The Effects of Fishing on Marine Ecosystems

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1. GENERAL INTRODUCTION

Fishing is the most widespread human exploitative activity in the marine environment and Pauly and Christensen (1995) estimated that over 20% of primary production is required to sustain fisheries in many intensively fished coastal ecosystems (Figure 1). Previous estimates of the primary production required were much lower and led Vitousek *et al.* (1986) to conclude that fishing had few fundamental effects on the structure or function of marine ecosystems apart from those on fished species. These views were widely accepted at the time since they were in accordance with the overriding philosophy of many fisheries scientists who based their assessment and management actions upon the short-term dynamics of target fish populations (Frank and Leggett, 1994; Smith, 1994). However, studies such as those of Pauly and Christensen (1995), coupled with empirical evidence for shifts in marine ecosystems, imply that the actions of fishers may have important effects on ecosystem function (Sherman and Alexander, 1986). As a result the emphasis of marine fisheries research is beginning to shift from population to ecosystem based concerns (Langton *et al.,* 1996; Auster *et al.* 1997), and this has been reflected in a number of recent reviews describing the effects of fishing on ecosystem structure and processes (Munro *et al.*, 1987; McClanahan and Muthiga, 1988; Hutchings, 1990; Russ, 1991; Jones, 1992; Gislason, 1994; Hughes, 1994; Matishov and Pavlova, 1994; Anon, 1995b; Dayton *et al.*, 1995; McClanahan and Obura, 1995; Roberts, 1995; Jennings and Lock, 1996; Jennings and Polunin, 1996b, Birkeland, 1997).

As early as the fourteenth century there were concerns about the effects of fishing on the marine environment and these effects were discussed in detail by a number of Government Commissions in the United Kingdom (Anon, 1885). However, the scientific basis for the management of fisheries was founded in the study of exploited fish populations and it was not surprising that these were the primary unit of concern since species or intraspecific stocks were the targets of fishers, the categories favoured by buyers or consumers, and the groupings in which fishing effects were most readily recognised. Early studies of fish population dynamics (Petersen, 1894; Garstang, 1900; Hjort, 1914; Hjort *et al.*, 1933) were paralleled by the wide-ranging studies of ecologists and mathematicians such as Malthus (1798), Lotka (1925) and Volterra (1926) who discussed the impacts of resource limitation on population growth and mathematical approaches for describing population fluctuations. In subsequent years, mathematical descriptions of fish population dynamics and the effects of exploitation were developed by Russell (1931), Graham (1935), Russell (1939), Schaefer (1954), Beverton and Holt (1957) and Ricker (1958) whose models had considerable influence on wider scientific thinking at that time. As applied fisheries science continued to develop, there was relatively little concern about the functional role of fishes within the marine ecosystem and the indirect effects of changes in their abundance or diversity. Indeed, the study of food webs (Elton, 1927), had considerable influence on the development of terrestrial ecology, but little or no impact on the development of fishery science.

Throughout the early twentieth century the discussion between fishery scientists and those working on the dynamics of other populations continued, but in subsequent years it was notable that fisheries science was increasingly viewed as a field of study in its own right. With few exceptions (May, 1984), fisheries scientists did not respond to many major theoretical advances in the description of ecosystem structure and function (May, 1973; Pimm, 1982; Pimm, 1991). This was strange since influential studies of the processes driving fish production had been conducted by scientists who worked in laboratories charged with fisheries assessment and whose interests freely transcended the boundaries between fish population biology, marine ecology and oceanographic science (Hjort, 1914; Ryther, 1969; Gulland, 1970; Steele, 1974; Cushing, 1975, 1982; Andersen and Ursin, 1977; Andersen and Ursin, 1978; Steele and Henderson, 1984; Sharp, 1988; Southward *et al*. 1988). Their ideas, however, were rarely translated into practical management advice since social and political pressures focused attention on the fish stock as the prime management unit and the study of management measures such as changes in mesh sizes or fishing mortality had become a central component of population based research (Smith, 1994).

The study of fish population dynamics continues to provide the basis for most present day management decisions. In those countries with the resources to implement procedures such as virtual population analysis and multispecies virtual population analysis (Pope, 1979; Sparre, 1991), the short-term predictions of stock structure and potential yield are remarkably accurate. Indeed, many practitioners continue to argue that the methods of enforcing management advice are of vastly more concern than the scientific details of the stock assessment models which they prefer (Anon, 1997). From the fisheries scientists' viewpoint, it is the lack of clear necessity that kept the ecosystems perspective from advancing in a field whose pragmatic concern is the mechanics of short-term fishery management.

The existing concerns of fisheries scientists in relation to human activities have largely focused on the dramatic collapse of a few stocks such as the Peruvian anchovy *Engraulis ringens* and Atlantic cod *Gadus morhua* (Idyll, 1973; Myers *et al*., 1996). Wider concerns that the rate of increase in the global fish catch is declining as demand is increasing (Anon, 1997), that the proportion of fish caught in many fisheries leaves little latitude for recruitment failure (Myers *et al*., 1995; Cook *et al*., 1997) and that unwanted by-catch often forms a relatively large proportion of the total catch (Alverson *et al*., 1994; Hall, 1996) also focus upon fish populations. Conversely, the concerns of terrestrial ecologists are rapidly moving from species to focus on habitats and ecosystems in recognition of the need to maintain ecosystem integrity and function rather than simply preserving entities (Gaston, 1996). Many of the key scientists in this field are now assessing the impact of human activities on the structure and function of ecosystems and the ways in which production processes and ecosystem stability are affected by reductions in species diversity (Ehrlich and Wilson, 1991; Walker, 1992; Ehrlich and Daily, 1993; Huston, 1994; Lawton, 1994; Naeem *et al*., 1994; Tilman and Downing, 1994; Anon, 1995f; Naeem *et al*., 1995; Gadgil, 1996; Johnson *et al*., 1996; Kunin and Lawton, 1996; Vane-Wright, 1996).

The possibility that fisheries have major effects at the ecosystem level and that the ecosystem should be considered as an assessment and management unit have been expressed by some marine ecologists (Sherman and Alexander, 1986; Sherman *et al*., 1991, 1993). Fishing has a number of direct effects on marine ecosystems because it is responsible for increasing the mortality of target and by-catch species and disturbing marine habitats. The direct effects of fishing have many indirect implications for other species. Thus fishers may remove some of the prey that piscivorous fishes, birds and mammals would otherwise consume, or may remove predators that would otherwise control prey populations. Moreover, reductions in the density of some species may affect competitive interactions and result in the proliferation of non-target species. The activities of fishers also provide food for scavenging species since fishes, benthic organisms and other unwanted by-catch are often discarded and because a range of species are killed, but not retained, by towed gears.

Our aim is to compile evidence for the effects of fishing on ecosystem structure or function and to determine whether there is a scientific basis for the prediction or management of changes in marine ecosystems. We believe that ecological questions relevant to the marine environment must be studied on many spatial and temporal scales and suggest that an understanding of fishing effects requires the integration of population and ecosystem-centred research. This review describes the effects of fishing on benthic fauna and habitat, community structure and trophic interactions. The divisions serve to structure the review, but they are primarily artificial because the effects of fishing are not mutually exclusive. For example, the intensive fishing of invertebrate-feeding fishes on Kenyan coral reefs has led to reductions in fish species diversity and reduced predation on sea urchins. In the longer term, sea urchin biomass has increased leading to a reduction in algal biomass and bioerosion of the reef matrix with corresponding reductions in the numerical abundance and diversity of fishes which can use the reef habitat (McClanahan and Muthiga, 1988; McClanahan, 1990; McClanahan, 1992; McClanahan, 1994a; McClanahan, 1995b; McClanahan, 1995a).

Our review is wide-ranging but selective. In particular, we have largely disregarded the direct effects of fishing on target and by-catch species. The effects of fishing on target species are described in a number of texts and form the basis of traditional fisheries science (Beverton and Holt, 1957; Beverton, 1963; Cushing, 1968; Nikolskii, 1969; Gulland, 1977; Munro and Williams, 1985; Hilborn and Walters, 1992; Appeldoorn, 1996) and there are a number of reviews that have described the type and magnitude of by-catch in many fisheries (Beddington *et al.*, 1985; Andrew and Pepperell, 1992; Alverson *et al.*, 1994; Anon, 1995b; Anon, 1996c; Hall, 1996; Simmonds and Hutchinson, 1996). In examining the indirect effects of fishing on the ecosystem, it is important to recognise that some by-catch species have been affected dramatically by fishing. For example, Smith (1983) estimated that the population sizes of three dolphin species caught by tuna boats in the eastern tropical Pacific were reduced to 20%, 35-50% and 58-72% of pre-exploitation levels by 1979. By-catches of marine mammals, birds and sea turtles have become a dominant political issue in the management of many fisheries (Hall, 1996) and even when rates of mortality have negligible effects on the populations, they may be politically significant. To some extent the value of biological significance is arbitrary (Hall, 1996). Thus the proposal that a by-catch mortality equivalent to 0.5% of cetacean population size is acceptable (Perrin *et al.*, 1994) may satisfy those who hope that the removal of dolphins will not affect ecosystem function but will not placate those concerned for the welfare of individual dolphins. Such issues are outside the scope of this review. Our consideration of by-catch is limited to the indirect effects of discarding on scavenger communities. The portion of the total catch which is discarded dead or dying, either because it is illegal to land or because there is little or no economic gain associated with sorting or retaining it, constitutes approximately 27% of global fish catches (Alverson *et al.*, 1994). Thus fishing activities subsidise marine foodwebs with carrion that would be unavailable under natural conditions, which may have profound effects on scavenging species (Britton and Morton, 1994). Moreover, in some fisheries, the ratio of by-catch to landings is so high that the removal of target species may not constitute the main impact of the fishery (Figure 2).

Having reviewed the evidence for the ecosystem effects of fishing we consider whether description can be used as a basis for prediction and whether an understanding of the ecosystem effects of fishing could be translated into effective management. Such considerations are timely given the increasing public and scientific disillusionment with existing fishery management strategies and that policy makers need a scientific basis for deciding whether they should respond to social, economic and political demands for instituting or preventing ecosystem-based management.

2. BENTHIC FAUNA AND HABITAT

2.1 Introduction

Fishing activities lead to changes in the structure of marine habitats and can determine the diversity, composition, biomass and productivity of the associated biota. The effects of fishing on habitats are often large scale ramifications of the cumulative effects on many individual plants and invertebrates since habitats such as kelp forests, coral reefs or bryozoan beds are formed by living organisms. Many fishing gears have direct effects on habitat structure, but indirect effects occur when fishing initiates shifts in the relationships between those organisms responsible for habitat development and degradation. The direct effects of fishing vary according to the gears used and the habitats fished, but they usually include the scraping, scouring and resuspension of the substratum. The magnitude of changes which can be attributed to fishing often depend upon the nature of the physical environment in which a given habitat is found. Thus the effects of fishing on communities of short-lived burrowing worms that temporarily inhabit mobile sediments in shallow shelf seas will be harder to detect than the effects on coral communities that structure equatorial coral reefs. The indirect effects of fishing on non-target fishes and invertebrates may lead to changes in community structure and habitat type. For example, there is increasingly good evidence to show that the indirect effects of fishing have caused some reef communities to shift from coral to algal or urchin-dominated phases. In section 2.2 we describe fishing methods that impact the marine ecosystem directly and their effects on habitat structure, benthic communities and non-target species. In section 2.3 we discuss the indirect effects of fisheries on habitat structure and production processes, and the ramifications of such changes for fish and invertebrate communities. The final section (2.4) considers the relative roles of natural and fishing disturbance in the marine environment.

2.2 Direct effects of fishing gears

Fishing techniques that affect benthic fauna and habitats can be grouped into two categories: active and passive. Active fishing methods usually involve towing trawls or dredges on continental shelves. However, artisanal fishers operating on tropical coasts also use a range of active techniques such as drive netting, spearing and fishing with chemicals or explosives. Passive fishing techniques include the use of pots or traps, baited hooks on set lines, gill nets and drift nets. Actively or passively fished surface, midwater and bottom fishing gears can have direct effects on non-target animals such as birds, marine mammals and reptiles and fishes which are taken as by-catch. In addition, the actions of fishers and their gears extensively modify seabed habitats and their associated benthic communities. In this section we describe the main fishing gears and their effects on benthic fauna and habitats.

2.2.1 Active fishing techniques

2.2.1.1 Trawls and dredges

The majority of mobile demersal fishing gears can be described as trawls or dredges. Both types of gear are used to capture species that live or feed in benthic habitats, and thus they have been designed to maximise their contact with the seabed. Fishing techniques and equipment have been fine-tuned to exploit the behaviour and habitat preferences of target species and to achieve the maximum catch-per-unit-effort. Presumably, fishers use the most effective techniques currently available. As commercial stocks have diminished, so fishing gears have been modified to maintain yield. The increasing power of fishing vessels has permitted the use of larger and heavier trawls and dredges. Towing larger gears incurs higher fuel costs which have to be offset by higher catches. However, these financial considerations take no account of the concomitant increase in environmental damage to non-target benthic communities.

Trawls generally fall into two categories, otter and beam trawls. Otter trawls derive their name from the two rectangular otter boards or doors, attached to the towing warps, which act as paravanes to maintain the lateral opening at the mouth of the net. The boards can weigh several t in air and are towed at an oblique angle across the seabed (Jones, 1992). When fished over fine muddy sediments the boards are sometimes fitted with metal shoes up to 30 cm wide which are designed to prevent the boards digging too far into the sediment (M.J. Kaiser, personal observations). Nevertheless, Krost *et al*. (1990) estimated that otter boards penetrated soft mud to a depth of 15 cm in the Baltic Sea. In the simplest otter trawls, the ground gear comprises a foot rope protected by sacrificial twine or rubber bobbins, which will be less intrusive than the otter doors. However, when used to catch flatfishes, varying numbers of tickler chains are attached between the otter boards (Harden Jones and Scholes, 1974; Sainsbury, 1987). Rockhopper gear represents the most extreme type of ground gear fitted to otter trawls. As its name suggests, this gear is used over rocky substrata. The groundrope is fitted with large rubber discs (> 50 cm diameter) and metal bobbins, which each weigh > 10 kg. The discs are held in position by a wire which runs the length of the ground rope and is threaded through their rear half. When the discs foul, they partially rotate against the tension imposed by the wire and then 'spring' clear, allowing the gear to hop over solid obstructions. Otter trawls are used at depths of up to 1500 m, which is far in excess of any other towed fishing net (Jones, 1992; Clark, 1996). To date, the incidental effects of these deep water fisheries are unknown although some unpublished data on by-catches are now available. These fisheries target pelagic species such as orange roughy, *Hoplostethus atlanticus* Collett, which aggregate in association with reef structures over which the gear is towed. Physical contact of these trawls with the reef substratum is likely to damage the epifaunal community.

Beam trawls comprise a rigid beam held off the seabed by two beam shoes. The net headline is attached to the beam and the footrope is attached to the beam shoes; thus the mouth of the net is fixed in an open position. Beam trawls are towed at speeds of up to 7 knots (Kaiser *et al.*, 1996b). Decreasing fish stocks have necessitated gear modifications such as increasing beam width and the addition of more tickler chains or the use of chain mats and flip-up ropes. Consequently, beam trawls have increased in weight from a mean of 3.5 t in the 1960's (Cole, 1971) up to 10 t in the early 1980's (Beek *et al.*, 1990). Beam trawlers specifically target benthic species such as sole, *Solea solea* (L.), plaice, *Pleuronectes platessa* L. and shrimp, *Crangon crangon* L. which are normally buried in, or rest on, surface sediments. The number of tickler chains fitted to the gear depends on the sediment characteristics of the fishing grounds, and 17 to 25 may be used on some of the largest trawls (Polet *et al.*, 1994). The tickler chains are specifically designed to penetrate the upper layers of the sediment, disturbing those target species that are buried in the sediment so that they swim up into the path of the trawl. Successive chains dig deeper as the leading chains "fluidise" the sediment. The heaviest trawls are used over rough grounds and are fitted with a chain matrix ('stone mat' gear) which prevents large rocks entering the net and causing damage to the gear and catch.

Dredges can be categorised as hydraulic or mechanical. Hydraulic dredges lift the sediment, non-target and target species whereas mechanical dredges physically dig target species out of the sediment. Hydraulic dredges use jets of water or air to create a venturi effect, which lifts the dredgings onto a boat for further processing on fixed or mechanical riddles (Meyer *et al*. 1981). Some of the largest commercial hydraulic dredgers harvest lugworms, *Arenicola marina* L., in the Dutch Wadden Sea. These leave furrows 1 m wide and 40 cm deep (Beukema, 1995). Similar devices are used to harvest cockles, *Cerastoderma edule* (L.) and Manila clams, *Tapes philippinarum* Adams and Reeve, at mid to high tide on sandflats in northern Europe (Hall and Harding, 1997; Spencer *et al*. 1997). Suction dredges are also used on a much smaller scale by divers to remove razor clams, *Ensis siliqua* (L.); although the area disturbed is relatively small, pits are often excavated to depths of 60 cm (Hall *et al*. 1990 a).

Mechanical dredges differ from trawls because they are designed to dig further into the substratum than beam trawls. Most dredges are used to target epi- or infaunal bivalves such as scallops, *Pecten maximus* (L.), clams, *Mercenaria mercenaria* (L.) and razor clams. Most dredge designs incorporate similar features such as a heavy duty bag or net attached to a rigid metal frame. Tooth bars or cutting blades of various designs are usually fitted to the frame. For example, the Newhaven dredge is fitted with a tooth bar bearing teeth approximately 11 cm long. The tooth bars are designed to disturb scallops which lie in shallow depressions in the seabed. Since scallop dredges tend to be used over rough ground, steel ring bellies are usually fitted to the net bag. Large scallop boats fish between 36 and 40 dredges simultaneously and these are attached to beams fitted with rollers that reduce drag. The total width and weight of a set of scallop gear is comparable with some of the larger beam trawls (Kaiser *et al.*, 1996b). Deep burrowing species such as razor clams are caught in dredges fitted with teeth up to 30 cm long (Gaspar *et al.*, 1994). The drag created by such a deep-digging dredge prevents small inshore boats fishing more than two at a time. Dredges are rarely towed at speeds in excess of 2.5 knots since the gear is less efficient at higher speeds (Caddy, 1968; Caddy, 1973; Dare *et al.*, 1993). Consequently, scallop dredges disturb smaller areas of seabed per unit time than beam trawls (Anon, 1995b; Kaiser *et al.*, 1996b).

Trawls and dredges have marked impacts on the substratum. Physical disturbance of the substratum results from direct contact with the fishing gear and the turbulent resuspension of surface sediments. The magnitude of the impact is determined by the speed of towing, physical dimensions and weight of the gear, type of substratum and strength of currents or tides in the area fished. The effects may persist for a few hours in shallow waters with strong tides or for decades in the deep sea.

In many shelf seas fishing intensity is very high and most fishable grounds will be impacted at intervals of less than one year. On Georges Bank, Caddy (1973) reported that 3% of the seabed in his study area was covered with trawl marks, but the persistence of the marks was unknown. More recently, Churchill (1989) estimated that 18% of a 259 km^2 area in the Middle Atlantic Bight was trawled in a 6 day period of intense fishing activity and Twichell *et al*. (1981) recorded up to 20 trawl tracks per 100 m^2 in the New York Bight, at a depth of 100 m, where current action was weak. Similarly, Krost *et al*. (1990) found that trawl tracks occupied 19% of their muddy and relatively deep study area. Churchill (1989) calculated that the effective area trawled on an annual basis in a number of 30' latitude by 30' longitude areas in the Middle Atlantic Bight was up to three times their actual area and Welleman (1989) and Rijnsdorp *et al*. (1991b) reported that some intensively fished regions of the southern North Sea were swept by trawls several times each year (Figure 3).

If observations of trawl marks are to be used to provide an index of fishing intensity then some knowledge of their persistence, as determined from experimental studies, is required.

High resolution video images of sediment surfaces before and after otter trawling indicate that trawling reduces the overall surface roughness of the seabed (Schwinghamer *et al.*, 1996) although trawl doors may leave depressions. Ripples, detrital aggregations and surface traces of bioturbation are smoothed over by the mechanical action of the trawl and the suspension and subsequent redeposition of the surface sediment. Acoustic data collected on trawled experimental sites on the eastern Grand Banks, Canada, showed the effects of trawling could be detected to a depth of at least 4.5cm within the sediment (hard packed sand), and there was a general, although uneven, reduction in the complexity of the internal sediment structure (Schwinghamer *et al.*, 1996). The physical disturbance of sediment can result in a loss of biological organisation and reduce species richness (Hall, 1994).

It is clear that all mobile bottom gears scrape the surface of, or dig into, the seabed to varying degrees. Hence, it is not surprising that non-target fishes and benthic invertebrate species comprise a large proportion of the catch in some fisheries (Andrew and Pepperell, 1992; Robin, 1992; de Groot and Lindeboom, 1994; Anon, 1996b; Raloff, 1996). While gear modifications such as the addition of extra tickler chains increase the catch of target species, there is an unavoidable and concomitant increase in the catch of non-target species (Cruetzberg *et al.*, 1987; Kaiser *et al.*, 1994). While nets have been refined to reduce by-catch of non-target and undersized commercial species (e.g. Briggs, 1992), few attempts have been made to reduce by-catch or the physical effects of fishing gears on invertebrate benthic species. For the purposes of this review we define infauna as those animals living entirely within the sediment, whereas epifauna are defined as those animals living on, protruding from, anchored in, or attached to, the sediment.

2.2.1.2 Effects of trawls and dredges on infauna

By-catches of non-target infaunal species indicate the extent to which benthic communities are perturbed by a particular gear. For example, the occurrence the infaunal bivalve, *Arctica islandica* (L.), and the heart urchin, *Echinocardium cordatum* (Pennant), in a 12 m beam trawl catch suggested that the tickler chains had penetrated hard sandy substrata to a depth of at least 6 cm (Bergman and Hup, 1992); although Steve Lockwood (CEFAS Conwy, pers. comm.) has reported catches of *E. cordatum* from trawls which penetrate less than 1 cm. The position of small urchins within the sediment column, and not their size, makes them vulnerable: smaller size-classes of heart urchins were found closer to the sediment surface and were most vulnerable to physical damage. Bergman and Hup (1992) emphasised the importance of considering the vulnerability of animals at different stages of their life history. In their study, it was estimated that 90% of the *A. islandica* in the catch had broken shells; although they did not provide information on the number that were damaged but remained in the sediment and were not able to sample this species adequately in order to determine changes in density. However, the prevalence of *A. islandica* in the stomach contents of Atlantic cod at times of intensive otter trawling in Kiel Bay, indicates that large numbers of these bivalves are damaged by trawling (Arntz and Weber, 1970). Rumohr and Krost (1991) found larger numbers of damaged *A. islandica* in a dredge towed directly behind an otter board than in the centre of the net. Furthermore, damaged *A. islandica* have been observed by divers while surveying areas of the seabed disturbed by beam trawls (Kaiser and Spencer, 1996a). Although *A. islandica* are vulnerable to damage by trawls, those that are slightly damaged can repair cracks in their shell matrix. As a consequence of physical damage, 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 and Klein, 1994). Witbaard and Klein (1994) studied annual growth rings in the shells of *A. islandica,* and were able to back-calculate 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 (Figure 4; Witbaard and Klein, 1994). Witbaard and Klein (1994) concluded that their study site had been disturbed by demersal fishing gear at least once per year during this period.

While it has been relatively simple to detect the changes in abundance of large macroinfauna which result from fishing disturbance, smaller fauna (< 10 mm) show conflicting responses. Furthermore, a recent study suggests that fauna below a certain body size or mass are resuspended by a pressure wave in advance of otter trawl doors, and are redistributed to the sides of the gear (Gilkinson *et al.* in press). Bergman and Hup (1992) found both decreases and increases in the abundance of smaller invertebrates after fishing an area of seabed with a beam trawl. A species-by-species analysis of responses to fishing gear disturbance (Bergman and Hup, 1992; Eleftheriou and Robertson, 1992) may have been less effective than the multivariate approaches adopted in more recent studies (Thrush *et al*., 1995; Currie and Parry, 1996; Kaiser and Spencer, 1996b). Furthermore, studies in the southern North Sea have been hampered by the inescapable fact that this area has already been disturbed by fishing for at least 100 yr (Figure 5).

Kaiser and Spencer (1996b) studied the effects of beam trawl disturbance at a site 27-40 m deep in the Irish Sea. Their experimental site encompassed two distinct habitats: stable sediments composed of coarse sand, gravel and shell debris, which supported a rich epifaunal filter-feeding community of soft corals and hydroids, and mobile sediments characterised by ribbons of megaripples with few sessile epifaunal species. Despite a robust experimental design with paired treatment and control areas, the effects of beam trawl disturbance were undetectable in the mobile sediments. This is not surprising given the levels of natural disturbance experienced in megaripple habitats (Shepherd, 1983). Similarly, de Wolf and Mulder (1985) reported that they could not provide accurate estimates of the abundance of benthic species in megaripple habitats because of the spatial variability within this type of habitat. In addition, animals living in the troughs of megaripples were less likely to be disturbed by fishing since the gears rode over the crest of each sand wave. Brylinsky *et al*. (1994) were also unable to detect any adverse effects of otter trawling over intertidal mud flats that are regularly exposed to large-scale disturbances such as ice-scour. Conversely, in stable sediments the effects of fishing are more noticeable. Kaiser and Spencer (1996b) found that the number of species and individuals in the stable sediment community was reduced by two and three-fold respectively. Their analysis also revealed that less common species were most severely depleted by beam trawling. In a similar study, Thrush *et al*. (1995) studied the effects of scallop dredging on a coarse sand community at a depth of 27 m. They were able to detect changes in the populations of individuals and compositional differences in the community that lasted for at least 3 mo after initial disturbance. Thrush *et al.* (1995) emphasised that their study was conservative as they were unable to simulate the effects of an entire fishing fleet, implying that at larger scales of disturbance recolonisation may take longer. Infauna that live within a few cm of the sediment surface at depths < 30 m tend to be small opportunistic species (e.g. spionid and capitellid polychaetes and amphipods) that quickly recolonise areas after disturbance (Dauer, 1984; Levin, 1984). As a consequence, the effects of trawling on this component of the infaunal community are unlikely to last more than 6 to 12 mo. However, a recent study by (Posey *et al*., 1996) suggested that deeper burrowing fauna were not affected by severe episodic storms. Their study site was at a depth of 13 m, and samples were collected to a depth of 15 cm. 'Deeper burrowing' was not defined, but it implies fauna living at a depth of 7-15 cm which is well within the depths disturbed by trawls and dredges (Krost *et al*., 1990; Bergman and Hup, 1992). If these fauna are less well adapted to periodic natural disturbances, they may be more severely affected by trawling activity.

In general, it seems reasonable to predict that the effects of physical disturbance will be short-lived in communities adapted to frequent natural perturbations in contrast to those communities found in habitats exposed to fewer disturbances. An extreme example of the former situation is Hall and Harding's (1997) study of the effects of mechanical and suction dredging and the scale of disturbance on an intertidal benthic community in the Solway Firth, Scotland. The immediate effects of cockle harvesting were obvious with a drastic reduction in the abundance of individuals; however the community in disturbed areas was comparable to that in control undisturbed areas after only 8 wk. This rapid recolonisation was attributed to the immigration of adults against a background of seasonal recruitment (Hall and Harding, 1997). This study contrasts with an investigation of the effects of suction dredging for manganese nodules on the abyssal plain of the Pacific Ocean (Thiel and Schriever, 1990; Thiel, 1992). Trenches created by the suction dredge head persisted for at least 2 years in this stable environment. While the persistence of disturbance effects may be approximately correlated to the level of natural disturbance experienced in a particular habitat, there are some exceptions. This is well illustrated in a recent study in which the effects of the scale of sediment defaunation were studied on an intertidal sandflat in New Zealand (Thrush *et al*., 1996). In contrast to Hall and Harding's (1997) findings, recolonisation rate was reduced at larger scales of disturbance. The main difference between these two studies was the presence, in the New Zealand study, of dense mats of tube building spionid worms which stabilised the sandflat sediments. Removal of these animals destabilised the sediment and exacerbated the effects of disturbance. Furthermore, while the changes associated with disturbance are relatively short-lived for the majority of small species, longer-lived organisms recolonise more slowly. For example, Beukema (1995) reported that the biomass of gaper clams, *Mya arenaria* L., took 2 yr to recover after commercial lugworm dredging in areas of the Wadden Sea, whereas small polychaetes and bivalves had recolonised the dredged areas within 12 mo. Long-lived epifaunal organisms frequently have a structural role within benthic communities, providing a microhabitat for a large number of species (see section 2.2.1.3). Calcareous algae of the genus *Lithothamnion* are amongst the oldest living marine plants in Europe and provide a substratum that can take hundreds of years to accumulate (Potin *et al*., 1990). The branching structure of the thalli provide a unique habitat for a diverse community of animals including commercial species such as scallops. Not surprisingly, scallop dredging in this habitat causes destruction of the interstices between the thalli and causes long-term changes to the composition of the associated benthic fauna (Hall-Spencer, 1995).

To date, most studies have been centred on the hypothesis that "..trawling/dredging has the potential to bring about long-term changes in community structure..", and have measured changes observed after an experimental fishing disturbance (Bergman and Hup, 1992; Eleftheriou and Robertson, 1992; Thrush *et al*., 1995; Currie and Parry, 1996; Kaiser and Spencer, 1996b; Pitcher *et al*. 1997). An alternative approach is to examine benthic community changes after closing areas that have been subjected to fishing disturbance for many years. Hill *et al.* (unpublished data) examined changes after the closure of an area within a scallop ground that had been heavily fished for over 50 years (Brand *et al*., 1991). After several years of closure, they found that the variation between infaunal samples within the closed area was greater than in the adjacent dredged areas. This suggests that intensive dredging leads to a more homogeneous environment, in a manner analogous to a tractor ploughing a meadow.

Van Dolah *et al.* (1991) studied changes in infaunal communities over a period of 5 mo within areas closed to fishing and in adjacent areas fished by shrimp trawlers. They concluded that seasonal reductions in the abundance and number of species sampled had a much greater effect than fishing disturbance. However, in a power analysis of their sampling strategy, only changes in the abundance of individuals and the number of species were considered. This assumes that the response of the infauna to trawling disturbance was unidirectional, whereas a consideration of changes in partial dominance might have been more sensitive to subtle changes in the fauna. While their results should be interpreted with caution it remains plausible that light shrimp trawls do not cause significant disturbance to communities in poorly sorted sediments in shallow water (Van Dolah *et al*., 1991). In addition, Van Dolah *et al.* (1991) sampled fauna from fished areas located between shoals and their study indicated that the local sediments were probably mobile and inhabited by fauna adapted to frequent disturbance (Kaiser and Spencer, 1996b).

Thus far, we have only considered the effects of fishing on infaunal communities living in coarse substrata. Most animals are found within the top 10 cm of these sediment habitats. However, in soft mud communities a large proportion of the fauna live in burrows up to 2 m deep (Atkinson and Nash, 1990). Consequently few of these deep burrowing fauna, such as thalassinid shrimps, are likely to be affected by passing trawls. Although upper burrow structures are collapsed by passing fishing gear, they are rapidly reconstructed (R.J.A. Atkinson personal communication). However, the energetic costs of repeated burrow reconstruction may have long-term implications for the survivorship of individuals. In addition, diel variation in behaviour may periodically increase the vulnerability of some species to fishing activities. For example, the burrowing shrimp *Jaxea nocturna* Nardo moves to the entrance of its burrow to feed at night (Nickell and Atkinson, 1995). These animals, along with other bioturbators, have an important role in maintaining the structure and oxygenation of muddy sediment habitats (Reise, 1981; Rowden and Jones, 1993; Fenchel and Finlay, 1995; Fenchel, 1996). Consequently, any adverse effects of fishing on these organisms would presumably lead to changes in habitat complexity and community structure.

2.2.1.3 Effects of trawls and dredges on epifauna

Intuitively, sessile epibenthic species are most likely to be vulnerable to the passage of bottom gears. Accordingly, observations of the changes in epifaunal communities in heavily fished areas have provided some of the first indications of the potential long-term effects of fishing on benthic communities. The disappearance of reefs of the calcareous tube building worm, *Sabellaria spinulosa* Leukart and their replacement by small polychaete communities, indicated that dredging activity had caused measurable changes in the Wadden Sea benthic community (Riesen and Riese, 1982). Similarly, Sainsbury (1987) reported a measurable decrease in the biomass of the sponge by-catch in the Australian north-west Shelf pair-trawl fishery from 1967 to 1985. Loss of the sponge community and associated fauna such as alcyonarians and gorgonians led to a reduction in the catches of emperors, *Lethrinus* spp., and snappers, *Lutjanus* spp. which sheltered and fed among the emergent fauna (Sainsbury, 1988). Langton and Robinson (1990) observed a c. 26% reduction in the mean density of the sabellid worm, *Myxicola infundibulum* (Renier, 1804) and the cerianthid anemone, *Cerianthus borealis* Verrill after one season of intense commercial scallop dredging on the Fippenies Ledges, Gulf of Maine. In addition, the significant negative association between these species became random after intensive fishing (Langton and Robinson, 1990). These authors hypothesised that cerianthid predation of scallop and sabellid worm larvae was an important factor controlling their spatial distribution. Thus the species association was broken down by dredging disturbance. Using a combination of fishing effort data and direct observations from side-scan sonar surveys, Collie *et al.* (1997) were able to identify comparable substrata that experienced different intensities of scallop dredging on the Georges Bank, north-west Atlantic. Areas that were less frequently fished were characterised by abundant bryozoans, hydroids and worm tubes which increased the three-dimensional complexity of the habitat (Figure 6). Furthermore, examination of evenness within the community suggested dominance by these structural organisms, which indicated that this environment was relatively undisturbed. In contrast, the more intensively dredged areas had lower species diversity, lower biomass of fauna, and were dominated by hard-shelled bivalves (e.g. *Astarte* spp.), echinoderms and scavenging decapods. The higher diversity indices observed at the less intensively dredged sites were attributable to the large number of organisms, such as polychaetes, shrimp, brittle stars, mussels and small fishes, that were associated with the biogenic fauna (Collie *et al.*, 1997). Many of these associated species were also important prey for commercially exploited fishes such as cod (Bowman and Michaels, 1984). Similarly, Auster *et al.* (1996) reported a reduction in habitat complexity as a result of fishing (trawling and scallop dredging) activity at three sites in the Gulf of Maine. Video observations made with an remote operated vehicle (ROV) revealed cleared swaths in the epifaunal cover on the border of the Swans Island conservation area which has been closed to fishing with mobile gears since 1983. As in other studies (Bradstock and Gordon, 1983; Sainsbury, 1987; Collie *et al.*, 1997), hydroids, bryozoans, sponges and serpulid worm matrices were greatly reduced in the fished areas. In addition, there was a reduction in the habitat features produced by some of the target species, e.g. pits created by scallops and crabs (Auster *et al.*, 1996). The Jeffreys Bank site was surveyed by submersible in 1987 and again in 1993. Boulders, 2 m wide, were a prominent feature of the site where towed fishing gear had been excluded until 1987. However, when the site was resurveyed, the percentage cover of sponges was greatly reduced, the thin mud veneer that previously covered the underlying gravel was no longer evident, and boulders appeared to have been moved across the seabed. The Stellwagen Bank area ranged in depth from 20 to 50 m, with a mixture of sand, gravel and shell debris habitats formed by large storm waves. These storm events are intermittent compared with the daily scallop dredging activity in the area. ROV surveys revealed that the area was characterised by dense aggregations of the hydrozoan *Corymorpha pendula* (Agassiz) which provided shelter for shrimp, *Dichelopandalus leptoceros* (Smith). Wide linear swathes through benthic microalgal cover indicated the occurrence of recent trawling and scallop dredging activity. The hydrozoans and associated shrimps were absent from these fished areas (Auster *et al.*, 1996). Recovery from disturbance may be rapid. Collie *et al.* (1997) found that the biogenic epifauna at a site, which had previously been dredged for scallops, and then closed to fishing, showed signs of recovery after 2 years and Kaiser *et al.* (1997) found that epifaunal communities that had been trawled over experimentally in relatively shallow (35 m) water were indistinguishable from control unfished areas after 6 months.

The effects of fishing on epifaunal communities may have ramifications for plankton communities which are often dominated by the larvae of invertebrates. The mesozooplankton taken in continuous plankton recorder samples in the central North Sea were numerically dominated by calanoid copepods from 1958 to the late 1970s whereas samples taken from the same stations from the early 1980s to early 1990s were dominated by the pluteus larvae of echinoid and ophiuroid echinoderms. This trend is consistent with the reported increases in the abundance of echinoderms in benthic communities which may have been stimulated, in part, by bottom trawling (Lindley *et al.*, 1995).

Where fishing occurs in shallow clear waters, marine plant communities are likely to be affected. In particular, seagrass meadows are vulnerable to physical disturbance as dredges and trawls reduce plant biomass and abundance by shearing off fronds, exposing rhizomes,digging shoots from the substratum and increasing local turbidity through sediment resuspension (Fonseca *et al.*, 1984). Guillén *et al.* (1994) reported that 45% of a *Posidonia oceanica* meadow in SE Spain was damaged by trawling and that in some areas the meadow no longer bound sediment effectively. Seagrass meadows are highly productive, support complex trophic food webs, provide sediment and nutrient filtration, enhance sediment stabilization and act as breeding and nursery areas for species of commercial importance (Short and Wyllie-Echeverria, 1996).

The studies that we have reviewed clearly illustrate the two main effects of mobile gears on epifaunal communities *i)* modification of substrata (shell debris, boulders, mud veneers) and *ii)* removal of biogenic taxa and a consequent decline in the abundance of fauna associated with them (see section 2.3). The loss of biogenic species not only reduces the supply of important prey species, but also increases predation risk for juvenile commercial species thereby lowering subsequent recruitment to the adult stocks (Walters and Juanes, 1993). Bradstock and Gordon (1983) reported the removal of extensive beds of bryozoans as a result of trawling activity and advocated the protection of these communities, noting that they provided an important habitat for juvenile commercial fishes. Moreover, Dayton *et al.* (1995) discuss the importance of different functional groups in maintaining community structure. Communities dominated by long-lived suspension feeders are most likely to be replaced by a community of opportunistic deposit-feeding species and mobile epifauna when subjected to large-scale and intense fishing disturbance. More dramatically, biogenic structures that increase the complexity of the epibenthic habitat (e.g. corals, bryozoans, worm tubes) create specialised environmental conditions by altering local hydrographic conditions that encourage the development of a specialised associated community. Loss of such structures will also affect the survivorship of any associated species and prolong the recolonisation process.

2.2.2 Static fishing gears

Static bottom gears are anchored to the seabed and left to fish passively. The most commonly used are gill, trammel or tangle nets, which are designed to capture target species by enmeshing or tangling them (Miller, 1985b; Potter and Pawson, 1991). Traps and pots are commonly anchored to the seabed in fleets, each pot or trap is baited to attract target species through one or more entrances into chambers in which the animals are trapped. Reefs are frequently damaged by the hauling of set nets, and the problem has been exacerbated by the use of mechanical net haulers or power blocks (Munro *et al.* 1987). The effects are regarded as minor in comparison with those attributable to drive netting and other active fishing techniques (see section 2.2.3). Since set net and pot fisheries are static the areas of seabed affected by each gear is likely to be insignificant compared with the widespread effects of mobile fishing gears. However, effort may be significant if concentrated in relatively small areas with communities of long-lived fauna. A recent study evaluated the effects of pot deployment and retrieval on supposedly fragile epifauna that are the subject of conservation interest in northern Europe (Eno *et al.*, 1996). Not surprisingly, pots that landed on, or were hauled through beds of the foliose bryozoan *Pentapora foliacea* (Ellis and Solander) caused physical damage to the brittle colonies. However, contrary to expectations, sea pens, *Pennatula phosphorea, Virgularia mirabilis* O.F. Muller and *Funiculina quadrangularis* Pallas bent in response to the pressure wave created by the descending pot and lay flat on the seabed. Moreover, when uprooted, the sea pens were able to re-establish themselves in the sediment. Sea fans, *Eunicella verrucosa,* (Pallas) were also found to be more flexible than anticipated, and were not severely damaged when pots were hauled over them (Eno *et al.*, 1996). These observations were interesting, because sea pens and sea fans were considered to be highly vulnerable to fishing activities (MacDonald *et al.*, 1997). The study of Eno et al. (1996) suggests that the direct contact of fishing gears with fauna may not be the primary cause of mortality and the frequency and intensity of physical contact is more likely to be important.

When nets or pots are lost, either because of bad weather, snagging or when towed away by mobile fishing gears, they may continue to fish. This phenomenon is known as 'ghost-fishing'. In contrast to the numerous records of bird, reptile and cetacean entanglement in set gears (see Dayton *et al.,* 1995 and references therein), little is known about the frequency of net loss or for how long lost gear is likely to fish. This lack of knowledge results from the reluctance of fishers to report such incidents and the difficulty in undertaking long-term studies in a realistic manner. Estimates of the proportion of nets lost from commercial fleets have been reported in a variety of studies reviewed by Dayton *et al.*, (1995). Losses of gear appear to be substantial. Approximately 7,000 km (20-30% of the total set each day) of drift nets were lost per year in a north Pacific fishery (Eisenbud, 1985). Complaints by fishers, prompted a grapnel survey of the seabed on Georges Bank which yielded 341 actively fishing ghost nets from 286 tows (Brothers, 1992). The phenomenon of ghost fishing was clearly perceived to have negative effects on commercial stocks by commercial fishers in the Greenland halibut fishery, who instigated their own voluntary clean-up programme (Bech, 1995). Considerable numbers of pots are also lost each year in North America. It was estimated that the 31,600 pots lost in the Bristol Bay king crab fishery removed c. 80,000 kg of crabs from the stock (Kruse and Kimber, 1993). In another study, Breen (1987) reports an annual loss of c. 11% of the traps used in the Dungeness crab *Cancer magister* Dana fishery in British Columbia.

Both lost nets and pots can persist and continue to fish in the marine environment for several years (Carr *et al.*, 1992), although their actual persistence will depend on the prevailing environmental conditions. Nets lost in areas exposed to large swells and storm activity are rapidly destroyed by physical forces (E. Puente, personal communication). Those lost in shallow, clear waters are rapidly overgrown with epibiota which makes them highly visible, reducing their fishing capabilities (K. Erzini personal communication). However, in circumstances where nets or pots are snagged onto rocks, holding the net in place, or lost in deep water in a relatively stable environment, they may continue to fish indefinitely (Carr *et al.*, 1992). Recent studies have shown that in these cases, a typical pattern of capture is observed. Over the first few days, catches decline almost exponentially as the increasing weight of catch causes the net to collapse. Then, for the next few weeks, the decaying bodies of fishes and crustacea attract large number of scavenging crustaceans, many of which are valuable commercial species and also become entangled in the net. Thereafter, there appears to be a continuous cycle of capture, decay and attraction for as long as the net has some entanglement properties (Carr *et al.*, 1992; Kaiser *et al.*, 1996a).

Pots tend to be constructed of robust materials and have a rigid structure which means that lost pots are likely to maintain a higher capture efficiency for much longer than lost nets. Not surprisingly, ghost-fishing mortality rates of up to 55% of the mortality rates recorded in attended pots have been reported (High, 1976; Miller, 1977). A rebaiting cycle occurs in lost pots as described for lost nets above, which suggests that an intact pot could fish indefinitely (B. Bullimore, personal communication). The 'ghost-fishing' potential of pots also varies for different fisheries and pot designs. For example, Parrish and Kazama (1992) found that the majority of Hawaiian spiny lobster, *Palinurus marginatus* and slipper lobster, *Scyllarisdes squammosus* were able to escape traps, whereas parlour-type traps lead to mortalities of 12-25% for American lobster, *Homarus americanus* (Smolowitz, 1978).

Compared with the proportions of target species removed by mobile fishing gears, the number of organisms removed by ghost-fishing is probably small. However, these fisheries tend to be highly localised leading to a concentration of lost gear within relatively small areas. Consequently, the proportion of local stocks removed can be significant (Kruse and Kimber, 1993). Furthermore, many of these species have a high individual value and hence represent a large economic loss to the local fishing industry. In order to reduce these losses for undersized specimens, escape panels are now fitted to many pots used in North America and biodegradable materials are used to ameliorate losses from 'ghost-fishing' (Guillory, 1993; Polovina, 1994).

2.2.3 Drive netting, poisons and explosives

Techniques such as drive-netting, pull-seining, poison and explosive fishing are principally used by small scale and artisanal fishers fishing on tropical reefs. Although the effects attributable to the activities of individual fishers are often small in comparison with those attributable to commercial fishing boats using towed gears, the combined effects of their activities are considerable given the large proportion of the coastal population involved in fishing (Pauly, 1988; Pauly *et al.*, 1989; Dalzell *et al.*, 1996). Many of the fishing techniques used to catch reef associated fishes cause direct physical damage to the reef substratum. The most widely used destructive fishing techniques are drive netting (Carpenter and Alcala, 1977; Gomez *et al.*, 1987), trapping (Munro *et al.*, 1987) and explosive fishing (Munro *et al.*, 1987). In addition, those poisons widely used to catch fishes for the aquarium trade and consumption have the potential to cause chemical damage to corals and non-target fishes and invertebrates (Rubec, 1986; Eldredge, 1987; McAllister, 1988; Pyle, 1993).

Corals perform several important functions in tropical environments. They provide substrata for primary production, habitats for invertebrates and fishes and often play a key role in protecting coasts from wave exposure and erosion. The rate at which reefs develop is determined by the balance between rates of accretion owing to the growth of corals, hydrocorals and coralline algae and erosion owing to mechanical processes and bioerosion. Fishing affects reefs directly when gears contact the reef substratum or indirectly by altering the relationships between those communities of plants, invertebrates and fishes which determine rates of reef accretion and bioerosion (see section 2.3). Coral accretion relies upon the successful settlement of young corals, and the maintenance of suitable conditions for their growth (Pearson, 1981). These processes may be affected by fishing activities.

Drive netting techniques are used to catch a range of reef associated fishes which shelter within the reef matrix or shoal above the reef. These techniques are extensively used on coral reefs, and may range from small scale village-based operations involving four or five fishers to large commercial operations which target offshore reefs in the Philippines and South China Sea and involve hundreds of divers (McManus, 1996). The process of drive netting requires that the fishers (who stand on the reef or dive) scare reef-associated fishes towards an encircling net or trap, using scaring devices such as weighted lines or poles. In shallow water, corals are often broken deliberately to scare closely reef-associated fishes such as groupers (Epinephelinae), snappers or emperors from their refuges. In deeper water, the *Kayakas* and *muro-ami* drive-netting techniques involve teams of swimmers which repeatedly drop weighted scarelines onto the reef in order to drive fishes towards a bag net. Carpenter and Alcala (1977) calculated the damage to one hectare of reef during a single *muro-ami* operation involving 50 fishers who each struck the bottom 50 times with a 4 kg weighted scareline. Six percent of the total area of coral present was damaged.

Blast fishing is practised on many reefs in the Atlantic, Pacific and Indian Oceans (Gomez *et al*., 1981; Polunin, 1983; Galvez and Sadorra, 1988; Ruddle, 1996). A variety of explosives are used including those obtained from mines or removed from armaments. Pelagic fishes living above the reef are often targeted rather than fishes living in direct association with the reef (Saila *et al*., 1993). Owing to the considerable variation in the types and sizes of charges used, and the depths at that they explode, it is difficult to make useful generalisations about the damage which they will cause. Alcala and Gomez (1987) report that a bottle bomb exploding at or near the bottom will shatter all corals within a radius of 1.15 m, and that a gallon-sized drum will have the same effect within a radius of 5 m. A 'typical' charge will kill most marine organisms including invertebrates within a radius of 77 m. Such techniques are highly unselective and Munro *et al*. (1987) report that post-larval and juvenile fishes are also killed. These young fishes would be about to recruit to the reef habitat, and the repeated effects of blast fishing on a large scale would reduce fish production from the reef. On those reefs from 15-30° either side of the equator, which are susceptible to hurricane damage, the effects of blast fishing are often localised and negligible in comparison with those of hurricanes (S. Jennings, personal observation). In other areas, especially in the Philippines, damage attributable to blast fishing is an increasing cause of concern.

Stupefacients are widely used by reef fishers. Traditionally, poisons extracted from plants were extensively used for reef fishing, but in the last few decades, synthetic chemicals such as sodium cyanide and chlorine have been used more frequently (Rubec, 1986; Eldredge, 1987). McAllister (1988) estimated that 150 t of sodium cyanide is used annually on Philippine reefs to catch aquarium fishes. There is little knowledge of the effects of these chemicals on the various life-history stages of the reef biota (Rubec, 1986; Pyle, 1993) and while concentrations of stupefacients which have an acute effect are quickly dispersed, the chronic effects may be significant.

The long-term direct effects of fishing on reefs are largely determined by the rate at which coral can accrete in relation to the rate at which it is damaged. The recovery and recolonization of coral communities following mechanical damage by fishing gears takes place when partially damaged colonies or coral fragments regrow and when the substratum becomes suitable for coral settlement (Pearson, 1981). Saila *et al*. (1993) developed a model to examine the effects of blast fishing on reefs in the Philippines. At present fishing intensities, the loss of diversity and coral cover would continue for approximately 25 years before recovery is expected. Coral growth rates are highly variable: 0.7 to 17.2 cm y^{-1} for branching species and 0.5-1.9 cm y^{-1} for massive species (Loya, 1976; Huston, 1985; Witman, 1988). Several studies of reef development following hurricanes and other natural events provide a useful guide to recovery rates. Published estimates of recovery time often vary widely because they reflect differences in the authors' assumptions regarding the organisation of coral communities and the meaning of 'stability' (Moran, 1986; Done, 1987; Done, 1988; Done *et al*., 1988; Endean *et al*., 1988; Moran, 1990; Turner, 1994; McClanahan *et al*. 1996). However, a coral community dominated by fast growing branching species and which provides a suitable habitat for many reef fishes would develop within five years (Pearson, 1981).

2.3 Indirect effects on habitat

The direct effects of fishing change the structure of fish and benthic communities and may lead to the resuspension of sediments. Changes in the structure of fish and benthic communities may affect the growth of those organisms which are responsible for structuring habitats. The resuspension, transport and subsequent deposition of sediment may affect the settlement and feeding of the biota in other areas. Trawling, in particular, can be responsible for resuspending a large proportion of the sediment load in some marine environments. Those parts of the trawl net that come into contact with the sea bed will cause bottom sediments to be resuspended but the turbulence created by the trawl doors suspends most material and plays a key role in herding fishes towards the net (Main and Sangster, 1981). The quantity of sediment resuspended by trawling depends on sediment grain size and the degree of compaction which is higher on mud and fine sand than on coarse sand. Sediment concentrations of 100-550 mg l^{-1} have been recorded 100 m astern of shrimp trawls in the muddy Corpus Christie Bay (Schubel *et al*., 1978) and Churchill (1989) reported that transmissometers, which had been employed to record turbid water parcels, frequently recorded the highest levels of turbidity during periods of trawling activity. In deeper areas where storm-related bottom stresses were generally weak, the quantity of sediment resuspended by otter trawling was significant. Churchill (1989) produced sediment budgets for parts of the mid-Atlantic Bight and concluded that trawling was the main factor initiating the offshore transport of sediment at depths of 100-140 m (Figure 7). However, the transport of sediment resulting from fishing activities would not produce significant large scale erosion over a period of a few years. In deeper water, where currents are weak and sediment is rarely in suspension, the effects of resuspension and subsequent deposition are readily detected. Thiel and Schriever (1990) investigated the potential effects of mining polymetallic nodules at depths > 4000 m by harrowing the sediment with an 8 m wide rake. Having harrowed 20% of the study area during 78 traverses, the remaining 80% of the area was affected by the redeposition of sediment. The potential effects of sediment resuspension include clogging of feeding apparatus or reduction of light availability (Rhoads, 1974) and sediment deposition has been shown to inhibit the settlement and growth of oysters and scallops (Moore, 1977; Jones, 1992). However, given the range of sediment types in the marine environment and the natural spatial and temporal variations in sediment load (Moore, 1977), it is unlikely that the population level consequences of sediment resuspension and deposition can be determined from small scale studies of siltation effects.

The surface of marine sediments is an important site of benthic production. Brylinsky *et al.* (1994) demonstrated that the biomass of benthic diatoms (measured as chlorophyll *a*) was significantly less in trawl door furrows on a muddy substratum in shallow water. However, one month after the trawling had taken place there was a diatom bloom in the furrow, which Brylinsky *et al.* (1994) attributed to the release of nutrients from the sediment. Emerson (1989) considered the effects of sediment disturbance resulting from wind stress on production in the southern North Sea, and found a significant negative correlation between wind stress and total macro- and meiobenthic production. The intensive trawling of *Posidonia oceanica* meadows in the Mediterranean Sea may lead to reductions in littoral primary productivity since large areas of *P. oceanica* are reported to have been killed by the mechanical action of fishing gears and the deposition of resuspended sediment (Guillén *et al.*, 1994). These meadows are known to be important sources of primary production although the consequences of losses in production are not known. It is unlikely that large scale changes in primary production could be reliably correlated with changes in fishing intensity using existing data. However, given that a large proportion of the continental shelf area is now trawled, and that tools such as stable isotope analysis can be used to trace the origins and transformations of organic matter in the marine environment (Owens, 1987; see section 5.3) it is increasingly likely that the impacts of fishing on the relative roles of benthic and planktonic based food chains could be investigated.

The most convincing evidence for the indirect effects of fishing on habitat structure comes from the study of fishing effects on coral reefs. The direct effects of fishing (see section 2.2.3) have been widely reported because popular reef fishing techniques often cause rapid and highly visible damage. However, the intensity and selectivity of fishing practices may have been responsible for initiating the transition of reef communities between relatively stable algal and coral-dominated phases. Understanding the ways in which fishing can lead to shifts in ecosystem state is dependent on an understanding of the roles of herbivores and corallivores in the reef ecosystem. Herbivorous and corallivorous species both erode the reef matrix and the rate at which coral reefs grow is determined by the relative rates of coral accretion and erosion. Some species of parrotfishes (Scaridae) and urchins erode the reef matrix while feeding on algae (Birkeland, 1989; Bak, 1990, 1994; McClanahan, 1992, 1995a; Bellwood, 1995) and may markedly reduce rates of reef accretion (Glynn *et al.*, 1979; Birkeland, 1989; Macintyre *et al.*, 1992). Corallivorous species such as the crown of thorns starfish *Acanthaster planci* (L.) and the gastropod *Drupella* spp. cause erosion by feeding directly on coral (Moran, 1986; Turner, 1994).

Herbivorous fishes and invertebrates not only determine rates of reef accretion but may also have a substantial impact on the distribution and abundance of reef algae (Brock *et al.*, 1979; Hay, 1984; Hay, 1985; Hay and Taylor, 1985; Lewis and Wainwright, 1985; Carpenter, 1986; Lewis, 1986). Herbivorous fishes may clear space for coral settlement and thereby enhance the survival and growth of young coral colonies but, unlike urchins, most herbivorous fishes do not damage these colonies once they are growing (Potts, 1977; Bak and Engel, 1979; Brock *et al.*, 1979; Sammarco, 1980; Lessios *et al.*, 1984; Hughes *et al.*, 1987b).

Herbivorous fishes are targeted by many reef fishers and their abundance may be significantly reduced on intensively fished reefs. Sea urchins, however, are rarely important target species and once the biomass of herbivorous fishes is reduced by fishing the urchins begin to dominate the grazing community. In addition, the biomass of those fishes which prey on urchins (Hiatt and Strasburg, 1960; Randall, 1967; Hoffman and Robertson, 1983; Reinthal *et al.*, 1984; McClanahan, 1995b) is also reduced by fishing since many of these species, in particular triggerfishes (Balistidae) and emperors, are targets of reef fishers or are easily caught because of their aggresive behaviour. McClanahan (1992) developed a biomass based energetic model to describe algal grazing by sea urchins and herbivorous fishes which suggested that sea-urchins would tolerate low algal biomass owing to their low consumption and respiration rates. This enables them to persist at low levels of algal biomass and productivity, out-competing herbivorous fishes and reaching maximum biomass levels an order of magnitude higher. As a result, once an urchin-dominated community is established it is unlikely that herbivorous fishes can re-establish themselves (McClanahan and Shafir, 1990; McClanahan, 1992).

Relationships between predatory fishes and their urchin prey have been explored on Kenyan reefs by comparing herbivore communities at a series of sites subject to different fishing intensities (McClanahan and Muthiga, 1988; McClanahan and Shafir, 1990; McClanahan and Obura, 1995) where the triggerfish *Balistapus undulatus* (Park) and wrasse *Chelinus trilobatus* (Linnaeus) are the main urchin predators (McClanahan, 1995b). Predator removal through fishing appeared to result in the ecological release of sea urchins and the competitive exclusion of weaker competitors such as herbivorous fishes. Thus the more heavily exploited Kenyan reef lagoons were characterised by denser populations of larger sea urchins, fewer and smaller fishes and reduced coral cover (McClanahan and Muthiga, 1988). Changes in fishing pressure and urchin mortality and urchin recruitment are responsible for shifting these Kenyan reef ecosystems to different, and relatively stable, states (Figure 8). McClanahan (1992) suggested that the persistence of herbivorous fishes on many reefs may be dependent on the presence of sea urchin predators which maintain sea urchins at a level that prevents them becoming dominant. Similarly, the structure of urchin *Paracentrotus lividus* (Lck) populations in the north-western Mediterranean also appear to be controlled by fish predators which are affected by fishing. Sala and Zabala (1996) demonstrated that the density of urchin populations in a marine reserve where their potential fish predators were abundant was significantly lower and that the urchins tended to adopt a crevice dwelling behaviour rather than feeding on exposed surfaces.

When the effects of intensive exploitation on herbivorous fish populations are coupled with a decrease in the abundance of invertebrate herbivores, the resulting increase in algal biomass may have a marked influence on the development of coral reefs. Thus the mass mortality of the algal feeding sea-urchin *Diadema antillarum* in those intensively fished regions of the Caribbean where herbivorous fishes were already scarce (Bak *et al*., 1984; Lessios *et al*., 1984, 1985; Carpenter, 1985, 1988a, 1990; Hughes *et al*., 1987a, b; Lessios, 1988) was followed by significant increases in algal cover and significant decreases in coral cover (Hughes *et al*., 1987b; Done, 1992; Knowlton, 1992; Hughes, 1994).

Crown-of-thorns starfish feed directly on living coral and outbreaks of this species have led to widespread decreases in live coral cover and reef structural complexity (Goreau *et al*., 1972; Endean and Stablum, 1973; Glynn, 1973; Nishihira and Yanmazato, 1974; Faure, 1989; Zann *et al*., 1990) reducing the availability of suitable habitat for reef fish communities (Sano *et al*., 1984; Bouchon-Navaro *et al*., 1985; Williams, 1986). The existence of an inverse relationship between the abundance of crown-of-thorns starfish and their fish predators suggests that starfish population outbreaks could have resulted from the removal of fishes such as emperors and triggerfishes that prey upon juvenile starfish (Ormond *et al*., 1991). Keesing and Halford (1992) documented mortality rates of over 6% day $^{-1}$ for crown-of-thorns starfish which had recently settled to the benthic habitat and attributed this to predation. Sweatman (1995) studied predation on juvenile crown-of-thorns starfish in one location on the Great Barrier Reef and his data suggested that the predation rates would be too low to regulate crown-of-thorns starfish populations. At present, there is only weak inference to suggest that removal of predators is responsible for outbreaks of crown of thorns starfish. Further studies to test quantitative hypotheses on larger temporal and spatial scales are needed to determine the indirect impacts of fishing on crown-of-thorns starfish populations. If intensive fishing can lead to crown-of-thorns outbreaks then there is good evidence to suggest that this would reduce the potential fish production from a reef ecosystem.

The muricid gastropod *Drupella* spp. is corallivorous and rapid increases in its population density have led to coral mortality approaching that caused by crown-of-thorns starfish (Turner, 1994). The removal of *Drupella* predators by fishers has been cited as a possible cause of these outbreaks (Turner, 1994) but the significance of fishing cannot reliably be determined using the limited data currently available (McClanahan, 1994b; Ayling and Ayling, unpublished).

Degradation of reef habitats which results from the direct or indirect effects of fishing will affect fish yield, both by causing a redistribution of the exploitable fish biomass and, in severe cases, by reducing the potential production of that ecosystem. Russ and Alcala (1989) suggested that reduced butterflyfish (Chaetodontidae) abundance in a newly exploited Philippine reserve was a result of a reduction in live coral cover associated with destructive fishing techniques, although they commented on the difficulty of differentiating between effects resulting from direct removal of fishes and those resulting from habitat modification. Porter *et al.* (1977) noted a significantly lower biomass of zooplankton was associated with rubble rather than coral habitats and it might be expected that fish density would change in response to such changes in food supply. The abundance of many reef fishes is positively correlated with topographic complexity (Risk, 1972; Porter *et al.*, 1977; de Boer, 1978; Luckhurst and Luckhurst, 1978; Carpenter *et al.*, 1981; Thresher, 1983; Kaufman and Ebersole, 1984; Patton *et al.*, 1985; Roberts and Ormond, 1987; Grigg, 1994; Jennings *et al.*, 1996a) and habitat complexity will also influence the rates at which larval fish recruit to the reef from the plankton (Jones, 1988; Connell and Jones, 1991). Most of these studies demonstrate habitat effects by making comparisons between sites within regions of high habitat complexity. The differences are greater when large well-developed areas of reef are compared with areas that have been fished destructively until little topographic complexity remains (Pauly *et al.*, 1989).

Changes to kelp bed habitats in temperate waters have been attributed to the indirect effects of fishing, but subsequent re-examination of the evidence for these changes suggested that fishing was not the cause. On the Atlantic coast of Nova Scotia, the reduction in the biomass of American lobster was assumed to have led a reduction in the predation rates on the sea urchin *Strongylocentrotus droebachiensis* (O.F. Müller). As a result, urchin populations flourished, leading to the destruction of kelp beds (Mann and Breen, 1972; Mann, 1982). However, more detailed analysis of feeding rates, stomach contents and biomass of lobsters indicated that they could not have controlled the population structure of urchins (Miller, 1985a) and that the increases in urchin populations which led to the destruction of kelp beds may have been stimulated by increased larval recruitment (Hart and Scheibling, 1988) .

2.4. Natural versus fishing disturbance

To date, most studies have investigated the effects of fishing on benthic communities in shallow seas on the continental shelf at depths < 100 m. This is not surprising as the majority of demersal fishing activity occurs in this depth range, and quantitative ecological studies become logistically complex at greater depths. Benthic communities in these environments experience continual disturbance at various scales (Hall, 1994). Large-scale natural disturbances, such as seasonal storms and strong tidal currents, form a background against which other smaller disturbances occur, such as those induced by predator feeding activities (Von Blaricom, 1982; Oliver and Slattery, 1985; Hall *et al.*, 1994). Hall *et al.* (1994) suggested 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 and Saunders, 1973; Connell, 1978). They concluded, however, that while it was possible to detect short-term effects of predator disturbance, large-scale effects could not be inferred. This implies that small-scale disturbance events, even when frequent, are masked by a background of large-scale disturbances or that the small-scale of disturbance permits rapid recolonisation such that large-scale effects never become apparent. These observations are summarised in Figure 9.

Clearly, the scale and frequency of disturbance events can increase until lasting ecological effects can be observed against a background of natural disturbance. The additive effects of an entire fishing fleet may reach such a threshold. Moreover, fishing effort in shelf seas is not homogeneously distributed. Fishers 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 severely restricted in some areas, such as shipping lanes and around oil rigs. Consequently, early estimates of area swept by bottom gears are unintentionally misleading as they imply physical disturbance spread homogeneously across large (> 100 km^2) areas (Welleman, 1989). More recently, ‘black box’ recorders have been fitted to a proportion of the Dutch beam trawl fleet which has allowed satellite tracking during fishing operations. The Dutch fleet accounts for 50-70% of the total beam trawling effort in the North Sea (Rijnsdorp *et al.*, 1996a). These records indicate that beam trawling effort is very patchily distributed in the North Sea; while it is estimated that some areas are visited > 400 times per year, others are never fished (Rijnsdorp *et al.*, 1996a). 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. Up to 55% of the starfish, *Astropecten irregularis* Pennant had lost arms in a heavily beam-trawled area of the Irish Sea, compared with only 7% in a less intensively fished area (Kaiser, 1996). Within intensively fished grounds, the background levels of natural disturbance may have been exceeded leading to long-term changes in the local benthic community. However, as pointed out by many previous authors, communities observed at the present time may be the product of decades of continuous fishing disturbance (Bergman and Hup, 1992; de Groot and Lindeboom, 1994; Dayton *et al.*, 1995).

Detecting those long-term changes in benthic fauna which can be attributed to fishing activities has been problematic in all but the most obvious cases (Riesen and Riese, 1982; Sainsbury, 1987). However, a few long-term datasets which record by-catches of benthic species have revealed reductions in potentially vulnerable species or changes in epibenthic communities. Philippart (1997) examined a dataset of returns of epibenthic by-catch species from the southern North Sea dating back to the 1930's. Fishers were paid to retain examples of a 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 as beam trawls catch a larger proportion of benthic species compared with otter trawls. However, the decrease in the incidence of species returned to the laboratory continued after 1970. Furthermore, Holtmann *et al.* (1996) reported a decrease in the abundance of the fragile burrowing heart urchin and the brittlestar *Amphiura filiformis* O.F. Muller in areas of the southern North Sea between 1990 and 1995. These trends suggest that fishing activity may have been the main cause of these changes. However, it is problematic to attribute these changes to fishing alone, as the southern North Sea has been influenced by eutrophication events leading to increases in the abundance of polychaete species and echinoderms such as *A. filiformis* (Pearson *et al.*, 1985) and by oceanographic changes (Lindeboom *et al.*, 1995). These observations emphasise the value of time-series data for identifying the factors which have had most influence on changes in community structure (see chapter 5).

2.5. Conclusions

Fishing activities lead to changes in the structure of marine habitats and influence the diversity, composition, biomass and productivity of the associated biota. The direct effects of fishing vary according to the gears used and the habitats fished, but they usually include the scraping, scouring and resuspension of substratum and occur against a background of natural disturbance. The relative impact of fishing on habitat and benthic community structure is determined by the magnitude of natural disturbance. The direct effects of a given fishing method on infaunal and epifaunal communities will tend to increase with depth and the stability of the substrate. In sheltered areas where complex habitats develop at minimal depth, such as coral reefs, the direct effects of fishing may be marked and have profound effects on the ability of the habitat to sustain fish production.

The indirect effects of fishing on sea urchin populations and their subsequent effects on the rate of accretion and bioerosion in the reef habitat are one of the few well documented examples of top-down control in marine ecosystems (see chapter 4). When a few species of predator, all of which may be fished, selectively feed upon one or two species of urchin which otherwise dominate the herbivore community on a reef, they have an unusual role of keystone species in a marine system. However, the tightly coupled relationships between urchins and their fished predators should not be regarded as ubiquitous and further work is needed to determine the relative roles of predator and environmental control in other ecosystems.

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