
Significance of Bottom-Fishing Disturbance

MICHEL J. KAISER

School of Ocean Sciences, University of Wales-Bangor, Menai Bridge, Gwynedd, LL59 5EY, United Kingdom,
email m.j.kaiser@sos.bangor.ac.uk

Abstract: *Since the early 1970s there has been increasing interest in the ecological effects of bottom-fishing activities on the benthic ecology of the seas of northern Europe. The majority of studies have examined the short-term effects of disturbance on benthic fauna. Some areas, however, such as the southern North Sea, have been subjected to fishing disturbance for over 50 years, which complicates predictions of long-term ecological change inferred from recent experimental studies. I highlight the importance of evaluating the ecological relevance of fishing disturbance versus natural perturbations, which varies among different habitats. Most experimental studies have shown that it is possible to detect short-term changes in community structure in response to fishing disturbance. Evidence suggests that long-term changes are probably restricted to long-lived fragile species or communities found in environments that are infrequently disturbed by natural phenomena. Understanding the relative ecological importance of physical disturbance by fishing versus natural events would provide a basis for predicting the outcome of fishing activities in different marine habitats. I suggest approaches that may refine attempts to correlate fishing intensity and frequency with community change, such as the use of tracking devices fitted to trawlers and surveys of fauna, such as bivalves and echinoderms, that record disturbance events of the past in their shells or body structure.*

Importancia de la Perturbación de la Pesca de Fondo

Resumen: *Desde principios de los años 70's ha habido un creciente interés en los efectos ecológicos de las actividades de pesca de fondo en la ecología béntica de los mares del Norte de Europa. La mayoría de estos estudios han examinado los efectos de las perturbaciones sobre la fauna bentónica a corto plazo. Sin embargo, en algunas áreas como la zona sur del Mar del Norte, han sido sujetas a perturbaciones por pesca por mas de 50 años, lo cual complica las predicciones de cambio ecológico a largo plazo establecidas a partir de estudios experimentales recientes. Remarco la importancia de la evaluación de la relevancia ecológica de la perturbación pesquera contra perturbaciones naturales que varían entre diferentes hábitats. La mayoría de los estudios experimentales han mostrado que es posible detectar cambios a corto plazo en la estructura comunitaria en respuesta a perturbaciones pesqueras. Las evidencias sugieren que los cambios a largo plazo están probablemente restringidos a especies frágiles de vida larga o a comunidades encontradas en ambientes que no son perturbados frecuentemente por fenómenos naturales. El entendimiento de la importancia ecológica relativa de las perturbaciones físicas debidas a la pesca comparada con eventos naturales podría proveer una base para la predicción de los resultados de la pesca en diferentes hábitats marinos. Sugiero aproximaciones que podrían refinar esfuerzos para correlacionar la intensidad pesquera y su frecuencia con cambios en las comunidades como lo son el uso de artefactos adaptados a los sistemas de arrastre y muestreos de fauna—como los bivalvos y equinodermos—que registran eventos pasados de perturbación en sus conchas o en la estructura de sus cuerpos.*

Introduction

The seas of northern Europe are among the most heavily fished in the world, leading to speculation that shifts in

some benthic communities may have occurred as a result of physical disturbance of the seabed by bottom-fishing gear. The earliest studies to address this issue were conducted in the North Sea and provided basic information such as the depth to which trawls penetrated the substratum and the number and identity of non-target benthic biota removed from the seabed (Graham

Paper submitted July 17, 1997; revised manuscript accepted July 1, 1998.

1230

1955; de Groot & Apeldoorn 1971; Margetts & Bridger 1971; Bridger 1972; de Groot 1984).

Many types of bottom-fishing gear are used in European waters, of which scallop dredges and otter and beam trawls disturb the largest areas of seabed annually (North Sea Task Force 1993; Anonymous 1995; Kaiser et al. 1996). Since the early 1970s there has been a large increase in the size of the beam trawl fleet (Heessen & Daan 1996; Rijnsdorp & van Leeuwen 1996). Beam trawls are towed at speeds up to twice as fast (4–7 knots) as other gear, and the entire width of the gear is designed to remain in close contact with the seabed. As a consequence, beam trawls disturb much greater areas of the seabed per hour of effort than other bottom-fishing (demersal) gear, with the main effort concentrated in the southern North Sea (North Sea Task Force 1993).

The disappearance of reefs of the tubicolous polychaete *Sabellaria spinulosa* was attributed to intense trawling activity in the Wadden Sea (Riesen & Reise 1982) and led to concern that bottom fishing, in particular beam trawling, may have caused similar changes in benthic communities elsewhere in the North Sea. This prompted a number of studies that have examined the changes that occur in benthic community structure as a result of trawling disturbance. Many of these have examined the effects of beam trawls, although other gears may cause considerable and comparable disturbance in certain areas (Table 1; Jennings & Kaiser 1998).

Fishing versus Natural Disturbance

To date, the majority of studies of the effects of fishing disturbance on the seabed have examined the short-term responses of benthic infauna and populations of scavengers (Table 1). Although these studies have yielded useful information on short-term changes in relative abundance, few have investigated potential long-term recovery (beyond 1 year) or alterations in community composition (Table 1; but see Tuck et al. 1998). Most of these studies have been undertaken in shallow seas on the continental shelf at depths below 100 m. This is not surprising because the majority of demersal fishing activity occurs in this depth range, and quantitative ecological studies become logistically complex at greater depths. Benthic communities within these environments experience continual disturbance at various scales (Hall 1994). Large-scale natural disturbances, such as seasonal storms and daily scouring by tidal currents, form a background against which other, smaller disturbances occur, such as those induced by predator feeding activities (Oliver & Slattery 1985; Hall et al. 1993a). Hall et al. (1993a) postulated that frequent small-scale predator disturbances may have a considerable additive effect on benthic communities, creating a long-term mosaic of patches in various states of climax or recolonization (Grassle & Saunders

1973; Connell 1978). They concluded, however, that while it was possible to detect the short-term effects of predator disturbance, large-scale effects were never manifested for two possible reasons: (1) they are masked by a background of large-scale natural disturbances, or (2) small-scale disturbances permit such rapid recolonization that large-scale effects never become apparent.

Presumably, the scale and frequency of physical disturbance events can increase to a point where lasting ecological effects are observed even against a background of natural disturbance. The additive effects of an entire fishing fleet may reach such a threshold. So far there is little evidence to suggest that this threshold may have been exceeded in the naturally perturbed sediments of the southern North Sea. Moreover, Posey et al. (1996) recently demonstrated that even large-scale disturbances such as hurricanes have relatively short-term effects on shallow-water communities adapted to frequent physical disturbance (but see Rees et al. 1977). Hence, benthic communities that inhabit frequently disturbed environments are less likely to exhibit long-term changes in their structure and composition in response to fishing activity (Shepherd 1983; Kaiser & Spencer 1996a; Kaiser et al. 1998; Posey et al. 1996) than those in more stable habitats (Fig. 1; Thiel & Schriever 1990; Kaiser & Spencer 1996a; Auster, this issue).

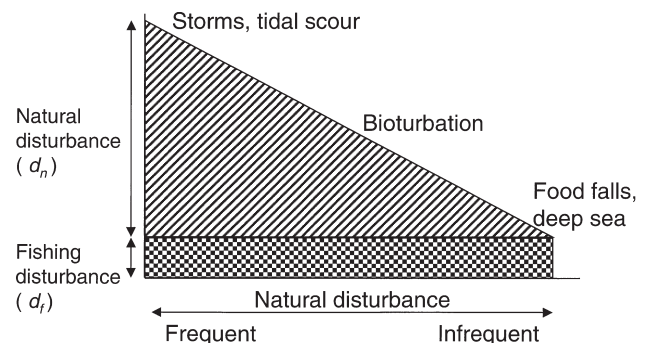


Figure 1. A simplistic model to illustrate the relative importance of a constant level of fishing disturbance in different habitats that are subjected to different levels of natural disturbance. As levels of natural disturbance decline, fishing disturbance accounts for a greater proportion of the total disturbance experienced ($d_n + d_f$) and becomes increasingly important. An example that illustrates a situation on the extreme left-hand side of the x axis is the mobile sediment community described by Kaiser and Spencer (1996a), whereas the extreme right-hand side is illustrated by the deep-water habitats described by Thiel and Schriever (1990). The addition of a z axis could incorporate habitat and substratum stability into the model.

Table 1. A list of the major studies undertaken or currently in progress in northern Europe that examine the effects of the physical disturbance of benthic communities by mobile demersal fishing gear.

<i>Gear studied</i>	<i>Area</i>	<i>Main objectives</i>	<i>Author or contact*</i>
Completed			
Otter trawl	North Sea	benthic by-catch	Graham 1995
Beam trawl	North Sea	benthic by-catch	de Groot & Apeldoorn 1971
Beam trawl	North Sea	benthic by-catch	Margetts & Bridger 1971
Beam trawl	North Sea	penetration of gear into sediment	Bridger 1972
Scallop dredge	Irish Sea	physical damage to epifauna	Bullimore 1985
Hydraulic dredge	North Sea	changes in infauna	Hall et al. 1990
Beam trawl	North Sea	changes in benthic communities	BEON 1990
Beam trawl	North Sea	changes in benthic communities	BEON 1991
Otter trawl	North Sea	damage to infauna caused by different parts of the gear	Rumohr & Krost 1991
Beam trawl	North Sea	catch composition, survival of by-catch	Fonds 1994
Beam trawl	North Sea	changes in macroinfauna	Bergman & Hup 1992
Scallop dredge	Scottish sealoch	changes in epi- and infauna	Eleftheriou & Robertson 1992
Demersal trawls	North Sea	use of wrecks as control areas	Hall et al. 1993 <i>b</i>
Beam trawl	Irish Sea	scavenger aggregation in trawled areas	Kaiser & Spencer 1994
Beam trawl	North & Irish Seas	effects of beam trawling on the seabed	de Groot & Lindeboom 1994
Beam trawl	North Sea	incidence of damage in bivalve shells	Witbaard & Klein 1994
Beam trawl	Irish Sea	survival of benthic by-catch	Kaiser & Spencer 1995
Scallop dredge	Irish Sea	changes in epibenthic communities	MacDonald 1993
Scallop dredge	Clyde Sea	effects of dredging on maerl beds	Hall-Spencer 1995
Scallop dredge	Irish Sea	benthic by-catches and survival	Hill et al. 1996
Beam trawl	Irish Sea	incidence of damaged mobile epifauna	Kaiser 1996
Beam trawl	Irish Sea	changes in macroinfauna	Kaiser & Spencer 1996 <i>a</i>
Beam trawl	Irish Sea	scavenger aggregation in trawled areas	Kaiser & Spencer 1996 <i>b</i>
Various	Irish Sea	comparison of disturbance effects by different fishing gears	Kaiser et al. 1996
Beam trawl	Irish Sea	intra- and interspecific competition between scavengers	Ramsay et al. 1996, 1997 <i>a</i> , 1997 <i>b</i> , 1998
Beam trawl	North Sea	microdistribution of fishing effort	Rijnsdorp et al. 1998
Beam trawl	Irish Sea	changes in epifaunal communities	Kaiser et al. 1998
Beam trawl	North Sea	historical changes in epifauna	Philippart 1998
Various	North & Irish Seas	effects of trawling on the seabed	de Groot & Lindeboom 1998
Otter trawl	Scottish sealoch	effects of trawling on habitat and fauna	Tuck et al. 1998
In progress*			
Various	English Channel, North Sea	long-term effects of different intensities of fishing, comparisons with areas closed to fishing	M. J. Kaiser
Various	English Channel, Irish & North Seas	bivalves and echinoderms as indicators of fishing disturbance	C. A. Richardson
Otter trawl	Northwestern Mediterranean	effects of trawling on infauna and sediment	P. Sanchez
Otter trawl	North Sea	long-term effects of trawling estimated from data on flatfish stomach contents	C. L. J. Frid
Scallop dredge	Irish Sea	long-term effects of different intensities of dredging effort and seasonal variation	A. R. Brand
Various	North & Irish Seas	methods to reduce the impact of fishing gear	W. Van Maaren

*Contact addresses available on request from author.

Can Long-Term Trends Be Detected?

In sedimentary habitats, the detection of long-term benthic community changes that are attributable to fishing activities has been problematic for all but the most obvious cases (Riesen & Reise 1982). But a long-term dataset of by-catches of benthic species has revealed reductions in potentially vulnerable species or changes in epibenthic communities. Philippart (1998) analyzed a dataset of returns of epibenthic by-catch species from the southern

North Sea dating back to the 1930s. Fishermen were paid to retain examples of a predetermined selection of species and deliver them to the Netherlands Institute for Sea Research. Beam trawling superseded otter trawling as the main Dutch fishery from about 1970. Consequently, landings of benthic species might have been expected to increase because beam trawls catch benthic species more effectively than otter trawls do. Nevertheless, the number of individuals of certain species returned to the laboratory declined steeply from 1970 onward (Philip-

part 1998). Species that showed the greatest decline tended to be slow-growing, low in fecundity, or physically vulnerable to damage by physical contact with fishing gear.

It is difficult to extricate the possible effects of fishing activities from other environmental or anthropogenic perturbations, especially in the North Sea. For example, eutrophication in the eastern North Sea is strongly linked with increases in populations of polychaetes and brittlestars (Pearson et al. 1985), which are thought to have influenced the observed increase in the size and growth rate of plaice (*Pleuronectes platessa* [L.]) populations (Rijnsdorp & van Leeuwen 1996). Similarly, the demise of the common whelk (*Buccinum undatum* [L.]) in the southern North Sea is thought to be partly attributable to the effects of tributyl tin, which causes reproductive failure in female whelks. Alternatively, increased whelk mortality may be associated with the beam trawl fishery, which damages their shells and increases their vulnerability to predation (ten Hallers-Tjabbes et al. 1996; Ramsay & Kaiser 1998). Furthermore, recent studies suggest that oceanic influences in the North Sea may have had greater ecological effects than the relatively localized effects of eutrophication and fishing disturbance (Lindeboom 1995). This emphasizes the value of time-series data, especially when trying to determine which factors have had the most influence on changes in community structure.

Solutions

Studies conducted in the North Sea have been hampered by the lack of comparable control areas that have been protected from fishing over the last century. The communities observed presently may be the products of decades of continuous fishing disturbance (de Groot & Lindeboom 1994; Dayton et al. 1995), so it is difficult to infer the ecological implications of the results of short-term experiments conducted in an environment that is potentially predisturbed. Moreover, fishing effort in shelf seas is not homogeneously distributed. Fishermen concentrate their effort in grounds that yield the best catches of commercial species and avoid areas with obstructions and rough ground that would damage their gear. In addition, fishing is restricted in some areas, such as in shipping lanes and around oil rigs. One method of resolving this problem is to identify those areas that have been fished—disturbed—most intensively. Fishing effort data have been analyzed by a number of workers, who assessed how often areas of the seabed were disturbed by fishing activities. Initially, Welleman (1989) estimated that some areas of the southern North Sea were swept, on average, three to seven times per year. These estimates were based on data collected for areas that measure 30' latitude by 30' longitude. Although data at this scale have yielded important information on the approximate dis-

tribution of different forms of fishing disturbance (Kaiser et al. 1996), it provides an unintentionally misleading representation of its microdistribution, implying that it is homogeneous across large areas. More recently, Rijnsdorp et al. (1998) have emphasized the patchy distribution of fishing effort by collecting data from areas that measure approximately 9 km². This analysis has revealed that, whereas some areas of the North Sea are visited more than 400 times per year, others are probably never fished (Rijnsdorp et al. 1998). The improved ability to pinpoint areas that experience different frequencies of disturbance will aid the interpretation of future studies. It is unlikely that these data can be used to interpret many of the findings of past studies because the distribution of fishing effort has altered with technological developments and fluctuations in fisheries (Anonymous 1995). Consequently, more-recent studies tend toward comparisons of present-day benthic community data with those collected prior to the start of intense fishing activity (Table 1; Philippart 1998; de Groot & Lindeboom 1998).

In certain localities, the distribution of bottom-trawling disturbance can also be ascertained from the occurrence of physical damage in populations of animals that are able to withstand such injuries. More than half of the starfish (*Astropecten irregularis*; Pennant 1777) sampled from a heavily beam-trawled area of the Irish Sea had lost arms, compared with only 7% in a less intensively fished area (Kaiser 1996). Bivalves may also provide a useful long-term indication of fishing disturbance. When bivalves are damaged physically by fishing gear, some are killed immediately and others are eaten by scavengers; those that survive are able to repair their shell matrix. During the repair process, sand grains become lodged between the mantle and the growing edge of the shell, eventually becoming incorporated into the shell matrix (Gaspar et al. 1994; Witbaard & Klein 1994). Witbaard and Klein (1994) studied annual growth rings in the shells of quahogs (*Arctica islandica* [L.]) and were able to determine the years in which they had been damaged by noting the occurrence of sand grains in the shell matrix. The incidence of shell damage correlated with increasing beam-trawling activity between 1972 and 1991 at a study site in the southern North Sea (Witbaard & Klein 1994). They were able to conclude that the study site had been disturbed by demersal fishing gear at least once per year during this period (Witbaard & Klein 1994). Long-lived sessile organisms, such as quahogs, could be used to provide an accurate record of the historical disturbance regime of small areas (<10 m²) of the seabed.

Summary

Recent and past studies of the possible long-term changes in benthic ecosystems caused by fishing disturbance have been hampered by a lack of control (unfished) areas for

comparative analysis. Analysis of long-term data sets, where they exist, should provide a useful insight into possible long-term changes associated with bottom-fishing activity. The use of species that provide a historical record of fishing disturbance events could greatly enhance the interpretation of perceived changes ascertained from samples of present-day benthic communities. The use of automated activity recorders or tracking devices would provide a means for identifying the most heavily fished areas and those, if any, that are presently unfished. This information would then provide a sound basis for comparative studies of the effects of different intensities of fishing and how they vary between different habitats and with season.

Literature Cited

- Anonymous. 1995. Report of the study group on the ecosystem effects of fishing activities. Cooperative research report 200. International Council for the Exploration of the Sea, Copenhagen, Denmark.
- Auster, P. J. 1998. A conceptual model of the impacts of fishing gear on the integrity of fish habitats. *Conservation Biology* **12**:1198–1203.
- BEON (Beleidsgericht Ecologisch Onderzoek Noordzee). 1990. Effects of bottom trawl fishery on the bottom fauna in the North Sea. Report no. 13. Den Burg, Texel, The Netherlands.
- BEON (Beleidsgericht Ecologisch Onderzoek Noordzee). 1991. Effects of bottom trawl fishery on the bottom fauna in the North Sea. II. The 1990 studies. Report no. 13. Den Burg, Texel, The Netherlands.
- Bergman, M. J. N., and M. Hup. 1992. Direct effects of beamtrawling on macrofauna in a sandy sediment in the southern North Sea. *International Council for the Exploration of the Sea Journal of Marine Science* **49**:5–13.
- Bridger, J. 1972. Some observations on the penetration into the sea bed of tickler chains on a beam trawl. CM 1972/B:7. International Council for the Exploration of the Sea, Copenhagen, Denmark.
- Bullimore, B. 1985. An investigation into the effects of scallop dredging within the Skomer Marine Reserve. Report to the Nature Conservancy Council. Skomer Marine Reserve subtidal monitoring project no. 3. Joint Nature Conservation Committee, Peterborough, United Kingdom.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**:1302–1310.
- Dayton, P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman. 1995. Environmental effects of fishing. *Aquatic Conservation: Marine and Freshwater Ecosystems* **5**:205–232.
- de Groot, S. J. 1984. The impact of bottom trawling on the benthic fauna of the North Sea. *Ocean Management* **10**:21–36.
- de Groot, S. J., and J. M. Apeldoorn. 1971. Some experiments on the influence of the beam-trawl on the bottom fauna. 1971/B:2. International Council for the Exploration of the Sea, Copenhagen, Denmark.
- de Groot, S. J., and H. J. Lindeboom, editors. 1994. Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea. Netherlands Institute for Sea Research, Den Burg, Texel, The Netherlands.
- Eleftheriou, A., and M. R. Robertson. 1992. The effects of experimental scallop dredging on the fauna and physical environment of a shallow sandy community. *Netherlands Journal of Sea Research* **30**: 289–299.
- Fonds, M. 1994. Mortality of fish and invertebrates in beam trawl catches and the survival chances of discards. Pages 131–146 in S. J. de Groot and H. J. Lindeboom, editors. Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea. Netherlands Institute for Sea Research, Den Burg, Texel, The Netherlands.
- Gaspar, M. B., C. A. Richardson, and C. C. Monteiro. 1994. The effects of dredging on shell formation in the razor clam *Ensis siliqua* from Barrinha, southern Portugal. *Journal of the Marine Biological Association of the United Kingdom* **74**:927–938.
- Graham, M. 1955. Effect of trawling on animals of the seabed. *Deep Sea Research, Suppl.* **3**:1–16.
- Grassle, J. F., and H. L. Saunders. 1973. Life-histories and the role of disturbance. *Deep Sea Research* **20**:643–659.
- Hall, S. J. 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanography and Marine Biology Annual Review* **32**:179–239.
- Hall, S. J., D. J. Basford, and M. R. Robertson. 1990. The impact of hydraulic dredging for razor clams *Ensis* sp. on an infaunal community. *Netherlands Journal of Sea Research* **27**:119–125.
- Hall, S. J., M. R. Robertson, D. J. Basford, and R. Fryer. 1993a. Pit-digging by the crab *Cancer pagurus*: a test for long-term, large-scale effects on infaunal community structure. *Journal of Animal Ecology* **62**:59–66.
- Hall, S. J., M. R. Robertson, D. J. Basford, and S. Heaney. 1993b. The possible effects of fishing disturbance in the northern North Sea: an analysis of spatial patterns in community structure around a wreck. *Netherlands Journal of Sea Research* **31**:201–208.
- Hall-Spencer, J.M. 1995. Evaluation of the direct impact of fishing gears on the substratum and on the benthos. Final project report to DGXIV (Directorate General). European Commission, Brussels, Belgium.
- Heessen, H. J. L., and N. Daan. 1996. Long-term trends in ten non-target North Sea fish species. ICES (International Council for the Exploration of the Sea) *Journal of Marine Science* **53**:1063–1078.
- Hill, A. S., A. R. Brand, U. A. W. Wilson, L. O. Veale, and S. J. Hawkins. 1996. Estimation of by-catch composition and annual by-catch mortality on Manx scallop fishing grounds. Pages 111–115 in S. P. R. Greenstreet and M. L. Tasker, editors. *Aquatic predators and their prey*. Blackwell Scientific Publications, Oxford, United Kingdom.
- Jennings, S., and M. J. Kaiser. 1998. The effects of fishing on marine ecosystems. *Advances in Marine Biology* **34**:201–351.
- Kaiser, M. J. 1996. Starfish damage as an indicator of trawling intensity. *Marine Ecology Progress Series* **134**:303–307.
- Kaiser, M. J., and B. E. Spencer. 1994. Fish scavenging behaviour in recently trawled areas. *Marine Ecology Progress Series* **112**:41–49.
- Kaiser, M. J., and B. E. Spencer. 1995. Survival of by-catch from a beam-trawl. *Marine Ecology Progress Series* **126**:31–39.
- Kaiser, M. J., and K. Ramsay. 1997. Opportunistic feeding by dabs within areas of trawl disturbance: possible implications for increased survival. *Marine Ecology Progress Series* **152**:307–310.
- Kaiser, M. J., and B. E. Spencer. 1996a. The effects of beam-trawl disturbance on infaunal communities in different habitats. *Journal of Animal Ecology* **65**:348–358.
- Kaiser, M. J., and B. E. Spencer. 1996b. Behavioural responses of scavengers to beam trawl disturbance. Pages 117–123 in *Aquatic predators and their prey*. S. P. R. Greenstreet and M. L. Tasker, editors. Blackwell Scientific Publications, Oxford, United Kingdom.
- Kaiser, M.J., et al. 1996. An estimate of fishing gear disturbance intensities in the Irish Sea: a comparison of beam trawling and scallop dredging. *Aquatic Conservation: Marine and Freshwater Ecosystems* **6**:269–287.
- Kaiser, M. J., D. B. Edwards, P. J. Armstrong, K. Radford, N. E. L. Lough, R. P. Flatt, and H. L. Jones. 1998. Changes in megafaunal benthic communities in different habitats after trawling disturbance. ICES (International Council for the Exploration of the Sea) *Journal of Marine Science* **55**:353–362.
- Lindeboom, H. J. 1995. Protected areas in the North Sea: an absolute need for future marine research. Pages 591–602 in H. D. Franke and K. Luening, editors. *The challenge to marine biology in a changing world*. Biologische Anstalt Helgoland, Hamburg, Germany.

- Lindeboom, H. J., and S. J. de Groot. 1998. The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystems. Report no. 1. Netherlands Institute for Sea Research, Den Burg, Texel, The Netherlands.
- MacDonald, D. S. 1993. Ecological studies on the effects of scallop dredging on the benthos of the north Irish Sea. Ph.D. thesis, University of Liverpool, United Kingdom.
- Margetts, A. R., and J. P. Bridger. 1971. The effect of a beam trawl on the seabed. CM 1971/B:8. International Council for the Exploration of the Sea, Copenhagen, Denmark.
- North Sea Task Force. 1993. North Sea quality status report. Olsen & Olsen, Fredensborg, Denmark.
- Oliver, R. S., and P. N. Slattery. 1985. Destruction and opportunity on the sea floor: effects of gray whale feeding. *Ecology* **66**:1965-1975.
- Pearson, T. H., A. B. Josefson, and R. Rosenberg. 1985. Petersen's stations revisited. I. Is the Kattegatt becoming eutrophic? *Journal of Experimental Marine Biology and Ecology* **92**:157-206.
- Philippart, C. J. M. 1998. Long-term impacts of bottom fisheries on several by-catch species of demersal fish and benthic invertebrates. ICES (International Council for the Exploration of the Sea) *Journal of Marine Science* **55**:342-352.
- Posey, M., W. Lindberg, T. Alphin, and F. Vose. 1996. Influence of storm disturbance on an offshore benthic community. *Bulletin of Marine Science* **59**:523-529.
- Ramsay, K., and M. J. Kaiser. 1998. Demersal fishing increases predation risk for whelks *Buccinum undatum* (L.). *Journal of Sea Research* **39**:299-304.
- Ramsay, K., M. J. Kaiser, and R. N. Hughes. 1996. Changes in hermit crab feeding patterns in response to trawling disturbance. *Marine Ecology Progress Series* **144**:63-72.
- Ramsay, K., M. J. Kaiser, and R. N. Hughes. 1997a. A field study of intraspecific competition for food in hermit crabs (*Pagurus bernhardus*). *Estuarine Coastal and Shelf Science* **44**:213-220.
- Ramsay, K., M. J. Kaiser, and R. N. Hughes. 1998. The responses of benthic scavengers to fishing disturbance in different habitats. *Journal of Experimental Marine Biology and Ecology* **224**:73-89.
- Ramsay, K., M. J. Kaiser, P. G. Moore, and R. N. Hughes. 1997b. Consumption of fisheries discards by benthic scavengers: utilisation of energy subsidies in different marine habitats. *Journal of Animal Ecology* **66**:884-896.
- Rees, E. I. S., A. Nicholaidou, and P. Laskaridou. 1977. The effects of storms on the dynamics of shallow water benthic associations. Pages 465-474 in B. F. Keegan, P. O. Ceidigh, and P. J. S. Boaden, editors. *Biology of benthic organisms*. Pergamon, Oxford, United Kingdom.
- Riesen, W., and K. Reise. 1982. Macrobenthos of the subtidal Wadden Sea: revisited after 55 years. *Helgolander Meeresuntersuchungen* **35**:409-423.
- Rijnsdorp, A. D., and P. I. van Leeuwen. 1996. Changes in growth of North Sea plaice since 1950 in relation to density, eutrophication, beam-trawl effort, and temperature. ICES (International Council for the Exploration of the Sea) *Journal of Marine Science* **53**:1199-1213.
- Rijnsdorp, A. D., A. M. Buijs, F. Storbeck, and E. Visser. 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 (International Council for the Exploration of the Sea) *Journal of Marine Science* **55**:403-419.
- Rumohr, H., and P. Krost. 1991. Experimental evidence of damage to the benthos by bottom trawling with special reference to *Arctica islandica*. *Helgolander Meeresuntersuchungen* **33**:340-345.
- Shepherd, S. A. 1983. The epifauna of megaripples: species' adaptations and population responses to disturbance. *Australian Journal of Ecology* **8**:3-8.
- ten Hallers-Tjabbes, C. C., J. M. Everaarts, B. P. Mensink, and J. P. Boon. 1996. The decline of the North Sea whelk (*Buccinum undatum* L.) between 1970 and 1990: a natural or a human-induced event? *Marine Ecology* **17**:333-343.
- Thiel, H., and G. Schriever. 1990. Deep-sea mining, environmental impact and the DISCOL project. *Ambio* **19**:245-250.
- Tuck, I. D., S. J. Hall, M. R. Robertson, E. Armstrong, and D. J. Basford. 1998. Effects of physical trawling disturbance in a previously un-fished sheltered Scottish sea loch. *Marine Ecology Progress Series* **162**:227-242.
- Welleman, H. 1989. De verspreiding van een aantal macrobenthos soorten in de Noordzee. Report no. 1. Netherlands Institute for Sea Research, Den Burg, Texel, The Netherlands.
- Witbaard, R., and R. Klein. 1994. Long-term trends on the effects of the southern North Sea beamtrawl fishery on the bivalve mollusc *Arctica islandica* L. (Mollusca, bivalvia). ICES (International Council for the Exploration of the Sea) *Journal of Marine Science* **51**:99-105.

