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Distribution of Diatoms and Development of Diatom-Based Models for Inferring Salinity and Nutrient Concentrations in Florida Bay and Adjacent Coastal Wetlands of South Florida (USA)

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Abstract The composition and distribution of diatom algae inhabiting estuaries and coasts of the subtropical Americas are poorly documented, especially relative to the central role diatoms play in coastal food webs and to their potential utility as sentinels of environmental change in these threatened ecosystems. Here, we document the distribution of diatoms among the diverse habitat types and long environmental gradients represented by the shallow topographic relief of the South Florida, USA, coastline. A total of 592 species were encountered from 38 freshwater, mangrove, and marine locations in the Everglades wetland and Florida Bay during two seasonal collections, with the highest diversity occurring at sites of high salinity and low water column organic carbon concentration (WTOC). Freshwater, mangrove, and estuarine assemblages were compositionally distinct, but seasonal differences were only detected in mangrove and estuarine sites where solute concentration differed greatly between wet and dry seasons. Epiphytic, planktonic, and sediment assemblages were compositionally similar, implying a high degree of mixing along the shallow, tidal, and storm-prone coast. The relationships between diatom taxa and salinity, water total phosphorus (WTP), water total nitrogen (WTN), and WTOC concentrations were determined and incorporated into weighted averaging partial least squares regression models. Salinity was the most influential variable, resulting in a highly predictive model ($r_{\mathrm{apparent}}^2=0.97$, $r_{\mathrm{jackknife}}^2=0.95$) that can be used in the future to infer changes in coastal freshwater delivery or sea-level rise in South Florida and compositionally similar environments. Models predicting WTN ($r_{\mathrm{apparent}}^2=0.75$, $r_{\mathrm{jackknife}}^2=0.46$), WTP ($r_{\mathrm{apparent}}^2=0.75$, $r_{\mathrm{jackknife}}^2=0.49$), and WTOC ($r_{\mathrm{apparent}}^2=0.79$, $r_{\mathrm{jackknife}}^2=0.57$) were also strong, suggesting that diatoms can provide reliable inferences of changes in solute delivery to the coastal ecosystem.

Keywords Diatoms · Prediction models · Diversity · Salinity · Nutrients · Florida Bay

Introduction

Estuaries and shallow coastal embayments around the world have been heavily impacted by human activities in the last few centuries (Lotze et al. 2006) and are among the ecosystems most threatened by urbanization and sea-level rise (Nicholls et al. 1999; Carnahan et al. 2008). Land conversion and saltwater encroachment "squeeze" coastal ecosystems (Silver and DeFries 1990) and alter their productivity, although long-term, spatially explicit data necessary to document these changes are sparse. Algal community changes often serve as an early warning of environmental change along coasts (Linton and Warner 2003; Niemi et al. 2004; Niemi and McDonald 2004), but

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their successful application requires a precise understanding of species identities and habitat preferences.

Many of the most densely populated and fastest developing coastal areas are located in subtropical regions of the Caribbean and North America (Schwartz 2005), where coastal water masses are particularly subject to anthropogenic stressors due to poorly developed environmental protection practices. Although the Everglades and coastal environments of South Florida have received considerable scientific and political attention in comparison to neighboring Caribbean coastal regions, decades of unregulated development have replaced much of the natural environment with a built, agricultural landscape that has left an unprecedented legacy of hydrologic engineering and ecological alteration. This legacy is evident in a severely fragmented hydroscape where a highly developed drainage system controls the flow paths, quantity, and quality of water delivered to the Everglades marshes and adjacent estuaries (McIvor et al. 1994). This has altered the distribution, composition, and productivity of many freshwater and marine organisms and plants, which has had system-level consequences (Tilmant 1989; Nance 1994; Butler et al. 1995; Fourqurean and Robblee 1999; Boyer et al. 1999). The threat of these local, directional changes resulting from specific land use alterations is now amplified by those imposed by a changing climate. Unraveling the sequence of environmental changes resulting in current biotic distributions will therefore partly depend on an understanding of how biota respond to the breadth of environmental variability to which they are now exposed. Biological assessment is widely recommended in the management of aquatic ecosystems (US EPA 1990), and diatoms represent one of the most important groups of organisms for evaluating water quality (Niemi et al. 2004) due to their widespread occurrence, high species diversity, and short reproductive rates that result in a quick response to environmental changes (Battarbee 1986). Where the relationships of diatom taxa to environmental variables are strong, diatom-based transfer functions can be used to infer environmental quality and improve the assessment of aquatic environments such as lakes and streams (Ramstack et al. 2004; Philibert et al. 2006; Fritz 2007; Ponader et al. 2007). More recently, ecological response functions have been developed for diatoms in coastal regions (Juggins 1992; Clarke et al. 2003; Jiang et al. 2004; Weckström and Juggins 2005), although few studies have described these relationships for subtropical coastal habitats (Taffs et al. 2008). The South Florida diatom flora is poorly resolved taxonomically, and although several diatom investigations have been conducted in this region (Gaiser et al. 2005, 2006; Wachnicka and Gaiser 2007), they have not produced a detailed account of species affinities across the full gradients of water quality and salinity occurring in these systems. The goal of this study was to document the diatom flora occupying Florida Bay and the adjacent coastal habitats of South Florida, determine their habitat affinities and environmental preferences, and develop quantitative models for inferring environmental conditions from diatom species composition. Specifically, we aimed to (1) determine how accurately habitat characteristics (such as coastal vegetation zone and substrate preference) can be inferred from diatom assemblages and (2) investigate the influence of physicochemical variability on diatom diversity and composition. Quantitative prediction models for inferring salinity and primary water column variables (nitrogen, phosphorus, organic carbon concentrations) have the potential to assist the understanding of environmental changes due to climatic fluctuations and water management strategies along the coast. This is particularly important for South Florida, where comprehensive water delivery changes are underway that may rehabilitate coastal ecosystems. If environmental preferences are identifiable and repeatable, these models can also enable precise paleoecological inferences from fossil diatom assemblages, to provide a long-term context for distinguishing the effects of climate variability from those imposed by water management. Additionally, we discuss the applicability of these transfer functions in other regions, particularly along Caribbean coasts where diatom assemblages and trajectories of environmental stressors may be comparable.

Study Area

A total of 38 sites were selected in Florida Bay and the adjacent coastal wetlands of South Florida, USA (Fig. 1), to encompass the gradients of salinity, nutrient availability, and habitat structure characterizing this region. Because rainfall at this subtropical latitude is highly seasonal and regulates solute concentrations in the estuaries (Boyer et al. 1999), we sampled during the “wet season” (September–October 2006) when freshwater flow is greatest and again in the following “dry season” (March–April 2007). The study area included freshwater, brackish, and marine areas.

Freshwater sites were located in the upper part of Taylor Slough (sites 34–38; Fig. 1), one of the largest sources of freshwater for Everglades National Park (ENP) and northeastern Florida Bay (McIvor et al. 1994). These sites were characterized by <0.5 salinity in both seasons (Appendix).

Sites adjacent to Florida Bay in the lower part of Taylor Slough (sites 29–33; Fig. 1) and the southwestern part of the Everglades containing lakes and small embayments (sites 22–28; Fig. 1) were located in a mangrove-dominated ecosystem that experienced brackish water conditions (salinity between 0.5 and 30) in both seasons (Appendix).

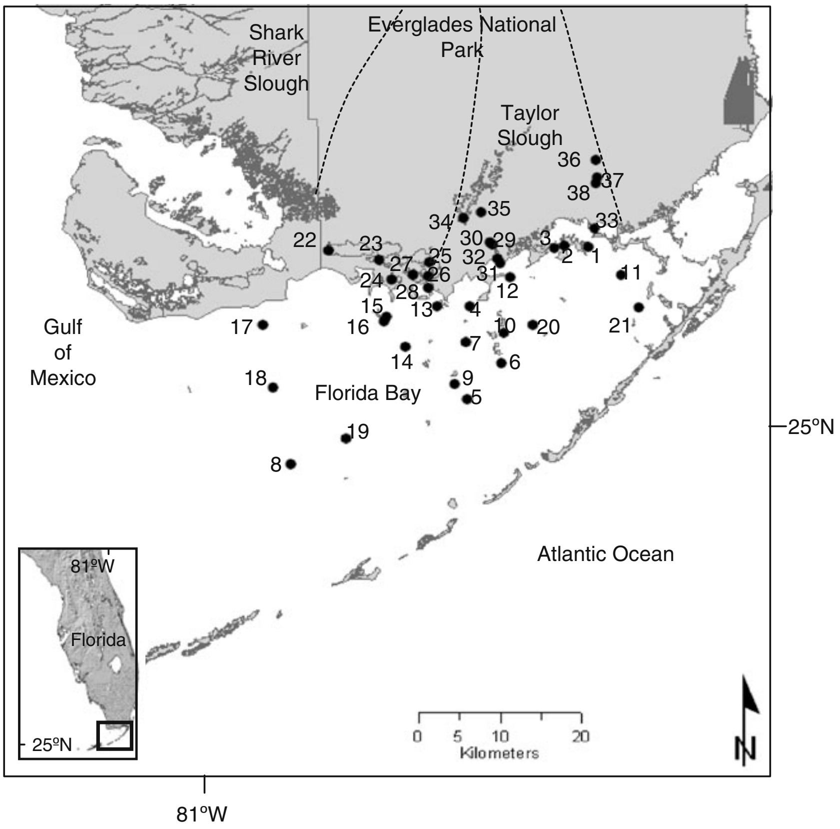

Fig. 1 Map showing location of the sampling sites in Florida Bay and adjacent coastal wetlands, USA. *Gray color* indicates terrestrial areas and the surrounding *white color* indicates marine areas

During wet seasons, water from Taylor River floods the surrounding mangrove areas and delivers large amounts of freshwater into Florida Bay, while during dry seasons high evaporation in the Everglades marshes combined with reduced rainfall result in high salinity (up to 50) throughout this region (McIvor et al. 1994; Davis et al. 2001). The lakes and embayments in southwestern ENP are oriented along freshwater flow paths from the freshwater Everglades to Florida Bay. The bathymetry of this area is shaped by storms, tides, freshwater flow, and sea-level change (Browder and Ogden 1999). In wet seasons, the lakes and coastal embayments become highly stained by humic substances from flooding of the surrounding mangroves, whereas in dry seasons, the water transparency either increases or algal blooms result in yellow coloration of the water (A.W., personal observation).

Marine sites in Florida Bay included nearshore sites in the northern portion of the Bay (sites 1–4 and 12–16; Fig. 1) and offshore sites (sites 5–11, 17–21; Fig. 1). The nearshore locations were characterized by brackish water conditions in the wet season (site 1 also in the dry season) and saline conditions (salinity 30–50) in the dry season, while the offshore sites encountered saline conditions in both seasons (except for sites 10 and 20 that were brackish in the wet season; Appendix). Florida Bay is a shallow estuary (~1-m mean depth) that is divided into a series of small basins separated from each other by carbonate mud banks and small islands (McIvor et al. 1994). There are three major sources of freshwater for the Bay: precipitation; freshwater flow from the mainland through Taylor Slough, the C111 canal, natural creeks, and groundwater; and indirect flow from Shark River Slough (Swart and Price 2002). The eastern portion of the Bay is phosphorus-limited (Boyer et al. 1997) and experiences the greatest annual salinity variations (McIvor et al. 1994). The central Bay has a long history of hypersaline conditions that reach 70 (Finucane and Dragovich 1959) due to a limited freshwater supply and restricted exchange with adjacent waters, high turbidity levels (Burd and Jackson 2002), and an inorganic nitrogen to phosphorus (N/P) ratio close to the Redfield ratio (Brand 2002). The western part of Florida Bay is strongly influenced by tidal exchange of water with the Gulf of Mexico (Burd and Jackson 2002) and has a salinity close to 35 throughout the year and a near-Redfield N/P ratio (Boyer et al. 1997). The southern part is influenced by inflow of water from the Atlantic Ocean and the Gulf Stream and has salinity values between 35 and 40 (Fourqurean et al. 1993).

Most of the sites located in Florida Bay and Taylor Slough are part of the Long-Term Ecological Research and Water Quality Monitoring programs (http://fcelter.fiu.edu/; http://serc.fiu.edu/wqmnetwork/). Additionally, several sites have been selected along coastal and mangrove zones to ensure long gradients of salinity and nutrient concentrations, ranging from freshwater to marine and high- to low-nutrient areas.

Methods

Sample Collection, Preparation, and Laboratory Analysis

In order to determine species habitat affinities, diatoms were collected from three habitat types at each location: surface sediment, plants (epiphyton), and the water column (plankton). Surface sediments were collected using a 3-cm-diameter syringe that was pushed into the sediment to collect the upper approximately 0.5–1-cm layer. Based on ^{210}Pb- and ^{137}Cs-calibrated accumulation rates from nearby sediment cores, 1 cm corresponds to approximately 0.2–8 years of sediment accumulation, depending on the location of the site (Reddy et al. 1993; Craft and Richardson 1998; Holmes et al. 2001). Epiphytes were obtained from at least ten leaves of the dominant submerged aquatic plant species cut at their attachment to the substrate. Plankton were collected by pumping water from a mid-depth in the water column onto a 20-µm mesh. Samples were transported to the laboratory on ice and kept frozen until they could be processed.

In the laboratory, samples were thawed and sediment samples were homogenized with a biohomogenizer to break down large particles. Epiphytes were scraped from the plant leaves using a blade, and plankton that had accumulated on the meshes were removed by spraying with deionized water. A 10-ml volume of slurry obtained from each of the sample types was collected for diatom analysis. Samples were cleaned for diatom analysis using the oxidation method described by Battarbee (1986). Approximately 1 ml of slurry was placed on no. 1 coverslips, air-dried, and then mounted onto glass slides using Naphrax®. At least 500 diatom valves were counted on each slide along random transects. Identification and enumeration of diatoms were made using a Nikon E400 light microscope at ×788 magnification (NA=1.4). The identification of species was based on the local and standard diatom taxonomic literature (e.g., Schmidt 1874–1959; Peragallo and Peragallo 1897–1908; Hustedt 1930; Navarro 1981a, b, 1982a, b, c, d, 1983a, b; Foged 1984; Podzorski 1985; Witkowski et al. 2000; Wachnicka and Gaiser 2007; Hein et al. 2008).

In order to characterize the physicochemical environment, salinity, oxygen, pH, turbidity, and temperature were recorded during each sampling event using a multiparameter sonde YSI 6600 EDS. Water depth was measured using a handheld sonar depth sounder. A portion of the sediment sample collected for diatoms was retained and dried and ground for sediment total phosphorus (STP), sediment total nitrogen (STN), and sediment total carbon (STC) analyses. WTP and STP were analyzed with a UV-2101PC Scanning Spectrophotometer using a dry-ashing, acid hydrolysis technique (Solorzano and Sharp 1980). WTN was measured with an ANTEK 7000 N Nitrogen Analyzer using oxygen as the carrier gas to promote a complete recovery of nitrogen in the water samples (Frankovich and Jones 1998). STN and STC were analyzed in a Perkin Elmer Series II CHNS/O (2400) Analyzer by using high-temperature catalytic combustion (Nelson and Sommers 1996). WTOC was measured with a Shimadzu TOC-5000 following methods described by the US EPA (1983).

Data Analysis

The relative abundance of all species was used for statistical analyses, and the Shannon–Wiener index was used to measure alpha (α) diversity at the sampling sites. In statistical analyses, only taxa occurring in more than 5% of the samples and having a mean relative abundance of over 0.5% were included, since the occurrence of rare species is often due to chance and increases noise in the dataset. The relative abundance was arcsine square-root-transformed to more closely approximate a normal distribution. Environmental data with a skewness of >1 were square-root-transformed and adjusted to standard deviates ("*z*-scored") in order to equalize variable distribution to a common scale (Clarke and Warwick 2001; McCune and Grace 2002).

The similarity in diatom composition among samples was examined using cluster analysis, tested using analysis of community similarity, and visualized in ordination space. Hierarchical clustering was performed using the Sørensen distance measure and flexible beta ($\beta=-0.25$) linage method (McCune and Grace 2002).

The statistical significance of differences in diatom community structure among habitats (plankton, sediments, or epiphytes), seasons (wet, dry), and groups defined by cluster analysis was tested with an analysis of similarities (Clarke and Gorley 2001). Results were reported as the Global R, which is based on the difference of the mean ranks of species by relative abundance within and among groups and increases from 0 to 1 with increasing dissimilarity among samples (Clarke and Warwick 2001).

Nonmetric multidimensional scaling (NMDS) ordination (Kruskal and Wish 1978) was used to illustrate differences in diatom community structure, measured by the Sørensen similarity index (Bray and Curtis 1957) among sample groups (clusters, habitat, and season). Samples were coded by location on joint plots, and "vectors" for each environmental variable were expressed in the plane of multidimensional space representing the direction and strength of the plane of maximum correlation with assemblage similarity.

To determine which individual species contributed most to the separation of the groups defined in the cluster analysis, we used the species contribution to similarity method (SIMPER), which measures the percentage each species contributes to average dissimilarity between two groups (an average of all possible pairs of dissimilarity coefficient taking one sample from each group; Clarke 1993).

Indicator Species Analysis (ISA) was used to identify indicator taxa, which were the most abundant and most frequently occurring taxa at each of the localities and habitats. The indicator value (IV_{kj}), which can vary between 0 and 100 (where 100 represents the best indicator of a particular group and is expressed as a percentage), was calculated by multiplying the value of proportional abundance of each taxon in a designated group relative to the abundance of that taxon in all groups by the proportional frequency of the same taxon in each group (Dufrêne and Legendre 1997; McCune and Grace 2002).

To determine the strength of the environmental relationships indicated by the NMDS ordination, we compared species and environmental similarity matrices using a Mantel test, determined the importance of environmental variables using BIO-ENV, and then employed weighted averaging partial least squares (WA-PLS) regression to build prediction models of the environmental variables of interest in this study.

We first determined the correlation among environmental variables using Spearman rank correlation analysis and the Kruskal–Wallis test. Spatial differences in environmental parameters among major clusters were detected with an analysis of variance followed by a post hoc Tukey test (Quinn and Keough 2002). The Mantel test determined the relationships between diatom assemblages and environmental matrices (McCune and Grace 2002). The BIO-ENV procedure with Spearman correlation (ρ_w) determined which parameters were likely to be important in describing the correlations between these distance matrices (Clarke and Ainsworth 1993; Clarke and Warwick 1994). All of the aforementioned analyses were performed using the software PC-ORD version 5.0 (McCune and Mefford 1999), Primer version 5.2.9, and SPSS version 13.0 (Levesque 2007).

The optima of each species along the gradients of interest (salinity, WTN, WTP, and WTOC) was determined by averaging all values for each variable from the sites where the taxon occurred, weighted by its abundance at each site. The taxon's tolerance along each gradient was then calculated as an abundance-weighted standard deviation of the environmental variable (Birks 1995).

The WA-PLS regression (Ter Braak et al. 1993) with jackknife cross-validation (Dixon 1993) was used to develop statistical prediction models. This method combines the features of weighted averaging (WA) and partial least squares (PLS) and uses the residual correlation structure in the data to improve the fit between the biological data and environmental data in the training set (Birks 1995). The predictive abilities of transfer functions were assessed by examining the relationship between the observed and diatom-inferred values, as well as the observed and jackknife-estimated values of the variables of interest in the training set ($r_{\mathrm{apparent}}{}^2$ and $r^2{}_{\mathrm{jackknife}}$), and evaluation of root mean square error (RMSE) and root mean square error of prediction (RMSEP) from repeated randomization, and maximum and average bias in the models that contained the smallest useful PLS components (Birks et al. 1990). The observed values of the variables were plotted against the residuals in order to look for trends that could explain the bias of the prediction models. We also plotted the residuals between the observed and inferred salinity, WTN, WTP, and WTOC against each of the other measured environmental factors and looked for relationships that could provide any additional information about the bias. We further validated the ability to predict each variable through an independent intraset cross-validation. We used the data from the 37 sites sampled during the dry season to develop transfer functions and tested their precision using the independent, 38-site wet season test set. These analyses were performed using C2 version 1.4.2 software (Juggins 2005).

Results

Distributional Patterns and Diatom Species Composition

A total of 592 diatom species were identified in both sampling seasons from 38 sites in the Everglades wetlands, coastal mangroves, and Florida Bay. Species richness ranged from 4 to 89, and the average α-diversity among sites was generally higher in the dry season. The offshore sites in Florida Bay had more diverse diatom assemblages than the nearshore, mangrove, and freshwater sites (α of 3.9, 3.6, 3.2, and 1.3, respectively), and sediment assemblages were more diverse than planktonic and epiphytic (α of 2.9, 2.5, and 2.3, respectively). Diatom diversity was significantly correlated with salinity and WTOC (Table 1).

After removing rare taxa from the dataset, 215 species remained in the dry season and 177 in the wet season datasets. The most common genera in both seasons were *Mastogloia* Thwaites (43 and 40 taxa in the dry and wet seasons, respectively) and *Amphora* Ehrenberg (32 and 20 taxa in the dry and wet seasons, respectively). A total of 51 and 38 taxa occurred in more than 50% of the dry and wet season samples, respectively. The most frequently occurring taxa in the dry season were *Cocconeis placentula* var. *euglypta* (Ehrenberg) Grunow (91.9%), *Amphora tenerrima*

Table 1 Spearman rank correlation coefficients (quantitative variables) matrix and Kruskal–Wallis values (categorical variables) of the mean values of the environmental variables among seasons and clusters

Variables	WTN (ppm)	WTP (ppm)	WTOC (ppm)	S	Clusters	Seasons
WTN (ppm)	1.00	0.79^{a}	0.54^{a}	0.30	5.13	0.25
WTP (ppm)	0.79^{a}	1.00	0.35^{a}	0.26	8.88^{a}	27.97^{a}
WTOC (ppm)	0.54^{a}	0.35^{a}	1.00	−0.21	6.41	3.13
D (m)	0.46^{a}	0.27	0.15	0.46^{a}	18.05^{a}	1.97
O_2 (mg L^{-1})	−0.05	0.09	0.16	0.18	5.73	2.60
Turb. (NTU)	0.51^{a}	0.48^{a}	0.12	0.38^{a}	17.15^{a}	1.07
S	0.30	0.26	−0.21	1.00	46.73^{a}	13.37^{a}
T (°C)	−0.26	0.06	0.13	−0.15	0.97	52.08^{a}
pH	0.23	0.32^{a}	−0.08	0.68^{a}	25.76^{a}	18.11^{a}
STN (ppm)	−0.20	−0.22	0.15	−0.61^{a}	29.29^{a}	8.22^{a}
STP (ppm)	0.03	0.23	−0.12	0.12	22.45^{a}	2.73
STC (ppm)	−0.40^{a}	−0.39^{a}	0.17	−0.78^{a}	40.32^{a}	3.70
α-Diversity	0.07	−0.01	−0.39^{a}	0.63^{a}	19.31^{a}	6.90^{a}

WTN water total nitrogen, *WTP* water total phosphorus, *WTOC* water total organic carbon, *D* depth, *O_2* oxygen, *Turb.* turbidity, *S* salinity, *T* temperature, *STN* sediment total nitrogen, *STP* sediment total phosphorus, *STC* sediment total carbon

[a] Significant correlations at $\alpha<0.05$

Aleem and Hustedt (86.5%), *Cyclotella choctawhatcheeana* Prasad (86.5%), and *Brachysira aponina* Kützing (86.5%), while in the wet season *B. aponina* (86.8%), *C. placentula* var. *euglypta* (86.8%), *Hyalosynedra laevigata* (Grunow) Williams and Round (81.6%), and *Mastogloia pusilla* (Grunow) Cleve (78.9%) were most frequent.

In both seasons, diatom assemblages from the freshwater Everglades (cluster 1; Fig. 2) and Florida Bay (cluster 3; Fig. 2) were completely different ($R=1$, $p=0.001$), while the mangrove area (cluster 2; Fig. 2) included some taxa typical for both of the regions. Differences between the coastal mangrove area and the freshwater Everglades were larger in the wet season ($R=0.992$, $p=0.001$ vs. $R=0.922$, $p=0.001$ in the dry season), while between the coastal mangrove area and Florida Bay (cluster 3) in the dry season ($R=0.820$, $p=0.001$ vs. $R=0.778$, $p=0.001$ in the wet season; Fig. 2).

In the dry season, Florida Bay assemblages differed significantly among the northern (subcluster 3a), eastern and central (subcluster 3b), and western (subcluster 3c) parts ($R=0.604$, $p=0.001$; Fig. 2a). Additionally, the mangrove communities were considerably different between southern Taylor Slough (subcluster 2a) and the mangrove lakes (subcluster 2b; $R=0.863$, $p=0.01$; Fig. 2a). In the wet season, differences between the communities in the northeastern (subcluster 3a), central and eastern (subcluster 3b), northwestern (subcluster 3c), and western (subcluster 3d) parts of the Bay increased ($R=0.846$, $p=0.001$; Fig. 2b). At the same time, mangrove communities in southern Taylor Slough (subcluster 2a) became slightly more similar to those in the coastal lakes (subcluster 2b; $R=0.817$, $p=0.003$). Compositional differences in the assemblages among the freshwater sites (cluster 1) were statistically significant in neither season ($p>0.05$; Fig. 2a, b).

Differences in communities among the sites for both seasons were captured in two-dimensional NMDS ordinations (Fig. 3a, b). A Mantel test revealed significant relationships between diatom species composition and environmental conditions in the dry and wet seasons ($r=0.72$, $p=0.001$ and $r=0.54$, $p=0.001$, respectively), and the single variable that best grouped the sites in a manner consistent with the diatom assemblage patterns was, in both seasons, salinity ($\rho_w=0.784$ in the dry season and $\rho_w=0.673$ in the wet season) represented by the longest vectors in the NMDS ordinations (Fig. 3a, b). WTN, WTP, and WTOC played smaller roles in influencing diatom communities ($\rho_w=0.142$, $\rho_w=0.128$, and $\rho_w=0.069$ in the dry season, and $\rho_w=0.140$, $\rho_w=0.202$, and $\rho_w=0.092$ in the wet season, respectively).

The average contributions of the diatom taxa to the total average dissimilarities between freshwater Everglades and the adjacent mangrove areas (clusters 1 and 2) were 93.11 and 92.54 out of 100, in the dry and wet seasons, respectively. Much of this difference was controlled by the presence of two species, *Encyonema evergladianum* Krammer and *Mastogloia smithii* Thwaites, which together contributed 15.87% and 17.64% of the differences in the dry and wet seasons, respectively. Additionally, *Fragilaria synegrotesca* Lange-Bertalot and *B. aponina* were also important in the dry season, while *C. choctawhatcheeana*, *Brachysira neoexilis* Lange-Bertalot, and *Nitzschia serpentiraphe* Lange-Bertalot were important in the wet season. The average contributions of the species to the total dissimilarities between the coastal mangrove zone and neighboring Florida Bay (clusters 2 and 3, respectively) were 76.61 in the dry season and 72.22 in the wet season, and the best discriminators between these regions, in order of decreasing importance, were *Cyclotella litoralis* Lange and Syvertsen, *C. placentula* var. *euglypta*, *M. pusilla*, *H. laevigata*, *Tabularia waernii* Snoeijs, and *Navicula pseudocrassirostris* Hustedt (10.55% of cumulative contribution) in the dry season, and *C. choctawhatcheeana*, *H.*

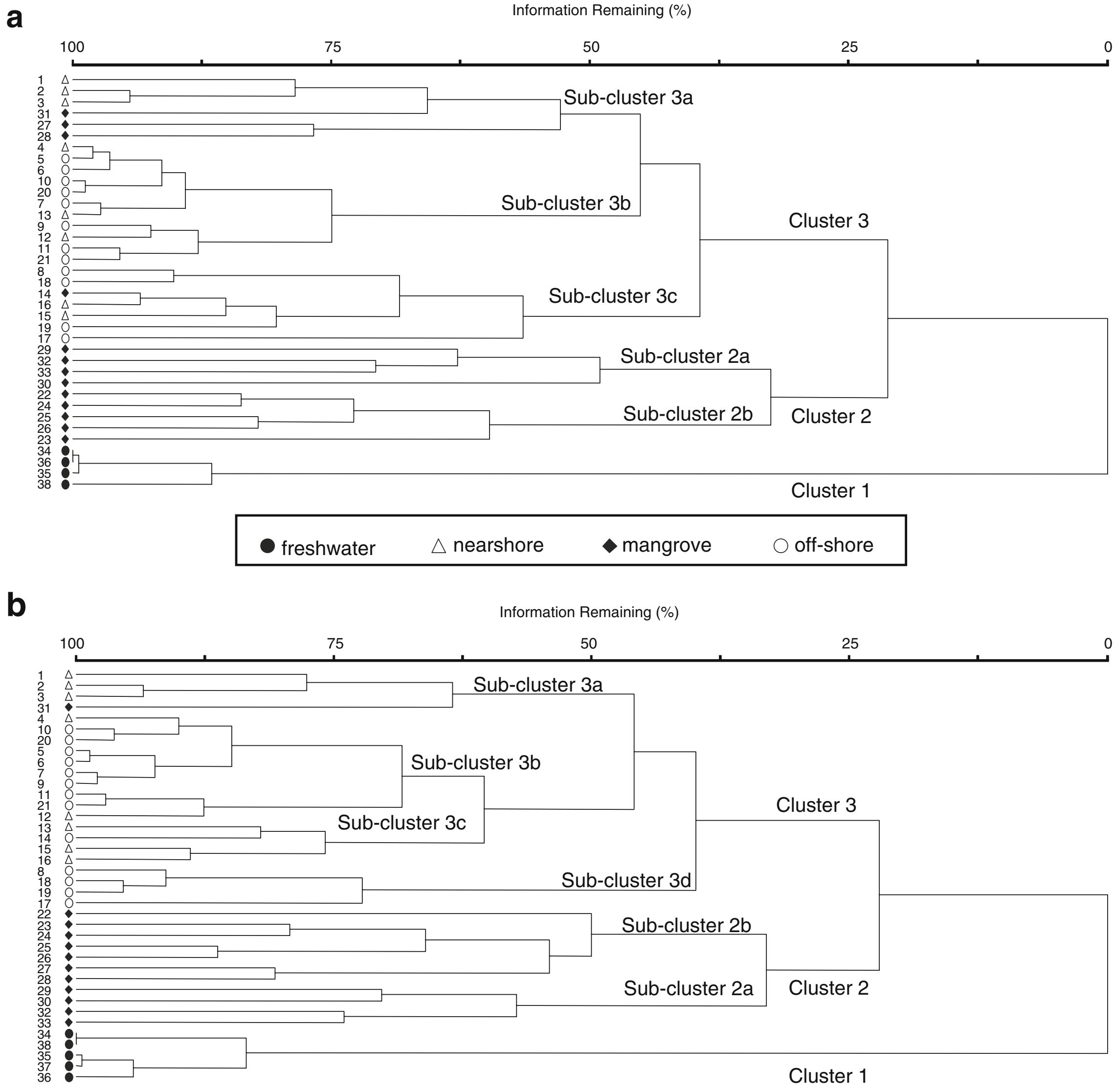

Fig. 2 Sampling locations grouped together by the cluster analysis based on diatom compositional similarity in the dry (**a**) and wet (**b**) seasons

laevigata, *B. aponina*, and *Mastogloia braunii* Grunow (10.89% of cumulative contribution) in the wet season.

Planktonic, epiphytic, and sediment assemblages inhabiting the coastal mangrove area encountered larger mixing in the dry season (R=0.400, p=0.001 vs. R=0.502, p=0.001 in the wet season; Fig. 4a), while Florida Bay assemblages were mixed more in the wet season (R=0.339, p=0.001 vs. R=0.508, p=0.001 in the dry season; Fig. 4b). In the dry season, planktonic assemblages in northeastern and central Florida Bay differed from those in the southeastern and western parts of the Bay (R=0.425, p=0.001), while in the wet season the assemblages were less diverse, and the largest differences were observed between the eastern and western parts of the Bay (R=0.671, p=0.001). Planktonic communities also differed between the western and eastern mangrove lakes in the dry season (R=0.73, p=0.01) and between the southernmost and more inland lakes in the wet season (R=0.939, p=0.001). During the wet season, diatom assemblages from the southernmost sites in Taylor Slough and coastal lagoons in the western portion of ENP became compositionally more similar to assemblages of the nearshore sites in Florida Bay. Differences in sediment assemblages among the northeastern, central and eastern, and western parts of Florida Bay and between southern Taylor Slough and the coastal lakes were more pronounced in the dry season (R=0.864, p=0.001 vs. R=0.793, p=0.001 and R=0.972, p=0.01 vs. R=0.914, p=0.01, in the wet season). Epiphytic assemblages in Florida Bay differed between the eastern and central and western parts of the Bay in the dry season (R=0.602, p=0.001) and among the northern, central and eastern, and western parts of the Bay in the wet season (R=0.59, p=0.001), while in

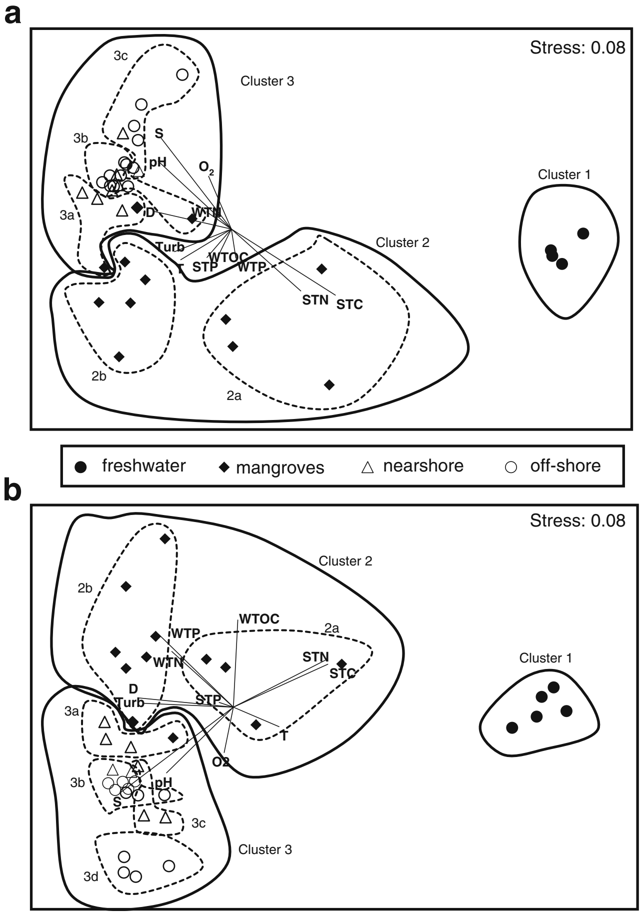

Fig. 3 Nonmetric multidimensional scaling ordination diagram of sites based on Bray–Curtis similarity in diatom composition in the dry (**a**) and wet (**b**) seasons. Sites are coded by sampling locations and surrounded areas represent clusters and subclusters. *Arrows* show the direction and magnitude of correlation of environmental variables with species compositional differences

the coastal mangrove area they were more distinct between southern Taylor Slough and the coastal lakes in the wet season (R=0.9, p=0.001 vs. R=0.778, p=0.001 in the dry season). The epiphytic and sediment assemblages did not differ significantly among the freshwater Everglades sites in either the wet or dry seasons (p>0.05).

The ISA revealed that most of the indicator taxa were associated with Florida Bay sites and were least associated with the mangrove sites (Table 2). Additionally, the highest number of indicators was associated with the plankton habitat (Table 3).

Environmental Conditions

Sites differed spatially and seasonally in salinity, WTN, WTP, and WTOC concentrations (Table 4; Appendix). Differences were significant among clusters (defined earlier based on compositional similarity among sites) for all measured water parameters except for WTN, turbidity, and temperature. Among the environmental variables that were of greatest interest in this study, salinity showed the greatest difference among clusters and was strongly correlated with many other water chemistry variables, clusters, and seasons (Table 1). Significant differences in WTP and WTOC were observed among freshwater Everglades, coastal mangroves, and Florida Bay sites (the mangrove sites had, on average, higher WTP and WTOC levels compared to the freshwater Everglades and offshore sites in Florida Bay, in both seasons), but no differences in WTN were observed among clusters. WTN, WTP, and WTOC were strongly correlated with each other and with several other variables (Table 1). WTP was also significantly correlated with clusters and seasons (Table 1).

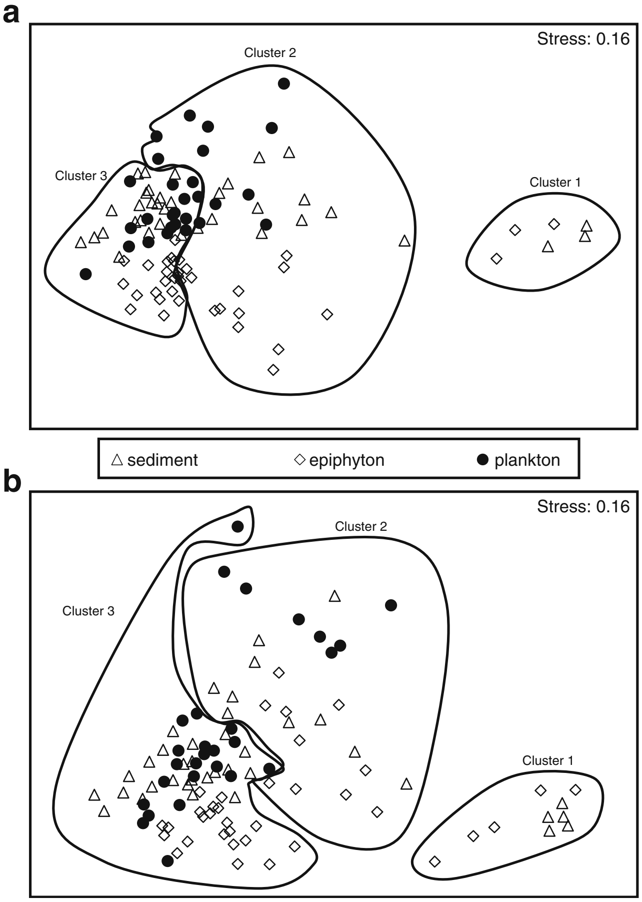

Fig. 4 Nonmetric multidimensional scaling ordination of sites based on Bray–Curtis similarity in diatom composition in the dry (**a**) and wet (**b**) seasons. Sites are coded by habitat type

Environmental Preferences and Transfer Functions

Optima and tolerances for the averaged values of salinity, WTN, WTP, and WTOC were determined for the 215 diatom taxa that occurred in both seasons. From these, only a few had very narrow tolerances around optima for salinity

Table 2 Diatom species identified by indicator species analysis as good indicators of coastal zones (having high observed indicator value (OIV)) distinguished by cluster analysis based on their relative abundance and frequency of occurrence in these clusters

Taxon name	OIV	S opt.	S tol.	WTN (ppm) opt.	WTN (ppm) tol.	WTP (ppm) opt.	WTP (ppm) tol.	WTOC (ppm) opt.	WTOC (ppm) tol.
Freshwater Everglades									
Encyonema evergladianum	97.2	2.6	8.3	0.46	0.25	0.01	0.01	12.2	4.7
Mastogloia smithii	97	2.8	7.6	0.48	0.26	0.01	0.02	11.8	4.9
Brachysira neoexilis	82.6	3.2	6.7	0.45	0.23	0.01	0.01	13.0	4.9
Nitzschia palea var. *debilis*	82	3.2	5.6	0.45	0.19	0.01	0	10.6	2.7
Fragilaria synegrotesca	77.2	5.0	7.3	0.46	0.25	0.01	0.01	11.7	4.1
Nitzschia serpentiraphe	75	1.6	7.7	0.45	0.26	0.01	0	12.3	3.9
Coastal Mangroves									
Navicula pseudocrassirostris	62.9	19.3	7.0	0.94	0.47	0.05	0.05	18.5	10.3
Mastogloia braunii	46.8	18.4	6.9	0.98	0.41	0.05	0.05	19.5	10.5
Achnanthes submarina	44.9	16.7	6.1	0.8	0.44	0.04	0.05	16.3	10.1
Open-bay Florida Bay									
Hyalosynedra laevigata	61.3	31.7	7.6	0.73	0.25	0.02	0.02	11.0	4.6
Rhopalodia pacifica	57.2	32.8	7.1	0.7	0.27	0.02	0.02	10.5	4.9
Grammatophora oceanica	47.3	33.4	6.0	0.68	0.29	0.02	0.02	10.5	5.7
Mastogloia crucicula	45.3	30.4	7.2	0.73	0.26	0.02	0.02	11.0	5.2
Synedra sp. 01	45.2	31.7	6.9	0.76	0.16	0.02	0.01	11.8	2.4
Mastogloia lacrimata	45.1	34.9	3.3	0.71	0.21	0.02	0.01	10.3	3.2
Nearshore Florida Bay									
Mastogloia halophila	52.2	27.4	7.6	0.79	0.3	0.03	0.03	12.4	6.9
Mastogloia cyclops	49.2	30.1	6.5	0.7	0.22	0.02	0.01	10.3	3.8
Cyclotella distinguenda	46.9	27.5	7.3	0.75	0.24	0.02	0.02	11.7	5.2
Climaconeis colemaniae	46.3	28.5	6.0	0.74	0.19	0.02	0.01	10.8	3.6
Brachysira aponina	45.1	25.9	9.7	0.73	0.25	0.02	0.02	11.7	5.0
Mastogloia gibbosa	40.2	27.3	7.9	0.69	0.2	0.02	0.01	9.9	2.5

Taxa optima (Opt.) and tolerances (Tol.) for salinity (S), water total nitrogen (WTN), water total phosphorus (WTP), and water total organic carbon (WTOC) calculated by weighted averaging regression are also provided

(four species could tolerate salinity less than ±2). WA regression showed that species inhabiting all sampling locations could tolerate wider changes in salinity, but only taxa occupying the mangrove ecosystem could tolerate significant changes in nutrient concentrations (Table 2).

The WA-PLS technique revealed that the most parsimonious models for inference of the aforementioned variables would be the two-component models. The relationship between observed and predicted values of salinity, WTN, WTP, and WTOC were very strong (Table 5; Fig. 5a–d). However, the models still to some extent overestimated the values of these variables at the low end of the gradients and slightly underestimated the values at the high end, which was exposed in residual values. Significant correlations were found between residual values for the final salinity, WTN, WTP, and WTOC models and observed values for several other water parameter variables (Table 6).

The intraset cross-validation transfer functions for the 37-site dry season training set and the 38-site wet season test set were based on a similar number of diatom taxa as the combined season dataset (Fig. 6a–d). As a result of significant seasonal differences in salinity, WTN, WTP, and WTOC, training and test sets included different ranges of these variables. Performance statistics of the 37-site, dry season training set transfer functions (salinity, WTN, WTP, and WTOC) were slightly different than for the combined seasons training set transfer functions (Figs. 5a–d and 6a–d). Overall, the models had higher prediction errors, and most of them (except for the salinity model) displayed slightly stronger relationships between observed and predicted values than the models based on combined dry and wet season data (Figs. 5a–d, 6a–d). Additionally, the intraset cross-validation showed that the salinity, WTN, WTP, and WTOC transfer functions based on the 37-site training set provided a good estimation of measured values of these variables in the 38-site test set for the sites where the annual variability of the above-mentioned water quality variables was the lowest (Fig. 6a–d).

Table 3 Diatom taxa identified by indicator species analysis as good indicators of planktonic, epiphytic, and sediment habitats (having high observed indicator value (OIV)) based on their relative abundance and frequency of occurrence in these groups

Taxon Name	% of samples in given group where taxon was present			OIV
	Sediment	Epiphyton	Plankton	
Plankton				
Entomoneis cf. *gigantea*	3	6	61	57.5
Cyclotella choctawhatcheeana	72	61	86	52.1
Amphora cf. *leavis*	14	0	57	50.8
Cyclotella litoralis	64	31	75	49.4
Navicula sp. 05	8	0	54	47.2
Climaconeis colemaniae	36	42	79	46.7
Pleurosigma cf. *salinarum*	17	11	57	43.5
Thalassiophysa hyalina var. *insecta*	3	8	46	41.5
Hyalosynedra laevigata var. *angustata*	11	17	57	41.4
Epiphytes				
Cocconeis placentula	75	89	71	56.8
Brachysira aponina	44	83	71	53.2
Navicula durrenbergiana	11	81	71	51.1
Amphora sp. 05	14	67	29	49.3
Mastogloia pusilla	55	78	54	45.1
Sediment				
Diploneis suborbicularis	58	3	4	53.8
Amphora cymbifera var. *heritierarum*	53	11	7	44.1
Rhopalodia acuminata	58	14	14	42.4
Cyclotella distinguenda	76	31	43	40.4

Discussion

Our study showed that not only can we quantify change in a single environmental variable from diatom communities in Florida Bay, but we can also quantify the impact of multiple environmental factors on the inferences. Diatoms, therefore, have great potential for discerning interacting influences of climate and water delivery change in the South Florida coastal environment. Because of their strong relationships with many important water quality variables, they can be used to assess

Table 4 Average, maximum, and minimum values of water quality variables and sediment nutrient concentrations recorded during the dry and wet seasons sampling events at 38 sampling locations in Florida Bay and adjacent coastal wetlands

Variables	Dry Season			Wet Season		
	Mean	Max	Min	Mean	Max	Min
D (m)	0.7	1.9	0.0	0.9	2.0	0.1
O_2 (mg L^{-1})	7.2	10.4	4.6	6.5	11.7	2.4
Turb. (NTU)	8.9	81.9	0.5	5.4	20.5	0.0
S	28.7	41.4	0.3	18.1	46.6	0.1
T (°C)	24.1	28.3	16.3	29.6	33.1	25.6
pH	8.3	8.9	7.6	7.9	8.5	7.2
WTN (ppm)	0.76	2.49	0.31	0.67	1.23	0.16
WTP (ppm)	0.020	0.139	0.005	0.032	0.112	0.006
WTOC (ppm)	12.2	43.5	5.2	12.2	23.5	2.0
STN (ppm)	7770.3	20400.0	400.0	5142.1	26100.0	600.0
STP (ppm)	371.5	1670.0	23.8	234.6	726.1	49.8
STC (ppm)	142,040.5	271,800.0	87,500.0	163,121.1	397,300.0	108,700.0

WTN water total nitrogen, *WTP* water total phosphorus, *WTOC* water total organic carbon, *D* depth, O_2 oxygen, *Turb*. turbidity, *S* salinity, *T* temperature, *STN* sediment total nitrogen, *STP* sediment total phosphorus, *STC* sediment total carbon

Table 5 Performance statistics for weighted averaging partial least squares (WA-PLS)-based diatom salinity, water total nitrogen (WTN), water total phosphorus (WTP), and water total organic carbon (WTOC) inference models for Florida Bay and adjacent coastal wetlands

Variable	WA-PLS components	$r_{(\text{apparent})}^2$	$r_{(\text{jackknife})}^2$	RMSE	RMSEP	% change	p values
Salinity	2	0.97	0.95	0.30	0.39	35.60	0.001
WTN (ppm)	2	0.75	0.46	0.09	0.13	22.56	0.019
WTP (ppm)	2	0.75	0.49	0.03	0.04	22.83	0.009
WTOC (ppm)	2	0.79	0.57	0.36	0.51	20.04	0.006

The percent change values represent percent reduction in root mean square error of prediction (RMSEP) between components 1 and 2, and p values obtained from t test indicate the statistical significance of these differences. The results are based on square-root-transformed water quality data

the current state of Florida Bay and adjacent environments and to determine the impact that anthropogenic and climate stressors have on those ecosystems. Additionally, diatoms can be used in paleoenvironmental studies in this region to identify reference salinity and water quality conditions within Florida Bay and the adjacent coastal wetlands. Assessment of these benchmark values, which is imperative to the Everglades and Florida Bay restoration, is impossible with data that come from current monitoring because of the extent to which environmental conditions have been changed by the twentieth century water management practices in this region (Sklar et al. 2005).

Our study showed that a high degree of spatial variability in water chemistry controlled, to a large extent, the distribution and composition of diatom assemblages in Florida Bay and the adjacent coastal wetlands. The most influential variable was salinity, commonly recognized by many as an important factor controlling the distribution of microorganisms in estuarine environments (Snoeijs 1994; Underwood et al. 1998; Weckström and Juggins 2005; Frankovich et al. 2006). Additionally, nutrient availability, which has been found to structure algal communities (including diatoms) in this region (Armitage et al. 2006; Frankovich et al. 2009), played an important role in structuring species composition, especially in the coastal mangrove zone. The assemblages at P-limited sites in eastern and central Florida Bay were dominated by *Amphicocconeis disculoides* (Hustedt) De Stefano and Marino, *B. aponina*, *H. laevigata*, and *Nitzschia*

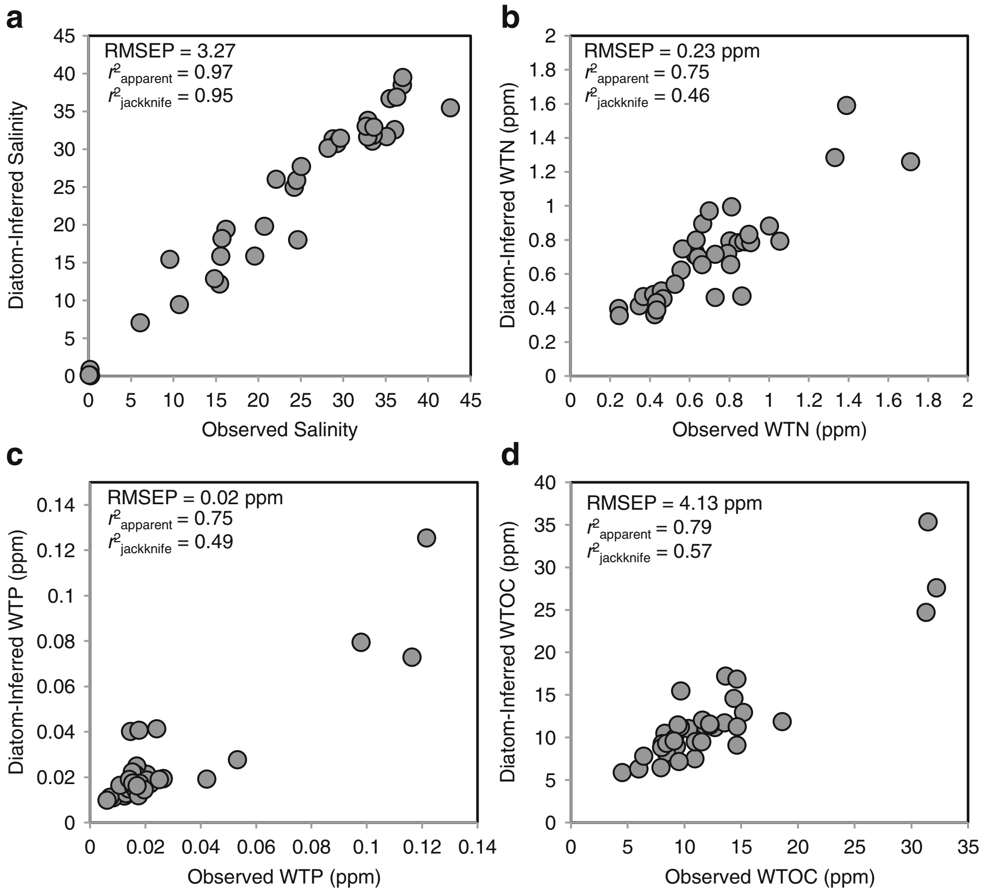

Fig. 5 Plots of observed vs. predicted salinity (**a**), WTN (ppm) (**b**), WTP (ppm) (**c**), and WTOC (ppm) (**d**) using weighted averaging partial least squares regression with jackknife cross-validation on the combined wet and dry season dataset

Table 6 Pearson correlation coefficients for correlations between residual values of salinity (S), water total nitrogen (WTN), water total phosphorus (WTP), and water total organic carbon (WTOC) derived for the final transfer function models and mean annual values of other measured chemical and physical water variables

Residuals	Salinity	WTN (ppm)	WTP (ppm)	WTOC (ppm)
WTN (ppm)	−0.37[a]	−0.49[a]	−0.58[a]	−0.08
WTP ppm	−0.34[a]	−0.27	−0.58[a]	−0.13
WTOC (ppm)	−0.39[a]	−0.17	−0.41[a]	−0.40[a]
D (m)	0.10	0.13	0.10	0.32[a]
O_2 (mg l^{-1})	0.14	0.21	0.06	−0.09
Turb. (NTU)	−0.38[a]	−0.33[a]	−0.31	0.02
Salinity	−0.20	−0.19	−0.22	0.23
T (°C)	0.12	0.23	0.09	−0.22
pH	0.10	0.05	−0.05	0.20
STN (ppm)	−0.14	−0.06	0.12	−0.09
STP (ppm)	−0.10	0.08	0.00	0.22
STC (ppm)	0.01	0.11	0.17	−0.34[a]

D depth, O_2 oxygen, *Turb.* turbidity, *T* temperature, *STN* sediment total nitrogen, *STP* sediment total phosphorus, *STC* sediment total carbon

[a] Significant correlation at $\alpha<0.05$

liebetruthii Rabenhorst, also characterized by Frankovich et al. (2006) as taxa often associated with seagrass-vegetated sites in the Bay. The mangrove ecotone is a transitional zone between Florida Bay and the freshwater Everglades marshes that acts as a buffer zone to intercept marine (e.g., *Cyclotella distinguenda* Hustedt, *M. pusilla*, *C. choctawhatcheeana*, *C. litoralis*), brackish (e.g., *Tryblionella granulata* (Grunow) Mann, *M. braunii*, *N. pseudocrassirostris*), and freshwater taxa (e.g., *M. smithii*, *E. evergladianum*, *F. synegrotesca*). Turbid and nutrient-rich coastal lakes in this zone contained assemblages dominated by small planktonic *Cyclotella* species (e.g., *C. choctawhatcheeana*, *Cyclotella meneghiniana* Kützing, *Cyclotella atomus* Hustedt), which have also been reported by Cooper (1995), Andrén et al. (2000), and Weckström and Juggins (2005) in highly disturbed, nutrient-rich waters of Chesapeake Bay and the Baltic Sea. Additionally, these lakes contained taxa that were seldom or never found at any other sampling locations (e.g., *Gyrosigma* sp. 04, *Navicula* sp. 01, *Pravifusus hyalinus* Witkowski). This is possibly a consequence of the relative geographic isolation of this region, also suggested by Davis and Williams (1950), who studied the plankton distribution in this area. The shallow freshwater sites in northern Taylor Slough had assemblages dominated by *E. evergladianum* and *M. smithii*—species often associated with unenriched periphyton mats in short-hydroperiod marshes throughout the freshwater Everglades (Gaiser et al. 2006; Gottlieb et al. 2006).

Seasonal disparities in water quality conditions were clearly responsible for intersite and intrasite compositional differences, which were more pronounced in the dry season. In the wet season, when freshwater flow from mainland and precipitation increased, resulting in comparable water quality conditions, and mixing of assemblages among different habitats increased (especially at shallow sites in Florida Bay), compositional differences among the studied regions (especially between nearshore Florida Bay and the neighboring coastal mangroves) and habitats decreased. In the coastal mangroves, *C. litoralis*, *Thalassiosira* sp. 01, and *M. pusilla* were the most abundant species in the dry season, while in the wet season they were replaced by *C. choctawhatcheeana*, *N. pseudocrassirostris*, and *C. atomus*. In Florida Bay, *C. placentula* var. *euglypta*, *H. laevigata*, *B. aponina*, and *C. litoralis* were the most abundant species in the dry season, but in the wet season *C. placentula* var. *euglypta* and *B. aponina* increased in abundance even more and were joined by *C. choctawhatcheeana* and *C. distinguenda* that are typically recorded in the coastal mangroves.

Improved quantification of the autecology of South Florida estuarine and coastal diatoms will enhance interpretation of current and past environments in South Florida and the adjacent Caribbean region. The distinct community structure along the environmental gradients covered by this study has great potential for use in detecting eutrophication in nearshore Florida Bay zones and salinization of the South Florida coastal wetlands. Both of these scenarios are rather inevitable in this region, where future increase of freshwater delivery, which is part of the Everglades restoration project, will most likely transport more nutrients to the coastal wetlands and adjacent estuaries (Rudnick et al. 2005) and where continuous sea-level rise and water management practices are already implicated in increased rates of saltwater encroachment and intrusion into low-lying areas of South Florida (Wanless et al. 1994; Gaiser et al. 2006). Appearance of taxa that flourish in high-nutrient environments, in nutrient-starved aquatic systems such as eastern Florida Bay, can serve as an early warning sign of declining water quality. Similarly, the increased abundance of brackish and marine taxa in freshwater wetlands of the Everglades can help to assess the progress and extent of saltwater encroachment.

The relationship of species richness and diversity to salinity is expected, given the inherent differences in diversity between marine and freshwater diatom floras

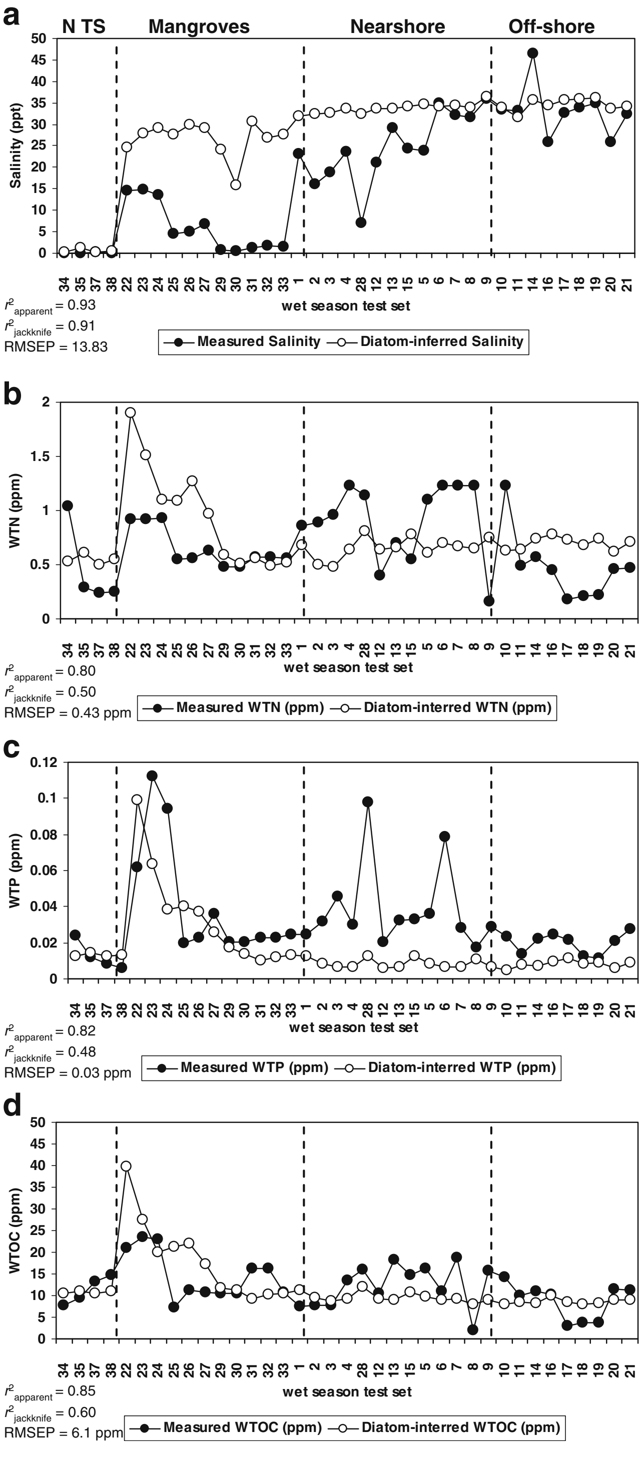

Fig. 6 Diatom-based weighted averaging partial least squares predictions of salinity (**a**), WTN (**b**), WTP (**c**), and WTOC (**d**) based on the 37-site dry season training set for 38-site wet season test set compared to the measured values of these variables. *NTS* northern Taylor Slough

(Round et al. 1990). Additionally, severe and unpredictable physical conditions such as desiccation most likely further reduce the species pool in short-hydroperiod Everglades marshes. Desiccation was blamed by McIntire and Overton (1971) for low diatom diversity in Yaquina Estuary, Oregon (USA). This relationship provides an additional proxy for interpreting salinity changes due to sea-level rise and encroachment in coastal regions. Furthermore, light limitation by suspended organic material in the water column is most likely a reason for low diversity at many sites in the mangrove zone and nearshore Florida Bay sites, as shown by a negative correlation between diversity and WTOC. The presence of numerous microhabitats and the influx of nutrient-rich waters from the Gulf of Mexico are most likely responsible for highly diverse diatom assemblages in Florida Bay, so the positive correlation of diversity with salinity is interpreted as an increase in marine influence. Moderate nutrient enrichment was shown to be an important factor in diversity increases in the Gulf of Finland (Weckström and Juggins 2005) and other marine ecosystems around the world (Irigoien et al. 2004). A higher species diversity in sediment assemblages compared to epiphytic assemblages, also reported by Montgomery (1978) who discovered that the ecologic diversity of diatoms in coral sand habitats of Florida Bay was higher than in *Thalassia testudinum* habitats, is probably due to the fact that the sediment assemblages include many taxa that originated in other habitats. Diversity in planktonic samples is likely overestimated in our study due to the dynamic nature of Florida Bay that often results in resuspension of benthic forms into the water column and creation of pseudoplankton.

The dynamic hydrology of South Florida can also be blamed for a relatively small number of indicator taxa identified by ISA for different habitats and locations. Diatom assemblages are easily transported by flow from the freshwater region of the Everglades towards the mangroves and with currents and tides between the nearshore regions of Florida Bay and the mangroves. Sherrod (1999) reported that offshore taxa are often redeposited in the marshes during high tides, and De Jonge (1985) found that loosely attached diatoms living on mudflats and in channels may be scoured off the substratum by tidal currents and transported into adjacent environments. Additionally, vertical mixing of sediments, especially in the shallow-water central and northern parts of Florida Bay (Prager and Halley 1999), also contributes to the small number of indicator species identified for assemblages occupying sediment, plants, and water column, but mostly for the first two habitats. For example, many taxa that were found in the water column and were identified by ISA as good indicators of planktonic communities (e.g., *Amphora* cf. *laevis* Gregory, *Navicula* sp. 05, *Climaconeis colemaniae* Prasad, and *H. laevigata*) are tychoplanktonic (i.e., they are pseudoplankton). This assumption is based on the original description of the habitats in which they were found, which was usually sediment or epiphyton (Prasad et al. 2000; Reid and Williams 2002). Consequently, it is difficult to separate true epiphytic, planktonic, and sediment-occupying forms or to determine if taxa were transported from the nearshore or mangrove areas. These results imply that more research is needed to determine true diatom habitat affinity in order to use this information in future reconstructions of vegetation abundance changes and algal blooms in Florida Bay.

The salinity optima and tolerances of diatoms living in different locations along this gradient differ (from 0.1 to 3 at the Florida Bay sites to up to 10 at the mangrove sites) from the values reported earlier by Frankovich et al. (2006), Gaiser et al. (2005), and Huvane (2002) from a more limited number of sites in Florida Bay and the adjacent coastal wetlands. The WTP optima and tolerances for species indicative of Florida Bay are very close to those reported by Frankovich et al. (2006). The differences are most likely due to the fact that we investigated a greater number of sites along broader salinity and nutrient gradients during the two sampling events, and therefore we provided a more comprehensive interpretation of taxon preferences. Our discovery of wider tolerances for salinity and nutrients for taxa living in northern Taylor Slough, coastal mangroves, and nearshore zone is similar to that reported by Admiraal (1984) for most of the epipelic diatoms in Ems-Dollard Estuary in the Netherlands and Tibby et al. (2007) for diatoms in coastal wetlands in southeast Australia. Both authors reported that the extreme variability in conditions at these locations selects for taxa with broad tolerances.

The prediction models obtained from the WA-PLS regression are strong, but some of them (e.g., WTN model) slightly overestimate values at the low end and underestimate values at the high end of the represented gradients. This condition is most likely due to the “edge effect” (truncation at the gradient edges) and inverse deshrinking (inverse linear regression) that are known to introduce such a bias between measured and inferred values (Birks 1998). The inference model for salinity allows this variable to be predicted from diatom assemblages with a very small prediction error (smaller than 14% of the average salinity recorded at the sampling sites in both seasons). The prediction errors were almost twice as large for WTN and WTOC and four times as large for WTP. The predictive power of our salinity and water quality models is similar to those reported in earlier investigations in South Florida and other regions of the world (for salinity, r_{apparent}^2=0.97 vs. r^2=0.91 in Fritz et al. 1991; r^2=0.91 in Gaiser et al. 2005; for WTN, r_{apparent}^2= 0.75 vs. r^2=0.84 in Clarke et al. 2003 and r^2=0.73 in Weckström et al. 2004; for WTP r_{apparent}^2=0.75 vs. r^2=0.68 in Ramstack et al. 2003 and r^2=0.57 in Weckström et al. 2004; for WTOC r_{apparent}^2=0.79 vs. r^2=0.94 in Rosen et al. 2000). The differences in model strengths may be due to the gradient length studied, the number of samples collected to develop the transfer functions, the methods used to analyze the data, and how diatoms perceive and react to changing environments. The errors in estimations in our prediction models are most likely due to the species’ responses to gradients in other measured water quality variables. For example, errors in estimating salinity may be in part caused by variation in nutrient levels (WTN, WTP) and degree of light limitation (correlation with WTOC and turbidity) across the salinity gradient, causing different responses of diatoms to this driving variable. WTN estimation error may result from variation in turbidity, WTP estimation error from variation in WTN and WTOC, and WTOC error from changes of depth and STC. These results agree with earlier findings that highlighted the influences of salinity, nutrient, and light limitation on diatoms (Frankovich et al. 2006; Jurado et al. 2007).

The question of whether only one season of measured water quality and diatom data can be used in the development of such transfer functions was addressed by the intraset cross-validation procedure. This procedure showed that the salinity, WTN, WTP, and WTOC transfer functions based on the 37-site dry season training set estimated (with some discrepancies) the measured values of these variables obtained during our sampling event in an independent 38-site wet season test set. Due to the high intra-annual variability of these variables in the nearshore and mangrove areas, a perfect relationship between diatoms and salinity and nutrient levels can most likely never be obtained in these areas if only one season of measured data is included in predictions (the predictive powers for sites with highly variable hydrology will be low). However, if more frequent sampling cannot be done, the diatom models should be used with prior knowledge of the natural conditions present at the study sites during the year. The predictions based on one-season sampling would be accurate for the freshwater Everglades and offshore Florida Bay locations, where seasonal variations in salinity do not exist or are small.

In general, our models provide a very powerful and reliable tool for quantitative salinity predictions, and even though WTN, WTP, and WTOC are highly correlated with each other, either one of these models (depending on the need) can be used in estimations of the past water quality at locations with less variable water parameter conditions in Florida Bay. As in the above-mentioned cases, the diatom-based quantitative predictions were strong and provide a tool for interpreting change in Florida Bay that can be used with other nonquantitative ecological models available in this area to detect the source and identity of ecosystem stressors. Additionally, because diatom communities in South Florida and the Caribbean significantly overlap (Navarro 1981a, b, 1982a, b, c, d, 1983a, b; Foged 1984; Wachnicka and Gaiser 2007; Hein et al. 2008) because of the subcosmopolitan nature of many diatom taxa (Kelly et al. 1998; Taylor et al. 2007), transfer functions developed in this study should perform well along other coasts of South Florida and the Caribbean. The performance of these transfer functions could be further enhanced by adding information about ecological preferences for new taxa and the unique conditions conferred by the karstic, carbonate-rich environment recorded in those regions, which may experience future of changes similar to those that have influenced South Florida.

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Conflict of Interest I do not have any financial relationship with the organization that sponsored the research. I have a full control of all primary data and I agree to allow the journal to review the data if requested.

Appendix

Table 7 Water quality data and sediment nutrient concentrations recorded at 38 sampling locations during the dry and wet season sampling events

Sampling sites	D (m)	O_2 (mgl^{-1})	Turb. (NTU)	S	T (°C)	pH	WTN (ppm)	WTP (ppm)	WTOC (ppm)	STN (ppm)	STP (ppm)	STC (ppm)
Dry season												
1	0.55	6.96	4.1	25.4	24.8	8.4	0.40	0.011	9.06	1,600	64.9	117,200
2	0.5	6.9	4.2	32.8	26.6	8.4	0.36	0.009	8.77	900	1230.2	116,100
3	0.65	7.78	4.1	31.3	26.4	8.5	0.32	0.007	8.40	1,000	50.3	115,900
4	0.57	6.47	6.7	34.8	22.1	8.3	0.46	0.005	11.79	9,200	446.4	87,500
5	0.5	7.44	8.9	37.2	23.9	8.4	0.54	0.007	7.22	4,600	198.1	97,100
6	0.67	7.34	43.5	33.7	24.3	8.3	0.88	0.006	9.84	7,000	258.8	104,900
7	1.71	6.38	4.0	35.1	23.4	8.4	0.52	0.007	8.22	3,400	97.0	120,500
8	0.55	8.41	1.7	37.9	24.2	8.7	0.33	0.008	7.10	3,600	302.7	117,800
9	0.45	7.95	81.9	36.9	24.2	8.4	0.59	0.005	7.57	1,800	97.8	122,900
10	1.76	6.76	15.3	33.8	23.8	8.3	0.50	0.005	9.29	1,900	107.4	113,600
11	1.35	6.69	2.4	33.9	24.2	8.4	0.62	0.008	6.79	17,900	1286.6	135,000
12	1.24	7.36	5.0	35.3	22.9	8.3	0.73	0.008	8.79	3,200	152.9	105,100
13	1.25	7.47	1.6	36.7	26.8	8.5	1.10	0.008	12.14	8,000	317.7	94,400
14	1.8	7	2.2	38.6	25.1	8.7	1.01	0.009	13.43	3,200	102.5	125,000
15	0.7	8.96	4.5	41.4	27.0	8.9	1.06	0.017	14.60	3,600	231.9	119,200
16	0.32	8.01	7.2	39.6	28.3	8.7	1.01	0.011	14.21	7,000	493.6	109,000
17	0.75	8.92	14.4	38.2	22.9	8.3	0.69	0.011	8.94	400	258.8	105,200
18	1.3	6.55	0.5	40.1	24.1	8.8	1.25	0.022	12.24	6,800	456.1	109,100
19	0.23	8.4	1.8	37.6	25.0	8.6	0.83	0.028	9.15	5,500	419.3	128,300
20	1.9	6.21	4.5	33.5	25.0	8.2	0.80	0.010	7.34	6,400	275.0	107,400
21	0.52	4.6	5.7	34.9	23.1	8.4	0.85	0.007	6.82	13,500	475.4	108,300
22	1.12	7.38	11.8	16.6	22.7	8.5	1.74	0.134	43.45	6,200	426.4	129,500
23	0.75	5.73	19.5	24.4	23.6	8.2	1.86	0.131	39.37	19,500	1670.0	184,200
24	0.55	8.05	27.3	35.6	23.8	8.3	2.49	0.139	39.68	11,300	443.1	151,500
25	1.32	7.75	1.2	14.7	24.8	8.4	0.78	0.009	12.09	8,100	180.9	246,800
26	1.15	7.75	2.2	27.3	26.0	8.4	0.84	0.013	15.94	10,200	341.5	189,200
27	1.05	10.43	1.0	34.5	27.9	8.5	0.99	0.012	18.53	9,300	266.0	154,800
28	0.75	6.58	0.7	37.2	27.1	8.3	0.86	0.009	12.84	11,500	755.9	105,800
29	0	5.5	2.8	20.8	24.5	7.7	0.36	0.013	7.92	14,400	107.4	136,200

Table 7 (continued)

Sampling sites	D (m)	O_2 (mgl^{-1})	Turb. (NTU)	*S*	*T* (°C)	pH	WTN (ppm)	WTP (ppm)	WTOC (ppm)	STN (ppm)	STP (ppm)	STC (ppm)
30	0.13	6.36	1.8	11.7	24.8	7.7	0.37	0.008	8.66	20,400	440.7	271,800
31	0	6.37	5.7	30.2	25.0	7.9	0.34	0.005	5.80	4,900	467.1	157,300
32	0.42	6.03	3.3	29.2	25.9	7.9	0.36	0.010	6.91	7,400	248.3	156,100
33	0.39	6.35	20.5	28.2	25.8	8.0	0.31	0.006	5.23	11,200	806.6	123,800
34	0.23	5.92	1.6	0.3	16.4	7.6	0.68	0.011	10.88	14,200	145.6	259,200
35	0.11	6.41	2.1	0.3	16.3	7.6	0.49	0.005	7.28	10,000	34.5	223,400
36	0.12	7.73	0.9	0.3	18.7	7.7	0.39	0.005	8.08	10,300	66.1	206,900
38	0.14	10.2	1.8	0.3	21.2	8.0	0.50	0.006	8.72	8,100	23.8	199,500
Wet season												
1	0.8	9.51	5.6	23.0	30.1	8.3	0.86	0.024	7.50	2,000	107.9	121,700
2	0.6	7.05	8.8	16.2	29.7	8.2	0.89	0.032	7.70	800	66.6	122,100
3	0.6	6.95	19.0	18.8	30.3	8.1	0.96	0.046	7.69	1,200	71.4	122,000
4	0.8	7.1	20.5	23.7	28.5	8.3	1.23	0.030	13.57	1,300	77.5	122,800
5	0.4	6.2	18.0	34.9	27.8	8.2	1.23	0.036	16.36	1,900	91.6	127,700
6	0.8	6.8	4.4	32.3	27.9	8.0	1.23	0.079	10.89	1,400	76.3	118,500
7	0.4	6.35	5.1	31.7	28.8	8.0	1.23	0.028	18.86	2,000	158.8	124,900
8	0.63	9.44	1.6	36.0	30.3	8.4	0.16	0.017	1.96	3,300	352.2	126,700
9	0.3	5.51	11.0	33.3	28.0	7.8	1.23	0.029	15.63	1,000	79.0	122,700
10	2	6.29	7.5	23.8	27.5	8.0	1.10	0.023	14.30	1,100	60.6	118,200
11	1.6	4.93	8.7	33.1	27.5	8.0	0.49	0.014	10.07	2,600	153.5	128,500
12	0.6	6	5.5	21.0	29.2	8.1	0.40	0.021	10.47	600	65.5	123,400
13	1.1	9.81	7.1	29.0	31.5	7.9	0.70	0.033	18.28	2,800	149.3	129,900
14	1.8	8.54	3.8	46.6	29.6	8.3	0.57	0.022	11.08	3,700	203.4	127,200
15	0.9	6.16	10.0	24.4	32.5	8.4	0.55	0.033	14.73	4,200	474.4	121,600
16	0.45	9.15	8.2	25.8	30.9	8.5	0.45	0.024	10.24	3,200	245.8	118,000
17	0.75	5.02	0.8	32.8	28.6	8.0	0.18	0.022	3.02	700	305.5	108,700
18	1.55	6.08	0.0	33.9	29.6	8.3	0.21	0.013	3.64	3,900	396.9	130,000
19	1.45	9.93	0.3	35.0	30.7	8.3	0.22	0.011	3.68	2,700	518.9	127,700
20	2	6.47	5.6	25.9	27.6	8.1	0.46	0.021	11.51	1,200	52.8	118,500
21	0.95	8.06	5.5	32.3	30.0	8.1	0.47	0.028	11.37	4,200	334.8	132,500
22	1.6	6.92	8.0	14.6	27.9	8.3	0.92	0.062	20.96	3,500	166.8	128,300
23	1.25	2.41	8.3	14.7	25.6	7.4	0.92	0.112	23.55	6,300	425.7	145,700
24	0.95	6.6	10.3	13.7	29.5	7.6	0.93	0.094	22.91	1,700	153.1	122,500
25	1.6	7.82	0.2	4.5	29.9	8.1	0.55	0.020	7.28	2,800	157.0	126,400
26	1.4	11.7	0.5	5.1	29.9	8.3	0.56	0.023	11.33	4,800	275.4	132,000
27	1.2	5.3	1.4	6.9	30.1	7.5	0.63	0.036	10.74	1,700	143.4	118,900
28	0.85	4.93	3.2	7.0	31.7	7.4	1.14	0.098	15.90	2,400	164.4	123,700
29	0.35	2.95	1.3	0.6	30.0	7.2	0.48	0.020	10.39	20,200	726.1	397,300
30	0.37	2.98	0.5	0.5	30.3	7.3	0.48	0.020	10.39	26,100	696.1	335,100
31	1.3	2.89	1.2	1.3	29.7	7.3	0.57	0.023	16.13	6,200	417.8	207,400
32	0.52	2.37	0.2	1.7	30.2	7.2	0.57	0.023	16.13	17,500	462.2	394,100
33	0.65	5.13	11.0	1.5	31.1	7.9	0.56	0.024	10.78	10,800	600.7	238,800
34	0.49	4.02	0.0	0.1	28.9	7.2	1.04	0.024	7.72	14,400	165.4	259,900
35	0.55	4.82	0.1	0.1	29.2	7.5	0.29	0.012	9.56	10,500	87.4	235,200
36	0.21	7.64	0.1	0.1	31.4	7.8	0.25	0.006	14.63	7,900	64.2	230,500
37	0.14	9.14	0.5	0.3	29.4	7.6	0.35	0.013	18.62	6,600	117.6	205,100
38	0.25	9.14	0.0	0.2	33.1	7.9	0.24	0.009	13.13	6,200	49.8	204,400

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