

# The Response of Fishes to Physicochemical Changes in the Mangroves of Northeast Florida Bay

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**ABSTRACT:** Historically, large volumes of fresh water from the Everglades reached Florida Bay in the form of overland sheet flow. South Florida's extensive canal system has diverted fresh water from its historic course, resulting in shorter hydroperiods and higher salinities than would have occurred in an unaltered system. The mixing zone between the freshwater Everglades and euryhaline Florida Bay is primarily characterized as a dwarf red mangrove forest. The small, demersal fishes found in this habitat are an important food source for a variety of predators and are excellent bio-indicators for both short-term and long-term perturbations in the system. I examine the effect of fluctuating water level, salinity, and temperature on this fish community in order to better understand the impact water diversion has had on the ecotone. Fish were collected at four sites within the ecotone over a 5-yr period using a 9-m<sup>2</sup> drop trap. Principal components analysis was used to generate 10 composite variables (PCs) from a temporal array of 59 physicochemical variables. These composite variables were used in regression analyses to evaluate spatial and temporal changes in the fish community. Regression analysis indicated fish density was significantly related to short-term and long-term changes in water level and with long-term temperature variation ( $r^2 = 0.50$ ). An ANOVA of density between sites supports the regression results, indicating that sites with longer hydroperiod had higher density than sites with shorter hydroperiod. The impact of changes in density on biomass was reflected by regression analysis, which indicated that increased water level and decreased variability in depth were correlated with higher biomass ( $r^2 = 0.61$ ). Biomass was also influenced by changes in the salinity regime, presumably through increases in individual fish body size or through a shift in the community toward heavier-bodied fish species. An ANOVA of biomass between sites indicates sites with longer freshwater periods had higher biomass than sites with shorter freshwater periods. The first two axes of a detrended correspondence analysis on community biomass explained 59.2% of the variance in the community and supported the hypothesis that salinity was a primary determinant of community structure. These results indicate historic changes in water delivery could have altered the mangrove fish community, thereby lowering prey availability for higher trophic levels.

## Introduction

Large volumes of fresh water from the Everglades historically reached Florida Bay via sheet flow through Taylor Slough (Fig. 1). Since 1960, flow patterns have been altered by the construction and operation of a series of canals known as the South Dade Conveyance System (SDCS). The SDCS was designed, in part, to supply the eastern Everglades and Florida Bay with appropriate water deliveries from upstream sources (Light and Di-  
neen 1994; United States Army Corps of Engineers 1994). In contrast to the original design, the SDCS has functioned primarily as a flood control system which ultimately drained that part of the Everglades it was designed to support (United States Army Corps of Engineers 1994). Many researchers have concluded that the resulting reduction in freshwater flow from the Everglades is at least partially responsible for recent ecological changes in Florida Bay (Boesch et al. 1993). Loftus and Ek-  
lund (1994) suggest canal operation has disrupted

the natural pattern of water quantity, flow, and hydroperiod in the Everglades, resulting in reduced abundance of demersal marsh fishes. Bancroft et al. (1994) propose that a decline in the available prey base may account for the observed reduction in Everglades wading bird populations. Similar impacts may be occurring in Florida Bay and associated wetlands due to construction and operation of the SDCS.

Hydrologic models indicate the amount of water flowing through the Everglades toward Florida Bay has been greatly reduced compared to historic flows (Fennema et al. 1994). A consequence of water diversion is that less fresh water reaches the mangrove zone and Florida Bay (McIvor et al. 1994). McIvor et al. (1994) developed a model of historic salinities for the euryhaline area between the freshwater Everglades and saltwater Florida Bay. The model indicated that since construction of the SDCS, marine conditions have occurred more frequently and brackish and marine periods have been longer in duration than in the pre-canal period. Meeder et al. (1996) used paleoecological techniques to demonstrate the marine environ-

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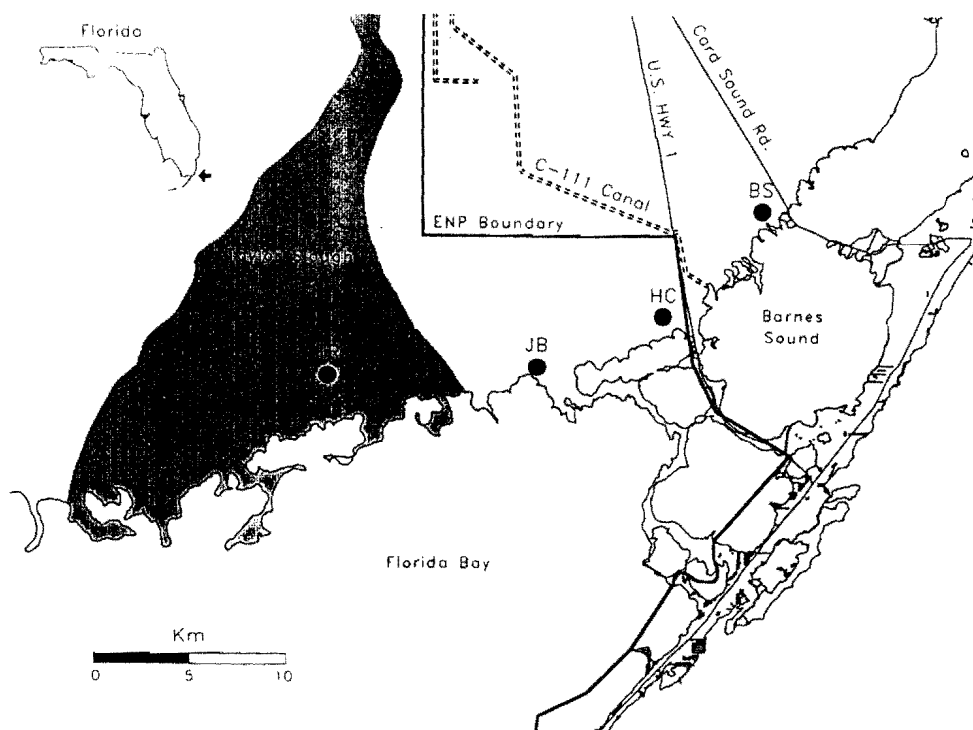


Fig. 1. Map of Southern Florida and Florida Bay showing the locations of the sampling sites, Taylor Slough, Everglades National Park (ENP) boundary, and the southern terminus of the South Dade Conveyance System (C-111 Canal). Site locations are Taylor River (TR), north of Joe Bay (JB), west of Highway Creek (HC), and north of Barnes Sound (BS).

ment had intruded into the historically freshwater wetlands north of Florida Bay at a rate faster than could be accounted for by sea-level rise. They also showed changes in the rate of marine intrusion were correlated with the construction and changes in operation of the SDCS. Ross et al. (in press) performed vegetation surveys between the C-111 Canal (the southern most canal in the SDCS) and Florida Bay and compared the results to similar surveys of the area performed by Egler in 1948 (Egler 1952). The comparisons indicated the mangrove-dominated area has expanded inland by as much as 3.3 km since the 1948 study, supplanting historic freshwater sawgrass marshes. Cumulatively, these studies indicate the wetlands north of Florida Bay have experienced higher salinities, longer periods of saline intrusion, and shorter hydroperiods due to anthropogenic manipulation of water resources than would have happen in a nonmanaged system.

Only a few studies have been initiated that directly link water deliveries to the changes in the fauna of Florida Bay. The underlying hypothesis of the research presented here was that alterations in the resident fish fauna would have occurred along with the historic changes in hydrology and vegetation. Because historical data are unavailable to test this hypothesis an alternative strategy was

adopted—the impact of fluctuations in physico-chemical variables (i.e., salinity, water level, and temperature) on the demersal mangrove fish community was examined as a means of assessing the implications of historical anthropogenic changes in these parameters on these ecologically important animals.

The community of demersal euryhaline fishes is an excellent subject for studies relating physical conditions to the biota. Most of these fishes are considered to be annual fishes (Loftus and Kushlan 1987), so comparisons from year to year are unencumbered by year classes as in many other fisheries studies. Several species have generation periods as short as of 60 d (Foster 1967; Haake and Dean 1983). As a result of their high reproductive and mortality rates, the demersal fish community responds very quickly to changes in hydrology. Unlike larger fish species, birds, and reptiles, many of these fish cannot leave the system when adverse conditions arise and then return when conditions improve, which makes them better indicators of short-term perturbations (e.g., Frederick and Loftus 1993). Top predators such as piscivorous fishes, alligators, crocodiles, and birds (especially wading birds of the order Ciconiiformes), are directly or indirectly dependent on these small fishes. If past changes in water delivery to the mixing zone can

be linked to a negative impact on this prey base, it may help explain the imperiled state of many of these animal populations in the Florida Bay area.

## Methods

### STUDY LOCATION

Browder and Moore (1981) proposed that secondary production in the estuarine mixing zone is a function of the degree of overlap between the stationary habitat (e.g., substrate type, vegetation, etc.) and the dynamic habitat (e.g., hydrology and hydrography). When comparing fish communities from multiple locations, observed differences in the community could be due to differences in the stationary habitat, dynamic habitat, or both. The focus of this study was the impact that anthropogenic changes to the dynamic habitat (specifically hydroperiod and salinity regimes) had on the fish community. To effectively determine this, sites were selected that were similar in stationary habitat but different in these key aspects of the dynamic habitat.

The four sampling sites (Fig. 1) were located in similar dwarf mangrove habitat and each was characterized by a deep central creek (creek microhabitat) surrounded by shallow flats (flats microhabitat) that were exposed seasonally. The percentage of sampling sites of the flats microhabitat ranged from about 75% to 90%. Vegetation consisted of widely spaced dwarf red mangrove (*Rhizophora mangle*) trees (0.5–2.0 m tall, 0.5–5.0 m between trees), with varying amounts of vegetation between the trees. The substrate at all sites was flocculent, unconsolidated, carbonate marl (Browder et al. 1994).

General areas for sampling sites were selected based on the potential to show spatial and temporal differences in water level, salinity, and temperature. Specific sampling sites were selected based on proximity (within 1 km) to Everglades National Park (ENP) hydrological monitoring stations so that data collected at these stations could be used to interpret the results of fish collections. The eastern most sampling site was located on Biscayne Bay near the northern end of Card Sound Bridge on Barnes Sound (25°17.65'N, 80°24.57'W). This site was impounded by roadbeds and received no freshwater sheet flow from the Everglades, therefore, all freshwater input to Barnes Sound was from local rainfall or groundwater seepage. The Barnes Sound site experienced diurnal tides approximately 7–12 cm in amplitude.

The other three sites were nontidal and were located just north of Florida Bay in the Taylor Slough, C-111 drainage area of ENP (Fig. 1). These sites were located north of Little Madeira Bay on

Taylor River (25°13.20'N, 80°39.00'W), north of the eastern end of Joe Bay (25°15.00'N, 80°31.92'W), and on a tributary west of Highway Creek (25°15.25'N, 80°27.28'W) near US Highway 1. The amount of fresh water these three sites historically received from the Everglades presumably decreased from west (Taylor River) to east (Highway Creek) based on site proximity to Taylor Slough. Sheet flow currently reaches northeastern Florida Bay via both Taylor Slough and the C-111 Canal. Water from the C-111 Canal exits the canal through 55 gaps in the southern levee along the lower (east to west) reach of the canal, resulting in sheet flow into northeastern Florida Bay (Ley et al. 1995). Between 1983 and 1990, approximately 75–90% of water arriving at Florida Bay was delivered via the C-111 Canal (Ley et al. 1995; Chiappone 1996). Because the easternmost gaps were at a lower elevation than the central or western gaps, most of this water exited the canal near US Highway 1. This resulted in the majority of fresh water being delivered to the Highway Creek region (the Highway Creek site) of Florida Bay, with decreasing amounts of fresh water being delivered to the bay at more western locations (Ley et al. 1995). Starting in about 1990, a series of operational changes were made concerning the C-111 Canal so that a more equitable distribution of water was delivered across the northeastern coast of Florida Bay (Ley et al. 1995). These changes resulted in a variety of hydrological regimes at the three Florida Bay mangrove sampling sites since 1990 (Ley et al. 1995). Based on these conditions, the four sites were assumed to experience high spatial and temporal variation in the dynamic habitat while the stationary habitat remained relatively constant.

### HYDROLOGIC MONITORING

In addition to the ENP hydrostations, water levels were monitored continuously at each site using a Telog 2108 potentiometric recorder with a float and pulley design. Accuracy of the equipment was checked by comparing the current measurement of the recorder against a nearby staff gauge each time the system was downloaded. Gaps in the water record were supplemented with data from nearby ENP waterlevel recorders. Salinity was measured at the site on the day of fish collections with an optical refractometer. These data were strongly correlated to the data recorded by the ENP hydrostations; there were minor differences between the two at the Joe Bay, Highway Creek, and Barnes Sound sites (the hydrostation at Taylor River was located immediately adjacent to the site). The continuous records from the ENP hydrostations were refined to better reflect conditions at the sites through the application of regression models gen-

erated from salinity data collected on the same dates at both the site and the hydrostation. All regression equations were significant ( $p < 0.001$ ) and the adjusted  $R^2$  for the equations were 0.96, 0.92, and 0.98 respectively for Joe Bay, Highway Creek, and Barnes Sound. A review of residuals indicated none of the assumptions for regression analysis were violated (Neter et al. 1996).

To investigate changes in fish abundance along a time gradient, means for hydrologic variables were calculated for a series of time steps prior to each sample. Means and standard deviations for salinity, water level, and temperature were calculated for the day on which each sample was collected and for the 30 d, 60 d, 90 d, 120 d, 180 d, 240 d, 300 d, and 360 d prior to each sample. A dryness index (DI) was calculated for the same time intervals. The DI was the number of days out of the period that the water level was below the point where the flats began to dry. For example, a 30-d DI of 5 indicates the flats were exposed 5 d of the 30 d prior to the sample.

The time series array of variables resulted in a very large number (59) of potential independent physical variables that could be used to derive linear models of fish abundance (Table 1). The variables were highly collinear since subsets of the data used to generate the long-term variables were also used to generate the short-term variables. These problems precluded the direct use of the time series array of variables in any meaningful linear model of fish abundance. Principal Components Analysis (PCA) was used as a data reduction tool so that a smaller, orthogonal set of physical composite variables (PCs) could be derived for use in the analysis of fish abundance (Ludwig and Reynolds 1988; Statsoft 1995). The PCA solution was VARIMAX rotated to facilitate interpretation of the principal components. All principal components with an eigenvalue greater than 1 were retained (Kaiser 1960) and the factor scores used in the analysis of fish abundance.

To investigate the impact of the periodicity of physical conditions, thresholds were established for each physical variable and the number of days that the threshold was exceeded was calculated for the period just prior to sample collection (hereafter called threshold period variables). Thresholds were set at greater than 5 cm relative water depth, less than 5‰ salinity, and less than 18°C for temperature. A relative water depth of 5 cm was chosen because this was the point at which the flats began to become exposed (flats were fully dry at a relative depth of 0 cm). The salinity threshold was chosen based on the observation that some species of submerged aquatic vegetation (important to fishes as habitat and food source) were neg-

atively impacted by salinity above 5‰. The temperature threshold was chosen based on the work of Frederick and Loftus (1993), which indicated that Everglades fish behavior was unaltered by temperatures at or above this temperature but was altered at lower temperatures. As an example, a salinity threshold period of 250 indicates salinity was less than 5‰ for the 250 d prior to collection of the sample. Inclusion of these variables in the PCA would have resulted in their elimination from further analyses because the large number of closely related variables in the PCA would have caused the threshold period variables to have eigenvalues of less than 1. As a result, these variables were used in addition to the composite variables from the PCA in the analyses of fish abundance.

#### FISH COLLECTIONS

A sampling method that employs a 9-m<sup>2</sup> drop net was developed for this study and has been demonstrated to be an effective and unbiased sampling method in this habitat (Lorenz et al. 1997). Nets were set up, left overnight, and deployed the following day within 2 h after sunrise. Each net surrounded an individual dwarf mangrove tree, thereby sampling both prop root habitat and the open area between trees. Trees were selected for sampling such that each site had a similar array of tree sizes with roughly equivalent prop root density so that there was consistent sampling of the stationary habitat (as per Browder and Moore 1981) from site to site. Fish were cleared from the net using the fish toxicant Rotenone. Any fish missed in the initial collection and found floating on the surface the next day were added to the sample (Lorenz et al. 1997). Net clearing efficiencies ranged from 78% to 90% for the most common fish species and averaged 86% for all marked and recaptured fish (Lorenz et al. 1997). All fish collected were identified, weighed, and measured. Weights for specimens collected during the second day of collection were calculated from length-weight regressions generated from the first day of collection.

Fish were collected from Highway Creek and Joe Bay starting in September 1990. Taylor River was first sampled in December 1991 and Barnes Sound in April 1992. Data through April 1996 are presented. The majority of fish collections were made during the dry season and transitional periods so that the impact of fluctuations in hydrology could be assessed. Sample collections were made in June, September, and monthly from November through April. Samples were not collected in December 1993, February, June, and September 1994, and June and December 1995 for financial reasons. Three nets were deployed in each microhabitat

TABLE 1. Results of principal components analysis shown as factor loadings for the first 10 principal components after VARIMAX rotation. Highlighted loadings indicate absolute scores >0.7 except for PC<sub>IX</sub>, for which the highest scores were 0.34 to 0.38. Parameters are calculated from continuously recorded data for the period (# d) indicated prior to the date of fish collections.

| Parameter                             | Period | PC <sub>I</sub> | PC <sub>II</sub> | PC <sub>III</sub> | PC <sub>IV</sub> | PC <sub>V</sub> | PC <sub>VI</sub> | PC <sub>VII</sub> | PC <sub>VIII</sub> | PC <sub>IX</sub> | PC <sub>X</sub> |
|---------------------------------------|--------|-----------------|------------------|-------------------|------------------|-----------------|------------------|-------------------|--------------------|------------------|-----------------|
| Mean level water                      | 1      | -0.27           | 0.13             | -0.01             | 0.02             | 0.1             | -0.11            | <b>0.72</b>       | -0.1               | 0.16             | 0.03            |
|                                       | 30     | -0.38           | 0.01             | -0.09             | -0.08            | 0.02            | 0                | <b>0.83</b>       | -0.07              | 0.15             | -0.04           |
|                                       | 60     | -0.44           | -0.03            | -0.09             | -0.12            | 0.01            | 0.06             | <b>0.81</b>       | -0.14              | 0.09             | -0.14           |
|                                       | 90     | -0.5            | -0.08            | -0.05             | -0.16            | 0.02            | 0.09             | <b>0.77</b>       | -0.14              | 0                | -0.18           |
|                                       | 120    | -0.62           | -0.1             | -0.02             | -0.16            | 0.01            | 0.11             | 0.65              | -0.16              | -0.06            | -0.22           |
|                                       | 180    | <b>-0.83</b>    | -0.09            | -0.01             | -0.11            | 0.04            | 0.09             | 0.39              | -0.16              | -0.11            | -0.18           |
|                                       | 240    | <b>-0.94</b>    | -0.02            | 0.02              | -0.02            | 0.1             | 0                | 0.19              | -0.14              | 0.01             | -0.06           |
|                                       | 300    | <b>-0.94</b>    | 0.07             | 0.05              | 0.1              | 0.13            | -0.07            | 0.13              | -0.11              | 0.1              | 0.04            |
| Water level SD                        | 360    | <b>-0.87</b>    | 0.13             | 0.06              | 0.17             | 0.17            | -0.09            | 0.21              | -0.12              | 0.15             | 0.08            |
|                                       | 30     | -0.01           | 0.23             | -0.03             | -0.01            | 0.04            | <b>0.75</b>      | 0.04              | 0.15               | 0.13             | -0.02           |
|                                       | 60     | 0.03            | 0.17             | 0.02              | 0.05             | 0.11            | <b>0.86</b>      | 0.09              | -0.02              | 0                | -0.12           |
|                                       | 90     | -0.05           | 0.19             | 0.06              | 0.06             | 0.3             | <b>0.76</b>      | 0.05              | 0.01               | -0.23            | -0.18           |
|                                       | 120    | -0.06           | 0.13             | 0.08              | 0.07             | 0.47            | 0.52             | 0.06              | 0.13               | -0.38            | -0.27           |
|                                       | 180    | -0.12           | 0.06             | -0.05             | 0.2              | <b>0.76</b>     | 0.21             | -0.07             | 0.16               | -0.37            | -0.14           |
|                                       | 240    | -0.03           | 0.04             | 0.16              | -0.02            | <b>0.9</b>      | 0.1              | -0.1              | -0.08              | 0.08             | 0.05            |
|                                       | 300    | -0.12           | -0.1             | 0.24              | -0.3             | <b>0.79</b>     | 0.15             | -0.03             | -0.16              | 0.17             | 0.08            |
| Dryness index                         | 360    | -0.22           | -0.21            | 0.17              | -0.4             | <b>0.74</b>     | 0.08             | -0.01             | -0.13              | 0.08             | 0.13            |
|                                       | 30     | 0.41            | 0.13             | 0.02              | 0.02             | 0.16            | 0.05             | <b>-0.76</b>      | -0.04              | 0.02             | 0               |
|                                       | 60     | 0.48            | 0.16             | 0.03              | 0.05             | 0.16            | 0.02             | <b>-0.76</b>      | -0.01              | 0.15             | 0.04            |
|                                       | 90     | 0.53            | 0.2              | 0.03              | 0.05             | 0.12            | -0.01            | <b>-0.73</b>      | -0.05              | 0.22             | 0.05            |
|                                       | 120    | 0.62            | 0.21             | 0.02              | 0.06             | 0.1             | -0.06            | -0.65             | -0.05              | 0.24             | 0.06            |
|                                       | 180    | <b>0.8</b>      | 0.17             | 0.05              | 0.03             | 0.07            | -0.13            | -0.42             | -0.01              | 0.23             | 0.04            |
|                                       | 240    | <b>0.92</b>     | 0.07             | 0.04              | -0.08            | 0               | -0.08            | -0.21             | 0.01               | 0.15             | -0.01           |
|                                       | 300    | <b>0.92</b>     | -0.05            | 0.01              | -0.23            | -0.09           | 0.04             | -0.14             | 0.02               | 0.02             | -0.05           |
| Mean salinity                         | 360    | <b>0.84</b>     | -0.13            | -0.04             | -0.31            | -0.17           | 0.09             | -0.23             | 0.06               | -0.07            | -0.08           |
|                                       | 1      | -0.02           | <b>0.87</b>      | -0.03             | 0.07             | 0.14            | 0.07             | -0.26             | 0.05               | 0.12             | 0.01            |
|                                       | 30     | 0.01            | <b>0.92</b>      | 0.04              | 0.11             | 0.01            | 0.06             | -0.2              | 0.09               | 0.14             | 0.05            |
|                                       | 60     | 0.02            | <b>0.94</b>      | 0.02              | 0.12             | -0.01           | 0.08             | -0.17             | 0.06               | 0.14             | 0.06            |
|                                       | 90     | 0.02            | <b>0.96</b>      | 0.02              | 0.13             | -0.01           | 0.08             | -0.1              | 0.05               | 0.09             | 0.08            |
|                                       | 120    | 0.07            | <b>0.96</b>      | 0.03              | 0.11             | 0.01            | 0.03             | 0.02              | 0.08               | 0.02             | 0.1             |
|                                       | 180    | 0.1             | <b>0.94</b>      | 0.02              | 0.03             | 0.01            | 0.02             | 0.22              | 0.12               | -0.06            | 0.08            |
|                                       | 240    | 0.07            | <b>0.89</b>      | 0.05              | -0.14            | -0.03           | 0.11             | 0.32              | 0.08               | -0.11            | 0.06            |
| Salinity SD                           | 300    | -0.01           | <b>0.87</b>      | 0.03              | -0.25            | -0.08           | 0.16             | 0.28              | 0.1                | -0.19            | 0.02            |
|                                       | 360    | -0.06           | <b>0.86</b>      | -0.03             | -0.28            | -0.1            | 0.17             | 0.18              | 0.14               | -0.2             | 0               |
|                                       | 30     | -0.03           | 0.15             | 0.02              | -0.11            | -0.24           | 0.14             | -0.08             | <b>0.78</b>        | 0.08             | 0.09            |
|                                       | 60     | 0.21            | 0.18             | 0.01              | -0.07            | -0.12           | 0.15             | -0.21             | <b>0.79</b>        | 0.02             | 0.13            |
|                                       | 90     | 0.4             | 0.25             | 0.01              | -0.17            | 0.14            | -0.05            | -0.07             | <b>0.76</b>        | -0.06            | 0.14            |
|                                       | 120    | 0.49            | 0.19             | 0.01              | -0.23            | 0.27            | -0.18            | 0.15              | 0.55               | -0.16            | 0.17            |
|                                       | 180    | 0.58            | 0.2              | -0.11             | -0.38            | 0.28            | -0.2             | 0.24              | 0.33               | -0.02            | 0.05            |
|                                       | 240    | 0.43            | 0.09             | 0.04              | <b>-0.77</b>     | 0.13            | 0.04             | 0.23              | 0.07               | 0.05             | -0.03           |
| Mean temp.                            | 300    | 0.19            | -0.02            | -0.05             | <b>-0.9</b>      | 0.07            | -0.03            | 0.01              | 0.12               | -0.04            | -0.14           |
|                                       | 360    | 0.1             | -0.07            | -0.17             | <b>-0.86</b>     | 0.08            | -0.11            | -0.14             | 0.17               | -0.02            | -0.13           |
|                                       | 1      | -0.03           | 0.09             | -0.04             | 0.29             | -0.01           | -0.22            | -0.33             | 0.12               | 0.16             | 0.5             |
|                                       | 30     | 0.12            | 0.2              | -0.05             | 0.22             | 0.08            | -0.32            | -0.3              | 0.25               | 0.29             | 0.67            |
|                                       | 60     | 0.22            | 0.2              | -0.09             | 0.22             | 0.09            | -0.26            | -0.07             | 0.28               | <b>0.34</b>      | <b>0.71</b>     |
|                                       | 90     | 0.27            | 0.19             | -0.18             | 0.22             | 0.08            | -0.19            | 0.15              | 0.24               | <b>0.38</b>      | 0.69            |
|                                       | 120    | 0.31            | 0.19             | -0.22             | 0.2              | 0.08            | -0.12            | 0.4               | 0.21               | <b>0.38</b>      | 0.58            |
|                                       | 180    | 0.26            | 0.2              | -0.27             | 0.11             | 0.03            | 0.07             | <b>0.75</b>       | 0.09               | 0.21             | 0.26            |
| Temp SD                               | 240    | 0.09            | 0.26             | -0.32             | 0.12             | -0.01           | 0.17             | <b>0.82</b>       | 0                  | -0.07            | 0.01            |
|                                       | 300    | -0.03           | 0.33             | -0.31             | 0.22             | -0.03           | 0.17             | <b>0.73</b>       | -0.11              | -0.26            | -0.01           |
|                                       | 360    | -0.1            | 0.41             | -0.25             | 0.36             | -0.05           | 0.04             | 0.51              | -0.11              | -0.33            | 0.23            |
|                                       | 30     | 0.04            | -0.05            | 0.15              | -0.06            | -0.08           | 0.12             | 0.13              | 0.01               | 0.08             | <b>-0.85</b>    |
|                                       | 60     | 0.04            | -0.03            | 0.19              | -0.02            | 0               | -0.03            | 0.02              | -0.05              | 0.05             | <b>-0.93</b>    |
|                                       | 90     | 0.07            | 0.01             | 0.3               | 0.06             | 0.08            | -0.07            | -0.04             | 0.03               | 0.09             | <b>-0.89</b>    |
|                                       | 120    | 0.06            | -0.01            | 0.44              | 0.17             | 0.11            | -0.04            | -0.12             | 0.01               | 0.19             | <b>-0.73</b>    |
|                                       | 180    | 0.12            | -0.07            | <b>0.79</b>       | 0.1              | 0.11            | 0.03             | -0.1              | -0.06              | 0.12             | -0.33           |
| % Total variance                      | 240    | -0.04           | 0                | <b>0.88</b>       | 0.04             | 0.03            | 0                | -0.16             | -0.01              | -0.08            | -0.28           |
|                                       | 300    | -0.07           | 0.09             | <b>0.87</b>       | 0.02             | 0.11            | 0.02             | -0.22             | 0.03               | -0.11            | -0.24           |
|                                       | 360    | -0.03           | 0.15             | <b>0.83</b>       | 0                | 0.2             | 0.04             | -0.15             | 0.07               | 0.03             | -0.24           |
| Cumulative Variance Explained = 87.8% |        | 240.5           | 170.4            | 120.7             | 90.9             | 60.6            | 40.8             | 40.4              | 30.5               | 20.1             | 20.0            |

(creek and flats) at each site, for a total of six nets per sample.

While the 9-m<sup>2</sup> drop net was designed to catch small, demersal fish (Lorenz et al. 1997), incidental collections of larger fishes did occur. A single large fish could weigh more than the entire sample of smaller fish, thereby biasing estimates of biomass. Length frequency distributions indicated the collection of fish larger than 6.5 cm was rare in the creek microhabitat and did not occur on the flats. The flats microhabitat made up 75–90% of the habitat utilized by the demersal fish community, indicating that fish larger than 6.5 cm were not functioning as an integral part of the demersal fish community. To analyze accurately the community of small, demersal fishes, all fish larger than 6.5 cm (3.2% of total fish collected) were eliminated from the dataset.

Preliminary data indicated the abundance of demersal fishes differed between creek and flats habitats even though the physicochemical parameters were uniform across the two microhabitats. For example, during periods of declining water level, high mortality may occur as fish on the flats are stranded. Those that survive are forced into the creeks. Sampling only the creek microhabitat would result in the conclusion that sharp declines in water level resulted in increased fish abundance (due to the concentration of fishes into the remaining wetted habitat). When the entire landscape subject to declining water level is considered, the observed effect would be that decreasing water level resulted in fewer fish overall (due to stranding mortality). The concentration effect obfuscates the impact of declining water levels on the demersal fish community across the entire landscape. In order to make statements about the impact of water level (or other physiochemical parameters) on the community as a whole, the estimated abundance of fishes in both microhabitats would have to be combined into a single meaningful estimate of abundance that is uniform across the entire landscape. Therefore, a stratified mean biomass and number of fish per m<sup>2</sup> (density) was calculated for each sample by averaging the weighted means for each habitat type (Cochran 1963). These data were log-transformed for use in regression and analysis of variance (ANOVA) models.

Calculation of a stratified estimate requires that the weight of each strata (in this case the wetted area of the creeks and the flats respectively) be known. Since wetted area changed in response to water-level variations, remote sensing techniques were employed to estimate wetted area of each strata at any given water depth. High-altitude false-color images (1:1800 scale) depicting 1 km<sup>2</sup> of wetland centered on each sampling site were acquired

from ENP. Using the selection criteria of the Idrisi GIS package (Eastman 1995), each image was separated into several discrete color bands representing small incremental changes (on the order of about 5 cm) in wetland surface elevation. Each site was then surveyed physically to determine the depth range of each color relative to the continuous water-level recorder. The ground-truthed GIS images could then be used to estimate wetted area for each sample and a stratified mean biomass and density calculated based on the strata weights.

#### STATISTICAL ANALYSIS

Spatial differences in density and biomass were examined by a one-way analysis of variance (ANOVA) between sites. Significant ANOVA were followed by Student-Newman-Keuls multiple range tests to determine the relationship among sites.

To determine which aspects of hydrology best explained the variance among samples, stepwise regressions were performed for each dependent variable (biomass and density) using the composite variable factor scores from the PCA and the threshold period variables as independent variables. The use of stepwise regression as a screening technique for large sets of independent variables has been brought into question because the sequence in which the variables are entered into the stepwise process can impact the results (James and McCulloch 1990). Because forward and backward stepwise techniques enter the variables in a different order (Neter et al. 1996), both techniques were employed to determine if the order in which the variables entered had an impact on the model outcome.

Annual community composition at each site was analyzed by applying detrended correspondence analysis (DCA) (ter Braak 1995) to 12 of the most common species. DCA is an ordination technique that can be used to evaluate differences in community structure between samples (Ludwig and Reynolds 1988; ter Braak 1995). Interpretation of the DCA is such that samples proximal to one another on a plot of the ordination scores have similar species structure (ter Braak 1995). Species were selected for inclusion in DCA if they made up more than 5% of the catch in any given sample (Table 2). Evaluating the results of a DCA of 120 samples from four sites and 5 yr proved difficult, so the dataset was simplified by calculating total biomass for each of the 12 species for each year at each site. A hydrologic year was defined as June 1 to May 31 to coincide with one cycle of wet season-dry season (Kushlan 1980). To determine if any environmental parameters were correlated with the DCA axes, various estimators of annual water level, salinity, and temperature (annual mean, stan-

TABLE 2. Phylogenetic list of all species sampled and the percent of catch at each site. Percent catch for all sites combined, total fish collected per site, number of species collected, number of dates, and total nets sampled are also included. All fish collected are represented; however, only fish less than 6.5 cm were used in subsequent analyses. Species used in the community analysis (DCA) are marked with an asterisk (\*).

| Order<br>Family<br>Genus species | Common Name           | TR    | JB    | HC    | BS    | All Sites |
|----------------------------------|-----------------------|-------|-------|-------|-------|-----------|
| <b>SILURIFORMES</b>              |                       |       |       |       |       |           |
| Ictaluridae                      | Freshwater catfish    |       |       |       |       |           |
| <i>Ameiurus natalis</i>          | Yellow Bullhead       |       | 0.02  |       |       | 0.01      |
| <i>Notturus gyrinus</i>          | Tadpole Madtom        |       |       | 0.02  |       | < 0.01    |
| Clariidae                        | Labyrinth catfishes   |       |       |       |       |           |
| <i>Clarius batrachus</i>         | Walking catfish       |       | 0.02  |       |       | 0.01      |
| <b>BATRACHOIDIFORMES</b>         |                       |       |       |       |       |           |
| Batrachoididae                   | Toadfishes            |       |       |       |       |           |
| <i>Opsanus beta</i> (juv)        | Gulf Toadfish         |       | 0.01  |       | 0.24  | 0.04      |
| <b>ATHERINIFORMES</b>            |                       |       |       |       |       |           |
| Atherinidae                      | Silversides           |       |       |       |       |           |
| <i>Menidia sp</i>                | Inland Silverside     | 2.72  | 4.10  | 0.98  | 6.61  | 3.45      |
| Belonidae                        | Needlefishes          |       |       |       |       |           |
| <i>Strongylura notata</i> (juv)  | Redfin Needlefish     | 0.01  | 0.06  | 0.02  | 0.32  | 0.08      |
| Cyprinodontidae                  | Killifishes           |       |       |       |       |           |
| <i>Adenia xenica</i>             | Diamond Killifish     |       | 0.09  | 1.54  | 0.28  | 0.42      |
| <i>Cyprinodon variegatus</i> *   | Sheepshead Minnow     | 5.18  | 17.25 | 37.90 | 14.10 | 18.05     |
| <i>Floridichthys carpio</i> *    | Goldspotted Killifish | 0.44  | 1.11  | 6.30  | 29.21 | 6.94      |
| <i>Fundulus chrysotus</i>        | Golden Topminnow      | 0.29  | 0.35  | 0.02  |       | 0.20      |
| <i>F. confluentus</i> *          | Marsh Killifish       | 0.52  | 4.61  | 9.17  | 0.18  | 3.76      |
| <i>F. grandis</i> *              | Gulf Killifish        | 0.09  | 2.79  | 8.61  | 1.30  | 3.10      |
| <i>F. seminolus</i>              | Seminole Killifish    | 0.06  |       |       |       | 0.02      |
| <i>F. similis</i>                | Longnose Killifish    | 0.07  | 0.28  | 0.77  | 0.22  | 0.32      |
| <i>Jordinella floridae</i> *     | Florida Flagfish      | 0.02  | 0.23  | 0.09  |       | 0.10      |
| <i>Lucania goodei</i> *          | Bluefinned Killifish  | 14.13 | 1.98  | 0.89  |       | 4.71      |
| <i>Lucania parva</i> *           | Rainwater Killifish   | 32.17 | 25.86 | 13.49 | 16.02 | 23.10     |
| Poeciliidae                      | Livebearers           |       |       |       |       |           |
| <i>Belonesox belizanus</i>       | Pike Killifish        | 0.24  | 0.49  | 0.11  | 0.02  | 0.25      |
| <i>Gambusia affinis</i> *        | Mosquitofish          | 1.11  | 2.00  | 2.86  | 0.81  | 1.74      |
| <i>Poecilia latipinna</i> *      | Sailfin Molly         | 5.83  | 13.14 | 9.91  | 5.88  | 9.17      |
| <b>CYPRINIFORMES</b>             |                       |       |       |       |       |           |
| Cyprinidae                       | Minnows               |       |       |       |       |           |
| <i>Notropis sp</i>               | Shiner                | 0.50  | 0.01  |       |       | 0.14      |
| Catostomidae                     | Suckers               |       |       |       |       |           |
| <i>Erimyzon succella</i>         | Lake Chubsucker       |       | 0.01  |       |       | < 0.01    |
| <b>GASTEROSTEIFORMES</b>         |                       |       |       |       |       |           |
| Syngnathidae                     | Pipefishes            |       |       |       |       |           |
| <i>Syngnathus louisianae</i>     | Chain Pipefish        |       |       |       | 0.12  | 0.02      |
| <b>PERCIFORMES</b>               |                       |       |       |       |       |           |
| Gerreidae                        | Mojarras              | 0.04  | 0.05  | 0.03  | 3.47  | 0.63      |
| Gobiidae                         | Gobies                |       |       |       |       |           |
| <i>Gobiosoma bosc</i>            | Naked Goby            | 0.29  | 0.02  |       |       | 0.08      |
| <i>Gobiosoma robustum</i>        | Code Goby             | 0.01  |       |       |       | < 0.01    |
| <i>Lophogobius cyprinoides</i> * | Crested Goby          | 8.01  | 0.02  |       |       | 2.19      |
| <i>Microgobius gulosus</i> *     | Clown Goby            | 8.31  | 1.13  | 0.45  | 21.10 | 6.38      |
| Centrarchidae                    | Sunfish spp.          | 0.37  | 0.96  | 0.02  |       | 0.42      |
| <i>Elassoma evergladi</i>        | Pygmy sunfish         | 0.12  |       |       |       | 0.03      |
| <i>Enneacanthus gloriatus</i>    | Blue Spotted Sunfish  | 0.09  |       | 0.02  |       | 0.03      |
| <i>Lepomis marginatus</i>        | Dollar Sunfish        | 0.05  | 0.08  | 0.02  |       | 0.04      |
| <i>Lepomis punctatus</i>         | Spotted Sunfish       | 0.24  | 0.26  | 0.03  |       | 0.16      |
| <i>Lepomis microlophus</i>       | Redear Sunfish        |       |       | 0.02  |       | < 0.01    |
| <i>Micropterus salmoides</i>     | Large mouth Bass      | 0.05  |       |       |       | 0.01      |
| Cichlidae                        | Cichlids              |       |       |       |       |           |
| <i>Cichlasoma bimaculatum</i>    | Black Acara           |       | 0.02  | 0.03  |       | 0.01      |
| <i>C. urophthalmus</i> *         | Mayan Cichlid         | 14.73 | 22.49 | 6.60  |       | 12.93     |
| <i>Tilapia mariae</i>            | Spotted Tilapia       | 4.31  | 0.55  | 0.09  |       | 1.38      |

TABLE 2. Continued.

| Order<br>Family<br>Genus species | Common Name | TR    | JB    | HC    | BS    | All Sites |
|----------------------------------|-------------|-------|-------|-------|-------|-----------|
| PLEURONECTIFORMES                |             |       |       |       |       |           |
| Soledae                          | Soles       |       |       |       |       |           |
| <i>Trinectes maculatus</i>       | Hogchoker   |       | 0.01  | 0.02  | 0.14  | 0.03      |
| Totals                           |             | 8,026 | 9,711 | 6,607 | 5,070 | 29,414    |
| Number of species                |             | 29    | 31    | 26    | 17    | 39        |
| Number of nets sampled           |             | 149   | 187   | 172   | 152   | 660       |
| Number of dates sampled          |             | 29    | 39    | 37    | 27    | 132       |

dard deviation, minimum, maximum, total number of days per year less than the threshold, longest continuous period per year less than the threshold) were compared with their associated ordination scores using indirect gradient analysis (Ludwig and Reynolds 1988; ter Braak 1995).

### Results

#### DYNAMIC HABITAT

There was a high degree of spatial, interannual, and intraannual variation of physical conditions in the mangrove zone (Fig. 2). However, the means of daily water level and salinity at each site indicate a typical annual cycle in the physical environment (Fig. 2). The cycle began in June when water level started to rise following the dry season (Fig. 2a; Kushlan 1980). High temperatures (Fig. 2c) play a role in increasing sea level (Holmquist et al. 1989) and rainfall (Duever et al. 1994) during the summer months, thus explaining this increase in water level. Water levels typically climbed throughout the summer (with the exception of a slight dip in August) and peaked in late September or early October. As temperature cooled (Fig. 2c), water level declined through October and November, culminating in dry season conditions from February through April and early May (Fig. 2a). Salinity (Fig. 2b) had an inverse pattern to that of water level. Salt concentrations were typically highest in late May and declined over the summer months. Freshwater or near freshwater conditions occurred in September and October, followed by a steady rise in salinity beginning in November and continuing through February. In March there was a sharp rise in salinity, with the highest salinity generally occurring in April or May.

The PCA identified 10 composite variables (hereafter called PC<sub>I</sub>, PC<sub>II</sub>, etc.) that had eigenvalues greater than 1 and that accounted for 87.8% of the variability in the physicochemical data. The factor loadings (Table 1) indicate the variation explained by each composite variable (PC) was correlated with the means or standard deviations of one of the three main physical variables (water lev-

el, salinity, or temperature). The factor loadings indicated the composite variables accounted for variability in the physical data along temporal lines by distinguishing relatively short-term from long-term trends (Table 1).

Physicochemical differences between the sites were examined using the factor scores for the composite variables. The median factor score and the 10th, 25th, 75th, and 90th percentiles are presented for the water level (Fig. 3), salinity (Fig. 4), and temperature (Fig. 5) composite variables for each site. To relate the PC factor score variability with actual physicochemical variation, the same parameters (median and CIs) are presented for the physicochemical variable with the highest factor loading for each PC (Table 1). Box plots for threshold period variables are presented in Fig. 6.

Composite variables for water level (Fig. 3) and continuous hydroperiod (Fig. 6a) allow the general characterization (relative to one another) of Taylor Creek and Barnes Sound as high-water sites, Highway Creek as a low-water site, and Joe Bay as intermediate. Short-term water-level variability was very similar across the sites except at Taylor River, which was less variable than the other sites (Fig. 3c). All four sites had similar ranges of long-term standard deviations in water level (Fig. 3d).

Composite variables for salinity (Fig. 4) and continuous low-salinity period (Fig. 6b) allow the general characterization (relative to one another) of Barnes Sound as a high-salinity site, Taylor River as a low-salinity site, and Joe Bay and Highway Creek as intermediate. The factor scores for PC<sub>VIII</sub> (short-term salinity variability) indicated salinity at Taylor River did not change much over relatively short periods when compared to the other sites (Fig. 4b); however, over the long term the range in salinity variation was relatively wide at Taylor River (Fig. 4c). The salinity period of record (Fig. 2b) indicated Taylor River had long periods of freshwater conditions (explaining the low short-term variability) punctuated by sharply rising then falling salinity in the late spring, thereby increasing the standard deviation around the mean (explain-

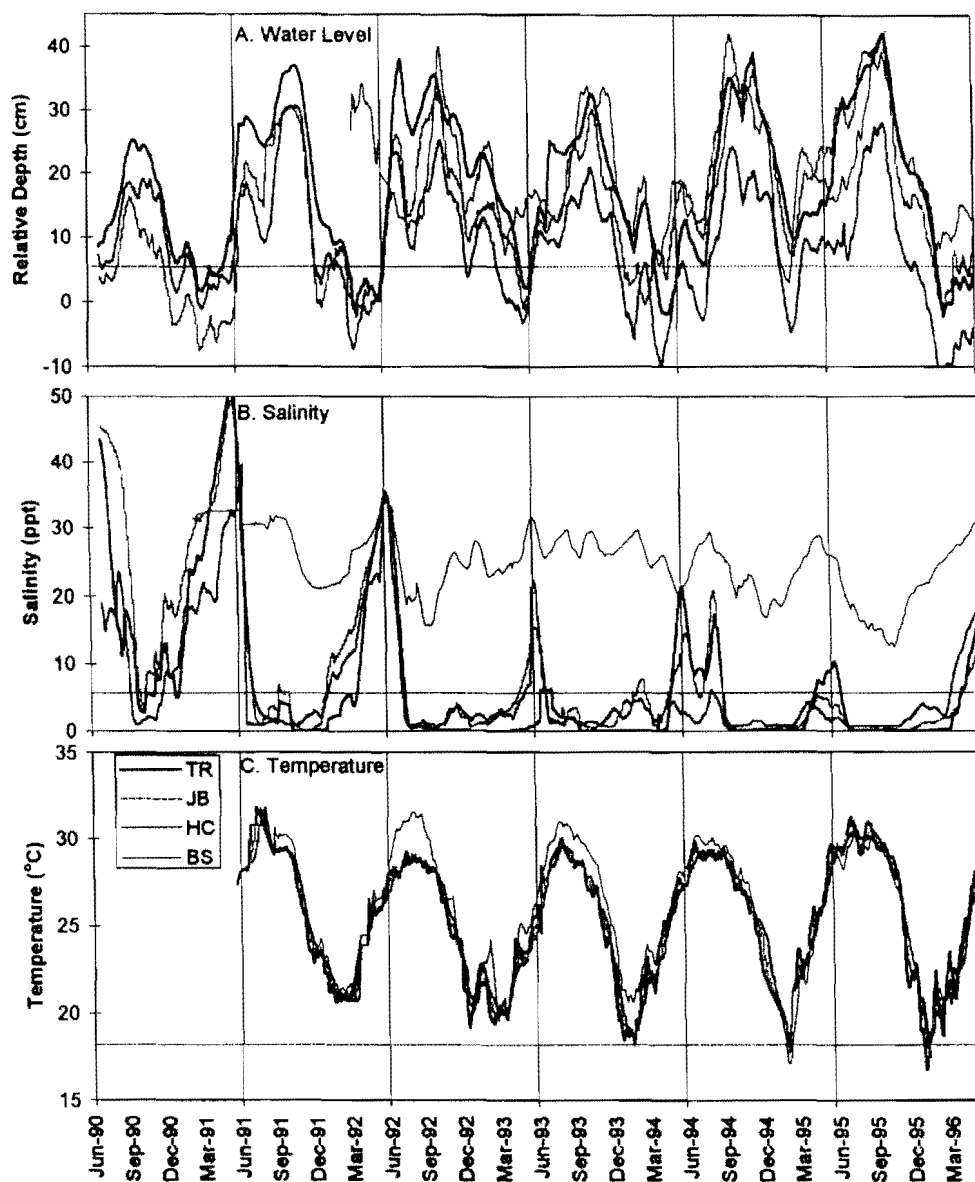


Fig. 2. Period of record for water level (a), salinity (b), and temperature (c) from continuous data recorders. Data presented are 30-d running averages. Horizontal lines on each graph indicate the threshold set for each parameter (water level = 5 cm, salinity = 5‰, temperature = 18°C). Temperature data from 1990 to 1991 are unavailable.

ing the wide range in variation over the long term). When considering the other three sites, salinity variability was similar between Barnes Sound and Highway Creek and these two sites had lower variability than Joe Bay (Fig. 4b,c).

The four sites exhibited great similarity in temperature-related composite variables (Fig. 5) and in low-temperature period (Fig. 6c). Temporal variation in temperature was pronounced (Fig. 2c) and, therefore, could explain some of the variability observed in the system as whole.

#### FISH DENSITY

Table 2 lists the species collected and their relative abundance by percent catch for each site. The most abundant species were the members of the families Cyprinodontidae, Poeciliidae, and Cichlidae. The results of the one-way ANOVA indicated there was an effect of site on density ( $F = 20.03$ ;  $p < 0.001$ ;  $df = 3, 127$ ) and the Student-Newman-Keuls test results showed the sites were all different from one another ( $p < 0.05$ ). Taylor River had the highest density followed by (in order)

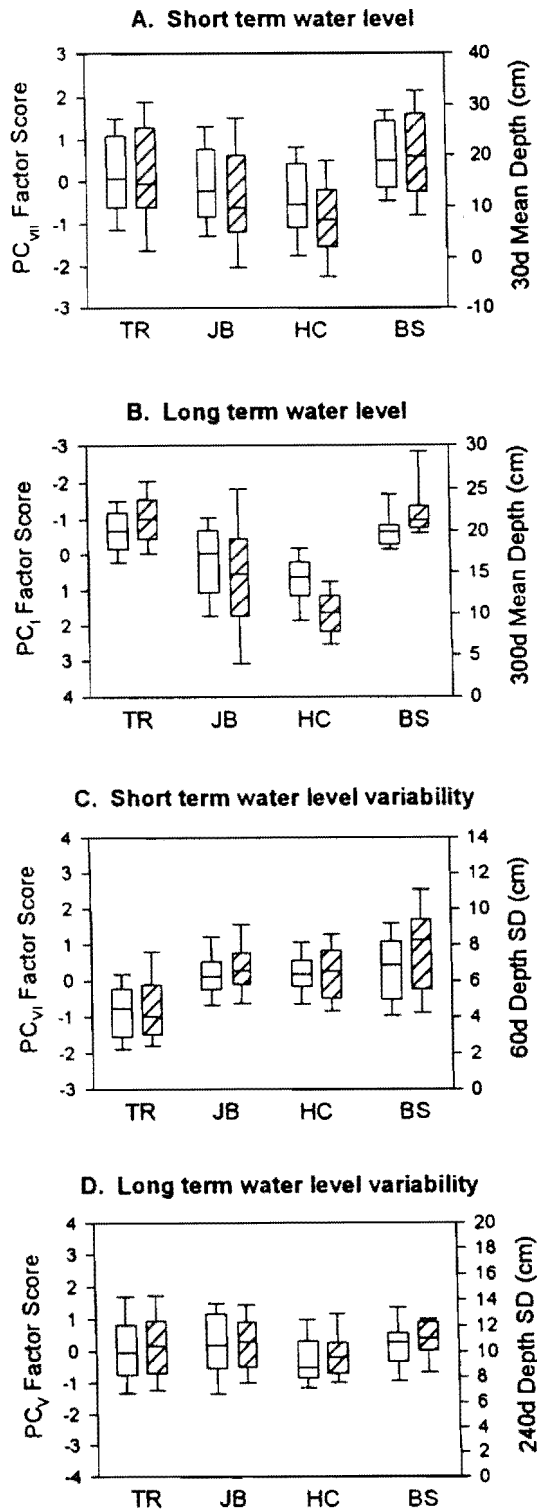


Fig. 3. Box-and-whisker plots for water-level composite variables (PCs). To relate the variability of the PC factor score with actual physicochemical variation, the physicochemical variable with the highest factor loading for each PC (see Table 1) is also presented. The left and right Y-axes are arranged so the medians for the PCs and the physicochemical variables are synchro-

Barnes Sound, Joe Bay, and Highway Creek. An examination of the stratified mean density estimates used in the analyses clearly indicates the differences among sites (Fig. 7).

Stepwise regression analysis of the three threshold period variables and the factor scores from the 10 PCs indicated PC<sub>VII</sub> (short-term mean water-level), PC<sub>I</sub> (long-term mean water-level), PC<sub>V</sub> (short-term variation in water level), and PC<sub>III</sub> (long-term variation in temperature) significantly contributed to explaining 50% of the variance in fish density (Table 3 and Fig. 8). Fish density was positively related to PC<sub>VII</sub>, PC<sub>I</sub>, and PC<sub>III</sub>, and negatively related to PC<sub>V</sub> (Table 3). Identical regression equations resulted from forward and backward procedures, indicating the outcome of the stepwise procedure was not biased by the order in which the variables were entered. Residuals were evaluated according to Neter et al. (1996) and indicated that none of the assumptions for regression analysis were violated.

#### FISH BIOMASS

The results of the ANOVA indicated an effect of site on density ( $F = 34.18$ ;  $p < 0.001$ ;  $df = 3, 127$ ), and the Student-Newman-Keuls test results showed the sites were all different from one another ( $p < 0.005$ ). Taylor River had the highest biomass followed by (in order) Joe Bay, Highway Creek, and Barnes Sound. An examination of the stratified mean biomass estimates used in the analyses indicates clearly the differences among sites (Fig. 9).

Stepwise regression analysis of the three threshold period variables and the factor scores from the 10 PCs indicated low salinity period (number of days prior to sampling that salinity was  $< 5\text{‰}$ ), PC<sub>IV</sub> (long-term variation in salinity), PC<sub>V</sub> (short-term variation in water level), PC<sub>II</sub> (mean salinity), and PC<sub>I</sub> (longterm mean water-level) significantly contributed to explaining 61% of the variance in fish biomass (Table 3 and Fig. 10). Fish biomass was positively related to low salinity period, PC<sub>IV</sub>, and PC<sub>I</sub>, and negatively related to PC<sub>V</sub> and PC<sub>II</sub> (Table 3). Identical regression equations resulted from forward and backward procedures, indicating the outcome of the stepwise procedure was not biased by the order in which the variables were entered. Residuals were evaluated according to Neter et al. (1996) and indicated that none of the assumptions for regression analysis were violated.

nous. For ease of comparison the PCs having a negative factor loading with the correlated physicochemical variable are presented with an inverted axis.

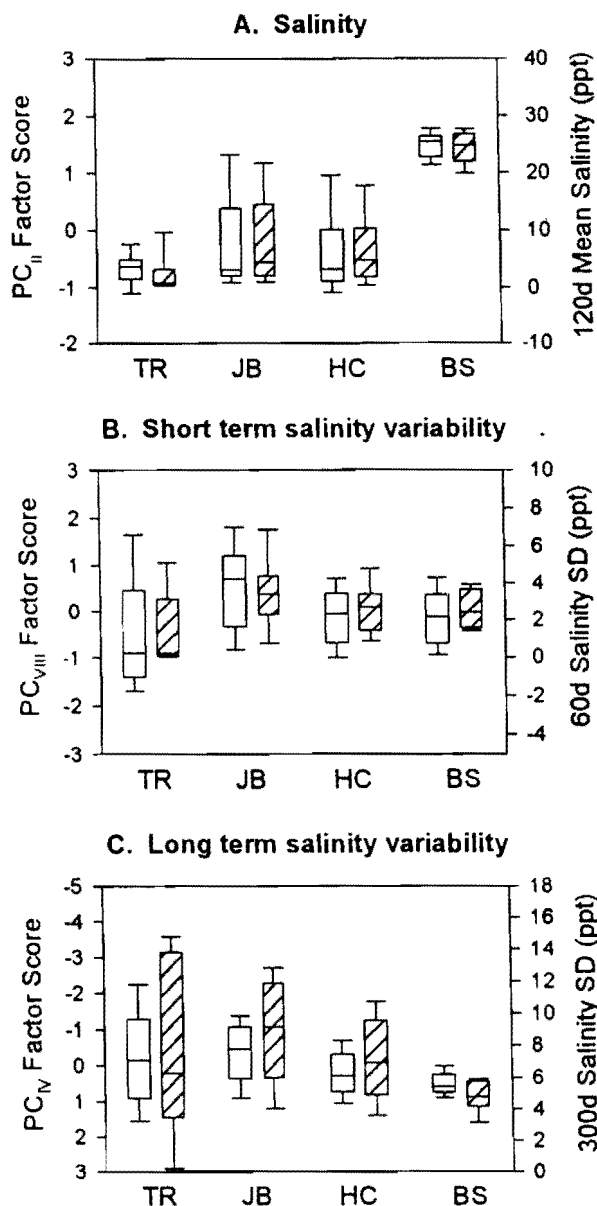


Fig. 4. Box-and-whisker plots for salinity composite variables (PCs).

#### COMMUNITY ANALYSIS

Species used in the DCA are listed in Table 2. Axis 1, Axis 2, and Axis 3 of the DCA ordination explained 45.2%, 14.0%, and 3.5%, respectively, of the variance in the mangrove fish community. Axis 3 will not be discussed further since it only explained a small amount of the variance. The ordination along the first two axes split the yearly estimators of community into groupings well defined by site (Fig. 11). Coefficients of correlation between the DCA axes and hydrologic parameters indicate Axis 1 separated annual communities by the

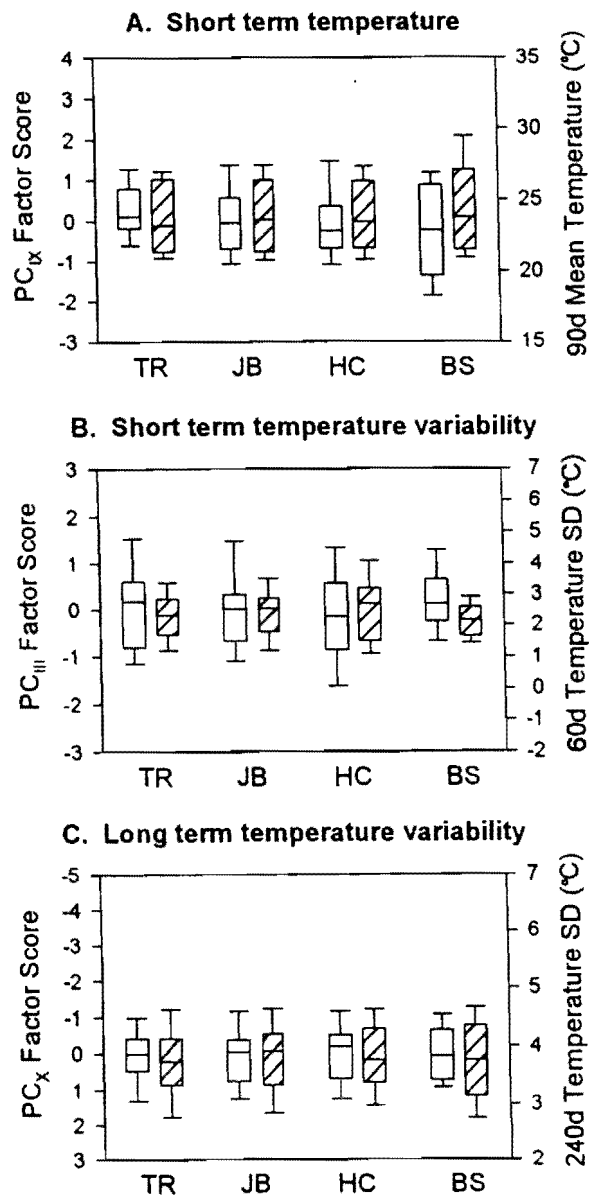


Fig. 5. Box-and-whisker plots for temperature composite variables (PCs).

number of low salinity days and the length of the longest low salinity period (Table 4). Axis 2 was correlated with a variety of parameters, half of which were also estimators of salinity (Table 4).

#### Discussion

##### DYNAMIC HABITAT

The results of the PCA indicate clear distinctions among sites for dynamic habitat. Differences in water level allow the sites to be characterized as high water, long hydroperiod (Taylor River and Barnes Sound); low water, short hydroperiod (Higway

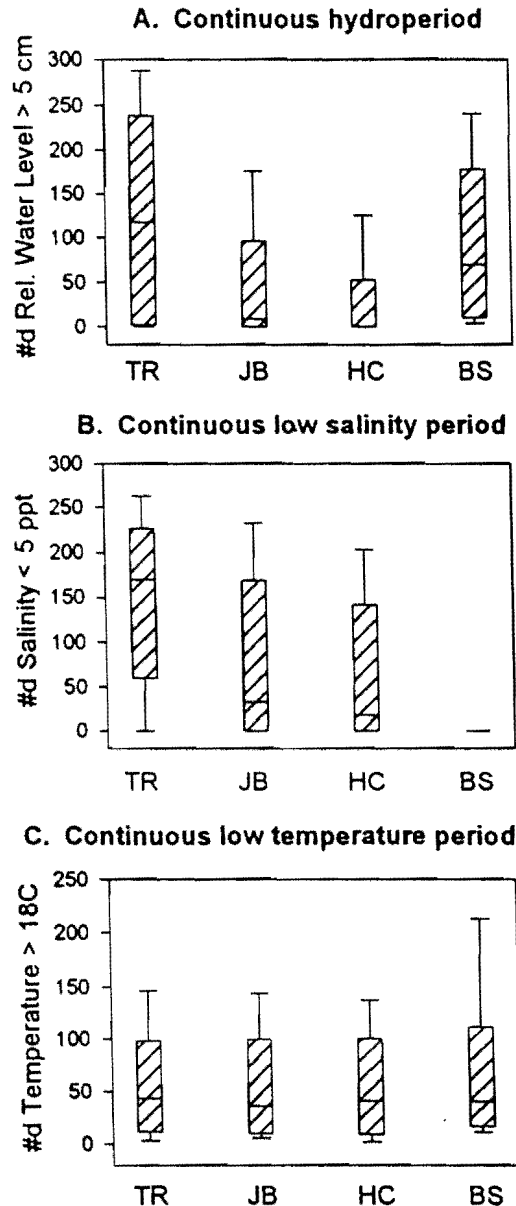


Fig. 6. Box-and-whisker plots for threshold period variables. The center horizontal line in the box is the median number of days the threshold was exceeded (water level > 5 cm, salinity < 5‰, and temperature < 18°C). The top and bottom of the box are the 25th and 75th percentiles (quartiles) and the ends of the whiskers are the 10th and 90th percentiles.

Creek); and variable in hydroperiod (Joe Bay). The salinity regime allows for further classification of sites by long periods of high salinity (Barnes Sound), long periods of low salinity (Taylor River), and variable in salinity and salinity periodicity (Joe Bay and Highway Creek). Also the sites can be classified by salinity range; Taylor River had the widest range followed by (in order) Joe Bay, Highway Creek, and Barnes Sound. The site-effect (ANO-

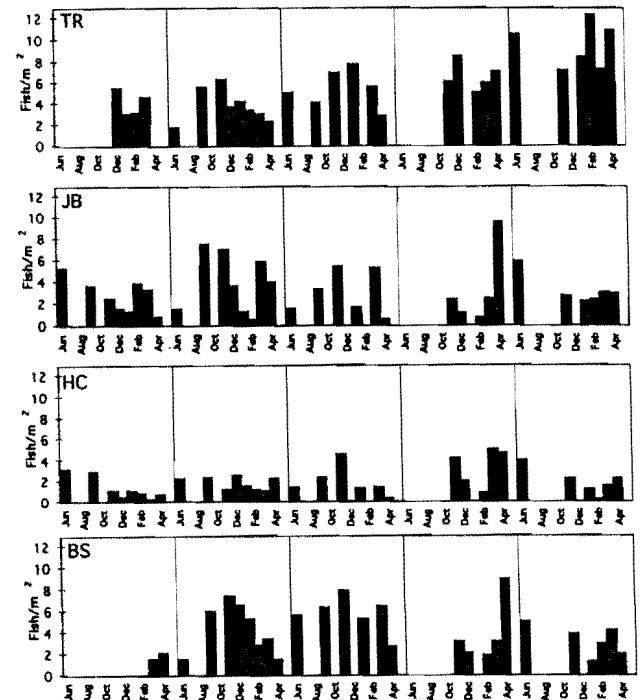


Fig. 7. Stratified mean density of fish for every sample collection. Sites as ranked by density are Taylor River > Barnes Sound > Joe Bay > Highway Creek; all sites are significantly different from each other. Sampling did not begin at Taylor River and Barnes Sound until December 1991 and March 1992 respectively. Ideally, samples were scheduled for June, September, and monthly from November through April; however, not all months were sampled every year.

VA) for both density and biomass indicate these differences in the dynamic habitat may have had a measurable impact on the abundance of fishes within the ubiquitous dwarf mangrove stationary habitat. Regression analyses were used to indicate specific aspects of the dynamic habitat that impact fish abundance.

#### FISH DENSITY

Regression results indicate density of fish was positively related to higher water levels over both short-term ( $PC_{VII}$ ) and long-term ( $PC_I$ ) periods. The short-term response of density to water level can be explained by the annual cycle in water level, which causes the flats to dry for parts of the year. During low-water periods, many fish may become stranded on the wetland surface (personal observation), resulting in a decrease in the number of fish. This may also explain the negative relationship between density and short-term fluctuations in water level ( $PC_{VI}$ ). Higher frequency of fluctuations would result in multiple strandings as fish try to exploit the flats between dry periods. Individuals that escape the drying wetland are concen-

TABLE 3. Results of regression analyses. Forward and backward stepwise regressions yielded identical equations for both independent variables. The factor loadings for  $PC_I$  and  $PC_{IV}$  were negative and they were negative in the regression, resulting in a positive relationship between these variables and biomass.

| Ind. Variable | ANOVA       | r <sup>2</sup> | Y-Int | Dependent Variable                                    | B      | t     | p       |  |  |
|---------------|-------------|----------------|-------|-------------------------------------------------------|--------|-------|---------|--|--|
| Log Density   | n = 121     | 0.50           | 0.594 | PC <sub>VII</sub> : Short-term Mean Water Level       | 0.132  | 8.82  | < 0.001 |  |  |
|               | F = 26.65   |                |       | PC <sub>I</sub> : Neg Long-term Mean Water Level      | -0.086 | -5.37 | < 0.001 |  |  |
|               | p < 0.0001  |                |       | PC <sub>VI</sub> : Short-term Water-level Variability | -0.051 | -3.42 | < 0.001 |  |  |
|               | df = 4, 116 |                |       | PC <sub>III</sub> : Long-term Temperature Variability | 0.039  | 2.52  | 0.013   |  |  |
| Log biomass   | n = 121     | 0.61           | 0.477 | Low Salinity Period                                   | 0.063  | 3.39  | < 0.001 |  |  |
|               | F = 37.72   |                |       | PC <sub>IV</sub> : Neg Long-Term Salinity Variation   | -0.079 | -5.94 | < 0.001 |  |  |
|               | p < 0.0001  |                |       | PC <sub>VI</sub> : Short-Term Water-level Variation   | -0.057 | -4.52 | < 0.001 |  |  |
|               | df = 5, 115 |                |       | PC <sub>II</sub> : Mean Salinity                      | -0.071 | -4.13 | < 0.001 |  |  |
|               |             |                |       | PC <sub>I</sub> : Neg Long-term Water Level           | -0.053 | -3.96 | < 0.001 |  |  |

trated into any remaining deeper water habitats, resulting in the number of fish per square meter being initially very high (Higer and Kolipinski 1967; Kushlan 1976a, 1980; Loftus and Eklund 1994). This concentration effect attracts predators and depletes oxygen, resulting in additional mass mortality of fishes (Hunt 1952; Odum and Heald 1975; Kushlan 1976b; Tramer 1977; Loftus and Kushlan 1987; Master 1992; Bancroft 1994). Based on these observations, low-water events would quickly result in an overall decline in the number of resident fish (Kushlan 1976b; Masters 1992; Loftus and Eklund 1994).

The longer term response of density to water level may indicate the time needed for fish to recover from drying events. As early colonizers of newly inundated wetlands, these species have a very quick reproductive response to increasing water levels and, thereby, can successfully take advantage of ephemeral wetlands (Harrington 1959; Foster 1967; Wourms 1972; Haake and Dean 1983; Loftus and Kushlan 1987). However, it may take several reproductive events for the population to recover after experiencing significant losses to drying events (Heald et al 1974; Kushlan 1980; Loftus and Kushlan 1987; Loftus and Eklund 1994). As a

result, the increases in the number of fish may be a long-term response of the fish populations.

The finding that increased water level is positively related to fish density is supported by the ANOVA post-hoc tests. Either Taylor River or Barnes Sound had the longest hydroperiod, longest continuous flooded period, and the highest mean water level every year and also had the greatest density of fishes. Highway Creek was a relatively shallow site with a short hydroperiod, and experi-

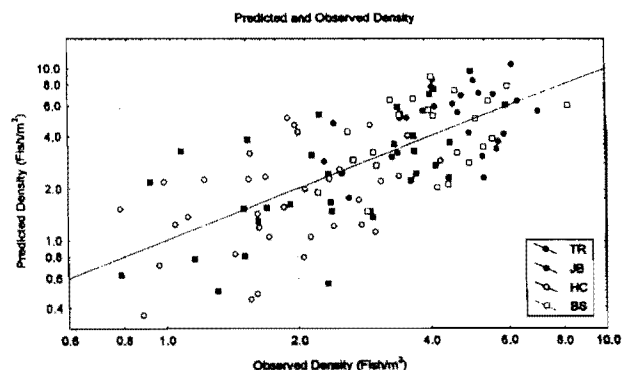


Fig. 8. Log-Log plot of predicted and observed (stratified mean per  $m^2$ ) density of fishes for each sample by site.

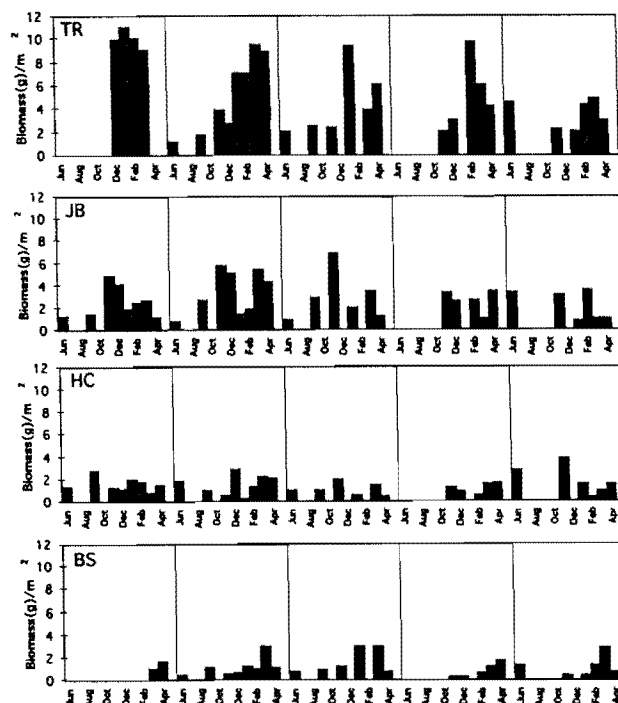


Fig. 9. Stratified mean biomass of fish for every sample collection. Sites as ranked by biomass are Taylor River > Joe Bay > Highway Creek > Barnes Sound and sites are all significantly different from each other. Sampling did not begin at Taylor River and Barnes Sound until December 1991 and March 1992 respectively. Ideally, samples were scheduled for June, September, and monthly from November through April; however, not all months were sampled every year.

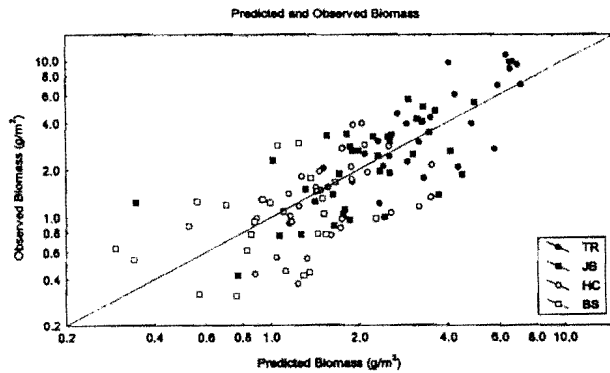


Fig. 10. Log-Log plot of predicted and observed (stratified mean per  $m^2$ ) biomass of fishes for each sample by site.

enced lower fish density. Joe Bay was intermediate in regard to estimates of water level and density.

Long-term variation in temperature ( $PC_{III}$ ) was also positively correlated with density. Taylor (1990) stated that temperature was one of the primary controllers of reproduction in estuarine fishes, particularly athrinids and cyprinodontids. Changes in temperature would, therefore, be expected to impact reproductive output and influence fish density through recruitment potential. The optimal temperature range for oocyte growth and egg hatching is both much narrower and well defined than for other physiological processes in many fishes (Gerking 1980; Munro 1990). Increased long-term variation in temperatures might indicate a diverse set of fish species had been within their optimum reproductive range during a discrete time period (e.g., 240 d) such that recruitment was enhanced and overall density increased over that time period.

#### FISH BIOMASS

Fish biomass can increase through 1) an increase in the number of fish within the existing populations; 2) an increase in the mean size of fishes (i.e., condition factor) within the existing population; and 3) a change in community species structure, with the new populations having biomass in excess of any populations that were displaced over the same time period (Kushlan 1976a). The duplication of two water-level-related regression variables ( $PC_I$ : long-term mean water-level, and  $PC_{VI}$ : short-term water-level variation) in both the density and biomass models indicates at least some of the changes in biomass were the result of changes in recruitment due to hydroperiod length. However, the other biomass regression components (low salinity period,  $PC_{II}$ : mean salinity, and  $PC_{IV}$ : long-term variation in salinity) were different than those for the density regression, indicating changes in biomass were not simply due to changes in

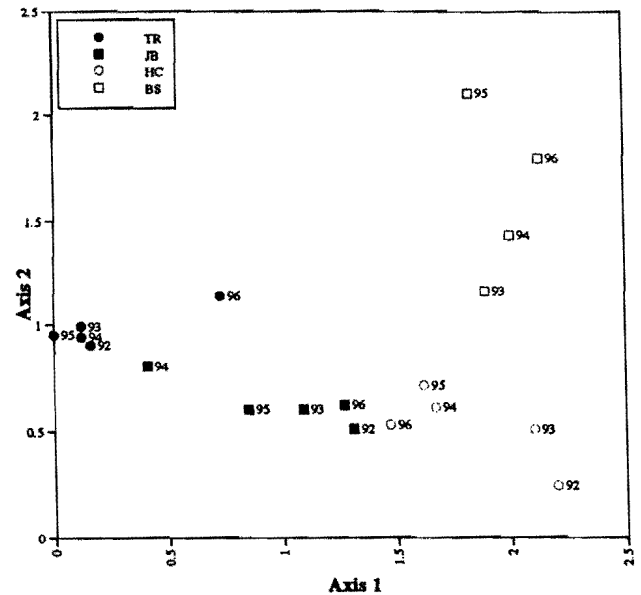


Fig. 11. Plot of detrended correspondence analysis Axis 1 and Axis 2 scores for annual collections at four sampling sites. Axis 1 and Axis 2 account for 45.2% and 14.0% respectively of the variation in community structure. Axis 1 separated sampling sites by the number of low salinity days and the length of the longest low salinity period. Axis 2 was associated with several parameters, half of which were estimators of salinity.

density but were independently impacted by the salinity regime.

Fish biomass responded negatively to periods of high salinity as indicated by inclusion of  $PC_{II}$  (mean salinity) in the regression model. The model also indicated biomass was positively correlated with long freshwater periods (low salinity period), further indicating fishes were negatively impacted by chronically high salinity. The ANOVA post-hoc tests supported these findings. Barnes Sound experienced near marine salinities year round and had the lowest biomass of the sites. Taylor River generally exhibited a prolonged annual freshwater

TABLE 4. Coefficients of correlation ( $r$ ) for hydrologic factors with annual scores on the first two DCA axes. Period and # Days Per Year refer to the longest continuous period and the total number of days per year (respectively) that temperature was below  $18^\circ C$ , water level was above 5 cm on the flats or salinity was less than 5‰. ns = not significant at  $p < 0.01$ .

|                 | AXIS 1   |             |      | AXIS 2   |             |      |
|-----------------|----------|-------------|------|----------|-------------|------|
|                 | Salinity | Water Level | Temp | Salinity | Water Level | Temp |
| Mean            | ns       | ns          | ns   | 0.69     | ns          | 0.57 |
| Std Dev         | ns       | ns          | ns   | ns       | ns          | ns   |
| Min             | ns       | ns          | ns   | 0.67     | ns          | ns   |
| Max             | ns       | ns          | ns   | ns       | 0.67        | ns   |
| Range           | ns       | ns          | ns   | ns       | ns          | ns   |
| # Days Per Year | -0.67    | ns          | ns   | -0.63    | 0.58        | ns   |
| Period          | -0.67    | ns          | ns   | ns       | ns          | ns   |

period compared to the other sites and had the highest biomass. Joe Bay and Highway Creek had similar salinity regimes; however, Joe Bay experienced longer periods of low salinity than Highway Creek, possibly explaining the lower biomass at Highway Creek than at Joe Bay.

Presumably the salinity regime impacted biomass by either changing the individual fish size within the existing community or changing the species structure of the community toward smaller or larger species. The indirect gradient analysis of DCA scores showed community structure was associated with changes in salinity, possibly indicating the latter. Furthermore, the regression analysis indicated high mean salinity ( $PC_{II}$ ) had a negative impact on mangrove-resident fishes even though most of the species commonly collected were euryhaline (Simpson and Gunter 1956; Foster 1967; Loftus and Kushlan 1987; Nordlie et al. 1992). Since the biomass of euryhaline species should remain relatively unaffected by changes in mean salinity, the implication is that observed changes in biomass were most likely the result of adding species sensitive to salinity during low-salinity periods.

The concept that increased mean salinity negatively impacted fishes on the individual level can not be fully dismissed from these findings, however. Although the euryhaline fish themselves may be physiologically unaffected by changes in salinity, the availability of preferred food items may be lower during high-salinity periods, thereby resulting in less or lower quality food for these fish. Consequently, the habitat available to fishes may be inferior at even moderate salinity levels. In a study of submerged aquatic macrophytes of northeastern Florida Bay, Montague and Ley (1993) demonstrated the importance of the salinity regime on primary production. In an associated manuscript, Ley et al. (1994) indicated that locations with impoverished primary production due to the salinity regime resulted in lower quality diets of mangrove fishes. Preliminary results from standardized counts of aquatic macrophytes at the sampling sites indicated submerged vegetation was negatively impacted by ambient salinities above  $\sim 5\text{‰}$ , potentially explaining the biomass-salinity relationship. A more detailed analysis of both plant and fish communities, an examination of fish condition factor at the population level, and controlled field and laboratory growth-salinity experiments on the most common species would help resolve this question.

An enigmatic result of the regression analysis was that biomass was positively correlated with variables that represented both stable salinity (low salinity period) and variable salinity ( $PC_{IV}$ : long-term variation in salinity) over relatively long periods. One possible explanation is that there was a bi-

model response at the community level. Prolonged low salinity would favor oligohaline species while high variation favors true euryhaline fishes. Extremes in either parameter might result in increased biomass overall. The findings of the DCA (that salinity was a major factor in determining the species composition) could be interpreted as supporting this possibility; however, a more detailed analysis of community structure and population responses to salinity would be needed to successfully evaluate this possibility.

A second possible explanation is that, although pulsed salinity events may be detrimental to some submerged plants (Montague and Ley 1993) and fish (Serafy et al. 1997) in the short term, the long-term effect may be positive (Odum et al. 1995). Infrequent pulses of marine water into the mangrove system might deliver to, or cause deposition of, biotically important compounds (e.g., sulfate, bicarbonate, orthophosphate) and thus facilitate greater primary and secondary production (Kemp 1989). If followed by relatively long periods of low salinity, oligohaline plant species may exploit the relative abundance of these compounds (as compared to freshwater systems), resulting in increased production. Over time these compounds may again become limiting if not replenished by a pulse of marine water, resulting in a decline in production (Odum et al. 1995). In this study, samples were collected with both long periods of low salinity and high long-term salinity variation. This could happen only if salinity immediately preceding the sample was below  $5\text{‰}$  for a prolonged period ( $> 200$  d) and if prior to the low-salinity period the salinity was relatively high ( $20\text{‰}$ ). Perhaps the pulses of marine water into the mangroves provided the raw materials for high primary productivity and resultant secondary productivity. The relative low stress of the stable salinity period following the pulses allowed the deposited compounds to be fully exploited (Montague and Ley 1993), resulting in the observed high biomass of fish under these circumstances.

Montague and Ley (1993) periodically sampled Florida Bay macrophytes and benthic crustaceans in conjunction with a variety of physicochemical parameters and found that variation in salinity had a negative impact on the flora and fauna examined. Ley (1992) found the standard deviation of mean salinity was negatively correlated with fish biomass. Finally, Ley et al. (1994) concluded that the diets of fishes in areas of high salinity variation were inferior to those of more stable salinity environments. The authors speculated that higher variance in ambient salinity caused reduced productivity in benthic plants and crustaceans, resulting in lower quality prey and lower biomass in fishes (Ley

et al. 1994). Stable salinity had the opposite effect. These findings support the inclusion of low salinity period as a positive correlate with biomass but are contradictory to the inclusion of  $PC_{IV}$  (long-term salinity variation).

It is possible that the seemingly contradictory components of the biomass regression model (low salinity period and  $PC_{IV}$ : long-term salinity variation) are an artifact of the annual cycling of physicochemical parameters within the dwarf mangrove sites. During a given year, peak salinity was about the same at all sites so the major difference among sites was the period of low salinity. Sites with a longer low-salinity period had lower mean salinity than sites with shorter periods (Figs. 4a and 6b). Since peak salinity was about the same at all sites, the standard deviation of the mean would be higher at the site with the lower mean salinity. The result is that prolonged periods of low salinity tend to co-occur with high long-term salinity standard deviations. Given the results of Ley (1992), Montague and Ley (1993), and Ley et al. (1994), the possibility exists that in the current analysis the period of low salinity was a determining factor in fish biomass but the inclusion of high salinity variation in the regression model was an artifact of the parameters included for the analysis. The very weak relationship between the variables  $PC_{IV}$  and low salinity period ( $r = -0.24$ ) places some doubt about this being simply an analytical artifact.

In summary, fish density was found to be correlated primarily with hydroperiod and water level, presumably through greater recruitment during high-water periods and high mortality during low-water periods. The response of density to water level was also reflected by increases in biomass with increased water level and decreased variability in depth. In addition to increased biomass through increased density, biomass was also influenced by changes in the salinity regime. Presumably this occurred through increases in individual fish body size or through a shift in the community toward heavier bodied fish species. The regression analysis and the ANOVA indicated higher mean salinity resulted in lower biomass within the demersal fish community. Prolonged periods of low salinity and high salinity variability over relatively long-term periods (e.g., 300 d) were both correlated with increased biomass. Three plausible explanations for the inclusion of these seemingly contradictory variables were suggested. 1) The presence of oligohaline specialists and euryhaline species in the community resulted in a bimodal pattern in biomass. 2) The combination of low-salinity periods punctuated by high-salinity events promotes primary and resultant secondary production. 3) The observed contradiction was an artifact of the param-

eters used in the analysis and long periods of stable salinity were the more likely determinant of biomass.

This exploratory study established correlations but did not establish causal relationships (Neter et al. 1996). Observed differences in fish abundance and community structure among sites could be the result of factors other than salinity, water level, and temperature. Differential predation rates, interspecies competition, historical artifacts in site conditions, or random chance could have resulted in the observed differences among sites. Although the analyses suggest a causal relationship between hydroperiod and salinity and the demersal fish community, controlled experiments and further analyses are needed to verify this conclusion.

Anthropogenic diversion of water has resulted in shortened hydroperiods and longer periods of relatively high salinity in the mangrove zone (McIvor et al. 1994). The data presented indicate such changes would have resulted in a restructuring of the demersal fish community in the mangrove habitat. The resulting community would have been less robust than the historic one. Fewer fish (due to shortened hydroperiod) and lower biomass (due to higher and more variable salinity) would have widespread implications for higher trophic levels. An implication of this study is that negative aspects of past water management practices may have impacted a wide variety of fauna in and around Florida Bay through declines in this prey base community. Plans to reverse these effects and restore Florida Bay to a more pristine state will, by definition, require that the wetlands north of Florida Bay be restored to its natural level of productivity.

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