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The Role of Zooplankton Grazing and Nutrient Loading in the Occurrence of Harmful Cyanobacterial Blooms in Florida Bay, USA

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Abstract Florida Bay is Florida's (USA) largest estuary and has experienced harmful picocyanobacteria blooms for nearly two decades. While nutrient loading is the most commonly cited cause of algal blooms in Florida Bay, the role of zooplankton grazing pressure in bloom occurrence has not been considered. For this study, the spatial and temporal dynamics of cyanobacteria blooms, the microbial food web, microzooplankton and mesozooplankton grazing rates of picoplankton, and the effects of nutrients on plankton groups in Florida Bay were quantified. During the study, cyanobacteria blooms ($>3\times10^5$ cells mL^{-1}) persisted in the eastern and central regions of Florida Bay for more than a year. Locations with elevated abundance of cyanobacteria hosted microzooplankton grazing rates on cyanobacteria that were significantly lower ($p<0.001$) and less frequently detectable compared to sites without blooms. Consistent with this observation, cyanobacteria abundances were significantly correlated with ciliates and heterotrophic nanoflagellates at low cyanobacteria densities ($p<0.001$) but were not correlated during bloom events. The experimental enrichment of mesozooplankton abundance during blooms yielded a significant decrease in the net growth rate of picoplankton but had the opposite effect when blooms were absent, suggesting that the cascading effect of mesozooplankton grazing on the microbial food web was also altered during blooms. While inorganic nutrient enrichment significantly increased the net growth rates of eukaryotic phytoplankton and heterotrophic bacteria, such nutrient loading had no effect on the net growth rates of cyanobacteria. Hence, this study demonstrates that low rates of zooplankton grazing and low rates of inorganic nutrient loading contribute to the persistence of cyanobacteria blooms in Florida Bay.

Keywords Florida Bay · Estuary · HABs · Cyanobacteria · Nutrients · Zooplankton · Microbial food web · Microzooplankton · Grazing · Mesozooplankton · Algal bloom

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Introduction

Harmful algal bloom (HAB) is the term used to denote the growth of planktonic microalgae to levels that have a negative impact on coastal ecosystems and/or nearby human populations due to the synthesis of toxins and/or high levels of algal biomass (Sunda et al. 2006). HABs afflict most temperate and tropical coastal nations, and the frequency of HAB events and their negative impacts on fisheries have increased markedly in recent decades (Heisler et al. 2008; Jin and Hoagland 2008). Increased nutrient loading is often suspected as a primary cause of algal blooms (Berman et al. 2005; Heisler et al. 2008; Anderson et al. 2008). However, in some cases, a loss of top–down control by pelagic (Turner and Tester 1997; Gobler et al. 2002; Irigoien et al. 2005) or benthic grazers (Shumway 1990; Cerrato et al. 2004) can also be responsible for the development of algal blooms (Mitra and Flynn 2006; Sunda et al. 2006).

Florida Bay, located between the Florida Keys and peninsular Florida to the north, is Florida's (USA) largest estuary and has experienced a series of ecological disturbances since the late 1980s, including the occurrence of HABs (Walters et al. 1992; Boesch et al. 1993; Fourqurean and Robblee 1999; Sunda et al. 2006). These blooms cover large areas in the North-Central basin, can last for months, and are formed by the picocyanobacteria *Synechococcus* spp. (Boesch et al. 1993; Phlips et al. 1999). While the Eastern basin of Florida Bay has been historically free of blooms (chlorophyll *a* levels typically <1 μg L^{-1}; Phlips et al. 1995, 1999), this basin has also began to experience intense cyanobacterial blooms in 2005 (SERC 1989–2007; this study).

Cyanobacterial blooms in Florida Bay have resulted in a number of negative impacts on the ecosystem, such as anoxic events and increased light attenuation (Phlips and Badylak 1996; Phlips et al. 1999), which has reduced the distribution of seagrass beds (Hall et al. 1999). The blooms are detrimental to fish (Boesch et al. 1993; Chasar et al. 2005), sponges (Butler et al. 1994; Peterson et al. 2006), and spiny lobsters (Butler et al. 1995). Recent research also suggests that primary production associated with these blooms is cycling primarily through the microbial loop rather than reaching upper trophic levels and supporting fisheries (Chasar et al. 2005). Because these blooms have severely altered and degraded ecosystem function, they have been classified as ecosystem disruptive algal blooms (EDABs) by Sunda et al. (2006).

Nutrient loading has been hypothesized as a prime cause of algal blooms in Florida Bay (Phlips et al. 1999) and has been the focus of water quality management and restoration efforts there (Boesch et al. 1993). However, increased levels of nutrients generally relieve the nutrient stress, and favor the growth, of larger phytoplankton (Raven and Kubler 2002), suggesting that other factors could be contributing to the blooms of small (~1 μm) cyanobacteria cells, including low predation rates. The sponge die-offs in Florida Bay (Peterson et al. 2006) may have shifted grazing pressure from the benthic community to the planktonic community. Microzooplankton feed efficiently on picoplankton and act as an important link in the food chain by making picoplankton energy available to upper trophic levels (Sherr and Sherr 2002). High microzooplankton growth rates create a usually tight coupling between picophytoplankton growth and microzooplankton grazing (Calbet and Landry 2004; Strom 2008), which should generally prevent pico-algal bloom formation (Landry et al. 1997). As such, the bloom events in Florida Bay and other EDABs are indicative of a disruption in this relationship (Sunda et al. 2006). To our knowledge, zooplankton grazing rates on *Synechococcus* sp. or other plankton groups have never been measured in Florida Bay.

The primary goal of this study was to determine the extent to which cyanobacteria and other plankton in Florida Bay are under top–down control by zooplankton grazing. The spatial and temporal dynamics of phytoplankton (cyanobacteria and eukaryotic algae), zooplankton (mesozooplankton, microzooplankton, heterotrophic nanoflagellates), and heterotrophic bacteria were established during summer and fall of 2006 and winter and spring of 2007 throughout Florida Bay. In parallel, mesozooplankton and microzooplankton grazing rates on eukaryotic algae, cyanobacteria, bacteria, and the total phytoplankton community were measured. Comparisons of grazing rates on multiple prey items were made, as were comparisons of the net growth rates of various planktonic groups under ambient and nutrient saturated conditions.

Materials and Methods

Field Sampling

Field sampling in Florida Bay was conducted at duplicate stations in the western (25.12°N, 80.97°W; 25.00°N, 80.93°W; sites 1 and 2), north-central (25.12°N, 80.80°W; 25.13°N, 80.72°W; sites 4 and 5), southern (24.98°N, 80.80°W; 24.97°N, 80.70°W; sites 3 and 6), and eastern (25.08°N, 80.55°W; 25.17°N, 80.52°W; sites 7 and 8) basins and at one station within Blackwater Sound (25.18°N, 80.40°W; BWS, site 9), which is in the far eastern portion of the bay (Fig. 1). Seasonal sampling at these sites occurred in the summer from July 19 through 24 of 2006, in the fall from November 6 through 10 of 2006, in the winter from January 8 through 13 of 2007, and in the spring from March 30 through April 4 of 2007. Thus, the spatial extent of the sampling was across the entire boundaries of the Florida Bay National Park and the temporal extent included quarterly samples over an annual cycle.

Water Quality and Plankton Community Composition

Surface and bottom temperature and salinity were measured with a YSI 556 probe. A Secchi disk was used to determine water clarity. Water samples from a depth of 0.5 m were collected gently in replicated 20-L carboys (n=3) with minimal bubbling and transported back to the Florida Bay Interagency Science Center at the Everglades National Park Ranger Station in Key Largo, FL, USA, for analysis. The well-mixed (personal observation of surface and bottom temperature and salinity) and shallow nature (<3 m) of Florida Bay ensured that sub-surface samples were representative of the whole-water column. Whole-water samples were preserved in 1% buffered formalin and analyzed flow cytometrically to assess picoplankton abundance (Olson et

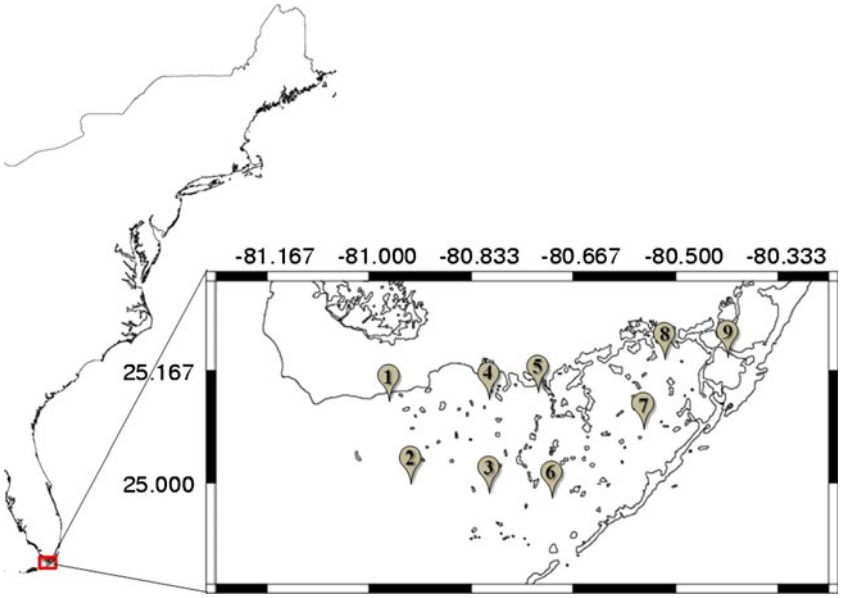

Fig. 1 Study sites in Florida Bay, FL, USA in the western (25.12°N, 80.97°W; 25.00°N, 80.93°W; sites 1 and 2), north-central (25.13°N, 80.80°W; 25.12°N, 80.72°W; sites 4 and 5), southern (24.98°N, 80.80°W; 24.97°N, 80.70°W; sites 3 and 6), and eastern (25.08°N, 80.55°W; 25.17°N, 80.52°W; sites 7 and 8) basins and at one station within Blackwater Sound (25.18°N, 80.40°W; sites 9), which is in the far eastern portion of the bay

al. 1991). Following preservation, samples were flash-frozen in liquid nitrogen. Abundance of heterotrophic bacteria (stained with SYBR Green I; Jochem 2001), picocyanobacteria, and photosynthetic picoeukaryotes was determined by a FACSort (Becton-Dickinson) flow cytometer using fluorescence patterns and particle size from side angle light scatter (Olson et al. 1991). Whole-water samples (40 mL) were also preserved with glutaraldehyde (2% v/v, final) and stored in the dark in sterile polypropylene tubes at 4°C. These samples were examined by epifluorescence microscopy at high resolution (×1000) to confirm the identification of picoplankton made by the flow cytometer.

Seawater samples for phototrophic and heterotrophic nanoplankton were preserved with 10% glutaraldehyde to a final concentration of 1%. Triplicate samples were stained with DAPI within 24 h of collection, and autotrophs and heterotrophs were differentiated and enumerated by epifluorescence microscopy (Sherr et al. 1993). At least 100 autotrophs and heterotrophs were counted per slide. Duplicate microplankton samples were analyzed according to Hasle (1978) to identify and quantify the major taxonomic categories of microzooplankton and phytoplankton present in the water column. Because of their well-known phagotrophic capabilities (e.g., Jeong 1999; Jeong et al. 2001, 2005), dinoflagellates were grouped among microzooplankton. Seawater samples (180 mL) were preserved with acid Lugol's solution (final concentration, 5%) and counted using an inverted microscope. A minimum of 200 organisms or 100 grids (microplankton enumerations) were counted per sample (Omori and Ikeda 1984). Forty-liter water samples were passed through a 64-μm sieve, and the contents collected on the sieve were preserved in 4% buffered formalin. These samples were analyzed for large microzooplankton (64–200 μm; primarily copepod nauplii) and mesozooplankton (>200 μm; grouped as meroplanktonic larvae and copepodites) identification and enumeration using a dissecting microscope (Harris et al. 2000). Whole seawater (WSW) was filtered for size fractionation of chlorophyll *a* using 2- and 20-μm polycarbonate filters and glass fiber filters (GFFs, nominal pore size 0.7 μm). Chlorophyll *a* was analyzed by standard fluorometric methods (Parsons et al. 1984).

Microzooplankton Grazing Rates

Microzooplankton grazing rates were assessed in serial dilution experiments (Landry et al. 1995). A series of dilutions were established using 100%, 70%, 40%, and 15% WSW diluted with 0.2 μm filtered seawater obtained via gravity filtration through filter capsules (Pall Life Sciences #12117) with vents, which eliminated bubbling of water as it entered the capsules. The experiments also included a 100% filtrate control and 100% WSW without nutrient enrichment control. All other treatments were enriched with nutrients (10 μM N, 1 μM P, 10 μM Si: Landry et al. 1995) and were executed in triplicate 1-L bottles. Experimental bottles were incubated in Florida Bay at the Florida Bay Interagency Science Center with one layer of neutral density screening (33% reduction in light) to mimic ambient light and temperature conditions. After 24 h, experimental bottles were processed and subsequently analyzed for chlorophyll *a* and flow cytometric counts of picocyanobacteria, picoeukaryotic phytoplankton, and heterotrophic bacteria as described above. Net growth rates of the various components of the plankton community were

calculated as: $\mu = \ln[B_t/B_o]/t$, where μ is the net growth rate (day^{-1}), B_o and B_t are the initial and final biomass (pigment or cell density) respectively, and t is the incubation duration. Plotting the linear regression of the dilutions versus the calculated net growth rates allowed the grazing rate and nutrient-enriched intrinsic growth rates to be determined. Grazing rates per day were determined from the slope of the line while nutrient-enriched intrinsic growth rates (μ_n) were determined from the y-intercept of these plots (Landry et al. 1995). The net growth rates of the planktonic prey group in enriched and non-enriched 100% WSW bottles were compared to assess the impacts of nutrients on these groups. The difference between these groups was subtracted from the nutrient-enriched intrinsic growth rates (μ_n) to obtain unenriched intrinsic growth rates from the dilution series (Landry et al. 1995). Three-point regressions of dilution curves during this study did not indicate saturation of grazing during experiments (Gallegos 1989).

Mesozooplankton Grazing Impacts

Experiments were conducted to elucidate the trophic impact of mesozooplankton (> 200 μm) on components of the microbial food web in Florida Bay. Mesozooplankton were carefully concentrated in the field over a submerged 200-μm mesh. Organisms on the mesh were carefully rinsed into 200-μm filtered seawater and stored in the dark. Within 3 h of collection, this suspension was then gently mixed and the volume required to attain 2×, 4×, and 8× ambient mesozooplankton concentrations was transferred into experimental bottles filled with 200-μm filtered seawater. This enrichment of mesozooplankton is within the range of variability among sites during samples periods and at individual sites during this study. A control treatment of 200 μm filtrate was also established (0× mesozooplankton). Five replicate bottles were established for each treatment and two bottles were immediately sacrificed following experimental setup to obtain T_0 samples for quantification of mesozooplankton and triplicate chlorophyll *a* analyses. Experimental bottles were incubated in the manner described above and net growth rates of whole chlorophyll *a*, picocyanobacteria, picoeukaryotic phytoplankton, and heterotrophic bacteria were determined as described above. The slope of the linear regression growth rate for each plankton group plotted against increasing mesozooplankton concentration provided a quantitative estimate of the trophic impact of mesozooplankton on each prey item (Lehman and Sandgren 1982; Carrick et al. 1991).

Statistical Analyses

Comparisons among variables (e.g., microbial groups) were made via one-way ANOVA with multiple comparison tests or appropriate non-parametric tests (e.g., Mann–Whitney rank sum test). Comparison of variables between bloom and non-bloom conditions (> and <3× 10^5 cells mL^{-1}; Phlips et al. 1999) were made with *t* tests or non-parametric equivalents. This bloom threshold was consistent with water clarity/discoloration in Florida Bay as well as changes in microbial populations during this study. The degree to which individual variables were correlated was evaluated by a Spearman's Rank Order Correlation Matrix. In all cases, a significance level of 0.05 was applied to justify statistically significant differences or correlations.

Results

Spatial and Temporal Dynamics of Plankton Communities

Summer During July 2006, temperatures averaged 29.6± 1.0°C and salinities ranged from 27.1 (site 8) to 37.6 (site 5; Table 1) across Florida Bay. Site 9 (Blackwater Sound, eastern Florida Bay; Fig. 1) experienced a relatively large cyanobacteria bloom with cell abundances exceeding 2× 10^6 cells mL^{-1} (Fig. 2). Concurrently, a smaller cyanobacteria bloom (0.4×10^6 cells mL^{-1}) occurred at site 4 (north-central basin) while cyanobacteria were less abundant throughout the rest of the bay ($0.12\pm0.8\times10^6$ cells mL^{-1}; Fig. 2). Chlorophyll *a* concentrations were slightly elevated at bloom locations (2.2±0.6 μg L^{-1} at sites 9 and 4; Fig. 2) and relatively low elsewhere (1.2± 0.9 μg L^{-1}; Fig. 2). Eukaryotic phytoplankton abundance was elevated at site 1 ($5.5\pm0.5\times10^3$ cells mL^{-1}) and at site 9 ($3.5\pm2.0\times10^4$ cells mL^{-1}; Fig. 2) but lower in the central and eastern basins ($0.7\pm0.4\times10^3$ cells mL^{-1}; Fig. 2). Abundances of heterotrophic bacteria were fairly consistent at $1.1\pm0.4\times10^6$ cells mL^{-1} throughout the Bay, except for site 9 (Blackwater Sound) where they reached almost 8×10^6 cells mL^{-1} (Fig. 2).

The abundance of heterotrophic nanoplankton was generally consistent throughout Florida Bay, averaging $0.59\pm1.2\times10^4$ cells mL^{-1} (sites 1–8). The exception to this pattern was at site 9 where their abundance was ~5 times higher ($3.0\pm0.49\times10^4$ cells mL^{-1}, Blackwater Sound; Fig. 3). Dinoflagellates were most abundant at site 4 in the north-central basin ($5.7\pm1.5\times10^4$ cells L^{-1}; Fig. 3), comprised mainly of *Prorocentrum* spp. Ciliates were most abundant at site 9 (Blackwater Sound, $4.6\pm0.4\times10^4$ cells L^{-1}; Fig. 3), being co-dominated by *Mesodinium rubrum* and *Laboea* spp. The remaining sites (1–8) exhibited mean ciliate abundances of $2.0\pm0.8\times10^4$ cells L^{-1}. Copepod abundance ranged from $0.31\pm0.05\times10^3$ individuals m^{-3} (site 6) to $24.3\pm2.6\times10^3$ individuals m^{-3} (site 3), with most sites hosting ~3×10^3 individuals m^{-3} (Table 1). *Acartia*

Table 1 Temperature (°C), salinity, and mesozooplankton abundance (× 10^3 individuals m^{-3})

Date	Site	Temperature	Salinity	Copepods	Nauplii	Larvae	Mysids	Forams	Other
7/19/2006	1	30.2	29.7	6.95	0.78	0.59	0.56	0.58	0.11
7/19/2006	2	30.9	31.0	2.26	3.15	0.63	0.03	0.25	0.34
7/19/2006	3	30.7	33.4	24.3	8.08	0.90	0.25	0.00	0.23
7/21/2006	4	28.1	31.4	2.88	0.89	0.00	0.00	0.00	0.11
7/21/2006	5	28.5	37.6	0.99	8.22	0.04	0.01	0.06	0.08
7/21/2006	6	29.1	36.1	0.31	0.08	0.00	0.00	0.00	0.04
7/24/2006	7	29.5	36.9	3.84	2.45	0.00	0.00	0.00	0.04
7/24/2006	8	29.3	27.1	3.57	2.79	0.00	0.00	0.00	0.00
7/24/2006	9	30.0	33.0	1.86	1.90	0.00	0.00	0.00	0.00
11/10/2006	1	24.5	34.8	4.63	0.39	0.85	0.15	0.00	0.24
11/8/2006	2	25.1	37.6	4.39	3.18	0.22	0.09	0.00	0.23
11/8/2006	3	25.2	36.6	2.85	0.71	0.08	0.04	0.08	0.06
11/10/2006	4	24.3	33.5	3.83	2.49	0.04	0.00	0.03	0.06
11/10/2006	5	26.0	30.9	0.36	0.48	0.10	0.15	0.00	0.78
11/8/2006	6	25.3	36.4	2.03	1.06	0.03	0.09	0.00	0.13
11/6/2006	7	23.1	31.4	1.34	0.33	0.00	0.00	0.00	0.00
11/6/2006	8	23.2	30.0	3.70	1.30	0.00	0.00	0.00	0.00
11/6/2006	9	23.7	30.2	8.91	1.46	0.10	0.00	0.00	0.00
1/13/2007	1	20.85	34.9	3.75	0.37	0.16	0.00	0.00	0.04
1/8/2007	2		37.3	2.58	0.13	0.00	0.05	0.00	0.30
1/8/2007	3		37.1	5.78	0.55	0.00	0.25	0.13	0.20
1/13/2007	4	20.8	33.0	2.07	0.90	0.00	0.00	0.00	0.00
1/13/2007	5	21.0	32.8	1.53	1.78	0.00	0.01	0.03	0.00
1/8/2007	6		35.7	6.23	1.55	0.08	0.10	0.03	0.13
1/10/2007	7	19.9	31.8	1.59	0.49	0.00	0.01	0.00	0.01
1/10/2007	8	18.5	31.7	3.94	1.60	0.08	0.00	0.00	0.01
1/10/2007	9	21.3	32.1	3.33	2.30	0.04	0.01	0.00	0.51
4/4/2007	1	24.3	38.1	4.64	0.76	0.00	0.15	0.00	1.18
4/4/2007	2	26.9	40.2	1.33	0.03	0.09	0.18	0.00	0.03
4/2/2007	3	23.6	38.0	5.60	0.68	0.35	0.06	0.06	0.24
4/4/2007	4	25.1	39.5	2.20	1.58	0.17	0.48	0.08	0.24
4/2/2007	6	23.6	38.8	2.43	0.17	0.09	0.04	0.04	0.01
3/30/2007	7	23.4	35.4	5.71	0.49	0.01	0.01	0.03	0.01
3/30/2007	8	22.9	36.1	0.83	0.08	0.04	0.00	0.00	0.00
3/30/2007	9	23.3	35.7	3.98	0.76	0.08	0.00	0.04	0.03

Relative standard deviation of replicated counts were 11%

tonsa was the dominant mesozooplankton species in Florida Bay at this time.

Fall November temperatures in Florida Bay averaged 24.5± 1.0°C while salinities ranged from 30.0 (site 8) to 37.6 (site 2; Table 1). The cyanobacteria bloom at site 9 persisted during the fall (0.8×10^6 cells mL^{-1}; Blackwater Sound) and expanded westward into Florida Bay (0.5×10^6 cells mL^{-1}; site 8; Fig. 2). The cyanobacteria bloom at site 4 (north-central basin) expanded southward to site 3 and increased in density as the bloom at both sites exceeded 3×10^6 cells mL^{-1}. The north-central bloom also seemed to expand eastward as to site 5 at this time (0.4×10^6 cells mL^{-1}; Fig. 2). Eukaryotic phytoplankton and heterotrophic bacteria abundance as well as chlorophyll *a* concentrations were 4–5 times higher at bloom sites (3, 4, 5, 8, and 9) compared to non-bloom locations (2, 6, and 7), except for site 1, which continued to display elevated levels of chlorophyll *a* and eukaryotic phytoplankton (Fig. 2).

Heterotrophic nanoplankton abundances were relatively low at sites 1, 2, 6, 7, and 8 (western and eastern locations of Florida Bay), averaging $0.27\pm0.11\times10^4$ cells mL^{-1}. By

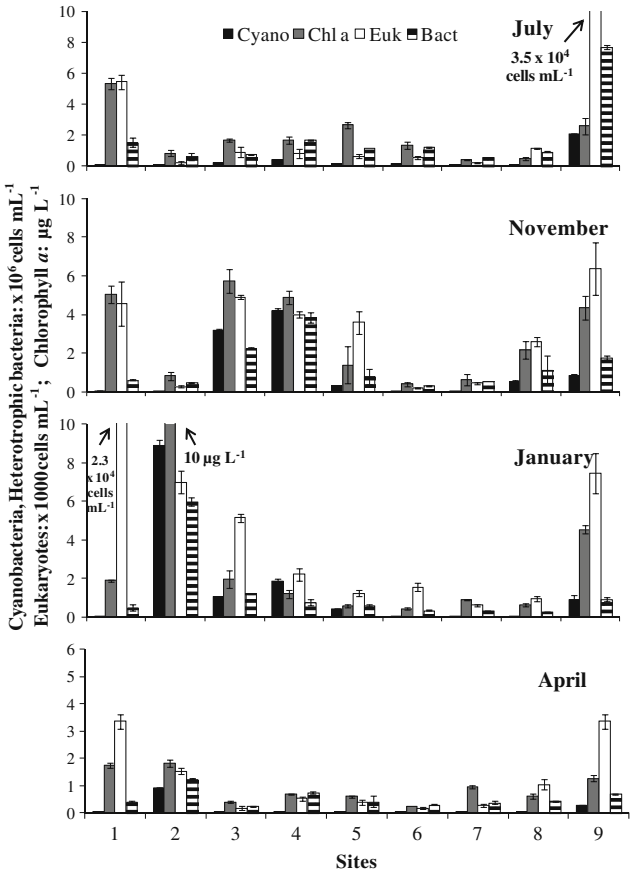

Fig. 2 Densities of cyanobacteria (*Cyano*), eukaryotic algae (*Euk*), heterotrophic bacteria (*Bact*) and chlorophyll *a* (*Chl a*) in July 2006, November 2006, January 2007, and April 2007. *Error bars* are means ± SD of triplicate measurements

contrast, abundances were elevated at sites 3, 4, and 5 (central basin) and highest at site 9 (Blackwater Sound), reaching $3.1\pm0.57\times10^4$ cells mL^{-1} (Fig. 3). Dinoflagellates (primarily *Gyrodinium spirale*) were most abundant at site 9 ($10.7\pm0.15\times10^4$ cells L^{-1}; Fig. 3), while ciliates were abundant at sites 3 and 5 with $7.5\pm0.47\times10^4$ cells L^{-1} and $7.0\pm0.66\times10^4$ cells L^{-1}, respectively (Fig. 3). *M. rubrum* was the dominant ciliate at most sites except at site 9 (Blackwater Sound), which was dominated by *Laboea* spp. The highest copepod abundance was found at site 9 (Blackwater Sound) with $8.9\pm0.6\times10^3$ individuals m^{-3} (Table 1), numerically dominated by *A. tonsa*.

Winter Temperatures in January were similar throughout Florida Bay, averaging 20.4±1.0°C, while salinity was lowest at site 8 (31.7) and highest at site 2 with (37.3; Table 1). The eastern basin cyanobacteria bloom was found exclusively at site 9 (Blackwater Sound) by January and maintained densities of ~0.5×10^6 cells mL^{-1} (Fig. 2). In contrast, the cyanobacteria bloom in the central region expanded to occupy sites 2, 3, 4, and 5, much of the central and southeastern portion of Florida Bay with $>10^6$ cells mL^{-1} (Fig. 2). Once again, bloom site (sites 2, 3, 4, 5, and 9) levels of eukaryotic phytoplankton, heterotrophic bacteria, and chlorophyll *a* were 5–7 times higher than those at non-bloom stations (6, 7, and 8) but similar to those at the non-bloom site 1 (northwestern basin; Fig. 2).

From November 2006 to January of 2007, site 9 (Blackwater Sound) experienced a fourfold decrease in heterotrophic nanoplankton abundance to $0.8\pm0.2\times10^4$ cells mL^{-1}. Site 2 hosted the highest levels of heterotrophic nanoplankton ($1.8\pm0.4\times10^4$ cells mL^{-1}) while moderate concentrations were found elsewhere in the Bay (sites 1 and 3–8; $0.53\pm0.37\times10^4$ cells mL^{-1}; Fig. 3). Dinoflagellates peaked at site 2 ($12.2\pm1.3\times10^4$ cells L^{-1}; Fig. 3), dominated by *Gyrodinium* spp. and *Heterocapsa* sp. Similar dinoflagellate concentrations were found at site 9 (Blackwater Sound; $1.22\pm1.8\times10^4$ cells L^{-1}), dominated by *Gyrodinium* spp. Ciliate abundances were lower compared to fall with an average of 1.4×10^4 cells L^{-1} (Fig. 3) and populations generally being dominated by *M. rubrum*. Sites 3 and 6 exhibited high copepod abundance of 5.8±0.2 and $6.2\pm0.2\times10^3$ individuals m^{-3}, respectively (Table 1). *A. tonsa* was dominant at site 3 while *Paracalanus* sp. was dominant at site 6.

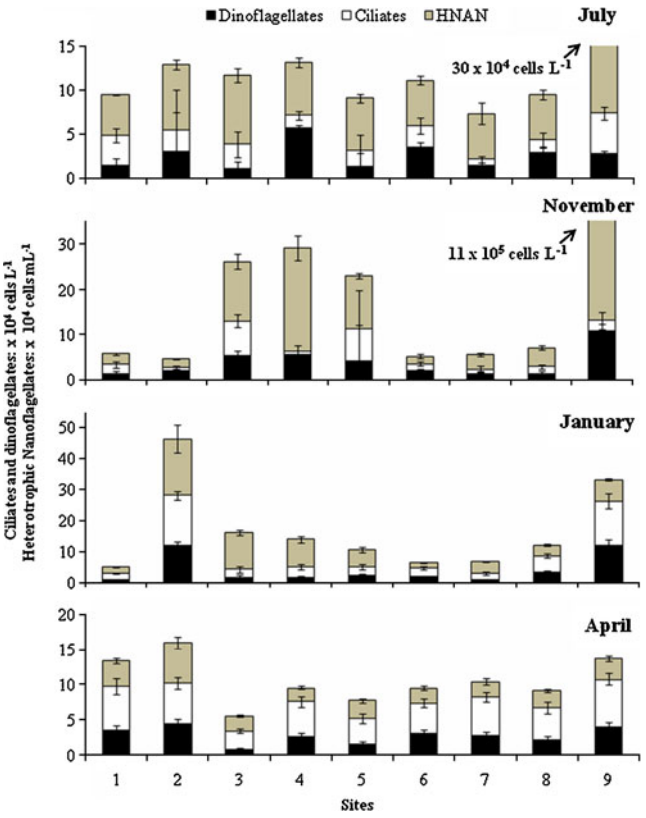

Fig. 3 Microzooplankton and heterotrophic nanoflagellate abundances in July 2006, November 2006, January 2007 and April 2007. *HNAN*= heterotrophic nanoflagellates. *Error bars* represent SD of triplicate counts

Spring Spring temperatures averaged 24.1±1.3°C. Salinity peaked again at site 2 at 40.2 and ranged from 35 to 39.5 elsewhere (Table 1). The bloom that had occupied the central and southeastern regions of Florida Bay diminished and was now restricted to the southwestern portion of the bay at site 2 (0.9×10^6 cells mL^{-1}; Fig. 2). The cyanobacteria bloom also continued at site 9 during the spring (Blackwater Sound; 0.4×10^6 cells mL^{-1}). Eukaryotic picophytoplankton abundances were above 3×10^3 cells mL^{-1} at sites 1 and 9 but lower elsewhere. Chlorophyll *a* concentrations were elevated at bloom sites (2 and 9) and site 1 but were lower elsewhere (0.58±0.25 μg L^{-1}). Heterotrophic bacteria abundances were lower in the spring ($0.55\pm0.31\times10^6$ cells mL^{-1}).

Heterotrophic nanoplankton abundance became more uniform during the spring, averaging $0.24\pm0.06\times10^4$ cells mL^{-1} for all sites (Fig. 3), except within the cyanobacteria bloom at site 2 where concentrations were twice the bay mean ($0.58\pm0.09\times10^4$ cells mL^{-1}; Fig. 3). Similarly, the blooms at sites 2 and 9 also harbored elevated levels of dinoflagellates ($4.4\pm0.62\times10^4$ cells L^{-1} and $4.0\pm0.61\times10^4$ cells L^{-1}, respectively; Fig. 3). In contrast, ciliate abundances (primarily *M. rubrum*) were fairly consistent throughout Florida Bay, averaging $2.2\pm0.06\times10^4$ cells L^{-1} (Fig. 3). The highest copepod densities occurred at sites 3 and 7 with 5.6±0.99 and $5.7\pm0.34\times10^3$ individuals m^{-3}, respectively (Table 1); site 3 was dominated by *A. tonsa* and site 7 by both *A. tonsa* and *Temora* sp.

Microzooplankton Grazing

Microzooplankton grazing rates were detectable on at least one of the microbial prey groups [total phytoplankton community (based on chl *a*), eukaryotic algae, cyanobacteria, or heterotrophic bacteria] during every experiment conducted during this study (n=36). Mean grazing rates on all populations during all experiments were approximately 0.8 day^{-1}. However, grazing rates and the ability to quantify microzooplankton grazing on various planktonic groups co-varied with the ambient abundance of cyanobacteria (Fig. 4).

Summer Microzooplankton grazing on cyanobacteria was undetectable by the dilution technique during the central Florida Bay bloom event at site 4 and at another central Bay site (site 6). Additionally, microzooplankton grazing rates on cyanobacteria were low in Blackwater Sound (0.20±0.09 day^{-1}; Table 2) compared to other sites (mean ± SD=1.1±0.76 day^{-1}; Table 3). In other regions of Florida Bay, microzooplankton grazing was detected at all stations on at least one prey group and rates were relatively high, averaging 0.73±0.41 day^{-1} on eukaryotic prey (chl *a*, eukaryotes) and 1.2±0.61 day^{-1} for prokaryotic prey (cyanobacteria, bacteria). High bacterivory (grazing on heterotrophic bacteria) persisted throughout the bay (mean ± SD=1.31±0.43 day^{-1}), with lower rates occurring at bloom sites 4 (0.81±0.10 day^{-1}) and 9 (0.52±0.09 day^{-1}; Table 2).

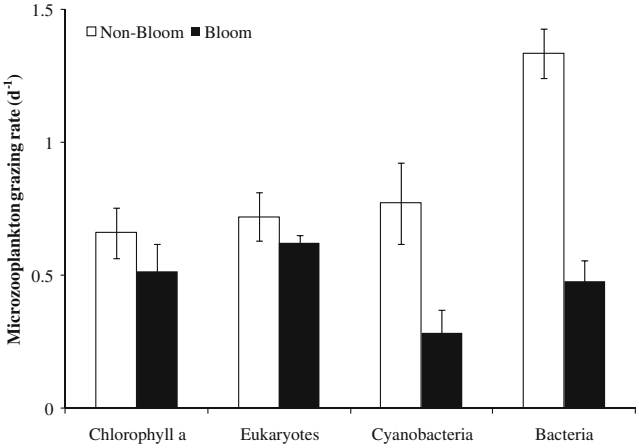

Fig. 4 Average microzooplankton grazing rates per day on various prey items for July 2006, November 2006, January 2007, and April 2007. *Error bars* represent standard error

Fall Microzooplankton grazing rates on cyanobacteria at bloom sites were either low (0.20±0.09 day^{-1}; site 8; Table 2) or undetectable (5 of 6 experiments; sites 3, 4, 5, 7, and 9) during the fall. At non-bloom locations, grazing rates on cyanobacteria were more than four times higher (mean ± SD=0.87±0.47 day^{-1}; Table 2). Microzooplankton grazing on eukaryotic phytoplankton ranged from 0.61± 0.20 day^{-1} (site 2) to 1.2±0.46 day^{-1} (site 7) and averaged 0.79±0.29 day^{-1}. Grazing on total phytoplankton (chl *a*) was highest at site 7 (1.2±0.24 day^{-1}), lowest at site 8 (0.25±0.12 day^{-1}), and averaged 0.66±0.31 day^{-1}. Bacterivory was high in the west (0.94±0.05 day^{-1} at site 1 and 0.78±0.13 day^{-1} at site 2) and low or non-detectable in the central Florida Bay cyanobacteria bloom: 0.21± 0.05 day^{-1} at site 3, undetectable at site 4, and 0.26± 0.06 day^{-1} at site 5 (Table 2).

Winter Although bacterivory was quantifiable at all locations during the winter, microzooplankton grazing on other prey was detectable in fewer than half of the experiments conducted with bloom levels of cyanobacteria (7 of 15 experiments; Table 2). Bacterivory was low within cyanobacteria blooms (mean ± SD=0.43±0.32 day^{-1}) and higher elsewhere (mean ± SD=1.2±0.23 day^{-1}). Mean microzooplankton grazing rates on eukaryotic algae, cyanobacteria, and the total phytoplankton community during winter were 0.32±0.13 day^{-1}, 0.31±0.12 day^{-1}, and 0.36± 0.23 day^{-1}, respectively (Table 2).

Table 2 Microzooplankton grazing rates per day ± standard error

Date	Site	Chlorophyll *a*	Eukaryotes	Cyanobacteria	Bacteria
7/19/2006	1	1.6±0.37	1.2±0.17	1.6±0.16	1.6±0.17
7/19/2006	2	ND	ND	0.73±0.11	1.8±0.46
7/19/2006	3	ND	0.22±0.07	1.2±0.14	1.1±0.10
7/21/2006	**4**	**ND**	**ND**	**ND**	**0.81±0.10**
7/21/2006	5	1.0±0.22	ND	0.35±0.14	1.4±0.13
7/21/2006	6	0.62±0.10	ND	ND	1.5±0.16
7/24/2006	7	0.64±0.27	ND	2.3±0.63	1.5±0.16
7/24/2006	8	0.63±0.14	0.35±0.11	0.46±0.05	1.7±0.14
7/24/2006	**9**	**0.78±0.25**	**0.65±0.10**	**0.20±0.09**	**0.52±0.09**
11/10/2006	1	0.94±0.22	1.06±0.08	1.2±0.05	0.94±0.05
11/8/2006	2	0.42±0.15	0.61±0.20	ND	0.78±0.13
11/8/2006	**3**	**ND**	**ND**	**ND**	**0.21±0.05**
11/10/2006	**4**	**0.78±0.28**	**ND**	**ND**	**ND**
11/10/2006	**5**	**0.70±0.25**	**0.43±0.15**	**ND**	**0.26±0.06**
11/8/2006	6	0.37±0.16	0.99±0.12	0.54±0.14	1.0±0.12
11/6/2006	7	1.2±0.24	1.2±0.46	ND	0.88±0.12
11/6/2006	**8**	**0.25±0.12**	**0.60±0.16**	**0.20±0.09**	**0.61±0.60**
11/6/2006	**9**	**0.66±0.10**	**ND**	**ND**	**0.33±0.04**
1/13/2007	1	0.75±0.10	ND	ND	1.4±0.17
1/8/2007	**2**	**ND**	**ND**	**ND**	**0.25±0.12**
1/8/2007	**3**	**0.25±0.11**	**ND**	**ND**	**0.27±0.06**
1/13/2007	**4**	**0.36±0.13**	**ND**	**ND**	**0.37±0.10**
1/13/2007	**5**	**ND**	**ND**	**0.46±0.15**	**0.97±0.09**
1/8/2007	6	0.16±0.08	ND	0.37±0.07	1.3±0.16
1/10/2007	7	ND	0.48±0.16	0.22±0.04	1.2±0.15
1/10/2007	8	ND	0.23±0.10	ND	0.85±0.06
1/10/2007	**9**	**ND**	**ND**	**ND**	**0.42±0.13**
4/4/2007	1	0.55±0.14	0.87±0.15	0.42±0.12	2.0±0.28
4/4/2007	**2**	**ND**	**ND**	**ND**	**0.60±0.10**
4/2/2007	3	0.44±0.20	0.76±0.32	0.55±0.16	1.7±0.27
4/4/2007	4	0.20±0.10	ND	1.4±0.39	1.8±0.20
4/2/2007	6	ND	0.71±0.32	0.37±0.05	2.1±0.34
3/30/2007	7	0.38±0.15	0.97±0.11	0.35±0.10	1.7±0.30
3/30/2007	8	ND	ND	0.21±0.07	1.4±0.19
3/30/2007	**9**	**ND**	**ND**	**ND**	**1.0±0.25**

Bloom events are shown in bold

ND non-detectable grazing

Spring During the spring, bacterivory and grazing on cyanobacteria were detectable in 88% of the experiments (Table 2). As was found during other seasons, grazing on cyanobacteria was undetectable at sites with a sizeable cyanobacteria population (>3×10^5 cells mL^{-1}; sites 2 and 9). Bacterivory was high at most stations (mean ± SD=1.8± 0.22 day^{-1}) but lower at sites with cyanobacteria blooms (mean ± SD=0.81±0.29 day^{-1}). In contrast to the prokaryotes, microzooplankton grazing on eukaryotic populations (chl *a*, eukaryotes) was undetectable in 50% of spring experiments (Table 2). Where grazing rates on the total phytoplankton population and eukaryotic algae were established, they were similar to rates recorded during winter, averaging 0.36±0.23 day^{-1} and 0.32±0.13 day^{-1}, respectively (Table 2).

Mesozooplankton Enrichment Experiments

Enriching mesozooplankton abundance yielded a significant, linear response from at least one of the microbial prey groups [total phytoplankton community (based on chl *a*), eukaryotic algae, cyanobacteria, and heterotrophic bacteria] in 86% of the experiments. During summer, mesozooplankton enrichment resulted in a significant, linear growth response from microbial prey in most experiments, the

Table 3 Mesozooplankton grazing rates per day ± standard error

Date	Site	Chlorophyll *a*	Eukaryotes	Cyanobacteria	Bacteria
7/19/2006	1	0.14±0.04	0.03±0.01	ND	0.01±0.01
7/19/2006	2	0.03±0.01	0.05±0.01	0.07±0.02	ND
7/19/2006	3	-0.04±0.01	ND	0.04±0.01	0.05±0.01
7/21/2006	**4**	**−0.07±0.02**	**ND**	**ND**	**ND**
7/21/2006	5	0.11±0.02	−0.05±0.02	ND	ND
7/21/2006	6	ND	ND	0.06±0.01	ND
7/24/2006	7	−0.06±0.03	ND	0.14±0.05	0.02±0.00
7/24/2006	8	ND	ND	−0.01±0.01	0.01±0.00
7/24/2006	**9**	**0.06±0.01**	**ND**	**ND**	**ND**
11/10/2006	1	ND	ND	ND	0.01±0.00
11/8/2006	2	ND	ND	ND	0.02±0.01
11/8/2006	**3**	**−0.03±0.01**	**ND**	**ND**	**ND**
11/10/2006	**4**	**−0.10±0.03**	**−0.11±0.03**	**ND**	**ND**
11/10/2006	**5**	**ND**	**ND**	**ND**	**ND**
11/8/2006	6	0.11±0.03	ND	ND	−0.01±0.01
11/6/2006	7	−0.03±0.02	ND	ND	0.01±0.00
11/6/2006	**8**	**ND**	**ND**	**ND**	**−0.01±0.01**
11/6/2006	**9**	**0.04±0.01**	**−0.10±0.02**	**−0.09±0.02**	**ND**
1/13/2007	1	0.09±0.02	0.04±0.02	0.06±0.01	ND
1/8/2007	**2**	**0.10±0.03**	**ND**	**ND**	**ND**
1/8/2007	**3**	**−0.06±0.01**	**ND**	**0.01±0.01**	**ND**
1/13/2007	**4**	**−0.05±0.02**	**ND**	**−0.01±0.01**	**−0.01±0.01**
1/13/2007	**5**	**ND**	**ND**	**ND**	**ND**
1/8/2007	6	0.05±0.02	0.05±0.01	ND	ND
1/10/2007	7	ND	0.04±0.02	ND	ND
1/10/2007	8	−0.02±0.01	0.11±0.03	−0.20±0.07	ND
1/10/2007	**9**	**0.01±0.00**	**ND**	**ND**	**ND**
4/4/2007	1	ND	ND	ND	ND
4/4/2007	**2**	**0.07±0.03**	**ND**	**−0.01±0.01**	**−0.03±0.01**
4/2/2007	3	ND	ND	ND	ND
4/4/2007	4	ND	ND	ND	−0.02±0.01
4/2/2007	6	ND	ND	ND	ND
3/30/2007	7	0.03±0.01	−0.04±0.02	ND	−0.01±0.00
3/30/2007	8	−0.07±0.01	ND	−0.03±0.01	−0.01±0.00
3/30/2007	**9**	**−0.12±0.04**	**ND**	**−0.02±0.01**	**ND**

A nonlinear response between the enrichment of mesozooplankton and microbial net growth rates was noted by ND. Bloom events are shown in bold

majority of which yielded negative net growth rates of all microbial prey groups (Table 3). During fall, winter, and spring, statistically significant linear responses among all prey groups were less common (40% of experiments; Table 3). For the entire study, the relative impact of enriching mesozooplankton on the net growth rates of microbial prey differed between stations with and without cyanobacteria blooms (Fig. 5). At locales with low cyanobacteria abundance, enriching mesozooplankton, on average, allowed for positive growth rates of all microbial populations (Fig. 5). In contrast, during bloom events, enrichment of mesozooplankton yielded progressively negative net growth rates of microbial populations (Fig. 5).

Effects of Nutrient Enrichment on Microbial Net Growth Rates

Nutrient enrichment had a large effect on the total phytoplankton community (chlorophyll *a*) in all experiments. Nutrient additions increased net growth rates by an average of 0.44±0.07 day^{-1}, an effect significantly larger than recorded for the individual plankton groups (Tukey test; $p<0.05$, Fig. 6). Eukaryotic algae and heterotrophic bacteria displayed more moderate responses to nutrient enrichment, with an average nutrient-induced increase in net growth rates of 0.16±0.06 day^{-1} and 0.12±0.04 day^{-1}, respectively. In contrast, nutrient enrichment elicited almost

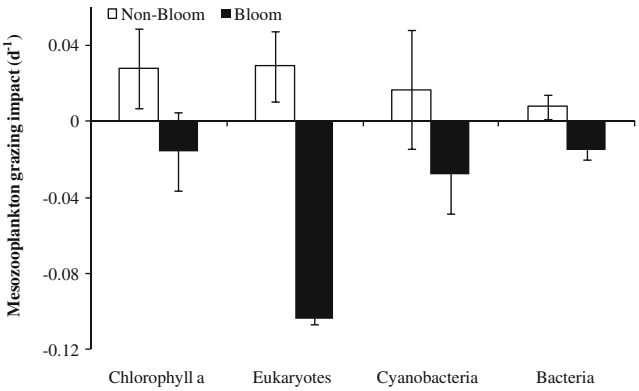

Fig. 5 Average mesozooplankton grazing rates per day on various prey items for July 2006, November 2006, January 2007, and April 2007. *Error bars* represent standard error

no change in net growth rates of cyanobacteria (average increase, 0.01 ± 0.07 day^{-1}). The responses of each group's net growth rate to nutrient loading were not significantly different between bloom and non-bloom conditions.

Discussion

During this study, blooms of cyanobacteria persisted during all seasons in both the eastern and central regions of Florida Bay, expanding during the fall and winter and retracting during the spring. This study is among the first reports of dense cyanobacteria blooms in eastern Florida Bay, a region previously characterized by very low levels of algal biomass (Phlips et al. 1999; Glibert et al. 2004). Cyanobacteria blooms in Florida Bay were accompanied by a microbial consortium comprised of high levels of chlorophyll *a*, heterotrophic bacteria, autotrophic nanoflagellates, and autotrophic microflagellates. While microzooplankton grazing on all members of the picoplankton community was high when cyanobacteria abundances were low, grazing rates were frequently undetectable during bloom events and quantifiable grazing rates on cyanobacteria and heterotrophic bacteria were substantially lower than that in non-bloom regions. These results suggest that decreased zooplankton grazing pressure may play a central role in facilitating the occurrence of cyanobacteria blooms in Florida Bay.

The composition of the microbial food web in Florida Bay changed with the onset of dense cyanobacteria blooms. When cyanobacteria abundances were low ($<3.0 \times 10^5$ cells mL^{-1}), they correlated positively with those of ciliates ($p<0.001$; $R=0.65$) and heterotrophic nanoflagellates ($p<0.0001$; $R=0.83$), two common grazers of picoplanktonic prey (Caron et al. 1991; Christaki et al. 1999; Jürgens and Massana 2000). In contrast, during cyanobacteria blooms in Florida Bay, the microbial consortium associated with cyanobacteria changed. For example, during blooms, densities of cyanobacteria abundance correlated significantly with chlorophyll *a* concentrations, heterotrophic bacteria, autotrophic nanoflagellates, and autotrophic microflagellates ($p<0.0001$, $R=0.89$; $p<0.01$, $R=0.67$; $p<0.01$, $R=0.68$; $p<0.0001$, $R=0.90$, respectively) but were no longer correlated with any zooplankton group including ciliates and heterotrophic nanoflagellates. These results indicate that the grazers whose abundances paralleled cyanobacteria abundance at low cyanobacteria population densities did not keep pace with increasingly dense cyanobacteria blooms in Florida Bay. It is possible that the presence of grazers at densities too low to control blooms allowed for the concurrent increase in other potential autotrophic and picoplanktonic prey such as heterotrophic bacteria, autotrophic nanoflagellates, and autotrophic microflagellates, all of which were well correlated with cyanobacterial densities at stations with cyanobacteria blooms.

Changes in the Florida Bay microbial food web occurred in concert with changes in grazing pressure on microbial populations. During non-bloom conditions, microzooplankton grazing was detectable on at least one prey group in every experiment (Table 2) and measurable grazing on cyanobacteria, eukaryotic algae, and the total phytoplankton community in 76%, 67%, and 71% of experiments, respectively (Table 2). With the onset of bloom conditions, the frequency of detectable microzooplankton grazing was significantly lower for these prey groups (cyanobacteria=29%, eukaryotic algae=50%, total phytoplankton community=57%; chi-square test, $p<0.01$ for each group; Table 2). When detectable, microzooplankton grazing rates on prokaryotic prey during cyanobacteria blooms were threefold lower than rates quantified under non-bloom conditions (*t* tests, $p<0.001$; Fig. 4). In contrast, the absolute rate of grazing on eukaryotic algae and the total phytoplankton

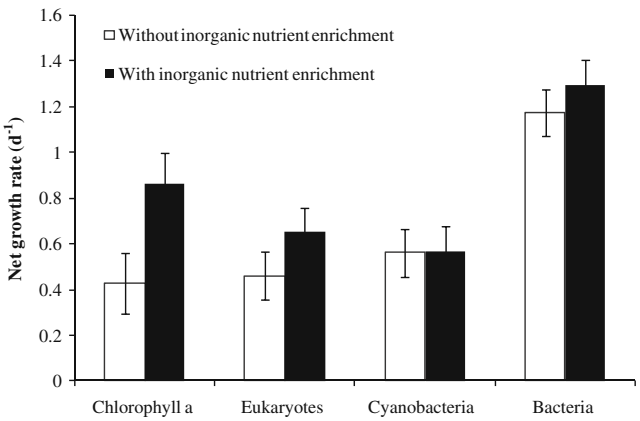

Fig. 6 Mean net growth rates per day for each of the four primary microbial populations studied with (*black bars*) and without (*white bars*) enrichment with inorganic nutrients (nitrate and phosphate) during all experiments. *Error bars* represent standard error

community did not change during cyanobacteria blooms (Fig. 4). Microzooplankton grazing rates on autotrophic prey under non-bloom conditions were generally equal to or slightly higher than those reported previously as typical of tropical regions and estuaries (~0.5 day^{-1}; Calbet and Landry 2004). However, mean microzooplankton grazing rates on cyanobacteria during bloom events were markedly lower (0.3 day^{-1}; Fig. 4). Such changes in grazing control of phytoplankton have been predicted to result in the outbreak of an algal bloom (Mitra and Flynn 2006; Sunda et al. 2006).

The observed absence of, or decrease in, microzooplankton grazing during cyanobacteria blooms in Florida Bay could be due to a variety of factors. Besides the inability of grazer populations to increase at the same pace as cyanobacteria, extracellular polysaccharides and/or cellular toxins secreted by the cyanobacteria (Mitsui et al. 1989; Phlips et al. 1989; Carmichael and Li 2006), both of which would be produced at high amounts during blooms, could discourage zooplankton grazing. It has recently been established that marine *Synechococcus*, the genus of cyanobacteria blooming in Florida Bay (Phlips et al. 1999; Lynch and Phlips 2000), produce microcystin (Carmichael and Li 2006), a putative zooplankton grazing deterrent (de Bernardi and Giussani 1990; Christoffersen 1996; Rohrlack et al. 1999). In addition, *Synechococcus* spp., which bloom in Florida Bay, are known to produce extracellular polysaccharides (EPS; Phlips et al. 1989; Lynch and Phlips 2000). These polysaccharides can adhere to the cilia of benthic and protozoan grazers and might inhibit feeding by causing the cessation of cilia movement (Draper et al. 1990; Gainey and Shumway 1991; Liu and Buskey 2000; Strom 2008). In a manner consistent with models of HABs (Flynn 2008; Flynn and Irigoien 2009), the inability of microzooplankton densities to keep pace with cyanobacterial blooms, coupled with decreases in grazing prompted by anti-grazing capacities, coupled further with any shift in the balance of grazing losses to net from pico-phytoplankton (with associated reduced inorganc nutrient regeneration), all likely conspire to promote blooms in Florida Bay. Therefore, low zooplankton grazing pressure on bloom-forming phytoplankton may be a primary cause of HABs and EDABs such as *Synechococcus* blooms in Florida Bay (Gobler et al. 2004a, b; Sunda et al. 2006).

The trophic impact of mesozooplankton on microbial prey also changed with the onset of cyanobacteria blooms in Florida Bay. When cyanobacteria abundance was low, enriching of mesozooplankton resulted in increased net growth rates for the picoplankton (Fig. 5). In this case, consumption of picoplankton predators such as microzooplankton by the mesozooplankton may have released picoplanktonic prey from predation pressure (Calbet and Landry 1999; Deonarine et al. 2006). However, under bloom conditions, enhancing mesozooplankton had a predatory affect on microbial prey, with net growth rates of each prey population decreasing significantly and linearly with increasing mesozooplankton abundances (most notably for eukaryotic algae; Fig. 5). While this could have been due to direct predation by mesozooplankton on these microbes, their small size makes it more likely that this was the result of a trophic cascade (Cushing 1990; Calbet and Landry 1999; Deonarine et al. 2006). This observed change suggests a shift in trophic structure perhaps with bloom sites having had an even number of trophic levels from mesozooplankton to the picoplanktonic prey (likely four levels) and non-bloom sites had an odd number of trophic levels (likely three levels). The proposed longer food chain during blooms might partly be facilitated by the dominance of picoplankton during those times (Fig. 2), which may lead to a decrease in the availability of autotrophic prey of a suitable size for mesozooplankton (Cushing 1990; Calbet and Landry 1999; Jürgens and Massana 2000). As such, the significant correlation of dinoflagellates and heterotrophic nanoflagellates with cyanobacteria under non-bloom ($p<0.001$, $R=0.83$; $p<0.001$, $R=0.83$, respectively), but not bloom conditions, might be partly due to higher mesozooplankton grazing on these groups during blooms. If this were the case, cyanobacteria blooms may also be partly promoted via trophic cascades.

Traditionally, the occurrence of algal blooms has been associated with eutrophication (Berman et al. 2005; Anderson et al. 2008), and it has been hypothesized previously that cyanobacteria blooms in Florida Bay are due to nutrient loading to this estuary (Phlips et al. 1999). Comparisons of the net growth rates of each plankton group with and without nutrient enrichment demonstrated that the total phytoplankton community (chlorophyll *a*) was most affected by nutrients, with net growth rates increasing by an average of 0.44±0.07 day^{-1} (Fig. 6). While some of these changes might be attributed to light or nutrient-induced adjustment of cellular chlorophyll content, nutrient enrichment also significantly increased the growth rates of eukaryotic algae and heterotrophic bacteria, raising their net growth rates by 0.16±0.06 day^{-1} and 0.12±0.04 day^{-1}, respectively, compared to unamended controls (*t* test; $p<0.05$; Fig. 6). Conversely, nutrient enrichment had virtually no effect on cyanobacteria net growth rates in Florida Bay (0.01±0.07 day^{-1} increase, Fig. 6). These results suggest that inorganic nutrient loading in Florida Bay is likely to discourage the occurrence of cyanobacteria dominance and would be more likely to promote the growth of eukaryotic phytoplankton rather than cyanobacteria blooms. A similar conclusion has been reached for other HAB species that rely on organic forms of nutrients during blooms (Gobler et al. 2004a, b, 2005). Like these other bloom-forming

phytoplankton, cyanobacteria blooms in Florida Bay are known to exploit organic matter for growth (Glibert et al. 2004; Boyer et al. 2006) and are therefore more likely to dominate under low inorganic nutrient conditions. The present study suggests that inorganic nutrient loading is unlikely to directly promote cyanobacteria blooms in Florida Bay and thus further supports the notion that a lack of adequate grazing pressure from zooplankton and perhaps sponges (Peterson et al. 2006) is likely a central cause of these extended and prolonged blooms.

In summary, it seems that Florida Bay has experienced an ecosystem shift from an estuary that once hosted dense populations of benthic and pelagic grazers that kept algal blooms in check (Peterson et al. 2006), to one which today suffers from frequent cyanobacteria blooms. The low zooplankton grazing pressure on cyanobacteria during blooms (Fig. 4) combined with the inability of cyanobacteria to dominate phytoplankton assemblages when inorganic nutrients levels are high (Fig. 6) are prime characteristics of EDABs (Sunda et al. 2006). Other such blooms include brown tides formed by *Aureococcus anophagefferens* in New York, USA, and *Aureoumbra lagunensis* in Texas, USA (Buskey et al. 1997; Gobler et al. 2005). A commonality among EDABs in these three distinct ecosystems is the shallow nature (2–4 m) of the lagoons within which these blooms occur, which makes them prone to strong benthic–pelagic coupling including processes such a diffusive benthic fluxes of organic nutrients (MacIntyre et al. 2004), which may be an important nutrient source in Florida Bay. While the shallow nature of lagoons may also facilitate the control of algal blooms when grazers are abundant, once grazing pressure has been lost, algal blooms have become common in these systems (Buskey et al. 1997; Gobler et al. 2005; this study).

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