

Experimental otter trawling on a sandy bottom ecosystem of the Grand Banks of Newfoundland: analysis of trawl bycatch and effects on epifauna

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ABSTRACT: An experimental study of the effects of otter trawling was conducted in a deep (120 to 146 m) sandy bottom ecosystem of the Grand Banks of Newfoundland from 1993 to 1995. Each year, three 13 km long corridors were trawled 12 times within 31 to 34 h with an Engel 145 otter trawl equipped with rockhopper foot gear. The width of the disturbance zones created was on the order of 120 to 250 m. The total biomass of invertebrate bycatch in the trawl decreased significantly over the 12 sets, even though only a very small proportion of the biomass present was removed and each set did not pass over exactly the same area of seabed. An influx of scavenging snow crabs *Chionoecetes opilio* into the trawled corridors was observed after the first 6 sets (approximately 10 to 12 h). Benthic organisms in trawled and nearby reference corridors were sampled with an epibenthic sled. Their biomass was on average 24% lower in trawled corridors than in reference corridors. At the species level, this biomass difference was significant for snow crabs *C. opilio*, sand dollars *Echinarachnius parma*, brittle stars *Ophiura sarsi*, sea urchins *Strongylocentrotus pallidus* and soft corals *Gersemia* sp. The reduced biomass of epibenthic organisms in trawled corridors is thought to be due to several interacting factors including direct removal by the trawl, mortality, damage, predation and migration. The homogeneity of the macro-invertebrate community collected by epibenthic sled was lower in trawled corridors. Sand dollars, brittle stars and sea urchins demonstrated significant levels of damage from trawling. The mean individual biomass of epibenthic organisms was lower in trawled corridors suggesting size specific impacts of trawling, especially for sand dollars. No significant effect of trawling was observed in the 4 dominant mollusc species captured by the sled (*Astarte borealis*, *Margarites sordidus*, *Clinocardium ciliatum* and *Cyclocardia novangliae*). This experiment indicates that otter trawling on a sandy bottom ecosystem can produce detectable changes on both benthic habitat and communities, in particular a significant reduction in the biomass of large epibenthic fauna.

KEY WORDS: Mobile fishing gear impacts · Otter trawling · Bycatch · Epibenthic organisms · Marine biodiversity · Grand Banks

INTRODUCTION

Mobile fishing gear is a widespread cause of physical disturbance to the global continental shelf benthos (Dayton et al. 1995). Mobile gear such as beam trawls, otter trawls, scallop rakes and clam dredges inflict damage

and mortality on benthic invertebrates as well as on target species (e.g. Gruffydd 1972, Caddy 1973, Meyer et al. 1981, McLoughlin et al. 1991, Andrew & Pepperell 1992, Bergman & Hup 1992, Fonds et al. 1992, Suuronen et al. 1996). Of the variety of mobile gear types used, the otter trawl is considered to be one of the more environmentally benign (Hall 1994); nonetheless, it is still capable of inflicting considerable disturbance on benthic ecosystems (Raloff 1996, Jennings & Kaiser 1998).

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Over the past 50 yr, otter trawls have been the most commonly used mobile fishing gear on the Atlantic continental shelf of Canada (Messieh et al. 1991). Throughout this period, there has been debate concerning the ecological effects of this gear. This debate has recently gained intensity with the collapse of groundfish stocks in the region in the early 1990s (Hutchings 1996). Past scientific studies have demonstrated that mobile gear can disturb benthic habitats and communities, with the discernable effects depending upon the scale of resolution, the kind of gear, the nature of the substrate and the kind of organisms present. Until recently, it has been difficult to experimentally demonstrate the anticipated impacts of otter trawling on offshore fishing banks, owing largely to limitations in experimental design and the technology required for trawling and sampling within a precisely defined area on the seabed. Another complicating factor has been that any impacts must be detected against a background of considerable natural variability in organism abundance and community structure which is poorly understood. Nevertheless, studies to date indicate that larger, longer-lived epibenthic organ-

isms, especially sedentary and attached forms, can be adversely affected by mobile fishing gear that comes into contact with the seabed (Caddy 1973, de Groot 1984, Messieh et al. 1991, Bergman & Hup 1992, Eleftheriou & Robertson 1992, Jones 1992, Thrush et al. 1995, Collie et al. 1997, Jennings & Kaiser 1998).

In 1990, the Department of Fisheries and Oceans (DFO) initiated a long-term, multi-disciplinary program to study the impacts of mobile fishing gear on the marine benthic habitat and communities of Atlantic Canada. 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 but the results should not be extrapolated to offshore fishing banks because of the major differences in water depth, sediment type, energy levels and biological communities. Another early initiative was to compile information on the extent and intensity of otter trawling off eastern Canada. Analysis of archived side-scan sonar data, collected by the Geological Survey of Canada for other purposes, indicated that less than 2% of the available records showed any visible trawling disturbance on the Scotian Shelf (Jenner et al. 1991) while less than 10% showed evidence of trawling disturbance on the Grand Banks (P. Schwinghamer unpubl. data). Disturbance from mobile fishing gear was usually found only in areas of low sediment transport suggesting that effects might be rapidly obliterated on high energy seabeds and that side-scan sonar records are inadequate for estimating the distribution of trawling activity. Krost et al. (1990) recorded higher frequencies of trawl door tracks with increasing depth which they interpreted as being partially the result of decreasing wave energy. Subsequently, a detailed study of the spatial pattern of otter trawling was conducted for the Grand Banks and Labrador Shelf using DFO data on commercial fishing effort for the period of 1980 to 1991 (P. Schwinghamer & D. W. Kulka unpubl. data). The results showed a very patchy distribution of trawling effort in this region (Fig. 1). The most intense effort was limited to a relatively small area (within which 8% or more of the seabed was disturbed in a particular year) while large areas were untrawled each year.

In 1993, once adequate sampling equipment had been developed and suitable navigation instrumentation was available, a major 3 yr experiment on the effects of otter trawling on a sandy bottom ecosystem was initiated on the Grand Banks of Newfoundland. This paper presents an analysis of the otter trawl bycatch data and the effects of the otter trawling on benthic organisms collected with an epibenthic sled. No attempt is made to discuss the effects of trawling on infaunal species since an extensive series of grab samples was also collected and will be reported in a future publication.

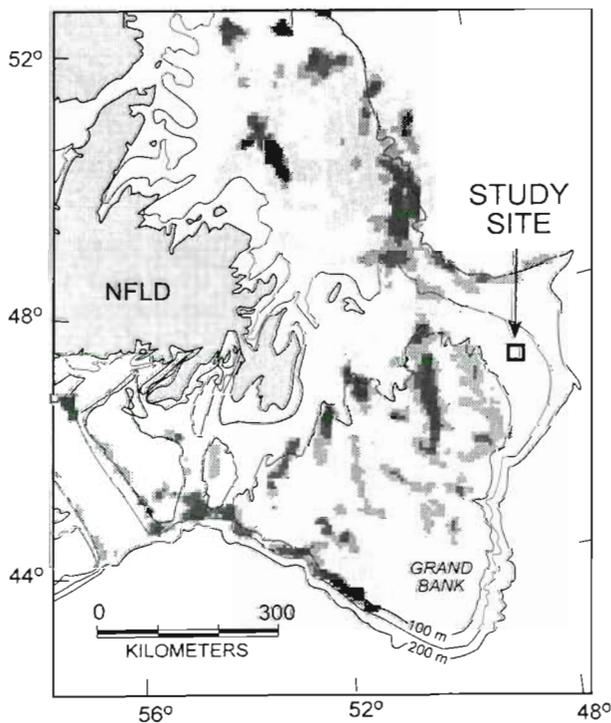


Fig. 1 Location of the study site on the Grand Banks, Newfoundland. Estimated intensity of seabed disturbance by otter trawling on the Grand Banks and Labrador Shelf in 1990 expressed as the percent of the sampling area swept by a trawl in 1 yr (P. Schwinghamer & D. W. Kulka unpubl. data). The darkest shade represents a trawling intensity greater than 8%.

METHODS

Study site. The 20 × 20 km study site centred at 47° 10' N, 48° 17' W was established on the northeastern part of the Grand Banks of Newfoundland (Fig. 1). Until the early 1990s, the fishery in this general region was for mixed groundfish, mostly American plaice *Hippoglossoides platessoides*, with about 15 to 20% Atlantic cod *Gadus morhua*. Analysis of fishing effort records indicated that the study site had not been fished intensively since the early 1980s (Kulka 1991). In 1992, the DFO formally closed the site to all fishing activity for the duration of the experiment. In addition, as a result of the collapse of the northern cod and other groundfish stocks in the region, a general moratorium on groundfish harvesting has been in effect for the Newfoundland and Labrador continental shelf since 1992. Therefore, we are confident that the only trawling which took place at the study site in recent years was that conducted in the experiment.

The depth range at the study site is 120 to 146 m. Surficial sediments are composed of Adolphus sand, a moderately to well sorted fine- to medium-grained sand (mean grain size ~170 µm) found around the perimeter of the Grand Banks and on the Flemish Cap (Fader & Miller 1986). The seabed at this depth is relatively stable with no evidence of wave-induced ripples on the smooth continuous surface (Barrie et al. 1984). However, interannual variations in sediment grain size and acoustic properties were observed during the experiment, possibly caused by winter storms (Schwinghamer et al. 1998). Exploratory sampling, conducted in 1992, demonstrated that the benthic community was species rich (at least 139 macrofaunal species), had a high number of epibenthic species, was high in biomass (mean of 6 grabs was 650 g wet wt m⁻²) and had a relatively homogeneous species composition (Prena et al. 1996). Secondary hard-bottom structures such as mussel reefs are not present and sessile epifaunal species (e.g. the soft coral *Gersemia* sp. and the bryozoan *Myriapora* sp.) occur in low densities. The patchiness of epibenthic megafauna in this region of the Grand Banks has been described by Schneider et al. (1987).

Experimental design. Complete details of experimental design are given in Rowell et al. (1997) and briefly summarized here. Based on the experience of Dutch colleagues investigating the effect of beam trawls (e.g. Bergman & Hup 1992), it was decided to conduct a multi-year experiment that included initial sampling, experimental trawling of known intensity with commercial fishing gear and post-trawling sampling. Three 13 km long experimental corridors were established for trawling (Fig. 2). Parallel reference corridors were established 300 m to one side. Each corri-

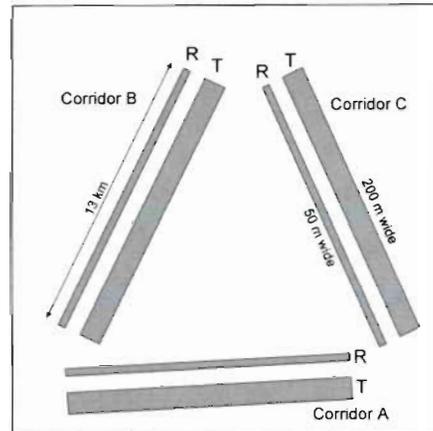


Fig. 2. Relative position and orientation of Corridors A, B and C in the study area (20 × 20 km) (not to scale). The central axis of reference corridors (R) was 300 m to one side of the trawled corridors (T). Ends of the corridors are approximately 3.5 km apart

dor was divided into 260 sampling blocks (50 m long and 200 m wide). Different blocks were selected for sampling on each cruise using a random procedure (McKeown & Gordon 1997). The 3 experimental corridors were trawled by the CSS 'Wilfred Templeman', as described below, in early July for 3 successive years (1993, 1994 and 1995). Pre- and post-trawl benthic surveying and sampling were conducted each year by the CSS 'Parizeau'. Benthic surveying and sampling were also conducted in September 1993, about 10 wk after the initial trawling disturbance.

Navigation. The 'Parizeau' was positioned with an accuracy of 3 to 4 m throughout the study using the Differential Global Positioning System (dGPS). During the first year of the experiment, the 'Templeman' was navigated along the trawled corridors using Loran-C and non-differential GPS. However, dGPS was installed on the 'Templeman' for trawling in 1994 and 1995. The otter trawl, sampling and surveying equipment were positioned relative to the 'Parizeau' by means of an ORE International Inc. model 4410C Trackpoint II ultra-short baseline acoustic tracking system. The accuracy of these geo-referenced positions varied on the order of 4 to 20 m depending upon the distance between the equipment and the ship. Navigation information (dGPS position, Trackpoint fix, gyro, log and echo sounder) was merged into a single ASCII data stream which was then supplied to the ship's bridge and the scientific laboratories. The software package AGCNAV was used to graphically display and record the navigation information. This graphics-based real-time PC display proved to be the key to the efficient prosecution of the surveying and sampling strategies. The tracks of the epibenthic sled while sam-

pling on the seabed (approximately 50 m long), determined by Trackpoint, were plotted over the paths of the otter trawl doors estimated from the navigation data (McKeown & Gordon 1997). This analysis confirmed that, with just 1 exception, all sled samples in the trawled corridors were collected entirely within the area that had been trawled, and that all reference samples were collected well outside the disturbed zone.

Experimental trawling. Experimental trawling was carried out using an Engel 145 otter trawl with 1250 kg polyvalent oval otter boards (McCallum & Walsh 1997). Approximate door spread was 60 m. This gear was standard for both commercial fishing and, until 1995, DFO research surveys in the Newfoundland Region. Since industry was using rockhopper foot gear, we used 46 cm (18") rockhopper foot gear rather than the steel bobbin foot gear used in DFO surveys. The mesh size (as used in commercial gear) was 180 mm on the wings and belly of the net and 150 to 130 mm in the codend. As in DFO surveys, a 30 mm square mesh liner was installed in the final 9 m of the 18.5 m long codend in order to capture invertebrates which may be damaged but not retained by commercial gear. Behaviour of the trawl was monitored with a Scanmar net mensuration system. Trawling speed was approximately 7 km h⁻¹.

The 3 experimental corridors were trawled within a 5 d period in late June/early July each year (Table 1). Each year, the corridors were trawled 12 times with

Table 1. Start and end times of the 12 otter trawl sets conducted by the CSS 'Wilfred Templeman' in the 3 experimental corridors. Also listed are the time intervals between the end of the last trawl set and epibenthic sled samples. Sled samples were not collected in Corridor C

Year	Corridor	Trawling starts		Trawling ends		Interval between last trawl set and sled samples (h)
		Date	GMT	Date	GMT	
1993	A	6 Jul	11:30	7 Jul	21:57	45–93
	B ^a	7 Jul	23:16	10 Jul	01:20	10–37
	C ^a	8 Jul	18:40	10 Jul	22:38	–
1994	A	9 Jul	17:31	11 Jul	00:24	12–42
	B	12 Jul	23:20	14 Jul	06:14	6–13
	C	11 Jul	01:59	12 Jul	08:57	–
1995	A	30 Jun	16:34	2 Jul	00:07	9–22
	B	2 Jul	00:43	3 Jul	08:40	1–5
	C	3 Jul	10:50	4 Jul	18:50	–

^aDue to equipment problems in 1993, there was a 19 h gap between Sets 6 and 7 in Corridor B and an 18 h gap between Sets 5 and 6 in Corridor C

direction alternating on each set. The time required to trawl the 12 sets in 1 corridor was generally on the order of 31 to 34 h. Each trawl set was initiated when the 'Templeman' was about 500 m from the end of the experimental corridor so that the trawl, which had a layback on the order of 500 m, would settle into its bottom configuration before entering the corridor. At the end of each set, the trawl was not retrieved until the ship was at least 500 m beyond the end of the corridor. Therefore, the trawl was on the bottom for slightly more than 13 km for each set. The intention was to keep all trawling disturbance within 100 m of the centre line. Each year, the 'Parizeau' tracked the position of the otter trawl for some sets using Trackpoint with a transponder placed on the head-line. The width of the disturbance zones was estimated using navigation data.

Analysis of trawl catch. Trawl catch data were collected in all 3 corridors (Fig. 2). Fish were separated by species, weighed using gimbaled electronic balances and sized in the ship-board laboratory. The invertebrate bycatch was also sorted by species and weighed. Subsamples of snow crabs *Chionoecetes opilio* were collected for determination of sex, maturity, and shell condition.

Epibenthic sled sampling. Samples of benthic organisms were collected with an Aquareve III epibenthic sled (Thouzeau & Vine 1991). This gear was selected because it was available to us and it was felt that it would collect suitable quantitative samples of epibenthic organisms at the experimental site if substantially modified. Modifications included decreasing the width of the sampling blade to 0.34 m, installing a closing door, widening the runners, and adding wings to increase stability (Rowell et al. 1997). The sled cuts to a depth of 2 to 3 cm and therefore can collect some infaunal species as well as epifaunal species. Towing distance over the seabed, measured by 2 odometer wheels, averaged 50 m (i.e. each sample represented about 17 m²). At the end of the tow, the door was closed electronically and the sled retrieved. Sampling performance was monitored using a video camera mounted on the sled frame which was directed backward toward the sled's mouth. Tows of dubious quality (i.e. lifting off the bottom) were aborted and repeated. A disadvantage of using an epibenthic sled of this type is the damage inflicted on captured organisms.

Due to time constraints, sled samples were only collected in Corridors A and B (Fig. 2). Five continuous sampling blocks were designated for each sled tow (i.e. 250 m along the axis of the corridor). The sled was equipped with a transponder so that its exact location on the seabed could be determined using the Trackpoint system. Throughout the entire experiment, 105 sled samples were collected (Table 2). Trawled and

Table 2. Summary of epibenthic sled samples collected during the 3 yr experiment. Sleds were collected either before trawling (B) or after (A). There was no trawling done on Cruise 93-029

Cruise no.	Timing	Corridor A		Corridor B	
		Trawled	Reference	Trawled	Reference
93-021	B	2	2	2	2
	A	4	–	4	–
93-029	–	3	4	1	1
94-015	B	–	–	–	–
	A	10	10	10	10
95-013	B	–	10	–	10
	A	10	–	10	–

reference samples were taken from the same box numbers of the parallel corridors (Fig. 2) (i.e. about 300 m apart), except in 1993. On the initial cruise (93-021), 2 sled samples were collected from neighbouring blocks in each of the trawled and reference corridors before trawling, and 4 samples were collected in other blocks of the trawled corridors after trawling. On the second cruise (93-029), only half the intended samples were collected because of bad weather. As a consequence of incomplete experimental blocks, these data are not included here. Based on an evaluation of the 1993 data, the number of sled samples was increased to 10 in each reference and trawled corridor during 1994 and 1995. Unfortunately, time constraints made it impossible to collect sled samples from the trawled corridors before re-trawling in 1994 and 1995. Therefore, the only opportunity to collect sled samples in the trawled corridors immediately before and after trawling occurred in 1993. The resulting sled data set provides no opportunity to examine the possible recovery of epibenthic organisms in the trawled corridors before re-trawling. The interval between the completion of experimental trawling and the collection of sled samples in trawled corridors was quite variable and an attempt was made in 1994 and 1995 to reduce it as much as possible (Table 1). It was planned to sample the reference corridors before trawling. However, due to operational constraints, in 1994 reference samples had to be collected after trawling (Table 2).

The sled catch was washed with seawater, under low pressure, over a 1 mm mesh screen. Common invertebrates were sorted by species and damage categories, counted and weighed on-board using suspended spring balances. Less common species were frozen for later processing ashore. Sled catch data were converted to units per m² of seabed using odometer data. Physical damage to echinoderms (e.g. broken test) and molluscs (e.g. broken shell) was assessed during sorting and the number of damaged organisms was expressed as a percentage of the total number of indi-

viduals in the sample. The only exception was that biomass rather than abundance was used for sand dollars because the weight of fragments could be more accurately determined than the number of individuals they represented. Chipped mollusc shells and missing or broken brittle star arms were not considered as damage in our analysis. No damage was assessed for soft corals *Gersemia* sp. and snow crabs *Chionoecetes opilio*.

Statistics. Invertebrate bycatch biomass data were analysed using a repeated measures ANOVA with corridors (A, B, C) as experimental subjects, nested in years (1993, 1994 and 1995), and bycatch in the 12 consecutive trawl sets as repeated measures. Biomass data were log-transformed in order to satisfy assumptions of the ANOVA. Where it was necessary to use ranked data, ranks were re-expressed as folded logs according to Mosteller & Tukey (1977) for parametric tests of significance. Statistical analyses were performed with Minitab Version 11 (Minitab 1996).

In processing the epibenthic sled data, a 3-way ANOVA for aggregate data and a 3-way MANOVA for dominant species were used to determine the statistical significance of the 3 main factors incorporated in the experimental design; namely trawling (comparing reference and trawled corridors), corridor (comparing A and B) and year (comparing 1993, 1994 and 1995). For statistical analysis, experimental units were defined as sampling blocks (i.e. stations) within the 2 corridors that were sampled. A paired test design gave very similar results and is not presented. MANOVA of acceptable fit (criterion F_{error}) could be computed for mean individual biomass and physical damage only when raw data were ranked or re-expressed by principal components. Both versions yielded similar results. Here we present MANOVA of those data sets based on principal components. For this reason the ANOVA of Table 7 was computed for each species separately and is not based on the MANOVA shown in Table 6. Assumptions of ANOVA could usually be met by applying log or root-transformations. Where it was necessary to use ranked data, ranks were re-expressed as folded logs according to Mosteller & Tukey (1977) for parametric tests of significance. The nominal significance level of 5% was Bonferroni adjusted (by dividing through the number of univariate tests) to control for compounding of the experimental error rate.

Homogeneity of the benthic community in trawled and reference corridors was examined by regression of mean and standard deviation of the abundance for all species within each combination of main effects (as described above for ANOVA). Warwick & Clarke (1993) showed that means and standard deviations can be described by linear relationships after transformation which can be used to compare the relative degree

of variability between samples, or as an index of aggregation. An increase of the standard deviation relative to the mean, measured by the slope of the regression, is interpreted as a decrease in homogeneity of the species community (or increase in aggregation). A sixth root transformation was applied to reduce the strong influence of the dominant sand dollars and brittle stars on the slope and to obtain a balanced distribution of data points along the regression line. Statistical analyses were performed using Systat 5.2 (Systat 1992).

RESULTS

Distribution of trawling disturbance

Navigation data were not logged for the 'Templeman' during trawling in 1993, so it was not possible to plot the exact course relative to the intended line. However, the Trackpoint data on trawl position indicated that the vessel wandered off course at times as much as several hundred meters. Navigation data were logged in 1994 and 1995 when the 'Templeman' was equipped with dGPS. In 1994, the vessel stayed very close to the intended line, usually within 20 m. In 1995, the vessel deliberately steered a sinusoidal course in order to distribute the trawling disturbance more widely across the trawled corridor.

Scanmar data indicated that the trawl, once settled into its fishing configuration, had a wing spread (i.e. net opening) of 20 ± 2 m and a door spread (i.e. distance between the otter boards) of 60 ± 5 m on all sets. Trackpoint data indicated that, while fishing, the trawl was consistently set to port relative to the ship position on the order of 20 to 35 m regardless of the direction steamed along the corridor (McKeown & Gordon

1997). It appears that this offset was due to slight differences in the length of the warps. The estimated widths of the disturbance zones for Corridors A and B are given in Table 3. The mean width was greatest in 1993, in excess of the intended 200 m but was reduced substantially in 1994 and 1995 to approximately 120 m or less.

Trawl bycatch

Snow crabs *Chionoecetes opilio*, basket stars *Gorgonocephalus arcticus* and sea urchins *Strongylocentrotus pallidus* dominated the trawl invertebrate bycatch and were consistently caught in large enough quantities to allow analysis of the relationship of bycatch with set number. Soft corals *Gersemia* sp., whelks *Buccinum* sp. and hermit crabs *Pagurus* sp. were commonly encountered in the small amount of other material that made up the bycatch. Iceland scallops *Chlamys islandica* and a few other bivalve molluscs were occasionally captured by the trawl.

The invertebrate bycatch biomass (both total and major components), averaged for all 3 corridors and 3 years, is presented by consecutive trawl set in Fig. 3A. The mean biomass was on the order of 10 kg (wet

Table 3. Estimated width of the disturbance zones created by otter trawling as estimated from the navigation data (McKeown & Gordon 1997). Individual estimates (N) were made by measuring the distance between the outermost door tracks in those boxes where samples were collected. Door track positions were estimated using either the position of the headline as determined by Trackpoint, if available, or vessel position

Year	Corridor	Mean (m)	SD (m)	Min (m)	Max (m)	N
1993	A	264	55	160	360	34
	B	204	102	80	420	33
1994	A	81	10	75	125	30
	B	119	15	90	150	30
1995	A	121	9	110	140	19
	B	112	16	90	160	20

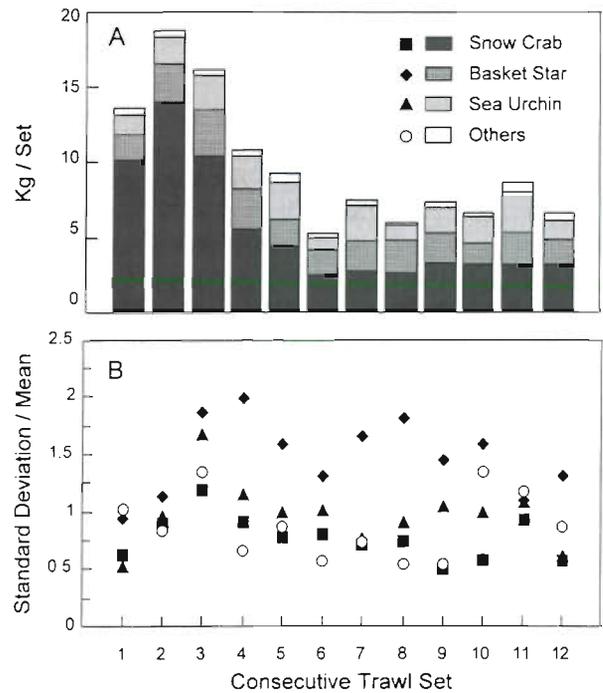


Fig. 3. (A) Mean and (B) coefficient of variation of invertebrate bycatch biomass plotted against otter trawl set (1 to 12). Each trawl set was 13 km long. Time needed to conduct the 12 trawl sets was 31 to 34 h. Average of 3 corridors (A, B and C) and 3 years (1993–95)

weight) for a 13 km set. There was a trend of decreasing bycatch in the first 6 sets, due primarily to a decline in snow crabs, with relatively constant levels thereafter. The biomass of basket stars tended to be slightly lower in later tows but there was no clear trend in sea urchin biomass. The coefficient of variation (standard deviation/mean) of snow crab, basket star and sea urchin bycatch increased markedly on the first 3 sets (Fig. 3B), suggesting increasing patchiness. A regression analysis of ranked invertebrate bycatch against trawl set, while highly variable, indicated a significant decrease in biomass with increasing set ($p < 0.05$) (Fig. 4).

It appears as if some of the non-linearity in bycatch decline with increasing trawl set (Fig. 3A) may be due to a behavioural response of snow crabs which are highly mobile. Ranked numerical abundance of adult and immediately pre-adult male snow crabs (carapace width >60 mm), which made up more than 70% of the crab bycatch biomass, is plotted against set number in Fig. 5. Biomass decreased markedly during the first 6 sets (approximately 15 to 17 h). Thereafter, biomass increased again but never reached initial levels.

The fish catch was extremely low and averaged on the order of 18 kg (wet weight) for a 13 km set (Fig. 6). It was dominated by American plaice *Hippoglossoides platessoides*, but thorny skate *Raja radiata* were also abundant. Capelin *Mallotus villosus* were caught primarily during the daytime. Arctic cod *Boreogadus saida* and sand lance *Ammodytes dubius* were caught in small quantities. Individuals of other fish species common to this area of the Grand Banks were occasionally captured. Very few Atlantic cod *Gadus morhua* were caught over the 3 yr experimental period. There was no indication of any trend in the fish catch with increasing set number or of differences between the 3 corridors.

ANOVA of total invertebrate bycatch biomass demonstrated that the effects of year (1993, 1994, 1995), corridor (A, B, C nested in year) and consecutive trawl set (1 to 12, repeated measure) were statistically significant ($p < 0.001$). The drop each year in the mean biomass of snow crabs, basket stars, sea urchins, other invertebrates, and fish collected by the otter trawl is illustrated in Fig. 6.

Macrofaunal community sampled by the epibenthic sled

General description of epifauna community

The total biomass of organisms collected by the epibenthic sled along the reference corridors ranged between 317 and 475 g (wet wt) m⁻² (Table 4). Nine

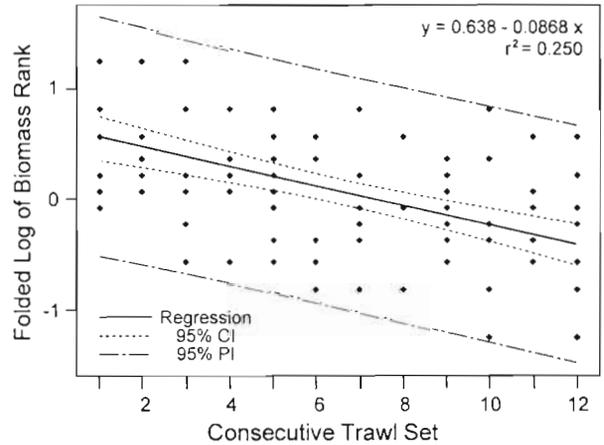


Fig. 4. Relationship of total invertebrate bycatch biomass (folded log ranks) to otter trawl set (1 to 12). Data from 3 corridors (A, B and C) and 3 years (1993–95) ($p < 0.05$). CI: confidence interval, PI: prediction interval

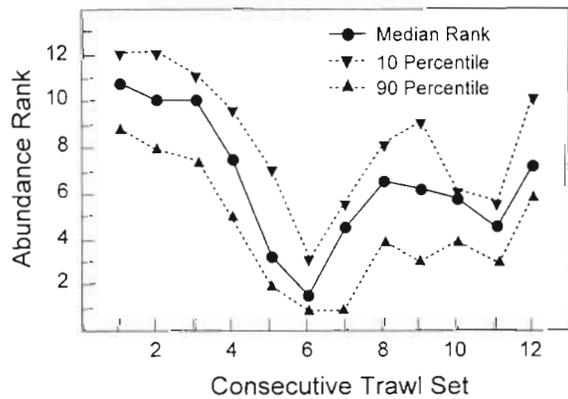


Fig. 5. Relationship of male snow crab (>60 mm carapace width) biomass to otter trawl set (1 to 12). Data are ranked relative abundance (Rank 12 = highest per 12 sets). Average of 3 corridors (A, B and C) and 2 years (1994–95). Time needed to conduct the 12 trawl sets was 31 to 34 h

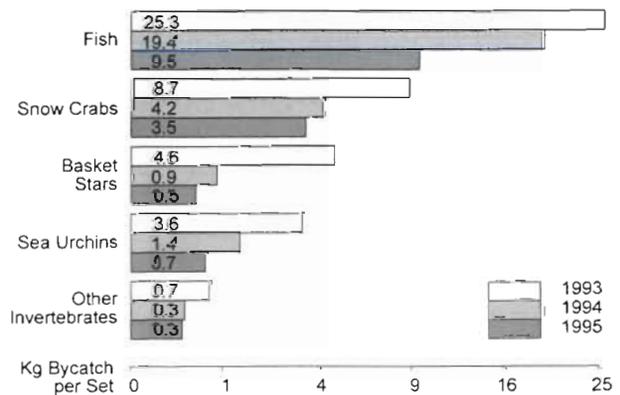


Fig. 6. Otter trawl fish catch and invertebrate bycatch by year (1993–95) expressed as wet weight biomass per trawl set. Average of all sets and 3 corridors (A, B and C)

Table 4. Mean and standard deviation (in brackets) of wet weight (g m^{-2}) for the 9 dominant species and the total sample (all species) collected by epibenthic sled. T: trawled; R: reference. E: Echinodermata, A: Arthropoda, M: Mollusca, C: Coelenterata

	Treatment	1993		1994		1995	
		Corridor A	Corridor B	Corridor A	Corridor B	Corridor A	Corridor B
<i>Echinarachnius parma</i> (E)	T	221 (27)	168 (73)	222 (48)	162 (69)	218 (49)	180 (69)
	R	230 (82)	296 (23)	243 (70)	181 (54)	321 (65)	275 (68)
<i>Ophiura sarsi</i> (E)	T	46 (14)	68 (9)	36 (14)	76 (27)	41 (15)	40 (39)
	R	75 (16)	71 (11)	56 (21)	73 (21)	81 (23)	88 (22)
<i>Strongylocentrotus pallidus</i> (E)	T	21 (10)	37 (19)	13 (8)	42 (24)	34 (20)	23 (19)
	R	39 (10)	41 (10)	24 (10)	35 (13)	35 (9)	34 (10)
<i>Astarte borealis</i> (M)	T	9.6 (9.6)	9.9 (13.9)	10.4 (7.2)	3.7 (2.4)	10.4 (4.4)	3.8 (2.8)
	R	5.8 (4.6)	7.9 (1.2)	9.6 (5.2)	4.0 (3.4)	7.2 (7.2)	6.0 (7.1)
<i>Chionoecetes opilio</i> (A)	T	0.3 (0.2)	8.2 (13.4)	2.1 (4.8)	2.8 (3.7)	8.5 (8.2)	4.3 (6.0)
	R	4.9 (6.9)	4.9 (6.9)	3.0 (2.6)	5.7 (9.4)	13.7 (15.9)	11.1 (9.8)
<i>Gersemia</i> sp. (C)	T	1.7 (0.8)	0.6 (1.0)	1.6 (1.4)	2.0 (1.3)	1.6 (1.0)	2.2 (2.4)
	R	1.9 (0.6)	2.6 (1.2)	3.3 (2.1)	3.3 (2.8)	2.2 (1.4)	2.0 (1.3)
<i>Margarites sordidus</i> (M)	T	0.5 (0.2)	1.6 (1.8)	0.5 (0.4)	0.7 (0.4)	0.6 (0.5)	0.4 (0.3)
	R	0.8 (0.2)	0.9 (0.4)	0.5 (0.3)	0.5 (0.3)	0.7 (0.4)	0.5 (0.3)
<i>Clinocardium ciliatum</i> (M)	T	0.2 (0.2)	1.0 (1.3)	0.4 (0.2)	0.7 (0.7)	0.4 (0.7)	1.3 (0.6)
	R	0.0 (0.0)	0.9 (0.6)	0.6 (0.5)	0.4 (0.4)	0.4 (0.5)	0.7 (1.0)
<i>Cyclocardia novangliae</i> (M)	T	0.5 (0.2)	0.1 (0.1)	0.6 (0.4)	0.2 (0.2)	0.5 (0.3)	0.3 (0.4)
	R	0.5 (0.4)	0.7 (0.5)	1.0 (0.8)	0.3 (0.3)	0.7 (0.6)	0.3 (0.4)
Total sample (all species)	T	316 (19)	305 (62)	291 (55)	303 (72)	327 (59)	261 (76)
	R	377 (75)	433 (42)	352 (48)	317 (50)	475 (78)	426 (61)

dominant species were present in more than 90% of the 96 samples included in the data analysis and made up 95 to 98% of the total biomass. They are, in decreasing order of mean biomass, the sand dollar *Echinarachnius parma*, the brittle star *Ophiura sarsi*, the sea urchin *Strongylocentrotus pallidus*, the snow crab *Chionoecetes opilio*, the mollusc *Astarte borealis*, the soft coral *Gersemia* sp. and the molluscs *Margarites sordidus*, *Clinocardium ciliatum* and *Cyclocardia novangliae*. The 3 most dominant species were echinoderms. The polychaete *Nothria conchylega* was also abundant in all sled samples but not processed because of the extensive sorting time required. The total number of species collected in all sled samples was 115 (list available on request). Since the sled blade cuts to a depth of several centimeters into the sandy sediment found at the study site, some infaunal organisms were collected (e.g. certain molluscs). Only sea urchins and snow crabs were commonly caught by both the otter trawl and sled.

Biomass

The mean total biomass of organisms sampled by the epibenthic sled in reference and trawled corridors over the entire experiment is presented in Table 4 and Fig. 7. The reference samples in 1993 include the sled samples taken from the trawled corridors before the

initial disturbance (Table 2). In all 3 years, the biomass in trawled corridors was lower than in reference corridors. Biomass in reference corridors showed considerable interannual variability, while biomass in the trawled corridors stayed relatively constant with time despite repeated trawling. The greatest difference in total biomass between reference and trawled corridors occurred in the final year of the experiment (1995). The least difference occurred in 1994 when the reference corridors were sampled after trawling (Table 2) and

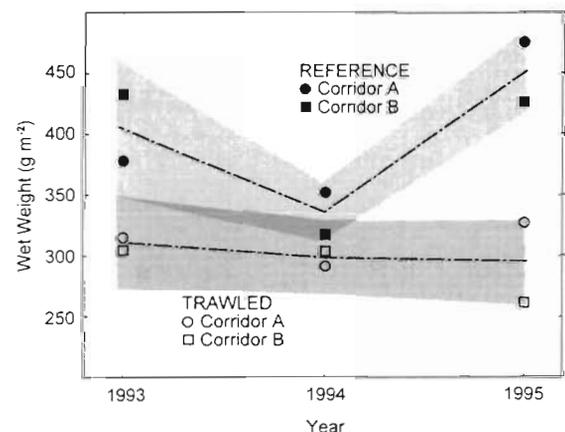


Fig. 7. Total biomass of invertebrates collected by the epibenthic sled in trawled and reference corridors (A and B only) each year of the experiment. Shaded areas represent 95% confidence intervals

Table 5. Three-way ANOVA of total biomass and mean individual biomass of organisms collected in the epibenthic sled for effects of corridor (A and B), trawling (trawled and reference) and year (1993, 1994 and 1995). Sources of variance in bold are statistically significant

Variable	Source	df	MS	F	p
Total biomass	Corridor	1	1.958	3.215	0.076
	Trawling	1	29.080	47.754	0.000
	Year	2	4.272	7.015	0.001
	Error	91	0.609		
Mean individual biomass	Corridor	1	3.258	3.585	0.061
	Trawling	1	5.679	6.248	0.014
	Year	2	1.674	1.842	0.164
	Error	91	0.909		

migration of scavengers in response to trawling may have reduced the biomass in reference corridors. The 3-way ANOVA indicated that the differences in total biomass between the trawled and reference corridors and year were statistically significant and that trawling accounted for most of the variance in the data (Table 5). Differences in total biomass between Corridors A and B were not significant. Overall, the total biomass in the trawled corridors was on the order of 24% less than in the reference corridors. A 3-way MANOVA indicates that the effects of trawling, year and corridor are significant when the biomass of the 9 dominant species is tested (Table 6). Again, the greatest variance is associated with trawling.

A 3-way ANOVA indicates that the biomass of 5 of the 9 dominant species was significantly lower in the trawled corridors than in the reference corridors (Table 7). Sand dollars *Echinarachnius parma* and brittle stars *Ophiura sarsi* had the greatest probability of being affected followed by soft corals *Gersemia* sp., snow crabs *Chionoecetes opilio* and sea urchins *Strongylocentrotus pallidus*. There were trends of lower biomass of the mollusc *Cyclocardia novangliae* and increasing biomass of the mollusc *Clinocardium ciliatum* in trawled corridors (Table 4) but these were not statistically significant by our criterion of significance ($p < 0.017$) (Table 7). The ANOVA indicated that the biomass of the molluscs *Astarte borealis* and *Margarites sordidus* had the least probability of being affected by trawling.

Mean individual biomass

Analyses of the abundance data gave similar results as the biomass data and are therefore not presented. However, the potential effects of trawling on organism size was examined by dividing biomass by abundance

Table 6. Three-way MANOVA of biomass, mean individual biomass and physical damage (without soft corals and snow crabs) of the 9 dominant species collected in the epibenthic sled on effects of corridor, trawling and year. Sources of variance in bold are statistically significant

Variable	Source	Wilks' λ	F	df 1, 2	p
Biomass (9 species)	Corridor	0.596	6.168	9, 82	0.000
	Trawling	0.520	8.421	9, 82	0.000
	Year	0.624	2.421	18, 164	0.002
	Error	0.962	0.364	9, 82	0.949
Mean individual biomass (9 species)	Corridor	0.670	3.178	9, 58	0.003
	Trawling	0.823	1.389	9, 58	0.214
	Year	0.469	2.961	18, 116	0.000
	Error	0.920	0.561	9, 58	0.823
Physical damage (7 species)	Corridor	0.848	1.689	7, 66	0.127
	Trawling	0.469	10.662	7, 66	0.000
	Year	0.662	2.162	14, 132	0.012
	Error	0.938	0.620	7, 66	0.738

to obtain mean individual biomass (Table 8). With the exception of Corridor A in 1994, the mean individual biomass for all species captured was less in the trawled corridors. The difference was statistically significant by 3-way ANOVA (Table 5). This difference in size was not significantly related to trawling when the mean individual biomass of the 9 dominant species was tested by the 3-way MANOVA (Table 6). This test also demonstrated a significant effect of both corridor (smaller in Corridor B) and year. The 3-way ANOVA of the mean individual biomass of the separate 9 dominant species indicates that only the sand dollar *Echinarachnius parma* was significantly affected by trawling (Table 7). A similar trend of smaller mean individual biomass in trawled corridors was apparent in the mollusc *Cyclocardia novangliae* but was not significant ($p = 0.105$).

Damage

Physical damage was quite variable by species (Table 9). Approximately half of some species were damaged (e.g. the molluscs *Astarte borealis* and *Clinocardium ciliatum*) while others suffered lower levels of damage (e.g. the brittle star *Ophiura sarsi* and the mollusc *Margarites sordidus*). The high percentage of damage for some species collected from reference corridors indicates that considerable damage was inflicted by the sled during sampling. For example, sampling apparently damaged 15 to 60% of the mollusc *A. borealis*, 8 to 23% of the sand dollars *Echinarachnius parma* and 1 to 5% of the sea urchins *Strongylocentrotus pallidus*. However, there was a general trend of

Table 7. Specific effect of trawling on biomass, mean individual biomass and physical damage of dominant benthic species collected by epibenthic sled. Three-way ANOVA with the effects trawling, corridor and year. Biomass model based on MANOVA shown in Table 6. Sources of variance in bold are statistically significant. Criterion of significance is 0.017 after Bonferroni adjustment. E: Echinodermata; A: Arthropoda; M: Mollusca; C: Coelenterata

Variable	Species	MS effect	MS error	df error	F	p
Biomass	<i>Astarte borealis</i> (M)	0.417	0.886	90	0.470	0.495
	<i>Clinocardium ciliatum</i> (M)	2.269	0.883	90	2.569	0.112
	<i>Cyclocardia novangliae</i> (M)	4.363	0.772	90	5.652	0.020
	<i>Chionoecetes opilio</i> (A)	5.782	0.800	90	7.230	0.009
	<i>Echinarachnius parma</i> (E)	16.394	0.715	90	22.924	0.000
	<i>Gersemia</i> sp. (C)	6.965	0.930	90	7.491	0.007
	<i>Margarites sordidus</i> (M)	0.185	0.951	90	0.194	0.660
	<i>Ophiura sarsi</i> (E)	16.978	0.748	90	22.702	0.000
	<i>Strongylocentrotus pallidus</i> (E)	5.759	0.909	90	6.333	0.014
Mean individual biomass	<i>Astarte borealis</i> (M)	0.537	0.828	90	0.648	0.423
	<i>Clinocardium ciliatum</i> (M)	1.066	0.538	83	1.983	0.163
	<i>Cyclocardia novangliae</i> ^a (M)	2.246	0.835	83	2.691	0.105
	<i>Chionoecetes opilio</i> (A)	3.099	1.774	85	1.747	0.190
	<i>Echinarachnius parma</i> (E)	11.975	0.884	91	13.543	0.000
	<i>Gersemia</i> sp. (C)	0.476	0.626	89	0.760	0.386
	<i>Margarites sordidus</i> (M)	0.036	0.115	88	0.314	0.577
	<i>Ophiura sarsi</i> ^a (E)	0.013	0.734	90	0.017	0.896
	<i>Strongylocentrotus pallidus</i> ^a (E)	0.439	0.852	90	0.515	0.475
Physical damage	<i>Astarte borealis</i> ^a (M)	0.493	2.785	90	0.177	0.675
	<i>Echinarachnius parma</i> (E)	3.810	0.193	91	19.719	0.000
	<i>Ophiura sarsi</i> (E)	8.144	0.207	88	39.250	0.000
	<i>Strongylocentrotus pallidus</i>^a (E)	72.753	1.600	90	45.457	0.000

^aData ranked

Table 8. Mean and standard deviation (in parentheses) of mean individual biomass (g wet weight) for the 9 dominant species and the total sample (all species) collected by epibenthic sled. Undamaged specimens of *Echinarachnius parma* were considered only. T: trawled; R: reference. E: Echinodermata; A: Arthropoda; M: Mollusca; C: Coelenterata

	Treatment	1993		1994		1995	
		Corridor A	Corridor B	Corridor A	Corridor B	Corridor A	Corridor B
<i>Chionoecetes opilio</i> (A)	T	1.5 (1.1)	9.8 (9.6)	8.9 (18.4)	19.6 (34.3)	55.2 (37.6)	16.9 (18.2)
	R	9.4 (9.8)	7.3 (8.1)	4.9 (3.5)	11.4 (14.6)	33.3 (47.1)	57.1 (34.0)
<i>Strongylocentrotus pallidus</i> (E)	T	16.6 (2.0)	9.5 (0.6)	15.4 (4.2)	15.3 (3.0)	16.2 (6.1)	15.3 (2.5)
	R	13.8 (3.8)	12.4 (1.8)	14.7 (3.2)	14.1 (1.7)	19.5 (3.2)	16.9 (3.7)
<i>Astarte borealis</i> (M)	T	8.6 (1.1)	8.2 (4.4)	8.1 (2.3)	5.5 (2.8)	8.9 (2.6)	7.6 (2.1)
	R	11.5 (4.8)	7.0 (0.5)	7.0 (1.8)	5.4 (3.2)	8.5 (3.1)	6.4 (3.2)
<i>Echinarachnius parma</i> (E)	T	4.5 (0.5)	4.2 (0.7)	4.7 (1.3)	4.1 (1.7)	3.8 (0.6)	3.9 (1.3)
	R	5.1 (0.6)	5.4 (0.5)	4.4 (1.2)	4.4 (1.5)	5.8 (1.4)	5.9 (1.4)
<i>Ophiura sarsi</i> (E)	T	3.7 (0.5)	2.5 (0.9)	4.9 (0.7)	3.5 (1.4)	5.7 (1.2)	4.5 (2.2)
	R	3.6 (0.6)	3.6 (0.2)	4.8 (0.6)	3.5 (1.2)	5.9 (3.8)	6.6 (7.3)
<i>Gersemia</i> sp. (C)	T	2.0 (1.6)	0.8 (0.3)	1.9 (1.8)	3.9 (2.8)	1.9 (1.0)	2.5 (1.9)
	R	1.4 (0.9)	5.7 (2.1)	1.4 (0.9)	3.9 (3.2)	1.5 (0.8)	3.6 (2.7)
<i>Clinocardium ciliatum</i> (M)	T	1.8 (0.4)	1.9 (1.9)	2.1 (1.8)	1.8 (1.0)	2.4 (2.9)	4.1 (5.0)
	R	0.6 (0.3)	3.6 (3.1)	1.5 (0.9)	1.6 (1.5)	1.6 (1.0)	1.8 (0.6)
<i>Margarites sordidus</i> (M)	T	1.4 (0.3)	2.9 (2.8)	1.2 (0.4)	1.3 (0.4)	1.5 (0.4)	1.2 (0.3)
	R	1.7 (0.4)	1.3 (0.2)	1.2 (0.4)	1.4 (0.5)	1.4 (0.3)	1.1 (0.3)
<i>Cyclocardia novangliae</i> (M)	T	1.1 (0.3)	1.1 (0.3)	1.2 (0.1)	0.8 (0.4)	1.3 (0.3)	1.1 (0.4)
	R	1.2 (0.1)	1.7 (0.4)	1.4 (0.2)	0.9 (0.3)	1.4 (0.2)	1.1 (0.5)
Total sample (all species)	T	5.3 (0.2)	3.9 (1.0)	5.2 (1.2)	4.5 (1.9)	4.9 (0.7)	4.5 (1.6)
	R	5.5 (0.5)	5.4 (0.5)	4.9 (1.0)	4.6 (1.5)	6.0 (1.1)	5.6 (1.9)

Table 9. Mean and standard deviation (in parentheses) of the percentage of 7 dominant species collected by epibenthic sled that were damaged. T: trawled; R: reference. E: Echinodermata; M: Mollusca. Soft corals and snow crabs could not be assessed for damage

	Treatment	1993		1994		1995	
		Corridor A	Corridor B	Corridor A	Corridor B	Corridor A	Corridor B
<i>Astarte borealis</i> (M)	T	72.8 (20.2)	40.1 (10.8)	55.5 (12.0)	47.9 (26.0)	60.5 (8.2)	55.0 (13.0)
	R	14.8 (11.1)	38.3 (4.7)	58.0 (21.7)	54.6 (25.2)	60.3 (17.0)	56.0 (25.0)
<i>Clinocardium ciliatum</i> (M)	T	20.9 (13.4)	45.1 (26.2)	44.0 (28.6)	59.4 (32.2)	66.9 (32.5)	67.2 (18.2)
	R	10.6 (17.4)	42.2 (7.2)	51.1 (29.8)	59.1 (35.3)	45.7 (34.8)	63.8 (19.9)
<i>Cyclocardia novangliae</i> (M)	T	41.7 (22.0)	16.7 (28.9)	17.9 (11.6)	15.9 (32.0)	31.1 (28.1)	36.9 (42.5)
	R	0	9.7 (11.6)	26.4 (27.8)	38.5 (38.9)	17.6 (14.7)	21.7 (23.0)
<i>Echinarachnius parma</i> (E)	T	21.9 (4.1)	18.6 (9.0)	14.8 (5.1)	27.6 (9.5)	28.8 (7.6)	30.8 (5.1)
	R	22.8 (6.2)	8.4 (5.1)	15.5 (3.9)	22.8 (6.8)	15.2 (7.9)	13.7 (5.8)
<i>Strongylocentrotus pallidus</i> (E)	T	7.0 (8.4)	1.8 (1.6)	17.9 (25.8)	12.1 (12.0)	13.3 (6.7)	16.2 (13.4)
	R	0.5 (1.0)	2.0 (1.5)	4.6 (4.3)	0.5 (1.2)	2.4 (2.8)	3.9 (3.6)
<i>Margarites sordidus</i> (M)	T	2.3 (0.6)	1.5 (1.0)	8.2 (16.5)	1.2 (4.0)	7.0 (9.5)	3.2 (7.1)
	R	2.5 (5.0)	2.5 (5.0)	0	0.7 (2.3)	0	2.0 (6.3)
<i>Ophiura sarsi</i> (E)	T	1.8 (0.6)	1.4 (1.0)	2.3 (1.6)	1.1 (1.0)	3.6 (2.2)	1.6 (1.4)
	R	1.5 (1.8)	1.3 (0.5)	0.3 (0.5)	0.3 (0.4)	0.4 (0.4)	0.7 (0.7)

greater damage in trawled corridors compared to reference corridors for all species (Table 9). The 3-way MANOVA indicated that there were significant effects of both trawling and year on damage but not of corridor (Table 6). Analysis of the effect of trawling on individual species indicated that only the 3 echinoderm species had significantly higher damage in the trawled corridors (Table 7), with the greatest probability of

impact on the sea urchins (on the order of 10% damage). Trawling did not have a significant effect on the damage of *A. borealis*. Because of the relatively large proportion of samples without damaged specimens, it was not possible to perform a parametric test of significance on the influence of trawling on the molluscs *M. sordidus*, *C. ciliatum*, and *Cyclocardia novangliae*. However, all dominant species could be used in the above mentioned MANOVA after principal component analysis.

Table 10. Regression of root-transformed means and standard deviations for the abundance of all species collected by epibenthic sled in each combination of the main effects of trawling, corridor and year. N: number of taxa; SE: standard error

Corridor	Treatment	N	R ²	Slope (SE)	Intercept (SE)
1993					
A	Reference	45	0.968	0.729 (0.020)	0.210 (0.016)
	Trawled	36	0.921	0.640 (0.032)	0.261 (0.025)
	Reference ^a	44	0.952	0.724 (0.025)	0.213 (0.019)
	Trawled ^a	35	0.944	0.740 (0.031)	0.193 (0.023)
B	Reference	51	0.946	0.569 (0.019)	0.306 (0.015)
	Trawled	48	0.929	0.799 (0.033)	0.146 (0.025)
1994					
A	Reference	66	0.972	0.662 (0.014)	0.253 (0.010)
	Trawled	60	0.975	0.736 (0.015)	0.213 (0.011)
B	Reference	70	0.956	0.751 (0.020)	0.202 (0.014)
	Trawled	70	0.969	0.803 (0.017)	0.168 (0.012)
1995					
A	Reference	60	0.956	0.691 (0.019)	0.241 (0.014)
	Trawled	71	0.933	0.735 (0.024)	0.208 (0.016)
B	Reference	68	0.943	0.761 (0.023)	0.200 (0.016)
	Trawled	64	0.956	0.818 (0.022)	0.164 (0.016)

^aSand dollars excluded

Species homogeneity

A linear relationship between the mean abundance and standard deviation of all species in each treatment group (year, corridor and trawling) was established by applying root-transformation (Fig. 8). Since sand dollars *Echinarachnius parma* and brittle stars *Ophiura sarsi* were very dominant, a sixth root transformation was used to achieve a more even distribution of the data points along the regression lines. The coefficient of determination was >0.92 for all regressions (Table 10). The slopes of the regressions of trawled corridors were greater than those of reference corridors, except for Corridor A in 1993 (Fig. 8). However, elimination of the sand dollar data in this instance improved the coefficient of determination for the trawled corridor and reversed the relationship of the regression coefficients between trawled and untrawled areas (Table 10). With

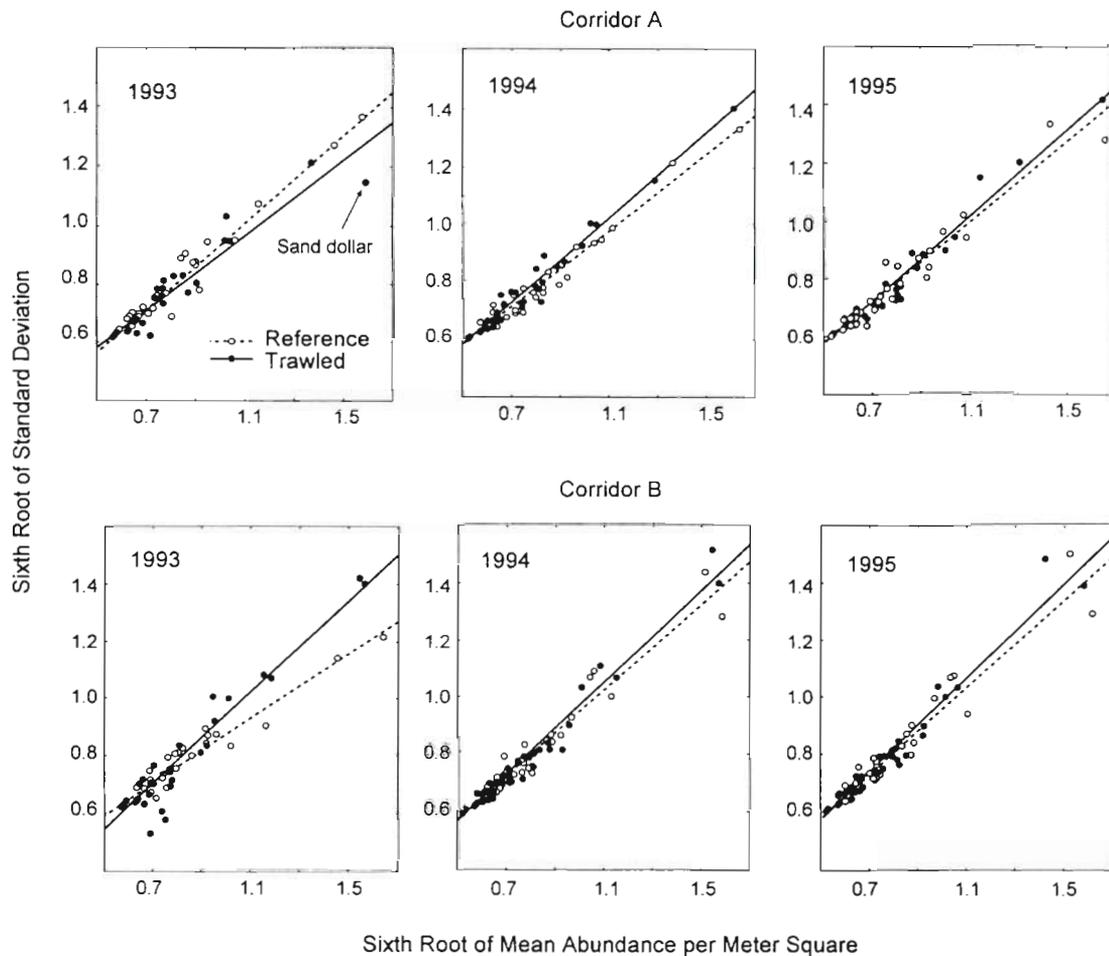


Fig. 8. Linear regression of root-transformed standard deviations and means for the abundance of all species sampled by the epibenthic sled in trawled and reference corridors (A and B) in 1993–95. Regression parameters are given in Table 10

this restriction, there was a general increase in the standard deviations relative to the means in the trawled corridors, indicating decreased homogeneity and increased aggregation in the benthic community.

DISCUSSION

The intensity of trawling applied in this experiment, 12 sets along the same line in each of 3 consecutive years, was intentionally designed to be high. Since the width of the disturbance zone within the trawled corridors (Table 3) was on the order of 2 to 4 times greater than the spread of the otter trawl doors (about 60 m), the same area of seabed was not disturbed on all sets and the average trawling intensity for a given location on the seabed was probably on the order of 3 to 6 sets per year. This trawling intensity appears to be higher than has occurred on the Grand Banks in recent years as estimated from effort data (Fig. 1). As noted above,

only a small area of the Grand Banks was fished in 1990 at a level where 8% or more of the seabed had been trawled. This is the equivalent of 1 trawling disturbance every 12 yr. However, commercial fishing effort can be more intense in other nearby regions. For example, Auster et al. (1996), using effort data collected between 1976 and 1992, estimate that on average the U.S. sector of the Gulf of Maine is trawled once a year while the U.S. sector of Georges Bank is trawled 3 to 4 times a year. Because of the pronounced patchiness of trawling effort (Fig. 1), targeted fishing grounds can receive an even higher level of disturbance, since it is common practice to fish a productive area heavily until catch declines to the point where further effort is not cost effective. Therefore, the intensity of trawling used in our experiment is not unrealistic.

The effects of the otter trawling on the physical habitat observed in this experiment have been presented by Schwinghamer et al. (1998) but are briefly summarized here. Trawling had no observed effect on sedi-

ment grain size. There was an immediate effect on sediment surface topography due to the berms and furrows created by the trawl doors which were readily detected by sidescan sonar and at times visible in video imagery. In most instances, they disappeared within 1 yr. RoxAnn™ data also indicated changes in sediment surface topography with increasing trawl set. Changes caused by trawling in the acoustical properties of the upper 4.5 cm of sediment were detected by DRUMS™ and suggest decreased habitat complexity through destruction of biogenic structures such as tubes and burrows (Schwinghamer et al. 1996). High resolution colour video observations indicated that trawling reduces biogenic sediment structures and the abundance of flocculated organic matter on the sediment surface. However, these visual effects disappeared in less than a year. In summary, these observations indicate that the physical habitat at the study site recovered from the experimental trawling disturbance within approximately 1 yr. It is important to note that there were significant interannual changes in both sediment grain size and acoustic properties that could not be attributed to trawling. Possible natural sources of this variability include bioturbation and winter storms.

As expected, the epibenthic sled catch was quite different from the invertebrate bycatch of the otter trawl. Only the snow crab *Chionoecetes opilio* and the sea urchin *Strongylocentrotus pallidus* were common in both. The third dominant invertebrate in the trawl bycatch, the basket star *Gorgonocephalus arcticus*, was only occasionally captured by the sled. Assuming an average invertebrate bycatch of 10 kg tow⁻¹ (Fig. 3), taking into account the length of the tow (13 km) and the width of the area sampled (20 m), the otter trawl captured an average invertebrate biomass on the order of 38 mg m⁻², which is only 0.01% of that captured by the sled (Table 4). A more conservative estimate of 0.5% is obtained using only the 3 dominant species of the invertebrate bycatch and a sampling width of 5 m (i.e. codend with smaller mesh). These results indicate that the otter trawl is very inefficient in catching epibenthic species, presumably due to its larger mesh size and its practice of travelling just above the sediment surface rather than cutting through it as the sled does. Different modes of capture (e.g. turbulent displacement into the otter trawl versus scooping up into the sled) also may have contributed to the observed differences in catches.

Even though the trawl is very inefficient in sampling epibenthic organisms and did not pass over exactly the same area of seabed on each set, there was a significant decrease of invertebrate bycatch in the otter trawl over the 12 consecutive sets (Figs. 3 & 4). It is questionable whether this decrease was caused entirely by the

direct removal of epibenthic organisms by the trawl. Another contributing factor could be that, once disturbed or damaged, epibenthic organisms are more difficult to capture in the trawl during later sets. The biological damage inflicted by the otter trawl was much greater than indicated by the biomass of invertebrate bycatch. The remains of dead organisms were commonly seen fouling the wings and belly of the net. In addition, large numbers of damaged organisms left behind on the seabed were detected in the sled samples collected soon after trawling (Table 9). The 3 species significantly damaged were sand dollars *Echinarrachnius parma*, brittle stars *Ophiura sarsi* and sea urchins *Strongylocentrotus pallidus*, all echinoderms (Table 7). These estimates of damage may be low because of predation by scavengers during the interval between trawling and sampling which in some instances was greater than several days (Table 1). Video imagery showed that basket stars *Gorgonocephalus arcticus* were coiled into tight balls after passage of the otter trawl but many seemed to recover within a day (Schwinghamer et al. 1998). The relative consistency of basket star and sea urchin biomass in the invertebrate bycatch (Fig. 3) reflects their low catchability by the trawl and the likely possibility that later sets passed over substantial areas of unsampled bottom because of variability in the path of the trawl.

The total biomass of organisms captured by the epibenthic sled was consistently lower in the trawled corridors in each of the 3 years of the experiment (Table 4, Fig. 7). The decrease averaged 24% and was statistically significant (Tables 5 & 6). Analysis at the species level indicated that the decreases were due primarily to reductions in the biomass of sand dollars *Echinarrachnius parma*, brittle stars *Ophiura sarsi*, soft corals *Gersemia* sp., sea urchins *Strongylocentrotus pallidus*, and snow crabs *Chionoecetes opilio* (Table 7). Because of its relative abundance in the invertebrate bycatch of the otter trawl (Fig. 3), it is possible that the biomass of the basket star *Gorgonocephalus arcticus* was also reduced by trawling. However, we were unable to detect this in the sled data because this species was poorly sampled. This is likely due to its rather sparse distribution and large size relative to the mouth of the sled. It is not surprising that the greatest difference in biomass between reference and trawled corridors occurred in 1995 (Fig. 7) since, by then, the trawled corridors had been trawled in 3 successive years. However, it is puzzling that the least difference occurred in 1994. This could be due to the fact that, in that year, the reference corridors were sampled after trawling instead of before (Table 2) and outward migration of mobile species from the reference corridors into the trawled corridors may have reduced biomass.

The lower biomass of epibenthic invertebrates observed in the trawled corridors can be due to several factors which operate over different time scales. Direct removal by the otter trawl appears to be insignificant since, as discussed above, the otter trawl is very inefficient in collecting the epibenthic species common at the study site. A more likely factor, with a time scale on the order of hours to days, is predation by scavengers on dead or damaged organisms left behind on the seabed. Scavenging by finfish in the wake of trawling or dredging has been documented by Caddy (1973) and Kaiser & Spencer (1994) but was probably negligible in our experiment because of the extremely low abundance of fish (Fig. 6). Due to there being no evidence of any increase in finfish abundance with increasing trawl set, there is nothing to suggest an inward migration of fish to feed.

A potential problem that arises with spatially separated treatments is confounding of treatment effects with location effects (Underwood 1992). However, we feel that our results reflect true trawling effects and are not the result of chance differences between the trawled and reference corridors (300 m apart) in our 13 km long experimental corridors (Fig. 2). Chance physical effects acting upon the seabed, obscuring trawling effects, are unlikely since imaging of the seabed within all corridors was comprehensive both before and after trawling and showed no apparent natural differences between trawled and reference corridors (Schwinghamer et al. 1998). Similarly, no natural biological processes can be envisioned operating in a strictly linear fashion in this relatively homogeneous habitat. For instance, recruitment of bivalves occurred throughout the entire study area during the 3 yr period of the experiment (unpubl. data). In addition, grab sampling conducted prior to the first trawling event in 1993 indicated no significant differences between reference and trawled corridors in total biomass of macrofauna, the biomass of 27 dominant macrofauna species, and size distributions of annelids, crustaceans and molluscs (unpubl. data).

Increased attention has recently been given to the role of invertebrate scavengers (Kaiser & Spencer 1996, Ramsey et al. 1996). The importance of scavengers in marine ecosystems disturbed by human activities has been recognised (Britton & Morton 1994). The snow crab *Chionoecetes opilio* and sea urchin *Strongylocentrotus pallidus* are well known scavengers on the Grand Banks and responses of these species to mobile gear can be expected. On one hand, they can be removed, damaged, or killed by the gear while, on the other hand, those that survive the disturbance, or can migrate into the disturbed area, may benefit from the increased availability of food items for scavenging and perhaps from decreased predation by

groundfish because of their removal. This appears to be the case for snow crabs. The 'functional' response of snow crab depletion by trawling during the first 6 sets (Fig. 3) appears to be followed by a behavioural or 'adaptive' response as adult male snow crabs migrated into the disturbed area during the later sets (Fig. 5). Direct evidence of this inward migration by snow crabs was seen in the video imagery obtained using BRUTIV (Schwinghamer et al. 1998). The snow crabs collected in sled samples represent the animals not removed by the trawl plus those entering the trawled corridor to scavenge. Therefore, our estimates of the impact of trawling on snow crab biomass (Tables 4 & 7) are probably low. The available data indicate a net negative effect of repeated trawling on snow crabs but not a simple linear relationship. If sea urchins have a similar migratory response, we were unable to detect it quantitatively with our sampling program. However, video observations were made of sea urchins apparently scavenging on dead snow crabs in trawled corridors (Schwinghamer et al. 1998). The possibility also exists that some mobile organisms could migrate out of the disturbed area.

The ICES Working Group on Ecosystem Effects of Fishing Activities (ICES 1996) formulated hypotheses on how the benthic community may change in areas where trawling is precluded. Closed area studies were considered as an indirect approach to evaluating the effects of trawling on seabed habitats. One prediction was that there would be a shift in size structure toward large individuals. Our experiment provided direct evidence that otter trawling does decrease the mean individual biomass of epibenthic species (Table 5). However, at the species level, only the sand dollar *Echinarachnius parma* was significantly smaller in trawled corridors compared to reference corridors (Table 7). All other species demonstrating significant biomass reduction had comparatively narrow size spectra, and immediate effects on their mean individual biomass were not detected. Longer-term effects on the size composition of sand dollars could not be evaluated due to the narrowness of the trawled corridors and possible migration. The trawl bycatch indicates inward migration of adult male snow crabs during trawling (Fig. 5) but this did not significantly alter the mean individual biomass of the snow crabs collected with the sled. This was likely a reflection of the low catchability of large crabs by the sled, as clearly observable in video records of sled sampling.

Varying levels of damage on epibenthic and shallow infaunal bivalves have been reported for different types of mobile fishing gear (e.g. Arntz & Weber 1972, Caddy 1973, Rumohr & Krost 1991, Shepard & Auster 1991, Bergman & Santbrink 1994, Santbrink & Bergman 1994, Witbaard & Klein 1994, Kaiser &

Spencer 1996, Tuck et al. 1998). Existing theories concerning susceptibility of bivalves to damage are based primarily on shell mechanical strength relationships. In general, thin-shelled bivalves are more easily damaged by otter trawl doors than thick-shelled bivalves (Rumohr & Krost 1991). However, there is conflicting evidence of the effect of shell size on damage. For example, Rumohr & Krost (1991) reported that damage to *Arctica islandica* increased with size while Witbaard & Klein (1994) concluded that intermediate sizes were most susceptible to damage. We observed no significant damage from trawling in the 4 dominant species of molluscs collected by the epibenthic sled (Tables 7 & 9). These results were surprising at first since the epibenthic sled samples organisms which live on or near the sediment surface (i.e. upper 2 to 3 cm) and therefore are exposed to the destructive forces of the otter trawl. However, Gilkinson et al. (1998) have shown experimentally that, on sandy substrata, small and medium size bivalves living on or near the sediment surface are 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. These were a large *Clinocardium ciliatum* at the sediment-water interface and a medium *Macoma calcarea* at a depth of 2 cm. It appears that burial depth combined with size is a key sensitivity parameter for bivalves.

The undisturbed benthic community at the study site is relatively homogeneous which was one of the reasons for selecting it (Prena et al. 1996). Regression analysis of organism abundance data collected with the sled clearly indicates an increase in the standard deviation relative to the mean in the trawled corridors (Fig. 8, Table 10). An increase in the standard deviation relative to the mean was also evident in the trawl bycatch data (Fig. 3B). This increased variability can be interpreted as an indication of decreased homogeneity and increased aggregation of the benthic community resulting from stress (Warwick & Clarke 1993). In this experiment, the stress of trawling could not be applied uniformly. As a consequence, the level of disturbance in a given sample is dependent on the number of trawl sets and the components of the trawl contacting each individual sample site. The 2 doors, which are in continuous contact with the seabed, have the greatest physical impact and affect 2 linear zones about 1 to 2 m wide. The rockhopper gear and net, which are in contact with the seabed most of the time during a set, affect an area about 20 m wide midway between the doors. The remaining path of the trawl is influenced by the ground warps which, while not in direct contact with the seabed, can create turbulence that resuspends sediment. Another possibility for the

decreased homogeneity observed in the trawled corridors is that organisms were redistributed unevenly after passage of the trawl as suggested by Bergman & Hup (1992) and Eleftheriou & Robertson (1992).

No attempt was made in this experiment to study the condition of the invertebrate bycatch once on board the 'Templeman'. Some individuals may have been able to survive if immediately dumped overboard. One of us (K.G.) has observed that in general a high proportion of gastropods in the bycatch of otter trawls on the Grand Banks appear to be in good condition. Survival experiments of bycatch in beam trawls have been conducted (van Beek et al. 1990, Fonds et al. 1992, Kaiser & Spencer 1995). The results indicate that the mortality of discards is relatively low for starfish (<10%), intermediate for most crustaceans and shellfish, but quite high for small fish (>90%). The principal cause of damage in these beam trawl studies appeared to be the chain matrix and tickler chains fitted to the gear. These were not present on the otter trawl used in our experiment. Therefore, it is reasonable to expect that the survival of bycatch in otter trawls could potentially be higher than in beam trawls; however, proper experiments are needed to prove this. Demersal fishing may increase whelk mortality in those individuals that are not captured but which come into contact with the gear as a result of diminished escape responses from predators (Ramsey & Kaiser 1998).

Over the longer term, other factors having the potential to affect the biomass of epibenthic organisms in the trawled corridors include changes in habitat structure and biogeochemical exchanges between the sediment and the water column. These could affect the suitability of the seabed as habitat for both adults and younger life stages. As discussed above, the observed effects of the experimental trawling on habitat structure seem to disappear in about 1 yr (Schwinghamer et al. 1998). We have no information on possible changes in biogeochemical exchanges. One final factor that may also have influenced the observed difference in epibenthic biomass between trawled and reference corridors is changes in the catchability of organisms by the sled (e.g. burial by resuspended sediment).

The gradual reduction in the biomass of both fish and invertebrate bycatch in the otter trawl over the 3 yr experiment is striking (Fig. 6). However, these changes are not necessarily due to the experimental trawling but could reflect natural variability or human impacts over much larger temporal and spatial scales than included in the design of this experiment. Unfortunately, there are no suitable data bases available for the general region of the study site that can be used for comparison. It is well known that there has been a steady decline in groundfish stocks in recent years on the Grand Banks. This has brought about the current

fishing moratorium (Hutchings 1996). This suggests that the observed drop in fish biomass (Fig. 6) is plausible and probably reflects declines independent of our experiment. Such a drop in fish biomass should also reduce predation on benthic organisms which, in turn, could increase benthic biomass. However, just the opposite was observed in the invertebrate bycatch by the otter trawl over the 3 yr experiment (Fig. 6). This observed decrease is highly suspect. As discussed above, the otter trawl is very inefficient in collecting epibenthic organisms. Furthermore, the biomass of organisms collected by the epibenthic sled (a much more quantitative device for collecting epibenthic organisms) in both trawled and reference corridors did not drop steadily with year (Fig. 7).

Five species were adversely affected by the otter trawling disturbance applied in our experiment. They are the snow crab *Chionoecetes opilio*, sand dollar *Echinarachnius parma*, sea urchin *Strongylocentrotus pallidus*, brittle star *Ophiura sarsi* and soft coral *Gersemia* sp. (Table 7). These are all relatively large epibenthic forms that live on the sediment surface and are therefore most susceptible to capture and damage from the otter trawl. The 4 dominant species captured by the sled for which there were no clear evidence of trawling effects were all molluscs (*Astarte borealis*, *Margarites sordidus*, *Clinocardium ciliatum* and *Cylocardia novangliae*). These observations are consistent with the results of other impact studies conducted with otter trawls and beam trawls. In general, the organisms most affected include epibenthic forms of molluscs, echinoderms, crustaceans, sponges, hydrozoans, bryozoans, and fish (e.g. Graham 1955, Caddy 1973, de Groot 1984, Rumohr & Krost 1991, Bergman & Hup 1992, Eleftheriou & Robertson 1992, Kaiser & Spencer 1994, Auster et al. 1996, Collie et al. 1997, Jennings & Kaiser 1998). On the other hand, the effects of trawling are less apparent on infaunal species (e.g. van Dolah et al. 1991, Bergman & Hup 1992, Brylinsky et al. 1994, Gilkinson et al. 1998).

In conclusion, this experiment demonstrates that, along with the obvious immediate impacts of removal, mortality and injury on benthic invertebrates seen in the otter trawl bycatch, other less visible but nevertheless significant impacts on both benthic habitat and communities can be induced by otter trawling on a sandy seabed. This is a habitat exposed to storm waves and iceberg scouring where it would be expected that the benthic fauna would be already adapted to some degree of physical disturbance. In particular, by sampling the benthic community with an epibenthic sled, we were able to detect decreases in total and mean individual biomass, damage to organisms and decreases in species homogeneity in corridors that were trawled repeatedly by an Engel 145 otter trawl.

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