REVISITING COPANO BAY, TEXAS: AN EXCEPTIONAL LONG-TERM RECORD OF ECOLOGICAL COMMUNITIES AND THEIR ASSOCIATED DEATH ASSEMBLAGES

A Thesis

by

DANIELLE DAWN EBNOTHER

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

August 2006

Major Subject: Geology

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Approved by:

Chair of Committee,	Thomas D. Olszewski
Committee Members,	Anne L. Raymond
	Stephen E. Davis, III
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ABSTRACT

Revisiting Copano Bay, Texas: An Exceptional Long-Term Record of Ecological
Communities and Their Associated Death Assemblages. (August 2006)

Danielle Dawn Ebnother, B.S., Southern Oregon University
Chair of Advisory Committee: Dr. Thomas D. Olszewski

Thanks to previous work conducted by Staff et al. (1986), Copano Bay on the Texas coast presents an exceptional research area for studying 1) the effect of living volatility on death assemblage diversity and composition and 2) the stability of death assemblage diversity. Staff et al. (1986) revisited one site in Copano Bay every six weeks for 18 months in 1981-1982. In order to test the variability of both the live and dead assemblages of Copano Bay, Texas, the transect originally established by Staff et al. (1981) in 1981-1983, was reestablished in 2004 and sampled every six weeks for a duration of one year. Taxonomic abundance, diversity, and composition of these assemblages were compared to each other and those of Staff et al. (1981) in order to understand how both the living and dead assemblages have changed in the intervening 22 years.

Important findings include: 1. Death assemblage composition in Copano Bay changed over 22 years more than expected based on short-term variation; 2. The death assemblages in Copano Bay reflected changes in taxonomic composition of the corresponding living community; 3. The death assemblages of Copano Bay were found to predominantly reflect the local, rather than the entire regional, species pool; and

4. Variation in diversity occurred at both six-week and 22-year time scales, indicating that the death assemblages at the study site are variable.

Understanding time averaging and its effects on death assemblages will not only aid in paleocommunity reconstruction, but also aid in the construction of modern ecologic baselines.

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To my father, Daniel V. Ebnother, who helped me to find the shiny rocks and catch the big lizards as a child.

ACKNOWLEDGEMENTS

This thesis exists as a result of the encouragement and support of my family and friends who provided immeasurable amounts of comfort and amusement throughout the entire duration of this project. My parents, Dan and Susan Ebnother, have always had faith in me in my various endeavors and have fully nurtured my academic growth. My grandparents, Llowel and Glorian Ebnother, have been like a second set of parents to me, and along with spoiling me rotten, have always encouraged me to ‘stand on my own two feet’. My friends Katie Poole, Coco Sta. Ana, Ben Eckstein, Meaghan Julian, and Leigh Fall were particularly helpful by providing insightful commentary, aiding with sample collection, and giving me a good reason to take a break from this thesis. Additionally, this project would not have been possible without the love and support of Charles Strickler.

I would like to thank my advisor, Tom Olszewski, for provoking my curiosity and challenging me to formulate new questions and find their corresponding answers. Dr. Olszewski boldly accepted me as his student, fully aware that I had absolutely no prior experience in the discipline of paleontology, and patiently guided me as I embarked upon a previously foreign field of study. The experience really was truly ‘character building’.

Additionally, I would like to thank Dr. Anne Raymond, Dr. Steve Davis, and Dr. George Staff for advice throughout this project and for enriching my experience at Texas A&M. Lastly, I would like to thank Mark Fisher of the Texas Parks and Wildlife Commission for providing me with environmental data for Copano Bay, Texas.

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INTRODUCTION

Death assemblages are collections of dead organisms that represent the initial step in the formation of fossil assemblages (Cummins et al., 1986b). Understanding the processes that influence death assemblage diversity and species abundances, such as the mixing of noncontemporaneous remains (time averaging) and differential loss among species, is critical to understanding the fossil record.

In soft-bottom marine settings along the Texas coast, death assemblages do not accumulate at the average rate at which individuals die; rather, individuals are added to the death assemblage in episodic pulses, usually after the occurrence of larval settlements (Cummins et al., 1986b; Powell et al., 1989). Immediately after death, shells become subject to processes such as transport, fracture, abrasion, bioerosion, and dissolution (Kidwell and Bosence, 1991). Even if burial occurs rapidly, subsequent bioturbation and physical re-working may re-expose shells to taphonomic alteration (Powell et al., 1989; Olszewski, 1999). The processes of time averaging and taphonomy can severely complicate the fidelity of death assemblages relative to their associated living assemblages.

On average, time averaging has been found to result in marine, molluscan death assemblages 22% more rich than corresponding living communities (Kidwell, 2001), interpreted to be due to mixing of multiple communities. Unless an assemblage was rapidly buried, multiple studies using radiocarbon and amino acid racemization dating

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This thesis follows the style and format of Palaios.

techniques, have revealed that the average scale of time averaging in marine settings on invertebrate shells (>3mm in size) ranges from 10^2 to 10^4 years (Flessa et al., 1993; Meldahl et al., 1997; Kowalewski et al., 1998; Carroll et al., 2003; Goodwin et al., 2004). Time averaging occurs on a much longer time scale than that of living community volatility (10^0-10^1 years) (Kidwell and Bosence, 1991). Because long-term time averaging allows mixing of multiple communities and community states over areas much larger than the corresponding local living community, it might be expected to result in stable, homogenized death assemblages. However, fossil assemblages, the end product of death assemblages, are commonly not homogenized; fossil assemblages from the same depositional setting can vary significantly (e.g., Olszewski and West, 1997; Bennington, 2003; Webber, 2005), indicating that the response of death assemblages to variability in the living community remains poorly constrained (e.g., Walker and Bambach, 1971; Peterson, 1976; Powell and Davies, 1990; Kowalewski et al., 1998).

The primary goal of this study is to address this problem by studying the variability of both the living and the dead assemblages at a site in Copano Bay, Texas (Figure 1). Thanks to previous work conducted by Staff et al. (1981), Copano Bay, Texas presents an exceptional research area for studying 1) the effect of living volatility on death assemblage diversity and composition at a six-week time scale and 2) the stability of death assemblage diversity at a decadal time scale. In order to test the variability of both the live and dead assemblages of Copano Bay, Texas, the transect originally established by Staff et al. (1981) in 1981-1983, was reestablished in 2004 and sampled every six weeks for a duration of one year. Taxonomic abundance, diversity, and composition of these assemblages were compared to each other and those of Staff et al. (1981) in order to understand how both the living and dead assemblages have changed in the intervening 22 years.

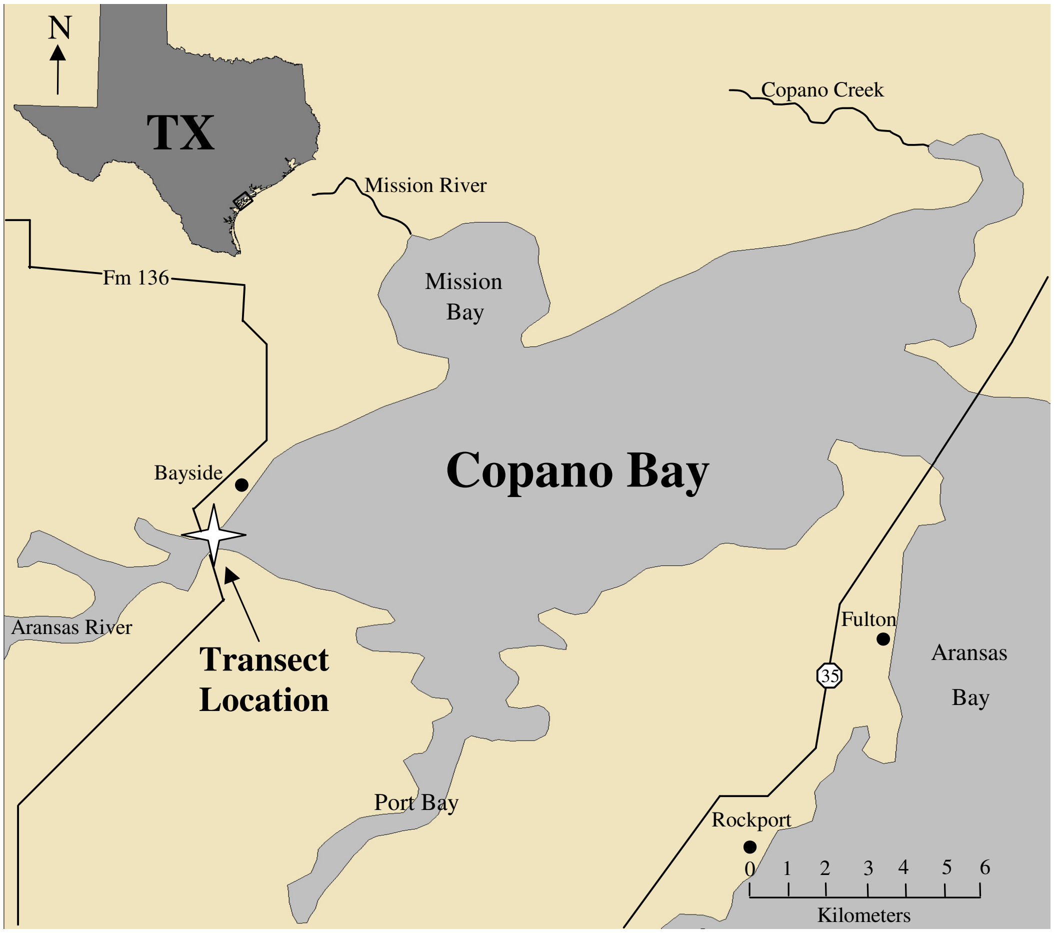

FIGURE 1—Location map of Copano Bay, Texas.

Results from this study will address: 1) the volatility of death assemblage composition at decadal and 6-week time scales, 2) whether death assemblages reflect the volatility of the living community, 3) the ability of local death assemblages to reflect the regional species pool, and 4) if death assemblages should be treated as stable or variable systems.

These findings will help guide the construction of modern ecologic baselines using death assemblages and aid in the interpretation of diversity in the fossil record. If death assemblage composition and diversity vary significantly through time and differ considerably from corresponding living communities, then perhaps fossil assemblages in the rock record are being interpreted beyond the limits of accuracy. However, if death assemblages are found to reflect the volatility of corresponding living communities, the temporal resolution of death assemblages may be more similar to living communities than previously thought.

TIME AVERAGING

In order to optimize paleocommunity reconstruction, much paleoecological research has focused on determining how closely death assemblages reflect attributes of their corresponding living communities, such as species diversity, species abundances, and taxonomic composition (e.g., Parker, 1960; Peterson, 1976; Cummins et al., 1986b; Staff et al., 1986; Fürsich and Flessa, 1987; Miller, 1988; Powell et al., 1992; Flessa and Kowalewski, 1994; Meldahl et al., 1997; Kidwell, 2001; Ferguson and Miller, 2003; Olszewski, 2004). Extensive investigations (e.g., Calnan, 1980; Cummins et al., 1986b; Staff et al., 1986; Miller, 1988; Powell et al., 1992; Ferguson and Miller, 2003) have been conducted on death assemblages in modern settings in order to understand how time averaging, which is the mixing of noncontemporaneous material (Walker and Bambach, 1971), and the postmortem alteration of biological remains affect death assemblages.

Previous work has demonstrated that attributes of a particular living community may be preserved in a death assemblage (e.g., Warme et al., 1976; Staff et al., 1986; Fürsich and Aberhan, 1990). Generally, 95.5 ± 5% of all preservable species sampled in the living community also occur in the corresponding death assemblage (Powell et al., 1982; Kidwell, 2001). In addition, trophic structure can be preserved from the living community in the corresponding death assemblage (Staff et al., 1986; Kidwell and Bosence, 1991; Kidwell, 2001). However, death assemblages are generally not exact representations of corresponding living communities: time averaging, the supply of dead remains, the inherent susceptibility of remains to postmortem destruction, the environment of accumulation, the time scale of accumulation, and sampling biases all result in variation between live and dead assemblages (Kidwell and Bosence, 1991).

Multiple studies have revealed that the average scale of time averaging, for marine invertebrate shells, ranges from 10^2 to 10^4 years (Flessa et al., 1993; Meldahl et al., 1997; Kowalewski et al., 1998; Carroll et al., 2003; Goodwin et al., 2004), which makes it difficult to distinguish distinct events in time within this duration and distorts diversity, morphometric variability, and size variation in death assemblages (e.g., Wilson, 1988; Fürsich and Aberhan, 1990; Kidwell and Bosence, 1991; Flessa et al., 1993; Kowalewski et al., 1998; Olszewski, 1999). In addition, the amount of time averaging has been found to vary greatly between different environments (Meldahl et al., 1997) and even within deposits formed in the same environmental setting (Kowalewski et al., 1998).

Time averaging cannot be thought of as a completely negative process; it dampens the ‘noise’ caused by ecologically disruptive, short-term perturbations, producing an assemblage that reflects long-term conditions before the period of final burial (Peterson, 1977; Kidwell and Bosence, 1991; Olszewski, 1999). Although time-averaged assemblages may represent thousands of years of accumulation, many time-averaged assemblages lack evidence for between-habitat transport; this indicates that the structure and composition of such assemblages may accurately reflect the corresponding living community from which they were derived (Kidwell and Bosence, 1991; Kidwell and Flessa, 1995). Additionally, numerical models of time averaging in death assemblages consistently predict that young shells should greatly outnumber old shells in death assemblages (Powell, 1992; Olszewski, 1999, 2004; Tomašovỳch, 2004), indicating that death assemblages are biased towards conditions at the time of burial rather than a record of previous conditions (e.g., Flessa and Kowalewski, 1994; Meldahl et al., 1997).

Although many advances have been made in our knowledge of the processes of time averaging and taphonomy, long-term stability of death assemblages is relatively unknown. Recent research in Smuggler's Cove, U.S. Virgin Islands examined the temporal stability of death assemblages over a period of 22 years (Ferguson and Miller, 2003). Results from this study indicated that species richness and composition of the death assemblage continued to reflect a sampled living biotic gradient after a 22-year interval. However, a change in key taxa occurred between the two studies; this finding suggests that death assemblages are unstable, but the degree of instability remains unquantified.

STUDY AREA

Located in a dry, subhumid climate zone, Copano Bay is a shallow (~2-4 meters depth), microtidal, lagoonal estuary in south-central Texas (Calnan, 1980) (Figure 1), formed as a result of the most recent Holocene transgression (Parker, 1960; Wilkinson, 1975; Weiss and Wilkinson, 1988; Paine, 1993; Morton et al., 2000; Blum et al., 2001). The salinity of Copano Bay ranges from 5‰ during wet years to 40‰ during droughts (Parker, 1960) and the majority of species within Copano Bay are tolerant of a broad range of salinity conditions (Calnan, 1980). Long-term tidal records (Martinez-Andrade et al., 2005) indicate that, from August 1981 to August 2005, average salinity was 11.84‰, average water temperature was 25°C, and average dissolved oxygen was 8.1 mgl^{-1}. Copano Bay has three primary sources of freshwater input: the Mission River, the Aransas River, and Copano Creek (Figure 1). The average discharge of each from April 1981 through September 2005 was 4.5 m^3s^{-1} for the Mission River, 1.2 m^3s^{-1} for the Aransas River, and 1.3 m^3s^{-1} for Copano Creek (United States Geological Survey, 2005).

FIELD METHODS

Live and dead assemblages were collected at six-week intervals for a period of 12 months, near the mouth of the Aransas River in Copano Bay, Texas (Figure 1). Samples consisted of two shallow push cores (176 cm^2 area and 17 cm depth) and a surface scrape (24 cm wide by 5 cm deep by 3 m long) collected at the same location used by Staff et al. (1986). To avoid re-sampling previously disturbed sites, each collection was taken from a random position along a 100-meter, shore-parallel, sampling transect, established 50 meters offshore in about one meter of water (water depth varied depending on season and wind direction) (Figure 2). Collection sites were sampled at random positions along the transect in order to distinguish temporal from spatial variation.

Shells collected for this study were sieved through >2.0 mm, 1.0 –2.0 mm, and 0.5-1.0 mm size classes. In contrast, Staff et al. (1986) combined all shells >0.5 mm. Each sieve size in the 2004-2005 dataset was analyzed independently in order to ensure that any size-dependent differences in composition, richness, and evenness were captured (Callaway et al., 2002; Kidwell et al., 2001; Kowalewski and Hoffmeister, 2003) and to be able to compare the dataset to that of other studies which may have utilized sieves of different sizes. In accordance with Staff et al. (1986), bivalves were identified and counted only if they retained a beak, and gastropods only if they retained an apex. Following Staff et al. (1981), disarticulated and articulated specimens were each counted as a whole individual for all calculations.

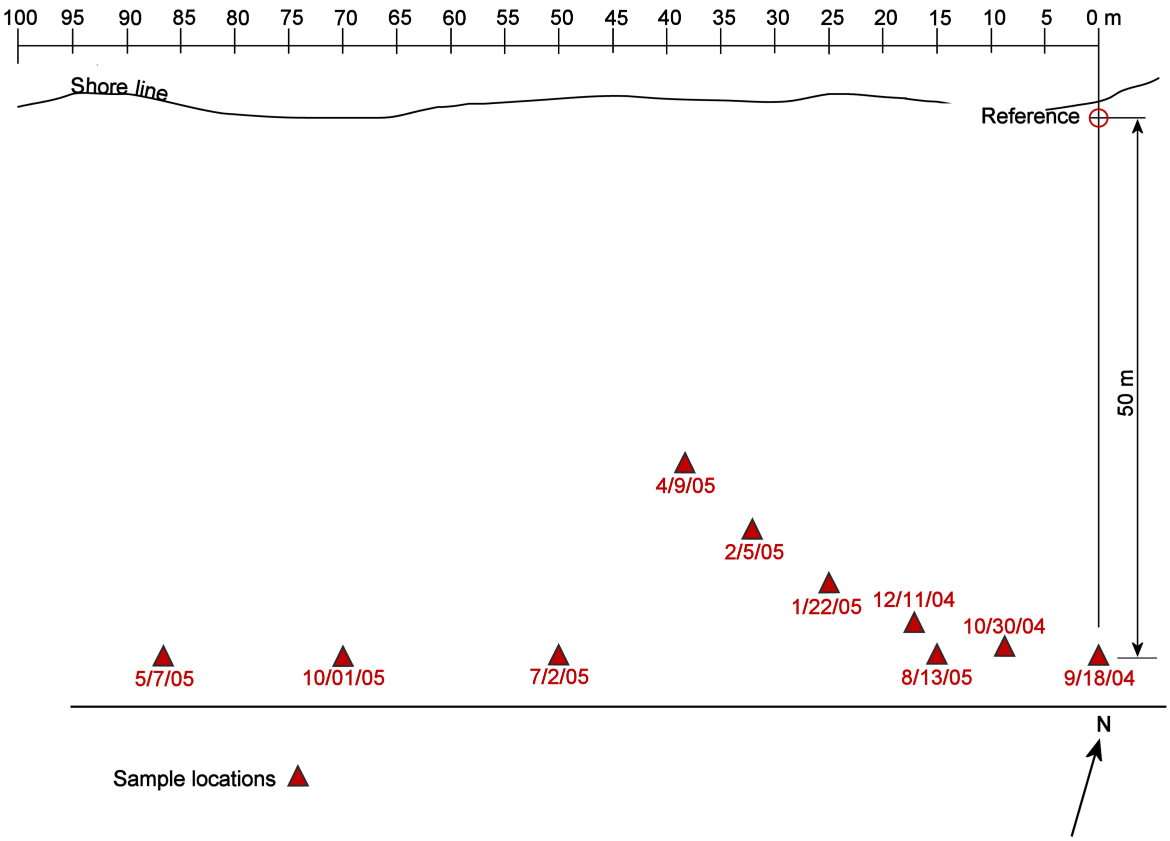

FIGURE 2—Dates and locations of each collection along the sampling transect. Samples were chosen at random along the 100 meter transect to avoid re-sampling previously disturbed sites.

RESULTS

Volatility of Death Assemblage Composition at Decadal and Six-Week Time Scales

Understanding the compositional stability of death assemblages at multiple time scales will lead to a better understanding of the compositional consistency of fossil assemblages. Correspondence analysis was employed to compare the composition of the 1981-1982 and 2004-2005 datasets. Prior to ordination, a double square root transformation was applied to the species abundances to reduce the influence of dominant species such as *Mulinia lateralis* and *Texadina sphinctostoma* (Clarke and Warwick, 2001). To ensure that rare species would not obscure results, all species occurring in three or fewer sites were deleted, as were sites containing fewer than three species.

Additionally, the taxonomic identifications of the 1981-1982 and 2004-2005 species were synonymized to ensure that differences in identifications and names did not influence any potential multivariate patterns. However, even at the genus level, similar morphology at very small sizes of *Odostomia spp*., *Sayella spp*., and *Texadina spp.,* complicated identification. *Solariorbis spp*. and *Vitrinella spp*. were also grouped together for the same reasons. Although combined, these genera are not necessarily closely related. Combining these taxa was intended to avoid the potential of identification errors between the 1981-1982 and 2004-2005 studies.

Correspondence analysis revealed that the 1981-1982 and 2004-2005 death assemblages formed distinct groups with minimal overlap (Figure 3). Species such as *Bulla striata*, *Macoma constricta*, and *Anomalocardia auberiana* occurred only in the 1981-1982 dataset, resulting in the cluster of species seen on the far left of the ordination plot (Figure 3). Species such as *Diastoma varium*, *Chione cancellata*, and *Mulinia lateralis* were present in both datasets, resulting in the cluster of species in the center of the ordination plot (Figure 3). Species such as *Chione intrapurpurea*, *Seila adamsi*, and *Alabina cerithidiodes* occurred only in the 2004-2005 dataset, resulting in the species seen on the far right of the ordination plot (Figure 3).

The string of species associated with the 2004-2005 dataset seen on the right-hand side of Figure 3 is interpreted to represent a compositional gradient. With the exception of two of the 2004-2005 sites (10/30/04 at 8.7m and 8/16/05 at 15m), all 2004-2005 sites roughly correspond to a spatial gradient. Physical evidence of the compositional gradient was noted in the field as the substrate east of the 50 meter point along the sampling transect was more mud-rich, whereas west of the 50 meter point, the substrate was more shell rich. The species *Vermicularia cf. spirata*, *Natica tectonatica pusilla*, *Ischadium recurvum*, *Lucina pectinata*, and *Truncatella caribaeensis* roughly correspond to the shelly end of the transect (100 m), whereas the species *Alabina cerithidiodes*, *Ischnochiton pappillosus*, *Mactra fragilis*, *Rangia flexuosa*, *Dentalium texasianum*, and *Seila adamsi* correspond to the muddy end of the transect (0 m) (Figure 3).

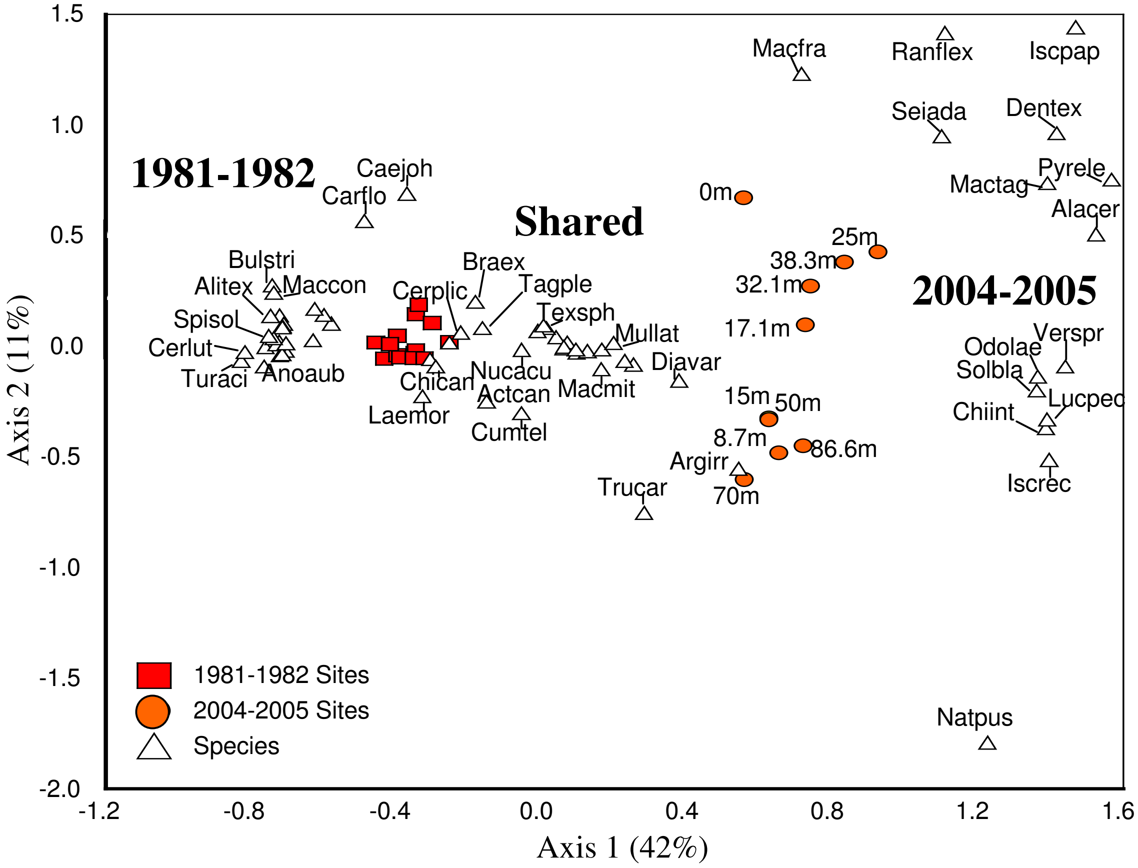

FIGURE 3—Correspondence analysis of the 1981-1982 and 2004-2005 death assemblages. Total inertia=0.632; percents reflect fraction of total inertia. Data were modified using a double square root transformation of abundances. Not all species are labeled in order to avoid overlap of names. Species on the far left of the plot occur only in the 1981-1982 dataset. Species in the middle of the plot occur in both 1981-1982 and 2004-2005 datasets. Species on the far right occur only in the 2004-2005 dataset; the string of species on the right side of axis 1 corresponds to a compositional gradient parallel to the sampling transect in the 2004-2005 dataset. Positions of each sample along the 2004-2005 transect are recorded in meters. Names of species correspond to the first three letters of the genus name and the first three letters of the species name; full species lists can be found in Tables 3 and 4. Dates and sample locations along the 2004-2005 transect are as follows: Sample 1-9/18/04 at 0m; Sample 2-10/30/04 at 8.7m; Sample 3-12/11/04 at 17.1m; Sample 4-1/22/05 at 25m; Sample 5-2/5/05 at 32.6m; Sample 6-4/9/05 at 38.3m; Sample 7-5/7/05 at 86.6; Sample 8-7/2/05 at 50m; Sample 9-8/13/05 at 15m; and Sample 10-9/24/04 at 70m.

If time averaging is significant, compositional gradients are not expected to be preserved in death assemblages due to the opportunity for mixing of living communities at different sites along the gradient. The presence of a gradient in the 2004-2005 death assemblages suggests that time averaging may be minimal in Copano Bay. In contrast, the close grouping of sites in the ordination plot in Figure 3 indicates that the 1981-1982 death assemblages do not display a gradient; exploration of higher ordination axes also confirmed this result.

Unlike the dead, the living 1981-1982 assemblages display a potential compositional gradient in the ordination (Figure 4); however, the physical position of each collection along the transect in the 1981-1982 dataset is unknown, so the presence of a spatial gradient cannot be validated. However, the samples do not occur in the order in which they were collected, so the gradient does not represent change through time. The 2004-2005 living communities displayed no discernable gradient; exploration of higher ordination axes confirmed this result (Figure 4). Since the 2004-2005 death assemblages displayed a compositional gradient, it is expected that the 2004-2005 living assemblages would also display such a gradient. However, species richness of 2004-2005 living assemblages (ten species) may not have been diverse enough to display a spatial gradient.

Overall, the 1981-1982 and 2004-2005 datasets each formed distinct groups, indicating that composition of both live and dead assemblages has changed over the 22-year interval separating the studies.

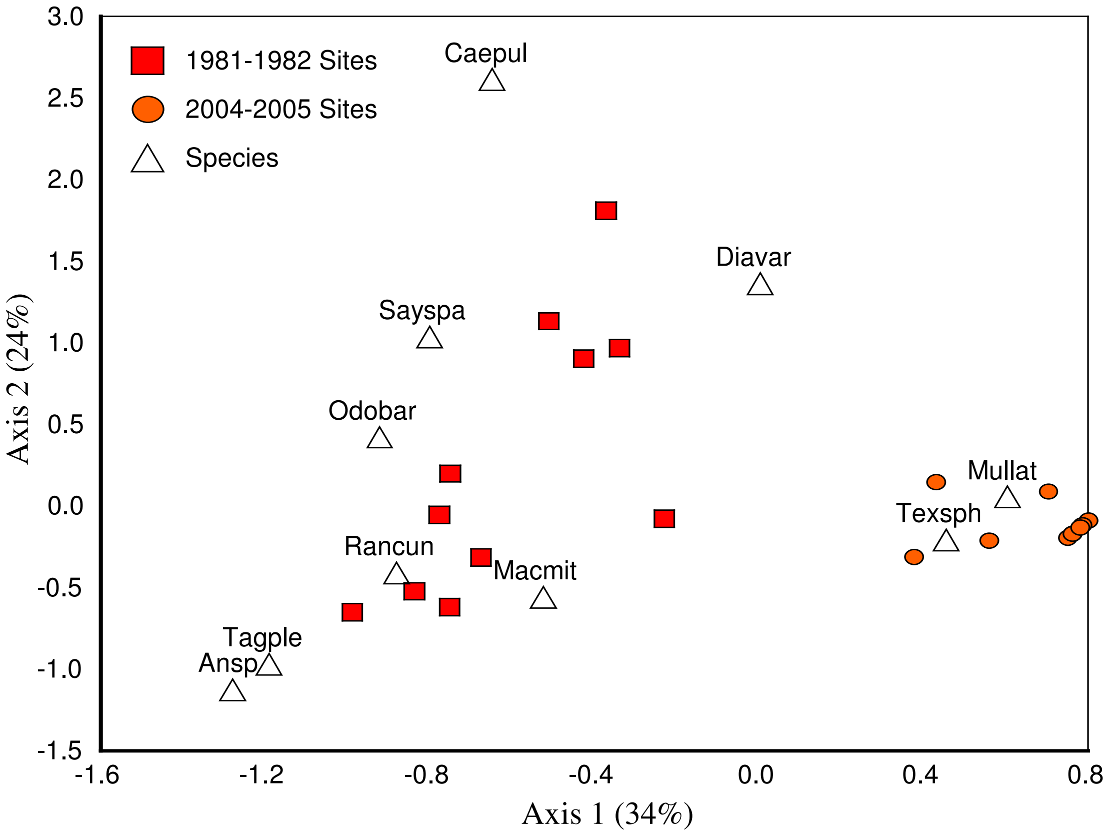

FIGURE 4—Correspondence analysis of the 1981-1982 and 2004-2005 living assemblages. Total inertia=1.343; percents reflect fraction of total inertia. Data were modified using a double square root transformation of raw abundances. Names of species correspond to the first three letters of the genus name and the last three letters of the species name; full species lists can be found in Table 2. The physical position of each collection along the transect in the 1981-1982 dataset is unknown.

Reflection of Living Community Volatility in the Composition of Death Assemblages

A common goal for ecologists is to assess community change over a particular interval of time, whereas paleoecologists only have access to death and fossil assemblages that accumulate over much longer timescales than living communities. The 22-year record of study from Copano Bay provides the opportunity to assess living community change and see how this change might be reflected in death assemblages. The Spearman rank correlation coefficient was used to compare abundance distributions in order to see how live and dead assemblages in Copano Bay have varied over 22 years.

Only 10 species were present in the live 2004-2005 dataset; together, the gastropod *Texadina sphinctostoma* and the bivalve *Mulinia lateralis* represent 99.57 percent of all live species collected (Table 1; Appendix A). Although the sample sizes of the living community in the 1981-1982 dataset were smaller than those of the 2004-2005 dataset, the 1981-1982 samples were more rich; 18 live species comprised the 357 live individuals that were identified in the live Staff et al. (1986) collection. The gastropods *Odostomia barretti* (59 % of the collection) and *Texadina sphinctostoma* (16 % of the collection) dominated the living 1981-1982 dataset (Table 1). The correlation of rank order between the 1981-1982 and 2004-2005 living assemblages was not significant ($r_s=0.078< r_{s\ \alpha=0.05,\ df=20}=0.428$ including all species observed in either or both datasets; $r_s=-0.096< r_{s\ \alpha=0.05,\ df=4}=0.886$ including only species occurring in both). The lack of significant correlation in rank abundances between the 1981-1982

TABLE 1—Raw counts and relative abundance (percent) of the 2004-2005 and 1981-1982 living assemblages

Species (2004-2005)	**Raw**	**Percent**	**Species (1981-1982)**	**Raw**	**Percent**
Mulinia lateralis	2486	51.56	*Odostomia barretti*	211	59.10
Texadina sphinctostoma	2315	48.01	*Texadina sphinctostoma*	56	15.69
Brachidontes exustus	8	0.17	*Rangia cuneata*	21	5.88
Macoma mitchelli	5	0.10	*Mulinia lateralis*	14	3.92
Diastoma varium	3	0.06	*Tagelus plebius*	14	3.92
Tricola aff. cruenta	1	0.02	*Macoma mitchelli*	11	3.08
Chione cancellata	1	0.02	*Anomia sp.*	10	2.80
Lucina pectinata	1	0.02	*Diastoma varium*	4	1.12
Nuculana acuta	1	0.02	*Odostomia c.f. teres*	4	1.12
Rangia cuneata	1	0.02	*Acteon punctostriatus*	2	0.56
Total	**4,822**	**100%**	*Caecum pulchellum*	2	0.56
			Sayella sp. A	2	0.56
			Acteocina candei	1	0.28
			Bulla striata	1	0.28
			Odostomia weberi	1	0.28
			Tricola sp.	1	0.28
			Brachidontes exustus	1	0.28
			Ensitellops sp.	1	0.28
			Total	**357**	**100%**

and the 2004-2005 datasets indicates a shift of dominant species in the living molluscan community between 1982 and 2005 (Table 1).

The 2004-2005 death assemblages contained a total of 57 species, whereas the 1981-1982 death assemblages contained a total of 80 species (Tables 2 and 3; Appendix B). The correlation of rank order between the 1981-1982 and 2004-2005 death assemblages was marginally significant ($r_s=0.193 < r_{s\ \alpha=0.05,\ df=98}=0.195$ including all species observed in either or both datasets; $r_s=0.5389 > r_{s\ \alpha=0.05,\ df=34}=0.325$ including only species occurring in both). Using only the top ten dominant individuals in each death assemblage resulted in a higher correlation for rank abundance when including only species occurring in both datasets ($r_s=0.750 > r_{s\ \alpha=0.05,\ df=6}=0.738$); however, this correlation was not as high when including all species observed in either or both datasets ($r_s=0.270 < r_{s\ \alpha=0.05,\ df=10}=0.564$). The volatility of rare, low abundance species decreases the correlation between the death assemblages. Although rank order of the dominant species in the death assemblages was similar, the actual proportions of the dominant species changed dramatically; *Mulinia lateralis* and *Texadina sphinctostoma* were much more abundant in the 2004-2005 death assemblages (Tables 2, 3).

In both the 2004-2005 and 1981-1982 assemblages, all living species were also found in the corresponding death assemblages. In the 2004-2005 dataset, 18 percent of the dead species were present in the living community (10 live species/57 dead species), whereas 23 percent of the dead were present in the 1981-1982 living community (18 live species/80 dead species). At the genus level, all taxa from the 1981-1982 living assemblage are also present in the 2004-2005 death assemblage. A tabulated list of species membership for both live and dead species in the 1981-1982 and 2004-2005 datasets is located in Appendix C.

TABLE 2—Raw counts and relative abundance (percent) of the 2004-2005 death assemblages

Species (2004-2005)	Raw	Percent
Mulinia lateralis	5497	30.27
Diastoma varium	4755	26.19
Texadina sphinctostoma	4546	25.04
Brachidontes exustus	672	3.7
Acteocina candei	494	2.72
Caecum pulchellum	310	1.71
Chione cancellata	270	1.49
Nuculana acuta	185	1.02
Tagelus plebius	165	0.91
Macoma mitchelli	160	0.88
Odostomia laevigata	155	0.85
Rangia flexuosa	112	0.62
Laevicardium mortoni	101	0.56
Chione intrapurpurea	86	0.47
Caecum nitidum	79	0.44
Lucina pectinata	64	0.35
Rangia cuneata	53	0.29
Truncatella caribaeensis	44	0.24
Vitrinella floridana	40	0.22
Acteon punctostriatus	37	0.20
Solariorbis blakei	34	0.19
Tellina Angulus texana	33	0.18
Cumingia tellinoides	25	0.14
Modulus modulus	23	0.13
Macoma tageliformis	22	0.12
Cerithidea pliculosa	16	0.09
Seila adamsi	16	0.09
Crepidula fornicata	15	0.08
Species (2004-2005) Cont.	**Raw**	**Percent**
Crepidula plana	14	0.08
Ischadium recurvum	14	0.08
Cerithiopsis greeni	12	0.07
Crepidula convexa	12	0.07
Boonea impressa	9	0.05
Pyrgiscus cf elegantula	9	0.05
Tricola aff. cruenta	8	0.04
Alabina cerithidiodes	7	0.04
Ischnochiton papillosus	7	0.04
Vermicularia cf. V spirata	7	0.04
Mactra fragilis	7	0.04
Natica Tectonatica pusilla	6	0.03
Polinices Nererita duplicatus	6	0.03
Musculus lateralis	5	0.03
Dentalium texasianum	5	0.03
Congeria leucophaeta	4	0.02
Argopecten irradians	3	0.02
Haminoea succinea	2	0.01
Pyrgiscus cf. portoricana	2	0.01
Anomalocardia auberiana	2	0.01
Caecum johnsoni	1	0.01
Eulimastoma cf. E. canaliculata	1	0.01
Sayella sp. A	1	0.01
Carditamera floridana	1	0.01
Chione clenchi	1	0.01
Macoma constricta	1	0.01
Mysella planulata	1	0.01
Tagelus divisus	1	0.01
Total	**18,158**	**100%**

TABLE 3—Raw counts and relative abundance (percent) of the 1981-1982 death assemblages

Species (1981-1982)	**Raw**	**Percent**	**Species(1981-1982) Cont.**	**Raw**	**Percent**
Diastoma varium	4055	21.47	*Cerithiopsis greeni*	17	0.09
Brachidontes exustus	3322	17.59	*Pseudosyrena floridana*	16	0.08
Texadina sphinctostoma	2357	12.48	*Amygdalum papyria*	16	0.08
Acteocina candei	1469	7.78	*Fargoa dianthophila*	15	0.08
Mulinia lateralis	1217	6.44	*Aligena texasiana*	13	0.07
Laevicardium mortoni	957	5.07	*Caecum lutosum*	12	0.06
Caecum pulchellum	776	4.11	*Odostomia bartschi*	11	0.06
Tagelus plebeius	748	3.96	*Syrnola sp. A*	11	0.06
Chione cancellata	627	3.32	*Turbonilla speira*	11	0.06
Odostomia barretti	284	1.5	*Truncatella caribaeensis*	10	0.05
Nuculana acuta	201	1.06	*Tellina tampaensis*	9	0.05
Rangia cuneata	194	1.03	*Turbonilla interupta*	8	0.04
Anomalocardia auberiana	183	0.97	*Bulla striata*	7	0.04
Odostomia c.f. teres	174	0.92	*Carditamera floridana*	7	0.04
Caecum nitidum	173	0.92	*Mactra fragilis*	7	0.04
Odostomia weberi	165	0.87	*Haminoea succinea*	5	0.03
Sayella sp. A	145	0.77	*Caecum johnsoni*	4	0.02
Boonea impressa	134	0.71	*Rissoina catesbyana*	4	0.02
Vitrinella floridana	132	0.7	*Crassostrea virginica*	4	0.02
Macoma mitchelli	120	0.64	*Lucinid sp. A*	4	0.02
Modulus modulus	119	0.63	*Anachis avara*	3	0.02
Cerithidea pliculosa	104	0.55	*Mitrella lunata*	3	0.02
Macoma constricta	98	0.52	*Nassarius vibex*	3	0.02
Tellina texana	95	0.5	*Seila adamsi*	3	0.02
Tricola aff. cruenta	92	0.49	*Tricola sp.*	3	0.02
Anomia sp.	87	0.46	*Circulus suppressus*	2	0.01
Crepidula convexa	74	0.39	Argopecten irradians	2	0.01
Cumingia tellinoides	73	0.39	*Ensitellops sp.*	2	0.01
Mysella planulata	73	0.39	*Montacula sp.*	2	0.01
Lucinid sp. B	64	0.34	*Rangia flexuosa*	2	0.01
Acteon punctostriatus	61	0.32	*Cyclostremella sp.*	1	0.01
Crepidula fornicata	50	0.26	*Lucapinella limatula*	1	0.01
Spissula solidissima	45	0.24	*Odostomia seminuda*	1	0.01
Teinostoma lerma	38	0.2	*Triphora pervervia*	1	0.01
Cerithium lutosum	35	0.19	*Turbonilla w.*	1	0.01
Nuculana concentrica	35	0.19	*Vitrinella thomasi*	1	0.01
Vermicularia fargoi	22	0.12	*Abra equalis*	1	0.01
Gemma sp.	22	0.12	*Anadara sp.*	1	0.01
Crepidula plana	21	0.11	*Cytopleura costata*	1	0.01
Turbonilla acicula	19	0.1	*Diplodont sp.*	1	0.01
			Total	**18,886**	**100%**

The 1981-1982 and 2004-2005 living assemblages have different top species and very different species rankings, indicating species turnover (Table 1). The 2004-2005 death assemblages recorded increases in rank order of the species that gained dominance in the 2004-2005 living assemblages. This result indicates that death assemblages at this site reflect changes in taxonomic composition of the living community over the observed 22-year timescale. However, the use of rank abundance data on death assemblages is contingent upon the assumption that death assemblages accurately reflect the species abundance patterns of living communities (Kidwell, 2001). The different inherent susceptibility of shells of different microstructure, age, and size to abrasion, dissolution, bioerosion, and breakage can cause death assemblages to differ in composition from corresponding living communities (Cummins, 1986a, Powell et al, 1989); death assemblages should be biased toward species that are resistant to destruction and short-lived (Kidwell and Flessa, 1995). In addition, population biology of different species can also influence death assemblage species rankings (Vermeij and Herbert, 2004). In a meta-analysis of nearly 85 studies in which living and dead assemblages were analyzed, Kidwell (2001) concluded that the rank order of species in living communities is preserved in death assemblages, indicating that changes seen in rank order suggest species turnover, as opposed to susceptibility and transport of shells.

Kidwell and Flessa (1995) suggested that low compositional agreement between live and dead assemblages arises from inadequate sampling of the living community as opposed to shell destruction and transport. Living communities often occur in patches (i.e., exhibit spatial heterogeneity), which can be inadvertently missed, omitting the majority of the living community from a sample (Warme et al., 1976; Miller and Cummins, 1990; Kidwell and Bosence, 1991). A large number of paleoecologic studies have reported patchiness of living communities as a common reason accounting for the inadequate sample size of such communities to account for much larger death assemblages (Warme et al, 1976; Peterson, 1975; Miller, 1988; Ferguson and Miller, 2003); however, it is unlikely that so many studies consistently miss the hypothesized community patches. The 1981-1982 and 2004-2005 studies each sampled along the same, 100-meter transect, making it unlikely that both studies inadequately sampled the living community by missing community patches. The patchiness of living communities may bias results when comparing them with corresponding death assemblages, but the consistent pattern of missing live individuals in multiple studies suggests that more than just inadequate sampling of community patches is necessary to explain the much larger size of equivalent dead samples.

Local versus Regional Range in Variation of Death Assemblages

To test if the fauna from the localized 2004-2005 transect are related to fauna from other sites within the Copano Bay region, the 2004-2005 death assemblages were compared to data collected by Calnan (1980). Calnan (1980) sampled 93 sites throughout Copano Bay during March and April of 1976 (Figure 5). He established that different dead molluscan associations occurred in different habitats; these associations were primarily controlled by factors such as sediment type, salinity, and total organic carbon content. Correspondence analysis of Calnan's (1980) dataset and the 2004-2005 dataset demonstrates that the sites of Copano Bay can roughly be divided into three primary groups depending upon whether the substrate is sand, mud, or shell (Figure 5).

Data from Staff et al. (1986) were omitted in this analysis because Calnan (1980) only sampled the one-millimeter or greater size community, whereas Staff et al. (1986) used a 0.5 mm sieve to process their samples. Such differences in mesh size strongly influence perceived community patterns (Kidwell et al., 2001; Callaway et al., 2002; Kowalewski and Hoffmeister, 2003). Only the >1mm mesh size categories of the 2004-2005 death assemblages were utilized for comparison. Ordination analysis revealed that the 2004-2005 death assemblages are closely related to only ten of the 93 Calnan (1980) sites (Figure 5). These ten sites are not geographically near the 2004-2005 sampling transect; rather, they are located apparently at random throughout Copano Bay (Figure 5). Seven of the ten sites are associated with a muddy substrate (the remaining three are associated with sandy substrate), suggesting that the 2004-2005 death assemblages are most closely related to sites containing a muddy substrate. The presence of *Mulinia lateralis* and *Texadina sphinctostoma* are the primary factors relating the ten Calnan (1980) sites to the 2004-2005 death assemblages. Subsidiary species tying together the Calnan (1980) and 2004-2005 data include *Tellina texana*, *Macoma mitchelli*, *Lucina pectinata,* and *Musculus lateralis*.

Warwick and Light (2002) suggested that death assemblages could be used to approximate the regional species pool; however, the composition of the 2004-2005 death assemblages is clearly not representative of the regional species pool from all habitats

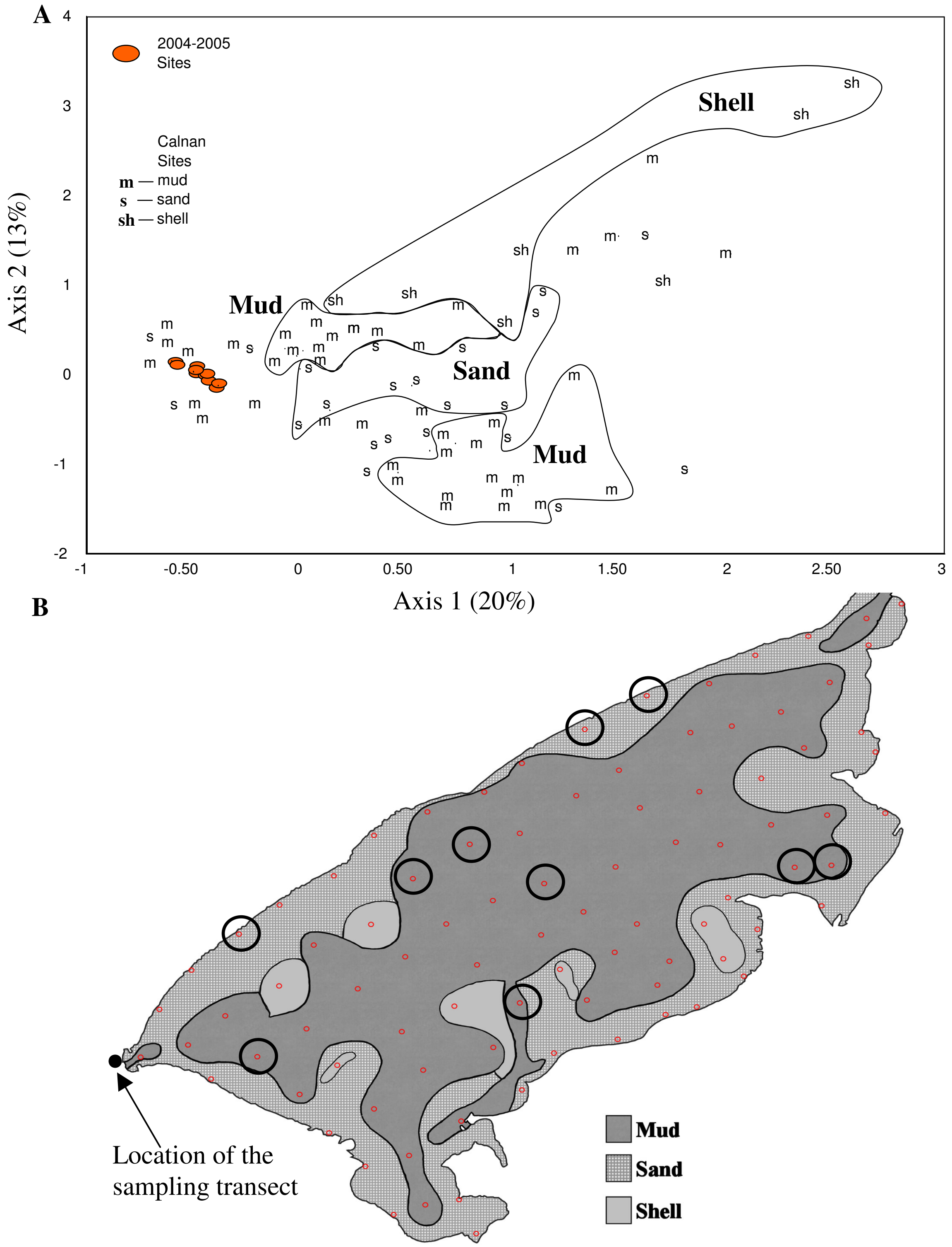

FIGURE 5—(A) Correspondence analysis of the dead data from Calnan (1980) and the 2004-2005 dataset (total inertia =2.60; percents reflect fraction of total inertia) and (B) Circles mark the 2004-2005 sites related to Calnan's (1980) sites.

within Copano Bay.

The 2004-2005 death assemblages contain *Brachidontes exustus* and *Ischadium recurvum,* species that prefer a hard substrate as opposed to the muddy substrate of the sampling area, indicating that the 2004-2005 death assemblages do reflect habitats other than that characteristic of the sampling transect. In Copano Bay, mixing of species from significantly different habitats along the transect has occurred; however, mixing has not been great enough to cause species from all habitats within Copano Bay to become homogenized at the Aransas River site.

Local death assemblages have been used to approximate the regional species pool (Warwick and Light, 2002). However, if local death assemblages are unable to approximate the regional species pool, then local fossil assemblages may not be able to approximate the regional species pool either.

Staff et al. (1986) assumed that revisiting the same sampling location multiple times (i.e., replicate sampling) would provide an effective method for establishing the range in variation through time for that particular site. If the 2004-2005 death assemblages are treated as replicate samples, then the range of variability they display in Figure 5 can be used as a model to predict the expected variability of other individual sampling locations within Copano Bay.

Variability of Death Assemblage Diversity

A concern for paleoecologists is how well single-census death assemblages (those based on one collection) represent the entire population of possible death assemblages from which they were derived (e.g., Bennington, 2003; Holland, 2005; Webber, 2005). Death assemblages are expected to be homogenized and relatively stable due to the mixing of multiple living communities during long-term time averaging, suggesting that they can be treated as steady-state systems. However, recent research has indicated that time-averaged assemblages are not simply a homogenized mix of shells and that death assemblages may be more dynamic than previously thought (e.g., Meldahl et al., 1997). In order to test whether single-census death assemblages should be treated as stable or varying systems, the evenness and richness of the 1981-1982 and 2004-2005 datasets were compared at both the six-week sampling interval within each study and the 22-year interval separating the two studies. If the richness and evenness of the 1981-1982 and 2004-2005 datasets show little variation at the six-week time scale, and are the same after 22 years, then single-census death assemblages can be treated as representative samples of stable systems at these scales. However, if the richness and evenness of the 1981-1982 and 2004-2005 datasets vary greatly at the six-week time scale, and are significantly different after 22 years, then single-census death assemblages should be treated as samples of highly varying systems.

Time series of richness of live and dead assemblages are shown in Figure 6. Student's *t*-tests for the death assemblages indicate that the richness values from the

2004-2005 dataset are significantly lower than those of 1981-1982 ($t=6.137$; $t_{\alpha=0.01,\ df=22}=2.819$); the richness values from the living 2004-2005 dataset are not significantly lower than those of 1981-1982 ($t=0.568$; $t_{\alpha=0.01,\ df=22}=2.819$).

To correct for the influence of sample size differences on richness, the live and dead assemblages were rarefied to a sample size of ten individuals for the living assemblages and 400 individuals for the death assemblages. These sample sizes were the smallest shared sample sizes common to both the 1981-1982 and 2004-2005 datasets. Several of the individual samples in the living community contained only one species, and thus could not be rarefied (8/81, 12/81, and 3/82). Additionally, two individual samples in the living community were of insufficient sample size (<10) and also could not be rarefied (9/81 and 1/82). Despite rarefaction, the richness values from the 2004-2005 death assemblages remained significantly lower than those of the 1981-1982 dataset ($t=8.617$; $t_{\alpha=0.01,\ df=22}=2.819$).

Like richness, the 2004-2005 dataset was found to be less even, using Hurlbert's PIE (Probability of Interspecific Encounter), than the 1981-1982 dataset (Figure 7). Hurlbert's PIE ($PIE=[N/(N-1)][1-\Sigma^{S}{}_{i=1}\, p_i^2]$ where N=sample size, S=sample richness, and p_i=proportion of species i), is a sample-size independent evenness metric that is equivalent to the slope of the steepest portion of a rarefaction curve (Hurlbert, 1971; Olszewski, 2004).

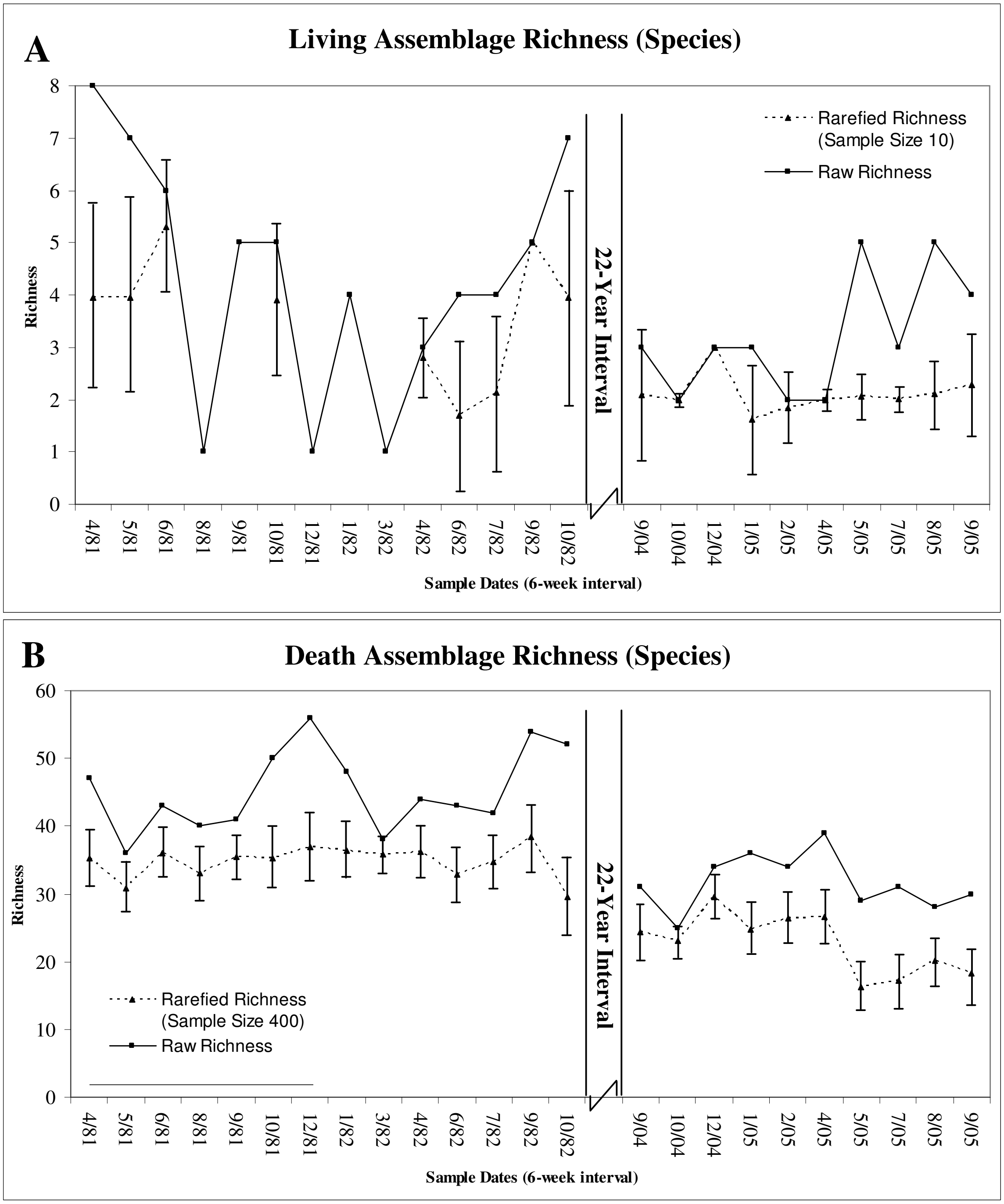

FIGURE 6—Live (A) and dead (B) assemblages of Copano Bay, Texas, listed in order of the date collected. Error bars show 95% confidence intervals. Richness was rarefied to a sample size of 10 individuals for the live and 400 individuals for the dead.

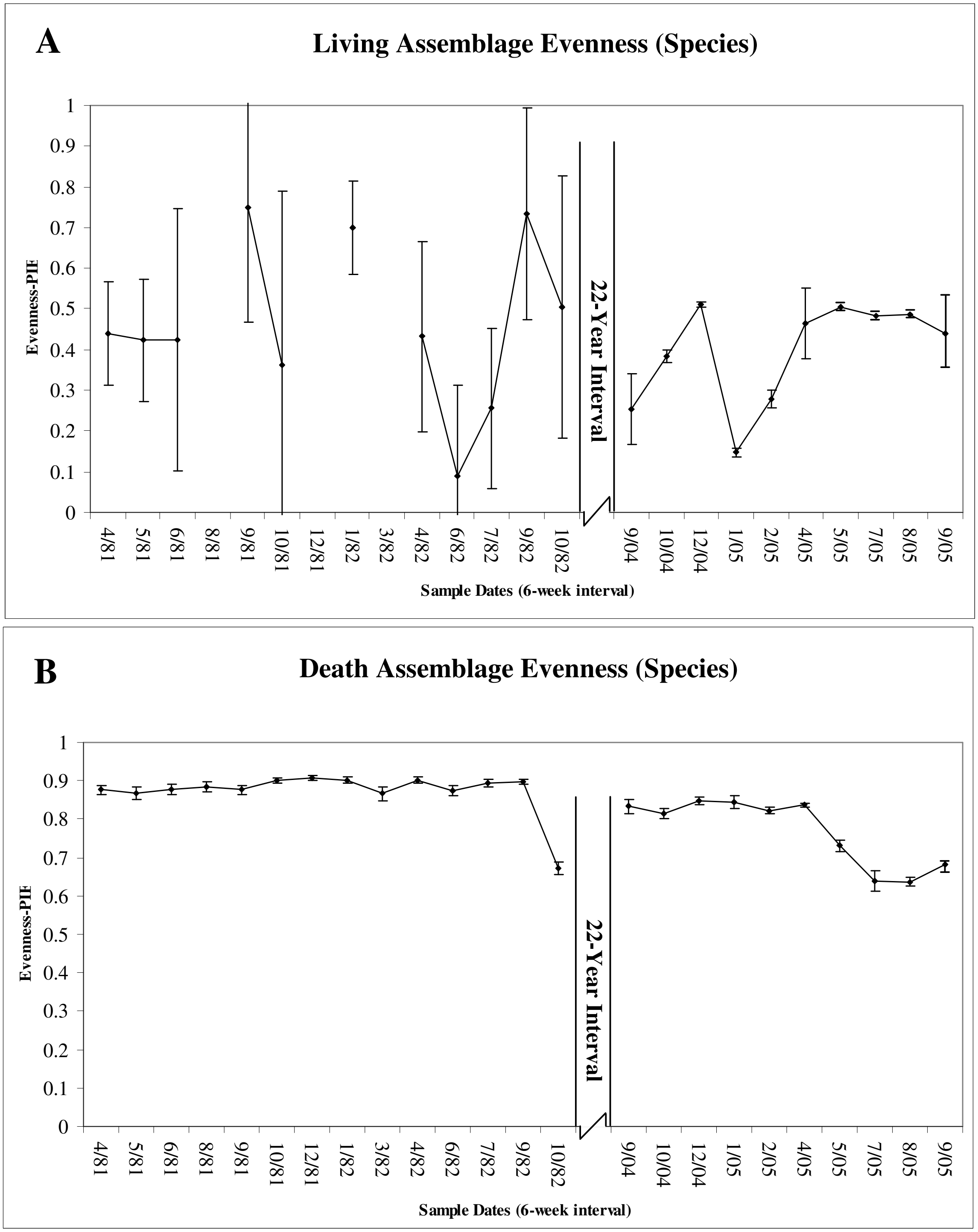

FIGURE 7—Evenness (Hurlbert's PIE) of live (A) and dead (B) assemblages of Copano Bay, Texas, listed in order of the date collected. Gaps in the living assemblage data (A) are caused by complete dominance of one species. Error bars show 95% confidence intervals. The live and dead assemblages of 1981-1982 are more even than those of 2004-2005.

Hurlbert's PIE ranges from zero (complete dominance) to one (complete evenness) (Hurlbert, 1971). Student's *t*-tests for both the live and dead assemblages confirmed that the evenness values from the 2004-2005 collection are significantly lower than those of 1981-1982 (Figure 7; Live: $t=2.07$; $t_{\alpha=0.01,\ df=22}=2.819$; Dead: $t=3.49$; $t_{\alpha=0.01,\ df=22}=2.819$).

Large drops in both richness and evenness occurred in the last four samples of the 2004-2005 dataset (5/05, 7/05, 8/05, 9/05; Figures 6 & 7), which can primarily be attributed to overwhelming dominance of *Mulinia lateralis*, *Texadina sphinctostoma*, and *Diastoma varium*. In order to test whether the drop in both richness and evenness within the 2004-2005 dataset could reflect spatial rather than temporal influences (given the previously recognized spatial gradient in substrate and composition), the sites were arranged in geographic order along the transect (Figures 8 & 9). Figures 8 and 9 revealed that although samples 7/05, 9/05, and 5/05 were located near one another at one end of the transect, sample 8/05 was located near the other end, indicating that the sites are not similar simply due to close spatial proximity. Unfortunately, the position along the transect for each collection in the 1981-1982 dataset is unknown, so it is not possible to repeat this analysis for the earlier dataset.

Variation in richness and evenness (Hurlbert's PIE) of death assemblages was found to occur at two time scales: 1) the six-week scale of the 1981-1982 and 2004-2005 studies and 2) the 22-year period separating the studies. These results indicate that single-census death assemblages should be treated as varying, rather than stable, systems.

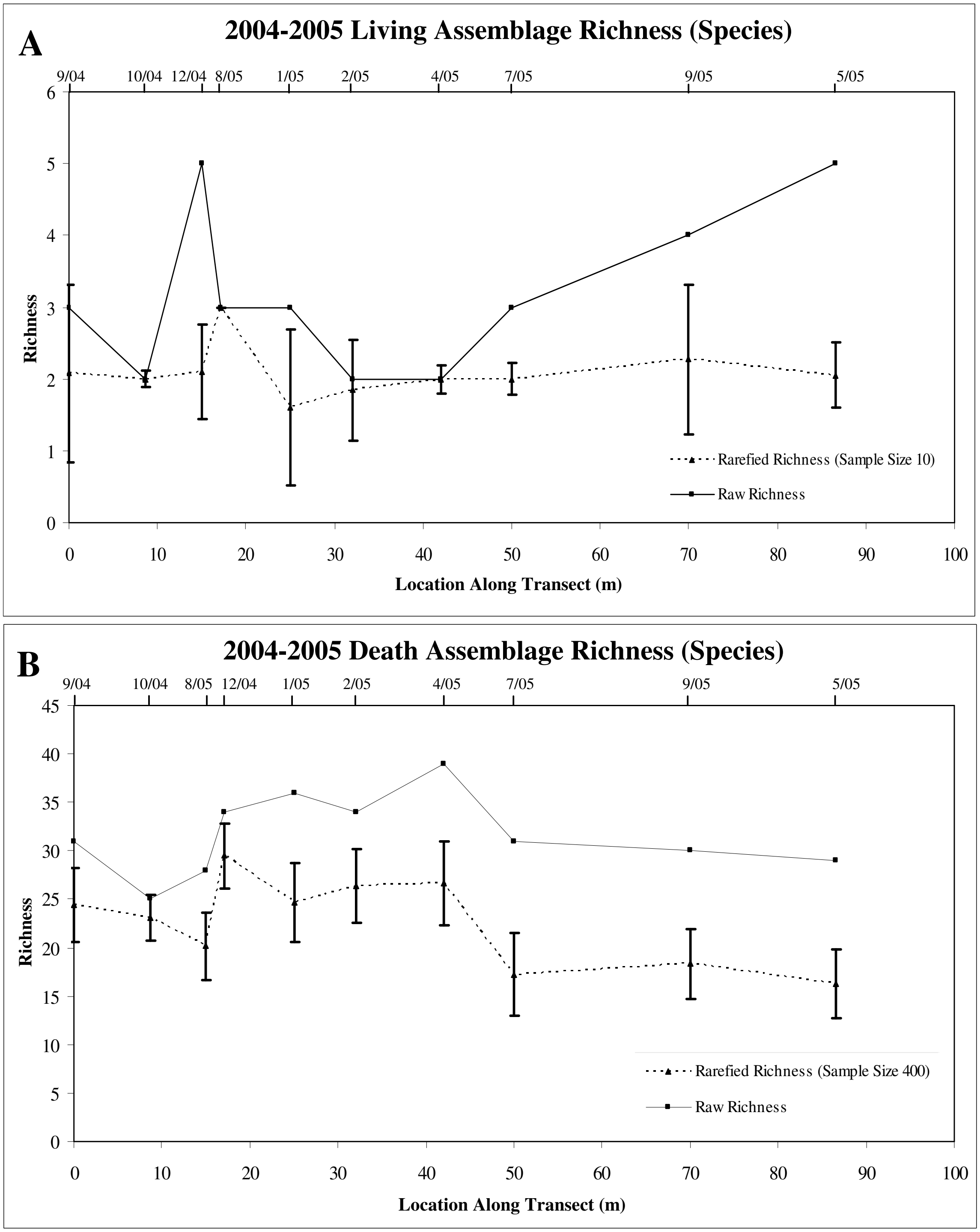

FIGURE 8—Richness of the 2004-2005 live (A) and dead (B) assemblages arranged in geographic order along the transect (as opposed to the date they were collected). Error bars represent 95% confidence intervals.

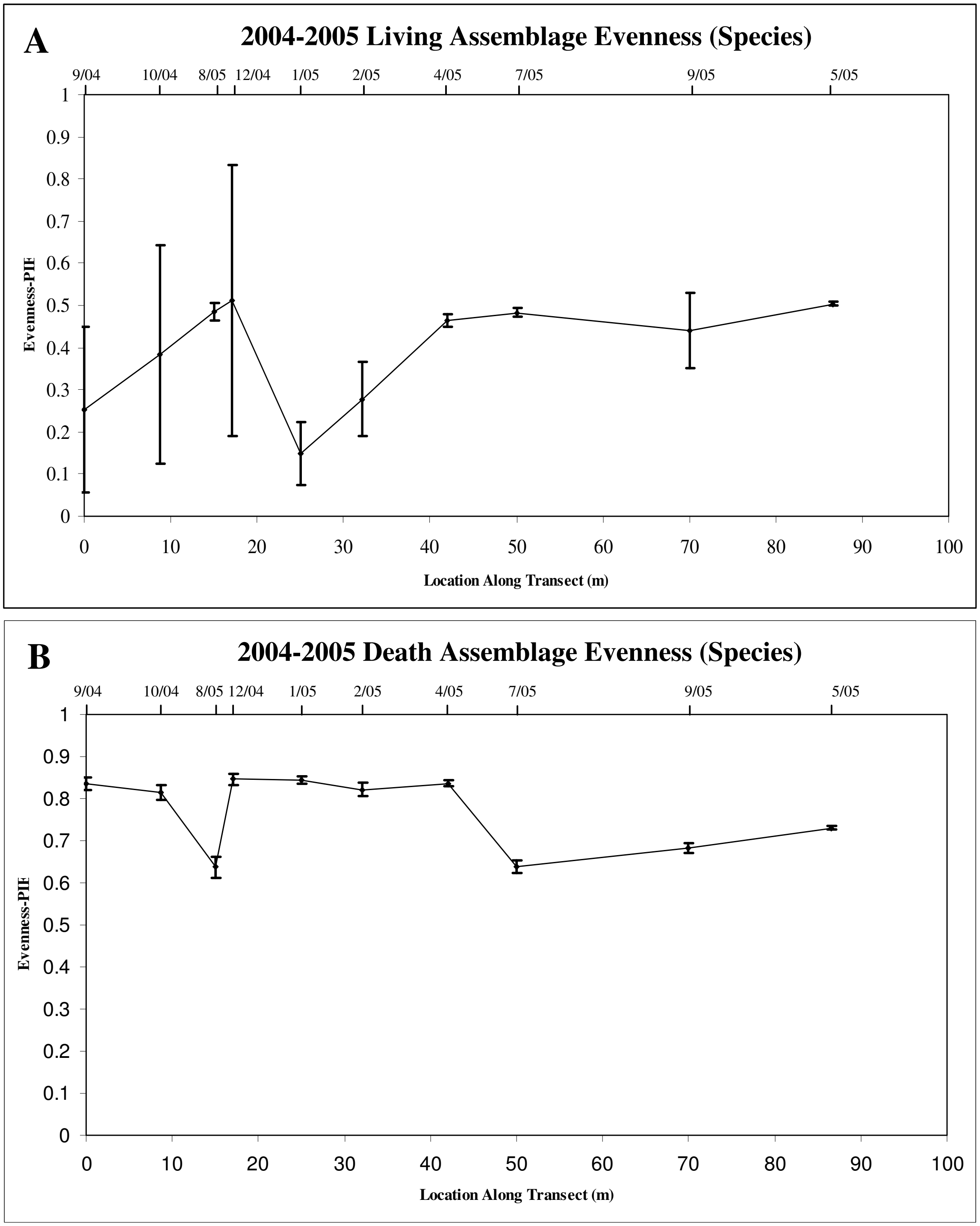

FIGURE 9—Evenness (Hurlbert's PIE) of the 2004-2005 live (A) and dead (B) assemblages arranged in geographic order along the transect (as opposed to the date they were collected). Error bars represent 95% confidence intervals.

Effect of Death Assemblage Composition on Cumulative Diversity

Total diversity can be partitioned into additive components in order to evaluate spatial patterns in species diversity (Lande, 1996; Veech et al., 2002). A diversity metric can be partitioned as long as its value for summed individual samples (ΣPIE) is greater than the weighted mean of the individual values (µPIE) (Lande, 1996). If the composition of individual samples differs from the whole more than expected by random chance, µPIE will be significantly smaller than ΣPIE. To test whether changes in the composition of the 1981-1982 and 2004-2005 datasets represent significant community change, the summed samples (ΣPIE) were compared to the mean of individual sample values (µPIE) (Table 4).

For both the 1981-1982 and 2004-2005 datasets, the evenness of the summed samples (ΣPIE) was greater than the mean of individual sample values (µPIE) at both the genus and species levels, suggesting compositional variation (Table 4). However, this difference is not significant, indicating compositional differences among samples *within* the 1981-1982 and 2004-2005 datasets cannot be distinguished from random variation among samples from the same community.

The differences between average evenness (µPIE) and summed evenness (ΣPIE) are similar between live and dead datasets. This result suggests that the death assemblages are not homogenized any more than the living community; this is unexpected because extended time averaging is hypothesized to cause death assemblages to become homogenized from the mixing of multiple assemblages (Warme et al., 1976).

TABLE 4—Sample size (N), richness (S), and evenness metrics for the 2004-2005 and 1981-1982 datasets for genera (A) and species (B)

A: GENERA	**N**	**S**	**Additive PIE (ΣPIE)**	**Weighted Average PIE (μPIE)**	**Weighted Standard Deviation**	**Difference (ΣPIE-μPIE)**
1981-1982 Live	357	14	0.404	0.381	0.161	0.023
2004-2005 Live	4,822	10	0.504	0.467	0.070	0.037
1981-1982 Dead	18,886	59	0.876	0.835	0.083	0.041
2004-2005 Dead	18,159	43	0.769	0.732	0.073	0.037

B: SPECIES	**N**	**S**	**Additive PIE (ΣPIE)**	**Weighted Average PIE (μPIE)**	**Weighted Standard Deviation**	**Difference (ΣPIE-μPIE)**
1981-1982 Live	357	18	0.619	0.581	0.265	0.038
2004-2005 Live	4,822	10	0.504	0.467	0.070	0.037
1981-1982 Dead	18,886	80	0.889	0.848	0.087	0.041
2004-2005 Dead	18,159	56	0.774	0.737	0.076	0.037

Living communities should are expected to be more volatile than death assemblages due to their smaller sample sizes, patchiness of occurrence, and greater temporal independence (Warme et al., 1976; Miller and Cummins, 1990; Kidwell and Bosence, 1991).

Synopsis

1) Correspondence analysis revealed that both the 1981-1982 and 2004-2005 datasets formed distinct groups with minimal overlap, indicating that death assemblage composition in Copano Bay changed over 22 years more than expected based on short-term variation.

2) Analysis of the taxonomic composition, using the Spearman rank correlation coefficient, revealed that the rank order of the 2004-2005 assemblages has significantly changed from that of the 1981-1982 assemblages. Change in the dominant species in the living assemblages was recorded in the 2004-2005 death assemblages, indicating that death assemblages at this site are reflective of changes in taxonomic composition of the living community.

3) The 2004-2005 death assemblages of Copano Bay were found to predominantly reflect the local, rather than the entire regional, species pool. However, species from non-local habitats were included in the 2004-2005 death assemblages, requiring at least some mixing.

4) Change in richness and evenness (Hurlbert's PIE) was found to occur at two time scales: 1) the six-week scale of the 1981-1982 and 2004-2005 studies and 2) the 22-year period separating the studies, indicating that the death assemblage at the study site should not be treated as a steady-state system.

5) Comparing average evenness (μPIE) and summed evenness (ΣPIE) of both live and dead assemblages revealed that the death assemblages are not homogenized any more than the living community despite their greater size and diversity.

DISCUSSION

Long-term differences between the 2004-2005 and the 1981-1982 datasets, and the short-term differences within them, suggest that single-census death assemblages are variable and cannot be treated as stable systems. The amount of volatility in the death assemblages of Copano Bay indicates that it is possible for death assemblage composition and diversity to rapidly change as a result of volatility in the living community.

Aspects of the physical environment, such as water temperature, salinity, dissolved oxygen (Figure 10), and stream discharge (Figure 11), could not be linked to the variability of the living community or fluctuations in mortality over the duration of this study. Analysis of water temperature, salinity, dissolved oxygen, and stream discharge data prior to 1981-1982 also discounted the potential of a lagged community response in the 1981-1982 dataset. Additionally, since Copano Bay remains relatively secluded from human influences, major water quality pollution events have not been recorded in Copano Bay since the 1940's to early 1970's when oil-field brine was being discharged into the bay through the Aransas River (Mosely and Copeland, 1974). Interestingly, the discharge of the brine had no long-term effects on salinity (Staff et al., 1986). Currently, only large changes in abundances of *Texadina sphinctostoma* and *Mulinia lateralis* can be linked to changes in evenness of the 2004-2005 dataset; although *Mulinia lateralis* exists in a wide variety of salinity conditions (5‰-80‰), *Texadina sphinctostoma* is indicative of lower salinity conditions (3‰-8‰) (Parker, 1960; Calnan, 1980).

In principle, long-term time averaging can significantly alter the diversity and composition of death assemblages, relative to corresponding living assemblages, through the mixing of communities from different sites and habitats (Cummins et al., 1986a). The presence of a compositional gradient within the 2004-2005 death assemblages indicates that long-term, continuous time averaging in Copano Bay is negligible during death assemblage accumulation because compositional gradients are not expected to be preserved in death assemblages due to the mixing of multiple communities and community states. However, the presence of *Brachidontes exustus* and *Ischadium recurvum,* species that prefer a hard substrate as opposed to the muddy substrate of the sampling area, indicate that at least some transportation between different habitats must be occurring.

Additionally, the lack of homogenization of death assemblages seen in the diversity partitioning analysis also suggests that time averaging is minimal in Copano Bay. Diversity partitioning indicated that the variation between average and summed evenness is not greatly different between the live and dead datasets, suggesting that the death assemblages are not homogenized any more than the living community. Death assemblages are expected to be more homogenized and

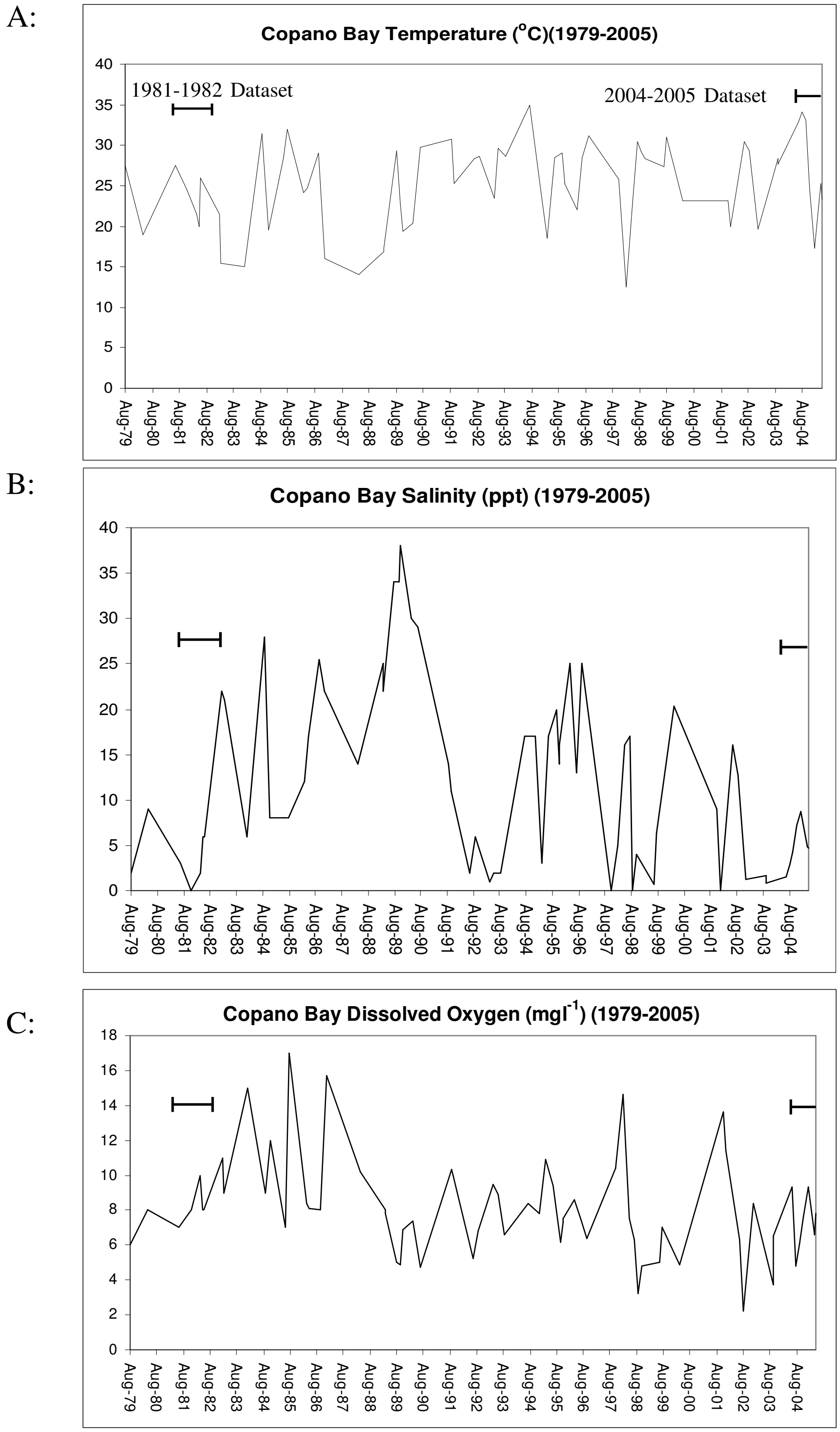

FIGURE 10—Water temperature (A), salinity (B), dissolved oxygen (C) for Copano Bay. Data for last four samples of the 2004-2005 dataset (5/05, 7/05, 8/05, 9/05) were not available at the time these graphs were produced. Data were roughly collected at tri-yearly intervals (Martinez-Andrade et al., 2005).

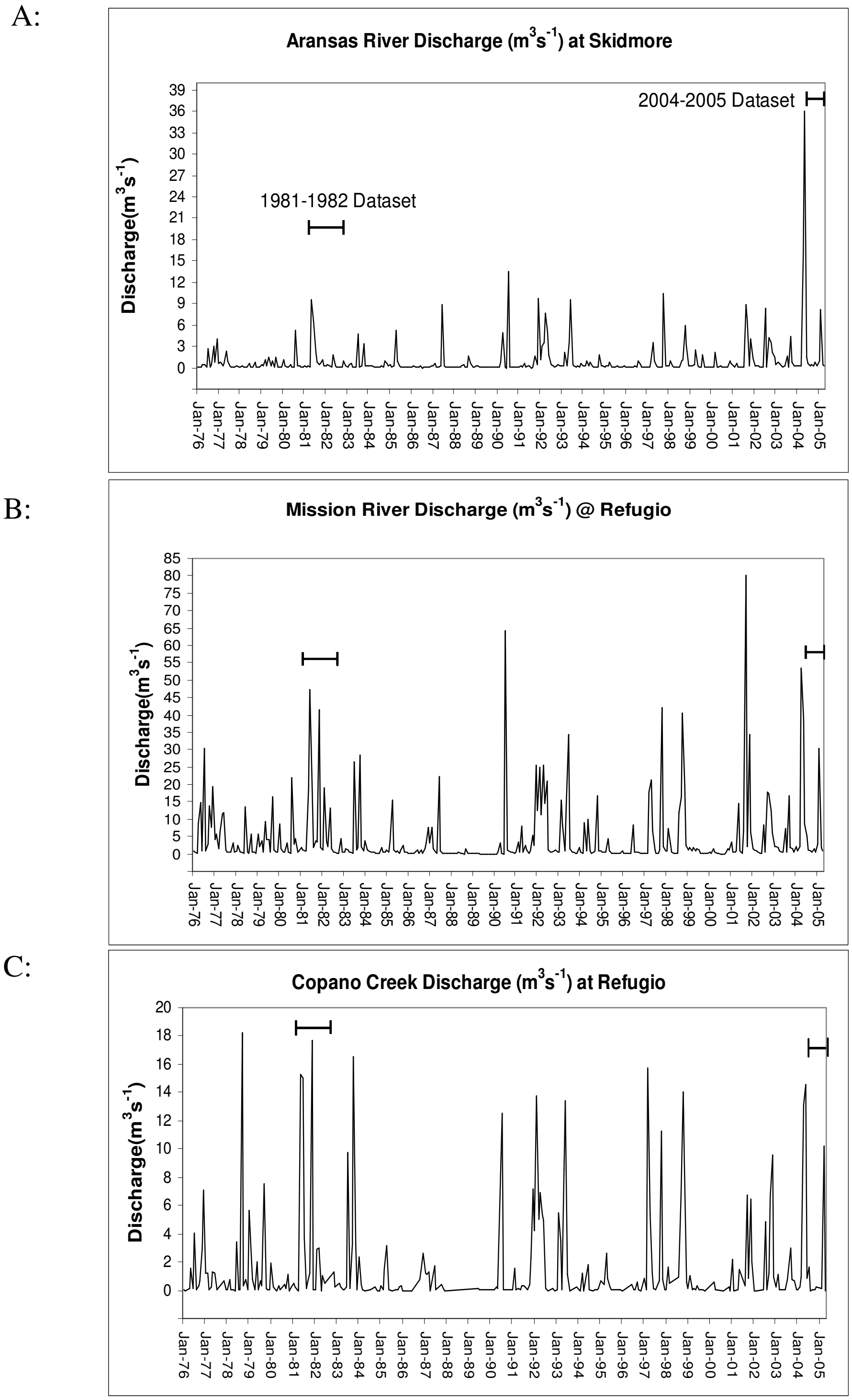

FIGURE 11—Stream discharge in cubic meters per second (m^3s^{-1}) for the Aransas River (A), Mission River (B), and Copano Creek (C). Data were obtained from the United States Geological Survey (2005). Data are reported at monthly intervals.

relatively stable in comparison to living communities due to the mixing of multiple communities during long-term time averaging; this lack of homogenization in the death assemblages may indicate that time averaging is negligible.

Conversely, the large collection sizes of the death assemblages, relative to the small sample sizes of the living community from the same volume of sediment, suggests that significant time averaging has occurred; mixing over time or influx due to transportation are needed in order reconcile the accumulation of large death assemblages relative to a small living community. The 2004-2005 living community is 0.25 times of the size of the corresponding death assemblage while the 1981-1982 living community is only 0.02 times of the size of the corresponding death assemblage. However, numerous studies have reported that living communities are often patchy and difficult to accurately sample (Warme et al., 1976; Miller and Cummins, 1990; Kidwell and Bosence, 1991) suggesting that neither the 1981-1982 nor the 2004-2005 datasets may have fully captured the extent of variation in the living community. A better understanding of the spatial patchiness of living communities within Copano Bay may reveal whether further sampling of the living community could result in larger, more adequate, sample sizes of the living community.

The death assemblages of Copano Bay should be relatively small based on rapid rates of shell dissolution calculated by Powell et al. (1984). Powell et al. (1984) observed molluscan shell half-lives (time required for the destruction of 50% of the individuals added to a death assemblage), in Texas lagoons to be as rapid as 40 days for individuals <3mm in size. Even the longest half-life (157 days) observed by Powell et al. (1984) for individuals <3mm suggests rapid shell destruction. Death assemblages should be small in Copano Bay given rapid rates of shell loss and destruction. However, the death assemblages of Copano Bay are large; in order to accrue large death assemblages with rapid rates of shell destruction, mixing of multiple communities from different sites and habitats must be contributing to and replenishing the supply of shells, suggesting a high degree of time averaging in Copano Bay.

A compositional gradient and the partitioning of diversity analysis in this study suggest minimal time averaging, while large death assemblages suggest much longer time averaging. These contradictory results could be resolved if time averaging in Copano Bay is a punctuated, rather than a continuous, process. If time averaging is a continuous process within Copano Bay, the spatial relationships of previous communities should not be preserved due to the intermixing of differing multiple communities and community states; however, a compositional gradient in the 2004-2005 death assemblages indicates that a spatial record of previous communities has been preserved.

Punctuated time averaging, potentially caused by a past record of storm events, could account for the occurrence of large death assemblages, relative to the living community. Coastal storm events in Copano Bay cover a variety of different wind regimes ranging from frequent (seasonal) rapidly moving polar fronts to infrequent (decadal) hurricanes (Simpson and Lawrence, 1971). These storm events have the potential to increase species richness through transportation and rapidly bury shells in enough sediment to sequester them from taphonomic processes. In between these storm events, minimal admixing into the death assemblages may occur. In Copano Bay, the 2004-2005 death assemblages display a compositional gradient, indicating that these death assemblages have accumulated without major transport and disruption. However, a few species (*Brachidontes exustus* and *Ischadium recurvum*) in the 2004-2005 death assemblages do reflect habitats other than that characteristic of the sampling transect, indicating that at least some transportation between different habitats must be occurring. Minor disruptions in the accumulation of the 2004-2005 death assemblages could be explained by polar fronts, which occur in the area during the winter months and create winds in excess of 50 miles per hour (Brown et al., 1976).

Hurricane Claudette, a Category 1 hurricane, was the only hurricane on record in close vicinity to Copano Bay in the past 25 years; Claudette made landfall on the Texas Coast at Matagorda Island on July of 2003 (Sheremet et al., 2005). Hurricane frequency in the Copano Bay region was calculated to be seven percent for any one year (Simpson and Lawrence, 1971), indicating that death assemblages have the potential to accumulate without significant interruption on average for 14-year intervals within Copano Bay.

Powell et al. (1992) described two vibracores (82 and 97 cm long) collected from a locality near the sampling transect which were estimated to cover 300-400 years of community history in Copano Bay. Unfortunately, short-term events such as hurricanes were below the resolution reported in the Powell et al. (1992) study. However, Powell et al. (1992) were able to conclude, using amino acid dating techniques, that substantial time averaging was not occurring in the upper 70 centimeters of the vibracores.

CONCLUSIONS

Time averaging has been hypothesized to cause diversity of death assemblages to differ significantly from that of corresponding living communities. Long-term time averaging has the potential to allow postmortem mixing over areas much larger than the corresponding local living community, so it might be expected to result in stable, homogenized death assemblages through the mixing of multiple communities and community states, which reflect different habitats and different stages of ecological succession. However, results from this study illustrate that the composition and diversity of the death assemblages in Copano Bay, Texas can change significantly over decadal and 6-week time scales, indicating that death assemblages at the study site are not homogenized.

The presence of a compositional gradient in the 2004-2005 death assemblages suggests that time averaging is minimal in Copano Bay because compositional gradients are not expected to be preserved due the mixing of multiple communities caused by continuous time averaging. However, death assemblages much larger than corresponding living assemblages, suggest much longer durations of time averaging; mixing of the same, or potentially multiple communities, is needed in order reconcile the accumulation of large death assemblages relative to a small living community. These contradictory results could be resolved if time averaging in Copano Bay is a punctuated, rather than a continuous, process.

Punctuated time averaging, potentially caused by a past record of storm events such as polar fronts or hurricanes, could account for the occurrence death assemblages much larger than corresponding living assemblages as well as the presence of the compositional gradient in the 2004-2005 death assemblages. Large storm events can transport and bury great numbers of shells that normally would not have occurred in the study area. In between storm events death assemblages have the potential to accumulate continuously without interruption.

Understanding time averaging and its effects on death assemblages aids in the construction of modern ecologic baselines. If time averaging can be accurately quantified, then death assemblages can reliably be used to provide records of previous conditions in a particular habitat, which in turn can be used to evaluate the welfare of the habitat, establish a natural range of variation for the habitat, and aid in restoration projects. Results from this study may be applicable to a broad array of other coastal, partially enclosed, shallow-water environments.

Additionally, these results have significant implications for interpretation of the reliability of diversity and composition of local fossil assemblages. Death assemblage richness, evenness, and taxonomic abundance in Copano Bay varied significantly over a 22-year period, indicating that death assemblages, and potentially fossil assemblages, are more dynamic than previously thought. If the 1981-1982 and 2004-2005 death assemblages were to become fossilized independently of one another, then they would each reflect a significantly different community, despite the small 22-year period separating the studies. The variability of death assemblages at decadal time scales indicates that corresponding local fossil assemblages are also variable.

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APPENDIX A

2004-2005 LIVING COMMUNITY

GASTROPODS	**9/04**	**10/04**	**12/04**	**1/05**	**2/05**	**4/05**	**5/05**	**7/05**	**8/05**	**9/05**
Diastoma varium	0	0	0	0	0	0	0	1	0	2
Texadina sphinctostoma	25	10	7	11	21	419	680	748	328	66
Tricola aff. Cruenta	0	0	0	0	0	0	1	0	0	0
BIVALVES										
Brachidontes exustus	0	0	0	0	0	0	6	0	2	0
Chione cancellata	0	0	1	0	0	0	0	0	0	0
Lucina pectinata	0	0	0	0	0	0	1	0	0	0
Macoma mitchelli	0	0	0	1	0	0	0	0	3	1
Mulinia lateralis	3	3	2	139	106	727	770	506	205	25
Nuculana acuta	1	0	0	0	0	0	0	0	0	0
Rangia cuneata	0	0	0	0	0	0	0	0	1	0

APPENDIX B

2004-2005 DEATH ASSEMBLAGES

GASTROPODS	**9/04**	**10/04**	**12/04**	**1/05**	**2/05**	**4/05**	**5/05**	**7/05**	**8/05**	**9/05**
Acteocina candei	33	34	40	61	39	77	93	34	26	57
Acteon punctostriatus	2	1	0	1	10	8	10	1	1	3
Alabina cerithidiodes	0	1	2	2	0	2	0	0	0	0
Boonea impressa	0	0	3	1	1	1	0	1	0	2
Caecum johnsoni	1	0	0	0	0	0	0	0	0	0
Caecum nitidum	9	6	8	12	3	12	8	5	11	5
Caecum pulchellum	31	7	29	41	18	59	52	14	10	49
Cerithidea pliculosa	0	1	0	2	1	3	0	0	0	9
Cerithiopsis greeni	0	0	0	0	0	2	0	0	4	6
Crepidula convexa	0	0	3	0	1	5	2	1	0	0
Crepidula fornicate	1	0	1	1	1	3	4	3	0	1
Crepidula plana	0	0	3	2	3	1	0	2	2	1
Diastoma varium	124	86	143	263	189	396	1448	379	132	1595
Eulimastoma cf. E. c.	0	0	0	1	0	0	0	0	0	0
Haminoea succinea	0	0	0	0	0	0	0	0	2	0
Ischnochiton papillosus	1	0	3	1	0	2	0	0	0	0
Texadina sphinctostoma	208	157	142	322	303	464	1590	562	244	554
Modulus modulus	0	0	4	3	1	4	2	3	4	2
Natica Tectonatica pusilla	0	1	0	0	0	0	1	2	0	2
Odostomia laevigata	5	4	10	20	9	35	34	11	5	22
Polinices Nererita duplicatus	0	0	0	0	1	4	1	0	0	0
Pyrgiscus cf. elegantula	0	0	0	3	2	3	1	0	0	0
Pyrgiscus cf. portoricana	0	0	1	0	0	0	0	0	0	1
Sayella sp A	0	0	1	0	0	0	0	0	0	0
Seila adamsi	1	0	0	1	7	6	0	1	0	0
Solariorbis blakei	1	4	4	8	0	7	1	4	2	3
Tricola aff. Cruenta	0	1	1	0	1	0	2	3	0	0
Truncatella caribaeensis	0	0	0	0	0	1	8	3	0	32
Turbonilla strioturb.cf T.h.	0	0	0	0	0	0	0	0	0	1
Vermicularia cf. V spirata	0	0	1	1	1	0	3	0	1	0
Vitrinella floridana	7	0	2	5	0	2	24	0	0	0
BIVALVES										
Anomalocardia auberiana	1	0	0	0	0	0	0	1	0	0
Argopecten irradians	0	1	1	0	0	0	0	0	1	0
Brachidontes exustus	36	33	35	97	68	144	111	46	32	70
Carditamera floridana	1	0	0	0	0	0	0	0	0	0
Chione cancellata	19	16	18	46	17	39	44	19	19	33
Chione clenchi	1	0	0	0	0	0	0	0	0	0
Chione intrapurpurea	0	8	8	12	11	14	14	5	6	8
Congeria leucophaeta	0	0	1	0	3	0	0	0	0	0
Cumingia tellinoides	0	1	2	0	0	5	6	2	1	8

	9/04	**10/04**	**12/04**	**1/05**	**2/05**	**4/05**	**5/05**	**7/05**	**8/05**	**9/05**
Ischadium recurvum	0	2	0	1	1	2	6	0	1	1
Laevicardium mortoni	0	7	0	0	1	0	0	7	43	43
Lucina pectinata	0	0	1	4	8	10	26	5	3	7
Macoma constricta	0	0	0	0	0	1	0	0	0	0
Macoma mitchelli	2	4	7	24	18	26	41	6	9	23
Macoma tagelifromis	2	0	3	1	0	4	0	12	0	0
Mactra fragilis	1	0	0	2	3	1	0	0	0	0
Mulinia lateralis	147	139	156	264	137	408	1525	1306	776	639
Musculus lateralis	2	0	0	1	2	0	0	0	0	0
Mysella planulata	1	0	0	0	0	0	0	0	0	0
Nuculana acuta	15	6	21	29	16	31	23	7	17	20
Rangia cuneata	14	8	6	14	2	4	1	2	1	1
Rangia flexuosa	6	0	0	18	24	64	0	0	0	0
Tagelus divisus	1	0	0	0	0	0	0	0	0	0
Tagelus plebius	46	8	4	32	26	18	8	3	9	11
Tellina Ang.texana	1	4	6	1	3	8	0	1	9	0
Dentalium tex.	1	0	1	1	0	1	0	0	1	0

APPENDIX C

TABULATED LIST OF SPECIES MEMBERSHIP FOR BOTH LIVE AND DEAD SPECIES OF THE 1981-1982 AND 2004-2005 DATASETS

Species	**Present Live 1981-1982**	**Present Live 2004-2005**	**Present Dead 1981-1982**	**Present Dead 2004-2005**
GASTROPODS				
Acteocina candei	X		X	X
Acteon punctostriatus	X		X	X
Alabina cerithidiodes				X
Anachis avara			X	
Boonea impressa			X	X
Bulla impressa			X	
Caecum johnsoni			X	X
Caecum Lutosum			X	
Caecum nitidum			X	X
Caecum pulchellum	X		X	X
Cerithidea pliculosa			X	X
Cerithiopsis greeni			X	X
Cerithium lutosum			X	
Circulus suppressus			X	
Crepidula convexa			X	X
Crepidula fornicata			X	X
Crepidula plana			X	X
Cyclostremella sp.			X	
Diastoma varium	X	X	X	X
Eulimastoma cf. E. c.				X
Fargoa dianthophilia			X	
Haminoea succinea			X	X
Ischnochiton papillosus				X
Lucapinella limatula			X	
Mitrella lunata			X	
Modulus modulus			X	X
Nassarius vibex			X	X
Natica Tectonatica pusilla				X
Odostomia barretti	X		X	
Odostomia bartschi			X	
Odostomia c.f. teres	X		X	
Odostomia seminuda			X	
Odostomia weberi	X		X	
Odostomia laevigata				X
Polinices Nererita duplicatus				X
Pseudosyrena floridana			X	
Pyrgiscus cf. elegantula				X

Species	**Present Live 1981-1982**	**Present Live 2004-2005**	**Present Dead 1981-1982**	**Present Dead 2004-2005**
Pyrgiscus cf. portoricana				X
Rissoina catesbyana			X	
Sayella sp A	X		X	X
Seila adamsi			X	X
Solariorbis blakei				X
Syrnola sp. A			X	
Teinostoma lerma			X	
Texadina sphinctostoma	X	X	X	X
Tricola aff. Cruenta		X	X	X
Tricola sp.	X		X	
Triphora perveria			X	
Truncatella caribaeensis			X	X
Turbonilla acicula			X	
Turbonilla interupta			X	
Turbonilla speira			X	
Turbonilla wrightsvillensis			X	
Turbonilla strioturb.cf T.h.				X
Vermicularia cf. V spirata				X
Vermicularia fargoi			X	
Vitrinella floridana			X	X
Vitrinella thomasi			X	
BIVALVES			X	
Abra equalis			X	
Aligena texasiana			X	
Amygdalum papyria			X	
Anadara sp.			X	
Anomalocardia auberiana			X	X
Anomia sp.	X		X	
Argopecten irradians			X	X
Brachidontes exustus	X	X	X	X
Carditamera floridana			X	X
Chione cancellata		X	X	X
Chione clenchi				X
Chione intrapurpurea				X
Congeria leucophaeta				X
Crassostrea virginica			X	
Cumingia tellinoides			X	X
Cytopleura costata			X	
Diplodont sp.			X	
Ensitellops sp.	X		X	
Gemma sp.			X	
Ischadium recurvum				X
Laevicardium mortoni			X	X
Lucina pectinata		X		X
Lucinid sp. A			X	

Species	**Present Live 1981-1982**	**Present Live 2004-2005**	**Present Dead 1981-1982**	**Present Dead 2004-2005**
Lucinid sp. B			X	
Macoma constricta			X	X
Macoma mitchelli	X	X	X	X
Macoma tagelifromis				X
Mactra fragilis			X	X
Montacula SP.			X	
Mulinia lateralis	X	X	X	X
Musculus lateralis				X
Mysella planulata			X	X
Nuculana acuta		X	X	X
Nuculana concentrica			X	
Rangia cuneata	X	X	X	X
Rangia flexuosa			X	X
Spissula solidissima			X	
Tagelus divisus				X
Tagelus plebius	X		X	X
Tellina Ang.texana			X	X
Tellina tampaensis			X	
Dentalium tex.				X

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