

## A CASE FOR LONG-TERM MONITORING OF THE INDIAN RIVER LAGOON, FLORIDA: FORAMINIFERAL DENSITIES, 1977-1996

*Martin A. Buzas and Lee-Ann C. Hayek*

### ABSTRACT

Replicate observations on foraminiferal densities were made at a single station in the IRL near the Harbor Branch Oceanographic Institution's jetty at Link Port, Florida during the 20-yr span, 1977-1996. At each sampling time, the densities of living (stained) individuals were recorded for five taxa in four replicates. During the years 1993 through 1996 sampling was on a monthly basis. Analyses of these data indicate a significant difference in density among years with 1994 exhibiting the lowest density for most (4 of 5) taxa. Seasonal differences were also significant for most (4 of 5) taxa with maximum densities in summer. For all taxa the interaction hypothesis for years by season was significant. During the 1970s and 1980s mostly summer data are available. Thus, we tested summer data only for yearly differences during the period 1993 through 1996. For all taxa, 1994 was a time of low densities. With this assurance, we proceeded to analyze equivalent data for the years 1977 thru 1996. In general, the years 1979 and 1994 were times of low densities while 1984 and 1987 were high. For all taxa, the 1980s had higher densities than the 1970s and 1990s, and taxa maintained the same rank order of abundance with no trend for an overall increase or decrease of densities evident. The seasonal and yearly observations of the pattern of foraminiferal densities are similar to those of the seagrasses and fish. However, the lack of similarity of sample timing, location, replication, and methods of analysis makes comparisons equivocal at best. Long-term monitoring by a number of specialists in different groups of organisms at the same times and places is needed. Before such simultaneous observations are begun, the researchers must all agree on a suitable statistical experimental design allowing for comprehensive analysis of the data.

The Indian River Lagoon, Florida (IRL) is biologically highly diverse, and the preservation of its biodiversity is of sufficiently great concern to have warranted a conference in 1994 (Swain et al., 1995). Effective conservation strategies require not only assessment of the current condition, but also measurement of change with time. An integral component of biodiversity is population size or density (Swain et al., 1995). Because of the great variability of natural populations, documentation of changes in population densities with time require carefully replicated observations (Hayek and Buzas, 1997). Unfortunately, as the conference results document, studies with long-term replicated observations are sparse. Here, we present replicated observations on foraminiferal densities for 11 yrs spanning a period of 20 yrs at a single station. The station, just north of the Link Port jetty, has been the site of a number of ecological investigations on the macro-fauna and flora (Young et al., 1976; Virnstein, 1995).

Buzas and Severin (1982) studied the distribution and systematics of the foraminifera for the entire IRL. In all, 94 species were recognized with species richness increasing from north to south. Canonical variate analysis on the densities of the 15 most abundant species discriminates the inlets from the lagoon and arranges the entire ensemble into a north-south pattern. At Link Port, which is centrally located within the IRL, 24 species were recorded. The Link Port station has been used to investigate predation on foramin-

ifera, substrate preference, vertical distribution within the sediment and rate of colonization (Buzas, 1977, 1978, 1982, 1989; Buzas and Carle, 1979).

The purpose of the present paper is to present and analyze replicated observations on foraminifera at the Link Port station over the span of 20 yrs. The difficulty encountered in comparisons across taxa while trying to compare our results with those obtained by others, illustrates the need for long-term monitoring with standardized methods.

## METHODS

**FIELD AND LABORATORY.**—The station used in this study is north of the Harbor Branch Oceanographic Foundation jetty at 27°32.1'N, 80°20.9'W. The water depth is about 1 m and the distance from shore is about 25 m. As indicated by Virnstein (1995), at this distance from shore, the sandy substrate is covered mostly by the sea grass *Halodule wrightii*. At each sampling time four replicates were collected within an area of about 1 m<sup>2</sup> by inserting plastic core liners of 3.5 cm diameter into the sediment. Upon return to the laboratory (within an hour), 5 ml of sediment was removed from the top of each core, washed over a 63 micron sieve and fixed in 95% ethyl alcohol. Before enumeration, samples were stained overnight with rose bengal (Walton, 1952; Murray and Bowser, 2000), washed over a 63-micron sieve, dried, concentrated by floating in sodium polytungstate, and rewet. To insure recognition of living individuals, counting of the number of individuals in each of the five most abundant taxa that comprise about 90% of the total living number of individuals was always done wet. The taxa counted were *Quinqueloculina* (mostly, *Q. impressa* and *Q. seminulum*), *Elphidium* (mostly *E. mexicanum* and *E. gunteri*), *Ammonia* (*A. beccarii*), *Bolivina* (mostly *B. striatula*) and *Ammobaculites* (*A. exiguus*); all belong in different Families and are easily recognized.

**STATISTICAL.**—At each sampling time  $n = 4$  replicates were taken. This number was chosen as a compromise between cost (laboratory time) and maximizing statistical confidence (Hayek and Buzas, 1997). Before analysis, counts were transformed to  $\ln(x+1)$  to stabilize the variance. Observations from 1993 through 1996 represent a complete, continuous, monthly sampling sequence. Therefore, univariate general linear models (GLM) for each taxa were fit to the complete data set with  $n = 4$  replicates each month (except for August 1994) for these years. Null hypotheses for differences among years, seasons and their interaction were tested.

To obtain seasons, the months were grouped as follows: Winter: Dec., Jan., Feb.; Spring: Mar., April, May; Summer: June, July, Aug.; Fall: Sept., Oct., Nov. The long-term monitoring data set consists of mainly spring-summer observations spanning the years 1977 through 1992. Consequently, we modeled on the 1993 through 1996 data set using summer data only in order to compare results with the complete monitoring data set. Finally, univariate GLM's were fit separately for each taxa for spring-summer data that spanned the period 1977 through 1996. To test contrasts between years or among groups of years, we used the S-method (Scheffé, 1959), a linear combination of means with coefficients adding to zero:  $H_0: a_1\mu_1 + a_2\mu_2 + \dots + a_k\mu_k = 0$ .

In order to test the efficacy of the replicates, GLM's were also formulated to test the hypotheses for replicates and all possible interactions. We do not include these results here. However, in all cases, hypotheses for replicates and their interactions were not significant indicating that observed differences in densities were due to years and seasons rather than spatial heterogeneity.

## RESULTS

In 1993, monthly sampling with four replicates was initiated at the Link Port station and continues through the present. Enumeration of the five taxa considered is complete for 1993 through 1996. Each of the four seasons has  $n = 12$  observations so that each year

Table 1. Fit of linear statistical models to long-term monitoring data for five species in the IRL, 1993-1996.  $n = 188$ . Total d.f. = 172 for each species. 3 d.f. for Year; 3 d.f. for Season; 9 d.f. for Season by Year Interaction. Results of fit are given as observed probability (P) values (ns indicates non-significance), F-test statistic value (F), mean square (MS) and multiple correlation coefficient  $r^2$ . An observed probability of 0.0001 indicates  $P < 0.0001$ .

Species		Species Models			$r^2$
		Year	Season	Interaction	
<i>Quinqueloculina</i>	P	0.0001	0.0001	0.0001	0.48
	F	12.730	9.920	9.990	
	MS	16.528	12.880	12.971	
<i>Elphidium</i>	P	0.004	0.033	0.0001	0.37
	F	4.703	2.984	8.557	
	MS	5.082	3.225	9.246	
<i>Ammonia</i>	P	0.0001	0.798 ns	0.0001	0.44
	F	21.483	0.337	8.419	
	MS	18.709	0.294	7.332	
<i>Bolivina</i>	P	0.004	0.042	0.001	0.23
	F	4.643	2.791	3.227	
	MS	0.550	0.330	0.382	
<i>Ammobaculites</i>	P	0.144 ns	0.021	0.0001	0.31
	F	1.829	3.318	6.803	
	MS	1.133	2.055	4.215	

has  $n = 48$  observations, and the entire ensemble of 4 yrs has  $n = 192$ . Unfortunately, August 1994 is missing and, therefore,  $n = 192 - 4 = 188$  observations. We fit the densities with linear models that considered the effects of Years, Seasons, and the Interactions of these two factors. Results of the modeling and hypotheses tests in terms of mean squares, F-ratios, observed probability levels, and  $r^2$  are shown in Table 1. Most of the test results are highly significant, with model fits at levels of  $P < 0.001$ . The models for *Quinqueloculina* and *Ammonia* account for almost half of the observed variation, with  $r^2$  values of 0.48 and 0.44, respectively. These two taxa account for about 85% of the individuals observed in all five taxa. For *Ammonia*, the model included no detectable seasonal differences ( $P = 0.80$  ns), while for *Ammobaculites*, the Year factor was not significant ( $P = 0.14$  ns). For each of the taxa the Season by Year interaction was highly significant ( $P < 0.0001$ ). Contrasts to examine differences among Years and Seasons were carried out using Scheffe's one degree of freedom F-tests. For the four taxa with significant Year differences (Table 1), the contrasts indicate that the year 1994 had significantly lower densities than the other years. For the four taxa with significant Seasonal differences (Table 1), the contrasts indicate that summer had significantly higher densities than the other seasons, except for *Ammobaculites*.

Using only the summer observations for the years 1993 through 1996, we fit models to each taxon's densities to examine yearly differences (Table 2). All models showed the Year effect to be significant. For the three most abundant taxa (*Quinqueloculina*, *Elphidium*, *Ammonia*) comprising 96% of the individuals counted, 1994 had significantly lower densities. For the remaining two rare taxa, 1994 and 1996 had lower densities than 1993 and 1995. Overall, the results of the summer-only analyses show that the summer data at the Link Port station is predictive of the entire year's data set in terms of maximal and mini-

Table 2. Fit of linear statistical models to long-term monitoring data for five species in the IRL, Summer seasons for 1993–1996. Total d.f. = 40 for each species. 3 d.f. for Year. Results of fit are given as observed probability (P) values, F-test statistic value (F), mean square (MS) and multiple correlation coefficient  $r^2$ .

Species	Species Models			
	P	F	MS	$r^2$
<i>Quinqueloculina</i>	0.0180	3.777	6.310	0.22
<i>Elphidium</i>	0.0010	7.237	6.885	0.35
<i>Ammonia</i>	0.0001	8.823	8.952	0.40
<i>Bolivina</i>	0.0150	3.941	1.118	0.23
<i>Ammobaculites</i>	0.0001	9.899	6.162	0.43

mal yearly trends and patterns (Fig. 1). We can now proceed to examine the entire set of yearly monitoring observations.

All available data, May through August from 1977 through 1996 was used to examine yearly differences with a linear model having  $n = 184$  (Table 3). For all taxa, the Year effect was highly significant ( $P < 0.0001$ ). Figure 2 shows plots of the five taxa's densities versus years. The plots for *Quinqueloculina* and *Ammonia* as well as contrasts show similar results. In both taxa, the years 1984 and 1987 were times of significant density maxima and 1979 and 1994 minima. (These two taxa account for about 85% of the total number of individuals counted). The third most abundant taxon, *Elphidium*, accounting for about 12% of the total has a maximum in 1977, which is significantly higher than all other years, while 1994 is lower than all the rest (Fig. 2). For *Bolivina* the years 1984 and 1985 were significantly higher than all the rest and the years 1979, 1992, 1994 and 1996 significantly lower than all the rest (Fig. 2). For *Ammobaculites* the years 1984, 1985, 1986 and 1987 were significantly higher and 1979 significantly lower than the remaining years. Overall, 1984 and 1987 were times of maxima and 1979 and 1994 times of minima. For all taxa, contrasts of the 70s and 90s versus the 80s were significant. In general, the 80s were times of high densities while the 70s and 90s were lower.

No simple trend of increasing or decreasing density during the observational period is evident.

Table 3. Fit of linear statistical models to Spring/Summer long-term monitoring data for five species in the IRL, 1977–1996. Error d.f. = 173 for each species. 10 d.f. for Year. Results of fit are given as observed probability (P) values, F-test statistic value (F), mean square (MS) and multiple correlation coefficient  $r^2$ .

Species	Species Models			
	P	F	MS	$r^2$
<i>Quinqueloculina</i>	0.0001	10.125	9.635	0.37
<i>Elphidium</i>	0.0001	20.921	15.663	0.55
<i>Ammonia</i>	0.0001	37.722	19.213	0.69
<i>Bolivina</i>	0.0001	53.995	15.089	0.76
<i>Ammobaculites</i>	0.0001	55.743	20.208	0.76

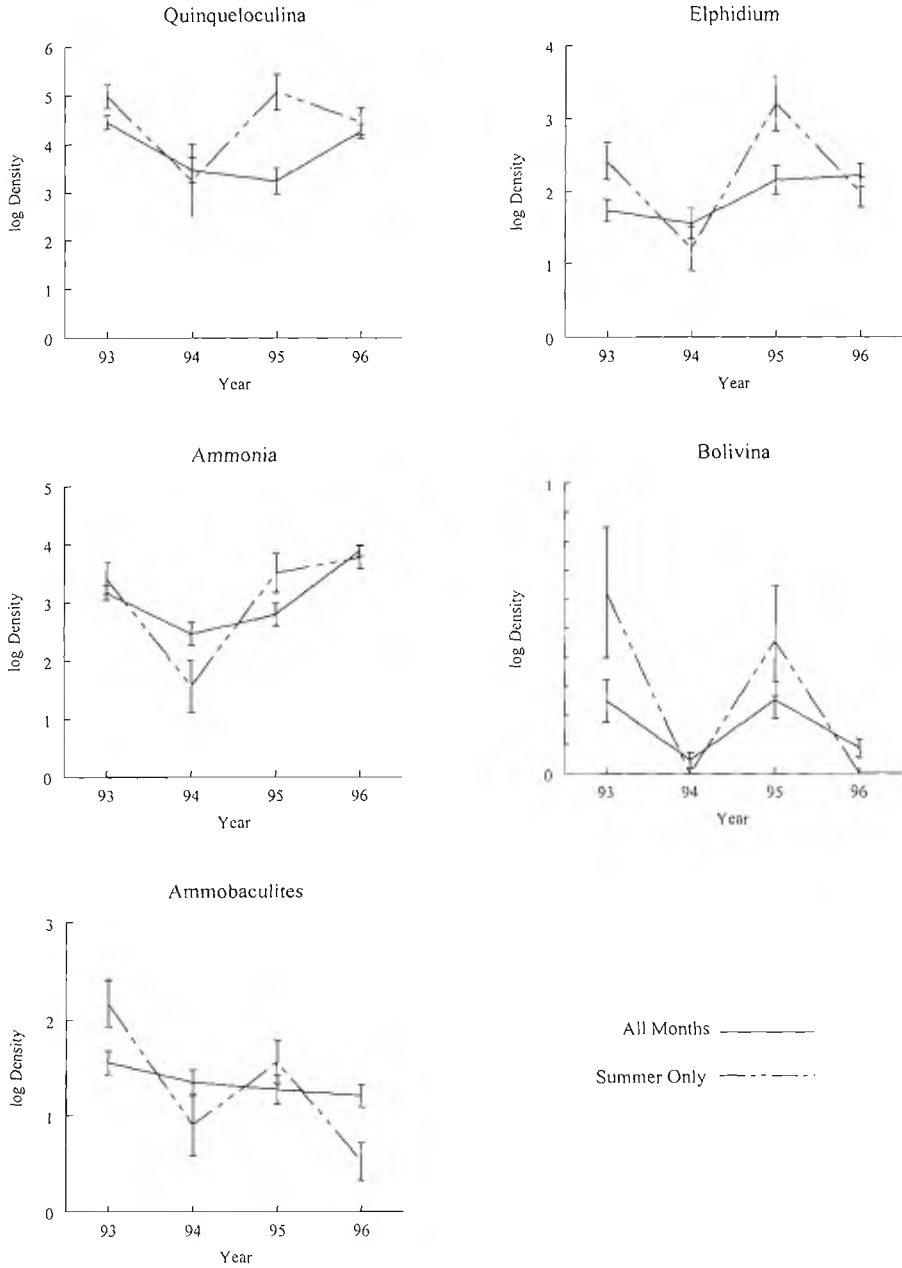


Figure 1. Plots of mean density (log transformed) with standard error bars at the Link Port station for the years 1993 through 1996. All months are averages of four replicates taken each month over a year. Summer only are averages for June, July and August.

## DISCUSSION AND CONCLUSIONS

Summarizing the results, we began our analyses with four replicate observations taken monthly for the years 1993 through 1996, with August 1994 missing. These  $n = 188$  observations were tested by a model considering differences in mean densities for years, seasons and their interaction (Table 1). Except for the relatively rare *Ammobaculites*, the difference among years was always significant, with 1994 having the lowest densities. Except for *Ammonia*, differences among seasons were always significant, and, in general, summer had the highest densities while winter had the lowest. The interaction (season by year) hypothesis was significant for all five taxa with densities for all taxa relatively low in the fall of 1995, and high in the fall of 1994. Because observations in the 1970s and 1980s contained mostly summer observations, we decided to test the summer observations for 1993 through 1996 to ascertain if the differences among years found for the complete data set would be apparent in an abbreviated one. Differences among years were significant for all taxa, and, as with the complete data set, 1994 exhibited significantly lower densities. With these encouraging results, we analyzed the  $n = 184$  observations from 11 yrs of the 20-yr time span 1977 to 1996. Once again the hypothesis for difference among years was significant for all taxa, and contrasts indicated that 1994 along with 1979 were years with low densities while 1984 and 1987 were high (Table 3). Contrasts for all taxa indicate densities in the 1970s and 1990s versus 1980s were significant, with the 1980s as a time of maximum densities (Fig. 2). The most important conclusion, however, is that large variations are exhibited and, consequently, expected with seasons, years and decades. Overall, no simple linear trend is observed over the 20-yr period.

The observations presented here cover the longest time span of any foraminiferal observations anywhere. A few foraminiferal studies (Lutze, 1968; Boltovskoy and Lena, 1969; Scott and Mediolì, 1980; Murray, 1983; Basson and Murray, 1995) have conducted monthly sampling over periods of 2 to 2.5 yrs. In all of these studies, contiguous years indicated differences in density between years. Consequently, the large changes in density among years demonstrated here (Fig. 2) are not surprising. Perhaps, it is more remarkable that for *Quinqueloculina* and *Ammonia*, which comprise about 85% of the individuals, densities for the years 1992, 1993, 1995 and 1996 are so similar. During the 1990s only 1994 exhibited low densities.

Long-term observations on other groups of organisms in the IRL are scarce. The estimated cover of seagrass, submerged aquatic vegetation (SAV), in the Link Port area and the entire South IRL was greater in 1986 than in 1970–1974 and 1992 (Fletcher and Fletcher, 1995), and maximum biomass occurs in summer (Virmstein and Carbonara, 1985; Dawes et al., 1995). While this pattern is consistent with the foraminiferal observations presented here, the effect of SAV on foraminiferal density is more complicated (Buzas and Severin, 1993). In an area of SAV about 100 m south of the Link Port jetty, Buzas and Severin (1993) observed foraminiferal densities every fortnight for 9 mo in 1978. The sediment from two localities was sampled: one within the seagrass beds; the other about 10 m distant on bare sand. No significant difference in overall density between the seagrass substrate and bare sand substrate was found. However, the periodicity at the two stations differed. At the bare sand station, peak density occurred in March–April, 1978, while peak density at the grass station was in July, 1978. Therefore, if observations had been restricted to particular sampling times, Buzas and Severin (1993) might have concluded higher densities in sand, higher densities in seagrass, or no difference between them.

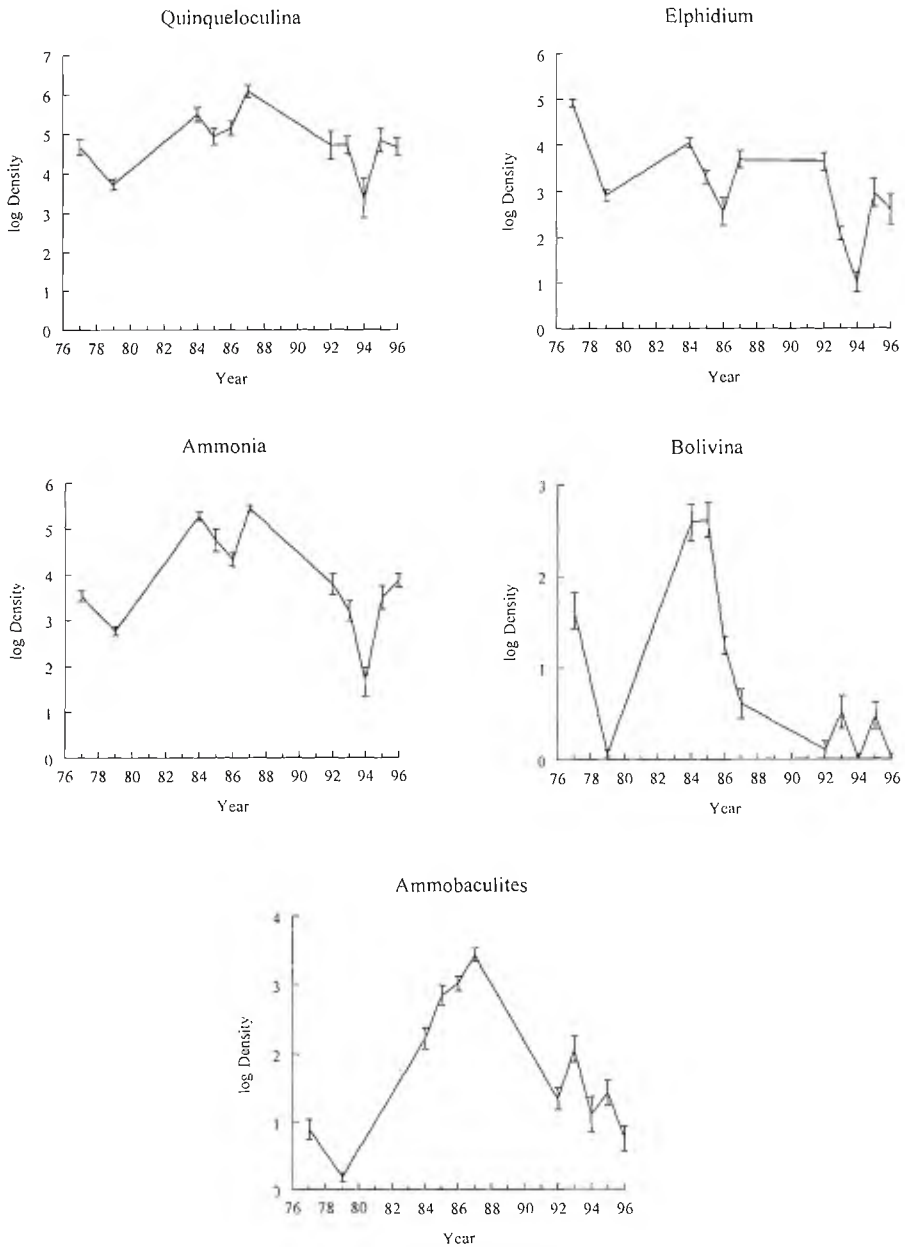


Figure 2. Plots of mean density (log transformed) with standard error bars at the Link Port station for the years 1977, 1979, 1984, 1985, 1986, 1987, 1992, 1993, 1994, 1995, and 1996. Means are for the months of May, June, July and August.

Mikkelsen et al. (1995) reported more mollusk species from seagrass stations (177) vs sand (166) in the IRL. However, there were more than twice as many stations (292) in the seagrass as on sand (130). Virnstein et al. (1983) sampled an area close to the foraminiferal monitoring station during April, May and June 1978 and found a higher density for



the macrofauna in seagrass vs bare sand. However, most of the difference was in densities of epifaunal species. At Carrie Bow Cay, Belize, Young and Young (1982) found no significant difference in species richness or densities for polychaetes or mollusks in seagrass vs bare sand localities sampled in March, 1976. The seagrass in Belize was *Thalassia testudinum* while at the IRL station it was a mixture of *T. testudinum* and *H. wrightii*. As Virnstein (1995) has pointed out, the pattern and scale as well as the species composition of seagrass meadows are probably important in assessing habitat diversity. As a further complication, the research of Buzas and Severin (1993) indicates that sampling over an extended period may be necessary to evaluate the importance of SAV for infaunal organisms. Consequently, the importance of SAV for the well being of at least some benthic infaunal organisms is equivocal. Studies are needed with proper statistical experimental design of field observations with replication and attention to pattern, scale and composition of seagrass communities.

During the years 1974 to 1979 observations on the densities of isopods (Kensley et al., 1995) and amphipods (Nelson, 1995) were made at Haulover, Link Port and St. Lucie. These three locations in the IRL were the study sites of Young et al. (1976) and Young and Young (1977). At the Link Port station, no differences in densities between years were observed. The significantly lower densities observed for the foraminifera at the same Link Port site in 1979 did not occur for the isopods and amphipods. Moreover, the isopods and amphipods exhibited lower densities in summer while the foraminifera, during the years 1993 through 1996, exhibited maximum densities in summer. Kensley et al. (1995) and Nelson (1995) suggested that the lower densities of pods in the summer was due to more intensive predation by fish, shrimp and crabs. Supporting this view, Tremain and Adams (1995) found higher densities and species richness of fish (similar to the foraminiferal pattern) during summer and fall between 1990 and 1993. However, within the IRL fish, crabs, shrimp, gastropods, bivalves, polychaetes and sipunculids (Rice et al., 1995) were all also found to ingest foraminifera (Buzas and Carle, 1979). Evidently, predation intensity affects one group differently from another. The advice given by Young and Young (1978) urging caution in extrapolation from species or species groups to the community level is still germane.

Based on the 11 yrs of sampling the 20-yr span from 1977 to 1996, we can document neither an overall increasing trend, nor an overall decreasing trend in foraminiferal densities. In general, the 1970s and 1990s had lower densities than the 1980s. In particular, the years 1979 and 1994 had low densities while 1984 and 1987 had high densities. Extreme caution must be exercised in the determination of long-term trends. For example, had we been unfortunate enough to have sampled only the years 1987, 1992 and 1994 (Fig. 2), we would have concluded that the foraminifera are undergoing an alarming decreasing trend in species densities. And yet, this is not the case at all.

The variances associated with mean densities of natural populations are relatively large and, consequently, recognition of differences with time requires replication at each sampling time (Hayek and Buzas, 1997). This study indicates that even with replication substantial differences among seasons and years are to be expected. The analyses presented here were complicated by a lack of monthly sampling prior to the 1990s. In the future, our long-term monitoring will take monthly replicated samples. As the discussion above indicates, all species and species groups do not exhibit the same patterns, long-term monitoring with a proper statistical design should be undertaken simultaneously by a number of specialists in different groups of organisms. By doing so, the equivocal relationship be-



tween seagrass and infaunal organisms as well as long-term trends in population densities can be evaluated with robust statistical analysis. In this way, deviations from the expected variability of natural populations over long periods of time can be recognized, and conservation strategies planned accordingly.

#### ACKNOWLEDGMENTS

We thank K. Carle and S. Reed for their outstanding contributions in the field and laboratory. The help of K. D. Cairns, L. B. Isham, M. A. Middleton, J. A. Jett, J. E. Miller, D. H. Mook, R. W. Virnstein, T. Wolcott, D. K. Young, and M. W. Young is greatly appreciated. This is contribution number 501 from the Smithsonian Marine Station at Fort Pierce.

#### LITERATURE CITED

- Basson, P. W. and J. W. Murray. 1995. Temporal variations in four species of intertidal foraminifera, Bahrain, Arabian Gulf. *Micropaleontology* 41: 69-76.
- Boltovskoy, E. and H. Lena. 1969. Seasonal occurrences, standing crop, and production in benthic foraminifera of Puerto Deseado. *Contrib. Cushman Fdn. Foram. Res.* 20: 87-95.
- Buzas, M. A. 1977. Vertical distribution of foraminifera in the Indian River, Florida. *J. Foram. Res.* 7: 234-237.
- \_\_\_\_\_. 1978. Foraminifera as prey for benthic deposit feeders: results of predator exclusion experiments. *J. Mar. Res.* 36: 617-625.
- \_\_\_\_\_. 1982. Regulation of foraminiferal densities by predation in the Indian River, Florida. *J. Foram. Res.* 12: 66-71.
- \_\_\_\_\_. 1989. The effect of quartz versus calcareous sand on the density of living foraminifera. *Micropaleontology* 35: 135-141.
- \_\_\_\_\_ and K. Carle. 1979. Predators of foraminifera in the Indian River, Florida. *J. Foram. Res.* 9: 336-340.
- \_\_\_\_\_ and K. P. Severin. 1982. Distribution and systematics of foraminifera in the Indian River, Florida. *Smithson. Contrib. Mar. Sci.* 16: 1-73.
- \_\_\_\_\_ and \_\_\_\_\_. 1993. Foraminiferal densities and pore water chemistry in the Indian River, Florida. *Smithson. Contrib. Mar. Sci.* 36: 1-38.
- Dawes, C. J., D. Hanisak and W. J. Kenworthy. 1995. Seagrass biodiversity in the Indian River Lagoon. *Bull. Mar. Sci.* 57: 59-66.
- Fletcher, S. W. and W. W. Fletcher. 1995. Factors affecting changes in seagrass distribution and diversity patterns in the Indian River Lagoon complex between 1940 and 1992. *Bull. Mar. Sci.* 57: 49-58.
- Hayek, L. C. and M. A. Buzas. 1997. *Surveying natural populations*. Columbia Univ. Press, New York. 563 p.
- Kensley, B., W. G. Nelson and M. Schotte. 1995. Marine isopod biodiversity of the Indian River Lagoon, Florida. *Bull. Mar. Sci.* 57: 136-142.
- Lutze, G. F. 1968. Jahresgang der foraminiferen-fauna in der Bottsand Lagune (Westlich Ostee). *Meyniana* 18: 13-30.
- Mikkelsen, P. M., P. S. Mikkelsen and D. J. Karlen. 1995. Molluscan biodiversity in the Indian River Lagoon, Florida. *Bull. Mar. Sci.* 57: 94-137.
- Murray, J. W. 1983. Population dynamics of benthic foraminifera: results from the Exe Estuary, England. *J. Foram. Res.* 13: 1-12.
- \_\_\_\_\_ and S. S. Bowser. 2000. Mortality, protoplasm decay rate, and reliability of staining techniques to recognize 'living' foraminifera: a review. *J. Foram. Res.* 30: 66-70.

- Nelson, W. G. 1995. Amphipod crustaceans of the Indian River Lagoon: current status and threats to biodiversity. *Bull. Mar. Sci.* 57: 143–152.
- Rice, M. E., J. Piraino and H. F. Reichardt. 1995. A survey of the sipuncula of the Indian River Lagoon. *Bull. Mar. Sci.* 57: 128–135.
- Scheffé, H. 1959. *The analysis of variance*. John Wiley & Sons, Inc. New York. 477 p.
- Scott, D. B. and F. S. Medioli. 1980. Living vs. total foraminiferal populations: their relative usefulness in paleoecology. *J. Paleo.* 54: 814–831.
- Swain, H. M., D. R. Breiningner, D. S. Busby, K. B. Clark, S. B. Cook, R. A. Day, D. E. De Freese, R. G. Gilmore, A. W. Hart, C. R. Hinkle, D. A. McArdle, P. M. Mikkelsen, W. G. Nelson and A. J. Zahorecak. 1995. Introduction. *Bull. Mar. Sci.* 57: 1–7.
- Tremain, D. M. and D. H. Adams. 1995. Seasonal variations in species diversity, abundance, and composition of fish communities in the northern Indian River Lagoon, Florida. *Bull. Mar. Sci.* 57: 171–192.
- Virnstein, R. W. 1995. Seagrass landscape diversity in the Indian River Lagoon, Florida: The importance of geographic scale and pattern. *Bull. Mar. Sci.* 57: 67–74.
- \_\_\_\_\_ and P. A. Carbonara. 1985. Seasonal abundance and distribution of seagrass beds in the Indian River Lagoon, Florida. *Aquat. Bot.* 23: 67–82.
- \_\_\_\_\_, P. S. Mikkelsen, K. D. Cairns and M. A. Capone. 1983. Seagrass beds versus sand bottoms: the trophic importance of their associated benthic invertebrates. *Fla. Sci.* 46: 363–381.
- Walton, W. R. 1952. Techniques for the recognition of living foraminifera. *Contrib. Cushman Fdn. Foram. Res.* 3: 56–60.
- Young, D. K. and M. W. Young. 1977. Community structure of the macrobenthos associated with seagrass of the Indian River Estuary, Florida. Pages 359–381 in B. C. Coull, ed. *Ecology of marine benthos*, no. 6, Univ. South Carolina Press, Columbia.
- \_\_\_\_\_ and \_\_\_\_\_. 1978. Regulation of species densities of seagrass-associated macrobenthos: Evidence from field experiments in the Indian River Estuary, Florida. *J. Mar. Res.* 36: 569–593.
- \_\_\_\_\_ and \_\_\_\_\_. 1982. Macrobenthic invertebrates in bare sand and seagrass (*Thalassia testudinum*) at Carrie Bow Cay, Belize. Pages 115–126 in K. Rutzler and I. G. Macintyre, eds. *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize*, 1: Structure and communities. *Smithson. Contrib. Mar. Sci.* 12.
- \_\_\_\_\_, M. A. Buzas and M. W. Young. 1976. Species densities of macrobenthos associated with seagrass: A field experimental study of predation. *J. Mar. Res.* 34: 577–592.

DATE SUBMITTED: March 6, 2000.

DATE ACCEPTED: July 21, 2000.

ADDRESSES: (M.A.B.) *Smithsonian Institution, Washington, D.C. 20560-0121*; (L.C.H.) *Smithsonian Institution, Washington, D.C. 20560-0136*.