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Research article

Influence of regulated water discharges on phytoplankton composition and biomass in a subtropical canal

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ABSTRACT

Phytoplankton composition and biomass were investigated in the C-43 Canal in southwest Florida during a period of shifting discharges from water control structures. The canal receives regulated discharges from eutrophic Lake Okeechobee via the S77 structure. During periods of high S77 discharge in spring and early summer, cyanobacteria biomass dominated the phytoplankton community, including blooms of the harmful algal bloom (HAB) species *Raphidiopsis raciborskii*, *Limnothrix redekei* and *Microcystis aeruginosa*. During periods of low discharges from the lake, in mid-summer and autumn, water inputs to the canal came primarily from tributaries in the watershed surrounding the C-43. Phytoplankton biomass decreased, but the relative importance of dinoflagellates increased, including a bloom in July. The dinoflagellate community included *Ceratium, Durinskia baltica, Glochidinium penardiforme, Gymnodinium fuscum, Parvodinium goslaviense, Parvodinium umbonatum/inconspicuum* complex, *Peridiniopsis quadridens, Woloszynskia reticulata*, and an unidentified thecate and athecate species. *D. baltica* and *P. goslaviense* were recorded for the first time in Florida. Data was also obtained on water temperature, conductivity, fluorescent dissolved organic matter, chlorophyll $\underline{a}$, total nitrogen, dissolved inorganic nitrogen, total phosphorus, PO_4, discharge rates from water control structures, and water residence times. Results show that temporal shifts in the sources and rates of water inputs to the C-43 influence the character of environmental conditions that define phytoplankton composition and biomass in the canal. This suggests that management of discharges can play a role in mitigating HABs in the canal and downstream coastal environments receiving water from the canal.

1. Introduction

The frequency and intensity of harmful algal blooms (HABs) in lakes and reservoirs in many regions worldwide have increased over the past century in response to increases in cultural eutrophication (O'Neil et al., 2012; Paerl et al., 2016; Huisman et al., 2018). In part, this is also a product of the extended water residence times in many lentic ecosystems that provide sufficient time for the accumulation of phytoplankton biomass to bloom levels. By contrast, many lotic systems (e.g., creeks and rivers) are less prone to intense planktonic HABs because of shorter water residence times and high flushing rates (Hilton et al., 2006). The introduction of water control structures (e.g., dams, locks, weirs, pumping stations) to many lotic systems for a wide range of objectives (e.g., flood prevention, water supply needs, hydroelectric power, navigation) have altered their hydrology and in some cases increased the potential for planktonic HABs (Sin and Jeong, 2015; Cheng et al., 2019; Kim et al., 2021; Ruan et al., 2024). The trend has led to increased efforts to develop management strategies that use regulation of water discharge schedules as a means of minimizing the potential for HABs (Mitrovic et al., 2003, 2011; Sin and Jeong, 2015, Sin et al., 2013; Xin et al., 2020). A prominent example of this issue is the canal systems that link the west and east coasts of the Florida peninsula, with Lake Okeechobee at the epicenter. Regulated discharges of water from the lake into the C-43 Canal (aka, Caloosahatchee River) on the west side of the lake and C-44 Canal (aka, St. Lucie River) on the east side occur throughout the year. Because the lake is eutrophic (Phlips et al., 1993; Missimer et al., 2021), and subject to frequent and intense cyanobacteria blooms (Phlips et al., 2015; McCarthy et al., 2009; Beaver et al., 2013; Rosen et al., 2017; Krimsky et al., 2019), the discharges periodically result in the introduction of disruptive HABs into the canals, which can ultimately impact downstream coastal ecosystems, i.e., the Caloosahatchee Estuary on the west coast (Fig. 1) and St. Lucie Estuary on the east coast (Phlips et al., 2012, 2020; Rosen et al., 2017; Krimsky et al., 2019; Metcalf et al., 2021; Uejio et al., 2022).

Over the past few decades attention has been focused on the dynamics of cyanobacteria HABs in Lake Okeechobee, but less is known

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Fig. 1. The S79 water control structure located at the lower end of the C-43 Canal at the boundary with the Caloosahatchee Estuary, showing accumulation of a cyanobacteria bloom at the upstream side of the S79 (Milbrandt, SCCF).

about the character and dynamics of phytoplankton communities in the canals that connect the lake to coastal environments on the west and east coasts of Florida. In this study we focused attention on the spatial and temporal distribution of phytoplankton composition and biomass in the C-43 Canal during a year when there were major shifts in discharge rates into the canal from Lake Okeechobee via the S77 water control structure, and inputs to the Canal from the surrounding watershed. The study had four major objectives addressing key questions about the phytoplankton community of the C-43 ecosystem; 1) Is there a potential for autochthonous blooms in the Canal, in addition to the allochthonous HABs that are periodically introduced to the Canal from Lake Okeechobee? 2) Are cyanobacteria the exclusive dominant taxa in the Canal? 3) How do temporal variations in the amount of water introduced to the Canal from Lake Okeechobee versus the surrounding watershed affect phytoplankton composition and biomass? 4) How do seasonal, event-driven (e.g., hurricanes), and management-driven (e.g., regulation of discharges from the S77 and S79 water control structures) variations in key environmental factors (e.g., light availability, temperature, rainfall, nutrient levels, water residence times) affect phytoplankton composition and biomass? The results highlight the importance of discharge regulation in defining the character of key environmental conditions in the C-43 that impact phytoplankton community structure and biomass, including HABs, which can impact the health of the Canal and downstream coastal environments. The results also provide a broad view of the dominant elements of the phytoplankton communities in the Canal, including the importance of dinoflagellates in this subtropical freshwater ecosystem.

2. Material and methods

2.1. Sample site description and collection

Climatic conditions in Florida range from the tropical regime in the Florida Keys and the southern tip of the peninsula, to humid sub-tropical conditions in the rest of Florida (prism.oregonstate.edu). The C-43 Canal and Caloosahatchee Estuary (Fig. 2) are located near the boundary of the two climatic regimes. The C-43 Canal was completed in 1966 (Antonini et al., 2002), and connects Lake Okeechobee, Florida's largest lake, to the Caloosahatchee Estuary. The Canal is part of a navigable passage for boats from the west to east coast of Florida via Lake Okeechobee and the St. Lucie Canal on the east coast of Florida. The Canal, on the west coast, includes three water control structures, with locks that facilitate transport of vessels, i.e., S77 adjacent to the Lake, the S78 approximately mid-way down the Canal, and the S79 at the upper reach of the estuary (Fig. 2). Freshwater releases from the water control structures are regulated by the U.S. Army Corps of Engineers and South Florida Water Management District to achieve several goals, including, *i.e.*, 1) Maintaining prescribed water levels in Lake Okeechobee, the C-43 Canal and its surrounding watershed, 2) Managing water resources needed for the agricultural interests in the region, and 3) Managing the environmental health of the Lake, Caloosahatchee Estuary, St. Lucie Estuary, and adjacent coastal environment (Flaig and Capece, 1998; Doering and Chamberlain, 1999; Buzzelli et al., 2014; Rumbold and Doering, 2020). The C-43 watershed basin covers 3625 km^2 and has extensive agricultural areas and urban/residential areas adjacent to the Canal (Knight and Steele, 2005; FDEP, 2020). In addition to discharges from Lake Okeechobee into the Canal, numerous small tributaries connect the surrounding watershed to the Canal (FDEP, 2020).

Five sampling sites were included in this study of freshwater phytoplankton. Site 1 was in the northern reach of the C-43 Canal near the S-77 water control structure at Lake Okeechobee (Fig. 2). Site 2 was located just downstream of the S78 water control structure. Sites 3–5 were located between the S78 and S79 water control structures (Fig. 2).

Depths at all sampling sites were shallow, between 2 and 3 m. Integrated water samples were collected with a 1¼ inch diameter Schedule 40 PVC tube that evenly collected water from the surface to near 0.2 m from the bottom of the water column. Samples were collected monthly from November 2021 through October 2022.

For seasonal descriptions, winter was defined as December, January and February, spring as March, April and May, summer as June, July, and August and autumn as September, October, and November.

2.2. Water analyses and measurements

Surface water temperature, salinity and fluorescent dissolved organic matter (FDOM) were measured at the five C-43 Canal sites with a YSI EXO2 sonde environmental multi-probe (Xylem, Washington, DC, USA).

Chlorophyll *a* was analyzed using a Trilogy laboratory fluorometer with EPA Method 445.0. Water samples were put in a pre-rinsed 500 mL polypropylene brown screw cap bottle and stored on ice. Samples were filtered onto GF/F glass fiber filters and extracted in 95% acetone overnight and centrifuged. The supernatant was analyzed using the Trilogy fluorometer followed by adding 0.03 ml of 0.1 N HCl to obtain pheophytin. Chlorophyll *a* (corrected) and pheophytin a concentrations were calculated according to equations in EPA Method 445.0.

Samples for total nitrogen (TN) and total phosphorus (TP) determinations were collected from integrated water column water and acidified ($pH < 2.0$) using H_2SO_4 then stored on ice. Benchmark EnviroAnalytical Labs (North Port, Florida, USA) conducted total phosphorus (TP) and PO_4 following EPA Method 365.3. Total nitrogen was calculated from the total Kjeldahl nitrogen method (EPA Method 351.2), plus nitrate/nitrite (Systea Easy Method). NH_4 was determined using EPA Method 350.1.

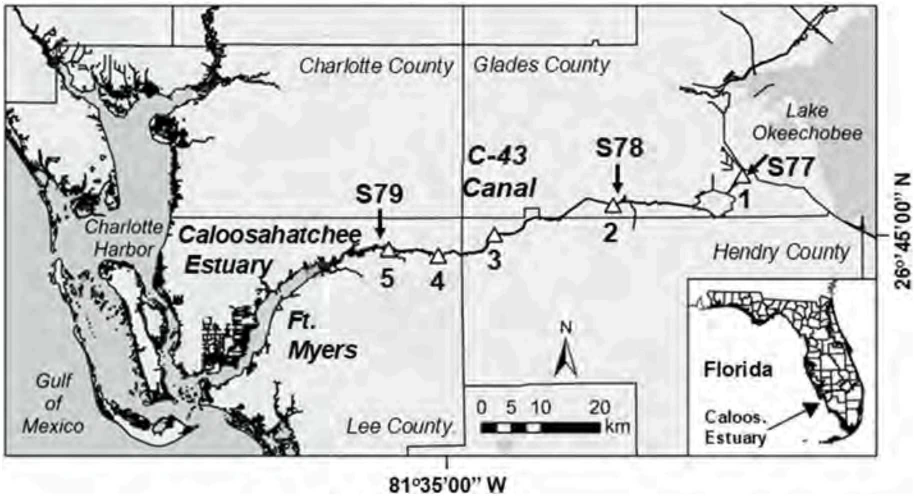

Fig. 2. Location of sampling sites in the study region. Grid lines are county boundaries.

2.3. Rainfall levels, discharge rates, and water residence times

Rainfall levels in the study region were obtained from the NOAA National Climatic Data Center – Climatological Data, Florida (www.ncdc.noaa.gov/IPS) for the Ft. Myers Page FLD AP meteorological station. Daily discharge rates for the S77, S78 and S79 water control structures were obtained from USGS web site (waterdata.usgs.gov/nwis/inventory). Estimates of median water residence times for the upper section of the C-43 Canal (i.e., between the S77 and S78) and the lower section of the C-43 Canal (i.e., between the S78 and S79) were determined using discharge rates at the S78 and S79 water control structures during designated time periods. The estimates used the approximate volume of each section, i.e., 10,000 ac-ft for the S77-S78 section and 30,000 ac-ft for the S78-S79 section. Volumes were converted to ft^3, and the converted volumes were divided by the selected discharge rates (cfs) to estimate the median water residence times in days for each section.

2.4. Microscopy

General phytoplankton composition and abundance were determined using the Utermöhl method (1958) with a Leica phase contrast inverted microscope on Lugol preserved samples as described in Badylak et al. (2014a). Samples preserved in Lugol's were settled in 19 mm diameter cylindrical chambers. Phytoplankton cells were identified and counted at 400x and 100x. At 400x a minimum of 100 cells of a single taxon and 30 grids were counted until 100 cells of a single taxon were reached. If 100 cells of a taxon were not reached in 30 grids counting continued until 100 grids were reached. At 100x, total bottom counts were completed for taxa greater than 25-30µ in size. Morphological descriptions of dinoflagellates and dominant cyanobacteria were based on light microscopy, SEM or captured images of live cells. For purposes of analysis the five major groups of phytoplankton are defined as dinoflagellates, diatoms, picocyanobacteria (cells $\leq$ 2µ), other cyanobacteria (excluding picocyanobacteria), and all other taxa (chlorophytes, cryptophytes and other nanoplanktonic eukaryotes).

Picoplanktonic cyanobacteria abundances were determined using a Zeiss Axio compound microscope using green and blue light excitation (Fahnenstiel and Carrick, 1992; Phlips et al., 1999). Samples were preserved with buffered glutaraldehyde. Subsamples of water were filtered onto a 0.2 µm Nucleopore filters and mounted between a microscope slide and cover slip with immersion oil. Picoplankton was counted at 1000x oil immersion magnification.

SEM samples were prepared from buffered glutaraldehyde preserved samples. Samples were immersed into 4% paraformaldehyde and 2.5% glutaraldehyde in cacodylate buffer overnight at 4^{o}C. The fixed sample was deposited onto poly-L-lysine treated 0.2um polycarbonate filters, washed with 0.1 M cacodylate buffer, followed by 2% buffered osmium tetroxide. After post-fixation, the sample was water-washed and dehydrated in a graded ethanol series of 25% through 100% with increasing concentrations of 5%–10%. Following ethanol dehydration, the sample was critical point dried (Autosamdri-815; Tousimis, Rockville, MD, USA). The dried sample was mounted on carbon adhesive tabs on aluminum specimen mounts and gold-palladium sputter coated and examined by secondary electrons (SE) on a field emission SEM (SU-5000; Hitachi High Technologies America, Schaumburg, IL, USA).

Count data was converted to phytoplankton biovolume using the closest geometric shapes method (Smayda, 1978; Sun and Liu, 2003). Phytoplankton carbon values (as µg carbon L $^{-1}$) were estimated by applying conversion factors for different taxonomic groups to biovolume estimates (expressed as 10^6 µm^3 ml^{-1}), i.e., 0.065 x biovolume/10^6 of diatoms, 0.16 x biovolume/10^6 for dinoflagellates 0.22 x biovolume/10^6, for cyanobacteria and other taxa (Strathmann, 1967; Ahlgren, 1983; Sicko-Goad et al., 1984; Verity et al., 1992; Work et al., 2005).

2.5. Statistical methods

Basic statistical procedures (e.g., determination of mean values, standard deviations) were carried out using SAS v9.4 (SAS Institute, Cary, North Carolina, USA). The means of the variables were compared using the *t.test* function in R (R Core Team, 2024). The variance was not presumed to be equal. The means for Site 1 and combined Sites 2–5 were compared for the months during active discharge from the S77 (March–June), versus months when discharge from the S77 was zero or minimal (i.e., <100 cfs) (July–September).

3. Results

3.1. Rainfall, discharges rates, and water residence time estimates

Monthly rainfall totals at the Fort Myers meteorological station ranged from 1.09 cm in March 2022 to 41.6 cm in September 2022 (Table 1). From November 2021 to March 2022 rainfall levels were consistently below long-term averages. Conversely, rainfall levels were significantly above normal from April to June 2022, and in September 2022, coincident with Category 4 Hurricane Ian. In July and August 2022 rainfall levels were near average long-term levels.

Rates of discharge of water from the S77 water control structure (i.e., from Lake Okeechobee) into the C-43 and S79 water control structure into the Caloosahatchee Estuary were similar from December 2021 to April 2022, at moderate levels of 1500–2000 cfs (Fig. 3). From mid-April to mid-June 2022 discharges from the S77 and S79 were lowered. From July through October discharges from the S77 were very low (i.e., <100 cfs) or negligible. At the same time discharges from the S79 were periodically increased, particularly in June and September–October, due to well above average rainfall levels in the region from April through June, and in September (i.e., largely due to Hurricane Ian) (Table 1).

Changes in discharge levels affected water residence times in the C-43 Canal. During the winter (December 2021 through February 2022), the estimate of median water residence time in the upper Canal (S77-S78) was 3.5 days (Std. dev., 0.5 days), and median water residence time in the lower Canal (S78 to S79) was 7.5 days (Std. dev., 0.2 days), for a total of 11.0 days for the overall Canal. In May 2022, discharge rates were lower, yielding an increase in median water residence time to 7.8 days (Std. dev., 2.5 days) in the upper Canal and 12.2 days (Std. dev., 2.0 days) in the lower Canal, for an overall total of 20.0 days. In June, discharge rates from the S78 and S79 were increased in response to continued above average rainfall levels in the region (Table 1). As a result median water residence times decreased from May to 6.2 days (Std. dev., 6.1 days) in the upper Canal and 6.8 days (Std. dev., 3.33 days) in the lower Canal. In July and August rainfall levels were near long-term average levels and daily discharge rates from the S78 and S79 were highly variable, with estimated median water residence times of 18.8 days (Std. dev., 18.2 days) in the upper Canal and 12.9 days (Std. dev., 4.7 days) in the lower Canal. In September, Hurricane Ian directly impacted the region with high rainfall resulting in increased discharge rates, and comparatively low median water residence times of 5.7 days (Std. dev., 11.5 days) in the upper Canal and 3.4 days (Std. dev., 2.9 days) in the lower Canal.

3.2. Water column conditions

Surface water temperatures ranged from near 20°C in the winter of 2021/22 to highs of 30–33°C in the summer of 2022 (Fig. 4). Temperatures were 25°C or higher from March through November. All five sites in the study showed similar temporal patterns of water temperature.

The C-43 Canal was fresh throughout the study period. Seasonal mean conductivities ranged from 346 to 389 μS/cm in the winter to 588–614 μS/cm in the summer (Table 2). The increases in conductivity during the rainy season (i.e., May–October) in part reflects the increase in comparatively high conductivity of water flowing into the C-43 Canal from the surrounding watershed versus the water entering the Canal from Lake Okeechobee via the S77. In order to exam the impacts of changes in discharges of water from the S77 on conductivity, and other key parameters, we compared mean values at Site 1 (just downstream of the S77 discharge), and a combination of Sites 2–5 in the Canal between the S78 and S79 for two time periods, 1) when S77 and S79 discharge rates were similar (March–June 2022), and 2) after S77 discharge rates were reduced to negligible or very low (i.e., <100 cfs) levels (July–September 2022). At both Sites 1 and combined Sites 2–5, mean conductivities increased by about 20% from Period 1 to 2 (Table 3).

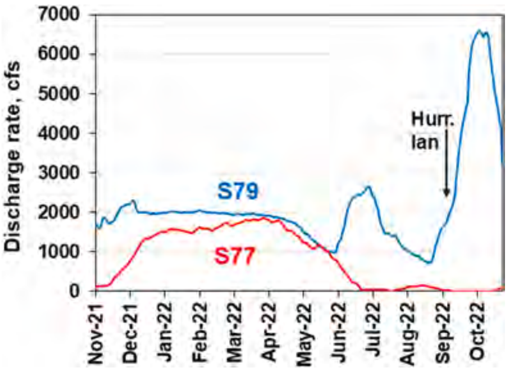

Fig. 3. Discharge rates at the S77 (red line) and S79 (blue line) water control structures (waterdata.usgs.gov/nwis/). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Monthly rainfall totals, and departure from long-term averages.

Month	Rainfall (cm)	Departure From Normal
Nov-21	6.22	1.24
Dec-21	1.37	−2.97
Jan-22	5.21	−0.97
Feb-22	1.22	−3.30
Mar-22	1.09	−4.17
Apr-22	14.81	8.61
May-22	22.02	13.23
Jun-22	35.76	11.23
Jul-22	24.18	0.36
Aug-22	26.72	0.23
Sep-22	41.61	18.75
Oct-22	4.04	−3.78

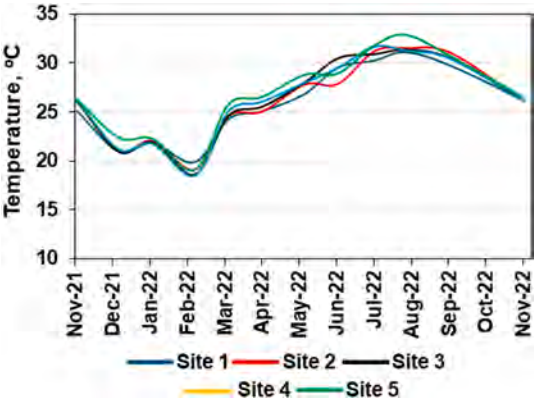

Fig. 4. Surface water temperature at the five sampling sites in the C-43 Canal.

Seasonal mean fluorescent dissolved organic matter (FDOM) levels were high (i.e., >100 qsu) at all five Canal sites in all four seasons of the year (Table 2). The lowest seasonal mean values were in the Spring, ranging from 120 to 177 qsu. The highest values were in the summer and autumn, ranging from 219 to 278 qsu. In the comparison of the March–June and July–September periods, mean FDOM levels for both Site 1 and combined Sites 2–5 went up significantly, roughly doubling (Table 3). The large increase reflects the high color levels in water flowing into the C-43 from the surrounding watershed.

Seasonal mean total nitrogen (TN) concentrations at the five sampling sites were lowest in the winter 2021/22, ranging from 1.10 to 1.21 mg L^{-1} (Table 2). Mean values increased at all sites in the spring 2022. In the summer, mean TN concentrations continued to increase at Site 1 to a peak in the autumn of 2.62 mg L^{-1}, while at Sites 2–5 TN decreased in the summer, before increasing again in autumn. The autumn peaks in part reflect the influence of major Hurricane Ian in September, which resulted in exceptionally high levels of water flowing from the watershed into the Canal, resulting in an extended period of high discharges (i.e., 4000–6500 cfs) from the S79 (Fig. 3). In the comparison of the March–June and July–September periods, no significant differences in mean TN concentrations were observed for either Site 1 or combined Sites 2–5, but mean TN values were higher for Site 1 than for combined Sites 2–5 (Table 3). In an additional comparison of mean values for dissolved inorganic nitrogen (DIN), no significant differences were observed between the March–June and July–September periods at Site 1, but there was a large decline in mean DIN at combined Sites 2–5

Table 2

Seasonal mean conductivity, FDOM, TN, TP and chlorophyll *a* levels at the five sampling sites in the C-43 Canal. Standard deviations are shown in italics.

Site	Mean Conductivity, µS/cm				FDOM, qsu			
	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
1	**346**	**446**	**594**	**457**	**164**	**120**	**241**	**239**
	26	*53*	*56*	*161*	*38*	*17*	*29*	*76*
2	**348**	**536**	**614**	**503**	**190**	**177**	**275**	**278**
	12	*143*	*62*	*84*	*22*	*46*	*18*	*17*
3	**359**	**460**	**613**	**478**	**198**	**147**	**239**	**260**
	14	*50*	*79*	*50*	*12*	*10*	*55*	*22*
4	**368**	**462**	**588**	**532**	**200**	**153**	**230**	**250**
	26	*57*	*62*	*92*	*16*	*12*	*51*	*12*
5	**389**	**463**	**599**	**497**	**198**	**148**	**219**	**237**
	31	*48*	*63*	*31*	*13*	*14*	*33*	*1*

Site	**Mean TN, mg L^{-1}**				**Mean TP, mg L^{-1}**			
	Winter	**Spring**	**Summer**	**Autumn**	**Winter**	**Spring**	**Summer**	**Autumn**
1	**1.21**	**2.01**	**2.26**	**2.62**	**0.028**	**0.066**	**0.075**	**0.202**
	0.16	*0.21*	*0.27*	*0.02*	*0.008*	*0.014*	*0.027*	*0.127*
2	**1.18**	**2.15**	**1.46**	**1.75**	**0.070**	**0.071**	**0.108**	**0.166**
	0.22	*0.41*	*0.18*	*0.25*	*0.041*	*0.021*	*0.009*	*0.076*
3	**1.11**	**1.59**	**1.26**	**1.72**	**0.066**	**0.069**	**0.103**	**0.173**
	0.16	*0.25*	*0.43*	*0.10*	*0.027*	*0.003*	*0.064*	*0.026*
4	**1.10**	**1.89**	**1.29**	**1.62**	**0.049**	**0.072**	**0.094**	**0.162**
	0.19	*0.66*	*0.46*	*0.08*	*0.032*	*0.017*	*0.056*	*0.037*
5	**1.14**	**1.89**	**1.20**	**1.60**	**0.057**	**0.088**	**0.155**	**0.169**
	0.30	*0.22*	*0.40*	*0.11*	*0.019*	*0.005*	*0.095*	*0.026*

Site	Mean Chlorophyll *a*, µg L^{-1}			
	Winter	Spring	Summer	Autumn
1	**16**	**36**	**65**	**24**
	11	*16*	*15*	*5*
2	**15**	**39**	**28**	**15**
	13	*15*	*6*	*13*
3	**10**	**37**	**26**	**19**
	7	*11*	*16*	*16*
4	**13**	**40**	**50**	**14**
	14	*16*	*31*	*16*
5	**15**	**56**	**65**	**30**
	9	*18*	*13*	*6*

Table 3

A comparison of mean values of conductivity, FDOM, TN, DIN, TP and PO_4 for Site 1 and combined Sites 2–5 for the March–June and July–September time periods. Mean values that were significantly different between time periods are indicated by asterisks: $^{*}\rho \leq 0.05$, $^{**}\rho \leq 0.001$, $^{***}\rho \leq 0.00001$. Standard deviations are shown in italics.

Parameters	Sites	March–June	July–September
Conductivity, µs cm^{-1}	1	**488**	**601**
		94	*60*
	2–5	499*	593*
		80	*82*
FDOM, qsu	1	144*	271*
		51	*38*
	2–5	166*	260***
		33	*22*
TN, mg L^{-1}	1	**2.00**	**2.47**
		0.17	*0.17*
	2–5	**1.66**	**1.56**
		0.54	*0.20*
DIN, mg L^{-1}	1	**0.209**	**0.217**
		0.247	*0.103*
	2–5	0.158*	0.032*
		0.157	*0.019*
TP, mg L^{-1}	1	0.061*	0.097*
		0.015	*0.016*
	2–5	0.072**	0.139**
		0.018	*0.045*
PO_4, mg L^{-1}	1	0.018*	0.053*
		0.014	*0.025*
	2–5	0.021*	0.098*
		0.014	*0.028*

(Table 3). The difference is also reflected in the significantly higher mean DIN at Site 1 than combined Sites 2–5 in the July–September period.

Seasonal mean total phosphorus (TP) concentrations were lowest in the winter 2021/22, with values from 0.028 to 0.070 mg L^{-1} (Table 2). Mean concentrations steadily increased from spring through autumn, peaking with values ranging from 0.162 mg L^{-1} at Site 4 to 0.202 mg L^{-1} at Site 1. In the comparison of the March–June and July–September periods, mean TP concentrations for both Site 1 and combined Sites 2–5 increased significantly from the first to the second period, with a 1.6-fold increase at the former site and a 1.9-fold increase at the latter site (Table 3). In an additional comparison of mean values for PO_4, Site 1 had a significant increase of 3-fold from March–June to July–September and combined Sites 2–5 had a 5-fold increase (Table 3). This indicates major inputs of inorganic phosphorus into the Canal from the watershed during the second period.

3.3. *Spatial and temporal patterns of phytoplankton biomass*

Seasonal mean corrected chlorophyll *a* concentrations at the five sample sites were lowest in the winter 2021/22, with values ranging from 10 to 16 µg L^{-1} (Table 2). Mean values increased by 2-4-fold in the spring. The highest mean value reached was 65 µg L^{-1} at Sites 1 and 5 in the summer. Mean concentrations decreased in autumn at all five sites.

Total phytoplankton biomass (as µg carbon ml^{-1}) followed the same general seasonal pattern as chlorophyll *a* values, with increasing values in the early spring, peaking in late spring/early summer, then declining in the late summer/fall, as illustrated by the time-series for Sites 1–5 (Fig. 5). In Fig. 5 the five major groups of phytoplankton are subdivided

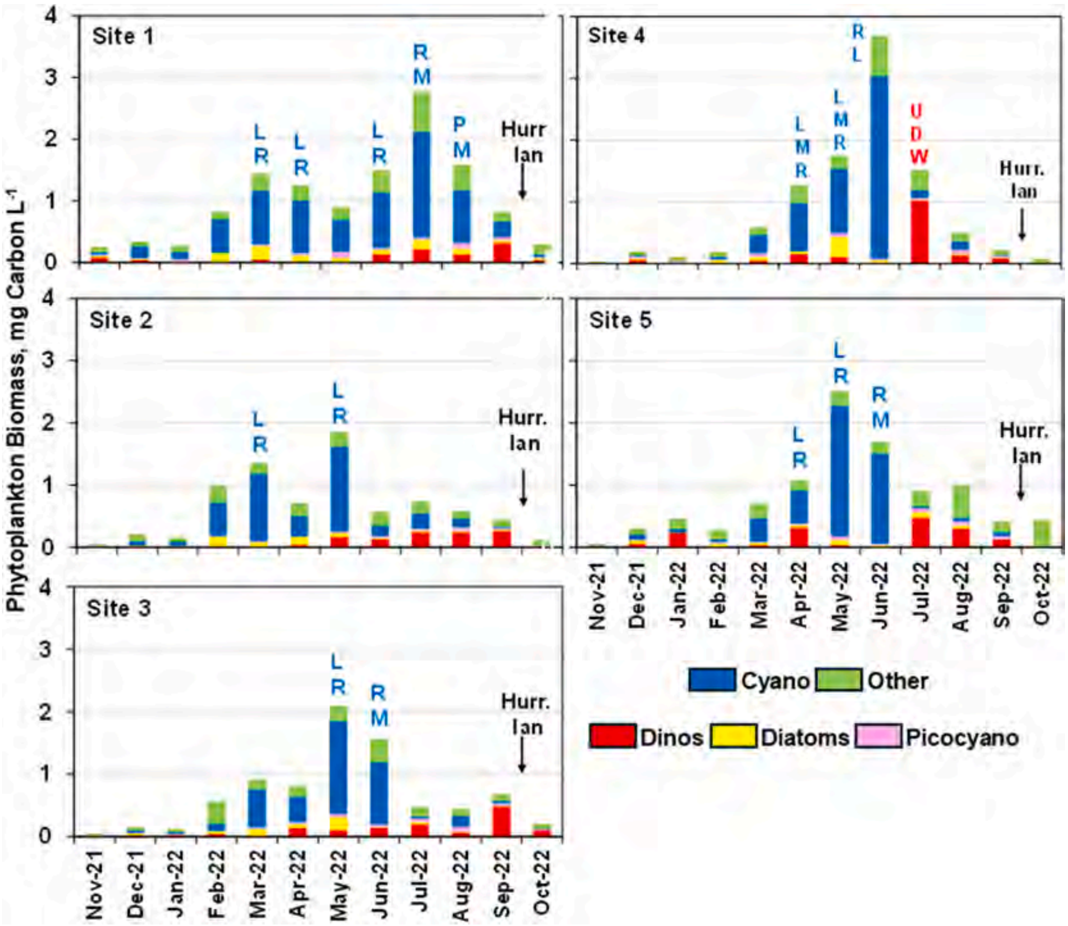

Fig. 5. Total phytoplankton biomass (as μg carbon ml^{-1}) at Sites 1–5 in the C-43 Canal. Total biomass is subdivided into five major phytoplankton groupings, i.e., dinoflagellates (red), diatoms (yellow), picoplanktonic cyanobacteria (pink), other cyanobacteria (blue), and all other taxa (green). The letters above the bars with bloom levels of biomass (i.e. ≥ 1 μg carbon ml^{-1}) represent the dominant species in the bloom, i.e., cyanobacteria: L – *Limnothrix redekei*, M – *Microcystis aeruginosa*, P – *Planktolyngbya limnetica*, R – *Raphidiopsis raciborskii*, and dinoflagellates: D – *Durinskia baltica* **U** – Unidentified thecate sp, W – *Woloszynskia reticulata*. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

as dinoflagellates, diatoms, cyanobacteria (excluding picocyanobacteria), picocyanobacteria (cells $\leq 2\mu$), and all other taxa (chlorophytes, cryptophytes and other nanoplanktonic eukaryotes).

At Site 1, just downstream of the S77, total phytoplankton biomass increased in the early spring, peaked in July at 2.8 mg carbon L^{-1}, then declined sharply through September (Fig. 5). Phytoplankton biomass was dominated by cyanobacteria from December 2021 through July 2022 (Fig. 6). In months with bloom levels of biomass (i.e., >1 mg carbon L^{-1}), four species of cyanobacteria dominated the filamentous taxa *Limnothrix redekei*, *Raphidiopsis raciborskii*, *Planktolyngbya limnetica*, and the colonial species *Microcystis aeruginosa* (Fig. 5).

At Site 2, just downstream of the S78 water control structure, total phytoplankton biomass increased in the spring, peaked in May near 2 mg carbon L^{-1} (Fig. 5). During the latter period cyanobacteria dominated the phytoplankton community, most prominently *L. redekei* and *R. raciborskii* (Fig. 5). After May, total phytoplankton biomass declined, and the relative importance of dinoflagellates increased significantly (Fig. 6).

Patterns of total phytoplankton biomass at Sites 3–5 followed the same general trends as observed at Site 2, except elevated levels of cyanobacteria biomass extended into June, involving the same dominant species observed at Site 1 (Fig. 5). As in the case of Site 2, dinoflagellates played a major role in total phytoplankton biomass (Fig. 6), including a bloom at Site 4 in July, dominated by three species *Durinskia baltica*, an unidentified thecate sp., and *Woloszynskia reticulata*.

The shift in dominance from cyanobacteria to dinoflagellates at Sites 2–5 in the summer coincided with a dramatic reduction in water discharges from Lake Okeechobee into the C-43 via S77 from late June through October 2022 (Fig. 3). The shift in the distribution of phytoplankton biomass is illustrated by a comparison of mean relative biomass of the five major groups of phytoplankton at Site 1 and Sites 2–5 prior to the decline in S77 discharge in March–June 2022, versus mean relative biomass after the decline in S77 discharge in July–September 2022 (Table 4). At Site 1, There were no significant differences in the mean relative biomass between the March–June and July–September time periods. The two largest contributors to mean biomass at Site 1 were ‘other cyanobacteria’ (i.e., mostly filamentous and colonial forms) at 62 and 50%, and ‘all other taxa’ (i.e., mostly nanoplanktonic eukaryotes) at 20 and 21%.

At Sites 2–5 the ‘other cyanobacteria’ group represented the highest mean relative biomass from March–June at 64%, and the ‘all other taxa’ category were second highest at 17%. In July–September there was a significant shift, dinoflagellates becoming the dominant group in terms of mean relative biomass at 48%, and the representation by the ‘other cyanobacteria’ group dropped to 13% (Table 4). Mean relative biomass of diatoms declined from 7% in March–June to 3% in July–September. Mean relative biomass of picocyanobacteria increased from 3% in March–June to 10% in July–September, and ‘all other taxa’ increased from 17% to 26%.

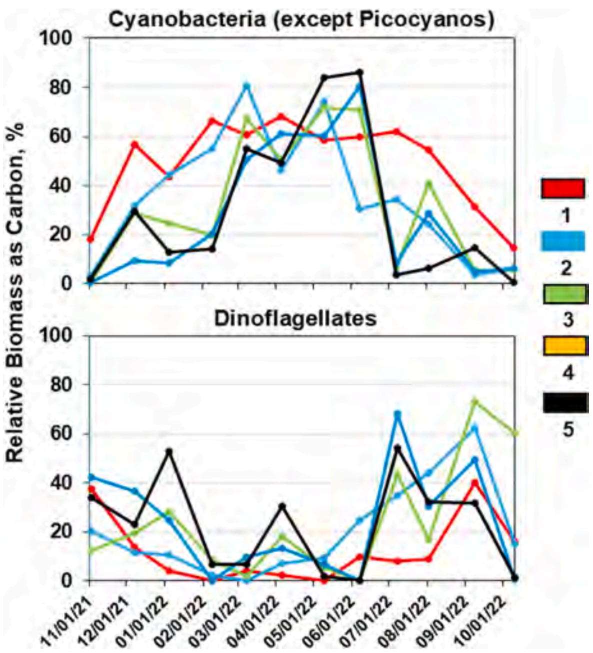

Fig. 6. A comparison of relative contributions (%) of cyanobacteria (except picocyanobacteria) and dinoflagellates to total phytoplankton biomass (as carbon) at the five sampling sites; Site 1 (red), Site 2 (blue), Site 3 (green), Site 4 (orange, and Site 5 (black). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 4

A comparison of mean relative biomass contributions of the five major groupings of phytoplankton for Site 1 and combined Sites 2–5 for the March–June and July–September time periods. Mean values that were significantly different between time periods are indicated by asterisks: $^{*}\rho \le 0.05$, $^{**}\rho \le 0.001$, $^{***}\rho \le 0.00001$. Standard deviations are shown in italics.

Sites	Group	Mean Relative Biomass, %	
		March–June	July–September
Site 1	**Dinoflagellates**	**4**	**19**
		4	*18*
	Diatoms	**9**	**5**
		5	*2*
	Picocyanobacteria	**5**	**5**
		4	*3*
	Other Cyanobacteria	**62**	**50**
		4	*16*
	All other taxa	**20**	**21**
		3	*4*
Sites 2–5	**Dinoflagellates**	**9*****	**48*****
		9	*15*
	Diatoms	**7***	**3***
		6	*3*
	Picocyanobacteria	**3****	**10****
		3	*6*
	Other Cyanobacteria	**64*****	**13*****
		16	*11*
	All other taxa	**17***	**26***
		8	*10*

3.4. *Dinoflagellate community of the C–43 canal*

Freshwater dinoflagellates from the genera *Ceratium, Durinskia, Glochidinium, Gymnodinium, Parvodinium, Peridiniopsis, Woloszynskia*, an unidentified thecate sp., and small athecate cells (<20μ) were present in depth-integrated sample water collected from November 2021 to October 2022, at the five sampling sites located in the C-43 Canal.

Two distinct morphological forms of *Ceratium* (Schrank, 1793), were observed with light microscopy (Fig. 7A and B). *Ceratium* abundances were highest in the spring season (Table 5).

The observation of *Durinskia baltica* (Levander) Carty and Cox 1986 in this study is the first account for Florida. It was observed in all seasons at four of five sites, with highest densities in the summer (Table 5. Peak cell densities were in excess of 150 cells ml^{-1} at three of five sites, reaching up to 302 cells ml^{-1}. The name *D. baltica* is considered a heterotypic synonym of *Durinskia dybowskii* (Woloszyńska) Carty, but the acceptability of the name *D. dybowskii* is in doubt (Lira et al., 2022). *D. baltica* is the most widely used name with an unambiguous nomenclatural type (Cavalcante et al., 2017; Lira et al., 2022, 2023). *D. baltica* appeared as a round brownish cell with a median cingulum and a central nucleus (arrow) (Fig. 7E). SEM images of *D. baltica* displayed smooth thin plates and sutures that were difficult to see, and a Sd plate appeared as a flap over the sulcal area (arrow) (Fig. 7C). A linear row of pores was present above the cingulum (arrows) (Fig. 7D).

Glochidinium penardiforme (Lindemann) Boltovskoy 1999 was observed at all sites, reaching its highest densities during the summer (Table 5)). An SEM image of the cell displays a flattened antapical, distinctive $3'$ plate (arrow) and a visible raised ridge around the apical pore (arrow) (Fig. 7F). A Lugol preserved sample using light microscopy revealed a strongly bilobed hypotheca (Fig. 7G).

Gymnodinium fuscum (Ehrenberg) Stein 1883, was observed during winter and spring, with highest densities in the spring (Table V). Cells often exhibited a mucoid halo during the study period (Fig. 7H).

This is the first record of *Parvodinium goslaviense* (Woloszyńska) Carty 2008, in Florida. It occurred during both the summer and autumn seasons and its highest density was during the summer (Table 5). In live cells, colored bodies were present in the epitheca, and the nucleus was visible in the hypotheca (Fig. 7I). A single antapical spine was visible (Fig. 7J).

Parvodinium umbonatum/inconspicuum species complex was observed at all five sites and reached the highest densities in the summer (Table 5). The *Parvodinium umbonatum/inconspicuum* species complex was created to address the uncertainties associated with this taxonomic group (Cavalcante et al. 2017; Kretschmann et al., 2018; Luo et al., 2021; Pandeirada et al., 2023). Cells observed in this study had a pentangular shape, with an apical pore and flattened posterior (Fig. 7K). SEM revealed the $3'$ and $4''$ plate a dorsal epitheca conjunctum arrangement, reticulate surface plate ornamentation, wide intercalary bands, a wide cingulum, and slightly larger epitheca. (Fig. 7L).

An unidentified thecate sp. was common at all sites, with highest cell densities in the summer and autumn (Table 5). Peak cell densities were in excess of 200 cells ml^{-1} at four of five sites, reaching up to 589 cells ml^{-1}. Cells had a pentagonal shape with a rounded epitheca (Fig. 7M). SEM revealed reticulate surface ornamentation, and a sulcus which widens in the hypotheca to antapex and a $1'$ plate not visible (Fig. 7N). An SEM anterior view shows the apical pore (Fig. 7O).

Peridiniopsis quadridens (Stein) Bourrelly 1968 was observed at all sites, with the highest cell densities in the summer (Table 5). Cells were conical with an angled epitheca with a short horn, two antapical spines and two postcingular spines that were often difficult to see without fine focus using light microscopy (Fig. 7P). The four sided $4''$ plate is shown in an empty cell (arrow) (Fig. 7Q). Postcingular spines were more apparent in the SEM view (Fig. 7R).

Woloszynskia reticulata Thompson 1950, was observed at all sites during the summer and autumn, with a highest densities in the summer (Table 5). Cells had a conical epitheca and a scalloped uneven hypotheca (Fig. 7S). SEM revealed an apical carina (see arrow) and thick hypotheca plate margins (Fig. 7T).

An unidentified athecate cells (<20 μm) was observed at all five sites, with highest cell densities in the summer and autumn (Table 5). Peak cell densities exceeded 200 cells ml^{-1} at four of five sites, reaching up to 775 cells ml^{-1}. Cells had a rounded epicone and hypocone (Fig. 7U). Empty cells revealed a thin wall structure (Fig. 7V).

Additional morphological information for dinoflagellate taxa observed in this study is available in Appendix A (Supplemental Data).

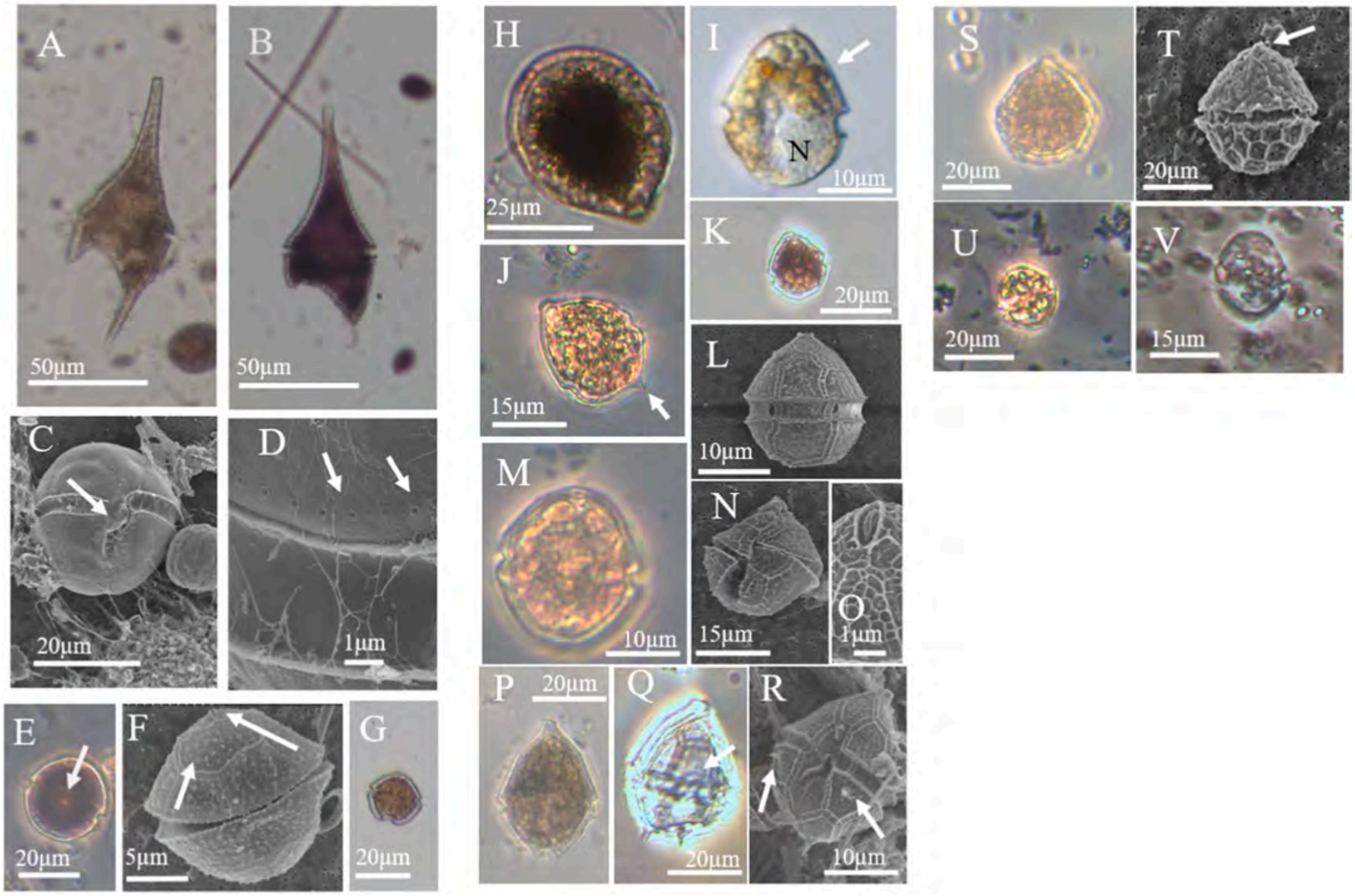

Fig. 7. Dinoflagellates observed in the C-43.

(A) and **(B)** Lugol's preserved sample images of *Ceratium* cells, ventral view.

(C) *Durinskia baltica,* SEM micrograph displaying ventral view of cell with slightly descending cingulum and Sd plate (arrow).

(D) *Durinskia baltica,* SEM micrograph of linear row of pores above cingulum (arrows).

(E) *Durinskia baltica,* Lugol's preserved sample image of a cell showing central nucleus (arrow).

(F) *Glochidinium penardiforme,* SEM dorsal view of raised ridge around canal plates and apical pore (arrow), 3′ plate (arrow).

(G) *Glochidinium penardiforme,* Lugol's preserved sample image of a ventral view.

(H) *Gymnodinium fuscum,* Lugol's preserved sample image of a cell.

(I) *Parvodinium goslaviense*, Live image with reddish colored bodies in epitheca (arrows) and Nucleus in hypotheca.

(J) *Parvodinium goslaviense* Lugol preserved image with singular antapical spine (arrow).

(K) *Parvodinium umbonatum/inconspicuum,* Lugol's preserved sample image of a cell.

(L) *Parvodinium umbonatum/inconspicuum,* SEM dorsal view.

(M) Unidentified thecate sp., Lugol's preserved sample image of a cell.

(N) Unidentified thecate sp., SEM micrograph ventral view displaying sulcus extending to antapex.

(O) Unidentified thecate sp. SEM micrograph of apical pore.

(P) *Peridiniopsis quadridens*, Lugol's preserved sample image of cell displaying slightly larger epitheca than hypotheca and antapical spines.

(Q) *Peridiniopsis quadridens*, *Peridiniopsis quadridens,* Lugol's preserved sample image of empty theca displaying four-sided 4″ plate (arrow).

(R) *Peridiniopsis quadridens*, SEM micrograph of two postcingular spines (arrows).

(S) *Woloszynskia reticulata,* Lugol's preserved sample image of a cell with sculpted hypotheca appearance.

(T) *Woloszynskia reticulata,* SEM micrograph with epitheca apical carina (arrow) and heavy sutures in hypotheca.

(U) Athecate cells <20 µm, Lugol's preserved sample image.

(V) Athecate cells < 20 µm*,* Lugol's preserved sample image of empty thin wall structure.

3.5. *Dominant cyanobacteria of the C-43 canal*

During high discharge periods into the C–43 Canal from the S77 during the spring and early summer, the dominant cyanobacteria taxa during bloom events in terms of biomass were three HAB species, *R. raciborskii*, *L. redekei* and *M. aeruginosa*, as well as *Planktolyngbya limnetica* (Fig. 5).

Raphidiopsis raciborskii (Woloszyńska) Aguilera et al. 2018 (previously known as *Cylindrospermopsis raciborskii* (Woloszyńska) Seenayya and Subba Raju 1972 is a filamentous species observed at all sites and was most abundant during the spring and early summer, sometimes at bloom levels of biomass (i.e., ≥1 µg carbon ml^{-1}) (Fig. 5). Trichomes were composed of cylindrical cells in a filament that is straight or slightly curved. Two types of trichomes were observed during this study, trichomes with a heterocyst at one or both terminal ends (Fig. 8A–C) and trichomes lacking a heterocyst but displaying pointed terminal cells (Fig. 8B and C). The observation of a form of *R. raciborskii* not containing heterocysts is the first record of the form in Florida, but it has been observed in other ecosystems and appears to be the same species as the form with terminal heterocysts (Aguilera et al., 2018).

Microcystis aeruginosa (Kützing) Lemmermann 1907, was observed in the C-43 Canal in the form of large amorphous colonies, sometimes

Table 5

Observations of dinoflagellates at the five sampling sites. Range of dinoflagellate cell ml^{-1} for each species at each sampling site. Number in parentheses indicates the number of times each species was observed at each site. Letter designations show the seasons when each taxon was observed at each site, i.e., S – Summer, A – Autumn, W – Winter, and SP – Spring. The season when the highest cell density of each species was observed at each site is shown in red.

Dinoflagellate	Site 1	Site 2	Site 3	Site 4	Site 5
Ceratium	0	1 – 2 (2) SP	1 (1) SP	0	1 – 5 (4) W, SP
Durinskia baltica	30 -151 (4) S, A, W	5 – 302 (9) S, A, W, SP	15 – 91 (6) S, A, W, SP	9 – 272 (7) S, A, W, SP	60 – 181 (8) S, A, W, SP
Glochidinium penardiforme	60 -165 (3) A, SP	70 (1) W	15 – 50 (4) S, W, SP	101 – 362 (2) S, SP	10 – 106 (4) S, A, W
Gymnodinium fuscum	0	0	30 – 151 (2) W, SP	28 – 101 (2) SP	295 (1) SP
Parvodinium goslaviense	30 (1) A	101 (1) S	0	23 – 90 (3) S, A	91 – 202 (2) S
Parvodinium umbonatum / inconspicuum	151 (1) S	15 – 107 (3) S	19 – 91 (2) S, A	23 – 36 (2) S, A	15 – 101 (3) S, A
Unidentified thecate sp.	14 - 353 (5) S, A, W	5 – 38 (5) S, A, W	5 – 246 (7) S, A, W, SP	5 -589 (8) S, A, W, SP	10 – 227 (7) S, A, W, SP
Peridiniopsis quadridens	1 – 3 (2) S	1 – 7 (2) S, A	1 – 5 (3) S, A	1 – 15 (5) S, A	1 – 21 (5) S, A, SP
Woloszynskia reticulata	2 – 14 (3) S, A, SP	1 – 13 (3) S, A, W	2 – 4 (3) S, A	1 – 74 (3) S, A	1 – 34 (4) S, A, W
Unidentified athecate < 20μ	30 – 202 (3) A, SP	13 – 76 (4) S, A, W, SP	5 – 775 (6) S, A, W, SP	5 – 227 (5) S, A, W	30 – 272 (4) S, A

greater than 1 mm in size (Fig. 8D). *M. aeruginosa* was most abundant in the spring and early summer (Fig. 5).

Limnothrix redekei (Van Goor) Meffert 1988 emend Suda et al., 2002, is a filamentous species, most frequently observed in the spring (Fig. 5). Trichomes had cylindrical cells and were slightly flexuous with rounded terminal cells. Thin cross walls (Fig. 8E) and aerotopes were present (Fig. 8E inset) but not always clearly visible.

*Planktolyngbya limnetica (*Lemmermann) Komárková-Legnerová and Cronberg, 1992, is a filamentous species observed at highest densities in early summer (Fig. 5). Trichomes were composed of cylindrical cells with thin colorless sheaths (Fig. 8F).

Additional morphological information for cyanobacteria taxa observed in this study is available in Appendix A (Supplemental Data).

4. Discussion

4.1. Cyanobacteria in the C-43 canal

The focus of many studies of phytoplankton in freshwater ecosystems of Florida has been on cyanobacteria, in large part because of the high frequency and wide distribution of harmful algal blooms (HABs) dominated by this taxonomic group in numerous eutrophic lakes in Florida (Canfield et al., 1989; Phlips, 2002). The results of our study of the C-43 Canal fall in line with this trend, with observations of spring/early summer blooms of cyanobacteria representing 50–85% of total phytoplankton biomass (as carbon equivalents). The dominant taxa included many of the HAB species observed in other eutrophic freshwater ecosystems in Florida, including *Raphidiopsis raciborskii* (formerly called *Cylindrospermopsis raciborskii*), *Microcystis aeruginosa* and *Limnothrix redekei* (Phlips, 2002; McCarthy et al., 2009; Humpage et al., 2012; Rosen et al., 2017), as well as the non-HAB species *Planktolyngbya limnetica*. Another important HAB species observed during the study period, but at comparatively low abundances, was the potential neurotoxin producing HAB species *Dolichospermum circinale* (formally called *Anabaena circinalis*) (Chorus and Welker, 2021). The importance of cyanobacteria in the C-43 Canal is in part related to the fact that the Canal regularly receives water from Lake Okeechobee via the S77 water control structure. Lake Okeechobee is eutrophic and characterized by frequent and intense blooms of the aforementioned cyanobacteria species, which can be introduced to the C-43 via the S77 (Cichra et al., 1995; Phlips et al., 1997; McCarthy et al., 2009; Beaver et al., 2013; Rosen et al., 2017; Metcalf et al., 2021; Uejio et al., 2022).

During our study, *R. raciborskii* reached bloom levels of biomass (i.e., ≥1 μg carbon ml^{-}) on several dates. *R. raciborskii* is a globally important HAB species often associated with the production of toxins (Padisak, 1997; Vico et al., 2020; Tan et al., 2021). The most prominent toxin associated with *R. raciborskii* is the hepatotoxin cylindrospermopsin, but recent evidence suggests that many strains in the western hemisphere may not be capable of producing cylindrospermopsin, including some strains found in Florida (Yilmaz and Phlips, 2011; Vico et al., 2020).

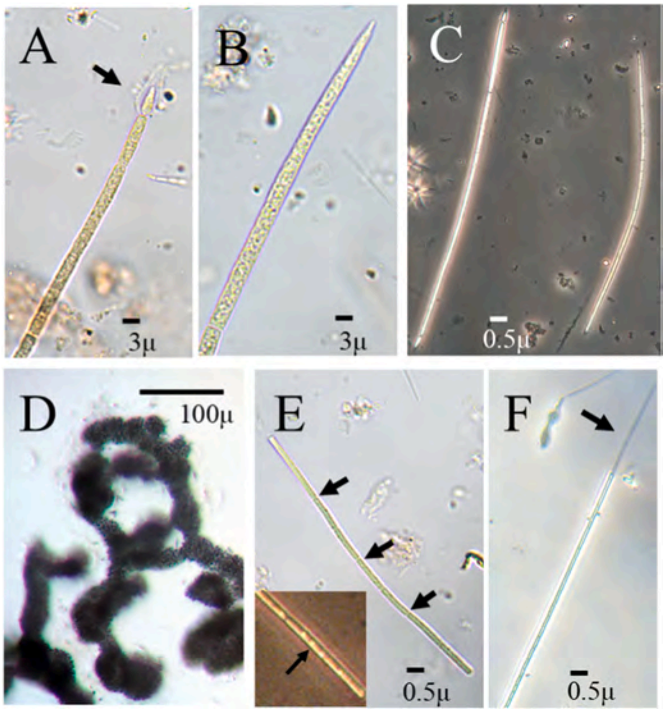

Fig. 8. Dominant cyanobacteria observed in the C-43 Canal
(A) Terminal heterocyst (arrow) of *Raphidiopsis raciborskii*.
(B) Terminal pointed cell of *Raphidiopsis raciborskii*.
(C) View of *Raphidiopsis raciborskii* filaments with terminal heterocyst's and no terminal heterocyst.
(D) Amorphous colony of *Microcystis aeruginosa*.
(E) Limnothrix redekei filament with slight indistinct thin cross walls (arrows) and inset displaying aerotopes (arrow).
(F) Planktolyngbya limnetica with thin colorless sheath (arrow).

Several strains in the western hemisphere have been shown to produce the neurotoxin saxitoxin (Vico et al., 2020).

Microcystis aeruginosa was frequently observed during the study period but mostly at low-moderate levels of biomass. However, several previous studies have shown that the C-43 Canal has experienced intense blooms of *M. aeruginosa* (Rosen et al., 2017; Metcalf et al., 2021; Uejio et al., 2022). *M. aeruginosa* is one of the most important and widespread toxin-producing freshwater HAB species in the world (Harke et al., 2016; Ibelings et al., 2021b). It is most often associated with the production of the hepatotoxin microcystin, which has serious implications for ecosystem, animal and human health (Ibelings et al., 2014, 2021a; Preece et al., 2017; Chorus and Welker, 2021). One of the characteristics of *M. aeruginosa* that may give it an advantage over many other freshwater phytoplankton species is its strong buoyancy regulation capabilities, that give it the ability to find optimal light conditions within the water column (Agusti and Phlips, 1992; Xu et al., 2023). The C-43 Canal is an environment with low light transmission, in part because of the high color levels, as reflected in the high FDOM concentrations observed in this study, which favors species with the ability to move vertically in the water column.

4.2. Dinoflagellates in the C-43 canal

The focus of attention on cyanobacteria in many studies of freshwater ecosystems of Florida is understandable given their tendency to be important bloom-formers in eutrophic lakes and rivers (Canfield et al., 1989; Phlips, 2002, Ibelings et al., 2021), but the results of our study highlight that dinoflagellates also play important roles in the phytoplankton communities of the C-43 Canal. Dinoflagellates are important components of planktonic communities in both marine and freshwater ecosystems (Smayda, 1997; Carty, 2003; Hallegraeff, 2003; Moestrup and Calado, 2018; Anderson et al., 2021). There has been widespread and extensive research on harmful algal blooms (HABs) involving dinoflagellates in marine environments around the world (Hallegraeff, 2003; Phlips et al., 2006; Heil et al., 2014; Lassus et al., 2016; Anderson et al., 2021). Freshwater dinoflagellates have been known to form blooms that result in harmful effects in lake and river ecosystems, but the scope of these studies has been more limited (Jurgens, 1953; Hashimoto et al., 1968; Wu et al., 1998; Rengefors and Legrand, 2001; Carty, 2003; Moestrup and Calado, 2018) in part because of the outsized role of cyanobacteria in many freshwater HABs (Paerl et al., 2016; Chorus and Welker, 2021). Information on dinoflagellates in freshwater ecosystems of Florida is limited and generally as lists of taxa in broad ecological studies (Bailey, 1850; Van Meter-Kasanof, 1973; Taylor et al., 1978; Dawes and Jewett-Smith, 1985; Sullivan et al., 2022).

In our study, dinoflagellates frequently represented 40–70% of total phytoplankton biomass in the summer, winter and autumn seasons in the C-43 Canal. The latter observation warrants a closer examination of the dinoflagellate species that played dominant roles in the phytoplankton community of the C-43, including two species not previously reported for Florida, *Durinskia baltica* and *Parvodinium goslaviense*. The freshwater dinoflagellates observed during this study have worldwide distributions spanning temperate to tropical climates, and oligotrophic to eutrophic environments (Carty, 2014; Moestrup and Calado, 2018), including streams, reservoirs, lakes, ponds, and swamps, and in some cases brackish waters (Boltovskoy, 1999; Hansen and Flaim, 2007; Pandeirada et al., 2013; Cavalcante et al., 2017; Bustamante-Gil et al., 2022).

Some of the physical/chemical characteristics of the C-43 Canal may help to explain the basis for the success of dinoflagellates. One of the most direct influences may be the importance of diverse inputs from many tributaries flowing into the C-43 Canal from local watersheds. A recent study of Ten-mile Creek, a tributary of the St. Lucie estuary in east-central Florida, showed that phytoplankton communities were often characterized by diverse communities of dinoflagellates, chlorophytes, diatoms and small-celled eukaryotes and cyanobacteria (Badylak et al., 2015), as opposed to the more common dominance by cyanobacteria in Lake Okeechobee observed in other studies (Cichra et al., 1995; Phlips et al., 1997; McCarthy et al., 2009; Beaver et al., 2013; Rosen et al., 2017; Krimsky et al., 2019). Similar observations have been made in a current study of freshwater creeks flowing into the Caloosahatchee estuary (Phlips and Badylak, 2024). The inoculation of dinoflagellates from watershed tributaries into the C-43 may help to explain the shift toward greater relative dinoflagellate biomass after the sharp reduction of inputs from the S77 (i.e., Lake Okeechobee), resulting in dominance of watershed inflows to the Canal.

Another important characteristic of the C-43 Canal is its brown color from the tannins in surface water runoff originating from the many watershed tributaries that empty into the canal, as reflected in the high FDOM levels recorded during our study. The dinoflagellates *D. baltica, P. goslaviense, Gymnodinium fuscum, Parvodinium inconspicuum, Glochidinium penardiforme* have all been observed in other brown-colored water ecosystems (Höll, 1928; Canion and Ochs, 2005; Bustamante-Gil et al., 2022, Sullivan et al., 2022). The motility of dinoflagellates provides them the ability to move upward in the water column in search of better light conditions for photosynthesis (Rengefors and Kremp, 2018), and move downward to avoid damaging high light fluxes, as observed in the marine dinoflagellate *Pyrodinium bahamense* (Phlips et al., 2011).

Another noteworthy feature of many dinoflagellate species is the ability to survive and grow mixotrophically, i.e., both photosynthetically and phagotrophically (the ingestion of other organisms) (Stoecker, 1999; Burkholder et al., 2008; Cecchi et al., 2016; Stoecker, 1999; Jeong et al., 2021). The dual ability provides these dinoflagellates with the ability to obtain organic carbon and essential nutrients, even when light and soluble nutrients are in limited supply. A number of the dinoflagellate taxa observed in C-43 in this study have been reported to be mixotrophic, such as *Durinskia* and *Woloszynskia* (Kang et al., 2011; Hehenberger et al., 2016; Onuma et al., 2020). In addition, some dinoflagellates have been shown to have the ability to store nutrients as a means of surviving periods of low inorganic nutrient availability (Barton et al., 2013; Dagenais-Bellefeuille and Morse, 2013).

In terms of dominant species observed during the current study, *D. baltica* was observed at all sites within the C-43 Canal during periods of both low and high freshwater inputs. During the summer, *D. baltica* was a dominant species, reaching bloom levels of biomass (i.e., $\geq$1 μg carbon ml^{-1}) in July. *D. baltica* has been reported from other eutrophic ecosystems associated with watersheds subject to intensive agricultural land uses and freshwater ponds rich in humus (Zhang et al., 2011; Lira et al., 2017). This is comparable to the eutrophic status of the C-43 Canal which is also surrounded by an extensive agricultural region. Another factor contributing to the broad spatial distribution and high frequency of *D. baltica* observations, and several other dinoflagellates, in the C-43 Canal may be the existence of cyst beds. For example, cysts of *D. baltica* in the sediments of eutrophic canals in Mexico have been shown to provide inoculum for blooms (Lira et al., 2017). The importance of cysts in dinoflagellate blooms in Florida has been previously shown in relation to blooms of the marine HAB dinoflagellates *Akashiwo sanguinea* in the Caloosahatchee Estuary and *Pyrodinium bahamense* in the Indian River Lagoon on the east coast of Florida (Badylak et al., 2014a, 2017; Phlips et al., 2023). Cysts play an important role in adapting to adverse environmental conditions in both freshwater and marine ecosystems (Wall et al., 1977; Mertens et al., 2012).

Another noteworthy observation is the high levels of mucilage associated with observations of *G. fuscum* during this study. Mucilage associated with *G. fuscum* has been previously reported in other studies (Thompson, 1947; Dodge and Crawford, 1969; Hansen and Flaim, 2007). The mucilage production of *G. fuscum* could act as a protective barrier against adverse environmental conditions encountered in the C-43 canal. Mucilage production has also been observed downstream of the Canal in the Caloosahatchee estuary by the marine dinoflagellate *A. sanguinea* (Badylak et al., 2014b). Excessive mucilage production can have ecosystem disruptive effects, such as inhibition of grazing (Liu and Buskey, 2000).

Another potential issue often associated with dinoflagellates is toxin production. Many marine species have been shown to produce toxins and/or allelopathic compounds that affect the growth, survival, or behavior (e.g., grazing) of other aquatic organisms (Granéli and Hansen, 2006; Granéli et al., 2008; Lassus et al., 2016), but similar research on freshwater species has been more limited, with only a few preliminary observations of toxin production (Moestrup and Calado, 2018).

Information is scarce regarding freshwater dinoflagellates in Florida. Future research should include further focus on two of most abundant and frequently encountered dinoflagellates observed in this study, the unidentified thecate sp. (previously undescribed S. Carty, Ohio, USA, personal communication July 2023), and unidentified athecate sp. < 20 μm sp. Their prominence in the C-43 emphasizes the need for additional taxonomic assessments and definitions of their potential functional roles, including possible toxin production and other negative impacts of future blooms. In the case of the unidentified thecate sp. information on the entire plate tabulation and apical pore complex is needed to support identification. The unidentified athecate sp. <20 μm requires further examination for the presence of thin plates and other morphological criteria not obtainable from the samples collected in this study.

4.3. Spatial/temporal patterns of phytoplankton biomass

Based on the high chlorophyll *a* levels observed in the C-43 Canal during our study, it would fit into a classification of a eutrophic ecosystem (Carlson, 1977; Carlson and Simpson, 1996). From the perspective of autochthonous phytoplankton production in the Canal, the classification is reflective of the nutrient inputs received from Lake Okeechobee, which is eutrophic (Phlips et al., 1993; Missimer et al., 2021), and inputs from the C-43 watershed (Montefiore et al., 2024), which includes extensive agricultural and residential land uses (Flaig and Capece, 1998; Mulkey et al., 2005; Hindle et al., 2020; FDEP, 2020). There is also a potential for allochthonous phytoplankton biomass inputs from Lake Okeechobee via the S77 water control structure. Historically, large releases of water from Lake Okeechobee into the C-43 during periods of intense blooms in the lake have resulted in peaks of high cyanobacteria biomass in the C-43 (Rosen et al., 2017; Krimsky et al., 2019; Metcalf et al., 2021; Uejio et al., 2022). Similar introductions of intense blooms have been observed in the St. Lucie Canal and estuary, which are connected to Lake Okeechobee on the east coast of Florida (Phlips et al., 2012, 2020; Rosen et al., 2017; Krimsky et al., 2019). Hydrologic characteristics of the C-43 Canal (e.g., flow rates, sources of water inputs) vary seasonally, annually, and due to changes in regulated discharges from the S77 and the S79 water control structures, which defines the volume of water leaving the Canal and entering the Caloosahatchee estuary. Changes in discharges from the water control structures are used to maintain desired water levels and environmental conditions in Lake Okeechobee, the C-43 Canal, the C-43 watershed and the Caloosahatchee estuary (Doering and Chamberlain, 1999; Julien and Osborne, 2018; SFWMD, 2018; FDEP, 2020). In turn, these changes impact the composition, biomass and dynamics of phytoplankton populations in the Canal.

Phytoplankton composition and biomass in the C-43 Canal are dictated by two processes: 1) Allochthonous (external) inputs of phytoplankton from Lake Okeechobee and the C-43 watershed, and 2) Autochthonous (internal) production within the Canal. The magnitude of external inputs depends on the rates, sources, and character (e.g., nutrient levels, phytoplankton composition) of discharges into the Canal from S77 and tributaries within the Canals watershed. Internal increases of phytoplankton biomass depend on factors that influence rates of phytoplankton production and biomass accumulation, such as light flux, temperature, nutrient levels, grazing loses, dilution rates (e.g., rainfall, watershed trinitary inflows) and water residence times in the Canal. These influences vary seasonally (e.g., wet versus dry season), cyclically (e.g., El Niño/La Niña) and in response to stochastic weather events (e.g., tropical storms, droughts) (Phlips et al., 2020). Temporal changes in the structure and biomass of phytoplankton, including shifts in the relative roles of cyanobacteria and dinoflagellates, can be viewed within the context of temporal changes in hydrologic conditions and how they impact phytoplankton composition, biomass, nutrient levels, water residence time, and external introductions of phytoplankton biomass.

Winter is the dry season in South Florida, when runoff from the C-43 watershed is low, elevating the relative importance of inputs of water from Lake Okeechobee (Doering and Chamberlain, 1999; SFWMD, 2018). Winter lows in temperature and light flux limit phytoplankton growth rates and the potential for high phytoplankton biomass, in part because of relatively short water residence times in the Canal. In the winter, estimated median water residence time was around 11 days. Given the low water temperatures (i.e., around 20^{o}C) and incident irradiances in the winter (i.e., approximately half the daily incident photosynthetically active radiation as in the late spring/early summer, Oswald and Gataas, 1957), maximum growth rates for phytoplankton would be significantly lower than observed in warmer months of the year. Since reported values of *in situ* maximum growth rates of most phytoplankton taxa are between 0.2 and 1.0 d^{-1} (Stolte and Garcés, 2006), rates under sub-optimal conditions in the winter would be considerably lower, and likely limit biomass potential given water residence times as short as 11 days. The latter considerations help to explain why winter biomass levels in the C-43 were lower than in the other three seasons. Dinoflagellates were major components of total biomass in the winter. The success of dinoflagellates during this season of lower light and temperature may in part be due to several key characteristics of the group (Smayda, 1997; Smayda and Reynolds, 2003; Cecchi et al., 2016). Dinoflagellates can adapt to low light transmission through the water column because of their motility and ability to vertically migrate, which can also aid in the search for light (Doblin et al., 2006; Ji and Franks, 2007). Many dinoflagellates are mixotrophic, and can grow both photosynthetically and heterotrophically, an advantage under light limited conditions (Stoecker, 1999). Dinoflagellates may also be able to deal with the lower growth rates associated with cooler water temperatures because of lower grazing loss rates compared to other important phytoplankton groups (Breier and Buskey, 2007; Xu and Kiørboe, 2018; Lürling, 2021).

In spring and early summer, large increases in phytoplankton biomass were observed in the C-43 Canal, largely dominated by cyanobacteria. The spring increases in biomass in part reflect seasonal increases in temperature, light availability and rainfall-induced nutrient loads to the Canal from Lake Okeechobee and the C-43 watershed. The dominance of cyanobacteria during the spring rise in biomass is in part driven by inputs from Lake Okeechobee, a lake typically dominated by cyanobacteria (Cichra et al., 1995; Phlips et al., 1997, 2020; McCarthy et al., 2009; Beaver et al., 2013; Rosen et al., 2017). The dominance of filamentous and colonial cyanobacteria observed at Site 1 near the S77 structure for most of the study period in part reflects inputs from the lake. Once introduced to the Canal the inputs can serve as seed for further biomass increases. During the current study period, well above average rainfall levels were observed from April to June and were associated with increases in TN and TP levels in the Canal, which likely supported spring phytoplankton production in the Canal. In addition, long median water residence time of 20 days in the C-43 in May provided the additional time needed for the accumulation of biomass to bloom levels.

In mid-summer, phytoplankton biomass declined from the peak in June, and the dominant group became dinoflagellates, except at Site 1 near the S77 outflow. The greater importance of dinoflagellates in mid-summer than spring/early summer may be viewed from the perspective of the impacts of shifts in climatic conditions and the relative influences of Lake Okeechobee and the C-43 watershed discharges. In part the shift away from cyanobacteria as the dominant species to dinoflagellates likely reflects the cessation of discharges from Lake Okeechobee into the C-43 Canal from June through December 2022. Without the major source of cyanobacteria-rich water from Lake Okeechobee, inputs from C-43 watershed tributaries dominate inflows to the Canal. Phytoplankton in these tributary inputs are likely comparatively low in biomass due to short water residence time in the tributaries. Phytoplankton composition in the watershed tributaries is also likely more diverse in taxonomic composition, including significant representation of dinoflagellates (as detailed the previous sub-section of the discussion), which could serve as inoculum for further growth in the nutrient-rich waters of the Canal, but can also dilute phytoplankton biomass when biomass levels in the Canal are higher. The highest dinoflagellate biomass in the C-43 Canal was a bloom in July.

The high rainfall levels in the region from April–September resulted in elevated concentrations of TP and soluble inorganic phosphorus (i.e., PO_4) in the summer. By contrast, the summer was characterized by lower levels of dissolved inorganic nitrogen (DIN) and low DIN/PO_4 ratios (i.e., 0.4 by weight), suggesting a potential for nitrogen limiting conditions in terms of DIN. One of the reasons for the increased importance of dinoflagellates in the mid-summer of 2022 may relate reduced DIN levels. As noted above, many dinoflagellate species are mixotrophic, giving them the dual capability of photoautotrophic and/or heterotrophic based growth, including phagotrophic consumption of bacteria and small-celled phytoplankton (Stoecker, 1999; Burkholder et al., 2008; Cecchi et al., 2016; Jeong et al., 2021). Dinoflagellates would be capable of adapting to low DIN conditions by consuming prey or nitrogen-rich particulate matter as a source of nitrogen, as well as using organic forms of nitrogen for growth (Burkholder et al., 2008). Another important group of phytoplankton in the C-43 Canal that may benefit from mixotrophy are nanoplanktonic eukaryotes, including some species of haptophytes, raphidophytes, cryptophytes and chlorophytes (Tranvik et al., 1989; Burkholder et al., 2008; McKie-Krisberg and Sanders, 2014). Similarly, the increased relative importance of picoplanktonic cyanobacteria in the summer may in part be related to their ability to use organic forms of nitrogen and compete for DIN at low concentrations (Raven, 1998; Burkholder et al., 2008; Liu et al., 2019; Reinl et al., 2022; Papacek et al., 2024).

In autumn, overall phytoplankton biomass levels continued to decline in the C-43 Canal, during which dinoflagellates were major components of total biomass. The period was characterized by high discharge rates (up to 6600 cfs) from the S79 in September–October, in response to the effects of Hurricane Ian. The extended period of high discharge coincided with short median water residence times, i.e., 5.7 days in the upper Canal and 3.4 days in the lower Canal. The combination of negligible inputs of water from Lake Okeechobee via the S77 and short water residence times help to explain the low phytoplankton biomass levels observed in the autumn. The temporal shifts in water residence times observed over the study period and their correlation to changes in phytoplankton biomass highlight the potential role discharge management could play in effecting bloom dynamics in the Canal.

5. Summary

The results of this study show that the composition and biomass of phytoplankton communities in the C-43 Canal are influenced by both allochthonous sources of water entering the system and autochthonous processes. Large inputs of water from Lake Okeechobee can introduce major blooms of cyanobacteria to the C-43, but even smaller inputs of cyanobacteria can provide the inoculum for the formation of blooms in the C-43, particularly in the spring and early summer. By contrast, during periods when the major sources of water to the C-43 come from the surrounding watershed phytoplankton composition is more diverse, sometimes dominated by dinoflagellates, with a potential for blooms, but generally of lesser peak biomass. The intensity and composition of blooms of autochthonous origin in the canal are influenced by nutrient levels, light, temperature and hydrodynamic conditions, such as water residence time and dilution rates, which are affected by discharge rates from the water control structures and regional rainfall levels leading to inflows of water from local C-43 watersheds. In a more general sense, the results of this study show that defining the drivers of change in phytoplankton composition and biomass in ecosystems subject to anthropogenically regulated water inflows and outflows present both unique challenges and opportunities in terms of management of algal blooms, as highlighted in studies of other ecosystems (e.g., Humborg et al., 1997; Domingues et al., 2012; Sin and Joeng, 2015; Arthington et al., 2018; Morrison et al., 2023; Qian et al., 2023). In as much as the character of external water sources for the canal and water residence times in the canal are regulated by water control structures, there is a potential to use management of discharges to help mitigate negative impacts of HABs in the C-43 and downstream marine ecosystems.

CRediT authorship contribution statement

Susan Badylak: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Edward J. Phlips:** Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Eric C. Milbrandt:** Writing – review & editing, Resources, Investigation. **Elise S. Morrison:** Writing – review & editing, Investigation. **Benjamin D. Stelling:** Writing – review & editing, Investigation. **Shin-Ah Lee:** Writing – review & editing, Investigation. **Thomas A. Frankovich:** Writing – review & editing, Investigation. **David Kaplan:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Edward Phlips reports financial support was provided by US Army Corps of Engineers. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2024.123470.

Data availability

Data will be made available on request.

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