ICES Journal of Marine Science

An evaluation of benthic community structure in and around the Sackville Spur closed area (Northwest Atlantic) in relation to the protection of vulnerable marine ecosystems

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The benthic macrofaunal community structure is investigated within and around a closed area at Sackville Spur in the Northwest Atlantic to ascertain whether continued exclusion of bottom fishing can be justified. This and other similar closed areas have been introduced by the Northwest Atlantic Fisheries Organisation (NAFO) to protect areas of likely occurrence of taxa that are indicative of vulnerable marine ecosystems (VMEs) from the damaging effects of bottom-contact fishing gear. Results reveal subtle yet significant differences in macrofaunal assemblage composition and community structure between inside and outside the closed area, between above and below the 1200-m depth contour (i.e. the historical depth limit of fishing), and between areas where dense sponge spicule mats are either present or absent. Differences were observed in many assemblage metrics; however, the most revealing was the greater abundance, biomass, diversity, and number of VME indicative taxa inside the closed area than outside. Overall community composition is also significantly different between treatments. Depth, sediment temperature, and the proportion of clay within sediments are important in shaping the faunal assemblage. The importance of the effects of fishing is discussed, although it is not possible to ascertain if fishing is the direct cause behind observed differences in the macrofaunal assemblage. A continued closure of the area is recommended, as well as options for streamlining the evaluation process of other closed areas.

Keywords: fishing exclusion zone, NAFO, Northwest Atlantic, Sackville Spur, vulnerable marine ecosystem (VME).

Introduction

In January 2010, as a precautionary measure, the Northwest Atlantic Fisheries Organisation (NAFO) imposed 11 interim exclusion zones on all bottom fishing activities on the slopes adjacent to the Grand Banks of Newfoundland (Canada; NAFO, 2010). These closures, which collectively cover an area of ∼8600 km^2, were introduced in response to the United Nations General Assembly (UNGA) Sustainable Fisheries Resolution (61/105), in which countries have agreed that they and the regional fisheries management organizations will take measures to mitigate impacts on vulnerable marine ecosystems (VMEs) arising from bottom fishing. The suitability of such closures is to be reviewed by NAFO in 2014. It is within this regulatory context and time frame that the present study has sought to characterize the little-known benthic invertebrate assemblage in and around one of the designated closed areas.

The 11 designated area closures have been placed around aggregations of deep-sea sponges and corals known to occur on the fringes of the Grand Banks and the Flemish Cap. Some deep-sea sponges and corals are thought to be indicative of VMEs, particularly those that are fragile, with slow growth and propagation rates (FAO, 2008). Present knowledge suggests that their distribution is limited to a depth band between 250 and 1300 m, where water temperature ranges from 4 to 10°C and there is moderate
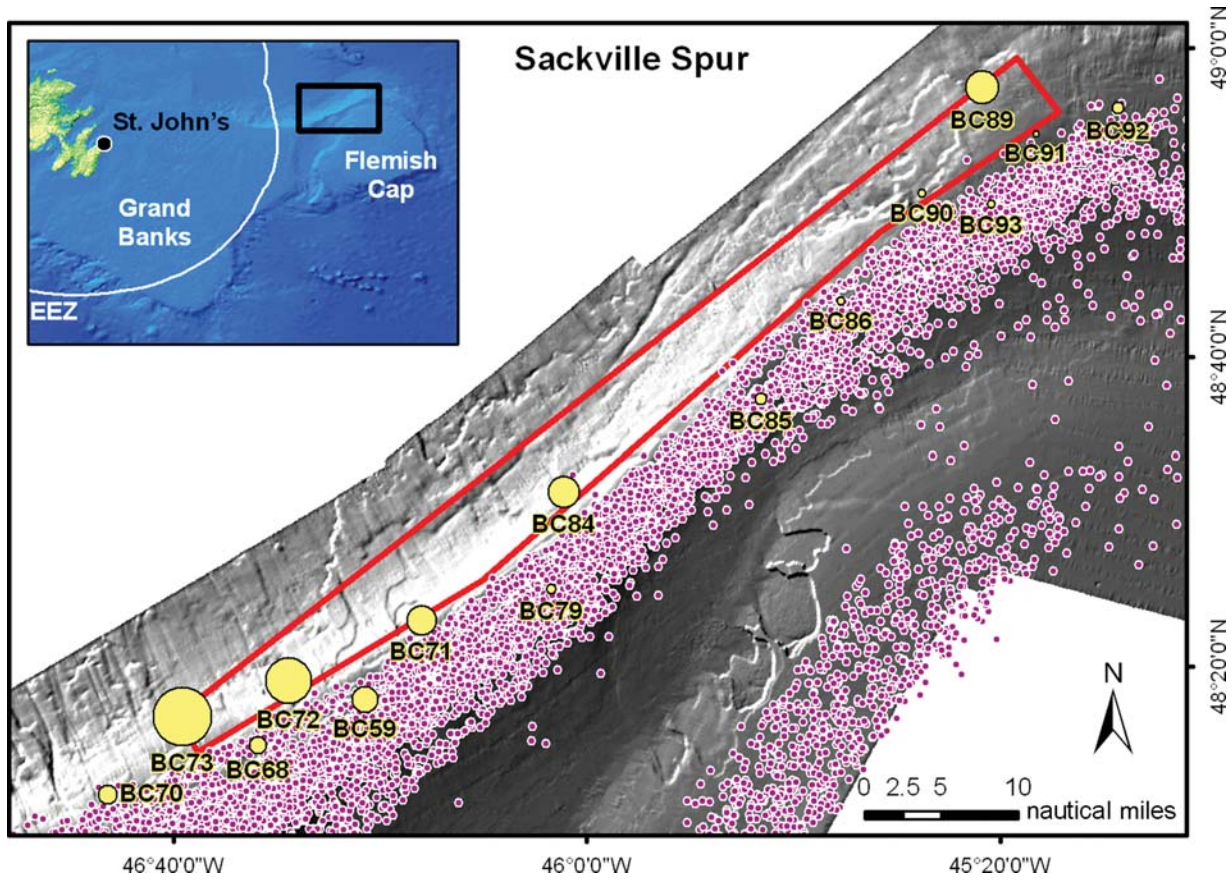
Figure 1. Map of the Sackville Spur showing the boundary of the designated closed area. The size of symbols showing the location of each sampling station is proportional to the abundance of VME indicative taxa at each station. Smaller, more densely packed symbols represent the fishing footprint of the Spanish Greenland halibut fishing fleet between January 1992 and December 2006.

current velocity (∼0.5 knots; Bett and Rice, 1992; Kenchington *et al.*, 2010a; Murillo *et al.*, 2010; Vinnichenko, 2010). Given that bottom-contact fishing gear can now reach depths of up to 2000 m (FAO, 2001–2011), it is important that known ecosystems recognized as vulnerable are protected from any detrimental effects of bottom fishing.

One of the largest areas to be closed to fishing is on the northwest-facing flank of the Sackville Spur, where this investigation has focused. The closed area is a near rectangle, ∼128 km long by 10 km wide, and adjoins along its longest axis the 1200-m depth contour on the northwest-facing slope of the Spur (Figure 1). The enclosure covers an area of 996 km^2 and reaches a maximum depth of ∼1400 m. The Spur itself is a sediment drift feature that forms a northeastward extension of the Grand Banks continental slope, between 900 and 2500 m deep near latitude 48°N (Kennard *et al.*, 1990). Its emergence from the surrounding deeper seafloor causes the acceleration of the deep offshore component of the Labrador Current, simultaneously winnowing finer sediment particles to expose a lag deposit suitable for faunal attachment, and delivering suspended food particles at an increased rate (Genin *et al.*, 1986; Genin, 2004). These conditions create favourable habitats for sessile suspension-feeders such as sponges and corals, which, in turn, can exert a major influence on species diversity by locally increasing habitat heterogeneity (Buhl-Mortensen *et al.*, 2010; Kenchington *et al.*, 2010b). The increased occurrence of sponges in particular can alter the

characteristics of surrounding sediments, as dense mats of siliceous spicules accumulated from previous generations may stabilize the sediment and inhibit colonization by some infaunal animals, resulting in a prominence of epifaunal organisms (Bett and Rice, 1992; Gubbay, 2002).

The crest of the Sackville Spur has been subjected to intense bottom fishing pressure by the Greenland halibut fishery, especially during the early 1990s. Fishing intensity declined after regulation of the fishery was introduced in 1994 (Bowering *et al.*, 2000), though bottom-fishing continues in the area throughout the year. Most of the fishing occurrs above the 1200-m depth contour, so that the deeper reaches of the slopes of the Spur to the north and south have received little direct impact.

The primary aim of the present investigation is to characterize and compare the benthic assemblage inhabiting the sediments inside and outside the Sackville Spur closed area to ascertain whether the maintenance of the closed area and its current boundaries are appropriate. Observed differences between assemblages inside and outside the closed area may count as evidence in support of the continued closure. A secondary aim is to ascertain the most effective way of conducting future evaluations of the suitability of other closed areas in the NAFO regulatory area. Tracking patterns in assemblage composition at different levels in the taxonomic hierarchy could help differentiate between patterns attributable to natural causes or those influenced by anthropogenic

activity (Warwick, 1998), as well as help speed up the assessment process for other closed areas.

Methods
Field protocol
Collection of data from the Sackville Spur was carried out as part of a large-scale international multidisciplinary habitat mapping survey (NEREIDA; http://www.nafo.int/science/frames/nereida.html) conducted aboard the Spanish research vessel "Miguel Oliver" during the summer months of 2009 and 2010. Data acquisition included 100% coverage of acoustic multibeam and seismic profile data for the seabed immediately adjacent to the limit of Canada's 200-nautical mile EEZ, between 700 and 2000 m depth. In addition, over 460 ground-truthing samples were taken over the entire survey area using a combination of mega boxcore and rock dredge samplers. Water column characteristics (e.g. conductivity, temperature, depth, fluorescence, and oxygen content) were measured at every ground-truthing station by deploying a CTD probe. Mega-boxcore samples were subsampled for stratigraphic, granulometric, and geochemical analyses. For the purposes of the present investigation on the Sackville Spur, only data obtained from 15 mega-boxcore samples (targeting benthic infauna) have been used, in combination with supplementary information which is known to be of influence on the distribution of benthic organisms (e.g. depth, temperature, fishing effort, sediment composition).

Onboard the survey vessel, mega-boxcore samples (sampling area: 0.25 m^2) were drained of any excess water before describing the undisturbed surface of the sample. Sediment temperature was measured at ~5-cm depth, as well as pore-water conductivity. Conspicuous epifaunal organisms were collected for future identification prior to the removal of sediment subsamples for particle size distribution analysis (PSA) and geochemical processing. After the removal of all subsamples, the top 5 cm of the remaining sediment was washed with seawater over a 0.5-mm mesh sieve to extract the infauna. All remaining sediment from the corer was washed separately and material retained on the sieve kept for future inspection. All biological material was fixed in 4% buffered formalin and eventually transported to the laboratory for processing.

Laboratory processing
In the laboratory, the 15 samples taken from within and around the Sackville Spur closed area (six from inside and nine from outside the area boundary) were washed again and the fauna separated from heavier material by elutriation, followed by visual inspection under magnification of the heavier material. Fauna were identified to the lowest possible taxonomic level given the available expertise and desire to perform a relatively rapid assessment. This approach meant that most identifications did not go beyond the taxonomic level of family. The resultant operational taxonomic units—or taxa, for short—were enumerated (colonial organisms were given a value of 1, though separate colonies were counted individually) and weighed after blotting on tissue paper to the nearest 0.0001 g. All biological material was preserved in either 4% formalin or 70% industrial methylated spirit for future reference.

Data analysis
A taxon abundance-by-sample matrix was generated, as well as a taxonomic aggregation file, a biomass-by-sample matrix, and a list of various environmental variables measured at each sampling station. Measured environmental variables included depth, sediment temperature, % clay, % silt, and % sand. In addition, a relative measure of historical fishing effort was attained by counting the number of trawl starting positions within a 5-km radius of each mega-boxcore sample over a period spanning from 1992 to 2006. This information was made available by the Spanish Institute of Oceanography, which holds the trawl data records taken by fisheries observers onboard the Spanish fishing fleet.

Initial analyses involved the calculation of several assemblage metrics per sample, such as total number of taxa (S), total abundance (N), total biomass (B), Hill's (1973) taxon diversity index (N1), and Hill's modified evenness index (N2-1/N1-1 or N21'). Statistical comparison of mean values for each of these metrics was conducted between predefined treatments, such as whether samples were inside or outside the Sackville Spur closed area, whether they lay above or below the 1200-m depth contour, or whether the sample contained evidence of dense spicule mats. Analysis of variance tests to compare these treatments statistically were performed using the Minitab 15 software package. Further multivariate analyses were conducted on datasets aggregated to different levels of taxonomic resolution using the PRIMER v6 software package. Variable-by-sample matrices were subjected to dispersion-based weighting to downweigh the influence of highly clustered taxa within each of the predefined treatments being compared (Clarke et al., 2006). Bray–Curtis similarity was calculated between all sample pairs and patterns in similarity displayed using agglomerative clustering (CLUSTER) and multidimensional scaling (MDS) routines. SIMPROF and ANOSIM tests were applied where necessary to test for any statistical differences observed within the data or between predefined treatments. Where statistically significant differences were observed, the SIMPER routine was applied to identify the taxa responsible for those differences. Lastly, the BIOENV and principal component analysis (PCA) routines were performed to ascertain and illustrate which environmental variables, either in isolation or in combination, were most highly correlated with the patterns observed in the faunal assemblage. Maps illustrating observed patterns in the data were generated using the ArcGIS mapping package.

Results
The range in depth from which all 15 samples were collected is 981–1612 m, with sediment temperature ranging between 3.3 and 4.8°C (Table 1). Six samples fell inside the boundary of the designated closed area, the remaining nine samples being outside. Deeper samples also tended to fall inside the closed area. Similarly, half of the samples showed evidence of dense spicule mats, all but one being inside the closed area. Most samples had a greater proportion of silt than of clay and sand, silt often accounting for over 50% of the total volume (Table 1). The proportion of clay, however, was significantly correlated with depth; deeper samples having a greater proportion of clay than shallower ones (Table 2). Fishing effort was also strongly correlated with depth, shallower sampling sites being subjected to much higher levels of disturbance by fishing gear than deeper sites. Differences in depth accounted for 81% of the variation in fishing effort between sites (Table 2). The differentiation of samples based on their measured environmental characteristics is best appreciated in a PCA plot (Figure 2), where the horizontal axis separates samples based largely on differences in depth, fishing effort, and the proportion of clay, and the vertical axis separates

Table 1. Summary of biological and environmental variables measured from samples collected in and around the Sackville Spur closed area (samples listed in order of increasing depth).

| Sample	Latitude (°N)	Longitude (°W)	Depth (m)	Closed area	Sponge spicules	Number of taxa (S)	Abundance (N)	Biomass (B; g)	Diversity (N1)	Evenness (N21')	Sediment temperature (°C)	% Clay	% Silt	% Sand	Fishing effort[a]
BC59	48.360	46.344	981	Outside	Absent	51	902	3.2662	9.81	0.35	4.1	31.7	52.7	15.5	202
BC79	48.466	46.032	1027	Outside	Absent	29	399	1.0152	3.85	0.37	4.8	20.9	60.9	18.2	167
BC68	48.317	46.522	1050	Outside	Absent	48	768	6.1987	10.72	0.36	3.5	14.6	39.1	46.4	148
BC85	48.656	45.671	1104	Outside	Absent	52	621	6.2788	15.93	0.50	3.9	17.7	52.2	30.1	152
BC86	48.755	45.529	1148	Outside	Absent	36	288	1.0928	17.45	0.65	3.6	34.4	60.3	5.3	99
BC93	48.848	45.272	1187	Outside	Absent	31	283	0.6173	9.32	0.49	3.7	18.4	62.8	18.8	51
BC70	48.273	46.769	1234	Outside	Absent	74	1661	6.7065	12.51	0.35	3.7	19.7	44.1	36.2	70
BC71	48.442	46.245	1260	Inside	Present	51	1405	6.2216	5.03	0.43	4.1	32.0	62.7	5.3	63
BC91	48.920	45.190	1280	Outside	Absent	53	608	4.7978	14.87	0.49	4.3	37.8	50.7	11.5	21
BC90	48.865	45.384	1325	Inside	Present	56	641	2.4215	12.63	0.49	3.9	37.5	53.8	8.7	7
BC92	48.941	45.054	1404	Outside	Present	48	387	0.8682	13.07	0.31	4.3	38.0	47.4	14.5	15
BC72	48.385	46.467	1443	Inside	Present	63	721	9.6478	12.83	0.38	3.4	34.3	57.2	8.5	28
BC84	48.570	46.001	1505	Inside	Present	45	1518	11.5490	3.46	0.44	3.4	34.4	45.9	19.7	4
BC89	48.974	45.273	1574	Inside	Present	56	173	51.3955	32.87	0.62	3.3	49.3	45.2	5.5	0
BC73	48.352	46.642	1612	Inside	Present	65	687	11.1134	14.08	0.29	3.7	38.5	57.1	4.3	5

[a]Fishing effort is the number of fishing gear deployments within a 5-km radius of the mega-boxcore sample between January 1992 and December 2006.

Table 2. Summary of R^2 values from standard regression tests between pairs of measured variables.

Variable	Depth	Temperature	% Clay	% Silt	% Sand	Fishing effort
Depth	–					
Temperature	20.5	–				
% Clay	**51.4**	n.a.	–			
% Silt	1.8	n.a.	n.a.	–		
% Sand	24.8	n.a.	n.a.	n.a.	–	
Fishing effort	**81.0**	n.a.	n.a.	n.a.	n.a.	–
No. of taxa (S)	20.5	11.8	6.6	16.8	0.1	11.5
Abundance (N)	0.1	1.6	4.1	6.2	9.7	0.0
Biomass (B)[a]	**85.5**	**40.0**	19.1	15.7	1.3	17.4
Diversity (N1)	13.4	17.2	25.3	8.2	5.5	7.9
Evenness (N21')	0.0	9.9	6.7	2.0	8.4	1.8
No. of VME taxa	**53.7**	**39.1**	17.6	3.2	5.3	20.8
Abund. VME taxa	**41.9**	14.2	14.1	1.5	14.2	12.9
Biomass VME taxa[a]	**56.6**	**39.6**	**29.0**	5.3	8.8	24.0

Statistically significant correlations between variables are shown emboldened ($p < 0.05$).
[a]Regression conducted excluding a single outlier value belonging to a large sponge specimen in sample BC89. Statistical significance of regression tests was not affected by the exclusion.
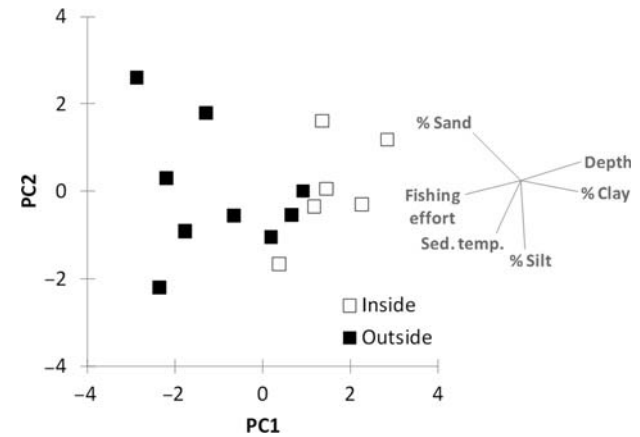
Figure 2. PCA plot of environmental variables measured at each of the sampling sites. Sites are coded according to whether they fell inside or outside the designated closed area.

samples according to the relative proportions of silt and sand, and sediment temperature. The location of sampling sites in relation to the closed area is reiterated in the plot, with those from inside the area generally being deeper, less disturbed, etc., and *vice versa*. Naturally, a degree of overlap is also observed.

A total of 11 062 organisms were processed, representing 165 taxa. Almost half of all organisms sampled (49%) were crustacean arthropods, the remaining half comprised polychaetous annelids (21%), nematodes (20%), mostly bivalve molluscs (6%), echinoderms (2%), and "others" (2%). The breakdown of wet-weight biomass among phyla was much more equitable, with sponges accounting for 23% of the biomass, followed by molluscs (17%), ascideans (chordata—15%), crustaceans (15%), annelids (14%), echinoderms (10%), and "others" (6%; note: a single, large sponge specimen accounting for almost half of all wet biomass recorded was omitted from these results, as it was the water retained within it that contributed the most to its weight).

Table 3. Taxonomic groups recognized as being indicative of VMEs in NAFO regulatory area (based on Fuller *et al.,* 2008).

Phylum	Taxon	Common name
Arthropoda	Cirripedia (Infraclass)	Barnacles
Brachiopoda	Brachiopoda (Phylum)	Brachiopods
Bryozoa	Bryozoa (Phylum)	Lace corals
Chordata	Ascidiacea (Class)	Sea squirts
Cnidaria	Antipatharia (Order)	Black corals
	Gorgonacea (Order)	Sea fans
	Scleractinia (Order)	Stony corals
	Pennatulacea (Order)	Sea pens
	Ceriantharia (Order)	Tube anemones
	Actinaria (Order)	Sea anemones
	Zoanthidea (Order)	Zoanthids
	Hydrozoa (Order)	Hydroids
Echinodermata	Crinoidea (Class)	Sea lilies
	Echinoidea (Class)	Urchins
	Asteroidea (Class)	Starfish
	Holothuroidea (Class)	Sea cucumbers
	Ophiuroidea (Class)	Brittlestars
Foraminifera	Xenophyophorea (Class)	Giant, single-celled protozoans
Mollusca	Limidae (Family)	File clams
Porifera	Demospongiae (Class)	Siliceous sponges
	Godiidae (Family)	Siliceous sponges
	Theneidae (Family)	Siliceous sponges
	Hexactinellida (Class)	Glass sponges

Not all taxa listed were recorded in this study and not every species within a taxon is indicative of VMEs.

Abundance values per sample ranged from 173 (BC89) to 1661 (BC70), and the number of taxa recorded varied between 29 (BC79) and 74 (BC70; Table 1). Biomass values per sample were even more variable, ranging from 0.6 g (BC93) to 51.4 g (BC89), though most of this higher value was contributed by a single sponge specimen. Excluding this specimen, biomass at BC89 was still the highest recorded in the study (17.4 g). Of all three variables, only biomass was correlated with changes in depth and sediment temperature, each accounting for 86 and 40% respectively, to differences in biomass (Table 2). Biomass was higher at deeper and colder sampling stations.

Based on published literature (Fuller *et al.*, 2008 and references therein), taxa were further classified into two broad categories, depending on whether they could be considered indicative of VMEs or not (Table 3). Subsequently, a number of analyses were performed using only the list of taxa considered indicative of VMEs. The number of VME indicative taxa, their abundance, and their biomass were all correlated with depth, differences in depth contributing to ~50% of the variation in all three variables (Table 2). Differences in temperature were also correlated with differences in the number and biomass of VME indicative taxa, accounting for 40% of the variation in both. Lastly, variation in the proportion of clay in the sediment at different sampling sites was responsible for 29% of the variation in the biomass of VME indicative taxa.

Comparing the macrofaunal assemblage living inside and outside the closed area, it is evident that there is little difference between the two, based on the relative values of metrics and indices calculated (Figure 3). Only biomass appeared to be significantly higher inside the closed area than outside. It is worth noting that variability in biomass was also much greater inside the closed area, samples outside yielding consistently low levels of biomass. The subsample of taxa that are considered indicative of VMEs,

on the other hand, showed clear differences between inside and outside the closed area, with all metrics except taxon evenness being significantly different. VME taxa were present in significantly greater numbers, indicative of a greater diversity inside the closed area than outside (Figure 1).

Differences in calculated metrics were also evident between the assemblages living above or below the 1200-m depth contour. Specifically, the biomass, the number of all taxa, and the number of VME indicative taxa were all significantly higher at depths greater than 1200 m (Figure 3), as was the diversity of VME indicative taxa. Lastly, only the assemblage comprising just VME indicative taxa was significantly affected by the presence of spicule mats, with their number, abundance, and biomass being higher in samples showing evidence of dense spicule mats.

Multivariate analyses revealed several noteworthy patterns in the dataset. According to the results form ANOSIM tests, there appear to be significant differences in macrofaunal community structure between samples inside and outside the closed area (Table 4). This difference is not only apparent at the finest level of taxonomic resolution afforded by the dataset, but can also be detected after the data have been aggregated to higher taxonomic levels. It would appear, therefore, that differences in community structure that exist between inside and outside the closed area are deeply rooted in the taxonomic composition of the assemblage, and are not simply a reflection of slight differences in the relative abundance of some species. Even after the dataset has been reduced to just two variables (VME taxa and non-VME taxa), the difference in community structure between inside and outside the closed area is still statistically significant.

Although similar significant differences in community structure were evident between samples above and below the 1200-m depth contour, such differences were no longer apparent after the data were aggregated to the level of class (Table 4). Conversely, the presence of spicule mats appeared to influence macrofaunal community structure even after the data were aggregated to the level of phylum, as differences in community structure at this level were still apparent. However, this difference in community structure was no longer evident at the coarsest level of aggregation (VME and non-VME indicative taxa). Moreover, results from a simultaneous CLUSTER and SIMPROF routine on the fully resolved dataset revealed seven statistically distinct assemblages, four of which each represented by a single sampling site (data not shown). After data were aggregated to class, the same routine produced just three statistically distinct assemblages, only one represented by a single sample. The remaining two distinct assemblages were broadly differentiated by whether they contained dense spicule mats or not (data not shown). Based on these results, it would seem that the presence of spicule mats and the location of samples in relation to the closed area have a greater power to explain patterns in the structure of the macrofaunal assemblage than a 1200-m depth boundary.

Conducting a SIMPER test on the dataset aggregated to class generates the relative contribution of each class to the observed differences between treatments (Table 5). It is clear from the colour scale used to ease interpretation of the results that relative abundance of classes was generally higher inside the closed area than outside (i.e. orange and yellow shades—representing higher values—are more prominent down the column labelled "Inside" in Table 5). Of the five taxa with the highest % contribution to the dissimilarity between treatments, only the polychaets were found at lower abundance inside the closed area. Similarly, relative abundance values for most taxa were perceptibly higher in samples
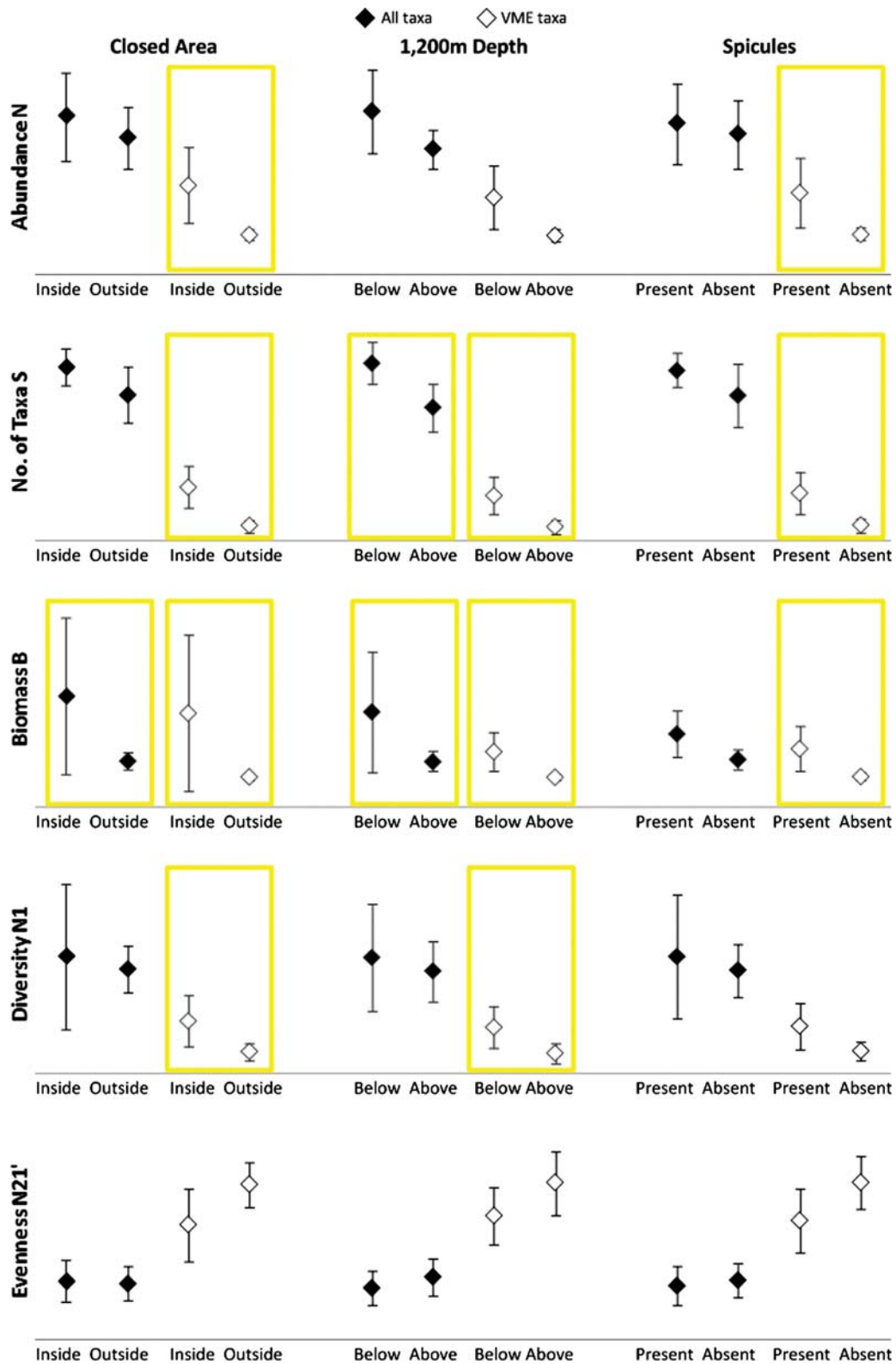
Figure 3. Pairwise comparisons of the sampled macrofaunal assemblage divided between the various treatments. Treatments include inside vs. outside the closed area, above vs. below the 1200-m depth contour and presence vs. absence of spicule mats. Comparisons are made using the whole sampled assemblage, as well as just those taxa that are indicative of VMEs. Statistical significance of differences in assemblages between treatments is illustrated by a coloured box ($p < 0.05$).

Table 4. Summary of results from ANOSIM tests performed on the dataset at different levels of taxonomic aggregation, comparing the assemblage between different treatments.

Taxon aggregation level	Number of variables	ANOSIM *R*-value	Significance level (%)
Inside vs. outside			
Taxa (raw data)	165	0.550	0.1
Family	110	0.503	0.2
Class	23	0.476	0.2
Phylum	11	0.353	0.8
VME/not VME	2	0.431	0.8
Above vs. below 1200 m			
Taxa (raw data)	165	0.420	0.3
Family	110	0.426	0.3
Class	23	0.156	5.4
Phylum	11	0.163	5.0
VME/not VME	2	0.165	6.1
Presence vs. absence of spicules			
Taxa (raw data)	165	0.485	0.2
Family	110	0.494	0.1
Class	23	0.246	0.9
Phylum	11	0.268	0.5
VME/not VME	2	0.179	5.4

that contained evidence of dense spicule mats. It is also interesting to note that taxa which are indicative of VMEs are always found in greater abundance in samples inside the closed area and supporting spicule mats. VME indicative taxa, however, are not among the highest contributors to the dissimilarity between assemblages characterizing each treatment. Taxa that show a higher relative abundance outside the closed area and where no spicule mats were observed are the polychaetes, gastropods, nemerteans, bivalves, scaphopods (tusk shells), maxilopods (mostly copepods), and anthozoans (stony corals). Most of these taxa can be considered as fairly resilient and not necessarily indicative of VMEs.

Finally, results from the BIOENV routine reveal which of the measured environmental variables have the greatest influence—either in isolation or in combination—on macrofaunal community structure. Again, both the full faunal dataset and that comprising just VME indicative taxa were analysed. When all faunal data are used, the single environmental variable which best explains observed patterns in community structure is depth (Spearman's correlation: 0.457). A combination of three variables showed the highest correlation with the faunal dataset (0.594); they were depth, sediment temperature, and % silt. However, there was very little difference in the correlation value when any

Table 5. Summary of results from SIMPER tests, showing the relative abundance values for each class within each treatment and the % contribution of each class to the dissimilarity between treatments.

Closed Area

Taxa	Inside	Outside	% Contrib.
Polychaeta	3.21	4.01	7.88
Nematoda	3.24	1.16	9.20
Ophiuroidea	3.22	0.26	10.55
Gastropoda	1.33	2.11	5.17
Nemertea	1.31	1.75	5.47
Bivalvia	0.87	1.79	4.47
Aplacophora	1.17	1.44	5.71
Hydrozoa	2.00	0.11	7.31
Demospongiae	1.87	0.11	7.14
Malacostraca	0.95	0.78	3.38
Scaphopoda	0.17	1.56	5.43
Crinoidea	1.33	0.11	4.65
Sipunculida	1.16	0.16	3.44
Maxillopoda	0.47	0.82	2.83
Holothuroidea	1.18	0.04	3.66
Ascidiacea	0.83	0.33	2.97
Anthozoa	0.15	0.73	2.44
Porifera	0.77	0.00	2.70
Pycnogonida	0.67	0.00	2.41
Ostracoda	0.00	0.37	1.22
Priapulida	0.17	0.11	0.85
Asteroidea	0.17	0.00	0.49
Cnidaria	0.17	0.00	0.65
TOTAL	26.41	17.75	

Spicules

Taxa	Present	Absent	% Contrib.
Polychaeta	2.99	4.3	8.98
Nematoda	3.11	1.02	9.30
Gastropoda	1.14	2.38	6.21
Nemertea	1.58	1.58	5.80
Ophiuroidea	2.85	0.21	9.39
Bivalvia	0.84	1.94	5.04
Aplacophora	1.14	1.5	5.74
Scaphopoda	0.14	1.75	6.51
Hydrozoa	1.71	0.13	6.22
Demospongiae	1.6	0.12	6.06
Malacostraca	0.85	0.85	3.39
Maxillopoda	0.4	0.92	3.12
Crinoidea	1.29	0	4.92
Sipunculida	1.04	0.13	3.11
Ascidiacea	0.71	0.38	2.71
Holothuroidea	1.01	0.04	3.11
Anthozoa	0.13	0.83	2.88
Porifera	0.66	0	2.27
Pycnogonida	0.57	0	2.03
Ostracoda	0	0.41	1.46
Priapulida	0.14	0.13	0.80
Asteroidea	0.14	0	0.41
Cnidaria	0.14	0	0.55
TOTAL	24.18	18.62	

For each comparison, classes are ordered in decreasing order of combined abundance, and each cell is colour-coded on a colour scale to reflect the relative contribution of each class to the whole assemblage (red, high; yellow, medium; green, low). Taxa broadly considered as indicative of VMEs are emboldened.

other combination of variables were compared. When just the VME taxa are used, the single environmental variable showing the highest correlation with VME community structure is fishing effort (Spearman's correlation: 0.330). No combination of variables showed a higher correlation with VME community structure, but the next highest correlation value was assigned to a combination of % clay and fishing effort (0.308), followed by the same two variables and depth (0.261).

Discussion
Macrofaunal characterization

There are limitations to the type of study like the one presented here which must be acknowledged. First, the data selected to conduct this investigation were acquired by a method used to target infauna. Epifauna are underrepresented in boxcore samples, and since most taxa indicative of VMEs are epifaunal, any conclusions based on their observed patterns of distribution must be treated with caution. However, this does not mean that the study and reporting of patterns in infaunal assemblage composition cannot provide useful insights to the management of benthic habitats, as infaunal community structure is influenced by the epifauna and observed differences in the infaunal assemblage can reflect differences in the function of benthic ecosystems (Biles *et al.*, 2002). Second, because the closed area at the Sackville Spur was put in place after much of the bottom fishing activity had occurred in the surrounding area, it is important not to attribute directly any differences observed in the macrofaunal assemblage from inside and outside the closed area to the deliberate exclusion of fishing. Historical bottom fishing activity has been concentrated mostly in areas above the 1200-m depth contour, avoiding deeper waters (Figure 1). The lack of sufficient macrofaunal samples representing areas above the 1200-m depth contour that are untouched by fishing and equally, samples representing areas below that depth which have been subject to intense fishing activity, precludes rigorous statistical testing of the true effects of fishing on the sampled macrofaunal assemblage at various depths. With the level of sampling effort and replication within different treatments afforded by the present study, it cannot be stated categorically that any difference in community structure is due solely to fishing or its exclusion.

What is apparent from the results here reported is that differences in the macrofaunal assemblage in and around the Sackville Spur closed area do exist, and that there are several likely explanations. Depth is certainly a key consideration, given that total biomass and the abundance, number, and biomass of VME indicative taxa were all correlated with depth (Table 2), as well as some of those same variables and community structure being significantly different above and below the 1200-m depth contour (Figure 3 and Table 4). However, evidence also suggests that depth may not be the most influential of all the factors considered in this study (see Flach, 2002, for a similar result from the European continental slope). Perhaps the most telling piece of evidence to undermine the influence of depth as the primary driver for the differences observed is that differences in assemblage composition between deeper and shallower samples are not preserved when data are aggregated above the level of class (Table 4). This suggests that depth alone is only of influence superficially, affecting the abundance, number, identity, and diversity of species, but does not have as big an influence on the higher taxonomic levels that are at the foundation of community structure. In other words, assemblages at all depths within the range sampled can potentially accommodate any

indigenous taxa, but the exact mix of those taxa will be influenced more strongly by factors other than depth. It has been suggested that anthropogenic disturbance can modify community composition at a higher taxonomic level than natural variability in the environment, which influences the fauna more by species replacement (Warwick, 1988). Factors such as sediment composition or the presence or absence of spicule mats, more readily altered by bottom-contact fishing activity and not as readily affected by depth alone, appear to have a greater influence on how communities around the Sackville Spur are structured, often right up to the highest level of taxonomic aggregation.

That sediment composition, or substrate type, should have an influence on the structure of the macrofaunal community around the Sackville Spur is not unexpected. Taxa indicative of VMEs select their preferred substrate type on which to settle and some, in turn, can themselves provide substrates for other organisms to inhabit. Clay was observed to comprise a smaller proportion of the sediment at shallower depths (Figure 2 and Table 2), which supports the notion of finer particles being winnowed out as deep-water currents accelerate when they are deflected up the slopes of the Spur (Genin *et al.*, 1986; Genin, 2004). The sedimentary profile resulting from this phenomenon, namely an increased exposure of coarser, more stable substrate at shallower depths, is favoured by epifaunal taxa seeking attachment spots, like sponges. It follows that VME indicative taxa ought to be more prevalent at shallower depths on the Spur (see Hughes and Gage, 2004, for examples where this is the case in the Northeast Atlantic), where the substrate is relatively harder than at depth. However, this was not the case. Something is clearly disrupting this expected distribution of VME indicative taxa in the samples.

Despite the theoretical limitations of the present study (outlined above), fishing effort cannot be disregarded as an influential factor on the patterns observed in the macrofaunal assemblage, especially given its strong inverse correlation with depth. Bottom trawling, in particular, is known to significantly impact habitats and fauna long after the initial disturbance (Mortensen *et al.*, 2005; Queirós *et al.*, 2006; Engel and Kvitek, 2008; Althaus *et al.*, 2009; Clark and Rowden, 2009; Murillo *et al.*, 2011). However, on its own, fishing effort did not appear to influence any of the calculated assemblage metrics (Table 2). Variability in fishing effort did, however, show the highest (though weak) correlation with the community structure of VME indicative taxa. Leaving the paucity of direct correlations aside, it is difficult to ignore the fact that significantly higher values of many of the assemblage metrics calculated were recorded from within the closed area and below the 1200-m depth contour (Figure 3), beyond the limit of most fishing effort. The presence of dense spicule mats, which have also been shown to greatly influence macrofaunal community structure (Bett and Rice, 1992), was also broadly confined to areas beyond the reach of most fishing gears. It is possible that repeated disturbance of the seabed by bottom fishing gears can disrupt the integrity of dense spicule mats, which can then no longer inhibit certain infaunal taxa or provide the hard substrate sought by some epifaunal taxa for attachment. This is a likely explanation for the disruption of the expected distribution of more VME indicative taxa at shallower depths on the crest of the Spur.

The difference in relative abundance values of certain taxa between inside and outside the closed area, and between samples with and without spicule mats, can be informative of the conditions these organisms encounter (Table 5). Organisms recorded in greater abundance outside the closed area and where spicule

mats were mostly absent, tend to be either soft-bodied or hard-shelled soft-sediment dwellers (i.e. intolerant or indifferent to a matrix of sharp sponge spicules), predatory, scavenging, or detritus-feeders and generally characteristic of disturbed environments (e.g. polychaetes, nemerteans, gastropods, bivalves, scaphopods). Some such organisms are also present inside the closed area and where spicule mats are present, but in addition to other more abundant organisms with their own particular characteristics. Organisms that were most abundant inside the closed area and in association with spicule mats tended to be more robust, often able to protrude above the sediment surface for suspension or filter feeding (e.g. hydroids, sponges, crinoids, ascideans), able to climb or live upon epifauna (e.g. filter feeding ophiuroids, errant predatory, or tube-dwelling deposit/filter-feeding polychaetes), or take advantage of the increased textural complexity by living within sponges and the spicule matrix (e.g. nematodes; Buhl-Mortensen *et al.*, 2010). The added structural complexity afforded by such robust-looking organisms disguises the fact that they are in fact extremely fragile and vulnerable to damage by direct disturbance such as bottom trawling. Further work on faunal associations is necessary to add detail to the generalized patterns observed in this study.

Recommendations

The macrofaunal assemblage (as sampled by boxcores) inside the exclusion zone has a greater abundance, biomass, diversity, and number of VME indicative taxa than sediments outside the zone, and it is fundamentally different in community structure. Given that the rationale for implementing the closed areas is to protect and safeguard the future of VMEs, it is recommended that, for the time being, the Sackville Spur closed area is maintained in its current form. Results from analyses of megafaunal assemblages currently underway will assist in the decision of whether the closure should be made indefinite.

Formal scientific investigations to confirm the effectiveness of closed areas can be costly and time-consuming, often taking longer to accomplish than the timelines allocated for reaching management decisions. The fact that traits that make taxa indicative of VMEs tend to be expressed at a high level of taxonomic resolution suggests that one time-consuming element that could be streamlined for future similar assessments is the formal taxonomic identification of specimens.

Deep-sea invertebrate taxonomy is in its infancy; this, coupled with the small number of deep-sea taxonomy practitioners, often results in there being a taxonomic impediment or bottleneck to identify with competence the many specimens that are often recovered by surveys of this kind. This study has revealed that many of the differences in macrofaunal community structure between sediments inside and outside closed areas are still evident at higher levels in the taxonomic hierarchy. Under similar circumstances (i.e. where the level of sampling effort and spatial coverage are similar), therefore, the assessment of such differences could be fast-tracked by limiting the formal identification of organisms to higher taxonomic levels. Identification of organisms at such a level may enable non-specialist taxonomists to generate datasets suitable for this type of investigation, which in turn could speed up the process of assessment and decision-making by the management organizations. However, the acquisition and repeated handling of such specimens are very expensive, and the chances of a specialist finding the time to revisit them after initial viewing are slim. Far from strongly recommending that,

for convenience or expediency, taxonomic identification stops short of what is capable by the available experts, it is preferable that as much information is extracted from organisms when the opportunity arises (and have the option to not use it) than to find out at a later stage that insufficient information is available to the study in hand. Ultimately, should resources only stretch to cover basic taxonomic identification, coarse level data may still suffice to detect patterns which can support decisions for management purposes.

Acknowledgements

References

Althaus, F., Williams, A., Schlacher, T. A., Kloser, R. J., Green, M. A., Barker, B. A., Bax, N. J., *et al.* 2009. Impacts of bottom trawling on deep-coral ecosystems of seamounts are long-lasting. Marine Ecology Progress Series, 397: 279–294.

Bett, B. J., and Rice, A. L. 1992. The influence of hexactinellid sponge (*Pheronema carpenteri*) spicules on the patchy distribution of macrobenthos in the Porcupine Seabight (bathyal NE Atlantic). Ophelia, 36: 217–226.

Biles, C., Paterson, D., Ford, R., Solan, M., and Raffaelli, D. 2002. Bioturbation, ecosystem functioning and community structure. Hydrology and Earth System Sciences, 6: 999–1005.

Bowering, W. R., Brodie, W. B., Morgan, M. J., Power, D., and Rivard, D. 2000. An Assessment of Greenland Halibut in NAFO Subarea 2 and Divisions 3KLMNO. NAFO SCR Document 00/43, Serial No. N4274. 33 pp.

Buhl-Mortensen, L., Vanreusel, A., Gooday, A. J., Levin, L. A., Priede, I. G., Mortensen, P. B., Gheerardyn, H., *et al.* 2010. Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Marine Ecology, 31: 21–50.

Clarke, K. R., Chapman, M. G., Somerfield, P. J., and Needham, H. R. 2006. Dispersion-based weighting of species counts in assemblage analyses. Marine Ecology Progress Series, 320: 11–27.

Clark, M. R., and Rowden, A. A. 2009. Effect of deep water trawling on the macro-invertebrate assemblages of seamounts on the Chatham Rise, New Zealand. Deep Sea Research I, 56: 1540–1554.

Engel, J., and Kvitek, R. 2008. Effects of otter trawling on a benthic community in Monterey Bay National Marine Sanctuary. Conservation Biology, 12: 1204–1214.

FAO. 2001–2011. Fishing ear types. Bottom otter trawls. Technology fact sheets [online]. FAO Fisheries and Aquaculture Department, Rome. Updated 13 September 2001. http://www.fao.org/fishery/geartype/306/en (last accessed 15 July 2011).

FAO. 2008. Report of the FAO Workshop on Vulnerable Ecosystems and Destructive Fishing in Deep-Sea Fisheries, 26–29 June 2007, Rome. FAO Fisheries Report, 829. 27 pp.

Flach, E. C. 2002. Factors controlling soft bottom macrofauna along and across European continental margins. *In* Ocean Margin Systems, pp. 351–363. Ed. by G. Wefer, D. Billett, D. Hebbeln, B. B. Jørgensen, M. Schlüter, and T. Van Weering. Springer-Verlag, Berlin, Heidelberg.

Fuller, S. D., Murillo Perez, F. J., Wareham, V., and Kenchington, E. 2008. Vulnerable marine ecosystems dominated by deep-water corals and sponges in the NAFO convention area. NAFO SCR Document 08/22, Serial No. N5524. 24 pp.

Genin, A. 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. Journal of Marine Systems, 50: 3–20.

Genin, A., Dayton, P. K., Lonsdale, P. F., and Spiess, F. N. 1986. Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. Nature, 322: 59–61.

Gubbay, S. 2002. The Offshore Directory: review of a selection of habitats, communities and species of the north-east Atlantic. WWF-UK: North-East Atlantic Programme. 108 pp.

Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology, 54: 427–432.

Hughes, D. J., and Gage, J. D. 2004. Benthic metazoan biomass, community structure and bioturbation at three contrasting deep-water sites on the northwest European continental margin. Progress in Oceanography, 63: 29–55.

Kenchington, E., Lirette, C., Cogswell, A., Archambault, D., Archambault, P., Benoit, H., Bernier, D., *et al.* 2010a. Delineating coral and sponge concentrations in the biogeographic regions of the east coast of Canada using spatial analyses. Canadian Science Advisory Secretariat (CSAS) Research Document, 2010/041. Fisheries and Oceans Canada. 208 pp.

Kenchington, E., Power, D., and Koen-Alonso, M. 2010b. Associations of demersal fish with sponge grounds in the Northwest Atlantic Fisheries Organisation Regulatory Area and adjacent Canadian waters. Canadian Science Advisory Secretariat (CSAS) Research Document, 2010/039. Fisheries and Oceans Canada. 33 pp.

Kennard, L., Schafer, C., and Carter, L. 1990. Late Cenozoic evolution of Sackville Spur: a sediment drift on the Newfoundland continental slope. Canadian Journal of Earth Sciences, 27: 863–878.

Mortensen, P. B., Buhl-Mortensen, L., Gordon, D. C., Fader, G. B. J., McKeown, D. L., and Fenton, D. G. 2005. Effects of fisheries on deep-water gorgonian corals in the Northeast Channel, Nova Scotia (Canada). American Fisheries Society Symposium, 41: 369–382.

Murillo, F. J., Durán Muñoz, P., Altuna, A., and Serrano, A. 2011. Distribution of deep-water corals of the Flemish Cap, Flemish Pass, and the Grand Banks of Newfoundland (Northwest Atlantic Ocean): interaction with fishing activities. ICES Journal of Marine Science, 68: 319–332.

Murillo, F. J., Kenchington, E., Gonzalez, C., and Sacau, M. 2010. The use of density analyses to delineate significant concentrations of pennatulaceans from trawl survey data. NAFO SCR Document 10/07, Serial No. N5753. 7 pp.

NAFO 2010. Northwest Atlantic Fisheries Organization—conservation and enforcement measures. NAFO/FC Document 11/1, Serial No. N5867. 98 pp.

Queirós, A. M., Hiddink, G., Kaiser, M. J., and Hinz, H. 2006. Effects of chronic bottom trawling disturbance on benthic biomass, production and size spectra in different habitats. Journal of Experimental Marine Biology and Ecology, 335: 91–103.

Vinnichenko, V. I. 2010. Russian investigations of Vulnerable Marine Ecosystems in the Newfoundland area. Working Document included in the ICES. Report of the ICES/NAFO Joint Working Group on Deep-water Ecology (WGDEC), 22–26 March 2010, Copenhagen, Denmark. ICES Document CM 2010/ACOM: 26. 160 pp.

Warwick, R. M. 1998. The level of taxonomic discrimination required to detect pollution effects on marine benthic communities. Marine Pollution Bulletin, 19: 259–268.

Handling editor: Howard Browman