

A small hotspot of benthic biodiversity on the northwest Atlantic continental shelf

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Abstract

The northern edge of Georges Bank supports a highly productive and diverse benthic community. Our study area is the gravel pavement on the Canadian side of Georges Bank in water depths of 72-90 m. This area has been surveyed periodically by Canadian and U.S. researchers because of its importance as fish and scallop habitat. On joint cruises from 1994 to 2005, the substrate has been characterized with side-scan and single-beam sonar. Site-specific sampling has been conducted with photo/video transects, and benthic samplers. Much of the gravel habitat over thousands of square kilometers is disturbed by bottom fishing gear and exhibits relatively low biodiversity. However, in some small areas the gravel has a biogenic covering of colonial epifauna and exhibits high benthic diversity. In one 14 km² area, dubbed the “mussel bed”, the substrate is almost completely covered with hydroid and bryozoan colonies. This epifaunal habitat contains the highest numerical abundance, biomass, and species richness of benthic megafauna that we have observed on Georges Bank. High benthic productivity in this area is fueled by upwelled waters from the Gulf of Maine. The shelf-edge front moves over the northern edge of the bank such that the water column is well mixed in winter and stratified in summer. The gravel substrate is undisturbed by winter storms, thus providing a stable substrate for mussel and epifaunal growth. This benthic community is vulnerable to potential oil and gas development, bottom-fishing disturbance, and to colonization by invasive species.

Keywords: benthic biodiversity, colonial epifauna, Georges Bank, outer continental shelf

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Introduction

The continental shelf occupies a large fraction of the area within the EEZs of ICES member countries and other nations. Mixing of the water column above the continental shelf retains nutrients in the euphotic zone, leading to higher biological production than in the adjacent open ocean (Kaiser *et al.* 2005). Benthic-pelagic coupling enhances benthic production and the benthic consumers.

Owing to the vastness of the continental shelf, detailed mapping and fine-scale surveys have been made only in selected areas. The continental shelves produce 20% of the global marine fish catch and, because of this importance, much of the biological information comes from fisheries surveys. The continental shelf is also the site of oil exploration and production; and benthic surveys have been conducted to monitor the potential impacts of the oil and gas industries (e.g. Battelle & WHOI 1985). More recently, areas of the continental shelf have been mapped because of their importance as fish habitat (e.g. Wakefield *et al.* 2005), but few studies have focused on biodiversity. Large areas of the northwest Atlantic continental shelf are covered with homogeneous sandy sediments. These habitats are generally expected to support low-diversity communities that are adapted to seasonal disturbance by winter storms.

Georges Bank is a shallow submarine plateau off the east coast of North America (Fig. 1). The center and southern flank of the bank is predominantly sandy sediments. On the northeastern part of the bank strong currents have transported sand into deep water, leaving behind a thin gravel pavement that extends 150 km along the northern edge and covers more than 3000 km² (Valentine & Lough 1989). Biological production is fuelled by nutrient-rich water upwelled from the Gulf of Maine and concentrated by the shelf-edge front, which moves over the northern edge such that the water column is well mixed in winter and stratified in summer.

A synoptic survey of the macrobenthos on Georges Bank was made between 1956 and 1965 (Theroux & Wigley 1998), but the grab sampler used in the study was not well suited to collecting representative samples of the gravel substrate on the northern edge. A systematic survey of benthic epifauna was made on the Canadian side of Georges Bank with a 1-m wide camera-equipped dredge (Thouzeau *et al.* 1991). This study was the first to identify “biogenic” habitats on the northeast part of Georges Bank, which supported high diversity of benthic epifauna. The emergent epifauna (hydroids, bryozoans, and polychaete tubes) create a three-dimensional habitat for benthic invertebrates such as shrimp and brittle stars.

The gravel pavement was identified as an important nursery area for juvenile cod and haddock (Lough *et al.* 1989), which provides abundant invertebrate food and protection from predators. These epifaunal communities are sensitive to bottom fishing with otter trawls and scallop dredges. Spatial comparisons showed that disturbed sites had lower

epifaunal cover and lower abundance, biomass, production and species richness of benthic megafauna (Hermsen *et al.* 2003, Collie *et al.* 2005).

Between 2001 and 2005 three research cruises were conducted by the present authors on northeast Georges Bank. Objectives of these cruises were to map benthic habitats with acoustic and photographic surveys and to characterize the benthic communities with direct sampling. In this study we synthesize the results of these three cruises. Our main objective is to describe the benthic diversity at these sites and to examine the factors responsible for maintaining biodiversity.

Acoustic backscatter from the seabed can reveal differences in the seabed surficial substrates. On the continental shelves in the northwest Atlantic, normal incidence sonar, sidescan sonar, and multibeam acoustic systems can distinguish among sand, gravel, and boulder habitats (Courtney *et al.* 2005, Kostylev *et al.* 2005). In this study we examined backscatter from a normal incidence fisheries acoustic system to determine if there were differences in seabed substrate and epifauna along a 12-km sampling corridor on northern Georges Bank (Fig. 1).

Methods

Sampling

Three cruises were made to northeastern Georges Bank between 2001 and 2005 (Table 1). Two of the study areas (13 and 20) were selected from sidescan sonar surveys conducted in 1994 (Collie *et al.* 1997). The third area, dubbed the mussel bed, was selected in 2002 (Fig. 1).

In October 2001, the *CCGS Hudson* ran a series of five diagonal transects NW to SE in the study area to collect acoustical and optical data. The first line was sampled simultaneously with both normal incidence and sidescan sonar systems. Four lines were sampled with normal incidence acoustic and a towed camera system (Towcam, Gordon *et al.* 2000). These transects were all sampled at approximately 1.3 m s^{-1} (2.5 knots) over 10 to 12 km distances except the first line which spanned 16 km (Fig. 2). Two additional lines were sampled with only the normal incidence acoustic system at speeds of 2.7 m s^{-1} (5.3 knots) and included transects that crossed the diagonal lines as a measure of sampling direction on acoustic backscatter. The backscatter image from the sidescan sonar was used to select eight sampling locations along the study corridor for still photos with a camera system that is lowered to the sea floor (Campod, Gordon *et al.* 2000). The altitude of the Campod was 0.7 m and the field of view measured 37 by 52 cm. Between three and nine still photos (39 total) were taken at each location. Data from the Towcam and sidescan sonar are not presented in this study.

Normal incidence sonar data were collected with a calibrated dual beam 120-kHz Biosonics DTX echosounder. Data were collected at 1 pps with a pulse width of 0.4 ms. The wide beam (17.8°) data were used to estimate backscatter from the seabed. The sonar signals were digitized at a rate of 42 kHz with a 24-bit A/D, yielding a potential 132 dB

of dynamic range; over 70 dB of effective signal range was observed in the data. The raw echo envelope was recorded during the cruise in DT4 format.

On the 2002 and 2005 cruises, photo transects were made with the SEABed Observing and Sampling System (SEABOSS). This system consists of a grab sampler with forward and bottom-looking video cameras and a bottom-looking still camera (Blackwood & Parolski 2001). SEABOSS transects were 15-25 minutes in duration with a still photograph taken at 30-60 sec intervals. These still photos were taken at approximately 0.76 m off the bottom with an approximate field of view of 51 by 76 cm.

Samples of the benthic megafauna were collected with a 1-m Naturalists dredge fitted with a 6.4-mm liner. Tow duration was short (~ 1 min) to avoid overfilling the dredge bag with gravel. Each dredge sample was sorted on deck and all animals placed in trays with sea water. The volume of the remaining gravel was measured by shoveling it into 9-1 pails. One pail full of gravel was sieved over a 5-mm screen as a quality control measure to collect any animals that were missed during the initial sorting process. Scallops were weighed and measured on board. All other animals were preserved in 5% formalin for laboratory analysis.

Analysis

Fishing effort data were extracted from three databases maintained by the Canada Department of Fisheries and Oceans. For the years 1992-2001, we used log book reports from the Zonal Interchange Format (ZIF) database. Data on scallop dredging and bottom trawling are recorded to the closest minute of longitude and latitude. To reconstruct the fishing history of the corridor sampled by the *CCGS Hudson* in 2001, we selected all records of scallop and groundfish effort from 1992-2001 that were located within 1.25 km of the easternmost transect. The coordinates of these fishing locations (which fell on even minutes) were projected perpendicularly to the acoustic transect and converted to distance (km) along transect. Finally, the fishing effort records were binned into 2-km intervals along the transect, recognizing that the precision of the fishing locations is on the order of 1-2 km.

Since 2002, logbook landings by gear type have been recorded at one-minute resolution in the MARFIS database. The two mobile bottom gear types are scallops drags and otter trawls. Fishing locations have also been recorded for scallop draggers carrying satellite vessel monitoring systems (VMS). Scallopers were assumed to be dragging when their vessel speed, as interpolated between successive VMS positions, was between 0 and 6 knots. These fishing positions were aggregated at 0.25, 0.5, and 1 minute resolution.

The raw hydro-acoustic data were converted to volume backscattering strength, Sv, with custom software (Simard *et al.* 2000). Estimates of on-axis (R1) and off-axis (R2) backscatter from the echo envelope followed the methods of Courtney *et al.* (2005). R1 was defined as the mean Sv response in dB within 5° of nadir. R2 was defined as the mean Sv response between 15° and 25° off nadir. These two metrics define the peak and

the width of the specular zone of the scattering model response curve. These metrics are often described as hardness (R1) and roughness (R2) of the seabed, respectively.

The seabed was detected with the bottom pick algorithm using commercial software (QTC IMPACT 2004). To minimize noise associated with ship motion and DGPS error (± 3 m), five consecutive pings were normalized to generate a bottom pick, smoothed with a five-point running average and offset by 5 m to account for the transducer depth relative to the surface. Latitude and longitude were converted into UTM units from which distance (m) between observations was calculated. Relief (rugosity) was calculated as the change in depth (m) between observations standardized to one kilometer horizontal distance (m km⁻¹) following Schneider et al. (1987) and Anderson et al. (2005). Typical distances between observations averaged 6 to 7 m for the slow lines and 13 to 14 m for the faster lines. Rugosity was estimated separately for the slow and fast lines due to the scale-dependent nature of the estimates.

Three types of information were extracted from the bottom photos with a Matlab graphical user interface. The sediment in each photograph was visually categorized as sand, pebble, cobble, or boulder, with size categories corresponding to the Wentworth scale. The dominant sediment categories were designed with a two-letter code in which the first, upper-case letter indicates the sediment category covering more than 50% of the photo and the second, lower-case letter indicates the sediment type covering >20% of the remaining area (Wakefield *et al.* 2005).

The “point count” method was used to measure the percent cover of colonial epifauna. Seventy random dots were superimposed on each photo and the substrate under each dot categorized into five classes: *Filograna* (tubicolous polychaete), Hydroid, Bryozoan, Sponge, and Other (including bare substrate). Empirical confidence intervals were obtained by bootstrapping the random dots. In a test set, 100 random dots were classified for each of 39 Photographs. Bootstrap analysis of these results indicated that the accuracy of the percent cover was acceptable above 50 points, and the precision was not substantially improved beyond 70 points. Finally, free-living animals were identified in each photograph and their locations recorded.

The Naturalist dredge samples were sorted to the lowest taxonomic level possible (generally species) and counted. The wet weight of each taxon was determined (± 1 mg) after blotting. The sample data were normalized by the volume of sediment collected. After being sorted separately, the numbers in the sieved (5 mm) subsample were multiplied by total sediment volume and added to the total sample numbers, to account for animals overlooked during the initial sorting on deck. The species list was screened to identify species (sometimes higher taxonomic levels) that were uniquely and consistently identified. This species list was used to calculate species richness and to perform analyses on the basis of presence/absence data. The species list was further screened to remove species that were not quantitatively sampled by the Naturalist’s dredge, either because they were too small to be consistently retained on the 5-mm sieve, or because they were attached to the substrate.

Univariate indices calculated from the dredge data included abundance, biomass, species richness, and species diversity. After appropriate transformation, the univariate indices were compared among sites with ANOVA. For the significant ANOVAs, multiple comparison tests were used to determine which sites were significantly different.

The multivariate data were square-root transformed to reduce the influence of dominant species. Bray-Curtis similarity was calculated among samples and the samples were ordinated with Multidimensional Scaling (MDS). Analysis of Similarities (ANOSIM) was used to test for significant differences in species composition among samples grouped by site. (Clarke & Warwick 2001). The Similarity of Percentages (SIMPER) routine was used to identify species that contributed most to the similarity within a site and the dissimilarity among sites (Clarke & Warwick 2001).

Results

The study site is on the northern edge of Georges Bank inside of the 100 m contour where waters rapidly deepen to > 200 m (Fig. 1). The 12-km acoustic sampling corridor ranged in depth from 72 m to 90 m with deeper depths occurring at either end (Fig. 2). However, most of the study area (91%) ranged between 72 m to 82 m depth.

Backscatter for R1 (seabed hardness) averaged -22.6 dB and ranged from -61.6 dB to -7.2 dB while R2 (seabed roughness) averaged -86.0 dB and ranged from -101.9 dB to -57.2 dB. Examination of the backscatter data indicated there was a single distribution for both R1 and R2 and no apparent clustering of the data that would indicate classes of backscatter (Fig. 3). There was no large-scale spatial pattern in the distribution of R1 or R2 along the sampling corridor (Fig. 4). In particular, there was no clear distinction between the predominantly Sand/pebble substrate at the NW end of the corridor compared with the Pebble/pebble substrate that occurred over most of the area. However, there was a clear association of the lowest backscatter where *Filograna implexa* occurred in an area that extended for approximately 1.5 km at the SE end of transect (Fig. 4 arrows). This result indicates that the acoustic reflectivity was influenced more by differences in the biota than by the physical substrate; the presence of the dense beds of *F. implexa* had the effect of producing a softer and smoother signal. Backscatter tended to be higher on the western side of the sampling area especially towards the SE end of the corridor. In addition, the east/west crossing lines tended to have higher backscatter than the lines sampled along the corridor. Together these signals indicate there may be some degree of directionality in the seabed structure in an east/west orientation.

Seabed rugosity tended to be lower at the SE end of the corridor where the epifauna was dominated by *F. implexa* and higher at the NW end of the corridor, where epifauna biodiversity was greater (Fig. 5). For the slow lines, rugosity averaged 3.5 m km^{-1} and ranged from 0 to 35.1 m km^{-1} and for the fast lines averaged 3.5 km^{-1} and ranged from 0 to 19.8 m km^{-1} . There was no apparent difference in the spatial distributions of the two estimates.

Several properties were plotted along the eastern-most transect, which extended for 16 km (Fig. 6). Along this transect (NW to SE), the seafloor was relatively flat between km 2-12, ranging between 79 and 86 m depth. Rugosity was highest at the ends of the transect (km 0-2 and 12-16) where the relief and slope were greatest (Fig. 6B). Groundfish and scallop effort had inverse patterns along the transect (Fig. 6C). Groundfish effort was highest at the NW end and generally decreased toward the SE, with a minor peak between km 12 and 14. Scallop dredging effort was very low at the NW end of the transect, and increased toward the SE.

Sediment composition inside the mussel bed was entirely pebble gravel. In many photos, the substrate was obscured by the epifauna, which was a combination of hydroids and bushy bryozoans (Fig. 8). The mussel bed (Fig. 1) is characterized by concentrations of the horse mussel, *Modiolus modiolus*, which attach themselves to the gravel substrate with byssal threads. Most of the shells visible in Fig. 7A are dead *Modiolus* shells. The gravel and shells are covered with a miniature forest of hydroids and bushy bryozoans, which provide habitat to numerous species, especially shrimps and brittle stars.

The sediment composition at the Campod stations was entirely pebble gravel, except at C1 and C2 where some sand was also observed. The bare gravel substrate is apparent in Fig. 7B, with traces of *Filograna implexa* on some pebbles. Colonies of *Filograna* grow on pebbles, cobbles, and dead shells (Fig. 7C) and also provide habitat for numerous invertebrate species. The percent cover of epifauna was averaged over the photographs taken at each Campod station (Fig. 8). At the NW end of the transect, *Filograna implexa* was relatively abundant (Station C1). At Stations C2, C3, and C4 hydroids were the dominant epifauna. These stations are located between km 2-6, where there was high groundfish effort and almost no scallop effort. The hydroid cover may be reflected in somewhat lower backscatter in this interval. The bare gravel with no epifauna observed at Stations C5 and C6 (Fig. 8) corresponds to the higher backscatter observed between km 8 and 10 (Fig. 6A). In this interval, there was lower groundfishing effort and higher scallop effort. Of particular note in this transect is the interval from 10-12 km which is very flat (79-81 m) and has low backscatter (~60 dB). Rugosity is also low, indicating a lack of vertical relief (Fig. 6B). Groundfish effort is at its lowest level in this interval and scallop effort is relatively low (Fig. 6C), indicating that there was relatively little bottom fishing in this area. This interval corresponds to the dense patch of *Filograna*, which can be detected acoustically from its low backscatter (R1, seabed hardness).

From the Naturalists' dredge samples, 90 species were selected as being quantitatively sampled and consistently identified. Of these 90 species, all were identified to the species level, except the nudibranch, *Psolus* sp. Significant differences among sites ($p < 0.05$) were found for numerical abundance, biomass, and number of species (Fig. 9). Total numerical abundance was consistently higher at Site 20 than at the adjacent Site 13 and higher inside the mussel bed (M-in) than at a control site outside the mussel bed (M-out; Fig. 9A). There was no significant difference between abundance at Site 20 and M-In or between Site 13 and M-out. The difference among sites was particularly apparent in total biomass, as biomass inside the mussel bed was three times

the biomass at any of the other sites (Fig. 9B). Biomass was statistically higher inside the Mussel Bed than at Sites 13 or 20. The main species that accounted for the biomass inside the mussel bed were *Asterias vulgaris*, *Placopecten magellanicus*, *Modiolus modiolus*, *Astarte undata*, *Buccinum undatum*, *Cucumaria frondosa*, and *Boltenia ovifera*. To estimate species richness, we included all species that were consistently identified, in addition to those that were quantitatively sampled, increasing the total species pool to 115. The number of species was higher inside the mussel bed compared with the other sites (Fig. 9C); only the difference between Site 20 and M-In was statistically significant.

Ordination of the dredge samples revealed two distinct clusters of samples that differed at 40% similarity and were separated mainly along the horizontal MDS axis (Fig. 10). Species composition at Site 20 is most similar to that inside the mussel bed, whereas Site 13 is most similar to outside the mussel bed. There is also a suggestion of separation along the vertical MDS axis, between the Mussel Bed and Sites 13 and 20. A one-way ANOSIM indicated significant differences in the megafaunal communities among the sites ($p < 0.01$). The pairwise R values indicated significant differences between sites in the difference clusters but not between sites within the clusters. Most species were more abundant at Site 20 and Mbi than at Site 13 and Mbo, with the exception of the bivalve molluscs, *Placopecten magellanicus*, *Astarte spp.*, and *Cyclocardia borealis* (Table 2). The top discriminating species between the clusters were the brittle star, *Ophiopholis aculeata*, which lives in the colonial epifauna, and the sea anenome, *Urticina felina*. Five shrimp species (*Eulis pusiolus*, *Spirontocarus spinus*, *Lebbeus groenlandicus*, *Dichelopandalus leptocerus*, and *Pandalus montagui*) were more abundant at Sites 20 and Mbi than at Site 13 and Mbo (Table 2).

Discussion

We have described a distinctive habitat on northern Georges Bank that is defined by pebble-gravel substrate surrounded by unconsolidated sand. Located between 72 and 90 m, this gravel is too deep to be resuspended by winter storms. The gravel therefore provides a stable substrate for colonial epifauna, mainly hydroids, bushy bryozoans, and the tubeworm, *Filograna implexa*, which feed on the suspension of plankton in the strong tidal currents. The epifauna create three-dimensional habitat structure on an otherwise two-dimensional gravel pavement, decreasing the water velocity at the sediment-water interface. The epifauna provide protection from predators for invertebrates and small fish and trap particulate matter that is food for deposit feeders such as brittle stars (Nalesso *et al.* 1995). The invertebrates living in the epifauna (e.g. shrimps, crabs) are, in turn, prey of demersal fish. This area contains the highest diversity of benthic megafauna that we have measured on Georges Bank (Collie *et al.* 2005). Our results confirm those of Thouzeau *et al.* (1991) who found the highest numbers of epifauna species (45-65 per sample) on “biogenic bottom.”

At spatial scales of 1-10 km, there is patchiness in the percent cover and species composition of the epifauna. Given the small spatial scales and limited depth range, this patchiness on the uniform pebble gravel substrate (as indicated by the single backscatter

mode and confirmed from the seabed photographs) is unlikely to be caused by physical differences in the water column or bottom currents.

Within the gravel category, subtle differences in sediment grain size could affect the settlement and growth of epifauna, if for example, hydroids can colonize small pebbles, but *Filograna* requires large pebbles or cobbles. The epifauna may also affect the surficial sediments by trapping sand. Subtle differences in sediment composition have been observed in previous analyses of photographs from Sites 13 and 20 (Asch 2006). According to results of BIO-ENV statistical analysis, epifaunal composition at Sites 13 and 20 was most highly correlated with scallop dredging effort, and the percent composition of small pebbles and sand. There may be an interaction between bottom fishing and sediment composition, to the extent that bottom fishing digs into the sediment, exposing the sand beneath the gravel.

Colonial epifauna on gravel substrates is particularly sensitive to bottom fishing effort with scallop dredges and otter trawls (Collie *et al.* 2000). Previous analyses of the benthic megafauna at Sites 13 and 20 attributed the differences between these sites to bottom fishing, primarily scallop dredging (Collie *et al.* 2005). The distribution of bottom fishing effort is patchy at 1-10 km scales and could therefore account for the patchy distribution of epifauna. Along our acoustic corridor, there was a gradient in fishing effort, with higher groundfish effort at the northwest end and higher scallop effort at the southeast end. This partitioning of scallop and groundfish effort is apparent over a wide area. A possible explanation of this pattern is that scallop density is higher over bare gravel, which provides attachment sites for juvenile scallops. Areas with high epifaunal cover may be less suitable for scallops due to lack of attachment sites and more numerous predators. These areas may provide better feeding opportunities for demersal fish.

Great care must be taken not to over-interpret the distribution of fishing effort because of the coarse precision of fishing locations (1-2 km). There is a fundamental mismatch between our ability to map benthic habitats at meter resolution and the use of these habitats by fish and fishermen, which integrate over 1-10 km scales (Fig. 8). Spatial management operates on 10-100 km scales (e.g. closed areas on fishing banks) and therefore incorporates heterogeneous habitat types.

The backscatter data from the acoustic corridor indicate a hard and smooth substrate. We found only one acoustic class, in contrast to a study area on Western Bank, Scotian Shelf, where there were two distinct acoustic classes associated with sand and gravel (Courtney *et al.* 2005). On Western Bank there were three categories of sand and five categories of gravel, including boulders. Therefore, in comparison with Western Bank, the study area on Georges Bank has much more uniform sediments.

Our study area appears to be near the boundary between “gravel” and “sand” as mapped by Kostylev *et al.* (2005). In their study of the Canadian portion of Georges Bank, higher backscatter values were associated with gravel and lower values with sand. However, we cannot compare our study site with their map as it has no coordinates. High

backscatter (-10 to -30 dB) is generally classified as “gravel” and low backscatter (-30 to -60 dB) as “fine-grained sand” (Mitchell & Hughes Clarke 1994). Most of our R1 (seabed hardness) data (Figure 3a) fell between -10 and -30 dB, which implies that our study area occurred over “gravel” and not “sand”. Our results show that Georges Bank is harder (R1= -21.6 dB) and smoother (R2= -94.2 dB) than Western Bank (R1=-34.0 dB, R2=-86.0 dB) based on the results of Courtney *et al.* (2005).

A surprising result of the present study is the relationship between dense *Filograna implexa* and acoustic backscatter on a pebble-gravel seabed. It appears that *Filograna* reduced the backscatter of both the R1 and R2 components on an otherwise hard seabed. Nominally, the acoustic backscatter of R1 was < -25 dB where otherwise it was > -20 dB on a pebble-gravel seabed. Note that the low backscatter occurred primarily on the eastern-most lines while high backscatter occurred on the western-most lines (Fig. 4). This difference implies that the transects mapped the western edge of a *Filograna* patch.

Rugosity measures vertical relief standardized to horizontal distance. We found greater rugosity on the northwest end of the transects, where there was greater epifaunal diversity. A more rugged sea-floor has more surface area and potentially more refuges for animals. On the Grand Banks of Newfoundland, higher biodiversity of benthos was associated with rugosity > 1 m km⁻¹ (Schneider *et al.* 1987). Preferred fish habitats on Emerald, Western and Sable Island Banks had rugosity ranging from 3.0 to 5.3 m km⁻¹ (with comparable ship speed/distance) compared with non-preferred habitats where rugosity ranged from 2.7 to 3.2 m km⁻¹ (Anderson *et al.* 2005). In comparison, our study area on Georges Bank averaged 3.5 m km⁻¹; and the seabed in the northwest part of the area exhibited values of 5.7 m km⁻¹ and greater, suggesting the presence of relatively good fish habitat.

In summary, our results show that the distinctive “biogenic” areas on Georges Bank can be mapped with acoustic data and that there is a relationship between seabed characteristics and preferred fish habitat.

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Table 1. Summary of samples collected on three research cruises to northeastern Georges Bank.

Date	October 2001	August 2002	August 2005
Research Vessel	<i>CCGS Hudson</i>	<i>RV Albatross IV</i>	<i>RV Delaware II</i>
Side scan transects	1	0	0
Acoustic transects	6	0	0
Video transects	4	5	35
Still photos	39		
Dredge samples	0	5	8
Beam trawl samples	0	0	5
Otter trawl samples	0	7	

Table 2. List of species accounting for the dissimilarity in species composition between the two clusters of sites in Fig. 10. Abundance is averaged among the samples in each cluster. Bray-Curtis dissimilarity was averaged over pair-wise between-cluster combinations of samples. Species with the highest average dissimilarity divided by the within-cluster standard deviation of abundance are best at discriminating the clusters.

Species	Av.Abund 20, Mbi	Av.Abund 13, Mbi	Average Diss.	Diss/SD	Cum.% Diss.
<i>Thelepus cincinnatus</i>	3.26	0.63	6.40	1.85	9.61
<i>Ophiopholis aculeata</i>	2.53	0.37	5.65	4.81	18.10
<i>Eualus pusiolus</i>	1.80	0.08	4.12	1.27	24.29
<i>Hyas coarctatus</i>	2.07	0.67	3.53	1.81	29.59
<i>Potamilla neglecta</i>	1.53	0.53	3.11	1.31	34.27
<i>Spirontocaris spinus</i>	1.02	0.02	2.60	2.59	38.17
<i>Lebbeus groenlandicus</i>	0.92	0.02	2.28	2.10	41.59
<i>Anachis haliaecti</i>	0.85	0.04	1.96	1.27	44.53
<i>Dichelopandalus leptocerus</i>	0.99	0.36	1.93	1.13	47.43
<i>Pandalus montagui</i>	0.82	0.18	1.71	2.25	49.99
<i>Placopecten magellanicus</i>	0.09	0.60	1.46	1.51	52.19
<i>Pagurus pubescens</i>	1.11	0.59	1.46	1.89	54.38
<i>Urticina felina</i>	0.60	0.06	1.42	3.73	56.51
<i>Ophiomitrella clavigera</i>	0.59	0.10	1.31	1.54	58.47
<i>Modiolus modiolus</i>	0.43	0.02	1.06	2.10	60.06
<i>Eunice pennata</i>	0.41	0.11	1.03	1.36	61.60
<i>Henricia sanguinolenta</i>	0.49	0.19	1.01	1.69	63.12
<i>Potamilla reniformis</i>	0.33	0.00	0.92	2.38	64.50
<i>Astarte undata</i>	0.30	0.41	0.91	1.48	65.86
<i>Calliostoma occidentale</i>	0.35	0.08	0.83	1.75	67.11
<i>Boltenia echinata</i>	0.34	0.03	0.83	1.93	68.36
<i>Nereis zonata</i>	0.37	0.13	0.82	1.64	69.59
<i>Strongylocentrotus droebachiensis</i>	0.06	0.32	0.79	1.49	70.78
<i>Buccinum undatum</i>	0.30	0.26	0.69	1.43	71.81
<i>Asterias vulgaris</i>	0.32	0.14	0.68	1.79	72.83
<i>Musculus discors</i>	0.27	0.08	0.66	1.55	73.83
<i>Pagurus acadianus</i>	0.08	0.28	0.62	1.48	74.76
<i>Nymphon grossipes</i>	0.26	0.03	0.62	1.10	75.69
<i>Neptunea decemcostata</i>	0.24	0.09	0.60	1.22	76.60
<i>Asterias tanneri</i>	0.40	0.24	0.59	1.25	77.48
<i>Onuphis conchylega</i>	0.14	0.07	0.59	0.59	78.37
<i>Pagurus arcuatus</i>	0.17	0.15	0.58	1.30	79.23
<i>Astarte montagui</i>	0.12	0.26	0.56	1.42	80.07
<i>Cyclocardia borealis</i>	0.16	0.31	0.52	1.14	80.86
<i>Nereis pelagica</i>	0.15	0.00	0.51	0.80	81.62
<i>Velutina velutina</i>	0.19	0.03	0.51	0.97	82.39
<i>Astarte elliptica</i>	0.30	0.44	0.47	1.01	83.10
<i>Crossaster papposus</i>	0.09	0.15	0.46	1.12	83.78
<i>Dendrodoa carnea</i>	0.17	0.00	0.45	0.97	84.46
<i>Epitonium greenlandicum</i>	0.05	0.15	0.44	1.78	85.12
<i>Cerastoderma pinnulatum</i>	0.13	0.17	0.44	1.57	85.78
<i>Aspidophoroides monopterygius</i>	0.14	0.04	0.43	0.87	86.42
<i>Boltenia ovifera</i>	0.13	0.09	0.40	1.07	87.03
<i>Astarte subaequilatera</i>	0.09	0.17	0.38	1.43	87.59
<i>Ischnochiton albus</i>	0.11	0.08	0.36	0.87	88.13

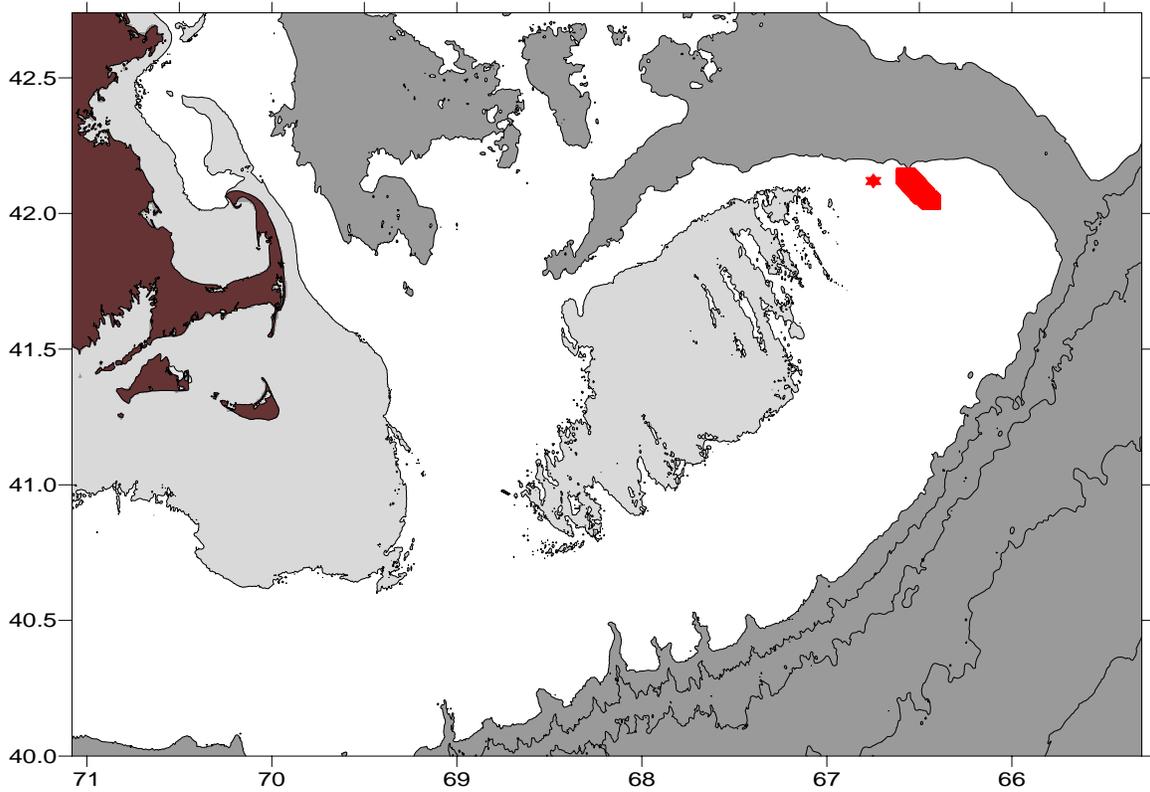


Figure 1. Georges Bank, indicating the study corridor on the northern edge (red polygon) and the mussel bed (red star). Bathymetry is represented by shading where light grey is < 50 m, white is 50 m to 100 m and the dark grey is > 200 m. Bathymetric contours beyond 200 m start at 1000 m and increment to 4000 m. Land is shaded dark brown. For scale, one-half degree of latitude represents 56 km.

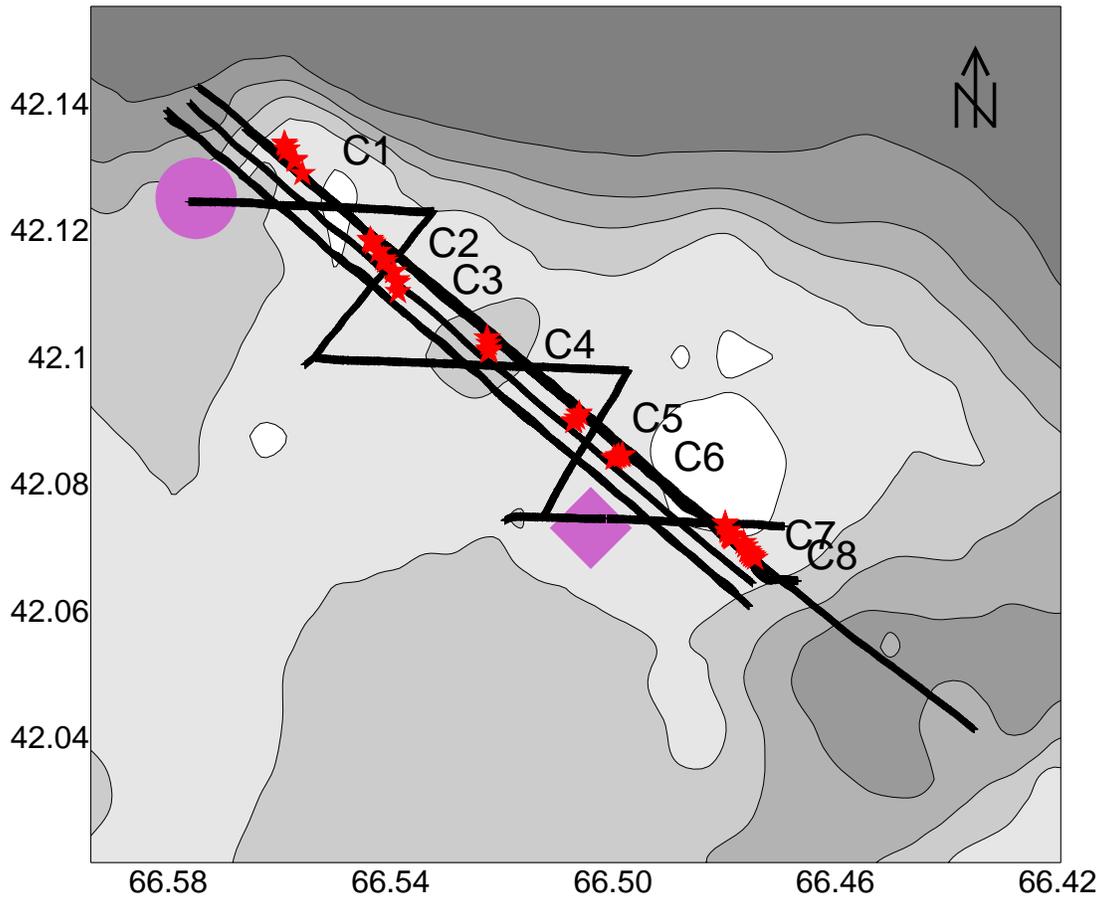


Figure 2. Acoustic sampling lines (black), 8 Campod photo stations (39 photos, red stars, stations C1 – C8), and sampling sites 13 (purple diamond) and 20 (purple circle). The depth is shaded from the shallowest areas (75 m, white), to 80 m, 85 m, 90 m, 100 m and 200 m with increasing degree of grey shading. For scale, each increment of latitude represents 2.2 km.

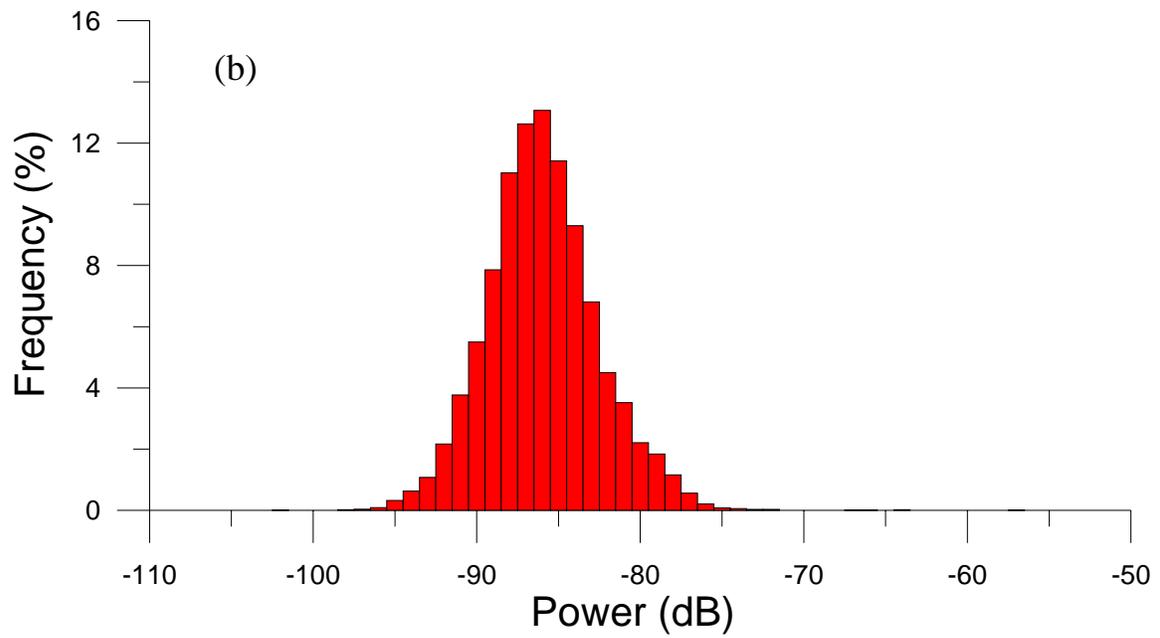
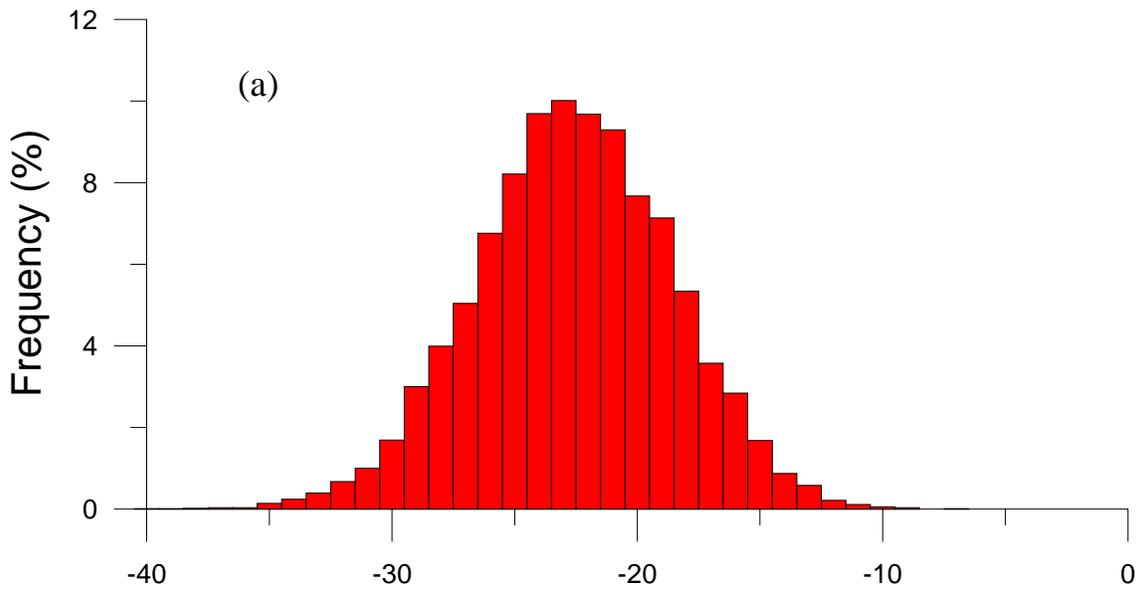


Figure 3. Acoustic backscatter (dB) frequency distribution (%) for (a) R1, seabed hardness, and (b) R2, seabed roughness.

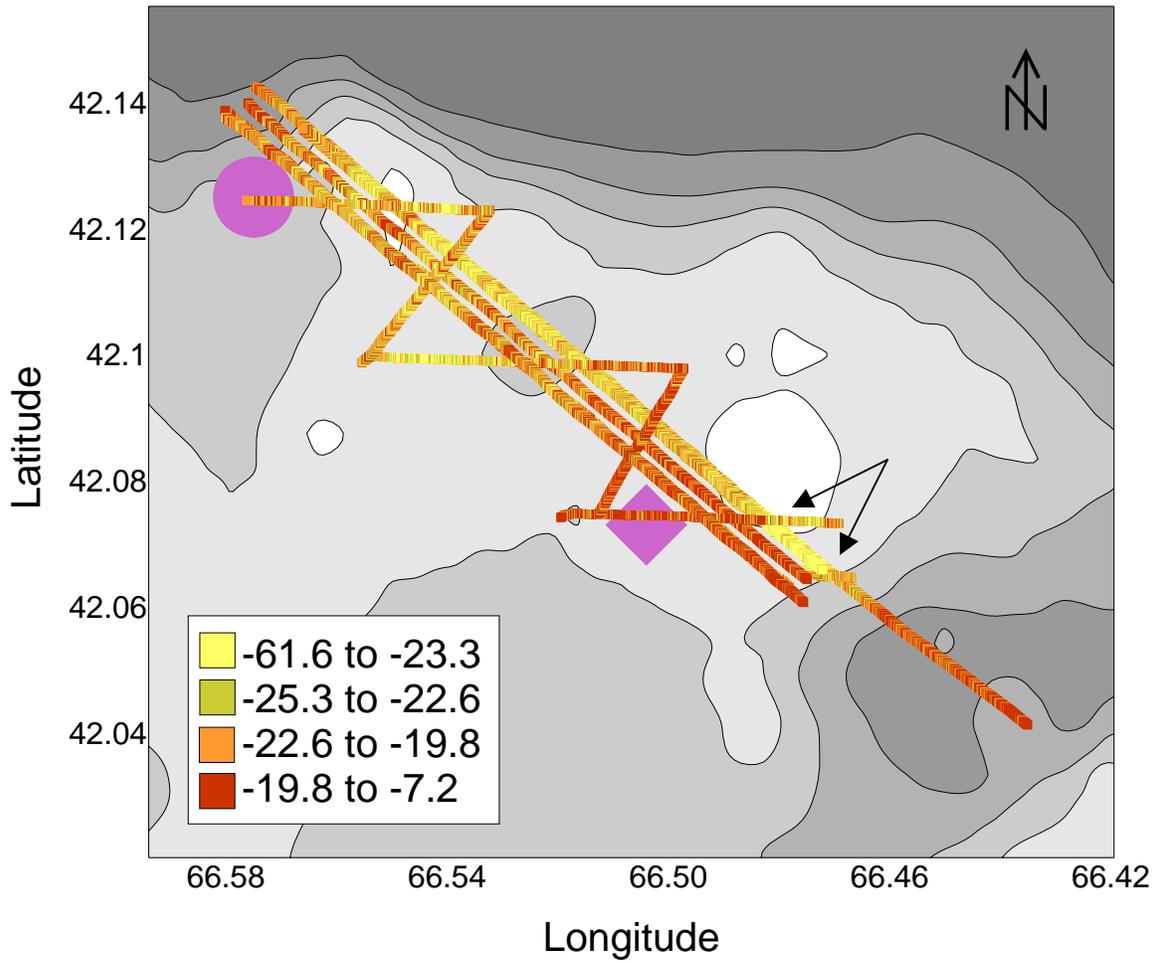


Figure 4. Acoustic backscatter (dB) expressed in quartiles where the lowest backscatter is in yellow and the highest backscatter is in red. Arrows point to the occurrence of *Filigrana implexa*. Sampling site 13 (purple diamond) and site 20 (purple circle). The depth is shaded from the shallowest areas (75 m, white), to 80 m, 85 m, 90 m, 100 m and 200 m with increasing degree of grey shading. For scale, each increment of latitude represents 2.2 km.

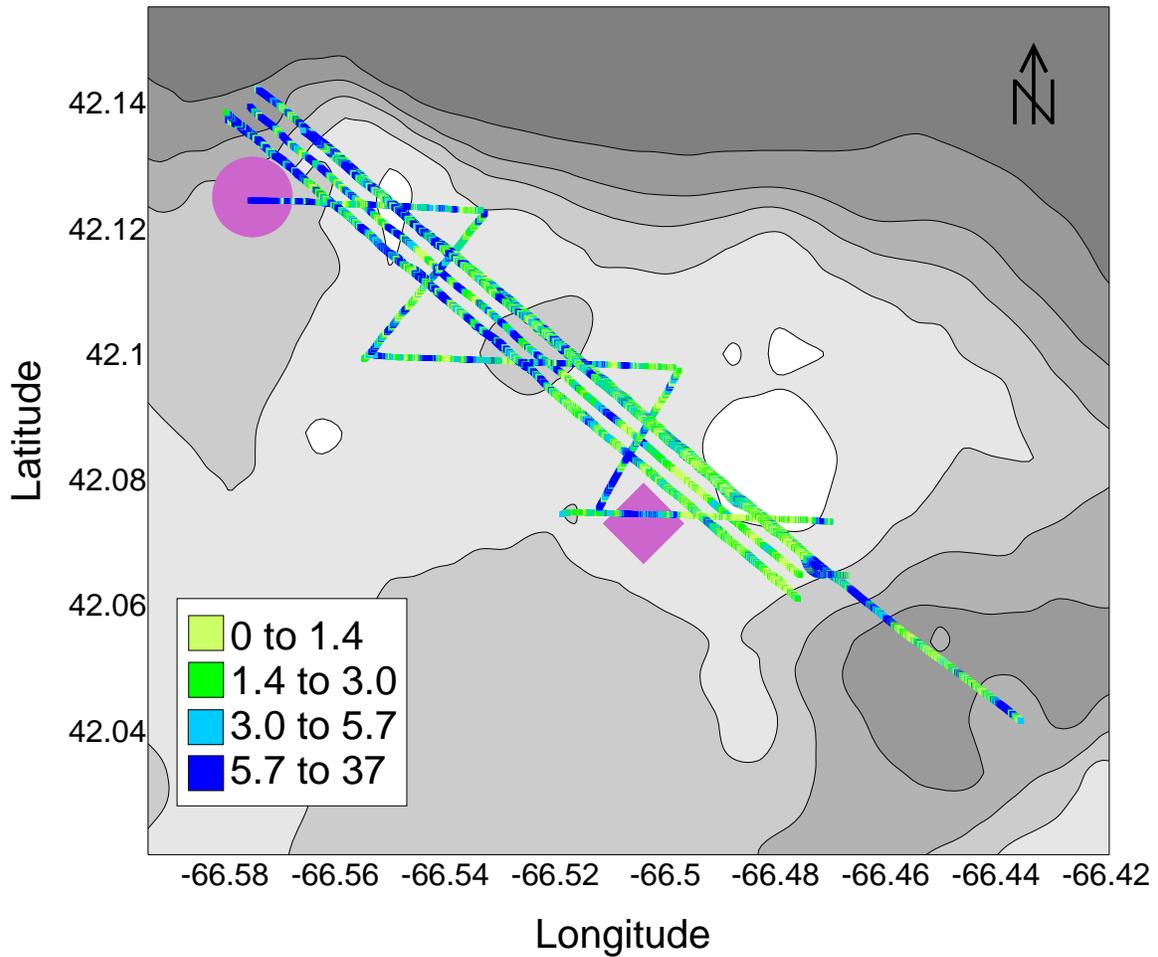
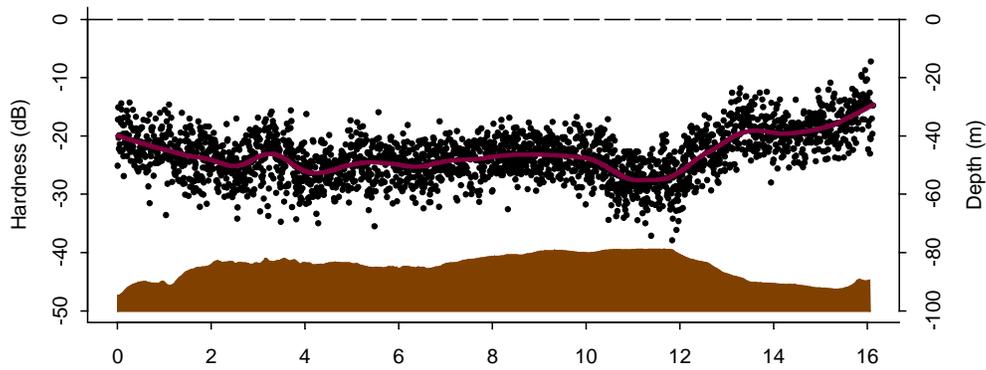
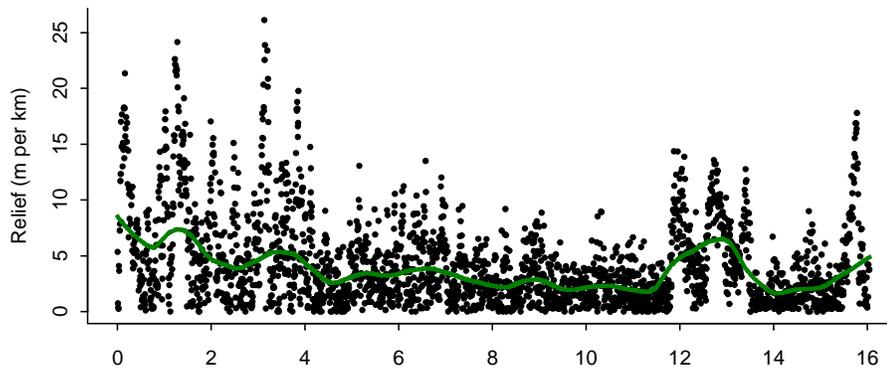


Figure 5. Surface rugosity (m km^{-1}) expressed in quartiles where the lowest levels are in green and highest levels in dark blue. Sampling site 13 (purple diamond) and site 20 (purple circle). The depth is shaded from the shallowest areas (75 m, white), to 80 m, 85 m, 90 m, 100 m and 200 m with increasing degree of grey shading. For scale, each increment of latitude represents 2.2 km.

A. Bottom Hardness (R1) and Depth



B. Rugosity



C. Fishing Effort 1992-2001

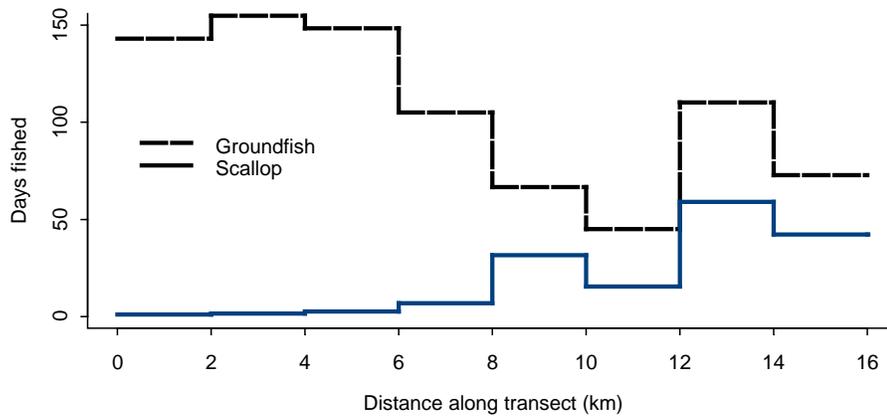


Figure 6. Eastern-most acoustic sampling transect (Fig. 2) from NW (0km) to SE (16km). Lowess smoothers were applied to the R1 (seabed hardness) and rugosity data, with spans equal to 1/12 of the data series (coloured lines). Fishing effort data were summed over years 1992-2001 for 2-km bins.

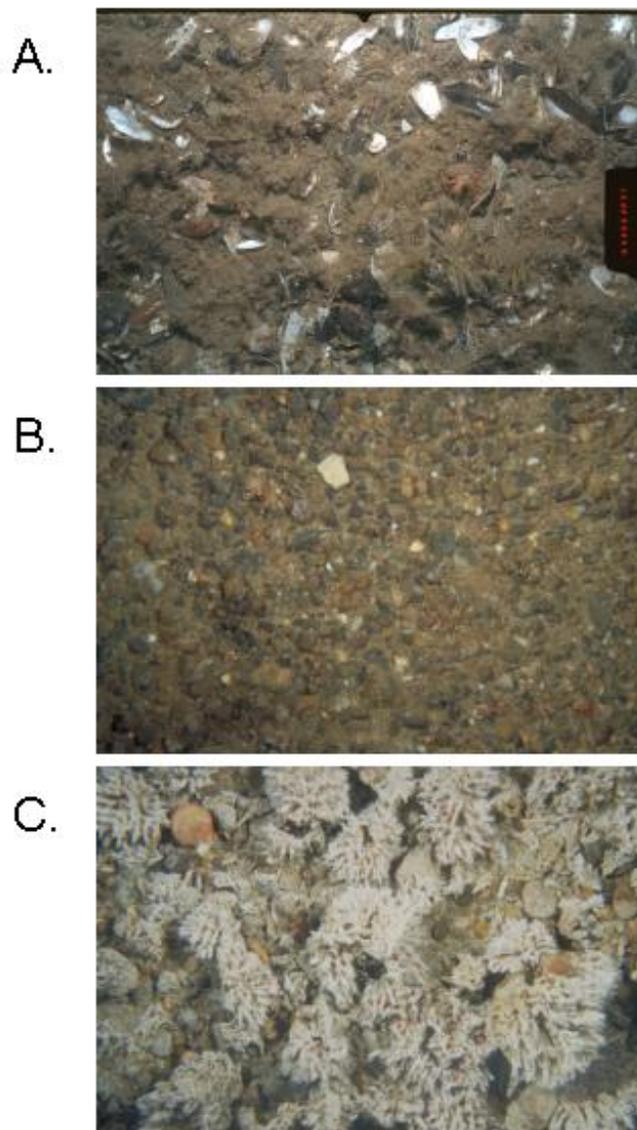


Figure 7. Bottom photographs from northern Georges Bank. A. Inside the mussel bed in 2005. Note the dense cover of hydroids and bushy bryozoans over the horse mussels, *Modiolus modiolus*. B. Campod station C5 in 2001. C. Campod station C7 in 2001. Note the Iceland scallop, *Chlamys islandica*, and the dense cover of *Filograna implexa*.

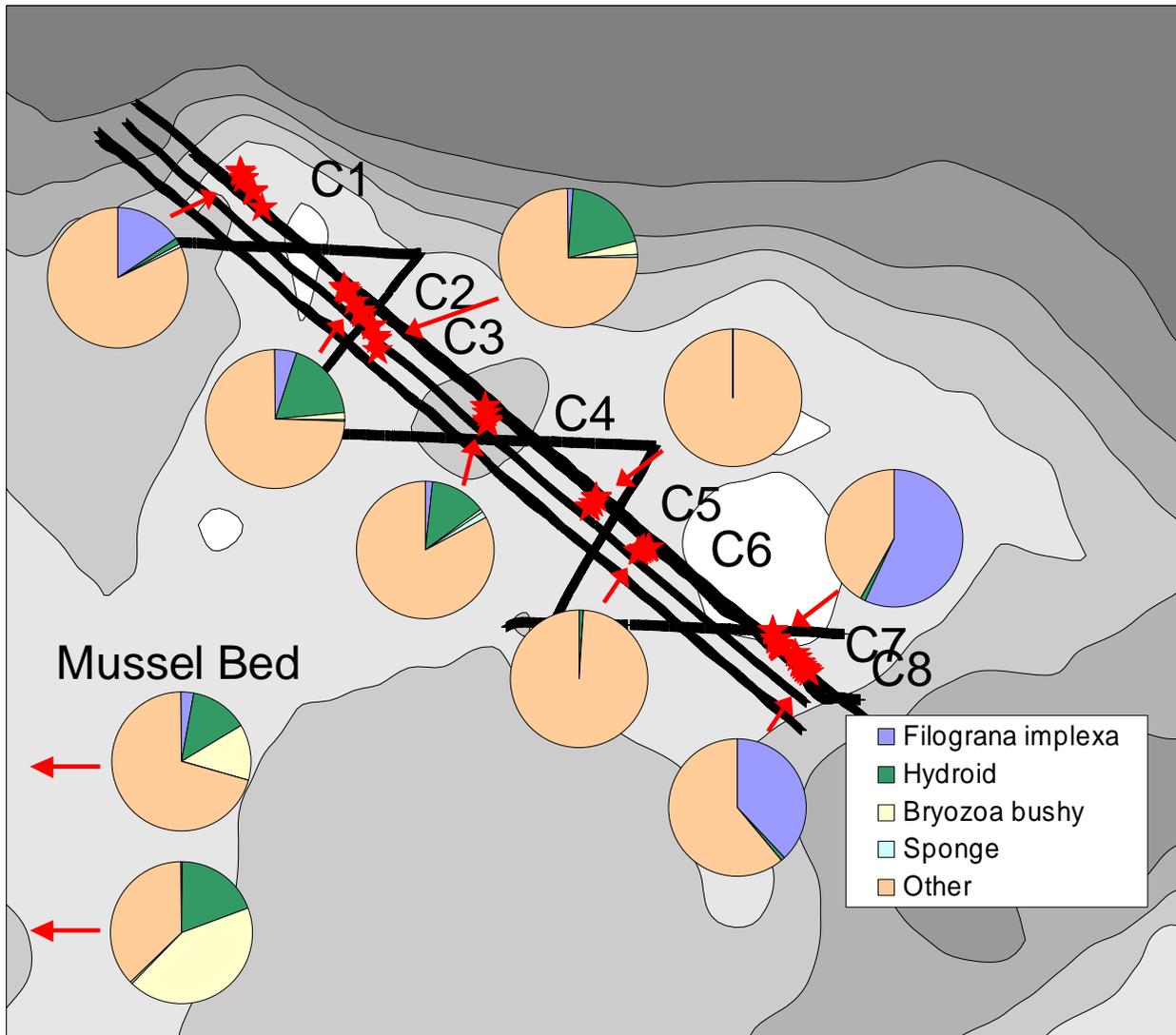


Figure 8. Percent cover of colonial epifauna at Campod stations C1 to C8. The mussel bed is located to the west of the acoustic transect (Fig. 1) and is represented by two stations. Each pie chart represents the mean percent cover in the photographs taken at that station. The “Other” category is mainly bare gravel. The acoustic transects are 12 km long.

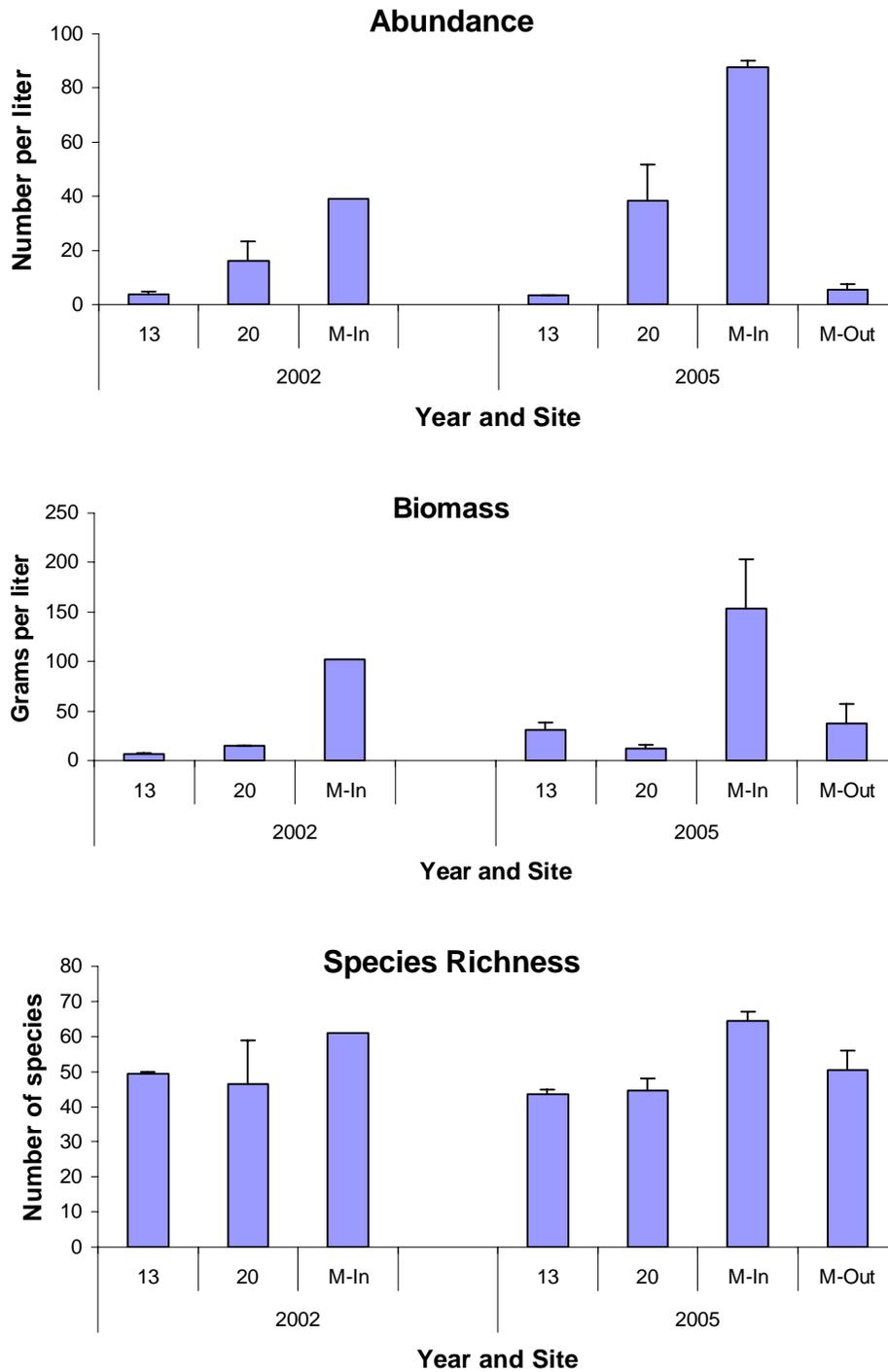


Figure 9. Benthic megafauna at sites 13, 20, and the mussel bed on northern Georges Bank. M-In and M-out refer to inside and outside the mussel bed. Error bars are standard errors of the means.

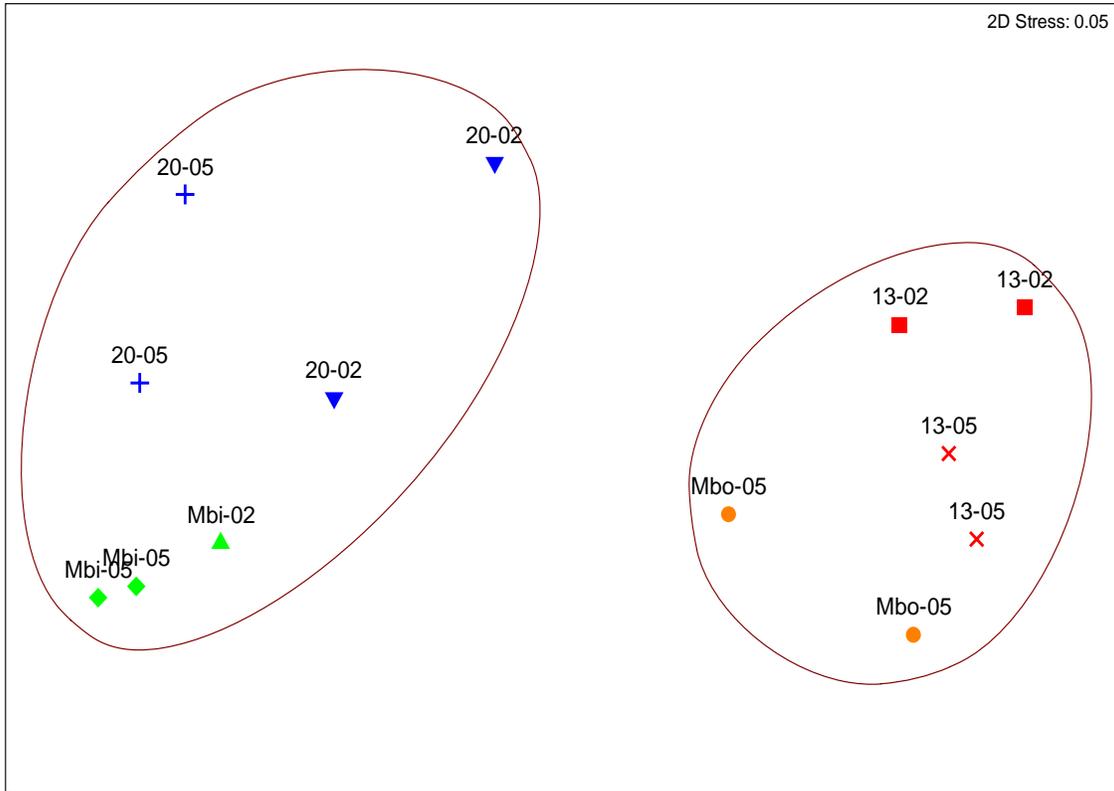


Figure 10. Numerical abundance data from dredge samples collected on the northern edge of Georges Bank. Each point represents the abundance of 90 species in one dredge sample. The labels indicate the sites (13, 20, Mussel bed inside, Mussel bed outside) and years (2002, 2005). The samples were ordinated with Multi-Dimensional Scaling of the Bray-Curtis similarity matrix calculated from square-root transformed abundance data. The contours enclose clusters that differ at 40% similarity.