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Marine fish diversity on the Scotian Shelf, Canada

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ABSTRACT

1. Marine life in offshore regions has not been fully censused, yet related conservation policy relies on our ability to identify areas of high biodiversity.
2. We assessed the census of marine finfish on the Scotian Shelf, Northwest Atlantic using data collected during annual research vessel surveys between 1970 and 2000. The species accumulation curve did not reach an asymptote reflecting that new species continued to be discovered throughout the survey period. Only 0.12% of the area of the Scotian Shelf has been sampled since 1970.
3. Since 1974, when over 50% of the species had been discovered, the community composition has been relatively constant. However, the dominance structure has changed dramatically as reflected in the geographic contraction of the formerly abundant, large-bodied piscivores concomitant with the geographic expansion of their prey species.
4. The region is under-sampled, and species' distribution and abundance are changing. A precise estimate of diversity is elusive. As an alternative, we searched for physical correlates of finfish diversity to identify its possible surrogates. Surrogates have potential both as a method for understanding process and as a tool for conservation management. We examined the effect of area and depth range on species richness. High species richness was associated with larger areas and greater depth range at large spatial scales.
5. Highly diverse areas include the Bay of Fundy, the Eastern Gully, the slopes, Western Bank and the northeastern shelf. Until now, the northeastern shelf has been under-appreciated as a highly diverse area. Such information will be important for environmental impact assessments as well as selection of 'sensitive' or protected areas.
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KEY WORDS: Marine fish diversity; census; species accumulation curve; conservation; diversity surrogates

INTRODUCTION

Many nations are creating policy to conserve marine biodiversity. The rate of policy development currently exceeds that of its related science even though a great deal of scientific progress has been made. Indices of biodiversity are much coveted as they can be used to monitor change and to design marine protected areas. Ideally, a complete census would exist but it is more typical that only a small proportion of an area is

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sampled and considered representative of a larger region. Because the probability of detecting individuals from small populations is lower than that from large populations, less common species may be overlooked.

An alternative to the use of a complete census is to use physiographic/oceanographic features and/or physical correlates of biodiversity in conservation planning (Ward *et al*., 1999; Zacharias and Roff, 2000; Ponder *et al*., 2001). For example, species diversity is predictably related to area — i.e. the species–area relationship. Species–area relationships have been proposed for use in the design of protected areas with equivocal response because the ecological basis of the species–area relationship is elusive and non-singular (McGuinness, 1984; Ricklefs and Lovette, 1999; Connor and McCoy, 2000). Another and related indicator of biodiversity is habitat diversity (Rosenzweig, 1995). Since different species can show preferences for different depths (Mahon and Smith, 1989), the range of available depths in a given area can be used as an index of habitat diversity.

In this paper, we evaluated the census of finfish on the Scotian Shelf to determine whether it could be used to monitor diversity. We then evaluated area and depth range as possible surrogates of species richness. We present the relationship of species richness, area and depth range at two spatial scales to demonstrate that the functional relationship between species richness and physical correlates is scale-dependent. We also examined the temporal changes in species composition and geographic distributions, and discuss how a dynamic community structure can affect local estimates of diversity. Finally, we discuss whether diversity can be monitored given the information available, and how our results can be used to identify areas of potentially high species diversity.

METHODS

The Canadian Department of Fisheries and Oceans has conducted summer research bottom trawl surveys of the Scotian Shelf annually since 1970. The survey uses a stratified random sampling design with stratification by depth and geographic location. The shelf is divided into 48 sampling strata (Figure 1). At each stratum, finfish were captured using a standard bottom trawl equipped with a 19 mm codend liner that was towed at a constant speed of 3.5 knots for approximately 30 min (referred to as a set). The area swept by the trawl during this sampling interval was 0.0404 km^2. Set allocation was generally proportional to stratum area. Sampling was conducted around the clock. Because there was no fixed schedule, the allocation of day and night samples varied randomly among strata and years. In general, 4 weeks were required to complete a single survey.

Census

Censuses of biodiversity are commonly incomplete. Fortunately, methods have been developed to estimate and/or extrapolate species richness when the true richness is unknown. These methods can be based on aspects of the species accumulation curve, as well as on how rare species are represented in a sample (see Colwell and Coddington, 1994). Such methods can also be used to assess the completeness of a census by comparing the expected theoretical estimate of species richness with the observed.

Sampling effort, in the study reported herein, has been low relative to the size of the Scotian Shelf. We therefore used a method that does not assume the existence of an asymptote but is instead based on the rarity of species. We compared the *Chao* 1 and *Chao* 2 non-parametric estimators of species richness with the observed, using the EstimateS program developed by Colwell (1997). *Chao* 1 is based on the number of species represented by 1 and 2 individuals (following notation in Colwell and Coddington, 1994):

$$Chao_1 = S_{\text{obs}} + (a^2/2b)$$

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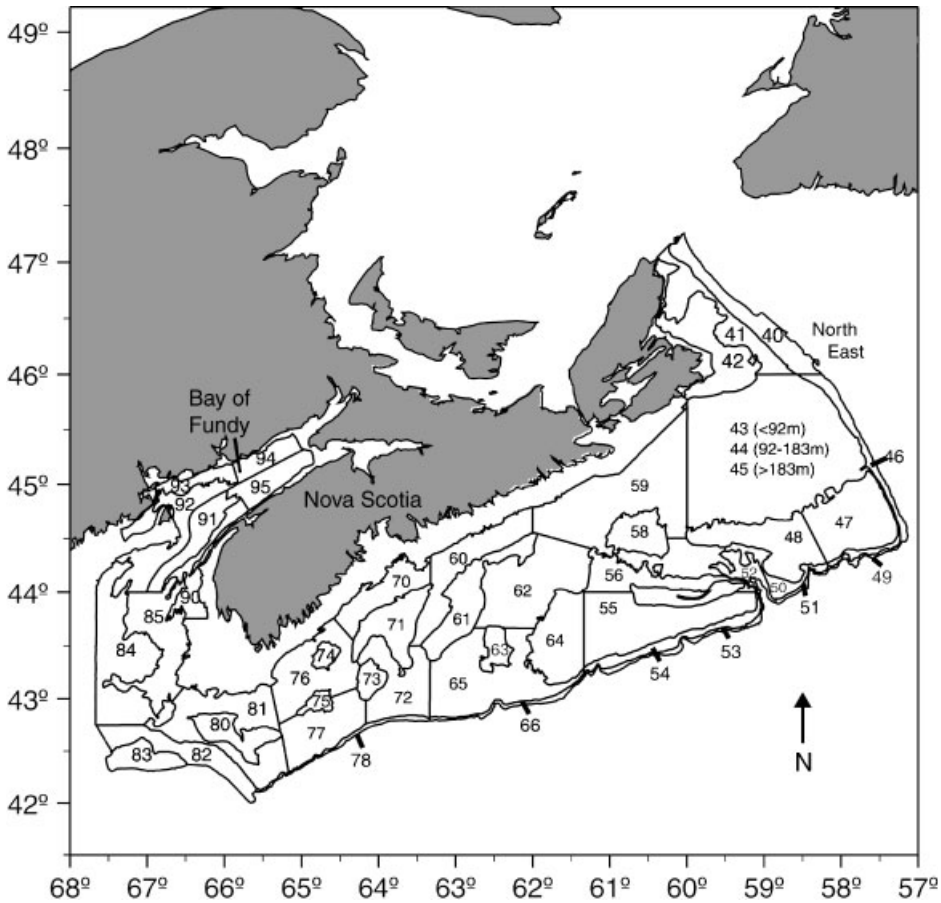

Figure 1. Scotian Shelf and Bay of Fundy. Lines delineate strata and numbers refer to strata codes as defined in the annual stratified random research vessel survey.

where S_{obs} is the observed number of species, a is the number of species represented by one individual and b is the number of species represented by two individuals. *Chao* 2 is based on the number of species that were found in only one or two samples:

$$Chao_2 = S_{\text{obs}} + (L^2/2M)$$

where L is the number of species that were found in only one sample and M is the number that were found in only two samples.

It is possible to compare the observed with the expected number of species at different levels of sampling effort. A species accumulation curve describes how the number of newly discovered species accumulates with sampling effort. Typically, the number of newly discovered species rises rapidly during the initial sampling phase, then levels off as the system becomes fully sampled. A species list from 31 years of sampling (1970–2000) was compiled for the whole Scotian Shelf region. We used EstimateS randomization re-sampling program (Colwell, 1997) to remove the bias introduced by the order of samples. This generated the average number of species from 50 randomizations for each level of sampling effort (1–31 years). We then compared the observed species accumulation curve with the expected species richness at all sample sizes as estimated by *Chao* 1 and *Chao* 2.

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Regional species pool

The use of cumulative species number as an index of species richness assumes that the true number of species cannot be detected in a single sample and that there is little species turnover among samples. In our system, we evaluated the possible influence of regional-scale turnover by calculating the similarity of species composition of the Scotian Shelf between 1974 (when 54% of species had been discovered) and all successive samples until 2000. A decreasing trend in similarity between 1974 and successive years would reflect a significant turnover due to regional colonizations and extinctions. We used the Bray–Curtis Index of Similarity based on (1) incidence (presence/absence) and (2) abundance (Primer-E Ltd. 2001).

Physical correlates of species richness

Species diversity is dependent on scale. Ideally, we would be able to measure diversity within a habitat or species assemblage from local to regional scales. However, the sampling survey was designed for the scale of strata (100–1000 s km^2). We analysed species diversity at two large spatial scales. The larger spatial scale reflects the survey sampling design. The smaller spatial scale (300 km^2) reflects structure within strata. Note that both scales are sufficiently large so as to be considered as 'large area species richness' as defined by Gray (2000).

The goal was to determine the relationship between species richness, and swept area and depth range. For each sampling unit (strata or 300 km^2 grid), we used the cumulative number of species from 31 years of sampling as an index of species richness. Species abundance data were not used to modify the species diversity index (see Magurran, 1988) because the vessel trawl is designed to catch demersal fish and so preferentially catches fish close to the bottom. The measure of area was the total area trawled (swept) per strata over the time series. Mahon and Smith (1989) examined finfish assemblages on the Scotian Shelf and determined that assemblages are loosely defined by variation in depth and seasonal temperatures. We used the range of available depths sampled within the summer season as an index of depth-habitat diversity. Depth range was measured as the difference between the maximum and minimum depth sampled within a stratum. After preliminary analyses, we determined that the model which best described the relationship between species richness and depth range and swept area at the strata level was

$$\mathrm{SR} = a + b(\text{depth range}) + \left(\frac{c}{\text{swept area}}\right)$$

where SR = is the species richness, a, b, c the parameters (coefficients), depth range = maximum sampled depth − minimum sampled depth, swept area = the area swept by trawl.

The model parameters were estimated by minimizing the residual sums of squares (the loss function) using an iterative estimation algorithm in the non-linear statistical package of SPSS Inc., 1999.

The model most appropriate at the grid scale (300 km^2) was

$$\mathrm{SR} = a + b(\mathrm{Log}(\text{depth range})) + c(\mathrm{Log}(\text{swept area}))$$

The model input and parameters were the same as for the strata-level analysis (above). Model parameters were estimated by minimizing the residual sums of squares of a linear model.

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RESULTS

Census

The first research vessel survey in 1970 yielded 50 species. By the year 2000, the total number of species had increased by almost 3-fold to 140 species (Table 1; Figure 2(a)). Species number ranged from 27 to 57 (mean = 44, S.D. = 8) among the 48 strata.

Based on the distribution of rare species in 31 samples, the expected species richness was 172.2 ± 18 (*Chao* 1) and 164 ± 12 (*Chao* 2). Both theoretically expected estimates are greater than the observed 140 species (Figure 2(a)). If we accept that the pattern of how rare species are sampled can be used to estimate the 'true' species richness, then there are quite a few species that have not yet been discovered on the Scotian Shelf. Ideally, species richness estimators, such as *Chao* 1 and *Chao* 2, would be verified by comparing the theoretical estimates at different levels of sampling effort, with an observed estimate from an exhaustive sampling program (Colwell and Coddington, 1994). Since we do not know the 'true' species number, is there additional information that would support the use of these species richness estimators to evaluate the census sufficiency?

Sampling effort has been extremely low relative to the size of the shelf. Twenty-four per cent of the newly discovered species since 1971 were only found once. Further, the total amount of area that has been sampled by the research vessel survey since 1970 represents only 0.12% of the Scotian Shelf. Finally, the number of new species per set is higher in the first 5 years of the survey, but then fluctuates between 0% and 4% (Figure 2(b)). Our results suggest that the survey-species accumulation curve represents the ascending limb of the sampling curve, albeit flatter than the first 5 years of the survey, and has not yet reached a final asymptote. Multiple asymptotes would be common at large spatial scales. With respect to rarer species, the census is incomplete. However, we show below that the census can be used to monitor particular aspects of diversity as well as ecosystem change.

Regional species pool

Bray–Curtis's Index of Similarity based on presence/absence was constant over the time series. That is, the species composition in 1974 did not change significantly over time. The value of the index is less than 100 as species are discovered but are also lost continuously throughout the time series. In contrast, Bray–Curtis's Index of Similarity based on species abundance declined (Figure 3) reflecting a change in the dominance structure among species. A change in dominance has been documented elsewhere, the abundance of commercial, demersal fish has decreased while the abundance of pelagic species has increased (Zwanenburg, 2000). While no significant change in the core species composition occurred over the time series, note that a change in dominance structure may lead to species turnover.

We explored the effect of changing community structure on the quality of the census to estimate diversity on smaller geographic scales within the region. We tested for increasing or decreasing trends in the area occupied over the time series, for each species that occurred in 10 or more years. For each species, the percentage of area occupied (arcsin square-root transformed) was regressed on survey year to test for significant linear increases or decreases in geographic distribution. Out of 63 species, 7 species demonstrated significant negative relationships, 23 species showed significant positive relationships while 33 showed no trend (Table 2). The significant trends may originate from the changing dominance structure. Firstly, the abundance of cod and other large piscivores has declined dramatically (Zwanenburg, 2000) due to overfishing. The amount of area occupied by cod has also decreased significantly (Table 2). Concurrently, species that are known to be important prey items of the previously abundant groundfish, such as herring, sand lance and snake blenny showed significant geographic expansion.

Abundance and geographic distributions of species are in a dynamic state on the Scotian Shelf. This dynamism may be a result of fishing and/or environmental change, and may even reflect a normal level of

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Table 1. Species list of the Scotian Shelf: column labelled 'year' represents survey year in which species was first observed

Year	Species name	Common name	Total no. sets
1970	*Agonus decagonus*	Atlantic sea poacher	118
	Alosa pseudoharengus	Alewife	430
	Alosa sapidissima	American shad	161
	Ammodytes dubius	Northern sandlance	390
	Anarhichas denticulatus	Northern wolffish	12
	Anarhichas lupus	Striped Atlantic wolffish	1081
	Anarhichas minor	Spotted wolffish	14
	Argentina silus	Atlantic argentine	753
	Artediellus uncinatus	Arctic Hookear sculpin	245
	Aspidophoroides monopterygius	Alligatorfish	396
	Brosme brosme	Cusk	584
	Clupea harengus	Herring	1276
	Cottunculus microps	Polar sculpin	18
	Cryptacanthodes maculatus	Wrymouth	68
	Cyclopterus lumpus	Lumpfish	120
	Enchelyopus cimbrius	Fourbeard rockling	342
	Eumicrotremus spinosus	Spiny lumpsucker	91
	Gadus morhua	Cod	3557
	Glyptocephalus cynoglossus	Witch flounder	2315
	Hemitripterus americanus	Sea raven	1149
	Hippoglossoides platessoides	American plaice	3657
	Hippoglossus hippoglossus	Atlantic halibut	742
	Limanda ferruginea	Yellowtail flounder	1823
	Liparis fabricii	Gelatinous seasnail	13
	Lophius americanus	Monkfish	1244
	Lumpenus lumpretaeformis	Snake blenny	193
	Lumpenus maculatus	Daubed shanny	117
	Macrozoarces americanus	Ocean pout	957
	Mallotus villosus	Capelin	292
	Melanogrammus aeglefinus	Haddock	3138
	Merluccius bilinearis	Silver hake	2463
	Myoxocephalus octodecemspinosus	Longhorn sculpin	1845
	Myxine glutinosa	Northern hagfish	304
	Nezumia bairdi	Marlin-spike grenadier	347
	Pholis gunnellus	Rock gunnel	9
	Phycis chesteri	Longfin hake	514
	Pollachius virens	Pollock	1636
	Pseudopleuronectes americanus	Winter flounder	764
	Raja erinacea	Little skate	320
	Raja laevis	Barndoor skate	39
	Raja ocellata	Winter skate	751
	Raja radiata	Thorny skate	2954
	Raja senta	Smooth skate	1183
	Reinhardtius hippoglossoides	Greenland halibut	288
	Scomber scombrus	Mackerel	374
	Sebastes sp.	Sebastes spp.	2157
	Squalus acanthias	Spiny dogfish	1195
	Triglops murrayi	Mailed sculpin	696
	Urophycis chuss	Red hake	947
	Urophycis tenuis	White hake	2096
Total	50		
1971	*Lycenchelys verrilli*	Wolf eelpout	15
	Maurolicus muelleri	Muller's pearlsides	7

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Table 1 (*continued*)

Year	Species name	Common name	Total no. sets
	Osmerus mordax	Rainbow smelt	21
	Paralichthys oblongus	Fourspot flounder	20
	Peprilus triacanthus	Butterfish	155
	Scophthalmus aquosus	Windowpane flounder	42
	Tautogolabrus adspersus	Cunner	28
Total	7		
1972	*Gadus ogac*	Greenland cod	4
	Lycodes reticulatus	Arctic eelpout	70
	Microgadus tomcod	Tomcod	5
	Myoxocephalus scorpius	Shorthorn sculpin	28
Total	4		
1973	*Lycodes esmarki*	Vachon's eelpout	2
	Prionotus carolinus	Northern searobin	1
Total	2		
1974	*Citharichthys arctifrons*	Gulf stream flounder	127
	Dibranchus atlanticus	Atlantic batfish	9
	Gonostoma elongatum	Longtooth anglemouth	4
	Helicolenus dactylopterus	Blackbelly rosefish	240
	Hyperoglyphe perciformis	American barrelfish	1
	Liparis liparis	Striped seasnail	2
	Lycodes vahlii	Shorttailed eelpout	332
	Merluccius albidus	Offshore hake	110
	Paralepis atlantica	Short barracudina	2
	Polymixia nobilis	Stout beard fish	2
	Trachyrhynchus murrayi	Roughnose grenadier	16
	Ulvaria subbifurcata	Radiated shanny	51
Total	12		
1975	*Stomias boa ferox*	Boa dragonfish	6
Total	1		
1976	*Peristedion miniatum*	Armored searobin	1
	Raja spinicauda	Spinytail skate	1
Total	2		
1978	*Gaidropsarus ensis*	Threebeard rockling	3
	Zenopsis ocellata	John dory	16
Total	2		
1979	*Coryphaenoides rupestris*	Rock grenadier	15
	Epigonus denticulatus	Epigonus denticulatus	1
	Lycodes lavalaei	Laval's eelpout	11
	Notolepis rissoi	White barracudina	13
Total	4		
1980	*Careproctus longipinnus*	Longfin seasnail	3
	Chlorophthalmus agassizi	Shortnose greeneye	33
	Gymnelis viridis	Fish doctor	2
	Lycenchelys paxillus	Common wolf eel	3
	Polymixia lowei	Beardfish	5
Total	5		

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Table 1 (*continued*)

Year	Species name	Common name	Total no. sets
1981	*Coelorhynchus carminatus*	Longnose grenadier	1
	Monolene sessilicauda	Deepwater flounder	1
	Myctophum punctatum	Spotted lanternfish	1
	Petromyzon marinus	Sea lamprey	7
Total	4		
1982	*Benthodesmus elongatus simonyi*	Frostfish	1
Total	1		
1983	*Acipenser oxyrhynchus*	Atlantic sturgeon	1
	Centroscyllium fabricii	Black dogfish	19
	Chauliodus sloani	Viperfish	4
	Cottunculus thompsoni	Pallid sculpin	4
	Nemichthys scolopaceus	Snipe eel	7
	Salmo salar	Atlantic salmon	1
Total	6		
1984	*Cyttus roseus*	Red dory	2
	Notolepis rissoi kroyeri	White barracudina	55
Total	2		
1985	*Aspidophoroides olriki*	Arctic alligatorfish	6
	Etmopterus princeps	Rough sagre	1
	Eumesogrammus praecisus	4-line snake blenny	12
	Scomberesox saurus	Atlantic saury	16
Total	4		
1986	*Malacocephalus occidentalis*	Straptail grenadier	4
Total	1		
1987	*Grammatostomias dentatus*	Torpedo dragonfish	1
	Micromesistius poutassou	Blue whiting	3
Total	2		
1988	*Sphoeroides maculatus*	Northern puffer	1
Total	1		
1990	*Pristipomoides aquilonaris*	Pristipomoides aquilonaris	1
Total	1		
1991	*Lumpenus fabricii*	Slender eelblenny	6
	Lycodes terraenova	Newfoundland eelpout	12
Total	2		
1992	*Alosa aestivalis*	Blueback herring	3
	Careproctus reinhardi	Sea tadpole	9
	Liparis gibbus	Dusky seasnail	2
	Paralichthys dentatus	Summer flounder	1
Total	4		
1993	*Anoplogaster cornuta*	Ogrefish	1
	Ceratoscopelus maderensis	Horned lanternfish	2
	Conger oceanicus	Conger eel	1

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Table 1 (*continued*)

Year	Species name	Common name	Total no. sets
	Liparis atlanticus	Atlantic seasnail	17
	Myoxocephalus scorpioides	Arctic sculpin	2
	Parasudis truculenta	Longnose greeneye	8
Total	6		
1994	*Cubiceps pauciradiatus*	Cubiceps pauciradiatus	1
	Lycodes pallidus	Pale eelpout	1
	Urophycis regius	Spotted hake	4
Total	3		
1995	*Artediellus atlanticus*	Hookear sculpin	42
	Icelus spatula	Spatulate sculpin	6
	Liparis inquilinus	Inquiline seasnail	2
	Macrourus berglax	Roughhead grenadier	2
	Myoxocephalus aeneus	Grubby	4
	Synaphobranchus kaupi	Gray's cutthroat eel	1
Total	6		
1996	*Callionymus agassizi*	Spotted dragonet	1
	Icelus bicornis	Twohorn sculpin	5
	Melanostigma atlanticum	Atlantic soft pout	8
	Torpedo nobiliana	Atlantic torpedo	1
Total	4		
1997	*Argyropelecus aculeatus*	Atlantic silver hatchfish	2
	Liparis coheni	Gulf seasnail	2
Total	2		
2000	*Raja fyllae*	Round skate	2
	Stenotomus chrysops	Scup	1
Total	2		
Total	140		

Total in column labelled 'Year' refers to the total number of species which were newly discovered in that year. The 'Total no. sets' represents the number of sets in which species occurred from first discovery to 2000.

community change. While this will affect measures of diversity on smaller 'local' scales, it is also true that the low annual sampling effort renders the cumulative species number a better measure of species richness. Therefore, the local measures of cumulative species richness includes geographic changes in species composition as a result of the changing dominance structure. In this manner, the cumulative species number that we use as an index of local diversity represents the possible species richness of an area.

Physical correlates of species richness

Strata-scale analysis (100–1000 km^2)

The variance explained by the non-linear regression model relating species richness to swept area and depth range was $R^2 = 0.67$ (Table 3(a)). Strata with a greater depth range had a greater species richness (Figure 4(a)). Larger areas held a greater number of species, although the relationship is weak, and reaches

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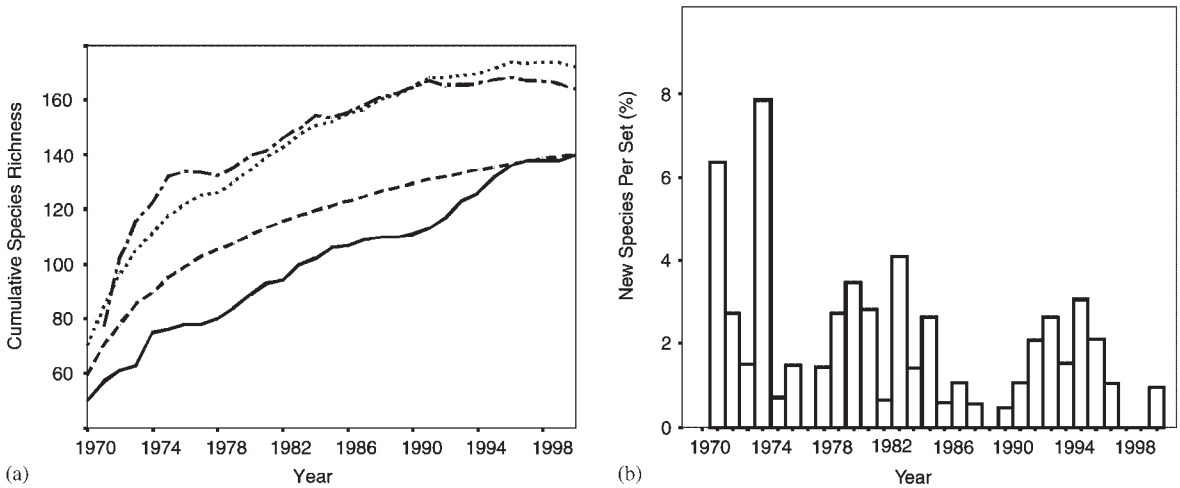

Figure 2. (a) Observed species richness:-solid line; Smoothed species richness (bias of sample order removed) — long dash; Estimated species richness *Chao* 1 — short dash; Estimated species richness *Chao* 2 — long/short dash combined. For all curves except the observed (solid line), each year represents the average species richness from 50 randomizations of samples/years (pooled for each survey year 2–31). (b) Number of newly discovered species per set in each survey year.

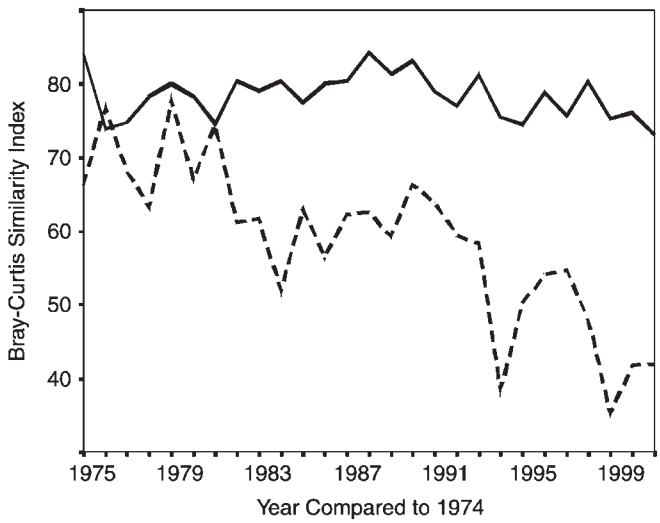

Figure 3. Bray–Curtis's Index of similarity of species composition between year 1974 and all successive years until 2000. Solid line is Bray–Curtis's Index based on incidence data; Dashed line is Bray–Curtis's index based on abundance data.

an asymptote quickly as swept area increases (Figure 4(b); Table 3). Depth range and swept area were not correlated at the strata scale. The spatial distribution of high positive residuals showed that the NE inshore, NE plain, NE slope (strata 40–42), inner Bay of Fundy (93–95) and Ba (75) had relatively higher species richness than would be predicted from the model. The Banquereau Bank and adjacent areas had a relatively lower species richness than would be expected (strata 47–51,58) (Figures 1 and 4(c)). These strata are influenced by factors other than depth range and swept area.

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Table 2. Species that demonstrated a significant increasing or decreasing trend in area occupied in the Research Vessel Survey (1970–2000)

Common name	r	N	p
Decreasing Area Occupied			
Thorny skate	−0.86	31	<0.001
Cusk	−0.84	31	<0.001
Northern wolffish	−0.79	11	0.004
Smooth skate	−0.72	31	<0.001
Cod	−0.67	31	<0.001
Striped Atlantic wolffish	−0.53	31	0.002
White hake	−0.50	31	0.004
Increasing area occupied			
Winter flounder	0.89	31	<0.001
Pollock	0.83	31	<0.001
Alligatorfish	0.83	27	<0.001
Northern sandlance	0.79	31	<0.001
Red hake	0.78	30	<0.001
Herring	0.77	31	<0.001
Capelin	0.75	22	<0.001
Atlantic sea poacher	0.71	20	<0.001
Snake blenny	0.69	28	<0.001
Longhorn sculpin	0.68	31	<0.001
Alewife	0.67	31	<0.001
American shad	0.67	30	<0.001
Little skate	0.65	30	<0.001
Blackbelly rosefish	0.64	25	0.001
Spiny lumpsucker	0.63	16	0.009
Mailed sculpin	0.62	31	<0.001
Gulf stream flounder	0.59	23	0.003
Fourbeard rockling	0.59	30	0.001
Northern hagfish	0.56	30	0.001
Greenland halibut	0.52	31	0.003
Spiny dogfish	0.51	31	0.003
Silver hake	0.50	31	0.005
Mackerel	0.46	31	0.009

r refers to Pearson correlation coefficient; N denotes the number of samples and p refers to the level of probability.

Grid-scale analysis (300 km^2)

The linear model relating species richness to swept area and depth range accounted for 55% of the observed variation (Table 3(b); Figure 5). Species richness increased linearly with the log of depth range and the log of swept area (Figures 5(a) and (b)). At this spatial scale, log swept area and log depth range were significantly correlated ($r = 0.3$, $p < 0.001$, $n = 510$) implying that the regression coefficients should not be directly interpreted because the independent effects of each variable are confounded. However, the effects of colinearity were not severe as indicated by the model diagnostics (variance inflation factor = 1.1). We can be confident that, at this scale, swept area accounts for proportionally more of the variation in species richness than does depth range (Table 3(b)). The location of the most negative residuals showed that Banquereau Bank (strata 47–48, refer to Figure 1) had fewer species than would be predicted from the model. There was no spatial pattern of the positive residuals.

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Table 3. Summary results of functional models explaining species richness

(a) Strata level: species richness = a+b(depth range) + (c/swept area): $R^2 = 0.67$

	Parameter estimates	Parameter standard error
A	44.2	2.39
B	0.082	0.01
C	−34.07	6.63

(b) Grid (300 km^2) level: species richness = a+b(Log(depth range)) + c(Log(area)): $R^2 = 0.55$.

	Coefficients	Std. Error	Standardized Coefficients	t	p	Correlation Zero-order	Partial
Constant	24.347	0.799		30.5	0.000		
Log (Depth Range)	3.623	0.440	0.263	8.3	0.000	0.45	0.34
Log (Area)	12.769	0.678	0.602	18.8	0.000	0.68	0.64

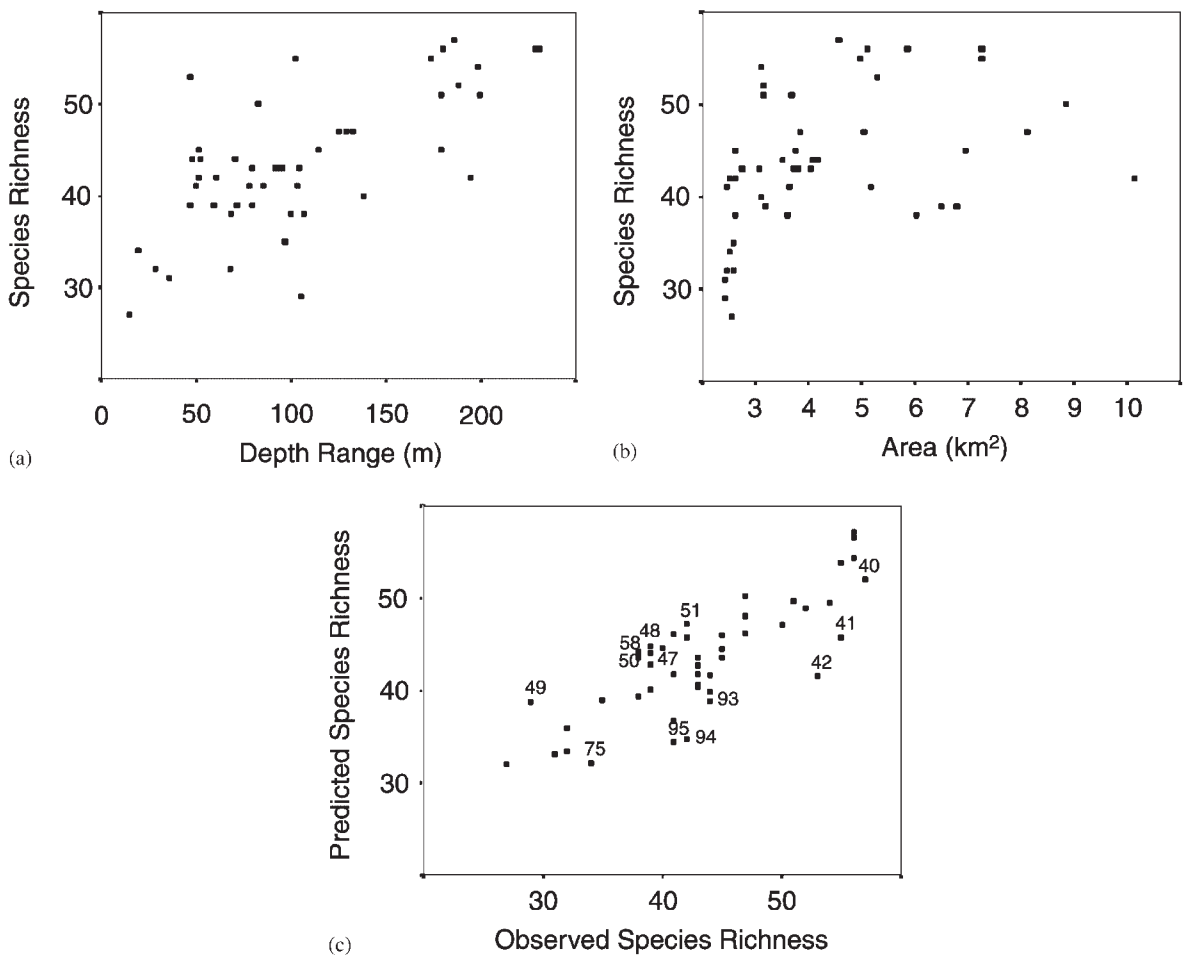

Figure 4. Summary results of strata-level analysis of Model: species richness = a+b(depth range) + (c/swept area). (a) species richness and depth range (b) species richness and swept area, (c) adjusted predicted values and observed species richness.

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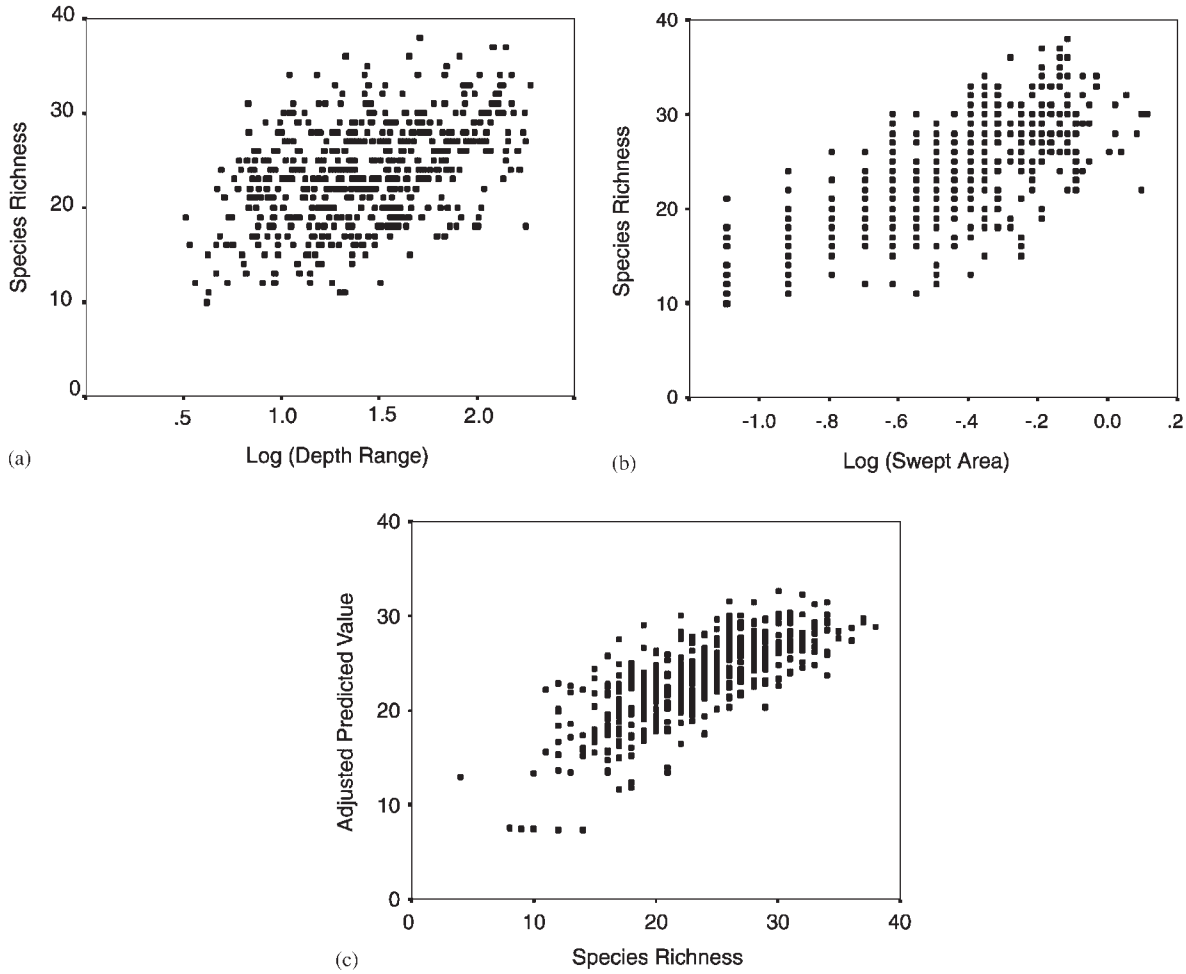

Figure 5. Summary results of grid-level analysis of Model: species richness = a + b(Log (depth range)) + *c*(Log (swept area)). (a) species richness and depth range, (b) species richness and swept area, (c) adjusted predicted values and observed species richness.

The geographic distribution of species richness shows that it is relatively higher along the northeast coast, along the slopes, on Western/Emerald Bank (strata 63–64) and in the Bay of Fundy (Plate 1(a)). If the effect of swept area is removed, the general pattern is the same but the larger banks appear to have a lower species richness (Plate 1(b)). The problem, however, of correcting for differences in area swept among grids is that it may result in an over-correction. Given the same sampling effort, species accumulate at different rates in different grids. If the species richness in an area has reached an asymptote, but continues to be sampled year after year, then any correction will be excessive, rendering an artificially low estimate of species richness. It is notable that the larger banks have been sampled relatively more than other areas. It is unlikely that the species accumulation curves within all grids are at the same stage, and species richness estimated by these two different methods must be qualified. The major disadvantage in our study is that sampling effort has been relatively low in any given year and our cumulative estimates include temporal and spatial population dynamics. Only intensive synoptic sampling with replication well in excess of the research survey protocol employed herein will yield asymptotic species-accumulation curves.

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Areal effect

Area has an effect at both spatial scales examined herein. The effect of area on species richness has been attributed to various mechanisms (Hart and Horwitz, 1991; Connor and McCoy, 2000). Most notable hypotheses include the MacArthur and Wilson Equilibrium theory of Island Biogeography (area *per se*), William's Habitat Diversity hypothesis, the Resource Concentration Hypothesis (*cf*. Connor *et al*., 2000), and the Random Placement or Passive Sampling hypothesis (Connor and McCoy, 1979; Coleman, 1981). The area *per se* hypothesis maintains that larger areas have a greater number of species because individual population sizes are larger and are not as vulnerable to extinction through stochastic events. The habitat diversity hypothesis states that as area increases, the number of habitats increases and therefore so do the number of species. The resource concentration hypothesis explains that if population density is higher in larger patches it is because either animals can find and remain longer in large areas of food than in small areas of food, or larger patches are safer from predators. In addition, higher density on larger patches can lead to lower rates of extinction by damping demographic and environmental stochasticity. Passive sampling can result in a species–area relationship because as the number of individuals increases with sample size, so does the probability of sampling new species.

We explored whether the results from the strata-level analysis were consistent with any of these theories. In a previous study, we examined the relationship between species and area on banks alone (<92 m) (Frank and Shackell, 2001). We observed that density and total abundance of several species increased with bank area, and suggested that larger areas have greater resources, as proposed by the resource concentration hypothesis (*cf*. Connor and McCoy, 2000). Larger areas may also support larger populations that are less susceptible to stochastic extinction processes (Frank and Shackell, 2001). In the present study, we examined the relationship between density and stratum area for 58 individual species that occurred in 10 or more strata. In examining the entire Scotian Shelf, there was one positive and 2 negative correlations between density of individual species and area significant at the 0.01 level. Clearly, the resource concentration hypothesis does not apply at the regional scale. Habitats vary greatly on a large spatial scale and it can be imagined, for a given species, that a small patch of a suitable habitat will be preferred over a large patch of unsuitable habitat. Dissimilar results between density and area on the bank and regional scales occur as we have mixed suitable and unsuitable habitats at the regional scale.

Finally, to test whether the effect of area was a result of passive sampling, we sub-sampled equal samples from each stratum (2 sets per year from 1970 to 2000). When samples were equal among strata, area had no effect on species richness, although depth range did. At this large spatial scale in which habitat heterogeneity is high, area *per se* has no effect but is a result of passive sampling (Connor and McCoy, 1979).

DISCUSSION

Census

New species continue to be discovered in the research vessel survey conducted annually on the Scotian Shelf. Annual sampling effort is low relative to the size of the Shelf, and species' abundance and distribution are continually changing. The discovery of a new species occurs if (1) a species has immigrated into the region, (2) the probability of capture has increased due to increase in sampling effort, an increase in abundance or sampling of additional habitats, or (3) identification skills have improved and interest in non-commercial species has increased. The latter effect is suspected to have occurred during the conduct of the survey, but is not quantifiable (M.Strong, pers.comm., DFO, St Andrew's, NB, E5B 2L9; J. Simon, pers. comm., DFO, Dartmouth, NS, B2Y 4A2). It is also true that the demersal trawl survey is designed to catch

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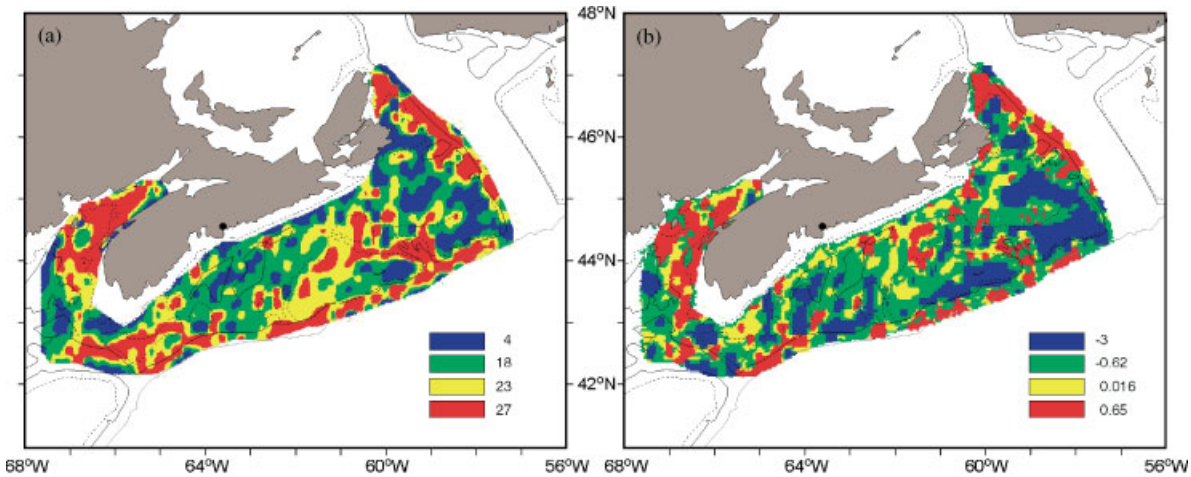

Plate 1. (a) Species richness (number of species) on the Scotian Shelf on 300 km^2 scale, and (b) Species richness after removing the sample effect (residuals of species richness regressed on swept area).

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bottom-dwelling fish and preferentially does so. Differential catchability cannot, however, explain why many demersal fish species were newly discovered during the 1980s and 1990s (Table 1).

Unfortunately, there is no clear method to partition the causes of a newly discovered species. We infer that a few new species may have colonized the Scotian Shelf over the last 31 years but the majority of newly observed species have resident but low population sizes. Many of the species discovered later in the survey series had relatively low population abundances. Twenty-four per cent of the species sampled were observed only once after 1970. Only a small proportion of the Scotian Shelf was sampled from 1970 to 2000 (0.12%). While this amount is sufficient to characterize the distribution and abundance of common species, it is insufficient to characterize the less abundant ones. Themelis (1996) conducted an intensive study of mesopelagic fish on a relatively small area on the continental slope of Canada. She discovered that 39.6% of her collected species had never been recorded in Atlantic Canada. There is undoubtedly a higher level of diversity than has been currently measured, particularly in slope waters. We predict additional discoveries of rarer species as the survey census accrues.

When only a small proportion of an area is sampled on an annual basis, it is important to use the cumulative number over the entire time series as an index of diversity. Strong and Hanke (1995) used the composite of annual surveys, or the average in 5 year-time blocks, to evaluate species richness on the Scotian Shelf. There are common areas of high diversity between our results and theirs, yet there are also important differences we believe stem from the scale of temporal aggregation. This raises the important question, is the cumulative species number estimated from a long survey time series equivalent to the synoptic/instantaneous species number estimated from an intensive and sufficient sampling program? It would be of great interest to exhaustively sample an area on the Scotian shelf to determine the answer.

Monitoring biodiversity

Can the survey database be used to monitor biodiversity? At a superficial level, it would appear that biodiversity has increased over the course of the research vessel surveys because new species are continually being discovered. Our analysis has shown this to be a function of sampling effort. It is, however, possible to monitor change in commoner species. Increasing or decreasing trends may be a precursor to a change in diversity level. We examined the percent of area occupied by each species over time to determine how the distribution of the community has changed. There has been a geographic expansion of the prey species of the formerly abundant cod, as well as for species that may have radiated as a result of competitive release (e.g. winter flounder, spiny dogfish, hagfish). The existence of a large area closure on the eastern Scotian Shelf may also have contributed to an increase in abundance and range expansion of several species.

An important question is whether geographic expansion/contraction reflects a metapopulation structure, or distinct populations. Protection of a network of habitats may be important for a species long-term viability (Marsh and Trenham, 2001). The declining trend in the similarity of species using an abundance-based index reflects a change in dominance structure. A change in dominance structure will precede a change in composition, as a population declines towards local extinction. The community on the Scotian Shelf is changing and the survey database can be used to address those changes.

Regional pattern of diversity

On the Scotian shelf, larger areas with a greater depth range have a greater number of species. Maximizing habitat heterogeneity and area are included in many Marine Protected Area selection criteria and our results reinforce that notion. However, the amount of variation explained by the functional models is 55–67%. Depth range is a crude measure of habitat diversity. Although it is comparable to the use of maximum elevation as has been used in terrestrial studies, depth range cannot be considered to characterize fully habitat diversity even though depth is correlated with substrate type, water temperature, light levels and other properties on the Scotian Shelf (Mahon and Smith, 1989). More of the variation in species

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richness could be explained were we to include other aspects of habitat diversity. The northeast region demonstrates our inability to capture fully habitat heterogeneity using our chosen metric. It is a very species-rich area, even after accounting for the effects of area and depth. The North East area is species rich possibly because it is influenced by its proximity to the Gulf of St. Lawrence, both as a conduit for colonizing species and that the water flowing from there is colder and less saline, introducing another level of habitat heterogeneity. Similarly, the Bay of Fundy is a species rich area, greater than could be explained by depth range and area. The Bay of Fundy habitat differs in several regards, several anadromous species are found there returning to rivers (e.g. shad). Habitat heterogeneity in the Bay of Fundy could also include less saline waters due to river discharge. It is a tidally dominated system with muddy substrates, quite different from the offshore areas.

The combined influences of area (through passive sampling) and depth range support the current dialectic notion that species richness on a regional scale is influenced by more than one factor (Connor and McCoy, 2000). The depth range effect conforms to the idea that greater heterogeneity of habitat results in greater species richness. Indeed, large-scale species richness of benthic organisms has been observed to increase with increased environmental heterogeneity (Ellingsen and Gray, 2002). Again we emphasize the effect of spatial scale. Herein, we examined slopes, plains, basins and banks across the Scotian Shelf. When shallow banks were analysed separately, depth range, due to its relatively low variation on shallow banks, had no influence whereas area had a strong effect (Frank and Shackell, 2001). In addition, species density increases with area on a bank-scale, implying larger areas are in some manner superior (Frank and Shackell, 2001). Species density does not increase with area on a regional scale because so many different habitats exist on a large scale: a mesopelagic species which prefers a slope would prefer a small slope over a large plain.

A summary question is, what is the best measure of local diversity in an incompletely censused area in which there is dynamic geographic expansion/contraction within the region? The ideal measure of species richness is a synoptic measure estimated from exhaustive sampling. We have presented, we believe, the best possible, but not perfect, depiction of regional scale diversity. We have also presented surrogates as indicators of species diversity both as a method for understanding process and as a potential tool for conservation management. However, these tools are not powerful. The use of surrogate variables in conservation planning is economical but somewhat simplistic. There is accruing evidence that habitat quality and spatial configuration are important determinants of diversity patterns (e.g. Oertli *et al*., 2002). We are currently exploring whether quality can be defined by location of core habitat, and how spatial configuration can affect dispersal.

We have used a database designed to monitor commercial species. As international commitments to preserve diversity translate to field programs, a course of action would be to verify and determine true species richness through establishing reference sites and sampling protocols at a range of scales (Colwell and Coddington, 1994). The use of surrogates of diversity will be scale-dependent but the range of spatial scales may be important for conservation planning. We support the development of additional habitat measures that may be measured at multiple scales. The present contribution can be used as a basis for designing such a program.

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