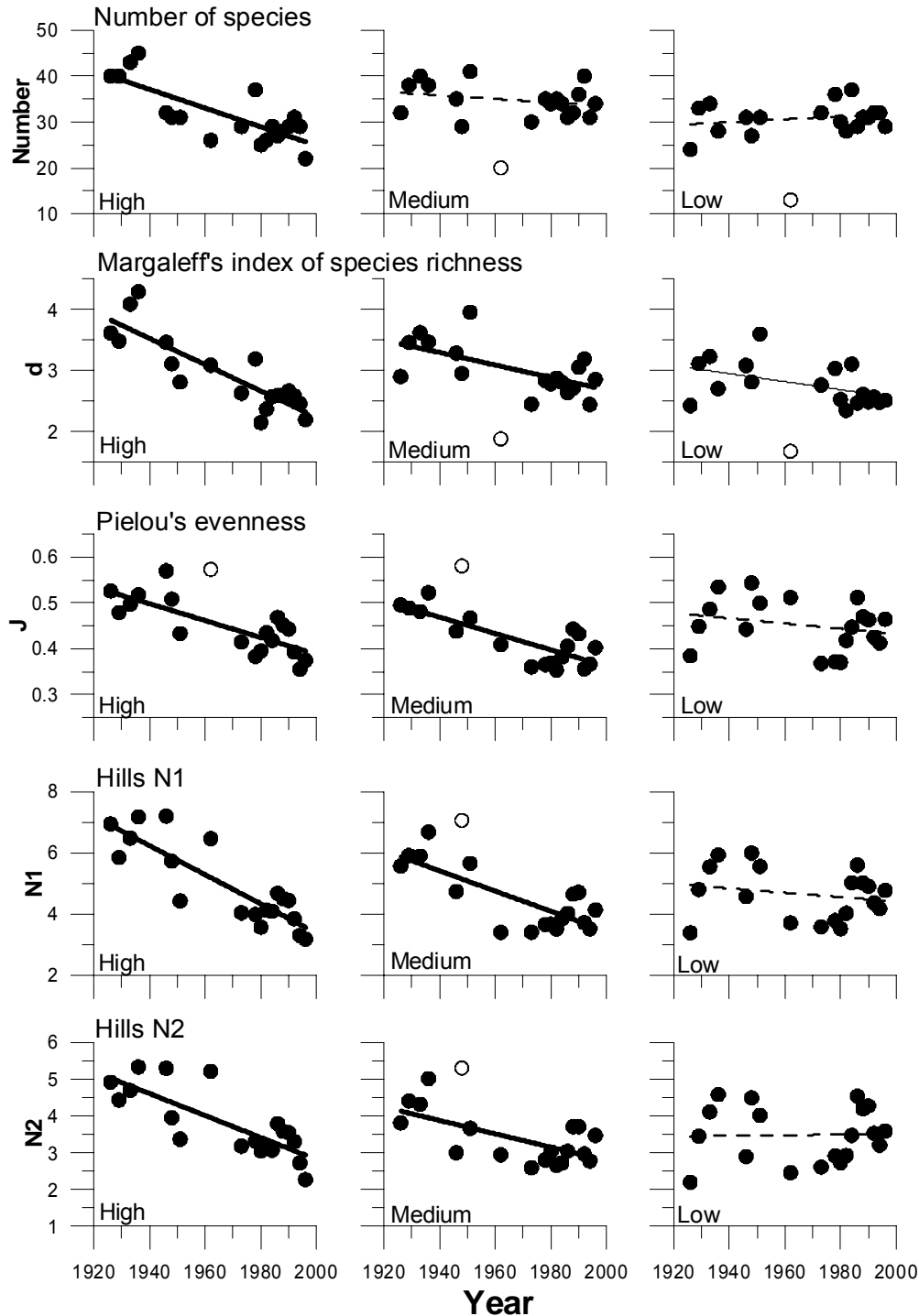
Figure 1.2.3.2: Long term trends in five metrics of the species richness and species diversity of the demersal fish community in ICES rectangles in the northwestern North Sea assigned to low, medium and high otter trawling "treatments" (from Greenstreet and Rogers 2006).

Other studies of long-term trends in species diversity in the North Sea are either not so clear cut or are not in agreement with the studies carried out in the northwestern North Sea. Piet and Jennings (2005) for example examined trends in species richness and species diversity based on mean values for single 30 minute duration trawl samples in the quarter 3 ICES International Bottom Trawl Survey (IBTS) and observed no significant long-term trends. Following sample rarefaction and accumulation analyses, Greenstreet and Hall (1996) pointed out that at least five one hour trawl samples needed to be aggregated before Hill's N_1 and N_2 stabilise and start to represent actual community values. Thus the statistical power of analyses based on the means of single 30min samples is unlikely to be adequate to detect trends (see Greenstreet and Rogers 2006 and Greenstreet et al 2007a) for more detailed discussions of this issue). Rogers and Ellis (2000) compared recent groundfish survey collected over the period 1989 to 1997 with archive research vessel catch data collected over the period 1901 to 1907. Records of mesh size and other gear characteristics suggested that these data were broadly comparable. Their analysis suggests that, in English coastal regions in the southern North Sea, species diversity of the demersal fish assemblage increased over an interval of 80 years. In the recent period the abundance of a number of small species, such as the dragonets (Callionymiidae), bib (*Trisopterus luscus*) and bullrout (*Myoxocephalus scorpius*) had increased, while the previous levels of dominance by plaice (*Pleuronectes platessa*) and whiting (*Merlangius merlangius*) had decreased. A similar increase in diversity in the southern North Sea was indicated by analysis of Dutch beam trawl survey data collected over the period 1985 to 2001 (Piet and Jennings 2005).

Consideration of these studies of long-term change in the composition and diversity of the North Sea demersal fish assemblage (Greenstreet & Hall 1996; Greenstreet et al 1999; Greenstreet & Rogers 2000; Rogers and Ellis 2000; Piet and Jennings 2005) raises the possibility that increased fishing activity over the course of the 20th century has caused species diversity to decrease in the northern North Sea and to increase in the southern North Sea. Such a situation is not altogether without some credibility. Huston's (1994) dynamic equilibrium model suggest that the response of species diversity to increased disturbance may be both positive or negative depending upon the productivity in the region: in areas of low productivity a negative response is anticipated, while in areas of high productivity positive relationships are more likely. Primary productivity in the southern North Sea, characterised by shallow, mixed, warmer water is greater than in the deeper, stratified, cooler northern North Sea (Reid et al 1990). Thus Huston's model actually predicts the apparently contradictory trends in species diversity found in the northern and southern North Sea. However, not all long-term studies of trends in demersal fish species diversity in the southern North Sea indicate the same increasing trends. In a similar study covering the southeastern North Sea, recent groundfish survey data were again compared with archive data collected early in the 20th century, and this comparison showed that increased dominance by two species, dab (*Limanda limanda*) and whiting, had caused a reduction in demersal fish species diversity over the intervening period (Rijnsdorp et al 1996).

1.3.   Development of an Ecosystem Approach to Management

With the addition of Annex V to the OSPAR Convention, OSPAR was considered to be the competent authority with primary responsibility for the development of the ecosystem approach to management. Under the auspices of OSPAR therefore, a series of workshops were convened with this purpose in mind. The first workshop in Oslo in June 1998 recognised the need not only for objectives at a "general" level, but also the requirement for "specific" objectives to serve as detailed operational goals. At the workshop at Scheveningen in September 1999, the basic template for an ecosystem approach to management was proposed. Ten "issues"

were identified for which Ecological Quality Objectives (EcoQOs) would be set (Figure 1.3.1). Ecological Quality (EcoQ) was defined as the "Ecological quality of ecosystems is an overall expression of the structure and function of the aquatic systems, taking into account the biological community and natural physiographic, geographic and climatic factors as well as physical and chemical conditions including those resulting from human activities". EcoQOs were defined as "the desired level of EcoQ relative to a reference level" where reference levels were defined as "the level of the EcoQ where the anthropogenic influence on the ecological system is minimal" (Skjoldal *et al*. 1999). However, with respect to fisheries, the Esbjerg Declaration acknowledged that legal competence for fisheries management policy within the North Sea lay with the European Commission (EC), implemented through the European Union's (EU) Common Fisheries Policy (CFP), and with the Norwegian authorities in Norwegian waters. Thus any regulation of fisheries necessary to achieve EcoQOs would have to be realised through cooperation with these authorities.
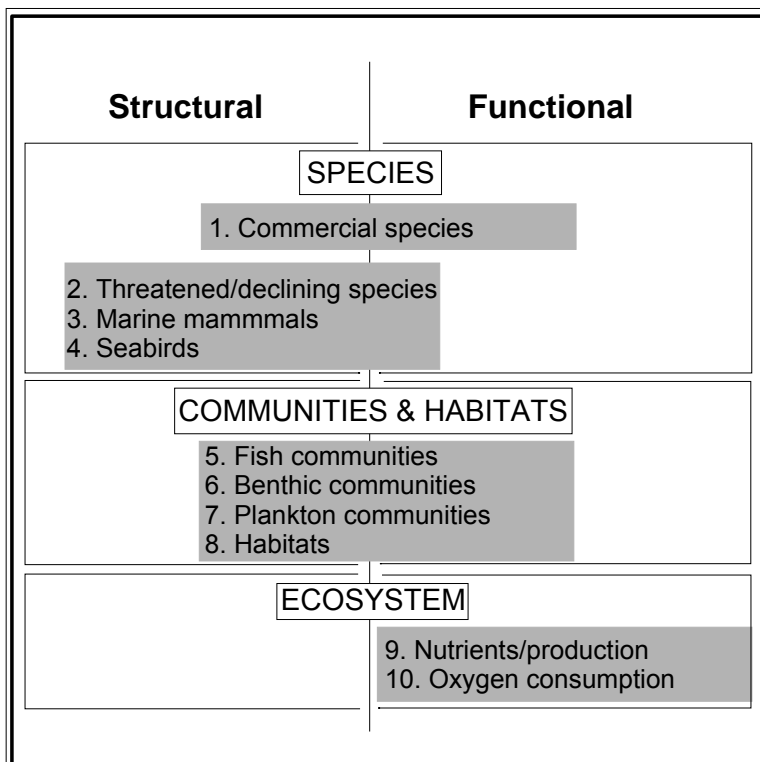
Figure 1.3.1: Ten OSPAR Ecological Quality Issues for each of which Ecological Quality Objectives will be set. The diagram indicates the level at which objectives are intended to be set, ie at species level or at community level, and the extent to which these objectives will address structural or functional attributes of the marine ecosystem.

Issues 1 to 4 were intended primarily to involve EcoQOs based at the level of individual species. Thus conservation objectives currently used in the single species assessments and management of commercial fish stocks could be carried over as EcoQOs for Issue 1. Likewise, where scientific knowledge suggested that particular species may be either threatened or declining, appropriate EcoQOs could be readily conceived to counter such problems. Similarly, appropriate EcoQOs could be introduced for EcoQ Issues 3 and 4 that would address specific problems identified for particular marine mammal and seabird species. Issues 5 to 7 move beyond species level and are intended to operate at the level of the "community". For these

issues, it was anticipated that EcoQOs would be directed towards multi-species, community, or assemblage level attributes and this has initiated a "hunt" for appropriate indicators of community or assemblage health (Frid 2003). EcoQ Issues 5 and 6 are "Fish Communities" and "Benthic Communities" respectively. Thus depiction of the ecosystem approach to the management of the natural resources of the North Sea specifically requires that EcoQOs be set for the fish and benthic invertebrate communities of the North Sea. The evidence presented in Section 1.2 provides a strong case that the species diversity of both these communities has been adversely affected by centuries of fishing activity. Given, as we have shown in Section 1.1, that the major policy drivers that have influenced the development of an ecosystem approach to fisheries management are primarily concerned with the conservation and restoration of biodiversity, two immediate principal objectives for management are implicit.

1.   Further decline in the species diversity of fish and benthic invertebrate communities of the North Sea should be halted immediately so that remaining biodiversity might be conserved.

2.   Action should be taken to restore the species diversity of the fish and benthic invertebrate communities of the North Sea to some predefined previous historical level in an attempt to restore biodiversity in a degraded system.

1.4.   Managing Fisheries to Conserve/Restore Species Diversity

Despite the strong evidence that fishing has adversely affected the species diversity of both benthic and fish communities, our understanding of the processes involved are not clear. Most of the studies demonstrating an effect are correlative in nature (eg Greenstreet and Hall 1996; Greenstreet *et al* 1999; Rogers and Ellis 2000; Piet and Jennings 2005; Greenstreet and Rogers 2006) and these fail to clearly elucidate the mechanistic relationship between fishing disturbance and species diversity. Several studies have considered how fishing affects communities from a mechanistic perspective, considering for example how species with particular life-history characteristics might be affected (eg Jennings *et al* 1998; Gilkensen *et al*. 1998; Schroeder and Knust 1999; Jennings *et al* 1999; Greenstreet and Rogers 2000), or how fishing might affect the size structure of the community (Duplisea and Kerr 1995; Duplisea *et al* 1997; Jennings *et al* 2001a; Jennings *et al* 2001b; Jennings *et al* 2002; Duplisea *et al* 2002; Blanchard *et al* 2005), but the link between these attributes of communities to changes in the species diversity of communities has not been explicitly studied and it is not immediately obvious that the relationships between community averaged life-history characteristics, or mean size, and community species diversity are altogether intuitive.

Commercial species remains EcoQ Issue number 1 in the ecosystem approach to management proposed by OSPAR (Figure 1.3.1). Consequently, the long-standing, traditional single-species approach to fisheries management will need to be maintained so as to meet objectives set for this Issue. Yet if the consequences of any specific management scenario (a particular suite of TACs for example) are to be taken account of, so as to ensure that species diversity objectives set for fish and benthic invertebrate communities (Issue 5 and 6) are not compromised, then the mechanistic relationship between fishing activity and species diversity needs to be much better understood. The management proceedings themselves will also need to be expanded so as to include the routine examination of consequences of proposed management actions. If species diversity objectives for fish and benthic invertebrate communities take on higher priority, ie if managers start to attempt to restore species diversity in degraded areas, then the importance of understanding the processes by which these communities are structured, and how these are

affected by fishing disturbance, becomes even more critical. Under these circumstances managers will be attempting to manipulate fishing activity so as to achieve specific diversity objectives and the order of emphasis on the three EcoQ Issues will have reversed.

The incorporation of fish and benthic species diversity objectives into fisheries management therefore involves two distinct steps. Firstly; the mechanistic relationship between fishing activity and species diversity needs to be clearly outlined and understood. Only then will scientists be able to provide the specific advice that managers require – ie to achieve specific goals for fish and benthic invertebrate community species diversity, exactly what changes to current levels of fishing pressure need to be made. Secondly, the current management process needs to be expanded to include assessment of the consequences of proposed management action on other components of the marine ecosystem beyond just the commercially exploited species. Addressing these two tasks has been the purpose of the SEERAD funded MF0753 and EC funded "Managing Fisheries to Conserve Groundfish and Benthic Invertebrate Species Diversity" (MAFCONS, Q5RS-2002-00856) projects. This combined project assessed the utility of Huston's (1994) dynamic equilibrium model to determine whether it might provide the theoretical basis linking changes in fishing disturbance to changes in the species diversity of fish and benthic invertebrate communities (See Section 2). An initial "management protocol" whereby such a theoretical model might be incorporated into the current management proceedings so as to include species diversity objectives was described in the EC project's Technical Annex and this is reviewed and revised in Section 3, where its practicality is assessed and alternative approaches are considered. Even at the proposal stage it was recognised that the dynamic equilibrium model could fail to predict the diversity response of fish and benthic invertebrate communities to variation in fishing disturbance. As insurance against this eventuality, a thorough review of the theoretical community ecology literature was undertaken so as to identify the processes by which fish and benthic invertebrate communities are structured (Greenstreet *et al* 2007b). On the basis of this review, a proposed alternative theoretical model is described in Section 4. Finally Section 5 discusses key issues emerging from project that need consideration if an ecosystem approach to fisheries management is to be successfully developed, and more importantly, successfully implemented.

2. TESTS OF HUSTON'S (1994) DYNAMIC EQUILIBRIUM MODEL

2.1. Introduction

In Section 1.2.3, examining the effects of fishing on the species diversity of the demersal fish community in the North Sea, the long-term increases in species diversity noted by Rogers and Ellis (2000) in the southern North Sea were contrasted with the negative trends observed in studies undertaken in the northern North Sea (Greenstreet *et al* 1999b). Huston's dynamic equilibrium model, which predicts that both positive and negative responses to increased disturbance are possible, dependent upon local productivity, was put forward as a possible explanation for these apparently contradictory results. Thus it was suggested that the negative response in the less productive northern North Sea and the positive response in the highly productive southern North Sea were in line with model predictions.

In this Section the basis of each of the tests is presented. The following Sections present a series of individual tests of Huston's (1994) dynamic equilibrium model. Only the specific data used for each test are presented here. The detailed derivation of each of these test data sets is described in full in Callaway *et al* (2007) and Greenstreet *et al* (2007a; 2007c; 2007d).

2.2.   Huston's Dynamic Equilibrium Model

After exhaustive review of the literature, Huston (1994) proposed that two unimodal relationships underpinned the species diversity of communities; thus both the relationships between species diversity and disturbance and between species diversity and productivity were unimodal in shape (Figure 2.2.1:A). Huston (1994) believed this was because competition provided the major force in structuring communities (eg Schoener 1983; Connell 1983; Ferson *et al* 1986; Greenstreet *et al* 2007b). At low productivity, insufficient resources to support specialist species would result in communities dominated by a small number of generalists. Higher resource levels are sufficient to support specialists, effectively reducing niche width and increasing niche packing, allowing more species to be supported and increasing diversity. With further increase in productivity, limitations on the population growth of dominant competitors are removed. Consequently, their populations expand, using more of the available resources, resulting in the elimination of competing species and reduced diversity. At low levels of disturbance, the population growth of dominant competitors is not limited by anything other than resource supply. Populations of dominant competitors therefore expand till they reach their carrying capacity, out-competing and excluding subordinate competitors for the same resource and keeping diversity low. As disturbance increases, population growth of the dominant competitors is checked, leaving resources available for subordinate competitors so that diversity increases. As disturbance increases still further, some species in the assemblage, increasingly unable to sustain the rising levels of mortality, go extinct causing diversity to decline.

Huston (1994) combined these two unimodal relationships to form a three dimensional model, the dynamic equilibrium model (Figure 2.2.1:B). Essentially this model maintains that community structure is not a stable equilibrium between resource supply and utilisation, rather that the equilibrium between community structure and resources is constantly disturbed by perturbations that vary in their extent and frequency. Huston (1994) examined species abundance data originating from a wide range of habitats and environments to demonstrate the "universal nature" of his dynamic equilibrium model. The outcome of this model is that it predicts very different relationships between diversity and productivity, depending on the disturbance regime and, more importantly as far as the MAFCONS project is concerned, very different relationships between diversity and disturbance, depending on the productivity regime (Figure 2.2.1:C). Thus Huston's dynamic equilibrium model provides specific hypotheses regarding the relationship between disturbance and the species diversity of fish and benthic invertebrate communities; it suggests that in areas of low productivity, we should expect to find a negative relationship, but that positive relationships might be anticipated in areas of high productivity. These hypotheses are tested in this chapter using spatial data, whereby at each point in space, three parameter values are required to be estimated: fishing disturbance, productivity and species diversity. If Huston's model holds, then three dimensional relationships between these three parameters similar to the one shown in Figure 2.2.1:B should be obtained, and specific relationships between diversity and disturbance at different productivity levels, such as the ones shown in Figure 2.2.1:C, should be observed.
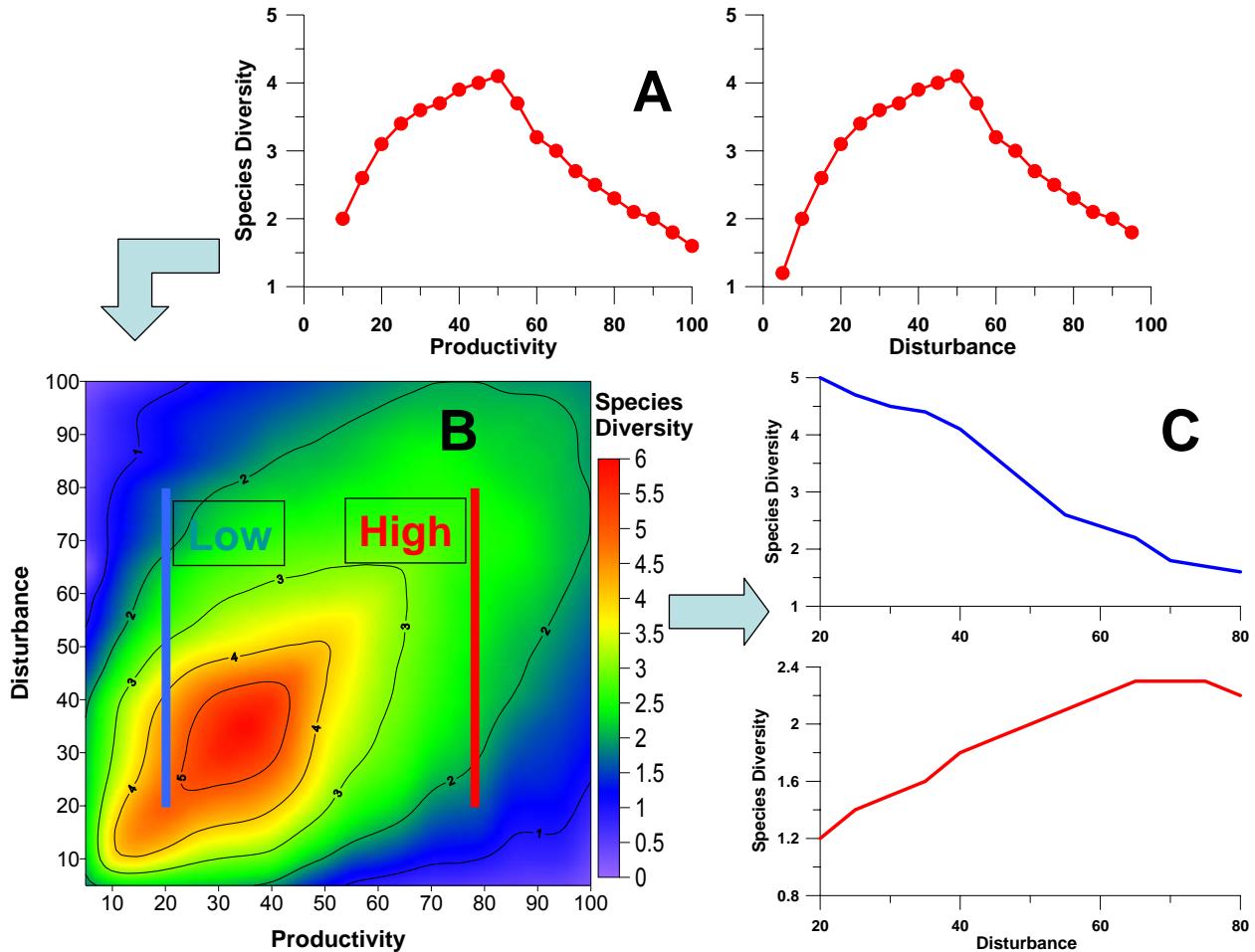
Figure 2.2.1: Schematic illustrating the evolution of Huston's dynamic equilibrium model and the relationships between species diversity and disturbance predicted by the model at low and high levels of productivity. A: unimodal relationships between species diversity and productivity and between species diversity and disturbance. B: Combination of the two relationships to produce the three dimensional "model" relating species diversity simultaneously to both productivity and disturbance. C: Predicted relationships between diversity and disturbance at the two productivity levels indicated in panel B.

As already explained, Huston's model is firmly founded in competition theory. Thus in selecting data to test hypotheses it has been essential to define the community whose species diversity (the "subject community") we are concerned about, so that the appropriate productivity parameters can be identified. Thus in this chapter we have defined "subject communities" along trophic level criteria. The appropriate productivity parameter value for hypothesis testing is then productivity by the community of organisms in the trophic level below that of the "subject community"; the "resource source community". For each test of the dynamic equilibrium model, specific "subject" and "resource source" communities are defined and spatial variation in the diversity of the former and productivity of the latter are presented. Disturbance is considered to be the total mortality experienced by the "subject community" at any location and spatial variation in this parameter is also presented. Thus each test of the dynamic equilibrium model starts by presenting spatial variation in the three input parameters to the model. Next the two relationships that are the basis of Huston's dynamic equilibrium model are examined; between productivity of the "resource source community" and diversity of the "subject community" and between disturbance and diversity of the "subject community". Here we would hope that some

part of the unimodal relationships on which the model is based would be revealed. The three values at each of the ICES rectangles where data are available are then input into a 3D plotting process with productivity on the *x* axis, disturbance on the *y* axis and diversity on the *z* axis, which if the model is supported, should resemble panel B in Figure 2.2.1. Finally data are classified into several productivity classes and the relationships between diversity and disturbance in each class are examined. Relationship similar to those shown in panel C of Figure 2.2.1 should be observed in the highest and lowest productivity categories.

2.3.   Summary of Methods

All data analysed were collected in August, the time of year when productivity in the North Sea is generally highest. Data for the fish community were derived from the ICES International Bottom Trawl Survey and Dutch Beam Trawl Survey data sets for the period 1998 to 2004. Two distinct benthic invertebrate communities are considered, the epifaunal community and the infaunal community. Data for these communities were collected specifically for this project by deploying a 2m epibenthic beam trawl (for epifauna) and a van Veen grab (for infauna) at selected groundfish survey stations in 2003 and 2004. Some additional benthic invertebrate data collected by FRS in 2001 and 2002 were also available, as were data collected in previous "Biodiversity" projects (Callaway *et al* 2002). All the samples were size structured so as to permit the individual organisms to be assigned to "same trophic level communities" on the basis of their size (eg. Duplisea and Kerr 1995; Duplisea *et al* 1997; 2002; Kerr and Dickie 2001; Jennings *et al* 2001a; 2001b; 2002a; 2002b. The methods involved in sample collection and processing, data extraction and archiving and data analysis are all described in detail by Callaway *et al* (2007). When considering the fish communities only species considered to be part of the "demersal fish assemblage" where included. Following Greenstreet and Hall (1996) and Greenstreet *et al* (1999) pelagic species such as herring, sprats, and sandeels that were not considered to be uniformly sampled by the GOV or 8m beam-trawl relative to their density in any specific ICES rectangle were all excluded from the analysis.

Three main indices of diversity were applied to the species abundance data for each "subject community", Hill's (1973) N_0, N_1, and N_2 (species richness, the exponential of the Shannon-Weiner index, and the reciprocal of the Simpson's index). Problems associated with the sampling of rare "events" (eg rare species or dense patches of a shoaling species) when considering species diversity issues make it critically important to assess the sampling effort required (eg Soetaert and Heip 1990) and considerable attention was paid to this issue (see Greenstreet *et al* 2007a; 2007c). Furthermore, because different species have different "catchabilities" in the samplers used in this study, it is important to realise that at all times the species diversity values for any particular "subject community" are only the values for that component of the community sampled by the gear – they are gear-biased views of the community. Such sampling bias is most likely to have the largest impact on measure of species diversity, although estimates of productivity may also be affected. Methods for estimating the secondary productivity of the fish and benthic invertebrate communities are described by Greenstreet *et al* 2007a; 2007c), while estimation of the fishing disturbance suffered by each community is carried out by Greenstreet *et al* (2007d)

## 2.4.   Test 1: Diversity of the Whole Fish Species Assemblage

In this test we examine the original basic premise of the project; that the demersal fish assemblage of the North Sea is essentially dependent on the benthic community as the principal supplier of its energy resources. Consequently the relationship between the species

diversity of the groundfish assemblage and disturbance to this assemblage caused by fishing activity should be dependent on variation in the productivity of benthic invertebrates.

2.4.1. Test input data

We will examine two sets of diversity data; diversity metric derived straight from the raw uncorrected IBTS GOV density estimates and data from the same survey corrected to take account of species- and size-related variation in catchability in the GOV trawl gear. Thus for Hill's N_1 and N_2 metrics the data shown are taken from Greenstreet *et al* (2007a: Figures 3.3.2.1.1 and 3.3.2.1.2 respectively, panels A and B). Our method for correcting for catchability cannot correct for species missed by the gear. So there is only one species richness estimate available to us. These data were established in Greenstreet *et al* (2007a: Figure 3.3.1.1). The suite of diversity test data used in this test is therefore shown in Figure 2.4.1.1. Greenstreet *et al* (2007d) describes how annual catch densities were calculated and the spatial distribution of catch density was given in their Figure 9.1. To convert these catch data to daily exploitation rates, the catch densities in each rectangle need to be divided by the density of fish present. This was done for the larger size classes of fish present in the fish assemblage in Greenstreet *et al* (2007d: Figure 9.3). For the purposes of this test, we calculate similar exploitation rates, but using the densities for the entire fish assemblage. These whole fish assemblage data are illustrated in Greenstreet *et al* (2007a: Figure 3.4.1.1 top panels A and C). Figure 2.4.1.2 shows the catch densities and two exploitation rate distributions, one based on the raw estimates of density and the second based on the density estimates corrected to take account of catchability. Estimates of epibenthic biomass density, productivity and production-biomass (P/B) ratio were given for six categories of epibenthic invertebrates in Greenstreet *et al* (2007c: Figures 1.3.5.5, 1.3.5.6 and 1.3.5.7 respectively). Summing biomass and productivity estimates over all six categories provides estimates of these variables for the entire epibenthic assemblage in each rectangle. Dividing production by biomass then produces a P/B estimate for the complete epibenthic community at each location (Figure 2.4.1.3). Estimates of infauna productivity were given in Greenstreet *et al* (2007c: Figure 2.3.4.1). These were calculated on AFDW biomass data, but still allow P/B ratios to be determined, which when applied to the biomass density data presented in Greenstreet *et al* (2007c: Figure 2.3.1.1, provide estimates of productivity in terms of wet weight (Figure 2.4.1.3).   Biomass and productivity in the infaunal component of the benthic community far exceeded epibenthic biomass and production. In examining the effect of the production by the benthic community on the relationships between fish diversity and disturbance of the fish community, one is essentially simply examining the impact of infaunal production (Figure 2.4.1.3). To determine whether production by epibenthic organisms played a role, the analysis were also run using epibenthic production only.
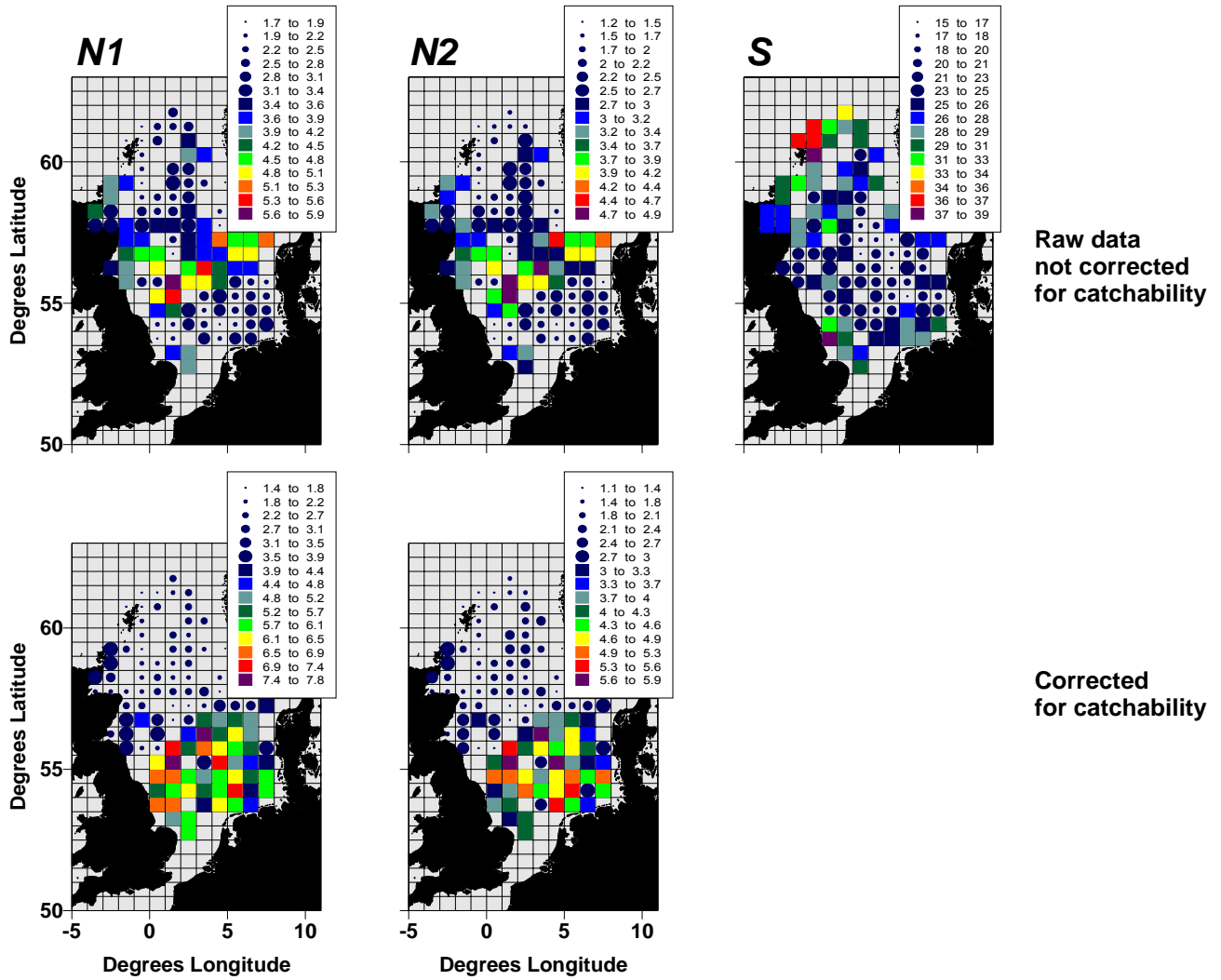
Figure 2.4.1.1: Spatial variation in Hill's N1, Hills N2, and species richness (S) based on raw GOV survey data and data corrected to account for species- and size-related catchability in the trawl gear.
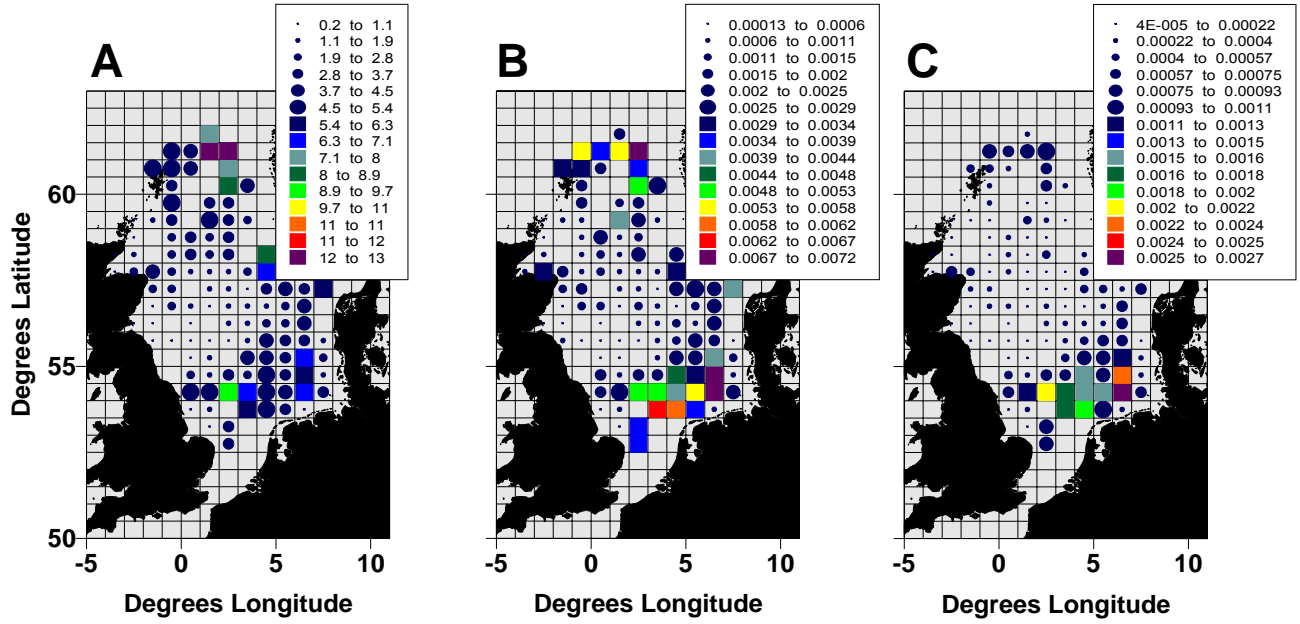
Figure 2.4.1.2: Spatial variation in catch density (g.m^{-2}) (A), exploitation rate based on raw survey density data (B) and exploitation rate based on estimates of density corrected to account for species- and size-related catchability in the trawl gear.
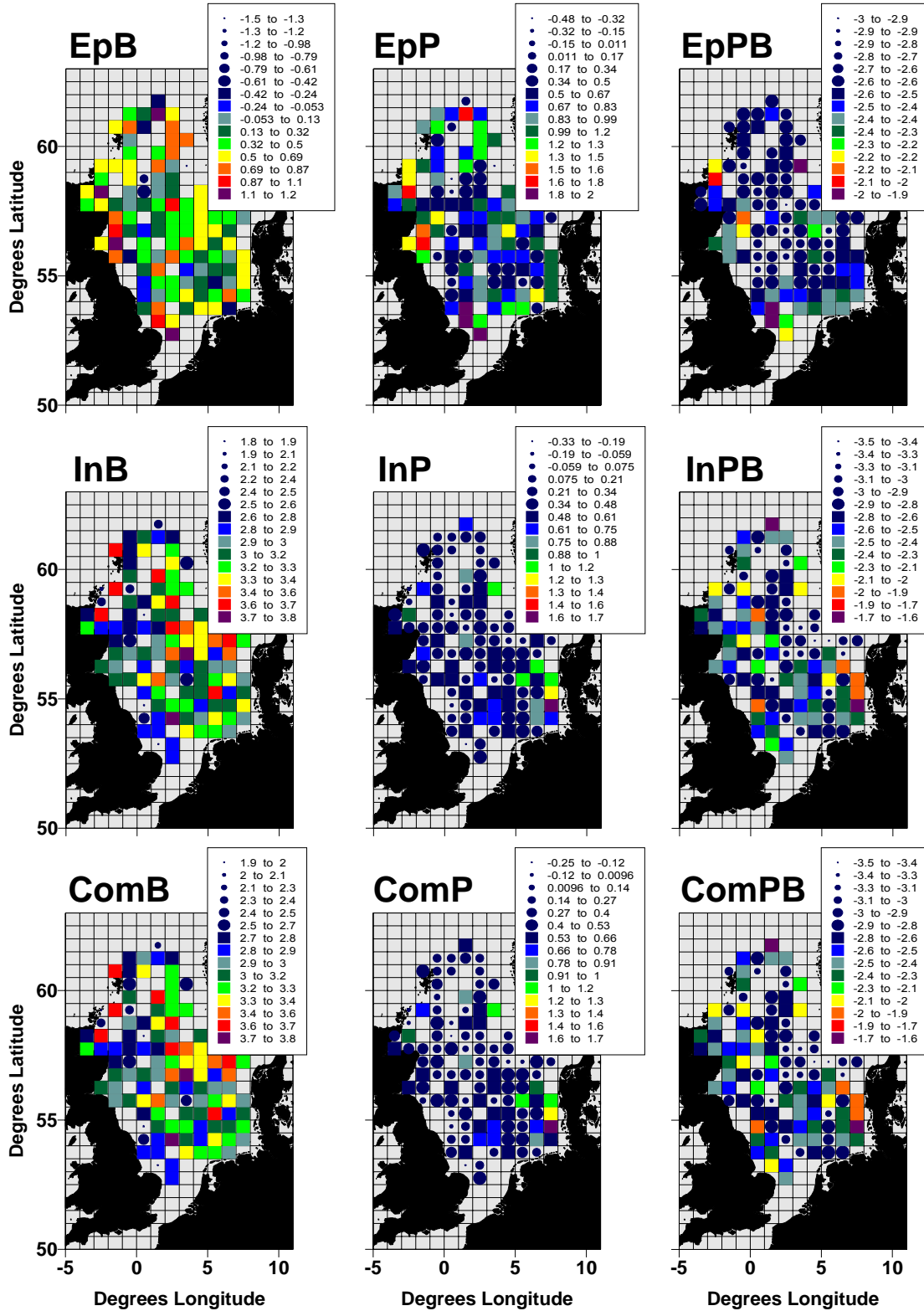
Figure 2.4.1.3: Spatial variation in the biomass density (B), production density (P), and P/B ratio (PB) of the epibenthic (Ep), infaunal (In) and combined (Com) components of the benthic invertebrate community.

2.4.2. Relationships between diversity and disturbance and between productivity and disturbance

Relationships between the five diversity metrics and three measures of disturbance are illustrated in Figure 2.4.2.1. Polynomial fits are plotted, since these were the relationships predicted by Huston's DEM, but in most cases the fits are far from convincing. Only the two relationships between the Hills N_1 and N_2 corrected to account for variability in catchability show any real indication of the expected unimodal relationship with the exploitation rate, also corrected to account for catchability (R^2 = 0.124 and 0.146 respectively). The major feature of the data appears to be a reduction in the variance of the various diversity metrics with increasing disturbance index values. Similar relationships between diversity and benthic productivity are explored in Figures 2.4.2.2 and 2.4.2.3. Again the unimodal relationships predicted by the DEM were not apparent, apart from some slight indication of a hump-shaped relationship between species richness and the P/B ratio of the infaunal component of the benthic invertebrate community. But yet again, the R^2 value of 0.065 was far from convincing.
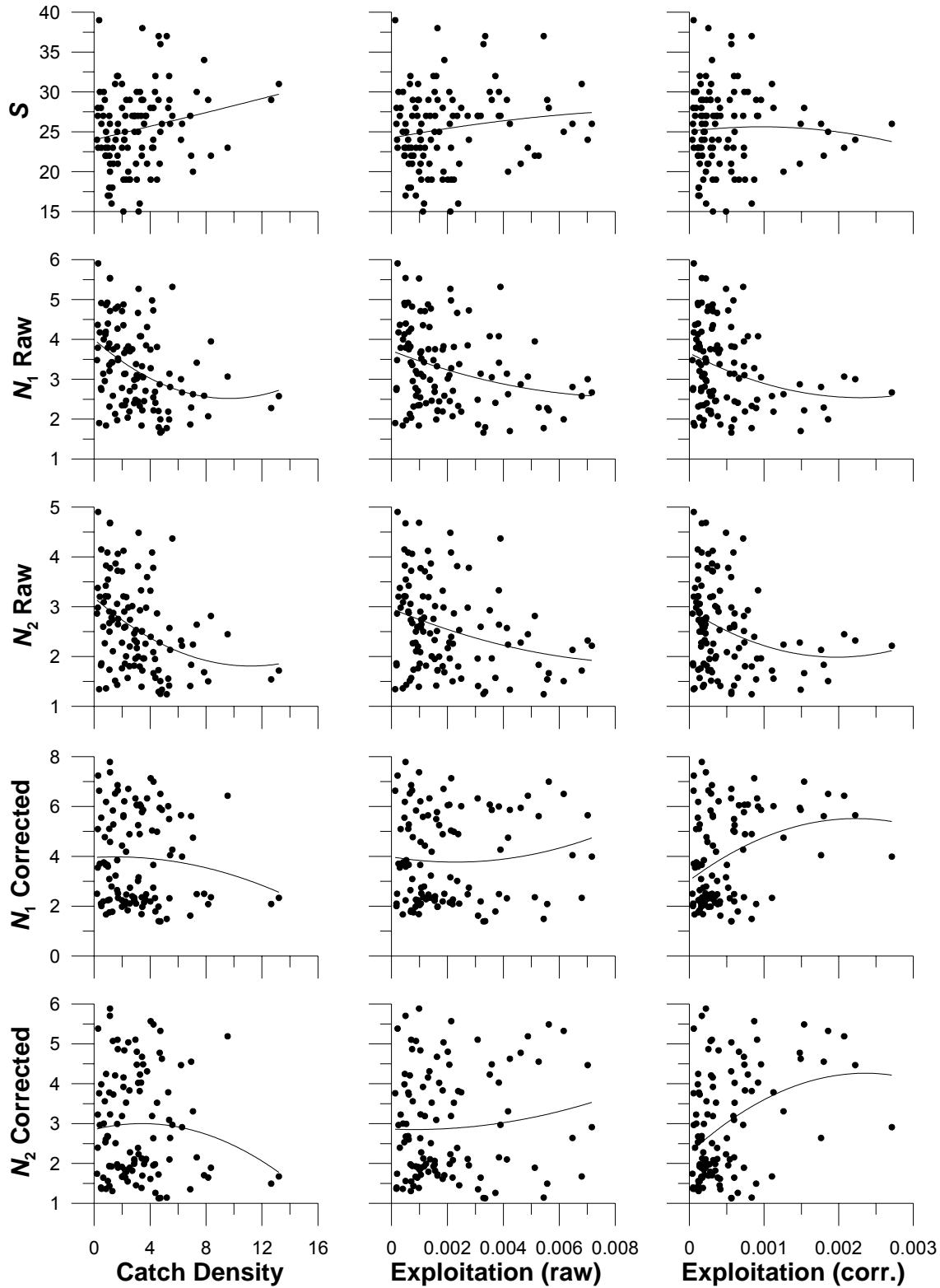
Figure 2.4.2.1: Relationships between species richness (S) and Hills N_1 and N_2, both raw and corrected to account for catchability and three indices of disturbance, the catch density and the exploitation rate both raw and corrected to account for catchability.
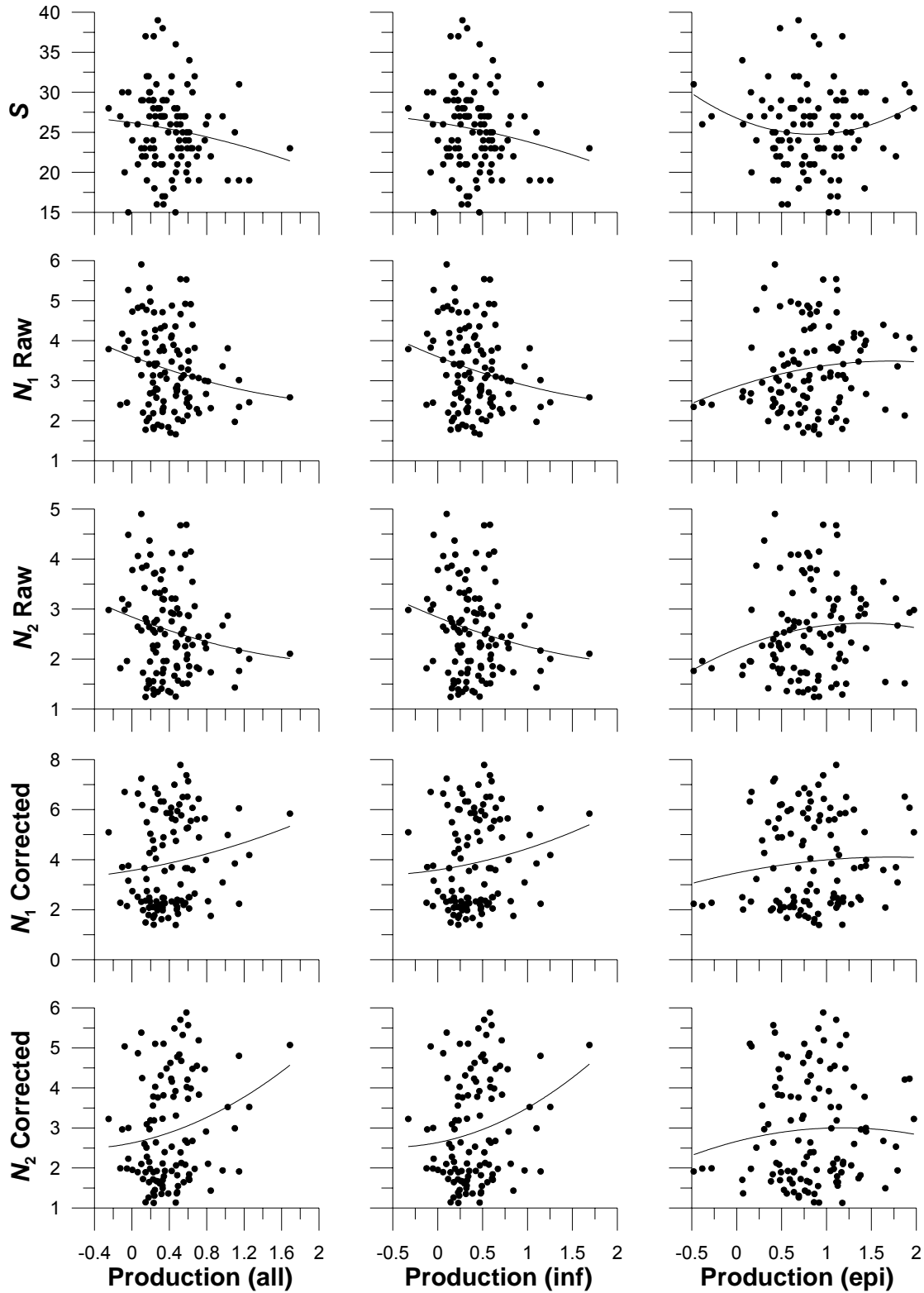
Figure 2.4.2.2: Relationships between species richness (S) and Hills N_1 and N_2, both raw and corrected to account for catchability and estimates of benthic secondary production by the whole benthic invertebrate community (all) and by the epifauna (epi) and infauna (inf) components separately.
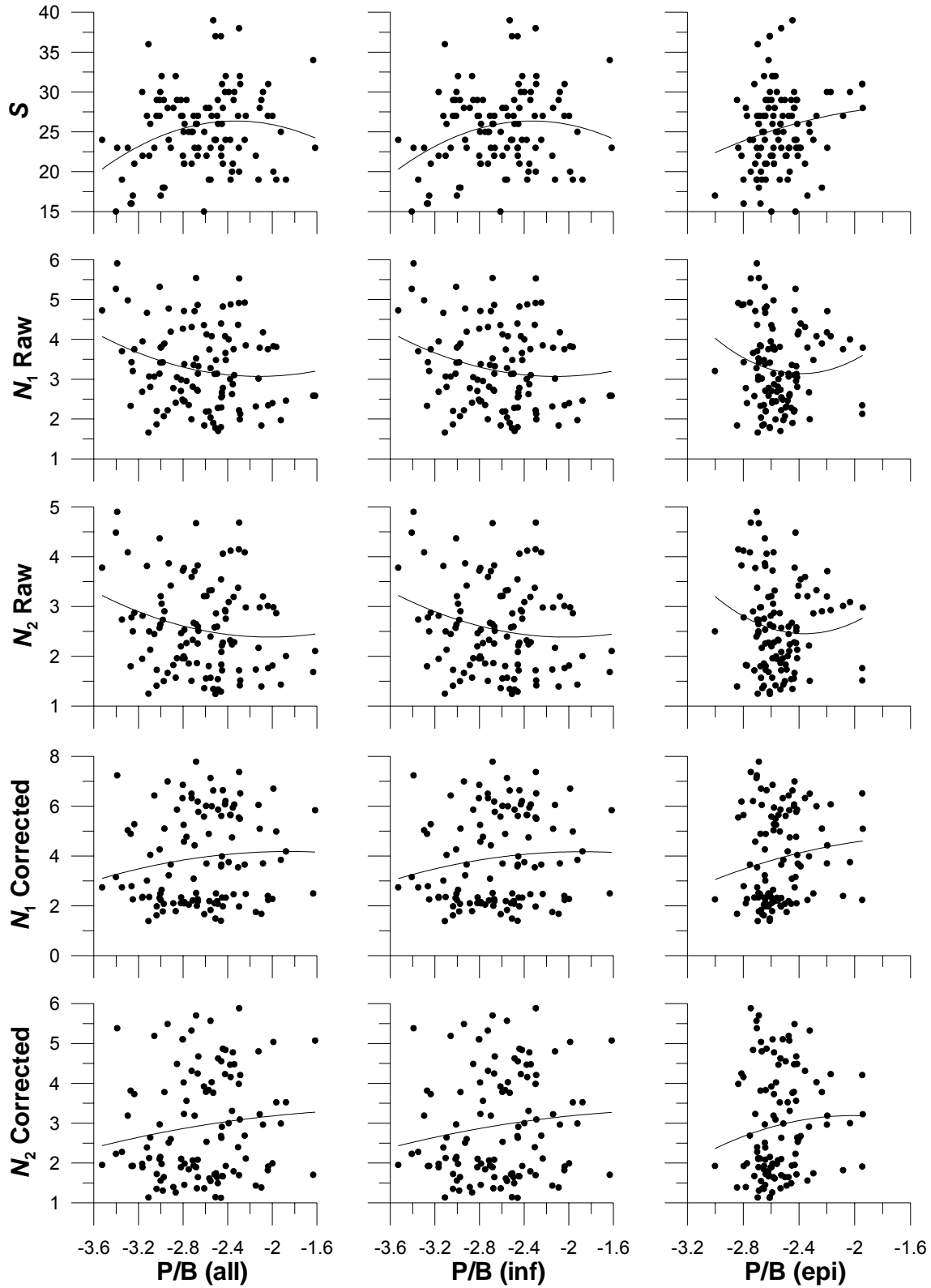
Figure 2.4.2.3: Relationships between species richness (S) and Hills N_1 and N_2, both raw and corrected to account for catchability and estimates of benthic P/B ratios for the whole benthic invertebrate community (all) and for the epifauna (epi) and infauna (inf) components separately.

2.4.3. Three-dimensional representation of the inter-relationships between diversity, production and disturbance.

Figures 2.4.3.1 to 2.4.3.4 illustrate the three dimensional representations of Huston's DEM relating diversity of the fish assemblage to disturbance caused by fish and production from the benthic invertebrate community. None of the plots suggested the distinctive cone-shaped 3D structure predicted by the model.
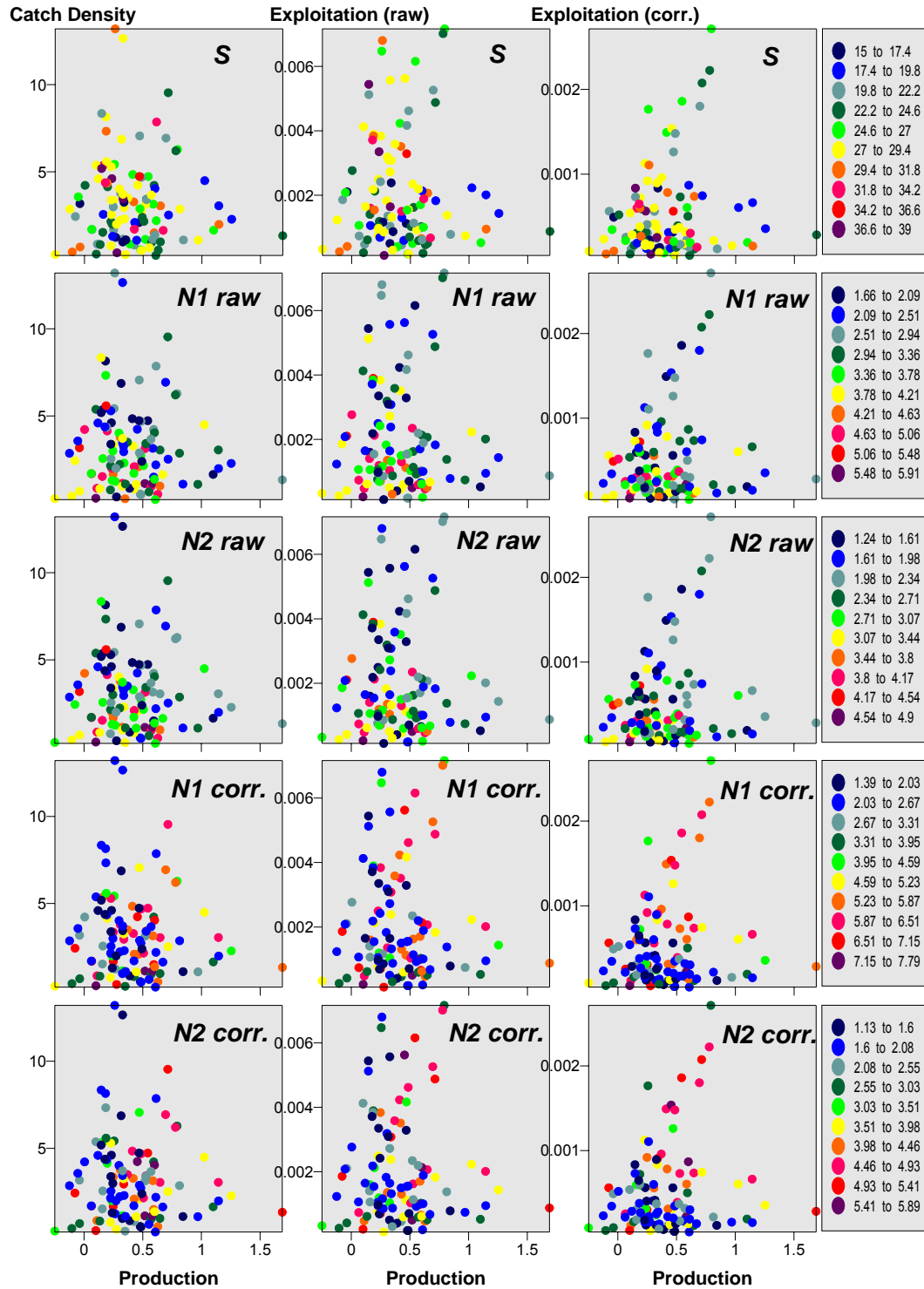
Figure 2.4.3.1: Three dimensional representations of the inter-relationships between productivity of the whole benthic invertebrate community, disturbance caused by fishing to the demersal fish community (as indicated by catch density and exploitation rates calculated on raw density estimates and density estimates corrected to account for variation in catchability in the GOV trawl), and species richness and diversity of the fish assemblage calculated on both raw survey data and survey data raised to take account of catchability.
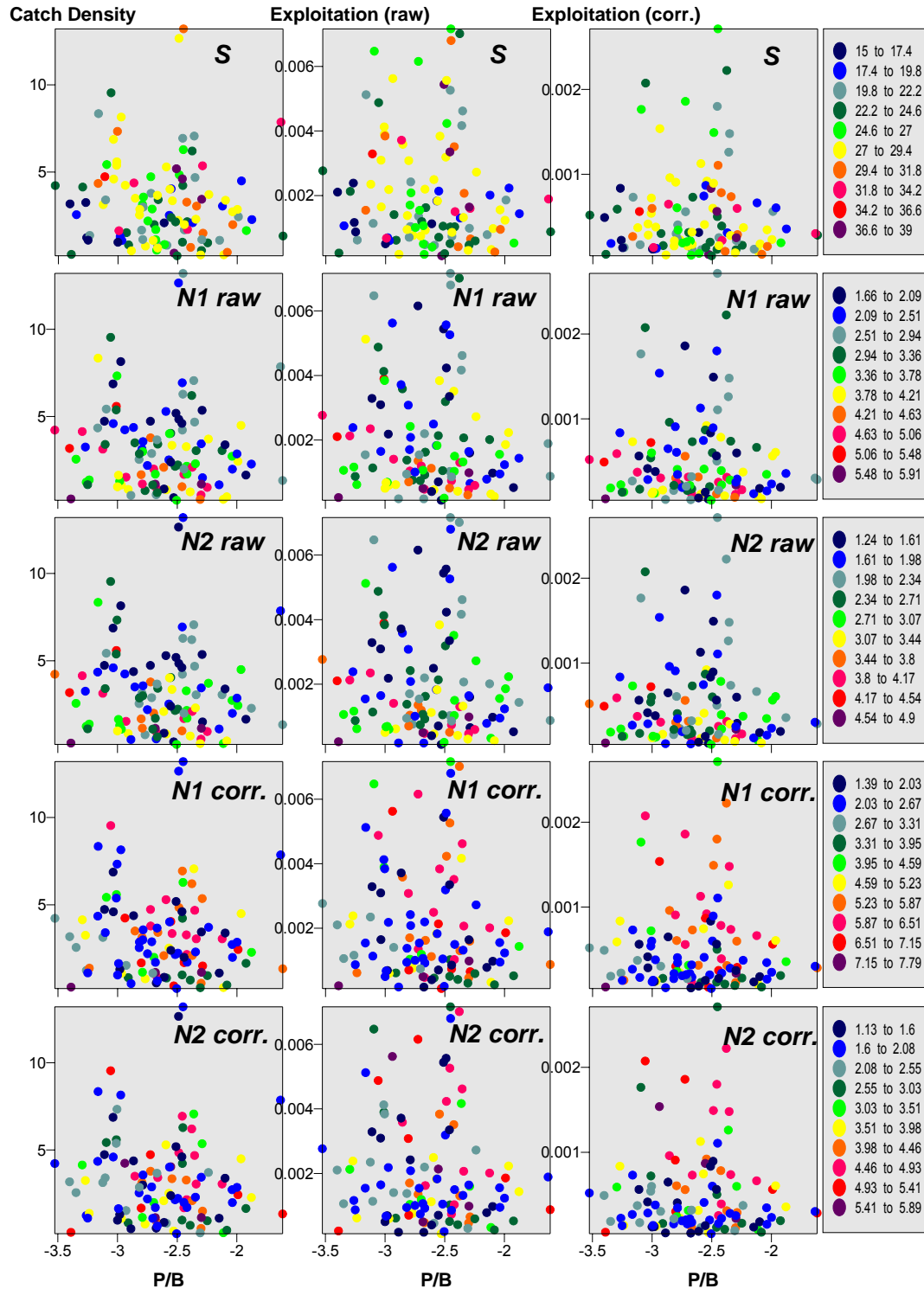
Figure 2.4.3.2: Three dimensional representations of the inter-relationships between the whole benthic invertebrate community P/B ratio, disturbance caused by fishing to the demersal fish community (as indicated by catch density and exploitation rates calculated on raw density estimates and density estimates corrected to account for variation in catchability in the GOV trawl), and species richness and diversity of the fish assemblage calculated on both raw survey data and survey data raised to take account of catchability.
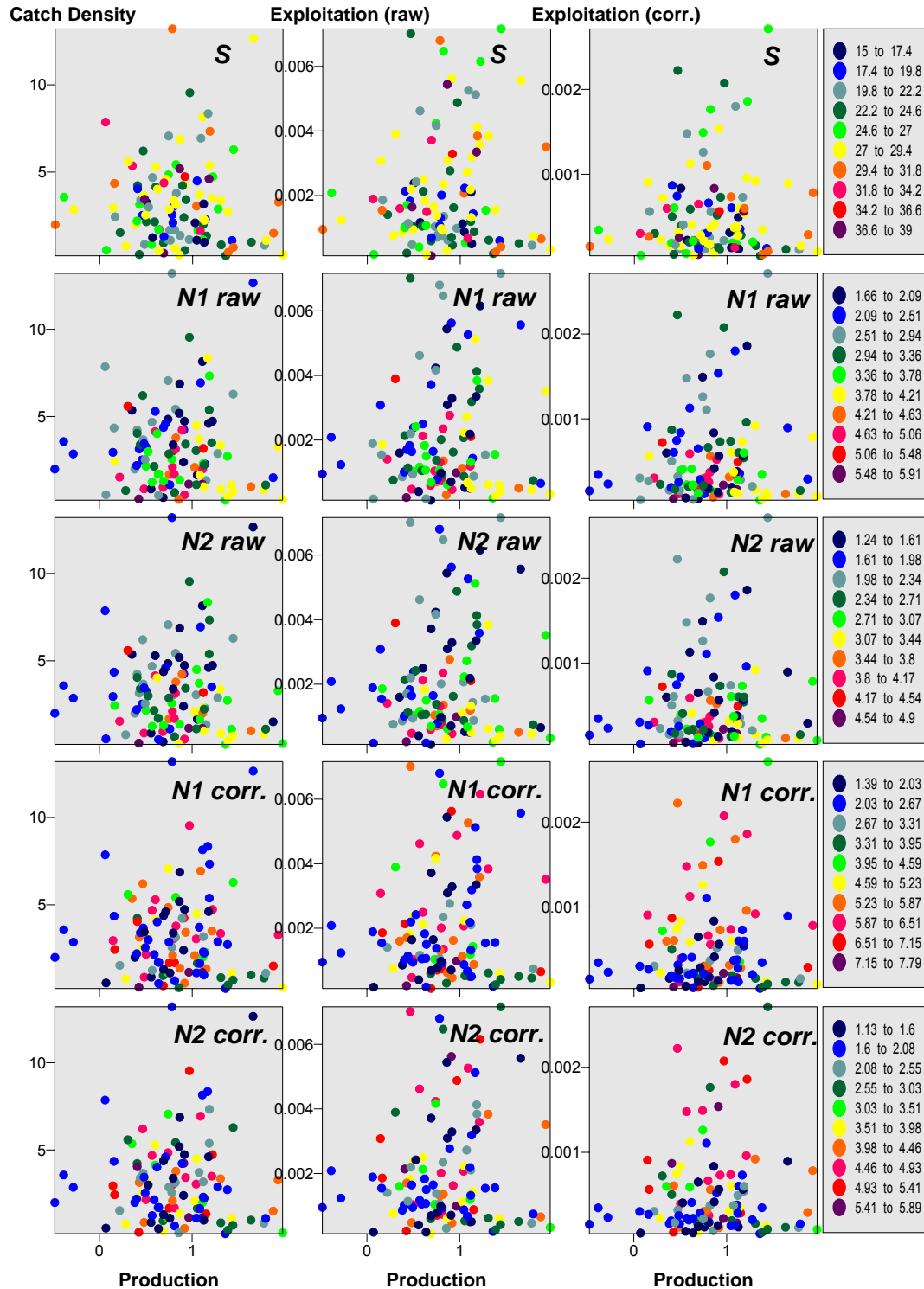
Figure 2.4.3.3: Three dimensional representations of the inter-relationships between productivity of the epifauna component of the benthic invertebrate community, disturbance caused by fishing to the demersal fish community (as indicated by catch density and exploitation rates calculated on raw density estimates and density estimates corrected to account for variation in catchability in the GOV trawl), and species richness and diversity of the fish assemblage calculated on both raw survey data and survey data raised to take account of catchability.
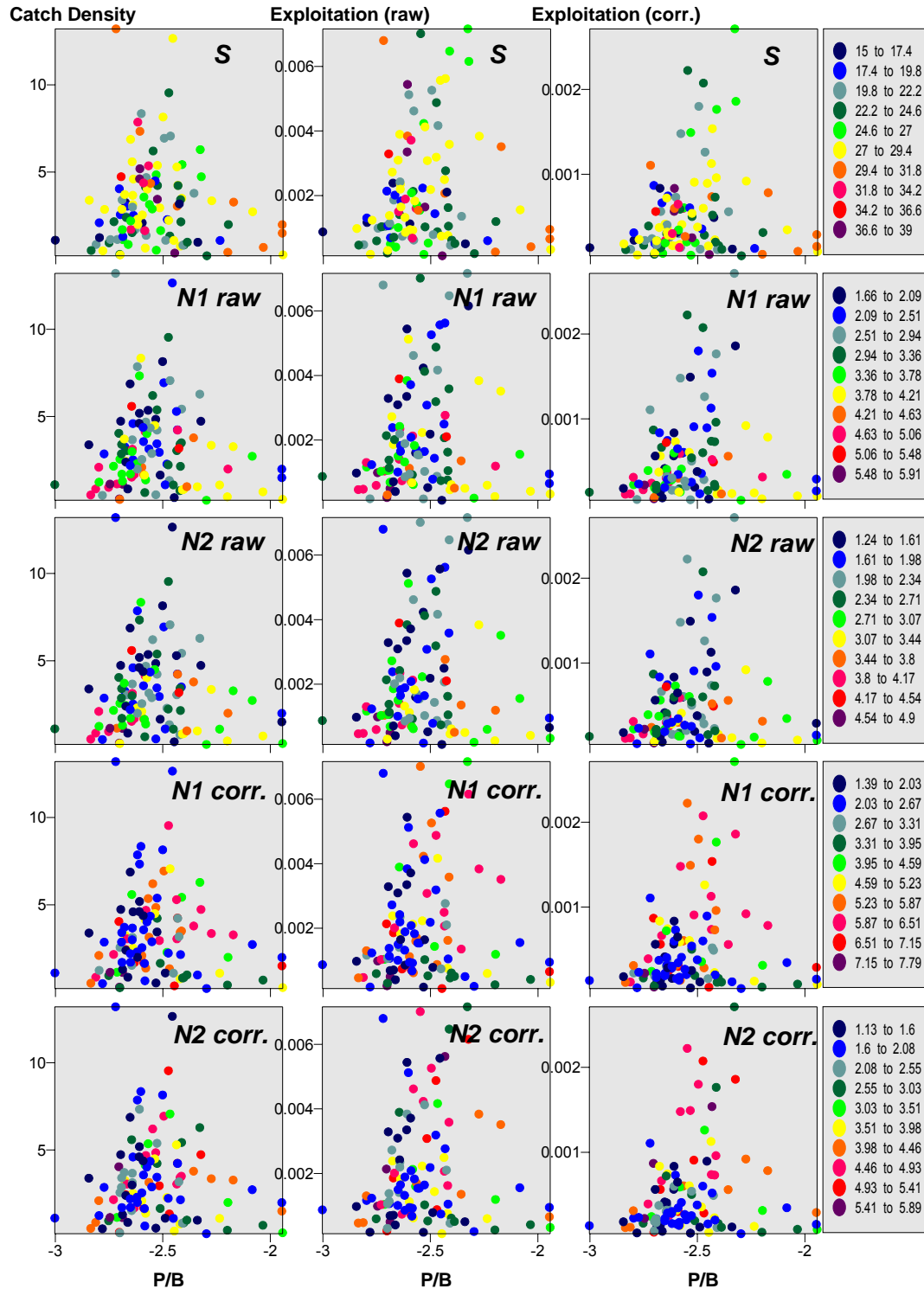
Figure 2.4.3.4: Three dimensional representations of the inter-relationships between the epifauna component of the benthic invertebrate community P/B ratio, disturbance caused by fishing to the demersal fish community (as indicated by catch density and exploitation rates calculated on raw density estimates and density estimates corrected to account for variation in catchability in the GOV trawl), and species richness and diversity of the fish assemblage calculated on both raw survey data and survey data raised to take account of catchability.

2.4.4. Relationships between diversity and disturbance at varying levels of productivity

None of the results displayed in section 2.4.3 above suggested that the relationships predicted between diversity and disturbance would be found. Given the data patterns, it was actually difficult to decide on particular productivity ranges to examine. Consequently for each productivity parameter, the data were split into three groups with approximately equal numbers of data points. Whilst numerous significant relationships between the fishing disturbance metrics and diversity indices were detected (Table 2.4.4.1), confirming that fishing affects fish diversity, examination of the data showed no real indication of a tendency for negative relationships at low productivity and positive relationships at high productivity predicted by the DEM (Figures 2.4.4.1 and 2.4.4.2).
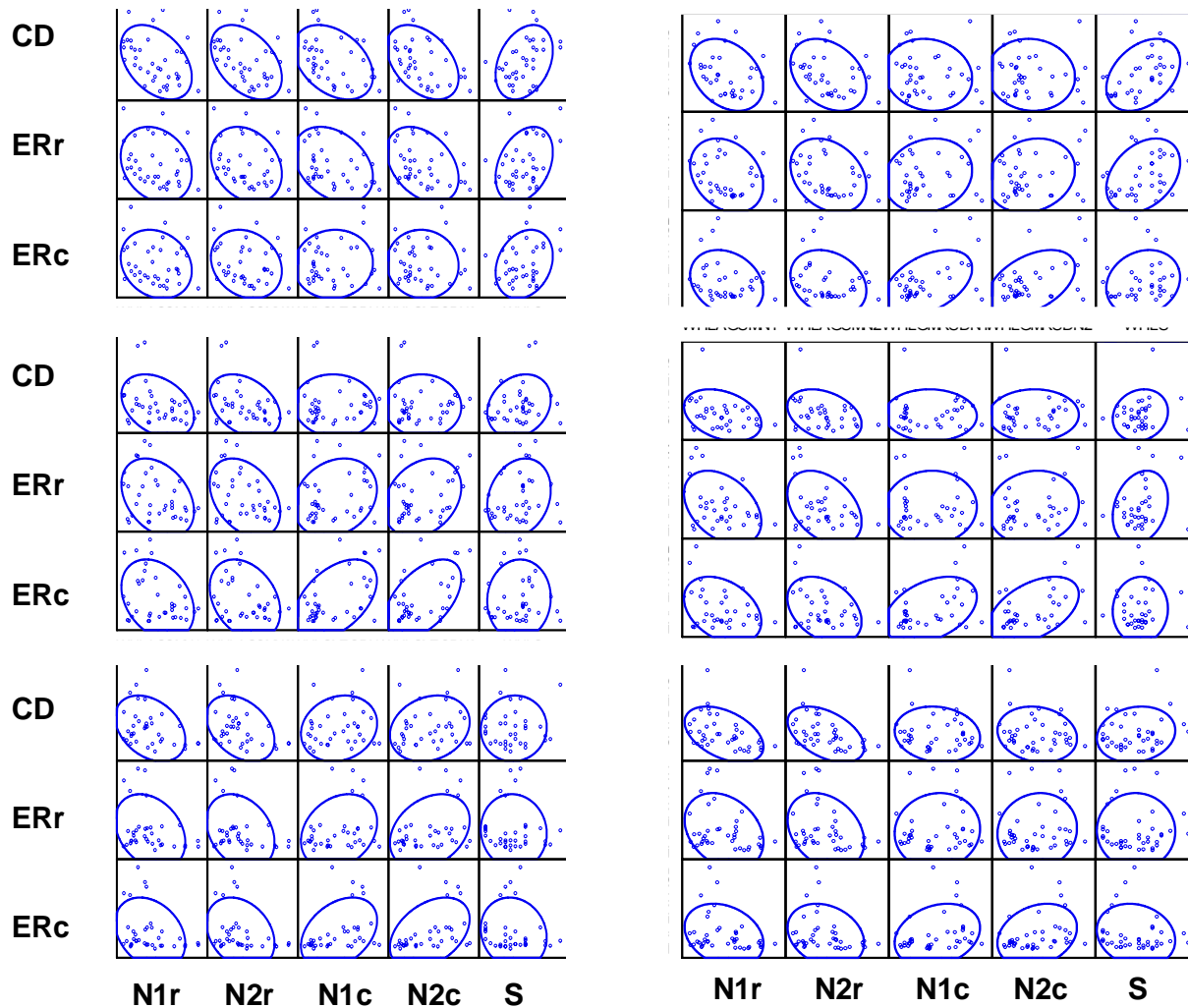
Figure 2.4.4.1: Relationships between Hills N_1 and N_2 based on raw (r) and catchability corrected (c) data and species richness (*S*) and the catch density (*CD*) and exploitation rates (*ER*) based on raw (r) and corrected (c) density data at low (top panels), medium (middle panels) and high (bottom panels) levels of productivity (left panels) and P/B ratios (right panels) for the whole benthic invertebrate assemblage.
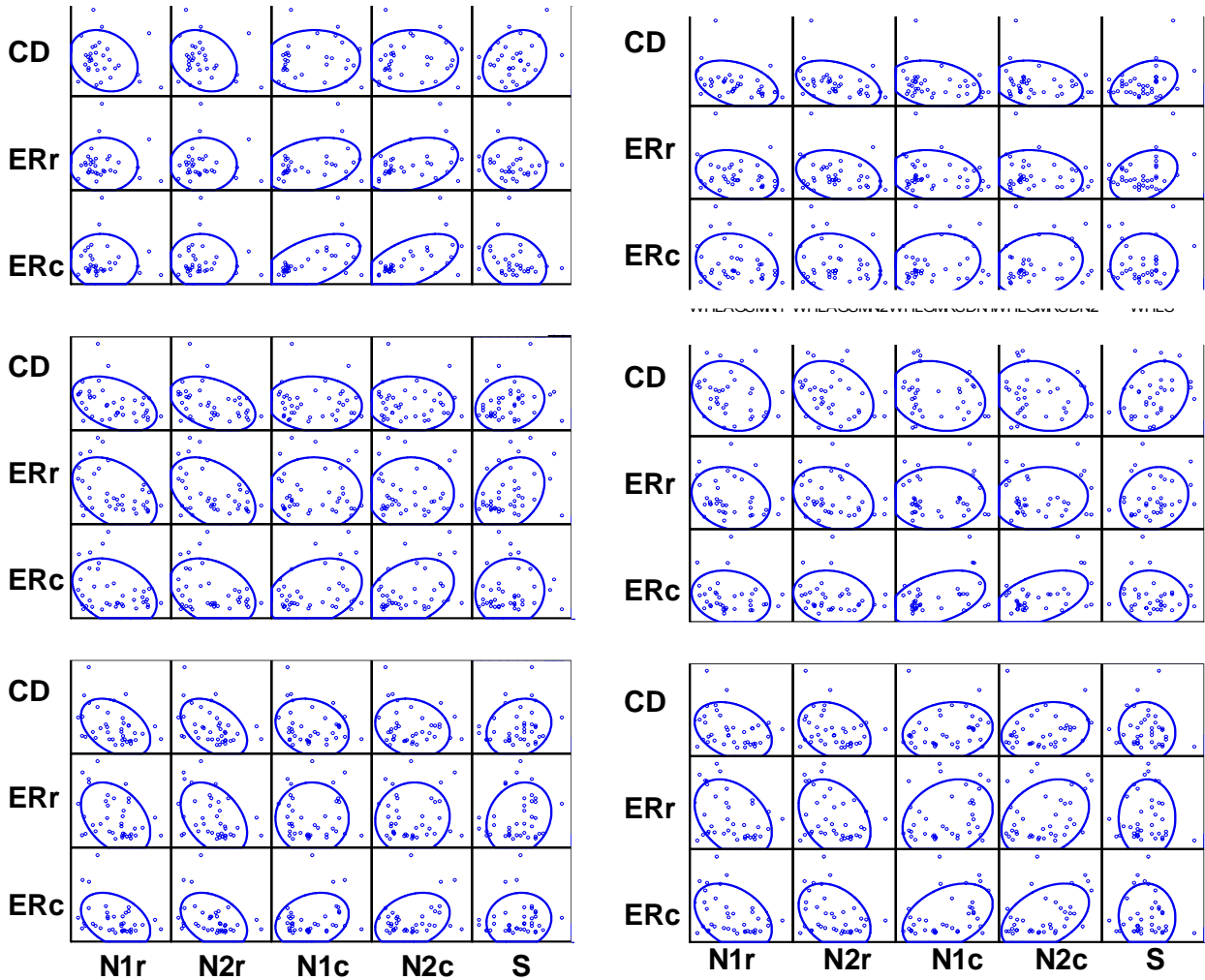
Figure 2.4.4.2: Relationships between Hills N_1 and N_2 based on raw (r) and catchability corrected (c) data and species richness (*S*) and the catch density (*CD*) and exploitation rates (*ER*) based on raw (r) and corrected (c) density data at low (top panels), medium (middle panels) and high (bottom panels) levels of productivity (left panels) and P/B ratios (right panels) for the epibenthic invertebrate assemblage.

Component	Log range	Disturbance	N_1 (raw)	N_2 (raw)	N_1 (cor)	N_2 (cor)	S
Whole P	<0.25	Catch density	.013	.009	.022	.011	.050
		Exploit. Rt. (raw)	.173	.134	.045	.026	.044
		Exploit. Rt. (cor)	.260	.230	.782	.792	.154
	0.25 to 0.50	Catch density	.035	.030	.728	.851	.205
		Exploit. Rt. (raw)	.036	.028	.198	.108	.228
		Exploit. Rt. (cor)	.060	.065	.003	.001	.813
	≥0.5	Catch density	.042	.028	.353	.241	.822
		Exploit. Rt. (raw)	.083	.092	.134	.074	.740
		Exploit. Rt. (cor)	.084	.095	.029	.016	.468
Whole P/B	<-2.8	Catch density	.059	.053	.547	.739	.025
		Exploit. Rt. (raw)	.119	.091	.394	.333	.038
		Exploit. Rt. (cor)	.166	.156	.007	.005	.334
	-2.8 to -2.48	Catch density	.054	.045	.868	.928	.421
		Exploit. Rt. (raw)	.025	.025	.861	.578	.164
		Exploit. Rt. (cor)	.040	.041	.021	.005	.839
	≥-2.48	Catch density	.004	.002	.453	.370	.378
		Exploit. Rt. (raw)	.073	.068	.700	.621	.923
		Exploit. Rt. (cor)	.101	.128	.133	.116	.305
Epi-benthos P	<0.6	Catch density	.223	.169	.794	.864	.130
		Exploit. Rt. (raw)	.966	.973	.090	.052	.554
		Exploit. Rt. (cor)	.704	.713	.003	.001	.162
	0.6 to 1.0	Catch density	.014	.014	.651	.763	.222
		Exploit. Rt. (raw)	.009	.009	.899	.980	.061
		Exploit. Rt. (cor)	.040	.047	.051	.035	.685
	≥1.0	Catch density	.011	.005	.172	.287	.245
		Exploit. Rt. (raw)	.015	.011	.993	.738	.267
		Exploit. Rt. (cor)	.017	.020	.144	.082	.627
Epi-benthos PB	<-2.64	Catch density	.020	.015	.137	.163	.027
		Exploit. Rt. (raw)	.141	.110	.282	.298	.046
		Exploit. Rt. (cor)	.251	.184	.340	.296	.823
	-2.64 to -2.5	Catch density	.220	.100	.289	.300	.121
		Exploit. Rt. (raw)	.259	.177	.926	.636	.427
		Exploit. Rt. (cor)	.300	.304	.012	.004	.436
	≥-2.5	Catch density	.050	.057	.386	.263	.706
		Exploit. Rt. (raw)	.028	.034	.132	.066	.953
		Exploit. Rt. (cor)	.018	.029	.016	.006	.868

Table 2.4.4.1: Correlation probabilities between groundfish diversity and disturbance metrics at different ranges of benthic invertebrate productivity.

2.4.5. Conclusions on Test 1

Relationships between the species richness and species diversity of the demersal fish assemblage of the North Sea, the exploitation rates by which these fish are impacted and the productivity of their benthic invertebrate prey resources failed to comply with Huston's dynamic equilibrium model.

2.5. Test 2: Diversity of Fish in the Fished Weight Classes

2.5.1. Test input data

Fishing is a size selective activity. Market forces encourage fishermen preferentially to target the larger fish since larger fish attract an economic premium. Fishing legislation also dictates size selection since almost all the commercially valuable species have a legal minimum landing size and minimum mesh sizes are enforced for all towed fishing gears in order to reduce the catches of under-sized fish. As a consequence, fishing disturbance on larger fish in the demersal fish community of the North Sea will be quite different to that on the smaller fish. Thus in assessing the effects of fishing on the species diversity of the demersal fish assemblage of the North Sea, such size-related differences in fishing disturbance inflicted on the community need to be taken into account. In this test of Huston's dynamic equilibrium model, we do this explicitly by considering as the "subject community", the species diversity of only fish in Log_2 weight classes 8 and above Figure 2.5.1.1. This corresponds generally to fish of 25cm and larger, around the minimum landing size for most commercial species (see Greenstreet *et al* 2007a: section 3.3.2.2 for derivation of these data). Many fish of this size in the North Sea are piscivorous to a very large extent, so the daily specific growth productivity of fish in the prey fish Log_2 weight classes 3 and 4 (between 8 and 32g in weight) provides an indication of the trophic resources available to the fished demersal fish community (Figure 2.5.1.2, see Greenstreet *et al* 2007a: section 3.4.2 for derivation of these data). Landings data, when raised to take account of discarding, indicate spatial variation in the amount of biomass removed by the fisheries from each ICES rectangle. Relating these catch estimates to the biomass present then produces estimates of spatial variation in fishing exploitation rates (Figure 2.5.1.3, see Greenstreet *et al* 2007d: section 9 for derivation of these data).
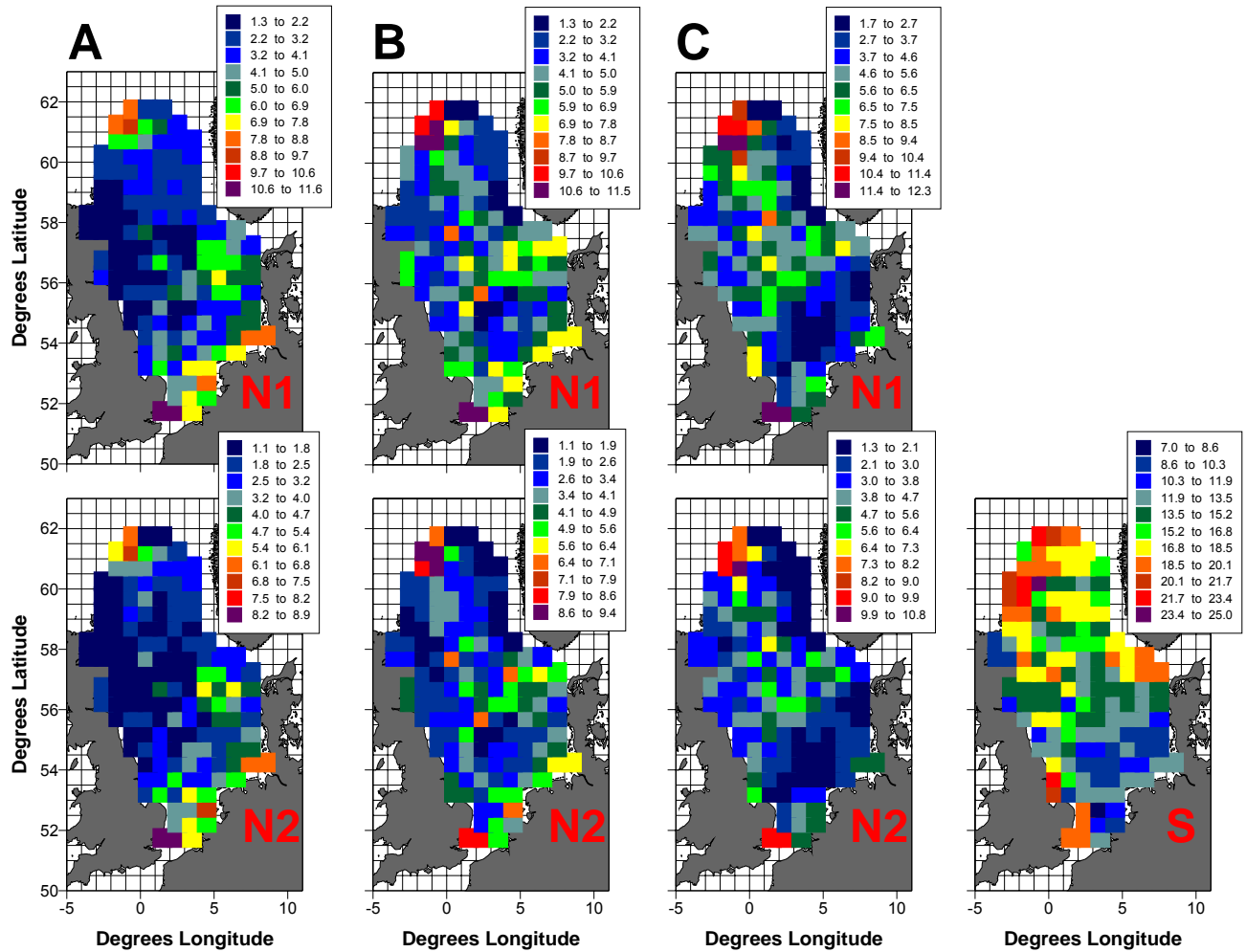
Figure 2.5.1.1: Spatial variation in the species richness (S) and species diversity (Hill's N1 and N2) of North Sea demersal fish belonging to the fished weight classes, Log$_2$ weight classes 8 and higher. A: Aggregated species totals across all 20 hauls in each rectangle. B: Based on geometric mean 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.
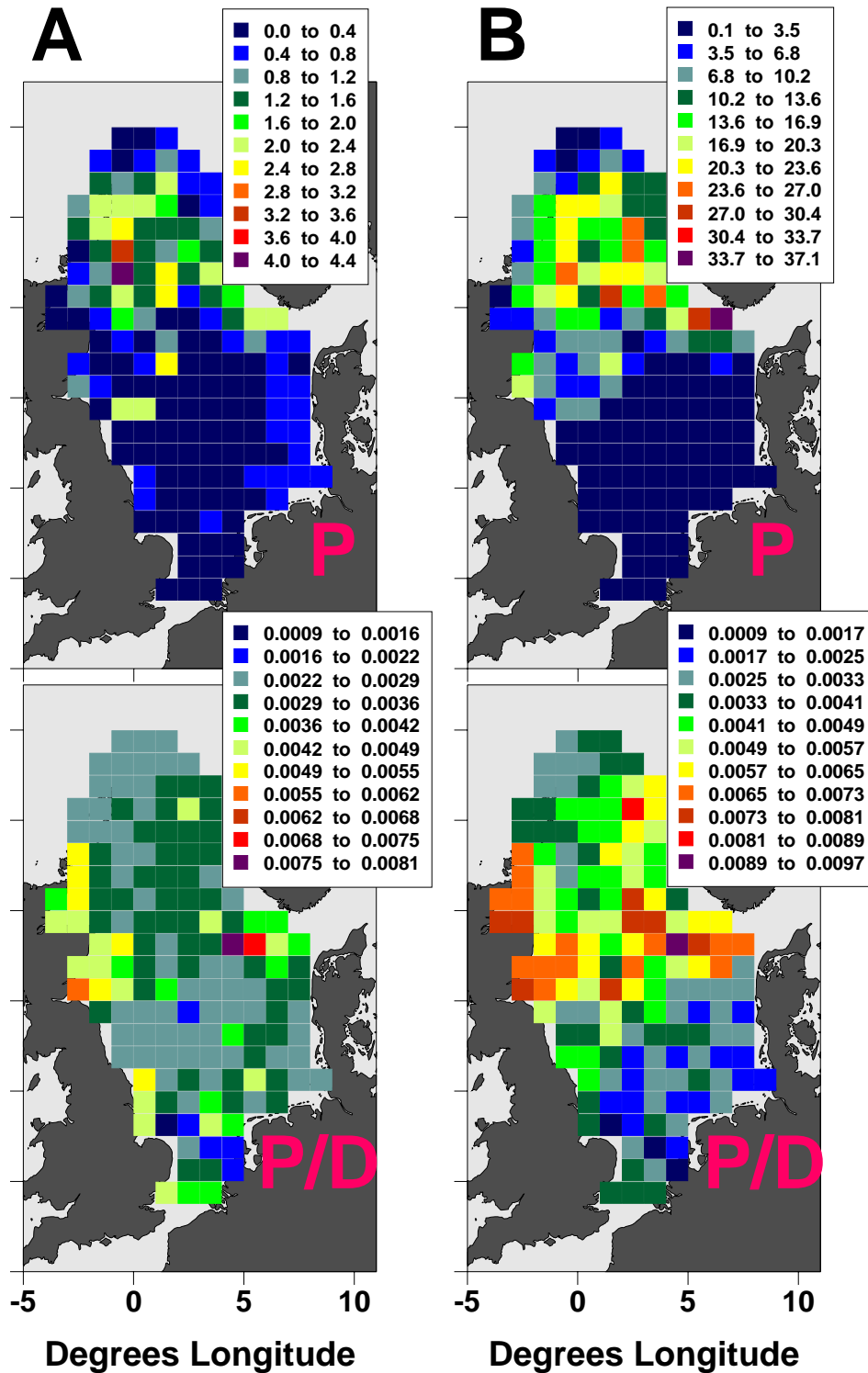
Figure 2.5.1.2: Spatial variation in the growth production (P, Kg.Km^{-2}.d^{-1}), and production per unit biomass (P/D) of demersal fish in the "prey-fish" weight range, Log$_2$ weight classes 3 and 4. A: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raw uncorrected (for catchability) trawl densities. B: Based on geometric mean densities calculated across all 20 hauls in each rectangle on the raised corrected (for catchability) trawl densities
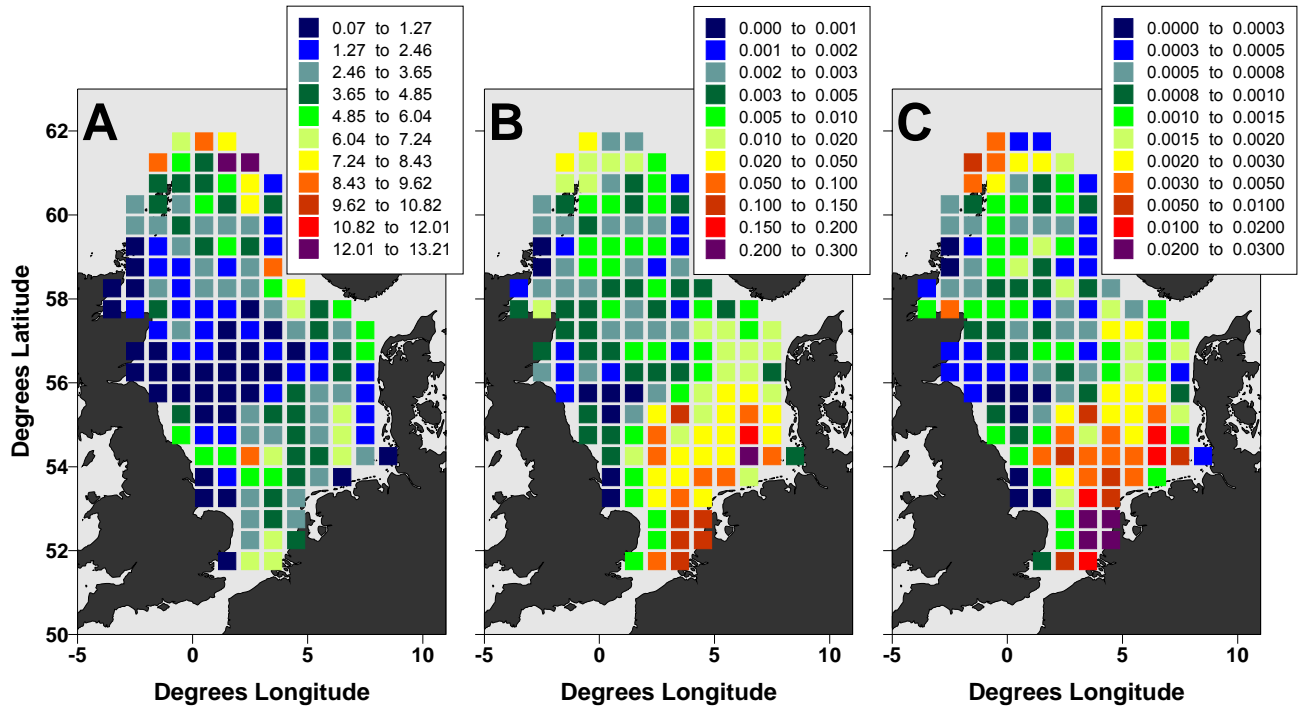
Figure 2.5.1.3: Spatial variation in daily third quarter catch densities (kg.km^{-2}.d^{-1}) (A) and exploitation rates of cod, haddock, whiting, saithe, plaice, and sole combined belonging to Log$_2$ weight-classes 7 and higher averaged over the period 1997 to 2004 based on geometric mean densities calculated on the raw uncorrected (for catchability) trawl densities (B) and based on geometric mean densities calculated on the raised corrected (for catchability) trawl densities (C) across all 20 hauls in each rectangle. Note non-linear scaling in panels B and C.

2.5.2. Relationships between diversity and disturbance and between productivity and disturbance

Significant unimodal relationships were detected between species richness of the fished component of the demersal fish community and productivity in the prey fish component of the community for three of the four productivity parameters. Only *P/B* ratios based on the raw GOV trawl survey data (not correcteded to take account of species- and size-related catchability) failed to produce a significant relationship (Figure 2.5.2.1). However, both Hill's N_1 and N_2 diversity indices calculated for the fished component of the demersal fish community, whether calculated on aggregated sums or geometric means of the raw survey data, or geometric means of the catchability-corrected survey data, appeared unrelated to variation in the productivity of the prey fish weight classes, however this was calculated (Figure 2.5.2.1). Figure 2.5.2.1 shows data only for Hill's N_2. Relationships for Hill's N_1 were similar to these, so only Hill's N_2 plots are shown since this index is less closely related to species richness, which is essentially Hill's N_0 index (Hill 1973). Examination of the effect of fishing disturbance on the fished component of the demersal fish community again suggested that only species richness was affected. Species richness was negatively and linearly related to the log transformed exploitation rate, whether calculated on the raw or the catchability-corrected survey data (Figure 2.5.2.2). Log transformation was necessary because of the extremely skewed distributions of the exploitation rate data, which tended to be low in most ICES rectangles, and relatively high in just a few. However, none of the species diversity indices was related to any of the disturbance indicators, no matter how these parameters were derived (Figure 2.5.2.2).
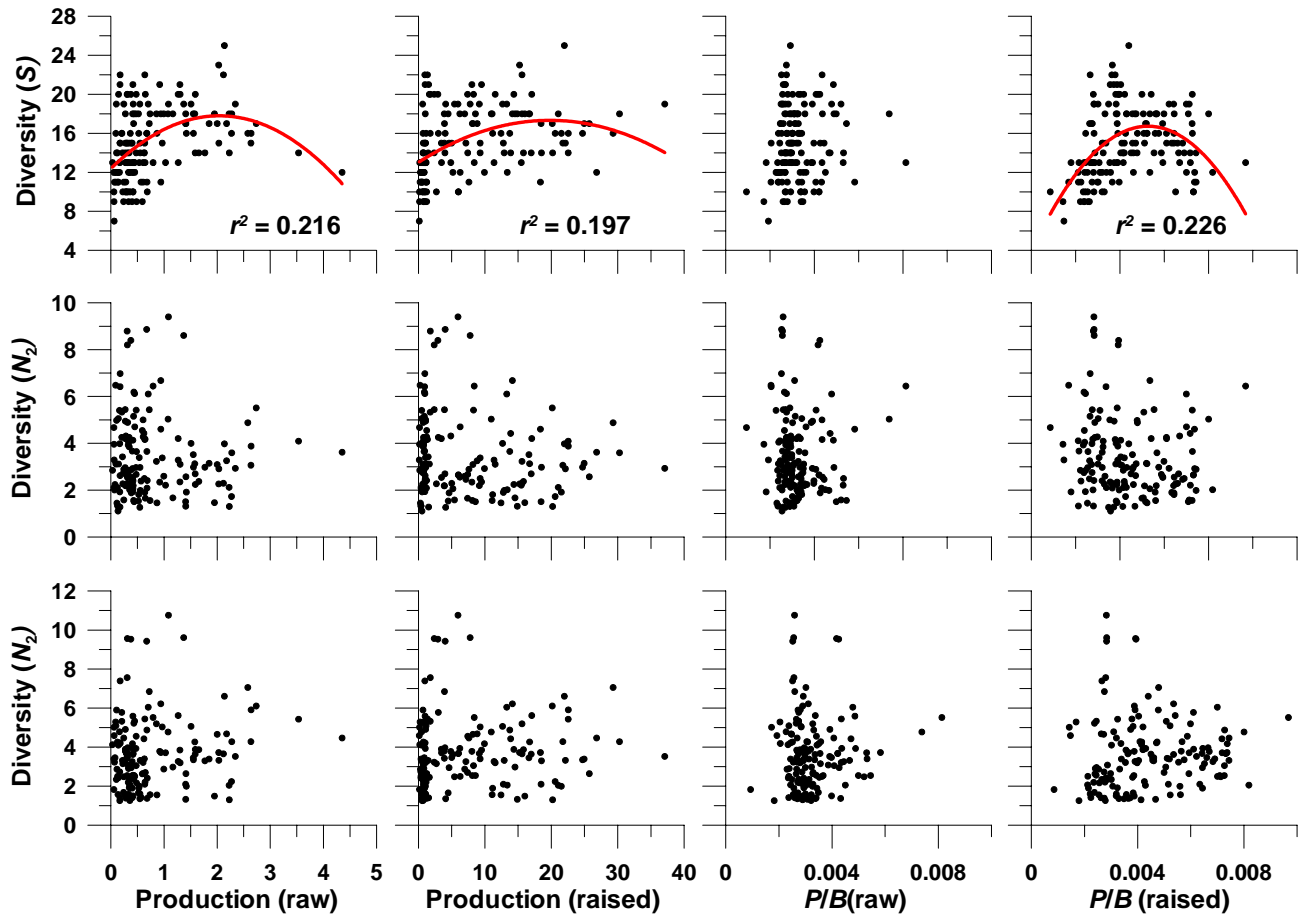
Figure 2.5.2.1: Relationships between species richness (upper panels), species diversity represented by Hill's N_2 based on the raw survey data (middle panels), and species diversity represented Hill's N_2 calculated on the catchability-corrected survey data (lower panels) of the fished component of the demersal fish community (Log$_2$ weight classes 8 and higher) and four indicators of the productivity of the prey fish component Log$_2$ weight classes 3 and 4) of the demersal fish community. Production is the daily biomass increase resulting from fish growth calculated on both the raw and the catch-corrected (raised) survey data (kg.km^{-2}.d^{-1}), and the P/B data are these production quantities divided by the biomass density present, again based on both the raw and the raised survey data.
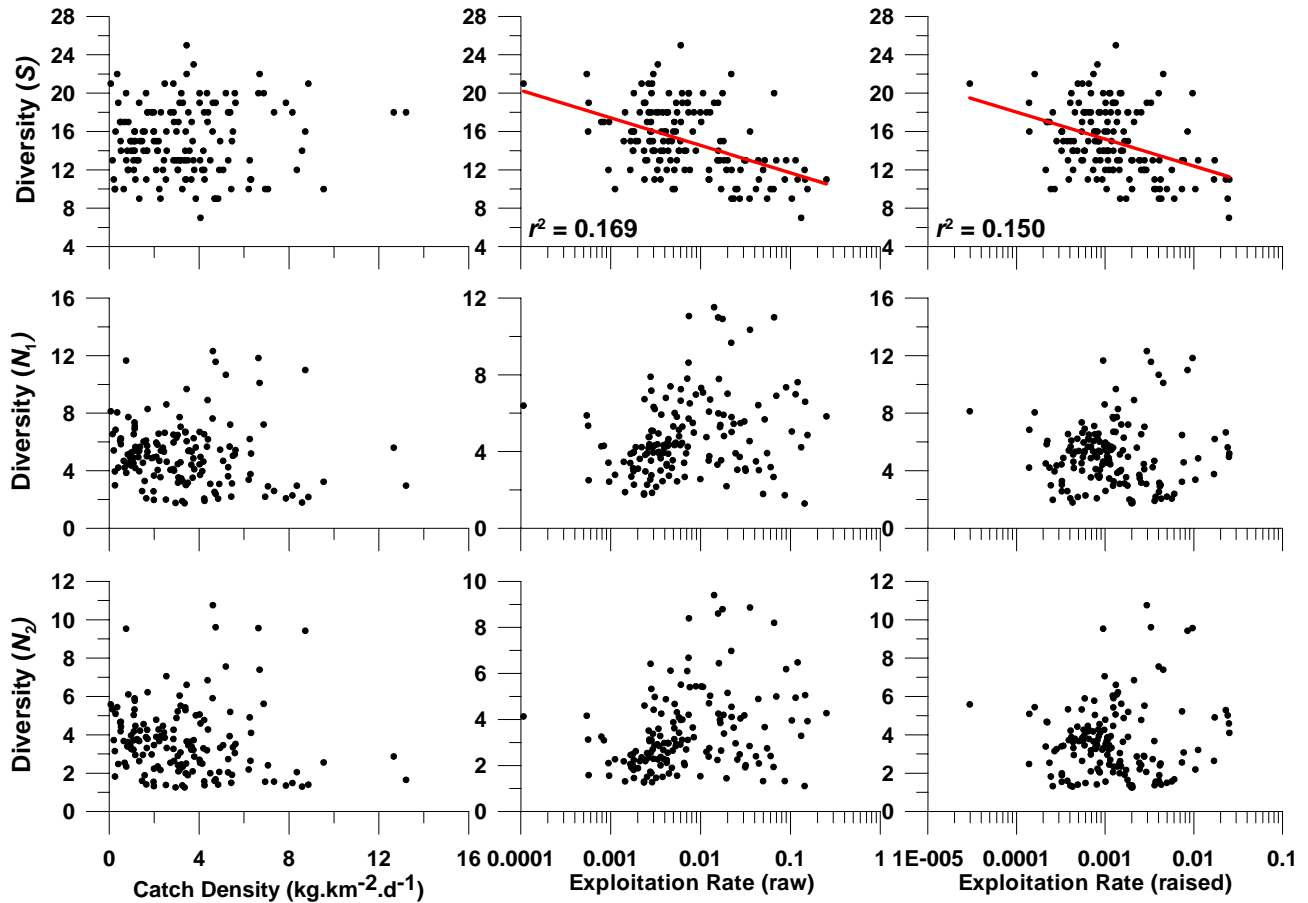
Figure 2.5.2.2: Relationships between (upper panels) species richness, (middle panels) species diversity represented by Hill's N_1 based on the catchability-corrected survey data (left and right panels) and raw survey data (centre panel), and (lower panels) species diversity represented Hill's N_2 calculated on the catchability-corrected survey data (left and right panels) and raw survey data (centre panel) of the fished component of the demersal fish community (Log_2 weight classes 8 and higher) and three indicators of the disturbance to this component of the demersal fish community caused by fishing. Catch density is the actual biomass of fish caught per day per square kilometre (taking account of discarding), while the exploitation rates are the catch density divided by the density of fish of Log_2 weight classes 7 and higher (including weight classes discarded) calculated on the raw survey data and the survey data raised to take account of species- and size-related variation in catchability in the GOV trawl.

2.5.3. Three-dimensional representation of the inter-relationships between diversity, production and disturbance.

Prior to plotting Huston's three-dimensional representation of the relationships between productivity, disturbance and diversity, the relationship between disturbance and productivity was examined (Figure 2.5.3.1). This revealed highly skewed, non-normal bivariate distributions. These appeared to indicate that the exploitation rate, in particular, of fish in the fished weight-classes component of the demersal fish community was highest in ICES rectangles where productivity of the prey-fish weight-classes was lowest. These distributions would have made three dimensional representation of the inter-relationships between productivity, disturbance and diversity extremely difficult. However, log transformation of both the productivity and the disturbance parameters produced more normalised bivariate distributions enabling this to be done. After log-transformation, the exploitation rates based on the

catch-corrected survey data remained significantly negatively correlated with both the daily production and the production:biomass ratio when both parameters were also calculated on the catch-corrected survey data.
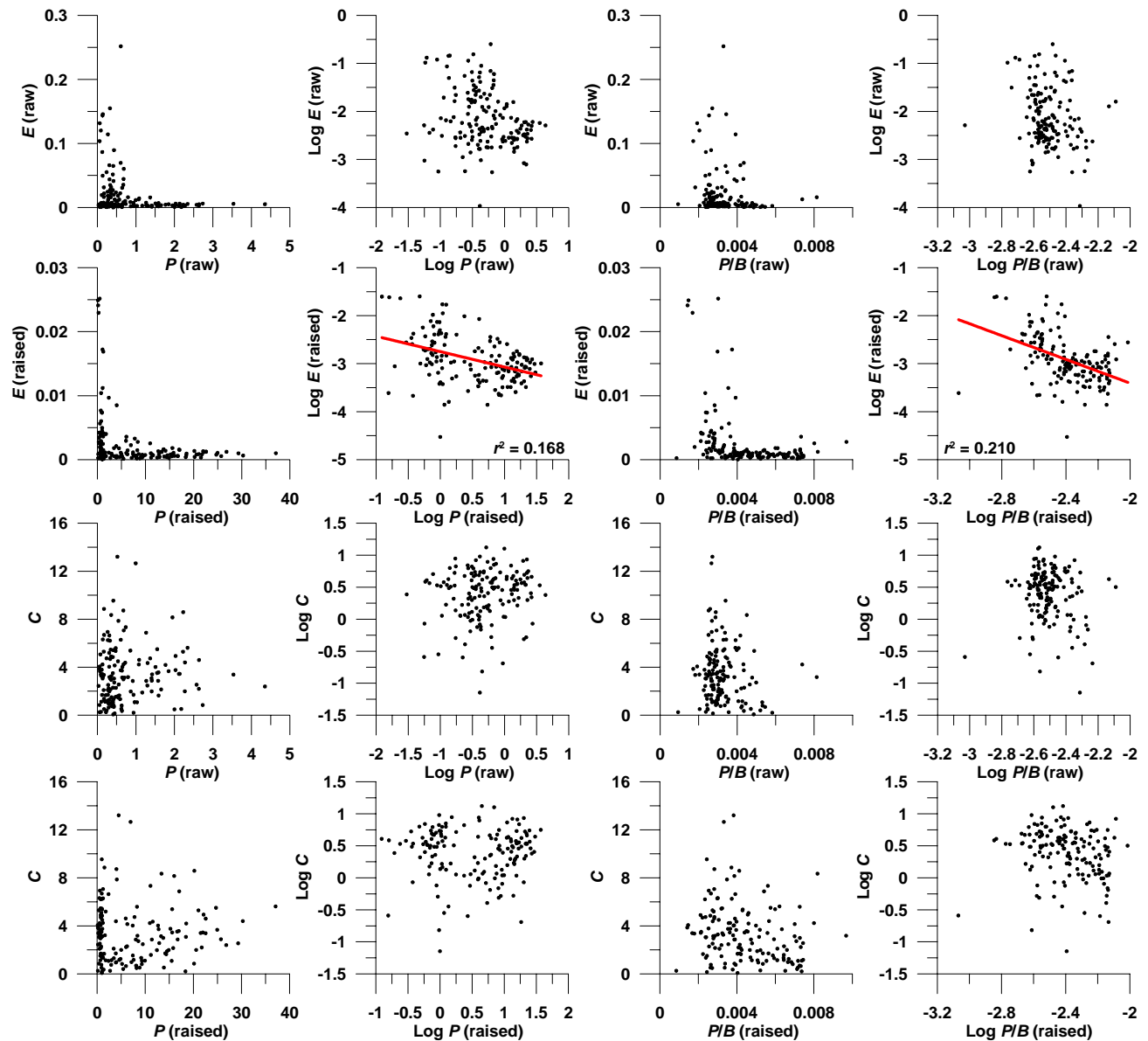
Figure 2.5.3.1: Examination of the relationships between disturbance (where C is the daily catch density (kg.km^{-2}.d^{-1}), E(raw) is the exploitation rate calculated on the estimates of density derived from the raw survey data, and E(raised) is the exploitation rate calculated on the catch-corrected estimates of density) and production (where P(raw) and P/B(raw) are the daily production densities (kg.km^{-2}.d^{-1}) and production: biomass ratios calculated on the estimates of density derived from the raw survey data and P(raised) and P/B(raised) are the same parameters calculated on the catch-corrected estimates of density).

Three dimensional, Huston style, representations of the inter-relationships between productivity, disturbance, and diversity were constructed for a variety of different parameter derivations and combinations (Figures 2.5.3.2 to 2.5.3.9). None of the Hill's N_1 and N_2 "tests" came close to

suggesting the 3D conical shape that characterises the dynamic equilibrium model. At any point in the 2D productivity-disturbance space, N_1 and N_2 values were extremely variable and both high and low N_1 and N_2 values were distributed throughout the 2D disturbance-productivity domain. However more of a pattern was evident for species richness. High species richness values tended to be located in the high productivity – low disturbance quadrant of the 2D productivity-disturbance space, while low species richness values tended to be located in the opposite corner of the domain. This was particularly true when disturbance was measured as one of the two exploitation rate parameters. When catch density was used as the disturbance parameter, species richness tended to be high in the high catch – high productivity zone. This was because high catch densities tended to occur where biomass densities were also highest, giving rise to relatively low exploitation rates.
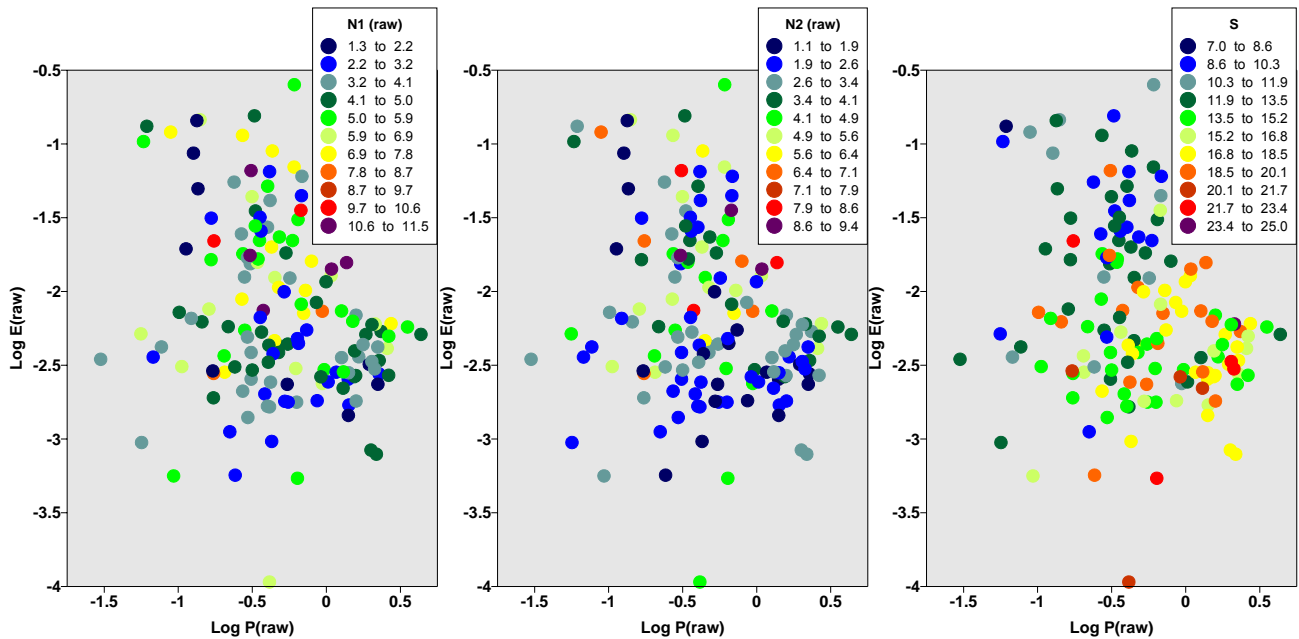
Figure 2.5.3.2: Three dimensional representations of the inter-relationships between productivity of the prey-fish component of the demersal fish community, disturbance caused by fishing to the fished component of the demersal fish community, and species richness and diversity of the fished component of the demersal fish community. P is the production density ($kg.km^{-2}.d^{-1}$), E the exploitation rate, and S, $N1$ and $N2$ are the species richness and Hill's diversity indices, all calculated on the raw survey data.
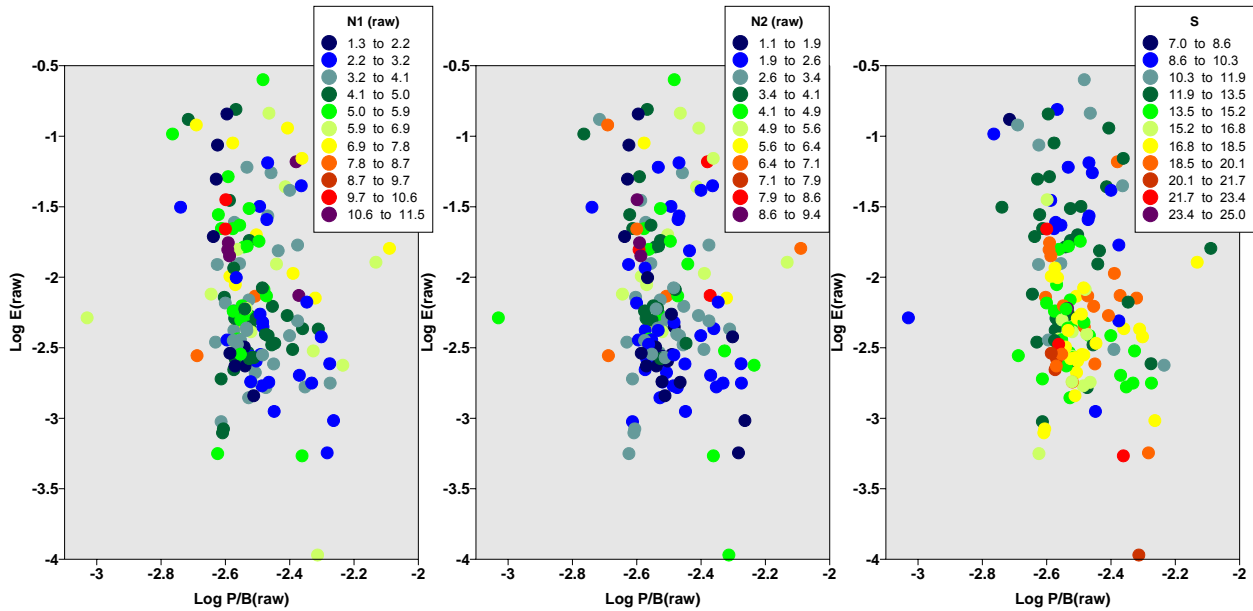
Figure 2.5.3.3: Three dimensional representations of the inter-relationships between productivity of the prey-fish component of the demersal fish community, disturbance caused by fishing to the fished component of the demersal fish community, and species richness and diversity of the fished component of the demersal fish community. *P/B* is the production:biomass ratio, *E* the exploitation rate, and *S*, *N*1 and *N*2 are the species richness and Hill's diversity indices, all calculated on the raw survey data.

Figure 2.5.3.4: Three dimensional representations of the inter-relationships between productivity of the prey-fish component of the demersal fish community, disturbance caused by fishing to the fished component of the demersal fish community, and species richness and diversity of the fished component of the demersal fish community. *P* is the production density (kg.km^{-2}.d^{-1}), *E* the exploitation rate, and *S*, *N*1 and *N*2 are the species richness and Hill's diversity indices, all calculated on the catchability-corrected raised survey data.

Figure 2.5.3.5: Three dimensional representations of the inter-relationships between productivity of the prey-fish component of the demersal fish community, disturbance caused by fishing to the fished component of the demersal fish community, and species richness and diversity of the fished component of the demersal fish community. *P/B* is the production:biomass ratio, *E* the exploitation rate, and *S*, *N*1 and *N*2 are the species richness and Hill's diversity indices, all calculated on the catchability-corrected raised survey data.

Figure 2.5.3.6: Three dimensional representations of the inter-relationships between productivity of the prey-fish component of the demersal fish community, disturbance caused by fishing to the fished component of the demersal fish community, and species richness and diversity of the fished component of the demersal fish community. *P* is the production density (kg.km^{-2}.d^{-1}), *C* the catch density (kg.km^{-2}.d^{-1}), and *S*, *N*1 and *N*2 are the species richness and Hill's diversity indices, all calculated on the raw survey data.

Figure 2.5.3.7: Three dimensional representations of the inter-relationships between productivity of the prey-fish component of the demersal fish community, disturbance caused by fishing to the fished component of the demersal fish community, and species richness and diversity of the fished component of the demersal fish community. *P/B* is the production:biomass ratio, *C* the catch density (kg.km^{-2}.d^{-1}), and *S*, *N*1 and *N*2 are the species richness and Hill's diversity indices, all calculated on the raw survey data.
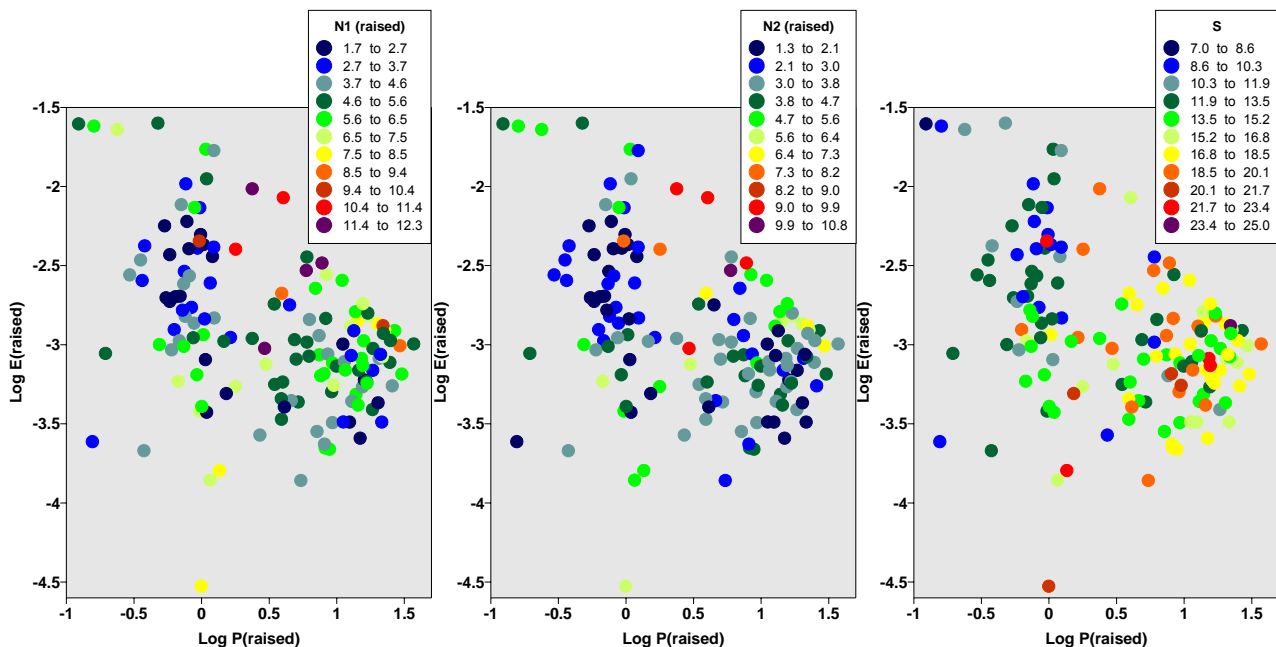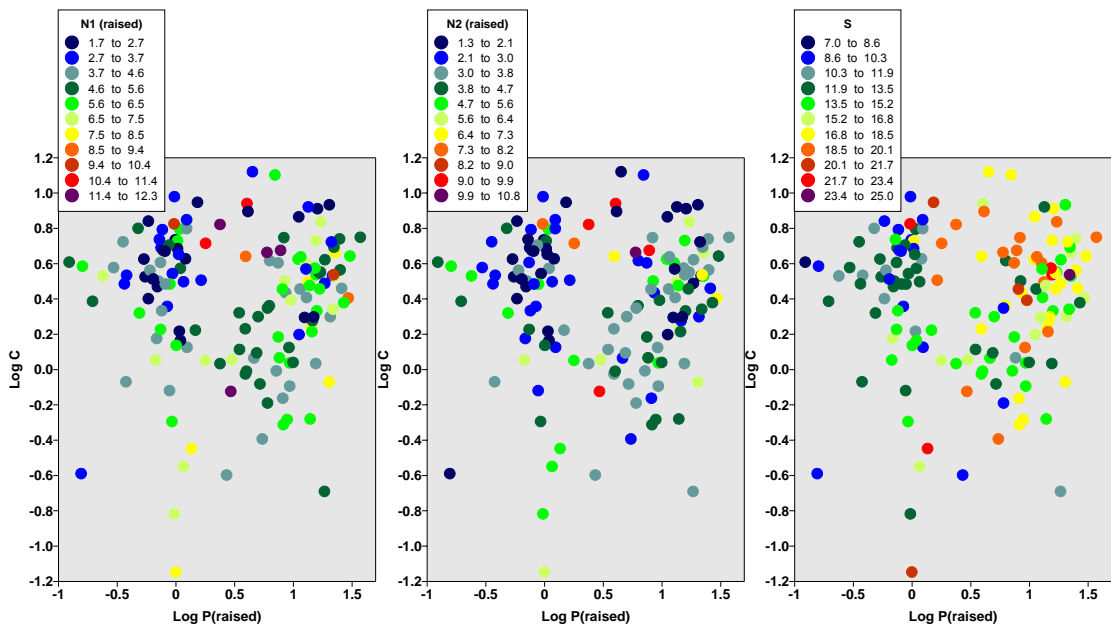

Figure 2.5.3.8: Three dimensional representations of the inter-relationships between productivity of the prey-fish component of the demersal fish community, disturbance caused by fishing to the fished component of the demersal fish community, and species richness and diversity of the fished component of the demersal fish community. *P* is the production density (kg.km^{-2}.d^{-1}), *C* the catch density (kg.km^{-2}.d^{1}), and *S*, *N*1 and *N*2 are the species richness and Hill's diversity indices, all calculated on the raised survey data.
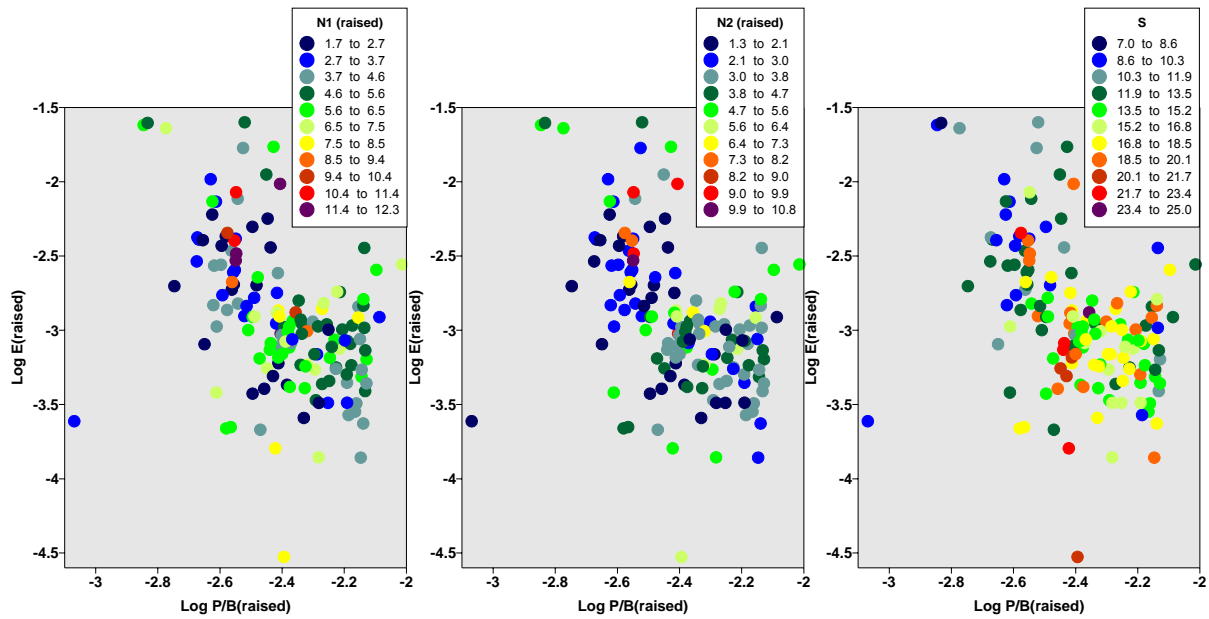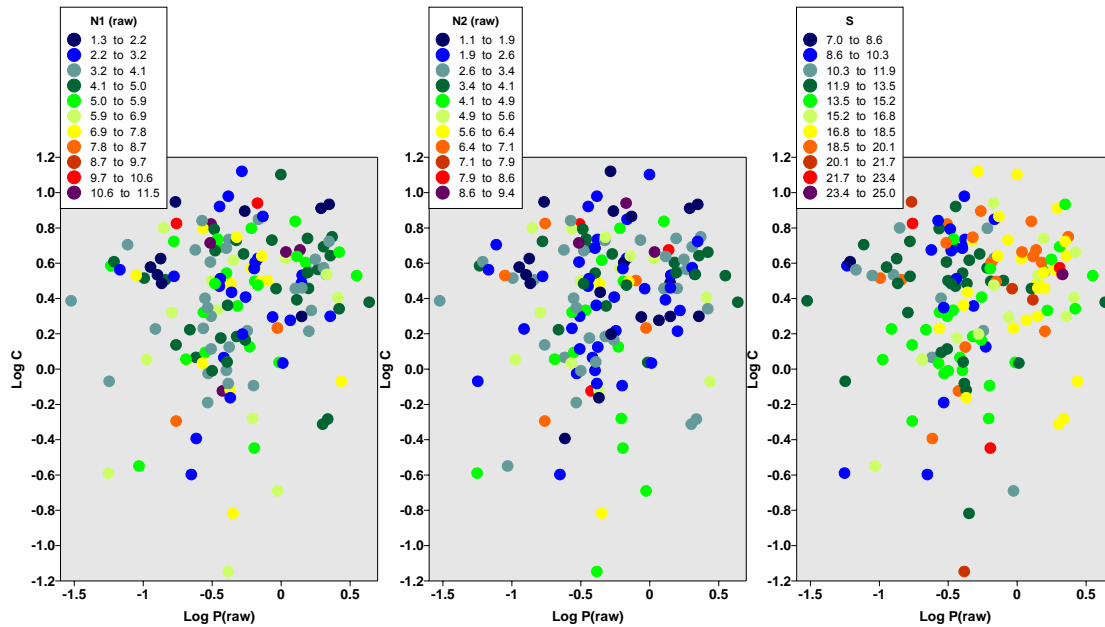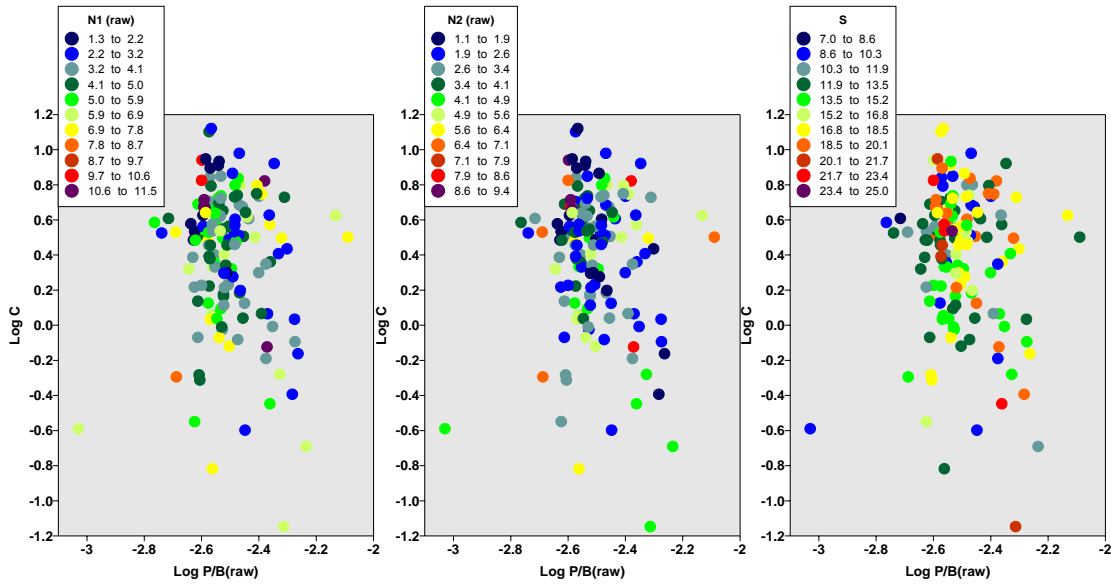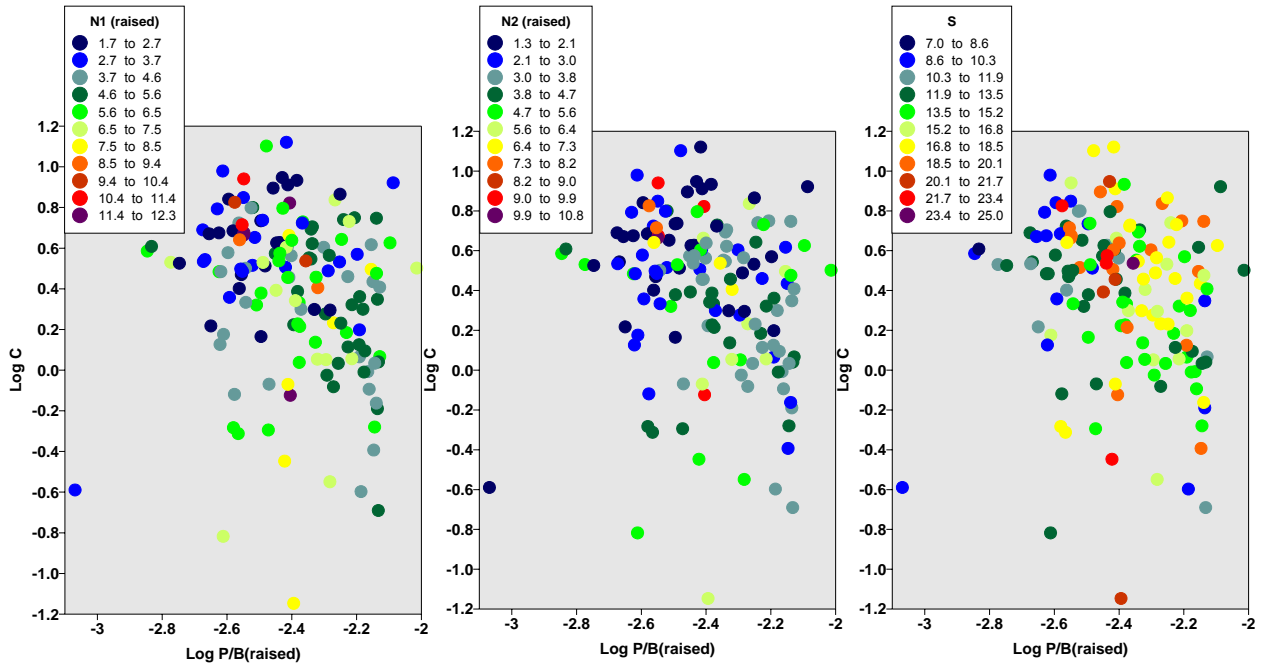
Figure 2.5.3.9: Three dimensional representations of the inter-relationships between productivity of the prey-fish component of the demersal fish community, disturbance caused by fishing to the fished component of the demersal fish community, and species richness and diversity of the fished component of the demersal fish community. *P/B* is the production:biomass ratio, *C* the catch density (kg.km^{-2}.d^{-1}), and *S*, *N*1 and *N*2 are the species richness and Hill's diversity indices, all calculated on the raised survey data.

2.5.4. Relationships between diversity and disturbance at varying levels of productivity

The three dimensional representations of inter-relationships between productivity, disturbance, and diversity presented in section 2.5.3 all generally failed to comply with the pattern anticipated by Huston's dynamic equilibrium model. Only for species richness of the fished component of the demersal fish community was there any indication that examination of the relationships between diversity and disturbance at varying levels of productivity within the prey-fish weight classes of the community might be worthwhile. This was done for the two exploitation rates, calculated on the raw survey data (Figure 2.5.4.1) and on the catchability-corrected raised survey data (Figure 2.5.4.2). For the former productivity of prey fish was also calculated on the raw survey data, while for the latter it was calculated on the raised survey data. Again these results are difficult to interpr*et al*ong the lines of the dynamic equilibrium, but they tended to confirm that species richness of the fished component of the demersal community was significantly negatively correlated with the extent to which that component of the assemblage was exploited by demersal fisheries, and that this relationship was ameliorated by increased productivity. Multiple linear regression confirmed this view. For both derivations of the productivity and exploitation parameters, both productivity and exploitation rate significantly influenced species richness (Table 2.5.4.1).
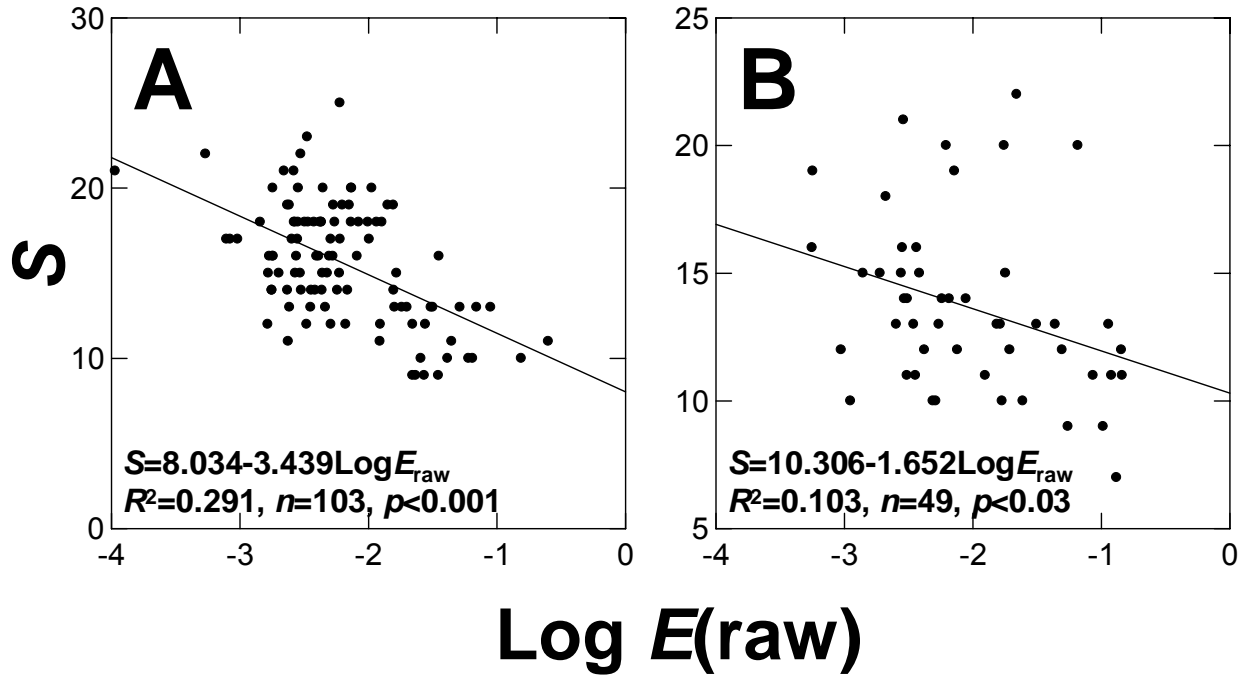
Figure 2.5.4.1: Examination of the relationship between species richness (S) of the fished component of the demersal fish community with variation in exploitation rate (E) at two levels of productivity of the prey-fish component of the demersal fish community (with both E and P calculated on the raw survey data). A: Log P(raw) $\geq$0.05; B: Log P(raw) <0.05.
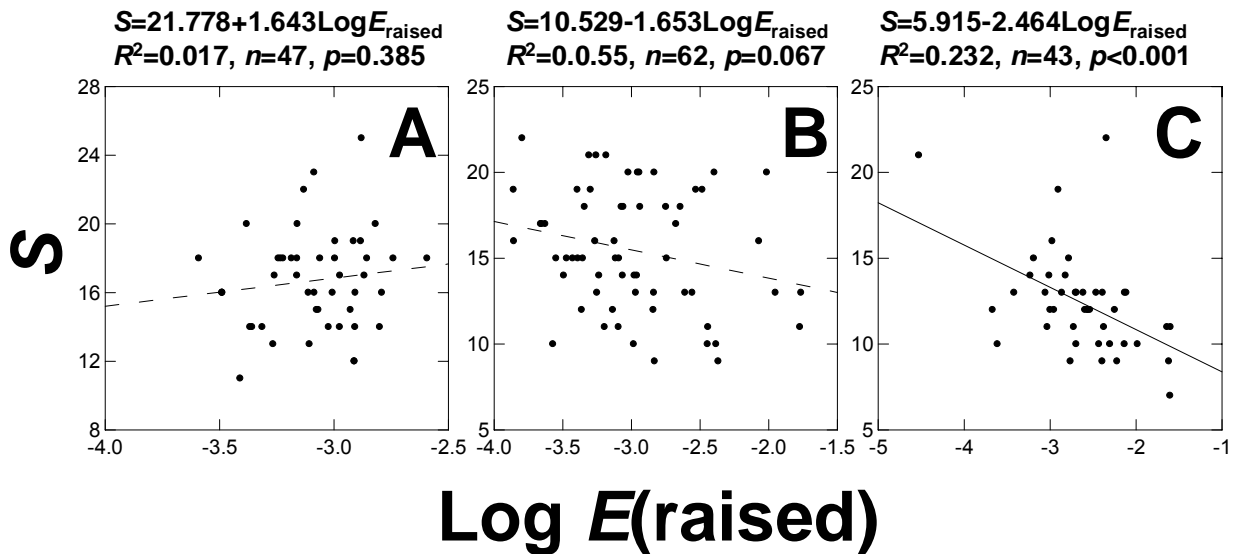
Figure 2.5.4.2: Examination of the relationship between species richness (S) of the fished component of the demersal fish community with variation in exploitation rate (E) at two levels of productivity of the prey-fish component of the demersal fish community (with both E and P calculated on the catchability-corrected raised survey data). A: Log P(raised) $\geq$1.0; B: Log P(raised) <1.0 and $\geq$0.0; C: Log P(raised) <0.0.

E and P parameters based on:	Equation	p (E)	p (P)	r²
Raw data	$S = 10.678 - 2.367\log E + 2.570\log P$	0.000	0.000	0.316
Raised data	$S = 9.150 - 1.566\log E + 2.373\log P$	0.005	0.000	0.295

Table 2.5.4.1: Results of multiple linear regression analysis relating species richness of the fished component of the demersal fish community to variation in exploitation rate and productivity of the prey fish weight classes of the demersal fish community.

2.5.5. Conclusions on Test 2

Relationships between the species richness and species diversity of the exploited weight classes of the demersal fish assemblage of the North Sea, the exploitation rates by which these fish are impacted and the productivity of their fish prey resources failed to comply with Huston's dynamic equilibrium model.

2.6. Test 3: Diversity of the Epibenthic Invertebrate Species Assemblage

In this test we determine the extent to which productivity in the infaunal component of the benthic invertebrate community might influence any relationships between fishing disturbance and species diversity and richness of epibenthic invertebrates.

2.6.1. Test input data

Spatial variation in species richness and diversity of the epibenthic invertebrate community was determined by Greenstreet *et al* (2007c: section 1.3.4) and presented for metrics based on abundance in the top panels of their Figure 1.3.4.1. These data are presented again here (Figure 2.6.1). Spatial variation in the productivity of the infaunal benthic invertebrates was determined by Greenstreet *et al* (2007c: section 2.3.4, panel (a) of Figure 2.3.4.1), in terms of Ash Free Dry Weight. As for Test 1 (section 2.4.1), these productivity data were reworked to give production in terms of wet weight (Figure 2.6.2). Benthic invertebrate mortality caused by fishing activity was modelled by Greenstreet *et al* (2007d: section 7), with a map of spatial variation in mortality presented as their Figure 7.4.5.2 for the years 2001 to 2004. We use these data as our index of disturbance to the epibenthic community (Figure 2.6.3).
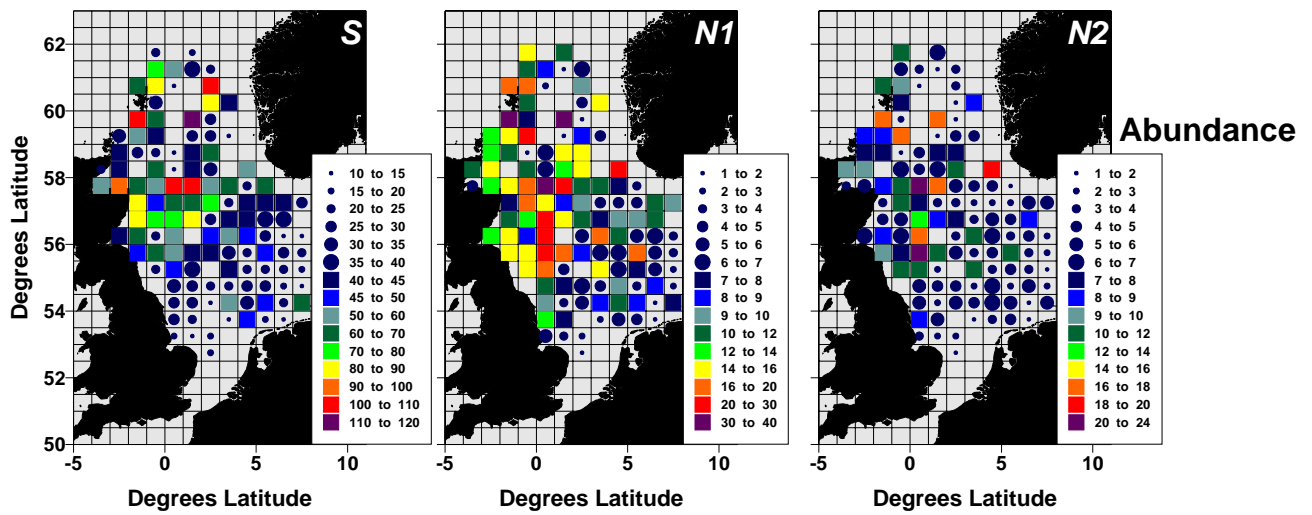
Figure 2.6.1: Spatial variation in the species richness (*S*) and diversity (Hill's N_1 and N_2) of the epibenthic invertebrate community of the North Sea.
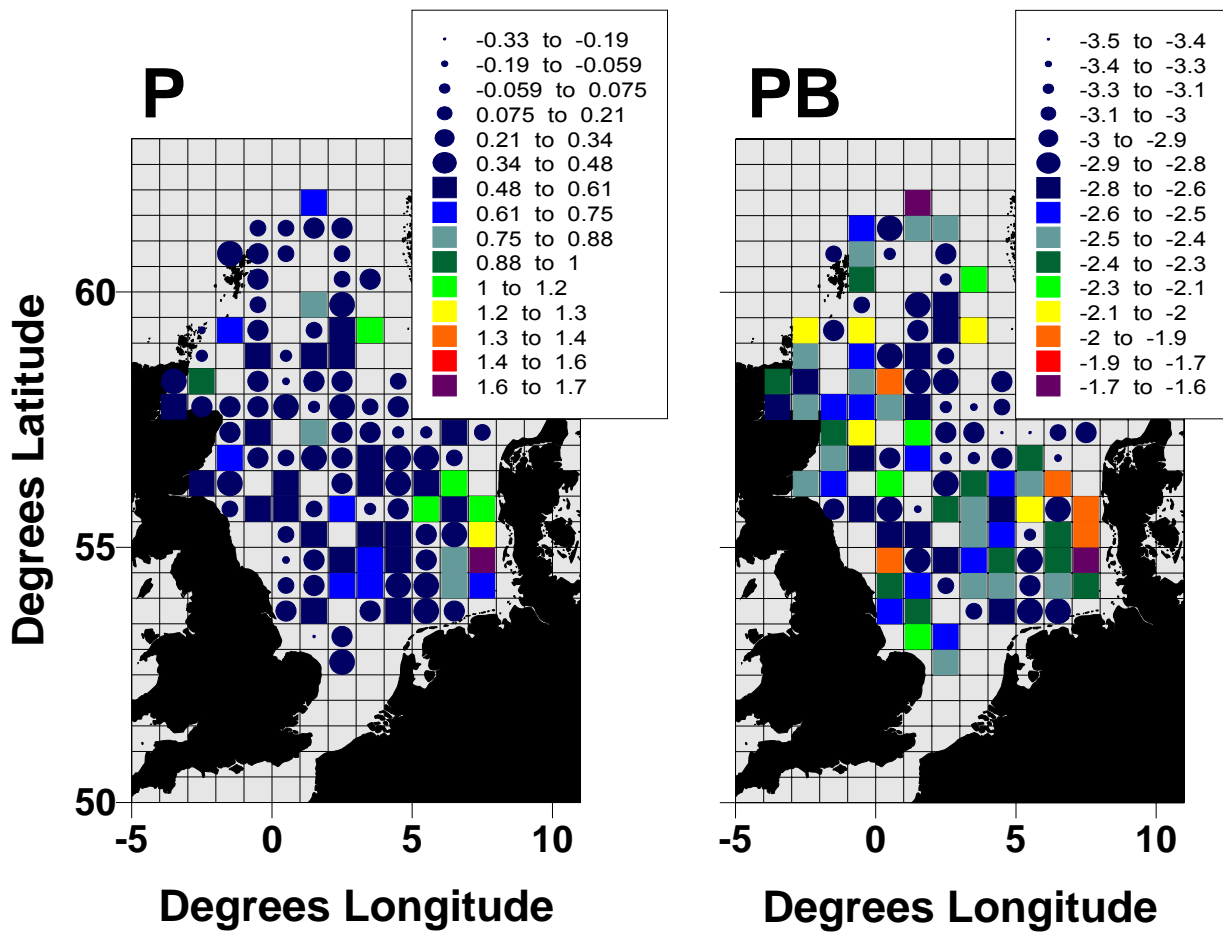
Figure 2.6.2: Spatial variation in the productivity (*P*) and productivity-biomass ratio (*P/B*) of the infaunal component of the benthic invertebrate community.

2001 to 2004
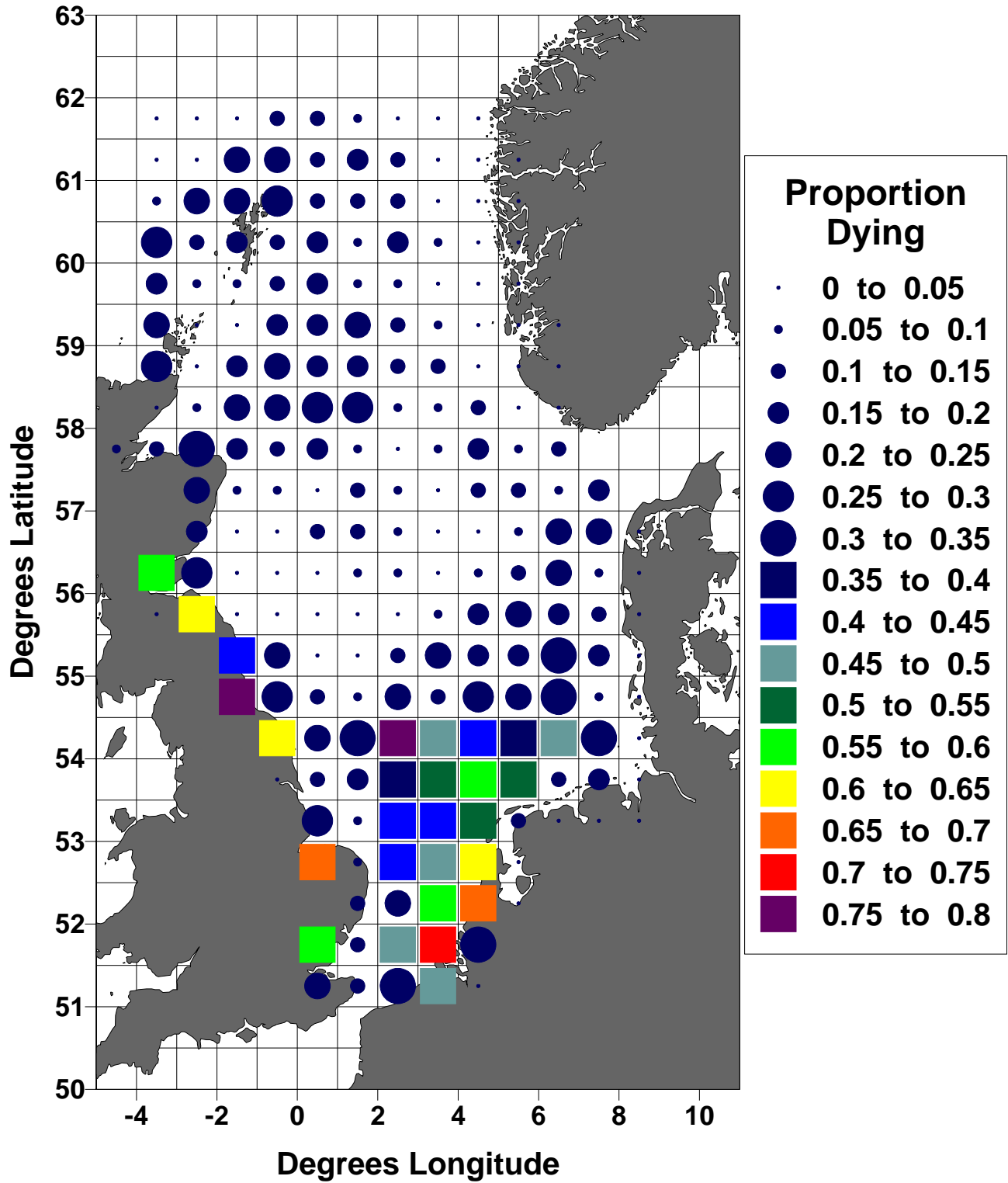
Figure 2.6.3: Spatial variation in the mortality of epibenthic invertebrates caused by fishing activity.

2.6.2. Relationships between diversity and disturbance and between productivity and disturbance

Polynomial fits were applied to the data relating epibenthic species richness and diversity to epibenthic fishing mortality and infaunal productivity to search for the unimodal relationships predicted by Huston's DEM (Figure 2.6.2.1). The relationships between species richness/diversity and productivity appeared promising, however, the R^2 values, whilst significant, suggest that 5% or less of the variance was explained by the fitted functions. No unimodal relationships were apparent between species richness/diversity and disturbance. Instead a linear negative relationship was indicated, although once again the relationship was weak.
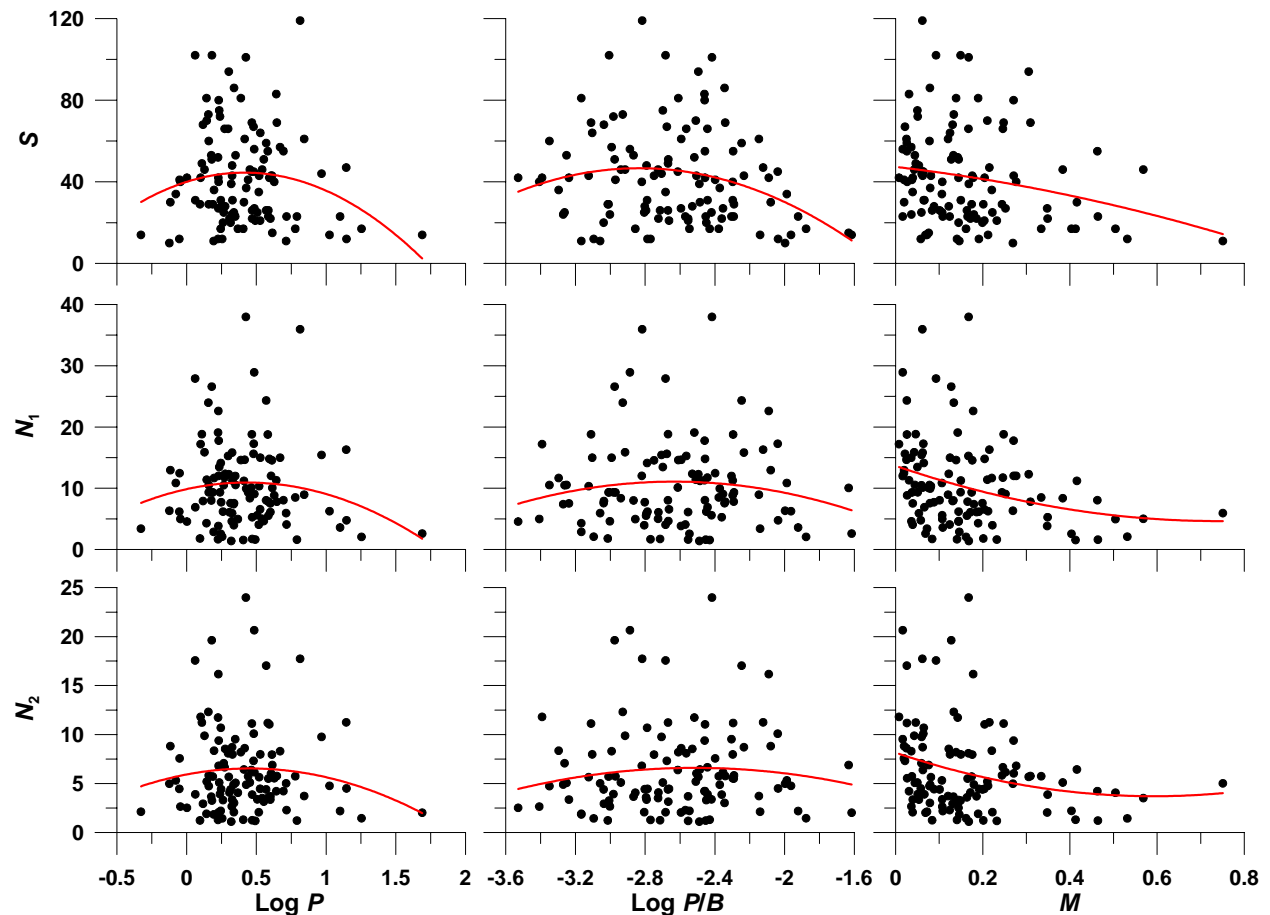
Figure 2.6.2: Relationships between species richness (*S*) and diversity (Hill's N_1 and N_2) of epifaunal benthic invertebrates and disturbance caused by fishing to epibenthic fauna (*M*) and productivity of the infaunal component of the benthic invertebrate community (Log *P* and Log *P*/*B*)

2.6.3. Three-dimensional representation of the inter-relationships between diversity, production and disturbance.

Three dimensional plotting of epifaunal species richness/diversity, infaunal productivity, and epibenthic fishing mortality revealed no indication of the characteristic cone shape to the 3D surface predicted by the DEM (Figure 2.6.3.1).
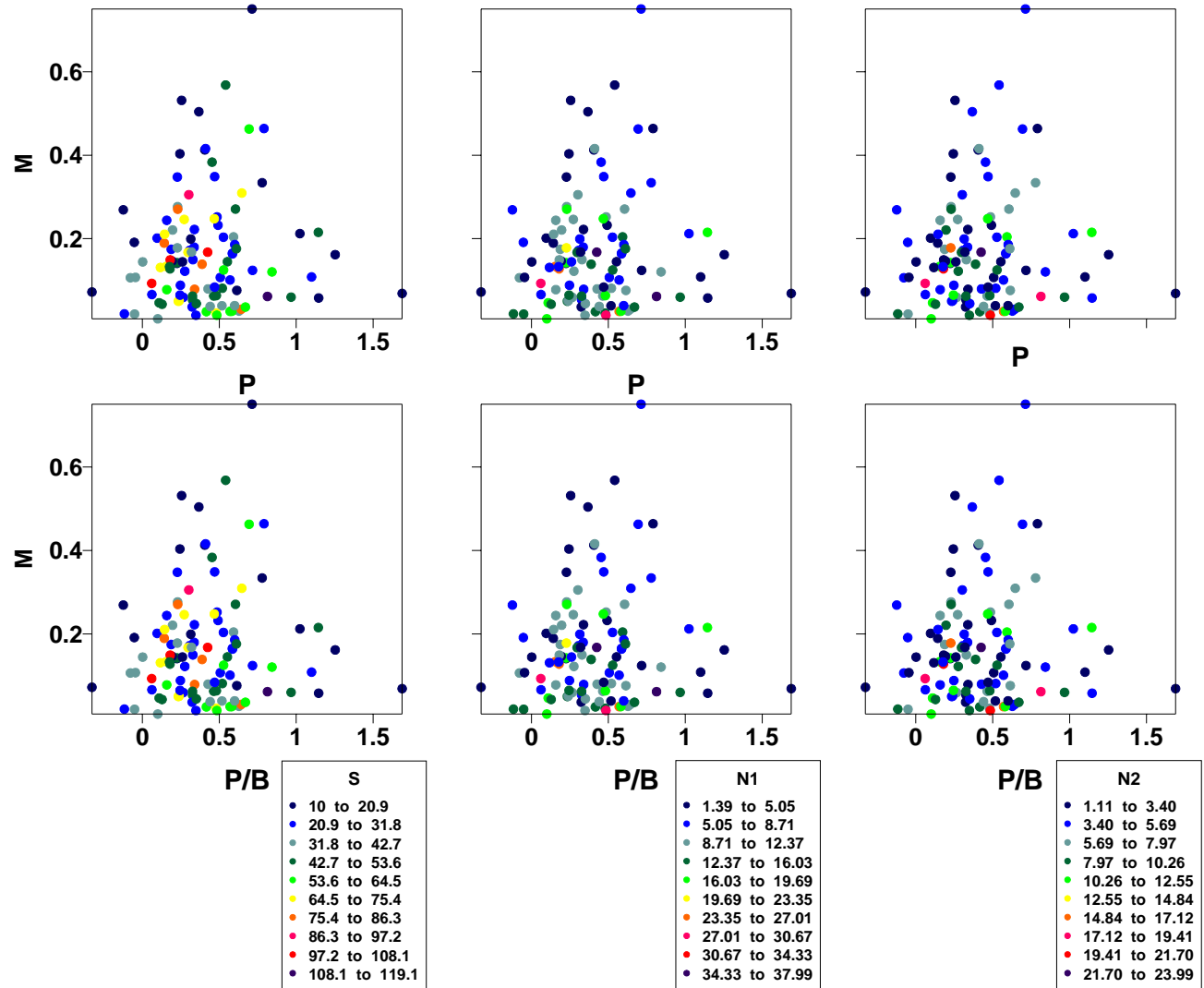
Figure 2.6.3.1: Three dimensional representation of the interrelationships between epifauna diversity (species richness (S) and Hill's N_1 and N_2), infauna productivity (P and P/B), and epifauna fishing mortality (M).

2.6.4. Relationships between diversity and disturbance at varying levels of productivity

Despite the lack of convincing three dimensional relationships between diversity, productivity and disturbance, plots of epibenthic richness/diversity against epibenthic fishing mortality tended to show the negative relationships at low productivity and positive relationships at high productivity predicted by Huston's DEM (Figure 2.6.4.1). However, all the relationships were

weak and not statistically significant. When infaunal P/B ratios were used instead a slightly different picture emerged. Now clear negative relationships were apparent between fishing disturbance and diversity, but these relationships weakened as infaunal productivity per unit biomass increased (Figure 2.6.4.2).
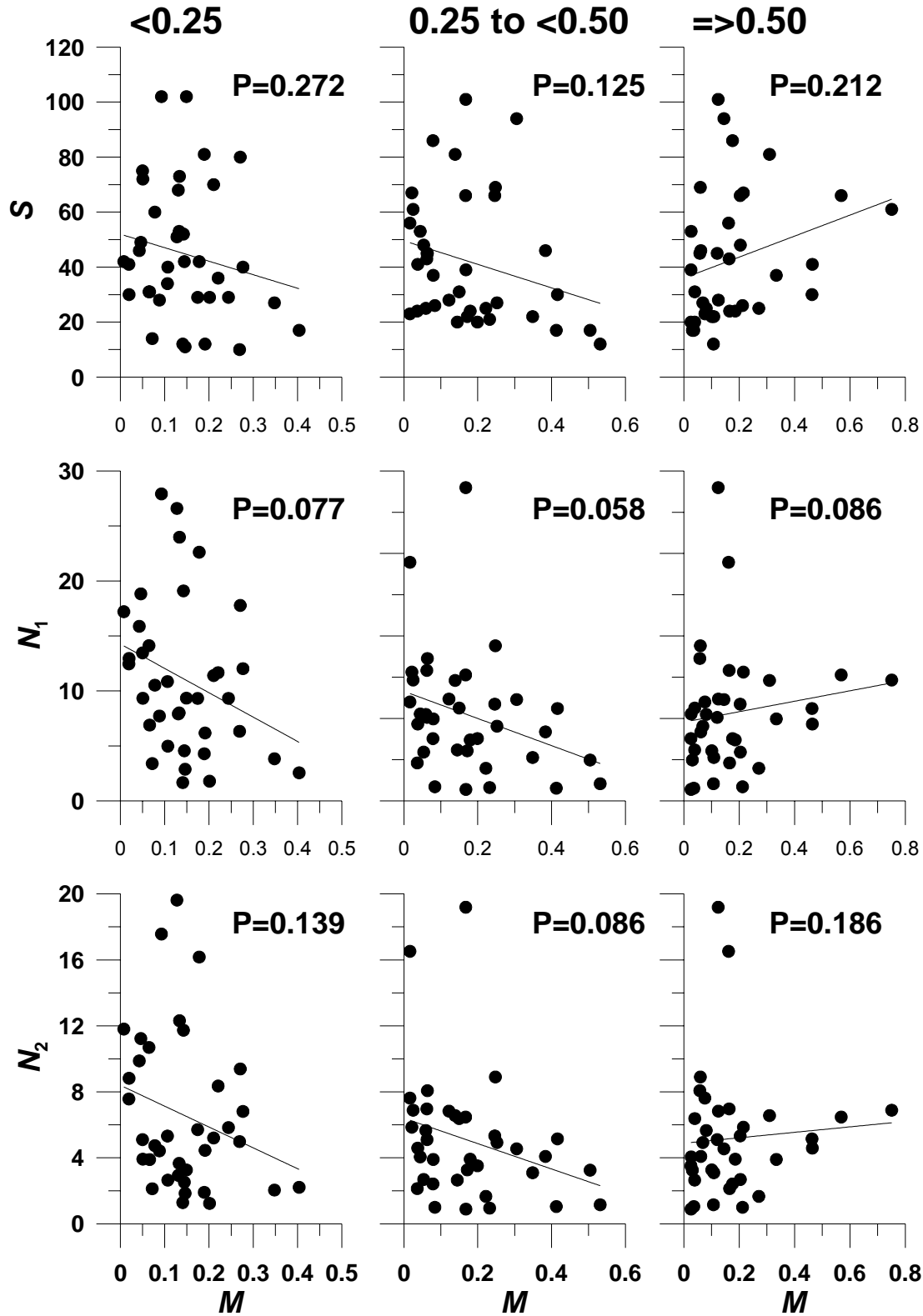
Figure 2.6.4.1: Relationships between epibenthic species richness (*S*) and diversity (N_1 and N_2) and epibenthic fishing mortality (*M*) at three levels of infaunal productivity (*P*); <0.25 g.m^{-2}.d^{-1}, 0.25 to <0.5 g.m^{-2}.d^{-1}, and ≥ 0.5 g.m^{-2}.d^{-1}.
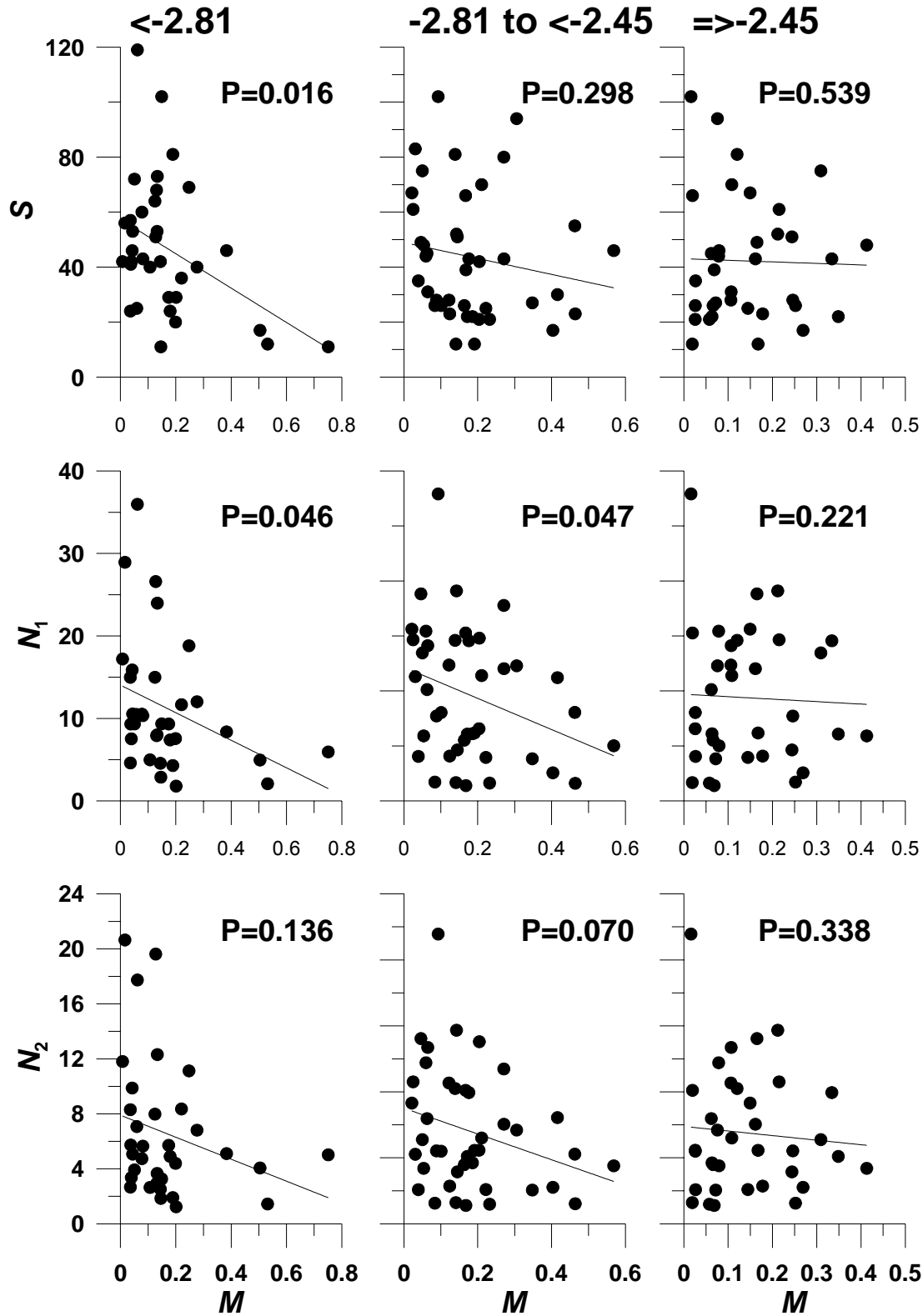
Figure 2.6.4.2: Relationships between epibenthic species richness (S) and diversity (N_1 and N_2) and epibenthic fishing mortality (M) at three levels of infaunal productivity:biomass ratio (P/B); <-2.81 $m^{-2}.d^{-1}$, -2.81 to <-2.45 $m^{-2}.d^{-1}$, and $\geq$ -2.45 $m^{-2}.d^{-1}$.

2.6.5. Conclusions on Test 3

Relationships between the species richness and species diversity of the epibenthic component of the benthic invertebrate assemblage of the North Sea, and the mortality rates caused by fishing to these epibenthic invertebrates and the productivity of their infaunal invertebrate prey resources failed to comply with Huston's dynamic equilibrium model. There was some suggestion of DEM-like processes working in the benthic community, but the relationships were too weak to be convincing, and certainly too weak to provide the basis of a management protocol.

2.7. General Conclusions: Applicability of Huston's DEM to Marine Communities

In collecting the data to test Huston's dynamic equilibrium model, we assumed that fishing disturbance would vary in space independently of spatial variation in productivity. Thus by sampling randomly (or evenly) in space, or at least by sampling without prior knowledge of the spatial patterns of either disturbance or productivity, so with no stratification with respect to these two variables, we expected to obtain data that were more or less independently distributed across the full range of values of each. In other words, within the two dimensional space defined by the full spread of values for both disturbance and productivity, we anticipated obtaining a relatively even distribution of data. However, this assumption appears to have failed in many instances. Thus for example in test 2 (section 2.4), fishing disturbance imposed on the fished component of the demersal fish community (Log_2 weight classes 7 and above) tended to be concentrated within a relatively limited fraction of the full range of productivity of the prey fish component of the demersal fish community (Log_2 weight classes 3 and 4). This restriction of the bulk of the data to only a very limited section of the 2D productivity-disturbance domain (see Figure 2.4.3.1 for example) made 3D representation of the inter-relationships between productivity, disturbance, and diversity very difficult, with log-transformation of both variables required in order to achieve a distribution of data that was sufficiently bi-variate normal. However, it is difficult to then reconcile this treatment of the data with Huston's original concept that underpins the dynamic equilibrium model.

In none of the test situations that we have examined was there any convincing indication that Huston's dynamic equilibrium model provided any sort of basis for predicting the relationship between diversity and disturbance. Given that the data sets that we have available to us are probably some of the most exhaustive that there are ever likely to be. It seems unlikely that this model could ever provide a basis for management advice.

3. THE MANAGEMENT PROTOCOL

3.1. The Original Concept

The original concept for managing fisheries in the North Sea so as to conserve demersal fish and benthic invertebrate species diversity was based on the premise that, through the manipulation of Total Allowable Catch (TAC) levels, the spatial distribution of fishing activity could be influenced. Huston's (1994) Dynamic Equilibrium Model suggests that the relationship between ecological disturbance and species diversity depends on local productivity. The model predicts that in regions of the North Sea where productivity is high, increased fishing disturbance would illicit an increase in species diversity. Conversely, where productivity was

low, any increase in fishing disturbance would cause species diversity to decline. Therefore, the principle on which the original management protocol was founded was that levels of species diversity might be maintained, or even increased, by manipulating TACs to direct fishing activity towards the higher productivity regions of the North Sea, and away from regions of low productivity.

The flow chart shown in Figure 3.1.1 illustrates the original management protocol envisaged at the start of the project. This protocol was intended to be implemented as an additional procedure in the annual stock assessment and management advice process, rather than as an alternative to this process. There are several key components to this protocol. Firstly, current fisheries management operates primarily through catch limitation, through the setting of Total Allowable Catches (TACs) for each coming year for each of the major commercially targeted species. Thus the starting point for the protocol is the suite of TACs decided for each year. Through the restriction of catches, TACs are intended to control the mortality rates imposed by fishing exploitation to within predefined (sustainable) ranges for each species. The estimates of fishing mortality provided by the stock assessments (e.g. ICES 2005) actually provide an indication of the "ecological disturbance" suffered by each of the targeted species as a result of fishing activity, at least at the North Sea scale. However, the TACs themselves, whilst providing an indication of the numbers of fish likely to be caught and killed in the coming year, do not on their own provide an indication of impending "fishing disturbance". This is because mortality rates are dependent not only on the numbers of fish caught, but also on the population abundance of each species present prior to the disturbance event. Critically, as far as this project is concerned, TACs and their associated estimates of mortality relate to large geographic areas, e.g. the North Sea or larger; no breakdown of this information to finer spatial resolution is provided. Furthermore, as indicators of the impact of fishing in the year ahead, TACs and their associated estimates of mortality are really only of relevance to the small proportion of the North Sea taxa that constitute the commercially targeted species. TACs (or the commercial species mortality estimates associated with them) provide little or no indication of the disturbance to which the greater fraction of the North Sea demersal fish or benthic invertebrate species, which constitute non-targeted species, will be subjected to as a result of the coming year's fishing activity. For the vast majority of fish and benthic invertebrate species in the North Sea therefore, determining the disturbance to which they are likely to be subjected as a result of fishing activity is best modelled using data that quantifies the level of activity itself: fishing effort data. So in order to apply the protocol to the broader demersal fish and benthic invertebrate communities, the necessary first step was to convert the suite of TACs proposed by managers in any given year to likely patterns of fishing activity, the amount of fishing effort required and its spatial distribution, that would produce these levels of landings. To do this the relationships between landings and fishing effort needed to be understood and modelled. This task was the addressed by work package 6 (Figure 3.1.2), and the results are reported in Greenstreet *et al* (2007e).
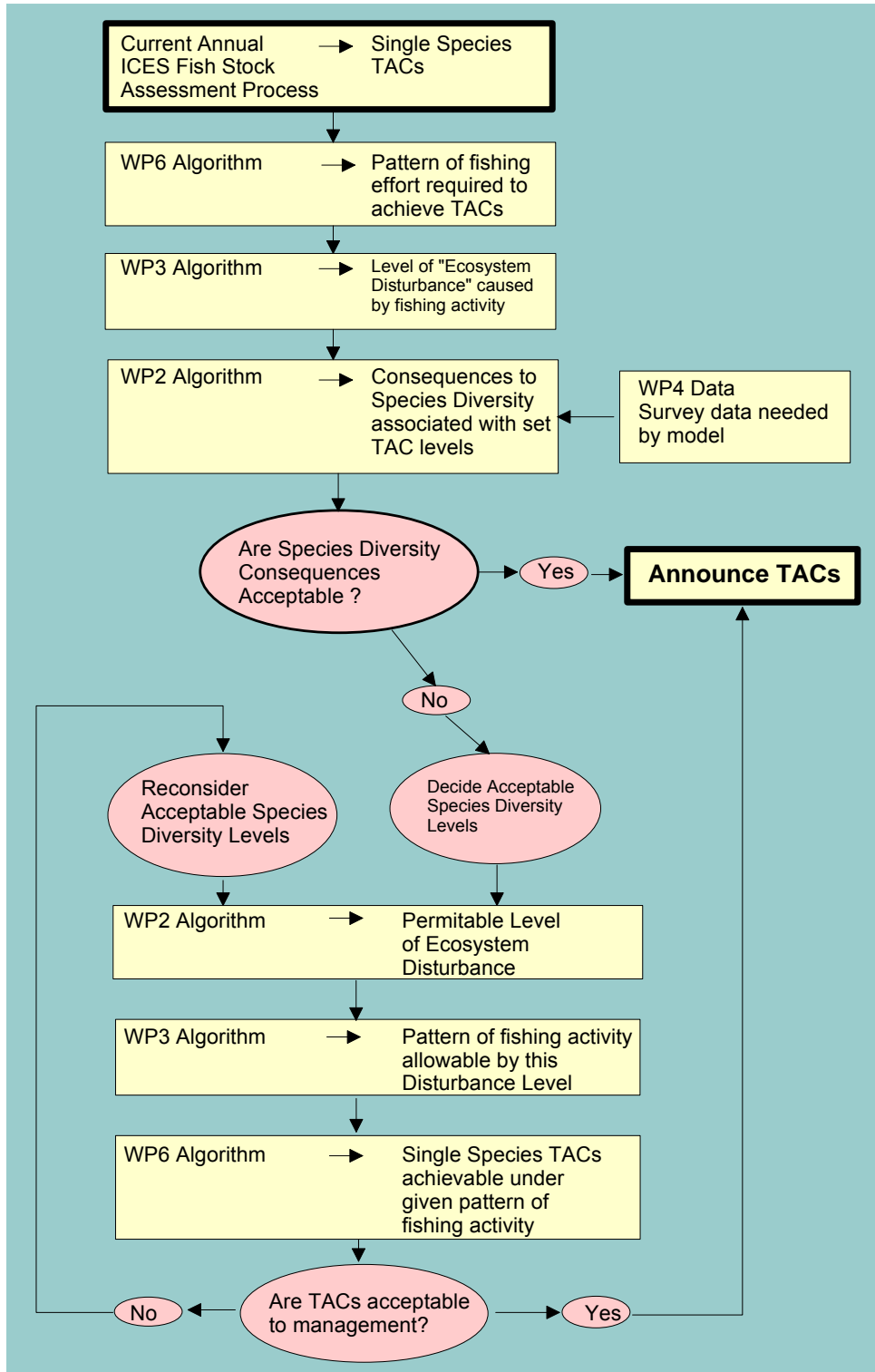
Figure 3.1.1: Flowchart for initial proposed "management protocol"
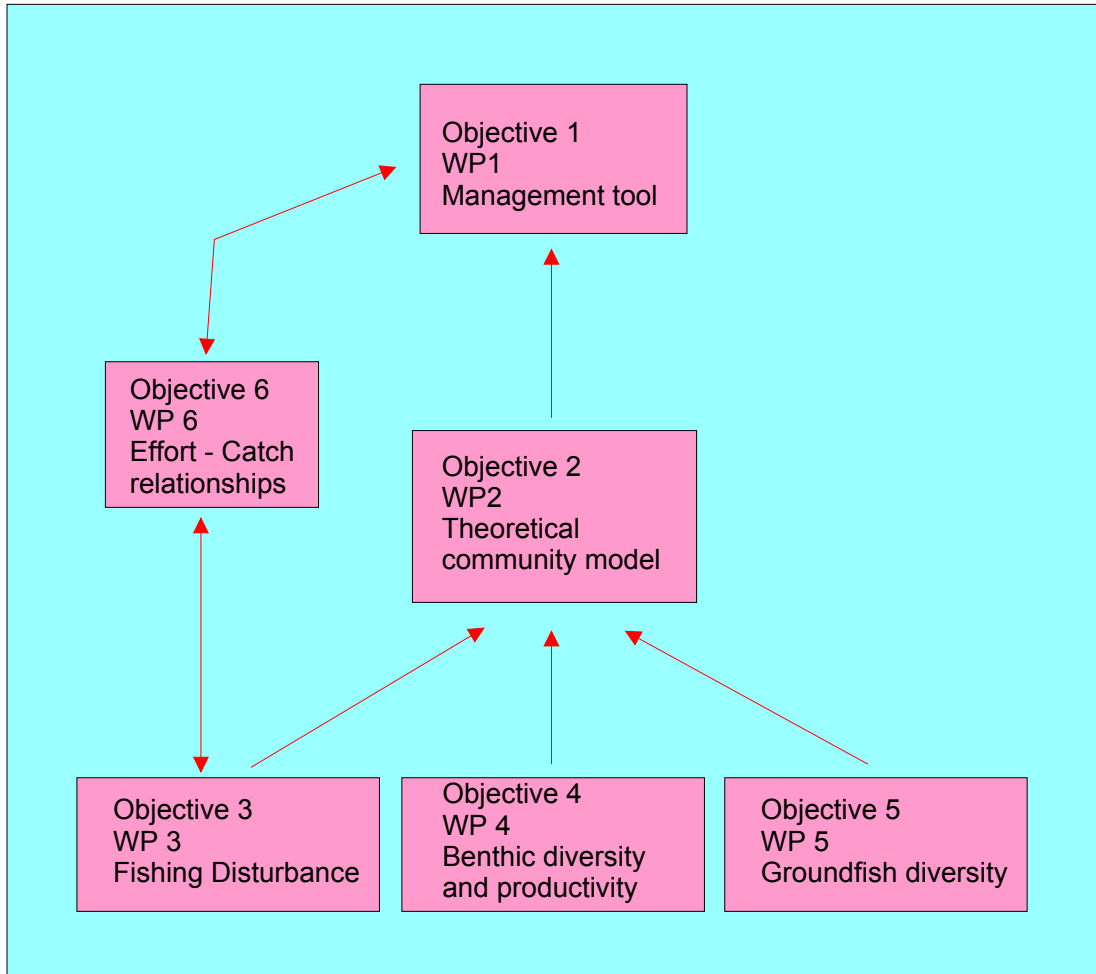
Figure 3.1.2: Project work-package structure and interaction chains.

Fishing effort statistics describe the anthropogenic activity itself. In many published studies the implicit assumption is that such statistics are equivalent to the ecological disturbance caused by fishing (e.g. Greenstreet & Hall 1996; Jennings *et al* 1999; Greenstreet & Rogers 2006). However, it is clear in Huston's (1994) derivation of the DEM that he considers the disturbance variable in his model to be the biological consequences of the disturbing perturbation, not the perturbation itself. In other words, it is the changes in mortality rate that occur as a result of the perturbation that alter the population dynamics of the species affected, thereby altering their competitive ability and their capacity to influence bottom and top down processes within trophically interacting species assemblages. If the relationship between fishing activity and its immediate ecological consequences (i.e. mortality rates), is linear (i.e. directly proportional) then fishing activity statistics may provide a useful proxy for ecological disturbance. However, if the relationship between these parameters is not linear, then simply using fishing effort statistics as the indicator of disturbance in the DEM could be miss-leading (e.g. Piet *et al* in Press), compromising the advice coming out of the protocol. To cover this possibility, the next step required in the original management protocol concept was the translation of spatial patterns of fishing activity to corresponding distributions of ecological disturbance. Elucidating the relationships between fishing effort and ecological disturbance for the different components of the benthic/demersal fauna of the North Sea occupied a considerable proportion of the

resources of the combined MF0753 and MAFCONS projects; both compiling the effort statistics themselves and developing the necessary biological models that relate fishing activity to the mortality caused by fishing. This work, which was the focus of work package 3 (see Figure 3.1.2), is described in detail in Greenstreet *et al* (2007d).

Having determined the patterns of ecological disturbance associated with any given set of TACs, the third step in the original management protocol concept involved inputting these data into a theoretical ecology module to predict the consequences of the proposed management action on the species diversity of the demersal fish and benthic invertebrate communities. Work package 2 covered this part of the project's work (see Figure 3.1.2). Huston's (1994) DEM (see Section 2) was initially identified as the most promising candidate to form the basis of this theoretical module, so a major part of the work was directed towards the testing of hypotheses derived from the DEM (reported in Section 2) to ensure that it could adequately serve this purpose. The hope was that, should the model withstand this rigorous testing, a simple function might be parameterised that related species diversity (*S*) to both disturbance from fishing (*F*) and productivity (*P*), thus;

$$S = f(F).f(P)$$
3.1.1

The first two steps of the management protocol would provide the input data for the disturbance component of this function. Parameterisation of the productivity aspect required the collection of new data and the development and application of new size-based methods of estimating local productivity from size-structured fish and benthic invertebrate biomass data. Finally, to fully develop the theoretical ecology module, the combined influence of productivity and disturbance on species diversity has to be determined. This involved the application of a suite of diversity indices to size-structured fish and benthos abundance data. This work was covered by work packages 4 and 5 (see Figure 3.1.2) and is reported in Greenstreet (2007a; 2007c).

At this point, the original concept for the management protocol has produced estimates of the species diversity consequences associated with specific fisheries management proposals (a given suite of TACs). The remainder of the protocol involves attempting to reconcile any unwelcome ecological consequences arising from the proposed fisheries regime against the economic benefits to be gained from landing the specified quantities of fish. If the estimated species diversity consequences are deemed acceptable, then there is no problem and the proposed TACs might be accepted and published. However, if this was not the case, and the species diversity consequences are considered unacceptable, then the management protocol could be re-run, either in the same direction with a new set of TACs, or in reverse with acceptable species diversity levels input and the algorithms run backwards to identify a set of TACs commensurate with management objectives for species diversity. TACs derived in this way may well be considered politically unacceptable in the context of supporting a viable fishing industry. Minimum acceptable TACs could then be input to determine the species diversity consequences associated with these. In effect, this original concept for a management protocol could be run and re-run in an iterative process to identify the best compromise between the needs of the fishing industry, and political obligations to conserve and restore species diversity.

3.2. Problems with the Original Management Protocol Concept

Over the course of the project it became clear that the original concept for the Management Protocol was seriously flawed. Major problems emerged in two of the steps in the protocol; the theoretical community ecology stage and the step relating TACs, landings and effort.

3.2.1. Problems with the DEM

In Section 2 we test a number of specific hypotheses derived from the DEM for explicitly defined components of the demersal fish and benthic invertebrate communities of the North Sea. In each case the model failed to explain spatial variation in species diversity. No function relating species diversity to variation in disturbance and productivity could be established in any of the analyses performed. It became obvious therefore that the DEM could not provide the theoretical basis for the community ecology stage of the Management Protocol. Following our review of the theoretical community ecology literature (Greenstreet 2007b), this result was not entirely unexpected. The DEM is founded strongly in competition and niche theory. Such a model may therefore be appropriate for communities consisting primarily of species displaying deterministic growth. In such communities all mature adult individuals of any particular species have approximately the same body mass, so that species might be considered to be the fundamental ecological functional unit. In communities consisting mainly of species displaying non-deterministic growth patterns, such as demersal fish and benthic invertebrate communities in the North Sea, individuals belonging to the same species vary markedly in size. Consequently their ecological roles also differ considerably (Jennings *et al* 2001; 2002a; 2002b; Kerr & Dickie 2001). In such communities, individuals of similar size, regardless of species, may more appropriately be considered to be the fundamental ecological unit. Under such circumstances, the DEM is unlikely to explain variation in species diversity. In the next Section we discuss these issues at much greater length.

Failure of the DEM to provide the basis for the theoretical community ecology step in the Management Protocol does not necessarily spell the end for the protocol. It simply means that the DEM is the wrong model and that an alternative is required. In Section 4 we develop an alternative theoretical species diversity model that is size structured and that takes account of both bottom up limitation and top down control processes and allows the impact of fishing on these processes to be modelled. Such a model, if developed, could well predict the changes in species abundance that occur as a result of varying fishing exploitation regimes, thereby allowing the effects of fishing activity on species diversity to be predicted. However, the disadvantage of the model is that it is species-specific and therefore much more demanding with respect to data requirements for parameterisation.

3.2.2. Problems with catch limitation fisheries management

Current fisheries management involves an annual process whereby the current state of the commercially targeted fish stocks is assessed in order to determine the level of fishing mortality that they can sustain. Once determined, these mortality rates are converted into potential catches, and these Total Allowable Catches (TACs) are divided into the individual member state quotas. Over the years, as the state of the stocks has waxed and waned, TACs have varied considerably, as the management process (including the scientific advice input) has attempted to maintain the individual fish stocks within sustainable bounds, whilst simultaneously trying minimise restrictions to fishing activity. Since 1994, there has been a clear decreasing trend in the TACs for the main demersal fish species (Figure 3.2.2.1). Prior to this, the data suggest that TAC levels were relatively stable.
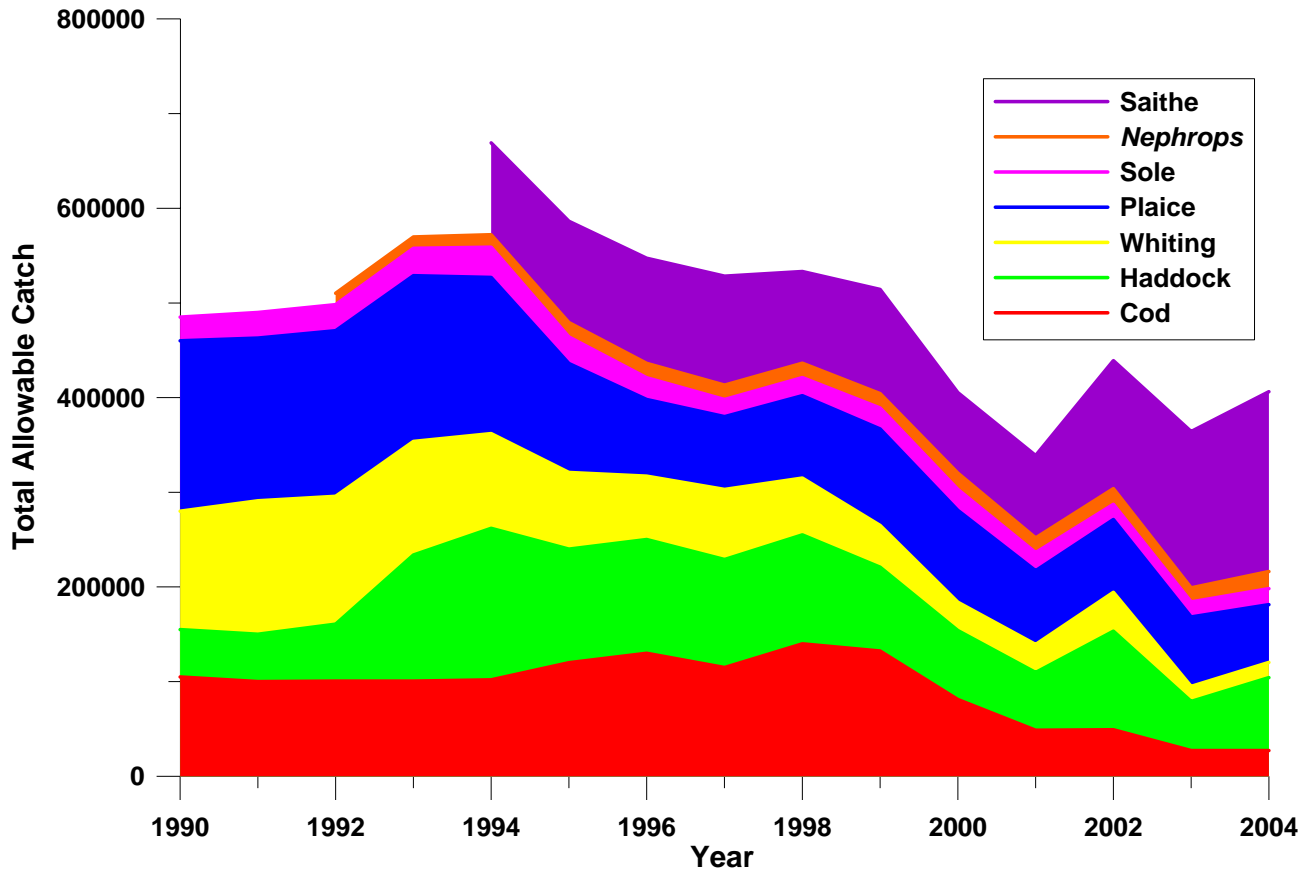
Figure 3.2.2.1: Annual variation in TAC of the main commercially targeted demersal fish stocks.

Whilst it is relatively easy to access data for North Sea landings and TACs, at least at the scale of the whole North Sea, accessing data to examine trends in fishing effort is considerably more difficult. Only two studies have attempted to compile international fishing effort databases over any appreciable period of time; the current study (Greenstreet *et al* 2007d) and the earlier EC funded "Biodiversity" study (Jennings *et al* 1999). The "Biodiversity" project covered the period 1990 to 1995, whilst the data presented by Greenstreet *et al* (2007d) cover the period 1997 to 2004. When data for the two periods were plotted together the data suggest that levels of fishing effort only started to decline from around 1997 onwards (Figure 3.2.2.2A). However, these two studies did not include participants from all nations operating fisheries in the North Sea. Greenstreet *et al* (2007d) have attempted to model fishing effort data for the four countries with significant North Sea quotas that did not contribute to the later effort database, Denmark, France, Sweden, and Belgium. Trends in total fishing effort suggest that effort really only started to decline in the North Sea from around 2000 onwards with the introduction of decommissioning and limitation of the numbers of days absence from port each month (Figure 3.2.2.2B). These conclusions seem a little tenuous because of the short duration of the data available. However, Scottish effort data covering the period 1960 to 2004 have been analysed and these certainly indicate a sharp decline in fishing effort since 1998 (Greenstreet *et al* 1999; 2006) (Figure 3.2.2.3). The increase in otter trawl through to the late 1980s was mainly associated with decreasing use of seine gear, with fishing vessels switching to otter trawl so that, by the late 1990s, otter trawl was the principal gear used by Scottish fishermen. The implication from this assessment of the available fishing effort data is that reductions in TAC had little or no effect on fishing effort levels until moves to control fishing effort directly were

introduced. At the very best, a lag of several years was apparent following reduction in TACs
before fishing effort levels started to decline. Greenstreet *et al* (2007e) explore the relationships
between TACs, landings and fishing effort explicitly. They conclude that it would be difficult to
estimate the spatial distribution of fishing effort associated with any given set of TACs with
sufficient precision as to provide adequate input into the next stage of the Management
Protocol. Consequently, the level of uncertainty involved with any advice regarding the species
diversity consequences associated with each set of TACs would be too high to be of value for
management purposes.
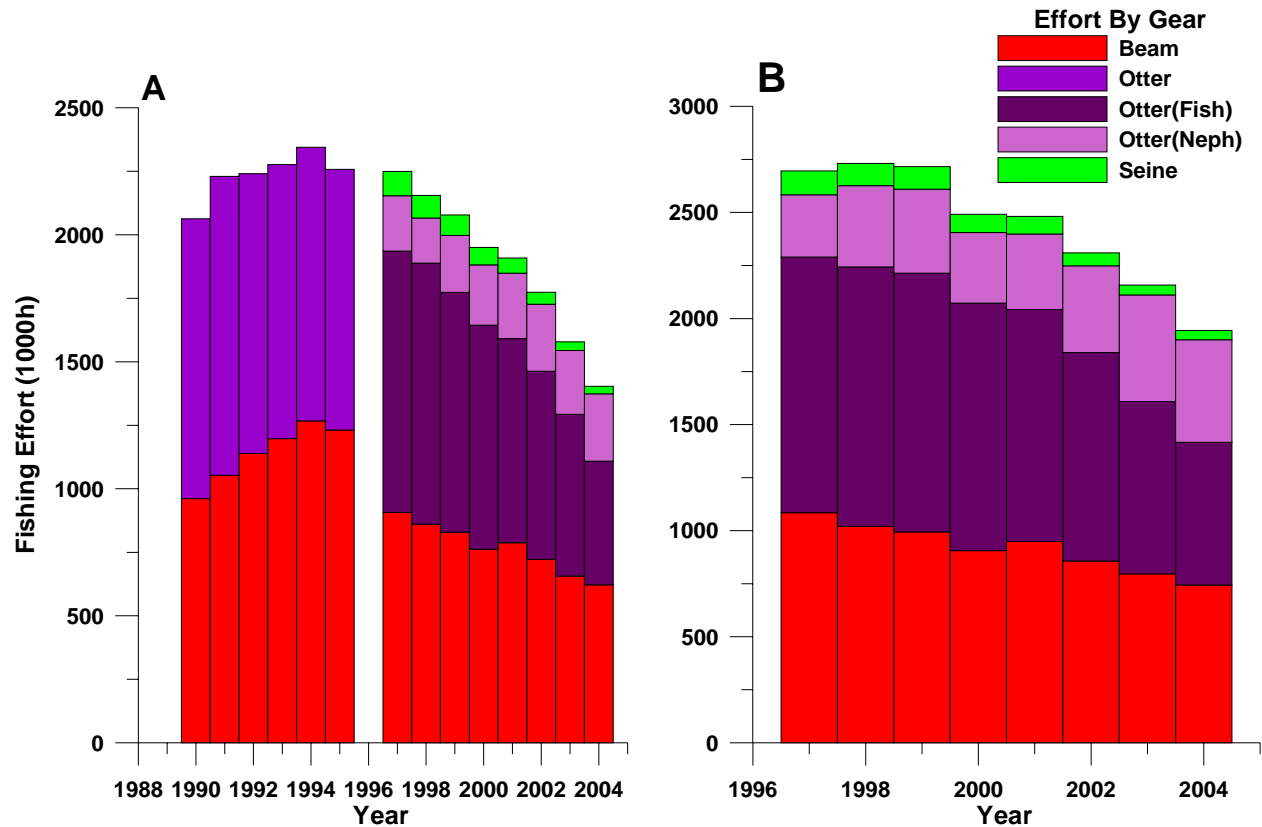
Figure 3.2.2.2: Temporal trends in international fishing effort in the North Sea. A: Data submitted to the
Biodiversity project (1990 to 1995) and to the MAFCONS project (1997 to 2004) showing only the data
submitted by the participating countries (1990 to 1995 excludes France, Belgium and Sweden; 1997 to
2004 excludes Denmark, France, Belgium and Sweden). B: Total North Sea effort between 1997 and
2004 including modelled estimates of effort by the four countries that did not contribute to the data base.
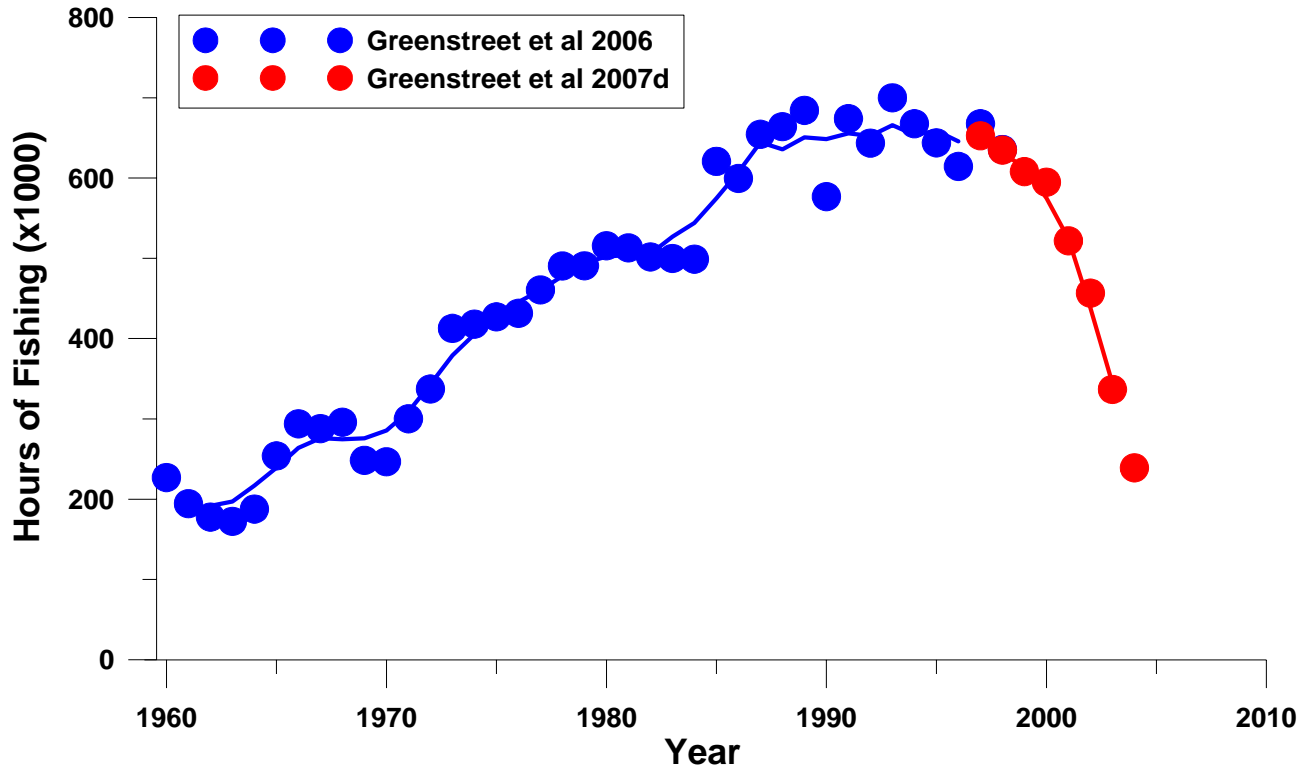
Figure 3.2.2.3: Long-term trends in Scottish Otter Trawl Effort derived from two separate studies. Lines show moving average fits to the two data sets.

A further consideration was the fact that whilst TACs may serve to limit officially recorded landings, their relationship to actual catches was far more obscure. For years now official landings data have failed to represent the actual quantities of fish landed because of the illegal landings of fish caught over-quota. In addition, the wide-spread practice of discarding under-sized fish, fish of lower value, over-quota fish and fish of no commercial value further extends the difference between the actual amount of fish caught, and hence the effort required to catch them, and the original TACs set by management. Discarding is an inevitable consequence of TAC/quota based management, especially in situations involving mixed-species fisheries, the situation prevalent throughout the North Sea.

Finally, TACs and fishing effort levels tend to be decoupled because of confounding variation in stock size. TACs tend to decrease when stock sizes decline so as to control rates of fishing mortality. But as stocks become less abundant, so they become more difficult to catch, and catch per unit effort (CPUE) declines. Consequently, the most common situation would be for TACs and CPUE to decrease in tandem, thus requiring the same, or even increasing, levels of fishing effort to take smaller and smaller catches.

3.3.   An Alternative Approach for Management

A major assumption underpinning the original concept for a Management Protocol was that in order to achieve ecological objectives as part of an ecosystem approach to fisheries management, not only would the amount of fishing activity need to be controlled, but also its spatial distribution. The fundamental principle at the heart of the protocol was that fishing activity should be directed away from areas considered to be the most vulnerable or most

valuable in terms of their intrinsic ecological worth, and shifted where necessary to less vulnerable areas or to areas of less value. Rather than attempting to do this through the manipulation of TACs, this can be achieved directly through the establishment of Marine Protected Areas (MPAs) (Pikitch *et al* 2004; Norse *et al* 2005).

Globally Marine Protected Areas (MPAs) are a commonly used marine management tool to protect commercial fish stocks, particular marine species, communities and habitats (Carr & Reed 1993; Allison *et al* 1998; Houde 2001; Roberts *et al* 2001; Botsford *et al* 2003; Gerber *et al* 2003). In recent years within Europe, increased awareness of the importance of the environment in maintaining the general health of marine ecosystems has generated considerable interest in the establishment of MPAs. The use of Marine Protected Areas (MPAs), in this context taken to mean areas closed to fishing, to achieve management objectives for broader marine ecosystem issues has been explicitly proposed in policy drivers such as the Convention on Biological Diversity, the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR), The World Summit on Sustainable Development, The 2002 Bergen North Sea Ministerial Conference, the EC Habitats, Birds, and Marine Strategy Directives, and UK Marine Strategy documents such as The Review of Marine Nature Conservation, Net Benefits (The PM's strategy unit 2004), "Charting Progress" and "Seas the Opportunity". Application of the Habitats Directives to the offshore zone will lead to the establishment of new MPAs around European coasts designed to protect vulnerable seabed habitats (EEC 1992). Under OSPAR, nations are further obliged to establish a coherent network of MPAs by 2010. The forthcoming UK Marine Bill, for example, is likely to feature a new mechanism to enable further MPAs to be established to protect features of national importance.

As pressure to designate MPAs increases, several important issues need examination. Firstly, how successful are MPAs in delivering their ecological objectives? Currently it is not clear precisely what closed areas can and can not deliver. World-wide there is certainly a considerable body of evidence to suggest that MPAs are beneficial at the local scale, i.e. within the boundaries of the designated closed area (Halpern 2003), but data indicating that MPAs are useful in achieving global scale (e.g. North Sea wide) management objectives are scarce. Since the majority of MPA sites will be subject to some form of fisheries restrictions, one major concern focuses on the effects of fishing activity displaced from areas closed to fishing to alternative locations. There is a real risk that in some situations such displaced fishing activity may have serious unintended consequences, perhaps even resulting in net losses for the marine ecosystem rather than gains. This raises the possibility that particular closed area proposals may not achieve the ecological gains anticipated, thereby proving inadequate to meet specified global scale management objectives.

A greater understanding of the circumstances whereby the establishment of MPAs results in net ecological benefits, and the scale of these benefits, is required in order to support evidence based policy making and management. Scientists need the tools to allow them to assess the costs and benefits, both ecological and economic, of each individual MPA proposal, in order to evaluate the sort of large scale ecological objectives that might best be addressed through closed area management. Parts of the original Management Protocol concept can be developed to meet this requirement, particularly step two, the fishing activity and disturbance modeling stage. The wealth of information obtained during this project regarding spatial variation in the abundance, biomass, production and species diversity of the fish and benthic infauna across the North Sea will be invaluable in identifying potential MPA locations. The comprehensive total international effort and landings data sets can be interrogated to assess

the consequential costs of closing particular areas to fishing activity. For a specified area, the loss of access to potential landings of each species by each of the countries operating in the North Sea can be estimated. If TACs are not reduced by equivalent amounts, it is anticipated that these landings will be made up by fishermen relocating to alternative grounds. If these new grounds are less productive, this may cause overall effort to increase. Knowing landings per unit effort at each ICES rectangle, this increase in effort can be quantified. It is entirely possible that any increase in overall effort, particularly when displaced to areas that previously might have only been lightly fished, may actually cause ecological damage that outweighs any gains achieved from the MPA. The ecological disturbance models can be used to determine the ecological damage associated with this displaced fishing activity, so enabling ecological costs-benefits analysis to be undertaken.

3.3.1. Protocols to assess the potential of MPA proposals

Set aside for nature conservation purposes in terrestrial systems amounts to approximately 8 to 10% of total land cover. If MPAs were to cover a similar percentage of the North Sea, then this would equate to closing some 17 to 22 ICES statistical rectangles to fishing. For the purposes of our demonstration, we therefore assume that up to 20 ICES rectangles will be closed to fishing in order to achieve specific ecological objectives. We now demonstrate how the databases and disturbance models developed during the project might be used to ascertain the most appropriate rectangles for closure and to explore the consequences of the closures on various aspects of the marine ecosystem of the North Sea.

As already discussed, a major concern over the designation of MPAs is what happens to the fishing activity that would normally have occurred in the closed area? If displaced to alternative areas, then where to? If these areas are less productive, does this result in increased effort. From a management perspective it is essential to know that the benefits derived from the establishment of each MPA are not outweighed by the detrimental consequences arising from this displaced fishing activity. If the ecological costs associated with the establishment of a particular MPA outweigh the anticipated benefits, then this may seriously call into question the wisdom of using closed area management to address the issue concerned. Alternatively action might also be taken to mitigate against the disadvantages by introducing steps to reduce fishing activity displacement. Such measures might, for example, include concomitant reductions in TACs associated with specific MPA proposals. In which case it would be important to know which TACs should be reduced, and by how much? Again the data sets and models developed during the project can be used to address questions such as these.

For the purposes of our demonstration of this alternative Management Protocol, we consider two potential ecological quality objectives that managers might well be required to address in the near future. These are:

- Use MPAs to protect those regions of the North Sea where the species diversity of the demersal fish community is highest.

- Use MPAs as a means of reducing the overall impact of fishing on the benthic invertebrate community by 30%.

3.3.1.1. *MPAs and the Conservation of Fish Species Diversity*

For this case study our objective is to select up to 10% of the area of the North Sea that might be considered to have the highest conservation value in terms of its fish community species diversity and to consider the implications of setting this area aside as MPAs with the complete abolition of fishing within them. Firstly we only have species diversity data for 152 ICES statistical rectangles covering a total area of 496,424Km^2, thus the total extent of our closed areas should amount to around 15 ICES rectangles covering an area of approximately 49,000Km^2. The data we used to guide our selection of closed areas is the GOV Q3 IBTS data set raised to account for catchability. In Chapter 9, Figures 9.3.3.2.1.3 and 9.3.3.2.1.4 suggest that the fish communities occupying the northern and southern halves of the North Sea are quite distinct, with each community differing markedly in species diversity. Under these circumstances we would wish to protect "examples" of both types of fish assemblage, and so would not locate all the MPAs in the most species diverse region, the southern North Sea. Figure 3.3.1.1.1 shows the spatial demarcation of the main assemblage types across the North Sea along with a plot of spatial variation in Hills N_1. In selecting ICES rectangles to set aside as MPAs to protect species diversity we did not simply select the 7 or 8 most species diverse rectangles in each assemblage type, instead we attempted to select groups of rectangles with relatively high species diversity that were contiguous with one another. Our intention here was to reduce the number of individual MPAs, and increase the size of each area. We believe this to be a better design strategy for the conservation of species diversity (Halpern 2003; Neigel 2003), more easily enforced, and perhaps of greater benefit in terms of the export of fish out of the MPAs into areas where they might be exploited. Figure 3.3.1.1.1 shows the 14 rectangles selected as MPAs, covering a total combined area of 46,595Km^2, or 9.4% of the area surveyed by the GOV.
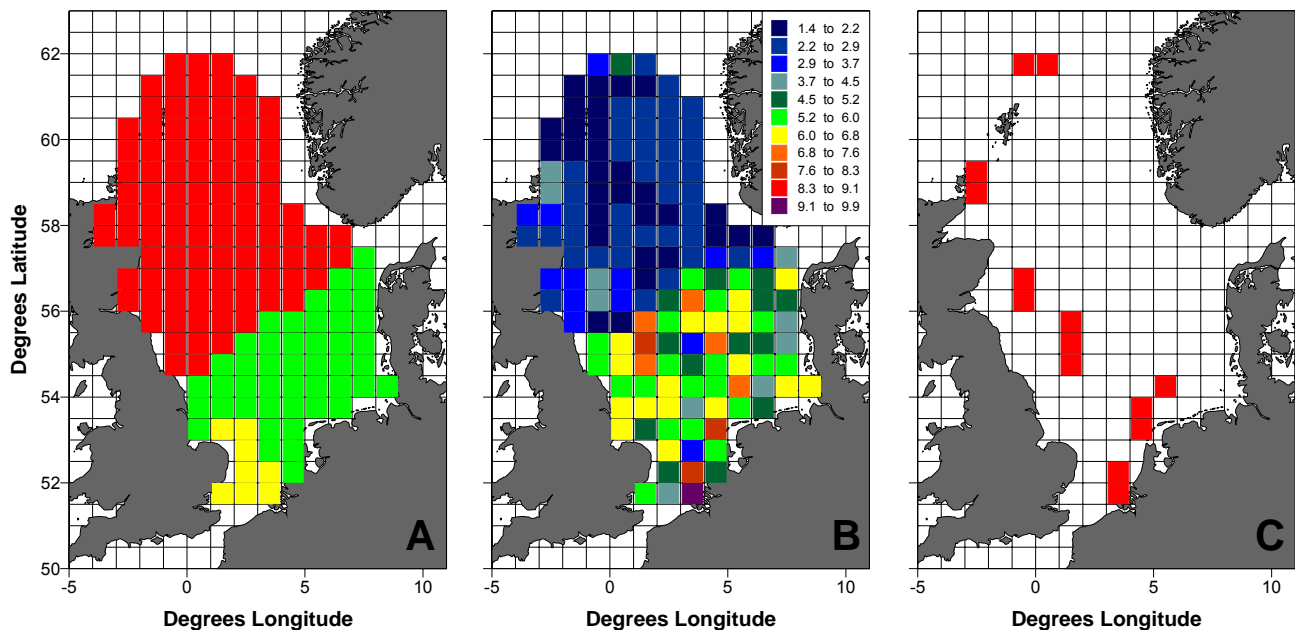
Figure 3.3.1.1.1: Spatial variation in groundfish species assemblage type (A) and Hills N_1 based on the GOV data raised to account for catchability (B) and the selection of approximately 10% of the surveyed area as MPAs designed to conserve the most species diverse regions within the area occupied by the two main assemblage types (C).

Landings and effort data were determined for 215 ICES statistical rectangles in ICES area IV (the North Sea), covering an area of 608,122Km^2 (Greenstreet *et al* 2007d). The 14 rectangles selected as MPAs to conserve groundfish species diversity constitute 7.7% of this total area. Only small quantities of *Nephrops* were landed from these MPA rectangles. The proportion of total landings of cod, haddock and whiting originating from the proposed MPA rectangles, at 3.7%, 3.5% and 4.2% respectively, were considerably less than the expected 7.7%, but the proportions of saithe, plaice and sole, at 11.7%, 10.9% and 23.0% were markedly higher (Figure 3.3.1.1.2A) . Not surprisingly, given these figures, the beam trawl fishery would be the most affected by the closure of these 14 rectangles to fishing; 22% of the total annual beam trawl effort occurred in the areas selected as possible MPAs. Other métiers were much less affected with only 4.1% of otter trawl effort directed at fish, 0.2% of otter trawl effort directed at *Nephrops*, and 5.5% of seine gear effort on average occurring in the 14 selected rectangles (Figure 3.3.1.1.2B).
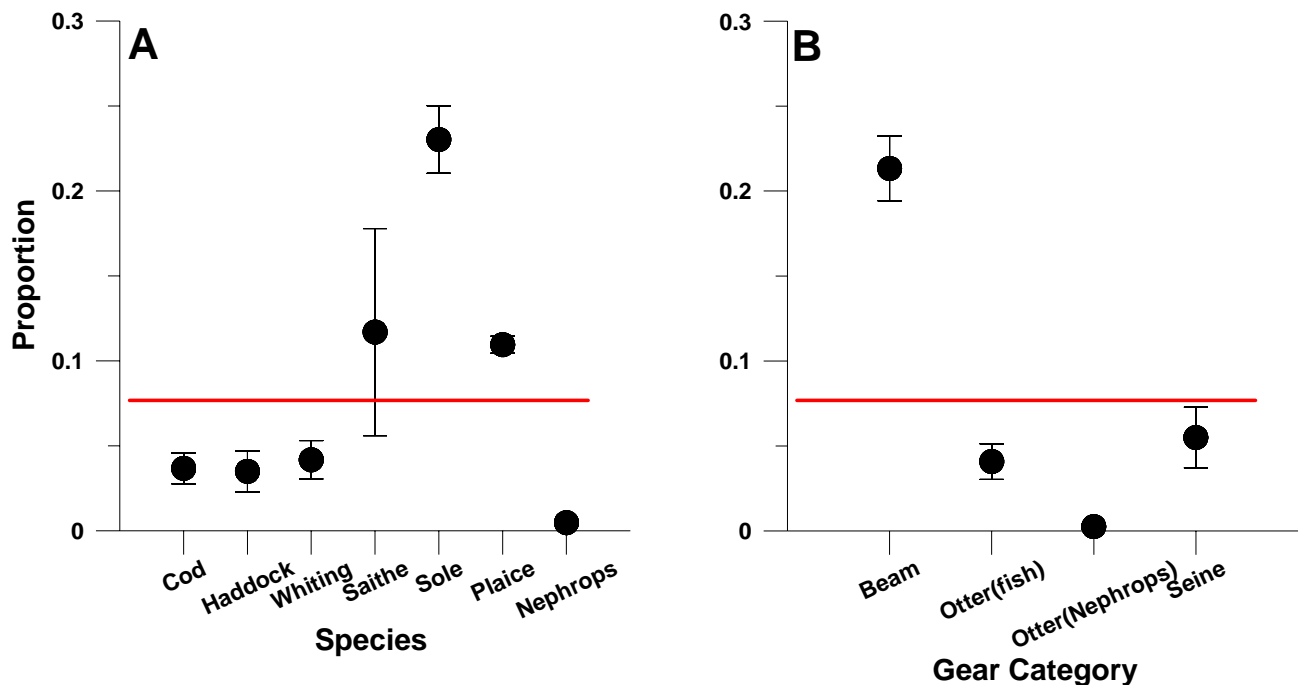
Figure 3.3.1.1.2: Mean proportion (±1 Std.Dev.) of total North Sea landings of each species (A) and fishing effort for each main gear category (B) reported from 14 ICES rectangles selected as MPAs to conserve groundfish species diversity over the period 1997 to 2004. Red lines indicate the expected fractions given the fraction of the area of the North Sea included within the proposed MPAs.

To avoid the displacement of this fishing effort to areas outside the proposed MPA would require a simultaneous reduction in TAC by the percentages indicated in Figure 3.3.1.1.2A). Without this reduction in TACs, then fishing effort is likely to be displaced to ICES rectangles remaining open to fishing outside those designated as MPAs, so as to make up the shortfalls in landed fish normally taken from within the MPA designated rectangles. The spatially referenced international landings and effort data compiled by the project allow this displaced effort to be modelled. To demonstrate this model we consider two time periods, 1997 to 2000 and 2001 to 2004, and use averaged annual data for these two periods. Spatial distributions of average annual landings of each species by each main gear category for these two periods are given by

Greenstreet *et al* (2007d: Figures 6.1.2.1 to 6.1.2.7). Spatial distributions of effort by each main gear category in each year are also given in their Figures 6.2.2.1 to 6.2.2.4. From these latter data, spatial distributions of averaged annual spatial variation in effort for each of the two time periods are easily calculated. From these two sets of data, average annual catch per unit effort (CPUE) for each species in each main gear category can be determined (Figures 3.3.1.1.3 to Figures 3.3.1.1.9).
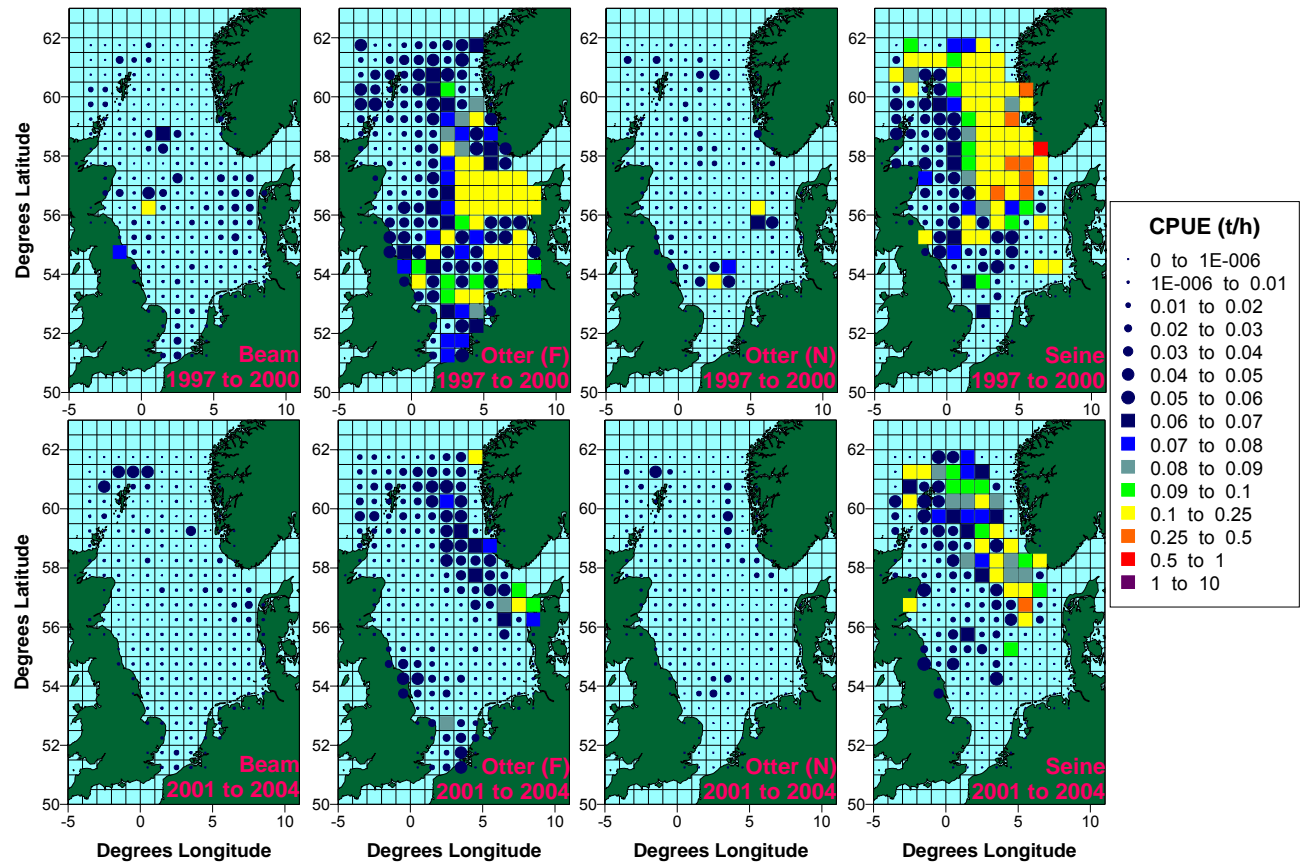
Figure 3.3.1.1.3: Spatial variation in average annual CPUE (t.h^{-1}) of cod in each of the main fishing gear categories (F indicates otter trawl directed at fish, N indicates otter trawl directed at *Nephrops*) in two time periods, 1997 to 2000 and 2001 to 2004.
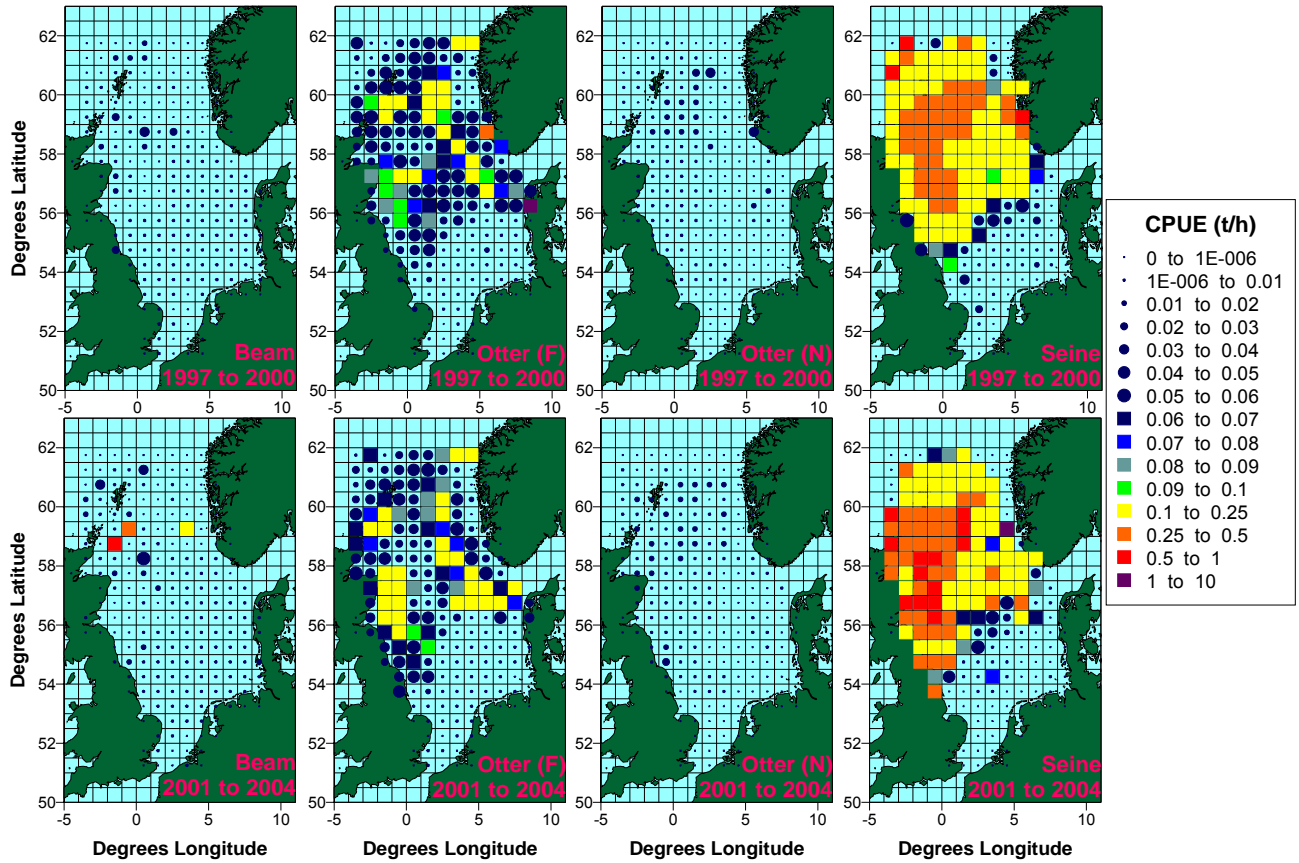
Figure 3.3.1.1.4: Spatial variation in average annual CPUE (t.h^{-1}) of haddock in each of the main fishing gear categories (F indicates otter trawl directed at fish, N indicates otter trawl directed at *Nephrops*) in two time periods, 1997 to 2000 and 2001 to 2004.
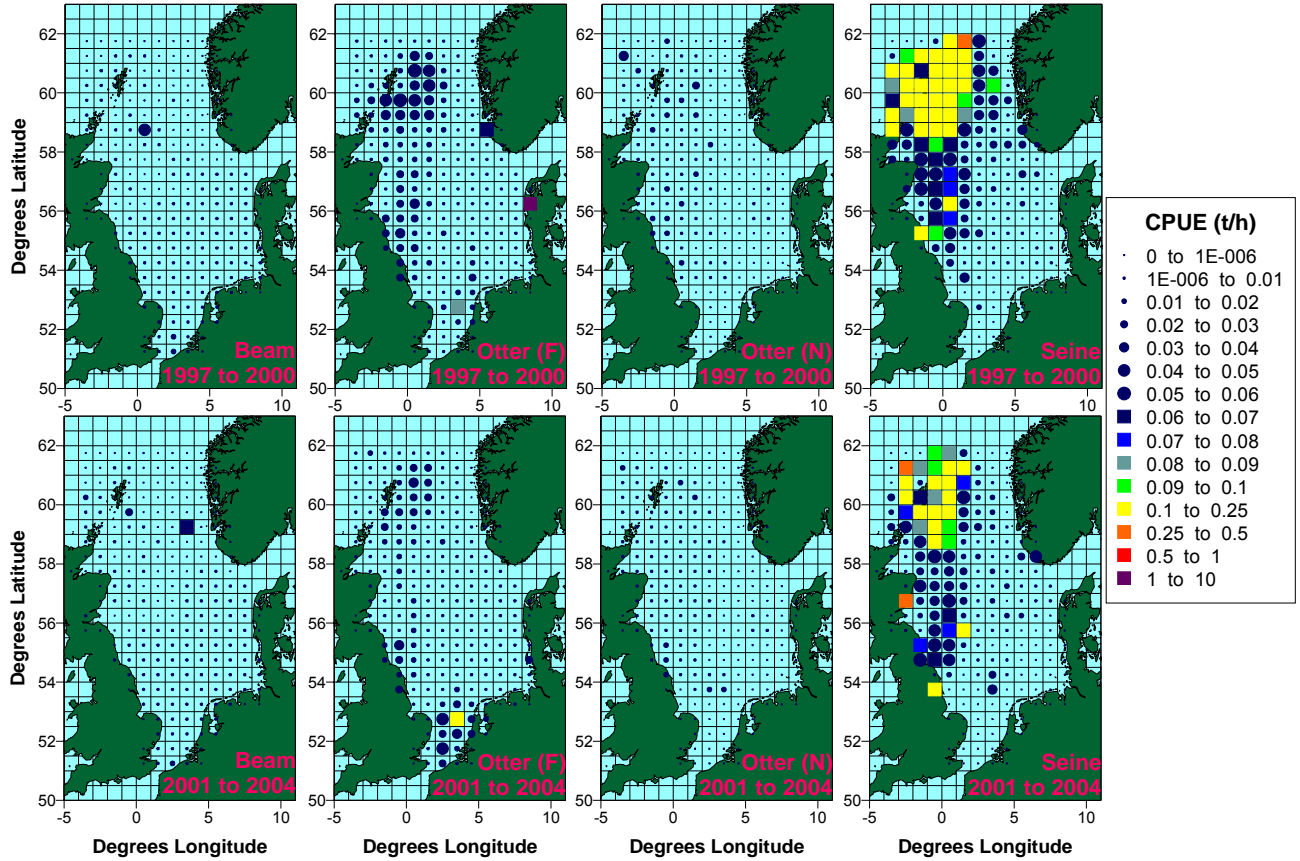
Figure 3.3.1.1.5: Spatial variation in average annual CPUE (t.h^{-1}) of whiting in each of the main fishing gear categories (F indicates otter trawl directed at fish, N indicates otter trawl directed at *Nephrops*) in two time periods, 1997 to 2000 and 2001 to 2004.
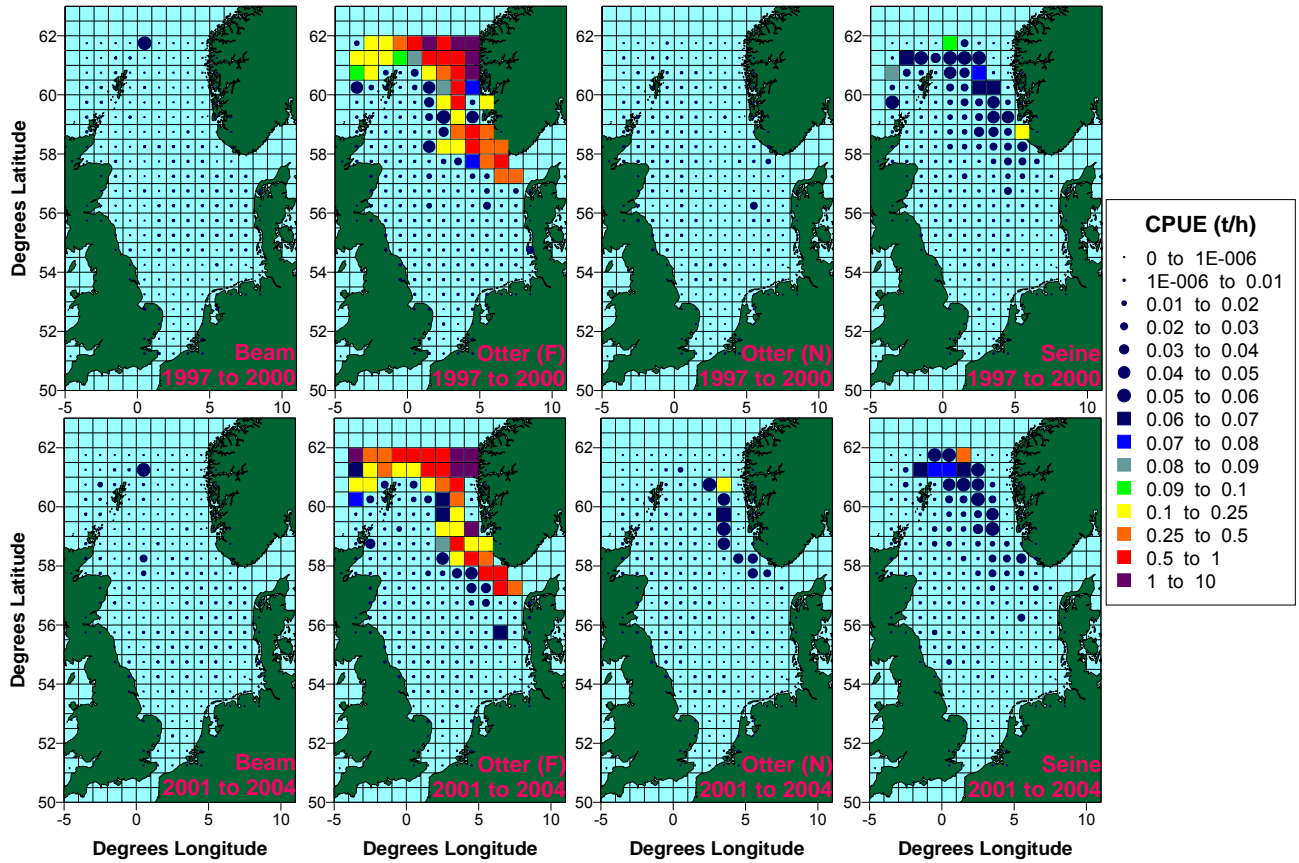
Figure 3.3.1.1.6: Spatial variation in average annual CPUE (t.h^{-1}) of saithe in each of the main fishing gear categories (F indicates otter trawl directed at fish, N indicates otter trawl directed at *Nephrops*) in two time periods, 1997 to 2000 and 2001 to 2004.
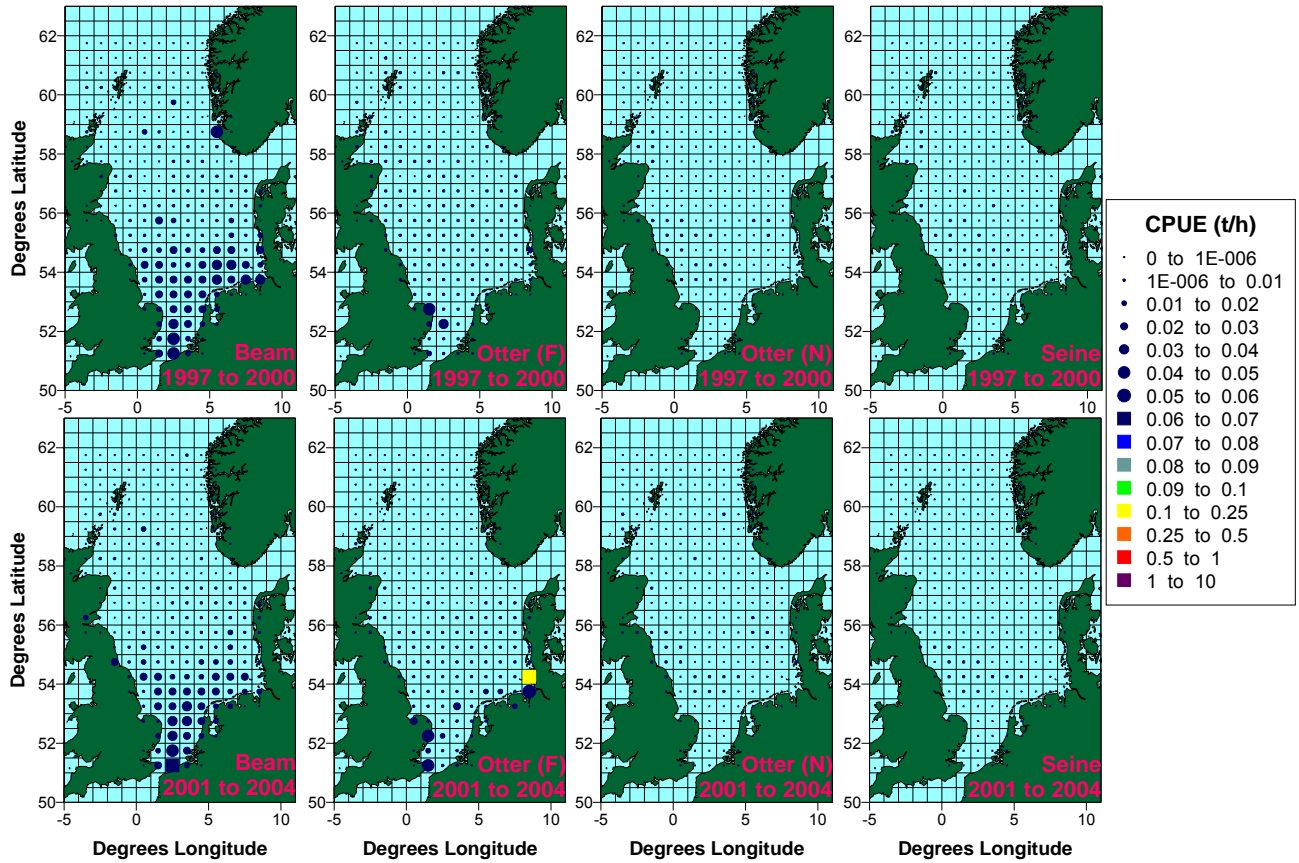
Figure 3.3.1.1.7: Spatial variation in average annual CPUE (t.h^{-1}) of sole in each of the main fishing gear categories (F indicates otter trawl directed at fish, N indicates otter trawl directed at *Nephrops*) in two time periods, 1997 to 2000 and 2001 to 2004.
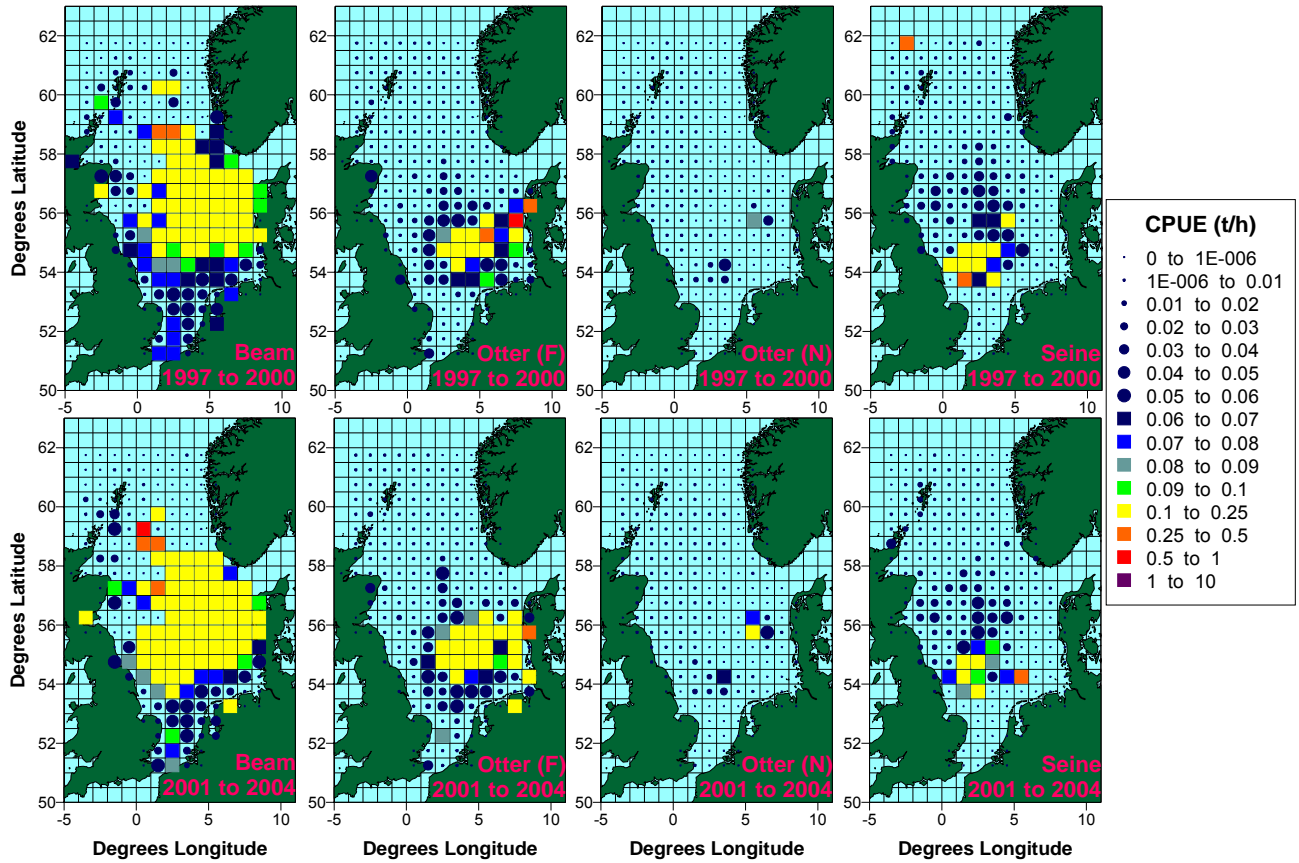
Figure 3.3.1.1.8: Spatial variation in average annual CPUE (t.h^{-1}) of plaice in each of the main fishing gear categories (F indicates otter trawl directed at fish, N indicates otter trawl directed at *Nephrops*) in two time periods, 1997 to 2000 and 2001 to 2004.
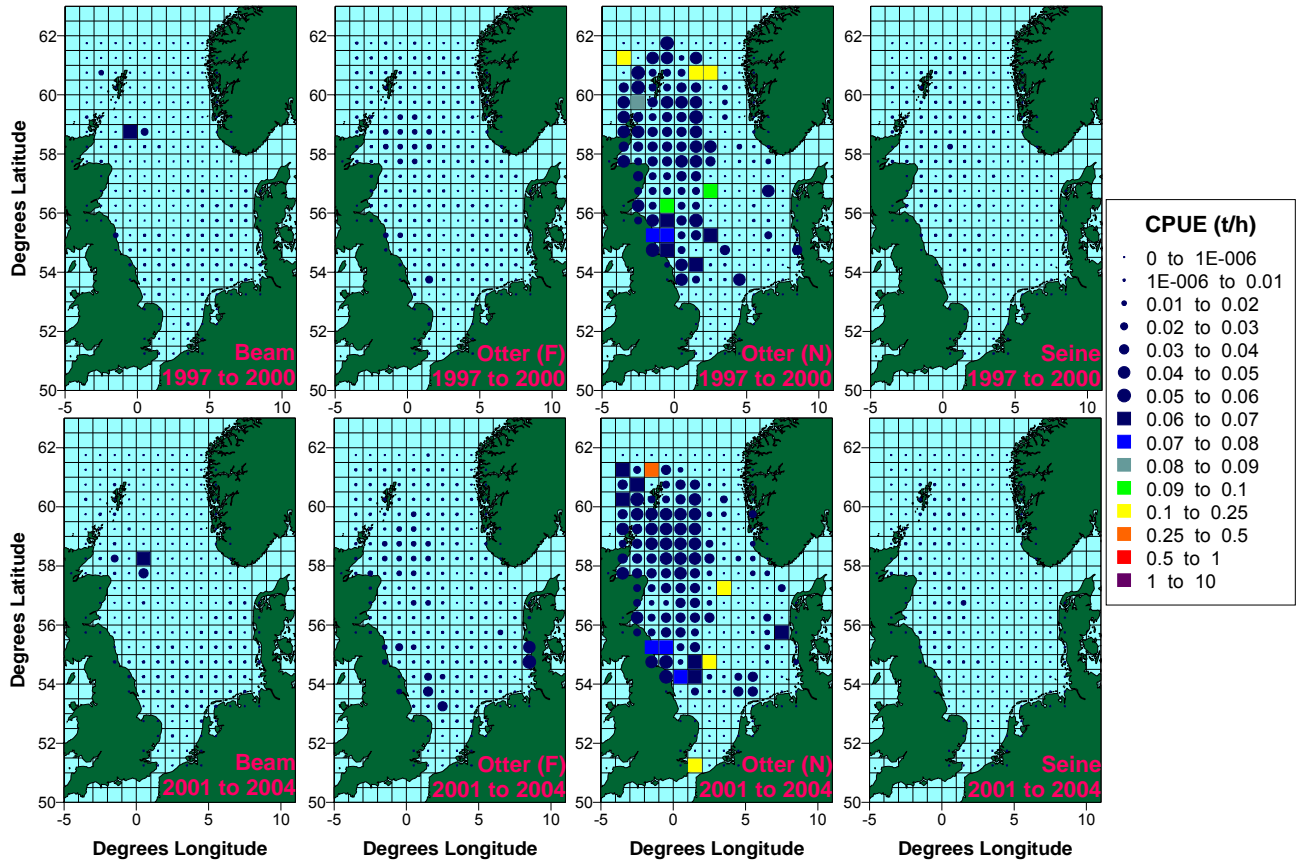
Figure 3.3.1.1.9: Spatial variation in average annual CPUE (t.h^{-1}) of *Neprops* in each of the main fishing gear categories (F indicates otter trawl directed at fish, N indicates otter trawl directed at *Nephrops*) in two time periods, 1997 to 2000 and 2001 to 2004.

The first step in modeling the redistribution of fishing effort, following closure of ICES rectangles designated as MPAs, is to estimate the additional landings of the principal species (*sg*) targeted by each main gear category (*g*) from each rectangle (*r*) remaining open to fishing required to balance the total quantity of that species normally landed from the closed rectangles prior to their closure. The model assumes that the total amount of landings normally originating from the MPA rectangles is, following their closure, now obtained from the rectangles remaining open to fishing *pro rata* to landings from these rectangles prior to the establishment of the MPAs, so that:

$$L_{sg,g,r,add} = \frac{L_{sg,g,r,prior}}{\sum\limits_{r=x}^{OPEN} L_{sg,g,r,prior}} . \sum\limits_{r=y}^{MPA} L_{sg,g,r,prior} \qquad \text{3.3.1.1.1}$$

$L_{sg,g,r,add}$ and $L_{sg,g,r,prior}$ are respectively, the additional landings in a given ICES rectangle remaining open to fishing following cessation of fishing in the MPA rectangles, and the landings in that rectangle prior to the establishment of the MPAs. $\sum\limits_{r=x}^{OPEN} L_{sg,g,r,prior}$ and $\sum\limits_{r=y}^{MPA} L_{sg,g,r,prior}$ are the total landings prior to the establishment of the MPAs from all rectangles remaining open to fishing and all rectangles designated as part of an MPA respectively. Next, the additional effort by each gear in each rectangle ($E_{sg,g,r,add}$) remaining open to fishing required to take the additional landings of principal species targeted by the gear needs to calculated. This is easily

done knowing the catch per unit effort (CPUE) of each species in question in each of the main gears in each rectangle ($CPUE_{sg,g,r}$) by:

$$E_{sg,g,r,add} = \frac{L_{sg,g,r,add}}{CPUE_{sg,g,r}}$$ 3.3.1.1.2

Finally, as a result of the additional fishing effort in the rectangles remaining open to fishing required to make up the shortfall in landings of the principal targeted species of each gear resulting from the closure of the MPA rectangles to fishing, other species of commercial value will also be caught. The additional landings of these commercially important "bycatch" species from each rectangle open to fishing can be determined knowing the CPUE of each species in each main gear in each rectangle:

$$L_{s,g,r,add} = E_{sg,g,r,add}.Cpue_{s,g,r}$$ 3.3.1.1.3

Note the change in the subscript, from *sg* to *s*, in the Landings and CPUE terms to denote that we are no longer considering the species that are the principal target species of each gear.

Figure 3.3.1.1.2 indicated that the landings of sole, plaice and saithe would be the most affected by closure of the 14 rectangles indicated in Figure 3.3.1.1.1C. The two flatfish are primarily taken by beam trawl (Greenstreet *et al* 2007d) and use of this gear in the proposed MPA rectangles was higher than average across the North Sea. Saithe are primarily landed from otter trawlers targeting fish, and presumably effort by this quite specific fishery would be affected the most out of all otter trawling activity (Greenstreet *et al* 2007d). The results of the effort displacement models applied to beam trawl targeting sole and otter trawl targeting saithe are summarised in Table 3.3.1.1.1. The model output indicated that just these changes to the beam trawl and otter trawl fishery, driven by the targeting of sole and saithe respectively, were sufficient to make up the deficits in landings that would normally have been taken in the MPA rectangles for all species. In fact the data suggest that high levels of discarding (as high as 100% of landings) of cod, haddock, plaice and whiting may result from these changes. However, we have no way of assessing how excessive such discard levels may be, since we have no explicit data detailing discard levels that would have been associated with the landings of these species had they been taken as normal from the MPA rectangles. Figure 3.3.1.1.10 compares the spatial distributions of beam trawl and otter effort before and after the closure of the 14 ICES rectangles to form the MPAs. The maps show the redistributed effort predicted by the model. Figure 3.3.1.1.11 presents similar data for otter trawl effort directed at *Nephrops* and seine net, but in this instance, the MPAs are simply overlaid on the original effort patterns as the model suggested that little redistribution of effort by these gears would have been necessary.

Main Gear Category		Beam Trawl		Otter Trawl (Fish)	
Principal Target Species		Sole		Saithe	
Time Period		1997-2000	2001-2004	1997-2000	2001-2004
Landings from rectangles designated as MPAs (t)		4,628	4,331	6,584	14,620
Effort expended in MPA rectangles to take landings (h)		199,416	189,067	42,467	40,312
Additional effort in "Open" rectangles to make up landings deficit (h)		231,213	211,205	97,405	155,127
Change in fishing effort over whole North Sea (h)		+31,797	+22,138	+54,939	+114,815
Effort in "Open" rectangles prior to MPA management (h)		801,901	647,316	1,160,913	850,006
Effort in "Open" rectangles after MPA management (h)		1,033,115	858,521	1,258,318	1,005,133
Percentage change in effort in "Open" rectangles		28.8%	32.6%	8.4%	18.3%
Percentage change in effort across the whole North Sea		3.2%	2.6%	4.6%	12.9%

Table 3.3.1.1.1: Results of applying the effort displacement model to beam trawlers targeting sole and otter trawlers targeting saithe to determine the effects of closing 14 ICES rectangles to conserve species diversity in the demersal fish community.
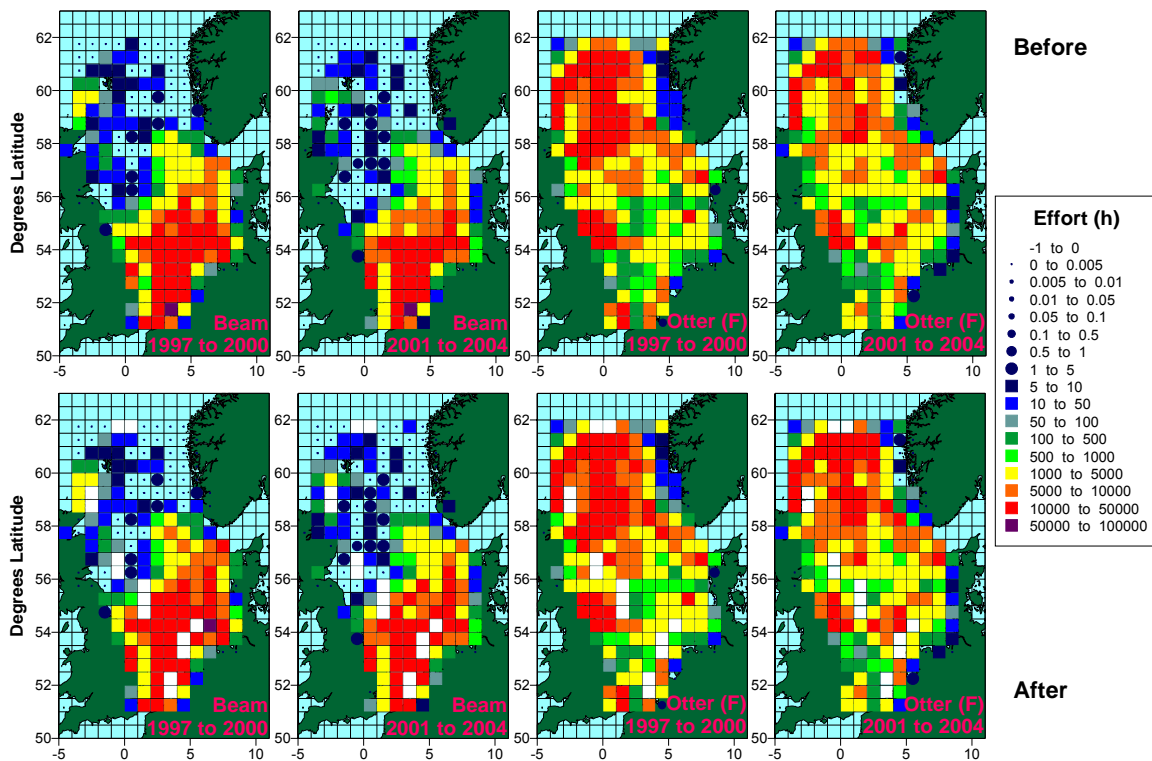
Figure 3.3.1.1.10: Spatial distributions of beam trawl and otter trawl effort directed at fish in two time periods, 1997 to 2000 and 2001 to 2004, before and after the designation of 14 ICES rectangles as MPAs designed to protect areas of high groundfish species diversity. After closure of the MPAs, effort is redistributed to make up the deficits of the two principal target species, sole and saithe, most affected by the locations of the MPAs.
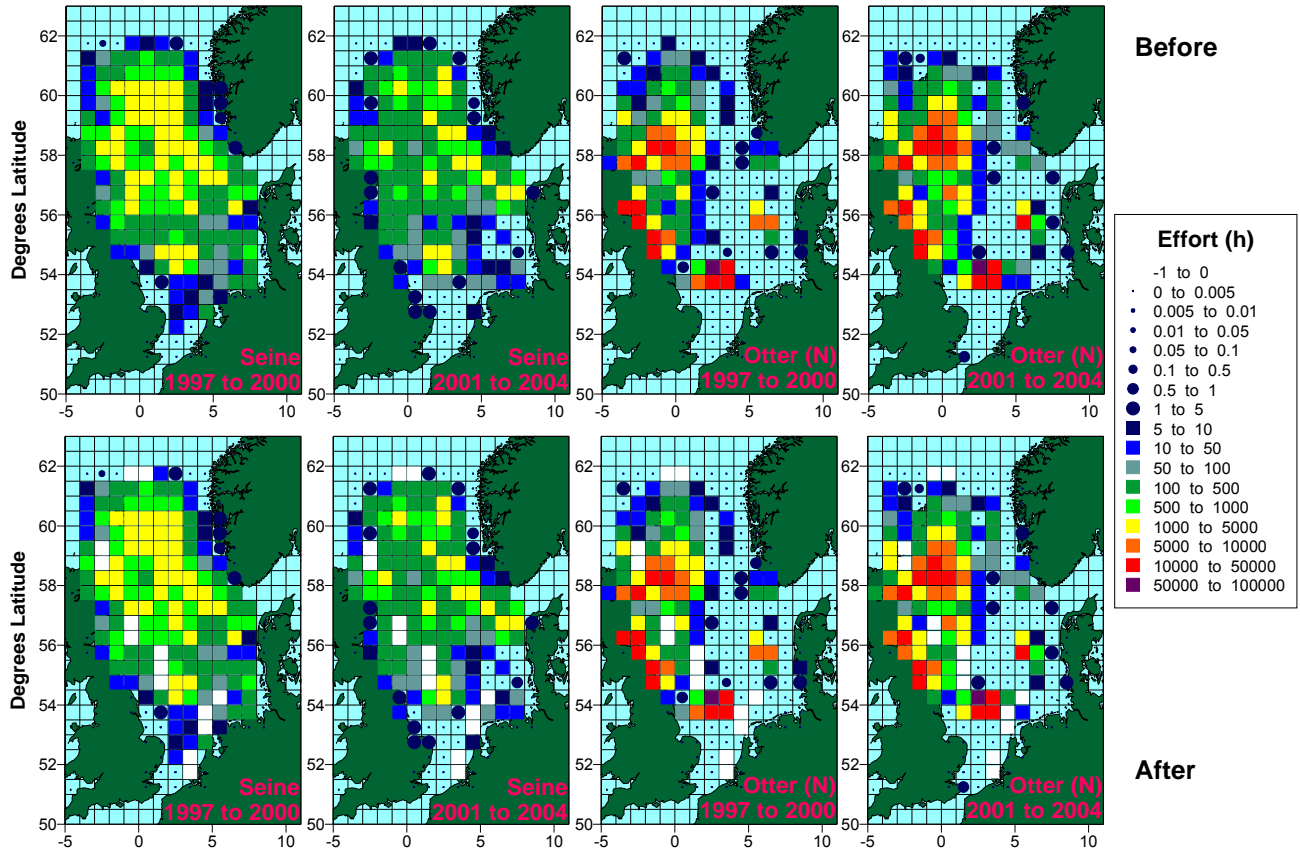
Figure 3.3.1.1.11: Spatial distributions of otter trawl effort directed at *Nephrops* and seine net effort in two time periods, 1997 to 2000 and 2001 to 2004, before and after the designation of 14 ICES rectangles as MPAs designed to protect areas of high groundfish species diversity.

Greenstreet *et al* (2007d) present a benthic invertebrate disturbance model. This model estimates the percentage of benthic invertebrates that are killed each year in each ICES rectangle as a result of the fishing effort expended by each main gear category. This model can now be applied to the effort distribution data presented in Figures 3.3.1.1.10 and 3.3.1.1.11 to examine what effect closing 14 ICES rectangles to conserve groundfish species diversity has on benthic invertebrate communities in the North Sea. Greenstreet *et al* (2007d: Figure 7.4.5.2) presents the mortality rate data for the two time periods, 1997 to 2000 and 2001 to 2004, that we have considered here, so we start from this point. Prior to the designation of 14 ICES rectangles as MPAs, average benthic invertebrate mortality across the whole North Sea was 19.8%.y^{-1} between 1997 and 2000 and 16.5%.y^{-1} over the period 2001 to 2004. These average values were based on the individual rectangle mortality rates weighted by rectangle area. If the 14 rectangles indicated in Figure 3.3.1.1.1 were closed to fishing and fishing effort was redistributed as indicated in Figures 3.3.1.1.10 and 3.3.1.1.11 to make up the deficit in landings that would normally have been taken in these MPAs, then average benthic mortality across the North Sea over these two periods predicted by the benthic disturbance model would be 20.1%.y^{-1} and 17.1%.y^{-1} respectively. Despite nearly 8% of the sea area of the North Sea being set aside as MPAs, in which all fishing activity was prohibited, overall impact on the benthic invertebrate communities across the entire North Sea increased in both time periods, by 1.2% in 1997 to 2000 and by 3.5% between 2001 and 2004, as a result of the introduction of closed area management. In both time periods, the overall increase in fishing effort required to make

up the landings deficit, resulting from the considerable increase in effort outside the MPAs, combined with the fact that in many instances this increase in effort affected rectangles that had previously been relatively lightly fished, caused increased disturbance to benthic communities that outweighed any benefits gained from the introduction of the MPAs themselves. The actual spatial distributions of benthic annual mortality caused by fishing activity, before and after the introduction of the MPAs designed to conserve groundfish species diversity are shown in Figure 3.3.1.1.12.
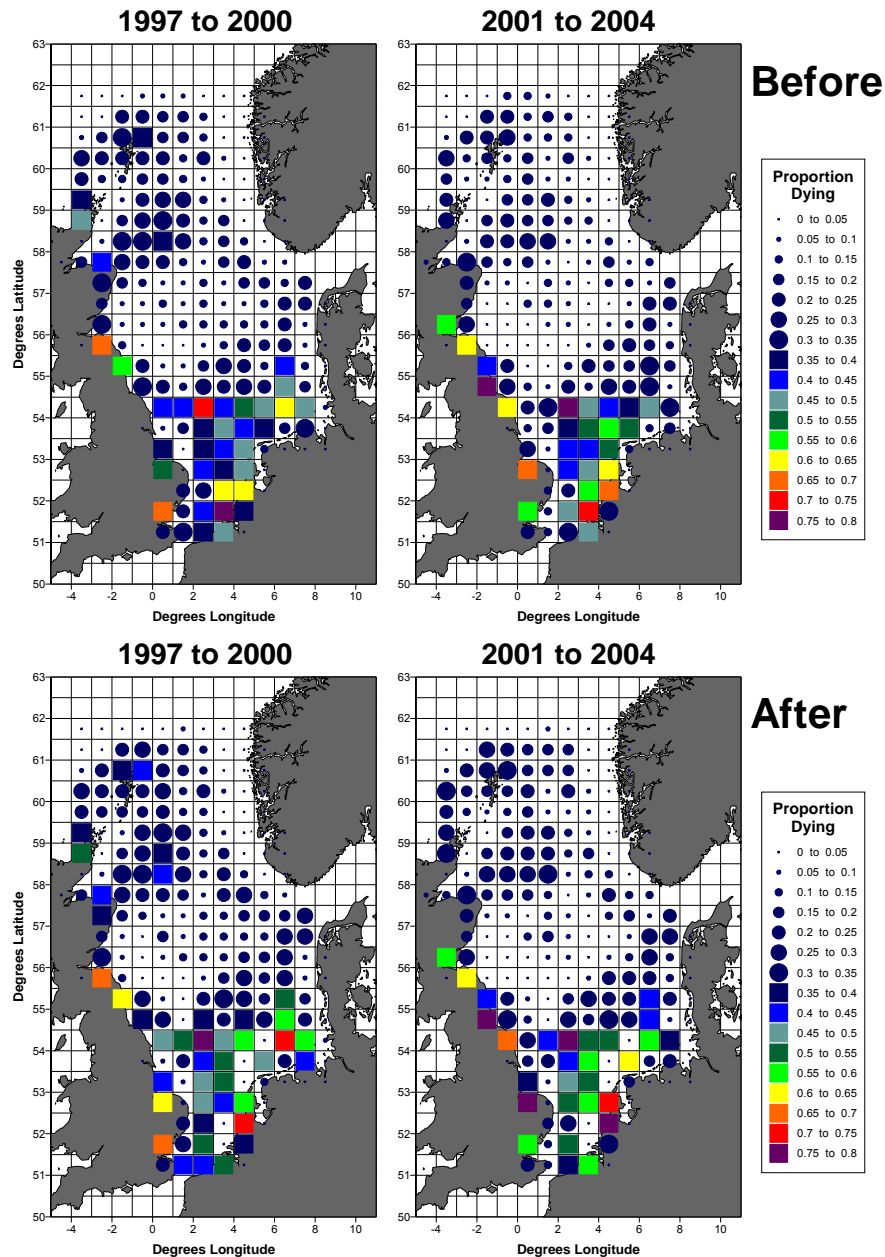
Figure 3.3.1.1.12: Spatial variation in the annual mortality of benthic invertebrates resulting from the combined fishing activity of beam trawlers, otter trawlers directed at fish, otter trawlers directed at *Nephrops*, and seine netters before and after the designation of 14 ICES rectangles as MPAs designed to conserve areas of high groundfish species diversity.

In conclusion, simply closing nearly 8% of the North Sea sea-area to protect regions of high species diversity in the groundfish community, without reducing TACs accordingly, results in an overall increase in fishing effort as fishermen attempt to make up the deficit in landings, normally taken from the MPA rectangles, by increasing fishing effort outside the closed areas. The increase in fishing effort in rectangles remaining open to fishing is substantial, resulting in increased impact on benthic invertebrate communities. Over the whole North Sea, the increased impact on the benthos in rectangles outside the closed areas outweighs any benefits gained from prohibiting fishing in the MPAs. For the fish community, the overall increase in fishing effort also has an impact, with indications of higher discard levels and greater impact on the non-target non-commercial species in the community. On balance, simply closing areas to fishing would appear to be of dubious value to the marine ecosystem. Real benefits may only be gained, making management through closing areas to fishing a viable tool for managers implementing an ecosystem approach to fisheries management, if at the same time TACs are also reduced accordingly. For the particular scenario on which this demonstration was based, Table 3.3.1.1.2 gives the reductions in TAC required.

	1997 - 2000			2001 - 2004		
	TAC	Reduction	% Reduction	TAC	Reduction	% Reduction
Cod	117100.0	3709.1	3.2	38125.0	1017.2	2.7
Had	97637.5	2454.5	2.5	73441.3	2175.6	3.0
Whiting	52000.0	1041.4	2.0	23500.0	699.9	3.0
Saithe	101750.0	6588.9	6.5	144250.0	14621.9	10.1
Sole	20250.0	4655.5	23.0	16962.5	4385.8	25.9
Plaice	94250.0	10337.2	11.0	72312.5	9651.8	13.3
Nephrops	15700.0	71.6	0.5	17420.8	73.0	0.4

Table 3.3.1.1.2: Average annual TACs of each of the main commercial species over the periods 1997 to 2000 and 2001 to 2004, and absolute reduction and percentage reductions in TAC required in order to prevent redistribution of fishing effort following the establishment of MPAs covering 7.7% of the North Sea sea-area (14 ICES statistical rectangles) to protect areas of high species diversity in the groundfish community.

3.3.1.2. *MPAs and the reduction off fishing disturbance to the benthic invertebrates*

Like the groundfish community, benthic invertebrate communities vary in species composition and structure across the North Sea with clear differences apparent between the northern and southern North Sea (Greenstreet *et al* 2007c).   In order to safeguard all types of benthic invertebrate community, we selected groups of rectangles subject to high disturbance from fishing from across the entire North Sea, rather than concentrating potential MPA sites predominantly in the southern North Sea, where in general disturbance was highest. Distributions of benthic disturbance were shown in the preceding section (Figure 3.3.1.1.12). On the basis of these distributions we have selected the rectangles indicated in Figure 3.3.1.2.1 as potential MPAs with the objective of using these MPAs to reduce the overall impact of fishing activity on benthic communities throughout the North Sea. Rectangles where fishing mortality was amongst the highest within each local region of the North Sea were selected on the basis that this would have result in the greatest reduction in benthic mortality for the smallest area closed. The 15 ICES rectangles selected cover an area of 44,255km^{-2}, 7.3% of the sea-area of the North Sea.
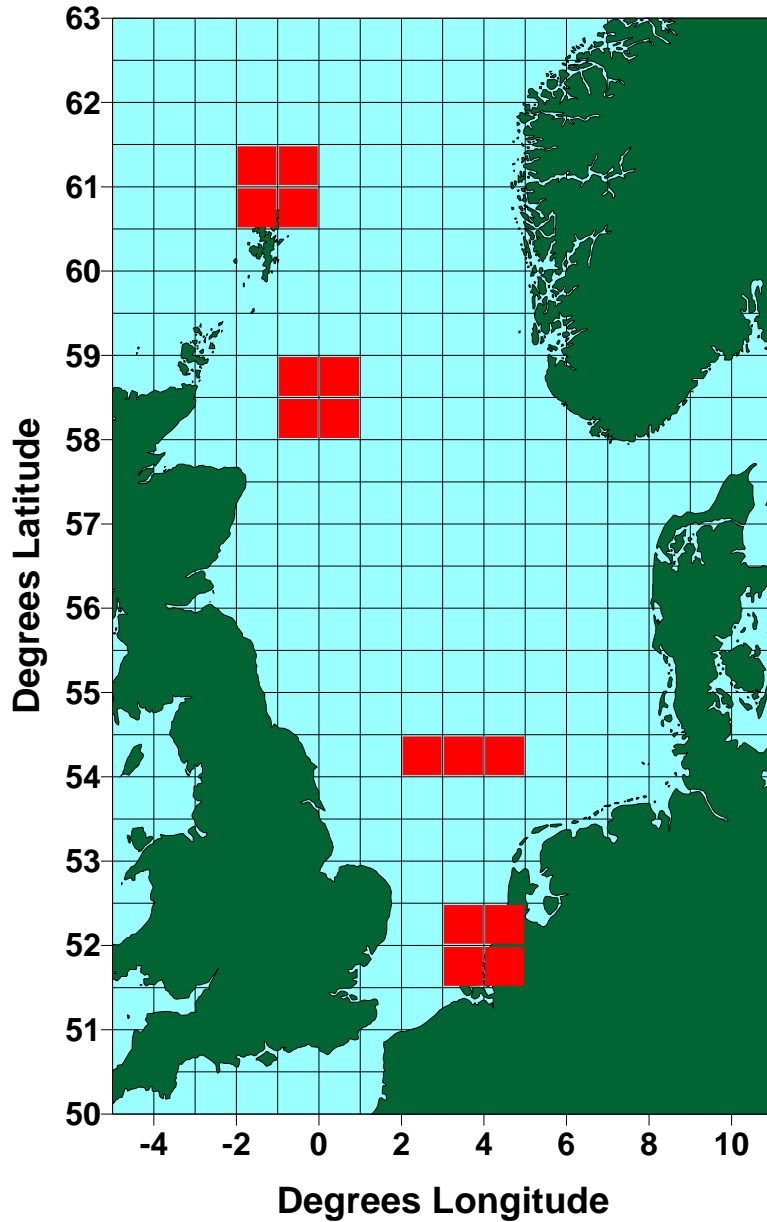
Figure 3.3.1.2.1: Location of four closed areas, including 15 ICES statistical rectangles covering 7.3% of the sea-area of the North Sea, designed to reduce the impact of fishing on the benthic invertebrate communities of the North Sea, in terms of reducing overall average annual benthic fishing mortality rates.

Since rectangles with amongst the highest benthic fishing mortality were selected for designation as MPAs, it is not surprising that the proportion of total North Sea landings of most species originating from the MPA rectangles was considerably higher than the proportion of the North Sea area set aside as MPAs. The location of the MPAs would appear to have the least affect on landings of haddock and saithe, but fishing activity for all other species, particularly *Nephrops*, seems likely to be severely affected by these MPAs (Figure 3.3.1.2.2A). With respect to the proportion of fishing effort by each of the main gear categories, all but seine fishing looks to be seriously affected by the location of the MPAs, and this is particularly the case with respect to otter trawl directed at *Nephrops* (Figure 3.3.1.2.2B).
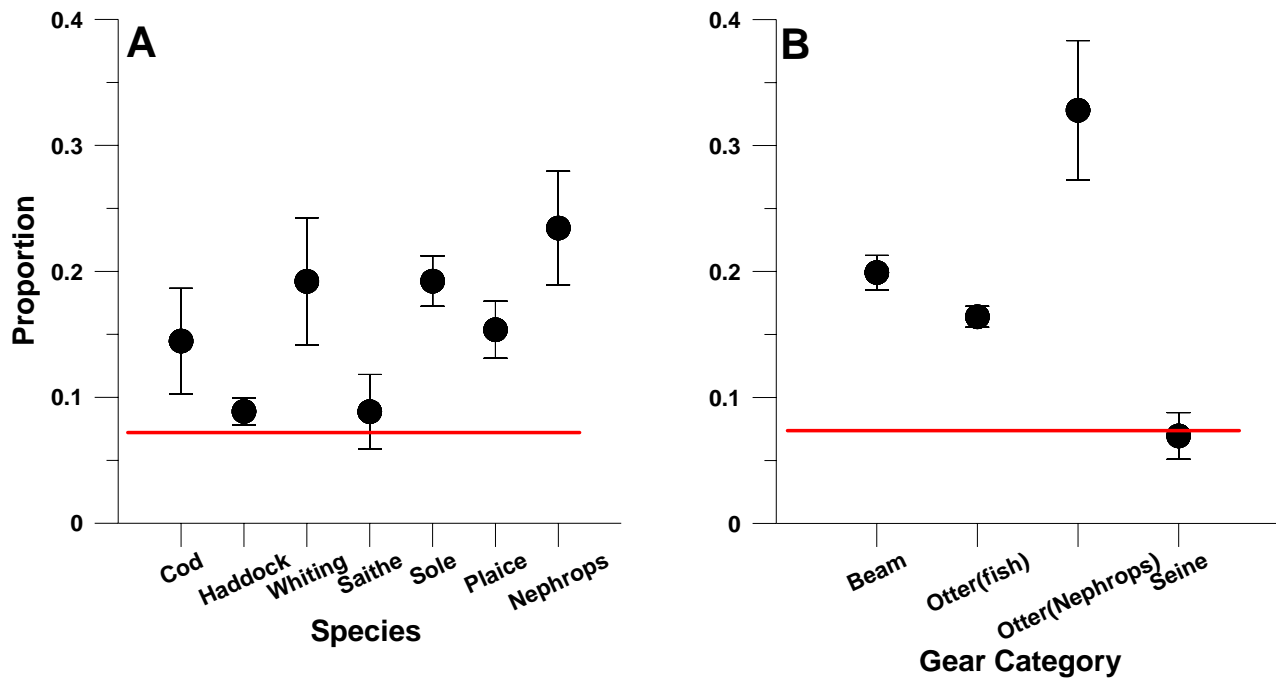
Figure 3.3.1.2.2: Mean proportion (±1 Std.Dev.) of total North Sea landings of each species (A) and fishing effort for each main gear category (B) reported from 15 ICES rectangles selected as MPAs to reduce the disturbance caused by fishing to benthic invertebrates over the period 1997 to 2004. Red lines indicate the expected fractions given the fraction of the area of the North Sea included within the proposed MPAs.

In the absence of concomitant reductions in TACs, to the extent indicated in Figure 3.3.1.2.2A, fishing effort is likely to be displaced to rectangles remaining open to fishing in order to make up the deficit in landings normally taken from within the MPAs. The effort displacement model described in section 3.3.1.1 was used to model the effort displacement required to make up the deficits in landings (Table 3.3.1.2.1). As suggested by Figure 3.3.1.2.2, it was only necessary to model effort displacement by three specific métiers to make up the deficits in landings normally taken in the closed areas; otter trawl targeting *Nephrops*, beam trawl targeting sole and otter trawl targeting whiting. In five out of six cases, overall effort declined following area closures and effort displacement, implying that the rectangles to which effort was displaced were more productive. For otter trawl targeting whiting and beam trawl targeting sole, the difference was negligible, but the reduction in overall effort by otter trawlers targeting *Nephrops* was quite marked. The *Nephrops* fishery is relatively restricted spatially and it just happened that the proposed MPA rectangles constituted a relatively high proportion of this area, and so included a high proportion of the landings and effort. But the rectangles closed to fishing tended to be the lower productivity rectangles (low CPUE). Closing these rectangles effectively forced fishing vessels into rectangles with higher CPUE. Trawlers utilized these lower CPUE rectangles because the gadoid bycatch was high and was commercially important to these vessels. Following displacement to rectangles outside the designated MPAs, CPUE of *Nephrops* was higher, resulting in a substantial net decrease in effort required to make up the *Nephrops* deficit. However, the bycatch of gadoid species was approximately halved. With respect to whiting, the bycatch taken by *Nephrops* trawlers made up a substantial fraction of the whiting taken in the MPA rectangles. As a result, following redistribution of effort by beam trawlers and otter trawlers targeting whiting, the deficit of whiting landings previously taken in the MPA rectangles

was not entirely made up. However, any attempt to rectify this resulted in substantial over-catches of saithe, cod and haddock.

Main Gear Category	Otter Trawl (*Nephrops*)		Beam Trawl		Otter trawl (Fish)	
Principal Target Species	*Nephrops*		Sole		Whiting	
Time Period	1997-2000	2001-2004	1997-2000	2001-2004	1997-2000	2001-2004
Landings from rectangles designated as MPAs (t)	1,782	3,273	3,816	3,484	2,729	1,594
Effort expended in MPA rectangles to take landings (h)	106,249	159,227	199,404	166,467	200,195	143,997
Additional effort in "Open" rectangles to make up landings deficit (h)	51,375	100,657	182,173	166,008	166,020	163,168
Change in fishing effort over whole North Sea (h)	-54,874	-58,570	-17,231	-459	-34,175	+19,171
Effort in "Open" rectangles prior to MPA management (h)	245,072	278,664	801,913	669,916	1,003,185	746,321
Effort in "Open" rectangles after MPA management (h)	296,447	379,321	984,086	835,924	1,169,205	909,489
Percentage change in effort in "Open" rectangles	21.0%	36.1%	22.7%	24.8%	16.5%	21.9%
Percentage change in effort across the whole North Sea	-15.6%	-13.4%	-1.7%	-0.1%	-2.8%	+2.2%

Table 3.3.1.2.1: Results of applying the effort displacement model to otter trawlers targeting *Nephrops*, beam trawlers targeting sole, and otter trawlers targeting whiting to determine the effects of closing 15 ICES rectangles to reduce the impact of fishing on benthic invertebrate communities.

Figures 3.3.1.2.3 and 3.3.1.2.4 compare maps of spatial variation in fishing effort before and after the establishment of the MPAs designed to reduce the impact of fishing on the benthos. The benthic invertebrate effort model was then run using these effort distributions to assess the effectiveness of these closed areas as a mechanism to reduce the impact of fishing on benthic communities. As we have already discussed in the previous section, prior to the introduction of any closed areas, benthic invertebrate fishing mortality was on average 19.8%.y^{-1} over the period 1997 to 2000 and 16.5%.y^{-1} between 2001 and 2004. After closing 15 ICES rectangles, 7.3% of the total sea-area of the North Sea, the model suggests that these overall mortality rates would have declined to 19.1%.y^{-1} and 16.3%.y^{-1}, 3.8% and 1.7% reductions in the pre-closed area annual mortality rates over the two time periods respectively. Spatial plots of the distributions of benthic invertebrate fishing mortality in both time periods, before and after the introduction of MPAs, are shown in Figure 3.3.1.2.5.
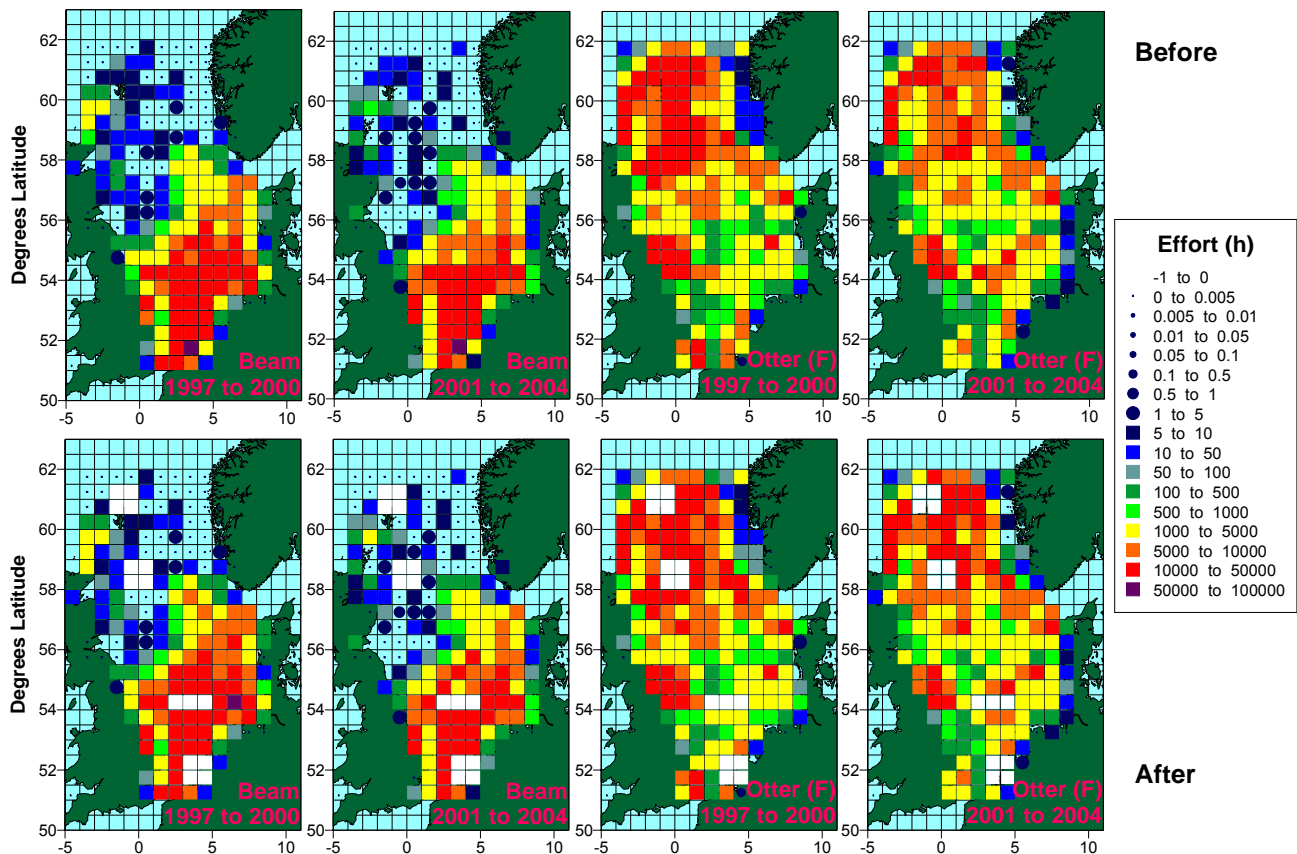
Figure 3.3.1.2.3: Spatial distributions of beam trawl and otter trawl effort directed at fish in two time periods, 1997 to 2000 and 2001 to 2004, before and after the designation of 15 ICES rectangles as MPAs designed to reduce the impact of fishing on North Sea benthic communities. After closure of the MPAs, effort is redistributed to make up the deficits of the two principal target species, sole and whiting, most affected by the locations of the MPAs.
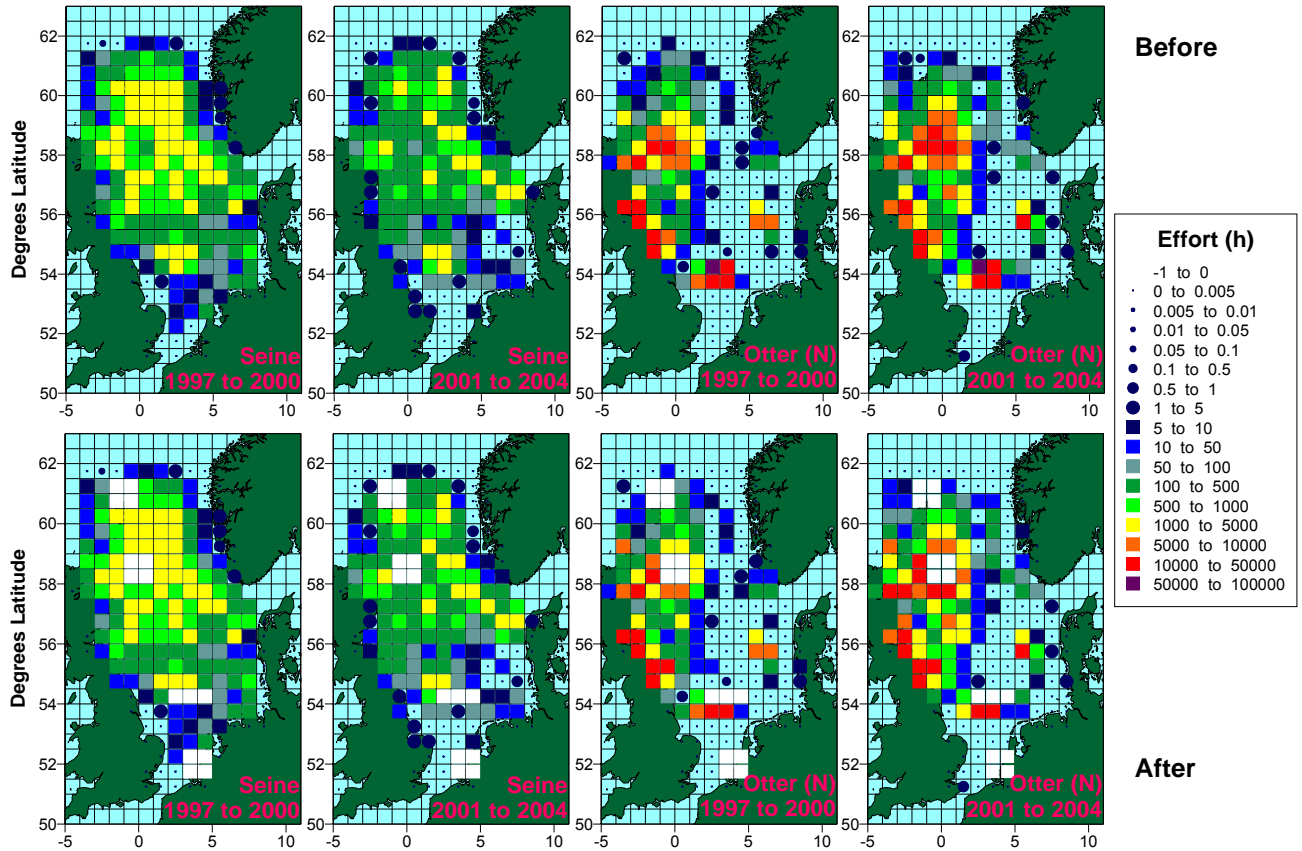
Figure 3.3.1.2.4: Spatial distributions of otter trawl effort directed at *Nephrops* and seine net effort in two time periods, 1997 to 2000 and 2001 to 2004, before and after the designation of 15 ICES rectangles as MPAs designed to reduce the impact of fishing on North Sea benthic communities. After closure of the MPAs, otter trawl effort is redistributed to make up the deficits of the principal target species, *Nephrops*, most affected by the locations of the MPAs. Redistribution of Seine effort was deemed unnecessary.
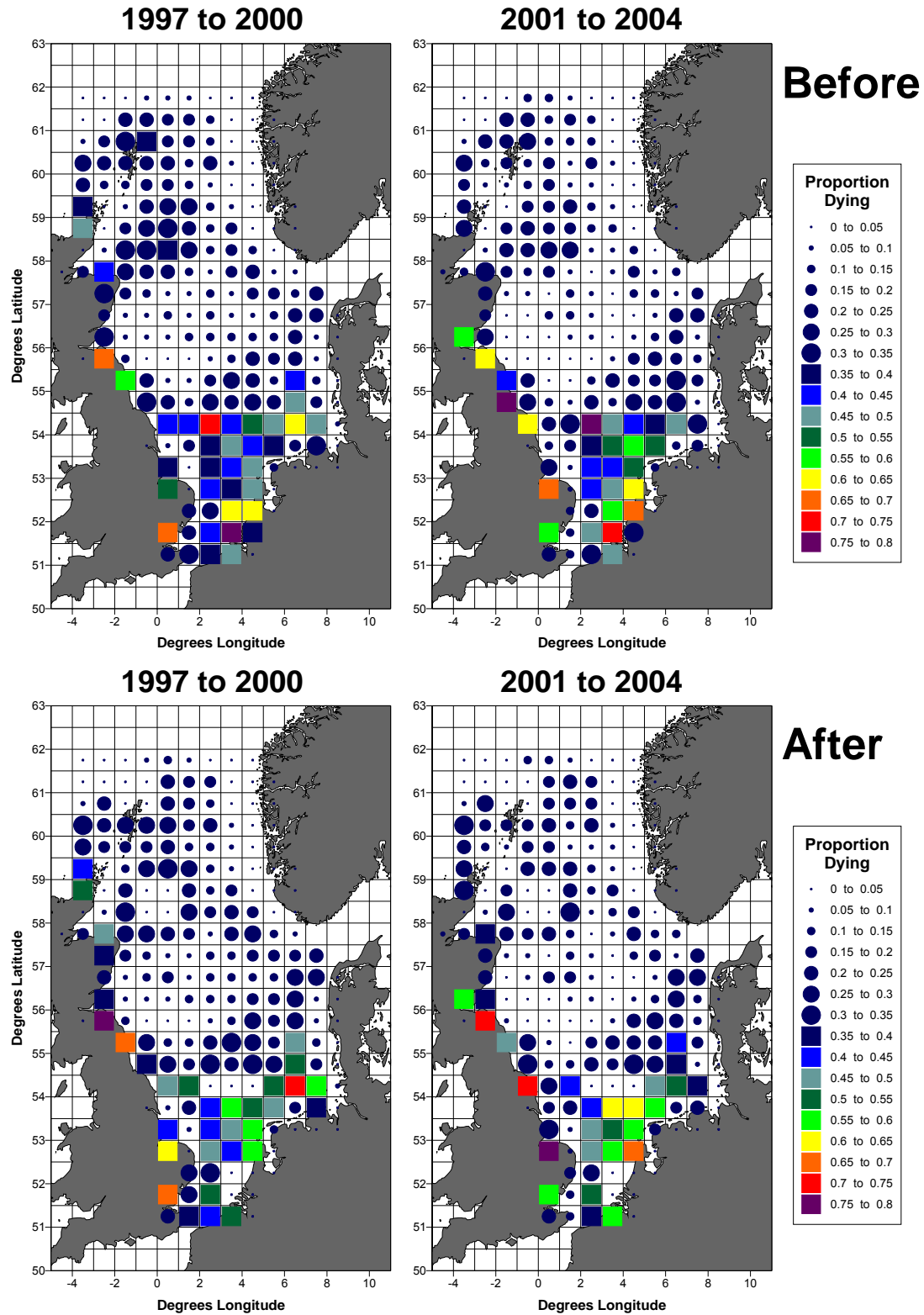
Figure 3.3.1.2.5: Spatial variation in the annual mortality of benthic invertebrates resulting from the combined fishing activity of beam trawlers, otter trawlers directed at fish, otter trawlers directed at *Nephrops*, and seine netters before and after the designation of 15 ICES rectangles as MPAs designed to reduce the overall impact of fishing on the benthic invertebrate communities of the North Sea.

Considering that approximately 7.3% of the North Sea was closed to achieve 3.8% and 1.7% reductions in overall North Sea benthic fishing mortality, closed area management with no other supporting action appears to be a relatively inefficient means of addressing such global scale ecological objectives. It is perhaps through the sheer chance that the rectangles selected for closure tended to result in the displacement of fishing activity to areas with higher CPUE, resulting in most instances in a reduction in overall effort, that any benefit in terms of reduced benthic fishing mortality was realised at all. The protocol described here can be used to examine the benefits of different closed area selections. In the scenario examined here we targeted rectangles with the highest benthic mortality rates, those with the highest levels of fishing effort. The relationship between fishing effort and benthic mortality is asymptotic in shape, not linear. Careful selection of rectangles could be employed so as to ensure that effort is displaced to areas higher up such curves. This should help to ensure that gains, in terms of reduced mortality, in closed areas always outweigh losses associated with increased mortality in areas to which effort is displaced. Once again, however, it seems that closed area management without associated reductions in TAC is relatively ineffective in addressing ecological objectives at the scale of the whole North Sea; the impact from fishing effort displaced throughout the remainder of the North Sea remaining open to fishing tends to negate much of the benefit achieved from the closed areas themselves. For the particular scenario on which this demonstration is based, Table 3.3.1.2.2 gives the reductions in TAC required. The combination of closing the 15 ICES rectangles along with the TAC reductions shown in Table 3.3.1.2.2, thereby assuming no effort redistribution, was examined using the benthic disturbance model. Under this set of conditions overall benthic invertebrate fishing mortality across the whole North Sea was reduced to $16.6\%.y^{-1}$ over the period 1997 to 2000 and $13.7\%.y^{-1}$ between 2001 and 2004; reductions in fishing mortality in each time period of 16.2% and 17.4% respectively.

	1997 - 2000			2001 - 2004		
	TAC	Reduction	% Reduction	TAC	Reduction	% Reduction
Cod	117100	11067	9.5	38125	4873	12.8
Had	97638	7092	7.3	73441	4817	6.6
Whiting	52000	4363	8.4	23500	3243	13.8
Saithe	101750	6592	6.5	144250	9063	6.3
Sole	20250	3904	19.3	16963	3585	21.1
Plaice	94250	12780	13.6	72313	15168	21.0
Nephrops	15700	3116	19.8	17421	4121	23.7

Table 3.3.1.2.2: Average annual TACs of each of the main commercial species over the periods 1997 to 2000 and 2001 to 2004, and absolute reduction and percentage reductions in TAC required in order to prevent redistribution of fishing effort following the establishment of MPAs covering 7.7% of the North Sea sea-area (14 ICES statistical rectangles) to protect areas of high species diversity in the groundfish community.

3.3.2. Concluding comments

We have demonstrated how the data sets compiled during this project, in conjunction with disturbance and effort redistribution models that we have developed, can be used to aid the selection of closed areas to achieve global scale ecological objectives for management in the North Sea. Our models are still at a preliminary stage. The benthic disturbance model can, for example, be improved to take account of mobility in benthic fauna. The effort redistribution model is currently very simple in concept, only utilizing information concerning spatial variation

in landings, effort and landings per unit effort. This model can certainly be enhanced to take account of many additional factors, such as distance to home port, fuel costs, labour costs, fish market values, etc, all of which are bound to influence the decision processes of skippers faced with area closures on their favoured fishing grounds. For both the disturbance and effort redistribution models as they currently stand, accurate spatially referenced landings and effort data are essential. Already our data sets are becoming dated, and our ability as scientists to access the data necessary to keep these databases current seems limited. To provide relevant advice into the future, advice that reflects the prevailing situation, it is essential that the appropriate data are easily accessible. We return to this issue in Section 5.

Several points emerge from our two initial demonstrations of the MPA management protocol. Firstly, as the benthic mortality scenario illustrated, even with unrestricted effort displacement, it may not always prove possible to make up the deficits in landings normally taken in the closed areas, at least not without considerable extra effort, and associated with markedly increased discarding. This will certainly have economic implications for the fishing industry. Secondly, an ecosystem approach to management will need to address numerous ecological objectives simultaneously. Considerable care will be required to ensure that MPAs established to address one specific ecological objective do not result in effort displacement that has detrimental impacts on other aspects of the marine ecosystem. Finally, closed area management alone may not be as effective a management tool to address North Sea-wide ecological objectives as many would hope. Effort displacement is a serious issue and the ecological consequences of increased effort in areas outside the MPAs may, over the North Sea as a whole, undermine much of the benefits gained from the closed areas themselves. However, MPAs combined with TAC reductions to reduce the need for effort displacement appears to hold considerable promise. Major steps forward towards the implementation of an ecosystem approach to management may be achieved through the combination of these two actions. The protocol we have started to develop here could provide scientists with exactly the tool needed to ensure that the advice scientists provide is adequate to support managers taking these steps.

4. ALTERNATIVE THEORETICAL MODEL

4.1. Introduction

In Section 2 a number of different tests of Huston's Dynamic Equilibrium Model (DEM) are presented. For the most part, these tests suggest that the DEM fails to predict the response of species diversity to variation in productivity and disturbance in fish and benthic invertebrate communities in the North Sea. Under these circumstances, the DEM cannot provide the theoretical basis for a management protocol aimed at predicting diversity consequences resulting from specific disturbance regimes. Nevertheless, since the conservation and restoration of biodiversity is at the heart of many of the principal policy drivers facing managers today, understanding the processes that structure marine communities, and affects their species diversity, remains an essential goal for marine scientists tasked with providing the scientific advice necessary to underpin an "ecosystem approach to management" (EAM).

It is widely recognised that the EAM will be heavily reliant on the use of "indicators". Currently there is considerable emphasis on the development of frameworks wherein indicators can be employed to inform and guide management. Many of these frameworks, for example the "Pressure-State-Response" (PSR) framework, rely on the application of a suite of indicators that are theoretically mechanistically linked (Figure 4.1.1). "Pressure" indicators relate variation an

anthropogenic activity, or the anthropogenic disturbance caused to the system. Such indicators
might include fishing effort statistics, or the mortality indices derived from models that use these
statistics to provide more biologically meaningful measures of the actual impact caused by any
given activity regime (Greenstreet *et al* 2007d). "State" indicators then reflect changes in the
state of the biological system. Such indicators are normally (but need not necessarily be)
specific to particular components of the marine ecosystem, for example the demersal fish
community or the epibenthic invertebrate community, and to particular characteristics of these
components, for example species diversity or mean body size (Greenstreet 2007a; 2007c). In
order for there to be a management issue, application of relevant "State" indicators will usually
have provided evidence of a change in "State" that is deemed undesirable, for example the
long-term declines in the species diversity of fish or benthic communities noted in chapter 1, and
which managers will wish to rectify. To initiate the remedial process, objectives for state
(Ecological Quality Objectives, {EcoQOs}) will be set and managers will then commence
mitigating action, the "Response", for example reducing Total Allowable Catches (TACs),
whereby the TACs themselves become the third, or "Response", indicator in the series
(Figure 4.1.1).
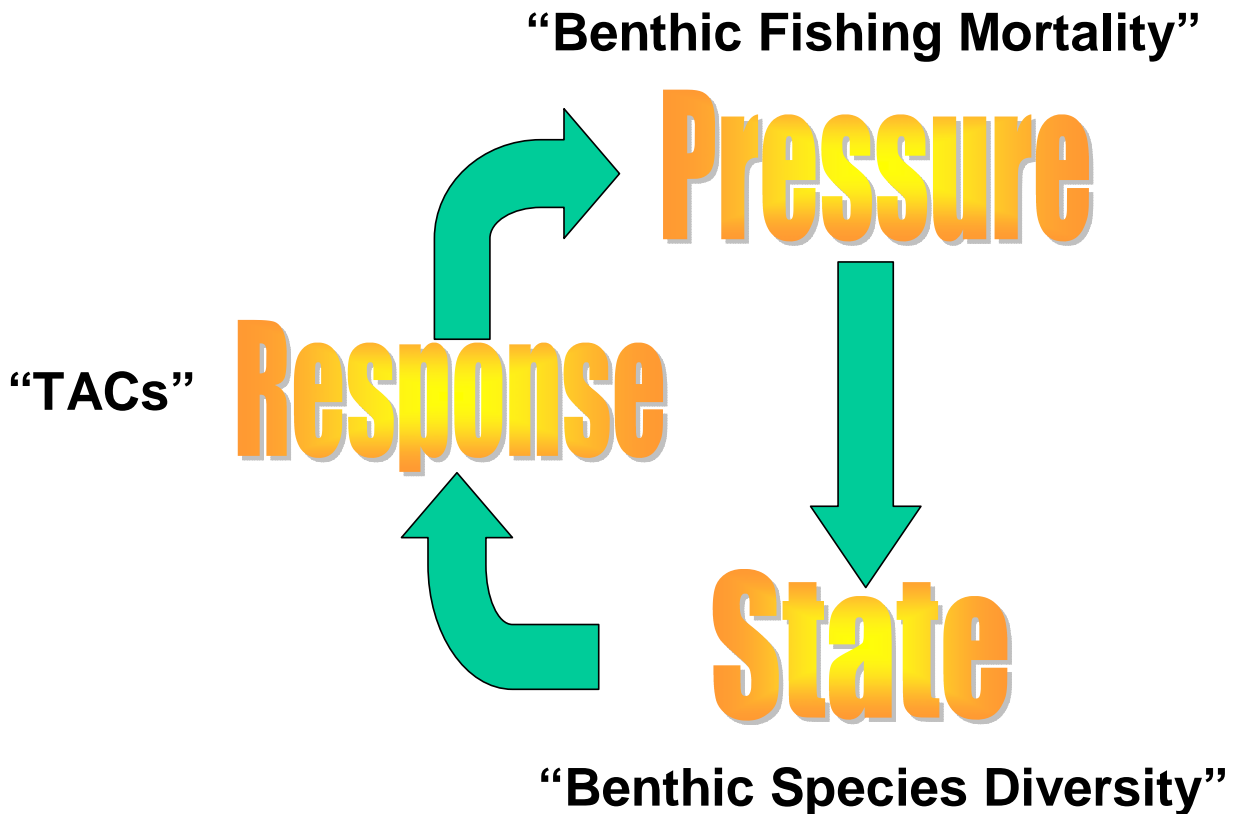
Figure 4.1.1: Representation of the "Pressure-State-Response" indicator based management framework.

For such management frameworks to be successful, appropriate indicators have to be
identified, and the mechanistic linkages between these indicators have to be well understood.
In the example considered in Figure 4.1.1, the relationship between TACs and fishing activity
regime needs to be well defined to ensure that a specific change in the suite of single species
TACs (the "Response" indicator) brings about a predictable change in benthic mortality caused

by fishing (the "Pressure" indicator), for example, a particular spatial distribution of a given level of fishing effort by a specific set of fishing gears that gives rise to unique distribution of benthic mortality. Most critically of all, it is important the relationship between the "Pressure" and "State" indicators are well known. This is essential if the change in "Pressure" brought about by the" Response" is to have the desired effect on "State". Failure to properly define the relationship between "Pressure" and "State" indicators may result in fisheries being constrained more than is necessary, or insufficiently constrained, to achieve management objectives. At worst, failure to elucidate and understand this link in the PSR framework my cause fisheries to be blamed and penalised for changes in state brought about by other factors altogether.

It is clear from the above discussion that this project was set up with the clear intention of providing the scientific support to management frameworks such as the PSR framework. The link between "Response" and "Pressure" indicators has largely been addressed elsewhere in the report (Greenstreet *et al* 2007e and Section 3). Here we devote our attention towards progressing our knowledge regarding the relationship between fishing activity ("Pressure") and the species diversity ("State") of fish and benthic invertebrate communities. Greenstreet *et al* (2007b) provide an in depth review of the literature on the subject, and start to apply what is largely (but not entirely) a set of terrestrial paradigms to the marine situation. This review considers the "forces" that contribute to Huston's DEM and in Section 2 the DEM is described in more detail with regard to the derivation of specific hypotheses from the model that were testable with the available data. In Section 2, where we test these hypotheses directly, we demonstrate that the DEM fails to predict variation in species diversity of fish and benthic communities in the North Sea; certainly it fails to do this with the precision required to form the basis for management decision making. However, the importance of understanding the link between ecological disturbance and species diversity with respect to the EAM remains undiminished. Here we consider why the DEM failed when applied to marine communities and we return to what was learnt by our review of theoretical community ecology so as to consider a possible alternative theoretical model.

4.2. The Shortcomings of Traditional Community Ecology Theory when Applied to Marine Fish and Benthic Invertebrate Communities

In communities consisting of species with deterministic growth, it makes sense to consider species as the "individual units" that make up the community. Individuals of each species quickly grow through their juvenile phase and mature as fully-grown adults occupying the adult "niche". The greater part of any individual's life span is spent as the mature adult, generally eating the same type of prey and occupying the same habitat. In communities of species that for the most part display non-deterministic growth, the idea of the species as the community unit makes far less sense (Persson 1988). An archetypal demersal fish in the North Sea, for example, may start life as a pelagic or demersal egg, hatch into a pelagic larval form preying on zooplankton such as copepods. As it grows it preys increasingly on larger planktonic prey, which may include the larvae of other fish. The larva metamorphoses and often, for a short while, goes through a pelagic juvenile phase, continuing to consume planktonic prey, which at this stage can consist of adult crustaceans, as well as the larvae of fish and benthic invertebrates (Robb and Hislop 1980; Robb 1981). After several months the juvenile fish settles to the seabed, now preying on benthic invertebrates and hyper-benthic crustaceans. The young fish continues to grow, and as it does so, its diet continues to change to include larger and larger prey, which at this stage may start to include fish, either the adults of small species such as gobies, or the juveniles of larger species (Hislop *et al* 1991; Greenstreet 1996; Hislop 1997; Greenstreet *et al* 1998). Some demersal fish species may not change to a piscivorous diet, but

nevertheless their diets also change so that they prey on ever larger invertebrate species, such as squat lobsters, hermit crabs, whelks and *Nephrops* (Daan 1973; 1989). As these fish grow, their habitat preferences may also change, for example, moving from shallow areas into deeper waters. Many marine species can increase in body mass through more than five orders of magnitude (Cushing 1975; Cohen *et al*. 2003) It is difficult to reconcile the changes in life-style that occur as the result of the continued growth of such non-deterministic growth species with the concept of the species niche. It would perhaps make more sense to consider particular organism size classes as the community unit, rather than maintaining the focus on species. In communities of non-deterministic growth species, differences in "ecological function" between the size classes of individuals within the community tend to be at least as great, if not greater, than the differences between species when all life-history phases of each species are considered (Werner & Gilliam 1984). Interaction strengths between different cohorts of both predators and prey will change continuously as both increase at varying rates and to different ultimate body-lengths. Different cohorts of the same species may interact, through cannibalism, or through mediation of prey responses to predators of different length for example, to alter species interactions between predators and prey and between competitors (Biro *et al* 2003; Rudolf 2006).

Unicellular algae are the principal primary producers in marine ecosystems (Duarte and Cebrián 1996). These support strongly size-structured food chains in which predators tend to be larger than their prey (Pope *et al* 1994). This, together with the transient predator-prey relationships that occur as individuals of any one species pass through so many different size-classes (e.g. Daan, 1973; 1989; Hislop *et al* 1991; Boyle and Pierce 1994; Greenstreet 1996; Hislop 1997; Greenstreet *et al* 1998), has led many scientists to undertake size based, rather than species oriented, analyses of food webs. Since non-deterministic growth is more prevalent in marine and aquatic environments, a high proportion of such studies have involved marine and aquatic communities (Platt and Denman 1978; Sheldon and Parsons 1967; Sheldon *et al*. 1972; 1973; Sprules 1980; Sprules and Goyke 1994; Sprules and Munawar 1986; see also references in Kerr and Dickie 2001). One of the principal features of many of these studies is the use of "biomass-size spectra" to describe the structure of the community in question. Such spectra have been used to describe the structure of both fish and benthic communities in the North Sea and elsewhere (Pope and Knights 1982; Pope *et al* 1988; Murawski and Idoine 1992; Duplisea and Kerr 1995; Rice and Gislason 1996; Duplisea *et al* 1997; 2002; Gislason and Rice 1998; Bianchi *et al* 2000; Jennings *et al* 2002a; 2002b; 2002c; Daan *et al* 2005). Because energy transfer between trophic levels is inefficient, production in lower trophic levels will always exceed production in the next higher trophic level. Consequently, and because predators tend to be larger than their prey (Warren and Lawton 1987; Cohen *et al* 1993), biomass-size spectra tend to demonstrate a typical form whereby biomass decreases in progressively heavier size classes (Kerr 1974, Dickie *et al* 1987; Boudreau *et al* 1991; Thiebaux and Dickie 1992, 1993; Kerr and Dickie 2001).

Long-term changes in the shape of fish and benthic community biomass spectra in the North Sea (and other seas) where fishing constitutes a major cause of mortality are often characterised by an increase in the gradient of the negative slope (Rice and Gislason 1996; Gislason and Rice 1998; Duplisea *et al* 2002; Jennings *et al* 2002a). The communities have changed such that the biomass of small organisms has increased while the biomass of large size class animals has decreased. Such changes in biomass size-spectra imply major changes in energy flow through the food webs involved. Production at higher trophic level will be reduced, whilst lower down food chains, production will be increased. The numbers of top predators in systems will be reduced, while their potential prey abundance will have increased

(Pinnegar *et al* 2002). Because of the profound implications that these observed changes in biomass size-spectra hold for marine ecosystem function (e.g. Jennings *et al* 2002a), considerable effort has been spent confirming the relationship between biomass size-spectra and trophic structure (Fry and Quinones 1994; France *et al* 1998; Jennings *et al* 2001a; 2001b; 2002c; 2002d; 2003). In most instances, this linkage has been established, leading to the inevitable conclusion that the changes in size composition within these communities has coincided with change in their trophic structure (Pinnegar *et al* 2002; Jennings *et al* 2002a; Jennings and Warr 2003). If so, then any consideration of marine fish and benthic invertebrate community species diversity must also take account of community biomass size-spectra. The observed changes in size-spectra imply major disruption to top-down, bottom-up, and competitive processes that may be operating between and within size classes to determine the number of coexisting species within each size class. Thus models of marine community species diversity also need to be size-based, particularly where non-deterministic growth is the norm for most species in the community.

To sum up therefore, consideration of the size-based processes common in marine fish and benthic invertebrate communities consisting of species with non-deterministic growth has several implications that species-based models, such as Huston's dynamic equilibrium model, simply do not take into account. Firstly, fishing is itself a size-based activity, encouraged by the higher value attributed to larger fish and regulated through minimum legal landing sizes and minimum legal mesh sizes, so that only the larger individuals in any species suffer the highest "fishing disturbance", or mortality. Secondly, as a result of size-based trophic structuring, not all individuals in a population are competing for the same prey resource. With increase in size, individuals of each species are involved in competitive interactions with a variety of different species at different trophic levels. Thirdly, as a corollary of this, not all individuals are subjected to the same levels of predation mortality, inflicted by the same predator species. Furthermore, through varying top-down predatory processes, large individuals of a particular species have the capacity to influence the outcome of competitive interactions in their smaller sized conspecifics (e.g. Biro *et al* 2003; Svanbäck & Persson 2004). Consequently, individuals of any given species in marine fish and benthic invertebrate communities are likely to be "limited" or "controlled" to differing extents by different "top-down control" and "bottom-up limiting" processes (Rudolf 2006).

In addition, models such as the dynamic equilibrium model, and indeed much of the theory relating to the mechanisms believed to structure communities, assume Lokta-Voltera type *per capita* population growth. Population dynamics of this type infer that the potential for population growth at any particular point in time is a function of the current population size. Fish communities in particular, but also in all likelihood benthic invertebrate communities as well, are instead characterised by what has been termed "storage" and "lottery" model population growth potential (see Greenstreet *et al* 2007b). The "storage" model infers that future population growth potential is, for a considerable period of time, decoupled from current population size and such population dynamics seem particularly appropriate for populations of species that are characterised by non-deterministic growth, and where individual fecundity is a function of individual body mass (McLaren 1965; Griffiths 1977; Achituv & Barnes 1978; Strong & Daborn 1979; Hughes & Roberts 1981; Emerson *et al* 1990; Bliel & Oberst 2005). Thus, a population of fish where recruitment, immigration, and emigration rates are set to zero (i.e. a single annual cohort in a closed population) will decline in number at a predictable rate dependent on the rate of mortality. However, the survivors will continue to grow in body mass such that, with the passage of time, the population will consist of a dwindling number of increasingly large individuals. Since fecundity in fish is tightly linked to body mass (Hislop 1988; Emerson *et al*

1990; Marteinsdottir & Begg 2002; Bliel & Oberst 2005), total population fecundity may remain constant, or even increase with time, despite decreasing numbers of spawners present in the population (Figure 4.2.1). In the example illustrated in Figure 4.2.1, loosely based on cod life-history characteristics, population growth potential (gamete mass) in the population increases for the first six years and it is not until seven years have passed that a serious decline begins. By this stage, the number of individuals in the population (cohort) has been reduced by 74% by an annual mortality of 20%. By age 7 in this example, the modelled fish have reached 80% of their ultimate body length and it is only from this point on that the loss of potential gamete mass through mortality losses each year exceeds the gains achieved through growth in body size in the surviving individuals.
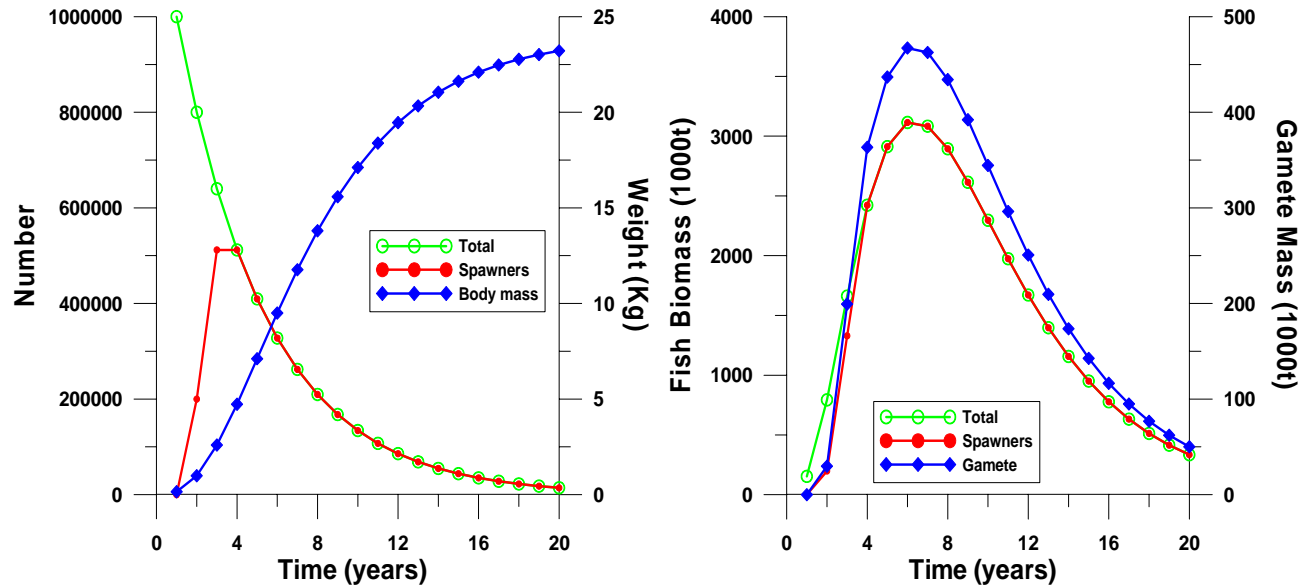
Figure 4.2.1: Illustration of the "storage" model based on life-history characteristics of a cohort of cod. Growth in length is driven by the von Bertalanffy growth function with L_∞=123.1 and K=0.230. Conversion to weight assumes values of c=0.0051 and b=3.192 in the weight at length power function. Cohort "seed" size at t=1 is 1000000. Mortality losses are assumed to be 20% per year and the proportions mature at t=1, t=2, t=3, and t=4+ are assumed to be 0%, 25%, 80% and 100% respectively. Gamete mass in a mature fish is assumed to be 15% of body mass. Left panel shows variation in total number of fish, number of spawners, and individual body mass of fish with time. Right panel shows variation in total cohort biomass, spawner biomass and gamete biomass with time.

The "lottery" model refers to the stochastic nature of recruitment that is a well known characteristic of marine fish and benthic invertebrate populations. Thus frequently, many years pass and despite high levels of gamete production, recruitment to the population may be relatively low. But on occasion, various factors combine to produce highly favourable conditions for larval/juvenile survival – the "lottery win" effect – resulting in markedly higher level of recruitment. The combination of both the "storage" and "lottery" effects means that despite declining numbers of individuals in a population due to mortality, arising through both natural processes and anthropogenic activities, relatively long periods of low recruitment rates may be sustainable due to the "storage" effect, until the "lottery" pays off and a single cohort of offspring experiences unusually high survival so that exceptionally high numbers recruit to the population and the population size recovers.

4.3.   An Alternative Size-Structured Species-Interactive Model

Figure 4.3.1 illustrates the type of form that a size-structured species-interactive model to simulate the effects of fishing activity on species diversity at various community organisational levels might have. In this example, which we describe here as it might be applied to a fish community, 10 species are modelled, labelled A through J, with a variable number, between 5 and 11, of Log_2 body-mass classes. For each species, the number of possible Log_2 body-mass classes is dependent upon the species ultimate body size, characterised by the von Bertalanffy growth curve Length$_{infinity}$ L_∞, parameter. Logged body-mass weight classes would be used so as to produce the linear Log total biomass – log body-mass biomass spectra predicted across all taxa from metabolic theory (Kerr & Dickie 2001). By convention, Logs to the base 2 are used so that each successive body-mass class represents a doubling in body-mass over the previous class. Provided abundance in the "mature" body-mass classes of each modelled species exceeded a set limit, then annual recruitment to the smallest body-mass class would be randomly generated based on observed mean and variance in recruitment for each species concerned. Should abundance in the "mature" body-mass classes fall below the set limit, then species-specific stock-recruit relationship would be assumed. Greenstreet *et al* (2007a: Section 2.5.2) present a method by which species specific daily growth rates as a percentage of current body-mass can be determined. These growth rates would be used to progress individuals of each species through successive body-mass classes.
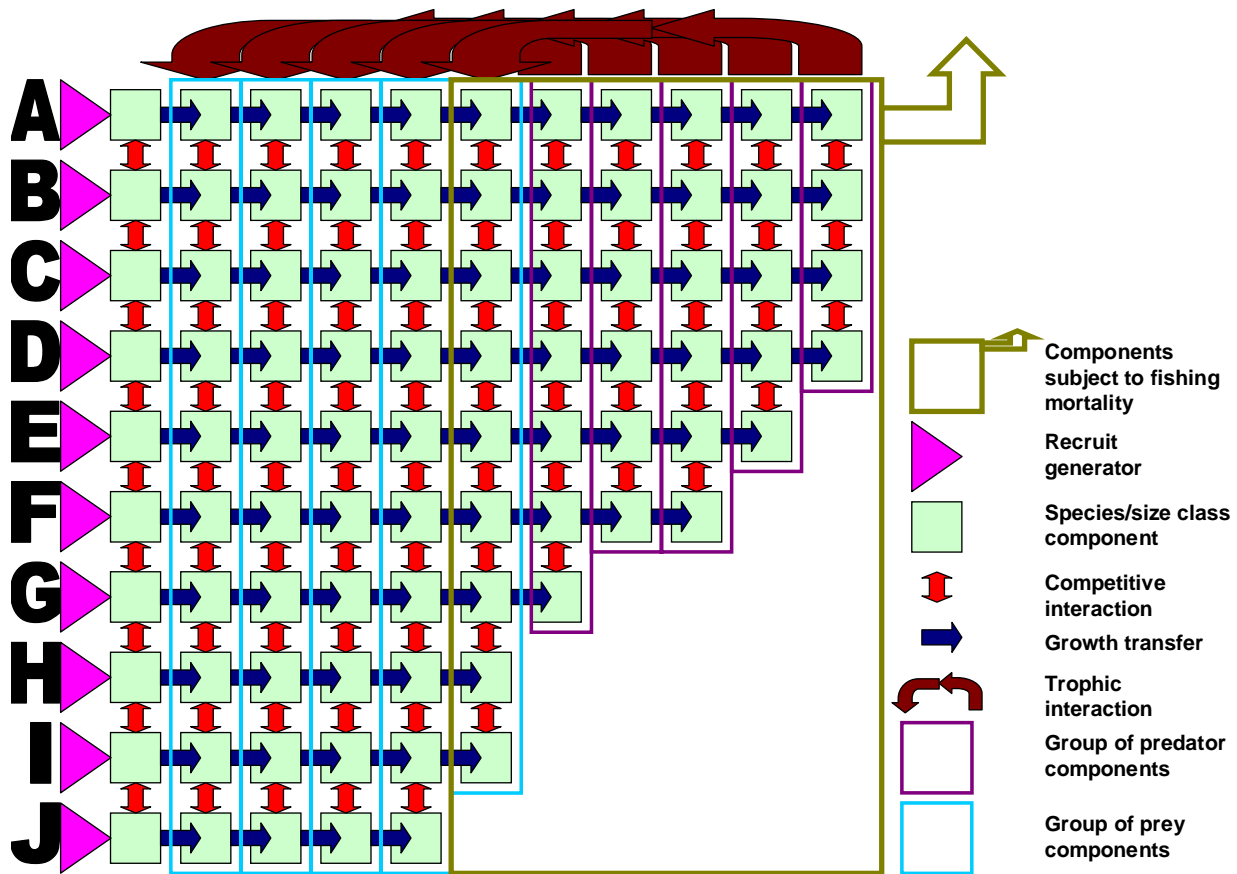
Figure 4.3.1: Proposed form for a size-structured species-interactive model to simulate the effect of fishing disturbance on the relative abundance of species with differing life-history characteristics.

To model top-down predatory forces, specific predator mass – prey mass ratios would be assumed (e.g. Jennings *et al* 2002; Jennings & Warr 2003). These predator-prey size ratios can be parameterised through stable isotope analyses for both fish and benthic communities, but in addition a wealth of feeding ecology data are available for fish from numerous North Sea diet and food consumption studies (e.g. Daan 1989; Hislop *et al* 1997; Greenstreet 2006). These would also allow direct estimation of predator-prey size ratios for fish predators consuming fish prey. Actual predation loadings on the prey body-mass classes will depend on abundance in the predator body-mass classes. Individual predation rates can be fixed as a function of their daily specific growth rate, i.e. assuming set trophic transfer efficiency rates, for example of 10% to 20%. Thus if the daily specific growth rate of predators in a given body-mass class was $0.3\%bw.day^{-1}$, consumption rates on the prey body-mass class might need to be 1.5% to 3.0% of biomass in the predator body-mass class in order for such growth rates to be achievable with the specified trophic transfer efficiency. Consumption rates determined in this way can be validated by the data available from diet and food consumption studies such as those cited above. Alternatively, such data can be used to parameterise consumption rates directly for predators of given body-mass.

In the absence of data to the contrary, there is no absolute imperative to model specific competition coefficients between individuals of different species within a given body-mass class. Simply, if productivity in a given prey-body mass class is insufficient to meet the consumption needs in the predator body-mass class preying on it, then growth in the predator body-mass class would be reduced across all species as a constant proportion of each individual species' daily specific growth rate. That is to say, all the daily specific growth rates of each species in the predator body-mass class would be reduced by a constant fraction. Under such circumstances, the life history characteristics of the species in the predator body-mass class will determine which species perform best under situations of strong competition and limiting prey resources. However, the model could also be structured so as to allow a variety of different competitive processes to be explored, depending upon the most likely scenarios suggested by developing theory.

Finally, to explore the effects of fishing disturbance, an additional fishing mortality can be imposed on the body-mass classes deemed to be exploitable. The effects of this on the relative abundance of individuals of different species and body-mass classes can then be followed.

This model form addresses all the short-comings in the DEM and any alternative species-centric models that might be considered instead. It takes account of variable top-down forces as total abundance in the larger piscivorous body mass classes varies. Variable bottom-up (competitive) forces are also accounted for as abundance in the prey body-mass classes varies, affecting the resources available to the predator body-mass classes, thereby influencing predator growth rates. The inclusion of biologically realistic recruitment random generators disconnects the population growth potential of each species from their standing spawning stock abundance. By summing individuals of each species across all body-mass classes, the effects of size and species selective fishing exploitation patterns on diversity at the species level can still be explored. Such output can be compared with the data available from field studies (Greensteet & Hall 1996; Greenstreet *et al* 1999; Piet & Jennings 2005; Greenstreet & Rogers 2006), and used to form the basis for advice to managers attempting to achieve community level EcoQOs. Size-structured modelling of fish communities so as to explore the effects of fishing on community size-structure is a new development, but one that has already started

(e.g. Pope *et al* 2006). Development of such models, particularly to take account of competitive interactions, will provide powerful tools for scientists providing advice in support of the EAM.

4.4. Theoretical Size-Based Maximum Species Richness Profiles

In Figure 4.3.1 illustrating the proposed form for a size-structured species-interactive community model not all species were represented by all size classes. As pointed out in the description of the proposed model, species ultimate body-lengths vary, as determined by their von Bertalanffy growth function L_∞ parameter, result in only a small proportion of species growing large enough to enter the largest Log_2 body-weight classes. If L_∞ parameter values can be determined for all species in a particular species "pool", then theoretical size based species richness profiles can be determined for the "pool".

Greenstreet *et al* (2007a: Section 2.5.2) developed a regression model to parameterise the von Bertalanffy growth function for each species sampled by the different groundfish surveys. Thus for each species the ultimate body-length of a fully grown individual, L_∞, if not available from appropriate published growth studies, could be estimated given values of L_{max}, the maximum recorded body-length from *FishBase* (Greenstreet *et al* 2007a: Section 4 Appendix 2). For each species, the ultimate body-weight of a fully grown individual, W_∞, can be determined by from the weight at length relationship $W_\infty = cL_\infty{}^b$, given the species specific c and b parameter values also provided in Section 9.4 Appendix 2. Assuming that each species might be expected to be found in all Log_2 weight classes up to and including the weight class that included its calculated W_∞, then the maximum species richness at each Log_2 body-mass size-class profile for each survey data set can be determined (Figure 4.4.1). The SAGFS data set had no abundance data for individual goby species, all gobies had been given a single, unidentified goby code. Eight goby species were identified between the IBTS and DBTS surveys, six species in the former and 5 in the latter. Three species were common to both data sets; sand goby, black goby and Fries's goby. The SAGFS unidentified goby code was therefore considered to consist of these three species and these species were added to the SAGFS species list.
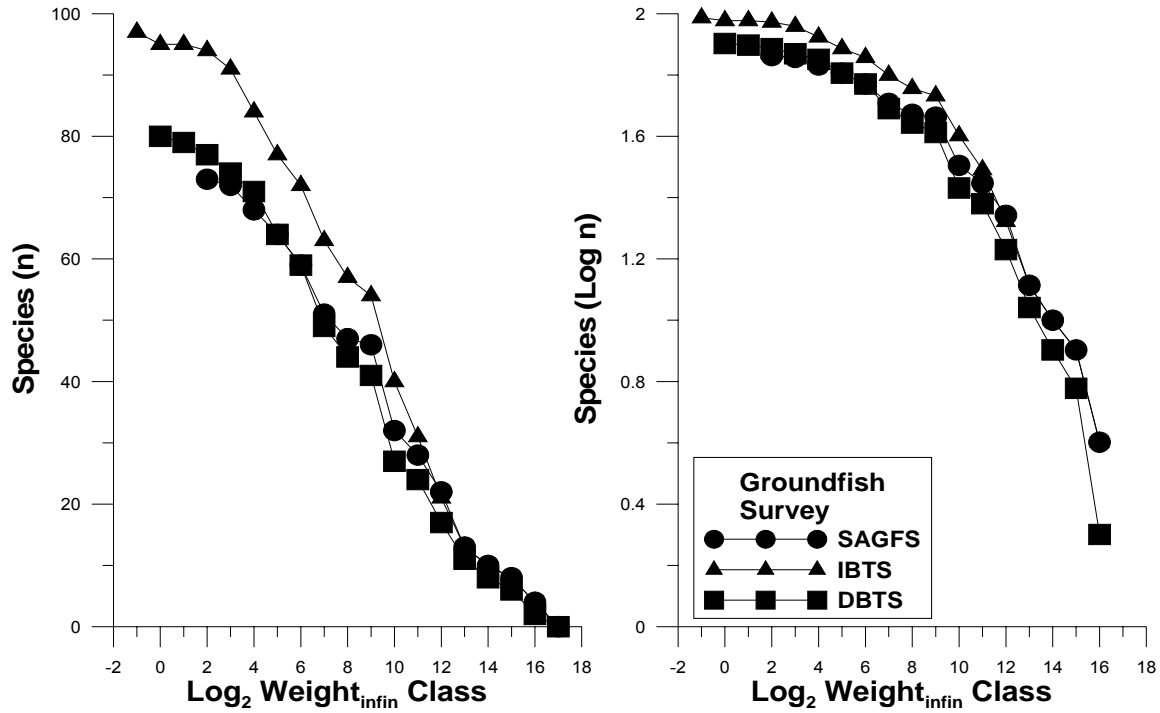
Figure 4.4.1: Relationships between maximum potential species richness in each Log_2 body-mass size class with increase in body-mass size class for the species suites sampled by each of the three main groundfish surveys for which data were available; the Scottish August Groundfish Survey (SAGFS), ICES Q3 International Bottom Trawl Survey (IBTS), and the Dutch Q3 Beam Trawl Survey (DBTS). Left panel show species richness in each body-mass class on a linear scale, while right panel shows Log_{10} of number of species.

4.5. Evidence for Size-based Diversity Processes

4.5.1. Relationships between species richness and abundance with body-mass

Many studies have demonstrated unimodal relationships between species richness and body-size class (Blackburn and Gaston 1994a; 1994b 1994c; Brown 1995; Brown, Marquet and Taper 1993; Cotgreave and Harvey 1994; Erwin and Scott 1980; May 1986; Morse, Stork and Lawton 1988; Navarrete and Menge 1997; Stanley 1973), while others have demonstrated similar unimodal relationships between abundance and body-size class (Bassett and Kitching 1991; Brown 1995; Janzen 1973; Morse *et al* 1985; Morse *et al* 1988). Few studies, however, have undertaken a detailed analysis of these relationships simultaneously. In two studies where variation in both the number of individuals and the number of species in body-mass size classes of increasing size on a log scale were examined together, remarkable similarities were observed despite one study focusing on grassland arthropod communities (Siemann, Tilman and Haarstad 1996; 1999), while the other examined a marine demersal fish assemblage (Hall and Greenstreet 1996).

Both studies demonstrated similar unimodal relationships between the number of individuals (I_m) or the number of species (S_m) and body mass size class (m). In each of the studies, S_m and I_m tended to peak at the same, or similar, body-mass class and in both cases, power functions of the form $S_m = c I_m{}^a$ were observed. Furthermore, these relationships held irrespective of whether data from only the ascending (smaller body-mass classes), descending (larger body-mass classes), or both sides of the unimodal relationships were analysed. In the arthropod study, the constant c=1.05 while the exponent a=0.51. Little variation in the values of these parameters was observed when each of the five most abundant arthropod orders was examined independently, despite the peaks of species richness and abundance occurring at different body-mass class in different taxonomic groups. In the demersal fish study, the constant c=1.72, while the exponent a=0.25. Thus while the shapes of the relationships were similar, species richness per individual in each body mass class in the demersal fish assemblage was considerably lower than in the arthropod communities.

In both studies, far from finding the descending sigmoid shaped theoretical size based species richness profiles shown in Figure 4.3.1, the observed profiles were unimodal in shape. We return to this point towards the end of section 4.5.2.

4.5.2. Fishing effects on size-based species richness and abundance profiles

Here we look at the effect of fishing on the relationships between species richness and abundance at different body-mass size classes in the demersal fish assemblage of the northwestern North Sea. Our purpose is twofold. Firstly we wish to explore the relationships to gain insight as to the processes operating to structure the fish community and the extent to which these processes might be modulated by size dependent variation in fishing mortality. Secondly we intend to explore the potential for these relationships to provide indications of a "fishing effect" that might be useful within a management context. We follow the analytical design described by Greenstreet & Rogers (2006).

Firstly, we compared the fish communities sampled in 75 ICES statistical rectangles assigned to three international otter trawl fishing effort "treatments"; "Low" (40 rectangles with an average annual otter trawl activity of 0 to 4999 h.y^{-1}), "Medium" (25 rectangles with an average annual

otter trawl activity of 5000 to 19,999 h.y^{-1}), and "High" (10 rectangles with an average annual otter trawl activity of 20,000 to 65,000 h.y^{-1}). For each rectangle, 10 Scottish August Groundfish Survey (SAGFS) trawl samples were selected from the data set for the 14 year period 1983 to 1996. To reduce the number of trawl samples to 10 per rectangle, samples collected in 1983, 1985, 1987 or 1995 were selected at random and excluded from the data set. In this way sampling effort per rectangle was as standardised as possible (for further details of the SAGFS and international fishing effort data sets see Greenstreet and Hall 1996; Greenstreet *et al* 1999a; 1999b; Greenstreet and Rogers 2006; Jennings *et al* 1999). All 10 samples in each rectangle were combined to give a single demersal fish community sample for each rectangle.

The relationships between Log$_2$ body-mass class (m) and both Log$_{10}$ of the number of species per body-mass class (S_m) and Log$_{10}$ of the number of individuals per body-mass class (I_m) were examined. For each of the 75 rectangles, unimodal relationships for both parameters were observed. The mean relationships for each effort treatment are shown in Figure 4.5.2.1, in which the mean S_m and mean I_m in each Log$_2$ body-mass class for all rectangles assigned to each effort treatment are plotted. The unimodal relationships for both are clear, however, contrary to the earlier study (Hall and Greenstreet 1996), there is some indication that the peaks in S_m and I_m do not always coincide. Divergence between the peaks was most apparent in the Low effort treatment, less so in the Medium effort treatment, while in High effort treatment rectangles, the two peaks tended to coincide. Divergence between the two distribution peaks, in terms of the mean number of Log$_2$ body-mass classes separating the peaks, was examined explicitly (Figure 4.5.2.2). Both mean maximum S_m and mean maximum I_m were significantly higher in ICES rectangles of high and medium fishing effort (One Way ANOVA, $p<0.001$ in both cases). However, this was essentially because there was a trend for the Log$_2$ body-mass class at which the peaks of the curves occurred to be smaller in rectangles assigned to the medium and high fishing effort treatments (significant in respect of Log$_2 W_{max} S_m$, One Way ANOVA, $p<0.01$) and, according to biomass spectrum theory, abundance would be expected to be inversely related to body-mass (Kerr & Dickie 2001). In rectangles of low fishing effort, divergence between the peaks of I_m and S_m was around two Log$_2$ body-mass classes, but in rectangles of medium and high fishing effort, the level of divergence was reduced to around 1.6 Log$_2$ body-mass classes (Figure 4.5.2.2).
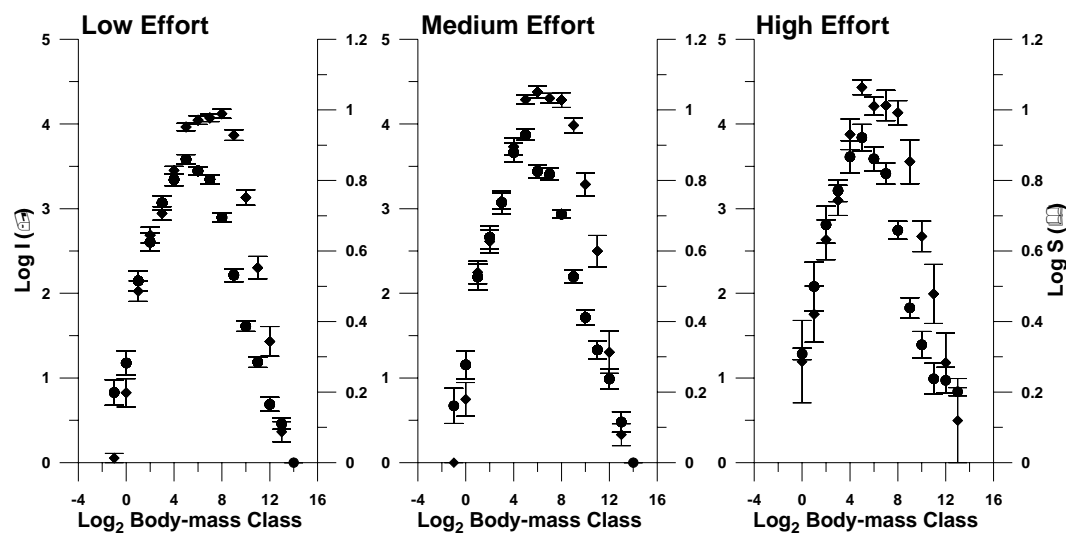
Figure 4.5.2.1: Mean ($\pm$ 1 S.E.M.) of the number of individuals (*I*) and the number of species (*S*) recorded at each log$_2$ body-mass class for rectangles assigned to one of three different fishing effort treatments.
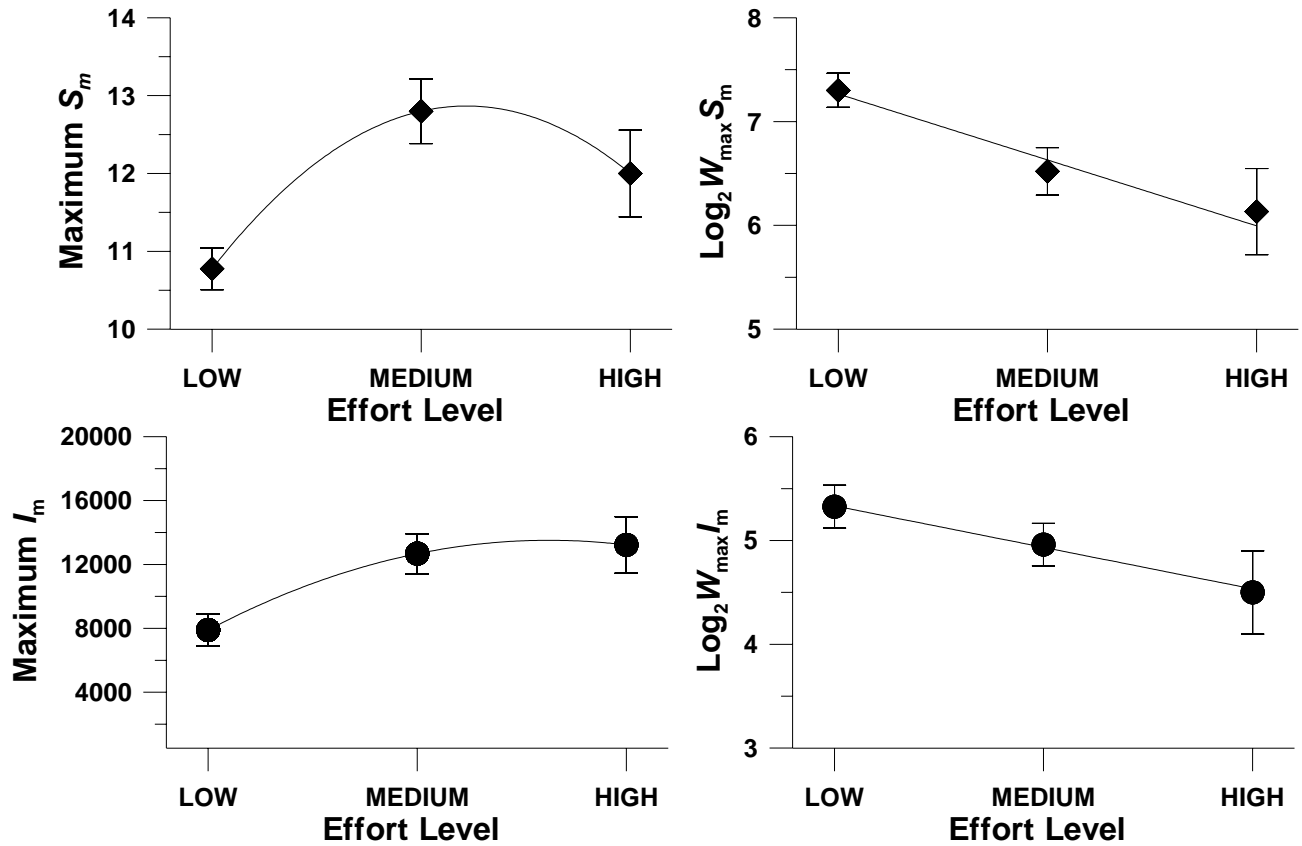
Figure 4.5.2.2: Plots showing mean ($\pm$ 1 S.E.M.) maximum I_m and S_m at the peaks of the unimodal curves for I_m and S_m against Log_2 body-mass class and the mean ($\pm$ 1 S.E.M.) Log2 body-mass class at which these peaks occurred in rectangles assigned to treatments of low, medium and medium fishing effort.

After first $\log_{10}$-transforming both variables, the number of individuals (I_m) per Log_2 body-mass class was regressed on the number of species (S_m) per Log_2 body-mass class to estimate the parameters c and a in the relationship $S_m = cI_m{}^a$ for each individual ICES rectangle. All 75 individual rectangle regressions were statistically significant at P<0.05 or less. The mean parameter values obtained for rectangles assigned to each otter trawl effort treatment were compared by ANOVA (Figure 4.5.3.3). Variation in the level of otter trawling had no significant effect on the exponent values, however the mean constant value in high otter trawl effort rectangles was significantly higher than values estimated in low otter trawl effort rectangles (ANOVA P=0.36, post-hoc Tukey comparison P=0.028).
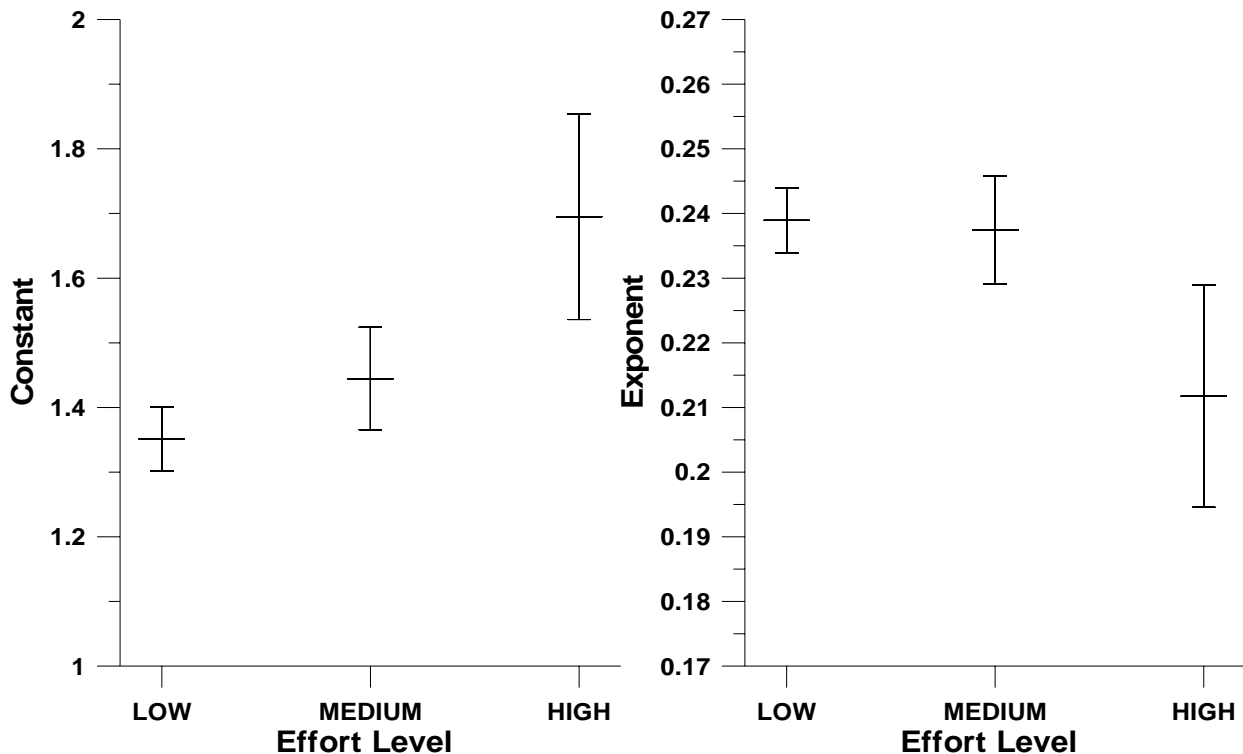
Figure 4.5.2.3: Mean (± 1 SE of Mean) constant and exponent values for the relationship $S_i = cI_i^{\,a}$ for 40 ICES rectangles with low otter trawl effort (0 to 4999h.y^{-1}), 25 rectangles with medium otter trawl effort (5000 to 19,999h.y^{-1}), and 10 rectangles with high otter trawl effort (20,000 to 65,000h.y^{-1}).

These preliminary analyses demonstrate a number of points. Firstly, the distributions of individuals and species across body-mass classes do appear to follow fairly rigidly defined general patterns, but the precise distributions are affected by fishing activity. This tends to confirm that the development of size-structured species interactive models certainly has potential to be of great values in aiding the development and implementation of an ecosystem approach to management. Secondly, the parameters obtained from the power function $S_m = cI_m^{\,a}$, particularly the constant, offer potential for use as indicators of the effects of fishing on the distributions of individual and species across body-mass classes in fish communities.

Finally we return to the discrepancy in the shapes of the expected and observed species richness – body mass profiles. Observed peaks in species richness occurred at Log$_2$ body-mass of around 7 (Figure 4.5.2.1 and Figure 4.5.2.2), close to the steepest part of the downward slope of the descending sigmoid curve of the theoretical species richness body-mass profile. Thus for the larger Log$_2$ body-mass classes, the observed and theoretical plots were similar. However, it is clear that not all species are equally likely to be represented at smaller size classes. In retrospect, the explanation for this is obvious. These smaller body mass classes consist largely of the younger individuals of larger growing species. At young age, overlap in body mass between different aged cohorts is much smaller, and may even be zero if comparing 0 group and 1 group fish of any particular species. Thus whilst fish certainly grow continuously, at any single time point, for example sampling in quarter 3, younger fish in the smaller body-mass classes of any one species will only have a very limited range of possible

sizes. Thus smaller bodied fish of any given species cannot be distributed across all possible Log_2 body-mass classes at the lighter end of the range.

Biomass spectrum theory predicts a linear relationship between Log abundance and Log body-mass class, yet the observed distributions being unimodal were far from linear. A similar discrepancy to that noted above for the species v body-mass class profile. Kerr and Dickie (2001) explain such discrepancies on the basis that no one taxa can vary along the full body-mass range. In other words you can only be so small and still be a fish! In essence, according to Kerr and Dickie (2001), the complete abundance body-mass spectrum may well be linear, but that the smaller body-mass classes in Figure 4.5.2.1 are increasingly dominated by taxa other than fish.

5. IMPORTANT ISSUES

5.1. The Need for Fishing Effort Data

An ecosystem approach to fisheries management is not about managing the marine ecosystem, it is about managing man's activities that adversely affect the ecosystem and threaten its capacity to continue to provide the ecosystem goods and services that we currently enjoy long into the future. This is best summed up in the Pressure-State-Response (PSR) framework for an indicator based ecosystem approach to management (Figure 5.1). Changes in "Pressure", reflected by variation in the pressure indicator, bring about changes in "State", reflected by changes in the state indicator. Management responds to this change in state, and this "Response" is reflected by changes in the response indicator. If the response is effective, it should illicit the anticipated change in the pressure indicator. The resulting change in pressure should then bring about the desired change in state. This simple concept absolutely encapsulates what we can aspire to as custodians of the world's marine natural resources. Our knowledge and our control over all the processes that structure and influence marine ecosystems is simply far too incomplete for us currently to consider that we can manage the marine ecosystem, and this may always be the case. The best that we can do therefore is to try and understand how man's activities impinge on marine ecosystems and to manage these activities so that detrimental impacts are kept to a minimum.
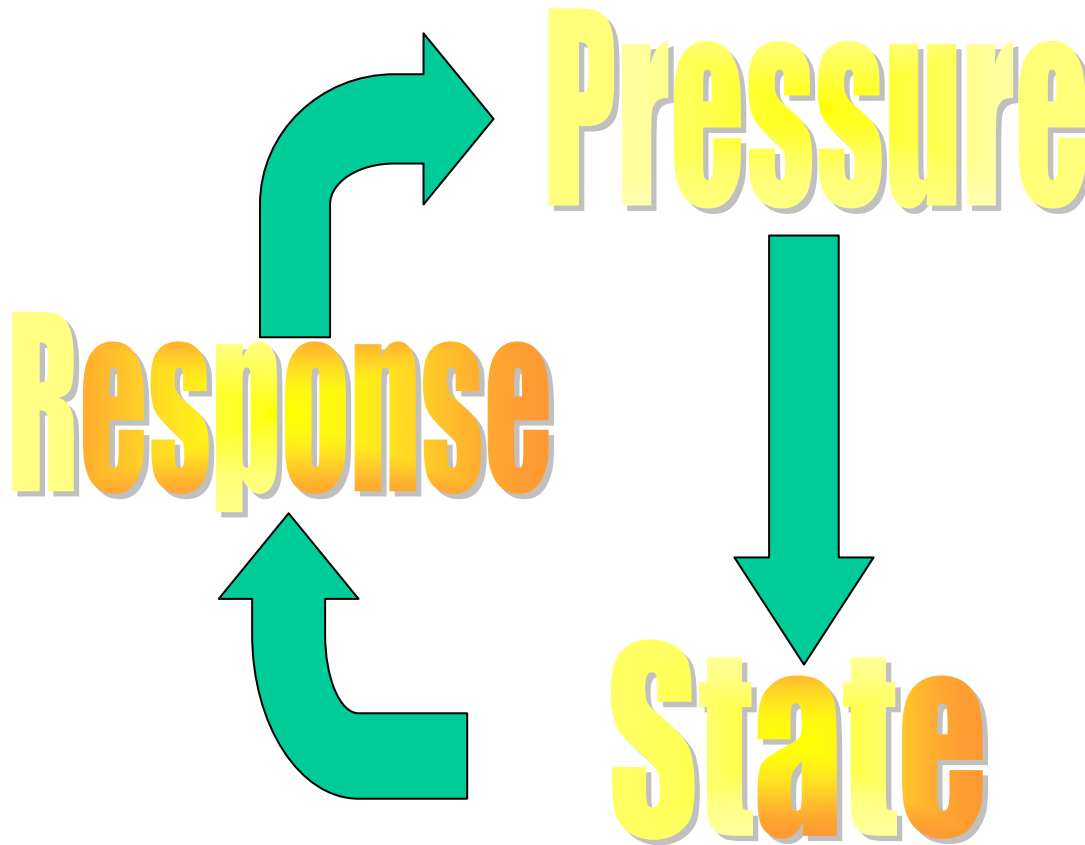
Figure 5.1: Representation of the Pressure-State-Response ecosystem approach to management framework.

Within such a framework it becomes abundantly clear that the relationship between "Pressure" and "State" is critical. Essentially, scientists providing the advice necessary to implement an ecosystem approach to management absolutely have to understand how man's activities work to effect changes in the state of the system. If these relationships are poorly understood, then advice as to the correct "Response" will always be based on weak foundations. If this relationship is to be properly understood then accurate data describing the pressure is required. Of all man's activities in the North Sea, fishing is the single activity that has the greatest impact on many diverse components of the marine ecosystem, from seabed habitats, through the benthic invertebrate communities and on up to the fish communities that constitute the resource being exploited. The need for accurate data describing the fishing "Pressure" is therefore of paramount importance to the successful implementation of an ecosystem approach to management. The need for such information has been amply demonstrated in the preceding four sections of this report, and the problems faced by scientists in accessing such data are evident in the analyses discussed by Greenstreet *et al* (2007d; 2007e).

The traditional single species approach to fisheries management has evolved over several decades. Landings data collected through each nation's market sampling programme provide the essential data for the stock assessment process. These data are analysed to provide estimates of fishing mortality for each individual stock. These mortality estimates provide the indicators of "Pressure" imposed by the fishing activity on each stock and are a vital component of the population dynamics models that form the basis of each assessment. These models produce estimates of stock abundance, the indicators of "State", for each of the assessed

stocks. Based on these estimates of the "State" of each stock, managers decide what level of catch can be sustained, and set TACs accordingly. These TACs therefore effectively provide the indicators of "Response" by management. In this example of the application of the PSR framework to a fisheries management context we argue that landings data provide the indicators of "Pressure". Essentially market sampling schemes provide an indication of the numbers of fish landed, i.e. directly killed by the fishing activity. But on their own, market sampling data provide only a poor indication of the actual total numbers of fish being killed. Many fish are killed and landed illegally, or discarded at sea. Only by combining data collected by market sampling with information provided by discard observer schemes and fisheries protection and enforcement agencies, can estimates of the true numbers of fish being killed be determined that are adequate for the stock assessment and management process. It is clear from this discussion that in the application of the PSR framework to fisheries management, huge resources are expended in obtaining the necessary "Pressure" indicator data. The successful implementation of an ecosystem approach to fisheries management requires similar levels of effort to be directed towards obtaining accurate indicators of "Pressure" on other components of marine ecosystems. Currently such data are not available and there is little to suggest any major commitment to rectifying this situation.

For many non-target fish species, some indication of the impact of fishing on their populations may be obtained from discard observer schemes. But currently in the North Sea, only a small percentage of fishing trips carry an observer. Sampling effort is therefore low and any indicators of "Pressure" derived from such data will carry low levels of precision. For benthic invertebrates and seabed habitats, even data such as these are scarce or absent. For these components of the marine ecosystem of the North Sea it seems inconceivable that we will ever be able to directly assess the impact of fishing in terms of monitoring the numbers of non-target fish and benthic invertebrates killed, or the amount of seabed habitat altered, by fishing. In these instances, the most profitable approach lies in modelling the impact of fishing based on data that quantify levels of fishing activity in an appropriate way. This approach is exemplified by Greenstreet *et al* (2007d). Fishing effort statistics provide exactly the sort of quantitative measure of fishing activity required for this purpose. Landings data cannot be used as a proxy for this information because, as shown by Greenstreet *et al* (2007e), landings and effort are so poorly related. There are several reasons for this, but principal among these is the fact that the relationship between landings and effort is heavily influenced by variation in stock abundance. The practices of discarding, inevitable in mixed fisheries situations regulated by catch limitation, and illegal landings further decouple the relationship between officially reported landings and fishing effort. In order to implement an ecosystem approach to management, scientists therefore have to have access to fishing effort data of a quality, consistency, and as comprehensive as the landings data currently used in traditional fisheries management.

Currently, access to reliable fishing effort statistics is extremely restricted. No co-ordinated international initiative, similar to the market sampling and discard observer schemes has been initiated. The data that are currently available have largely been compiled by two separate EC funded research projects; the Biodiversity project covering the period 1990 to 1995 (Jennings *et al* 1999) and the MAFCONS project covering the period 1997 to 2004 (Greenstreet *et al* 2007d). For neither of these projects were the databases fully comprehensive since not all countries operating fisheries in the North Sea were included in the project consortia. In the MAFCONS project, missing effort data for the countries that were not part of the project were modelled. However, such modelled data are a poor substitute for the real thing. In compiling these databases, the lack of co-ordination between the different countries quickly became apparent, with different countries using different gear codes and recording the data with different

units (hours-fishing or days absent from port). In order to render the data from different sources compatible, gear codes had to be combined until a "lowest common denominator" between the different countries was found, with considerable information loss as a result. Ultimately data could only be compiled for a few major gear-type categories (e.g. beam trawl, otter trawl, etc). For two countries, it was necessary to model hours-fishing from days absent from port to make the units in data from different countries compatible. The fact that the recording of effort data by fishing skippers appears not to be mandatory also caused problems in this respect. Compilation of a single comprehensive database from such disparate sets of data can only be achieved with the loss of information and a reduction in data accuracy.   If the development and implementation of an ecosystem approach to management is to be a serious proposition, then the provision of routine fishing effort statistics is an absolute necessity. The accurate logging of such data by fishing skippers must be considered to be mandatory, with all countries recording similar data in an identical format. Such data collection needs to be co-ordinated and managed centrally, with the data fully accessible to scientists whose role it is to provide advice in support of management.

The two databases that have been compiled to date hold data as the number of hours fishing by main gear category in each ICES rectangle in each year. Thus both the spatial and temporal resolution of the data is relatively low. With centralised co-ordination, the provision of effort data on much finer temporal resolution (i.e., by month, or week) should be easily achievable. The provision of finer scale spatial resolution is more problematic, and in all likelihood is the more important.   In modelling the impact of fishing activity on benthic invertebrate populations (i.e. fishing mortality within the benthos), it was evident that effort data at the spatial scale of the ICES statistical rectangle was insufficient (Greenstreet *et al* 2007d). Data for the Dutch beam trawl fisheries were available at a 1x1NM scale (Rijnsdorp *et al* 1998; Piet *et al* 2000; In Press) that allowed a benthic invertebrate model to be developed (Greenstreet *et al* 2007d), but similar data were not readily available to the project for otter trawls. Thus in modelling the mortality caused by otter trawls, major assumptions had to be made that at present have not been verified. The provision of shoot and haul positions for each deployment of the gear by fishing skippers would help to provide such information, but for precise modelling of the impact of fishing on benthic invertebrates and seabed habitats, the spatial information provided by the Vessel Monitoring by Satellite (VMS) scheme would be invaluable. Currently not all fishing vessels are monitored by VMS, and positions are only recorded every two hours, which is barely adequate for scientific needs (Deng *et al* 2005). Again, the requirement for high quality fishing effort data in order to implement an ecosystem approach to fisheries management is such that the VMS scheme should be extended to include all fishing vessels fishing in European waters and the monitoring frequency should be markedly increased. Management of the database should continue to be centrally co-ordinated and the data made readily available to scientists working to support the ecosystem approach to management.

5.2.   The Issue of Catchability

Accurate assessment of the abundance of organisms is without doubt one of, if not, the most critical aspect of any study of ecological processes. Problems arising from species- and size-related variation in the catchability of surveyed marine fauna in the sampling equipment used affect marine science over a wide range of different topics. The issue of catchability is therefore of fundamental importance, not only to this study, but to all marine science undertaken in support of an ecosystem approach to management.

In studies of predator-prey interactions, knowledge of predator abundance is essential if total predation loadings are to be assessed (Bax 1991; Hislop *et al.,* 1991; Pierce and Santos, 1996; Mills and Shenk, 1992; Wanless *et al.*, 1998; Furness, 2002; Daunt *et al.*, submitted). Likewise, without knowing the abundance of prey organisms, these predation loadings cannot be converted to prey mortality rates (Sterner, 1986; Greenstreet *et al.*, 1997; Hebblewhite, 2005). Such interactions are summarised by the classical Lotka-Volterra type differential equations for two predator and prey interacting species (May, 1976). Quantitative analysis of tropho-dynamic rates in food webs simply expands this process to include all species in the "assemblage" with significant predator-prey interactions (Pimm, 1982; Bax, 1991; DeAngelis, 1992; Greenstreet *et al.,* 1997; Blanchard *et al.*, 2002; Araujo *et al.*, 2005). Estimation of natural mortality rates is a key aspect of the stock assessments that underpin fisheries management in the North Sea (ICES, 2005). Information for this is largely drawn from Multi-species Virtual Population Analysis (MSVPA) models. Predator diet information for the MSVPA model is largely invariable, being mainly reliant on two North Sea wide diet studies carried out in 1981 and 1991 (Daan, 1989; Hislop *et al.*, 1997). Most of the variation in estimates of natural mortality is driven by alteration of predator and prey species and size class abundance variable values (ICES, 2006a).

As we move from traditional fisheries management towards an "ecosystem approach to management" (Hall and Mainprize, 2004; Frid *et al.,* 2005), such considerations will need to be extended to include interactions between fish predators and a larger number of prey species belonging to a wider variety of taxa. Furthermore, while fisheries management has tended to operate at relatively large spatial scales (most stock assessments are undertaken at the North Sea wide scale or larger (ICES, 2005), such spatial scales may be entirely inappropriate for populations of some of these prey species, requiring estimation of fish predator abundance at much finer spatial resolution. For example, a considerable body of evidence now suggests that fishing has had a detrimental impact on benthic habitats and invertebrate communities in the North Sea (reviewed in Jennings and Kaiser, 1998; Collie *et al.,* 2000; Clark and Frid, 2001; Johnson, 2002; Kaiser *et al.,* 2006). Since "Benthic Communities" is Issue 6 in the list of ten issues for which Ecological Quality Objectives (EcoQOs) are intended to be set (Lanters *et al.*, 1999), mitigation of the impact of fishing on benthic invertebrates is likely to be a feature of the developing ecosystem approach to fisheries management. However, due to their smaller size and relatively sedentary nature, the impacts of fishing on the benthic invertebrate community are generally considered at spatial scales considerably below that of the whole North Sea, and often smaller than single ICES statistical rectangles (Kaiser *et al.*, 1998; Collie *et al.*, 2000; Craeymeersch *et al.,* 2000; Jennings *et al.*, 2001; Dinmore *et al.*, 2003; Kaiser *et al.*, 2006). Benthic invertebrates are also subject to mortality from many sources, including natural disturbance from storms and phytoplankton "die-offs" (Taylor *et al.,* 1985; Hall, 1994) and predation from fish (Duineveld and van Noort, 1986; Greenstreet *et al.,* 1997). Through altering the abundance of populations of fish predators that prey on benthic invertebrates, fishing is also likely to have indirectly affected benthic invertebrate population dynamics (Frid *et al.,* 1999; Frid and Clark, 2000). If the processes by which fishing affects benthic invertebrate communities are to be sufficiently well understood so as to provide the scientific advice required to achieve benthic community EcoQOs, then accurate estimates of spatial variation in fish predator abundance are necessary.

Of particular relevance to this project is the impact of fishing on the species diversity of fish and benthic invertebrate communities. Fishing activity in the North Sea has increased markedly over the course of the 20th century (Daan *et al.,* 1990; Greenstreet *et al.,* 1999a) and consideration of the effects of this on various attributes of the demersal fish community has

generated much interest (Gislason and Rice, 1998; Jennings *et al.,* 1999a; 2002; Piet and Jennings, 2005). There is now a large body of evidence to suggest that species diversity has been adversely affected, particularly in the northern North Sea (Greenstreet and Hall, 1996; Greenstreet *et al.,* 1999b; Hall and Greenstreet, 1998; Greenstreet and Rogers, 2000; 2006). In the southern North Sea the situation is less clear cut. Long-term declines in diversity have been noted (e.g. Rijnsdorp *et al.,* 1996), but other studies have suggested that groundfish diversity may have increased over time (Rogers and Ellis, 2000; Piet and Jennings, 2005). Huston's (1994) dynamic equilibrium model suggests that diversity may both increase or decrease in response to increased disturbance depending on local productivity. Thus increasing diversity in the shallow, hydrographically mixed, southern North Sea, where primary productivity is greatest (Reid *et al.,* 1990), may still be an "adverse" response to increased fishing disturbance. Policy drivers such as the Convention on Biological Diversity (CBD), Annex V of the Convention Protection of the Marine Environment of the North-East Atlantic (OSPAR), and the EC Marine Directive all stress the importance of conserving biodiversity. Such a goal should therefore feature highly in any ecosystem approach to the management of natural resources in the North Sea.

The use of protected areas to achieve ecological and conservation objectives is explicitly mentioned in several of these policy drivers. Article 8 of the CBD, for example, suggests that a system of protected areas be established where special measures are taken to conserve biological diversity. The UK marine strategy documents ("Seas the Opportunity" and "Charting Progress") and the EC Marine Strategy Directive both explicitly consider the use of Marine Protected Areas (MPAs) to achieve their goals of "clean, healthy, safe, productive and biologically diverse oceans and seas". Indeed, (MPAs) are widely considered as potentially one of the most useful tools available to managers tackling ecological objectives for marine ecosystems (Russ and Alcala, 1989; Roberts and Polunin, 1991; Dugan and Davis, 1993; Agardy, 1994; Lindeboom, 1995; Allison *et al.,* 1998; Lubchenco *et al.,* 2003; Hastings and Botsford, 2003; Micheli *et al.,* 2004). Most analyses of North Sea groundfish survey data to date have involved time series analyses, linking changes in the community over time to temporal variation in fishing activity to demonstrate fishing effects (see references cited above). However, the use of MPAs to conserve species diversity in the North Sea clearly requires detailed knowledge of spatial variation in this component of the marine ecosystem, making spatial analysis of these data and mapping of groundfish and benthic invertebrate species diversity now a priority for marine scientists.

Estimation of the abundance of organisms is fundamental to predator-prey studies and studies of biodiversity. Groundfish surveys have been carried out in the North Sea in some form or other since the early 1900's (Greenstreet *et al.,* 1999; Rjinsdorp *et al.,* 1996). Research surveys provide estimates of the abundance of each fish species sampled at any particular location. However, no trawl gear ever samples all the individuals present in the path of the net and catch rates of fish of different species and size in any given fishing gear vary considerably. Vertical distributions of many species vary with time of day affecting "availability" of fish to demersal trawl gears (Benoît and Swain, 2003; Casey and Myers, 1998; Korsbrekke and Nakken, 1999; Michalsen *et al.,* 1996). Different species of fish behave differently ahead of the trawl gear; some are herded into the path of the net by the action of the otter doors and trawl sweeps on the seabed stirring up a sediment cloud (Bublitz, 1996; Main and Sangster, 1981; Ramm and Xiao, 1995; Somerton, 2004), others show net avoidance behaviour (Main and Sangster, 1981). Variation in swimming endurance influences which individuals fall back into the net (Michalsen *et al.,* 1996; Wardle, 1983; Winger *et al.,* 1999; Winger *et al.,* 2000). 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 (Engås and Godø, 1989; Rose and Nunnallee, 1998; von Szalay and Somerton, 2005), trawl speed and duration (Ehrich and Stransky, 2001; Somerton and Weinberg, 2001; Weinberg *et al.,* 2002) and the size and type of trawl ground-gear (Main and Sangster, 1981; Ehrich, 1987; Engås *et al*., 1988; Engås and Godø, 1989; Walsh, 1992). Consequently, the catchability of particular species and sizes of fish varies markedly between different fishing gears, dependent upon the characteristics of the gear (Ehrich *et al*., 2004; Harley and Myers, 2001; Winger *et al.,* 2004). Therefore, all trawl surveys provide gear-biased perceptions of the actual abundance of different species and size-class at any particular location. In essence this means that any particular research trawl provides a biased sample of what is actually present in the path of the trawl. Thus, the Grande Overture Verticale otter trawl (GOV) used in the ICES quarter 1 and quarter 3 International Bottom Trawl Surveys (IBTSs) provides a GOV biased view of the fish community and likewise the 8m beam trawl fishing gear used in the quarter 3 Dutch Beam Trawl Survey (DBTS) provides an 8BT biased view of the fish community.

In the time series analyses mentioned above, the fact that the derived estimates of community species diversity were subject to such bias was not an important issue. The studies involved analysed data collected from the same areas each year, so bias would have remained relatively constant allowing trends to be discerned. The presence of bias should not therefore have unduly affected the conclusions drawn. However, this is not the case with respect to analyses directed towards the examination of spatial variation within the same data. The species composition of the groundfish assemblage of the North Sea varies markedly across the region, being dominated by roundfish species in the north and flatfish species in the south (Daan *et al.,* 1990). Catchabilities of roundfish are much higher than flatfish in otter trawl gears, like the GOV, while the converse is true in respect to beam trawls (Ehrich *et al*., 2004), hence the reason why otter trawling dominates commercial fishing activity in the northern North Sea, while beam trawling predominates in the south (Jennings *et al.,* 1999b). Spatial patterns of the species diversity of demersal fish community derived from the GOV and 8BT are therefore strongly gear dependent and differ considerably (Figure 5.2.1). Furthermore, neither may reflect the real spatial pattern in species diversity of the actual demersal fish community present across the North Sea. Without knowledge of the bias caused by variation in the catchability of the different sizes and species of fish in different research trawls, maps of the species diversity of the North Sea demersal fish community derived from spatial analysis of groundfish survey data may well prove to be miss-leading. Under such circumstances, their use to underpin advice on which to base closed area management would appear to be seriously flawed.
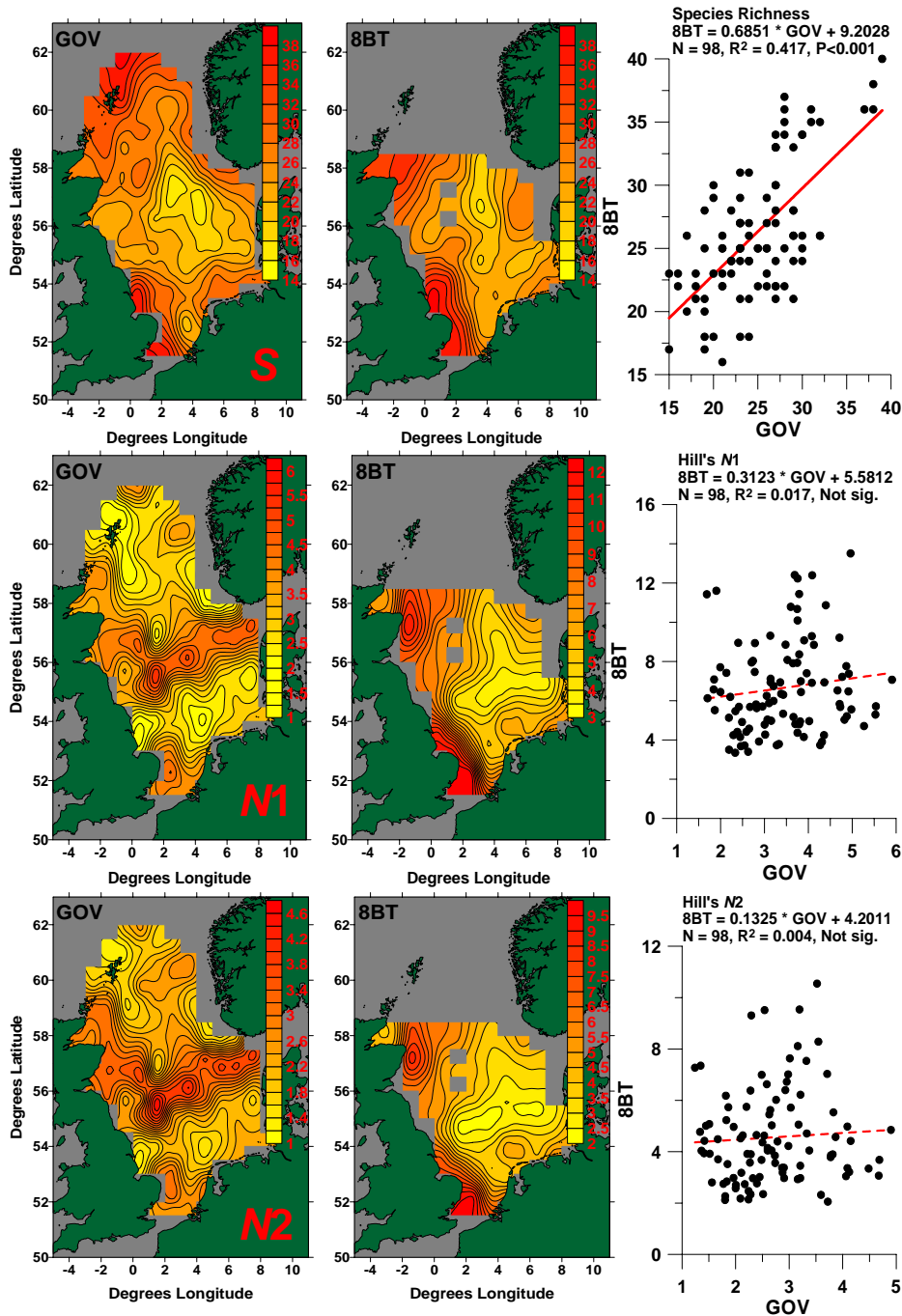
Figure 5.2.1: Spatial variation in species richness (*S*) and Hill's N_1 and N_2 indices of species diversity derived from the GOV (IBTS) and 8BT (DBTS) data sets. Correlations in index values obtained from each data set are also shown.

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). The issue of catchability in sampling gears is not just restricted to the estimation of fish abundance, determining the abundance of benthic invertebrates is subject to similar difficulties

(Reiss *et al* 2006). Issues of species catchability in IBTS trawls have come to the fore in previous studies that attempted to estimate the total biomass of fish in the North Sea (Yang 1982; Daan *et al.,* 1990; Sparholt 1990). These studies equated groundfish survey catch rates of the main assessed commercial species with estimates of their biomass in the North Sea derived from the ICES stock assessment process. All the non-assessed species were then assigned to a "fish-type" group, each of which was headed up by one or more of the assessed species. Within each of the "fish-type" groups, biomass of the non-assessed species (B_{na}) was estimated by:

$$B_{na} = \frac{C_{na}}{C_a} \times B_a$$

where C_{na} and C_a are the catch rates of the non-assessed and assessed species in each group respectively and B_a is the biomass of the assessed species in the group.

During this study we have developed this approach further, utilising data collected in two surveys that used very different research trawls, the GOV and the 8BT, to model variation in catchability, q, for each 1cm size class of every species sampled by the GOV trawl in the ICES quarter 3 IBTS (Fraser *et al.,* 2006 submitted; Chapter 9). Application of the catchability correction factors to the GOV sample data to derive estimates of true abundance had a profound effect on our interpretation of spatial variation of both the species diversity (Figure 5.2.2) and productivity (Figure 5.2.3) of the groundfish assemblage. Failure to take account of the catchability of different species and size classes of fish in the GOV produces a miss-leading impression of where species diversity and productivity hotspots are located. Any attempt to understand the processes that influence, structure and control these attributes of the fish community would therefore be entirely false. Add to this similar difficulties with respect to benthic organisms and it is soon apparent that our understanding how marine ecosystems operate may be seriously flawed. Assessing the catchability of marine organisms in the samplers used to assess their abundance is therefore a critical issue that needs serious and urgent attention. Failure to address this question could seriously compromise the scientific advice provided in support of an ecosystem approach to management at just about every level. If as a consequence management action consistently fails to produce the anticipated response so that managers lose faith in the process, this may eventually jeopardise the management approach itself. But ultimately, consistent ill-advised and inappropriate management may put the marine ecosystem at risk.
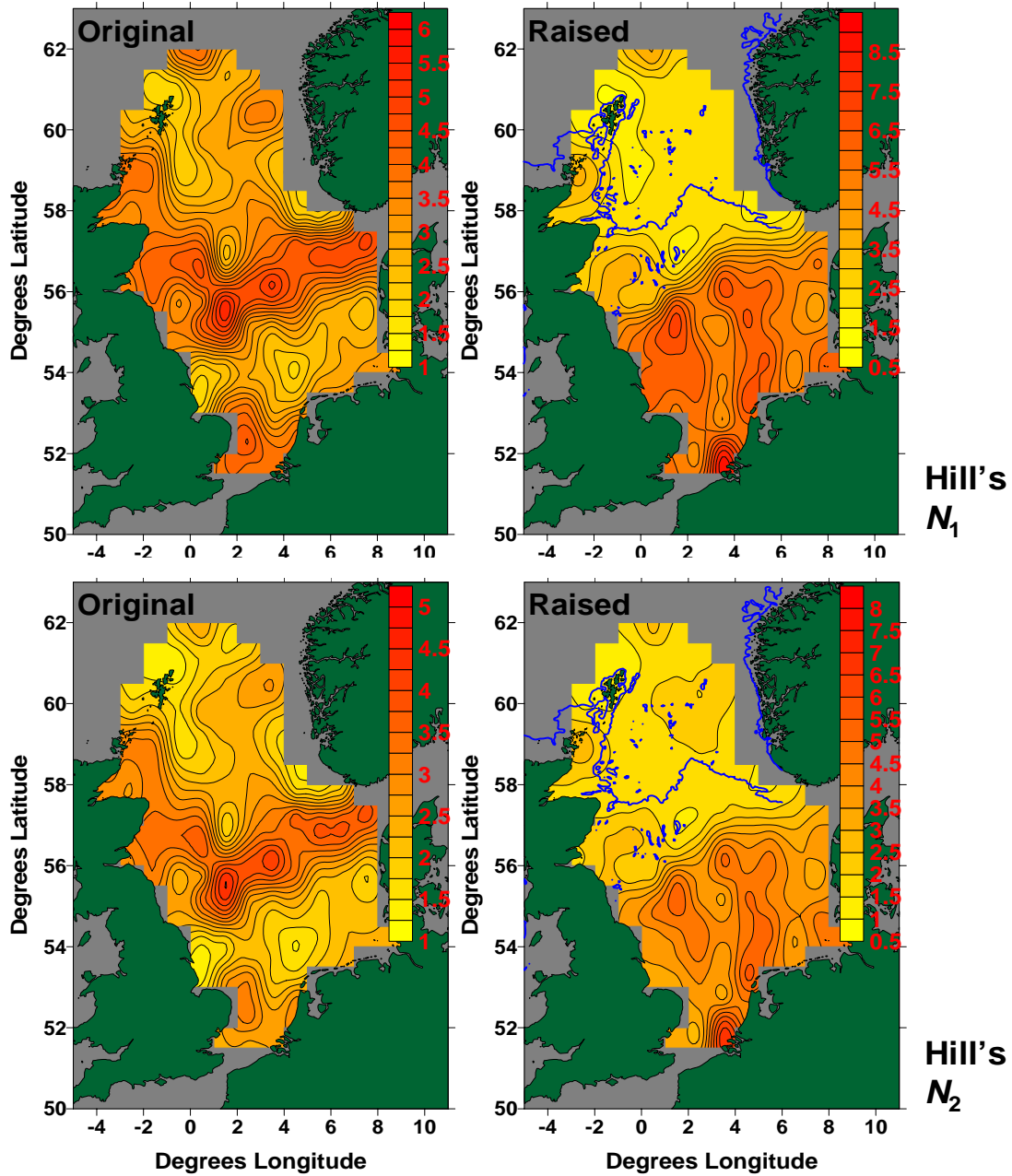
Figure 5.2.2: The effects of taking catchability into account on spatial variation in Hill's N_2 based on the IBTS GOV data-set. Original: based on the raw trawl data. Raised: based on the raw trawl data corrected for catchability.
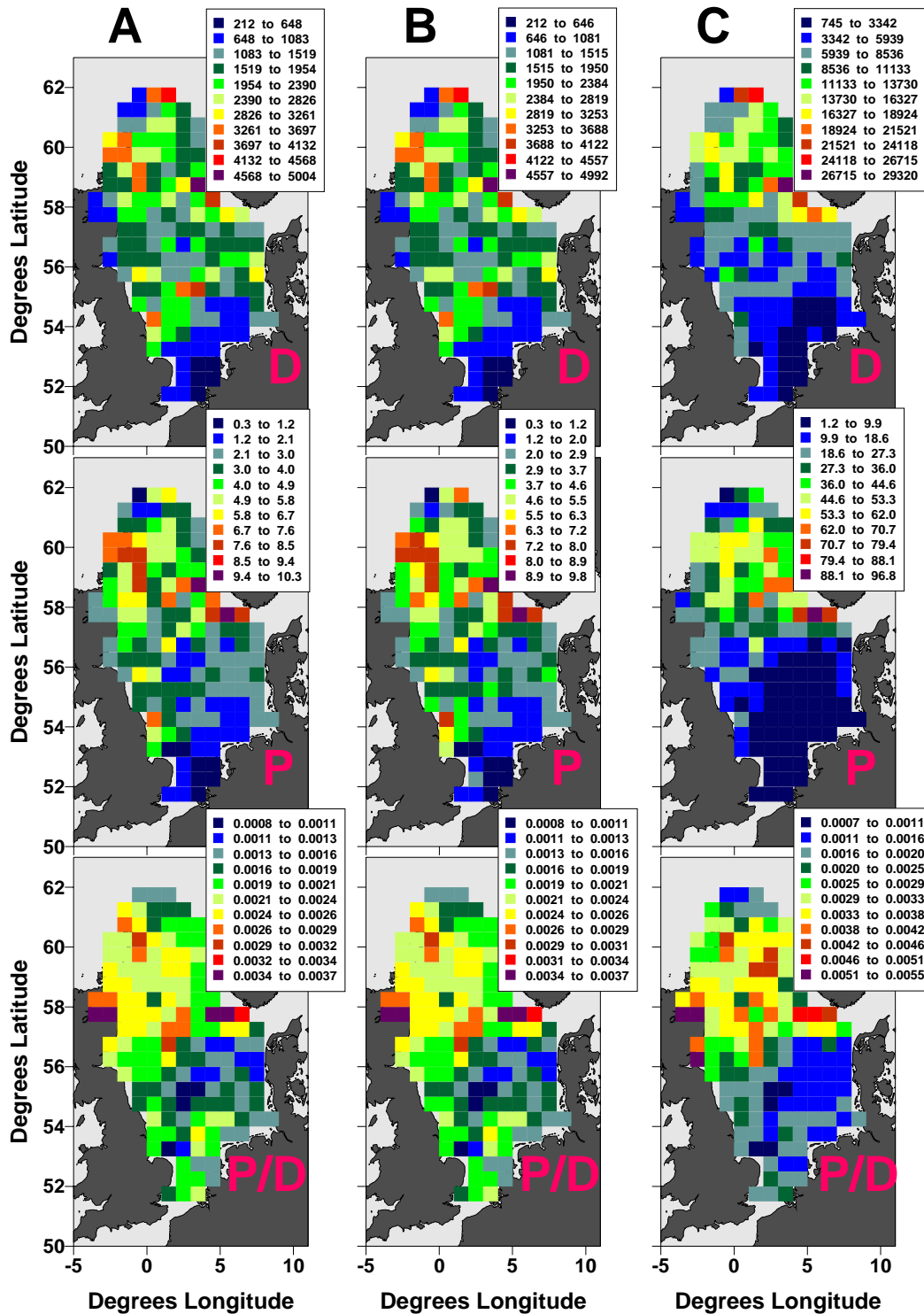
Figure 5.2.3: Spatial variation in the biomass density (D, Kg.Km^{-2}), growth production (P, Kg.Km^{-2}.d^{-1}), and production per unit biomass (P/D) of the demersal fish community. A: Based on arithmetic mean densities calculated across all 20 hauls in each rectangle on the raw uncorrected (for catchability) 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.

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