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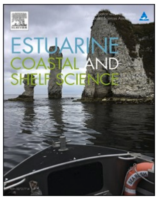

Long-term patterns and trends in water column biogeochemistry in a changing environment

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ABSTRACT

Water column nutrient concentrations and autotrophy in oligotrophic ecosystems are sensitive to eutrophication and other long-term environmental changes and disturbances. Disturbance can be defined as an event or process that changes the structure and response of an ecosystem to other environmental drivers. The role disturbance plays in regulating ecosystem functions is challenging because the effect of the disturbance can vary in magnitude, duration, and extent spatially and temporally. We measured changes in total nitrogen (TN), dissolved inorganic nutrient (DIN), total phosphorus (TP), soluble reactive phosphorus (SRP), total organic carbon (TOC), and chlorophyll-a (Chl-*a*) concentrations throughout the Everglades, Florida Bay, and the Florida Keys. This region has been subjected to a variety of natural and anthropogenic disturbances including tropical storms, fires, eutrophication, and rapid increases in water levels from sea-level rise and freshwater restoration. We hypothesized that the rate of change in water quality would be greatest in the coastal ecotone where disturbance frequencies and marine P concentrations are highest, and in freshwater marshes closest to hydrologic changes from restoration. We applied trend analyses on multi-decadal data (1996–2019) collected from 461 locations distributed from inland freshwater Everglades (ridge and slough) to outer marine reefs along the Florida Keys, USA. Total Organic Carbon decreased throughout the study area and was the only parameter with a systematic trend throughout the study area. All other parameters had spatially heterogeneous patterns in long-term trends. Results indicate more variability across a large spatial and temporal extent associated with changes in biogeochemical indicators and water quality conditions. Chemical and biological changes in oligotrophic ecosystems are important indicators of environmental change, and our regional ridge-to-reef assessment revealed ecosystem-specific responses to both long-term environmental changes and disturbance legacies.

1. Introduction

Ecological change is a function of press and pulse disturbances that lead to shifts in ecosystem drivers such as nutrients, water or material (Kaushal et al., 2018; Chen et al., 2021). Press disturbances such as sea-level rise and even hydrologic restoration can lead to gradual long-term shifts (Sarker et al., 2020; Gaiser et al., 2020). In contrast, pulse events such as hurricanes, fires, and cold snaps produce dramatic shifts in inland and nearshore water quality that can be sustained for varying periods of time (Davis et al., 2018). These forces interact to create a complex response with a significant degree of spatial heterogeneity in the rates of change of a given ecosystem characteristic (Millette et al., 2019). This spatial heterogeneity can be the result of distance from a disturbance epicenter or extreme events that potentially result in

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changes to physical and biological processes across space and time, and/or changes in biogeochemical cycling (McClain et al., 2003; Kaushal et al., 2018).

Along the aquatic continuum, organic matter (OM) plays a critical role in regulating ecosystem function and productivity at both the local and global scales. Locally, OM is an energy source for heterotrophic organisms, attenuates sunlight, buffers pH, chelated metals, and other functions in the aquatic ecosystem (Vannote et al., 1980; Dittmar and Stubbins, 2014). On the global scale, OM is one of the largest mobile carbon pools. Across all scales, the biogeochemical cycling of OM is intricately associated with nutrient and element cycling, potentially modulating nutrient limitations within given systems. In coastal wetlands, OM sources can vary and decomposition can be relatively rapid (Chen and Jaffé, 2014, 2016; Wagner et al., 2015). Dissolved OC, the backbone of OM undergoes several transformations as it flows from land to ocean (Berggren et al., 2022). The relative concentrations of carbon (C), nitrogen (N) and phosphorus (P) can vary widely across OM sources potentially driving changes in stoichiometric composition within and between ecosystem compartments (Elser et al., 2000; Lenton and Watson, 2000; Frost et al., 2002; Cleveland and Liptzin, 2007).

Coastal waters, where land and sea OM pools mix, are amongst the most productive and biogeochemically active zone of the marine biosphere accounting for greater than a third of the ocean productivity and up to 80% of OM burial (Gattuso et al., 1998). In this zone, OM and nutrients within the OM pool are either from autochthonous sources (i.e., bacteria, plankton, algae, macrophytes, sediment or other biota) or allochthonous (i.e., derived from groundwater discharge, rivers, streams, and overland flow) (Lønborg et al., 2018). Degradation of OM can be a dominant source of total bioavailable N and P (Lønborg et al., 2018); therefore, allochthonous supplementation of nutrients either from eutrophication or disturbances can result in shifts in limiting nutrient concentrations, nutrient stoichiometry, and productivity (Kominoski et al., 2020).

Aquatic systems are often investigated as freshwater, estuarine, or marine ecosystems independently, but the underlying linkages between these ecosystems and the inherent spatial heterogeneity necessitate integrated investigations across freshwater to marine ecosystems. This is especially true for the Everglades (FL, USA), where freshwater mixes with offshore waters along much of the South Florida coastline through the myriad of channels, sloughs, and groundwater discharge points. Evaluating spatio-temporal differences can help to pinpoint the ecological processes and patterns causing changes in freshwater to marine ecosystems that are influenced by multiple, interacting stressors from disturbances to climate change (Paerl, 2009; Wurtsbaugh et al., 2019; Schafer et al., 2020). The objective of this paper was to evaluate biogeochemical signals in multi-decadal datasets of total and dissolved nutrients, chlorophyll-*a* (Chl-*a*), and total organic carbon concentrations across a large spatial scale spanning the freshwater coastal wetland-estuary-marine continuum around South Florida. We hypothesized that the rate of directional change in water quality constituents would be greatest in the coastal ecotone where the long-term presses of sea-level rise, eutrophication, and freshwater restoration interact with episodic exposure to pulses of marine and freshwater will affect nutrient cycling and limitations in this region.

2. Methods

2.1. Study area

This study spans the freshwater Everglades, coastal mangrove fringe, Florida Bay, Southwest Florida Shelf, and the Florida Keys to the Dry Tortugas (Fig. 1). The coastal Everglades is comprised of the largest mangrove forest in the Western Hemisphere, characterized by a complex pattern of mangrove islands with natural braided streams fed by the Everglades marshes. Florida Bay is located south of the freshwater Everglades and is bordered by the Florida Keys to the south and west Florida Shelf to the west. Florida Bay and the coastal waters around south Florida receive freshwater runoff from the upstream Everglades via Lostmans and Shark River Sloughs on the southwest coast and via Taylor Slough and the C-111 Basins to the south (Boyer et al., 1997). The

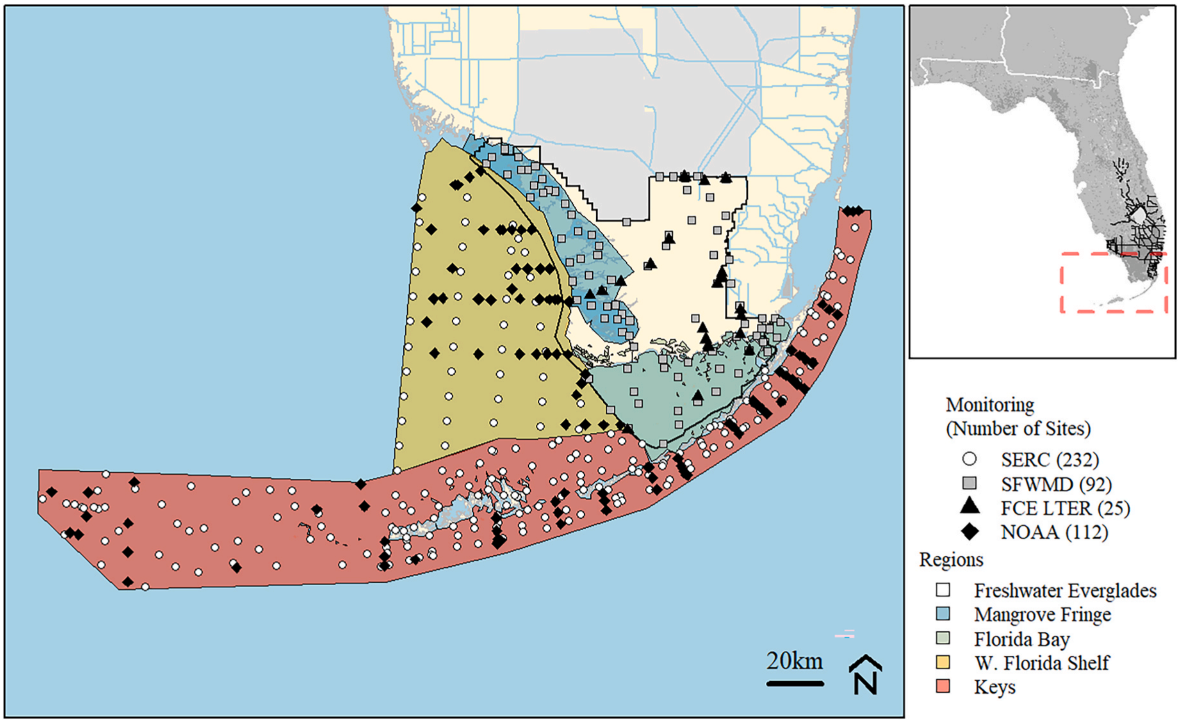

Fig. 1. Southeast Environmental Research Center (SERC), South Florida Water Management District (SFWMD), Florida Coastal Everglades Long Term Ecological Research (FCE LTER), and National Oceanic and Atmospheric Administration (NOAA) long-term monitoring networks across the southern Everglades, Florida Bay, and the Florida Keys.

Florida Keys is a 350 km long archipelago that stretches southwesterly from Miami to the Dry Tortugas. Water from the Gulf of Mexico and Florida Bay passes through the Florida Keys from the north and its southern coastline faces the Florida Straits bounded by the Gulf Stream (Briceño et al., 2013).

2.2. Data sources

Water quality grab sample data were compiled from the Southeast Environmental Research Center of Florida International University (SERC FIU), Florida Coastal Everglades Long-Term Ecological Research program (FCE LTER; Troxler, 2019a; b; Troxler and Childers, 2019; Gaiser and Childers, 2020), South Florida Water Management District (SFWMD) and the South Florida Ecosystem Restoration program at the Atlantic Oceanographic and Meteorological Laboratory of the National Oceanic and Atmospheric Administration (NOAA/AOML) (Julian, 2022). Across these four programs, 461 monitoring locations span the freshwater Everglades, coastal mangrove fringe, Florida Bay, Southwest Florida Shelf, and the Florida Keys National Marine Sanctuary (Fig. 1 and Table S1). Collectively, these independent monitoring programs provide a synoptic evaluation of water quality across the region. Data collected between water year (WY) 1996–2019 (May 1, 1995–April 30, 2019) were selected for this study as it coincided with a stable positive phase of the Atlantic Multidecadal Oscillation (AMO; Fig. S1) and spanned a period of pre-restoration/early restoration activities within the upstream Everglades (Briceño and Boyer, 2010; Millette et al., 2019; Julian et al., 2021). The water quality parameters considered for this study were total phosphorus (TP), soluble-reactive phosphorus (SRP/ortho-phosphate), total nitrogen (TN), dissolved inorganic nitrogen (DIN; calculated as nitrate + nitrite + ammonium), Chl-*a*, and total organic carbon (TOC) (Table S2). Water quality data were screened based on laboratory or field qualifier codes such that any datum associated with a fatal qualifier indicating a potential data quality problem was removed from the analysis. Total and dissolved fractions of nutrients were checked to ensure data integrity so that if the dissolved fraction (i.e., DIN and SRP) were 30% greater than the total fraction (i.e., TN and TP), the sample was excluded from the analysis consistent with Julian et al. (2021). For purposes of data analyses and summary statistics, data reported less than the method detection limit (MDL) was assigned a value of one-half the MDL.

2.3. Data analyses

Similar to Millette et al. (2019), stations were deemed to have sufficient data if they had at least five consecutive WYs of data at any point between WYs 1996; 2019. Daily average concentrations were computed for more than one sample collected in a day. In addition to period of record (POR) screening, within-year screening was also applied, stations with $\geq$ four samples per year and at least one in the wet (May–October) and dry (November–April) seasons were considered for analysis. Annual (WY) geometric mean (AGM) concentrations were computed for each monitoring location for TN, DIN, TP, SRP, TOC, and Chl-*a*. Stoichiometric ratios of TN:TP, TOC:TP and TOC:TN were calculated for individual sample by converting concentrations from mass per volume (mg L^{-1}) to molar concentrations (mM) and AGM were calculated on individual ratios for a given site and year.

Sites were grouped into five broad geographical groups based on Briceño et al. (2013) and are identified as freshwater Everglades National Park (ENP), Coastal Mangrove fringe, Florida Bay, West Florida Shelf, and Florida Keys (Fig. 1). Annual geometric mean concentrations were compared between regions using Dunn's test of multiple comparisons to perform pairwise comparisons of TN, DIN, TP, SRP, and Chl-*a* concentrations between regions (dunn.test R-package; Dinno, 2015). To visualize pairwise comparisons, a custom cldList function was used (see supplemental material; based on the cldList function in the rcompanion R-package; Mangiafico and Mangiafico, 2017). Spatial pattern of directional change, was evaluated using temporal trend analysis on AGM concentration at sites across the study using Kendall's tau correlation analysis and Thiel-Sen slope estimate (zyp R-package; Bronaugh and Werner, 2019). For visualization purposes, Thiel-Sen slope and average AGM concentrations were spatially interpolated using thin-plate spline interpolation (fields R-package; Nychka et al., 2017) and clipped to the study area. Site-specific Kendall trend and Thiel-Sen results are located in Table S3.

To evaluate long-term trends and the effects of salinity on TP and TN, spatiotemporal generalized additive models (GAM; mgcv R-package; Wood, 2017) were fit for annual mean TP and TN, separately. Annualized data (i.e. annual mean) were used in this effort due to the spatial and temporal coverage of the data and computational time needed to fit the models. The models were constructed consistent with Eq (1) for both parameters. Both TP and TN models fit using a Gamma log-linked distribution. Degrees of smoothing (knots = k) were initially used to minimize the generalized cross-validation score, followed by post hoc adjustments of "k" for individual terms using the function "gam.check." The first derivative of the fitted trend was evaluated using finite differences (gratia R-package; Simpson, 2021). Significant changes were identified when the confidence interval of the first derivative for annual mean salinity and WY splines did not include zero, consistent with (Simpson, 2018).

$$E(y) = \alpha + s(salinity) + s(WY) + s(UTMX, UTMY) + ti(UTMX, UTMY, WY) \qquad \text{Equation 1}$$

All statistical operations were performed with R © (Ver 4.1.0, R Foundation for Statistical Computing, Vienna Austria). Unless otherwise stated, all statistical operations were performed using the base R library. The critical level of significance was set at $\alpha = 0.05$.

3. Results

3.1. Regional comparison

There were regional differences for all parameters investigated in this study (Fig. 2). Across regions, TN AGM concentrations were different across all regions ($\chi^2 = 2871$, df = 4, $\rho < 0.01$; Fig. 2) with AGM concentrations ranging from 0.04 to 2.20 mg N L^{-1} (Table 1). Similarly, DIN AGM concentrations varied across all regions ($\chi^2 = 3579$, df = 4, $\rho < 0.01$; Fig. 2) with concentrations ranging from 0.001 to 1.82 mg N L^{-1} (Table 1). Both TN and DIN showed trends of decreasing concentrations as you moved downstream from the freshwater to marine systems (Fig. 2). Total P AGM concentrations were different across regions ($\chi^2 = 2010$, df = 4, $\rho < 0.01$) but similar between ENP and Florida Keys (Fig. 2). Total P had the largest range in AGM concentrations from 1.5 to 48.0 μg P L^{-1} (Fig. 2 and Table 1) and did not show a clear relationship between regions but concentrations were highest among coastal ecosystems (i.e., coastal ecotones, mangrove fringe, West Florida Shelf, and Florida Bay) and lowest within freshwater ENP and offshore in the Florida Keys. Soluble reactive P AGM concentrations were different across all regions ($\chi^2 = 1019$, df = 4, $\rho < 0.01$; Fig. 2 and Table 1) with concentrations ranging from 0.12 to 22.87 μg P L^{-1}. Similar to TP, SRP did not have a clear trend as you moved downstream from freshwater to marine, but instead had peaks in the coastal ecotones; although SRP concentrations in ENP were closer to the coastal values. Chl-*a* AGM concentrations were different across regions ($\chi^2 = 3628$, df = 4, $\rho < 0.01$) with ENP and West Florida Shelf being similar and all other pairwise comparisons having greater differences (Fig. 2 and Table 1). The highest chlorophyll-*a* concentrations were in the coastal Mangrove fringe followed by West Florida Shelf and ENP then Florida Bay, and the lowest Chl-*a* concentrations were in the Florida Keys. Annual geometric mean TOC concentrations were different across regions with concentrations in ENP and mangrove fringe being similar and all other pairwise comparisons being different ($\chi^2 = 2693$, df = 4, $\rho < 0.01$; Fig. 2) with

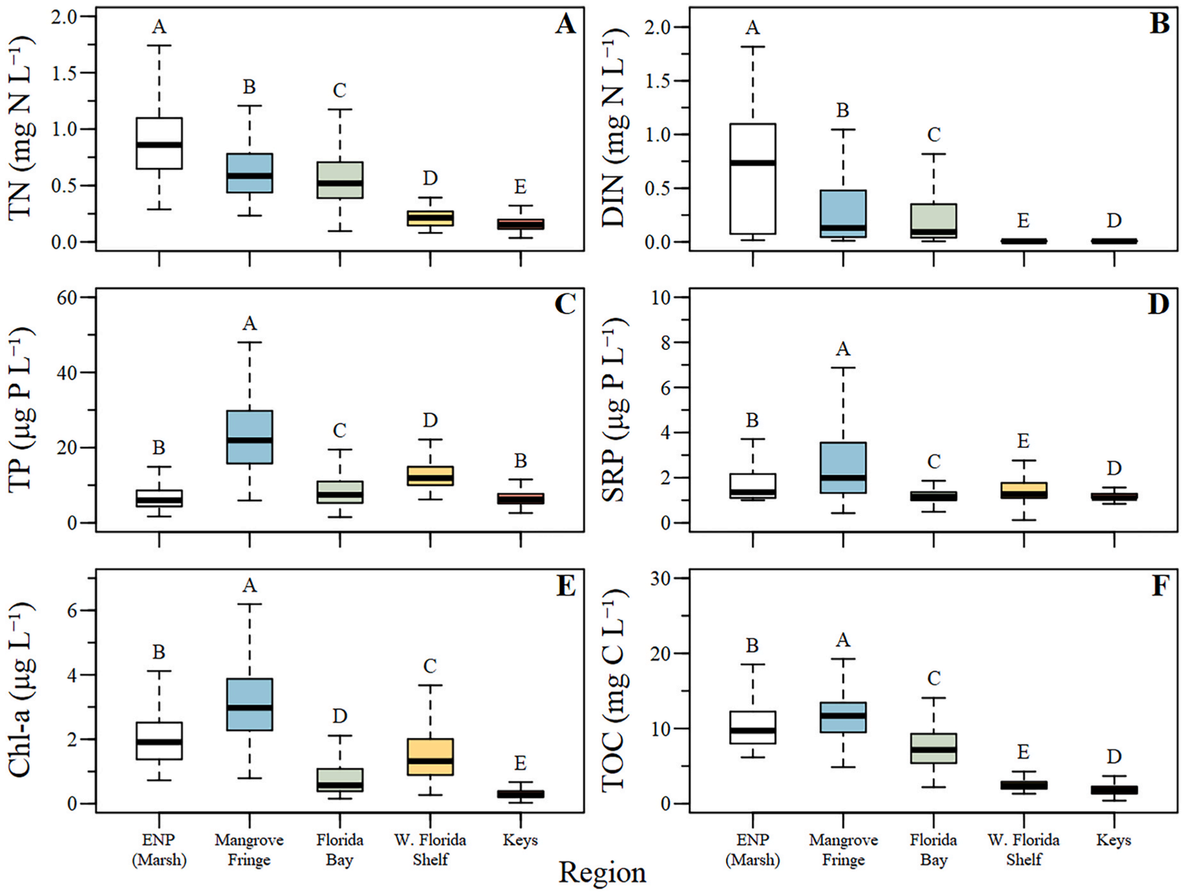

Fig. 2. Comparison of A) annual geometric mean total nitrogen (TN), B) dissolved inorganic nutrient (DIN), C) total phosphorous (TP), D) soluble reactive phosphorus (SRP), E) chlorophyll-*a* (Chl-*a*), and F) total organic carbon (TOC) concentrations across the five regions across the study area. Letters above boxplots indicate pairwise comparisons between regions using Dunn's test of multiple comparisons.

Table 1
Summary statistics of annual geometric mean concentrations by region and parameter.

Parameter (Units)	Region	N	Minimum	Median	Mean	Maximum
TN (mg N L^{-1})	ENP (Marsh)	557	0.289	0.863	0.880	1.817
	Mangrove Fringe	614	0.233	0.586	0.614	1.207
	Florida Bay	685	0.096	0.518	0.572	2.200
	W. Florida Shelf	393	0.080	0.214	0.212	0.393
	Keys	2506	0.035	0.152	0.162	0.429
DIN (mg N L^{-1})	ENP (Marsh)	463	0.016	0.732	0.672	1.817
	Mangrove Fringe	594	0.011	0.129	0.283	1.207
	Florida Bay	671	0.005	0.093	0.240	1.405
	W. Florida Shelf	665	0.001	0.007	0.008	0.030
	Keys	2630	0.001	0.007	0.009	0.055
TP (µg P L^{-1})	ENP (Marsh)	637	1.69	5.91	6.83	25.22
	Mangrove Fringe	701	5.92	21.89	22.88	47.99
	Florida Bay	708	1.51	7.35	9.18	43.17
	W. Florida Shelf	393	6.20	11.88	12.62	26.20
	Keys	2503	1.92	6.19	6.57	17.30
SRP (µg P L^{-1})	ENP (Marsh)	553	1.00	1.40	1.78	15.11
	Mangrove Fringe	676	0.43	1.97	2.84	22.87
	Florida Bay	701	0.18	1.16	1.23	5.09
	W. Florida Shelf	849	0.12	1.27	1.58	9.39
	Keys	2458	0.12	1.10	1.12	4.66
Chl-a (µg L^{-1})	ENP (Marsh)	87	0.73	1.91	2.24	8.22
	Mangrove Fringe	647	0.79	2.97	3.19	9.34
	Florida Bay	636	0.16	0.57	1.04	15.71
	W. Florida Shelf	894	0.27	1.32	1.60	6.05
	Keys	2686	0.03	0.27	0.32	1.62
TOC (mg C L^{-1})	ENP (Marsh)	40	6.17	9.71	10.85	20.95
	Mangrove Fringe	659	4.85	11.69	11.49	23.95
	Florida Bay	708	2.19	7.16	7.51	26.61
	W. Florida Shelf	389	1.32	2.40	2.49	4.52
	Keys	2465	0.40	1.81	1.89	5.17

concentrations ranging from 0.4 to 26.6 mg C L^{-1} (Table 1). Spatially, TOC did show a downstream decrease in TOC with ENP and Mangrove fringe having the highest concentrations and TOC decreasing in Florida Bay and the West Florida Shelf and Florida Keys having much lower TOC concentrations (Fig. 2 and Table 1).

Stoichiometric ratios of TN:TP, TOC:TP and TOC:TN were significantly different between regions ($\chi^2 = 2234.7$, $\rho < 0.01$; $\chi^2 = 1889.2$, $\rho < 0.01$ and $\chi^2 = 597.6$, $\rho < 0.01$, respectively). Each region is stoichiometrically distinct, despite some similarity in TOC:TN between the West Florida Shelf and Florida Keys (Fig. 3). Generally, TN:TP, TOC:TP and TOC:TN significantly decrease from freshwater to marine regions, but in the case of TOC:TN, stoichiometric ratios exhibited an increase in variability along the continuum (Fig. 3 and Table 2).

3.2. Spatial and temporal trends

Generally, TN, DIN, and TOC concentrations were greatest in the freshwater Everglades with a precipitous drop in concentrations along the ridge-to-reef aquatic continuum (Figs. 4–6). Meanwhile, TP was greatest close to the coastline, particularly along the coastline in the northern reaches of the study area. SRP concentrations had a similar pattern with greatest concentrations along the coastline in the northern reaches of the study area and elevated concentrations along the western mangrove fringe of ENP. Average AGM concentrations of Chl-*a* remained relatively low with a maximum period of record average concentration of ~6.0 μg L^{-1} observed throughout the entire study area (Fig. 6). Generally, areas of high Chl-*a* concentrations were along the coastline corresponding with high TP concentrations meanwhile Chl-*a* concentrations remained relatively low along the Florida Keys reef tract (Fig. 6 and Table S3).

Increasing trends in TN were observed at several locations within Florida Bay, the mangrove fringe of ENP, freshwater portions of ENP and the Florida Keys. The region with the greatest increase in TN concentration over time was the northern ENP mangrove fringe (Fig. 4). Meanwhile, DIN increased in coastal and nearshore areas of the study area, including the mangrove fringe (Fig. 4). There were slight decreases in DIN in the most offshore West Florida Shelf.

Annual trends in TP concentration were more variable across the study area with a dominance of declining values in Florida Bay, and the adjacent upstream portions of the Everglades while increasing trends were observed in specific areas along the western mangrove fringe near the Broad and Shark Rivers and in some specific areas of the Florida Keys (Fig. 4). Annual trends in SRP concentrations were significantly declining in the most upstream freshwater Everglades (Fig. 5). However, SRP AGMs increased in the mangrove fringe and in numerous locations within the Florida Keys and southern Florida Bay regions SRP increased at marginal rates of change (0.0–0.042 μg P L^{-1} WY^{-1}; Fig. 4).

As expected, annual trends in N:P were variable across the entire study area with most areas increasing, especially Florida Bay and the mangrove fringe of northern Florida Bay. On average, the freshwater portion of the study areas (ENP marsh) and Florida Bay is and remains P-limited (high N:P values), and Florida Keys and West Florida Shelf are generally N-limited (low N:P). The majority of the changes in N:P ratios are limited to highly dynamic parts of the system with a change of >3.4 yr^{-1} change in N:P ratios over the multidecadal period (Fig. 4).

Annual trends in Chl-*a* had variable rates of change. The greatest

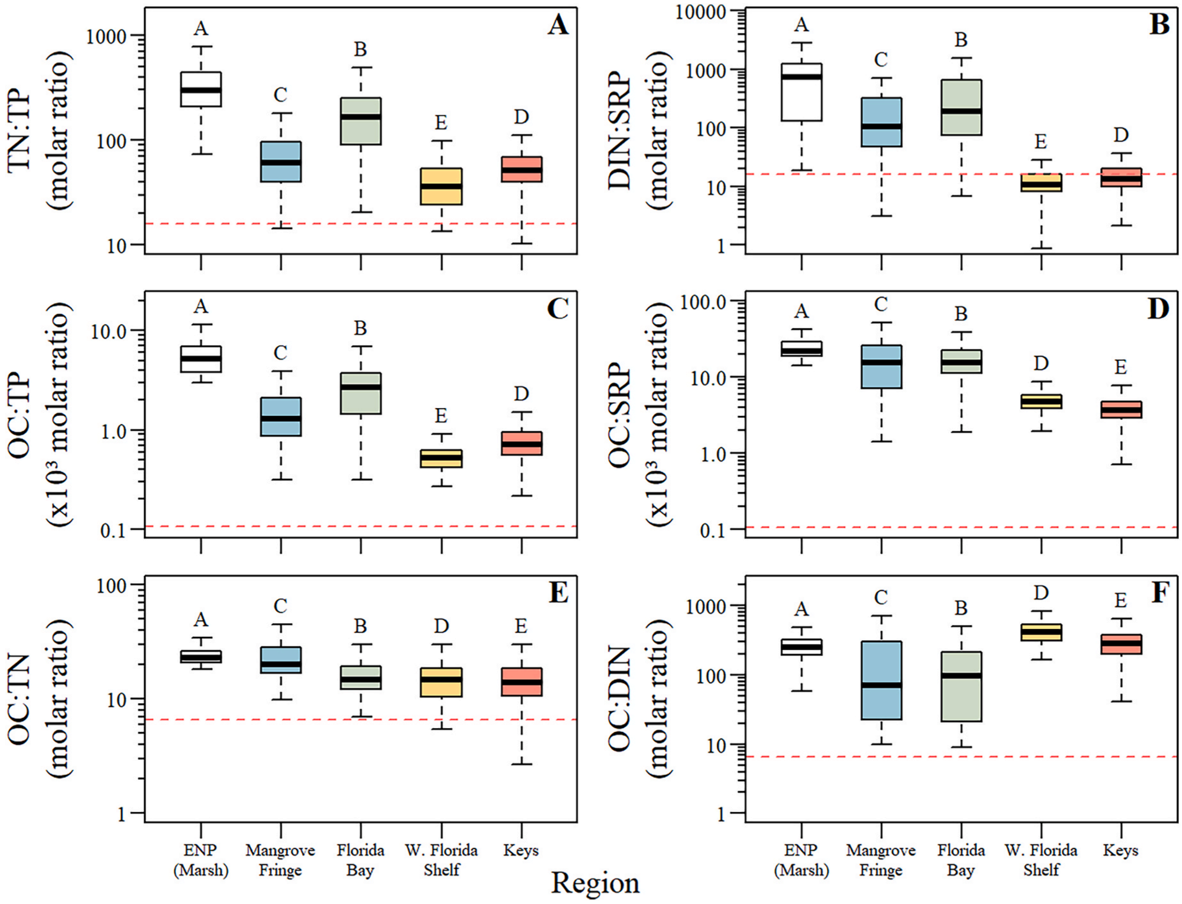

Fig. 3. Comparison of annual geometric mean A) total nitrogen to total phosphorus (TN:TP), B) total organic carbon to TP (TOC:TP) and C) TOC to TN molar ratio across the five regions across the study area. Letters above boxplots indicate pairwise comparisons between regions using Dunn's test of multiple comparisons. Red dashed line indicating the 16:1 TN:TP, 106:1 TOC:TP, and 106:16 TOC:TN Redfield molar ratios. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Summary statistics of annual geometric mean stoichiometric ratios by region and parameter.

Parameter (Units)	Region	N	Minimum	Median	Mean	Maximum
TN:TP (molar ratio)	ENP (Marsh)	550	73	298	347	1016
	Mangrove Fringe	600	14	61	73	245
	Florida Bay	680	20	164	189	1015
	W. Florida Shelf	393	13	36	41	112
	Keys	2503	10	52	59	243
TOC:TP (molar ratio) [a]	ENP (Marsh)	38	2969	5172	5867	11955
	Mangrove Fringe	659	316	1289	1542	5637
	Florida Bay	708	317	2681	2775	12607
	W. Florida Shelf	389	268	518	529	908
	Keys	2462	214	714	785	3000
TOC:TN (molar ratio) [a]	ENP (Marsh)	40	18	23	24	37
	Mangrove Fringe	558	10	20	23	46
	Florida Bay	680	7	15	17	76
	W. Florida Shelf	389	5	15	15	38
	Keys	2465	3	14	15	45

[a] Limited availability of TOC measurements in ENP (Marsh) restricted sample size.

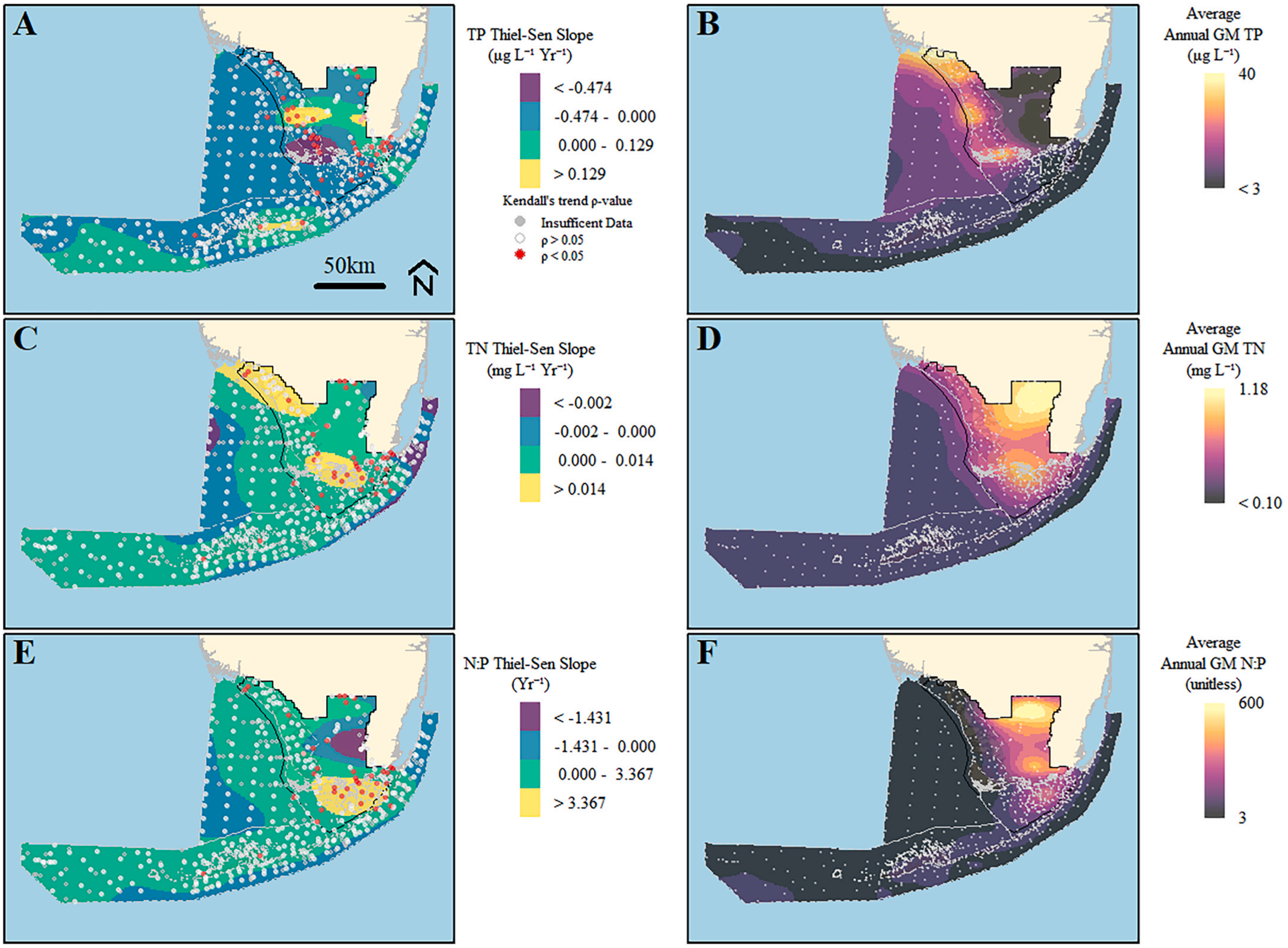

Fig. 4. Annual rate of change for geometric mean A) total phosphorus (TP), C) total nitrogen (TN) concentration, and E) total nitrogen to total phosphorus molar ratio (N:P) at individual stations across the Everglades-Florida Bay-West Florida Shelf-Keys ecosystem during the period of record. Average annual geometric mean TP (B) TN (D), and N:P (F) concentrations across the study area.

increases in Chl-*a* were observed in the northern mangrove fringe and northern West Florida Shelf. Florida Bay and the most southern mangrove fringe had declining trends in Chl-*a* (Fig. 6). Many regions of the Florida Keys also showed slight increases in Chl-*a*. Furthermore, the extent and magnitude of these trends appear to be disjunct from those observed for N and P fractions. The relative magnitude of Chl-*a* across the study area varies with relatively higher concentrations being observed along the mangrove fringe and West Florida Shelf. Annual trends in TOC consistently declined across nearly all of the study area. The lone exception was a single station at the mouth of Taylor Slough

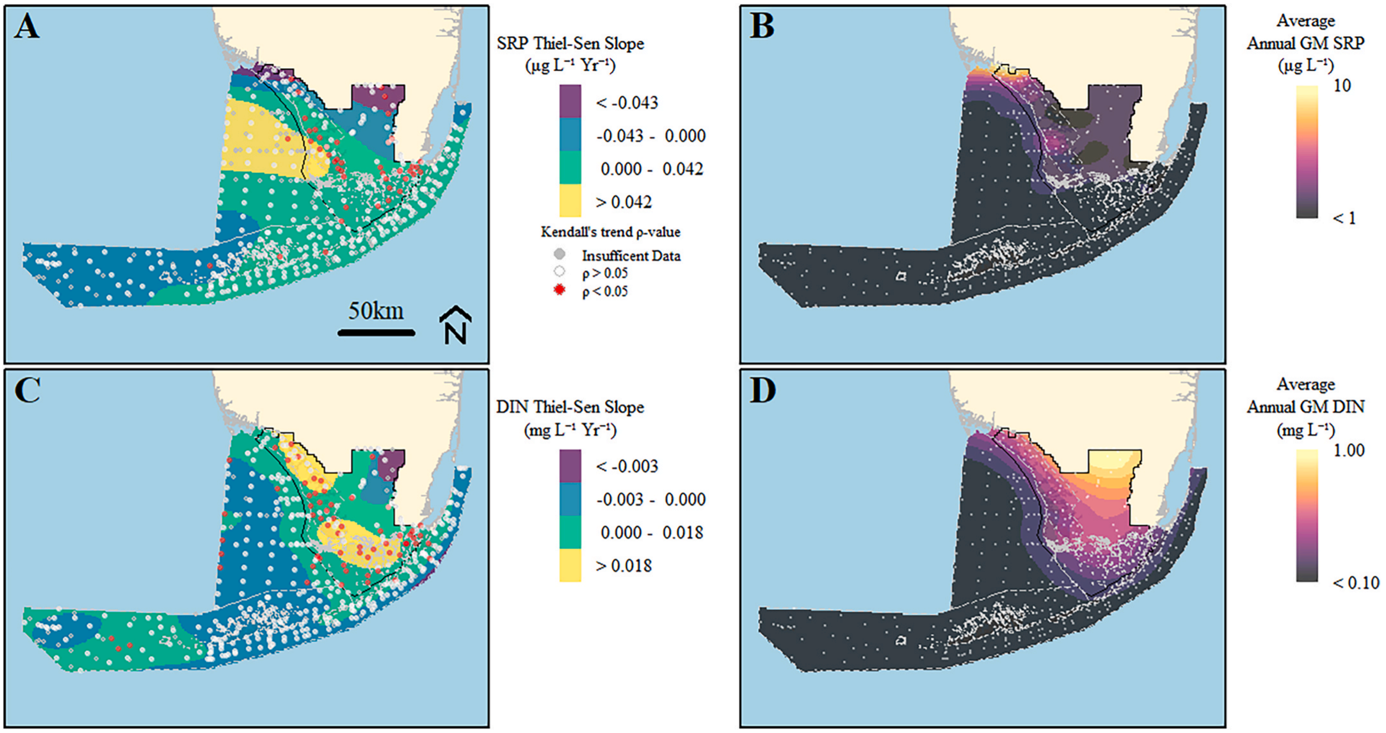

Fig. 5. Annual rate of change for geometric mean A) soluble reactive phosphorus (SRP) and C) dissolved inorganic nitrogen (DIN) concentrations at individual stations across the Everglades-Florida Bay-West Florida Shelf-Keys ecosystem during the period of record. Average annual geometric mean SRP (B) and DIN (D) concentrations across the study area.

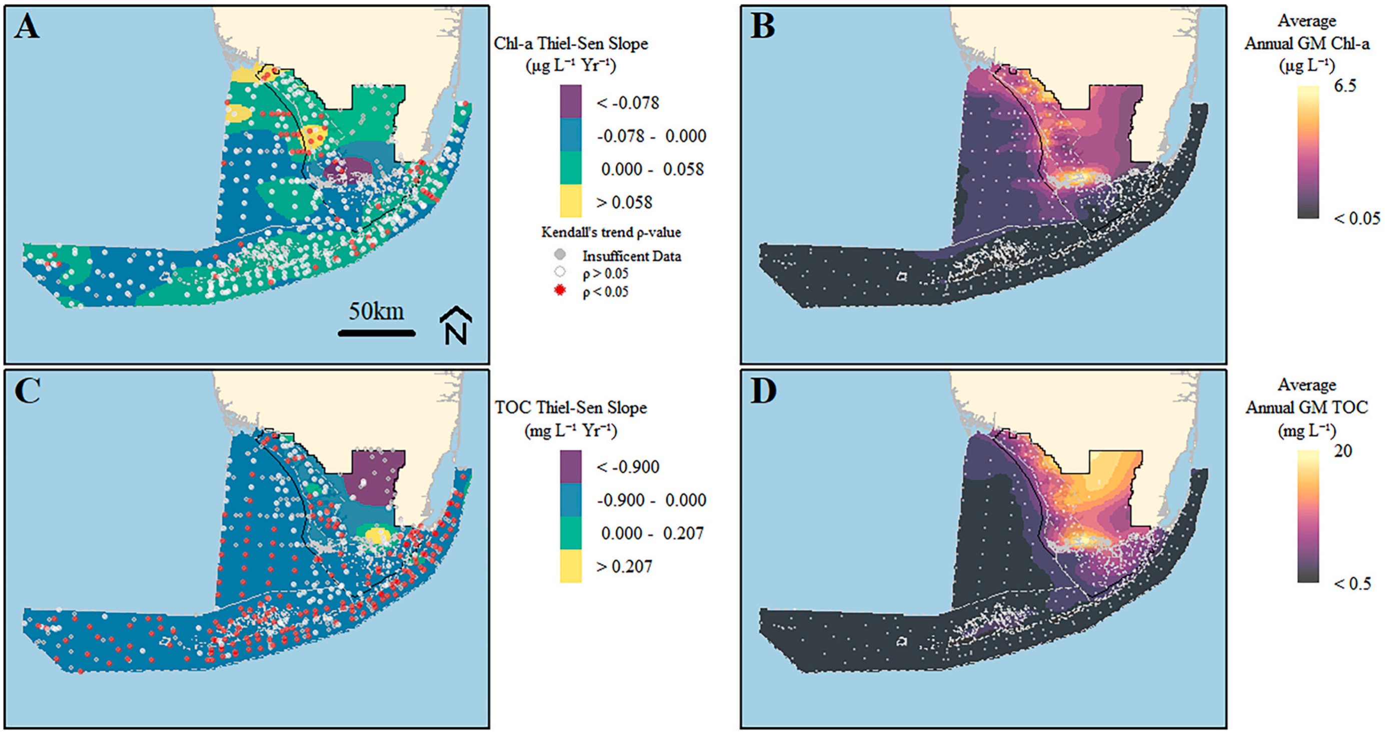

Fig. 6. Annual rate of change for geometric mean A) chlorophyll-a (Chl-a) and C) total organic carbon (TOC) concentrations at individual stations across the Everglades-Florida Bay-West Florida Shelf-Keys ecosystem during the period of record. Average annual geometric mean Chl-a (B) and TOC (D) concentrations across the study area.

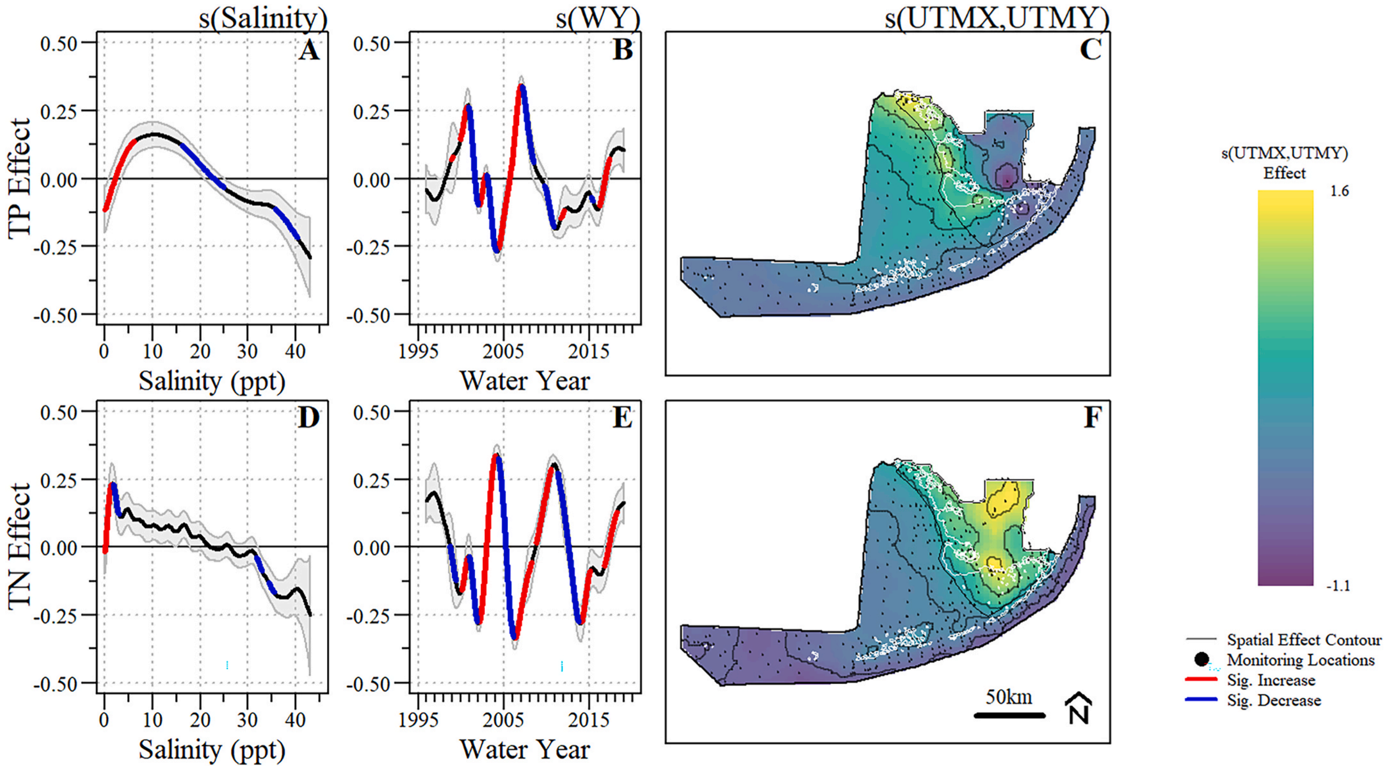

Fig. 7. Generalized additive model effect plots for the TP (A, B and C) and TN (D, E and F) spatiotemporal models. The effect of salinity (A and D), water year (B and E) and spatial (C and F) for the TP and TN models, respectively. Significant changes were identified for salinity and water year effects with red line segments indicating significantly increasing effects and blue line segments indicating significantly decreasing effects. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

which had increasing TOC at rates of change ~0.2 mg C L^{-1} WY^{-1} (Fig. 6).

3.3. Salinity spatiotemporal models

The annual geometric mean TP and TN varied across space and time (Fig. 7), with the models explaining 95% and 96% of the deviance in the observed data (akin to R^2) for TP and TN, respectively (Table 3). Spatially, the largest positive effect for TP is located along the northwestern coastline of Everglades National Park and adjacent to the shoreline where the Shark River Slough estuary enters the Gulf of Mexico meanwhile the smallest spatial effect is located in Taylor Slough, northeastern Florida Bay, and the entire stretch of the reef track (Atlantic Ocean side of the Florida Keys; Fig. 7C). The effect of WY was highly dynamic with several periods of significant change (increases and decreases) being detected (Fig. 7B). Significantly changes throughout the POR were detected following a general cyclic pattern with periods of significant increases including two short periods in the late 1990s, a short period spanning 2002, a prolonged event spanning 2004 to 2006, a brief period in mid-2011 to early 2012, and 2016 to 2017. Generally, periods of significant increases are followed by periods of significant declines (Fig. 7B). These changes in WY correspond closely to either the occurrence of disturbance events or during periods of recovery (post-disturbance; Table 4). The effect of salinity on annual geometric mean

Table 3

Spatio-temporal generalized additive model results for two models including (1) annual geometric mean total phosphorus and (2) annual geometric mean total nitrogen across the study area. Minimum selection criteria and method are defined as fREML (restricted maximum likelihood). Other values provided include effective degrees of freedom (edf), reference degrees of freedom (Ref df), adjusted R^2 and deviation explained (akin to R^2).

Predicted Variable	Term	Estimate	Standard Error	t-value	ρ-value	edf (Ref df)	F-value	ρ-value	Adj R^2 (Dev. Exp.)	Minimum Selection Criterion	Scale (n)
(1) Annual Geometric Mean Total Phosphorus	Intercept	2.22	0.03	76.74	*< 0.01*	–	–	–	0.95 (0.94)	−624.48 (fREML)	0.03 (4622)
	s(Salinity)	–	–	–	–	7.95 (9.93)	9.75	*< 0.01*			
	s(UTMX, UTMY)	–	–	–	–	209.64 (315.00)	65.07	*< 0.01*			
	s(WY)	–	–	–	–	21.12 (21.73)	50.35	*< 0.01*			
	ti(WY,UTMX, UTMY)	–	–	–	–	560.70 (3646.00)	1.04	0.39			
(2) Annual Geometric Mean Total Nitrogen	Intercept	−1.32	0.03	−48.70	*< 0.01*	–	–	–	0.96 (0.98)	−1015.74 (fREML)	0.02 (4524)
	s(Salinity)	–	–	–	–	21.54 (24.68)	3.04	*< 0.01*			
	s(UTMX, UTMY)	–	–	–	–	188.22 (290.00)	120.90	*< 0.01*			
	s(WY)	–	–	–	–	20.31 (20.78)	76.32	*< 0.01*			
	ti(WY,UTMX, UTMY)	–	–	–	–	867.62 (4440.00)	2.11	*< 0.01*			

Table 4
Inventory of disturbance events and potential drivers of ecological change experienced across the study area including tropical storm/hurricanes, drought, floods, cold snaps, fire, and climate shifts.

Event Type	Name	Year(s)	Date(s)	Additional Information	References
Tropical Storm	Harvey	1999	Sept 21	Heavy rain	Davis et al. (2004)
Hurricane	Irene	1999	Oct 15	Storm surge and rain	Davis et al. (2004)
Hurricane	Katrina	2005	Aug 25	Heavy rain	Zhang et al. (2009)
Hurricane	Wilma	2005	Oct 24	Storm surge, rain, sediment, and legacy P	Castañeda-Moya et al. (2010) Davis et al. (2018) Kominoski et al. (2020)
Hurricane	Irma	2017	Sept 10	Storm surge, rain, vegetation damage	Castañeda-Moya et al. (2020)
Drought		2001			Smith et al. (2003)
Drought		2007		Record low lake stage 8.82 ft NGVD	Unpublished Data, South Florida Water Management District
Drought		2011			Kominoski et al. (2020)
Drought		2015		Seagrass dieoff	Hall et al. (2016)
Flood		2016			Kominoski et al. (2020)
Cold snap		2010	Jan 2–13	vegetation loss and faunal mortality	Boucek and Rehage (2014)
Fire	Mustang	2008	May		Smith et al. (2015) Davis et al. (2018)
Strong el Niño conditions[a]		1997–98 2009–10 2015–16		Wetter than average dry seasons) that lead to high discharge	Unpublished Data, South Florida Water Management District

[a] See Fig. S2 for Niño 3.4 index time-series.

TP concentrations was non-linear (Table 3) with edf values > 1.0, with a steep significant increase between salinity values of 0 and 6 ppt, a brief plateau followed by two significant decreases between salinity values of 16 and 24 ppt and 36 and 40 ppt (Fig. 7A).

The spatial effect for annual mean TN concentrations was markedly different than that of the TP model with the greatest effect being located in the freshwater ENP and northern Florida Bay and lowest along the reef track (Fig. 7F). The effect of WY was similar to that of the TP model in that the change in annual effect was cyclical, however, the effects were notably shifted (Fig. 7E). Some short periods of non-significant change were apparent during transitional times but generally, the mid to late 1990s, early 2006, 2015 to 2016 and > 2018 in periods of non-significant change. Periods of significant increases include early to mid- 2000, 2002 to 2004, 2006 to 2010, 2014 to 2015, and 2016 to 2015. The effect of salinity on annual geometric mean TN concentrations was non-linear (Table 3) with a gradually negatively sloping line between salinity values of 1.3 and 30 ppt, a significantly decreasing dip occurred between salinities of 1.7–3 ppt, 32–33 ppt, and 34–36 ppt (Fig. 7D).

4. Discussion

Across the Everglades ridge-to-reef ecosystem structure, there were distinct variations along spatial gradients for N, P, C, and Chl-*a* over time (Figs. 2–5). To understand this variation, we quantified long-term trends in water column biogeochemical characteristics to understand how spatiotemporal changes varied across the ridge-to-reef ecosystem structure and observed the variation in water column characteristics consistent with the occurrence of several and often distinct drivers of ecosystem change (Table 4). Herein we describe some potential drivers of biogeochemical changes across the different ecosystems evaluated in this study.

Disturbance legacies are known drivers of biogeochemical variation in Everglades habitats. These habitats have adapted to long-term persistent disturbances (e.g., hurricanes, droughts) (Davis et al., 2018; Kominoski et al., 2020). However, they are still being modified along divergent trajectories in response to relatively recent disturbances (e.g., management operations, anthropogenic-driven eutrophication). Based on the magnitude, variation, and rate of change of N and P, some regions such as the mangrove fringe and coastal nearshore regions reflect biogeochemical hotspots (Cheng and Basu, 2017) responding, in part, to the legacy effects of significant disturbance events (Table 4). These biogeochemical hotspots typically occur in ecotonal regions and are generally nutrient sinks with a high rate of change. This is apparent with respect to P in the mangrove fringe region and N in northern/northeastern Florida Bay (Fig. 4). Additionally, across the study area, temporal trends varied spatially for some parameters such as Chl-*a* and SRP increasing in the mangrove fringe (Fig. 6) whilst declining in Florida Bay and ENP (Fig. 5). Regional changes in N and P trends are expected given the disturbance legacy (Table 4) in those regions such as changes in P in the mangrove fringe (Castañeda-Moya et al., 2010, 2020), changes in N in Florida Bay (Davis et al., 2004; Glibert et al., 2009, 2021) and ongoing restoration efforts.

In coastal oligotrophic ecosystems, spatiotemporal variation of biogeochemical characteristics can be strongly driven by episodic short-term events and long-term disturbance legacies (Davis et al., 2018; Kominoski et al., 2020). The year-to-year variation in TN and TP across the study area, at times, corresponds with pulse events (Table 4; i.e., hurricanes/tropical activity, fire, cold snaps, and seagrass die-offs) and press events (Table 4 and Fig. S1; i.e., drought, high water in Everglades, climate shifts, restoration, eutrophication, etc) suggesting a push-pull dynamic between events and the spatiotemporal variation in nutrients (Fig. 7B and E). The interaction between these disturbance events combined with end-member sources of nutrients can be influenced by regional climate and upstream water management (Kwon et al., 2006; Boyer et al., 2009; Briceño and Boyer, 2010; Dessu et al., 2018). As suggested by Davis et al. (2018) in the freshwater (and estuarine) Everglades episodic events are linked to temporal changes in N and P such as sediment and P redistribution post-major hurricane (Castañeda-Moya et al., 2020). Additionally, press events or an interaction of press events can also manifest in gradual changes in N and P indirectly via sea-level rise and rapid loss of organic soils due to salinization of freshwater soils (e.g. peat-collapse; Wilson et al., 2018; Servais et al., 2019; Andres et al., 2019) or more directly through eutrophication. A combination of sea-level rise, peat-collapse, and eutrophication could provide context to changes in SRP and Chl-*a* concentrations in the northwestern portion of the study area (Figs. 5 and 6). This paradigm could also be extended into the larger system, albeit each region attenuates these changes differently due to different hydrologic and biogeochemical factors unique to each region.

The results demonstrate the need to look at biogeochemical patterns across the freshwater to marine ecosystems to fully understand the causes of biogeochemical changes. Recent studies from nearby Biscayne Bay highlighted the increased eutrophication being caused by land-based sources (Millette et al., 2019). However, there are freshwater and marine drivers of eutrophication at this nexus and without evaluating both a full understanding of eutrophication drivers cannot be ascertained. As such, mitigation strategies could be hampered by implementing strategies formulated with incomplete information. While the majority of the study area includes estuarine (brackish) and marine portions of the system, the inclusion of the freshwater marsh aids in understanding the nature of nutrient changes in adjacent ecosystems.

An integrated view of spatial and temporal changes and drivers of biogeochemical cycles relative to landscape-scale processes such as disturbances is key to understanding the resilience of important ecosystems. The results presented here establish large-scale spatial and temporal trends in biogeochemical cycles in the region with the intent of facilitating future research that can link these trends to the well-established drivers in the region. Along the freshwater-to-marine aquatic continuum, the downstream estuarine or marine system is hydrologically linked to the upstream freshwater systems. In south Florida, the oligotrophic estuaries of the Florida Everglades are coupled to the upstream freshwater wetlands of the Everglades (Childers et al., 2006). This hydrologic linkage is important for the sources and timing of the delivery of organic matter and nutrients (Kominoski et al., 2020). Disturbances and long-term hydrologic changes have been suspected to influence the quantity, quality, and timing of basal resources by affecting organic matter and nutrients (Erlandsson et al., 2008; Kominoski and Rosemond, 2011; Solomon et al., 2015). In the Florida Everglades, hydrologic conditions in the freshwater system have varied in response to climate and ongoing restoration (Kotun and Renshaw, 2014; Harvey et al., 2017; Paudel et al., 2020, Fig. 7), and water management and climate (i.e., El Niño-Southern Oscillation) can strongly influence water quality patterns in estuaries (Childers et al., 2006).

Everglades restoration has been a major driver of P reduction (Fig. 4; Julian et al., 2021) in water delivered to the freshwater Everglades which developed as a P-limited system. A reduction in P loading to the Everglades should result in lower nutrients delivered to the downstream estuaries. However, the estuaries of the Everglades ecosystem have been coined “upside-down” or reverse estuaries where concentrations of the limiting element (P) increase (Figs. 4, 5 and 7C), and N concentrations decrease toward the marine end-member (Childers et al., 2006, Figs. 3 and 7F). At the interface between marine and freshwater systems, the coastal mangrove fringe ecotone is a biogeochemical hotspot with high soil P and other constituents (Chambers and Pederson, 2006; River-a-Monroy et al., 2011). Additionally, the effect of salinity across space and time is further demonstrated by the spatiotemporal GAM models (Fig. 7) highlighting the “upside-down” estuary but also gaining an insightful landscape-scale view of potential nutrient source (positive spatial effect) and sinks (negative spatial effect). Furthermore, these landscape-scale patterns provide additional insight into the potential drivers of organic matter dynamics through time.

Contrasting the low P concentrations of the freshwater Everglades, N concentrations are generally higher in the freshwater portion than in downstream estuaries, which is driven largely by biomass turnover, relatively higher dissolved organic matter (DOM)/OC concentrations, and cycling of N (i.e., N_2 fixation and denitrification; Sutula et al., 2003; Inglett et al., 2011, Fig. 7F). Moreover, the calcareous periphyton of the southern Everglades is a significant transformer and fixer of N in the freshwater Everglades (Hagerthey et al., 2011). While surface water TN concentrations are generally greater in the freshwater Everglades (Fig. 4), central Florida Bay also has relatively high concentrations of N. Moreover, significant increases in TN and DIN concentrations were detected in central Florida Bay, Whitewater Bay, and the northern extent of the mangrove fringe (Figs. 4 and 5). These observed trends could be the results of biomass turnover due to large-scale mortality events in the coastal mangrove fringe and seagrass beds of Florida Bay. Additionally, this region has been the epicenter of historic widespread mortality of seagrass in the late 1980s and early 1990s (Zieman et al., 1989, 1999) and more recently in 2015 (Hall et al., 2016) as well as mangrove die-back due to tropical storm impacts (Lagomasino et al., 2021). Specific to Florida Bay, belowground seagrass biomass, living and dead could be a local, *in-situ* source of N resulting in a steady increase in water column N (Figs. 4–7).

Several environmental and biological drivers are thought to have contributed to seagrass die-off events in Florida Bay including seagrass density, temperature, salinity, sulfide toxicity, pathogenic infections, and TP concentrations (Fredley et al., 2019). After the 2015 seagrass die-off, Glibert et al. (2021) noted exceptionally high ammonium concentrations in Florida Bay following the event. These high ammonium concentrations could be the result of biological remineralization, sponge-mediated N release (Hoer et al., 2020), or a combination of these factors. Long-term data from Florida Bay suggest significant increases in DIN concentrations (this study; Fig. 5). While regions of seagrass die-off have unique physical (i.e., sediment depth, hypersalinity, etc.) and biogeochemical (sulfide cycling) characteristics it would appear these regions are a major source of N to the system through decaying biomass, remineralization, and other benthic organisms contributing major N-fluxes. Although large-scale seagrass die-off events happen infrequently (documented only in the late 1980s and again in 2015; Hall et al., 2016), the decay of biomass and “normal” annual turnover of these communities can be a major source of N to the surrounding oligotrophic systems (Fig. 7). However, disturbances such as hurricanes, climate cycles, changes in freshwater flow/salinity regimes, and nutrient inputs can influence the local and regional ecology of the press and pulse dynamics and or changes to stable states.

Estuaries are conduits of DOM and, more importantly, DOC between the catchment/watershed to the coastal nearshore and offshore environments. Estuaries and nearshore environments also modify the DOM load through conversion via productivity and abiotic processes (Maher and Eyre, 2011; Julian and Osborne, 2018). Hydrology, climate, and water management are long-term drivers of OC export or flux in the freshwater and estuarine portions of the Everglades ecosystem (Regier and Jaffé, 2016; Regier et al., 2016). In the mangrove estuary of the Everglades, water management had a strong (positive) influence on OC dynamics by restoring salinity gradients after significant droughts and elevated sea levels (Regier and Jaffé, 2016). Changes in DOM/OC concentrations and flux can influence ecosystem productivity. As observed in lake ecosystems changes in DOM/OC can have a variety of effects ranging from increased productivity via phytoplankton growth or decreased productivity due to reducing light availability and mixing due to heat absorption (Solomon et al., 2015). Across the coastal Everglades (from freshwater to estuarine ecosystems), DOC was positively correlated with bacterioplankton productivity (Kominoski et al., 2020). In some cases, changes in OC trends could also alter localized ecosystem phytoplankton productivity. In this study, we observed most of the study area experiencing significantly declining TOC trends (Fig. 6), combined with observed changes in plankton productivity (Kominoski et al., 2020) this change in TOC concentrations could suggest a shift in phytoplankton productivity. However, while not significant it would appear a portion of Taylor Slough/Taylor River has a strong positive rate of change potentially signaling a “browning” of this region as observed in other freshwater systems (Blanchet et al., 2022). This potential browning signal could be partly explained by the immediate and delayed effects of mass mangrove mortality caused by Hurricane Irma (Lagomasino et al., 2021) where living and dead mangrove biomass is contributing to the organic carbon pool.

Nutrient and light availability are major bottom-up drivers that stimulate primary production in brown (heterotroph-dominated) and green (autotroph-dominated) aquatic food webs (Evans-White and Halvorson, 2017). Organic C and chlorophyll have been used as metrics of aquatic primary producer biomass and are typically correlated (Burt et al., 2018); therefore, it would be reasonable to expect TOC and Chl-*a* trends to correspond. In some regions such as Florida Bay, it would appear Chl-*a* and TOC are both indicating a shift in aquatic productivity over time. Meanwhile, in other areas (northern mangrove fringe) significantly increasing trends in algal biomass (as indicated by Chl-*a*) and decreasing trends in TOC (Fig. 6) have been observed potentially pointing to other drivers such as nutrient availability for algal biomass proliferation. Pulse disturbance events such as seagrass die-offs, fires, cold snaps, hurricanes, etc. can mobilize nutrients for algal consumption. Ultimately the trends in water quality observed across the system are the combined response of press and pulse events transposed over decadal or multi-decadal climatic forcing factors (Briceño and Boyer, 2010, Fig. 6).

Another potential driver of ecosystem and biogeochemical process in the study area, in the form of a press event is sea-level rise (SLR; Dessu et al., 2018). Global eustatic sea-level rise (SLR) is currently 3.6 mm year^{-1} leading to many coastal ecosystems being exposed to saltwater intrusion and prolonged tidal inundation (Oppenheimer et al., 2019) resulting in the salinization of oligohaline and freshwater wetlands. In south Florida, the local rate of SLR can be much more variable depending on location and timeframe ranging from 2.4 to 5.9 mm yr $^{-1}$ (Wdowinski et al., 2016; Breithaupt et al., 2017; Meeder et al., 2021). Coastal ecosystems have a natural positive feedback mechanism that allows them to adapt to SLR through the build-up of organic matter (Chambers et al., 2014; Breithaupt et al., 2017). Coastal freshwater peat-based wetlands are especially susceptible to saltwater intrusion and changes in water depth (Herbert et al., 2015). The effect of SLR has the greatest potential to influence these regions by altering organic C accumulation processes and associated biogeochemical cycling (Wilson et al., 2018). Therefore, as SLR increases ecosystems at the brackish or estuarine interface have the greatest potential to see changes from this prolonged press and could in part explain the P trends in the nearshore environment observed in this study (Fig. 4). However, increases in freshwater flow through hydrologic restoration in the Florida Everglades have the potential to reduce the negative impacts of sea-level rise in ecologically sensitive coastal habitats (Dessu et al., 2021).

Disturbance events have shaped the ecology and biogeochemical processes across the Everglades-Florida Bay-West Florida Shelf-Key by changing sources and sinks of nutrients across the system. Similar to the conceptual model proposed by Briceño and Boyer (2010), changes in water column TN and TP across the system could be the result of a tug of war between decadal or multi-decadal climate patterns, press and pulse disturbance legacies, and long-term changes in hydrology due to restoration activities. Disturbance legacies combined with planned restoration efforts and forecasted SLR will influence spatial and temporal trends in water quality across the Greater Everglades Ecosystem with landscape-level implications and connections with adjacent marine ecosystems (e.g., Florida Reef). However, at this time, the influence of restoration projects on the directionality of change for selected biogeochemical parameters is uncertain. As more freshwater is moved south through ENP towards the estuaries, restoration modeling efforts indicate saltwater intrusion be reduced and salinization of freshwater marshes would be stayed. The increase in freshwater flow will have an effect on nutrient fluxes and concentrations. Along with this increased freshwater flow, nutrient loading could also increase despite achieving near-ambient nutrient concentrations. The objective of Everglades restoration is to improve the quality, quantity, timing, and distribution of water to the Greater Everglades Ecosystem, well beyond the conventionally viewed boundaries of the Everglades ecosystem that include the Water Conservation Areas, Everglades National Park, and Florida Bay.

5. Conclusions

The interactions between disturbance legacies and ecosystem trajectories can be complicated as disturbance and ecosystem response depend on numerous factors (Gaiser et al., 2020). Ecological theory and specifically disturbance ecology predict that ecosystems are maintained and enhanced through disturbances by the release and redistribution of nutrients and organic matter (Junk et al., 1989; Odum et al., 1995). Ecosystem responses to disturbances, legacies, and interactions with other environmental and global factors can lead to non-linearities (Bestelmeyer et al., 2011; Dakos et al., 2015). The holistic analysis of long-term trends in biogeochemical indicators at individual locations across a large spatial area exposed a large degree of spatial variability not observed at smaller spatial scales (Figs. 4–6). Our study illustrates the cumulative effect of disturbance, legacy impacts and ongoing restoration efforts across a freshwater-estuarine-marine aquatic continuum over a multi-decadal timestep and the associated changes in biogeochemical indicators. A limitation of this study is that cause-and-effect determinations are not possible and through the weight of evidence we can hypothesize based on spatial and temporal correlation with the magnitude and rate of change of biogeochemical indicators. Regardless, how ecosystem drivers interact to increase or decrease nutrient, organic matter, and sediment retention is critical to the long-term trajectories of ecosystems (Kominoski et al., 2018; Breithaupt et al., 2020). Additionally, this highlights the value of long-term datasets encompassing large spatial scales to evaluate the potential change in ecosystem variables across space and time relative to other ecosystem drivers. Further understanding of biogeochemical trends and potential drivers and mechanisms of change are important to the conservation, management, and restoration of ecosystems in the face of rapidly changing climate.

CRediT authorship contribution statement

Paul Julian: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **James W. Fourqurean:** Writing – original draft. **Stephen E. Davis:** Writing – review & editing, Writing – original draft. **Donatto Surratt:** Writing – original draft, Data curation. **Evelyn E. Gaiser:** Writing – review & editing, Writing – original draft, Data curation. **John S. Kominoski:** Writing – review & editing, Writing – original draft, Data curation. **Tiffany G. Troxler:** Writing – review & editing, Writing – original draft, Data curation. **Joseph N. Boyer:** Writing – review & editing, Writing – original draft, Data curation. **Serge Thomas:** Writing – review & editing, Writing – original draft. **Henry O. Briceño:** Writing – original draft, Data curation. **Christopher J. Madden:** Writing – original draft, Data curation. **Enrique Montes:** Writing – original draft, Data curation. **Chris R. Kelble:** Writing – original draft, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data used in this study can be found here https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-fce.1248.1 and in the supplemental material. Additionally, R-script used to analyze these data are available in the Supplemental Material.

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Appendix A. Supplementary data

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