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by

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ABSTRACT

A three-year experiment was conducted to examine the effects of repetetive otter trawling on a sandy bottom ecosystem at a depth of 120-146 m on the Grand Banks of Newfoundland. The most pronounced impacts were the immediate effects on habitat physical structure. However, these effects were relatively short-lived since the available evidence shows that the habitat recovered in about a year or less. Except for snow crabs and basket stars, direct removal of epibenthic fauna by the otter trawl appeared to be insignificant because of its very low efficiency in catching benthic organisms. Immediately after trawling, the mean biomass of epibenthic organisms (as sampled with an epibenthic sled) was reduced on average by 24%. The most affected species were snow crabs, basket stars, sand dollars, brittle stars, sea urchins and soft corals. Both the immediate and long-term impacts of otter trawling, as applied in this experiment, on the resident benthic infauna (as sampled by a large videograb) appeared to be minor. Significant effects could not be detected on the majority of species found at the study site, including all the molluscs. All available evidence suggests that the biological community recovered from the annual trawling disturbance in less than a year, and no significant effects could be seen on benthic community structure after three years of otter trawling. The habitat and biological community at the experimental site are naturally dynamic and exhibited marked changes irrespective of trawling activity, and this natural variability appeared to over-shadow the effects of trawling.

The results of this experiment are specific to the conditions under which it was conducted (i.e. annual otter trawling on a deep sandy bottom with few structure-forming organisms), and one must be very cautious in extrapolating them to other conditions. Further research is needed to improve our knowledge of otter trawling impacts, and to develop the information needed to adopt a more ecosystem-oriented approach to fisheries, habitat and oceans management. Information requirements include further gear impact experiments, improving our understanding of the role that benthic habitat and communities play in marine ecosystems, mapping benthic habitat and communities, and mapping the fine-scale spatial distribution of fishing effort. Possible management actions that should be considered to protect sensitive benthic habitat and communities include control of fishing effort, gear usage and modification, gear substitution, and area closures.

RÉSUMÉ

On a réalisé une expérience sur trois ans afin d'examiner les effets du passage répété de chaluts à panneaux sur l'écosystème d'un fond sableux, à une profondeur de 120-146 m, sur les Grands Bancs de Terre-Neuve. Les incidences immédiates sur la structure physique de l'habitat étaient les plus marquées. Toutefois, elles étaient de durée relativement courte, puisque, selon les preuves dont on dispose, l'habitat s'en remettait dans environ un an ou moins. Sauf pour ce qui est des crabes des neiges et des fausses étoiles de mer, le retrait direct de faune épibenthique par le chalut à panneaux semblait négligeable, à cause de la très faible efficacité du chalut pour la capture d'organismes benthiques. Immédiatement après le chalutage, la biomasse moyenne des organismes épibenthiques (échantillonnée au moyen d'une traîne épibenthique) était réduite en moyenne de 24 %. Les espèces les plus touchées étaient les crabes des neiges, les fausses étoiles de mer, les clypéastres, les ophiures, les oursins et les mains de mer. Dans les conditions d'expérience, les effets, tant immédiats qu'à long terme, du chalut à panneaux sur l'endofaune benthique résidente (échantillonnée au moyen d'une grande benne-vidéo) semblaient minimes. On n'a pas décelé d'effet important sur la majorité des espèces trouvées sur les lieux de l'expérience, y compris tous les mollusques. Tout semble indiquer que la communauté biologique s'est remise en moins d'un an des perturbations annuelles dues au chalutage et qu'aucune incidence importante n'a été observée sur la structure de la communauté benthique après trois années de chalutage. L'habitat et la communauté biologique sur le lieu de l'expérience ont une dynamique naturelle et présentaient des changements marqués, indépendamment de l'activité de chalutage; cette variabilité naturelle semblait éclipser les effets du chalutage.

Les résultats de cette expérience sont propres aux conditions dans lesquelles celle-ci a été réalisée (c'est-à-dire opération de chalutage annuelle sur un fond sableux profond comportant peu d'organismes qui élaborent des structures). Il convient d'être très prudent dans leur extrapolation à d'autres conditions. De plus amples recherches sont nécessaires pour améliorer notre connaissance des incidences de l'utilisation des chaluts à panneaux et pour obtenir l'information nécessaire à l'adoption d'une gestion des pêches, de l'habitat et des océans davantage axée sur l'écosystème. Il nous faut, notamment, réaliser d'autres expériences sur les incidences des engins, mieux comprendre le rôle que jouent l'habitat et les communautés benthiques dans les écosystèmes marins et établir des cartes à petite échelle de la distribution spatiale de l'effort de pêche. Pour protéger l'habitat et les communautés benthiques vulnérables, on pourrait, par exemple, régir l'effort de pêche, l'utilisation et la modification des engins ainsi que les substitutions d'engin, et établir des zones de fermeture.

DEDICATION

This report is dedicated to the memory of our colleague Peter Schwinghamer who died on 22 May 1999 after a long and courageous battle with a brain tumour. He played a leading role in the design and execution of the Grand Banks otter trawling experiment, as well as in the early stages of data analysis and interpretation. During his all-too-brief scientific career, Peter earned an excellent international reputation as an innovative benthic ecologist (Gordon et al. 1999). He was an independent thinker who constantly and effectively challenged the status quo and was a continuous source of new ideas. We are richer for having had the privilege of working with him.

INTRODUCTION

Mobile fishing gear such as beam trawls, otter trawls, scallop rakes and clam dredges are widely used around the world to harvest benthic fishery resources, and concerns have been raised about their environmental effects. A large number of scientific studies of their impacts on benthic habitat and communities have been conducted, and numerous reviews have been published (e.g. Jones 1992, Dayton et al. 1995, Dorsey and Pederson 1998, Lindeboom and de Groot 1998, Jennings and Kaiser 1998, Watling and Norse 1998, Auster and Langton 1999, Hall 1999, Collie et al. 2000a, WGECO 2000, Northeast Region Essential Fish Habitat Steering Committee 2002, National Research Council 2002).

Understanding the impacts of mobile gear on benthic habitat and communities is a difficult and expensive undertaking, especially in offshore marine environments. Benthic habitats and communities display considerable natural variability, both spatial and temporal, which must be factored into the design of research programs. Sources of natural variation include storm waves, tidal currents, ice, bioturbation and foraging by predators. While some useful information can be obtained from laboratory experiments, well-designed field programs are essential. Small-scale manipulative experiments can provide direct evidence on immediate impacts of a known disturbance event (e.g. gear type, location, intensity) on a particular habitat but, to date, most of these have been conducted in relatively shallow water (where wave-generated natural disturbances frequently affect the seabed), have been of limited spatial extent, and have been short-term in nature. Alternatively, observational studies comparing areas with different fishing histories, or observations over time in the same area, can provide indirect evidence of longer-term impacts at the spatial scale of whole fishing grounds, though the conclusions may be equivocal as natural fluctuations may be mistakenly attributed to human impacts. With observational studies, it can be difficult to study the impacts of specific gear types since fished areas often have histories of multiple gear usage. Regardless of the experimental approach taken, it is necessary to include observations in reference areas not influenced by previous fishing disturbance. Because of the widespread use of mobile fishing gear, these can be difficult to find.

Over the past 50 years, otter trawls have been widely used on the continental shelf of Atlantic Canada to capture bottom dwelling species such as cod, haddock, plaice, flounder and shrimp (Messieh et al. 1991). Throughout this period, there has been increasing concern about the potential effects of this gear on benthic habitat and communities. More recently there has been debate over the possible role of trawling effects in the collapse of regional groundfish stocks that occurred in the early 1990's.

Investigating the effects of bottom fishing gear has a long history in Canada (e.g. Ketchen 1947, Caddy 1973, Scarratt 1973, Pringle and Jones 1980, Jamieson and Campbell 1985, Robichaud et al. 1987). In 1990, the Department of Fisheries and Oceans began a long-term multidisciplinary research program to study the impacts of mobile fishing gear on the benthic habitat and communities of Atlantic Canada. From the very beginning, this has been a collaborative effort between the Newfoundland and Maritime Regions. One of the first initiatives was to conduct an experiment on the effects of otter trawling on the intertidal habitat and communities in the Minas Basin of the Bay of Fundy (Brylinsky et al. 1994). The observed impacts were minor, and can not be extrapolated to offshore sites because of major differences in water depth, energy levels, habitat type and biological communities. Another early initiative was to compile information on the extent and intensity of otter trawling off eastern Canada using archived sidescan sonar data from the Scotian Shelf and Grand Banks (Jenner et al. 1991, Harrison et al. 1991). Disturbance from otter trawling and other gear types was readily visible in many of the records but usually found only in areas of low sediment transport suggesting that trawling disturbance might be readily obliterated on high energy seabeds and that sidescan sonar records are inadequate for estimating the distribution of trawling activity. Another early initiative was to develop adequate sampling equipment and navigational procedures for conducting mobile gear impact experiments on offshore ecosystems.

During 1993-1995, the Department of Fisheries and Oceans (DFO) conducted a manipulative experiment on the effects of otter trawling on a deep sandy bottom ecosystem on the Grand Banks of Newfoundland. Site selection procedures, methodology and results have been presented in a series of technical reports (Prena et al. 1996, McKeown and Gordon 1997, Rowell et al. 1997), scientific papers (Schwinghamer et al. 1996, Gilkinson et al. 1998, Schwinghamer et al. 1998, Prena et al. 1999, Kenchington et al. 2001) and a thesis (Gilkinson 1999). In addition, a brief summary of the Canadian program on the impacts of mobile gear on benthic habitat and communities has been prepared (Gordon et al. 1998).

This technical report provides an overview of this major experiment. The intended audience includes fisheries and habitat managers, the fishing industry and environmental organizations. It briefly summarizes the experimental design and methodology, reviews the principal results (already published in the scientific literature), and synthesizes and discusses all results in the context of other recent scientific studies on otter trawling impacts. In addition, it presents some general conclusions from all the otter trawling impact experiments that have been conducted around the world, as well as some thoughts on future information needs and the implications of this new knowledge for habitat and resource management.

OTTER TRAWLS AND THEIR POTENTIAL EFFECTS ON BENTHIC HABITAT AND ORGANISMS

Otter trawls consist of a funnel-shaped net towed at a speed of 2-4 knots across the seabed by a single vessel. They have four major components: doors (also called otter boards), ground warps, footgear and net. All components create turbulence that can affect both habitat and organisms. This turbulence is intended and is part of the working principle of the gear. The two doors keep the gear on the seabed and provide horizontal spread to the net. They can be quite large and heavy, and are usually in continuous contact with the seabed, often leaving well-defined tracks that, depending upon sediment composition, can be as deep as 30 cm (Linnane et al. 2000). The cloud of sediment stirred up by passing doors tends to herd fish toward the mouth of the net. The ground warps, leading from the doors to the net, can periodically come into contact with the seabed but the disturbance they create is much less than the doors. The footgear is found at the leading edge of the lower part of the trawl net. It is usually fitted with different kinds of bobbins or rollers that maintain constant contact with the seabed, except when they skip over features on rough bottom. Therefore, the footgear can cause substantial disturbance. The bottom of the trawl net can also come into contact with the seabed, especially the codend when the net is full, disturbing the area already passed over by the footgear. In some applications, such as towing for shrimp on a smooth bottom, tickler chains are installed in front of the footgear to stir up sediment and improve the capture rate of target organisms. When first developed, otter trawling was limited mainly to smooth bottoms. However, technology has evolved to the point where otter trawling can now be carried out on almost any kind of bottom, no matter how rough.

Otter trawls can potentially effect benthic habitat and organisms in a wide variety of ways. Immediate impacts can include:

- Resuspension and displacement of sediment, organic matter, shells and small organisms.
- Burial of habitat structures and organisms by redeposited sediment.
- Digging of furrows, creation of berms, realignment of rocks and shells, and generally smoothing of surficial sediment features.
- Destruction of habitat structures (mounds, tubes, burrows, etc.).
- Capture and removal of organisms including target species (i.e. haddock, cod, pollock, etc.) and bycatch (both fish and invertebrates).
- Damaging or killing organisms which are left on the seabed exposed to predation, including juvenile fish and structure forming organisms such as sponges and corals.
- Temporary exposure of sediment dwelling organisms (i.e. infauna), making them more available to predators.
- Attraction of scavengers because of the increased availability of prey.

Longer-term impacts, especially if otter trawling is repeated frequently over the same bottom, can potentially include:

- Altering the sediment habitat structure which could affect its suitability for particular species and the rates of biogeochemical fluxes between the sediment and water column.
- Changing the composition of benthic communities (e.g. presence/absence, relative abundance, biomass and size of individual species).

- Changing ecosystem processes such as the rates of primary and secondary production and organic matter dynamics.
- Altering fisheries recruitment through changes in physical habitat and food supply which affect the survival of juvenile fish.

SITE SELECTION PROCEDURES

As explained in Prena et al. (1996), considerable care and effort went into the selection of the site for this experiment. Several locations on Western Bank (Scotian Shelf) and the Grand Banks were initially considered and examined on exploratory cruises in 1991 and 1992. After assessing the available information, a site on the northeastern part of the Grand Banks (47° 10', 48° 17'W) (Fig. 1) was selected for the following reasons:

- Analysis of commercial fishing effort data indicated that the site had not been subjected to trawling since at least 1980. Therefore, the benthic habitat and community at this site had at least 13 years to recover from any previous trawling disturbance. Sidescan sonar surveys indicated no visible disturbance of the seabed by trawling activity. It seemed safe to assume that the benthic ecosystem at this site was in a natural state with little if any modification by human disturbance.
- The sandy bottom was representative of large areas of the continental shelf off Atlantic Canada, and the general area of the experimental site had earlier been commercially fished for mixed groundfish, mostly American plaice with about 15-20% Atlantic cod.
- DFO was willing to close a 20 x 20 km experimental area to all fishing activity for the duration of the experiment. The general moratorium on groundfisheries on the Grand Banks, established in 1992, provided an additional degree of protection from fishing disturbance.
- The environmental conditions of the seabed were relatively uniform, both spatially and temporally, making it potentially easier to detect trawling effects above natural variability. The seabed was relatively flat and featureless (except on a micro-scale). Water depth averaged 137 m (range of 120 to 146 m) which is deeper than the effects of most storms. The seabed was relatively stable with no evidence of wave or current-induced ripples. Some iceberg scours were present but not abundant enough to interfere with the experiment.
- The sand bottom was easily and accurately sampled with our sampling gear, and samples could be quickly processed in a reasonable time.
- The benthic community was composed of a diverse number of species with high abundance and biomass, including abundant epibenthic species which are those most likely affected by trawling. The species composition showed a relatively high level of homogeneity, again making it easier to detect trawling effects above natural variability.

EXPERIMENTAL DESIGN

The three-year experiment was designed to determine the immediate and medium-term effects of repetitive otter trawling on the sandy bottom ecosystem present at the experimental site. The basic questions asked were:

- Could effects of an annual trawling disturbance be observed above natural variability?
- What components of the benthic ecosystem are affected?
- What are the recovery rates?

Full details of experimental design are given in Rowell et al. (1997). Extensive surveys of the experimental site were conducted before any trawling disturbance was applied. Three, 13 km long experimental corridors were established within the 20 x 20 km experimental box, each with a different heading (Fig.1). Each had a parallel reference corridor established 300 m to one side. The experimental corridors were trawled twelve times in July of each year. This was considered to be a relatively high level of trawling disturbance, roughly equivalent to the greatest commercial trawling intensity on the Grand Banks in recent years (Prena et al. 1999, Kulka and Pitcher 2001). Both experimental and reference corridors were surveyed and sampled with a wide variety of equipment at different spatial scales. Whenever possible, reference corridors were sampled before trawling, and experimental corridors were sampled both before and after trawling. Changes in the reference corridors were assumed to reflect natural variability.

SUMMARY OF METHODS

Navigation

The use of dGPS, a Trackpoint II acoustic tracking system, and the AGCNav navigation display and logging system ensured the positioning of vessels, the otter trawl and all sampling equipment within an accuracy of 4-20 m (McKeown and Gordon 1997). It was confirmed that all samples were collected from either disturbed or reference areas as intended.

Experimental Trawling

Each year in July, the three experimental corridors were trawled twelve times with an Engel 145 otter trawl, equipped with 1250 kg polyvalent oval doors and rockhopper footgear, using the C.C.G.S. *Wilfred Templeman*. This trawl has an average door spread of 60 m and wing spread (i.e. footgear) of about 20 m. The rockhopper footgear had a diameter of 46 cm. Mesh size was 18 cm on the wings and belly of the net and 13-15 cm in the codend. A 3 cm square mesh liner was installed in the codend to capture organisms damaged but not retained by commercial gear.

The widths of the disturbance zones created were estimated from the navigation data (McKeown and Gordon 1997, Prena et al. 1999) and were on the order of 120-250 m depending upon year. Cumulative trawling disturbance was greatest nearer the centre lines of the trawled corridors, but the local intensity of the impact from doors, ground warps, footgear, and net was necessarily uneven within the trawled area.

Trawl Catch and RoxAnn

Trawl catch data were collected each year in all three corridors (Prena et al. 1999). Fish and invertebrates were separated by species and weighed. In 1995, the *Templeman* was equipped with a RoxAnn^{TM} acoustic bottom classification system and collected data during all trawl sets (Schwinghamer et al. 1998).

Sidescan Sonar

Sidescan sonar surveys were run each year in all corridors before and after experimental trawling using the C.C.G.S. *Parizeau* (Rowell et al. 1997, Schwinghamer et al. 1998). Additional surveys were run in September 1993 and 1994. The results were used to provide a general description of the seabed at the experimental site, ensure that there was no recent seabed disturbance (e.g. commercial trawling, icebergs) that might influence experimental results, provide a general picture of the degree and distribution of the trawling disturbance, and provide information on the persistence of trawl marks on the seabed.

BRUTIV

In 1993 and 1995, black and white video surveys of the seabed in both experimental and reference corridors were conducted using BRUTIV (Bottom Referencing Underwater Towed Instrument Vehicle), an underwater vehicle flown at a constant altitude over the seabed (Rowell et al. 1997, Schwinghamer et al. 1998).

Epibenthic Sled

Large epibenthic (i.e. surface dwelling) organisms were collected with the modified Aquareve III epibenthic sled (Rowell et al. 1997, Prena et al. 1999). Each tow was about 50 m long and sampled an area of the seabed on the order of 17 m^2. The sled cuts to a depth of several centimeters in a sandy substrate and therefore collected some shallow-living infaunal organisms. The collection box had 1-cm diameter holes so smaller organisms were not retained. Performance was monitored by a colour video camera directed backwards showing the sled opening, and tows of dubious quality (i.e. lifting off the seabed) were aborted and repeated.

Due to time constraints, sled samples were not collected from Corridor C. Also, it was not possible to collect sled samples in experimental corridors before retrawling in 1994 and 1995. In 1993 and 1995, reference samples were collected before trawling. Unfortunately, due to operational constraints, reference samples in 1994 had to be collected after retrawling. As discussed later, this may have influenced the results.

Immediately after retrieval, the sled catch was washed with seawater over a 1 mm mesh screen, and organisms were sorted by species, counted and weighed (Prena et al. 1999). Damage was also assessed for some species. Processing time was on the order of one hour for each sample.

Videograb

Macrobenthic communities were sampled with the DFO videograb that was developed specifically for this experiment (Schwinghamer et al. 1996, Rowell et al. 1997, Gordon et al. 2000, Kenchington et al. 2001). This hydraulically-actuated bucket grab equipped with colour video cameras provides the scientific operator the ability to visually select the precise sampling area on the seabed, close and open the bucket remotely, and verify that the bucket closed properly prior to recovery. If a sample is considered not suitable for any reason, the videograb can be lifted off the bottom, opened and landed in a new location. It samples an area of 0.5 m^2. Sampling depth is on the order of 10-25 cm, and at full penetration the sediment volume is about 100 L. Most previous gear impact studies have used grabs that sampled a much smaller area (<0.2 m^2) and gave limited penetration on hard sand.

Due to time constraints, as with the epibenthic sled, videograb samples were not collected from Corridor C. Reference samples were collected before trawling each year of the experiment but time constraints prevented the sampling of reference corridors immediately after trawling (Kenchington et al. 2001). However, in contrast to the epibenthic sled sampling, it was possible to sample the experimental corridors both before and after trawling each year. An attempt was made to collect the videograb samples from the disturbed areas as soon as possible after trawling. In 1993 and 1995, the delay was less than a day but, in 1994, weather and logistic problems increased the delay to over a day in Corridor B and over five days in Corridor A.

Immediately upon retrieval, subsamples of surface sediment were taken for grain size and organic carbon/nitrogen analysis. The contents of the videograb (average volume collected during this experiment was 87 L with a standard deviation of 11 L) were then washed with seawater over a 1 mm mesh screen, and all retained material (i.e. organisms and gravel) was preserved in formalin. Processing time on deck was on the order of half an hour for each sample. Samples were subsequently processed ashore using standard procedures (Kenchington et al. 2001), including identification to the lowest possible taxon and determination of abundance and biomass by taxon. Damage was also assessed for some species. Detailed damage classification and length measurements were made on all molluscs since this group is known to leave records of encounters with fishing gear (Witbaard and Klein 1994).

In 1994 and 1995, a dynamically responding underwater matrix sonar (DRUMS^{TM}) was mounted in the videograb to provide high resolution information on small-scale structural properties of surficial sediments (Schwinghamer et al. 1996, Schwinghamer et al. 1998). Acoustic images were collected of the precise area of the seabed to be sampled before the videograb bucket was closed.

Laboratory Experiments

Experiments investigating the effects of otter doors on molluscs buried in sediment were conducted in an instrumented tank using a full-scale model of an otter door shoe (Gilkinson et al. 1998). Burrowing experiments with bivalves were also conducted (Gilkinson 1999) using common species collected from the study site with the videograb and transported live back to the Northwest Atlantic Fisheries Centre. Species-specific burrowing rates and depths were determined in sediment held in flowing seawater aquaria.

Statistics

A variety of uni- and multivariate statistical methods were used to process the data. These included analysis of variance (ANOVA) and multi-dimentional scaling (MDS) ordination. Full details, including probability values, are described in Schwinghamer et al. 1996, Schwinghamer et al. 1998, Prena et al. 1999, Gilkinson 1999, and Kenchington et al. 2001.

SUMMARY OF RESULTS

Otter Trawl Catch

The fish catch in the otter trawl was extremely low and averaged just 18 kg (wet weight) for a 13 km long set over the entire experiment (Prena et al. 1999). The dominant species caught were American plaice (*Hippoglossoides platessoides*) and thorny skate (*Raja radiata*). Other species captured in smaller quantities were capelin (*Mallotus villosus*), Arctic cod (*Boreogadus saida*), sand lance (*Ammodytes dubius*) and Atlantic cod (*Gadus morhua*). There was no statistically significant differences in fish catch with increasing trawl set or between corridors. However, the average fish catch gradually decreased each year of the experiment. Such poor catches attest to the depressed state of groundfish resources on the Grand Banks at the time of the experiment.

The invertebrate bycatch, which averaged 10 kg (wet weight) for a 13 km long set, was dominated by snow crabs (*Chionoecetes opilio*), basket stars (*Gorgonocephalus arcticus*) and sea urchins (*Strongylocentrotus pallidus*) (Prena et al. 1999). Other species included soft corals (*Gersemia* sp.), whelks (*Buccinum* sp.), and hermit crabs (*Pagurus* sp.). Iceland scallops (*Chlamys islandica*) were only occasionally caught on the sandy bottom since their preferred habitat is gravel. These are all large surface dwelling species and most have some degree of mobility. The average catch of invertebrates captured by the trawl (per square meter of bottom sampled) was just 0.01% that captured by the epibenthic sled, which indicates the extremely low efficiency of the otter trawl in collecting the epibenthic organisms present at the study site. However, the trawl was relatively efficient in capturing snow crabs and basket stars, and their biomass decreased over the twelve trawl sets. An influx of adult male snow crabs into the trawled corridors was observed after the first six trawl sets (approximately 10-12 h). It is presumed that they were migrating into the disturbed zone to feed on damaged organisms. There were significant differences in the biomass of invertebrate bycatch between trawl set, corridor and year.

Effects on Habitat

The experimental otter trawling had no apparent effect on the grain size of surficial sediments (Schwinghamer et al. 1998). However, there was a suggestion of some temporal changes in the finer fractions over the three-year experiment which are thought to be natural in origin. The trawling did not appear to affect organic carbon and nitrogen in surficial sediments in the first two years while, in 1995, concentrations were significantly lower after trawling (Kenchington et al. 2001).

Sidescan sonar surveys at the start of the experiment revealed a physically uniform seabed with no evidence of any large-scale features indicating sediment transport. Some iceberg furrows were observed but to our knowledge were never sampled. There was no evidence of fishing disturbance other than from our experimental trawling. Otter door tracks, and in some cases disturbance from footgear, were readily visible on sidescan sonar records immediately after trawling and ten weeks later. The 1993 tracks were not visible a year later but the 1994 tracks were faintly visible in 1995.

Continuous video observations made with BRUTIV (Rowell et al. 1997) revealed that the seabed in freshly trawled corridors was lighter in colour than reference corridors, and that organisms and shell hash tended to be organized into linear features parallel to the direction of trawling (Schwinghamer et al. 1998). Door tracks and damaged organisms were also visible on occasion. High-resolution video observations with the videograb indicated that untrawled seabed had a hummocky, mottled appearance with abundant organic detritus, while recently trawled seabed was generally smoother and cleaner. While some new structural features were created by the doors (i.e. furrows and berms), the visual observations showed a generally smooth sediment surface with an overall decrease in habitat complexity. There was no visible difference in seabed surface structures of trawled and reference corridors before retrawling in 1994 and 1995, suggesting habitat recovery over the intervening twelve months.

There was a significant increase in the RoxAnn^{TM} E2 signal during trawling in 1995 (Schwinghamer et al. 1998). The E2 signal is considered to be a proxy for sediment hardness (in the original reference the E2 signal was mistakenly attributed to sediment roughness). DRUMS^{TM} acoustic data indicated that trawling caused significant changes in small-scale subsurface sediment structure down to depths of 4.5 cm (Schwinghamer et al. 1996, 1998). These results were interpreted to indicate that the trawling destroyed biogenic structures such as mounds, tubes and burrows and thereby reduced habitat complexity.

In summary, immediate physical impacts of the experimental trawling on benthic habitat were readily visible and tended to decrease habitat complexity, but it appears that recovery from the disturbance occurred within a year.

Effects on Organisms Sampled with the Epibenthic Sled

Most organisms collected with the epibenthic sled were large, epibenthic species, but since the blade penetrates several centimeters into the sand some shallow burrowing infauna were also collected. The total biomass of organisms sampled by the epibenthic sled averaged 400 g (wet weight) m^{-2} and the total number of species captured was 115 (in 96 samples) (Prena et al. 1999). The dominant epibenthic species at the study site, which comprised 95-98% of the biomass, were sand dollars (*Echinarachnius parma*), brittle stars (*Ophiura sarsi*), sea urchins (*Strongylocentrotus pallidus*), snow crabs (*Chionoecetes opilio*), soft corals (*Gersemia* sp.) and four molluscs (*Astarte borealis*, *Margarites sordidus*, *Clinocardium ciliatum*, and *Cyclocardia novangliae*). With the exception of *M. sordidus*, the molluscs were shallow infaunal species. A tube dwelling polychaete (*Nothria conchylega*) was also abundant in epibenthic sled samples but was not processed because of the extensive sorting time required (however, it was processed in the videograb samples). Only sea urchins and snow crabs were commonly caught by both the epibenthic sled and the otter trawl.

Immediately after trawling each year, the total biomass of organisms was significantly lower in trawled corridors than in reference corridors (Prena et al. 1999). This difference was greatest after the third trawling event in 1995, and averaged 24% over the entire experiment. At the species level, this biomass reduction immediately after trawling was significant for snow crabs, sand dollars, brittle stars, sea urchins and soft corals. Actual impacts on snow crabs were probably greater than the analyses showed because of their rapid migration into trawled corridors (i.e. some of the snow crabs sampled after trawling were not present before). Judging by their capture rate in the otter trawl, there probably was a similar reduction in the biomass of basket stars but this was not detected in the epibenthic sled data, probably because this species was poorly sampled. The homogeneity of epibenthic organisms collected by epibenthic sled was lower in trawled corridors immediately after trawling than in nearby reference corridors. This presumably reflects the realignment of organisms into rows as seen in the BRUTIV video footage. Sand dollars, brittle stars and sea urchins demonstrated significant levels of damage from trawling. In addition, the mean individual biomass of epibenthic organisms was lower in trawled corridors suggesting size specific impacts of trawling, especially for sand dollars (Prena et a. 1999). However, no significant effects of trawling were observed on the four mollusc species commonly captured by the epibenthic sled.

The reduced biomass of epibenthic organisms in trawled corridors immediately after trawling is presumably due to several factors including direct removal by the trawl, displacement, predation and possibly migration of non-captured organisms. Since it was not possible to collect epibenthic sled samples before retrawling in 1994 and 1995, there are no direct data on the recovery rates of epibenthic organisms in the trawled corridors. However, the fact that most of the affected species have some degree of mobility and that the biomass of epibenthic species in the trawled corridors was relatively constant over the three year experiment suggests that recovery time for most affected species is on the order of a year or less.

In summary, significant immediate effects of the experimental trawling were detected on some species of large epibenthic organisms, in particular snow crabs, sand dollars, brittle stars, sea urchins and soft corals. Indirect evidence suggests that recovery of these species took place within a year, most likely through migration and transport from undisturbed areas immediately outside the narrow trawled corridors.

Effects on Organisms Sampled with the Videograb

A rich and diverse infaunal community was present at the experimental site (Kenchington et al. 2001). A total of 246 invertebrate taxa were identified in the 200 videograb samples, with an average of 68 taxa per sample. Mean biomass and abundance were on the order of 1 kg (wet weight) m^{-2} and 2100 individuals m^{-2}, respectively. With respect to biomass, the dominant taxa were molluscs and echinoderms. The most abundant taxonomic groups were polychaetes, molluscs and crustaceans. Twenty-seven taxa occurred in more than 90% of the samples and accounted for 89% of the total biomass and 87% of the numerical abundance. The videograb also collected abundant epibenthic species (e.g. sand dollars and brittle stars).

Considerable temporal variability was observed in the community properties of reference corridors (Kenchington et al. 2001). These were always sampled before trawling and to the best of our knowledge were not directly affected by the otter trawling. There was a clear trend of decreasing abundance and number of species during the three-year experiment. Multivariate analyses (i.e. MDS) indicated marked temporal changes in community structure. These results indicate that the benthic communities at the study site are naturally dynamic and exhibit temporal changes irrespective of trawling disturbance. This natural variability makes it more difficult to detect the effects of otter trawling.

The immediate effects of trawling were examined by comparing community properties before and after trawling each year in the trawled corridors (Kenchington et al. 2001). Few significant effects were observed in 1993 and 1995. However, in 1994 there was a significant drop in total community abundance immediately after trawling, with polychaetes being the most affected taxonomic group. In the same year, there was no significant drop in the total community biomass but sand dollars and several species of polychaetes were negatively affected. No significant immediate effects of trawling were detected on the number of species present, species diversity or evenness. No significant damage to sand dollars or brittle stars could be detected in the videograb samples. Multivariate analysis indicated changes in community structure only in 1994. It may have been easier to detect immediate impacts in 1994 because that year the trawling disturbance was more concentrated along the centre line of trawled corridors and there was a longer delay between the cessation of trawling and videograb sampling which provided more time for predators to feed on dead, damaged or exposed organisms.

The annual trawling had no significant effect on the abundance of adult or juvenile molluscs in any year (Gilkinson 1999). Recruitment rates of bivalves were similar in both reference and trawled corridors. There was no evidence that trawling affected either the size structure or species composition of molluscs. In addition, there was no detectable difference in mollusc damage between reference and trawled corridors.

The long-term effects of trawling were examined by comparing community properties in trawled corridors before trawling with reference corridors (Kenchington et al. 2001). Few significant long-term effects on macrofauna abundance and biomass were observed. These were restricted primarily to eight species of polycheates in 1994. It is not clear whether these apparent effects were due to otter trawling or the natural spatial and temporal variability in the benthic communities. However, there was a significant increase in the frequency of damaged sand dollars in trawled corridors, especially for the larger organisms. There was no evidence of any cumulative effect of trawling disturbance on community structure over the three-year experiment. Ten dominant species were remarkably stable during the experiment and showed no effect of either natural or trawling disturbance.

In summary, it appears that the effects of otter trawling on the abundant and diverse macrobenthic organisms present at the study site, as sampled by the videograb, are relatively minor and restricted primarily to sand dollars and some species of polychaetes. A significant effect on sand dollars was also evident in the epibenthic sled data. Some of the observed drop in polychaete abundance is most likely due to predation but some could also be due to displacement outside the trawled corridors. Echinoderms (except sand dollars), molluscs and crustaceans showed little or no effect. The major signal observed in the data was a natural temporal trend over the three-year experiment. The minor impacts observed appear to have shifted the benthic community in the same direction as the natural changes. The macrobenthic community appears to have recovered fully from the trawling disturbance within a year and no long-term effects could be detected.

Laboratory Experiments

The results of the laboratory experiments (Gilkinson et al. 1998) indicated that small and medium size bivalves living on or near the surface of a sandy seabed were displaced in fluidized sediment ahead of the trawl doors and thereby escape direct hits. Only 2 out of 42 recovered bivalves which had originally been buried in the scour path of the door were damaged. Large near-surface bivalves, which are not common at the study site, were not displaced and could be damaged by direct hits from the trawl door. These results are consistent with the observations of no significant detectable impacts of otter trawling on molluscs in the field experiment (Prena et al. 1999, Kenchington et al. 2001). Burrowing experiments indicated that the majority of bivalve taxa (70%) at the study site were shallow burrowers and that most of the species tested were slow to very slow burrowers (Gilkinson 1999).

SYNTHESIS AND DISCUSSION

Experimental Design

This experiment is one of approximately thirty that have been conducted around the world to study the effects of otter trawling on benthic ecosystems under a wide range of conditions (Table 1). Many of the earliest experiments were done in relatively shallow water, were of limited spatial extent, and were short term in nature (Auster and Langton 1999, Collie et al. 2000a). Therefore, when we designed our experiment in 1993, we attempted to incorporate features that would extend the understanding of otter trawl impacts over broader scales of depth, space, time and variables measured.

The major features of our experimental design are summarized as follows:

- Considerable effort went into the site selection process, in particular picking an area that had not been subjected to recent trawling activity and that had an abundant, diverse, representative, and relatively uniform biological community.
- The sandy bottom habitat selected is widespread on the Canadian continental shelf (i.e. about 70% of the Grand Banks), supports commercial fisheries, and is easily sampled.
- The study site was located in relatively deep water (120-146 m) on an offshore fishing bank.
- A manipulative experimental approach was taken.
- Three replicate corridors, each 13 km long, were subjected to a high level of trawling disturbance (i.e. 12 sets) once a year for three years in a row.
- Parallel reference corridors were sampled frequently to provide information on natural variability.
- A wide variety of sampling methods was employed to investigate trawling impacts at different spatial scales and on different physical and biological characteristics of the benthic ecosystem.

This design allowed three separate assessments of immediate impacts and two assessments of recovery over one year. It also allowed assessment of possible cumulative effects of repetitive trawling on the same bottom over a three-year period, as well as a thorough assessment of natural variability in the benthic ecosystem. Overall, this experimental design provides a high probability of detecting any impacts of otter trawling on the benthic ecosystem at the study site.

In comparison to the other otter trawling experiments that have been conducted (Table 1), our experiment remains unique in terms of its depth, repeat nature of trawling disturbance, duration, and scope of data collected. Only three other offshore, deep-water otter trawling impact experiments have been reported. Engel and Kvitek (1998) studied otter trawling effects on mixed sediment at 180 m in Monterey Bay off California by comparing two adjacent areas subjected to different levels of commercial trawling intensity. Smith et al. (2000) investigated the effects of commercial trawling on a soft bottom habitat at 200 m in the Mediterranean Sea off Greece by comparing a heavily trawled lane with nearby untrawled reference areas. In a manipulative experiment like ours, Freese et al. (1999) examined the effects of single otter trawl sets on a hard bottom habitat at 206-274 m in the Gulf of Alaska.

General Description of Habitat and Biological Community

The seabed at the study site (120-146 m) was relatively flat and uniform. The surface of the well-sorted sand was hummocked, with small mounds rising to heights of a few centimetres (Schwinghamer et al. 1998). These are not wave-generated bedforms, such as the ripples and megaripples seen at shallower depths on the Grand Banks, because the site is too deep for extensive disturbance by wave action (Barrie et al. 1984). Rather, they are likely created by the activities of the abundant benthic organisms living on and in the sediment (i.e. bioturbation). There was also an abundance of dark coloured organic floc on the seabed that was patchily distributed and accumulated in depressions. Bottom water temperature at the experimental site is on the order of 0° C, or just below, year round.

A rich and diverse biological community was present at the experimental site (Prena et al. 1999, Kenchington et al. 2001). A total of 246 invertebrate taxa were present, including both epifauna and infauna. Mean biomass and abundance were on the order of 1 kg (wet weight) m^{-2} and 2100 individuals m^{-2}, respectively. The dominant taxonomic groups were echinoderms, polychaetes, molluscs and crustaceans. Being a sandy habitat, most species were free-living or burrowing. There were some tube-building species but very few sessile species due to the absence of stable substrata. Except for scattered shells and hummocks, there were no biogenic physical structures. The only abundant sessile species were soft corals (*Gersemia* sp.) attached to shells.

Natural Variability

Benthic habitat and communities, even at depths of 120-146 m on the Grand Banks, are not static, but subject to considerable temporal and spatial variability. The natural variability of benthic ecosystems in Atlantic Canada is poorly understood because of the limited number of quantitative benthic surveys that have been conducted and the absence of any time series data. However, it must be documented in temporal experiments like this since it could be confused with possible trawling impacts. In this experiment, natural variability was assessed by sampling in the parallel reference corridors 300 m to one side of the trawled corridors (Fig. 1).

Various observations suggested that sediment transport processes were more active in the winter of 1993-94 than in the winter of 1994-95 (Schwinghamer et al. 1998). The biomass of epibenthic organisms in reference corridors showed considerable interannual variability (Prena et al. 1999). However, the lower values observed in 1994 may have been influenced by the fact that, due to operational constraints, reference corridors had to be sampled after trawling, and therefore mobile species such as snow crabs had an opportunity to immigrate into the nearby experimental corridors to scavenge dead or damaged organisms. The most pronounced natural changes were observed in the videograb data (Kenchington et al. 2001). There was a clear trend of decreasing total abundance with time in the macrobenthic communities in the reference corridors, dropping about 50% between 1993 and 1995. The number of species per sample also decreased significantly during the experiment. Approximately 20% of the species tested showed significant date effects for both abundance and biomass in the reference corridors. These combined results demonstrate that the habitat and biological community at the study site are naturally dynamic and exhibit marked changes irrespective of trawling activity.

With the possible exception of the epibenthic sled samples collected in 1994, as described above, we feel that the changes observed in the reference corridors reflect natural variation and are not influenced by the trawling. All videograb samples and the epibenthic sled samples in 1993 and 1995 in the reference corridors were collected before trawling. It is possible that the reference corridors may have been influenced by the deposition of organic floc or small organisms resuspended by the trawling. However, if this took place, there was a year for recovery before the reference corridors were sampled again.

The average biomass of fish catch in the trawl decreased each year of the experiment (Prena et al. 1999) but it can not be determined with certainty whether this trend was due to natural variability or the continuing effects of overfishing before the groundfish moratorium initiated in 1992. The effects of dramatically reduced groundfish populations on benthic community structure on the Grand Banks is unknown but potentially significant because of the importance of benthic invertebrates in the diet of demersal fish (Methven 1999).

Pattern of Trawling Disturbance and Features Sampled by Different Gears

The width of the disturbance zone created by the experimental trawling, defined by the distance between the outermost door tracks, varied considerably but averaged on the order of 120-250 m (McKeown and Gordon 1997, Prena et al. 1999). It was greatest in 1993, when the trawler was not equipped with dGPS, and least in 1994. Since the average width of the disturbance zone was several times the spread of the otter trawl doors (60 m), the trawling disturbance was clearly not evenly distributed in this zone. Probably a very small area of the seabed was swept by all twelve sets each year. Some areas, especially near the outer boundaries, may have been swept only once. It is estimated that a given location on the seabed well within the disturbed zone was probably swept by the trawl on the order of 3 to 6 sets each year, with frequency being greater near the centre line.

As also noted by Smith et al. (2000), the degree of disturbance at a particular spot will depend upon the part of the otter trawl that comes into contact with the seabed. The greatest damage is expected from the doors, which under ideal conditions are in near constant contact with the seabed. However, the tracks they create are narrow, about 1 m wide, and so they disturb only about 3% of the area swept by the trawl (i.e. 60 m between the doors in this experiment). The next most damaging component of the otter trawl is probably the rockhopper footgear, also in constant contact with the seabed, which has a width on the order 20 m or about 33% of area swept by the trawl. The net follows behind the footgear and therefore can potentially affect the same area. More than 60% of the area swept by the trawl is affected only by the ground warps which can contact the seabed periodically.

The sidescan sonar surveys covered the entire disturbed zone and door tracks were clearly visible immediately after trawling and several months after. They were also faintly visible before retrawling in 1995. RoxAnn data (1995 only) were collected from an area of approximately 200 m^2 directly under the *Templeman* while trawling and should have integrated the disturbance created by different gear components. BRUTIV video imagery was collected along a path several meters wide which passed over seabed influenced by all trawl components. Door tracks were clearly visible in some instances. The epibenthic sled tows, which averaged 50 m in length, should have sampled door tracks and areas passed over by the footgear, as well as areas swept by the groundwarps. Videograb samples were taken as close to the centre line of the corridors as possible (usually within 25 m). Since the videograb samples an area of just 0.5 m^2, the influence of different trawl components is not integrated in a single sample. Relatively few deployments of the videograb probably sampled directly in a door track (i.e. only about 3% of the area swept by the trawl was disturbed by the doors) but rather areas influenced by the footgear (and net) or ground warps. Therefore, higher variance can be expected in videograb data. The chances of detecting immediate impacts with all sampling gears should be highest in 1994 when the trawling disturbance was most concentrated along the centre line.

Intensity of Experimental Trawling

The general level of trawling effort, twelve sets along the same line once a year, was much higher than usually occurred on the Grand Banks before the groundfish moratorium in 1992. Most areas in the disturbed zones were probably swept by 3 to 6 sets of the otter trawl each year (i.e. 300-600% per year). Analysis of the DFO offshore trawler Observer Program database from Atlantic Canada, collected between 1980 and 1998 and scaled up to total effort, indicated that the detailed distribution of effort was very patchy (Kulka and Pitcher 2001). Most trawling was concentrated in specific regions, and large areas appear to be untrawled,. The area of seabed swept by otter trawls at an intensity greater than 100% (i.e. more than once a year) was generally less than 1.5% of the total shelf area. Presumably, these are the preferred areas where fish are most abundant and the bottom is fishable. The maximum trawling intensity estimated from this database ranged from 141% to 644 % per year (i.e. the seabed was swept by a trawl 1 to 6 times a year) which is comparable to the intensity applied in this experiment. Therefore, the intensity of trawling used in our experiment (twelve sets once a year over the same bottom) is high, at the upper end of the range of effort applied by the commercial fleet in recent years. However, it should be kept in mind that this effort was concentrated into just a few days each year while commercial effort is generally spread out over the entire year. This difference could have implications for recovery potential.

Comparison of Sampling Gear

The kind and magnitude of impacts detected in field experiments such as this will be very dependent upon the sampling gear and how it is used. Therefore, it is important to understand the differences in the effectiveness of the otter trawl, epibenthic sled and videograb in collecting benthic organisms, and to take these into account when interpreting the results. These gears are designed to capture different kinds of organisms over quite different spatial scales. The otter trawl, which samples a large area of the seabed approximately 20 m wide and many kilometers long (i.e. a 13 km set sampled an area of 26×10^4 m^2), is designed to capture demersal fish, not benthic invertebrates. However, some large epibenthic species were captured in low numbers as bycatch. The epibenthic sled was designed to capture large epibenthic species living on the sediment surface, and each tow sampled an area approximately 17 m^2 to an average depth of 2-3 cm. The videograb was designed to capture organisms of all sizes living on and in 0.5 m^2 of sediment to an average depth of about 17 cm (an average of 87 L of sediment in the 200 videograb samples processed in this experiment).

The most common benthic organisms captured in the otter trawl were snow crabs (*Chionoecetes opilio*), basket stars (*Gorgonocephalus arcticus*), and sea urchins (*Strongylocentrotus pallidus*), all relatively large surface-dwelling forms. Soft corals (*Gersemia* sp.), whelks (*Buccinum* sp.), bivalves (e.g. *Chlamys islandica*) and hermit crabs (*Pagurus* sp.) were also captured in small numbers. Comparison of the total invertebrate biomass to that captured by the epibenthic sled indicated that the Engel otter trawl as used in this experiment sampled only about 0.01% of the epibenthic invertebrate biomass at the experiment site (Prena et al. 1999). This inefficiency of the otter trawl in capturing epibenthic organisms is not surprising since the rock hopper footgear (46 cm in diameter) kept the ground line of the trawl well above the sediment surface. A similar low efficiency was also observed for the Campelen 1800 otter trawl (Gilkinson 1999). The low efficiency of otter trawls in capturing epibenthic organisms has also been reported by Sainsbury et al. (1997) and Moran and Stevensen (2000).

Efficiency of capture by the otter trawl will vary with species, and the most susceptible species at our experimental site appears to be the snow crab, followed by the basket star. Declines in the biomass of snow crabs and basket stars in the bycatch were observed each year Prena et al. (1999). There also was evidence of an immigration of scavenging snow crabs after approximately fifteen hours of fishing that compensated for further declines in that species. The average snow crab bycatch per set was 0.19 $g\ m^{-2}$ (assuming the effective sampling width of the net is 20 m), while the first five sets each year, on average, took more than two thirds of the total amount of snow crab captured over twelve sets. That catch, 1.52 g m^{-2}, was a significant fraction of the snow crab biomass estimated from epibenthic sled catches (average 4.37 g m^{-2}). Thus, the otter trawl is relatively effective in capturing snow crabs and direct removal appears to explain most of their observed decrease.

Eighty-seven species of invertebrates were captured by both the epibenthic sled (Prena et al. 1999) and the videograb (Kenchington et al. 2001) during this experiment (Table 2). The 105 epibenthic sled samples (about 17 m^2 each) sampled a total area of about 1785 m^2 while the 200 videograb samples (0.5 m^2 each) sampled a total area of 100 m^2. Despite the much smaller area sampled, the majority of the species had higher biomass in the videograb samples. For example, the biomass values observed with the videograb were 26% higher for sand dollars, 42% higher for soft coral, 29% higher for sea urchins and 17% higher for brittle stars (Table 2). Only 17 of the 87 species sampled by both gears had a higher biomass in the epibenthic sled samples (shown in bold in Table 2). These were primarily dispersed, surface-living organisms, in particular gastropods, bryozoans, crustaceans and ascidians. These differences can be explained by several factors including the greater sampling depth of the videograb, the loss of small organisms through the holes in the collection box of the epibenthic sled, and the occasional decline in the collection efficiency of the epibenthic sled (as observed in the video). Of the two gear types, the videograb is more quantitative.

The comparisons in Table 2 are based upon all the epibenthic sled and videograb samples collected during the experiment. In Table 3, the mean biomass of sand dollars, brittle stars, sea urchins and soft corals, four dominant epibenthic species at the experimental site, is compared for both gear types in the reference corridors and experimental corridors immediately after trawling. Again, in all cases, biomass is higher in the videograb samples, despite the much smaller area sampled. However, it is interesting to note that the difference in the biomass collected by the two gears is greater after trawling for brittle stars, sea urchins and soft corals, suggesting that the efficiency of the epibenthic sled in capturing these three common species is reduced immediately after trawling. This could be due to trawl-induced turbulence which resuspends sediment that subsequently buries some individuals (perhaps just temporarily) when it resettles so that they are below the sampling depth of the epibenthic sled (just few centimeters). These results suggest that some of the reduction in biomass immediately after trawling observed in the epibenthic sled data (Prena et al. 1999) may be a sampling artefact.

The coefficients of variation were calculated for the biomass of sand dollars and brittle stars, as sampled by the epibenthic sled and videograb (Table 4). The coefficient of variation estimated from the videograb data was almost twice that calculated for the epibenthic sled data. The lower values for the epibenthic sled data are presumably due to the larger sample size (approximately 17 m^2) that integrates much of the small scale patchiness in organism distribution, while the videograb (0.5 m^2) has a much greater chance of hitting small patches with either high or low biomass. Therefore, statistical analyses using the epibenthic sled data should have higher power than those using the videograb data.

Immediate Impacts on Habitat

In this experiment, habitat features were examined at spatial scales of hundreds of metres down to millimetres using sidescan sonar, RoxAnn, video imagery and DRUMS (Schwinghamer et al. 1996, 1998). Numerous immediate physical changes to benthic habitat caused by the otter trawling disturbance were detected.

The tracks (i.e. furrows and berms) made by the otter boards were readily apparent on the sidescan sonar images, although their depths of penetration could not be determined with certainty (Schwinghamer et al. 1998). They were also occasionally seen in the video imagery collected with BRUTIV, but were not evident in the video imagery collected by the videograb. RoxAnn data showed no effect of trawling on the El signal, which is an index for seabed roughness, but the E2 signal did indicate that repeated trawling increased the hardness of the seabed surface.

Video imagery of the seabed collected by BRUTIV and the videograb revealed signs of additional disturbance from the experimental otter trawling (Schwinghamer et al. 1998). Immediately after trawling each year, the sediment surface was generally flatter, the hummocks being reduced or eliminated, and showed linear features, presumably created by the rockhopper footgear, while organic floc was either absent or less abundant, presumably due to resuspension and redistribution outside the disturbed zone. The trawl track, or perhaps more specifically the track of the rockhopper footgear and net, had a "swept" appearance. It was this surface which the epibenthic sled and videograb likely sampled most of the time since the area of seabed disturbed by the doors was much smaller (about 15% that disturbed by the footgear and net).

There was no detectable effect of trawling on the grain size of sediment (Schwinghamer et al. 1999). In 1993 and 1994, there was no apparent effect of trawling on the concentrations of organic carbon and nitrogen in surficial sediments. However, in 1995, concentrations were significantly lower immediately after trawling. This is in agreement with the video observations indicating that the dark-coloured organic floc was less abundant immediately after trawling.

The DRUMS data indicated that the otter trawling caused a significant change in sediment structure to depths of at least 4.5 cm (Schwinghamer et al. 1996, 1998). There seems to have been a reduction in the structural complexity of the sediment at scales of millimetres, probably due to the destruction of biogenic structures including hummocks, burrows, and other traces of bioturbation, rather than changes in grain size. This reduction in structure may explain the increase in sediment hardness detected by RoxAnn.

The other studies of otter trawling effects, conducted under somewhat different conditions, have reported similar observations. Caddy (1973) observed that doors could cut through surficial gravel and exposed finer sediments below. A number of field studies have reported reductions in sediment structure and complexity consistent with those seen in our experiment (Bridger 1970, Krost et al. 1990, Auster et al. 1991 and 1996, Jenner et al. 1991, Mayer et al. 1991, Brylinsky et al. 1994, Auster and Malatesta 1995, Lindeboom and de Groot 1998). More specifically, Engel and Kvitek (1998) report that door tracks, exposed sediment and shell fragments were readily visible in their heavily trawled area off California. In addition, there were fewer rocks and mounds plus less flocculant organic matter in the heavily trawled area. They too report a general decrease in habitat complexity in their heavily trawled area. Tuck et al. (1998) and Ball et al. (2000a) report that physical habitat disturbance was readily seen in the Loch Gareloch experiment in Scotland. Auster et al. (1996) and Freese et al. (1999) report displaced boulders as a result of otter trawling, while Smith et al. (2000) report the visibility of door tracks and a general flattening of the microtopography in their deepwater experiment in the Mediterranean Sea.

The general homogenization of the seabed, the smoothing of three-dimensional structures, and the reduction in sediment microstructure as a result of otter trawling, as seen in this and other experiments, may be more critical than it might first appear. While the functional significance of infaunal burrows to benthic ecosystems is still poorly understood, they may be important to the biogeochemical fluxes that link sediment pore waters to the overlying water column since the burrows greatly increase the surface area for ecologically-important chemical exchanges between sediment and the water column. The case for significant effects of trawling impacts on sediment structures has been developed primarily for silt and mud seabeds (e.g. Mayer et al. 1991, Pilskaln et al. 1998, Watling 1998). While the impact on sandy substrates is likely to be less, since biogenic structures are less abundant than in muddy substrates, it remains an unresolved but potentially important concern.

The argument has been advanced by Auster et al. (1991, 1996) that habitat structure is advantageous to many species, assisting them to obtain food while avoiding predators, and hence that the smoothing of the seabed may reduce survival of a range of organisms, including such commercial species as Atlantic cod (*Gadus morhua*). Juvenile cod are known to associate with structurally-complex habitat (Gregory and Anderson 1997), particularly cobble-gravel sediment and emergent epifauna on Georges Bank (Valentine and Lough 1991). Such habitats are widespread on the offshore banks of the northwest Atlantic where they provide nursery areas for a number of fish species. These observations suggest that juvenile cod are best able to avoid predators and find prey in these habitats which are essential for their survival and recruitment to the fishery (Collie et al. 1997). The importance of structurally-complex algal habitats to juvenile cod in coastal areas has been recently demonstrated (e.g. Anderson and Gregory 2000).

The importance of biogenic structures, such as hummocks and various other bedforms (e.g. megaripples), in providing cover to juvenile flatfish and their prey are unknown.

However, unlike young gadids which seek concealment amongst above-surface cover or in rock crevices, flatfish will cover themselves with sand to varying degrees, probably primarily to avoid predation (Van der Veer and Bergman 1987, Gibson and Robb 1992). In the case of juvenile European plaice (*Pleuronectes platessa*), there is a strong compulsion to bury themselves in sand, and a clear relationship between body length, sediment grain size and the extent to which individuals can bury (Gibson and Robb 1992). Thus, sediment composition, rather than three-dimensional structure, may be of more importance to flatfish. In this experiment, there was no evidence of a significant trawling effect on the sediment grain size so impacts of this kind appear unlikely.

Immediate Impacts on Benthic Organisms

The most obvious immediate biological impact observed in this experiment was the capture and removal of large epibenthic organisms from the seabed by the otter trawl. The affected species in this experiment were snow crabs (*Chionoecetes opilio*), basket stars (*Gorgonocephalus arcticus*), sea urchins (*Strongylocentrotus pallidus*), soft corals (*Gersemia* sp.), whelks (*Buccinum* spp.), bivalves (e.g. *Chlamys islandica*) and hermit crabs (*Pagurus* sp.)(Prena et al. 1999). However, because of the very low efficiency of capture, on the order of 0.01%, a very low percentage of the total biomass on the seafloor was actually removed. Therefore, the impacts of direct removal on most species were small and difficult to detect above natural variability. The only exception appears to be snow crabs and perhaps basket stars and whelks.

No attempt was made in this experiment to study the condition of the invertebrate bycatch, and some individuals may have survived if immediately dumped overboard. Other studies (e.g. van Beek et al. 1990, Fonds et al. 1992, Kaiser and Spencer 1995) have indicated that the mortality of discards is low for starfish (<10%), intermediate for most crustaceans and shellfish, but quite high for small fish (>90%).

Less obvious, but possibly more important, are the indirect effects on organisms that are disturbed by the trawl but escape capture and remain on the seabed. Ramsey and Kaiser (1998) observed delayed mortality in whelks contacted but not captured by trawls. Samples collected in this experiment using the epibenthic sled indicated that the experimental otter trawling caused a significant reduction in the biomass of snow crabs, sand dollars, brittle stars, sea urchins and soft corals (Prena et al. 1999). Sand dollars, brittle stars and sea urchins demonstrated significant levels of damage, and the mean individual biomass of epibenthic organisms was lower in trawled corridors suggesting size specific impacts of trawling, especially for sand dollars. However, no impacts could be detected on the four species of molluscs commonly captured by the epibenthic sled. This observation was somewhat surprising at first since other studies have demonstrated the susceptibility of molluscs to otter trawling. The explanation seems to be that most of near-surface bivalves at the experimental site are small or medium in size and appear to be displaced with fluidized sediment ahead of the trawl doors (Gilkinson et al. 1998).

Considerably fewer immediate impacts of otter trawling were detected in the videograb samples (Kenchington et al. 2001) compared to the epibenthic sled samples. Few significant effects were observed in 1993 and 1995. However, in 1994 there was a significant decrease in total community abundance immediately after trawling, with polychaetes being the most affected taxonomic group. In the same year, there was no significant change in the total community biomass but several species of polychaetes, as well as sand dollars, were negatively affected. No significant immediate effects of trawling were detected on the number of species, species diversity or evenness. In addition, no significant damage to sand dollars or brittle stars could be detected. It is suspected that it was easier to detect immediate impacts in 1994 because in that year the disturbance was more concentrated along the centre line of trawled corridors and there was a longer delay between the cessation of trawling and videograb sampling which gave more time for scavengers to feed on dead, damaged or exposed organisms. The trawling had no detectable effects on the abundance, recruitment, size structure, species composition or damage of molluscs collected by the videograb (Gilkinson 1999).

Analysis of the epibenthic sled data demonstrated that the biomass of sand dollars, soft corals, sea urchins and brittle stars was significantly lower after trawling (Prena et al. 1999). In contrast, the videograb data demonstrated a drop only in the biomass of sand dollars (and only in 1994), but no significant effects on the other three species (Kenchington et al. 2001). Why is it that more significant immediate effects were observed with the database collected with the epibenthic sled compared to that collected using the videograb? There are several possible explanations.

- **Sampling design**

  Since it was not possible to collect samples in the disturbed corridors before re-trawling in 1994 and 1995, the epibenthic sled samples compared community properties in the reference corridors to those in experimental corridors immediately after trawling. In comparison, videograb samples were collected in the experimental corridors both immediately before and after trawling all three years, and the same blocks were sampled in 1994 and 1995. Therefore, one would expect that the videograb data would be more likely to detect any immediate trawling effects, but they did not.

- **Statistical models**

  Another possible explanation could lie in the statistical models used to analyze the data. Prena et al. (1999) used an ANOVA model for the epibenthic sled data that assumed all differences between the trawled and reference corridors resulted from the experimental trawling. In contrast, Kenchington et al. (2001) used an ANOVA model that acknowledged natural differences among the corridors and used interaction terms as indicative of trawling effects. Again, one would expect that the videograb data would be more likely to detect any immediate trawling effects, but they did not.

- **Sampling efficiency**

  As discussed earlier, there is some evidence that the effectiveness of the epibenthic sled in catching large epibenthic organisms such as sand dollars, brittle stars, sea urchins and soft corals may have been reduced immediately after trawling because of partial burial by resuspended sediment (Table 3). If true, the epibenthic sled samples collected after trawling could have underestimated the biomass of these species and therefore overestimated the apparent trawling effect. The videograb data would not be subjected to this possible error.

- **Area sampled**

  The most logical explanation of the differences in the results from the two databases is the area of seabed sampled. Each epibenthic sled tow sampled an area on the order of 17 m^2 while each videograb sampled an area of only 0.5 m^2. The larger area sampled by the epibenthic sled reduced the variability due to small-scale spatial patchiness (Table 4) and therefore gave more power to the statistical analyses, making it easier to detect significant differences (i.e. the detectable effect size was smaller).

Several different mechanisms are probably responsible for the immediate impacts observed. As stated above, direct removal by the otter trawl is probably not very important, except for snow crabs and perhaps basket stars and whelks. All parts of the otter trawl, but particularly the doors, can resuspend sediment and organisms. Most of the sandy sediment and larger organisms are probably re-deposited in the trawled corridors, and it is possible that this could lead to the burial of some organisms. As discussed above, there is some evidence that the epibenthic sled was less efficient in capturing some species immediately after trawling because of burial (Table 4). Video observations indicate that the resuspended organic floc is transported out of the trawled corridors before it resettles. The same could have happened with smaller organisms. It is possible that the observed reductions in small polychaetes, most pronounced in 1994, do not represent a loss from the ecosystem through mortality but merely a horizontal displacement.

Undoubtedly, another important process in the disappearance of organisms immediately after trawling is predation by scavengers on individuals killed, damaged, or exposed by trawling. In many other experiments, increased predation in freshly disturbed areas has been observed by both fish (e.g. Caddy 1973 and Kaiser and Spencer 1994) and invertebrates (e.g. Kaiser and Spencer 1996, Ramsey et al. 1996, Ramsey et al.1998). Numerous studies have indicated that damaged organisms may be exposed to increased predation risk (e.g. Ramsey and Kaiser 1998). Many of the scavengers may migrate into the disturbed areas from outside. In this experiment, an influx of snow crabs into the trawled corridors while trawling was taking place was clearly observed, presumably to take advantage of increased prey availability (Schwinghamer et al. 1998). Sea urchins feeding on dead snow crabs were seen in some of the video footage. Feeding by demersal fish was probably not a major factor in this experiment because of the extremely low fish abundance at the study site at the time of the experiment (Prena et al. 1999). Impacts might have been greater if demersal fish populations were not so depressed. There also is the possibility that some organisms may have emigrated from the disturbed area.

Numerous observational studies have reported immediate impacts of otter trawling on benthic fauna, including starfish and bivalves being damaged (Rumohr and Krost 1991), sea cucumbers being depleted (Auster et al. 1991, 1996), scallops and moulting crabs being broken up (Hamon et al. 1991), and infaunal bivalves being dug out and left on the surface, some too damaged to reburrow (Arntz and Weber 1972, Rumohr and Krost 1991). Carr and Milliken (1998) provided an anecdotal observation of otter boards impacting beds of decorator worms (*Diopatra cupraea*) in the Gulf of Maine, while Rumohr (1989) contributed a similar claim of trawls removing "lawns" of the polychaete *Polydora*. Most of these effects are probably attributable to the otter boards and thus not directly comparable with the results of this experiment which integrated the impacts of all gear components.

The immediate biological impacts we observed in our experiment appear to be generally consistent with those obtained from other otter trawling experiments (Table 1), realizing of course that some differences should be expected because of variations in habitat, experimental design and sampling gear.

Impacts on epibenthic organisms have been seen in most otter trawling experiments (Table 1). In North America, Auster et al. (1996) report damage to epifaunal species at several locations in the Gulf of Maine. Collie et al. (1997, 2000b) have compared areas on Georges Bank that are exposed to different levels of fishing effort. They report that disturbed sites have lower abundance, biomass, species richness and diversity, as well as a reduced abundance of bushy epifauna that provides structural habitat for other species. Off California, Engel and Kvitek (1998) report that a heavily-trawled area had lower densities of sea pens, starfish, sea anemones and sea slugs compared to a nearby reference site that was subjected to much less trawling disturbance. The reverse trend was seen in oligochaete worms, nematodes, ophiuroid brittlestars, and particularly the polychaete worm *Chloeia pinnata* (which is an important food item for commercial fish). In general, they observed decreased diversity and enhanced abundance of opportunistic species in the heavily trawled area. Freese et al. (1999) report that just a single pass of an otter trawl removed or damaged large epifauna on a hard bottom in the Gulf of Alaska. MacConnaughey et al. (2000), working in the Eastern Bering Sea, observed that sedentary epifauna and whelks were more abundant in untrawled areas compared to trawled areas. In particular, they observed a decrease in abundance and increased damage to sponges and anthozoans. Working on a hard bottom in coastal waters of Georgia, Van Dolah et al. (1987) reported damage to sponges.

Numerous otter trawling studies have been conducted in Australia and New Zealand. Bradstock and Gordon (1983) report extensive damage to coral-like bryozoans. Observations by Koslow and Gowlett-Holmes (1998) indicate that otter trawling can severely damage beds of deepwater corals. There is also compelling evidence from northwest Australia that trawling has caused a marked depletion of sponges and gorgonian corals which in turn has had a negative effect on commercial fisheries (Sainsbury, 1987, 1988, 1991, Sainsbury et al., 1997). Working in the same region, Moran and Stevenson (2000) report that four passes of an otter trawl reduced the density of epibenthic organisms by approximately one half. Pitcher et al. (1999) conducted a depletion experiment in the Great Barrier Reef and report that each set of the otter trawl removed about 5-20 % of the sessile epibenthic biomass. And finally, Thrush et al. (1998) report a decrease in the density of echinoderms, long-lived surface dwellers, total number of species and individuals, and diversity with increased fishing pressure. Overall, increased fishing pressure reduced the abundance of large epifauna.

In European experiments, Bergman and van Santbrink (2000a) have demonstrated that in the Dutch Sector of the North Sea trawling-induced mortalities for gastropods, starfish, crustaceans and annelid worms are on the order of 5-40%, while those for bivalves tend to be higher (20-65%). Bergman and van Santbrink (2000b) suggest that small-sized organisms are affected mainly by perturbation of the sediments (which is comparable to natural disturbances such as storms) while larger organisms are affected primarily by direct physical contact. In the Mediterranean Sea, Smith et al. (2000) observed a greater abundance of epifaunal species (especially echinoderms), higher diversity and lower evenness in reference areas outside a trawled lane, while species number, abundance and biomass were lower in the trawled lane.

The immediate impacts of otter trawling on infaunal organisms have also been shown in other experiments to be relatively minor and difficult to detect at times above natural variability. Van Dolah et al. (1991) could not find any significant differences in community properties between trawled and non-trawled areas in coastal waters of South Carolina. Identical results were obtained from a similar experiment conducted in Australia (Gibbs et al. 1980). In the Loch Gareloch experiment, Tuck et al. (1998) observed that trawling increased the number of species and abundance, while measures of diversity and evenness decreased. As in our experiment, the MDS analyses conducted by Tuck et al. (1998) suggest that subtle natural temporal changes in the macrobenthic community were more pronounced than any trawling effects. In general, only minor effects on infauna were observed in experiments conducted in the Irish Sea (Ball et al. 2000a, 2000b). Relatively minor effects were also observed in the Gullmarsfjorden experiment (Hannson et al. 2000, Lindegarth et al. 2000a, Lindegarth et al. 2000b) as well as an experiment in the Aegean Sea (Simboura et al. 1998). Sanchez et al. (2000) report that otter trawling had no detectable effect on a muddy community in the

Mediterranean Sea and suggest that sporadic trawling disturbance in muddy habitats may have few effects on the benthic communities.

Recovery of Habitat

It is important to document the recovery time of both habitat and organisms from trawling disturbance, and our experiment is one of the few that have attempted to do this. The door tracks were still detectable in sidescan sonar images two months after trawling in both 1993 and 1994. The tracks made in 1993 were not visible in 1994, but those made in 1994 were still faintly visible before retrawling in 1995 (Schwinghamer et al. 1998). Hence, the time for door tracks to disappear in our experiment was on the order of one year. Little information on recovery time scales could be extracted from the acoustic data (Schwinghamer et al. 1998). RoxAnn was only used the last year of the experiment (1995). DRUMS data were collected in both 1994 and 1995, but strong interannual variability precluded an unequivocal assessment of recovery rates. Qualitative examination of the video imagery collected with the videograb in 1994 and 1995 indicated no visual difference in habitat structure (i.e. hummocks, floc, etc.) between reference corridors and experimental corridors before retrawling. These observations suggest that the habitat structure is recovering in less than a year. The most important process affecting recovery of habitat structure is thought to be bioturbation by benthic organisms, but storm-generated sediment transport might also play a minor role, despite the relatively deep depth of the study site. Therefore, all available physical and visual evidence indicates that habitat structure in this experiment appears to have recovered in about a year or less.

Our observations of door tracks persisting for up to a year is the first of its kind reported for a deep (120-146 m) sandy offshore area. They have been reported to persist for at least four months at 200 m in the Mediterranean Sea (Smith et al. 2000), seven months in the intertidal zone of the Bay of Fundy (Brylinsky et al. 1994), at least a year in muddy sediments at 30-40 m in the Mediterranean Sea (Palanques et al. 2001), eighteen months in the muddy bottom of a sheltered Scottish sea loch (Tuck et al. 1998) and, in one instance, as long as five years (Jones 1992).

Recovery of Benthic Organisms

The biomass of fish, snow crabs, basket stars, sea urchins and other invertebrates caught in the otter trawl decreased each year (Prena et al. 1999). These results could be interpreted to indicate that the recovery period of these large epibenthic organisms may be greater than a year. However, the same trends were not visible for these species as sampled by the epibenthic sled which, as described above, is much more efficient in capturing epibenthic organisms than the otter trawl. Unfortunately, due to operational constraints, we were unable to sample the experimental corridors with the epibenthic sled before retrawling in 1994 and 1995, and therefore do not have any direct observations of recovery over the intervening year. However, the abundance and biomass of snow crabs, sea urchins and total invertebrates in trawled corridors was relatively constant during the experiment (Prena et al. 1999). This suggests that recovery from the observed impacts occurred within a year. Such a relatively short recovery time seems reasonable. Most of the affected species (i.e. snow crabs, sand dollars, brittle stars, sea urchins) are mobile and can readily migrate into the trawled corridors from undisturbed areas just a few hundred meters away. In fact, a rapid migratory response was observed for snow crabs (Prena et al. 1999).

Immediate effects of trawling on benthic organisms, as sampled by the videograb, were only observed in 1994 (Kenchington et al. 2001). Since no consistent long-term effect could be attributed to trawling disturbance, it would appear that recovery for those few species affected, mostly small polychaetes, required less than a year. Within this time frame, the actual recovery period is unknown. Rapid recovery of polychaetes is not unexpected. Many are opportunistic species and most can reproduce rapidly. For example, the abundance of *Capitella capitella*, one of the impacted species, has been shown to recover from experimental disturbance in two days (Bonsdorff and Pearson 1997).

In summary, as with habitat, all the available data suggest that organisms recovered from the immediate impacts of the experimental trawling within one year or less. Smith et al. (2000) observed that the recovery period for benthic organisms at their deep water study site in the Mediterranean Sea was in excess of four months. Van Dolah et al. (1987) reported that the corals and sponges at their shallow water site appeared to recover from damage within a year. However, their study employed a very light degree of disturbance (a single set) and they did not specifically examine the tracks of the otter boards where damage was probably most intense. In the Loch Gareloch experiment, Tuck et al (1998) observed that epifauna appeared to have recovered in six months but that some community changes were still evident after 18 months of recovery. Collie (1998) reported the recovery of sponges, bryozoans, crabs, scallops and sea urchins on Georges Bank over several years following the closure of an area to otter trawling and scallop dragging. In general, recovery rates should be relatively high for mobile organisms but much lower for sessile forms that must re-establish by recruitment and growth.

Long-Term Effects on Benthic Communities

During this three-year experiment, we were unable to detect any statistically significant long-term effects of trawling on the benthic community above natural variability over the three year period of this experiment (Kenchington et al. 2001). The non-significant trawling-related trends that were observed in the community analyses paralleled the natural variability documented in the reference corridors, suggesting that any trawling disturbance may have been affecting the benthic community in a similar manner as natural disturbance. After three years of heavy trawling disturbance, twelve sets along the same line each year, there was no distinctive trawling disturbance signal in the benthic community data in the trawled corridors. This observation indicates that the disturbance regime applied in this experiment had no detectable effect on the biodiversity of the benthic community at the experimental site.

It has been argued that benthic communities exposed to repetitive trawling disturbance over long time periods, typical of commercial fishing conditions, can evolve into states that are more tolerant of disturbance and therefore are less likely to exhibit effects from single trawling events . However, this should not be a factor at our experimental site because effort data clearly indicate that it had not been exposed to appreciable trawling activity for at least 13 years (Prena et al. 1999, Kulka and Pitcher 2001), a period of time that we think is ample enough to allow the dominant invertebrate species to recover if previously impacted.

Some other otter trawling experiments have also demonstrated a lack of or limited long-term biological effects. For example, Van Dolah et al. (1991) report that five months of otter trawling did not have a pronounced effect on the abundance, diversity or species composition of a shallow water, soft-bottom community. Ball et al. (2000b) report some possible effects at their offshore site in the Irish Sea, but there is some uncertainty in these results because of the lack of proper reference sites. Pitcher et al. (1999) report few long-term differences between open and closed areas in the Great Barrier Reef. They speculate that impacts may not be detectable where trawling is sparse or infrequent, but that cumulative effects of frequent trawls over the same ground could be substantial.

In contrast, other otter trawling experiments have reported more significant long-term biological effects. These are more likely to be detected when the frequency of disturbance is greater than the recovery period (i.e. frequency of trawling is monthly but it takes a year to recover) as usually occurs under commercial fishing conditions. Continuous fishing pressure could keep benthic habitat and communities in a permanently altered state. Benthic habitats and communities substantially altered by otter trawling will not necessarily return to their original state once the disturbance is removed.

Working on Georges Bank, Collie et al. (1997, 2000b) report that undisturbed sites were characterized by an abundance of bushy epifaunal taxa and had higher numbers of individuals, biomass, species richness and species diversity, while disturbed sites were dominated by larger, hard-shelled molluscs, and scavenging crabs and echinoderms. They concluded that bottom fishing on gravel habitat removes the epifauna and thereby reduces the complexity and diversity of the benthic community. Engel and Kvitek (1998) present evidence off California that high levels of trawling can decrease habitat complexity and biodiversity, and can enhance the abundance of opportunistic and prey species. Thrush et al. (1998), working in New Zealand coastal waters, report increases in the density of echinoderms, long-lived surface dwellers, total numbers of species and individuals, and diversity and decreases in the density of deposit feeders and small opportunists with decreasing fishing pressure. Sainsbury et al. (1997) report long-term decreases in the abundance of fish and benthos in areas open to trawling on the northwest coast of Australia compared to closed areas. Tuck et al. (1998) report long-term impacts on the soft bottom infaunal community of Loch Gareloch, and suggest that even fishing during a restrictive part of the year may be sufficient to maintain the biological community in an altered state. And finally, Smith et al. (2000) demonstrated that overall diversity was higher and evenness lower at reference stations compared to the trawled lane in their deepwater experiment in the Mediterranean Sea.

Perhaps a long-term trawling impact signal would have been detected in our experiment if the annual trawling had continued for more than three years, as could be expected from normal fishing activity. Unfortunately, there are no long-term data sets of benthic community properties on the continental shelf off eastern Canada that can be used to investigate possible long-term impacts of trawling (Stewart et al. 2001). However, there are time series data from the North Sea that indicate long term changes in benthic communities which could be due in part to trawling. For example, Lindeboom and de Groot (1998) report during the 1900s a significant increase in biomass and a change in community structure with a shift towards dominance by opportunistic short-lived species and a decrease in long-lived sessile organisms such as molluscs. They attribute these changes to the cumulative direct and indirect effects of fishing, although recognizing that eutrophication and pollution may also be causative factors. Frid and Hall (1999) have also presented evidence of long-term changes in North Sea benthos, in this case inferred from the analysis of fish stomach contents. Comparing the early 1950s with 1996/97, they observed an increased prevalence of scavengers and decreased occurrence of sedentary polychaetes in the diet, both observations consistent with the hypothesized effects of fishing. Frid and Clark (2000) report reduced abundances of long-lived bivalves and increased abundances of scavenging crustacea and sea stars in the German Bight, as well as altered community structure on some fishing grounds. Frid et al. (2000) have concluded that increases in the areas trawled and the use of heavier and potentially more destructive gears has probably had effects on the North Sea benthic community. Hill et al. (1999) report that forty years of scallop dredging in the Irish Sea has led to an increase in the polychaete to mollusc ratio, loss of some fragile species, and an increase in scavenger species. However, not all the changes observed could be attributed to fishing activities. These studies have considered different kinds of gear and bottom and therefore are not directly comparable to our experiment, but the results illustrate the kind of long-term changes that can occur as a result of commercial fishing activity under certain conditions.

Sensitivity of Benthic Organisms to Trawling Disturbance

Benthic organisms can be expected to vary in their sensitivity to trawling disturbance due to factors such as size and life habits. In our experiment, just 25 species out of a total of 246 taxa were negatively affected to some degree, in the short term, by the repetitive otter trawling (Table 5). Large epibenthic species are vulnerable to direct capture by the trawl. These include snow crabs, basket stars, sea urchins, soft corals, whelks, hermit crabs and Iceland scallops (Prena et al. 1999). However, with the exception of snow crabs and perhaps basket stars, the efficiency of capture is extremely low (0.01%) so only a very small percentage of the population is removed on each pass of the trawl. However, dead, damaged and disturbed organisms not captured by the trawl are exposed to predation. Smaller epibenthic and infaunal species left behind on the seabed can be affected indirectly. On at least one occasion, the biomass and/or abundance of snow crabs, sea urchins, soft corals, sand dollars, two species of crustaceans, thirteen species of polychaetes, and oligochaetes were significantly lower immediately after trawling (Prena et al. 1999, Kenchington et al. 2001). Significant levels of damage were observed in sand dollars, brittle stars and sea urchins and there also was a significant reduction in the mean biomass of sand dollars (Prena et al. 1999). With the exception of some of the crustaceans, all the polychaetes and the oligochaetes, all the species affected by the otter trawling disturbance in this experiment were epibenthic.

Not all the immediate impacts observed in this experiment were negative. For example, three species, all infaunal, showed a significant increase in either abundance or biomass on occasion (Table 6)(Kenchington et al. 2001). In addition, there were thirteen species common at the study site which appeared to be unaffected by both trawling and natural variation (Table 7), including one amphipod, one gastropod, five bivalves and six polychaetes (Kenchington et al. 2001). With one exception, all are infaunal species. These species showed little variation around their mean abundances suggesting genuine stability with time rather than a lack of detectable change.

Overall, it appears that the most sensitive organism to otter trawling at the experimental site was the sand dollar. This is not surprising since it is abundant (~100 of all sizes m^2), attains a large size (~8 cm in diameter), has a fragile test, and lives on the sediment surface.

In general, our results agree with the conclusions of other studies that the species most vulnerable to otter trawling are large, epibenthic and slow growing (e.g. Auster and Langton 1999, Collie et al. 2000b). Bergman and van Santbrink (2000b) have demonstrated that in general small species tend to show lower direct mortalities compared to large species. MacDonald et al. (1996) have developed procedures for calculating an index of sensitivity to trawling disturbance that is based on the intensity of impact, the fragility of the species and the recovery time. They conclude that fragile, slow recruiting organisms are most susceptible to disturbance while the least sensitive species are generally fast growing and have good recruitment.

Possible Effects Not Detected

Despite the care that went into the design and execution of this experiment, it is possible that some trawling effects may have been missed. In any study of this type, it must be remembered that the lack of proof of an effect is not synonymous with proof of an absence of impacts. Factors such as inadequate sampling and natural variation can weaken the power of statistical analyses so that real effects are not detected (Type II error). However, we feel that the chances are low that we missed any major effects of otter trawling on this sandy bottom ecosystem, especially since the sampling program was able to resolve significant levels of natural variability in the reference corridors. A possible exception to this could be effects on large, thinly-distributed epibenthic organisms such as basket stars and whelks which could have been substantially damaged by the repetitive trawling but which were not adequately sampled by either the epibenthic sled or the videograb. Another possible exception might be effects on large sessile epibenthic organisms. Such organisms are particularly vulnerable, however, with the exception of soft corals, they were not abundant at the study site, presumably because of the lack of stable substrata. We do not feel that their scarcity is due to the effects of previous fishing activity since we know for certain that the study site had not been subjected to trawling for at least thirteen years before the experiment, and we consider this to be sufficient time for these organisms to recover from any previous impacts.

Lessons Learned about Experimental Design

This experiment was a major and expensive field effort. Two initial cruises were devoted to site selection and equipment development. The actual experiment required 80 ship days (trawling and sampling combined) over a three-year period. A total of 108 otter trawl sets were made and processed. A total of 105 epibenthic sled and 200 videograb samples were collected and processed. In addition, numerous sidescan sonar and BRUTIV video surveys were run and processed. On the basis of what we have learned, it is reasonable to re-examine our experimental design and consider what we would do differently to maximize the return for the effort expended if we were going to repeat this experiment.

As a general rule, we always tried to sample our reference corridors before trawling, just in case they might be affected by sedimentation. Unfortunately, we were unable to do so with the epibenthic sled in 1994 and, as discussed by Prena et al. (1999), this may have confounded the results due to possible emigration of mobile organisms to feed on dead or damaged organisms in the nearby trawled corridors. As a general rule, in experiments of this kind, reference sites should always be sampled before the trawling disturbance. Ideally, it would have been valuable to have sampled the reference corridors both before and after trawling. This would have given us a full BACI (Before-After, Control-Impact) experimental design and verified our assumption that the reference corridors were not affected by trawling. Time constraints prevented this, but it should be attempted in future experiments.

It was our original intention to sample the trawled corridors with the epibenthic sled before retrawling in 1994 and 1995 as we did with the videograb. This would have provided direct information on both the immediate impacts of trawling and the recovery rate of the benthic organisms over the intervening year. However, time constraints again prevented this, and this is probably the major shortcoming in our experiment, especially since the major biological effects were observed in the epibenthic sled database. Although more difficult to collect than videograb samples, epibenthic sled samples required much less time for processing (most of which was done at sea). In retrospect, we regret not collecting more epibenthic sled samples. Due to the rapid response of migrating organisms (e.g. snowcrabs), it is also important to standardize the time interval between trawling and the biological sampling immediately after.

We have considered whether it is necessary to identify all organisms to the lowest taxonomic level, especially in the videograb samples which had 246 taxa. Analyses at higher levels of aggregation generally showed similar results (Kenchington et al. 2001), but we concluded that the effort needed to identify organisms to the lowest possible taxonomic level was justified because of the additional information it provided. For example, this experiment has provided a detailed description of the benthic community for a representative region of the Grand Banks that can be used in the future as a baseline for assessing long-term variations in biodiversity.

There is no one correct trawling regime to use in manipulative experiments such as this because commercial fishing disturbance covers a continuum of intensity and frequency. However, the trawling disturbance regime we applied was clearly quite different from that usually expected from commercial trawling in an offshore setting. For example, the disturbance was limited to a narrow corridor and therefore undisturbed seabed was immediately adjacent on both sides. In addition, it probably would have been more realistic to trawl once a month instead of twelve times once a year, but this was impossible because of constraints in scheduling research vessel time. Difference in the timing of the disturbance in relation to natural biological cycles (e.g. growth, spawning, migration, etc.) could potentially affect both the immediate impacts and recovery period. This inability to completely replicate the disturbance imposed by commercial trawling constitutes the principal shortcoming of the manipulative experimental approach to study gear impacts. However, its distinct advantages, such as knowing and controlling the exact disturbance regime and accounting for natural variability, still makes it a valuable approach to follow. In future experiments, consideration should be given to having the gear disturbance applied by a commercial fishing vessel following standard fishing practices, within the constraints of an experimental approach.

Potential Effects on Demersal Fisheries

We can only speculate on how the trawling disturbance imposed may have impacted the resident demersal fish population, which was quite depauperate at the study site when the experiment was conducted (Prena et al. 1999). Many of the benthic organisms found at the study site are important prey items for demersal fish (Methven 1999) so the presence of dead, damaged and exposed organisms on the seabed immediately after trawling probably constituted a short-term increase in food supply. However, no evidence of a behavioural response was detected in the fish catch (i.e. increasing abundance with each successive set as was observed with snowcrabs), and stomach contents were not analyzed. Effects of the observed changes in habitat structure on the growth and survival of demersal fish are of course possible but were not investigated. Considering that all the evidence indicates that both habitat and organisms recovered from the trawling disturbance in less than a year, any long-term effects of this particular experiment on demersal fish populations were probably small and difficult to detect.

The major impact on the sparse fish populations at the experimental site was most likely direct removal by the otter trawl.

There was no clear evidence from our experiment to indicate that the effects of intensive otter trawling on benthic habitat and communities were a major factor in the crash of groundfish stocks on the Grand Banks in the early 1990's. However, it is recognized that otter trawling may have greater potential effects on demersal fish on gravel habitats that have been shown to play an important role in providing shelter for early life stages (e.g. Valentine and Lough 1991, Collie et al. 1997, Gregory and Anderson 1997). Nonetheless, there is evidence that the groundfish crash on the Grand Banks can be explained entirely by excessive fishing mortality (i.e. overfishing) (Hutchings 1996).

Extrapolation of Results to Other Conditions

The conclusions of this experiment are specific to the conditions of the disturbance regime employed (i.e. annual experimental trawling along narrow corridors surrounded by undisturbed seabed) and the characteristics of the benthic habitat and community at the study site (i.e. sandy bottom with few sessile epifauna). It can not be assumed that the same conclusions would be reached for different disturbance regimes and different benthic ecosystems for numerous reasons. The disturbance regime employed in this experiment did not completely replicate that imposed by commercial fishing activity. While the annual intensity of trawling may have been realistic (at the upper end of the range estimated from past trawling activity on the Grand Banks), the pattern, timing and duration of trawling were not. Despite the considerable length of our trawled corridors (13 km), because of their narrowness they do not adequately replicate the scale of the disturbance regime that would be expected from commercial fishing. The disturbed zone was only 120-250 m wide and bordered on both sides by undisturbed habitat and communities. The zone of disturbance under commercial fishing pressure can be expected in most cases to be more widespread. Therefore, the rate of biological recovery observed in our experiment is probably higher than would take place under conditions of a wider disturbance zone where mobile organisms would have to travel greater distances to re-colonize.

With regard to timing, all the experimental trawling was done within a few days each year in early July. In contrast, commercial trawling generally takes place throughout the year, subject to regulations. Impacts may have been different if this concentrated disturbance had been applied at other times of the year when organisms were possibly more vulnerable. In addition, impacts may have been different if the study site had been trawled once a month. Spreading the trawling intensity over the year would most likely slow down the rate of recovery since the seabed would be disturbed more frequently. Finally, commercial trawl fisheries usually operate in a given area for more than three years, the time span of this experiment. We may have observed some long-term changes if we had extended the length of the experiment.

Otter trawls are designed to capture demersal species while being towed in limited contact with the seabed, but other gear types such as scallop rakes and clam dredges are designed to collect benthic species that live on or in the seabed. Therefore the physical disturbance they create is much greater for each square meter of the seabed contacted. As the intensity of use increases, so does the potential for lasting effects, especially if the time interval between disturbance events is less than the recovery period of the benthic ecosystem. Sandy bottom habitats are generally subjected to considerable physical stress through waves and currents, and tend to be relatively robust and self-healing. Other benthic habitat types, including both mud and gravel bottoms, are more prone to physical damage. There are anecdotal reports from fishers that intensive use of mobile gear has changed the topography of the seabed in some locations (e.g. Fuller and Cameron 1998). Our experiment site had very few sessile epibenthic species (the dominant one being the soft coral). Such species, which stand erect attached to the seabed, are particularly vulnerable to damage from mobile gear, and, being non-mobile, will take longer to recover. These include mussels, corals, sponges, anemones and seapens. Therefore, the conclusions of this experiment would have been quite different if it had been conducted on a different bottom or with different gear.

GENERAL CONCLUSIONS OF TRAWLING IMPACT STUDIES

A large number of scientific studies have investigated the impacts of trawling on seabed habitat and communities (Table 1). Most of these have been conducted within the past decade in Europe, Canada, the US, New Zealand and Australia. Different experimental approaches have been applied in a wide variety of habitats. While the results of specific experiments are very dependent on the conditions under which they were conducted, it is clear from the recent reviews of the scientific literature (e.g. MacDonald et al. 1996, Jennings and Kaiser 1998, Lindeboom and de Groot 1998, Watling and Norse 1998, Hall 1999, Auster and Langton 1999, Collie et al. 2000a, WGECO 2000, Northeast Region Essential Fish Habitat Steering Committee 2002, National Research Council 2002) that a number of general and widely accepted conclusions are emerging which illustrate the general type and direction of impacts that can be expected. These are summarized below. They were compiled with the impacts of otter trawling foremost in mind but most of them also hold true for other mobile gear types.

- Benthic habitats and communities are not static but change naturally through weather-mediated oceanographic events and physical stresses imposed by storm waves, tidal currents, ice scour, sediment transport, foraging, and bioturbation. This natural variation, both spatial and temporal, must be understood and not confused with changes caused by human activities. Therefore, experiments designed to investigate trawling effects must include adequate reference areas.
- Effects of otter trawling on seabed habitat and communities can be detected but are highly dependent upon many factors including: 1) previous fishing history, 2) the intensity and frequency of trawling, 3) the type of habitat and 4) the kind of

organisms present. In some instances, effects are negligible and short-lived, while in other cases they may be profound and long lasting.

- Otter trawls appear to disturb the seabed less than beam trawls, scallop rakes and clam dredges but their overall footprint is generally much greater.
- In general, the magnitude of natural variability relative to fishing stress decreases with increasing water depth.
- Disturbance by otter trawling (and other bottom fishing gears) is widespread but within a given area appears to be quite patchy (i.e. most of the effort is concentrated in a relatively small area). In heavily fished regions, it can be difficult to find undisturbed seabed habitat and communities.
- There are limited data on the characteristics of seabed habitat and communities before fishing began which complicates understanding long-term changes.
- The greatest impacts probably occur when an area is fished for the first time. As the seabed habitat and communities adapt to fishing disturbance, the effects of future fishing become less. Many of the studies of gear impacts have been conducted in previously fished areas and so effects may be underestimated.
- Otter trawling can alter the physical structure of seabed habitat. Berms and furrows are created by the doors. Lighter sediments are resuspended. The sediment surface is flattened and biogenic sediment structures are damaged. In general, there is a reduction in habitat structural complexity.
- The most vulnerable seabed habitats appear to be those with a high degree of structural complexity. These tend to be most common in low-energy environments but can also be found in deepwater areas with high currents (i.e. deepwater corals). The most resilient habitats appear to be those found in high-energy environments exposed to frequent storm waves and tidal current activity (i.e. sands).
- Direct removal by the otter trawl (i.e. bycatch) is very limited for most benthic species (except large epibenthic forms). Most of the observed mortality is through damage and predation on organisms left exposed on the seabed behind the otter trawl.
- Effects on benthic organisms are quite variable and depend upon life history characteristics, life habit, size and morphology. Highest mortalities are generally found for organisms that are large, fragile, live on or near the seabed surface, sessile, long-lived, and have slow growth and recruitment rates. Conversely, the lowest mortalities are generally found for organisms that are small, robust, live deep in the seabed, mobile, short-lived and have high growth and recruitment rates.
- As a result of the varying susceptibility of individual species, changes in community structure (i.e. various indices of diversity and evenness) can be expected to take place with repeated trawling. More vulnerable species can decrease in abundance while opportunistic species can increase.
- Biological communities in variable environments dominated by less vulnerable species appear to be quite resilient to disturbance. For example, impacts can be expected to be less on sandy bottoms where organisms are adapted to sediment resuspension, especially in shallow water. Under these conditions, impacts may fall within the range of natural perturbations and be difficult to detect. On the other

hand, impacts on communities occurring in stable environments dominated by vulnerable species can be substantial and long lasting.

- Organisms killed, damaged or exposed by otter trawling, as well as discarded bycatch, attract benthic scavengers (e.g. fish, crabs, gastropods, echinoderms, etc.) into recently disturbed areas.
- The recovery period for habitat damage is highly variable. It can range from just a few days for high-energy sand habitats to tens of years for stable, structurally complex habitats in low-energy environments.
- The recovery period for biological communities is also highly variable and covers the same range of time scales. Those communities dominated by opportunistic species can be expected to recover the fastest. The principal mechanisms of biological recovery are immigration (for mobile species only) and recruitment.
- Rate of recovery depends upon the spatial scale of the fishing disturbance. In general, the smaller the disturbed area, the faster the recovery. Single, widely spaced disturbances (Type 1) should recover relatively quickly, in part due to immigration of mobile species. However, spatially extensive disturbances with a few isolated undisturbed patches (Type 2) can be expected to recovery more slowly, through both immigration and recruitment.
- Since most trawling impact experiments have been done at a small spatial scale, not at the scale of commercial fisheries, observed rates of recovery are probably artificially high.

In addition, there are a number of speculative impacts that are still at the hypothesis stage and yet to be proven. Further research is needed to determine if they are real. These include:

- Few studies have been conducted on the impacts of fixed gear (e.g. gillnets, longlines, traps, etc.) on seabed habitat and communities, but these are expected to be substantially less than those of mobile gear.
- Changes in physical habitat structure may affect the survival of various organisms, including juvenile forms of commercial fish species.
- Where the frequency of disturbance is greater than the recovery period, long-term effects on seabed habitat and communities can be expected. Heavily fished areas, especially those with the most vulnerable habitats and organisms, are likely to be maintained in a permanently altered state. Detecting these long-term effects is difficult and subject to controversy, largely due to a lack of predisturbance data but also due to coincidental confounding disturbances. In general, a shift from communities dominated from relatively high biomass species toward dominance by high abundances of small-sized organisms is anticipated.
- The most convincing evidence for long-term effects of trawling activity comes from the heavily-fished North Sea, although it is difficult to separate fishing impacts from changes due to pollution, eutrophication and natural processes. There appear to have been declines in deposit feeders, bivalves and long-lived, sessile species, but

increases in total biomass, suspension feeders, scavengers, predators and opportunistic, short-lived species.

- Otter trawling may also have effects on important ecological processes such as chemical exchanges between sediments and the water column, nutrient regeneration, primary production and organic matter dynamics but these are generally not well understood.

FUTURE INFORMATION NEEDS

Further research is needed to improve our knowledge of otter trawling impacts, as well as the impacts of other gear types, and to develop the information needed to adopt a more ecosystem-oriented approach to fisheries, habitat and oceans management. As a result of the experience gained in the past decade, the way forward is quite clear. Some of the major recommendations for future research presented in recent reviews (e.g. Auster and Langton 1999, Collie et al. 2000a), augmented by our own thoughts, are summarized as follows.

Gear Impact Experiments

Understanding the effects of otter trawling on benthic habitat and communities is a difficult task. Despite the large number of gear impact experiments conducted (Table 1), there still is a need for more. These should be conducted over a gradient of disturbance intensities on specific habitats and benthic communities, and seek to understand the mechanisms of both initial impact and recovery. More information is needed on the relative sensitivity of different habitats and communities to fishing disturbance and their recovery periods. It is particularly important to determine what habitats have long recovery times (i.e. more than one year).

Different experimental approaches should continue to be pursued, acknowledging that each has its own benefits and shortcomings and that the most appropriate one depends upon the specific questions being asked and the resources at hand. Laboratory experiments allow detailed observations to be made on specific processes under highly controlled conditions, such as the interactions between trawl doors and bivalves (Gilkinson et al. 1998), burrowing behaviour (Gilkinson 1999), and determining the shell strength of bivalves (Coffen-Smout 1998, Gilkinson et al. 1998).

Manipulative field experiments, such as ours and many others (e.g. Tuck et al. 1998, Freese et al. 1999, Bergman and van Santbrink 2000a, Hannson et al. 2000, Sanchez et al. 2000, Moran and Stevenson 2000), have the advantages that a specific kind of habitat and gear can be targeted, the disturbance regime is well documented, and natural variability (both spatial and temporal) can be accurately assessed. However, a major disadvantage is that the trawling disturbance is usually of limited spatial extent and does not always truly replicate commercial fishing.

Another approach is to compare areas that have been subjected to different levels of commercial fishing effort (e.g. Thrush et al. 1998, Engel and Kvitek 1998, Simboura et al. 1998, Collie et al. 2000b, MacConnaughey et al. 2000, Smith et al. 2000). This approach works well if georeferenced effort data are available and the spatially separated seabed habitats can be shown to be comparable. The major disadvantage to this approach is that proper reference areas can be hard to find making it difficult to distinguish gear effects from natural variation or the influence of other human activities. Also the use of multiple gears makes it difficult to determine with certainty what kind of gear is causing the observed effects.

A fourth approach is to collect time series data on benthic communities at a particular site and compare them with changes in fishing effort over relatively long time periods (e.g. Lindeboom and de Groot 1998, Frid and Hall 1999, Hill et al. 1999, Frid and Clarke 2000). However, interpretation of these data is again complicated by the usual lack of adequate reference sites to document natural variation and the influence of other human activities.

In particular, more experiments are needed to better understand:

- Long-term natural variations in benthic habitat and communities unaffected by human activity.
- Impacts on and recovery of habitats and communities not yet subjected to fishing, especially those for which new fisheries are proposed.
- Impacts on and recovery of stable, mud habitats and communities at all depths including the continental shelf, slope and seamounts.
- Impacts on and recovery of stable, structurally complex habitats at all depths including the continental shelf, slope and seamounts.

Wherever possible, experiments should be large-scale and investigate the effects of fishing disturbance imposed by commercial fleets. Sainsbury et al. (1997) describe such experiments that have been carried out in Australia to examine the links between gear impacts on habitat structure and population responses. It has been argued by Collie et al. (2000a) that short-term, small-scale pulsed experiments should be abandoned and replaced by large-scale press and release experiments. They suggest that some heavily fished areas should be closed and the recovery process followed. The advantages of this approach are that the results obtained can be interpreted in terms of realistic intensities of fishing disturbance, the closed areas could be relatively small, and the experiments would be conducted on the very habitats and communities (i.e. important fishing grounds) for which questions of recovery are being asked. Conducting research at the scale of fish populations will make it easier to apply the results to management questions.

Understanding the Role that Different Benthic Habitats and Communities Play in Marine Ecosystems

There is a general lack of knowledge on the linkages between benthic habitat and the productivity of fish populations on the continental shelf. This information is needed to understand the potential impact of past fishing disturbance and to predict the effects of future disturbance. More work is needed on understanding the dependence of fish communities on particular habitats and their structural features. It is important to define what constitutes essential fish habitat for different species, to understand how it is utilized by different life stages, and to determine how much is necessary to support healthy populations. This information is needed for the design and management of marine protected areas.

Mapping the Fine-Scale Spatial Distribution of Benthic Habitat and Communities

Our knowledge of benthic habitat and communities and their spatial distribution on the continental shelf of Atlantic Canada remains rudimentary. A wide range of different habitats and communities is known to exist and they need to be systematically classified and mapped at a small spatial scale. Fortunately, the technology exists to do this. Available tools include multibeam bathymetry, sidescan sonar, acoustic seabed classification systems (e.g. RoxAnn, Quester Tangent), and various video and photographic platforms. Pilot benthic mapping projects have been conducted on Browns Bank (Kostylev et al. 2001) and in the Gully (Kostylev 2002). The SEAMAP program has been proposed to systematically map the entire Canadian seabed over the next 25 years. This information will allow us to map the spatial distribution of benthic habitat and communities over large geographic areas. Combined with knowledge of gear impacts and essential fish habitat, this information will allow the identification of specific areas that are potentially more vulnerable to fishing impacts, as well as those areas least likely to show impacts.

Mapping the Fine-Scale Spatial Distribution of Fishing Effort

It is important to collect information on the fine-scale spatial distribution of commercial fishing-induced disturbance. Where they exist, historical data can be used to determine both the extent and distribution of past fishing disturbance (e.g. Rijnsdorp et al. 1998, MacConnaughey et al. 2000, Kulka and Pitcher 2001). The recent analyses by Kulka and Pitcher (2001) provide a detailed picture of recent seabed disturbance by otter trawling off the Atlantic and Pacific coasts of Canada. The distribution of fishing disturbance is very patchy. These data can be used to identify highly stressed areas of the seabed as well as areas subjected to little or no fishing disturbance. High priority should be given to collecting and analyzing these data in the future. Again, the necessary technology is available (i.e. satellite tracking). This information will have many applications in understanding and managing fishing gear impacts on benthic habitat and communities. For example, it can be used to predict the extent of past damage, to identify areas of the seabed that have not been affected by mobile fishing gear, and to design marine protected areas.

MANAGEMENT IMPLICATIONS

In order to maintain the long-term integrity, biodiversity and productivity of benthic habitat and communities, as well as the sustainability of the commercial fisheries that they support, it is essential to incorporate our newly acquired knowledge of gear impacts into management regimes. Most fisheries management measures today are based solely on the population dynamics of exploited fish populations and do not take into account information on the benthic ecosystem. This shortcoming is now recognized and steps are underway to develop more ecosystem-oriented approaches to fisheries management (e.g. Murphy and O'Boyle 2000). Different management approaches are suggested by Auster (2001).

While there is value in conducting retrospective analyses of past fishing disturbance, the ultimate goal of research should be to develop the ability to predict the outcomes of particular management regimes in the future. We need a system of ecosystem-based management where the benefits of fishing can be evaluated against its side effects which may negatively influence other valuable functions provided by benthic ecosystems. Because of our rudimentary level of knowledge of benthic ecosystems, predictive numerical models are not available at this time. However, as discussed above, on the basis of recent research we have a general idea of the kinds of impacts that can be expected from otter trawling (and other mobile gear types) and the likely direction of change. There also is a growing understanding of habitat and organism sensitivity. Some conceptual models of the vulnerability of benthic habitats to gear impacts have also been developed (e.g. Auster 1998, Auster and Langton 1999, Duplisea et al. 2001, Jennings et al. 2001). This knowledge must be incorporated into new management regimes.

In developing new and effective management procedures based on ecological relationships, it is important that scientists, managers, industry and conservation organizations work together. One well-known example of a productive approach is the work of Sainsbury et al. (1997) in northwest Australia. On the basis of existing knowledge, they drafted a series of hypotheses regarding the dependence of harvested species on habitat. Management regulations were then adopted and applied to test these hypotheses over a period of years, and the research results were used to modify subsequent management decisions. This is an excellent example of adaptive environmental management, and more of this kind of approach is needed.

The basic challenge is to develop procedures to incorporate our rapidly increasing knowledge of benthic ecosystems and gear impacts into the decision-making process. We now have a good understanding of which ecosystems are most vulnerable to fishing disturbance and, with time, will hopefully gain a much better understanding of their fine-scale spatial distribution. We will need to take steps to protect sensitive habitats and minimize disturbance. In particular, we must determine the kinds and levels of fishing disturbance that different habitats can withstand without altering the ecosystem to the point where recovery is retarded or the system shifted to an alternative, less desirable state.

The application of scientific information to management decisions will always be complicated by the natural variation inherent in marine ecosystems which is substantial and unpredictable. Because of this, and our rudimentary knowledge of benthic ecosystems, there is clearly a need for a precautionary approach to the management of fisheries, other human activities and benthic ecosystems.

Some of the recommendations for specific management actions presented in recent reviews (e.g. Auster and Langton 1999, WGECO 2000), augmented by our own thoughts, are summarized as follows.

Control of Fishing Effort

The single most effective measure to protect fish populations and the benthic ecosystem is to reduce the overall fishing effort, both significantly and permanently. Some populations may respond to permanent reductions in effort rather quickly, while recovery of benthic ecosystems will probably take longer, especially those which are structurally complex and populated with long-lived species (i.e. deep water corals).

Steps could also be introduced to control the distribution of effort within fishing grounds, both spatially and temporally. With today's technology, it is relatively easy and inexpensive to control and monitor effort down to very small spatial scales. For example, patches or strips of productive bottom could be left undisturbed and serve as a source of recruitment for the recolonization of fished areas. More controls could also be set on the frequency of effort. For example, as a general principle, a given area of the seabed should not be retrawled until the habitat and communities have been able to recover from previous disturbance. An acceptable return period would be quite variable depending on ecosystem conditions and range anywhere from a few months to tens of years. In the case of our Grand Banks experiment, it appears that the sandy bottom ecosystem can withstand intensive otter trawling once a year without showing long-term effects, as long as nearby areas remain undisturbed.

Gear Usage and Modification

Altering the way that gear is used also has the potential to reduce environmental impacts (Linnane et al. 2000). For example, shorter tows could increase the survival of bycatch. Re-engineering the different gear components and how they are rigged to reduce contact with the bottom would also lessen environmental impacts. For example, using lighter doors and footgear should decrease the degree of bottom disturbance. Despite FAO's guidelines for the precautionary approach to management and numerous countries advocating a conservation-minded approach to the use of fishing gear, limited effort has been devoted to looking at desirable gear modifications. This requires an immediate and concerted effort in partnership between industry and government. Various options for reducing the seabed impacts of trawling gear where discussed at a DFO/industry workshop in October 1999 (DFO 1999).

Gear Substitution

Where effort controls will not work, benthic ecosystems can be protected to some degree by selecting the least-damaging gear type, that is matching the fishing gear to bottom type. This would be most effective in areas that have the most sensitive habitat, such as hard bottoms with abundant emergent, sessile, structure-forming epifauna. Replacing bottom trawls with fixed gear (gillnets, longline, traps, etc.) should reduce the degradation of sensitive habitats and, in some cases, mortality of non-target species. However, fixed gears have their own set of environmental concerns (e.g. bycatch of seabirds and cetaceans, entanglement in deep water corals, etc.) which must be considered. In addition, their potential benthic impacts are still poorly understood.

Area Closures

Where effort and gear controls will not work, area closures can be an effective measure in protecting benthic ecosystems from fishing disturbance. They should be selected and designed with a clear purpose in mind, taking into account all available knowledge of the characteristics of benthic habitat and communities, including both traditional ecological knowledge possessed by the fishing community and the results of scientific investigations. While different spatial scales are possible, the most suitable depending upon local environmental conditions, larger areas will probably be the most effective, especially since at the moment we do not have a good idea as to how big is enough. Such closed areas can protect sensitive and valuable areas of the seabed not yet affected by fishing disturbance, and also allow disturbed areas an opportunity to recover (or reach a new state of equilibrium). To be most effective, closed areas should be established concurrently with effort reductions so that the displaced effort is not transferred to other areas creating new problems. Equally important to identifying areas to protect from trawling is the identification of areas where trawling has little or no environmental impact and is an acceptable method of harvesting fish.

Closed areas offer many advantages. They can serve as a source of new recruits to re-populate disturbed areas immediately outside. They can also serve as natural control areas valuable for scientific research on undisturbed benthic ecosystems, including long-term studies of natural variability. Where closed areas are established, it is important to conduct long-term scientific studies of their effectiveness. Such studies should be based on testable scientific hypotheses and the results used in adaptive management. For example, if the anticipated benefits are not being achieved, the design of the closed areas should be reconsidered and modified as necessary to meet the management objectives.

Examples of how closed areas have been effectively used in research programs are given in Bradstock and Gordon (1983), Sainsbury et al. (1997), Pitcher et al. (1999), Moran and Stevenson (2000) and Collie et al. (2000b). An example of a large-scale area closure in Canada is the haddock nursery box on Emerald/Western Bank which has been closed to mobile groundfish gear (but not scalloping) since 1987 to protect juvenile haddock. The effectiveness of this management action has been recently evaluated by Frank et al. (2000). The degree to which management objectives may have been compromised by allowing scalloping to continue is not known.

The effectiveness of these different potential management measures will depend upon the specific habitat and communities present in a given area, the scale at which they are employed, and their duration. There will be no generic approach for mitigating the effects of otter trawling on all habitats and species. The best approach will depend upon the local environmental conditions and specific management objectives.

CONCLUSIONS

- A carefully designed, three-year experiment (1993-1995) was conducted to examine the effects of intensive otter trawling on a sandy bottom ecosystem at a depth of 120-146 m on the Grand Banks of Newfoundland. Three, 13 km long experimental corridors were trawled twelve times each year with an Engel 145 otter trawl equipped with rockhopper footgear. A broad array of imaging and sampling instrumentation was used to survey both trawled and nearby reference corridors over different spatial scales.

- Most pronounced impacts were the immediate physical effects on habitat. Sediment was resuspended by all parts of the otter trawl, furrows and berms were formed by the doors, biological sediment structures were either modified or destroyed, and organic detritus was dispersed. However, these physical effects appear to be relatively short-lived for the available evidence suggests that the habitat recovered in about a year or less.

- The most immediately obvious biological effect was the direct removal of large epibenthic organisms by the otter trawl. However, except for snow crabs and basket stars, direct removal appears to be insignificant at the population level because of the very low efficiency of the otter trawl in catching benthic organisms.

- Less obvious, but more significant, was the immediate damage done to epibenthic organisms that were left behind on the seabed. Some were been killed outright while others may have been damaged or exposed. Most susceptible were the larger epibenthic organisms that live on the sediment surface and were subject to direct contact with the otter trawl. The species most affected in this experiment were snow crabs, basket stars, sand dollars, brittle stars, sea urchins and soft corals. The net effect was a reduction in mean biomass, averaging 24 %, within a few days after trawling. This reduction in biomass is thought to be due primarily to direct removal by the otter trawl, predation by scavenging organisms, displacement outside the disturbed area, and perhaps burial by resuspended sediment.

- Both the immediate and medium-term impacts of otter trawling on benthic infauna appear to be very minor. For the most part, significant effects were seen in just a limited number of polychaetes and were restricted to just one year of the experiment (1994).

- All available evidence suggests that the biological community recovered from the trawling disturbance in less than a year. Most of the affected epibenthic species have some power of locomotion and migration into the disturbed area from the surrounding undisturbed area is highly probable. This was in fact documented for snow crabs.

- Negative effects were observed on only 25 species out of 246 taxa. The majority of species at the study site were not affected by otter trawling. This included all the molluscs, including the shallow-burrowing species. No significant effects could be seen on the benthic community after three years of trawling.

- Long-term effects were not observed because it appears that the frequency of trawling (i.e. annual) was greater than the recovery period of both the habitat and biological communities.

- The habitat and biological community at the experimental site are naturally dynamic and exhibit marked changes irrespective of trawling activity. The effects of natural variability on the infaunal benthic community at the study site appear to over-shadow the effects of trawling.

- Limitations in experimental design, constraints on conducting the field program influenced by the vagaries of weather and scheduling research vessels, and the considerable natural spatial and temporal variability inherent in benthic communities mean that some effects of otter trawling may have gone undetected in this experiment. However, if so, they are expected to be relatively minor.

- There is evidence from other scientific studies that the observed impacts of otter trawling will be less on benthic ecosystems that have already been stressed by previous fishing activity. Analysis of historical effort data clearly indicates that the study site had not been actively trawled for at least 13 years before this experiment was conducted which strongly suggests that the benthic ecosystem was in a natural state when the experiment began in 1993.

- This experiment is one of approximately thirty that have been conducted using different approaches to study the effects of otter trawling on benthic ecosystems under a wide range of conditions. It remains unique in terms of its depth, repeat nature of trawling disturbance, duration, and scope of data collected. Only three other offshore, deep-water otter trawling impact experiments have been reported. The results of our study are in general agreement with those of other otter trawling experiments, taking into account differences in experimental design, habitat and biological communities.

- The scientific literature indicates that the effects of otter trawling on benthic habitat and communities are quite variable and depend upon numerous factors such as previous fishing history, how the otter trawl is deployed, the intensity and frequency of use, the type of habitat, and the kind of organisms present. In some instances, effects are negligible and short-lived, while in other cases they may be profound and long lasting.

- The kind and magnitude of impacts detected will depend upon the kind of sampling gear and how it is used. It is important that future experiments employ different gear types that sample over a wide range of spatial scales (hundreds of meters to centimeters).

- The results of this experiment are specific to the conditions under which it was conducted, and one must be very cautious in extrapolating them to other conditions. The trawling disturbance was not fully representative of commercial fishing activity, and there is good reason to suspect the observed rate of biological recovery may be higher than would be expected under normal fishing activity.

- There is no clear evidence from this experiment that otter trawling damage to benthic habitat and communities was a major factor in the crash of groundfish stocks on the Grand Banks in the early 1990s.

- Further research is needed to improve our knowledge of otter trawling and to develop the information needed to adopt a more ecosystem-oriented approach to fisheries, habitat and oceans management. Information requirements include further gear impact experiments, improving our understanding of the role that benthic habitat and communities play in marine ecosystems, mapping benthic habitat and communities, and mapping the fine-scale spatial distribution of fishing effort.

- Possible management actions that should be considered to protect sensitive benthic habitat and communities include control of fishing effort, gear usage and modification, gear substitution, and area closures.

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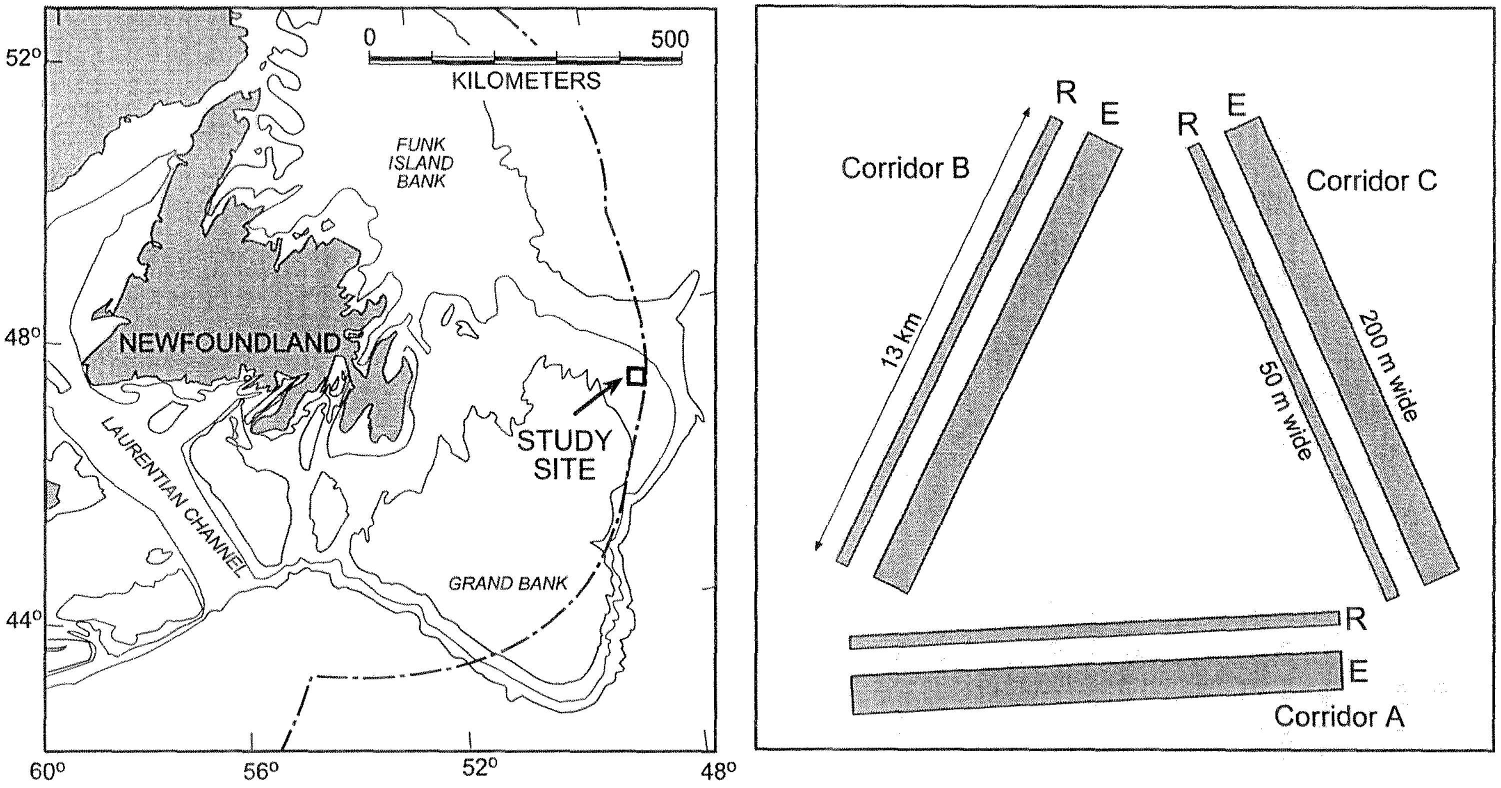

Figure 1. Location of the experimental site (20 X 20 km) on the Grand Banks, and the relative position of Corridors A, B and C (not to scale). The central axis of reference corridors (R) was 300 m to one side of the experimental (i.e. trawled) corridors (E). Ends of the corridors are about 3.5 km apart.

Table 1. Must insert later.

Table 1. Summary of experiments conducted around the world to investigate the effects of otter trawling on benthic habitat and communities. Experiments are listed in the order in which they were initiated. Manipulative experiments include observations before and after a controlled trawling disturbance and are usually of limited spatial scale. Comparative experiments are usually of larger spatial scale and compare areas subjected to different levels of commercial fishing, or the same area over time. Some comparative experiments include the impacts of other mobile gear types.

Location	Year	Depth (m)	Habitat	Experimental Design	Reference
Botany Bay, Australia	1975-76	Shallow	Sand	Comparative and Manipulative	Gibbs et al. 1980
Tasman Bay, New Zealand	1980	10-35	Hard bottom with bryozoans	Comparative	Bradstock and Gordon 1983
Georgia, USA	1982	20	Hard bottom with sponges and corals	Manipulative	Van Dohal et al. 1987
Northwest shelf, Australia	1985 to present	<200	Mixed but included hard bottom with attached epifauna	Comparative	Sainsbury et al. 1997
South Carolina, USA	1987	8-30	Sand	Comparative	Van Dolah et al. 1991
Gulf of Maine, USA	1987-93	94	Gravel with boulders	Comparative	Auster et al. 1996
Limfjord, Denmark	1988	7-11	Soft bottom	Manipulative	Riemann and Hoffman 1991
Kiel Bay, Germany	1989	20	Sand	Manipulative	Rumohr and Krost 1991

Location	Year	Depth (m)	Habitat	Experimental Design	Reference
Hauraki Gulf, New Zealand	1994	17-35	Mud and sand	Comparative	Thrush et al. 1998
Monterey Bay, USA	1994-96	180	Mixed sediments	Comparative	Engel and Kvitek 1998
Georges Bank, USA	1994 to present	40-90	Gravel pavement	Comparative	Collie et al. 1997, Collie et al. 2000b
Northwest Irish Sea, Ireland	1994-96	35-75	Silty sand	Comparative and manipulative	Ball et al. 2000b
Mediterranean Sea, Greece	1995-96	200	Clay	Comparative	Smith et al. 2000
Eastern Gulf of Alaska, USA	1996	206-274	Pebble, cobble and boulder	Manipulative	Freese et al. 1999
Aegean Sea, Greece	1996	60-70	Silty sand	Comparative	Simboura et al. 1998
Gullmarsfjorden, Sweden	1996-97	<120	Soft bottom	Manipulative	Hannson et al. 2000, Lindegarth et al. 2000a, Lindegarth et al. 2000b
Eastern Bering Sea, USA	1996	48	Rippled sand	Comparative	MacConnaughey et al. 2000
Mediterranean Sea, Spain	1997	30-40	Mud	Manipulative	Demestre et al. 2000, Sanchez et al. 2000, Palanques et al. 2001

Location	Year	Depth (m)	Habitat	Experimental Design	Reference
Bay of Fundy, Canada	1990-91	Intertidal	Silty sand	Manipulative	Brylinsky et al. 1994
Strangford Lough, Northern Ireland	1990-93	Shallow	Mixed sediments with horse mussel beds	Comparative	Magorrian et al. 1995, Service and Magorrian 1997
Great Barrier Reef, Australia	1991-96	Shallow	Coral reef	Comparative and manipulative	Pitcher et al. 1999
Northwest Shelf, Australia	1992-93	50	Hard bottom with sponges, soft corals and gorgonians	Manipulative	Moran and Stevenson 2000
North Sea, Netherlands	1992-95	<30-50	Sand and silt	Manipulative	Bergman and van Santbrink 2000a, Bergman and van Santbrink 2000b
Gulf of Maine, USA	1993	20-55	Sand and gravel	Comparative	Auster et al. 1996
Gulf of Maine, USA	1993	30-40	Cobble, sand and shell	Comparative	Auster et al. 1996
Grand Banks, Canada	1993-95	120-146	Sand	Manipulative	Schwinghamer et al. 1996, Schwinghamer et al. 1998, Prena et al. 1999, Kenchington et al. 2001
Loch Gareloch, Scotland	1993-96	30-35	Mud	Manipulative	Tuck et al. 1998, Ball et al. 2000a

Table 2. Comparison of the rank order and biomass of the 87 species common to both the videograb and epibenthic sled samples by gear type. All samples are combined (i.e. reference, before trawling, after trawling). For videograb, n = 200. For epipbenthic sled, n = 105. Ranking is based on the frequency of occurrence in the total number of samples per gear type. Taxa shown in bold had higher biomass in the epibenthic sled samples. (E) Echinodermata, (B) Bivalvia, (P) Polychaeta, (G) Gastropoda, (R) Ribbon worms, (A) Arthropoda, (C) Cnidaria, (Br) Bryozoa, and (U) Urochordata.

Taxon	Rank		Biomass (mg m^{-2})	
	Grab	Sled	Grab	Sled
Echinarachnius parma (E)	1	1	288816.1	231461.3
Macoma calcarea (B)	1	18	89025.9	10.3
Ophiura sarsi (E)	1	4	76102.1	61716.2
Maldanid group (P)	1	68	13082.5	1.0
Eteone longa (P)	1	85	181.7	0.0
Nephtys caeca (P)	6	79	9073.3	1.5
Harmothoe imbricata (P)	7	54	230.0	1.4
Astarte borealis (B)	8	1	39291.8	6791.8
Cylichna alba (G)	8	65	172.7	0.1
Cyrtodaria siliqua (B)	10	61	380409.6	126.8
Clinocardium ciliatum (B)	11	8	17242.9	587.9
Yoldia myalis (B)	11	39	1318.2	4.6
Nemertea (R)	13	65	434.4	3.6
Strongylocentrotus pallidus (E)	14	1	43438.9	30697.9
Gattyana cirrosa (P)	15	63	144.1	4.0
Cyclocardia novangliae (B)	16	11	917.0	456.1
Leaena ebranchiata (P)	17	79	37.1	0.2
Solariella obscura (G)	18	35	85.4	1.3
Melita dentata (A)	19	68	118.6	0.3
Gersemia sp. (C)	20	5	4080.4	2348.6
Anonyx sp. (A)	21	54	24.9	1.3
Liocyma fluctuosa (B)	22	12	414.6	79.4
Nuculana minuta (B)	23	21	117.0	8.9
Margarites sordidus (G)	24	6	901.4	593.4
Astarte sp. (B)	24	39	78.1	1.3
Curitotoma violacea (G)	26	45	118.5	0.4

Taxon	Rank		Biomass (mg m^{-2})	
	Grab	Sled	Grab	Sled
Curitotoma incisula (G)	27	32	33.3	1.0
Curitotoma laurenciana (G)	28	41	29.2	1.5
Cyclocardia sp. A (B)	29	15	783.4	379.0
Solariella varicosa (G)	30	27	48.0	2.9
Curitotoma trevelliana (G)	31	44	24.0	1.0
Hydrozoa (C)	32	58	23.4	1.0
Propebela rugulata (G)	33	54	20.9	0.3
Cryptonatica affinis (G)	34	8	559.3	307.7
Chionoecetes opilio (A)	**35**	**7**	**5340.7**	**6009.0**
Musculus discors (B)	36	51	198.0	3.2
Polinices pallida (G)	37	23	796.4	61.6
Buccinidae (G)	37	54	406.5	21.7
Ophiacantha bidentata (E)	39	16	732.7	709.5
Trochidae (G)	40	45	11.8	0.8
Gastropoda (G)	**41**	**47**	**19.3**	**23.7**
Astarte sp. A (B)	42	32	34.0	3.1
Gorgonocephalus arcticus (E)	**43**	**14**	**3846.5**	**4059.1**
Admete viridula (G)	43	41	17.1	4.6
Chiridota laevis (E)	45	68	1694.1	2.2
Serripes groenlandicus (B)	46	17	6236.6	119.2
Buccinum totteni (G)	46	12	1147.8	726.7
Lepeta caeca (G)	48	74	5.5	0.1
Tealia felina (C)	49	19	521.6	141.8
Panomya arctica (B)	50	35	9666.2	42.4
Oenopota sp. (G)	50	51	4.6	0.5
***Buccinum* sp.** (G)	**52**	**26**	**39.3**	**161.4**
Oenopota impressa (G)	53	74	7.2	0.2
Nudibranchia (G)	54	74	18.7	0.5
Hyas coarctatus (A)	**55**	**21**	**143.8**	**183.1**
***Myriapora* sp.** (Br)	**56**	**10**	**25.2**	**294.9**
Lyonsia arenosa (B)	56	58	19.3	5.1
Amauropsis islandica (G)	58	74	74.5	3.2
Tachyrhynchus reticulatus (G)	58	30	12.5	5.3
Nereis zonata (P)	58	85	0.4	0.1
Buccinum scalariforme (G)	61	32	178.5	64.9
Pandora gouldiana (B)	61	27	39.0	17.0

Taxon	Rank		Biomass (mg m^{-2})	
	Grab	Sled	Grab	Sled
Buccinum inexhaustum (G)	63	65	360.0	63.1
Ophiopholis aculeata (E)	63	23	155.4	113.5
Obestoma gigantea (G)	63	51	11.4	4.7
Asteriidae (E)	**63**	**48**	**1.8**	**5.6**
Hiatella arctica (B)	**63**	**79**	**0.1**	**0.3**
Pagurus pubescens (A)	68	27	136.0	132.6
Colus sabini (G)	69	25	133.1	131.7
Colus sp. (G)	69	49	89.3	13.6
Volutopsius norvegicus (G)	71	31	731.7	451.4
Chlamys islandica (B)	**71**	**38**	**293.4**	**667.0**
Aporrhais occidentalis (G)	**71**	**20**	**106.3**	**365.9**
Velutina undata (G)	71	68	6.0	1.6
Trophon clathratus (G)	**71**	**35**	**1.3**	**27.6**
***Neptunea* sp.** (G)	**71**	**79**	**0.5**	**4.2**
Margarites striatus (G)	**71**	**68**	**0.2**	**3.3**
Campylaspis rubicunda (A)	**71**	**85**	**0.0**	**0.2**
Colus sp. B (G)	79	58	29.1	5.2
Henricia sp. (E)	79	61	21.3	7.2
Corymorpha groenlandica (C)	79	79	17.1	2.2
Eunoe nodosa (P)	79	68	4.8	2.6
Ctenodiscus crispatus (E)	**79**	**63**	**4.1**	**35.8**
Oenopota pyramidalis (G)	79	74	1.3	0.4
Propebela viridula (G)	79	79	0.4	0.1
Ascidiacea (U)	**79**	**41**	**0.1**	**24.6**
Trichotropis borealis (G)	**79**	**49**	**0.1**	**6.3**

Table 3. Comparing the average biomass (mg m^{-2}) of four dominant epibenthic species captured by the epibenthic sled and videograb in reference and trawled corridors immediately after trawling. Epibenthic sled/reference, n = 47; Epibenthic sled/trawled, n = 53; Videograb/reference, n = 40; Videograb/trawled, n = 30. (E) Echinodermata, (C) Cnidaria.

Treatment	Species	Sled	Grab	Difference	Proportion
Reference	*Echinarachnius parma* (E) (Sand dollar)	256718	326822	70104	0.21
	Ophiura sarsi (E) (Brittle star)	75033	84210	9177	0.11
	Strongylocentrotus pallidus (E) (Sea urchin)	33451	45455	12004	0.26
	Gersemia spp. (C) (Soft coral)	2716	3350	634	0.19
After Trawling	*Echinarachnius parma* (E) (Sand dollar)	197332	263111	65779	0.25
	Ophiura sarsi (E) (Brittle star)	51126	76154	25028	0.33
	Strongylocentrotus pallidus (E) (Sea urchin)	28754	53109	24355	0.46
	Gersemia spp. (C) (Soft coral)	1755	5402	3647	0.68

Table 4. Coefficient of variation (standard deviation/mean * 100) of the biomass for two common epibenthic species, brittle stars (*Ophiura sarsi*) and sand dollars (*Echinarachnius parma*) that were well-sampled by the epibenthic sled and videograb. Samples from trawled and reference corridors combined.

Gear Type	Brittle stars	Sand dollars
Videograb	63	45
Epibenthic Sled	34	27

Table 5. Common species at the study site that showed an immediate negative effect of repetitive otter trawling based upon the analysis of samples collected by the otter trawl, epibenthic sled and videograb. While the distinction between epibenthic and infaunal is not always clear for some species, predominant life mode is shown.

Species	Taxon	Sampling Gear	Life Mode
Chionoecetes opillo (Snow crab)	Arthropod	Trawl, sled	Epibenthic
Gorgonocephalus arcticus (Basket star)	Echinoderm	Trawl	Epibenthic
Strongylocentrotus pallidus (Sea urchin)	Echinoderm	Trawl, sled	Epibenthic
Gersemia sp. (Soft coral)	Cnidarian	Trawl, sled	Epibenthic
Buccinum sp. (Whelk)	Gastropod	Trawl	Epibenthic
Pagurus sp. (Hermit crab)	Crustacean	Trawl	Epibenthic
Chlamys islandica (Iceland scallop)	Bivalve	Trawl	Epibenthic
Echinarachnius parma (Sand dollar)	Echinoderm	Sled, grab	Epibenthic
Ophuria sarsi (Brittle star)	Echinoderm	Sled	Epibenthic
Protomedeia fasciata	Arthropod	Grab	Infaunal
Monoculodes intermedius	Arthropod	Grab	Infaunal
Capitella capitella	Polychaete	Grab	Infaunal
Mediomastus ambiseta	Polychaete	Grab	Infaunal
Eteone longa	Polychaete	Grab	Infaunal
Apistobranchus typicus	Polychaete	Grab	Infaunal
Chaetozone setosa	Polychaete	Grab	Infaunal
Polydora socialis	Polychaete	Grab	Infaunal
Prionospio steenstrupi	Polychaete	Grab	Infaunal
Spio filicornis	Polychaete	Grab	Infaunal
Ophelina breviata	Polychaete	Grab	Infaunal
Arcidea catherinae	Polychaete	Grab	Infaunal
Arcidea wassi	Polychaete	Grab	Infaunal
Polynoidae juvenile	Polychaete	Grab	Infaunal
Oligochaeta undetermined	Oligochaete	Grab	Infaunal
Ophelia limacina	Polychaete	Grab	Infaunal

Table 6. Species positively affected by repetitive otter trawling in this experiment.

Species	Taxon	Sampling Gear	Life Mode
Yoldia myalis	Bivalve	Grab	Infaunal
Protomedeia grandimana	Arthropod	Grab	Infaunal
Ophelia limacina	Polychaete	Grab	Infaunal

Table 7. Common species at the study site that were not affected by repetitive otter trawling or natural variation.

Species	Taxon	Sampling Gear	Life Mode
Margarites sordidus	Gastropod	Sled	Epibenthic
Astarte borealis	Bivalve	Sled, Grab	Infaunal
Clinocardium ciliatum	Bivalve	Sled	Infaunal
Cyclocardia novangliae	Bivalve	Sled	Infaunal
Cyrtodaria siliqua	Bivalve	Grab	Infaunal
Macoma calcarea	Bivalve	Grab	Infaunal
Ampharete finmarchica	Polychaete	Grab	Infaunal
Lysippe labiata	Polychaete	Grab	Infaunal
Laphania boecki	Polychaete	Grab	Infaunal
Scoloplos armiger	Polychaete	Grab	Infaunal
Nephtys caeca	Polychaete	Grab	Infaunal
Maldanid group	Polychaete	Grab	Infaunal
Priscillina armata	Arthropod	Grab	Infaunal