

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, ie. 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 of relevance to MAFCONS. 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 (eg 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 (eg. 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.

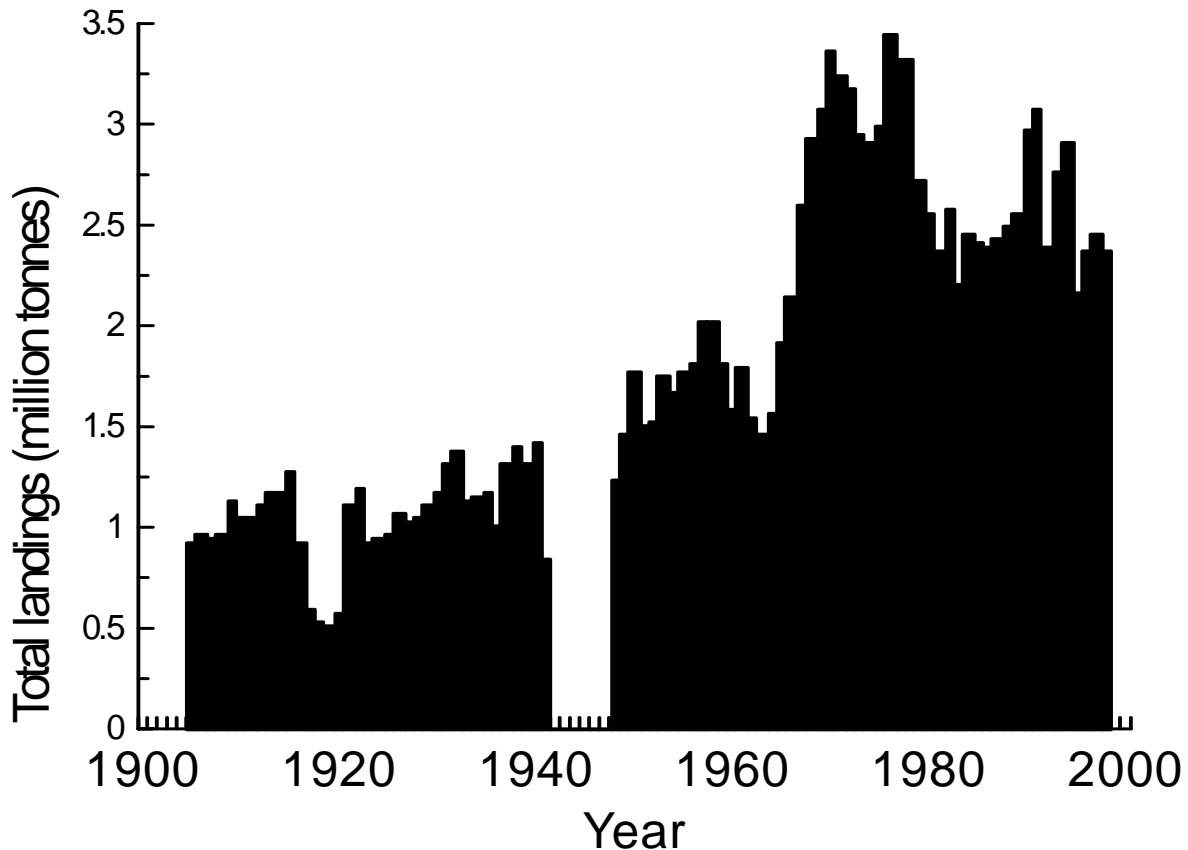


Figure 1.2.1.1. Trends in landings of fish taken from the North Sea over the course of the 20th century.

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).

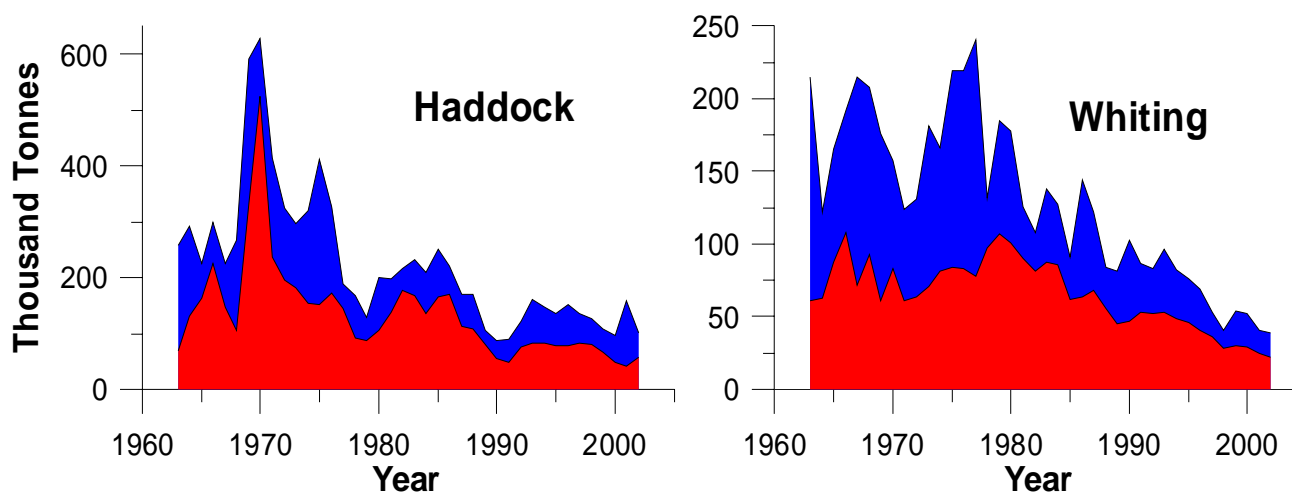


Figure 1.2.1.2. Trends in landings (red fill) and discarding (blue fill) of haddock and whiting (data from ICES 2005).

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 world's 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.

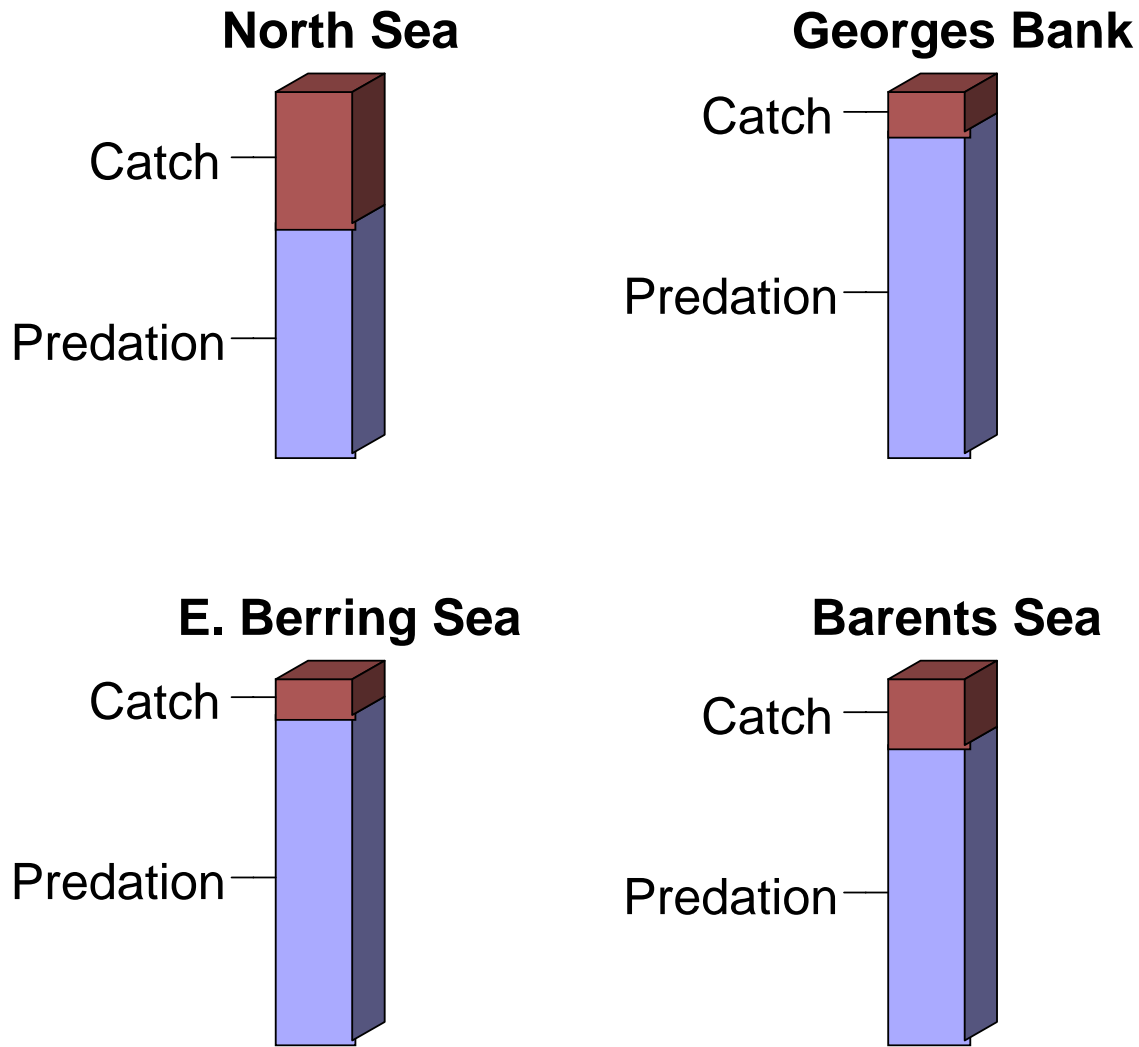


Figure 1.2.1.3. Comparison of catch and predation mortality of fish in four continental shelf seas.

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 Kvittek 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 (eg 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 (eg. 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 (eg 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 (eg 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 (eg 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 (eg. 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 (eg 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).

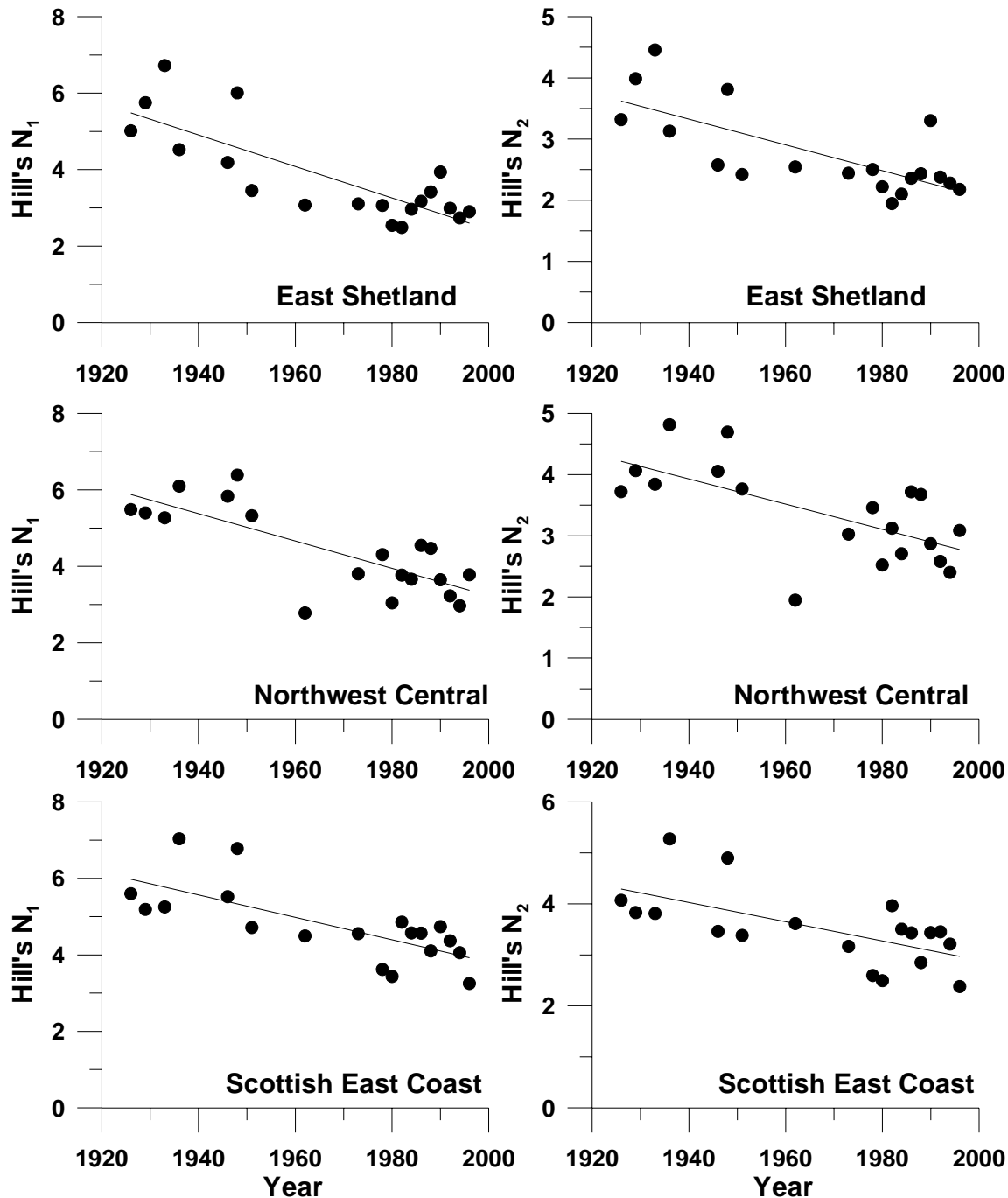


Figure 1.2.3.1. Long-term trends in Hill's N_1 and N_2 indices of demersal fish species diversity in three regions of the northwestern North Sea (from Greenstreet et al 1999b). See Greenstreet and Hall (1996) for map showing the precise location and boundaries of the three regions.

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 fourth 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 ($<5,000\text{h}\cdot\text{y}^{-1}$), medium ($5,000\text{h}\cdot\text{y}^{-1}$ to $20,000\text{h}\cdot\text{y}^{-1}$) and high ($>20,000\text{h}\cdot\text{y}^{-1}$). 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.

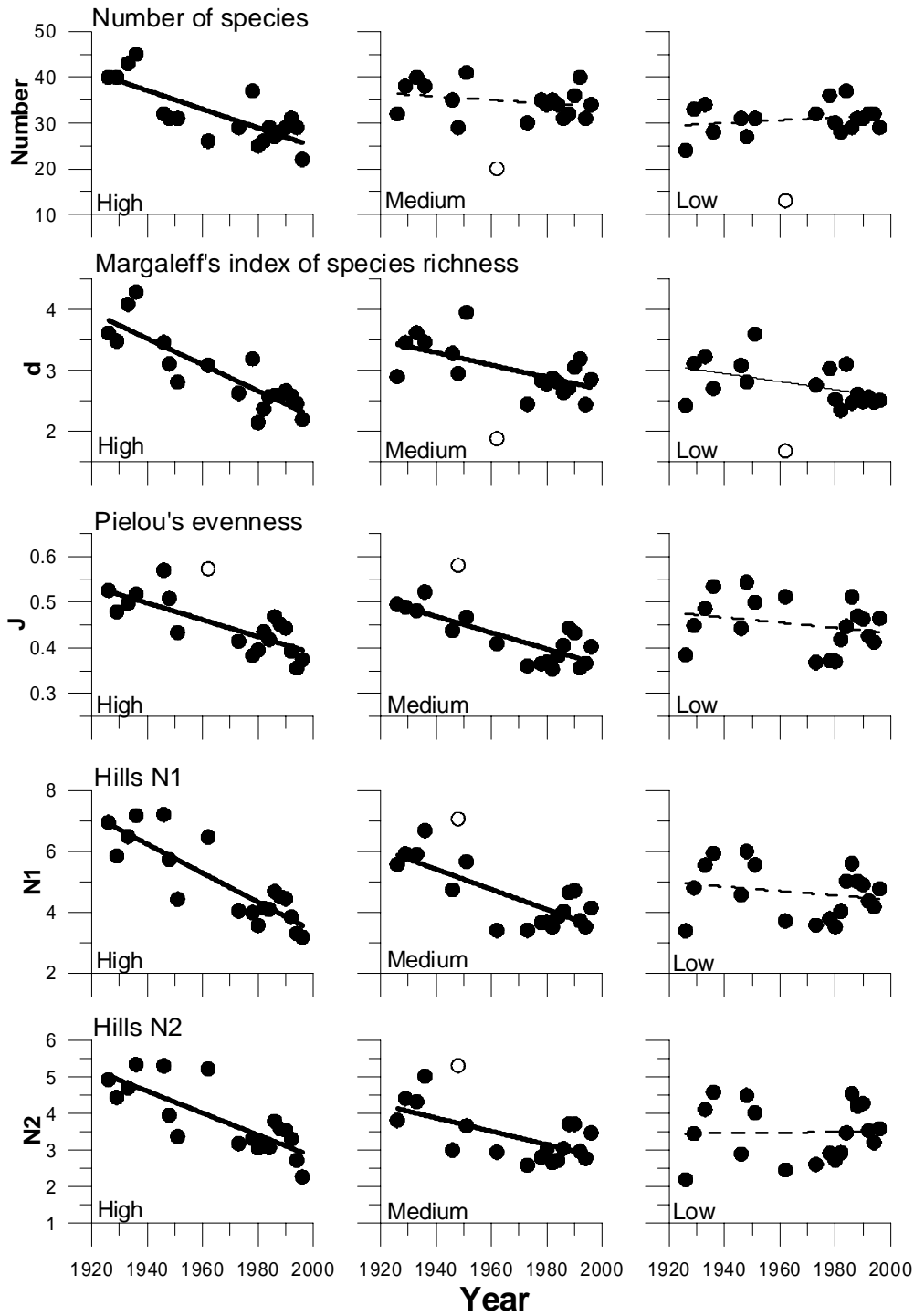


Figure 1.2.3.2. Long term trends in five metrics of the species richness and species diversity of the demersal fish community in ICES rectangles in the northwestern North Sea assigned to low, medium and high otter trawling “treatments” (from Greenstreet and Rogers 2006).

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 Chapter 9 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 date 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 (*Callionymidae*), 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.

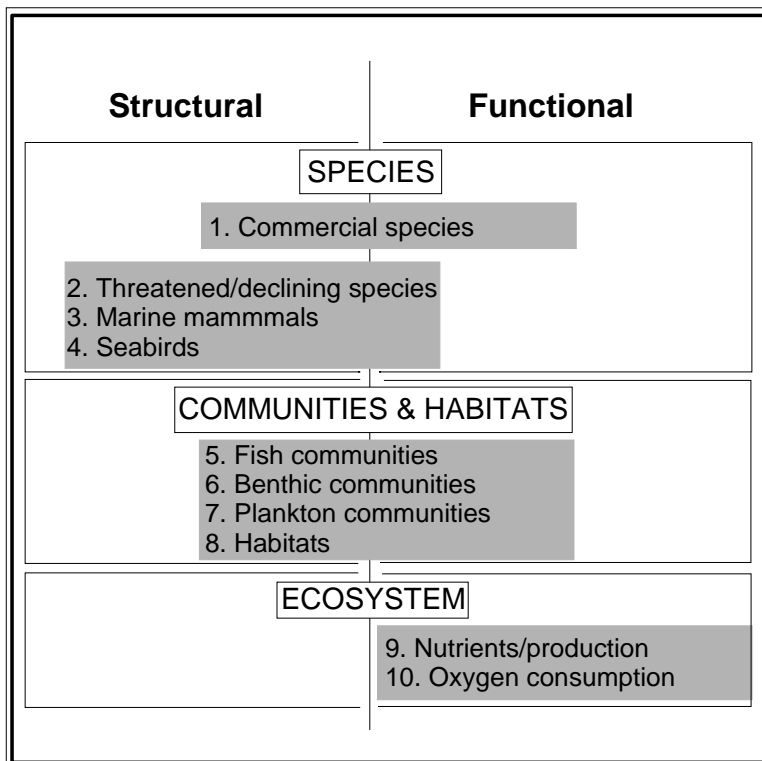


Figure 1.3.1. Ten OSPAR Ecological Quality Issues for each of which Ecological Quality Objectives will be set. The diagram indicates the level at which objectives are intended to be set, ie at species level or at community level, and the extent to which these objectives will address structural or functional 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 processes needs to be expanded to included 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 MAFCONS project. MAFCONS has 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 (Chapter 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 Technical Annex and is reviewed below. The practicality of such a protocol is assessed in Chapter 3.

1.4.1. Huston's dynamic equilibrium model

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.

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 1.4.1.1:A). His explanation for these relationships was steeped in the belief that competition was the major force in structuring communities (eg Schoener 1983; Connell 1983; Ferson et al 1986, see also review in Chapter 7). At low levels of productivity, resources would be insufficient to support specialist species and the community is dominated by a small number of generalists. As resources increase, the resource supply becomes sufficient to support specialists, thereby effectively allowing species niche widths to decrease enabling increased niche packing. More species can be supported and diversity increases. As productivity increases further, limitations to population growth are reduced allowing dominant competitors populations to expand so that they utilise an increasingly broad spectrum of the resource, resulting in the elimination of competing species and lowering 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) examined species abundance data originating from a wide range of habitats and environments to demonstrate the "universal nature" of his dynamic equilibrium model.

Huston (1994) combined these two unimodal relationships to form a three dimensional model, the dynamic equilibrium model (Figure 1.4.1.1: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. 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 1.4.1.1: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 can be tested 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 1.4.1.1:B should be obtained, and specific relationships between diversity and disturbance at different productivity levels, such as the ones shown in Figure 1.4.1.1:C, should be observed.

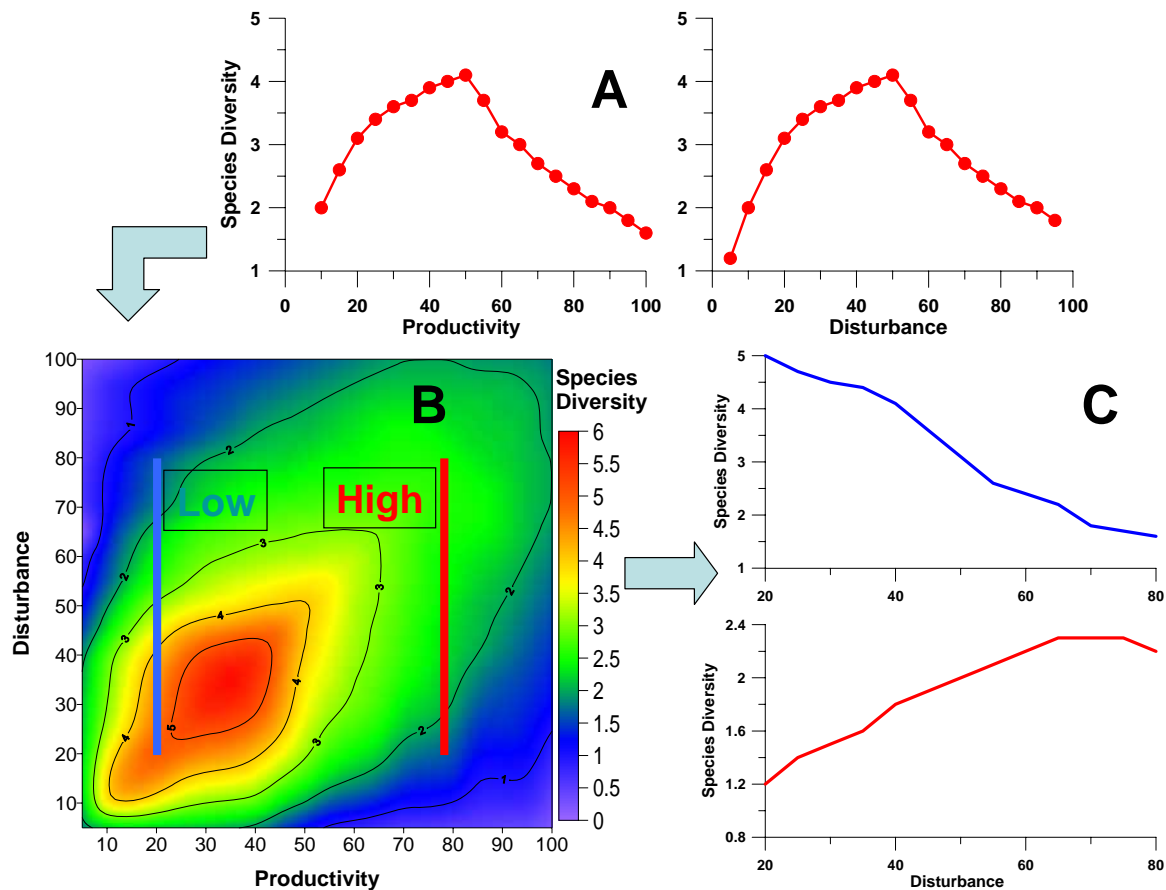


Figure 1.4.1.1. Schematic illustrating the evolution of Huston’s dynamic equilibrium model and the relationships between species diversity and disturbance predicted by the model at low and high levels of productivity. A: unimodal relationships between species diversity and productivity and between species 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 determined. Throughout the ensuing report we have attempted to define "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". Testing the applicability of Huston's dynamic equilibrium model was the subject of work package 2. In chapter 2 several tests of hypotheses derived from Huston's dynamic equilibrium model are presented. For each test, 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 presents spatial variation in the three input parameters to the model. The three values at each of the ICES rectangles where data are available are then input into a gridding process to construct 3D images 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 1.4.1.1. 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 1.4.1.1 should be observed in the highest and lowest productivity categories.

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 epifaunal) 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 in Chapter 6. When considering the fish communities only species considered to be part of the "demersal fish assemblage" were 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 Chapters 9 and 10). 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.

1.4.2. A preliminary management protocol – the MAFCONS project

The initial proposals for the MAFCONS project included a preliminary outline of a “management protocol” that would enable species diversity objectives to be taken into consideration prior to finally deciding on TAC levels (Figure 1.4.2.1). It was always intended that this should add on to the existing management process, rather than replace the process with something entirely different. There are several key components to this protocol. Firstly, current fisheries management operates through catch limitation, the imposition of a Total Allowable Catch (TAC) for each of the major commercially targeted species. By restricting catches to these levels, managers attempt to maintain fishing mortality to within a predefined range for each species. The estimates of fishing mortality provided by the stock assessments (eg 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 breakdown of this information to finer spatial resolution is not provided. The TACs themselves do not provide “fishing disturbance” information, as mortality rates are dependent not only on the numbers of fish caught, but also the population abundance of each species prior to the disturbance event. For all other components of the marine ecosystem, TACs or estimates of fishing mortality for the commercial species provide little or no indication of disturbance. For the vast majority of fish and benthic invertebrate species in the North Sea, determining the disturbance to which they are subjected as a result of fishing activity is best modelled using data that quantifies the level of activity itself: fishing effort data. Thus, in order to apply the protocol to the broader demersal fish and benthic invertebrate communities, the first step is to convert the suite of TACs proposed by managers in any given year to patterns of fishing activity that would produce these levels of landings. To do this the relationships between landings and fishing effort need to be understood and modelled. This task was the addressed by work package 6 (Figure 1.4.2.2), and the results are reported in Chapter 12.

Fishing activity statistics, however, do not provide the measures of fishing activity required by the theoretical model. As stated above, fisheries managers are actually concerned about fishing mortality. Similarly, theoretical community ecology models, such as the dynamic equilibrium model, require mortality data to be input as the disturbance parameter values. Only if measures of fishing activity are linearly related to mortality could they provide a proxy for disturbance. Because fishing activity is patchily distributed (Jennings et al 1999; Rijnsdorp et al 1998; Piet et al 2000) this is highly unlikely to be the case (Piet et al 2000; Piet et al In Press). The second key step in developing the management protocol therefore is the modelling of mortality caused by given patterns of activity for whichever component of the marine ecosystem is the focus of species diversity objectives. Modelling the mortality of fish and benthic invertebrate organisms was the focus of work package 3 (Figure 1.4.2.2) and the results of this work are documented in Chapter 8.

The third key stage in the development of the management protocol was the development of the theoretical model that translated patterns ecological disturbance (mortality caused by fishing) into patterns of species diversity for each “subject community” under consideration, As stated in section 1.4.1, the initial candidate for such a model was Huston’s (1994) dynamic equilibrium model, and

one of the principal objectives of the MAFCONS project was to thoroughly test this model to determine its usefulness in this role. The results of this testing process are presented in Chapter 2. However, 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, the project consortium undertook to carry out a review of the theoretical community ecology literature so as to identify the processes by which fish and benthic invertebrate communities are structured. This review is presented in Chapter 7. On the basis of this review, the project consortium undertook to consider how an alternative model might be structured. The development of ideas for an alternative theoretical model is described in Chapter 4. This review and the consideration of alternatives to Huston's dynamic equilibrium model also constituted part of work package 2 (Figure 1.4.2.2).

Which ever theoretical community ecology model is ultimately used to drive the management protocol, it will have data requirements. The disturbance inputs have already been covered (WP 3, Chapter 8), but information will also be required to support whatever input parameters the model may require with respect to the demersal fish and benthic invertebrate communities whose species diversity is the focus of attention. With regard to Huston's dynamic equilibrium model, the main input parameters related to the productivity in the community in the trophic level below the "subject community". Abundance data for organisms occupying the "subject community" will also be required to monitor the performance of the management protocol with respect to meeting species diversity objectives. The collection of these data, used in MAFCONS to test the dynamic equilibrium model, was covered in work package 4 in respect of the benthic invertebrate community and in work package 5 covering the demersal fish community (Figure 1.4.2.2). Chapter 6 presents a full description of the sampling, processing, data collection and data archiving methods used in the project. This chapter was produced as a manual early on in the project to serve as a guide as to how all the field and practical work undertaken as part of the project should actually be carried out. The results of all the diversity and productivity analyses carried out on these data are presented in Chapters 9, 10 and 11 for the demersal fish, epibenthic invertebrate and benthic infaunal communities respectively.

Reconsideration of the management protocol and the application of the data collected and analysed over the course of the MAFCONS project to support management towards species diversity objectives comprised the work undertaken for work package 1 (Figure 1.4.2.2). This is summarised in Chapter 4. Finally Chapter 5 discusses key conclusions drawn from the work undertaken by the MAFCONS project that need consideration if an ecosystem approach to fisheries management is to be successfully developed, and more importantly, successfully implemented.

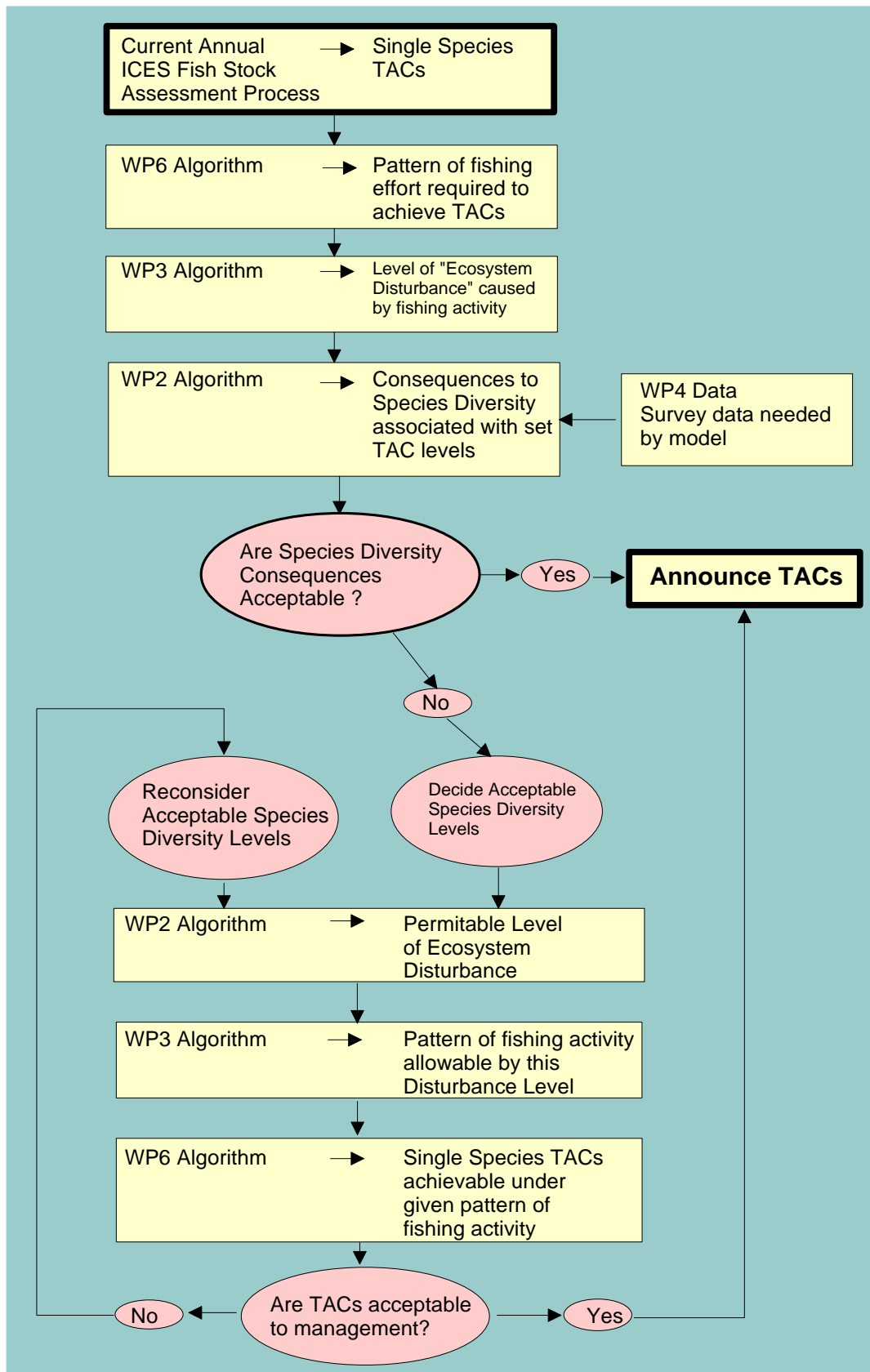


Figure 1.4.2.1. Flowchart for initial proposed "management protocol"

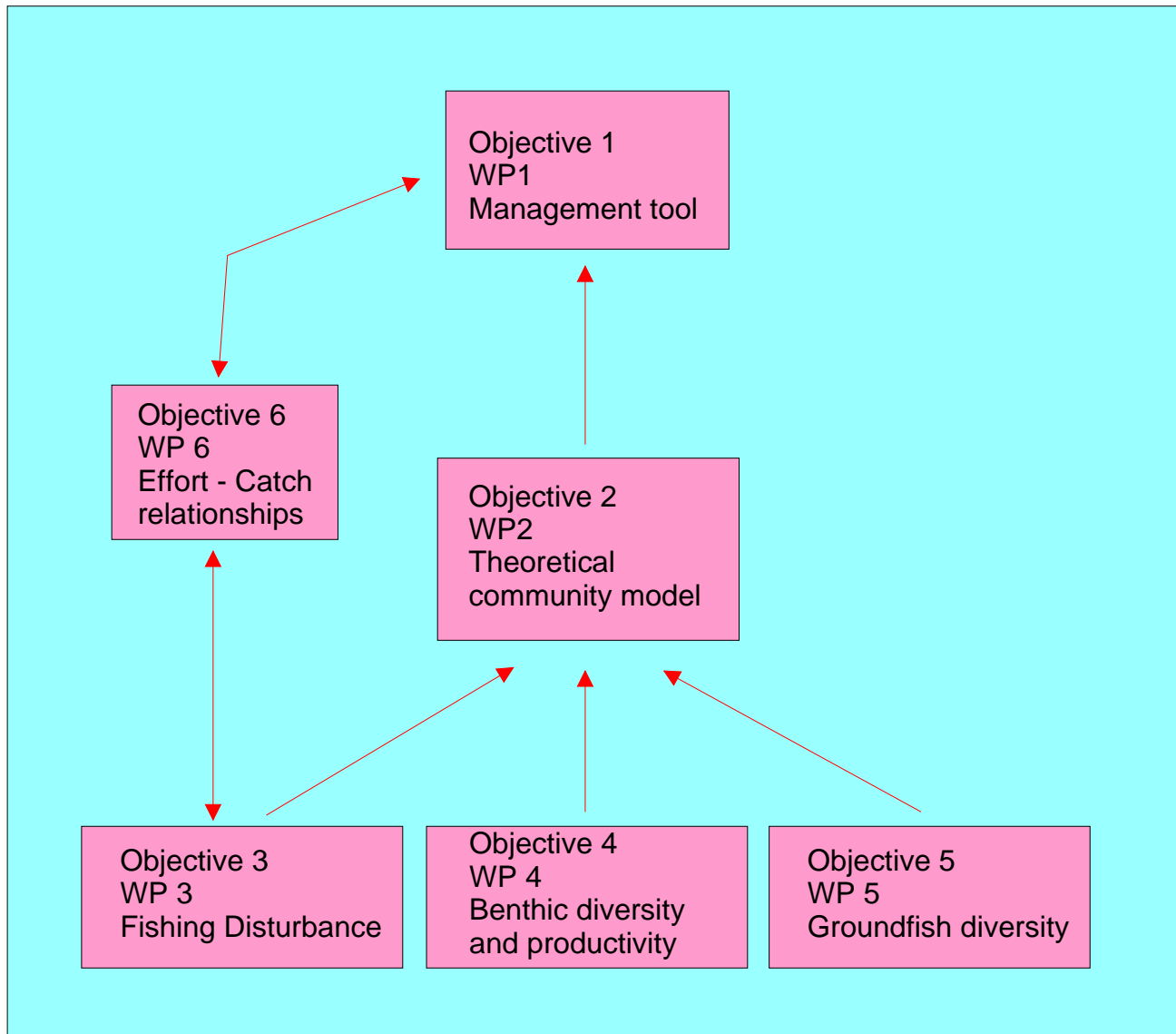


Figure 1.4.2.2. MAFCONS project work-package structure and interaction chains.

1.5. References

Auster, P. J., Malatesta, R. J., Langton, R. W., Watling, L., Valentine, P. C., Donaldson, C. L. S., Langton, E. W., Shepard, A. N. & Babb, I. G. (1996) The impacts of mobile fishing gear on seafloor habitats in the gulf of Maine (northwest Atlantic): implications for conservation of fish populations. *Reviews in Fisheries Science*, **4**, 185-202.

Bartol, I. K., Mann, R. & Luckenbach, M. (1999) Growth and mortality of oysters (*Crassostrea virginica*) on constructed intertidal reefs: effects of tidal height and substrate level. *Journal of Experimental Marine Biology and Ecology*, **237**, 157-184.

Bax, N. J. (1991) A comparison of the fish biomass flow to fish, fisheries, and mammals in six marine ecosystems. *ICES Marine Science Symposia*, **193**, 217-224.

Beddington, J. R. (1995) The primary requirements. *Nature*, **374**, 213-214.

Bergman, M. J. N. & Hup, M. (1992) Direct effects of beamtrawling on macrofauna in a sandy sediment in the southern North Sea. *ICES Journal of Marine Science*, **49**, 5-11.

Bergman, M. J. N. & van Santbrink, J. W. (2000) Fishing mortality of populations of megafauna in sandy sediments. *Effects of Fishing on Non-Target Species and Habitats: Biological, Conservation and Socio-economic Issues*. (ed M. J. & d. G. S. J. Kaiser), pp. 49-68. Blackwell Science, Oxford, UK.

Bergmann, M. (2000) The fate of discarded invertebrates from the Clyde Nephrops fishery. University of London.

Bergmann, M. & Moore, P. G. (2001) Mortality of *Asterias rubens* and *Ophiura ophiura* discarded in the Nephrops fishery of the Clyde Sea area, Scotland. *ICES Journal of Marine Science*, **58**, 531-542.

Bergmann, M. & Moore, P. G. (2001) Survival of decapod crustaceans discarded in the *Nephrops* fishery of the Clyde Sea area, Scotland. *ICES Journal of Marine Science*, **58**, 163-171.

Blanchard, F., LeLoc'k, F., Hily, C. & Boucher, J. (2004) Fishing effects on diversity, size and community structure of the benthic invertebrate and fish megafauna on the Bay of Biscay coast of France. *Marine Ecology Progress Series*, **280**, 249-260.

Blanchard, J. L., Dulvy, N. K., Jennings, S., Ellis, J. R., Pinnegar, J. K., Tidd, A. & Kell, L. T. (2005) Do climate and fishing influence size-based indicators of Celtic Sea fish community structure. *ICES Journal of Marine Science*, **62**, 405-411.

Blyth, R. E., Kaiser, M. J., Edwards-Jones, G. & Hart, P. J. B. (2004) Implications of a zoned fishery management system for marine benthic communities. *Journal of Applied Ecology*, **41**, 951-961.

Bundy, A., Fanning, P. & Zwanenburg, C. T. (2005) Balancing exploitation and conservation of the eastern Scotian Shelf ecosystem: application of a 4D ecosystem exploitation index. *ICES Journal of Marine Science*, **62**, 503-510.

Callaway R (2003) Long-term effects of imitation polychaete tubes on benthic fauna: they anchor *Mytilus edulis* (L.) banks. *Journal of Experimental Marine Biology and Ecology*, **283**, 115-132.

Callaway, R., Alsvag, J., de Boois, I., Cotter, J., Ford, A., Hinz, H., Jennings, S., Kröncke, I., Lancaster, J., Piet, G., Prince, P. & Ehrich, S. (2002) Diversity and community structure of epibenthic invertebrates and fish in the North Sea. *ICES Journal of Marine Science*, **59**, 1199-1214.

Churchill, J. H. (1989) The effect of commercial trawling on sediment resuspension and transport over the Middle Atlantic Bight continental shelf. *Continental Shelf Research*, **9**, 841-864.

- Collie, J. S., Escanero, G. A. & Valentine, P. C. (1997) Effects of bottom fishing on the benthic megafauna of Georges Bank. *Marine Ecology Progress Series*, **155**, 159-172.
- Collie, J. S., Hall, S. J., Kaiser, M. J. & Poiner, I. R. (2000) A quantitative analysis of fishing impacts on shelf-sea benthos. *Journal of Animal Ecology*, **69**, 785-799.
- Connell, J. H. (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist*, **122**, 661-696.
- Corten, A. & van den Kamp, G. (1996) Variation in the abundance of southern fish species in the southern North sea in relation to hydrography and wind. *ICES Journal of Marine Science*, **53**, 1113-1119.
- Crowder, L. B. & Cooper, W. E. (1982) Habitat structural complexity and the interaction between bluegills and their prey. *Ecology*, **63**, 1802-1813.
- Daan, N., Bromley, P. J., Hislop, J. R. G. & Nielsen, N. A. (1990) Ecology of North Sea fish. *Netherlands Journal of Sea Research*, **26**, 343-386.
- Dayton, P. K., Thrush, S. F., Agardy, M. T. & Hoffman, R. J. (1995) Environmental effects of marine fishing. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **5**, 205-232.
- Dean, T. A. (1981) Structural aspects of sessile invertebrates as organizing forces in an estuarine fouling community. *Journal of Experimental Marine Biology and Ecology*, **53**, 163-180.
- Dewarumez, J. M., Davoult, D., Anorve, L. E. S. & Frontier, S. (1992) Is the muddy heterogeneous sediment assemblage an ecotone between the Pebbles community and the Abra-Alba community in the Southern Bight of the North Sea. *Netherlands Journal of Sea Research.*, **30**, 229-238.
- Duplisea, D. E. (2005) Running the gauntlet: the predation environment of small fish in the northern Gulf of St Lawrence, Canada. *ICES Journal of Marine Science*, **62**, 412-416.
- Duplisea, D. E. & Kerr, S. R. (1995) Application of a biomass spectrum model to demersal fish data from the scotian shelf. *Journal of Theoretical Biology*, **117**, 263-269.
- Duplisea, D. E., Kerr, S. R. & Dickie, L. M. (1997) Demersal fish biomass size spectra on the Scotian Shelf, Canada: species replacement at the shelfwide scale. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 1725-1735.
- Duplisea, D. E., Jennings, S., Warr, K. J. & Dinmore, T. A. (2002) A size-based model of the impacts of bottom trawling on benthic community structure. *Canadian Journal of Fisheries and Aquatic Science*, **59**, 1785-1795.
- Eckman, J. E. (1983) Hydrodynamic processes affecting benthic recruitment. *Limnology and Oceanography*, **28**, 241-257.

- Engel, J. & Kvitek, R. (1998) Effects of otter trawling on a benthic community in Monterey Bay National Marine Sanctuary. *Conservation Biology*, **12**, 1204-1214.
- Eno, N. C., MacDonald, D. S., Kinnear J.A.M., Amos, S. C., Chapman, C. J., Clark, R. A., Bunker, F. P. D. & Munro, C. (2001) Effects of crustacean traps on benthic fauna. *ICES Journal of Marine Science*, **58**, 11-20.
- Erzini, K., Inejih, C. A. O. & Stobberup, K. A. (2005) An application of two techniques for the analysis of short, multivariate non-stationary time-series of Mauritanian trawl survey data. *ICES Journal of Marine Science*, **62**, 353-359.
- Fager, E. W. (1964) Marine sediments: Effects of a Tube-Building Polychaete. *Science*, **143**, 356-358.
- Featherstone, R. & Risk, M. (1977) Effect of tube-building polychaetes on intertidal sediments of the Minas Basin, Bay of Fundy. *Journal of Sedimentary Petrology*, **47**, 446-450.
- Ferson, S., Stewart, S., Downey, P., Jacquez, G., Klerks, P., Ssemakula, J., Weissburg, M., Malenkey, R., Kroot, I. & Anderson, K. (1986) Competing reviews, or why do Connell and Schoener disagree? *American Naturalist*, **127**, 571-576.
- Forster, S. & Graf, G. (1995) Impact of irrigation on oxygen flux into the sediment: Intermittent pumping by *Callianassa subterranea* and "piston-pumping" by *Lanice conchilega*. *Marine biology*, **123**, 335-346.
- Frid, C. L. J. & Clark, R. A. (2000) Long-term changes in the North Sea Benthos: discerning the role of fisheries. *Effects of Fishing on Non-target Species and Habitats: Biological, Conservation and Socio-economic Issues*. (eds M. J. Kaiser & S. J. de Groot), pp. 198-216. Blackwell Science, Oxford, UK.
- Frid, C. L. J., Clark, R. A. & Hall, J. A. (1999) Long-term changes in the benthos on a heavily fished ground off the NE coast of England. *Marine Ecology Progress Series*, **188**, 13-20.
- Frid, C. L. J., Harwood, K. G., Hall, S. J. & Hall, J. A. (2000) Long-term trends in the benthic communities on North Sea fishing grounds. *ICES Journal of Marine Science*, **57**, 1303-1309.
- Frid, C. L. J. (2003) Managing the health of the seafloor. *Frontiers in Ecology and the Environment*, **1**, 429-436.
- Friederichs, M., Graf, G. & Springer, B. (2000) Skimming flow induced over a simulated polychaete tube lawn at low population densities. *Marine Ecology Progress Series*, **192**, 219-228.
- Gabriel, W. L. (1992) Persistence of demersal fish assemblages between Cape Hatteras and Nova Scotia, Northwest Atlantic. *Journal of the Northwest Atlantic Fisheries Society*, **14**, 29-46.
- Gallagher, E. D., Jumars, P. A. & Trueblood, D. D. (1983) Facilitation of soft-bottom benthic succession by tube builders. *Ecology*, **64**, 1200-1216.

Garthe, S., Camphuysen, C. J. & Furness, R. W. (1996) Amounts of discards by commercial fisheries and their significance for food for seabirds in the North Sea. *Marine Ecology Progress Series*, **136**, 1-11.

Garthe, S. & Damm, U. (1997) Discards from beam trawl fisheries in the German Bight (North Sea). *Archives of Fisheries and Marine Research*, **45**, 232-242.

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

Gilkinson, K., Paulin, M., Hurley, S. & Schwinghamer, P. (1998) Impacts of trawl door scouring on infaunal bivalves: results of a physical trawl door model/dense sand interaction. *Journal of Experimental Marine Biology and Ecology*, **224**, 291-312.

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

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

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

Greenstreet, S. P. R., Spence, F. E., Shanks, A. M. & McMillan, J. A. (1999) Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. II. Trends in fishing effort in the North Sea by U.K. registered vessels landing in Scotland. *Fisheries Research*, **40**, 107-124.

Greenstreet, S. P. R. & Rogers, S. I. (2000) Effects of fishing on non-target fish species. *Effects of Fishing on Non-Target Species and Habitats: Biological, Conservation and Socio-economic Issues*. (eds M. J. Kaiser & B. de Groot), pp. 217-234. Blackwell Science, Oxford, U.K.

Greenstreet, S. P. R., Shanks, A. M. & Buckett, B.-E. (2006) Trends in fishing activity in the North Sea by U.K. registered vessels landing in Scotland over the period 1960 to 1998. *Fisheries Research Services Collaborative Reports*, **02/06**, 27pp.

Groenewold, S. & Fonds, M. (2000) Effects of benthic scavengers of discards and damaged benthos produced by the beam-trawl fishery in the southern North Sea. *ICES Journal of Marine Science*, **57**, 1395-1406.

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

Heessen, H. J. L. (1996) Time series data for a selection of forty fish species caught during the International Beam Trawl Survey. *ICES Journal of Marine Science*, **53**, 1079-1084.

Heessen, H. J. L. & Daan, N. (1996) Long-term trends in ten non-target North Sea fish species. *ICES Journal of Marine Science*, **53**, 1063-1078.

Hill, A. S., Brand, A. R., Wilson, U. A. W., Veale, L. O. & Hawkins, S. J. (1996) Estimation of by-catch composition and the numbers of by-catch animals killed annually in the Manx scallop fishing grounds. *Aquatic Predators and their Prey*. (ed S. P. R. & T. M. L. Greenstreet), pp. 111-115. Blackwells Science, Oxford, UK.

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

Hinz, H., Kröncke, I. & Ehrich, S. (2004) Seasonal and annual variability in an epifaunal community in the German Bight. *Marine Biology*, **144**, 735-745.

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

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

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

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

Jennings, S., Bouille, D. P. & Polunin, N. V. C. (1996) Habitat correlates of the distribution and biomass of Seychelles' reef fishes. *Environmental Biology of Fishes*, **46**, 15-25.

Jennings, S., Dinmore, T. A., Duplisea, D. E. & Lancaster, J. E. (2001) Trawling disturbance can modify benthic production processes. *Journal of Animal Ecology*, **70**.

Jennings, S., Grandcourt, E. M. & Polunin, N. V. C. (1995) The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. *Coral reefs*, **14**, 225-235.

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

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

Jennings, S. & Kaiser M.J. (1998) The effects of fishing on marine ecosystems. *Advances in Marine Biology*, **34**, 203-314.

Jennings, S., Kaiser, M. J. & Reynolds, J. D. (2001) *Marine Fisheries Ecology*. Blackwell Science, Oxford, UK.

Jennings, S., Marshall, S. S. & Polunin, N. V. C. (1996) Seychelles' marine protected areas: Comparative structure and status of reef fish communities. *Biological Conservation*, **75**, 201-209.

Jennings, S., Pinnegar, J. K., Polunin, N. V. C. & Boon, T. (2001) Weak cross species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology*, **70**, 934-944.

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

Jennings, S. & Polunin, N. V. C. (1997) Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. *Coral Reefs*, **16**, 71-82.

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

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

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

Jennings, S., Nicholson, M. D., Dinmore, T. A. & Lancaster, J. E. (2002) Effects of chronic trawling disturbance on the production of infaunal communities. *Marine Ecology Progress Series*, **243**, 251-260.

Jennings, S., Pinnegar, J. K., Polunin, N. V. C. & Boon, T. W. (2001) Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology*, **70**, 934-944.

Jennings, S., Pinnegar, J. K., Polunin, N. V. C. & Warr, K. J. (2001) Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. *Marine Ecology Progress Series*, **213**, 127-142.

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

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

- Jennings, S., Greenstreet, S. P. R. & Reynolds, J. (1999) Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology*, **68**, 617-627.
- Jennings, S., Greenstreet, S. P. R., Hill, L., Piet, G. J., Pinnegar, J. K. & Warr, K. J. (2002) Long-term trends in the trophic structure of the North Sea fish community: evidence from stable isotope analysis, size spectra and community metrics. *Marine Biology*, **141**, 1085-1097.
- Johnson, K. A. A Review of National and International Literature on the Effects of Fishing on Benthic Habitats. 2002. NOAA Technical Memorandum.
- Jones, S. E. & Jago, C. F. (1993) In situ Assessment of Modification of Sediment Properties by Burrowing Invertebrates. *Marine Biology*, **115**, 133-142.
- Jouffre, D. & Inejih, C. A. (2005) Assessing the impact of fisheries on demersal fish assemblages of the Mauritanian continental shelf, 1987-1999, using dominance curves. *ICES Journal of Marine Science*, **62**, 380-383.
- Kaiser, M. J., Clarke, K. R., Hinz, H., Austen, M. C., Somerfield, P. J. & Karakassis, I. (2006) Global analysis of the response and recovery of benthic biota to fishing. *Marine Ecology Progress Series*, **311**, 1-14.
- Kaiser, M. J., Ramsay, K., Richardson, C. A., Spence, F. E. & Brand, A. R. (2000) Chronic fishing disturbance has changes shelf sea benthic community structure. *Journal of Animal Ecology*, **69**, 494-503.
- Kaiser, M. J., Spence, F. E. & Hart, P. J. (2000) Fishing-Gear Restrictions and Conservation of Benthic Habitat Complexity. *Conservation Biology*, **14**, 1512-1525.
- Kaiser, M. J. & Spencer, B. E. (1996) Behavioural responses of scavengers to beam trawl disturbance. *Aquatic Predators and their Prey* (eds S. P. R. Greenstreet & M. L. Tasker), pp. 116-123. Blackwells Science, Oxford, UK.
- Kaiser, M. J. & Spencer, B. E. (1996) The effects of beam-trawl disturbance on infaunal communities in different habitats. *Journal of Animal Ecology*, **65**, 348-358.
- Kerr, S. R. & Dickie, L. M. (2001) *The Biomass Spectrum: A Predator Prey Theory of Aquatic Production*. Columbia University Press, New York.
- Kohn, A. J. (1967) Environmental complexity and species diversity in the gastropod genus *Conus* on Indo-West Pacific reef platforms. *American Naturalist*, **101**, 251-260.
- Kohn, A. J. (1968) Microhabitats, abundance and food of *Conus* on atoll reefs in the Maldives and Chagos Islands. *Ecology*, **49**, 1046-1062.
- Kotler, B. P. & Brown, J. S. (1988) Environmental heterogeneity and the coexistence of desert rodents. *Annual Review of Ecology and Systematics*, **19**, 281-307.

- Kröncke, I. (1990) Macrofauna standing stock of the Dogger Bank, a comparison 1950-1954 versus 1985-1987. *ICES paper*, **CM 1990/Mini 3**, 1-22.
- Krost, P., Bernhard, M., Werner, F. & Hukriede, W. (1990) Otter trawl tracks in Kiel Bay (western Baltic) mapped by side-scan sonar. *Meeresforsch*, **32**, 344-353.
- Kröncke, I. (1992) Macrofauna standing stock of the Dogger Bank - a comparison. 2. 1950-1954 versus 1985-1987 - a final summary. *Helgolander Meeresuntersuchungen*, **46**, 137-169.
- Kröncke, I. & Bergfeld, C. (2001) Review of the current knowledge on North Sea benthos. Zentrum für Meeres- und Klimaforschung der Universität, Hamburg, Germany.
- Künitzer, A. (1990) The infauna and epifauna of the Central North Sea. *Kiel Meeresforsch*, **33**, 23-37.
- Lackschewitz, D. & Reise, K. (1998) Macrofauna on flood delta shoals in the Wadden Sea with an underground association between the lugworm *Arenicola marina* and the amphipod *Urothoe poseidonis*. *Helgoländer Meeresuntersuchungen*, **52**, 147-158.
- Langton, R. W. & Robinson, W. E. (1990) Faunal associations on scallop grounds in the western Gulf of Maine. *Journal of Experimental Marine Biology and Ecology*, **144**, 157-171.
- Lindeboom, H. J. & De Groot, S. J. (1998) IMPACT II. The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystems. Netherlands Institute for Sea Research.
- Lubchenco, J. (1983) *Littorina* and *Fucus* : Effects of herbivores, substratum heterogeneity, and plant escapes during succession. **64**.
- MacArthur, R. H. & MacArthur, J. W. (1961) On bird species diversity. *Ecology*, **42**, 594-598.
- Magnussen, E. (2002) Demersal fish assemblages of the Faroe Bank; species composition, distribution, biomass spectrum and diversity. *Marine Ecology Progress Series*, **238**, 211-225.
- Mayer, L. M., Schick, D. F., Findlay, R. H. & Rice, D. L. (1991) Effects of commercial dragging on sedimentary organic matter. *Marine Environmental Research*, **31**, 249-261.
- Messieh, S. N., Rowell, T. W., Peer, D. L. & Cranford, P. J. (1991) The effects of trawling, dredging and ocean dumping on the eastern Canadian continental shelf seabed. *Continental Shelf Research*, **11**, 1237-1263.
- Mueter, F. J. & Megrey, B. A. (2005) Distribution of population-based indicators across multiple taxa to assess the status of Gulf of Alaska and Bering Sea groundfish communities. *ICES Journal of Marine Science*, **62**, 344-352.
- Overholtz, W. J. & Tyler, A. V. (1985) Long-term responses of the demersal fish assemblages of Georges Bank. *Fishery Bulletin*, **83**, 507-520.
- Pauly, D. & Christensen, V. (1995) Primary production required to sustain global fisheries. *Nature*, **374**, 255-257.

- Pederson, E. J. & Peterson, M. S. (2002) Bryozoans as ephemeral estuarine habitat and a larval transport mechanism for mobile benthos and young fishes in the north- central Gulf of Mexico. *Marine Biology*, **140**, 935-947.
- Pianka, E. R. (1966) Convexity, desert lizards and spatial heterogeneity. *Ecology*, **47**, 1055-1059.
- Pianka, E. R. (1967) On lizard species diversity: North American flatland deserts. *Ecology*, **48**, 333-350.
- Piet, G. J. & Jennings, S. (2005) Response of potential fish community indicators to fishing. *ICES Journal of Marine Science*, **62**, 214-225.
- Piet, G. J., Quirijns, F., Robinson, L. & Greenstreet, S. P. R. (In Press) Potential pressure indicators for fishing and their data requirements. *ICES Journal of Marine Science*.
- Piet, G. J., Rijnsdorp, A. D., Bergman, M. J. N., van Santbrink, J. W., Craeymeersch, J. & Buijs, J. (2000) A quantitative evaluation of the impact of beam trawling on benthic fauna in the southern North Sea. *Ices Journal of Marine Science*, **57**, 1332-1339.
- Platt, T., Sathyendranath, S., Joint, I. & Fasham, M. J. R. (1993) Photosynthesis characteristics of the phytoplankton in the Celtic Sea during late spring. *Fisheries Oceanography*, **2**.
- Pringle, C. M. (1990) Nutrient spatial heterogeneity: effects on community structure, physiognomy, and diversity of stream algae. *Ecology*, **71**, 905-920.
- Qian, P. Y., Rittschof, D., Sreedhar, B. & Chia, F. S. (1999) Macrofouling in unidirectional flow: miniature pipes as experimental models for studying the effects of hydrodynamics on invertebrate larval settlement. *Marine Ecology Progress Series*, **191**, 141-151.
- Ragnarsson, S. A. & Raffaelli, D. (1999) Effects of the mussel *Mytilus edulis* L. on the invertebrate fauna of sediments. *Journal of Experimental Marine Biology and Ecology*, **241**, 31-43.
- Ramsay, K., Kaiser, M. J. & Hughes, R. N. (1998) Responses of benthic scavengers to fishing disturbance by towed gears in different habitats. *Journal of Experimental Marine Biology and Ecology*, **224**, 73-98.
- Recher, H. F. (1969) Bird species diversity and habitat diversity in Australia and North America. *American Naturalist*, **103**, 75-80.
- Rees, H. L., Pendle, M. A., Waldcock, R., Limpenny, D. S. & Boyd, S. E. (1999) A comparison of benthic biodiversity in the North Sea, English Channel, and Celtic Seas. *ICES Journal of Marine Science*, **56**, 228-246.
- Reid, P. C., Lancelot, C., Gieskes, W. W. C., Hagmeier, E. & Weichart, G. (1990) Phytoplankton of the North Sea and its dynamics: a review. *Netherlands Journal of Sea Research*, **26**, 295-331.

- Reise, K. (1983) Biotic enrichment of intertidal sediments by experimental aggregates of the deposit-feeding bivalve *Macoma balthica*. *Marine Ecology Progress Series*, **12**, 229-236.
- Riemann, B. & Hoffmann, E. (1991) Ecological consequences of dredging and bottom trawling in the Limfjord, Denmark. *Marine Ecology Progress Series*, **69**, 171-178.
- Rijnsdorp, A. D., Buys, A. M., Storbeck, F. & Visser, E. G. (1998) Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. *Ices Journal of Marine Science*, **55**, 403-419.
- Rijnsdorp, A. D., Leeuwen, P. I. v., Daan, N. & Heessen, H. J. L. (1996) Changes in the abundance of demersal fish species in the North Sea between 1906-1909 and 1990-1995. *ICES Journal of Marine Science*, **53**, 1054-1062.
- Roberts, C. M. & Polunin, N. V. C. (1991) Are marine reserves effective in management of reef fisheries? *Reviews in Fish Biology and Fisheries*, **1**, 65-91.
- Roberts, C. M. & Polunin, N. V. C. (1993) Marine reserves: Simple solutions to managing complex fisheries? *Ambio*, **22**, 363-368.
- Rogers, S. I. & Ellis, J. R. (2000) Changes in the demersal fish assemblages of British coastal waters during the 20th century. *ICES Journal of Marine Science*, **57**, 866-881.
- Rogers, S. I. & Millner, R. S. (1996) Factors affecting the annual abundance and regional distribution of English inshore demersal fish populations: 1973 to 1995. *ICES Journal of Marine Science*, **53**, 1094-1112.
- Rosenzweig, M. L. & Winakur, J. (1969) Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology*, **50**, 558-572.
- Rumohr, H. & Krost, P. (1991) Experimental evidence of damage to benthos by bottom trawling with special reference to *Arctica islandica*. *Meeresforsch*, **33**, 340-345.
- Rumohr, H. & Kujawski, T. (2000) The impact of trawl fishery on the epifauna of the southern North Sea. *ICES Journal of Marine Science*, **57**, 1389-1394.
- Samoilys, M. A. (1988) Abundance and species richness of coral reef fish on the Kenyan coast: The effects of protective management and fishing. (eds J. H. Choat, D. Barnes, M. A. Borowitzka, J. C. Coll, P. J. Davies, P. Flood, B. G. Hatcher & D. e. al. Hopley), Townsville, Australia.
- Schoener, T. W. (1983) Field experiments on interspecific competition. *American Naturalist*, **122**, 240-285.
- Schroeder, A. & Knust, R. (1999) Long-term changes in the benthos of the German Bight (North Sea) - possible influences of fisheries. *ICES Journal of Marine Science*, **56**.

Schwinghamer, P., Guigné, J. Y. & Siu, W. C. (1996) Quantifying the impact of trawling on benthic habitat structure using high resolution acoustics and chaos theory. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 288-296.

Skjoldal, H. R., van Gool, S. & Offringa, H. (1999) Workshop on Ecological Quality Objectives (EcoQOs) for the North Sea. 1-3 September 1999; Scheveningen, Netherlands. TemaNord, The Hague, Netherlands.

Soetaert, K. & Heip, C. (1990) Sample-size dependence of diversity indices and the determination of sufficient sample size in a high-diversity deep-sea environment. *Marine Ecology Progress Series*, **59**, 305-307.

Sparholt, H. (1990) An estimate of the total biomass of fish in the North Sea. *Journal du Conseil International pour l'Exploration de la Mer*, **46**, 200-210.

Stobberup, K. A., Inejih, C. A. O., Traore, S., Monteiro, C., Amorim, P. & Erzini, K. (2005) Analysis of size-spectra off northwest Africa: a useful indicator in tropical areas? *ICES Journal of Marine Science*, **62**, 424-429.

Stratoudakis, Y., Fryer, R. J. & Cook, R. M. (1998) Discarding practices for commercial gadoids in the North Sea. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1632-1644.

Stratoudakis, Y., Fryer, R. J., Cook, R. M. & Pierce, G. J. (1999) Fish discarded from Scottish demersal vessels: Estimators of total discards and annual estimates for targeted gadoids. *ICES Journal of Marine Science*, **56**, 592-605.

Talman, S. G., Norkko, A., Thrush, S. F. & Hewitt, J.E. (2004) Habitat structure and the survival of juvenile scallops *Pecten novaezelandiae*: comparing predation in habitats with varying complexity. *Marine Ecology Progress Series*, **269**, 197-207.

Thrush, S. F., Hewitt, J. E., Cummings, V. J., Dayton, P. K., Cryer, M., Turner, S. J., Funnell G.A., Budd R.G., Milburn, C. J. & Wilkinson, M. R. (1998) Disturbance of the marine benthic habitat by commercial fishing: impacts at the scale of the fishery. *Ecological Applications*, **8**, 866-879.

Thrush, S. F., Hewitt, J. E., Funnell G.A., Cummings, V. J., Ellis, J., Schultz D., Talley, D. & Norkko, A. (2001) Fishing disturbance and marine biodiversity: the role of habitat structure in simple soft sediment systems. *Marine Ecology Progress Series*, **221**, 255-264.

Tuck, I. D., Hall, S. J., Robertson, M. R., Armstrong, E. & Basford, D. J. (1998) Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch. *Marine Ecology Progress Series*, **162**, 227-242.

Van Beek, F. A., Van-Leeuwen, P. I. & Rijnsdorp, A. D. (1990) On the survival of plaice and sole discards in the otter trawl and beam trawl fisheries in the North Sea. *Netherlands Journal of Sea Research*, **26**, 151-160.

Watling, L. & Norse, E. A. (1998) Disturbance of the Seabed by Mobile Fishing Gear: A Comparison to Forest Clearcutting. *Conservation Biology*, **12**, 1180-1197. Notes: In 'Benthic Ecology' file - waiting to be filed.

Watson, M. & Ormond, R. F. G. (1994) Effect of an artisanal fishery on the fish and urchin populations of a Kenyan coral reef. *Marine Ecology Progress Series*, **109**, 115-129.

Woodin, S. A. (1978) Refuges, disturbance, and community structure: A marine soft-bottom example. *Ecology*, **59**, 274-284.

Yang, J. (1982) The dominant fish fauna in the North Sea and its determination. *Journal of Fish Biology*, **20**, 635-643.

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

Yemane, D., Field, J. G. & Leslie, R. W. (2005) Exploring the effects of fishing on fish assemblages using Abundance Biomass Comparison curves. *ICES Journal of Marine Science*, **62**.