



# Process-Driven Characterization and Mapping of Seabed Habitats

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## Abstract

*The creation of habitat maps commonly is based on defining regions having similar chemical, physical and biological characteristics. Traditionally, the boundaries between habitat types are established on arbitrarily-chosen levels of physical variables and on approximation of spatial location. Here, we demonstrate a practical method for creating seabed habitat maps using the habitat template approach to integrate multiple environmental fields into a single map. The resulting map shows the distribution of habitats where organisms with particular life history traits are likely to flourish, and provides a spatial framework for integrated management of ocean uses. A case study for the Scotian Shelf and Bay of Fundy in the northwest Atlantic Ocean illustrates that the parsimonious nature of the modelling approach allows prediction of spatial patterns in benthic habitat types based on readily available oceanographic data.*

## Résumé

La création de cartes d'habitat est fréquemment basée sur la définition de régions présentant des caractéristiques chimiques, physiques et biologiques communes. Traditionnellement, les limites entre les types d'habitat sont établies à l'aide de paramètres physiques, selon des niveaux définis de façon arbitraire, ainsi que sur une approximation de la localisation spatiale. Nous offrons ici une démonstration d'une méthode pratique pour générer des cartes d'habitat du fond marin, en utilisant l'approche par modèle d'habitat qui permet d'intégrer plusieurs paramètres environnementaux dans une seule carte. La carte qui en résulte montre la répartition des habitats où des organismes dont le cycle biologique présente des caractéristiques spécifiques sont plus susceptibles de proliférer, et fournit un cadre spatial pour la gestion intégrée des interventions en milieu océanique. Un exemple provenant du plateau néo-écossais et de la baie de Fundy dans le nord-ouest de l'Océan Atlantique illustre le fait que la nature parcimonieuse de l'approche modélisée permet de prédire la répartition spatiale des types d'habitats benthiques à l'aide de données océanographiques facilement accessibles.

**INTRODUCTION**

Our knowledge of seabed ecosystems is fragmentary because it is constructed from ‘snapshots’ speckled through space and time. The perception of the seabed obtained from these snapshots (in the form of physical bottom samples and photograph and video observations) is not comparable to the appreciation of the diversity of terrestrial life and landforms that is gained from a walk in the forest or a low-altitude flight over land because of the lack of continuity of observations and the disparity of scale. Nevertheless, ocean management, based on zoning (restricting certain human activities to geographically-defined areas), presupposes the existence of maps that are equivalent to detailed land use and habitat maps for the terrestrial environment. Creation of such maps is difficult because visual observations of the seafloor are unavoidably fragmentary and remote sensing techniques in the marine realm are mainly limited to structural descriptions of the seabed (acoustic surveying) and to depictions of the ocean surface (*e.g.*, satellite imagery). Benthic habitat maps for relatively small areas, such as harbours and offshore banks, can be created using high-resolution acoustic surveying, cores, grabs and optical samples (Kostylev *et al.*, 2001, 2005). However, practical constraints on geophysical and biological observations and on mapping of large areas of the seabed, such as continental shelves, call for the development of new approaches with reduced demands for data quality and quantity (Roff and Taylor, 2000; Roff *et al.*, 2003).

Our approach is based on ecological theory that relates species life history traits to the properties of the environment. Many authors have argued that characteristics of habitats impose selective forces through a variety of biotic and abiotic factors; these factors affect the fitness of individual organisms by modifying their growth rate, survival, fecundity, *etc.* (Southwood, 1977, 1988; Grime, 1977, 1979; Margalef *et al.*, 1979; Huston, 1994; Reynolds, 1999). The two major selective forces are physical disturbance and adversity of the environment. This disturbance–adversity continuum has been used to predict traits of species occurring in different quadrants of the habitat template (Table 1; Southwood, 1977, 1988), emergent properties of ecological communities, such as competition and bio-

diversity (Southwood, 1988; Huston, 1994), and has been used in the classification of terrestrial habitats (Grime, 1977, 1979). The summary of existing habitat template models, exhibited in a common system of coordinates, is presented in Figure 1(A-D). In this paper, we use the habitat template shown in Figure 1E as a framework for transforming maps of the physical environment into a map of benthic habitat types; these habitats support species populations that have different life history traits, and species assemblages having characteristic sensitivity to human impacts. Instead of the term ‘adversity’, which may be easily confused with ‘disturbance’, we use the term ‘scope for growth’ which is reciprocal to ‘adversity’ (compare Figures 1A and 1E).

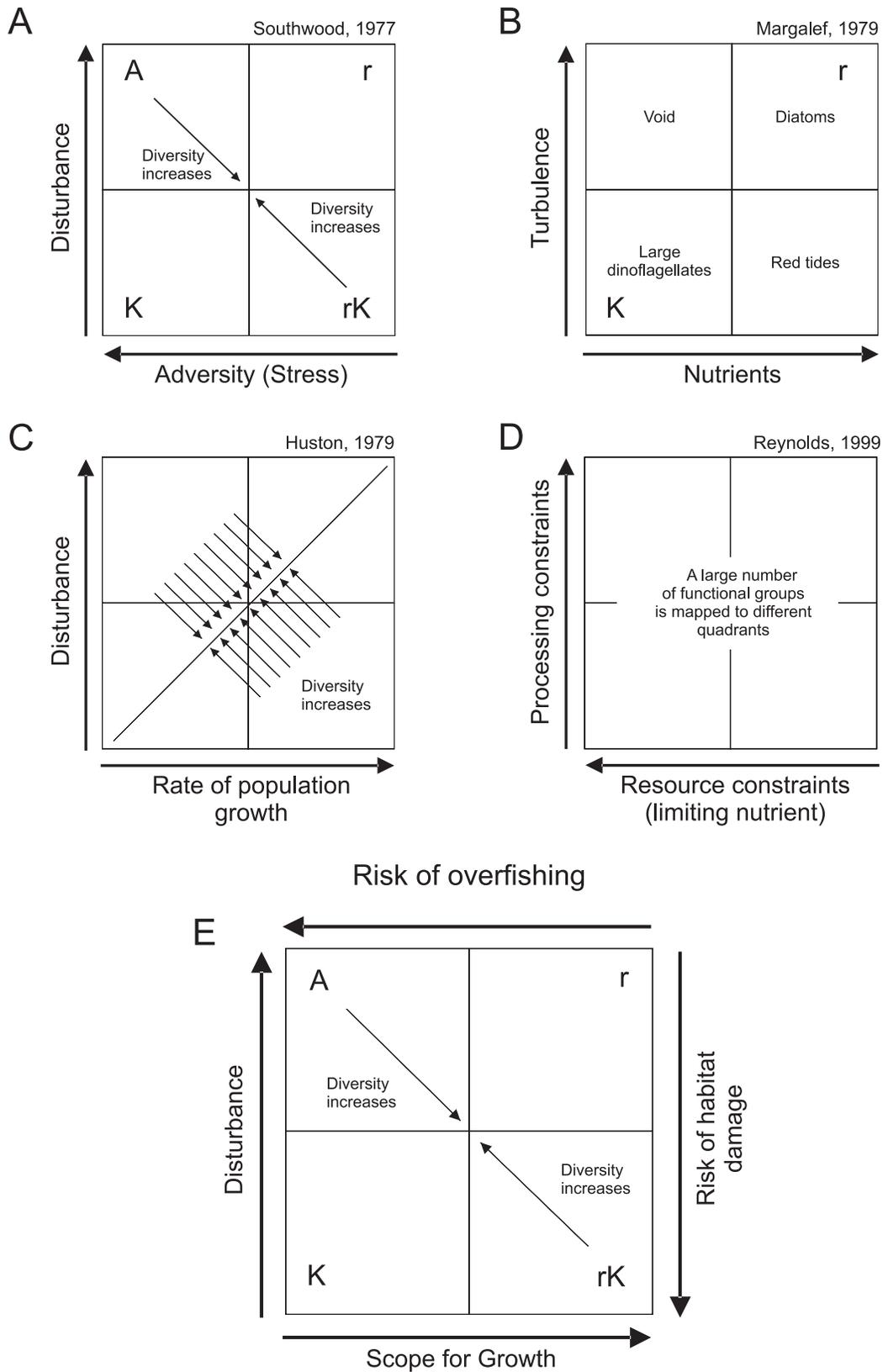
The ‘disturbance’ axis reflects the intensity of habitat alteration or destruction, or the durational stability of habitats, including only natural seabed processes responsible for selection of species’ life history traits on the evolutionary time scale. We define disturbance as the ratio of the characteristic friction velocity to the critical shear stress required for initiation of sediment movement, where friction velocity is computed using surface wave data, tidal currents, sediment grain size and water depth. The critical stress required for resuspension of bottom sediment is a function of grain size. In the Canadian Scotian Shelf case study presented here, we do not take into consideration episodic events such as turbidity currents down steep slopes, ice scouring, or anthropogenic disturbances such as bottom trawling.

Shallow offshore banks covered by coarse sandy sediments often experience high sediment mobility. Such disturbed environments would favour species capable of tolerating or escaping disturbance, for example, mobile or tough-shelled animals, fast-growing species capable of reaching maturity before the next major disturbance, broadcast spawners, or species with short life spans that can quickly colonize an area and leave offspring.

The ‘scope for growth’ axis (Figure 1E) considers environmental stressors that pose a cost for physiological functioning of organisms and limit somatic growth and reproduction. We propose that the scope for growth axis is an estimate of energy available for growth and reproduction of a species after accounting for energy spent adapting to the environment. Our definition of scope for growth is based on four factors: food availability (which combines stratification and surface chlorophyll as a measure of benthic–pelagic coupling), annual bottom temperature (as an indicator of metabolic rates), temperature variability (as an indicator of both thermal stress and temporal uncertainty for reproduction), and oxygen saturation (as a measure of metabolic stress). Indices, based on these factors, are additive, following fuzzy logic theory (Zadeh, 1965), which allows characterization of the environment on a continuous scale between ‘benign’ (high scope for growth) and ‘adverse’ (low scope for growth). This is not an explicit model of ecological and physiological processes in benthic communities, but rather an evaluation of the benthic environment in terms of the amount of energy available to animals for growth and reproduction.

**Table 1.** The life history traits associated with the 4 quadrants of the habitat template with characteristic species from the Scotian Shelf. The traits are based on Southwood (1977); high adversity correlates to Southwood’s low scope for growth, and low adversity correlates with high scope for growth

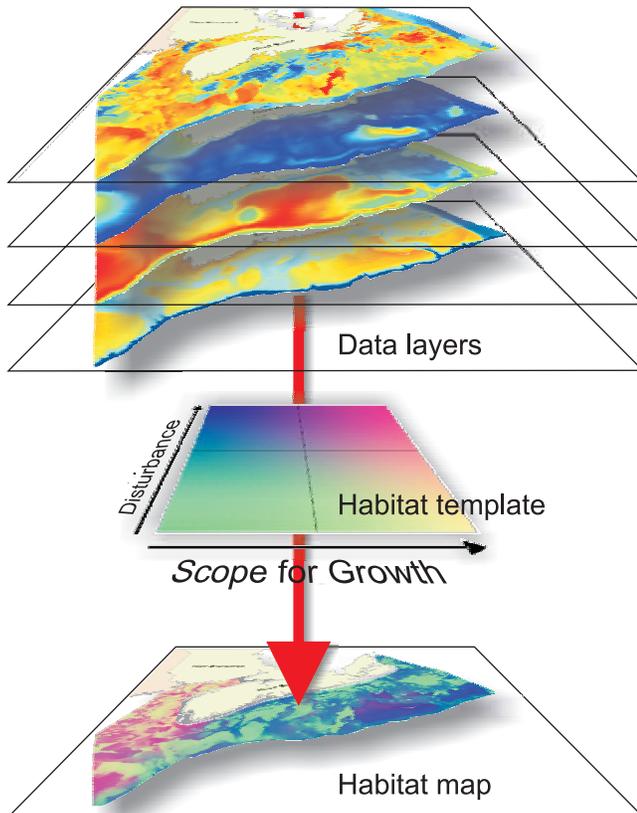
	<b>Low Scope for Growth</b>	<b>High Scope for Growth</b>
<b>Low Disturbance</b>	Defence: high Migration: low Offspring: few and large Longevity: great  Example: cold water corals	Defence: medium Migration: low Offspring: medium and small Longevity: medium  Example: tube-building polychaetes
<b>High Disturbance</b>	Defence: high Migration: high Offspring: medium large Longevity: medium  Example: quahogs	Defence: low Migration: high Offspring: many small Longevity: small  Example: scallops



**Figure 1.** A-D) Habitat templates developed by different authors, brought into a common system of coordinates. E) Habitat template for benthic habitat mapping, representing our summary of existing habitat models. Expected life history traits are shown in each quadrant: r- 'opportunistic' strategies; K- 'equilibrium' strategies; rK-mixed strategies; A-adversity tolerators. These terms are used for convenience and are not in strict accordance with deterministic model of life history strategies (MacArthur and Wilson, 1967).

## METHODS

Here we provide a brief description of the data and sources. Underlying the scope for growth and disturbance axes (Figure 1E) are eight data layers. A schematic of the process for transforming the data layers into the habitat map using the habitat template is shown in Figure 2. A map of the study area in the Atlantic Ocean off eastern Canada (Scotian Shelf and Bay of Fundy), with geographical names mentioned in the text, is shown in Figure 3.



**Figure 2.** Schematic of the process for transforming the data layers into the habitat map using the habitat template. The nine environmental data layers for the Scotian Shelf application are described in the Methods Section, and the habitat template is presented in Figure 1 and Table 1.

All of the data fields have been created in MapInfo™ GIS using Vertical Mapper™ as raster grids with 500 m pixel size (the analysis grid) to achieve a good representation of the gradients that exist in each data layer. This does not mean that the data layers or the final map have a spatial accuracy of 500 m, rather the analysis grid provides an underlying structure that resolves the gradients and will accommodate future improvements in horizontal resolution of the data layers.

### Bathymetry

The bathymetry data has been provided by the Canadian Hydrographic Service (G. Costello, pers. comm., 2002). The source data are a combination of traditional soundings and modern multi-

beam sonar bathymetric data. After substantial quality control and editing, the data are gridded to 500 m horizontal resolution (Figure 4A). This dataset controlled the horizontal resolution of the analysis grid. Data close to the coast were excluded because of the spatial complexity and legal issues related to navigation.

### Stratification

The typical upper ocean stratification for summer (July-September) was estimated from the Bedford Institute of Oceanography (BIO) hydrographic database (Gregory, 2004; [www.mar.dfo-mpo.gc.ca/science/ocean/database/data\\_query.html](http://www.mar.dfo-mpo.gc.ca/science/ocean/database/data_query.html)). For each month, all the temperature and salinity data covering the period 1950 to 2001 were binned into a 0.5° horizontal grid at 0 m depth (all data between 0 and 5 m) and 30 m depth (25 and 35 m). The binned data were then linearly interpolated into a 5 km (north-south) by 10 km (east-west) grid. The temperature and salinity at each grid point were then used to compute water density. Stratification was defined as the density difference between 30 m and 0 m depth (V. Soukhovtsev, pers. comm., 2003). This numerical field was then interpolated to the analysis grid using MapInfo, and the summer stratification was computed as the average of the July, August and September fields (Figure 4B).

### Chlorophyll

Following the suggestion by Hargrave and Peer (1973) that benthic productivity has the strongest relationship with spring blooms, a composite map of chlorophyll-*a* distribution in the spring, estimated from Sea-viewing Wide Field-of-view Sensor data (SeaWiFS, <http://oceancolor.gsfc.nasa.gov/SeaWiFS/>) for the period 1997 to 2003, was used as a proxy for primary production reaching seafloor. The map (Figure 4C) was computed from the semi-monthly composites that are produced at BIO by combining all of the data available for each half-month and averaging multiple pixels at any location. These images cover the area 39°N to 62.5°N and 42°W to 71°W, have data resolution of about 1.5 km per pixel, and are available online ([http://www.mar.dfo-mpo.gc.ca/science/ocean/ias/seawifs/seawifs\\_1.html](http://www.mar.dfo-mpo.gc.ca/science/ocean/ias/seawifs/seawifs_1.html); G. Harrison, BIO, pers. comm., 2004). The mapped pattern was interpreted using caution because it represents only fluorescence of the surficial water masses and may be influenced by suspended inorganic particles. For example, unusually high chlorophyll-*a* values in the Bay of Fundy are likely artefacts caused by suspended mud (B. Hargrave, BIO, pers. comm., 2003). For our calculations, concentrations in excess of 7 µg ml<sup>-1</sup> were truncated to 7 µg ml<sup>-1</sup>.

### Oxygen Saturation

Bottom oxygen saturation data representing typical conditions for July were mapped. Oxygen saturation data from the annual July summer groundfish cruises were extracted for the period 1997-2003 from the BioChem database (Department of Fisheries and Oceans Canada, 2006; Gregory and Narayanan, 2003). The bottom values from each profile were extracted and maps were generated on a 5-km grid using the 'griddata' function in Matlab™. The mean July conditions were obtained by temporal averaging at each grid point. The field was then mapped to the analysis grid using MapInfo (Figure 4D). The resulting map is similar to that published by Harrison *et al.* (2004).

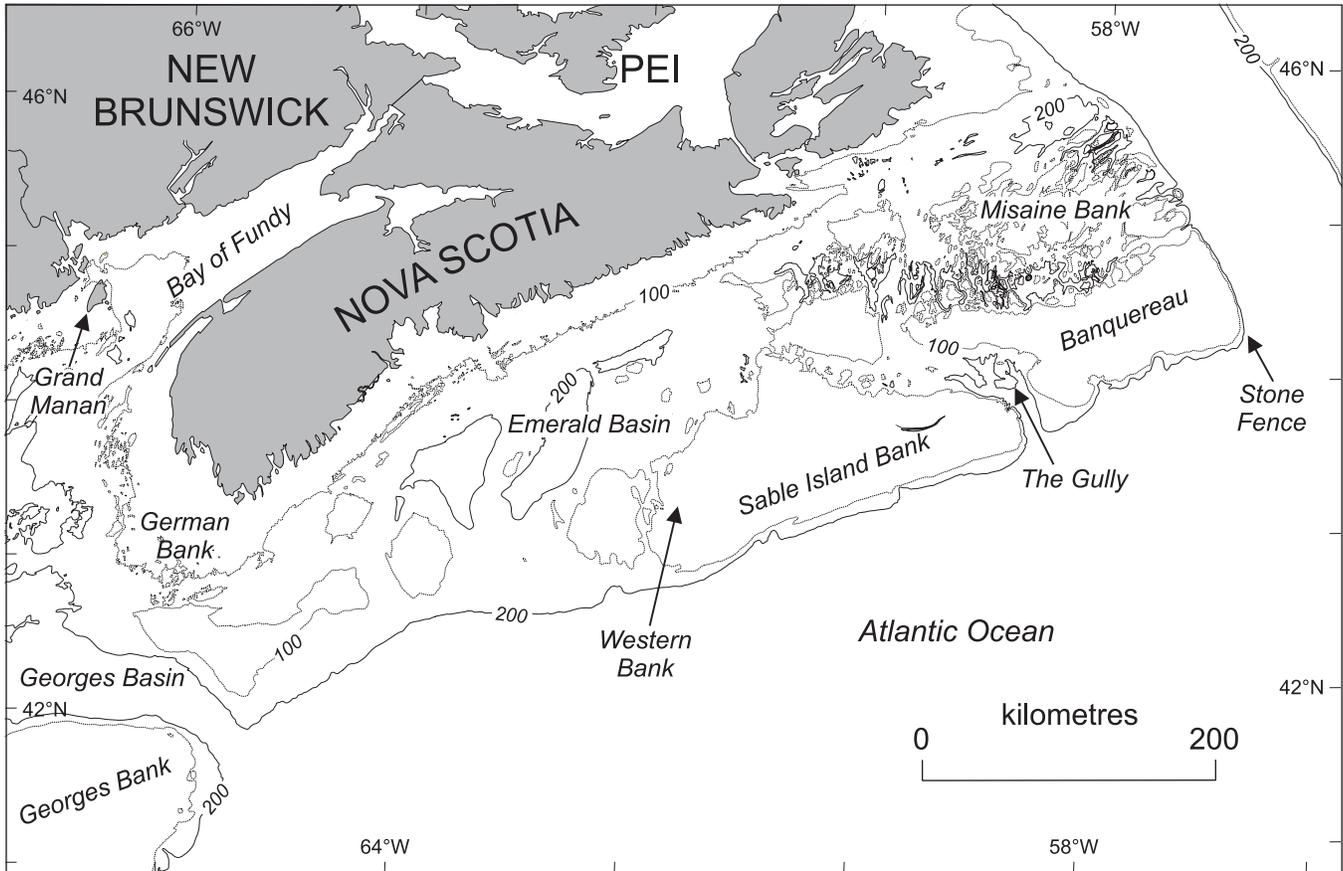


Figure 3. Location map of the Scotian Shelf and Bay of Fundy with geographical names indicated.

### Bottom Temperature

Seasonal mean averages of the near-bottom temperatures were taken from the modelling results of Hannah *et al.* (2001) and Han *et al.* (1999), which were based on the analysis of Loder *et al.* (1997). The combined fields covering the entire region are shown in Breeze *et al.* (2002). The annual average (Figure 4E) and amplitude of the seasonal cycle (Figure 4F) were computed from the seasonal means. Estimates of the Root Mean Square (RMS) magnitude of the interannual temperature variability (V. Soukhovtsev, pers. comm., 2003) were made using the BIO hydrographic database (Gregory, 2004; Petrie *et al.*, 1996; [www.mar.dfo-mpo.gc.ca/science/ocean/database/data\\_query.html](http://www.mar.dfo-mpo.gc.ca/science/ocean/database/data_query.html)). Monthly means (using data from the period 1950 to 2001) were computed on a  $0.5^\circ$  horizontal resolution grid at standard oceanographic depths: 0-5 m for 0 m, 5-15 m for 10 m, 25-35 m for 30 m, 45-55 m for 50 m, 70-80 m for 75 m, 90-110 m for 100 m, and 140-160 m for 150 m. The RMS interannual variability was estimated for each month by computing the standard deviation of the temperature observations in the  $0.5^\circ$  grid squares (thus ignoring the annual cycle within a month and spatial variability within each grid cell). Vertical interpolation was then used to estimate near-bottom values. For depths greater than 150 m, the value at 150 m was used. Two-dimensional linear interpolation was used to map the monthly fields to a 20 km grid. This interannual variability field was then interpolated to the analysis grid using MapInfo and the annual average variability was computed as the average of the 12 monthly values (Figure 4G).

### Sediment Grain Size

Grain size was mapped on the basis of approximately 10,000 sediment samples obtained from the Scotian Shelf by Natural Resources Canada (NRCan) and the US Geological Survey (USGS). Mean grain sizes for the upper 10 cm of each sample were interpolated within similar sedimentary facies and the resulting interpolations were merged and spatially smoothed. This approach allowed us to use acoustically-verified boundaries between sedimentary formations as defined by a facies map (King and MacLean, 1976; Fader *et al.*, 2004) while preserving patterns of grain size variability within them. The resulting grain size distribution map (Figure 4H) is the first attempt to recreate a continuous sediment texture for the entire Scotian Shelf.

### Characteristic Bottom Stress

The characteristic bottom stress (Figure 4I) was the synthesis of four data products: 1) high-resolution bathymetry of the region (the analysis grid), 2) 42-year hindcast of the wave height and period data, 3) near-bottom estimates of tidal current extracted from various models, and 4) median grain size estimates. These data were used as inputs for the calculation of bottom stress using SEDTRANS96 (Li and Amos, 2001). The bottom stress is represented by a friction velocity ( $\text{cm s}^{-1}$ ) which is the square root of the bottom stress divided by the density of water.

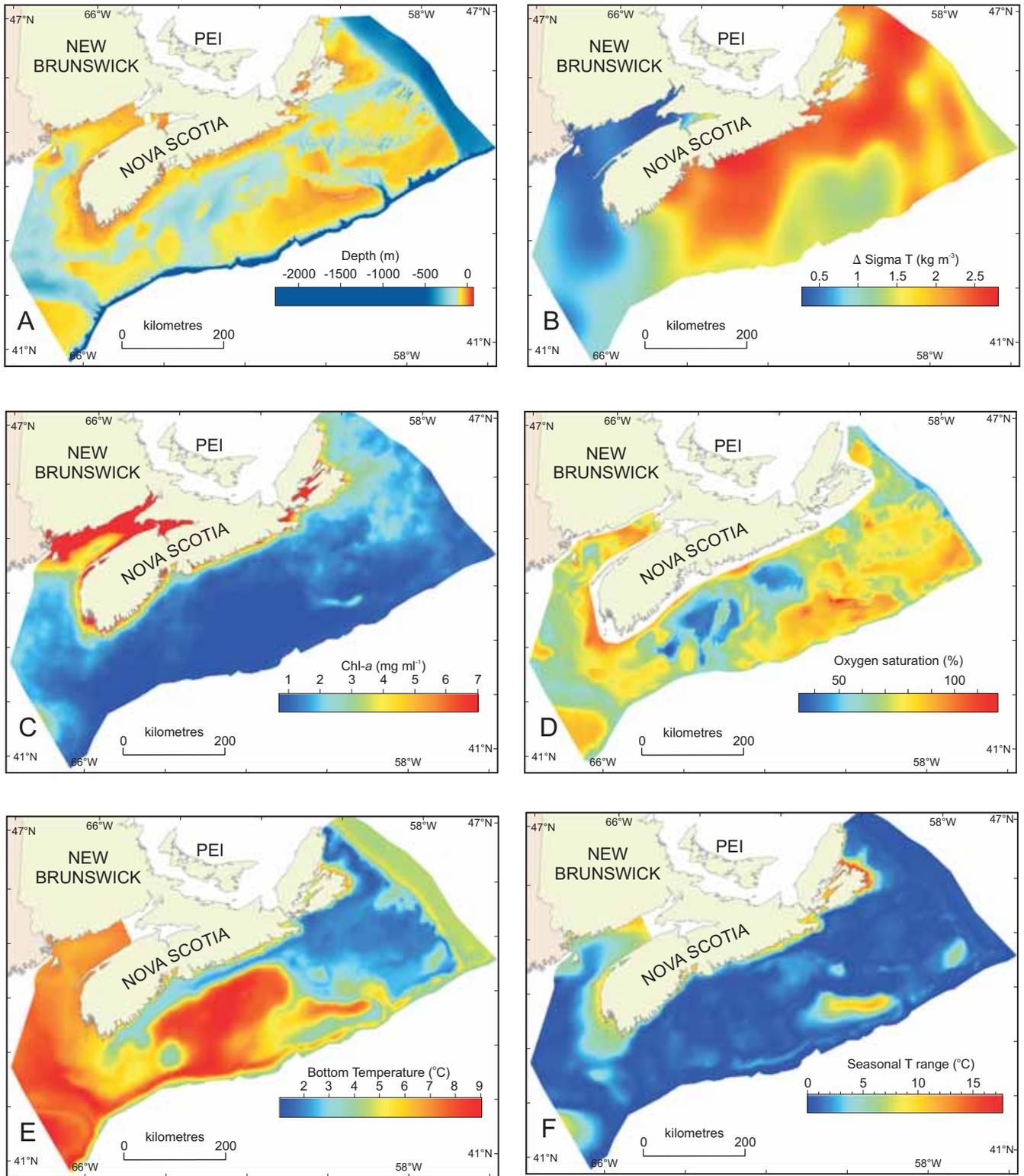
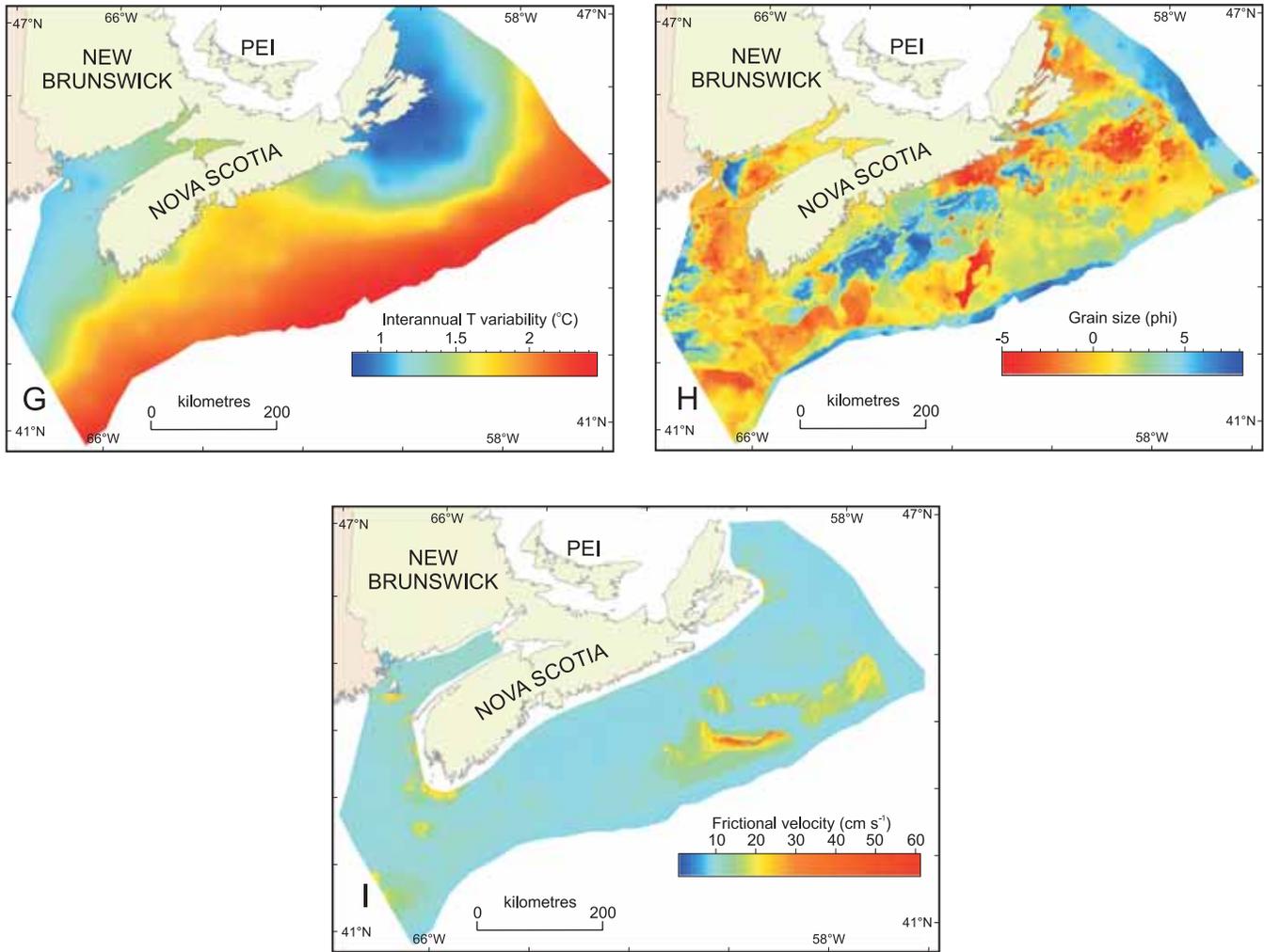


Figure 4. Caption and continuation of Figure on opposite page.



**Figure 4.** A) Gridded bathymetry of the Scotian Shelf and the Bay of Fundy area; B)  $\Delta$  Sigma T (density) difference ( $\text{kg m}^{-3}$ ) between surface and 30 m water depth (July-September) from Scotian Shelf climatology (C.G. Hannah and V. Soukhovtsev, pers. comm., based on Petrie et al., 1996; C) Spring chlorophyll-a climate derived from SeaWiFS surface chlorophyll-a. An upper bound of  $7 \mu\text{g ml}^{-1}$  was imposed; D) Bottom oxygen saturation (%) in July, based on optimal extrapolation of available observations for the period 1933-2003; E) Average annual bottom temperature ( $^{\circ}\text{C}$ ) from Breeze et al. (2002) based on results of Hannah et al. (2001) and Han et al. (1999); F) Amplitude of seasonal bottom temperature cycle ( $^{\circ}\text{C}$ ) calculated from seasonal temperatures shown in Breeze et al. (2002), based on results of Hannah et al. (2001) and Han et al. (1999). G) Interannual variability in bottom temperature ( $^{\circ}\text{C}$ ) (data from C.G. Hannah and V. Soukhovtsev pers. comm., 2003), unpublished analysis based on the BIO data archives (Petrie et al., 1996); H) Median grain size (phi) estimates obtained by facies-constrained interpolation; I) Frictional velocity ( $\text{cm s}^{-1}$ ) calculated from high-resolution bathymetry of the region (the analysis grid), 42 year hindcast of the wave height and period data, near-bottom estimates of tidal current and grain size estimates.

The wave climate data were obtained from the 42-year wind and wave hindcast of Swail and Cox (2000). The spatial resolution was  $0.625^{\circ}$  in the north-south direction and  $0.833^{\circ}$  in the east-west direction. Temporal resolution was 6 hours. In the analysis, fields were created of the 90th percentile of the significant wave height and period for the 42 years of data for the Scotian Shelf study area. These fields were then linearly interpolated to the analysis grid.

Near-bottom tidal currents were expressed as the RMS tidal currents based on the 5 major constituents: M2, N2, S2, O1, and K1 (with corresponding periods of 12.42, 12.00, 12.66, 23.93, and 25.82 hours). As no 3-D model solutions were available that cover

the Scotian Shelf region with all 5 constituents, tidal currents were used from two 3-D models (Hannah *et al.*, 2001; Han and Loder, 2003) to estimate the relationship between the depth-averaged tidal and near-bottom tidal currents. These relationships were used to estimate near-bottom currents from depth-averaged currents from two regional tidal models (Dupont *et al.*, 2002, 2005). The horizontal interpolation of the RMS tidal currents to the analysis grid was done by interpolating the product of RMS velocity and model depth and then dividing by the local bathymetry. This process better preserves the relationship between the bathymetry and tidal currents when interpolating from model horizontal resolutions of 4-10 km to the analysis grid of 500 m horizontal resolution.

At each point in the analysis grid, the 90th percentile wave height and period, the grain size, and the RMS tidal currents were used to compute the total friction velocity (sum of skin friction and bed friction) with SEDTRANS96. The friction velocity calculation is sensitive to whether the wave- and tide-generated currents are directionally aligned. For this application, the average of the cases with the two aligned and at right angles was used. In addition, a uniform  $1 \text{ cm s}^{-1}$  was added to the friction velocity field because comparison with calculations using observed near-bottom currents and wave information for the appropriate time period showed a bias of about  $1 \text{ cm s}^{-1}$ . The final result is shown in Figure 4I.

**Disturbance Axis**

The disturbance axis was defined as the ratio of the characteristic friction velocity to the critical shear stress. This ratio was log-transformed and scaled from 0 to 1. The log transformation ensured that the frequency distribution of map cell values is approximately mezkurtic and not skewed. It also provided a better representation of the dynamic range.

The critical shear stress ( $V_c$ ,  $\text{cm s}^{-1}$ ) for initiation of motion is a function of grain size ( $m$ , mm) and was derived from the Hjulstrom (1935) diagram. The empirical approximation used was:

$$\text{Log}(V_c) = -0.027 \log(m)^4 - 0.091 \log(m)^3 + 0.241 \log(m)^2 + 0.469 \log(m) + 1.876$$

The resulting map of seabed disturbance is shown on Figure 5A.

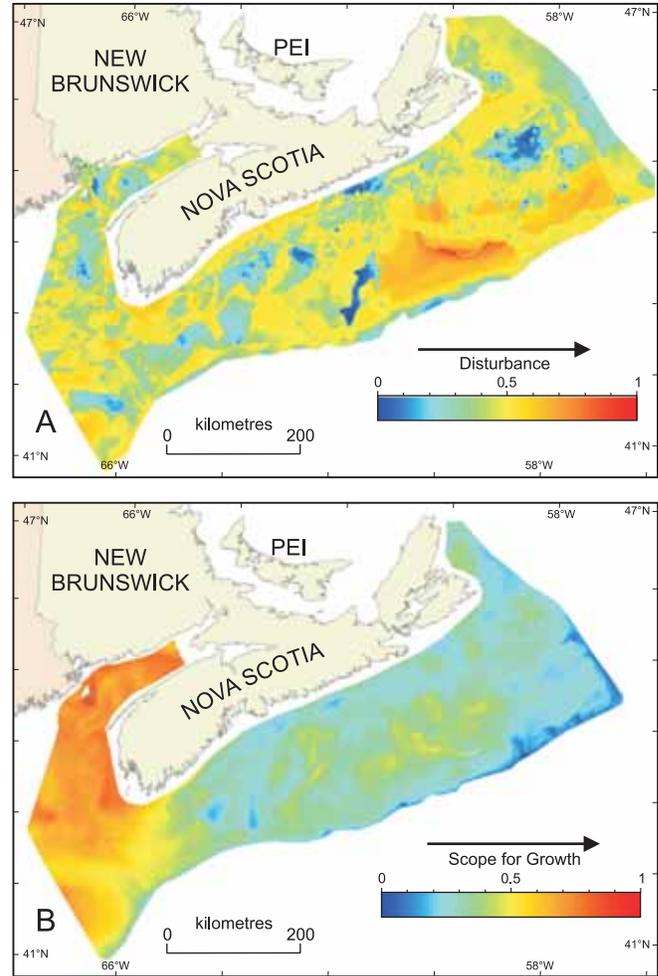
**Scope for Growth**

Scope for growth was calculated using five data layers: a food availability index that combines stratification and surface chlorophyll as a measure of benthic-pelagic coupling, annual bottom temperature as an indicator of metabolic rates, annual and interannual temperature variability as an indicator of thermal stress and a measure of temporal uncertainty for reproduction, and oxygen saturation as a measure of metabolic stress. For calculation, each data layer was converted into an index by linear scaling from 0 to 1 based on the minimums and maximums provided in Table 2. We chose these layers because each layer is indicative of an important bioenergetic process and sufficient data were available to map the bottom distributions for the Scotian Shelf.

To calculate scope for growth, these indices were combined in an additive model, where an increasing linear membership function indicates that the index increases scope for growth and a decreasing

**Table 2.** Data layers for the scope for growth axis, showing the minimum and maximum values used to create the indices

Data layer	Minimum	Maximum
Surface stratification ( $\text{kg m}^{-3}$ )	0.28	2.80
Spring chlorophyll-a ( $\mu\text{g ml}^{-1}$ )	0.69	7.00
Mean bottom temperature ( $^{\circ}\text{C}$ )	0.5	9.1
Annual range of bottom temperature ( $^{\circ}\text{C}$ )	0.0	17.6
Interannual RMS of bottom temperature ( $^{\circ}\text{C}$ )	0.8	2.5
Oxygen saturation (%)	32.89	118.47



**Figure 5.** A) Map of the natural disturbance axis of the habitat template model; B) Map of the scope for growth axis of the habitat template model.

linear membership function indicates that the index decreases scope for growth.

The food availability layer ( $F_a$ ) was defined as  $F_a = \log(C/B) - S$ , where  $C/B$  is the ratio of chlorophyll-*a* concentration ( $C$ ) to water depth ( $B$ ) and  $S$  is the stratification index;  $\log(C/B)$  and  $S$  were rescaled from 0 to 1 as well as the resulting  $F_a$ .

The scope for growth ( $S_g$ ) axis was then defined as

$$S_g = (F_a + T_m - T_a - T_i + O)/5$$

where  $T_m$  is the mean bottom temperature index,  $T_a$  is the annual temperature variability index,  $T_i$  is the interannual temperature variability index, and  $O$  is the oxygen saturation index.

The data layers represent the variables that are considered to be important. They were transformed into the scope for growth axis using linear scaling and equal weights in an additive model. This is likely the simplest choice from a large number of possible transformation models. The resulting map of seabed scope for growth is shown in Figure 5B.

The final habitat template map for the Scotian Shelf and Bay of Fundy is shown in Figure 6. In order to simultaneously display two template axes in geographical space, a red–green–blue (RGB) colour map was used, where disturbance corresponds to green, and the scope for growth corresponds to red.

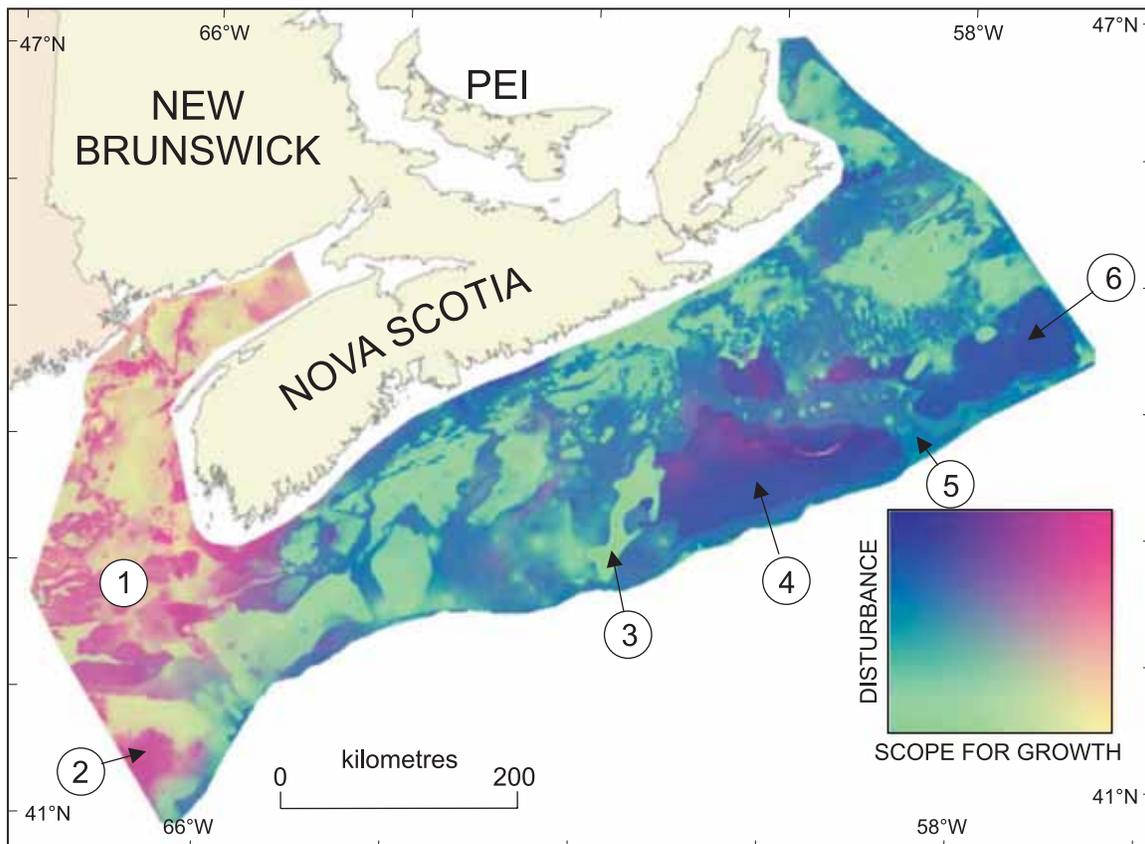
**TESTING THE HABITAT MODEL**

As in any habitat map, the map is a visual representation of a conceptual model and can be considered as a hypothesis to be tested. Our approach to model validation was to test whether similarity in template values (proximity of samples within the disturbance–scope for growth continuum) was a better predictor of similarity in species composition than geographical distance between samples (spatial proximity). The rationale behind this approach is based on the supposition that if the species composition of two samples is similar it is likely that these samples come from similar habitats. At the same time, in the absence of information on the physical environment, spatial proximity between samples is often used to interpolate similar community types (as in kriging, inverse distance weighting, etc.). We assumed that if the habitat template successfully captures ecologically important information on habitat characteristics, it will serve as a better predictor of species composition than spatial proximity between stations alone. The Bray–Curtis similarity (Bray and Curtis, 1957) between samples was compared to the similarity between associated habitat template values and to the geographical

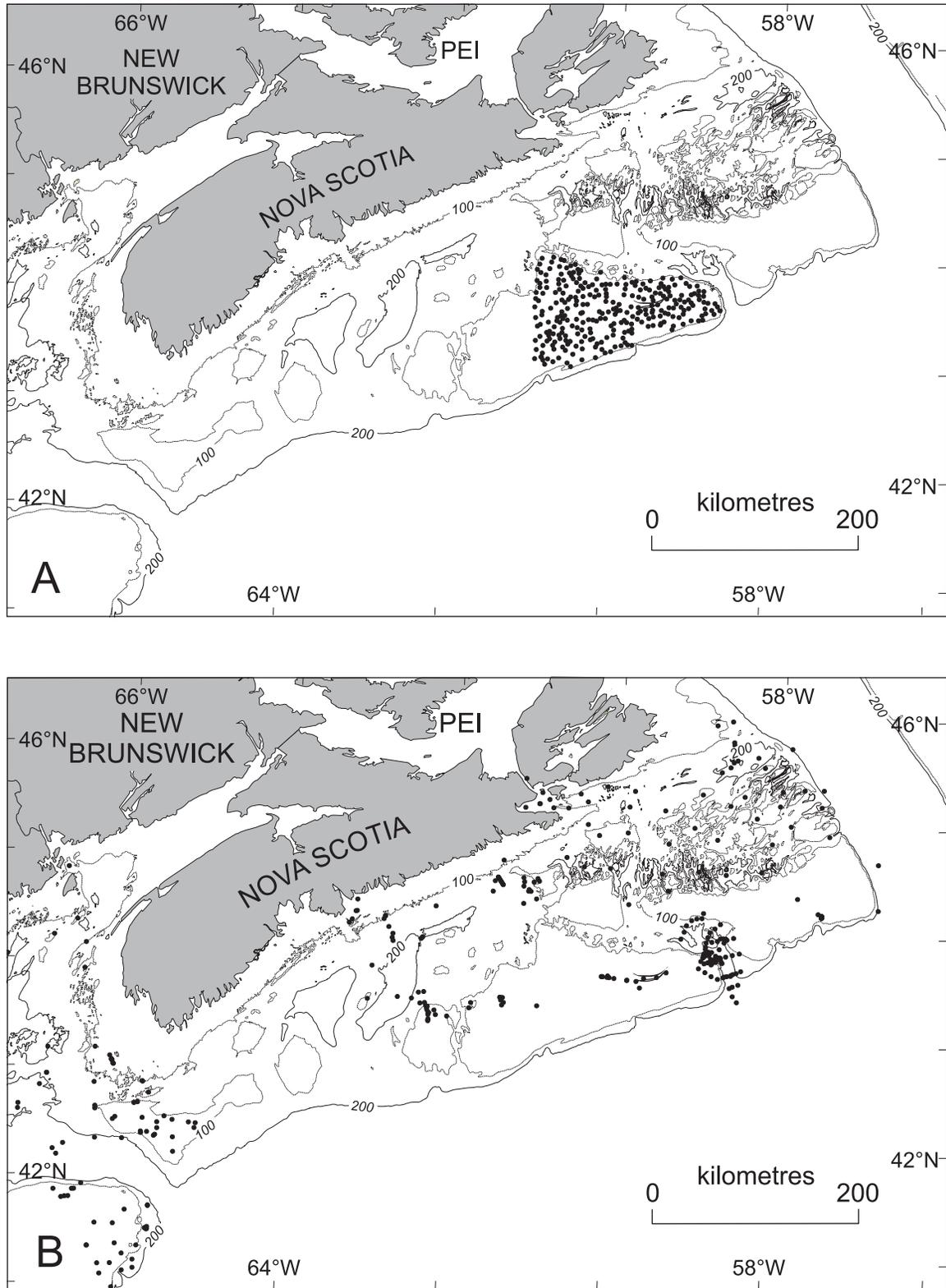
distance between the compared samples using Spearman’s rank order correlations.

The first dataset tested was from Sable Island Bank on eastern Scotian Shelf and comprised 281 grab samples with a typical station spacing of 5 km (Figure 7A) and covering 13,000 km<sup>2</sup> (D. Roddick, BIO, pers. comm., 2003). Analysis showed that the habitat template is a much better predictor of similarity in species composition than the geographical distance ( $r_s = 0.47$  compared to  $r_s = 0.09$ , both with  $p < 0.05$ ; Figure 8). For this dataset, all of the predictive power is in the scope for growth axis ( $r_s = 0.5$ ,  $p < 0.05$ ), which ranged from 0.15 to 0.49. The disturbance axis has a similar range over this dataset (0.52-0.84) but provides less predictive power ( $r = 0.19$ ,  $p < 0.05$ ) than scope for growth. Nevertheless, disturbance is a better predictor than distance between samples (Table 3).

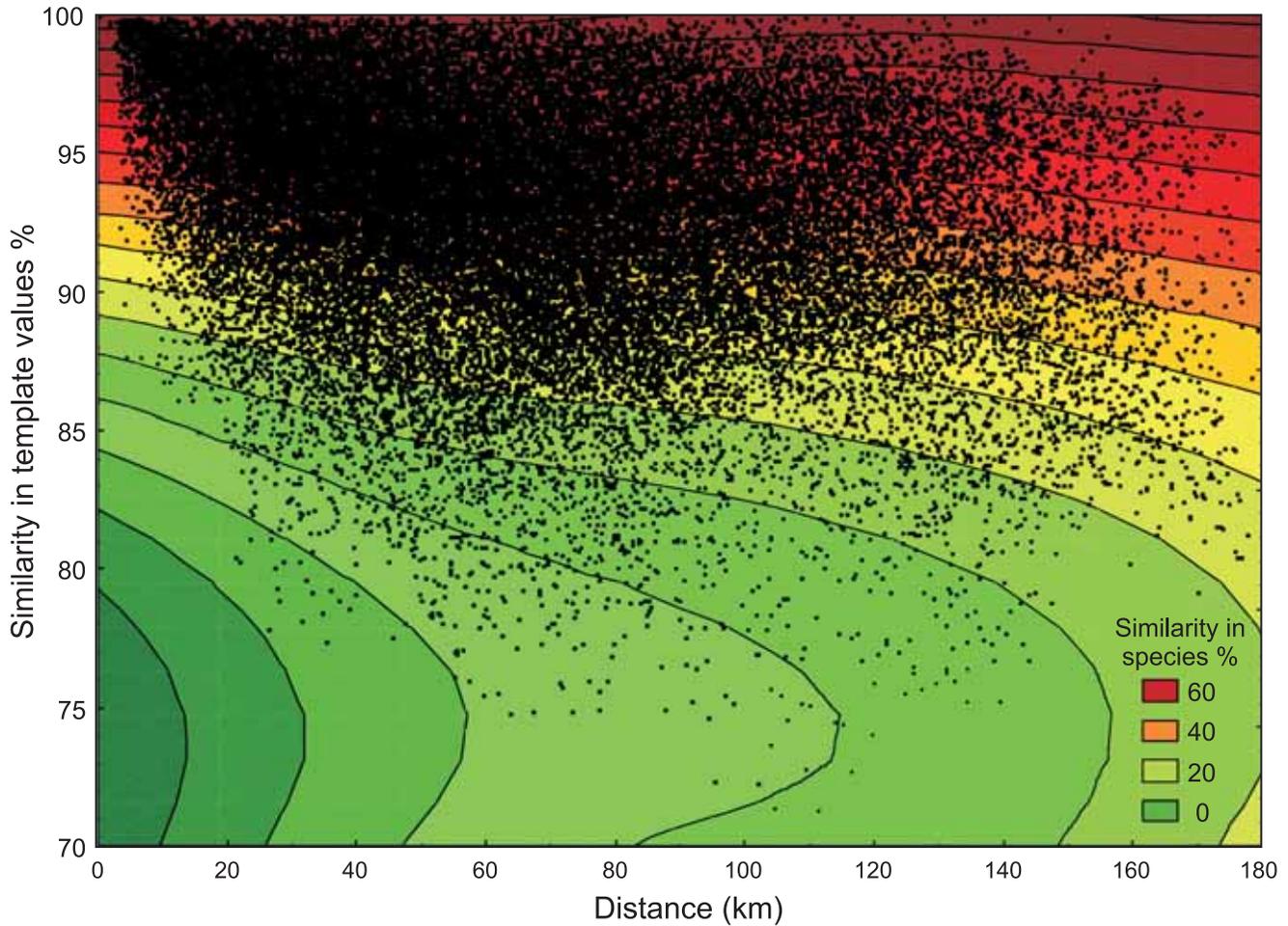
A validation on the shelf-wide scale (the survey area of 160,000 km<sup>2</sup>), using identifications of epifauna obtained from 251 seabed photographic stations (Figure 7B) again demonstrates that the habitat template is a better predictor of species similarity ( $r_s = 0.078$ ,  $p < 0.05$ ) than distance between stations ( $r_s = -0.019$ ,  $p < 0.05$ ). Scope for growth, ranging from 0.10 to 0.77, serves as a better predictor ( $r_s = 0.1$ ,  $p < 0.05$ ) than the disturbance ( $r_s = 0.02$ ,  $p < 0.05$ ), which ranged from 0.06-0.79. However, the relationship breaks down at a distance of about 400 km, likely because the species pool is limited to this geographical scale (Table 3).



**Figure 6.** Habitat template map for the Scotian Shelf and eastern Gulf of Maine, constructed as red–green–blue (RGB) colour map, where disturbance corresponds to green, and the scope for growth to red. The following features are referred to in the text: 1) Gulf of Maine; 2) Georges Bank; 3) Western Bank; 4) Sable Island Bank; 5) The Gully and 6) Banquereau.



**Figure 7.** Data used for testing the habitat template: A) Distribution of sampling stations from the Sable Island Bank data set; B) Distribution of sampling stations for the Scotian Shelf photographic data set.



**Figure 8.** Comparison of the relationship of Bray–Curtis similarity in species composition with distance between samples and with similarity in habitat template values. The closer two samples are within the habitat template space, the more likely they are to have similar faunas, while their spatial proximity is a poor predictor. Points on this graph correspond to each comparison between a pair of samples. Colour background shows spline-interpolated similarity in species composition, red is high, green is low.

Spearman’s rank order correlation coefficients for distances <400 km and >400 km were also calculated (Table 3). At a sample separation of more than 400 km, there were no significant correlations between similarity in species composition and template or distance between stations. Taken separately, the scope for growth and disturbance were still significantly correlated to species similarity, with the scope for growth being the stronger correlate.

**DISCUSSION**

The habitat template map for the Scotian Shelf and the eastern Gulf of Maine (Figure 6) shows a broad-scale, east-west gradient in scope for growth while disturbance produces a complex spatial pattern of different habitat types. The western part of the study area (the Gulf of Maine) has generally high scope for growth with areas of both high (red) and low (yellow) disturbance. The eastern Scotian Shelf has generally lower scope for growth, with areas of both high (dark blue) and low (light green) disturbance. Another view of the map is the phase portrait (Figure 9); by locating different geographical locations in the disturbance-scope for growth

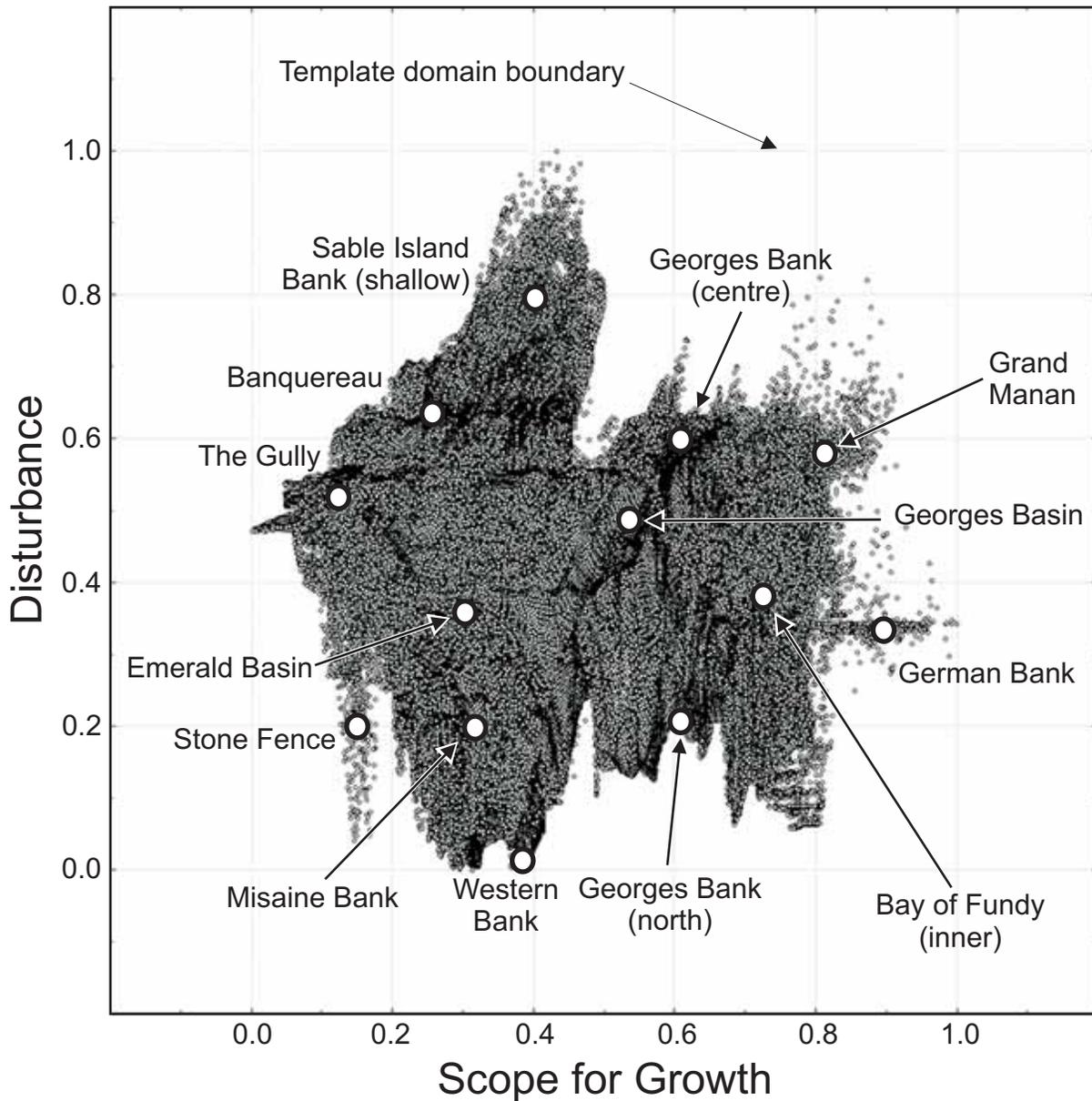
**Table 3.** Spearman’s rank order correlations between similarities in environmental factors and similarities in species composition for the Sable Island Bank (dredge) and Scotian Shelf (photograph) datasets. All correlations are significant at  $p < 0.05$ , except those in italics

Species composition	Distance between samples	Template values	Disturbance	Scope for Growth
Sable Island Bank	0.094	0.470	0.190	0.500
Scotian Shelf	-0.019	0.078	0.020	0.102
Scotian Shelf <400 km	-0.026	0.110	0.039	0.139
Scotian Shelf >400 km	<i>0.011</i>	<i>0.014</i>	-0.018	0.058

phase space, the magnitude of habitat differences between locations can be appreciated. The differences in disturbance are a function of both water depth (primarily the influence of wave activity) and sediment type. For example, Banquereau (shallow and sandy) has high disturbance, whereas the gravely areas of Western Bank have very low disturbance. The generally lower scope for growth on the eastern banks relative to the western banks is consistent with the different benthic communities that exist in the east. This lower scope for growth predicts slower recovery from bottom disturbances and biomass removals for communities on the eastern banks relative to the western ones. Such a difference has been reported in terms of cod growth (Campana *et al.*, 1995), ground fish recovery (Frank *et al.*, 2005) and sensitivity to bottom trawling on the eastern Scotian

Shelf (Messieh *et al.*, 1991). Species with traits typical for a disturbed environment are known to be abundant on the outer banks of Scotian Shelf. For example, giant scallop (*Placopecten magellanicus*) is a fast-growing broadcast spawner, hermit crabs (*Pagurus* sp.) are very mobile, and sand dollars (*Echinarachnius parma*) are well adapted to sediment burial.

The disturbance–scope for growth continuum (Figure 9) also assists in visualizing the extent of environmental variability on Scotian Shelf. Scotian Shelf habitats largely fill the phase space of the template, thus both axes are required for interpretation of the environment, and there is no one-dimensional approximation to the two-dimensional habitat template. The notable exceptions to the space fill-



**Figure 9.** The habitat phase space with geographic locations. Each point on the plot corresponds to, and summarises, average disturbance and scope for growth conditions in a grid cell located on Scotian Shelf. The centroids of select geomorphologic features (representative points, marked by larger circles) that are used for reference on the Scotian Shelf (e.g., banks, basins, channels) can be located in the phase space with a certain degree of accuracy, limited by imprecision of their spatial definition.

ing are that highly disturbed seabed environments with very low and very high scope for growth are under-represented in the study area. The high disturbance values are dominated by Sable Island Bank which is both shallow (implying large bottom stresses due to waves) and sandy (very mobile sediment). This suggests that the continental shelf will have relatively few species that can be characterized as either extreme adversity tolerators or clearly defined *r* strategists (following terminology of MacArthur and Wilson, 1967).

In testing the predictability of species composition by similarity in template values against spatial separation between stations, we discovered that the habitat template is a better predictor of species similarity than spatial proximity. For both datasets, the scope for growth had a stronger effect on the similarity in species composition than the natural seabed disturbance, likely because of the deficiency in grain size interpolation (which underlies the disturbance calculations). These findings confirm the assumptions that benthic habitats can be mapped based on the similarity of physical factors and that interpolation of seabed fauna based on spatial proximity of samples may be misleading.

The habitat template map (Figure 6) predicts which life history traits will be favoured in a particular place (Table 1) and not which species will live there. In this sense, it is analogous to the climate zone classification used by gardeners (USDA Plant Hardiness Zone Map, <http://www.usna.usda.gov/Hardzone/ushzmap.html>). For example, organisms that inhabit the low disturbance and low scope for growth quadrant of the template (Figure 6, light green) are likely to be long-lived, slow-growing, slow-reproducing, and have limited dispersal. This has direct management implications, because such species are vulnerable to trawling, dredging, mineral extraction, and directed fishing. In fact, our template allows prediction of two kinds of risks (Figure 1E): the risk of habitat destruction (reciprocal of natural habitat disturbance) and the risk of population extinction due to such activities as over-fishing (reciprocal of the scope for growth).

A common limitation of any classification system based on physical factors is the assumption of 'natural environment'. It is evident that, during the past 50 years of resource extraction on the Scotian Shelf, species composition has changed (Frank *et al.*, 2005). In addition, emergent community traits and species composition are hard to predict with confidence. Specific limitations are that temporal dynamics (such as short-term changes in the environment), changes in the climate, natural ecosystem dynamics, and human activities all affect the types of organisms inhabiting a region at a particular time, and there is always spatial heterogeneity at scales finer than the map resolution.

The habitat template approach described here differs from other approaches used for habitat mapping in general and on the Scotian Shelf in particular (*e.g.*, Roff and Taylor, 2000; Roff *et al.*, 2003) in how the variables are translated into habitat maps. Traditionally, seabed habitat mapping was based on descriptions of separate features of the physical environment (*e.g.*, geological settings) or on classification systems which are typically intersections of single-factor maps (combinations of univariate classes). In this traditional approach, the significance of each habitat class to seabed management is often obscure to decision-makers. The habitat tem-

plate approach avoids arbitrary subdivisions of each physical layer into classes by recognizing the inherent blurriness of ecological gradients. The resulting habitat map is a continuum where the gradients arise naturally from the data layers. In addition, the method reduces multiple environmental variables to the most important factors related to the major selective forces responsible for defining the life history traits of species.

The individual axes in the habitat map also have direct management applications. The disturbance map provides a scale against which to measure disturbances from human activities such as bottom trawling, pipeline construction, dredging, and seabed mining. Areas with high rates of natural disturbance (*e.g.*, shallow sandy banks) are less likely to suffer harmful alteration and destruction of habitat. The scope for growth map serves as guide for estimating relative time scales for population recovery from impacts. Thus, areas with low scope for growth are more likely to suffer from over-fishing. These ideas can be used to inform discussions of sensitivity (of species or habitats), which has become an important concept in ocean management and conservation (Laffoley *et al.*, 2000; OSPAR, 2003). Definitions of sensitivity generally have two components: 1) the habitat or species is easily disturbed, and 2) the expected recovery time is long. In the template used here, organisms in a low scope for growth environment will exhibit slow recovery and those in a low disturbance environment will be vulnerable to physical disturbance. Thus, with respect to physical disturbance, the most sensitive habitats and communities are likely those in the low disturbance–low scope for growth quadrant (*e.g.*, cold-water coral ecosystems).

Disturbance and productivity regimes have also been used to predict trends in biodiversity in different habitats (Huston, 1994). The applications of the regional template to predict biodiversity has limitations because the template values occupy only a fraction of the global template space. Therefore, the maximum biodiversity may not occur at the centre of the regional template as assumed by the model (Figure 1); it may change monotonically across the template.

## CONCLUSIONS

Habitat mapping is done by modelling natural disturbance and scope for growth based on georeferenced physical information. Benthic habitats are particularly appropriate for this approach because benthic communities are more spatially and temporally stable than pelagic systems and therefore are amenable to mapping based on fixed geographical coordinates. An important benefit of this approach is that condensing a number of environmental variables into a single map in an ecologically meaningful manner has the potential to be more useful for management than a set of maps depicting separate physical factors. A second benefit is the capacity for capturing environmental gradients better than can be achieved by statistical interpolation between benthic samples. The resulting map predicts species and community traits, which allows drawing conclusions on their vulnerability, and is suitable for managing human activities and preserving seabed habitats on the continental shelf. For example, the Marine Protected Area around The Gully near Sable Island (Figure 6) contains a variety of habitats, ranging from low- to intermediate-scope for growth and low- to high-disturbance, leading to a diversity of habitat types and life history traits in the area.

The ecological theory behind our approach is general. Given the potential shown on the Scotian Shelf, we intend to develop a global habitat template map for the World Oceans. To achieve this, information on seabed bathymetry, geology and oceanography needs to be compiled and standardized and additional physical factors will need to be introduced to the modelling. For example, sources of seabed disturbance, such as ice scouring in polar and subpolar regions and turbidity flows on shelf slopes, need to be added. Additional variables will need to be considered in the scope for growth model and the ranges of the productivity and temperature models need to be expanded. Finally, a better estimate of food availability to seabed fauna should be achieved through physically explicit benthic–pelagic coupling models.

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