Gulf and Caribbean Research

Volume 17 | Issue 1

January 2005

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Recommended Citation

Murrell, M. C. and J. M. Caffrey. 2005. High Cyanobacterial Abundance in Three Northeastern Gulf of Mexico Estuaries. Gulf and Caribbean Research 17 (1): 95-106.
Retrieved from https://aquila.usm.edu/gcr/vol17/iss1/8
DOI: https://doi.org/10.18785/gcr.1701.08

Gulf and Caribbean Research Vol 17, 95–106, 2005 Manuscript received December 10, 2004; accepted January 31, 2005

HIGH CYANOBACTERIAL ABUNDANCE IN THREE NORTHEASTERN GULF OF MEXICO ESTUARIES

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ABSTRACT Aquatic phytoplankton comprise a wide variety of taxa spanning more than 2 orders of magnitude in size, yet studies of estuarine phytoplankton often overlook the picoplankton, particularly chroococcoid cyanobacteria (cf. *Synechococcus*). Three Gulf of Mexico estuaries (Apalachicola Bay, FL; Pensacola Bay, FL; Weeks Bay, AL) were sampled during summer and fall 2001 to quantify cyanobacterial abundance, to examine how cyanobacterial abundance varied with hydrographic and nutrient distributions, and to estimate the contribution of cyanobacteria to the bulk phytoplankton community. Cyanobacterial abundances in all 3 estuaries were high, averaging 0.59 ± 0.76 X 10^9 L^{-1} in Apalachicola Bay, 1.7 ± 1.2 X 10^9 L^{-1} in Pensacola Bay and 2.4 ± 1.9 X 10^9 L^{-1} in Weeks Bay (mean ± standard deviation). Peak abundances typically occurred in the oligohaline zone (low salinity estuarine zone) during the summer. Freshwater sites had nearly undetectable abundances, and marine sites had abundances several-fold lower than the oligohaline zone. When converted to equivalent chlorophyll *a* concentrations, cyanobacteria comprised a large fraction of the total phytoplankton biomass, at times approaching 100% in all 3 systems. These observations clearly indicate a cyanobacterial community of estuarine origin that can make up a large proportion of phytoplankton biomass.

INTRODUCTION

Phytoplankton are responsible for about 40% of global primary production and form the base of the aquatic food web; they are thus critically important mediators of carbon and energy (Falkowski 1994). Quantitative measures of phytoplankton biomass, size distribution, and community composition are important indicators of the trophic state of aquatic systems and provide insight into the environmental forcings that affect phytoplankton dynamics (Chisholm, 1992). Phytoplankton taxonomic and size composition can also provide insight into the trophic transfer to zooplankton grazers and help predict the resulting zooplankton community composition (Hansen et al. 1994).

In the open ocean, phytoplankton biomass and production are typically dominated by the picophytoplankton (phytoplankton < 2 µm), which are largely comprised of cyanobacteria (e.g., *Synechococcus*) and prochlorophytes (Li 1998). In estuaries, however, the importance of picophytoplankton is not well understood, because estuarine studies often overlook cyanobacteria. A commonly used method for enumerating phytoplankton relies on settling of organisms from a water sample (Utermol 1958). However, particles of 1–2 µm are effectively colloidal and do not sink. Therefore, such studies are biased towards organisms larger than 5–10 µm, thereby overlooking the potential contribution of picophytoplankton (e.g., Livingston 2001, 2003). Nevertheless, there is a growing body of literature showing that estuaries have high cyanobacterial abundances, particularly during the summer, but often their contribution to the total phytoplankton biomass is relatively small (Pinckney et al. 1998, Ning et al. 2000). Notable exceptions include studies in subtropical systems such as Florida Bay (Phlips et al. 1999) and Pensacola Bay (Murrell and Lores 2004), where cyanobacteria can dominate the phytoplankton biomass.

The purpose of this study was to enumerate cyanobacteria in 3 Gulf of Mexico (GOM) estuaries: Apalachicola Bay, Florida; Pensacola Bay, Florida; and Weeks Bay, Alabama. We examined their distribution along the salinity gradient and examined their relationship with chlorophyll *a* (Chl *a*) and dissolved inorganic nitrogen (DIN) concentrations. Additionally, we estimated the cyanobacterial contribution to total Chl *a*, using an estimate of their cell-specific Chl *a* content. Data on cyanobacterial abundances and Chl *a* from Pensacola Bay are a subset of a larger dataset originally reported in Murrell and Lores (2004) and were included here for comparative purposes.

MATERIALS AND METHODS

Study sites

The 3 estuaries chosen for this study are all located along the northeastern coastline of the GOM (Figure 1) and therefore share similar patterns of solar radiation and rainfall. All sites are quite shallow, averaging from 2 to 3 m depth, but vary in estuarine area, watershed area and freshwater flow (Table 1). Apalachicola Bay, located in the middle of the Florida panhandle, is 593 km^2 in size and receives freshwater from the Apalachicola River. Land cover in the Apalachicola portion of the watershed is pri-

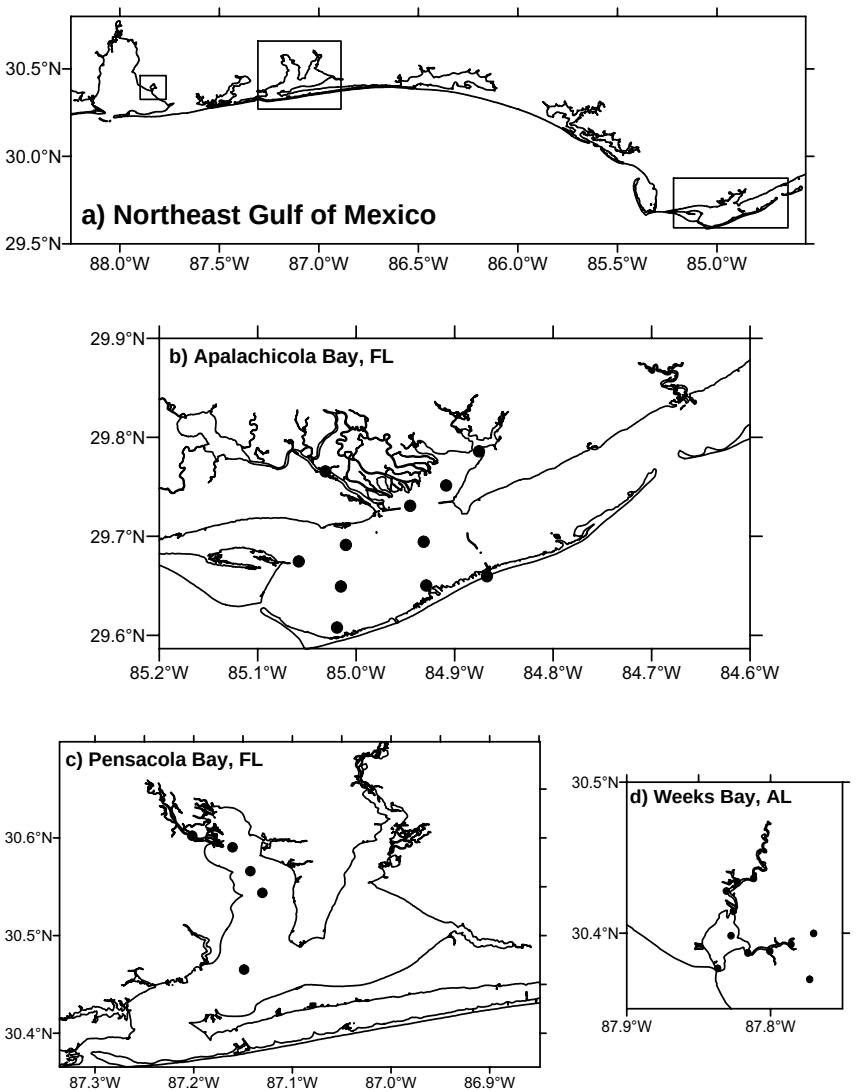

Figure 1. a) Map of study area in the northeastern Gulf of Mexico. Inset maps are included for b) Apalachicola Bay, FL; c) Pensacola Bay, FL; and d) Weeks Bay, AL.

marily forest, including pine flatwoods and bottomland hardwood, with little residential and commercial development. Pensacola Bay is a moderately sized (370 km^2) estuary in the western panhandle of Florida. The major freshwater source is the Escambia River (180 $m^3\ s^{-1}$), which empties into the western side of the system. Other rivers include the Yellow (45 $m^3\ s^{-1}$), and Blackwater (9.2 $m^3\ s^{-1}$), which flow into the eastern side of the system. The watershed is comprised of pine forests (74%), croplands (12%), pastures (7%) and urban development (2%) that is concentrated near the shoreline of the bay. Weeks Bay is a sub-estuary of Mobile Bay, Alabama, and is much smaller (7 km^2) than Pensacola and Apalachicola Bays. The Fish River contributes 90% of the freshwater flow into Weeks Bay, and at the seaward end, Weeks Bay empties into Mobile Bay. Land use is dominated by agriculture, both timber production and cropland, which together represent 68% of the land use in Baldwin County, where Weeks Bay is located (Arcenaux 1996). Agricultural lands are rapidly being converted to suburban developments as population growth increases throughout the county.

Field collection

Samples were collected during summer and fall 2001 (Table 2). In general, sampling sites were oriented along major salinity gradients. Apalachicola Bay was sampled on 3 dates (Sep, Oct, Nov) at seven sites. In November, 4 additional sites were sampled. Pensacola Bay was sampled on five dates (Jul, Aug, Sep, Oct, Nov) at 5 sites on the western side of the system. The Pensacola Bay data are a

TABLE 1

Summary of key physical and environmental characteristics of the 3 Gulf of Mexico estuaries sampled in this study. Rainfall and river flow data are long term means. Residence times are calculated via the fraction of freshwater method of Dyer 1973.

Estuary	Mean annual rainfall (cm)	Estuarine area (km^2)	Watershed area (km^2)	Watershed area: Estuarine area	Mean depth (m)	Mean river flow ($m^3\ s^{-1}$)	Mean residence time (d)
Apalachicola Bay	143	593	51000	86	2.9	710	6
Pensacola Bay	163	370	13500	37	3.3	234	25
Weeks Bay	165	7.0	510	73	2.0	3.4	6

TABLE 2

Station names and locations sampled in this study. The mean salinity from all sampling dates and stations is provided to indicate the station's relative position within the estuary.

Estuary	Station	Latitude	Longitude	Mean salinity (psu)
Apalachicola Bay	Apalachicola River	29° 45.93'N	85° 01.87'W	2
	ANERR 5	29° 41.48'N	85° 00.63'W	18
	Dry Bar	29° 40.48'N	85° 03.50'W	22
	ANERR 4	29° 38.96'N	85° 00.93'W	23
	ANEER 8	29° 43.85'N	84° 56.71'W	23
	East Bay	29° 47.15'N	84° 52.52'W	24
	ANERR 3	29° 36.47'N	85° 01.17'W	25
	ANERR 9	29° 45.08'N	84° 54.52'W	27
	ANERR 6	29° 39.02'N	84° 55.73'W	30
	ANERR 7	29° 41.67'N	84° 55.89'W	30
	Gulf	29° 39.58'N	84° 52.03'W	31
Pensacola Bay	P01	30° 33.13'N	87° 12.09'W	1
	P02	30° 32.42'N	87° 09.64'W	10
	P03	30° 30.95'N	87° 08.56'W	15
	P04	30° 29.62'N	87° 07.83'W	17
	P06	30° 24.91'N	87° 08.94'W	21
Weeks Bay	Weeks Creek, Upper	30° 22.17'N	87°46.37'W	0
	Magnolia River, Upper	30° 23.99'N	87° 46.20'W	1
	Fish River	30° 26.18'N	87° 48.71'W	3
	Waterhole Branch	30° 26.04'N	87° 49.39'W	3
	Turkey Branch	30° 25.67'N	87° 49.84'W	4
	Lulu Dock	30° 24.88'N	87° 49.55'W	5
	Weeks Creek, Lower	30° 23.56'N	87° 47.15'W	6
	Nolte Creek	30° 23.29'N	87° 48.03'W	8
	Magnolia River, Lower	30° 23.21'N	87° 48.95'W	9
	Mid Bay	30° 23.90'N	87° 49.65'W	11
	Mouth	30° 22.60'N	87° 50.20'W	14

subset of a 2 year study examining phytoplankton and zooplankton dynamics previously reported in Murrell and Lores (2004). The dates chosen for inclusion in this study overlap the time frame of the other 2 sites. Weeks Bay was sampled on 3 dates (Jul, Sep, Nov) at 11 sites.

Water samples were collected from the surface layer (top 0.5 m) into clean polyethylene bottles and processed at the lab within hours. Salinity (psu) was measured either with a Hyrolab multimeter (Pensacola Bay) or with a Thermo Orion Model 150A+ conductivity meter (Apalachicola and Weeks Bays). Chl *a* samples were filtered onto Whatman 25 mm GF/F filters (50 to 200 ml) and frozen (–20 °C) until analysis. Chl *a* was extracted in 90% acetone (Strickland and Parsons 1972), and fluorescence was measured with a Turner Designs TD 700 fluorometer calibrated using commercially available Chl *a* standards (Sigma Chemicals). Cyanobacterial samples were collected into 20 ml vials, fixed with 2% final concentration formaldehyde and stored at 4 °C until cell counts were performed via epifluorescence microscopy, as described in Murrell and Lores (2004). Samples for nutrients (NH_4^+, NO_2^-, NO_3^-, PO_4^{3-}) were stored in clean glass or HDPE vials and analyzed using standard methods (APHA 1989). DIP (dissolved inorganic phosphorus) is used to denote PO_4^{3-}, while DIN is the sum of $NO_2^- + NO_3^- + NH_4^+$.

RESULTS

Weather conditions during this study were typical for summer and early fall in the region, including warm water temperatures (28–30 °C) and episodic rainfall events due to thunderstorm activity. River flow during this period was lower than normal for the region. Mean flows (from July through November 2001) were 60% (Apalachicola River), 72% (Fish River), and 89% (Escambia River) of long term means for the same time window (http://water.usgs.gov).

Over all sites and dates, Chl *a* concentration varied widely from 1 to > 250 µg L^{-1} (Table 3). Weeks Bay had the highest Chl *a* concentration peaking at over 200 µg L^{-1} at the Turkey Branch site, but also exceeding 100 µg L^{-1} at several other sites (Figure 2). In contrast, Chl *a* in Apalachicola Bay and Pensacola Bay never exceeded 20 µg L^{-1} and had ranges and means similar to each other (Figure 2). One common finding in all 3 systems was that Chl *a* tended to peak at the mid-estuarine sites on a given date (Figure 2). DIN concentrations ranged from below detection to 148 µM, exhibiting a typical spatial pattern with highest concentrations at the freshwater sites decreasing along the freshwater to marine estuarine gradient (Figure 3). Weeks Bay had by far the highest DIN concentrations, with peak concentrations at the Upper Magnolia River site, ranging 94.2 to 148 µM (Figure 3). As with Chl *a*, Apalachicola and Pensacola Bays had similar but much lower DIN concentrations, rarely exceeding 20 µM. DIP concentrations were generally low in all estuaries, never exceeding 1 µM (Table 3), and there were no obvious DIP-salinity gradients (data not shown). Cyanobacterial abundance varied by over 3 orders of magnitude from 0.004 to 5.8 X 10^9 L^{-1} and, similar to bulk Chl *a*, were generally most abundant at the mid-estuarine sites (Figure 4), peaking at salinities near 5–10 psu in Weeks Bay, 10 psu in Pensacola Bay, and 22 psu in Apalachicola Bay (Figure 5a). Similar to DIN and Chl *a* concentrations, mean cyanobacterial abundance was highest in Weeks Bay and lower in Apalachicola and Pensacola Bays (Table 3, Figure 4). However, in contrast with DIN, the freshwater sites had the lowest cyanobacterial abundances, usually one or 2 orders of magnitude lower than nearby estuarine sites. This pattern was most evident in Pensacola Bay (P01) and Weeks Bay (Weeks Creek, Magnolia River). At the marine sites, cyanobacteria abundances were lower than at the mid-estuarine sites, but not nearly as low as the freshwater sites. In Apalachicola Bay, only the East Bay site had high cyanobacterial abundances, averaging 2.3 X 10^9 L^{-1}, 2 to 3 times higher than the other sites. In contrast, Weeks Bay and Pensacola Bay had high cyanobacterial abundances at most estuarine sites, peaking at 5.8 X 10^9 L^{-1} and 4.6 X 10^9 L^{-1}, respectively.

Although there were only 3 sampling dates, there was a consistent temporal pattern in Weeks Bay and Pensacola Bay (Figure 4). In general, cyanobacterial abundance peaked during summer when temperatures are warmest (ca. 30 °C). In Pensacola Bay, peak abundances occurred during August, whereas, in Weeks Bay, a similar peak occurred during July (there was no August sampling in Weeks Bay). This temporal pattern was not evident in Apalachicola Bay where cyanobacterial abundances were similar on all dates; however, this may be due to inadequate sampling earlier in the summer, as the first sampling date was not until September.

In order to gauge the importance of the cyanobacterial component of the phytoplankton community, we converted cyanobacterial abundance to equivalent Chl *a* concentration using a factor of 3.4 fg chl *a* $cell^{-1}$ (see Murrell and Lores 2004). Cyanobacterial Chl *a* was then normalized to the total Chl *a* concentration and plotted as a function of salinity (Figure 5b). This analysis showed that cyanobacteria contributed a large fraction of the total Chl *a*, especially in the low- to mid-salinity zone of the all 3 estuaries. In Weeks Bay, for example, many values were at or near 100%, suggesting that virtually all of the phyto-

TABLE 3

Mean values and ranges for salinity, DIN, DIP, Chl *a*, and cyanobacterial abundances during 2001.

Estuary	Date	# Sites	Salinity (psu)		DIN (µM)		DIP (µM)		Chl *a* (µg L^{-1})		Cyanobacteria (X 10^9 L^{-1})	
			Mean	Range	Mean	Range	Mean	Range	Mean	Range	Avg.	Range
Apalachicola	14 Sep	7	25.1	2.5–32.0	1.7	0.0–10.3	0.39	0.09–0.58	9.9	4.9–17.7	0.77	0.11–3.10
Bay	12 Oct	7	26.4	2.4–33.1	3.0	0.0–20.5	0.26	0.10–0.52	6.4	2.3–12.7	0.46	0.14–1.42
	20 Nov	11	21.1	1.8–28.5	3.0	0.0–21.3	0.32	0.22–0.43	3.3	1.6–6.2	0.48	0.11–2.35
	Avg.		24.2		2.6		0.32		6.4		0.57	
Pensacola	10 Jul	5	8.3	0.0–17.9	5.2	0.7–10.8	0.07	0.01–0.19	12.0	4.2–18.2	1.50	0.07–2.92
Bay	8 Aug	5	8.2	0.4–19.8	4.2	0.2–8.3	0.07	0.06–0.09	11.2	4.8–15.7	2.41	0.12–4.58
	11 Sep	5	7.9	0.1–13.4	3.9	0.3–8.6	0.07	0.01–0.17	10.4	1.9–16.5	1.68	0.02–2.79
	16 Oct	5	17.6	0.5–25.7	6.8	1.0–15.9	0.06	0.01–0.15	9.2	1.5–15.6	0.46	0.01–0.73
	13 Nov	5	22.2	4.9–29.2	6.6	2.7–18.8	0.08	0.01–0.13	5.0	1.9–8.5	0.67	0.04–1.15
	Avg.		12.9		5.3		0.07		10.4		1.35	
Weeks	19 Jul	11	4.0	0.1–11.0	17.1	0.0–148.1	0.25	0.04–0.45	25.2	1.0–99.5	3.04	0.06–5.79
Bay	4 Sep	11	3.5	0.0–7.8	23.1	0.0–94.2	0.47	0.17–0.90	75.1	2.9–253.6	1.64	0.004–5.20
	27 Nov	11	9.6	0.1–22.0	46.6	1.4–139.3	0.20	0.01–0.90	24.6	0.9–171.0	1.23	0.02–2.84
	Avg.		5.7		28.9		0.31		25.2		1.97	

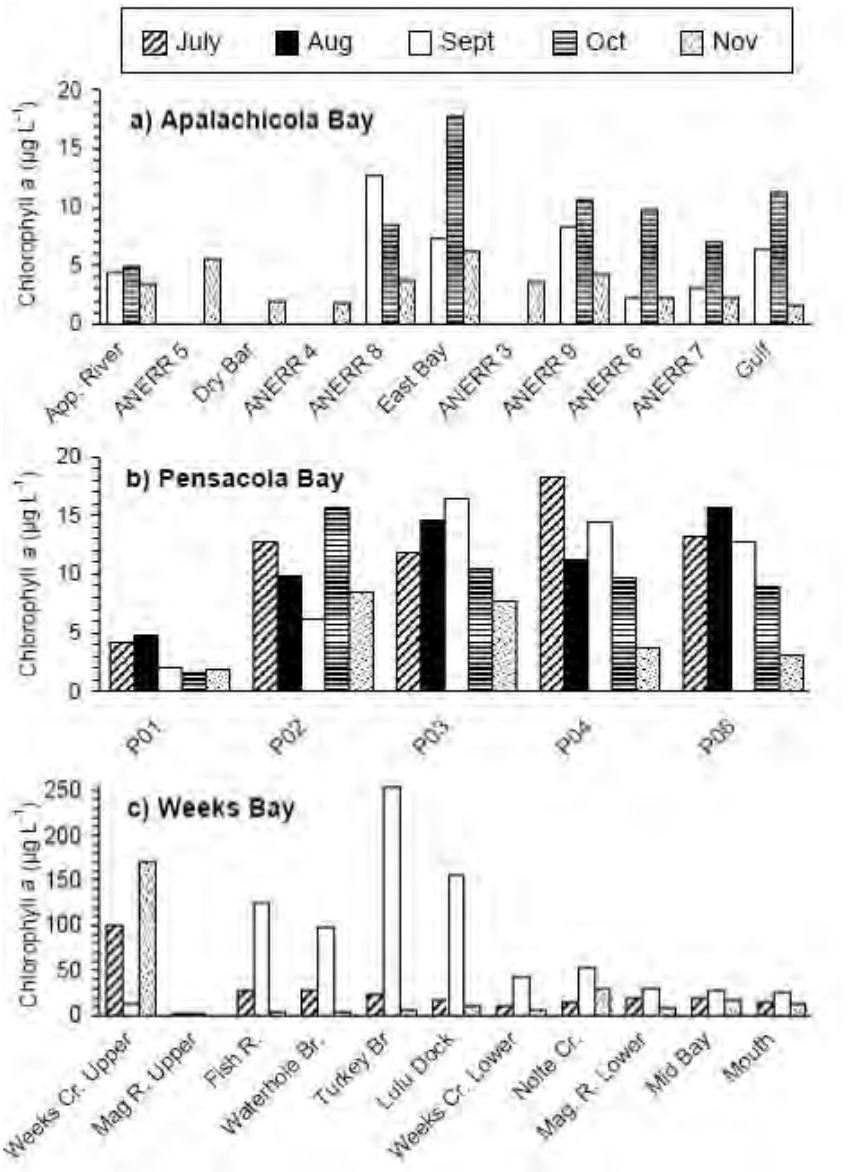

Figure. 2. Chl *a* concentration at all sites and dates sampled during the study: a) Apalachicola Bay, FL; b) Pensacola Bay, FL; c) Weeks Bay, AL (note different scaling). The sites were arranged in order of increasing mean salinity for each system as listed in Table 2.

plankton was comprised of cyanobacteria. In the other 2 systems, this fraction was not usually so high, but frequently exceeded 50%. Interestingly, when averaged across all sites and dates, the percentage of cyanobacterial Chl *a* was similar in all 3 systems; 31% for Apalachicola Bay, 39% for Pensacola Bay, and 36% for Weeks Bay. However, these global means can be considered biased low because the freshwater sites are clearly unsuitable habitat for cyanobacteria, where they contribute virtually 0% to total Chl *a*. Including only estuarine sites (mean salinity > 2, Table 2), the mean cyanobacterial contribution to total Chl *a* increased to 32%, 47% and 43%, respectively.

DISCUSSION

The physical settings of the 3 estuarine systems (Table1) have important similarities (e.g., rainfall, water depth) and differences (e.g., estuarine area, watershed area, freshwater flow) which help provide a context for interpreting the biological and chemical data. Apalachicola Bay is the largest system, with the largest watershed and is least impacted by anthropogenic nutrient inputs, as indicated by the low mean DIN at the freshwater source (mean 17.4 µM). Baywide mean Chl *a* and cyanobacterial concentrations were lower than those of the other 2 estuaries. Apalachicola Bay has a strong marine influence and a rel-

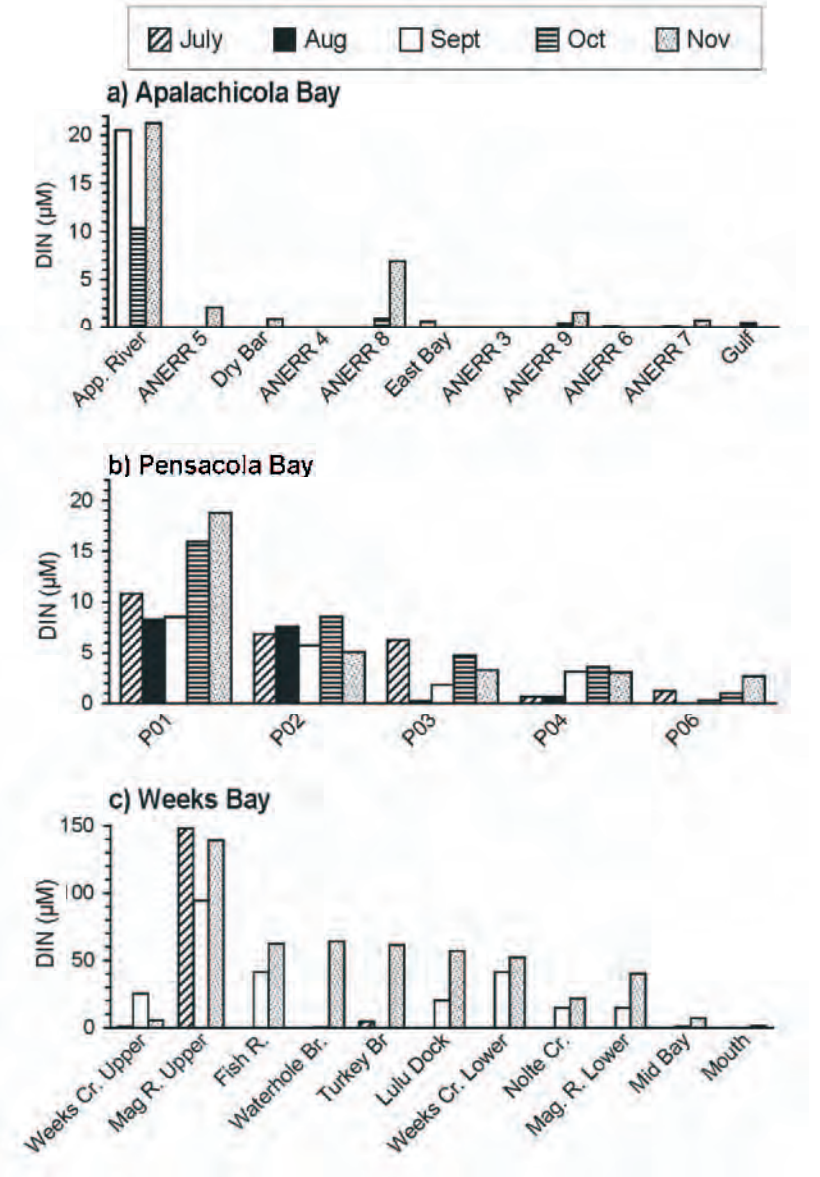

Figure 3. Dissolved inorganic nitrogen (DIN) concentration at all sites and dates sampled during the study: a) Apalachicola Bay, FL; b) Pensacola Bay, FL; c) Weeks Bay, AL (note different scaling). The sites were arranged in order of increasing mean salinity for each system as listed in Table 2.

atively short residence time (6 d), explaining the high mean salinity (24.2). The rapid Gulf exchange probably acts to dilute nutrient, Chl *a*, and cyanobacterial concentrations.

Pensacola Bay is intermediate in size, with moderate anthropogenic impacts from the watershed. Exchange with the GOM is narrowly constricted at Pensacola Pass, contributing to its relatively long residence time (25 d) and a lower mean salinity (12.9) than Apalachicola Bay. At the Escambia River site (P01) DIN averaged 12.5 µM, somewhat lower than the Apalachicola River mean; however, non-riverine sources of DIN (e.g. sewage treatment plants, urban storm-water runoff) are relatively more important in Pensacola Bay, given the relatively high human population (ca. 300,000 people) surrounding the bay. This may in part explain the higher bay-wide mean DIN, Chl *a*, and cyanobacterial concentrations in Pensacola Bay compared to Apalachicola Bay.

Weeks Bay has a much smaller watershed and estuarine area, nearly 2 orders of magnitude smaller than Apalachicola Bay or Pensacola Bay, and on the marine end exchanges with Mobile Bay estuary rather than the GOM proper, explaining the low mean salinity (5.7) we observed. The rate of water exchange between the 2 bays is strongly dependent on river discharge and wind forcing (Schroeder et al. 1990), but the mean freshwater residence

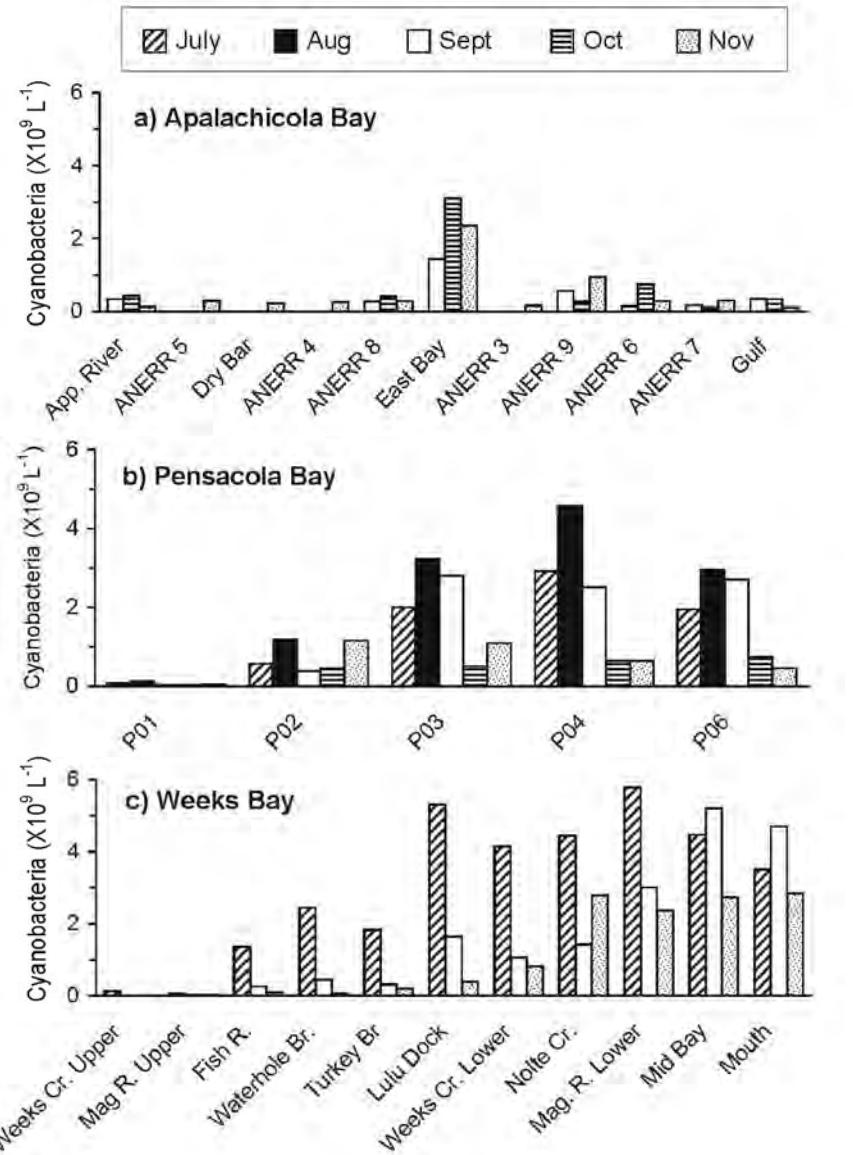

Figure 4. Cyanobacterial abundance at all sites and dates sampled during the study: a) Apalachicola Bay, FL; b) Pensacola Bay, FL; c) Weeks Bay, AL. Within each system, the sites were arranged in order of increasing mean salinity as listed in Table 2.

time is short (6 d) similar to Apalachicola Bay. It has high anthropogenic nutrient loading as evidenced by high freshwater DIN concentrations averaging 51 µM in the Fish River and 127 µM in the Magnolia River. It also has the highest baywide mean Chl *a* concentrations and cyanobacterial abundances. Mean cyanobacterial abundances were about 350% higher than Apalachicola Bay and 50% higher than Pensacola Bay.

In this study, peak cyanobacterial abundances ranged from about 3 X 10^9 L^{-1} (Apalachicola Bay) to nearly 6 X 10^9 L^{-1} (Weeks Bay) and are among the highest reported in the literature (Table 4). Cyanobacteria have been enumerated in a wide range of estuarine and near-coastal environments, ranging from tropical (e.g., Phlips et al. 1999) to northern latitude systems (e.g., Kuosa 1988). Cyanobacteria abundances in these systems vary considerably, but highest abundances always tend to occur during summer, and lower latitude systems tend to have higher peak abundances than higher latitude systems.

Because the time frame of this study was restricted to one summer-fall period, we acknowledge that the results may not be representative of longer-term patterns. As mentioned earlier, freshwater flows were below long-term averages, which likely caused higher salinities and lower water column stratification than expected to occur during more normal flow conditions. While interannual variation in such factors likely affect the location and extent of high cyanobacterial abundances, it seems clear from longer-

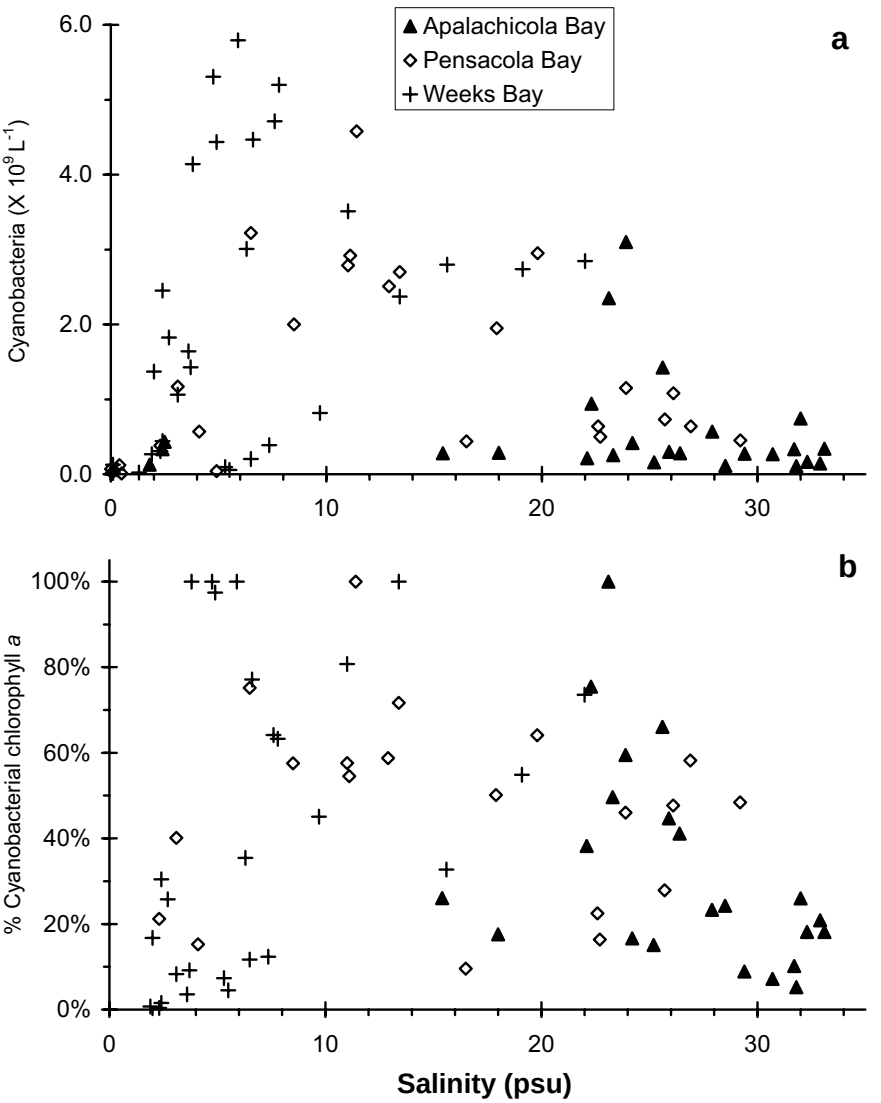

Figure 5. Distribution of cyanobacteria as a function of salinity: a) cyanobacterial abundance, and b) cyanobacterial percentage of bulk Chl *a*. The 3 estuaries are distinguished by different plot symbols.

term datasets (e.g., Marshall and Nesius 1996, Phlips et al. 1999, Murrell and Lores 2004) that high cyanobacterial abundances are a common summer-time feature of estuaries.

It is further clear from this study that cyanobacteria can be an important component of the phytoplankton community in these GOM estuaries, despite considerable variability in hydrology and anthropogenic impacts. Assuming a nominal cellular Chl *a* content, cyanobacteria contribute from 30 to 50% of the total Chl *a* in all 3 estuarine systems. This percentage agrees well with the 2+ year average of 43% reported for Pensacola Bay (Murrell and Lores 2004), and is among the highest reported in the literature. For example, in San Francisco Bay, cyanobacteria mean 15% (maximum 38%) of total Chl *a* (Ning et al. 2000). In the Neuse River estuary, cyanobacteria represented 18% of total Chl *a* based on HPLC pigment analysis (Pinckney et al. 1998). In the York River estuary, pico-phytoplankton comprised 7% of Chl *a* over an annual cycle, peaking at 14% during summer (Ray et al. 1989). In the Kiel Bight, cyanobacteria contributed up to 52% of the total Chl *a* during summer (Jochem 1988), while in Southhampton estuary cyanobacteria contributed 10% or less to bulk Chl *a* (Iriarte and Purdie 1994). It should be noted that normalizing cyanobacteria to Chl *a* likely underestimates their true contribution to phytoplankton carbon biomass and productivity, given that cyanobacteria have relatively low chlorophyll content per unit of carbon compared to eukaryotic algae, particularly diatoms (MacIntyre et al. 2002).

One pattern noted by Iriarte and Purdie (1994) was that the relative importance of picoplankton appears to diminish with increasing trophic state, ultimately con-

TABLE 4

Peak abundances of cyanobacteria reported from various estuaries and inland seas. When available, temperature and salinity data at the time of collection are included and the month of the year the sample was collected.

Location	Temp °C	Salinity psu	Peak Abundance (cells X $10^6 L^{-1}$)	Month	Reference
St. Lawrence River (Canada)	21	0.1	17	Jun	Bertrand and Vincent1994
North Inlet (SC, USA)	NA	NA	55	Sep	Lewitus et al. 1998
Southampton (UK)	19–20	34	130	Jul	Iriarte and Purdie 1994
Yangtze River (China)	25–30		200	Jul	Vaulot and Xiuren 1988
Long Island Sound (NY, USA)	24.3	NA	232	Aug	Carpenter and Campbell 1988
San Francisco Bay (CA, USA)	22	20	234	July	Ning et al.2000
Gulf of Finland	12–13	6	243	Jun	Kuosa 1988
Kiel Bight (Baltic Sea)	22	14	260	Jul–Aug	Jochem 1988
York River Estuary (VA, USA)	28	22	750	Sep	Ray et al. 1989
Chesapeake Bay (VA, USA)	26	NA	920	Jul	Affronti and Marshall 1994
Chesapeake (MD & VA, USA)	NA	NA	> 2000	Jul	Marshall and Nesius1996
Apalachicola Bay (FL, USA)	25	24	3100	Sep	This Study
Pensacola Bay (FL, USA)	29	11	4600	Aug	Murrell and Lores 2004, This Study
Weeks Bay (AL, USA)	30	6	5800	Jul	This Study
Florida Bay (FL, USA)	NA	35	> 5000	Oct	Phlips et al. 1999
Mississippi River Plume (USA)	NA	8	> 5000	Jul	Dortch 1998

tributing < 5% when Chl *a* concentrations exceed 5 µg L^{-1}. In this study, cyanobacteria appeared to dominate the phytoplankton well beyond this 5 µg L^{-1} threshold. The estuarine sites with the smallest cyanobacterial contribution (excluding freshwater sites) were the highly eutrophic sites (e.g. Weeks Bay) where total Chl *a* concentrations exceeded 100 µg L^{-1}. Instead, phytoplankton at these sites were comprised of small diatoms (up to 6 X 10^7 L^{-1}) and cryptophytes (up to 2.6 X 10^7 L^{-1}). However, such highly eutrophic conditions are relatively rare in GOM estuaries, and seasonal maxima for Chl *a* more typically range from 10 to 20 µg L^{-1} (Pennock et al. 1999). In this range, the potential for cyanobacteria to dominate the phytoplankton is quite likely, given that an abundance of 5 X 10^9 L^{-1} corresponds to 17 µg L^{-1} Chl *a* (assuming 3.4 fg Chl *a* $cell^{-1}$). Therefore, data from this and related studies (e.g., Phlips et al. 1999, Murrell and Lores 2004) appear to challenge the generalized pattern observed by Iriarte and Purdie (1994), showing that cyanobacteria can be dominant in GOM estuaries and can represent nearly 100% of the Chl *a*, especially during summer.

While there are several reports of cyanobacterial abundances in estuaries, cyanobacterial growth rates and productivity are more rarely quantified. However, studies conducted in several estuaries, including Chesapeake Bay (Affronti and Marshall 1994), Long Island Sound (Carpenter and Campbell 1988), the South China Sea (Agawin et al. 2003), and Santa Rosa Sound (Juhl and Murrell in press) have consistently found that peak specific growth rates range from 1 to 1.5 d^{-1} (1.4 to 2.2 divisions d^{-1}). One consistent finding in these and related studies is a strong temperature-dependence on cyanobacterial growth, being repeatedly noted in estuarine (Carpenter and Campbell 1988, Ray et al. 1989, Iriarte and Purdie 1994, Juhl and Murrell in press) and oceanic environments (Li 1998). Based on these observations, it is clear that estuarine cyanobacteria actively grow during warm periods and significantly contribute to bulk productivity. Furthermore, given their characteristically low chlorophyll content relative to carbon (MacIntyre et al. 2002), cyanobacterial contribution to bulk phytoplankton productivity probably exceeds their contribution to bulk Chl *a*. Thus, cyanobacteria appear to be major mediators of carbon flow in subtropical estuarine systems and deserve further study to better quantify their role in estuarine productivity.

The size structure of the phytoplankton community has a profound influence on the pathways by which organic matter is transferred through aquatic food webs. Perhaps most importantly, cyanobacteria in the 1 to 2 µm size range cannot be directly consumed by mesozooplankton and demersal fish species. For example, Nival and Nival (1976) found that even naupliar stages of the ubiquitous genus *Acartia* was unable to efficiently collect and consume particles less than 3 µm in size. Similarly, Durbin and Durbin

(1975) found that the Atlantic menhaden (*Brevoortia tyrannus*), a major phytoplanktivorous fish in estuaries, was unable to consume phytoplankton less than 13–16 µm in size. So the route by which cyanobacteria become available to higher trophic levels requires one or more intermediate trophic steps (i.e. the microzooplankton), with respiratory losses of carbon and energy at each step. The existence of such trophic linkages has been demonstrated, in particular between cyanobacteria and microzooplankton (Caron et al. 1991, Ayukai 1992, Lessard and Murrell 1998, Juhl and Murrell in press), and between microzooplankton and mesozooplankton (Lonsdale et al. 1996, Sipura et al. 2003). However, the inefficiency of such indirect pathways, when compared to more direct pathways, constrains the degree to which cyanobacteria can ultimately support production of top predators.

In summary, this study found high abundances of chroococcoid cyanobacteria in 3 estuaries along the northeastern GOM. Cyanobacterial abundances peaked in the oligohaline reach of each system and appeared to positively covary with the degree of eutrophication. While cyanobacteria have long been known to play a dominant role in oceanic environments, their role in estuaries is not as well understood. This study adds to a small but growing body of literature suggesting that cyanobacteria can be dominant in estuaries, which has broad implications for how primary production is transferred to higher trophic levels. Future studies should consider the potential role of cyanobacterial dominance on various topics ranging from fish productivity to eutrophication effects.

ACKNOWLEDGMENTS

This study was supported by CICEET grants (99-298 and 01-452) to JMC. We thank Scott Phipps and Lee Edmiston for field assistance. We further thank Scott Phipps and 2 anonymous reviewers for useful comments to improve the manuscript. Contribution No. 1229 US EPA, Gulf Breeze, FL, USA. Mention of trade names or commercial products does not constitute endorsement by the US EPA.

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