Quantitative Definition of Viosca Knoll Biotopes Available to Fishes of the Continental Slope, 325-500 m, Northern Gulf of Mexico

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Abstract

The megafaunal invertebrate fauna of *Lophelia pertusa* coral reefs and associated hard-bottom biotopes was investigated at two depth horizons (325 m and 500 m depth) on Viosca Knoll in the northern Gulf of Mexico using a manned submersible. Megafaunal invertebrates were quantified by occurrence from high-quality digital video frame grabs using Coral Point Count software. Megafaunal invertebrate assemblages identified by Primer v6 multivariate analyses of the occurrence data were used to characterize and differentiate key biotopes used by demersal fishes associated with *Lophelia* coral and comparative biotopes. Multivariate analyses fundamentally supported the a priori empirical classification of biotopes on Viosca Knoll, including *Lophelia* coral 'Thicket', 'Rock', 'Plate', 'Plate/Chemo' and 'Open'. In striking contrast to *Lophelia* reefs in the northeastern Atlantic and off the southeastern U.S. East Coast, coral 'Rubble' biotope was essentially absent in this study. *Lophelia* coral 'Thicket' biotope was extensively developed on the 500 m site. *Lophelia* occurred only sporadically and as individual colonies on the 325 m site. Mixed species oases comprised of *Lophelia*, black corals, sponges and other taxa occurred primarily on the shallower site. In places clusters of individuals of a single species inhabited broad expanses of 'Plate' and 'Rock' biotopes. Among hard-substrate and structured biotopes, species richness was highest for 'Rock' biotope, and lowest on *Lophelia* 'Thicket'. Thus, contrary to expectations, *Lophelia* biotope in the northern Gulf of Mexico does not support a richer invertebrate megafaunal assemblage than that found on comparative hard-substrate or soft-substrate biotopes. Another surprising finding in this study, compared to *Lophelia* reefs in the northeastern Atlantic and off the southeastern U.S. East Coast, is the virtual absence of *Lophelia* 'Rubble' biotope. The height and slope of the rarefaction curve for 'Open' biotope suggested that this inadequately sampled biotope probably supports the highest megafaunal invertebrate species richness, also contrary to expectations. This study represents

the first statistically robust quantitative analysis of biotopes available to fishes associated with *Lophelia* reefs in the Gulf of Mexico, and generally in the western North Atlantic.

INTRODUCTION

Hardgrounds on the continental slope (300-550 m depth) in the northern Gulf of Mexico (NEGOM) have formed by deposition of carbonate rock in areas of hydrocarbon seepage (MacDonald, 1992; Roberts and Aharon, 1994; Schroeder, 2002; but also see Sulak, (Chapter 8). On the slope in the NEGOM, hard grounds support diverse assemblages of sponges, anemones, gorgonians, black corals, bamboo corals, and hard corals, prominently including the matrix-building scleractinian coral, *Lophelia pertusa* (Linnaeus, 1758). In contrast to the essentially 2-D soft-substrate biome of the open continental slope, the hard-ground biome, populated by sessile invertebrates, provides complex 3-D habitats for demersal fishes and mobile megafaunal invertebrates, and small-scale habitats for macrofaunal invertebrates (Teichert, 1958; Jensen and Frederiksen, 1992; Mortensen et al., 1995; Fosså and Mortensen, 1998; Husebø et al., 2002; Costello et al., 2005; Reed et al., 2005; Reed et al., 2006; Sulak et al., (Chapter 2) within living coral structures, in and on coral rubble, or within associated reef-derived sands. An analysis of demersal fishes inhabiting two hard-ground sites on the NEGOM slope (Sulak et al., Chapter 2) empirically differentiated the overall Viosca Knoll demersal habitat into four major biotope categories ('Thicket', 'Rock', 'Plate', and 'Open': examples shown in Master Appendix E) based on topography, substrate, and qualitative occurrence of *L. pertusa*. A first order chi-square statistical test demonstrated that twelve key dominant demersal fish taxa were not randomly distributed among these four biotope categories. Deviation from expected random distribution frequencies among the fish taxa suggested strong affinities with different biotopes. Accordingly, Sulak et al.'s (Chapter 2) original empirical definition of biotopes was supported by fish faunal differentiation results. Nine of the dominant 12 fish taxa displayed a particular bias in occurrence toward one or more biotopes; only three approached the critical chi-square value for random, non-selective distribution across all available biotopes. However, the very low per-unit-area abundances of demersal fish species precluded a more definitive quantitative definition of specific habitat affinities.

In 2004 and 2005, the U.S. Geological Survey (USGS) conducted two multidisciplinary submersible missions targeting deep *Lophelia pertusa* coral reef sites on the continental slope in the northern Gulf of Mexico. The present study represents one among a suite of investigations focused on slope-depth hard-grounds that support *Lophelia* reefs and assemblages of other sessile invertebrates. This study was undertaken by the USGS on behalf of the Minerals

Management Service (MMS) to address living resource information needs to facilitate resource management. The MMS exercises an environmental stewardship role for deep-water 'live-bottom' habitats in areas of oil and gas exploration and development in the Gulf of Mexico.

The objective of the present investigation is to analyze the demersal megafauna (invertebrates only, focusing primarily on sessile species) of Viosca Knoll to provide a more robust, statistically-based quantitative biological differentiation of the biotopes utilized by demersal fishes between 300-550 m depth. As Reed et al. (2005, 2006) have previously observed, few studies have documented the characteristic associations of species with deep-reef habitats in the western Atlantic region.

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MATERIALS AND METHODS

Biotope differentiation in this study is based upon abundance and occurrence data for key invertebrate taxa, as scored by analysis of submersible video frame grabs using Coral Point Count (CPCe©) software. For this investigation of megafaunal invertebrates, individual frame grabs were selected for analysis, rather than sequential along a dedicated moving transect (e.g., Burnham et al., 1980, Butler et al., 1991; Adams et al., 1995; Sulak et al., Chapter 2). This methodology was adopted to obtain high resolution from images taken with the submersible either stationary or moving very slowly, in order to facilitate critical image analysis. Since the central objective was to define and differentiate biotopes in terms of differential megafaunal invertebrate assemblages characteristic of the respective biotopes, percent cover of substrate by sessile invertebrates was not a metric analyzed.

Bottom video was obtained during two missions of the Harbor Branch Oceanographic Institution's manned Johnson-Sea-Link (JSL) submersibles conducted in July-August 2004 and September 2005. Study sites and submersible methods have previously been detailed (Randall et al., Chapter 1; Sulak et al., Chapter 2). Both missions targeted two prominent elevated topographic features on the continental slope of the northern Gulf of Mexico (Fig. 3.1). These two features have been designated Viosca Knoll 826 (VK-826) and Viosca Knoll 906/862 (VK-906/862) with reference to the MMS oil lease blocks in which they lie. The two sites represent two distinct depth horizons (Sulak et al., Chapter 2), centered on depths of approximately 500 m and 325 m, respectively (Figs. 3.2, 3.3). Much of the substrate capping these topographic features is hardground, consisting of extensive deposits of authigenic goethite, hydrated ferric oxide/hydroxide (Sulak, Chapter 8) formed in areas of hydrocarbon seepage. The clean, hard surface of the black goethite rock provides a settlement substrate for the larvae, and a holdfast substrate for the adults, of diverse sessile invertebrates. Depending upon taxonomic composition, population density, and differential growth forms of sessile invertebrates inhabiting the carbonate substrate, the hard-ground biome is comprised of several distinct biotopes available to mobile megafaunal invertebrates and demersal fishes, and also to associated macrofaunal invertebrates.

Twenty submersible dives were accomplished during the combined missions, 12 on the VK-826 site (Fig. 3.2), and eight on the VK-906/862 site (Fig. 3.3). Ship's position was determined via differential GPS, accurate to within 5 m. Station position data (latitude and longitude coordinates) are surface vessel position data (Randall et al., Chapter 1, Table 1.2). Submersible positions on the bottom were estimated via Trackpoint II© "Integrated Positioning System" (ORE Offshore) using dual acoustic beacons interpreted topside by HBOI submersible operations personnel. Only returns with signal strength above a predetermined threshold (signal strength of 8 on an arbitrary scale of 10) were accepted in plotting the most probable bottom positions of the submersible. High-probability submersible bottom positions to anchor plots of dive tracks were obtained as 'fixes' with the submersible remaining stationary on the bottom for a length of time, several times throughout a given dive. Well-resolved individual dive tracks are presented in interactive video format in Master Appendix A.

Each dive had multiple objectives, mostly involving collection of *Lophelia* samples for research largely unrelated to the present study (Randall et al., Chapter 1; Master Appendix A). Although all dives at both study sites targeted known or suspected *Lophelia* coral areas, each dive typically traversed several distinct biotopes in the course of visiting widely separated sampling areas (Master Appendix A). However, given the overarching bottom time bias toward locations where *Lophelia* could be sampled, imaging of 'Open' biotope for image analysis was comparatively limited.

SUBMERSIBLE VIDEO IMAGING - Color video imagery was obtained using a Sony DX2 3000A 3-chip CCD camera, with 6-48 mm zoom lens, mounted in a pressure housing on an extensible arm on the port side of the submersible sphere, 1.37 m above the bottom of the vehicle (when the arm is fully retracted). The area in view with the video camera was typically illuminated by two high intensity 400 W, 5600°K HMI lights affixed to the submersible's forward upper work bar, and by four additional individually-selectable HMI lights surrounding the video camera. Video was viewed on a flat screen monitor aboard the submersible, and recorded to a mini-DV tape recorder (and to an S-digital backup recorder). A virtual data display (time, date, temperature, depth, salinity) was continuously overlaid onto the video record on all dives (except for certain periods of failure of this utility). Two lasers mounted astride the video camera projected parallel beams 25 cm apart, in a horizontal plane, which were used as one reference scale to determine size of objects imaged, but due to typical submersible attitude parallel to the substrate were only occasionally useful in this regard. Two invertebrate taxa of very constant size dimensions, and very frequent occurrence, were also utilized as reference scales (below). Most video imagery was obtained with the submersible parallel to the substrate and the video camera trained downward at a 45º angle.

VIDEO FRAME ANALYSIS - In the laboratory, all original mini-DV tapes were first copied onto digital video disk (DVD). The entire video record of each dive (ca 2 hr total bottom time) was then converted to a series of sequential still frames using VideoCharge© 3.0 frame-grab software, adjacent frames each representing an interval of approximately one second (0.996 sec). The entire still-frame record of each dive was then scanned to select frames for analysis of megafaunal invertebrate assemblages. Individual frames were referenced by the time display in the submersible's digital data overlay (or by DVD run time when the virtual overlay failed). Frames representing VK-826 and VK-906/862, respectively (two distinct depth horizons), were analyzed separately. Frame selection and exclusion criteria for analysis were as follows:

1. Frames were selected only during bottom operations when the submersible was stationary or traversing very slowly (< 0.3 kt, 0.6 m s^{-1}).
2. A frame with a field of view that overlapped that of a previously selected preceding frame was not selected to avoid duplication.
3. Only frames where the counting field of view was evenly-illuminated were chosen.
4. Only frames in which the substrate fully occupied the lower two-thirds of the total field of view were chosen.

All frames meeting these criteria were accepted (n = 459, Table 3.1). Each frame grab was converted from .tif format to .jpg format at the highest possible resolution, and cropped 112 pixels from the top margin using ReaConverter© v4.0 Pro software (ReaSoft Development). The format conversion to .jpg format was necessary to enable the application of Coral Point Count with Excel© extensions (CPCe) software (Kohler and Gill, 2006). Images were cropped down from the top border to remove open-water background area occupying the upper portion of the field of view, as well as to remove the overlaid data display (time, date, temperature, depth, salinity).

The area of each image was determined using the following size references: 1) parallel submersible laser beam spaced 25 cm apart and projected onto the substrate as a pair of dots; 2) the mean basal stalk width of the common and distinctive orange-lipped white anemone (taxonomic identify under investigation) measured from collected specimens (mean = 2.202 cm ± 0.236 cm SD) (Fig. 3.4A); or 3) the distance along one calyx (basal branching axil to tip of coral cup) of the common open growth form of *L. pertusa* coral, measured from collected specimens (mean = 2.048 cm ± 0.247 cm SD)) (Fig. 3.4B). Areas of many images could not be determined directly when reference taxa used for scaling were absent. Images lacking the specified taxa for size reference (n = 371) were assigned the mean area for the remaining images from which areas were obtained by scaling to reference taxa (Fig. 3.5). The mean area determined was 19.2×10^3 cm^2 ± SD (9.4×10^3 cm^2); the mode was 20.0×10^3 cm^2.

Images that met all four criteria above were analyzed using CPCe software, as follows:

1. <u>Creation of a Megafaunal Invertebrate Code File</u> - A new code file (ASCII text file) containing broad species categories, individual codes and species identifiers of convenience (where taxa could be visually differentiated, but taxonomic identifiers could not be firmly assigned) was created and imported into CPCe for use in this study. This code file contained all megafaunal taxa (hereafter understood in this chapter to include only invertebrates) observed within the two study sites, in addition to four non-biological codes: 1) "No Invertebrate" (a virtual taxon or 'dummy species' discussed below) - when boxes fell on unoccupied substrate, 2) "Shadow" - when open space and substrate was occluded from view (and thus unavailable for analysis) by disturbed sediment, 3) "Tape" - when a portion of the time/date overlay remained in partial view in some of the cropped images, and 4) "Wand" when fish or research equipment partially occluded the field of view, preventing CPCe scoring. The last three codes are CPCe defined immutable codes.
2. <u>Determination of the Number of Points to Project and Point Overlay</u> - A grid array of 60 evenly-spaced (10 columns by 6 rows) boxes (each 20 x 20 pixels) was overlaid

on each cropped image (Fig. 3.6). The number of boxes to be overlaid to provide adequate sampling of the megafauna was determined empirically prior to image analysis. Ten images were selected as a test sample to ground truth the number of boxes to be projected. A progressively increasing number of regularly distributed boxes were overlaid on each image, in increments of ten (i.e., 10-100), and the total number of invertebrates found was scored. The mean number of overlaid boxes beyond which no additional invertebrate hits were scored (i.e., positive hits had approached an asymptote) was 60.

3. Defining the Frame Border - The effective outside borders for scoring each image were offset inwards from the image perimeter by 10 pixels on each side. This was necessary so that the outermost boxes would not fall partially off the image, biasing the results from those outer boxes relative to the remaining scoring boxes.
4. Megafaunal Scoring - The area under each overlaid box was examined to score the occurrence of the individual megafaunal taxon wholly or partially present within that box, or otherwise to score the box as unoccupied substrate (scored as 'No Invertebrate' dummy taxon), or alternatively as one of the three CPCe designated image artifacts (tape, wand, or shadow). Scores were recorded using the CPCe on-screen data columns. Each occurrence of an individual taxon, 'no-invertebrate' dummy taxon, or CPCe artifact category received a score of '1'.
5. Scoring Criteria – 1) If a box contained more than one megafaunal invertebrate taxon, then only the spatially dominant taxon within that box was scored; and 2) Invertebrate taxa too small in scale to resolve individually visually or to identify with the naked eye (= macrofauna), and/or otherwise too abundant and ubiquitous to score (e.g., carpets of tiny macrofaunal bryzoans, hydroids, and diminutive anemone species), were excluded from this megafaunal analysis.
6. Biotope Classification – Each frame was classified (by concensus of three evaluating scientists: ADN, KEL, KJS) as representing one of these six biotope categories: 'Open', 'Plate', 'Plate/Chemo', 'Rock', 'Thicket', or 'Rubble'. The new 'Plate/Chemo' category was previously included within 'Plate' in the moving transect analysis of Sulak et al. (Chapter 2). This new category became recognizably distinct when evaluating megafaunal invertebrate occurrences in digital still imagery.

Biotope categories are defined in Table 3.2, with representative images given in Master Appendix E to show the range of biotope variation within each category. The criterion for classification of any given frame by biotope category was that within the defined frame border, >50% of the area in view corresponded with specified category, as defined in Table 3.2.

7. <u>Data Archiving</u> - Scores for each sample were saved to a CPCe .cpc format data file, and then processed to individual Microsoft Excel spreadsheets. Subsequently, all individual Excel spreadsheets were combined into one master data matrix.

SUPPLEMENTARY VIDEO – The present investigation was originally intended to include submersible dives on Green Canyon and Mississippi Canyon sites where *Lophelia* also occurs, although more sporadically and sparsely than on Viosca Knoll (unpublished observations: W. Schroeder, Dauphin Island Marine Laboratory; S. Viada, Continental Shelf Associates, CSA). Copies of Green Canyon and Mississippi Canyon dive videos obtained courtesy of S. Viada (CSA) were examined qualitatively for comparative reference in empirically categorizing NEGOM slope biotopes, and in qualitatively evaluating fish species use of differential biotopes, defined in part by megafaunal communities.

TAXONOMIC VALIDATION – Except during designated video transects, the submersible was periodically stopped to conduct sampling operations (Sulak et al., Chapter 2). At the same time, high-quality close-up images of sessile invertebrates were obtained using the submersible video camera (with close-up zoom) and digital still camera. Accompanying voucher specimens for taxonomic identification were obtained via in situ submersible collections (suction sampler, manipulator claw) and via remote sampling from the surface vessel. Specimens obtained were transferred to the surface for preparation of laboratory layout images to supplement underwater images. Selected voucher specimens and images were subsequently sent to appropriate taxonomic experts for identification, and a master appendices of taxonomic voucher images prepared for reference. Reserve voucher specimens documenting this investigation were retained at the Florida Integrated Science Center, Gainesville, Florida (FISC). They will ultimately be curated in the cataloged collection of the U.S. National Museum of Natural History, Smithsonian Institution. Since the primary goal of this investigation was ecological, not taxonomic, vernacular identifiers of convenience were used in establishing a master working CPCe code file.

The master taxonomic voucher image appendices (Master Appendices C and D) maintained at FISC, will be updated as definitive scientific names for individual taxa are received back from expert taxonomists.

MULTIVARIATE ANALYSES: METHODS, OPTIONS, AND RATIONALE

1 - DATA MATRIX MANIPULATION – The master matrix of raw CPCe scores for samples (entities) versus megafaunal species occurrences (attributes) was standardized by station total (total occurrences of all taxa in a given sample) (Boesch and Swartz, 1977) for use in multivariate analyses. This standardization adjusts for differences in area 'sampled' by each submersible frame grab image, converting raw scores from CPCe to proportional occurrence scores. Such data standardization is appropriate and desirable for multivariate procedures when sampled area cannot be strictly controlled (Clarke and Gorley, 2006).

2 - MULTIVARIATE ANALYSIS OF SIMILARITY (ANOSIM) - The Canberra metric data matrix derived from the standardized master data matrix of sample data was analyzed statistically using the ANOSIM (nonparametric one-way analysis of similarity) utility in Primer 6©. Prior to engaging in clustering and ordination operations, two null hypotheses were advanced for testing via the nonparametric ANOSIM utility, using 999 permutations of the data (the maximum number of permutations allowable in ANOSIM):

Null hypothesis H1: *No significant differences exist between the megafaunal assemblages determined by CPCe analysis of comparative species occurrence data for the two sampling sites, VK-906/906 and VK-826 (respectively representing two distinct depth horizons, 325 m and 500 m, utilized by demersal fishes associated with hard-bottom slope biotopes in the northern Gulf of Mexico).*

Null hypothesis H2: *No significant differences exist among the megafaunal assemblages determined by CPCe analysis of comparative species occurrence data for the five empirically-defined megafaunal biotopes available to demersal fishes on Viosca Knoll in the northern Gulf of Mexico.*[1]

[1] During the course of the present study, the 'Plate' biotope category of Sulak et al. (Chapter 2) determined empirically for demersal fishes on Viosca Knoll study sites, was subdivided into 'Plate' and 'Plate/Chemo' categories, relative to megafaunal invertebrate occurrences. Additionally, coral 'Rubble' biotope, although rarely encountered, was maintained as a category for CPCe scoring. Thus the present study recognizes six, not four, fundamental empirical biotopes.

3 - SPECIES RICHNESS VIA RAREFACTION CURVES – Species accumulation, or rarefaction, curves were determined utilizing EstimateS© software (Colwell, 2005). EstimateS uses multiple random draws from within pooled sample data to determine the expected number of species at any given sample size (number of specimens) up to the maximum size of the pooled sample (i.e., pooled occurrence data from CPCe). The expected number of species is outputted as the 'Mao Tau' statistic ±95% CIs. Results were plotted as comparative rarefaction curves (both with and without CIs) from five pooled samples, respectively comprising each of the five empirically-defined biotope categories (excluding 'Rubble') to test this null hypothesis:

Null hypothesis H3: *No significant differences exist in species richness among the megafaunal assemblages comprising the respective pooled samples for the five empirically-defined megafaunal biotopes under study.*

The number of random draws (with replacement) used for each pooled biotope sample was set to 100 (i.e., 100 virtual samples of the megafaunal community). The number of species and image samples available for input into EstimateS per pooled biotope sample were as follows: 'Open': 9 species and 55 images; 'Plate': 20 species and 148 images; 'Plate/Chemo': 11 species and 53 images; 'Rock': 20 species and 86 images; 'Thicket': 24 species and 117 images.

4 - CLUSTER ANALYSIS - Sample groups, groups of images statistically-defining living biotopes on the NEGOM continental slope, were resolved and differentiated via cluster analysis using the Primer core applications (Clarke, 1993) and the version 6 software package (Clarke and Warwick, 2001; Clarke and Gorley, 2006). Standardization on species total (as above) was employed as a clustering pretreatment to suppress the contribution of extralimital species (e.g., stochastic occurrences of monospecific schools of fishes) when clustering sample groups, while maintaining the more predictable contribution of less-abundant, but regularly-occurring species. This converts raw counts into relative percentages. This is particularly appropriate where the unit of sampling cannot be tightly controlled (Clarke and Gorley, 2006), which is the case for submersible video frame grabs in the present study, despite the application of rigorous criteria for submersible and camera operations. For cluster analysis of sample groups only, the taxon category 'No Invertebrate' was removed from the data matrix, such that negative data entries (joint absences of all taxa from comparative samples) did not play a role in cluster analyses otherwise defining biotopes by the positive co-occurrences of actual taxa. The 'No Invertebrate'

virtual taxon, or 'Dummy Species' (Clarke and Gorley, 2006; Clarke et al., 2006), was created in the present study to eliminate zeros from the data matrix when CPCe scoring boxes fell on unoccupied substrate. No data transformations were undertaken before or after matrix standardization.

Cluster analysis methods undertaken in this study followed the terminology of Boesch and Swartz (1977), interpreted as follows. Thus, methods employed in the present study were 'exclusive' (at the highest similarity level in the cluster dendrogram, a given entity can belong to only one cluster group), 'intrinsic' (based solely on entity attribute scores, with no environmental variables included), 'hierarchical' and 'agglomerative' (proceeding by a chain of progressive fusions), and 'combinatorial' (resemblance measures calculated successively down the matrix).

Clustering by samples (frame grab images in the present study), or 'normal' analysis, (Boesch and Swartz, 1977) was accomplished using the Canberra metric similarity coefficient (Lance and Williams, 1966; Lance and Williams, 1967b; Boesch and Swartz, 1977), calculated in its dissimilarity form. This coefficient is 'metric' in that distances in mathematical space used for clustering entities remain constant (do not contract or dilate depending on direction of measurement). The more commonly-employed (in ecological analyses) Bray-Curtis coefficient is not strictly metric [i.e., described as semi-metric by Gotelli and Ellison (2004)], such that differences in scale (e.g., magnitude of species scores due to sizes of sampled areas) excessively influence the clusters resolved. That is, the Bray-Curtis coefficient, and related 'dominance similarity' or 'percent similarity' coefficients, tend to resolve clusters dominated by a small number of entities (samples or species) with high scores in the data matrix (Boesch and Swartz, 1977), and greatly dilute the importance of less abundant entities. The Canberra metric coefficient, which is particularly useful in holistic community structure analyses, was specifically designed (Lance and Williams, 1966; 1967b) to overcome this characteristic of the Bray-Curtis coefficient, resulting instead in clusters in which the entities tend to co-occur in a consistent proportional order relative to one another, regardless of scale differences.

The combinatorial method employed (Lance and Williams, 1967a) to express linkage among members of a cluster group was the 'group average' linkage (Boesch and Swartz, 1977; McGarigal et al., 2000), also known as the 'unweighted pair-group' method using arithmetic averages (UPGMA) (Sneath and Sokal, 1973). This is the most widely-employed linkage method in ecological studies. Group average linkage avoids both excessive chaining and intense clustering at low hierarchical levels in the analysis (Boesch and Swartz, 1977), which can lead to artificial groupings. The group average algorithm tends to maximize 'cophenetic correlation' resulting in a faithful representation in the resolved cluster groups of the structure of the original data matrix (McGarigal et al., 2000). The 'sorting strategy', or cluster intensity coefficient [the '*ß*' parameter in the Lance and Williams (1967a) clustering Equation 31: linear solution for computation of inter-group resemblance] was zero (space conserving), the fixed value specified for group average linkage in Primer.

The same methods and options utilized for clustering samples to define biotopes were employed to cluster species to identify recurrent megafaunal invertebrate groups inhabiting and characterizing those biotopes. However, for species, or 'inverse' clustering, pretreatment of the data matrix included flipping the matrix such that the species became the entities, and the samples the attributes. Additionally, samples were standardized on species total instead of sample total. That is, each species score in the matrix was converted to a proportion of the total score for the species across all samples.

Results of both sample and species clusters were presented as hierarchical dendrograms of resemblance measured in Canberra metric 'distance'. Defined clusters were tested for mutual statistical differences at the 95% confidence level using the Primer v6 SIMPROF utility (Clarke and Gorley, 2006), based on 1,000 permutations and 999 simulations. The lowest level of similarity (highest dissimilarity) at which major clusters were identified as statistically significant by SIMPROF served as a first-order criterion for comparison of clusters identified by cluster analysis versus ordination (below), although definitive acceptance of cluster groupings depended as well on ecological interpretations. Although only intrinsic species occurrence data from the overall data matrix were used to calculate dissimilarity values, extrinsic parameters including sampling site depth and biotope designation (either empirical assigned a priori, or statistically defined by SIMPROF analysis) were symbolically overlaid on the x-axis of the site cluster dendrograms to assist in ecological interpretation of comparative biotopes differentiated by cluster analysis.

5 - ORDINATION. - Non-metric Multidimensional Scaling (MDS) was employed as a second independent multivariate method for defining groups of samples based on species occurrence and abundance (versus cluster analysis). MDS is an ordination method that utilizes only rank order information from the similarity or dissimilarity matrix of samples versus species data (McGarigal et al., 2000) to map the spatial configuration of the samples (Clarke and Warwick 2001). Compared to other ordination techniques (e.g., the widely-applied Principal Components Analysis or PCA), MDS makes fewer assumptions regarding the data (Clarke and Warwick, 2001). Accordingly, it has been considered one of the most effective ordination methods for community analyses (Everitt 1978; Kenkel and Orloci, 1986). The goodness-of-fit of an MDS ordination plot is revealed by the "stress" value calculated during MDS analysis in Primer v6. The stress value is a chi-square-like statistic (Gotelli and Ellison, 2004) that measures scatter of data points about the nonparametric regression line of 2-D or 3-D MDS distance versus similarity (or dissimilarity) values in a Shepard diagram (Clarke and Warwick 2001). Ideally, zero stress indicates no scatter, i.e., no departure from a perfect data fit. Stress values under 0.20 indicate data trends that may have nonparametric statistical rigor, and should be explored.

In the MDS ordination plot, points that lie in close proximity represent samples that are similar in community composition (Clarke and Gorley, 2006). Plots of MDS configurations are arbitrarily scaled and aligned, thus graphical distance cannot be used as a metric to compare distance among entities or clusters in MDS space. Angular orientation of MDS plots is similarly non-informational. MDS does not utilize extrinsic (i.e., environmental) data.

The same Canberra metric similarity data matrix used for cluster analysis was also used for ordination analyses. Sample groupings resolved in the 2-D MDS ordination plot from the present study were compared to those resolved by Canberra metric cluster analysis, via graphical overlay of both results using the Primer v6 'Configuration Plot' utility. Based on Primer v6 SIMPROF utility definition of statistically different cluster groups (Clarke and Gorley, 2006), a Canberra metric distance of 10 (out of a maximum dissimilarity distance of 15) and a 'slack' level of 30% (tightness of graphical fit) were chosen as the criteria determining cluster group ellipses enclosing MDS groups of sample points. For MDS calculation, 50 restarts (alternative fittings of the data from 50 random iterations) were selected, and a minimum stress of 0.01 specified. Both 2-D and 3-D Shepard diagrams were produced to evaluate stress statistic values defining strength of clusters identified (lower stress = greater strength). Similarly, MDS ordination plots in both 2-D and 3-D space were produced for empirical evaluation of clusters resolved, with sample points alternatively coded by site depth or empirical biotope assignment for analysis via inspection.

6 - HABITAT COMPLEXITY - The CPCe software was designed in part to assess percent cover of hermatypic corals on shallow tropical coral reefs. Percent cover by individual taxa, or by individual frame grabs, was not a community parameter or habitat metric quantified in the present study. However, the relative proportion of open versus structured habitat across samples representing the respective biotopes was of interest as an index of the relative megafaunal complexity and heterogeneity characterizing each of the respective biotopes. In the present study the percent of bare substrate was determined for the total sample representing each biotope.

RESULTS

SAMPLES - Nineteen dives were accomplished yielding 229 samples (frame grab digital stills from video) within the VK-906/862 sample site depth horizon, and 230 samples within the VK-826 sample site depth horizon, yielding a total of 459 samples for analysis (Table 3.1). Biotope categories established empirically from initial screening of submersible video were: 'Open', 'Plate', 'Plate/Chemo' 'Rock', 'Rubble', and 'Thicket' (Table 3.2; Figs. 3.7-3.12). These six categories were largely consistent with those used in our analysis of demersal fish community structure (Sulak et al., Chapter 2; Sulak et al., 2007), except for the addition of 'Plate/Chemo' (Table 3.2). Furthermore, the biotope category 'Rubble' (Table 3.2) was earlier determined to be so rarely encountered on the Viosca Knoll submersible transects that it was eliminated as a fish biotope from Chapter 2 analyses (Sulak et al., Chapter 2). This category has also been excluded from most analyses in the current investigation, but retained for comparative discussion. The greatest development of high-diversity sessile invertebrate assemblages occurred on 'Plate' and 'Rock' hard-bottom substrates (Fig. 3.13). Coral 'Thicket' biotope was essentially a dense monoculture of *L. pertusa*.

All images combined covered an area of 8.825 x 10^6 cm^2. Individual samples ranged in area between 8.88-64.0 x 10^3 cm^2, mean image area = 19.2 x 10^3 cm^2, (9.4 x 10^3 cm^2), mode = 20.0 x 10^3 cm^2 (Fig. 3.5). Fifty-five distinct types of megafauna were recognized. These were comprised of 54 distinguishable taxa (some of which were composite groups), and one 'unknown' taxon category for animals that could be recognized and scored as living megafaunal organisms, but not otherwise unidentifiable taxonomically. Entities that could be distinguished to individual taxa were coded for analysis and were selected empirically during initial screening of video (Table 3.3). Of the 55 megafaunal types, 39 were scored one or more times during CPCe from the overall set of frames selected for analysis (Table 3.3). Additionally, the virtual or dummy taxon 'no-invertebrate' was scored, as well as three types of CPCe methodological artifacts (shadow, tape, and wand) (Table 3.3). Definitive taxonomic determinations for all megafaunal entities will be accomplished by collaborating experts following this report.

MULTIVARIATE ANALYSES

1 – RAW DATA MATRIX – The master matrix of raw CPCe scores for samples (entities) versus megafaunal species occurrences (attributes) is presented as Master Appendix G.

2 - MULTIVARIATE ANALYSIS OF SIMILARITY (ANOSIM) - ANOSIM tests of two *a priori* hypotheses of megafaunal-defined biotope differentiation on the Viosca Knoll study sites yielded the following results:

Null hypothesis H1 (no significant differences between the megafaunal assemblage occurrences between the two sampling sites, VK-906/862 and VK-826, respectively representing two distinct depth horizons, 325 m and 500 m) was rejected. That is, the megafaunal assemblages of VK-906/862 and VK-826 differed significantly (459 samples, 999 permutations, p>0.01) (Table 3.4). No individual permutation closely approached or exceeded the Global 'R' statistic value of 0.534; 'R' values were symmetrical around a zero mode, with maximum value <0.025 (Fig. 3.14).

Null hypothesis H2 (no significant differences among the megafaunal assemblages representing the five empirically-defined megafaunal biotopes available to demersal fishes on Viosca Knoll in the northern Gulf of Mexico) was rejected. That is, statistically significant differences exist among the megafaunal assemblages of the five respective biotopes (459 samples, 999 permutations, p>0.01) (Table 3.5A). No individual permutation closely approached or exceeded the ANOSIM Global 'R' statistic value of 0.534; 'R' values were symmetrical arrayed around a zero mode, with maximum value <0.050 (Fig. 3.15). ANOSIM pairwise contrasts among data for the five biotopes also revealed statistically significant differences among the biotopes (p <0.1%) (Tables 3.5B, 3.5C). Highly significant differences are revealed when the pairwise R statistic approaches 1.0 ($p < 0.1\%$); ‘Thicket’ differed from all other biotopes (‘Rock’, ‘Plate’, ‘Plate/Chemo’, and ‘Open’) ($R > 0.7$) (Tables 3.5B, 3.5C). ‘Plate’ also differed significantly from ‘Rock’ ($p < 0.1\%$), but at a relatively low R (< 0.3) (Tables 3.5B, 3.5C). Similarly, ‘Plate/Chemo’ also differed significantly from ‘Rock’, ‘Plate’, and ‘Open’ ($p < 0.1\%$), but at low R (< 0.5) (Tables 3.5B, 3.5C). These first-order indications of significant differences among the empirically-defined Viosca Knoll biotopes provided an objective statistical basis for proceeding with ordination and cluster analysis of megafaunal samples by empirical biotope categories (below).

3 - Species Richness via Rarefaction Curves – Rarefaction curves by biotope with 95% CI envelopes (Figs. 3.16-3.18; Appendix 3-I,) revealed a statistically significant difference in species richness only between ‘Thicket’ and ‘Rock’ biotopes (Fig. 3.16), with an expected number of species at N = 2,400 specimens of 13.4 ± 4.2, and 20.0 ± 1.9, respectively. The number of specimens in the pooled samples of ‘Open’ and ‘Plate/Chemo’ were too low to enable substantive comparison with the much larger samples representing the other three biotopes. However, the curve for ‘Open’ was still rising steeply at 70 specimens for that biotope, had not approached an asymptote (Fig. 3.17), and, from its steep initial slope, appeared headed for the highest species richness among the five comparative Viosca Knoll biotopes (Fig. 3.18). In contrast, the curve for ‘Plate/Chemo’ had already flattened at 454 specimens for that biotope (Fig. 3.17), and appeared headed for the lowest species richness among the five biotopes. At a cutoff pooled sample size of N = 200 specimens across the biotopes, the order of increasing species richness was: ‘Thicket’, ‘Plate/Chemo’, ‘Plate’, and ‘Rock’ (Fig. 3.18). At a cutoff of N = 2,400 specimens, the order of increasing species richness was: ‘Thicket’, ‘Plate’, and ‘Rock’ (Fig. 3.17).

4A - Cluster Analysis, Part A: Site & Biotope Analyses – Using the Canberra metric dissimilarity maximum metric distance (arbitrary units) determined in Primer 6 for scaling of cluster dendrograms by sites or biotopes was 10. Low dissimilarity distance values indicated high similarity among samples comprising a Primer-defined cluster group.

Site Clustergram - Samples (CPCe analyzed digital images) evaluated by sampling site (N = 419 total, after removal of ‘No Invertebrate’ samples; 195 representing the VK-826 sampling site; 224 representing the VK-906/862 site) clustered into six major groupings, designated 'A'-'F' (Fig. 3.19, Appendix 3-II). Both SIMPROF and inspection of group attributes (site fidelity, biotope fidelity) were used in accepting validity of defined cluster groups. Group 'A' was comprised of 138 samples, all clustered at a Canberra metric dissimilarity of less than 5.0 distance units (out of the maximum dissimilarity of 10 units). All members forming this group came from VK-826, and all but nine samples represented 'Thicket' biotope. Since the non-'Thicket' members (2 'Plate', 6 'Plate-Chemo', 2 'Rock') were non-systematically distributed among several subgroups (Appendix 3-II), subgroups were not further analyzed relative to extrinsic factors (site, biotope), or individually numbered.

Site Group 'B' was statistically distinct (SIMPROF, $p < 0.05$) from Group 'A'. Group B was comprised of 247 samples, united at a dissimilarity distance of less than 6.0 units, and subdivided into two large cohesive subgroups, B1 and B2 (mutually differentiated at less than 5.0 distance units), and several smaller, less-cohesive subgroups, B3-B7. Although not statistically different by SIMPROF, Subgroups B1 and B2 were highly sampling-site specific, and internally very homogenous in terms of biotope composition, when extrinsic factors (sampling site, biotope type) were considered in post-classification inspection (Boesch and Swartz, 1977). Thus, Subgroup 'B1' comprised 59 samples (53 from VK-826. six from VK-906/862), all but two ('Plate') characterized as 'Open' or 'Plate/Chemo' biotopes (Appendix 3-II). Upon inspection, Group A and Subgroup B1 were recognized as allied by site, together accounting for 191 of the 195 VK-826 samples.

Upon inspection, Subgroups B2-B7 were recognized as united by both site and biotope. Together, these subgroups included 188 samples (185 from VK-906/862, three from VK-826), all but four ('Open') categorized as 'Plate' or 'Rock' biotopes (Appendix 3-II). The large cohesive Subgroup B2 (internally united at less than 5.0 distance units) accounted for 161, with Subgroups B3-B7 adding 27 samples, linked to B2 at lower similarity (less than 6.5 distance units). Site Groups C through F included four small, less well-defined groups (34 total samples), linked to Subgroups B2-B7 (via Group B) and to each other at distances of 6.0-9.5 units (relatively low similarities) (Fig. 3.19). Postclassification inspection revealed that Subgroups B2-B7 and C-F were allied by site and biotope, with 218 of the combined 222 samples coming from VK906/862, and 215 representing 'Plate' or 'Rock' biotopes.

Samples (Biotope) Clustergram - After removal of non-informational 'No Invertebrate' only samples, 491 remained for cluster analysis by biotope. Of these, 195 represented VK-826, and 224 represented VK-906/862. Six major groupings were defined in the analysis, designated Groups 1-6 (Fig. 3.20; Appendix 3-III).

Two major statistically distinct assemblages (SIMPROF, $p < 0.05$) defined were Groups 1 (138 samples united at high similarity, less than 5 distance units) and 2 (281 samples, united at less than 6 distance units). Group 1 was further divided into two statistically-distinct Subgroups 1A (112 samples) and 1B (18 samples), plus a heterogeneous catch-basket combination of Subgroups 1C-F (8 stations). However, both 1A and 1B were both dominated by 'Thicket' samples, and could not be differentiated by inspection. Of the Group 1 samples, 115 of 138 were classified as 'Thicket' biotope, all of which came from the deeper (500 m) VK-826 depth horizon. The remaining non-'Thicket' samples included 12 'Plate', 9 'Plate/Chemo', and 2 'Rock' image grab samples, from both depth horizons, distributed fairly evenly among all subgroups. Upon postclassification sample (image) inspection, the presence of *Lophelia* coral was the single most unifying characteristic of Biotope Group 1.

Group 2 was also subdivided into two major cohesive (but not significantly different, SIMPROF, $p > 0.05$) subgroups (linked together at less than 5 distance units). Subgroup 2A (161 samples) consisted entirely (158) of 'Plate' and 'Rock' classified samples, all but one from the shallower (325 m) VK-906/862 depth horizon (Appendix 3-III). Subgroup 2B (59 samples) consisted predominantly of 'Plate/Chemo' (38) and 'Open' (19) classified images, plus two 'Plate' samples. This subgroup, representing both hard and soft substrates, was characterized by low-relief biotopes (i.e., absence of 'Rock'), and the absence of *Lophelia* coral.

In addition to Subgroups 2A and 2B, Group 2 also included five minor subgroups, Subgroups 2C-G (27 samples), mutually linked in chained fashion at a dissimilarity distance of less than 6 units. The assemblage includes 18 'Rock' and 9 'Plate' samples, all from the shallower VK906/862 depth horizon. This Subgroup 2C-G assemblage bears a strong affinity to the remaining biotope Groups 3 through 6. Taken together these four groups (mutually statistically distinct, SIMPROF, $p < 0.05$) chained together at progressively lower similarity, are comprised of 34 samples, also classified predominantly as 'Rock' (29 samples) from the shallower depth horizon. The remaining samples are 3 'Plate' and 2 'Plate/Chemo' images. Together, the combination of Subgroup assemblage '2C-G' plus Group assemblage '3-6' is characterized predominantly by high-relief 'Rock' biotope at the shallower Viosca Knoll depth horizon (325 m), with a general rarity of *Lophelia* coral. This is the same biotope identified above by rarefaction curve analysis as statistically distinct (EstimateS, no overlap in 95% CIs) from 'Thicket', and displaying the greatest species richness among the hard-substrate biotopes on Viosca Knoll. Thus, there is general coorespondence in the two biotope analyses.

4B - CLUSTER ANALYSIS, PART A: SPECIES GROUP ANALYSES – Maximum Canberra metric dissimilarity distance (arbitrary units) determined in Primer 6 for scaling of CLUSTER DENDROGRAMS BY 'SPECIES' (MEGAFAUNAL ENTITY) was 250 units. Low dissimilarity distance values indicated high similarity among taxonomic/ecological entities comprising a Primer-defined megafaunal 'SPECIES' CLUSTER GROUP.

Megafaunal entities tended not to group in well-defined fashion, but to form a serial chain of linked taxa (Fig. 3.21). However, at the lowest tiers of this stair-step series, a group of 22 entities (Group XV) linked together at very high mutual similarity (<20 arbitrary distance units out of 250). At the highest levels of dissimilarity, three groups stood out as distinct from all remaining entities. They were mutually statistically different (SIMPROF, $p < 0.05$), as well as statistically different from the remaining entities. The red-lipped white anemone (linked with the 'unknown taxon' category) formed one distinct group (Group I), followed by live (white) and presumably dead (brown) *Lophelia* (Group II), followed by bamboo coral (Group III). Group III was linked to a stair-step chained series of 12 megafaunal entities (Groups IV-XIV), in turn linked to the internally cohesive Group XV.

5A – ORDINATION, PART A: SITE & BIOTOPE ANALYSES - Both 2-D (Fig. 3.22) and 3-D (Fig. 3.23) MDS ordination on invertebrate megafaunal score data categorized by sample site (depth horizon) showed complete spatial distinction between the two sampling sites (325 m and 500 m depth horizons). However, considerable internal heterogeneity was revealed within the two distinct groups of samples [stress statistic value of 0.15 in both the MDS plot (Fig. 3.22A) and the accompanying Shepard diagram (Fig. 3.22B)]. Statistically stronger spatial resolution was observed in the 3-D analysis (stress = 0.11; Figs. 3.23A, B). When CPCe megafaunal score data categorized by EMPIRICAL BIOTOPE CATEGORY were analyzed, incomplete spatial of biotope groups was facilitated by comparative overlay of previously-defined biotope cluster distinction among five biotopes included ('Rubble' excluded) was observed in both 2-D and 3-D plots (Figs. 3.24A, B). Visualization groups. At a dissimilarity cutoff of 5.5 arbitrary distance units, eight cluster groups were defined. In the 2-D display, a 'Thicket' biotope group is both spatially distinct and well-supported by the cluster group overlay. 'Rock' and 'Plate' overlap extensively, as do 'Plate', 'Plate/Chemo', and 'Open'. Analyzed in 3-D space, the stress statistic drops from 0.15 to 0.11, indicating better inter-group distinction. Viewed in 3-D, 'Plate/Chemo' and 'Rock' tend to stand out more distinctly than in 2-D from the central tightly-bound core of 'Plate' samples.

5B – ORDINATION, PART B: SPECIES GROUPS ANALYSES Both 2-D (stress = 0.03) and 3-D (stress = 0.02) MDS ordination of CPCe megafaunal score data categorized by 'SPECIES' (MEGAFAUNAL ENTITY) showed a very tight assemblage of entities (Fig. 3.25A, B) anchoring the center of the spatial plot, within a diffuse cloud of the remaining entities. The central assemblage is confined within an ellipse at 50 distance units from the center of the plot (out of a total of 350 units) (Fig. 3.25B). This assemblage consisted of cluster groups VIII through XV (Fig. 3.21), including 29 of the total 38 megafaunal entities in the analysis (excluding the 'no invertebrate' dummy species). These extremely low stress statistics indicate tight conformity with the predicted Shepard diagram regression plots (Figs. 3.26A, B), suggesting that the 30-entity taxonomic assemblage is a very cohesive group, highly associated with the Viosca Knoll sites. This result is in close agreement with the 'Species' clustergram, where these same 29 entities are mutually linked at 50 (on a scale 250) Canberra metric dissimilarity units. The nine MDS outlier entities (those in the outer cloud in Fig. 3.25) are associated with the larger central assemblage over a broad range of dissimilarity distance (Fig. 3.21). The outlier assemblage includes these CPCe coded entities: white anemone, unknown, brown *Lophelia* coral, white *Lophelia* coral, bamboo coral, Venus flytrap anemone, red black coral, white black coral, and bacterial mat. The expanded view of the MDS plot (Fig. 3.25B) reveals that the last four entities listed lie just slightly outside the central ellipse (>50 to 80 distance units from the center), while white anemone, unknown, brown *Lophelia*, white *Lophelia*, and bamboo coral are much more distant (>125 distance units). Overall, the MDS plot and the associated Shepard plots statistically reinforce the qualitative observation that *Lophelia* on Viosca Knoll appears to exist as a monoculture (i.e., 'Thicket' biotope), essentially independent of the remaining invertebrate megafauna. The MDS results indicate that the same is true for the common orange-lipped white anemone, and for the bamboo coral, *Keratoisis flexibilis* (Pourtalés, 1868). EstimateS species richness was highest for 'Rock' and 'Plate' biotopes, where, in contrast to 'Thicket', the majority of the MDS central assemblage of 33 (29 + 4) entities most commonly occurred.

6 – HABITAT COMPLEXITY The five primary biotopes recognized in this study represent a serial gradient in habitat complexity, in terms of both the physical (2-D versus 3-D topographic complexity) and living structure (occurrence of emergent sessile megafauna). Viewed in inverse fashion (i.e., declining structural complexity) the gradient is quantitatively expressed as the mean proportion of area unpopulated by recognizable megafauna across CPCe analyzed images (including "No Invertebrate" scored images) comprising each of the respective biotope samples. The result (Fig. 3.27) is a nearly linear decrease in biotope complexity ($y = 20.05x + 0.5915$, $r^2 = 0.9543$) from 'Thicket' (most complex) to 'Rock' to 'Plate/Chemo' to Plate' to 'Open' (least complex) (Fig. 3.27).

DISCUSSION

MULTIVARIATE ANALYSIS OF SIMILARITY (ANOSIM) - The result of the nonparametric ANOSIM test of *Null Hypothesis H1 (Site Test)* demonstrated that megafaunal composition differed significantly between the two sampling sites, VK-906/862 and VK-826. The simplest hypothesis regarding the source of megafaunal differentiation in community structure between the two sampling sites is that faunal transition depends upon depth. Costello et al. (2005) have advanced depth as the more important parameter influencing faunal transition in *Lophelia*-associated fishes. Precisely how depth operates in this regard has not been explained. Sulak et al. (Chapter 2) have argued that in fishes, mobile visual predators and visual plankton-pickers drop out in coordination with increased depth (500 m) on VK-826. Among sessile particulate feeders, increased feeding efficiency relative to a diminished food supply (which may be hypothesized to decrease progressively with depth) may determine relative success among competing taxa. Temperature may be a controlling factor for some species, such as *Lophelia*. The general range within which *Lophelia* prospers is 8-10ºC. *Lophelia* typically occurs as isolated sporadic bushes on the shallower (325 m) VK-906/862 site, where temperatures are probably frequently at or above 10ºC. Substrate would not appear to be a factor in faunal differentiation between the two study sites since the entire range of biotope substrates occurs at both the 325 m and 500 m sites. The ANOSIM site test result provided an objective statistical basis for proceeding with ordination and cluster analysis of megafaunal differentiation by sampling site.

The result of the nonparametric ANOSIM test of *Null Hypothesis H2 (Biotope Test)* demonstrated that megafaunal composition also differs significantly among the empirically-defined Viosca Knoll biotopes. Analyzed further via pairwise contrasts between biotopes, 'Rock' differed significantly from 'Open', as did 'Plate'. These findings are not surprising, given that 'Rock' and 'Plate' are the dominant hardpan substrate biotopes on Viosca Knoll, while 'Open' biotope represents the broader soft-substrate regime of the overall open slope. 'Rock' and 'Plate' provide the solid surface for the settling of larvae of sessile invertebrates (gorgonians, black corals, anemones, sponges), and the anchored substrate for the attachment of sessile particulate feeders. Both biotopes appear to be stable over time (at least 300 years, based on antipatharian age determinations; Williams et al. Chapter 7), enabling the development of oases of diverse invertebrate taxa (Fig. 3.13), dense monocultures of dominant taxa (Fig. 3.10) and the continuous existence of individual large gorgonians and old black corals (Fig. 3.8A; Sulak, Chapter 8, Fig. 8-3; Williams et al., Chapter 7). In contrast, 'Plate/Chemo' typically appears weathered and eroded (Figs. 3.9A, 3.9B, 3.9D), and may not provide stable substrate for long-lived colonial invertebrates. On Viosca Knoll at least, 'Thicket' also does not appear to be a biotope preferred by many sessile invertebrates. Perhaps this is due to the unusual preponderance of live white *Lophelia* on Viosca Knoll, and the relative rarity of dead standing coral and rubble. In live *Lophelia*, the living tissue sheath, or coenosarc, coats the calcareous stalk of the coral calyx, retarding colonization of the coral by other invertebrates (Mortensen, 2001). Many authors have reported that, compared to living coral, dead standing coral and coral rubble harbor a much higher diversity and abundance of associated invertebrate taxa (Wilson, 1979; Jensen and Frederiksen, 1992; Mortensen et al., 1995; Costello et al., 2005).

The ANOSIM determination of significant differences among the empirically-defined Viosca Knoll biotopes provided an objective basis for proceeding with ordination and cluster analyses.

SPECIES RICHNESS VIA RAREFACTION CURVES – Rarefaction curves (Figs. 3.16-3.18) provided three surprising results: 1) *Lophelia* 'Thicket' biotope harbored the fewest number of megafaunal taxa at any given sample size (Figs. 3.16-3.18); 2) The inadequately sampled 'Open' biotope nonetheless demonstrated the highest and fastest-rising megafaunal taxa accumulation curve (Fig. 3.18), suggesting the highest species richness at equivalent sample sizes; and 3) Species richness for 'Rock' biotope was significantly higher than for coral 'Thicket' biotope (Fig. 3.16). These findings seem contrary to expectations based on species richness determined for invertebrates associated with *Lophelia* reefs versus comparative biotopes in the northeastern Atlantic (Wilson, 1979; Jensen and Frederiksen, 1992; Mortensen et al., 1995; Costello et al., 2005: Raes and VanReusel, 2005). However, these previous studies tallying numbers of associated taxa included the invertebrate macrofauna (the 'minifauna' of many European authors, typically defined as animals retained on a 420 μm or 500 μm mesh sieve), a major community component not assessed in the present study. Furthermore, much of the species richness registered on coral biotopes among these previous studies derived from extensive dead standing coral and loose coral rubble, habitat components that are rare on Viosca Knoll. Live coral appears to resist colonization (e.g., Mortensen, 2001). However, even if the northeastern Atlantic versus northern Gulf of Mexico contrast in species richness were limited only to the megafauna, and only taxa found on live *Lophelia*, Viosca Knoll reefs would still appear comparatively depauperate in terms of associated gorgonian, sponge, and echinoderm species.

Based on qualitative observations, the same conclusion would seem to apply to a contrast of species richness of *Lophelia* reefs off the southeastern coast of the U.S. versus those studied by us in the northern Gulf of Mexico (K.J.S., personal observations based on NOAA Ocean Exploration 2001-2004 cruises). Differences in substrate, current, and food supply may all contribute to lower megafaunal species richness for Viosca Knoll reefs. However, food supply in particular may be limiting in the northern Gulf of Mexico. *Lophelia* reefs in the northeastern Atlantic under the North Atlantic (Norway) Current and off the southeastern U.S. under the Gulf Stream lie in oceanographically dynamic regions of enhanced surface productivity and fallout of organic carbon to the slope.

Other factors limiting the richness of the Viosca Knoll coral-associated megafauna may be comparative isolation, together with limited area available for colonization. To date, the *Lophelia* thickets on VK-826 are the only examples of well-developed *Lophelia* coral reefs on the slope in the northern Gulf of Mexico, and indeed, in the entire Gulf of Mexico. Thus, VK-826 is essentially a small island of *Lophelia* reef, without neighboring reefs across a vast area of the ocean. This situation is very different from that of the Florida-Hatteras Slope and Blake Plateau, and also that of the northeastern Atlantic. In these comparative regions, large *Lophelia* banks number in the thousands (Teichert, 1958; Stetson et al., 1962: Neumann et al., 1977; Mullins et al., 1981; Messing et al., 1990; Mortensen et al., 1995; Paull et al., 2000; Reed, 2004; Costello et al., 2005). The well-known island biogeography effect may thus be operative. That is, species richness tends to be a direct function of (i.e., positively correlated with) the area of an island (or of groups of adjacent islands taken together). Therefore, although somewhat contrary to expectations based on earlier studies (e.g., Mortensen et al., 1995), it seems logical (and in conformity with the species-area concept) that total species richness of the vast soft-substrate biome of the open continental slope would exceed that of the very limited area of *Lophelia* reef in the northern Gulf of Mexico. At a sample size of 200 individuals (maximum number of individuals scored from limited 'Open' biotope transects), the EstimateS rarefaction curve for 'Open' biotope has the highest and steepest species accumulation trajectory of all biotopes (Fig. 3.18). This suggests that this biotope supports higher species richness than the comparative structured biotopes of more limited areal extent on the slope.

The finding that 3-D 'Rock' biotope supports the highest species richness among the hard-substrate and reef biotopes adds strength to the hypothesis of Auster (2005, 2007) that structured abiotic (geological) habitat may function equivalently to structured biotic habitat (i.e., living coral reef) in determining community structure in deep water. Auster's hypothesis pertains to the linkage between deep-water corals and fish populations, but this hypothesis might logically be extended to the invertebrate megafauna in deep water. On the Viosca Knoll study sites, for example, otherwise barren goethite rock substrate appears to be the preferred substrate for extensive colonization by both individual megafaunal species like the orange-lipped white anemone (Figs. 3.10A-D) and by mixed oases of sessile invertbrates (Figs. 3.13A-D). We might have predicted at the outset that species richness would decline in harmony with a serial decline in habitat complexity from 'Thicket' to 'Rock' to 'Plate/Chemo' to 'Plate' to 'Open'. However, no such pattern was observed. Rarefaction results coordinate more closely, if imprecisely, with Auster's (2005, 2007) hypothesis.

MULTIVARIATE ANALYSES PART A: SITE & BIOTOPE ANALYSES – Both clustering and MDS ordination substantiated distinct megafaunal community differentiation between the VK-906/862 (325 m) and the VK-826 (500 m) sites. The empirically-defined biotopes were largely differentiated as well by multivariate analyses. Additionally, the relative homogeneity of empirical biotope assignments for samples clustered into most multivariate groups reinforces the correspondence of our empirical biotope categories with natural ecological differentiation. However, in both the site clustergram and the biotope clustergram, some small groups and subgroups are unnatural paraphyletic or polyphyletic catch-baskets, comprised of odd samples of low similarity (e.g., Group '6' and Subgroups '2C-2G' in the biotope clustergram, Fig. 3.20). However, the parameter or parameters responsible for faunal differentiation between the two study sites and among the biotopes has not been determined in this study. Clustering simply identifies taxonomic entities that associate in mathematical space due to mutual similarities in occurrence data, expressed in a similarity coefficient. Nor can the underlying nature of the MDS dimensions be identified in the ordination analysis. However, probable candidates at play in faunal differentiation do emerge from examination of cluster group composition in relation to habitat parameters. Those candidates include: depth (shallow versus deep), substrate (hard versus soft), relief (high versus low), and *Lophelia* coral (presence versus absence). The reduced stress level between the 2-D (0.15) and 3-D (0.11) analyses indicates that at least two habitat parameters are responsible for differential megafaunal community structure. However, one parameter alone accounts for most of the faunal structuring, both between the study sites, and among the biotopes.

Two potentially key parameters that were not examined in the present multivariate analyses are 1) differential planktonic prey availability, and 2) prevailing current regime. Without an intensive field study of local hydrography, the second parameter will remain illusive. However, with respect to the first parameter, trophodynamic research entailing both tissue stable isotope analysis (carbon and nitrogen), and conventional food habits analysis are proceeding to be reported later (FISC, Gainesville, FL, K.J.S., PI; samples for analysis detailed in Randall et al., Master Appendix B, Table 1.7).

MULTIVARIATE ANALYSES, PART B: SPECIES GROUP ANALYSES – The 'species' clustergram (Fig. 3.21) revealed that the common orange-lipped white anemone, *Lophelia*, and the bamboo coral *K. flexibilis* (Groups I, II, and III) are distributed almost independently of one another and of all other megafauna taxa. The remaining taxa (Groups IV-XIV) occur in tight coordination at high mutual similarity, particularly the 22 taxa comprising Group XV (Appendix 3-IV), statistically distinct (Primer SIMPROF utility) as a group from all other taxa (Fig. 3.21). MDS ordination (Figs. 3.25A, B) confirms that this core group is very tightly conjoined in space. The 3-D Shepard diagram (Fig. 3.26B) portrays the marked stepwise distinction between the inner core of 22 taxa and the secondary donut of linked taxa, and between the secondary group and the diffuse and distant outer cloud of dissimilar taxa (white anemone, white and brown *Lophelia*, bamboo coral, and unknown). The multivariate results suggest that occurrence of taxa in the outer group is controlled by different parameters than those operating upon the remaining taxa, particularly the inner core group. Furthermore, the absence of statistical differentiation (SIMPROF) among the 22 taxa comprising the inner core group, indicates that which of those taxa occurs in any given place at any given time is entirely stochastic. This suggests colonization of hard substrate biotopes by these 22 taxa occurs at random with equal probability. In contrast, more deterministic processes with unequal probabilities might reasonably be hypothesized to operate in controlling the spatial occurrence of *Lophelia*, white anemones, and bamboo coral.

BIOTOPES VERSUS ECOTONES - The approach employed in the present megafaunal invertebrate biotope study and in the companion fish community study (Sulak et al., Chapter 2) is based on the concept that fish communities on Viosca Knoll are organized primarily among biotopes characterized by differential physical (geological) and biological features (resident megafaunal species). This approach may be insufficient to holistically comprehend the structuring of fish communities in relation to megafaunal invertebrate assemblages in the deep ocean. A competing, or perhaps an adjunct, concept is that of ecotones, the narrow transitional borderlands between larger areas of distinctly different biotopes. Analysis of neither the mobile demersal fish fauna (Sulak et al., Chapter 2), nor the sessile/sedentary invertebrate megafauna via submersible video transects or sequential frame grabs, is adept at quantifying and characterizing faunal associations with ecotones. Nonetheless, ecotones are ecologically important in the structuring of fish and megafaunal communities. A particularly notable ecotone on Viosca Knoll study sites is the often abrupt transition between plate and rock. This ecotone presents a ridge line or platform edge predatory vantage point utilized by mobile fishes, but also a feeding vantage point for sessile megafauna that intercept current-borne plankton. Our qualitative submersible observations suggest that ecotones are nodes of particular activity and faunal complexity. Oases of mixed sessile invertebrates appear to be best developed at ecotones (e.g., Fig. 3.13A, B), and fish abundance appears to peak along ecotones as well. Another notable ecotone occurs within 'Rock' biotope, where large crevasses or cavities occur between boulders or the edges of rock plates. Again, fish abundance appears much higher within the narrow ecotone, which is difficult or impossible to 'sample' effectively or to quantify using submersible video.

REGIONAL BIOTOPE CONTRASTS -

COMPARATIVE MEGAFAUNAL INVERTEBRATE DIVERSITY – Well-developed *Lophelia* 'Thicket' biotope in the northern Gulf of Mexico gives the appearance of a single-species monoculture, dominated by *L. pertusa* coral (Fig. 3.12), and sparsely populated otherwise by other large invertebrate megafauna, sessile or mobile. Overall, the impression is one of a winnowed, depauperate community, relative to megafaunal communities in and around *Lophelia* reefs in other regions. This qualitative observation from analysis of submersible dive video is substantiated quantitatively by comparative species richness analyses among the biotopes using EstimateS (Figs. 3.16-3.18). Thus, at sample sizes of both 200 and 2,400 total individuals, the comparative expected number of megafaunal invertebrate species is least for 'Thicket' among all comparative biotopes (Figs. 3.17, 3.18). At a sample size of 2,400 individuals, predicted species richness of 'Thicket' is only 13 species, versus 18-20 for 'Rock' and 'Plate' (Fig. 3.17). The expected number of species for 'Thicket' is significantly and consistently less (no overlap in respective 95% CIs of the respective biotope curves) than the number predicted for 'Rock' biotope (Fig. 3.17), and appears to have the flattest rate (slope of curve) of species accumulation with increasing sample size (Figs. 3.17, 3.18).

On our study sites, *Lophelia* was the only scleractinian framework coral found. Elsewhere, a companion scleractinian species typically co-occurs. In various regions of the world ocean, these companion framework corals are as follow: *Enallopsammia profunda* (Pourtales, 1867), *Enallopsammia* sp., and/or *Madrepora oculata* Linnaeus, 1758, off the southeastern U.S. (Stetson et al., 1962; Neumann et al., 1977; Mullins et al., 1981; Rogers, 1999; Reed, 2002); *M. oculata*, *Solensmilia variabilis* Duncan, 1873, or *Dendrophyllia cornigera*

(Lamarck, 1830) in the northeastern Atlantic (Rogers, 1999). Even when the companion framework species is not evident on living reefs, it leaves a legacy of rubble to document its episodic importance. Thus, for example, on Florida-Hatteras Slope *Lophelia* reefs, living *E. profunda* is rare, but this species is abundantly represented in the coral rubble (K.J.S., unpublished observations, NOAA Ocean Exploration 2001-2004 cruises).

On the Norwegian Shelf, Mortensen et al. (1995) found several large gorgonian species, including *Paragorgia arborea* Linnaeus, 1758; *Paramuricea placomus* Linnaeus, 1758; and *Primnoa resedaeformis* (Gunnerus, 1763) to be prominent members of *Lophelia* coral bioherms. On the Florida-Hatteras Slope, at Site 'C', Reed (2002) also reported gorgonians (including *Plumarella pourtalessi* (Verrill, 1883) and *Eunicella* sp. to be prominent and abundant on *Lophelia* habitat (but only habitat consisting mostly of rubble and dead standing colonies). However, gorgonians were very rarely observed by us within or adjacent to Viosca Knoll reef thickets. None of the same genera reported by Mortensen et al. (1995) from the northeastern Atlantic, or Reed (2002) from the northwestern Atlantic, were recorded during the present study in the northern Gulf of Mexico. The only large, prominent gorgonian we recorded was *Callogorgia americana delta* Cairns and Bayer, 2002 (Master Appendix D, Plate 3B), but this species was not found in association with *Lophelia*. Very large gorgonians, black corals, and bamboo corals do occur on the Viosca Knoll study sites, but typically only on 'Plate' biotope, and predominantly on the shallower study site, VK-906/862 (Master Appendix D, Plates 2B-D, 3C). Only rarely are these large sessile colonial 'soft' corals found in close proximity to *Lophelia* colonies (Figs. 3.8A, 3.13C). Messing et al. (1990) also reported a spatial separation (interpreted in relation to differences in bottom current regime associations) between the large zoanthid *Gerardia* sp. and the scleractinian *Lophelia* on deep-water lithoherms in the northeastern Florida Straits.

Hexactinellid glass sponges and other small sponges occur more frequently within Viosca Knoll *Lophelia* 'Thicket' biotope (Master Appendix D, Plates 9A-D) or mixed megafaunal 'oases' containing *Lophelia* (Fig. 3.13B). However, sponges are a minor megafaunal component of northern Gulf of Mexico *Lophelia* reefs, as Reed (2002) also reported for his Site 'C' off Georgia.

Among invertebrates found within *Lophelia* habitats, Jensen and Frederiksen (1992) have concluded that none are found exclusively on *L. pertusa*, and none are obligate associates. Our results for demersal fishes provide essentially the same conclusion (Sulak et al., Chapter 2). However, in the present investigation, certain invertebrate species would not otherwise be found on the northern Gulf of Mexico continental slope, if *Lophelia* were absent. One such species is the gastropod, *Coralliophila abbreviata* (Lamarck, 1816) (Master Appendix D, Plates 27A-B), which feeds on the sort tissues of *Lophelia*. Another is a potentially undescribed species of *Periclimenes*, a 2.0 cm long abundant pure white shrimp (Master Appendix D, Plates 24C-D) that is superbly camouflaged to shelter among the living *Lophelia* matrix. This species would be much more vulnerable to predation on any other substrate. Finally, the large tube-dwelling polychaete, *Eunice* sp. (Master Appendix D, Plate 18B), lives in intimate association with *Lophelia*. The coral is induced to secrete a calcareous sheath around the polychaete's tube (Jensen and Frederiksen, 1992), permanently and cryptically incorporating the worm's home into the coral colony's skeleton. Mortenson (2001) considers the *Eunice-Lophelia* relationship one of non-obligate mutualism since the polychaete can also associate with other scleractinians including *M. oculata*. Nonetheless, living white *Lophelia* does provide special habitat for a number of small megafaunal invertebrate species on Viosca Knoll reefs. Such species may form an important part of the prey of *Lophelia*-associated fishes like *Grammicolepis brachiusculus*, which appears to be an epifaunal cropper or picker (Sulak et al., Chapter 2), and its probable trophic counterpart in the northeastern Atlantic counterpart, *Neocyttus helgae*. On New England seamounts, *N. helgae* also uses large gorgonians like *Paragorgia* for shelter, feeding both as an epifaunal picker (picking at items on the gorgonian) (Gartner et al., 1997; Auster et al., 2005) and/or on plankton (P. Auster, pers. comm.). It seems probable that *Lophelia* 'Thicket' biotope shelters a number of small, cryptic, and/or crepuscular invertebrates that form important food resources for *Lophelia*-associated fishes. Jensen and Frederiksen (1992) reported that the tanaid *Apseudes spinosus* was associated with live coral. Husebø et al. (2002) reported that the copepod, *Euchaeta* sp., was a major food item of plankivorous redfishes (*Sebastes* spp.), but that *Euchaeta* was not found in non-coral habitats. Apparently this copepod shelters within the coral, and is exploited by redfish when it emerges into the water column. Hyperiid amphipods (e.g., *Themisto* sp.) may similarly shelter within the coral matrix, becoming major fish prey (Husebø et al., 2002) only upon emerging into adjacent unprotected biotopes. In the present study, small ophidiid fishes like *Neobythites marginatus* and *Bassogigas?* sp. (Master Appendix B, Plates 5A) were observed similarly sheltering within 'Thicket' biotope.

<u>*COMPARATIVE COMMUNITY COMPOSITION AND POPULATION DENSITY*</u> - There appears to be a second major contrast in invertebrate megafaunal communities between Viosca Knoll *Lophelia* reefs, and those off the southeastern coast of U.S., and in the northeastern Atlantic. Jensen and Frederiksen (1992) have reported high abundance of the suspension feeding brittle star, *Ophiactis balli,* on Faroe shelf *Lophelia* reefs. Similarly, the brittle star, *Ophiacantha bidentata*, occurs in enormous numbers per unit area within the basal matrix of *Lophelia* colonies off the U.S. southeastern coast (unpublished observations, 2001-2004 NOAA Ocean Exploration cruises: M. Nizinski, NOAA Systematics Laboratory, Smithsonian Institution; R. Allen Brooks, ENSR, St. Petersburg, Florida; and K.J.S.). The comparable suspension feeding brittle star niche appears unoccupied on Viosca Knoll reefs. Similarly, while suspension feeding crinoids occur in sporadic clusters on Viosca Knoll (Master Appendix D, Plates 16B-D), their overall occurrence and abundance seems very low in contrast to the high numbers of crinoids reported by Neumann et al. (1977) and Messing (1984) for *Lophelia* banks in the Atlantic Ocean off eastern Florida. There appear to be regional contrasts in the relative utilization of other equivalent trophic niches as well. Thus, even for prominent invertebrate taxa co-occuring on both East Coast and Viosca Knoll reefs (e.g., the galatheid squat lobster, *Eumunida picta*; the large red brisingid seastar, *Novodina antillensis*), submersible observations (K.J.S.) suggest markedly lower population abundances per unit area for the northern Gulf of Mexico reefs.

<u>*COMPARATIVE BIOTOPES*</u> - Another striking difference between Viosca Knoll *Lophelia* reefs and northeastern Atlantic *Lophelia* reefs is the virtual absence of the coral rubble and patch reef transition zones (Mortensen et al., 1995; Freiwald et al., 2002) on the northern Gulf of Mexico reefs, and the apparently very high proportion of living white (versus dead brown-gray) coral in the Gulf of Mexico (Schroeder, 2002; Sulak et al., Chapter 2). Both *Lophelia* rubble and dead coral have been reported to be important high-density, high-diversity invertebrate habitats in the northeastern Atlantic (Wilson, 1979; Jensen and Frederiksen, 1992; Mortensen et al., 1995; Costello et al., 2005). Jensen and Frederiksen (1992) reported 42 invertebrate species specifically utilizing loose *Lophelia* rubble biotope. Furthermore, these authors reported that the abundance of all invertebrates (excluding colonial forms) found on analyzed blocks of *Lophelia* was twice as high on dead versus living blocks of coral matrix quantitatively analyzed. Indeed,

for selected taxa the difference was remarkable, as follows by taxon: brachiopods (50 times more abundant); ascidians, anthozoans, and echinoderms (10 times); siphunculids, crustaceans, bivalves and nematodes (4-8 times). Mortensen et al. (1995) also reported that the diversity of taxa associated with *Lophelia* (standing live and dead forms taken together, corresponding to our 'Thicket' biotope) was threefold higher that than of the surrounding soft substrate (equivalent to our 'Open' biotope). Thus, on northeastern Atlantic deep reefs, 'Rubble' biotope (.e., expanses of dead *Lophelia* branches) appears to form a distinct and important biotope relative to standing coral on the one hand, and open sediment on the other. Indeed, in contrast to standing *Lophelia*, Mortensen et al. (1995) reported lower species richness for rubble, but the highest population density of all non-colonial invertebrates among the habitats analyzed. In contrast to adjacent soft sediment biotope, the common squat lobster, *Munida sarsi*, was 10 times more abundant on coral rubble. In the western North Atlantic, Messing et al. (1990) reported that the upcurrent ends of *Lophelia*-topped lithoherms in the Florida Straits were covered with *Lophelia* rubble. Rubble was reported to extend beyond the foot of the lithoherms forming a talus apron, much like the rubble zones described for *Lophelia* reefs in the northeastern Atlantic. Similarly, Reed (2002) observed that for a site at 700-800 m depth at the base of the Florida-Hatteras Slope, nearly 100% of *Lophelia* consisted of fields of dead rubble. Reed et al. (2005, 2006) have reiterated this observation. Live coral comprised only about 5% cover on the peak of the site, where rubble was again dominant, but standing dead *Lophelia* was also found. Among Norwegian bioherms studied, dead coral has been reported to cover an average basal area nearly 8-fold larger than that occupied by living coral (Mortensen et al., 1995). Elsewhere, *Lophelia* rubble is utilized as habitat by demersal fish species (Costello et al., 2005), and may form a distinct biotope for certain species, e.g., *Lophiodes beroe* Caruso, 1981, and *Chaunax stigmaeus* Fowler, 1946, both found preferentially on *Lophelia* rubble on the Blake Plateau (J. H. Caruso, Tulane University, pers. comm.).

A unique and striking feature of Viosca Knoll study sites is the prevalence of hardpan 'Plate' and 'Rock' biotopes on the Viosca Knoll study sites, and the complementary rarity to near absence of soft substrate. Aside from the stony matrix of live and dead coral, and coral rubble, hard substrate is virtually nonexistent on *Lophelia* reefs off the southeastern U.S. (K.J.S., unpublished observations). Alternately, on the rock-capped tops of VK-906/862 and VK-826, soft substrate is virtually absent. A thin veneer of reef-derived sand thinly coats the underlying hardpan substrate in places (Fig. 3.8), but soft substrate is often completely absent. Thick soft substrate (Fig. 3.7) occurs only on the flanks of the knolls and ridges, or within in-filled valleys (Sulak et al., Chapter 2, Fig. 2.4) or structural collapse depressions in the geological diapar mound as visited on Dive 4750 (Fig. 3.2). Although important demersal fish habitat is provided by *Lophelia* on Viosca Knoll, in the form of both the dense thickets (Fig. 3.12) and oases of mixed sessile megafauna including *Lophelia* (Fig. 3.13), high-relief, 3-D 'Rock' biotope generally appears to function as a structured fish biotope that is equivalent to living reef, except for a few fish species that are tightly tied to living 'Thicket' (Sulak et al., Chapter 2).

RECOMMENDATIONS

Recommendations for future research on *Lophelia* megafaunal invertebrate communities generally adhere to those presented in Sulak et al. (Chapter 2). A further recommendation, however, is greater emphasis on comparative on-reef versus off-reef sampling and imaging. Companion research on the invertebrate macrofauna, using well-controlled extreme close-up imagery, should also be undertaken, again with incorporation of comparative on-reef versus off-reef analyses. Finally, it is appropriate to again emphasize the fundamental importance of high-resolution multibeam bathymetric/topographic/acoustic reflectance mapping to identify and define high-quality reef sites prior to launching expensive and time-limited submersible and ROV missions.

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DISCLAIMER

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Table 3.1. Synopsis of sampling operations conducted during two USGS submersible and one surface vessel cruise, 2004-2005. Key: JSL = Johnson-Sea-Link submersible, USGS = sampling stations conducted remotely from a surface research vessel, VK = the Viosca Knoll study area, V = video operations, FC = JSL fish and invertebrate collections, BT = bottom trawl collections, BS = epibenthic sled collections.

USGS Cruise number	Station number	Study site	Depth (m)	Sample type	Video bottom time (hh:mm:ss)	Number of video frame grabs analyzed
2004-03	JSL-4744	VK-906/862	315	V & FC	2:44:46	24
2004-03	JSL-4745	VK-906/862	336	V & FC	0:58:01	4
2004-03	JSL-4746	VK-906/862	345	V & FC	2:01:58	31
2004-03	JSL-4747	VK-906/862	316	V & FC	2:58:00	17
2004-03	JSL-4748	VK-826	446	V & FC	2:24:17	10
2004-03	JSL-4749	VK-826	511	V	2:29:23	8
2004-03	JSL-4750	VK-826	528	V & FC	2:32:01	0
2004-03	JSL-4751	VK-826	462	V & FC	2:46:07	21
2004-03	JSL-4752	VK-826	469	V	2:40:44	23

Table 3.1 (continued)

USGS Cruise number	Station number	Study site	Depth (m)	Sample type	Video bottom time (hh:mm:ss)	Number of video frame grabs analyzed
2004-03	JSL-4753	VK-826	475	V	2:37:41	6
2004-03	USGS-9004	VK-906/862	327	BT	NA	NA
2004-03	USGS-9007	VK-826	536	BT	NA	NA
2004-03	USGS-9013	VK-826	457	BS	NA	NA
2004-03	USGS-9014	VK-826	382	BS	NA	NA
2004-03	USGS-9017	VK-826	308	BT	NA	NA
2004-03	USGS-9018	VK-826	325	BT	NA	NA
2005-03	USGS-0017/0073	VK-906/862	360	FT	NA	NA
2005-03	USGS-0018/0074	VK-906/862	360	FT	NA	NA
2005-03	USGS-0025/0075	VK-826	486	FT	NA	NA
2005-03	USGS-0027/0076	VK-826	486	FT	NA	NA
2005-04	JSL-4873	VK-906/862	315	V	1:49:18	3
2005-04	JSL-4874	VK-906/862	315	V	1:43:31	37

Table 3.1 (continued)

USGS Cruise number	Station number	Study site	Depth (m)	Sample type	Video bottom time (hh:mm:ss)	Number of video frame grabs analyzed
2005-04	JSL-4875	VK-906/862	337	V	2:19:49	69
2005-04	JSL-4876	VK-906/862	312	V	2:47:16	44
2005-04	JSL-4877	VK-826	479	V	2:28:35	13
2005-04	JSL-4878	VK-826	465	V	1:02:06	6
2005-04	JSL-4879	VK-826	454	V & FC	2:29:28	53
2005-04	JSL-4880	VK-826	455	V	2:25:50	61
2005-04	JSL-4881	VK-826	451	V	2:31:18	17
2005-04	JSL-4882	VK-826	478	V	0:55:17	12
Totals			315-536		44:45:26	459

Table 3.2. Biotope category descriptions, Viosca Knoll study sites, based on physical structure and characteristic sessile megafauna. Descriptions are from Sulak et al., Chapter 2), further amplified from the present study of megafaunal assemblages.

Biotope Category	Assignment criterion when scoring images: Biotope category was assigned when a particular biotope covered >50% of the analyzed field of view; field of view = the lower two-thirds of video screen. Mean area covered = 19.2 x 10^3 cm^2, ±SD (9.4 x 10^3 cm^2), mode = 20.0 x 10^3 cm^2.
Open (non-coral)	Terrain flat or undulating, comprised of deep soft sediment, often hummocky with obvious biogenic burrows and mounds. Key indicator taxa: black ceranthiid anemones (burrowers).
Plate (non-coral)	Terrain flat or terraced hardpan, often with a thin veneer of surficial sediment. Maximum relief less than 10 cm. Substrate is typically populated by attached sessile invertebrates. Key indicator taxa: white anemones, glass sponges, gorgonians, bamboo corals, black corals, and/or isolated *Lophelia* colonies.
Plate/Chemo	Terrain flat or terraced hardpan, often with extensive features suggesting chemical erosion: pock marks, knobs, channels, and ragged-edged plates. Sparsely-populated, characteristic megafauna include tube worms, bacterial mats, dead vent clam valves.
Rock (non-coral)	Terrain uneven and either highly eroded, sculpted, or fragmented, with outcropping edge, and large crevices or pockets. Maximum relief greater than 10 cm. Substrate barren, or sparsely to densely populated by sessile invertebrates. Key indicator taxa: white anemones, glass sponges, gorgonians, bamboo corals, black corals.
Rubble (coral debris)	Terrain either hard or soft, but with broken and scattered live and/or dead *Lophelia pertusa* coral branches and fragments covering >50% of field of view.
Thicket (live *Lophelia* coral)	Terrain either hard or soft, predominantly live (white) coral developed into expanses of tall, extensively-branched *Lophelia* coral bushes covering >50% of field of view.

Table 3.3. Megafaunal invertebrate taxa recorded from USGS JSL video operations on VK-826 and VK-906/862, 2004-2005.

CPCe Code	CPCe Description	Count
BLC	Brown *Lophelia* coral	2,824
WLC	White *Lophelia* coral	2,995
BAM	Bamboo coral	972
POBC	Pink black coral	11
RBC	Red black coral (‘spaghetti’ coral)	372
UBC	Unknown black coral	4
WBC	White black coral	352
FG	Fan gorgonian	6
UG	Unknown gorgonians	0
BA	Bamboo coral anemone	1
BWA	Big white anemone	0
BCYR	Black cerianthid	23
DA	Dandelion anemone	10
PCYR	Pink cerianthid	1
UA	Unknown anemones	32
VFT	Venus fly trap anemone	170
WA	White anemone (orange lip)	2,411
AS	Amorphous sponge	0
DS	Demo sponge	19
FS	Finger sponge	1
GS	Glass sponge	105
SS	Sulphur sponge	0
US	Unknown sponges	0
VS	Vase sponge	2
BL	*Bathynectes longispina*	0

Table 3.3 (continued)

CPCe Code	CPCe Description	Count
CS	Cleaner shrimp	1
SBC	Square bodied crab	0
SL	Squat lobster	42
UCL	Unknown crabs and lobsters	3
EURC	Echinus	7
HURC	Heart urchin	0
PENU	Pencil urchin	9
UURC	Unknown urchin	0
LST	*Luidia* seastar	4
PST	Pillow seastar	2
SST	Snakestar	0
UST	Unknown starfish	0
BR	Brisingid	15
BRT	Brittlestar	0
CRI	Crinoid	34
UCR	Unknown crinoids and brittlestars	9
FDW	Feather duster worms	0
SW	Serpulid worms	6
TW	Tube worms	102
UW	Unknown worms	0
UNK	Unknown	401
BAC	Bacterial mat	199
BLU	Blue sponge	7
BRY	Bryozoans	0
CLAM	Dead clam	34
FHYD	Fan hydroid	1
HYD	Hydroids	83

Table 3.3 (continued)

CPCe Code	CPCe Description	Count
SB	Starburst coral	0
UAL	Unknown alcyonarian	21
UOC	Unknown octopus	1
NONE	No invertebrate (virtual taxon)	15,640
SHAD	Shadow	461
TAPE	Tape	69
WAND	Wand	78
	Total (excluding tape, wand, and shadow) = 55 Entities	26,932 Images

Table 3.4. Results of ANOSIM test of Null Hypothesis H_1 (sampling site test).

Analysis Type	One-Way Analysis
Data Type	Multivariate Distance
Factor	Site(s)
Sites	VK-826, VK-906/862
ANOSIM output:	
Global R statistic	0.534
Significance level of R statistic	0.1%
Number of permutations	999
Number of permutated statistics ≥ Global R	0
Result	H_1 rejected; megafaunal assemblages of VK-826 and VK-906/862 differ significantly.

Table 3.5A. Results of ANOSIM test of Null Hypothesis H_2 (biotope contrast test).

Analysis Type	One-Way Analysis
Data Type	Multivariate Distance
Factor	Biotope(s)
Biotopes	Rock, Plate, Open, Thicket, Plate/Chemo
ANOSIM output:	
Global R statistic	0.534
Significance level of R statistic	0.1%
Number of permutations	999
Number of permutated statistics ≥ Global R	0
Result	H_2 rejected; significant differences in megafaunal assemblages were detected among the contrasted biotopes.

Table 3.5B. Pairwise tests from results of ANOSIM test of Null Hypothesis H_2 (biotope contrast test). Asterisk and bold font denotes a statistically highly significant difference between two test biotopes, as indicated by a Pairwise R Statistic approaching 1.0 (p<0.1%).

Groups (Biotopes)	Pairwise R Statistic	Significance Level %	Possible Permutations	Actual Permutations	Number ≥ Observed
Rock, Plate	0.283	0.1	Very large	999	0
Rock, Open	0.123	4.4	Very large	999	43
Rock, Thicket	**0.784**	0.1	Very large	999	0
Rock, Plate/Chemo	0.440	0.1	Very large	999	0
Plate, Open	0.076	14.6	Very large	999	145
Plate, Thicket	**0.704**	0.1	Very large	999	0
Plate, Plate/Chemo	0.359	0.1	Very large	999	0
Open, Thicket	**0.796**	0.1	Very large	999	0
Open, Plate/Chemo	0.285	0.1	Very large	999	0
Thicket, Plate/Chemo	**0.709**	0.1	Very large	999	0

Table 3.5C. Triangle table of ANOSIM Pairwise 'R' statistic values from test of Null Hypothesis H_2 (biotope contrast test). Bold denotes a highly statistically significant pairwise contrast, as indicated by a Pairwise R Statistic approaching 1.0 ($p<0.1\%$).

Biotope Category	**Rock**	**Plate**	**Open**	**Thicket**	**Plate/Chemo**
Rock	xxxxx				
Plate	0.282624	xxxxx			
Open	0.123228	0.076036	xxxxx		
Thicket	**0.783810**	**0.703827**	**0.796260**	xxxxx	
Plate/Chemo	0.439879	0.358646	0.284524	**0.709220**	xxxxx

Table 3.6. Dominance rank (by numerical occurrence) of key taxa characteristic of biotope categories.

Biotope Category	**Rock**	**Plate**	**Plate/Chemo**	**Thicket**	**Open**
Total Area Sampled (cm sq)	2,542,031	2,529,080	67,500	1,042,851	373,447
Taxon & (CODE)					
Brown *Lophelia* coral (BLC)	10			2	
White *Lophelia* coral (WLC)	5	9		1	6
Bamboo coral (BAM)	2	2			
Pink black coral (POBC)		10			6
Red black coral (RBC)	8	3		5	
Unknown black coral (UBC)					
White black coral (WBC)	4	4			
Fan gorgonian (FG)					
Bamboo coral anemone (BA)					
Black cerianthid (BCYR)					2
Dandelion anemone (DA)					
Pink cerianthid (PCYR)					6
Unknown anemones (UA)		7			5
Venus fly trap (VFT)	6	6			
White anemone (WA)	1	1			4
Demo sponge (DS)		10			
Finger sponge (FS)					
Glass sponge (GS)	7	8			
Vase sponge (VS)					
Cleaner shrimp (CS)					
Squat lobster (SL)				4	
Unknown crabs and lobsters (UCL)				10	
Echinus (EURC)			5	9	

Table 3.6 (continued)

Biotope Category	**Rock**	**Plate**	**Plate/Chemo**	**Thicket**	**Open**
Total Area Sampled (cm sq)	2,542,031	2,529,080	67,500	1,042,851	373,447
Taxon & (CODE)					
Pencil urchin (PENU)					
Luidia seastar (LST)					
Pillow seastar (PST)					
Brisingid (BR)				8	
Crinoid (CRI)				5	
Unknown crinoids and brittlestars (UCR)					
Serpulid worms (SW)					
Tube worms (TW)			2		
Unknown (UNK)	3	5	3	7	1
Bacterial mat (BAC)			4		3
Blue sponge (BLU)					
Dead clam (CLAM)			1		
Fan hydroid (FHYD)					
Hydroids (HYD)	9				
Unknown alcyonarian (UAL)				3	
Unknown octopus (UOC)					

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Figure 3.25. A) 2-D, nonmetric multidimensional scaling (MDS) ordination plot using Primer 6 from SPECIES OCCURRENCE DATA, with SIMPROF species clusters (Figure 3.24) overlaid at slack level = 30.

Figure 3.26. A) 2-D Shepard plot to accompany Figure 3.25, stress statistic = 0.03; B) 3-D Shepard plot for same data matrix (3-D MDS plot not shown), stress statistic = 0.01.

Figure 3.27. Comparative proportion of unpopulated substrate (percentage of 'No Invertebrate' scores in CPCe raw data matrix) among the five empirical biotope categories.

NOTE: The study site designation "906/907" in some figures corresponds with sampling actually conducted in VK 906/862.

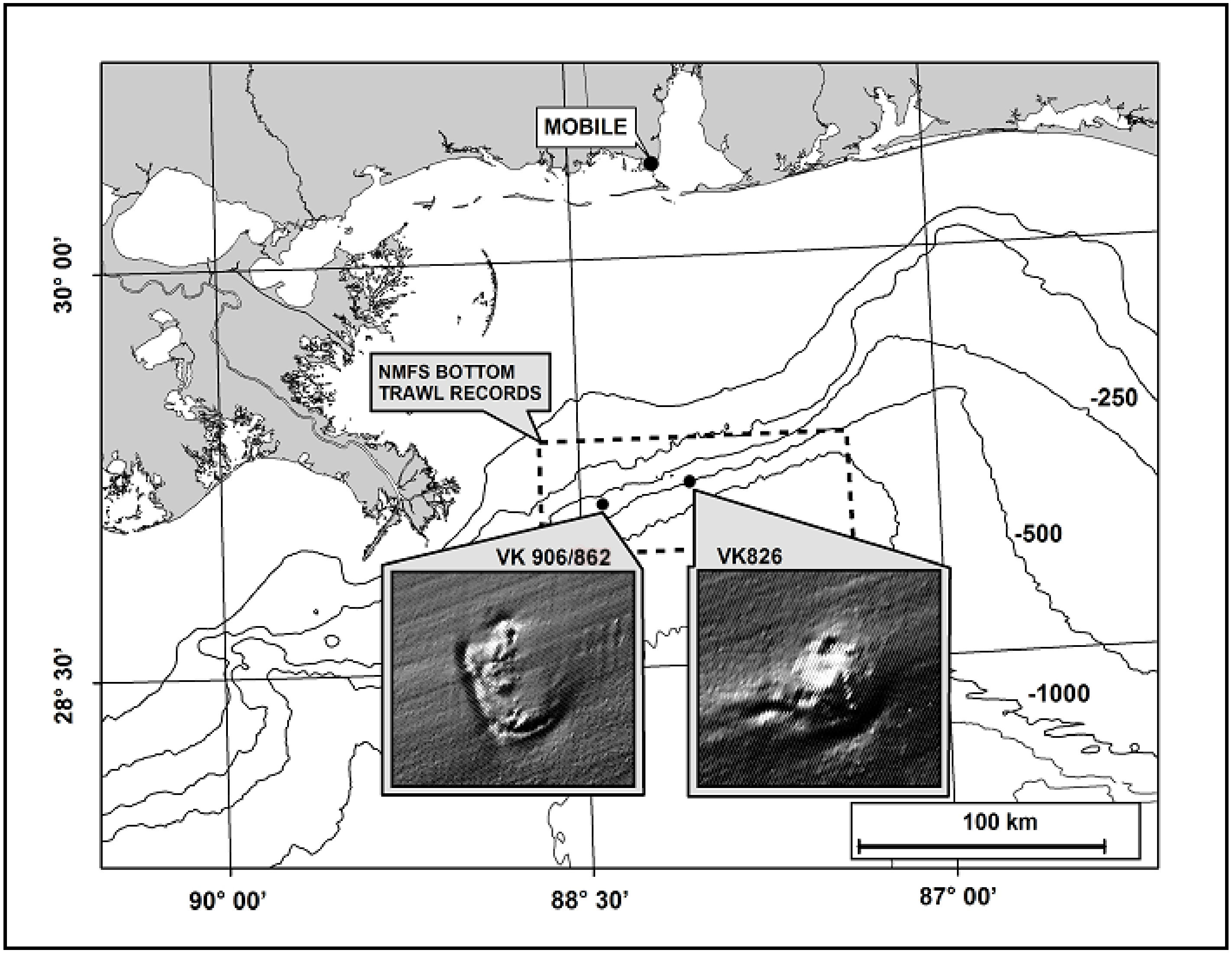


Figure 3.1. Location of two Viosca Knoll 826 submersible *Lophelia* reef study sites in the northern Gulf of Mexico, and location of comparative NOAA bottom trawl records (open rectangle). Depth contours are in meters.

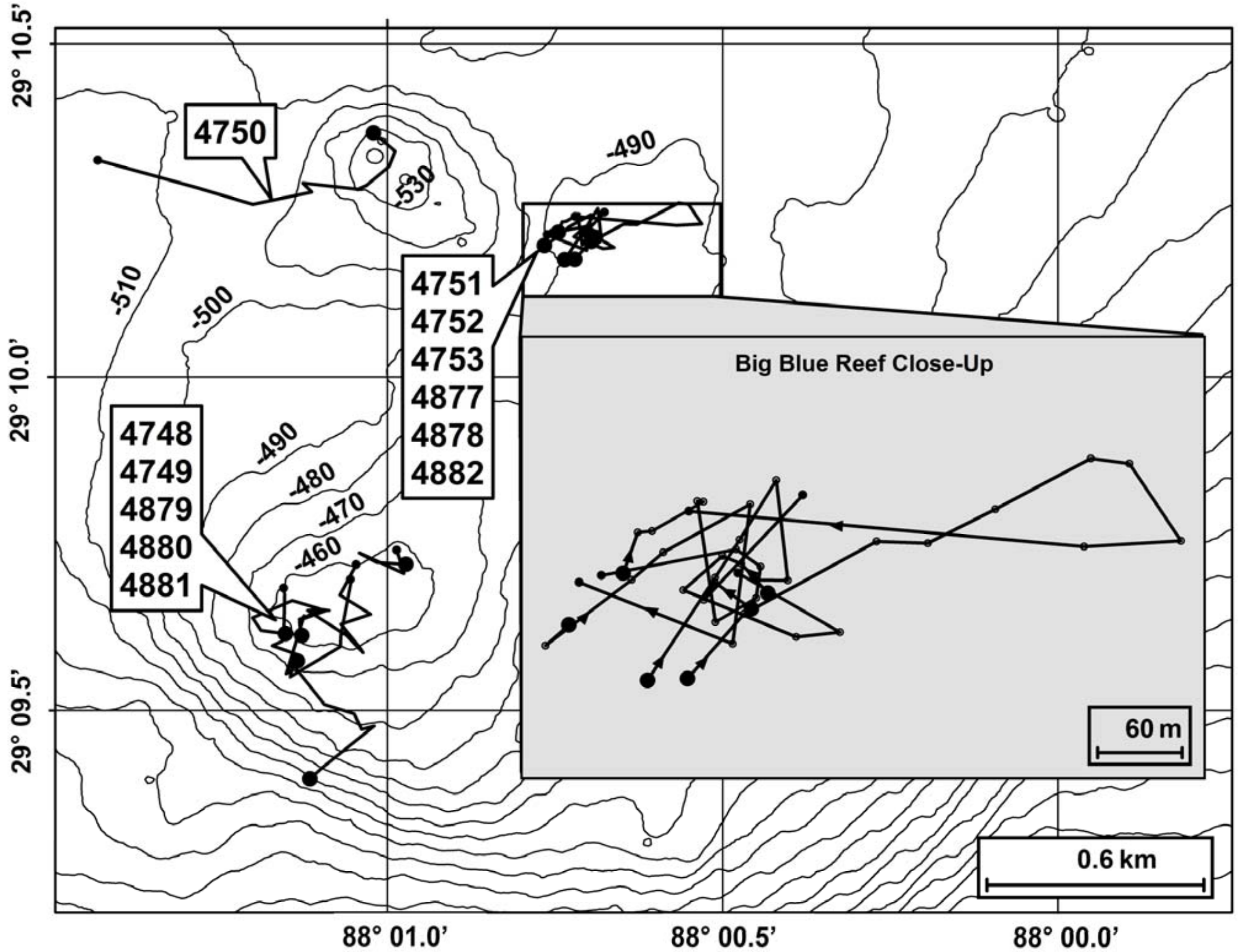


Figure 3.2. Bathymetric chart (10-m isobaths) of Viosca Knoll 826 *Lophelia* reef study site, showing tracks of 12 USGS submersible dives undertaken in 2004-2005: A = "Big Blue Reef" on northeastern sector of overall feature; B = 100 m deep depression; C = main knoll on southwestern sector of feature (with *Lophelia*). Inset shows detail of eight dives conducted on "Big Blue Reef". Key: large dots = beginning of bottom time; small dots = Trackpoint II navigation fixes during the course of a dive, including final fix at end of bottom time; arrowheads indicate direction of submersible movement.

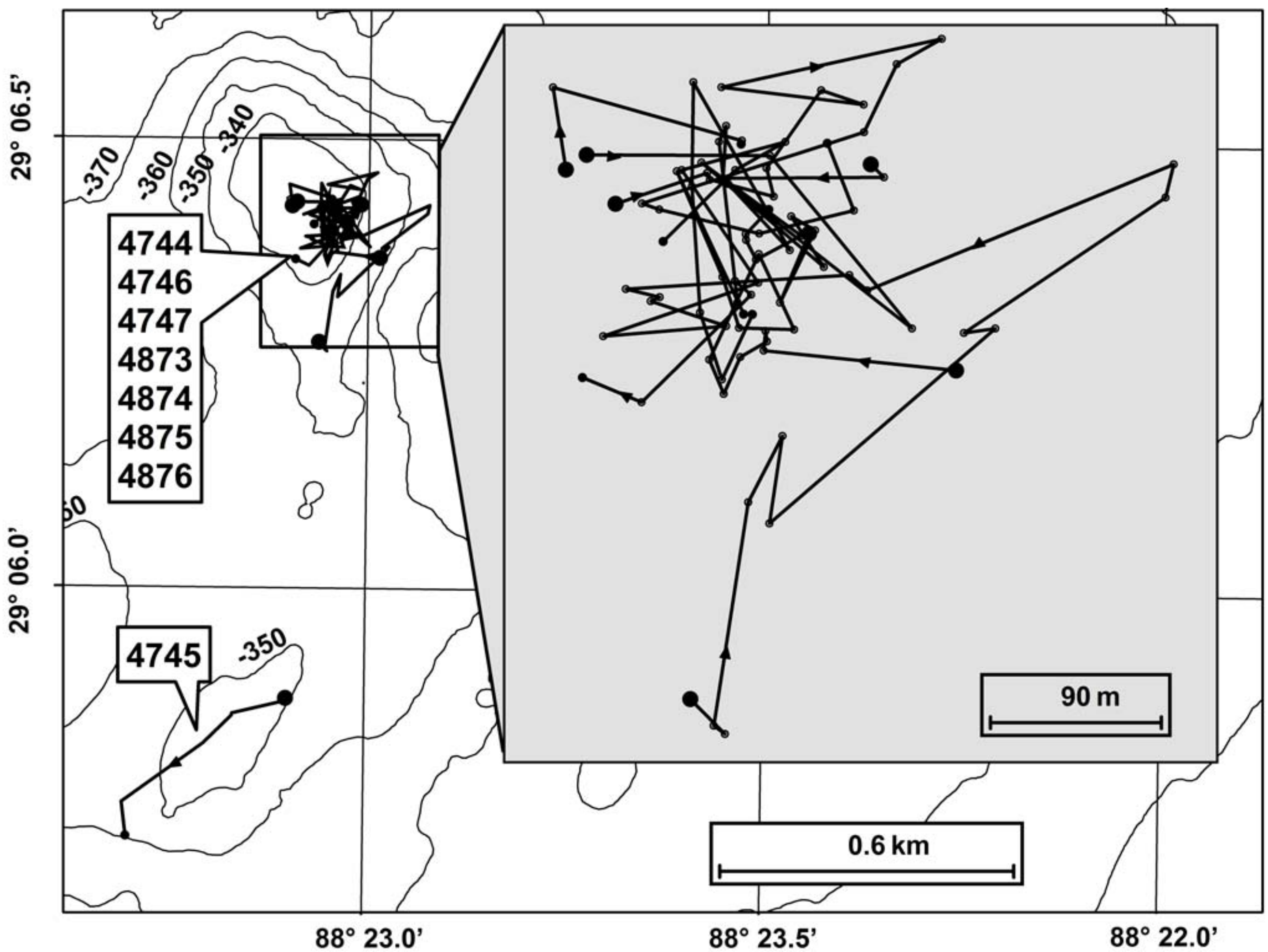


Figure 3.3. Bathymetric chart (10-m isobaths) of Viosca Knoll 906/862 *Lophelia* reef study site, showing tracks of eight USGS submersible dives undertaken in 2004-2005: A = area of live-bottom development, including *Lophelia* coral; B = area visited on one exploratory dive. Key: large dots = beginning of bottom time; small dots = Trackpoint II navigation fixes during the course of a dive, including final fix at end of bottom time; arrowheads indicate direction of submersible movement.

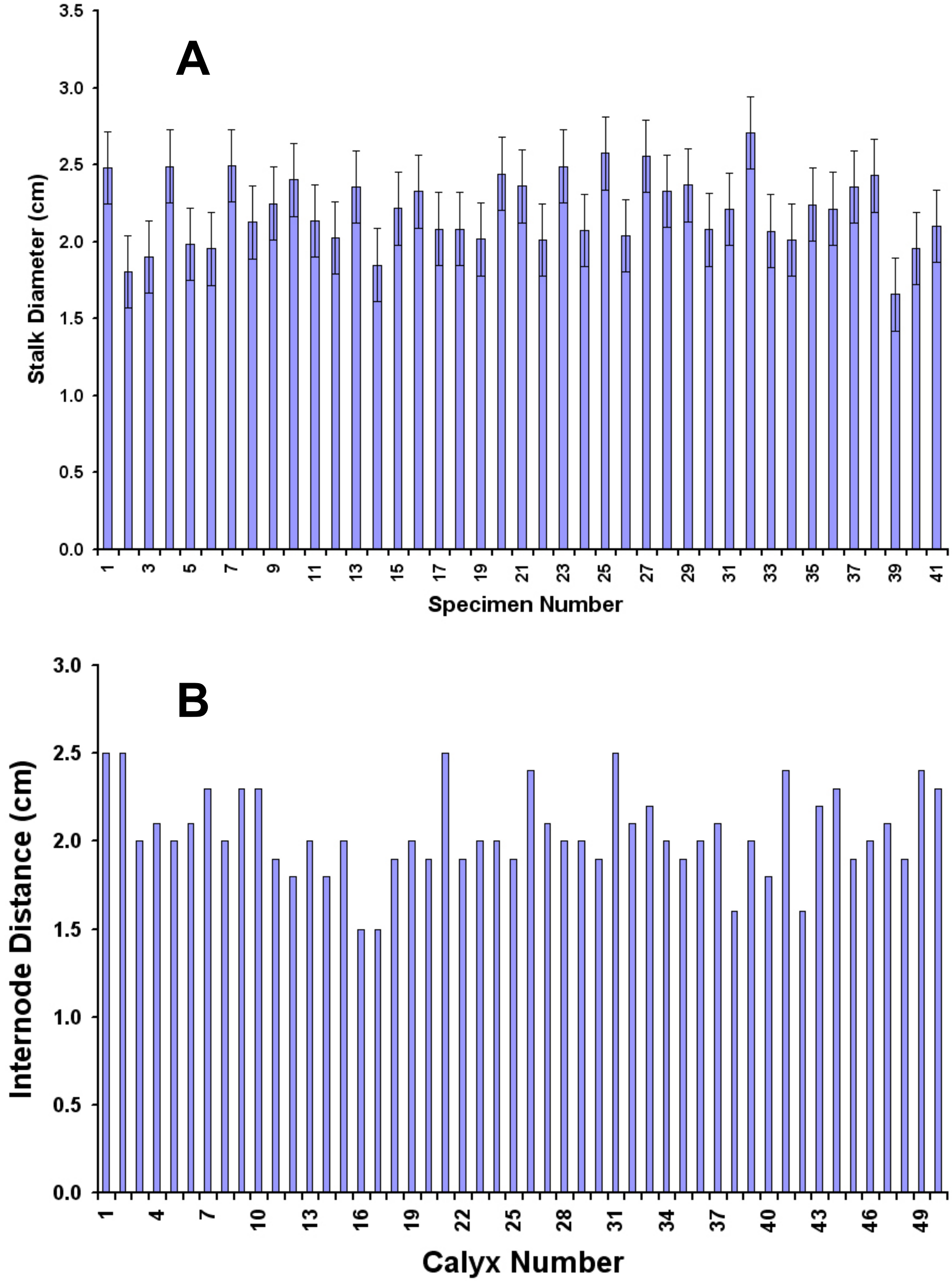


Figure 3.4. Measurements of common invertebrates used to scale frame grab image field of view for CPCe analyses: A) Orange-lipped white anemone, stalk base diameter: N = 41 individuals, mean diameter = 2.202 cm ±SD (0.236 cm), median = 2.212 cm. Error bars on individual histobars indicate methodological standard error; B) *Lophelia pertusa* coral, calyx length = distance between adjacent branching nodes: N = 50 measurements, mean = 2.048 cm ±SD (0.247 cm). Methodological error bars omitted.

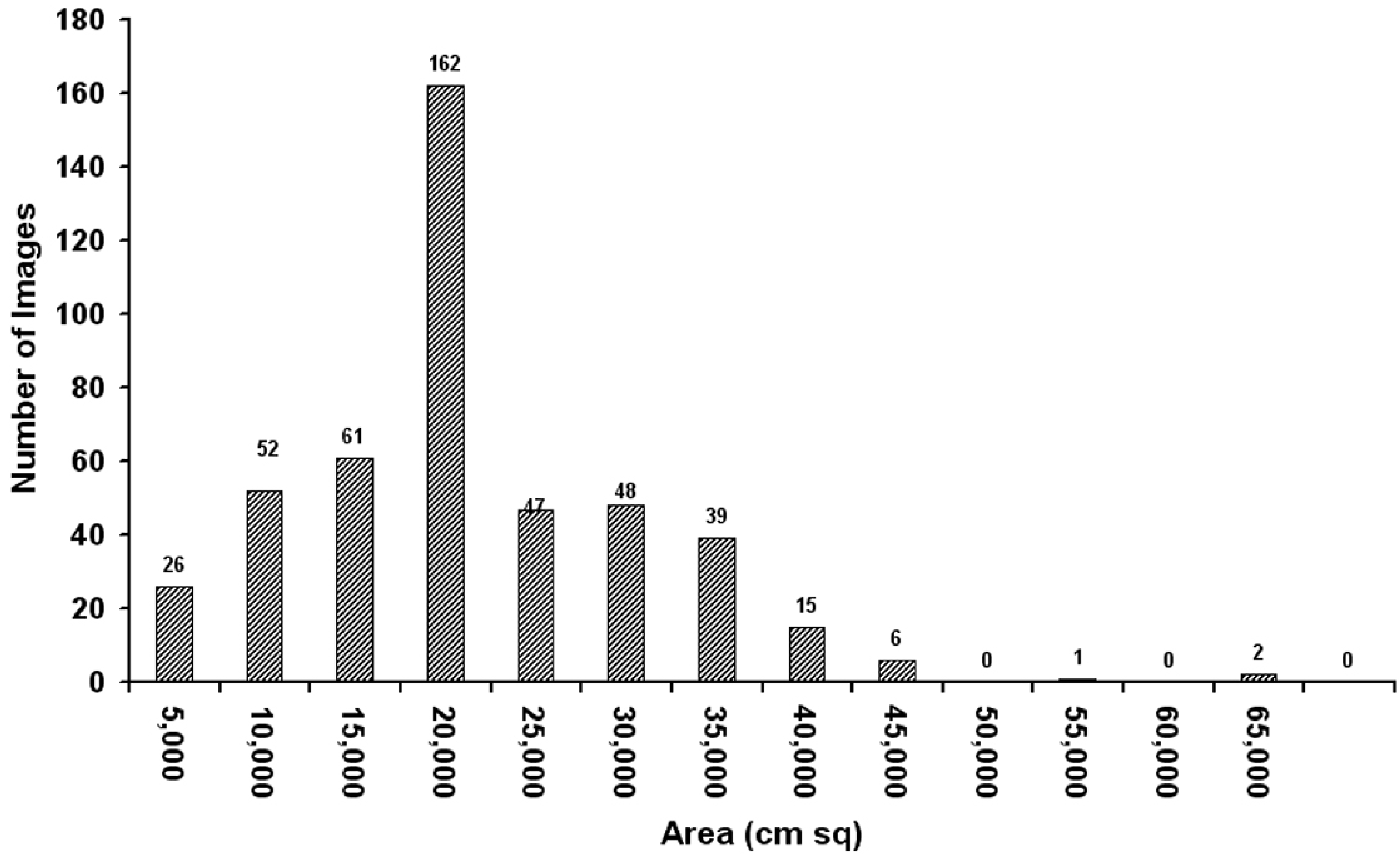


Figure 3.5. Frequency plot (in intervals of 5,000 cm^2) of the area of the field of view in 459 video frame grab images analyzed in this study. Mean area = 19.2 x 10^3 cm^2, ±SD (9.4 x 10^3 cm^2), mode = 20.0 10^3 cm^2.

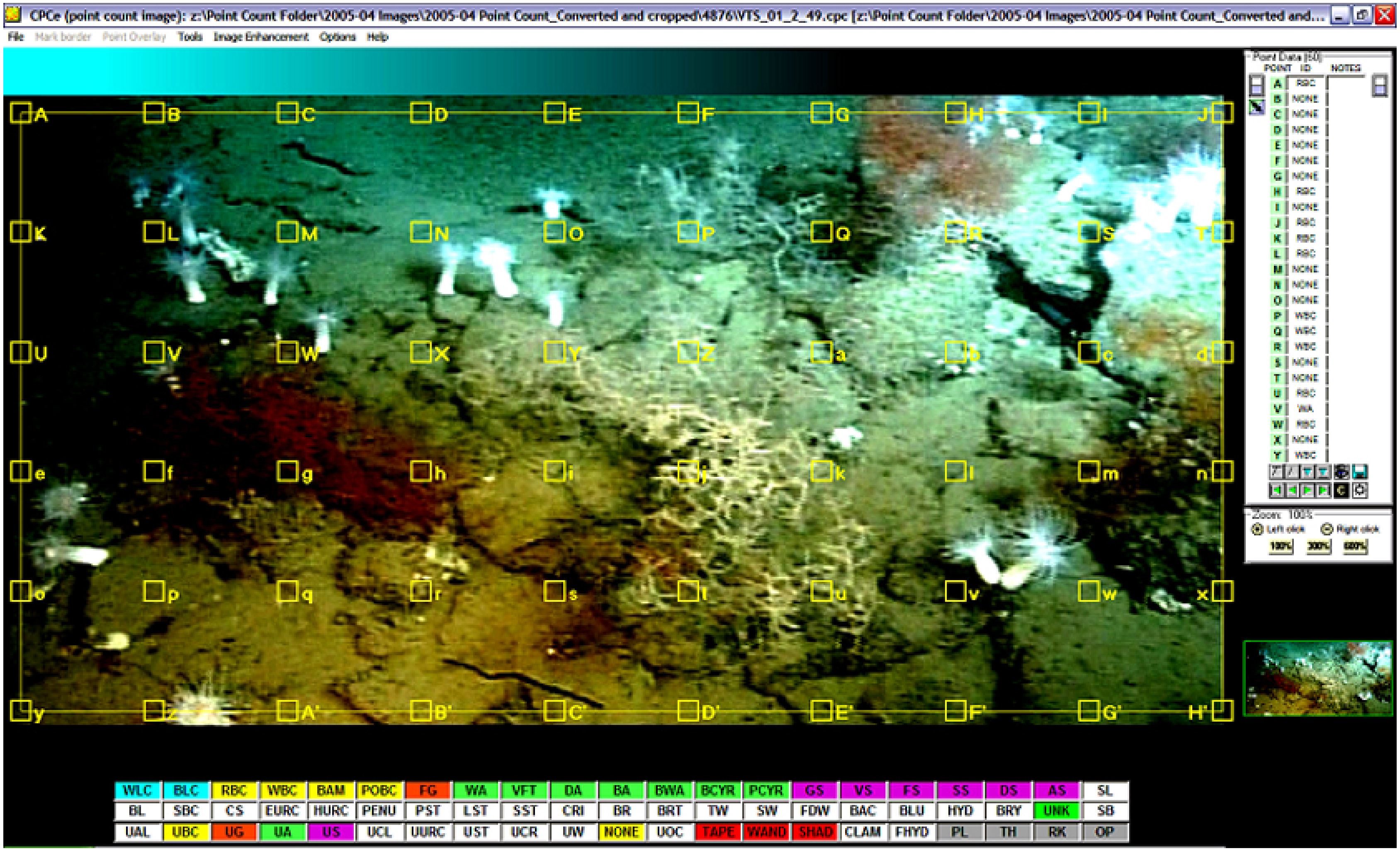


Figure 3.6. Computer screen grab to display a typical Viosca Knoll frame grab in the process of megafaunal invertebrate occurrence scoring via projection of a grid of 60 open boxes (10 columns by 6 rows) using Coral Point Count (CPCe).

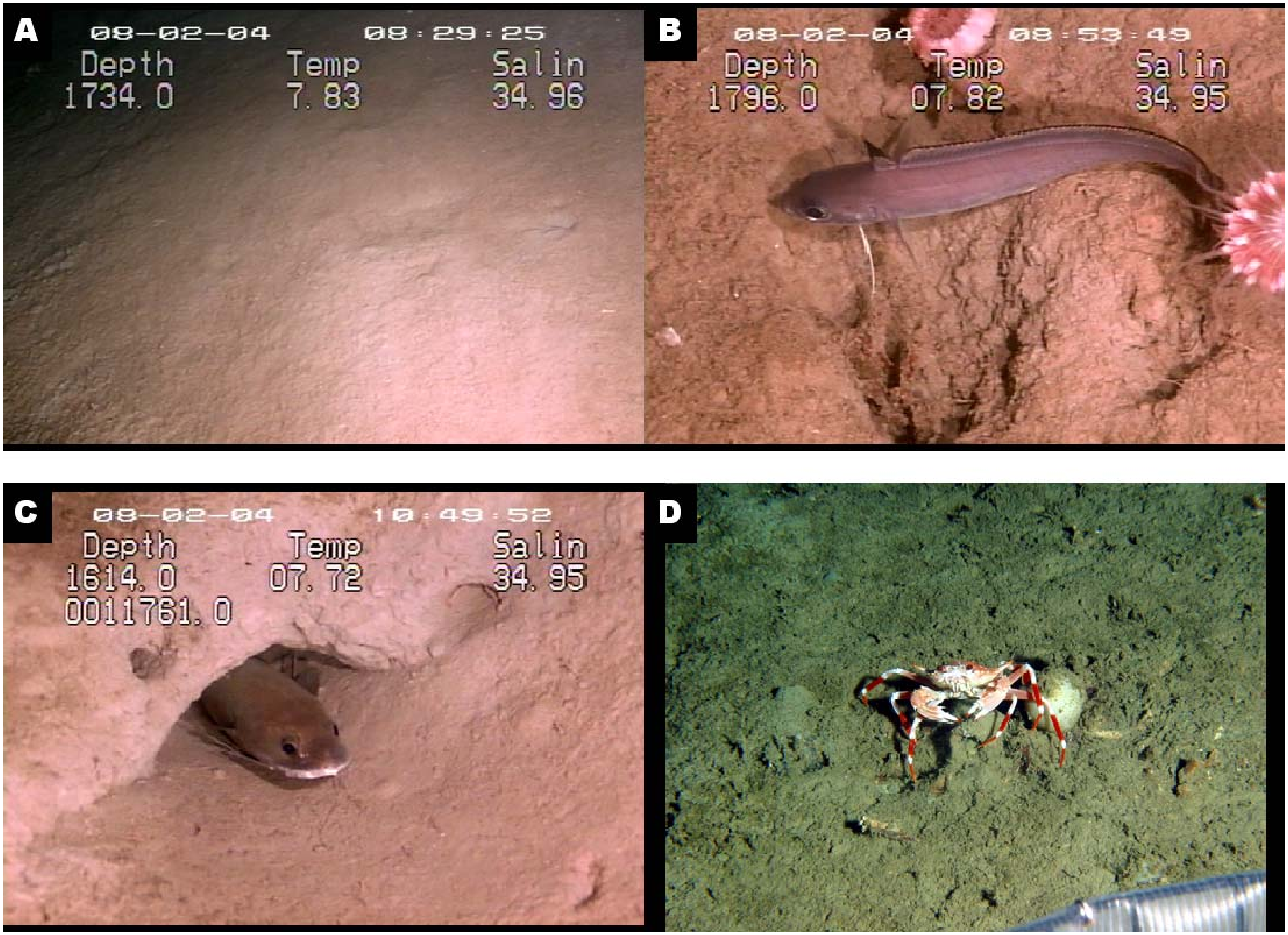


Figure 3.7. Four Viosca Knoll digital images categorized as representing typical 'Open' soft-bottom biotope. (Refer to Key to Master Appendix E for data on individual images.)

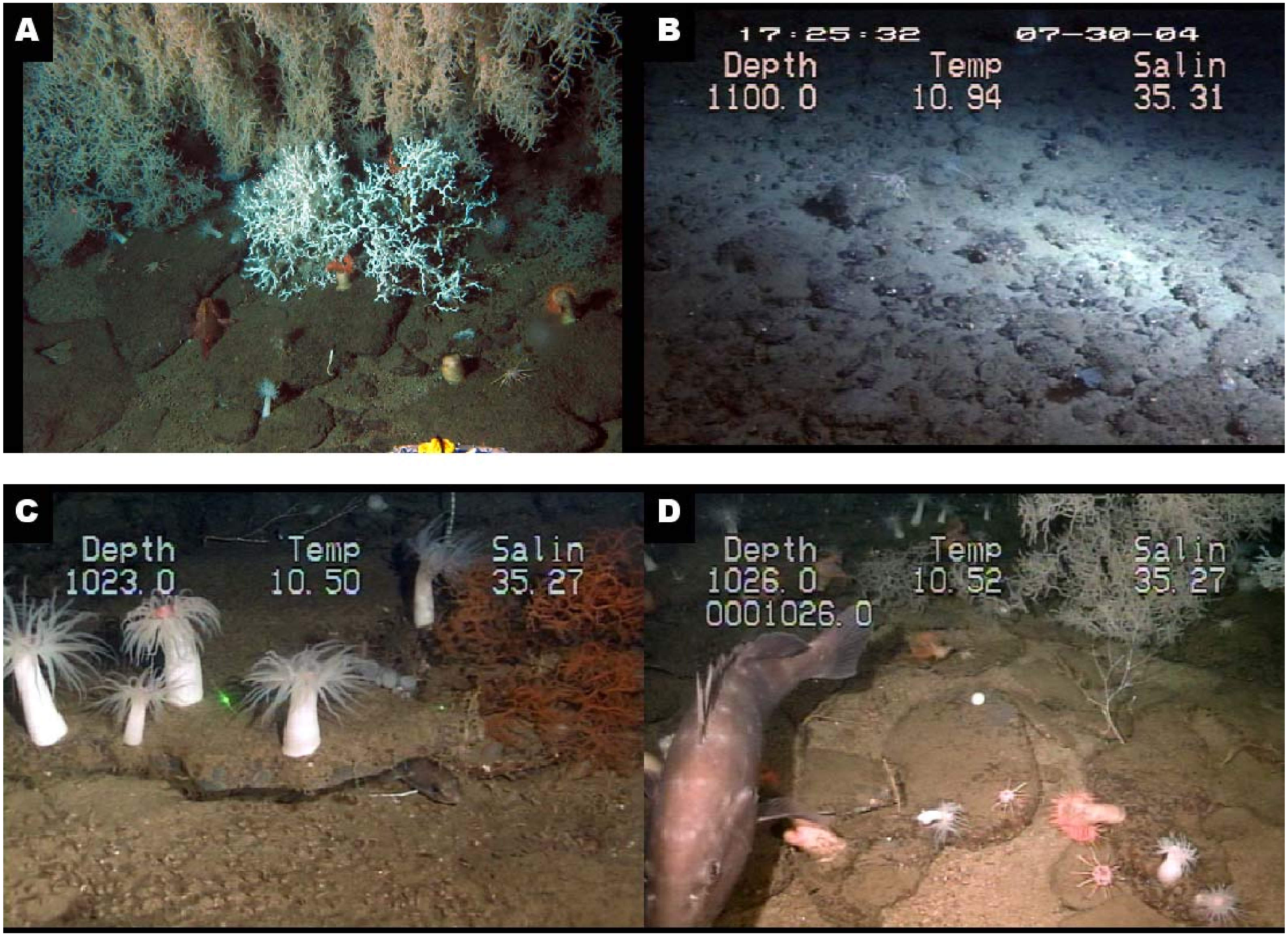


Figure 3.8. Four Viosca Knoll digital images categorized as representing typical ‘Plate’’ hard-bottom biotope. (Refer to Key to Master Appendix E for data on individual images.)

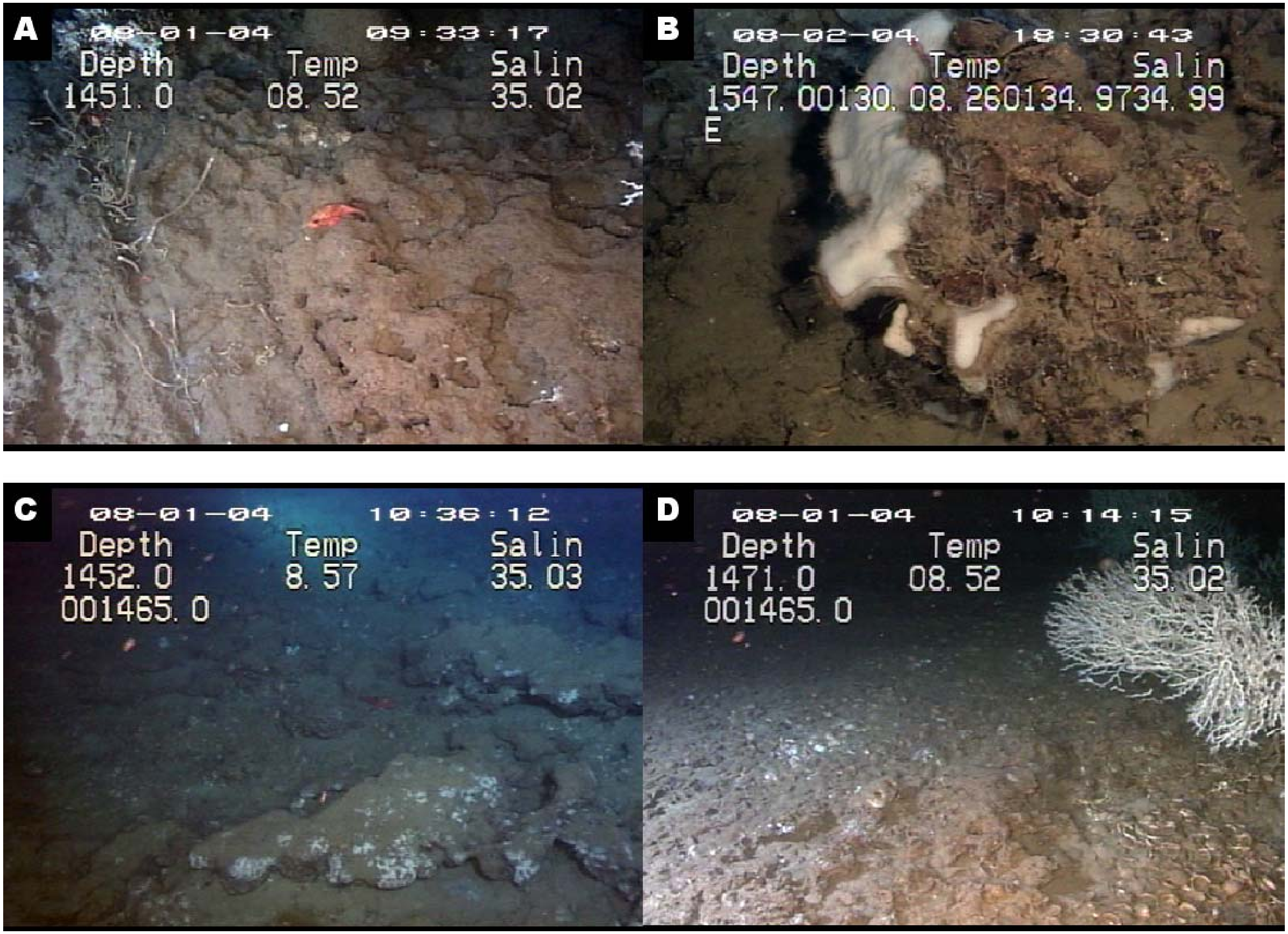


Figure 3.9. Four Viosca Knoll digital images categorized as representing typical ‘Plate/Chemo’ hard-bottom biotope. (Refer to Key to Master Appendix E for data on individual images.)

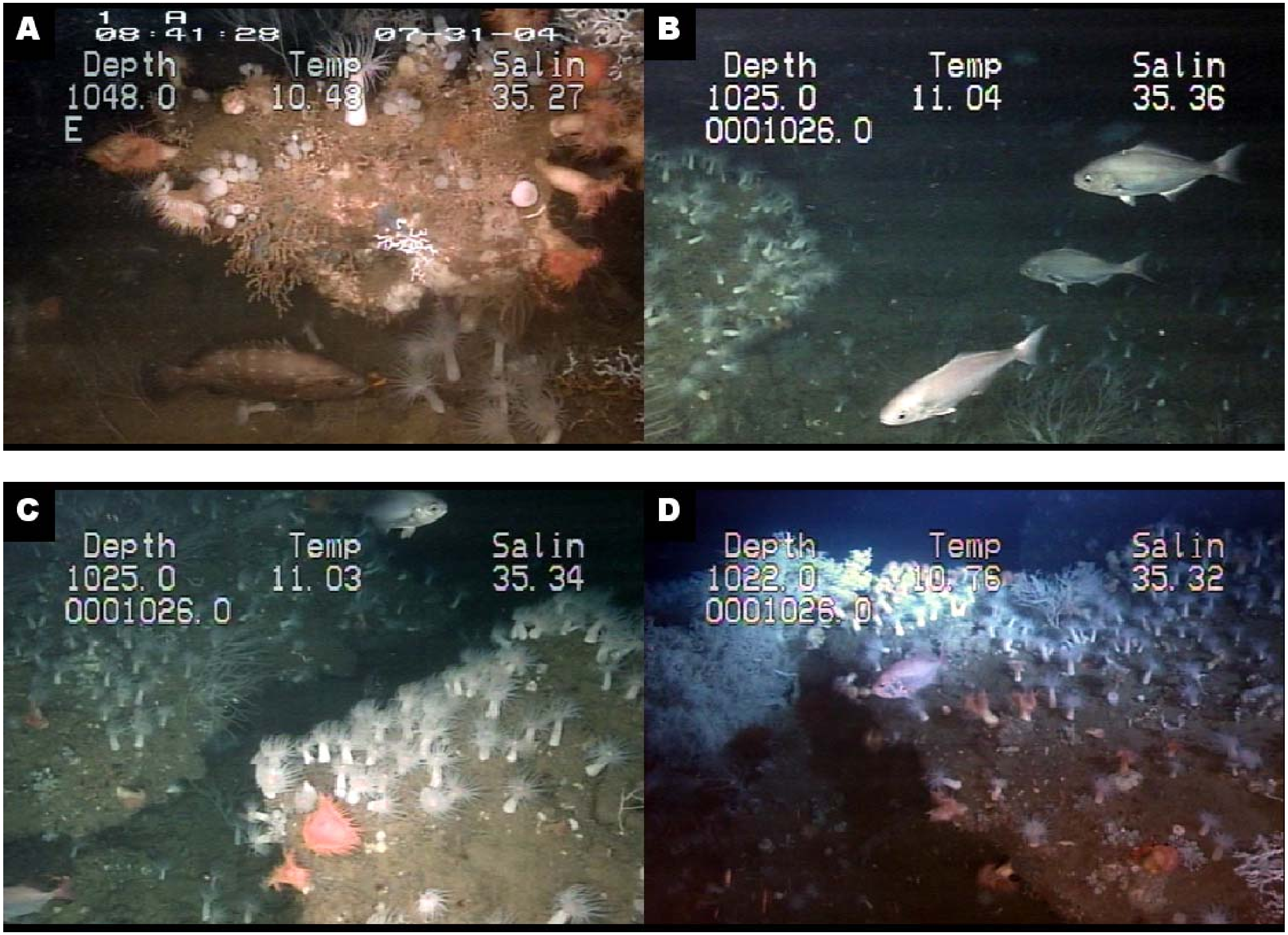


Figure 3.10. Four Viosca Knoll digital images categorized as representing typical 'Rock' hard-substrate biotope. (Refer to Refer to Key to Master Appendix E for data on individual images.)

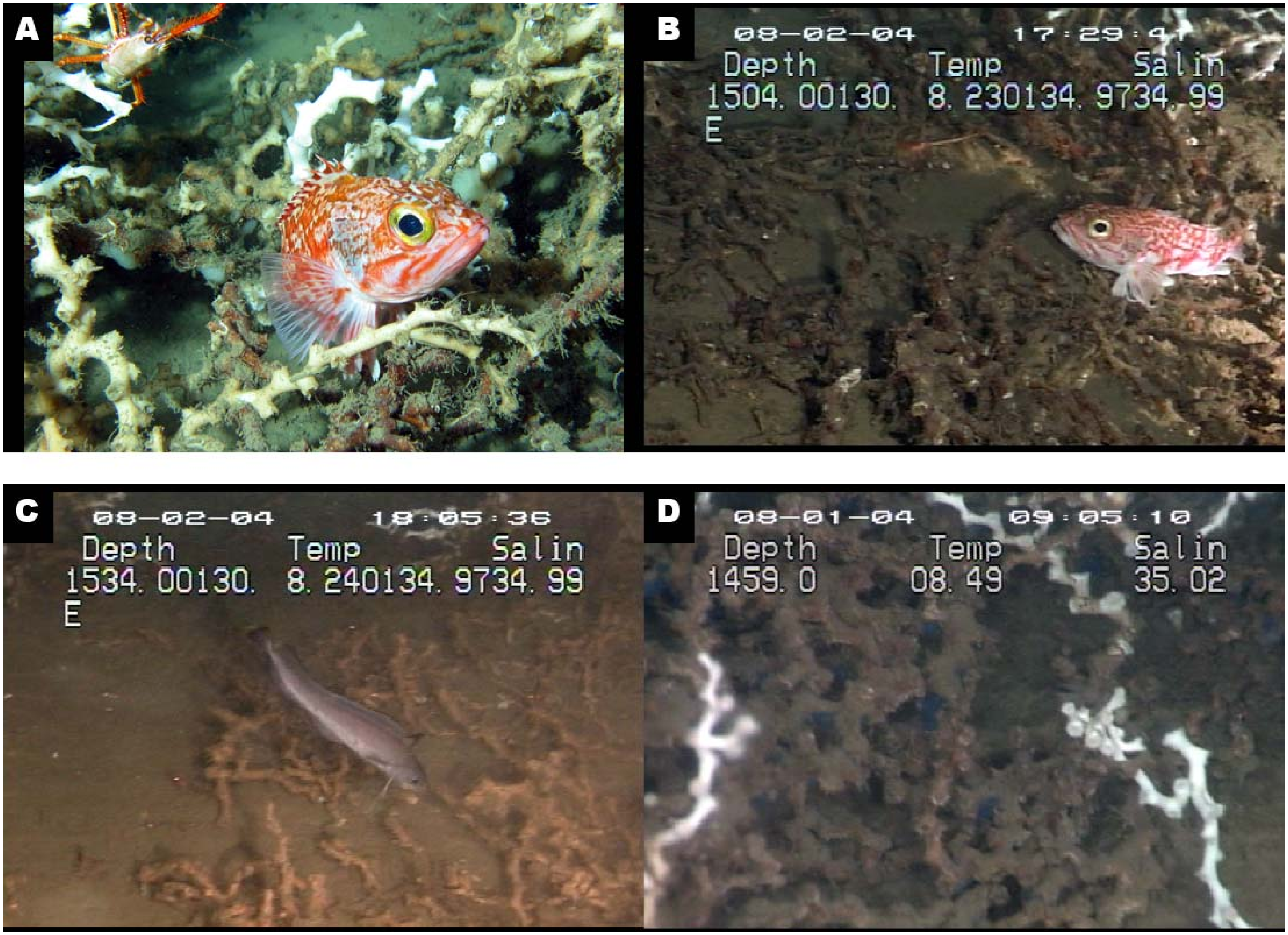


Figure 3.11. Four Viosca Knoll digital images categorized as representing typical *Lophelia* coral 'Rubble' biotope. (Refer to Key to Master Appendix E for data on individual images.)

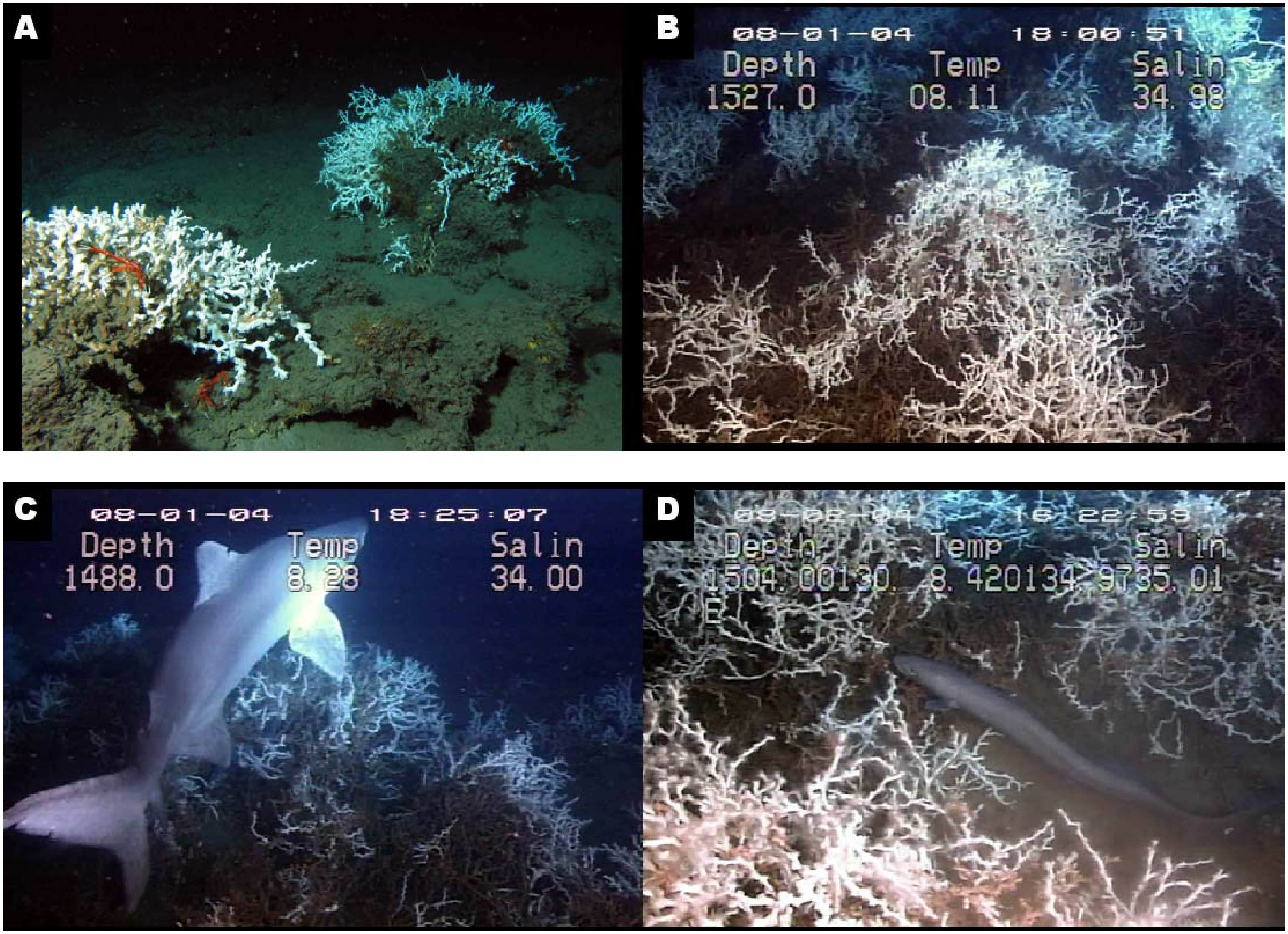


Figure 3.12. Four Viosca Knoll digital images categorized as representing typical 'Thicket' *Lophelia* coral biotope. (Refer to Key to Master Appendix E for data on individual images.)

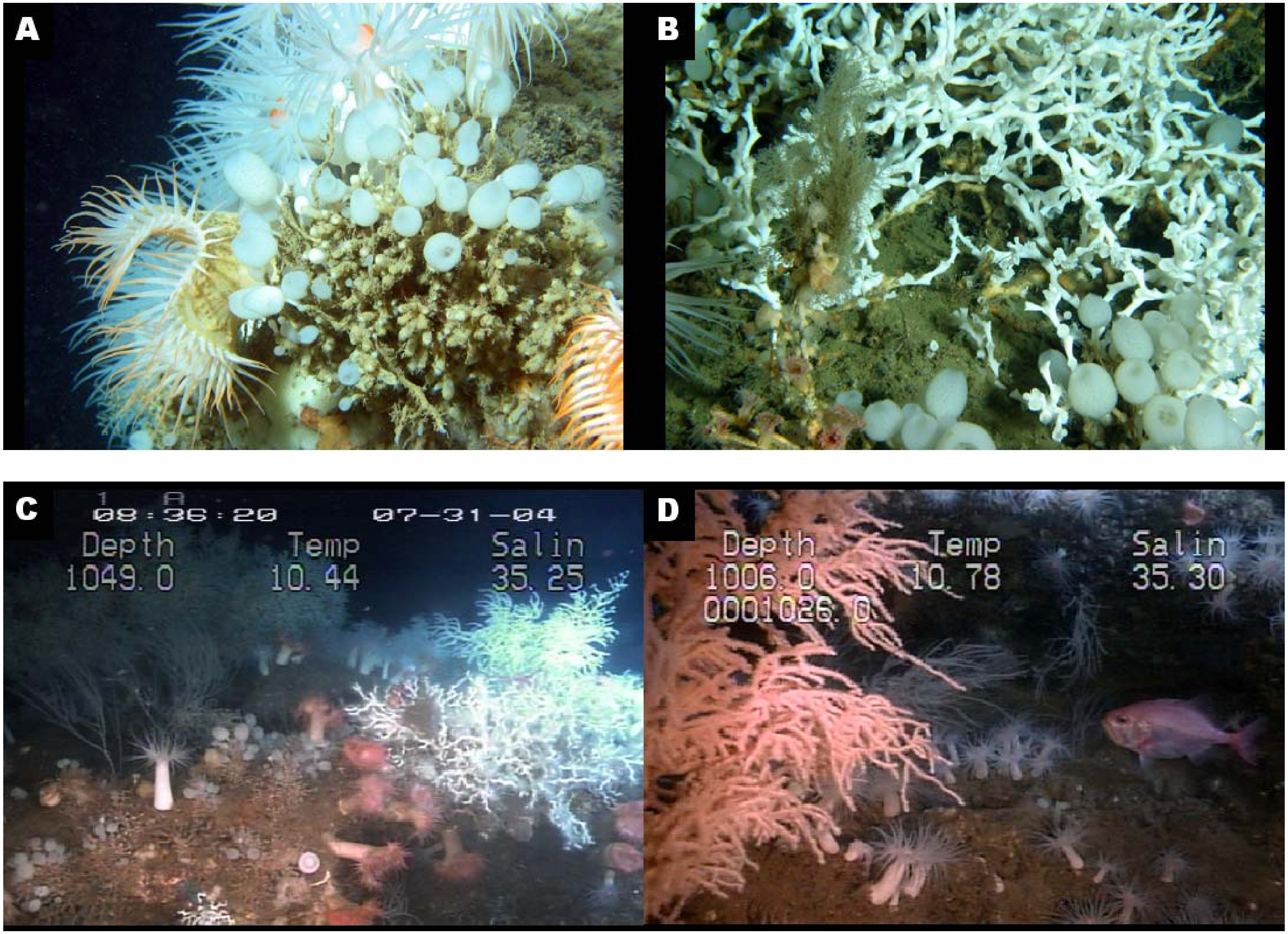


Figure 3.13. Four Viosca Knoll digital images displaying examples of high-diversity megafaunal invertebrate ‘oases’, which form primarily on plate and rock hardpan goethite substrate biotopes.

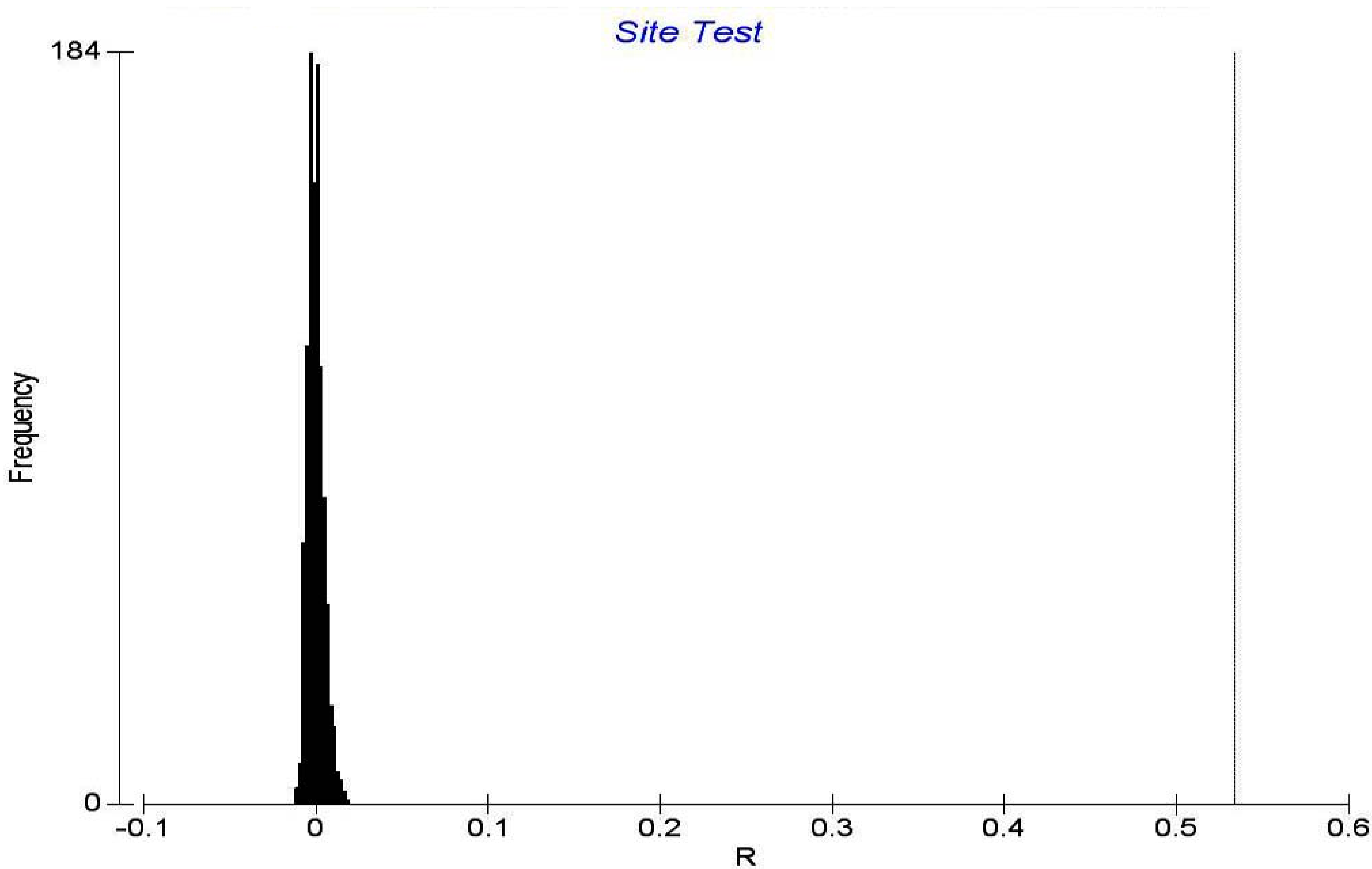


Figure 3.14. ANOSIM results of sampling site differentiation hypothesis test (VK-826 versus VK-906/862) accomplished from Primer 6. N = 459; critical value of Global ‘R’ statistic = 0.534. No values exceed ‘R’; thus H_1 is rejected: VK-906/862 and VK-826 differ significantly at $p < 0.1\%$.

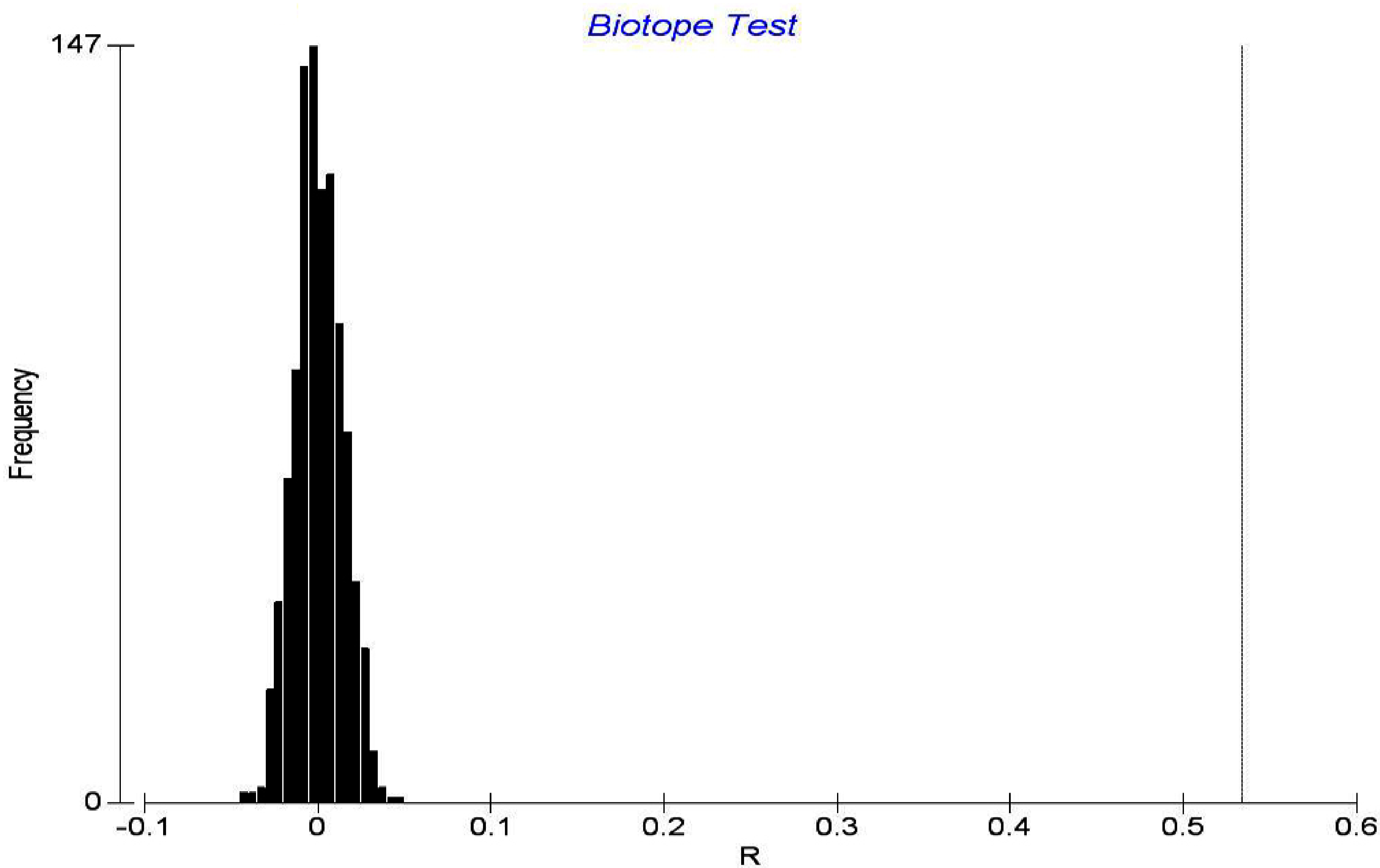


Figure 3.15. ANOSIM results of biotope differentiation hypothesis test (VK-826 versus VK-906/862) accomplished from Primer 6. N = 459; critical value of Global 'R' statistic = 0.534. No values exceed 'R'; thus H_2 is rejected: Significant differences ($p < 0.1\%$) exist among the five Viosca Knoll biotopes.

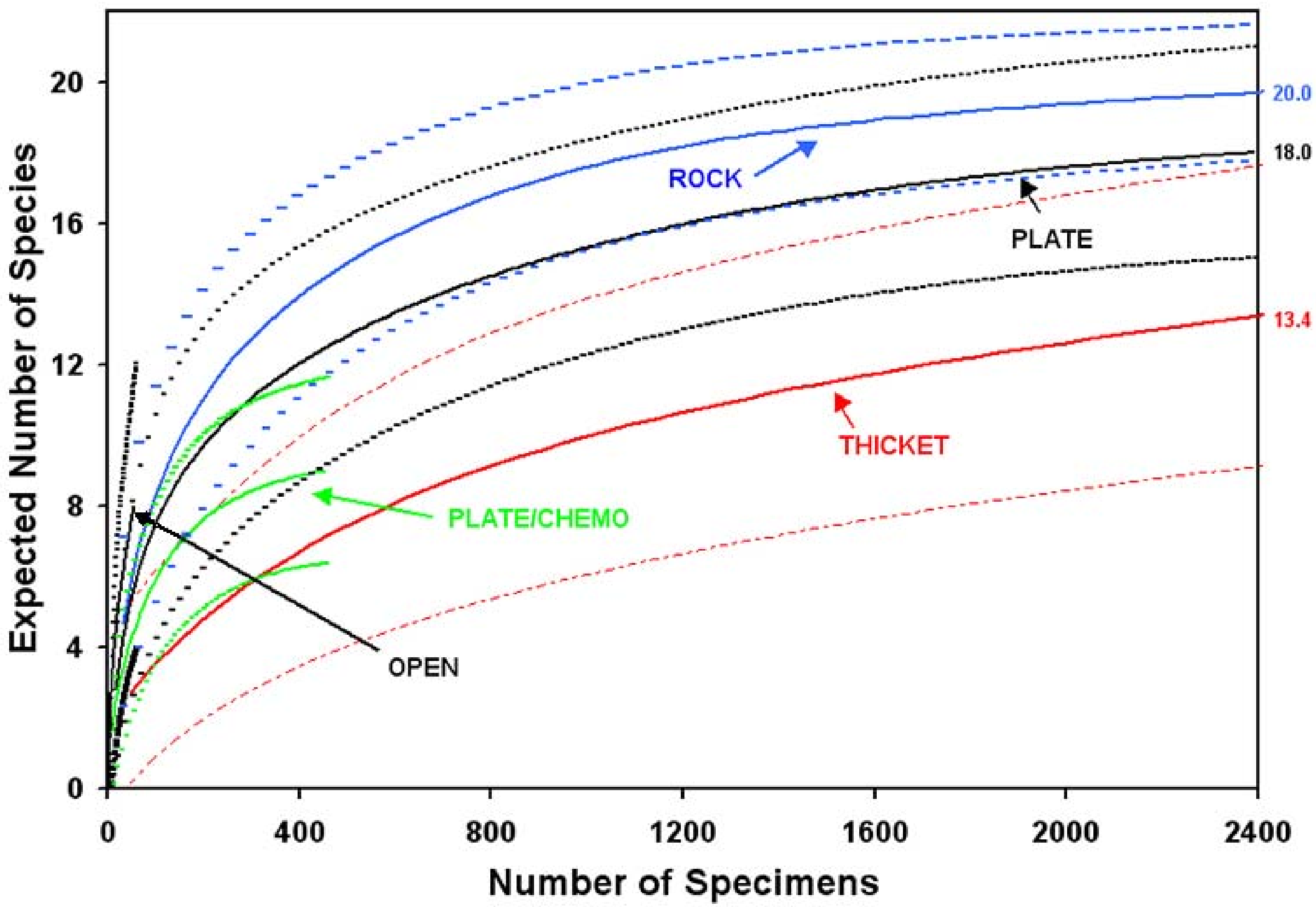


Figure 3.16. Species richness rarefaction curves (solid lines) and 95% CIs (dotted or dashed lines) for Viosca Knoll empirically-defined biotopes. Curves were prepared from EstimateS data (Mao Tau statistic). Curves were truncated at N = 2,400 specimens where necessary. Expected number of species at N = 2,400 specimens is indicated along the right margin. For supporting data refer to Appendix 3-I.

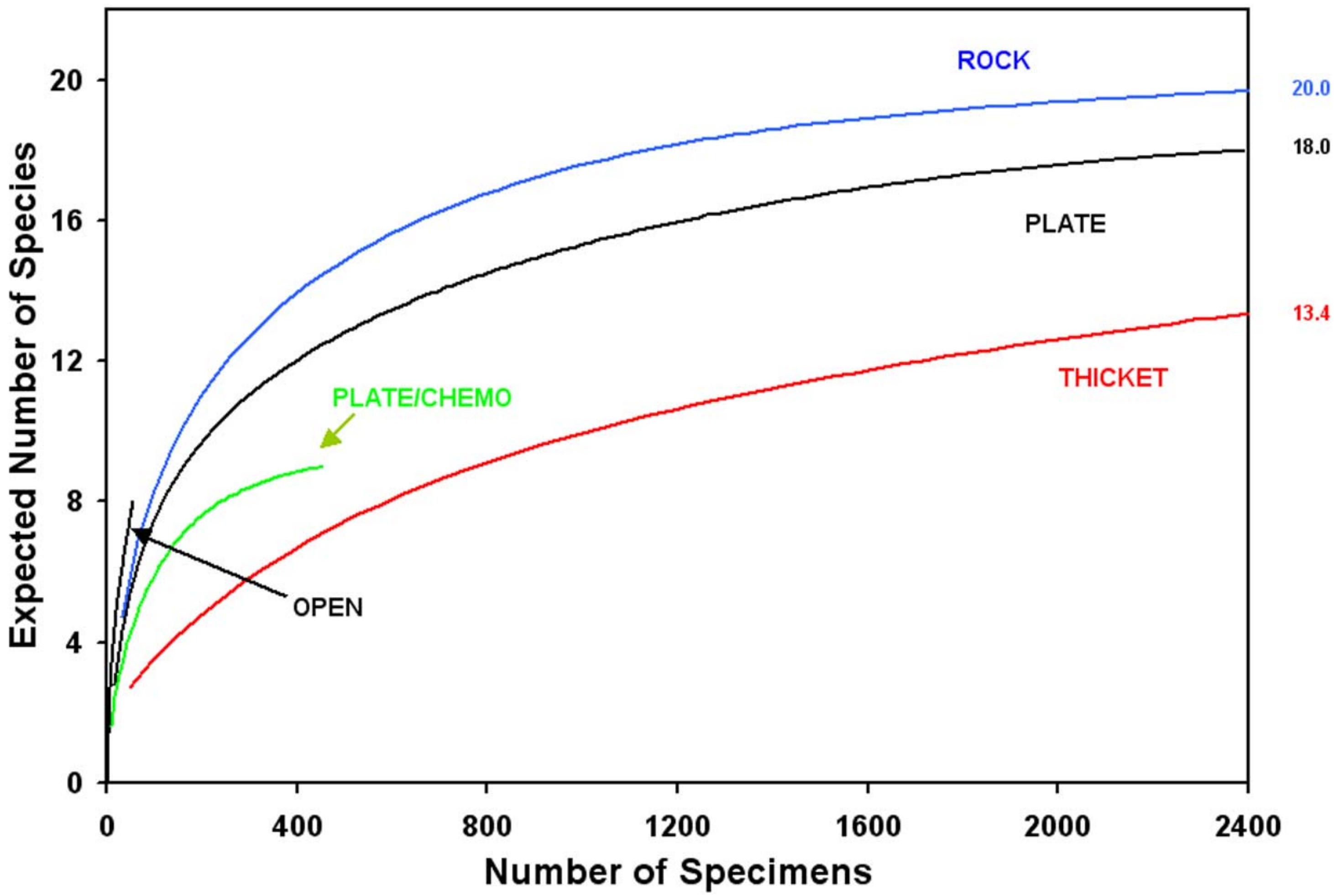


Figure 3.17. Species richness rarefaction curves (solid lines) without 95% CIs for Viosca Knoll empirically-defined biotopes. Curves were prepared from EstimateS data (Mao Tau statistic). Curves were truncated at N = 2,400 specimens where necessary; numbers outside right-hand margin are expected number of species at the N = 2,400 specimens cutoff level. For supporting data refer to Appendix 3-I.

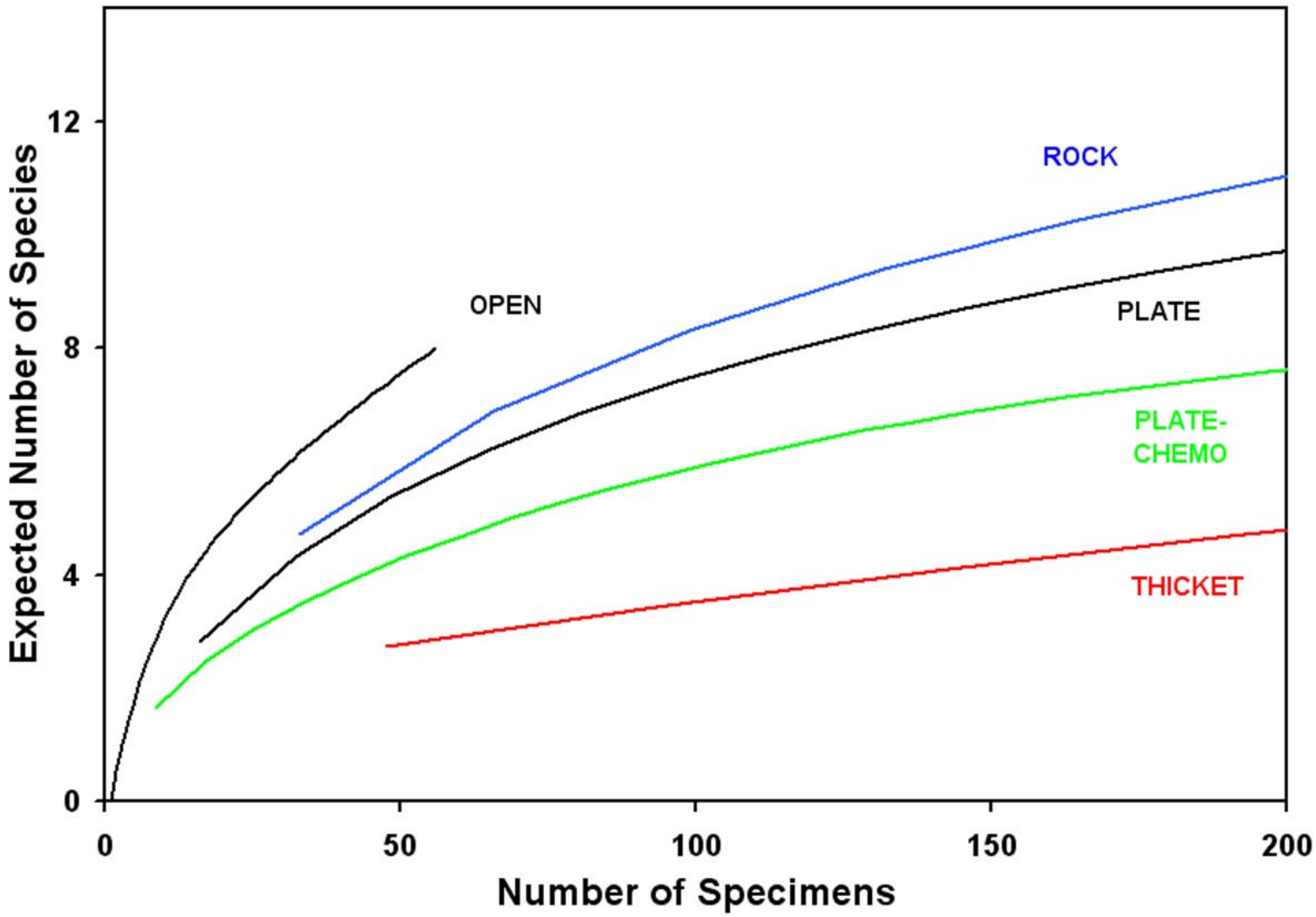


Figure 3.18. Species richness rarefaction curves (solid lines) without 95% CIs for Viosca Knoll empirically-defined biotopes. Curves were prepared from EstimateS data (Mao Tau statistic). Curves were truncated at N=200 specimens maximum. For supporting data refer to Appendix 3-I.

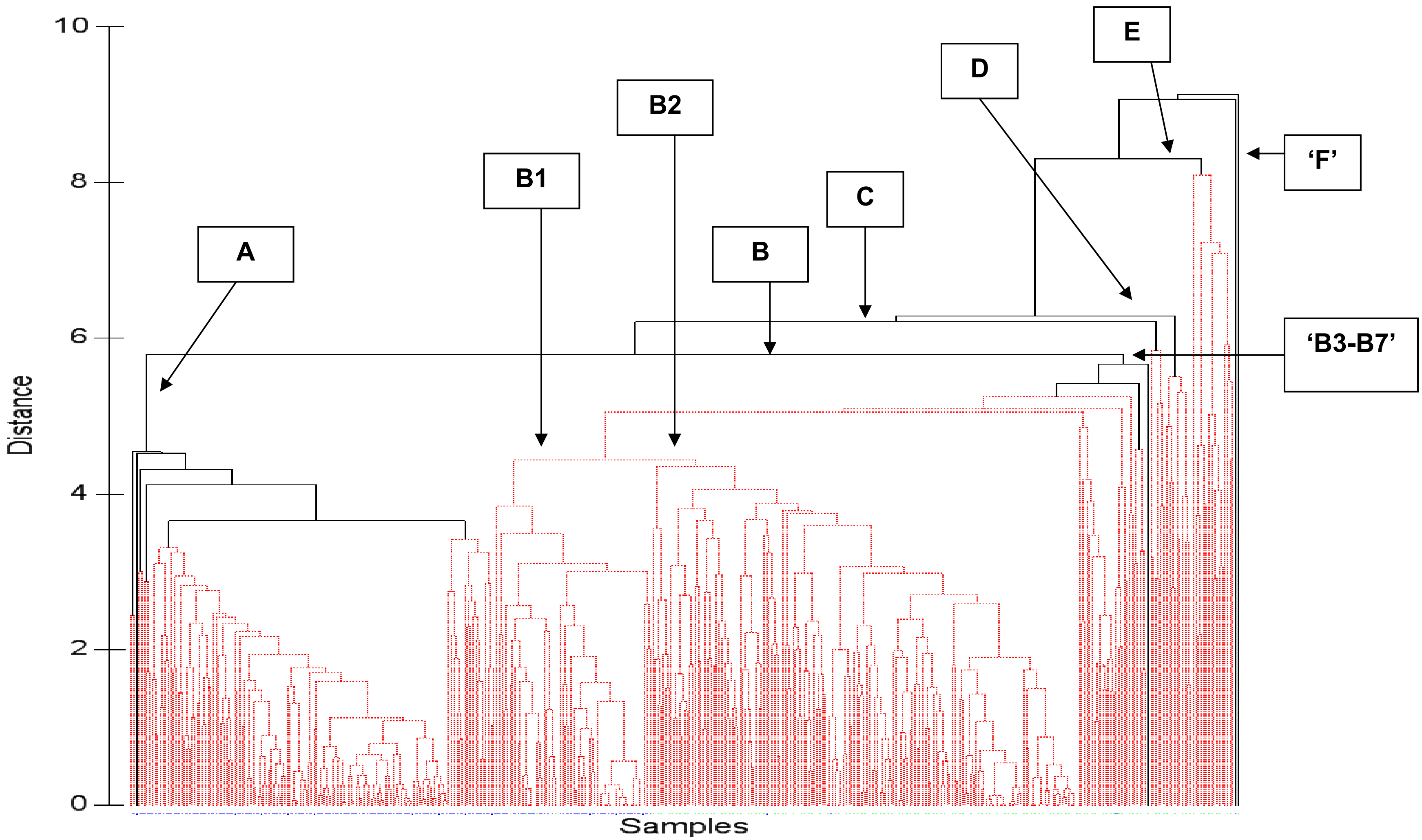


Figure 3.19. Primer 6-produced sampling SITE CLUSTERGRAM from Coral Point Count (CPCe) analysis of 459 digital still frame grabs. Cluster options: Canberra metric, group-average, data standardized on sample (image) total. Sites with 'no invertebrates' scored (N_0=40) were removed. SIMPROF determined statistically distinct species groups are identified in solid black (versus dotted red) lines. Refer to Appendix 3-II for composition of groups and subgroups identified by alphabetical designations.

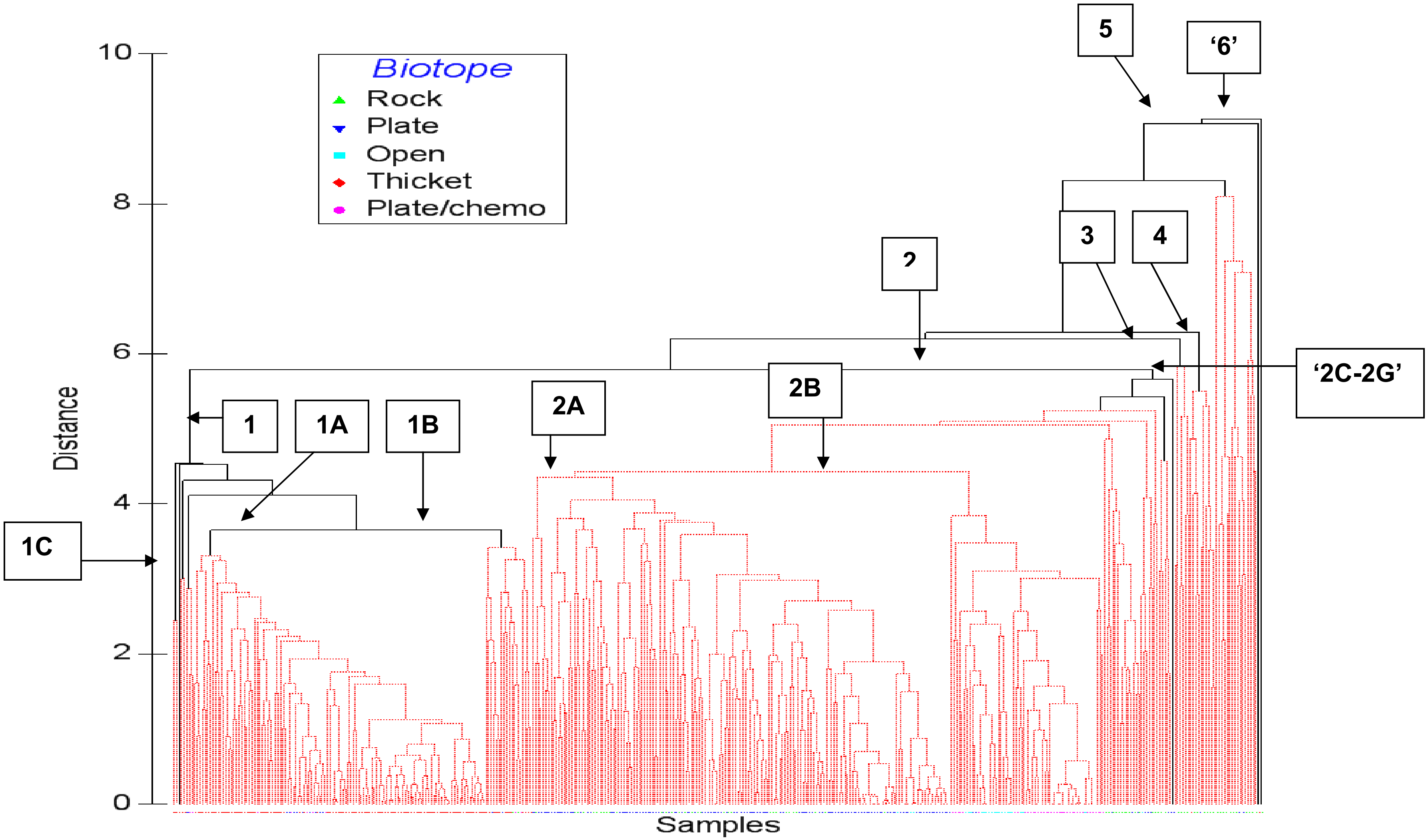


Figure 3.20. Primer 6-produced BIOTOPE CLUSTERGRAM from Coral Point Count (CPCe) analysis of 419 digital still frame grabs. Cluster options: Canberra metric, group-average, data standardized on sample (image) total. Images with 'no invertebrates' scored (N_0=40) were removed. SIMPROF determined statistically distinct species groups are identified in solid black (versus dotted red) lines. Refer to Appendix 3-III for composition of groups and subgroups identified by numerical designations.

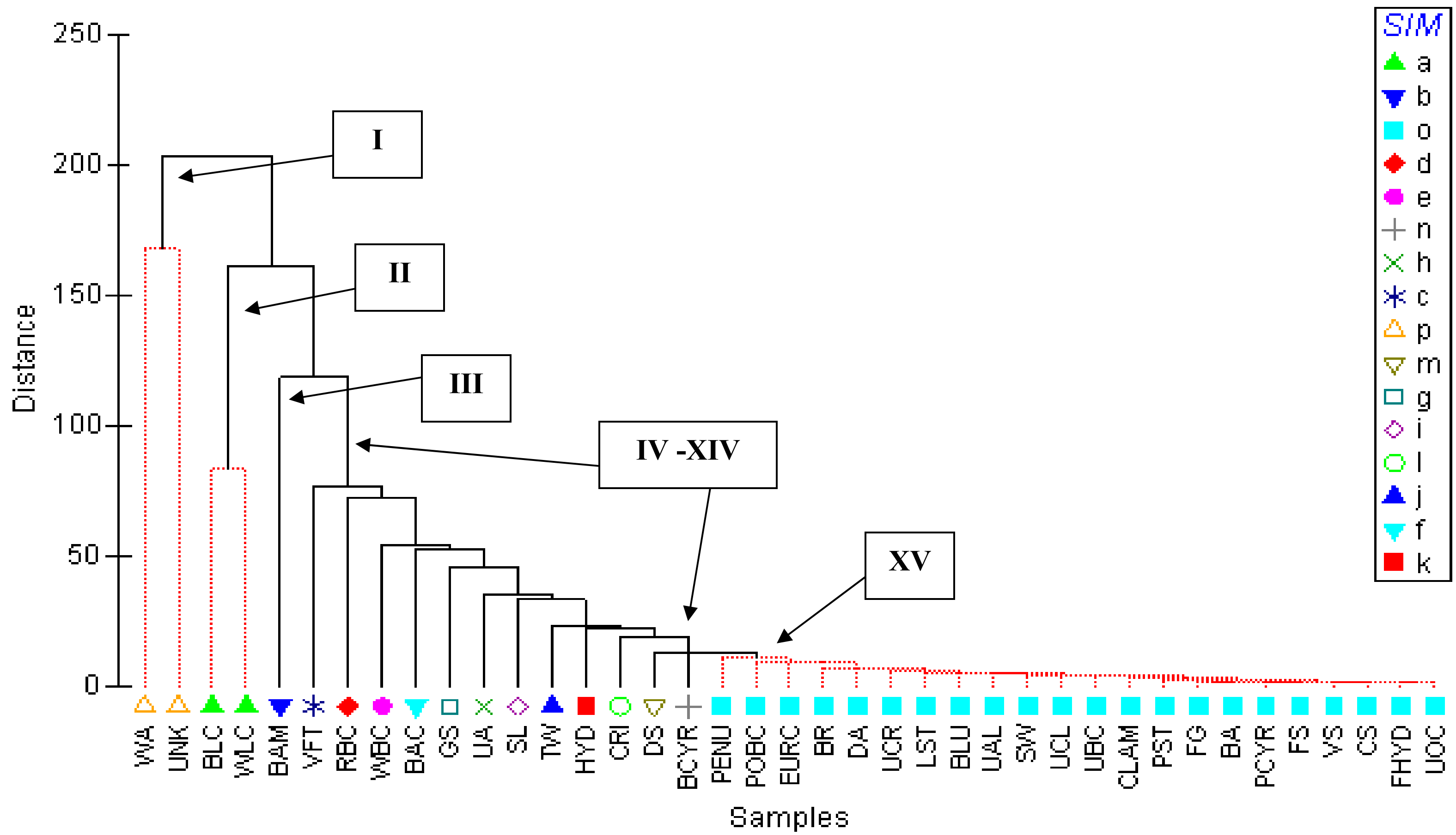


Figure 3.21. Primer 6-produced megafaunal invertebrate SPECIES CLUSTERGRAM from Coral Point Count (CPCe) analysis of 459 digital still frame grabs. Cluster options: Canberra metric, group-average, data standardized on species total. Sites with 'no invertebrates' scored (N_0=40) were removed. Refer to Appendix 3-IV for composition of groups and subgroups identified by Roman numeral designations. SIMPROF-determined statistically-distinct (p = 0.5) species groups are identified in solid black (versus dotted red) lines.

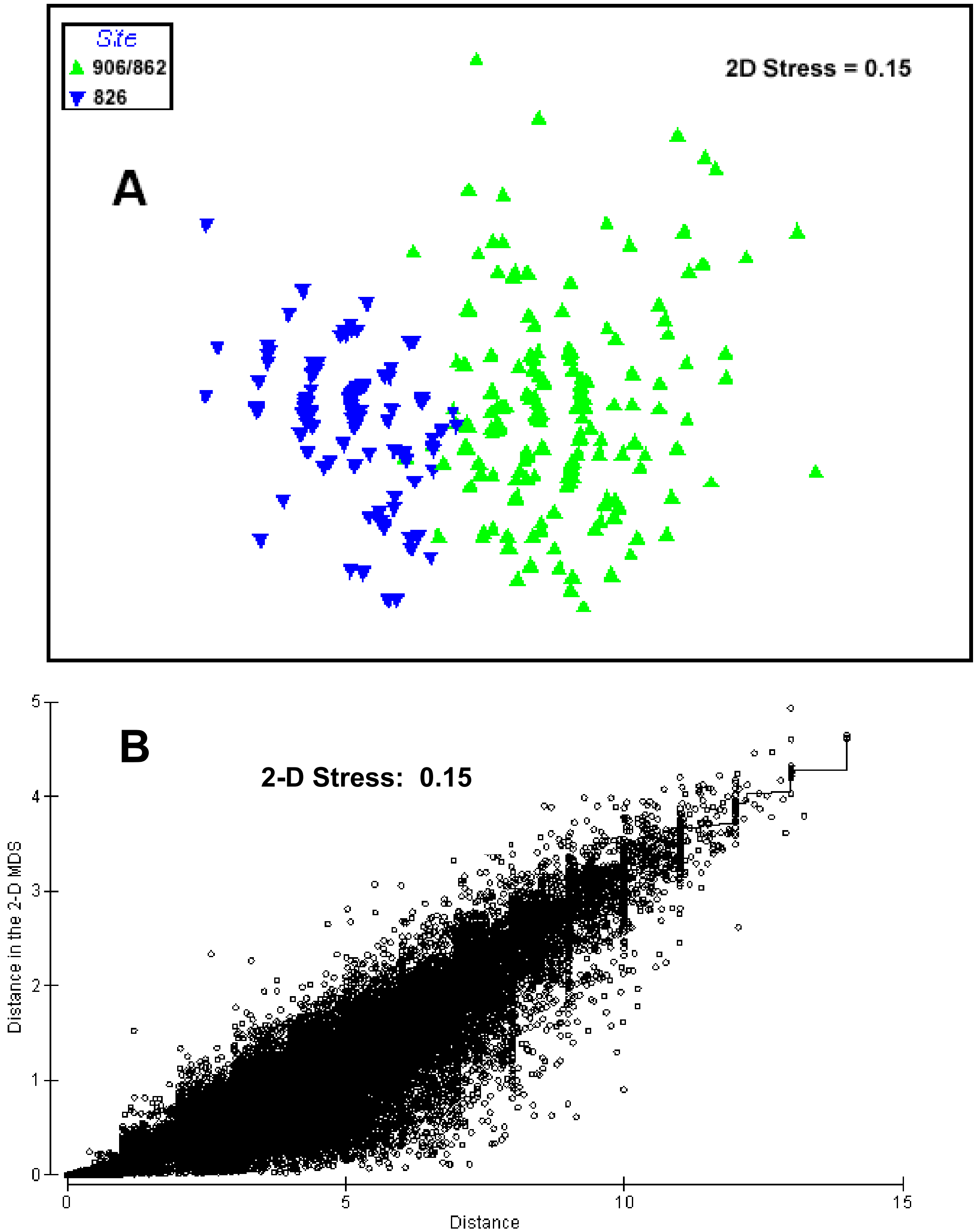


Figure 3.22. A) 2-D, nonmetric multidimensional scaling (MDS) ordination plot using Primer 6 from data categorized by SAMPLE SITE (DEPTH HORIZON). Data in matrix was first standardized by sample total from the original CPCe raw data matrix of species occurrences across all samples (images), N = 459. B) 2-D Shepard plot from the same data matrix. Stress statistic indicated is a measure of deviation around the predicted curve; 0.0 = minimum stress, or no deviation from the predicted model curve.

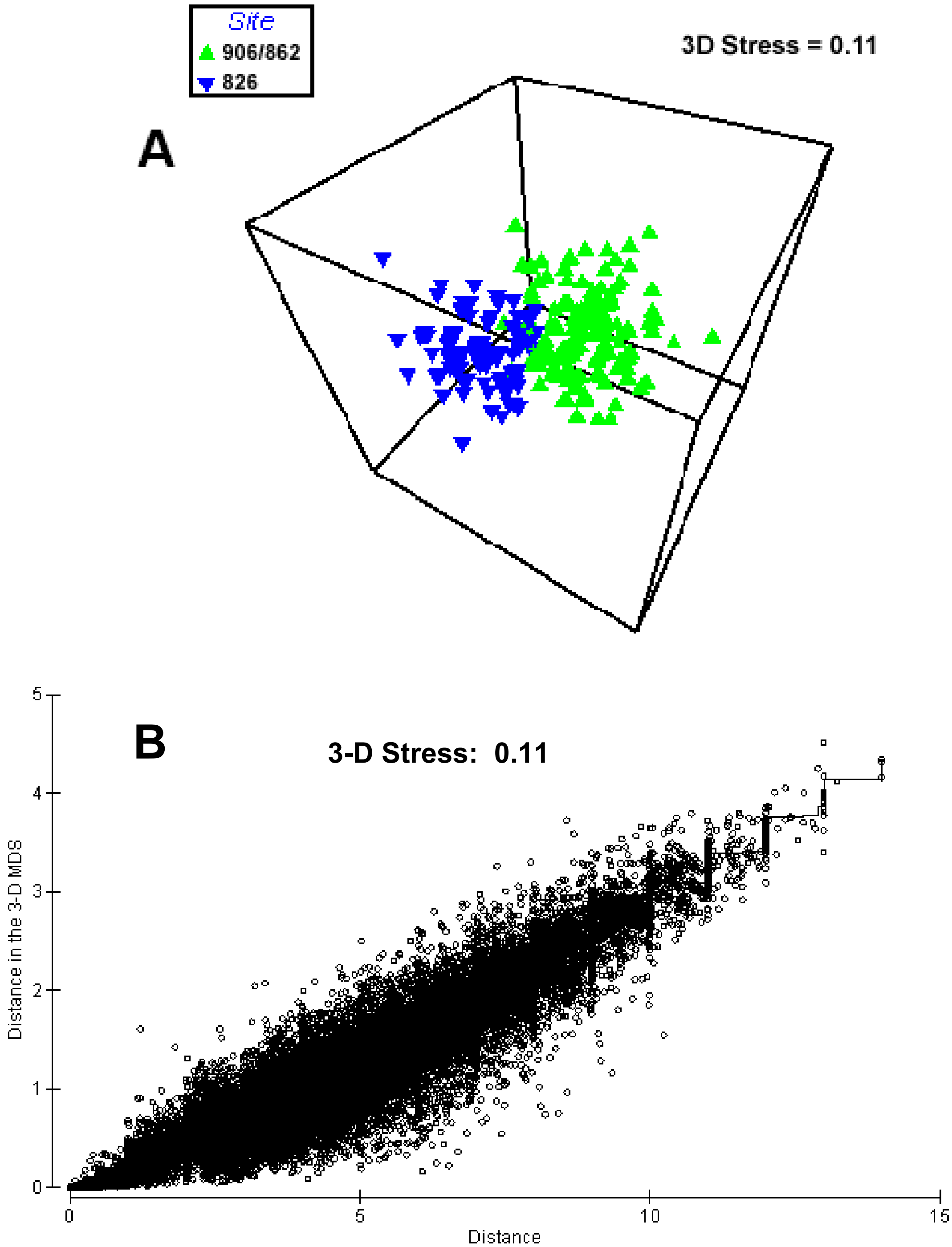
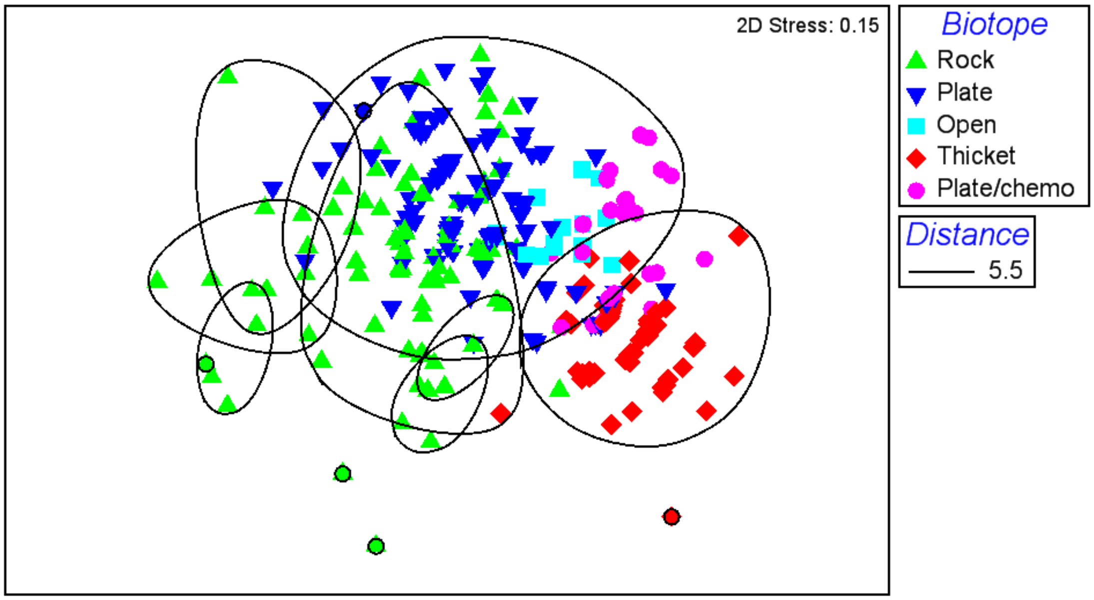


Figure 3.23. A) 3-D, nonmetric multidimensional scaling (MDS) ordination plot using Primer 6 from data categorized by SAMPLE SITE (DEPTH HORIZON); B) 3-D Shepard plot from the same data matrix.



B

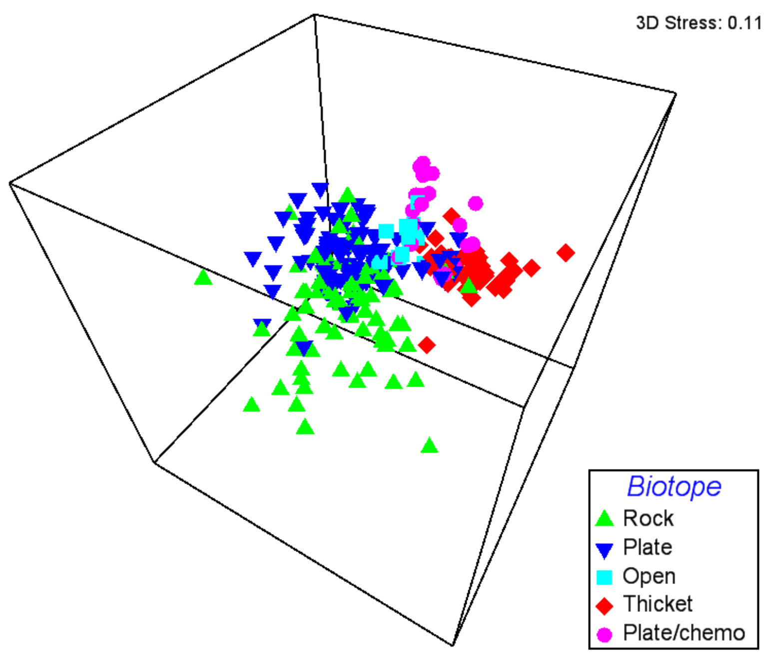


Figure 3.24. A) 2-D, nonmetric multidimensional scaling (MDS) ordination plot using Primer 6 from data categorized into EMPIRICALLY-DEFINED BIOTOPES, with SIMPROF sample clusters (Figure 3.20) overlaid at slack level = 30. Data in matrix was first standardized by sample total from the original CPCe raw data matrix of species occurrences across all samples (images), N = 459; B) 3-D MDS ordination plot similarly produced. Note: 2-D and 3-D Shepard plots (not shown here), and stress statistics, are identical to those in Figs. 3.21 and 3.22 above.

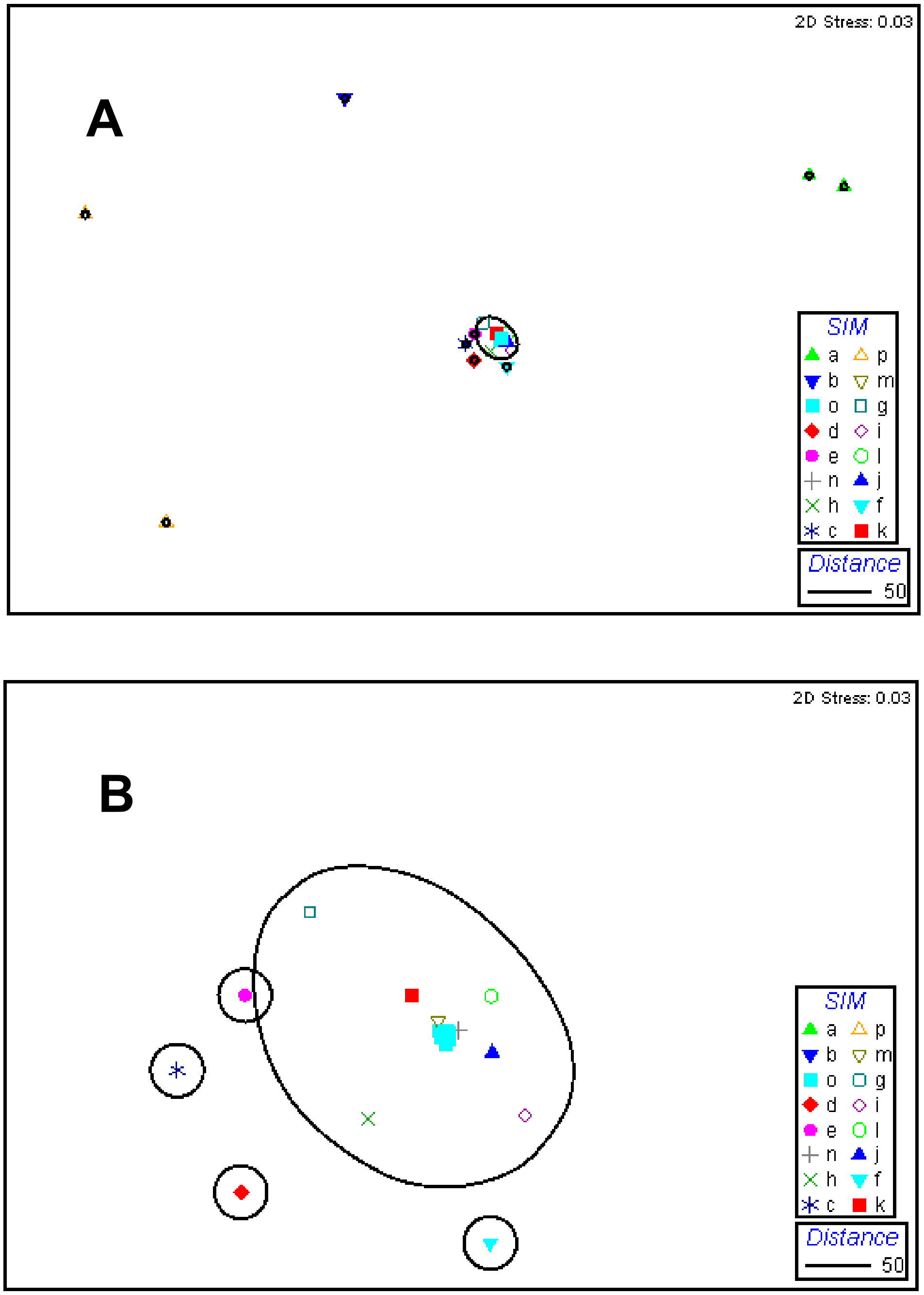
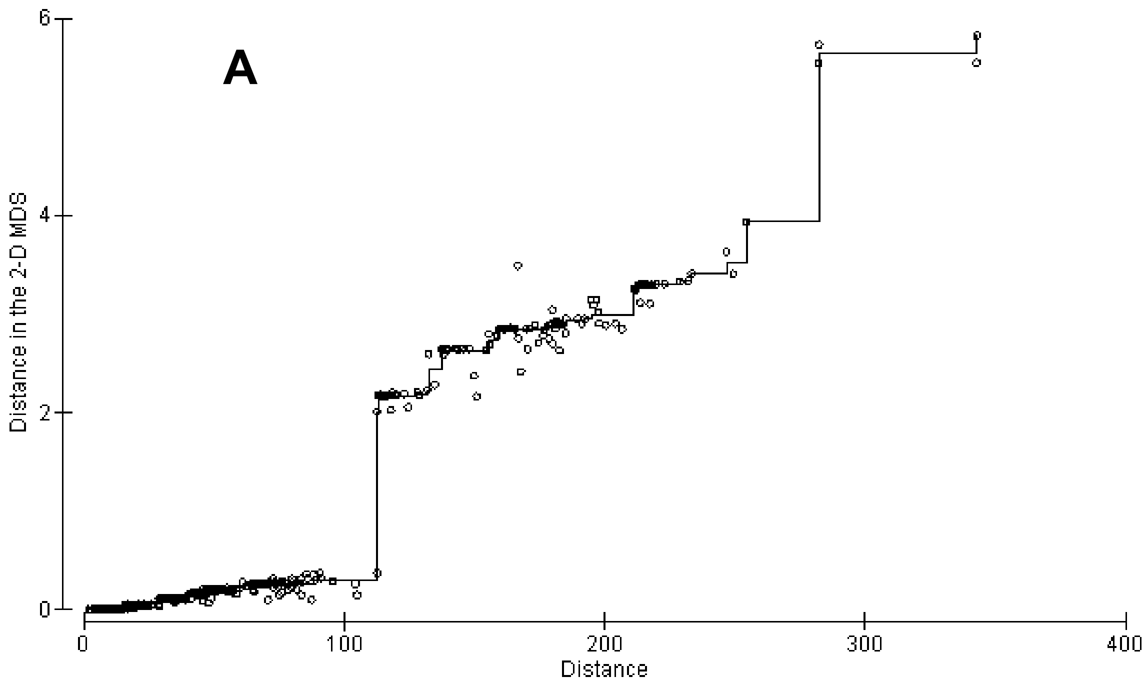


Figure 3.25. A) 2-D, nonmetric multidimensional scaling (MDS) ordination plot using Primer 6 from species occurrence data, with SIMPROF species clusters (Figure 3.24) overlaid at slack level = 30. Data in matrix was first standardized by species total from the original CPCe raw data matrix of species occurrences across all samples (images) analyzed, N = 419; images with 'no invertebrates' scored (N_0=40) were removed; B) Expanded view of the central region of the same MDS plot from (A).



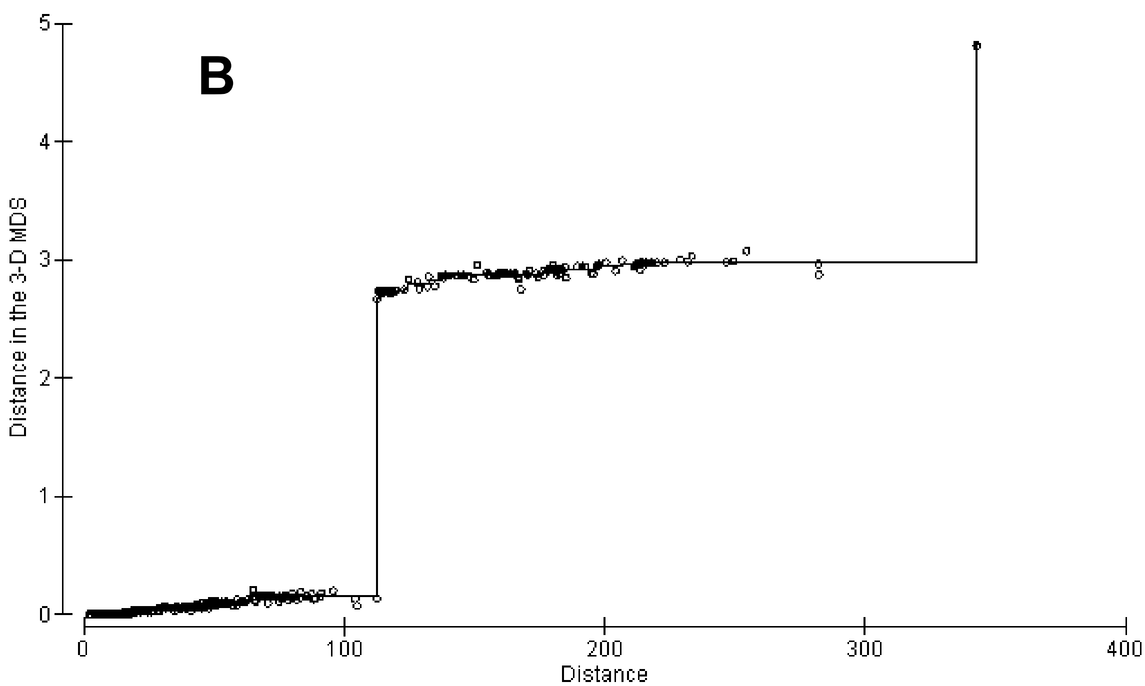


Figure 3.26. A) 2-D Shepard plot to accompany Figure 3.25, stress statistic = 0.03; B) 3-D Shepard plot for same data matrix (3-D MDS plot not shown), stress statistic = 0.01.

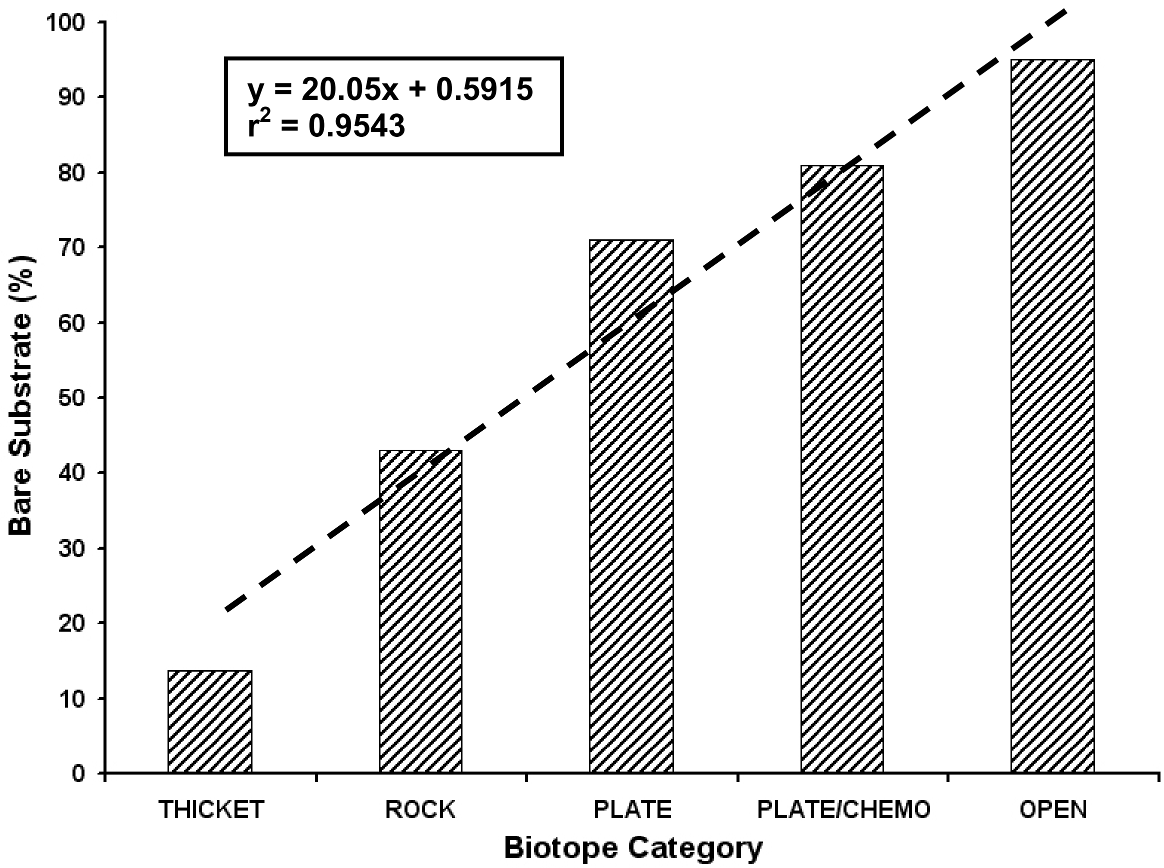


Figure 3.27. Comparative proportion of unpopulated substrate (percentage of 'no invertebrate' scores in CPCe raw data matrix) among the five empirical biotope categories. Refer to Appendix 3-IV for supporting matrix of raw CPCe data.

LIST OF APPENDICES

Appendix 3-I. 'EstimateS' EXPECTED NUMBER OF SPECIES (Sobs = Mao Tau statistic) and 95% confidence intervals determined from multiple random draws upon pooled sample data for each empirically-defined biotope group. 'No Invertebrate' scores (N_0=40) were deleted from the data matrix, resulting in a combined sample, N_T = 419. Data support Figures 16-18.

Appendix 3-I. 'EstimateS' EXPECTED NUMBER OF SPECIES data

Biotope Category	Individuals (computed)	Sobs (Mao Tau)	Sobs 95% CI Lower Bound	Sobs 95% CI Upper Bound
Open	1.27	0.53	0.09	0.97
Open	2.53	1.00	0.18	1.81
Open	3.80	1.41	0.29	2.54
Open	5.07	1.79	0.40	3.18
Open	6.34	2.13	0.51	3.74
Open	7.60	2.43	0.62	4.24
Open	8.87	2.71	0.74	4.68
Open	10.14	2.96	0.85	5.07
Open	11.41	3.19	0.96	5.42
Open	12.67	3.40	1.07	5.73
Open	13.94	3.60	1.17	6.02
Open	15.21	3.78	1.28	6.29
Open	16.47	3.95	1.38	6.53
Open	17.74	4.11	1.48	6.75
Open	19.01	4.27	1.57	6.96
Open	20.28	4.41	1.67	7.15
Open	21.54	4.55	1.76	7.34
Open	22.81	4.68	1.85	7.51
Open	24.08	4.80	1.93	7.67
Open	25.35	4.92	2.02	7.83
Open	26.61	5.04	2.10	7.98
Open	27.88	5.15	2.18	8.13
Open	29.15	5.26	2.26	8.27
Open	30.41	5.37	2.33	8.41
Open	31.68	5.47	2.41	8.54
Open	32.95	5.58	2.48	8.67
Open	34.22	5.67	2.55	8.80
Open	35.48	5.77	2.62	8.93
Open	36.75	5.87	2.69	9.05
Open	38.02	5.96	2.75	9.17
Open	39.29	6.05	2.82	9.29
Open	40.55	6.15	2.88	9.41
Open	41.82	6.24	2.94	9.53
Open	43.09	6.32	3.00	9.65
Open	44.35	6.41	3.06	9.77
Open	45.62	6.50	3.11	9.88

Appendix 3-I. 'EstimateS' EXPECTED NUMBER OF SPECIES data

Biotope Category	Individuals (computed)	Sobs (Mao Tau)	Sobs 95% CI Lower Bound	Sobs 95% CI Upper Bound
Open	46.89	6.58	3.17	10.00
Open	48.16	6.67	3.22	10.12
Open	49.42	6.75	3.28	10.23
Open	50.69	6.84	3.33	10.35
Open	51.96	6.92	3.38	10.46
Open	53.23	7.01	3.43	10.58
Open	54.49	7.08	3.48	10.69
Open	55.76	7.16	3.53	10.80
Open	57.03	7.24	3.57	10.91
Open	58.29	7.32	3.62	11.02
Open	59.56	7.40	3.66	11.14
Open	60.83	7.48	3.71	11.25
Open	62.10	7.55	3.75	11.36
Open	63.36	7.63	3.79	11.47
Open	64.63	7.71	3.83	11.58
Open	65.90	7.78	3.87	11.69
Open	67.17	7.85	3.91	11.80
Open	68.43	7.93	3.95	11.91
Open	69.70	8.00	3.98	12.02
Plate	16.15	2.82	0.91	4.72
Plate	32.30	4.32	1.87	6.76
Plate	48.46	5.37	2.62	8.12
Plate	64.61	6.19	3.25	9.14
Plate	80.76	6.86	3.78	9.94
Plate	96.91	7.42	4.24	10.59
Plate	113.06	7.90	4.65	11.14
Plate	129.21	8.31	5.03	11.60
Plate	145.37	8.69	5.37	12.01
Plate	161.52	9.03	5.68	12.37
Plate	177.67	9.33	5.97	12.70
Plate	193.82	9.61	6.24	12.99
Plate	209.97	9.88	6.49	13.26
Plate	226.12	10.12	6.73	13.51
Plate	242.28	10.35	6.96	13.73
Plate	258.43	10.56	7.18	13.95
Plate	274.58	10.76	7.38	14.14
Plate	290.73	10.95	7.58	14.33
Plate	306.88	11.14	7.77	14.51
Plate	323.03	11.31	7.95	14.67
Plate	339.19	11.48	8.12	14.83
Plate	355.34	11.63	8.29	14.98

Appendix 3-I. 'EstimateS' EXPECTED NUMBER OF SPECIES data

Biotope Category	Individuals (computed)	Sobs (Mao Tau)	Sobs 95% CI Lower Bound	Sobs 95% CI Upper Bound
Plate	371.49	11.79	8.45	15.12
Plate	387.64	11.93	8.61	15.26
Plate	403.79	12.07	8.76	15.39
Plate	419.94	12.21	8.90	15.52
Plate	436.10	12.34	9.04	15.64
Plate	452.25	12.47	9.18	15.76
Plate	468.40	12.59	9.31	15.87
Plate	484.55	12.71	9.44	15.98
Plate	500.70	12.83	9.57	16.08
Plate	516.85	12.94	9.69	16.19
Plate	533.01	13.05	9.81	16.29
Plate	549.16	13.16	9.93	16.38
Plate	565.31	13.26	10.04	16.48
Plate	581.46	13.36	10.15	16.57
Plate	597.61	13.46	10.26	16.66
Plate	613.76	13.55	10.36	16.74
Plate	629.92	13.65	10.47	16.83
Plate	646.07	13.74	10.57	16.91
Plate	662.22	13.83	10.67	16.99
Plate	678.37	13.92	10.76	17.07
Plate	694.52	14.00	10.86	17.15
Plate	710.67	14.09	10.95	17.22
Plate	726.83	14.17	11.04	17.30
Plate	742.98	14.25	11.12	17.37
Plate	759.13	14.33	11.21	17.44
Plate	775.28	14.40	11.29	17.51
Plate	791.43	14.48	11.38	17.58
Plate	807.58	14.55	11.46	17.65
Plate	823.74	14.62	11.54	17.71
Plate	839.89	14.69	11.61	17.77
Plate	856.04	14.76	11.69	17.84
Plate	872.19	14.83	11.76	17.90
Plate	888.34	14.90	11.84	17.96
Plate	904.49	14.96	11.91	18.02
Plate	920.65	15.03	11.98	18.08
Plate	936.80	15.09	12.05	18.14
Plate	952.95	15.15	12.11	18.19
Plate	969.10	15.21	12.18	18.25
Plate	985.25	15.27	12.24	18.30
Plate	1001.40	15.33	12.31	18.36
Plate	1017.56	15.39	12.37	18.41

Appendix 3-I. 'EstimateS' EXPECTED NUMBER OF SPECIES data

Biotope Category	Individuals (computed)	Sobs (Mao Tau)	Sobs 95% CI Lower Bound	Sobs 95% CI Upper Bound
Plate	1033.71	15.45	12.43	18.46
Plate	1049.86	15.50	12.49	18.51
Plate	1066.01	15.56	12.55	18.56
Plate	1082.16	15.61	12.61	18.61
Plate	1098.31	15.66	12.67	18.66
Plate	1114.47	15.72	12.72	18.71
Plate	1130.62	15.77	12.78	18.76
Plate	1146.77	15.82	12.83	18.81
Plate	1162.92	15.87	12.88	18.85
Plate	1179.07	15.92	12.93	18.90
Plate	1195.23	15.96	12.98	18.94
Plate	1211.38	16.01	13.03	18.99
Plate	1227.53	16.06	13.08	19.03
Plate	1243.68	16.10	13.13	19.07
Plate	1259.83	16.15	13.18	19.12
Plate	1275.98	16.19	13.23	19.16
Plate	1292.14	16.23	13.27	19.20
Plate	1308.29	16.28	13.32	19.24
Plate	1324.44	16.32	13.36	19.28
Plate	1340.59	16.36	13.40	19.32
Plate	1356.74	16.40	13.45	19.36
Plate	1372.89	16.44	13.49	19.39
Plate	1389.05	16.48	13.53	19.43
Plate	1405.20	16.52	13.57	19.47
Plate	1421.35	16.56	13.61	19.51
Plate	1437.50	16.60	13.65	19.54
Plate	1453.65	16.63	13.69	19.58
Plate	1469.80	16.67	13.72	19.61
Plate	1485.96	16.70	13.76	19.65
Plate	1502.11	16.74	13.80	19.68
Plate	1518.26	16.77	13.83	19.72
Plate	1534.41	16.81	13.87	19.75
Plate	1550.56	16.84	13.90	19.78
Plate	1566.71	16.87	13.93	19.81
Plate	1582.87	16.91	13.97	19.85
Plate	1599.02	16.94	14.00	19.88
Plate	1615.17	16.97	14.03	19.91
Plate	1631.32	17.00	14.06	19.94
Plate	1647.47	17.03	14.09	19.97
Plate	1663.62	17.06	14.12	20.00
Plate	1679.78	17.09	14.15	20.03

Appendix 3-I. 'EstimateS' EXPECTED NUMBER OF SPECIES data				
Biotope Category	Individuals (computed)	Sobs (Mao Tau)	Sobs 95% CI Lower Bound	Sobs 95% CI Upper Bound
Plate	1695.93	17.12	14.18	20.06
Plate	1712.08	17.15	14.21	20.09
Plate	1728.23	17.18	14.24	20.12
Plate	1744.38	17.21	14.27	20.14
Plate	1760.53	17.23	14.30	20.17
Plate	1776.69	17.26	14.32	20.20
Plate	1792.84	17.29	14.35	20.22
Plate	1808.99	17.31	14.37	20.25
Plate	1825.14	17.34	14.40	20.28
Plate	1841.29	17.36	14.42	20.30
Plate	1857.44	17.39	14.45	20.33
Plate	1873.60	17.41	14.47	20.35
Plate	1889.75	17.44	14.49	20.38
Plate	1905.90	17.46	14.52	20.40
Plate	1922.05	17.48	14.54	20.42
Plate	1938.20	17.50	14.56	20.45
Plate	1954.35	17.53	14.58	20.47
Plate	1970.51	17.55	14.60	20.49
Plate	1986.66	17.57	14.62	20.52
Plate	2002.81	17.59	14.64	20.54
Plate	2018.96	17.61	14.66	20.56
Plate	2035.11	17.63	14.68	20.58
Plate	2051.26	17.65	14.70	20.60
Plate	2067.42	17.67	14.72	20.62
Plate	2083.57	17.69	14.74	20.64
Plate	2099.72	17.71	14.76	20.67
Plate	2115.87	17.73	14.78	20.69
Plate	2132.02	17.75	14.79	20.70
Plate	2148.17	17.77	14.81	20.72
Plate	2164.33	17.78	14.83	20.74
Plate	2180.48	17.80	14.84	20.76
Plate	2196.63	17.82	14.86	20.78
Plate	2212.78	17.84	14.87	20.80
Plate	2228.93	17.85	14.89	20.82
Plate	2245.08	17.87	14.90	20.84
Plate	2261.24	17.88	14.92	20.85
Plate	2277.39	17.90	14.93	20.87
Plate	2293.54	17.91	14.94	20.89
Plate	2309.69	17.93	14.96	20.90
Plate	2325.84	17.94	14.97	20.92
Plate	2341.99	17.96	14.98	20.94

Appendix 3-I. 'EstimateS' EXPECTED NUMBER OF SPECIES data

Biotope Category	Individuals (computed)	Sobs (Mao Tau)	Sobs 95% CI Lower Bound	Sobs 95% CI Upper Bound
Plate	2358.15	17.97	14.99	20.95
Plate	2374.30	17.99	15.00	20.97
Plate	2390.45	18.00	15.02	20.98
Thicket	47.59	2.73	0.16	5.29
Thicket	95.18	3.47	0.82	6.11
Thicket	142.77	4.10	1.39	6.81
Thicket	190.36	4.68	1.88	7.48
Thicket	237.95	5.21	2.31	8.11
Thicket	285.54	5.69	2.69	8.70
Thicket	333.13	6.14	3.03	9.25
Thicket	380.72	6.55	3.35	9.75
Thicket	428.31	6.93	3.64	10.22
Thicket	475.90	7.28	3.91	10.66
Thicket	523.49	7.61	4.16	11.06
Thicket	571.08	7.91	4.40	11.43
Thicket	618.67	8.20	4.62	11.78
Thicket	666.26	8.47	4.83	12.10
Thicket	713.86	8.72	5.03	12.40
Thicket	761.45	8.95	5.22	12.68
Thicket	809.04	9.18	5.41	12.94
Thicket	856.63	9.39	5.58	13.19
Thicket	904.22	9.59	5.75	13.43
Thicket	951.81	9.78	5.91	13.65
Thicket	999.40	9.96	6.06	13.86
Thicket	1046.99	10.13	6.21	14.06
Thicket	1094.58	10.30	6.36	14.24
Thicket	1142.17	10.46	6.50	14.43
Thicket	1189.76	10.61	6.63	14.60
Thicket	1237.35	10.76	6.76	14.76
Thicket	1284.94	10.90	6.89	14.92
Thicket	1332.53	11.04	7.01	15.08
Thicket	1380.12	11.18	7.13	15.22
Thicket	1427.71	11.31	7.25	15.37
Thicket	1475.30	11.43	7.36	15.50
Thicket	1522.89	11.55	7.47	15.64
Thicket	1570.48	11.67	7.58	15.77
Thicket	1618.07	11.79	7.68	15.89
Thicket	1665.66	11.90	7.79	16.02
Thicket	1713.25	12.01	7.89	16.14
Thicket	1760.84	12.12	7.98	16.25
Thicket	1808.43	12.22	8.08	16.37

Appendix 3-I. 'EstimateS' EXPECTED NUMBER OF SPECIES data

Biotope Category	Individuals (computed)	Sobs (Mao Tau)	Sobs 95% CI Lower Bound	Sobs 95% CI Upper Bound
Thicket	1856.02	12.33	8.17	16.48
Thicket	1903.61	12.43	8.26	16.59
Thicket	1951.20	12.53	8.35	16.70
Thicket	1998.79	12.62	8.44	16.80
Thicket	2046.38	12.72	8.53	16.91
Thicket	2093.98	12.81	8.61	17.01
Thicket	2141.57	12.90	8.70	17.11
Thicket	2189.16	12.99	8.78	17.21
Thicket	2236.75	13.08	8.86	17.30
Thicket	2284.34	13.17	8.94	17.40
Thicket	2331.93	13.25	9.01	17.49
Thicket	2379.52	13.34	9.09	17.59
Thicket	2427.11	13.42	9.16	17.68
Thicket	2474.70	13.50	9.24	17.77
Thicket	2522.29	13.58	9.31	17.86
Thicket	2569.88	13.66	9.38	17.94
Thicket	2617.47	13.74	9.45	18.03
Thicket	2665.06	13.82	9.52	18.12
Thicket	2712.65	13.89	9.58	18.20
Thicket	2760.24	13.97	9.65	18.28
Thicket	2807.83	14.04	9.71	18.37
Thicket	2855.42	14.11	9.78	18.45
Thicket	2903.01	14.19	9.84	18.53
Thicket	2950.60	14.26	9.90	18.61
Thicket	2998.19	14.33	9.96	18.69
Thicket	3045.78	14.39	10.02	18.77
Thicket	3093.37	14.46	10.08	18.84
Thicket	3140.96	14.53	10.14	18.92
Thicket	3188.55	14.60	10.20	18.99
Thicket	3236.14	14.66	10.25	19.07
Thicket	3283.73	14.73	10.31	19.14
Thicket	3331.32	14.79	10.36	19.21
Thicket	3378.91	14.85	10.42	19.29
Thicket	3426.50	14.91	10.47	19.36
Thicket	3474.09	14.97	10.52	19.43
Thicket	3521.69	15.03	10.57	19.50
Thicket	3569.28	15.09	10.62	19.57
Thicket	3616.87	15.15	10.67	19.63
Thicket	3664.46	15.21	10.72	19.70
Thicket	3712.05	15.27	10.77	19.77
Thicket	3759.64	15.32	10.82	19.83

Appendix 3-I. 'EstimateS' EXPECTED NUMBER OF SPECIES data

Biotope Category	Individuals (computed)	Sobs (Mao Tau)	Sobs 95% CI Lower Bound	Sobs 95% CI Upper Bound
Thicket	3807.23	15.38	10.86	19.90
Thicket	3854.82	15.44	10.91	19.96
Thicket	3902.41	15.49	10.95	20.03
Thicket	3950.00	15.54	11.00	20.09
Thicket	3997.59	15.60	11.04	20.15
Thicket	4045.18	15.65	11.08	20.21
Thicket	4092.77	15.70	11.13	20.27
Thicket	4140.36	15.75	11.17	20.33
Thicket	4187.95	15.80	11.21	20.39
Thicket	4235.54	15.85	11.25	20.45
Thicket	4283.13	15.90	11.29	20.51
Thicket	4330.72	15.95	11.33	20.57
Thicket	4378.31	15.99	11.37	20.62
Thicket	4425.90	16.04	11.40	20.68
Thicket	4473.49	16.09	11.44	20.73
Thicket	4521.08	16.13	11.48	20.79
Thicket	4568.67	16.18	11.51	20.84
Thicket	4616.26	16.22	11.55	20.90
Thicket	4663.85	16.27	11.58	20.95
Thicket	4711.44	16.31	11.62	21.00
Thicket	4759.03	16.35	11.65	21.06
Thicket	4806.62	16.40	11.68	21.11
Thicket	4854.21	16.44	11.72	21.16
Thicket	4901.81	16.48	11.75	21.21
Thicket	4949.40	16.52	11.78	21.26
Thicket	4996.99	16.56	11.81	21.31
Thicket	5044.58	16.60	11.84	21.36
Thicket	5092.17	16.64	11.87	21.40
Thicket	5139.76	16.68	11.90	21.45
Thicket	5187.35	16.71	11.93	21.50
Thicket	5234.94	16.75	11.96	21.55
Thicket	5282.53	16.79	11.98	21.59
Thicket	5330.12	16.82	12.01	21.64
Thicket	5377.71	16.86	12.04	21.68
Thicket	5425.30	16.90	12.06	21.73
Thicket	5472.89	16.93	12.09	21.77
Thicket	5520.48	16.97	12.11	21.82
Thicket	5568.07	17.00	12.14	21.86
Rock	32.94	4.72	2.31	7.13
Rock	65.89	6.89	4.00	9.78
Rock	98.83	8.31	5.27	11.36

Appendix 3-I. 'EstimateS' EXPECTED NUMBER OF SPECIES data

Biotope Category	Individuals (computed)	Sobs (Mao Tau)	Sobs 95% CI Lower Bound	Sobs 95% CI Upper Bound
Rock	131.77	9.39	6.29	12.49
Rock	164.72	10.26	7.15	13.37
Rock	197.66	11.00	7.90	14.09
Rock	230.60	11.63	8.56	14.70
Rock	263.55	12.19	9.15	15.22
Rock	296.49	12.68	9.68	15.68
Rock	329.43	13.12	10.17	16.08
Rock	362.37	13.53	10.62	16.44
Rock	395.32	13.89	11.03	16.76
Rock	428.26	14.23	11.41	17.05
Rock	461.20	14.54	11.76	17.32
Rock	494.15	14.83	12.09	17.57
Rock	527.09	15.10	12.40	17.81
Rock	560.03	15.35	12.68	18.02
Rock	592.98	15.59	12.95	18.23
Rock	625.92	15.81	13.21	18.42
Rock	658.86	16.02	13.44	18.60
Rock	691.81	16.22	13.67	18.76
Rock	724.75	16.40	13.88	18.92
Rock	757.69	16.57	14.07	19.07
Rock	790.64	16.74	14.26	19.22
Rock	823.58	16.89	14.44	19.35
Rock	856.52	17.04	14.60	19.48
Rock	889.46	17.18	14.76	19.60
Rock	922.41	17.31	14.91	19.72
Rock	955.35	17.44	15.05	19.82
Rock	988.29	17.56	15.19	19.92
Rock	1021.24	17.67	15.31	20.02
Rock	1054.18	17.77	15.43	20.11
Rock	1087.12	17.87	15.55	20.20
Rock	1120.07	17.97	15.66	20.28
Rock	1153.01	18.06	15.76	20.36
Rock	1185.95	18.15	15.86	20.43
Rock	1218.90	18.23	15.96	20.50
Rock	1251.84	18.30	16.05	20.56
Rock	1284.78	18.38	16.14	20.62
Rock	1317.73	18.45	16.22	20.68
Rock	1350.67	18.51	16.30	20.73
Rock	1383.61	18.58	16.37	20.78
Rock	1416.56	18.64	16.45	20.83
Rock	1449.50	18.70	16.52	20.87

Appendix 3-I. 'EstimateS' EXPECTED NUMBER OF SPECIES data

Biotope Category	Individuals (computed)	Sobs (Mao Tau)	Sobs 95% CI Lower Bound	Sobs 95% CI Upper Bound
Rock	1482.44	18.75	16.58	20.92
Rock	1515.38	18.80	16.65	20.96
Rock	1548.33	18.85	16.71	20.99
Rock	1581.27	18.90	16.77	21.03
Rock	1614.21	18.95	16.83	21.06
Rock	1647.16	18.99	16.88	21.10
Rock	1680.10	19.03	16.94	21.13
Rock	1713.04	19.07	16.99	21.16
Rock	1745.99	19.11	17.04	21.18
Rock	1778.93	19.15	17.09	21.21
Rock	1811.87	19.18	17.13	21.24
Rock	1844.82	19.22	17.18	21.26
Rock	1877.76	19.25	17.22	21.28
Rock	1910.70	19.29	17.26	21.31
Rock	1943.65	19.32	17.31	21.33
Rock	1976.59	19.35	17.35	21.35
Rock	2009.53	19.38	17.38	21.37
Rock	2042.47	19.41	17.42	21.39
Rock	2075.42	19.44	17.46	21.41
Rock	2108.36	19.46	17.49	21.43
Rock	2141.30	19.49	17.53	21.45
Rock	2174.25	19.52	17.56	21.47
Rock	2207.19	19.54	17.60	21.49
Rock	2240.13	19.57	17.63	21.51
Rock	2273.08	19.59	17.66	21.53
Rock	2306.02	19.62	17.69	21.55
Rock	2338.96	19.64	17.72	21.57
Rock	2371.91	19.67	17.75	21.59
Rock	2404.85	19.70	17.78	21.61
Rock	2437.79	19.72	17.81	21.63
Rock	2470.74	19.74	17.83	21.65
Rock	2503.68	19.77	17.86	21.67
Rock	2536.62	19.79	17.89	21.69
Rock	2569.56	19.81	17.91	21.71
Rock	2602.51	19.84	17.94	21.74
Rock	2635.45	19.86	17.96	21.76
Rock	2668.39	19.88	17.99	21.78
Rock	2701.34	19.91	18.01	21.80
Rock	2734.28	19.93	18.03	21.83
Rock	2767.22	19.95	18.05	21.85
Rock	2800.17	19.98	18.08	21.88

Appendix 3-I. 'EstimateS' EXPECTED NUMBER OF SPECIES data

Biotope Category	Individuals (computed)	Sobs (Mao Tau)	Sobs 95% CI Lower Bound	Sobs 95% CI Upper Bound
Rock	2833.11	20.00	18.10	21.90
Plate-Chemo	8.55	1.64	0.14	3.14
Plate-Chemo	17.10	2.47	0.62	4.32
Plate-Chemo	25.65	3.06	1.09	5.04
Plate-Chemo	34.20	3.55	1.50	5.59
Plate-Chemo	42.76	3.97	1.87	6.06
Plate-Chemo	51.31	4.34	2.20	6.47
Plate-Chemo	59.86	4.67	2.51	6.84
Plate-Chemo	68.41	4.98	2.78	7.17
Plate-Chemo	76.96	5.26	3.04	7.48
Plate-Chemo	85.51	5.51	3.27	7.76
Plate-Chemo	94.06	5.75	3.48	8.02
Plate-Chemo	102.61	5.97	3.67	8.27
Plate-Chemo	111.16	6.17	3.86	8.49
Plate-Chemo	119.72	6.36	4.02	8.70
Plate-Chemo	128.27	6.54	4.18	8.90
Plate-Chemo	136.82	6.70	4.33	9.08
Plate-Chemo	145.37	6.86	4.46	9.25
Plate-Chemo	153.92	7.00	4.59	9.41
Plate-Chemo	162.47	7.13	4.71	9.56
Plate-Chemo	171.02	7.26	4.82	9.70
Plate-Chemo	179.57	7.37	4.92	9.82
Plate-Chemo	188.12	7.48	5.02	9.94
Plate-Chemo	196.68	7.58	5.11	10.05
Plate-Chemo	205.23	7.68	5.20	10.16
Plate-Chemo	213.78	7.77	5.28	10.25
Plate-Chemo	222.33	7.85	5.36	10.34
Plate-Chemo	230.88	7.93	5.43	10.43
Plate-Chemo	239.43	8.00	5.50	10.51
Plate-Chemo	247.98	8.07	5.57	10.58
Plate-Chemo	256.53	8.14	5.63	10.65
Plate-Chemo	265.09	8.20	5.68	10.72
Plate-Chemo	273.64	8.26	5.74	10.79
Plate-Chemo	282.19	8.32	5.79	10.85
Plate-Chemo	290.74	8.37	5.84	10.90
Plate-Chemo	299.29	8.42	5.88	10.96
Plate-Chemo	307.84	8.47	5.93	11.01
Plate-Chemo	316.39	8.51	5.97	11.06
Plate-Chemo	324.94	8.56	6.01	11.11
Plate-Chemo	333.49	8.60	6.04	11.16
Plate-Chemo	342.05	8.64	6.08	11.20

Appendix 3-I. 'EstimateS' EXPECTED NUMBER OF SPECIES data				
Biotope Category	Individuals (computed)	Sobs (Mao Tau)	Sobs 95% CI Lower Bound	Sobs 95% CI Upper Bound
Plate-Chemo	350.60	8.68	6.11	11.24
Plate-Chemo	359.15	8.71	6.14	11.28
Plate-Chemo	367.70	8.75	6.17	11.32
Plate-Chemo	376.25	8.78	6.20	11.36
Plate-Chemo	384.80	8.81	6.22	11.39
Plate-Chemo	393.35	8.84	6.25	11.43
Plate-Chemo	401.90	8.86	6.27	11.46
Plate-Chemo	410.45	8.89	6.29	11.49
Plate-Chemo	419.01	8.92	6.31	11.52
Plate-Chemo	427.56	8.94	6.33	11.55
Plate-Chemo	436.11	8.96	6.34	11.58
Plate-Chemo	444.66	8.98	6.36	11.60
Plate-Chemo	453.21	9.00	6.37	11.63

Appendix 3-II. Multivariate determined sampling SITE CLUSTER GROUPS AND SUBGROUPS by alphabetical designation, with list of component images (N_T = 419) and original empirical biotope designations. Images are identified by USGS station number, Viosca Knoll site number, digital images designation, and original empirical biotope category. Images with no megafauna scored are omitted (N_0=40). SITE GROUP AND SUBGROUP clustergram is presented in Figure 3.19. Note: 906/907 designation within Station-Site-Image-Biotope equals 906/862 in text.

Appendix 3-II. Multivariate determined sampling SITE CLUSTER GROUPS			
Group	Subgroup	No.	Station-Site-Image-Biotope
A (all VK-826; mostly Thicket)		138	4751_826_VTS_01_2_1123_Thicket 4882_826_VTS_01_1_1164_Thicket 4749_826_VTS_01_4_1234_Thicket 4751_826_VTS_01_2_921_Thicket 4751_826_VTS_01_3_951_Thicket 4879_826_VTS_01_4_603_Plate 4879_826_VTS_01_1_23_Plate/Chemo 4880_826_VTS_01_4_449_Plate/Chemo
			4752_826_VTS_01_3_85_Thicket 4749_826_VTS_01_5_37_Thicket 4751_826_VTS_01_2_709_Thicket 4877_826_VTS_01_2_809_Thicket 4879_826_VTS_01_2_726_Thicket 4749_826_VTS_01_1_280_Thicket 4749_826_VTS_01_4_729_Thicket 4748_826_VTS_01_4_1251_Thicket 4752_826_VTS_01_1_726_Thicket 4752_826_VTS_01_3_483_Thicket 4748_826_VTS_01_2_214_Thicket 4882_826_VTS_01_2_155_Thicket 4878_826_VTS_01_1_467_Thicket 4753_826_VTS_01_1_939_Thicket 4751_826_VTS_01_2_1002_Thicket 4751_826_VTS_01_2_690_Thicket 4880_826_VTS_01_1_317_Thicket 4751_826_VTS_01_1_599 _Thicket 4880_826_VTS_01_1_707_Thicket 4878_826_VTS_01_3_4_Thicket 4879_826_VTS_01_2_766_Thicket 4751_826_VTS_01_1_688_Thicket 4879_826_VTS_01_3_1217_Thicket 4880_826_VTS_01_1_482_Thicket 4881_826_VTS_01_3_817_Plate/Chemo 4753_826_VTS_01_4_18_Thicket 4751_826_VTS_01_3_1191_Thicket 4880_826_VTS_01_1_650_Thicket

Appendix 3-II. Multivariate determined sampling SITE CLUSTER GROUPS			
Group	Subgroup	No.	Station-Site-Image-Biotope
			4880_826_VTS_01_1_781_Thicket 4749_826_VTS_01_4_689_Thicket 4752_826_VTS_01_3_85_Thicket 4749_826_VTS_01_5_37_Thicket 4751_826_VTS_01_2_709_Thicket 4877_826_VTS_01_2_809_Thicket 4879_826_VTS_01_2_726_Thicket 4749_826_VTS_01_1_280_Thicket 4749_826_VTS_01_4_729_Thicket 4748_826_VTS_01_4_1251_Thicket 4752_826_VTS_01_1_726_Thicket 4752_826_VTS_01_3_483_Thicket 4748_826_VTS_01_2_214_Thicket 4882_826_VTS_01_2_155_Thicket 4878_826_VTS_01_1_467_Thicket 4753_826_VTS_01_1_939_Thicket 4751_826_VTS_01_2_1002_Thicket 4751_826_VTS_01_2_690_Thicket 4880_826_VTS_01_1_317_Thicket 4751_826_VTS_01_1_599 _Thicket 4880_826_VTS_01_1_707_Thicket 4878_826_VTS_01_3_4_Thicket 4879_826_VTS_01_2_766_Thicket 4751_826_VTS_01_1_688_Thicket 4879_826_VTS_01_3_1217_Thicket 4880_826_VTS_01_1_482_Thicket 4881_826_VTS_01_3_817_Plate/Chemo 4753_826_VTS_01_4_18_Thicket 4751_826_VTS_01_3_1191_Thicket 4880_826_VTS_01_1_650_Thicket 4880_826_VTS_01_1_781_Thicket 4749_826_VTS_01_4_689_Thicket
			4752_826_VTS_01_2_1015_Thicket 4753_826_VTS_01_4_1052_Thicket 4752_826_VTS_01_1_800_Thicket 4882_826_VTS_01_2_702_Thicket 4877_826_VTS_01_2_623_Thicket 4877_826_VTS_01_2_764_Thicket 4878_826_VTS_01_3_446_Thicket 4880_826_VTS_01_4_1134_Thicket 4752_826_VTS_01_2_854_Thicket 4877_826_VTS_01_4_1044_Thicket 4751_826_VTS_01_1_133 _Thicket 4878_826_VTS_01_3_985_Thicket

Appendix 3-II. Multivariate determined sampling SITE CLUSTER GROUPS			
Group	Subgroup	No.	Station-Site-Image-Biotope
			4881_826_VTS_01_2_967_Thicket 4752_826_VTS_01_2_882_Thicket 4753_826_VTS_01_3_808_Thicket 4748_826_VTS_01_3_65_Thicket 4752_826_VTS_01_2_1088_Thicket 4879_826_VTS_01_5_5_Thicket 4751_826_VTS_01_1_660 _Thicket 4879_826_VTS_01_1_402_Thicket 4882_826_VTS_01_3_319_Thicket 4879_826_VTS_01_1_514_Thicket 4752_826_VTS_01_2_828_Thicket 4751_826_VTS_01_4_753_Thicket 4880_826_VTS_01_1_684_Thicket 4880_826_VTS_01_1_745_Thicket 4880_826_VTS_01_3_569_Thicket 4879_826_VTS_01_1_347_Thicket 4881_826_VTS_01_1_725_Thicket 4879_826_VTS_01_1_223_Thicket 4881_826_VTS_01_1_738_Thicket 4881_826_VTS_01_1_820_Thicket 4881_826_VTS_01_1_834_Thicket 4752_826_VTS_01_2_1073_Thicket 4752_826_VTS_01_3_385_Thicket 4882_826_VTS_01_1_438_Thicket 4878_826_VTS_01_1_31_Thicket 4880_826_VTS_01_1_41_Thicket 4880_826_VTS_01_4_1169_Thicket 4882_826_VTS_01_1_692_Thicket 4879_826_VTS_01_3_464_Thicket 4748_826_VTS_01_4_1104_Plate 4881_826_VTS_01_2_1291_Thicket 4753_826_VTS_01_2_408_Thicket 4880_826_VTS_01_4_605_Thicket 4879_826_VTS_01_2_267_Plate 4752_826_VTS_01_3_393_Thicket 4881_826_VTS_01_2_901_Thicket 4882_826_VTS_01_1_385_Thicket 4881_826_VTS_01_1_565_Rock 4881_826_VTS_01_1_111_Plate/Chemo 4748_826_VTS_01_2_655_Rock 4880_826_VTS_01_1_1119_Plate/Chemo 4748_826_VTS_01_3_272_Thicket 4879_826_VTS_01_1_110_Thicket 4753_826_VTS_01_2_335_Thicket

Appendix 3-II. Multivariate determined sampling SITE CLUSTER GROUPS			
Group	Subgroup	No.	Station-Site-Image-Biotope
			4880_826_VTS_01_1_453_Thicket
B (B1)	B1 (almost all VK-826; mostly Open and Plate/Chemo)	59	4877_826_VTS_01_1_1169_Plate/Chemo 4748_826_VTS_01_1_337_Plate/Chemo 4880_826_VTS_01_4_470_Plate/Chemo 4748_826_VTS_01_2_792_Plate/Chemo 4880_826_VTS_01_3_1171_Plate/Chemo 4746_906/907_VTS_01_1_194_Open 4752_826_VTS_01_4_1237_Open 4752_826_VTS_01_2_677_Open 4879_826_VTS_01_2_15_Plate 4879_826_VTS_01_4_509_Plate 4879_826_VTS_01_5_6_Plate/Chemo 4875_906/907_VTS_01_3_1025_Open 4880_826_VTS_01_2_657_Open 4752_826_VTS_01_4_420_Open 4877_826_VTS_01_2_149_Open 4746_906/907_VTS_01_1_130_Open 4752_826_VTS_01_1_123_Open 4752_826_VTS_01_1_1158_Open 4877_826_VTS_01_2_755_Open 4877_826_VTS_01_2_172_Open 4744_906/907_VTS_01_3_957_Open 4877_826_VTS_01_2_183_Open 4746_906/907_VTS_01_1_101_Open 4746_906/907_VTS_01_1_115_Open 4879_826_VTS_01_1_301_Plate/Chemo 4748_826_VTS_01_1_729_Plate/Chemo 4752_826_VTS_01_1_1_Open 4752_826_VTS_01_4_769_Open 4880_826_VTS_01_2_1118_Plate/Chemo 4880_826_VTS_01_4_349_Plate/Chemo 4880_826_VTS_01_4_378_Plate/Chemo 4879_826_VTS_01_1_157_Plate/Chemo 4879_826_VTS_01_4_645_Plate/Chemo 4879_826_VTS_01_1_899_Plate/Chemo 4880_826_VTS_01_2_1020_Plate/Chemo 4880_826_VTS_01_4_428_Plate/Chemo 4879_826_VTS_01_1_337_Plate/Chemo 4880_826_VTS_01_4_517_Plate/Chemo 4879_826_VTS_01_1_120_Plate/Chemo 4880_826_VTS_01_1_1043_Plate/Chemo 4880_826_VTS_01_2_1067_Plate/Chemo 4879_826_VTS_01_1_175_Plate/Chemo 4879_826_VTS_01_1_867_Plate/Chemo

Appendix 3-II. Multivariate determined sampling SITE CLUSTER GROUPS			
Group	Subgroup	No.	Station-Site-Image-Biotope
			4880_826_VTS_01_2_1155_Plate/Chemo 4880_826_VTS_01_2_1195_Plate/Chemo 4879_826_VTS_01_1_138_Plate/Chemo 4880_826_VTS_01_2_1208_Plate/Chemo 4880_826_VTS_01_4_490_Plate/Chemo 4879_826_VTS_01_1_55_Plate/Chemo 4879_826_VTS_01_1_93_Plate/Chemo 4879_826_VTS_01_1_835_Plate/Chemo 4879_826_VTS_01_3_345_Open 4880_826_VTS_01_1_829_Plate/Chemo 4880_826_VTS_01_1_1182_Plate/Chemo 4880_826_VTS_01_1_1010_Plate/Chemo 4880_826_VTS_01_1_1094_Plate/Chemo 4879_826_VTS_01_1_479_Plate/Chemo 4879_826_VTS_01_1_801_Plate/Chemo 4880_826_VTS_01_4_402_Plate/Chemo
B (B2-B7)	B2-B7 (almost all VK-906/907; mostly Plate and Rock)	188	4746_906/907_VTS_01_4_217_Plate 4744_906/907_VTS_01_1_1102_Rock 4744_906/907_VTS_01_3_906_Plate 4874_906/907_VTS_01_2_573_Plate 4874_906/907_VTS_01_1_671_Plate 4744_906/907_VTS_01_3_1078_Plate 4744_906/907_VTS_01_3_1123_Plate 4876_906/907_VTS_01_2_901_Plate 4873_906/907_VTS_01_4_264_Plate 4875_906/907_VTS_01_1_272_Plate 4875_906/907_VTS_01_1_350_Plate 4876_906/907_VTS_01_2_21_Plate 4875_906/907_VTS_01_1_335_Plate 4876_906/907_VTS_01_2_92_Plate 4875_906/907_VTS_01_1_368_Plate 4876_906/907_VTS_01_1_322_Plate

Appendix 3-II. Multivariate determined sampling SITE CLUSTER GROUPS			
Group	Subgroup	No.	Station-Site-Image-Biotope
			4744_906/907_VTS_01_2_1253_Rock 4744_906/907_VTS_01_2_834_Rock 4746_906/907_VTS_01_1_1251_Plate 4874_906/907_VTS_01_1_1120_Rock 4875_906/907_VTS_01_2_427_Rock 4874_906/907_VTS_01_1_11_Plate 4874_906/907_VTS_01_1_1083_Plate 4874_906/907_VTS_01_2_671_Rock 4876_906/907_VTS_01_2_698_Rock 4744_906/907_VTS_01_2_1024_Rock 4874_906/907_VTS_01_2_246_Rock 4744_906/907_VTS_01_1_238_Rock 4874_906/907_VTS_01_1_345_Rock 4875_906/907_VTS_01_2_740_Rock 4874_906/907_VTS_01_1_1064_Plate 4874_906/907_VTS_01_2_933_Plate 4876_906/907_VTS_01_1_412_Rock 4875_906/907_VTS_01_1_676_Plate 4876_906/907_VTS_01_4_248_Plate 4874_906/907_VTS_01_3_274_Plate 4874_906/907_VTS_01_3_257_Plate 4874_906/907_VTS_01_3_244_Plate 4874_906/907_VTS_01_3_280_Plate 4874_906/907_VTS_01_3_1126_Plate 4875_906/907_VTS_01_1_1291_Plate 4876_906/907_VTS_01_2_1154_Plate 4876_906/907_VTS_01_3_769_Plate 4751_826_VTS_01_1_41 _Plate 4876_906/907_VTS_01_2_24_Plate 4873_906/907_VTS_01_1_156_Plate 4876_906/907_VTS_01_2_49_Plate 4876_906/907_VTS_01_1_259_Plate 4876_906/907_VTS_01_2_923_Plate 4746_906/907_VTS_01_3_488_Rock 4875_906/907_VTS_01_3_506_Plate 4875_906/907_VTS_01_2_503_Rock 4876_906/907_VTS_01_2_136_Plate 4747_906/907_VTS_01_1_3_1057_Rock 4875_906/907_VTS_01_2_290_Plae 4874_906/907_VTS_01_1_966_Plate 4874_906/907_VTS_01_3_305_Rock 4746_906/907_VTS_01_3_579_Plate 4875_906/907_VTS_01_4_251_Rock

Appendix 3-II. Multivariate determined sampling SITE CLUSTER GROUPS			
Group	Subgroup	No.	Station-Site-Image-Biotope
			4874_906/907_VTS_01_2_510_Plate 4876_906/907_VTS_01_2_1085_Plate 4875_906/907_VTS_01_4_908_Rock 4747_906/907_VTS_01_1_1054_Plate 4874_906/907_VTS_01_2_700_Rock 4874_906/907_VTS_01_3_963_Rock 4875_906/907_VTS_01_1_941_Plate 4875_906/907_VTS_01_1_98_Plate 4879_826_VTS_01_3_596_Plate 4876_906/907_VTS_01_2_877_Plate 4875_906/907_VTS_01_1_12_Plate 4875_906/907_VTS_01_1_117_Plate 4875_906/907_VTS_01_1_313_Plate 4747_906/907_VTS_01_1_2_928_Plate 4874_906/907_VTS_01_2_969_Rock 4746_906/907_VTS_01_3_719_Plate 4747_906/907_VTS_01_1_1166_Rock 4875_906/907_VTS_01_3_308_Rock 4876_906/907_VTS_01_2_1039_Plate 4876_906/907_VTS_01_4_472_Plate 4874_906/907_VTS_01_2_526_Rock 4875_906/907_VTS_01_1_652_Plate 4876_906/907_VTS_01_4_68_Plate 4876_906/907_VTS_01_3_713_Plate 4876_906/907_VTS_01_1_1262_Plate 4876_906/907_VTS_01_2_73_Plate 4876_906/907_VTS_01_3_916_Plate 4875_906/907_VTS_01_4_209_Plate 4876_906/907_VTS_01_2_953_Plate 4876_906/907_VTS_01_1_1282_Plate 4876_906/907_VTS_01_1_1279_Plate 4876_906/907_VTS_01_2_971_Plate 4874_906/907_VTS_01_3_317_Rock 4747_906/907_VTS_01_1_2_637_Rock 4874_906/907_VTS_01_1_998_Rock 4874_906/907_VTS_01_2_714_Rock 4746_906/907_VTS_01_4_843_Plate 4874_906/907_VTS_01_1_367_Plate 4744_906/907_VTS_01_2_610_Rock 4874_906/907_VTS_01_1_1040_Rock 4875_906/907_VTS_01_4_566_Rock 4744_906/907_VTS_01_2_586_Rock 4744_906/907_VTS_01_2_659_Rock

Appendix 3-II. Multivariate determined sampling SITE CLUSTER GROUPS			
Group	Subgroup	No.	Station-Site-Image-Biotope
			4876_906/907_VTS_01_1_859_Plate 4876_906/907_VTS_01_2_114_Plate 4874_906/907_VTS_01_1_376_Plate 4876_906/907_VTS_01_3_1064_Plate 4744_906/907_VTS_01_2_772_Plate 4876_906/907_VTS_01_3_448_Plate 4874_906/907_VTS_01_2_733_Rock 4744_906/907_VTS_01_1_1004_Rock 4744_906/907_VTS_01_3_1066_Plate 4747_906/907_VTS_01_1_1157_Plate 4874_906/907_VTS_01_3_1156_Rock 4876_906/907_VTS_01_2_1064_Plate 4873_906/907_VTS_01_3_282_Plate 4875_906/907_VTS_01_1_251_Plate 4747_906/907_VTS_01_1_1009_Plate 4875_906/907_VTS_01_3_950_Plate 4875_906/907_VTS_01_1_73_Plate 4875_906/907_VTS_01_1_184_Plate 4875_906/907_VTS_01_1_162_Plate 4875_906/907_VTS_01_1_205_Plate 4876_906/907_VTS_01_1_768_Plate 4875_906/907_VTS_01_3_926_Plate 4874_906/907_VTS_01_2_561_Plate 4875_906/907_VTS_01_3_802_Plate 4875_906/907_VTS_01_1_228_Plate 4875_906/907_VTS_01_3_985_Plate 4875_906/907_VTS_01_1_290_Plate 4875_906/907_VTS_01_3_848_Plate 4875_906/907_VTS_01_3_960_Plate 4745_906/907_VTS_01_2_621_Plate 4875_906/907_VTS_01_3_833_Plate 4875_906/907_VTS_01_3_876_Plate 4875_906/907_VTS_01_3_901_Plate 4876_906/907_VTS_01_1_784_Rock 4875_906/907_VTS_01_1_384_Plate 4875_906/907_VTS_01_4_219_Plate 4874_906/907_VTS_01_2_490_Plate 4876_906/907_VTS_01_1_834_Plate 4875_906/907_VTS_01_3_1037_Open 4747_906/907_VTS_01_1_2_943_Plate 4876_906/907_VTS_01_3_747_Plate 4876_906/907_VTS_01_1_1304_Plate 4875_906/907_VTS_01_3_815_Plate 4875_906/907_VTS_01_3_998_Open

Appendix 3-II. Multivariate determined sampling SITE CLUSTER GROUPS			
Group	Subgroup	No.	Station-Site-Image-Biotope
			4875_906/907_VTS_01_3_1012_Open 4876_906/907_VTS_01_1_1299_Plate 4874_906/907_VTS_01_2_615_Plate 4874_906/907_VTS_01_1_1121_Plate 4875_906/907_VTS_01_1_136_Plate 4745_906/907_VTS_01_3_697_Plate 4745_906/907_VTS_01_2_613_Plate 4875_906/907_VTS_01_3_915_Plate 4875_906/907_VTS_01_3_974_Plate 4875_906/907_VTS_01_3_1082_Plate 4875_906/907_VTS_01_3_1094_Plate 4875_906/907_VTS_01_3_939_Plate 4875_906/907_VTS_01_3_1111_Plate 4875_906/907_VTS_01_3_783_Plate 4875_906/907_VTS_01_3_863_Plate 4876_906/907_VTS_01_3_119_Rock 4746_906/907_VTS_01_1_306_Rock 4746_906/907_VTS_01_4_926_Plate 4744_906/907_VTS_01_1_578_Rock 4744_906/907_VTS_01_2_621_Rock 4747_906/907_VTS_01_1_1066_Rock 4744_906/907_VTS_01_3_888_Rock 4747_906/907_VTS_01_1_930_Rock 4875_906/907_VTS_01_3_177_Rock 4744_906/907_VTS_01_1_563_Rock 4744_906/907_VTS_01_4_50_Plate 4875_906/907_VTS_01_4_52_Rock 4747_906/907_VTS_01_1_1103_Plate 4875_906/907_VTS_01_4_134_Rock 4749_826_VTS_01_4_897_Open 4747_906/907_VTS_01_1_880_Plate 4747_906/907_VTS_01_1_2_920_Plate 4747_906/907_VTS_01_1_961_Plate 4747_906/907_VTS_01_1_3_38_Rock 4747_906/907_VTS_01_1_1183_Rock 4875_906/907_VTS_01_4_358_Rock 4744_906/907_VTS_01_1_1022_Rock 4746_906/907_VTS_01_1_213_Rock 4746_906/907_VTS_01_4_731_Rock 4876_906/907_VTS_01_3_363_Plate 4876_906/907_VTS_01_3_418_Plate 4876_906/907_VTS_01_2_1017_Plate

Appendix 3-II. Multivariate determined sampling SITE CLUSTER GROUPS			
Group	Subgroup	No.	Station-Site-Image-Biotope
C, D, E, F (almost all VK-906/907; almost all Rock)		34	4875_906/907_VTS_01_4_510_Rock 4875_906/907_VTS_01_4_921_Rock 4744_906/907_VTS_01_1_5_Rock 4744_906/907_VTS_01_4_1176_Rock 4747_906/907_VTS_01_1_1177_Rock 4876_906/907_VTS_01_1_100_Rock 4746_906/907_VTS_01_3_263_Thicket 4875_906/907_VTS_01_3_1128_Rock 4746_906/907_VTS_01_2_1296_Rock 4876_906/907_VTS_01_2_1117_Plate 4744_906/907_VTS_01_1_107_Rock 4746_906/907_VTS_01_4_692_Rock 4874_906/907_VTS_01_3_495_Rock 4746_906/907_VTS_01_4_1088_Rock 4746_906/907_VTS_01_4_1066_Rock 4875_906/907_VTS_01_1_852_Rock 4874_906/907_VTS_01_3_1198_Rock 4875_906/907_VTS_01_4_1177_Rock 4875_906/907_VTS_01_1_568_Rock 4875_906/907_VTS_01_4_1212_Rock 4875_906/907_VTS_01_1_373_Rock 4875_906/907_VTS_01_4_289_Rock 4746_906/907_VTS_01_1_203_Rock 4746_906/907_VTS_01_1_227_Rock 4746_906/907_VTS_01_4_244_Plate 4746_906/907_VTS_01_4_663_Rock 4746_906/907_VTS_01_4_839_Plate 4874_906/907_VTS_01_3_950_Rock 4746_906/907_VTS_01_3_54_Rock 4746_906/907_VTS_01_1__826_Rock 4746_906/907_VTS_01_2_78_Rock 4746_906/907_VTS_01_2_163_Rock 4751_826_VTS_01_1_623_Thicket 4746_906/907_VTS_01_3_312_Rock

Appendix 3-III. Multivariate determined BIOTOPE CLUSTER GROUPS AND SUBGROUPS by numeric designation, with list of component images (N_T = 419) and original empirical biotope designations. Images are identified by USGS station number, Viosca Knoll site number, digital images designation, and original empirical biotope category. Images with no megafauna scored are omitted (N_0=40). A few weakly-associated subgroups were combined for convenience into para-topic groups (i.e., 1A). BIOTOPE GROUP AND SUBGROUP clustergram is presented in Figure 3.20. Note: 906/907 designation within Station-Site-Image-Biotope equals 906/862 in text.

Appendix 3-III. Multivariate determined BIOTOPE CLUSTER GROUPS/SUBGROUPS				
Group	Subgroup	No.	Station-Site-Image-Biotope	Designation
1	1A	112	4752_826_VTS_01_3_85_Thicket 4749_826_VTS_01_5_37_Thicket 4751_826_VTS_01_2_709_Thicket 4877_826_VTS_01_2_809_Thicket 4879_826_VTS_01_2_726_Thicket 4749_826_VTS_01_1_280_Thicket 4749_826_VTS_01_4_729_Thicket 4748_826_VTS_01_4_1251_Thicket 4752_826_VTS_01_1_726_Thicket 4752_826_VTS_01_3_483_Thicket 4748_826_VTS_01_2_214_Thicket 4882_826_VTS_01_2_155_Thicket 4878_826_VTS_01_1_467_Thicket 4753_826_VTS_01_1_939_Thicket 4751_826_VTS_01_2_1002_Thicket 4751_826_VTS_01_2_690_Thicket 4880_826_VTS_01_1_317_Thicket 4751_826_VTS_01_1_599 _Thicket 4880_826_VTS_01_1_707_Thicket 4878_826_VTS_01_3_4_Thicket 4879_826_VTS_01_2_766_Thicket 4751_826_VTS_01_1_688_Thicket 4879_826_VTS_01_3_1217_Thicket 4880_826_VTS_01_1_482_Thicket 4881_826_VTS_01_3_817_Plate/Chemo 4753_826_VTS_01_4_18_Thicket 4751_826_VTS_01_3_1191_Thicket 4880_826_VTS_01_1_650_Thicket 4880_826_VTS_01_1_781_Thicket 4749_826_VTS_01_4_689_Thicket 4880_826_VTS_01_1_816_Thicket 4752_826_VTS_01_4_163_Thicket 4881_826_VTS_01_2_984_Thicket 4882_826_VTS_01_3_434_Thicket 4882_826_VTS_01_1_672_Thicket	Thicket Subgroup 1A

Appendix 3-III. Multivariate determined BIOTOPE CLUSTER GROUPS/SUBGROUPS				
Group	Subgroup	No.	Station-Site-Image-Biotope	Designation
			4880_826_VTS_01_4_545_Plate 4879_826_VTS_01_4_953_Plate 4880_826_VTS_01_2_1247_Plate/Chemo 4879_826_VTS_01_1_269_Plate 4879_826_VTS_01_1_294_Plate 4879_826_VTS_01_4_485_Thicket 4879_826_VTS_01_4_538_Plate 4879_826_VTS_01_4_563_Thicket 4880_826_VTS_01_1_772_Plate/Chemo 4879_826_VTS_01_4_380_Plate 4880_826_VTS_01_4_574_Plate/Chemo 4879_826_VTS_01_1_176_Plate 4879_826_VTS_01_1_36_Thicket 4881_826_VTS_01_2_998_Plate 4879_826_VTS_01_4_1207_Plate 4881_826_VTS_01_2_548_Plate/Chemo 4879_826_VTS_01_1_128_Thicket 4751_826_VTS_01_2_620_Thicket 4879_826_VTS_01_1_1077_Thicket 4749_826_VTS_01_4_1202_Thicket 4882_826_VTS_01_3_322_Thicket 4751_826_VTS_01_3_974 _Thicket 4749_826_VTS_01_4_110_Thicket 4882_826_VTS_01_3_131_Thicket 4752_826_VTS_01_1_569_Thicket 4752_826_VTS_01_1_861_Thicket 4751_826_VTS_01_1_568 _Thicket 4751_826_VTS_01_1_609_Thicket 4751_826_VTS_01_1_581 _Thicket 4880_826_VTS_01_1_1141_Thicket 4751_826_VTS_01_1_382 _Thicket 4879_826_VTS_01_1_677_Thicket 4882_826_VTS_01_4_4_Thicket 4877_826_VTS_01_3_1058_Thicket 4878_826_VTS_01_1_284_Thicket 4752_826_VTS_01_1_746_Thicket 4881_826_VTS_01_2_982_Thicket 4748_826_VTS_01_3_828_Thicket 4752_826_VTS_01_2_1015_Thicket 4753_826_VTS_01_4_1052_Thicket 4752_826_VTS_01_1_800_Thicket 4882_826_VTS_01_2_702_Thicket 4877_826_VTS_01_2_623_Thicket 4877_826_VTS_01_2_764_Thicket	

Appendix 3-III. Multivariate determined BIOTOPE CLUSTER GROUPS/SUBGROUPS				
Group	Subgroup	No.	Station-Site-Image-Biotope	Designation
			4878_826_VTS_01_3_446_Thicket 4880_826_VTS_01_4_1134_Thicket 4752_826_VTS_01_2_854_Thicket 4877_826_VTS_01_4_1044_Thicket 4751_826_VTS_01_1_133 _Thicket 4878_826_VTS_01_3_985_Thicket 4881_826_VTS_01_2_967_Thicket 4752_826_VTS_01_2_882_Thicket 4753_826_VTS_01_3_808_Thicket 4748_826_VTS_01_3_65_Thicket 4752_826_VTS_01_2_1088_Thicket 4879_826_VTS_01_5_5_Thicket 4751_826_VTS_01_1_660 _Thicket 4879_826_VTS_01_1_402_Thicket 4882_826_VTS_01_3_319_Thicket 4879_826_VTS_01_1_514_Thicket 4752_826_VTS_01_2_828_Thicket 4751_826_VTS_01_4_753_Thicket 4880_826_VTS_01_1_684_Thicket 4880_826_VTS_01_1_745_Thicket 4880_826_VTS_01_3_569_Thicket 4879_826_VTS_01_1_347_Thicket 4881_826_VTS_01_1_725_Thicket 4879_826_VTS_01_1_223_Thicket 4881_826_VTS_01_1_738_Thicket 4881_826_VTS_01_1_820_Thicket 4881_826_VTS_01_1_834_Thicket 4752_826_VTS_01_2_1073_Thicket 4752_826_VTS_01_3_385_Thicket 4882_826_VTS_01_1_438_Thicket 4878_826_VTS_01_1_31_Thicket 4880_826_VTS_01_1_41_Thicket 4880_826_VTS_01_4_1169_Thicket	
1	1B	18	4882_826_VTS_01_1_692_Thicket 4879_826_VTS_01_3_464_Thicket 4748_826_VTS_01_4_1104_Plate 4881_826_VTS_01_2_1291_Thicket 4753_826_VTS_01_2_408_Thicket 4880_826_VTS_01_4_605_Thicket 4879_826_VTS_01_2_267_Plate 4752_826_VTS_01_3_393_Thicket 4881_826_VTS_01_2_901_Thicket 4882_826_VTS_01_1_385_Thicket 4881_826_VTS_01_1_565_Rock	Thicket Subgroup 1B

Appendix 3-III. Multivariate determined BIOTOPE CLUSTER GROUPS/SUBGROUPS				
Group	Subgroup	No.	Station-Site-Image-Biotope	Designation
			4881_826_VTS_01_1_111_Plate/Chemo 4748_826_VTS_01_2_655_Rock 4880_826_VTS_01_1_1119_Plate/Chemo 4748_826_VTS_01_3_272_Thicket 4879_826_VTS_01_1_110_Thicket 4753_826_VTS_01_2_335_Thicket 4880_826_VTS_01_1_453_Thicket	
1	1C-1F	8	4751_826_VTS_01_2_1123_Thicket 4882_826_VTS_01_1_1164_Thicket 4749_826_VTS_01_4_1234_Thicket 4751_826_VTS_01_2_921_Thicket 4751_826_VTS_01_3_951_Thicket 4879_826_VTS_01_4_603_Plate 4879_826_VTS_01_1_23_Plate/Chemo 4880_826_VTS_01_4_449_Plate/Chemo	Thicket Para-Subgroup 1C/1F
2	2A	161	4746_906/907_VTS_01_4_217_Plate 4744_906/907_VTS_01_1_1102_Rock 4744_906/907_VTS_01_3_906_Plate 4874_906/907_VTS_01_2_573_Plate 4874_906/907_VTS_01_1_671_Plate 4744_906/907_VTS_01_3_1078_Plate 4744_906/907_VTS_01_3_1123_Plate 4876_906/907_VTS_01_2_901_Plate 4873_906/907_VTS_01_4_264_Plate 4875_906/907_VTS_01_1_272_Plate 4875_906/907_VTS_01_1_350_Plate 4876_906/907_VTS_01_2_21_Plate 4875_906/907_VTS_01_1_335_Plate 4876_906/907_VTS_01_2_92_Plate 4875_906/907_VTS_01_1_368_Plate 4876_906/907_VTS_01_1_322_Plate 4744_906/907_VTS_01_2_1253_Rock 4744_906/907_VTS_01_2_834_Rock 4746_906/907_VTS_01_1_1251_Plate 4874_906/907_VTS_01_1_1120_Rock 4875_906/907_VTS_01_2_427_Rock 4874_906/907_VTS_01_1_11_Plate 4874_906/907_VTS_01_1_1083_Plate 4874_906/907_VTS_01_2_671_Rock 4876_906/907_VTS_01_2_698_Rock 4744_906/907_VTS_01_2_1024_Rock 4874_906/907_VTS_01_2_246_Rock 4744_906/907_VTS_01_1_238_Rock 4874_906/907_VTS_01_1_345_Rock	Shallow Plate & Rock Subgroup 2A-1

Appendix 3-III. Multivariate determined BIOTOPE CLUSTER GROUPS/SUBGROUPS				
Group	Subgroup	No.	Station-Site-Image-Biotope	Designation
			4875_906/907_VTS_01_2_740_Rock 4874_906/907_VTS_01_1_1064_Plate 4874_906/907_VTS_01_2_933_Plate 4876_906/907_VTS_01_1_412_Rock 4875_906/907_VTS_01_1_676_Plate 4876_906/907_VTS_01_4_248_Plate 4874_906/907_VTS_01_3_274_Plate 4874_906/907_VTS_01_3_257_Plate 4874_906/907_VTS_01_3_244_Plate 4874_906/907_VTS_01_3_280_Plate 4874_906/907_VTS_01_3_1126_Plate 4875_906/907_VTS_01_1_1291_Plate 4876_906/907_VTS_01_2_1154_Plate 4876_906/907_VTS_01_3_769_Plate 4751_826_VTS_01_1_41 _Plate 4876_906/907_VTS_01_2_24_Plate 4873_906/907_VTS_01_1_156_Plate 4876_906/907_VTS_01_2_49_Plate 4876_906/907_VTS_01_1_259_Plate 4876_906/907_VTS_01_2_923_Plate 4746_906/907_VTS_01_3_488_Rock 4875_906/907_VTS_01_3_506_Plate 4875_906/907_VTS_01_2_503_Rock 4876_906/907_VTS_01_2_136_Plate 4747_906/907_VTS_01_1_3_1057_Rock 4875_906/907_VTS_01_2_290_Plate 4874_906/907_VTS_01_1_966_Plate 4874_906/907_VTS_01_3_305_Rock 4746_906/907_VTS_01_3_579_Plate 4875_906/907_VTS_01_4_251_Rock 4874_906/907_VTS_01_2_510_Plate 4876_906/907_VTS_01_2_1085_Plate 4875_906/907_VTS_01_4_908_Rock 4747_906/907_VTS_01_1_1054_Plate 4874_906/907_VTS_01_2_700_Rock 4874_906/907_VTS_01_3_963_Rock 4875_906/907_VTS_01_1_941_Plate 4875_906/907_VTS_01_1_98_Plate 4879_826_VTS_01_3_596_Plate 4876_906/907_VTS_01_2_877_Plate 4875_906/907_VTS_01_1_12_Plate 4875_906/907_VTS_01_1_117_Plate 4875_906/907_VTS_01_1_313_Plate 4747_906/907_VTS_01_1_2_928_Plate	

Appendix 3-III. Multivariate determined BIOTOPE CLUSTER GROUPS/SUBGROUPS				
Group	Subgroup	No.	Station-Site-Image-Biotope	Designation
			4874_906/907_VTS_01_2_969_Rock	
			4746_906/907_VTS_01_3_719_Plate	
			4747_906/907_VTS_01_1_1166_Rock	
			4875_906/907_VTS_01_3_308_Rock	
			4876_906/907_VTS_01_2_1039_Plate	
			4876_906/907_VTS_01_4_472_Plate	
			4874_906/907_VTS_01_2_526_Rock	
			4875_906/907_VTS_01_1_652_Plate	
			4876_906/907_VTS_01_4_68_Plate	
			4876_906/907_VTS_01_3_713_Plate	
			4876_906/907_VTS_01_1_1262_Plate	
			4876_906/907_VTS_01_2_73_Plate	
			4876_906/907_VTS_01_3_916_Plate	
			4875_906/907_VTS_01_4_209_Plate	
			4876_906/907_VTS_01_2_953_Plate	
			4876_906/907_VTS_01_1_1282_Plate	
			4876_906/907_VTS_01_1_1279_Plate	
			4876_906/907_VTS_01_2_971_Plate	
			4874_906/907_VTS_01_3_317_Rock	
			4747_906/907_VTS_01_1_2_637_Rock	
			4874_906/907_VTS_01_1_998_Rock	
			4874_906/907_VTS_01_2_714_Rock	
			4746_906/907_VTS_01_4_843_Plate	
			4874_906/907_VTS_01_1_367_Plate	
			4744_906/907_VTS_01_2_610_Rock	
			4874_906/907_VTS_01_1_1040_Rock	
			4875_906/907_VTS_01_4_566_Rock	
			4744_906/907_VTS_01_2_586_Rock	
			4744_906/907_VTS_01_2_659_Rock	
			4876_906/907_VTS_01_1_859_Plate	
			4876_906/907_VTS_01_2_114_Plate	
			4874_906/907_VTS_01_1_376_Plate	
			4876_906/907_VTS_01_3_1064_Plate	
			4744_906/907_VTS_01_2_772_Plate	
			4876_906/907_VTS_01_3_448_Plate	
			4874_906/907_VTS_01_2_733_Rock	
			4744_906/907_VTS_01_1_1004_Rock	
			4744_906/907_VTS_01_3_1066_Plate	
			4747_906/907_VTS_01_1_1157_Plate	
			4874_906/907_VTS_01_3_1156_Rock	
			4876_906/907_VTS_01_2_1064_Plate	
			4873_906/907_VTS_01_3_282_Plate	
			4875_906/907_VTS_01_1_251_Plate	
			4747_906/907_VTS_01_1_1009_Plate	

Appendix 3-III. Multivariate determined BIOTOPE CLUSTER GROUPS/SUBGROUPS				
Group	Subgroup	No.	Station-Site-Image-Biotope	Designation
			4875_906/907_VTS_01_3_950_Plate 4875_906/907_VTS_01_1_73_Plate 4875_906/907_VTS_01_1_184_Plate 4875_906/907_VTS_01_1_162_Plate 4875_906/907_VTS_01_1_205_Plate 4876_906/907_VTS_01_1_768_Plate 4875_906/907_VTS_01_3_926_Plate 4874_906/907_VTS_01_2_561_Plate 4875_906/907_VTS_01_3_802_Plate 4875_906/907_VTS_01_1_228_Plate 4875_906/907_VTS_01_3_985_Plate 4875_906/907_VTS_01_1_290_Plate 4875_906/907_VTS_01_3_848_Plate 4875_906/907_VTS_01_3_960_Plate 4745_906/907_VTS_01_2_621_Plate 4875_906/907_VTS_01_3_833_Plate 4875_906/907_VTS_01_3_876_Plate 4875_906/907_VTS_01_3_901_Plate 4876_906/907_VTS_01_1_784_Rock 4875_906/907_VTS_01_1_384_Plate 4875_906/907_VTS_01_4_219_Plate 4874_906/907_VTS_01_2_490_Plate 4876_906/907_VTS_01_1_834_Plate 4875_906/907_VTS_01_3_1037_Open 4747_906/907_VTS_01_1_2_943_Plate 4876_906/907_VTS_01_3_747_Plate 4876_906/907_VTS_01_1_1304_Plate 4875_906/907_VTS_01_3_815_Plate 4875_906/907_VTS_01_3_998_Open 4875_906/907_VTS_01_3_1012_Open 4876_906/907_VTS_01_1_1299_Plate 4874_906/907_VTS_01_2_615_Plate 4874_906/907_VTS_01_1_1121_Plate 4875_906/907_VTS_01_1_136_Plate 4745_906/907_VTS_01_3_697_Plate 4745_906/907_VTS_01_2_613_Plate 4875_906/907_VTS_01_3_915_Plate 4875_906/907_VTS_01_3_974_Plate 4875_906/907_VTS_01_3_1082_Plate 4875_906/907_VTS_01_3_1094_Plate 4875_906/907_VTS_01_3_939_Plate 4875_906/907_VTS_01_3_1111_Plate 4875_906/907_VTS_01_3_783_Plate 4875_906/907_VTS_01_3_863_Plate	

Appendix 3-III. Multivariate determined BIOTOPE CLUSTER GROUPS/SUBGROUPS				
Group	Subgroup	No.	Station-Site-Image-Biotope	Designation
2	2B	59	4877_826_VTS_01_1_1169_Plate/Chemo 4748_826_VTS_01_1_337_Plate/Chemo 4880_826_VTS_01_4_470_Plate/Chemo 4748_826_VTS_01_2_792_Plate/Chemo 4880_826_VTS_01_3_1171_Plate/Chemo 4746_906/907_VTS_01_1_194_Open 4752_826_VTS_01_4_1237_Open 4752_826_VTS_01_2_677_Open 4879_826_VTS_01_2_15_Plate 4879_826_VTS_01_4_509_Plate 4879_826_VTS_01_5_6_Plate/Chemo 4875_906/907_VTS_01_3_1025_Open 4880_826_VTS_01_2_657_Open 4752_826_VTS_01_4_420_Open 4877_826_VTS_01_2_149_Open 4746_906/907_VTS_01_1_130_Open 4752_826_VTS_01_1_123_Open 4752_826_VTS_01_1_1158_Open 4877_826_VTS_01_2_755_Open 4877_826_VTS_01_2_172_Open 4744_906/907_VTS_01_3_957_Open 4877_826_VTS_01_2_183_Open 4746_906/907_VTS_01_1_101_Open 4746_906/907_VTS_01_1_115_Open 4879_826_VTS_01_1_301_Plate/Chemo 4748_826_VTS_01_1_729_Plate/Chemo 4752_826_VTS_01_1_1_Open 4752_826_VTS_01_4_769_Open 4880_826_VTS_01_2_1118_Plate/Chemo 4880_826_VTS_01_4_349_Plate/Chemo 4880_826_VTS_01_4_378_Plate/Chemo 4879_826_VTS_01_1_157_Plate/Chemo 4879_826_VTS_01_4_645_Plate/Chemo 4879_826_VTS_01_1_899_Plate/Chemo 4880_826_VTS_01_2_1020_Plate/Chemo 4880_826_VTS_01_4_428_Plate/Chemo 4879_826_VTS_01_1_337_Plate/Chemo 4880_826_VTS_01_4_517_Plate/Chemo 4879_826_VTS_01_1_120_Plate/Chemo 4880_826_VTS_01_1_1043_Plate/Chemo 4880_826_VTS_01_2_1067_Plate/Chemo 4879_826_VTS_01_1_175_Plate/Chemo	Deep Plate/Chemo & Open Subgroup 2A-2

Appendix 3-III. Multivariate determined BIOTOPE CLUSTER GROUPS/SUBGROUPS				
Group	Subgroup	No.	Station-Site-Image-Biotope	Designation
			4879_826_VTS_01_1_867_Plate/Chemo 4880_826_VTS_01_2_1155_Plate/Chemo 4880_826_VTS_01_2_1195_Plate/Chemo 4879_826_VTS_01_1_138_Plate/Chemo 4880_826_VTS_01_2_1208_Plate/Chemo 4880_826_VTS_01_4_490_Plate/Chemo 4879_826_VTS_01_1_55_Plate/Chemo 4879_826_VTS_01_1_93_Plate/Chemo 4879_826_VTS_01_1_835_Plate/Chemo 4879_826_VTS_01_3_345_Open 4880_826_VTS_01_1_829_Plate/Chemo 4880_826_VTS_01_1_1182_Plate/Chemo 4880_826_VTS_01_1_1010_Plate/Chemo 4880_826_VTS_01_1_1094_Plate/Chemo 4879_826_VTS_01_1_479_Plate/Chemo 4879_826_VTS_01_1_801_Plate/Chemo 4880_826_VTS_01_4_402_Plate/Chemo	
2B	2B-2G	27	4876_906/907_VTS_01_3_119_Rock 4746_906/907_VTS_01_1_306_Rock 4746_906/907_VTS_01_4_926_Plate 4744_906/907_VTS_01_1_578_Rock 4744_906/907_VTS_01_2_621_Rock 4747_906/907_VTS_01_1_1066_Rock 4744_906/907_VTS_01_3_888_Rock 4747_906/907_VTS_01_1_930_Rock 4875_906/907_VTS_01_3_177_Rock 4744_906/907_VTS_01_1_563_Rock 4744_906/907_VTS_01_4_50_Plate 4875_906/907_VTS_01_4_52_Rock 4747_906/907_VTS_01_1_1103_Plate 4875_906/907_VTS_01_4_134_Rock 4749_826_VTS_01_4_897_Open 4747_906/907_VTS_01_1_880_Plate 4747_906/907_VTS_01_1_2_920_Plate 4747_906/907_VTS_01_1_961_Plate 4747_906/907_VTS_01_1_3_38_Rock 4747_906/907_VTS_01_1_1183_Rock 4875_906/907_VTS_01_4_358_Rock 4744_906/907_VTS_01_1_1022_Rock 4746_906/907_VTS_01_1_213_Rock 4746_906/907_VTS_01_4_731_Rock 4876_906/907_VTS_01_3_363_Plate 4876_906/907_VTS_01_3_418_Plate 4876_906/907_VTS_01_2_1017_Plate	Mostly Shallow, Mostly Rock Para-Group 2B/6

Appendix 3-III. Multivariate determined BIOTOPE CLUSTER GROUPS/SUBGROUPS				
Group	Subgroup	No.	Station-Site-Image-Biotope	Designation
3-6		34	4875_906/907_VTS_01_4_510_Rock 4875_906/907_VTS_01_4_921_Rock 4744_906/907_VTS_01_1_5_Rock 4744_906/907_VTS_01_4_1176_Rock 4747_906/907_VTS_01_1_1177_Rock 4876_906/907_VTS_01_1_100_Rock 4746_906/907_VTS_01_3_263_Thicket 4875_906/907_VTS_01_3_1128_Rock 4746_906/907_VTS_01_2_1296_Rock 4876_906/907_VTS_01_2_1117_Plate 4744_906/907_VTS_01_1_107_Rock 4746_906/907_VTS_01_4_692_Rock 4874_906/907_VTS_01_3_495_Rock 4746_906/907_VTS_01_4_1088_Rock 4746_906/907_VTS_01_4_1066_Rock 4875_906/907_VTS_01_1_852_Rock 4874_906/907_VTS_01_3_1198_Rock 4875_906/907_VTS_01_4_1177_Rock 4875_906/907_VTS_01_1_568_Rock 4875_906/907_VTS_01_4_1212_Rock 4875_906/907_VTS_01_1_373_Rock 4875_906/907_VTS_01_4_289_Rock 4746_906/907_VTS_01_1_203_Rock 4746_906/907_VTS_01_1_227_Rock 4746_906/907_VTS_01_4_244_Plate 4746_906/907_VTS_01_4_663_Rock 4746_906/907_VTS_01_4_839_Plate 4874_906/907_VTS_01_3_950_Rock 4746_906/907_VTS_01_3_54_Rock 4746_906/907_VTS_01_1__826_Rock 4746_906/907_VTS_01_2_78_Rock 4746_906/907_VTS_01_2_163_Rock 4751_826_VTS_01_1_623_Thicket 4746_906/907_VTS_01_3_312_Rock	

Appendix 3-IV. SPECIES CLUSTER GROUP composition (refer to Figure 3.24).

Group	CPCe Code	CPCe Description
I	WA	White anemone
	UNK	Unknown
II	BLC	Brown *Lophelia* coral
	WLC	White *Lophelia* coral
III	BAM	Bamboo coral
IV-XIV	RBC	Red black coral
	WBC	White black coral
	BAC	Bacterial mat
	GS	Glass sponge
	UA	Unidentified anemones
	SL	Squat lobster
	TW	Tube worms
	HYD	Hydroids
	CRI	Crinoid
	DS	Desmo sponge
	BCYR	Black Cerianthid
XV	PENU	Pencil urchin
	POBC	Pink black coral
	EURC	Echinus
	BR	Brisingid
	DA	Dandelion anemone
	UCR	Unidentified crinoids and brittlestars
	LST	Luidia star
	BLU	Blue biofilm
	UAL	Unknown Alcyonarian
	SW	Serpulid worms
	UCL	Unidentified crab and lobster
	UBC	Unidentified black coral
	CLAM	Dead clam
	PST	Pillow star
	FG	Fan gorgonian
	BA	Bamboo coral anemone
	PCYR	Pink cerianthid
	FS	Finger sponge
	VS	Vase sponge
	CS	Cleaner shrimp
	FHYD	Fan hydroid
	UOC	Unidentified octopus