COMMUNITY STRUCTURE OF DEEP-SEA BIVALVE MOLLUSKS

FROM THE NORTHERN GULF OF MEXICO

A Thesis

by

MIN CHEN

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

December 2003

Major Subject: Oceanography

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ABSTRACT

Community Structure of Deep-sea Bivalve Mollusks from

the Northern Gulf of Mexico. (December 2003)

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Density, species diversity, species richness, and evenness of bivalve mollusks were measured in the deep (0.2km to 3.7km) northern Gulf of Mexico to describe the community structure of benthic bivalve mollusks. Density decreased gradually from shallow continental slope depths, with remarkably high values in the Mississippi canyon, to the deepest sites. Diversity of bivalve mollusks increased from shallow continental slope depths, with low values in the Mississippi canyon, to a maximum at intermediate depths (1-2km), followed by a decrease down to the deepest locations (3.7km). Nine distinct groups were formed on the basis of the similarity in species composition. The pattern varied more abruptly on the slope compared to the deeper depths, possibly due to steeper gradients in physical variables.

ANOVA indicated that the density of bivalve mollusks was not significantly different at different depths, was not significantly different on different transects, was not significantly different between basin and non-basin, but was significantly different in canyon and non-canyon locations. Similar distinctions were observed in diversity, except that basins were lower than non-basins. The patterns observed reflect the intense

elevated input of terrigenous sediments accompanied by high surface-water plankton

production from the Mississippi River to the north central gulf.

DEDICATION

TO MY FAMILY

ACKNOWLEDGEMENTS

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INTRODUCTION

Mollusks are distributed widely from shallow water to the deep sea. They provide clues about the deep-sea bottom conditions. Some mollusks such as mussels can be important indicators for hydrothermal vents and hydrocarbon seeps. The "health" of the ecosystem in the area can be evaluated based on the community structure of mollusks. By understanding the natural range of variability that exists within mollusk populations, mollusks can be used to assess the effects of natural and human disturbance.

Mollusks are one of the dominant invertebrate groups in the deep sea. Wigley and McIntyre (1964) found the most important taxonomic groups were Crustacea, Mollusca and Polychaeta offshore south of Martha's Vineyard, Massachusetts. Rowe, et al. (1982) found the principal deep-sea macrobenthos were the polychaete annelid worms, bivalve mollusks, and crustaceans on the continental margin of the northwest Atlantic Ocean. In the comparative study of Sanders (1968), the polychaetes and bivalves of the samples were compared since these two groups comprised about 80% of the macrobenthos by number in most of the samples. From 1960 to 1966, Sanders and Hessler (1969) studied a transect of the ocean floor between southern New England and Bermuda to the tropical Atlantic. The samples were mainly composed of Polychaeta, Crustacea, and Bivalvia. On the continental slope off New Jersey and Delaware, annelids, arthropods and mollusks formed 84% of the benthic macrofauna (Grassle and Maciolek,1992). In this study, density, zonation and species diversity were used to

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This thesis follows the style and format of Deep-Sea Research I.

describe the community structure of benthic mollusks in the northern Gulf of Mexico.

Density

The deep sea is a nutrient-poor environment. Nutrients come from extrinsic sources and reach the deep sea in the form of small particulate organic material, feces and large sinking particles. In the world ocean, the density of the macrofauna generally diminishes with depth and distance from shore, as well as from polar and temperate to tropical latitudes (Filatova, 1982). The dependence of benthic fauna on available food resources is the crucial controlling factor (Belyaev, 1966).

Sanders et al. (1965) found that bivalve density decreased with depth and distance from the continent along the Gay Head-Bermuda transect. Moreover, the Eulamellibranchiata formed 77 and 95% of the bivalves on the outer continental shelf and upper continental slope, respectively. Thereafter, their percent composition diminished continuously with distance from the continent. The Protobranchiata showed the contrasting distribution pattern.

Diversity

Species diversity in the deep-sea benthos is higher than originally expected. It is as high as that in other physically stable, shallow, tropical marine environment (Sanders,1969). Rex (1981, 1983) suggested that all macrofaunal taxa have a parabolic pattern in diversity with respect to depth. Species diversity in the bivalves (H. L. Sanders, unpublished data), gastropods (Rex, 1973, 1976), polychaetes (Hartman, 1965), and cumaceans (Johnes and Sanders, 1972) increase with depth to a maximum at intermediate depths of about 3km and then decrease at abyssal depths in the

northwestern Atlantic (Rex, 1983).

Theories that explain the high deep-sea benthic diversity include the stability-time hypothesis (Sanders, 1968), biological disturbance (Dayton and Hessler, 1972), contemporaneous disequilibrium (Grassle and Sanders, 1973; Jumars, 1975, 1976), both predation and competition mediated by productivity (Rex, 1976), and dynamic equilibrium between rates of competitive displacement and the frequency of population reduction (Huston, 1979). The stability-time hypothesis proposed that on an evolutionary time-scale a physically predictable environment allows biological interactions to stabilize and this leads to highly diverse and "biologically accommodated" communities (Sanders, 1968). Dayton and Hessler (1972) proposed that high diversity may be maintained by biological disturbance in the form of "cropping" by large epibenthic invertebrates and fish that could reduce the importance of competitive exclusion and permit the coexistence of many species which shared the same resources. Grassle and Sanders (1973) suggested that niche diversification can be multidimensional, including numerous biotic, biochemical, physical and temporal differences, so that diversity could be maintained. Jumars (1975, 1976) pointed out that the stability of deep-sea sediments may allow exploitation of microhabitats by either contemporaneous disequilibrium, grain specialization, or both. Rex (1976) suggested that both competition and predation are important but that their relative significance varies with depth and depends on the rate and stability of production. Huston's (1979) dynamic equilibrium model suggests the parabolic pattern of species diversity in macrobenthos reflects a dynamic balance between rates of competitive displacement and the frequency of population reduction by

predation. At shelf depths, low species diversity may result from high rates of displacement, counteracted only by a low level of predation. The high diversity at intermediate depths is maintained by moderate rates of displacement, and the approach to equilibrium is interrupted by the moderately high levels of predation disturbance. At abyssal depths, rates of displacement are probably low, but infrequent reduction by predation permit sufficient time for the community to approach competitive equilibrium, resulting in a decline in diversity. However, food availability, competition, predation, and spatiotemporal heterogeneity all appear to be important, according to Rex (1983), including the relative geographic scales over which these factors vary.

Zonation

The benthic macrofaunal community changes in species composition with depth. Faunal changes have been related to physical factors, such as sediment type, temperature, strength of the currents and topography (Day and Pearcy, 1968; Rowe and Menzies, 1969; Haedrich et al., 1975). Siebenaller and Somero (1978) argued that zonation may mirror responses to the pressure gradient over depth. However, the relative significance of physical factors to zonation in the deep-sea is still uncertain. Carney et al. (1983) suggested that three types of depth-related gradient could regulate the distribution of organisms. The first group was physiologically important factors, including temperature, salinity and pressure. The second group was composed of resources that changed with depth, such as sediment type. The third was resources that changed in availability with depth, including food and space.

Sanders and Hessler (1969) found bivalve species composition changed abruptly at the shelf-slope break within the depth range of 100 to 300 meters. The bivalve composition was far more sensitive to change in depth than to the effects of distance from land. They believed that the zonation was related to temperature variation.

Rex (1977) found that the deep-sea gastropods from the western North Atlantic changed continuously from the upper slope to the abyss and the rate of change was proportional to the rate of change in depth, with the highest on the slope, lowest on the abyss and intermediate on the abyssal rise. This pattern may result from the deep-sea environment becoming increasingly uniform at greater depths. He proposed that rates of zonation were partly determined by biological interactions. Predation alleviated competition among infaunal groups at lower trophic levels, allowing their ranges to overlap more extensively and consequently diminishing their rates of faunal change with depth. Rex presented data suggesting that rates of zonation in the epifauna, gastropods and the infaunal polychaete-bivalve fraction were correlated with their relative positions in the trophic structure.

Studies in the Gulf of Mexico

Macrobenthic invertebrate communities have been studied in the deep Gulf of Mexico previously. The macrofauna is known to be dominated by polychaetes, ostracods, bivalves, tanaids, bryozoans, and isopods, in that order, and together these make up 86% of the fauna (Pequegnat et al., 1990). Densities of macrofauna were highest in the north central region, and decreased with depth. Spring densities were higher than fall densities. Diversity decreased from east to west and was higher in fall

than in spring on the Central Gulf of Mexico. Diversity increased slightly from the shallow stations to 1400m and then decreased markedly down to the deepest station in the eastern GoM. Gastropod densities were about 10% of bivalve densities and greatest densities were at depths of less than 900m. However, greatest densities in bivalves were achieved at 1000-1500m (Pequegnat et al., 1990).

Diversity in macrofauna showed a parabolic pattern in the western Gulf of Mexico, increasing from a minimum in estuaries, to maximum diversity on the continental shelf (~100-500m), then decreasing to the lower continental slope and abyssal plain (Lohse, 1999). It was suggested that, in the estuary, salinity and temperature controlled diversity (Lohse, 1999). The high diversity on the continental shelf was due to mild physical fluctuations and predation (Lohse, 1999). The reason for diversity decreasing from the continental shelf to the continental slope and abyssal plain were hypothesized to be the basin's young age, higher temperature compared to similar depths in the Atlantic, limiting sill depth and intermittent turbidity currents or slumps coming from the Mississippi Canyon (Lohse, 1999).

James (1972) found approximately 300 live bivalves and 2,800 dead bivalves from a total of 91 stations in the Gulf of Mexico. He found 34 species representing 11 genera. The composition based on the live specimens, changed at depths around 2,000 meters. James (1972) concluded that the Gulf of Mexico had an abyssal zone.

This study was a part of Deepwater Program: Northern Gulf of Mexico Continental Slope Habitats and Benthic Ecology" (DGoMB) program (MMS solicitation 1435-01-99-RP-30991, 1999-2003) which was funded by the Minerals Management

Services (MMS). The program is intended to provide information that will be potentially

impacted by current and future exploration and production of fossil fuel reserves in the

deep water Gulf of Mexico (GOM).

HYPOTHESES TO BE TESTED

In this study, four hypotheses were proposed to better describe the community structure of bivalve mollusks.

Hypothesis 1a: There is no difference in benthic bivalve density with depth. Hypothesis 1b: There is no difference in benthic bivalve diversity with depth.

Density of bivalve mollusks declines with depth because food resources diminished with depth and distance from land. Diversity of bivalve mollusks is hypothesized to be low on the continental shelf, high on the continental intermediate depth and then declined at deeper depths, which reflected the dynamic balance between rates of competitive displacement and the frequency of population reduction by predation.

Hypothesis 2a: There is no difference in benthic bivalve density along an east to west gradient. Hypothesis 2b: There is no difference in benthic bivalve diversity along an east to west gradient.

It is hypothesized that the organic input from the Mississippi River might enhance food availability for benthic bivalve mollusks in the central transects compared to the western and eastern transects. Furthermore, the broad continental shelf off Florida and nutrient sources of the Florida rivers might bring more organic material for the deep-sea organisms than the western region. The community structure of bivalve mollusks could be different along an east to west gradient.

Hypothesis 3a: There is no difference in benthic bivalve density between basin and non-basin. Hypothesis 3b: There is no difference in benthic bivalve diversity

between basin and non-basin.

Basins could trap more different types of sediment than non-basin stations, resulting in community structure differences between basin and non-basin.

Hypothesis 4a: There is no difference in benthic bivalve density between canyon and non-canyon. Hypothesis 4b: There is no difference in benthic bivalve diversity between canyon and non-canyon.

Canyons can trap and funnel organic matter. An organic enriched environment could change the community structure.

AREA OF STUDY

The Gulf of Mexico is a semi-closed basin with a maximum depth of 3840 m. The eastern Gulf of Mexico is characterized with an anticyclonic Loop Current and the western Gulf is characterized with anticyclonic Loop Current eddies and associated cyclones. The world's third largest river, the Mississippi River, brings large amounts of freshwater, sediment and organic material to the Gulf from the middle of the northern boundary (Pequegnat et al., 1990). Some sediment falls to the bottom westward, but more moves southwestward to the Mississippi Fan or to the abyssal plain to the west (Pequegnat et al., 1990). The East Gulf Loop Current, an extension of one branch of the Gulf Stream, enters the Gulf from the Caribbean via the Yucatan Channel and exits via the Florida Straits to the Atlantic, where it joins the main Gulf Stream. This Caribbean Current brings fishes, larvae, plant material and heat to the Gulf. Since nutrients in the deep sea come from extrinsic sources, the materials brought from the Caribbean via the Yucatan Channel could be the principal source of organisms recruited into the populations being studied.

MATERIALS AND METHODS

Selection of sites

A total of 48 sites were sampled in the Gulf of Mexico in this study (Fig. 1). General site information was given in Table 1. Stations RW1, RW4, RW6, W1, W4, W6, C1, C4, C12, MT1, MT4, MT6, S39, S42, S44 stations were sampled to test the hypothesis 1. These stations were chosen because they were along isobaths at different depths in western, central and eastern transects. The same stations were sampled to test the hypothesis 2. These stations were selected because they were along isobaths at similar distance from shore and at different distances from the Mississippi River. B1-B3, NB2-NB5 stations were sampled to test the hypothesis 3. These stations were within and outside of basins at similar water depths and distances from the shore and the Mississippi River. Data from stations MT1, MT2, MT3, C1, C4, C7 stations were used to test the hypothesis 4. These stations were chosen because they were either within or outside of canyons at similar water depths and distances from the shore and the Mississippi River.

Sample collection and analyses

Macrofauna samples were collected with a GOMEX box core, which was used because it is safe and easy to handle (Boland and Rowe, 1991). The GOMEX box core has an area of $0.1725m^2$ (Fig. 2). The top 15cm of sediments within the core were washed through a 300um sieve. The material retained on the sieve was put into an appropriately sized container. Buffered formalin (10%) with filtered seawater was added
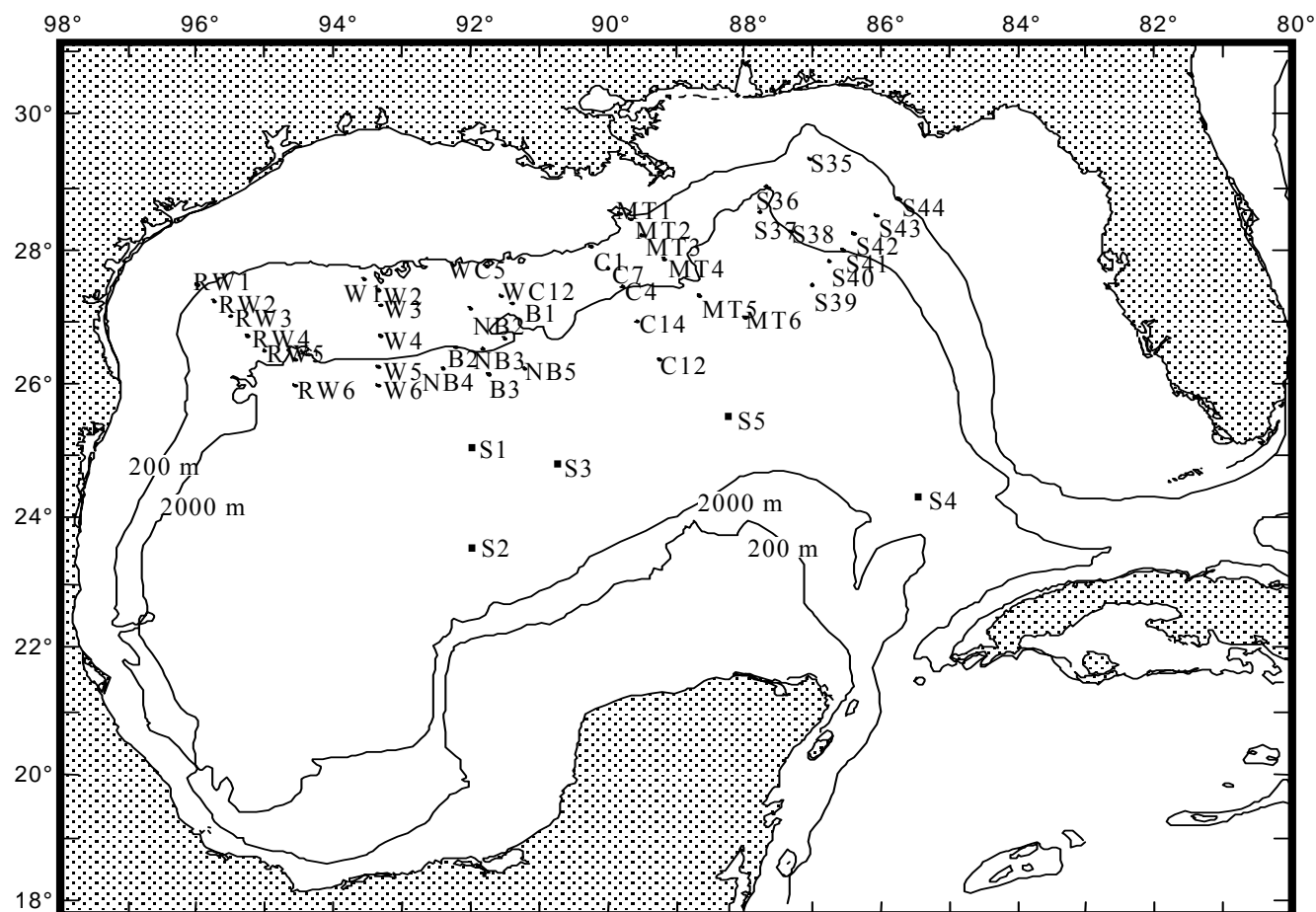
Fig. 1. Station locations in the Gulf of Mexico.

Table 1
General site information

Site	Date	Depth(m)	Longitude	Latitude
C1	05/30/00	335	90.2562	28.0571
C4	05/31/00	1457	89.7857	27.4594
C7	05/31/00	1072	89.9820	27.7304
C12	06/03/00	2922	89.2414	26.3794
C14	06/01/00	2490	89.5725	26.9382
WC5	05/05/00	356	91.7647	27.7832
WC12	05/05/00	1156	91.5558	27.3232
NB2	05/07/00	1530	91.9993	27.1337
NB3	05/08/00	1875	91.8252	26.5384
NB4	05/11/00	2033	92.3950	26.2545
NB5	05/09/00	2063	91.2102	26.2519
RW1	05/23/00	213	96.0028	27.5001
RW2	05/22/00	950	95.7436	27.2541
RW3	05/22/00	1327	95.4924	27.0084
RW4	05/21/00	1575	95.2461	26.7481
RW5	05/21/00	1620	94.9967	26.5075
RW6	05/18/00	3010	94.4960	25.9987
S35	06/12/00	664	87.0464	29.3352
S36	06/12/00	1828	87.6704	28.9194
S37	06/13/00	2386	87.7668	28.5536
S38	06/14/00	2635	87.3253	28.2719
S39	06/06/00	3002	86.9998	27.4837
S40	06/07/00	2974	86.7526	27.8389
S41	06/09/00	2974	86.5733	28.0136
S42	06/10/00	766	86.4178	28.2526
S43	06/10/00	363	86.0768	28.5029
S44	06/11/00	213	85.7494	28.7502
B1	05/06/00	2256	91.4018	27.2034
B2	05/12/00	2629	92.2167	26.5513
B3	05/10/00	2620	91.7351	26.1644
AC1	05/19/00	2469	94.5596	26.3917
W1	05/14/00	396	93.5510	27.5772
W2	05/14/00	625	93.3376	27.4133
W3	05/15/00	865	93.3233	27.1724
W4	05/15/00	1447	93.3195	26.7317
W5	05/16/00	2748	93.3327	26.2678
W6	05/17/00	3145	93.3203	26.0028
S1	06/05/02	3525	92.0066	25.0060
S2	06/06/02	3732	92.0039	23.4919
S3	06/08/02	3670	90.7549	24.7554
S4	06/10/02	3410	85.4838	24.2502
S5	06/13/02	3314	88.2704	25.4890
MT1	06/17/00	481	89.8289	28.5419
MT2	06/17/00	677	89.6719	28.4479
MT3	06/16/00	987	89.4961	28.2204
MT4	06/16/00	1401	89.1661	27.8276
MT5	06/04/00	2277	88.6595	27.3365
MT6	06/05/00	2746	87.9978	27.0001
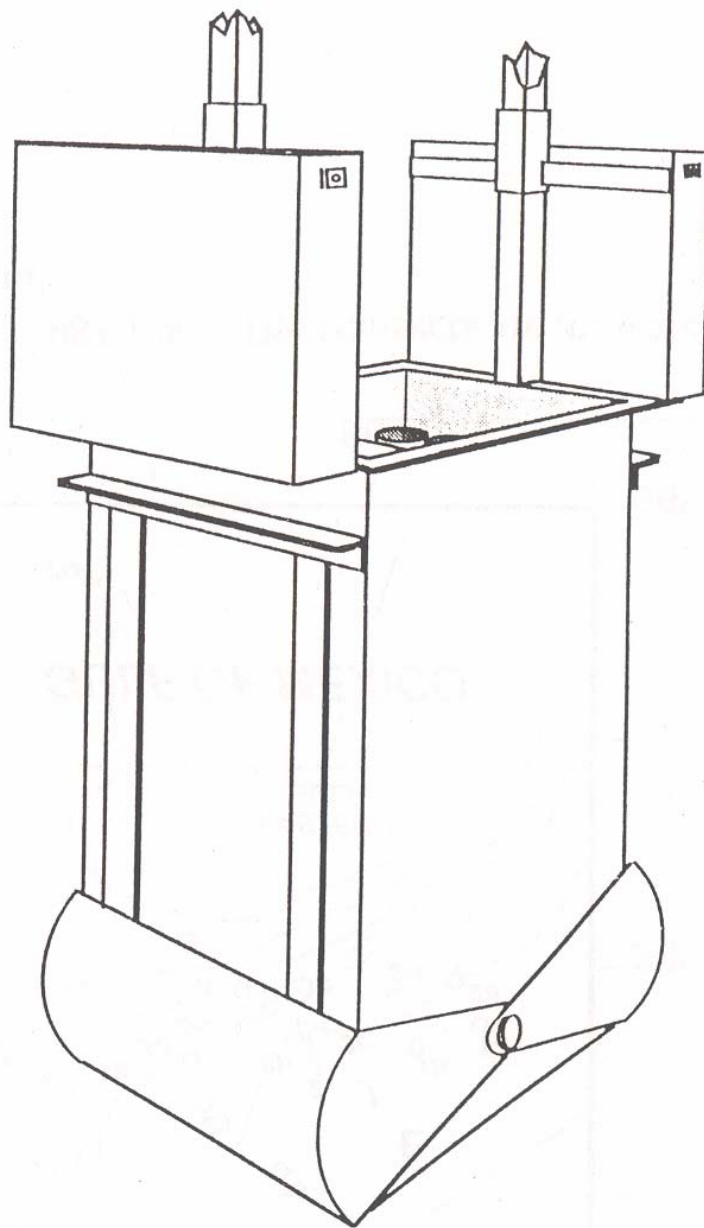
Fig. 2. GOMEX box core used for the sampling of macrofauna (Hubbard, 1995).

and the container was labeled inside and out.

At the laboratory, sorters stained organisms with 5% rose bengal for 24 hours, then removed the formalin, rose bengal and any remaining fine sediment by rinsing with fresh water through a 300 um sieve. The stain color aided in the sorting of organisms into major taxonomic groups. The mollusks of each sample were separated to the lowest distinguishable taxonomic unit based on shell morphology and enumerated.

Measures of community structure

Species abundance was proportionately measured by the number of individuals of each species m^{-2} and the number of species per station. Clustering was performed to determine the similarity among stations in terms of species composition. Similarity was calculated using percentage similarity (Whittaker and Fairbanks, 1958). According to the equation:

$$PS=100\Sigma min(P_a, P_b)$$

in which P_a and P_b are, for a given species, the percentages of samples A and B which that species represents.

Species diversity, which describes the distribution of individuals of the species present, was determined using the Shannon-Wiener information theory function (Shannon and Weaver, 1963).

$$H'=-\Sigma(n_i/Nlogn_i/N)$$

where n_i= the number of individuals of the ith species, and N=the total number of individuals in the whole sample. The Shannon-Wiener diversity index (1963) expresses the relative importance of different species in a population of unknown size. It is less

sensitive to sample size than those approaches which require an estimate of the total

number of species, and is dimensionless. This formula will be used because the

population is indefinitely large and randomly sampled.

Evenness was calculated using Pielou's J' (1966) equitability index:

$$J'=H'/H'max,$$

where H'max=logS, which is the maximum species diversity of a sample (H'max) when

all species in the sample are equally distributed and S=the number of species present in

the sample. Evenness is near zero when dominance is high and is 1.0 when all species

present are represented by the same number of individuals (Rowe et al., 1982). The

species diversity measurement and the evenness measurement assume all species in the

community are present in the sample.

The expected species number was calculated using Hulbert's expected species

number (Hurlbert 1971; Heck et al. 1975):

$$E(S_n)=S-\sum(1-n_i/N)^n$$

where S=the number of species present in the sample, n_i= the number of individuals of

the ith species, N=the total number of individuals in the whole sample, and n=number of

individuals selected at random. Because species richness tends to increase with sample

size, it is necessary to scale down all collections to the same number of individuals to

compare species richness. In this study, samples were decreased to 50 individuals.

Statistical Analyses

Different statistical tests were used to assess the difference in the community

structure in different locations. Linear regressions of abundance and species diversity

were plotted against depth. Differences in abundance and species diversity of bivalve

mollusks were tested using an ANOVA among different depths, eastern central and

western transects, between basin and non-basin, canyon and non-canyon. Furthermore,

similarity dendrograms were plotted based on similarity indices. The analyses were

performed using a variety of programs including Microsoft Excel[©], Microsoft

Powerpoint[©] , SPSS[©] and PRIMER[©].

RESULTS

General

There were 144 samples collected at 48 sites in this study which yielded total of 3615 individuals and 94 species of bivalves from the depths of 213 m to 3732 m in the Northern Gulf of Mexico (Table 2). The mean density was 147 bivalves m^{-2}, with a standard deviation of 104. The site MT3 had the maximum density of 439, and site S3 had the minimum density of 35 individuals m^{-2}. All taxa are listed in the Appendix.

Density

Bivalve density was highest near the coast, with particularly high values in the Mississippi Canyon and decreased with depth and distance from the shore (Fig. 3). A linear relationship was found between log10 bivalve density and depth (y = -0.17x + 2.40, R^2 = 0.41, p<0.01) (Fig. 4). Site S5 had extraordinarily high density among the deep stations at which depths exceeded 3 km. Hypothesis 1a, there is no difference in benthic bivalve density with depth, and Hypothesis 2a, there is no difference in benthic bivalve density along an east to west gradient, were tested using a randomized complete block design analysis of variance where the depth was the main factor with 3 levels and transect was the blocking factor with 5 levels. The result indicated that the mean values for the bivalve density at different depths were not significantly different (F$_{2,8}$=2.823, p=0.118) and the mean values for the bivalve density in western, central and eastern transects were not significantly different (F$_{4,8}$=0.561, p=0.698), i.e., there was no difference in bivalve mollusks density among transects (Table 3). The mean value of bivalve density in 0.3km is 225±129 individuals m^{-2} whereas the mean value of bivalve

Table 2
Depth (m), total individuals per site, number of individuals m^{-2}, total number of species, species richness, Pielou's evenness (J'), expected number of species (50), and Shannon-Wiener species index (H') for bivalves. The sample area per replicate was 0.1725 m^2 and three replicates were collected for each location

Site	Depth(m)	Total Individuals (N)	Number of Individuals m^{-2}	Total Species(S)	Species Richness(d)	Pielou's Evenness(J')	Expected Number of Species(50)	Shannon-Wiener Species Index (H)
C1	335	67	129	23	5.23	0.82	20	2.58
C4	1457	107	207	34	7.06	0.91	24	3.19
C7	1072	112	216	27	5.51	0.88	20	2.91
C12	2922	91	176	25	5.32	0.83	19	2.68
C14	2490	89	172	22	4.68	0.81	17	2.50
NB2	1530	69	133	22	4.96	0.91	20	2.81
NB3	1875	45	87	22	5.52	0.93	22	2.87
NB4	2033	65	126	27	6.23	0.91	23	2.99
NB5	2063	27	52	17	4.85	0.93	17	2.64
RW1	213	104	201	23	4.74	0.85	17	2.66
RW2	950	112	216	33	6.78	0.86	22	3.02
RW3	1327	39	75	18	4.64	0.92	18	2.67
RW4	1575	70	135	21	4.71	0.91	18	2.77
RW5	1620	70	135	23	5.18	0.91	20	2.85
RW6	3010	33	64	14	3.72	0.91	14	2.41

Table 2
Continued

Site	Depth(m)	Total Individuals (N)	Number of Individuals m^{-2}	Total Species(S)	Species Richness(d)	Pielou's Evenness(J')	Expected Number of Species(50)	Shannon-Wiener Species Index (H)
WC5	356	90	174	24	5.11	0.85	18	2.69
WC12	1156	69	133	26	5.90	0.92	23	3.01
S35	664	159	307	28	5.33	0.68	16	2.26
S36	1828	142	274	28	5.45	0.72	15	2.40
S37	2386	79	153	13	2.75	0.89	12	2.29
S38	2635	45	87	11	2.63	0.82	11	1.97
S39	3002	29	56	15	4.16	0.94	15	2.55
S40	2974	27	52	13	3.64	0.93	13	2.38
S41	2974	30	58	15	4.12	0.90	15	2.44
S42	766	68	131	18	4.03	0.85	16	2.45
S43	363	121	234	18	3.54	0.74	12	2.15
S44	213	61	118	15	3.41	0.88	14	2.37
B1	2256	29	56	15	4.16	0.89	15	2.42
B2	2629	44	85	12	2.91	0.83	12	2.07
B3	2620	79	153	23	5.03	0.77	17	2.40
AC1	2469	30	58	10	2.65	0.87	10	2.00

Table 2
Continued

Site	Depth(m)	Total Individuals (N)	Number of Individuals m^{-2}	Total Species(S)	Species Richness(d)	Pielou's Evenness(J')	Expected Number of Species(50)	Shannon-Wiener Species Index (H)
W1	396	124	240	19	3.73	0.81	14	2.39
W2	625	77	149	16	3.45	0.76	13	2.10
W3	865	46	89	25	6.27	0.91	25	2.93
W4	1447	45	87	22	5.52	0.93	22	2.88
W5	2748	24	46	9	2.52	0.85	9	1.86
W6	3145	55	106	11	2.50	0.78	11	1.88
S1	3525	22	43	4	0.97	0.83	4	1.16
S2	3732	24	46	8	2.20	0.96	8	2.00
S3	3670	18	35	5	1.38	0.97	5	1.56
S4	3410	33	64	11	2.86	0.96	11	2.29
S5	3314	160	309	15	2.76	0.72	11	1.95
MT1	481	226	437	13	2.21	0.23	5	0.59
MT2	677	226	437	21	3.69	0.47	10	1.44
MT3	987	227	439	27	4.79	0.76	15	2.51
MT4	1401	70	135	23	5.18	0.87	20	2.74
MT5	2277	42	81	18	4.55	0.92	18	2.65
MT6	2746	24	46	10	2.83	0.85	10	1.95
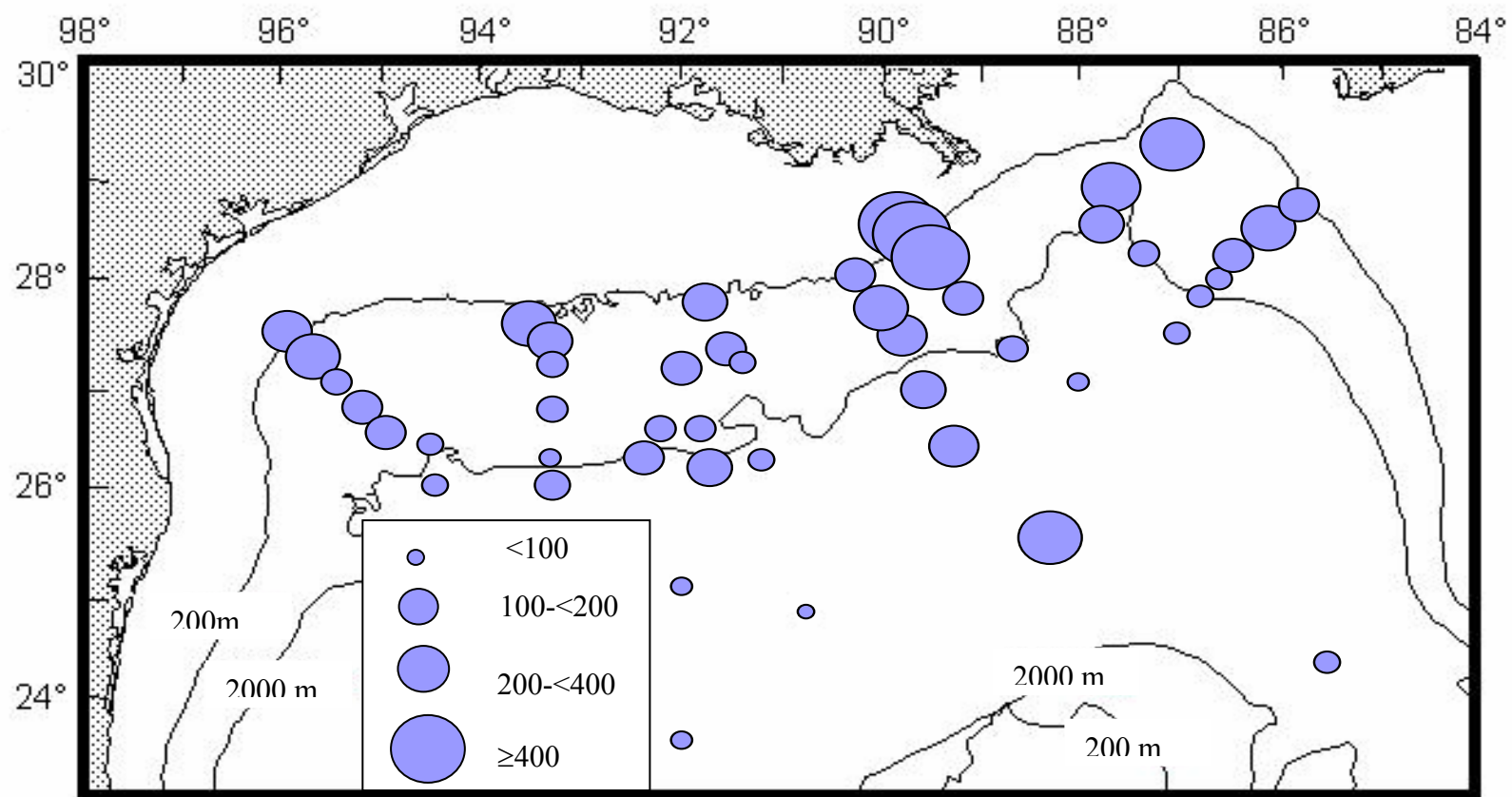
Fig. 3. Map of density distribution of bivalves in the Gulf of Mexico.
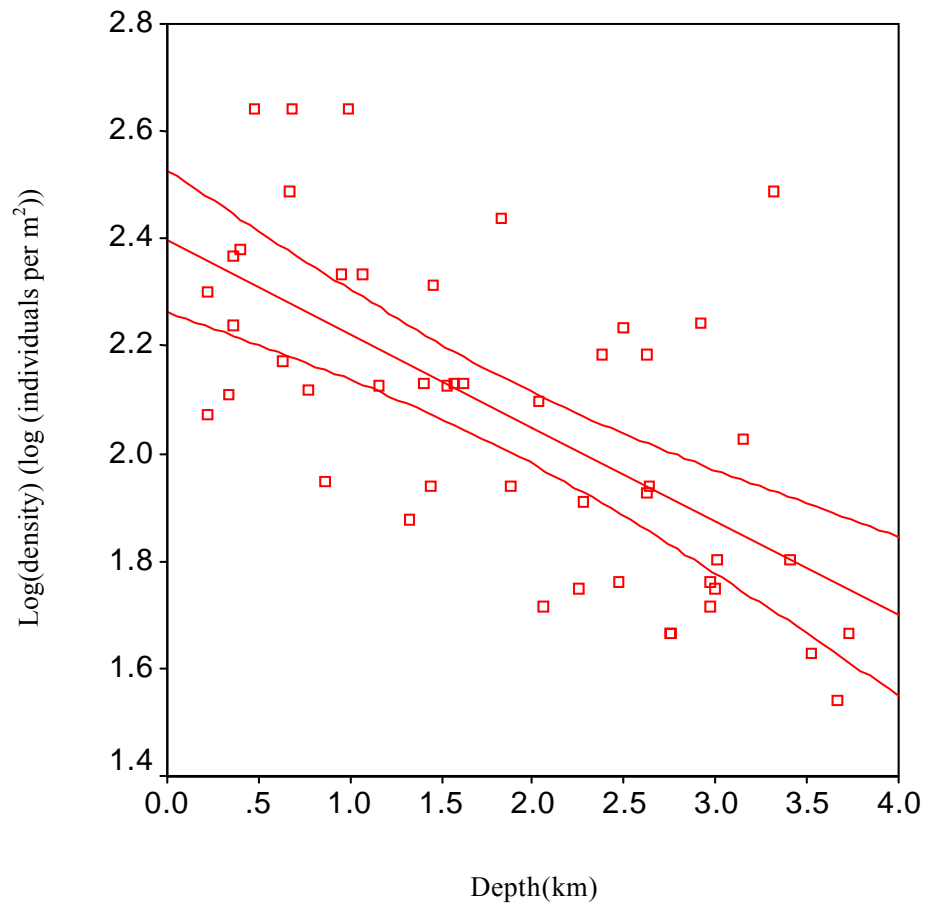
Fig. 4. Linear regression plot of bivalve log density against depth ($Y=-0.17x+2.40$ $R^2=0.41$).

Table 3

ANOVA table for the analysis of the depth and transect factors for bivalve density

Tests of Between-Subjects Effects

Dependent Variable: DENSITY

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
Corrected Model	65460.758[b]	6	10910.126	1.315	.350	7.891	.277
Intercept	343102.772	1	343102.772	41.361	.000	41.361	1.000
DEPTH	46841.824	2	23420.912	2.823	.118	5.647	.403
TRANSECT	18618.933	4	4654.733	.561	.698	2.245	.127
Error	66361.907	8	8295.238				
Total	474925.436	15					
Corrected Total	131822.664	14					

a. Computed using alpha = .05

b. R Squared = .497 (Adjusted R Squared = .119)

DENSITY

DEPTH	Mean	Std. Deviation	Minimum	Maximum
~0.5km	224.9275	128.66286	117.87	436.71
~1.5km	139.1304	42.97074	86.96	206.76
~3km	89.6618	53.33473	46.38	175.85
Total	151.2399	97.03558	46.38	436.71

density in 1.5km was 139±43 individuals m^{-2}. The mean value of bivalve density in 3 km

is 90±53 individuals m^{-2}. The least squares regression analysis of density and depth

showed there was a linear correlation between bivalve density and depth (Table 4).

Hypothesis 3a, there is no difference in benthic bivalve density between basin and non-

basin, was tested using a single-factor analysis of variance which indicated that the mean

values for the basin bivalve density and non-basin bivalve density were not significantly

different ($F_{1,5}$=.002, p=0.963) (Table 5). The mean value of bivalve density in basin

stations was 98±50 individuals m^{-2} and 100±38 individuals m^{-2} at non-basin stations.

Hypothesis 4a, there is no difference in benthic bivalve density between canyon and

non-canyon, was tested using a single-factor analysis of variance which indicated that

the mean values for the canyon and non-canyon bivalve density were significantly

different ($F_{1,4}$=84.583, p=0.001) (Table 6). The mean value of bivalve density in canyon

stations was 437±1 individuals m^{-2} while the mean value in non-canyon stations was

184±48 individuals m^{-2}.

Diversity

Diversity of bivalves increased slightly from the shallow stations, with especially

low values in the Mississippi canyon, to the maximum in the intermediate depth, and

then decreased down to the deepest station (Fig. 5). A parabolic (quadratic) relationship

was found between bivalve diversity and depth. The Shannon-Wiener Species Index

(Fig. 6a) and the expected number of species (Fig. 6b) displayed the same pattern. The

three sites that had lowest diversity were MT1, MT2, and S1. Hypothesis 1b, there is no

Table 4
 The least squares regression analysis of density and depth

Tests of Between-Subjects Effects

Dependent Variable: DENSITY

Source	Type I Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
Corrected Model	143659.800[b]	1	143659.800	18.234	.000	18.234	.987
Intercept	1033120.1	1	1033120.083	131.132	.000	131.132	1.000
DEPTH	143659.800	1	143659.800	18.234	.000	18.234	.987
Error	362410.116	46	7878.481				
Total	1539190.0	48					
Corrected Total	506069.917	47					

a. Computed using alpha = .05

b. R Squared = .284 (Adjusted R Squared = .268)

Table 5
 ANOVA table for the analysis of the bivalve density between the basin and non-basin stations

Tests of Between-Subjects Effects

Dependent Variable: DENSITY

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	4.445[a]	1	4.445	.002	.963
Intercept	66816.073	1	66816.073	36.553	.002
BASIN	4.445	1	4.445	.002	.963
Error	9139.692	5	1827.938		
Total	77511.260	7			
Corrected Total	9144.137	6			

a. R Squared = .000 (Adjusted R Squared = -.199)

DENSITY

BASIN	Mean	Std. Deviation	Minimum	Maximum
basin	97.9066	49.58069	56.04	152.66
non-basin	99.5169	37.51978	52.17	133.33
Total	98.8268	39.03874	52.17	152.66

Table 6

ANOVA table for the analysis of the bivalve density between the canyon and non-canyon stations

Tests of Between-Subjects Effects

Dependent Variable: DENSITY

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	25741.500[a]	1	25741.500	84.583	.001
Intercept	155204.167	1	155204.167	509.981	.000
CANYON	25741.500	1	25741.500	84.583	.001
Error	1217.333	4	304.333		
Total	182163.000	6			
Corrected Total	26958.833	5			

a. R Squared = .955 (Adjusted R Squared = .944)

DENSITY

CANYON	Mean	Std. Deviation	Minimum	Maximum
canyon	437.3591	1.11565	436.71	438.65
non-canyon	184.2190	47.66070	129.47	216.43
Total	310.7890	141.89111	129.47	438.65
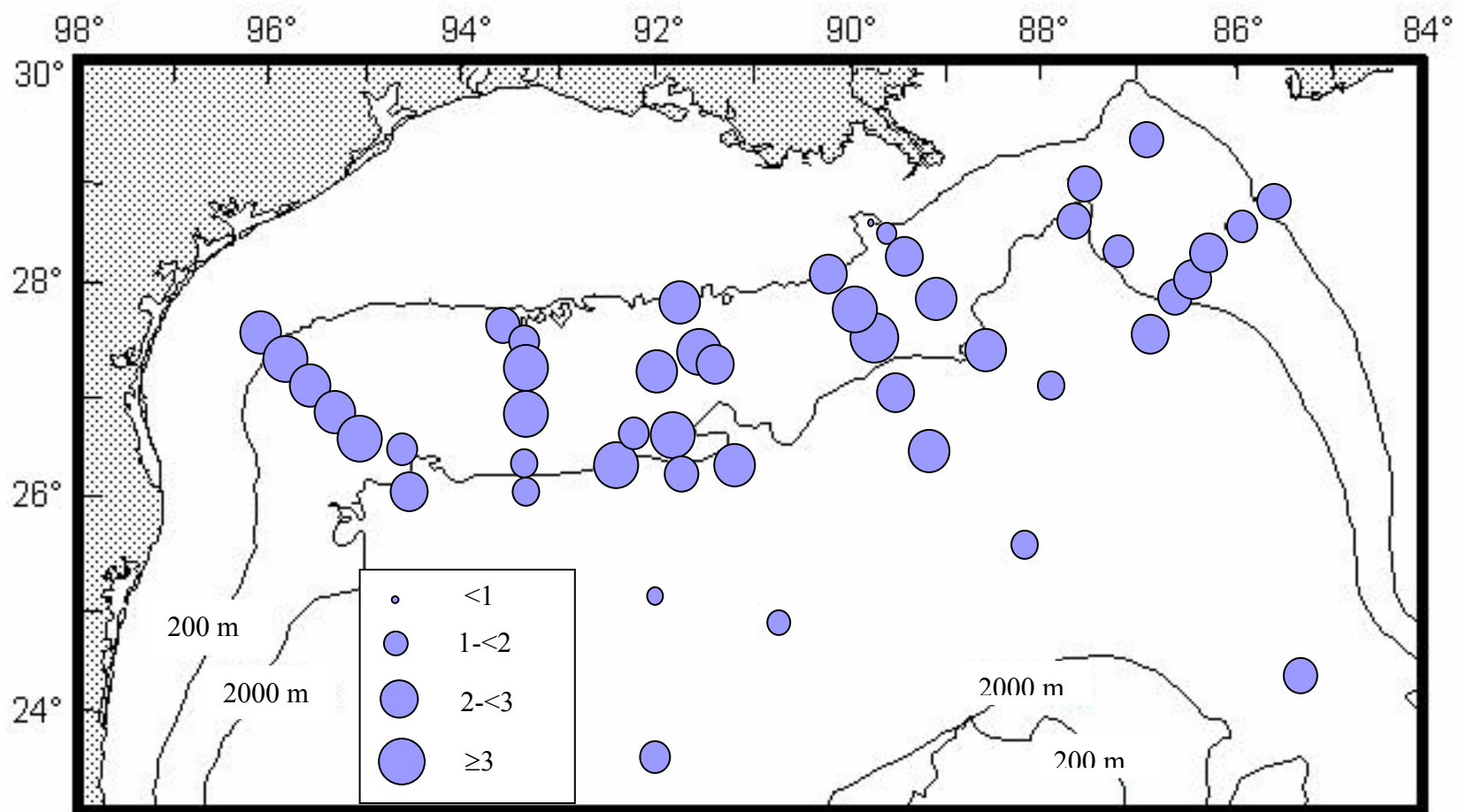
Fig. 5. Map of diversity (Shannon-Wiener Species Index) distribution of bivalves in the Gulf of Mexico.
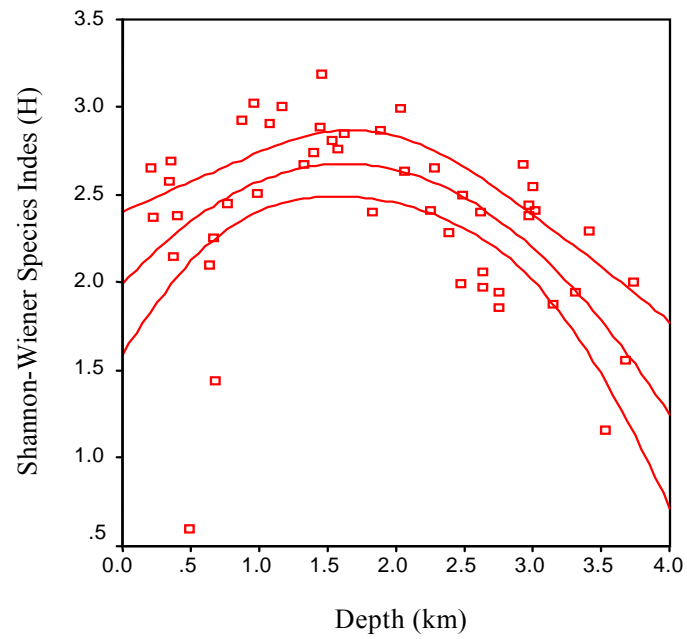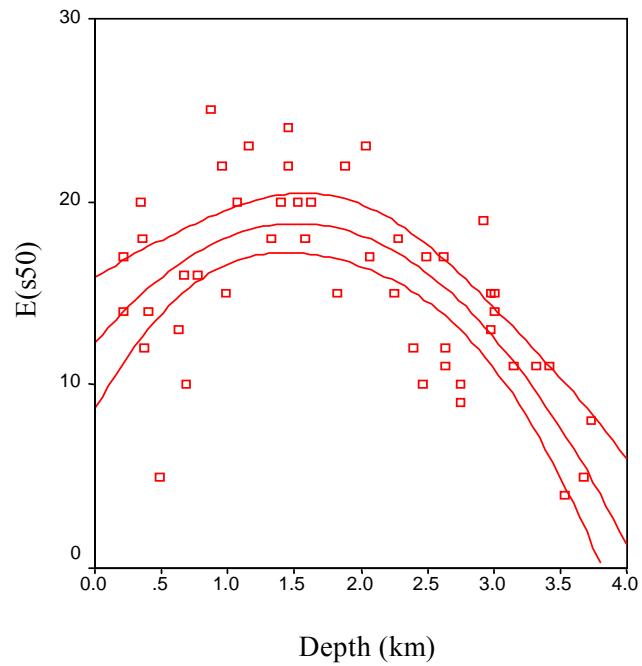
Fig. 6. Curvilinear regression plot of bivalve diversity against depth. Reported are: curves created from Shannon-Wiener Species Index (H) ($y=-0.26x^2+0.84x+2.00$ $R^2=0.31$) (a) and for expected number of species (50) ($y=-2.84x^2+8.62x+12.28$ $R^2=0.47$) (b).

difference in benthic bivalve diversity with depth, and Hypothesis 2b, there is no difference in benthic bivalve diversity along an east to west gradient, were tested using a randomized complete block analysis of variance where the depth was the main factor with 3 levels and transect was the blocking factor with 5 levels. The result indicated that the mean values for bivalve diversity at different depths were not significantly different ($F_{2,8}$=2.709, p=0.126) and the mean values for bivalve diversity in western, central and eastern transects were not significantly different ($F_{4,8}$=2.010, p=0.186), i.e., there was no difference in bivalve mollusks diversity among transects (Table 7). The least squares regression analysis of diversity and depth showed there was a quadratic correlation between bivalve diversity and depth (Table 8). Hypothesis 3b, there is no difference in benthic bivalve diversity between basin and non-basin, was tested using a single-factor analysis of variance which indicated that the mean values for the basin bivalve diversity and non-basin bivalve diversity were significantly different ($F_{1,5}$=17.137, p=0.009) (Table 9). The mean value of bivalve diversity in basin stations was 2.30±0.11. The mean value in non-basin stations was 2.83±0.07. Hypothesis 4b, there is no difference in benthic bivalve diversity between canyon and non-canyon, was tested using a single-factor analysis of variance which indicated that the mean values for canyon bivalve diversity (H') and non-canyon bivalve diversity were not significantly different ($F_{1,4}$=5.61, p=0.08) (Table 10). The mean value of bivalve diversity in canyon stations was 1.51±0.96, whereas the mean value in non-canyon stations was 2.89±0.31. Evenness of bivalves had no clear tendency in the Gulf of Mexico (Fig. 7). However, the dominance

Table 7

ANOVA table for the analysis of depth and transect factors for bivalve diversity

Tests of Between-Subjects Effects

Dependent Variable: DIVERSITY

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
Corrected Model	3.174[b]	6	.529	2.243	.144	13.458	.459
Intercept	86.833	1	86.833	368.241	.000	368.241	1.000
DEPTH	1.277	2	.639	2.709	.126	5.417	.389
TRANSECT	1.896	4	.474	2.010	.186	8.041	.371
Error	1.886	8	.236				
Total	91.893	15					
Corrected Total	5.060	14					

a. Computed using alpha = .05

b. R Squared = .627 (Adjusted R Squared = .348)

Report

DIVERSITY

DEPTH	Mean	Std. Error of Mean
~0.5km	2.1180	.38597
~1.5km	2.8060	.11944
~3km	2.2940	.16089
Total	2.4060	.15523

Table 8

The least squares regression analysis of diversity and depth

Tests of Between-Subjects Effects

Dependent Variable: DIVERSITY

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
Corrected Model	3.701[b]	2	1.850	9.951	.000	19.902	.978
Intercept	18.467	1	18.467	99.307	.000	99.307	1.000
DEPTH	2.083	1	2.083	11.201	.002	11.201	.906
$DEPTH^2$	2.899	1	2.899	15.589	.000	15.589	.971
Error	8.368	45	.186				
Total	284.187	48					
Corrected Total	12.069	47					

a. Computed using alpha = .05

b. R Squared = .307 (Adjusted R Squared = .276)

Table 9

ANOVA table for the analysis of the bivalve diversity between the basin and non-basin stations

Tests of Between-Subjects Effects

Dependent Variable: DIVERSITY

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	.483 [a]	1	.483	17.137	.009
Intercept	45.012	1	45.012	1596.836	.000
BASIN	.483	1	.483	17.137	.009
Error	.141	5	2.819E-02		
Total	47.944	7			
Corrected Total	.624	6			

a. R Squared = .774 (Adjusted R Squared = .729)

Report

DIVERSITY

BASIN	Mean	Std. Error of Mean
basin	2.2967	.11348
non-basin	2.8275	.07284
Total	2.6000	.12189

Table 10
ANOVA table for the analysis of the bivalve diversity between the canyon and non-canyon stations

Tests of Between-Subjects Effects

Dependent Variable: DIVERSITY

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	2.857[a]	1	2.857	5.607	.077
Intercept	29.128	1	29.128	57.177	.002
CANYON	2.857	1	2.857	5.607	.077
Error	2.038	4	.509		
Total	34.022	6			
Corrected Total	4.894	5			

a. R Squared = .584 (Adjusted R Squared = .480)

Report

DIVERSITY

CANYON	Mean	Std. Deviation
canyon	1.5133	.96210
non-canyon	2.8933	.30534
Total	2.2033	.98938
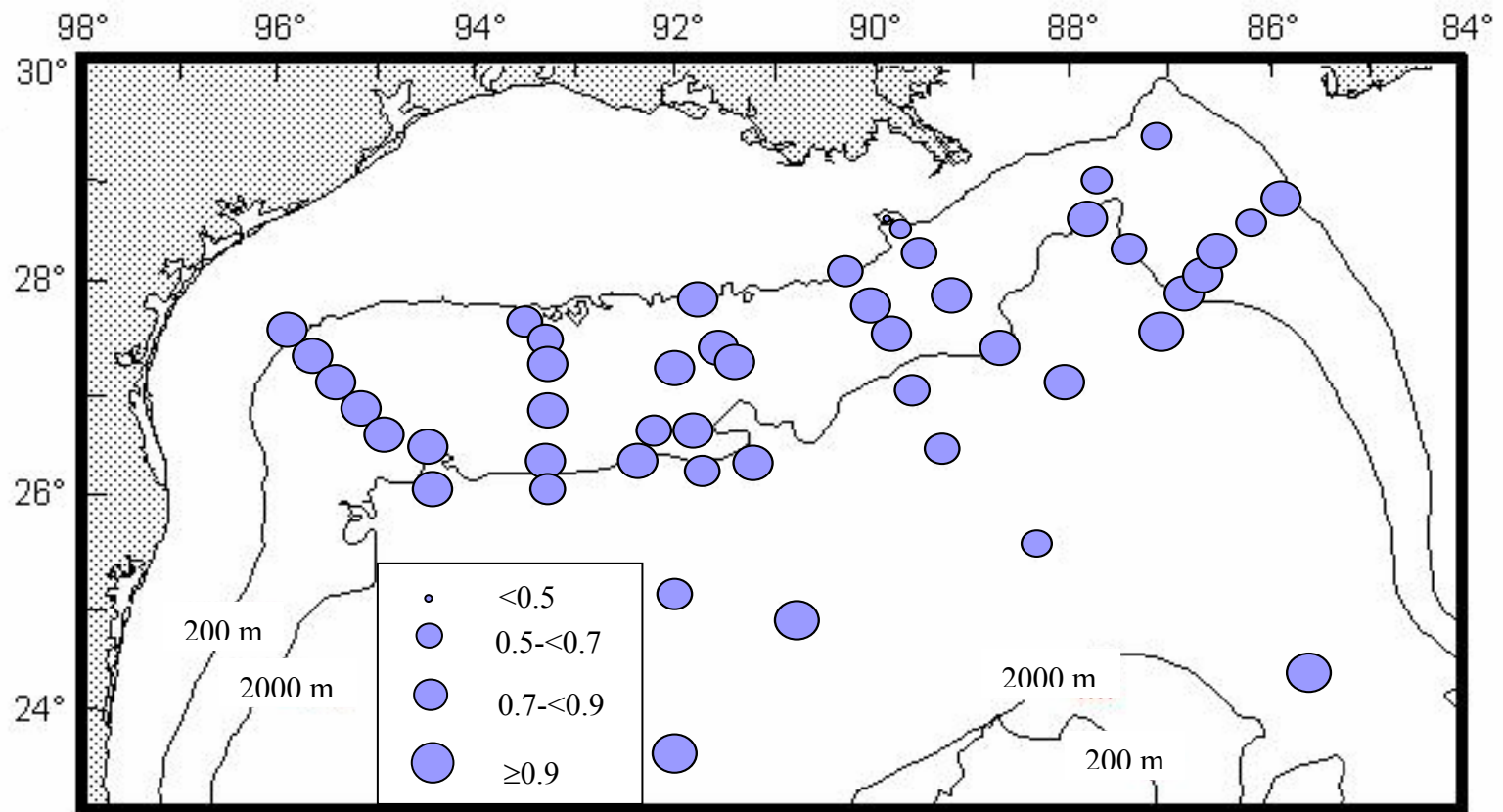
Fig. 7. Map of evenness distribution of bivalves in the Gulf of Mexico.

in MT1 and MT2 were high with evenness of 0.23 and 0.47 respectively (Fig. 8).

Zonation

The stations were separated into nine groups according to percent similarity of species composition (Fig. 9). Within each group, the stations shared at least 25% of the species, except group 4 which shared at least 20% of the species. The species composition appeared to change with depth. Group 1 included MT1and MT2, which ranged from 481m to 677m in the Mississippi Canyon (Table 11). Group 2 included RW1 and WC5, which ranged from 213m to 356m in western Gulf. Group 3 included MT3, MT4, and S36, which ranged from 987m to 1828m, which is in the eastern and central Gulf. Group 4 included S44, S35, S43, and W1, which ranged from 213m to 664m in eastern and western Gulf. Group 5 included W2, RW2, C7, W4, NB3, WC12, S42, W3, RW3, RW4, C4, and NB2, which ranged from 625m to 1875m. Group 6 included MT5, RW5, NB4, NB5, B2, B1, AC1, W5, and RW6, which ranged from 1620m to 3010m. Group 7 included S4, S2, S41, S3, MT6, S1, S40, and S39, which ranged from 2746m to 3732m. Group 8 included central site C1 which is 335m.Group 9 included S38, S37, S5, W6, C14, B3, and C12, which ranged from 2386m to 3314m.

From 213m to 677m, there were 4 groups that fell in this range. They are group 1, group 2, group 4, and group 8. From 625m to 1875m, there were two groups that fell in this range. They are group 3 and group 5. There were 3 groups fell in the range of 1620m to 3732m. They are group 6, group 7, and group 9.
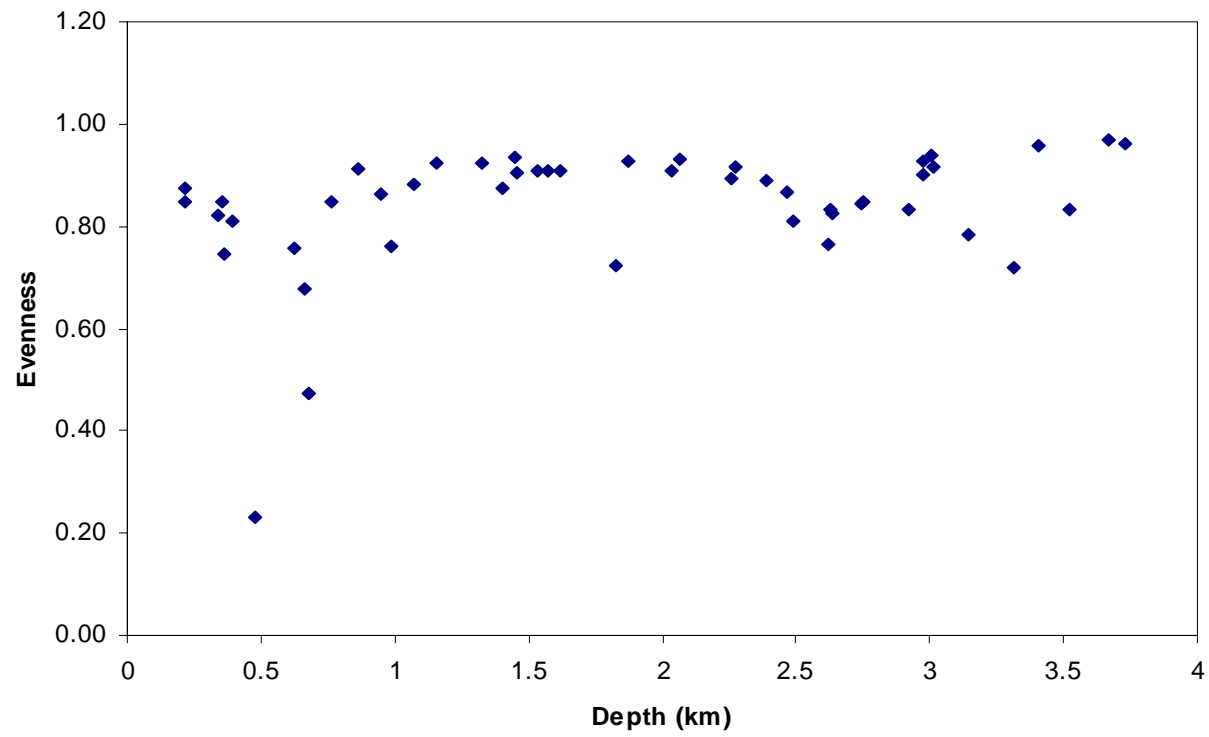
Fig. 8. Scatter plot of bivalve evenness against depth.
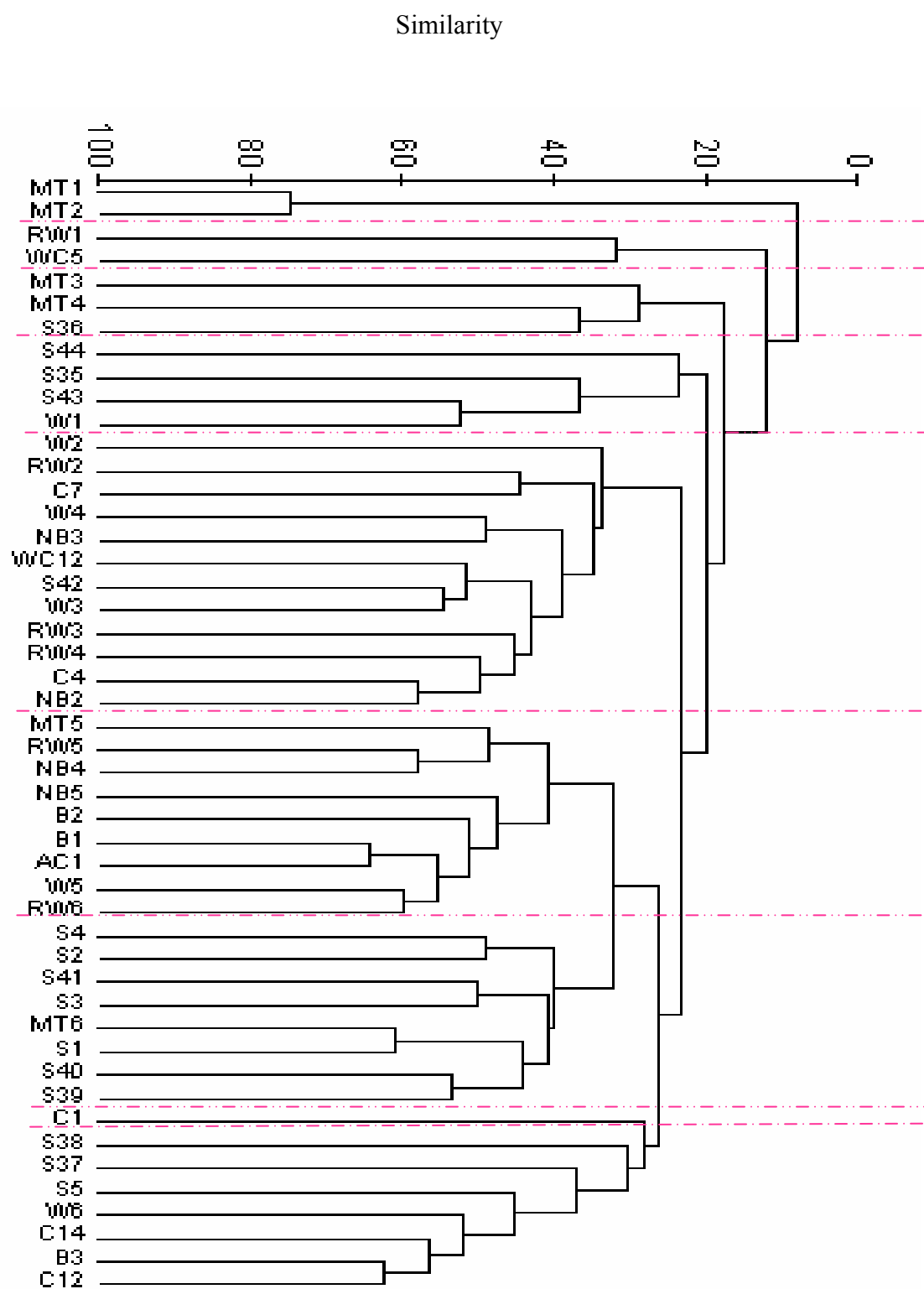
Similarity

Fig. 9. Dendrogram showing the similarity among the stations.

Table 11
List of station groups based on percent similarity with respect to species composition.

Group	Description	Stations	Depth(m)	Group	Description	Stations	Depth(m)
1	Shallow, Mississippi Canyon	MT1	481	6	Deep area	MT5	2277
		MT2	677			RW5	1620
						NB4	2033
2	Shallow, non-canyon	RW1	213			NB5	2063
		WC5	356			B2	2629
						B1	2256
3	Mid-slope, eastern and cental area	MT3	987			AC1	2469
		MT4	1401			W5	2748
		S36	1828			RW6	3010
4	Shallow, eastern and west-central area	S44	213	7	Deep area	S4	3410
		S35	664			S2	3732
		S43	363			S41	2974
		W1	396			S3	3670
						MT6	2746
5	Mid-slope area, most inclusive	W2	625			S1	3525
		RW2	950			S40	2974
		C7	1072			S39	3002
		W4	1447				
		NB3	1875	8	Shallow, central area	C1	335
		WC12	1156				
		S42	766	9	Deep area	S38	2635
		W3	865			S37	2386
		RW3	1327			S5	3314
		RW4	1575			W6	3145
		C4	1457			C14	2490
		NB2	1530			B3	2620
						C12	2922

DISCUSSION

Density

The least squares regression analysis showed that there was a linear relationship between density and depth. The p-value was less than 0.01. The test had a power of 0.987 (Table 4). The density of bivalve mollusks decreased with depth, with especially high values in the Mississippi Canyon. The explanation for the observed pattern has traditionally been that food resources diminish with depth and distance from land. However, the ANOVA test showed no difference in density of bivalve mollusks for different depth. The reason that the test was not statistically significant could be explained by the sample size not being big enough. Furthermore, the ANOVA test only used a few levels of depth which could not supply enough information for detecting the correlation between depth and density. The ANOVA test for the depth factor only had a power of 0.403 (Table 3). The probability of failing to detect the different density with depth was 59.7%.

The enhanced density in the Mississippi Canyon could be explained by a large amount of organic input from the Mississippi river that was entrapped in the canyon. The central transects density was not different from the eastern and western transects. It seemed the organic input from the Mississippi River may have had higher influence in the central transects than the western and eastern transects. It was surprising that the western transects had almost the same density as the eastern transects, even though the broad continental shelf off Florida and nutrient sources of the Florida rivers might be expected to bring more organic material for the deep-sea organisms than the western

region. The common basins found on the slope had the same density as non basin

because the basins trap similar sediments as the adjacent non basins.

Of particular interest was the observed enhancement of bivalve mollusks in Site

S5 among the deep stations where depths exceed 3km. The total density of macrofauna

and megafauna groups showed extraordinarily high values compared to sites deeper than

3km in the Gulf of Mexico as well. The reason for enhanced density of organisms could

be explained by enhanced organic material brought by Mississippi River.

Diversity

The least squares regression analysis showed there was a quadratic relationship

between diversity and depth. For linear term the p-value was 0.002 and the power was

0.906 (Table 8). For quadratic term the p-value was less than 0.01 and the power was

0.971. The diversity of bivalve mollusks increased from shallow continental slope

depths, with especially low values in the Mississippi Canyon, to a maximum at

intermediate depths (1-2km), followed by a decrease down to the deepest areas (3.7km)

in the Gulf of Mexico. However, the ANOVA test showed no difference in diversity of

bivalve mollusks for different depth. The reason that the test was not statistically

significant could be explained by the sample size not being big enough. Furthermore, the

ANOVA test only used a few levels of depth which could not supply enough

information for detecting the correlation between depth and diversity. The test for the

depth factor only had a power of 0.389 (Table 7). The probability of failing to detect the

different diversity with depth was 61.1%.

In accordance with dynamic equilibrium (Huston, 1979), low species diversity

may have resulted from severe biotic and physical disturbances on the upper slope. One of the extraordinary physical disturbances in the Mississippi Canyon was Mississippi River flows which transported a large amount of sediment and organic material into the canyon. Due to the severe and frequent disturbance by the Mississippi River currents, bivalve mollusks may have especially low diversity values in the Mississippi Canyon (Huston, 1979).

The same theory of dynamic equilibrium (Huston, 1979) was suggested to explain the high diversity on the northern Gulf of Mexico continental slope. High diversity at intermediate depths is probably maintained by moderate rates of displacement, with the approach to equilibrium interrupted by fairly high levels of predation disturbance. Moving from the continental shelf to the continental slope, the intensity of the turbidity currents and sediment transportation decreases to a moderate level, which maintains the high diversity at the intermediate depths of the northern Gulf of Mexico.

On the abyssal plain (3.5 to 3.7 km), rates of displacement are probably low, but infrequent predation may permit sufficient time for the community to approach competitive equilibrium, resulting in a decline in diversity (Huston, 1979).

A parabolic relationship was found between diversity (H'(S)) of bivalves and depth ($y = -0.24x^2 + 0.79x + 1.99$, $R^2 = 0.29$, p-value=0.0003), but the maximum was found on the upper continental slope (1-2km), rather than the upper continental rise (3 km), where a maximum has been observed in the northwestern Atlantic (Rex, 1983). The difference may be due to the shallower nature of Gulf of Mexico (Lohse, 1999). Another

explanation could be that the Gulf of Mexico is a semi-closed basin, and the intensity of the turbidity currents and sediment transport influence by Mississippi River on the upper continental slope are different from those in the northwestern Atlantic.

To reduce the influence of the outlier diversity (H'(S)) of MT1 which had standardized residual –4.05, iteratively reweighted least squares was used by applying weights that varied inversely with the size of the residual. Outlying case diversity (H'(S)) of MT1 that had largest residual was thereby given smallest weight. The iteratively reweighted least squares robust regression for diversity (H'(S)) became $y = -0.22x^2 + 0.66x + 2.20$, $R^2 = 0.40$, p-value<0.01.

Zonation

Nine distinct groups were formed on the basis of the similarity in species composition (Fig. 10). Species composition of bivalve mollusks changed with depth. The pattern varied more abruptly on the slope compared to the deeper depths. There are four groups which fell within 213m to 677m. Moving from shallower area to deeper sites, each group covered eastern, central and western Gulf of Mexico. The pattern could be due to the more stable environment including temperature, strength of the currents and topography, in the deep sea rather than shallower depths.

The sites MT1 and MT2 species compositions were dramatically different from other stations. The high nutrients and strong current brought by Mississippi River could be the main factors forming the species community in this specific area. The distinct physical environment around MT3, MT4 and S36 caused by Mississippi River input,

compared to intermediate depths in other areas, probably plays an important role in

forming the bivalve community in this regime.
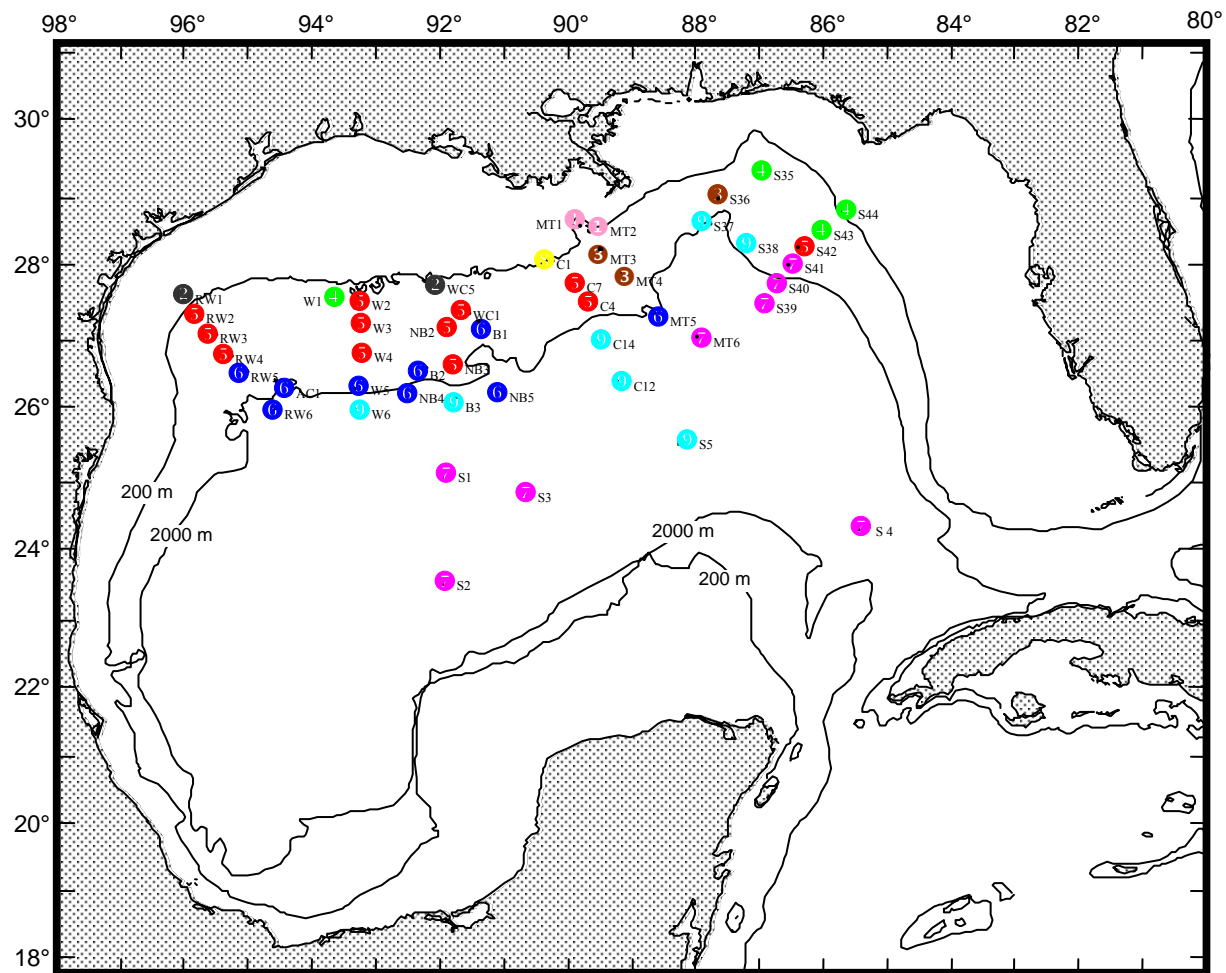
Fig. 10. Map of grouping stations based on similarity.

SUMMARY

Density of bivalve mollusks decreased gradually from shallow continental slope depths, with remarkably high values in the Mississippi canyon, to the deepest sites. Diversity of bivalve mollusks increased from shallow continental slope depths, with low values in the Mississippi canyon, to a maximum at intermediate depths (1-2km), followed by a decrease down to the deepest locations (3.7km). Maximum diversity was found on the upper continental slope (1-2km) in the Gulf of Mexico, rather than the upper continental rise (3 km), where a maximum has been observed in other ocean basins (Rex, 1983). Nine distinct groups were formed on the basis of the similarity in species composition. The pattern varied more abruptly on the slope compared to the deeper depths. The pattern was hypothesized to be due to steeper gradients in physical variables in shallow continental slope depths compared to the deeper depths.

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APPENDIX

Table 12
List of bivalves by site

Taxa	C1	C4	C7	C12	C14	WC5	WC12	NB2	NB3	NB4	NB5	RW1
1	3	2	21	0	12	0	1	0	2	2	1	2
2	2	5	0	14	22	1	2	11	3	8	1	0
3	22	1	0	20	14	0	0	1	2	5	5	1
4	0	6	4	0	5	0	0	0	2	0	2	1
5	1	8	5	1	0	0	9	3	0	0	0	0
6	0	8	5	1	0	16	5	6	0	1	0	14
7	2	5	7	2	1	7	7	3	7	2	2	0
8	0	9	0	1	2	0	5	8	2	3	4	0
9	0	2	2	4	0	0	3	2	0	1	0	0
10	0	0	0	13	8	1	0	0	0	1	1	0
11	0	5	6	0	1	1	1	4	2	7	2	1
12	0	0	0	0	0	0	1	2	6	4	1	4
13	0	7	10	0	0	1	5	5	0	0	0	0
14	0	1	0	3	0	0	4	4	1	1	0	0
15	0	0	11	0	0	0	2	0	0	0	0	0
16	0	4	2	0	0	0	1	2	2	0	0	11
17	1	0	0	4	0	4	0	0	0	0	0	0
18	0	0	2	3	1	0	2	0	0	0	1	0
19	1	12	2	2	0	0	0	4	1	0	1	0
20	0	0	8	2	0	0	0	0	0	0	0	0
21	0	1	2	0	0	1	0	1	0	0	1	0
22	0	2	0	4	1	0	0	0	1	1	1	0
23	0	1	0	1	0	0	2	3	0	5	1	0
24	0	0	0	0	0	0	3	0	0	0	0	10
25	1	0	2	0	0	0	0	0	0	0	0	0
26	0	1	0	0	1	0	0	0	1	1	0	0
27	0	2	0	0	0	0	0	0	3	5	1	0
28	0	0	0	1	3	0	0	0	2	2	0	0
29	0	0	0	3	2	2	0	1	1	1	0	0
30	0	0	1	0	1	10	0	0	0	0	0	1
31	0	2	2	3	1	0	0	0	0	0	0	0
32	0	3	0	0	0	5	0	4	2	0	0	0
33	0	0	0	1	0	0	3	0	1	0	0	2
34	1	2	0	0	4	0	0	0	0	0	0	0
35	0	1	0	0	0	0	0	0	0	0	0	12
36	1	0	0	0	1	0	0	0	0	0	0	1
37	0	0	0	0	0	16	0	0	0	0	0	8
38	1	0	0	0	0	0	0	0	0	0	0	18
39	0	2	1	0	0	0	2	0	1	1	0	0
40	3	0	3	0	0	0	1	0	0	0	0	0
41	3	0	2	2	0	0	0	1	0	1	0	0
42	0	4	0	0	0	2	0	0	0	1	0	1
43	0	0	0	0	0	0	0	0	0	0	0	2
44	0	0	0	0	2	0	1	0	0	2	0	0
45	0	0	0	0	0	5	0	0	0	0	0	3
46	0	1	1	0	0	0	0	0	0	1	0	2

Table 12
Continued

Taxa	C1	C4	C7	C12	C14	WC5	WC12	NB2	NB3	NB4	NB5	RW1
47	0	2	5	0	0	0	1	0	0	0	0	0
48	4	1	2	0	0	0	3	1	0	0	0	0
49	0	0	1	0	0	2	0	0	0	0	0	0
50	4	0	0	0	0	0	0	0	0	0	0	0
51	0	1	0	2	0	1	0	0	0	0	0	0
52	0	0	0	1	2	0	0	0	0	0	0	0
53	1	0	1	0	0	0	0	0	1	1	0	0
54	6	0	0	0	0	0	0	0	0	0	0	0
55	0	1	0	0	0	0	2	0	0	5	0	0
56	0	0	0	0	1	0	0	1	0	1	0	0
57	0	0	2	0	0	0	1	1	0	0	0	0
58	0	1	0	1	0	0	0	1	0	0	0	0
59	0	0	0	0	0	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0	0	0	0	0	0
61	0	0	0	0	0	0	0	0	0	0	0	0
62	0	0	0	0	0	0	0	0	0	0	0	0
63	0	0	0	1	2	0	0	0	0	0	0	0
64	0	0	0	0	0	0	0	0	0	0	0	1
65	0	0	0	0	0	1	1	0	1	1	1	0
66	0	0	0	0	0	3	0	0	0	0	0	0
67	0	0	0	0	0	4	1	0	0	0	0	0
68	0	0	0	0	0	0	0	0	0	1	0	0
69	0	0	0	0	0	2	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	0	0	0	0	0	0	0	0
72	3	0	0	0	0	0	0	0	0	0	0	0
73	3	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	1	0
76	0	0	0	0	2	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0	0
78	0	0	0	0	0	0	0	0	1	0	0	0
79	0	0	0	0	0	0	0	0	0	0	0	3
80	0	1	0	0	0	0	0	0	0	0	0	0
81	0	0	0	0	0	1	0	0	0	0	0	0
82	1	0	0	0	0	2	0	0	0	0	0	2
83	1	0	2	0	0	0	0	0	0	0	0	0
84	0	1	0	0	0	0	0	0	0	0	0	0
85	0	2	0	0	0	0	0	0	0	0	0	0
86	0	0	0	1	0	0	0	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	0	0
88	1	0	0	0	0	1	0	0	0	0	0	0
89	0	0	0	0	0	1	0	0	0	0	0	2
90	1	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	2
92	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0

Table 12
Continued

Taxa	RW2	RW3	RW4	RW5	RW6	S35	S36	S37	S38	S39	S40	S41
1	5	1	1	0	4	11	5	0	15	2	0	0
2	15	6	11	8	5	71	13	1	2	2	4	8
3	1	0	0	2	5	0	8	12	5	2	1	0
4	2	0	0	0	0	11	42	0	0	0	0	0
5	8	4	1	0	1	4	1	0	0	1	2	0
6	0	2	1	4	0	1	1	0	1	0	2	0
7	5	0	4	2	5	0	1	3	0	1	1	3
8	0	3	5	5	1	0	16	5	0	1	0	0
9	3	0	0	2	0	5	0	0	0	1	2	1
10	0	0	0	0	2	0	1	11	0	0	0	0
11	0	4	5	11	0	1	1	0	0	0	0	2
12	1	1	2	4	1	0	0	0	1	0	2	0
13	13	5	0	1	0	2	0	0	0	0	0	0
14	1	0	0	2	2	4	0	0	0	0	1	0
15	8	0	0	0	0	17	0	0	0	0	0	0
16	11	2	4	2	0	0	1	0	0	0	0	0
17	0	0	0	0	3	0	0	0	3	5	5	3
18	0	0	0	0	1	1	0	14	10	0	0	0
19	2	1	5	0	0	0	0	0	0	0	0	1
20	0	0	0	0	0	0	1	0	0	2	0	0
21	2	0	4	2	0	2	25	0	0	0	0	0
22	0	0	0	0	0	0	3	11	2	3	1	2
23	0	1	0	3	0	0	1	0	0	0	0	0
24	2	0	0	7	0	0	0	0	0	0	0	0
25	0	0	1	0	0	0	0	0	0	0	0	0
26	0	0	0	4	0	0	7	7	2	0	0	1
27	0	0	0	0	1	0	0	0	0	4	1	0
28	0	0	1	1	0	0	1	6	3	0	0	0
29	0	1	0	2	0	0	1	0	0	2	1	2
30	10	1	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	1	0	0	1	0	0
32	1	1	3	0	0	0	0	0	0	0	0	0
33	2	0	0	0	0	1	1	0	0	0	0	0
34	0	0	1	0	0	2	0	1	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	2	0	5	0	0	0	0
37	0	0	0	0	0	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0	0	1	0	0
39	0	0	7	3	0	0	0	0	0	0	0	0
40	0	0	7	0	0	4	1	0	0	0	0	0
41	1	0	0	1	1	0	0	1	0	0	0	0
42	1	0	1	0	0	0	0	0	0	1	4	1
43	0	0	0	0	0	3	0	0	0	0	0	0
44	0	0	0	0	0	0	1	0	1	0	0	1
45	0	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	1	0	2	0	0	0	0	0	0
47	1	0	3	0	0	0	0	0	0	0	0	0

Table 12
Continued

Taxa	RW2	RW3	RW4	RW5	RW6	S35	S36	S37	S38	S39	S40	S41
48	2	0	0	0	0	1	0	0	0	0	0	0
49	0	2	0	0	0	0	1	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0
51	0	1	0	0	0	0	0	0	0	0	0	1
52	0	0	0	0	0	0	0	2	0	0	0	0
53	0	0	0	0	0	2	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0
56	2	0	0	0	1	0	0	0	0	0	0	1
57	2	0	0	1	0	1	0	0	0	0	0	0
58	0	0	0	0	0	0	0	0	0	0	0	0
59	0	0	0	0	0	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0	0	0	0	0	0
61	1	0	0	0	0	3	0	0	0	0	0	0
62	0	0	0	0	0	1	0	0	0	0	0	0
63	0	0	0	0	0	0	1	0	0	0	0	0
64	0	0	0	0	0	0	0	0	0	0	0	0
65	0	1	0	1	0	0	0	0	0	0	0	0
66	1	2	0	0	0	0	0	0	0	0	0	0
67	0	0	0	0	0	0	0	0	0	0	0	0
68	0	0	0	0	0	0	1	0	0	0	0	1
69	0	0	0	0	0	0	0	0	0	0	0	0
70	0	0	0	0	0	3	0	0	0	0	0	0
71	0	0	2	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	1	4	0	0	0	0	0
73	1	0	0	0	0	0	0	0	0	0	0	0
74	2	0	0	1	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	2
76	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	1	0	0	0	0	0	0	0	0	0
78	1	0	0	0	0	0	0	0	0	0	0	0
79	0	0	0	0	0	0	0	0	0	0	0	0
80	1	0	0	0	0	1	0	0	0	0	0	0
81	1	0	0	0	0	1	0	0	0	0	0	0
82	0	0	0	0	0	0	0	0	0	0	0	0
83	0	0	0	0	0	0	0	0	0	0	0	0
84	0	0	0	0	0	0	0	0	0	0	0	0
85	0	0	0	0	0	0	1	0	0	0	0	0
86	1	0	0	0	0	0	0	0	0	0	0	0
87	2	0	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	1	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	1	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0

Table 12
Continued

Taxa	S42	S43	S44	B1	B2	B3	AC1	W1	W2	W3	W4	W5
1	0	16	9	1	3	1	0	35	2	0	0	1
2	10	42	9	6	16	23	10	8	19	5	2	8
3	1	15	0	6	5	12	6	6	0	0	0	5
4	0	0	0	0	1	1	0	1	0	1	0	0
5	9	2	0	1	0	0	0	5	25	7	2	0
6	15	0	0	0	0	1	0	2	2	1	2	0
7	6	0	0	2	4	4	2	0	3	6	6	0
8	0	0	0	3	1	4	2	0	0	0	2	0
9	1	11	0	1	0	0	0	13	0	1	2	0
10	0	0	0	1	0	14	2	0	0	0	0	4
11	0	1	0	1	0	1	2	0	0	1	1	0
12	1	12	2	1	1	1	2	13	1	2	5	0
13	5	0	0	0	0	0	0	0	6	3	1	0
14	3	0	2	0	0	2	0	2	2	2	4	2
15	4	0	0	0	0	0	0	0	1	1	0	0
16	5	0	0	1	0	0	0	0	0	2	4	0
17	0	0	0	0	0	0	0	0	0	0	0	1
18	0	0	0	0	0	2	0	2	0	0	0	0
19	1	0	2	0	0	0	0	3	1	1	1	0
20	0	0	0	0	0	0	0	0	0	0	0	0
21	0	1	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	3	1	0	0	0	0	0	0
23	0	0	2	1	4	1	0	0	0	0	3	1
24	0	2	0	0	0	0	0	7	1	0	2	0
25	0	5	0	0	0	0	0	17	0	1	1	0
26	0	0	0	0	0	0	0	0	0	0	0	0
27	1	0	0	0	1	2	1	0	0	0	0	1
28	0	0	0	1	4	1	0	0	0	0	0	0
29	0	0	0	0	1	0	2	0	0	0	0	0
30	1	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	2	0	0	1	0
32	0	0	8	0	0	0	0	1	0	0	0	0
33	0	0	0	2	0	0	0	0	0	0	1	0
34	0	5	0	0	0	0	0	2	0	0	1	0
35	0	0	10	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	0	0	0	0	0
38	0	0	2	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0	0	0	0	0	0	0	0
40	0	0	0	0	0	0	0	0	0	0	0	0
41	1	1	0	0	0	1	0	0	0	0	1	0
42	0	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	1	0	1	0	0	0	0	0	0
45	0	0	8	0	0	0	0	0	0	0	0	0
46	0	0	3	0	0	0	0	1	0	1	0	0
47	0	0	0	0	0	0	0	0	0	2	0	0

Table 12
Continued

Taxa	S42	S43	S44	B1	B2	B3	AC1	W1	W2	W3	W4	W5
48	1	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	7	1	0	0
50	0	1	0	0	0	0	0	0	0	0	0	0
51	0	0	0	0	0	1	0	3	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	1	0	0	1
54	0	2	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	1	0	0
56	0	0	1	0	0	0	0	0	0	0	0	0
57	0	0	0	0	0	0	0	0	0	1	0	0
58	0	0	0	0	0	1	1	0	0	0	1	0
59	0	0	0	0	0	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0	0	0	0	0	0
61	0	2	0	0	0	0	0	0	0	0	0	0
62	0	0	0	0	0	0	0	0	0	0	0	0
63	0	0	0	0	0	0	0	0	0	0	0	0
64	0	0	1	0	0	0	0	1	3	1	0	0
65	0	0	0	0	0	0	0	0	0	0	0	0
66	0	0	0	0	0	0	0	0	0	0	0	0
67	0	0	0	0	0	0	0	0	2	0	0	0
68	0	0	0	0	0	0	0	0	0	0	0	0
69	0	1	1	0	0	0	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	1	0	0
71	0	0	0	0	0	0	0	0	1	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0
75	0	1	0	0	0	0	0	0	0	0	1	0
76	0	0	0	0	0	0	0	0	0	0	0	0
77	2	0	0	0	0	0	0	0	0	1	0	0
78	0	0	0	0	0	0	0	0	0	0	1	0
79	0	0	1	0	0	0	0	0	0	0	0	0
80	0	0	0	0	0	0	0	0	0	1	0	0
81	0	1	0	0	0	0	0	0	0	0	0	0
82	0	0	0	0	0	0	0	0	0	0	0	0
83	0	0	0	0	0	0	0	0	0	0	0	0
84	1	0	0	0	0	1	0	0	0	0	0	0
85	0	0	0	0	0	0	0	0	0	0	0	0
86	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	1	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	1	0	0	0	0	0	0
93	0	0	0	0	0	2	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	1	0	0

Table 12
Continued

Taxa	W6	S1	S2	S3	S4	S5	MT1	MT2	MT3	MT4	MT5	MT6
1	0	0	0	0	0	18	201	152	31	6	0	0
2	15	3	3	6	3	20	4	3	0	2	8	6
3	17	12	0	0	3	68	0	0	0	0	4	6
4	0	0	0	0	0	2	0	0	59	17	0	0
5	2	0	0	3	2	3	1	21	0	1	0	0
6	1	2	5	3	3	0	0	1	18	5	0	0
7	6	0	2	3	0	0	0	0	1	4	0	1
8	0	0	0	0	0	0	0	0	0	4	5	0
9	0	0	0	0	0	3	0	4	15	0	0	1
10	0	0	0	0	0	20	0	0	0	0	0	0
11	0	0	5	0	2	0	0	0	0	2	2	1
12	0	0	0	0	0	0	0	0	1	0	0	0
13	0	0	0	0	0	0	0	0	1	0	0	0
14	4	0	0	0	6	6	0	1	2	0	0	1
15	0	0	0	0	0	0	0	0	15	2	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0
17	1	5	2	3	6	2	0	0	0	0	0	5
18	6	0	0	0	0	0	1	2	0	0	1	0
19	0	0	0	0	2	0	1	1	0	0	0	0
20	0	0	0	0	0	0	0	0	25	4	2	1
21	0	0	0	0	0	0	0	0	0	0	3	0
22	0	0	0	0	0	2	0	0	0	0	2	0
23	0	0	0	0	0	2	0	0	6	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	2	0	2	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	4	3	0
27	0	0	3	0	2	0	0	0	0	0	3	0
28	0	0	0	0	2	0	0	0	0	0	2	0
29	0	0	2	0	0	5	0	0	0	0	1	0
30	0	0	0	0	0	0	0	0	4	1	0	0
31	0	0	0	0	0	0	0	0	16	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	2	9	2	0	0
34	0	0	0	0	0	0	3	1	2	1	0	0
35	0	0	0	0	0	0	0	0	0	2	0	0
36	0	0	0	0	0	0	6	8	1	0	0	0
37	0	0	0	0	0	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0	2	0	0	1	0	1	0
40	0	0	0	0	0	0	0	0	4	0	0	0
41	0	0	0	0	0	0	0	0	0	1	1	0
42	0	0	0	0	0	0	0	0	0	1	0	0
43	0	0	0	0	0	0	1	10	0	0	0	0
44	0	0	0	0	0	0	0	0	0	5	0	1
45	0	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	1	0	0	1	0	0
47	0	0	0	0	0	0	0	0	1	0	0	0

Table 12
Continued

Taxa	W6	S1	S2	S3	S4	S5	MT1	MT2	MT3	MT4	MT5	MT6
48	0	0	0	0	0	0	0	0	2	1	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	1	5	0	0	0	0
51	0	0	0	0	0	0	0	0	0	0	1	0
52	0	0	0	0	0	5	0	0	0	0	0	0
53	0	0	0	0	0	0	0	1	0	0	0	0
54	0	0	0	0	0	0	0	2	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0
56	1	0	0	0	0	0	0	0	0	0	0	0
57	0	0	0	0	0	0	0	0	0	0	0	0
58	0	0	0	0	0	0	0	0	0	0	0	1
59	0	0	0	0	0	0	0	2	5	0	0	0
60	0	0	0	0	0	0	0	5	2	0	0	0
61	0	0	0	0	0	0	0	0	1	0	0	0
62	0	0	0	0	0	0	4	2	0	0	0	0
63	0	0	0	0	0	0	0	0	2	0	1	0
64	0	0	0	0	0	0	0	0	0	0	0	0
65	0	0	0	0	0	0	0	0	0	0	0	0
66	1	0	0	0	0	0	0	0	0	0	0	0
67	0	0	0	0	0	0	0	0	0	0	0	0
68	1	0	0	0	0	0	1	0	1	0	0	0
69	0	0	0	0	0	0	1	0	0	0	1	0
70	0	0	0	0	0	0	0	0	1	0	0	0
71	0	0	0	0	0	0	0	0	0	2	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	1	0	0	0	0
74	0	0	0	0	0	0	0	1	0	1	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	2	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0	0
78	0	0	0	0	0	0	0	0	0	0	1	0
79	0	0	0	0	0	0	0	0	0	0	0	0
80	0	0	0	0	0	0	0	0	0	0	0	0
81	0	0	0	0	0	0	0	0	0	0	0	0
82	0	0	0	0	0	0	0	0	0	0	0	0
83	0	0	0	0	0	0	0	0	1	0	0	0
84	0	0	0	0	0	0	0	0	0	0	0	0
85	0	0	0	0	0	0	0	0	2	0	0	0
86	0	0	0	0	0	0	0	1	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	1	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	1	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0

Table 13

List of species names of bivalves

Label	Taxa	Label	Taxa
1	Heterodonta sp. A	48	Neilonella sp.
2	Heterodonta sp. B	49	Bivalve sp. G
3	Heterodonta sp. C	50	Heterodonta sp. K
4	Heterodonta sp. D	51	Nuculana sp. B
5	Nucula sp. A	52	Heterodonta sp. L
6	Vesicomya vesica	53	Neilo sp.
7	Bathyarca sp. A	54	Heterodonta sp. M
8	Tindariopsis aeolata	55	Bivalve sp. H
9	Palaeotaxodonta sp. A	56	Limopsis sp. D
10	Tindariopsis sp. A	57	Bivalve sp. I
11	Nuculana sp. A	58	Limopsacea sp.
12	Heterodonta sp. E	59	Bivalve sp. J
13	Tellina sp.	60	Nuculana sp. C
14	Limopsis sp. A	61	Limopsis sp. E
15	Heterodonta sp. F	62	Anodontia sp.
16	Limopsis sp. B	63	Palaeotaxodonta sp. D
17	Dacrydium vitreum	64	Bivalve sp. K
18	Heterodonta sp. G	65	Bivalve sp. L
19	Pristigloma nitens	66	Bivalve sp. M
20	Heterodonta sp. H	67	Verticordia sp.
21	Bivalve sp. A	68	Cyrtodaria sp.
22	Malletiidae sp. A	69	Palaeotaxodonta sp. E
23	Tindariopsis agathida	70	Limopsis sp. F
24	Heterodonta sp. I	71	Tindaria sp A.
25	Limopsis sp. C	72	Tindaria sp B
26	Modiolinae sp. A	73	Palaeotaxodonta sp. F
27	Palaeotaxodonta sp. B	74	Bivalve sp. N
28	Bivalve sp. B	75	Malletia sp.
29	Tindariopsis sp. B	76	Neilonella sp.
30	Bivalve sp. C	77	Bivalve sp. O
31	Nucula sp. B	78	Cuspidaria sp.
32	Nucula sp. C	79	Limea sp.
33	Bathyarca sp. B	80	Verticordia sp.
34	Lucina sp. A	81	Malletiidae sp. C
35	Limea sp.	82	Tindaria sp. C
36	Bivalve sp. D	83	Bivalve sp. P
37	Nucula sp.	84	Modiolinae sp. B
38	Bivalve sp. E	85	Bivalve sp. Q
39	Heterodonta sp. J	86	Palaeotaxodonta sp. G
40	Bivalve sp. F	87	Palaeotaxodonta sp. H
41	Lucina sp. B	88	Heterodonta sp. N
42	Palaeotaxodonta sp. C	89	Palaeotaxodonta sp. I
43	Pectinidae sp.	90	Astarte sp.
44	Bathyarca sp. C	91	Nuculana platessa
45	Nuculanidae	92	Periploma sp.
46	Malletiidae sp. B	93	Nuculana solidula
47	Nucula sp. D	94	Bivalve sp. R

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