THE MARTYRDOM OF ST. LUCIE: DECIMATION OF A MEIOFAUNA

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ABSTRACT

St. Lucie, the southernmost inlet of the Indian River Lagoon, Florida, is affected by a variety of stresses including dumping from Lake Okeechobee, the second-largest freshwater lake in the U.S., through a system of canals. Foraminifera, a major component of the meiofauna, are utilized as a source of nutrition by a large assortment of deposit feeders in this area. Just as pollutants, spills, and organic enrichment are obvious sublethal effects of estuarine health, so too is the disappearance of organisms constituting essential links in the food web. Because the meiofauna is at the base of the food web, the consequences of major declines and local extinctions clearly are indicators of serious damage to the health of the entire ecosystem. To establish a baseline, foraminiferal density, species richness, evenness, and community structure were examined in 1975/1976. Thirty years later in 2005, the same area was re-sampled. In 1975/1976 the mean density was 280 per 20 ml of sediment. In 2005, we observed a mean of 46 per 20 ml, a decline of 83%. In 1975/1976, we observed 62 species while in 2005 we observed 13, a decline of 79%. The most abundant species constituted 42% of the fauna in 1975/1976; by 2005 it had risen to 76%, a dramatic increase in dominance. Based upon our newly-developed three-stage evaluation system of ecosystem decline over time, we find that the St. Lucie area is nearing, if not at, the beginning of Stage 3 (local extinction).

In the fourth century, the purportedly rich and beautiful Lucia de Syracuse was tortured and martyred. Now, 17 centuries later, the beautiful Inlet and area named after her is close to suffering the same fate. The Indian River Lagoon (IRL), the most diverse estuary in North America (Swain et al., 1995), extends 156-mi from New Smyrna Beach in Volusia County, Florida to Jupiter Inlet in Palm Beach County, Florida. There are four major inlets in the IRL: Sebastian, Jupiter, Ft. Pierce, and St. Lucie. The latter is the subject of this investigation (Fig. 1).

Naturally during the change of seasons from rainy to dry, estuaries are known to receive an excess of fresh or salt water. Extraordinary occurrences like major storms can lead to excessively high variability in the fresh-salt water cycle and in turn can result in suppression of diversity (Lauff, 1967); those species that cannot tolerate high salinity variance (Sime, 2005) die off or cannot reproduce, while freshwater species have little chance to establish. Alternatively, many species are uniquely suited for this environment and have adapted well to these natural cycles.

However, human influences also affect the balances. At present the IRL (Virnstein, 1990; Virnstein and Morris, 1996), and in particular, the area of the southernmost inlet at St. Lucie, experiences an extremely wide variability from both natural and synthetic systems in variables such as salinity (Sime, 2005) and dissolved oxygen levels (www.sfwmd.gov). Beginning in the 1920s, the areas west of the St. Lucie Inlet were drained into the IRL for agricultural purposes. Much of the water that supports the IRL estuarine system in south Florida is supplied by a series of canals built in the late 1940s. The canal at St. Lucie (C-44) was built during 1916–1928, while the entire system of canals began after 1947. This canal system protects the area from flooding and supplies water for agriculture, residential, municipality, and industrial
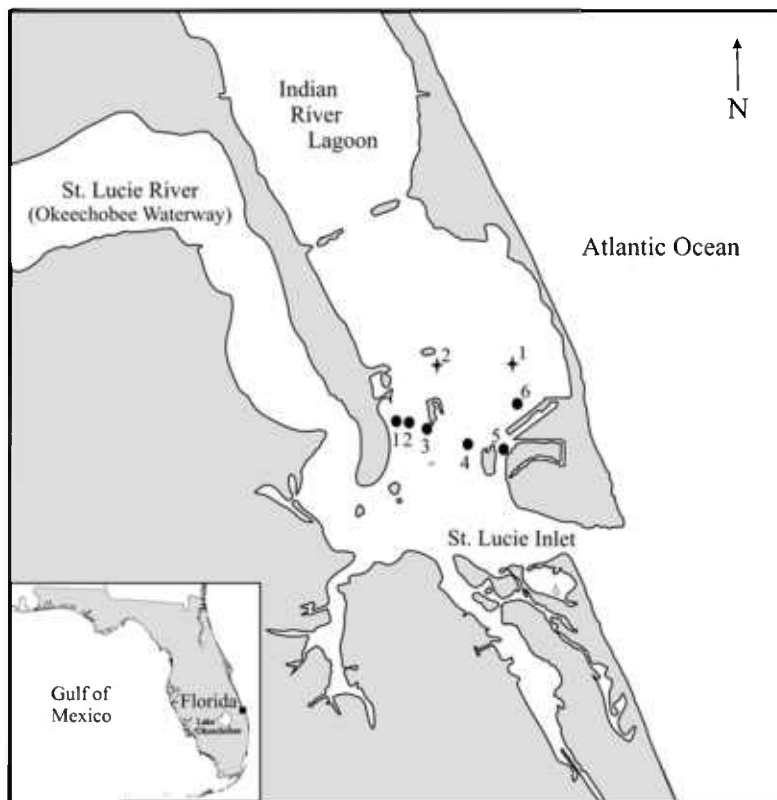
Figure 1. Location map. Stations 1, 2, 3, 4, and 5 (points) of the St. Lucie transect were sampled with two replicates each in February 1976. Station 6 was sampled with four replicates in June 1975. Stations 1 and 2 (stars) were sampled with 4 four replicates each in July 2005.

use (Sime, 2005). However, the canal system also has increased the land area that feeds water into the inlet and estuary, thus allowing natural phenomena like storms to force water into the estuary areas faster and with a stronger pulsating action. In particular, the St. Lucie has been artificially connected to Lake Okeechobee for purposes of water and flood control (www.sfwmd.gov).

Further affecting water quality, dikes for mosquito control were established, while with population increase came increased wastewater, discharges, pollutant saturation, and in turn, algae overgrowth and seagrass destruction, all of which have been documented from that time through the present (www.riverscoalition.org; Sime, 2005). The result of this forcing and unnatural infusion of fresh pollutant-saturated water into the IRL environment has been losses in seagrass and bivalves (www.rivercoalition.org), diminished recruitment (Gaines and Bertress, 1992), and diseased and dying fish and other organisms (www.sfwmd.gov; www.floridaoceanographic.org/riveralert.html; Sime, 2005). In polluted areas, the frequency of abnormalities increases over time (Gassman et al., 1994; Fournie et al., 1996; Browder et al., 1997; Sime, 2005 and references therein). Early in the 1970s, this naturally regulated environment became almost totally influenced by human activity with over 75% of the salt marshes found to be dead by the end of that decade (www.sjr.state.fl.us).

In 1975 and 1976, as part of an extensive foraminiferal survey program throughout the entire IRL, Buzas and Severin (1982) sampled, with replicates, the St. Lucie area, providing baseline data for future work (Fig. 1). The purpose of the present study is to document and assess the dramatic ecological situation at the St. Lucie Inlet area both at the beginning of the affected period and at present. There has been little, if any, investigation of the basic chains of life, predator-prey dependencies, or the extent of sublethal effects within this system. Such investigation ought to involve the bottom of the food web rather than just the obvious effects recognizable in the top-level organisms. Buzas (1978, 1982) and Buzas and Carle (1979) assessed the importance of the foraminifera as food source for a wide range of predators throughout the IRL. These predators included major commercial species from fish to crab to shellfish as well as a myriad of macrofaunal organisms. The health of the components of the meiofauna as lower order prey has not been investigated at St. Lucie since 1975/1976 and here we rectify the situation.

Methods

Field Sampling.—The sampling plan for the entire IRL area from Haulover in the north to St. Lucie in the south allowed for a combination of replicates taken at single stations and multiple samples taken along a transect at multiple stations. At each transect station, two replicate cores were obtained. Four benthic foraminiferal samples were collected in June 1975 at St. Lucie Inlet station. Using available resource maps at that time, coordinates were given by Buzas and Severin (1982) as 27°11.0′ N/80°10.1′ W. In February 1976, 10 replicate samples (two from each of five stations) were obtained from a transect at St Lucie with coordinates given as 27°10.9′ N/80°11.2′ W (Fig. 1). Detailed field methods for this study are presented in Buzas and Severin (1982).

In July 2005, two sets of four replicate cores were obtained from the same general area as those from the baseline study. However, over the 30 yrs, technology has changed and GIS systems have become available. Therefore, the coordinates of the stations are more precise: 27°11.121′ N/80°10.079′ W and 27°11.468′ N/80°10.800′ W (Fig. 1). All sample cores were inserted by hand and returned to the Smithsonian Marine Station at Ft. Pierce, Florida (SMS) laboratory for processing.

Laboratory Methods.—Laboratory methods for the 1975/1976 baseline study and 2005 study adhere to standard micropaleontological procedures. In both of these studies 20 ml (top 2 cm of sediment) were removed from the core, washed over a 63 μm sieve, stained with rose Bengal, washed again, floated in sodium polytungstate to remove the quartz sand, washed again, and placed wet in Petri dishes. Live (stained) foraminifera were then picked with a fine brush, placed on slides, enumerated, and identified. For the 2005 sampling, a preliminary examination of the first two sets of samples took place at the SMS after which all samples were shipped to the foraminiferal Laboratory at National Museum of Natural History (NMNH) for final analysis.

Statistical Methods.—Data were analyzed with both SYSTAT and SPSS (version 13.0). Formulae required for some calculations were written and executed in Mathcad 12. SHE analysis, used to identify community structure, was run on a program written by P. Karlsson (SMS) and L. Runsten (SMS) and C. Grand Pre (East Carolina State Univ.). The program is available from the authors by request. SHE analysis (Buzas and Hayek, 1996; Hayek and Buzas, 1997) is a succinct and efficient way of examining biodiversity changes over time by accumulating the observed sample results and producing familiar (Colwell et al, 2004) species accumulation curves. A cumulative S, or total observed sample richness, is obtained with accumulating N as new species are encountered in each successive sample. For example, if we

found 10 species in the first 100 individuals and then found two additional species in the next 100 individuals our cumulative entries for S and N would be: 10, 100, and 12, 200.

In addition, for each successively accumulated value of N, a value for the information function (H) and the logarithm of a measure of evenness for that assemblage (lnE) is also obtained. In 1996 Buzas and Hayek provided the basis for the integration of biodiversity study when they showed that H = lnS + lnE, which effectively separated richness and evenness within a single community. Because lnS, the logarithm of species richness, is a function of the sample size lnN, in turn H and lnE also were shown to be functions of lnN. The measure of evenness we have chosen to present in this paper is the well-known $E = e^H / S$ (Buzas and Gibson, 1969), where H is the information function and S denotes species richness. Consequently, through the unified mathematical framework of Buzas and Hayek (2005) we are able to examine the entire ensemble of biodiversity; namely, density, species richness, evenness, and compound diversity in a single diagram we introduce and call a Biodiversity-gram (BDG). General linear models for species density comparisons utilized natural log (n+1), where n represents the number of individuals of each species.

RESULTS

In 1975/1976, throughout the IRL there were 94 living species representative of 47 genera observed (Buzas and Severin, 1982). Mirroring the IRL as a whole, the most abundant 15 species at St. Lucie Inlet area likewise comprised approximately 95% of the living population of forams. At St. Lucie Inlet locations there were 3917 individuals (in 14 20-ml samples) representing 62 species and 37 different genera. The counts are given in Buzas and Severin (1982).

Data from 1975/1976 were used to construct a BDG (Fig. 2). Ecologists have long realized that the number of species observed is a function of the number of individuals (for a review see, Hayek and Buzas, 1997). In 1975/1976, the 3917 individuals counted in 14 (20 ml each) sediment samples gave a mean number per sample of 279.8. In 2005, eight sediment samples were taken with an observed mean value of 46.3 per sample for a total of 371 individuals. The number of individuals expected in 2005 based upon the initial sample period would be (279.8 × 8) or 2238. Counts for species found in 2005 samples are given in Appendix A.

DENSITY.—Table 1 lists the mean number of individuals of each species per 20 ml sample at both sampling times in the St. Lucie area. General linear models, with time as a factor, indicated that the mean number of total living individuals changed significantly (83.4% decrease; $F_{(1,20)} = 13.94$; $P < 0.001$) from 1975/1976 to 2005. In general, each species showed significant decline over time (each $F_{(1,20)}$ was $P < 0.001$) with a large effect size (Cohen, 1977) over 0.30. Only the number of *Elphidium excavatum* (Terquem, 1875) showed no difference over time. With observed power of only 26% and a small effect size of only 0.13, *E. excavatum's* result is not surprising based upon the small sample sizes obtained. In this study, despite the fact that we were not able to reject the null hypothesis of no difference over time, we can indeed rely upon the dimensionless observed effect size measure (Cohen, 1977; Hayek and Heyer, 2005) to indicate that with increased sample size we might well observe significant difference in this species.

RICHNESS.—There were 62 species representing 37 different genera at the St. Lucie locations. By 2005, only 13 species within 10 genera were detected (Table 2). Observed richness across time decreased significantly ($F_{(1,20)} = 19.07$; $P < 0.001$). A regression of the values of lnS accumulated against those of lnN was performed on the 1975/1976
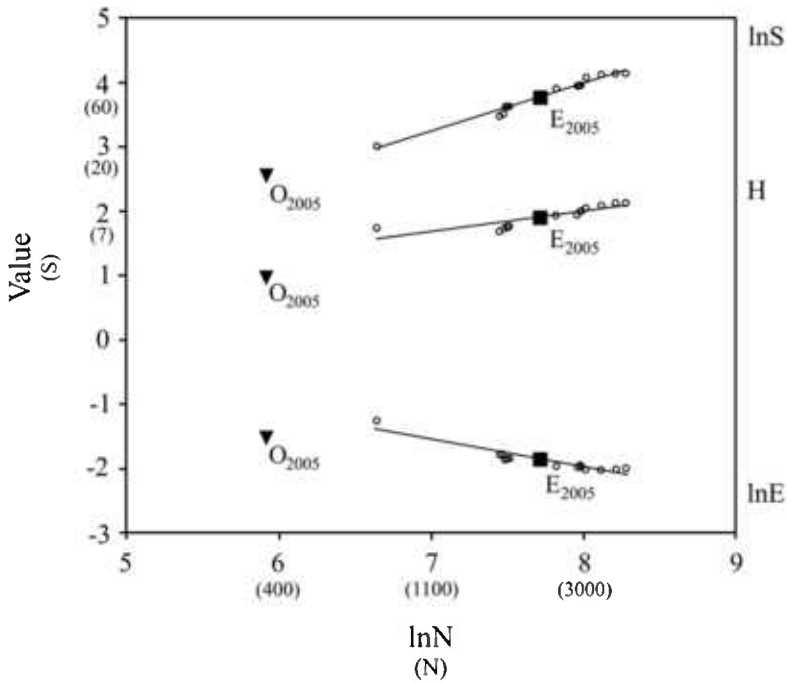
Figure 2. Biodiversity-Gram (BDG). SHE analysis for 1975/1976 foraminifera data and expected (EX) and observed (O) values for 2005. SHE analysis successively accumulates individuals for each of the 14 samples of 1975/1976, notes the logarithmic observed richness (lnS) and calculates the information function (H) obtaining the logarithmic evenness as the difference: $lnE = H − lnS$, at each of the 14 points. lnN is presented on the x-axis with corresponding values of N in parentheses. The regression lines are: $lnS = −2.05 + 0.75lnN$, $P = 0.00$, $R^2 = 0.99$; $H = −0.60 + 0.32lnN$, $P = 0.00$, $R^2 = 0.86$; $lnE = 1.45 − 0.43lnN$, $P = 0.00$, $R^2 = 0.94$; $lnS = 0.88 − 1.54lnE$, $P = 0.00$, $R^2 = 0.93$. The expected value for N in 2005 is the mean total number of individuals observed in 1975/1976 times the number of samples in 2005, $(3917/14)(8) = 2238.29$. Using this N, the expected values for 2005 of lnS, H, and lnE are calculated from the regressions given above. The observed values (O) for 2005 are the N and S observed in the accumulated samples, with H and lnE calculated from them.

data (Fig. 2). The percent change from the expected number of species in 2005 to the observed was −69.8%. The percent change from the observed 1975/1976 richness S to the observed richness in 2005 was −78.3%. Consequently, even when N is not taken into account, the results are similar (about −70% and −78%, respectively).

EVENNESS.—The expected values of both lnS and H for 2005 were considerably larger than those actually observed, while the expected value of lnE was smaller than the observed (Fig. 2). However, a comparison of values of evenness at the observed density of N = 371 indicates that evenness should be 0.33 (from regression), yet it was only 0.22. Consequently, the 2005 fauna showed increased dominance. This excess dominance is dramatically illustrated by the change in relative abundance of the most abundant species *Ammonia tepida* (Cushman, 1926). In 1975/1976 *A. tepida* comprised 42% of the fauna, while in 2005 this species constituted 76%.

Plots of ranked dominance in species abundance indicate that among the 14 samples from 1975/1976 there is comparatively little indication of stress (Fig. 3A). Most of the species are neither abundant nor rare and the range of the ranks is within acceptable bounds for the IRL (Buzas and Severin, 1982). In contrast, samples from 2005

Table 1. Mean numbers of individuals per sample observed at St. Lucie in 1975/1976 and 2005. Species are listed in order of abundance as of the first sampling period. NF indicates that the species was not found during that sampling period.

Species	Sample data	
	1975/1976	2005
1. *Ammonia beccarii* (Linné, 1758)*	117.1	35.1
2. *Buliminella elegantissima* (d'Orbigny, 1839)	37.6	0.4
3. *Quinqueloculina seminula* (Linné, 1758)	30.4	1.9
4. *Bolivina striatula* Cushman, 1922	29.4	1.1
5. *Elphidium mexicanum* Kornfeld, 1931	16.2	0.8
6. *Nonionella auricula* Heron-Allen and Earland, 1930	9.4	NF
7. *Elphidium excavatum* (Terquem, 1875)	6.5	4.8
8. *Quinqueloculina impressa* Reuss, 1851	4.1	NF
9. *Rosalina globularis* d'Orbigny, 1826	4.1	0.1
10. *Gaudyrina exilis* Cushman and Bronnimann, 1948	2.9	NF
11. *Cyclogyra planorbis* (Schultze, 1854)	2.6	1.3
12. *Rosalina floridana* (Cushman, 1922)	2.1	NF
13. *Bolivina paula* Cushman and Cahill, 1932	1.6	NF
14. *Elphidium kugleri* (Cushman and Bronnimann, 1948)	1.3	NF
15. *Weisnerella auriculata* (Egger, 1893)	1.2	NF
16. *Trochamina ochracea* (Williamson, 1858)	1.1	NF
17. *Bolivina subexcavata* Cushman and Wickendon, 1929	1.1	NF
Ammonia parkinsoniana (d'Orbigny, 1839)	NF	0.1
Cassidulina sp.	NF	0.1
Nonionella atlantica Cushman, 1947	0.2	0.3
Quinqueloculina sp.	NF	0.1
Trifarina occidentalis (Cushman, 1922)	0.0	0.1
Percent of total fauna	96%	100%
Total N	3,917	371
Total S	60	13

*Now called *Ammonia tepida* (Cushman, 1926), (Buzas-Stephens et al., 2002; Hayward et al., 2003).

(Fig. 3B) exhibit a relatively high degree of stress as indicated by the clear decrease in diversity over time, higher dominance, and a more limited set of species ranks.

Discussion

Foraminifera, one of the most abundant components of the meiofauna, are at the base of the marine food chain. Their important contribution as prey for deposit feeders is well documented by field experiments (Buzas 1978, 1982) and the examination of the gut contents from a wide variety of organisms (Buzas and Carle, 1979) in the Indian River Lagoon. The decline of any major component of the food web, not merely the top predators, must be recognized as a sublethal effect on the vitality of the entire ecosystem. Perturbations in such components, particularly at the base, can trigger ecological cascades (Vermeij, 1989). However, scientists are still a long way from understanding population dynamics, a requirement for management of marine systems (Schaaf et al., 1987).

The short life cycle of the foraminifera as well as their abundant and ubiquitous distribution make them ideally suited to measure the health of an ecosystem. Indeed,

Table 2. Observed and expected values of number of individuals (N) and species richness (S). The expected number of individuals EX(N) is obtained by multiplying the mean number of individuals observed in 1975/1976 by eight the number of samples taken in 2005. The expected value of species richness EX(S) is obtained from a regression based on the 1975/1976 data: ln S = −2.05 + 0.75lnN.

Observed 1975/1976		Expected 2005		Observed 2005	
N	S	EX(N)	EX(S)	N	S
3,917	60	2,238	43	371	13

in recent years a proliferation of studies has been devoted to the effects of anthropogenic contamination on foraminifera (Alve, 1995; Culver and Buzas, 1995; Scott et al., 2001). Many sources of stress and pollution on meiofauna have been examined, for example, point sources of discharge of fresh water, organic enrichment and other contaminants such as heavy metals and oil (Alve, 1995).

Historically, after any general environmental stress on a fauna, lower richness and density plus higher dominance have been noted (Allee et al., 1949). However, these
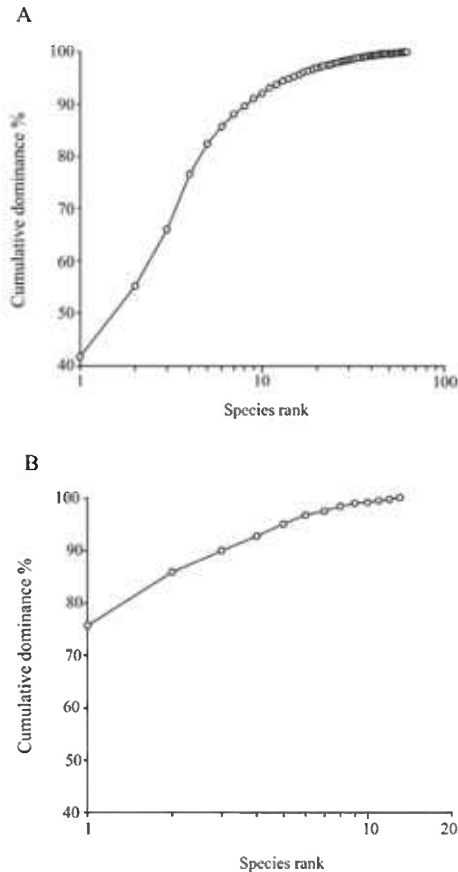

Figure 3. Cumulative percentage of species of foraminifera versus species rank for (A) 1975/1976 data and (B) 2005 data. Plots of ranked dominance in species abundance are composed of species ranking in decreasing order of their influence or importance to the total abundance in 1975/1976 and 2005. These ranked values are expressed as percentages for the total of all observed species and plotted against species rank. Using log-rank allows for clearer representation of the more common species. These plots are the reverse of rarefaction curves because the higher the curve the lower the diversity (Lambshead et al., 1983).

relationships may be only an observable endpoint in either a sudden or a continuing degradation. Here we conveniently group the actual time sequence of effects of polluting by organic enrichment and develop an ecosystem evaluation system with three recognizable and sequential categories or stages.

Stage 1. Slight amounts of organic enrichment often increase the density of foraminifera because their food source of diatoms and bacteria are increased (Alve, 1995). If their metazoan predators, which are more susceptible to organic pollution (Josefson and Widbom, 1988), are reduced in density, the density of foraminifera may be further enhanced. Under these circumstances of beginning or intermediate levels of disturbance, we would expect both density and species richness to peak (Connell, 1978). An example, of such a situation is found in Nueces Bay, Texas, where both density and species richness are higher on the south shore of the Bay that receives effluents from the Nueces River as well as industries (Buzas-Stephens and Buzas, 2005).

Stage 2. As the amounts of organic enrichment increase further, episodes of hypoxia occur and, in turn, density and species richness of foraminifera decrease. An example is Long Island Sound, where density and species richness have decreased since the 1960s as the supply of organic matter to the benthos has increased (Thomas et al., 2000). The relative abundance of *Ammonia,* a group shown to be tolerant of low oxygen conditions (Moodley and Hess, 1992), has increased in Long Island Sound along with episodes of anoxia/hypoxia (Thomas et al., 2000).

Stage 3. Under the most severe conditions in which hypoxia/anoxia occur over extended periods of time, the area may have greatly reduced or zero densities of foraminifera. The area close to the outfall in Sandebutka inlet of the Oslo Fjord is devoid of foraminifera (Alve and Nagy, 1986). Such a condition may also be simulated by examining a foraminiferal fauna with depth in the sediment. In the Indian River Lagoon near Fort Pierce at a depth of 10 cm oxygen is most often zero with high concentrations of NH_3 and highly negative values of Eh (oxidation reduction potential). In this situation the highly abundant foraminiferal fauna at the surface was reduced to extremely low to zero densities (Buzas and Severin, 1993).

In 1975/1976 at St. Lucie, each 20 ml of sediment contained an average of 280 living individuals distributed among 62 species. At the present time, we have no way of knowing whether or not these numbers represent a completely natural situation or the stage 1 scenario outlined above. However, in the first stage of pollution stress over time, the number of rare species is large relative to the other values, a situation evident in the 1975/1976 dataset.

By 2005, the mean density of foraminifera had been reduced to 46 living individuals per 20 ml of sediment and only 13 species were present. According to Gray and Pearson (1982), in unpolluted environments the number of rare species is large relative to other classes, and a smooth curve results with the mode far to the left (Fig. 4A). Lower abundance under environmental stress is observed clearly in 2005 (Fig. 4B), as evidenced by the number of geometric classes and less smooth curves (deviation from smoothness is as yet an unquantified concept by these authors). The relative abundance of *A. tepida* increased from 42% to 76% so that the evenness measure for 2005 fell below that predicted from the regressions of the 1975/1976 data. Increased abundance during 1975/1976 is evident also by the larger number of geometric classes, and by 2005, both numbers of individuals and numbers of species
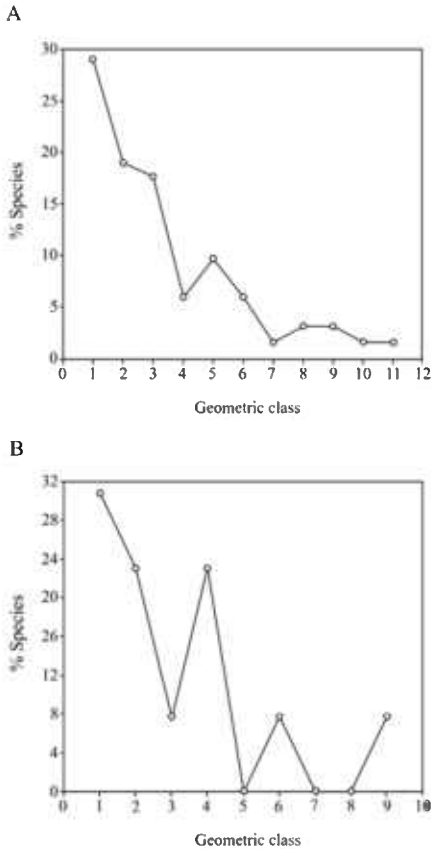
A

B

Figure 4. Percentage of species of foraminifera in geometric classes for (A) 1975/1976 data and (B) 2005 data. Geometric class plots have number of species represented by only 1 individual in a sample, 2–3 individuals, 4–7 individuals, and so on. These summaries are denoted on the x-axis by k geometrically-increasing group sizes each of size 2^k (k = 0, 1, 2..., n) denoted by class 1, class 2, and so on, respectively, for the 1975/1976 data and 2005 data.

were reduced to a smaller number of classes. The 2005 samples reflected increased dominance as well as evidence of stress.

Gray and Pearson (1982) discussed the possibility of selecting stress "indicator species" "objectively" by examining those in intermediate classes on the geometric class plot. The following species in intermediate classes in1975/1976 disappeared entirely after 30 yrs: *Ammobaculites exiguus* Cushman and Bronniman, *Fissurina lucida* (Williamson), *Glabratellina sagrai* (Todd and Bronniman), *Hanzawaia con-centrica* (Cushman), *Haynesiana germanica* (Ehrenberg), *Peneroplis pertusis* (For-skal), *Reophax nana* Rhumbler, *Rosalina concinna* (Brady), *Scutuloris* sp. A, *Sorites marginalis* (Lamarck), *Stetsonia minuta* Parker, *Elphidium advenum* (Cushman), *Quinqueloculina* cf. *Q. akneriana*, *Quinqueloculina poeyana* d'Orbingy, *Rosalina subaraucana* (Cushman), *Bolivina paula* Cushman and Cahill, *Bolivina subexcava-tum* Cushman and Wickenden, *Elphidium kugleri* (Cushman and Bronniman), *Tro-chamina ochracea* (Williamson) and *Weisnerella auriculata* (Egger).

Indeed, based upon our 2005 results, if the paradigm of Gray and Pearson were to hold, the species that are the most threatened at the present time and therefore the

most likely to decrease to local extinction in that area are: *Elphidium mexicanum* Korfeld, *Bolivina striatula* Cushman and *Quinqueloculina seminula* (Linneus). The dramatic change of about 80% in species richness, density, and relative abundance indicates that the foraminifera fauna of St. Lucie are well into Stage 2 if not early Stage 3.

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