COPANO BAY: ASSESSING THE ACCOUNTABILITY OF SPATIAL/TEMPORAL VARIABILITY IN BENTHIC MOLLUSCAN PALEOCOMMUNITIES

A Senior Scholars Thesis

by

ADAM MICHAEL HORBACZEWSKI

Submitted to the Office of Undergraduate Research
Texas A&M University
in partial fulfillment of the requirements for the designation as

UNDERGRADUATE RESEARCH SCHOLAR

April 2008

Major: Geology

COPANO BAY: ASSESSING THE ACCOUNTABILITY OF SPATIAL/TEMPORAL VARIABILITY IN BENTHIC MOLLUSCAN PALEOCOMMUNITIES

A Senior Scholars Thesis

by

ADAM MICHAEL HORBACZEWSKI

Submitted to the Office of Undergraduate Research
Texas A&M University
in partial fulfillment of the requirements for designation as

UNDERGRADUATE RESEARCH SCHOLAR

Approved by:

Research Advisor: Thomas Olszewski
Associate Dean for Undergraduate Research: Robert C. Webb

April 2008

Major: Geology

ABSTRACT

Copano Bay: Assessing the Accountability of Spatial/Temporal Variability in Benthic Molluscan Paleocommunities (April 2008)

Adam Michael Horbaczewski
Department of Geology & Geophysics
Texas A&M University

Research Advisor: Dr. Thomas Olszewski
Department of Geology & Geophysics

Increasing attention has been directed towards paleoecolological studies in understanding the relationship between modern live communities and death assemblages as a means of better understanding fossil assemblages preserved in the rock record. In order to study this relationship, benthic molluscan live and dead assemblages are being collected from an ongoing time series and a spatial transect from Copano Bay, Texas. Previous work on this time series transect has demonstrated that death assemblages are more dynamic than previously recognized, and that they reflect short-term fluctuations in their living community counterpart. The spatial transect, collected in June 2007, and the time series transect are considered here to further assess this relationship as well as estimate the full range of variation in the site locality and identify any significant change through time.

Results show that richness corrected for sample size and evenness are highly variable for the live communities and has been considerably variable for the death assemblages for new samples added to the time series. Furthermore, cluster analysis and non-metric

multidimensional scaling ordinations indicate a compositional shift in the new data (last seven samples) for the living community, and a compositional rebound toward samples collected 22-years ago for the death assemblages. In addition, additive partitioning of evenness on the spatial transect does not indicate any detectable gradient at the time of collection.

DEDICATION

This work is dedicated to everyone who has helped me along my way.

ACKNOWLEDGMENTS

First, I would like to thank my advisor and teacher, Dr. Thomas Olszewski, for introducing me to this project and guiding me through the scientific process.

I would like also to thank George Staff and Danielle Ebnother whose work, for the past year, became my own. Without their work, this project would necessarily have been very different.

My thanks go out to Chris Klug and Meaghen Julien for their indispensable help with collecting the spatial transect samples in June 2007 that are included in this work.

Thanks also to Jason Moore for his stimulus and helpful commentary.

Lastly, I would like to thank in particular Leigh Fall for all her help and especially her willingness to share her lab with this green undergraduate.

TABLE OF CONTENTS

Page

LIST OF FIGURES

LIST OF TABLES

CHAPTER I

INTRODUCTION

Paleoecologists observe changes in the dead remains of once living communities to infer environmental conditions in the past and to develop paleoecological reconstructions. However, postmortem mixing, destruction, or transport can greatly distort both the size and composition of death assemblages and thereby hinder their reliability for interpreting the past.

One pervasive aim in paleoecological studies is to understand the relationship between live and dead assemblages as a means of understanding fossil assemblages preserved in the rock record. Understanding how the dynamics of living communities are reflected in death assemblages is crucial for the development of paleoecological reconstructions. Likewise, it can lend itself to a whole host of other practical and beneficial applications. For example, an improved understanding of death assemblage dynamics can help establish ecological baselines for interpreting the biological effects of recent environmental changes, as well as aid in coastal wetland restoration projects (Wardlaw 2001; Lichlyter and Olszewski 2005; Ebnother and Olszewski 2005).

Earlier studies have concentrated on the variation seen in both living communities and their corresponding death assemblages within benthic molluscan communities, in

---

This thesis follows the style and format of Paleobiology.

particular over decadal time scales (e.g., Ferguson and Miller 2003; Ebnother and Olszewski 2005); yet few studies have also accounted for spatial variability in the living assemblage, and no time series are sufficiently complete and long enough to capture the full range of variation within a locality. Consequently, the present study aims to address these two issues by assessing the amount of variation observed in both living communities and death assemblages in space as well as through time by both measuring spatial variation and increasing the duration of an ongoing time series.

Previous work and a continuing time series along a pre-established transect in Copano Bay, Texas offers an excellent opportunity for addressing the issue of living and death assemblage volatility (Staff 1983; Ebnother and Olszewski 2005). In 1981, Staff established a transect at Copano Bay from which he collected samples of benthic mollusks in living communities and death assemblages every six weeks and created a time series spanning eighteen months. In 2004, Ebnother revisited this transect and reestablished the time series and compared her data (spanning twelve months) to Staff's to see if the death assemblage had changed after 23 years. Her results demonstrated that death assemblages are more dynamic than previously recognized, and that they reflect short-term fluctuations in their living community counterparts (Ebnother and Olszewski 2005). However, what Ebnother's work did not address was the effects of spatial variation. This study will both increase the duration and resolution of the time series (extending it an additional nine months) as well as account for spatial variability (using a spatial transect).

The time series and spatial transect, collected in June 2007, are considered here with the objective to 1) assess the fidelity of changes in living communities with respect to their corresponding death assemblages in space as well as through time, 2) estimate the range of variation in the site locality, 3) identify any significant change through time, and 4) better understand the reliability of subfossil assemblages for the interpretation of fossil assemblages in the rock record.

The hypotheses underlying this research are 1) spatial variation will be significantly smaller than variation recorded through time, and 2) changes in variation at the decadal scale will be larger than changes in variation seen at the six-week scale. Therefore, the spatial transect is expected to show less variation than both six-week or decadal scales, and variation within any six-week time interval is not expected to exceed that observed at the decadal scale.

If temporal variability is greater that spatial variability for the death assemblages, the implication is that time-dependent, post mortem processes (i.e., intrinsic decay rates, taphonomic destruction, etc.) are significant factors for the amount of change observed through time and any significant change will be discernible. However, if the converse is true (spatial variability is greater than temporal variability), the implication is that death assemblages may be poor indicators of substantial environmental or ecological shifts in the past.

CHAPTER II

METHODS

Field and laboratory

Both live and dead assemblages are being sampled from the southwest corner of Copano Bay, Texas, at a shallow inlet area (depth varies seasonally between two to five feet) near the mouth of the Aransas River (see Fig. 1). Time series samples are collected at approximately six-week intervals along a 100 meter transect parallel to the shore and at random positions to avoid resampling previously disturbed sites. Samples are collected using a push core (15 cm diameter, 17 cm deep) pressed into the substrate (repeated once), and a surface scrape (24 cm wide, 300 cm long, 5 cm deep). The seven samples in this study that have been added to the time series begin November 2005 and end July 2006. The spatial transect was collected using only one core and no surface scrape every five meters ten meters further offshore and parallel to the time series in two consecutive days in June, 2007. The five spatial transect samples used in this study were taken at 25 meter intervals along this 100 meter transect.

Samples are then taken back to the laboratory, washed through three progressively finer sieves (2.0mm, 1.0mm, and 0.5mm) to separate the shells from the muddy substrate, and then placed in a bath of rose bengal overnight to allow all living tissue to be dyed pink. Soaking samples in rose bengal aids in keeping both live and dead specimens distinguishable within a given sample. Species are sorted carefully and identified under

microscope while marking method of collection (box core or surface scrape) and sieve

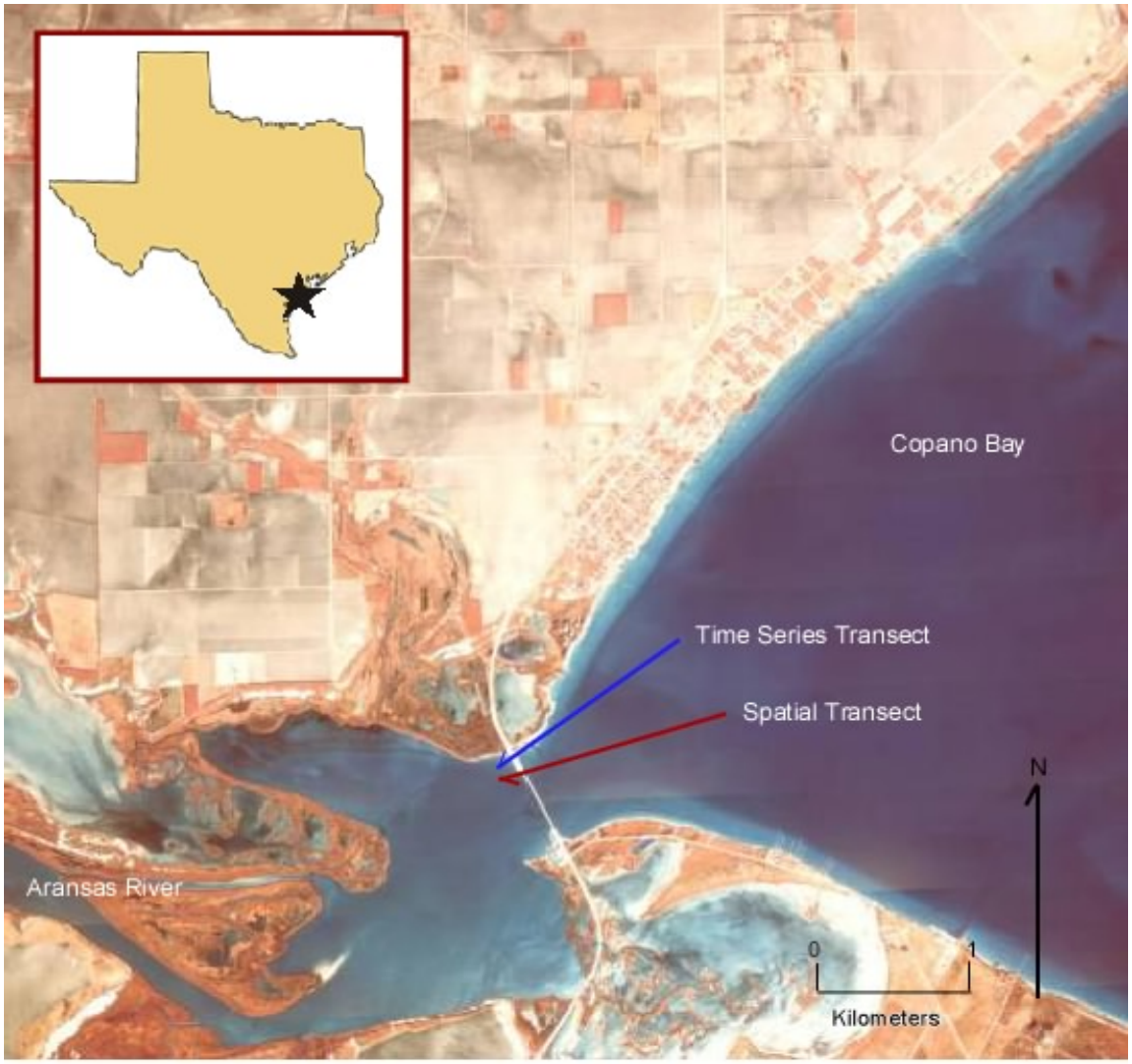

FIGURE 1. Satellite image of the study site at the mouth of the Aransas River, Copano Bay, Texas. Relative locations of time series and spatial transects indicated with the blue and red arrows, respectively. Image modified from www.texmaps.com.

size. Species are only counted if, for bivalves, they retain a beak and complete hinge line, and for gastropods, only if they retain the apex. As it is difficult to determine whether or not two shells in a given sample represent a single individual, bivalve counts were obtained by dividing the total number of single valves by two.

Analyses

Sample rarefaction and composite rarefaction were computed using Holland's online rarefaction program (http://www.uga.edu/strata/software/). Collector's curves were computed using EstimateS (Version 7.5, R. K. Colwell, http://purl.oclc.org/estimates). Non-metric multidimensional scaling ordinations and cluster analyses were generated using Paleontological Statistics (PAST), a program that can be found at http://folk.uio.no/ohammer/past/.

All samples collected by Ebnother are being housed in a Texas A&M laboratory and were accessible for comparison, so that the author feels confident that the results presented in this study do not reflect differences in taxonomic identification between workers. Staff's data, however, were destroyed shortly after an attempt to preserve the specimens in formalin, and so are no longer available for taxonomic identification comparison.

To eliminate the influence of questionable species (both rare and infrequent) present only in Staff's data and others in Ebnother's data, species that made fewer than two

appearances in the death assemblages throughout the whole time series were selectively deleted prior to clustering and ordination. No species were ignored for the live community samples. To normalize abundances for super-abundant species (namely, *Diastoma varium*, *Mulinia lateralis*, and *Texadina sphinctostoma*) a log(x + 1) transformation was used. Bray-Curtis distance (measures similarity by taking number of shared species for any two samples divided by the total number of species present in those two samples; McCune and Grace, 2002) and the Paired Group linkage algorithm were used for clustering.

CHAPTER III

RESULTS

Time series

Seven samples, beginning November 2005 and ending July 2006, collected at six week intervals, have been added to the time series established by Ebnother in September of 2004 (see methods section).

30,115 new individuals of bivalves and gastropods are considered in the new samples: 27,231 from the death assemblages and 2,884 for the live communities. Single valves were counted individually and divided by two to come up with the individual bivalve count (see methods section). The seven samples include fifty species.

Raw counts and relative abundances for the live communities are shown in Table 1 (see Appendix A for raw counts and relative abundances for the death assemblages). Three species (out of fourteen) were found to dominate more than ninety percent of the live individuals for the seven samples: *Texadina sphinctostoma* (36.7%), *Mulinia lateralis* (31.3%), and *Acteon punctostriatus* (22.5%). Only one species, *Montacula sp.*, in the live individuals was not found in the corresponding death assemblages. Over eighty-six percent of the death assemblage samples taken together were likewise dominated by only three species (out of forty-one): *Diastoma varium* (51.7%), *Texadina sphinctostoma* (19.2%), and *Mulinia lateralis* (15.5%).

TABLE 1. Total raw counts and relative abundances for the time series live communities. Only counts from the last seven samples of the time series are included in this table.

Taxa		Raw	Relative Abundance (%)
Texadina	*sphinctostoma*	1057	36.650
Mulinia	*lateralis*	904	31.345
Acteon	*punctostriatus*	650	22.538
Montacula	*sp.*	170	5.895
Macoma	*mitchelli*	56	1.942
Laevicardium	*mortoni*	23	0.798
Brachidontes	*exustus*	11	0.381
Macoma	*tageliformis*	5	0.173
Lucina	*pectinata*	2	0.069
Rangia	*flexuosa*	2	0.069
Boonea	*impressa*	1	0.035
Chione	*cancellata*	1	0.035
Tagelus	*plebeius*	1	0.035
Tellina	*tampaensis*	1	0.035
	Total	**2884**	**100**

Richness and evenness trends were used to assess temporal diversity in terms of number of species present and their distribution within a given sample. Richness (S) is the total number of species in the sample, and evenness (Hurlbert's Probability of Interspecific Encounter, or PIE) is the probability that two individuals picked at random from some sample will be different species (PIE = $\left(\frac{N}{N-1}\right)\left(1-\sum_{i=1}^{S} p_i^2\right)$; $p_i = \frac{n_i}{N}$, N = total number of individuals in a sample, n_i = the number of individuals of the i^{th} species in the sample; Hurlbert 1971).

Trends showing both richness and evenness for the whole time series are shown in Figure 2. Figure 2A shows trends in raw richness and evenness for the live communities. Richness never exceeded ten species, which occurred in June 2006. Moreover, evenness drops down to zero on four occasions: 8/81, 12/81, 3/82, and 11/05. This corresponds with complete dominance, that is, the appearance of a single species in these samples.

Samples were then rarefied to determine whether and to what degree sample size influenced species richness. Figure 2B shows raw richness and rarefied richness trends for the live communities. All samples were rarefied to a sample size of ten individuals. Gaps in the rarefaction trend correspond with samples that either contained too few species, or too few individuals to be rarefied. Rarefied trends mirror raw richness in the new samples which seems to indicate that sample size was an insignificant factor in the observed richness trend for these samples. Furthermore, raw richness for the last four samples of the time series fall within the 95% confidence intervals of the rarefied richness, indicating that samples were sufficiently large to capture the expected richness during the collection of the samples. Conversely, samples collected in December 2005 and January 2006 show raw richness that falls outside the 95% confidence intervals of the rarefied richness. This indicates that these samples may not have been large enough to capture the expected richness during collection.

Figure 3A shows trends in raw richness and evenness for the death assemblages. Species richness was never observed to exceed 56 for the death assemblages. In contrast with the living communities, evenness is steady until May of 2005 which marks the onset of variable evenness in the succeeding samples. A similarly abrupt drop in evenness occurred just before the twenty-two year hiatus in the time series. Rarefaction trends shown in Figure 3B indicate similar variability in the species richness and a rise in species richness beginning in April 2006 after a level species richness of eleven months (5/05--3/06).

Figure 2 and Figure 3 both demonstrate that live communities are much more variable than death assemblages.

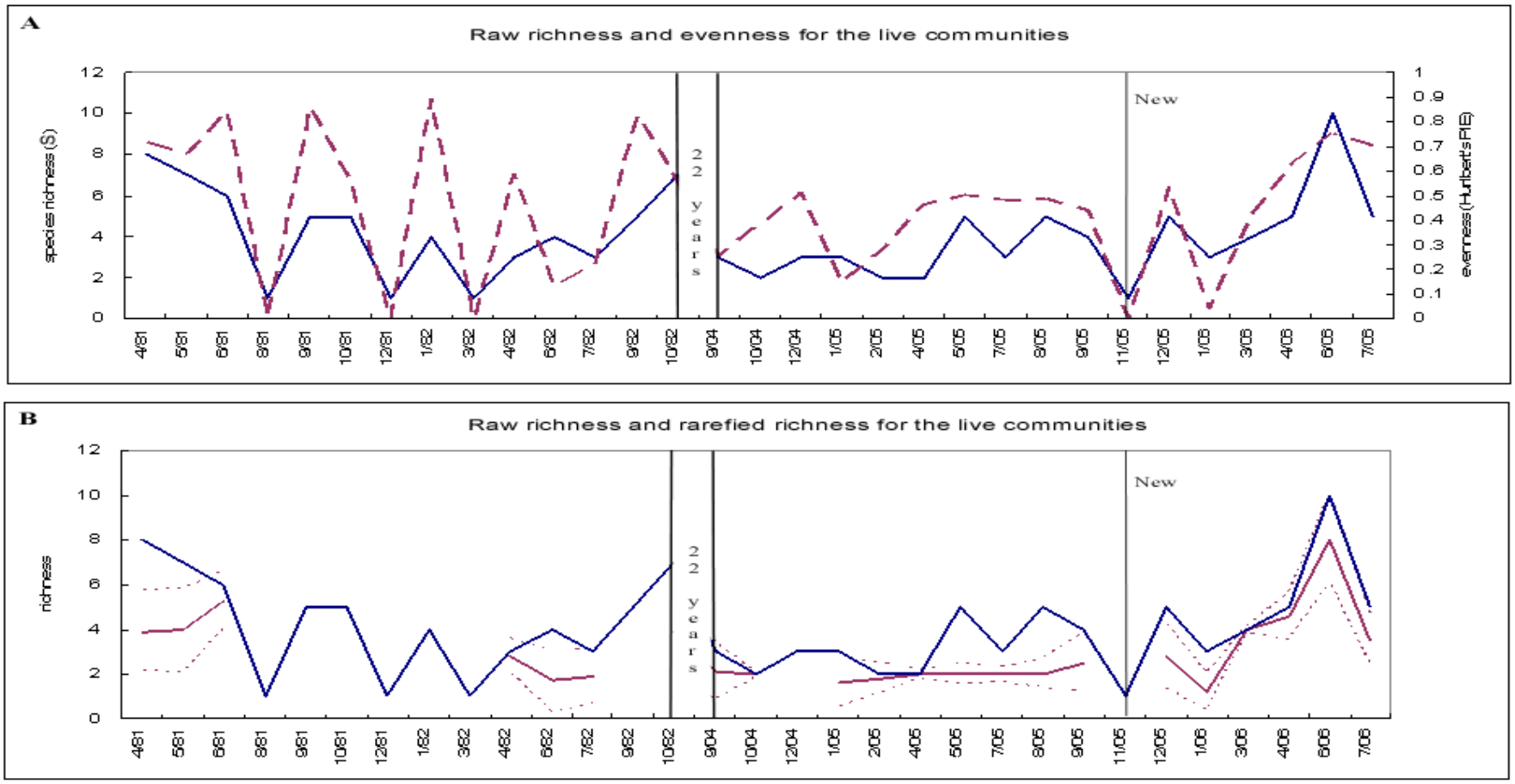

FIGURE 2. Sample richness, evenness. and rarefied richness trends for the live communities collected for the time series. New samples are labeled. (A) Solid blue line is raw richness and dashed maroon line is evenness (Hurlbert's PIE). Note that zero evenness (i.e., complete dominance by one species) occurs in four samples: 8/81, 12/81, 3/82, and 11/05. (B) Raw richness (solid blue line) was rarefied to a sample size of ten individuals (solid maroon line enclosed with 95% confidence intervals). Gaps in rarefaction trend correspond with samples too small (i.e., one species) or with insufficient abundance (number of individuals) to be rarefied.

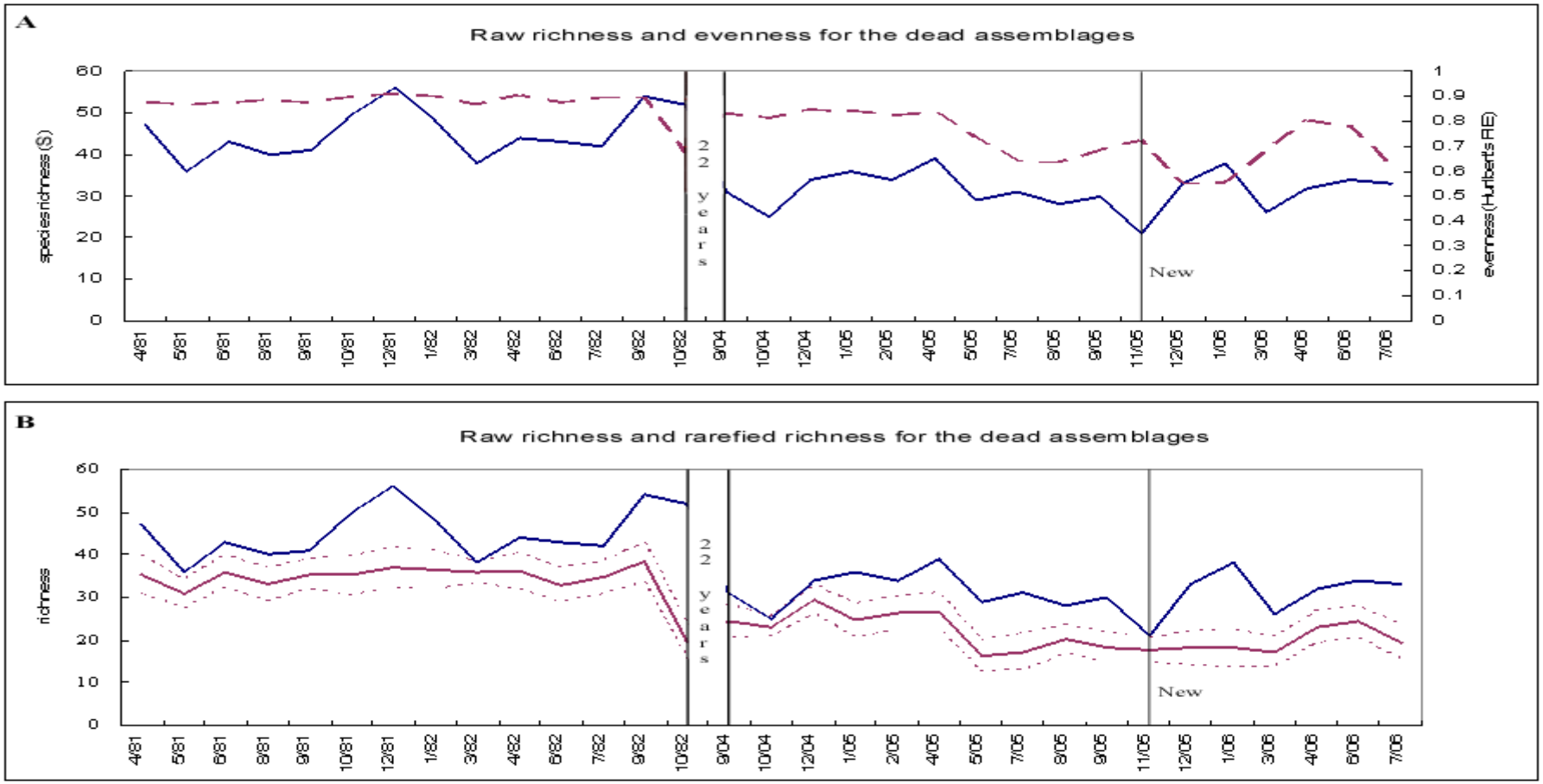

FIGURE 3. Sample richness, evenness, and rarefied richness trends for the dead assemblages collected for the time series. New samples are labeled. (A) Solid blue line is raw richness and dashed maroon line is evenness (Hurlbert's PIE). (B) Solid blue line is raw richness, and solid maroon line enclosed with 95% confidence intervals is rarefied richness (sample size of 400 individuals). Note that zero evenness did not occur in any of the samples, and all were large enough to be rarefied.

Additive diversity partitioning was used to explore the contribution of the individual samples of the time series to the total diversity of the set of collections. Diversity can be partitioned additively into three hierarchical scales. By definition, gamma (γ) diversity is the total regional diversity, beta (β) diversity is the diversity among samples in a habitat, and alpha (α) diversity the diversity within samples (Lande 1996; Olszewski 2004; Olszewski and Kidwell 2007). Using the additive diversity partitioning model, ($\gamma = \alpha + \beta$) beta diversity is simply the difference between gamma and beta diversities.

Because PIE is a diversity metric that can be partitioned additively using this formula, ADP evenness values for the time series were computed and are included in Table 2. Sample collections were divided into three groups corresponding with data collected by Staff, Ebnother, and the current study.

For the 14 samples collected from 4/81 to 10/82 and the 10 samples collected from 9/04 to 9/05, ∑PIE and μPIE are both considerably larger for the death assemblages than for the live communities. However, this pattern stops in the newly added samples to the time series (11/05--7/06) which show that ∑PIE for the death assemblages falls below that of the live communities, but μPIE remains larger, if only slightly, in the dead than the live collections. In addition, the largest difference between ∑PIE and μPIE occurs in the live collections for the new samples (∑PIE – μPIE = 0.136). This difference is

considerably larger than that for all other sample collections (the second largest difference occurring in the live samples for 4/81--10/82; ∑PIE – μPIE = .075).

TABLE 2. Evenness statistics for the time series transect. N = composite sample size, S = species richness, X = number of collections, ΣPIE = PIE of composite sample (i.e., gamma), and μPIE = weighted average PIE of the individual collections (i.e., alpha).

LIVE	N	S	X	ΣPIE	μPIE
4/81--10/82	357	18	14	0.619	0.544
9/04--9/05	4822	10	10	0.504	0.467
11/05--7/06	2884	14	7	0.713	0.577
DEAD	N	S	X	ΣPIE	μPIE
4/81--10/82	18886	80	14	0.889	0.848
9/04--9/05	18159	57	10	0.774	0.737
11/05--7/06	27231	49	7	0.669	0.608

Cluster analysis and ordination were used in order to explore significant compositional change through time among the samples. Cluster analysis dendrograms are shown in Figures 4 and 5 for the live communities and death assemblages, respectively. Corresponding non-metric multidimensional (NMDS) ordinations are shown in Figures 6 and 7. Samples are color coded by worker: Staff's samples are shown in red, Ebnother's in blue, and the new samples are shown in green.

Death assemblage cluster analyses and ordinations show that samples collected 22 years ago are compositionally different from samples collected in the past two years. The NMDS ordination in Figure 7 demonstrates a general trend in the last seven samples of the time series back toward samples collected 22 years ago; however, the dendrogram of Figure 5 stresses that these samples remain compositionally distinct. The ordination also reveals that samples collected after the time interval are compositionally richer and hence plot more diffusely in the ordination than earlier samples. Alternatively, however, all samples for the live communities cluster closely together (Fig. 6), despite the increased numbers in *Mulinia lateralis* and *Acteon punctostriatus* in the samples collected after the 22 year time interval. In addition, the NMDS live ordination fails to capture some of what the cluster dendrogram preserves (Fig. 4); namely, the total disappearance of the relatively abundant species *Odostomia barretti* after the time interval, which appropriately cluster together on the far right of the dendrogram.

The March 1982 outlier in Figures 4 and 6 cannot be explained by the species composition of this sample or each species' richness: the two gastropods *Texadina sphinctostoma* (2) and *Odostomia barretti* (1), and the two bivalves *Mulinia lateralis* (1) and *Rangia cuneata* (1).

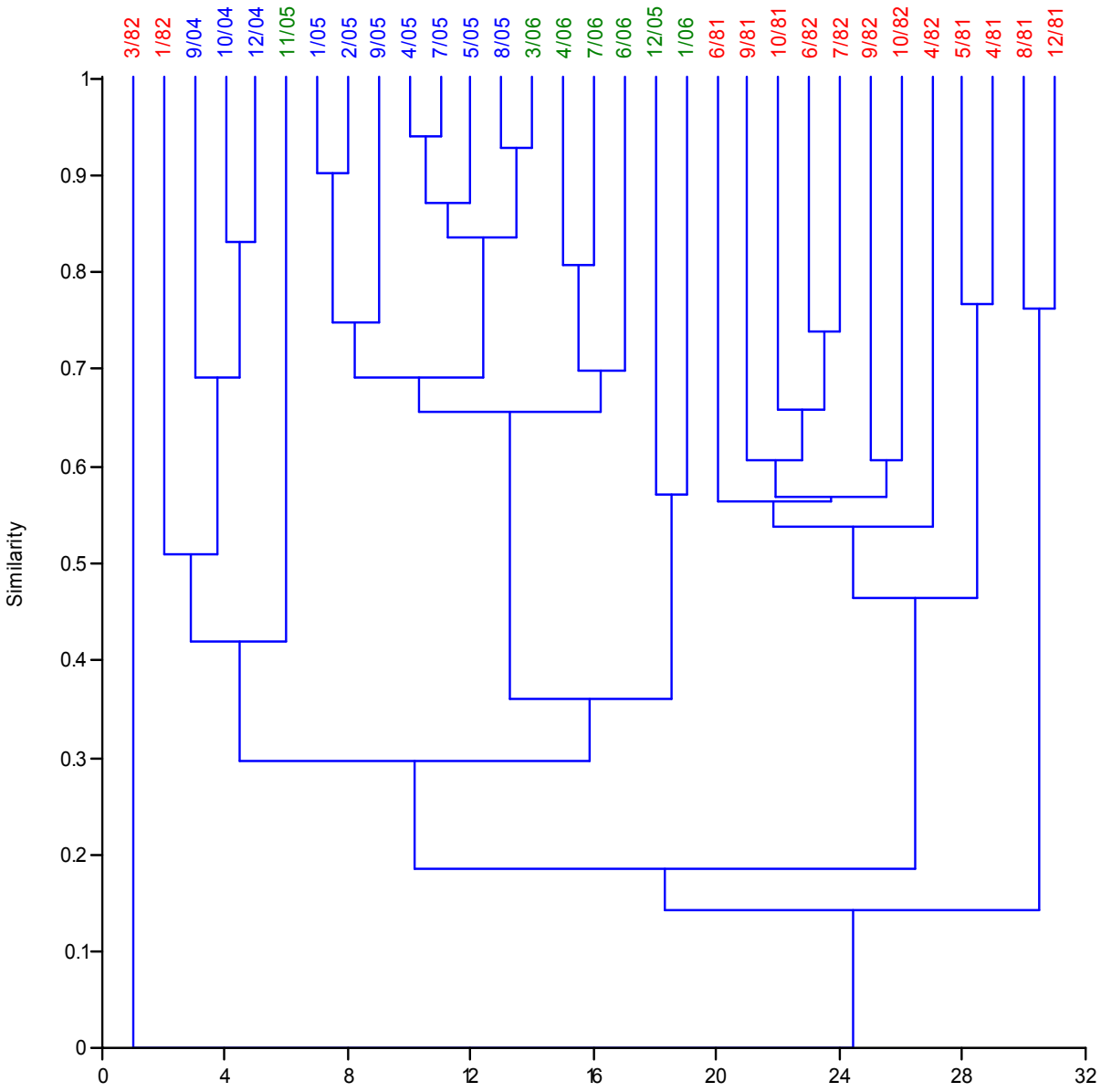

FIGURE 4. Cluster analysis dendrogram for the live communities. Transformation – Log (x+1); Distance measure -- Bray-Curtis; Linkage algorithm -- Paired group. Sample dates are color coded to distinguish workers: Staff's data shown in red, Ebnother's in blue, and the new data in green.

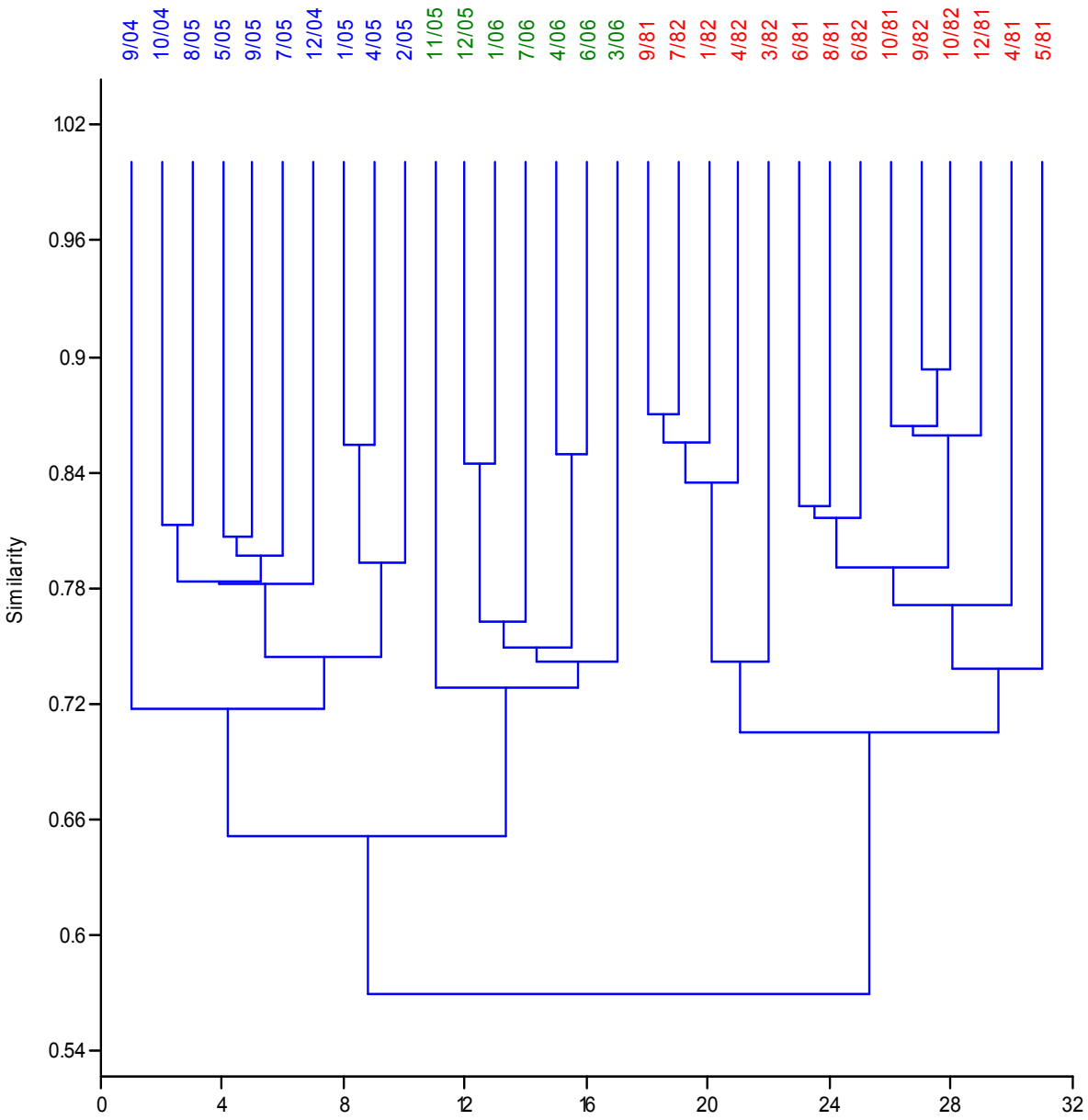

FIGURE 5. Cluster analysis dendrogram for the death assemblages. Transformation – Log (x+1); Distance measure -- Bray-Curtis; Linkage algorithm -- Paired group. Sample dates are color coded to distinguish workers: Staff's data shown in red, Ebnother's in blue, and the new data in green.

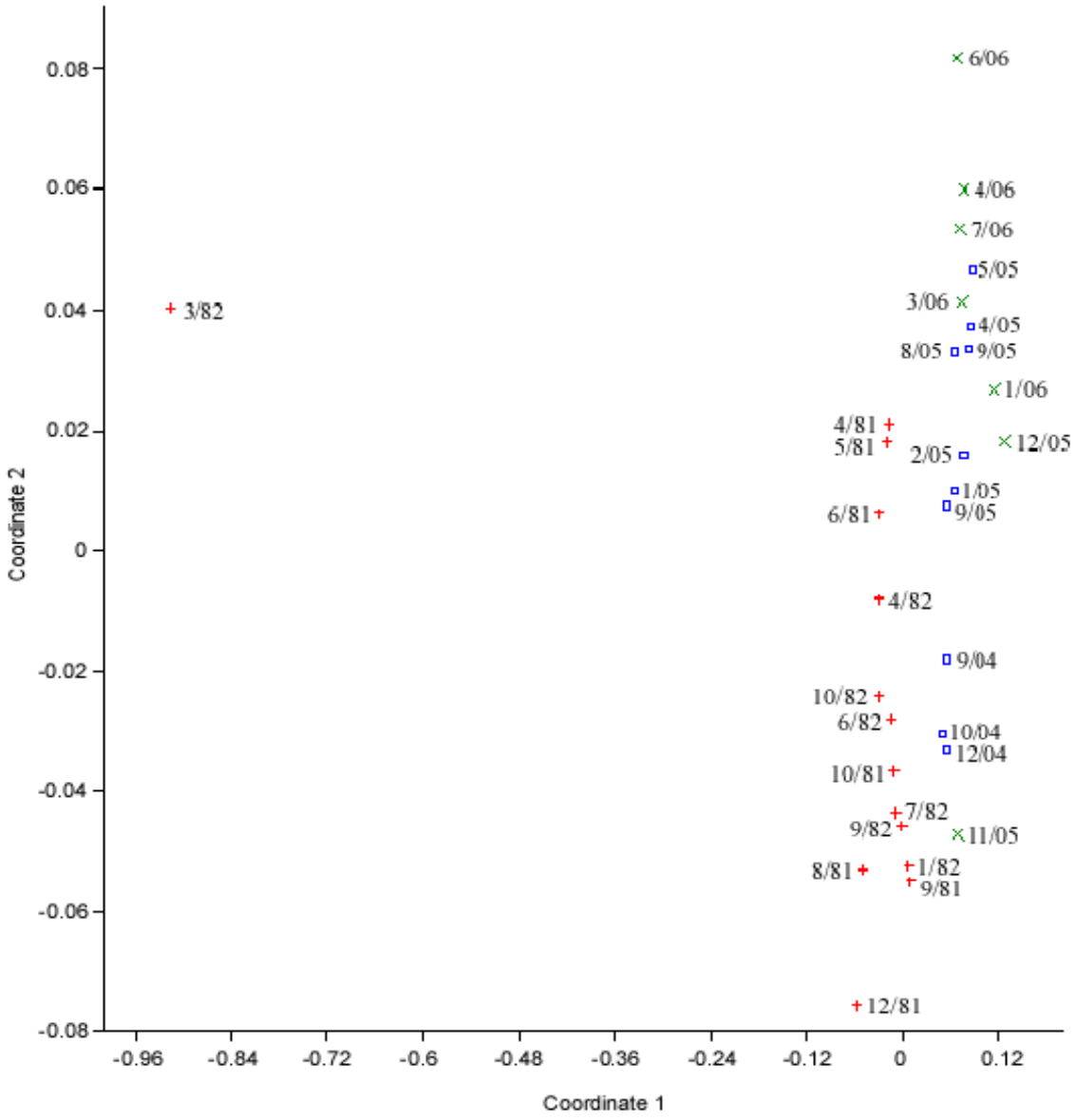

FIGURE 6. Non-metric multidimensional scaling (NMDS) ordination of the live communities. Transformation -- Log (x+1); Distance measure -- Bray-Curtis. As for the dendrogram, samples are colored accordingly: Staff's data are shown here as red crosses, Ebnother's with blue squares, and the new data with green crosses. Samples are labeled by date.

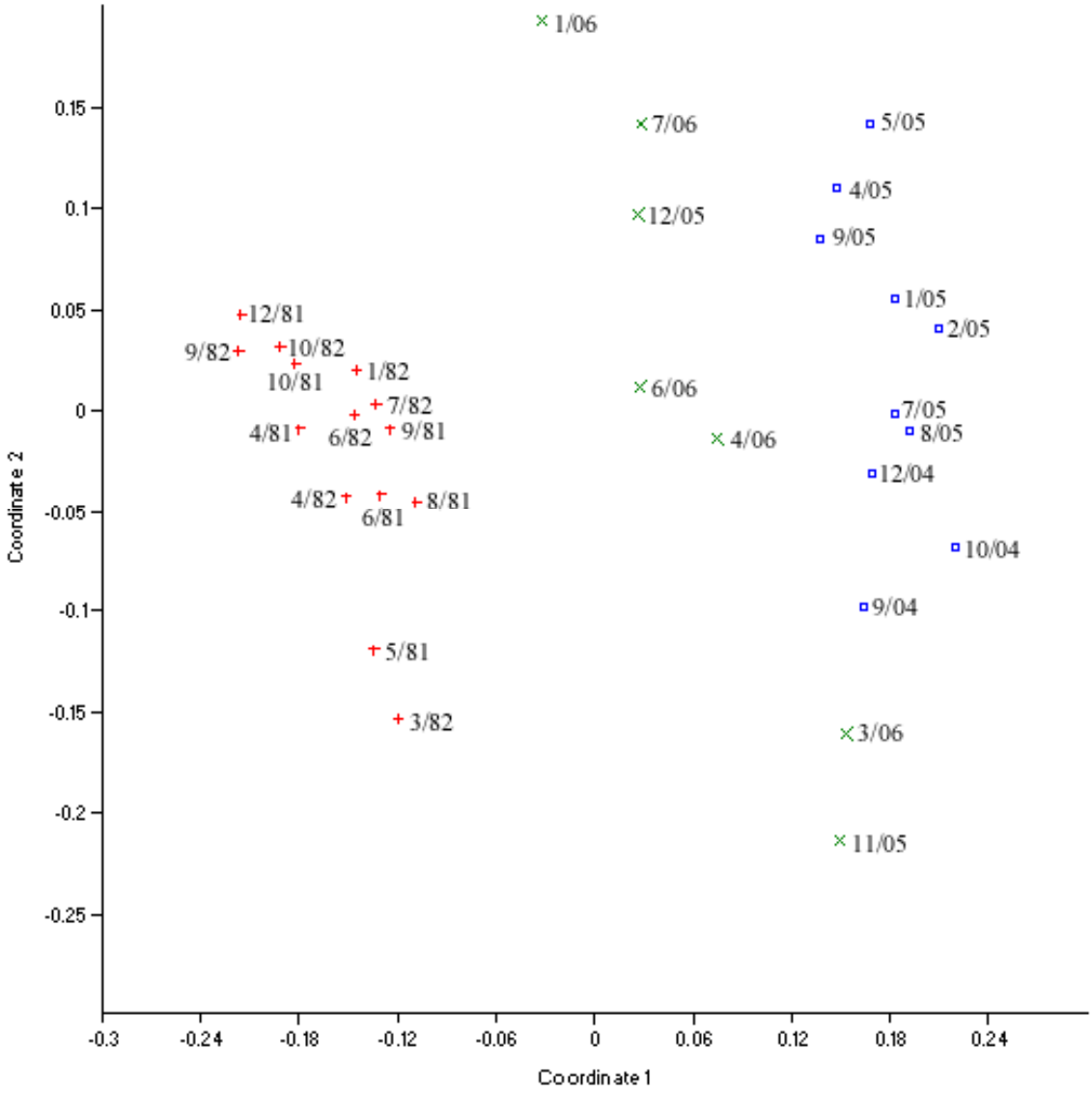

FIGURE 7. Non-metric multidimensional scaling (NMDS) ordination of the death assemblages. Transformation -- Log (x+1); Distance measure -- Bray-Curtis. As for the dendrogram, samples are colored accordingly: Staff's data are shown here as red crosses, Ebnother's with blue squares, and the new data with green crosses. Samples are labeled by date.

Spatial transect

The spatial transect was collected to assess both the living community and its corresponding death assemblage at Copano Bay at any moment in time, and therefore should show a reasonable estimate of the range of local variability at any moment in time and any compositional gradients present.

A total of 1,226 live and dead individuals collected along the 100 meter spatial transect at 25 meter intervals are considered here: 1,117 for the death assemblage, and 109 for the live individuals. Taken together, both the live and dead individuals include forty-five species. Raw counts and relative abundances for the live individuals can be found in Table 3 (see Appendix B for raw counts and relative abundances for the death assemblages).

For the live individuals, two species (out of seven) made up more than ninety-one percent of the total individuals: *Texadina sphinctostoma* (75.2%) and *Mulinia lateralis* (16.5%). One species, *Macoma constricta*, in the live individuals was not found in the death assemblages. The same three dominant species found in the time series here comprised more than sixty-seven percent of the death assemblage for the spatial transect (three from a total of forty-four species): *Texadina sphinctostoma* (27.3%), *Mulinia lateralis* (23.6%), and *Diastoma varium* (16.7%).

TABLE 3. Total raw counts and relative abundances for the living community (spatial transect).

Taxa		Raw	Relative Abundance (%)
Texadina	*sphinctostoma*	82	75.23
Mulinia	*Lateralis*	18	16.51
Macoma	*Mitchelli*	4	3.67
Macoma	*constricta*	2	1.83
Tagelus	*plebeius*	1	0.92
Tellina	*tampaensis*	1	0.92
Turbonilla	*sp.D(Andrews)*	1	0.92
	Total	**109**	**100**

Composite rarefaction curves and collector's curves have served to be a useful means of graphically assessing beta diversity among a set of collections (Gotelli and Colwell 2001; Olszewski 2004; Olszewski and Kidwell 2007). Composite rarefaction curves differ from collector's curves in that rarefaction curves compute the expected richness as sample size increases by accumulating specimens individually, whereas collector's curves compute expected richness as sample size increases by accumulating whole samples. As the distribution of diversity among samples, whether patchy or homogenized, will determine the growth of the collector's curve, it can be demonstrated that the graphical difference between these two curves is in fact beta diversity. Therefore, any deviation of the collector's curve from the composite rarefaction curve must indicate measurable beta diversity (i.e., variation in species composition among individual samples; Olszewski 2004).

Composite rarefaction and collector's curves for both the live community and death assemblage are shown in Figure 8. Evenness statistics are included in Table 4 for comparison. Composite rarefaction and collector's curves for the live community (Fig. 8A) show expected species richness as sample size increases to 106 individuals, the composite abundance for the five samples considered for the spatial transect. Figure 8B shows expected species richness as sample size increases to 1117 individuals for the death assemblage in accumulating the same five samples.

The collector's curves in Figure 8 are not identical to the composite rarefaction curves, indicating at least some heterogeneity among samples (i.e., measurable beta diversity) along the transect. Table 4 reveals the same pattern for much of the collections in the time series; namely, ∑PIE and μPIE both are significantly larger in the death assemblage than in the corresponding living community. In addition, ∑PIE - μPIE for the living community (0.194) is much larger than that of the death assemblage (0.027).

TABLE 4. Evenness statistics for the spatial transect. N is composite sample size, S species richness, X number of collections, ΣPIE PIE of composite sample, and μPIE weighted average PIE of the individual collections.

LIVE	N	S	X	ΣPIE	μPIE
6/07	109	8	5	0.588	0.394
DEAD	N	S	X	ΣPIE	μPIE
6/08	1117	44	5	0.836	0.809

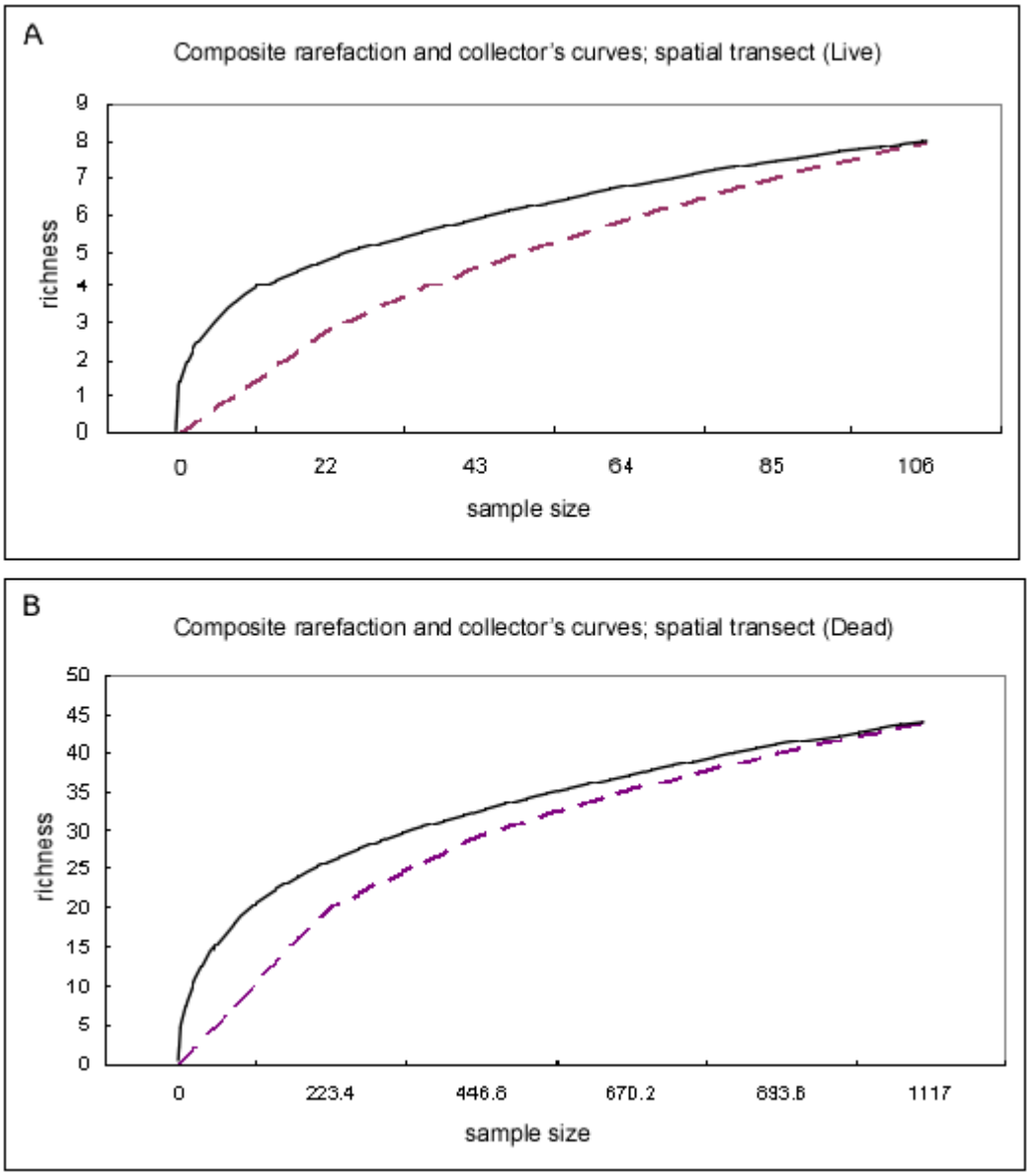

FIGURE 8. Composite rarefaction and collector's curves for both the live community and death assemblage (spatial transect). In both (A) and (B) the composite rarefaction curve is indicated with the solid black curve and the collector's curve with the dashed maroon curve. Note the difference in scale for both figures. In theory, collector's curves should be indistinguishable from composite rarefaction curves when beta = 0. Any deviation is an indicator of variation *among* samples (measurable beta diversity).

Summary of results

1.) Sample size corrected richness and evenness trends for the live communities are highly variable; sample size corrected richness for the death assemblages show a true rise in species richness beginning in April 2006 after a level species richness of ten months (6/05--3/06), and a pattern of markedly variable evenness beginning April 2005.

2.) Additive diversity partitioning revealed a large value for ∑PIE in the living versus the dead collections for the last seven samples of the time series and a small difference in ∑PIE and μPIE (0.061) which interprets the death assemblage as relatively stable (despite what would appear to be a variable trend in Figure 3A), though it cannot be explained by the highly variable nature of the living communities.

3.) NMDS ordination and cluster analysis revealed a compositional rebound in the death assemblages, where samples recently collected for the time series become compositionally more similar to samples collected 23 years ago; this was explained to be the result of reintroduction of species in the new samples collected from 11/06 to 7/06 and the disappearance of other species after samples collected from 9/04 to 9/05.

4.) Composite rarefaction and collector's curves and additive partitioning of evenness for the spatial transect do not indicate any compositional gradients present, and can be used as a fairly reliable estimate of the beta diversity within the locality for any moment in time.

CHAPTER IV

DISCUSSION

The spatial/temporal relationship

Additive partitioning of evenness for the spatial transect revealed that death assemblages are stable (∑PIE – μPIE was very small), though the large difference for the live community (0.194) suggested considerable variation among the samples. As species richness in the live community never exceeded 4 for any of the samples and evenness plotted versus distance along the transect did not seem to suggest any compositional gradients present, this variation was interpreted to be a fairly reliable estimate of the beta diversity within the locality.

Partitioning of evenness for the time series revealed the highly variable nature of the living communities which is evident in Figure 2A. The fact that ∑PIE and μPIE were much larger in the death assemblages than in the live communities for collections made from 4/81 to 10/82 and from 9/04 to 9/05 suggested that there was sufficient time averaging (the mixing of noncontemporaneously deposited remains; Olszewski 1999) or spatial mixing to have produced a stable death assemblage. However, although μPIE was much larger in the death assemblages than in the live communities for samples collected from 11/05 to 7/06, the opposite was true for ∑PIE. The large value for ∑PIE in the living versus the dead collections taken together with the small difference in ∑PIE and μPIE (0.061) revealed that though the death assemblage can be interpreted as stable

(despite what would appear to be a variable trend in Figure 3A) it cannot be explained by the highly variable nature of the living communities.

Compositionally, both living communities and death assemblages at Copano Bay have been replaced by new dominant species after a 22 year time interval (Fig. 4, 5). Figure 7 reveals what is interpreted to be a compositional rebound in the death assemblages, where samples recently collected for the time series become compositionally more similar to samples collected 23 years ago. In choosing the Bray-Curtis distance measure, this can be explained by the reappearance of species in the new samples collected from 11/06 to 7/06 (e.g., *Mitrella lunata*, *Triphora perversa nigrocinta*, *Aligena texasiana*, *Teinostoma lerema*, *Turbonilla interrupta*, *Vermicularia fargoi*, *Nuculana concentrica*) and the disappearance of other species after samples collected from 9/04 to 9/05 (e.g., *Haminoea succinea*, *Seila adamsi*, *Argopecten irradians*, *Mactra fragilis*, *Macoma constricta*). Alternatively, the living communities showed no such patterns in the ordination (Fig. 6) and demonstrated only that species composition did not significantly change for the last two years of the time series. Figure 4 emphasizes, however, that a significant change in species composition has occurred over the 22 year time interval.

CHAPTER V

CONCLUSIONS

In this study, temporal and spatial variability were investigated in benthic molluscan living communities and death assemblages collected from Copano Bay, a shallow inlet bay located on the coast of Texas. Species richness corrected for sample size and evenness trends for the time series indicated that species richness can be highly variable through time; however, species richness for living communities is always significantly smaller than their corresponding death assemblages. Additive diversity partitioning also demonstrated that no detectable compositional gradients were present at this locality at the time the spatial transect was collected in June 2007, and that the species richness along this transect can be used a fairly reliable estimate of the amount of beta diversity in the locality.

Compositional shifts through time for the live communities and death assemblages were seen in the cluster analyses and non-metric multidimensional scaling ordinations. Both live and dead cluster analyses demonstrated that samples collected 23 years ago are compositionally distinct from samples collected 22 years later. Ordinations revealed that for the death assemblages there occurs a compositional rebound in the most recent samples of the time series toward those collected 23 years ago, and can be interpreted as the result of the reintroduction of species that were not present in any of the samples collected from 9/04 to 9/05. However, the live community ordination does not reveal a

corresponding living community rebound, but only a slight trend in the new samples away from those collected previously.

LITERATURE CITED

Colwell, R. K. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide and application published at: http://purl.oclc.org/estimates.

Ebnother, D.D. and Olszewski, T. D., 2005. Revisiting Copano Bay, Texas: An exceptional long-term record of ecological communities and their associated molluscan death assemblages. GSA Abs. Prog. 37:136

Ferguson, C.A. and Miller, A.I., 2007. A sea change in Smuggler's Cove? Detection of decadal-scale compositional transitions in the subfossil record. Paleogeography, Paleoclimatology, Palaeoecology 254: 418-429.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379-391.

Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4(1): 1-9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52: 577-586.

Lande, R., 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76: 5-13

Lichlyter, S.A. and Olszewski, T.D., 2005. An applied paleoecology case study: Bahia Grande, Texas prior to construction of the Brownsville Ship Channel. GSA Abs. Prog. 37:136

Olszewski, T.D., 1999. Taking advantage of time-averaging. Paleobiology 25(2): 226-238.

Olszewski, T.D., 2004. A unified mathematical framework for the measurement of Richness and evenness within and among multiple communities. Oikos 104: 377-387.

Olszewski, T.D., Kidwell, S.M., 2007. The preservational fidelity of evenness in molluscan death assemblages. Paleobiology 33(1): 1-23.

Staff, G.M., 1983, The nature of information loss in the paleoecological

reconstruction of Benthic macrofaunal communities using faunal assemblages from the recent Texas coastal environment. Ph.D. Diss., Texas A&M Univ., College Station, TX, 211 p.

Wardlaw, B.R., 2001, Paleoecological Studies of South Florida. Bull. Am. Paleo. 361, 280 p.

Literature consulted

Abbot, R.T., 1974. American Seashells: the marine mollusca of the Atlantic and Pacific Coasts of North America. Van Nostrand Reinhold Company, New York, NY. 663p.

Adler, P.B., White, E.P., Lauenroth, W.K., Kaufman, D.M., Rassweiler, A., and Rusak, J.A., 2005. Evidence for a general species-time-area relationship. Ecology 86(8):2032-2039.

Adler, P.B., and Lauenroth, W.K., 2003. The power of time: spatiotemporal scaling of species diversity. Ecology Letters 6: 749-756.

Andrews, J. 1971. Seashells of the Texas Coast. The University of Texas Press, Austin. 298p.

Bennington, J.B., 2003. Transcending patchiness in the comparative analysis of paleocommunities: a test case from the Upper Cretaceous of New Jersey. Palaios 18: 22-33.

Carey, S., Ostling, A., Harte, J., and Del Moral, R., 2007. Impact of curve construction and community dynamics on the species-time relationship. Ecology 88(9): 2145-2153.

Davis, J. C., 1986. Statistics and data analysis in geology. John Wiley & Sons, New York 646 p.

Ferguson, C.A. and Miller, A.I., 2003. A sea change in Smuggler's Cove: compositional dynamics of subfossil molluscan assemblages. GSA Prog. Abs. 35:591.

Gering, J.C., Crist, T.O., and Veech, J.A., 2003. Additive partitioning of species diversity across multiple spatial scales: implications for regional conservation of biodiversity. Conservation Biology 17: 488-499.

Kowalewski, M., and Hoffmeister, A., 2003. Sieves and fossils: effects of mesh size on paleontological patterns. Palaios 18: 460-469.

Mcune, B., and Grace, J.B., 2002. Analysis of ecological communities. MJM Software Design, Glendon Beach, Oregon. 300pp.

Preston, F.W., 1960. Time and space and the variation of species. Ecology 41: 611-627.

Peterson, C.H., 1977. The paleoecological significance of undetected short-term temporal variability. Journal of Paleontology 51: 976-981.

APPENDIX A

Table A.1 Total raw counts and relative abundances for newly sampled death assemblages (time series).

Taxa		Raw	Relative Abundance (%)
Diastoma	*varium*	14087	51.731
Texadina	*sphinctostoma*	5240	19.243
Mulinia	*lateralis*	4227	15.523
Brachidontes	*exustus*	642	2.358
Caecum	*pulchellum*	588	2.159
Acteocina	*candei*	370	1.359
Laevicardium	*mortoni*	295	1.083
Acteon	*punctostriatus*	219	0.804
Macoma	*mitchelli*	167	0.613
Macoma	*tageliformis*	154	0.566
Chione	*cancellata*	150	0.551
Nuculana	*acuta*	134	0.492
Truncatella	*caribaeensis*	121	0.444
Cerithiopsis	*greeni*	103	0.378
Rangia	*cuneata*	101	0.371
Caecum	*nitidum*	86	0.316
Lucina	*pectinata*	57	0.209
Tagelus	*plebeius*	53	0.195
Crepidula	*convexa*	48	0.176
Anomalocardia	*auberiana*	37	0.136
Rangia	*flexuosa*	36	0.132
Boonea	*impressa*	33	0.121
Mitrella	*lunata*	25	0.092
Teinostoma	*lerma*	25	0.092
Vitrinella	*floridana*	25	0.092
Tellina Angulus	*texana*	24	0.088
Cerithidea	*pliculosa*	20	0.073
Sayella	*sp.A(Andrews)*	20	0.073
Modulus	*modulus*	19	0.070
Triphora	*perveria*	19	0.070
Cumingia	*tellinoides*	19	0.070
Congeria	*leucophaeta*	16	0.059
Odostomia	*laevigata*	11	0.040
Chione	*clenchi*	11	0.040
Vermicularia cf. V	*spirata*	8	0.029
Mysella	*planulata*	7	0.026
Tricola	*aff. cruenta*	6	0.022
Tellina	*tampaensis*	5	0.018
Eulimastoma cf. E.	*canaliculata*	4	0.015
Ischadium	*recurvum*	4	0.015

Taxa cont.		Raw	Relative Abundance (%)
Nuculana	*concentrica*	4	0.015
Carditamera	*floridana*	3	0.011
Crepidula	*fornicata*	2	0.007
Alabina	*cerithidiodes*	1	0.004
Caecum	*johnsoni*	1	0.004
Crepidula	*plana*	1	0.004
Turbonilla	*interupta*	1	0.004
Vermicularia	*fargoi*	1	0.004
Aligena	*texasiana*	1	0.004
	Total	**27231**	**100**

APPENDIX B

Table B.1 Total raw counts and relative abundances for death assemblage (spatial transect).

Taxa		Raw	Relative Abundance (%)
Texadina	*sphinctostoma*	305	27.31
Mulinia	*lateralis*	263	23.55
Diastoma	*varium*	186	16.65
Acteocina	*candei*	46	4.12
Brachidontes	*exustus*	35	3.13
Caecum	*pulchellum*	32	2.86
Acteon	*punctostriatus*	31	2.78
Laevicardium	*mortoni*	31	2.78
Rangia	*cuneata*	25	2.24
Odostomia	*seminuda*	22	1.97
Chione	*cancellata*	21	1.88
Caecum	*nitidum*	16	1.43
Cerithidea	*pliculosa*	12	1.07
Nuculana	*acuta*	11	0.98
Macoma	*mitchelli*	10	0.90
Retusa	*canaliculata*	8	0.72
Crepidula	*convexa*	7	0.63
Sayella	*livida*	6	0.54
Tagelus	*plebeius*	6	0.54
Cumingia	*tellinoides*	5	0.45
Teinostoma	*lerma*	5	0.45
Anomalocardia	*auberiana*	4	0.36
Crepidula	*fornicata*	4	0.36
Lucina	*pectinata*	3	0.27
Turbonilla	*sp.D (andrews)*	2	0.18
Vermicularia cf. V	*spirata*	2	0.18
Vitrinella	*floridana*	2	0.18
Aligena	*texasiana*	1	0.09
Anomalocardia	*cuneimens*	1	0.09
Boonea	*impressa*	1	0.09
Carditamera	*floridana*	1	0.09
Congeria	*leucophaeta*	1	0.09
Meioceras	*nitidum*	1	0.09
Modulus	*modulus*	1	0.09
Rangia	*flexuosa*	1	0.09
Teinostoma	*leremum*	1	0.09
Trifora	*perversa nigrocinta*	1	0.09
Turbonilla	*sp.A (Andrews)*	1	0.09
Tellina	*tampaensis*	1	0.09

Taxa cont.		Raw	Relative Abundance (%)
Tricola	*affinis cruenta*	1	0.09
Turbonilla	*strioturbinalla cf. T hemphilli*	1	0.09
Turbonilla	*sp. C (Andrews)*	1	0.09
Vermicularia	*fargoi*	1	0.09
Vitrinella	*texana*	1	0.09
	Total	**1117**	**100**

APPENDIX C

Table C.1 Abundance data for the newly sampled live communities (time series).

Taxa		11/5/2005	12/17/2005	1/29/2006	3/11/2006	4/22/2006	6/7/2006	7/19/2006
Acteon	*punctostriatus*	0	0	0	0	452	143	55
Boonea	*impressa*	0	0	0	0	0	1	0
Texadina	*sphinctostoma*	0	0	0	389	316	270	82
Brachidontes	*exustus*	0	0	0	4	0	7	0
Chione	*cancellata*	0	0	0	0	0	1	0
Laevicardium	*mortoni*	0	23	0	0	0	0	0
Lucina	*pectinata*	0	1	0	0	0	0	1
Macoma	*mitchelli*	0	3	3	5	5	15	25
Macoma	*tageliformis*	0	3	0	0	2	0	0
Montacula	*sp.*	0	0	0	0	0	170	0
Mulinia	*lateralis*	3	48	242	149	179	173	110
Rangia	*flexuosa*	0	0	2	0	0	0	0
Tagelus	*plebeius*	0	0	0	0	0	1	0
Tellina	*tampaensis*	0	0	0	0	0	1	0

APPENDIX D

Table D.1 Abundance data for the newly sampled death assemblages (time series).

Taxa		11/5/2005	12/17/2005	1/29/2006	3/11/2006	4/22/2006	6/7/2006	7/19/2006
Acteocina	*candei*	36	71	99	17	53	50	44
Acteon	*punctostriatus*	0	4	5	0	155	11	44
Alabina	*cerithidiodes*	0	0	0	1	0	0	0
Boonea	*impressa*	2	3	16	2	2	1	7
Caecum	*johnsoni*	0	0	0	0	0	0	1
Caecum	*nitidum*	6	14	23	2	8	17	16
Caecum	*pulchellum*	15	87	255	31	31	40	129
Cerithidea	*pliculosa*	0	0	0	0	6	3	11
Cerithiopsis	*greeni*	0	37	46	0	0	0	20
Crepidula	*convexa*	1	5	23	1	6	9	3
Crepidula	*fornicata*	0	0	0	0	0	0	2
Crepidula	*plana*	0	0	0	0	1	0	0
Diastoma	*varium*	87	3625	6983	357	131	283	2621
Eulimastoma	*canaliculata*	1	0	2	0	0	1	0
Texadina	*sphinctostoma*	251	756	1284	1052	477	599	821
Mitrella	*lunata*	0	3	17	0	0	0	5
Modulus	*modulus*	2	4	5	1	2	5	0
Odostomia	*laevigata*	0	3	0	0	3	0	5
Sayella	*sp. A*	0	3	8	3	0	0	6
Teinostoma	*lerma*	2	4	6	1	1	2	9
Tricola	*aff. cruenta*	0	0	0	0	3	2	1
Triphora	*perveria*	0	5	10	0	0	0	4
Truncatella	*caribaeensis*	0	30	61	0	0	1	29
Turbonilla	*interupta*	0	0	0	0	0	1	0
Vermicularia	*fargoi*	0	0	1	0	0	0	0
Vermicularia	*spirata*	0	1	0	0	2	4	1
Vitrinella	*floridana*	0	6	11	0	2	6	0
Aligena	*texasiana*	1	0	0	0	0	0	0
Anomalocardia	*auberiana*	2	8	8	5	2	5	7
Brachidontes	*exustus*	9	127	240	47	22	57	140
Carditamera	*floridana*	0	0	0	0	2	1	0
Chione	*cancellata*	8	24	39	10	21	23	25
Chione	*clenchi*	0	0	4	7	0	0	0
Congeria	*leucophaeta*	2	0	2	3	1	3	5
Cumingia	*tellinoides*	0	2	5	3	1	5	3
Ischadium	*recurvum*	0	0	3	0	1	0	0
Laevicardium	*mortoni*	14	56	84	11	56	51	23
Lucina	*pectinata*	0	9	10	15	6	8	9
Macoma	*mitchelli*	7	42	12	12	14	19	61
Macoma	*tageliformis*	1	12	91	19	20	11	0

Taxa cont.		11/5/2005	12/17/2005	1/29/2006	3/11/2006	4/22/2006	6/7/2006	7/19/2006
Mulinia	*lateralis*	277	564	1443	603	408	458	474
Mysella	*planulata*	0	0	3	0	0	2	2
Nuculana	*acuta*	5	44	32	4	19	16	14
Nuculana	*concentrica*	0	1	2	1	0	0	0
Rangia	*cuneata*	0	7	16	19	33	26	0
Rangia	*flexuosa*	0	0	24	12	0	0	0
Tagelus	*plebeius*	0	19	15	0	2	8	9
Tellina	*tampaensis*	0	2	1	0	0	2	0
Tellina	*texana*	1	4	9	0	7	1	2

CONTACT INFORMATION

Name:	Adam Michael Horbaczewski
Address:	Department of Geology & Geophysics Texas A&M University College Station, TX, 77843
Email Address:	adam_horb@neo.tamu.edu
Education:	B.S., Geology/Geological Engineering, Minor in Mathematics Texas A&M University, 2008 Undergraduate Research Scholar