

Immediate impacts and recovery trajectories of macrofaunal communities following hydraulic clam dredging on Banquereau, eastern Canada

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A hydraulic clam dredging experiment, designed to mimic offshore commercial dredging practices, was carried out at a depth of approximately 70 m on a sandy seabed on Banquereau, on the Scotian Shelf, eastern Canada. The experiment was designed to study the separate and combined effects of dredging through three treatment boxes (Dredging Only, Dredging and Discarding, Discarding Only) and two spatially separated reference boxes. In all, 270 taxa were identified from grab samples. Of these, four bivalves are targeted in the commercial fishery (*Arctica islandica*, *Cyrtodaria siliqua*, *Mactromeris polymyma*, and *Serripes groenlandicus*) while 266 taxa were non-target species. Sample biomass was dominated by the propellerclam, *C. siliqua*, and the echinoderm, *Echinarachnius parma*, while the polychaete, *Spiophanes bombyx*, was the numerical dominant. The dredges captured 33 invertebrate and two fish taxa, although >80% of the catch biomass comprised propellerclams and echinoderms. Immediately after dredging, most macrofaunal species decreased in abundance, with the greatest declines inside dredge furrows (which covered 53–68% of the area inside the dredged boxes). Large numbers of propellerclams were excavated to the seabed surface, with a large proportion showing massive damage. There were few signs of discards on the sediment surface. Recovery trajectories of target and non-target species were followed for 2 years. Following initial declines in abundance and biomass of most taxa immediately after dredging, there were marked increases in abundance of polychaetes and amphipods after 1 year. Two years after dredging, abundances of opportunistic species were generally elevated by >>100% relative to pre-dredging levels. Two years after dredging, average taxonomic distinctness had decreased (i.e. taxonomic relatedness between species had increased) due, in part, to increased numbers of species of certain polychaetes and amphipods, while communities had become numerically dominated (50–70%) by *S. bombyx*. It is concluded that the disturbed community was still in the colonizing phase 2 years after dredging. The mobile brittlestar, *Ophiura sarsi*, displayed increases in abundance ranging from 200% to 300% in the dredged and reference boxes over the 2-year post-dredging. A similar response of non-target macrofauna in the reference boxes suggests, possibly, a coincident natural recruitment pulse. Dredging resulted in pronounced, sustained reductions in biomass (up to 67%) of the target bivalves with no signs of recovery after 2 years. Recruitment of target bivalves (>1-mm shell length) was very low throughout the experimental area during this interval.

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Introduction

Hydraulic clam dredges are a unique class of mobile bottom fishing gear given that their effectiveness depends on an ability to dig deeply into sediments in order to harvest infaunal bivalves. While dredge designs vary, all offshore deepwater dredges are large and of heavy construction.

Although their footprint is relatively small compared with that of otter trawls, hydraulic clam dredges produce the most dramatic effects on seabed habitat of any gear type (see Meyer *et al.*, 1981; Hall *et al.*, 1990; Gilkinson *et al.*, 2003). More so than for other gear types, less is known about the environmental impacts of hydraulic clam dredging even though this technology has been in use in the Northwest Atlantic since the 1940s (Serchuk and Murawski, 1997). In addition to physical effects, biological impacts can be pronounced and include dispersal and burial of epifauna (Hauton *et al.*, 2003b), reductions in the abundance, biomass, and diversity of benthos (Kauwling and Bakus, 1979; Murawski and Serchuk, 1989; Hall *et al.*, 1990; Pranovi and Giovanardi, 1994; Kaiser *et al.*, 1996), as well as a temporary increase in numbers of scavengers feeding on exposed infauna (e.g. Kauwling and Bakus, 1979; Meyer *et al.*, 1981; Murawski and Serchuk, 1989). Significant damage to clams, not retained by the dredge, has also been reported (Lambert and Goudreau, 1996; Hauton *et al.*, 2003a). However, most of the reported impacts have been based on short-term experiments in shallow water with a range of hydraulic dredge designs and modes of operation. Very little is known about impacts of hydraulic clam dredging on benthic communities in deeper offshore areas.

Hydraulic dredges have been used to harvest clams on the Scotian Shelf since the mid-1980s and on the Grand Banks off Newfoundland since the early 1990s (Roddick, 1996). The principal target species is the Arctic surfclam (*Mactromeris polynyma*), but the propellerclam (*Cyrtodaria silqua*), the ocean quahog (*Arctica islandica*), and the Greenland smoothcockle (*Serripes groenlandicus*) are also harvested. At present, three factory freezer vessels participate year round in this fishery, which has annual sales of Can \$50 million. Working at depths between 50 and 80 m, these vessels deploy paired hydraulic dredges, each approximately 4 m wide and weighing 12 tonnes, that create furrows on the order of 4 m wide by 20 cm deep.

Critical information gaps relating to the environmental impacts of hydraulic dredging include an understanding of longer-term impacts and rates and processes of recovery. For instance, hydraulic clam dredges have high capture efficiencies for target bivalve species (Lambert and Goudreau, 1996). Therefore, within a dredged patch of seabed, a substantial proportion of benthic biomass, in the form of large, long-lived bivalves, can be removed. It is the practice in the Canadian fishery to dredge localized areas (tens of thousands m²) and then to leave this fallow for a period of approximately 10 years in order to allow time for re-establishment and growth to commercial size of the

target species. At the scale of fishing banks, this results in a mosaic pattern of seabed of varying “dredging age”. In order to better manage the fishery using an ecosystem approach, it is vital to understand recovery trajectories within these dredged areas with regard to physical habitat and benthos.

In order to investigate the immediate impacts of hydraulic clam dredging on macrofaunal communities and to follow rates of recovery, a manipulative offshore field experiment was conducted on Banquereau, an important fishing bank off eastern Canada. A key aspect of the experiment was the collaboration with industry, which ensured that the design and execution closely followed standard commercial dredging practices. Recovery processes were followed over 2 years. Effects on seabed habitat and soft corals are presented elsewhere (Gilkinson *et al.*, 2003; Gilkinson *et al.*, 2003, *in press*).

Material and methods

Experimental site

The experimental site (44°26'N 57°54'W) was selected after surveying several potential sites in 1997. Selection criteria included commercial concentrations of clams, not previously dredged, homogeneous sandy sediments, and diverse and abundant macrofaunal communities. The experimental site is located on Banquereau, the easternmost outer shelf bank on the Scotian Shelf, Southeast Atlantic Canada (Figure 1). Surficial sediments on Banquereau consist of well-sorted medium-grained sands (Amos and Fader, 1988). Water depths at the experimental site ranged from 70 to 80 m.

Experimental design

Biological impacts associated with hydraulic clam dredging include: (i) incidental damage and mortalities in non-harvested organisms, (ii) removal of benthos, and (iii) secondary impacts associated with discards (fish and invertebrates, including unused portions of the harvested clams, e.g. viscera and shells). The impacts of dredging (i, ii) and discarding (iii) were studied separately, as well as in combination, in three experimental treatment boxes (Dredging Only, Discarding Only, Dredging and Discarding) established inside an experimental frame measuring 1.5 km by 2 km (Figure 1). The present paper focuses on the two dredging treatments, since impacts in the Discarding Only box were expected to be relatively transient, affecting scavengers primarily.

Both dredging treatment boxes measured 100 m by 500 m. A length of 500 m was selected so that the dredges would not overfill with benthos. Two reference boxes (North and South) were situated so that each was separated from any of the treatment boxes by a distance of at least 500 m. This spacing reduced the chances of re-suspended

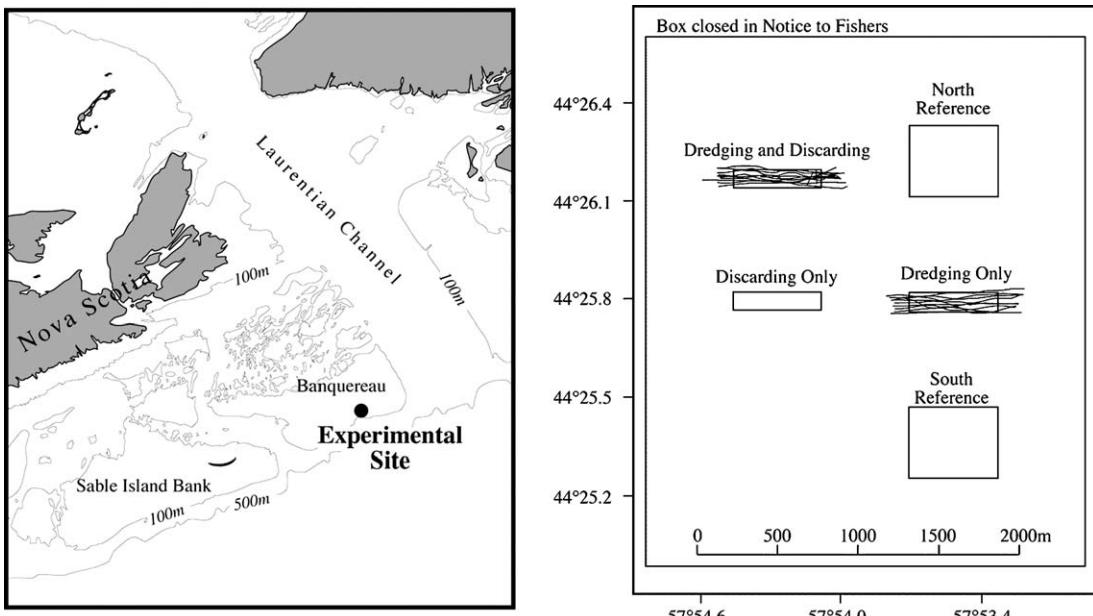


Figure 1. Location of experimental site on Banquereau, Scotian Shelf, off eastern Canada, and schematic representation of the relative positions and orientation of the Dredging, Discarding, and reference boxes. Note: grab sampling was not done in the Discarding Only box.

sediment entering and settling inside the reference boxes. The experiment was designed as an asymmetrical BACI (Before-After-Control-Impact) (Underwood, 1994) with multiple reference areas and temporal replication in both treatment and reference areas. This design is appropriate for detecting impacts from pulse disturbances and reducing the chances of confounding treatment and location effects. The experimental design was also driven by the need to closely follow standard commercial dredging practices in order for the results to be broadly applicable to this type of fishing.

Experimental dredging

Experimental dredging was done by the "Atlantic Pursuit"; a Canadian commercial offshore clam vessel that tows two hydraulic dredges from the stern. Each dredge measured 4 m (wide opening) by 3.6 m (length) by 1 m (height) and weighed approximately 12 tonnes. The bottom of the dredge was lined with 17.5-mm-diameter steel bars spaced approximately 4 cm apart. In front of the dredge opening was a blade set at a cutting depth of 20 cm. A manifold directed jets of water under pressure (130-psi exit pressure) into the sediment in front of the blade in order to loosen the sediment.

The experimental dredging boxes were displayed on the ship's plotter to aid in keeping the tows inside the box boundaries and distributed throughout. A RoxAnn system logged the differential GPS ship's position at approximately 2-s intervals during the experimental dredging. In all, 12 tows were made in alternating directions within each box with sufficient lead-ins and exits to ensure that the dredges

were on-bottom over the entire length of the box. The total catch was processed on-board. In the Dredging and Discarding box, after each tow the dredges were brought on-board and dumped for processing and subsequently redeployed for the next tow. Bycatch, consisting of non-target fish and invertebrates, and the shells and viscera of clams, was continuously discarded while dredging proceeded. In the Dredging Only box, the total catch was stored in the hoppers and processing and discarding occurred in the Discarding Only box.

Sidescan sonar surveys were accomplished immediately after dredging, providing complete coverage of the seabed within each dredged box. The sidescan digital data were processed by the Geological Survey of Canada and mosaics were constructed (see Gilkinson *et al.*, 2003). The total area covered by dredge furrows in each dredged box was determined using a planimeter and expressed as a percentage of the total area ($50\,000\text{ m}^2$).

Sampling the dredge catch

After the dredges were retrieved, the volume of the catch was visually estimated by comparing the level to a diagram giving the volume at each crossbar on the side of the dredge. Tows were done and the catch accumulated until the hoppers on the back of the vessel were full. Once the hoppers were full and the vessel was within the appropriate discard area, processing of the catch began. Subsamples of the catch (1–2% of total catch volume) were taken from the conveyor belt feeding out from the hoppers before any mechanical separation took place. The catch in the

Dredging Only box was relatively low and all 12 tows could be stored in the hoppers. Five bushels (182 l) were sampled from each dredge hopper (0.36 m^3 in total). Catch volume in the Dredging and Discarding box was higher, and samples of two bushels were taken from each hopper after three consecutive series of tows (1–3, 4–7, 8–12) for a total subsample volume of 0.43 m^3 . Subsamples of the catch were shovelled from the conveyor belt into bushel baskets. The subsamples were then weighed and sorted by taxa. Based on subsample weights, estimates were made of the biomass of the total catch, and by species, captured by the dredge in each dredging box.

Grab sample collection and processing

Grab sample collection and initial processing was carried out on the "C.S.S. Hudson". Sampling was done in May/June of each year inside the treatment and reference boxes at the following time intervals: before dredging, immediately after dredging, and 1 and 2 years after dredging (Table 1). A total of 180 samples was collected using the Department of Fisheries and Oceans (DFO) 0.5-m² hydraulic videograb. Details of the grab design and operation can be found in *Rowell et al.* (1997) and *Gordon et al.* (2000). During the design phase, both dredging treatment boxes had three survey lines established along the long axis (centre line and lines offset by 50 m). Each line was subdivided into ten segments (each 50 m long). The centre of each segment represented one potential grab sampling station. Ten stations were then randomly selected from each box. Using a similar procedure, ten stations were randomly selected from the two reference boxes, six from the northern box and four from the southern. The grab was positioned at each station using differential GPS ship's position in conjunction with an ORE International Inc., Model 4410C Trackpoint II ultra-short baseline (USBL) acoustic tracking system. An AGCNav computer-based navigation display and logging program was used to log all the navigation data and to display ship and grab positions in

Table 1. Numbers of videograb samples (0.5 m^2) collected during the experiment.

Date	Sampling period	Reference box		Dredging	
		North	South	Only box	Dredging and Discarding box
May/June 1998	Before dredging	6	4	10	10
	Immediately after dredging	6	4	20	20
May 1999	1 year after dredging	6	4	20	20
June 2000	2 years after dredging	6	4	20	20

real time on both the ship's bridges and in the scientific laboratories. Navigation accuracy was approximately $\pm 6 \text{ m}$. Further details of this equipment can be found in *McKeown and Gordon* (1997).

Grab samples were sieved through a 1-mm mesh screen and the retained material was preserved in 10% buffered formalin. Subsequent onshore processing consisted of identification of all macrofauna, where possible, to species. Due to gaps in taxonomic knowledge, some groups could not be identified to species; in particular, the actinarians, ascophoran Bryozoa, Nemertea, and Platyhelminthes. Sample abundance and biomass (formalin wet weight) were determined for each taxon. Individuals of the target bivalve species were measured for shell length in order to monitor recruitment patterns over the 3-year extent of the experiment.

An attempt was made to sample within two categories of dredging disturbance: (i) *primary*: samples taken inside dredge furrows and, (ii) *secondary*: samples taken outside furrows in areas subjected to secondary sedimentation and/or burial in berms immediately adjacent the furrows. Classification was done using real-time imagery of the seabed using a grab-mounted video camera. Appearance of the seabed surface, as seen in video, was judged to be the most unbiased source of information for classifying type of disturbance since it was based on physical disturbance to the seabed rather than on status or appearance of the biological communities. Since the spatial pattern of dredging disturbance (i.e. proportion of the seabed covered by furrows) was not known at the time of sampling, an industry estimate of 50–60% was used to allocate the samples to areas inside furrows vs. outside. Although subsequent MDS analyses (not presented) based on macrofaunal species abundances showed very good separation of samples that had been assigned, *a priori*, as either inside or outside furrows, there was still uncertainty associated with this classification. This paper focuses on an average effect on a dredging ground (i.e. samples taken both inside and outside furrows). Where differences exist between the average effect and the maximum effect (i.e. samples taken only from within furrows), these are highlighted. This analysis could only be done in the first year of the experiment since dredge furrows were no longer discernible in video surveys done 1 year after dredging.

Data analyses

Community indices

For each grab sample, biomass (B) and abundance (N) of target and non-target species, average weight of individuals (B/N), and number of species were calculated. Tests of each of the hypotheses listed below were carried out separately on these community indices.

Effects on target and non-target species were analysed separately in order to obtain a better understanding of

impacts on the biomass dominant target species from impacts on the remaining species that dominate the benthic community in terms of numbers of species (99%) and numbers of individuals (98%). For comparisons with the dredging treatments, the North and South reference boxes were combined in order to provide an average picture of benthic community structure in non-dredged habitat within the study area.

Analysis of variance

The following two-way analysis of variance (ANOVA) was used to test the hypothesis that dredging had no immediate effect on macrofauna:

$$(i) \text{ Model A: } Y_{ijl} = \mu + D_i + T_j + DT_{ij} + \varepsilon_{ijl}$$

where factor D_i represents a dredging treatment effect (Dredging Only or Dredging and Discarding) contrasted with effects in the combined reference boxes, and T_j represents a time effect with two levels (before dredging, immediately after dredging).

A two-way ANOVA was used to test the hypothesis that dredging had no longer-term effects on macrofauna:

$$(ii) \text{ Model B: } Y_{ijl} = \mu + D_i + T_j + DT_{ij} + \varepsilon_{ijl}$$

where factor D_i represents a dredging treatment effect (Dredging Only or Dredging and Discarding) contrasted with effects in the combined reference boxes, and T_j represents a time effect with three levels (before dredging, 1 year after dredging, 2 years after dredging).

Data were transformed ($\log_{10}(x + 1)$) prior to analysis. Tukey's honestly significant difference test was used as a *post hoc* analysis to determine which pairs of sample means were significantly different.

Multidimensional scaling ordination

Non-target macrofaunal community structure before and after dredging was contrasted with natural temporal and spatial patterns seen in the reference boxes using non-metric multidimensional scaling ordination (MDS) using PRIMER v.5 (Clarke and Gorley, 2001). A Bray–Curtis similarity matrix was constructed for both species abundances and biomass. The data were $\log_{10}(x + 1)$ transformed prior to calculation of dissimilarities. Two-dimensional MDS plots were constructed in order to examine the immediate effects of dredging on community structure and longer-term effects using the same time periods used in the ANOVA models. Significant differences between samples were determined using the analysis of similarities (ANOSIM) routine in PRIMER, while the species accounting for these differences were identified using the SIMPER routine.

Taxonomic distinctness

Longer-term effects of dredging on macrofaunal biodiversity were examined. The metric used was average taxonomic distinctness, which measures the average taxonomic relatedness of species in a sample and compares this to expected values based on a larger regional pool of species. For the purposes of this study, the regional pool comprised the non-target species pool (266 species) found in the experimental frame. Conventional diversity indices, which use only the relative abundance of species, do not describe the degree of taxonomic relatedness of those species (Rogers *et al.*, 1999). Benthic communities that have been disturbed often have low diversity and consist of species that are closely related. Conversely, undisturbed communities often consist of a wider range of taxonomically distinct species (Warwick and Clarke, 1995). An advantage of using taxonomic distinctness is that it is independent of sampling effort, which can strongly influence the values of other commonly used diversity indices owing to the influence of sampling effort on species richness (Warwick and Clarke, 1998). This was a consideration in the present study since sampling effort was greater in the “after dredging” samplings and in the dredging treatment boxes. Funnel plots, delineating predicted mean average taxonomic distinctness as a function of species number and 95% confidence limits, were generated from samples collected before dredging and 2 years after dredging for each treatment box. Statistical tests for taxonomic distinctness, based on species presence–absence data, were made using the Taxdist routine in PRIMER.

Results

General description of the macrobenthic community

In all, 270 species, including species groups, representing nine phyla were identified from 180 grab samples (Table 2). Of these, 266 were non-target species while four bivalves, the Arctic surfclam (*Mactromeris polynyma*), the propellerclam (*Cyrtodaria siliqua*), the ocean quahog (*Arctica islandica*), and the Greenland smoothcockle (*Serripes groenlandicus*) comprise the target species in the commercial dredge fishery on Banquereau. The mean number of non-target species in a videogram sample ranged from approximately 48 to 73. Overall, the temporal pattern in numbers of species was similar between treatments, with average number of species per sample increasing slightly over the 2-year post-dredging interval (Figure 2). In terms of number of species, arthropods (mostly amphipods) (89), annelids (mostly polychaetes) (84), and molluscs (65) dominated. Combined, these three phyla accounted for 86% of all species. A total of 19 species (7% of all species) occurred in greater than 90% of the samples (Table 2), while 140 species (52%) were found in less than 10% of the samples.

Table 2. Number of species, by phylum, of macrofauna collected by the videograb at the experimental site. Species with frequencies of occurrence > 90% are listed.

Phylum	# Species	>90%
Arthropoda	89	<i>Ampelisca macrocephala</i> (Lilljeborg, 1852) <i>Eudorellopsis deformis</i> (Kroyer, 1846) <i>Priscillina armata</i> (Boeck, 1861)
Annelida	84	<i>Aglaophamus circinata</i> (Verrill, 1874) <i>Chaetozone setosa</i> (Malmgren, 1867) <i>Euchone papillosa</i> (M. Sars, 1851) <i>Goniada maculata</i> (Oerstad, 1843) <i>Nephtys caeca</i> (Fabricius, 1780) Oligochaeta spp. <i>Ophelia limacine</i> (Rathke, 1843) <i>Pectinaria granulata</i> (Linnaeus, 1767) <i>Polydora concharum</i> (Verrill, 1880) <i>Polydora</i> sp. (Bosc, 1802) <i>Scoloplos armiger</i> (O.F. Müller, 1776) <i>Spiophanes bombyx</i> (Claparède, 1870) <i>Spio filicornis</i> (O.F. Müller, 1776)
Mollusca	65	<i>Cyrtodaria siliqua</i> (Spengler, 1793)
Cnidaria	12	
Echinodermata	11	<i>Echinorachnius parma</i> (Lamarck, 1816) <i>Ophiura sarsi</i> (Lutken, 1855)
Bryozoa	4	
Chordata	3	
Nemertea	1	
Platyhelminthes	1	

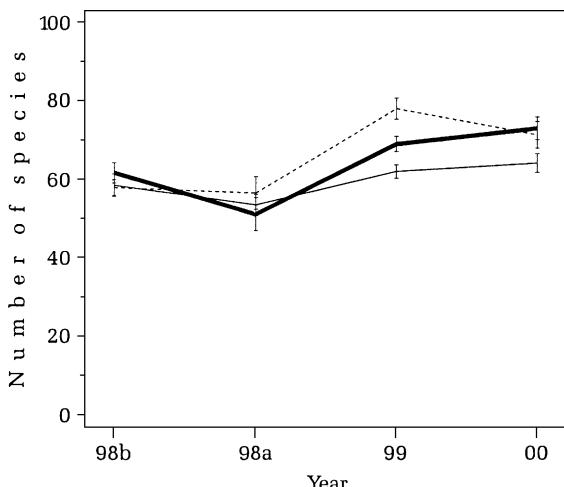


Figure 2. Mean (\pm standard error) number of species per grab sample (0.5 m^2) for the combined reference boxes (----), the Dredging Only (—), and Dredging and Discarding boxes (—). Years: 98b (before dredging, 1998), 98a (immediately after dredging, 1998), 99 (1 year after dredging, 1999), 00 (2 years after dredging, 2000).

Abundance

The non-target species pool showed dramatic increases in abundance over the 3 years of the study (Figure 3a). In the Dredging and Discarding box in particular, average sample abundance increased from 564 individuals before dredging to 3505 individuals 2 years after dredging. In the study area, three species comprised 65% of total mean species abundance. These were the polychaete, *Spiophanes bombyx*, and the amphipods *Priscillina armata* and *Ampelisca macrocephala*. In particular, *S. bombyx* averaged 531 individuals per grab sample, representing 46% of total mean species abundance. The propellerclam, *Cyrtodaria siliqua*, was the numerically dominant target species, with pre-dredging average sample abundance ranging from approximately 17 to 48 individuals per 0.5 m^2 (Table 3). There was no change in the combined abundance of the target species in the reference boxes (Figure 3b). In the dredging boxes, declines in target species abundance over time were attributable primarily to declines in numbers of propellerclams (Figure 3b).

Biomass

Average total sample biomass of non-target species ranged from 117 g to 277 g. Three echinoderm species constituted approximately 70% of average sample biomass of non-target species in the study area. The sand dollar, *Echinorachnius parma*, accounted for 47% of total biomass while the sea cucumber, *Cucumaria frondosa*, and the brittlestar, *Ophiura sarsi*, accounted for 14% and 9% of sample biomass, respectively. Average sample biomass of non-target species fluctuated over time in the treatment boxes, although it was most stable in the Dredging Only box (Figure 4a). Average sample biomass of the target species remained relatively stable in the reference boxes over the 3 years of the study (Figure 4b). However, in the dredging treatments, temporal trends in average sample biomass of the four target species combined mirrored patterns of abundance with 46% (Dredging Only) and 67% (Dredging and Discarding) declines in average biomass from before dredging to 2 years after dredging (Figure 4b). The propellerclam dominated target species biomass, with pre-dredging average sample biomass ranging from 962 g to 1.2 kg (Table 3). Average sample biomass, of the second ranked target species (*M. polynyma*) was considerably lower and ranged from 39 g to 136 g. Temporal declines in target species sample biomass in the dredging boxes were attributable primarily to declines in propellerclam biomass.

Natural spatial and temporal variability of macrofauna

An MDS plot of reference box samples, based on the abundances of 266 non-target species, revealed consistent differences in community structure between the North and South reference boxes over the 3-year period (Figure 5a)

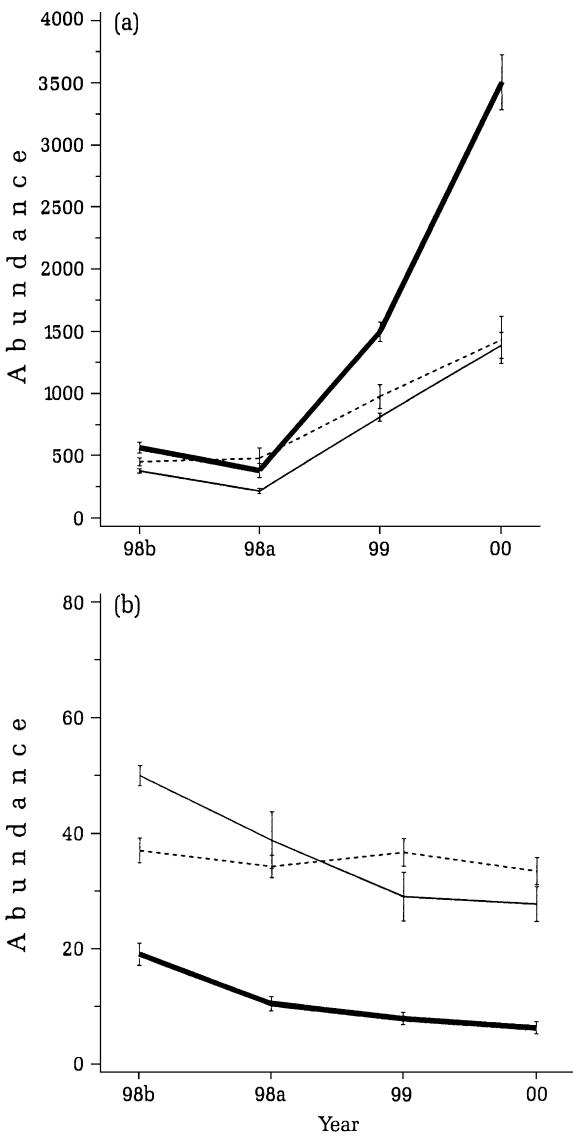


Figure 3. Mean (\pm standard error) abundances over time of non-target (a) and target species (b) per grab sample (0.5 m^2) for the combined reference boxes (----), Dredging Only (—), and Dredging and Discarding (—) boxes.

(ANOSIM, $R = 0.447$, $p = 0.001$). SIMPER analysis showed that 58 species accounted for two-thirds of the cumulative average dissimilarity between the North and South reference samples. The majority of these were annelids (primarily polychaetes) and arthropods (primarily amphipods). Of the 58 species, 40 (69%) had higher average abundances in the North box (3-year average).

There was also significant separation of North and South reference box samples based on biomass (ANOSIM, $R = 0.42$, $p = 0.001$) (Figure 5b). Similarly, average sample biomass for the majority of species (66%)

accounting for dissimilarity between the two reference boxes was higher in the North box.

Despite these differences, temporal trends in community structure were similar between the two reference boxes (Figure 5a, b). It is important to note that samples taken before and immediately after dredging in both boxes were not significantly different based on both abundance and biomass (ANOSIM, $R < 0.2$, $p > 0.05$). A major trend seen in both reference boxes was an increase over time in average abundance of many species, particularly polychaetes and small crustaceans.

There were differences in community structure of non-target species between the treatment boxes prior to dredging (Figure 6). Trends were similar for both abundance and biomass. Samples from the combined reference boxes and the Dredging Only box were not significantly different (ANOSIM: abundance, $R = 0.06$, $p = 0.17$; biomass, $R = 0.05$, $p = 0.17$). Samples taken from the Dredging and Discarding box were significantly different from those taken in both the combined references boxes and the Dredging Only box (ANOSIM, $p < 0.05$), although separation was more pronounced for species abundances where approximately 64% of non-target taxa had higher average abundances in the Dredging and Discarding box.

There were also natural spatial differences in the abundance and biomass of the target bivalve species. Prior to dredging, average abundance of propellerclams was significantly higher in the Dredging Only box (ANOVA, $p < 0.05$), while average abundance was significantly lower in the Dredging and Discarding box compared with either the reference or Dredging Only boxes (ANOVA, $p < 0.05$) (Table 3). However, there was no significant difference in average sample biomass of *C. siliqua* between treatments indicating fewer but larger propellerclams in the Dredging and Discarding box (Table 3). Average sample abundance and biomass for each of the other three target species were uniformly low in all treatment boxes (Table 3).

Dredge catch

A total of 35 taxa (33 invertebrates, two fish) was identified in subsamples of the dredge catch in the Dredging and Discarding box, while 29 invertebrate taxa were recorded in the Dredging Only box. Approximately 23 and 14 tonnes of benthos were captured by dredging in the Dredging and Discarding and Dredging Only boxes, respectively (Table 4). There were some differences between boxes in the proportions of various invertebrate taxa in the catch. In each box, propellerclams and echinoderms dominated the catch, constituting greater than 80% of total biomass. However, while the biomass of propellerclams and echinoderms was roughly equal in the Dredging Only box, the biomass of propellerclams caught in the Dredging and Discarding box was about twice that of echinoderms (Table 4). Non-target molluscs (primarily Buccinidae),

Table 3. Mean sample abundance and biomass (0.5 m^{-2}) of the four target bivalve species in the hydraulic dredge fishery prior to dredging. R — combined reference boxes, Dr — Dredging Only box, DD — Dredging and Discarding box. Standard errors are shown in parentheses. Note: common names are taken from Turgeon *et al.* (1998).

	Abundance			Biomass (g)		
	R	Dr	DD	R	Dr	DD
<i>Cyrtodaria siliqua</i> (Spengler, 1793) (propellerclam)	35.4 (2.04)	48.1 (1.67)	16.8 (1.82)	1006.84 (109.4)	1217.69 (111.66)	961.88 (83.89)
<i>Mactromeris polynyma</i> (Stimpson, 1860) (Arctic surfclam)	0.90 (0.28)	1.30 (0.33)	1.80 (0.42)	41.47 (16.75)	39.40 (16.06)	135.51 (73.19)
<i>Serripes groenlandicus</i> (Mohr, 1786) (Greenland smoothcockle)	0.70 (0.21)	0.60 (0.27)	0.50 (0.22)	11.92 (6.36)	13.37 (6.78)	22.21 (15.78)
<i>Arctica islandica</i> (Linnaeus, 1767) (ocean quahog)	0.10 (0.10)	0	0	2.54 (2.54)	0	0

other invertebrates (tunicates, anemones, polychaetes, hydrozoans, soft corals), and fish (grey sole, Cottidae) comprised approximately 1% of the total catch biomass in each box. A total of 145 grey sole and 82 sculpins (Cottidae) were estimated to have been captured in the Dredging and Discarding box, while no fish were subsampled in the Dredging Only box. Using estimates of densities of the target bivalves based on grab samples, dredge removal of these species was compared with estimated standing crop inside the dredging box boundaries (i.e. $100 \times 500 \text{ m}$). Approximately 5% and 13% of the standing crop of propellerclams, 17% and 38% of Arctic surfclams, and 36% and 63% of Greenland cockles were removed by dredging in the two boxes. No estimates could be made for the Ocean quahog, as this species was not sampled by the grab in either dredging box.

Immediate effects of dredging on macrofauna (1998)

Dredging Only box

Five samples taken immediately after dredging were excluded from the analysis since navigation data, combined with video observations, indicated that these samples lay outside the zone of dredging disturbance.

Non-target species. An MDS plot based on non-target species abundances showed that samples taken from the Dredging Only box immediately after dredging were significantly different from non-dredged samples (ANOSIM, $R = 0.3$, $p = 0.001$) (Figure 7a). Prior to dredging, there were no significant differences in species composition between reference and Dredging Only samples (ANOSIM, $R = 0.06$, $p = 0.18$). Considering just the Dredging Only box, average sample total abundance declined significantly immediately after dredging (Table 5, Figure 3a). A total of 50 species contributed to two-thirds of the cumulative average dissimilarity between the two time periods. Most of these were polychaetes and arthropods (mostly amphipods),

but, there were also four species of molluscs and two species of echinoderms. Of these 50 species, 45 (90%) declined in average abundance, with an overall average decline of 46%. Two polychaetes (*Euchone papillosa*, *Owenia fusiformis*), two crustaceans (*Anonyx* spp., *Lebbeus* sp.), and the echinoderm, *Echinarachnius parma*, showed little or no change in abundance. The other common and abundant echinoderm in the study area, the brittlestar, *Ophiura sarsi*, showed no change in average abundance before and after dredging.

An MDS plot based on biomass largely reflected that based on abundance (Figure 7b) although in the case of biomass, molluscs and echinoderms contributed more to cumulative dissimilarity between time periods than in the case of abundance.

Ten out of 15 (67%) samples were tentatively classified as taken from areas of primary disturbance (i.e. inside furrows) based on video taken at the time of sampling. For ease of interpretation, only macrofaunal abundances are discussed. The major difference seen in samples taken from within furrows was an overall greater (10%) decline in average abundance of individual species compared with the average effect. Approximately 75% of shared species (between average and maximum effect samples) showed greater average declines in abundance within furrows compared with the average effect. There was a significant increase (109%) in average body weight of macrofauna immediately after dredging when only those samples taken inside dredge furrows were included (ANOVA, $p < 0.05$). While there was a significant decline in average abundance of *O. sarsi* inside dredge furrows (9.5–5.7 individuals), there was no change in abundance of *E. parma*.

Target species. Although not statistically significant, average sample biomass and abundance of the four target bivalves combined declined immediately after dredging. Mean sample abundance declined by 22% (50–39 individuals per sample) (Figure 3b) while mean sample biomass declined by 26% (1.3–0.9 kg) (Figure 4b). This

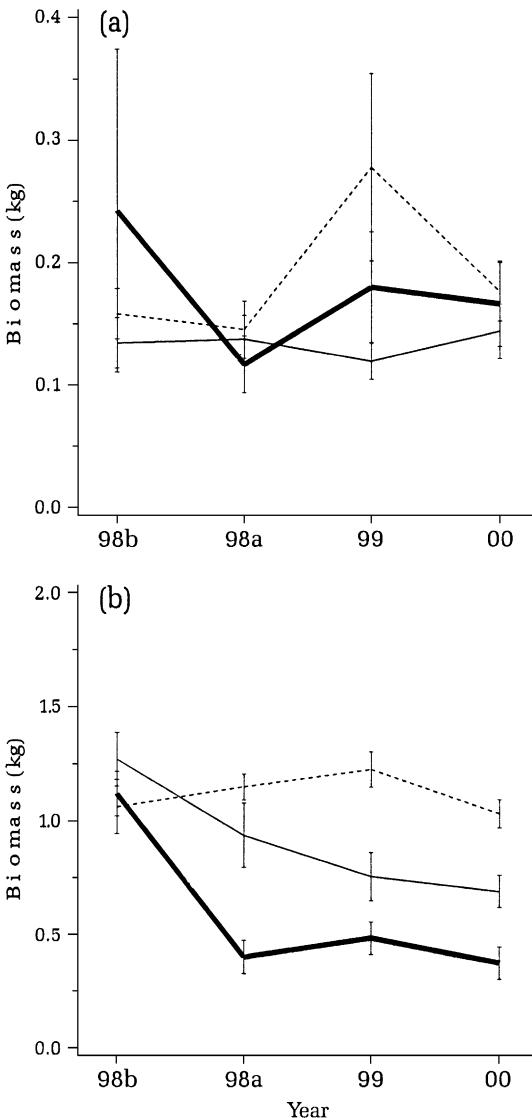


Figure 4. Mean (\pm standard error) biomass over time of non-target (a) and target species (b) per grab sample (0.5 m^2) for the combined reference boxes (----), Dredging Only (—), and Dredging and Discarding (—) boxes.

was largely due to declines in abundance and biomass of propellerclams.

Dredging and Discarding box

Non-target species. An MDS plot based on abundances of non-target species is shown in Figure 7c. While there was a trend for samples taken immediately after dredging to group separately from non-dredged samples, this was not significant due to the variation amongst samples taken after dredging. Reference samples taken before and after dredging were not significantly different (ANOSIM,

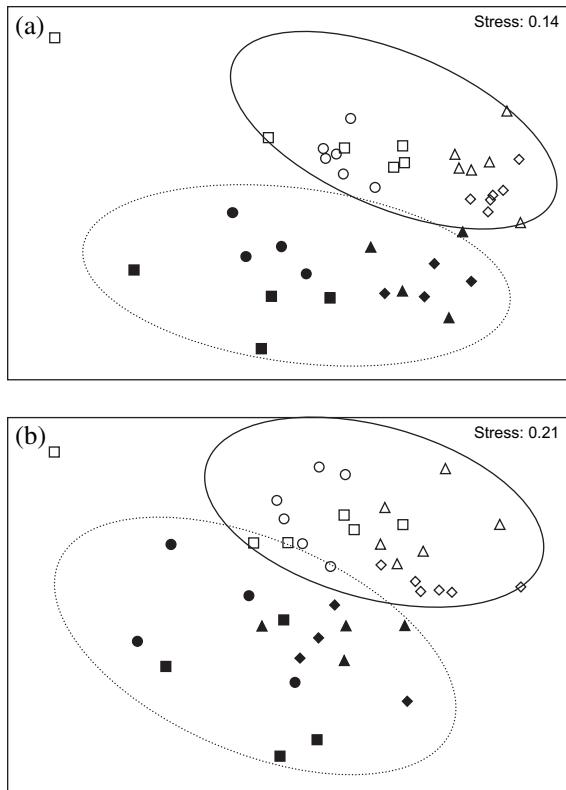


Figure 5. Two-dimensional MDS plot of the North (open symbols) and South (filled symbols) reference box samples based on Bray–Curtis similarity from log₁₀-transformed abundances (a) and biomass (b) of 266 non-target species. Symbols: before dredging (○ ●), immediately after dredging (□ ■), 1 year after dredging (△ ▲), 2 years after dredging (◊ ♦).

$R = 0.052$, $p = 0.145$). Considering only samples taken in the Dredging and Discarding box, a total of 48 species accounted for two-thirds of the cumulative dissimilarity between the two time periods. Of these, 42 species (88%) declined in average abundance immediately after dredging, with an overall average decline of 46%. The majority of species contributing to dissimilarity were polychaetes and micro-crustaceans, although two molluscs (*Cylichna alba*, Mytilidae) and one echinoderm (*Ophiura sarsi*) were included.

Including only ten out of 20 samples that were considered taken from inside furrows, there was a significant reduction in total sample abundance immediately after dredging (ANOVA, $p < 0.05$). Compared with samples taken before dredging, average abundance was 93% lower inside furrows.

An MDS plot based on biomass largely reflected that based on abundance (Figure 7d). Similarly, due to variation between samples taken after dredging, there was no significant difference in average biomass of non-target species before and after dredging (ANOSIM, $p > 0.05$). In the Dredging and Discarding box, a total of 37 out of 53

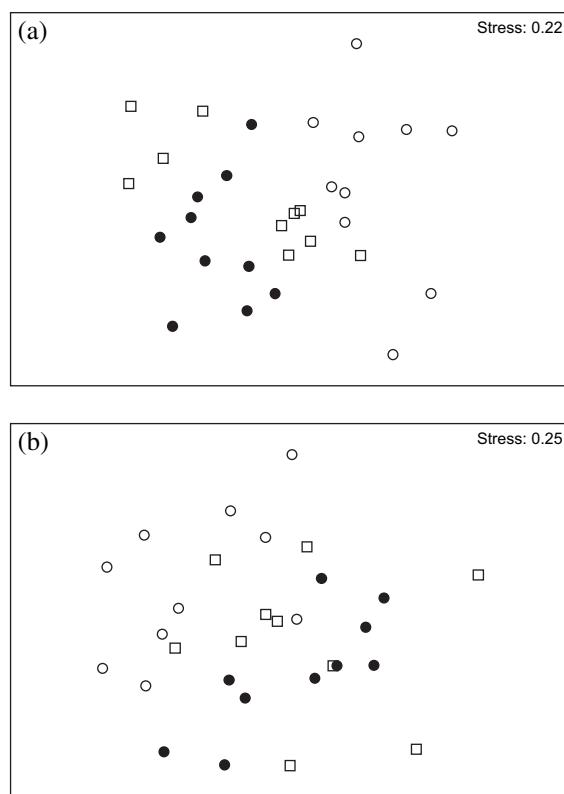


Figure 6. Two-dimensional MDS plot of pre-dredging samples based on Bray–Curtis similarity from log₁₀-transformed abundances (a) and biomass (b) of 266 non-target species. Symbols: reference samples (□), Dredging Only samples (●), Dredging and Discarding samples (○).

species (70%) contributing to two-thirds cumulative dissimilarity between time periods decreased in biomass after dredging, with an overall average decrease of 51%.

Target species. The average combined sample biomass and abundance of the four target bivalves declined significantly immediately after dredging (Table 5). Mean sample abundance declined by 42% (19–11 individuals per sample) (Figure 3b) while mean sample biomass declined by 64% (1.1–0.4 kg) (Figure 4b). These trends were largely due to declines in abundance and biomass of propeller-clams.

One year after dredging (1999)

Dredging Only box

Non-target species. One year after dredging, there was a pronounced increase in total sample abundance of non-target species (Figure 3a). In both the reference and Dredging Only boxes, the average increase was approximately 116%. There was a continuing significant dredging effect on average number of species. Average number of species was significantly lower in Dredging Only samples (62) compared with reference samples (78) (ANOVA, $p < 0.05$) (Figure 2).

An MDS plot of Dredging Only samples based on non-target species abundances is shown in Figure 8a. Samples taken 1 year after dredging were grouped separately from samples taken before dredging (ANOSIM, $R = 0.95$, $p = 0.0001$). SIMPER analysis showed that 54 species contributed to two-thirds cumulative dissimilarity between these time periods, and, of these species, 39 (72%) had increased in average abundance in the intervening year compared with pre-dredging levels with an overall average

Table 4. Estimated biomass (kg) of benthos and fish captured by the dredges in the two experimental dredging boxes and percentage of standing crop of target species removed inside the box boundaries (500 × 100 m).

Taxa	Dredging and Discarding			Dredging Only		
	Biomass captured	Standing crop	% Removed	Biomass captured	Standing crop	% Removed
Arctic surfclam	2 356	13 500	17	1 500	3 900	38
Propellerclam	12 579	96 100	13	5 977	120 000	5
Greenland cockle	1 377	2 200	63	470	1 300	36
Ocean quahog	40	—	—	0	—	—
Echinoderms*	6 059	—	—	5 902	—	—
Non-target molluscs/other invertebrates/fish†	245	—	—	116	—	—
Total	22 656			13 965		

**Echinarchnus parma*, *Ophiura sarsi*, *Ophiopholus aculeata*, *Strongylocentrotus* sp., *Asterias* sp., *Cucumaria frondosa*, *Psolus* sp., burrowing sea cucumbers.

†Buccinidae, Naticidae, *Panomya arctica*, *Gersemia rubiformis*, Ascidiacea, polychaeta, *Aplysia* sp., *Mytilus edulis*, *Musculus niger*, *Chlamys islandica*, *Aphrodita hastate*, grey sole, Cottidae.

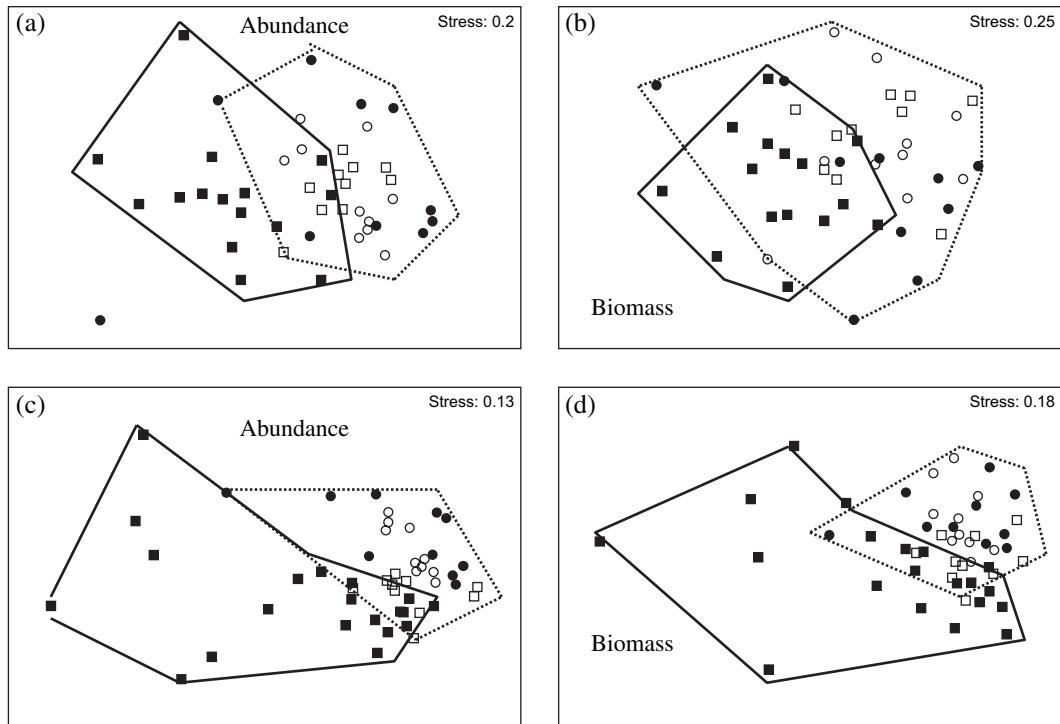


Figure 7. Two-dimensional MDS plot of before and immediately after dredging samples in the dredging boxes based on Bray–Curtis similarity from \log_{10} -transformed abundances and biomass of 266 non-target species. Dredging Only box (a, b), Dredging and Discarding box (c, d). Symbols: reference (○ ●) Dredging boxes (□ ■). Open symbols = 1998 before dredging; filled symbols = 1998 immediately after dredging.

increase of 419%. The majority of these species were polychaetes and micro-crustaceans (mostly amphipods), although the echinoderm *Ophiura sarsi* also increased in abundance by 63%. A total of 15 species (28%), mostly polychaetes, decreased in abundance, by on average, 56%.

Target species. There was a significant dredging effect on sample total biomass of the four target bivalves with average biomass decreasing from 1.27 kg before dredging

Table 5. Summaries of significant immediate dredging effects* based on interaction in the Model A ANOVA showing changes in average sample (0.5 m^2) abundance and biomass ($\alpha = 0.05$).

Treatment	Index	Before dredging	Immediately after	% Change
Dredging Only	Abundance (non-target species)	377	218	-42
Dredging and Discarding	Abundance (target species)	19	11	-42
Dredging and Discarding	Biomass (kg) (target species)	1.12	0.4	-64

*Includes samples taken inside and outside of dredge furrows.

to 0.75 kg 1 year after dredging (Figure 4b) (Table 6). Much of this decrease was attributed to declines in biomass of propellerclams. Both average biomass and abundance had declined further compared with immediately after dredging (Figures 3b and 4b).

Dredging and Discarding box

Non-target species. Similar to the Dredging Only box, average sample biomass of non-target species showed no significant change from before dredging to 1 year after dredging (Figure 4a) while average body weight was significantly lower 1 year after dredging (ANOVA, $p < 0.05$). There was a significant dredging effect on average total abundance of non-target species, with an increase from 568 individuals before dredging to 1503 individuals 1 year after dredging (Figure 3a) (Table 6). In the ANOVA, there was a significant effect of time on number of species with a greater number of species, 1 year after dredging compared with before dredging (Figure 2).

An MDS plot based on non-target macrofaunal abundances showed significant separation between samples collected before dredging and 1 year after dredging (ANOSIM, $R = 0.787$, $p = 0.001$) (Figure 8b). A total of 57 species (mostly polychaetes and micro-crustaceans)

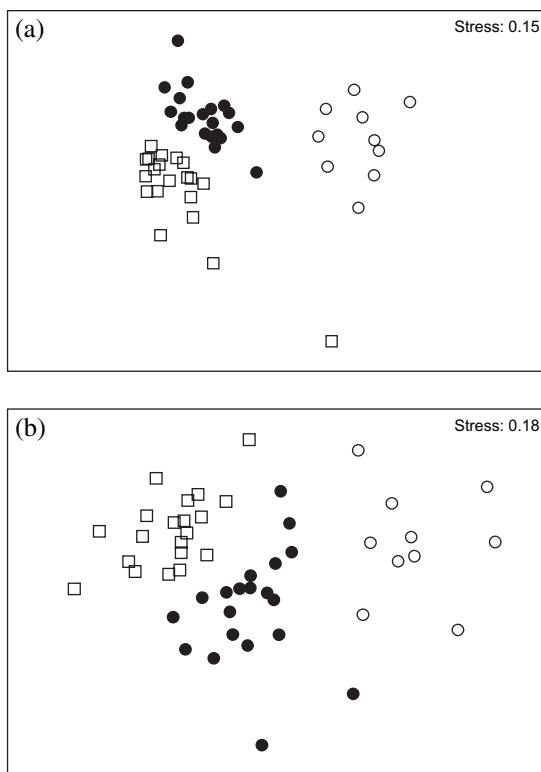


Figure 8. Two-dimensional MDS plot of samples taken before dredging (○), 1 year after dredging (●) and 2 years after dredging (□) based on Bray–Curtis similarity from \log_{10} -transformed abundances of 266 non-target species. (a) Dredging Only (b) Dredging and Discarding.

contributed to two-thirds cumulative dissimilarity between the time periods, with 43 species (75%) increasing in abundance with an overall average increase of 284%. A total of 14 species (25%) decreased in abundance, with an average decrease of 48%.

Target species. There was a continuing significant dredging effect on the target species, with reductions in average abundance and biomass of 58% compared with before

dredging (Figures 3b and 4b) (Table 6). Similar to the Dredging Only box, this was largely due to declines in abundance and biomass of propellerclams.

Two years after dredging (2000)

Dredging Only box

Non-target species. Average sample total abundance of non-target species increased from 815 individuals 1 year after dredging, to 1391 individuals 2 years after dredging (Figure 3a). This was largely due to dramatic increases in abundance of the spionid polychaete *Spiophanes bombyx*. This trend was largely matched in the reference boxes (Figure 9). In the Dredging Only box, *S. bombyx* had increased in average abundance tenfold, i.e. from 60 individuals before dredging to 678 individuals 2 years after dredging. There was a significant time effect in the Model B ANOVA, with average body weight decreasing and number of species increasing 2 years after dredging (Figure 2).

An MDS plot of samples based on non-target species abundances shows that samples collected 2 years after dredging were significantly different from samples taken before dredging in 1998 (ANOSIM, $R = 0.858$, $p = 0.001$) and 1 year after dredging in 1999 (ANOSIM, $R = 0.599$, $p = 0.001$) (Figure 8a). Comparing the 1998 and 2000 samples, a total of 51 species (mostly polychaetes and arthropods) contributed to two-thirds cumulative dissimilarity between these time periods. Of these, 35 species (69%) had higher average abundances 2 years after dredging compared with before dredging, with an average increase in the abundance of these species of 600%. A total of 16 species (polychaetes, oligochaetes, amphipods) (31%) decreased in abundance, although the overall average change (−54%) was much lower in this group than in those species that increased in abundance.

The k-dominance curves, showing proportional contribution of each non-target species to the overall population density in the Dredging Only box, are shown in Figure 10. Before dredging, the k-dominance curve was relatively steep, with the most abundant species, *Spiophanes bombyx*, accounting for approximately 16% of total macrofaunal

Table 6. Summary of significant longer-term dredging effects based on interaction in the Model B ANOVA showing changes in average sample (0.5 m^2) abundance and biomass 1 and 2 years after dredging compared with before dredging ($\alpha = 0.05$).

Treatment	Index	1998	1999	% Change (1998–1999)	2000	% Change (1998–2000)
Dredging Only	Biomass (kg) (target species)	1.27	0.75	−41	0.69	−46
Dredging and Discarding	Abundance (non-target species)	568	1 503	+165	3 506	+517
	(target species)	19	8	−58	7	−63
	Biomass (kg) (target species)	1.12	0.48	−58	0.37	−67

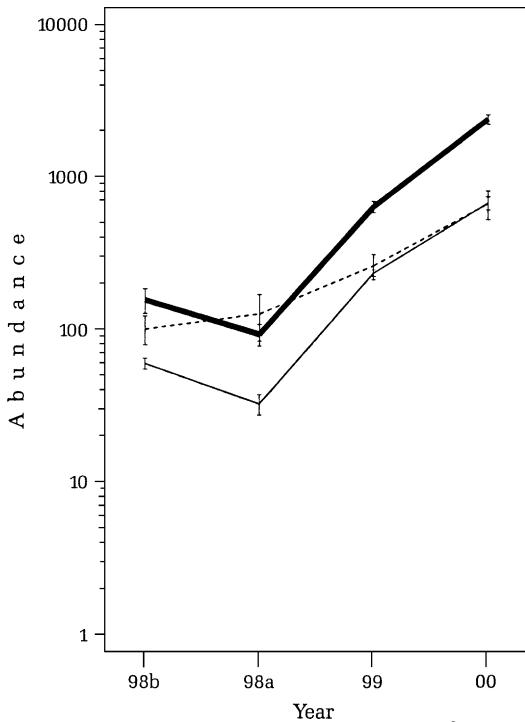


Figure 9. Mean (\pm standard error) abundances (0.5 m^2) over time of the polychaete, *Spiophanes bombyx*, in the dredging treatments. Reference boxes (---), Dredging and Discarding box (—■—), Dredging Only box (—○—).

abundance. A total of 20 species combined to make up 80% of total macrofaunal abundance. In contrast, 2 years after dredging the k-dominance curve was less steep and *S. bombyx* accounted for 49% of total abundance, while 80% of total abundance was attributable to just seven species. It is noted that the k-dominance curves for the reference boxes showed a similar pattern (Figure 10).

Target species. Target species abundance and biomass showed no signs of recovery 2 years after dredging. In particular, average sample biomass was significantly lower than before dredging (~46%) (Figure 4b) (Table 6).

Taxonomic distinctness. Funnel plots of average taxonomic distinctness (Delta+) for samples collected before and 2 years after dredging are shown in Figure 11. Before dredging, 20% of the samples had values of Delta+ that were significantly lower than expected, and this increased to 40% 2 years after dredging (Figure 11a, b). To assist in the interpretation of differences in taxonomic distinctness between groups of samples, it is useful to identify which taxa have contributed most to patterns in Delta+ (Rogers *et al.*, 1999). The number of species belonging to each of the 46 Orders identified in the data set was determined. Before dredging, the arthropod Order Amphipoda had the highest average number of species per sample (11),

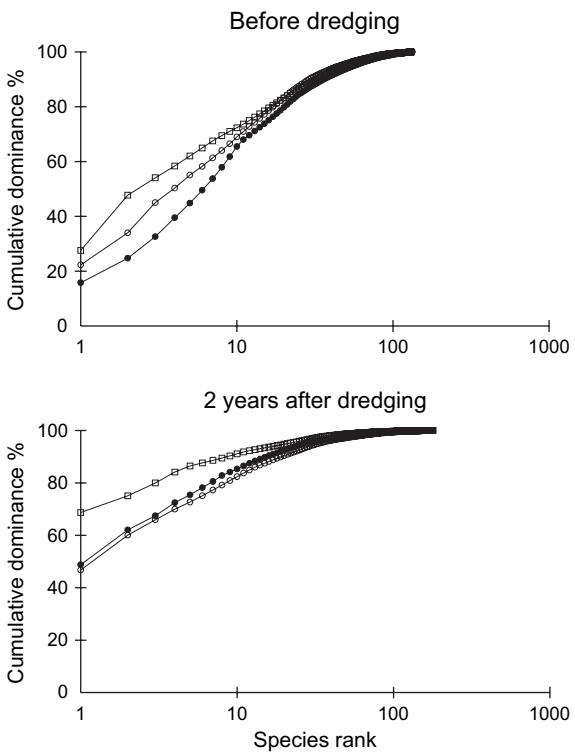


Figure 10. Species k-dominance curves based on pooled sample abundances for the treatment boxes before and 2 years after dredging. Reference (○), Dredging Only (●), Dredging and Discarding (□).

followed by the polychaete Orders Phyllodocida (eight) and Spionida (seven). Most of the remaining Orders had few species. While there were no marked changes 2 years after dredging, there were marginal increases in the number of species per sample for many of the annelid (primarily polychaetes) and arthropod Orders. In particular, the Order Amphipoda showed an average sample increase of four species, while the Phyllodocida increased by two. Also, the Cumacea increased by one species. Orders showing decreases in number of species were the bryozoan Cheliostomata (one) and the cnidarian Thecata (two).

Dredging and Discarding box

Non-target species. Temporal patterns of total sample abundance and biomass of non-target species and number of species in the Dredging and Discarding box were similar to those seen in the Dredging Only box. However, the overall increase in average sample abundance was greater in the Dredging and Discarding box. From before dredging to 2 years after dredging, average sample abundance increased from 568 individuals to 3506 individuals (Figure 3a) and the Model B ANOVA indicated a significant dredging effect on abundance (Table 6). Again, much of this increase was accounted for by the polychaete *S. bombyx* (Figure 9).

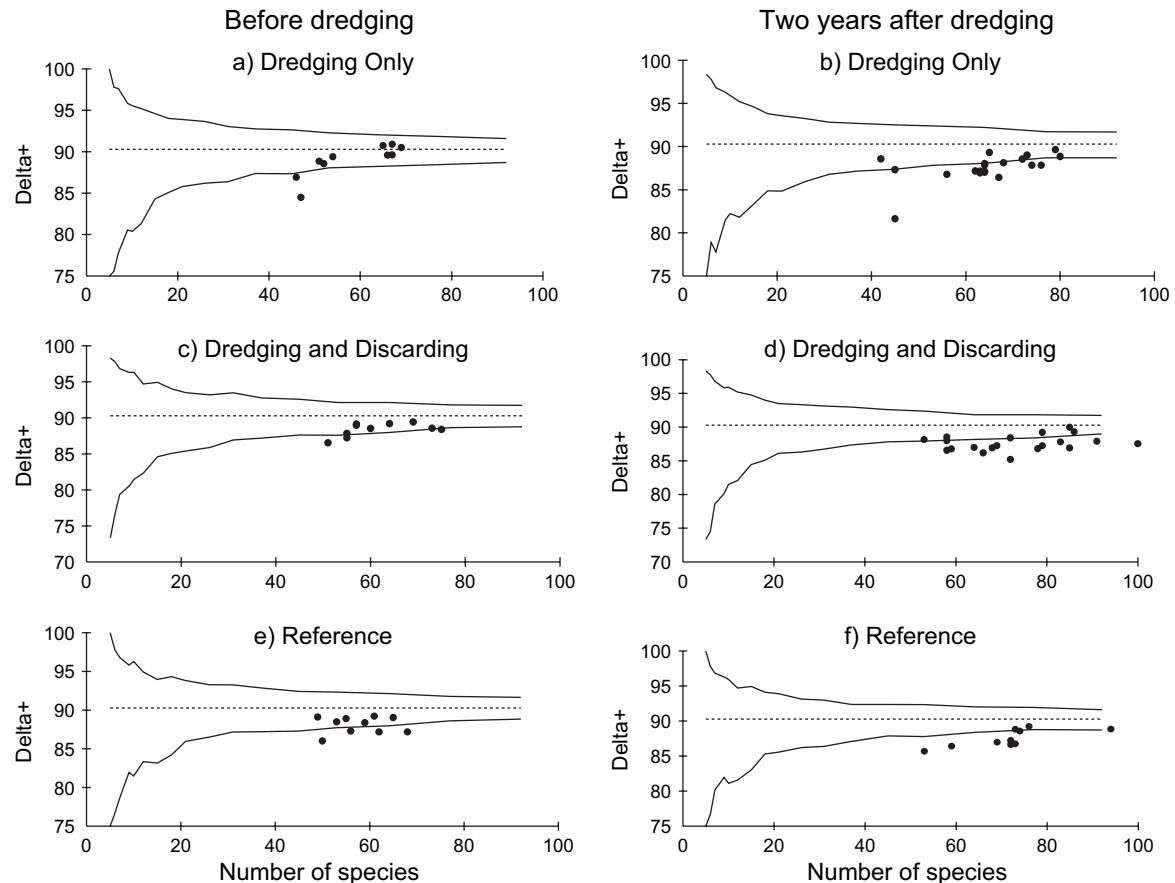


Figure 11. The departure from the theoretical mean taxonomic distinctness ($\Delta+$) (dashed line), and 95% confidence funnel, of macrofauna collected by grab in the experimental boxes before dredging and 2 years after dredging. All values of $\Delta+$ should fall within the confidence funnel assuming that each sample consists of species randomly selected from the total, regional species list.

Compared with an approximately 70% increase in abundance from 1999 to 2000 in the Dredging Only and reference boxes, average abundance increased by 133% in this time period in the Dredging and Discarding box.

An MDS plot based on non-target species abundances showed a similar clear separation of samples taken 2 years after dredging from the two other time periods (Figure 8b). Similar to the Dredging Only box, separation was greatest between the 2-year post-dredging samples and the before dredging samples (ANOSIM, $R = 0.959$, $p = 0.001$). Comparing before dredging and 2-year post-dredging samples, Simper analysis showed that a total of 53 species contributed to two-thirds of the cumulative dissimilarity. The majority of these were polychaetes and microcrustaceans, but also included the echinoderm, *Ophiura sarsi*. Of these species, 74% had increased in average abundance 2 years after dredging with an overall average increase of 916%. In contrast, 26% of the species decreased in abundance with an overall average decrease of 57%.

The k-dominance curve for non-target species before dredging was steep, and *S. bombyx* accounted for 28% of

total macrofaunal abundance, with 17 species accounting for 80% of cumulative abundance (Figure 10). Two years after dredging, the curve was less steep and *S. bombyx* accounted for 69% of total abundance, while only three species accounted for 80% of total abundance.

Target species. Similar to the Dredging Only box, there was no recovery in abundance or biomass of the target species 2 years after dredging (Figures 3b and 4b). However, decreases were greatest in the Dredging and Discarding box, with significant declines in both abundance (63% decline) and biomass (67% decline) (Table 6).

Taxonomic distinctness. Before dredging, 20% of the samples in the Dredging and Discarding box had significantly lower values for $\Delta+$ than expected, and this increased to 65% 2 years after dredging (Figure 11c, d). The longer-term patterns of $\Delta+$ in the reference samples showed a similar pattern to that seen in the dredging treatments and the Dredging and Discarding box in particular (Figure 11e, f). The pattern of distribution of

numbers of species by Order in the Dredging and Discarding box was very similar to that seen in the Dredging Only box. Similarly, patterns of increases and decreases in numbers of species by Order 2 years after dredging were similar between dredging boxes with increases in the Amphipoda, Phyllodocida, and Cumacea of five, three, and two species respectively, while both the Cheilostomata and the Thecata decreased by approximately two species.

Recruitment in the target species. Recruitment of small juveniles (1–16-mm shell length) of the target bivalve species at the experimental site was low over the 3-year period (1998–2000). Out of a total of 180 grab samples collected, total numbers of small juveniles recorded were: *M. polynyma* (15), *C. siliqua* (28), and *S. groenlandicus* (four) (Table 7). No small juveniles of *A. islandica* were observed. Most of the juveniles were >8-mm shell length.

Discussion

Immediate effects of dredging

The experimental hydraulic dredging affected a large number of macrofaunal species. Immediately after dredging in both dredging treatments, the average decrease in species abundance and biomass was typically >40%. Similarly, Hall *et al.* (1990) recorded a non-selective reduction in numbers of all infaunal taxa following suction dredging. On Banquereau, the majority of macrofauna are polychaetes and amphipods. Declines in abundance of these groups were

likely due to a combination of factors including resuspension/advection, and increased levels of predation. Unlike certain large-bodied epifauna (e.g. echinoderms), the dredge did not capture these small macrofauna to any extent. For at least a two-day period following dredging, numbers of flatfish counted in video surveys increased in both dredging boxes (including a fivefold increase in the Dredging and Discarding box). Yellowtail flounder (*Limanda ferruginea*) is one of two common flatfish species on Banquereau, and polychaetes and amphipods are an important part of their diet (Methven, 1999; Link *et al.*, 2002).

As expected, reductions in abundance and biomass of macrofauna were greatest inside dredge furrows compared with the average effect. Nonetheless, at the level of dredging disturbance applied in this experiment (i.e. 53–68% of the seabed covered by furrows), an average effect of dredging was clearly visible in terms of changes to non-target species community structure and reductions in biomass of the target species.

Compared with before dredging, the maximum decrease in biomass of the target bivalves was seen 1 and 2 years after dredging rather than immediately after dredging. Large numbers of damaged and dead propellerclams were observed lying on the seabed immediately after dredging, in video and still photographs. These would have been available for capture by the grab and included in the biomass estimates. In the case of the biomass dominant *C. siliqua*, 50–60% of individuals sampled by grab immediately after dredging in the dredging boxes had potentially lethal injuries compared with 11–17% of individuals collected

Table 7. Numbers of small juvenile Arctic surfclams (*M. polynyma*), propellerclams (*C. siliqua*), and Greenland cockles (*S. groenlandicus*) collected in 0.5-m² grab samples (n) in the treatment boxes over the 3-year duration of the experiment; 98 (before dredging 1998), 98a (immediately after dredging 1998), 99 (1 year after dredging 1999), 00 (2 years after dredging 2000).

Shell length (mm)	Species	Reference (n = 40)			Dredging and Discarding (n = 70)			Dredging Only (n = 70)			
		98	98a	99	98	98a	99	00	98	98a	99
1–2	<i>M. polynyma</i>			1							1
2.1–4	<i>M. polynyma</i>		1			1					
	<i>C. siliqua</i>										1
4.1–6	<i>C. siliqua</i>						1				
6.1–8	<i>M. polynyma</i>			1					1		
	<i>C. siliqua</i>							1	1		1
8.1–10	<i>M. polynyma</i>					1	2				1
	<i>C. siliqua</i>					1	1				1
10.1–12	<i>M. polynyma</i>	1				2	1				1
	<i>C. siliqua</i>		1		2	1	1				1
	<i>S. groenlandicus</i>									1	1
12.1–14	<i>M. polynyma</i>						1	1		1	
	<i>C. siliqua</i>	1		2		1	2	1		2	
	<i>S. groenlandicus</i>			1						1	
14.1–16	<i>C. siliqua</i>						2				

before dredging (Figure 12). This was largely substantiated when, 1 year after dredging, many of these whole clams had transformed into empty shells based on video surveys.

Recovery of macrofauna

While recognition of the point of recovery of impacted benthic communities should be a component of ecosystem-based fisheries management, in practice it may be difficult to implement. A fundamental problem relates to the definition of recovery. For instance, currently there are no standard recovery reference points for metrics of population or community status (see Rice, 2000, for a review of commonly used metrics). One challenge is to measure and show convincingly when recovery has reached an equilibrium state within continuously changing ecosystems (Ellis, 2003). The process of “recovery” following environmental disturbance has been defined as a succession of species, which progresses towards a community that is similar in numbers of species, abundance of individuals, and biomass (SAB) to that previously present (see Newell *et al.*, 1998). Newell *et al.* (1998) suggest that the point of recovery is when a community is capable of self-maintenance and in which at least 80% of the species diversity and biomass has

been restored, although no rationale is given for this benchmark. Ellis (2003) defines “biodiversity recovery” as the start of sustainable ecological succession, in which there is interannual persistence of a select number of macrofaunal species following a disturbance.

Rosenberg (2001) states that there are general patterns to trajectories of structural changes in marine benthic communities following different environmental disturbances which are predictable and follow SAB models developed by Pearson and Rosenberg (1978) and Rhoads and Germano (1986). In contrast to the generic model whereby numbers of individuals, fuelled by opportunists, increase dramatically following a disturbance, only to crash within 1–2 years, numbers of individuals in the Banquereau dredging boxes continued to increase dramatically 2 years after dredging while the total number of species increased marginally over the 3-year period (Figure 13). This trend was also reflected in the k-dominance curves, which showed moderate numerical dominance (50% of total abundance) by *S. bombyx* in the Dredging Only box and strong dominance (70%) by this species in the Dredging and Discarding box. In undisturbed habitats, each species makes a relatively small contribution to overall population density, whereas disturbed communities can

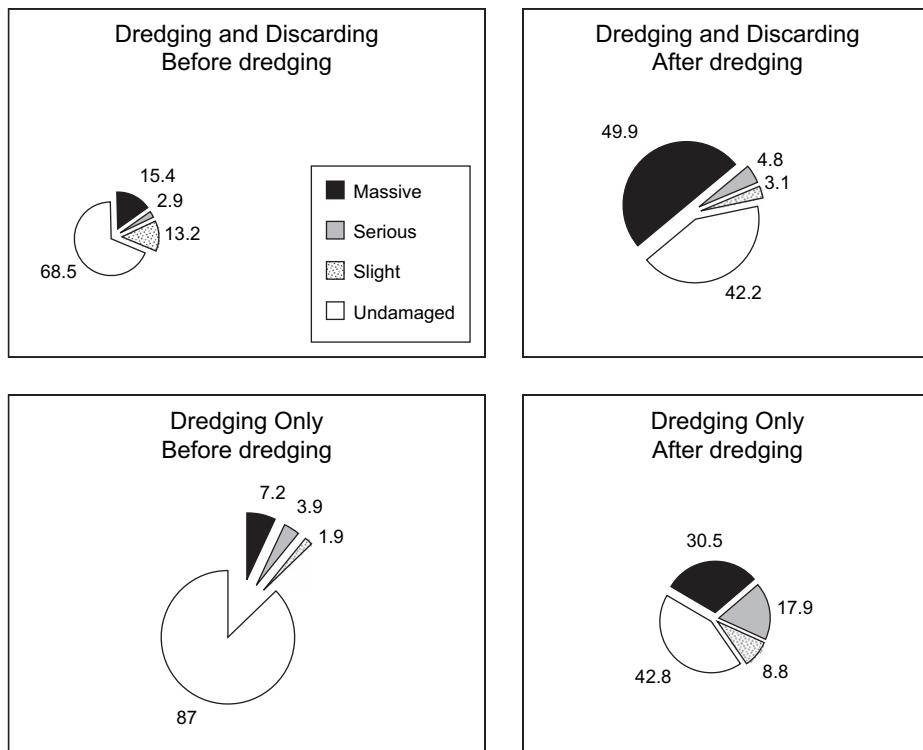


Figure 12. Percentage frequency of occurrence of physical damage categories recorded for *Cyrtodaria siliqua* collected by grab in the dredging boxes before dredging and immediately after dredging. Damage categories: massive – lethal damage involving severing, evisceration or complete crushing; serious – possibly lethal involving cracked shells or exposed tissue laceration (e.g. siphon); slight – likely non-lethal involving a scratch or chipped valve; undamaged – no visible signs of external damage to the shell or exposed tissues.

become numerically dominated by one or two opportunistic species (see Lambshead *et al.*, 1983; Warwick, 1986). It is apparent therefore, that the non-target macrofaunal community changed considerably over a 2-year post-dredging period, relative to before dredging, largely due to the increased abundance of a large number of small-bodied taxa (polychaetes, crustaceans). Populations of non-target species had shifted to higher levels of abundance, with no signs of having reached a plateau or equilibrium phase 2 years after dredging. Non-target species responsible for this are listed in Table 8. Four basic trends in abundance were identified:

- (i) *Large increases in abundance (> 100%) over 2 years following dredging.* Species in this group included the polychaetes *Euchone papillosa* and *Spiophanes bombyx*. Both are classified as sedentary tube-dwellers. In particular, populations of *S. bombyx* continued to increase 2 years after dredging. This was most

dramatic in the Dredging and Discarding box, where average densities of this species increased from 155 to 2406 individuals per 0.5 m^2 . The greater increase in abundance of this species seen in the Dredging and Discarding box may have been due partly to the higher initial densities of this species in this box than in the Dredging Only box. This species is a known opportunist, exploiting sediments that have been disturbed (Pearson and Rosenberg, 1978; Van Dalfsen and Essink, 2001). On Dogger Bank (in the southern central North Sea) the abundance of *S. bombyx* increased notably between the 1950s and late 1980s, and it was speculated that this was in response to environmental change and anthropogenic impacts, including fisheries impacts (Kröncke, 1990). Four amphipod species (*C. crassicornis*, *Unciola* spp., *L. pinguis*, and *S. crenulata*) also belong to this group. *Syrrhoe crenulata* is free-living while the other species are mobile tube-dwellers.

- (ii) *Greatest increase in abundance seen 1 year after dredging.* Three polychaetes (unidentified juvenile sabellids, *Capitella capitata*, *Chaetozone setosa*), three amphipods (*A. macrocephala*, *Anonyx* spp., *P. holboelli*), and two cumaceans (*D. sculpta*, *E. deformis*) constituted this group. Both *C. capitata* and *C. setosa* are regarded as opportunists and *C. capitata*, in particular, is able to respond to disturbance at any time of the year through a very flexible reproductive strategy that includes year-round breeding (Grassle and Grassle, 1974; Warren, 1976; Tsutsumi and Kikuchi, 1984; Mendez *et al.*, 1997). Similarly, *A. macrocephala* is known as a colonizer of areas that have undergone faunal reductions (Mills, 1969; McCall, 1977). It is often dominant in areas frequented by bottom-feeding grey whales, which target dense tube mats of this species (Oliver *et al.*, 1984). The genus *Anonyx* comprises species that are scavengers/carnivores, which also thrive in physically disturbed habitats (Oliver *et al.*, 1984).

- (iii) *Greatest increase in abundance seen 2 years after dredging.* The brittlestar, *Ophiura sarsi*, increased in abundance in both dredging boxes over the course of the experiment, with the largest increases seen 2 years after dredging. This was a result of adult immigration rather than larval recruitment. The source of attraction and retention of adult *O. sarsi* in the experimental area is not known, although it may be linked to increased food supply. This species is a mobile scavenger, and individuals were seen in photographs taken two weeks after dredging apparently feeding on tissue of exposed, damaged propellerclams. An examination of the stomach contents of several *O. sarsi* collected from the dredged boxes showed that their prey included *S. bombyx*, which, as previously discussed, had greatly increased in abundance at the experimental site. Brittlestars have been observed in large

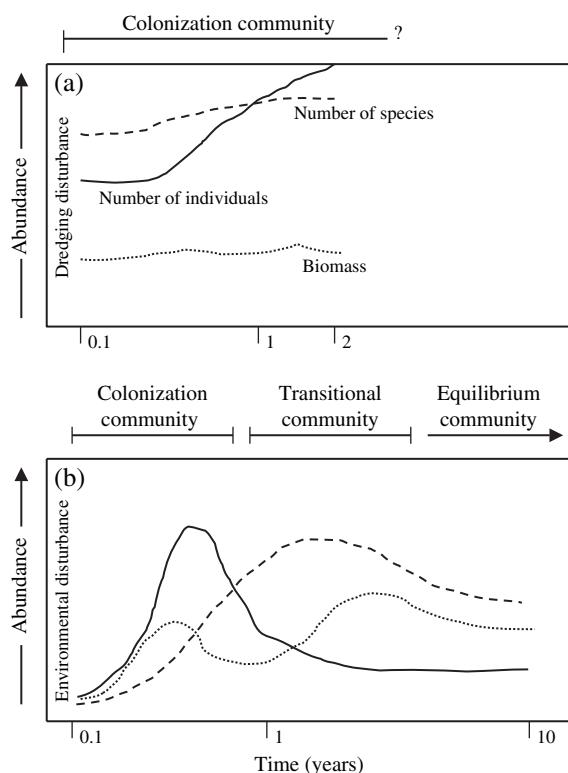


Figure 13. Schematic diagrams for recolonization trajectories for benthic communities following environmental disturbance. (a) Banquereau experimental dredging boxes. (b) General model for benthic communities (after Pearson and Rosenberg, 1978). Colonization community = Group I species comprised mainly of r-strategist opportunistic species; equilibrium community = Group III species including larger, slow-growing k-strategist species; transitional community = Group II species intermediate in life history strategies between Groups II and III (after McCall, 1977).

Table 8. Post-dredging annual changes in abundance of dominant non-target species. (+) Increase (-) decrease; large and small symbols represent changes in abundance >100% and <100%, respectively; Dredging and Discarding (DD), Dredging Only (Dr), combined reference (R); (99) 1998 before dredging to 1999; (00) 1999–2000.

Family/species	Feeding	Ecology	R	DD		Dr		R	
				99	00	99	00	99	00
Polychaeta									
Sabellidae									
<i>Euchone papillosa</i> (M. Sars, 1851)	S,D	T,S	P,A	+	+	+	+	+	+
Juveniles (unident.)	S,D	T,S		+	-	+	-	+	-
Spionidae									
<i>Spiophanes bombyx</i> (Claparède, 1870)	D,S	T,S	P	+	+	+	+	+	+
<i>Spio filicornis</i> (O.F. Müller, 1776)	D,S	T,S?	P	+	+	+	+	+	+
<i>Prionospio steenstrupi</i> (Malmgren, 1867)	D,S?	T,S	P	-	-	+	-	-	-
<i>Polydora concharum</i> (Verrill, 1880)	S?	B*	P	+	-	-	-	+	-
Nephtyidae									
Juveniles (unident.)	C	B,F		+	+	+	+	+	+
Pectinariidae									
<i>Pectinaria granulata</i> (Linnaeus, 1767)	D	T,S	P	+	+	+	-	+	+
Capitellidae									
<i>Capitella capitata</i> (Fabricius, 1780)	D	B,T	D,P	+	+	+	+	+	+
<i>Mediomastus ambiseta</i> (Hartman, 1947)	D	T,S?	D,P	-	-	+	-	+	-
Pholidae									
<i>Pholoe tecta</i> (Stimpson, 1854)	C	F	P	-	+	-	+	+	-
Cirratulidae									
<i>Chaetozone setosa</i> (Malmgren, 1867)	D	B,F	D,P	+	-	+	-	+	-
Oweniidae									
<i>Owenia fusiformis</i> (delle Chiaje, 1841)	S,D	T,S?	P,A?	+	-	-	-	+	-
Pyllodocidae									
<i>Phyllocoete mucosa</i> (Oersted, 1843)	C	F	P	+	+	+	+	+	+
<i>P. maculata</i> (Linnaeus, 1767)	C	F	P	+	+	-	+	+	-
Maldanidae									
<i>Petaloprotus tenuis</i> (Theel, 1879)	D?	T,S?	D	-	-	-	-	-	+
Ampharetidae									
<i>Asabellides siberica</i> (Wiren, 1883)	D	T,S?	D	-	+	-	-	-	-
Amphipoda									
Corophiidae									
<i>Corophium crassicornis</i> (Bruzelius, 1859)	G,S	T,M	D	+	+	+	+	+	+

Table 8 (continued)

Family/species	Feeding	Ecology	R	DD		Dr		R	
				99	00	99	00	99	00
<i>Unciola</i> spp. (Say, 1818)	G,S	T,M	D	+	+	+	+	+	+
Aoridae									
<i>Leptocheirus pinguis</i> (Stimpson, 1853)	S,G?	T,M	D	+	+	+	+	+	+
Ampeliscidae									
<i>Ampelisca macrocephala</i> (Lilljeborg, 1852)	S,D	T,M	D	+	+	+	+	+	+
<i>Protomediea fasciata</i> (Kroyer, 1842)	S?D?	T?	D	+	+	+	-	+	-
Lysianassidae									
<i>Anonyx</i> spp. (Kroyer, 1838)	Sc,C	F,M	D	+	+	+	-	+	-
Synopiidae									
<i>Syrhoe crenulata</i> (Goes, 1866)	?	?	?	+	+	+	+	+	-
Phoxocephalidae									
<i>Phoxocephalus holboelli</i> (Kröyer, 1842)	S,G	F,B	D	+	-	+	-	+	-
Haustoriidae									
<i>Priscillina armata</i> (Boeck, 1861)	S,Dr	F,M	D	+	-	+	+	+	+
Isaeidae									
<i>Erithonius rubricornis</i> (Stimpson, 1853)	Dr	T	?	+	-	-	+	+	-
Cumacea									
Diastyidae									
<i>Diastylis sculpta</i> (Sars, 1871)	S,Dr	F,B	D	+	+	+	-	+	+
Lampropidae									
<i>Lamprops fuscata</i> (Sars, 1865)	S,Dr	F,B	D	+	+	+	-	+	+
Leuconidae									
<i>Eudorellopsis deformis</i> (Kroyer, 1846)	S,Dr	F,B	D	+	+	+	-	+	-
Isopoda									
Idoteidae									
<i>Synidotea marmorata</i> (Packard, 1867)	C	F,M	D	+	+	+	-	+	+
Nemertea									
	C	F,M	D,P,A	+	-	+	-	+	-
Echinodermata									
Ophiolepididae									
<i>Ophiura sarsi</i> (Lutken, 1855)	Sc,C	F,M	P	+	+	+	+	+	+

Feeding: S – suspension; D – deposit; C – carnivorous; G – grazer; Sc – scavenger; Dr – detritivore. Ecology: T – tube-dweller; F – free living; B – burrower or occupying burrows; S – sedentary; M – mobile. R (Reproductive mode): P – planktotrophic; D – direct; A – asexual. * – in mollusc shells.

numbers in trawl tracks in Monterey Bay and in ice scours in the Canadian Arctic (see Engel and Kvitek, 1998).

- (iv) *Species that decreased in abundance over time.* This group comprised four species of polychaetes (*P. steenstrupi*, *P. concharum*, *M. ambiseta*, and *A. siberica*).

It is apparent that macrofaunal communities within the dredging boxes were still in the colonizing phase 2 years after dredging. It is noted that 48% of the species that showed relatively large post-dredging increases in abundance are relatively sedentary deposit-feeding tube-dwellers (Table 8). In general, Group I species (i.e. opportunists) characterizing successions are relatively immobile tube-dwellers and, typically, deposit-feeders (McCall, 1977). Spionid tube lawns or beds have been reported as very dense aggregations of up to 40 000 individuals m⁻² (Noji and Noji, 1991; Sisson et al., 2002). Although densities of *S. bombyx* at the experimental site did not approach this level, densities in the Dredging and Discarding box had increased to approximately 5000 m⁻² 2 years after dredging. The rate of increase in the second year (27%) was only slightly lower than in the first year (31%). There were also corresponding increased densities of polychaete tubes counted in still photographs (Gilkinson et al., 2003). Tubeworms at high densities can stabilize sediments against erosion (Eckman, 1985; Friedrichs et al., 2000) and can function as keystone resource modifiers through organic matter digenesis (Holte, 2001; Sisson et al., 2002). Dense spionid populations usually condition and improve disturbed sediments for future recolonization, and also, represent a source of food for flatfish (see Noji and Noji, 1991, and references therein). Polychaete tube beds can have positive effects on species richness and abundance and can enhance bivalve spat settlement (Zühlke et al., 1998; Bolam and Fernandes, 2002). It is also possible that *S. bombyx* could reach densities that would constitute “super-dominance” (*sensu* Holte), resulting in negative density-dependent interactions with other competing species.

A key objective of this experiment was to study rates of recovery of macrofaunal communities following hydraulic dredging. While the colonizing phase was observed in the non-target species, it is obvious that recovery is a much longer process in the case of the target bivalves. Unlike the population increases witnessed in the non-target species, there were no signs of recovery in these equilibrium species. It has been suggested that more attention should be placed on effects on equilibrium species rather than on opportunists (Boesch et al., 1976). The propellerclam *Cyrtodaria siliqua* was biomass dominant in the study area, and dredging reduced the average sample biomass of this species by up to 50% of pre-dredging levels. Although the maximum removal of *C. siliqua* by the dredges was only 13% of total standing

crop, this estimate was based on a subsample volume of <10%, which could have had a large associated sampling error (see Heales et al., 2003). Also, this estimate did not take into account mortality of clams left on the seabed, which was relatively high (based on recorded levels of physical damage). Although growth rates for *C. siliqua* are unknown, it is expected that it will take several more years before recovery is seen in this species. For the primary target species, *Mactromeris polynyma*, the industry applies a 10-year rule-of-thumb for returning to areas previously dredged, based on growth to commercial size. However, rates of recovery could be longer and temporally and spatially variable given the variability in successful recruitment in marine bivalve populations (Chintala and Grassle, 2001; Amaro et al., 2003; Maximovich and Guerassimova, 2003). This was quite apparent over the 3-year duration of the experiment, recruitment of the target species appearing to be very low if based on the scarcity of small juveniles (1–16-mm shell length).

Rates of recovery of macrofaunal communities following environmental disturbances will depend on habitat type and the extent of defaunation, among other factors. For instance, in coarser sediments (e.g. sands, gravels), with long-lived k-selected species, succession is held at the transitional phase longer than in finer sediments (Newell et al., 1998). In general, recovery rates can be significantly longer in cases of complete defauna relative to partial defauna (see Newell et al., 1998). Based on the proportion of seabed directly impacted by the dredges at the Banquereau site (53–68%), recolonization proceeded from a point of partial defauna, meaning that local recruitment could have contributed to recolonization.

Trends in abundance of non-target species witnessed in the dredging boxes 1 and 2 years after dredging were largely mirrored in the reference boxes. It is noted that there were no initial declines in species abundances in the reference boxes following dredging and, based on video surveys, the reference boxes were not affected by secondary disturbance (e.g. sedimentation, discards).

There are several possible explanations for the observed patterns of increasing abundance over time of non-target species in both the Dredging and reference boxes: (i) temporal increases in abundance were not a dredging effect, but represented natural population increases over large spatial scales; (ii) temporal increases were entirely due to dredging; or (iii) increases in abundance occurred through a combination of natural increases and dredging effects. We consider (iii) to be the most plausible. Using the example of *S. bombyx*, while a longer-term dredging effect could not be detected in the ANOVA due to coincidental similar increases in the reference boxes, a significant dredging effect was detected in the Dredging and Discarding box. As previously noted, the large increases in abundance of spionid polychaetes seen after dredging on Banquereau represent a general response to various environmental

disturbances, including anoxic events, dredging for aggregates, and storms (Rachor and Gerlach, 1978; Kröncke, 1990; Niermann *et al.*, 1990; Harvey *et al.*, 1998; Van Dalfsen *et al.*, 2000; Van Dalfsen and Essink, 2001). In those studies, following initial declines in abundance after the disturbance, most polychaete taxa recovered (in terms of abundance), typically within 1 year.

The similar response by species of polychaetes and amphipods in the reference boxes to that seen in the dredging boxes 1 year after dredging may be indicative of a larger-scale response to dredging, extending beyond the boundaries of the dredging boxes. The mechanism for this may be a combination of heightened reproductive activity within the dredged areas (i.e. in response to disturbance) with dispersal of larvae over a wider area, combined with external recruitment. Alternatively, the increases witnessed in the reference boxes may represent a natural recruitment event(s) within the general study area. At different locations, within restricted areas, time-series of abundance of many macrofaunal species often show synchronized patterns of abundance (Beukema *et al.*, 1996). In a 25-year time-series from the German Bight, Ziegelmeyer (1978) demonstrated relatively synchronous temporal fluctuations in abundance of *S. bombyx* at sites that were separated by several kilometres.

Increasingly, ecologists are faced with the task of predicting the functional consequences associated with structural changes in benthic communities resulting from anthropogenic impacts. Presently, our ability to address this is limited given the complexity of ecosystems and our limited knowledge of component species and their interactions. As a consequence, it is difficult to predict the effects of removing a large portion of benthic biomass and/or changing the species composition or abundance patterns of a myriad of species. Numerous k-selected equilibrium species (e.g. infaunal bivalves) are recognized now as ecosystem engineers. Arguably, there is a stronger theoretical framework for predicting the effects of removing ecosystem engineers and their associated biogenic structures compared with predicting the effects of changes in relative abundance of a large number of species. Through the creation of large burrows and elevated burrow openings, *C. siliqua* creates structural complexity in low-relief unconsolidated sediments and is an ecosystem engineer (see Jones *et al.*, 1994; Coleman and Williams, 2002). This species has a high *per capita* impact since it occurs at high densities over large areas and is long-lived. Through their burrows, propellerclams may play a key role in determining the biogeochemical properties of a seabed (see Aller, 1988). Also, given their high densities they may have significant effects on other species, including a role in the settlement success of benthic larvae and as competitors for food of other suspension-feeders. Therefore, the substantial removal of these ecosystem engineers, which will take a long time to recover, could be an important impact, which was not investigated in our experiment.

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