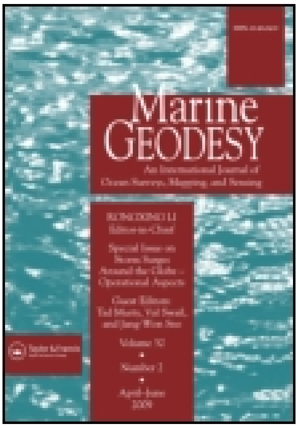

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Towards High-Resolution Habitat Suitability Modeling of Vulnerable Marine Ecosystems in the Deep-Sea: Resolving Terrain Attribute Dependencies

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Towards High-Resolution Habitat Suitability Modeling of Vulnerable Marine Ecosystems in the Deep-Sea: Resolving Terrain Attribute Dependencies

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Recent habitat suitability models used to predict the occurrence of vulnerable marine species, particularly framework building cold-water corals, have identified terrain attributes such as slope and bathymetric position index as important predictive parameters. Due to their scale-dependent nature, a realistic representation of terrain attributes is crucial for the development of reliable habitat suitability models. In this paper, three known coral areas and a noncoral control area off the west coast of Ireland were chosen to assess quantitative and distributional differences between terrain attributes derived from bathymetry grids of varying resolution and information content. Correlation analysis identified consistent changes of terrain attributes as grain size was altered. Response characteristics and dimensions depended on terrain attribute types and the dominant morphological length-scales within the study areas. The subsequent effect on habitat suitability maps was demonstrated by preliminary models generated at different grain sizes. This study demonstrates that high resolution habitat suitability models based on terrain parameters derived from multibeam generated bathymetry are required to detect many of the topographical features found in Irish waters that are associated with coral. This has implications for marine spatial planning in the deep sea. Supplemental materials are available for this article. Go to the publisher's online edition of Marine Geodesy *to view the free supplemental file.*

Keywords Carbonate mounds, cold-water coral, ecosystem-based management, habitat suitability modeling, spatial resolution, terrain analysis

Introduction

In late 2006, the United Nations General Assembly resolution 61/105 highlighted the major need to identify, map, and protect vulnerable marine ecosystems, including cold-water corals from anthropogenic impacts such as bottom trawling (UNGA 2006). In order to facilitate the design and implementation of effective marine protected areas (MPAs), extensive knowledge of habitat distribution and species-habitat relationships is needed. However, information on deep-sea habitats is generally limited, since ROV- or

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submarine-based surveys are expensive and time-consuming. In the absence of complete surveys, habitat suitability modeling (HSM) can be applied to predict full coverage distribution of key species based on available presence-only point data (Phillips et al. 2006; Hirzel et al. 2002). Resulting species distribution maps can provide useful and cost-effective support for future survey planning and the design of marine protected areas (Galparsoro et al. 2009).

There has been a rapid increase in the development and relevance of HSM in terrestrial ecology and natural resource management (Elith et al. 2006; Guisan and Thuiller 2005). More recently, advances in seabed mapping technologies (Anderson et al. 2008; Kenny et al. 2003) and benthic sampling and surveying techniques (Gage and Bett 2005) have facilitated the application of HSM in the marine environment (Davies et al. 2008; Degraer et al. 2008; Dolan et al. 2008; Galparsoro et al. 2009; Guinan et al. 2009a). In the deep sea, much of the development of HSM approaches has centered on cold-water corals, both because they are an emblematic vulnerable marine ecosystem and because our understanding of cold-water corals, particularly *Lophelia pertusa*, habitat requirements are now well constrained (Roberts et al. 2009).

Table 1 summarizes cold-water coral HSMs developed at different spatial scales using different modeling techniques. Analogous with the experience of terrestrial studies (MacKey and Lindenmayer 2001; Pearson and Dawson 2003), the dominant environmental factors for coral growth appear to vary over scales of investigation. In global HSMs, for example, cold-water coral distribution is determined by the availability of suitable temperatures, oxygen, and aragonite saturation state, as well as enhanced surface productivity (Clark et al. 2006; Tittensor et al. 2009; Davies et al. 2008). In regional and local HSMs, bathymetric terrain attributes such as slope and bathymetric position index (BPI) have shown good potential as environmental predictors as they act as proxies indicating areas of enhanced currents and food supply for the suspension-feeding corals (Dolan et al. 2008; Guinan et al. 2009a; Wilson et al. 2007). The summary of HSMs in Table 1 further demonstrates the frequently encountered trade-off between spatial (cell size) and thematic (range of environmental variables) resolution (Guisan and Thuiller 2005; Kendall and Miller 2008). Indeed, the lack of extensive high-resolution environmental datasets has been identified to be one of the major restrictions to the reliability and applicability of cold-water coral HSMs (Bryan and Metaxas 2007; Davies et al. 2008; Etnoyer and Morgan 2007; Tittensor et al. 2009). For example, a 1°x1° temperature grid was shown to be too coarse to accurately resolve rapid changes in water temperature, leading to a mismatch between coral occurrences and temperature values beyond the species' thermal tolerance limit (Davies et al. 2008). A precise spatial matching between presence data and environmental variables is necessary to avoid an artificial expansion of the species niche width, especially when modeling the distribution of sessile organisms (Guisan and Thuiller 2005).

Terrain attributes are increasingly applied in habitat classification and modeling studies, and seabed morphology has been shown to play a crucial role in the distribution of benthic biota (Dolan et al. 2008; Guinan et al. 2009a; Guinan et al. 2009b; Wilson et al. 2007; Holmes et al. 2008; Kostylev et al. 2001; Lundblad et al. 2006; Verfaillie et al. 2008). These attributes are frequently derived from readily available global bathymetry grids which combine quality-controlled ship depth soundings with satellite-derived gravity data (Marks and Smith 2006). While such hybrids provide full coverage of the world's ocean bathymetry, they are not reliable in resolving discrete morphological features on the seafloor. The global 1^{o}x1^{o} resolution GEBCO grid (http://www.bodc.ac.uk/data/online_delivery/gebco/), for example, proved to be too coarse to resolve many of the ocean's seamounts, which are known to be ecologically important biodiversity hotspots (Davies et al. 2008; Clark et al.

Table 1
Local, regional and global scale habitat suitability models for cold-water corals

Target Taxon	Predictive Model	Environmental Data	Cell Size	Source
Global				
Cold-water corals on Seamounts	ENFA	Alkalinity; Aragonite saturation state; Bathymetry; Current velocity; Dissolved inorganic carbon; Dissolved oxygen; Export primary Productivity; Productivity; Salinity; Seamount location; Temperature; % oxygen saturation	1°	Clark et al., 2006
Scleractinian corals *(Lophelia pertusa)*	ENFA	Alkalinity; Aragonita saturation state; Bathymetry; Aspect; Dissolved inorganic carbon; Dissolved oxygen; Hydrocarbon seeps/Pockmarks; Nitrate; Phosphate; Productivity; Salinity; Silicate; Slope; Temperature	1°	Davies et al., 2008
Sclerectinian corals on seamounts	ENFA; MAXENT	Alcalinity; Aragonite saturation state; Bathymetry; Current velocity; Dissolved inorganic carbon; Dissolved oxygen; Export primary productivity; Nitrate; Phosphate; Productivity; Salinity; Seamount location; Silicate; Temperature; % oxygen saturation	1°	Tittensor et al., 2009
Sclerectinian corals	MAXENT	Alkalinity; Apparent oxygen utilisation; Aragonite; Bathymetry; BPI; Calcite; Carbonate ion concentration; Current velocity; Dissolved inorganic carbon; Dissolved oxygen; Eastness /Northness; Nitrate; pH; Phosphate; Productivity; Salinity; Silicate; Slope; Rugosity; Temperature; Vertical flow; % oxygen saturation	0.0083°	Guinotte et al., 2009

(Continued on next page)

Table 1
Local, regional and global scale habitat suitability models for cold-water corals *(Continued)*

Target Taxon	Predictive Model	Environmental Data	Cell Size	Source
Regional				
Gorgonian corals *(Paragorgia arbore, Orimnoa resedaeformis)*	ENFA	Bathymetry; Current speed; Productivity; Slope; Substrate; Temperature	9 km	Leverette and Metaxas, 2005
Gorgonian corals *(Paragorgiidae, Primnoidae)*	ENFA	Bathymetry; Current velocity; Productivity; Slope; Temperature	a) 0.03° b) 0.08°	Bryan and Metaxas, 2007
Scleractinian corals *(Lophelia pertusa)*	ENFA; GARP	Aspect; BPI; Current velocity; Curvature; Rugosity; Salinity; Slope; Temperature	550 m	Guinan et al., 2008
Scleractinian corals *(Lophelia pertusa)*	ENFA	Aspect; Bathymetry; Current speed; Iceberg ploughmark areas; Productivity, Salinity, Slope, Temperature	0.25°	Davies et al., 2008
Cold-water corals	Logistic regression	Bathymetry, Rugosity, Slope	15-50 m	Woodby et al., 2009
Local				
Scleractinian corals *(Lophelia pertusa)*	ENFA; GARP	Aspect; BPI; Current velocity; Curvature; Rugosity; Salinity; Slope; Temperature	30 m	Guinan et al., 2008
Scleractinian corals *(Lophelia pertusa)*	ENFA	Aspect; BPI; Curvature; Fractal Dimension; Rugosity; Slope; TRI	0.5 m	Dolan et al., 2009

2006). By employing the GEBCO bathymetry with a 30 arc-second resolution, Guinotte et al. (2009) significantly improved the terrain detail in their global model, revealing suitable coral habitat on thousands of previously undetected seamounts.

In Irish waters, cold-water corals such as *Lophelia pertusa* and *Madrepora occulata* are often associated with areas of raised topography known as carbonate mounds. These are discrete morphological features of varying shape with heights ranging from tens to hundreds of meters (Wheeler et al. 2007). In this study, we investigate the effect of initial bathymetric grid resolution in the production of terrain attribute maps for carbonate mound areas on the Irish continental margin. The Irish National Seabed Survey bathymetric dataset was regridded at a grain size of 50 m x 50 m to provide a high resolution benchmark to measure the quality of terrain attributes derived from coarser resolutions. A grain size of 1000 m was chosen to be the upper limit of investigation, as it roughly corresponds to the 30 arc-second GEBCO grid (GEBCO 2009) used in the Guinotte et al. (2009) global model. The effects of terrain attribute resolution on the applicability of HSM are explored by means of preliminary "terrain suitability models" (i.e., habitat suitability models based on terrain parameters only) for cold-water corals.

Methods

Study Areas

Four study areas were chosen to represent large, medium and small carbonate mounds as well as a mound-less gently sloped area on the Irish continental margin in the depth range 550–1100 m (Figure 1a). Study areas A, B and D measure 15×15 km^2 while study area C measures $10{\times}9$ km^2. The main topographical features in the study areas are shown in Figure 1b. Study area A (55°28.21′N 16°6.23′W) is situated within the Logachev mound

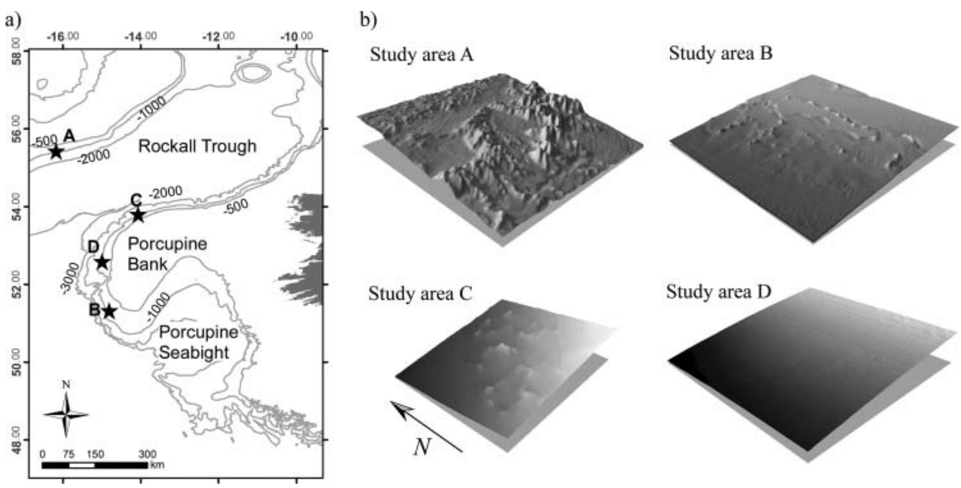

Figure 1. a) Overview of the study areas on the Irish continental margin: study area A (Logachev Mound Province), study area B (Arc Mound Province), study area C (R1 area) and study area D (control area). b) Terrain visualization of the study areas at $5\times$ vertical exaggeration based on INSS multibeam bathymetry at 50 m resolution. Projection is UTM Zone 28N (WGS84).

province, a belt of giant carbonate mounds stretching between 16°30'W and 15°15′W along the southern margin of the Rockall bank. The area's morphology and geology have been described in detail (Kenyon et al. 2003; Mienis et al. 2006; Wheeler et al. 2007). Mounds are predominantly arranged in down-slope oriented clusters, which may reach lengths of several km and heights of up to 380 m (Mienis et al. 2006). A large sediment wave field runs upslope and parallel to the mound belt. Previous video and photographic surveys revealed high densities of live corals on the summits and terraced flanks of the mounds (Mienis et al.; Olu-Le Roy et al. 2002). Study area B (55°19.56′N 14°45.74′W) comprises the Arc Mound province on the western Porcupine Bank. This area is characterized by a north-south oriented carbonate mound chain in the east and east-west oriented mound chains in the north. Some mound flanks drop into a channel or local depressions, resulting in steep slopes and larger mound heights on one side of the mounds. The mounds reach between 50 and 100 m in height and base lengths seldom exceed 500 m. Video surveys have revealed the existence of high density cold-water coral assemblages on the flanks and tops of the mounds (Grehan et al. 2005; Grehan et al. 2009). Study area C (53°46.47′N 13°58.24′W) in the southeast Rockall Trough covers the R1 area investigated by Guinan et al. (2009b). Carbonate mounds are aligned along a northeast–southwest trend. The tallest mound reaches approximately 200 m in height and has a base length of 1500 m. Multiscale relationships between coral presence points and terrain attributes in this area were studied by Guinan et al. (2009b). Study area D (52°36.82′N 14°57.74′W) is situated approximately 140 km north of the Arc mound province on the Western Porcupine Bank. It is a moundless, relatively smooth area and serves as control area.

Generation of Terrain Attribute Maps

Multibeam data covering the study areas were acquired as part of the Irish National Seabed Survey. The employed multibeam system was a Kongsberg Simrad EM120 multibeam system mounted to the hull of the survey vessel S.V. Bligh. Multibeam data were processed to hydrographic standards (GOTECH 2002). The clean *.xyz ASCII data were acquired from the Geological Survey of Ireland by the authors and Fledermaus v.7 gridding software was used to produce a digital elevation model (DEM) with a grain size of 0.0005° x 0.0005° (WGS84). The DEM was imported into ArcGIS v.9 and projected in UTM Zone 28N with a grain size of 50 m × 50 m. This original bathymetry grid (B_{50}) contained the maximum amount of information and served as a source and benchmark for all further produced grids. The Mean Aggregation strategy in ArcGIS v.9 was used to coarsen B_{50} to 100, 250, 500, and 1000 m spatial resolution (B_{100}, B_{250}, B_{500} and B_{1000}, respectively). Resampling by bilinear interpolation (ArcGIS v.9) was then applied to the B_{1000} grid in order to obtain bathymetry grids of 500, 250, 100, and 50 m spatial resolution (I_{500}, I_{250}, I_{100} and I_{50}, respectively), but with low information content. The purpose of these interpolated grids was to assess the utility of upscaling coarse global bathymetry models such as GEBCO to finer spatial resolutions. Additionally, information on how much of the variation between terrain attributes is due to the changing grid resolution (i.e., discretization effect) and how much is due to varying terrain information content (i.e., smoothing effect) (Gallant and Hutchinson 1996; Sørensen and Seibert 2007; Wolock and McCabe 2000) can be derived.

We calculated slope, aspect (as eastness and northness values), plan and profile curvatures, bathymetric position index (BPI), roughness, and rugosity for all bathymetry grids (B_{50}-B_{1000} and I_{50},-I_{500}) using ArcGIS v.9 and following parameter computation methods described by Wilson et al. (2007). The Benthic Terrain Modeller extension (Lundblad et al. 2006) was employed for the computation of terrain rugosity. A default neighborhood of

3×3 grid cells was employed for all terrain attributes, and for consistency in analyses no annulus was used for the computation of the BPI. To avoid including edge artifacts, the map borders for each study areas were clipped after terrain analysis. Cells per grid totaled 90000, 22500, 3600, 900, and 225 for study areas A, B, and D and 36000, 9000, 1440, 360, and 90 for study area C at grid cell sizes of 50, 100, 250, 500, and 1000 m, respectively.

Terrain Attribute Analyses

Terrain attributes of varying resolution and terrain information content were compared in three different ways:

(1) Maps were visually evaluated within ArcGIS v.9.
(2) Pearson correlation coefficients (r) between the terrain attributes of the 50 m benchmark (B_{50}) and coarser resolutions (B_{100}-B_{1000}) were calculated in order to assess the effects of decreasing resolution on a cell-by-cell basis. This analysis gave information on the spatial agreement between maps.
(3) For each study area, 500 random point locations were generated. These points were used to sample all underlying terrain attribute maps. The randomized sampling procedure was chosen because it simulated potential species-presence data with minimal spatial autocorrelation. Box-plots were computed for each set of sample points to obtain information on quantitative variations between terrain attribute maps of different resolutions and information content.

Generation of Preliminary Terrain Suitability Models

To investigate the effects of decreasing resolution and terrain information loss on HSM of cold-water corals, preliminary terrain suitability models were generated employing MAXENT (Phillips et al. 2006). This modeling software estimates the distribution of a certain species by relating known species occurrences with a series of environmental variables via a machine learning maximum entropy algorithm. MAXENT provides a user-friendly interface and has shown good performance in recent comparative modeling studies (Phillips et al. 2006; Elith et al. 2006; Guisan et al. 2007). Default parameters (convergence threshold of 10^{-5}, a maximum of 500 iterations, and a regularization multiplier of 1) of MAXENT version 3.31 (http://www.cs.princeton.edu/~schapire/maxent) were applied. Terrain suitability models for study area C were generated for each set of the above described terrain attributes (50, 100, 250, 500, and 1000 m resolution). The species sample data in this area consisted of 247 georeferenced video-derived coral presence points provided by Guinan et al. (2009a). MAXENT removed duplicate presence points within the grid cells, resulting in a reduction of sample points with increasing cell size (203 at 50 m, 44 at 100 m, 22 at 250 m, 13 at 500 m, and 6 at 1000 m). The trained model was then projected onto all study areas. MAXENT produces logistically scaled habitat suitability maps for each study area, with each pixel estimating the probability of species presence. Values close to zero indicate low probability, and values close to one suggest high probability of species presence.

For many HSM applications, continuous predictions need to be reduced to binary maps indicating species presence and absence. In order to assess the effect of grid resolution on the total area predicted suitable coral habitat (i.e., coral presence), all produced HSMs were converted into binary maps based on habitat suitability index thresholds of 0.4, 0.5, 0.6, and 0.7. All grid cells with habitat suitability values above the respective threshold were counted, and the total area was computed by multiplying the cell count with the respective grid cell size.

Results

Visual Evaluation of Computed Terrain Attributes

The generated terrain attribute maps varied considerably with resolution and terrain information content. Figure 2a shows the distribution of slope values in study area A as an example for the general pattern found. Even though dominant features were roughly preserved over a range of resolutions, terrain detail and smaller features were gradually lost with increasing cell size. For example, steep slopes were not resolved at coarse resolutions as they were increasingly aggregated with the adjacent valley bottom. The loss of high slope values was also visualized by the reduction of map contrast. Smaller features such as sediment waves in study area A or the Arc mounds in study area B entirely dissolved with coarsening resolution.

Lost terrain detail could not visibly be recovered by upscaling B_{1000} to finer resolutions. While I_{500} grid based terrain attribute maps appeared to be smoother versions of the B_{1000} terrain attribute maps, further interpolation resulted in artifacts reflecting the cell structure of the underlying B_{1000} bathymetry grid (Figure 2b). These square-shaped structures are most visible in the I_{50} and I_{100} maps and are probably a consequence of the bilinear interpolation method applied. Virtually constant attribute values within the original 1000 m $\times$ 1000 m window and rapidly changing values at the window borders resulted in a grate-like grid appearance.

Increasing the grid cell sizes also led to an emergence of new distributional properties within terrain attribute maps. Figure 3 shows BPI, eastness, profile curvature, and rugosity computed for study area B at 50, 250, and 1000 m resolution. While the grey-scales employed are map-specific and cannot be used as a basis for comparison between resolutions, it is clear that attribute maps based on B_{1000} fail to represent the terrain in a realistic manner.

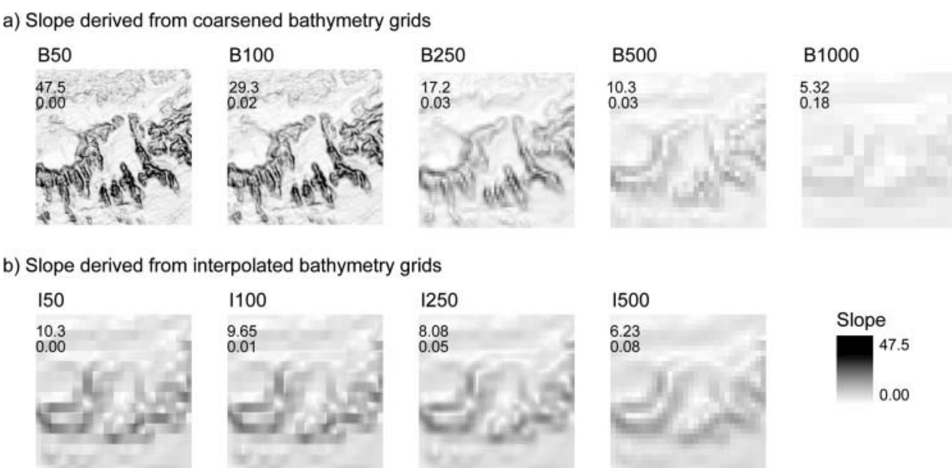

Figure 2. Slope maps of study area A derived from coarsened (a) and interpolated (b) bathymetry grids at 50, 100, 250, 500, and 1000 m resolutions. The minimum and maximum slope values of each individual map are indicated.

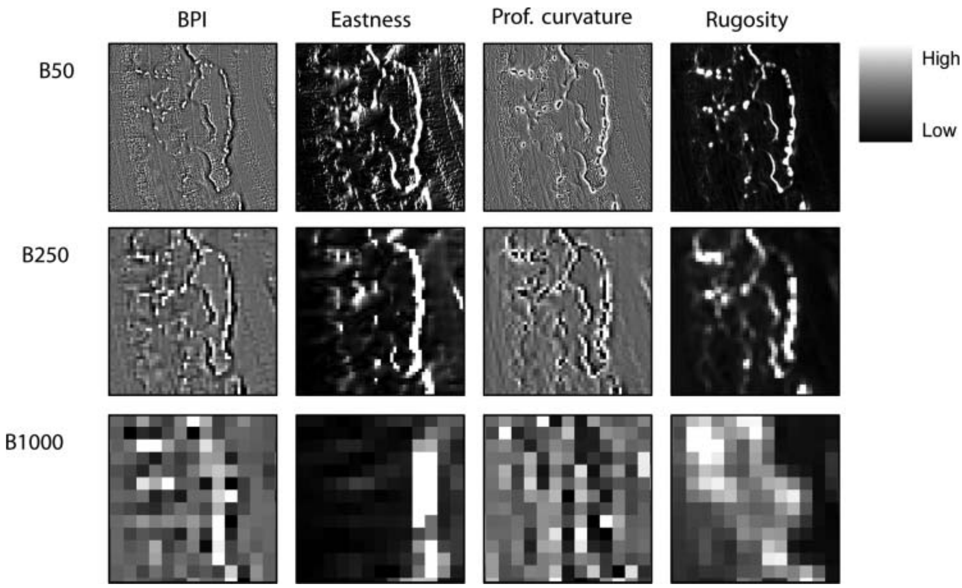

Figure 3. BPI, eastness, profile curvature, and rugosity maps computed for study area B based on varying initial grid resolutions. Grey-tone scale is computed individually for each parameter and resolution; range is too great to allow a common representation of changes within each parameter for all resolutions.

Frequently, an alternation between positive and negative terrain attribute values could be observed.

Spatial Agreement of Terrain Attributes Across Resolutions

The Pearson correlation coefficient (r) was used to describe the nature (i.e., positive or negative) and strength of spatial agreement between terrain attributes of 50 m and coarser resolutions. High r values (close to 1) indicated that the terrain attribute based on a certain grid resolution represented the respective 50 m benchmark grid well, while low values (close to 0) indicated a poor correlation. Correlation coefficients consistently decreased with coarsening resolutions (Figure 4). This suggests a general decrease of spatial agreement between terrain attribute values with increasing grid cell size, along with a decrease in predictability of the manner of change. An abrupt drop in r values mostly between 100 m and 250 m resolution indicated the potential crossing of a threshold, possibly reflecting dominant morphological length scales in the study areas. Interestingly, this drop was also observed for the BPI and curvatures in the moundless control area (study area D), suggesting that these attributes might be sensitive to artifacts which commonly exist in multibeam derived bathymetry. Slope, roughness, and rugosity within the control area showed generally higher correlations, with r values of $\sim$0.7 throughout resolutions. Averaged over all resolutions and study areas, slope, rugosity, and roughness were the terrain attributes most robust to resolution changes (r means and standard deviations of 0.62 ± 0.24, 0.61 ± 0.25, and 0.60 ± 0.25, respectively), while BPI, plan curvature and profile curvature were the most sensitive (0.34 ± 0.28, 0.27 ± 0.26, and 0.24 ± 0.27, respectively).

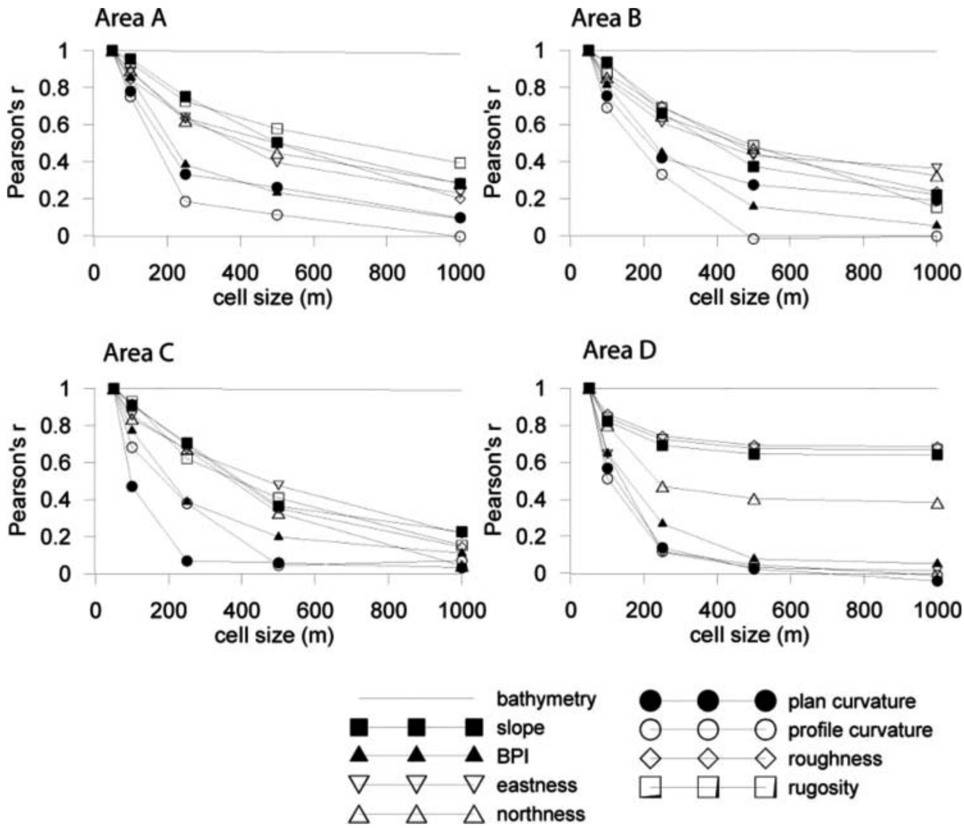

Figure 4. Pearson's correlation coefficients (r) between terrain attributes of 50m (B50) and coarser resolutions (B100–B1000).

Quantitative Variations in Terrain Attribute Values

All terrain attribute values varied dramatically with change in resolution and information content. Box-plots for all study areas followed the same patterns and only results for study area A are presented here (Figure 5, the figures for the remaining study areas are included in the online appendix, Figure A1, Figure A2, and Figure A3). However, the dimensions of the y-axes were throughout highest for study areas A and C, followed by area B. Within the control area changes in attribute values remained negligible.

Effects of bathymetry grid coarsening (B_{50} – B_{1000}). While the summary statistics of bathymetry remained generally constant throughout all grids, mean slope values decreased slowly and maximum values decreased sharply with increasing cell size. The underestimations of maximum slope values when calculated at 1000 m resolution reached as high as ~80% (in study areas A and C).

Aspect (orientation) was transformed into eastness and northness for a better quantification of the parameter (Wilson et al. 2007). Mean values of both parameters were largely preserved across resolutions and mirrored the overall orientation of the study areas; for example, study area C was dominated by negative eastness values (~−0.7) and positive northness values (~+0.8), reflecting the north-west facing slope of the continental margin

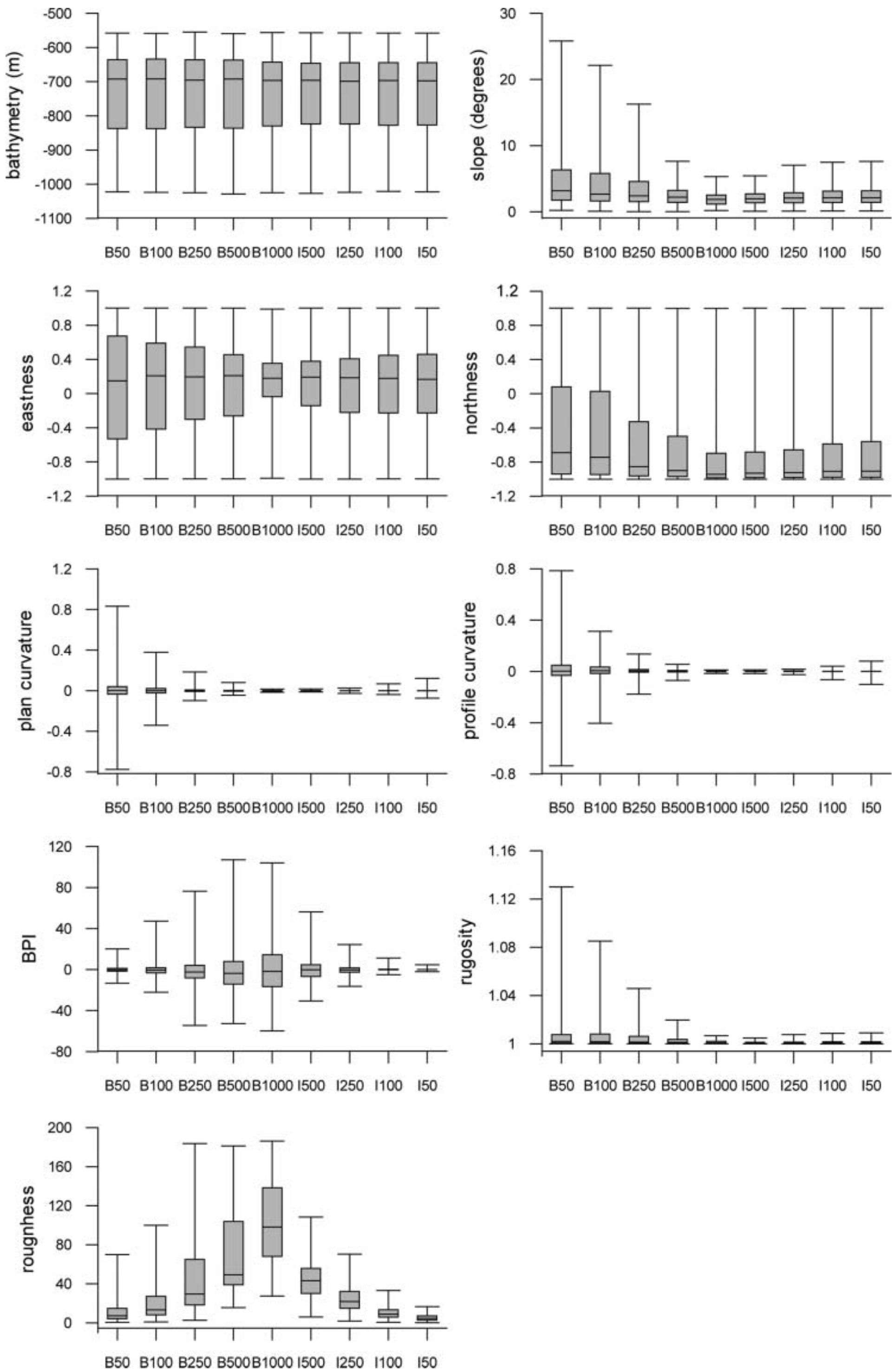

Figure 5. Box plots for the study area A illustrating the range, the median, and the upper and lower percentiles of terrain attribute values derived from grids of varying resolution (B_{50}-B_{1000}) and information content (I_{500}-I_{50}). The figures for study areas B-D are included in the online appendix.

in this area (Figure 1b). Generally, upper and lower percentiles converged towards the mean with coarsening resolution, reflecting the same terrain "smoothing" effect observed for slope.

Plan and profile curvature showed strong resolution sensitivity as positive and negative values converged towards zero with increasing grid cell size. Again the same pattern was found for all study areas; however, curvature values in study area D (control area) remained comparatively low and never exceeded $+/-$ 0.2. Generally, mean values remained close to zero throughout resolutions, indicating that approximately the same level of convexity and concavity occurs in the study areas.

The BPI is a measure of the relative position of an individual pixel in relation to its surrounding terrain (Weiss 2001). Coarsening grid resolution led to a strong overestimation of both positive and negative BPI values. Generally, the range of the percentiles expanded slowly while extreme values expanded rapidly with increasing grid cell size. Again, the same qualitative differences between areas could be observed, with BPI values expanding most in study area A, followed by area C and finally area B.

All statistical measures of roughness increased with decreasing resolution while maximum rugosity values sharply decreased and converged towards one.

Effects of bathymetry grid interpolation (I_{500} – I_{50}). The box-plots derived from the up-scaled bathymetry grids of low terrain information content (I_{50}, I_{100}, I_{250}, I_{500}) replicated a similar pattern as plots derived from original grids of the same resolution (B_{50}, B_{100}, B_{250}, B_{500}), even without reaching the extreme values observed for the higher resolution data. This similarity between box-plots suggests that resolution-dependent differences can partly be attributed to the change in grid cell size (i.e., discretization effect). However, a substantial part of the differences remains due to the actual loss of information content (i.e., smoothing effect) and cannot be recovered by bilinear interpolation to higher resolution.

Preliminary Terrain Suitability Models

Preliminary terrain suitability maps produced by MAXENT clearly reflect the resolution-effects observed during terrain analysis (Figure 6). Only models of higher resolution (i.e., B_{50} – B_{250}) successfully identified areas of small-scale terrain complexity as suitable coral habitat. The control area (area D) was predicted to be unsuitable at all resolutions. The degree of resolution sensitivity varied between study areas depending on average length-scales of the dominant morphological features (i.e., study area A shows less decrease in maximum habitat suitability values than study area B). Changes in extreme habitat suitability values further affected the total extent of area predicted suitable when different habitat suitability thresholds were applied. Interestingly, these responses were inconsistent between study areas (Figure 7). Study area A showed a constant pattern of overprediction of suitable habitat with increasing cell size at all tested thresholds. Based on a threshold of 0.5, the predicted coral habitat increased from 35 km^2 at 50 m resolution to 77 km^2 at 1000 m resolution. Study area B, on the other hand, showed a pronounced underprediction as grid cell size was increasing, with potentially suitable habitat decreasing from 3 km^2 at 50 m to 0 km^2 at 1000 m resolution. These contradicting trends are due to the above discussed qualitative differences in the study areas. Due to the large mound features in study area A, a suitable coral habitat is detected throughout resolutions, and the increasing cell size leads to an increase in predicted suitable area. Within study area B, however, the

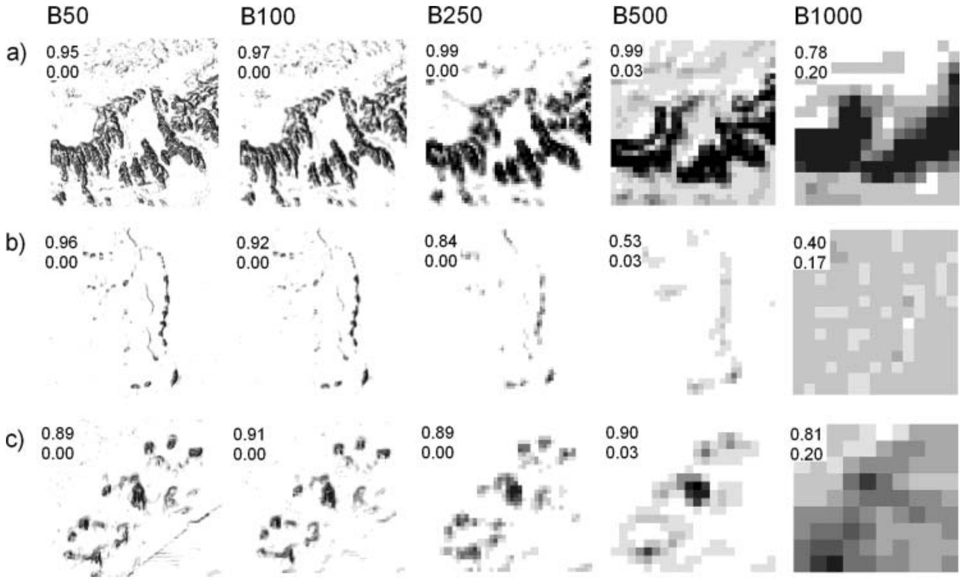

Figure 6. Terrain suitability maps based on a set of 247 training data points provided by Guinan et al. 2009a. Models were trained within study area C (c) and projected to the study areas A (a), B (b) and D (not displayed) employing terrain variables based on B_{50}–B_{1000} bathymetry grids. Terrain suitability ranges from low (0, white) to high (1, black). Maximum and minimum suitability values are indicated in each map.

smaller mound features become less distinguished at increasing cell sizes, and less suitable habitat can be detected by the HSM. The pattern observed in study area C suggests the existence of a cell size threshold between 500 m and 1000 m resolution, above which a marked overprediction will take place. Most of this overprediction could be attributed to an increase in area predicted suitable based on lower thresholds (0.4 and 0.5).

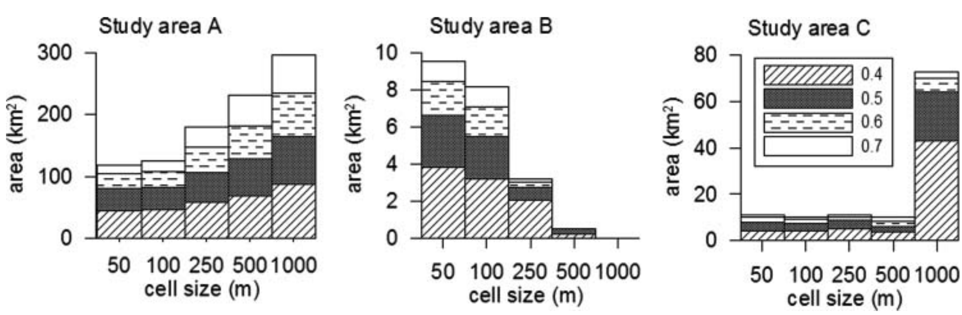

Figure 7. Stacked columns display the area (km^2) predicted to be suitable coral habitat based on binary maps resulting from a range of habitat suitability thresholds (from bottom to top: 0.4, 0.5, 0.6, and 0.7). Study area D is not displayed as less than 0.01 km^2 was predicted to be suitable.

Discussion

Terrain Analysis

Terrain attributes, by their nature, are scale-dependent. Numerous authors have addressed the issues of initial grid resolution (Deng et al. 2007; Kienzle 2004; Wolock and McCabe 2000) and analysis window size (Albani et al. 2004; Schmidt and Andrew 2005; Wilson et al. 2007; Wood 1996) in terrain analysis. Our results corroborate findings of studies investigating resolution dependency of topography derived terrain attributes (Deng et al.; Kienzle; Sørensen and Seibert 2007; Wolock and McCabe), despite the differences in the grid resolution coarsening techniques applied. Sørensen and Seibert employed pixel thinning methods implemented in Idrisi software (www.clarklabs.org). Other authors re-sampled the high resolution grids at every nth grid point to ensure exact matching between grid points on the coarse resolution grids with grid points on high resolution grid (Deng et al.; Wolock and McCabe). We tested the latter approach in a preliminary study and did not find any significant differences to the results presented here. Grid coarsening by means of the Mean Aggregation method was chosen because resulting grids better represented coarse bathymetry models such as the GEBCO grid. Terrain attribute distributions of interpolated grids (I_{50} – I_{500}) partially reproduced the ones of the original grids (B_{50} –B_{500}). From this one could conclude that upscaling coarse bathymetry to higher grid resolution is a way to obtain higher resolution terrain attribute maps. However, visual evaluation indicated significant differences between the coarsened and interpolated terrain attribute maps, including grate-like artifacts at the highest resolutions. Different upscaling methods should be considered if it is aimed to apply coarse bathymetry grids to terrain analysis of higher resolution. Interpolation techniques such as inverse distance weighing or kriging might prove more promising for such purpose; however, the evaluation of and comparison between interpolation methods is beyond the scope of this study.

A detailed review of novel methods and trends in terrain analysis is given by Deng (2007). One promising example to overcome the scale problem in terrain analysis could be the incorporation of fuzzy logic to produce multiscale parameters (Wood 1996) and multiscale fuzzy objects (Fisher et al. 2004). An alternative approach involves changing the analysis window size while maintaining a constant bathymetry grid resolution (Albani et al. 2004; Wilson et al. 2007). The applicability of the multiscale terrain analysis approach to benthic mapping and habitat suitability modeling has recently been explored and seen promising results (Dolan et al. 2008; Guinan et al. 2009a; Wilson et al. 2007; Verfaillie et al. 2008). While the multiscale analysis approach is useful, it is only feasible when high resolution bathymetric data are available in the first place.

Terrain Resolution Effects on HSM for Cold-Water Corals

All terrain attributes tested within this study (slope, eastness, northness, plan and profile curvature, BPI, roughness, and rugosity) varied dramatically with changes in resolution of the underlying bathymetry (Figure 5). This may affect HSM results in different ways.

Slope has been identified as important predictive parameter in virtually all published cold-water coral HSM studies (Table 1 and references therein). Guinan et al. (2009b) found high cold-water coral coverage percentage to be directly associated with steep slope values. The underestimation of maximum (steep) slope values at coarse resolutions has the effect of reducing the width of the slope-specific niche output by an HSM. In addition, the observed convergence of extreme values towards the mean (i.e., the loss in map contrast observed in Figure 2a) is likely to result in a loss in predictive power. Terrain aspect is intrinsically linked to slope and provides information on the exposure of seabed terrain to local and regional currents. We observed a substantial change of eastness and northness distributions with changing resolutions, as well as a resolution-dependent alternation between positive and negative values. Cold-water corals have been associated with positive BPI values corresponding to bathymetric highs such as crests and ridges (Dolan et al. 2008; Guinan et al. 2009a; Guinan et al. 2009b). We found the BPI to be highly resolution dependent, with a pronounced overestimation of extreme values at coarser resolutions. Recent HSM studies approached the scale-sensitivity of the BPI by computing both a small-scale BPI (calculated over a small analysis window size) and a large-scale BPI (calculated with a large analysis window size) (Lundblad et al. 2006; Guinotte et al. 2009).

Preliminary Terrain Suitability Models

The results presented in this study suggest that habitat suitability models employing terrain parameters based on bathymetry of 1000 m ($\sim$30 arc-seconds) resolution fail to detect many of the small carbonate mounds found in Irish waters. Bathymetry data of at least 250 m^2 resolution are required to identify these areas as suitable coral habitat. Care must be taken if the available bathymetric data does not reflect local surface variability, as matching between the target species presence points and flawed terrain attribute values is likely to occur. This mismatch might skew the species' niche width as well as the resulting habitat suitability maps, ultimately leading to ill-informed management decisions.

Binary coral habitat maps based on different thresholds have been shown to highly depend on terrain attribute resolution, and care must be taken when making assumptions on total area coverage of species predictions when coarse bathymetry grids are being used. Besides the resolution factor, the choice of threshold will further influence the total area predicted suitable. Several methods for choosing an appropriate threshold are discussed in the literature (Liu et al. 2005; Jiménez-Valverde and Lobo 2007), but to date no consensus for a best method has been reached, and different thresholds are being used to respond to different management issues. Further research will be necessary to better describe and understand the effect of terrain attribute resolution and HSM thresholds for the generation of binary habitat suitability maps for the purpose of ecosystem-based management.

Besides the effects of original bathymetry resolution discussed above, HSMs also show an intrinsic sensitivity to changes in grid cell size (Guisan et al. 2007; Seo et al. 2009). Increasing model resolution may potentially influence a species' presence-absence pattern (Wiens 2002) and may affect the relevance of the output for management applications. Seo et al. (2009) reported a threefold increase in suitable area when models were run at 64 km $\times$ 64 km resolution compared to models run at 1 km $\times$ 1 km resolution. While the present study did not incorporate an evaluation of model performance, as more species sample data would be required from all study areas to compute reliable model evaluation indices, the generation of preliminary terrain suitability models did illustrate the sensitivity of the model outcomes to initial bathymetry grid resolution.

The need for further information on local environmental drivers of cold-water coral distribution in order to improve their management has been identified by Duran Munoz et al. (2009) and others. In future work, we will use high-resolution hydrodynamic models to help identify whether regional and local oceanographic processes contribute to habitat optimization in Irish waters. Where 3D oceanographic models of sufficient resolution are unavailable, a hierarchical modeling framework (MacKey and Lindenmayer 2001; Pearson and Dawson 2003) should be employed, combining high resolution terrain information with lower resolution oceanographic parameters. Such hierarchical models would ensure the identification of suitable habitat on small morphological features while highlighting areas of unsuitable terrain in areas otherwise indicated as suitable by the oceanography. A hierarchical modeling framework could improve estimates of actual coral coverage and the identification of vulnerable marine ecosystems at scales that support management decision making, particularly spatial planning.

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