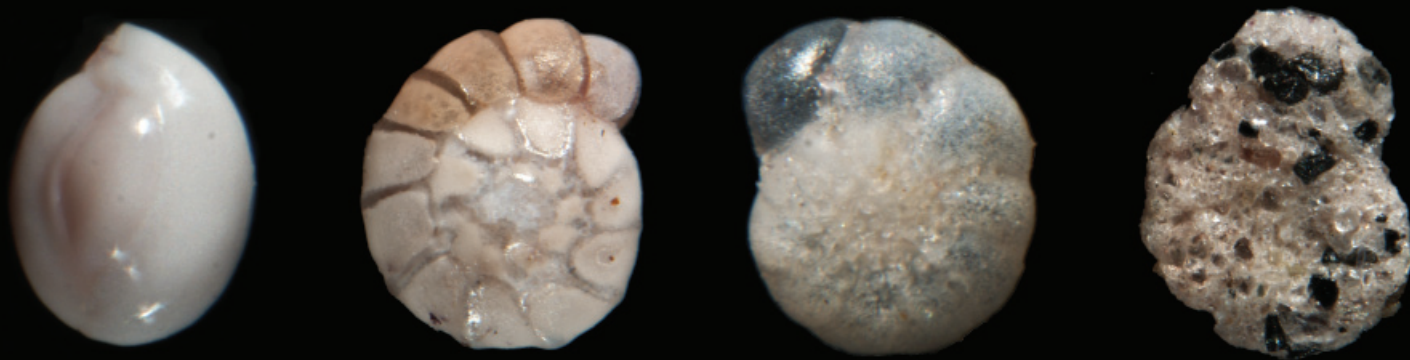




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Pulsating Patches

History and Analyses of Spatial, Seasonal, and Yearly Distribution of Living Benthic Foraminifera

*Martin A. Buzas, Lee-Ann C. Hayek,
Jennifer A. Jett, and Sherry A. Reed*

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ABSTRACT

Buzas, Martin, A., Lee-Ann C. Hayek, Jennifer A. Jett, and Sherry A. Reed. Pulsating Patches: History and Analyses of Spatial, Seasonal, and Yearly Distribution of Living Benthic Foraminifera. *Smithsonian Contributions to Paleobiology*, number 97, x + 91 pages, 69 figures, 39 tables, 2015. Within habitats the density of most organisms varies spatially and temporally. Patches are defined as density differences between stations. Pulses are defined as density differences with time (days, weeks, months, seasons, or years). When multiple samples are taken within a habitat at each sampling time, the possibility arises that we can detect that densities in space and time do not act in unison. The existence of significant statistical interaction between space and time is termed “pulsating patches.” Although our historical review and reanalysis of research on living foraminifera verified the existence of patches and pulses, the sampling design of most studies was inadequate to address the hypothesis of pulsating patches. To alleviate this deficiency, we designed an exemplar study in the Indian River Lagoon, Florida. At each of two scales, one with stations 1 m apart and another with stations 10 m apart, four stations were located in a square configuration. For each of these two studies, four sediment samples were taken at each station in the middle of each season, and this design was carried out for four years beginning in 2001. The densities of four taxa were enumerated in each sediment sample. We have then for each of four taxa, 4 replicates $\times$ 4 stations $\times$ 4 seasons $\times$ 4 years = 256 observations at each scale for each taxon. A three-way ANOVA was constructed for each taxon with hypotheses for (1) station difference, (2) seasonal difference, (3) yearly difference, and (4) their multiway interactions. The main and interaction hypotheses for station $\times$ time were significant for all taxa, which confirmed the existence of pulsating patches on varying spatial and temporal scales. Pulsating patches make the predictability of density difficult at any particular point in time and space, but this unpredictability may be a fundamental ecological strategy to avoid reduction of populations by predators and pathogens. Because many organisms exhibit within-habitat patchiness and pulses, it is likely that they may have as yet undetected pulsating patches.

Cover images, from left to right: *Quinqueloculina*, *Ammonia*, *Elphidium*, and *Ammobaculites* from station 1 (27°32.153 N and 80°20.948 W) Indian River Lagoon, Florida. Photos by Jennifer Jett.

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Pulsating Patches: History and Analyses of Spatial, Seasonal, and Yearly Distribution of Living Benthic Foraminifera

Martin A. Buzas,^{1} Lee-Ann C. Hayek,² Jennifer A. Jett,¹ and Sherry A. Reed³*

INTRODUCTION

The spatial and temporal distributions of organisms are primary ecological characteristics (Murray, 2000, 2006). Large-scale spatial distributions identify differences among biofacies or communities (Murray, 2000). Smaller-scale spatial distributions, of interest here, record the spatial arrangement among individuals within a habitat. Thus, for marine species, such as foraminifera, we document these distributions in marshes, bays, and the shelf, slope, and abyss of the open ocean. These habitats or environments are often subdivided further into subunits, for example, upper marsh, lower bay, inner shelf, and so on.

Herein we specify that spatial distribution refers to the distribution of individuals at a specified place at a moment in time. Temporal distribution then describes the distribution of individuals over time. For example, observations may be made weekly, monthly, seasonally, and occasionally over a period of years. We might think of the assemblage of individuals within a habitat over time as a motion picture. The players (individuals) change position and increase and decrease their numbers (density) with time. The spatial distribution is then a single frame of the motion picture. Temporal distributions are additional static frames allowing us a glimpse of the development and history of a species or community.

SPATIAL DISTRIBUTIONS: OBSERVATIONS FROM CONTIGUOUS SAMPLES

The most rewarding method by which to examine spatial distribution is to place a set of contiguous cells or quadrats over an entire habitat or section of a habitat of interest. If a habitat appears homogeneous to an individual, so that all areas within it are equally inhabitable, and the organisms are not social, then we expect the individuals to occupy the space at random. That is, the probability of an individual's occupying any particular cell in our sampler is equal to 1 divided by the number of cells. If the data appear not to be the result of a random process, two alternatives are possible. In the first case individuals are more evenly spaced than random, like trees in an orchard. In the second case, individuals are

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more aggregated or patchy than in a random configuration, like cows in a meadow. Recognizing a random pattern visually, however, is notoriously difficult, and several statistical techniques are available to help the researcher identify such randomness (Hayek and Buzas, 2010).

For larger organisms, such as trees, counting the number of individuals within cells is relatively simple, and the actual spatial distribution can be mapped over many meters. For smaller organisms with high densities, such as foraminifera, formidable obstacles exist. For suitable examination, the contiguous cells are necessarily small (Hayek and Buzas, 2010). In this case, only a few centimeters of a habitat can reasonably be examined because of time and effort constraints. Consequently, only two studies have used contiguous cells in studying the spatial distribution of foraminifera (Buzas, 1968; Olsson and Erikson, 1974). The results of these studies indicate that foraminifera, similar to most other organisms, are often patchy, but on a scale of centimeters.

SPATIAL DISTRIBUTIONS: OBSERVATIONS FROM NONCONTIGUOUS SAMPLES

Because of the physical impossibility of sampling by extending contiguous cells over larger areas such as meters, for the examination of the spatial distribution of microscopic organisms, an alternative method is chosen on the basis of time, cost, and effort limitations. Stations or localities are usually located meters apart within a habitat. Samples are then taken at each station, and densities between stations are compared. Consequently, with this type of noncontiguous sampling, homogeneity is defined as the lack of difference in density between stations. To measure the inherently large variability often exhibited between adjacent samples only centimeters apart, multiple observations or replicate samples must be taken at each station. Without replicates, statistical analyses and critical evaluation of spatial variability are not possible. When a number of stations are evaluated statistically, areas of high and low densities can become evident, and these areas can appear patchy.

TEMPORAL DISTRIBUTIONS

The procedure used in space can also be used in time, and herein we focus on seasonal and yearly distributions of foraminifera. Clearly, if information concerning possible seasonal variation in density is the goal of a study, then a single or multiple stations should be sampled repeatedly during the course of several seasons or time periods. In addition, because of the natural spatial variability,

multiple observations or replicates must be taken at each sampling time. The sampling times may then be compared statistically in the same manner as the samples were compared in space. If more than one station is sampled at each sampling time, then the analytical problem becomes more complicated. We now can have spatial variability between the multiple stations at each sampling time as well as variability across the different sampling times.

Hypotheses for differences in spatial and temporal distributions can be tested easily. However, now another hypothesis concerning the interface of distributions in space and time emerges, that is, the statistical interaction of station by time. Consideration and testing of this interaction hypothesis provides a statistical, quantifiable way to question if the stations are exhibiting different patterns of temporal variability (e.g., seasonality) at different times. In other words, stations may not be synchronized, and an increase in density may not occur everywhere at the same time. The importance of the significance of this statistical interaction hypothesis in reference to those of time and space was termed “pulsating patches” by Buzas et al. (2002). That is, at any given time we observe patches in density, but the location of these spatial patches themselves also changes with time. Maps showing areas of high and low densities within a habitat are not the same with time and represent only a single frame of a continuously varying landscape.

PURPOSE OF PRESENT CONTRIBUTION

The purpose of the present contribution is (1) to review, reanalyze where possible, and critique the historical and present literature on the methodology and results of observations on spatial and temporal distribution of living benthic foraminifera, (2) to provide a field design that can adequately examine both spatial and temporal distributions, including their interaction (pulsating patches) from new field observations from the Indian River Lagoon, Florida, and (3) to provide an exemplar with a suitable experimental design so that other marine organisms can be examined for pulsating patches.

Although many foraminiferal studies on spatial and seasonal distributions are reviewed, no attempt is made to ensure that the list is all-inclusive. Nevertheless, the number of studies (56) included is probably sufficient to judge the state of knowledge regarding these two fundamental ecological attributes. To simplify presentation, the original species names used by authors are given here even though to the experienced foraminiferal researcher they are currently not in use; for example, *Elphidium clavatum* is now called *E. excavatum*.

The advent of staining foraminifera for recognition of living individuals was a huge development and opened up entirely new avenues of foraminiferal research. The staining technique (Walton, 1952) marked the watershed for study of living populations. When living individuals and populations are referred to in this study, we are referring to stained individuals. All of the graphs, tables, and appendices in this study have numbers of living (stained) individuals.

The exemplar data for of this study are field observations on the density of four taxa from the same locality carried out in the Indian River Lagoon, Florida, on two scales, one with stations 1 m apart and another with stations 10 m apart. On each scale four replicates, a few centimeters apart, were taken at each of four stations, during each of four seasons over four years. In all, there are 512 observations on each of four taxa over a relatively small area. The data were analyzed by three-way ANOVA with hypotheses for stations, seasons, years, and their statistical interactions.

HISTORY, REANALYSIS, AND CRITIQUE OF SPATIAL STUDIES

SPATIAL DISTRIBUTION WITH CONTIGUOUS SAMPLES

The small size of foraminifera, their mainly infaunal habit, and surrounding sediment present numerous difficulties for examining the spatial distribution of individuals in their natural state. To try and circumvent this difficulty, Buzas (1968) designed a sampler consisting of 36 contiguous cells. The sampler covered an area of about 58 cm² in an array of 6 × 6 cells, with each cell containing about 2 mL of volume. Three such samples were taken in an area of about 1 m² in Rehoboth Bay, Delaware. The distributions of living and dead populations were tested for randomness (Poisson distribution) or aggregation (negative binomial distribution). Four species in the living population were analyzed in each of the three sets of 36 cells. Of the 12 possible analyses, 6 were designated as random and 6 as aggregated. Figure 1 illustrates the number of living individuals of *Ammonia beccarii* in each of the contiguous cells in one of the three sampling devices for which the distribution was fit by a negative binomial (aggregated). The values in the cells range from 0 to 17. The cell immediately next to the cell with 17 individuals, about a centimeter away, contains only 1 individual. In general, the more abundant taxa exhibit more patchiness, and the relationship is most easily expressed by a power function between the variance and the mean, $\sigma^2 = a\mu^b$. This functional

7.5 cm					
NS	3	1	1	7	4
0	3	5	1	4	15
NS	2	8	0	2	2
4	4	8	15	4	7
4	3	6	1	1	17
3	5	10	0	3	6

FIGURE 1. Number of living individuals of *Ammonia beccarii* in contiguous cells with 2 mL volume, Rehoboth Bay, Delaware. Data from Buzas (1968). NS = no samples.

relationship is a general property of organisms, and Hayek and Buzas (1997, 2010) give numerous examples of the applicability of the power function for the relationship of mean and variance for a variety of organisms.

In the only other study to utilize contiguous cells, Olsson and Eriksson (1974) used 81 contiguous cells to examine the spatial distribution of foraminifera as well as other meiofauna. The study differs in several respects from that of Buzas (1968). Each cell represents about 45 mL versus 2 mL for Buzas (1968). Instead of the standard 63 μ m sieve used in benthic foraminiferal studies, a 200 μ m sieve was used. Nevertheless, the results are remarkably similar. The rarer species are best fit by a Poisson distribution, and the more abundant species are best fit by a negative binomial. The relationship between the variance and the mean of each taxon over all samples appears as a power series.

SPATIAL DISTRIBUTION WITH NONCONTIGUOUS SAMPLES

Some authors presented only visual interpretation of their data, whereas others performed a quantitative analysis. Fortunately, a number of researchers gave tables of their original data, allowing us to reanalyze their data. We present the results of these reanalyses whenever possible. In

the Adriatic Sea, Hohenegger et al. (1993) sampled a 4 × 4 grid with stations 1 m apart at a water depth of 14.5 m. The 16 stations were sampled every centimeter to a depth of 5 cm. Using the Morisita index to discern patchiness, they discovered the spatial distribution at the surface was patchy for almost all of the more abundant species. Also, the abundant *Ammonia tepida* and *Bolivina striatula* were patchy at the surface, random at the second and third centimeters, and then patchy again. One species, *Elphidium granosum*, was exclusively infaunal, with low abundances in the top 2 cm. Attesting to the wide range of densities in a relatively small area, abundances (0–5 cm depth) at the 16 sampling points ranged from 67 to 313 for *Reophax nanus*, 21 to 104 for *Labrospira jeffreysii*, 35 to 230 for *Spiroplectinella sagittula*, 12 to 40 for *Elphidium advenum*, 6 to 98 for *Nonionella turgida*, and 30 to 79 for *Ammonia tepida*.

HOMOGENEITY OF NONCONTIGUOUS
SAMPLES BETWEEN STATIONS

Another way to examine and define spatial distribution is to look for homogeneity in mean values of individuals among stations. The null hypothesis is that there is no detectable difference in the mean density at each station. Increase or decrease in abundance with time also measures density. Therefore, using differences in mean density for both space and time makes sense.

In the Hohenegger et al. (1993) study, no replicates were taken at the stations, so we cannot test for differences between the 16 stations. However, these authors provided their data set, and the square 4 × 4 array allows us to test between rows and columns using a two-way ANOVA with one observation per cell. Using the data in their table 1 for abundances in the 0–5 cm sediment depth range, we ran analyses on the natural logarithm (ln) of abundances for *Reophax nanus*, *Labrospira jeffreysii*, *Spiroplectinella sagittula*, and *Ammonia tepida*. For the first three species, no significant difference between rows and columns was found. However, for *A. tepida* a significant difference, $p = 0.045$, was found between rows (Table 1, Figure 2). Tukey’s post

TABLE 1. ANOVA for station differences on $\ln(x + 1)$, where x is density of *Ammonia tepida*. Data from Hohenegger et al. (1993).

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Row	0.595	3	0.198	4.036	0.045
Column	0.024	3	0.008	0.160	0.920
Error	0.442	9	0.049		

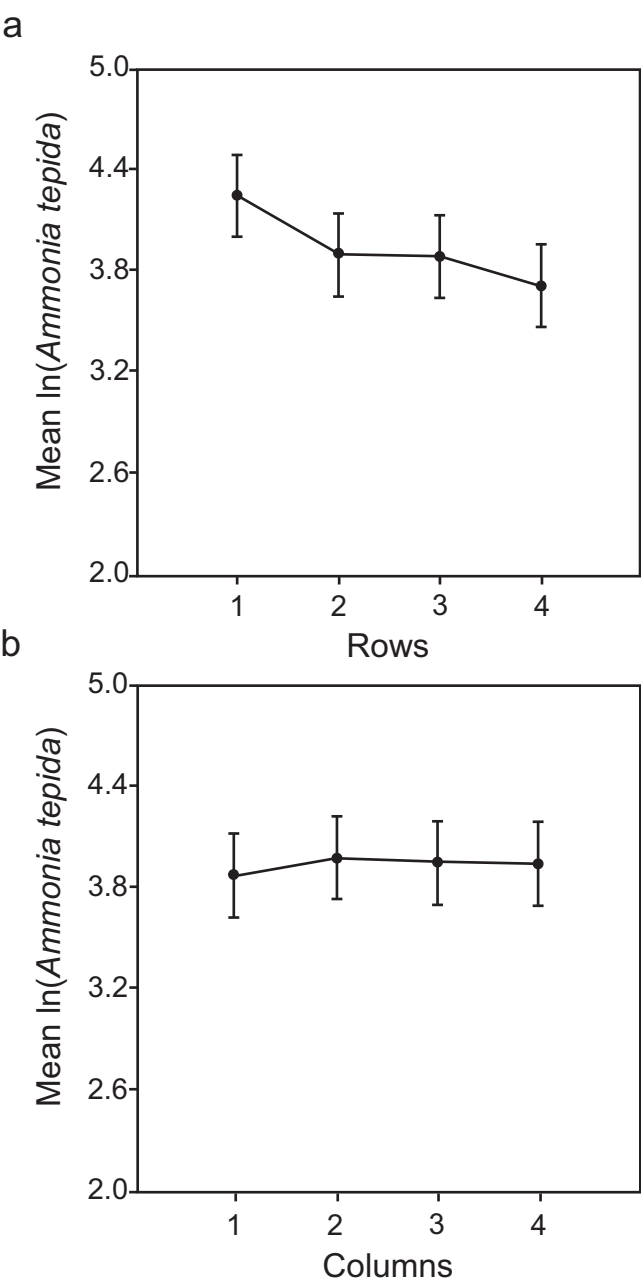


FIGURE 2. Mean number of living individuals for $\ln(Ammonia tepida)$ observed at 16 stations 1 m apart in the Adriatic Sea. (a) Between rows; (b) between columns. Data from Hohenegger et al. (1993).

hoc test indicates a significant difference in density between rows 1 and 4. (Note that the small number of degrees of freedom [df] in the error term precludes strong confidence in the result.) Although we did not analyze all of the species listed in table 1 of Hohenegger et al. (1993), the five species

we did test indicate that although patchy, a good deal of homogeneity between abundances exists. In the remaining examination of spatial distributions, only homogeneity of densities between stations will be considered.

Parker and Athearn (1959) took multiple (duplicate and triplicate) samples about six inches (15.24 cm) apart from each other in their study of eight stations from a marsh in Popponeset Bay, Massachusetts. Samples were stained with Rose Bengal, and living populations were examined while wet. Analysis consisted of visual examination of the data. One duplicate sample differed greatly from others, but the authors reported that, overall, the results concerning the reliability of samples were “reassuring.”

Buzas (1965) obtained 12 sample pairs or replicates while studying Long Island Sound. The distance between samples, although indeterminate, is probably on the order of meters (distance the boat drifted between samples). Homogeneity was ascertained by using a normal approximation to the binomial distribution. In the living population 7 of 12 sample pairs were homogeneous by these criteria.

Shifflett (1961) examined living, dead, and total populations from four localities in the vicinity of Heald Bank, Gulf of Mexico. At each of the localities three samples were taken within a radius of 100 feet (30.48 m). She indicated by inspection that faunal variations in short lateral distances were appreciable. We performed one-way ANOVA's on the living, dead, and total populations. For the living population the mean number of individuals was significantly smaller at the second locality (Table 2, Figure 3). We found no significant difference among the four localities for the dead and total populations.

Lynts (1966) examined the standing crop at 19 stations in Buttonwood Sound, Florida Bay, to establish the existence of “restricted foraminiferal colonies,” or patches. Samples from each station were taken at three sampling times in August 1962. Consequently, they do not measure spatial distribution at a single time but, instead, within a few weeks of each other. Nevertheless, the data were treated as a single-time spatial distribution. Each sample was estimated to be within a 3 m radius of the other samples. Statistical analysis by ANOVA indicated 9 of the 19 stations had significant

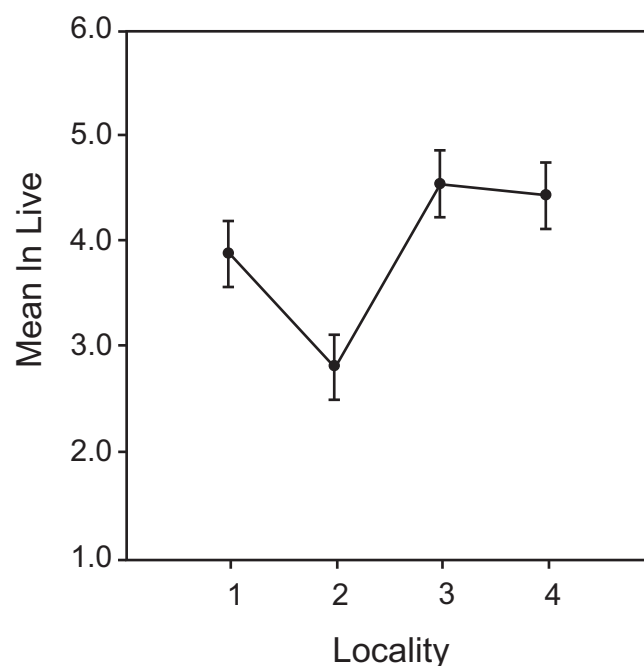


FIGURE 3. Mean number of living individuals observed at stations 30 m apart in the vicinity of Heald Bank, Gulf of Mexico. Data from Shifflett (1961).

variation in standing crop. Lynts (1966) concluded that the remaining 10 stations represented colonies, or patches, of at least 30 m². Using the same reasoning as in the 1966 paper, he concluded that Shifflett's (1961) data contained colonies of at least 2,900 m² (recall her stations were within a radius of about 30 m).

The living distribution of foraminifera was examined from six stations in Puerto Deseado, Patagonia, by Boltovskoy and Lena (1969). At five stations, 23 core samples were placed 1 m apart, and at the sixth station, 18 cores were taken 10 cm apart. The authors visually contoured the results to show areas of high and low density. The contours showed patches at both the 1 m and 10 cm levels, leading the authors to conclude that foraminifera live in “irregular colonies.” The sampling scheme, with unaligned rows and columns, for the 1 m scheme had five rows with five samples in rows 1, 3, and 5 and four samples in rows 2 and 4. We performed a one-way ANOVA on their data for rows for the species *Buliminella elegantissima* at stations 1 and 4 and for *Elphidium macellum* at stations 3 and 4. These four analyses indicated no significant differences among rows even though contouring (Boltovskoy and Lena, 1969, fig. 3) showed substantial patches. Similarly, for the live population from

TABLE 2. ANOVA for station differences on $\ln(x + 1)$, where x is density of living population. Data from Shifflett (1961).

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Station	5.636	3	1.879	6.247	0.017
Error	2.406	8	0.301		

the 18 samples placed 10 cm apart, there is no significant difference among the four rows. Although the paper has often been cited as evidence for a patchy distribution, the results of the analyses presented herein show a remarkable degree of homogeneity. The results also indicate how difficult it is to interpret visually or to evaluate graphic techniques without statistical analysis.

Buzas (1970) set up a 4×4 grid of stations placed 10 m apart with five replicates at each station in Rehoboth Bay, Delaware. The 80 samples were analyzed using an ANOVA model. For the three most abundant species, there was a significant difference among the 16 stations. For *Elphidium clavatum* one station had a very high density compared with the rest, whereas for *Elphidium tisburyensis* and *Ammonia beccarii*, various paired samples indicate a significant difference over stations. In the multivariate population considering four species with 80 samples at 16 stations, a discriminant analysis indicated only a single station stood out as different from the rest. Following the reasoning of Lynts (1966) for obtaining the size of patches, for comparison only, because the entire area represents 1,600 m², if we consider a single station to be 100 m², then patches of 1,500 m² and 100 m² exist for this multispecies population and for one species of *Elphidium*. Of course, such a configuration is unrealistic because patches exist on all scales (Buzas, 1968; Olsson and Erickson, 1974).

In the Gulf of Saint Lawrence, Schafer (1971) sampled 17 stations at depths from 17 to 53 m. Up to six replicates were taken at each station. The living population showed a good deal of variation, and the coefficient of variation suggested that deeper stations were more uniform. His figure 4 has a range of variation of about 15% to 58% for shallower waters and 8% to 15% for deeper waters. We could not reanalyze because data were not available.

On the Atlantic coast of France, Morvan et al. (2006) examined intertidal foraminifera from 10 stations along three traverses parallel to the shoreline. The traverses were at high marsh, intertidal, and at neap low tide, with each of the stations 10 m apart. The results were described only visually by a series of graphs indicating marked differences in densities between traverses and stations along traverses. No data were available for us to analyze.

SUMMARY

In summary, for stations only a few meters apart statistical analyses of 27 taxa indicated that 15 or 56% had a heterogeneous distribution between stations. Patches are, then, not universal, and about half of the examined

taxa were homogeneously distributed among stations. There is a distinct possibility, however, that patches were not discerned because of limited sample sizes. We will, however, discover the same situation when we examine temporal distributions.

HISTORY, REANALYSIS, AND CRITIQUE OF SEASONAL AND YEARLY STUDIES

Studies of seasonal or temporal variation sometimes use a single station and sometimes multiple stations to measure differences over time. In the latter case, spatial distribution at the multiple stations becomes important for discerning differences. The hypotheses we are interested in are differences in densities between stations, time, and their interaction. In research papers, time is measured by weeks, months, seasons, and years. For simplicity, we grouped weekly and monthly measurements into seasons. Therefore, hypotheses for differences between stations, seasons, years, station $\times$ seasons, station $\times$ years, seasons $\times$ years, and stations $\times$ seasons $\times$ years can be considered. The data from most studies are inadequate to address all of these hypotheses because of their inadequate sampling design. We arrange the review roughly by water depths.

Early research on the life cycle of *Elphidium crispum* indicated an annual cycle (yearly life cycle with alternating generations) of reproduction that could be correlated with the spring or summer phytoplankton bloom (Myers, 1943). Researchers in the new field of foraminiferal ecology at that time assumed that the foraminifera would exhibit a simple seasonal cycle related to phytoplankton blooms that, in turn, was regulated by temperature and the release of nutrients. The observations cited below, however, indicate that this simple cycle is seldom seen, and a search for simple generalities proved to be a search for the will-o'-the-wisp.

In Todos Santos Bay, Baja California, a seasonal traverse consisting of 9 to 16 stations ranging in depth from a few meters to about 900 m was sampled eight times during 1952 by Walton (1955). One sample (no replicates) was taken at each of the stations located about one mile apart. Visual inspection of the data indicated the largest living populations were at a depth of 50 m to 70 m in August, with smaller maxima in June and October. Walton (1955) suggested that the maximum abundance was associated with phytoplankton blooms and seasonal maximum temperature in August.

Phleger and Lankford (1957) recorded living populations from 32 stations distributed in the Aransas, Mesquite,

and San Antonio Bays, Texas. Sampling times were August and November 1954 and January, March, May, and June 1955. Visual inspection of the data indicated that the highest densities occurred in upper San Antonio Bay near the mouth of the Guadalupe River. In January and November individuals of *Ammobaculites salsus* were especially plentiful. In the lower bay the maximum density of each station appeared to occur independently of the others (possible season $\times$ station interaction). These authors noted that histograms of the test size distribution indicated reproduction was occurring during all seasons of the year. Although replicates were not usually taken, during March of 1955 they took four samples at station 15 and found a living population ranging from 19 to 23 individuals. At the same time, five samples collected from station 21 yielded 10–19 individuals. This surprisingly small variation, which was probably due to luck and the low densities observed, led them to conclude that variation in the field is within laboratory error. It also encouraged other workers, unfortunately, to continue sampling designs with only one sample per station.

The eight stations sampled by Parker and Athearn (1959) in the marsh at Popponesset Bay, Massachusetts, were examined for living foraminifera during the months of August, October, and December 1956 and February, April, June, and September 1957. Visual inspection of the data indicated high densities were recorded in August 1958 and June 1957. The August high was for *Ammobaculites dilatatus*, and the June high was for *Protelphidium tisuryense*. All species exhibited low densities in December 1956.

Berkeley et al. (2008) sampled a tropical marsh consisting of an upper mangrove environment (three stations) and a lower mangrove-mudflat environment (3 stations) in January and August 2005 in north Queensland, Australia. The abundance of living individuals was recorded every centimeter to a depth of 10 cm and at intervals to a depth of 90 cm. At each of the six stations the authors performed an ANOVA to compare the density of species between the summer and winter sampling. Five species had significantly higher densities in summer, and five had significantly higher densities in winter; 20 species showed no significant difference between seasons. In the upper mangrove environment, seven species were significantly different between seasons, whereas in the lower mangrove-mudflat environment only three were significantly different seasonally. Because of the lack of replication the interaction hypotheses could not be tested. However, the alternation of seasons for significance suggests interaction was occurring.

In Santa Monica Bay, California, Reiter (1959) established seven intertidal stations distributed over 58 km. He sampled weekly from September 1956 until April 1957, a total of 30 sampling times. The original counts per 100 g of sediment were not given, and plots show abundance data for only three stations. Visual inspection of the plots shows a great deal of variation and high abundances in November and April at station 1, none at station 2, or in October and February at station 5.

Boltovskoy (1964) sampled a single station weekly from April 1961 to May 1963 at Puerto Deseado, Patagonia, Argentina. A few weeks were missed, but in all 94 samples were taken and examined for living individuals. For *Elphidium macellum*, reproduction as evidenced by the appearance of juveniles began in September and concluded in March. In both years maximum densities (adults and juveniles) occurred in January. Boltovskoy concluded that like *Elphidium crispum*, a closely related species, the life span of an individual of *E. macellum* was also one year. Although represented by many fewer individuals, *Quinqueloculina seminulum* exhibited the same pattern. *Rotalia beccarii*, however, had living juveniles all year and indicated a short period of reproductive activity. A one-way ANOVA on the standing crop in this study by Murray (2000) indicated a significant difference between years.

Buzas (1965) sampled a single traverse in Long Island Sound seven times during 1961 and 1962. In 1961 the sampling months were June and October, whereas in 1962 they were January, March, June, September, and November. Stations were located about 1 nautical mile (1.85 km) apart. The central portion of the traverse consisted of 10 stations, the *Eggerella advena* zone (mean depth of 29 m), and showed less spatial variation than did shallower waters. This zone was analyzed statistically by the author for seasonal differences using the Wilcoxon two-sample test. For the total living population, October 1961 and June 1962 showed maximum densities. The October 1961 maximum was due to *E. advena*, whereas the June 1962 maximum was due to *E. advena*, *Elphidium clavatum*, and *Buccella frigida*. Although *E. clavatum* exhibited a maximum only in June 1962, Buzas noted that juveniles of this species were present throughout the year. He also speculated that the seasonal variation correlated in a general way with the phytoplankton cycle in Long Island Sound.

In Narragansett Bay, Rhode Island, Brooks (1967) examined the standing crop of *Ammonia beccarii* at a single station each month during 1963. During most of the sample times, six replicate cores were taken, and each of the top 4 cm was enumerated. After determining that the transformation of the counts to $\ln(x + 1)$ was best to

normalize the data, he analyzed the standing crop using ANOVA. The results indicated no significant difference between months at any of the four levels.

Haake (1967) examined populations of *Cribronionion excavatum* at Flensburg (1962), Kiel (1962–1964), Fehmarn Belt (1962–1964), and a tidal flat in the North Sea (1963–1964). At Kiel, temperature ranged from 1°C to 12°C, and salinity ranged from 16 to 25. Visual inspection indicated all localities except for the North Sea achieved high densities in summer. At all localities reproduction was observed throughout the year, and the severe winter of 1962–1963 resulted in low densities. Data were not available for quantitative reanalysis.

In Christchurch Harbour, England, Murray (1968) sampled 60 stations during September 1959, April 1960, and July 1960. Of these 60, only 39 could be sampled in January 1960 because of weather conditions. Through visual inspection he recognized four groups of fauna by their chlorinity preference and traced their seasonal changes in distribution and abundance within the estuary. For all species, minimum abundances were observed in winter. *Elphidium excavatum* exhibited seasonal changes in distribution and achieved maximum abundance in spring. Size relationships for individuals of each species indicated reproduction occurred once a year. Seasonal changes in distribution and abundance were attributed primarily to chlorinity and temperature.

Lutze (1968) sampled three stations monthly in the Bottsand Lagoon near Kiel, Germany, from December 1964 to June 1967. The temperature range was from about 0°C to 30°C, and salinity varied from about 10 to 18. The dominant species was *Cribronionion articulatum*. Visual examination indicated maximum densities in 1965 during September and November, but size measurement of tests indicated reproduction in the spring of 1965 resulted in the high autumn densities. Some juveniles also appeared all year long. In January 1966 a large decrease in density occurred, and densities remained low throughout 1966 and most of 1967. Murray (2000) performed a one-way ANOVA on the standing crop that indicated a significant difference between years.

Haman (1969) sampled Llandanwg Lagoon on the west coast of Wales at monthly intervals from February 1965 to January 1966. The surface temperature varied from 1°C to 17°C, and salinity ranged from 3 to 30. Only *Elphidium excavatum* had sufficient abundance in the living population to record seasonal changes. Visual examination indicated maximum densities occurred in spring and fall.

In the Choptank River, a subestuary of the Chesapeake Bay, Buzas (1969) sampled three stations for 12 successive months beginning in December 1965. At each station

four replicates were taken, and the densities of *Ammonia beccarii*, *Ammobaculites exiguus*, and *Elphidium clavatum* were recorded along with bottom temperature, salinity, oxygen, and chlorophyll *a*, *b*, and *c*. The temperature ranged from 1°C to 27°C, and the salinity varied from 11 to 16. The data were analyzed by a general linear model consisting of vectors for periodicity and environmental variables. Periodicity was evident throughout but varied among species as well as between stations, indicating continuous reproduction. The environmental variables were significant as a group. Because we are particularly interested in interaction hypotheses in the present study, we reanalyzed the data by two-way ANOVA with hypotheses for station differences, seasonal differences, and their interaction. All hypotheses were significant except for station differences for *A. exiguus*. For *E. clavatum* spring and summer showed maxima (Table 3, Figures 4 and 5), for *A. beccarii* summer and fall had maxima (Table 4, Figures 6 and 7), and for *A. exiguus* summer had a maximum (Table 5, Figures 8 and 9). Notice, however, that the stations displayed different behaviors with seasonal abundances (Figures 5, 7, and 9).

In the Rappahannock River, a subestuary of the Chesapeake Bay, Ellison and Nichols (1970) collected samples during five sampling periods from June 1962 to December 1965. Temperature varied from 4°C to 28°C, and salinity ranged from 0 to 16.5. Four biofacies were recognized: (1) a basin biofacies dominated by *Elphidium clavatum*, (2) a shoal biofacies dominated by *Ammobaculites crassus*, (3) an outer marsh biofacies dominated by *Miliammina fusca*, and (4) an inner marsh biofacies dominated by *Ammobaculites salsa*. The authors believed from visual inspection that densities of the species and, consequently, boundaries of the biofacies, varied with seasons and years.

Boltovskoy and Lena (1969) sampled weekly from February 1964 to March 1966 in the Quinta Island area, Puerto Deseado, Patagonia. Densities of *Buliminella*

TABLE 3. ANOVA for season, station, and interaction differences on $\ln(x + 1)$, where x is density of *Elphidium clavatum*. Data from Buzas (1969).

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Season	7.754	3	2.585	5.004	0.003
Station	436.210	2	218.105	422.211	0.000
Season × station	15.959	6	2.660	5.149	0.000
Error	68.188	132	0.517		

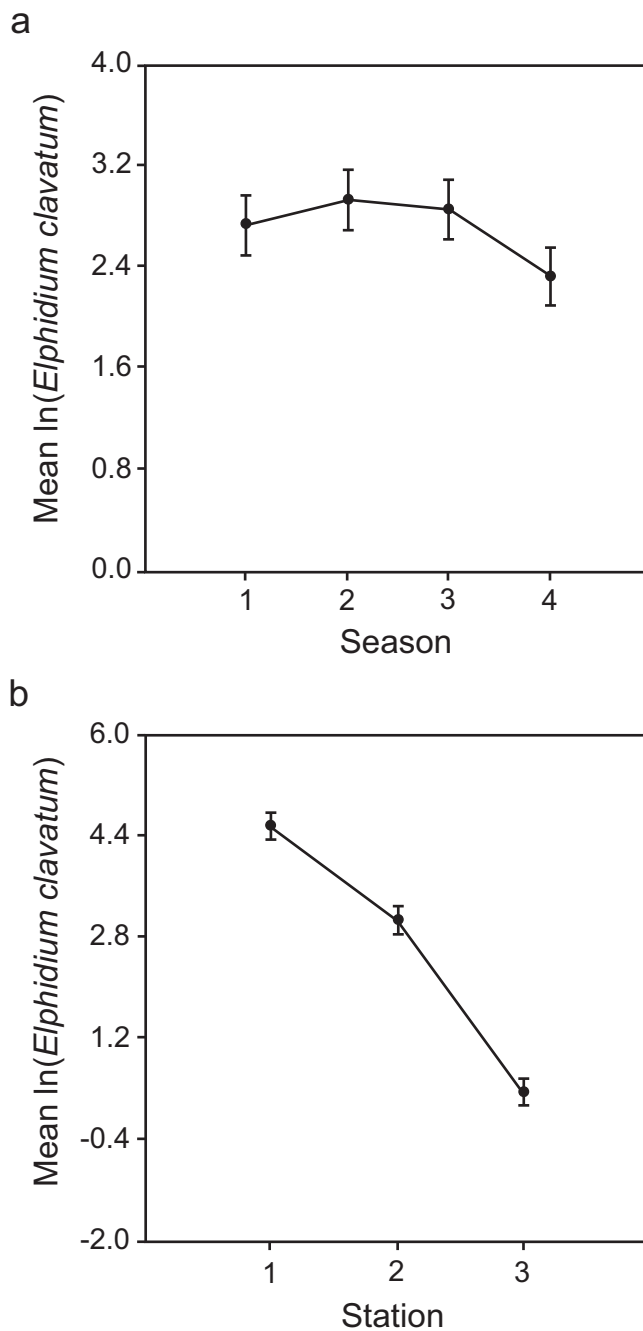


FIGURE 4. Mean number of $\ln(\text{Elphidium clavatum})$ in the Choptank River, Maryland. Data from Buzas (1969). (a) Seasons: 1 = winter, 2 = spring, 3 = summer, 4 = fall. (b) Stations 1 (downstream) to 3 (upstream). Stations 1 and 2 are about 10 km apart, and stations 2 and 3 are about 4 km apart.

elegantissima, *Elphidium articulatum*, *Epistominella exigua*, *Rotalia beccarii*, *Elphidium gunteri*, and *Buccella frigida* were recorded. Most species exhibited a maximum density in the winter of 1964 and, except for *B. frigida*,

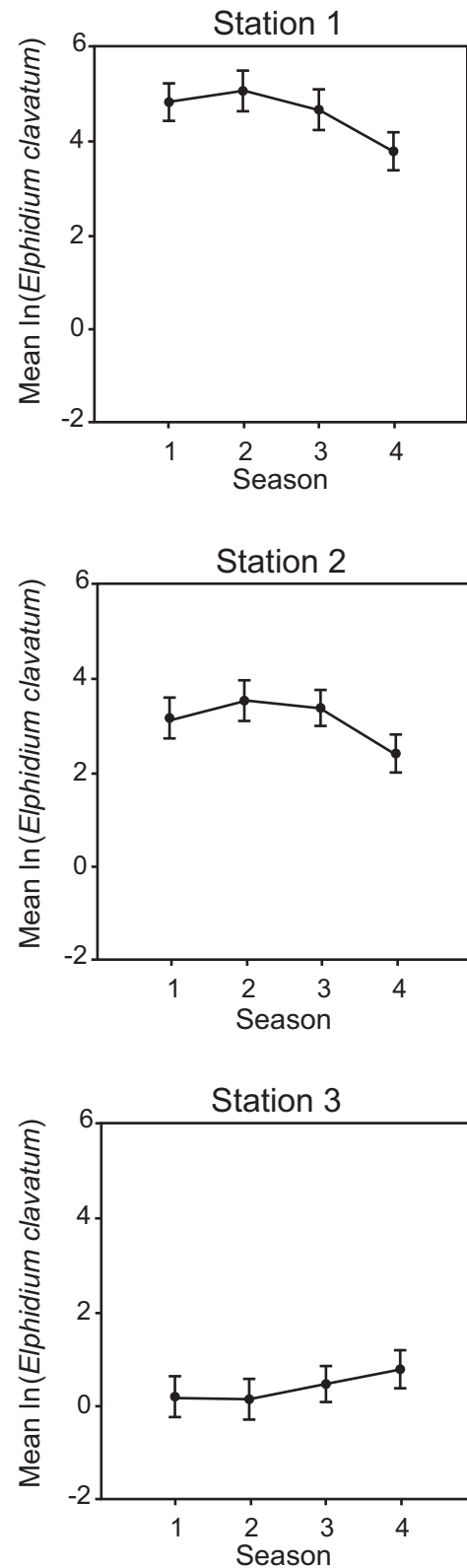


FIGURE 5. Mean number of $\ln(\text{Elphidium clavatum})$ in the Choptank River, Maryland, at stations 1, 2, and 3 during seasons 1 (winter), 2 (spring), 3 (summer), and 4 (fall). Data from Buzas (1969).

TABLE 4. ANOVA for season, station, and interaction differences on $\ln(x + 1)$, where x is density of *Ammonia beccarii*. Data from Buzas (1969).

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Season	17.521	3	5.840	6.506	0.000
Station	19.428	2	9.714	10.821	0.000
Season × station	14.992	6	2.499	2.783	0.014
Error	118.496	132	0.898		

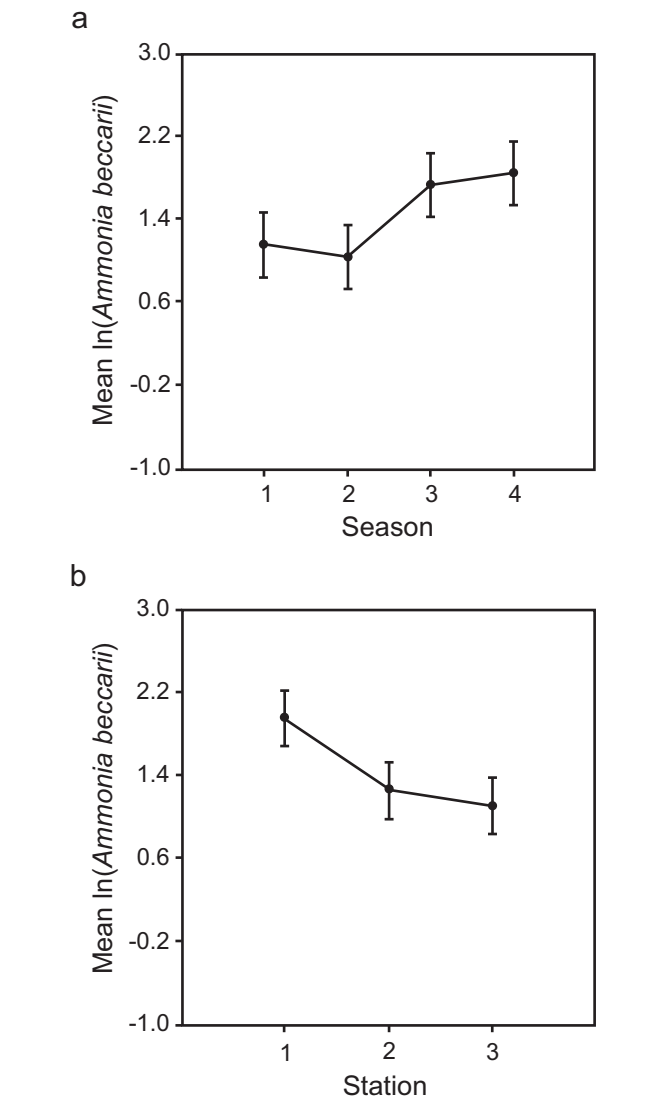


FIGURE 6. Mean number of $\ln(Ammonia beccarii)$ in the Choptank River, Maryland. Data from Buzas (1969). (a) Seasons: 1 = winter, 2 = spring, 3 = summer, 4 = fall. (b) Stations 1 (downstream) to 3 (upstream). Stations 1 and 2 are about 10 km apart, and stations 2 and 3 are about 4 km apart.

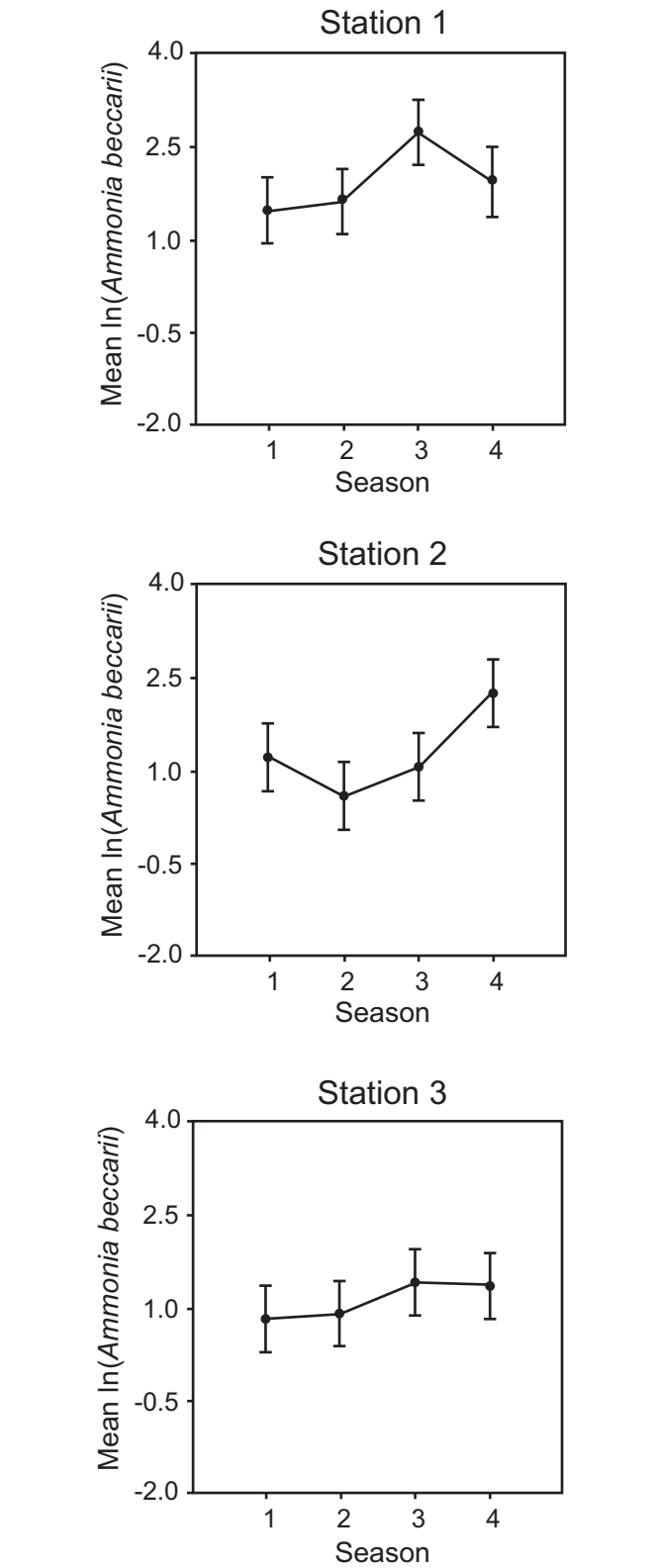


FIGURE 7. Mean number of $\ln(Ammonia beccarii)$ in the Choptank River, Maryland, at stations 1, 2, and 3 during seasons 1 (winter), 2 (spring), 3 (summer), and 4 (fall). Data from Buzas (1969).

TABLE 5. ANOVA for season, station, and interaction differences on $\ln(x + 1)$, where x is density of *Ammobaculites exiguus*. Data from Buzas (1969).

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Season	22.575	3	7.525	13.133	0.000
Station	3.186	2	1.593	2.780	0.066
Season $\times$ station	10.038	6	1.673	2.920	0.010
Error	75.632	132	0.573		

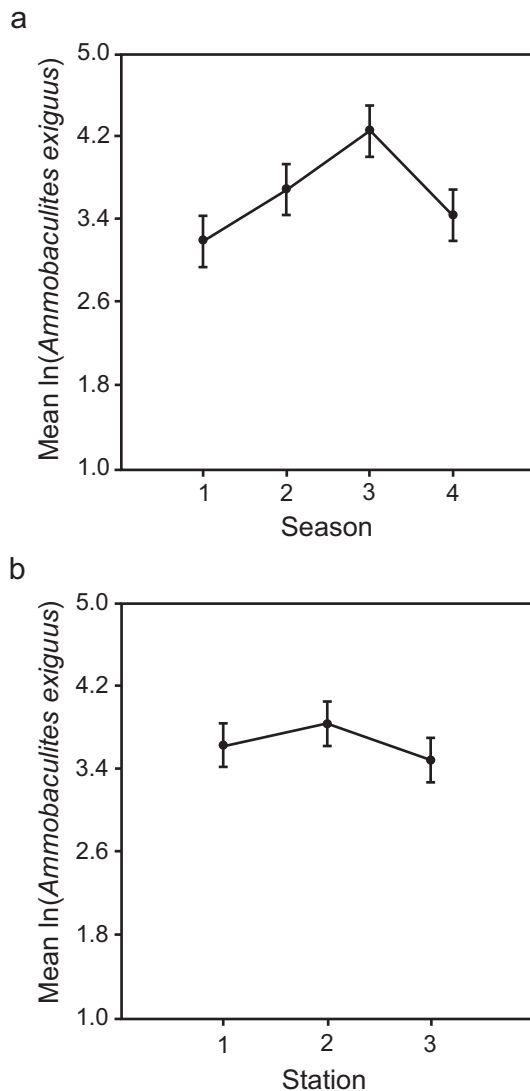


FIGURE 8. Mean number of $\ln(Ammobaculites\ exiguus)$ in the Choptank River, Maryland. Data from Buzas (1969). (a) Seasons: 1 = winter, 2 = spring, 3 = summer, 4 = fall. (b) Stations 1 (downstream) to 3 (upstream). Stations 1 and 2 are about 10 km apart, and stations 2 and 3 are about 4 km apart.

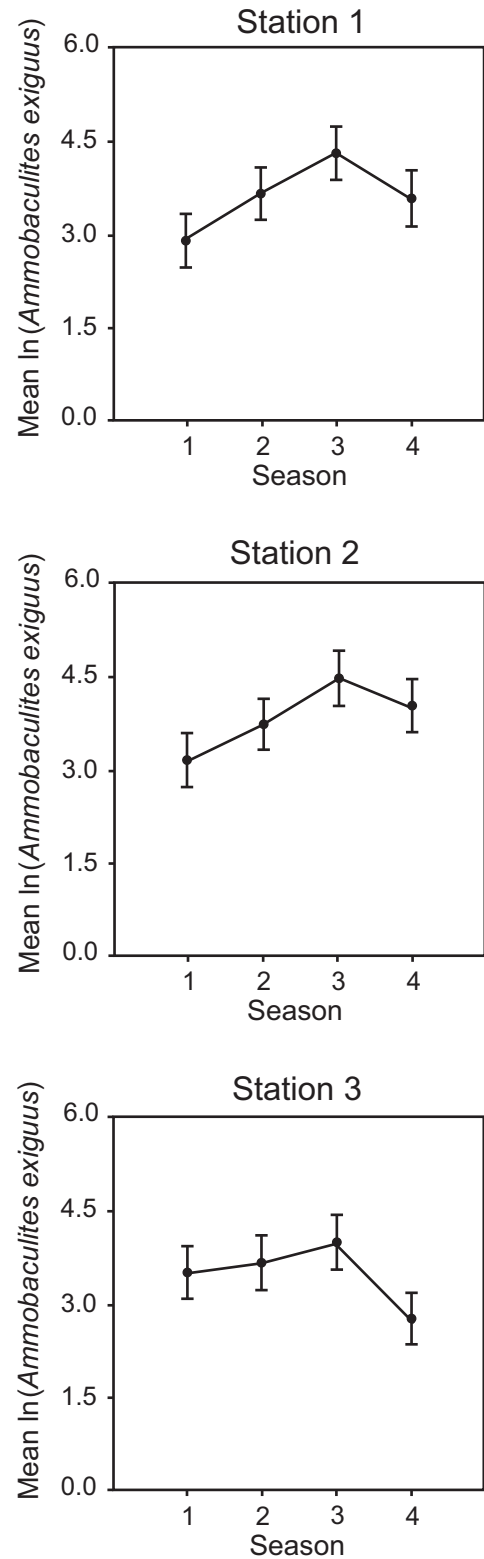


FIGURE 9. Mean number of $\ln(Ammobaculites\ exiguus)$ in the Choptank River, Maryland, at stations 1, 2, and 3 during seasons 1 (winter), 2 (spring), 3 (summer), and 4 (fall). Data from Buzas (1969).

indicated reproduction throughout the year. The very high densities observed in the winter of 1964 were not repeated in 1965. The authors commented that the high densities observed were mutual for all species at the same time. Murray (2000), using these data, performed a one-way ANOVA on the standing crop (number of living individuals at a particular time) and found significant differences between years.

Daniels (1970) sampled 11 stations from the open-ocean mouth to the terminus of the Limski Canal, Croatia, on a monthly basis from September 1967 until October 1968. Temperature varied from 9°C to 25°C, and salinity ranged from 37 to 38. Five faunal zones were recognized, and Daniels plotted the relative abundance of the major species and groups on a monthly basis per station. He noted that rotalids were more abundant in summer, and textularids were more abundant in winter. At six stations he plotted the density of *Nonionella opima*. The plots show maxima during summer and fall; however, stations do not exhibit similar patterns of differences even when they are in the same faunal zone.

Wefer (1976) sampled sediment and algae from July 1973 to May 1975 at two- to five-week intervals in the Eckernförder Bay, western Baltic Sea. Temperature in the bay varied from 2°C to 16°C, and salinity ranged from 18 to 24. He was concerned mainly with carbonate production yet did provide plots for changes in relative abundance over the sampling period. For *Elphidium excavatum excavatum*, the summer of 1974 was a period of high abundance. The monthly variation for all species was quite pronounced. Stations located at depths from 8 m to 27 m did not show the same patterns of differences. In this case, Murray (2000) reanalyzed and performed a one-way ANOVA on the standing crop and found significant differences between years.

Fourteen stations were sampled monthly from November 1999 to October 2000 by Debenay et al. (2006) in the Vie estuary, France. This temperate estuary had a range in temperature from 3.4°C to 27°C and in salinity from 0 to 45. In total, 13 environmental variables were measured. The densities of the five dominant species (*Haynesina germanica*, *Ammonia tepida*, *Cribrorhynchium excavatum*, *Brizalina striatula*, and *Trochammina inflata*) were all influenced by an interplay of oceanic and estuarine influences that varied seasonally.

In Jamaica, West Indies, Buzas et al. (1977) sampled two *Thalassia* habitats, one in a back-reef flat at a depth of less than 1 m and the other at about 3 m depth in Discovery Bay. Each habitat was sampled with four replicates each month from November 1969 to October 1970. Each

locality then had 48 observations for 12 successive months. In all, 143 species were recorded, 115 at the back-reef flat and 117 in Discovery Bay. Sediment temperature varied from about 26°C to 29°C. At the back-reef flat, salinity varied from about 28 to 35, whereas in Discovery Bay it ranged from 33 to 35. Thirteen environmental variables were measured. The 19 species with densities greater than 2.00/20 mL of sediment were analyzed by a general linear model. The environmental variables were not significant for any of the species. Two species had significant station and periodicity. Eight species exhibited no significant differences of any kind. The seven species with significant periodicity each had maxima in spring and summer. The dominant species, *Ammonia beccarii* and *Nonionella auricula*, had no significant test results, whereas *Amphistegina gibbosa* occurred almost exclusively at the 3 m deep station in Discovery Bay.

In Samish Bay, Washington, Jones and Ross (1979) sampled 10 intertidal stations during the months of April, June, July, August, October, November, and December 1976 and January and March 1977. The temperature range was about 5°C to 22°C, and salinity ranged from 21 to 27. The arenaceous species *Trochammina pacifica* and *Miliammina fusca* had a nearly constant number of living individuals throughout the sampling interval, whereas the calcareous species of *Elphidium* and *Ammonia beccarii* had the highest populations during the summer months.

Scott and Medioli (1980) examined living and total populations qualitatively during the period of September 1975 to August 1978 in the salt-marsh sequence at Chez-zetcook Inlet, Nova Scotia. Temperature varied from -5°C to 20°C, and salinity ranged from 1 or 2 to 28. Except for *Miliammina fusca*, living populations were largest in summer; however, the density of living populations varied greatly from year to year.

Murray (1983) sampled an intertidal station in the Exe estuary, England, on a monthly basis from January 1979 to July 1981 (31 sampling times). Temperature ranged from 5°C to 20°C, and salinity varied from 18 to 34. Although duplicate samples were taken because of the work intensity, only one sample was used throughout the study. However, in January 1979 and February 1979 duplicate samples were counted and yielded 255 and 329 and 168 and 201 tests, respectively. Like Phleger and Lankford (1957), Murray unfortunately felt the results were sufficiently close to warrant using only one sample in the rest of the study. The analysis focused on the most abundant species, *Nonion depressulus*. Size frequency distributions of test diameter indicated eight or nine generations per year. Maximum densities occurred in spring, summer, or

fall and did not coincide among years. However, Murray (2000) performed a one-way ANOVA on the standing crop and found no differences between years.

Erskian and Lipps (1987) followed populations of *Glauertella ornatissima* on algae and in sediments near the Bodega Marine Laboratory in northern California. Single observations were made weekly from 1975 to 1977 on algae as well as within the sediment. Water temperature varied from about 5°C to 13°C. Visual inspection indicated that this species has an orderly cycle of gamont and agamont populations. Agamont densities were high in the winter of 1976 and spring of 1977, with much higher population densities in 1977.

Wilson and Dawe (2006) reanalyzed the data of Erskian and Lipps (1987) quantitatively by time series analysis. A plot of two-year time series indicated maximum abundances differed between years, but 12 month seasonality could be confirmed only provisionally.

A study concentrating on the vertical distribution of benthic foraminifera was undertaken by Barmawidjaja et al. (1992). A single station in the Adriatic Sea at a water depth of 32 m was sampled seven times between December 1988 and November 1989. During this study sampling temperature varied from 9.5°C to 16.5°C, and salinity ranged from 37.26 to 38.79. The authors grouped their species into three depth categories based on their observed vertical distribution and found “no clear cut distinction between exclusively infaunal and exclusively epifaunal taxa” (p. 299). Maximal densities occurred in winter and minima in summer and fall. However, no replicates were made, and the authors state, “It is impossible to determine the significance of the differences between samples.”

In the Indian River Lagoon, Florida, Buzas and Severin (1993) sampled a bare-sand station and a grass-surface station (mostly *Halodule wrightii* with some *Thalassia testidium*) that were about 10 m apart. They collected four replicates at each station every two weeks from 27 March to 6 November 1978. There were 17 sampling times and a total of $N = 136$ samples. The densities of five taxa were enumerated, and 10 environmental variables were measured. The taxa *Quinqueloculina* (75%), *Elphidium* (14%), and *Ammonia* (8%) made up 97% of the living population. Temperature varied from 22°C to 32°C, and salinity ranged from 20 to 38. The observations were analyzed by a general linear model with vectors for station differences, environmental variables, time, and interaction of time with station differences. Surprisingly, overall densities between bare sand and grass were not significant for any of the three abundant taxa. The group of

environmental variables was significant for all three taxa. Time and interaction with station differences were significant for all three taxa. For *Quinqueloculina* maximum densities occurred in summer on the grass surface and in spring on bare sand. For *Elphidium* maximum densities occurred in summer and fall on the grass surface and in spring on bare sand. For *Ammonia* maximum densities occurred in summer on the grass surface and in spring, summer, and fall on bare sand.

Basson and Murray (1995) enumerated four infaunal taxa in duplicate samples over a 25 month period (February 1991 to February 1993) from a lower intertidal zone in Bahrain, Persian Gulf. The temperature ranged from 17°C to 31°C, and the salinity in this hypersaline environment was a constant 45. The authors presented their data in an appendix with one observation in November 1992 missing. Using the proportions observed in October and November 1992 in the other samples, we calculated the expected values for the missing observations. We then analyzed the data by two-way ANOVA's for differences between years and seasons for each of the four taxa. For all taxa, as pointed out by the authors from visual inspection, a significant increase in densities occurred between 1991 and 1992. For *Ammonia beccarii* (Table 6, Figure 10) seasonal differences were not statistically significant. For *Elphidium advenum*, *Brizalina* (or *Bolivina*) *pacifica*, and *Nonion* sp. (Tables 7, 8, 9, Figures 11, 12, 13), however, seasonal differences were statistically significant. Fall was the time of maximum abundance for each taxon. Size data for *A. beccarii* indicate that this species was reproducing throughout the year.

The intertidal foraminifera from two stations in Hamble estuary, England, were sampled over a 27 month period by Murray and Alve (2000). Station 1 was located at neap low water, whereas station 2 was located in the mid-intertidal zone. Temperature ranged from about 4°C to 25°C, and salinity varied from about 25 to 35. Two replicates were taken at the stations during the 24 month period from March 1994 to February 1996. Three species,

TABLE 6. ANOVA for season and year differences on $\ln(x + 1)$, where x is density of *Ammonia beccarii*. Data from Basson and Murray (1995).

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Season	2.930	3	0.977	1.493	0.230
Year	5.838	2	2.919	4.462	0.017
Error	28.783	44	0.654		

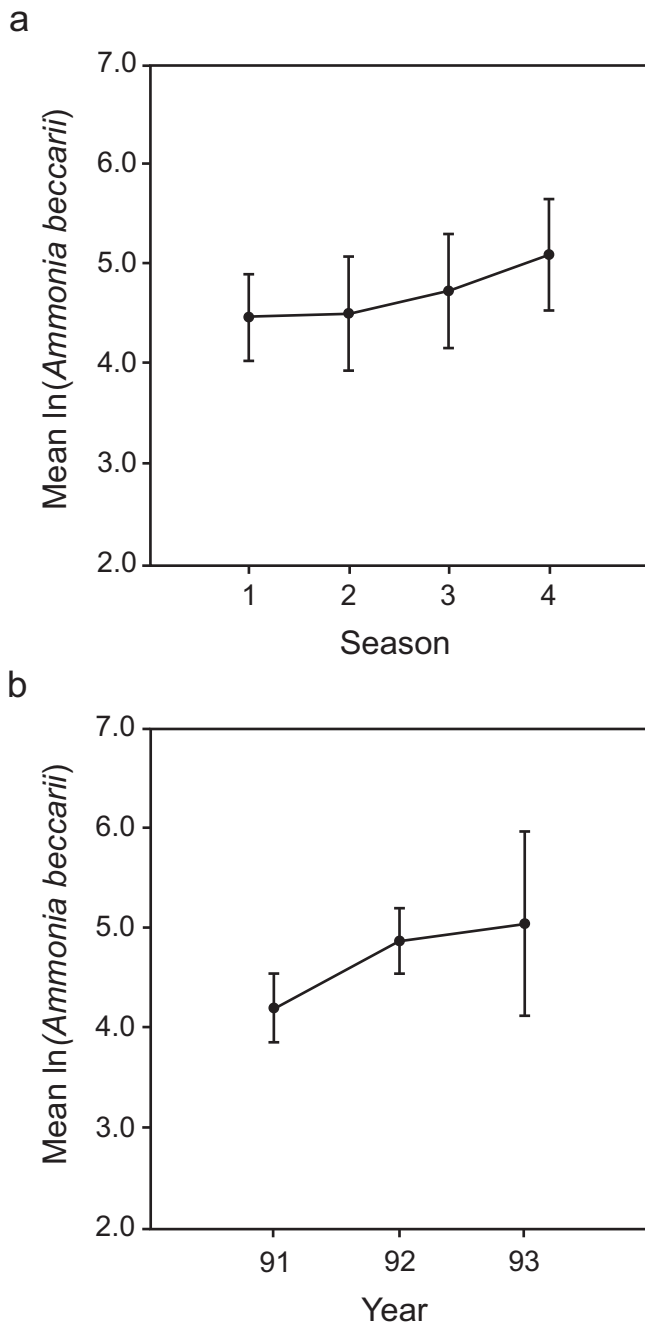


FIGURE 10. Mean number of *ln(Ammonia beccarii)* in the lower intertidal zone in Bahrain, Persian Gulf. Data from Basson and Murray (1995). (a) seasons: 1 = winter, 2 = spring, 3 = summer, 4 = fall. (b) Years.

Ammonia beccarii (forma *tepida*), *Elphidium excavatum*, and *Haynesina germanica*, constituted most of the standing crop (overall density). Juveniles were present throughout the year, indicating continuous reproduction. Plots of

TABLE 7. ANOVA for season and year differences on $\ln(x + 1)$, where x is density of *Elphidium advenum*. Data from Basson and Murray (1995).

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Season	12.176	3	4.059	4.104	0.012
Year	12.070	2	6.035	6.103	0.005
Error	43.510	44	0.989		

TABLE 8. ANOVA for season and year differences on $\ln(x + 1)$, where x is density of *Bolivina pacifica*. Data from Basson and Murray (1995).

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Season	40.368	3	13.456	6.210	0.001
Year	61.784	2	30.892	14.256	0.000
Error	95.347	44	2.167		

TABLE 9. ANOVA for season and year differences on $\ln(x + 1)$, where x is density of *Nonion* sp. Data from Basson and Murray (1995).

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Season	24.664	3	8.221	3.609	0.020
Year	48.344	2	24.172	10.612	0.000
Error	100.225	44	2.278		

standing crop indicated visually that there was cyclicity at station 2 but not at station 1. We used their data for statistical hypotheses testing by performing a three-way ANOVA for each of the three species. The hypotheses for differences were: station differences in density were equal; equality over years; equality over seasons; and equality over interactions of stations $\times$ years, stations $\times$ seasons, years $\times$ seasons, and stations $\times$ years $\times$ seasons. For each of the three species there was a significant difference between stations as well as seasons (Tables 10, 11, 12, Figures 14, 15, 16, 17, 18, 19), but yearly differences were significant for only *A. beccarii* (Table 10). All the analyses point to summer as a time of minimum density (Figures 14, 16, 18). Maxima occur in winter and fall for *A. beccarii* (Figure 14), in fall for *E. excavatum* (Figure 16), and in

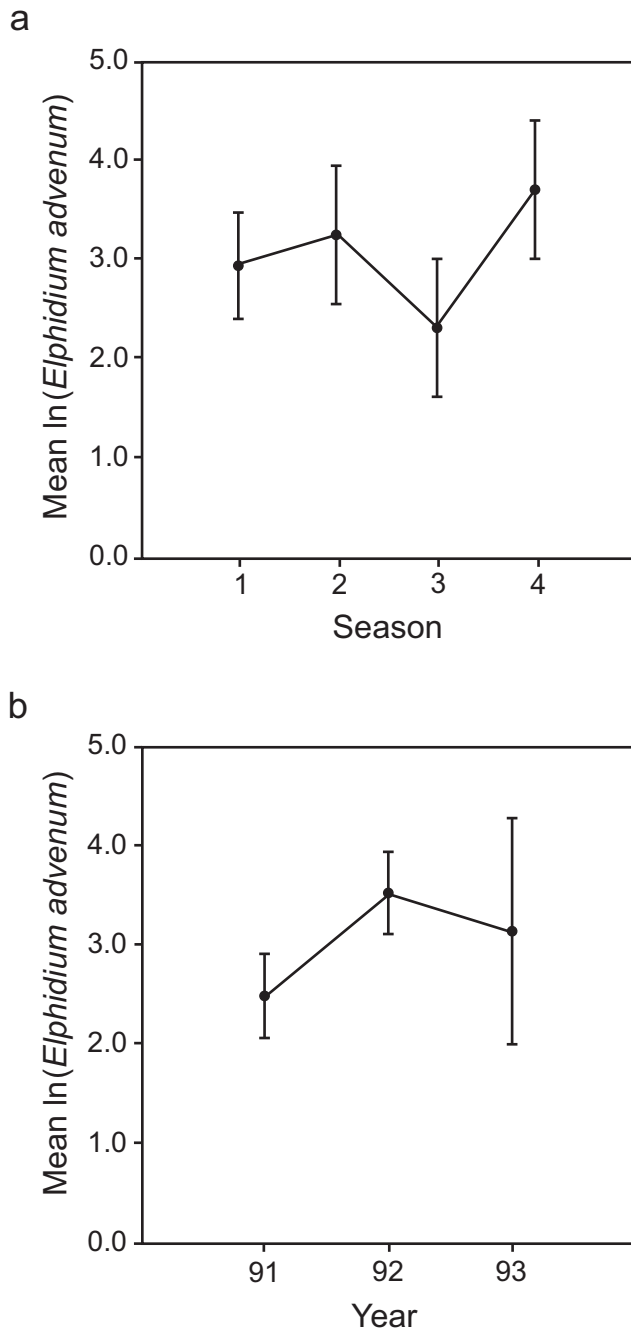


FIGURE 11. Mean number of $\ln(\text{Elphidium advenum})$ in the lower intertidal zone in Bahrain, Persian Gulf. Data from Basson and Murray (1995). (a) Seasons: 1 = winter, 2 = spring, 3 = summer, 4 = fall. (b) Years.

winter, spring, and fall for *H. germanica* (Figure 18). The interaction of stations $\times$ years $\times$ season was significant for each of the three species, but the plots vary for each of the species (Figures 15, 17, 19).

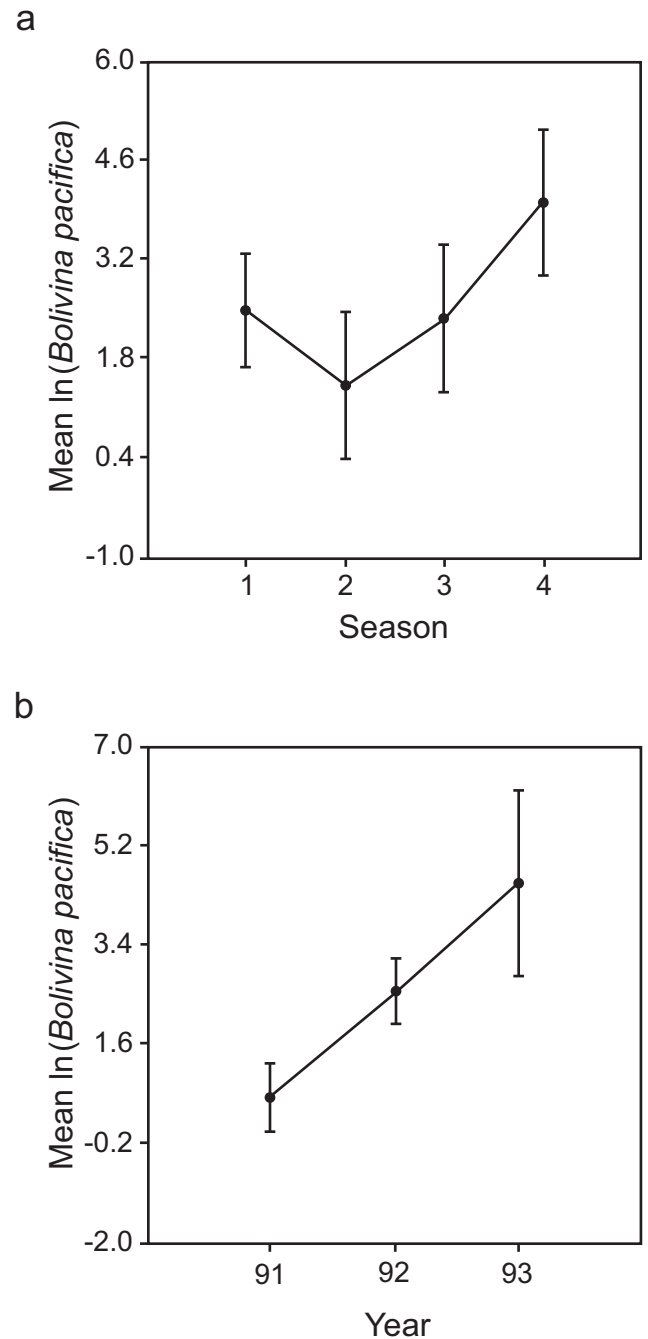


FIGURE 12. Mean number of $\ln(\text{Bolivina pacifica})$ in the lower intertidal zone in Bahrain, Persian Gulf. Data from Basson and Murray (1995). (a) Seasons: 1 = winter, 2 = spring, 3 = summer, 4 = fall. (b) Years.

The same two stations were examined to a depth of 4 cm during the first 14 months (Alve and Murray, 2001). The maximum abundance for all species was in the upper 0.25 cm of the sediment, and no change in the vertical distribution

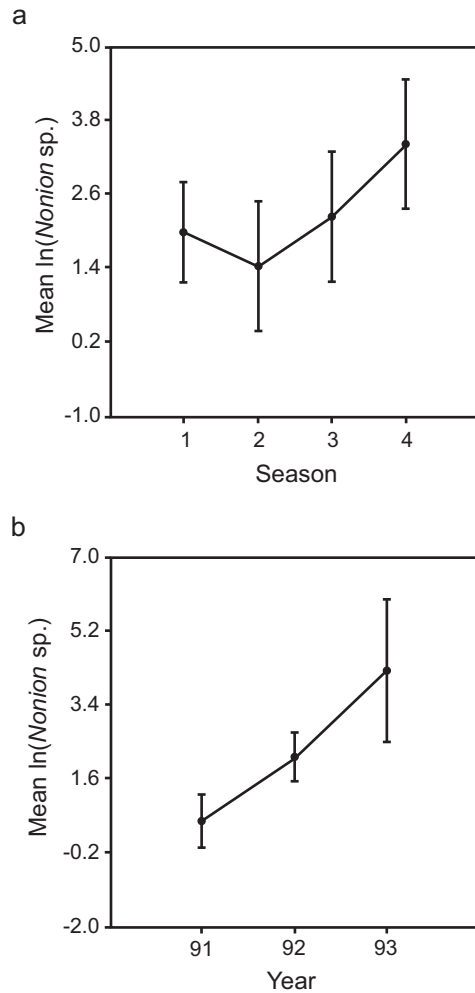


FIGURE 13. Mean number of *ln(Nonion sp.)* in the lower intertidal zone in Bahrain, Persian Gulf. Data from Basson and Murray (1995). (a) Seasons: 1 = winter, 2 = spring, 3 = summer, 4 = fall. (b) Years.

TABLE 10. ANOVA for season, year, station, and their interaction differences on $\ln(x + 1)$, where x is density of *Ammonia beccarii*. Data from Murray and Alve (2000).

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Season	19.166	3	6.389	20.043	0.000
Year	6.846	1	6.846	21.479	0.000
Station	19.471	1	19.471	61.085	0.000
Season $\times$ year	16.301	3	5.434	17.047	0.000
Season $\times$ station	5.088	3	1.696	5.321	0.002
Year $\times$ station	1.082	1	1.082	3.395	0.069
Season $\times$ year $\times$ station	7.099	3	2.366	7.423	0.000
Error	25.500	80	0.319		

TABLE 11. ANOVA for season, year, station, and their interaction differences on $\ln(x + 1)$, where x is density of *Elphidium excavatum*. Data from Murray and Alve (2000).

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Season	6.825	3	2.275	8.890	0.000
Year	0.785	1	0.785	3.066	0.084
Station	1.184	1	1.184	4.628	0.034
Season $\times$ year	11.396	3	3.799	14.844	0.000
Season $\times$ station	0.985	3	0.328	1.284	0.286
Year $\times$ station	0.408	1	0.408	1.594	0.210
Season $\times$ year $\times$ station	2.899	3	0.966	3.776	0.014
Error	20.473	80	0.256		

TABLE 12. ANOVA for season, year, station, and their interaction differences on $\ln(x + 1)$, where x is density of *Haynesina germanica*. Data from Murray and Alve (2000).

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Season	15.591	3	5.197	21.417	0.000
Year	0.111	1	0.111	0.459	0.500
Station	11.340	1	11.340	46.733	0.000
Season $\times$ year	0.953	3	0.318	1.308	0.277
Season $\times$ station	0.069	3	0.023	0.095	0.963
Year $\times$ station	0.633	1	0.633	2.608	0.110
Season $\times$ year $\times$ station	4.871	3	1.624	6.691	0.000
Error	19.413	80	0.243		

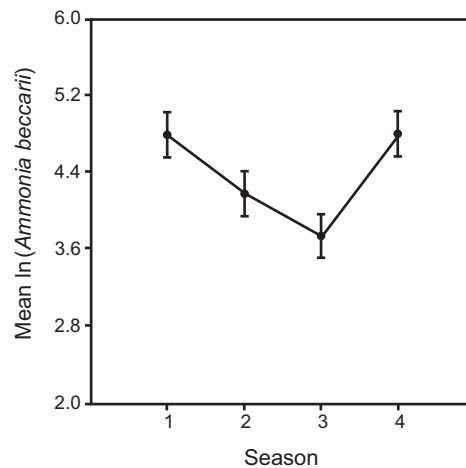


FIGURE 14. Mean number of *ln(Ammonia beccarii)* at two stations in the Hamble estuary, England. Seasons: 1 = winter, 2 = spring, 3 = summer, 4 = fall. Data from Murray and Alve (2000).

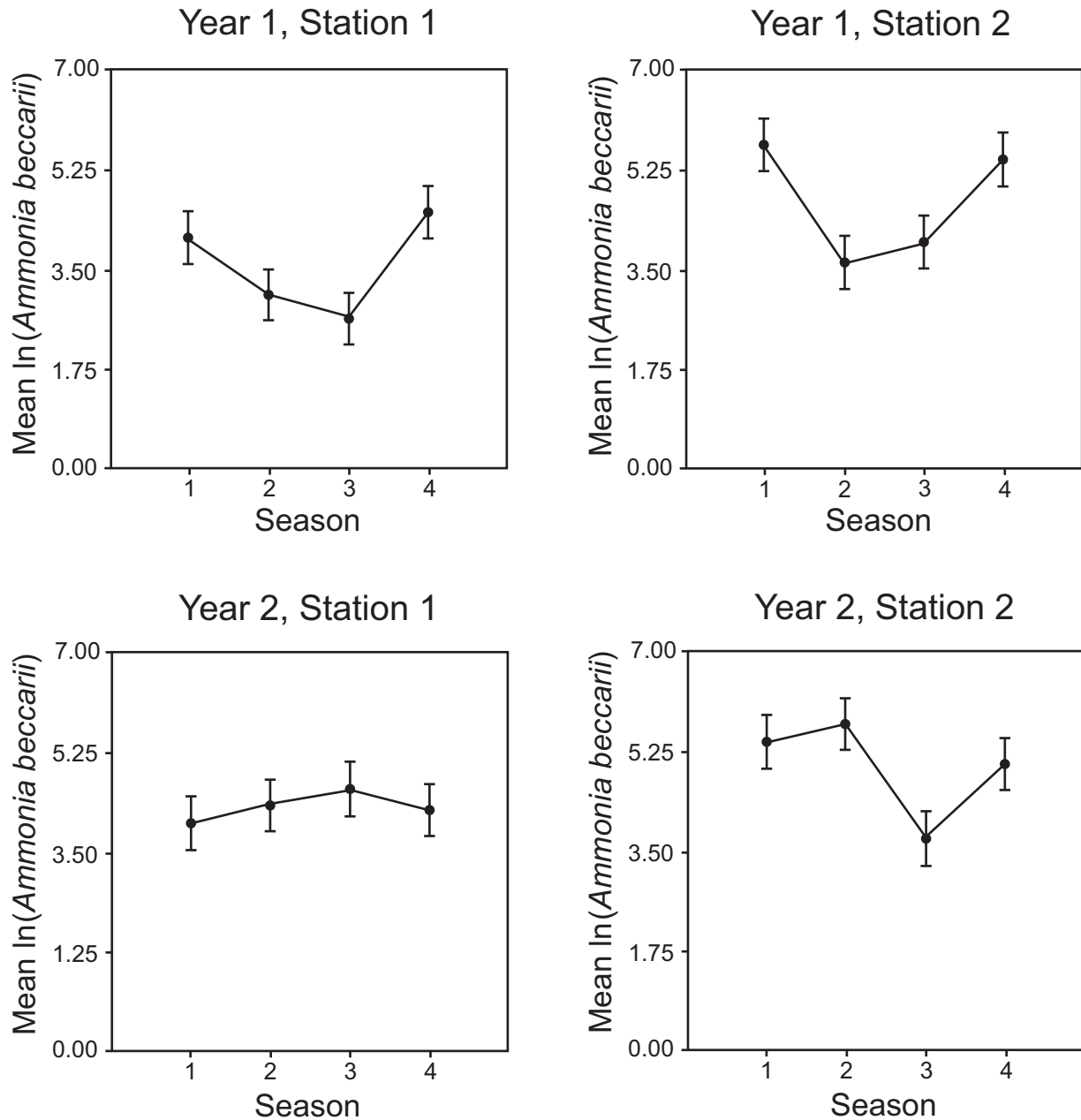


FIGURE 15. Mean number of $\ln(Ammonia\ beccarii)$ in the Hamble estuary, England, during two years from March 1994 to February 1996 at station 1 near neap tide and at station 2 in mid-intertidal during seasons 1 (winter), 2 (spring), 3 (summer), and 4 (fall). Data from Murray and Alve (2000).

of the foraminifera was observed. The low abundances in the subsurface were attributed to a lack of bioturbation in this area. A plot of the cumulative number of individuals versus the cumulative number of species indicated species accumulated with time faster at station 2. Buzas and Hayek (2011) evaluated the within-community beta diversity for these two stations, and the regression analysis of cumulative H versus $\ln N$ yielded a regression coefficient of $\beta_{1H} = 0.02$

(not significant) for station 1 and $\beta_{1H} = 0.18$ (significant) for station 2, which is consistent with the cumulative number of species observed by Alve and Murray (2001). We agree with Alve and Murray (2001) that species diversity is one of the principal methods for evaluating natural variability as well as possible human impact.

Buzas et al. (2002) sampled three stations in the Indian River Lagoon with four replicates at each station monthly

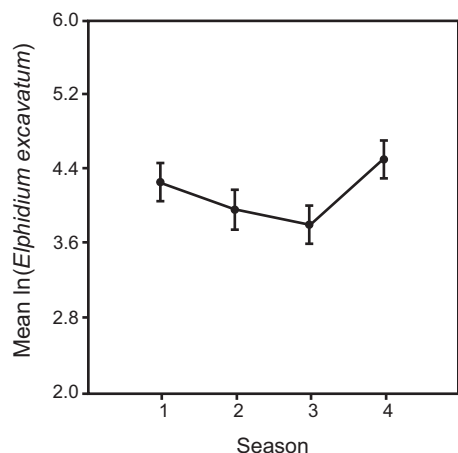


FIGURE 16. Mean number of $\ln(\textit{Elphidium excavatum})$ at two stations in the Hamble estuary, England. Seasons: 1 = winter, 2 = spring, 3 = summer, 4 = fall. Data from Murray and Alve (2000).

for five years (1992–1997). The densities of five taxa, *Quinqueloculina*, *Elphidium*, *Ammonia*, *Bolivina*, and *Ammobaculites*, were recorded along with seven environmental variables. The temperature ranged from 15°C to 37°C, averaging 26°C, and salinities varied from 18 to 40, averaging 28. In total, there are 720 observations for each taxon. The data were analyzed by general linear models with taxon density as the dependent variable. The environmental variables did not contribute significantly to explaining the observed variability in densities. However, the observed densities between taxa were highly correlated, and when a taxon is treated as a covariate, most of the variability in the density of a related taxon was explained. Differences between stations, years, seasons, and their interactions were all statistically significant. The authors proposed a model of pulsating patches on the basis of these results, wherein individual foraminifers are spatially

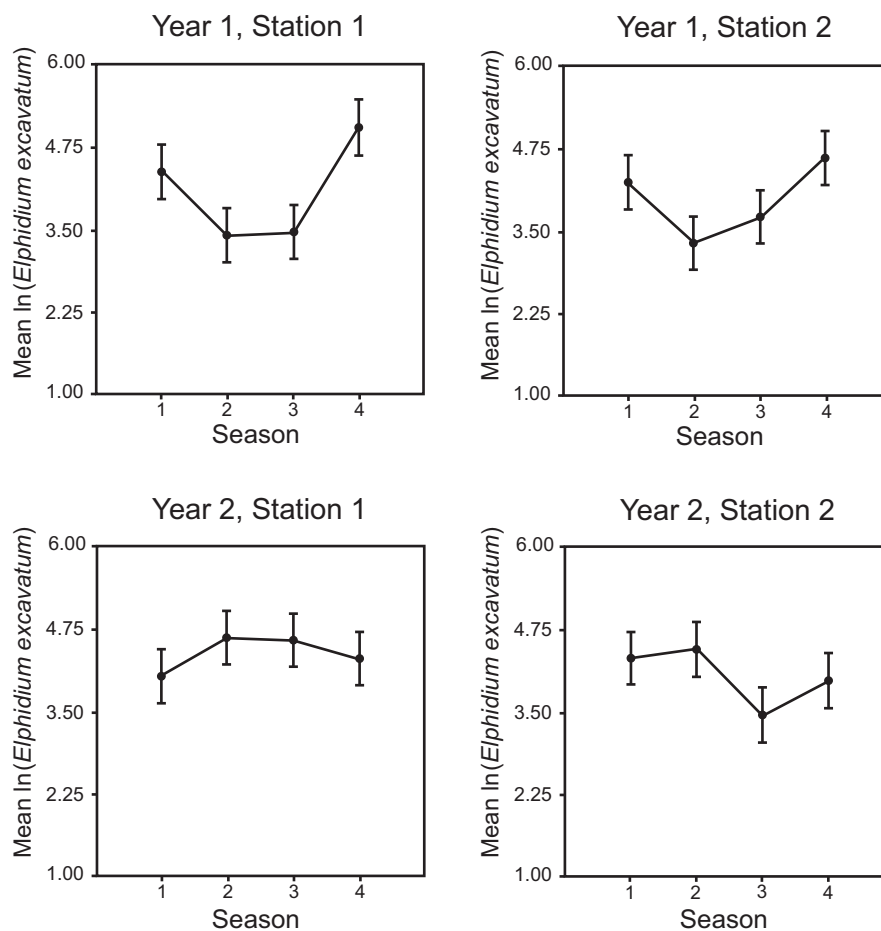


FIGURE 17. Mean number of $\ln(\textit{Elphidium excavatum})$ in the Hamble estuary, England, during two years from March 1994 to February 1996 at station 1 near neap tide and at station 2 in the mid-intertidal during seasons 1 (winter), 2 (spring), 3 (summer), and 4 (fall). Data from Murray and Alve (2000).

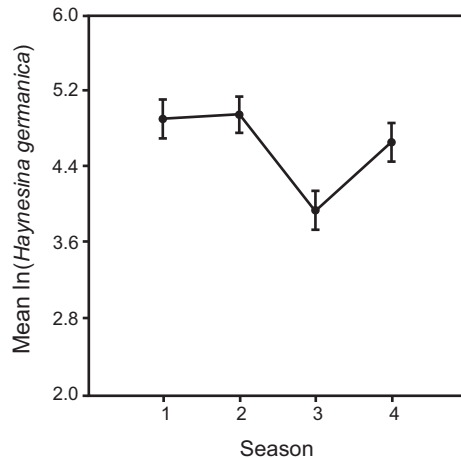


FIGURE 18. Mean number of $\ln(\textit{Haynesina germanica})$ at two stations in the Hamble estuary, England. Seasons: 1 = winter, 2 = spring, 3 = summer, 4 = fall. Data from Murray and Alve (2000).

distributed in a heterogeneous continuum forming patches with different densities that are only meters apart, with reproduction being asynchronous and thereby causing the patches to vary in space and time.

Wilson and Dawe (2006) reanalyzed the data for *Quinqueloculina* presented by Buzas et al. (2002) by statistical time series analysis. Their analysis confirmed seasonality. Stations 1 and 2 fluctuated in phase, whereas stations 2 and 3 fluctuated as well but out of phase, supporting the conclusions of Buzas et al. (2002).

Takata et al. (2006) documented the foraminifera in Lake Saroma Lagoon, Japan, with 11 samples in August 1994 and 54 samples in October 1995. At 15 m depth the water temperature varied from about 1°C to 20°C, and the salinity ranged from about 32 to 34. On the basis of the analysis of the October samples, three faunas are recognized: a lagoon bottom fauna dominated by *Haynesina* sp., a shallow-water fauna dominated

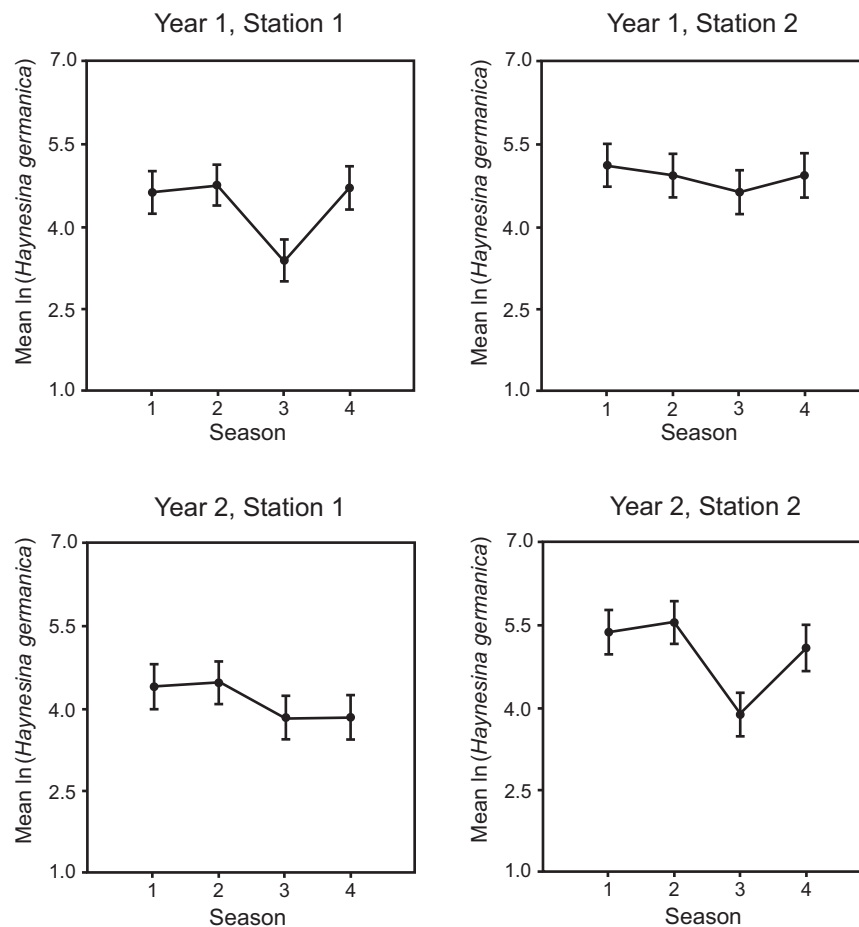


FIGURE 19. Mean number of $\ln(\textit{Haynesina germanica})$ in the Hamble estuary, England, during two years from March 1994 to February 1996 at station 1 near neap tide and at station 2 in the mid-intertidal during seasons 1 (winter), 2 (spring), 3 (summer), and 4 (fall). Data from Murray and Alve (2000).

by *Trochammina* cf. *japonica*, and a river mouth fauna dominated by *Elphidium excavatum*. Differences between August 1994 and October 1995 were striking. In August 1994, almost no calcareous fauna was observed. Living individuals of *Haynesina*, the dominant species of the lagoon bottom fauna, were absent. The authors suggested that low-oxygen conditions prevailed in the summer of 1994 (about 2.1 mL/L) and improved between August 1994 and October 1995, allowing for the migration of *Haynesina* into the lagoon bottom. However, these hypotheses could not be tested.

Larger foraminifera were sampled from reef rubble along a Florida reef tract (Baker et al., 2009). Quarterly samples were taken from 1995 to 2000 at Conch Reef at depths of 10, 18, and 30 m and at Tennessee Reef at depths of 8 m and 20 m. Three replicate sets of three or four palm-sized pieces of rubble were collected at each sampling time but were not tested statistically. The most abundant species was *Amphistegina gibbosa*, and it tended to be more abundant at deeper sites. The authors concluded that the densities of *A. gibbosa* do not show a seasonal trend. We assume they mean the same seasonality existed from year to year because their plots (figures 2 and 3 in Baker et al., 2009) do show seasonality but not the same seasonality from year to year. In other words, their results reviewed visually seem consistent with significant differences between depths, season, years, and their interaction.

Buzas-Stephens et al. (2011) measured foraminiferal densities with four replicates at each of five stations in Nueces Bay, Texas, during the years 2002, 2003, and 2007. Freshwater inflow was low during 2002, high in 2003, and low to moderate in 2007. The four most abundant species, *Ammonia parkinsoniana*, *Ammotium salsum*, *Elphidium excavatum*, and *Triloculina oblonga*, showed similar responses. A two-way ANOVA with interaction was used with hypotheses for station differences, time differences, and the interaction of these two factors. All hypotheses were significant, although the mean square for time (inflow) was an order of magnitude larger than for the other two hypotheses.

Monthly samples were taken at a single locality from June 2008 to May 2009 for *Amphistegina lobifera* in the Aegean Sea (Triantaphyllou et al., 2012). The temperature at this single locality ranged from 26.2°C in August to 13.8°C in January, whereas salinity ranged from 38.2 to 38.8. The authors concluded that monthly variations in size, frequency distribution, and abundance indicated reproduction primarily in summer. To reanalyze their data statistically, we grouped the monthly data given in their table 2 into four seasons and analyzed the total number

of living individuals as well as the percentage of small individuals by one-way ANOVA models. For the natural logarithm of the number of living individuals observed during the four seasons we found nonsignificance with $p = 0.559$ (Table 13). Figure 20 shows very little change from season to season. An ANOVA on the percentage of small individuals was likewise not significant ($p = 0.145$).

Gustafsson and Nordberg (2001) sampled the deepest part (116 m) of the Gullmar Fjord, Sweden, monthly from August 1993 to December 1994. The temperature varied from about 5.5°C to 7.8°C, and the salinity ranged from about 34.5 to 34.8. Replication was carried out at seven sampling times. For the dominant species, *Stainforthia fusiformis*, a peak was observed in autumn 1993 but

TABLE 13. ANOVA for season differences on $\ln(x + 1)$, where x is density of *Amphistegina lobifera*. Data from Triantaphyllou et al. (2012).

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Season	0.209	3	0.070	0.737	0.559
Error	0.758	8	0.095	—	—

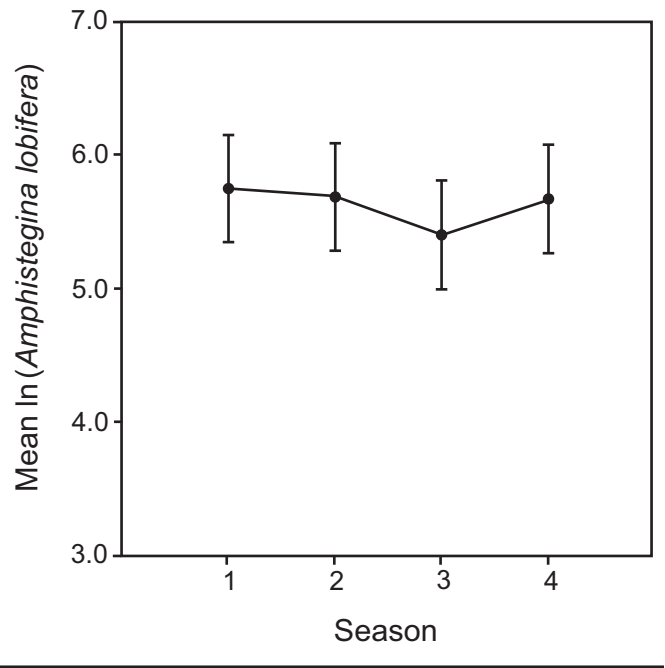


FIGURE 20. Mean number of $\ln(Amphistegina lobifera)$ in the Aegean Sea. Seasons: 1 = winter, 2 = spring, 3 = summer, 4 = fall. Data from Triantaphyllou et al. (2012).

was not confirmed in a replicate. However, a peak in late spring to early summer of 1994 was confirmed and occurred after the spring phytoplankton boom of 1994. The biota had changed since the sampling in 1927 according to Höglund (1947), and the authors believed that by 2001 at the time of their study the biota was more tolerant of low-oxygen conditions (minimum 0.6 mL/L).

Fontanier et al. (2003) sampled foraminifera at 10 sampling times between October 1997 and April 2000 at a depth of 550 m in the Bay of Biscay. At half of these times the authors used only single, unreplicated samples, although at five sampling times, October 1997, January 1998, April 1999, June 1999, and April 2000, duplicate cores were taken. The biota was analyzed in two fractions, >150 and 63–150 μm . The counts are included in the paper and are listed in tables 5 and 6. The Bay of Biscay is characterized by phytoplankton blooms in spring, summer, and fall, with the predominant bloom in spring. Although the spatial patchiness is considerable, especially in the 63–150 μm fraction, the authors state that the temporal variability is larger than the spatial variability. The >150 μm fraction is dominated by *Uvigerina peregrina* and *U. mediterranea*. After transforming the original counts to natural logarithms, we reanalyzed the five sampling times with duplicate samples by one-way ANOVA. For *U. peregrina*, a significant $p = 0.037$ was obtained (Table 14, Figure 21). Tukey's pairwise comparisons indicated October 1997 had higher densities than those from April 1999 and June 1999. For the most dominant species, *U. mediterranea*, a non-significant $p = 0.149$ was obtained. (Table 15, Figure 22). In the 63–150 μm fraction from Fontanier et al. (2003), the species *Epistominella exigua*, *Reophax guttiferus*, *Bolivina spathulata*, *Cassidulina carinata*, and *Nuttallides pusillus* were judged to be "most responsive." We reanalyzed the data for these species as well as those for *U. peregrina* and *U. mediterranea* by one-way ANOVA for differences between the five sampling times with duplicates. Only *C. carinata* and *B. spathulata* showed a significant difference with time. In both cases Tukey's pairwise comparison indicated that April 2000 had greater densities than April 1999. Analyses of total live foraminifera in both fractions indicated no significant differences. Finally, to examine the live population greater than 63 μm , we used these data and added together counts for both fractions of *U. peregrina* and *U. mediterranea* as well as total live counts to obtain live foraminifera greater than 63 μm . The analyses of these three data sets indicated no significant differences with time. Table 16 and Figure 23 show the results for

TABLE 14. ANOVA for sampling time differences on $\ln(x + 1)$, where x is density of *Uvigerina peregrina*. Data from Fontanier et al. (2003), >150 μm fraction.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Sampling times	6.542	4	1.636	6.032	0.037
Error	1.356	5	0.271		

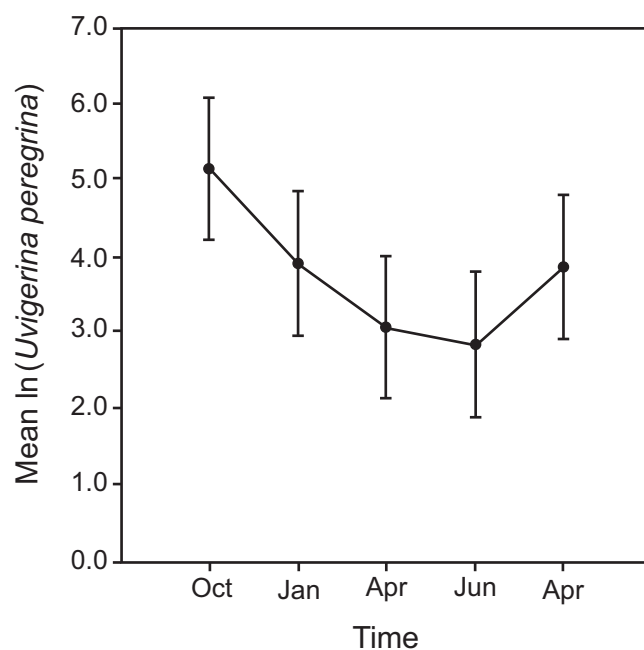


FIGURE 21. Mean number of $\ln(Uvigerina peregrina)$ in the Bay of Biscay at 550 m depth during the sampling times October 1997, January 1998, April 1999, June 1999, and April 2000, >150 μm fraction. Data from Fontanier et al. (2003).

these total living populations. Based on these results, we cannot state conclusively that the benthic foraminiferal densities were not influenced by phytoplankton blooms in the Bay of Biscay. We can only affirm that the spatial variability is sufficiently large that duplicate samples (error term has only 5 df) are insufficient to demonstrate this potential effect, except for three cases.

In San Pedro Basin, California, at a water depth of about 720 m, Silva et al. (1996) sampled with duplicate box cores in April, July, and October 1988. Sediment was sampled to a depth of 20 cm in both the 63–150 and >150 μm fractions. However, the duplicate samples were

TABLE 15. ANOVA for sampling time differences on $\ln(x + 1)$, where x is density of *Uvigerina mediterranea*. Data from Fontanier et al. (2003), >150 μm fraction.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Sampling times	2.355	4	0.589	2.740	0.149
Error	1.075	5	0.215		

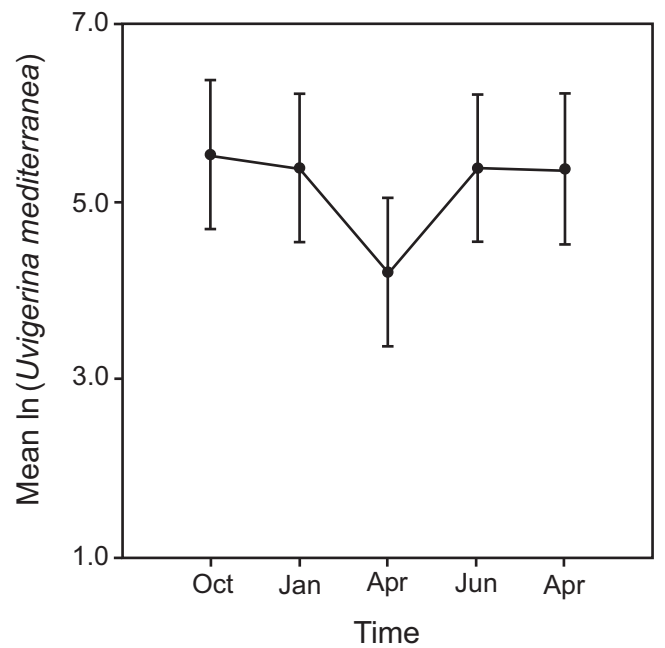


FIGURE 22. Mean number of $\ln(Uvigerina mediterranea)$ in the Bay of Biscay at 550 m depth during the sampling times October 1997, January 1998, April 1999, June 1999, and April 2000, >150 μm fraction. Data from Fontanier et al. (2003).

examined for only the >150 μm fraction. The authors state that variability in abundances in replicate cores is not as great as seasonality and list (for the >150 μm fraction) several species with maximum abundances in July or October. By using the counts in their tables we tested statistically some of these species with the live counts in the entire 20 cm using a one-way ANOVA and post hoc pairwise comparisons by Tukey's procedure. We discovered that for *Bolivina spissa*, although a maximum was observed in July ($p = 0.118$), it was not significant (Table 17, Figure 24). For *Chilostomella ovoidea* a maximum was observed in July, but $p = 0.065$ and likewise was not significant (Table 18,

TABLE 16. ANOVA for sampling time differences on $\ln(x + 1)$, where x is density of total live population. Data from Fontanier et al. (2003), >63 μm fraction.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Sampling times	2.078	4	0.520	2.149	0.212
Error	1.209	5	0.242		

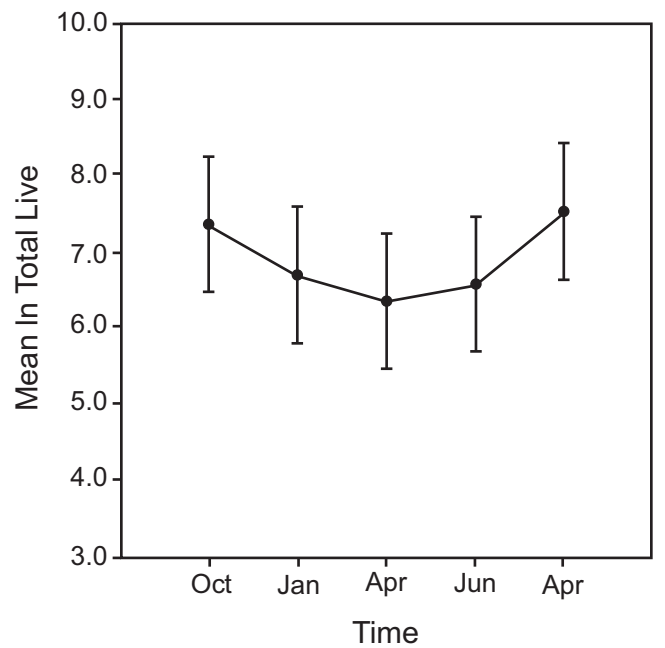


FIGURE 23. Mean number of total live population in the Bay of Biscay at 550 m depth during the sampling times October 1997, January 1998, April 1999, June 1999, and April 2000, >63 μm fraction. Data from Fontanier et al. (2003).

Figure 25). For *Globobulimina pacifica*, the authors state a maximum density was observed in July. July does, indeed, exhibit a visual high point but not in comparison to the other points in the plots, so the ANOVA resulted in $p = 0.260$ (Table 19, Figure 26). For *Nonionella stella* a visual maximum density was observed in October, but the ANOVA showed that $p = 0.087$ (Table 20, Figure 27). We also analyzed the total live foraminifera in the top 20 cm, and the ANOVA's observed significance value of $p = 0.008$ is significant (Table 21, Figure 28). Following this significant result, pairwise comparisons show that both July and October had statistically significant maxima, not

TABLE 17. ANOVA for sampling time differences on $\ln(x + 1)$, where x is density of *Bolivina spissa*. Data from Silva et al. (1996), >150 μm fraction.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Sampling times	0.521	2	0.256	4.719	0.118
Error	0.166	3	0.055		

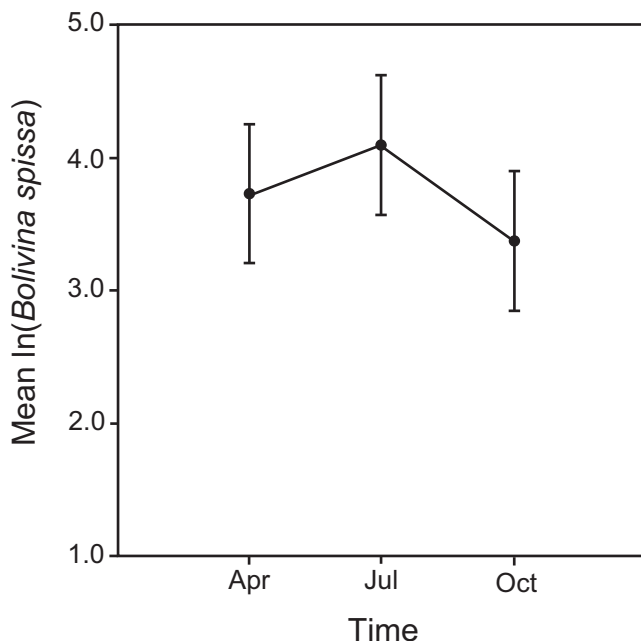


FIGURE 24. Mean number of $\ln(Bolivina\ spissa)$ in the San Pedro Basin, California, at 720 m depth during sampling times April, July, and October 1988, >150 μm fraction. Data from Silva et al. (1996).

merely visual high values. Seasonality is then demonstrably present for the total live population in the San Pedro Basin. Interestingly, we also ran an ANOVA on the total live foraminifera from only the top centimeter, and $p = 0.187$ (Table 22, Figure 29). Thus, the result is strikingly different from that for the entire ensemble. Silva et al.'s conclusion concerning stratification of species within the sediment is apparently justified. One note of caution is that with only two replicates, given the high natural variability for foraminiferal densities, it is highly probable that duplicate samples provide too low a power of the test to make definitive conclusions (error term has only 3 df).

In the Bay of Biscay, a station at 1,000 m water depth was sampled at 10 intervals from October 1997 to April

TABLE 18. ANOVA for sampling time differences on $\ln(x + 1)$, where x is density of *Chilostomella ovoidea*. Data from Silva et al. (1996), >150 μm fraction.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Sampling times	0.814	2	0.407	7.781	0.065
Error	0.157	3	0.052		

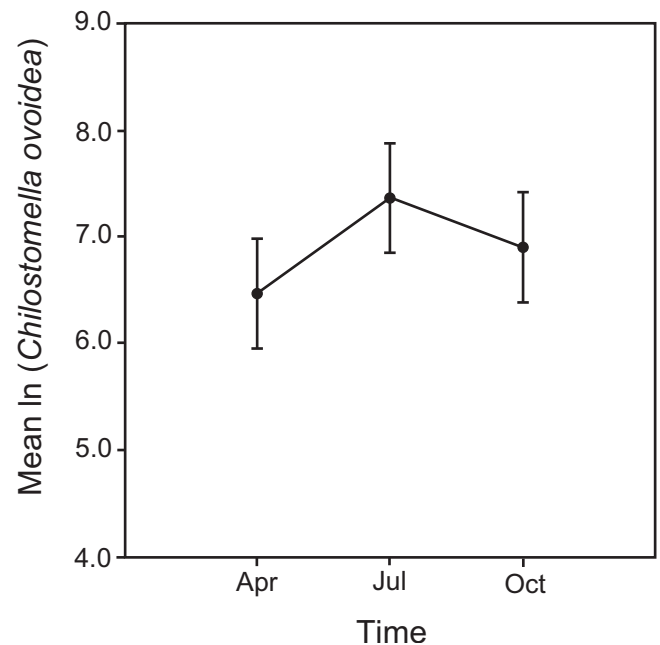


FIGURE 25. Mean number of $\ln(Chilostomella\ ovoidea)$ in the San Pedro Basin, California, at 720 m depth during sampling times April, July, and October 1988, >150 μm fraction. Data from Silva et al. (1996).

2001 by Fontanier et al. (2006). At sampling times January 1998 and April 2000 duplicate samples were taken. Samples were examined in the >150 and 63–150 μm fractions. The waters are characterized by high salinity of about 35.8 and moderate oxygen of about 3.8 mL/L. Spring blooms of phytoplankton were observed each year. The authors point out that they observed maxima in their counts in the >150 μm fraction in April 2000 (669) and April 2001 (444), which coincide with phytoplankton blooms. However, we calculated the observed confidence limits at each of the two duplicate sampling times as well as those for the four values observed in both duplicate cores (308, 238, 363, 669). All of the observations at the

TABLE 19. ANOVA for sampling time differences on $\ln(x + 1)$, where x is density of *Globobulimina pacifica*. Data from Silva et al. (1996), >150 μm fraction.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Sampling times	0.148	2	0.074	2.182	0.260
Error	0.102	3	0.034		

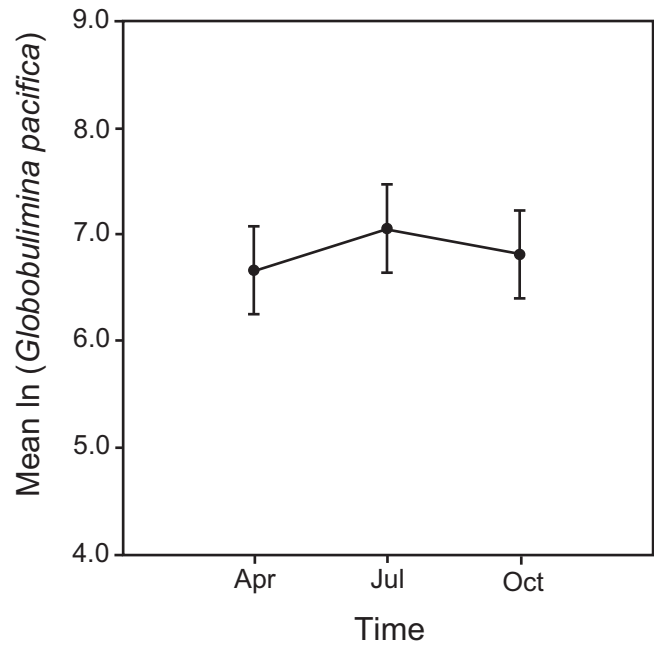


FIGURE 26. Mean number of $\ln(Globobulimina\ pacifica)$ in the San Pedro Basin, California, at 720 m depth during sampling times April, July, and October 1988, >150 μm fraction. Data from Silva et al. (1996).

10 sampling times fall well within the confidence limits. The same is true for the 63–150 μm fraction, and hence, we conclude for these observations that no statistically significant result can be demonstrated.

At bathyal depths, Ohga and Kitazato (1997) sampled Sagami Bay, Japan, during 1991 to 1994. The station located at a water depth of 1,450 m was sampled 19 times. Highest densities were observed in spring in conjunction with a light green phytodetrital layer deposited from a strong spring bloom. Test size distributions indicated that the shallow infaunal species *Bolivina pacifica* and *Textularia battegatensis* have annual life cycles, whereas growth

TABLE 20. ANOVA for sampling time differences on $\ln(x + 1)$, where x is density of *Nonionella stella*. Data from Silva et al. (1996), >150 μm fraction.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Sampling times	9.481	2	4.741	6.147	0.087
Error	2.314	3	0.771		

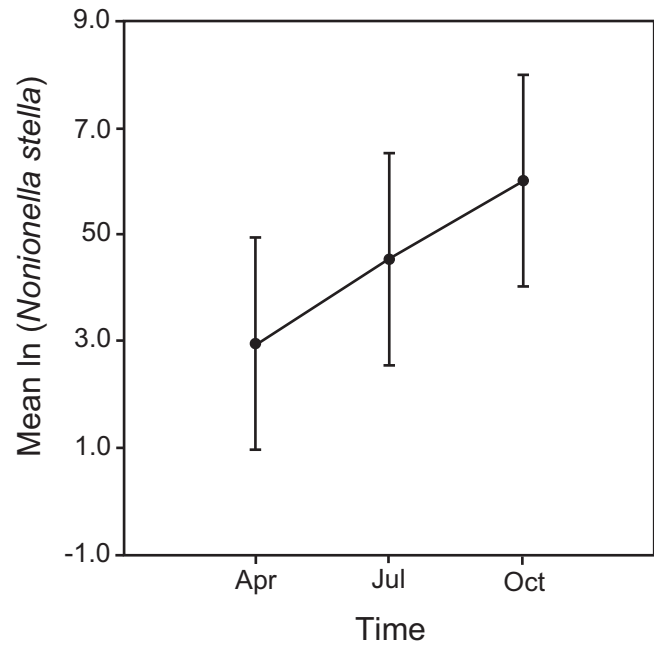


FIGURE 27. Mean number of $\ln(Nonionella\ stella)$ in the San Pedro Basin, California, at 720 m depth during sampling times April, July, and October 1988, >150 μm fraction. Data from Silva et al. (1996).

rates suggest a two-year or longer life cycle, and visual inspection showed no seasonality for the deeper infaunal species, *Globobulimina affinis* and *Chilostomella ovoidea*.

Cores were taken at 2,800 m in the Bay of Biscay at three sampling times, January and June 1999 and April 2000 (Fontanier et al., 2005). Only the April 2000 observation time had a duplicate sample. At this location the bottom water temperature was about 3.0°C, and the salinity was 34.95. Visual inspection indicated that the deep infaunal species *Globobulimina affinis* and *Melonis barleeanus* had very high densities in all except the duplicate April core B. The total live foraminifera count was 242 for winter, 413 for summer, 243 for spring core A, and

TABLE 21. ANOVA for sampling time differences on $\ln(x + 1)$, where x is density of total live population in the top 20 cm of sediment. Data from Silva et al. (1996).

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Sampling times	0.316	2	0.158	36.813	0.008
Error	0.013	3	0.004		

TABLE 22. ANOVA for sampling time differences on $\ln(x + 1)$, where x is density of total live population in the top 1 cm of sediment. Data from Silva et al. (1996).

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Sampling times	0.664	2	0.332	3.086	0.187
Error	0.323	3	0.108		

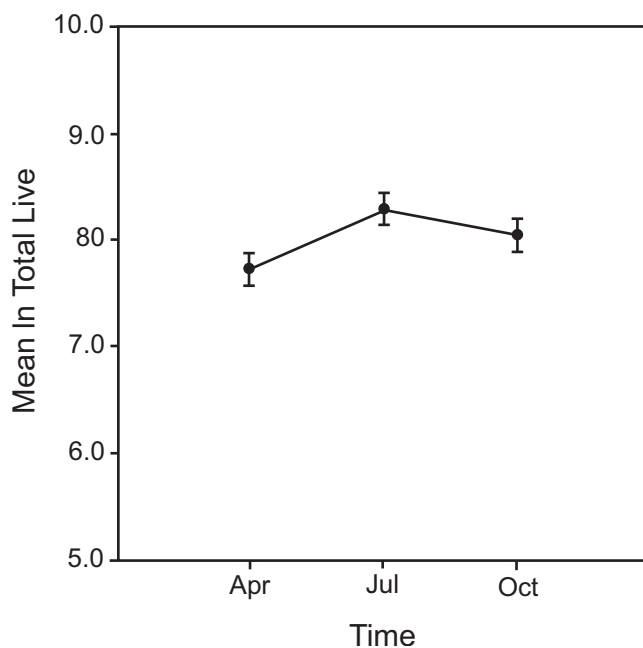


FIGURE 28. Mean total live population in the top 20 cm of sediment in San Pedro Basin, California, at 720 m depth. Data from Silva et al. (1996).

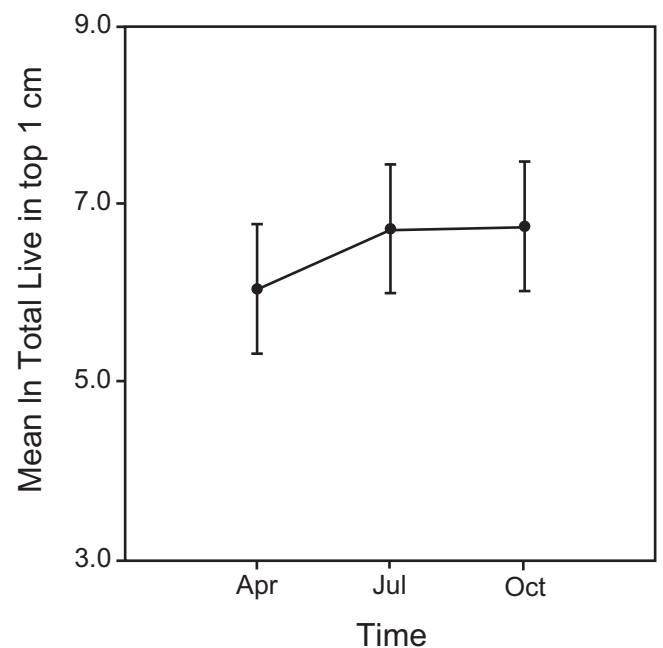


FIGURE 29. Mean total live population in the top 1 cm of sediment in San Pedro Basin, California, at 720 m depth. Data from Silva et al. (1996).

544 for core B. The high density in core B was attributed to macrofaunal burrowing activities. On the basis of their visual inspection, the authors concluded that the station has a very high infaunal population, but no seasonality could be demonstrated.

SUMMARY OF HISTORICAL REVIEW

The review presented here provides a summary of the results of over 60 years of distributional research on living benthic foraminifera. The majority, 25 of the 37 of the studies

we examined (see Table 23), or about 68% of the studies reviewed with original temporal data, based their conclusions on visual inspection. Publications include multiple taxa that range from total living population to genera to species. Table 23 shows also that 42 of 48 visual inspections of taxa by the original authors, or 88%, estimated that taxa exhibited seasonality. Visual inspection also indicated that 24 of 27 taxa, or 89%, exhibited yearly differences. In contrast, Table 24 shows that statistical analysis of sampling data revealed that only 43 of 89 taxa, or 48%, exhibited seasonal differences, whereas 22 of 35 taxa, or 63%, exhibited yearly differences.

TABLE 23. Evaluation by visual inspection of data. ST = station, SE = season, YR = year, S = deemed significant, NS = deemed not significant, dash (—) = not applicable.

Area and totals	ST	SE	YR	ST × SE	ST × YR	SE × YR	ST × SE × YR
Todos Santos Bay, California, 1955	—	1S	—	—	—	—	—
	—	0NS	—	—	—	—	—
Texas bays, 1957	1S	1S	1S	1S	1S	—	—
	0NS	0NS	0NS	0NS	0NS	—	—
Popponeset Bay marsh, Massachusetts, 1959	—	2S	2S	—	—	—	—
	—	0NS	0NS	—	—	—	—
Santa Monica Bay, California, 1959	1S	1S	—	1S	—	—	—
	0NS	0NS	—	0NS	—	—	—
Patagonia, Argentina, 1964	—	2S	0S	—	—	—	—
	—	1NS	3NS	—	—	—	—
Kiel, Germany, 1967	—	1S	1S	—	—	—	—
	—	0NS	0NS	—	—	—	—
Christchurch, England, 1968	—	1S	—	—	—	—	—
	—	0NS	—	—	—	—	—
Bottsand Lagoon, Germany, 1968	—	1S	1S	—	—	—	—
	—	0NS	0NS	—	—	—	—
Llandanwg Lagoon, Wales, 1969	—	1S	—	—	—	—	—
	—	0NS	—	—	—	—	—
Patagonia, Argentina, 1969	—	6S	6S	—	—	—	—
	—	0NS	0NS	—	—	—	—
Limski Canal, Croatia, 1970	—	1S	1S	1S	—	—	—
	—	0NS	0NS	—	—	—	—
Rappahannock River, Virginia, 1970	—	4S	4S	—	—	—	—
	—	0NS	0NS	—	—	—	—
Baltic Sea, 1976	1S	1S	1S	1S	—	—	—
	0NS	0NS	0NS	0NS	—	—	—
Samish Bay, Washington, 1979	—	2S	—	—	—	—	—
	—	2NS	—	—	—	—	—
Nova Scotia, Canada, 1980	—	1S	1S	—	—	—	—
	—	0NS	0NS	—	—	—	—
Exe Estuary, England, 1983	—	1S	1S	—	—	—	—
	—	0NS	0NS	—	—	—	—
Bodega, northern California, 1987	—	1S	1S	—	—	—	—
	—	0NS	0NS	—	—	—	—
Adriatic Sea, 1992	—	1S	—	—	—	—	—
	—	0NS	—	—	—	—	—
Sagami Bay, Japan, 1997	—	2S	—	—	—	—	—
	—	2NS	—	—	—	—	—
Gullmar Fjord, Sweden, 2001	—	1S	1S	—	—	—	—
	—	0NS	0NS	—	—	—	—
Vie estuary, France, 2006	—	5S	—	—	—	—	—
	—	0NS	—	—	—	—	—
Saroma Lagoon, Japan, 2006	—	3S	3S	—	—	—	—
	—	0NS	0NS	—	—	—	—
Bay of Biscay, 2006	—	0S	—	—	—	—	—
	—	1NS	—	—	—	—	—
Reef, Florida, 2009	1S	1S	1S	—	—	—	—
	0NS	0NS	0NS	—	—	—	—
Aegean Sea, Greece, 2012	—	1S	—	—	—	—	—
	—	0NS	—	—	—	—	—
Total significant	4	41	25	4	1	—	—
Total not significant	0	6	3	0	0	—	—

TABLE 24. Statistical evaluation of hypotheses. ST = station, SE = season, YR = year, S = significant at 0.05 level, NS = not significant at 0.05 level, dash (—) = not applicable.

Area and totals	ST	SE	YR	ST × SE	ST × YR	SE × YR	ST × SE × YR
Long Island Sound, USA, 1965	—	3S	2S	—	—	—	—
	—	0NS	1NS	—	—	—	—
Narragansett Bay, Rhode Island, 1967	—	0S	—	—	—	—	—
	—	1NS	—	—	—	—	—
Choptank River, Maryland, 1969	2S	3S	—	3S	—	—	—
	1NS	0NS	—	0NS	—	—	—
Jamaica, West Indies, 1977	6S	7S	—	5S	—	—	—
	13NS	12NS	—	14NS	—	—	—
Indian River Lagoon, Florida, 1993	0S	3S	—	3S	—	—	—
	3NS	0NS	—	0NS	—	—	—
Bahrain, Persian Gulf, 1995	—	3S	4S	—	—	—	—
	—	1NS	0NS	—	—	—	—
San Pedro Basin, 720 m, California, 1996	—	5S	—	—	—	—	—
	—	1NS	—	—	—	—	—
Hamble Estuary, England, 2000	3S	3S	1S	1S	0S	2S	3S
	0NS	0NS	2NS	2NS	3NS	1NS	1NS
Patagonia, Argentina, 2000	—	—	1S	—	—	—	—
	—	—	0NS	—	—	—	—
Bottsand Lagoon, Germany, 2000	—	—	1S	—	—	—	—
	—	—	0NS	—	—	—	—
Patagonia, Argentina, 2000	—	—	1S	—	—	—	—
	—	—	0NS	—	—	—	—
Baltic Sea, 2000	—	—	1S	—	—	—	—
	—	—	0NS	—	—	—	—
Exe estuary, England, 2000	—	—	0S	—	—	—	—
	—	—	1NS	—	—	—	—
Indian River Lagoon, Florida, 2002	5S	5S	4S	5S	5S	5S	5S
	0NS	0NS	1NS	0NS	0NS	0NS	0NS
Bay of Biscay, 550 m, Spain, 2003	—	1S	2S	—	—	—	—
	—	9NS	8NS	—	—	—	—
Bodega, California, 2006	—	0S	—	—	—	—	—
	—	1NS	—	—	—	—	—
Queensland, Australia, 2008	—	10S	—	—	—	—	—
	—	20NS	—	—	—	—	—
Nueces Bay, Texas, 2011	4S	—	4S	—	4S	—	—
	0NS	—	0NS	—	0NS	—	—
Aegean Sea, Greece, 2012	—	0S	—	—	—	—	—
	—	1NS	—	—	—	—	—
Total significant	20	43	22	17	9	7	8
Total not significant	17	46	13	16	3	1	

Examination of plots without any indication of confidence bars easily allows a researcher to state that highs and lows are meaningful, even when, on the basis of inherent variability, they are well within expectation. Because the researcher is looking for purported seasonal or yearly differences or

making the ontological assumption that such differences must exist, he or she finds them. When we analyzed statistically the data presented in papers that listed their data, our analyses often conflicted, at least in detail, with the conclusions based on visual inspection by the authors.

Although the need for replication to evaluate seasonal differences statistically was pointed out by Buzas (1969) and Hayek and Buzas (1997, 2010) and was urged by Murray and Alve (2000), foraminiferal researchers have not or could not follow this advice. Taking replicate samples in deeper water is often prohibitive either because of time or cost considerations or because of the mission of the vessel involved. In shallower water, time restrictions and effort are still germane limitations. However, the need to take replicate samples (Hayek and Buzas, 1997, 2010) is still paramount if we, as foraminiferalogists, expect to make definitive and predictive statements about these organisms' spatial and temporal distributions. In this study, only 11 of 35 studies, or 31%, reviewed here contained replicates, and these were often only duplicates, which are insufficient for a complete analysis of interaction. Only 6 of 35, or 17%, had station and time replicates suitable for analyses of interaction or pulsating patches. The studies with sampling that allowed for consideration of interaction hypotheses had 30 analyses, of which 28, or 93%, had significant interactions. It seems likely, therefore, that station $\times$ time interactions or pulsating patches are commonplace but have gone and still go largely undetected because of inadequate sampling protocols.

METHODS IN THE INDIAN RIVER LAGOON, FLORIDA

FIELD

This study is designed to provide a complete data set for the identification of and testing for the existence of patches. With this design we can evaluate the size of patches, the possible significance of seasonality, differences between years, and all of their interactions (pulsating patches). We provide this exemplar by sampling at multiple stations (at two scales), with multiple observations (replicates), multiple seasons, multiple years, and an analysis by three-way ANOVA with interactions and a general linear model using co-occurring taxa and environmental variables as covariates.

Station 1 in the Indian River Lagoon, Florida, is located just north of the Harbor Branch Oceanographic Institution jetty (Figure 30). This station, with GPS coordinates 27°32.153'N, 80°20.948'W and at a water depth of about 1 m, has been monitored continuously since 1977. In the present study this station acts as the anchoring station for both the 100 m² and 1 m² pulsating patch studies. For the 100 m² study at station 1 an aluminum pole was

positioned at the coordinates given above, and a second pole for station 2 was positioned 10 m to the east; a third pole was positioned 10 m to the south, and a fourth was placed 10 m to the west of the third. The arrangement is shown in Figure 31. For the 1 m² study, station 1 was denoted 1', and the second station (2') was located 1 m to the east; the third station (3') was 1 m to the south of 1', and the fourth (4') was 1 m to the east of 3'. The arrangement, then, was exactly like the one shown in Figure 31, except that the distance between stations was 1 m instead of 10 m.

At each sampling time, four plastic cores with an inner diameter of about 3.5 cm were inserted into the sediment within centimeters of each other at each station. Consequently, each of the four stations has four replicate sediment samples at each sampling time. There are then $4 \times 4 = 16 = N$ biological samples for the 100 m² study and also $N = 16$ for the 1 m² study at each sampling time. Sampling was carried out in the middle of the month in the middle month of each season, that is, January, April, July, and October. For each year, for each study, we have 4 replicates $\times$ 4 stations $\times$ 4 seasons = 64 = N biological samples. Sampling for the two studies began in July 2001 and was carried out for four years. In total for each study we have 4 replicates $\times$ 4 stations $\times$ 4 seasons $\times$ 4 years = 256 = N biological samples or statistical observations. For both studies combined there are a total of $2 \times 256 = 512 = N$ observations. Temperature, salinity, and oxygen were measured at station 1 at the time of each collection. All of these observations or samples are within a 100 m² area, making this study the most intensely sampled one ever conducted in foraminiferal research.

LABORATORY

Immediately after sampling (within an hour) the cores were taken into the laboratory, and by means of a spatula and measuring cylinder, 5 mL of sediment were removed from the top 1 or 2 cm of each core. The removed sediment was then washed over a 63 μ m sieve, and the fraction greater than 63 μ m was stored in a 95% solution of ethyl alcohol and Rose Bengal (Walton, 1952). Before specimens in a stored sample were counted, the sediment was rewashed over a 63 μ m sieve and placed in a gridded Petri dish. All specimens were counted while wet to ensure recognition of stained individuals. The taxa counted were *Quinqueloculina* (mostly *Q. impressa* and *Q. seminula*), *Ammonia* (mostly *A. tepida*, formerly counted as *A. beccarii*; Buzas et al., 2002), *Elphidium* (mostly *E. mexicanum* and *E. gunteri*), *Bolivina* (mostly *B. striatula*), and *Ammobaculites* (mostly *A. exiguus*).

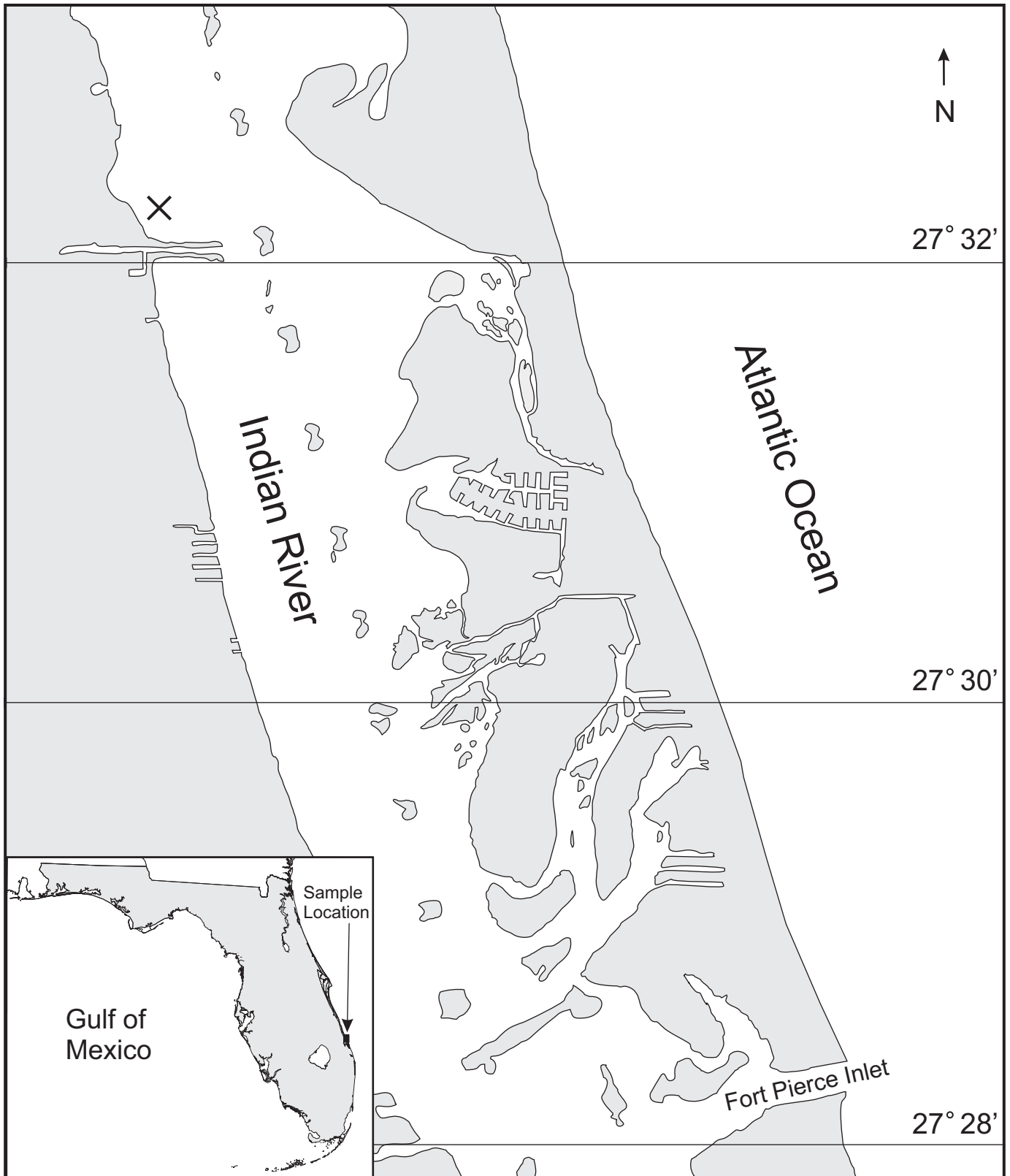


FIGURE 30. Location of station 1 (including substations 1, 2, 3, and 4 and 1', 2', 3', and 4') in the Indian River Lagoon Florida.

STATISTICAL ANALYSES

Recall from the field sampling that for each of the two studies there are four replicates, four stations, four seasons, and four years. The study was designed purposefully so that the $N = 4 \times 4 \times 4 \times 4 = 256$ observations could be analyzed by a three-way ANOVA with interaction (Buzas et al., 2002). The independent null hypotheses are that each of the following sets of means are equal: (1) stations, (2) seasons, (3) years, and (4) their interactions, namely, 1×2 , 1×3 , 2×3 , and $1 \times 2 \times 3$. Because we are interested in the hypothesis of pulsating patches, that is, that the stations do not coordinate changes in density with time, the interactions 1×2 , 1×3 , and $1 \times 2 \times 3$ are of particular interest.

We also constructed a general linear model (ANOVA with covariates) for each of the four taxa densities as dependent variables and 15 independent variables. The independent variables are listed along with our discussion of the results of the analysis. All calculations were made using SYSTAT 13.

RESULTS

The study began on 16 July 2001. One set of observations had four stations (numbered 1, 2, 3, 4) each 10 m apart; the other set of observations had four stations (numbered 1', 2', 3', 4') each 1 m apart (Figure 31). Stations 1 and 1' are the same. Each station was sampled

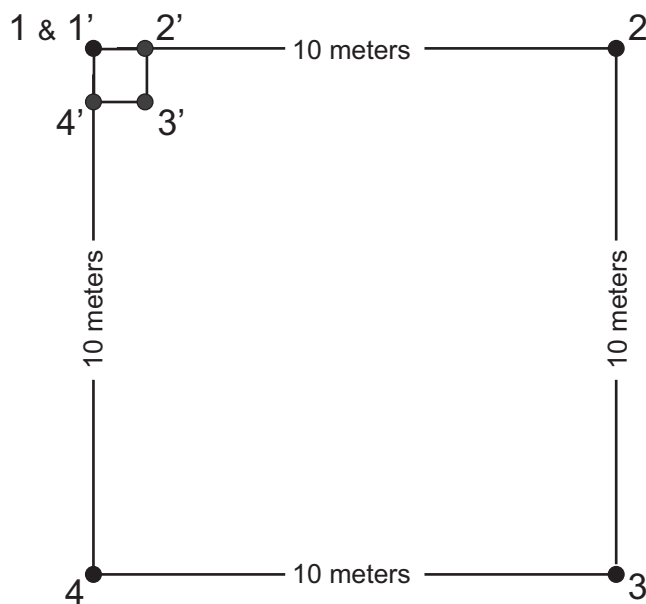


FIGURE 31. Layout for 100 m² study with stations 10 m apart. For the 1 m² study the layout is the same, with stations 1 m apart.

with four replicates at each sampling time. The sampling with replicates was repeated in the middle of each season for the next four years to yield 4 replicates $\times$ 4 stations $\times$ 4 seasons $\times$ 4 years = 256 = N observations or samples at each of the two sites. The counts in 5 mL samples for five taxa for the 100 m² site are shown in Appendix 1. Similarly, for the same taxa, the counts for the 1 m² site are shown in Appendix 2. Because *Bolivina* is so rare, only four taxa are subjected to statistical analysis. The counts were transformed to normalize the data and stabilize the variance with $\ln(x_{ijkl} + 1)$, where x is the number of individuals at the i th station ($i = 1, 2, \dots, 4$), j th season ($j = 1, 2, \dots, 4$), k th year ($k = 1, 2, \dots, 4$), and l th replicate ($l = 1, 2, \dots, 4$).

QUINQUELOCULINA

The results of the ANOVA for *Quinqueloculina* for the 100 m² study are shown in Table 25. Because we are interested in the detection of possible pulsating patches, the hypotheses of most interest are those involving interaction with stations and time by definition (Buzas et al., 2002). If all stations had equal densities with time, then neither the hypothesis for equality of station means nor the hypotheses for their interaction with stations would be significant. If the same station(s) always exhibited a high or low density, then the station hypothesis would be significant, but the interaction hypothesis would not be significant. Significance of interaction hypotheses involving stations and some measure of time indicates that the stations do not have a uniform response over some measure of time, which is the definition of pulsating patches. Table 25 shows that all of the hypotheses except for the interaction of station $\times$ year are significant. One of the major advantages of the ANOVA technique is that the ANOVA table allows us to view not only the significance of the hypothesis test results but also the apportioning of the sum of squares among the hypotheses. For the overall hypotheses, the mean square for station differences, which is a variance estimate, is less than those for seasons and years. The mean square for the interaction hypothesis for season $\times$ year is far greater than the rest. The result of the analysis, with significant results for each interaction with station except for year, shows that pulsating patches exist with seasons but not with years.

For stations positioned 10 m apart, the station differences and their interaction with seasons were significant at the 0.05 level, but they were not as large as differences noted with seasons and years (Table 25). It is reasonable, then, to suppose that stations positioned only 1 m apart would have even smaller differences.

TABLE 25. ANOVA for station, season, year, and their interaction differences on $\ln(x + 1)$, where x is density of *Quinqueloculina*, for stations 10 m apart.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Station	22.989	3	7.663	12.742	0.000
Season	103.772	3	34.591	57.517	0.000
Year	85.236	3	28.412	47.243	0.000
Station $\times$ season	11.998	9	1.333	2.217	0.023
Station $\times$ year	7.344	9	0.816	1.357	0.210
Season $\times$ year	209.021	9	23.225	38.618	0.000
Station $\times$ season $\times$ year	27.650	27	1.024	1.703	0.022
Error	115.469	192	0.601		

For the 1 m² study, the stations are labeled 1', 2', 3', and 4', and the counts of individuals in 5 mL of sediment were again transformed to $\ln(x_{ijkl} + 1)$. The results for the ANOVA on *Quinqueloculina* for the stations 1 m apart are shown in Table 26. Surprisingly, all of the hypotheses are significant, and the mean square for overall station differences is nearly identical to the mean square in the ANOVA result for stations positioned 10 m apart. The mean square for station differences is also smaller than those for season and year in this model, but all the interactions are significant, so that pulsating patches are apparent not only with seasons but also with years. However, in the smaller-plot study the magnitude of the variance estimate, or mean square, for each factor and interaction factor differs much less than those from the larger plot. Since the mean squares are not proportions of the total but estimates of the population variance, this result indicates

TABLE 26. ANOVA for station, season, year, and their interaction differences on $\ln(x + 1)$, where x is density of *Quinqueloculina*, for stations 1 m apart.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Station	22.983	3	7.661	10.720	0.000
Season	53.648	3	17.883	25.023	0.000
Year	37.364	3	12.455	17.427	0.000
Station $\times$ season	16.663	9	1.851	2.591	0.008
Station $\times$ year	20.635	9	2.293	3.208	0.001
Season $\times$ year	124.241	9	13.805	19.316	0.000
Station $\times$ season $\times$ year	92.559	27	3.428	4.797	0.000
Error	137.213	192	0.715		

that the model of pulsating patches fits better and with less variance at the 100 m² plot.

A scatterplot by stations for each study is shown in Figure 32. Stations 1 and 1' are the same (i.e., the same observations were used for both; station 1 is station 1'). At each station there are 4 replicates, 4 seasons, and

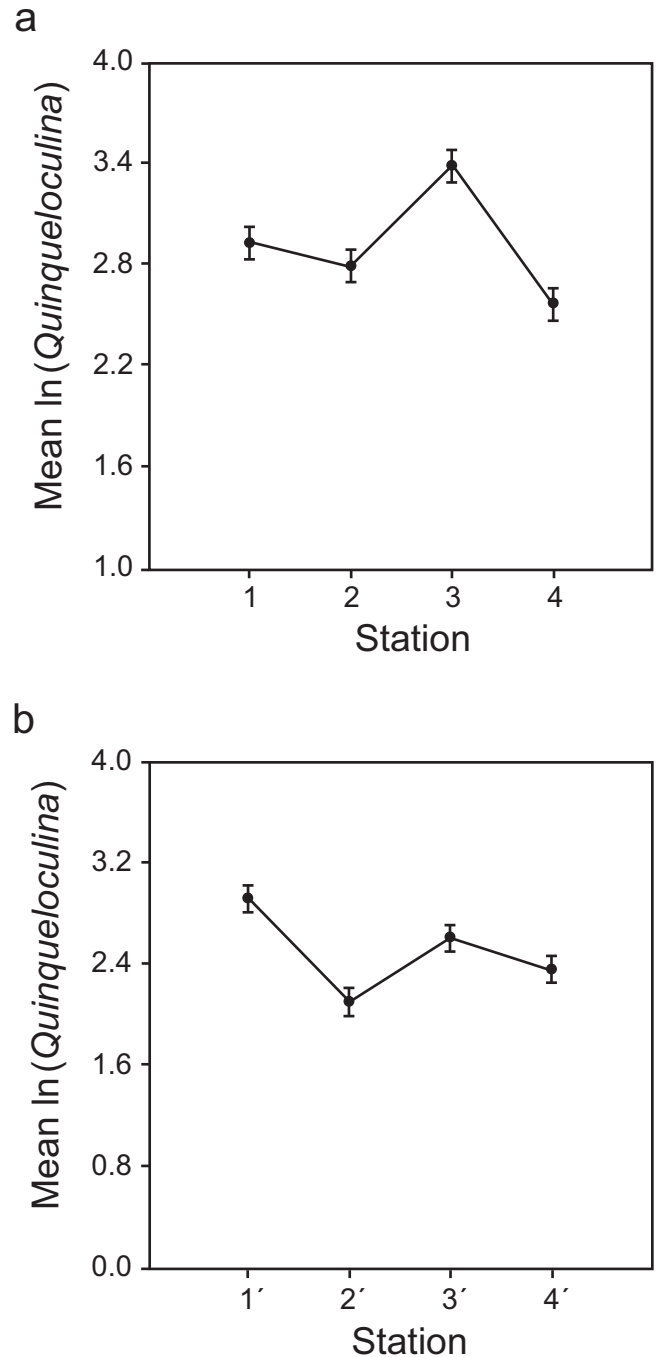


FIGURE 32. Mean number of $\ln(\text{Quinqueloculina})$ at stations. (a) Stations 10 m apart. (b) Stations 1 m apart.

4 years, giving a total of 64 observations comprising each plotted point on the figure. This figure shows that although significant station differences exist for both sets of observations, the pattern over stations for each design is not equivalent even though the mean squares are (Tables 25 and 26).

Figure 33 shows the overall results for *Quinqueloculina* for seasons at the 100 m² and 1 m² sites. If we were able to make predictive statements about the potential seasonality of *Quinqueloculina*, we would hope that the pattern of seasonal differences obtained by sampling would be equivalent for any sampled plot. In our study plots, in both cases the total in fall (season 4) is smaller than in the other seasons, and that in summer (season 3) is highest. However, for the 1 m² site the winter (season 1) and spring (season 2) densities are similar to those in summer, whereas at the 100 m² site, they are not. Overall, the two sites give a different pattern for seasonality over the four years.

Figure 34 shows the overall results for *Quinqueloculina* for years for the 100 m² and 1 m² studies. Again, we would hope the pattern for the years would be the same at both sites. At both sites, a high occurs in the third year (July 2003 to April 2004). However, the pattern for the 100 m² site shows that the results for years 1 and 2 are nearly equal but are lower than those for years 3 and 4, which are also nearly equal. On the other hand, for the 1 m² study an increase occurs from year 1 to 2 to 3, and then a decrease occurs in year 4, so that results for year 4 nearly equal those for year 2 (Figure 34). Except for year 2, the counts are higher at the 100 m² site. As with the seasons, the overall pattern is different depending on whether we choose 100 m² or 1 m².

Ideally, all stations would exhibit the same density in each season. However, the interaction hypothesis stations $\times$ season is significant at both the 100 m² and 1 m² sites, confirming our visual observation that these densities are not equivalent. At the 100 m² site, station 3 shows high points in winter, spring, and fall. At the 1 m² site maxima occur at station 1 in winter and summer. Except for summer at the 100 m² site, the densities between sites are comparable (Figure 35).

Ideally, all stations also would exhibit the same density each year, so that differences among years could be recognized at any station. The 100 m² site appears to meet this ideal. The interaction hypothesis for stations $\times$ year is not significant (Table 25). Note that the station densities are not significantly different, meaning all four years vary at random, even though Figure 36 shows station 3 usually has a higher density than the rest. High densities in years 3 and

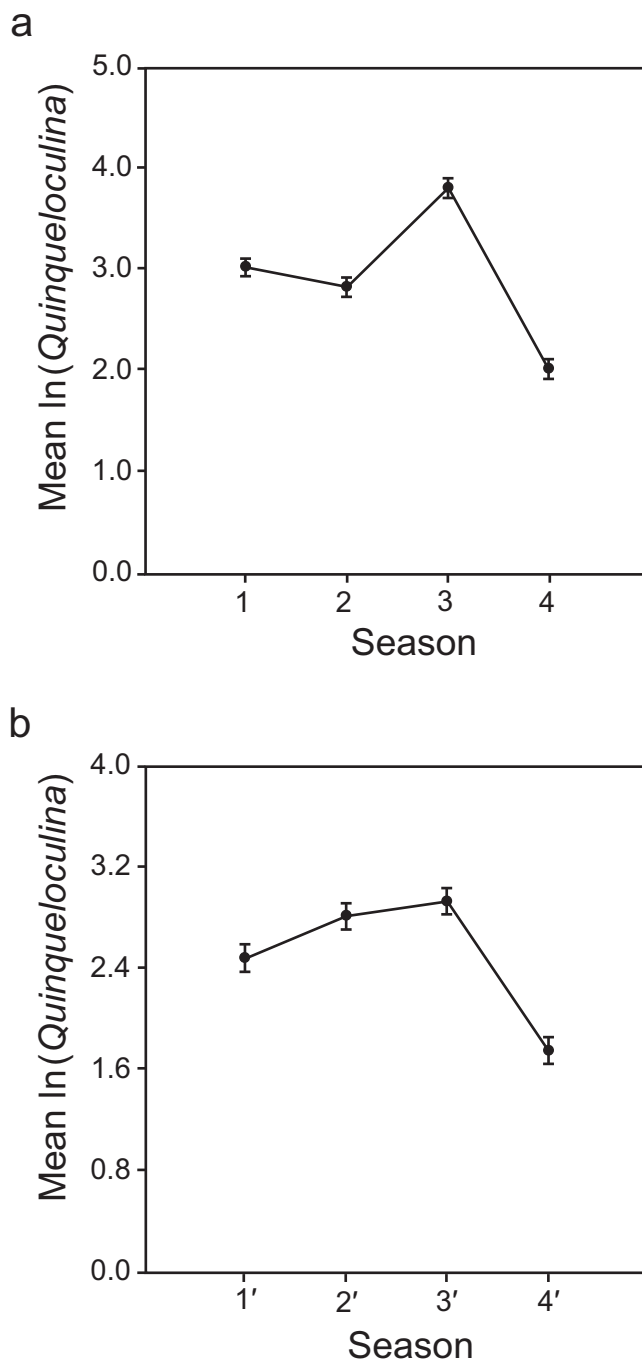


FIGURE 33. Mean number of $\ln(\text{Quinqueloculina})$ for seasons: 1 = winter, 2 = spring, 3 = summer, 4 = fall. (a) Stations 10 m apart. (b) Stations 1 m apart.

4 are evident in Figure 36 for the 100 m² site just as they are in Figure 34. Although we might expect less difference among more closely placed stations, the interaction hypothesis stations $\times$ years is significant for the 1 m² site. Otherwise,

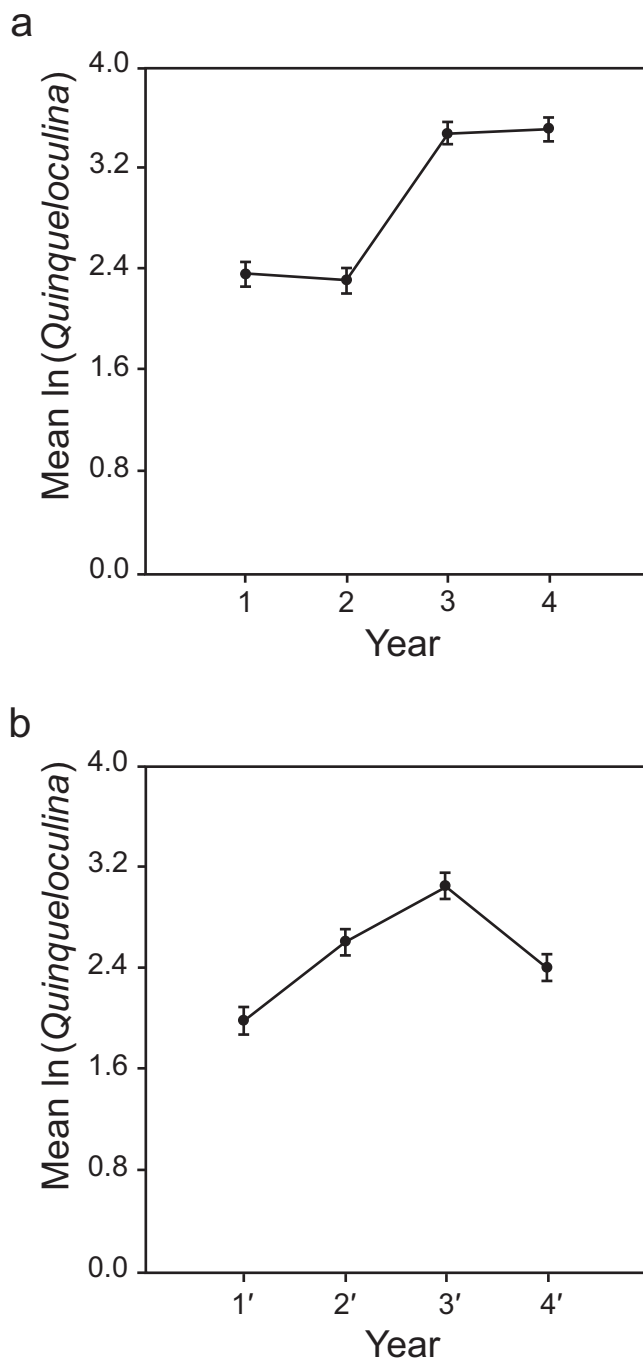


FIGURE 34. Mean number of *ln(Quinqueloculina)* for years: 1 = summer 2001 to spring 2002, 2 = summer 2002 to spring 2003, 3 = summer 2003 to spring 2004, 4 = summer 2004 to spring 2005. (a) Stations 10 m apart. (b) Stations 1 m apart.

the pattern of lowest densities in year 1 and highest in year 4 shown in Figure 34 is also evident in Figure 36.

The interaction hypothesis of season $\times$ year is significant for both studies, so the same seasons do not exhibit

high and low densities consistently from year to year. Hopefully, both sites will, however, show the same pattern. Figure 37 shows that for years 1 and 3 the patterns are quite similar. In year 1, summer has a high at both sites, and in year 3 spring shows the high. However, in years 2 and 4 the summer maximum seen at the 100 m² site does not appear at the 1 m² site. Similarly, the very low density in the fall of year 4 at the 1 m² site is not evident at the 100 m² site. A simple statement such as spring or summer always exhibits a high density cannot be made.

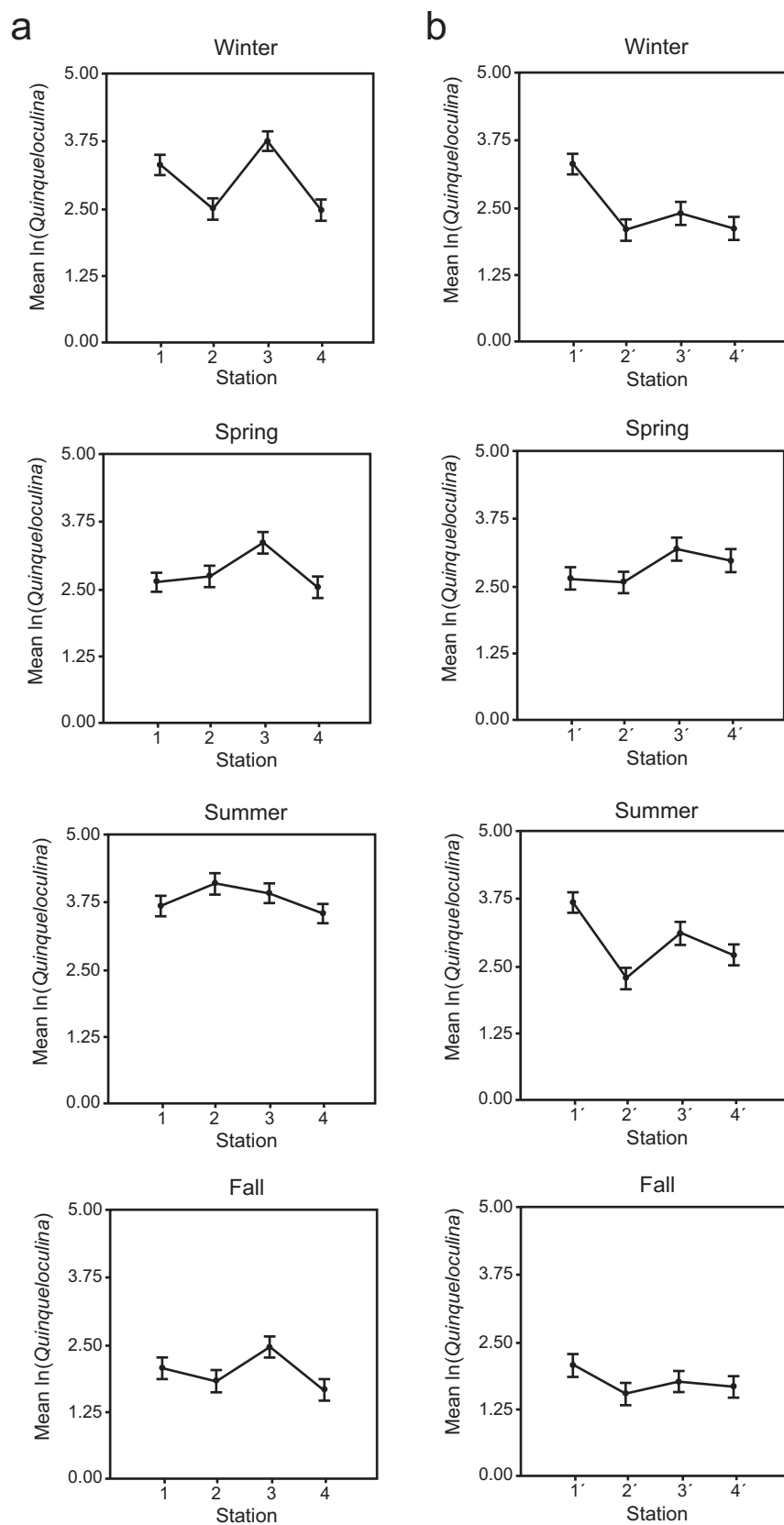
The three-way interaction hypothesis for testing station $\times$ season $\times$ year is significant for both the 100 and 1 m² sites (Tables 25 and 26). This interaction's significance, of course, indicates that as we make observations over a period of time, there is no consistency among stations, seasons, or years at either site.

Illustrating the interaction differences requires 16 plots for each of the sites. In Figure 38 we illustrate the 16 possibilities for the 100 m² site. What becomes immediately apparent is that at different times different stations have either low or high densities; these are the pulsating patches. For example, we noted in Figure 32 that overall, at the 100 m² site, station 3 has a higher density than the other stations. Upon visual examination of Figure 38, we observe that this is true only for winter and fall of year 1, winter and spring of year 2, winter and summer of year 3, and fall of year 4. The high overall spring density shown in Figure 33 was observed only in year 3. The high overall densities observed in years 3 and 4 (Figure 34) were actually because of high densities in spring of year 3 and summer of year 4.

In Figure 39 we illustrate the 16 possibilities for the study at the 1 m² site. Just as for the 100 m² site, different stations have high and low densities that differ with time, with pulsating patches at different scales. The overall low density observed at station 2 (Figure 32) was observed only in spring of year 1, summer of year 2, winter of year 3, and summer of year 4. The overall low density in fall (Figure 33) at all stations is evident except in year 2 (Figure 39). The overall high density in year 3 (Figure 34) was due mostly to spring in year 3, just as it was for the 100 m² site.

AMMONIA

The results of the ANOVA for *Ammonia* at the 100 m² site are shown in Table 27. All of the hypotheses are significant at the 95% level. Unlike *Quinqueloculina*, however, the mean square for seasons is much smaller than the mean square for years. Like *Quinqueloculina*, the interaction for season $\times$ year is the largest.

FIGURE 35. Mean number of $\ln(\text{Quinqueloculina})$ for station $\times$ season interaction. (a) Stations 10 m apart. (b) Stations 1 m apart.

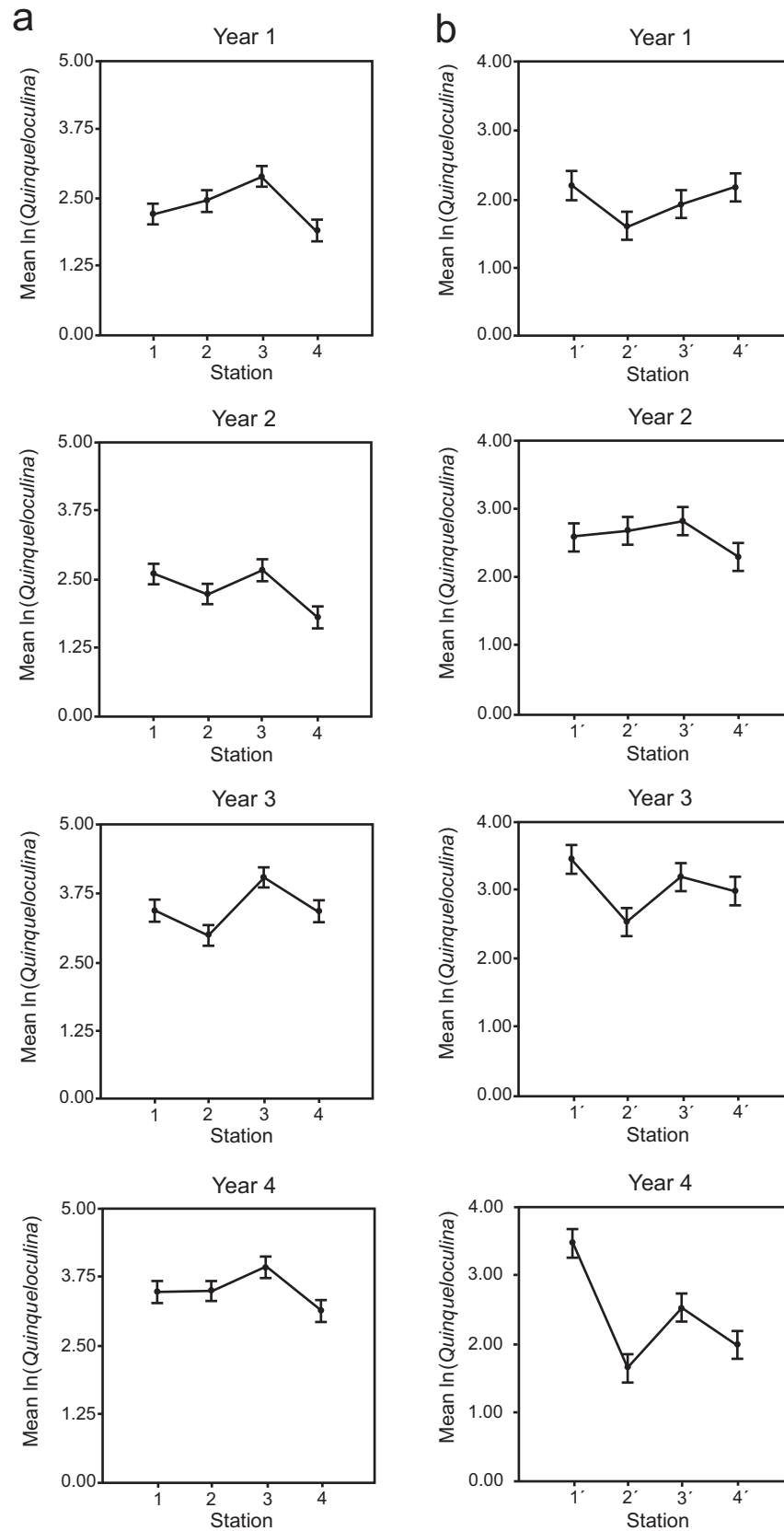


FIGURE 36. Mean number of $\ln(\text{Quinqueloculina})$ for station $\times$ year interaction. (a) Stations 10 m apart. (b) Stations 1 m apart.

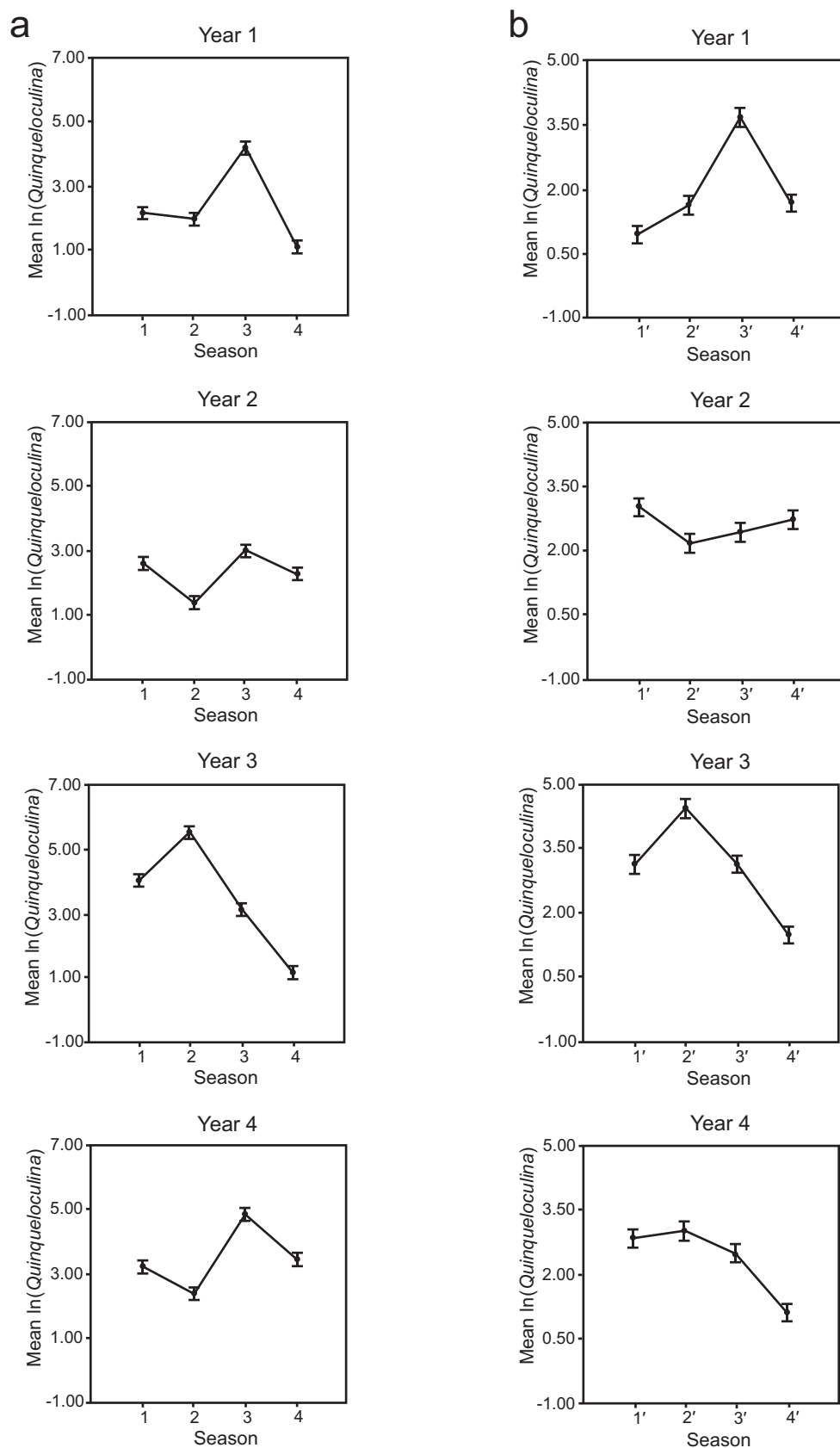


FIGURE 37. Mean number of $\ln(\text{Quinqueloculina})$ for season $\times$ year interaction. (a) Stations 10 m apart. (b) Stations 1 m apart.

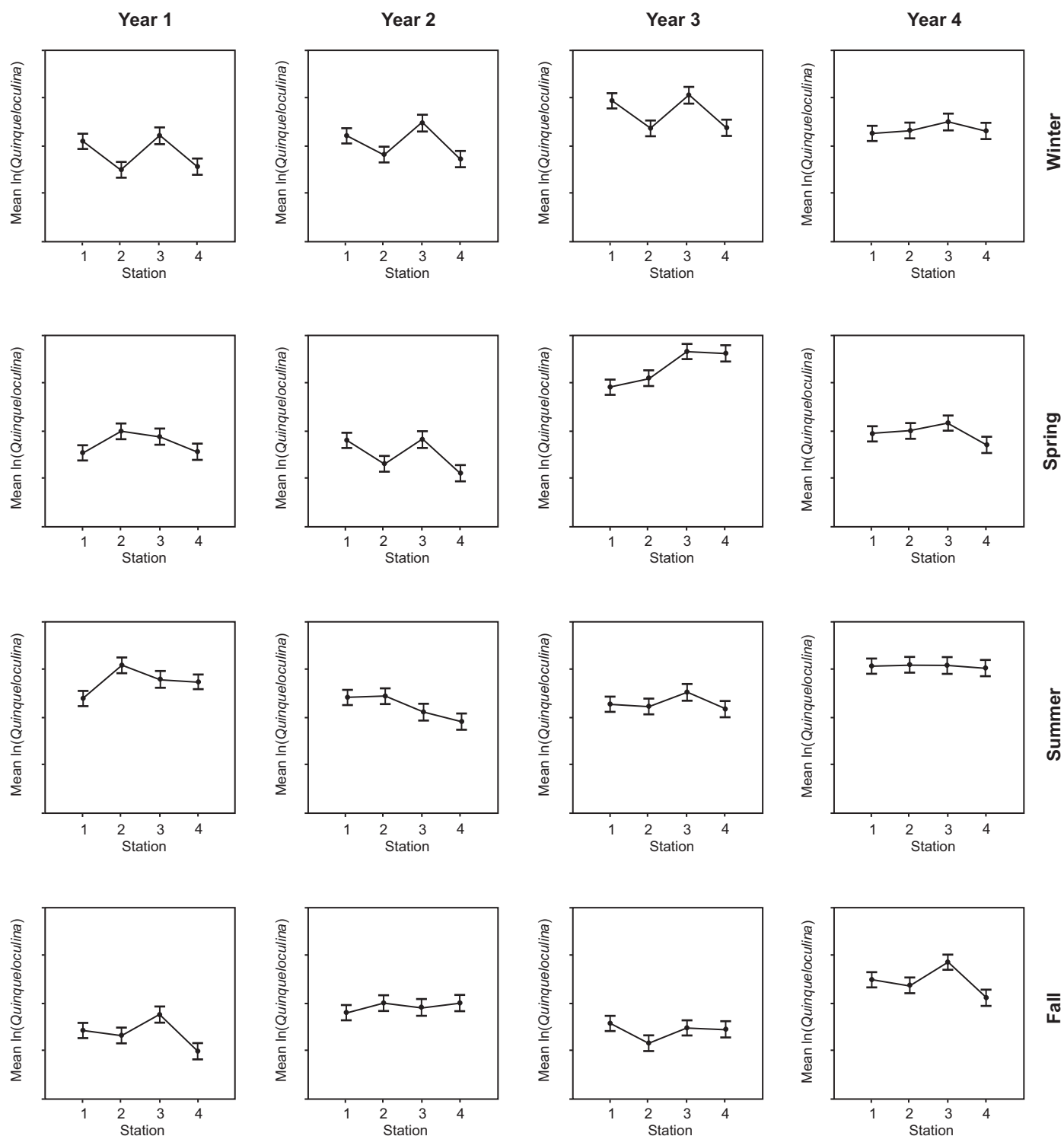


FIGURE 38. Mean number of $\ln(\text{Quinqueloculina})$ for station $\times$ season $\times$ year interaction for stations 10 m apart.

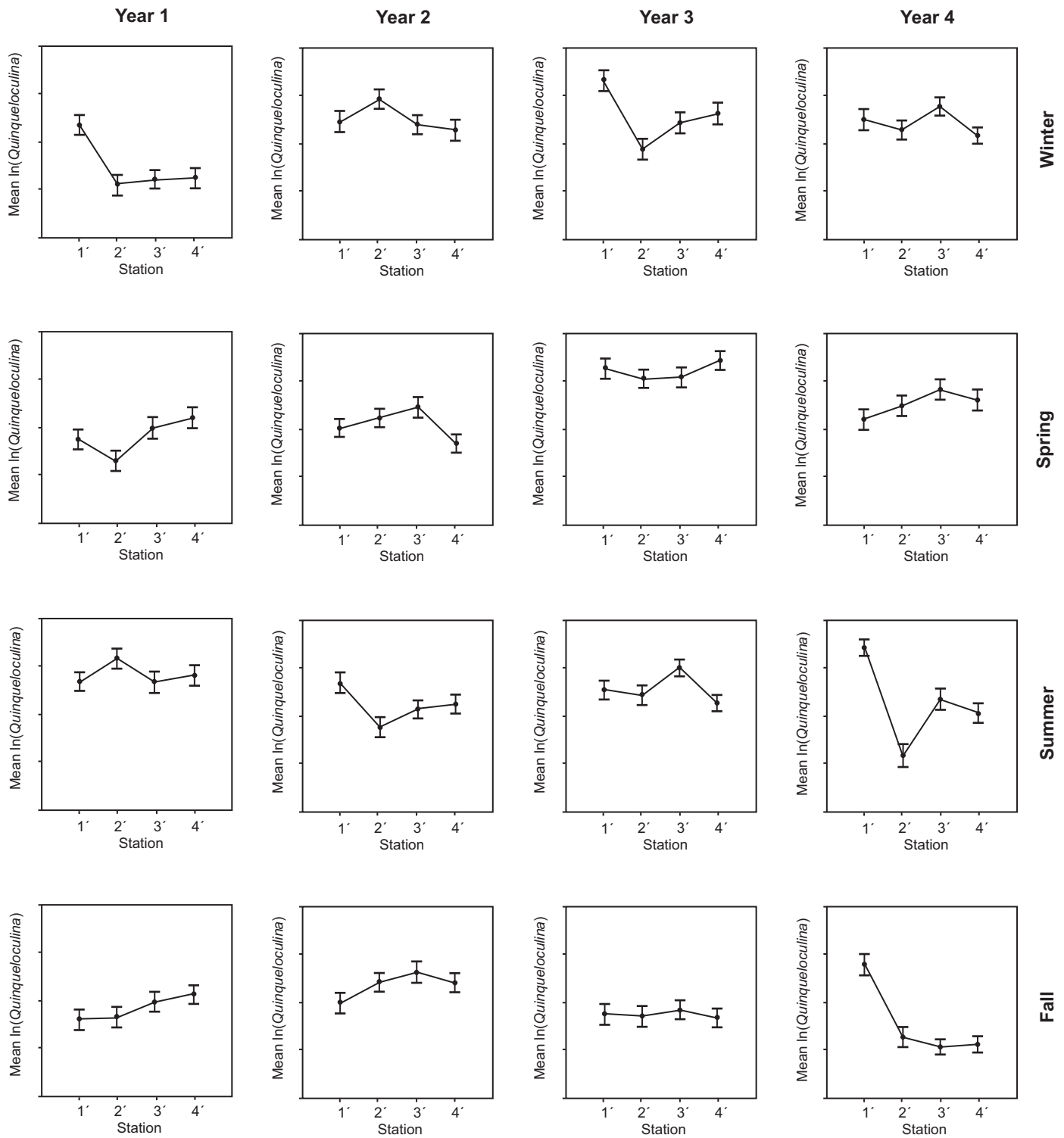


FIGURE 39. Mean number of $\ln(\text{Quinqueloculina})$ for station $\times$ season $\times$ year interaction for stations 1 m apart.

TABLE 27. ANOVA for station, season, year, and their interaction differences on $\ln(x + 1)$, where x is density of *Ammonia*, for stations 10 m apart.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Station	17.648	3	5.883	13.844	0.000
Season	20.289	3	6.763	15.916	0.000
Year	121.435	3	40.478	95.262	0.000
Station $\times$ season	9.314	9	1.035	2.435	0.012
Station $\times$ year	18.579	9	2.064	4.858	0.000
Season $\times$ year	61.322	9	6.814	16.035	0.000
Station $\times$ season $\times$ year	19.747	27	0.731	1.721	0.019
Error	81.584	192	0.425		

The results of the ANOVA for *Ammonia* at the 1 m² site are shown in Table 28. Like the 100 m² site result, the hypothesis test for years has the highest mean square. However, the interaction hypothesis of station $\times$ seasons is not significant. Recall that for *Quinqueloculina*, the interaction hypothesis for station $\times$ years was not significant at the 100 m² site.

A scatterplot of stations at the two sites is shown in Figure 40. The overall station differences are significant at both sites. Although the station densities for *Ammonia* are lower than those for *Quinqueloculina*, the patterns of highs and lows were remarkably similar, indicating that favorable conditions for an increase in density were mostly the same for both species (compare Figures 32 and 40).

However, Figure 41 shows the overall plot of seasonal density for *Ammonia* at the two sites for which the patterns of highs and lows were not the same. At the 100 m²

TABLE 28. ANOVA for station, season, year, and their interaction differences on $\ln(x + 1)$, where x is density of *Ammonia*, for stations 1 m apart.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Station	6.035	3	2.012	2.925	0.035
Season	16.022	3	5.341	70766	0.000
Year	103.921	3	34.640	50.371	0.000
Station $\times$ season	6.466	9	0.718	1.045	0.406
Station $\times$ year	12.605	9	1.401	2.037	0.037
Season $\times$ year	71.204	9	7.912	11.504	0.000
Station $\times$ season $\times$ year	60.389	27	2.237	3.252	0.000
Error	132.039	192	0.688		

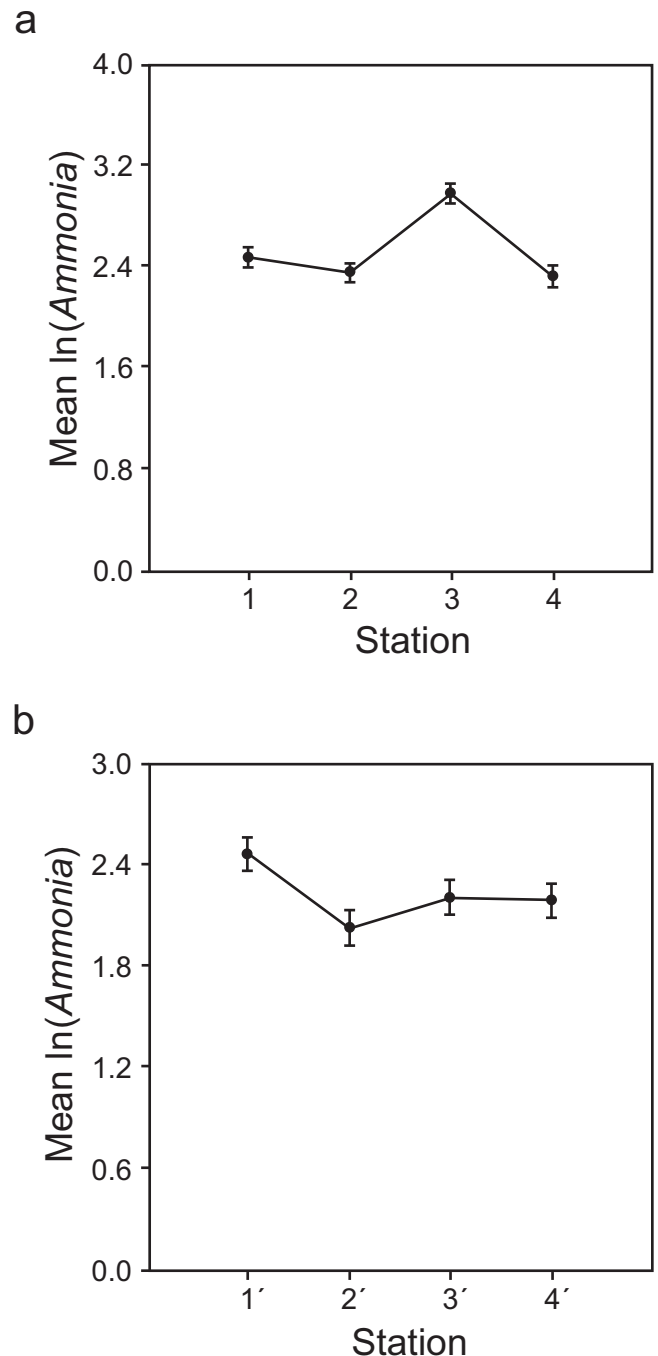


FIGURE 40. Mean number of $\ln(\text{Ammonia})$ at stations. (a) Stations 10 m apart. (b) Stations 1 m apart.

site winter and spring densities were higher than those of summer and fall, whereas at the 1 m² site, only summer had a lower density than the other three seasons. Comparing Figure 41 with Figure 33 shows that the two taxa behave quite differently with respect to seasons.

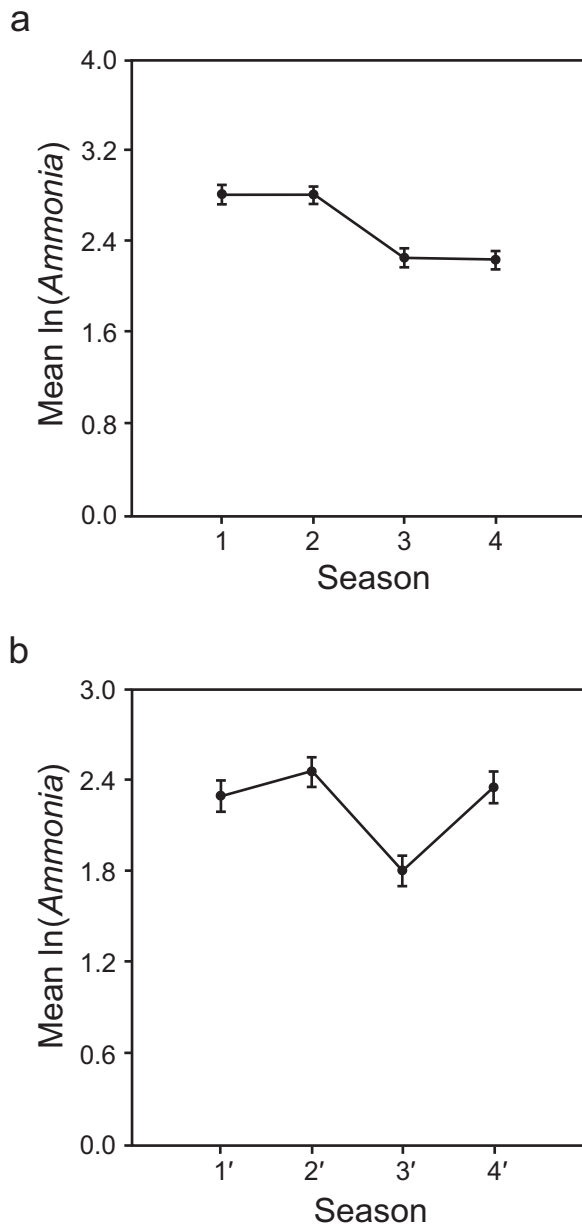


FIGURE 41. Mean number of $\ln(\text{Ammonia})$ for seasons: 1 = winter, 2 = spring, 3 = summer, 4 = fall. (a) Stations 10 m apart. (b) Stations 1 m apart.

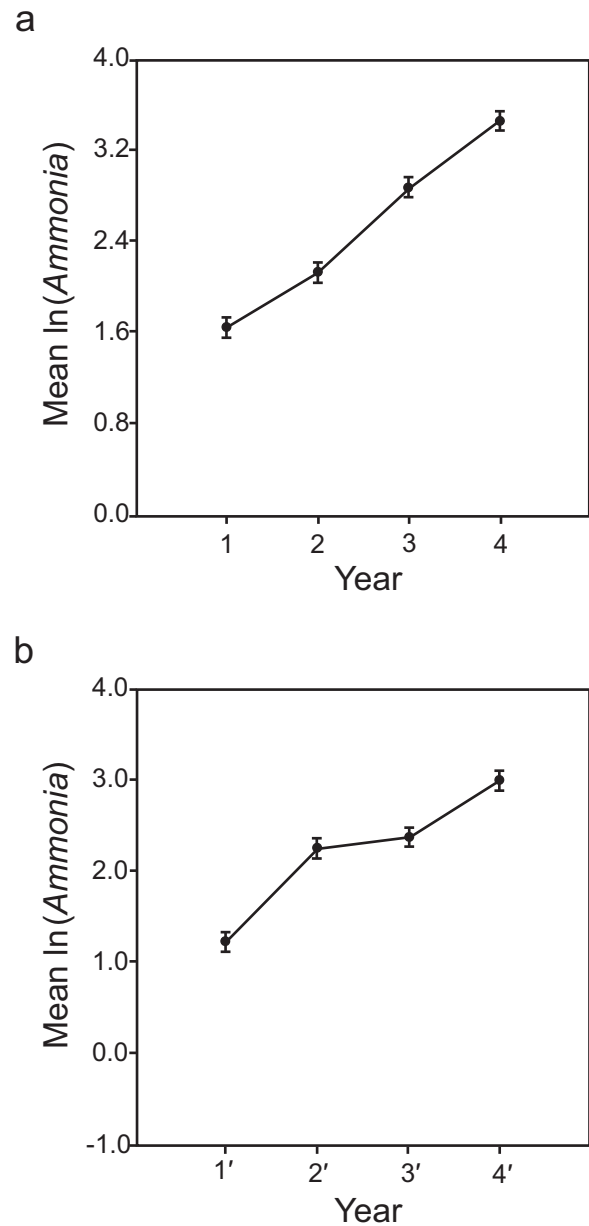


FIGURE 42. Mean number of $\ln(\text{Ammonia})$ for years: 1 = summer 2001 to spring 2002, 2 = summer 2002 to spring 2003, 3 = summer 2003 to spring 2004, 4 = summer 2004 to spring 2005. (a) Stations 10 m apart. (b) Stations 1 m apart.

Figure 42 is a scatterplot for overall differences among years at the two sites for *Ammonia*. At both sites density increases over the years of observation, and we can contrast this pattern with that of *Quinqueloculina* shown in Figure 34. For *Quinqueloculina* there is also an increase over years except for year 4 at the 1 m² site. Because of this decrease in year 4 at the 1 m² site, the rank order of dominance changes, and *Ammonia* has a higher

density than *Quinqueloculina* at the 1 m² site. A switch in the rank order of species would usually be regarded as an important event indicating a change in community structure. Here, however, it happens only at the 1 m² site, indicating caution in drawing conclusions is advisable.

Figure 43 shows interaction plots for station $\times$ season at the 100 and 1 m² sites. At the 100 m² site, station 3 appears to have high densities in all seasons; however,

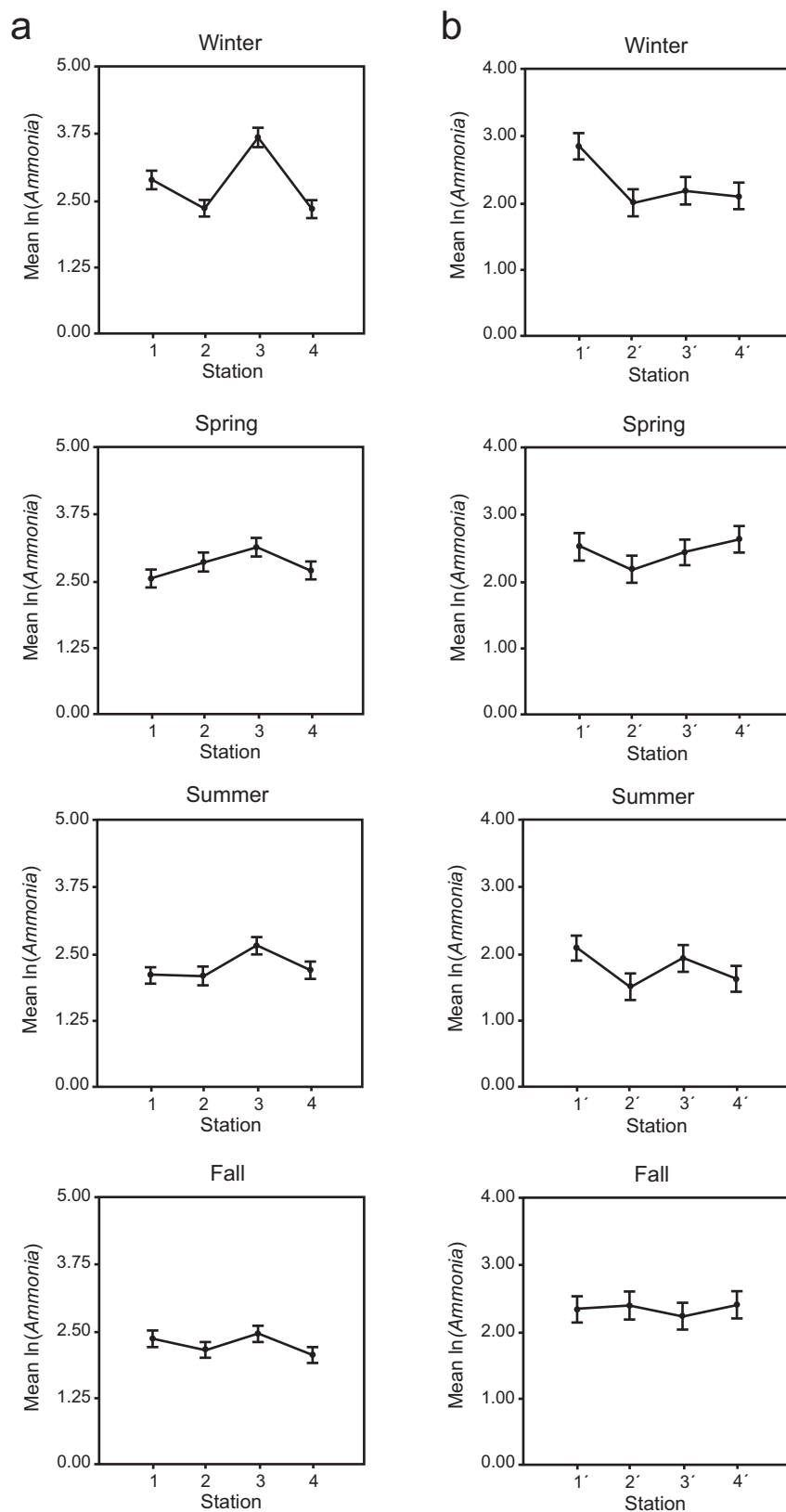


FIGURE 43. Mean number of $\ln(\text{Ammonia})$ for station $\times$ season interaction. (a) Stations 10 m apart. (b) Stations 1 m apart.

the interaction hypothesis was significant (Table 27). At the 1 m² site Figure 43 shows a high density in winter and summer at station 1. However, the hypothesis for station $\times$ season was not significant.

Figure 44 indicates that for the 100 m² site station 3 has high density in years 1 and 2, but in year 3 densities at both stations 3 and 4 are higher than in years 1 and 2. In the fourth year, the density at station 4 is slightly lower than in the other three years. Note also how the densities are increasing with years (see also Figure 43). For years 1 and 2, the 1 m² site shows little difference among stations (Figure 44). In year 3, stations 3 and 4 appear to have slightly higher densities, and in year 4 station 1 has higher density. Like the 100 m² site, the 1 m² site shows an increase in density over the years (Figure 43).

Figure 45 shows the interaction of seasons $\times$ years at the two sites. Except for the third year, high and low densities do not follow the same pattern over the four years of observations at the two sites. We have, then, a situation in which not only do different seasons exhibit high or low densities among years, but also in three of four years the two sites exhibit different seasonal patterns.

Figure 46 illustrates the 16 possibilities for the three-way interaction of station $\times$ season $\times$ year at the 100 m² site. As with *Quinqueloculina* different stations have low and high densities at different times; these are the pulsating patches.

Figure 47 illustrates the 16 possibilities for the interaction of station $\times$ season $\times$ year at the 1 m² site. Similar to the other examples of three-way interaction, the stations differ in high and low densities with time. The pattern of high and low densities is not the same as at the 100 m² site (Figure 46). Both sites exhibit high densities in the spring and winter of years 3 and 4. However, the high density in the fall of year 4 at the 100 m² site is not apparent visually at the 1 m² site.

In summary, Figures 38 and 46 show the patterns for the 100 m² site, and Figures 39 and 47 show patterns for the 1 m² site. These figures make clear that *Quinqueloculina* and *Ammonia* do not exhibit the same patterns for the three-way interactions.

ELPHIDIUM

The results for the three-way ANOVA for *Elphidium* at the 100 m² site are shown in Table 29. All of the hypothesis test results were significant at the $p < 0.05$ level. Like *Ammonia* (Table 27), the mean square for years is high for this taxon, an order of magnitude higher than the

rest. The interaction hypothesis for season $\times$ years also has a large mean square.

The results for the three-way ANOVA for *Elphidium* at the 1 m² site are shown in Table 30. The hypothesis for equality of overall station differences and that for the interaction of station $\times$ season differences were not significant. The mean square for overall yearly differences is by far the largest (Table 30).

Figure 48 shows the overall density at the stations at the two sites. At the 100 m² site the pattern is similar to that for *Quinqueloculina* (Figure 32) and for *Ammonia* (Figure 40). Unlike the other two taxa, however, at the 1 m² site there is no significant difference among stations for *Elphidium* (Figure 48).

Figure 49 shows the overall seasonal density at the two sites. In both cases there is a decrease from winter to fall. The pattern at the 100 m² site resembles that of *Ammonia* (Figure 41) at the same site, but the pattern at the 1 m² site is unique, although *Ammonia* also exhibits an overall summer low.

Figure 50 shows that at both sites there is an overall increase in densities of *Elphidium* with years. This pattern is very similar to that for *Ammonia* (Figure 42) but not to that of *Quinqueloculina* (Figure 34).

The interaction of station $\times$ season for the two sites is shown in Figure 51. As with *Ammonia* at the 1 m² site, the interaction is not significant. At the 100 m² site, in winter, stations 1 and 3 exhibit high densities. This same pattern is evident for *Quinqueloculina* (Figure 35) and for *Ammonia* (Figure 42). During the other seasons the patterns are different among the taxa.

The interaction of station $\times$ year for the two sites is shown in Figure 52. The pattern at the 100 m² site does not differ among the stations for the years to the extent that it does at the 1 m² site. Except for year 4, the pattern is not the same at the two sites, but unlike with seasonal densities both sites have a significant interaction and, therefore, pulsating patches over the years. For *Quinqueloculina* the interaction hypothesis for station $\times$ years was not significant at the 100 m² site. At the 1 m² site, except for year 4 when they were similar (Figure 36), the pattern for *Quinqueloculina* differs from that of *Elphidium* (Figure 52). The station $\times$ year patterns were more similar at both sites for *Ammonia* and *Elphidium* (Figures 44 and 52). This similarity is especially evident at the 1 m² site in year 4, when *Quinqueloculina*, *Ammonia*, and *Elphidium* all exhibit the same pattern (Figures 36, 44, and 52).

The magnitude of the value for the mean square of the interaction for season $\times$ year is second only to that for the

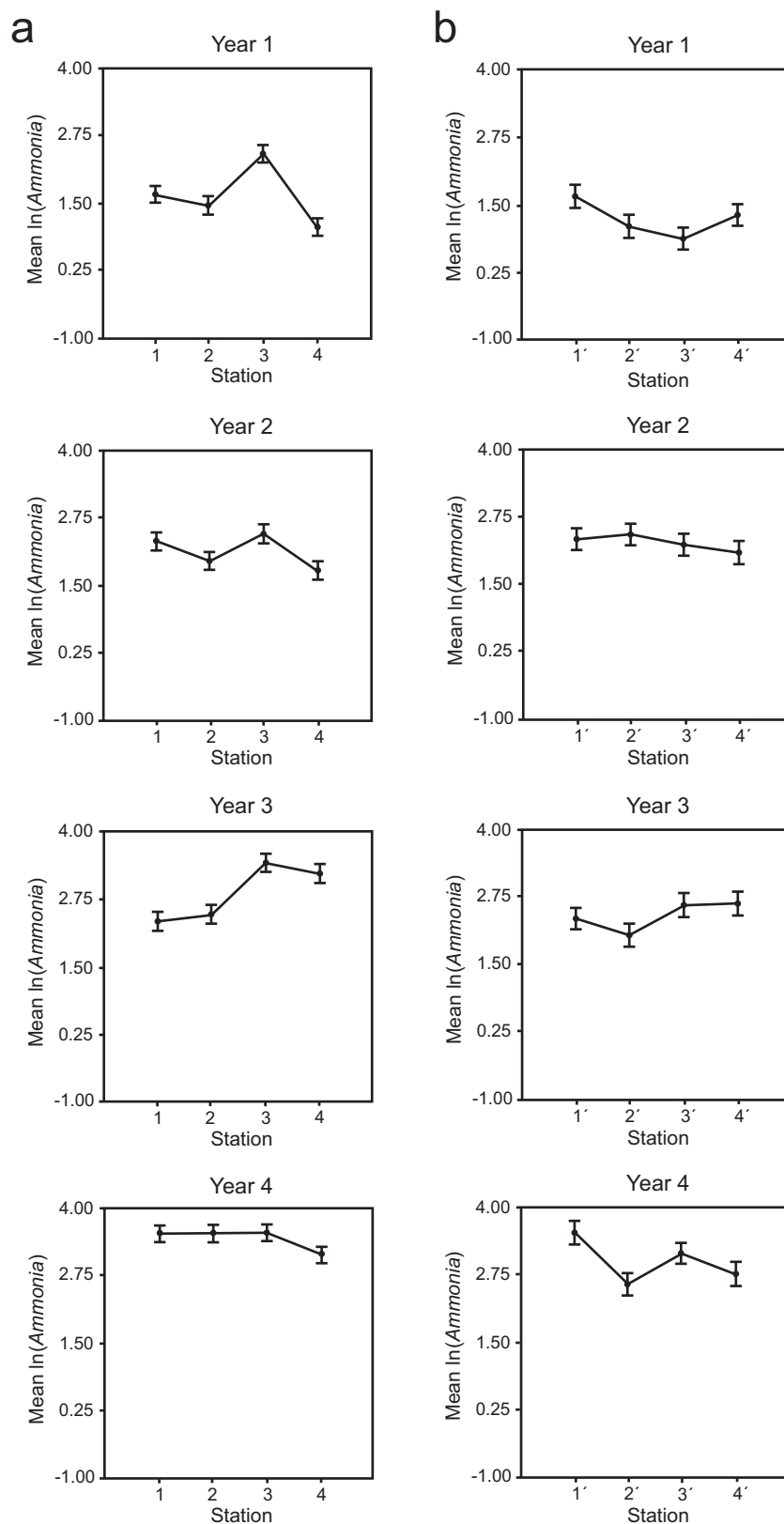


FIGURE 44. Mean number of $\ln(\text{Ammonia})$ for station $\times$ year interaction. (a) Stations 10 m apart. (b) Stations 1 m apart.

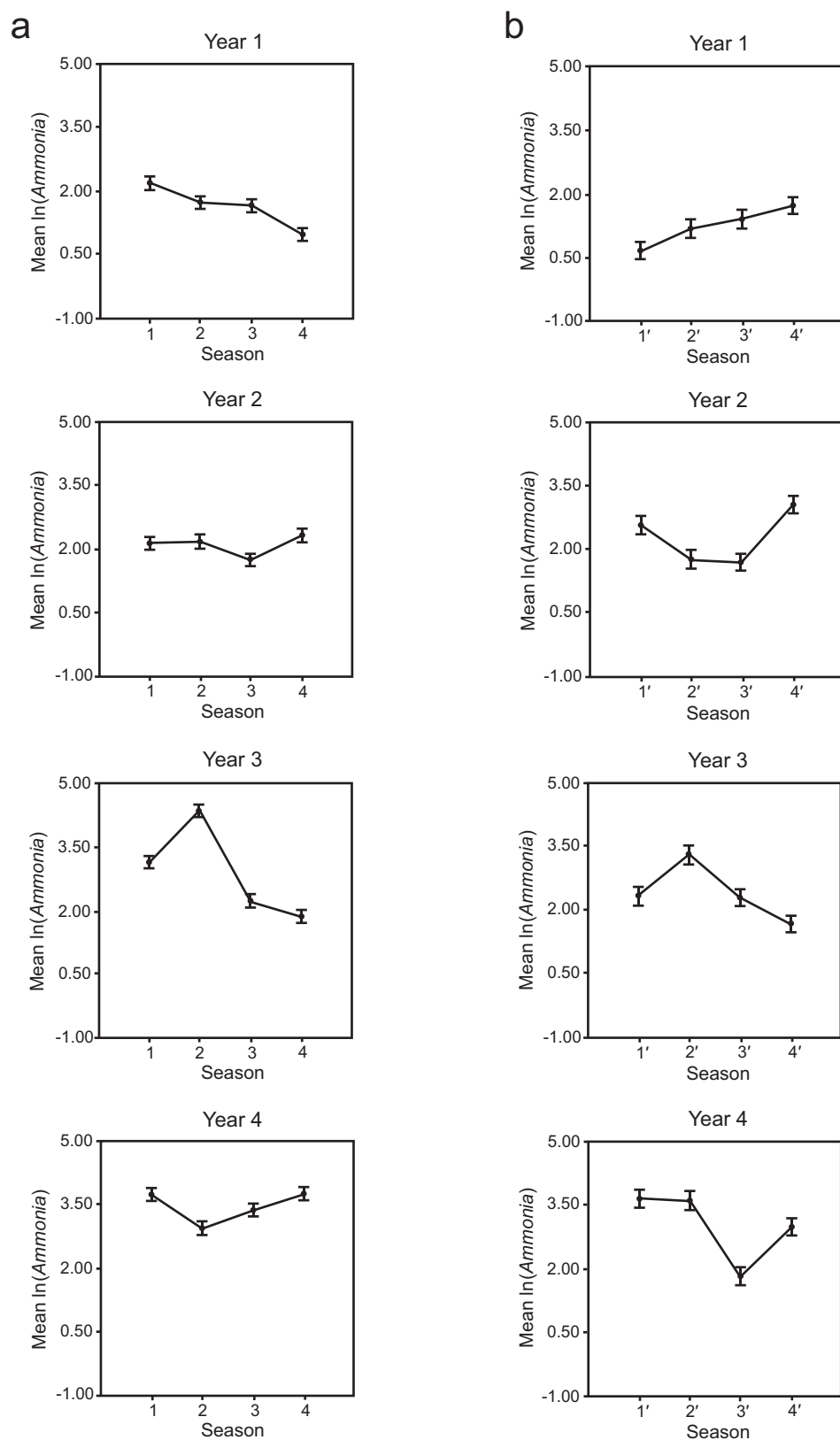


FIGURE 45. Mean number of $\ln(\text{Ammonia})$ for season $\times$ year interaction. (a) Stations 10 m apart. (b) Stations 1 m apart.

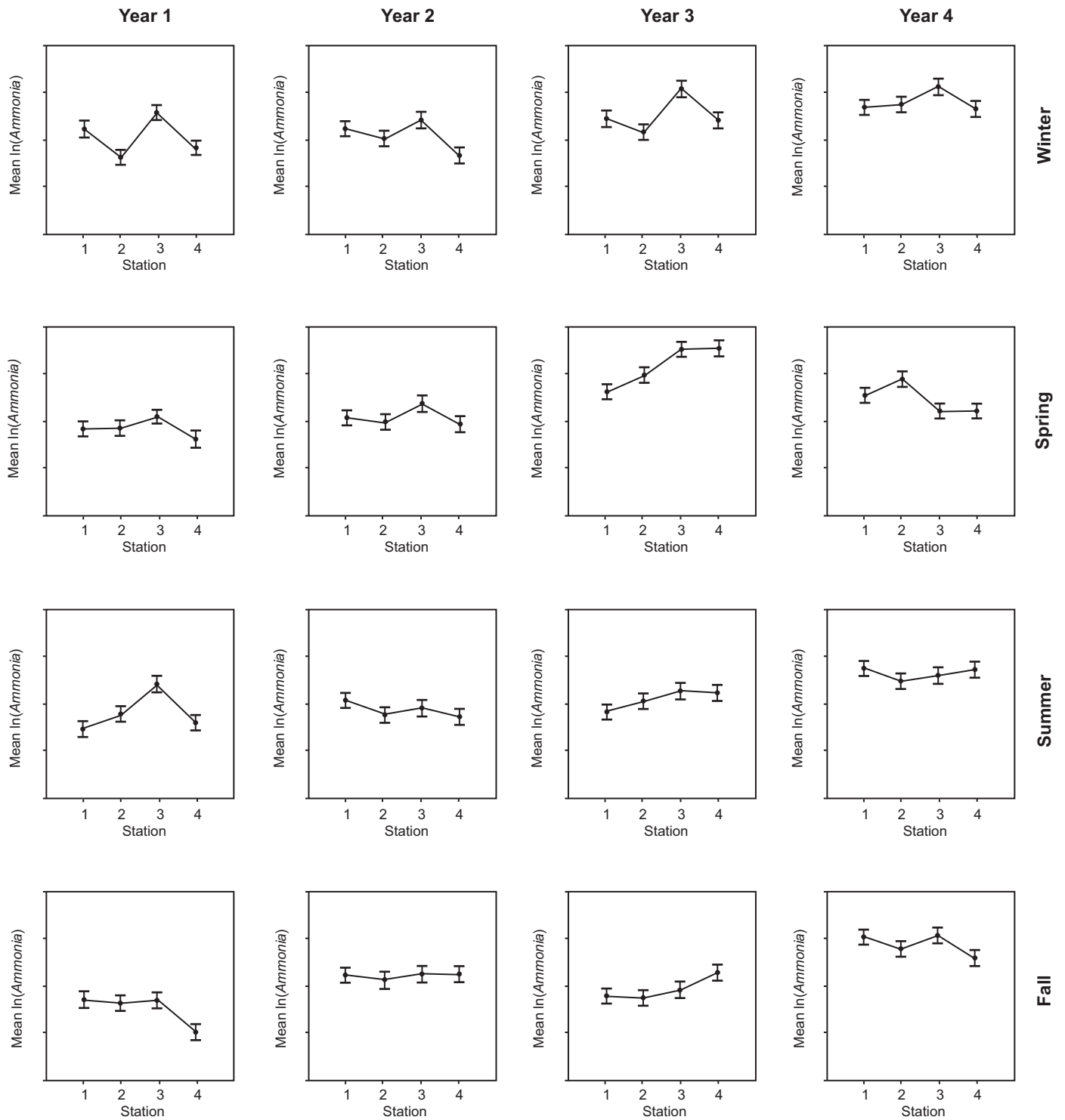


FIGURE 46. Mean number of $\ln(\text{Ammonia})$ for station $\times$ season $\times$ year interaction for stations 10 m apart.

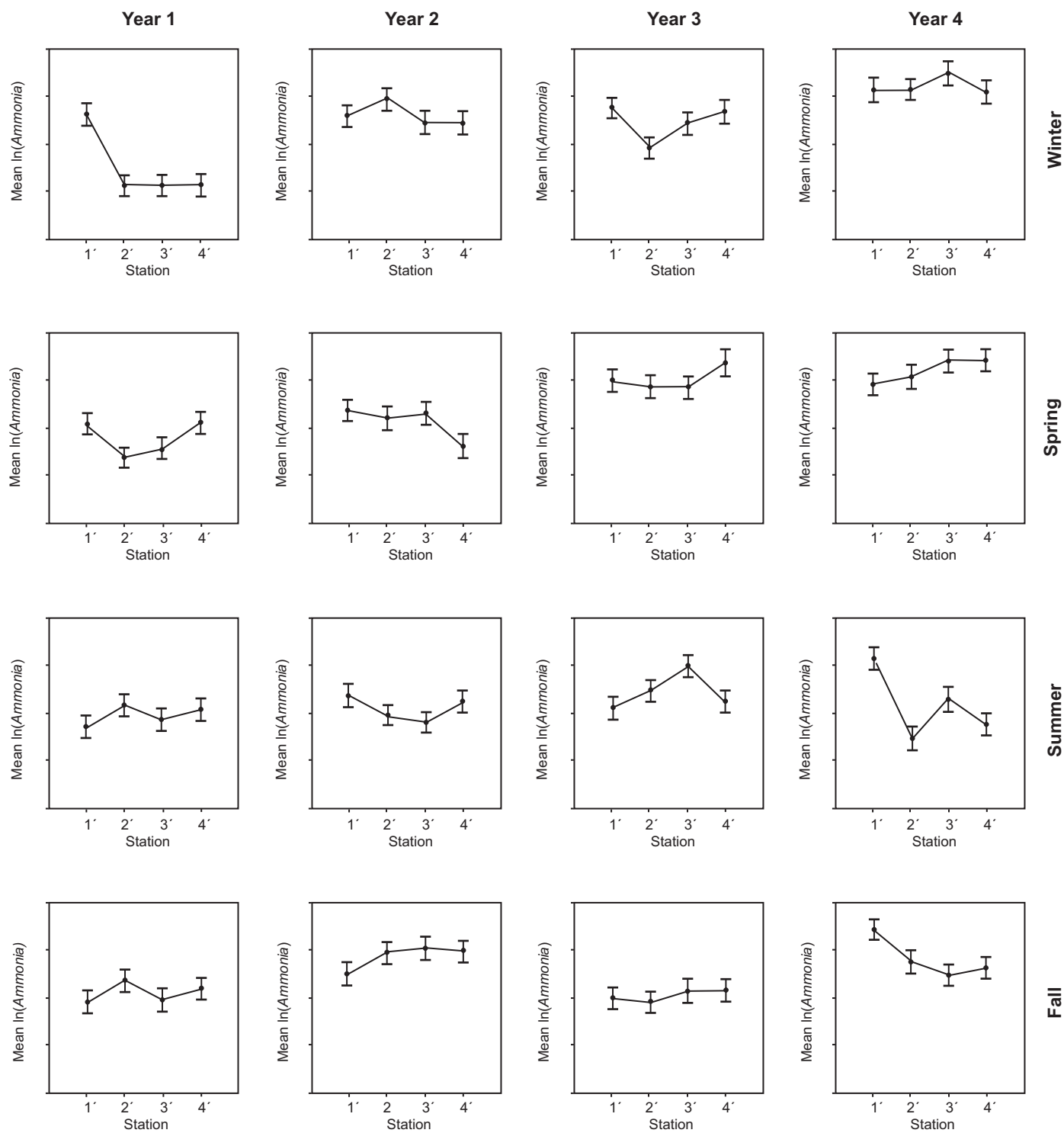


FIGURE 47. Mean number of $\ln(\text{Ammonia})$ for station $\times$ season $\times$ year interaction for stations 1 m apart.

TABLE 29. ANOVA for station, season, year, and their interaction differences on $\ln(x + 1)$, where x is density of *Elphidium*, for stations 10 m apart.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Station	18.942	3	6.314	13.805	0.000
Season	16.535	3	5.512	12.051	0.000
Year	225.575	3	75.192	164.403	0.000
Station $\times$ season	10.797	9	1.200	2.623	0.007
Station $\times$ year	12.133	9	1.348	2.948	0.003
Season $\times$ year	162.324	9	18.036	39.435	0.000
Station $\times$ season $\times$ year	30.371	27	1.125	2.459	0.000
Error	87.814	192	0.457		

TABLE 30. ANOVA for station, season, year, and their interaction differences on $\ln(x + 1)$, where x is density of *Elphidium*, for stations 1 m apart.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Station	2.603	3	0.868	1.351	0.259
Season	21.420	3	7.140	11.118	0.000
Year	166.537	3	55.512	86.442	0.000
Station $\times$ season	8.658	9	0.962	1.498	0.151
Station $\times$ year	30.479	9	3.387	5.273	0.000
Season $\times$ year	139.866	9	15.541	24.199	0.000
Station $\times$ season $\times$ year	67.998	27	2.518	3.922	0.000
Error	123.301	192	0.642		

hypothesis for overall years at both sites (Tables 29, 30). Recall this is also true for *Ammonia* (Tables 27, 28) but not for *Quinqueloculina* (Tables 25, 26). The interaction of season $\times$ year for the two sites is shown in Figure 53. At both sites spring shows high densities in year 3, but the two sites do not exhibit similar patterns for seasons in other years. The high density in spring of year 3 is also evident for *Quinqueloculina* (Figure 37) and *Ammonia* (Figure 45).

Figure 54 shows the 16 possibilities for the three-way interaction of station $\times$ season $\times$ year at the 100 m² site. In some of the plots a large visual difference among the stations can be seen, and in the remaining plots little difference

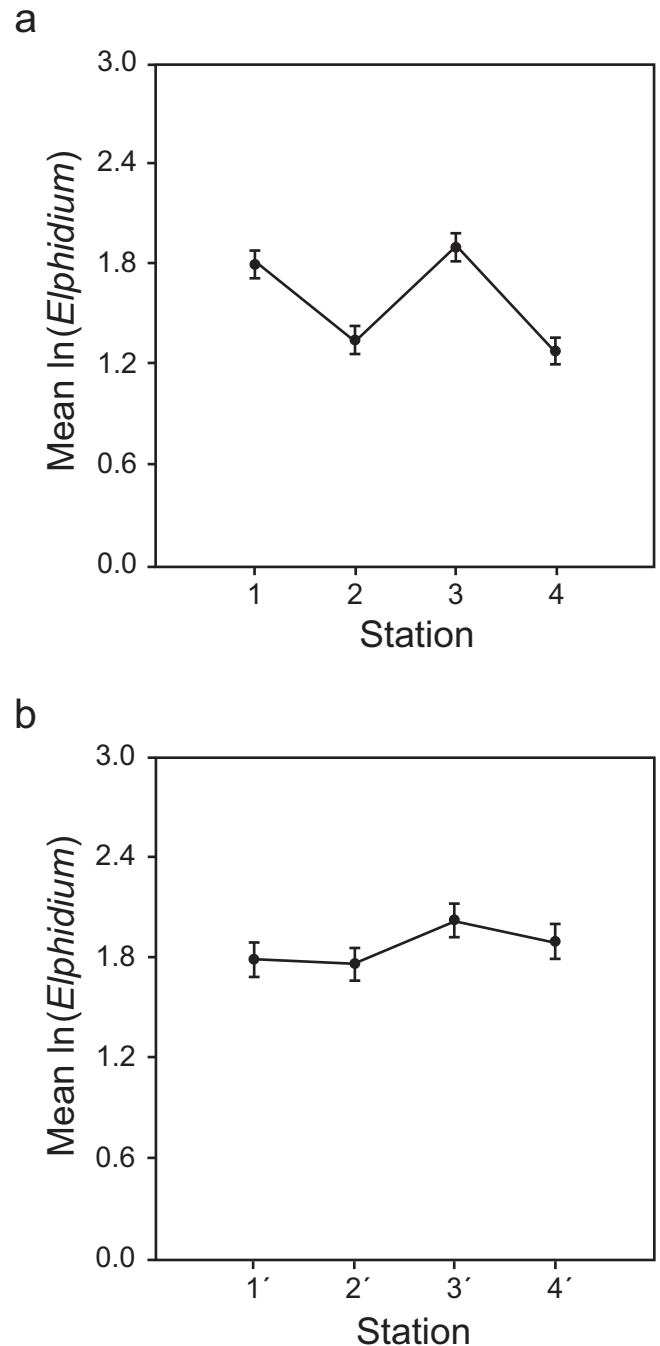


FIGURE 48. Mean number of $\ln(\text{Elphidium})$ at stations. (a) Stations 10 m apart. (b) Stations 1 m apart.

is evident. Although station 3 exhibited high densities, this is true only about half the time. In year 3, spring had the highest density observed, and in year 4, except for spring, densities were high in three of the seasons. Surprisingly,

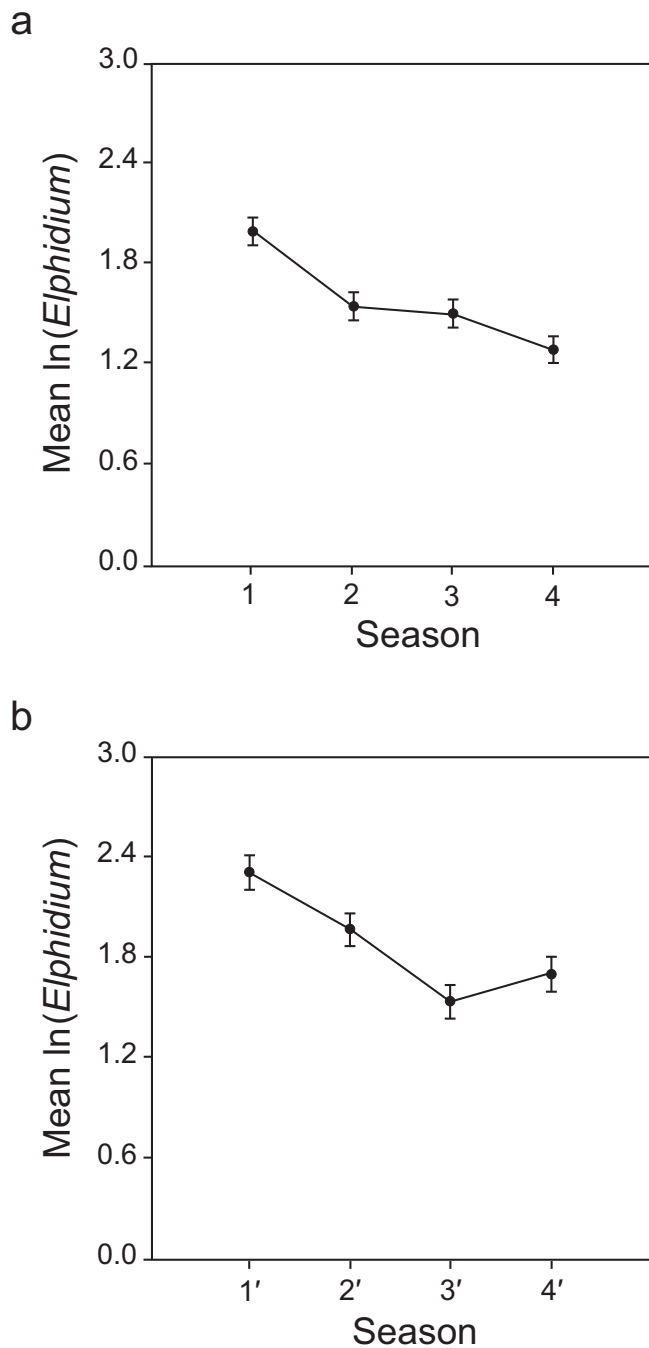


FIGURE 49. Mean number of $\ln(\text{Elphidium})$ for seasons: 1 = winter, 2 = spring, 3 = summer, 4 = fall. (a) Stations 10 m apart. (b) Stations 1 m apart.

winter had the highest density (see also Figure 49), and during the four years of observation these winter densities increased each year (see also Figure 40).

Figure 55 shows the 16 possibilities for the three-way interaction of station $\times$ season $\times$ year at the 1 m² site. Similar to the 100 m² site's behavior, the difference in densities

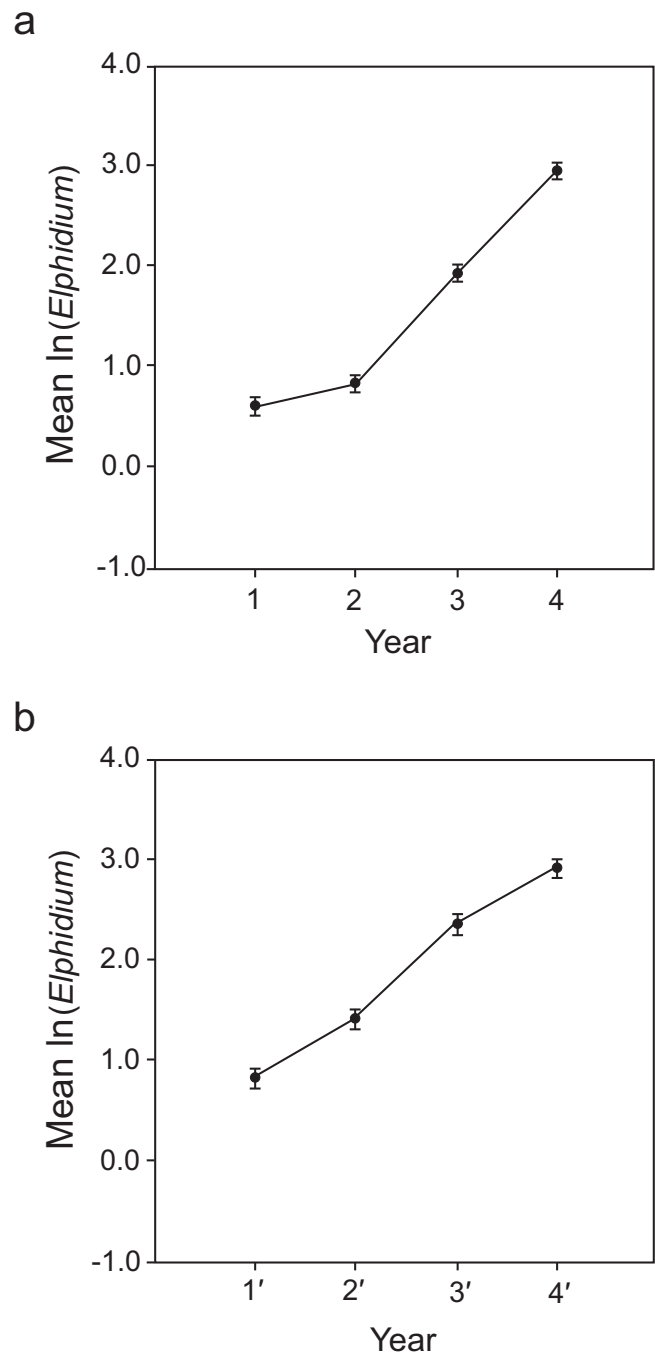


FIGURE 50. Mean number of $\ln(\text{Elphidium})$ for years: 1 = summer 2001 to spring 2002, 2 = summer 2002 to spring 2003, 3 = summer 2003 to spring 2004, 4 = spring 2004 to spring 2005. (a) Stations 10 m apart. (b) Stations 1 m apart.

among stations was sometimes large and sometimes very small. We would not expect the stations to show the same patterns, and they clearly do not (compare Figures 54 and 55). Both sites exhibit a high density in the spring of year

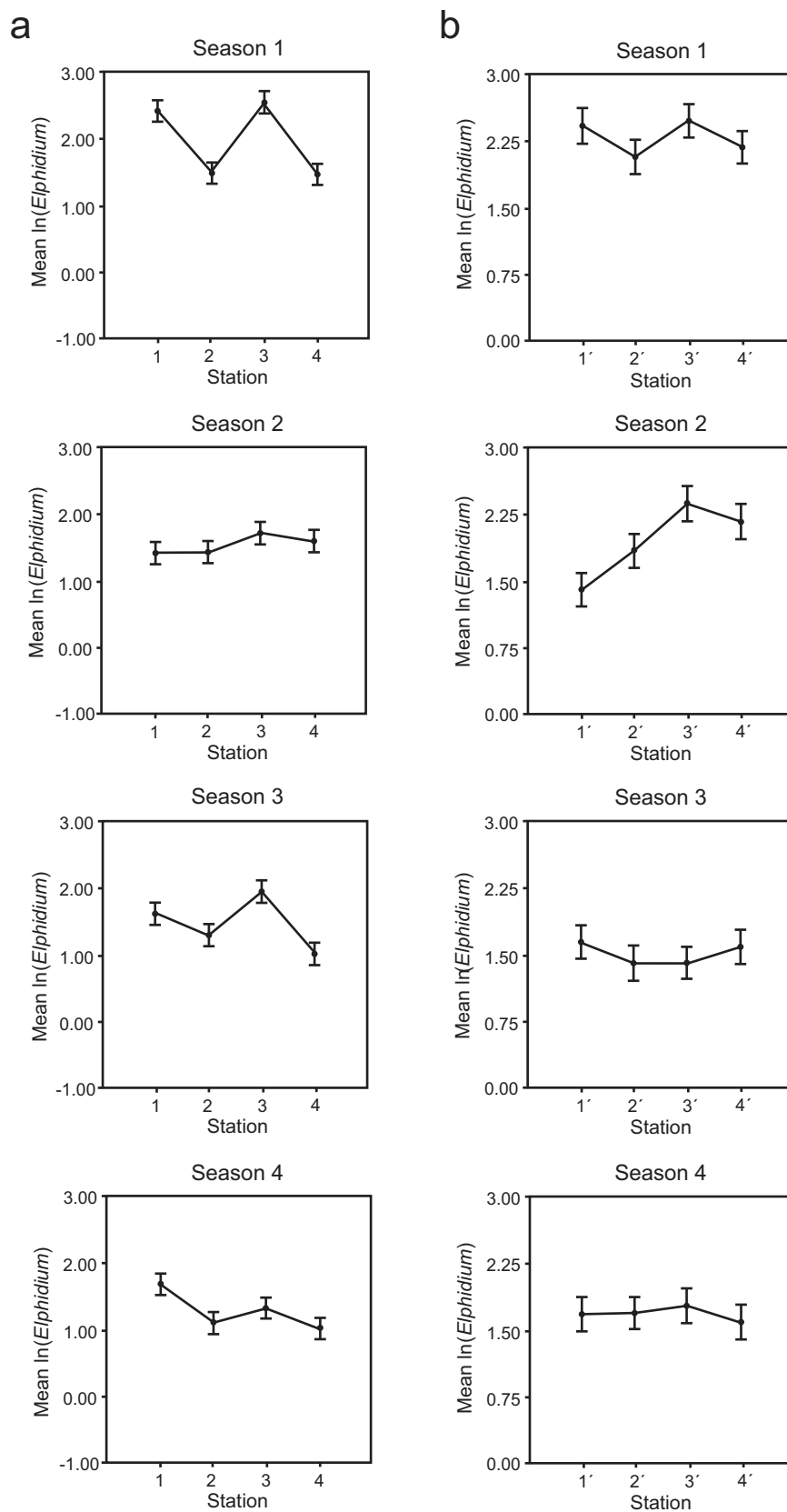


FIGURE 51. Mean number of $\ln(\textit{Elphidium})$ for station $\times$ season interaction. (a) Stations 10 m apart. (b) Stations 1 m apart.

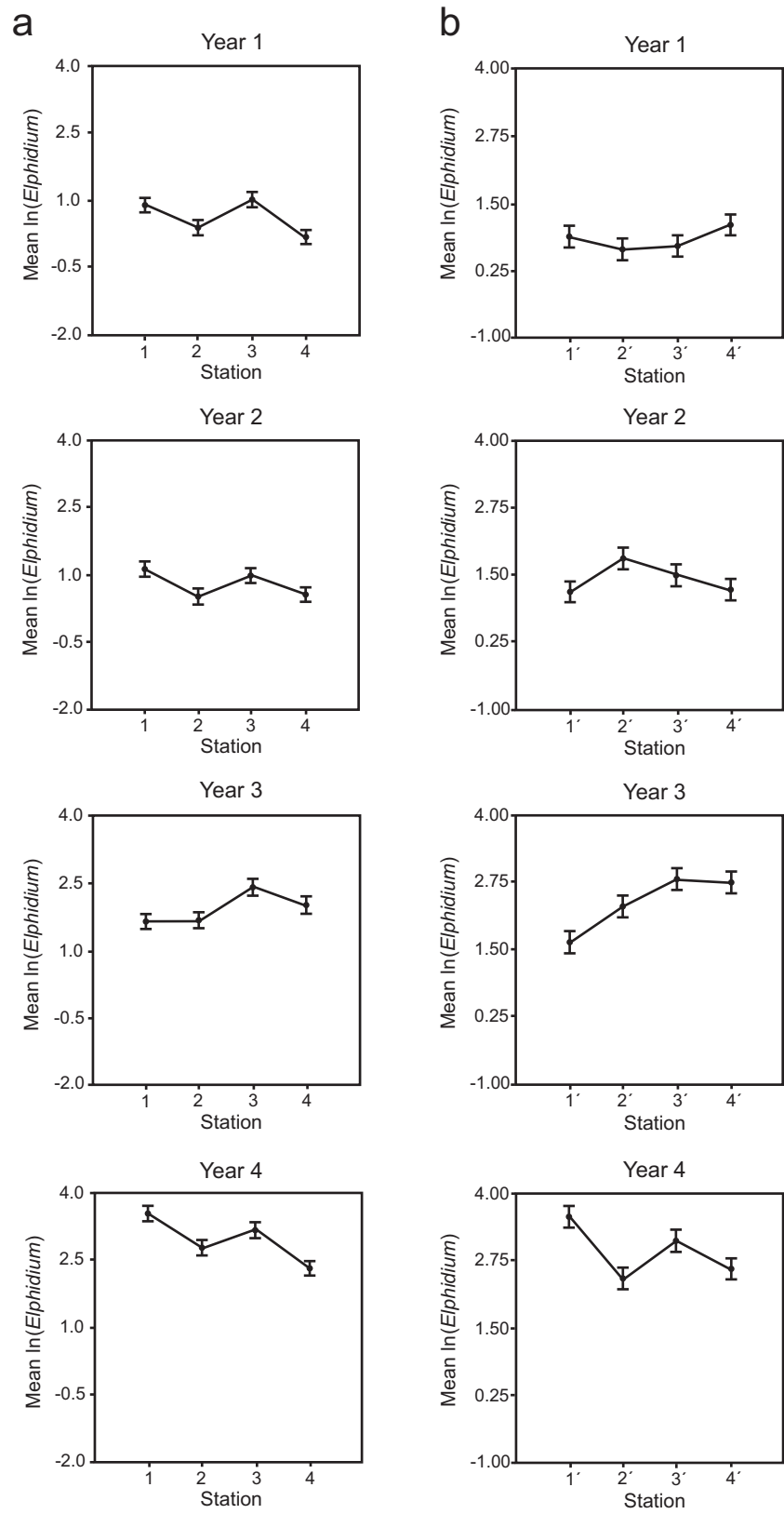


FIGURE 52. Mean number of $\ln(\text{Elphidium})$ for station $\times$ year interaction. (a) Stations 10 m apart. (b) Stations 1 m apart.

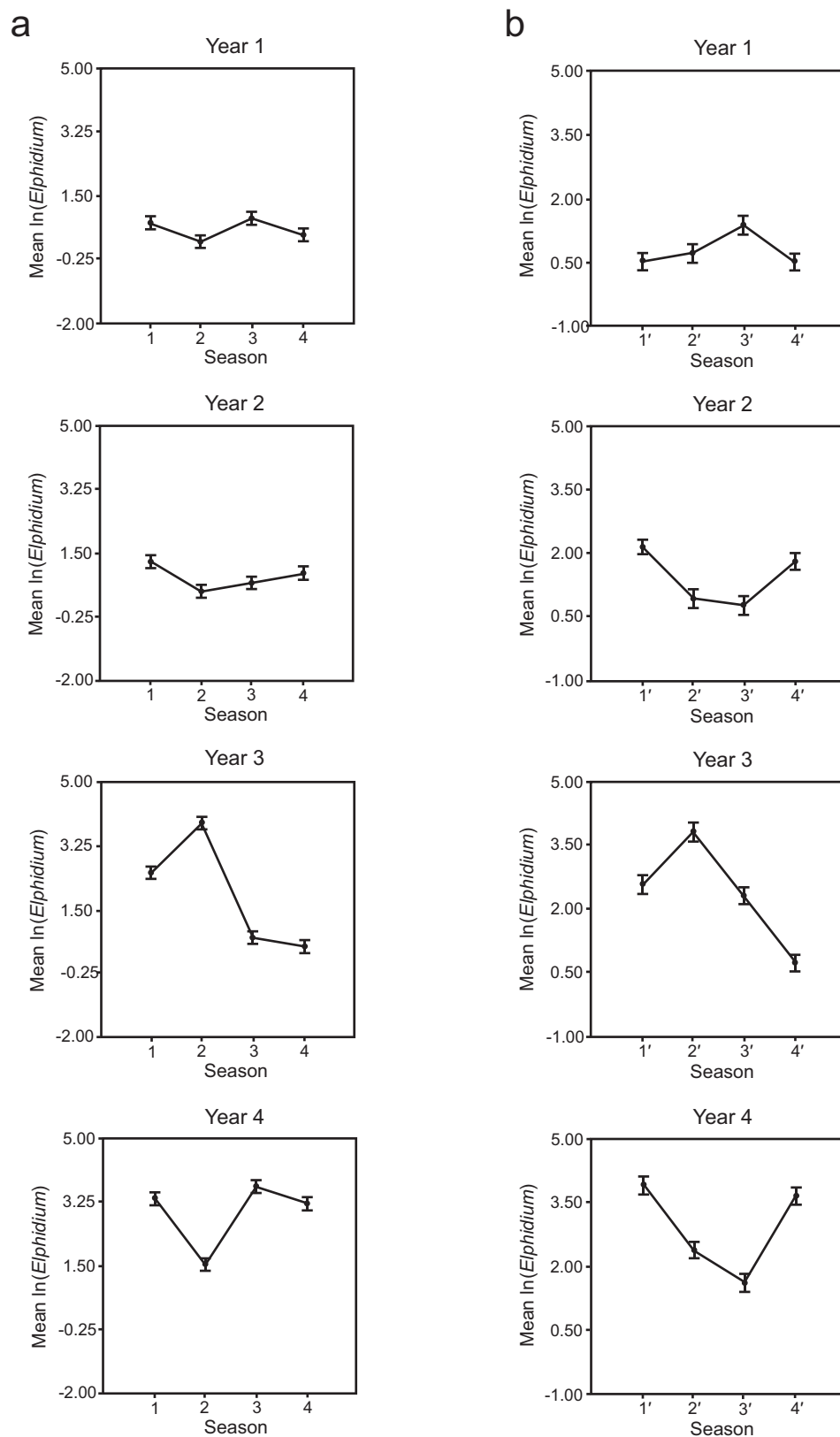
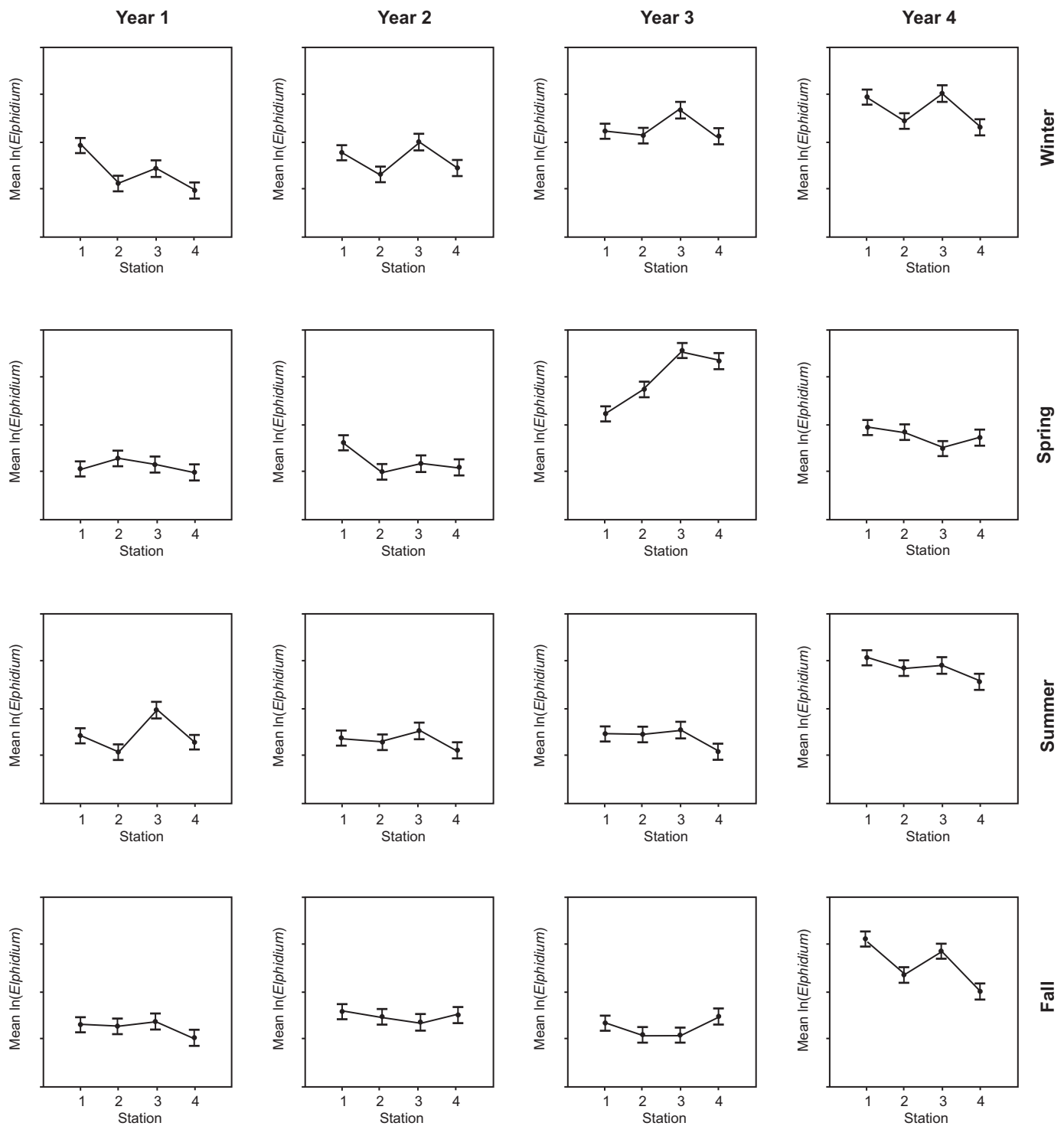


FIGURE 53. Mean number of $\ln(\text{Elphidium})$ for season $\times$ year interaction. (a) Stations 10 m apart. (b) Stations 1 m apart.

FIGURE 54. Mean number of $\ln(\text{Elphidium})$ for station $\times$ season $\times$ year interaction for stations 10 m apart.

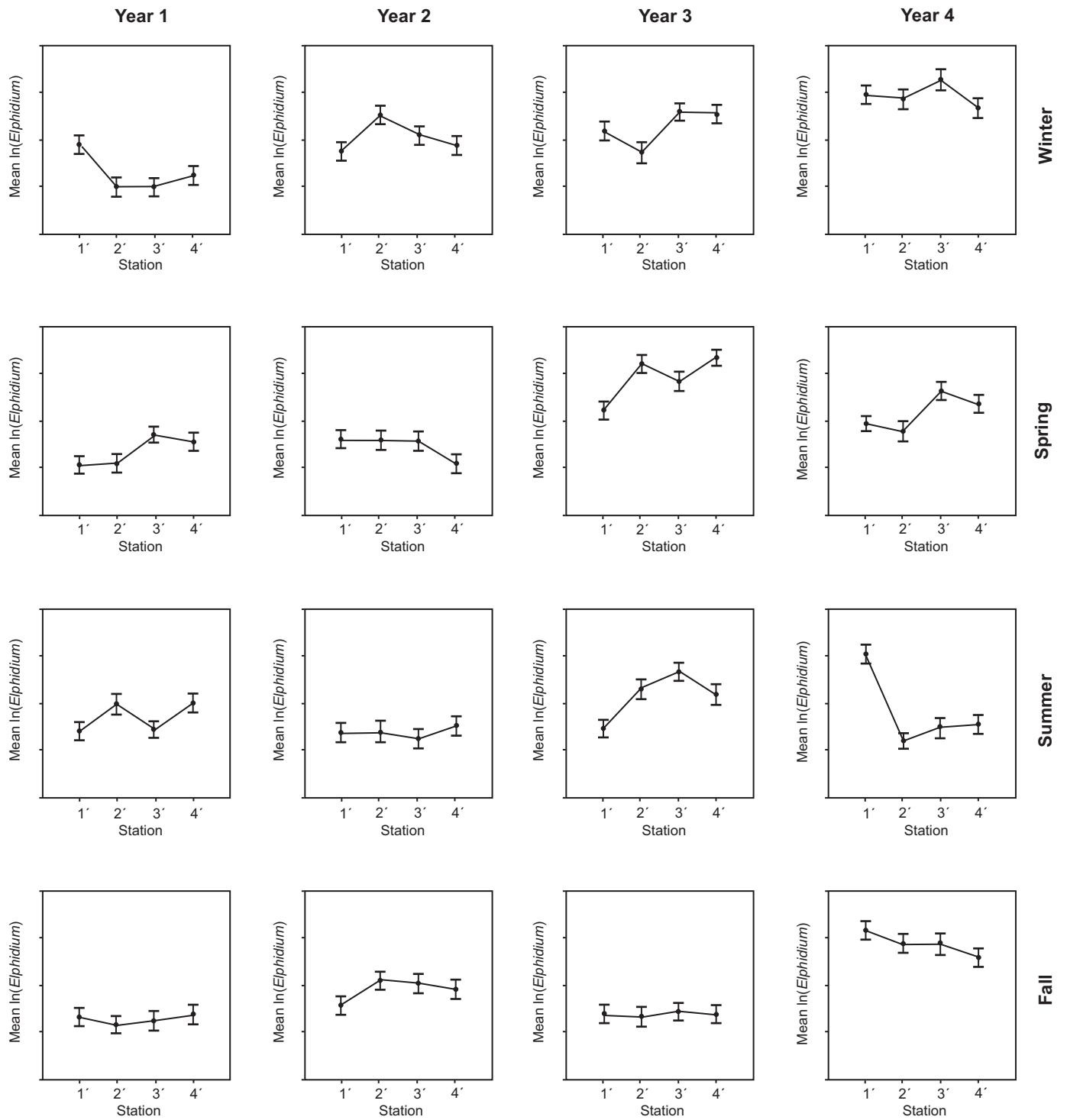


FIGURE 55. Mean number of $\ln(\text{Elphidium})$ for station $\times$ season $\times$ year interaction for stations 1 m apart.

3 and high winter and fall densities in year 4. At both sites, however, we observe an increase in densities during the four years of observation (see also Figure 50).

Visually, if we compare the 16 possibilities at the 100 m² site for *Quinqueloculina*, *Ammonia*, and *Elphidium* the patterns of pulsating patches at the stations are amazingly similar (Figures 38, 46, and 54). If we compare the pattern of pulsating patches (pattern at stations) at the 1m² site, the same phenomenon is apparent (Figures 39, 47, and 55). All three taxa exhibit a similar pattern and high densities in spring of year 3.

AMMOBACULITES

The results for the three-way ANOVA with interaction for *Ammobaculites* at the 100 m² site are shown in Table 31. All hypothesis test results were statistically significant. The largest mean square by far is for yearly differences followed by seasonal differences. Although all the interaction hypotheses are significant, as with the other taxa, the largest mean square is for season × year.

The results for the 1 m² site are shown in Table 32. Once again, all hypothesis test results were statistically significant. In contrast to the 100 m² site, the mean squares for the main factors of season and year are nearly equal. Similar to that for the 100 m² site, the mean square for the interaction of season × year was the highest among the set of all interactions.

Figure 56 shows the overall density at each of the stations at the two sites. If we compare Figures 32, 40, 48, and 56, the similarities for all taxa in their patterns of highs and lows for station differences at the two sites are

TABLE 31. ANOVA for station, season, year, and their interaction differences on ln(*x* + 1), where *x* is density of *Ammobaculites*, for stations 10 m apart.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Station	11.291	3	3.764	11.974	0.000
Season	19.086	3	6.362	20.239	0.000
Year	62.495	3	20.832	66.273	0.000
Station × season	13.391	9	1.488	4.734	0.000
Station × year	8.589	9	0.954	3.036	0.002
Season × year	27.761	9	3.085	9.813	0.000
Station × season × year	13.511	27	0.500	1.592	0.039
Error	60.352	192	0.314		

TABLE 32. ANOVA for station, season, year, and their interaction differences on ln(*x* + 1), where *x* is density of *Ammobaculites*, for stations 1 m apart.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Station	3.992	3	1.331	4.555	0.004
Season	22.969	3	7.656	26.210	0.000
Year	22.725	3	7.575	25.933	0.000
Station × season	5.935	9	0.659	2.258	0.020
Station × year	15.502	9	1.722	5.897	0.000
Season × year	44.393	9	4.933	16.886	0.000
Station × season × year	15.971	27	0.592	2.025	0.003
Error	56.084	192	0.292		

apparent. Especially at the 100 m² site, the high at station 3 is always noticeable.

The overall pattern for *Ammobaculites* with season is shown in Figure 57. The pattern for *Ammobaculites* with a relatively high density in the winter is similar to that for *Elphidium* (Figure 49) but distinct from both *Quinqueloculina* (Figure 33) and *Ammonia* (Figure 41).

Figure 58 shows the overall pattern for *Ammobaculites* over years. There is a general tendency of an increase in density over the four years, just as was observed for *Ammonia* (Figure 42) and *Elphidium* (Figure 50). The most abundant taxon, *Quinqueloculina*, however, has quite a dissimilar pattern with densities increasing at the 100 m² site in a step fashion and, more clearly, a decrease in density in year 4 at the 1 m² site.

Figure 59 shows interactions of station × season at the 100 and 1 m² sites for *Ammobaculites*. At the 100 m² site, station 3 exhibits a high density in winter. At the 1 m² site, the mean square is much lower than at the 100 m² site, and the *F* value, although significant at *p* = 0.020 (Table 32), also is much smaller. Note that we can make this comparative statement only because the degrees of freedom are the same for both tests. No large differences in densities occur among the stations at the 1 m² site. If we compare Figure 35 for *Quinqueloculina*, Figure 48 for *Ammonia*, Figure 51 for *Elphidium*, and Figure 59 for *Ammobaculites*, at the 100 m² site station, station 3 is generally high in winter. At the 1 m² site for *Ammonia* and *Elphidium* the hypothesis for station × season is not significant (Tables 28 and 30). The patterns for *Quinqueloculina* and *Ammobaculites* across the sites do not resemble one another.

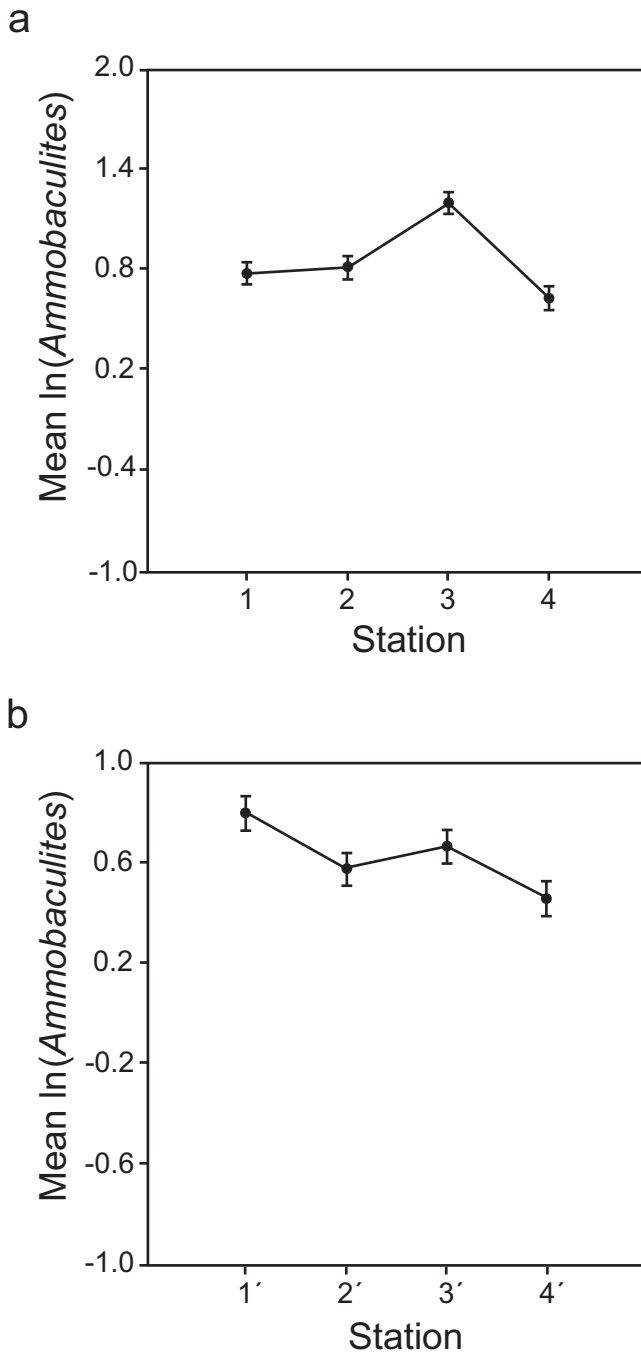


FIGURE 56. Mean number of $\ln(Ammobaculites)$ at stations. (a) Stations 10 m apart. (b) Stations 1 m apart.

The interaction hypothesis of station $\times$ year for the two sites is shown in Figure 60. In years 2 and 3, station 3 exhibits a high at the 100 m² site. At the 1 m² site station 1 has a high in year 4. When we compare Figure 36 for *Quinqueloculina*, Figure 44 for *Ammonia*, Figure 52 for

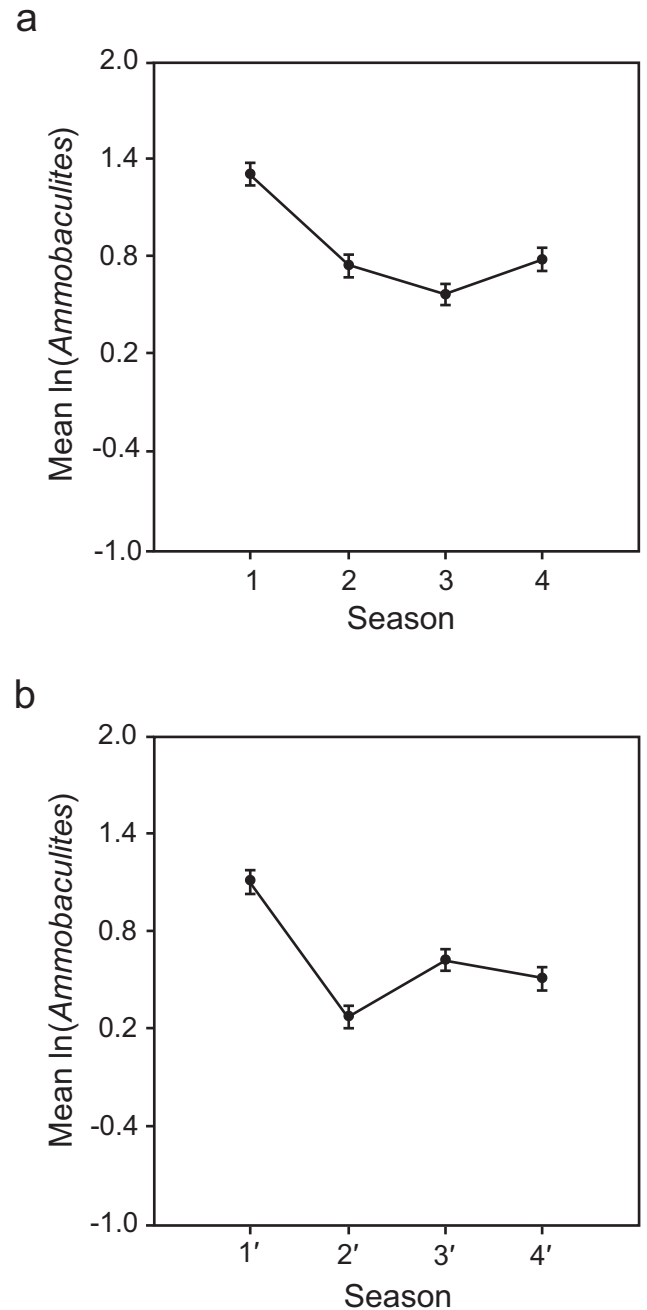


FIGURE 57. Mean number of $\ln(Ammobaculites)$ for seasons: 1 = winter, 2 = spring, 3 = summer, 4 = fall. (a) Stations 10 m apart. (b) Stations 1 m apart.

Elphidium, and Figure 60 for *Ammobaculites*, a high at station 3 is apparent in all the figures at the 100 m² site. Note, however, that the interaction hypothesis of station $\times$ year is not significant for *Quinqueloculina* (Table 25) at the 100 m² site. This result illustrates how difficult it is to detect differences on a visual basis alone.

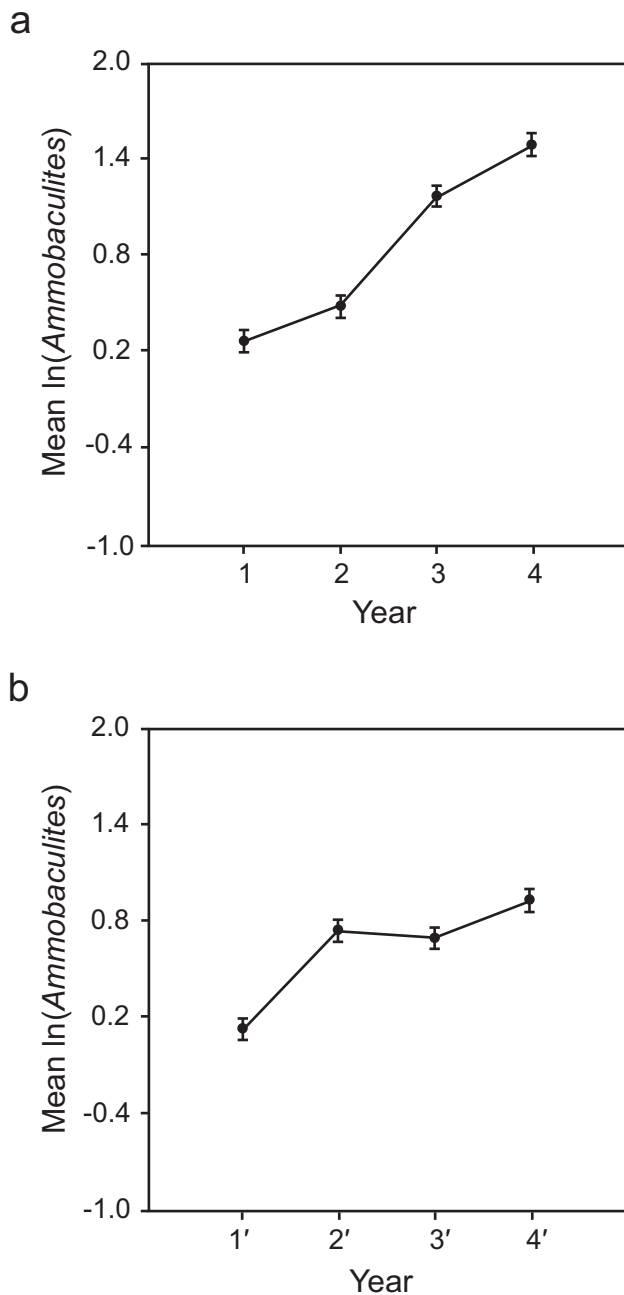


FIGURE 58. Mean number of $\ln(Ammobaculites)$ for years: 1 = summer 2001 to spring 2002, 2 = summer 2002 to spring 2003, 3 = summer 2003 to spring 2004, 4 = summer 2004 to spring 2005. (a) Stations 10 m apart. (b) Stations 1 m apart.

Among the interaction hypotheses, that for season $\times$ year has the highest mean square for both sites, as shown in Tables 31 and 32. From Figure 61 we observe clearly that the seasons do not behave in the same way from year to year. In year 1, both sites have similar

densities in all seasons, whereas in years 2 and 4 highs were seen in winter. In year 3, the 100 m² site has a high density in winter and spring, whereas at the 1 m² site the high density occurs in summer. Comparing Figure 37 for *Quinqueloculina*, Figure 45 for *Ammonia*, Figure 53 for *Elphidium*, and Figure 61 for *Ammobaculites*, a clear high density exists in the spring of year 3 for all taxa except *Ammobaculites*. Otherwise, the patterns are complex and vary from taxon to taxon. A simple hypothesis, such as a spring or summer high density is evidenced each year, clearly is not tenable.

The 16 interactions for station $\times$ season $\times$ year for *Ammobaculites* at the 100 m² site are shown in Figure 62. An increase in the overall densities occurs during the four years of observation (see also Figure 58). Winter is also a season of high density for *Ammobaculites* at the 100 m² site (Figures 62 and 57). It is clear from Figure 62 that during winter and spring there is more difference among stations than is evidenced in summer and fall.

In Figure 63, similarly to that seen at the 100 m² site, an increase in density over the four years is visible. It is, however, not as large as for the other site. Likewise, the 100 m² site has its highest density, on average, in winter. The spring high observed at the 100 m² site (Figure 62) was not observed at the 1 m² site; instead, a high was observed in the same year in summer (Figure 63). As density increases over the years, so does the difference among stations.

Comparing the 100 m² interaction of station $\times$ season $\times$ year for each of the taxa, *Quinqueloculina* (Figure 38), *Ammonia* (Figure 46), *Elphidium* (Figure 54), and *Ammobaculites* (Figure 62), we can see that all taxa increased in density over the years. However, *Quinqueloculina*, the most abundant taxon, had its maximum density in summer, whereas the others had their maxima in winter and/or spring.

The 1 m² site interaction of station $\times$ season $\times$ year for *Quinqueloculina* (Figure 39), *Ammonia* (Figure 47), *Elphidium* (Figure 55), and *Ammobaculites* (Figure 63) indicates an increase in density over the four years, except for the most abundant taxon, whose density decreases during the fourth year. Observe in Figure 38 for the 100 m² site that there are low variability and high densities among the stations in the summer and fall of year 4 yet high variability at the same time at the 1 m² site (Figure 39). Recall that stations 1 and 1' are the same, and thus, the large visual difference in density observed between the 100 m² and 1 m² sites over the seasons and years was due to the lower densities observed in the remaining stations that compose the 1 m² site.

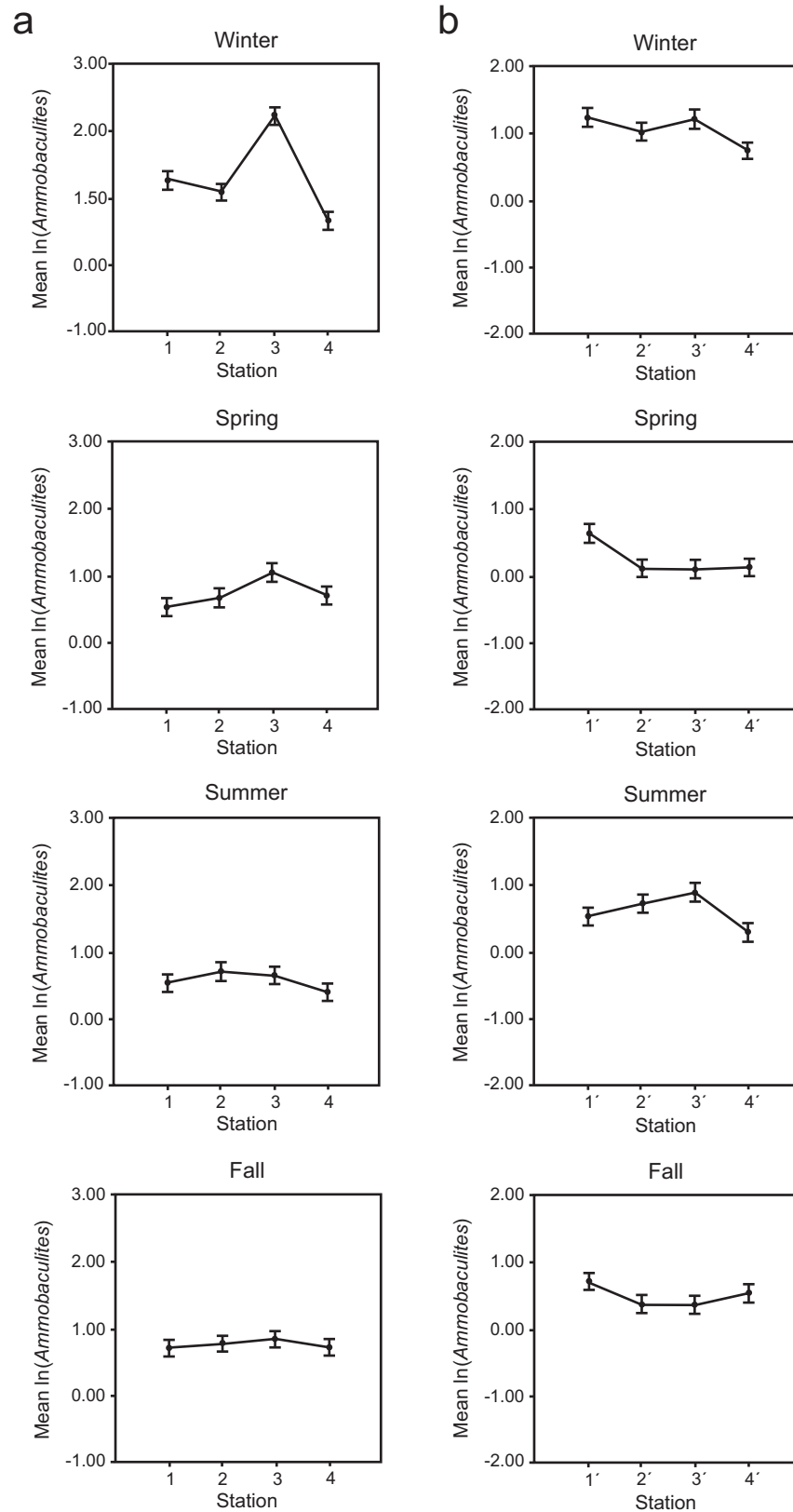


FIGURE 59. Mean number of $\ln(\text{Ammobaculites})$ for station $\times$ season interaction. (a) Stations 10 m apart. (b) Stations 1 m apart.

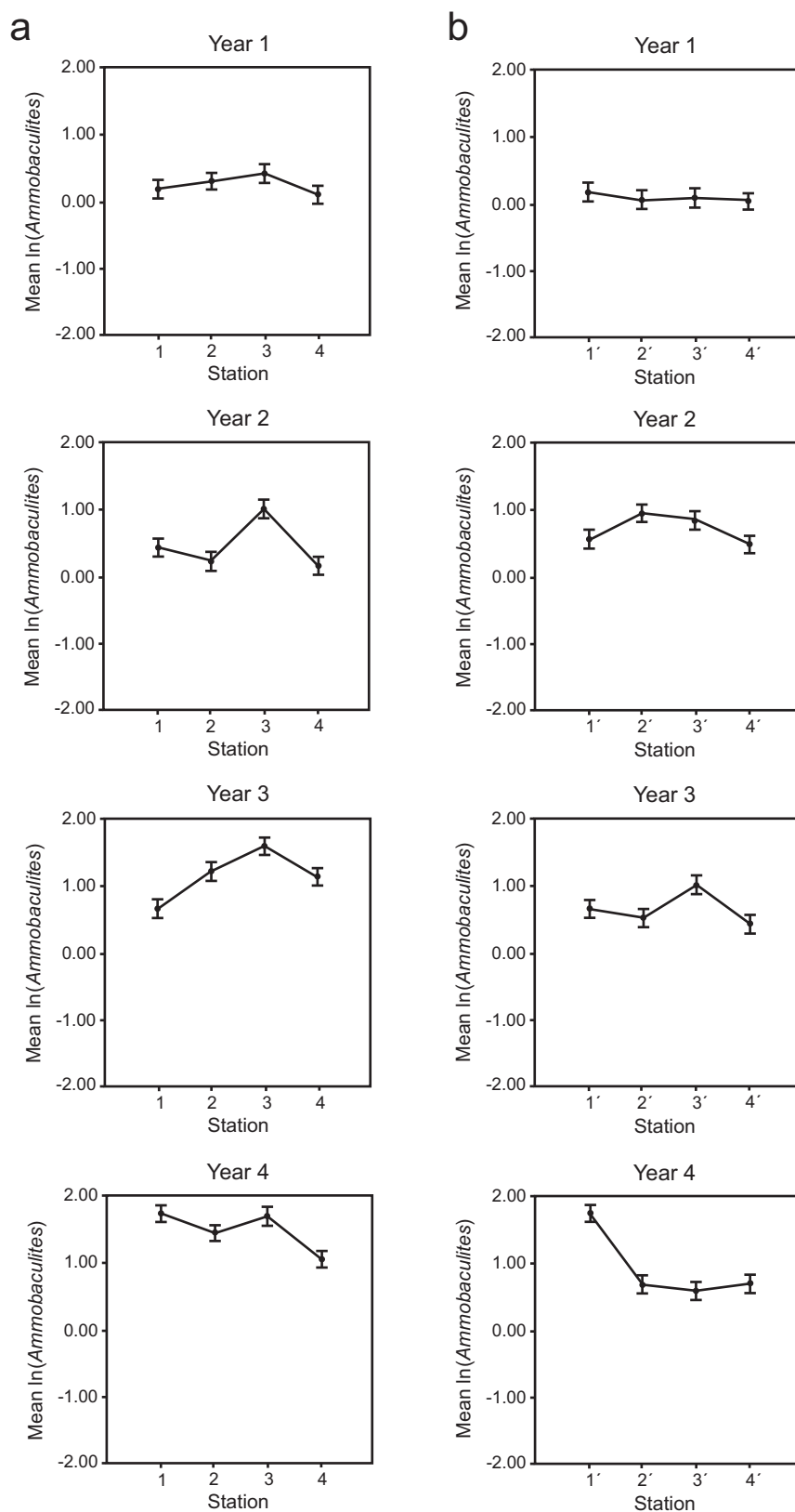


FIGURE 60. Mean number of $\ln(\text{Ammobaculites})$ for station $\times$ year interaction. (a) Stations 10 m apart. (b) Stations 1 m apart.

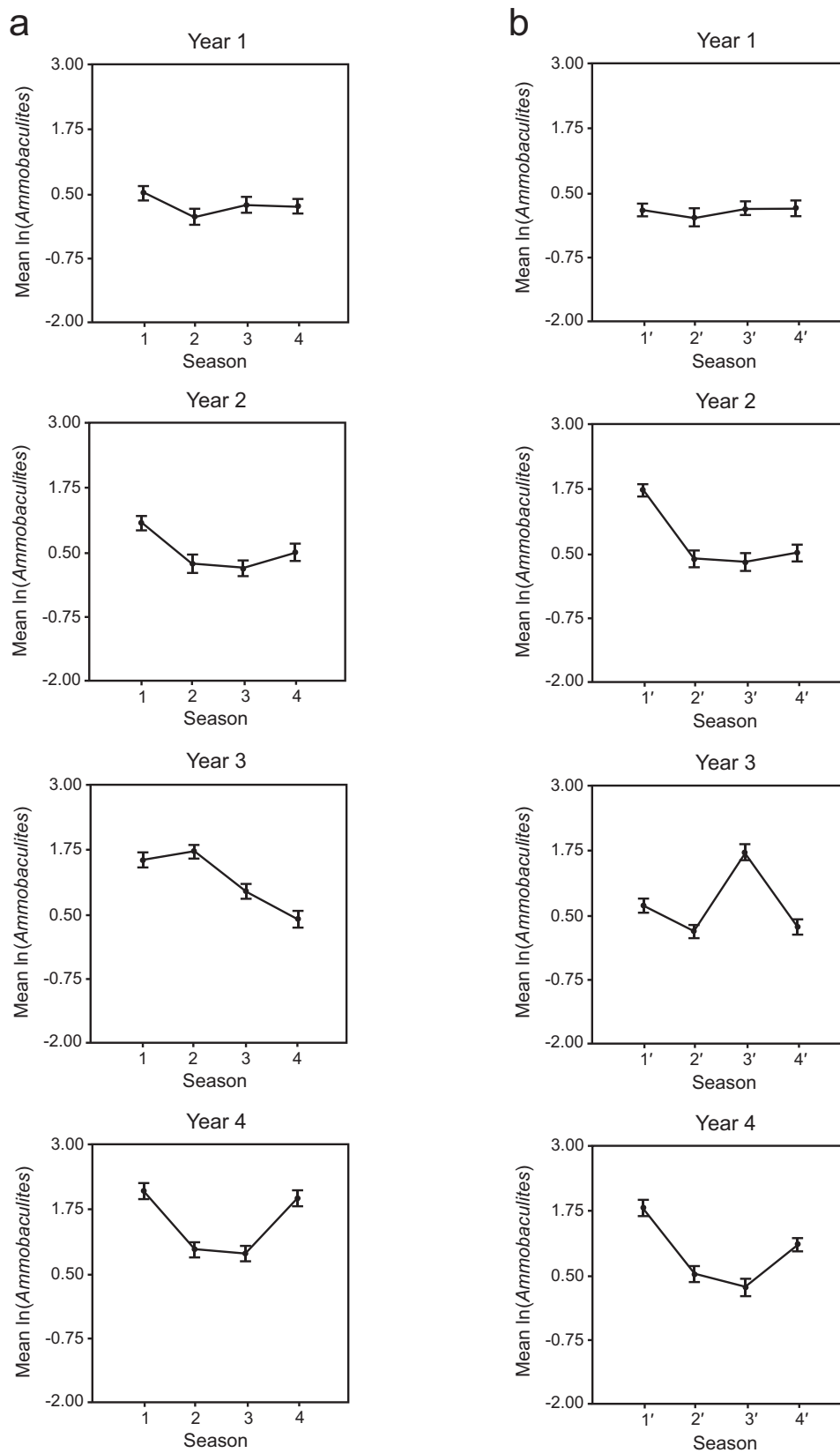


FIGURE 61. Mean number of $\ln(\text{Ammobaculites})$ for season $\times$ year interaction. (a) Stations 10 m apart. (b) Stations 1 m apart.

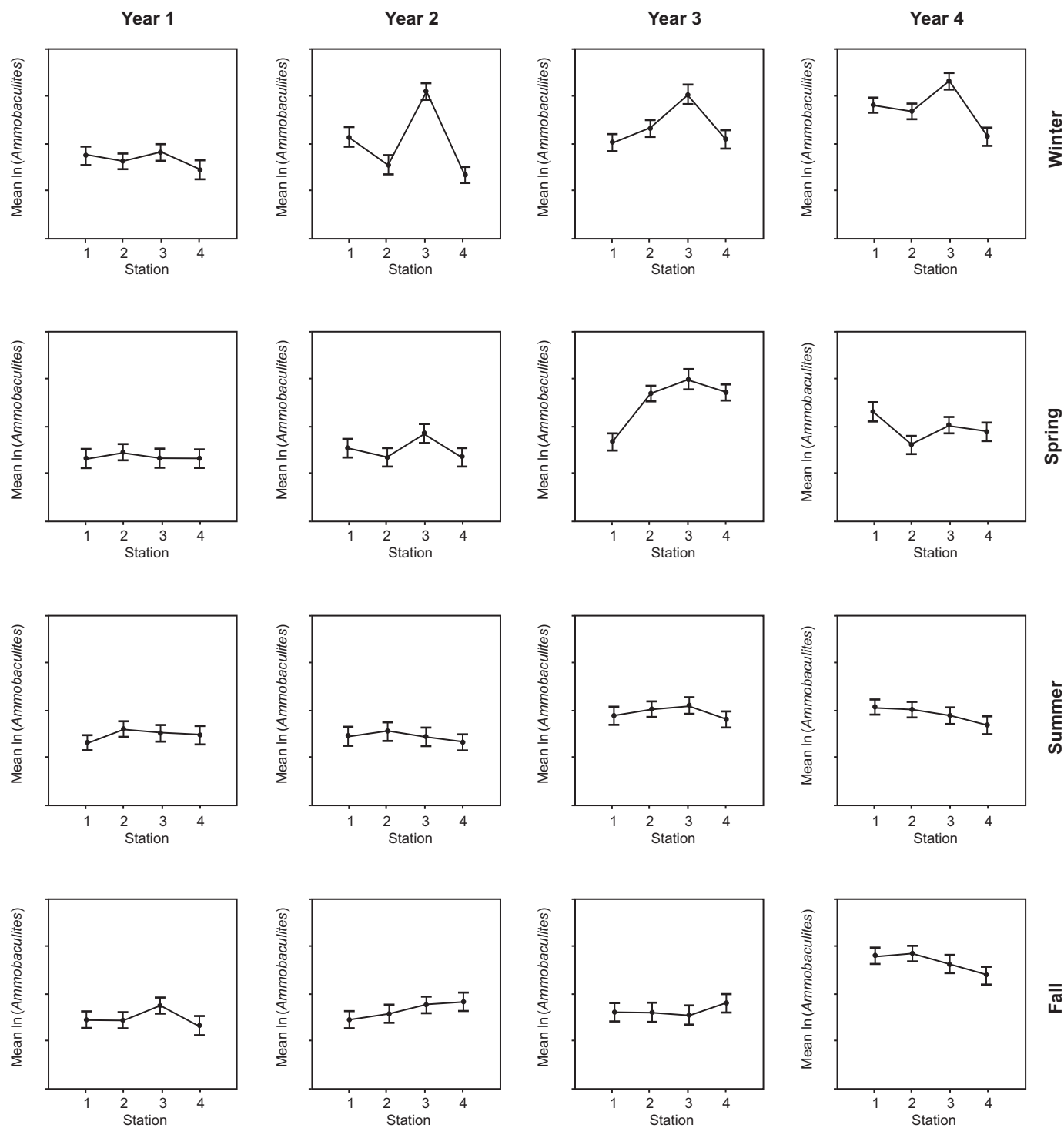


FIGURE 62. Mean number of $\ln(\text{Ammobaculites})$ for station $\times$ season $\times$ year interaction for stations 10 m apart.

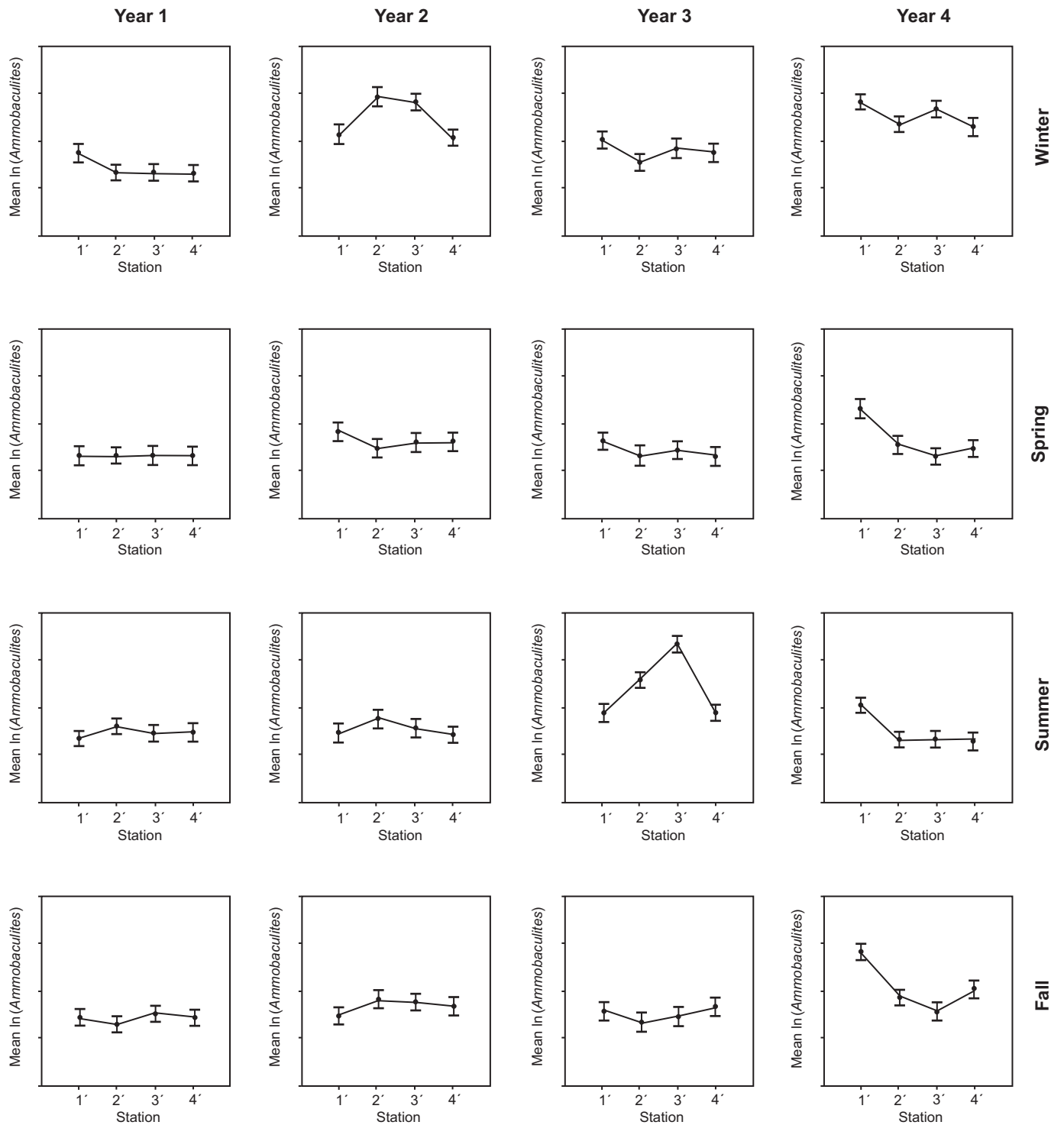


FIGURE 63. Mean number of $\ln(\text{Ammobaculites})$ for station $\times$ season $\times$ year interaction for stations 1 m apart.

The complexity involved with all the interactions does have serious consequences. Simple statements concerning stations, seasons, and years, such as station 3 is always high in the spring of each year, are quite impossible. Nevertheless, a striking pattern emerges. At both scales examined, the station $\times$ season and station $\times$ year interaction hypotheses were significant, and therefore, by definition pulsating patches are confirmed.

ENVIRONMENTAL VARIABLES

Temperature, salinity, and oxygen were recorded at station 1 for each sampling time and are assumed to be uniform through the entire 100 m² sampling area. Although these measurements do not record diurnal or large daily and weekly changes, they are indicators of the larger seasonal and yearly changes at the station. Although only seasonal counts of foraminifera were made for this study, the temperature, salinity, and oxygen were recorded monthly and indicate that the measurements used here are typical for the season. In July 2002 and October 2002 oxygen was not recorded, so the mean values from the previous and next month were used.

As expected in this area, the temperature is coldest in winter and warmest in summer. The range in temperature over the four years was from 16.9°C to 37.3°C. A two-way ANOVA with interaction using temperature as the dependent variable with season and year as independent variables indicated that not only are the seasons significantly different but so are the years and the interaction of seasons $\times$ years. In Figure 64, we show the interaction of seasons and years from this analysis at station 1. In winter and spring there is little difference among years; however, in year 3 the summer temperature was particularly high, whereas in year 2 the fall temperature was high.

Salinity also varied greatly during the four years, with a range of 15.4 to 38. These values span brackish to slightly above normal marine salinity. A two-way ANOVA with interaction using salinity as the dependent variable with season and year as independent variables shows that all three hypotheses tested are significant. Figure 65 shows an overall decrease in salinity over the four years, and Figure 66 indicates that in year 4 winter and fall had low salinities, whereas summer had the highest value recorded. Unlike temperature (Figure 64), salinity exhibits great variation among years and all seasons.

Oxygen varied from 0.5 to 12.9 mg O₂/L. Because oxygen saturation in seawater depends greatly on temperature as well as on salinity, barometric pressure, and biological activity, the maximum was observed in winter,

and the minimum was observed in summer. As with temperature and salinity, a two-way ANOVA with interaction using oxygen as the dependent variable with seasons and years as independent variables resulted in all hypothesis test results being significant. Figure 67, which depicts the interaction of seasons $\times$ years, shows that summer values of O₂ were particularly variable from year to year. Years 1 and 4 had low values of O₂; however, except for the summer of year 1, all values are above 1.0, which is considered oxic (Bernhard and Sen Gupta, 2002). In general, the sandy sediments of the Indian River Lagoon at station 1 are well oxygenated.

GENERAL LINEAR MODEL

Setup of Model

The observations at stations, seasons, and years were analyzed by a three-way ANOVA with interaction for the four taxa. The research design of the study ensured that all the hypotheses generated by ANOVA were independent (dummy variables or vectors are all orthogonal). Buzas et al. (2002) demonstrated the importance of other coexisting species as covariates. We now extend the analysis to include not only other species but also the environmental variables of temperature, salinity, and oxygen as covariates. Because the environmental variables were measured at station 1 or 1' we will make the analysis for the 1 m² observations because all of the observations are within a meter of the measured temperature, salinity, and oxygen. At each sampling time this research design gives 16 observations, with 4 seasons and 4 years, for a total of 256 observations of species densities.

Recall that the three most abundant taxa are *Quinqueloculina*, *Ammonia*, and *Elphidium*. In each analysis, when one taxon is the dependent variable, the other two will serve as independent variables. Thus, we will write a general linear model (GLM) in matrix notation:

$$\Omega: \mathbf{x}_{(256 \times 1)} = \mathbf{Z}_{(256 \times 15)} \boldsymbol{\beta}_{(15 \times 1)} + \mathbf{e}_{(256 \times 1)}$$

where $\mathbf{x}$ is the vector of 256 observations of density of species treated as the independent variable, $\mathbf{Z}$ is a matrix consisting of one column for the constant, density of one taxon, density of the second taxon, temperature, salinity, and oxygen and three columns of dummy variables each for station, season, and yearly differences (giving 15 vectors in all), $\boldsymbol{\beta}$ is the vector of associated coefficients, and $\mathbf{e}$ is the vector of residuals. This ANOVA model for each taxon, consisting of 15 independent variables, generates

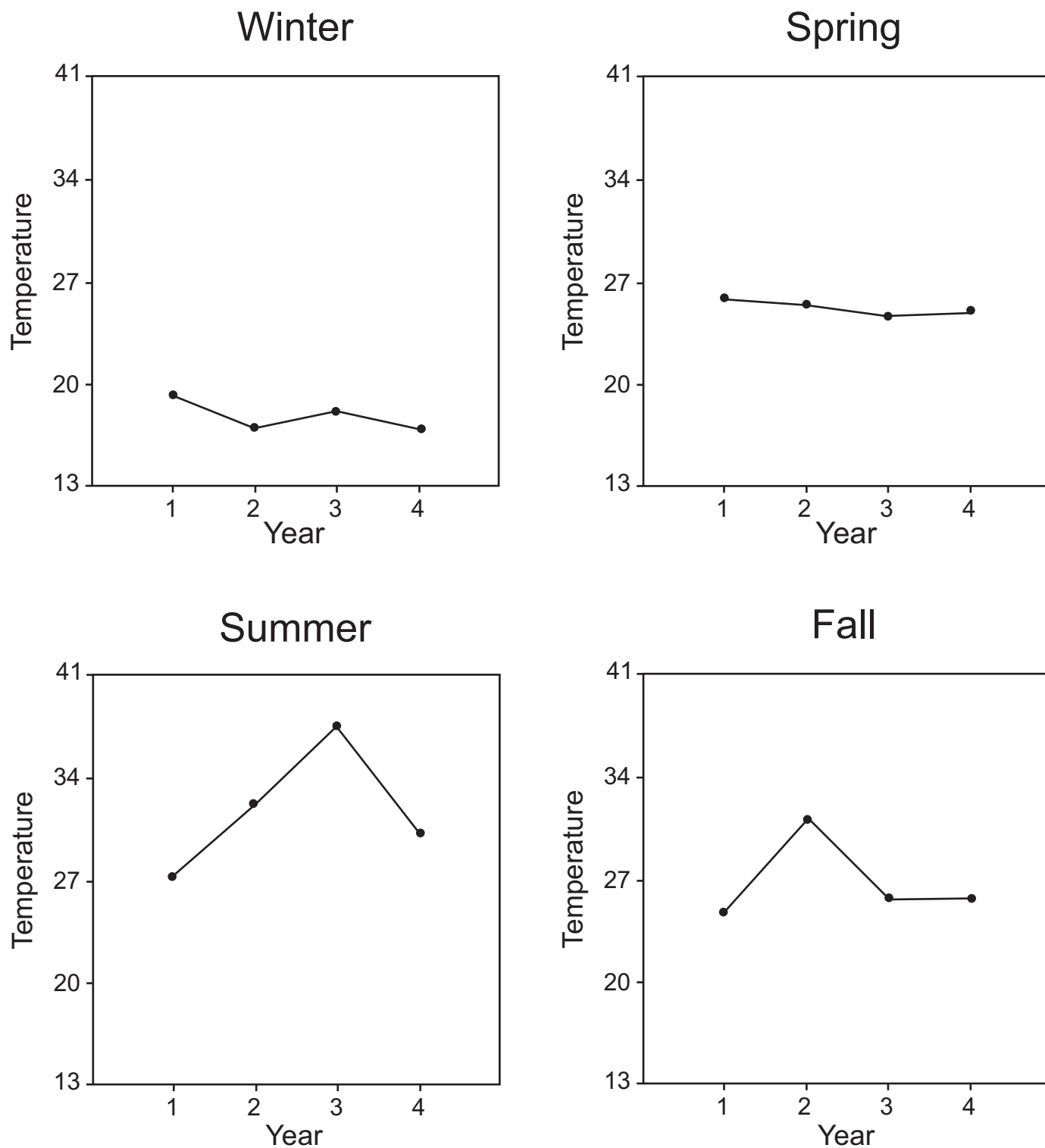


FIGURE 64. Temperature (in °C) by season and year at station 1.

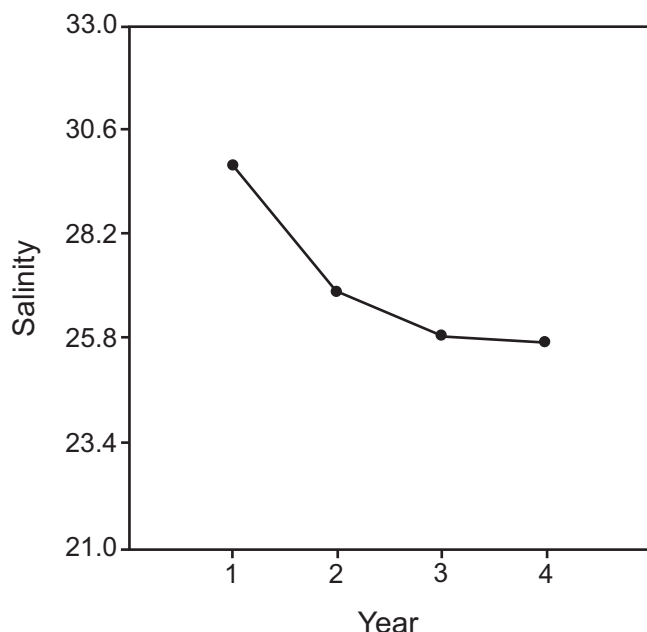


FIGURE 65. Salinity by year at station 1.

8 hypotheses to test: (1) density of taxon 1, (2) density of taxon 2, (3) temperature, (4) salinity, (5) oxygen, (6) stations, (7) seasons, and (8) years. We will analyze the four taxa as before and will arrange the ANOVA table in decreasing order of significant mean squares.

Results from Fitted Models

The results for *Quinqueloculina* are shown in Table 33. The statistical significance of the hypotheses for equality of mean densities for stations, seasons, and years agrees with our previous ANOVA (Table 26). That is, densities for seasons, years, and stations were each significant and in that order of descending mean square values. As Table 33 shows, however, the density of *Ammonia* explains most of the variability in the GLM. The environmental variables for salinity and temperature are significant.

For *Ammonia*, only five of the eight hypotheses are significant, and the results for this GLM are shown in Table 34. Unlike the analyses in Table 28, station differences for *Ammonia* are not significant. Most of the variability was due to the coexisting *Quinqueloculina* and *Elphidium*. The environmental variable oxygen explains a small amount of the total variability.

For *Elphidium* all eight hypotheses are significant (Table 35). The highest mean square is for *Ammonia*, but

salinity and oxygen have higher mean squares than those for years, seasons, or stations. The last three are all significant, and the order of their mean squares is the same as shown in Table 30 for the three-way ANOVA.

For *Ammobaculites*, a species observed with very low densities in the Indian River Lagoon, six hypothesis test results are significant, with oxygen having the highest mean square (Table 36). Unlike the three-way ANOVA shown in Table 32, the mean square for year is higher than that for season, and stations are not significant. The significance of the hypothesis for salinity agrees with previous observations on this species' distribution.

DISCUSSION

PATCH SIZE

Early work on spatial distribution was concerned with estimating the size of patches, or "colonies." Estimates of colony size ranged from 1 m² to tens of thousands of square meters (Lynts, 1966; Buzas, 1970; Buzas and Gibson, 1990). The results of the present study with stations 1 m apart and 10 m apart attest to the futility of such an approach. The size of foraminiferal colonies identified in these early studies clearly depended on the configuration of the sampling scheme. In the present study, patches were identified in both configurations (1 and 100 m²), were identified at particular times, and were shown to change with time. Thus, we have identified pulsating patches in the Indian River Lagoon at both scales of this design.

Aggregation or patchiness exists on a scale of centimeters (Buzas, 1968; Olsson and Eriksson, 1974; Murray and Alve, 2000). This is evident from the data in Appendices 1 and 2. For example, in Appendix 1 (100 m² study), in July 2001 (the first observational time) the counts for *Quinqueloculina* at station 3 vary by two orders of magnitude (range: 7 to 246). Looking at the data from cores, each 3.5 cm in diameter, the counts of the foraminifera vary greatly from observation to observation. The patches are on the centimeter scale, yet an ANOVA of this data set shows no significant differences between the mean numbers of individuals of *Quinqueloculina* at the four stations. The analysis, of course, takes into account the variation among observations, which a visual examination cannot do. This little exercise demonstrates that when comparing means among stations to examine homogeneous versus heterogeneous distributions, we are not simply defining the size of patches. Instead, we are setting up, at some arbitrary size

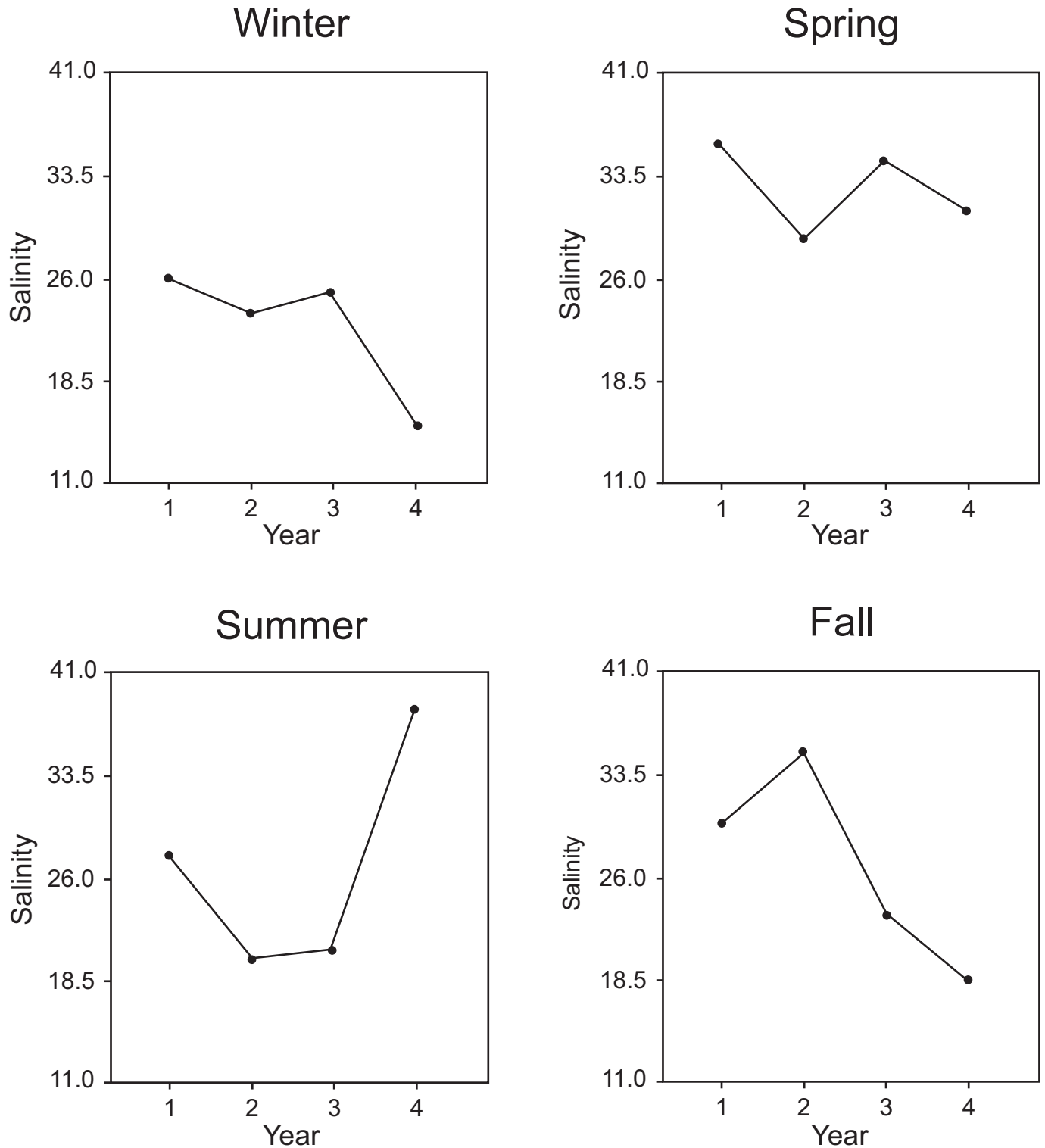


FIGURE 66. Salinity by season and year at station 1.

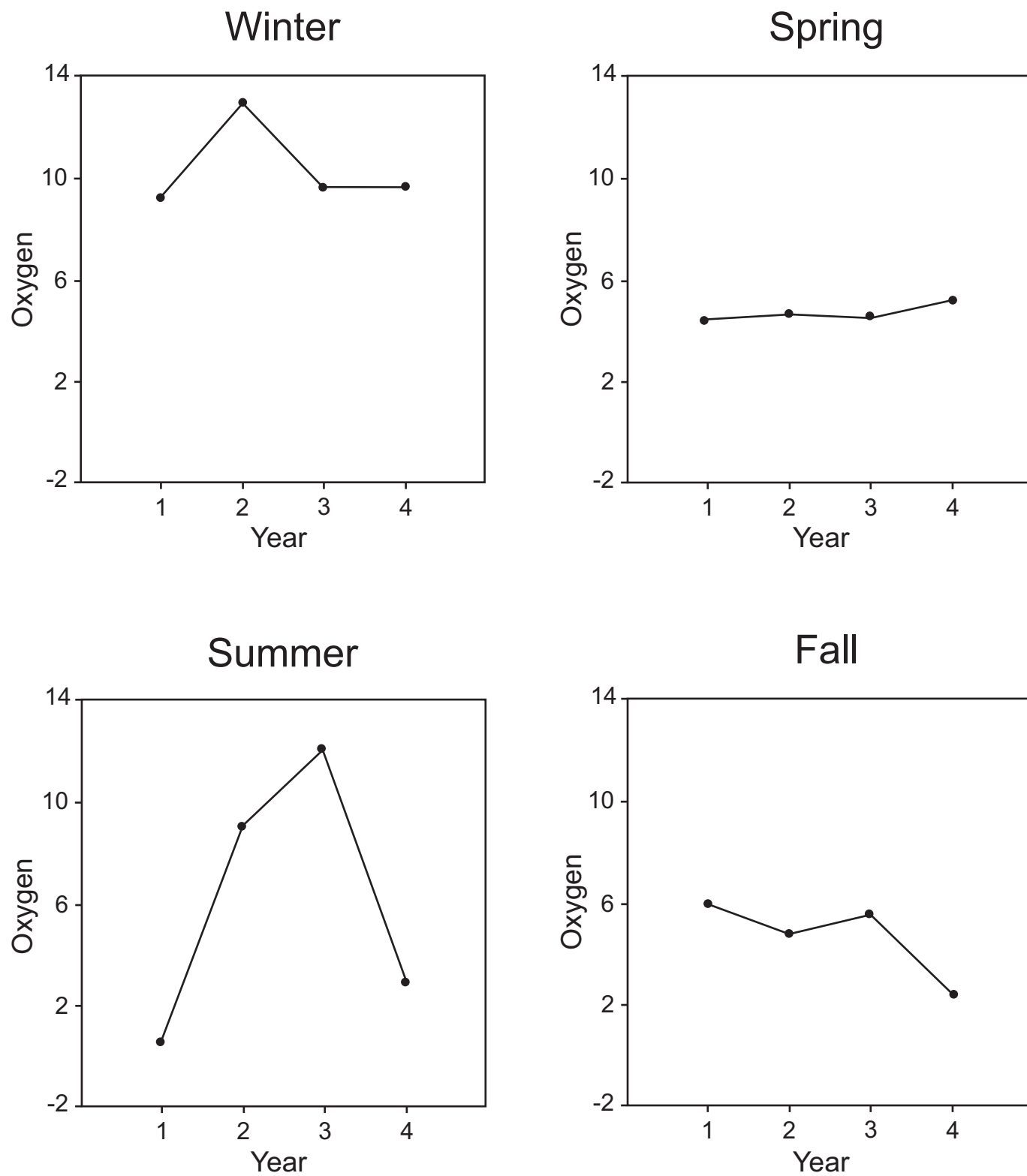


FIGURE 67. Oxygen (in mg O₂/L) by season and year at station 1.

TABLE 33. General linear model for *Quinqueloculina*.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
ln(<i>Ammonia</i>)	69.885	1	69.885	138.942	0.000
Season	90.662	3	30.221	60.084	0.000
Year	64.755	3	21.585	42.914	0.000
Salinity	14.637	1	14.637	29.101	0.000
Temperature	14.171	1	14.171	28.174	0.000
ln(<i>Elphidium</i>)	9.222	1	9.222	18.335	0.000
Station	8.910	3	2.970	5.905	0.001
Error	121.720	242	0.503		

TABLE 34. General linear model for *Ammonia*.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
ln(<i>Quinqueloculina</i>)	53.080	1	53.080	159.624	0.000
ln(<i>Elphidium</i>)	23.382	1	23.382	70.315	0.000
Season	37.739	3	12.580	37.829	0.000
Year	29.228	3	9.743	29.299	0.000
Oxygen	9.600	1	9.600	28.869	0.000
Error	81.803	246	0.333		

TABLE 35. General linear model for *Elphidium*.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
ln(<i>Ammonia</i>)	34.120	1	34.120	56.049	0.000
Salinity	12.874	1	12.874	21.148	0.000
Oxygen	12.504	1	12.504	20.541	0.000
ln(<i>Quinqueloculina</i>)	9.889	1	9.889	16.245	0.000
Year	26.199	3	8.733	14.346	0.000
Temperature	5.575	1	5.575	9.158	0.003
Season	12.903	3	4.301	7.065	0.000
Station	9.110	3	3.037	4.988	0.002
Error	146.709	241	0.609		

scale, a definition for homogeneity, but only for that scale. As observations are made over time, the interaction of station $\times$ time defines and quantifies the conceptual basis for pulsating patches.

In all of these studies utilizing the powerful ANOVA technique, the researcher is making an arbitrary (although

TABLE 36. General linear model for *Ammobaculites*.

Source	Sum of squares	df	Mean squares	F-ratio	p-Value
Oxygen	12.465	1	12.465	34.348	0.000
ln(<i>Quinqueloculina</i>)	7.090	1	7.090	19.537	0.000
ln(<i>Elphidium</i>)	4.736	1	4.736	13.049	0.000
Salinity	4.126	1	4.126	11.369	0.001
Year	8.502	3	2.834	7.809	0.000
Season	3.404	3	1.135	3.127	0.026
Error	88.908	245	0.363		

guided by experience with the natural world) decision regarding the scale examined. We can define patches at any scale we wish from centimeter to kilometer. All are legitimate, and the scale depends upon the question at hand.

PSEUDOREPLICATION

Ever since the publication of Hurlbert's (1984) paper on pseudoreplication, considerable misunderstanding has arisen among benthic ecologists about the use of multiple observations (samples) or replicates. Because of the large variation in the counts of individuals from closely spaced samples, researchers believe the counts may not be "true replicates" or may bias their observations of larger-scale patterns. Consequently, for example, Morvan et al. (2006) and Goldstein and Alve (2011), because they were interested in larger patterns, mixed or added together replicate samples. Although this procedure may seem logical or even desirable, it prevents any estimate of confidence limits on the observations and makes analysis by an ANOVA with a complete higher-way layout (two- or three-way ANOVA with interaction), as done here, impossible.

As a demonstration of this problem, in Figures 1 and 68, we show the microdistribution of *Ammonia* from a sample taken in Rehoboth Bay, Delaware (Buzas, 1968). The original sampler consisted of 36 contiguous cells with each sample having a volume of 2 mL. Samples 1 and 13 were lost during the sampling procedure and are indicated by NS on Figure 1. The data consist of the number of individuals of *Ammonia* observed in each cell.

A biologist might call each of the 34 cells a sample or subsample. Another biologist might call each cell a quadrat. If we observe more than one cell, the multiple samples (or subsamples or quadrats or observations) are called replicates. A statistician would call the number of individuals observed in each cell an observation, and using the counts

of more than one cell would be termed a sample. A more thorough discussion of the terms and the confusion resulting from them is given in Hayek and Buzas (2010).

The original counts were the number of individuals in each cell, but in Figure 68, we drew circles to represent the foraminifera and placed them at random in each cell to give an idea of what the actual spatial distribution looks like. Because we know the actual number observed in 34 cells (159), we know that the true mean is $\mu = 159/34 = 4.676$. If we wish to estimate the mean number of individuals without counting all 34 cells, a sample consisting of a smaller number could be taken. To illustrate, we shall consider our totals from the original sampler to be the “true values”; that is, we imagine the “true mean” is 4.676. Then we randomly select four cells (we selected numbers 13, 21, 20, and 12) and the related counts (8, 4, 15, 2) as recorded (Figure 1). Their sum is 29, so an estimate of the mean would be 7.250. If the samples were combined into a single total of 29, that is all the information that we would have available. Surely, no one would want to attest to the equality of 4.676 and 7.250. Now, in the field, the true mean is

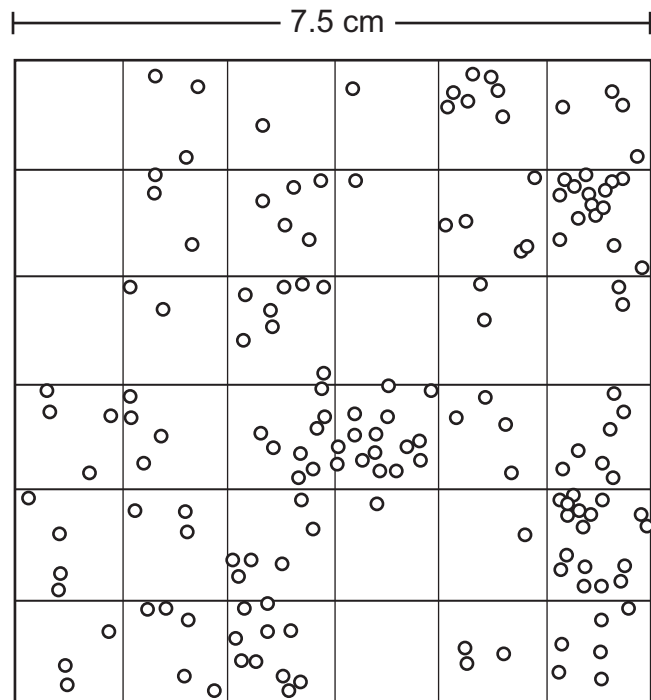


FIGURE 68. Numbers of individuals of *Ammonia* in contiguous cells with 2 mL volume, Rehoboth Bay, Delaware. Numbers are the same as in Figure 1; however, circles representing foraminifera are placed at random within cells to give an idea of actual spatial configuration. Data from Buzas (1968).

never known, and without a confidence statement we do not know how close our estimate is to the true mean. If, however, we utilize the separate information given in each of the four observations or replicates, statistical procedure allows us to formulate confidence limits on the true mean even though we do not know its actual value. Hayek and Buzas (2010) provide a thorough explanation with examples of how to calculate confidence limits. From the four observations for our example, we calculate the standard error as 2.869, so the 95% approximate confidence limits are $1.5 \leq \mu \leq 13.0$. In other words, we are 95% confident that the true mean lies between these numbers, and it does (4.676). The confidence limits are rather wide because the counts show a considerable amount of variability. Statistical procedure, however, allows us to make a confidence statement with a given probability even though we do not know the true value of the mean. The above exercise should make it clear that by calling multiple observations replicates, there is nothing “pseudo” involved. The confusion lies with the language and not the mathematics.

Another problem with mixing or adding samples, observations, or replicates together is that analysis with a higher-way all-inclusive model is impossible. Let us consider the number of observations N and the number of parameters (these are the population values, not the sampled estimates) in our three-way ANOVA. We obtained 4 observations or replicates at 4 stations at 4 seasons for 4 years. We have then $4 \times 4 \times 4 \times 4 = 256 = N$ observations. Testing between the 4 stations requires 3 vectors; another 3 vectors are needed to test between the 4 seasons, and 3 more vectors are needed to test between the 4 years. For the interaction of station $\times$ season we require $3 \times 3 = 9$, for station $\times$ year we require 9, for season $\times$ year we require 9, and finally, for station $\times$ season $\times$ year, there will be $3 \times 3 \times 3 = 27$ vectors. These vectors are listed as degrees of freedom in the ANOVA tables (Tables 25–32). In total, there are $3 + 3 + 3 + 9 + 9 + 9 + 27 + 1 = 64 = q$. Notice N is considerably larger than q , and this difference between N and q should be maintained to make confidence intervals small enough to be biologically meaningful.

If we mix or add together the replicates, resulting in only one total set of numbers (sample), the number of observations becomes 4 stations, 4 seasons, and 4 years, or $4 \times 4 \times 4 = 64$, and then we have $N = q$. When $N = q$, the case with no replicates or multiple observations, the error or residual term becomes zero, and no statistical testing with a complete model is possible. Because we define pulsating patches by the significance of the interaction effects, we therefore cannot analyze for pulsating patches or their importance over time.

SPACE AND TIME

Recall that we define pulsating patches by the existence of a statistically significant interaction hypothesis for station $\times$ time. We have shown in the ANOVA analysis (Tables 25–32) that the interaction of station $\times$ time, in which we considered time as season and year, was nearly always significant. The exceptions were station $\times$ season for *Ammonia* (1 m², Table 28) and *Elphidium* (1 m², Table 30). Perhaps, because both of these exceptions are on the 1 m² scale, there is less of an interaction effect of seasonal differences on close-by stations.

A great advantage of the ANOVA/GLM models is that not only are independent hypotheses tested for statistical significance, but also the amount of the total variability for which each hypothesis accounts can easily be determined from the standard ANOVA table. Thus, we can ask the question, How much of the total variability is accounted for by the pulsating patches (space), and how much is accounted for by seasonal and yearly differences (time)?

The sum of squares (SS) column in Tables 25–32 can be misleading because it does not take into account the degrees of freedom (df) associated with each hypothesis. However, by using the mean square (MS) column, SS/df, where these quantities are also scaled variance estimates, this pitfall is avoided. Table 37 is constructed by dividing each (MS) by the sum of all (MSs) and multiplying by 100. Table 37, then, gives the percentage of the total variability accounted for by each hypothesis for the four taxa at the 1 and 100 m² sites. Table 37 also gives the subtotals for space and time. Clearly, the hypotheses associated with time explain most of the variability.

Although pulsating patches (space $\times$ time) are statistically significant, most of the variability is explained

by season and year (time). For the most abundant taxon, *Quinqueloculina*, season amounts were 35% and 30%, which are greater than the values of 29% and 21% for year. For the other three taxa considered in this study, however, the percentage of mean square is larger for year than for season.

CHANGES OVER THE FOUR YEARS

The taxa observed in this study have highly intercorrelated densities. As observed during the study period of 1992 to 1996 (Buzas et al., 2002), a statistical model with another taxon as a covariate has the highest mean square of all the hypotheses considered. Consequently, usually, the densities of the taxa vary together, and “good times” are good for all (Boltovskoy and Lena, 1969). For the three most abundant taxa the highest mean square in the GLM is another species of foram (Tables 33, 34, and 35). Although this overall pattern of species varying together exists, some intriguing differences occur. Looking at Figures 42 and 50, at both the 100 m² and 1 m² localities we observed an increase in densities over the years for *Ammonia* and *Elphidium*. However, for *Quinqueloculina* (Figure 34), a marked decrease in density occurred at the 1 m² site in year 4. Because the density for *Ammonia* and *Elphidium* increased, the relative abundance relationships (rank order of abundance) changed. The observations given in Appendix 2 show that beginning in October 2004, the densities of *Ammonia* and *Elphidium* were higher than those for *Quinqueloculina*. In Figure 69 we show how the species proportions change at the 1 m² site for the four years. In years 1 and 2, the rank order is *Quinqueloculina*, *Ammonia*, *Elphidium*, *Ammobaculites*, in year 3 the rank order is *Quinqueloculina*, *Elphidium*,

TABLE 37. Percentage of total mean square explained by each hypothesis for space and time.

Hypothesis	<i>Quinqueloculina</i>		<i>Ammonia</i>		<i>Elphidium</i>		<i>Ammobaculites</i>	
	100 m ²	1 m ²	100 m ²	1 m ²	100 m ²	1 m ²	100 m ²	1 m ²
Station	8	13	9	4	6	1	10	5
Station $\times$ season	1	3	2	1	1	1	4	3
Station $\times$ year	1	4	3	2	1	4	3	7
Station $\times$ season $\times$ year	1	6	1	4	1	3	1	2
Subtotal space	11	26	15	11	9	9	18	17
Season	35	30	10	10	5	8	17	31
Year	29	21	63	63	69	64	56	31
Season $\times$ year	24	23	11	14	16	18	8	20
Subtotal time	88	74	84	87	90	90	81	82

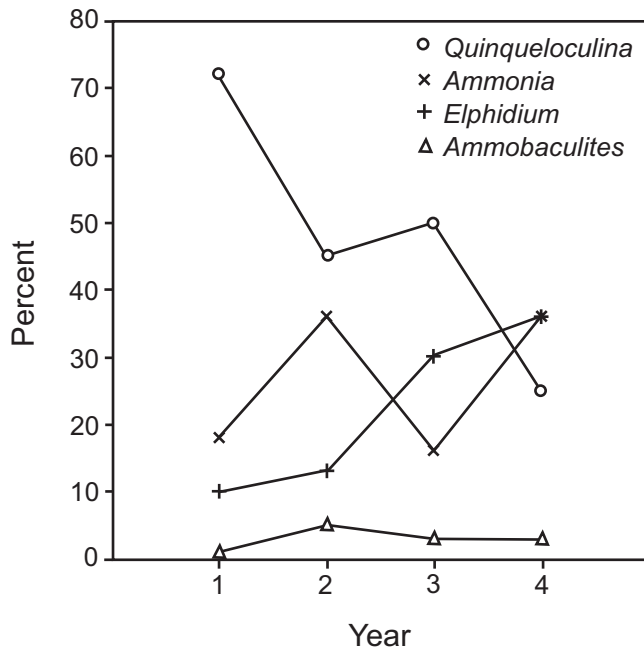


FIGURE 69. Proportions of taxa (in percent) by year with stations 1 m apart.

Ammonia, *Ammobaculites*, and in year 4 it is *Ammonia*, *Elphidium*, *Quinqueloculina*, *Ammobaculites*.

The analysis shown in Table 33 for *Quinqueloculina* indicates both salinity and temperature are significant in explaining the variability of *Quinqueloculina* over the four years of our observations. Temperature was higher in years 2 and 3 and lower in years 1 and 4. Perhaps the decrease in temperature from year 3 to 4 contributed to the decline in density. Salinity, on the other hand, showed a decrease during the four years (Figure 65), even though only the last year showed a corresponding decline in the density of *Quinqueloculina*. Perhaps the effect is cumulative. A shift to a less saline or more marginal marine environment is supported by the modern geographic distribution of *Quinqueloculina*. Culver and Buzas (1980) documented the distribution of all modern species off the North American Atlantic coast. Their documentation shows that most species of modern *Quinqueloculina* are distributed in southern waters and in open-ocean environments. A decrease in the density and proportion of *Quinqueloculina* is consistent with a decrease in temperature and a decrease in salinity.

Ammonia and *Elphidium* are common components of shallow-water systems not only off the North Atlantic coast (Culver and Buzas, 1980) but also worldwide

(Bernhard and Sen Gupta, 2002; Murray, 2006). In the modern environment off the North American Atlantic coast, *Ammonia* occurs in shallow waters and is a constituent of estuarine or marginal marine conditions. *Elphidium* has a wider geographic distribution (common in the Arctic) than *Ammonia* and also occurs at deeper depths.

The analyses shown in Tables 34 and 35 indicate that the largest contribution to the mean squares for *Ammonia* is that due to the coexistence of *Quinqueloculina*, whereas the largest contribution for *Elphidium* is *Ammonia*. In both analyses, however, *Elphidium* and *Quinqueloculina*, respectively, are also significant. For *Ammonia* the environmental variable oxygen is significant (Table 34), whereas for *Elphidium* salinity, oxygen, and temperature are significant factors (Table 35).

Both of these taxa tolerate marginal marine salinities. In the Choptank River, Maryland, the density of *Elphidium* sharply declined below about 12, whereas that of *Ammonia* declined only moderately (Buzas, 1969). As indicated earlier, the range in salinities in the present study is only between 15.8 and 38, well above the range of their tolerance. Nevertheless, the range in variability tolerated by these taxa on a worldwide basis (Sen Gupta, 2002; Murray, 2006) is substantiated by this study.

Using propagules for community assembly and different temperature regimes, Goldstein and Alve (2011) concluded that *Ammonia* grew more abundantly at higher temperatures and *Elphidium* grew more abundantly at lower temperatures. Biogeographic distribution off the North American Atlantic coast by Culver and Buzas (1980) also indicates that this is the case. *Elphidium* occurs in more northerly waters and at deeper depths (colder) than *Ammonia*. However, the temperature range of 16.9°C to 37.3°C in the present study is well within the tolerance of both species.

Oxygen is a significant factor for both *Ammonia* and *Elphidium* (Tables 34 and 35). Except for year 1, in which a low of 0.53 mg O₂/L was recorded, the oxygen measurements indicate station 1 is a well-oxygenated environment. Nevertheless, the observation of high densities for *Ammonia* during the first year and, correspondingly, low densities for *Elphidium* during the next year is consistent with *Ammonia* having greater tolerance for low oxygen.

On the continental shelf off Louisiana, Sen Gupta et al. (1996) showed that the ratio $N_{Ammonia} / (N_{Ammonia} + N_{Elphidium}) \times 100$ was related to bottom water hypoxia (<2 mg O₂/L). Higher values of the index (more *Ammonia*) were stated to indicate increased hypoxia (lower oxygen). If the relationship depicted in Figure 69 were observed in a core

(going from 1 to 4 up core), a reasonable interpretation based upon the use of this index would be that years 1 and 2 had lower O_2 than years 3 and 4. These numbers were summed for the two genera, and this index was calculated for each year. For year 1 the index is 64.2%, for year 2, it is 73.2%, and for years 3 and 4, the value of the index is 35.5% and 50.4%, respectively. The average oxygen values in milligrams of O_2 per liter per year were 5.0, 7.8, 8.0, and 5.0, respectively. Although the lowest value of the index, 35.5%, coincides with the highest oxygen value, 8.0, overall, the values of oxygen for the first two years are nearly identical to those for the next two years. The only low value (less than 2 mg/L) of oxygen observed was in July 2001 (year 1), when the value was 0.53. The index value for the 16 observations made in July 2001 was 47.8%. We must conclude that the Sen Gupta index is not particularly useful in well-oxygenated waters like those of the Indian River Lagoon.

PULSATING PATCHES AS A GENERAL PHENOMENON

The foraminifera, with their relatively small size, high density, and short generation time, are the ideal organisms for the recognition of pulsating patches. Nevertheless, the phenomenon was not discovered until spatial and temporal observations with replication were carried out simultaneously and properly analyzed. For larger organisms with longer generation times, the phenomenon is more difficult to observe. Recognition of pulsating patches for the trees in a forest, for example, would probably take longer than our own longevities.

In the Indian River Lagoon, sea grasses occur in patches of varying scales ranging from <1 to 10^9 m² (Virnstein, 1995). Choosing a scale and pattern depends on the research question. The unpredictability of long-term data (1994 to 2007) on the sea grass *Halophila johnsonii* from 35 transects in the Indian River Lagoon prompted Virnstein et al. (2009) to propose a model of pulsating patches to explain its distribution in space and time.

Temporal variability in the Indian River Lagoon is illustrated by isopods and amphipods (Kensley et al., 1995; Nelson, 1995). For each group, density was recorded at three sites over six years. For both groups the authors concluded that regions of the Indian River Lagoon were not biologically closely coupled. Although no statistical analysis was provided, these data suggest the existence of pulsating patches for these groups.

As more data become available from different localities and different groups of organisms, we believe the recognition of pulsating patches will become commonplace.

CONCLUSIONS

1. Within a habitat, the density of benthic foraminifera can vary spatially and temporally (e.g., daily, weekly, monthly, seasonally, and yearly).
2. Historically, most foraminiferal field studies have collected only one observation (sample) per sampling time at each station. Therefore, researchers experience great difficulty in separating spatial differences from temporal differences.
3. Historically, visual inspection of data with only a single observation per sampling time has led to the conclusion that seasonal and yearly differences are significant for most taxa.
4. Rigorous statistical analysis requires more than one observation per sampling time per station (replicates). More than two replicates are required for adequate analysis. Observations (samples) should not be added together for statistical evaluation.
5. In our summary of historical field sampling studies, statistical analyses indicate spatial, seasonal, and yearly differences within a habitat were actually significant in only about half of the taxa examined.
6. Examination of densities at multiple stations over seasons and years requires statistical testing by a three-way ANOVA model that includes interactions. The null hypotheses for this model are that mean densities are equal over stations, seasons, years, and the interactions of stations $\times$ seasons, stations $\times$ years, seasons $\times$ years, and stations $\times$ seasons $\times$ years. Depending on the actual data collected, this model may be abbreviated to include only the relevant temporal factors and their interactions.
7. The interaction hypotheses of stations with time (station $\times$ time) are tested to determine whether or not the stations behave the same or differently with time. That is, this is a test of possible asynchrony.
8. Significance of the interaction of stations $\times$ time defines the existence of pulsating patches (each sampling time has a patchy distribution, but the patches vary with time).
9. The most thorough examination of the pulsating patch hypothesis for foraminifera has been with a research design that included four stations within a 1 m² area and four stations within a 100 m² area sampled each season for four years in the Indian River Lagoon, Florida. Interaction hypotheses were determined to be statistically significant for the four taxa examined in the Indian River Lagoon at both scales and sites.

10. Hypotheses for seasons and years have the highest mean square values in each of the three-way ANOVAs. About 68% of the variability is due to these time components, about 7% to station differences, and 24% to interactions.
11. In the Indian River Lagoon at the 1 m² site, a general linear ANOVA model with covariates was constructed for each of the four taxa as the dependent variable and two coexistent taxa, seasonal differences, yearly differences, station differences, temperature, salinity, and oxygen as independent variables. For each of the analyses of the four taxa, most of the eight hypotheses that were generated were significant and provided evidence to reject equality. About half of the mean square values were attributable to the density of the other taxa, and time and environmental variables each accounted for about a quarter of this variability estimate.
12. The large amount of variability accounted for by the associated foraminifers suggests that the foraminifera constitute a community responding in unison to the environment about them. The results of the three-way ANOVAs agree with this conclusion in that about 75% of the variability is explained by overall station and time components, and only about 25% is explained by interactions.
13. Although only a small number of other studies have looked for the existence of pulsating patches, both the sea grass *Halophile johnsonii* (Virnstein et al., 2009) and cyanobacteria in the Indian River Lagoon (Hayek et al., unpublished data) appear to adhere to this model. We propose that a large number of taxa are actually well modeled by this approach.

ACKNOWLEDGMENTS

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Appendix 1

TABLE A.1. Number of individuals stained with Rose Bengal in 5 mL of sediment from top of cores. Stations: 1 to 4, arranged at the corners of a square with stations 10 m apart. Years: 1, July 2001 to October 2002; 2, July 2002 to October 2003; 3, July 2003 to October 2004; 4, July 2004 to October 2005. Seasons: 1, Winter (January); 2, Spring (April); 3, Summer (July); 4, Fall (October). Replicates: 1 to 4, cores taken within centimeters of each other. Counter: S. A. Reed.

Station	Year	Season	Replicate	<i>Quinqueloculina</i>	<i>Ammonia</i>	<i>Elphidium</i>	<i>Bolivina</i>	<i>Ammobaculites</i>
1	1	3	1	65	5	1	0	0
1	1	3	2	19	1	1	0	0
1	1	3	3	58	3	6	0	0
1	1	3	4	8	0	0	0	0
2	1	3	1	92	1	0	0	1
2	1	3	2	154	6	0	0	0
2	1	3	3	121	5	0	0	2
2	1	3	4	227	5	1	0	0
3	1	3	1	7	14	1	0	0
3	1	3	2	74	24	8	0	0
3	1	3	3	246	36	13	0	0
3	1	3	4	204	6	9	0	3
4	1	3	1	79	3	1	0	0
4	1	3	2	139	4	2	0	2
4	1	3	3	41	3	1	0	0
4	1	3	4	38	1	0	0	0
1	1	4	1	0	0	0	0	0
1	1	4	2	6	7	2	1	0
1	1	4	3	5	5	3	0	1
1	1	4	4	2	4	0	0	0
2	1	4	1	1	1	1	0	0
2	1	4	2	5	4	0	0	1
2	1	4	3	1	1	1	0	0
2	1	4	4	1	6	1	0	0
3	1	4	1	8	6	2	0	0
3	1	4	2	6	7	0	0	2
3	1	4	3	1	0	1	0	1
3	1	4	4	20	3	2	0	1
4	1	4	1	2	0	0	0	0
4	1	4	2	0	0	0	0	0
4	1	4	3	0	0	0	0	0
4	1	4	4	0	0	0	0	0
1	1	1	1	31	18	3	0	3
1	1	1	2	6	3	1	0	0
1	1	1	3	12	22	17	0	2
1	1	1	4	17	16	10	0	0
2	1	1	1	7	12	0	0	0

Station	Year	Season	Replicate	<i>Quinqueloculina</i>	<i>Ammonia</i>	<i>Elphidium</i>	<i>Bolivina</i>	<i>Ammobaculites</i>
2	1	1	2	0	1	0	0	1
2	1	1	3	3	0	0	0	2
2	1	1	4	7	6	2	0	0
3	1	1	1	81	35	2	0	2
3	1	1	2	28	48	3	0	5
3	1	1	3	13	17	2	0	0
3	1	1	4	4	11	0	0	0
4	1	1	1	6	5	0	0	1
4	1	1	2	4	3	0	0	0
4	1	1	3	2	5	0	0	0
4	1	1	4	4	5	0	0	0
1	1	2	1	2	5	0	0	0
1	1	2	2	10	5	0	0	0
1	1	2	3	3	5	1	0	0
1	1	2	4	2	3	0	0	0
2	1	2	1	11	2	4	0	0
2	1	2	2	14	5	1	0	1
2	1	2	3	6	5	0	0	0
2	1	2	4	19	8	0	0	0
3	1	2	1	8	7	0	0	0
3	1	2	2	10	16	0	0	0
3	1	2	3	5	4	3	0	0
3	1	2	4	15	11	0	0	0
4	1	2	1	4	2	0	0	0
4	1	2	2	1	2	0	0	0
4	1	2	3	18	9	0	0	0
4	1	2	4	2	1	0	0	0
1	2	3	1	26	11	0	0	0
1	2	3	2	12	6	1	0	0
1	2	3	3	41	8	4	0	1
1	2	3	4	58	7	1	0	0
2	2	3	1	21	3	1	0	1
2	2	3	2	30	3	0	0	1
2	2	3	3	32	5	0	0	0
2	2	3	4	53	5	4	0	0
3	2	3	1	4	0	0	0	0
3	2	3	2	15	12	5	0	0
3	2	3	3	24	16	5	0	1
3	2	3	4	33	6	1	0	0
4	2	3	1	6	2	0	0	0
4	2	3	2	11	3	0	0	0

Station	Year	Season	Replicate	<i>Quinqueloculina</i>	<i>Ammonia</i>	<i>Elphidium</i>	<i>Bolivina</i>	<i>Ammobaculites</i>
4	2	3	3	2	3	0	0	0
4	2	3	4	45	7	2	0	0
1	2	4	1	17	24	2	0	0
1	2	4	2	1	5	1	0	0
1	2	4	3	8	14	1	0	0
1	2	4	4	8	6	7	0	1
2	2	4	1	3	2	3	0	1
2	2	4	2	12	11	2	0	0
2	2	4	3	31	11	0	0	1
2	2	4	4	9	14	2	0	0
3	2	4	1	3	4	0	0	5
3	2	4	2	8	9	0	0	0
3	2	4	3	15	26	4	0	0
3	2	4	4	13	13	2	0	1
4	2	4	1	5	3	1	0	0
4	2	4	2	9	13	0	0	2
4	2	4	3	12	16	2	0	1
4	2	4	4	25	14	8	0	2
1	2	1	1	26	16	5	0	2
1	2	1	2	10	17	4	0	2
1	2	1	3	25	22	7	0	1
1	2	1	4	14	2	1	0	6
2	2	1	1	7	8	3	0	0
2	2	1	2	4	11	0	0	0
2	2	1	3	13	6	0	0	1
2	2	1	4	5	4	2	0	1
3	2	1	1	29	24	3	0	12
3	2	1	2	155	39	18	0	30
3	2	1	3	76	41	14	0	14
3	2	1	4	3	1	1	0	5
4	2	1	1	5	1	2	0	0
4	2	1	2	4	3	1	0	0
4	2	1	3	5	4	1	0	0
4	2	1	4	8	4	3	0	0
1	2	2	1	16	16	7	0	5
1	2	2	2	2	5	1	0	0
1	2	2	3	21	9	3	0	2
1	2	2	4	2	5	1	0	0
2	2	2	1	5	14	0	0	0
2	2	2	2	2	11	0	0	0
2	2	2	3	0	1	0	0	0

Station	Year	Season	Replicate	<i>Quinqueloculina</i>	<i>Ammonia</i>	<i>Elphidium</i>	<i>Bolivina</i>	<i>Ammobaculites</i>
2	2	2	4	1	6	0	0	0
3	2	2	1	5	16	1	0	1
3	2	2	2	4	8	0	0	2
3	2	2	3	5	5	0	0	0
3	2	2	4	22	63	1	0	2
4	2	2	1	3	10	0	0	0
4	2	2	2	0	6	0	0	0
4	2	2	3	1	5	0	0	0
4	2	2	4	0	4	1	0	0
1	3	3	1	36	9	3	0	4
1	3	3	2	17	3	0	0	0
1	3	3	3	19	4	2	0	1
1	3	3	4	16	3	2	0	2
2	3	3	1	17	7	2	0	0
2	3	3	2	32	21	0	0	6
2	3	3	3	9	5	4	0	2
2	3	3	4	24	3	1	0	2
3	3	3	1	40	13	3	0	0
3	3	3	2	41	13	3	0	2
3	3	3	3	28	8	1	0	3
3	3	3	4	45	15	1	0	8
4	3	3	1	2	5	0	0	0
4	3	3	2	38	17	0	0	4
4	3	3	3	24	10	0	0	1
4	3	3	4	36	14	1	0	1
1	3	4	1	2	0	1	0	0
1	3	4	2	24	7	2	0	0
1	3	4	3	2	7	2	0	1
1	3	4	4	1	6	0	0	1
2	3	4	1	0	3	0	0	1
2	3	4	2	1	4	0	0	0
2	3	4	3	1	5	0	0	0
2	3	4	4	2	2	1	0	1
3	3	4	1	8	4	0	0	0
3	3	4	2	2	8	1	0	0
3	3	4	3	1	5	0	0	0
3	3	4	4	3	4	0	0	2
4	3	4	1	1	9	1	0	1
4	3	4	2	7	12	0	0	0
4	3	4	3	9	19	11	0	6
4	3	4	4	0	9	1	0	0

Station	Year	Season	Replicate	<i>Quinqueloculina</i>	<i>Ammonia</i>	<i>Elphidium</i>	<i>Bolivina</i>	<i>Ammobaculites</i>
1	3	1	1	159	26	11	0	2
1	3	1	2	185	9	25	0	4
1	3	1	3	164	19	16	0	3
1	3	1	4	19	15	2	0	0
2	3	1	1	6	10	3	0	1
2	3	1	2	46	4	8	0	1
2	3	1	3	39	12	10	1	7
2	3	1	4	51	17	21	0	11
3	3	1	1	107	59	40	3	11
3	3	1	2	95	52	9	0	3
3	3	1	3	202	99	36	0	24
3	3	1	4	152	70	43	3	22
4	3	1	1	114	66	19	0	7
4	3	1	2	4	3	1	0	1
4	3	1	3	44	21	29	1	5
4	3	1	4	25	16	4	0	0
1	3	2	1	24	7	6	0	0
1	3	2	2	36	18	9	0	0
1	3	2	3	372	72	22	0	5
1	3	2	4	251	36	9	0	0
2	3	2	1	222	66	63	0	9
2	3	2	2	124	65	10	0	4
2	3	2	3	116	44	22	0	5
2	3	2	4	152	32	59	0	10
3	3	2	1	610	247	232	1	12
3	3	2	2	547	128	161	0	13
3	3	2	3	343	106	168	0	21
3	3	2	4	700	197	120	0	3
4	3	2	1	508	132	78	0	4
4	3	2	2	820	207	143	0	13
4	3	2	3	582	250	167	1	7
4	3	2	4	246	102	66	0	5
1	4	3	1	102	42	73	1	1
1	4	3	2	152	19	45	0	3
1	4	3	3	144	45	36	0	1
1	4	3	4	127	39	106	0	4
2	4	3	1	150	26	74	1	5
2	4	3	2	162	27	37	1	1
2	4	3	3	142	14	31	0	1
2	4	3	4	109	19	26	2	2
3	4	3	1	171	31	39	0	1

Station	Year	Season	Replicate	<i>Quinqueloculina</i>	<i>Ammonia</i>	<i>Elphidium</i>	<i>Bolivina</i>	<i>Ammobaculites</i>
3	4	3	2	158	45	59	0	2
3	4	3	3	143	12	39	0	0
3	4	3	4	83	27	42	0	4
4	4	3	1	95	48	28	2	2
4	4	3	2	76	41	20	0	2
4	4	3	3	142	33	19	0	0
4	4	3	4	193	20	21	0	0
1	4	4	1	36	79	96	2	11
1	4	4	2	42	55	78	4	11
1	4	4	3	18	36	70	2	4
1	4	4	4	51	61	44	1	7
2	4	4	1	18	23	7	2	11
2	4	4	2	34	35	21	0	4
2	4	4	3	23	41	19	3	13
2	4	4	4	31	46	22	3	9
3	4	4	1	59	61	56	1	5
3	4	4	2	49	56	32	3	9
3	4	4	3	117	91	48	0	6
3	4	4	4	123	47	33	0	4
4	4	4	1	39	25	3	2	2
4	4	4	2	22	31	17	1	4
4	4	4	3	8	21	9	0	6
4	4	4	4	6	19	5	0	4
1	4	1	1	4	4	19	0	2
1	4	1	2	19	24	49	0	10
1	4	1	3	45	95	73	0	20
1	4	1	4	42	95	78	0	9
2	4	1	1	23	41	13	0	9
2	4	1	2	37	88	24	0	12
2	4	1	3	16	27	25	0	5
2	4	1	4	25	19	8	0	3
3	4	1	1	40	86	58	0	15
3	4	1	2	21	47	41	0	11
3	4	1	3	52	106	90	0	26
3	4	1	4	36	92	48	0	27
4	4	1	1	45	74	28	0	8
4	4	1	2	52	35	31	0	3
4	4	1	3	7	12	3	0	0
4	4	1	4	15	27	9	0	3
1	4	2	1	17	30	19	1	5
1	4	2	2	22	24	3	1	2

Station	Year	Season	Replicate	<i>Quinqueloculina</i>	<i>Ammonia</i>	<i>Elphidium</i>	<i>Bolivina</i>	<i>Ammobaculites</i>
1	4	2	3	10	21	21	10	4
1	4	2	4	2	11	0	0	3
2	4	2	1	34	117	19	0	2
2	4	2	2	7	31	0	0	1
2	4	2	3	6	27	3	0	0
2	4	2	4	11	38	9	0	0
3	4	2	1	18	8	3	0	1
3	4	2	2	31	13	15	0	4
3	4	2	3	4	7	0	0	0
3	4	2	4	30	15	0	0	6
4	4	2	1	5	11	5	0	1
4	4	2	2	11	14	8	0	1
4	4	2	3	3	5	3	0	1
4	4	2	4	5	17	1	0	3

Appendix 2

TABLE A.2. Number of individuals stained with Rose Bengal in 5 mL of sediment from top of cores. Stations: 1' to 4', arranged at the corners of a square with stations 1 m apart. Station 1' is the same as station 1 in Appendix 1. Years: 1, July 2001 to October 2002; 2, July 2002 to October 2003; 3, July 2003 to October 2004; 4, July 2004 to October 2005. Seasons: 1, Winter (January); 2, Spring (April); 3, Summer (July); 4, Fall (October). Replicates: 1 to 4, cores taken within centimeters of each other. Counter: 1, S. A. Reed; 2, J. A. Jett.

Station	Year	Season	Replicate	Counter	<i>Quinqueloculina</i>	<i>Ammonia</i>	<i>Elphidium</i>	<i>Bolivina</i>	<i>Ammobaculites</i>
1'	1	3	1	1	65	5	1	0	0
1'	1	3	2	1	19	1	1	0	0
1'	1	3	3	1	58	3	6	0	0
1'	1	3	4	1	8	0	0	0	0
2'	1	3	1	2	77	7	7	2	0
2'	1	3	2	2	43	3	4	0	1
2'	1	3	3	2	151	11	4	3	1
2'	1	3	4	2	65	2	11	0	0
3'	1	3	1	2	126	11	7	4	0
3'	1	3	2	2	60	2	0	1	1
3'	1	3	3	2	6	1	0	0	0
3'	1	3	4	2	11	1	3	1	0
4'	1	3	1	2	52	7	11	11	0
4'	1	3	2	2	26	1	5	3	0
4'	1	3	3	2	73	8	9	4	0
4'	1	3	4	2	17	3	3	4	1
1'	1	4	1	1	0	0	0	0	0
1'	1	4	2	1	6	7	2	1	0
1'	1	4	3	1	5	5	3	0	1
1'	1	4	4	1	2	4	0	0	0
2'	1	4	1	2	0	3	0	0	0
2'	1	4	2	2	6	22	1	0	0
2'	1	4	3	2	6	6	1	0	0
2'	1	4	4	2	3	8	0	0	0
3'	1	4	1	2	3	7	1	0	1
3'	1	4	2	2	8	5	1	0	1
3'	1	4	3	2	17	0	0	0	0
3'	1	4	4	2	3	6	1	0	0
4'	1	4	1	2	5	0	2	0	0
4'	1	4	2	2	6	9	1	0	0
4'	1	4	3	2	20	27	2	0	1
4'	1	4	4	2	8	5	0	0	0
1'	1	1	1	1	31	18	3	0	3
1'	1	1	2	1	6	3	1	0	0
1'	1	1	3	1	12	22	17	0	2
1'	1	1	4	1	17	16	10	0	0
2'	1	1	1	2	0	0	0	0	0
2'	1	1	2	2	0	0	0	0	0
2'	1	1	3	2	0	0	0	0	0
2'	1	1	4	2	1	0	0	0	0
3'	1	1	1	2	0	0	0	0	0
3'	1	1	2	2	4	0	0	0	0
3'	1	1	3	2	0	0	0	0	0
3'	1	1	4	2	0	0	0	0	0
4'	1	1	1	2	0	0	0	0	0

Station	Year	Season	Replicate	Counter	<i>Quinqueloculina</i>	<i>Ammonia</i>	<i>Elphidium</i>	<i>Bolivina</i>	<i>Ammobaculites</i>
4'	1	1	2	2	6	0	6	0	0
4'	1	1	3	2	0	0	0	0	0
4'	1	1	4	2	0	0	0	0	0
1'	1	2	1	1	2	5	0	0	0
1'	1	2	2	1	10	5	0	0	0
1'	1	2	3	1	3	5	1	0	0
1'	1	2	4	1	2	3	0	0	0
2'	1	2	1	2	1	2	0	0	0
2'	1	2	2	2	2	0	0	0	0
2'	1	2	3	2	0	0	0	0	0
2'	1	2	4	2	1	1	2	0	0
3'	1	2	1	2	39	5	15	0	0
3'	1	2	2	2	8	3	8	0	0
3'	1	2	3	2	3	0	1	0	0
3'	1	2	4	2	1	0	0	0	0
4'	1	2	1	2	11	6	4	0	0
4'	1	2	2	2	16	8	1	0	0
4'	1	2	3	2	11	5	1	0	0
4'	1	2	4	2	5	2	4	0	0
1'	2	3	1	1	26	11	0	0	0
1'	2	3	2	1	12	6	1	0	0
1'	2	3	3	1	41	8	4	0	1
1'	2	3	4	1	58	7	1	0	0
2'	2	3	1	2	8	11	0	0	1
2'	2	3	2	2	18	13	6	2	2
2'	2	3	3	2	0	1	0	0	0
2'	2	3	4	2	2	0	2	1	1
3'	2	3	1	2	9	1	0	0	0
3'	2	3	2	2	8	3	1	0	1
3'	2	3	3	2	7	2	1	0	0
3'	2	3	4	2	13	4	1	0	1
4'	2	3	1	2	7	3	0	0	1
4'	2	3	2	2	5	5	3	0	0
4'	2	3	3	2	20	12	1	0	0
4'	2	3	4	2	22	7	6	0	0
1'	2	4	1	1	17	24	2	0	0
1'	2	4	2	1	1	5	1	0	0
1'	2	4	3	1	8	14	1	0	0
1'	2	4	4	1	8	6	7	0	1
2'	2	4	1	2	13	22	7	0	0
2'	2	4	2	2	47	34	13	0	3
2'	2	4	3	2	11	18	8	0	1
2'	2	4	4	2	10	19	5	0	1
3'	2	4	1	2	15	15	3	0	1
3'	2	4	2	2	90	163	33	0	5
3'	2	4	3	2	9	8	4	0	0
3'	2	4	4	2	34	29	5	0	0
4'	2	4	1	2	2	5	0	0	0
4'	2	4	2	2	25	27	5	0	0
4'	2	4	3	2	13	18	8	0	1
4'	2	4	4	2	75	131	26	0	3

Station	Year	Season	Replicate	Counter	<i>Quinqueloculina</i>	<i>Ammonia</i>	<i>Elphidium</i>	<i>Bolivina</i>	<i>Ammobaculites</i>
1'	2	1	1	1	26	16	5	0	2
1'	2	1	2	1	10	17	4	0	2
1'	2	1	3	1	25	22	7	0	1
1'	2	1	4	1	14	2	1	0	6
2'	2	1	1	2	37	26	24	0	15
2'	2	1	2	2	93	33	43	0	16
2'	2	1	3	2	26	10	9	0	8
2'	2	1	4	2	51	30	18	0	5
3'	2	1	1	2	9	7	8	0	6
3'	2	1	2	2	58	28	17	0	32
3'	2	1	3	2	30	38	21	0	10
3'	2	1	4	2	3	0	1	0	2
4'	2	1	1	2	23	16	14	0	8
4'	2	1	2	2	4	6	3	0	0
4'	2	1	3	2	10	4	3	0	2
4'	2	1	4	2	18	15	4	0	2
1'	2	2	1	1	16	16	7	0	5
1'	2	2	2	1	2	5	1	0	0
1'	2	2	3	1	21	9	3	0	2
1'	2	2	4	1	2	5	1	0	0
2'	2	2	1	2	9	0	1	0	1
2'	2	2	2	2	13	14	5	0	0
2'	2	2	3	2	15	7	0	0	0
2'	2	2	4	2	7	15	7	0	0
3'	2	2	1	2	18	15	4	0	1
3'	2	2	2	2	12	7	1	0	0
3'	2	2	3	2	54	27	9	0	1
3'	2	2	4	2	7	0	0	0	0
4'	2	2	1	2	5	5	1	0	1
4'	2	2	2	2	9	4	0	0	1
4'	2	2	3	2	0	0	0	0	0
4'	2	2	4	2	3	0	0	0	0
1'	3	3	1	1	36	9	3	0	4
1'	3	3	2	1	17	3	0	0	0
1'	3	3	3	1	19	4	2	0	1
1'	3	3	4	1	16	3	2	0	2
2'	3	3	1	2	4	2	2	0	2
2'	3	3	2	2	24	11	14	0	28
2'	3	3	3	2	33	38	41	0	2
2'	3	3	4	2	21	7	16	0	8
3'	3	3	1	2	65	23	27	0	25
3'	3	3	2	2	68	49	39	0	11
3'	3	3	3	2	45	20	27	0	13
3'	3	3	4	2	54	16	22	1	42
4'	3	3	1	2	42	2	8	0	3
4'	3	3	2	2	5	10	18	0	0
4'	3	3	3	2	41	15	10	0	8
4'	3	3	4	2	1	3	5	0	0
1'	3	4	1	1	2	0	1	0	0
1'	3	4	2	1	24	7	2	0	0

Station	Year	Season	Replicate	Counter	<i>Quinqueloculina</i>	<i>Ammonia</i>	<i>Elphidium</i>	<i>Bolivina</i>	<i>Ammobaculites</i>
1'	3	4	3	1	2	7	2	0	1
1'	3	4	4	1	1	6	0	0	1
2'	3	4	1	2	5	6	1	0	0
2'	3	4	2	2	10	5	2	0	0
2'	3	4	3	2	0	1	1	0	0
2'	3	4	4	2	3	2	0	0	0
3'	3	4	1	2	0	2	0	0	0
3'	3	4	2	2	4	2	2	0	0
3'	3	4	3	2	12	5	1	1	0
3'	3	4	4	2	12	23	5	0	1
4'	3	4	1	2	6	17	2	0	1
4'	3	4	2	2	3	7	1	0	0
4'	3	4	3	2	1	3	0	0	0
4'	3	4	4	2	3	2	2	0	2
1'	3	1	1	1	159	26	11	0	2
1'	3	1	2	1	185	9	25	0	4
1'	3	1	3	1	164	19	16	0	3
1'	3	1	4	1	19	15	2	0	0
2'	3	1	1	2	26	16	33	0	0
2'	3	1	2	2	10	14	9	0	2
2'	3	1	3	2	1	0	0	0	0
2'	3	1	4	2	1	0	0	0	0
3'	3	1	1	2	6	3	13	0	1
3'	3	1	2	2	37	24	40	0	4
3'	3	1	3	2	15	8	15	0	0
3'	3	1	4	2	20	10	37	0	1
4'	3	1	1	2	33	6	12	0	0
4'	3	1	2	2	7	6	7	0	0
4'	3	1	3	2	20	23	36	0	2
4'	3	1	4	2	64	44	68	1	3
1'	3	2	1	1	24	7	6	0	0
1'	3	2	2	1	36	18	9	0	0
1'	3	2	3	1	372	72	22	0	5
1'	3	2	4	1	251	36	9	0	0
2'	3	2	1	2	108	26	275	4	0
2'	3	2	2	2	30	11	24	1	0
2'	3	2	3	2	109	22	88	0	0
2'	3	2	4	2	39	21	81	0	0
3'	3	2	1	2	84	13	26	0	0
3'	3	2	2	2	48	18	14	0	0
3'	3	2	3	2	32	12	42	0	1
3'	3	2	4	2	138	40	136	0	0
4'	3	2	1	2	115	37	50	1	0
4'	3	2	2	2	93	53	78	2	0
4'	3	2	3	2	218	72	348	0	0
4'	3	2	4	2	137	49	102	0	0
1'	4	3	1	1	102	42	73	1	1
1'	4	3	2	1	152	19	45	0	3
1'	4	3	3	1	144	45	36	0	1
1'	4	3	4	1	127	39	106	0	4

Station	Year	Season	Replicate	Counter	<i>Quinqueloculina</i>	<i>Ammonia</i>	<i>Elphidium</i>	<i>Bolivina</i>	<i>Ammobaculites</i>
2'	4	3	1	2	1	1	0	0	0
2'	4	3	2	2	0	1	4	0	0
2'	4	3	3	2	0	1	0	0	0
2'	4	3	4	2	1	0	0	0	0
3'	4	3	1	2	11	16	6	0	0
3'	4	3	2	2	13	10	0	0	0
3'	4	3	3	2	18	11	6	0	0
3'	4	3	4	2	16	1	0	0	0
4'	4	3	1	2	5	0	0	0	0
4'	4	3	2	2	3	0	0	0	0
4'	4	3	3	2	25	9	7	0	0
4'	4	3	4	2	9	6	10	0	0
1'	4	4	1	1	36	79	96	2	11
1'	4	4	2	1	42	55	78	4	11
1'	4	4	3	1	18	36	70	2	4
1'	4	4	4	1	51	61	44	1	7
2'	4	4	1	2	0	14	53	0	1
2'	4	4	2	2	11	26	39	2	2
2'	4	4	3	2	0	15	25	0	1
2'	4	4	4	2	0	13	47	0	1
3'	4	4	1	2	0	12	46	0	1
3'	4	4	2	2	0	8	31	0	0
3'	4	4	3	2	0	14	46	1	0
3'	4	4	4	2	1	6	33	2	1
4'	4	4	1	2	2	21	21	1	1
4'	4	4	2	2	0	15	27	1	10
4'	4	4	3	2	0	5	12	0	2
4'	4	4	4	2	0	17	36	0	0
1'	4	1	1	1	4	4	19	0	2
1'	4	1	2	1	19	24	49	0	10
1'	4	1	3	1	45	95	73	0	20
1'	4	1	4	1	42	95	78	0	9
2'	4	1	1	2	15	47	58	0	1
2'	4	1	2	2	8	41	44	0	6
2'	4	1	3	2	6	15	20	0	2
2'	4	1	4	2	32	41	69	1	11
3'	4	1	1	2	45	87	110	0	12
3'	4	1	2	2	56	92	148	1	15
3'	4	1	3	2	33	56	84	0	4
3'	4	1	4	2	17	35	52	0	2
4'	4	1	1	2	8	40	35	0	3
4'	4	1	2	2	1	11	6	0	0
4'	4	1	3	2	25	53	69	0	9
4'	4	1	4	2	19	29	42	1	7
1'	4	2	1	1	17	30	19	1	5
1'	4	2	2	1	22	24	3	1	2
1'	4	2	3	1	10	21	21	10	4
1'	4	2	4	1	2	11	0	0	3
2'	4	2	1	2	21	59	17	0	0
2'	4	2	2	2	18	21	2	2	0

Station	Year	Season	Replicate	Counter	<i>Quinqueloculina</i>	<i>Ammonia</i>	<i>Elphidium</i>	<i>Bolivina</i>	<i>Ammobaculites</i>
2'	4	2	3	2	19	52	9	0	1
2'	4	2	4	2	17	9	0	0	1
3'	4	2	1	2	7	19	17	0	0
3'	4	2	2	2	53	41	13	2	0
3'	4	2	3	2	78	205	66	0	0
3'	4	2	4	2	63	46	31	0	0
4'	4	2	1	2	5	26	5	0	0
4'	4	2	2	2	28	28	13	0	0
4'	4	2	3	2	69	320	90	1	2
4'	4	2	4	2	24	29	6	2	0

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