ENVIRONMENTAL FACTORS INFLUENCING

BENTHIC MACROFAUNAL INVERTEBRATE COMMUNITY

STRUCTURE IN THE FLOWER GARDENS EAST BANK

An Undergraduate Research Scholars Thesis

by

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TABLE OF CONTENTS

ABSTRACT

Environmental Factors Influencing Benthic Macrofaunal Invertebrate Community Structure in the Flower Gardens East Bank. (May 2014)

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The Flower Garden Banks consist of two salt domes raised above the continental shelf in the Gulf of Mexico roughly 190 km southeast of Galveston, Texas. With mean annual temperature variations of 18 to 32°C and relatively low-turbidity water, the shallower portions of both banks provide ideal substrates for scleractinian coral growth, resulting in the formation of the two northernmost coral reefs in the continental U.S (Bright et al., 1984; Teague et al., 2013). Factors affecting macroinfaunal organism communities within the shallowest portions of these banks have so far been neglected, with the nearest assessments being conducted by Yingst and Rhoads in waters over 90 m deep and adjacent to the Banks, not within the Bank tops (1985).

The objectives of this study were twofold: to determine if there are statistically significant differences in composition between the polychaete communities of the coastal northwestern Gulf of Mexico and the East Flower Garden Bank (EFGB), and to look for correlations between the environmental parameters of percent carbonate content, particulate organic carbon (POC) content, and sediment grain size, and the community parameters of biomass, density, species richness, species evenness, and diversity of all macroinfaunal invertebrates at a depth of ~25 meters in the EFGB.

Eight box core samples were taken off the coast of Louisiana from August 21-September 9, 1978, and box core samples were taken from the EFGB on August 28-29, 2013. There was no overlap in species composition between the Louisiana samples and the EFGB samples, and the Louisiana samples were more diverse in general. Amphipod and isopod crustaceans dominated the EFGB macrofauna numerically in most samples, but polychaete worms comprised the largest percentage of biomass in all EFGB samples.

Mean sediment grain size was positively and significantly correlated with species count, Margalef's richness, and biomass. Particulate organic carbon content was positively and significantly correlated with every diversity measurement except species count and individual density. Sediment carbonate content was not significantly correlated with any biotic variable. No significant correlations were detected between the environmental variables.

ACKNOWLEDGEMENTS

CHAPTER I

INTRODUCTION

The Flower Garden Banks consist of two salt domes on the Gulf of Mexico continental shelf roughly 190 km southeast of Galveston, Texas. The East Flower Garden Bank (EFGB), which is part of the Flower Garden Banks National Marine Sanctuary, is approximately 5 km wide by 8 km long, with a shallowest depth of 18 m. With mean annual temperature variations of 18 to 32°C and relatively low-turbidity water, the shallower portions of both banks provide ideal substrates for scleractinian coral growth, resulting in the formation of the two northernmost tropical coral reefs in the continental U.S (Bright et al., 1984; Teague et al., 2013). Other salt domes near the banks harbor extensive oil and natural gas deposits, and by 1998 four drilling platforms had been constructed within 6.5 km of the EFGB.

In order to assess the impacts these drilling operations might have on the local fauna, the Minerals Management Service and the National Oceanic and Atmospheric Administration have been conducting surveys of the reef fishes, elasmobranchs, and sea turtles in the area, in addition to surveys of the diversity, abundance, and growth rates of the corals themselves (Gittings, 1998). However, although macrofauna censuses have been taken, factors affecting macroinfaunal organism communities within the shallowest portions of these banks have so far been neglected. The nearest assessments were conducted by Yingst and Rhoads in waters over 90 m deep and adjacent to the Banks, not within the Bank tops (1985). Bright et al. found that although 85% of the areas above 36 m in the Banks consist of coral growth and hard substrate,

the remaining 15% is comprised of gravel and carbonate sand, which could be suitable habitat for infauna (1984).

Due to the locally unique environmental conditions at the Flower Garden Banks (FGB), it is quite likely that the infaunal composition of the shallow FGB is significantly different from that of the surrounding continental shelf. Water clarity at the Banks is higher than that of inshore areas of similar depths, with mean light attenuation coefficients measuring 0.1 to 0.3 m^{-1} for most 20-100 m depths of similar distance from the Texas coast, while FGB light attenuation coefficients vary between 0.13 m^{-1} in January to 0.06 m^{-1} in August (Hagman et al., 1998; Lugo-Fernández et al., 2012). This greater light penetration could increase primary productivity in the FGB relative to inshore areas, and factors that depend on primary productivity, such as chlorophyll α content and meiofaunal biomass, have been shown to correlate positively with benthic macrofaunal species richness in the northern Gulf of Mexico (Haedrich et al., 2008).

Sediment grain size is another physical factor in the FGB that could create a unique infaunal community composition. Although this environmental variable has not proven significant in all marine benthic faunal studies, Byrnes et al. found that sediment grain size was the most crucial factor other than season that affected species composition and richness in benthic infauna off the coast of Alabama (1999). Regarding specific patterns, Martins et al. found that sediment grain size was positively correlated with measures of Shannon-Wiener diversity, Margalef's richness, and Simpson richness in polychaete communities off the coast of Portugal, which also shows that sediment type is an important community-driving factor in oceans worldwide (2013). A report published by the Minerals Management Service corroborates these data for the northern Gulf of

Mexico, particularly with regards to mollusks and crustaceans; however, this report also states that sediment grain size tends to be influenced by variables such as season, location, and water depth, so sediment texture could merely be an indicator of richness/diversity and not a proximate cause (Schroeder and Wood, 2000).

The percentage of particulate organic carbon in sediment is yet another important factor that must be examined when evaluating benthic habitats. For deposit-feeding animals, such as the polychaete worm *Nereis virens*, particulate organic carbon is a crucial metabolic component, being taken up preferentially to particulate organic nitrogen (Kristensen and Blackburn, 1987). Kristensen and Blackburn's study also implied that the percentage of particulate organic matter can affect the biomass and diversity of resident organisms, as they introduced *Nereis virens* to a controlled environment where only 0.25% of their sediment consisted of particulate organic carbon and found that the biomass and number of individuals had both decreased after 94 days (1987). For a species that is rare in a particular area, a decrease in individuals due to decreased nutrients could lead to extirpation, reducing local biodiversity.

Calcium carbonate content is another commonly measured sediment characteristic in benthic ecology studies. Like particulate organic carbon, the percentage of calcium carbonate in marine sediments can be used as a proxy for primary productivity because the majority is derived from shells of foraminiferans and pteropod molluscs (Levin and Thomas, 1989; Levin et al., 1991; Gage and Tyler, 1991). Due to the high concentration of scleractinian corals (which are also generally primary producers) in the FGB, there will likely be a significant $CaCO_3$ contribution

from them as well; however, the contributions of coral detritus to benthic food webs, if any, have not been investigated.

In addition to species richness and diversity, species composition is a dependent variable that will be examined in this study. Although infaunal invertebrate data from the EFGB is somewhat lacking (particularly regarding polychaetes), fish populations from the same area (<45 m depth) are dominated by species that are also found in Caribbean coral reefs; however, due to habitat patchiness and homogeneity, as well as the great distance between the FGB and the Caribbean reefs, reef fish diversity in the FGB is lower than that of similar habitat types in the Caribbean (Dennis and Bright, 1988). It remains to be seen if these factors will similarly affect the diversity of invertebrates, or if the invertebrates will be more highly influenced by the sediment grain size or primary productivity of the area. However, based on the abundance of tropical coral and fish species, it is reasonable to assume that the benthic infaunal invertebrate species found in the FGB will most closely resemble those found in the Caribbean Sea.

Benthic biomass has been measured as an indicator of primary productivity in multiple marine ecology studies, as particulate organic carbon is rapidly ingested by many deposit feeding invertebrate species in both shallow and deep water (Gage and Tyler, 1991). However, at subtropical and tropical latitudes <10% of primary productivity reaches the ocean bottom, possibly due to microbial or zooplanktonic activity (Ambrose and Renaud, 1995). In the present study biomass is used as primary productivity indicator due to the relatively shallow depth of the study site, which should minimize the opportunities for nutrient interception in the water column.

This study had two objectives: the first was to determine if there are statistically significant (p<0.05) differences in the density, species richness, species evenness, diversity, and composition of polychaetes at ~30 m depth in the coastal northwestern Gulf of Mexico and the Flower Garden Banks. The null hypothesis was that there are no significant differences in these variables between the two study sites; the experimental hypothesis was that there are significant differences in one or more of these variables between the two study sites.

The second objective of this study was to determine if there are statistically significant (p<0.05) correlations between the environmental parameters of sediment grain size, sediment carbonate content, and sediment particulate organic carbon (POC) content, and the community parameters of biomass, density, species richness, species evenness, and diversity of all macroinfaunal invertebrates at a depth of ~30 meters in the Flower Garden Banks. The null hypothesis was that there is no significant correlation between any of these environmental variables and any of the community variables; the experimental hypothesis was that there is a significant correlation between one or more of these environmental variables and one or more of the community variables.

CHAPTER II

METHODS

Sample collection

Sediment cores were collected from the East Flower Garden Bank on August 28-29, 2013.

Figure 1 shows a bathymetric map of the EFGB; Figure 2 shows an enlarged view of the study

site with buoy locations. Eight core samples were taken from random locations within a 30m

radius of Mooring Buoy #5, located at 27°54'35" N by 93°36'0" W, 113 km offshore

(NOAA, 2013). All sampling locations were retrieved from approximately 25 m depth. The first

two samples were obtained via 100 cm^2 box core, while divers manually scooped the following

six samples into glass jars of roughly equal volume. Samples were taken to a depth of

approximately 10 cm. These samples were preserved in 10% formalin/90% seawater solution.

Control samples were collected by Dr. Donald Harper from August 21 to September 9, 1978.

Samples were taken by a 897.6 cm^2 modified Smith-McIntyre grab at random cardinal directions

surrounding oil drilling Platforms 3 and 4, located at 28°40'02" N by 90°14'43" W and

28°34'09" by 90°24'32", respectively. Samples were taken to a depth of 9 to 16 cm, depending

on substrate. Platform 3 was located 42 km from shore in water 30 m deep, while Platform 4 was

located 53 km from shore in water 45 m deep. Samples were collected at intervals of 500 and

2,000 m from the platforms. Ten replicates were taken from each site. Each control sample was

coded as follows: P#, indicating whether the sample was taken near Platform 3 or Platform 4, a

number indicating the cardinal direction in relation to the platform, a number indicating the

distance from the platform, and, when more than one replicate from a single site is included, a

dash followed by a number between 1 and 10 (e.g. P3 E5-9 indicates the 9th replicate of a sample taken 2,000 m east of Platform 3) (Harper and Fitzhugh, unpublished). Eight of the total control samples were subsampled at random for comparison with the FGB samples.
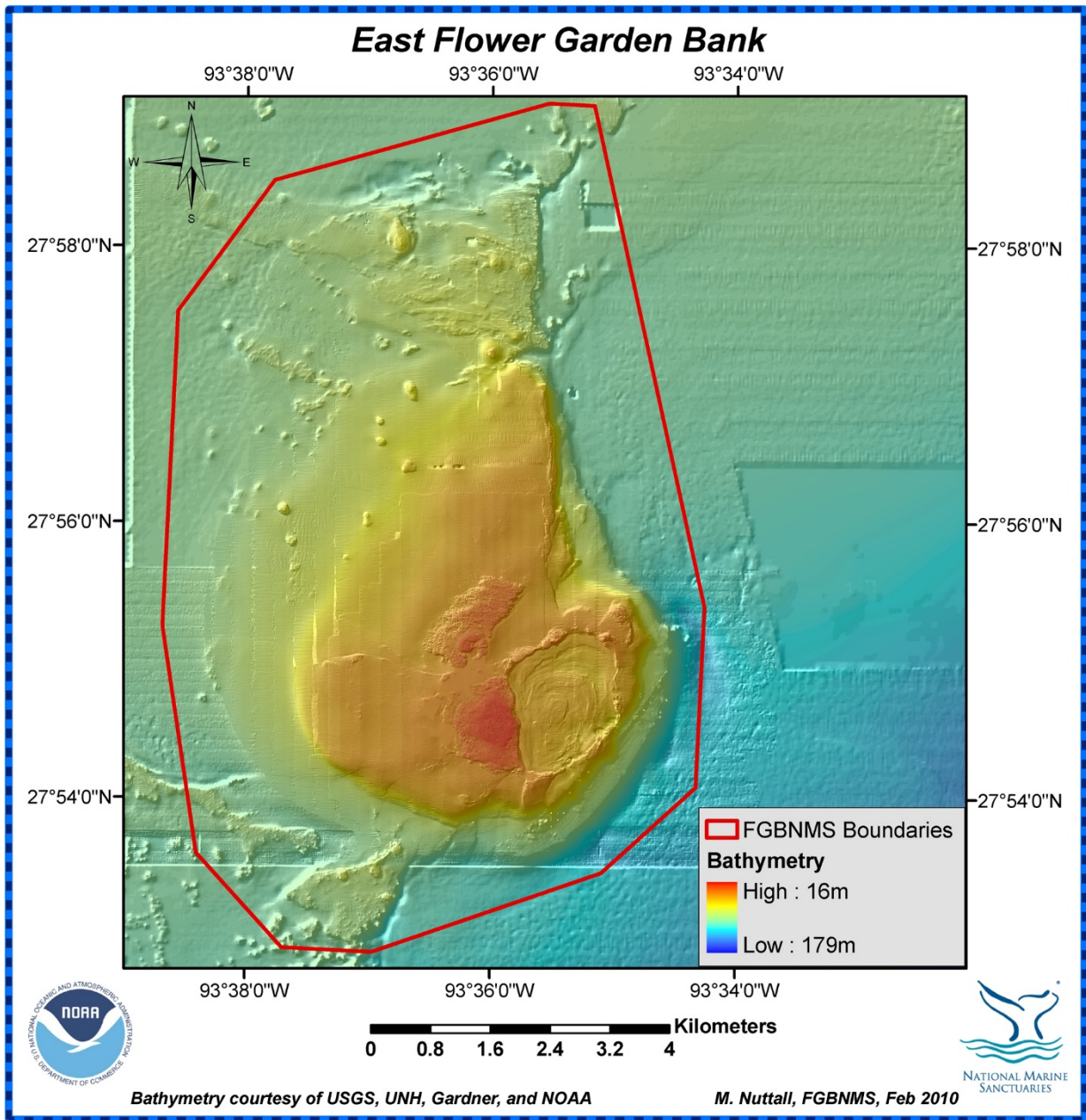

Figure 1. Bathymetric map of the East Flower Garden Bank. Image courtesy of NOAA.
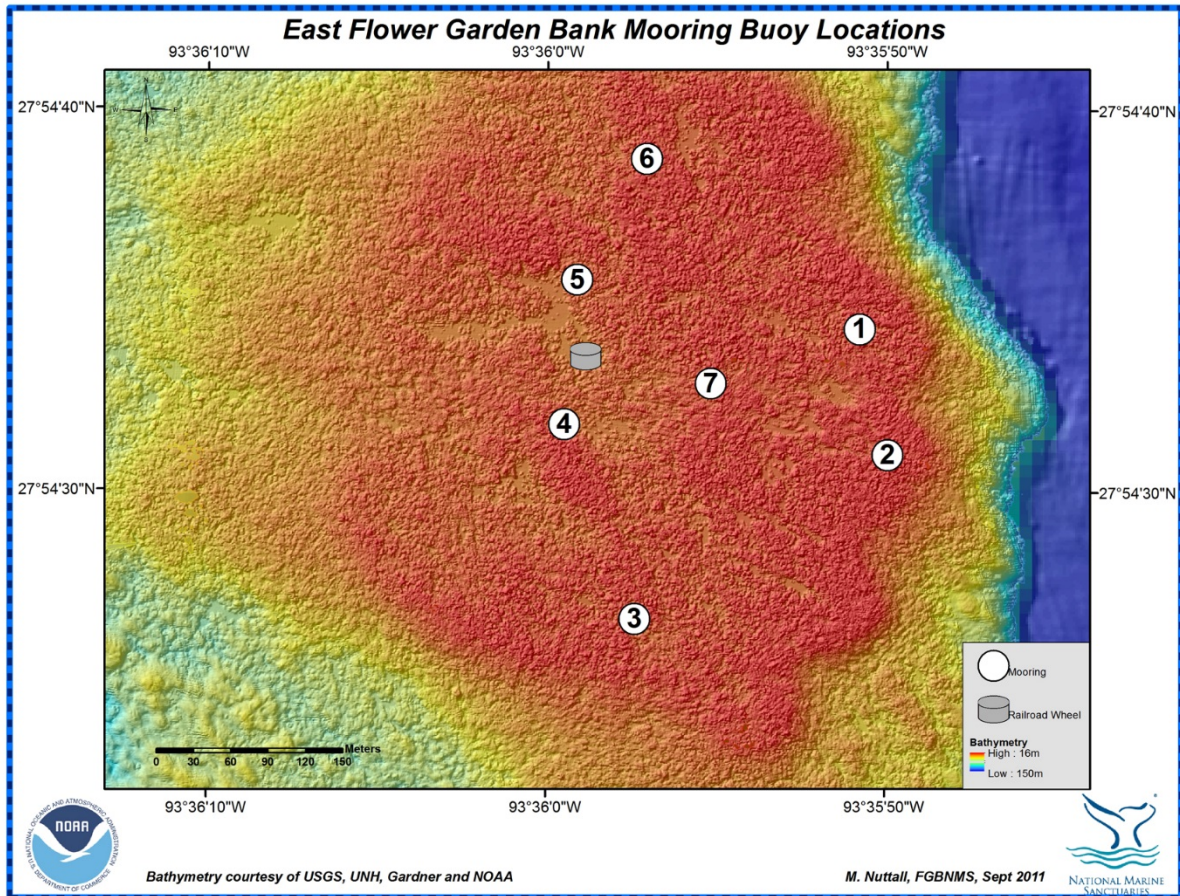
Figure 2. Bathymetric map of East Flower Garden Bank mooring buoy locations. Sampling was conducted within a 30m radius of Buoy #5. Image courtesy of NOAA.

Sample processing

In the lab, the FGB samples were stained with rose bengal to simplify differentiation and separation of fauna from the sediment. Macrofauna were removed from the samples and separated from meiofauna by filtration through a 0.5 mm sieve. Fauna retained by the sieve but belonging to taxa traditionally classified as meiofauna (nematodes, ostracods, and harpacticoid copepods) were omitted as in other macrofaunal community studies (Galéron et al., 2000). Macrofauna were then counted manually under a light microscope and identified to the lowest possible taxon.

Macrofaunal biomass for all taxa except cephalochordata and turbellaria was determined as ash free dry weight (AFDW) using the method of Galéron et al. (2000). Cephalochordate biomass was determined as AFDW by measuring each individual to the nearest centimeter and calculating based on the length/mass relationship determined by Stokes (1996) for the lancelet *Branchiostoma floridae*. An appropriate conversion factor for determining AFDW from wet weight could not be found for turbellarians, and since their mean wet weight contribution to the total biomass across all samples was found to be only 0.535%, they were omitted from this analysis. Ten-specimen subsamples were taken from animals in each taxon in each sediment sample, blotted dry with lint-free tissue wipes, and weighed on a microbalance to the nearest microgram to obtain a measure of wet weight. When fewer than ten specimens were present in a taxon, every specimen was weighed. These wet weights were changed to ash free dry weights using conversion data from Galéron et al. (2000). Mean ash free dry weight values were then calculated for each major taxon in each sediment sample.

After the macrofauna were removed, the sediment was heated at ~65°C until all moisture was evaporated. The dried sediment was then sieved through 1 mm, 0.5 mm, 0.25 mm, and 0.125 mm meshes, and the weight of each sediment fraction was recorded.

Particulate organic carbon (POC) content and calcium carbonate content were measured using the techniques of Heiri et al. (2001). POC was determined by combusting ~10g subsamples of the dry sediment at 500°C for 2 hours; calcium carbonate content was determined by taking these subsamples and further combusting them at 950°C for 3 hours.

Data analysis

A species-sample matrix containing all polychaete species from the FGB samples and the control samples was square-root transformed before being subjected to multivariate analysis.

The control samples consisted solely of polychaetes, so comparisons of all taxa were not viable. PRIMER 6.0 software was used to calculate Margalef's richness index, Pielou's evenness index, and $\log_e$ and $\log_{10}$ values of the Shannon-Wiener diversity index for the EFGB and Control polychaetes, as well as for the total EFGB macrofauna. An unpaired, two-tailed Student's t-test was used to test for significant differences ($p<0.05$) in the means of each of these values between the EFGB and control polychaetes. CLUSTER and Multidimensional Scaling (MDS) Analysis were applied to illustrate differences in faunal community structure between the study areas.

Means and standard deviations for sediment grain sizes were calculated using the method of moments detailed by Folk (1980). Spearman rank correlation was used to determine covariance between the FGB environmental factors and the biotic factors. The environmental factors included: the mean sediment grain size, the percentage of POC in the sediment, and the percentage of sediment carbonate. The biotic factors included biomass, individual count, individual density, species count, and the indices calculated using PRIMER 6.0 above. Since these comparisons only involved samples taken within the FGB, all macroinfaunal invertebrate taxa were included in determining the biotic factors. Spearman rank correlations were also performed between the environmental factors to determine if they were associated with each other.

The mean Margalef's richness, Pielou's evenness, and Shannon-Wiener diversity of polychaetes, shown in Table 1, were significantly ($p<0.05$) higher in the control samples than in the FGB samples. The mean number of species was significantly higher in control samples than in FGB samples, while the mean individual counts and individual densities were not significantly different between samples.

Table 1. Polychaete species counts (S), individual counts (N), individual densities (N/m^2) and diversities in Flower Garden Bank samples and control samples. FGB samples are in green; control samples are in blue; mean and standard deviation values for each sample group are in black. d is Margalef's richness index, J' is Pielou's evenness index, H' is the Shannon–Wiener diversity index ($\log_e$ and $\log_{10}$ values are both displayed). Mean values significantly different ($p<0.05$) between sample groups are denoted with an asterisk.

Sample	S	N	N/m^2	d	J'	H'($\log_e$)	H'($\log_2$)
Sample A	4	11	1100	1.251097	0.745557	1.033562	1.491115
Sample B	2	3	300	0.910239	0.918296	0.636514	0.918296
Sample C	4	9	900	1.365359	0.828871	1.14906	1.657743
Sample D	2	9	900	0.45512	0.503258	0.348832	0.503258
Sample E	6	54	5400	1.253452	0.554078	0.992775	1.432272
Sample F	6	306	30600	0.873578	0.070942	0.127111	0.183383
Sample G	10	49	4900	2.312543	0.746178	1.718139	2.478750
Sample H	4	22	2200	0.970546	0.621650	0.861790	1.243300
FGB mean	4.75*	57.875	5787.5	1.173992*	0.623604*	0.858473*	1.238515*
FGB σ	2.6	102.073	10207.3	0.542897	0.262850	0.495128	0.714318
P3 S2000-10	14	38	423	3.573799	0.848346	2.238835	3.229955
P3 S500-6	20	128	1426	3.915887	0.815655	2.443483	3.525201
P3 N2000-9	9	27	301	2.427305	0.795247	1.747336	2.520872
P4 W500-7	10	37	412	2.492441	0.837484	1.928377	2.782060
P4 W2000-5	6	24	267	1.573290	0.945452	1.694023	2.443959
P3 E500-10	14	60	668	3.175111	0.864145	2.280529	3.290107
P3 N500-5	21	60	668	4.884787	0.867489	2.641089	3.810286
P3 E500-9	22	125	1393	4.349345	0.797829	2.466125	3.557866
Control mean	14.5*	62.375	694.8	3.298996*	0.846456*	2.179975*	3.145038*
Control σ	6	41.751	465.3	1.100508	0.048661	0.351354	0.506897

When arranged in a CLUSTER dendrogram by Bray-Curtis similarity analysis (Figure 3), the

FGB samples show 0% community overlap with the control samples. Both groups also display

very close similarity levels, with all control samples sharing ~25% of polychaete species and all

FGB samples sharing ~22% of polychaete species. The MDS analysis did not reveal any

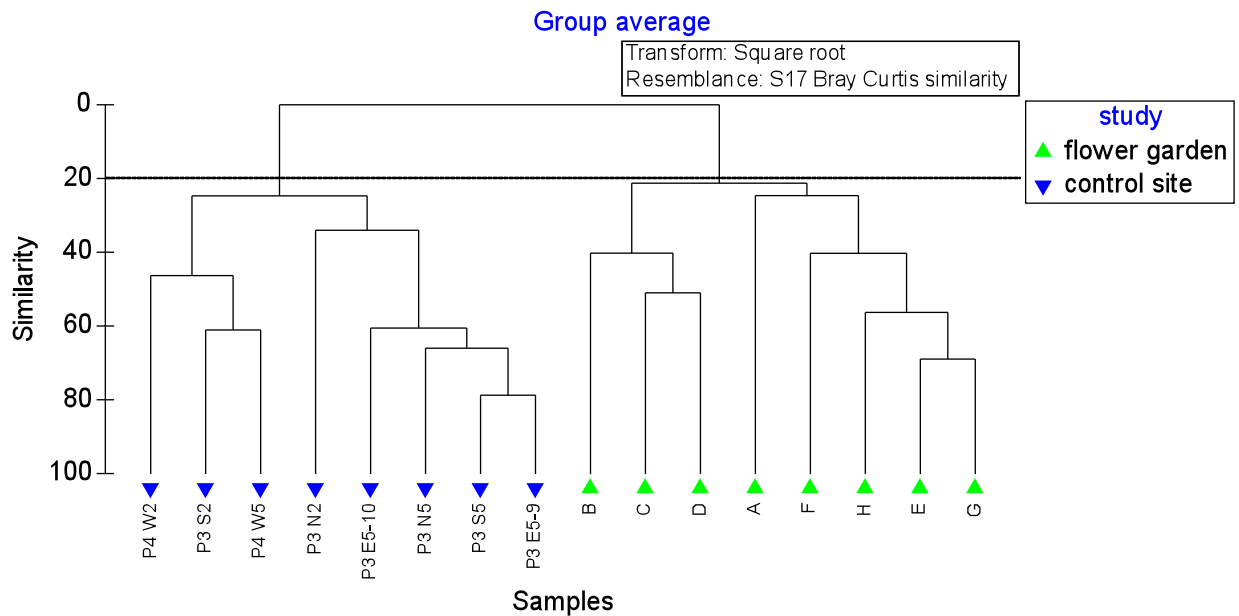significant relationships, so its results are not shown.

Figure 3. Dendrogram of Bray-Curtis similarities among locations in the FGB compared to the control sites.
The CLUSTER dendrogram illustrates 2 distinct groups in polychaete species composition between the 2 studies
based on a 20% similarity level. For the control site samples, the first number-letter pair denotes that the sample was
taken from Platform 3 or Platform 4. The second letter-number pair indicates the cardinal direction and distance
from the platform at which the sample was taken (e.g. W2 is 2,000 m west, N5 is 500 m north). Where multiple
replicates from a single site are included, the replicate number is separated from the second letter-number pair by a
dash.

The percent representation of all identified macroinfaunal taxa in each FGB sample is shown in

the two figures below. Figure 4 illustrates the percentage of total individuals present in each

taxon, while Figure 5 shows the percentage of total biomass represented by each taxon. Except

for Sample F, polychaetes are not numerically dominant in any sample; however, they constitute

a plurality of the biomass in every sample save Sample B, where they compose the smallest

15

percentage of the biomass. The control samples all had taxon representations consisting of 100% Polychaeta and are not shown.
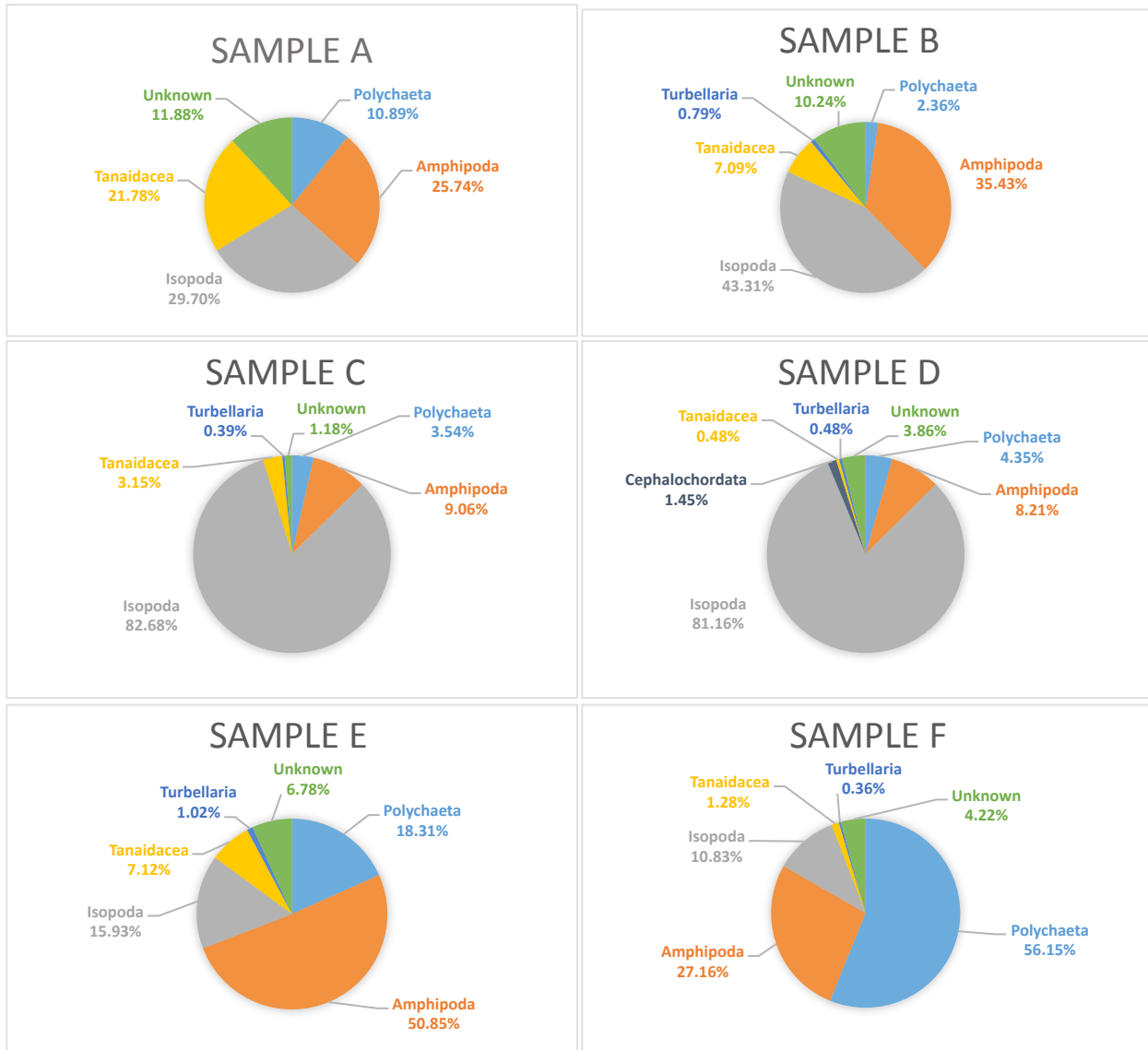
Figure 4. FGB taxon representation in each sample by number of individuals. Specimens that could not be identified to a specific taxon are listed as "unknown".

Figure 4. (Continued)

Figure 5. FGB taxon representation in each sample by biomass. Turbellaria and "unknown" specimens are not represented due to lack of suitable WW/AFDW conversion factors for determining biomass. Decapod biomass is absent from Sample G because the single specimen was not collected intact.

Figure 5. (Continued)

Sediment grain size varied widely, with phi standard deviations being much larger than phi means in all samples. The POC content of the sedime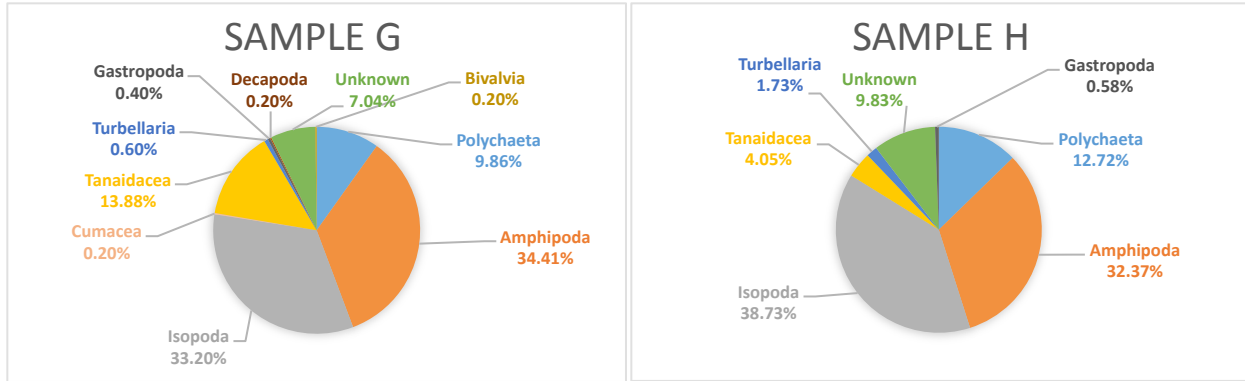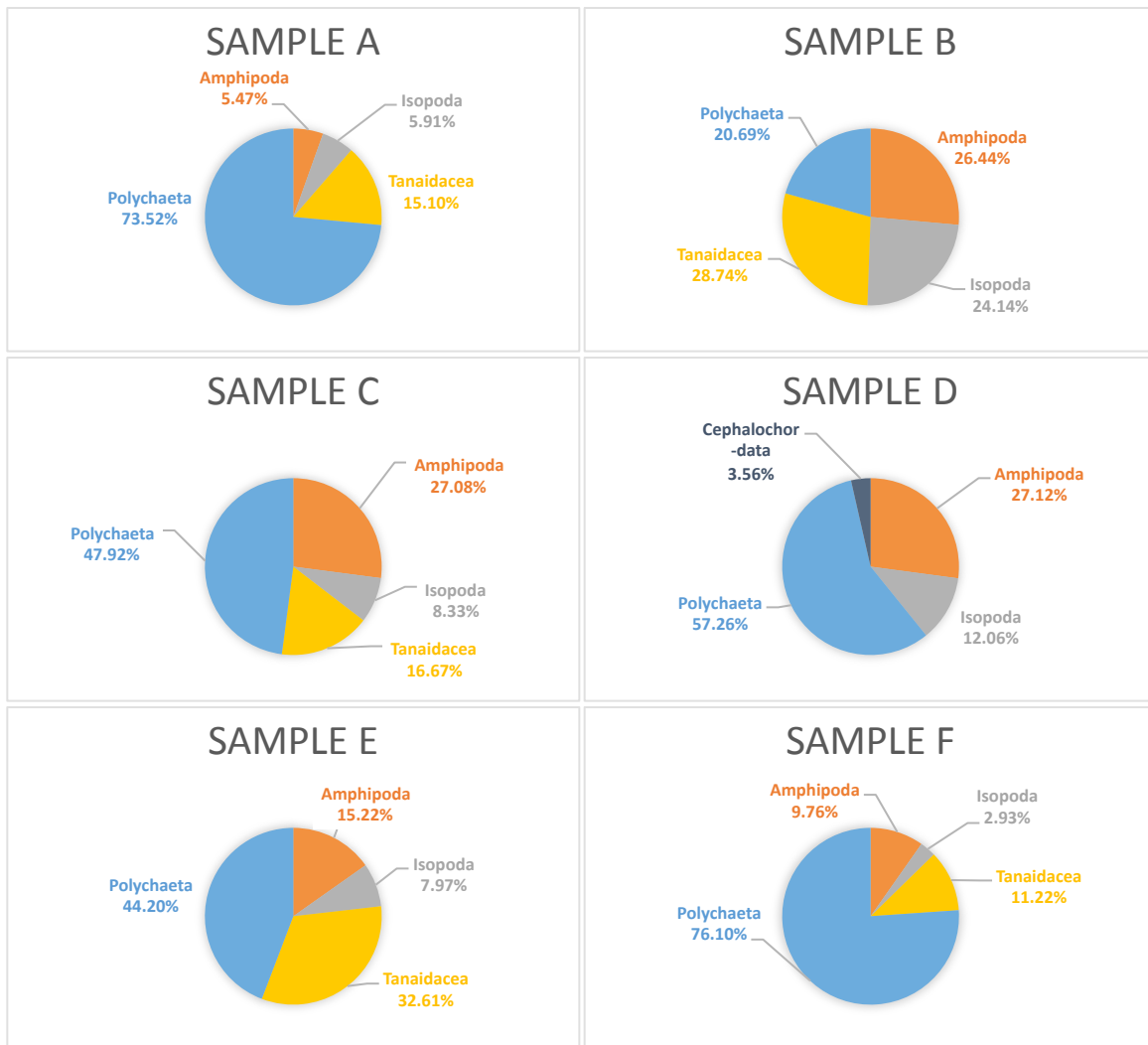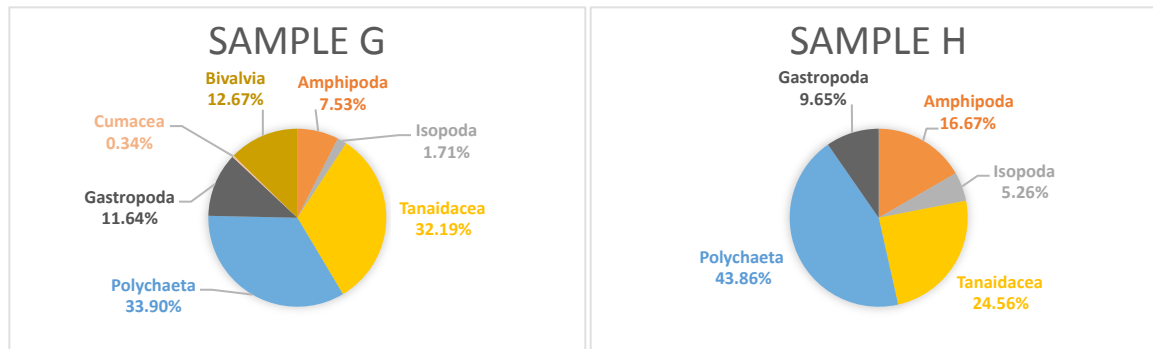nt had a mean of 2.520%, with a standard deviation of 0.056%. The sediment carbonate content of each sample was more uniform, with a mean of 39.278% and a standard deviation of 0.160%. The total biomass in each sample varied widely, having a mean of 0.714 mg and a standard deviation of 0.509 mg. The values for each individual sample are shown in Table 2 below.

Table 2. Mean sediment phi, sediment phi standard deviation, POC % content, calcium carbonate % content, and total biomass for samples A-H. Biomass is measured in milligrams of ash-free dry weight. POC and carbonate contents are measured as percentages to account for small sample volume differences. Sediment from sample F was contaminated with sediment from another sample and could not be used in this analysis.

Sample	Mean sediment φ	Sediment φ σ	POC % content	Carbonate % content	Total biomass (mg AFDW)
A	0.29	0.65	2.564	38.965	0.709
B	0.27	0.64	2.456	39.301	0.623
C	0.38	0.61	2.473	39.239	0.557
D	0.47	0.65	2.464	39.345	0.126
E	-0.31	0.42	2.604	39.394	1.021
G	-0.17	0.52	2.525	39.463	1.665
H	-0.10	0.57	2.557	39.241	0.295
mean	-	-	2.520	39.278	0.714
σ	-	-	0.057	0.160	0.509

Table 3 shows the species count, individual count, individual density, Margalef's richness, Pielou's evenness, Shannon-Wiener diversity (both $\log_e$ and $\log_{10}$), and biomass for all macroinfauna in the FGB samples. Table 4 shows the relationships determined by Spearman rank correlation between these biotic factors and the environmental factors listed above for all macroinfauna.

The mean sediment phi was significantly correlated with the number of macroinfaunal species, Margalef's richness index, and biomass. The percentage of POC content was significantly correlated with every biotic factor except number of species and number of individuals. Sediment grain size was more strongly correlated with Margalef's richness index than POC was, although both correlations were similarly significant ($0.025 > p > 0.01$). Sediment grain size was correlated more strongly and more significantly with biomass than POC ($0.05 > p > 0.025$ for POC, $0.025 > p > 0.01$ for grain size). The percentage of sediment carbonate content, however, was not correlated strongly or significantly with any biotic factor. Spearman rank correlation tests displayed no correlations between the three environmental factors.

Table 3. Macroinfauna species counts (S), individual counts (N), individual densities (N/m^2), and diversities in Flower Garden Bank samples. d is Margalef's richness index, J' is Pielou's evenness index, H' is the Shannon–Wiener diversity index ($\log_e$ and $\log_{10}$ values are both displayed).

Sample	S	N	N/m^2	d	J'	H'($\log_e$)	H'($\log_2$)
Sample A	9	89	8900	1.782278	0.737828	1.621173	2.338859
Sample B	9	114	11400	1.689118	0.539755	1.185964	1.710984
Sample C	9	251	25100	1.447845	0.306118	0.672609	0.97037
Sample D	7	199	19900	1.133507	0.321369	0.625355	0.902197
Sample E	12	275	27500	1.958421	0.593718	1.475334	2.128457
Sample F	12	522	52200	1.757843	0.442165	1.098739	1.585145
Sample G	21	462	46200	3.259684	0.561176	1.708511	2.464861
Sample H	11	156	15600	1.980254	0.591792	1.419055	2.047264
Mean	11.25	258.5	25850	1.876119	0.511740	1.225843	1.768517
σ	4.3	158.0	15804	0.623873	0.146792	0.409395	0.590632

Table 4. Spearman rank correlation values for relationships between environmental and biotic variables. S is species count, N/m^2 is individual density, d is Margalef's richness index, J' is Pielou's evenness index, and H' is the Shannon–Wiener diversity index. Individual counts are equal to $(N/m^2)*10^2$, so correlation values would be exactly the same as for individual density, and thus are not shown. Significant ($p<0.05$) r^2 values are indicated in bold.

	Mean sediment phi	POC	Carbonate content
S	**-0.947**	0.713	0.297
N/m^2	-0.304	0.214	0.593
d	**-0.893**	**0.794**	0.076
J'	-0.604	**0.813**	-0.065
H'($\log_e$)	-0.639	**0.810**	-0.244
H'($\log_2$)	-0.639	**0.810**	-0.244
biomass	**-0.869**	**0.743**	-0.025

CHAPTER IV

DISCUSSION

Very little work has been performed regarding the polychaete community of the EFGB.
Previously, only two species of polychaete had been identified from this area: *Hermodice
carunculata* and *Spirobranchus giganteus* (Bright et al., 1974; Wills, 1976). Neither of these
species were found in the present study, but the species that were recovered were entirely new to
the EFGB: *Chaetopteridae* sp., *Paleanotus heteroseta*, *Eurythoe* sp., *Nematonereis unicornis*,
Saccocirrus sp., *Paraonidae* sp., *Cirratulidae* sp., *Polydora aggregata*, *Dorvillea* sp.,
Caulleriella sp., *Syllis gracilis*, *Kefersteinia cirrata*, *Mooreonuphis pallidula*, *Sphaerosyllis* sp.,
and *Aricidea taylori*. Furthermore, the species *Paleanotus heteroseta*, *Saccocirrus* sp.,
Paraonidae sp., *Polydora aggregata*, *Caulleriella* sp., *Mooreonuphis pallidula*, *Sphaerosyllis*
sp., and *Aricidea taylori* have not been found previously in the Flower Gardens. At a higher
taxonomic level, the families Saccocirridae (represented by *Saccocirrus* sp.) and Paraonidae
(represented by *Aricidea taylori* and an unidentified species) are entirely absent from earlier
FGB records (Bright et al., 1974; Wills, 1976). This study was relatively small, with only eight
samples collected; even so, the discovery of species and families new to the area shows that
much more exploratory work is needed in order to thoroughly document the EFGB polychaetes.

As expected, the polychaete fauna of the EFGB differed markedly from that of the inshore
control samples, with no species being shared between them. However, the two groups did have
some families in common (Amphinomidae, Paraonidae, Cirratulidae, and Spionidae). Except for
the Amphinomidae, the species belonging to the shared families tend to be surface deposit-

21

feeders (Fauchald and Jumars, 1979), indicating that this feeding mode is a reliable method for gathering sustenance in both habitats. Still, it is important to note that the proportions of deposit-feeders in the control samples and in the EFGB samples are substantially different. The control samples totaled 32 polychaete species, 75% of which were deposit-feeders and 12.5% of which were predators; in contrast, the EFGB samples contained a total of 15 polychaete species, 46.7% of which were deposit-feeders and 26.7% of which were predators. Although deposit-feeding comprises the majority feeding style in the first sample group and the plurality feeding style in the second, predation appears to be a more viable lifestyle in the coral reef habitat than in soft, mud bottoms. This is probably best explained by the fact that three of the four carnivorous EFGB polychaete species (*Eurythoe* sp., *Nematonereis unicornis*, and *Syllis gracilis*) belong to families known for feeding on sessile, soft-bodied invertebrates, such as corals, sea anemones, hydroids, and bryozoans (Fauchald and Jumars, 1979).

Another possibility is that the smaller-sized sediment grains present at the control group sites would be more easily ingested by deposit-feeders than the relatively large-grained coral rubble in the FGB. Jumars et al. investigated the determinants of sediment particle preference in a few deposit-feeding polychaete species and found that, although particle size is important, particle specific gravity is also influential, with polychaetes preferring smaller-diameter, lighter particles over larger, heavier ones (1982). Specific-gravity measurements were not performed on the sediment in the present study, and sediment data for the control samples were not available, so the strength of this factor (and, due to their association, of sediment grain size) in determining polychaete species distributions cannot be assessed in this study. Further investigation into this phenomenon in the northwestern Gulf of Mexico is warranted.

The composition of the macrofauna from this bank top in the EFGB is especially interesting when compared with studies of nearby areas. In their study of five sites near both banks, Yingst and Rhoads found that polychaetes were the numerically dominant macrofaunal animals (mean density = 14.3 per 10 cm^2, S.D. = 7.9 per 10 cm^2) at every site, followed at a large gap by bivalve molluscs (mean density = 2.4 per 10 cm^2, S.D. = 2.0 per 10 cm^2) and, in one sample, sipunculids (mean density = 1 per 10 cm^2) (1985). However, as previously noted, these samples were not taken from the bank tops, but instead ranged from depths of 90-223 m (Yingst and Rhoads, 1985). In the current study, the most common taxon in all but three samples was the Isopoda (mean = 55.3%, S.D. = 24.9%), which was edged out by Amphipoda in samples E and G (mean = 42.6%, S.D. = 11.6%) and Polychaeta in sample F (56.2%). These results show that the taxon composition of the bank tops at the FGB is substantially different from that of the surrounding area, and also that there is little consistency even within the bank tops.

Without knowing the life histories of the individual species comprising these taxa, it is difficult to say why some of them are so much more abundant than others at specific sites. Despite these differences in numbers of individuals, polychaetes were the dominant biomass percentage in every sample, as the numerically superior crustaceans had very low ash-free dry weights consistent with their relatively low-carbon, high-$CaCO_3$ body morphologies. Thus, even though there were not as many individual polychaetes as there were crustaceans, the polychaete worms must have been consuming a greater amount of the total organic carbon in the area.

Increasing sediment grain size (decreasing phi values) was strongly correlated with the number of species and with Margalef's richness in each sample. Martins et al. found similar results when

studying polychaete diversity off the coast of Portugal, where increasing grain size was associated with increased diversity and abundance; they postulated that the larger interstitial spaces that accompany large grain sizes allow more living space for interstitial polychaetes, such as pisionids, syllids, and polygordiids (2013). Although sediment size in the FGB does not seem to be associated with all forms of diversity, the fact that the total number of species appears to increase as grain size increases, coupled with the fact that grain size is independent of the number of individuals, implies that the finer-grained sediments are dominated by a few abundant specialist species. This is supported by the two samples with the highest phi values, C and D, which were numerically dominated by a single species of blind, vermiform isopod. However, these isopods were relatively small, contributing little to each sample's biomass.

The association between biomass and sediment grain size was particularly unexpected. This could be due to the presence of tanaid shrimps, particularly in samples E and G, which were individually quite large, and may have been hampered by smaller sediment sizes inhibiting interstitial activity. It is important to note that, as expected, the particulate organic carbon content of the sediment was positively and significantly correlated with the macrofaunal biomass, but that this association was not as strong or as significant as the grain size-biomass correlation. Furthermore, when assessing these findings one must also account for the fact that no correlation was found between sediment grain size and POC content, as sediment grain size has been considered secondarily associated with POC content and current action, which are often believed to be the true drivers of infaunal community structure (Bergen et al., 2001; Hernández-Arana et al., 2003).

These results are not representative of worldwide trends, however. In contrast with present

results, a North Sea macrofauna study by Heip et al. found that biomass increased with

decreasing sediment grain size, and that diversity was not affected by grain size at all (1992).

Furthermore, this study found that latitude was a more important variable in determining

diversity and biomass of macrofauna than were sediment type or chlorophyll α content

(Heip et al., 1992). Conversely, Martins et al. did find strong correlations between multiple

measures of polychaete diversity and sediment grain size off the coast of Portugal, as mentioned

previously (2013). Due to this lack of consensus, regional studies may be more appropriate for

determining environmental drivers of diversity in macrofauna.

There is a possibility that the large mean sediment grain size at the FGB reflects strong,

persistent wave action and bottom currents, and disturbances at depths of <20 m have been

recorded from this area as affecting infauna diversity (Hernández-Arana et al., 2003). This would

explain the greater diversity of polychaetes at the control sites, which had finer sediments, but

were a few meters deeper than the FGB sites, which might protect the vulnerable polychaetes

from wind-induced currents (Harper and Fitzhugh, unpublished; Martins et al., 2013). However,

bottom current speeds are not regularly measured at the FGB, so a correlation with this variable

could not be investigated in this study.

The amount of particulate organic carbon present in the FGB sediment was strongly and

positively correlated with every biotic variable measured in this study except for individual

density, and every correlation was significant except the correlation with species count. This

result was expected, as sediment organic carbon content has been shown to correlate positively

with macrofaunal diversity at multiple benthic sites worldwide, in sites as diverse as the continental slope off North Carolina and in the bathyal Pacific Ocean (Levin and Gage, 1998; Gooday et al., 2001). However, the study by Gooday et al. also found that macrofaunal abundance increased with increasing carbon input, as a larger nutrient input was capable of supporting a greater number of individuals (2001). This stands in direct contrast with the results of the present study, where the correlation between POC content and individual density is relatively weak and insignificant. Along with the increase in biomass that accompanies the POC increase, this could indicate an association between individual animal size and food availability, with larger animals monopolizing available food in rich areas and driving out smaller competitors, keeping individual density equal to that of food-poor sites.

If this is the case, then the increased species richness, evenness, and diversity that accompanied higher POC availability could be due to a wider range of food items available in high-carbon sites. Samples E,G, and H had higher POC contents than samples B,C, and D, and the former group of samples also contained more species of polychaete worms, which in the FGB are predominantly deposit-feeders. This might indicate that the extra POC is comprised of minute particles only accessible to deposit-feeders, and non-appetizing to scavenging amphipods. A confounding example is that of sample A, which has a similarly high POC content that coincides with an abundance of tanaid shrimps not found in any other samples. Due to a lack of qualified personnel, these tanaids could not be identified to the species level, so their feeding habits and food source cannot be deduced at this time. A more detailed analysis of the benthic food supply at the FGB is warranted, as the loss on ignition measurements taken here cannot differentiate

between proteins, lipids, and carbohydrates, which can each correlate with benthic fauna differently (Albertelli et al., 1999).

Of the three environmental variables studied, the calcium carbonate content of the sediment appeared to be the least important ecologically, as it did not correlate significantly with any of the community variables. As stated earlier, this is not surprising, as all the sampling sites were located near coral heads, meaning that the majority of the carbonate is likely derived from coral skeletons. If this is the case, then one might expect occurrences of the polyp-consuming FGB polychaetes *Eurythoe* sp., *Nematonereis unicornis*, and *Syllis gracilis* to be more or less common depending on sediment carbonate concentration. However, the sites studied here possessed a standard deviation of only 0.4% in their carbonate content, so additional samples would need to be taken further from the coral heads to test this hypothesis.

This study is by no means comprehensive. Due to practical constraints, comparisons between sites could not be performed based on abiotic factors such as water movement, light attenuation, or phytopigment concentration, which could also heavily influence benthic macrofauna (Haedrich et al., 2008; Martins et al., 2013). The possibility of top-down, predator-based community control in this area also warrants investigation.

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SPECIES LISTS

Table 5. Individuals per species at each control site. Polychaete fragments (e.g. Magelona mid, Magelona serrate prostomium) were not assigned to species by Harper and Fitzhugh, so they are listed separately here.

Species	P3 S2	P3 S5	P3 N2	P4 W5	P4 W2	P3 E5-10	P3 N5	P3 E5-9
Aricidea fragilis		3				8	2	
Aricidea suecica		33				2	1	29
Cossura delta	2	2		3			1	4
Diopatra cuprea	1							1
Scoletoma tenuis	6	6	1	3		5	9	7
Magelona rosea	1	7					3	4
Magelona sp.		1						1
Magelona mid			1					
Magelona serrate prostomium					6	2		1
Mediomastus californiensis	3	10				1	2	17
Nephtys incisa	5			9	5			
Nereis sp.	3	25	6			15	13	23
Nereis sp. 2						1		1
Notomastus latericeus	1	4		2	2	6	2	2
Paraprionospio pinnata	11	2	1	12	6	1	3	1
Aonidella cirrobranchiata	1	1		1			1	1
Prionospio cirrifera		1					2	
Prionospio cristata		2					1	
Cirratulus hedgpethi	1							
Nereidae sp.	1							
Lepidasthenia sp.	1							
Nereis succinea								
Tharyx marioni		6	11			9	4	11
Tharyx setigera		7				4	2	5
Glycera americana		6				3	1	3
Ceratonereis irritabilis		3			2		7	3

Table 5. (Continued)

Species	P3 S2	P3 S5	P3 N2	P4 W5	P4 W2	P3 E5-10	P3 N5	P3 E5-9
Ampharete acutifrons		7	1			2	2	4
Aglaophamus verrilli			2				1	
Pista cristata			1					
Ninoe nigripes	1			2	3			
Sigambra tentaculata		1		3				1
Cirrophorus lyriformis				1			1	3
Ophioglycera sp.				1				2
Mooreonuphis nebulosa		1				1		
Lepidasthenia sp.							1	
Linopherus ambigua							1	1
Megalomma bioculatum			3					

Table 6. Polychaete individuals per species at each EFGB site.

Species	A	B	C	D	E	F	G	H
Saccocirrus sp. A		2	2	8	38	300	18	16
Chaetopteridae sp.	1		5					
Paleanotus heteroseta	2				1		2	2
Eurythos sp.	1					1	1	
Nematonereis unicornis	7	1			4	1	4	
Paraonidae sp.			1	1				
Cirratulidae sp.			1					
Polydora aggregate					1			
Dorvillea sp.					8	1	15	3
Caulleriella sp.					2		4	
Syllis gracilis						2	1	
Kefersteinia cirrata						1	2	
Mooreonuphis pallidula							1	
Sphaerosyllis sp.							1	
Aricidea taylori								1