

Modification of marine habitats by trawling activities: prognosis and solutions

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Abstract

Fishing affects the seabed habitat worldwide on the continental shelf. These impacts are patchily distributed according to the spatial and temporal variation in fishing effort that results from fishers' behaviour. As a consequence, the frequency and intensity of fishing disturbance varies among different habitat types. Different fishing methodologies vary in the degree to which they affect the seabed. Structurally complex habitats (e.g. sea-grass meadows, biogenic reefs) and those that are relatively undisturbed by natural perturbations (e.g. deep-water mud substrata) are more adversely affected by fishing than unconsolidated sediment habitats that occur in shallow coastal waters. These habitats also have the longest recovery trajectories in terms of the recolonization of the habitat by the associated fauna. Comparative studies of areas of the seabed that have experienced different levels of fishing activity demonstrate that chronic fishing disturbance leads to the removal of high-biomass species that are composed mostly of emergent seabed organisms. Contrary to the belief of fishers that fishing enhances seabed production and generates food for target fish species, productivity is actually lowered as fishing intensity increases and high-biomass species are removed from the benthic habitat. These organisms also increase the topographic complexity of the seabed which has been shown to provide shelter for juvenile fishes, reducing their vulnerability to predation. Conversely, scavengers and small-bodied organisms, such as polychaete worms, dominate heavily fished areas. Major changes in habitat can lead to changes in the composition of the resident fish fauna. Fishing has indirect effects on habitat through the removal of predators that control bio-engineering organisms such as algal-grazing urchins. Fishing gear resuspend the upper layers of sedimentary seabed habitats and hence remobilize contaminants and fine particulate matter into the water column. The ecological significance of these fishing effects has not yet been determined but could have implications for eutrophication and biogeochemical cycling. Simulation results suggest that the effects of low levels of trawling disturbance will be similar to those of natural bioturbators. In contrast, high levels of trawling disturbance cause sediment systems to become unstable due to large carbon fluxes between oxic and anoxic carbon compartments. In low energy habitats, intensive trawling disturbance may destabilize benthic system chemical fluxes, which has the potential to propagate more widely through the marine ecosystem. Management regimes that aim to incorporate both fisheries and habitat conservation objectives can be achieved through the appropriate use of a number of approaches, including total and partial exclusion of towed bottom fishing gears, and seasonal and rotational closure techniques. However, the inappropriate use of closed areas may displace fishing activities into habitats that

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are more vulnerable to disturbance than those currently trawled by fishers. In many cases, the behaviour of fishers constrains the extent of the impact of their fishing activities. Management actions that force them to redistribute their effort may be more damaging in the longer term.

Keywords closed areas, fisheries, habitat modification, management regimes, trawling

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Introduction

It is now well established that bottom-fishing activities that involve the use of mobile gear have a physical impact upon the seabed and the biota that lives

there. However, the ecological significance of these fishing disturbances for the immediate and wider ecosystem are coloured by differing views on their importance (e.g. Dayton *et al.* 1995; Kaiser 1998; Watling and Norse 1998; Kaiser and De Groot 2000; Kaiser and Jennings 2001; Thrush *et al.* 2002). The

wider ecosystem effects of fishing activities on the marine environment are widely considered to be crucial considerations in any future management plans (see Benaka 1999). The inclusion of ecosystem considerations in future fisheries management has become known as the 'ecosystem approach'. The objectives of the ecosystem approach to fisheries management vary in their definition and are themselves the subject of much discussion; indeed, many argue that effective single species management would ultimately achieve many ecosystem goals (Gislason *et al.* 2000). The ecosystem effects of fishing include: changes in predator-prey relationships leading to shifts in food-web structure that are not necessarily reversed by the reduction of fishing pressure (alternative stable states); effects on abundance and body-size distributions that can result in a fauna dominated by small body-sized individuals; genetic selection for different physical characteristics and reproductive traits (e.g. earlier age-at-maturity); effects on populations of nontarget species (e.g. cetaceans, birds, reptiles and elasmobranch fishes) as a result of by-catches or ghost fishing; reduction of habitat complexity, resuspension of surficial sediments and the alteration of benthic community structure. In this review we have focused our attention on the modification of benthic habitat by fishing activities, although it is necessary to appreciate that all of the fishing effects listed above can occur simultaneously and may have important additive effects at many scales. The increasing awareness of the effects of fishing on seabed communities is reflected by the increase in the research effort that has addressed these issues (for reviews see Dayton *et al.* 1995; Jennings and Kaiser 1998; Kaiser 1998; Watling and Norse 1998; Auster and Langton 1999; Kaiser and De Groot 2000). This continues to develop rapidly, although some stagnation has occurred with a tendency for some researchers to repeat the pulse type of experiments that were performed in the early and mid 1990s. Recent studies have increasingly focused on management techniques that may alleviate both the effects of fishing on target species and the impact on the seabed (Collie *et al.* 1997; Kaiser *et al.* 2000a; Murawski *et al.* 2000).

Marine habitats and demersal fishing

Definitions of the term 'habitat' in the ecological literature vary somewhat, but there is a general consensus that it entails the description of some key environmental features related to a species or communities distribution. Overlaid on the notions of

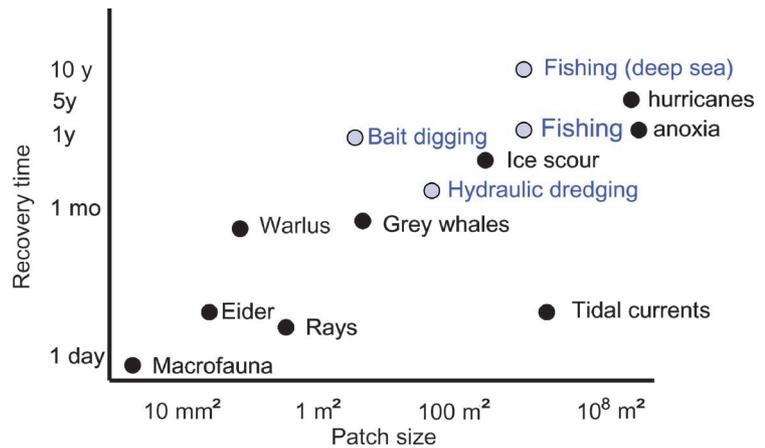
habitat arising primarily from the physical structure of the abiotic environment (e.g. sediment grain size, water flow, nutrient status) are the notions of habitat structure or architecture, provided by the resident animals and plants themselves. The effects of fishing on both the abiotic and biotic environment are of concern. For conservation the concept of the habitat is extremely important because efforts are largely directed at the classification, evaluation and preservation of representative areas including threatened species or their habitats.

With respect to fishing, discussion of effects on habitat is most appropriately applied to benthic communities because it is clearly more difficult to imagine that the pelagic habitat could be affected by fishing (although the effects of trawling on patterns of nutrient regeneration may lead to changes – see below). Perhaps because they are the most widely used demersal fishing gears, it is the effect of trawls on benthic habitats that has drawn most attention. The ubiquity of trawling is revealed by a recent analysis where catches were mapped to country continental shelves (refer to the effort data that Ian did for the Montpellier conference); trawling and dredging activity was reported from 19 984 200 km² of country continental shelves, which represents about 75% of the global continental shelf. Although there is significant variation in catch density (catch by a country divided by the area of continental shelf), it is clear that demersal trawling and dredging is an ubiquitous global activity on continental shelves. However, although mobile fishing gears are the major concern on a global scale, other physically destructive practices such as dynamite fishing or the 'muro-ami' fishery of the Philippines (Carpenter 1977), which employs stones, chains or poles to break up coral and drive fish out into nets, are also locally important. Below, we review the known and potential effects that fishing gears may have on the structure of marine habitats.

Putting fishing disturbance into context

The majority of seabed (demersal) fishing activity is undertaken in shallow seas on the continental shelf at depths of less than 200 m. However, as traditional stocks of fish dwindle, fishers have moved their attention to previously unexploited species. As a result, bottom trawling occurs around sea mounts and on the continental-shelf slope at depths greater than 1000 m. Benthic communities experience continual disturbance at various scales in time and space (for

Figure 1 The relative recovery rate of different scales of disturbance that occur in the marine environment. The figure shows various forms of fishing activity compared with naturally occurring disturbances such as predation effects and physical sources of disturbance (after Hall 1994).



more detail see Hall 1994 and Hall *et al.* 1994). In general, shallow continental-shelf sea environments experience more frequent disturbances than deeper sea environments that are not exposed to wave action and strong currents. Large-scale natural disturbances, such as seasonal storms and regular (daily) scouring by tidal currents, form a background against which other smaller disturbances occur, such as those induced by predator feeding activities (Fig. 1). The additive effects of many small-scale disturbances may oblit-

erate larger, but less frequent disturbance events (e.g. Hall *et al.* 1993). Thus, for fishing disturbance of the seabed to have an ecologically significant impact it must exceed the background levels and frequency of natural disturbance. It is important to consider the relative scale at which fishing disturbance occurs. Given a similar habitat, very intensive but highly localized fishing disturbance may have fewer ecological implications than less intense, but wide-spread fishing disturbance (Fig. 2). Many empirical studies of fishing

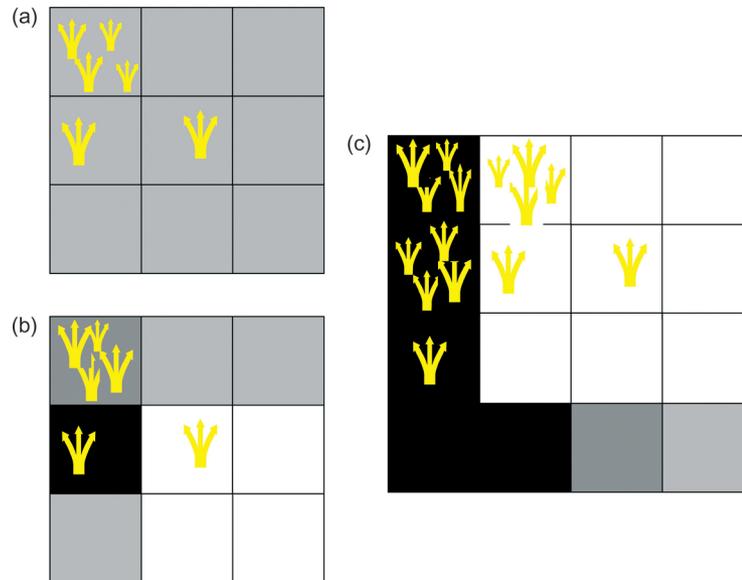


Figure 2 Three different scenarios of fishing disturbance intensity on the seabed in relation to the distribution of biogenic fauna (indicated by the three pronged trees). (A) A uniform distribution of fishing effort affects all areas of the seabed to the same extent; (B) a patchy distribution of effort, which is more representative of current fishing practices, has more severe effects on some patches of habitat but leaves others totally unaffected; (C) a scenario in which a total closure to fishing is imposed displacing fishing activity to the outside edges of the closed area (see Rijnsdorp *et al.* 2001). In this scenario, this inadvertently results in fishing disturbance occurring in a greater proportion of sensitive biogenic habitat. Black panels indicate intensive fishing, increasingly lighter grey panels indicate less intensive fishing, white panels indicate no fishing.

disturbance have failed to detect the anticipated reductions in many species. This is probably explained by the tendency of scientists to examine one-off pulse disturbance events as opposed to the effects of chronic disturbance (Tuck *et al.* 1998) that is probably more representative of commercial fishing practices (Rijnsdorp *et al.* 1998; Murawski *et al.* 2000).

In any particular habitat, the associated fauna and flora will presumably have adaptations or life styles that enable them to persist in that environment. In other words, most communities have an inherent resilience to a certain level of natural physical disturbance, although periodic extreme events can lead to widespread kills of biota (e.g. Rees *et al.* 1977). However, the scale and frequency of anthropogenic physical disturbance events may 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. Shallow-water communities on exposed coastlines are likely to be the most resilient to physical disturbance from bottom fishing (Fig. 3). For example, 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. Nevertheless, there are situations in which the associated fauna can increase the inherent stability of supposedly unstable habitats. For example, dense aggregations of spionid worms can increase the stability of intertidal sediments through their ability to bind sediment particles together (Thrush *et al.* 1996). There is no doubt that as habitat stability increases the relative effects of fishing will also increase as will the longevity and severity of its ecological effects (Thiel and Schriever 1990; Kaiser and Spencer 1996; Auster and Langton 1999). A single passage of a bottom trawl through a rich epifaunal community of filter-feeding organisms at a depth of 100 m will certainly have longer-term effects than the passage of the same gear through a mobile sand habitat at a depth of 10 m (Kaiser 1998; Collie *et al.* 2000).

Physical disturbance of marine habitats

Any fishing gear that is towed over the seabed will disturb the sediment and the resident community to some degree. Hence, it is pertinent to ask what these gears do to the physical structure of the unconsolidated sedimentary environment? In addressing this question, it is important to recognize at the outset that the intensity of disturbance and its magnitude relative to other disturbance agents will depend on the details of the gear, sediment type, water depth and other factors (see above). Although the details for many combinations of gear and sediment type remain unexamined, we probably know enough to arrive at a qualitative ranking under most circumstances. In general, the various types of shellfish dredge, rock-hopper otter trawls and the heavy flatfish beam trawls disturb the seabed most intensely, whereas for lighter gears such as smaller otter and prawn trawls, disturbance is largely restricted to the trawl boards. (It should be noted, however, that in areas where erect sponges and other biogenic structure are present, the warps and foot rope of even these lighter gears can detach individuals from the seabed – see below). Similarly, sandy substrata in higher energy environments are likely to be less affected by the physical impact of fishing gear for as long as physically stable muddy sediments. Although they also often occur in higher energy regimes, hard substrata are also likely to be vulnerable owing to the generally higher abundance of encrusting and erect biota that are damaged by trawls.

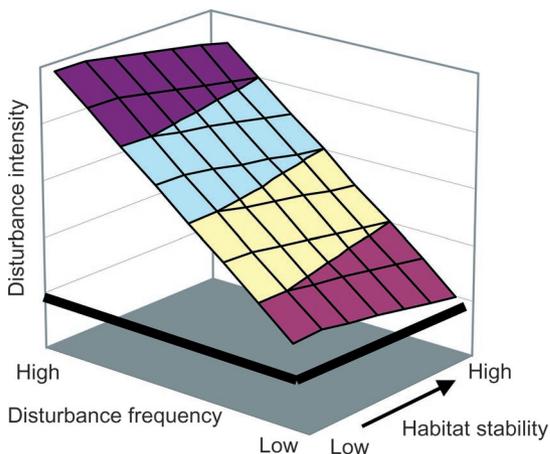


Figure 3 A simple model to illustrate the relative importance of a constant level of fishing disturbance (given an arbitrary value on the *y*-axis) in different habitats (habitat stability) that are subjected to different frequencies or levels of natural disturbance. As levels of natural disturbance decline, fishing disturbance accounts for a greater proportion of the total disturbance experienced and becomes increasingly important (adapted from Jennings and Kaiser 1998).

Alteration of surface topography

Perhaps the most obvious change that trawling can cause is in surface topography. Trawl tracks are readily apparent on sidescan sonar records taken on fishing grounds, and their frequency of occurrence has been used by a number of authors to estimate the intensity of trawl disturbance (e.g. Caddy 1973; Krost *et al.* 1990; Bergman and Hup 1992). Other acoustic methods have also been used to evaluate changes in surface topography after experimental trawling (e.g. Schwinghamer *et al.* 1996; Tuck *et al.* 1998). Using such methods, the general conclusion is that trawling increases surface roughness owing to the furrowing caused by trawl doors. An issue of scale is important here, however, because at a slightly smaller scale trawls generally lower surface topography by smoothening ripples, and mounds and other structures created either by fauna or the physical environment. This combination of changes should, perhaps, be viewed as the replacement of a landscape with widespread, small-scale, low-relief topographic features (ripples and mounds) with a rather smoother landscape, interspersed with higher relief, but less frequent features caused by the ploughing of trawl doors.

Paradoxically, it may be the loss of smaller scale features that should be of most concern. Currie and Parry (1996), for example, reported clear visible changes following scallop dredging which persisted for about a year. For the most part, these changes were associated with the destruction of mounds and depressions caused by the burrowing activities of Callinassid shrimps. In turn, this flattening led to the removal of unattached weed and seagrass which tends to accumulate around such features. The spatial heterogeneity that mounds and patches of organic matter provide is often considered to be an important factor controlling the diversity and species composition of benthic infaunal communities (e.g. Hall 1994), so their destruction would be expected to have effects. In addition, we know from field observations and experimental studies that juveniles of demersal fish on continental shelves might benefit from a high abundance of relatively small physical features (sponges, empty shells, small rocks, etc.) (Gotceitas and Brown 1993; Walters and Juanes 1993; Auster *et al.* 1997). Over time trawling can be expected to gradually lower the physical relief of the habitat with potentially deleterious consequences for some fish species. Such effects may account for notable increases in the dominance of flatfish in both tropical

and temperate systems (Hall 1999). Indeed, recent analyses that have related habitat complexity to fish assemblage composition suggest that habitat degradation would favour flatfishes such as Dover sole that are chemosensory over visual predators such as dabs and plaice that feed on mobile fauna associated with a low level of habitat complexity (Kaiser *et al.* 1999).

Effects of sediment resuspension

The direct physical contact of fishing gear with the substratum can lead to the resuspension of sediments and the fragmentation of rock and biogenic substrata. To date few studies have directly examined the potential ecological consequences of sediment resuspension attributed to trawling activities. Most studies have been focused on the effects of fishing on sediment biota. It is our opinion that studies that examine the contribution of fishing to sediment resuspension are urgently required.

The resuspension, transport and subsequent deposition of sediment may affect the settlement and feeding of the biota in other areas. Sediment resuspended as a result of bottom fishing will have a variety of effects including: the release of nutrients held in the sediment (Duplisea *et al.* 2002), exposure of anoxic layers, release of contaminants (see Olive 1993), increasing biological oxygen demand (Reimann and Hoffman 1991), smothering of feeding and respiratory organs. The quantity of sediment resuspended by trawling depends on sediment grain size and the degree of sediment compaction which is higher on mud and fine sand than on coarse sand.

Resuspended sediments must subsequently resettle, either *in situ* or after transport by water currents. Only a few estimates of the magnitude of these processes have been made (e.g. Churchill 1989; Pilskaln *et al.* 1998). Churchill (1989), for example, estimated that coarse sand was typically penetrated to a depth of 1 cm by otter boards, which resuspended approximately 39 kg sediment s⁻¹, whereas the figures for fine sand and muddy sand were 2 cm (78 kg s⁻¹) and 4 cm (112 kg s⁻¹), respectively. After monitoring salinity and suspended sediment load over a 3-month period at a 125-m deep site in the Middle Atlantic Bight, Churchill (1989) concluded that most of the suspended sediment load was advected from inshore. Storms in shallower water accounted for most of the suspended sediment pulses except for the most dramatic events during the fishing season, which coincided with intense fishing activity.

Transmissiometers that measure background light levels in water, frequently recorded the highest levels of turbidity during periods of trawling activity off the north-east coast of the United States (Churchill 1989). In deeper water where storm-related bottom stresses have less influence, otter trawling activity contributed significantly to the resuspension of fine material. Churchill (1989) calculated the sediment budget for certain areas of the mid-Atlantic Bight and concluded that trawling was the main factor that accounted for the offshore transport of sediment at depths between 100 and 140 m. However, Churchill (1989) calculated that the transport of sediment that resulted from fishing activities would not produce significant large-scale erosion over a period of a few years. However, Churchill (1989) made no inferences regarding the potential biological impact of this sediment transport.

Palanques *et al.* (2001) have undertaken the first observations of the sedimentological consequences of trawling on continental-shelf sediments. They used moored instruments and transmissiometers to quantify the effect of an experimentally fished otter trawl on the fine-mud sediment in water 20–40 m deep off the coast of Barcelona, Spain. They found that the disruption of the surface layers of the sediment led to elevated levels of tidally resuspended sediment for up to 5 days after the trawl disturbance event. The furrows made by the otter boards remained evident for at least one year after the initial disturbance which corroborates other similar examinations of trawl marks in muddy sediments (e.g. Tuck *et al.* 1998). The furrows made by trawling in these sediments have the potential to significantly increase topographic complexity. The ecological significance of this change to seabed surface is unknown.

The superficial physical effects of sediment resuspension are clearer in deep-water environments that are relatively unperturbed. Thiel and Schriever (1990) experimentally harrowed an area of seabed at a depth of 4000 m. Their observations revealed that 80% of their study site was covered by fine material that had settled out from the resultant sediment plume. Although this study was designed to imitate the effects of deep-sea mining, the observations are, nevertheless, relevant for deep-sea trawling activities. More recently, Roberts *et al.* (2000) undertook a photographic survey of the continental slope off the north-west of Scotland between depths of 700–1300 m. They also studied photographic material from a survey of the same area that had been undertaken in 1988. Evidence of scouring on the soft

sediment seabed was apparent in both periods which indicated that the continental slope in this region has been subject to disturbance for at least 10 years. In addition, they found that trawl disturbance was patchily distributed on the seabed as marks were evident in between 2 and 47% of the photographs taken on separate surveys. The observations of the sediment resuspension in the deep sea may have a similar effect to the seasonal settlement of organic material that occurs in deep-sea regions (Angel and Rice 1996).

Given that bottom trawling can lead to large-scale resuspension and transport of sediment it is reasonable to ask whether fishing changes the particle size distribution or the internal structure of sediments. One might imagine, for example, that finer sediments would be washed out and transported further by water currents, leading to a gradual coarsening of median sediment grain size. Little data are available to address this question, but efforts to use acoustic methods for evaluating changes to sediment structure have recently been developed (Schwinghamer *et al.* 1996). The results of an experimental trawling study on hard-packed sand described in Schwinghamer *et al.* (1996) indicated that trawling decreased the fractal geometry (structural complexity) of the internal sediment structure at millimetre scales – a characteristic that was not revealed by analysis of bulk sediment properties. The authors suggested that such changes might be due to collapse of burrow structures and sediment voids caused by fauna and that the structural change might affect exchange processes with overlying water column. In follow-up studies, however, acoustic estimates of internal sediment structure gave inconsistent results that were difficult to interpret with respect to experimental trawling (Schwinghamer *et al.* 1996). Similarly, changes in bulk sediment properties showed large spatial and temporal variability. On balance, it would appear that the kinds of changes in sediment structure due to trawling may be rather subtle compared to changes due to other factors.

Effects on biogeochemical processes

Bottom trawling is a key source of physical disturbance in shallow shelf seas, but little is known of the effects of trawling disturbance on functional processes despite the expectation that sediment community function, carbon mineralization and biogeochemical fluxes will be strongly affected by trawling disturbance. This is because trawling

reduces the abundance of bioturbating macrofauna that play a key role in biogeochemical processes and because the physical mixing by trawling, unlike the mixing by macrofauna, does not contribute directly to community metabolism (Duplisea *et al.* 2002). The relative impacts of trawling disturbance on biogeochemical fluxes in sediments are likely to depend on the relationship between trawling and natural disturbance. In shallow turbid regions such as the southern North Sea, wave and tidal action leads to bulk sediment disturbance/transport and the effects of trawling are likely to be negligible. Moreover, the fauna living in these areas are likely to be well adapted to continual disturbance and more resilient to the effects of trawling. Conversely, in deeper areas with less natural disturbance, such as parts of the central North Sea, trawling disturbance is likely to account for a significant proportion of total disturbance.

Duplisea *et al.* (2002) used an existing simulation model of a generalized soft sediment system to examine the effects of trawling disturbance on carbon mineralization and chemical concentrations. They contrasted the effects of a natural scenario, where bioturbation increases as a function of macrobenthos biomass, with those of a trawling disturbance scenario where physical disturbance results from trawling rather than the action of bioturbating macrofauna (which are killed by the action of the trawl gear). Simulation results suggest that the effects of low levels of trawling disturbance will be similar to those of natural bioturbators but that high levels of trawling disturbance cause the system to become unstable due to large carbon fluxes between oxic and anoxic carbon compartments. The presence of macrobenthos in the natural disturbance scenario stabilizes sediment chemical storage and fluxes because the macrobenthos are important participants in the total community metabolism. In soft sediment systems where physical disturbance due to waves and tides is low, they suggested that intensive trawling disturbance might destabilize benthic system chemical fluxes, and that this instability had the potential to propagate more widely through the marine ecosystem.

Nutrient regeneration – effects on pelagic habitats?

Work reviewed by Cloern (2001) provides convincing evidence for an increase in the nutrient levels of coastal ecosystems over the last half of the 20th

Century, driven largely by the nutrient loading of river systems from industrial and agricultural activity. There seems little doubt that it is this signal that dominates the anthropogenic influences on geochemical processes in coastal ecosystems. In the scheme of things the nutrient regeneration effected by trawling is likely to be much more limited, although not necessarily insignificant at a local scale.

Expected influences of nutrient regeneration from trawling should also be tempered by recent comparative analysis of the dose–response relationship between nutrient inputs and algal biomass in freshwater and marine systems (Cloern 2001). While lake systems usually show a tight positive correlation between nutrient loading and algal biomass or primary production, this does not seem to hold in the marine domain. In a review of 51 estuarine systems, for example, Borum and SandJensen (1996) found that only 36% of the variance in phytoplankton primary production is correlated with the N loading rate. Similarly, Meeuwig (1999) showed that chlorophyll yield per unit of N delivered was 10 times lower in small nonstratified estuarine systems compared to lakes.

In the present context, perhaps of greater significance than the contrast between freshwater and marine systems, is the difference between particular coastal environments. Evidence presented by Cloern (2001) has illustrated how different systems respond in quite different ways to alterations in nutrient inputs. For example, Chesapeake Bay shows marked increases in phytoplankton biomass and high likelihood of anoxia of bottom waters owing to nutrient enrichment, whereas San Francisco Bay shows no such response despite greater levels of nutrient supply. Clearly, the cycling of nutrients differs markedly in these two systems and we should not expect, therefore, to arrive at a generic model of how resuspension by trawling might impact on a given system. In speculating on the issue, however, it is important to recognize that a number of inherent biological and physical attributes operate in concert to determine the level of response we should expect in any given situation. These factors include tidal energy, horizontal transport processes (residence times), the optical properties of the water column and the density of suspension feeders (Cloern 2001). The importance of last of these implies that in some circumstances, fishing could play an important indirect role in patterns of nutrient cycling in addition to a direct role through sediment resuspension. It is noteworthy, for example, that chlorophyll a concentration in Canadian

estuaries is best predicted by the biomass of mussels, rather than any quantity related to nutrient fluxes or concentrations (Meeuwig 1999). The removal of mussels by fishing, therefore, could have a significant impact on the nutrient dynamics in these systems. Similar conclusions have been drawn concerning the fishery for oysters and its effects on water quality in Chesapeake Bay (Costanza and Greer 1998). Whether the shifts in community structure that have been observed on continental shelves from bivalve to polychaete domination are sufficiently large to also affect nutrient dynamics is an open question, but one that warrants further investigation.

Effects of fishing on the habitat: a global analysis

The short-term effects of fishing on seabed biota are well documented in recent studies (see Jennings and Kaiser 1998; Kaiser and De Groot 2000; for reviews). The results from short-term studies are informative and often have confirmed our expectations of the type of changes that might occur as a result of fishing activity. Nevertheless, the usefulness of each study on its own is limited by factors such as the specific location, type of gear used and season during which the study in question was undertaken. Viewed on their own, these individual studies can only be used to predict the outcome of fishing activities in a restricted number of situations. However, Collie *et al.* (2000) overcame this problem by extracting summary data from a population of fishing impact studies and undertook a meta-analysis (e.g. Gurevitch and Hedges 1999) of the combined data. Their analysis aimed to reveal any consistent patterns in the responses of benthic organisms to fishing disturbance, whether the magnitude of this response varied with habitat, depth, disturbance type and among taxa, and how the recovery rate of organisms varied with these same factors. Collie *et al.* (2000) found that the magnitude of the immediate response (i.e. change in abundance or biomass) of organisms to fishing disturbance varied significantly according to the type of fishing gear used in the study, the habitat in which the study was undertaken, and among different taxa. Here, we explore the reasons for these observations in more detail.

Effects of different gears

The initial impacts of different fishing gears were mainly consistent with expectations. Intertidal dredging

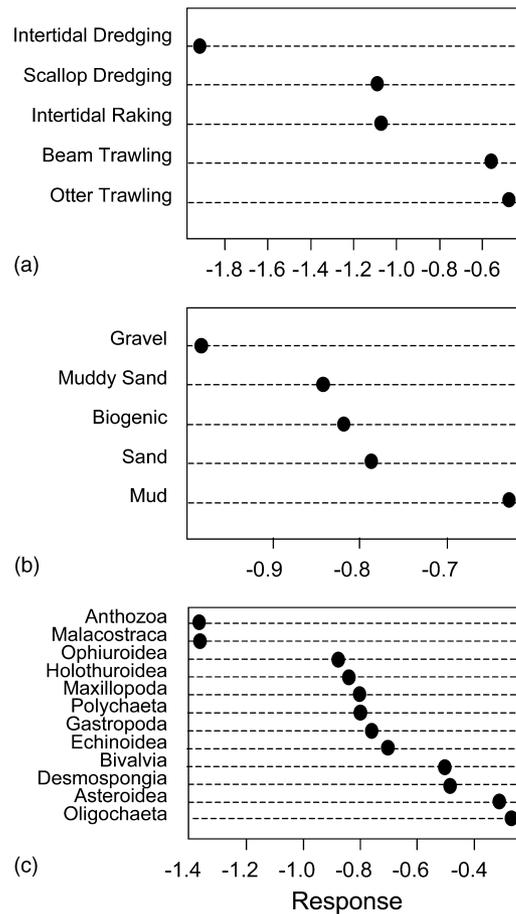


Figure 4 The predicted mean response derived from ANOVA of (a) the response of invertebrate abundance or biomass to different gear types; (b) the response of invertebrate abundance or biomass in different habitats; (c) the response of different taxa to physical disturbance that occurred immediately after that disturbance had occurred. Data are on a transformed scale where values correspond to percentage decline from control as follows: $-0.1 = 10\%$; $-0.22 = 20\%$; $-0.35 = 30\%$; $-0.5 = 40\%$; $-0.68 = 50\%$; $-1.35 = 75\%$; $-4.61 = 100\%$. In all cases, the initial response of the fauna was negative.

ging activities had a more marked effect than scallop dredging, which in turn had greater effects than otter trawling (Fig. 4). Although at first sight the apparent lack of effect from beam trawling is somewhat surprising, we suspect that the relative paucity of data for this gear is part of the explanation. It should also be borne in mind, however, that beam-trawling studies were generally conducted in relatively dynamic sandy areas, where initial effects may be less apparent or are less easily detected. Intertidal dredging is

likely to have the greatest initial effects on the biota because fishers are able to use the harvesting machinery accurately, working parallel lines along the shore. In contrast, fishers using towed nets in subtidal areas are unable to actually see precisely where their gear is fishing although technological advances in positioning systems are making it increasingly easier to achieve very accurate positioning of fishing gear on the seabed. It is also easier to study the impacts of intertidal fishing disturbances as the scientist can accurately collect samples from known (seen) impacted areas and adjacent undisturbed areas, whereas there is an inevitable chance of error when collecting subtidal samples. Otter trawling appears to have the least significant impact on fauna compared with other gears, although it is necessary to flag a few warnings about this observation. Firstly, it is the otter doors that hold the wings of the otter trawl open that have the greatest impact on the sediment habitat. However, the otter doors constitute a small proportion of the total width of the gear (c. 2 m cf. 40–60 m). Furthermore, none of the studies published at that time considered the effects of rockhopper otter trawls on seabed communities and these have been shown to have considerable negative short-term effects on emergent epifauna (Prena *et al.* 1999; McConnaughey *et al.* 2000; Pitcher *et al.* 2000).

Effects in different habitats

Several authors have suggested that the relative ecological importance of fishing disturbance will be related to the magnitude and frequency of background of natural disturbances that occur in a particular marine habitat (Kaiser 1998; Auster and Langton 1999). Certainly, it makes intuitive sense that organisms that inhabit unconsolidated sediments should be adapted to periodic sediment resuspension and smothering. Similarly, it seems plausible that organisms living in seagrass beds rarely experience repeated intense physical disturbances or elevated water turbidity as created by bottom fishing gears. Indeed, such intuition has been the cornerstone of hypotheses about impacts and recovery dynamics for benthos (e.g. Hall 1994; Jennings and Kaiser 1998). However, Collie *et al.* (2000) found that their initial impact results with respect to habitat were somewhat inconsistent among analyses. While the initial responses to fishing disturbance of taxa in sand habitats were usually less negative than in other habitats, a clear ranking for

expected impacts did not emerge (Fig. 4). Such inconsistencies may reflect interactions between the factors arising from the unbalanced nature of the data, with many combinations of gear and habitat absent. For example, the relatively low initial impact on mud habitats may be explained by the fact that most studies were done with otter trawls. If data were also available for the effect of dredgers on mud substrata, a more negative response for this habitat may have been observed. Nevertheless, it should be borne in mind that initial effects of disturbance may be hard to detect in mud communities that often have low abundances of biota which tend to be burrowed deep (10–200 cm) within the sediment. Presumably, the deeply burrowed fauna would be relatively well protected from the physical effects of disturbance, although the passage of the gear will cause their burrows to collapse. Whether these inconsistencies can be explained in this way can only await further study. It is also important to note that it is important not to classify habitats by the particular nature of the sediment. For example, intertidal sandflats inhabited by high densities of tubicolous worms such as spionids will be more stable (and hence, more adversely affected by fishing) than sandflats with relatively little infauna (Thrush *et al.* 1996).

Immediate effects on biota

Collie *et al.* (2000) found that the most consistently interpretable result within their meta-analysis was the vulnerability of fauna, with a ranking of initial impacts that concurred broadly with expectations based on morphology and behaviour. They undertook a regression tree analysis that perhaps provides the first quantitative basis for predicting the relative impacts of fishing under different situations. Following the tree from its root to the branches one can make predictions, for example, about how a particular taxon would be affected initially by disturbance from a particular fishing gear in a particular habitat. Thus, trawling would reduce anthozoa (anemones, soft corals, sea ferns) by 68%, whereas asteroid starfishes would only be reduced by 21%. Similarly, repeated (chronic) dredging is predicted to lead to 93% reductions for anthozoa, malacostraca (shrimps and prawns), ophiuroidea (brittlestars) and polychaeta (bristle worms), whereas a single (acute) dredge event is predicted to lead to a 76% reduction (Fig. 5). This approach might ultimately provide a useful quantitative framework for predicting instantaneous fishing impacts. However, it is probably more

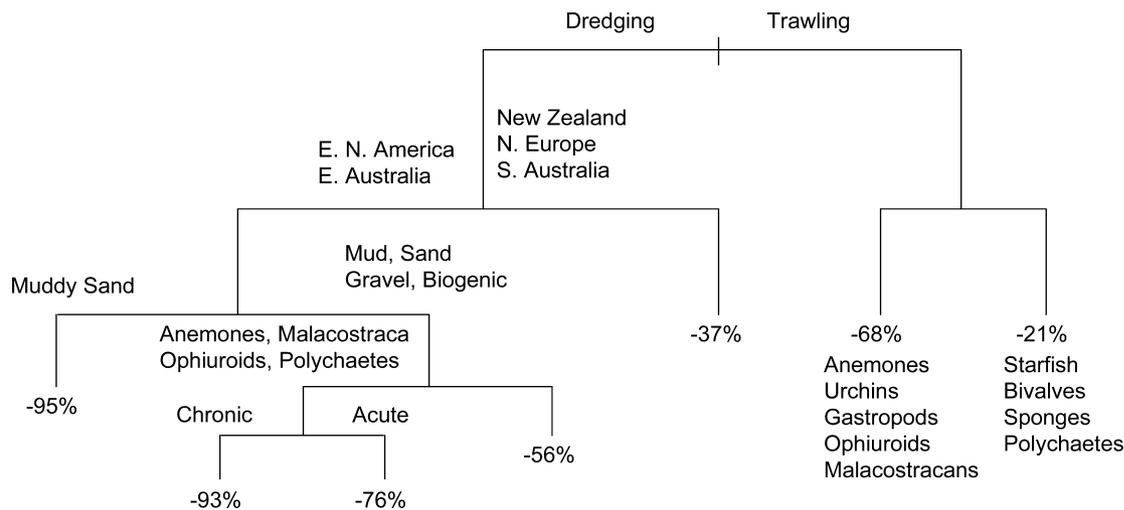


Figure 5 Regression tree of the data for the initial response of biota to fishing disturbance. A binary partitioning algorithm recursively splits the data in each node until the node is homogeneous or contains too few observations. The vertical height of each branch indicates the importance of that split. The number under each node is the mean response for that combination of variables. Working up from the root of the regression tree permits one to predict the response of a particular taxon to a particular type of fishing disturbance under particular scenarios (adapted from Collie *et al.* 2000).

useful to develop this approach for recovery rates of fauna and habitats (see below).

Recovery rates after trawl disturbance

Soft sediment habitats

From our perspective, the short-term effects of bottom-fishing disturbance on habitats and their biota are of interest but of far less ecological importance than the issue of the potential for recovery or restoration. The short-term outcome of disturbance experiments is often counter-intuitive and open to misinterpretation. Unfortunately, relatively few studies of trawl disturbance have included a temporal component of sufficient duration to address longer term changes that occur as a result of bottom fishing disturbance. This is almost certainly a result of the conflict between financial resources, project duration, statistical and analytical considerations. Nevertheless, Collie *et al.* (2000) were able to incorporate studies that included a recovery component into their analysis. This permitted them to speculate about the level at which physical disturbance becomes unsustainable in a particular habitat. For example, their study suggested that sandy sediment communities are able to recover within 100 days which implies that they could perhaps withstand two to three incidents of physical disturbance per

year without changing markedly in character (Fig. 6). If our recovery rate estimates for sandy habitats are realistic, this would suggest that areas of the seabed that are trawled more frequently than three times per year are held in a permanently altered state by the physical disturbance associated with fishing activities. As we discuss later, such levels of fishing disturbance exist in areas such as the North Sea and this outcome has important implications for predicting the outcome of management systems that may cause changes in the spatial pattern of seabed disturbance. This expectation is supported by a recent study that links the size and species composition of North Sea benthic communities to patterns of chronic beam-trawling disturbance (Jennings *et al.* 2001a). There was minimal evidence for trawling effects on size composition or benthic production in a series of sites trawled up to 2.3 times per year. However, at another series of sites trawled up to 6.5 times per year, the most heavily trawled sites were characterized by a fauna of low biomass and low production that consisted of very small individuals. Larger bivalves and burrowing sea urchins, that can dominate the biomass in infrequently trawled areas, were effectively absent (Jennings *et al.* 2001b).

At this point, it is important to acknowledge that there are some important limitations to the data compiled by Collie *et al.* (2000). First, the small spatial

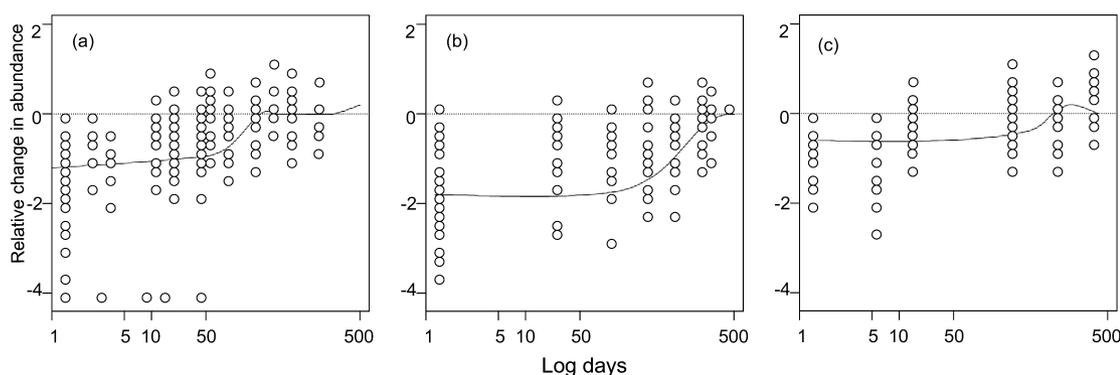


Figure 6 Results from a meta-analysis of the effects of fishing disturbance on benthic communities. The scatter plots of the relative change of all species (each datapoint represents the relative abundance of a different species on each different sampling date) in different habitats (a = sand, b = muddy sand, c = mud) at time intervals after the occurrence of a fishing disturbance. The fitted curves show the predicted time trajectory for recovery to occur. On the y -axis, 0 shows no relative change in abundance, negative values show a relative decrease in abundance (adapted from Collie *et al.* 2000).

scale of most of the trawl impact studies (the maximum width of most of the disturbed areas examined was < 50 m) made it likely that much of the recolonization was via active immigration into disturbed patches rather than reproduction within patches. Second, it should be noted that while we might accurately predict the recovery rate for small-bodied taxa such as polychaetes which dominate the data set, sandy sediment communities often contain one or two long-lived and, therefore, vulnerable species. Note, for example, the occurrence of the large bivalve *Mya arenaria* in the intertidal zone of the Wadden Sea. While the majority of the benthos in this environment recovered within 6 months of lugworm dredging, the biomass of *M. arenaria* remained depleted for at least 2 years afterwards (Beukema 1995). This delayed recovery of larger-bodied organisms is, no doubt, even more important in habitats that are formed by living organisms (e.g. soft corals, sea fans, mussels), as the habitat recovery rate is directly linked to the recolonization and growth rate of these organisms. By now, there is sufficient evidence in the literature to suggest that under conditions of repeated and intense bottom-fishing disturbance a shift from communities dominated by relatively high-biomass species towards dominance by high abundance of small-sized organisms is likely to occur (e.g. Kaiser *et al.* 2000a,b).

Effects on biogenic structure

The benthic communities with which human beings identify most strongly are those that are character-

ized by a rich epifauna that provides abundant biogenic structure. Coral reefs are the exemplar, but sponge gardens, calcareous algae, or maerl beds and various hard substratum communities are all valued targets for conservation. There is little doubt that put in the path of a trawl or subjected to dynamite or 'muro-ami' fishing, these communities are at risk. It is somewhat surprising, therefore, that there have been relatively few studies that examine the effects of trawling for such biogenic habitats, or the rates of recovery. In their meta-analysis of 57 trawl impact studies, Collie *et al.* (2000) found only 10 studies that focused on biogenic habitats and of these, only four contained data suitable for analysis. Part of the reason for this lack of studies is understandable because the vast majority of trawling occurs in sandy habitats where biogenic structure is absent. It should be noted, however, that even in these sandy habitats, smaller scale patches of biogenic habitat may be present and may have been markedly impacted on trawl grounds. A good example of the magnitude of effect is provided by Hall-Spencer and Moore (2000) who showed that scallop dredges have profound effects on calcareous algae (maerl) beds, with up to 70% of thalli in dredge tracks killed through burial. Similarly, Poiner *et al.* (1998) report the results of a trawl depletion experiment in the interreef areas of the Great Barrier Reef, which showed that each trawl removed and caught between 5 and 20% of the available biomass of sessile fauna, with 70–90% removed after 13 trawls. Note that the above estimate does not include fauna that were detached from the seabed but not caught. However, video analysis of the effects

of the trawl ground rope undertaken by Sainsbury (1987) for the Australian north-west shelf, indicate that about 89% of encounters lead to dislodgement of sponges and almost certainly subsequent death.

With respect to other forms of fishing that affect habitat structure, dynamite and cyanide fishing on coral reefs are probably the most obvious, but the removal of fish themselves may also affect the nature of the available habitat. Species that act as ecosystem engineers are being increasingly recognized as playing an important role in the marine systems. In the Gulf of Mexico, for example, where unconsolidated sediment overlies hard rock substratum, fish such as the red grouper have been shown to create burrows, or dig pits, down to the rock (Coleman and Williams 2002). This seabed excavation in turn allows a rich epifaunal community to colonize. In such circumstances, depletion of the fish resource will lead to concomitant effects on the biodiversity of the benthos. The extent of such phenomena is currently unknown.

It could certainly be argued that it is by effecting changes to biogenic structure that fishing is most likely to influence the benthic communities of marine systems. Although the data are relatively sparse and well-executed studies of effects of mobile bottom-fishing gears on many biogenic habitats are difficult to find (e.g. Collie *et al.* 2000), it seems self-evident that destroying the physical integrity of reefs or other biogenic structures will have profound consequences, both for fish populations and the other taxa. Indeed, on coral reefs, some of the most complex of biogenic habitats, there are significant positive relationships between fish biomass and topographic complexity (Luckhurst and Luckhurst 1978; Roberts and Ormond 1987). What is true for coral reefs is almost certainly true for other biogenic habitats. The issue here is not only that marked and undesirable effects ensue when trawling, dynamite fishing, or other physically disruptive practices take place, but the extent of the fishing activity and the distribution of sensitive habitats. The lack of high resolution (± 100 m) maps of benthic habitats and biota is probably the biggest current impediment to effective protection of vulnerable habitat from fishing activities. Only by combining such data with microscale data on the distribution and frequency of trawling disturbance for major fishing grounds can we accurately assess the extent of impact of fishing on benthic habitats. Such data will also provide a sound basis for developing mitigation strategies.

Case history of prolonged recovery

One analysis of recovery, which also demonstrates the importance of biogenic structure provided by benthic organisms, is that of Sainsbury (1988) who studied the fishery off the north-west shelf of Australia. Research survey data available from 1960 onward has shown that while the total biomass of fish has not changed as these fisheries have developed, the composition of the fish community has altered, with Lethrinids and Lutjanids declining and Saurids and Nemipterids increasing. The available data also indicated that the benthic environment has altered over the same period. In particular, the quantity of epibenthic fauna caught in trawls (mainly sponges, alcyonarians and gorgonians) is now considerably lower than it was prior to the development of the trawl fishery (Sainsbury 1987). Using video data Sainsbury (1988) identified four habitat types on the basis of dominant benthic fauna. Fish catch data was then examined in relation to habitat type, and the results indicated that Lethrinids and Lutjanids were almost exclusively associated with habitats supporting large epibenthos. In contrast, the Saurids and Nemipterids were only found on open sand. Subsequent comparison between a closed area and one open to trawling between 1985 and 1990 shows how the area closed to fishing experienced an increase in the density of *Lethrinus* and *Lutjanus* and in the abundance of small benthos. The abundance of larger epibenthos stayed the same or perhaps increased slightly. In the area open to trawling, the abundance of fish declined along with the small and large epibenthos.

The north-west shelf is a good example of where an interaction between fisheries and the structure of benthic communities may lead to both an enhanced fishery and a less disturbed benthic community. Such mechanisms may not happen everywhere; indeed, the habitats in which they operate might be quite restricted, but we should be alert to the possibility. Unfortunately, however, in the case of the north-west shelf, it is apparent that the time scales for recovery for epifaunal benthos are slower than previously thought. Rather than taking 6–10 years for sponges to grow to 25 cm it now appears that at least 15 years are required. This slow recovery dynamic, coupled with the apparently high probability that large benthos will be removed by a trawl, means that measures to protect the habitat would need to be very effective to maintain the habitat structure required to support this high-value fishery.

What would the seabed be like without fishing disturbance?

Comparative studies

It is unlikely that we will ever unearth sufficient datasets that will provide a good picture of the manner of change in benthic communities during the period when fishing developed. Hence, if we do not see major trends in time series or marked effects from experimental trawling, might it be that fishing removed or degraded the community to a considerable degree before we even started looking? The perceived problems that might be associated with intense and prolonged bottom-fishing disturbance have only been examined with any degree of rigour in the last 20 years. However, the bottom-fishing fleets have been in operation much longer (Jennings and Kaiser 1998). For example, the whole North Sea was already accessible to otter trawlers by 1900 and the beam trawl fleet in the southern North Sea expanded dramatically through the 1960s and 1970s and reached an asymptote in the mid 1980s. Consequently, many present-day studies have been undertaken in what is already a considerably altered environment from which certain vulnerable species have been extirpated (Philippart 1998). Despite our efforts to predict the outcome of fishing activities for existing benthic communities, we are often unable to deduce the original composition of the fauna because data gathered prior to the era of intensive bottom fishing are sparse and variable in quality. This is an important caveat because recent analyses of the few existing historical datasets suggest that larger bodied benthos were more prevalent prior to intensive bottom trawling (Frid *et al.* 2000; Rumohr and Kujawski 2000). Rumohr and Kujawski (2000) noted that 25% of the bivalve fauna recorded in the North Sea in the first half of the twentieth century are no longer present, although their data require careful interpretation. Perhaps, not surprisingly, present-day comparative studies (i.e. those studies that compare areas of the seabed subjected to different regimes of chronic disturbance from none upwards) indicate that epifaunal organisms are less prevalent in areas subjected to intensive bottom fishing (Collie *et al.* 1997; Sainsbury *et al.* 1997; Kaiser *et al.* 2000a,b; Koslow *et al.* 2000; McConnaughey *et al.* 2000; Rumohr and Kujawski 2000). An important consequence of this effect is the reduction in habitat complexity (architecture) that accompanies the removal of sessile epifauna. Nevertheless, it has been hard to convincingly

demonstrate that towed bottom fishing activity has been responsible for changes in bottom fauna and habitats. Often, effort data are lacking at a scale or over a time period that is relevant to ascertain the disturbance history of a particular area of seabed. Kaiser *et al.* (2000a) were able to overcome the problems associated with verification of disturbance history by recording the frequency of trawl-induced scars in the shell of a long-lived species of bivalve mollusc *Glycymeris glycymeris*. In the few instances when such data have been available, observations have indicated consistently a shift from dominance by high-biomass organisms towards communities dominated by small-bodied opportunistic species (Engel and Kvittek 1998; Bradshaw *et al.* 2000; Kaiser *et al.* 2000a,b; McConnaughey *et al.* 2000; Jennings *et al.* 2001a,b).

Fishing effects on production in different habitats

Complex biogenic and structured habitats harbour communities of higher biomass and diversity than adjacent habitats with less complex structure (Kaiser *et al.* 1999 and others?). Since trawling disturbance reduces habitat complexity, this may reduce the total production of the associated community. However, it has also been argued that frequent trawling disturbance may lead to the proliferation of smaller benthic species with faster life histories that can withstand the mortality imposed by trawling and are favoured as food by commercially fished species. Since smaller species are more productive, trawling disturbance may 'farm the sea', with knock-on benefits for consumers, including fish populations.

There have been few empirical tests of the impact of trawling disturbance on production, but one study of trawling impacts on a soft-sediment community suggests that the effects may be negative. In this study, benthic production was assessed across quantified gradients of trawling disturbance on real fishing grounds in the North Sea (Jennings *et al.* 2001b). Biomass fell with increased levels of trawling disturbance (Fig. 7). Production was estimated from size-spectra, using an allometric relationship between body mass and the production to biomass ($P : B$). In heavily fished areas, the abundance of larger individuals was depleted more than smaller ones, as reflected by the positive relationship between the slope of the normalized size-spectra and trawling disturbance. Relative infaunal production (production per unit biomass) rose with increased trawling disturbance, and this was largely attributable to the dominance of smaller animals in the disturbed

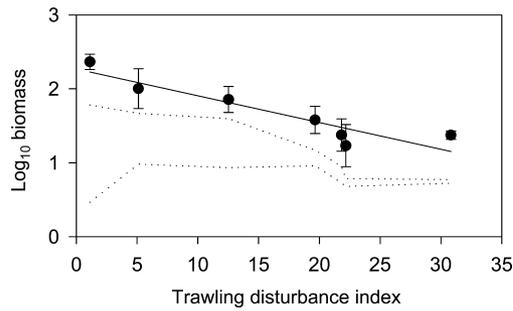


Figure 7 The relationship between trawling disturbance and the biomass of infauna in the Silver Pit region of the North Sea. The continuous line is the fitted relationship between biomass and trawling disturbance while the upper broken line shows the relationship between the biomass of bivalves/spatangoids and disturbance and the lower broken line shows the relationship between the biomass of polychaetes and disturbance. Preliminary multivariate analyses of these data showed that trawling disturbance alone accounted for more of the variance in total biomass than sediment characteristics and depth.

communities. The significant increase in relative production ($P : B$) did not compensate for the loss of total production that resulted from the depletion of large individuals (Fig. 8). Multivariate analyses have also

been used to show that bottom trawling disturbance had a dominant effect on the size-structure and production of the fauna of this soft-sediment benthic community and that the role of other environmental variables such as sediment particle size and depth was relatively weak (D. E. Duplisea *et al.* unpublished results). Given that trawling disturbance led to reductions in production in this relatively simple and unstructured habitat, it is expected that the effects may be even more profound when trawling leads to reductions in the complexity of highly structured biogenic habitats and their associated fauna.

It is also expected that trawling impacts on complex biogenic habitats will lead to changes in the trophic structure of the associated communities. One study of trawling impacts on trophic structure in a soft-sediment community demonstrated that chronic trawling disturbance led to dramatic reductions in the biomass of infauna and epifauna, but that these reductions were not reflected in changes to the mean trophic level of the community, or the relationships between the trophic levels of different size classes of epifauna. Despite order of magnitude decreases in biomass of infauna, and a shift from a community dominated by bivalves and spatangoids

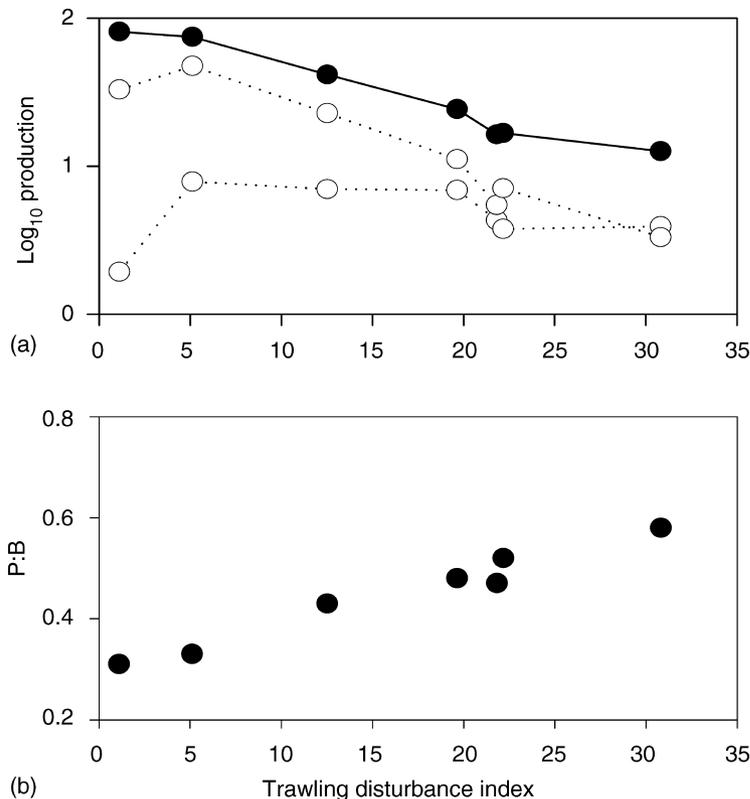


Figure 8 (a) The relationship between trawling disturbance and production for infauna in the Silver Pit region of the North Sea. The continuous line shows the relationship for the whole community, while the upper broken line shows the relationship for bivalves/spatangoids and the lower broken line shows the relationship for polychaetes (not significant). (b) The relationship between trawling disturbance and production to biomass ratios for the same infaunal community.

to one dominated by polychaetes, the mean trophic level of these communities differed by less than one trophic level between sites and differences were not linked to levels of fishing disturbance. The trophic structure of the benthic invertebrate community in this part of the North Sea may have been quite robust, thus ensuring the efficient processing of production within those animals that have sufficiently high intrinsic rates of population increase to withstand the levels of mortality imposed by trawling. The lack of changes in the trophic level of the benthos could imply that species less vulnerable to disturbance are taking the trophic roles of larger, more vulnerable species. It would be worthwhile to undertake an explicit study of whether smaller species with faster life histories begin to fill the trophic functions vacated by larger species with slower life histories because the latter cannot withstand the high mortality rates imposed by repeated trawling. Jennings *et al.* (2001a) emphasized that their results were only applicable to the free-living fauna of mobile substrates and that it was unlikely that they could be extrapolated to deeper areas with lower natural disturbance where many habitat-forming species are found (Auster *et al.* 1996). Here, loss of habitat would have important consequences for many species, and stability in trophic structure is unlikely to be observed as biomass falls.

The patchiness of trawling effects and its implications

The patchiness of trawling effort is a key determinant of the cumulative large-scale impacts of trawling disturbance on habitats. Trawling effort is patchy on a range of scales. Thus, even in the intensively fished North Sea at the scale of the ICES rectangle (areas of 0.5° latitude by 1° longitude = 3720 km^2 at 53°N used for the statistical collection of fisheries data), annual international beam and otter trawling effort ranges from 0 to over $50\,000 \text{ h year}^{-1}$ (Jennings *et al.* 1999). Half the ICES rectangles in the North Sea are beam trawled for less than 2000 h year^{-1} . Since a typical beam trawler tows two 12 m (width) beams at six knots (11.1 km h^{-1}), the trawler will impact $267\,264 \text{ m}^2 \text{ substratum hour}^{-1}$ or 534.5 km^2 in 2000 h. Thus, in rectangles subject to 2000-h beam trawling per year, and with a truly homogeneous effort distribution in the rectangle, it would take at least 7 years to trawl the entire rectangle once. This would have a limited effect on most benthic habitats, and such rectangles could be considered *de facto*

closed areas. At smaller scales, trawling effort is also very patchy. Rijnsdorp *et al.* (1998) examined effort data for their beam trawl fleet and have shown that effort is patchy at spatial scales of 30×30 , 10×10 , 3×3 and 1×1 nautical miles. Only at the smallest scale of 1×1 nautical miles was the effort distribution usually observed to be random. In practical terms, this research means that *de facto* closed areas where habitats are not impacted by fishing are likely to exist at many scales. Even in eight of the most heavily beam trawled ICES rectangles in the southern North Sea, 5% of the area is trawled less than once every 5 years (Rijnsdorp *et al.* 1998). We can only assume that the remaining presence of vulnerable habitat in many intensively fished areas is the consequence of patchiness in fishing effort. If this is the case, then management regulations that preserve such patchiness are desirable for conservation purposes.

The analysis of patterns in trawling effort shows that in the absence of radical changes in management practices, trawlers tend to target the same grounds year after year. However, there are usually seasonal (within years) changes in effort distributions. Once on the fishing grounds, many vessels will fish the same tows time after time as these tows are likely to be clear of obstructions. This means that in the short term (up to 5 years or so), the spatial distribution of effort from year to year tends to be quite consistent. However, since fishermen prefer to fish on certain types of ground, the areas that are unimpacted or lightly impacted by trawling will not necessarily be representative of all habitat types that are present.

If there are no major changes to fishery management regimes, trawlers tend to fish the same grounds year after year. This means that the same areas of the seabed are disturbed, and that areas of seabed are virtually unaffected by trawling. For most habitats that are vulnerable to fishing, a consistently patchy distribution of a given level of trawling effort from year to year is likely to have lower environmental impacts than if the same trawling effort were distributed evenly. This is because the recovery times of the vulnerable habitats are very long (Collie *et al.* 2000), and impacts by trawls at intervals of 4–5 years may be enough to cause habitat loss and structural change.

If closed areas are used as a fishery conservation tool, they will always cause changes in the spatial and temporal distribution of fishing effort. For example, the temporary closure of 40 000 square miles of

the North Sea to trawling from 14 February to 30 April 2001 (North Sea Cod Recovery Plan), led to trawlers operating in areas that were previously not fished (Rijnsdorp *et al.* 2001). As a result, while the effects of trawling on habitats may be mitigated within the closed area, the resultant changes in effort distribution may mean that the impacts of trawling are exacerbated outside the closed area. Any assessment of the potential benefits of closed area management must take into account the impacts both inside and outside the reserve. We can envisage a situation where a number of temporary closures of fishing grounds in different locations would, in the long term, result in greater overall homogeneity in trawling effort distributions than would otherwise exist. Redistribution would be a particular concern in relation to biodiversity conservation if, for example, there was a displacement of vessels from inshore fishing grounds to previously unfished continental shelves where cold-water corals and other fauna of conservation concern may be present (Roberts *et al.* 2000).

Essential Fish Habitat

Recent amendments to the U.S. Magnuson-Stevens Act require fisheries managers to address the impact of fishing gears upon fish habitat in their management plans (Benaka 1999). This will, no doubt, have a profound effect on the manner in which U.S. fisheries are managed. This legislation is one of the first measures to embrace an ecosystem perspective in fisheries management. While it is fairly simple to identify those habitats that might be considered essential to the life history of some fish, e.g. spawning and nursery areas. However, of equal relevance are the habitat quality issues that affect the acquisition of food and the avoidance of predators. Hence, there is an urgent need to identify those habitats that may have an important or 'essential' functional role for particular species or types of fish (e.g. piscivores/herbivores/omnivores or flatfish/roundfish) at other stages of their life history.

Previous studies of the relationship between fish and shellfish assemblages and their environment have focused on variables such as salinity, depth and substratum type (e.g. Overholtz and Tyler 1985; Smale *et al.* 1993). Yet, while such environmental parameters are in some cases good correlates of certain fish assemblages, they do not necessarily define the essential features of a specific habitat, rather they constitute a component of that habitat that may act as a surrogate for some other more important habitat

feature. Habitat complexity and structure (e.g. grain size composition) appear to be important physical features for some fish species (e.g. Sainsbury 1987; Gibson and Robb 1992; Auster *et al.* 1997). Many studies have already demonstrated the relationship between flatfish species and the sediment particle composition of the seabed, which may be more important than the occurrence of associated epibenthic structures or fauna that occur in that habitat (e.g. Gibson and Robb 1992; Rogers 1992). For example, plaice are better able to bury themselves in sediments that have a particular grain-size composition and hence, more effectively avoid predation. Hence, a specific particle-size composition may be essential for flatfish, whereas the presence of large sessile epifauna or rocky substrata might be considered non-essential. In contrast, there is good evidence to suggest that structural complexity can have important implications for the survival of roundfishes (e.g. Walters and Juanes 1993; Tupper and Boutilier 1995).

Habitat complexity is a product of the surface topography of the substratum and the sessile epifauna that grow upon it. Reef-forming organisms can result in habitats of very high complexity providing a multitude of refuges for a diverse range of species. More subtle features such as sand ridges and pits created by the feeding or burrowing action of benthic fauna may provide shelter for bottom-dwelling fish species (e.g. Auster *et al.* 1997). Bottom fishing activities are capable of greatly reducing habitat complexity by either direct modification of the substratum or removal of the fauna that contribute to surface topography (Jennings and Kaiser 1998; Auster and Langton 1999). Hence, degradation of habitat complexity by fishing activities may lead to changes in the associated fish assemblages (e.g. Sainsbury *et al.* 1997). Alteration of habitat features has been shown to have important consequences for freshwater fishes, and this is the caveat that underpins much of the ecological restoration projects centred on salmonid habitats that focus on the reconstruction of habitat features important for the life history of the fish (e.g. Cederholm *et al.* 1999). An initial study of habitat/fish assemblage relationships indicated that even subtle alterations in habitat characteristics are linked to changes in the dominance of certain fish species within the assemblage (Kaiser *et al.* 1999). Presumably, a good understanding of the link between fish and their habitat would enable us to predict the consequences of habitat alteration. For example, for certain species such as sole (*Solea solea*) that preferentially live in relatively uniform sandy areas,

the exclusion of towed bottom fishing gear from an area of the seabed could permit the growth of emergent sessile fauna. As sessile fauna attract decapod crustacea (Auster *et al.* 1996), this could make the sandy environment better suited to predatory flatfishes such as plaice (*Pleuronectes platessa*) and dab (*Limanda limanda*) (Kaiser *et al.* 1999). Thus, in the case of the sole fishery, the fishing activity may maintain the seabed habitat in a condition that favours the target species. Nevertheless, it is important to remember that excessive bottom disturbance will eventually result in reduced productivity.

Integrating habitat conservation into fisheries management

Fishery managers are unlikely to be concerned with habitat unless: (i) they are forced to take it into account by conservation legislation, (2), if it can be shown that the habitat is essential and that loss of habitat would cause a bottleneck in the life history that subsequently leads to a loss of yield. Fisheries management that also achieves habitat management can be realized through a number of different mechanisms. Total exclusion of all fishing effort will achieve habitat conservation provided that there are no other extrinsic factors that negatively affect the habitat (e.g. agricultural run-off from adjacent land masses). Other measures include networks of area closures at different spatial scales that are determined by the demography of the species to be protected. Temporal closures may achieve habitat

preservation if the habitat or species in question have generation times that fall within the time scale of the temporal closure.

The total exclusion of certain forms of fishing activities from areas of the seabed will often lead to opposition from the fishing industry. Nevertheless, a recent large-scale study on the north-west Atlantic coast of North America has demonstrated some potential benefits of large-scale closures. In New England, USA, seasonal closed areas have been an important component of fisheries management since the early 1970s but had little impact on the groundfish stocks that they were designed to protect. In 1994, three large areas that, in total, covered 17 000 km² of the seabed were closed all year to all fishing gears that might retain groundfish (trawls, scallop dredges, hooks, etc.). These closed areas were maintained for 5 years and were found to effectively protect the more sedentary components of the assemblage such as flatfishes, skates and scallops. Although less protection was afforded to cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), limits on the number of days fished lowered stock-wide mortality rates. The closures also protected important juvenile nursery areas. Scallop dredges were excluded because they took a by-catch of groundfish species. The relaxation of fishing effort on scallops had dramatic effects and led to a 14-fold increase in scallop biomass within the closed areas during 1994–1998 (Fig. 9). A portion of the closed areas was reopened to scallop dredging in 1999 (Murawski *et al.* 2000). The returns of scallops during this period were so encouraging that

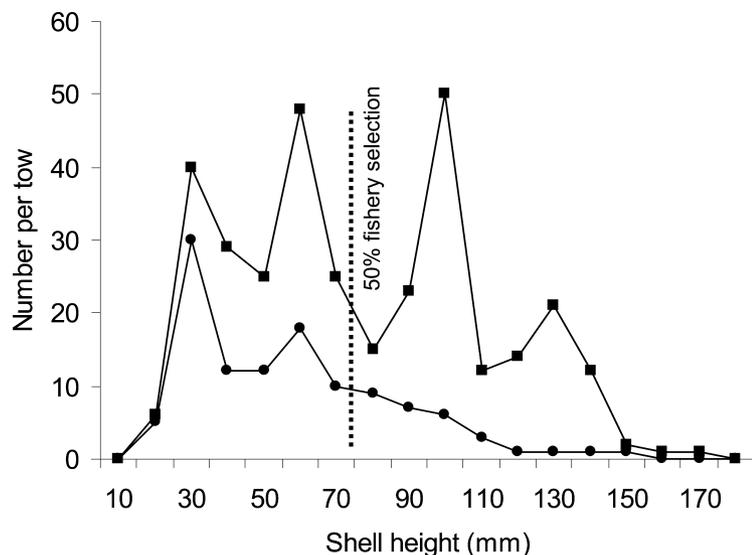


Figure 9 Standardized abundance of sea scallops (numbers per dredge tow) by shell height, taken in the July National Marine Fisheries Service dredge survey on Georges Bank. Data are presented separately for the areas closed (squares) and those open to scallop dredging (circles). Harvestable animals are indicated by the 50% selection line (from Murawski *et al.* 2000).

managers are now contemplating a formal 'area rotation' scheme for this fishery presumably on a time scale of 4–5 years.

Another approach to the protection of habitat is to partition fishing activities. In an inshore fishery off the south coast of England, two commercially important species coexist in the same habitat which has led to conflict between different sectors of the fishing industry. A good example of this situation is when fishers using towed bottom fishing gears (scallop dredges, beam trawls and otter trawls) operate in the same areas where fixed bottom gears (crab pots) are deployed. Kaiser *et al.* (2000b) examined an area subject to a voluntary agreement between these two sectors of the fishing industry such that some areas are used exclusively by fixed gear fishers, some are shared seasonally by both sectors, and others are open to all methods of fishing year round. This agreement was enacted to resolve conflict between the two sectors of the industry. An additional perceived benefit of this agreement was the possible protection of the seabed from towed bottom fishing gear. Kaiser *et al.* (2000b) undertook comparative surveys of the benthic habitat and communities within the area covered by the agreement and compared different areas subjected to a range of fishing disturbance regimes. Communities found within the areas closed to towed fishing gears were significantly different from those open to fishing either permanently or seasonally. Abundance/biomass curves plotted for the benthic fauna demonstrated that the communities within the closed areas had more large-bodied species (Fig. 10). Areas fished by towed gear were dominated by smaller bodied fauna and scavenging taxa.

While it would appear that gear restriction management regimes have the added benefit of conserving habitats, target species and benthic fauna within the management area, it is, at present, not possible to determine whether there are any wider benefits for the fishery that exploits the target species outside the management area.

With sufficient scientific information it should be possible to formulate a regime of fishing effort (i.e. physical disturbance for towed bottom fishing gear) that would be environmentally sustainable. Here, we define environmentally sustainable as the process by which the habitat and its associated biological assemblage can recover before a subsequent disturbance event. For example, in shallow sandy areas of the seabed two to three physical disturbances of the seabed every year may have little or no net effect on the habitat or resident assemblage. However, at present, the definition of sandy areas is too imprecise to allow us to select areas that would respond in the same way to a given management measure. We know, for example, that sand flats that are dominated by tube-building spionid worms take much longer to recover if these worms are removed through physical disturbance as the worms normally have a stabilizing effect on the habitat (Thrush *et al.* 1996).

It is pertinent to ask what we might expect to achieve by protecting certain 'essential' habitats from the standpoint of enhanced fisheries production. In many areas this secondary habitat is patchily distributed, and the question is whether such localized refugia are sufficiently widespread and important to make a difference for the fishery as a whole. This will often be a difficult question to answer. We know, for

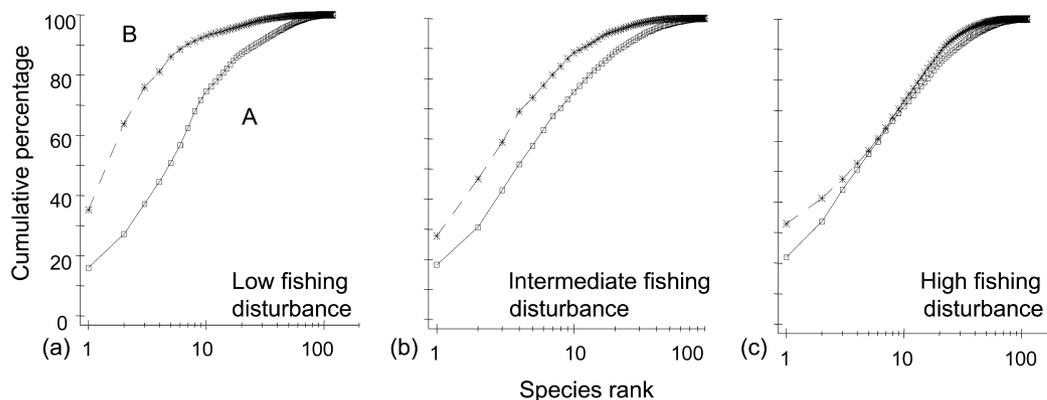


Figure 10 Abundance/biomass curves of samples collected from areas protected from towed bottom fishing gear (low disturbance), areas open seasonally to towed bottom fishing gear and those areas that are fished all year with towed bottom fishing gear (high disturbance). As the level of bottom fishing disturbance increases the biomass curve (B) converges with the abundance curve (A) which is a typical response in stressed communities (adapted from Kaiser *et al.* 2000b).

example, that juvenile cod that occupy the shallow subtidal region around the coasts of Europe and North America benefit from the shelter that algal cover can provide. Yet, the proportion of the total stock which survives and recruits into the fishery, which were afforded this protection is probably quite trivial compared to the numbers that survive from more open areas. On a *per capita* basis then, the margins may be better, but in terms of total contribution they are probably insignificant. When this is so, we might protect the habitat for other reasons, but enhancing fisheries would not be one of them.

Unfortunately, we have the additional question of whether habitats, which we now consider to be devoid of structure, used to afford protection to juveniles (the issue discussed in the previous section returns!). On the north-west shelf of Australia, it seems clear that habitats were rapidly affected by trawling and, as noted above, there is no real basis for supposing that this has not happened elsewhere. It should be recognized, however, that if benefits to a fishery can be shown if habitats are protected or restored, it is likely that those benefits will only be obtainable if alternative to trawling can be developed. Trawling and benthic habitat protection is largely incompatible. The one exception to this, of course, is if benefits accruing in an area closed to fishing spill over into trawled areas.

Future research priorities

With respect to the design of future studies, we feel that experimentalists wishing to address the fishing impacts issue will be best served by abandoning short-term, small-scale pulse experiments. Instead, the scientific community should argue for support to undertake much larger scale press and relaxation experiments. One half of the experiment has already been done because fishing activity has been providing the press for many years what we now require more carefully designed closed area contrasts. There are two principal advantages to this approach. First, the results obtained are clearly interpretable in terms of real world intensities of fishing disturbance. Second, the spatial scale of the protected areas could be relatively small (and hence, replicated to fulfil the requirements for sound experimental design) without compromising unduly the interpretation of recovery dynamics. Estimates of recovery in small protected areas in a sea of disturbance are likely to be conservative, while recovery in small deliberately disturbed patches are not. Third, the experiments

would be conducted in the very habitats (i.e. real fishing grounds) about which the question of recovery is actually being posed. The time has come to try some rotational type of closure system. This would provide the ideal 'experiment' at an appropriately large scale. In addition, we would recommend that any such management regime included a study of the changes in system productivity within these areas. At present, the only justification for funding a suitably replicated 'fishing disturbance' experiment as performed 'ad nauseam' by some of the present authors and others would be within a closure system as described above. This would demonstrate (or not) that you could drive the 'closed' system back to a state similar to areas open to continuous fishing.

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