Vol. 477: 217–230, 2013
doi: 10.3354/meps10127

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 12

Associations of demersal fish with sponge grounds on the continental slopes of the northwest Atlantic

E. Kenchington[1,*], D. Power[2], M. Koen-Alonso[2]

[1]Fisheries and Oceans Canada, Bedford Institute of Oceanography, 1 Challenger Drive, Dartmouth, Nova Scotia B2Y 4A2, Canada

[2]Fisheries and Oceans Canada, Northwest Atlantic Fisheries Centre, PO Box 5667, St. John's, Newfoundland A1C 5X1, Canada

ABSTRACT: Association of demersal fish taxa with *Geodia*-dominated temperate sponge grounds was examined in 104 research vessel survey trawl sets from 500 to 1500 m depth along the continental slopes of the Grand Banks and Flemish Cap, northwest Atlantic. The total number of fish taxa and their total biomass were negatively correlated with sponge biomass and catch depth, and sponge biomass increased with depth. ANOSIM identified significantly different fish communities (biomass and abundance composition) associated with 3 sponge catch weight classes, and multidimensional scaling plots showed separation of trawl sets labelled by this factor to be strongest for abundance. SIMPER analysis identified the fish assemblage associated with the sponge grounds (≥250 kg km^{-1}): roughhead grenadier *Macrourus berglax*, roundnose grenadier *Coryphaenoides rupestris*, blue hake *Antimora rostrata*, longnose eel *Synaphobranchus kaupii*, turbot *Reinhardtius hippoglossoides*, black dogfish *Centroscyllium fabricii* and deep-sea cat shark *Apristurus profundorum*. These contributed to 92 and 81% of the similarity (~50%) among trawl set catches using biomass and abundance data, respectively. Four additional taxa contributed to 92% similarity in abundance: common grenadier *Nezumia bairdii*, shortnose snipe eel *Serrivomer beanii*, lanternfish (Myctophidae) and goitre blacksmelts *Bathylagus euryops*. SIMPER dissimilarity identified 6 fish taxa with larger biomass in catches with high sponge catch weight: shortnose snipe eel, deep-sea cat shark, eelpout *Lycodes* spp., spinytail skate *Bathyraja spinicauda*, white skate *Dipturus linteus* and deepwater chimaeras *Hydrolagus affinis*. The first 3 species were also more abundant in those catches and are considered to be strongly associated with the sponge grounds. Future research focussing on these species identified as being associated with the sponge grounds may provide greater insight into the strength of the associations and the ecological linkages between these benthic and pelagic communities.

KEY WORDS: Demersal fish assemblages · Sponge grounds · Trawl catch

INTRODUCTION

The importance of individual sponges as microhabitat for invertebrate species has been widely demonstrated and includes a wide range of ecological interactions including both facultative and obligate commensalisms (see recent reviews by Wulff 2006 and Bell 2008, and articles specific to the North Atlantic by Bett & Rice 1992, Klitgaard 1995, Klitgaard & Tendal 2004, ICES 2009, Hogg et al. 2010, Barrio Froján et al. 2012). At these small spatial scales, sponge architecture is an important determinant of the type and strength of such interactions, as sponge morphology includes a wide diversity of forms.

At larger spatial scales, the use of temperate sponge grounds as habitat for fish assemblages has been less well documented, especially in terms of

---

*Email: ellen.kenchington@dfo-mpo.gc.ca

Publisher: Inter-Research · www.int-res.com

obligative, facultative, or opportunistic relationships (Hixon et al. 1991, ICES 2009, Hogg et al. 2010). Sponges can form dense aggregations in some temperate waters, including biogenic reefs (e.g. Hectate Glass Sponge Reefs in British Columbia, Canada; Chu & Leys 2010, Hogg et al. 2010) and sponge grounds (e.g. continental slope off Labrador, Canada; Kenchington et al. 2010). The latter are characterized by the presence of 1 or more dominant taxa which have a larger individual- and population-level biomass than smaller associated sponge species. Such structure-forming species include members of the genera *Geodia*, *Stryphnus*, *Asconema*, *Vazella* and *Stelletta*, amongst others (ICES 2009). Fish often use the structural habitat that sponge grounds provide for shelter, reproduction and to forage for food (Bell 2008). The 3-dimensional spatial complexity of sponge grounds also provides important nursery grounds for juvenile fish in their early stages of growth (Auster et al. 2003, Freese & Wing 2003) and shelter for all life stages (Brodeur 2001). Rockfish (or 'redfish') of the genus *Sebastes* are particularly prevalent in sponge grounds in some areas, living both inside and between the sponges (Richards 1986, Freese & Wing 2003, Marliave et al. 2009, Du Preez & Tunnicliffe 2011). Marliave et al. (2009) describe habitat partitioning by *Sebastes maliger* in which adults are associated with the reef structures (bioherms) and juveniles are associated with single sponges or lower density 'sponge gardens'. *S. maliger* feeds on benthic crustaceans, and the authors hypothesize that increased species richness in the food resource on the sponge gardens drives this distribution pattern. However, avoidance of certain sponges by some species may also occur. Bell (2008) cites a number of examples in which the chemical compounds of the sponges act as deterrents to other organisms. In temperate waters, Marliave et al. (2009) show regional patterns in British Columbian waters (Northeast Pacific) in the association of adult *S. maliger* with the sponge reef structures, with the fish absent from some sponge reefs entirely but present in nearby areas. There is also some evidence that removal of temperate sponge grounds by bottom trawling changes the composition of the fish fauna, providing weak evidence for the association of some fish with such habitats (cf. Klitgaard & Tendal 2004). Thus, it seems that temperate sponge grounds may be an important refuge and habitat for fish as well as invertebrates, although little ecological work has been carried out to understand the exact nature of this habitat use in the deep sea, and most studies to date are limited to tropical waters (e.g. McCormick 1994, Cleary & de Voogd 2007).

Given the limited evidence in the literature regarding temperate sponge and fish interactions, we identified a need to look at large-scale species associations. Fish species that are consistently associated with temperate sponge grounds, when alternative habitats are available, are likely to be actively selecting the sponge grounds for some purpose. Here we present novel data on the presence/absence of fish assemblages compared with sponge biomass in the temperate waters of the northwest Atlantic. We describe the relationship between the fish fauna associated with the sponge grounds on the continental slopes of the Grand Banks and Flemish Cap, off Newfoundland, Canada. We give a particular focus to the Northwest Atlantic Fisheries Organization (NAFO) Regulatory Area (NRA, seaward of the Canadian 200 mile limit), where these sponge grounds are located and have been verified with *in situ* photography (NAFO 2010). The sponges in this area are dominated by *Geodia* species, which are massive ball sponges found throughout the North Atlantic (ICES 2009). However, at least 27 different species have been identified in the study area (Murillo et al. 2012). *Geodia barretti*, *G. phlegraei*, *G. macandrewi*, *Stryphnus ponderosus* and *Stelletta normani* are the main structural sponges and constitute >99% of the total invertebrate biomass (Murillo et al. 2012). These species all have similar morphologies, being massive spherical/lobed sponges reaching diameters in the range of 20 to 55 cm (Best et al. 2010). Although pelagic fish may use sponge grounds as habitat, we expect that if there are any large-scale associations between fish assemblages and sponge grounds, they will be strongest in demersal fish assemblages which are more closely associated with the sea floor. Our hypothesis is that demersal fish assemblages caught in research vessel trawl catches will differ in areas of low, medium and/or high sponge biomass.

MATERIALS AND METHODS

Data sources and selection

Data used for these analyses come from the Fisheries and Oceans Canada (DFO) Newfoundland Region fall multispecies surveys of the Grand Banks inside and adjacent to Canada's exclusive economic zone. These surveys followed a depth-stratified random design to 1500 m and employed a Campelen 1800 shrimp trawl. The Campelen carries out 15 min tows using a towing speed of 3.0 knots. The catches were standardized to a 1 km distance towed. The average wingspread was 16.84 m. Because catchability of the standard survey trawl was unknown for most species, the indices were considered to be relative estimates only. A trawl-mounted CTD was used to collect temperature data. The trawl sets were almost evenly split between day and night times. The catch was sorted at sea, and the number and weight (kg) of each taxon were recorded using a standard set of species codes. Fish were generally identified to species level, whereas sponges were only recorded as Porifera and weighed collectively for each set (not counted). Only records from 2001 to 2007 were used in order to avoid confounding the results by temporal trends due to environmental factors (cf. Colbourne 2004) and to ensure consistency of reporting. These records were further reduced to include: (1) only those sets deeper than 500 m, to minimize confounding of the results by including both shelf and slope taxa; (2) only those sets from south of 50°N latitude, in order to reduce confounding the results by introducing biogeographic differences in community composition through disproportionate representation of arctic and boreal faunas; and (3) only records in which the sponge catch was verified at sea through species keys or identified via representative samples post-survey (to avoid false identification of bryozoans and other taxa as sponges). For (3), zero sponge catch records were not included, as we could not be certain that sponges were not caught, as they may have just not been recorded. These criteria produced 104 trawl records for analysis, with an average depth of 1096 m (range: 578 to 1446 m) (Fig. 1).

The 104 selected trawls contained non-zero records for 200 taxa of fish. The weights and abundance of each of the taxa were standardized to a 1 km trawl, using the start and end positions of the trawl to calculate distance on bottom. This involved only a minor adjustment to the data, as the average trawl length was 0.8 ± 0.07 km (range: 0.6 to 1.0).

The 200 taxa were reduced by: (1) combining some species to higher level groupings and (2) eliminating all rarities after combining the data to include only taxa >0.1% of total biomass/abundance. The first of these steps was done to avoid introducing errors due to taxonomic imprecision among trips and also sets within trips. The second was to eliminate taxa that may not be reliably caught in the trawl, or whose rarity may escape detection in the routine sorting and sub-sampling processes. To determine the low end cut off, decisions were made on the size of the taxon relative to the biomass record before removing it from the list.

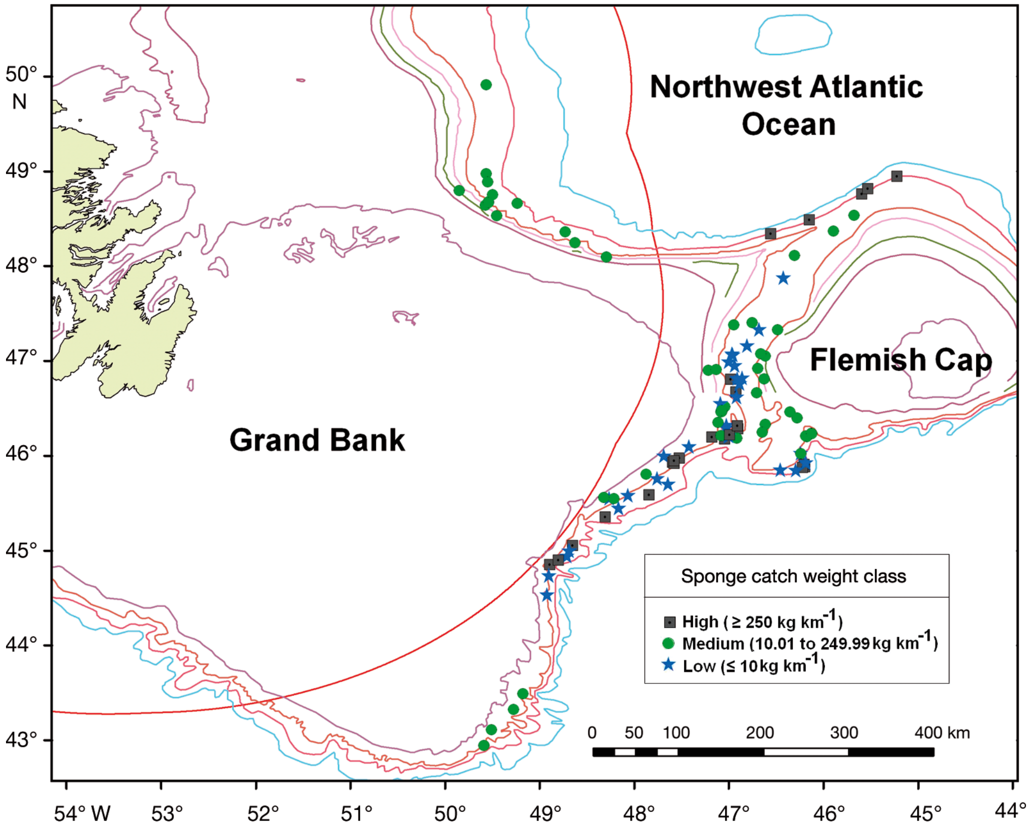

Fig. 1. Locations off Newfoundland, Canada, of the research vessel trawls used in our analyses, with corresponding sponge catch weight classes. Thick red line is the Canadian Exclusive Economic Zone (EEZ). Depth contours are shown for 200, 400, 600, 800, 1000, 1500 and 2000 m

Data analyses

The analytical variables used to describe the fish communities were: total number of fish taxa (number km^{-1} of the 34 species for which biomass was analyzed; see Table 1), total fish biomass (kg km^{-1}), total fish abundance (number km^{-1}), fish taxon biomass (weight in kg of each taxon, usually species, km^{-1}) and fish taxon abundance (number km^{-1}). Total sponge biomass (kg km^{-1}), average trawl depth (m) and bottom temperature (°C) were also recorded for each trawl set.

The cumulative distribution of total sponge biomass is highly right-skewed, that is, there are large numbers of very small catches and very few large ones (Kenchington et al. 2009). This distribution was used to categorize the trawl sets according to 1 of 3 arbitrary sponge catch weight classes which were selected to represent sponge grounds, transition areas and non-sponge ground, respectively (sponge catch weight class; see Supplement 1 at www.int-res.com/articles/suppl/m477p217_supp.pdf): high ($\geq$250 kg km^{-1}, which is the upper quartile of the distribution; N = 24), medium (10.01 to 249.99 kg km^{-1}; N = 30) and low ($\leq$10 kg km^{-1}, which is approximately the median of the distribution; N = 50). The high class equates to sponge grounds. The medium class may arise through trawl sets encountering the fringes of sponge grounds (research vessel trawl catches >75 kg of sponge per trawl set for this survey and area; Kenchington et al. 2009), or through the accumulation of smaller sponges that are not associated with sponge grounds (Kenchington et al. 2011). The low class is outside of the sponge grounds. The small weight threshold for this class could be achieved through collection of a single sponge.

The variance in average trawl depth (Supplement 1) was tested for equality among sponge catch weight classes using Levene's test and was found to be unequal (p = 0.04). This variable was analyzed in its untransformed state, and Welch's ANOVA was used to test for an effect of sponge catch weight class on average trawl depth. Tukey's HSD test was used for post hoc comparisons of the mean values to identify differences between factor levels. These and similar analyses below were performed with JMP v.6.0.3 software (SAS Institute). The locations of the trawl sets used in these analyses, identified by their sponge weight class, are illustrated in Fig. 1.

The variance of the total number of fish taxa (Supplement 1) was tested for equality among sponge catch weight classes using Levene's test and was found to be unequal; attempts to transform it did not improve its variance structure. This variable was analyzed in its untransformed state, and Welch's ANOVA was used to test for an effect of sponge catch weight class on total number of fish taxa. Tukey's HSD test was used for post hoc comparisons of the mean values to identify differences between factor levels. The total number of fish taxa was regressed against average trawl depth and log10-transformed total sponge biomass using a rank correlation.

Total fish biomass and total fish abundance (Supplement 1) were log10 transformed and their variances were found to be homogeneous among sponge catch weight classes using Levene's test. ANOVAs were used to assess whether mean total fish biomass and mean total fish abundance were equal among sponge catch weight classes. Tukey's HSD test was used for post hoc comparisons of the mean values to identify differences between factor levels. The variables were independently regressed against average trawl depth and log10-transformed total sponge biomass.

Differences in community composition among sponge weight classes were examined with ANOSIM (analysis of similarities; Clarke 1993). The test statistic, R, is based on comparing distances between groups with distances within groups using permutation. The degree of sensitivity of R to heterogeneity may be influenced by our unbalanced design, depending on whether the group with the larger numbers of samples (low sponge catch weight class) had greater or lesser dispersion than the other groups. In our data set, variance in fish taxon biomass was not statistically different among the sponge catch weight classes. Bray-Curtis similarity matrices of trawl set pairs were constructed based on the transformed fish taxon biomass (Table 1) and fish taxon abundance (Table 2) of the 34 fish taxa identified for each variable. A similarity of percentages (SIMPER) analysis was performed to quantify the level of similarity within and between groups and to identify the taxa contributing most to the dissimilarities. A multidimensional scaling (MDS) ordination of the Bray-Curtis similarity matrix was used to visualize the relationships among the trawl set catches. To select the environmental variables (total sponge biomass, average trawl depth and bottom temperature) that best explain the similarity of the demersal fish communities, the BIOENV procedure (BIOta ENVironment matching, Euclidean distance matrix for normalized environmental data, Spearman rank correlation method, 10 restarts, 99 permutations) was used. Unfortunately, the effect of sampling year could not be robustly tested due to small sample sizes and

Table 1. List of the 34 fish taxa analyzed for fish biomass association with sponge grounds, their common names, total fish taxon biomass (total B) and percent of total biomass (%) in 104 trawl sets standardized to 1 km distance

Fish taxon	Common name	Total B (kg km^{-1})	%
Somniosus microcephalus	Greenland shark	3555.56	26.56
Macrourus berglax	Roughhead grenadier	2477.42	18.51
Antimora rostrata	Blue hake	1738.51	12.99
Centroscyllium fabricii	Black dogfish	1091.65	8.16
Reinhardtius hippoglossoides	Turbot	846.83	6.33
Sebastes mentella	Deepwater redfish	574.43	4.29
Hippoglossoides platessoides	American plaice	546.04	4.08
Synaphobranchus kaupii	Longnose eel	543.07	4.06
Coryphaenoides rupestris	Roundnose grenadier	374.73	2.80
Apristurus profundorum	Deep-sea cat shark	185.44	1.39
Bathyraja spinicauda	Spinytail skate	171.28	1.28
Nezumia bairdii	Common grenadier	156.29	1.17
Anarhichas denticulatus	Broadhead wolffish	134.40	1.00
Notacanthus chemnitzii	Largescaled tapirfish	112.52	0.84
Amblyraja radiata	Thorny skate	109.71	0.82
Glyptocephalus cynoglossus	Witch glounder	96.09	0.72
Gaidropsarus spp.	Threebeard rockling	89.31	0.67
Hydrolagus affinis	Deepwater chimaera	87.46	0.65
Amblyraja jenseni	Jensen's skate	81.82	0.61
Dipturus linteus	White skate	62.07	0.46
Myctophidae	Lanternfishes	51.96	0.39
Notacanthidae	Spiny eels	38.78	0.29
Lycodes spp.	Eelpout	37.96	0.28
Lycodes vahlii	Vahl's eelpout	37.37	0.28
Serrivomer beanii	Shortnose snipe eel	31.25	0.23
Harriotta raleighana	Longnose chimaera	25.57	0.19
Phycis chesteri	Longfin hake	19.33	0.14
Bathylagus euryops	Goitre blacksmelts	19.22	0.14
Anarhichas minor	Spotted wolffish	16.41	0.12
Bathytroctes spp.	Black herring	16.39	0.12
Amblyraja hyperborea	Arctic skate	16.30	0.12
Chauliodus sloani	Viperfish	16.19	0.12
Rajella bathyphilia	Abyssal skate	12.63	0.09
Stomias boa ferox	Boa dragonfish	11.31	0.08

Table 2. List of the 34 fish taxa analyzed for fish abundance association with sponge grounds, their common names, total fish taxon abundance (total A) and percent of total abundance (%) in 104 trawl sets standardized to 1 km distance

Fish taxon	Common name	Total A (km^{-1})	%
Myctophidae	Lanternfishes	10214.69	25.25
Antimora rostrata	Blue hake	7006.51	17.32
Macrourus berglax	Roughhead grenadier	4875.68	12.05
Synaphobranchus kaupii	Longnose eel	4038.52	9.98
Coryphaenoides rupestris	Roundnose grenadier	3435.24	8.49
Nezumia bairdii	Common grenadier	1645.77	4.07
Sebastes mentella	Deepwater redfish	1570.75	3.88
Centroscyllium fabricii	Black dogfish	961.89	2.38
Reinhardtius hippoglossoides	Turbot	961.67	2.38
Hippoglossoides platessoides	American plaice	897.63	2.22
Stomias boa ferox	Boa dragonfish	867.42	2.14
Bathylagus euryops	Goitre blacksmelts	673.56	1.67
Chauliodus sloani	Viperfish	485.04	1.20
Notacanthidae	Spiny eels	333.03	0.82
Paralepididae	Barracudinas	322.96	0.80
Serrivomer beanii	Shortnose snipe eel	289.72	0.72
Gaidropsarus spp.	Threebeard rockling	283.74	0.70
Glyptocephalus cynoglossus	Witch flounder	209.09	0.52
Notacanthus chemnitzii	Largescale tapirfish	160.21	0.40
Lycodes vahlii	Vahl's eelpout	156.67	0.39
Polymixiidae	Beardfishes	114.87	0.28
Lycodes spp.	Eelpout	111.25	0.28
Phycis chesteri	Longfin hake	110.62	0.27
Apristurus profundorum	Deep-sea cat shark	99.65	0.25
Nemichthys scolopaceus	Atlantic snipe eel	97.60	0.24
Malacosteus niger	Loosejaw	89.99	0.22
Chiasmodon niger	Black swallower	83.95	0.21
Bathytroctes spp.	Black herring	61.06	0.15
Polyacanthonotus rissoanus	Shortspine tapirfish	58.04	0.14
Alepocephalidae	Smoothheads	52.30	0.13
Amblyraja radiata	Thorny skate	49.92	0.12
Cottunculus microps	Polar deep-sea sculpin	48.14	0.12
Stomiinae	Scaled dragonfishes	44.28	0.11
Anarhichas denticulatus	Broadhead wolffish	42.17	0.10

empty cells (Supplement 1). This procedure maximizes the rank correlation between the respective similarity matrices, and all permutations of the variables are assessed. The analyses and community analyses described above were performed with Primer v.6.1.5 software (2006 Primer-E).

RESULTS

There was a significant difference in depth among the sponge catch weight classes ($p < 0.0001$), and post hoc analyses showed that this difference was due to a shallower average trawl depth in the low sponge catch weight class than in the medium and high classes, which were not significantly different from each other. The average depths ± SD (range) for each class were: low: 981 ± 247 m (578 to 1420 m), medium: 1165 ± 205 m (589 to 1385 m) and high: 1237 ± 168 m (827 to 1446 m).

Thirty-four fish taxa had biomass values >0.1 % of the total biomass for the trawl sets (Table 1). Total fish biomass (kg km^{-1}) summed across the 104 trawl sets for the 34 selected taxa (Supplement 1) was 13 514.92 kg. Greenland shark *Somniosus microcephalus* accounted for 26 % of the total biomass in the data, with roughhead grenadier *Macrourus berglax* accounting for 19 %. Eleven taxa accounted for 90 % of the total biomass in these sets (Table 1).

A different set of 34 fish taxa showed abundance values >0.1 % of the total abundance for the trawl sets (Table 2). The total number of fish caught (km^{-1})

summed across the 104 trawl sets for the 34 selected taxa was 40 453.63. Eleven taxa accounted for 90 % of the total abundance, with lanternfish (Myctophidae) being the largest taxon and accounting for 25 % of total abundance (Table 2). Blue hake *Antimora rostrata* was the second most abundant taxon, and this species also ranked high in total biomass (Table 1).

The total number of fish taxa and the total fish biomass were significantly different among the sponge catch weight classes ($p < 0.001$). Post hoc analyses showed that fish biomass was not significantly different between the medium and high classes, but that the low class had significantly higher fish biomass. The total number of fish taxa was significantly lower in the high sponge catch weight class and did not differ between medium and low classes. Total fish abundance did not differ significantly among sponge catch weight classes ($p = 0.079$).

Linear regressions between fish biomass and sponge biomass by depth were statistically significant ($p < 0.0001$). Sponge biomass increased significantly with depth ($R^2 = 0.197$), while fish biomass significantly decreased ($R^2 = 0.182$). In contrast, the total number of fish taxa and total fish abundance were not significantly correlated with depth ($p = 0.249$ and $p = 0.797$, respectively). Total fish biomass and the total number of fish taxa were both significantly negatively correlated with total sponge biomass ($p < 0.0001$, $R^2 = 0.133$ and $R^2 = 0.209$, respectively), while there was no significant relationship with fish abundance. These p-values remained significant after correcting for multiple tests.

Community analyses: biomass

ANOSIM of the 104 trawl sets found a significant difference in community composition of the biomass between sponge catch weight classes (Global $R = 0.129$, $p = 0.001$). There was no significant difference between low and medium classes ($R = 0.056$, $p = 0.087$); however, there was a significant difference

Table 3. Taxa contributing to >90 % of the cumulative percent similarity in the biomass (kg km^{-1}) of research vessel trawl set catch composition (2001 to 2007) within each of the low, medium and high sponge catch weight classes

Species	Common name	Average similarity	% contribution	Cumulative %
Low sponge catch weight class — average similarity overall: 54.85				
Macrourus berglax	Roughhead grenadier	12.52	22.83	22.83
Antimora rostrata	Blue hake	10.79	19.68	42.50
Reinhardtius hippoglossoides	Turbot	8.06	14.69	57.20
Synaphobranchus kaupii	Longnose eel	4.76	8.68	65.88
Centroscyllium fabricii	Black dogfish	3.56	6.50	72.38
Coryphaenoides rupestris	Roundnose grenadier	3.48	6.35	78.73
Nezumia bairdii	Common grenadier	2.91	5.31	84.04
Myctophidae	Lanternfishes	1.46	2.66	86.70
Notacanthus chemnitzii	Largescaled tapirfish	1.28	2.34	89.04
Gaidropsarus spp.	Threebeard rockling	1.15	2.10	91.14
Medium sponge catch weight class — average similarity overall: 57.59				
Antimora rostrata	Blue hake	14.10	24.48	24.48
Macrourus berglax	Roughhead grenadier	13.34	23.16	47.63
Synaphobranchus kaupii	Longnose eel	6.50	11.29	58.93
Reinhardtius hippoglossoides	Turbot	5.51	9.56	68.49
Centroscyllium fabricii	Black dogfish	3.94	6.84	75.33
Coryphaenoides rupestris	Roundnose grenadier	3.82	6.64	81.97
Apristurus profundorum	Deep-sea cat shark	1.69	2.93	84.90
Nezumia bairdii	Common grenadier	1.59	2.76	87.67
Gaidropsarus spp.	Threebeard rockling	1.52	2.64	90.31
High sponge catch weight class — average similarity overall: 49.73				
Macrourus berglax	Roughhead grenadier	17.77	35.74	35.74
Reinhardtius hippoglossoides	Turbot	9.04	18.18	53.91
Antimora rostrata	Blue hake	8.66	17.41	71.32
Centroscyllium fabricii	Black dogfish	2.90	5.83	77.15
Synaphobranchus kaupii	Longnose eel	2.88	5.79	82.93
Coryphaenoides rupestris	Roundnose grenadier	2.87	5.77	88.70
Apristurus profundorum	Deep-sea cat shark	1.81	3.64	92.34

between the low and high classes (R = 0.232, p = 0.001) and between the medium and high classes (R = 0.122, p = 0.001) even after adjusting the p-value for multiple tests. SIMPER indicated an overall similarity of the fish assemblages within groups of 54 %. Similarities within the low (55 %), medium (58 %) and high (50 %) classes were not widely variant and included many of the same taxa in differing proportions. The taxa which accounted for 90 % of the similarity in biomass within each class are listed in Table 3. Average dissimilarity in the fish communities between the low and medium sponge weight classes was 46 %, between the low and high classes 52 % and between the medium and high classes 49 %. The taxa contributing to the dissimilarity between the low and high classes are shown in Table 4. Of the 22 taxa accounting for 90 % of the dissimilarity in biomass between these 2 classes, black dogfish *Centroscyllium fabricii*, blue hake and longnose eel *Synaphobranchus kaupii* accounted for a quarter of the dissimilarity (Table 4). All had higher biomass in the low sponge catch weight class, although they were also found in the high class. Only 6 taxa showed increased biomass in the high class, namely the deep-sea cat shark, spinytail skate *Bathyraja spinicauda*, white skate *Dipturus linteus*, shortnose snipe eel *Serrivomer beanii*, eelpout *Lycodes* spp. and deepwater chimaera *Hydrolagus affinis* (Table 4). Another 4 taxa were never found in association with high sponge catches, namely deepwater redfish *Sebastes mentella*, American plaice *Hippoglossoides platessoides*, witch flounder *Glyptocephalus cynoglossus* and thorny skate (*Amblyraja radiata*) (Table 4). Most other taxa showed increased biomass in the low class to varying degrees. These relationships are visualized in the MDS plot (Fig. 2), with trawl sets with an average similarity of 54 % circled. Owing to the high stress of the 2-dimensional presentation (0.20), the 3-dimensional presentation is also shown (stress = 0.15). Although some sets with high sponge catch cluster together, most of the trawl sets share a similarity of taxa that is not explained by the sponge catch weight class (Fig. 2). The relative proportions of biomass for selected pairs of taxa are indicated in the MDS ordination in Fig. 3. Each graph highlights a taxon which has increased biomass in the high or low sponge catch weight class and shows the discreteness of the groups. The BIOENV analysis identified 2 variables, total sponge biomass and average trawl depth, as having the largest rank correlation with the fish community patterns of similarity ($\rho = 0.490$, $p = 0.001$). All 3 variables together produced a lower correlation ($\rho = 0.450$), while average trawl depth had the highest rank correlation of the variables tested singly ($\rho = 0.446$).

Table 4. Taxa contributing to >90 % of the dissimilarity in the biomass (kg km^{-1}) of research vessel trawl set catch composition (2001 to 2007) between the low and high sponge catch weight classes. Arrowheads indicate the direction of change in biomass from low to high sponge catch weight class. ▼: decrease in biomass; ▼▼: decrease to zero biomass; ▲: increase in biomass

Taxon	Common name	Direction of change	Ave. $\log_{10}$ biomass Low	High	% contr. to diss.	Cum. contr. to diss.
Centroscyllium fabricii	Black dogfish	▼	1.53	1.22	9.23	9.23
Antimora rostrata	Blue hake	▼	2.58	2.13	7.83	17.05
Synaphobranchus kaupii	Longnose eel	▼	1.50	0.96	6.67	23.73
Reinhardtius hippoglossoides	Turbot	▼	2.10	1.76	6.04	29.77
Macrourus berglax	Roughhead grenadier	▼	3.00	2.79	5.87	35.64
Coryphaenoides rupestris	Roundnose grenadier	▼	1.24	0.74	5.74	41.38
Apristurus profundorum	Deep-sea cat shark	▲	0.29	0.93	5.08	46.46
Nezumia bairdii	Common grenadier	▼	0.95	0.37	4.54	51.00
Sebastes mentella	Deepwater redfish	▼▼	0.76	0.00	4.17	55.17
Hippoglossoides platessoides	American plaice	▼▼	0.79	0.00	4.12	59.29
Anarhichas denticulatus	Broadhead wolffish	▼	0.64	0.15	3.94	63.23
Bathyraja spinicauda	Spinytail skate	▲	0.34	0.42	3.73	66.96
Notacanthidae	Spiny eels	▼	0.59	0.31	3.65	70.61
Gaidropsarus spp.	Threebeard rockling	▼	0.55	0.16	3.20	73.80
Myctophidae	Lanternfishes	▼	0.47	0.11	2.53	76.34
Glyptocephalus cynoglossus	Witch flounder	▼▼	0.44	0.00	2.34	78.68
Dipturus linteus	White skate	▲	0.03	0.41	2.25	80.93
Amblyraja radiata	Thorny skate	▼▼	0.40	0.00	2.16	83.10
Serrivomer beanii	Shortnose snipe eel	▲	0.18	0.32	1.96	85.05
Lycodes spp.	Eelpout	▲	0.09	0.33	1.94	86.99
Hydrolagus affinis	Deepwater chimaera	▲	0.01	0.33	1.61	88.60
Amblyraja jenseni	Jensen's skate	▼	0.19	0.10	1.61	90.21

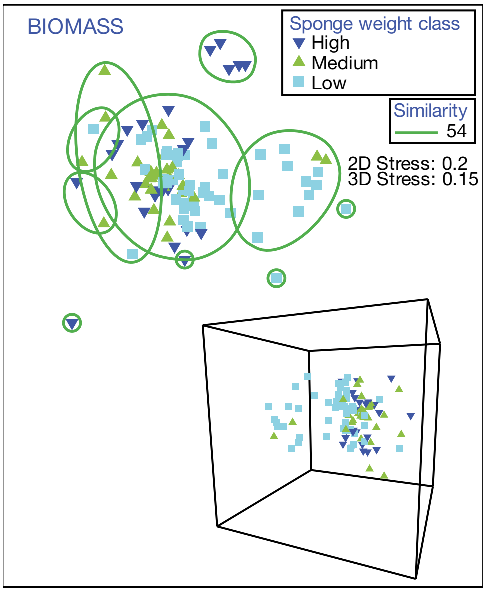

Fig. 2. Multidimensional scaling (MDS) configuration of the trawl catches (2001 to 2007) in 2D and 3D based on the Bray-Curtis similarity matrix calculated from $\log_{10}$-transformed biomass (kg km^{-1}) data for each of 34 fish taxa. Trawl set catches are labelled according to sponge catch weight class. In the 2D representation, trawl sets with 54% similarity to each other are indicated. This is the average similarity level within each of the 3 classes (see 'Results: Community analyses: biomass')

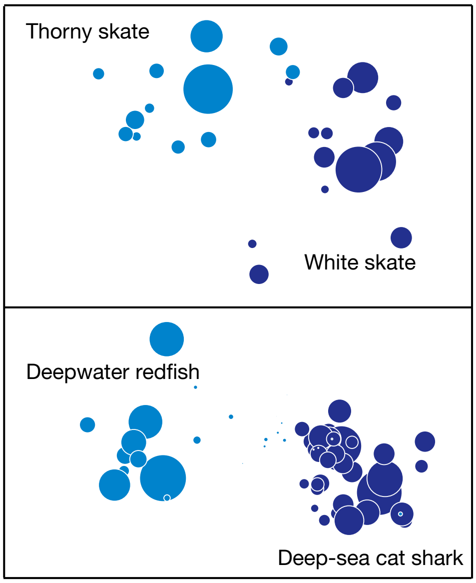

Fig. 3. MDS configuration of the trawl catches (2001 to 2007) based on the Bray-Curtis similarity matrix calculated from $\log_{10}$-transformed biomass data for each of 34 taxa. The proportional biomass (kg km^{-1}) of pairs of taxa which favour the sponge grounds (high sponge catch weight class; dark blue) or the low sponge areas (light blue) are illustrated. Note that proportions are relative to each taxon, and the values have not been added to allow comparisons as the purpose was largely to illustrate the non-overlap of the selected taxa

Community analyses: abundance

ANOSIM of the 104 trawl sets found a significant difference in community composition in abundance of taxa between sponge catch weight classes (Global R = 0.245, p = 0.001), and between all weight class pairs. However, there was a low R (0.083) produced between the low and medium classes, and the associated probability was 0.034, a value which would not be considered significant if corrected for the total number of tests performed. SIMPER indicated an overall similarity of the fish communities within groups of 59%; however, there was greater similarity within the low (63%) and medium (63%) classes than within the high class (51%). The taxa which account for 90% of the similarity in abundance within each class are listed in Table 5. Average dissimilarity in the fish communities between the low and medium classes was 39%, between the low and high classes was 52% and between the medium and high classes was 48%. The taxa contributing to the dissimilarity between the low and high classes are provided in Table 6. Of the 25 taxa accounting for 90% of the dissimilarity in abundance between these 2 classes, lanternfish, common grenadier *Nezamia bairdii* and roundnose grenadier *Coryphaenoides rupestris* accounted for a quarter of the dissimilarity (Table 6). These all have higher abundance in the low sponge catch weight class than in the high class. The only taxa which had increased abundance in the high class were the deep-sea cat shark, eelpout and the shortnose snipe eel. All other taxa (N = 22) had decreased abundance in the high class, and 4 taxa were not found in that class: deepwater redfish, American plaice, witch flounder and Vahl's eelpout *Lycodes vahlii* (Table 6). The relationships between the trawl sets labelled by sponge catch weight class are visualized in the MDS plot in Fig. 4, with trawl sets with an average similarity of 59% circled. It can be seen that, although some sets with high sponge catch cluster together, most of the trawl sets share a similarity of taxa that is not explained by the sponge catch weight classes (Fig. 4). Total sponge biomass and average trawl depth, which had the highest correlation in the BIOENV analyses with the pattern of similarity in fish biomass, also had the largest rank correlation with the fish community pattern calculated from abundance ($\rho = 0.558$, $p = 0.001$). However, in contrast to the analyses of biomass, total sponge biomass had the highest rank correlation of the variables tested singly ($\rho = 0.383$).

Table 5. Taxa contributing to >90% of the cumulative % similarity in the abundance (km^{-1}) of research vessel trawl set catch composition (2001 to 2007) within each of the low, medium and high sponge catch weight classes

Species	Common name	Average similarity	% contribution	Cumulative %
Low sponge catch weight class — average similarity overall: 62.58				
Myctophidae	Lanternfish	9.45	15.10	15.10
Antimora rostrata	Blue hake	9.27	14.81	29.91
Macrourus berglax	Roughhead grenadier	7.75	12.38	42.29
Synaphobranchus kaupii	Longnose eel	6.01	9.60	51.89
Coryphaenoides rupestris	Roundnose grenadier	4.73	7.55	59.45
Nezumia bairdii	Common grenadier	4.47	7.14	66.59
Reinhardtius hippoglossoides	Turbot	4.09	6.54	73.13
Stomias boa ferox	Boa dragonfish	3.36	5.37	78.50
Chauliodus sloani	Viperfish	1.67	2.66	81.16
Gaidropsarus spp.	Threebeard rockling	1.61	2.57	83.73
Paralepididae	Barracudinas	1.58	2.52	86.25
Bathylagus euryops	Goitre blacksmelts	1.55	2.48	88.73
Centroscyllium fabricii	Black dogfish	1.55	2.48	91.21
Medium sponge catch weight class — average similarity overall: 63.13				
Antimora rostrata	Blue hake	10.51	16.64	16.64
Macrourus berglax	Roughhead grenadier	8.86	14.04	30.69
Synaphobranchus kaupii	Longnose eel	7.47	11.84	42.52
Myctophidae	Lanternfishes	6.74	10.68	53.21
Coryphaenoides rupestris	Roundnose grenadier	5.49	8.69	61.90
Chauliodus sloani	Viperfish	3.46	5.49	67.39
Nezumia bairdii	Common grenadier	2.76	4.37	71.75
Reinhardtius hippoglossoides	Turbot	2.73	4.33	76.08
Stomias boa ferox	Boa dragonfish	2.51	3.97	80.05
Gaidropsarus spp.	Threebeard rockling	1.87	2.97	83.02
Centroscyllium fabricii	Black dogfish	1.74	2.75	85.76
Lycodes spp.	Eelpout	1.14	1.80	87.56
Serrivomer beanii	Shortnose snipe eel	1.10	1.74	89.31
Polymixiidae	Beardfishes	1.02	1.61	90.92
High sponge catch weight class — average similarity overall: 51.13				
Macrourus berglax	Roughhead grenadier	14.55	28.46	28.46
Antimora rostrata	Blue hake	8.34	16.30	44.76
Coryphaenoides rupestris	Roundnose grenadier	5.56	10.88	55.64
Synaphobranchus kaupii	Longnose eel	5.07	9.92	65.56
Reinhardtius hippoglossoides	Turbot	4.96	9.70	75.26
Centroscyllium fabricii	Black dogfish	2.01	3.93	79.19
Nezumia bairdii	Common grenadier	1.89	3.69	82.88
Serrivomer beanii	Shortnose snipe eel	1.60	3.14	86.02
Bathylagus euryops	Goitre blacksmelts	0.98	1.92	87.94
Myctophidae	Lanternfishes	0.86	1.67	89.61
Apristurus profundorum	Deep-sea cat shark	0.85	1.66	91.27

DISCUSSION

Temperate sponge grounds are considered vulnerable marine ecosystems (sensu FAO 2009) in the northwest Atlantic (Fuller et al. 2008), and in 2009 NAFO implemented Sponge Protection Zones in the international waters of the Grand Banks (NAFO 2009). Their upright nature and poor recovery potential if dislodged from the seafloor render them vulnerable to bottom-contact fishing gear. Large structure-forming sponges are considered to be ecosystem engineers through their modification of the seafloor (through altering bottom currents and depositing spicules), and, by adding structural complexity, provide habitat for a wide variety of benthic invertebrates (Klitgaard 1995). However, the association of demersal fish communities with these temperate sponge grounds has not been well documented. Our results show that the high biomass sponge grounds on the continental slopes off Newfoundland, Canada, have lower biomass and numbers of taxa of demersal fish relative to areas with low sponge bio-

Table 6. Taxa contributing to >90% of the dissimilarity in abundance (km^{-1}) of research vessel catch composition (2001 to 2007) between the low and high sponge catch weight classes. Arrowheads indicate the direction of change in fishtaxon abundance in going from the low to the high sponge catch weight class. ▼: decrease in abundance; ▼▼: decrease to zero abundance; ▲: increase in abundance

Taxon	Common name	Direction of change	Ave. log$_{10}$ abundance Low	High	% contr. to diss.	Cum. contr. to diss.
Myctophidae	Lanternfishes	▼	4.46	0.93	11.61	11.61
Nezumia bairdii	Common grenadier	▼	2.58	1.11	5.95	17.55
Coryphaenoides rupestris	Roundnose grenadier	▼	2.90	2.01	5.81	23.36
Synaphobranchus kaupii	Longnose eel	▼	3.21	2.23	5.80	29.16
Stomias boa ferox	Boa dragonfish	▼	2.02	0.55	5.28	34.44
Antimora rostrata	Blue hake	▼	4.13	3.06	5.22	39.66
Centroscyllium fabricii	Black dogfish	▼	1.41	1.24	4.68	44.34
Bathylagus euryops	Goitre blacksmelts	▼	1.44	0.74	4.35	48.69
Sebastes mentella	Deepwater redfish	▼▼	1.17	0.00	3.66	52.35
Paralepididae	Barracudinas	▼	1.24	0.28	3.55	55.90
Reinhardtius hippoglossoides	Turbot	▼	2.20	1.61	3.48	59.38
Chauliodus sloani	Viperfish	▼	1.28	0.60	3.45	62.84
Serrivomer beanii	Shortnose snipe eel	▲	0.79	1.04	3.20	66.04
Macrourus berglax	Roughhead grenadier	▼	3.66	3.48	3.08	69.12
Gaidropsarus spp.	Threebeard rockling	▼	1.11	0.45	2.99	72.11
Hippoglossoides platessoides	American plaice	▼▼	0.89	0.00	2.70	74.81
Notacanthus chemnitzii	Largescale tapirfish	▼	0.78	0.28	2.32	77.13
Apristurus profundorum	Deep-sea cat shark	▲	0.19	0.69	2.04	79.17
Lycodes spp.	Eelpout	▲	0.25	0.54	1.85	81.02
Glyptocephalus cynoglossus	Witch flounder	▼▼	0.59	0.00	1.82	82.84
Malacosteus niger	Loosejaw	▼	0.44	0.37	1.75	84.59
Chiasmodon niger	Black swallower	▼	0.41	0.31	1.57	86.16
Nemichthys scolopaceus	Atlantic snipe eel	▼	0.46	0.15	1.57	87.73
Phycis chesteri	Longfin hake	▼	0.51	0.03	1.55	89.27
Lycodes vahlii	Vahl's eelpout	▼▼	0.47	0.00	1.41	90.69

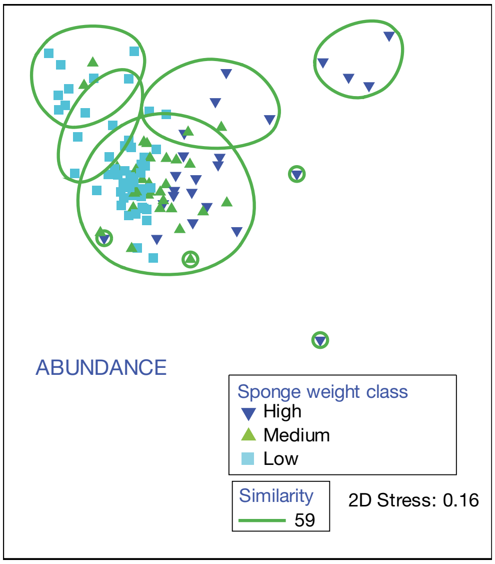

Fig. 4. MDS configuration of the trawl catches (2001 to 2007) in 2 dimensions (2D) based on the Bray-Curtis similarity matrix calculated from log$_{10}$-transformed abundance data for each of 34 taxa. Trawl catches are labelled according to sponge catch weight class. Trawl sets with 59% similarity to each other are indicated. This is the average similarity level within each of the 3 classes (see 'Results: Community analyses: abundance')

mass outside of the sponge grounds, a correlation not reflected in the abundance of fish. This scenario is created by small numbers of the larger bodied fish living where sponge biomass is significantly lower and where water depth is also shallower.

Although we attempted to narrow the depth range of our samples *a priori* by selecting trawl sets from the continental slope (578 to 1446 m) for analysis, depth together with sponge biomass explained the highest percentage of the variation in the fish communities, whether measured by biomass or abundance. Bottom temperature was not an important determinant either on its own or in combination with depth and sponge biomass. A significantly distinct fish assemblage based on both biomass and abundance metrics was associated with the sponge grounds (trawl sets with high sponge biomass ≥250 kg km^{-1}), despite the statistically similar depth of the trawl sets with medium sponge biomass (10 to 250 kg km^{-1} exclusive). The coherence amongst trawl set fish composition is relatively high for both biomass and abundance at about 50% similarity over the sponge grounds. Species which form the fish assemblage associated with the sponge grounds are the roughhead grenadier, roundnose grenadier, blue hake, longnose eel, turbot *Reinhardtius hippoglossoides*, black dogfish and deep-sea cat shark. SIMPER showed these fish to characterize sponge grounds both in terms of biomass and abundance, contributing to 92 and 81 %, respectively, of the similarity among trawl set fish composition. An additional 4 taxa, common grenadier, shortnose snipe eel, lanternfish and goitre blacksmelts *Bathylagus euryops*, were identified through characterization of abundance only, contributing an additional 10 % of the similarity among trawl sets. The association of these demersal fish with the sponge grounds further strengthens the role that sponge grounds play in marine ecosystems.

Only 6 taxa had higher abundance and/or biomass in trawl sets with high sponge catches compared to sets with low sponge catches (≤10 kg km^{-1}) (sponge grounds vs. non-sponge grounds). None are targeted in commercial fisheries in this area. These were deep-sea cat shark, spinytail skate, white skate, shortnose snipe eel, eelpout and deepwater chimaeras (Table 7), although none were exclusive to those sets. Only 2 (deep-sea cat shark and shortnose snipe eel) contributed to the SIMPER description of similarity amongst fish caught in the high sponge bycatch sets. This is because the remainder were also found in sets with medium sponge catch. All of these are deep-living fish (Rose 2005), and their associations with the sponges may be a coincidental one with depth, particularly for the 4 taxa that also occurred with medium sponge catches, as there was no significant difference in the depth of trawl sets between the medium and high sponge catch weight classes. However, all 6 taxa are also active predators, which may indicate a foraging relationship with the sponge grounds.

Previous studies have shown that the invertebrate fauna associated with sponge grounds has a higher species diversity compared to surrounding bottoms. This associated fauna is largely comprised of other smaller sponges (ICES 2009), hydroids, zoanthids, bryozoans and ascidians (Klitgaard 1995, Klitgaard & Tendal 2004). Klitgaard (1995) identified 242 taxa of epifauna and infauna associated with the sponge grounds, dominated by *Geodia* spp. and *Strychnus* spp. near the Faroe Islands, and considered that almost half of these formed obligate associations with the sponges. The spicule mats associated with the sponge communities' support increased biomass of macrofaunal species (Bett & Rice 1992). Preliminary evidence suggests that the sponge grounds in the northwest Atlantic also host a high diversity of benthic invertebrates (NAFO 2010, Barrio Froján et al. 2012), and foraging may be the mechanism which has produced the associated fish assemblage observed in our study. Eelpout are known to eat sponge remains (Table 7; Coad & Reist 2004) and so may feed directly on the sponges in the sponge grounds. The diet of shortnose snipe eel consists of crustaceans, cephalopods and teleosts (Geidner 2008). *Harriotta raleighana*, a chimaera related to the deepwater chimera, feeds on endo- and epibenthic organisms on the Grand Bank and at Flemish Cap (González et al. 2007). They found that *H. raleighana* in particular consumed a high proportion of benthic polychaetes and associated sediment. Little information is available on the diets of white or spinytail skate, but, in the Barents Sea, the white skate feeds on benthic invertebrates, including brittlestars, gammarids and shrimp, while the spinytail is largely piscivorous as an adult (Dolgov 2005), but feeds mainly on benthos as a juvenile (Dolgov 2002). Similarly, the diet of the deep-sea cat shark is not well documented, although congeneric species feed heavily on crustaceans (Cortés 1999), especially euphausiids and penaeid shrimp. Therefore, all of the 6 taxa identified as having a high biomass/abundance in association with the sponge grounds (Table 7) have dietary links to that habitat. The other fish taxa identified by SIMPER as descriptive of the high-density sponge grounds are also benthic feeders, that is, the roughhead grenadier (Eliassen & Jobling 1985), black dogfish (González et al. 2007), blue hake (Mauchline & Gordon 1984), turbot (Rodríguez-Marín et al. 1995) and juvenile longnose eel (Marques 1998), with only the lanternfish and goitre blacksmelts being predominately pelagic feeders. However, most demersal fish are benthivores; thus, more direct evidence is needed before conclusions can be drawn on how these fish may use the habitat offered by the sponge grounds.

There is no strong evidence for fish avoidance of the sponge grounds. The lower biomass of black dogfish, blue hake and longnose eel and the lower abundance of lanternfish, common grenadier and roundnose grenadier drove the distinction in the fish assemblages between trawl sets with high sponge biomass in the catch and those with low sponge catch, accounting for a quarter of the dissimilarity in both instances. These taxa only differ between the sponge weight classes in terms of relative biomass as all are found in both types of trawl sets. Only 5 species common in the low sponge biomass trawl sets were never reported in the catches with high sponge biomass and had only a small proportion of their bio-

Table 7. Summary of known habitat and diet characteristics of those fish taxa showing a positive association with sponge grounds in biomass (B) and/or abundance (A) and those never captured with high sponge catches in the study (Tables 4 & 6). This table was produced using information recorded on FishBase (www.fishbase.org) and from Coad & Reist (2004) and Troyanovsky (1992)

Common name (taxon)	Metric response	Zone	Ecology	Diet	Depth information
Fish taxa showing a positive association with sponge grounds in biomass and/or abundance					
Shortnose snipe eel (*Serrivomer beanii*)	Increase B, increase A	Epibenthic-mesopelagic	Exhibits vertical migrations to feed during the night	Shrimps, other crustaceans, small fish	To 5998 m, Canadian Atlantic: 850–925 m. Mostly at depths of 550–1000 m; present study (N = 57 sets): range = 768–1446 m median = 1211 m
Deep-sea cat shark (*Apristurus profundorum*)	Increase B, increase A	Bathydemersal, inhabits the continental slope	Relatively small, sluggish sharks; egg cases may be attached to biogenic structures as they are laid	Euphausiids, penaeid shrimp, crustaceans	1100–1750 m; present study (N = 37 sets): range = 871–1446 m median = 1303 m
Eelpout (*Lycodes* spp.)	Increase B, increase A	Demersal	Muddy bottoms. It seems to get the bulk of its food by burrowing in the sediment.	Small bivalves, polychaetes, small crustaceans. *L. terraenovae* eats sponge	19–1750 m; present study (N = 40 sets): range = 589–1410 m median = 1164 m
Spinytail skate (*Bathyraja spinicauda*)	Increase B	Benthic, bathydemersal	Boreal and arctic species found in water temperatures <8°C	Invertebrates as juveniles, fish as adults	140–1463 m, usually 65–255 m; present study (N = 17 sets): range = 601–1384 m, median = 1202 m
White skate (*Dipturus linteus*)	Increase B	Benthic, bathydemersal	Little known species is widespread but distributed deeply	Worms, crustaceans, fishes	150–1455 m, usually 250 m; present study (N = 14 sets): range = 1153–1446 m, median = 1357 m
Deepwater chimaera (*Hydrolagus affinis*)	Increase B	Epibenthic, bathydemersal	Deepwater slope, seamount and sea plain dwelling fish	Fish, invertebrates	Deep waters to 2400 m; 300–2400 m; present Study (N = 9 sets): range = 1058–1370 m, median = 1243 m
Fish taxa never captured with high sponge catches in the present study					
Deepwater redfish (*Sebastes mentella*)	Decrease B, decrease A	Epibenthic–pelagic, bathypelagic	Long-lived species (>65 yr)	Crustaceans, fish	300–1441 m; 500–700 m in NAFO Div.2J,3K; present study (N = 27 sets): range = 578–1243 m, median = 812 m
American plaice (*Hippoglossoides platessoides*)	Decrease B, decrease A	Benthic, demersal	Soft bottoms	Worms, molluscs, echinoderms, crustaceans, fish	10–3000 m, usually 9–250 m; present study (N = 18 sets): range = 589–1161 m, median = 739 m
Witch flounder (*Glyptocephalus cynoglossus*)	Decrease B, decrease A	Benthic, demersal	Soft mud bottoms in fairly deep water	Worms, crustaceans,molluscs, brittle stars, fish	8–1570 m, usually 45–366 m; present study (N = 14 sets): range = 578–1384 m, median = 622 m
Vahl's eelpout (*Lycodes vahlii*)	Decrease A	Benthic, bathydemersal	Lives at temperatures of 0–5°C	Worms, crustaceans, molluscs	65–1200 m; present study (N = 12 sets): range = 578–985 m, median = 630 m
Thorny skate (*Amblyraja radiata*)	Decrease B	Benthic, demersal	Sandy and muddy bottoms	Worms, crustaceans, fish	20–1000 m; present study (N = 12 sets): range = 578–1190 m, median = 655 m

mass/abundance in areas with medium sponge biomass: deepwater redfish, American plaice, witch flounder, Vahl's eelpout and thorny skate. These fish could be avoiding the sponges, as has been noted elsewhere (Bell 2008). American plaice, thorny skate and witch flounder are associated with mud or sandy bottoms and may actively avoid the sponge grounds which can have dense spicule mats forming biogenic substratum (Bett & Rice 1992) and creating a heterogenous surface. Further, some of these fish tend to prefer shallower waters (Table 7), and the significantly shallower average depth of the low sponge catch weight class may contribute to our findings.

Collectively our data suggest that the *Geodia*-dominated sponge grounds of the continental slopes off Newfoundland, northwest Atlantic, host distinctive fish assemblages, although the active or passive nature of this association is not known. We speculate that these fish use the sponge grounds to forage, although they may only be taking advantage of the presence of the physical structure created by the sponges. A more detailed analysis of these data using less coarse taxonomic categories may have revealed greater differences in community composition. However, trawl survey catch can only give a generalized picture of the species associations for those species that are caught by the gear. Other sampling tools are required to provide details for the smaller invertebrate and fish species and life-history stages that have been reported elsewhere as being associated with sponge grounds. Future research focussing on the species identified to be associated with the sponge grounds may provide greater insight into the strength and temporal stability of the associations and the ecological linkages between these benthic and pelagic communities.

Acknowledgements. This project was funded by the Department of Fisheries and Oceans, Canada International Governance Strategy to E. K. We thank the ICES Working Group on Deep-water Ecology (WGDEC) for useful discussion and comment on this work and the very helpful comments of 4 anonymous reviewers.

LITERATURE CITED

➤ Auster PJ, Lindholm J, Valentine PC (2003) Variation in habitat use by juvenile Acadian redfish, *Sebastes fasciatus.* Environ Biol Fishes 68:381–389

➤ Barrio Froján CRS, MacIsaac KG, McMillan AK, del Mar Sacau Cuadrado M and others (2012) 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. ICES J Mar Sci 69:213–222

➤ Bell JJ (2008) The functional roles of marine sponges. Estuar Coast Shelf Sci 79:341–353

➤ Best M, Kenchington E, MacIsaac K, Wareham V, Fuller SD, Thompson AB (2010) Sponge identification guide NAFO area. NAFO Sci Counc Stud 43:1–49

➤ Bett BJ, Rice AL (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

➤ Brodeur RD (2001) Habitat-specific distribution of Pacific ocean perch (*Sebastes alutus*) in Pribilof Canyon, Bering Sea. Cont Shelf Res 21:207–224

➤ Chu JWF, Leys SP (2010) High resolution mapping of community structure in three glass sponge reefs. Mar Ecol Prog Ser 417:97–113

➤ Clarke KR (1993) Non-parametric multivariate analysis of changes in community structure. Aust J Ecol 18:117–143

Cleary DFR, de Voogd NJ (2007) Environmental association of sponges in the Spermonde Archipelago, Indonesia. J Mar Biol Assoc UK 87:1669–1676

Coad BW, Reist JD (2004) Annotated list of the Arctic marine fishes of Canada. Can Manuscr Rep Fish Aquat Sci 2674: iv + 112 p

➤ Colbourne EB (2004) Decadal changes in the ocean climate in Newfoundland and Labrador waters from the 1950s to the 1990s. J Northw Atl Fish Sci 34:43–61

➤ Cortés E (1999) Standardized diet compositions and trophic levels of sharks. ICES J Mar Sci 56:707–717

Dolgov AV (2002) Feeding and food consumption by the Barents Sea skates. Serial No. N4714, NAFO SCR Doc 02/93, NAFO, Dartmouth

➤ Dolgov AV (2005) Feeding and food consumption by the Barents Sea skates. J Northw Atl Fish Sci 35:495–503

➤ Du Preez C, Tunnicliffe V (2011) Shortspine thornyhead and rockfish (Scorpaenidae) distribution in responses to substratum, biogenic structures and trawling. Mar Ecol Prog Ser 425:217–231

➤ Eliassen JE, Jobling M (1985) Food of the roughhead grenadier, *Macrourus berglax*, Lacepede in North Norwegian waters. J Fish Biol 26:367–376

FAO (Food and Agricultural Organization) (2009) Technical consultation on international guidelines for the management of deep-sea fisheries in the high seas. FAO Fisheries and Aquaculture report No. 881. ftp://ftp.fao.org/docrep/fao/011/

Freese JL, Wing BL (2003) Juvenile red rockfish *Sebastes* sp., associations with sponges in the Gulf of Alaska. Mar Fish Rev 65:38–42

Fuller SD, Murillo Perez FJ, Wareham V, Kenchington E (2008) Vulnerable marine ecosystems dominated by deep-water corals and sponges in the NAFO Convention Area. Serial No. N5524, NAFO SCR Doc 08/22, NAFO, Dartmouth

Geidner M (2008) Spatial and trophic ecology of the sawtooth eel, *Serrivomer beanii*, a biomass-dominant bathypelagic fish over the northern Mid-Atlantic Ridge. Florida Atlantic University, Boca Raton, FL

González C, Teruel J, López E, Paz X (2007) Feeding habits and biological features of deep-sea species of the Northwest Atlantic: large-eyed rabbitfish (*Hydrolagus mirabilis*), narrownose chimaera (*Harriotta raleighana*) and black dogfish (*Centroscyllium fabricii*). NAFO SC Rep. No. 07/63, NAFO, Dartmouth

Hixon MA, Tissot BN, Pearcy WG (1991) Fish assemblages of rocky banks of the Pacific Northwest (Heceta, Coquille, and Daisy Banks). OCS Study 91-0052, US Minerals Management Service, Camarillo, CA

Hogg MM, Tendal OS, Conway KW, Pomponi SA and others (2010) Deep-sea sponge grounds: reservoirs of biodiversity. UNEP-WCMC Biodiversity Series No. 32, UNEP-WCMC, Cambridge

ICES (International Council for the Exploration of the Sea) (2009) Report of the ICES-NAFO working group on deep-water ecology (WGDEC). ICES Comm Meet 2009\ACOM:23

Kenchington E, Cogswell A, Lirette C, Murillo Pérez FJ (2009) The use of density analyses to delineate sponge grounds and other benthic VMEs from trawl survey data. Serial N5626, NAFO Sci Coun Res Doc 09/6, NAFO, Dartmouth

Kenchington E, Lirette C, Cogswell A, Archambault D and others (2010) Delineating coral and sponge concentrations in the biogeographic regions of the east coast of Canada using spatial analyses. DFO Can Sci Adv Sec Res Doc 2010/041. vi + 203 pp

Kenchington E, Murillo FJ, Cogswell A, Lirette C (2011) Development of encounter protocols and assessment of significant adverse impact by bottom trawling for sponge grounds and sea pen fields in the NAFO regulatory area. NAFO Sci Coun Res Doc 11/75, NAFO, Dartmouth

Klitgaard AB (1995) The fauna associated with outer shelf and upper slope sponges (Porifera, Demospongiae) at the Faroe Islands, northeastern Atlantic. Sarsia 80: 1–20

➤ Klitgaard AB, Tendal OS (2004) Distribution and species composition of mass occurrences of large-sized sponges in the northeast Atlantic. Prog Oceanogr 61:57–98

➤ Marliave JB, Conway KW, Gibbs DM, Lamb A, Gibbs C (2009) Biodiversity and rockfish recruitment in sponge gardens and bioherms of southern British Columbia, Canada. Mar Biol 156:2247–2254

➤ Marques A (1998) A note on the diet of *Synaphobranchus kaupi* (Pisces: Synaphobranchidae) from the Porcupine Seabight, North-East Atlantic. J Mar Biol Assoc UK 78: 1385–1388

➤ Mauchline J, Gordon JDM (1984) Feeding and bathymetric distribution of the gadoid and morid fish of the Rockall Trough. J Mar Biol Assoc UK 64:657–665

➤ McCormick MI (1994) Comparison of field methods for measuring surface topography and their association with a tropical reef fish assemblage. Mar Ecol Prog Ser 112: 87–96

➤ Murillo FJ, Durán Muñoz P, Cristobo F, Ríos P, González C, Kenchington E, Serrano A (2012) Deep-sea sponge grounds of the Flemish Cap, Flemish Pass and the Grand Banks of Newfoundland (Northwest Atlantic Ocean): distribution and species composition. Mar Biol Res 8: 842–854

NAFO (Northwest Atlantic Fisheries Organization) (2009) Report of the fisheries commission and its subsidiary body (STACTIC). Serial No. N5735, NAFO/FC Doc 09/21, NAFO, Dartmouth

NAFO (2010) Report of the 3rd meeting of the NAFO Scientific Council Working Group on ecosystem approach to fisheries management (WGEAFM). Serial No. N5868, NAFO SCS Doc 10/24, NAFO, Dartmouth

➤ Richards LJ (1986) Depth and habitat distributions of three species of rockfish (*Sebastes*) in British Columbia: observations from the submersible PISCES IV. Environ Biol Fishes 17:13–21

Rodríguez-Marín E, Punzón A, Paz J (1995) Feeding patterns of Greenland halibut (*Reinhardtius hippoglossoides*) in Flemish Pass (Northwest Atlantic). NAFO Sci Counc Studies 23:43–54

➤ Rose GA (2005) On distributional responses of North Atlantic fish to climate change. ICES J Mar Sci 62:1360–1374

➤ Troyanovsky FM (1992) Observations on non-maturing redfish (*Sebastes mentella* Travin) in the Northwest Atlantic. J Northw Atl Fish Sci 14:145–147

➤ Wulff JL (2006) Ecological interactions of marine sponges. Can J Zool 84:146–166

Editorial responsibility: Hans Heinrich Janssen, Oldendorf/Luhe, Germany

Submitted: February 27, 2012; Accepted: October 17, 2012
Proofs received from author(s): February 4, 2013