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Research Article

Keywords:

Posted Date: October 15th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-11251382/v1>

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Extreme conditions and ecosystem disruptions of the relationships between phytoplankton, seagrass and macroalgal communities in the Indian River Lagoon, Florida, USA, 1997-2024

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ABSTRACT

From the 20th century, there have been progressive increases in cultural eutrophication and global temperatures resulting in disruptions of many coastal ecosystems. Imbedded in these trends is a growing potential for extreme events, such as exceptional temperature periods and intense storms, which can also lead to major shifts in the structure and function of ecosystems, as illustrated in this study. Temporal and spatial changes in the composition and biomass of phytoplankton, seagrasses and macroalgae were determined for the northern half of the Indian River Lagoon (IRL) ecosystem in Florida (USA) from 1997 to 2024, along with measurements of selected physical and chemical parameters. Two major shifts were observed in the relative importance of the three major primary producer communities in the IRL over the study period, each coinciding with extreme climatic conditions, i.e., a year of exceptionally low winter water temperatures in 2010 and a period of multiple hurricanes in 2017-18. The 2010 event was followed by a ten-year period of elevated nutrient levels in the water column, repeated intense harmful algal blooms, and severe losses in seagrass communities, associated with low light transmission. The 2017-18 period was associated with a widespread blooms of the benthic macroalga *Caulerpa*, which took advantage of the open benthic habitat resulting from the extensive losses of seagrass. The results of this study highlight that the structure and function of primary producer communities in aquatic ecosystems can be dramatically altered association with extreme short-term environmental events.

INTRODUCTION

Many estuarine ecosystems around the world are facing the dual threats of cultural eutrophication and climate changes, both of which are contributing to increases in the frequency and intensity of harmful algal blooms (HABs) (Heisler et al., 2008; Paerl et al., 2016; Glibert, 2020; Phlips et al., 2020; Anderson et al., 2021). Addressing the drivers and impacts of HABs requires not only an understanding of phytoplankton dynamics, but also the interactions between phytoplankton and other primary producer communities, such as seagrasses and macroalgae (Valiela et al., 1997; Burkholder et al., 2007; Dunic et al., 2021). From the perspective of basic growth requirements, the interactions are strongly influenced by availability of nutrients and light. Sustained high nutrient loads can lead to intense planktonic HABs that limit the availability of light for benthic primary producers, particularly in ecosystems subject to long water residence times, which allow for accumulation of high phytoplankton biomass. Numerous coastal environments around the world have experienced widespread losses of seagrasses linked to progressive cultural eutrophication (Havens et al., 2001; Burkholder et al., 2007; Waycotte et al., 2009; Han & Liu, 2014; Roca et al., 2016; Orth & Heck, 2023; Zuo et al., 2025).

Some ecosystems have observed recovery of seagrass communities following successful reductions in external nutrient loads, such as Tampa Bay (Greening et al., 2014; Sherwood et al., 2017) and Chesapeake Bay (Lefcheck et al., 2018) in the United States. However, these improvements can be difficult to sustain, especially in regions subject to high rates of human development. For example, in Tampa Bay, after an extended period of seagrass recovery from 2000 to 2016 (Lizcano-Sandoval et al., 2023), average coverage declined by a third by 2022, despite few notable changes in nutrient load characteristics in most of the bay (Beck et al., 2024). The recent losses have been attributed to environmental stress on seagrasses associated with expansions in periods of high-water temperatures and reductions in salinity related to high rainfall, including tropical storms (Beck et al., 2024). In addition, more tidally restricted regions of upper Tampa Bay (i.e., Old Tampa Bay and Hillsborough Bay) have been subject to disruptive HABs related to long water residence times (Weisberg & Zheng, 2006; Badylak et al., 2007; Greening et al., 2014; Corcoran et al., 2017). The influences of these factors help to explain the high seagrass losses in Old Tampa Bay and Hillsborough Bay post-2016, i.e., 62% and 80%, respectively (Beck et al., 2024). The recent changes in Tampa Bay highlight that a wide range of environmental factors beyond just eutrophication can influence the relationships between

phytoplankton and benthic primary producer communities, such as shifts in climatic conditions, and hydrology. While these changes are often incremental over time, major shifts in the structure and function of aquatic ecosystems can be sudden, dramatic and persistent, sometimes referred to as regime shifts (Folke et al., 2004; Krause-Jensen et al., 2012; Möllmann et al., 2015; Bode et al., 2020).

The current study examines the environmental drivers responsible for sudden, dramatic and persistent shifts in the composition and biomass of phytoplankton, seagrasses and macroalgae in the Indian River Lagoon (IRL) in Florida over the past 28 years. The IRL spans 156 miles along the sub-tropical east coast of Florida from the Ponce de Leon Inlet to Jupiter Inlet. The northern half of the IRL ecosystem is composed of four hydrologically connected sub-regions, the Mosquito Lagoon, Banana River Lagoon, northern portion of the IRL proper, and central IRL (Fig. 1). Because of large distances to the nearest inlets to the Atlantic Ocean and absence of major river inflows, water residence times in the sub-regions are long (i.e. averaging > 3-5 months) (Smith, 1987; Sheng & Davis, 2003; Steward et al., 2005). Long water residence times and shallow mean depths (i.e., approximately 1-2 m) provide the hydrologic and physical conditions favorable for the development of phytoplankton blooms (Phlips et al., 2004, 2011; Reynolds, 2006). However, shallow mean depths are also ideal for seagrass and benthic macroalgae, that have historically been major elements of the IRL ecosystem in terms of habitat and primary production (Virnstein et al., 2014; Morris et al., 2022; Hall et al., 2022).

In 2011, a sudden and dramatic shift occurred in the intensity, duration and composition of phytoplankton blooms in the IRL, which persisted for ten years (Phlips et al., 2015). The blooms reached previously unrecorded levels of peak biomass (e.g., chlorophyll *a* concentrations up to over 200 $\mu\text{g L}^{-1}$), and were mostly dominated by nanoplanktonic phytoplankton (e.g., *Aureoumbra lagunensis*) and/or picoplanktonic cyanobacteria (Gobler et al. 2013; Phlips et al. 2012, 2021; Lopez et al. 2021). The shift coincided with dramatic declines in seagrass and drift macroalgae (Hall et al., 2022; Morris et al., 2022). After a nearly ten-year period of frequent intense phytoplankton blooms, bloom biomass levels have declined with regional returns of seagrass, drift macroalgae and/or benthic macroalgae. The objectives of this study were to describe the changes in the major primary producer communities in the northern half of the IRL over the past 28 years and explore the drivers of the shifts in their composition and biomass. The results highlight the role of extreme climatic conditions in rapidly altering the relationships

between primary producer communities, with consequences for the structure and function of the ecosystem.

METHODS

Site Description – The study focused on four sub-regions of the Indian River Lagoon (IRL), the Mosquito Lagoon; Banana River Lagoon, northern IRL, and central IRL (Fig. 1). The southern Mosquito Lagoon is connected to the northern IRL via the Haulover Canal north of the City of Titusville. The Banana River Lagoon is connected to the northern IRL via the Barge Canal near the City of Cocoa, and a convergence to the IRL near the City of Melbourne.

Eight sampling sites were included in the study region (Fig. 1). Sites BR2, IR1, IR3 and IR4 were sampled monthly from September 1997 through 2005, with some monthly gaps. From 2006 to 2024 sites MQ1, and IR4 were sampled monthly, and MQ2, BR1, BR2, IR1, IR2, and IR3 were sampled twice per month.

The four sub-regions included in the study have watersheds that vary in terms of land-use (Sigua & Tweedale, 2003; Adkins et al., 2004; Steward et al. 2005; Gao, 2009, SFWMD, 2020). The watersheds of the central and southern Mosquito Lagoon are characterized by a high percentage of natural upland and wetland regions. The northern Banana River Lagoon watershed is characterized by a high percentage of natural upland regions along with residential and commercial uses. The watersheds of the central Banana River Lagoon and northern IRL are primarily urban/residential. The watersheds of the central IRL are primarily urban/residential but also include tributary inputs from agricultural land use.

Field Procedures –*In situ* water temperatures and salinities were measured on site with YSI or Hach/Hydrolab environmental multi-probes at the top and near the bottom of the water column. Additional water temperatures for key time periods were obtained from a USGS continuous monitoring site in the Haulover Canal near Titusville. Light transmission through the water column was measured using a Secchi disk (meters).

Water was collected for phytoplankton analyses using a vertically integrating sample tube that captured water evenly from the surface to approximately 0.2 m of the bottom. Split phytoplankton samples were preserved on site, one with Lugol's solution and the other with glutaraldehyde in 0.1 M sodium cacodylate buffer. Aliquots of water were kept on ice and processed upon return to the laboratory for analysis of picocyanobacteria densities.

Water samples for nutrient analyses were collected from 0.5 m below the surface, preserved and analyzed according to State of Florida Water Quality Standard Operating Procedures for analyses of total nitrogen (TN), total dissolved nitrogen (TNd), nitrate + nitrite (NO_x), ammonium (NH_4), total phosphorus (TP), total dissolved phosphorus (TPd), and orthophosphate (PO_4) (SJRWMD Environmental Data). For further details see Supplemental Information.

Rainfall Data - Rainfall data was obtained from the NOAA Climatological Data for Florida web site (www.ncdc.noaa.gov/IPS) for the Titusville Meteorological Station, located near site IR1.

Phytoplankton Composition and Biomass - General phytoplankton composition was determined using the Utermöhl method (Utermöhl, 1958; Badylak et al., 2004, 2012). Samples preserved in Lugol's were settled in 19-mm diameter cylindrical chambers. Phytoplankton cells were identified and counted at 400 $\times$ and 100 $\times$ with a Leica phase contrast inverted microscope. Fluorescence microscopy was used to enumerate picoplanktonic cyanobacteria at 1000 $\times$ magnification (Phlips et al., 1999). Subsamples of seawater were filtered onto 0.2- μm Nucleopore filters and mounted between a microscope slide and cover slip with immersion oil.

Cell biovolumes ($\mu\text{m}^3 \text{ cell}^{-1}$) were estimated by assigning combinations of geometric shapes to fit the characteristics of individual taxa (Smayda, 1978; Sun & Liu, 2003). Phytoplankton biomass as carbon values ($\mu\text{g carbon ml}^{-1}$) was estimated by using conversion factors for different taxonomic groups applied to biovolume estimates (Strathmann, 1967; Ahlgren, 1983; Sicko-Goad et al., 1984; Verity et al., 1992; Work et al., 2005). For further details see Supplemental Information.

For the purpose of discussion, “bloom” was defined as phytoplankton carbon values which fell within the top 20% of total phytoplankton carbon values for the three northern sub-regions of the IRL, i.e., $\geq 2 \text{ mg C L}^{-1}$. ‘Major bloom’ refers to top 10% of values, i.e. 4-8 mg C L^{-1} , and ‘intense bloom’ refers to top 5% of values, $> 8 \text{ mg C L}^{-1}$.

Bayesian Model Analyses - Spatiotemporal modeling - Multiple linear regression models accounting for both spatial and temporal autocorrelation were constructed in a Bayesian framework. All the modeling was done with the R package “spTimer,” designed for creating spatiotemporal Bayesian models (Bakar & Sahu, 2015). The package uses conjugate priors for all parameters except for ϕ and ν for spatial correlation, allowing for the use of Gibbs sampling and fast computation (Bakar & Sahu, 2015). Standard deviation for the proposal normal distribution

of the Metropolis algorithm was set as 0.02 for Autoregressive (AR) models (Bakar & Sahu, 2015; Gelman et al., 2004). Explanatory covariates included water temperatures, salinity, Secchi disk depth, MEI index, downstream influence on biomass, TN, TSN, NO_x and NH₄, TP, TSP, PO₄, and Si (for diatoms). Mean effect sizes for the covariates were determined for six phytoplankton groupings at the eight sampling sites. For further details see Supplemental Information.

Seagrass and Macroalgae Distribution and Biomass – Seagrass and macroalgae data were assessed from long-term fixed transects for determination of mean percent cover (Fig. S1; Morris et al. 2001). Data for seagrass, drift macroalgae, and the benthic macroalga *Caulerpa* spp. were collected during summer (June through August) at fixed transects from 1998-2024. Mean percent cover, taken within 1-m² quadrats, for every transect in every sampling event was calculated for each of the three parameters. Biomass of seagrass was calculated from the mean percent cover of the three canopy forming species, *Halodule wrightii*, *Syringodium filiforme*, and *Thalassia testudinum*. Biomass for drift macroalgae was calculated using a visual index method for transects (Hall et al., 2022). Biomass of *Caulerpa* was calculated using a linear regression model between mean cover and dry weight (Banquero, 2026). For further details see Supplemental Information.

Basic Statistical Methods – Basic statistical procedures (i.e., determination of mean values, standard deviations) were carried out using SAS v9.2 (SAS Institute, Cary, North Carolina, USA) or R (R Core Team, 2020).

RESULTS

Field and Climate Parameters

Surface water temperatures mostly ranged from lows near 15°C in the winter to near 30°C in the summer (Fig. 2A). Winter low temperatures were several degrees higher at the southernmost sampling site (IR4) than in the northern regions of the study. The winters of 2009/10 and 2010/11 had the lowest water temperatures over the 1997-2024 study period, with temperatures near sites MQ2 and IR1 as low as 3.5°C and 6°C (Fig. 2B).

Annual rainfall levels measured at the meteorological station in Titusville (near site IR1) ranged from 100 to 160 cm (Fig. 3). The average annual rainfall over the study period was 133 cm/year. The study period was characterized by ten time periods when hurricanes/tropical storms

impacted IRL with high winds and rainfall (Fig. 3): The Multivariate ENSO Index (Version 2) of El Niño and La Niña periods roughly followed trends in rainfall, with mostly higher annual rainfall levels during El Niño conditions than during La Niña conditions (Fig. 3).

Temporal trends in salinity reflected the major trends in rainfall, with overall declines during mostly above average rainfall years, versus overall increases during extended periods of below average rainfall (Fig. 4). The highest salinities during the study were observed in the southern Mosquito Lagoon (MQ2), where hypersaline conditions (i.e., salinities > 35) were common. IR 4 in the central IRL had the narrowest range of salinities (i.e. 20-35).

In the three sub-regions most susceptible to major algal blooms, i.e. Mosquito Lagoon, Banana River Lagoon and northern IRL, Secchi disk depths ranged from 0.1 to 2.7 m (Fig. 5). Secchi disk depths showed a high degree of variability between sampling dates at all sites mostly reflecting variability in tripton and phytoplankton biomass (Phlips et al. 2002). The frequency of low Secchi depths (i.e., <0.5 m) increased after 2010 at all three northern IRL sites.

Nutrient Concentrations

Temporal patterns of annual mean total nitrogen (TN) concentrations were similar at all four representative sites in the four regions of the study (Fig. 6). Annual mean concentrations started near 1.8 mg L⁻¹ at sites MQ2, IR1 and BR2 in the northern IRL, then declined to near 1.0 mg L⁻¹ by 2009. After 2009, concentrations increased to near 1.7 mg L⁻¹ by 2011 at all three sites. Following the 2011 peak, annual mean concentrations varied between 1.0 and 1.8 mg L⁻¹, with peaks in 2015-2016 and 2019 at MQ2 and IR1, and in 2018-20 at BR2. Annual mean TN concentrations at Site IR4 in the central IRL were considerably lower than at the other three sites, and generally declined from 1998 to 2000, then remained relatively stable through 2024.

Annual mean total phosphorus (TP) concentrations at sites MQ2, IR1 and BR2 started near 0.05 mg L⁻¹ in 1998, then declined to near 0.03 mg L⁻¹ at all three sites by 2009 (Fig. 6). After 2009, annual mean TP concentrations increased to 0.07 mg L⁻¹ at MQ2, and 0.10 mg L⁻¹ at IR1 and BR2 by 2011. Following 2011, annual mean TP concentration decreased to near 0.5 at all three sites by 2014, then peaked again in 2015-2016 and 2018. After 2018 annual mean TP concentrations declined at all sites. Annual mean TP concentrations at IR4 in the central IRL followed the same overall patterns as the sites in the northern sub-regions of the IRL, but at higher concentrations before 2011.

Annual mean TN/TP ratios showed the opposite trends as TN and TP concentrations, with major declines in the range of values 30-75 prior to 2011 to 15-30 after 2010 at MQ2, IR1 and BR2 (Fig. 7). By contrast, annual mean TN/TP ratios at IRL4 largely ranged between 5 and 22 through the study period, with ratios remaining below 10 after 2007.

Dissolved inorganic nitrogen (DIN) concentrations mostly ranged between non-detect at 0.01 to 0.746 mg L⁻¹ (Fig. 8). Average DIN concentrations across the four sites from 1997 – 2010 were 0.041, 0.057, 0.042, and 0.029 mg L⁻¹ while in 2011 – 2020 concentrations were 0.083, 0.086, 0.065, and 0.034 mg L⁻¹, and 2021 – 2024 concentrations were 0.015, 0.109, 0.015, and 0.026 mg L⁻¹. DIN peaks exceeding 0.07 mg L⁻¹ were observed in all regions for all the time periods selected, often associated with years of above average rainfall and hurricane activity. The peaks were dominated by elevated NH₄ concentrations.

Phytoplankton Composition and Biomass

In the Mosquito Lagoon, the phytoplankton biomass concentrations were consistently below bloom concentrations (i.e., < 2 mg carbon L⁻¹) (Fig. 9). The first major bloom in the Mosquito Lagoon was observed in 2011 at MQ2 and was dominated by picoplanktonic cyanobacteria and nanoplanktonic phytoplankton. After 2011, intense blooms were again observed in 2012, 2013 and 2015-2016 at both MQ1 and MQ2, primarily involving the brown tide species *A. lagunensis*, along with other nanoplanktonic phytoplankton. At MQ2, major blooms were again observed in 2018-2020. After 2020, major blooms were not observed in the Mosquito Lagoon. Temporal patterns of blooms in the Mosquito Lagoon are further reflected in the trends of annual mean phytoplankton biomass on an aerial basis (g carbon m⁻²) at MQ2 (Fig. 10).

In the northern IRL, multiple blooms of *P. bahamense* were observed from 1997-2010, reaching peak biomass concentrations up to 6 mg carbon L⁻¹ (Fig. 9). In 2011 a prolonged bloom of nanoplanktonic eukaryotes and picocyanobacteria was observed at both IR1 and IR2 from the spring through the fall. After 2011, major and intense blooms were observed at both sites in 2012, 2015-2016, 2018-2019 and 2020, often dominated by *A. lagunensis*, other nanoplanktonic phytoplankton, and sometimes the dinoflagellate *P. bahamense* at IR2. Temporal patterns of blooms in the northern IRL are further reflected in the trends of annual mean phytoplankton biomass on an aerial basis (g carbon m⁻²) at IR1 (Fig. 10).

In the central IRL at IR3 near Melbourne, intense *A. lagunensis* blooms were briefly observed in 2016 and 2018, after which peak biomass concentrations declined and were dominated by dinoflagellates, including *P. bahamense* and *Akashiwo sanguinea* (Fig. 9). In the central IRL near Sebastian (IR4) phytoplankton biomass was predominantly below bloom concentrations, except briefly in 2016 and 2018, as further reflected in the trends of annual mean phytoplankton biomass on an aerial basis (g carbon m^{-2}) at IR4 (Fig. 10).

In the Banana River Lagoon, the phytoplankton time series for BR1 in the northern region began in 2006, and for BR2 in the central region, extended back to 1997 (Fig. 9). From 1997 to 2010, the dominant bloom-forming phytoplankton species in both regions was *P. bahamense*, reaching major biomass peaks up to $6 \text{ mg carbon L}^{-1}$. In 2011, a protracted bloom of nanoplanktonic phytoplankton and picocyanobacteria species was observed at BR1 and BR2 from March through October. After a period of relatively lower phytoplankton biomass and nutrient concentrations in 2012 and 2013, major blooms of diatoms were observed at BR2 in late 2014, after which intense blooms of *A. lagunensis* and other nanoplanktonic phytoplankton were observed at both BR1 and BR2 in 2016 and 2018-2020, reaching intense biomass concentrations up to $30 \text{ mg carbon L}^{-1}$. Temporal patterns of blooms in the Banana River Lagoon sub-region are further reflected in the temporal trends of annual mean phytoplankton biomass on an aerial basis (g carbon m^{-2}) at BR2 (Fig. 10).

From a broad compositional perspective, the three sub-regions of the northern IRL shared a fundamental shift toward dominance of pico- and nano-phytoplankton (i.e., $0.5\text{-}20 \mu\text{m}$) over micro-phytoplankton (i.e., $>20 \mu\text{m}$) from 2011 to 2020 (Table 1). Mean pico- and nano-phytoplankton biomass levels during the latter years were up to 20-40 times higher than in the pre-2011 period. By contrast, micro-phytoplankton biomass levels in the 2011-2020 period were similar to or only up to 3 times higher than in the pre-2011 period. At Site IR4 in the central IRL, pico-/nano-phytoplankton biomass levels were mostly similar to micro-phytoplankton levels, except in 2011 and 2015-20.

Bayesian Model Analyses

The mean effect sizes of five physical-chemical parameters (i.e., water temperatures, salinity, Secchi disk depth, MEI index, and downstream influence on biomass) and seven nutrient parameters (TN, TNd, NO_x and NH_4 , TP, TPd, PO_4 , and Si for diatoms) were determined for six phytoplankton groupings.

279 **A) *A. lagunensis*/nanoplanktonic phytoplankton** – Mean effect sizes for water temperature and
280 salinity were only significant for salinity at MQ1 and IR1, both positive (Fig. 11). Mean effect
281 sizes for Secchi disk depth were uniformly negative at all eight sites but not significant. The
282 mean effect sizes for downstream influence were positive for IR2 on IR3 and IR3 on IR4.

283 Among the nutrient parameters, the largest mean effect sizes were positive for TN at all
284 eight sites (Fig. 12). Conversely, the effect sizes were negative for TNd, except at MQ1. There
285 were positive effects for TPd at all sites except IR4, and for PO₄ at BR1 and IR3.

286 **B) Cyanobacteria** – Mean effect sizes were positive for water temperature at six of eight sites
287 (Fig. 11). Secchi disk depth effect sizes were negative at all eight sites, but none were significant.
288 The mean effect sizes for downstream influence were positive for IR2 on IR3 and IR3 on IR4.

289 The dominant mean effect sizes among nutrient parameters were positive for TN at six of
290 eight sites (Fig. 12). The exception at BR2 is noteworthy considering the positive effect of TP,
291 suggesting that there are some regional differences in availability of nitrogen and phosphorus for
292 cyanobacteria.

293 **C) Diatoms** – Mean effect sizes varied widely between sites for diatoms. For the physical-
294 chemical parameters only a few sites showed significant positive mean effect sizes for water
295 temperature, salinity or MEI (Fig. 11). The largest negative effect was for salinity at IR4, but not
296 significant. The mean effect size for downstream influence was positive for IR3 on IR4.

297 In terms of nutrient parameters, two of the largest positive mean effect sizes were
298 associated with TN and NH₄ concentrations at IR4 (Fig. 12). Two other positive effects sizes
299 were for TP and PO₄ at IR1.

300 **D) Dinoflagellates** – Water temperature had significant positive mean effect sizes for
301 dinoflagellate biomass at all eight sites (Fig. 11). For BR2 and IR2, salinity had a modest
302 positive effect. The mean effect sizes for downstream influence were positive for IR2 on IR3 and
303 IR3 on IR4.

304 TN had significant positive effect sizes for dinoflagellate biomass at BR2, IR1 and IR2,
305 while TNd had negative effect sizes at BR2 and IR2 (Fig. 12). TNd, NO_x and NH₄ had negative
306 effect sizes at most sites except IR4. NH₄ concentrations had negative effect sizes for six of eight
307 sites except MQ1 And IR4.

E) *P. bahamense* – Water temperature had positive mean effect sizes for *P. bahamense* biomass at six of eight sites (Fig. 11). At three sites (MQ1, MQ2 and IR4) salinity had negative effect sizes on biomass. The mean effect size for downstream influence was positive for IR3 on IR4.

In terms of nutrients, the mean effect sizes of TN were positive for MQ2 and IR2, and negative for TNd at BR2, IR1 and IR2. TP had a positive effect size at IR3 (Fig. 12).

F) Total phytoplankton biomass – Significant effect sizes for physical-chemical parameters were limited to positive effects of water temperature at Sites MQ2, BR2, IR1 and IR4, along with positive effects of salinity at MQ1 and IR1 (Fig. 11). The mean effect sizes for downstream influence were positive for IR2 on IR3 and IR3 on IR4.

The strongest positive effect sizes of nutrient parameters on total phytoplankton biomass involved TN at all sites except IR4, but negative effect sizes for TNd at all sites except MQ1 and IR4 (Fig. 12). There were also moderate negative effect sizes of NO_x at Sites MQ1, BR1 and IR2, and for NH₄ at Sites MQ1, BR1, IR1 and IR1. There were positive effect sizes of TP at Sites BR1, BR2, IR1 and IR3, and positive effect sizes for TPd at MQ1, IR1 and IR2.

Seagrass and Macroalgae Distribution and Biomass

Changes in the amount of seagrass biomass were observed in all four sub-regions of the study (Fig. 10). In the southern Mosquito Lagoon, annual mean summer biomass varied around 5 g carbon m⁻² from 1998 to 2014, then declined steadily to negligible levels in 2020. Biomass levels surged back in 2021 to near 5 g carbon m⁻² by 2024. In the Banana River Lagoon, annual mean summer biomass varied between 5-9 g carbon m⁻² from 1998 to 2010, then declined dramatically to near zero in 2012. After 2012 biomass levels remained very low until a mild resurgence in 2024. In the northern IRL, annual mean summer biomass varied around 5 g carbon m⁻² from 1998 to 2014, then declined to negligible levels from 2016 to 2023, then increased in 2024. In the central IRL, seagrass biomass levels varied from 3-7.5 g carbon m⁻² through 2010, then declined to less than 1 g carbon m⁻² through the end of the study period.

Annual mean summer drift macroalgae biomass in the southern Mosquito Lagoon varied between near zero to 2.5 g carbon m⁻² from 1998 to 2010 (Fig. 10). After 2010, drift macroalgae biomass levels remained low and never exceeded 1 g carbon m⁻² until 2024, when levels reached 2.5 g carbon m⁻². In the Banana River Lagoon, biomass of drift macroalga varied from negligible to 4 g carbon m⁻² from 1998 to 2015, then declined to zero until 2021 when there was a mild resurgence to around 1 g carbon m⁻². In the northern IRL, drift macroalgae biomass was higher

than in the other two sub-regions, frequently in excess of 3 g carbon m⁻² until 2016 when peak levels were consistently below 2.5 g carbon m⁻². In all three northern sub-regions, temporal trends of annual summer mean drift macroalgal biomass often showed the opposite trend as annual mean phytoplankton biomass. In the central IRL drift algae biomass stayed between 2-4 g carbon m⁻² through 2010, then declined to near zero in 2011-13. After 2013, biomass levels increased to levels above 1 g carbon m⁻², with peaks up to 5 g carbon m⁻².

The benthic macroalga *Caulerpa* spp. (predominantly *C. prolifera*) was largely absent in the southern Mosquito Lagoon throughout the study period (2006 to 2024) (Fig. 10). In the Banana River Lagoon, annual mean summer biomass of *Caulerpa* spp. was negligible from 2006 to 2015 except for two peaks in 2007 and 2019 of 5 and 2 g carbon m⁻². After 2015, biomass of *Caulerpa* spp. increased with multiple peaks in excess of 20 g carbon m⁻² after 2019. In the northern IRL sub-region, biomass of *Caulerpa* spp. was largely negligible biomass from 2006 to 2018 except for four moderate peaks in 2007, 2009, 2016 and 2018. After 2018, there were four major peaks in excess of 15 g carbon m⁻². In the central IRL *Caulerpa* summer biomass levels ranged between 2-9 g carbon m⁻², then dropped to negligible levels from 2011-2014. After 2017 biomass levels increased dramatically with multiple peaks above 20 g carbon m⁻².

DISCUSSION

The 28-year record of phytoplankton, seagrass, drift macroalgae, the benthic macroalga *Caulerpa* spp. and environmental data for the northern half of the Indian River Lagoon (IRL) ecosystem provides an opportunity to examine the driving factors for the observed spatial and temporal shifts in their composition and biomass of these primary producer communities. The relationships between the communities play major roles in defining the structure and function of coastal ecosystems (Harlin, 1993; Valiella et al., 1997; Duarte et al., 2006; Burkholder et al., 2007). Historically, seagrass communities have been dominant benthic habitat features of the IRL, and major contributors to primary production (Thompson, 1978; Virnstein, 1995; Steward et al., 2005; Morris et al., 2022). The importance of seagrasses is manifested by their consistently high summer biomass levels during the first 13 years of our study in all four sub-regions of the northern half of the IRL (Fig. 10). Over the same time period, drift macroalgae and the benthic macroalga *Caulerpa* spp. were also important primary producers in all of the study regions, although their biomass levels varied by region, and *Caulerpa* spp. was negligible in the Mosquito

Lagoon. Mean annual phytoplankton biomass levels during the first 13 years of the study were consistently between 0.5-2 g carbon m⁻² in the northern IRL (IR1) and Banana River (BR2) (Fig. 10), with periodic bloom concentrations up to 6 g carbon L⁻¹ (Fig. 9). By contrast, mean biomass levels in the Mosquito Lagoon and central IRL were below 0.5 g carbon m⁻². The potential for phytoplankton blooms in the former two regions is in part attributable to long water residence times (i.e., E₅₀ turnover rates > 75 days, up to > 200 days) (Smith, 1993; Sheng & Davis, 2003; Steward et al., 2005), which provide adequate time for biomass to reach bloom levels, even at moderate phytoplankton growth rates (e.g., 0.1-0.5 d⁻¹) (Stolte & Garcés, 2006).

The importance of water residence time in the potential for blooms in the IRL is highlighted by the general absence of autochthonous blooms in the central IRL, despite regional inflows of nutrient-rich water (e.g., Sebastian River) from watersheds characterized by significant agricultural land uses (Sigua & Tweedale, 2003; Gao, 2009). Tidal water mixing with the Atlantic Ocean via the nearby Sebastian Inlet shortens water residence times (e.g., < 14 days), lowers nutrient concentrations, and dilutes phytoplankton biomass in the central IRL, all of which limit the potential for autochthonous blooms (Phlips et al., 2010). The absence of blooms observed in the Mosquito Lagoon up to 2011, despite long water residence times, was likely related to two factors, 1) the high percentage of marginally developed lands in the local watersheds (Sigua & Tweedale, 2003; Gao, 2009), as indicated by the low TP levels compared to the other three sub-regions, and 2) the very shallow mean depth in the lagoon (0.9 m), which increases the effects of competition for nutrients between phytoplankton and macrophyte communities (Viaroli et al., 2008; McGlathery et al., 2009; Wang et al., 20200).

Following the first thirteen years of the study there were two major regime shifts in the composition and biomass of phytoplankton, seagrass and macroalgae in the four sub-regions of the northern half of IRL (Fig. 13). The drivers of the shifts can be viewed in the context of changes in several environmental parameters over the study period, including extremes in temperature, changes in light availability in the water column, rainfall patterns, hurricanes, shifts in nutrient sources and concentrations, and changes in the interactions between the major primary producer communities.

Regime Shift 1, 2011– 2020: A Period of Intense Phytoplankton Blooms

In 2011, annual average phytoplankton biomass in the water column increased by 3 to 4.7-fold higher than the average for the previous thirteen-year period, in the Mosquito Lagoon

(MQ2), northern IRL (IR1), Banana River Lagoon (BR2), but only 1-fold higher in the central IRL (IR4). Annual average TN concentrations increased by 0.6 to 0.8-fold and average TP concentrations increased by 2.7 to 4.5-fold from 2009 to 2011 at the latter three sites, while TN increased by 0.5-fold and TP increased by 0.8-fold at IR4. The disproportionate increases in TP relative to TN resulted in an extended period of lower TN/TP ratios after 2009. The consistent decline in TN/TP ratios suggests an increase in the potential for nitrogen limitation of peak phytoplankton biomass potential. The 2009 to 2011 transition period was also associated with major losses in summer biomass of macrophytes, including 5, 33, 52 and 65% reductions in seagrass biomass, and 41, 75, 90 and 95% reductions in drift macroalgae biomass, in the Mosquito Lagoon, northern IRL, Banana River Lagoon and central IRL, respectively. In 2011, *Caulerpa* biomass was largely negligible in all four regions. These observations raise important questions about the drivers of the increases in nutrients that supported the 2011 phytoplankton blooms, and widespread losses in macrophyte biomass.

The displacement of benthic primary producer communities by phytoplankton in ecosystems in advanced stages of eutrophication is a growing concern in many coastal ecosystems around the world (Burkholder et al., 2007; Schmidt et al., 2012; Malone & Newton, 2020; Cui et al., 2021; Shayka & Allgeier, 2025). In the northern IRL sub-region, the rise in intensity and duration of phytoplankton blooms in 2011 was sudden and not related to a gradual increase in trophic state. Prior to 2011, the highest nutrient concentrations and bloom intensities were mostly associated with periods of elevated rainfall levels, which result in higher external nutrient loads (Atkins et al. 2004; Steward & Green, 2007; Gao, 2009; Philips et al., 2010, 2020). However, the large increases in nutrient concentrations in the 2009-2011 period were associated with a period of below average rainfall levels, suggesting a change in the sources of nutrients within the region favoring phytoplankton (Fig. 13). One of the drivers of the change appears to be the exceptionally low winter temperatures during 2009-2011. During the first eleven years of the study period (1997-2009) winter water temperatures in the northern sub-regions of the IRL were primarily confined to lows above 13°C, which has been used as a definer of sub-tropical aquatic ecosystems (Neilson, 1995). The sub-tropical climate along the central east coast of Florida provides conditions suitable for the survival of a wide range of temperate, subtropical, and tropical flora and fauna (Swain et al., 1995). In the winter of 2009/10 minimum water temperatures were near or below 5°C for 14 days, and air temperatures were as low as -4°C, and

below freezing for nine days in January (Boucek & Rehage, 2016; Stevens et al., 2016). Similarly, in the winter of 2010/11 water temperatures dropped to near 5°C, and air temperatures were as low as -2.8°C and below freezing for nine days in December 2010 (Boucek & Rehage, 2016; Stevens et al., 2016). Based on these low temperatures, and their long duration, 2010 was classified as a once-in-eighty-year cold event (Boucek & Rehage, 2014). The exceptionally low temperatures likely resulted in stress on marine subtropical and tropical flora and fauna in the region (Boucek et al. 2016), such as the observed mass mortalities of warm-water fish (Stevens et al., 2016).

In the terrestrial domain, recent studies of low temperature effects on mangroves in Florida have shown that prolonged below freezing air temperatures can result in damage, such as defoliation (Ross et al., 2009; Liu et al., 2014; Peereman et al., 2021; Kang et al., 2024). Mangroves are major features of shorelines throughout all four sub-regions of the northern IRL. The aforementioned observations, and evidence from other studies of the impacts of cold temperature events on subtropical and tropical ecosystems (Boucek & Rehage, 2014; Boucek et al., 2016), indicate that the low air and water temperatures experienced in the IRL in 2010 contributed to the production of dead and decaying faunal and floral biomass in the lagoons and their watersheds. Remineralization of nutrients from decaying biomass was likely one of the sources of the observed increases in TN and TP in 2011, which in turn provided fuel for the protracted major phytoplankton bloom of 2011 (Fig. 13). The disproportionately higher increases of TP than TN from 2009 to 2011 may in part reflect the higher rates of remineralization of phosphorus than nitrogen, as reported for other ecosystems (Garber, 1984; Flynn, 2008; Zhang et al., 2017; Lin et al., 2024). The importance of nutrient re-cycling and remineralization in the development and maintenance of phytoplankton blooms has been highlighted in a number of studies (Glibert, 2017; Jiang et al., 2019; Li et al., 2021; Xu et al., 2021; Xue et al., 2021; Chi et al., 2024).

After 2011, the Mosquito Lagoon, Banana River Lagoon and northern IRL were subject to an additional nine years of recurring intense phytoplankton blooms, often dominated by the brown tide HAB species *Aureoumbra lagunensis* and other small nanoplanktonic phytoplankton. Unlike the 2011 bloom period, which was associated with below average rainfall conditions, the most protracted and intense blooms after 2011 were associated with periods of mostly above average rainfall and accompanied elevated nitrogen concentrations. Overall, annual mean

monthly phytoplankton biomass levels in the 2011-2020 period were much higher than before 2011 in all three sub-regions. Peak phytoplankton biomass concentrations exceeded that encountered before 2011 by up to five-fold (i.e., 30 mg carbon L⁻¹ versus 6 mg carbon L⁻¹). In part, the differences in peak biomass levels are attributable to the observed increase in nutrient concentrations, but another factor is the low phosphorus quota for optimal growth of *Aureoumbra lagunensis* (i.e., 2 fmoles cell⁻¹) (Liu et al., 2001; Sun et al., 2012). This means that *A. lagunensis* can generate higher levels of carbon biomass relative to cellular phosphorus concentrations than many other bloom species. Temporal patterns in the dynamics of blooms generally mirrored patterns in TN concentrations, reinforcing the importance of nitrogen as a driving factor for defining peak phytoplankton biomass during the 2011-2020 period. The latter hypothesis is supported by the results of the Bayesian analyses, which show large significant positive effect sizes of TN on phytoplankton biomass at all sites in the study except IRL4.

The intensity and long duration of phytoplankton blooms in IRL during 2011-2020 regime shift was consequential in terms of light availability for seagrass communities, which remained severely depressed from 2016 until 2022 (Morris et al., 2022). In many shallow aquatic ecosystems, competition for light between phytoplankton and benthic macrophytes has been shown to impact biomass and distribution of benthic primary producer communities (Smith et al., 1988; Onuf, 1996; Pederson & Borum 1996; Valiela et al., 1997; Kendrick et al., 2019; Sfrisco et al., 2025). In the northern IRL the causal relationship between the intense phytoplankton blooms and declines in seagrass and macroalgal biomass is supported by data on light attenuation and light requirements for the two groups. For example, the blooms of 2011 resulted in very low light transmission in the water column from the spring through the winter of 2011/12: i.e., monthly Secchi disk depths from 0.3-0.5 m, 0.4-0.6 m and 0.2 – 0.7 m, in the Mosquito Lagoon, northern IRL and Banana River Lagoon, respectively. Since Secchi depths roughly represent the depth of 10-15% of surface light transmission, the latter ranges fall within a category that would limit net growth of seagrasses to the very shallowest nearshore regions, given that seagrasses typically require 10-25% of surface irradiance to sustain net biomass increases (Duarte, 1991; Kenworthy & Fonseca, 1996; Tomasko et al., 2001; Steward et al., 2005, 2007). The dominant seagrass species in the northern IRL is *Halodule wrightii* (Morris et al., 2021), which has been reported to have a minimum light requirement between 18-27% of surface irradiance (Dennison, 1987; Dunton, 1994; Burd & Dunton, 2001; Lee et al., 2007;

Choice et al., 2014; Lapointe et al., 2020; Morris et al., 2021). The latter thresholds for seagrass growth indicate that low light penetration in the northern IRL and Banana River Lagoon in 2011 was a factor in the declines of seagrass and drift macroalgae biomass. By contrast, seagrass biomass in the Mosquito Lagoon in the summer of 2011 was similar to prior years possibly due to two factors, 1) phytoplankton blooms in the southern Mosquito Lagoon did not begin until June 2011 allowing for growth in the spring, and 2) mean depth in the southern Mosquito Lagoon (i.e., 0.9 m) is shallower than in the northern IRL and Banana River Lagoon (i.e., 1.9 m and 1.7 m) (Steward et al., 2005). After 2011, even more intense and persistent phytoplankton blooms magnified the issue of light limitation for seagrass, resulting in negligible biomass in all three sub-regions from 2016-2021. The issue of light limitation on biomass also applies to drift macroalgae and benthic macroalgae (Lapointe et al. 1984; Malta et al., 2005; Hanisak, 2016). Hanisak (2016) carried out light and temperature tolerance experiments on drift algae from the IRL, including the dominant species *Gracilaria tikvahiae*, and concluded that low light conditions were likely a contributor to their low abundances during periods of intense blooms in 2011-2020 (Hall et al., 2022).

The observed declines in seagrass community and macroalgal biomass in the IRL may have also contributed to the longevity of phytoplankton blooms in 2011 by reducing competition for bioavailable nutrients in the water column (Viaroli et al., 2008; McGlathery et al., 2009; Wang et al., 2020). The losses of arial coverage of seagrass communities can also increase the potential for internal loading of nutrients from the bare and disrupted sediments associated with seagrass losses, through sediment resuspension and nutrient diffusion (Fox & Trefry, 2023).

During 2011-2020 bloom period there were moderate returns of drift macroalgae, particularly during periods of reduced bloom intensity. Even more dramatically, there were major blooms of the benthic macroalgae *Caulerpa* spp. (mostly *C. prolifera*) in the Banana River Lagoon, northern IRL and central IRL, particularly after 2016. The *C. prolifera* blooms coincided with a period of negligible seagrass biomass in all three regions, indicating that the macroalgae were taking advantage of the open benthic habitat (Stafford & Bell, 2006; Tuya et al., 2013; Brewton & Lapointe, 2023; Brewton & Lapointe, 2025). The ability of *Caulerpa* spp. to proliferate even during moderate bloom concentrations of phytoplankton biomass may be related to its tolerance for low light conditions and preference for high inorganic nitrogen levels (Taplin et al., 2005; García-Sánchez et al., 2012; Brewton & Lapointe, 2023; Banquero, 2026).

The timing of *Caulerpa* blooms in the northern IRL and Banana River Lagoon coincided with periods of elevated NO_x and NH_4 and concentrations, which predominantly coincided with years of above average rainfall and hurricane activity (Fig. 8). The contrast between temporal patterns of seagrasses and macroalgae biomass highlights the ability of the latter to respond quickly to limited windows of opportunity for recovery during years of moderate phytoplankton bloom intensity, given the presence of open sediment habitat.

The Rise of Picos and Nanos

The preeminence of pico- (e.g., cyanobacteria) and nanophytoplankton (e.g., *A. lagunensis*) in the 2011-2020 bloom period, compared to the pre-2011 dominance of blooms by micro-phytoplankton (e.g., *P. bahamense*) raises questions about the drivers of the shift in cell size and composition (Fig. 13). A number of traits of *A. lagunensis* and many other pico- and nanophytoplankton may help to explain their success in the post-2010 period. One factor is the ability to effectively utilize ammonium and organic forms of nitrogen and phosphorus to grow, as well as mixotrophic species capable of obtaining nutrition phagotrophically (Berg et al., 2002; Dyhrman & Ruttenberg, 2006; DeYoe et al., 2007; Muhlstein & Villareal, 2007; Burkholder et al., 2008; Altman & Pearl, 2012; Yuan et al., 2012; Wetz et al., 2017). Research on nutrient uptake by the picocyanobacteria and nanoeukaryotes associated with the 2011 algal bloom in the northern IRL has shown significant rates of uptake of organic forms of nitrogen and phosphorus (Papacek et al., 2024). This can be a competitive advantage in environments characterized by major contributions of re-cycled nutrients to total load from multiple sources, including remineralization of dead floral and faunal biomass, senescing phytoplankton blooms, mobilization of nutrients from sediments, and other sources, such as watershed inputs, ground water intrusion, and septic tank seepage (Swarzenski et al., 2001; Atkins et al., 2004; Macintyre et al., 2004; Steward & Green, 2007; Engelsens et al., 2008; Gao, 2009; Lapointe et al., 2015; Aoki et al., 2020; Trefry & Fox, 2021, Al-Taliby et al., 2023; Lapointe et al., 2023).

There is also a common theme that large-celled phytoplankton taxa are favored during periods of high inorganic nutrient concentrations and light availability, while the larger surface area to volume ratios of small-celled species (i.e., pico- and nanoplankton) provide a competitive advantage under lower rates of nutrient supply and more limited light availability (Guislain et al. 2024; Reynolds, 2006; Sunda & Hardison, 2010). In the IRL, blooms of the large-celled dinoflagellate *P. bahamense* were generally most intense during periods of elevated rainfall,

which are associated with higher external inorganic nutrient loads (Phlips et al., 2020, 2021). By contrast, the period leading up to the major 2011 bloom was characterized by below average rainfall, but large increases in nutrient levels, in part generated by sustained recycling of nutrients available from decomposing faunal and floral biomass associated with the impacts of the record cold temperatures of 2010. Another contributor to the success of *A. lagunensis*/other nanoplankton in the post-2010 period may be related to top-down control issues. *A. lagunensis* has been shown to have comparatively low grazing loss rates (Liu & Buskey, 2000; Kang et al., 2015; Galimany et al., 2020; Sweat et al., 2021). Low grazing losses contribute to the formation and longevity of HABs (Buskey, 2008; Smayda, 2008; Sunda & Hardison, 2010).

Overall, the regime shift from warm/wet season blooms of *P. bahamense* to more intense blooms dominated by pico- and nanoplanktonic phytoplankton (e.g., *A. lagunensis*) was particularly disruptive for seagrass and macroalgae communities because it transcended seasonal boundaries, limiting the temporal windows for recovery. The latter issue is highlighted by the correlation of the greatest losses in seagrass abundances to years of the most protracted intense phytoplankton blooms (i.e., 2011, 2015/16, 2018/20).

Regime Shift 2, 2021-2024: The Return of Seagrass and Macroalgae

The second major regime shift in the composition and biomass of phytoplankton, seagrass and macroalgae in the Mosquito Lagoon, Banana River Lagoon and northern IRL occurred in 2021. Declines in annual average phytoplankton biomass and the intensity/duration of blooms (Fig. 9) were accompanied by a return of *P. bahamense* as a major bloom species in the Banana River Lagoon and northern IRL. In the Mosquito Lagoon, *A. lagunensis* and other nanoeukaryotes continued to be dominant species, but at significantly lower peak biomass (i.e., < 2 mg carbon L⁻¹). The declines in peak biomass coincided with decreases in TN and TP concentrations. By contrast, seagrass and/or macroalgae showed major increases in biomass, with regional differences.

In the Banana River Lagoon, northern IRL and central IRL subregions there were dramatic peaks in biomass of the benthic macroalga *Caulerpa* spp. in 2017-2024. Negligible recovery of seagrass communities in the three sub-regions until after 2023 contributed to the habitat available for *Caulerpa* colonization (Brewton and Lapointe, 2025). *C. prolifera* has been shown to be very proficient at expanding into available habitats and out-competing seagrasses once they reach high percentage cover (Banquero et al., 2026). *C. prolifera* has been observed in

the IRL since at least the early 1980's (Jensen & Clark, 1983; White & Snodgrass, 1990). Blooms were observed in 1986 during a decline in seagrass abundance, but the bloom was short-lived due to a proliferation of the herbivorous sea slug *Elysia*, which is known to actively graze on *Caulerpa* (White & Snodgrass, 1990).

In the Mosquito Lagoon, increases in benthic primary producers after 2022 primarily involved seagrasses (e.g., *H. wrightii*). The lack of *Caulerpa* spp. over the study period in Mosquito Lagoon may be in part related to the high benthic light intensities associated with shallow mean depths (i.e., 0.8 m), which have been reported to disfavor the colonization of *C. prolifera* (Taplin et al., 2005). Another factor contributing to the lack of *Caulerpa* colonization in the Mosquito Lagoon may have been limited benthic habitat availability. The Mosquito Lagoon was the last sub-region to reach very low seagrass coverage in 2020, and seagrass recovery began in 2022, restricting the time available establishment of *Caulerpa*. Conversely, high benthic light fluxes provide an environment suited for increases in seagrass colonization. In addition, Insalaco et al. (2026) suggest that the hurricanes of 2022 (i.e. Nicole and Ian) may have enhanced seagrass coverage by distributing seagrass fragments around the Mosquito Lagoon. A similar argument may be made about the rapid spread of *Caulerpa* spp. in other subregions of the IRL in relationship to the multiple hurricanes impacting the IRL in 2017, 2019, 2022-2024..

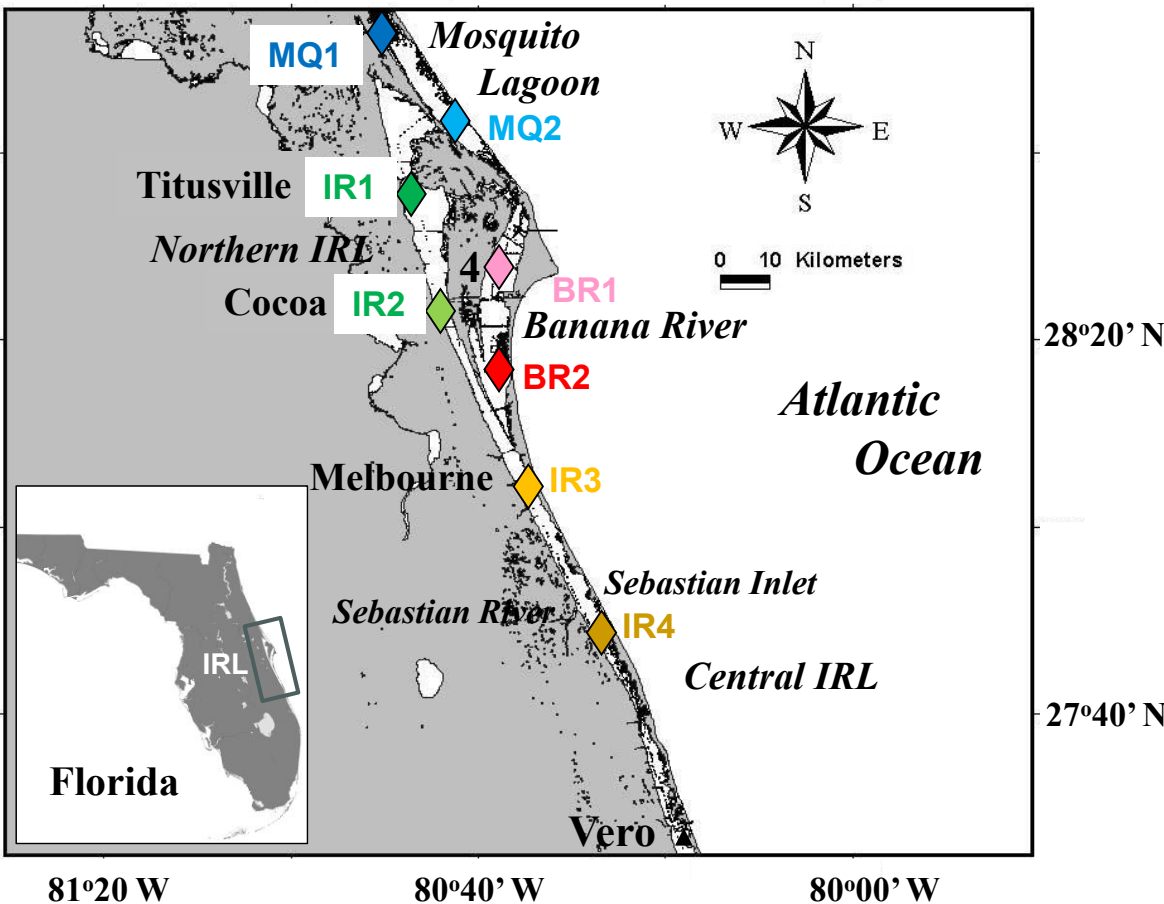
Regional differences in the colonization of open benthic habitat in IRL highlight the multi-variate nature of the drivers of competition between phytoplankton, macroalgae and seagrasses. The resurgence of benthic primary producer communities in northern IRL in the later years of the study period suggests a possible return to an alternative stable state more similar to the pre-2011 period, i.e., favoring seagrasses and macroalgae over phytoplankton biomass (Fig. 13). In the case of the prominence of *Caulerpa* spp. in the Banana River Lagoon, northern IRL and central IRL, three questions remain, 1) Do they provide the same ecosystem services as seagrasses, 2) What is the long-term sustainability of *Caulerpa* communities, and 3). Will dynamics of *Caulerpa* allow for the eventual re-establishment of robust seagrass communities (Orth et al., 2020; Parreira et al., 2021; Brewton & Lapointe, 2023, 2025). Past studies of the structure and function of *C. prolifera* in Indian River Lagoon and other regions of world provide a mixed picture. A recent study of fauna in regions of the northern IRL dominated by *C. prolifera* showed similar composition of taxa as found in regions dominated by the seagrass *Halodule wrightii*, but at lower levels of abundance, which could have cascading impacts on higher

618 trophic levels, such as fish (Brewton & Lapointe, 2025). From a broader temporal perspective,
619 uncertainties remain about the future trajectory of the *Caulerpa* spp. communities in the IRL,
620 given the previous record of similar expansions that have been suddenly cut short by outbreaks
621 of herbivorous macroinvertebrates (White & Snodgrass, 1990; Brewton & Lapointe, 2025).

622 CONCLUSION

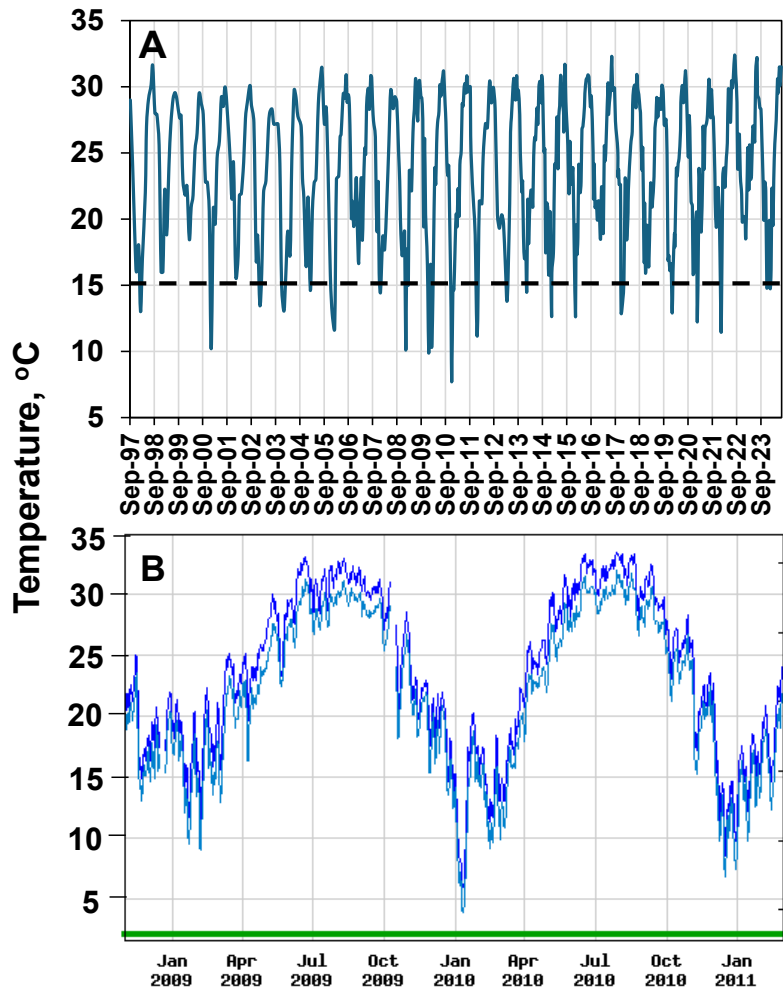
623 Results of this 28-year study of the northern IRL provide an example of how short
624 duration extreme environmental events can lead to sudden, dramatic and persistent shifts in the
625 structure and function of primary producer communities. The first shift in the IRL resulted from
626 a period of exceptionally cold winter temperatures that drove major increases in nutrient levels,
627 which precipitated a protracted ten-year period of intense HABs, that in turn helped to drive
628 dramatic losses of seagrass biomass, the historically dominant primary producer in the IRL. A
629 second regime shift occurred in the later years of the study, coinciding with the advent of
630 multiple major hurricanes, which were associated with peaks in inorganic nutrient levels and
631 widespread blooms of the benthic macroalga *Caulerpa*, that took advantage of the open benthic
632 habitat left behind by the extensive losses of seagrass communities. At the same time,
633 phytoplankton biomass levels decreased. The sequence of regime shifts highlights that even
634 short-duration extreme environmental conditions can result in major changes in the biomass and
635 composition of primary producer communities, that have cascading impacts on ecosystem
636 structure and function. Since the 20th century, there have been growing concerns about the
637 persistent increases in cultural eutrophication and global climate changes, and how these are
638 impacting primary producer communities (Glibert, 2020; Griffith & Gobler, 2020; Malone &
639 Newton, 2020; Paerl et al., 2016). Imbedded in these trends is the growing potential for extreme
640 events (Liu et al., 2019; Méndez-Tejeda & Hernández-Ayala; Wetz & Yoskowitz, 2013; Zhao &
641 Held, 2010), such as droughts, intense storms and extremes in temperature. The results of our
642 study highlight that these events can dramatically affect the structure and function of aquatic
643 ecosystems.

645 Figure 1. Sampling site map.



646

Figure 2. Surface water temperatures recorded during this study at Site IR1 (A). Daily water temperature range in the Haulover Canal from November 2008 to February 2011 at USGS continuous monitoring station (www.waterdata.usgs.gov) (B).



653 Figure 3. Rainfall totals for 12-month periods October through September, and the timing of El
 654 Niño (blue) and La Niña (pink) periods are shown as the header of the figure, based on the
 655 Multivariate ENSO Index Version 2 using JRA3Q (psl.noaa.gov/enso/mei/). The dashed line is
 656 the average annual rainfall over the study period. Periods of hurricane/tropical storms impacting
 657 the northern IRL: 1) Irene (Oct. '99), 2) Gabrielle (Sept. '01), 3) Charley (Aug. '04), Francis
 658 (Sept. '04), Jeanne (Sept. '04), 4) Tammy (Oct. '05), Wilma (Oct. '05), 5) Fay (Aug. '08), 6)
 659 Mathew (Oct. '16), Emily (Aug. '17), Irma (Sept. '17), 7) Dorian (Sept. '18), Humberto (Sept.
 660 '18), 8) Ian (Sept. '22), 9) Nicole (Nov. '22), 10) Milton (Oct. '24).

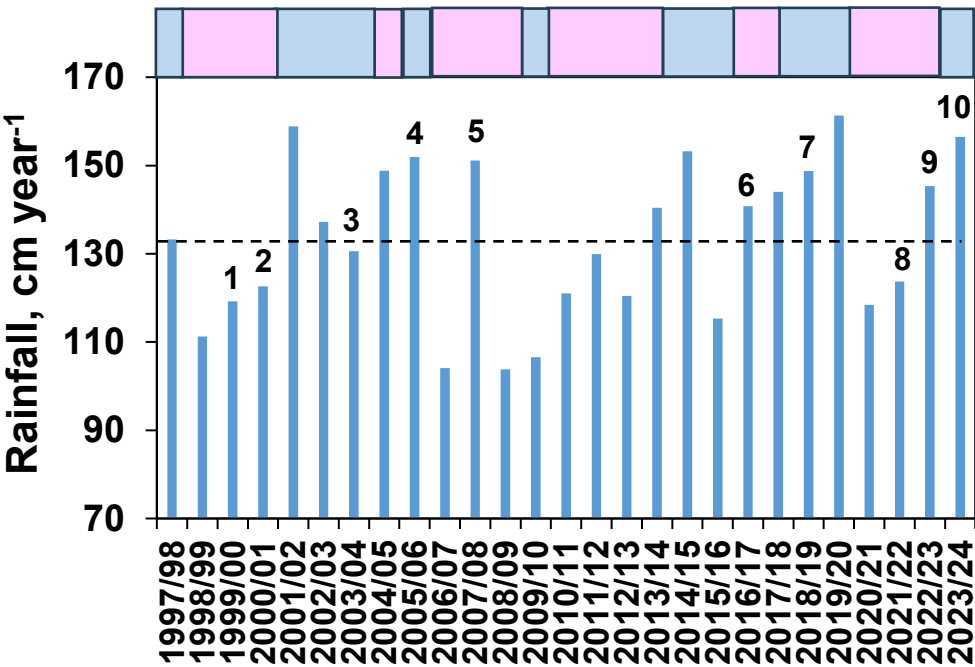
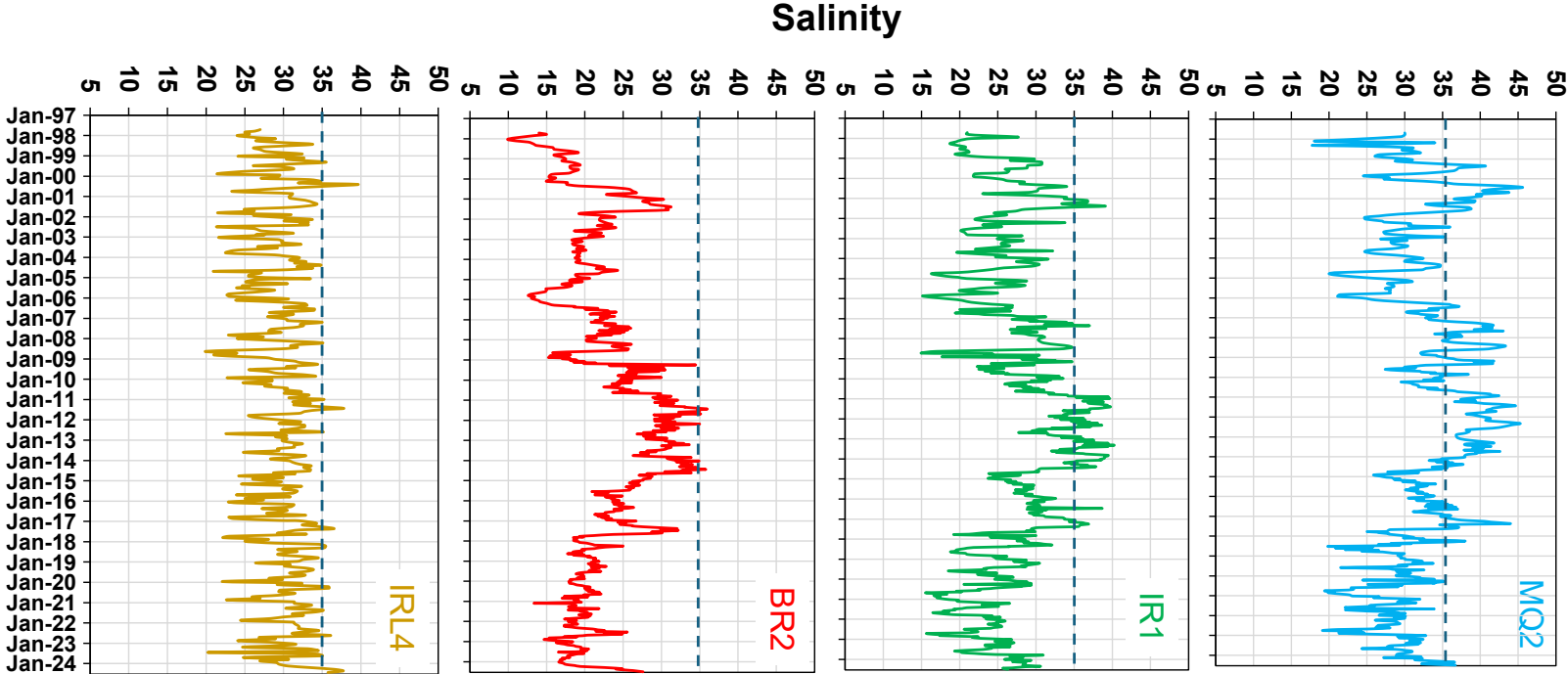
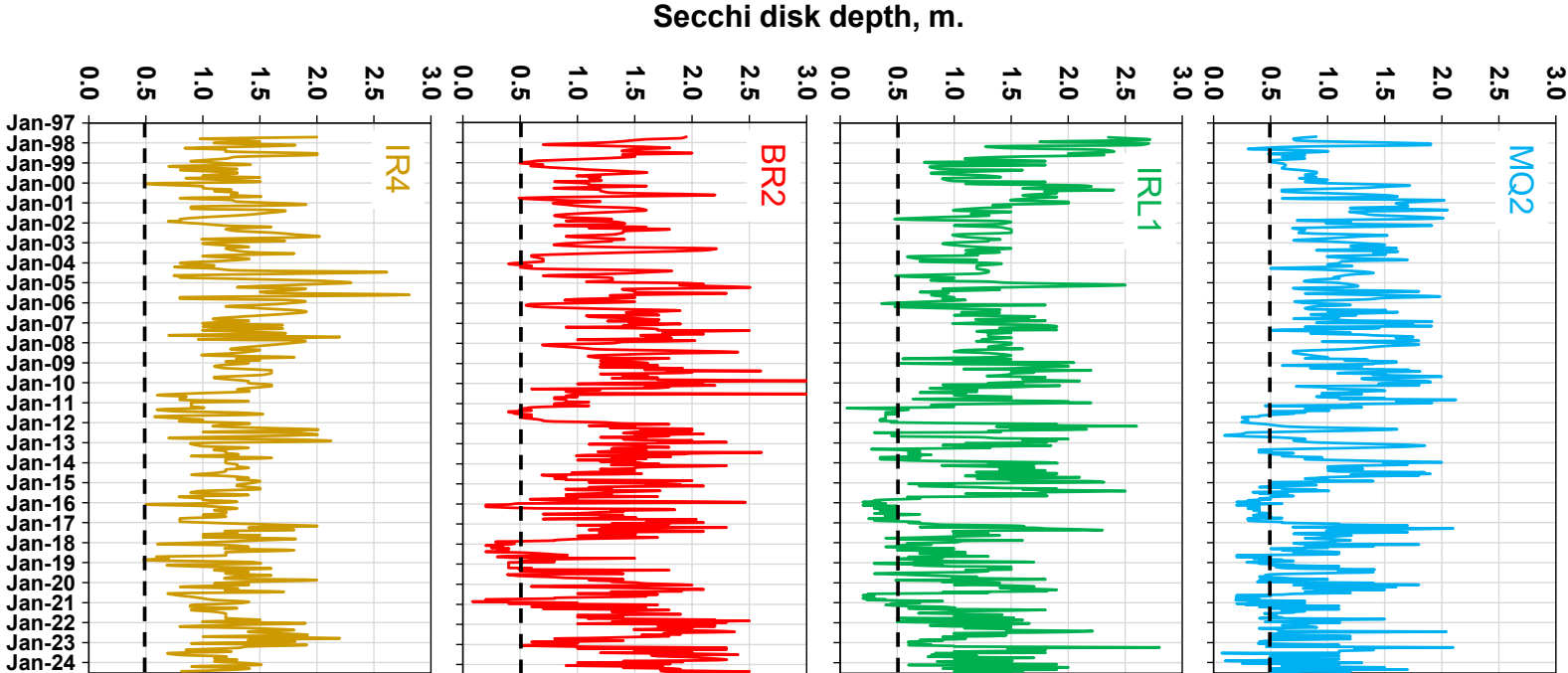


Figure 4 Salinities at four sites representative of the Mosquito Lagoon (MQ2), northern IRL (IR1), Banana River Lagoon (BR2) and Central IRL (IR4).



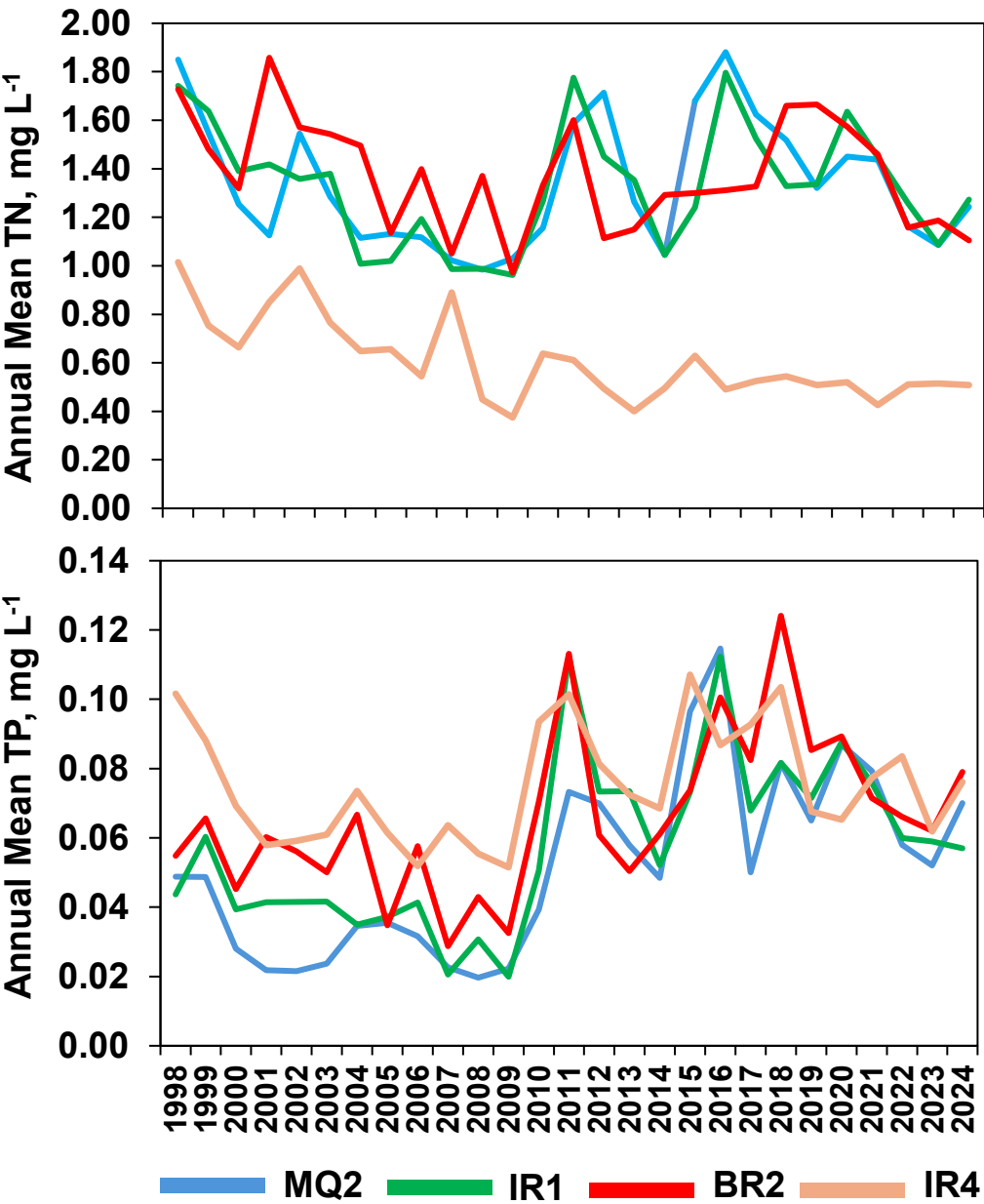
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667 Figure 5. Secchi disk depth at four sites representative of the Mosquito Lagoon (MQ2), northern
668 IRL (IRL1), Banana River Lagoon (BR2) and Central IRL (IR4).



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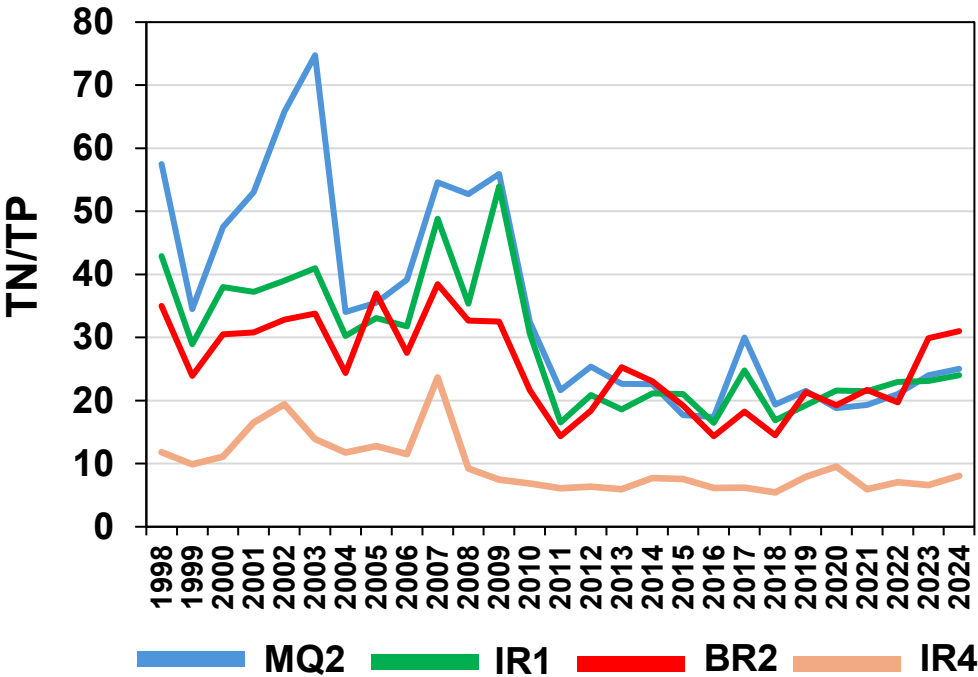
670 Figure 6. Annual mean TN (Top panel) and TP (Bottom Panel) concentrations at four
671 representative sites in the southern Mosquito Lagoon (MQ2), northern IRL (IR1), central
672 Banana River Lagoon (BR2), and central IRL (IR4).



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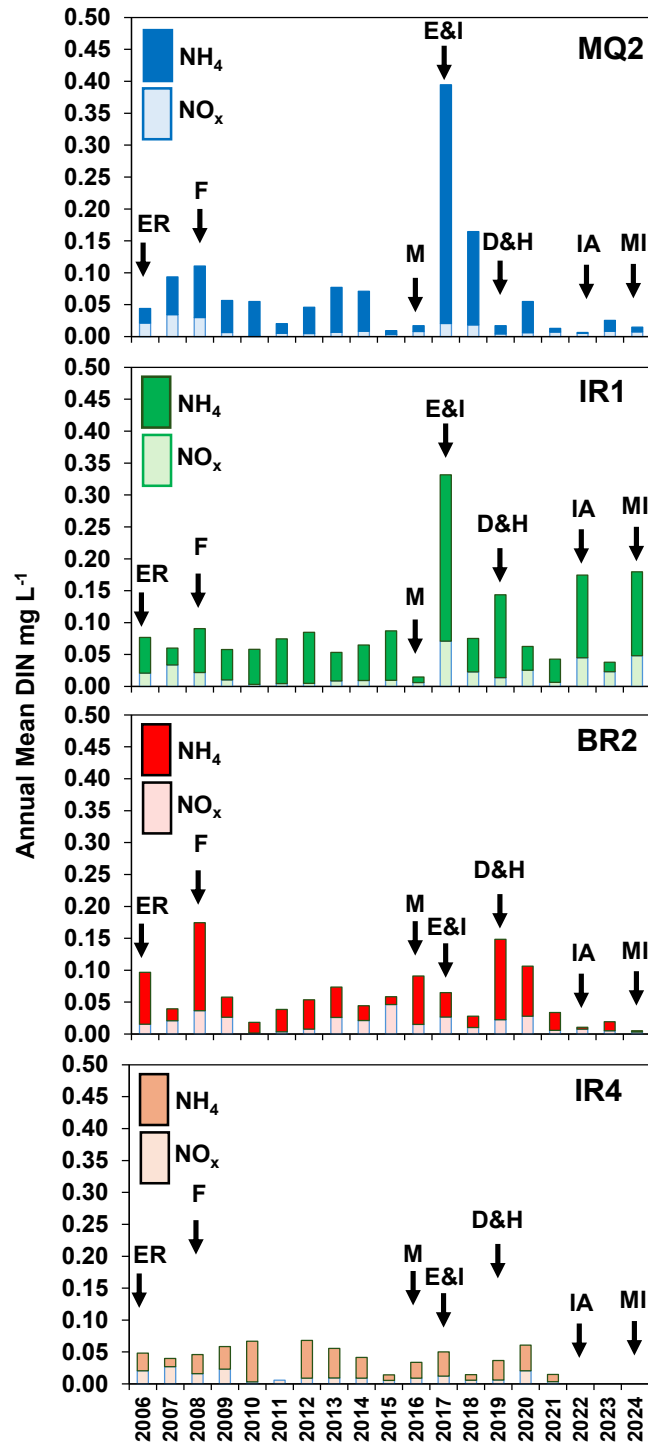
674

675 Figure 7. Annual mean TN/TP ratios at four representative sites in the southern Mosquito Lagoon
676 (MQ2), northern IRL (IR1), central Banana River Lagoon (BR2), and central IRL (IR4).



677

Figure 8. Annual mean NH_4 and NO_x concentrations at four representative sites in the Mosquito Lagoon (MQ2), N. IRL (IR1), C. Banana River Lagoon (BR2), and C. IRL (IR4). Timing of major hurricanes/tropical storms are indicated by arrows; ER – Ernesto, F – Fay, M – Mathew, E&I -Emily & Irma, D&H – Dorian & Humberto, IA – Ian, MI - Milton.



684 Figure 9. Biomass of five groupings of phytoplankton at the eight sampling sites, i.e.
685 dinoflagellates, diatoms, cyanobacteria, the raphidophyte *Aureoumbra lagunensis*, and 'other'
686 taxa. Letters associated with blooms indicate the dominant species in the bloom: A –
687 *Aureoumbra lagunensis*, Ak – *Akashiwo sanguinea*, C – picocyanobacteria, D – diatoms, N –
688 nanoeukaryote, nC – nano-cyanobacteria, P – *Pyrodinium bahamense*, Pd – Pedinophyte,

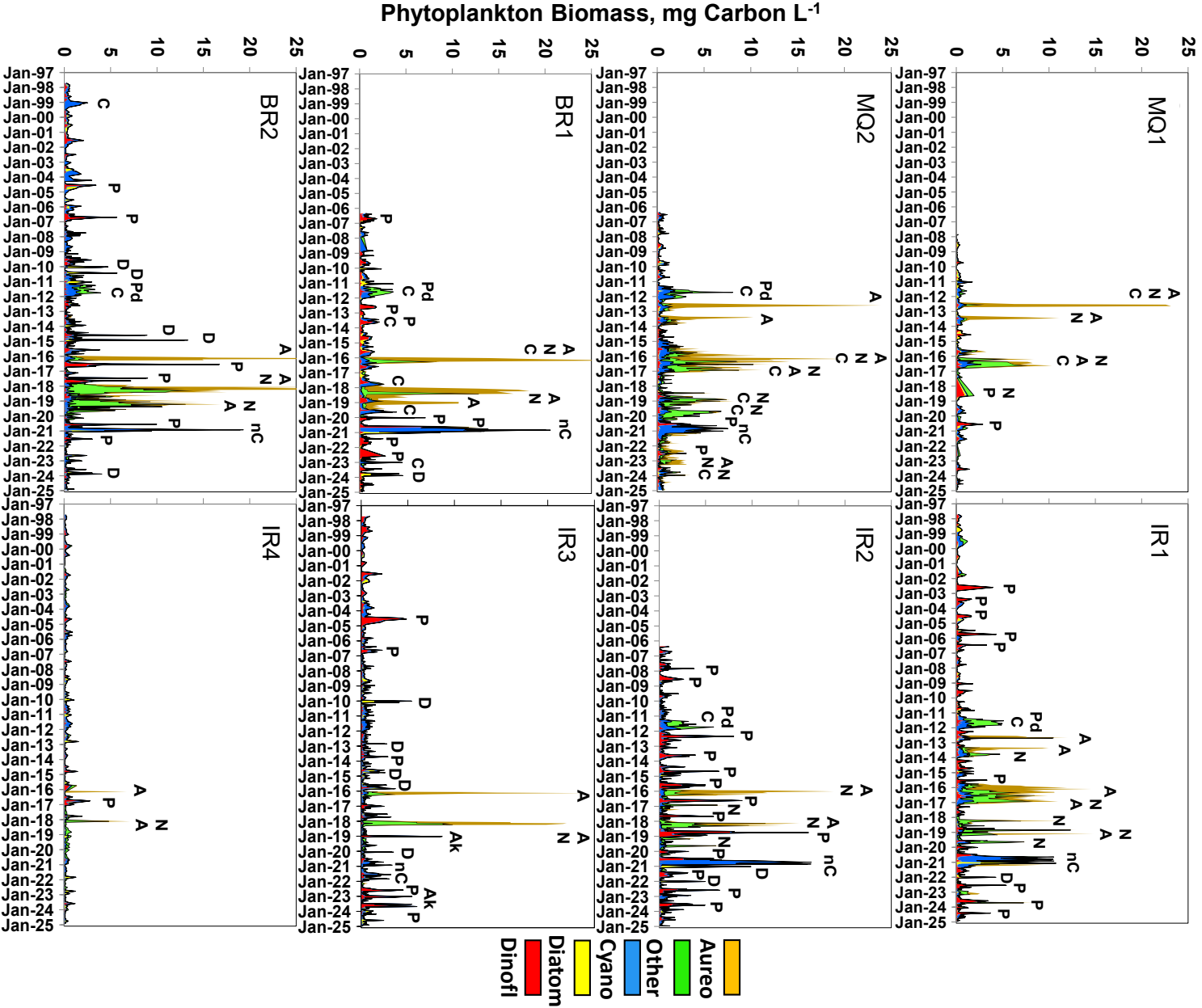


Figure 10. Mean summer carbon biomass (g m^{-2}) of seagrasses (summer survey), drift macroalgae (summer survey), the benthic macroalga *Caulerpa prolifera* (summer survey) and annual mean phytoplankton carbon biomass (g m^{-2}) for three phytoplankton bloom-prone sub-regions in the IRL ecosystem, i.e., southern Mosquito Lagoon, central Banana River and northern IRL.

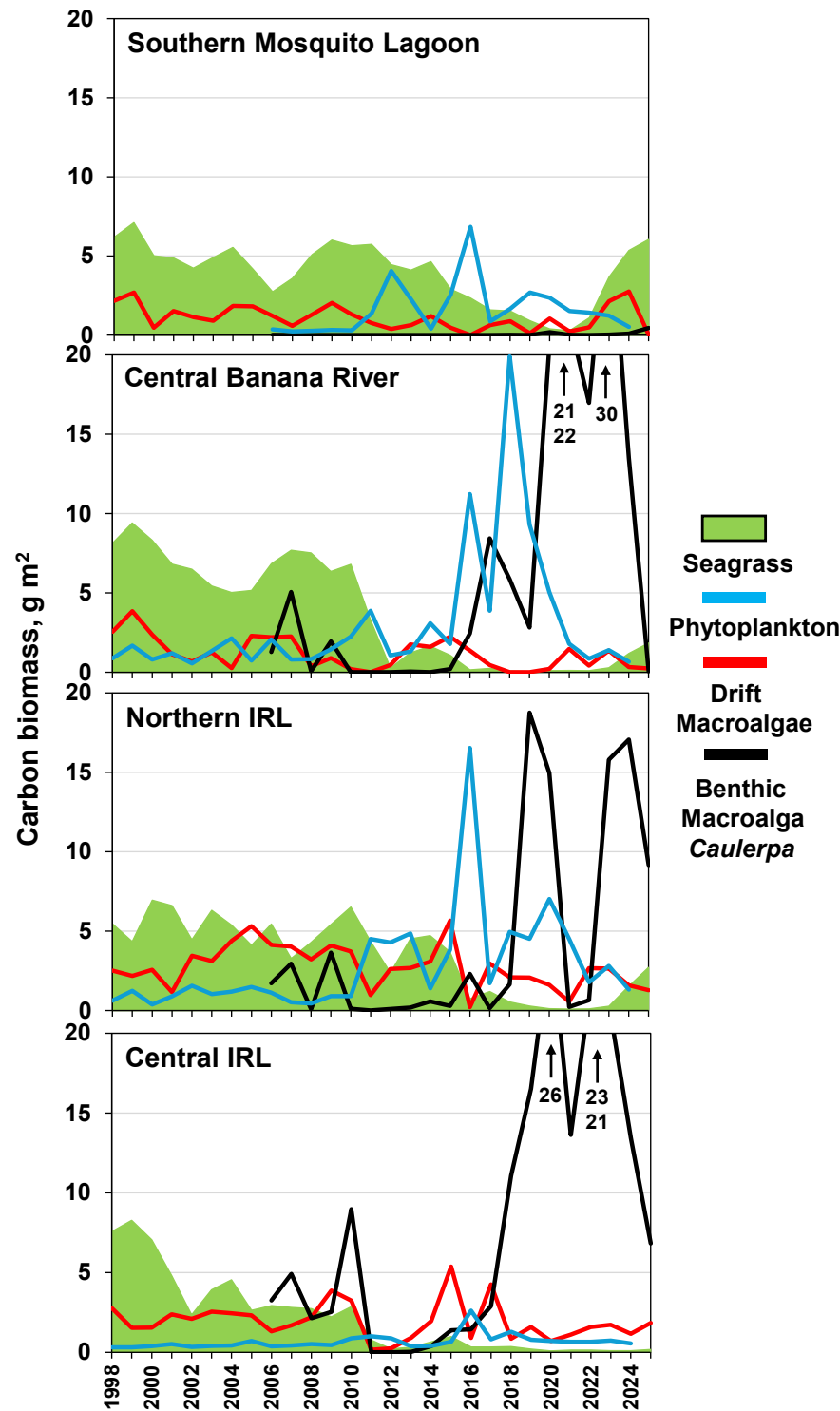


Figure 11. Mean effect sizes for physical, chemical, mei and upstream influence explanatory covariate across sites. Bar colors correspond to sites. When an asterisk is included, the 95% credible intervals did not contain zero, indicating significance.

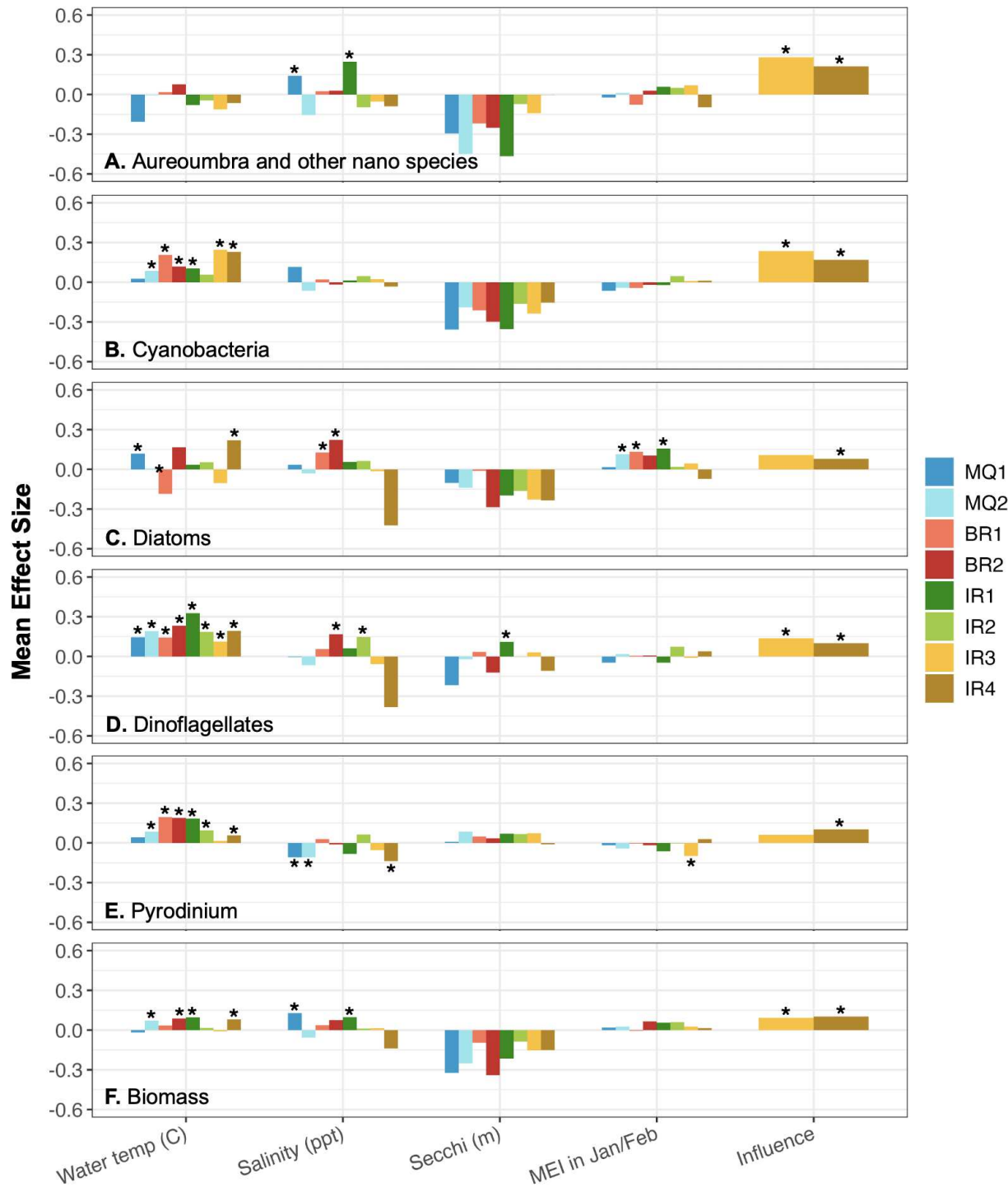


Figure 12. Mean effect sizes for nutrient explanatory covariate across sites. Bar colors correspond to sites. When an asterisk is included, the 95% credible intervals did not contain zero, indicating significance.

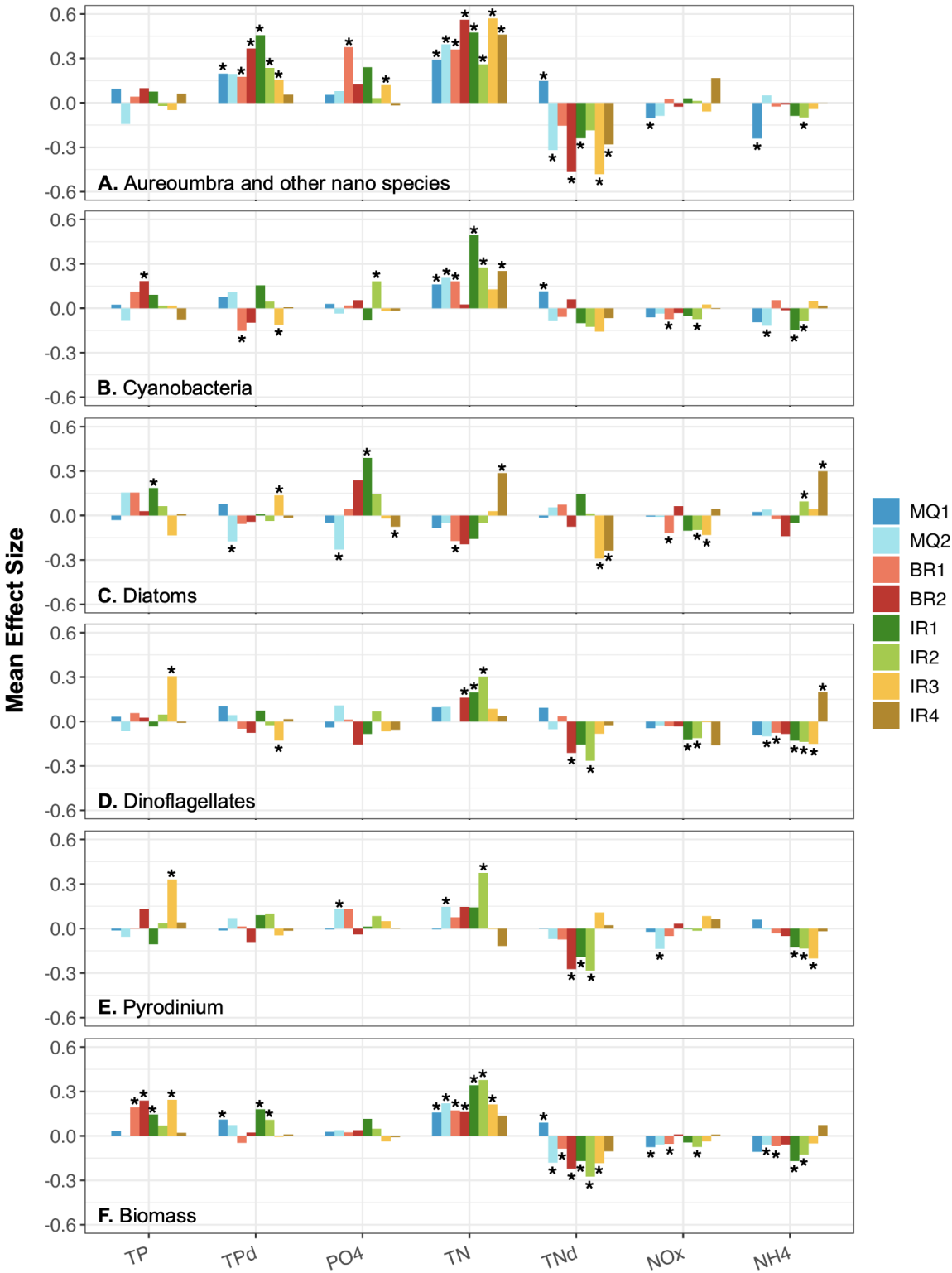


Figure 13. The schematic of the flow of external and internal nutrient sources to the three major primary producer communities in the IRL prior to the regime shift in 2011. Seagrass category includes epiphytes. The width of the arrows indicates the relative importance of the nutrient sources. Dashed arrows represent re-cycling of nutrients associated with the senescence of the three primary producer communities. Sizes of the green boxes show the approximate distribution of biomass of the primary producer communities.

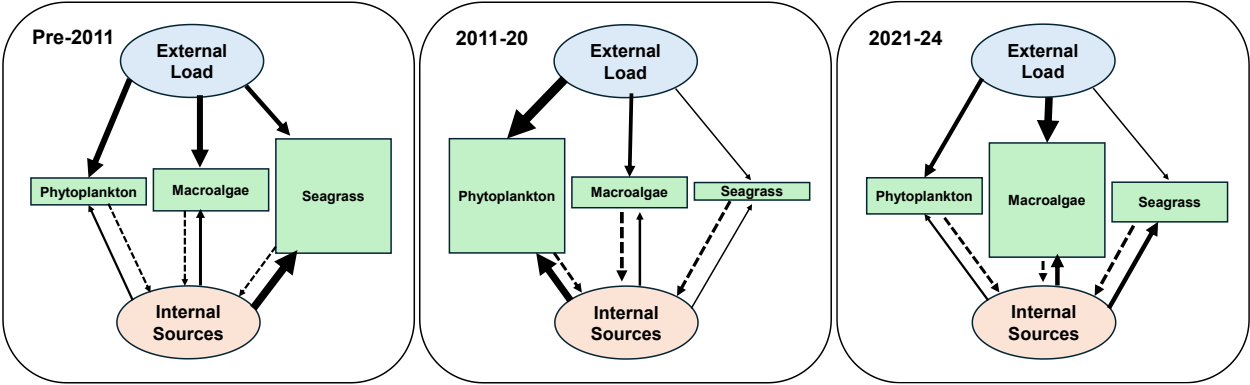


Table 1. Mean phytoplankton biomass ($\mu\text{g carbon ml}^{-1}$) for key time periods in the 28-year study period. Mean values are presented for Pico-Nano-phytoplankton (i.e., 0.5-20 μm), micro-phytoplankton (i.e., >20 μm), and total phytoplankton.

Southern Mosquito Lagoon - MQ2						
Period	Pico-Nano	<i>Std</i>	Micro	<i>Std</i>	Total	<i>Std</i>
2006-2009	0.19	0.19	0.19	0.22	0.37	0.30
2010	0.18	0.18	0.20	0.19	0.38	0.30
2011	1.58	1.96	0.12	0.15	1.70	2.01
2012	4.88	7.10	0.18	0.12	5.07	7.08
2013	2.49	2.73	0.27	0.22	2.76	2.83
2014	0.23	0.18	0.27	0.33	0.51	0.40
2015-2020	3.30	3.47	0.24	0.36	3.54	3.49
2021-2024	1.35	1.25	0.22	0.34	1.56	1.24

Northern IRL - IRL1						
Period	Pico-Nano	<i>Std</i>	Micro	<i>Std</i>	Total	<i>Std</i>
1997-2000	0.19	0.30	0.21	0.15	0.40	0.30
2001-2005	0.15	0.18	0.51	0.92	0.65	0.92
2006-2009	0.12	0.11	0.29	0.46	0.40	0.47
2010	0.14	0.11	0.34	0.44	0.48	0.52
2011	2.10	1.68	0.27	0.21	2.37	1.76
2012	1.50	2.23	0.76	1.82	2.25	3.03
2013	2.31	2.57	0.25	0.18	2.56	2.58
2014	0.18	0.13	0.55	0.56	0.74	0.56
2015-2020	3.05	3.77	0.32	0.55	3.38	3.77
2021-2024	0.79	1.59	0.70	1.38	1.48	2.07

Central Banana River - BR2						
Period	Pico-Nano	<i>Std</i>	Micro	<i>Std</i>	Total	<i>Std</i>
1997-2000	0.36	0.59	0.29	0.20	0.65	0.54
2001-2005	0.32	0.52	0.37	0.60	0.69	0.76
2006-2009	0.21	0.23	0.56	0.88	0.77	0.89
2010	0.42	0.54	0.90	1.54	1.32	1.51
2011	1.75	1.07	0.53	0.67	2.28	0.89
2012	0.19	0.14	0.44	0.40	0.63	0.43
2013	0.24	0.22	0.53	0.60	0.77	0.60
2014	0.34	0.22	1.48	2.94	1.82	3.00
2015-2020	4.14	7.53	0.91	1.96	5.05	7.43
2021-2024	0.62	2.17	0.62	1.43	1.23	2.55

Central IRL - IR4						
Period	Pico-Nano	<i>Std</i>	Micro	<i>Std</i>	Total	<i>Std</i>
1997-2000	0.10	0.07	0.13	0.15	0.23	0.19
2001-2005	0.14	0.11	0.13	0.18	0.26	0.23
2006-2009	0.13	0.10	0.10	0.12	0.23	0.17
2010	0.20	0.11	0.26	0.32	0.46	0.31
2011	0.38	0.18	0.15	0.11	0.53	0.23
2012	0.24	0.17	0.22	0.38	0.46	0.41
2013	0.12	0.05	0.08	0.06	0.20	0.10
2014	0.08	0.03	0.13	0.15	0.21	0.16
2015-2020	0.43	0.98	0.18	0.38	0.61	1.04
2021-2024	0.16	0.07	0.18	0.27	0.34	0.28

Author's Contributions

EJP: Research plan development, funding acquisition, project management, data interpretation, original manuscript drafting and editing. **SB:** Phytoplankton data curation, project management, manuscript drafting and editing. **LM:** Seagrass data curation and interpretation, manuscript drafting and editing. **LMH:** Macroalgal data curation and interpretation, manuscript drafting and editing. **SP:** Data analysis, Bayesian modeling and interpretation, manuscript editing. **BS:** Phytoplankton analyses data curation, manuscript editing. **SLC:** Chemical data curation and interpretation, manuscript editing. **LL:** Leader in field research efforts, field data curation. **NN:** Data analysis, Bayesian modeling and interpretation, manuscript editing. **LMB:** Macroalgal data curation and interpretation.

Acknowledgements

The research presented in this paper was in part funded by grants from the U.S.E.P.A. Indian River Lagoon National Estuarine Program, Sebastian, Florida, USA and the St. Johns River Water Management District, Palatka, Florida, USA. Edward Phlips, Susan Badylak, Leslie Landauer and Ben Stelling are in part supported by the USDA National Institute of Food and Agriculture, Hatch Project 1017098.

Statements and Declarations

The authors have no relevant financial or non-financial interests to disclose. The authors have no competing interests to declare that are relevant to the content of this article. All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript. The authors have no financial or proprietary interest in materials discussed in this article.

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