Deep-Sea Research II 56 (2009) 1830–1833

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Faunal zonation of large epibenthic invertebrates off North Carolina revisited

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ARTICLE INFO

Available online 28 May 2009

Keywords:
Deep-sea faunal zonation
Epibenthic invertebrates
North Carolina (USA)

ABSTRACT

The dominant populations of large epibenthic megafauna off North Carolina were mapped in the 1960s from the upper continental slope out to the Hatteras Abyssal Plain using multi-shot sea-floor photography. The present re-analysis of the original data using contemporary computer-based methods and geo-referenced mapping (GIS) reveal that the overall patterns inferred initially can be substantiated. Individual species occurred in narrow depth bands that hugged the topography along the entire sampling area, but multi-species assemblages emerge with the modern, more formal quantitative methods.

1. Introduction

The Census of Marine Life (CoML) has expectations that the Ocean Biological Information System (OBIS) will archive the locations where all species of marine life are encountered, thus eventually allowing maps of all species distributions to be mapped world-wide, a broad vision attributed to J. Frederick Grassle, to whom we are contributing this paper. This short note is an attempt to assemble a small subset of earlier data into the context of the Continental Margins Ecosystem (COMARGE) project, which is one of the many components of CoML initiatives. Most importantly, this area in the NW Atlantic off North Carolina is familiar to Fred Grassle and the second author, as they worked there, between touch football games, contemporaneously on the R/V EASTWARD, memories perhaps best forgotten.

The data involved were collected from the R/V EASTWARD using a multi-shot bottom pogo camera that captured 25–50 exposures, covering 6.3 m^2 of sea floor with each shot. The advantage of the pogo camera is that every picture was taken at the same height and angle above the sea floor, thus exposing a well-defined area, which allowed quantitative estimates of the densities of visible abundant organisms. By capturing dominant animals in bottom trawls at the same locations as the camera lowerings, the dominant animals in the photos could be identified to species. [Specific details on the methods are available in Rowe and Menzies (1969).] A total of 157 camera lowerings were accomplished, with 27 species identified over the area surveyed. The mapping extended from 32° and 34°N to 77° and 71°W. The original analyses were presented in the second author's Ph.D. thesis at Duke (1968). The patterns were also compared closely with those described by Grassle et al. (1975) off New England using DSRV ALVIN. The photographs provided accurate counts of the abundant species as a function of depth and latitude. Multi-species assemblages were defined as depth ranges with a minimum of change in species, whereas boundaries between assemblages were locations where the rate of change in species composition was a maximum (Menzies et al., 1973). This use of 'overlap frequencies' or numbers of first and last entries on the depth gradient has been a traditional approach to defining zonation (Carney, 2005). The depth bands of species which occurred together in high frequency were considered to be faunal zones (Rowe and Menzies, 1969; Menzies et al., 1973).

The objective of the present paper is to re-examine the 40-year-old data set with the new multivariate analytic methods now available in commercial statistical packages. The natural grouping of samples was identified based on the similarity of the multi-species database. A geo-referenced map was constructed to make the information more readily available through CoML and subject the earlier conclusions to an objective re-assessment.

2. Data analyses

For our re-assessment, species abundances (the number of individuals) at each location were 4th root transformed to construct a matrix of intra-sample similarities (Bray–Curtis similarity) to be analyzed using the package PRIMER version 6. At the same time, a modified Normalized Expected Shared Species (NNESS) index (Gallagher, 1996; Grassle and Smith, 1976) was computed using COMPAH96 to compare with Bray–Curtis similarity. Cluster analysis (group-average linkage) was done with SIMPROF, testing the null hypothesis that a sub-cluster within the

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doi:10.1016/j.dsr2.2009.05.006

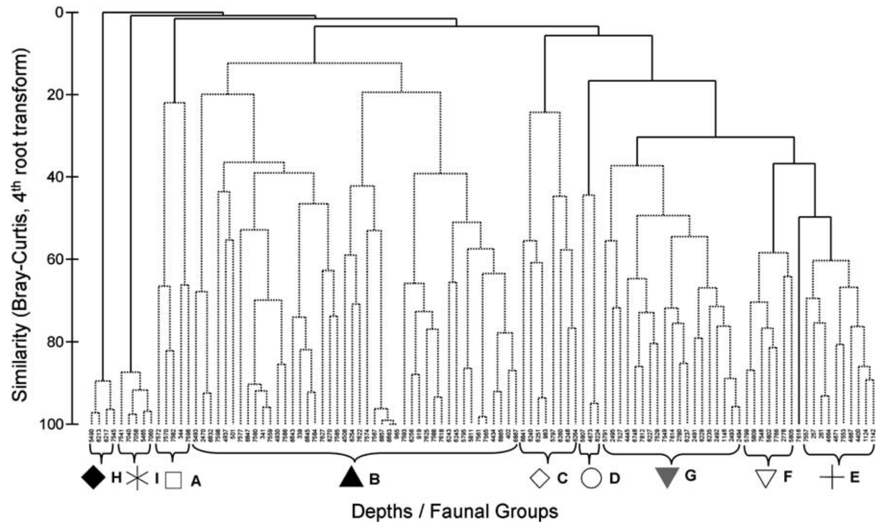

Fig. 1. Group-average clustering based on faunal similarity. The species abundances were 4th root transformed before converting to Bray–Curtis similarities. *X*-axis represents the sampling depth (m) and faunal zones. *Y*-axis represents the similarity (%). Solid lines indicate significant evidence of structure (SIMPROF test, $P<0.05$). Dotted lines indicate no evidence of structure.

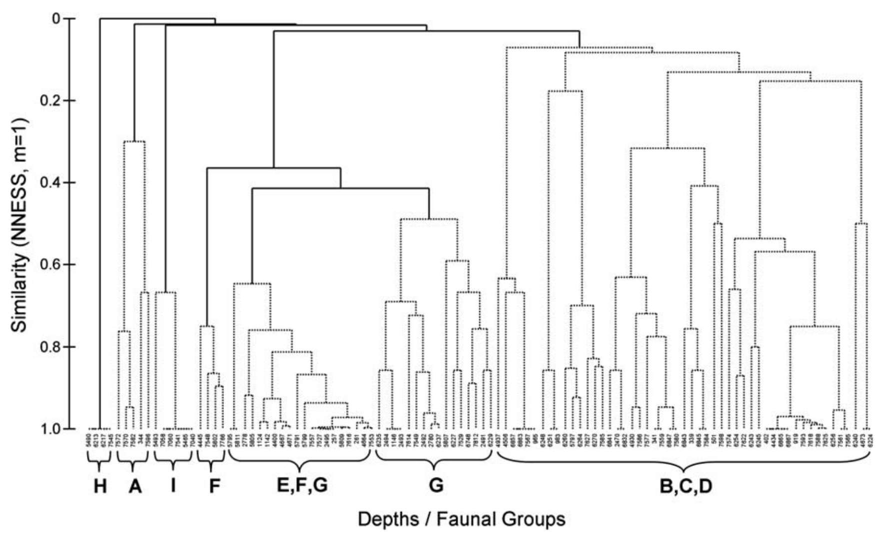

Fig. 2. Group-average clustering based on the modified Normalized Expected Shared Species (NNESS) at a random sample size (m) of 1. *X*-axis represents the sampling depth (m) and faunal zones. The symbols indicate significant faunal zones based on Fig. 1. *Y*-axis represents the NNESS coefficient. Solid lines indicate significant evidence of structure (SIMPROF test, $P<0.05$). Dotted lines indicate no evidence of structure.

dendrogram can be recreated by permuting the entry species and locations. Sub-clusters confirmed by SIMPROF ($P<0.05$) were considered to be natural faunal groups. The intra-sample similarities were used to compute non-metric multi-dimensional scaling (MDS) in which the faunal similarities between sites were represented by distances. The species in each faunal zone were broken down to percent contribution (SIMPER) to the average faunal similarity within the zone. Bathymetric data were derived from the NOAA National Geophysical Data Center and the map was produced using ArcGIS® 9.0.

3. Results

The original analysis, 40 years ago considered faunal discontinuities to be located at depths where the fewest species overlap. These minima were encountered at the outer margin of Blake Plateau (1000 m), the upper continental rise (3600 m), the lower rise and the Abyssal plain (Rowe, 1968; Rowe and Menzies, 1969). The highest densities were encountered along abrupt boundaries at the shallow end of distributions, tapering out with depth. Several species were thought to 're-appear' in a second band in deeper water, after a hiatus at intermediate depths.

The current analysis with PRIMER identified 9 significant faunal zones, assigned alphabetical labels from shallow to deep (Fig. 1). The shallow Zones A, B and C have very low within-zone faunal similarity ($<30\%$); the intermediate Zones D and G have faunal similarity of about 40%; the deeper Zones E and F have faunal similarity of about 60% and the deepest Zones I and H have faunal similarity of about 90%. Separated clustering based on NNESS ($m=1$) generally agrees with results of the Bray–Curtis similarity (Fig. 1), where Zones B, C, D and part of Zones E, F and G are lumped together (Fig. 2). The same symbols were used in the Map (Fig. 3) and MDS plot (Fig. 4) to see the relationships between the data and the geographic location of the population under scrutiny.

The faunal zones were distributed in narrow ribbons along the depth contours. Dense and narrow zones occurred at the area with

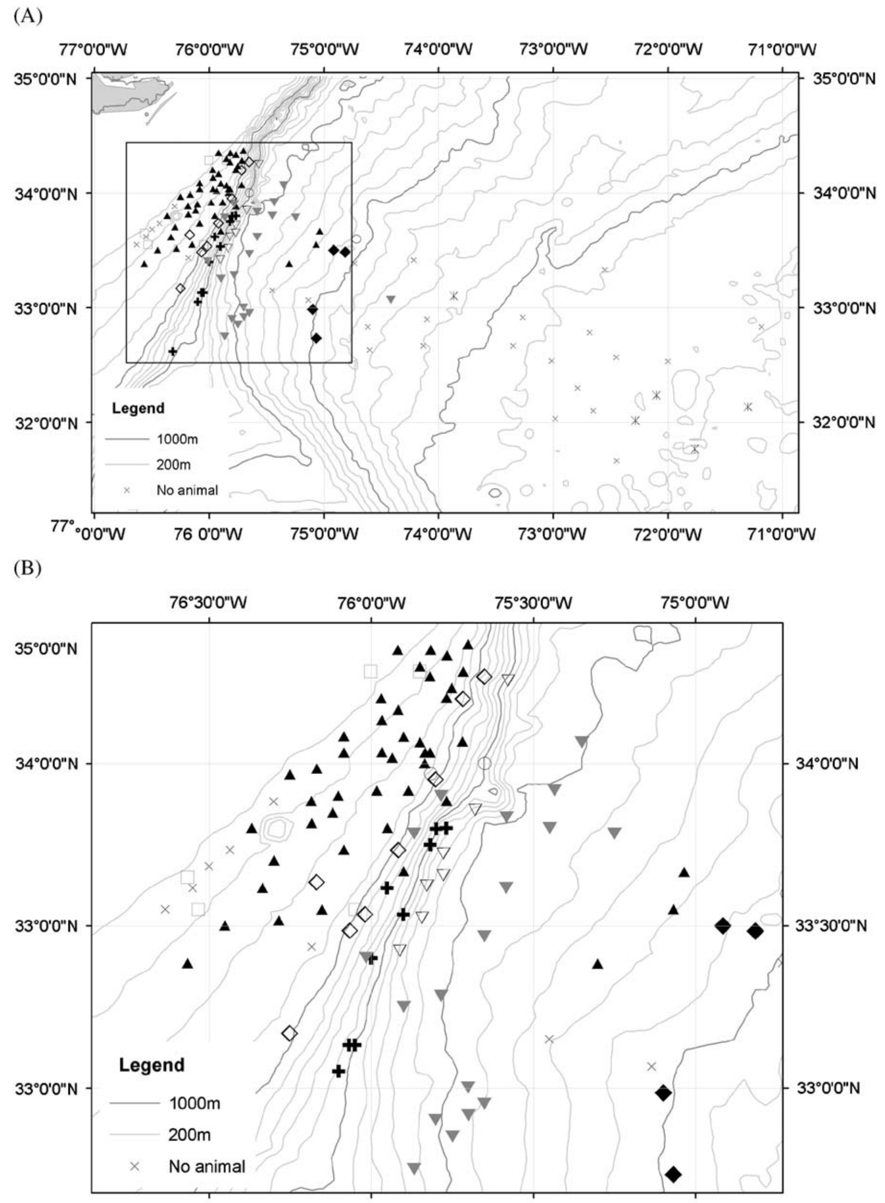

Fig. 3. Sampling area and distribution of significant faunal groups based on cluster analysis. Group symbols are identical to Fig. 1. The second figure is a close-up view of the square area in the first figure.

the steepest topography (1000–3000 m). Zones B and G occurred in bands at several depth ranges (expatriate/recurrent population). Large animals were absent between 4100 and 5300 m, separating the *Umbellula lindahli* population in Zone H from *Amphiophiura bullata* population in Zone I.

Non-metric MDS (Fig. 4) illustrates that the faunal composition in Zone H was very different from the rest of the zones that cluster together (faunal discontinuity). There was also one station in Zone A outside of that cluster. Faunal zones were generally distinct with little overlap. The faunal composition in Zones B, C, D, E, F and G are close, while Zones A and I appear to be more different from the subgroup mentioned above. Zones E, F and G overlap to some degree. Based on the MDS plot, 9 faunal zones can be lumped into 4 major depth zones with more similar faunal compositions, including (1) a shelf-transition (Zone A), (2) a continental slope and the upper rise (Zones B, C, D, E, F and G), (3) the lower continental rise (Zone H) and (4) the Abyssal Plain (Zone I).

4. Characteristics of each depth zone

The shelf-transition communities of Zone A (267–405 m), plus one outlier at 818 m, are composed of the hermit crab *Catapagurus sharreri*, and the anemones *Cidaris abyssicola* and *Actinauge logicornis* . These three species contributed more than 90% to the within-zone faunal similarity (Table 1). The continental slope and upper rise communities (287–3265 m), Zone B, covered most of the upper slope (287–890 m), but there were 2 reoccurring patches at the mid slope (1375–1547 m) and the upper rise (3428–3610 m). The large tubiculous polychaete *Hyalinoecia tubicola*, the squat lobster *Munida valida*, the hermit crab *Parapagurus pilosimanus* and the crab *Cancer borealis* were the most important species. Zone C occurred on the mid slope (992–1450 m), but there was one station at 620 m. The cnidarians *Flabellum Goodei* and *Cerianthis sp.* explained more than 90% of average similarity within Zone C. Zone E (1500–2170 m), Zone F

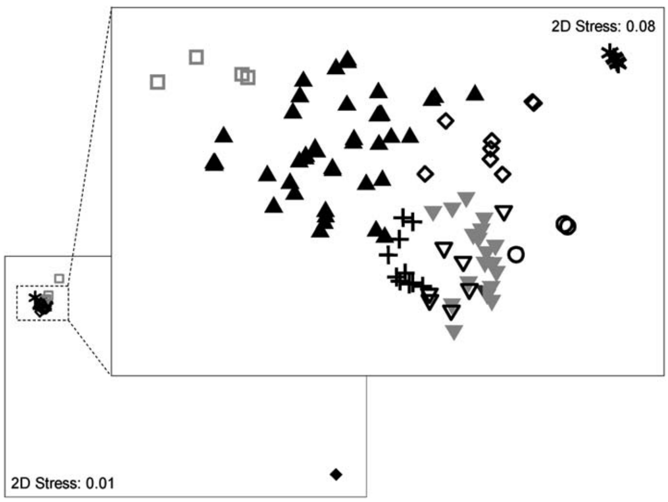

Fig. 4. Non-metric MDS plot for species abundance data. Group symbols are identical to Fig. 1. The analysis is based on 4th root transformed data and Bray–Curtis similarity. The bottom left figure is the MDS for all the samples. The upper right is a separate MDS that excluded outliers.

Table 1
Species contributing the most to average similarity within faunal zones.

Group	Av. Sim%	Species	Av. Abund	Contrib%	Cum%
A	41.32	*Catapagurus sharreri*	0.64	75.45	75.45
		Cidaris abyssicola	0.27	16.01	91.46
		Actinauge longicornis	0.25	8.54	100
B	25.17	*Hyalinoecia tubicola*	0.48	33.97	33.97
		Munida valida	0.42	32.9	66.87
		Parapagurus pilosimanus	0.28	14.38	81.25
		Cancer borealis	0.18	12.38	93.63
C	39.18	*Flabellum goodei*	0.68	70.52	70.52
		Cerianthis sp.	0.48	27.11	97.63
D	61.26	*Pennatula aculeata*	0.46	100	100
E	66.77	*Ophiomusium lymani*	2.09	67.11	67.11
		Ophiacanatha simulans	1.31	29.04	96.15
F	66.29	*Ophiomusium lymani*	1.32	48.56	48.56
		Anthomastus grandiflorus	1.06	48.49	97.06
G	52.16	*Ophiomusium lymani*	0.75	54.85	54.85
		Hyalonema boreale	0.73	29.36	84.2
		Pennatula aculeata	0.34	10.48	94.69
H	91.94	*Umbellula lindahli*	0.51	100	100
I	91.08	*Amphiophiura bullata*	0.55	100	100

Av. Sim is the average Bray–Curtis similarity within a faunal zone. Av. Abund is the animal abundance per photo within the faunal zones. Contrib% is the percent contribution of species to the average similarity within a faunal zone. Cum% is the cumulative percent contribution.

(2440–2810 m) and Zone G (2800–3265 m) stretched along the lower slope to upper rise. However, Zone G had another patch which re-occurred between 1392 and 1765 m, as well as one station at 4452 m. The brittle star *Ophiomusium lymani* was the most important species in these areas, contributing about 50% or more of the average within zone similarities. Zone D was patchily distributed at three different depths (1032, 2582 and 3830 m) where only one species (the stalked sea pen *Pennatula aculeate*) had been photographed. The lower rise community (3750–4050 m), Zone H, was broadly distributed with only the stalked anthozoan *U. lindahli* present in the photos. The Abyssal Plain community (5320–5340 m), Zone I, only had a single species, the large brittle star *A. bullata*. This species was also sampled at 4685 m.

5. Discussion

The general patterns of distributions of individual species in narrow depth bands remain the same, but the multivariate analyses reveal more nuanced information with greater confidence. Multiple sub-zones were defined with the new methods, accompanied by 'outliers', much of which was not recognized in Rowe and Menzies (1969).

The new analyses illustrate that 'depth' rarely forms an immutable boundary, especially on the lower end of distributions of individual species or of groups of species because the assemblages in several instances appear 'out of place (depth)'. If the fauna is particularly sparse, with only one or two species occurring at frequencies of only one or two per hectare, then machine-based analyses are hardly worthwhile.

What were called "recurrent zones" on the upper slope (the 'main' population), with repeats at mid slope and upper rise (Zone B), were confirmed, as was Zone G on the mid slope and upper rise (main population). The original study was based on the distribution of individual species. The current analyses suggest that the assemblages may recur as outliers at deeper depths.

Acknowledgements

This re-analysis was supported by the departments of Oceanography at TAMU and Marine Biology at TAMUG. The original data were derived from a dissertation at Duke by GTR, with support from a grant from the US NIH and an NSF Graduate Fellowship in Biological Oceanography under the direction of Robert J. Menzies. The captain and crew of the R/V EASTWARD, along with electronics technician James Cason, played pivotal roles in the sampling. The data have been deposited in the Ocean Biological Information System (OBIS) as a contribution to the Continental Margin Ecosystem (COMARGE), directed by Myriam Sibuet, a component of the Census of Marine Life (CoML), the inspiration of J. Fred Grassle.

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