

FORECASTING RESPONSES OF SEAGRASS DISTRIBUTIONS TO CHANGING WATER QUALITY USING MONITORING DATA

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Abstract. Extensive data sets on water quality and seagrass distributions in Florida Bay have been assembled under complementary, but independent, monitoring programs. This paper presents the landscape-scale results from these monitoring programs and outlines a method for exploring the relationships between two such data sets. Seagrass species occurrence and abundance data were used to define eight benthic habitat classes from 677 sampling locations in Florida Bay. Water quality data from 28 monitoring stations spread across the Bay were used to construct a discriminant function model that assigned a probability of a given benthic habitat class occurring for a given combination of water quality variables. Mean salinity, salinity variability, the amount of light reaching the benthos, sediment depth, and mean nutrient concentrations were important predictor variables in the discriminant function model. Using a cross-validated classification scheme, this discriminant function identified the most likely benthic habitat type as the actual habitat type in most cases. The model predicted that the distribution of benthic habitat types in Florida Bay would likely change if water quality and water delivery were changed by human engineering of freshwater discharge from the Everglades. Specifically, an increase in the seasonal delivery of freshwater to Florida Bay should cause an expansion of seagrass beds dominated by *Ruppia maritima* and *Halodule wrightii* at the expense of the *Thalassia testudinum*-dominated community that now occurs in northeast Florida Bay. These statistical techniques should prove useful for predicting landscape-scale changes in community composition in diverse systems where communities are in quasi-equilibrium with environmental drivers.

Key words: discriminant function analysis; Florida Bay; principal components analysis; seagrass; spatial pattern; water quality.

INTRODUCTION

To deal with environmental change, resource managers require tools that will allow them to predict the response of ecological communities to alterations, both anthropogenic and natural, in the environment (Clark et al. 2001). Often, simulation models based on mechanistic descriptions of species' responses to environmental changes have been used to make such predictions, but the construction of these models requires extensive knowledge of physiological ecology and interspecific interactions. In the absence of a reliable, mechanistic simulation model to use as a data synthesis and ecological forecasting tool, statistical models that describe the relationships between ecological response variables and the environment may provide tools for assessing potential ecological change. While the predictive power of such statistical models is constrained by the nature of the available data (Hobbie 2000), they

require much less knowledge of the biology and ecology of the target species and habitats to construct, and can be useful tools for both managers and ecologists in refining mechanistic simulation models.

Human population growth in coastal areas has resulted in changes in the quality, quantity, and timing of freshwater runoff into estuaries. The major water quality change has been an increase in nutrient loading, which has caused eutrophication of many estuaries and coastal marine areas; shifts in the relative importance of planktonic primary producers and submerged vascular plants are concomitant with eutrophication. Estuarine and marine macrophytes, common in relatively oligotrophic areas, have often been replaced by faster growing benthic microalgae and phytoplankton in areas with increased anthropogenic nutrient loading (see Duarte 1995 for review). Changes in the salinity of an estuary can also lead to changes in the structure of submerged aquatic vegetation communities (e.g., Quammen and Onuf 1993). Because of the well-recognized ecological importance of submerged aquatic vegetation beds in estuaries, preserving and restoring these beds is often a goal of environmental manage-

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ment programs (e.g., Chesapeake Bay [Dennison et al. 1993]).

Seagrasses are submerged vascular plants that grow in shallow marine and estuarine environments. Because of their extensive belowground roots and rhizomes, seagrasses have among the highest light requirements of all plants, requiring 10–30% of full surface-incident sunlight (Duarte 1991b). Knowledge of the relationship between commonly measured water quality parameters, like chlorophyll concentration and turbidity, has been used to predict light penetration in the water column and to define the water quality limits for survival of submerged aquatic vegetation. For example, submerged aquatic vegetation is persistent in water >1 m deep in Chesapeake Bay only in areas where median concentrations of chlorophyll and suspended solids were <15 $\mu\text{g/L}$ and <15 mg/L, respectively (Dennison et al. 1993). A refinement of this “habitat requirements” approach has been developed to predict the distribution of subtropical seagrasses in the Indian River Lagoon, Florida, as a function of multiple optically important water quality variables (Gallegos and Kenworthy 1996).

While it is an important determinant of the persistence of submerged aquatic vegetation, light availability is only one of a number of environmental factors that set the bounds of the habitat requirements of submerged aquatic vegetation (Koch 2001). Temperature, salinity, sediment accumulation, water currents, waves, and nutrient availability can also determine the suitability of a site for submerged aquatic vegetation. Further, different species of submerged plants have different habitat requirements.

Extensive modifications to the natural flow of freshwater through the Everglades ecosystem have been made over the past 70 years (Light and Dineen 1994). These modifications have drained water from historic freshwater marshes and sloughs and diverted water that once flowed through the Shark and Taylor Sloughs to Florida Bay. The ecological consequences of this diversion have yet to be fully explored, but it is clear that the flux of organic matter to Florida Bay (Smith et al. 1989), as well as the amount and variability of freshwater runoff and salinity of the Bay, have changed (Swart et al. 1996a, b, 1999, Brewster-Wingard and Ishman 1999, Halley and Roulier 1999). Paleocological evidence is mounting that the flora and fauna of the Bay may also have changed as a result of engineering of the Everglades watershed (Brewster-Wingard and Ishman 1999, Halley and Roulier 1999). It has been suggested that reduction in the variability and amount of freshwater runoff has caused a “marinization” of Florida Bay, leading to changes in the species composition and biomass of the seagrass beds (Zieman 1982). Human alteration of freshwater flow has also been implicated as a potential cause of the recent dieoff of seagrasses in western Florida Bay (Robblee et al. 1991).

There is currently an effort underway to understand the effects of past and planned changes in water management in south Florida (see Redfield 2000 for a description). This is largely a computer simulation exercise to assess different water management scenarios. Because of the sensitivity of Florida Bay to freshwater inflows, it is widely held that changes in water management may cause further changes in the biota. Unfortunately, there are few tools available to predict changes in Florida Bay that may occur under various management scenarios.

This paper outlines a method that uses the extensive monitoring data available for both water quality and seagrasses in Florida Bay to construct statistically based “habitat requirements” models. We show that, given the water quality characteristics that overlie a seagrass bed of known composition, it is possible to make predictions of changes in seagrass distribution within Florida Bay as a consequence of changing water management practice.

METHODS

Study site

Present-day Florida Bay (Fig. 1) supports one of the most extensive seagrass beds in the world, with >2000 km² of seagrass (Zieman et al. 1989). Species composition and density of seagrasses in the Bay have been shown to be controlled by salinity, sediment accumulation (Zieman et al. 1989), phosphorus availability (Fourqurean et al. 1992a), and herbivores (Peterson et al. 2002).

There is a spatial pattern to water quality in Florida Bay (Fourqurean et al. 1993, Boyer et al. 1997, 1999). In general, the mangrove-lined upper estuaries exhibit greater variability and lower mean salinity, while the western margin of Florida Bay within Everglades National Park has much more constant salinity. Average depth also increases from east to west; water depth, along with water clarity, control the amount of light reaching the benthos. Phosphorus availability increases from east to west in Florida Bay and phosphorus controls biomass of both seagrasses (Fourqurean et al. 1992a) and phytoplankton (Fourqurean et al. 1993) in the Bay.

Benthic habitat data

Data on the species composition and abundance of seagrass taxa were collected from 677 locations within Florida Bay between June and September of 2000 (Fig. 1). Data from four separate projects were combined for this analysis; similar methods were used by all projects. In all projects, site locations were determined using a stratified-random approach to ensure independence of sample locations and even coverage within the chosen sampling area. These preselected random coordinates were located in the field using a differentially corrected Global Positioning System with a horizontal accuracy

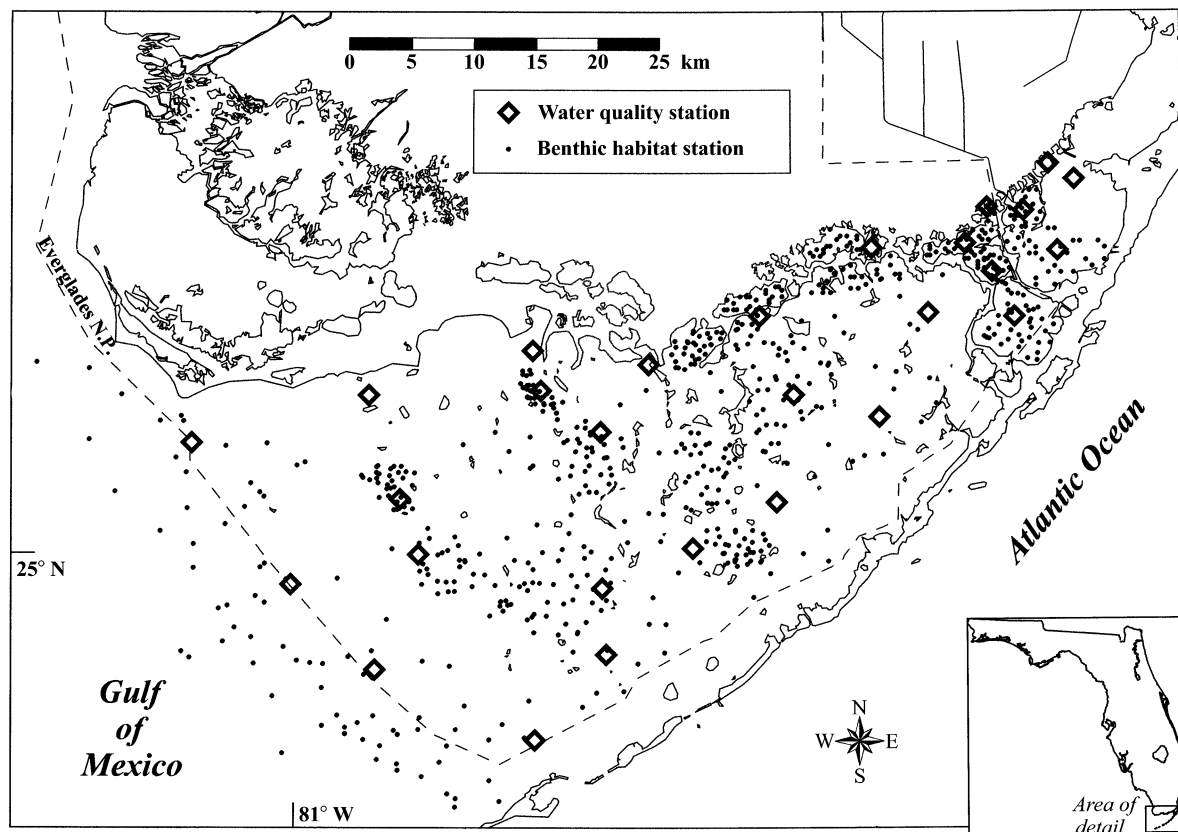


FIG. 1. Map of Florida Bay. Surveys of the benthic plant communities were made at the 677 stations indicated by small dots. Monthly water quality observations were made at the water quality stations (open diamonds) during the period March 1991–March 2000.

of ± 5 m. Abundance of all seagrass species at a site was estimated by using a modified Braun-Blanquet method, in which the abundance of all taxa in observed plots was assigned a score between 0 and 5 (Fourqurean et al. 2001, 2002). A score of 0 indicated that a species was absent; 0.1 indicated a solitary stem covering $<5\%$ of the plot; 0.5 indicated few stems that covered $<5\%$ of the plot; 1 indicated numerous stems covering $<5\%$ of the plot; 2 indicated 5–25% cover; 3 indicated 25–50% cover; 4 indicated 50–75% cover; and 5 indicated 75–100% cover. Depending on the data source, either 4 or 10 plots of 0.25 m^2 were sampled at each sample site. The average score for each species was computed for the plots within a site to yield a Braun-Blanquet density estimate. At each site, water depth was recorded, and at a subset of the sites, sediment depth was measured by probing with a steel rod to bedrock. For sites at which sediment depth was not measured, we estimated sediment depth by subtracting measured water depth from the depth to bedrock estimated from the surface given in Wanless and Tagett (1989).

Water quality data

Water quality data were collected on a monthly basis at 28 sampling stations across Florida Bay (Fig. 1) for

the period March 1991–March 2000, for a total of 3068 samples. Salinity and temperature were measured 10 cm below the surface using a combination salinity–conductivity–temperature probe. Surface and bottom-dissolved oxygen (DO) was measured using an oxygen electrode, corrected for salinity and temperature. Water samples were collected from 10 cm below the surface. These samples were analyzed for chlorophyll *a* (Chl *a*), total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), alkaline phosphatase activity (APA), turbidity (in nephelometric turbidity units, NTUs), and dissolved inorganic nutrients [soluble reactive phosphorus (SRP), nitrate (NO_3^-), nitrite (NO_2^-), and ammonium (NH_4^+)]. Total organic nitrogen (TON) was defined as the difference between TN and DIN (dissolved inorganic nitrogen). Analytical methods are described in Boyer et al. (1999).

For a subset of the samples (279 observations between November 1994 and December 1995), light attenuation by the water column was directly assessed in situ by measuring the light profile in the water column using a 4π PAR sensor (LI-COR, Lincoln, Nebraska). The diffuse attenuation coefficient (k_d) was estimated from the profile data according to the Lambert-Beer law. To estimate the water column light at-

tenuation for the remainder of the samples, we used multiple regression to derive a relationship between other more routinely measured water quality variables and the attenuation coefficient that was then used to predict k_d for each sample. The resulting regression model ($k_d = 1.97 \times 10^{-2} \times \text{TURB} + 0.710 \times \text{TP} + 4.03 \times 10^{-4}$; $r^2 = 0.87$; $P < 0.001$) was used to generate an estimate of the amount of light reaching the benthic community ($\%I_0$) using the Lambert-Beer law and the depth of each station; these predictions were compared with measured bottom light levels as an indication of the utility of the light attenuation predictions. These predicted k_d values produced estimates of bottom irradiance that in general agreed well with measured bottom irradiance ($r^2 = 0.61$, $n = 277$, $P < 0.001$).

Statistical methods

Benthic habitat survey locations were grouped into sets of similar benthic habitat using an hierarchical clustering algorithm. Each survey was treated as a separate case, and the Braun-Blanquet densities of the benthic plant taxa were used to define the groups. The goal of this was not to define "natural" benthic habitat types, but to separate the original 677 locations into groups of similar benthic vegetation composition. The number of groups identified was somewhat arbitrary; for this paper we found there were eight ecologically relevant groups. Further lumping or splitting led to either large groups that combined identifiably different communities or small groups with few cases in each group. A similar approach was used to delineate naturally occurring species associations in the submerged aquatic vegetation of the Chesapeake Bay (Moore et al. 2000).

Many of the water quality variables were correlated with one another. In order to describe the groups of related water quality variables, principal components analysis (PCA) was used to define groups of variables that behaved in a similar fashion (King and Jackson 1999). Before extracting the principal components (PCs), the data values were converted to Z scores to standardize the mean and range of each variable. Varimax rotation was used to facilitate interpretation of the composite variables.

One of the original variables that was highly correlated with each of the resultant principal components was chosen as a proxy to represent the group of correlated variables. This choice was guided by the strength of the association with the principal component, but consideration was also given to the likelihood that a variable would be measured in a monitoring program. For each water quality station, a mean and coefficient of variation ($CV = \bar{x}/SD$) was calculated for each of the proxy variables. Because the water quality and benthic habitat data were not collected at the same locations, fields of means and CVs for each of the water quality proxy variables (plus predicted diffuse attenuation coefficients) were computed for the spatial do-

main of the benthic survey data using a kriging interpolation routine (point kriging using a linear variogram and no nugget). For each benthic habitat survey location, estimates of the value of each of these variables were made by sampling these data fields at that location. The CVs were included specifically to incorporate the effects of intra annual variability (seasonality plus other effects) in water quality on benthic habitats.

We used Hierarchical Discriminant Function Analysis (HDFA [Tabachnick and Fidell 1983]) to generate discriminant functions that would predict the occurrence of a benthic habitat type as a function of water quality and sediment accumulation variables. We entered predictor variables (the proxy variables from the PCA, sediment depth and $\%I_0$) in an order that addressed local management concerns: first we entered salinity variables (salinity mean and salinity CV); then $\%I_0$, sediment depth, and the remaining water quality proxy variables. At each step, a cross-validated (i.e., jackknifed) classification (each case's group membership is predicted from all other cases) was made for each of the 677 benthic habitat locations. The validity of adding subsequent predictor variables to the discriminant model was assessed at each step using McNemar's χ^2 (Tabachnick and Fidell 1983).

The potential change in benthic habitat distribution as a function of changing water quality was assessed by predicting the distribution of benthic habitats using the discriminant functions from the ultimate significant step in the HDFA. For this analysis, we predicted benthic habitats for a situation in which the mean salinity was reduced by 50% and the CV of salinity was doubled—in essence, simulating an increase in the magnitude and variability of freshwater runoff from the Everglades watershed. All other predictor variables were held constant in this exercise.

RESULTS

Benthic habitat surveys

The cluster analysis identified eight distinct benthic macrophyte communities defined by species composition and density (Table 1). Of the 677 sampled locations, 25 had no seagrasses. By far the largest cluster contained 387 locations; the benthic community at these sites could be described as a sparse seagrass bed dominated by *Thalassia testudinum*, with occasional occurrence of *Syringodium filiforme* and *Halodule wrightii*. The mean Braun-Blanquet density of 2.1 at these locations indicates a *T. testudinum* cover of <25%, on average. The next largest cover had 88 locations; these stations had a dense cover of *T. testudinum* (>75% cover), with some sparse *S. filiforme* and *H. wrightii* intermixed. Almost as common was a group of 85 stations dominated by sparse cover of *H. wrightii* with occasional *T. testudinum*. A group of 37 stations had a dense *S. filiforme* bed. At 19 locations, a dense mixed-species assemblage was observed, with no clear

TABLE 1. Density, on a Braun-Blanquet scale, of species of seagrass in each one of the seagrass community types. The number of sites supporting each habitat type is indicated (*n*).

Seagrass community type	Sites, <i>n</i>	Braun-Blanquet density ($\bar{X} \pm 1$ SE)					
		<i>Thalassia testudinum</i>	<i>Syringodium filiforme</i>	<i>Halodule wrightii</i>	<i>Halophila decipiens</i>	<i>Halophila engelmanni</i>	<i>Ruppia maritima</i>
No seagrass	25	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
Sparse <i>Thalassia testudinum</i> bed	387	2.10 $\pm$ 0.05	0.02 $\pm$ 0.01	0.29 $\pm$ 0.03	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
Dense <i>Thalassia testudinum</i> bed	88	4.43 $\pm$ 0.04	1.28 $\pm$ 0.01	0.39 $\pm$ 0.07	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Halodule wrightii</i> bed	85	0.64 $\pm$ 0.09	0.05 $\pm$ 0.02	2.50 $\pm$ 0.14	0.00 $\pm$ 0.00	0.02 $\pm$ 0.01	0.00 $\pm$ 0.00
Dense mixed-species bed	19	1.91 $\pm$ 0.26	2.27 $\pm$ 0.19	2.32 $\pm$ 0.30	0.03 $\pm$ 0.03	0.09 $\pm$ 0.05	0.00 $\pm$ 0.00
<i>Syringodium filiforme</i> bed	37	0.85 $\pm$ 0.10	3.69 $\pm$ 0.17	0.29 $\pm$ 0.07	0.01 $\pm$ 0.01	0.02 $\pm$ 0.02	0.00 $\pm$ 0.00
<i>Halophila decipiens</i> community	16	0.00 $\pm$ 0.00	0.11 $\pm$ 0.07	0.48 $\pm$ 0.23	1.38 $\pm$ 0.20	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Ruppia maritima</i> – <i>Halodule wrightii</i> community	20	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.86 $\pm$ 0.29	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.74 $\pm$ 0.11

dominant species. At 16 of the sites, *Halophila decipiens* was the dominant seagrass in the community, and at the remaining 20 sites, the benthic community was dominated by a mixture of *Ruppia maritima* and *H. wrightii*.

There was a spatial pattern in the benthic habitat group membership (Fig. 2). The *Halophila decipiens* community was found predominantly in the northwest portion of our study area, while the *Syringodium filiforme* community was found in the southwest. The dense mixed-species community was found just east of the *S. filiforme* community. The eastern reaches of Florida Bay most often supported either sparse or dense *Thalassia testudinum* communities, with dense beds being more common to the west of this area. The *Halodule wrightii* community was found on the northern and western peripheries of the *T. testudinum*-dominated communities. Finally, the *Ruppia*–*Halodule* mixed community was found most often along the northern coastal region of Florida Bay. Locations with no seagrass were scattered throughout the study area.

Water quality data

There was substantial variability in all of the water quality parameters measured in this study as a consequence of the geographic extent of the sampling stations and the decade-long scope of the data (Table 2). The range in these variables was generally consistent with other published accounts of water quality in Florida Bay (Fourqurean et al. 1993, Boyer et al. 1997, 1999). On average, Florida Bay was a warm (median $T = 26.5^\circ\text{C}$) estuary (median salinity = 30.5, using the practical salinity scale) with relatively clear water (median $k_d = 0.64 \text{ m}^{-1}$) and high DO (median = 6.5 mg/L). Phytoplankton concentrations were low compared to most other estuaries (median Chl *a* = 0.90 $\mu\text{g/L}$), while TOC concentrations were relatively high (median = 691.3 $\mu\text{mol/L}$). Concentrations of dissolved inor-

ganic nutrients were quite low. Median DIN concentration was 3.56 $\mu\text{mol/L}$; DIN was usually dominated by NH_4^+ . SRP concentrations were very low (median = 0.03 $\mu\text{mol/L}$), as were TP concentrations (median = 0.31 $\mu\text{mol/L}$). Much of the observed range in water quality variables can be attributed to the strong seasonality in Florida Bay, which is described in detail elsewhere (Boyer et al. 1999).

PCA extracted five composite variables with eigenvalues >1 ; these composite variables captured 76.8% of the variation in the original data (Table 3). The first principal component (PC I) explained 22.8% of the variance, and was strongly associated with high values of TN, TON, APA, and TOC; we interpret PC I as an indicator of the size of the heterotrophic planktonic community. PC II explained another 16.9% of the variance, and had strong correlations with oxidized forms of inorganic nitrogen (NO_x , NO_2^- , NO_3^-). PC III explained 14.6% of the variance and was dominated by the NH_4^+ concentration; DIN also was highly correlated with PC III since NH_4^+ dominates the DIN (Table 2). PC IV was an indicator of the size of the phytoplankton community, and was highly correlated with Chl *a*, TURB, and TP; PC IV explained 13.3% of the original variance. The final PC (PC V) was negatively correlated with salinity and positively correlated with DO, and described an additional 9.2% of the variance. We chose TOC as the proxy for the group of variables correlated with PC I, NO_3^- as the proxy for PC II, NH_4^+ as the proxy for PC III, TP as the proxy for PC IV, and salinity as the proxy for PC V.

There were pronounced spatial patterns in the mean values for the proxy water quality variables; these patterns were very similar to the ones reported in earlier works (Fourqurean et al. 1993, Boyer et al. 1997, Frankovich and Fourqurean 1997). Salinity means decreased from >32 in the western portions of the Bay to <18 in the northeast portions of the Bay. Salinity

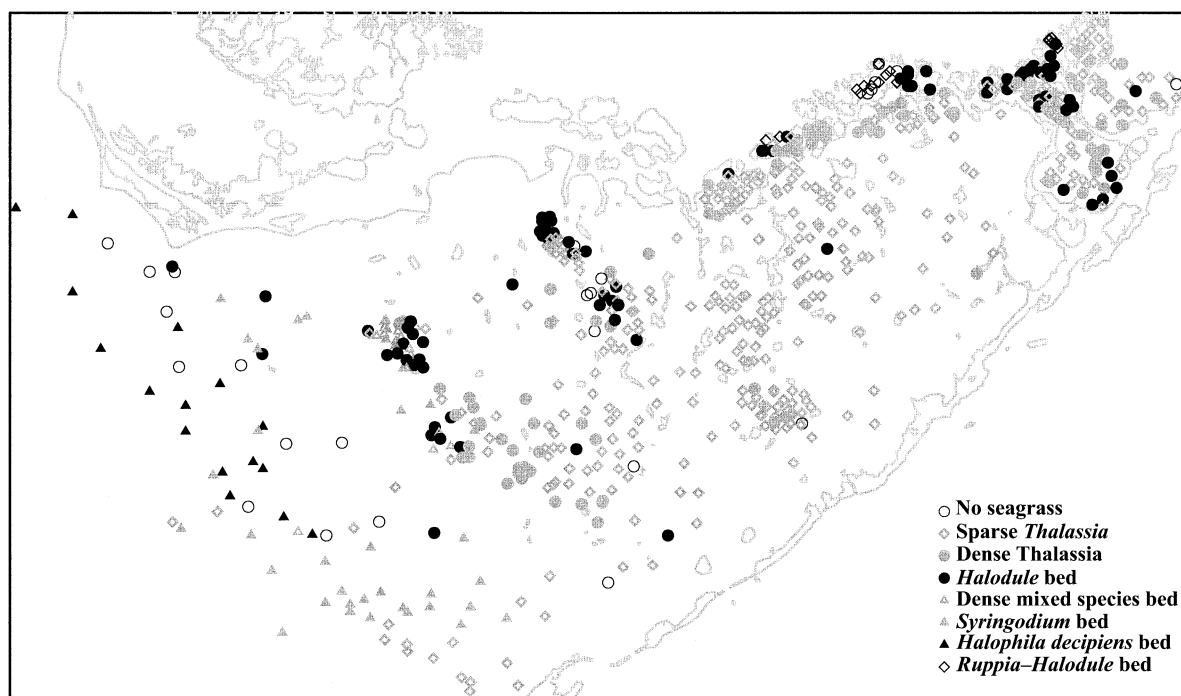


FIG. 2. Cluster analysis of benthic plant community data. Note the grouping in space of stations with the same habitat designation.

variability tended to increase as mean salinity decreased. TOC tended to be low in western Florida Bay, and reached a maximum of $>1200 \mu\text{mol/L}$ in north-central Florida Bay. In contrast, NO_3^- was low in western Florida Bay and reached a maximum of $2.1 \mu\text{mol/L}$ in eastern Florida Bay. In general, NH_4^+ concentrations were higher than NO_3^- ; NH_4^+ was at a maximum ($>14 \mu\text{mol/L}$) in central Florida Bay and decreased to the east, west, and south. TP concentrations, in contrast, were maximum ($>0.9 \mu\text{mol/L}$) in the northwest and decreased to the east.

The presence of spatial pattern in both water quality and benthic habitat distribution (Fig. 2) resulted in different water quality and environmental characteristics for different benthic habitats. The *Ruppia-Halodule* community tended to be found in shallower water and the *Halophila decipiens* community tended to be found in deeper water than the other benthic community types (Fig. 3). Accordingly, less light reached the bottom in *H. decipiens* communities than *Ruppia-Halodule* communities; the other benthic habitat types were found where intermediate amounts of light reached the bottom

TABLE 2. Water quality characteristics of Florida Bay. Distributions are based on monthly samples from 28 stations for the period March 1991–March 2000.

Water quality parameters	n	Median	MAD	Min	Max	Mean	1 SD	1 SE
Temperature ($^{\circ}\text{C}$)	3011	26.5	3.2	15.9	36.0	26.1	4.0	0.1
Salinity (psu)	3012	30.5	7.6	0.2	63.0	28.5	10.0	0.2
Dissolved oxygen (mg/L)	3005	6.5	0.9	0.4	15.2	6.6	1.2	0.0
Total organic carbon ($\mu\text{mol/L}$)	2981	691.3	259.6	99.9	4836.9	752.4	375.3	6.9
NO_3^- ($\mu\text{mol/L}$)	3011	0.41	0.81	BD	10.98	0.87	1.21	0.02
NO_2^- ($\mu\text{mol/L}$)	3011	0.18	0.18	BD	7.92	0.26	0.34	0.01
NH_4^+ ($\mu\text{mol/L}$)	3010	2.55	4.67	BD	120.04	5.18	8.01	0.15
Total nitrogen ($\mu\text{mol/L}$)	3011	48.70	19.83	6.23	314.88	53.20	28.11	0.51
Dissolved inorganic nitrogen ($\mu\text{mol/L}$)	3003	3.56	5.29	0.07	120.47	6.32	8.58	0.16
Total organic nitrogen ($\mu\text{mol/L}$)	3002	42.29	17.89	0.00	311.04	46.83	26.53	0.48
Total phosphorus ($\mu\text{mol/L}$)	3011	0.31	0.23	0.02	4.21	0.42	0.37	0.01
Soluble reactive phosphorus ($\mu\text{mol/L}$)	3011	0.03	0.04	BD	1.57	0.05	0.08	0.00
Alkaline phosphatase activity ($\mu\text{mol/L}$)	2975	0.39	0.71	0.01	6.44	0.80	1.03	0.02
Chlorophyll <i>a</i> ($\mu\text{g/L}$)	3002	0.90	1.26	0.02	35.61	1.55	2.08	0.04
Turbidity (NTU)	3010	3.4	7.2	BD	178.6	7.5	13.8	0.3
k_d (m^{-1})	279	0.64	0.45	0.04	3.85	0.83	0.63	0.04
I_z (fraction of I_0)	279	0.38	0.18	0.00	0.95	0.39	0.22	0.01

Notes: MAD = mean absolute deviation; BD = below detection. For other acronyms, see *Water quality data*.

TABLE 3. Factor loadings for the five significant rotated Principal Components (PCs) extracted from the water quality data set.

Water quality parameters	PC I	PC II	PC III	PC IV	PC V
Total nitrogen	0.903	0.050	0.282	0.120	-0.113
Total organic nitrogen	0.929	-0.047	0.001	0.128	-0.125
Total organic carbon	0.890	-0.036	0.083	0.094	0.040
Alkaline phosphatase activity	0.755	-0.192	-0.046	0.306	0.032
NO ₃ ⁻	-0.064	0.932	0.085	-0.027	0.169
NO ₂ ⁻	-0.007	0.670	0.441	0.060	-0.060
Dissolved inorganic nitrogen	0.076	0.312	0.931	-0.005	0.020
NH ₄ ⁺	0.091	0.164	0.965	-0.004	-0.001
Turbidity	-0.075	0.155	0.142	0.806	0.041
Total phosphorus	0.388	-0.059	-0.056	0.760	-0.107
Chlorophyll <i>a</i>	0.297	-0.118	-0.097	0.781	-0.010
Salinity	-0.051	-0.283	0.026	0.108	-0.745
Dissolved oxygen	-0.118	-0.057	0.048	0.066	0.828
Soluble reactive phosphorus	0.306	0.090	-0.175	-0.029	0.226
% of variance explained	22.8	16.9	14.6	13.3	9.2

Notes: Bold type indicates strong correlations between water quality variables and the PCs. Taken together, the principal components describe 76.8% of the variance in the water quality data.

(Fig. 3). *Ruppia-Halodule* communities had the lowest and most variable salinity (Fig. 4), while yearly mean salinity in the *H. decipiens*, *Syringodium filiforme*, and dense mixed-species beds was relatively high, with low variability. Intermediate yearly mean salinities and relatively high annual variability were found in the *Halodule wrightii*, dense *Thalassia*, and sparse *Thalassia* communities. TOC was highest in *Ruppia-Halodule* communities, and lowest in *H. decipiens* and *Syringodium filiforme* communities (Fig. 5); NO₃⁻ concentrations showed a similar pattern among habitat types as TOC. In contrast, NH₄⁺ concentrations were lowest in the *Ruppia-Halodule* communities and highest in the sparse *Thalassia testudinum* communities. TP was also lowest in the *Ruppia-Halodule* communities, but was highest in the dense mixed-species and *Syringodium filiforme* beds.

Discriminant Function Analyses

A discriminant function model using only mean salinity of a site correctly classified only 13.9% of the benthic habitat stations (Table 4). Adding salinity variability to the discriminant function led to a small but statistically significant increase in predictive ability, as did stepwise additions of %I₀ and sediment depth. Adding the mean NO₃⁻, TOC, NH₄⁺, and TP as a group increased the accuracy of classification further, but adding information on the variability of these parameters did not increase the predictive ability of the model. The final discriminant function model correctly classified 56.7% of the benthic habitat stations (Table 5), much better than the 12.5% expected by chance. Not all benthic habitat classes were predicted with equal accuracy. The model was very successful in predicting the occurrence of *Halophila decipiens* (93.8% accuracy) and dense mixed-species beds (84.2% accuracy), but was not successful in predicting the occurrence of benthic habitats with no seagrasses. For the sparse *Thalassia*,

dense *Thalassia*, *Halodule*, *Syringodium*, and *Ruppia-Halodule* communities, the most frequently predicted habitat type corresponded to the actual habitat, and the second-ranked predicted habitat classification was always biologically close to the actual habitat type. For example, 66.1% of sparse *Thalassia* beds were correctly classified, but 16.8% were incorrectly classified as dense *Thalassia* beds. Very few misclassifications of sparse *Thalassia* beds were scored as *H. decipiens* beds or *Ruppia-Halodule* beds—two communities with very dissimilar habitat requirements (Figs. 3–5).

The final discriminant function model was used to predict the probability of each benthic habitat class as a function of water quality across the spatial domain of the study. We used the mean and cv of the water quality parameters over the period of record as our base case for these predictions. For the entire eastern half of Florida Bay, the probability of encountering a sparse *Thalassia* community was >50% (Fig. 6). The probability of encountering a dense seagrass bed was highest in the south-central parts of our study area. In the extreme western end of our study area, a *Halophila decipiens* community was the most probable, while in the southwestern part of Florida Bay, a *Syringodium* community was most probable (Fig. 7). The dense mixed-species community was restricted to the area immediately east of the *Halophila* community, and the maximum probability of encountering a *Halodule* community was just east of that and in a narrow band close to the shoreline in the northeastern region. The water quality model predicted that the *Ruppia-Halodule* community would be restricted to the extreme northeast under current water quality characteristics (Fig. 8).

Changes in water quality caused a change in the predicted distribution of the habitat types. Under a hypothetical scenario in which mean annual salinity was reduced by one-half and the variance in the salinity was increased (cv increased by a factor of 2), the dis-

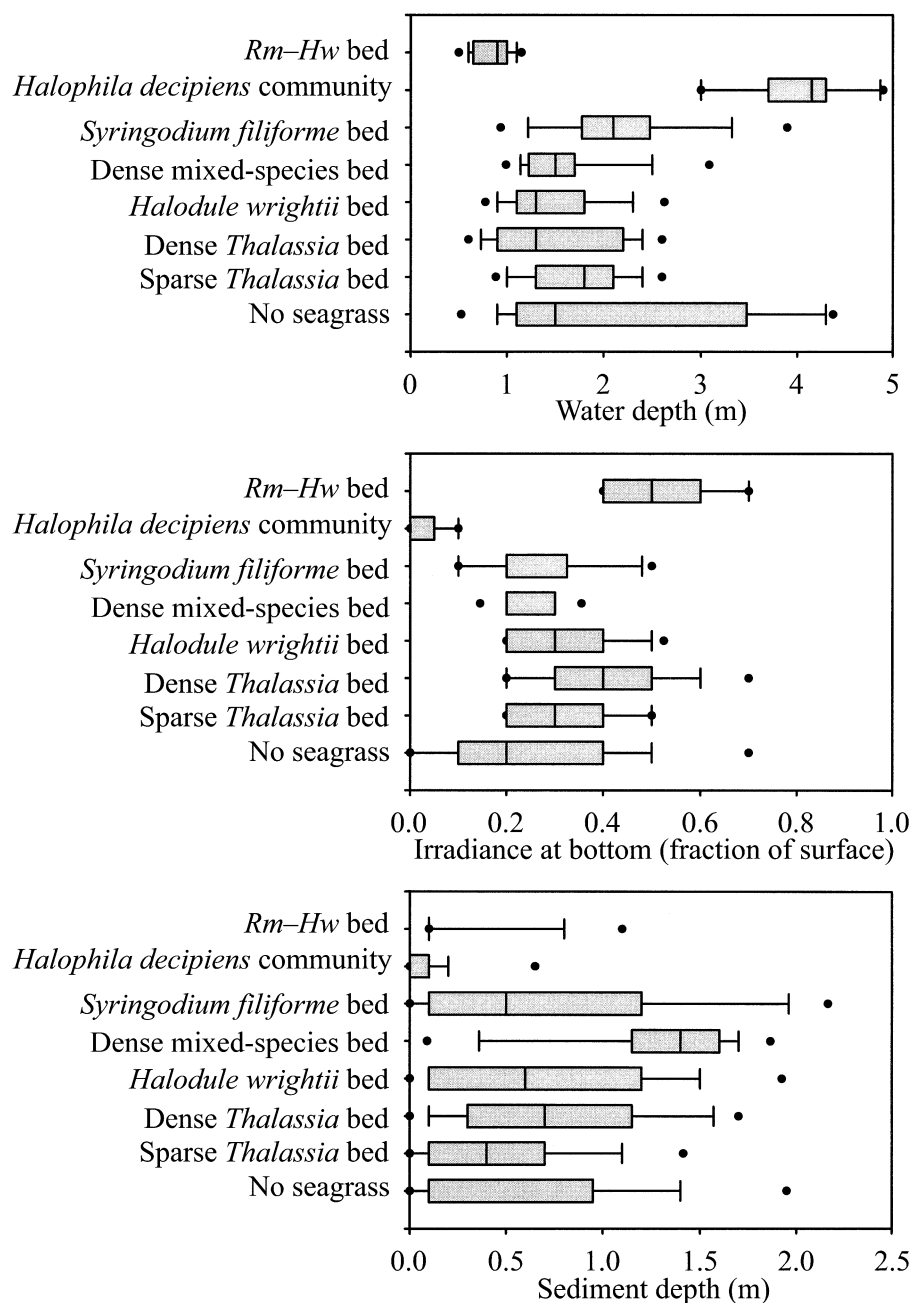


FIG. 3. Physical characteristics of benthic habitat sites belonging to the benthic habitat classes. The box indicates 25th and 75th percentiles, and error bars indicate 10th and 90th percentiles. The short vertical line within the box indicates the median value; solid dots are outliers. Top: Characteristics of water depth. Middle: Characteristics of the amount of surface irradiance that reaches the bottom. Bottom: Depth of unconsolidated sediment over bedrock.

criminant model predicts the southern expansion of the *Ruppia-Halodule* community into Florida Bay (Fig. 8) and a retreat of *Thalassia*-dominated communities away from sources of freshwater runoff (Fig. 9).

DISCUSSION

Monitoring data by themselves do not provide the information needed by resource managers to exercise

adequate environmental stewardship. Rather, explorations of the relationships between driving environmental variables (in this case water quality) of Florida Bay, and ecological response variables (in this case benthic habitat structure) can provide models that represent potential tools for the resource manager. One problem facing the development of such tools is that data on the driving variables and the response variables are

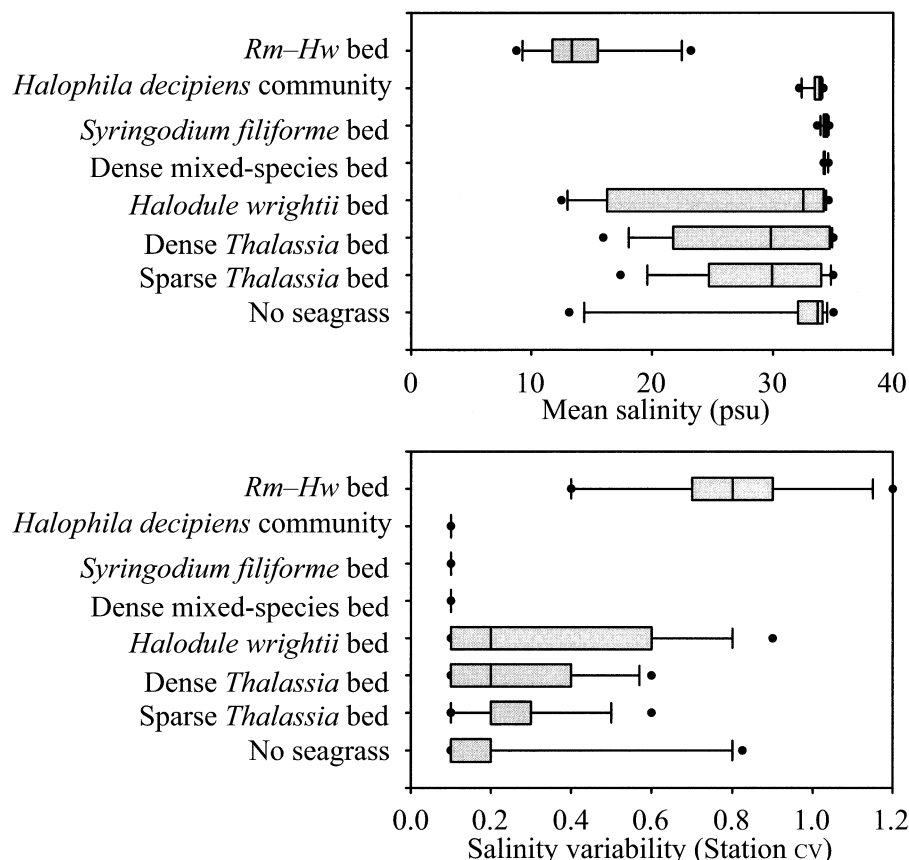


FIG. 4. Salinity characteristics of benthic habitat sites belonging to the benthic habitat classes. The box indicates 25th and 75th percentiles, and error bars indicate 10th and 90th percentiles. The short vertical line within the box indicates the median value; solid dots are outliers. Top: Mean station salinity. Bottom: Station salinity variability, expressed as coefficient of variation (cv, %).

often collected by different investigators at different locations and at different times, making simple correlational analysis difficult. The approach taken in this paper allows for spatial interpolation of descriptors of driving variables (i.e., water quality parameter mean and variability) and the creation of a probabilistic prediction about the occurrence of an ecological state (i.e., benthic habitat classification). Our approach is still constrained by the inability to draw statistical inference in cases where either the values or correlational structure of the predictor variables are different from those used to construct the model. However, in many situations, statistical models can provide useful tools to forecast ecological change (Hobbie 2000). The utility of this approach is not limited to the Florida Bay ecosystem; it should prove to be a valuable tool in other ecosystems in which gradients in environmental conditions produce patterns in distribution of habitats. It must be emphasized that such statistical models can only describe relationships among variables; they cannot shed light on causation.

The relationships between seagrass habitat structure and water quality are of interest largely because of the

history of seagrass losses caused by water quality degradation. Recovery of seagrass habitat in degraded areas is a goal of many restoration efforts, since seagrasses are known to contribute significantly to the high productivity of many estuaries (e.g., Chesapeake Bay [Kemp et al. 1983]). In Chesapeake Bay, statistical relationships between water quality variables and seagrass survival have been used to establish "habitat criteria" for the survival of seagrasses (Dennison et al. 1993); these criteria have in turn been used to set goals for restoration efforts. However, not all submerged aquatic vegetation communities have the same habitat value. For example, fish densities are higher in Florida Bay seagrass beds where *H. wrightii* and *S. filiforme* are present than in monotypic stands of *T. testudinum* (Thayer and Chester 1989). Hence, the ability to predict the species composition, not just the occurrence of submerged aquatic vegetation, will help resource managers predict the ecosystem-level changes wrought by environmental change.

The techniques employed herein rely on the implicit assumption that the ecological response variable is in equilibrium with the environmental forcing variables.

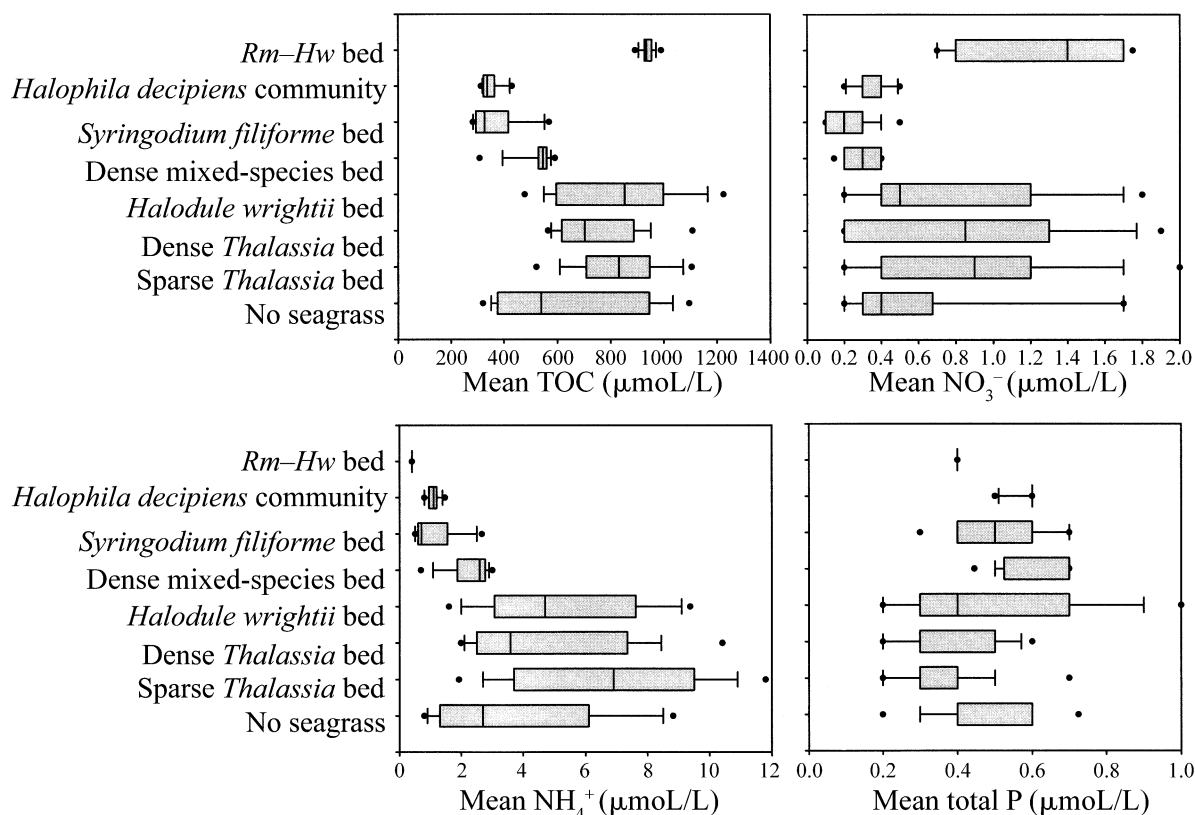


FIG. 5. Water quality characteristics of benthic habitat sites belonging to the benthic habitat classes. The box indicates 25th and 75th percentiles, and error bars indicate 10th and 90th percentiles. The short vertical line within the box indicates the median value; solid dots are outliers.

In most ecosystems, this assumption will not be strictly met. In this study, we used a 10-year record of antecedent water quality to predict benthic habitats surveyed at a single point in time. There are a number of lines of evidence that suggest decadal-scale water quality data are necessary to predict the makeup of benthic communities in Florida Bay. Seagrasses are clonal

plants; the median age of single shoots of *T. testudinum* in south Florida is >5 years (Peterson and Fourqurean 2001), and the average age of whole plants is on the order of decades. Sexual reproduction is rare in seagrasses, so colonization of new areas is generally a result of relatively slow vegetative growth (Hemminga and Duarte 2000). And, since most of the biomass of

TABLE 4. Summary of the results from the hierarchical discriminant function analysis.

Step	Variables entered	Cases correctly classified (%)	McNemar's χ^2	P
1	Mean salinity	13.9		
2	Salinity variability	16.7	3.84	0.05
3	% I_0	23.9	24.3	<0.001
4	Sediment depth	33.5	37.8	<0.001
5	Mean NO_3^-	56.7	104.5	<0.001
	Mean TOC			
	Mean NH_4^+			
	Mean total phosphorus			
6	NO_3^- variability	55.5	0.54	>0.10
	TOC variability			
	NH_4^+ variability			
	Total phosphorus variability			

Notes: Independent variables entered at each model step are given, along with an assessment of the increase in predictive ability of the model (McNemar's χ^2). Probabilities indicate whether the model step was a significant improvement over the previous step.

TABLE 5. Classification accuracy of the discriminant function model. Each cell is the percentage (%) of cases classified as a given habitat type (rows) predicted to support the benthic habitat type given in the column heading.

Actual benthic habitat	Predicted benthic habitat type (%)							
	No sea-grass	Sparse <i>Tt</i>	Dense <i>Tt</i>	<i>Hw</i> bed	Dense mix	<i>Sf</i> bed	<i>H. decipiens</i> bed	<i>Rm-Hw</i> bed
No seagrass	0.0	4.0	16.0	20.0	0.0	4.0	40.0	16.0
Sparse <i>Tt</i> bed	1.3	66.1	16.8	10.1	1.3	3.4	1.0	0.0
Dense <i>Tt</i> bed	8.0	33.0	43.2	6.8	6.8	0.0	0.0	2.3
<i>Hw</i> bed	4.7	18.8	12.9	30.6	17.6	1.2	1.2	12.9
Dense mixed species	5.3	0.0	0.0	0.0	84.2	5.3	5.3	0.0
<i>Sf</i> bed	5.4	0.0	0.0	0.0	27.0	51.4	16.2	0.0
<i>H. decipiens</i> bed	0.0	0.0	0.0	0.0	0.0	6.3	93.8	0.0
<i>Rm-Hw</i> bed	0.0	5.0	10.0	15.0	0.0	0.0	0.0	70.0

Notes: Classifications are based on a jackknife approach, in which each case's benthic habitat was predicted using equations based on all data except the data for that case. Cells in bold on the diagonal are the proportions of correctly classified sites. Of all cases, 56.7% were correctly classified. The benthic macrophyte communities are described in *Results: Benthic habitat surveys*.

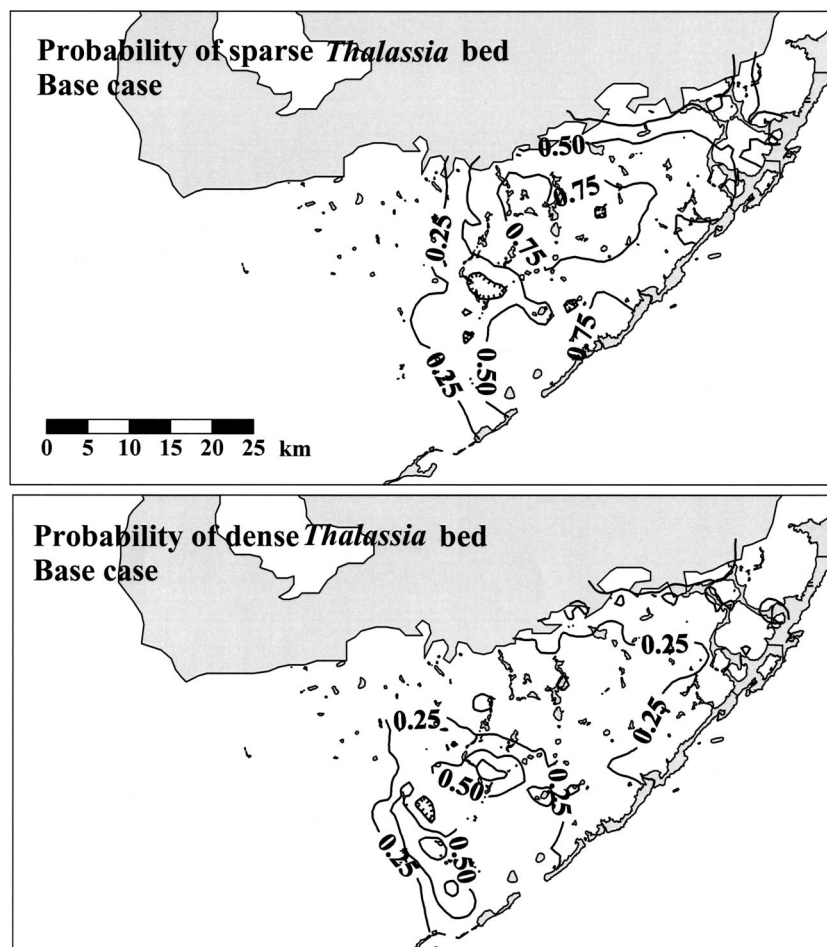


FIG. 6. Discriminant Function Model predictions: the probability of finding a given benthic habitat across Florida Bay as a function of water quality characteristics. Top: Sparse *Thalassia* community. Bottom: Dense *Thalassia* community.

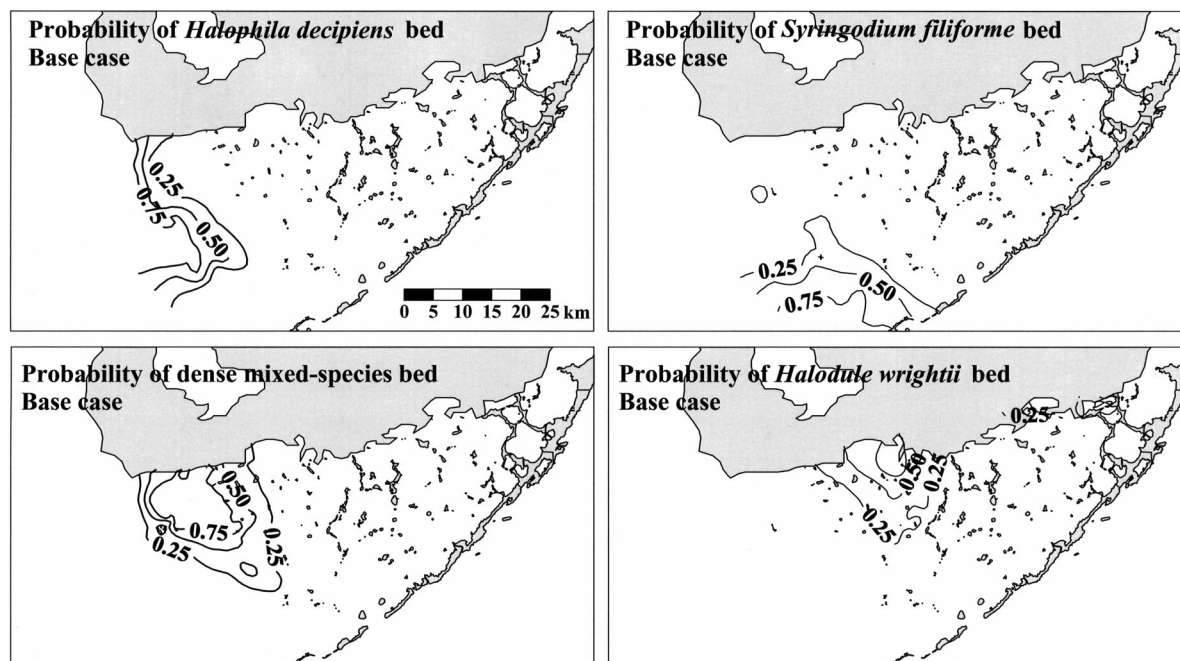


FIG. 7. Discriminant Function Model predictions: The probability of finding a given benthic habitat across Florida Bay as a function of water quality characteristics.

seagrasses is buried in sediments, they are protected to some degree against acute water quality problems. They can also rely on stored reserves in rhizomes to survive periods of unfavorable conditions (Hemminga and Duarte 2000). As a consequence, changes in species composition occur slowly as conditions change. In one fertilization experiment in Florida Bay, the relative biomass of different seagrasses was still responding nine years after alteration of nutrient loading rates (Fourqurean et al. 1995) as a result of stochastic variability in the recruitment of new species.

There are a number of factors that would upset the equilibrium between benthic habitat and water quality in Florida Bay. Disturbances such as grazing events or physical disturbances can alter the species composition or biomass of the seagrass bed. For example, grazing of sea urchins recently has been reported to denude dense *S. filiforme* beds in extreme western Florida Bay, leaving a sparse *T. testudinum* and calcareous green algae community in its place (Maciá and Lirman 1999, Rose et al. 1999, Peterson et al. 2002). Physical disturbance of seagrass beds by wave attack can also create a patch mosaic of species composition of seagrass beds in response to the migration of blowouts through the grass bed (Patriquin 1975).

Despite the evidence of disequilibrium between seagrass beds and water quality in some instances, the discriminant model was fairly accurate in predicting the occurrence of the eight benthic habitat classes identified for Florida Bay, with the exception of the “no seagrass” and “*H. wrightii*” classes (Table 5). Apparently, these latter two habitat classes are not always in

stable equilibrium with water quality in Florida Bay. Some sites that did not support seagrasses may have indeed been too deep for seagrasses to survive, but other sites were most likely responding to the recent, poorly understood seagrass dieoff in Florida Bay (Robblee et al. 1991, Zieman et al. 1999). Inaccuracies in predicting the occurrence of the *H. wrightii* class may have been a consequence of the pioneering life-history strategy of this species (see Zieman 1982 for review). In many instances, domination of the community by *H. wrightii* may indicate that the site was at an early successional stage following disturbance, and that another species, most likely *T. testudinum*, would eventually replace the *H. wrightii* as the benthic habitat reached equilibrium with the environmental variables.

A further assumption underlying these analyses is that the species responsible for structuring the different community types have different life history characteristics that bring about divergent habitat characteristics among the species. This is certainly the case for the seagrasses in south Florida. From experimental and observational work, it is known that fast-growing seagrasses (*R. maritima* and *H. wrightii*) have higher nutrient requirements than slow-growing species like *T. testudinum* (Powell et al. 1989, 1991, Fourqurean et al. 1992b). From distributions along depth gradients, it is known that *T. testudinum* has a higher light requirement than *S. filiforme*, *H. wrightii*, and *Halophila* spp. (Wiginton and McMillan 1979, Fourqurean et al. 2002). Differences in sexual and asexual reproduction rates lead to differences in the rate at which the species will colonize disturbed areas (Patriquin 1975, Duarte

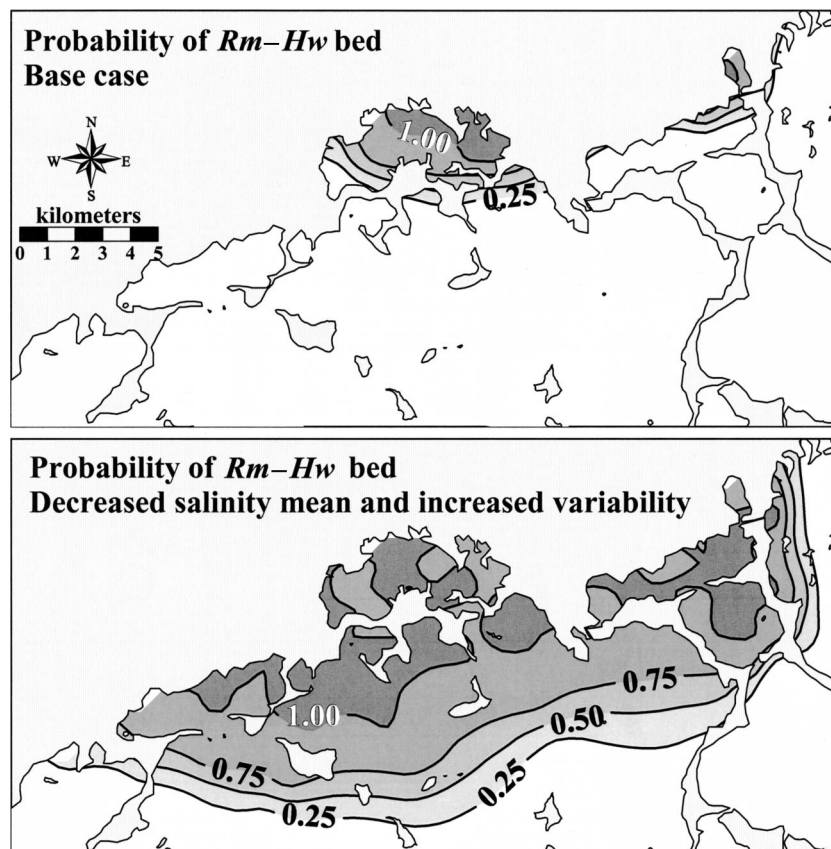


FIG. 8. Discriminant Function Model predictions: the probability of finding the *Ruppia-Halodule* benthic habitat across Florida Bay as a function of water quality characteristics. Top: Using the water quality data collected March 1991–March 2000 as a predictor (base case). Bottom: Predictions made if salinity mean were reduced by half and the variation in salinity were doubled over the base case.

1991a). In a situation without strong differences in habitat requirements among important species, the techniques used in this paper would not be effective.

In our stepwise addition of driving variables into the discriminant function model, we chose the order in which the variables were entered into the model. Rather than allowing the order to be based on the amount of variance explained, we entered the variables in an order based on knowledge of the system and the need of resource managers (Table 3). Of the potential driving variables assessed, salinity and salinity variability are the factors under the greatest control of managers, and were thus evaluated first. The subsequent order was determined by our assessment of the relative ease in obtaining values for the driving variables and their documented importance. In later steps of the model, we chose to enter all of the remaining proxy water column nutrient means in a single step, instead of evaluating them all independently. This was done to simplify the presentation of the approach in this paper. It would be a simple matter to evaluate the contribution of each of the independent proxy variables to the goodness-of-fit of the discriminant function model. Further, we chose to use a single original measured variable as a proxy

for all of the variables that were correlated to a single principal component in order to allow for a more straightforward application and explanation of the model. A slightly better predictive model would result if the factor scores of the component variables were used in the discriminant function model instead of the proxy variables.

Seagrass distributions within Florida Bay have not been static over the past few decades, indicating that environmental driving variables controlling seagrass distribution have changed over the same time period. In the 1960s and 1970s, much of northeastern Florida Bay that is presently occupied by sparse *T. testudinum* communities (Figs. 2 and 9) was instead dominated by a *H. wrightii* community (Schmidt 1979, Zieman 1982: 90–91). Currently, *H. wrightii* communities are typified by a lower mean and more variable salinity regime (Fig. 4) than sparse *T. testudinum* communities. We interpret this to indicate that the mean salinity increased and salinity variability decreased from the 1960s to the present in northeastern Florida Bay in response to the documented anthropogenic diversion of freshwater flow in the Everglades. These observations are consistent with paleoecological reconstructions based on coral skeleton

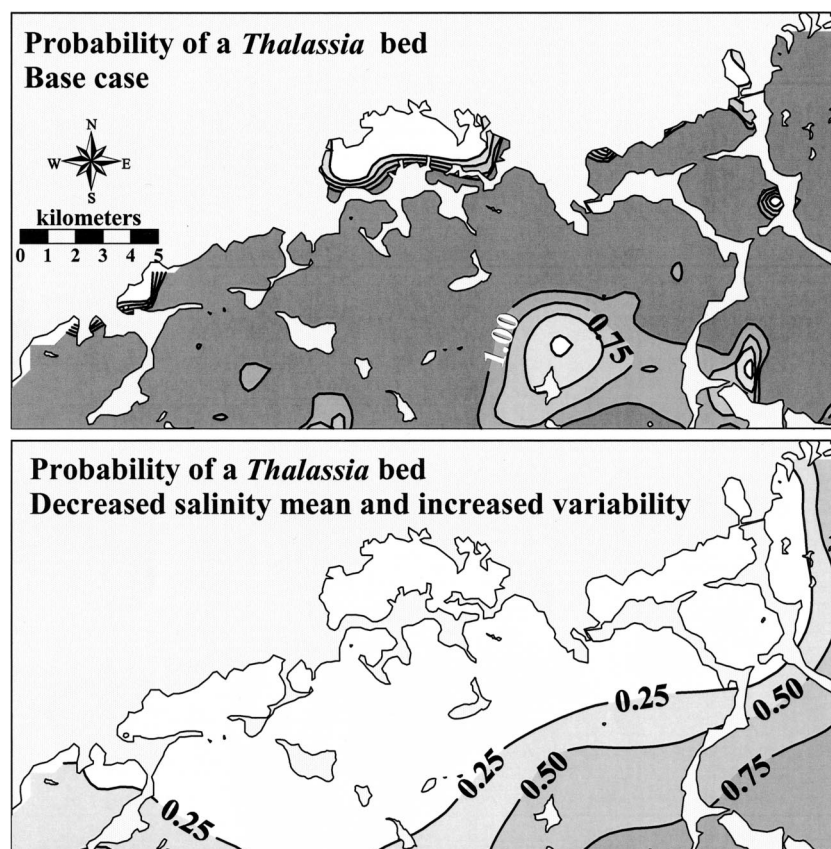


FIG. 9. Discriminant Function Model predictions: the probability of finding a *Thalassia*-dominated community (sparse *Thalassia* + dense *Thalassia*) in northeastern Florida Bay as a function of water quality characteristics. Top: Using the water quality data collected March 1991–March 2000 as a predictor (base case). Bottom: Predictions made if salinity mean were reduced by half and the variation in salinity were doubled over the base case.

stable isotope patterns (Swart et al. 1996b, 1999) and benthic infauna from sediment cores (Brewster-Wingard and Ishman 1999) that indicate mean salinity was lower and that patterns in salinity variability were different in the past than the present. In contrast to the *H. wrightii*-to-*T. testudinum* shift in eastern Florida Bay, *T. testudinum*-dominated communities that were typical of western Florida Bay in the early 1980s (Zieman et al. 1989) have largely been replaced by mixed-species and *H. wrightii*-dominated communities (Fig. 2). This shift has been attributed to the poorly understood dieoff of *T. testudinum* from Florida Bay and the subsequent increases in turbidity and decreases in light availability in western Florida Bay (Durako et al. 2002). In the present survey, dense mixed-species beds and *H. wrightii* communities were associated with increased TP concentration in the water column (Fig. 5) and decreased light availability (Fig. 3) than those of *T. testudinum* communities, consistent with the recorded increase in light attenuation and TP concentration of the water column from the late 1980s to the present (Boyer et al. 1999).

The consistency of recent changes in seagrass beds of Florida Bay and the relationships between seagrass

community characteristics and water quality that form the basis of the discriminant function model suggest that this model will prove a useful tool for resource managers interested in predicting the ecological responses of Florida Bay to changes in the amount, timing, and quality of freshwater flows. Predictions of new distributions of benthic community composition of eastern Florida Bay suggest that an increase in freshwater flow to Florida Bay of sufficient magnitude to reduce mean salinity to one-half of current means and increase the salinity variability will result in distributions of seagrass habitats in eastern Florida Bay that are closer to the distributions of the early 1970s (Schmidt 1979) than current distributions. Under such a regime, the *Ruppia*–*Halodule* community would encroach outwards into Florida Bay by 5–10 km (Fig. 8), while there would be a concomitant decrease in the presently dominant *T. testudinum*-dominated communities (Fig. 9). Because *T. testudinum* communities reach higher plant biomass than the *Ruppia*–*Halodule* communities of Florida Bay (compare cover values for the communities in Table 1), such a shift would possibly lead to a decrease in seagrass biomass and primary production. It is unclear how such a change in

seagrass community structure would affect the total ecosystem primary production.

Changes in the structure of the benthic plant communities is also likely to have a large impact on the food web in Florida Bay, since the animal communities in seagrass beds in Florida Bay are affected by the species composition and density of the seagrasses (Thayer and Chester 1989, Thayer et al. 1999). In addition, if the anecdotes in Zieman (1982:90–91) about the relative values of these different seagrass communities to hook-and-line fisherman are true, such a change could lead to an increase in production of sought-after game fish in Florida Bay, including sea-trout (*Cynoscion nebulosus*), redfish (*Sciaenops ocellata*), and snook (*Centropomus undecimalis*).

The statistical model developed herein offers a simple tool to predict changes in seagrass beds as a result of changes in water management practices in south Florida. The utility of the model would be increased if coupled with other geographically explicit models that will predict how water quality will be altered by such practices. Florida Bay is subdivided into many semi-isolated basins by shallow mud banks (see Fourqurean and Robblee 1999 for a description of the system), and exchange of water between these semi-enclosed basins will determine what water quality effects will result from management actions. Detailed three-dimensional hydrodynamic models for this purpose have proven elusive for Florida Bay because of the segmented, shallow nature of the system. Simpler, less detailed models of exchange of water and solutes between basins in the Bay (Nuttall et al. 2000) should provide the link necessary to explicitly couple water management activities to benthic habitat distribution. Developing a model with the ability to forecast ecological change, however, does not give guidance as to the proper target of restoration efforts. Different benthic habitat types have different habitat values for different animal species, so any restoration target is likely to favor one group of species, say wading birds and estuarine game fish, over another group of species, like spiny lobsters and juvenile reef fish.

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