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# Effect of Restored Freshwater Inflow on Macrofauna and Meiofauna in Upper Rincon Bayou, Texas, USA 

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#### Abstract

Construction of two dams in 1958 and 1982 reduced freshwater inflow events to Rincon Bayou, part of the Nueces Delta near Corpus Christi, Texas, USA. Inflow reduction led to a reverse estuary, where low-salinity water flooded the delta on incoming tides and higher salinities were found near the Nueces River. Hypersaline conditions caused by high evaporation rates and low water levels were common during summer in the upper reaches. In October 1995, an overflow diversion channel was created by lowering the bank of the Nueces River to restore inflow events into Rincon Bayou, which is the main stem creek that runs through the center of the Delta. Hypersaline conditions occurred four times from mid-1994 to mid-1997 and only once after mid-1997. Lower, rather than higher, salinity conditions were found after August 1997 in the upper reaches. Benthic faunal recovery was monitored by changes in macrofauna and meiofauna communities. Macrofauna responded to inflow events with increased abundances, biomass, and diversity but decreased during hypersaline conditions. Meiofauna abundance also increased with increasing inflow. Benthic characteristics were different in Rincon Bayou than in a reference site, upstream from introduced inflow. As inflow events have increased due to the diversion, the opportunities for positive responses to increased flow have increased. Although the overflow channel was filled in at the end of the demonstration project in fall 2000, the City of Corpus Christi reopened the channel in fall 2001 because the ecological benefits were credited toward the state-mandated minimum flow requirement for the Nueces Estuary.


## Introduction

Construction of two dams in the Nueces Basin reduced freshwater inflow events to the Nueces Delta, part of the Nueces estuary near Corpus Christi, Texas, USA. Wesley Seale Dam (Lake Corpus Christi) was built in 1958 on the Nueces River and Choke Canyon Dam (Choke Canyon Reservoir) was built in 1982 on the Frio River, just upstream from where it joins the Nueces River. From 1983-1996 (post-Choke Canyon), annual stream flow volumes in the Nueces River near Mathis, Texas deceased $55 \%$ relative to 1940-1982 (pre-Choke Canyon; Asquith et al. 1997). Salinity in Nueces Bay has increased on average $0.5 \%$ o $\mathrm{yr}^{-1}$ from 1958-1995 (Ward and Armstrong 1997). Inflow reduction and bypassing the Delta led to a reverse estuary, where freshwater flooded the Delta on incoming tides and higher salinity dominated the upper reaches of the Delta near the River. On October 26, 1995, the U.S. Bureau of Reclamation completed opening an overflow channel from the Nueces River to Rincon Bayou, which is the main stem channel of the Nueces Delta marsh (Fig. 1). The purpose of the channel was to increase opportunities for freshwater inflow to the delta marsh and associated tributaries to improve ecological value

[^0]of the marsh (Ward 1985). It was hypothesized that increased freshwater inflow to the delta would create or enhance marsh habitats (Stevens et al. 1995), stimulate primary productivity (Glenn et al. 1996), and consequently stimulate secondary productivity (Comin et al. 2001).

Abundance and biomass of benthic infauna increase when nutrient loading from river input is transformed into food for benthic animals (Montagna and Yoon 1991). This occurs because nutrients introduced by a river stimulate primary production (Deegan et al. 1986; Nixon et al. 1986). Primary production can be deposited locally or advected and deposited further downstream, potentially increasing benthic productivity away from the source of inflow. This assumes that freshwater and low salinity do not have a negative effect. Salinity stress on physiology (Finney 1979) and hypoxia (Ritter and Montagna 1999) could reduce benthic populations. The net effect of freshwater inflow on biological processes (enhanced productivity, recruitment gains, and losses via low-salinity intolerance) is a function of the interaction between physical processes (sedimentation, resuspension, advection, and seawater dilution) and chemical processes (nutrient enrichment and cycling; Longley 1994). If freshwater inflow enhanced benthic productivity, then increased abundance and biomass should be found if inflow is reintroduced to the Rincon Bayou Marsh.


Fig. 1. Rincon Bayou, Nueces Delta, Texas. Locations of stations in three sites: reference site (stations A and B), upper Rincon Bayou (stations C and D), and central Rincon Bayou (stations E and F).

The goal of the current study was to document change in benthos as a result of diverting and restoring freshwater inflow from the Nueces River into upper Rincon Bayou. Benthic infauna are useful indicators of long-term effects because they are relatively immobile and long-lived compared to plankton of similar sizes. Benthos also integrate the cascading interactions of increasing freshwater inflow, nutrients, and primary productivity. The two objectives were to assess the effect of the diversion project on benthic macroinfauna biomass, abundance, and diversity; and to assess the response of benthos with different ecological roles by examining meiofauna ( $<0.5$ and $>0.063 \mathrm{~mm}$ in size) and macrofauna ( $>0.5 \mathrm{~mm}$ in size).

## Materials and Methods

## Study Design

The Nueces River overflow channel was created by lowering the river bank leading to the head of Rincon Bayou (Fig. 1). The channel was created to increase the opportunity of freshwater inflow events into upper Rincon Bayou. The Rincon Bayou overflow channel was created by lowering the banks of Rincon Bayou to increase events into the upper Nueces Marsh. The Nueces River overflow channel was activated during 31 inflow events occurring over the course of this study, but the Rincon Bayou overflow channel was active only twice (Bureau of Reclamation 2000).

Sampling began (October 28, 1994) one year before the overflow channels were cut (October 29, 1995), and continued for five additional years (October 28, 1999). Samples were taken quarterly in January, April, July, and October of each year. Be-
cause the first sample of the second year was taken early (October 3, 1995) there are five pre-project samples and 16 post-project samples.

At each sampling period one reference and two impact sites were sampled. The reference site (stations A and B) was located upstream from the overflow channels, reflecting natural variability, but not diversion effects (Fig. 1). Rincon Bayou is subdivided by constrictions into three parts. The upper Rincon Bayou is nearest the Nueces overflow channel and has the most river influence. The central Rincon Bayou has potentially less river influence, but more tidal influence, and is below a road crossing constriction. Two stations were located in the upper Rincon Bayou site (stations C and D), and two stations were located in further downstream in the central Rincon Bayou site (stations E and F). The boundary for the lower Rincon Bayou is downstream of the railroad bridge. The current study is restricted to the upper and central Rincon Bayou.

The study was designed to test for differences in time and space. Samples were taken quarterly before and after the Rincon Bayou overflow channel was built. At each sampling period reference (without impacts) and impact sites were sampled. This is similar to a before versus after, control versus impact experimental design (Green 1979), but the reference site is not actually a control because other environmental differences could exist between any two sites. The reference stations (A and B) were not affected by freshwater diversions to Rincon Bayou (stations C, D, E, and F). The response variables measured are benthic macrofaunal biomass, abundance, and species diversity, and meiofaunal abundance and major taxa diversity. Three replicate samples were taken at each station during each sampling date.

## Environmental Measurements

The physical hydrographic conditions of the water column overlying sediments were measured at each station for each sampling period. Measurements were collected at the surface and near the bottom with a multiparameter instrument (Hydrolab Surveyor II). The following parameters are read from the digital display unit (accuracy and units): temperature ( $\pm 0.15^{\circ} \mathrm{C}$ ), pH ( $\pm 0.1$ units), dissolved oxygen ( $\mathrm{mg} \mathrm{L}^{-1} \pm 0.2$ ), specific conductivity ( $\pm 0.015-1.5 \mathrm{mmhos} \mathrm{cm}^{-1}$ depending on range), redox potential ( $\pm 0.05 \mathrm{mV}$ ), depth ( $\pm 0.1$ m ), and salinity in parts per thousand (\%o) automatically corrected to $25^{\circ} \mathrm{C}$.

Current flow and tidal elevation were obtained from U.S. Geological Survey gauges. One gauge was in the Nueces River at Calallen just above the diversion (station 08211500). The second gauge was in Rincon Bayou, just downstream from the
diversion point (station 08211503). Rainfall data was collected from the National Weather Service station at the Corpus Christi International Airport, about 10 km away from Rincon Bayou, through May 16, 1996 and at the Rincon Bayou gauge after that date.

## Benthos Measurements

Meiofauna were sampled by hand with a $1.8-\mathrm{cm}$ diameter core tube, and sectioned at depth intervals of $0-3 \mathrm{~cm}$ only (Montagna and Kalke 1992). Samples were preserved with $5 \%$ buffered formalin. In the laboratory, samples were sorted on $0.063-\mathrm{mm}$ sieves and identified to higher taxonomic levels (usually phylum, class, or order) and counted.

Macrofauna were sampled by hand with a $6.7-\mathrm{cm}$ diameter tube, and sectioned at depth intervals of $0-3$ and $3-10 \mathrm{~cm}$ and preserved with $5 \%$ buffered formalin. In the laboratory, macrofauna were sorted on $0.5-\mathrm{mm}$ sieves (Kalke and Montagna 1991). Macrofauna were identified to the lowest taxonomic level possible (usually the species level) and counted. Biomass was measured by combining individuals into higher taxa categories, i.e., Crustacea, Mollusca, Polychaeta, and others. Samples were then dried for 24 h at $55^{\circ} \mathrm{C}$ and weighed. Mollusks were placed in 1 N HCl until carbonate shells dissolved, washed before drying, and weighed to the nearest 0.01 mg for shell-free dry weight.
Species diversity was calculated by pooling all replicate cores for each site. Diversity is calculated using Hill's diversity number one (N1; Hill 1973). It indicates the number of abundant species in a sample and is a measure of the effective number of species (Ludwig and Reynolds 1988). The effective number of species is a measure of the degree to which proportional abundances are distributed among species (Hill 1973). It is calculated as the exponentiated form of the Shannon diversity index: $\mathrm{N} 1=e^{H^{\prime}}$. As diversity decreases N1 will tend toward one. The Shannon index is the average uncertainty per species in an infinite community made up of species with known proportional abundances. Hill's N1 was used because the unit, numbers of species, is easier to interpret than most other diversity indices.

## Statistical Analyses

Statistical analyses were performed using SAS software (SAS 1991). All data (except when calculating diversity) were log transformed prior to analysis. A 2 -way ANOVA was used to test for differences in meiofauna abundance, and macrofauna abundance, biomass, and diversity within sampling dates and sites. Because all samples were pooled to calculate diversity, there is no interaction for that
test. If a significant interaction was encountered then simple main effects were examined. Analysis of simple main effects is accomplished by converting the treatments into a one-way ANOVA for each date $\times$ site cell. Linear contrasts were used to test for differences before and after the diversion and between reference and impacted sites.

Community structure of macrofauna species was analyzed by multivariate methods. Ordination of samples was performed using the non-metric multidimensional scaling (MDS) procedure described by Clarke and Warwick (2001) and implemented in Primer software (Clarke and Gorley 2001). The software creates a Bray-Curtis similarity matrix among all samples and then an MDS plot of the spatial relationship among the samples. The data set contains two main effects, sampling date and site, so the MDS patterns were plotted twice, once using the site name as the symbol and once using the sample sequence number as the symbol.

The relationship between macrofauna characteristics and salinity were examined with a non-linear model. The assumption behind the model is that there is an optimal range for salinity and values decline prior to and after meeting this maximum value. That is, the relationship resembles a bellshaped curve. The shape of this curve can be predicted with a three-parameter, log normal model:

$$
\mathrm{Y}=\mathrm{a} \times \exp \left(-0.5 \times(\ln (\mathrm{X} / \mathrm{c}) / \mathrm{b})^{2}\right)
$$

The model was used to characterize the nonlinear relationship between a biological characteristic ( Y ) and salinity (X) and inflow (X). The three parameters characterize different attributes of the curve, where $a$ is the maximum value, $b$ is the skewness or rate of change of the response as a function of salinity, and $c$ the location of the peak response value on the salinity axis. The model was fit to data using the Regression Wizard in SigmaPlot, which uses the Marquardt-Levenberg algorithm to find coefficients (parameters) of the independent variables that give the best fit between the equation and the data (SigmaPlot 2000).

## Results

## Environmental Conditions

The water column overlying sediments changed on varying temporal scales because of natural freshwater inflow events, e.g., wet and dry periods, as well as the emplacement of the overflow channel. A total of 37 events occurred during the study period (Bureau of Reclamation 2000). Salinity ranges were extreme in Rincon Bayou, varying from freshwater conditions (near $<0.5 \%$ ) to hypersaline conditions ( $>36 \%$; Fig. 2). The highest salinity was $140 \%$ o in the upper site during July 1996. The temporal trends were similar at different


Fig. 2. Physical characteristics for sampling periods. A) Cumulative rainfall and inflow between sampling periods. B) Average salinity at all sites on sampling dates
sites, but were not always the same. Prior to the diversion (1994-1995), the reference site always had lower salinities (average $21.0 \%$ o) than Rincon sites (average $31.7 \%$ ), which were similar. After the diversion, the Rincon sites (average $20.4 \%$ o) were slightly less than the reference site (average $22.8 \%$ o).

Inflow into and out of Rincon Bayou was measured daily (Bureau of Reclamation 2000). Salinities at benthic stations were measured quarterly, so rain and inflow were summed for the quarterly sampling dates to compare cumulative effects of dilution on average salinity at all stations (Fig. 2). Cumulative inflow was correlated with cumulative rain, ( $\mathrm{r}=0.57, \mathrm{p}=0.0068$ ), and salinity was inversely correlated with cumulative inflow ( $\mathrm{r}=$ $-0.40, \mathrm{p}=0.0717$ ) and cumulative rain ( $\mathrm{r}=$ $-0.63, \mathrm{p}=0.0020$ ). The Rincon overflow channel gauge was not in place prior to May 1, 1996. There were no inflows prior to channel emplacement, and there was only one large rainfall event between channel opening and gauge deployment (October $26,1996)$. Over the entire period rainfall events occurred frequently, but there were only three periods with large inflow events (July through October 1997, October 1998, and October 1999). Only two of those events (October 1997 and 1998) were
sufficient to cause inflow to Rincon Bayou without the overflow channel. Hypersaline conditions resulted from near zero inflows and high evaporation rates, which typically occurred in summer. The difference between the dry summers of 1996 and 1998 demonstrate the reverse estuary conditions that existed in Rincon Bayou prior to overflow channel emplacement. The reverse estuary is where salinity patterns are reverse that expected, i.e., higher salinities occur at the river source because of evaporation rather than the tidal source. Early in the study, the estuary had higher salinities in the upper Rincon Bayou. Later, higher salinities occurred in the central Rincon Bayou.

Water temperature ranged from a maximum of $40.5^{\circ} \mathrm{C}$ to a minimum of $10.5^{\circ} \mathrm{C}$. Average July temperature was $30.3^{\circ} \mathrm{C}$ and average January temperature was $16.2^{\circ} \mathrm{C}$. There was considerable interannual variability, with a $5.7^{\circ} \mathrm{C}$ range between warmest (1995) and coldest (1997) years. The interannual range reflected inflow and water depth differences among years, not air temperature differences. Generally, the central Rincon had the highest temperatures (average $24.4^{\circ} \mathrm{C}$ ), followed by the upper Rincon (average $23.0^{\circ} \mathrm{C}$ ). The reference site had the lowest temperatures (average $22.1^{\circ} \mathrm{C}$ ). Although absolute differences in water temperature among sites were quite small (average $2.3^{\circ} \mathrm{C}$ ), the differences likely result from differences in water depth, because temperature changes more slowly in larger volumes of water. There was considerable variation in station differences between years.

Dissolved oxygen concentrations varied widely during the study period from hypoxic ( $<2 \mathrm{mg} \mathrm{L}^{-1}$ ) to supersaturated ( $8-15 \mathrm{mg} \mathrm{L}{ }^{-1}$ ). The Rincon sites had hypoxia only once in 21 sampling periods. The reference site was hypoxic 4 of 21 sampling times, and had values $<3 \mathrm{mg} \mathrm{L}^{-1}$ an additional five times. The reference site had seagrass beds, so decaying organic matter or night time respiration likely caused the hypoxia. Hypoxic events were most common in summer (Bureau of Reclamation 2000), because solubility of oxygen in water decreases with increasing temperature and salinity.

## Macroinfauna

The upper Rincon site, located closest to the river overflow channel, had the highest abundance of macrofauna before and after the diversion (Table 1). Biomass was higher in the upper Rincon site than the reference site before and after the diversion. The highest diversity was found in the reference site. There was a significant interaction (2-way ANOVA, $\mathrm{p}=0.0001$ ) between 21 sampling dates and three sites for biomass and abundance (Table 2). The nature of the interaction is clear

TABLE 1. Summary of macrofauna community characteristics at sites before and after the diversion was installed. Average by replicates for backtransformed biomass and abundance and average number of species ( N 0 ) in pooled replicate samples for each site and sampling period.

| Site | Station | Biomass <br> $\left(\mathrm{g} \mathrm{m}^{-2}\right)$ | Abundance <br> $\left(\mathrm{n} \mathrm{m}^{-2}\right)$ | Diversity <br> $\left(\mathrm{N} 00.02 \mathrm{~m}^{-2}\right)$ |
| :--- | :--- | :---: | :---: | :---: |
| Reference | Before | 1.88 | 3,200 | 8.2 |
|  | After | 1.32 | 2,200 | 5.6 |
| Upper Rincon | Before | 2.62 | 47,600 | 4.6 |
|  | After | 1.57 | 7,800 | 3.3 |
| Central Rincon | Before | 1.35 | 8,000 | 6.6 |
|  | After | 1.60 | 7,000 | 4.8 |

when examining temporal trends among sites (Fig. 3). At various times, the central Rincon site has the lowest biomass, at other times the reference site has the lowest biomass. After the diversion, the upper Rincon site had the highest abundances of all stations during periods of peak biomass blooms. There was a strong seasonal trend with highest biomass occurring in spring (April) and lowest biomass occurring in summer (July) or fall (October).

Biomass was significantly higher (linear contrast of simple main effects, $p=0.0003$ ) in the period before the diversion ( $1.90 \mathrm{~g} \mathrm{~m}^{-2}$ ) than after the diversion ( $1.43 \mathrm{~g} \mathrm{~m}^{-2}$; Table 2). Mean biomass was significantly higher (linear contrast of simple main effects, $\mathrm{p}=0.0008$ ) in Rincon Bayou ( $1.67 \mathrm{~g} \mathrm{~m}^{-2}$ ) than at the reference site ( $1.29 \mathrm{~g} \mathrm{~m}^{-2}$ ). Abundance was significantly higher (linear contrast of simple main effects, $p=0.0001$ ) in the period before the diversion ( $10,700 \mathrm{~m}^{-2}$ ) than before the diversion $\left(4,900 \mathrm{~m}^{-2}\right)$. Abundance was significantly higher ( $\mathrm{p}=0.0001$ ) in sites affected by the diversion ( 9,280 ind $\mathrm{m}^{-2}$ ) than at the reference site $(2,400$ ind $\mathrm{m}^{-2}$ ). Diversity (species number) was significantly ( $\mathrm{p}<0.0001$ ) lower ( 4.5 species) before the diversion than after the diversion ( 6.5 species). Species richness was significantly ( $\mathrm{p}<0.0001$ ) lower ( 2.8 species) in impact sites relative to the reference site ( 6.2 species).

Rainfall and inflow vary with seasons and between years (Fig. 2); macrofaunal dynamics in Rincon Bayou exhibit seasonal and interannual dynamics (Fig. 3). Seasonal and interannual trends are most evident when all samples at all stations are averaged together to form a marsh-wide (over all sites) average biomass or marsh-wide average abundance (Fig. 4). The marsh-wide averages are most useful because site differences are obscured by interaction effects with sampling dates. When the marsh-wide averages are compared to salinity, the effect of inflow becomes apparent. When salinities are high ( $>50 \%$ ) biomass decreases, often to near zero. During periods following inflow and salinity declines, the biomass increases as it does in

TABLE 2. Analysis of variance of macrofauna community characteristics. A. Probabilities for tests. B. Detransformed means for levels from main sources of variability.

|  |  |  | Probability |  |
| :--- | :---: | :---: | :---: | :---: |
| A. Source | df | Biomass | Abundance | N0 Diversity |
| Date | 20 | $<0.0001$ | $<0.0001$ | $<0.0001$ |
| Site | 2 | 0.0007 | $<0.0001$ | 0.0003 |
| Date $\times$ Site | 40 | $<0.0001$ | $<0.0001$ | - |
| B. Source | Level | $\left(\mathrm{g} \mathrm{m}^{-2}\right)$ | $\left(\mathrm{n} \mathrm{m}^{-2}\right)$ | $\left(\mathrm{n} \sigma .02 \mathrm{~m}^{-2}\right)$ |
| Period | Before | 1.90 | 10,700 | 4.5 |
|  | After | 1.43 | 4,900 | 6.5 |
| Site | Reference | 1.29 | 2,400 | 6.2 |
|  | Upper Rincon | 1.79 | 12,000 | 3.5 |
|  | Central Rincon | 1.54 | 7,200 | 5.2 |



Fig. 3. Macrofauna community response at sites through time. A) Abundance, B) biomass, and C) species richness.


Fig. 4. Macrofauna community response and salinity at each sampling period. A) Abundance, B) biomass, and C) N1 diversity.

January 1996, January 1997, January 1998, October 1998, and April 1999. Highest biomasses occurred in January (average $3.3 \mathrm{~g} \mathrm{~m}^{-2}$ ) or April (average $3.4 \mathrm{~g} \mathrm{~m}^{-2}$ ) of each year, and lowest biomasses in October (average $1.8 \mathrm{~g} \mathrm{~m}^{-2}$ ) or July (average 0.8 $\mathrm{g} \mathrm{m}^{-2}$ ) of each year. Another important trend is less variability in biomass fluctuations through time as the project progresses. The standard deviation for biomass was $3.0,1.5,1.9,1.6$, and 0.8 in 1995, 1996, 1997, 1998, and 1999, respectively.

Macrofauna diversity was very low ranging from 1 to 14 species (Fig. 3). Because diversity was so low, all six replicates at a site were pooled for species analyses leaving no replication. An interaction between stations and dates was evident. In 12 of 21 sampling periods the reference site had the highest diversity. Diversity (i.e., species richness) was highest when abundance was highest. Richness (i.e., species number) does not express the domi-


Fig. 5. Macrofauna community response as a function of salinity. Abundance (A), biomass (B), and N1 diversity (C). Data same as Fig. 4, and nonlinear response to salinity (solid line) at each time period. Circles ( $(\circ)$ represent periods of rising salinity and diamonds $(\diamond)$ represent periods of falling salinity. Dashed line is not significant.
nance or evenness of a sample. Because densities were so high and species numbers so low, the ecosystem was characterized by dominance of a few species. The diversity index N1 was used to calculate the average number of dominant species among all sites at each sampling period (Fig. 4). Generally, no more than two dominant species were present at each sampling period. Diversity, measured as the number of dominant species, increased following periods of low salinity and decreased when salinities were high.

Macrofauna characteristics have a strong nonlinear relationship with salinity, which appears to be a bell-shaped curve that is skewed to the left with a long tail to the right (Fig. 5). The logarithmic model fits biomass and diversity data reasonably well, explaining $58 \%$ and $76 \%$ of the variability, respectively. The model for abundance explains only $19 \%$ of the variability and is not significant. The coefficient of variation (i.e., standard devia-

TABLE 3. Parameters from nonlinear regressions to predict macrofauna characteristics from salinity (lines in Fig. 5) and inflow (line in Fig. 6). Probability ( $\mathbf{P}$ ) that model fits the data, percent of variance explained by data ( $\mathbf{R}^{2}$ ), parameters for maximum biological value (a), rate of change (b), and maximum salinity value (c), and coefficient of variation for parameters in parentheses.

|  |  | Salinity |  |  |
| :--- | :---: | :---: | :---: | :---: |
| Parameter | Abundance | Biomass | N1 Diversity | Inflow Biomass |
| $\mathbf{P}$ | 0.1584 | 0.0252 | 0.0004 | 0.0236 |
| $\mathrm{R}^{2}$ | 0.19 | 0.58 | 0.76 | 0.61 |
| a | $4.58 \times 10^{4}(25 \%)$ | $3.43(15 \%)$ | $2.361(7 \%)$ | $3.99(13 \%)$ |
| b | $0.666(31 \%)$ | $0.905(27 \%)$ | $1.70(13 \%)$ | $1.34(18 \%)$ |
| c | $32.7(17 \%)$ | $18.7 \quad(24 \%)$ | $9.08 \%(19 \%)$ | $1.25 \times 10^{5}(25 \%)$ |

tion divided by the mean) for each parameter range from $7 \%$ to $31 \%$ (Table 3). Using these parameters, abundance appears to peak at a high salinity around $32.7 \%$, biomass peaks at $18.7 \%$, and diversity peaks at $9.08 \%$. Central skewness (b) parameters indicate more narrow ranges of responses with respect to salinity. For the three characteristics, the salinity range of response (b) increases as the salinity peak value for the response increases (c).

The direction of salinity change during a sampling period is important for diversity but not abundance or biomass (Fig. 5). The lowest values of all biological responses occurred at the highest salinities, and the highest salinities always occurred during periods of rising salinity (observations in the graph with the circle symbols in Fig. 5). Low diversity occurred when salinity values were decreasing (observations in the graph with diamond symbols) and high diversity occurred when salinities were rising within normal salinity ranges (i.e., $<35 \%$ o)

Salinity is a surrogate of the actual flow rate. The same model was used to regress macrofaunal characteristics against non-zero, quarterly inflow rates.


Fig. 6. Macrofauna biomass response as a function of inflow. Average biomass (Fig. 4) predicted as a nonlinear response to inflow (solid line) at each time period. Circles ( 0 ) represent periods of rising salinity and diamonds $(\diamond)$ represent periods of falling salinity.

Only biomass was significant, explaining $61 \%$ of the variability (Table 3, Fig. 6). The peak biomass of $3.99 \mathrm{~g} \mathrm{~m}^{-2}$ occurred at a flow rate of 125,000 $\mathrm{m}^{3}$ per quarter.

In spite of the low average diversity on any given sampling date, a total of 37 species were found over the 5 -yr period of the study. The polychaete Streblospio benedicti was an overwhelmingly dominant species at all stations representing $84 \%$ of all individuals found over the study period. Only four other species contribute as much of $2 \%$ of the community: the polychaete Laeonereis culveri, the hydrobid snail Assiminea succinea, one unidentified species of ostracod, and unidentified chironomid larvae.

Benthic faunal communities in the two Rincon Bayou sites were similar, but the reference site was distinct (Fig. 7a). Rincon Bayou was dominated by the four most common species: S. benedicti, L. culveri, unidentified Ostracoda, and unidentified chironomid larvae. All other species were rare. The reference site was distinct because of the presence of A. succinea and insects. The insects included Chironomidae and Ceratopogonidae larvae, the coleopteran Berosus sp., the hemipteran Tricho corixa, and damselfly nymphs (Zygoptera).

The six most dominant species were found continuously throughout the study, except when salinities were high ( $>35 \%$ ) . Rare species generally occurred during periods of low salinity. The only species to occur consistently during hypersaline conditions was the insect, T. corixa, but it was also found when salinities were brackish, so it is not an indicator species. There appeared to be little evidence of succession because sampling date sequence codes are spread throughout the entire MDS space (Fig. 7b). There were two abrupt changes in community structure over time as indicated by the line through the center of the space for each sampling period (Fig. 7b). The most extreme drought occurred in July 1996 (7th sample) and these samples are skewed to the lower left of the MDS space. After that period samples move back to the center. The next break occurred in July 1997 (10th sample) when there was a large flood,


Fig. 7. Multidimensional scaling (MDS) plot produced by macrofauna species similarities over each sampling date $\times$ site combination. Stress $=0.15$. A) Plotted using sites as symbols: R $=$ reference, $\mathrm{U}=$ upper Rincon, and $\mathrm{C}=$ Central Rincon. Lines connect outer limits of each sites space. B) Plotted using the sampling sequence number, where $1=$ first sample $\ldots 21=$ twenty-first sample, with a line through center of each sampling dates space.
which is very unusual for the summer. From October 1997, all samples cluster together in the top right part of the MDS space.

## MEIOFAUNA

The meiofauna community was composed of Nematoda (84\%), Harpacticoida (11\%), and 12 other taxa ( $5 \%$ ). The other taxa consisted of permanent meiofauna (Turbellaria $0.7 \%$, Gastrotricha $0.01 \%$, Tardigrada $0.01 \%$, Cnidaria $0.01 \%$, and Ro-

TABLE 4. Meiofauna abundance ( $\mathrm{n} 10 \mathrm{~cm}^{-2}$ ) characteristics.

|  |  | Total | Nematoda | Harpacticoida | Others |
| :--- | :--- | ---: | :---: | :---: | :---: |
| Period | Before | 1,182 | 896 | 77 | 23 |
|  | After | 689 | 377 | 40 | 23 |
| Site | Reference | 373 | 132 | 92 | 11 |
|  | Upper Rincon | 979 | 773 | 28 | 35 |
|  | Central Rincon | 1,212 | 1,005 | 39 | 30 |



Fig. 8. Meiofauna community response at sites through time. Average of station responses at each sampling period for abundance and biomass, and species richness.
tifera $0.03 \%$ ) and temporary meiofauna (Polychaeta $2.5 \%$, Oligochaeta $0.03 \%$, Gastropoda $0.05 \%$, Bivalvia $0.02 \%$, Ostracoda $1.6 \%$, and Amphipoda $<0.01 \%$ ). Two groups of protozoans were found among the meiofauna: Ciliata and Foraminifera.

The average total number of metazoan meiofauna was 1,200 ind $\mathrm{cm}^{-2}$. There was a significant interaction between stations and dates (2-way ANOVA, $\mathrm{p}=0.0001$; Table 4) so simple main effects were analyzed to test hypotheses. Meiofauna densities were different in reference and Rincon sites (Fig. 8). The reference site had lower densities than Rincon sites for total metazoans ( $p=0.0001$ ), nematodes ( $\mathrm{p}=0.0001$ ), harpacticoids ( $\mathrm{p}=$ 0.0001 ), and other taxa ( $\mathrm{p}=0.0001$ ). There were higher densities before the diversion than after for total metazoans ( $\mathrm{p}=0.0001$ ), nematodes ( $\mathrm{p}=$ 0.0001 ), harpacticoids ( $\mathrm{p}=0.0001$ ), but not for other taxa ( $\mathrm{p}=0.9815$ ).

The average abundance of meiofauna among all sites at each sampling period changed throughout the study period (Fig. 9). Abundances were lowest when salinities were highest, e.g., in July 1996 and


Fig. 9. Biological standing stock at each sampling period. Average macrofauna and meiofauna abundance.

July 1998. The highest abundance occurred in January 1998 after steadily increasing following the flood of July 1997. The meiofauna abundance pattern was similar to the macrofauna abundance pattern during the first eight sampling periods (October 1994 through July 1996). Thereafter the patterns were different. There is no correlation ( $\mathrm{r}=$ $-0.11, \mathrm{p}=0.65$ ) between meiofauna and macrofauna abundance.

## Discussion

Rincon Bayou is an unusual marsh with extreme environmental variability. The variability is evidenced by wide ranges in salinity (from $0 \%$ o to $160 \%$ o), high temperature $\left(12^{\circ} \mathrm{C}\right.$ to $\left.40^{\circ} \mathrm{C}\right)$, and a tendency toward reverse salinity gradients with higher salinities in the upper marsh area near the freshwater source. The environmental extremes are partly due to geography (a semiarid climate and microtidal coast) and partly due to reduced inflow by reservoir construction. Macrofauna diversity in Rincon Bayou is generally lower than in either Nueces Bay or Corpus Christi Bay. The average number of dominant species (diversity index N1) per station was only 1.8 in Rincon Bayou but 3.5 in Nueces Bay stations (Mannino and Montagna 1997) and 7.0 in Corpus Christi Bay (Ritter and Montagna 1999). Hypoxic stations in Corpus Christi Bay average an N1 value of 1.5 (Ritter and Montagna 1999). The low diversity in Rincon Bayou reflects a relatively greater degree of stress caused by the higher environmental variability. Macrofaunal abundance in Rincon Bayou (10,000 ind $\mathrm{m}^{-2}$ ) is $40 \%$ less than that typically found in Nueces and Corpus Christi Bays ( 14,000 ind $\mathrm{m}^{-2}$ and $4.4 \mathrm{~g} \mathrm{~m}^{-2}$ ). Macrofaunal biomass in Rincon Bayou ( $1.7 \mathrm{~g} \mathrm{~m}^{-2}$ ) is less than half that found in Nueces and Corpus Christi Bays ( 14,000 ind $\mathrm{m}^{-2}$ and $4.4 \mathrm{~g} \mathrm{~m}^{-2}$ ). Meiofaunal abundance in Rincon Bayou ( 1,200 ind $10 \mathrm{~cm}^{-2}$ ) is also about half the value typically found in Nueces and Corpus Christi Bays ( 2,500 ind $10 \mathrm{~cm}^{-2}$ ). Benthic abundance and biomass are indicators of secondary productivity (Banse and Mosher 1980). Environmental conditions in Rincon Bayou appear to be affecting community structure and secondary productivity. Comparison between Rincon Bayou and the adjacent bay is striking because marsh habitats typically have greater secondary productivity than open bay habitats (Day et al. 1989). It is possible that current secondary production in the Nueces Marsh is not as high as its historical values before inflow was reduced.

The strongest evidence that the freshwater diversion project has increased productivity and ameliorated stresses on biodiversity is demonstrated by relationship of diversity and biomass with inflow
and salinity (Figs. 6 and 7). Peak biomass occurred near $19 \%$ ond peak diversity occurred near $9 \%$. Peak biomass occurred when inflow was near $125,000 \mathrm{~m}^{3}$. Beneficial benthic effects are caused by increased opportunities for freshwater inflow into the marsh, establishment of lower salinity regimes, and reduction of hypersaline conditions (Figs. 2-5). Seasonal increases of biomass occurred in spring, when salinities were lowest and water levels were highest. Biomass was always lowest (Fig. 3) during summer, when salinities were highest and water levels were lowest (Fig. 2), except for July 1997. Inflow events triggered bursts of productivity as indicated by increased abundance and biomass following periods of lower salinities. Biodiversity increases after inflow events and salinity begins to rise again indicating more brackish species are invading and using the marsh habitat as a result of increased inflow events. Different species appear after each inflow event (Bureau of Reclamation 2000). Prior to overflow channel construction, brackish conditions in April 1995 resulted in decreased diversity. After construction, brackish conditions in April (1997-1999) resulted in increased diversity (Figs. 3 and 4). The benthic responses follow inflow events, which establish or reestablish a normal estuarine salinity gradient in Rincon Bayou.

The responses of increased abundance to inflow by macrofauna and meiofauna were similar (Fig. 9) indicating both size levels of benthos are responding to inflow events caused by channel construction. Meiofauna and macrofauna have different ecological roles in marine ecosystems (Coull and Bell 1979; Coull and Palmer 1984) so macrofauna and meiofauna could respond to inflow at different spatial and temporal scales (Bell 1980). Macrofauna, with planktonic larval dispersal, could be indicative of effects over larger spatial scales and longer temporal scales. Meiofauna, with direct benthic development and generation times as short as one month, indicate effects over smaller spatial scales and shorter temporal scales. Because sampling was quarterly, it is possible that changes could have occurred in both groups, but especially meiofauna, that were not detected in the current study.

The mechanisms of infaunal response to inflow are likely physiological and trophic. The physiological response is controlled by increased survivability and tolerance to specific salinity ranges caused by inflow events (Fig. 4; Jassby et al. 1995). Trophic response is indirect and related to response by potential food items, which respond to nutrients and sediments carried to estuaries by inflow (Nixon et al. 1986). In theory, when primary producers respond to inflow by increased biomass, then in-
creased food levels could lead to increased secondary production (Deegan et al. 1986).

Nutrients and chlorophyll were measured monthly during this study by other authors (Bureau of Reclamation 2000). Dissolved inorganic nitrogen (DIN) concentration was positively correlated with chlorophyll $a$ (chl $a$; r $=0.68, \mathrm{p}<$ $0.0001, \mathrm{n}=51$ ) and primary productivity in water ( $\mathrm{r}=0.35, \mathrm{p}<0.0156, \mathrm{n}=46$ ). DIN was not correlated with salinity ( $\mathrm{p}=0.29$ ), but there was a positive correlation between salinity and nitrite ( r $=0.37, \mathrm{p}=0.0075$ ) and ammonia $(\mathrm{r}=0.28, \mathrm{p}=$ 0.0422 ), but not nitrate ( $p=0.64$ ). There was also no correlation between salinity and chl $a$ or productivity ( $\mathrm{p}=0.62$ and 0.30 , respectively). Salinity lagged by one month was inversely correlated with chl $a(\mathrm{r}=0312, \mathrm{p}=0.04)$, indicating biomass deceased one month after salinity increased. These results indicate there is no strong empirical relationship between inflow and consequent salinity decreases to indicators of primary production measured on monthly time scales.

Because infauna was sampled quarterly, indicators of primary production were averaged over the quarterly sampling period. Over quarterly time scales, there was a positive correlation between chl $a$ and inflow ( $\mathrm{r}=0.55, \mathrm{p}=0.0269, \mathrm{n}=21$ ), but there was no correlation between chl $a$ or productivity and macrofauna abundance, macrofauna biomass, or meiofauna abundance. The lack of correlation between animal response measures and potential food measures is surprising, because such correlations have been found in the past. Meiofauna are known to be grazers and respond the presence of chlorophyll (Montagna 1995; Montagna et al. 1995). In San Antonio Bay, Texas, meiofauna respond to freshwater inflow and increased chlorophyll with increased grazing rates (Montagna and Yoon 1991).

Flood events can be classified as a disturbance event because large changes in salinity can affect benthic infaunal communities. The effects of disturbance frequency and altered flow regimes on macrobenthic community structure and colonization were studied experimentally in upper Rincon Bayou during the current study period (Ritter 1999). Abundance and biomass decreased with increasing disturbance frequency, indicating succession could be disrupted by frequent disturbance. Abundance and biomass were higher in defaunated sediments relative to background sediments, indicating colonizers are important in community production of early succession communities. A flood in June 1997 drove salinities to near zero (Fig. 2) and changed the succession trajectory of the community. A S. benedicti recruitment event (resulting in densities as high as $1.310^{6} \mathrm{~m}^{-2}$ ) was re-
corded on June 20, 1997 and the flood event began just 2 d later (June 22, 1997). After the flood, S. benedicti density declined rapidly and freshwater species invaded, leading to three distinct community states over the 14 -wk period of the study. Shortterm (about 3 wk ) changes in community structure were larger than were the seasonal differences detected by quarterly monitoring. The recruitment and flood events were likely stochastic, but were very important in driving short term changes in the community.

Long-term (years) changes in community structure also occurred (Fig. 7b). There was a large state change in the community before and after the summer of 1996 , such that a new community succeeded the one established before the diversion. During the first seven sampling periods, the community was dominated by ostracods and $A$. succinea. After the ninth sampling period and regular inundation of Rincon Bayou, the community was dominated by $S$. benedicti and chironomid larvae. Dominance by insect larvae and a pioneer species indicates that the flooding was acting as a disturbance and this was responsible for increasing diversity in the period following the diversion.

Increased freshwater inflow restored functioning of the Nueces salt marsh as a nursery habitat for development of juvenile brown shrimp, Penaeus aztecus (Riera et al. 2000). Brown shrimp spawn offshore in the Gulf of Mexico, post-larvae are carried by onshore water movement and enter bays, and ultimately find productive shallow estuarine waters that are protected from storms and predators (Day et al. 1989). Larval brown shrimp enter marine bays from late winter through early spring, spend about 3 to 4 mo in estuarine nursery grounds, and return to the offshore Gulf of Mexico in early summer (Moffett 1970). The trophic dynamics of juvenile brown shrimp were investigated as they migrated from Aransas Pass to Corpus Christi Bay to Nueces Bay and to Nueces Delta using stable isotopes ratios of carbon ( $\delta^{13} \mathrm{C}$ ) and nitrogen ( $\delta^{13} \mathrm{~N}$; Riera et al. 2000). Because food sources change in different habitats, stable isotopes can also be used to assess migration of shrimp (Fry 1981). During the study period, shrimp lengths increased from $10-11 \mathrm{~mm}$ when the animals entered Corpus Christi Bay as larvae, to $80-90 \mathrm{~mm}$ when they returned to the Gulf of Mexico as subadults (Riera et al. 2000). Brown shrimp exhibited spatial and temporal $\delta^{13} \mathrm{C}$ variation (from $-25.2 \%$ o to $12.5 \%$ o) indicating a high diversity of food sources throughout their migration. From $\delta^{13} \mathrm{C}$ values, it appears the main food source used by juvenile brown shrimp in Rincon Bayou marsh were Spartina alterniflora and Spartina spartinae detritus and benthic diatoms. From $\delta^{13} \mathrm{C}$ and $\delta^{15} \mathrm{~N}$ values, it appears or-
ganic matter inputs carried by river inflow can also contribute significantly to the feeding of migratory brown shrimp. In Rincon Bayou marsh habitats, shrimp isotopic ratios changed rapidly indicating high tissue turnover rates and rapid growth. Reintroduction of freshwater inflow to the Nueces marsh provided nursery areas with high benthic biomass favorable for feeding and growth of juvenile brown shrimp.

The diversion project program was performed to support water resource management decision making. Wetland habitats and function have been lost in other areas where freshwater was impounded and diverted from coastal deltas, such as happened in the Colorado River Delta, Mexico (Glenn et al. 1996). Nesting bird populations birds declined when water flow was altered in the Everglades (Walters et al. 1992). Physical effects of reduced inflow to the coast include changes in nutrient cycling and sediment supply. Wetland restoration improved water quality in the Ebro Delta, Spain by enhancing nitrogen and phosphorous removal (Comín et al. 2001). The infauna in Rincon Bayou responded to inflow events that restored brackish salinities with increased abundances, biomass, and diversity (Fig. 5). Although inflow events increased as a result of the diversion project, the overflow channel was filled in at the end of the demonstration project in September 2000. The City of Corpus Christi re-opened the channel in October 2001 in return for a reduction in the State mandated a minimum flow requirement for the Nueces Estuary. Re-opening of the channel was largely justified by findings of the current research.

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