




Biogeochemistry of a River-Dominated Estuary Influenced by Drought and Storms

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Abstract

Increased frequency and severity of droughts, as well as growing human freshwater demands, in the Apalachicola-Chattahoochee-Flint River Basin are expected to lead to a long-term decrease in freshwater discharge to Apalachicola Bay (Florida). To date, no long-term studies have assessed how river discharge variability affects the Bay's phytoplankton community. Here a 14-year time series was used to assess the influence of hydrologic variability on the biogeochemistry and phytoplankton biomass in Apalachicola Bay. Data were collected at 10 sites in the bay along the salinity gradient and include drought and storm periods. Riverine dissolved inorganic nitrogen and phosphate inputs were correlated to river discharge, but chlorophyll *a* (Chl *a*) was similar between periods of drought and average/above-average river discharge in most of the Bay. Results suggest that the potentially negative impact of decreased riverine nutrient input on Bay phytoplankton biomass is mitigated by the nutrient buffering capacity of the estuary. Additionally, increased light availability, longer residence time, and decreased grazing pressures may allow more Chl *a* biomass to accumulate during drought. In contrast to droughts, tropical cyclones and subsequent increases in river discharge increased flushing and reduced light penetration, leading to reduced Chl *a* in the Bay. Analysis of the time series revealed that Chl *a* concentrations in the Bay do not directly mirror the effect of riverine nutrient input, which is masked by multiple interacting mechanisms (i.e., nutrient loading and retention, grazing, flushing, light penetration) that need to be considered when projecting the response of Bay Chl *a* to changes in freshwater input.

Keywords Apalachicola estuary · Drought · Storm · River discharge · Nutrients · Phytoplankton chlorophyll

Introduction

Estuarine biogeochemistry can have substantial temporal variability; therefore, long-term datasets are needed to assess trends as well as the effects of climatic and anthropogenic disturbances (Wetz and Yoskowitz 2013; Zingone et al. 2010). Variability in river discharge affects nutrient input, water residence time, and salinity gradients and thereby has

profound impacts on estuarine biology and biogeochemistry (e.g., Mallin et al. 1993; Murrell et al. 2007; Paerl et al. 2009; Wetz et al. 2011). Early studies in river-influenced estuaries suggested that phytoplankton production and/or biomass is positively correlated with river discharge, owing to the nutrients that are delivered to the estuaries (Cloern 1996; Mallin et al. 1993; Haertel et al. 1969). Other studies have shown that high phytoplankton biomass can also occur during low river discharge conditions. In Florida Bay (FL) and Baffin Bay (TX) for example, droughts have been linked to higher salinity and prevalence of phytoplankton blooms (Briceño and Boyer 2009; Wetz et al. 2017). High river discharge periods, as caused by hurricanes and tropical storms, can increase flushing rates, break down a stratified water column, reduce light availability, and reduce phytoplankton growth despite higher availability of nutrients (Paerl et al. 2009, 2014). Understanding the effects of hydrologic variability on estuary biogeochemistry and biology is critical for assessing long-term trends and for determining freshwater inflow needs in estuaries with human-controlled freshwater input (Montagna et al. 2012). This requires studies of individual

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estuaries because the effects of hydrologic variability depend on the environmental settings of the estuarine ecosystem under consideration (Wetz and Yoskowitz 2013).

In this study, a comprehensive multivariable time series is used to evaluate the influence of hydrologic variability on phytoplankton biomass and biogeochemistry in Apalachicola Bay (AB), a bar-built estuary in the northeastern Gulf of Mexico. The discharge of the Apalachicola River to AB is affected by upstream withdrawals as well as climatic changes in the southeastern USA (Huang and Spaulding 2000; Huang et al. 2004), and there is growing concern that river discharge will be much lower in the future as a result (Edmiston 2008; Light et al. 2006; Singh et al. 2017). A recent modeling study of Apalachicola-Chattahoochee-Flint (ACF) River Basin management implied that current strategies may be unable to mitigate deleterious effects of prolonged drought on AB due to limited reservoir storage (Leitman et al. 2016). The impacts of river discharge variability on the health and productivity of AB are largely unknown (Livingston 2014); therefore, it is difficult to project freshwater needs or the effects of future changes in discharge. Overall, an improved understanding is needed of the links between freshwater inflow and biogeochemical processes in AB to improve water resource planning.

In AB, attributes such as river discharge, residence time, and activity of oyster reefs all potentially modulate the impacts of climatic- and anthropogenic-induced hydrologic variability (Cloern 2001; Edmiston 2008; Kennish et al. 2014). We analyzed a 14-year dataset (2002–2015) of monthly nutrient and chlorophyll measurements collected by the Apalachicola National Estuarine Research Reserve (ANERR) to quantify spatial and interannual variability of estuarine biogeochemistry in relation to climatic and hydrologic variability. This dataset consists of measurements at 10 sites in the bay along the salinity gradient. The study period encompasses two “exceptional droughts” (National Integrated Drought Information System (NIDIS) 2017), including the 2010–2012 drought that preceded the Autumn 2012 population collapse of the economically important oyster, *Crassostrea virginica* (Camp et al. 2015; Havens et al. 2013; Pine et al. 2015). Several tropical storms also generated high river discharge to AB during the study period. These extreme events allowed an assessment of the sensitivity of the AB biology and biogeochemistry to changes in freshwater inflow. This study addresses the following questions:

1. How do temporal changes in river discharge affect the spatial distribution of biogeochemical characteristics, nutrients, and phytoplankton biomass along the estuarine gradient?
2. How do nutrients, phytoplankton biomass, and net ecosystem metabolism change during drought conditions?

3. How do major flood events affect estuarine phytoplankton biomass in space and time?

Methods

Study Site

Apalachicola Bay, Florida (Fig. 1) is a shallow, river-dominated estuary located in the northeastern Gulf of Mexico. The open water area is approximately 450 km² (Huang et al. 2002b), with an average water depth of 2–3 m in the greater extent of the Bay, and 0.9 m in the northeastern portion of the estuary known as East Bay (Edmiston 2008). Four barrier islands enclose the bay—Dog Island, St. George Island, Little St. George Island, and St. Vincent Island. Between the islands are four tidal inlets connecting the estuary to the Gulf of Mexico—East Pass, Sikes Cut, West Pass, and Indian Pass (Fig. 1).

The Apalachicola River supplies 90% of the freshwater entering the bay, while rain and groundwater supply the remaining 10% (Huang 2010). The Apalachicola River is the final section of the ACF river system that drains water from the 50,500-km² watershed of the ACF River Basin. The ACF river system begins as the Chattahoochee and Flint Rivers in Alabama and Georgia, which flow south and merge into Lake Seminole at the Florida state border. The Woodruff Dam at the southern boundary of the lake controls the water release to the Apalachicola River, which begins at the dam and then flows uninhibited for 180 km before discharging into AB.

Currents in AB are primarily controlled by tides, with a residual net westward flow generated by the surface gravity gradient that forms due to variations in tidal phase and water level at tidal inlets across the estuary (Huang et al. 2002b). Sustained winds can alter these tidal current velocities, as well as exchange rates of estuarine and Gulf water through the inlets (Edmiston 2008; Huang et al. 2002a). Although tides and winds can cause substantial short-term variability in currents and horizontal salinity gradients, the magnitude of freshwater input from the river has an overarching effect on the areal expanse of the salinity gradients such that reduced freshwater input results in the areal contraction of lower salinity water towards the river mouth (Geyer et al. 2018; Morey and Dukhovskoy 2012; Putland et al. 2013; Sun and Koch 1996). Mortazavi et al. (2000c) estimated residence time to be 25–2 days when river discharge ranged between ~400 and 2800 m³ s⁻¹.

Data Sources

Monthly inorganic nutrient (nitrate, nitrite, ammonium, phosphate) and chlorophyll *a* (Chl *a*) data were retrieved for 2002–2015 from the National Estuarine Research Reserve System

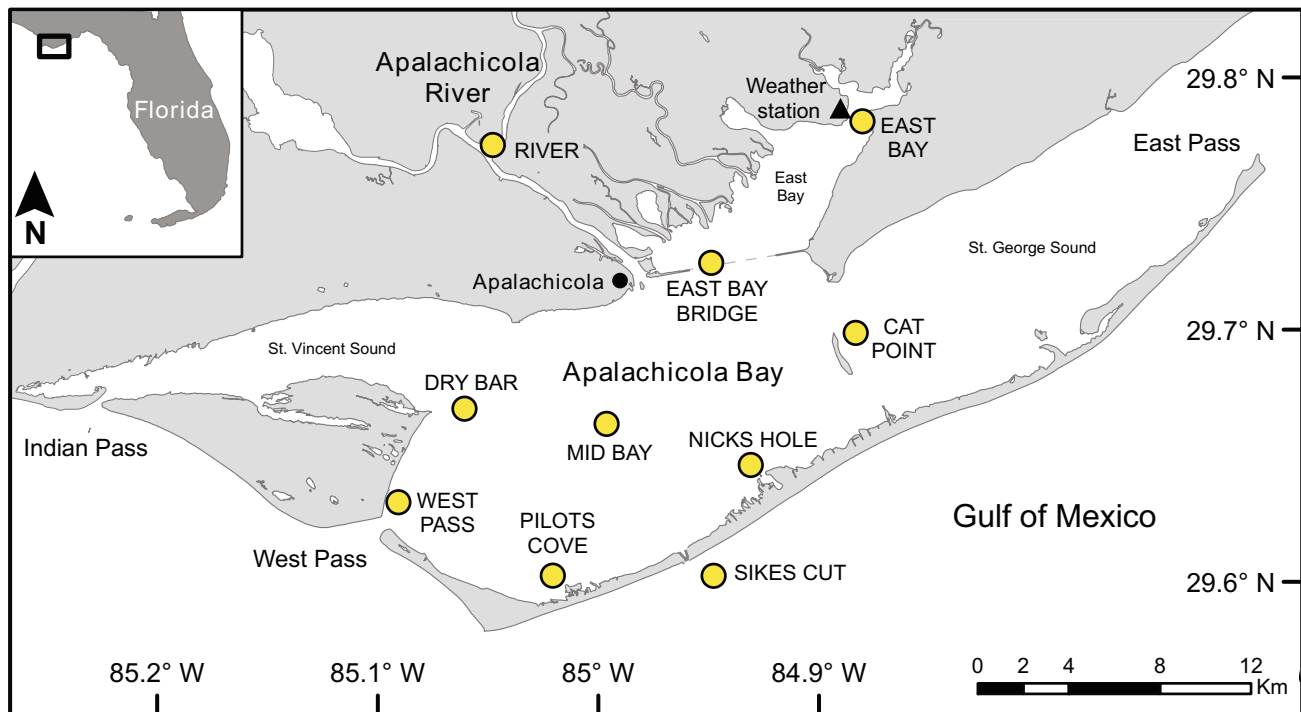


Fig. 1 Apalachicola National Estuary Research Reserve sampling stations in Apalachicola Bay, Florida (circles), and location of a weather station in East Bay (triangle)

Central Data Management Office (CDMO) website (<http://cdmo.baruch.sc.edu/>). Sample locations and descriptions are summarized in Fig. 1 and Table 1. The River site was ~9.7 km upstream from the river mouth and represents the freshwater endmember of the estuarine gradient. The Sikes Cut site was ~1.3 km outside the estuary in the Gulf of Mexico, to the southeast of Sikes Cut Inlet, and represents the marine endmember of the estuarine gradient. Water samples were collected 0.5 m below the surface at all sites except Dry Bar

and Cat Point, where water was collected at 1.5 m below the surface to correspond with the depth of moored YSI datasondes at these stations. The water column at these sites is typically well-mixed (with intermittent stratification at Dry Bar), which allows comparison of these data with data collected at 0.5-m water depth. At East Bay, water was collected at the surface (0.5 m) and near bottom (1.5 m) to correspond with moored datasondes at both depths. Associated water quality variables were measured at time of discrete water

Table 1 Environmental characteristics and discrete water sampling depths at the ANERR measurement sites

Site location	Bottom habitat	Average water depth (m)	Average tidal range (m)	Salinity range	Sampling depth (m)
River (29° 46.743' N, 85° 2.606' W)	Sandy silt, bare	3–4	0.7	0–0.5	0.5
East Bay (29° 47.147' N, 84° 52.512' W)	Clayey sand, bare	1.7	0.7	0.1–29.8	0.5, 1.5
East Bay (EB) Bridge (29° 43.848' N, 84° 56.711' W)	Silty clay, bare	1.6	0.7	0–30.7	0.5
Mid Bay (29° 40.061' N, 84° 59.641' W)	Sandy silt, bare	2.2	0.7	0.1–35.2	0.5
Dry Bar (29° 40.48' N, 85° 03.50' W)	Clayey sand, oyster bar	1.7	0.7	0.8–35.2	1.5
Cat Point (29° 42.128' N, 84° 52.811' W)	Clayey sand, oyster bar	1.8	0.7	0.2–35.2	1.5
Nick's Hole (29° 39.022' N, 84° 55.732' W)	Sandy silt, seagrass	1	0.7	0.5–35.4	0.5
Pilot's Cove (29° 36.473' N, 85° 1.173' W)	Sandy silt, seagrass	1.8	0.7	1.3–35.5	0.5
West Pass (29° 38.279' N, 84° 5.341' W)	Sand, bare	5.0	0.7	1.8–36.2	0.5
Sikes Cut Offshore (29° 36.401' N, 84° 56.799' W)	Sand, bare	>5	0.7	21.7–37.0	0.5

sample collection, including salinity, temperature, pH, Secchi depth, and turbidity.

Nutrient samples were filtered through 0.7- μm pore size glass fiber filters in the field and frozen at 4 °C until analysis. Samples were analyzed for nitrate + nitrite (NOx), ammonium (NH_4^+), and orthophosphate (PO_4^{3-}) using standard colorimetric methods (Grasshoff et al. 1999; Strickland and Parsons 1984). ANERR has shown that nitrite is a minor component of NOx compared to nitrate, and nitrite therefore was not measured separately after 2006. Dissolved inorganic nitrogen (DIN) was calculated as the sum of NOx and NH_4^+ concentrations. Total dissolved nitrogen (TDN) and phosphorus (TDP) samples were collected between March 2007 and June 2013. Samples for TDN and TDP were first digested (Grasshoff et al. 1999) and then analyzed with methods used for NOx and PO_4^{3-} , respectively. Dissolved organic nitrogen (DON) and phosphorus (DOP) were calculated as the difference between total and inorganic constituents ($\text{DON} = \text{TDN} - \text{DIN}$; $\text{DOP} = \text{TDP} - \text{PO}_4^{3-}$). Complete nutrient and Chl *a* analysis protocols are available in the metadata from CDMO.

High temporal resolution (15 min) water quality data were acquired from the CDMO for the Dry Bar permanent monitoring station, established in 1992. Salinity, temperature, dissolved oxygen (DO, in mg L^{-1} and % air saturation), pH, and pressure measurements were collected with a YSI 6600 multisensor moored on a piling 0.3 m above the sediment in approximately 2 m of water. Sensors were maintained and calibrated on a biweekly basis. Meteorological data were collected by ANERR in 15-min intervals at the East Bay weather station (29 46.472' N, 85 53.005' W) starting in 1999. Data flagged as rejected by the CDMO quality assurance checks were excluded from analysis.

Daily mean river discharge of the Apalachicola River was obtained from the USGS river gage (02359170) at Sumatra, Florida, 33 km upstream from the river mouth (<http://waterdata.usgs.gov>). Phases of the El Niño-Southern Oscillation (ENSO) were identified from the Oceanic Niño Index (<http://www.cpc.ncep.noaa.gov>).

Net Ecosystem Metabolism

Net ecosystem metabolism (NEM) is the daily integrated flux of DO measurements, which indicates the estuary's metabolic state as a balance between primary production and aerobic respiration. Positive NEM indicates greater production than respiration, whereby the system is net autotrophic and acts as a carbon source. In contrast, negative NEM indicates net heterotrophy in which the system acts as a carbon sink. Using the open water technique (Odum 1956), NEM was calculated with high frequency DO measurements collected at the ANERR Dry Bar monitoring station as described in Russell et al. (2006). First, the rate of change of DO (mg L^{-1}), *R*, between 15-min measurements was calculated. To correct

for atmospheric diffusion of oxygen into the water column, a diffusion correction factor was subtracted from *R*. This correction factor used the difference of percent saturation of DO in the water column at times 1 and 2, *S*₁ and *S*₂, the 15-min wind speed, *x*, from the ANERR East Bay weather station, and a diffusion coefficient, *K* ($\text{g O}_2 \text{ m}^{-2} \text{ h}^{-1}$), at 0% DO saturation (D'Avanzo et al. 1997).

$$K = 0.56e^{0.15x}$$

$$R_{dc} = R - \frac{K}{4} \left(1 - \left(\frac{S_1 + S_2}{200} \right) \right)$$

*R*_{dc} ($\text{mg O}_2 \text{ l}^{-1} \text{ 15 min}^{-1}$) is the wind-related diffusion corrected DO rate of change per 15 min. NEM is the sum of *R*_{dc} over a 24-h period starting at 08:00, which is referred to as a “metabolic day.”

The water column in the Bay was usually well-mixed, and for these calculations, we assumed that it was homogenous and biological activity more influential for DO variability than physical mixing. No stratification index correction was applied, and days with missing data were excluded. The time series was smoothed by a running average (centered moving average using a 30-day smoothing window) and plotted for evaluation of general trends.

Statistical Analysis

Drought and non-drought periods were categorized for statistical comparison of environmental variables. Drought periods were identified using historical records of river discharge and NIDIS (<http://www.drought.gov>). The first drought period (1999–2002) was already underway when sampling began in April 2002 and lasted through October 2002. During the second and third drought periods (January 2006–December 2008 and June 2010–January 2013), a large portion of the ACF River Basin was categorized as being in “exceptional drought” (NIDIS 2017). Periods with daily river discharge equal or higher than the 38-year average daily discharge were combined into a “non-drought” category. Years with average river discharge included 2004 and 2015. Years with above-average river discharge included 2003, 2005, 2009, 2010 (January–May), 2013, and 2014.

Linear regression, Student's *t* test, and analysis of variance (ANOVA) were performed in JMP 12.0.1 (SAS Institute Inc.). Where noted, data for regressions were log-transformed to normalize the distribution of the data (e.g., Chl *a*, turbidity). Averaging of time series curves from each site was performed in OriginPro 2016 (OriginLab Corporation).

Due to the short-term variability of salinity distributions in the bay, comparing other variables to salinity distribution (i.e., mixing diagram) produced large scatter of data. Therefore, in order to extract relationships between river discharge and key parameters in the bay, long-term averages were calculated to

smooth out the short-term variability. This revealed that river input of freshwater produces a general gradient of increasing salinity with increasing distance from the river mouth. Thus, to visualize the gradient of water quality variables in a spatial context, site means during drought and non-drought were plotted by distance from the river mouth. The River site was assumed to be representative of the river water up to the river mouth; therefore, the River site was assigned 0 km. The distance of sampling stations from the river mouth was measured in ArcGIS. East Bay was not included on the line connecting site means, as it is geographically isolated and does not fit the typical estuarine gradient observed for the other sites. For comparison, East Bay was assigned a distance of 2 km based on where the site's mean salinity would fit along a conservative mixing line. Water quality variables were analyzed for the main and interactive effects of site and climate period (drought and non-drought) using separate two-way ANOVA models.

Results

River Discharge and Nutrient Input

River discharge between 2002 and 2015 ranged from 125 to 4700 m³ s⁻¹ (Fig. 2). The average discharge during this period (572 ± 465 m³ s⁻¹) was lower than the 38-year mean (667 ± 506 m³ s⁻¹). The River site was fresh (*S* = 0–0.5) at the surface and usually also fresh at the bottom, with a few intrusions of brackish water (*S* = 1–20) observed along the bottom. Over 14 years, each site in the bay experienced a broad range of salinity from nearly fresh to nearly/fully marine (Table 1). The surface salinity at all estuary sites decreased significantly as discharge increased (*p* ≤ 0.0003, *R*² = 0.36–0.62, *n* = 130–156); salinity at the River and Sikes Cut was also correlated with discharge (*p* < 0.05) though less strongly (*R*² < 0.13). In the estuary, the largest differences between surface and bottom

salinity were at sites nearest the river mouth (Mid Bay and EB Bridge), whereas the water column at the other sites tended to be well-mixed (data not shown). Salinity at Sikes Cut ranged from brackish to marine (Table 1). Riverine input of DIN and PO₄³⁻ were calculated as the product of nutrient concentration at the River site and daily river discharge. DIN and PO₄³⁻ delivery from the river was correlated with river discharge rate (Fig. 3), with greater nutrient input occurring during higher discharge.

Mean Secchi Depths, Nutrients, and Chl *a* Along the Salinity Gradient

Secchi depth was greatest at Sikes Cut (2.2 ± 1.0 m) and lowest in East Bay (0.6 ± 0.3 m) (Table 2). The River had consistently high NO_x and low salinity, while Sikes Cut had low NO_x and high salinity (Tables 1 and 2). PO₄³⁻ had a similar spatial gradient as NO_x, with concentrations decreasing from the River to the Gulf (Table 2). The River had NO_x concentrations that were 30 times higher than the Gulf water at Sikes Cut but only 3 times higher PO₄³⁻ concentrations (Table 2). Mean molar DIN:DIP ratios were highest (80–145) at the River, EB Bridge, and Mid Bay and lowest (22 ± 18) at Sikes Cut (Table 2).

DON was greatest in East Bay (Table 2, 20.0 ± 10.8 μM), and generally similar at all other sites, with a slight spatial gradient of decreasing concentrations from the River (13.3 ± 8.5 μM) to the outer bay sites (e.g., Pilots Cove mean = 8.8 ± 5.3 μM) and Sikes Cut (7.5 ± 6.0 μM). In the River, DIN concentrations tended to exceed DON by about 60% (*n* = 76). The sign of the difference between DON and DIN was variable at the bay sites. In East Bay, DON exceeded DIN (paired *t* test, *p* < 0.0001, *df* = 75), and during drought, DON was twice as high as DIN (118 ± 57%, *n* = 54); whereas during non-drought, this difference was not as large (49 ± 90%, *n* = 22). DON at Sikes Cut also exceeded DIN (*p* < 0.0001, *df* = 60) by an average of 71 ± 82%. Mean DOP was similar

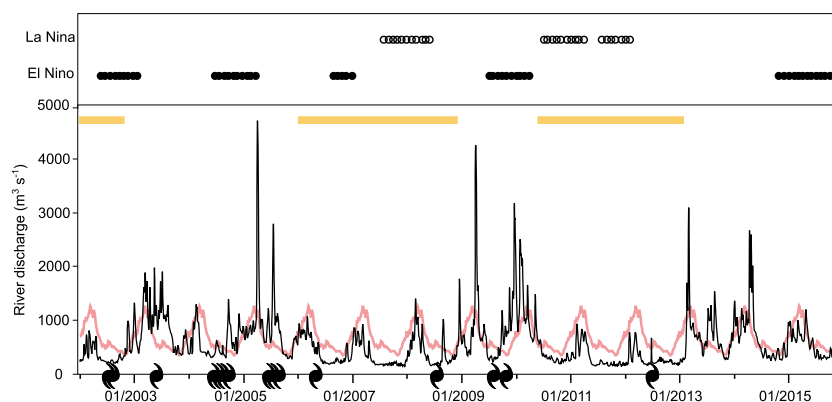


Fig. 2 Apalachicola River discharge. Daily mean discharge (thin black line) compared to the 38-year mean (thick pink line). Drought periods (horizontal yellow bars) and timing of El Niño (solid circles) and La Niña conditions (hollow circles). Timing of named storms is indicated by the

vortex symbols on the *X* axis (2002: Tropical Storm (T.S.) Hanna, T.S. Isidore; 2003: T.S. Bill; 2004: T.S. Bonnie, Hurricane (H.) Frances, H. Ivan, H. Jeanne; 2005: T.S. Arlene, H. Cindy, H. Dennis; 2006: T.S. Alberto; 2008: T.S. Fay; 2009: T.S. Claudette, H. Ida; 2012: T.S. Debby)

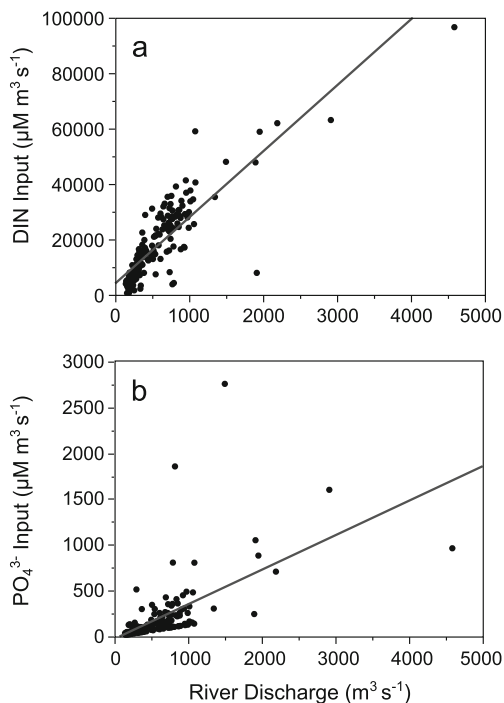


Fig. 3 Positive correlation between riverine input of **a** DIN ($p < 0.0001$, $R^2 = 0.72$, $n = 161$) and **b** PO_4^{3-} ($p < 0.0001$, $R^2 = 0.37$, $n = 160$) and river discharge rate

between most sites (Table 2), with lower DOP in the River ($0.2 \pm 0.1 \mu\text{M}$) than Sikes Cut ($0.5 \pm 0.5 \mu\text{M}$) and West Pass ($0.4 \pm 0.4 \mu\text{M}$). DOP and PO_4^{3-} concentrations were similar in the River (paired t test, $p > 0.05$). At all other sites, DOP exceeded PO_4^{3-} (paired t test, $p < 0.0001$, $df = 60\text{--}73$) by an average of $58 \pm 58\%$ ($n = 622$; varying from $29 \pm 73\%$ at EB Bridge, to $84 \pm 49\%$ at Sikes Cut).

Chl a was lowest in the River ($3.5 \pm 2.6 \mu\text{g L}^{-1}$) and at Sikes Cut ($3.3 \pm 2.6 \mu\text{g L}^{-1}$) (Table 2) and highest in East Bay ($12.6 \pm 8.3 \mu\text{g L}^{-1}$, surface and bottom concentrations were not statistically different). The remainder of the estuarine sites, which will be referred to collectively as “Bay sites,” had higher Chl a ($5.3\text{--}6.8 \mu\text{g L}^{-1}$) than both endmember stations but lower concentrations than East Bay (one-way ANOVA, $F_{9, 1497} = 54.0$, $p < 0.0001$).

Chl a , Inorganic Nutrient Input, and Net Ecosystem Metabolism Relative to River Discharge

Time series of riverine inorganic nutrient input and Chl a averaged for all 10 sites are shown in Fig. 4. Though DIN and PO_4^{3-} input were each correlated with river discharge, the magnitude of DIN and PO_4^{3-} input did not always change proportionally to each other (Fig. 4b); in particular, pulses of relatively high PO_4^{3-} input occasionally occurred concomitantly with high spring-time river discharge peaks. Time series of DIN (μM) and PO_4^{3-} (μM) concentrations averaged for all 10 sites are available in the Supplementary Material (ESM 1 and ESM 2). Annual average DIN (μM) for all 10 sites was correlated with annual river discharge ($p < 0.0001$, $R^2 = 0.8$, $n = 14$). Likewise, annual average PO_4^{3-} (μM) was correlated with annual river discharge when the 2003 outlier was excluded ($p < 0.0001$, $R^2 = 0.5$, $n = 13$).

At the beginning of 2005, Chl a concentrations decreased at all sites and remained relatively low for a year, corresponding with a period of high river discharge. In contrast, a

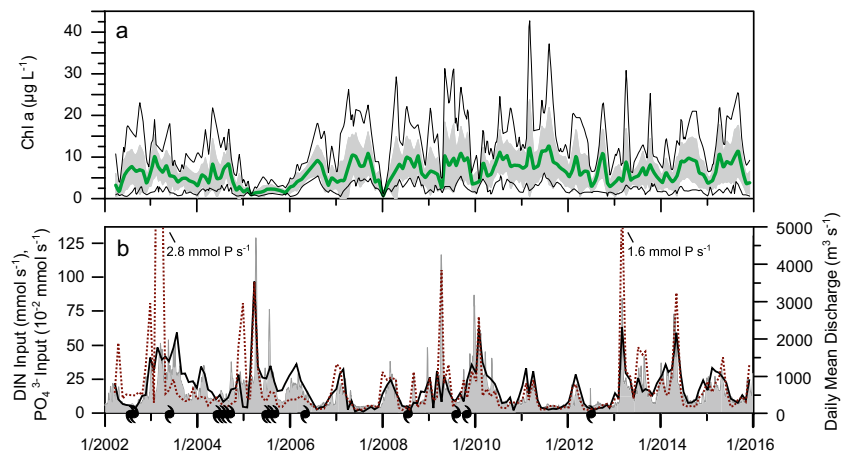
Table 2 Mean ± 1 standard deviation (SD) Secchi depth, surface turbidity, nutrients, and Chl a

Site	Secchi (m)	Turbidity (ntu)	NOx (μM)	NH_4^+ (μM)	DON (μM)	PO_4^{3-} (μM)	DOP (μM)	DIN:DIP	Chl a ($\mu\text{g L}^{-1}$)	n^a
River	1.1 ± 0.5	10.2 ± 6.7	27.9 ± 12.4	2.6 ± 1.6	13.3 ± 8.5	0.3 ± 0.3	0.2 ± 0.1	145 ± 93	3.5 ± 2.6	159
East Bay, sfc	0.6 ± 0.3	13.4 ± 8.6	4.4 ± 5.8	2.9 ± 2.5	20.0 ± 10.8	0.2 ± 0.3	0.3 ± 0.1	49 ± 48	12.6 ± 8.3	160
East Bay, btm	0.6 ± 0.3	13.4 ± 8.6	4.0 ± 5.3	3.3 ± 2.8	21.3 ± 11.3	0.2 ± 0.3	0.3 ± 0.2	50 ± 47	13.3 ± 8.9	161
EB Bridge	0.9 ± 0.3	10.4 ± 9.2	17.7 ± 11.5	2.6 ± 1.5	11.9 ± 8.3	0.2 ± 0.3	0.3 ± 0.1	122 ± 87	6.6 ± 4.3	156
Mid Bay	1.1 ± 0.4	9.9 ± 11.7	10.0 ± 9.8	2.4 ± 1.8	12.0 ± 7.2	0.2 ± 0.1	0.3 ± 0.3	80 ± 72	6.7 ± 4.0	156
Dry Bar	1.0 ± 0.4	10.7 ± 8.9	7.4 ± 8.0	2.5 ± 2.5	10.7 ± 6.3	0.2 ± 0.1	0.4 ± 0.3	68 ± 60	6.8 ± 3.8	157
Cat Point	1.0 ± 0.4	11.5 ± 9.4	7.2 ± 8.6	3.1 ± 2.2	12.5 ± 8.8	0.2 ± 0.1	0.4 ± 0.3	66 ± 58	6.0 ± 4.0	160
Nicks Hole	1.1 ± 0.4	7.4 ± 6.3	6.9 ± 8.1	2.1 ± 1.5	10.8 ± 6.6	0.2 ± 0.1	0.3 ± 0.2	61 ± 62	5.7 ± 3.3	141
Pilots Cove	1.2 ± 0.4	7.9 ± 7.0	5.3 ± 6.8	2.0 ± 1.3	8.8 ± 5.3	0.2 ± 0.1	0.4 ± 0.4	51 ± 49	5.3 ± 2.9	143
West Pass	1.2 ± 0.6	10.9 ± 11.0	6.2 ± 7.2	2.1 ± 1.3	9.0 ± 5.5	0.2 ± 0.1	0.4 ± 0.4	56 ± 50	6.1 ± 3.8	143
Sikes Cut	2.2 ± 1.0	5.3 ± 3.9	0.9 ± 1.4	2.1 ± 1.9	7.5 ± 6.0	0.1 ± 0.1	0.5 ± 0.5	22 ± 18	3.3 ± 2.6	133

Sites are delineated into zones based on water quality characteristics: (top to bottom) River, East Bay, Apalachicola Bay, and Gulf

^a DON and DOP: $n = 61\text{--}76$

Fig. 4 Time series of **a** mean Chl *a* (thick green line) \pm SD (gray area) from the 10 sampling sites. Thin black lines represent the Chl *a* min–max and **b** riverine input of DIN (solid black line) and PO_4^{3-} (dashed red line). Note different units for DIN and PO_4^{3-} . Daily mean discharge of the Apalachicola River (gray area) and timing of tropical cyclones (vortex symbol) are indicated



relatively prolonged period of above-average Chl *a* concentrations ($8.1 \pm 5.7 \mu\text{g L}^{-1}$, $n = 268$) was observed during the drought between mid-2010 and 2012, compared to the 14-year average ($6.3 \pm 4.9 \mu\text{g L}^{-1}$, $n = 1507$). Annual mean Chl *a* of the Bay sites did not vary significantly with annual mean river discharge (Fig. 5, $p = 0.1$, $R^2 = 0.18$, $n = 14$). All years, except those with prolonged extreme events (drought 2011, flood 2005), had annual means within $2 \mu\text{g L}^{-1}$ of the 14-year mean. The mean and variability (SD) in 2005 was much lower ($1.8 \pm 1.0 \mu\text{g L}^{-1}$, $n = 69$) than in other years. The mean in 2011 was higher ($9.3 \pm 4.0 \mu\text{g L}^{-1}$, $n = 68$) than in other years, with similar intra-annual variability.

Net ecosystem metabolism at Dry Bar during 2010–2015 suggests a net heterotrophic system, with lowest NEM occurring in the summer (mean = $-2.3 \pm 2.2 \text{ mg O}_2 \text{ L}^{-1} \text{ day}^{-1}$) and highest in the winter (mean = $-0.1 \pm 2.0 \text{ mg O}_2 \text{ L}^{-1} \text{ day}^{-1}$) (Fig. 6; $F_{3, 1931} = 89.8$, $p < 0.0001$). Annual mean NEM was significantly higher in 2011 and 2012 than in 2014 and 2015

($F_{5, 1911} = 13.1$, $p < 0.0001$), while river discharge was significantly lower in 2011 and 2012 than the other 4-years that NEM was analyzed ($F_{3, 1931} = 134$, $p < 0.0001$). Summer 2010 had significantly lower NEM than summer in 2011, 2012, and 2013 (two-way ANOVA, $F_{23, 1911} = 18.6$, $p < 0.0001$). Monthly mean NEM was negatively correlated with datasonde water temperature ($R^2 = 0.46$, $p < 0.0001$, $n = 71$). After removing the temperature trend, residual NEM was positively correlated with datasonde salinity ($R^2 = 0.39$, $p < 0.0001$, $n = 71$) and negatively correlated with river discharge ($R^2 = 0.44$, $p < 0.0001$, $n = 71$). The residual NEM was lower in spring and summer than autumn and winter ($F_{3, 1931} = 13.5$, $p < 0.0001$). The greatest differences between NEM and residual NEM were observed during summer (Fig. 6), when temperatures were greatest (mean $\sim 28 \text{ }^\circ\text{C}$).

Effects of Drought on Spatial Distribution of Biogeochemical Variables

Site mean values during drought and non-drought periods were compared with two-way ANOVAs ($\alpha = 0.05$). The statistical model and effect details are reported in the Supplementary Material (ESM 3). If the overall model was significant, the main and interactive effects were further investigated with a post hoc Tukey or Student's *t* test.

Surface water temperatures for a given sampling date were similar at all sampling sites ($p > 0.05$) and not influenced by drought. Salinity at the River, East Bay, and Sikes Cut sites was not significantly different during drought periods (Fig. 7). In contrast, all other Apalachicola Bay sites had significantly higher salinity (~ 6) during the droughts ($F_{19, 1482} = 132.8$, $p < 0.0001$). Collectively, for all 10 sites, pH was 0.2 higher during droughts ($F_{1, 1388} = 64.6$, $p < 0.0001$). Secchi depth was significantly deeper in the River during drought periods ($1.3 \pm 0.6 \text{ m}$) than non-drought periods ($0.9 \pm 0.3 \text{ m}$), whereas at Sikes Cut, Secchi depth was $\sim 0.3 \text{ m}$ deeper during non-drought periods ($F_{19, 1424} = 45.2$, $p < 0.0001$). There was no

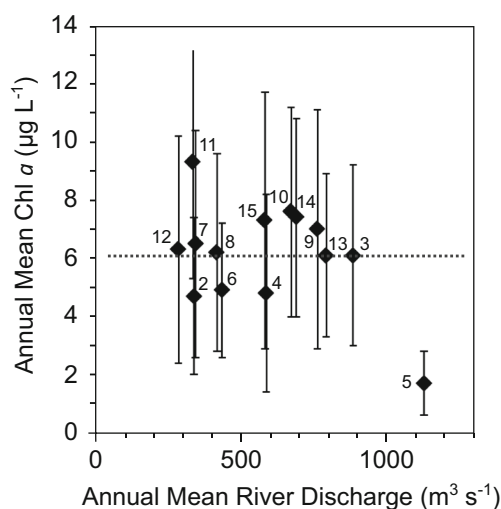
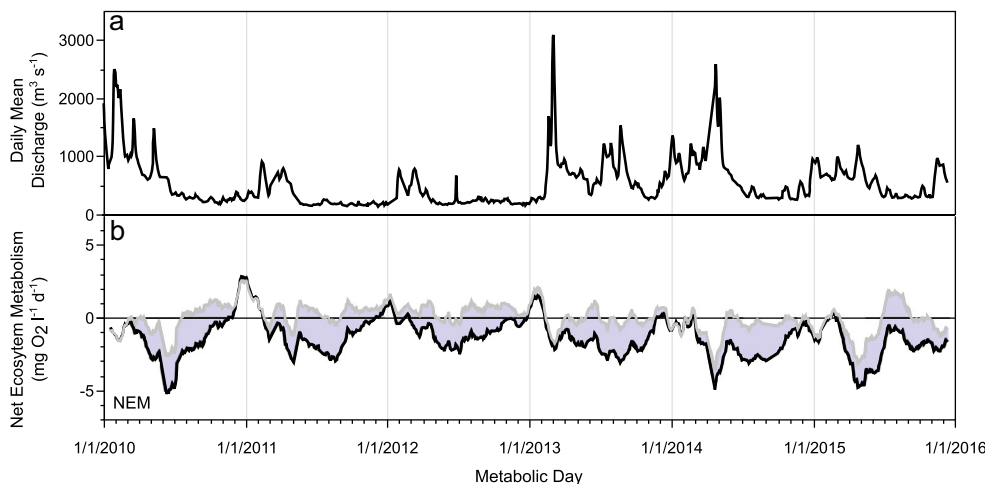


Fig. 5 Annual mean (\pm SD) Chl *a* of the Bay sites ($n = 63$ –84 per year) versus annual mean river discharge. The 14-year mean Chl *a* is indicated (6.2 ± 3.8 , $n = 1055$, dashed line). Year is indicated next to corresponding annual means (e.g., 2002 = 2)

Fig. 6 Time series of **a** daily mean river discharge and **b** smoothed (centered moving average using a 30-day smoothing window) daily NEM (black line) and residual NEM (gray line). Shaded area indicates difference between NEM and residual NEM



significant difference between drought and non-drought Secchi depths at the other sites.

East Bay had higher Chl *a* during drought periods ($F_{19, 1487} = 28.6; p = 0.02$), whereas at all other sites, Chl *a* concentrations were not significantly different during drought (Fig. 7). Turbidity did not differ significantly at any particular site between drought and non-drought nor was there an overall difference during drought when looking at all sites collectively ($p > 0.05$). However, turbidity and river discharge were positively correlated ($p < 0.05$) during non-drought at East Bay ($R^2 = 0.03$), EB Bridge ($R^2 = 0.49$), Mid Bay ($R^2 = 0.31$), Dry Bar ($R^2 = 0.08$), Cat Point ($R^2 = 0.09$), and Nicks Hole ($R^2 = 0.2$). In contrast, turbidity and river discharge were not correlated during drought periods ($p > 0.05$), except at Dry

Bar and West Pass, where there was a weak negative correlation during drought ($p = 0.03, R^2 = 0.07$).

Turbidity and Chl *a* were positively correlated in East Bay and all Bay sites during drought (ESM 4, $p < 0.01, R^2 = 0.11–0.40, n = 56–69$) but not during non-drought ($p > 0.05$), except at Pilots Cove ($p = 0.03, R^2 = 0.06, n = 76$). In the River, this correlation was negative during drought ($p < 0.0001, R^2 = 0.22, n = 67$) and not significant during non-drought ($p > 0.05$). At Sikes Cut, turbidity and Chl *a* were positively correlated during both drought and non-drought ($p = 0.0005, R^2 = 0.20, n = 56; p < 0.0001, R^2 = 0.29, n = 72$, respectively). Secchi depth and Chl *a* were negatively correlated at all Bay sites (except EB Bridge) and Sikes Cut during drought (ESM 5, $p < 0.01, R^2 = 0.10–0.42, n = 57–66$) and in Cat

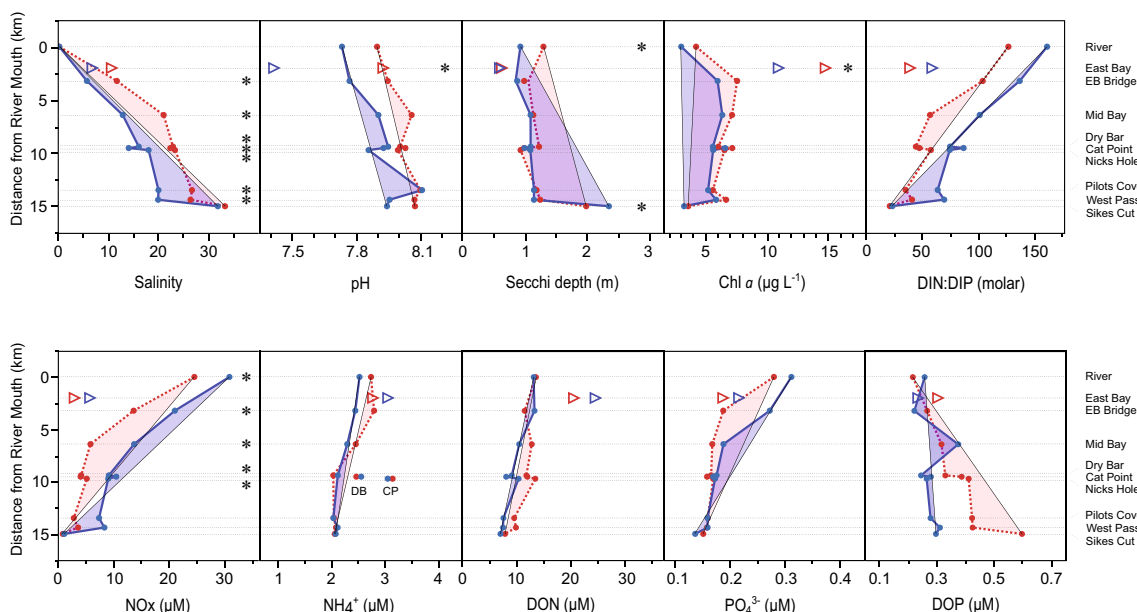


Fig. 7 Comparison of site means during drought (light-red shaded area, dashed red line) and non-drought (dark-blue shaded area, solid blue line) periods. Site means are indicated with circles, except East Bay (triangles).

Asterisks denote which sites had significantly different means in drought and non-drought (two-way ANOVA interaction, $\alpha = 0.05$)

Point, Pilots Cove, West Pass, and Sikes Cut during non-drought ($p < 0.01$, $R^2 = 0.09$ – 0.20 , $n = 66$ – 82).

NOx was significantly lower during drought years at the River, EB Bridge, Mid Bay, and Dry Bar and Nicks Hole ($F_{19, 1500} = 76.2$, $p < 0.0001$), but at stations farther away from the river than Nicks Hole, this difference was not statistically significant (Fig. 7). NH_4^+ had no overall or site-specific differences between drought and non-drought periods ($p > 0.05$). NH_4^+ was relatively high at Cat Point, Dry Bar, and East Bay (bottom), in part because these water samples were taken 0.5 m above the sediment surface. While mean PO_4^{3-} and DIN:DIP ratios for individual sites were not significantly different between drought and non-drought, when pooled, both PO_4^{3-} and DIN:DIP ratios were significantly higher during non-drought periods ($F_{1, 1509} = 4.2$, $p < 0.0001$; $F_{1, 1506} = 76.5$, $p < 0.0001$, respectively). DON was not significantly different during drought ($p > 0.05$). Collectively, DOP was significantly higher during drought ($F_{1, 1509} = 13.5$, $p < 0.0003$); however, the interactive effect between site and climate period was not significant.

Effects of Storm and Flood Events

From 2002 to 2015, several high discharge periods were observed (Fig. 2), some of which were related to tropical storm activity. Tropical cyclones during this time period had variable trajectories, wind strength, precipitation, and landfall locations (National Hurricane Center, <http://www.nhc.noaa.gov>). The effects of the tropical cyclones on river discharge were linked to the amount of precipitation over the ACF River Basin. For example, Tropical Storm (T.S.) Debby slowly passed over AB in June 2012, producing > 400 mm of local precipitation over 3 days (East Bay weather station); then T.S. Debby tracked to the east and had relatively little impact on the rest of the ACF watershed. The river had been historically low that summer, and with the passing of T.S. Debby, there was a threefold increase in discharge rates that persisted for about 3 days before returning to rates well below average (Fig. 2). One week after the passage of T.S. Debby, salinity returned to brackish-marine levels in the Bay, and much of the Bay had near average Chl *a* (5 – $6 \mu\text{g L}^{-1}$) (Geyer, unpublished data). In contrast, T.S. Fay directly hit AB in August 2008, producing heavy rainfall in the ACF River Basin that caused the Apalachicola River discharge to increase 4.5-fold within 1 week and remain elevated for 1 month. Water samples collected 2 weeks after the passing of T.S. Fay revealed elevated DIN and PO_4^{3-} input and concentrations. The increases in riverine PO_4^{3-} input were proportionally higher than DIN input (Fig. 4b).

Four tropical cyclones in August–September 2004 passed over the ACF River Basin, contributing to peaks in river discharge during Fall 2004, as well as a peak ($4700 \text{ m}^3 \text{ s}^{-1}$) in April 2005 that was in the upper 99.5 percentile of river

discharge recorded over the previous 38 years (Fig. 2). Three more tropical cyclones in June and July 2005 added another spike in river discharge ($2800 \text{ m}^3 \text{ s}^{-1}$) in July 2005. Among these was Hurricane Dennis, which made landfall to the west of AB in July 2005, causing a 2.5-m storm surge in AB (Edmiston et al. 2008) and heavy rainfall (80–250 + mm) over much of the ACF River Basin (Weather Prediction Center, <http://www.wpc.ncep.noaa.gov>). Both DIN and PO_4^{3-} input were elevated during these high river discharge periods (Fig. 4b). Meanwhile, Chl *a* was reduced across the estuary at the beginning of 2005 and remained below average through December 2005 (Fig. 4a).

Discussion

The response of estuarine phytoplankton to river discharge variability is a function of the riverine nutrient input, salinity gradients, turbidity, water residence time, and biological controls (Livingston et al. 1997; Mortazavi et al. 2000c; Murrell et al. 2007; Putland et al. 2013). The 14-year time series of river discharge and nutrient concentrations in AB illustrates the relationship of Apalachicola River discharge and phytoplankton dynamics. In this shallow, river-dominated estuary, the natural range of residence times (days to weeks) overlaps with timescales of phytoplankton growth, biomass accumulation, and bloom development. In the following, we discuss factors affecting phytoplankton biomass under varying freshwater inflow conditions in AB and the timescales of biogeochemical changes induced by droughts and high discharge events.

Mechanisms Influencing Estuarine Biogeochemistry Under Drought and Non-Drought Conditions

When data from the seven “Bay sites” were pooled, the Bay had similar Chl *a* during drought ($6.6 \pm 3.8 \mu\text{g L}^{-1}$, $n = 467$) and non-drought ($5.8 \pm 3.8 \mu\text{g L}^{-1}$, $n = 588$). Furthermore, when the unusually low Chl *a* data in 2005 were excluded, the non-drought mean ($6.4 \pm 3.7 \mu\text{g L}^{-1}$, $n = 519$) was statistically similar to the drought mean ($p > 0.05$). There was also no significant correlation between annual mean Chl *a* at the Bay sites and annual mean river discharge (Fig. 5). The annual mean and standard deviation of Chl *a* during 2005 were low for the entire Bay and not representative of other non-drought years. On the other extreme, annual mean Chl *a* was highest during 2011, a drought year, though variability (SD) during 2011 was similar to other years. These 2 years show how extreme events can affect phytoplankton biomass in AB, whereas all other years had near average concentrations and similar intra-annual variability.

The lack of a decrease in estuarine Chl *a* during drought is notable, as the expected response of reduced river discharge and associated decrease in nutrient input is reduced primary

productivity and biomass and thus reduced Chl *a* concentration (Livingston et al. 1997; Putland et al. 2013). The relatively consistent Chl *a* concentrations during drought and non-drought periods may be the result of equalizing mechanisms: Higher river discharge may deliver more nutrients to the Bay, but it also reduces residence time and light penetration, thereby also limiting the buildup of biomass. Livingston et al. (1997) observed that during drought, less precipitation and runoff lead to improved water clarity in East Bay. In the present study, Secchi depths were deeper in the River during drought. During non-drought, river discharge explained 54 and 23% of the variance observed in turbidity at the River and EB Bridge, respectively. Although the river water was significantly clearer during drought, the Bay sites did not have a difference in water clarity, suggesting that other mechanisms (e.g., sediment resuspension) are more important in controlling light penetration in the estuary when river discharge is low (May et al. 2003). The lack of different Secchi depths and turbidities in the Bay thus may reflect balancing effects between concentration of suspended sediment and detrital material and abundance of living cells (Kirk 1994; Swift et al. 2006). It is reasonable to conclude that there was less allochthonous material in the water column during drought, allowing for more light availability to the phytoplankton. Furthermore, the oyster population in the Bay may respond with stronger growth and associated higher filtration rates during periods of moderate to high river discharge and salinities < 25 (Wang et al. 2008), thereby limiting an increase of Chl *a* concentration proportional to freshwater inflow increase. In contrast, during drought, riverine nutrient loads are reduced, but residence time increases and oyster populations suffer increased predation and disease-related mortality at higher salinities (Garland and Kimbro 2015; Livingston et al. 2000; Petes et al. 2012). The combined effects of longer residence time and reduced filtration pressure may allow for sustained higher Chl *a* concentrations. From an ecological standpoint, it should be noted that bulk Chl *a* is an indicator of the collective

community response to changes in river discharge and does not necessarily represent the responses of specific taxa (Cloern and Dufford 2005; Li and Harrison 2008).

NO_x had an inverse relationship with salinity along the estuarine continuum except at East Bay. Lower NO_x during drought years was particularly evident at sites nearer the river mouth (Fig. 7). These lower NO_x concentrations were reflected in DIN:DIP ratios, which were also lower during drought. Previous studies suggest phytoplankton productivity is P-limited in regions nearer the river mouth where salinity is lower and N-limited in the outer portions of the bay that are more marine influenced (Fulmer 1997; Mortazavi et al. 2000a; 2000b; Viveros 2014); therefore, we expect N-limitation to become more widespread during drought when reduced freshwater input results in lowered nutrient delivery and greater salinities in the Bay. In a 2-year study, Mortazavi et al. (2000a) calculated that 66% of annual DIN input from the river was exported to the Gulf, suggesting AB has excess N available, but they also calculated phytoplankton nitrogen demand and concluded that these demands were not met in the summer when productivity was highest and N-input was relatively low, supporting the hypothesis of N-limitation during drought conditions.

NH₄⁺ concentrations were relatively low and did not differ significantly between drought and non-drought. In AB, pelagic and benthic regenerations of NH₄⁺ contribute to water column DIN (Gihring et al. 2010; Mortazavi et al. 2000a). Mobilization of benthic NH₄⁺ occurs through processes such as wind-driven (> 4 m s⁻¹) resuspension of the sediment (Myers 1977). Prior work concluded that these contributions supply the majority of the phytoplankton nitrogen demand during summer (Mortazavi et al. 2000a). At Cat Point and Dry Bar, nutrient samples collected from bottom water revealed NH₄⁺ concentrations that were much higher than expected compared to other bay sites (Fig. 7). Both of these sites

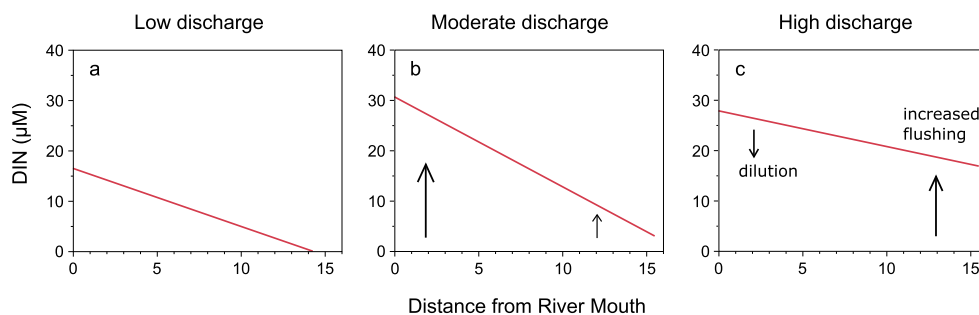


Fig. 8 Changes in DIN concentrations over the estuarine gradient during **a** low (100–300 m³ s⁻¹), **b** moderate (300–1100 m³ s⁻¹), and **c** high (1100–4500 m³ s⁻¹) river discharge rates (data points not shown). At low discharge, DIN in the river water was mixed with lower concentration estuarine water and utilized in the estuary ($p < 0.0001$, $R^2 = 0.45$, $n = 411$). As discharge increased, the increase of DIN in the

river was greater than in the estuary, leading to a steeper slope ($p < 0.0001$, $R^2 = 0.47$, $n = 882$). Instead of increasing further, DIN concentrations in the river were diluted during high discharge; furthermore, due to increased flushing and reduced residence time, more of the riverine DIN input was transported farther in the estuary ($p = 0.01$, $R^2 = 0.1$, $n = 65$)

are near oyster reefs, which may contribute to high NH_4^+ concentrations (Dame et al. 1989).

DIN concentrations were highest in the river at moderate discharge and slightly lower at very high discharge (ESM 6), likely due to dilution which has been observed in other systems as well, such as the Neuse River Estuary (Paerl et al. 2014). At low discharge ($100\text{--}300\text{ m}^3\text{ s}^{-1}$), DIN concentration in the river is reduced and river water mixes with the relatively low concentration brackish-marine water in the estuary (Fig. 8a). As discharge increases, DIN increases in the river water relatively more than in the estuary, leading to a steeper nutrient gradient (Fig. 8b). This was likewise observed with PO_4^{3-} concentrations (not shown). While the rate of PO_4^{3-} change continued to increase (steeper slope) with increasing river discharge, the rate of DIN change at higher discharge ($>1100\text{ m}^3\text{ s}^{-1}$) became less steep again (Fig. 8c). During high discharge periods, riverine DIN concentrations become diluted (ESM 6) and the outer estuary concentrations increase relatively more—leading to a less steep nutrient gradient within the estuary. While the slope of DIN change over distance is similar between low and high discharge periods, the magnitudes of the concentrations are different (Fig. 8). The nutrient input at low river discharge will be retained longer in the estuary due to longer residence times, allowing more of the available nutrients to be utilized (Mortazavi et al. 2000a). In contrast, at high river discharge, a greater amount of DIN may be flushed to the farther reaches of the estuary where it may be utilized or exported.

DON concentrations did not change during drought and decreased slightly between River and Sikes Cut, in contrast to the steep gradient observed in DIN. The DON pool can be large relative to DIN during drought, but the relatively small concentration gradient between River and Sikes Cut suggests that this material degrades slowly and thus has relatively little influence on the productivity in the Bay. Mortazavi et al. (2001) concluded that DON from the river is mostly exported from the bay because there is not enough time for it to be utilized in the estuary.

Overall, PO_4^{3-} in the Bay was reduced during drought. River PO_4^{3-} input increased with discharge rates, sometimes proportionally more than DIN (Fig. 4b), which may be due to enhanced mobilization of P from greater amounts of runoff during heavy precipitation or floods (Paerl et al. 2014). For example, in March 2003, within 3 days of sampling, there was a substantial amount of rain (114 mm) recorded at the East Bay weather station, which may explain the PO_4^{3-} peak ($\leq 2.1\text{ }\mu\text{M}$; ESM 2) observed in the river and upper estuary sites.

DOP concentrations were similar to PO_4^{3-} concentrations at the River station and during non-drought conditions showed no trend across the Bay. During drought, DOP concentrations increased from the River to Sikes Cut, which could be a consequence of DOP production by phytoplankton in the nearshore water. The DIN:DIP ratio can influence DOP

production rates when DIN becomes limiting (Ruttenberg and Dyhrman 2012; Yoshimura et al. 2014). DOP thus could provide additional P to the estuary during phases of high coastal primary production.

Runoff from the surrounding bottomland hardwood forests and adjacent marshes reduces the pH of the river water (Edmiston 2008). During drought and non-drought periods, lower pH river water mixes with higher pH marine water. Compared to the pH at River and Sikes Cut (Fig. 7), surface water pH was higher in the Bay than expected by conservative mixing, possibly due to a drawdown of carbon dioxide from increased primary productivity in the estuary as compared to the endmember sites. Overall, pH was higher during drought, which can be attributed to reduced riverine detritus input and degradation, and intrusion of buffered coastal seawater. The relatively high pH at Pilots Cove may be a result of photosynthesis of the seagrass meadows at this site (Hendriks et al. 2014). In contrast, Hu et al. (2015) observed long-term alkalinity decrease and acidification in estuaries in the Northwestern Gulf of Mexico and suggested that these changes are a result of precipitation decline under drought conditions and freshwater diversion for human consumption, as well as calcification in these bays.

Net Ecosystem Metabolism

NEM can offer additional insight into the effects of freshwater discharge on estuarine systems (Russell et al. 2006). The location of Dry Bar outside the river mouth provides an opportunity to evaluate the use of NEM as an indicator of the effects of river discharge variability. Stratification is a violation of the open water method assumptions and may cause systemic errors when estimating DO flux for the entire water column from data collected at a fixed depth (Murrell et al. 2017); however, at Dry Bar, no more than 15% of the monthly samples between 2010 and 2015 were affected by stratification.

NEM results indicated that AB was net heterotrophic, with lowest NEM values occurring during summer (Fig. 6) when water temperatures were warmer. This is in agreement with previous NEM calculations for AB using the open water method (Caffrey 2004; Caffrey et al. 2013). Caffrey et al. (2013) observed that the monthly trends of gross primary production (GPP) and ecosystem respiration (ER) calculated from DO measurements at East Bay, Dry Bar, and Cat Point were similar, though GPP rates at Cat Point tended to be $\sim 30\%$ lower than the other sites. Highest rates of GPP and ER occurred during summer, reflecting seasonal patterns consistent with temperature cycles. Respiration appeared to be more strongly affected by temperature than GPP, resulting in lower NEM during summer (Caffrey et al. 2013).

The effects of temperature on NEM may mask the influence of river discharge. Monthly NEM was not correlated with river discharge or salinity ($p > 0.05$), but removing the

temperature trend revealed a negative correlation between NEM (residuals) and river discharge and the inverse correlation with salinity. Russell et al. (2006) likewise observed decreasing NEM with increasing river discharge and decreasing salinity in upper Lavaca Bay (TX). At Dry Bar, river discharge explained 44% of the variance in residual NEM, with lower residual NEM occurring during higher river discharge, suggesting that low NEM is partially due to the delivery of terrestrial matter and inorganic nutrients during high river discharge, which supports secondary production and primary production, respectively (Chanton and Lewis 2002). Annual mean NEM was highest (less net heterotrophic) in 2011 and 2012, differing significantly from annual mean NEM in 2014 and 2015, which were non-drought years. Both 2011 and 2012 had significantly higher summer NEM than 2010 as well, which was the beginning of the 2010–2012 drought. Increased bacterial activity during warm summer months may have released nutrients from the sediment supporting the relatively high Chl *a* observed during the drought (Vouve et al. 2000). The influence of freshwater inflow on NEM is further evidenced by the correspondence of higher mean residual NEM and lower mean river discharge during 2011 and 2012, presumably due to less organic material delivered from the river during 2011–2012.

Timescales of Drought and Storm Effects on Estuarine Biogeochemistry

Interannual variability in river discharge is influenced by climatic cycles (e.g., Briceño and Boyer 2009; Cloern and Jassby 2010). The ACF River Basin is strongly affected by the ENSO phase, such that the southeastern USA experiences increased winter precipitation during El Niño and warmer and drier conditions during La Niña (Morey et al. 2009; Singh et al. 2015). Furthermore, multidecadal climate cycles such as the Atlantic Multidecadal Oscillation and the Pacific Decadal Oscillation modulate how the ENSO phase affects baseflow of the Flint and Apalachicola Rivers (Singh et al. 2015). The droughts of 1999–2002, 2007–2008, and 2011–2012 overlapped with La Niña phases (Fig. 2). Meanwhile, the tropical cyclones in 2005 were associated with the most active hurricane season on record (Beven et al. 2008). Tropical cyclones were associated with some of the river discharge peaks, but high discharge was not always dependent on tropical events (e.g., 2013–2015). Furthermore, tropical cyclones had variable impacts on the ACF River Basin, depending on their trajectory and precipitation. A storm with intense localized rainfall on the estuary but not the entire watershed, such as T.S. Debby in July 2012, had short-term (< 1 week) impacts on estuarine hydrology. In contrast, storms affecting the entire

watershed had long-lasting effects on estuarine hydrology by refilling the upstream rivers and reservoirs (Fig. 2).

There has been an increase in the frequency and severity of multiyear droughts in the ACF River Basin over the last two decades compared to the previous 100 years (Singh et al. 2015), and though there is uncertainty about the persistence of this trend (Seager et al. 2009), the increased water demands of upstream cities and agricultural irrigation will continue to cause concerns about how the ACF River Basin is managed (Leitman et al. 2016). How a drought affects estuarine phytoplankton will likely depend on its duration. Benthic regeneration of N, P, and Si that are temporarily sequestered in estuarine sediments (Froelich 1988; Hallas and Huettel 2013; Mortazavi et al. 2000a, b) may be regularly resuspended into the water column (Myers 1977; Percuoco et al. 2015). Weaker vertical stratification during drought may increase benthic-pelagic coupling (Koseff et al. 1993), thus leading to enhanced potential for the resuspension of benthic microalgae, remineralized nutrients, and sediment (Gabrielson and Lukatelich 1985; Myers 1977; Wengrove et al. 2015). During the initial phase of drought, these secondary sources of nutrients, in conjunction with increased residence time, may mitigate the negative effects of reduced riverine nutrient input on phytoplankton growth. Because nutrients will be exported less quickly, phytoplankton has more time to utilize these nutrients. The intrusion of higher salinity water into the upper estuary may also cause more sediment-bound P to be released from the sediment (Jordan et al. 2008).

High river discharge events can substantially reduce Chl *a* through enhanced flushing (Murrell et al. 2007; Paerl et al. 2009). Large freshwater pulses corresponded with reductions in Chl *a* throughout the study period (Fig. 4a). The duration of these reductions depended on the intensity and frequency of freshwater pulses. Long-term effects on riverine hydrology seem to be more strongly tied to a storm's trajectory and rainfall over the watershed. Storms and wind events also cause changes in turbidity that typically resolve within days, but water quality changes from prolonged or frequent high river discharge events can be slower to resolve (Edmiston et al. 2008). The frequency of tropical cyclones during 2004 and 2005 caused recurrent periods of high flushing and likely low light penetration, which prevented recovery of the standing stock of phytoplankton for an extended period (Murrell et al. 2007; Paerl et al. 2014).

Conclusions

Over the last two decades, there has been an increased frequency of multiyear droughts in the southeast USA (Leitman et al. 2016; Singh et al. 2015). This, along with growing human freshwater demands in the watershed, has raised concern

about the potential for lower freshwater discharge rates to AB in the future and subsequent environmental impacts (Fisch and Pine 2016; Kimbro et al. 2017; Leitman et al. 2017). To develop effective freshwater inflow management strategies, we must identify key environmental indicators and processes and ultimately determine how hydrologic variability and change will affect them (Montagna et al. 2013). Chlorophyll *a*, a proxy for phytoplankton biomass and water quality, is an important water column indicator of the effects of hydrological variability on the primary producers. This study has shown that although dissolved inorganic nitrogen and phosphate loadings to AB were correlated to river discharge, Chl *a* was similar between periods of drought and average/above-average river discharge in most of the Bay. This suggests that the potentially negative impact of decreased riverine nutrient input on Bay phytoplankton biomass is mitigated by the nutrient buffering capacity of the estuary. Due to the very shallow depths and vertically well-mixed water column in much of AB, benthic-pelagic interactions in terms of nutrient exchange are likely enhanced compared to deeper estuaries where watershed nutrient input tends to translate directly into phytoplankton biomass (Kennish et al. 2014). In some estuaries on the Texas Coast, droughts have been shown to cause measurable decreases in nutrient concentrations and chlorophyll concentrations (Palmer and Montagna 2015), yet in others (such as the shallow Baffin Bay), very high organic nitrogen concentrations and high rates of recycling allow for accumulation of phytoplankton biomass during droughts (e.g., Wetz et al. 2017). Although phytoplankton biomass may not be directly affected by reductions in freshwater inflow, the type(s) of phytoplankton present may still be. As demonstrated here and in other studies, changes in the influence of riverine versus internal recycled nutrients will alter the form(s) of nutrients present. Specifically, reductions in riverine nutrients allow for a greater proportion of the available nutrients to be in reduced form, such as ammonium and DON in the case of nitrogen. These differences in nutrient conditions will likely influence the size-structure and taxonomic composition of the phytoplankton community and thereby the estuarine food web. Thus, future studies should address this issue. Overall, findings in this study demonstrate that the relationship between Apalachicola River discharge and nutrient-phytoplankton dynamics in AB is complex, with a number of other factors such as light availability, residence time, and grazing affecting Chl *a* biomass in the bay. These factors should be considered when developing projections of potential changes in Apalachicola Bay ecosystem dynamics under future climate and upstream water withdrawal scenarios.

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