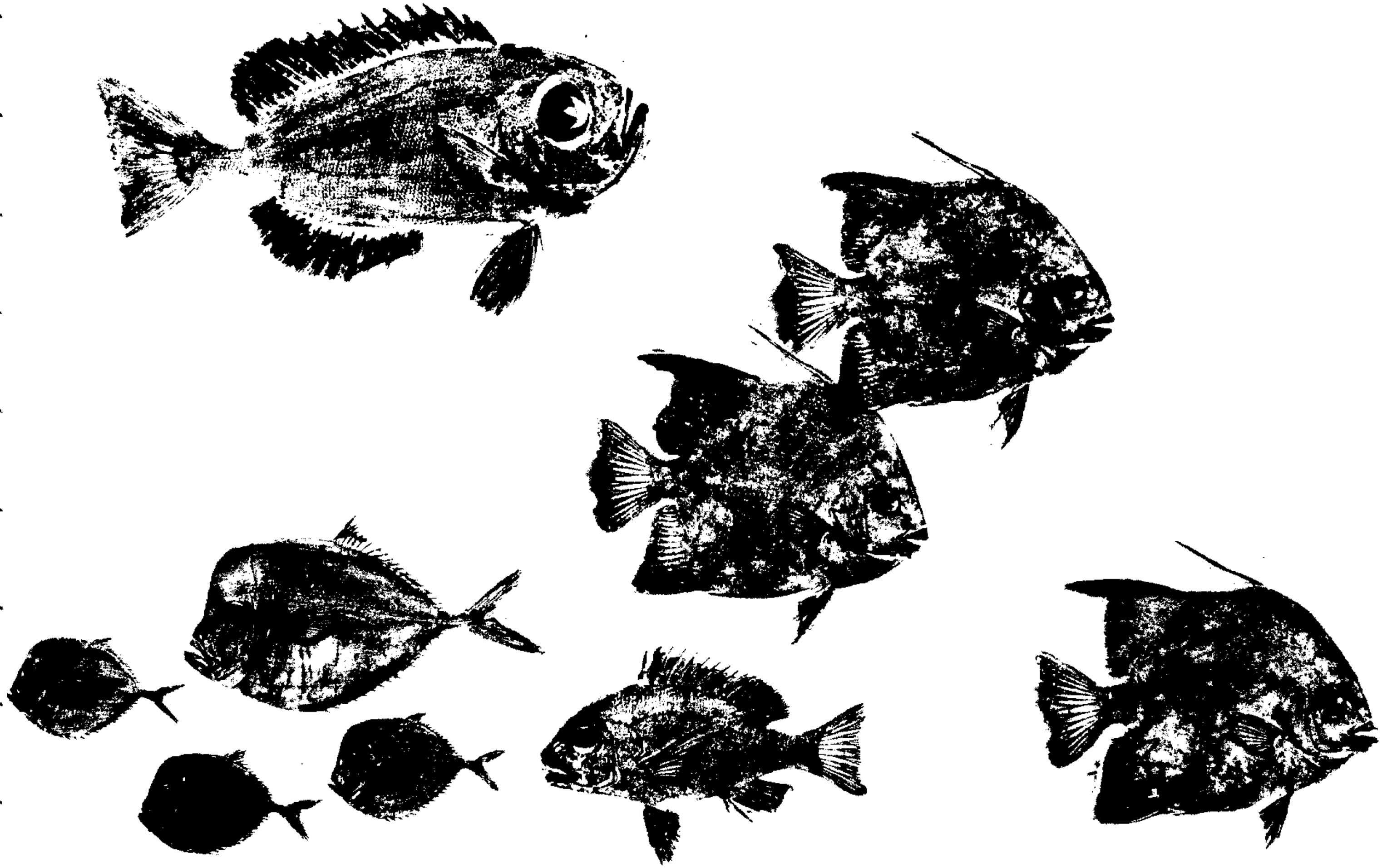

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PREDICTING LONG-TERM EFFECTS OF FRESHWATER INFLOW ON MACROBENTHOS IN THE LAVACA-COLORADO AND GUADALUPE ESTUARIES

Paul A. Montagna, Principal Investigator

TWDB Contract No. 91-483-787

Technical Report Number TR/91-004

FINAL REPORT

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by

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Texas Water Development Board
P.O. Box 13087 Capitol Station
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Interagency Cooperative Contract
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PREDICTING LONG-TERM EFFECTS OF FRESHWATER INFLOW ON MACROBENTHOS IN THE LAVACA-COLORADO AND GUADALUPE ESTUARIES

ABSTRACT

Two estuaries have been studied to determine the effect of year-to-year variation of freshwater inflow on macrobenthic infauna. The estuaries have similar inflow characteristics, but the Lavaca-Colorado has direct exchange of coastal marine water with the Gulf of Mexico and the Guadalupe does not. Studies in the Lavaca-Colorado began in 1984, and studies in the Guadalupe began in 1987. There are changes in community structure and function from year-to-year, which can be linked to the long-term cycle of wet and dry years along the Texas coast. There appears to be a long-term cycle of high-inflow stimulated recruitment, followed by nutrient depletion and recruitment of marine species during low-inflow periods, followed by declines in productivity until the next wet year. These cycles appear to have a period of 2-3 years, but it will take at least 3 more years of data to test this hypothesis.

INTRODUCTION

Prudent management of freshwater resources is required to meet residential, industrial, and agricultural needs while still protecting the natural resources in our environment. One aspect of environmental conservation (as evidenced by good management practices) is to ensure that there is adequate freshwater inflow to our estuaries. Data is needed to describe the effects of freshwater inflow on estuaries, so that an assessment of freshwater needs can be made.

The climate of Texas is characterized by a long-term cycle of floods and droughts. Yet, we have very little information about the scales of natural variability over the long-term. This makes it very difficult to create long-range plans for the management of water resources. Data is needed to describe the long-term variability of biological indicators of freshwater inflow effects.

Previous studies have shown that benthos are good indicators of freshwater inflow effects (Montagna, 1989; Kalke and Montagna, 1991; Montagna and Yoon, 1991; Montagna and Kalke, submitted ms.). However, all of these studies were carried out over a narrow time scale, from seven to 21 months. The studies spanning more than one year hint that there is a long-term effect associated with wet and dry years. The purpose of this study is to determine if freshwater inflow affects on benthos is greater for year-to-year variability than for seasonal variability. This would allow us to build better models of quantitative relationships between freshwater inflow and benthos in Texas estuaries.

METHODS

Why Study Benthos?

Benthos are the most economical and reliable indicators of the effects of freshwater inflow in Texas estuaries. This contradicts the conventional wisdom. Rivers transport nutrients to estuaries, which should stimulate phytoplankton production (Nixon et al., 1986). The benthos would benefit by this production if filter feeders, e.g., oysters consume phytoplankton in the water column or if the primary production is deposited to the bottom via gravity. Previous studies have shown that phytoplankton parameters are very variable. Primary production can vary as much over one or two days as it can over a week. Therefore, we have not been successful in correlating primary production with river inflow. We also don't know what taxonomic groups, let alone species, are responding to the inflow. It would be very labor intensive and expensive to generate enough data to fully describe the natural variability in primary production and phytoplankton species distributions to determine if man's activities in managing freshwater inflow would increase that variability. Benthos, on the other hand, are relatively fixed in space and easy to sample accurately, long-lived and integrate effects over a long time period, and many community characteristics can be measured inexpensively.

Study Design and Area

There are seven major estuarine systems along the Texas coast (Figure 1). Each system receives drainage from one to three major rivers. The northeastern most estuaries receive more freshwater inflow than the southwestern estuaries (Figure 2). Two estuarine systems were studied in detail (Figure 3). Both systems have similar freshwater inflow characteristics, but the Lavaca-Colorado has direct exchange of marine water with the Gulf of Mexico via Pass Cavallo, whereas the Guadalupe does not. To assess ecosystem-wide variability stations in the freshwater influenced and marine influenced zones were chosen. Two stations, which replicate each of the two treatment effects (freshwater and marine) influence, were sampled. Generally these stations were along the major axis of the estuarine system leading from river mouth to the foot of the estuary

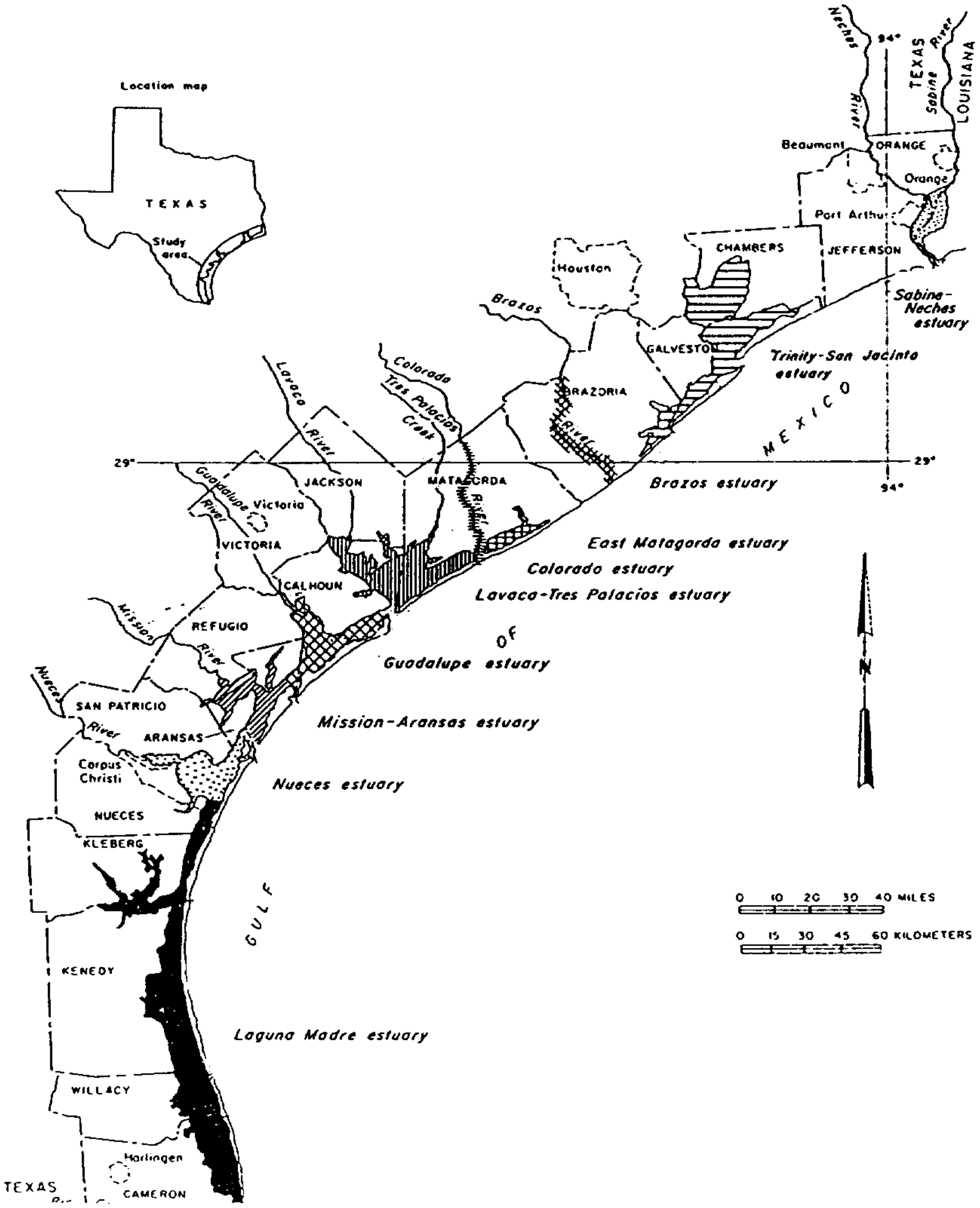


Figure 1. Location of Texas Estuaries.

47 – year (1941 – 1987) Average Freshwater Inflow Balance (10^9 acre – ft · y)

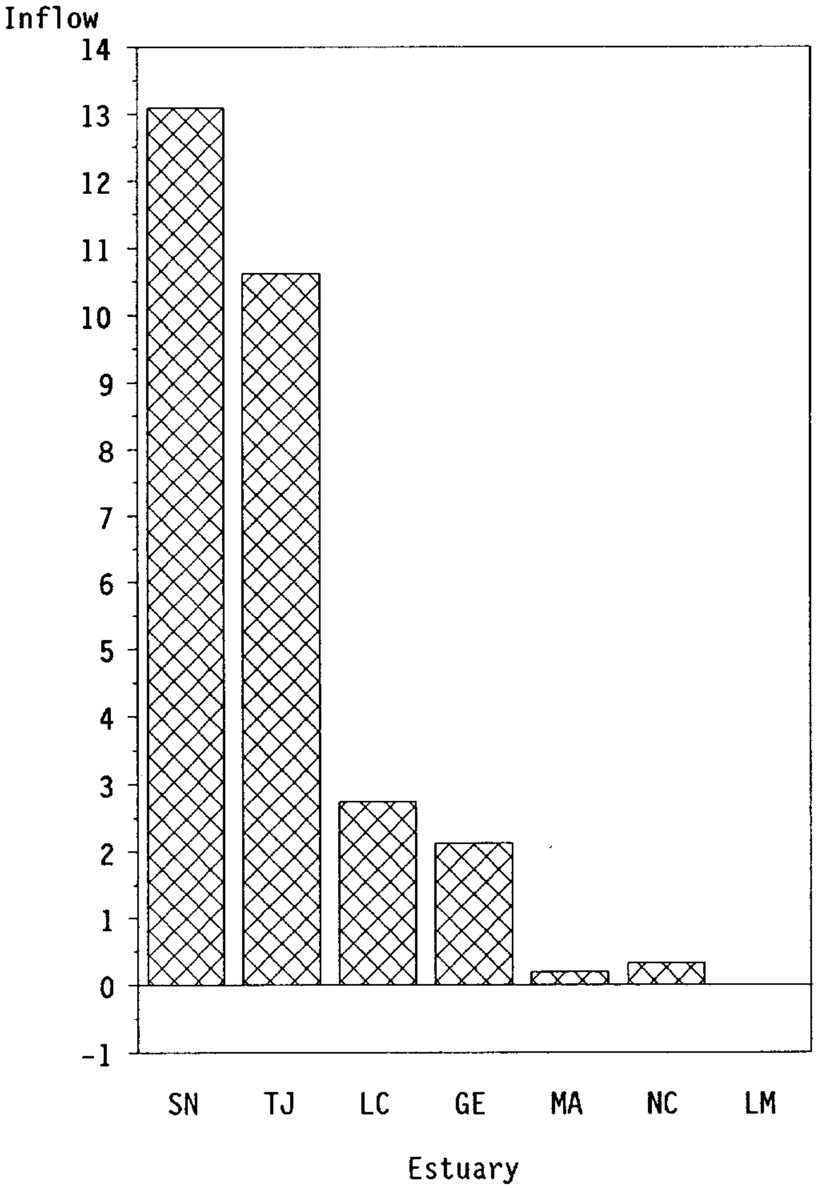


Figure 2. Annual average inflow in Texas Estuaries. SN = Sabine-Neches, TJ = Trinity-San Jacinto, LC = Lavaca-Colorado, GE = Guadalupe, MA = Mission-Aransas, NC = Nueces, LM = Laguna Madre (doesn't show at this scale).

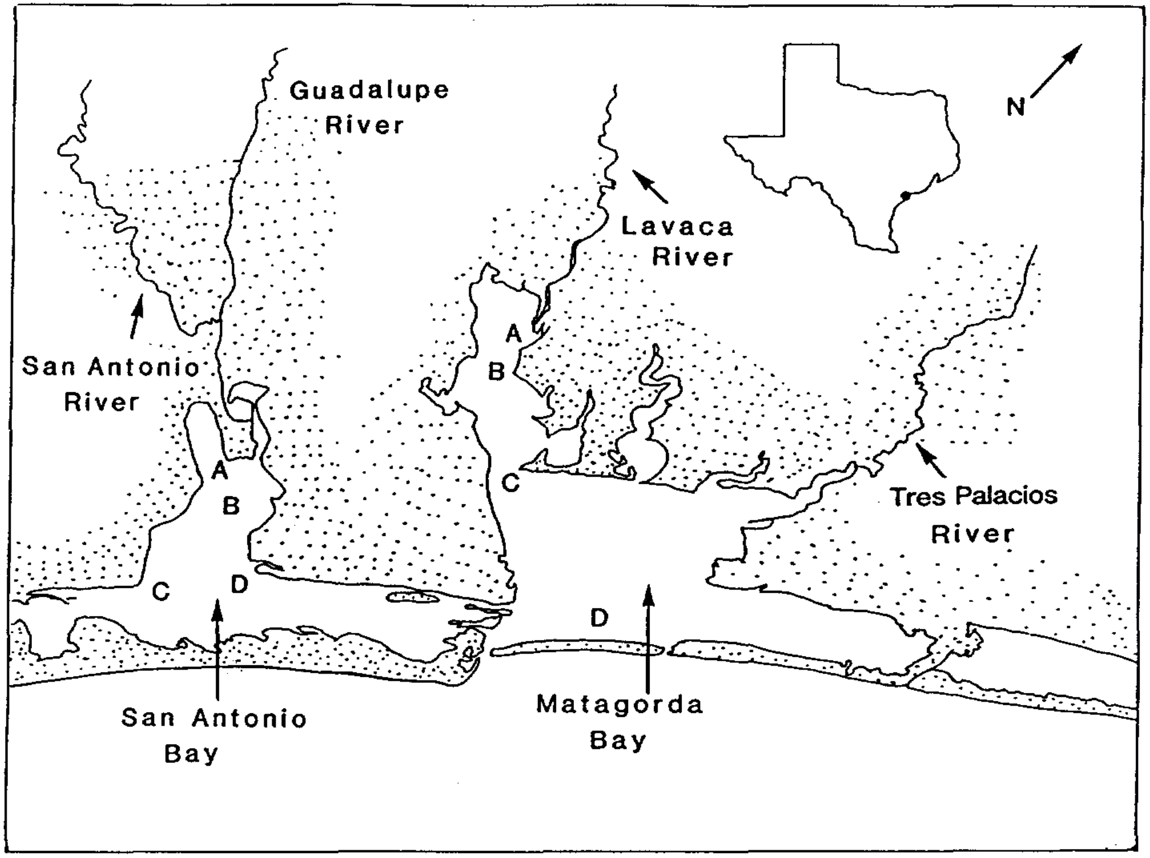


Figure 3. Sampling locations within the Guadalupe and Lavaca-Colorado Estuaries.

near the barrier island. This design avoids pseudoreplication, where only one station has the characteristic of the main effect, and it is not possible to distinguish between station differences and treatment differences.

The Lavaca River empties into Lavaca Bay, which is connected to Matagorda Bay. Matagorda Bay also has freshwater input from the Colorado and Tres Palacios River. Over a 47-year period (1941-1987) the Lavaca-Colorado Estuary received an average of 3.800×10^9 m^3 y^{-1} with a standard deviation of 2.080 m^3 y^{-1} (3.080 ± 1.686 $\times10^6$ ac-ft y^{-1}) of freshwater input, and the freshwater balance (input-output) was 3.392×10^9 m^3 y^{-1} with a standard deviation of 2.345×10^9 m^3 y^{-1} (2.750 ± 1.901 $\times10^6$ ac-ft y^{-1}) (TDWR, 1980a; TWDB unpublished data). Four Stations were occupied along the axis of the system. Two stations were in Lavaca Bay (A and B), and two stations were in Matagorda Bay (C and D) (Figure 3). Depths of stations A, B, C, and D were 1.3 m, 2.0 m, 3.1 m, and 4.2 m, respectively. Five field trips were performed. Station A in Lavaca Bay was the same station 85 sampled in 1984-1986 (Jones et al., 1986).

The San Antonio River joins the Guadalupe River that flows into San Antonio Bay. Over a 46-year period the Guadalupe Estuary received an average of 2.896×10^9 m^3 y^{-1} with a standard deviation of 1.597 m^3 y^{-1} (2.347 ± 1.295 $\times10^6$ ac-ft y^{-1}) of freshwater input, and the freshwater balance (input-output) was 2.624×10^9 m^3 y^{-1} with a standard deviation of 1.722×10^9 m^3 y^{-1} (2.127 ± 1.396 $\times10^6$ ac-ft y^{-1}) (TDWR, 1980b; TWDB unpublished data). This system was studied from January through July 1987. Four stations were occupied: freshwater influenced stations at the head of the bay (station A) and at mid-bay (station B), and two marine influenced stations near the Intracoastal Waterway, one at the southwestern foot of the bay (station C) and one at the southeastern foot of the bay (station D) (Fig. 1). Stations were sampled five times in the first year. All stations were in shallow water. Depths of stations A, B, C, and D were 1.3 m, 1.9 m, 2.0 m, and 1.6 m, respectively.

Hydrographic Measurements

Salinity, conductivity, temperature, pH, dissolved oxygen, and redox potential were measured at the surface and bottom at each station during each sampling trip. Measurements were made by lowering a probe made by Hydrolab Instruments. Salinities levels are automatically corrected to 25°C. The manufacturer states that the accuracy of salinity measurements are 0.1 ppt. When the Hydrolab instrument was not working, water samples were collected from just beneath the surface and from the bottom in jars, and refractometer readings were made at the surface.

Geological Measurements

Sediment grain size analysis was also performed. Sediment core samples were taken by diver and sectioned at depth intervals 0-3 cm and 3-10 cm. Analysis followed standard geologic procedures (Folk, 1964; E. W. Behrens, personal communication). Percent contribution by weight was measured for four components: rubble (e.g. shell hash), sand, silt, and clay. A 20 cm^3 sediment sample was mixed with 50 ml of hydrogen peroxide and 75 ml of deionized water to digest organic material in the sample. The sample was wet sieved through a 62 μm mesh stainless steel screen using a vacuum pump and a Millipore Hydrosol SST filter holder to separate rubble and sand from silt and clay. After drying, the rubble and sand were separated on a 125 μm screen. The silt and clay fractions were measured using pipette analysis.

Chemical Measurements

The vertical distribution of carbon and nitrogen content of sediments was measured in October 1990. One m cores were sectioned every 10 cm. Two replicate cores were taken at each station. The samples were frozen until they were prepared for analysis. Sediments were prepared for analysis of total carbon and nitrogen by drying at 50 °C for 24 h, after which they were ground into a fine powder with a mortar and pestle. A Perkin-Elmer 240B elemental analyzer was used for sample analysis. Sample sizes of about 120 mg for sediments were necessary for adequate detection of carbon.

Quality control was determined by running a blank, and standards at the beginning and ending of each days measurements. Blank values were used to determine the validity of the days runs. If blanks were too high, then the data were rejected. Caffeine was used as the standard. Over all runs, the average measured carbon value was 50.98% (± 2.14 SD), and the average nitrogen value was 31.23% (± 1.22). Indicating the precision for replicate measurements (i.e., the coefficient of variation) was ± 4.2% for carbon and ± 3.9% for nitrogen. The true values are 49.48% for carbon and 28.85% for nitrogen. Indicating the accuracy (calculated as 100×[observed-true]/true) was ± 3.3% for carbon and ± 8.2% for nitrogen.

Biological Measurements

Sediment was sampled with core tubes held by divers. The macrofauna were sampled with a tube 6.7 cm in diameter, and sectioned at depth intervals of 0-3 cm and 3-10 cm. Three replicates were taken within a 2 m radius. Samples were preserved with

5% buffered formalin, sieved on 0.5 mm mesh screens, sorted, identified, and counted.

Each macrofauna sample was also used to measure biomass. Individuals were combined into higher taxa categories, i.e., Crustacea, Mollusca, Polychaeta, Ophiuroidea, and all other taxa were placed together in one remaining sample. Samples were dried for 24 h at 55 °C, and weighed. Before drying, mollusks were placed in 1 N HCl for 1 min to 8 h to dissolve the carbonate shells, and washed with fresh water.

Statistical Analyses

Statistical analyses to reveal differences among cruises, stations and sediment depths were performed using general linear model procedures (SAS, 1985). Two-way analysis of variance (ANOVA) models were used where sampling dates and stations were the two main effects. Tukey multiple comparison procedures were used to find *a posteriori* differences among sample means (Kirk, 1982). Multivariate ANOVA was used to test for treatment effects on species data. Factor analysis and cluster analysis was used to determine if communities were similar on different sampling dates. Linear correlation coefficients were calculated to determine if salinity was correlated to macrofauna abundance, biomass or diversity. Diversity is calculated using Hill's diversity number one (N1) (Hill, 1973). It is a measure of the effective number of species in a sample, and indicates the number of abundant species. It is calculated as the exponentiated form of the Shannon diversity index:

$$N1 = eH' \tag{1}$$

The Shannon index is the average uncertainty per species in an infinite community made up of species with known proportional abundances (Shannon and Weaver, 1949). The Shannon index is calculated by:

$$H' = -\sum_{i=1}^{S}\left[\left(\frac{n_i}{n}\right)\ln\left(\frac{n_i}{n}\right)\right] \tag{2}$$

Where n_i is the number of individuals belonging to the ith of S species in the sample and n is the total number of individuals in the sample.

RESULTS

There is a linear decrease in average annual freshwater inflow from north to south along the Texas coast (one-way ANOVA, *P* = 0.0001, Figure 2). The Lavaca-Colorado and Guadalupe Estuaries have the same average inflow (linear contrast, *P* = 0.3333, Figure 2). Lavaca-Colorado and Guadalupe Estuaries are very different in certain respects. The Lavaca-Colorado is much larger, receives drainage from three rivers, has a typical primary and secondary bay configuration, and has excellent exchange with the Gulf of Mexico (Figure 3). The Guadalupe has restricted Gulf exchange and is composed of a single bay. The impact of human activities is very different also. The Guadalupe receives drainage from the San Antonio River, which passes through a major metropolitan area, yet San Antonio Bay is very rural. The Lavaca-Colorado watershed is mostly rural, but Lavaca Bay is heavily impacted by channels, ship traffic, and the chemical industry. I must use salinity as an indicator of freshwater inflow. Assessments of freshwater inflow into the Guadalupe and Lavaca-Colorado do not extend beyond 1988.

Guadalupe Estuary

Since 1987, the Guadalupe has gone through three different phases (Figure 4, Table 1). There was a great flood in the spring of 1987. In the summer of 1987, even the stations located in the zone of greatest marine influence had salinities of near zero. A two year drought followed that period. During the drought salinities rose to 20-30 ppt throughout the estuary. The period since April 1990 has been one of fluctuations. Salinities in the upper part of the estuary dropped to near zero during spring floods, but the salinities at the lower end of the estuary, only dropped to the 6-12 range. The period during the spring of 1991 looks a lot like the period prior to the flood of the spring of 1987.

The sediments of the upper part of the estuary are characterized by high silt and clay contents (Figure 5, Table 2). Only station D sediments were dominated by sand. Rubble was common in deep sediments from A, and shallow sediments in C. Correlated with the high sand content, station D had the lowest carbon (Figure 6) and nitrogen (Figure 7) contents of all stations (Table 3). There was considerably more carbon throughout the top m of sediment in stations A and B than in C and D. Nitrogen content was higher in A and B only in the top 40 cm.

Macrofauna abundance (Figure 8) and biomass (Figure 9) are generally higher in stations A and B in the upper end of the estuary than in stations C and D in the lower end of the estuary (linear contrast, *P*=0.0001 for both). The average density (in units of individuals • m^{-2}) over the entire study period was 44,512 at A, 35,318 at B, 17,474 at D, and 15,629 at C (Table 4). The average biomass (in units of g • m^{-2}) during the entire study period was 9.47 at A, 6.95 at B, 5.41 at D and 3.06 at C. An exception to the generality is biomass in station D when rare, but large, ophiuroids are present (Figure 9). There were large year-to-year fluctuations in both parameters during the course of the study, but in general, the station pairs changed in similar ways.

Average estuarine-wide salinity was plotted with average estuarine-wide abundance (Figure 10), average estuarine-wide biomass (Figure 11), and average estuarine-wide diversity (Figure 12) to determine the relationship between freshwater inflow and biological response. Over time, biomass was significantly correlated with changes in salinity ($r=0.59$, $P=0.0164$), but abundance was not ($r=0.32$, $P=0.2277$). However, simple correlation does not explain the response completely. The highest abundance, over 90,000•m^{-2}, occurred in 1988, following the flood of 1987. Density dropped with sustained high salinities during 1989 and 1990. Biomass also increased to peak levels after the flood of 1987, and was declining during the drought of 1989-1990. Together, these data suggest that periodic flooding, and resulting nutrient enrichment are required to maintain a productive benthic ecosystem. Hill's diversity index was highly correlated with salinity ($r=0.71$, $P=0.0020$). Diversity is most affected when there are floods. During floods diversity drops to very low levels. The lower diversity is probably resulting from displacement of marine species with freshwater species. There are fewer species present in the upper reaches of the estuary than in the lower reaches (Table 5). There appears to be a succession of species groups through time. The first two factors in a factor analysis of sampling dates accounts for 77% of the variability in the species dataset. The first factor appears to be related to suites of freshwater species since the dates during the flood of 1987 are separated from other groups along that axis (Figure 13). Marine conditions prevailed from July 1988 to July 1989 and these dates separate along the axis of the second factor, indicating the second factor is related to a suite of marine species. January 1987 also separates as a marine period. Transitional periods are in the center of the factor analysis. A cluster analysis shows a similar trend (Figure 14). In the cluster analysis dates from March 1987 to December 1989 separate from later dates, suggesting that succession to marine conditions were complete to that date. January 1987 separates out with the latter dates, since marine conditions prevailed prior to the 1987 flood.

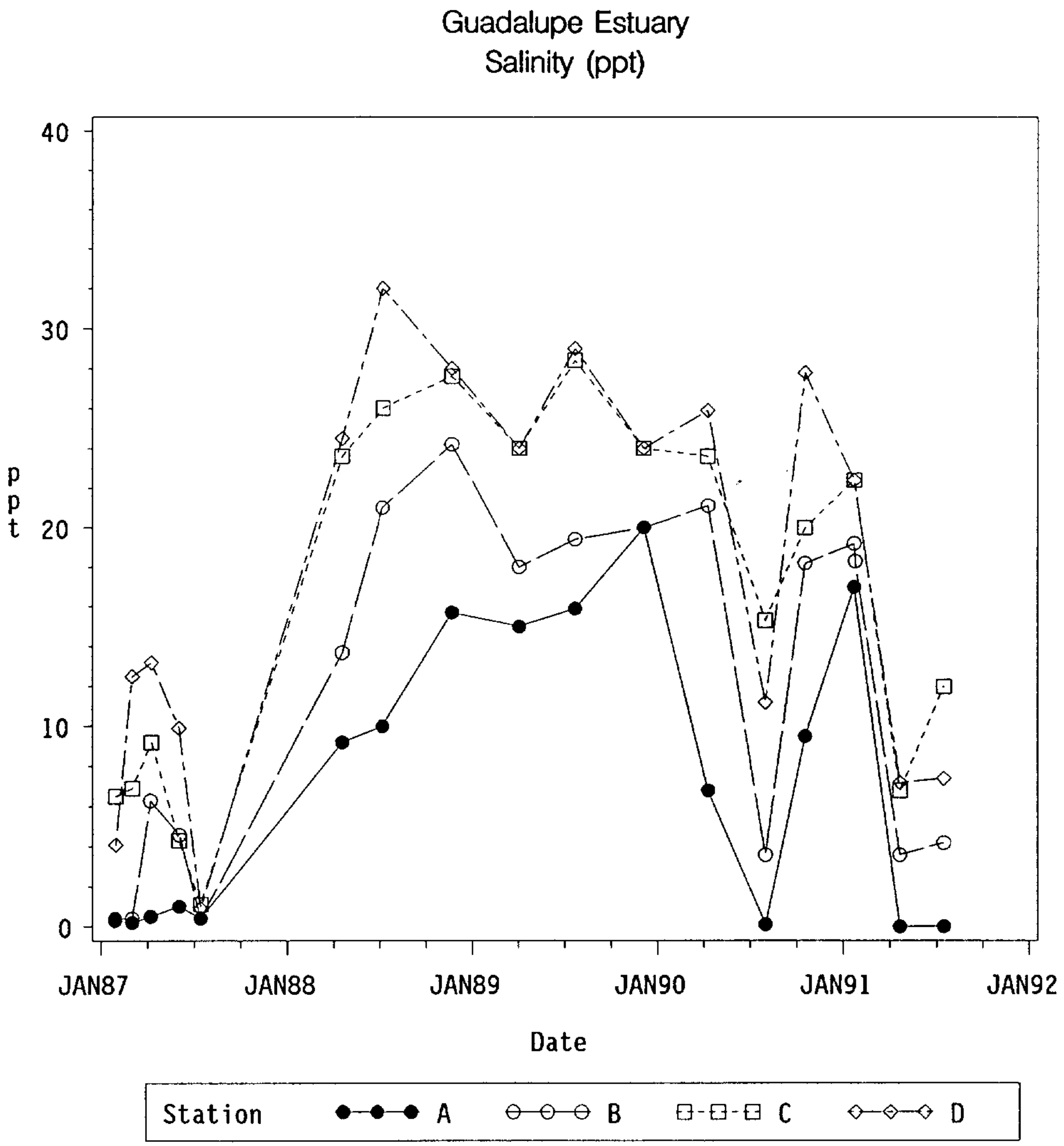
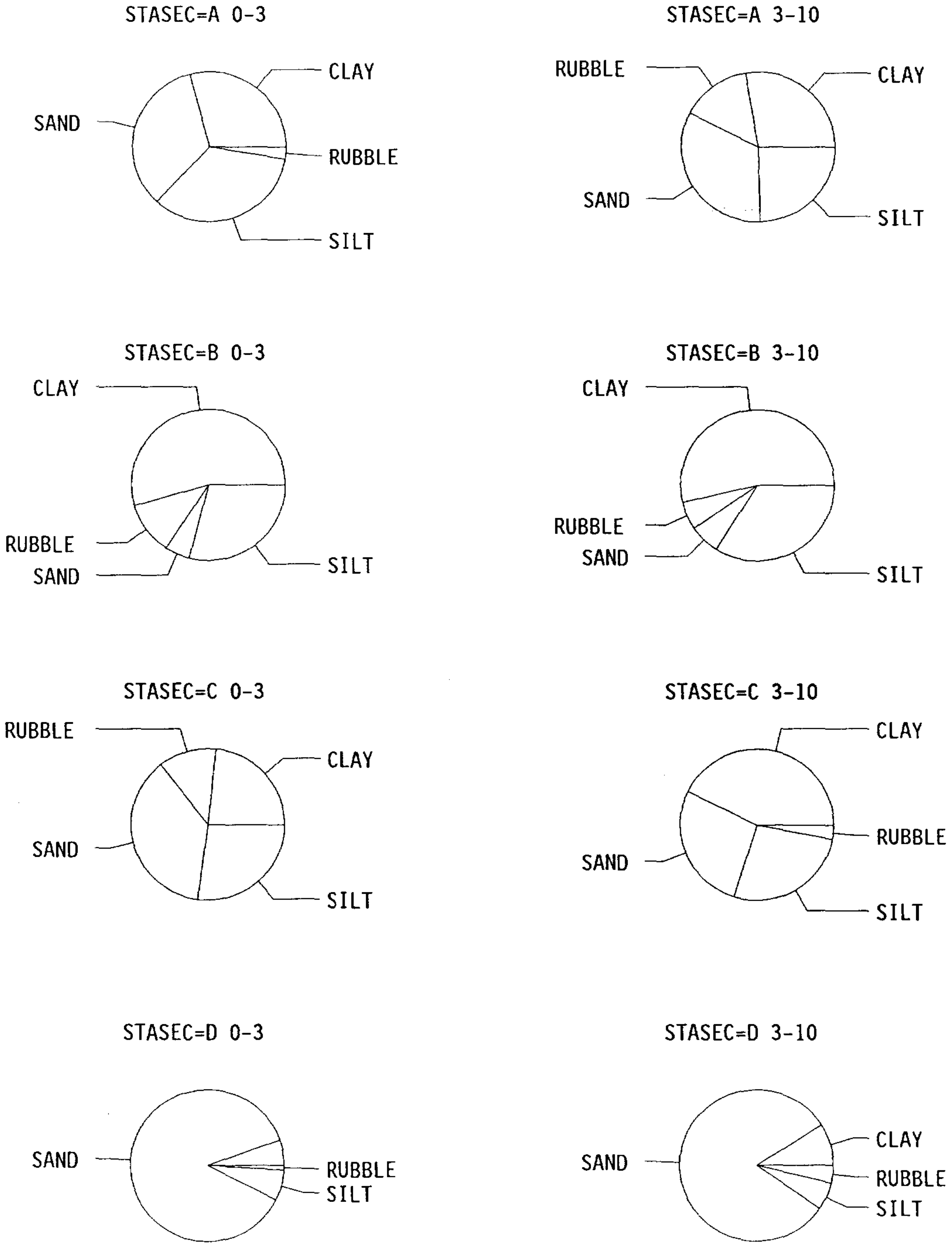


Figure 4. Bottom water salinity at four stations in the Guadalupe Estuary.

Figure 5. Sediment grain size in the Guadalupe Estuary. Samples taken in October 1990. STASEC=Station, vertical section combination. Section in cm.

Guadalupe Estuary Sediment Composition (% dry weight)



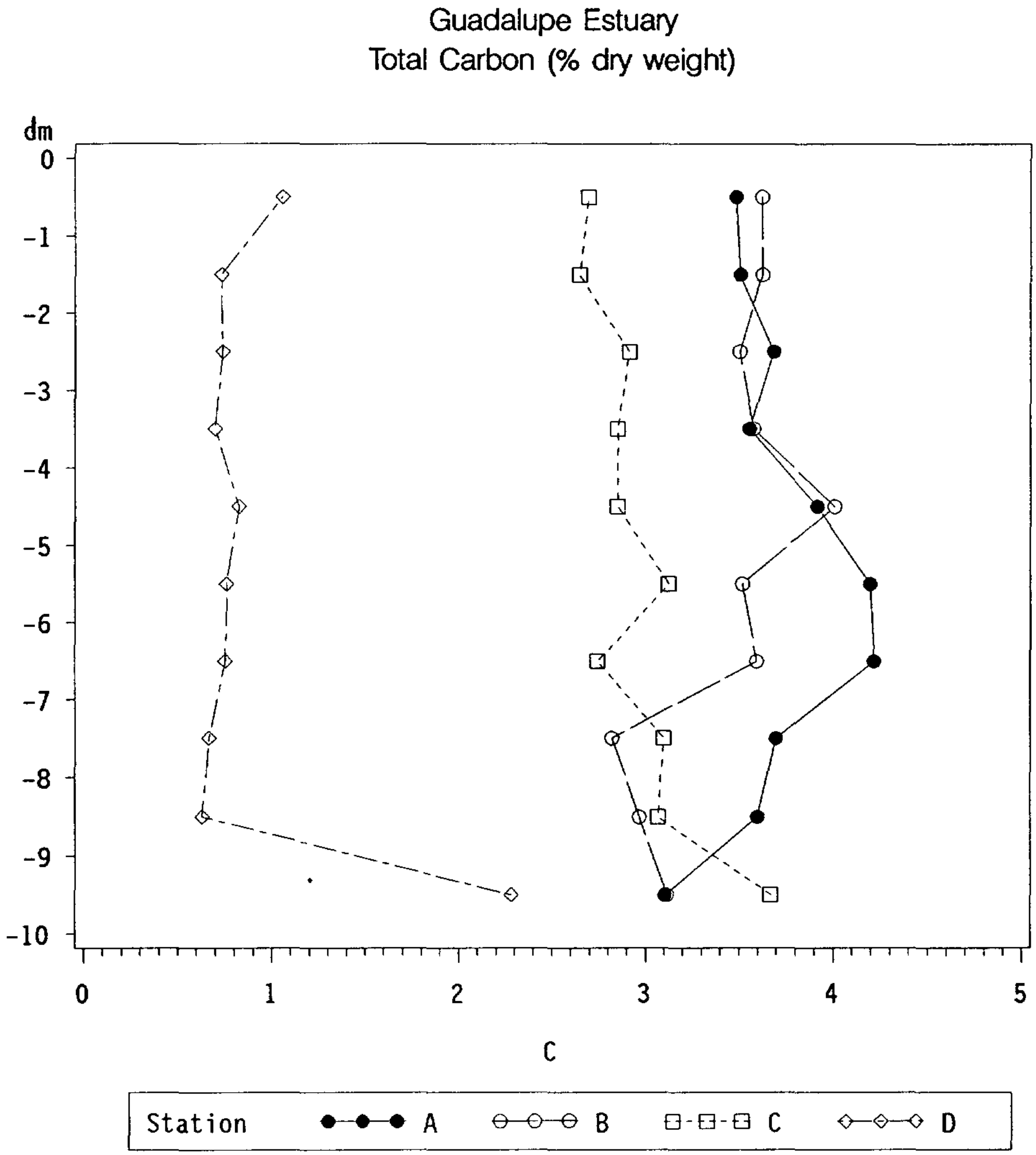


Figure 6. Vertical distribution of carbon in sediments from the Guadalupe Estuary. Samples taken October 1990 at 10 cm intervals, average of $n=2$, 1 dm = 10 cm.

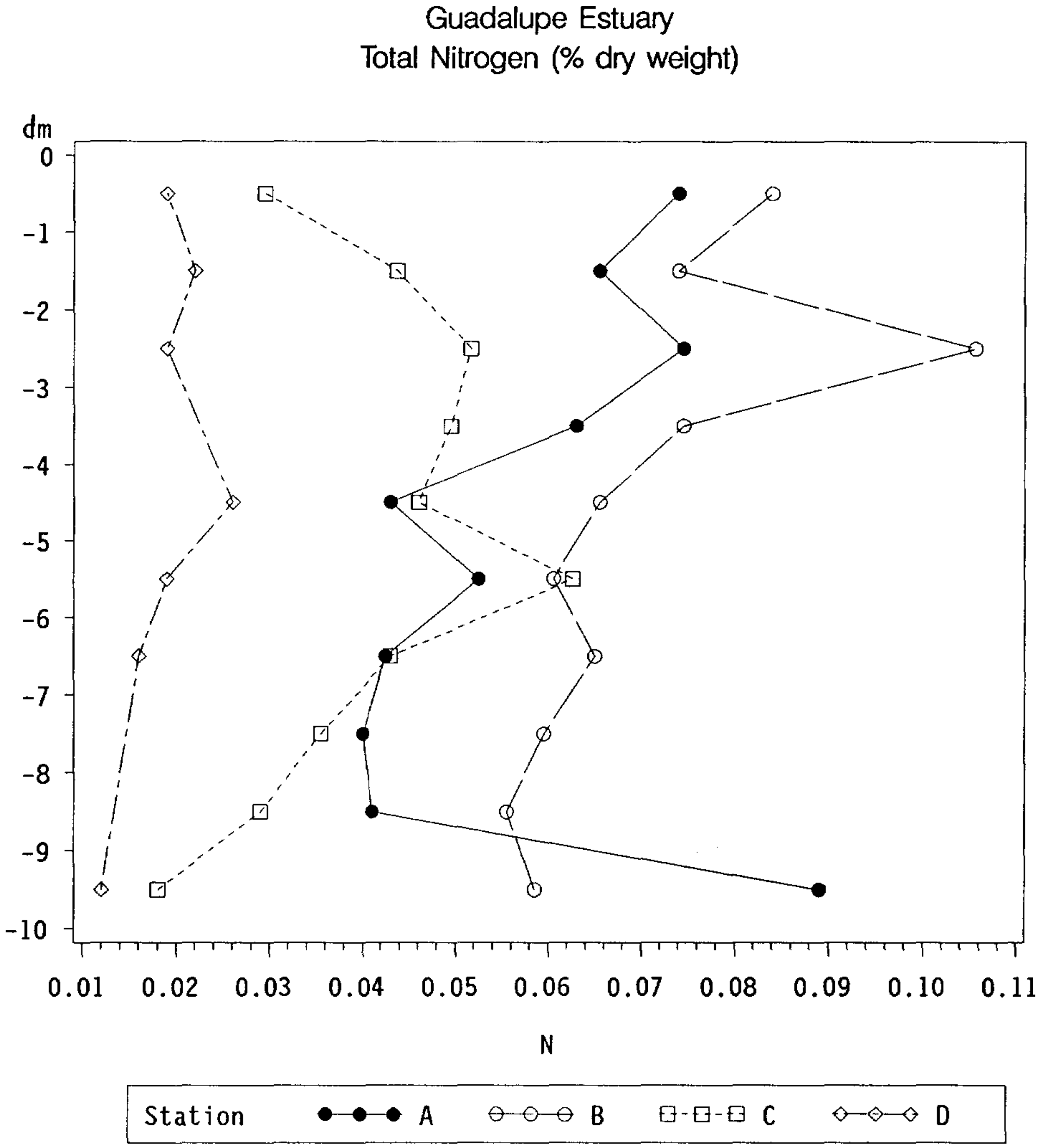


Figure 7. Vertical distribution of nitrogen in sediments from the Guadalupe Estuary. Samples taken in October 1990 at 10 cm intervals. 1 dm = 10 cm.

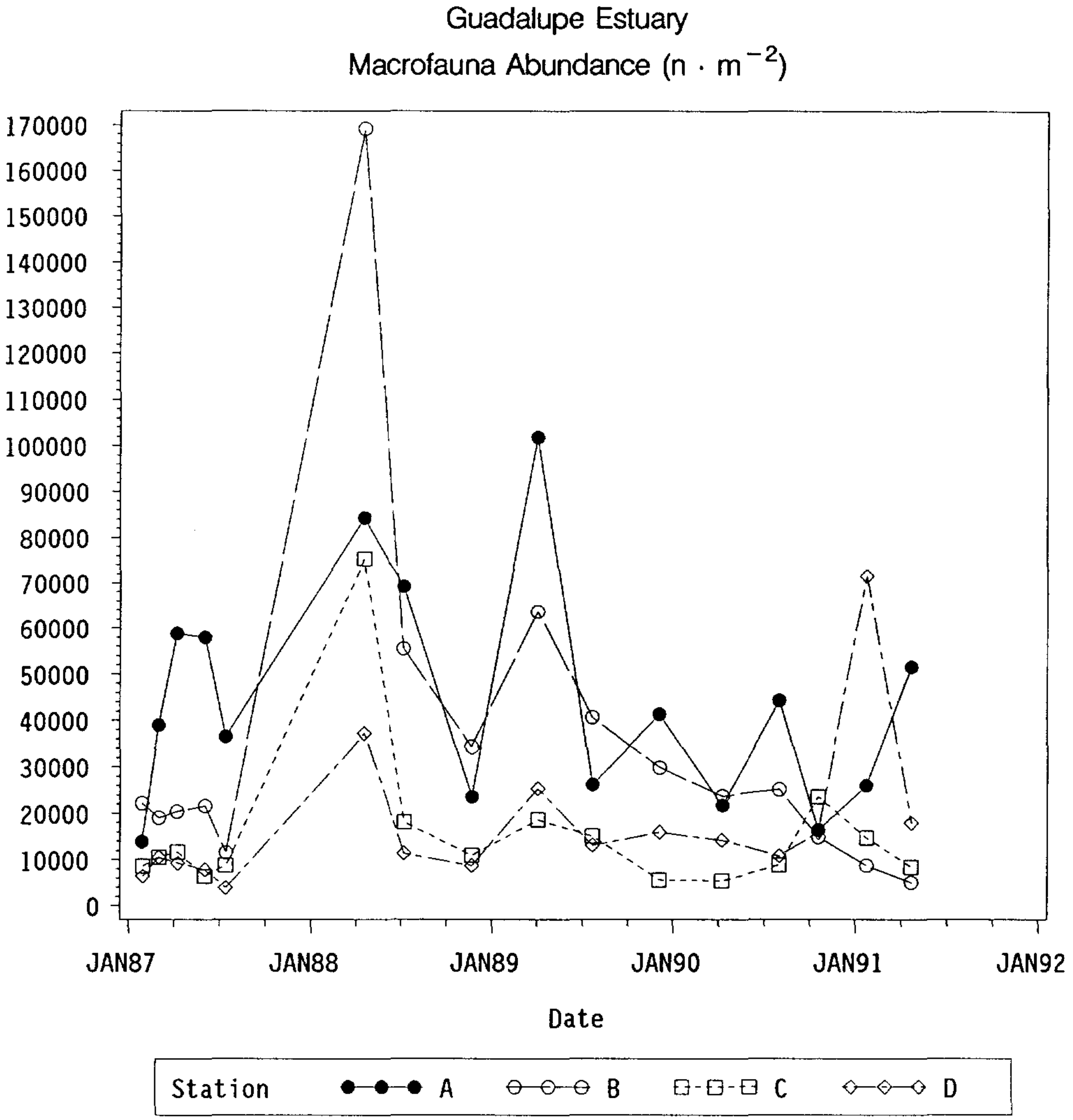


Figure 8. Macrofauna abundance at four stations in the Guadalupe Estuary. Samples taken to a depth of 10 cm, average of *n*=3.

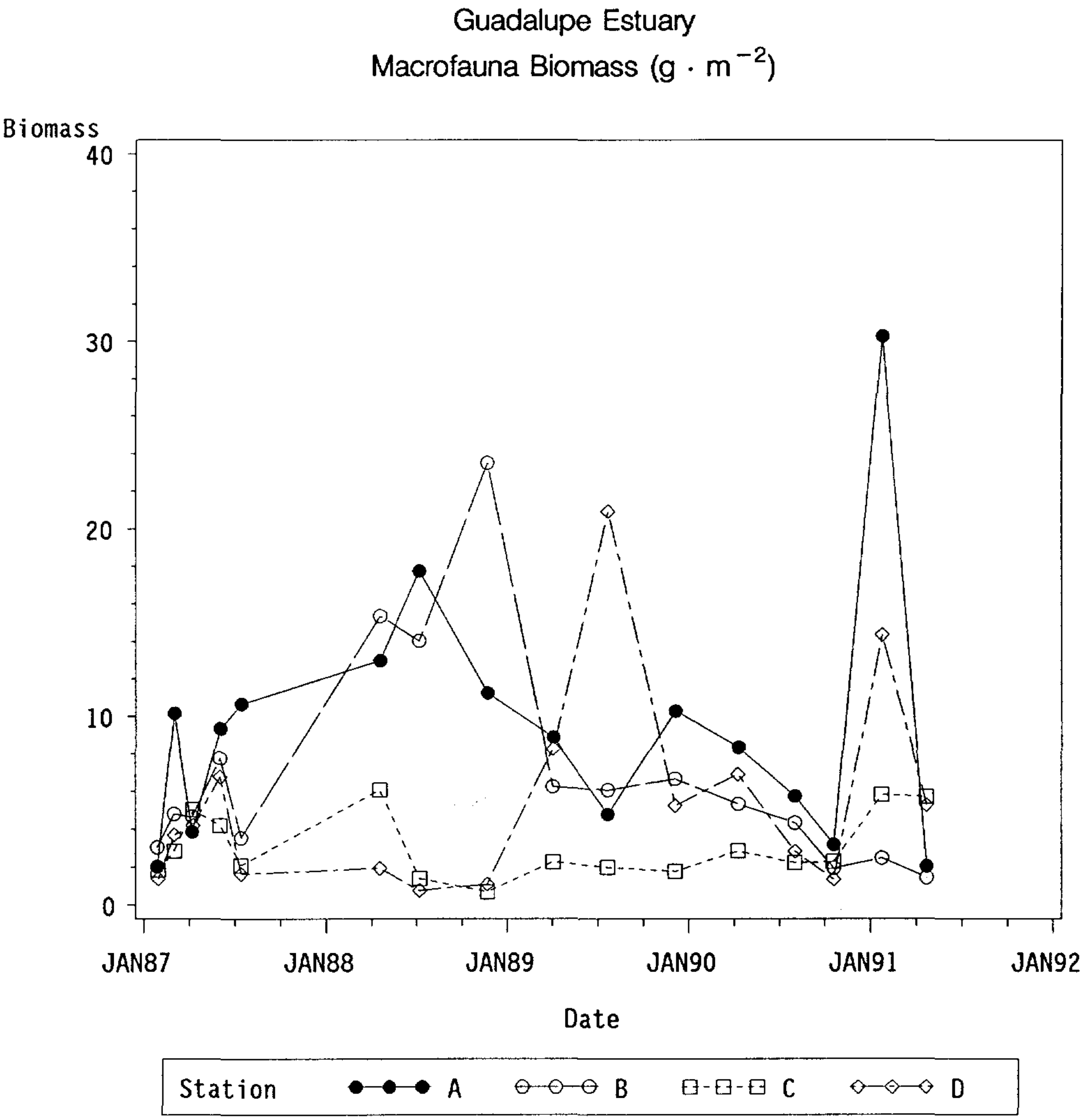


Figure 9. Macrofauna biomass at four stations in the Guadalupe Estuary. Samples taken to a depth of 10 cm, average of *n*=3.

Guadalupe Estuary

Macrofauna Abundance ($n \cdot m^{-2}$) and Salinity (ppt)

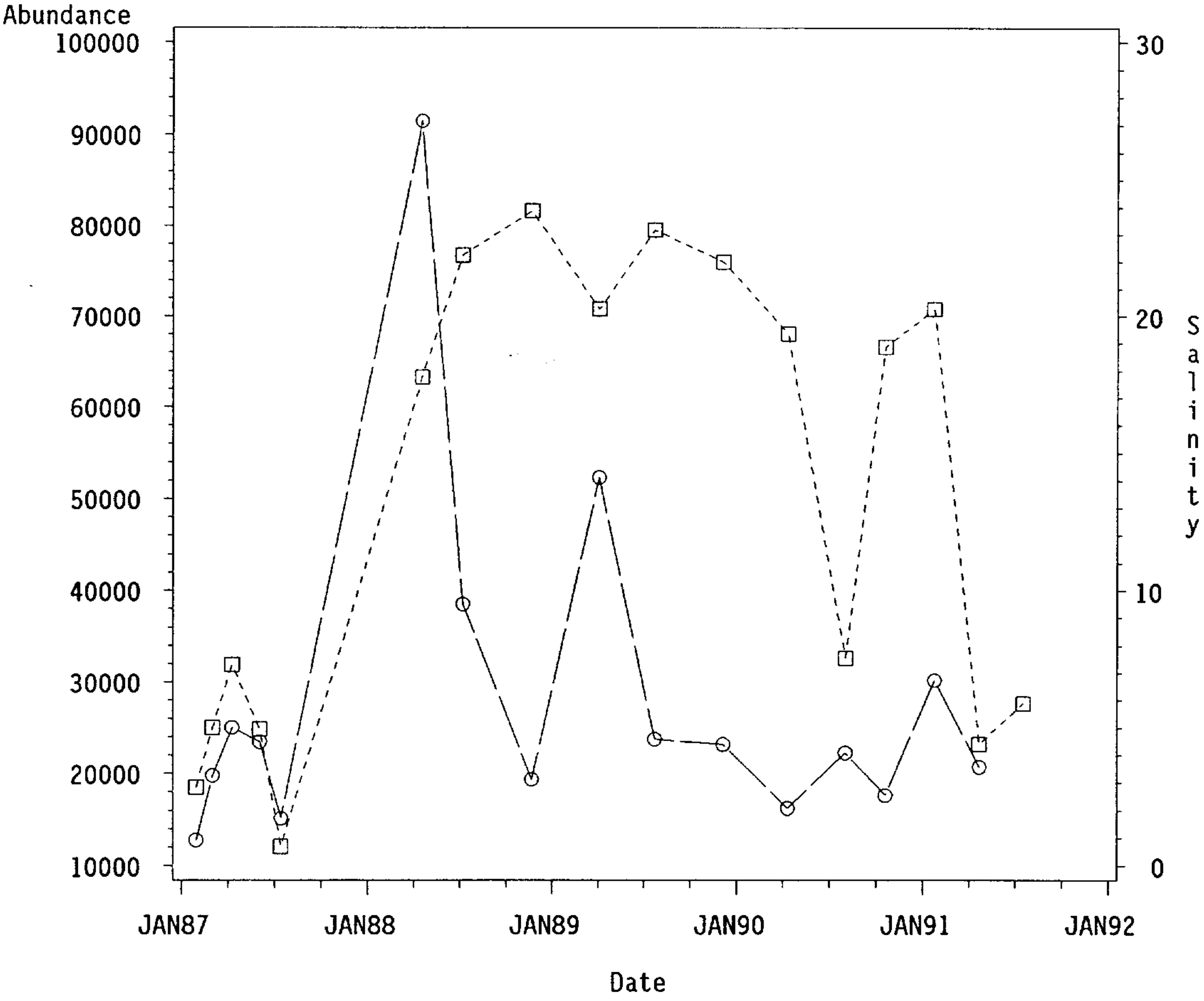


Figure 10. Relationships between macrofauna abundance (○) and salinity (□) in the Guadalupe Estuary. Average abundance and salinity at all stations.

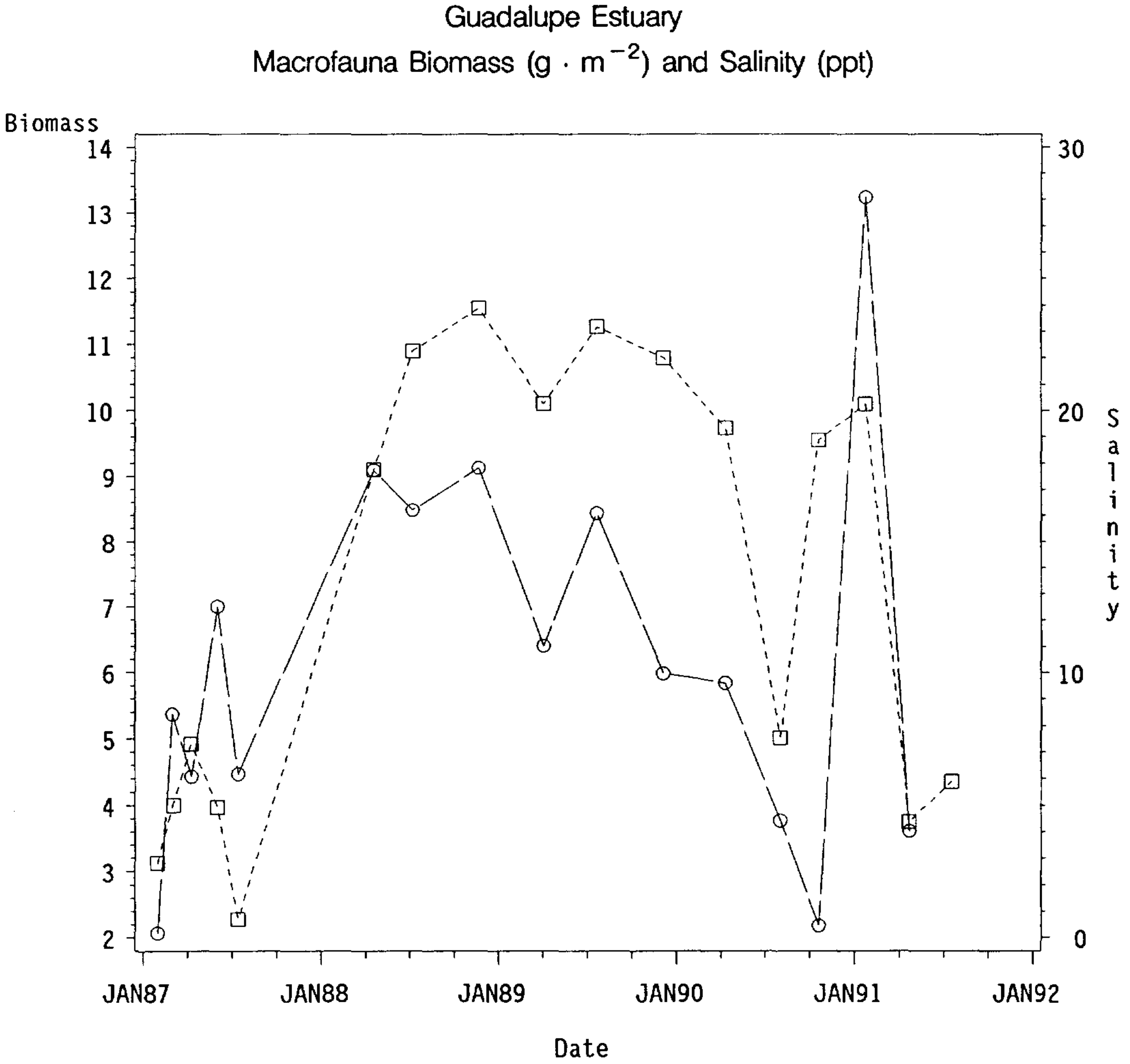


Figure 11. Relationships between macrofauna biomass (○) and salinity (□) in the Guadalupe Estuary. Average biomass and salinity at all stations.

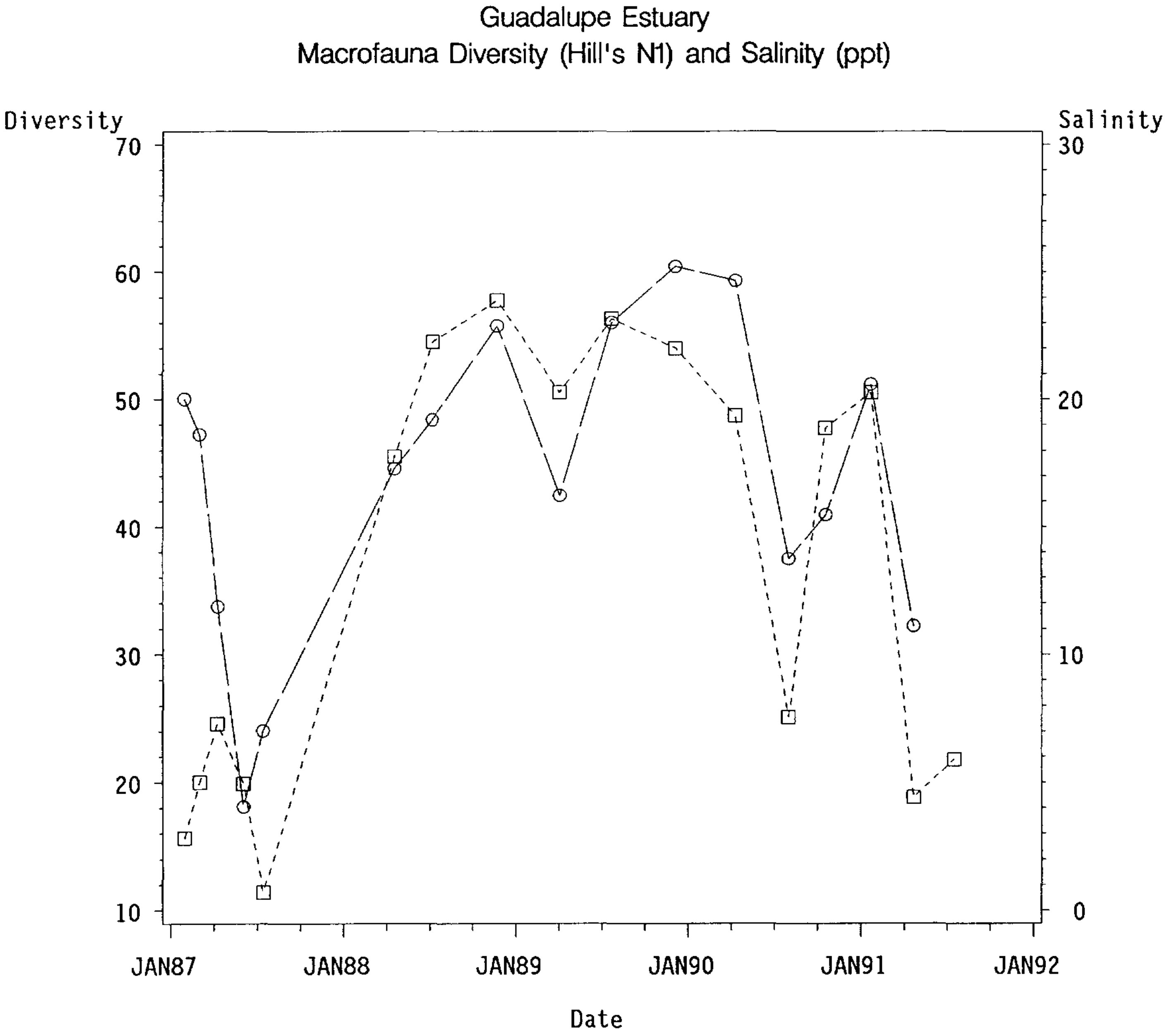
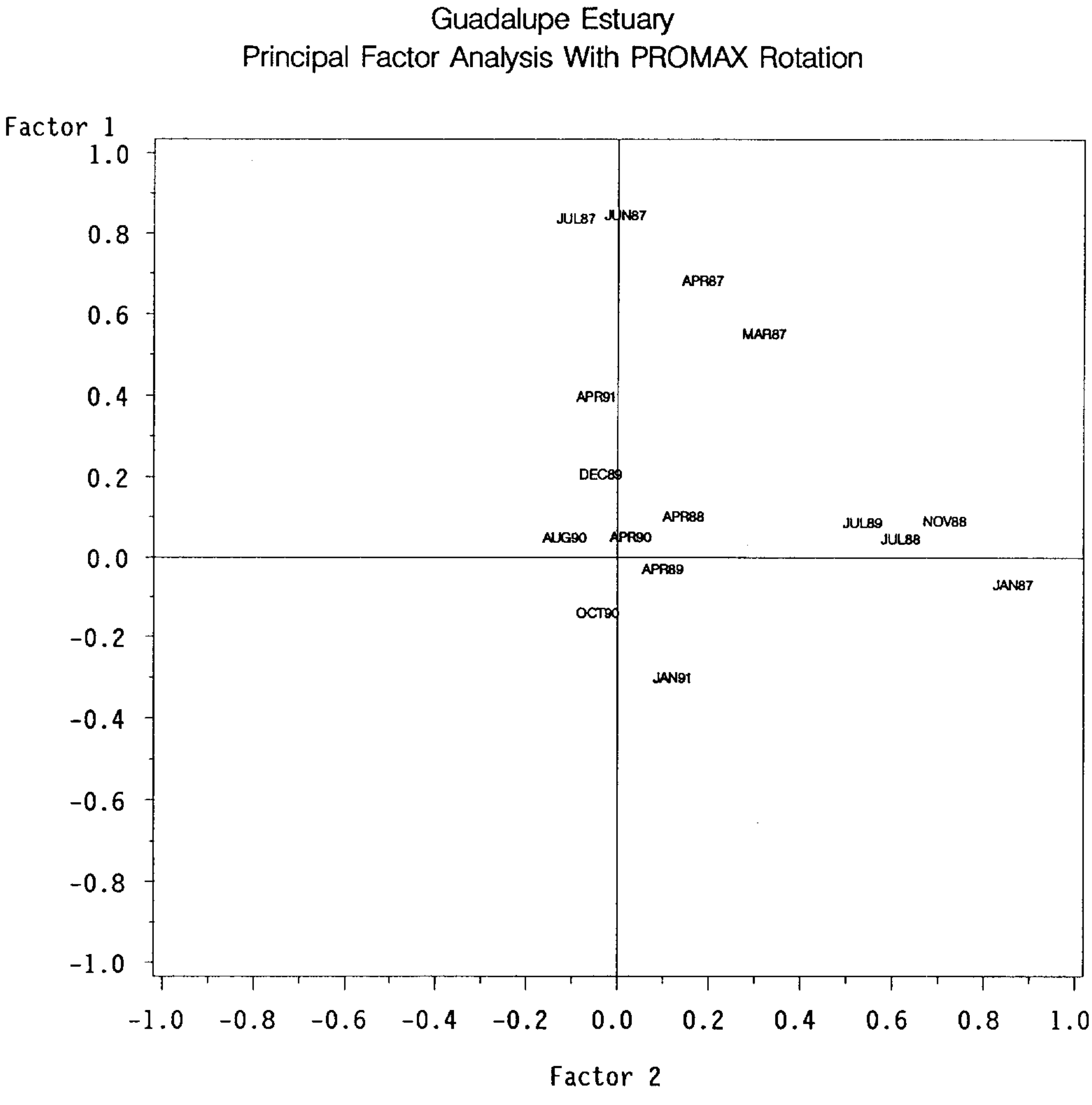


Figure 12. Relationships between macrofauna diversity (○) and salinity (□) in the Guadalupe Estuary. Average diversity and salinity at all stations.

Figure 13. Factor analysis for macrofauna species at all sampling dates in the Guadalupe Estuary. Species occurring at all stations for a given date.



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DISTANCE METRIC IS EUCLIDEAN DISTANCE
SINGLE LINKAGE METHOD (NEAREST NEIGHBOR)

TREE DIAGRAM
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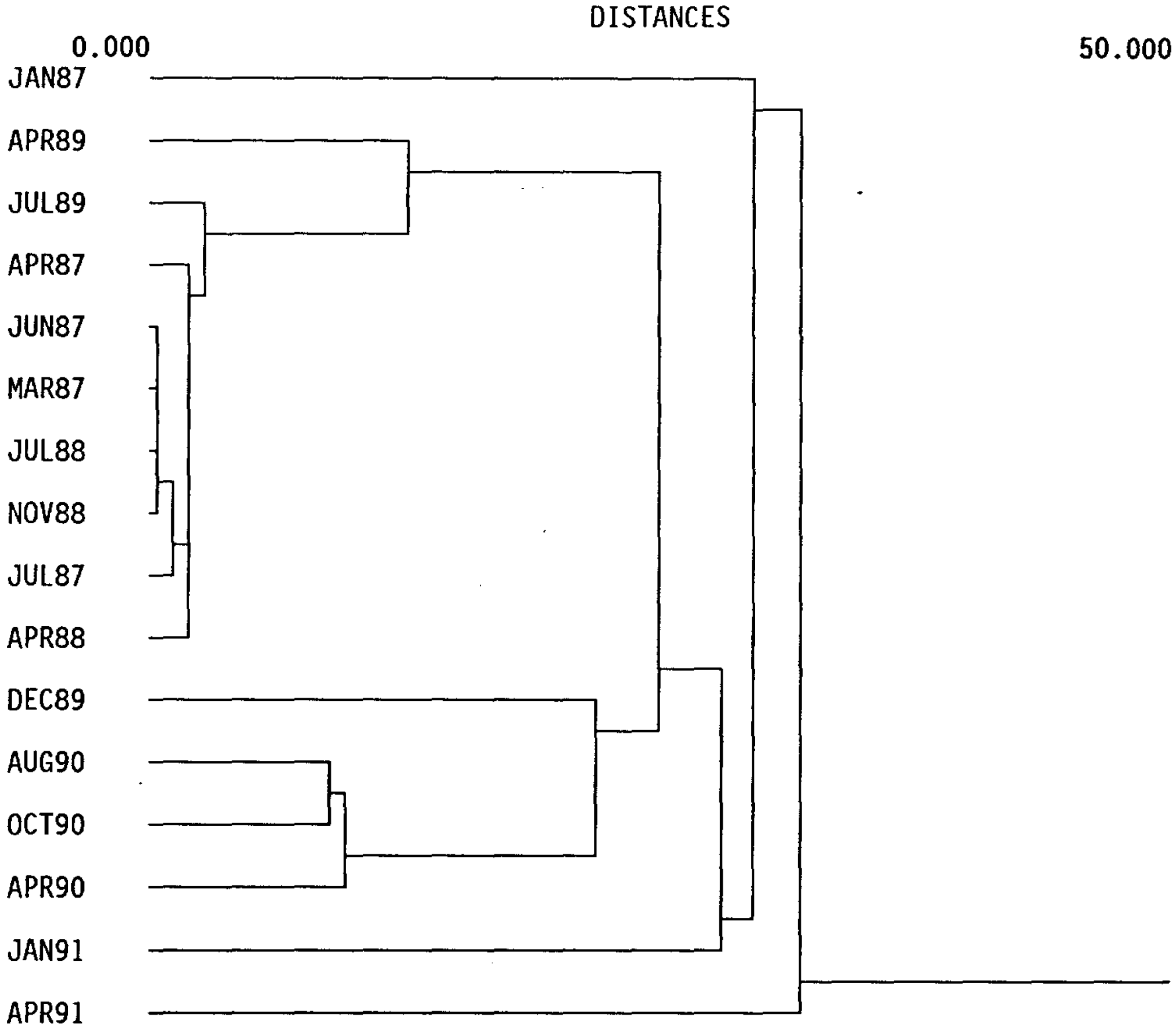


Figure 14. Cluster analysis of sampling dates for Guadalupe Estuary. Distance metric is euclidean distance single, linkage method (nearest neighbor)

Lavaca-Colorado Estuary

Station A was also studied during 1984-1986, and called station 85 in previous studies (Kalke and Montagna, 1991). Unfortunately, my record is incomplete during 1987, so we can not look at the effect of the spring flood in the Lavaca-Colorado Estuary (Table 6). However, the period between 1984 and 1985 was a very wet period indicated by low salinities in station A (Figure 15). 1986 to early 1987 was dry, and similar to the recent period from April 1990 to the present. 1988 through 1989 was the highest salinity period recorded.

The sediments of the upper part of the estuary are characterized by high silt and clay contents (Figure 16, Table 2). Station C sediments were dominated by rubble and sand. Sand, silt and clay are equally abundant at station D. Rubble was common in sediments from C. Correlated with the high sand content, station D had the lowest carbon (Figure 17) and nitrogen (Figure 18) contents of all stations (Table 3). The patterns of carbon content throughout the top m of sediment were different in the two parts of the estuary. Carbon was higher in the top 30 cm at stations C and D, but relatively uniform through the to m of sediment at stations A and B. Nitrogen content was higher in A and B than in C and D, but only in the top 50 cm.

Macrofauna abundance (Figure 19) and biomass (Figure 20) are generally higher in stations C and D in the lower end of the estuary than in stations A and B in the upper end of the estuary (linear contrast, $P=0.0001$ for both). The average density (in units of individuals $\cdot$ m^{-2}) over the entire study period was 10,347 at A, 10,012 at B, 20,909 at D, and 30,689 at C (Table 7). The average biomass (in units of g $\cdot$ m^{-2}) during the entire study period was 2.42 at A, 3.47 at B, 12.71 at C, and 19.22 at D. There were large year-to-year fluctuations in both parameters during the course of the study, but in general, the station pairs were changed in similar ways. There were more polychaete and crustacean species in the lower part of the estuary (stations C and D) than in the upper part of the estuary (stations A and B) (Table 8).

Average estuarine-wide salinity was plotted with average estuarine-wide abundance (Figure 21), average estuarine-wide biomass (Figure 22), and average estuarine-wide diversity (Figure 23) to determine the relationship between freshwater inflow and biological response. Although, both abundance and biomass seem to respond to salinity patterns over time, neither abundance ($r=0.19$, $P=0.5782$), nor biomass ($r=-0.04$, $P=0.8997$) was significantly correlated with changes in salinity. The lack of correlation is due to the period between April and July 1988. After that period, downward trends in salinity relate to downward trend in abundance and biomass. Hill's diversity index was also not correlated with salinity ($r=-0.40$, $P=0.2256$). Diversity seemed to be most affected by seasonal swings. There appears to be a succession of species groups through time. The first two factors in a factor analysis of sampling dates accounts for 91% of the variability in the species dataset. The first factor appears to be related to suites of species during the period between April 1988 July 1989 (Figure 24). The second factor is related to the community present from December 1989 to present. This latter period has been fresher than the preceding period. A cluster analysis shows a slightly different trend (Figure 25). In the cluster analysis dates April 1988 and July 1988 are sharply separated from one another. April 1988 is very different from all other communities.

Lavaca-Colorado Estuary Station A

Since station A was studied from 1984, we can look at the data from that station alone to try and discern long-term trends. Unfortunately, there was a 20-month break in records from August 1986 through April 1988. Biomass was measured differently during the 1984-1986 study, so we can only compare abundance and diversity with the current dataset. The trends are more clear in the long-term data set. Abundance and salinity were low from 1984 to 1986, they both increased from 1986 to 1987, were uniformly high from 1988 to 1990, and both declined in 1991 (Figure 26). Diversity exhibited the same trend (Figure 27). Within these general trends, small fluctuations are also obvious. During the height of the 1988 drought, both abundance and diversity dropped. This analysis confirms two ideas in the present study, that trends are only obvious over long periods of time, and that floods and droughts are both perturbations.

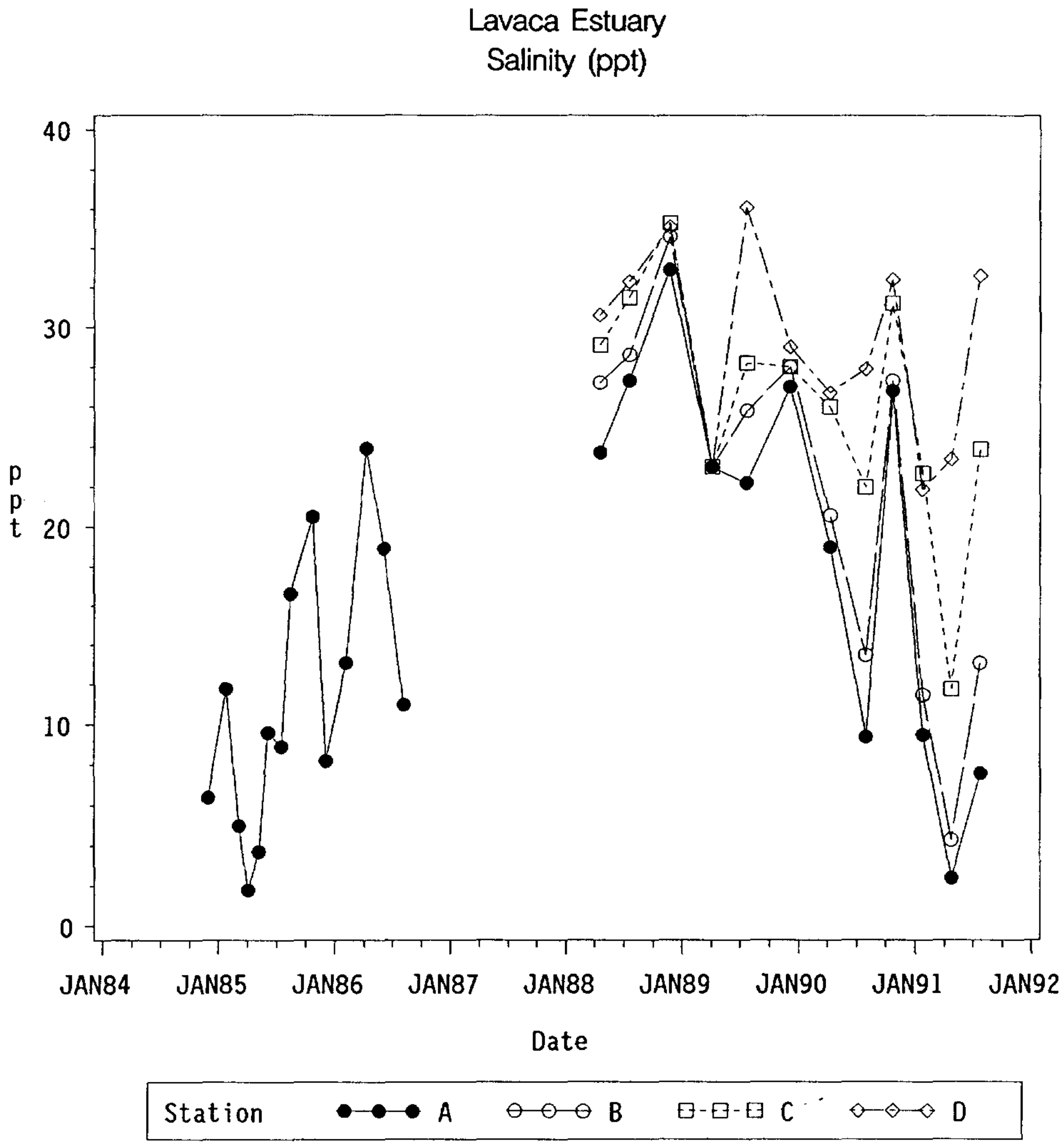
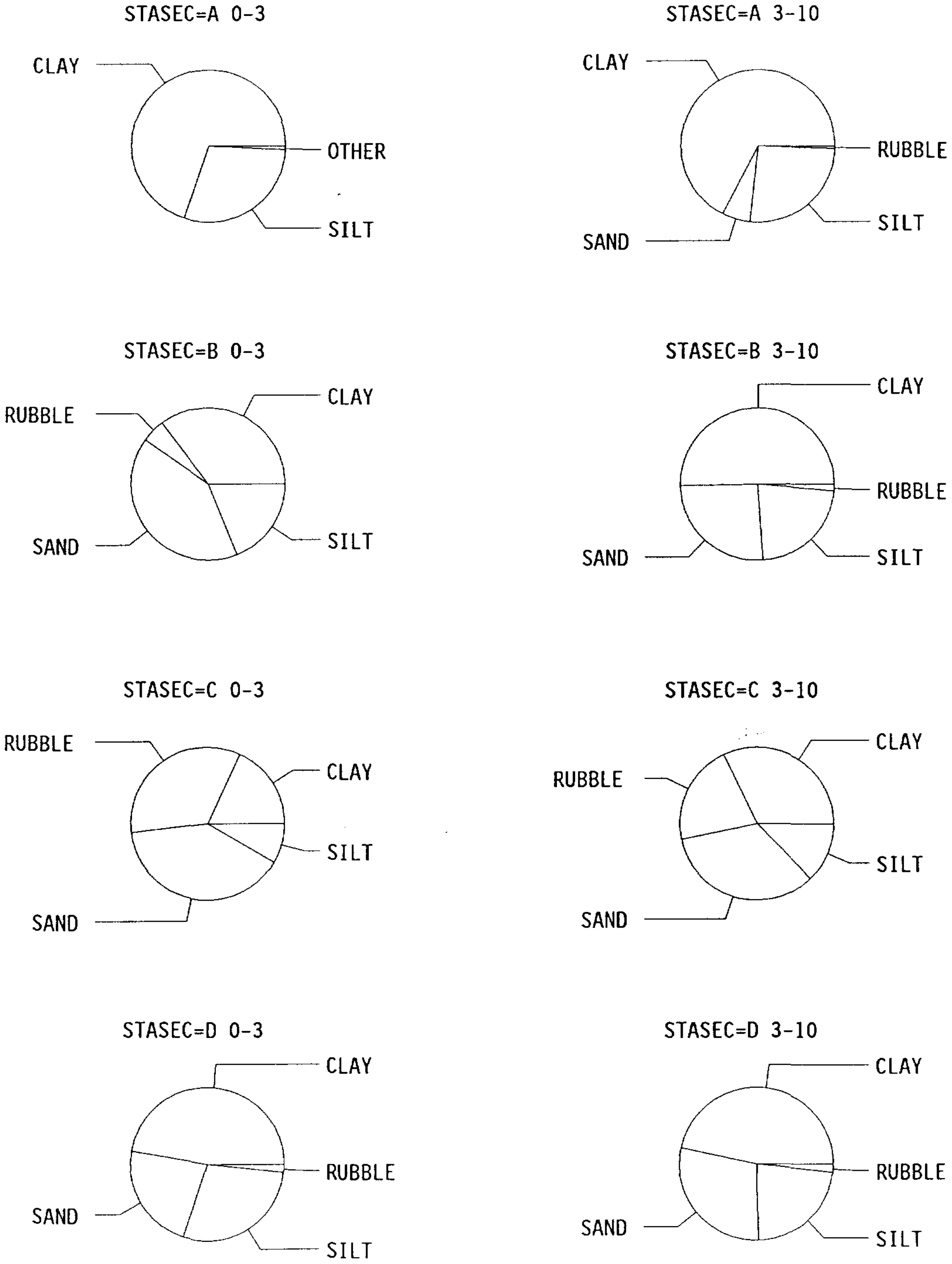


Figure 15. Bottom water salinity at four stations in the Lavaca-Colorado Estuary.

Figure 16. Sediment grain size in the Lavaca-Colorado Estuary. Samples taken in October 1990. STASEC=Station, vertical section combination. Section in cm.

Lavaca – Colorado Estuary Sediment Composition (% dry weight)



STASEC=A 0-3

STASEC=A 3-10

STASEC=B 0-3

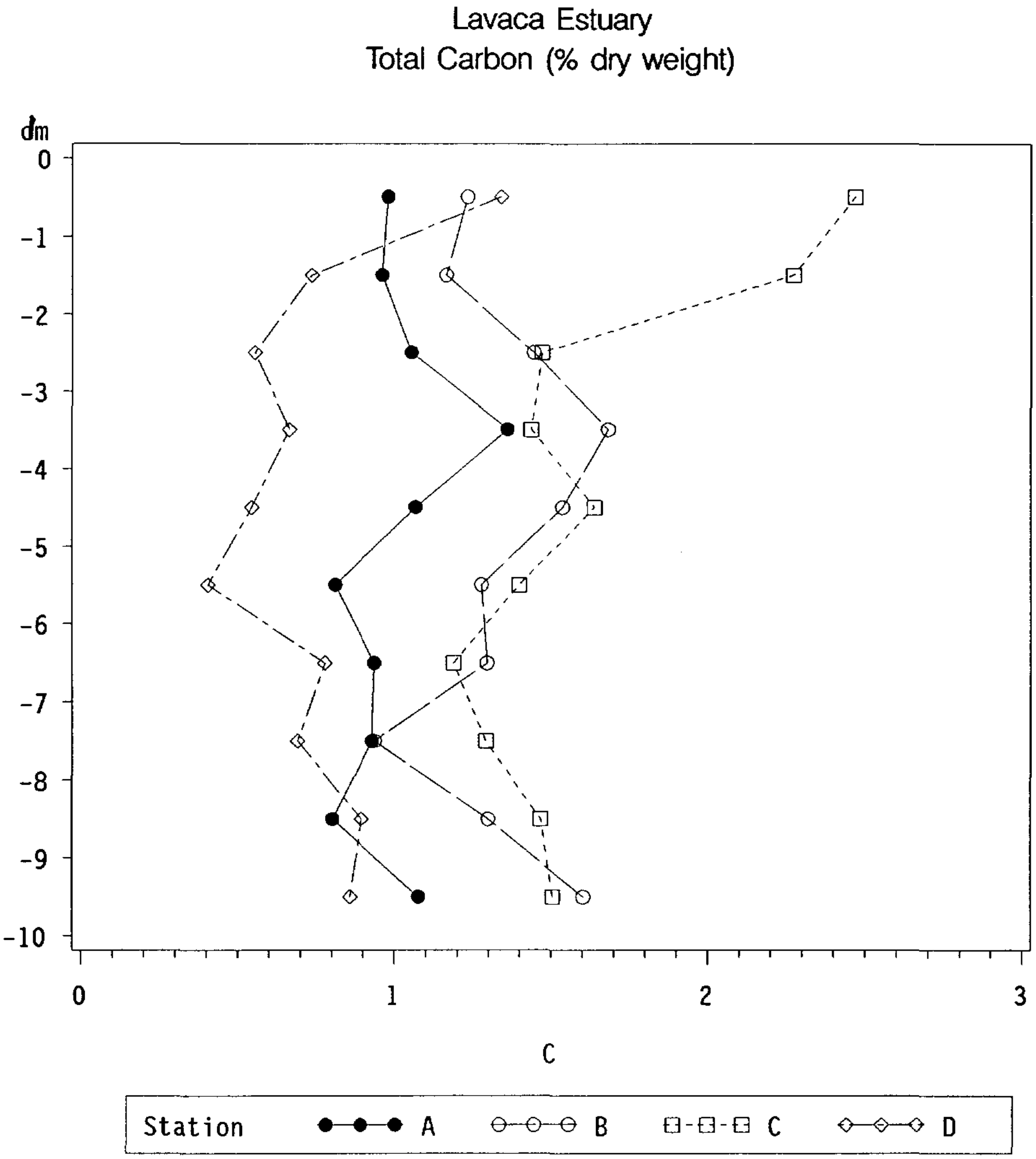
STASEC=B 3-10

STASEC=C 0-3

STASEC=C 3-10

STASEC=D 0-3

STASEC=D 3-10



Lavaca Estuary
Total Carbon (% dry weight)

Figure 17. Vertical distribution of carbon in sediments from the Lavaca-Colorado Estuary. Samples taken October 1990 at 10 cm intervals, $n=2$, 1 dm=10 cm.

Lavaca Estuary
Total Nitrogen (% dry weight)

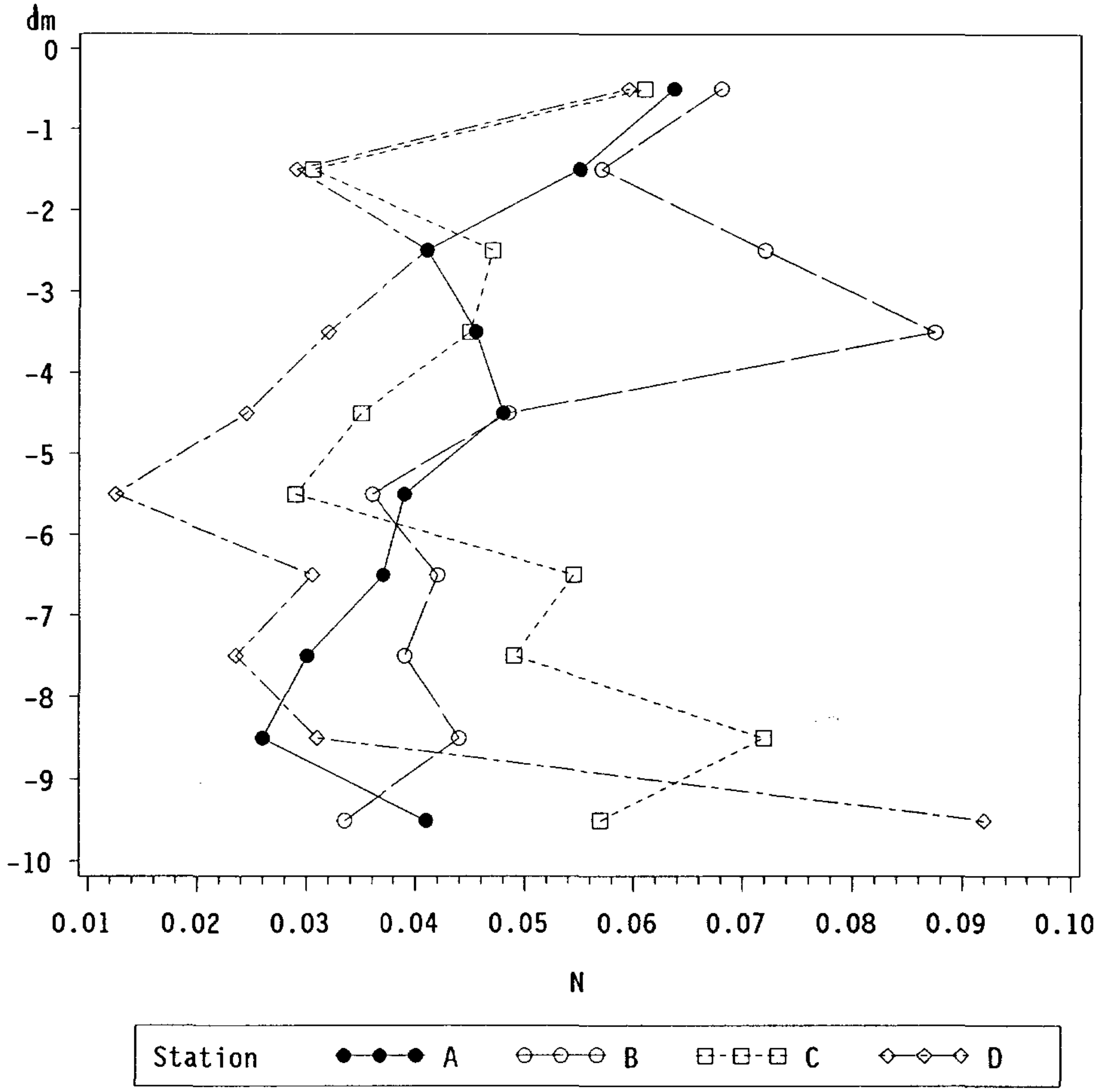


Figure 18. Vertical distribution of nitrogen in sediments from the Lavaca-Colorado Estuary. Samples taken in October 1990 at 10 cm intervals, $n=2$, 1 dm=10 cm.

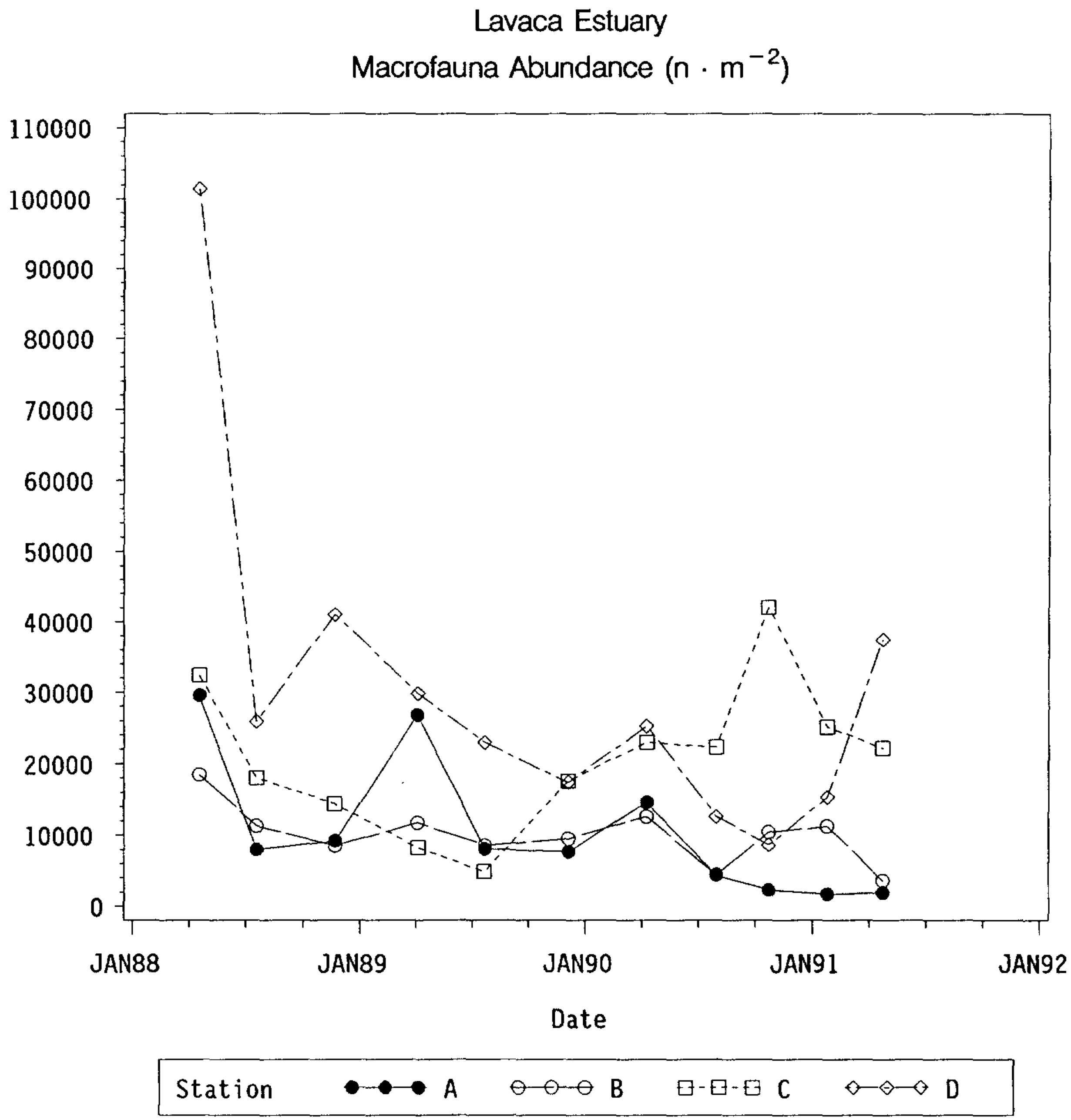


Figure 19. Macrofauna abundance at four stations in the Lavaca-Colorado Estuary. Samples taken to a depth of 10 cm, average of *n*=3.

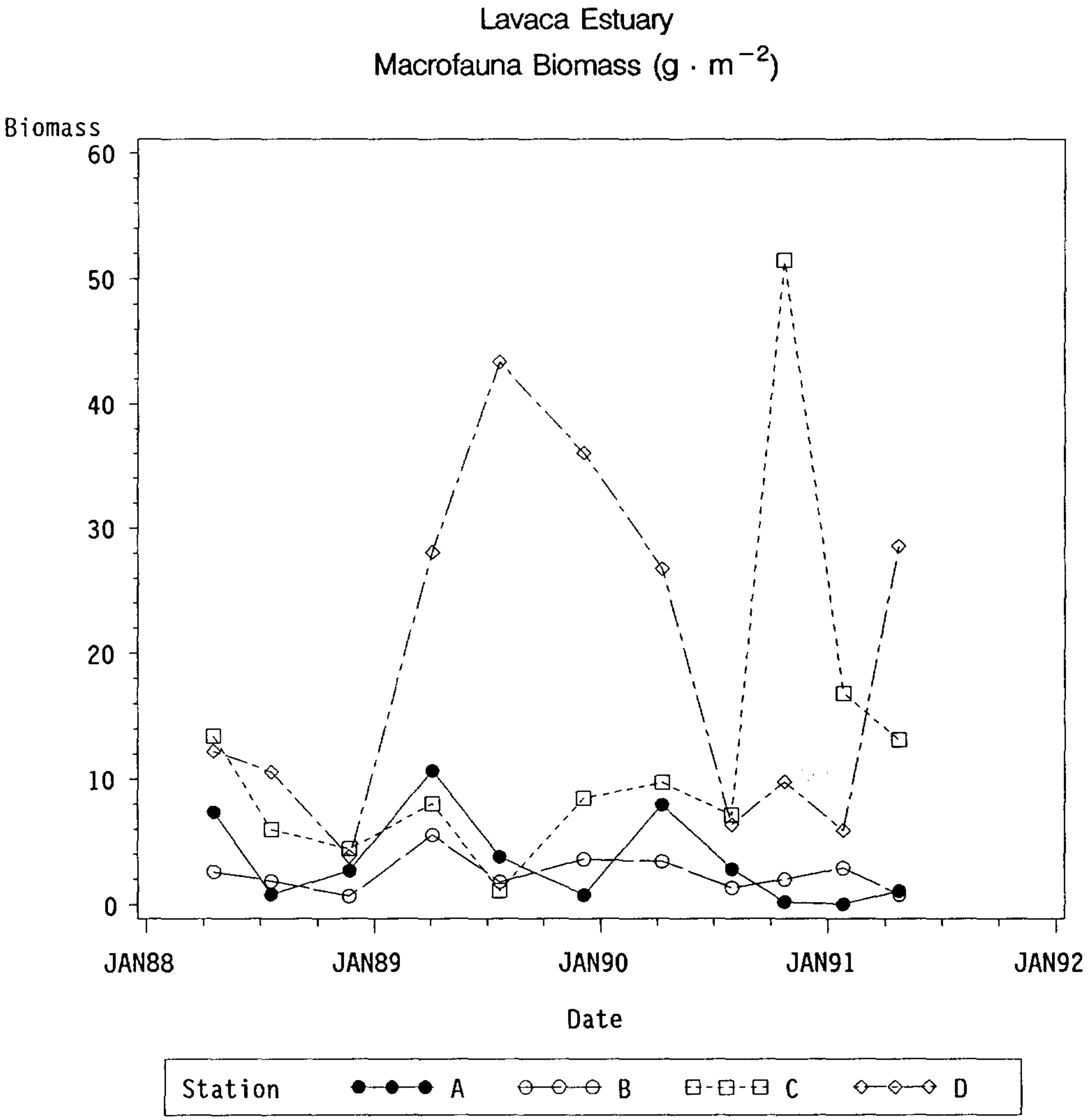


Figure 20. Macrofauna biomass at four stations in the Lavaca-Colorado Estuary. Samples taken to a depth of 10 cm, average of $n=3$.

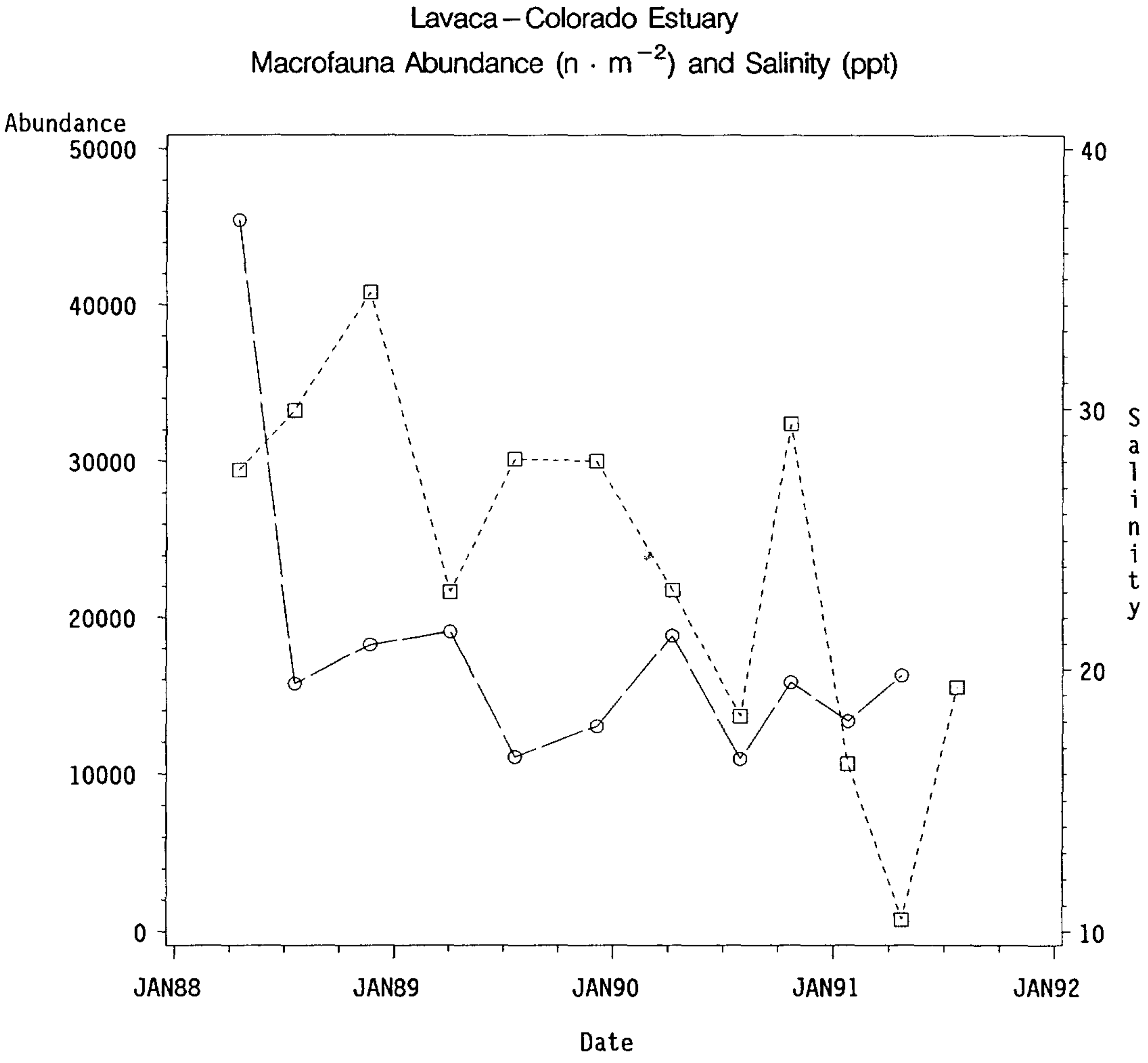


Figure 21. Relationships between macrofauna abundance (○) and salinity (□) in the Lavaca-Colorado Estuary. Average abundance and salinity at all stations.

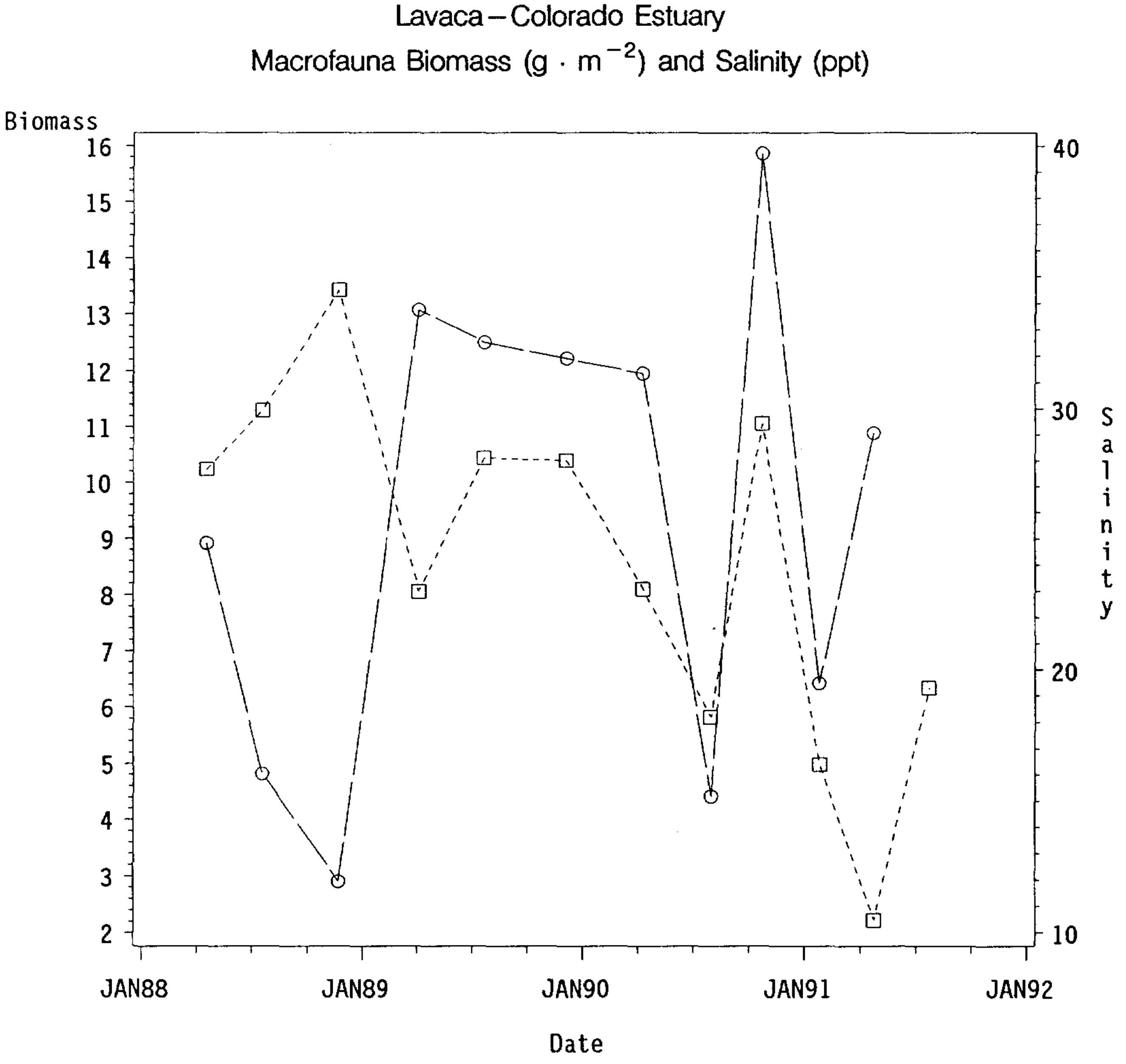


Figure 22. Relationships between macrofauna biomass (○) and salinity (□) in the Lavaca-Colorado Estuary. Average biomass and salinity at all stations.

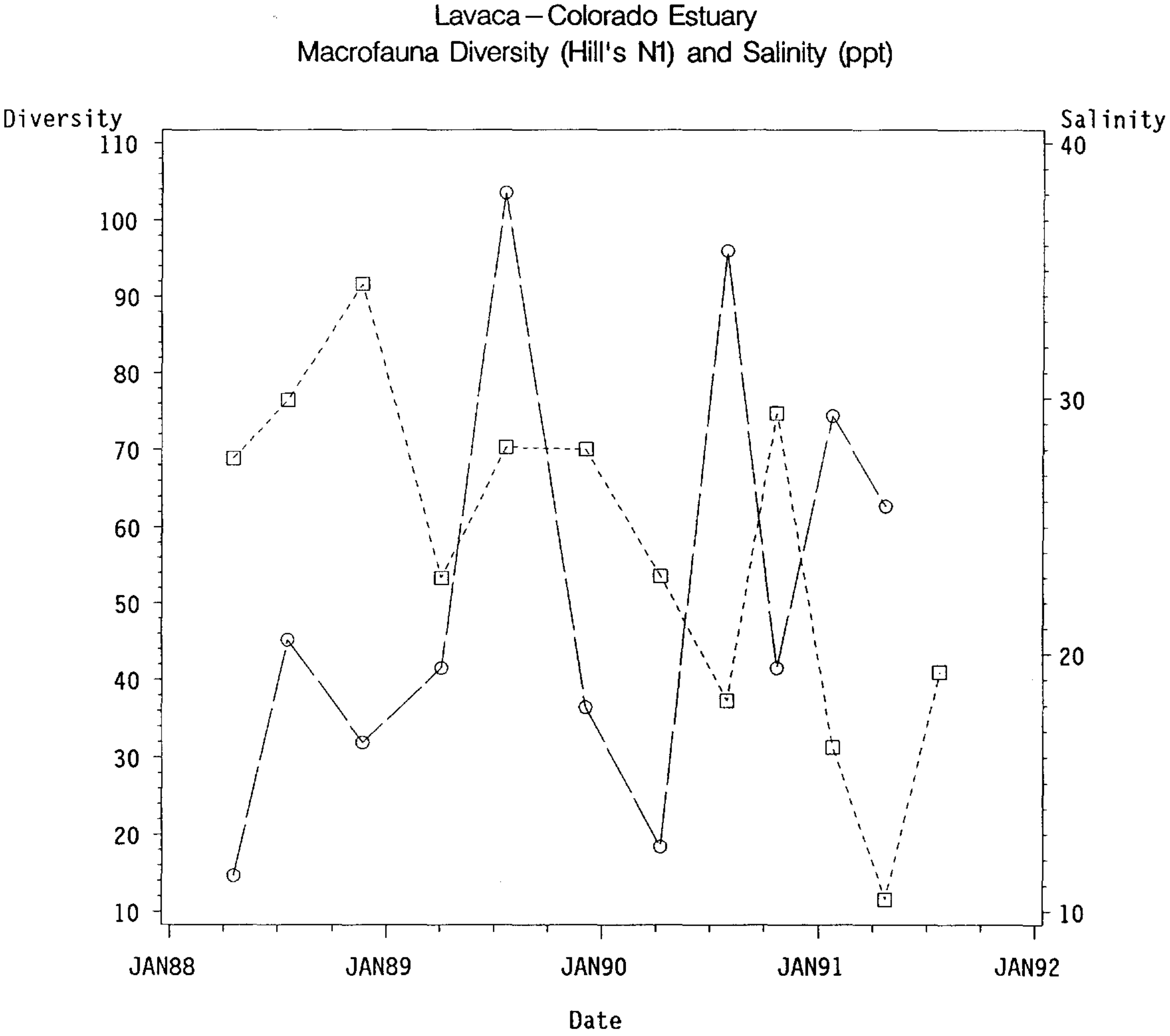


Figure 23. Relationships between macrofauna diversity (○) and salinity (□) in the Lavaca-Colorado Estuary. Average diversity and salinity at all stations.

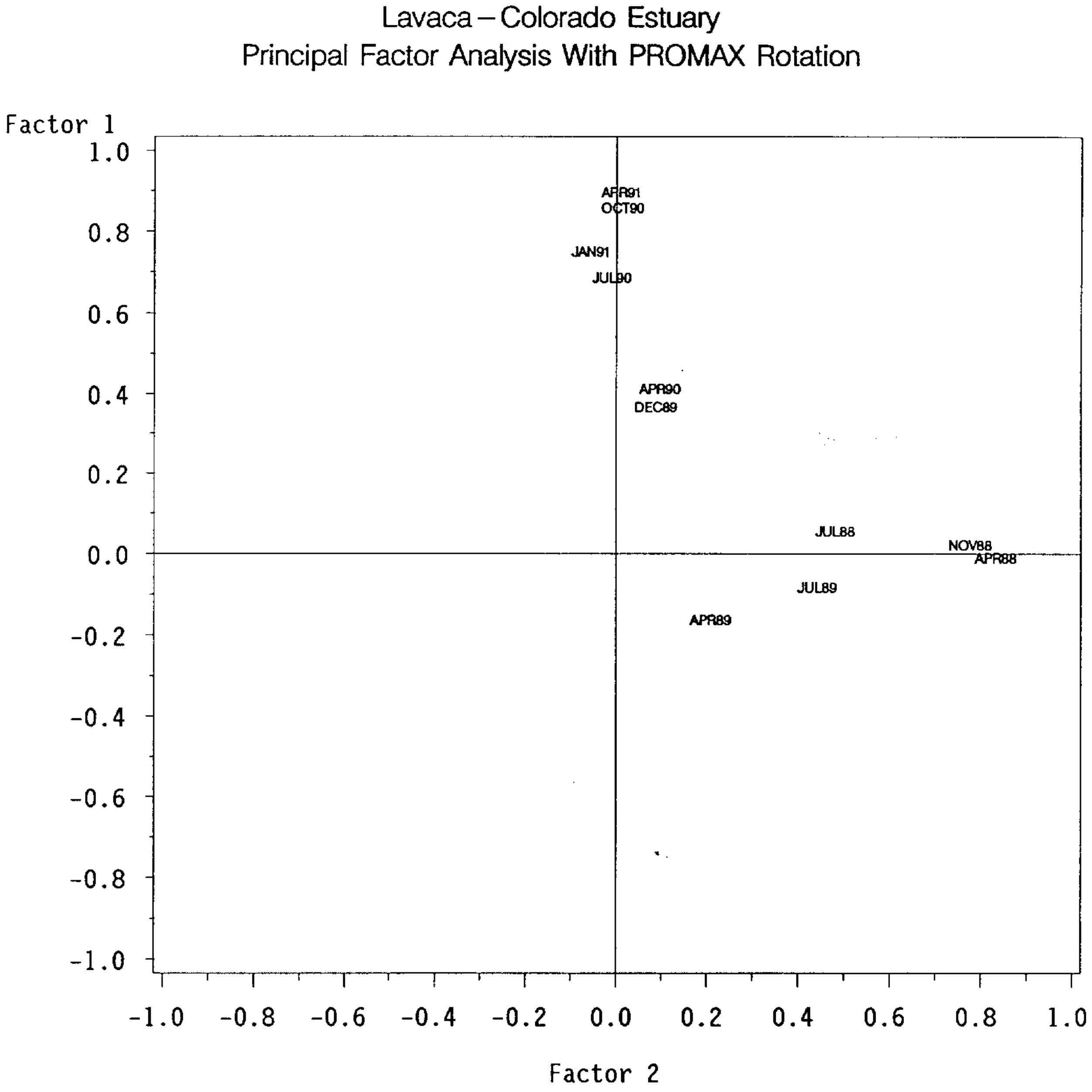


Figure 24. Factor analysis for macrofauna species at all sampling dates in the Lavaca-Colorado Estuary. Species occurring at all stations for a given date.

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DISTANCE METRIC IS EUCLIDEAN DISTANCE
SINGLE LINKAGE METHOD (NEAREST NEIGHBOR)

TREE DIAGRAM
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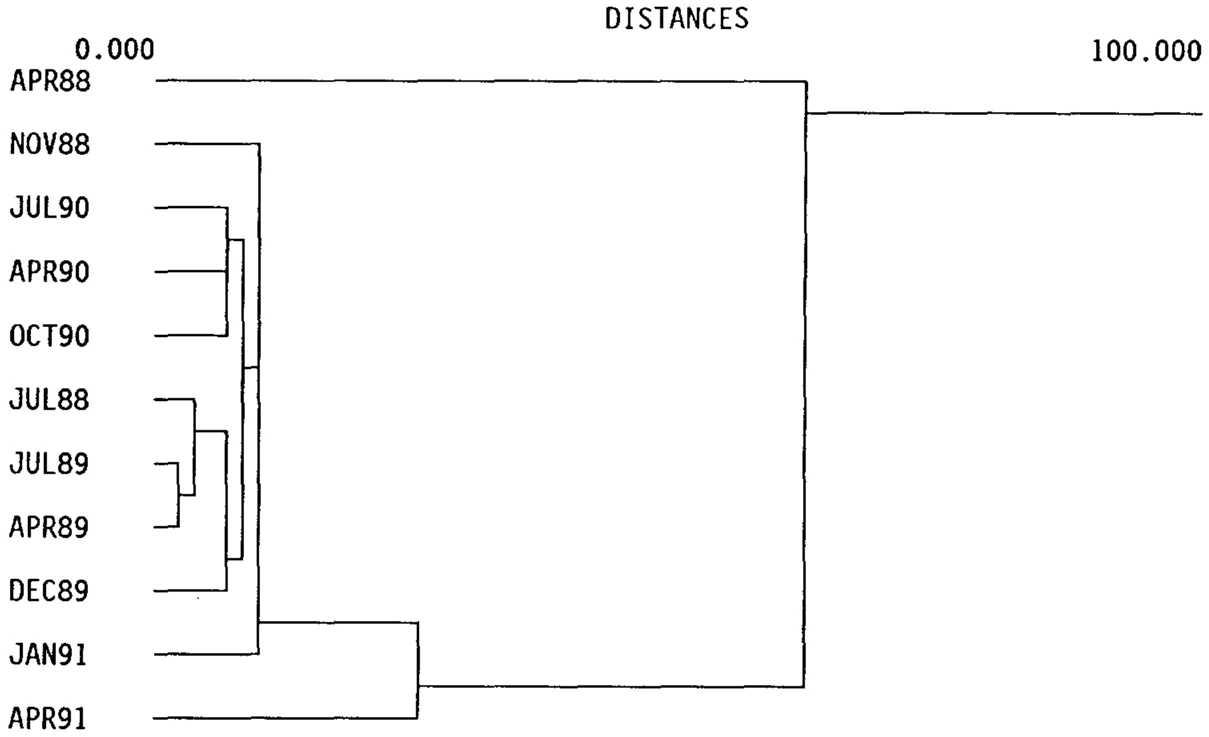

Figure 25. Cluster analysis of sampling dates for Lavaca-Colorado Estuary. Distance metric is euclidean distance, single linkage method (nearest neighbor).

Lavaca Bay (Station A)
Macrofauna Abundance ($n \cdot m^{-2}$) and Salinity (ppt)

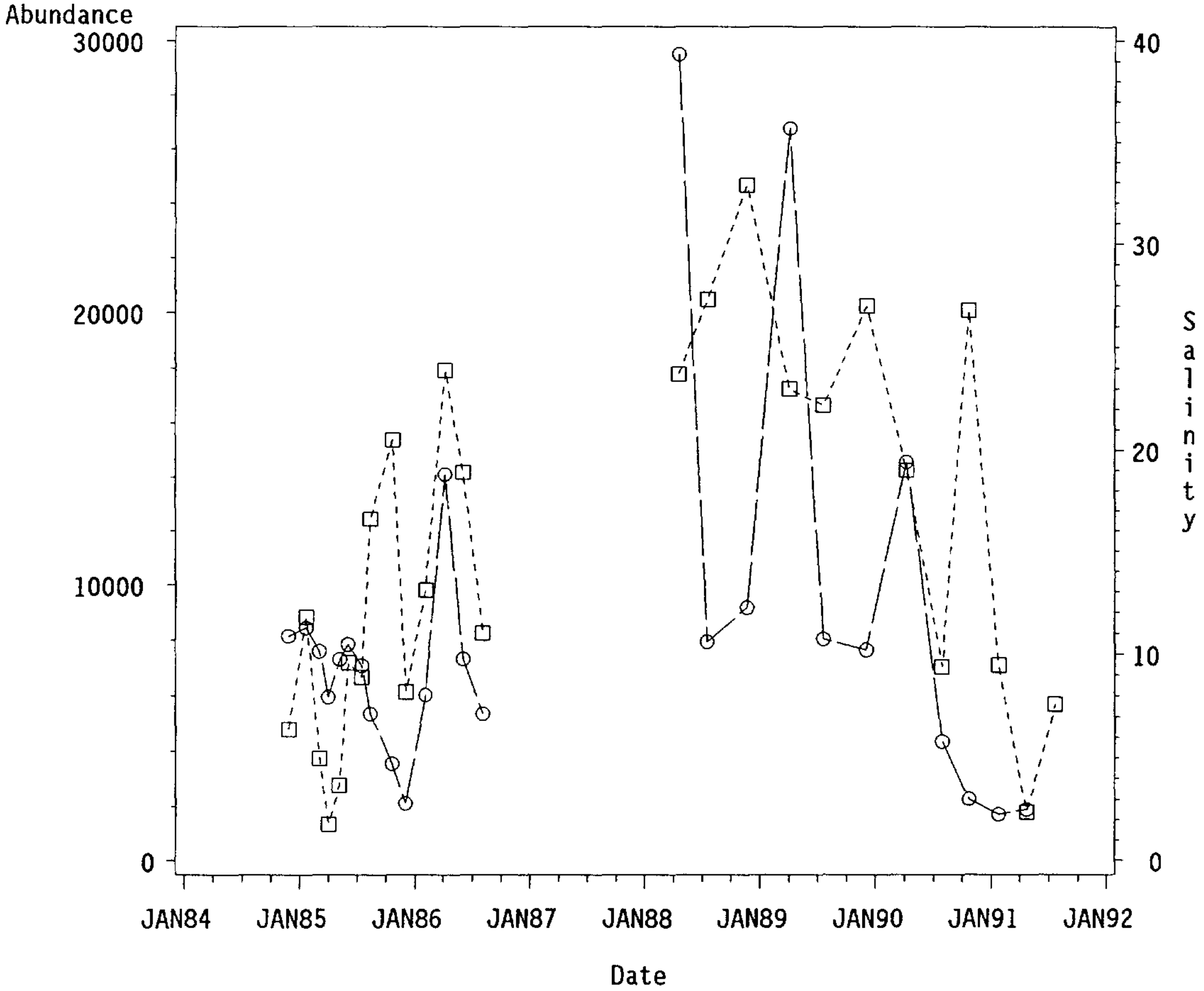

Figure 26. Relationships between macrofauna abundance (○) and salinity (□) in the Lavaca-Colorado Estuary, Station A, *n*=3.

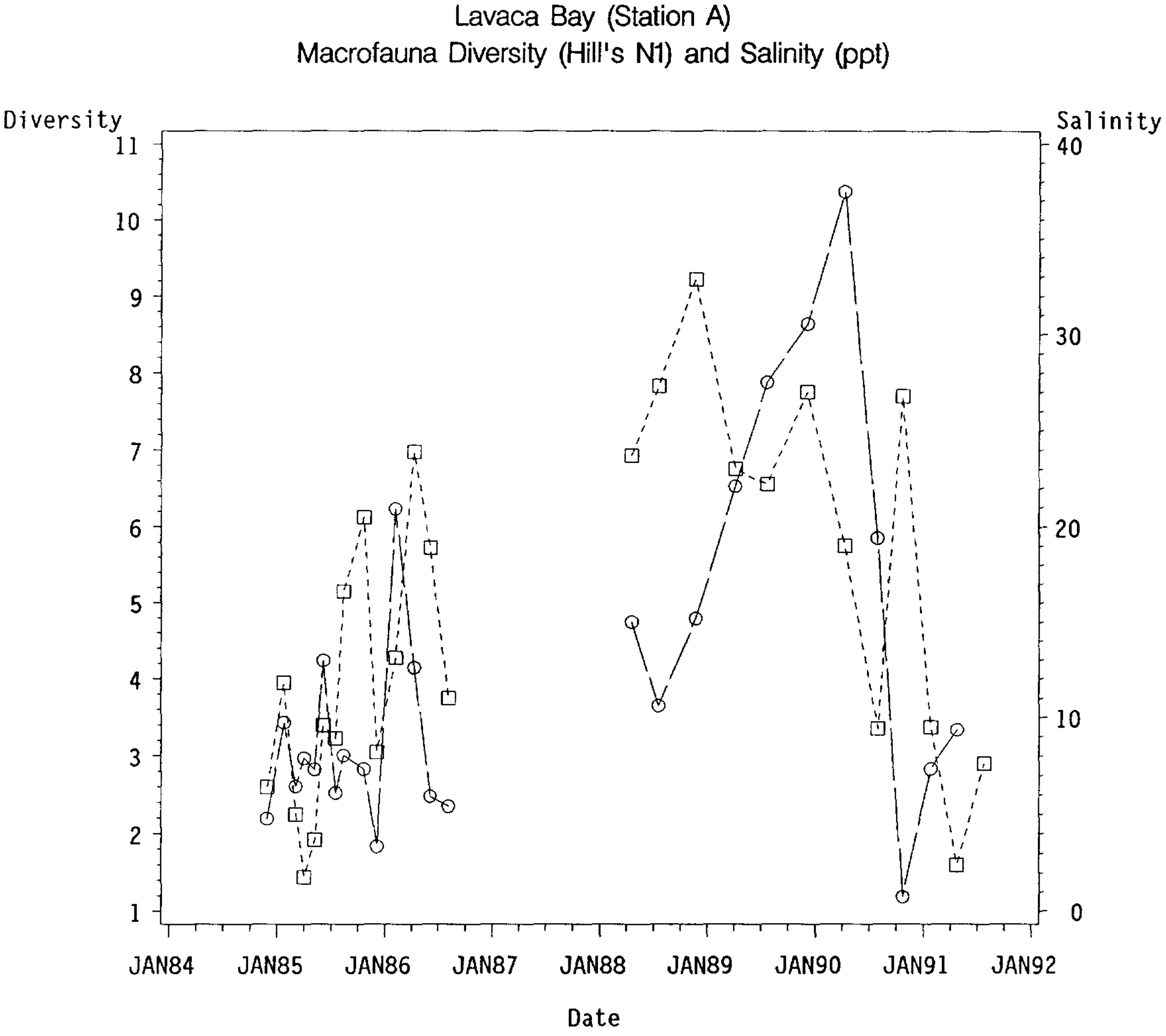

Figure 27. Relationships between macrofauna diversity (○) and salinity (□) in the Lavaca-Colorado Estuary, Station A, *n*=3.

DISCUSSION

The Lavaca-Colorado and Guadalupe Estuaries are similar in the amount of freshwater inflow (Figure 2), but different in two key attributes. The Lavaca-Colorado Estuary (910 km^2 at mean tide) is almost twice as large as the Guadalupe Estuary (579 km^2 at mean tide). The Lavaca-Colorado also has direct exchange of marine water with the Gulf of Mexico via Pass Cavallo and the Matagorda Ship Channel (Figure 3). Because it is smaller and has restricted exchange, the Guadalupe generally has lower salinities (average 13 ppt) than the Lavaca-Colorado (average 24 ppt). This indicates that freshwater inflow has a greater effect on the upper part of San Antonio Bay than on Lavaca Bay. This conclusion is supported by several pieces of data. The salinity time series show that at any given time the salinities are lower in the Guadalupe, both estuarine-wide, and particularly at stations A and B in both estuaries (Figures 4 and 15). The amount of total carbon in sediments is much greater in the Guadalupe than in the Lavaca-Colorado (Figure 6 and 17). Carbon content of Lavaca-Colorado sediments and Guadalupe-station D sediments are about 1%, but carbon content in the Guadalupe at station C is 3%, and at stations A and B around 4%. The carbon data indicate that organic matter is being trapped or not exported from the Guadalupe Estuary. Profiles of nitrogen content exhibit the same trends found in carbon, but there is less difference in total nitrogen content between the estuaries, both being about 0.05% (Figures 7 and 18). Sediment texture is similar in both estuaries (Figures 5 and 16). Both are characterized by silt-clay sediments, with increasing grain sizes from the upper to the lower parts of the estuaries. Differences in physiography between the two estuaries mitigate the similarities of inflow.

Macrofauna abundance is generally larger in the Guadalupe Estuary than in the Lavaca-Colorado Estuary (Figures 8 and 19), but macrofauna biomass is generally larger in the Lavaca-Colorado Estuary (Figures 8 and 19). The average abundance in the Lavaca-Colorado among all times and stations was 15,308 individuals$\cdot m^{-2}$, and the average biomass was 9.46 $g \cdot m^{-2}$. The average abundance in the Guadalupe among all times and stations was 28,233 individuals$\cdot m^{-2}$, and the average biomass was 6.22 $g \cdot m^{-2}$. The differences between the estuaries is due to a greater abundance of ophiuroids, which are rare and large, in the marine stations of the Lavaca-Colorado Estuary (Tables 5 and 8). Diversity is generally greater in the Lavaca-Colorado Estuary (N1=54 species) than in the Guadalupe Estuary (N1=44 species) (Figures 12 and 23). These results indicate that since the effect of freshwater inflow is less diluted by marine water in the Guadalupe Estuary, we find higher benthic productivity. The greater Gulf exchange in the Lavaca-Colorado leads to more oceanic species present in the that estuary, so we find higher diversity.

The time series data show that there are large year-to-year fluctuations in both estuaries for both freshwater inflow (as indicated by salinity changes in Figures 4 and 15) and benthic community response (Figures 10, 11, 12, 21, 22, and 23). The key to understanding the biological response to freshwater inflow is to not try and relate biological changes to inflow changes with simples linear models, e.g., regression or correlation. The proper model is a time series model.

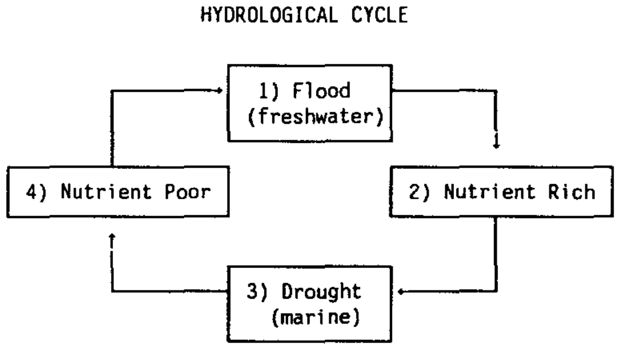

Figure 28. Conceptual model of the long-term effect of freshwater inflow on benthos.

Sine waves that are lag-synchronized could more likely be the true response of estuarine organisms to the inter-annual changes in inflow. We have a continuous cycle of drought and flood conditions. These cycles regulate freshwater inflow, and thus, directly affect the biological communities. The variability in the freshwater inflow cycle results in predictable changes in the estuary, which are diagrammed in a conceptual model of the temporal sequence of the hydrological cycle (Figure 28).

Our study of the Guadalupe Estuary demonstrates the biological effects of this cycle. Flood conditions introduce nutrient rich waters into the estuary which result in lower salinity. This happened in the spring of 1987. During these periods the spatial extent of the freshwater fauna is increased, and the estuarine fauna replaced the marine fauna in the lower end of the estuary. The high level of nutrients stimulated a burst of benthic productivity (of predominantly freshwater and estuarine organisms) in the spring and summer of 1988 (Figures 10 and 11). This was followed by a transition to a drought period with low inflow resulting in higher salinities, lower nutrients, marine fauna, decreased productivity and abundances. At first, the marine fauna responded with a burst of productivity as the remaining nutrients are utilized, but eventually nutrients are depleted resulting in lower densities from 1989 to 1990. The cycle repeated in the spring of 1990, with flooding and high freshwater inflows. However, the flood was not nearly as great as the one in 1987. Yet, the biological response in terms of biomass in the summer of 1991 was even larger. The response of abundance was small and hardly noticeable. We have currently gone through one complete cycle, a wet period in 1987 to a wet period in 1991. We must follow this succession for at least one more cycle, probably four more years, to be sure that the response was not by chance alone.

Macrofauna responded to annual variation in freshwater inflow in a similar fashion in the Lavaca-Colorado Estuary. Abundances and biomass were high in the spring of 1988, one year after the flood of 1987 (Figures 21 and 22). Both declined with increasing salinities in the last half of 1988. Abundances have remained relatively constant since 1989. Biomass rose again with lower salinities in the Spring of 1989, and decreased steadily through the drought of 1989-1990. Spring runoff in both 1990 and 1991 resulted in increased biomass. Salinities during 1987 are unknown, so the spring of 1991 is the lowest recorded salinity in this record.

A longer record is available for station A in Lavaca Bay of the Lavaca-Colorado Estuary (Figures 26 and 27). These data illustrate that the long-term trend is more obvious, and that records of eight years duration are much more revealing than records of only three years. There was a wet period in spring of 1985 that was of the same magnitude as the spring of 1991. Abundances were low during both wet periods, and increased in 1986 following the first wet period. The period in early 1988, following the flood of 1987, had the highest abundances. 1989 through 1990 was generally dry with high salinities. Ignoring seasonal changes, abundances generally decreased during this drought period to the lowest recorded. If my hypothesis on how freshwater affects benthos is correct, the there should be very high values in the spring of 1992. Time series analysis requires at least three cycles to have occurred. When we have enough data, we can fit the data to time series models.

CONCLUSION

The main difference between these two estuaries relate to both size and Gulf exchange. Freshwater inflow has a larger impact on the smaller-restricted Guadalupe Estuary than in the Lavaca-Colorado. Both the smaller size and restricted inflow have synergistic effects, thus the Guadalupe is generally fresher and has higher carbon content than the Lavaca-Colorado. These conditions lead to higher benthic productivity in the Guadalupe Estuary. On the other hand, higher salinities and invasion of marine species is responsible for a more diverse community in Lavaca-Colorado Estuary. There is long-term, year-to-year variability in inflow that drives benthic community succession, and results in different levels of productivity from year-to-year.

ACKNOWLEDGEMENTS

This study builds on a data base which originated in other Texas Water Development Board funded studies. Specifically, contract nos. 8-483-607, 9-483-705, and 9-483-706. The purpose of the studies was to determine the effects of freshwater inflow on benthic biological responses.

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Table 1. Guadalupe Estuary hydrographic measurements. Abbreviations: STA=Station, Z=Depth, SAL(R)=Salinity by refractometer, SAL(M)=Salinty by meter, COND=Conductivity, TEMP=Temperature, DO=dissolved oxygen, and ORP=oxidation redox potential. Missing values show with a period.

Date	STA	Z (m)	SAL(R) (ppt)	SAL(M) (ppt)	COND (uS/cm)	TEMP (°C)	pH	DO (mg·l^{-1})	ORP (mV)
28JAN87	A	1.25	.	0.3	.	14.40	.	.	.
28JAN87	B	1.80	.	0.4	.	14.80	.	.	.
30JAN87	C	2.00	.	6.5	.	15.50	.	.	.
30JAN87	D	1.50	.	4.1	.	15.80	.	.	.
03MAR87	A	1.25	.	0.2	.	15.00	.	.	.
03MAR87	B	1.80	.	0.4	.	16.00	.	.	.
03MAR87	C	2.00	.	6.9	.	16.00	.	.	.
03MAR87	D	1.50	.	12.5	.	17.50	.	.	.
08APR87	A	1.25	.	0.5	.	14.50	.	.	.
08APR87	B	1.80	.	6.3	.	15.20	.	.	.
10APR87	C	2.00	.	9.2	.	14.50	.	.	.
10APR87	D	1.50	.	13.2	.	14.90	.	.	.
03JUN87	A	0.00	.	0.5	1.50	26.70	.	9.40	.
03JUN87	A	1.25	.	1.0	1.50	26.20	.	9.40	.
03JUN87	B	0.00	.	4.3	7.70	26.00	7.90	.	.
03JUN87	B	1.80	.	4.6	.	26.70	.	.	.
03JUN87	C	0.00	.	3.4	6.30	26.50	.	.	.
03JUN87	C	2.00	.	4.3	6.60	26.20	.	.	.
03JUN87	D	0.00	.	7.6	13.00	25.90	.	9.40	.
03JUN87	D	1.50	.	9.9	13.00	26.40	.	9.20	.
15JUL87	A	1.25	.	0.4	.	30.50	.	.	.
15JUL87	B	1.80	.	0.4	.	30.00	.	.	.
15JUL87	C	2.00	.	1.1	.	30.50	.	.	.
15JUL87	D	1.50	.	0.9	.	30.50	.	.	.
18APR88	A	0.00	9	9.6	15.60	22.30	.	7.70	.
18APR88	A	1.25	.	9.2	16.20	21.90	.	.	.
18APR88	B	0.00	14	20.5	22.60	22.20	.	7.50	.
18APR88	B	1.75	.	13.7	32.70	22.00	.	.	.
18APR88	C	0.00	25	23.6	37.10	22.00	7.90	7.30	.
18APR88	C	2.00	.	23.6	37.10	22.10	.	22.10	.
18APR88	D	0.00	24	26.7	38.40	22.70	.	7.50	.
18APR88	D	1.60	.	24.5	41.50	22.10	.	7.10	.
07JUL88	A	0.00	10	10.0	.	28.40	.	.	.
07JUL88	A	1.25	10	10.0	.	28.40	.	.	.
07JUL88	B	0.00	21	21.0	.	29.30	.	.	.
07JUL88	B	1.80	21	21.0	.	29.30	.	.	.
08JUL88	C	0.00	26	26.0	.	28.90	.	.	.

08JUL88	C	2.00	26	26.0	.	28.90	.	.	.
08JUL88	D	0.00	32	32.0	.	28.90	.	.	.
08JUL88	D	1.50	32	32.0	.	28.90	.	.	.
06OCT88	A	0.00	15	15.0	.	24.00	.	.	.
06OCT88	B	0.00	22	22.0	.	24.00	.	.	.
06OCT88	C	0.00	29	29.0	.	24.00	.	.	.
22NOV88	A	0.00	.	18.5	25.60	16.10	.	10.30	.
22NOV88	A	1.25	.	15.7	29.70	15.50	.	10.10	.
22NOV88	B	0.00	.	24.9	38.00	16.50	.	9.60	.
22NOV88	B	1.75	.	24.2	39.00	15.40	.	8.20	.
22NOV88	C	0.00	.	30.2	42.80	17.00	.	9.80	.
22NOV88	C	1.78	.	27.6	46.40	16.00	.	9.20	.
22NOV88	D	0.00	.	30.7	43.30	15.70	.	9.90	.
22NOV88	D	1.50	.	28.0	47.00	15.90	.	12.30	.
04APR89	A	1.25	.	15.0	.	24.00	.	.	.
04APR89	B	1.80	.	18.0	.	23.70	.	.	.
04APR89	C	2.00	.	24.0	.	22.00	.	.	.
04APR89	D	1.50	.	24.0	.	23.90	.	.	.
23JUL89	A	1.25	.	15.9	.	31.50	.	.	.
23JUL89	B	1.80	.	19.4	.	31.50	.	.	.
23JUL89	C	2.00	.	28.4	.	31.30	.	.	.
23JUL89	D	1.50	.	29.0	.	31.50	.	.	.
05DEC89	A	0.00	20	.	.	12.00	7.90	13.20	.
05DEC89	A	1.25	.	20.0	.	11.40	8.00	14.50	.
05DEC89	B	0.00	20	.	.	11.40	7.90	12.20	.
05DEC89	B	1.75	.	20.0	.	11.30	8.00	14.80	.
05DEC89	C	0.00	24	.	.	11.70	7.80	10.70	.
05DEC89	C	2.00	.	24.0	.	11.00	7.90	11.80	.
05DEC89	D	0.00	24	.	.	11.80	7.90	12.00	.
05DEC89	D	1.60	.	24.0	.	11.50	7.90	12.60	.
10APR90	C	0.00	24	24.6	37.30	21.18	8.20	8.28	.
10APR90	C	2.20	.	23.6	38.80	20.56	8.16	7.36	.
10APR90	D	0.00	26	25.9	40.50	21.16	8.23	7.65	.
10APR90	D	1.70	.	25.9	40.50	20.91	8.22	7.38	.
11APR90	A	0.00	7	6.9	12.47	19.14	8.02	8.80	.
11APR90	A	1.50	.	6.8	12.51	19.12	8.20	8.60	.
11APR90	B	0.00	20	21.1	33.80	19.50	8.12	8.00	.
11APR90	B	2.10	.	21.1	33.80	19.53	8.10	7.80	.
02AUG90	A	0.00	.	0.1	1.27	29.34	8.73	7.04	0.105
02AUG90	A	1.30	.	0.1	1.27	29.34	8.72	6.70	0.106
02AUG90	B	.	.	5.4	7.12	29.70	.	6.68	1.700
02AUG90	B	1.80	.	3.6	8.75	29.65	.	5.57	1.635
02AUG90	C	0.00	.	15.2	25.30	29.00	.	6.31	0.810
02AUG90	C	1.80	.	15.3	25.40	29.81	8.35	5.94	0.666
02AUG90	D	0.00	.	11.2	19.20	29.46	8.25	6.05	0.143
02AUG90	D	1.20	.	11.2	19.30	29.48	8.25	5.74	0.141

19OCT90	A	0.00	10	9.4	16.40	22.35	9.07	12.93	0.106
19OCT90	A	1.70	.	9.5	16.50	22.26	9.05	12.10	0.107
19OCT90	B	0.00	18	18.0	29.40	22.19	8.67	5.09	0.113
19OCT90	B	2.20	.	18.2	29.70	21.71	8.60	3.40	0.115
19OCT90	C	0.00	20	20.0	32.20	22.25	8.41	4.98	0.121
19OCT90	C	2.30	.	20.0	32.20	21.60	8.41	3.69	0.121
19OCT90	D	0.00	27	27.8	43.20	21.57	8.54	4.25	0.105
19OCT90	D	2.00	.	27.8	43.20	21.50	8.53	4.09	0.106
23JAN91	A	0.00	3	5.1	9.75	10.41	8.17	9.04	0.155
23JAN91	A	1.20	3	17.0	28.00	10.67	8.39	5.86	0.162
23JAN91	B	0.00	18	19.0	30.80	9.98	8.69	11.96	0.157
23JAN91	B	2.00	18	19.2	31.40	10.29	8.58	8.24	0.160
23JAN91	C	0.00	21	22.4	35.60	10.01	8.47	10.40	0.173
23JAN91	C	1.90	21	22.4	35.70	10.01	8.47	10.25	0.173
23JAN91	D	0.00	24	22.3	35.40	10.34	8.37	9.45	0.208
23JAN91	D	1.50	24	22.4	35.60	10.31	8.37	9.40	0.207
25JAN91	B	0.00	9	8.9	16.00	12.38	8.87	15.29	0.138
25JAN91	B	1.80	9	18.3	30.10	11.12	8.52	9.40	0.152
22APR91	A	0.00	0	0.0	0.50	25.26	8.13	7.65	0.137
22APR91	A	1.20	0	0.0	0.51	25.17	8.08	7.35	0.141
22APR91	B	0.00	2	0.6	2.10	24.74	8.18	8.27	0.140
22APR91	B	1.70	2	3.6	7.29	24.19	8.04	6.49	0.150
22APR91	C	0.00	6	6.7	12.30	24.38	8.23	8.90	0.150
22APR91	C	1.80	6	6.8	12.79	24.28	8.18	7.34	0.151
22APR91	D	0.00	7	7.1	12.89	24.51	8.19	8.50	0.148
22APR91	D	1.50	7	7.2	13.31	24.74	8.19	7.90	0.148
17JUL91	A	0.00	0	0.0	0.73	29.98	8.39	7.41	0.131
17JUL91	A	1.20	0	0.0	0.74	29.98	8.44	7.25	0.131
17JUL91	B	0.00	4	4.2	8.20	30.04	8.23	5.75	0.140
17JUL91	B	1.70	4	4.2	8.24	30.07	8.22	5.44	0.142
17JUL91	C	0.00	10	9.3	16.20	30.92	8.49	7.55	0.126
17JUL91	C	1.90	10	12.0	20.70	30.92	8.53	5.96	0.128
17JUL91	D	0.00	7	7.1	12.92	30.65	8.44	6.70	0.120
17JUL91	D	1.50	7	7.4	13.47	30.46	8.46	5.91	0.121

Table 2. Sediment grain size in both estuaries measured in October 1990. Estuary abbreviations: GE=Guadalupe, and LA=Lavaca.

Estuary	Station	Depth (cm)	Rubble (%)	Sand (%)	Silt (%)	Clay (%)
GE	A	0-3	2.6	34.1	34.3	29.0
GE	A	3-10	14.8	33.1	24.5	27.6
GE	B	0-3	11.3	5.3	29.0	54.4
GE	B	3-10	6.0	6.3	34.0	53.7
GE	C	0-3	12.0	37.3	27.2	23.5
GE	C	3-10	3.1	27.4	26.8	42.7
GE	D	0-3	1.0	87.2	6.4	5.4
GE	D	3-10	3.8	81.4	5.8	9.0
LA	A	0-3	0.1	0.7	29.4	69.8
LA	A	3-10	0.5	5.9	26.2	67.4
LA	B	0-3	5.0	41.0	18.9	35.1
LA	B	3-10	1.3	25.8	22.5	50.3
LA	C	0-3	33.8	39.7	8.4	18.1
LA	C	3-10	21.2	34.0	12.7	32.1
LA	D	0-3	1.7	22.7	28.4	47.2
LA	D	3-10	1.9	28.8	22.7	46.6

Table 3. Sediment carbon and nitrogen inventories in both estuaries measured in October 1990. Estuary abbreviations: GE=Guadalupe, and LA=Lavaca.

Estuary	Station	Depth (cm)	Carbon (%)	Std (%)	Nitrogen (%)	Std (%)
GE	A	0-10	3.48	0.09	0.07	0.02
GE	A	10-20	3.50	0.28	0.07	0.03
GE	A	20-30	3.68	0.32	0.07	0.02
GE	A	30-40	3.56	0.28	0.06	0.02
GE	A	40-50	3.92	0.16	0.04	0.01
GE	A	50-60	4.20	0.37	0.05	0.00
GE	A	60-70	4.22	0.10	0.04	0.00
GE	A	70-80	3.70	0.21	0.04	0.02
GE	A	80-90	3.60	0.08	0.04	0.02
GE	A	90-100	3.10	0.32	0.09	0.03
GE	B	0-10	3.62	0.01	0.08	.
GE	B	10-20	3.62	0.00	0.07	0.00
GE	B	20-30	3.50	0.02	0.11	0.03
GE	B	30-40	3.58	0.16	0.07	0.00
GE	B	40-50	4.01	0.14	0.07	0.01
GE	B	50-60	3.52	0.55	0.06	0.00
GE	B	60-70	3.59	0.36	0.07	0.01
GE	B	70-80	2.82	0.72	0.06	0.00
GE	B	80-90	2.97	0.55	0.06	0.02
GE	B	90-100	3.12	0.04	0.06	0.00
GE	C	0-10	2.69	0.18	0.03	0.01
GE	C	10-20	2.64	0.09	0.04	0.04
GE	C	20-30	2.91	0.23	0.05	0.01
GE	C	30-40	2.85	0.29	0.05	0.00
GE	C	40-50	2.85	0.18	0.05	0.01
GE	C	50-60	3.12	0.02	0.06	0.01
GE	C	60-70	2.74	0.01	0.04	0.01
GE	C	70-80	3.10	0.15	0.04	0.01
GE	C	80-90	3.07	0.09	0.03	0.00
GE	C	90-100	3.67	0.55	0.02	0.01
GE	D	0-10	1.06	0.40	0.02	.
GE	D	10-20	0.73	0.27	0.02	.
GE	D	20-30	0.74	0.13	0.02	0.00
GE	D	30-40	0.70	0.30	.	.
GE	D	40-50	0.82	0.13	0.03	.
GE	D	50-60	0.76	0.15	0.02	.
GE	D	60-70	0.75	0.05	0.02	.
GE	D	70-80	0.67	0.04	.	.
GE	D	80-90	0.63	.	.	.
GE	D	90-100	2.28	1.97	0.01	0.01

LA	A	0-10	0.98	0.21	0.06	0.01
LA	A	10-20	0.96	0.09	0.05	0.01
LA	A	20-30	1.05	0.14	0.04	0.01
LA	A	30-40	1.36	0.03	0.05	0.03
LA	A	40-50	1.07	.	0.05	.
LA	A	50-60	0.81	.	0.04	.
LA	A	60-70	0.94	0.12	0.04	.
LA	A	70-80	0.93	0.20	0.03	.
LA	A	80-90	0.80	0.21	0.03	.
LA	A	90-100	1.08	.	0.04	.
LA	B	0-10	1.23	.	0.07	.
LA	B	10-20	1.17	0.14	0.06	0.02
LA	B	20-30	1.44	0.11	0.07	0.02
LA	B	30-40	1.68	0.03	0.09	0.01
LA	B	40-50	1.54	0.02	0.05	0.03
LA	B	50-60	1.28	0.10	0.04	0.04
LA	B	60-70	1.30	.	0.04	.
LA	B	70-80	0.94	.	0.04	.
LA	B	80-90	1.30	.	0.04	.
LA	B	90-100	1.60	0.07	0.03	0.04
LA	C	0-10	2.47	0.58	0.06	.
LA	C	10-20	2.27	0.73	0.03	0.03
LA	C	20-30	1.47	0.30	0.05	.
LA	C	30-40	1.44	0.15	0.04	0.00
LA	C	40-50	1.64	0.04	0.04	0.02
LA	C	50-60	1.40	0.14	0.03	0.01
LA	C	60-70	1.19	0.10	0.05	0.01
LA	C	70-80	1.29	0.06	0.05	0.01
LA	C	80-90	1.47	0.12	0.07	0.02
LA	C	90-100	1.51	0.02	0.06	0.02
LA	D	0-10	1.34	0.12	0.06	0.00
LA	D	10-20	0.74	0.51	0.03	0.03
LA	D	20-30	0.55	0.48	0.04	0.00
LA	D	30-40	0.67	0.05	0.03	0.00
LA	D	40-50	0.54	0.03	0.02	0.00
LA	D	50-60	0.41	0.03	0.01	0.00
LA	D	60-70	0.78	0.60	0.03	0.03
LA	D	70-80	0.69	0.11	0.02	0.00
LA	D	80-90	0.90	0.02	0.03	0.00
LA	D	90-100	0.86	0.04	0.09	0.09

Table 4. Guadalupe Estuary macrofauna abundance ($n \cdot m^{-2}$) and biomass ($g \cdot m^{-2}$).

Date	Station	Abundance	STD	Biomass	STD
28JAN87	A	13898	5580	2.024	0.703
03MAR87	A	38953	5604	10.154	9.162
08APR87	A	58805	43356	3.855	2.498
03JUN87	A	57949	27889	9.339	4.262
15JUL87	A	36495	6249	10.656	1.761
18APR88	A	84241	14393	12.985	2.692
07JUL88	A	69198	6806	17.751	1.373
22NOV88	A	23542	4403	11.243	2.398
04APR89	A	101827	7023	8.880	1.004
23JUL89	A	26186	5240	4.781	1.148
05DEC89	A	41317	7618	10.283	1.541
11APR90	A	21651	3226	8.333	2.516
02AUG90	A	44248	2948	5.738	2.177
19OCT90	A	16357	3124	3.174	0.594
23JAN91	A	26000	4523	30.276	47.281
22APR91	A	51528	4800	2.032	0.143
28JAN87	B	22124	5587	3.035	1.357
03MAR87	B	19004	6487	4.806	1.432
08APR87	B	20325	433	4.667	1.947
03JUN87	B	21554	8583	7.756	0.870
15JUL87	B	11535	6654	3.528	0.704
18APR88	B	169144	20768	15.364	4.243
07JUL88	B	55491	10673	14.040	2.556
22NOV88	B	34320	6542	23.485	1.591
04APR89	B	63630	5369	6.242	1.606
23JUL89	B	40649	3311	6.068	1.729
05DEC89	B	29877	1931	6.661	4.988
11APR90	B	23731	2129	5.328	0.796
02AUG90	B	25149	2681	4.331	0.490
19OCT90	B	14844	1662	1.937	0.959
23JAN91	B	8698	1562	2.470	1.715
22APR91	B	5011	714	1.440	1.613
30JAN87	C	8603	327	1.826	1.917
03MAR87	C	10589	590	2.835	0.772
10APR87	C	11629	1986	5.021	3.047
03JUN87	C	6428	3287	4.185	3.255
15JUL87	C	8698	2979	2.073	1.513
18APR88	C	75259	12918	6.082	0.611
08JUL88	C	18056	2855	1.386	0.513
22NOV88	C	10873	1662	0.688	0.152
04APR89	C	18531	3188	2.260	1.415
23JUL89	C	15031	2878	1.976	0.976

05DEC89	C	5578	1428	1.767	0.870
10APR90	C	5389	2141	2.825	2.553
02AUG90	C	8793	5434	2.218	0.943
19OCT90	C	23542	3439	2.263	0.442
23JAN91	C	14655	4541	5.826	0.959
22APR91	C	8415	2798	5.727	1.320
30JAN87	D	6428	590	1.386	0.874
03MAR87	D	10495	2215	3.685	0.751
10APR87	D	9264	3523	4.190	1.527
03JUN87	D	7846	433	6.767	4.867
15JUL87	D	3876	912	1.626	1.321
18APR88	D	37155	3070	1.933	0.313
08JUL88	D	11344	2599	0.751	0.350
22NOV88	D	8698	434	1.088	0.148
04APR89	D	25337	9652	8.259	4.467
23JUL89	D	13046	1965	20.909	13.294
05DEC89	D	15884	9952	5.249	1.672
10APR90	D	14182	1985	6.897	1.199
02AUG90	D	10778	2521	2.811	2.228
19OCT90	D	15789	6019	1.350	0.433
23JAN91	D	71572	21347	14.373	4.777
22APR91	D	17869	3271	5.284	1.520

Table 5. Guadalupe Estuary species list. Average density ($n \cdot m^{-2}$) over entire study period.

Taxa	A	B	C	D
Cnidaria				
Anthozoa				
Anthozoa (unidentified)	6	0	18	6
Platyhelminthes				
Turbellaria				
Turbellaria (unidentified)	18	6	160	30
Rynchocoela				
Rhynchocoel (unidentified)	414	467	408	207
Phoronida				
Phoronis architecta	0	0	219	71
Mollusca				
Gastropoda				
Gastropoda (unidentified)	780	0	0	18
Vitrinellidae				
Vitrinellidae (unidentified)	0	0	0	6
Caecidae				
Caecum pulchellum	0	6	0	6
Caecum johnsoni	0	0	6	6
Nassariidae				
Nassarius acutus	0	0	12	0
Pyramidellidae				
Odostomia sp.	0	0	6	0
Turbonilla sp.	0	0	12	41
Pyramidella crenulata	12	6	6	18
Pyramidella sp.	35	6	0	24
Retusidae				
Acteocina canaliculata	12	47	24	89
Crepidulidae				
Crepidula fornicata	0	0	6	0
Hydrobiidae				
Littoridina sphinctostoma	15592	5388	1253	266
Pelecypoda				
Pelecypoda (unidentified)	0	0	12	41
Nuculanidae				
Nuculana acuta	0	0	0	12
Nuculana concentrica	0	0	0	6
Mytilidae				
Brachidontes exustus	0	41	0	0
Cultellidae				
Ensis minor	0	6	6	53

Leptonidae				
Mysella planulata	0	0	0	195
Tellinidae				
Macoma tenta	0	0	0	6
Tellina sp	0	6	0	6
Macoma mitchelli	213	366	124	278
Veneridae				
Mercenaria campechiensis	0	0	6	6
Lyonsiidae				
Lyonsia hyalina floridana	0	0	6	0
Pandoridae				
Pandora trilineata	0	0	0	6
Sportellidae				
Aligena texasiana	0	0	6	77
Mactridae				
Mulinia lateralis	3001	4201	1371	756
Periploma cf. *orbiculare*	0	0	0	59
Rangia cuneata	30	18	0	0
Periplomatidae				
Periploma margaritaceum	0	0	6	0
Solecurtidae				
Tagelus plebeius	0	0	24	24
Annelida				
Polychaeta				
Sigalionidae				
Sigalionidae (unidentified)	0	0	0	6
Palmyridae (= Chrysopetalidae)				
Paleanotus heteroseta	0	0	0	12
Phyllodocidae				
Eteone heteropoda	0	65	6	12
Anaitides erythrophyllus	0	0	12	0
Pilargiidae				
Parandalia ocularis	53	0	6	30
Hesionidae				
Gyptis vittata	12	6	53	47
Podarke obscura	0	0	6	0
Hesionidae (unidentified)	0	0	0	6
Syllidae				
Sphaerosyllis cf. *sublaevis*	0	0	0	6
Exogone sp.	0	0	0	12
Nereidae				
Nereis succinea	0	0	12	65
Nereidae (unidentified)	0	0	18	18
Glyceridae				
Glycera americana	0	0	0	41
Glycera capitata	0	0	0	6

Goniadidae				
Glycinde solitaria	6	35	230	260
Onuphidae				
Diopatra cuprea	0	6	35	59
Arabellidae				
Drilonereis magna	0	0	6	0
Dorvilleidae				
Schistomeringos rudolphi	0	0	0	6
Spionidae				
Polydora ligni	0	0	0	30
Minuspio cirrifera	0	0	0	6
Paraprionospio pinnata	0	18	106	100
Scolelepis texana	0	6	24	41
Polydora websteri	30	0	0	24
Polydora socialis	0	6	59	18
Streblospio benedicti	13105	14286	2127	2541
Polydora caulleryi	0	0	12	1436
Polydora sp.	41	0	0	6
Scolelepis squamata	6	0	47	18
Spionidae (unidentified)	0	6	0	0
Chaetopteridae				
Spiochaetopterus costarum	0	0	177	1743
Cirratulidae				
Tharyx setigera	0	0	0	6
Cossuridae				
Cossura delta	0	0	89	95
Orbiniidae				
Haploscoloplos foliosus	136	408	331	148
Haploscoloplos fragilis	0	0	0	12
Capitellidae				
Capitella capitata	496	148	35	35
Mediomastus californiensis	4384	6257	5897	4668
Notomastus latericeus	0	0	0	6
Heteromastus filiformis	30	0	0	0
Mediomastus ambiseta	4449	2617	1566	2417
Capitellidae (unidentified)	0	0	0	18
Maldanidae				
Clymenella torquata	0	0	12	95
Asychis sp.	0	0	12	71
Clymenella mucosa	0	0	24	77
Maldanidae (unidentified)	0	0	35	65
Pectinariidae				
Pectinaria gouldii	0	6	6	6
Ampharetidae				
Isolda pulchella	0	0	0	6
Melinna maculata	0	6	24	30
Hobsonia florida	804	83	0	0

Terebellidae				
Pista palmata	0	6	118	12
Terebellidae (unidentified)	0	0	0	6
Sabellidae				
Megalomma bioculatum	0	24	18	24
Sabellidae (unidentified)	0	12	0	0
Serpulidae				
Eupomatus dianthus	0	0	0	6
Serpulidae (unidentified)	0	0	0	18
Polychaete juv. (unidentified)	0	6	6	0
Oligochaeta				
Oligochaetes (unidentified)	236	319	24	0
Crustacea				
Copepoda				
Calanoida				
Diaptomidae				
Pseudodiaptomus coronatus	6	6	24	6
Cyclopoida				
Cyclopidae				
Hemicyclops sp.	0	0	0	12
Cirripedia				
Balanus eburneus	18	12	0	0
Malacostraca				
Reptantia				
Callianassidae				
Callianassa sp.	0	0	6	6
Pinnotheridae				
Pinnixa chacei	0	0	0	6
Pinnotheridae (unidentified)	0	0	0	6
Brachyuran Larvae				
Megalops	6	6	0	0
Mysidacea				
Mysidopsis bahia	6	0	6	30
Bowmaniella sp.	6	0	0	0
Mysidopsis sp.	30	0	0	12
Mysidopsis almyra	18	24	0	0
Cumacea				
Cyclaspis varians	30	65	165	266
Oxyurostylis sp.	0	0	12	6
Leucon sp.	0	0	47	0
Oxyurostylis salinoi	0	18	18	18
Oxyurostylis smithi	12	30	201	177
Amphipoda				
Ampeliscidae				
Ampelisca abdita	30	12	12	30

Gammaridae				
Gammarus mucronatus	6	0	18	0
Oedicerotidae				
Monoculodes sp.	284	177	160	47
Synchelidium americanum	0	0	0	30
Corophiidae				
Erichthonias brasiliensis	0	0	0	47
Corophium ascherusicum	0	12	0	6
Corophium louisianum	0	6	18	0
Microprotopus spp.	6	6	6	6
Bateidae				
Batea catharinensis	0	0	6	6
Liljeborgiidae				
Listriella barnardi	0	0	6	30
Stenothoidae				
Parametopella sp.	0	0	0	6
Caprellidae				
Caprellid	12	0	53	12
Melitidae				
Elasmopus sp.	0	0	6	0
Melita sp.	0	0	18	6
Isopoda				
Anthuridae				
Xenanthura brevitelson	0	0	0	6
Idoteidae				
Edotea montosa	0	12	12	0
Sphaeromatidae				
Cassidinidea lunifrons	0	6	0	0
Echinodermata				
Ophiuroidea				
Ophiuroidea (unidentified)	0	0	6	24
Insecta				
Pterygota				
Diptera				
Chironomidae				
Chironomid larvae	142	35	12	6

Table 6. Lavaca-Colorado Estuary hydrographic measurements. Abbreviations: STA=Station, Z=Depth, SAL(R)=Salinity by refractometer, SAL(M)=Salinty by meter, COND=Conductivity, TEMP=Temperature, DO=dissolved oxygen, and ORP=oxidation redox potential. Missing values show with a period.

Date	STA	Z (m)	SAL(R) (ppt)	SAL(M) (ppt)	COND (uS/cm)	TEMP (°C)	pH	DO $(mg \cdot l^{-1})$	ORP (mV)
18APR88	A	0.00	25	23.7	37.30	24.10	.	8.50	.
18APR88	A	1.10	.	23.7	37.30	.	.	.	.
18APR88	B	0.00	29	27.3	42.20	23.30	.	8.80	.
18APR88	B	2.15	.	27.2	42.30	23.20	.	8.00	.
18APR88	C	0.00	34	31.0	44.80	22.90	.	.	.
18APR88	C	3.10	.	29.1	47.40	21.60	.	.	.
18APR88	D	0.00	34	31.2	46.90	22.40	.	8.30	.
18APR88	D	4.40	.	30.6	47.70	21.50	.	.	.
19JUL88	A	0.00	28	27.3	42.40	29.90	.	.	.
19JUL88	A	2.00	.	27.3	42.40	29.90	.	.	.
19JUL88	B	0.00	30	28.6	44.10	30.50	.	.	.
19JUL88	B	2.00	.	28.6	44.10	30.50	.	.	.
19JUL88	C	0.00	33	31.5	48.20	29.40	.	6.30	.
19JUL88	C	2.50	.	31.5	48.20	29.60	.	.	.
19JUL88	D	0.00	32	32.3	492.0	29.80	.	.	.
19JUL88	D	4.00	.	32.3	49.20	29.80	.	.	.
22NOV88	A	0.00	32	32.7	49.80	13.80	.	8.90	.
22NOV88	A	1.00	.	32.9	50.00	13.90	.	8.80	.
22NOV88	B	0.00	33	34.5	52.20	14.50	.	8.80	.
22NOV88	B	1.75	.	34.6	52.40	14.60	.	8.60	.
22NOV88	C	0.00	35	35.2	53.20	15.40	.	8.80	.
22NOV88	C	2.50	.	35.3	53.30	15.50	.	8.50	.
22NOV88	D	0.00	35	34.4	52.10	16.70	.	8.50	.
22NOV88	D	4.00	.	35.1	53.00	16.70	.	8.30	.
05APR89	A	1.10	.	23.0	.	21.80	.	.	.
05APR89	B	2.10	.	23.0	.	20.30	.	.	.
05APR89	C	3.10	.	23.0	.	21.40	.	.	.
05APR89	D	4.40	.	23.0	.	21.00	.	.	.
22JUL89	A	1.10	.	22.2	.	29.50	.	.	.
22JUL89	B	2.10	.	25.8	.	29.00	.	.	.
22JUL89	C	3.10	.	28.2	.	31.00	.	.	.
22JUL89	D	4.40	.	36.1	.	31.00	.	.	.
05DEC89	A	0.00	27	.	.	10.40	8.00	11.80	.
05DEC89	A	1.50	27	.	.	10.20	7.90	11.90	.
05DEC89	B	0.00	28	.	.	10.30	7.80	12.20	.
05DEC89	B	2.00	28	.	.	10.30	7.80	12.10	.
05DEC89	C	0.00	28	.	.	11.30	7.80	11.80	.

05DEC89	C	3.60	28	.	.	11.00	7.80	11.20	.
05DEC89	D	0.00	29	.	.	12.40	8.00	10.80	.
05DEC89	D	4.00	29	.	.	12.10	7.80	10.40	.
10APR90	A	0.00	20	19.4	31.00	19.77	8.23	8.20	.
10APR90	A	1.50	.	19.0	31.50	19.77	8.23	8.08	.
10APR90	B	0.00	20	21.6	33.10	19.96	8.26	8.67	.
10APR90	B	2.20	.	20.6	34.60	19.85	8.27	8.15	.
10APR90	C	0.00	26	26.1	40.50	19.90	8.25	8.15	.
10APR90	C	3.20	.	26.0	40.60	19.79	8.25	7.94	.
10APR90	D	0.00	27	27.6	41.70	20.41	8.34	8.63	.
10APR90	D	4.60	.	26.7	42.90	19.95	8.30	7.68	.
31JUL90	A	0.00	.	11.9	16.50	31.52	8.66	8.36	1.080
31JUL90	A	1.10	.	9.4	20.30	31.10	8.49	7.02	1.190
31JUL90	B	0.00	.	16.5	22.60	30.67	8.43	6.61	0.115
31JUL90	B	1.50	.	13.5	27.20	30.10	8.31	5.91	0.122
31JUL90	C	0.00	.	22.3	35.10	31.32	8.29	6.39	0.119
31JUL90	C	2.30	.	22.0	35.50	30.51	8.27	6.00	0.119
31JUL90	D	0.00	.	28.4	43.30	29.65	8.25	5.88	0.120
31JUL90	D	3.90	.	27.9	44.00	29.60	8.27	5.73	0.118
23OCT90	A	0.00	22	23.5	37.30	19.09	8.17	8.90	0.159
23OCT90	A	1.40	.	26.8	42.00	18.87	8.15	8.07	0.161
23OCT90	B	0.00	22	24.7	38.80	18.67	8.18	9.06	0.156
23OCT90	B	2.20	.	27.3	42.90	17.75	8.09	6.64	0.160
23OCT90	C	0.00	28	30.9	47.60	19.10	8.24	6.98	0.148
23OCT90	C	3.30	.	31.2	47.90	18.98	8.24	6.79	0.149
23OCT90	D	0.00	30	32.3	49.40	18.95	8.29	6.47	0.142
23OCT90	D	4.70	.	32.4	49.50	18.97	8.29	6.35	0.142
25JAN91	A	0.00	6	7.9	14.06	12.43	8.45	12.12	0.145
25JAN91	A	1.10	6	9.5	16.50	10.68	8.43	12.98	0.148
25JAN91	B	0.00	8	8.6	15.20	13.60	8.41	11.71	0.143
25JAN91	B	1.70	8	11.5	19.60	10.72	8.44	11.81	0.147
25JAN91	C	0.00	16	17.2	36.60	10.70	8.19	8.60	0.141
25JAN91	C	2.70	16	22.7	36.60	11.52	8.19	8.60	0.141
25JAN91	D	0.00	20	21.1	33.80	11.96	8.23	9.98	0.147
25JAN91	D	4.20	20	21.9	35.00	11.39	8.16	8.94	0.150
24APR91	A	0.00	3	2.4	5.21	24.98	7.95	8.48	0.143
24APR91	A	1.20	3	2.4	5.23	24.95	7.95	8.26	0.143
24APR91	B	0.00	4	4.3	8.35	24.31	7.92	8.24	0.147
24APR91	B	2.00	4	4.3	8.40	24.30	7.92	8.16	0.148
24APR91	C	0.00	10	10.4	18.10	23.64	7.88	8.03	0.145
24APR91	C	3.10	10	11.8	20.30	23.65	7.84	6.50	0.148
24APR91	D	0.00	20	20.9	33.50	23.79	7.87	7.34	0.152
24APR91	D	4.30	20	23.4	36.90	23.64	7.81	5.74	0.154

24JUL91	A	0.00	8	7.4	13.65	29.66	8.40	7.34	0.135
24JUL91	A	1.40	8	7.6	13.72	29.60	8.39	7.10	0.135
24JUL91	B	0.00	12	12.5	20.20	29.98	8.11	6.82	0.149
24JUL91	B	2.10	12	13.1	22.00	29.53	8.12	6.38	0.136
24JUL91	C	0.00	21	20.6	33.10	29.64	7.68	6.12	0.211
24JUL91	C	3.10	21	23.9	37.70	30.02	7.50	2.89	0.215
24JUL91	D	0.00	32	31.4	48.30	29.70	7.85	5.19	0.170
24JUL91	D	4.50	32	32.6	49.50	29.73	7.67	3.18	0.175

Table 7. Lavaca-Colorado Estuary macrofauna abundance ($n \cdot m^{-2}$) and biomass ($g \cdot m^{-2}$).

Date	Station	Abundance	STD	Biomass	STD
28NOV84	A	8149	2521	.	.
23JAN85	A	8451	4803	.	.
06MAR85	A	7621	3524	.	.
03APR85	A	5961	1925	.	.
08MAY85	A	7319	1699	.	.
05JUN85	A	7847	3073	.	.
17JUL85	A	7092	2483	.	.
14AUG85	A	5357	915	.	.
22OCT85	A	3546	692	.	.
04DEC85	A	2113	653	.	.
05FEB86	A	6036	1898	.	.
09APR86	A	14109	2911	.	.
04JUN86	A	7319	2267	.	.
06AUG86	A	5357	795	.	.
18APR88	A	29499	1771	7.381	2.875
19JUL88	A	7941	1725	0.824	0.633
22NOV88	A	9170	1181	2.687	1.577
05APR89	A	26757	6344	10.678	7.117
22JUL89	A	8035	2412	3.790	1.532
05DEC89	A	7658	2269	0.760	0.455
10APR90	A	14560	867	7.956	2.892
31JUL90	A	4349	1845	2.808	4.143
23OCT90	A	2269	750	0.208	0.046
25JAN91	A	1702	851	0.039	0.026
24APR91	A	1891	912	1.082	1.787
18APR88	B	18531	2412	2.605	0.494
19JUL88	B	11249	3124	1.886	1.578
22NOV88	B	8508	1860	0.667	0.450
05APR89	B	11629	2948	5.549	2.101
22JUL89	B	8508	2947	1.812	1.083
05DEC89	B	9455	1456	3.604	2.949
10APR90	B	12575	3592	3.418	1.567
31JUL90	B	4444	590	1.330	0.963
23OCT90	B	10400	3324	2.004	1.326
25JAN91	B	11251	1279	2.896	1.116
24APR91	B	3593	655	0.797	0.332
18APR88	C	32334	12286	13.456	12.015
19JUL88	C	17961	7553	5.989	3.402
22NOV88	C	14369	2147	4.429	1.452
05APR89	C	8226	4292	8.055	9.434
22JUL89	C	4821	2423	1.089	1.340

05DEC89	C	17586	7057	8.484	3.390
10APR90	C	22975	4687	9.729	5.110
31JUL90	C	22313	8069	7.154	1.831
23OCT90	C	42073	4932	51.454	34.782
25JAN91	C	25149	5746	16.861	7.671
24APR91	C	22218	4766	13.160	4.084
18APR88	D	101340	47872	12.249	4.113
19JUL88	D	25808	3196	10.579	5.802
22NOV88	D	41027	7851	3.817	1.118
05APR89	D	29782	2947	28.041	25.082
22JUL89	D	22972	3001	43.350	23.086
05DEC89	D	17397	4248	35.999	17.594
10APR90	D	25244	4643	26.730	13.264
31JUL90	D	12669	3934	6.370	5.801
23OCT90	D	8604	1889	9.814	3.021
25JAN91	D	15317	1300	5.895	2.275
24APR91	D	37440	10506	28.549	18.105

Table 8. Lavaca-Colorado Estuary species list. Average density ($n \cdot m^{-2}$) over entire study period.

Taxa	A	B	C	D
Cnidaria				
Anthozoa				
Anthozoa (unidentified)	0	17	17	95
Platyhelminthes				
Turbellaria				
Turbellaria (unidentified)	17	9	60	60
Rynchocoela				
Rhynchocoel (unidentified)	34	103	567	902
Phoronida				
Phoronis architecta	0	69	17	52
Mollusca				
Gastropoda				
Gastropoda (unidentified)	9	9	9	0
Caecidae				
Caecum johnsoni	0	0	17	34
Columbellidae				
Mitrella lunata	0	0	9	0
Nassariidae				
Nassarius acutus	34	43	34	34
Nassarius vibex	0	0	0	17
Pyramidellidae				
Odostomia sp.	26	17	0	0
Turbonilla sp.	0	26	103	9
Pyramidella crenulata	26	77	17	0
Pyramidella sp.	26	34	9	0
Retusidae				
Acteocina canaliculata	146	120	17	17
Crepidulidae				
Crepidula fornicata	0	0	0	26
Hydrobiidae				
Littoridina sphinctostoma	17	0	0	0
Scaphopoda				
Dentaliidae				
Dentalium texasianum	0	0	0	17
Pelecypoda				
Pelecypoda (unidentified)	43	26	43	576
Nuculanidae				
Nuculana acuta	0	0	9	60
Nuculana concentrica	26	52	43	43
Arcidae				
Anadara ovalis	0	0	0	9

Cultellidae				
Ensis minor	120	0	0	0
Leptonidae				
Mysella planulata	34	26	0	17
Tellinidae				
Macoma tenta	0	0	0	17
Tellina sp	69	52	0	9
Tellina texana	0	0	0	9
Macoma mitchelli	60	52	9	0
Semelidae				
Abra aequalis	0	0	0	95
Veneridae				
Mercenaria campechiensis	0	0	0	9
Corbulidae				
Corbula contracta	0	0	0	1057
Pandoridae				
Pandora trilineata	0	17	0	0
Sportellidae				
Aligena texasiana	0	0	17	0
Mactridae				
Mulinia lateralis	859	455	34	26
Periploma cf. *orbiculare*	0	0	129	1693
Periplomatidae				
Periploma margaritaceum	0	0	34	0
Solecurtidae				
Tagelus plebeius	69	0	0	0
Hiatellidae				
Hiatella arctica	0	0	0	138
Annelida				
Polychaeta				
Polychaete juv. (unidentified)	0	17	9	69
Polynoidae				
Eunoe cf. *nodulosa*	0	0	0	34
Polynoidae (unidentified)	0	0	0	9
Sigalionidae				
Sigalionidae (unidentified)	0	0	52	69
Palmyridae (= Chrysopetalidae)				
Paleanotus heteroseta	0	0	120	421
Phyllodocidae				
Eteone heteropoda	9	0	0	9
Anaitides erythrophyllus	9	0	0	0
Phyllodocidae (unidentified)	9	0	0	0
Pilargiidae				
Sigambra tentaculata	0	0	0	86
Ancistrosyllis groenlandica	0	0	9	17
Ancistrosyllis papillosa	0	0	9	17
Parandalia ocularis	69	0	17	0

Ancistrosyllis cf. *falcata*	0	0	0	9
Sigambra cf. *wassi*	0	0	0	9
Pilargiidae (unidentified)	0	0	9	17
Hesionidae				
Gyptis vittata	17	26	524	232
Podarke obscura	0	0	9	17
Syllidae				
Sphaerosyllis cf. *sublaevis*	0	0	0	9
Sphaerosyllis erinaceus	0	0	9	9
Brania clavata	0	0	455	9
Sphaerosyllis sp. A	26	17	26	163
Syllidae (unidentified)	0	0	60	9
Nereidae				
Ceratonereis irritabilis	0	0	9	0
Laeonereis culveri	9	9	0	0
Nereidae (unidentified)	34	0	17	86
Nephtyidae				
Aglaophamus verrilli	0	0	0	9
Glyceridae				
Glycera americana	0	9	43	26
Glycera capitata	0	0	0	9
Glyceridae (unidentified)	43	9	0	0
Goniadidae				
Glycinde solitaria	370	163	275	138
Onuphidae				
Diopatra cuprea	34	34	43	52
Arabellidae				
Drilonereis magna	0	9	1246	129
Dorvilleidae				
Schistomeringos rudolphi	0	0	9	26
Schistomeringos sp. A	0	0	26	0
Spionidae				
Polydora ligni	52	0	9	0
Minuspio cirrifera	0	0	395	1323
Paraprionospio pinnata	77	292	206	146
Apoprionospio pygmaea	0	0	17	0
Scolelepis texana	0	9	0	0
Polydora socialis	0	0	146	9
Streblospio benedicti	1229	2234	309	26
Polydora caulleryi	0	0	2432	1427
Polydora sp.	0	0	0	26
Scolelepis squamata	17	0	0	0
Spionidae (unidentified)	0	0	52	541
Magelonidae				
Magelona pettiboneae	0	0	26	0
Magelona phyllisae	0	0	9	9
Chaetopteridae				

Spiochaetopterus costarum	43	34	206	17
Cirratulidae				
Cirriformia filigera	0	0	9	0
Tharyx setigera	0	0	1435	17
Cossuridae				
Cossura delta	241	679	438	567
Orbiniidae				
Haploscoloplos foliosus	77	112	34	103
Naineris laevigata	0	0	17	352
Paraonidae				
Paraonidae Grp. A	0	0	275	34
Paraonidae Grp. B	0	0	963	524
Opheliidae				
Armandia maculata	0	0	0	69
Capitellidae				
Capitella capitata	26	9	0	0
Mediomastus californiensis	3334	2870	3730	4142
Notomastus latericeus	0	0	9	34
Notomastus cf. *latericeus*	0	0	26	52
Heteromastus filiformis	112	34	0	0
Mediomastus ambiseta	816	1461	3369	1899
Capitellidae (unidentified)	0	0	17	9
Maldanidae				
Branchioasychis americana	9	17	223	34
Clymenella torquata	17	0	103	26
Asychis sp.	9	0	258	0
Clymenella mucosa	52	69	318	17
Maldanidae (unidentified)	0	69	163	77
Oweniidae				
Owenia fusiformis	0	0	17	0
Flabelligeridae				
Brada cf. villosa capensis	0	0	0	9
Pectinariidae				
Pectinaria gouldii	0	0	0	9
Ampharetidae				
Melinna maculata	17	34	77	9
Terebellidae				
Amaenana trilobata	0	0	52	34
Pista palmata	0	0	17	0
Terebellidae (unidentified)	0	0	9	43
Sabellidae				
Sabella microphthalma	0	0	17	0
Megalomma bioculatum	0	9	17	0
Sabellidae (unidentified)	0	0	9	0
Oligochaeta				
Oligochaetes (unidentified)	0	0	86	756

Sipuncula				
Phascolion strombi	0	0	9	138
Sipuncula (unidentified)	0	0	0	9
Crustacea				
Ostracoda				
Myodocopa				
Sarsiella texana	17	0	17	0
Sarsiella spinosa	0	0	9	9
Copepoda				
Calanoida				
Diaptomidae				
Pseudodiaptomus coronatus	9	34	26	43
Cyclopoida				
Cyclopidae				
Hemicyclops sp.	9	0	0	0
Lichomolgidae				
Cyclopoid copepod (commensal)	95	26	0	0
Malacostraca				
Natantia				
Ogyrididae				
Ogyrides limicola	0	9	9	0
Reptantia				
Paguridae				
Pagurus annulipes	0	0	0	26
Pagurid juv.	0	0	17	0
Portunidae				
Callinectes similis	0	0	9	0
Xanthidae				
Xanthidae (unidentified)	0	0	9	0
Pinnotheridae				
Pinnixa sp.	0	0	0	43
Pinnixa cristata	0	0	17	0
Pinnixa chacei	0	0	17	120
Pinnixa retinens	0	0	17	0
Pinnotheridae (unidentified)	0	0	0	9
Brachyuran Larvae				
Megalops	0	0	0	9
Mysidacea				
Mysidopsis bigelowi	0	0	60	0
Mysidopsis bahia	17	9	26	17
Mysidopsis sp.	0	26	9	9
Cumacea				
Cyclaspis varians	95	103	0	0
Oxyurostylis sp.	0	9	26	9
Leucon sp.	77	120	9	0
Oxyurostylis salinoi	0	0	138	0
Oxyurostylis smithi	86	17	43	9

Eudorella sp.	0	43	17	0
Amphipoda				
Amphipoda (unidentified)	0	0	9	17
Ampeliscidae				
Ampelisca sp. B	0	0	9	43
Ampelisca abdita	1461	138	52	9
Ampelisca verrilli	0	0	17	0
Gammaridae				
Gammarus mucronatus	9	0	0	0
Oedicerotidae				
Monoculodes sp.	26	17	26	0
Corophiidae				
Erichthonias brasiliensis	0	0	0	34
Photis sp.	0	0	17	0
Microprotopus spp.	26	17	0	0
Liljeborgiidae				
Listriella barnardi	9	9	52	60
Listriella clymenellae	0	0	17	0
Caprellidae				
Caprellid	9	0	17	9
Amphilochidae				
Amphilochus sp.	0	0	9	0
Isopoda				
Idoteidae				
Edotea montosa	34	0	0	0
Tanaidacea				
Apseudidae				
Apseudes sp. A	0	0	9	9840
Echinodermata				
Ophiuroidea				
Ophiuroidea (unidentified)	0	0	249	576
Chordata				
Hemichordata				
Schizocardium sp.	0	9	284	610

EFFECTS OF THE LAGUNA MADRE, TEXAS BROWN TIDE ON BENTHOS

The Brown Tide Event

In January 1990, a bloom of an undescribed species of a chysophyte began in the upper reaches of Baffin Bay, Texas bordering the King Ranch. The chrysophyte is a small (5 μm in diameter) single cell diatom, with a crescent-shaped chloroplast. Bloom conditions did not exist until later in the spring. In fact, the brown tide was not noticed until it reached the adjacent Laguna Madre (Figure 1). The brown tide went unnoticed for 5 months, because it occurred in an unpopulated area. Sport or commercial fisherman did not report the event either. In the Laguna Madre it could not go unnoticed. The chlorophyll content in the water increased by almost two orders of magnitude, and the visibility over the seagrass beds dropped from 10 feet to less than 1 inch. You could not see you hand when it was placed just below the surface of the water. Once the brown tide bloom reached the Laguna Madre, it quickly spread to adjacent estuaries. By late summer 1990, the prevailing south-westerly winds had spread the tide north to (but not in) San Antonio Bay. The wind-reversing northerlies of fall 1990 and winter 1991 reversed the brown tide movement. The southern (or lower) Laguna Madre was completely covered during this period. Over the entire year the brown tide covered an area of about 150 linear miles. A wet spring and summer in 1991 has led to a decline in the bloom conditions, but the chrysophyte is still present.

It is impossible to know, in hindsight, exactly what caused the brown tide bloom. However, since several research projects were in progress at the time, more is probably known about the causes and effects of this brown tide than any other. Several events were coincident at the outset of the brown tide suggesting that there were multiple causes, and that they must occur at the same time, since these events occurred by themselves regularly in the past without causing brown tides. The 2-year period preceding the brown tide was very dry. Salinities rose from 30 ppt in 1986 to 45 ppt in 1989 during the drought. During the spring of 1990, the drought was broken by a spring flood event that elevated nutrient levels in Baffin Bay and Laguna Madre. There was also a freeze in December 1989 just prior to the first signs of the brown tide. The freeze occurred during a period of low tides. The combination of cold and shallow water led to an enormous fish kill. This resulted in an enormous amount of nitrogen, which had been locked up in fish biomass, being released into the water. It is probable that the combination of the freeze coming after a drought was the primary cause of the brown tide. Nutrients were dumped into a system that had low diversity, low stability, and was nutrient depleted. These are ideal conditions for a bloom event. Other conditions were also present and could have had a role in causing the bloom. Maintenance dredging was being performed in the Intracoastal Waterway (ICW), and the King Ranch had put a large tract close to Baffin Bay in agriculture. Finally, Baffin Bay and Laguna Madre are characterized by little circulation, and a microtidal range. The lack of adequate circulation also contributed to low flushing of the bloom organism.

The immediate concern of the brown tide was that the concomitant water transparency and light reductions could lead to loss of seagrass bed habitats. The degradation of the habitats would be an environmental disaster. The Laguna Madre and Baffin Bay have great value. This region of the Texas coast yielded 53% of the total commercial finfish harvest during the last 20 years. It is an overwintering ground for the endangered redhead ducks. It is one of the last relatively pristine areas, the human population density is low, and it is bordered by the King Ranch on one side and the Padre Island National Seashore on the other side. The principal human activities in the area are tourism, oil and gas production, and transportation (via the ICW). The local tourism and fishing industry was devastated by the brown tide during the summer of 1990, but has recovered significantly in the summer of 1991. Although, the potential for negative effects on seagrass exists, it probably has not occurred. The seagrasses had enough carbon stored in roots to survive and grow during the brown tide (at least down to a depth of 1 - 1.3 m). Fortunately, the beds were mapped in 1988 by the U.S. Fish and Wildlife Service and they plan a post-brown tide survey. Until the beds are mapped again, the extent of effects on seagrass won't be known.

The Effect of Brown Tide on Benthos

The main effect of brown tide on benthos in other areas of the U.S. was the decline of bivalve mollusk densities due to clogging of feeding appendages by the small chrysophyte. This led to a severe economic loss in shellfish fisheries of the northeast. In Texas, there is a climatic gradient from northeast to southwest of decreasing rainfall and concomitantly decreasing freshwater inflow to estuaries. Due to a lack of sufficient inflow, only the northeastern estuaries of Texas support a commercial oyster industry. Therefore, the economic effects of brown tide in south Texas would not be direct effects on benthos, but indirect effects could alter food webs and have dramatic consequences.

A variety of benthic studies have been performed to examine productivity of (both autotrophic and heterotrophic) microbial producers, and abundance and community structure of macrobenthic organisms. These studies were performed in Baffin Bay and the upper Laguna Madre. Benthic nutrient regeneration, oxygen consumption, and bacterial biomass and productivity were studied bimonthly for one year before the brown tide event. Biomass, productivity and responses to light by microphytobenthos were studied before and after the brown tide. Macrofauna were sampled bimonthly until January 1990 and quarterly thereafter.

Baffin Bay is deeper and more turbid than the Laguna Madre, so one may suppose that benthic primary production by microphytobenthos is low. Prior to the brown tide, the shade-adapted microphytobenthos produced up to 3 g $C \cdot m^{-2} \cdot d^{-1}$ in Baffin Bay sediments (Figure 2). The amount fluctuates daily, decreasing with wind-induced resuspension of sediments, which blocks light reaching the bottom. After the brown tide, no benthic photosynthesis occurred because of a lack of light reaching the bottom (Figure 3). This represents a great loss of autotrophic production, and consequently high quality food, to the benthic food web.

Sediment bacterial production is correlated with bacterial cell abundance (Table 1). Sediment oxygen consumption and inorganic nitrogen regeneration are correlated with bacterial production. Baffin Bay sediments are sources of regenerated nitrogen, and Laguna Madre sediments are sinks for nitrogen. The uptake of nitrogen by Laguna Madre sediments is probably due to absorption by seagrass roots.

There are indications that a disturbance of some sort was already occurring in the sediments of Baffin Bay and Laguna Madre prior to the brown tide. In early 1989, the macrofauna community was very abundant and diverse. However, from August 1989 to January 1990, abundance was increasing while diversity was decreasing (Figures 4-5). The community in Baffin Bay was dominated by a single species, the polychaete worm *Streblospio benedicti* (Table 2). This pattern is typical of a disturbed benthic community. During the onset of the brown tide, abundances and diversity decreased to near zero. As found in the northeast, bivalve mollusks disappeared within weeks after the brown tide onset. Baffin Bay is now completely dominated by *Streblospio*, while Laguna Madre is dominated by polychaetes and gastropods. *Streblopsio* is a suspension feeder and a deposit feeder. There has been a complete alteration of the benthic food web. The loss of the bivalves, particularly *Mulinia lateralis*, is of great concern, since it is reported to be the dominant food source of black drum.

The hypersaline Baffin Bay-Laguna Madre ecosystem is a very fragile environment. This is indicated by the lack of stability in the ecosystem. When the equilibrium was put out of balance by the loss of diversity, the benthic system rapidly deteriorated and crashed. This crash could be either a pre-condition, causal mechanism, or a contributing factor for the onset of the brown tide. The ecosystem was apparently already disturbed and did not have the stability to withstand further disturbance. An alternative hypothesis is that what ever caused the disturbance that led to the benthic response before the brown tide also caused the brown tide. If this is true then benthos could play the role of "canary" to future blooms.

Table 1. Descriptive statistics of microbial and sediment variables by station over the entire study period. Variables are follwed by abbrieviations in parentheses. Statistics include mean ± standard error and number of observations in parentheses.

		STATION		
VARIABLE	UNITS	VEGETATED	BARE-PATCH	MUD
Bacterial abundance (BA)	10^9 cells•cm^{-3}	5.41 ± 3.08 (36)	3.25 ± 2.76 (36)	5.72 ± 1.43 (36)
Bacterial production (BP)	μg C•cm^{-3}•h^{-1}	1.78 ± 2.13 (36)	0.43 ± 0.51 (36)	1.92 ± 2.09 (36)
Specific growth rate (SGR)	d^{-1}	0.25 ± 0.23 (36)	0.12 ± 0.11 (36)	0.28 ± 0.31 (36)
Oxygen metabolism (OM)	mmol•m^{-2}•h^{-1}	3.96 ± 2.12 (48)	1.42 ± 0.71 (48)	0.87 ± 0.46 (48)
Dissolved organic carbon (DOC)	μg C•cm^{-3}	30.7 ± 11.0 (36)	24.6 ± 7.86 (36)	14.6 ± 3.14 (36)
Total organic carbon (TOC)	mg C•cm^{-3}	13.6 ± 4.27 (11)	11.1 ± 2.52 (11)	5.99 ± 1.73 (11)
Organic carbon content (C)	%	1.96 ± 0.76 (11)	1.27 ± 0.90 (11)	1.82 ± 0.11 (11)
Total organic nitrogen (TON)	mg N•cm^{-3}	0.96 ± 0.26 (11)	0.78 ± 0.26 (11)	0.64 ± 0.10 (11)
Organic nitrogen content (N)	%	0.14 ± 0.08 (11)	0.09 ± 0.09 (11)	0.20 ± 0.04 (11)
Molar C to N ratio (CN)	--	16.6 ± 2.6 (11)	17.6 ± 4.6 (11)	10.8 ± 1.6 (11)
Ammonium concentration (NH4)	μM	55.3 ± 34.4 (36)	72.9 ± 60.6 (36)	138 ± 88.6 (36)
Nitrite concentration (NO2)	μM	3.47 ± 2.84 (36)	2.35 ± 3.73 (36)	2.38 ± 3.56 (36)
Nitrate concentration (NO3)	μM	4.11 ± 6.60 (36)	1.89 ± 3.26 (36)	3.77 ± 7.09 (36)
Chlorophyll concentration[a] (CHL)	mg•m^{-2}	20.8 ± 7.97 (36)	27.6 ± 8.38 (36)	11.1 ± 6.70 (36)
Phaeopigment concentration[a] (PHA)	mg•m^{-2}	111 ± 21.7 (36)	64.9 ± 17.3 (36)	59.1 ± 10.4 (36)
Water content (W)	%	45.7 ± 13.4 (11)	36.6 ± 14.3 (11)	72.7 ± 6.80 (11)
Percent sand[b] (SA)	%	77.07 (1)	81.55 (1)	30.67 (1)
Percent silt[b] (SI)	%	0.92 (1)	3.64 (1)	15.41 (1)
Percent clay[b] (CL)	%	5.71 (1)	3.99 (1)	48.36 (1)

[a] integrated to 1 cm depth.

[b] Results of single samples of 0-3cm strata sediment collected during the March 1989 sampling.

Table 2. Macrofauna community composition over two years. Brown tide started in January 1990 in Baffin Bay, and reached Laguna Madre in June 1990. Table finds average percent abundance from 6 replicates.

Taxa	1989 Mar	May	Jul	Nov	1990 Jan	Apr	Jul	Oct
BAFFIN BAY								
Mollusca	29	28	0	1	1	12	2	0
Polychaeta	63	66	†99	98	99	88	97	100
Crustacea	8	4	0	1	0	0	1	0
Other	0	2	1	0	0	0	0	0
LAGUNA MADRE								
Mollusca	23	14	17	14	10	-	-	‡80
Polychaeta	70	55	70	76	84	-	-	18
Crustacea	6	30	10	9	3	-	-	2
Other	1	1	3	1	3	-	-	0

†start *Streblospio benedicti* dominance
‡all Gastropoda

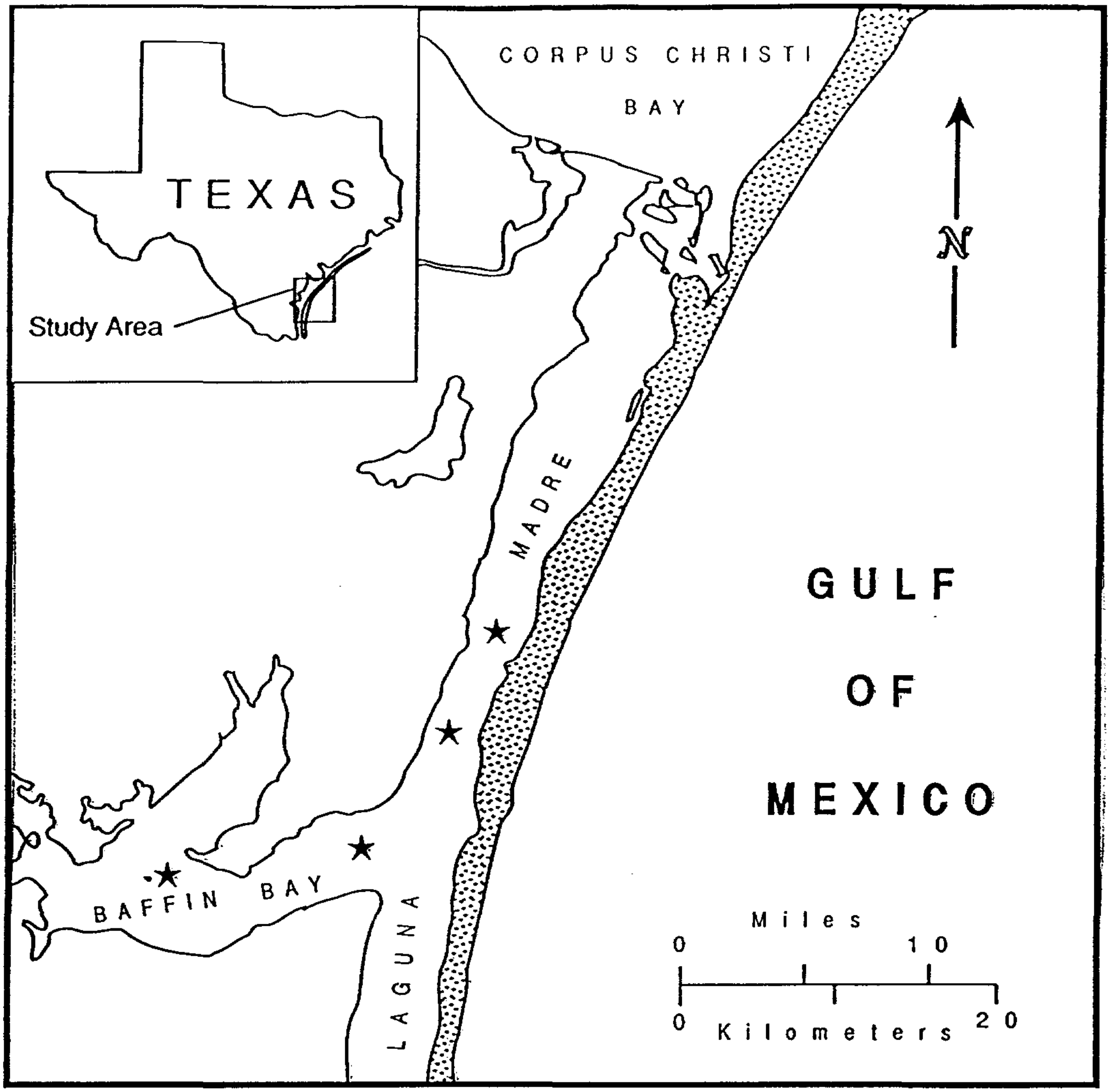

Figure 1. Study area. Stations sampled are marked with stars. The two stations in Laguna Madre were paired seagrass bed (*Halodule wrightii*) and bare patch stations.

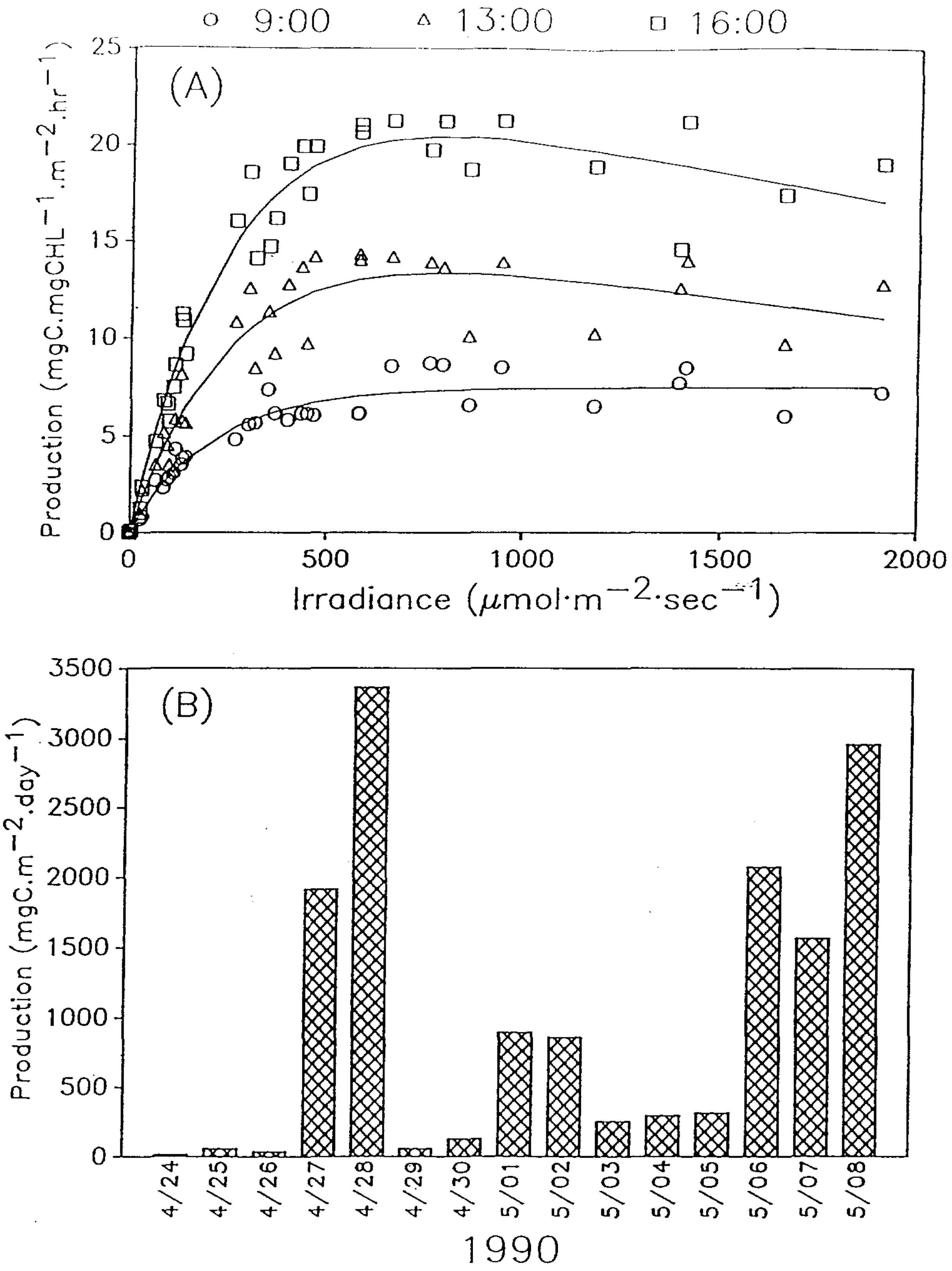

Figure 2. Microphytobenthos primary production. (A) Production as a function of light irradiance during the day. (B) Modeled daily production based on bottom light measurements and photosynthetic parameters calculated from A.

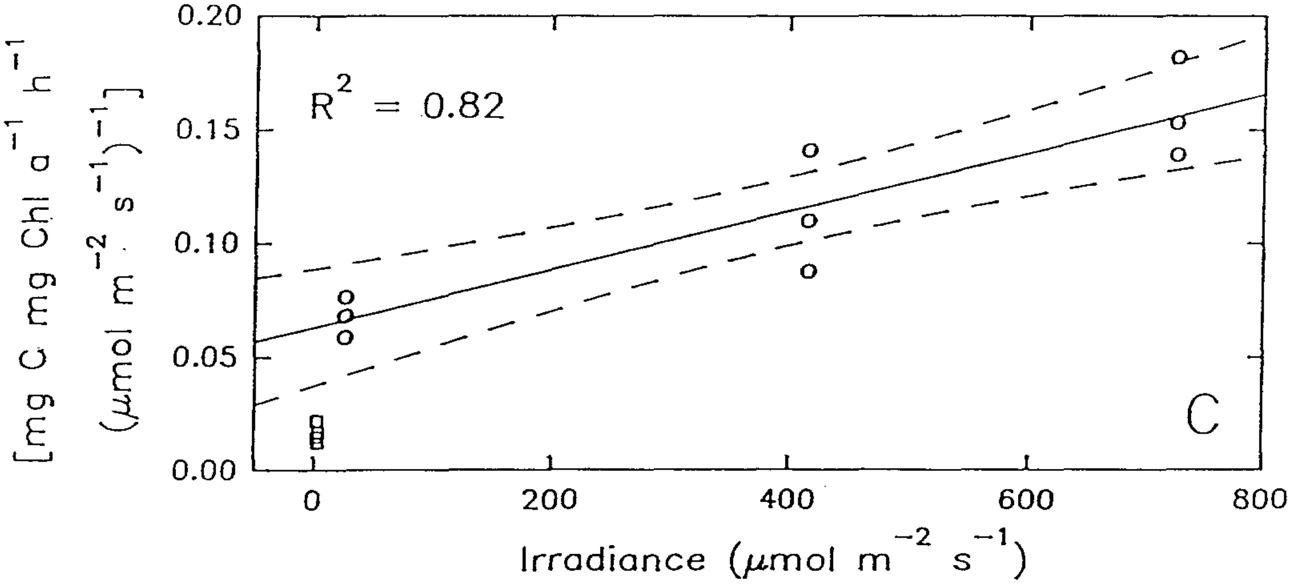

Figure 3. Effect of brown tide on photosynthetic parameters of microphytobenthos. o=May 1990 (before brown tide) and □=July 1990 (during brown tide).

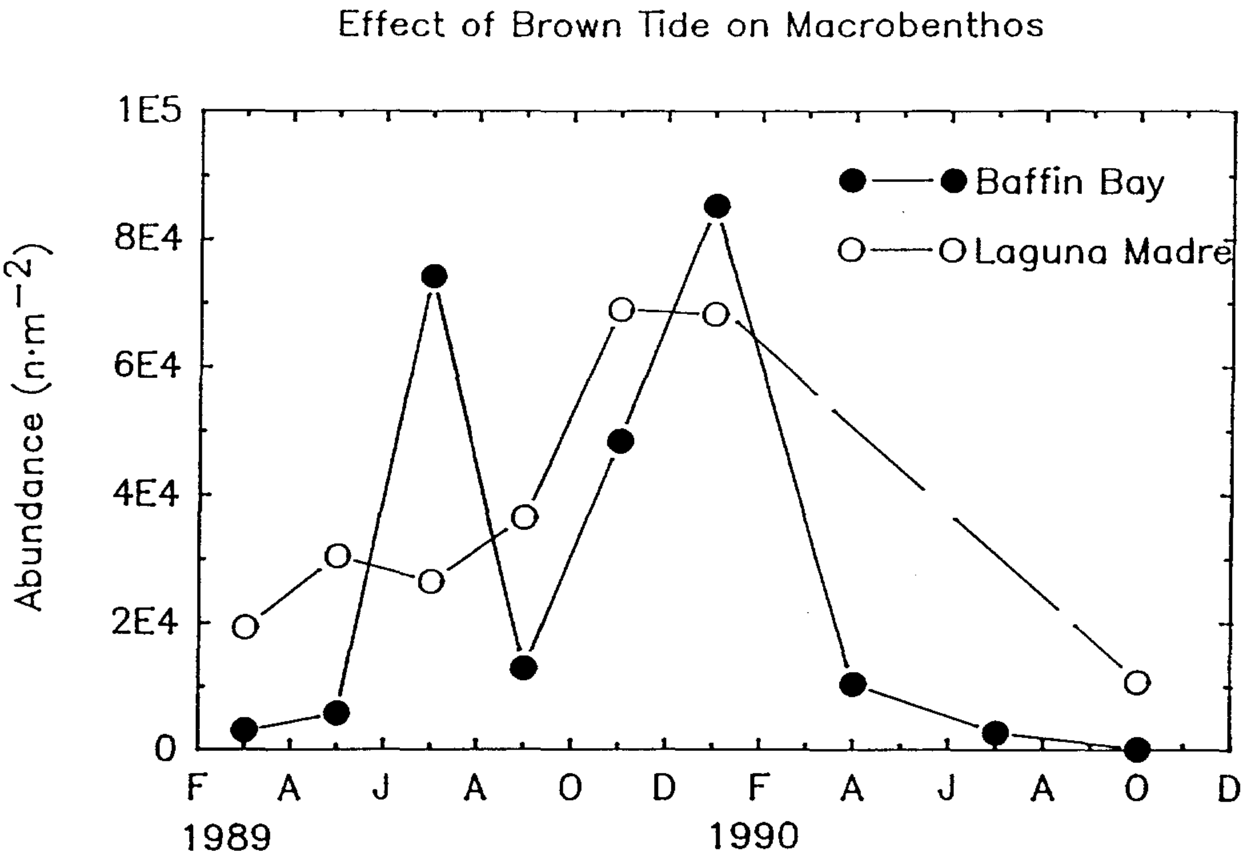

Figure 4. Effect of brown tide on macrobenthos abundance in Baffin Bay and Laguna Madre. Brown tide appeared at these station in June 1990.

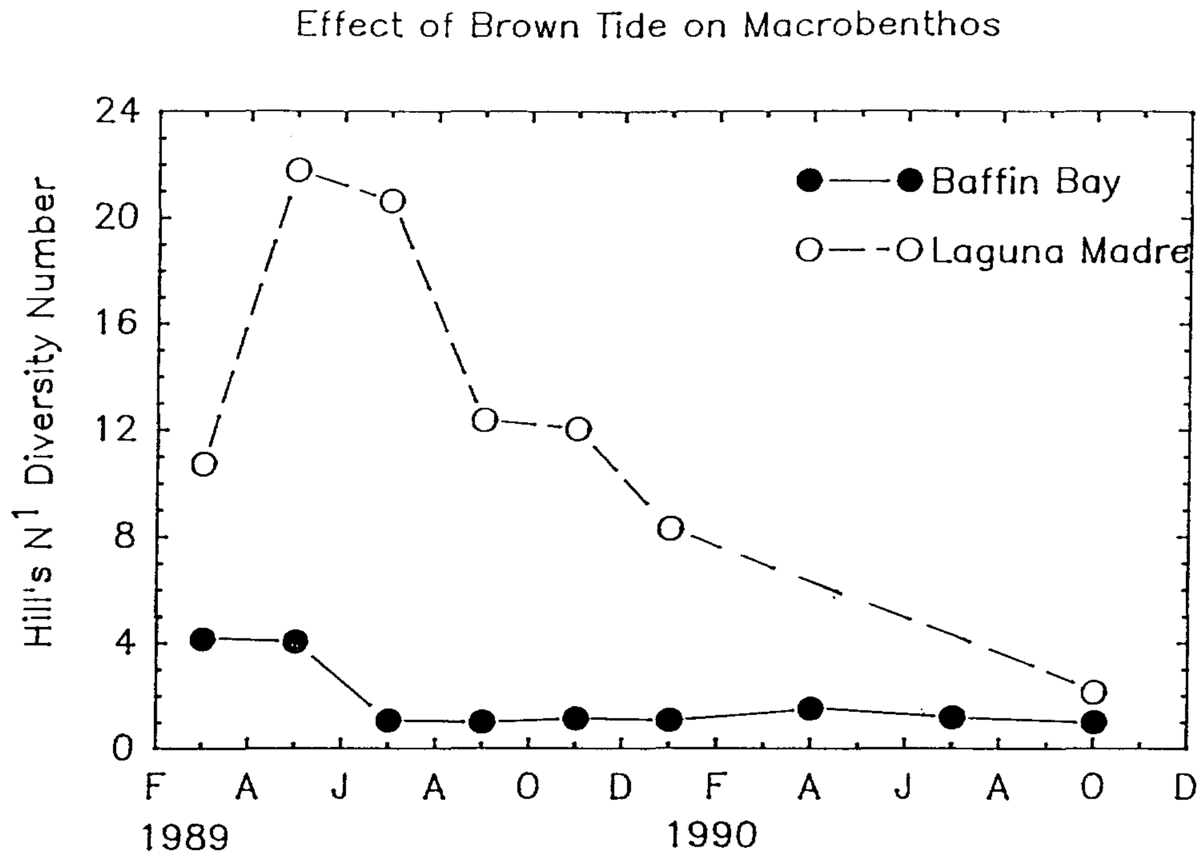

Figure 5. Effect of brown tide on macrobenthos diversity in Baffin Bay and Laguna Madre. Hill's diversity number is a measure of the number of dominant species.