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

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Abstract of the Thesis

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Florida Bay is Florida's (USA) largest estuary and has experienced harmful picocyanobacterial blooms for nearly two decades. While nutrient loading is the most commonly cited cause of algal blooms in Florida Bay and elsewhere, the role of zooplankton grazing pressure in bloom occurrence has never been considered. For this study, the spatial and temporal dynamics of cyanobacteria blooms, the microbial food web, and micro- and mesozooplankton grazing rates of picoplankton in Florida Bay were quantified. During the one-year study, cyanobacteria blooms ($> 3 \times 10^5$ cyanobacteria cells ml^{-1}) persisted in the eastern and central regions of Florida Bay. Blooms were associated with lower and less frequently detectable microzooplankton grazing on cyanobacteria compared to locations without blooms. Consistent with this observation, cyanobacterial densities were significantly correlated with ciliates and heterotrophic nanoflagellates when cyanobacteria densities were low, but not during bloom events. The experimental enrichment of mesozooplankton densities during blooms yielded a significant increase in the net growth rate of picoplankton, but had the opposite effect

when blooms were absent, suggesting the cascade of grazing pressure on the microbial food web was altered during blooms. While inorganic nutrient enrichment significantly increased the net growth rates of eukaryotic phytoplankton in Florida Bay, such nutrient loading had no effect on the net growth rates of cyanobacteria. The sum of these observations suggests that low rates of zooplankton grazing, not inorganic nutrient loading, contribute to the persistence of cyanobacteria blooms in Florida Bay.

Dedication

This thesis is dedicated to Aiden
who gave my life new meaning and purpose.

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INTRODUCTION

Florida Bay, located between the Florida Keys and peninsular Florida to the north, is Florida's (USA) largest estuary. Many of the organisms common to Florida Bay are commercially or recreationally important (Davis and Dodrill, 1989; Tilmant, 1989). Florida Bay has been plagued with a series of ecological disturbances since the late 1980s including the occurrence of harmful algal blooms (Walter *et al*., 1992; Boesch *et al*., 1993; Fourqurean and Robblee, 1999). These blooms cover large areas in the North-Central basin, can last for months, and are formed primarily 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 $\mu g\ l^{-1}$; Phlips *et al*., 1995, 1999), this basin has also began to experience intense cyanobacterial blooms in 2005 (D. Rudnick, pers. comm.; this study).

Algal 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). These blooms are detrimental to fish (Boesch *et al*., 1993; Chasar *et al*., 2005), sponges (Bulter *et al*., 1994; Stevely and Sweat, 1998; 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). The manner in which blooms are harmful to sponges and other organisms is unknown, but may be associated with toxins that *Synechococcus* has been known to produce (Mitsui *et al*., 1989; Carmichael and Li, 2006).

Increased nutrient loading is often suspected as a primary cause of algal blooms (Anderson *et al*., 2002; Berman *et al*., 2002) and has been the focus of Florida Bay water quality management and restoration efforts. However, increased levels of nutrients generally favor the growth of larger phytoplankton (Raven and Kubler, 2002) suggesting that other factors could be contributing to the picocyanobacterial blooms, such as low mortality pressure. 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 efficiently feed on picoplankton and act as an important link in the food chain by making energy from the picoplankton available to upper trophic levels (Sherr and Sherr, 2002). Due to the high growth rate of microzooplankton, there is usually tight coupling between picophytoplankton growth and microzooplankton grazing (Calbet and Landry, 2004) which would generally prevent bloom formation (Landry *et al*., 1997). As such, the bloom events occurring in Florida Bay are indicative of a disruption in this relationship. The *Synechococcus* spp. which bloom in Florida Bay are known to produce extracellular polysaccharides (EPS; Phlips *et al*., 1989; Lynch and Phlips, 2000) which can adhere to the cilia of, and thus inhibit feeding in, benthic and protozoan grazers by causing the cessation of cilia movement (Draper *et al*., 1990; Gainey and Shumway, 1991; Liu and Buskey, 2000). To date, zooplankton grazing rates on *Synechococcus* sp. or other plankton groups have never been measured in Florida Bay.

The 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, meso- 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.

METHODS

Field Sampling

Field sampling in Florida Bay was conducted at two stations in the western (25.12ºN, 80.97ºW; 25.00ºN, 80.93ºW; sites 1 and 2), north-central (25.12ºN, 80.80ºW; 25.13ºN, 80.72ºW; sites 4 and 5), southern (24.98ºN, 80.80ºW; 24.97ºN, 80.70ºW; sites 3 and 6), and eastern basins (25.08ºN, 80.55ºW; 25.17ºN, 80.52ºW; sites 7 and 8) and at one station within Blackwater Sound (25.18ºN, 80.40ºW; sites 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 winter from January 8 through 13 of 2007, and in the spring from March 30 through April 4 of 2007.

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 gently collected in replicated 20-liter carboys (n = 3) with minimal bubbling

and transported back to the laboratory for analysis. The well-mixed (pers. obs. of surface and bottom temperature and salinity) and shallow nature (< 3 m) of Florida Bay ensured sub-surface samples were representative of the whole water column. Whole water samples were preserved with 10% buffered formalin and analyzed flow cytometrically to assess picoplankton densities (Olson *et al*., 1991). Following preservation, samples were flash-frozen in liquid nitrogen. Abundance of heterotrophic bacteria (stained with SYBR Green I; Jochem, 2001), phycoerythrin-containing picocyanobacteria, phycocyanin-containing picocyanobacteria, and photosynthetic picoeukaryotes were determined using a FACScan (BD®) flow cytometer using fluorescence patterns and particle size from side angle light scatter (Olsen *el al*., 1991). Whole water samples (40 ml) were preserved with glutaraldehyde (2 % v/v, final) and stored in the dark in sterile polypropylene tubes at 4ºC. These samples were examined using an epifluorescence microscope at high resolution (1000X) to confirm the identification of picoplankton made with the flow cytometer. Two classes of cyanobacteria were quantified. One group consisted of small, unicellular cyanobacteria that contained phycoerythrin, resembling *Synechococcus* sp., while the second population consisted of coccoid, phycocyanin-containing cyanobacteria, which were slightly larger (ca. 1 μm) than *Synechococcus*-like cyanobacteria.

Seawater samples for photo- and heterotrophic nanoplankton were preserved with 10% glutaraldehyde. These samples were stained in triplicate with DAPI within 24 h of collection, and autotrophs and heterotrophs were differentiated and enumerated via epifluorescent 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 (Jeong *et al*., 1999, 2001, 2002, 2004, 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 mesozooplankton (meroplanktonic larvae, nauplii and copepodites) identification and enumeration using a dissecting microscope (Harris *et al*., 2000). Whole seawater was filtered for size-fractionation of chlorophyll *a* using 2- and 20-µm polycarbonate filters and 0.7-µm glass fiber filters. Chlorophyll *a* was analyzed by standard fluorometeric methods (Parsons *et al*., 1984).

Microzooplankton grazing rates

Dilution experiments were conducted to estimate microzooplankton grazing rates (Landry *et al*., 1995). A series of dilutions were established using 100, 70, 40, and 15% whole seawater (WSW) diluted with 0.2 µm filtered seawater obtained via gravity filtration through filter capsules (Pall) with vents which eliminated bubbling of water as it entered the capsules. The experiment 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-liter bottles. Experimental bottles was incubated in Florida Bay in the vicinity

of Key Largo region at the Everglades National Park Ranger Station with one layer of neutral density screening (33% reduction in light) to mimic ambient light and temperature conditions. After 24 hours 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 with the following equation: $\mu = \ln[B_t/B_o)]/t$ where μ is the net growth rate (d^{-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 (m) 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 an 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. This solution was then gently mixed and the volume required to attain 2x, 4x, and 8x 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 (Fig 5). A control treatment of 200 µm filtrate was also established (0x 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 of the plankton groups 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 ANOVAs with multiple comparison tests or appropriate non-parametric tests (*e.g.*, Mann-Whitney rank sum test). Comparison of variables between the bloom and non-bloom conditions, established as 3×10^5 cells ml^{-1} by Phlips *et al.* (1999) were made with T-tests. This threshold was consistent with water clarity observations in Florida Bay.

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 of 2006, Blackwater Sound (Site 9, eastern Florida Bay) experienced a relatively large picocyanobacterial bloom, consisting mostly of phycocyanin-containing cells (92% of total cell density), with total cyanobacterial densities exceeding 2 x 10^6 cells ml^{-1} (Fig. 2). Concurrently, a smaller cyanobacteria bloom (4 x 10^5 cells ml^{-1}) comprised primarily of *Synechoccocus*-like cells occurred in the north-central basin of the bay (Site 4) while cyanobacterial densities were lower throughout the rest of the bay (1.2 ± 0.8 x 10^5 cells ml^{-1}; Fig. 2). Chlorophyll *a* levels were slightly elevated at bloom locations (2.2 ± 0.6 µg l^{-1} at sites 9 and 4; Fig. 2) and were relatively low elsewhere (1.2 ± 0.9 µg l^{-1}; Fig. 2). Eukaryotic phytoplankton densities were elevated in the northwest (5.5 ± 0.5 x 10^3 cells ml^{-1} at site 1) and in Blackwater Sound (35 ± 2.0 x 10^3 cells ml^{-1}; Fig. 2) but were lower in the central and eastern basins (0.7 ± 0.4 x 10^3 cells ml^{-1}; Fig. 2). Diatom abundance was greatest at site 1 (3.74 ± 0.08 x 10^2 cells ml^{-1}; Fig. 4) being dominated by the *Rhizosolenia sp*. A smaller peak in abundance occurred at site 5 (2.42 ± 0.2 x 10^2 cells ml^{-1}; Fig. 4) dominated by the entric species *Thalassiosira* sp. Autotrophic microflagellates had a sizeable population at site 7 with 4.9 ± 0.3 x 10^4 cells l^{-1}. Densities of heterotrophic bacteria were fairly

consistent at 1.1 ± 0.4 x 10^6 cells ml^{-1} throughout the bay, except for Blackwater Sound where densities reached almost 8 x 10^6 cells ml^{-1} (Fig. 2).

The abundance of heterotrophic nanoplankton was generally consistent throughout Florida Bay averaging 5.9 ± 1.2 x 10^3 cells ml^{-1} (Sites 1-8). The exception to this pattern was Blackwater Sound where their abundance was more than five times higher (3.0 ± 0.49 x 10^4 cells ml^{-1}, Site 9, Fig. 3). Total microzooplankton abundance for Florida Bay averaged 7.1 ± 0.18 x 10^4 cells l^{-1}. Dinoflagellates were most abundant at site 4 with a density of 5.7 ± 1.5 x 10^4 cells l^{-1} (Fig. 4), comprised mainly of *Prorocentrum* spp. Ciliates were most abundant at Blackwater Sound (Site 9, 4.6 ± 0.4 x 10^4 cells l^{-1}; Fig. 4), being co-dominated by *Mesodinium rubrum* and *Loboea* spp. The remaining sites (1-8) had an average ciliate density of 2.0 ± 0.8 x 10^4 cells l^{-1}. Copepod abundances ranged from 0.31 ± 0.05 (site 6) to 24.3 ± 2.6 (site 3) individuals l^{-1}, with most sites throughout Florida Bay hosting ~3 individuals l^{-1} (Fig. 5). *Acartia tonsa* was the dominant mesozooplankton species in Florida Bay at this time.

Fall - The cyanobacteria bloom in Blackwater Sound diminished slightly in intensity during the fall (8 x 10^5 cells ml^{-1}; site 9) but expanded westward into Florida Bay (5 x 10^5 cells ml^{-1}; Site 8; Fig. 2), and was again comprised primarily of a phycocyanin-containing cells (85% of total cell density). The North-Central basin cyanobacteria bloom expanded southward and increased in density as two sampling sites had cell densities exceeding 3 x 10^6 cells ml^{-1} (sites 3 and 4) with a smaller bloom (3 x 10^5 cells ml^{-1}) occurring at site 5 (Fig. 2). These blooms consisted mostly of *Synechococcus*-like cyanobacteria (65% of cells of total cell density). Densities of eukaryotic phytoplankton, heterotrophic bacteria,

and chlorophyll *a* were 4 – 5 times higher at most bloom sites (3,4,5,8,9) compared to other locations (2,6,7), excluding site 1 which continued to have elevated levels of chlorophyll *a* and eukaryotic phytoplankton (Fig. 2). Site 1 also had the highest abundance of diatoms ($4.73 \pm 0.04 \times 10^5$ cells l^{-1}; Fig. 4); the dominant species were *Rhizosolenia setigera*, *Nitzschia* sp., and *Asterionellopsis* sp. Elsewhere, diatom abundances ranged from 2.4 ± 1.7 (site 3) to 166 ± 8.1 (site 7) $\times 10^3$ cells l^{-1} (Fig. 4). Autotrophic microflagellate abundance was the greatest at site 3 with $3.9 \pm 0.34 \times 10^4$ cells l^{-1}.

Heterotrophic nanoplanktonic abundances were relatively low in the western and eastern locations of Florida Bay (sites 1,2,6,7,8) averaging $2.7 \pm 1.1 \times 10^3$ cells ml^{-1}. By contrast, levels were elevated in the central basin (sites 3,4,5) and were highest in Blackwater Sound (site 9) reaching $3.1 \pm 0.57 \times 10^4$ cells ml^{-1} at Site 9 (Fig. 3). Total microzooplankton abundances were highest at site 3 ($1.72 \pm 0.22 \times 10^5$ cells l^{-1}) with a smaller peak at site 9 ($1.54 \pm 0.03 \times 10^5$ cells l^{-1}). Dinoflagellates (primarily *Gyrodinium spirale*) were most abundant at site 9 ($1.07 \pm 0.15 \times 10^5$ cells l^{-1}; Fig. 4). Ciliates were abundant at sites 3 and 5 with densities of $7.5 \pm 0.47 \times 10^4$ cells l^{-1} and $7.0 \pm 0.66 \times 10^4$ cells l^{-1}, respectively (Fig. 4). *Mesodinium rubum* was the dominant ciliate at most sites with the exception of Blackwater Sound (site 9) which was dominated by *Loboea* spp. The greatest copepod numerical density was found in Blackwater Sound with 8.9 ± 0.6 individuals l^{-1}, numerically dominated by *Acartia tonsa*. The lowest abundance of copepods was 0.36 ± 0.09 individuals l^{-1} at site 4 (Fig. 5).

Winter – Compared to the fall, the eastern basin cyanobacteria bloom retracted into Blackwater Sound by January (site 9) and became a mixed assemblage of *Synechococcus*-like and phycocyanin-containing cyanobacteria, but maintained densities of ~5 x 10^5 cells ml^{-1} (Fig. 2). In contrast, the cyanobacteria bloom in the central region continued to occupy much of the central and southeastern portion of Florida Bay (sites 2, 3, 4, 5), achieved densities of >10^6 cells ml^{-1}, and was comprised primarily of phycocyanin-containing cells. Once again, bloom sites (sites 2, 3, 4, 5, 9) contained levels of eukaryotic phytoplankton, heterotrophic bacteria, and chlorophyll *a* which were 5–7 times greater than the levels found in non-bloom stations (6,7,8), but were similar to the non-bloom northwestern site (Fig. 2). The highest abundance of diatoms was found in the western basin (site 7; 4.00 ± 0.02 x 10^5 cells l^{-1}; Fig. 4) and was dominated by *Nitzschia* sp. The rest of Florida Bay was characterized by lower levels of diatoms ranging from 3.6 ± 0.9 (site 3) to 91 ± 2.0 (site 8) x 10^3 cells l^{-1}; no diatoms were found at site 2 (Fig. 4). High abundances of autotrophic microflagellates occurred in the western sites 1 and 2 with 6.1 ± 0.13 and 7.1 ± 0.31 x 10^4 cells l^{-1}, respectively.

From November 2006 to January of 2007, Blackwater Sound experienced a four-fold decrease in heterotrophic nanoplankton abundance to 0.8 ± 0.2 x 10^4 cells ml^{-1}. Site 2 hosted the highest levels of heterotrophic nanoplankton (1.8 ± 0.4 x 10^4 cells ml^{-1}) while moderate levels were found throughout the rest of the Bay (Sites 1, 3-8; 5.3 ± 3.7 x 10^3 cells ml^{-1}; Fig. 3). Site 2 also had the largest abundance of microzooplankton with a density of 2.31 ± 0.18 x 10^5 cells l^{-1}. The largest density of dinoflagellates occurred at site 2 (1.22 ± 0.13 x 10^5 cells l^{-1}; Fig. 4), being comprised largely *Gyrodinium* spp. and *Heterocapsa* sp. Similar levels of dinoflagellates were found at site 9 (1.22 ± 0.18 x 10^5

cells l^{-1}) being comprised mainly of *Gyrodinium* spp. There was an overall decrease in ciliate abundance in Florida Bay compared to the fall with an average of 1.4 x 10^4 cells l^{-1} at this time (Fig. 4). The ciliate populations were dominated by *Mesodinium rubum* throughout Florida Bay and peaked at site 2 with 3.8 ± 0.16 x 10^4 cells l^{-1}. Sites 3 and 6 had high densities of copepods with 5.8 ± 0.2 and 6.2 ± 0.2 individuals l^{-1}, respectively (Fig. 5). *Acartia tonsa* was dominant at site 3 while *Paracalanus* sp. was dominant at site 6. Site 7 had the lowest density of copepods (1.6 ± 0.05 individuals l^{-1}; Fig. 5).

Spring - During the spring of 2007, the bloom that occupied the central and southeastern regions of Florida Bay diminished and was only found in the southwestern portion of the bay at site 2. This bloom was primarily comprised of phycocyanin-containing cyanobacteria (93% of total cell density) and contained 9 x 10^5 cells ml^{-1}. Cyanobacterial abundance was also high in Blackwater Sound (site 9) at 3 x 10^5 cells ml^{-1}; this bloom was mainly comprised of *Synechococcus*-like cyanobacteria (78% of total cell density). Eukaryotic picophytoplankton abundances were elevated just above 3 x 10^3 cells ml^{-1} at sites 1 and 9, but were lower elsewhere. Diatoms concentrations were lower throughout the bay (3.2 ± 1.9 x 10^4 cells l^{-1}; Fig. 4). Site 1 had high levels of autotrophic microflagellates (1.7 ± 0.09 x 10^4 cells l^{-1}). Chlorophyll *a* levels were elevated at bloom sites (2 and 9) and site 1, but were lower elsewhere (0.58 ± 0.25 µg l^{-1}). Heterotrophic bacterial abundances were lower in the spring as well (5.5 ± 3.1 x 10^3 cells ml^{-1}).

Heterotrophic nanoplanktonic abundances became more uniform during the spring, averaging 2.4 ± 0.6 x 10^3 cells ml^{-1} for all sites (Fig. 3) except within the cyanobacteria bloom at site 2 where levels were twice the bay mean (5.8 ± 0.87 x 10^3

cells ml^{-1}; Fig. 3). Microzooplankton abundances ranged from 3.2 ± 0.34 x 10^4 cells l^{-1} (site 3) to 8.1 ± 1.2 x 10^4 cells l^{-1} (site 1; Fig. 4). The bloom at site 2 had elevated levels of dinoflagellates (4.4 ± 0.62 x 10^4 cells l^{-1}), mainly *Prorocentrum* sp. Site 9 also had high levels of dinoflagellates at 4.0 ± 0.61 x 10^4 cells l^{-1} comprised of *Heterocapsa* sp., *Gyrodinium spirale*, and *Prorocentrum* sp (Fig. 4). Ciliate abundances, dominated by *Mesodinium rubum*, were fairly consistent throughout Florida Bay averaging 2.2 ± 0.06 x 10^4 cells l^{-1} (Fig. 4). The highest copepod densities occurred at sites 3 and 7 with abundances of 5.6 ± 0.99 and 5.7 ± 0.34 individuals l^{-1}, respectively, with site 3 dominated by *Acartia tonsa* and site 7 was dominated by *Acartia tonsa* and *Temora* sp. (Fig. 5). The lowest copepod density was at site 8 with 0.83 ± 0.20 individuals l^{-1} (Fig. 5).

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, and heterotrophic bacteria) during every experiment conducted during this study (n = 36). Mean grazing rates on all populations during all experiments were approximately 0.8 d^{-1}. However, grazing rates and our ability to quantify microzooplankton grazing on various planktonic groups co-varied in conjunction with the ambient densities of cyanobacteria.

Summer - Microzooplankton grazing on cyanobacteria was undetectable using the dilution technique during the central Florida Bay bloom event at site 4 and at another central site 6. Additionally, microzooplankton grazing rates on cyanobacteria were low

in Blackwater Sound (0.20 ± 0.09 d^{-1}; Table 1) compared to other sites (1.1 ± 0.76 d^{-1}; Table 1). 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 d^{-1} on eukaryotic prey (chl *a*, eukaryotes) and 1.2 ± 0.61 d^{-1} for prokaryotic prey (cyanobacteria, bacteria). There was relatively high bacterivory (grazing on heterotrophic bacteria) throughout the bay (1.31 ± 0.43 d^{-1}) with lower rates occurring at bloom sites 4 (0.81 ± 0.10 d^{-1}) and 9 (0.52 ± 0.09 d^{-1}; Table 1).

Fall - During the fall, microzooplankton grazing rates on cyanobacteria at sites with blooms were either low (0.20 ± 0.09 d^{-1}; Site 8; Table 1) or undetectable (4 of 5 experiments; sites 3, 4, 5, 9). For locations without blooms, grazing rates on cyanobacteria were more than four-times higher (0.87 ± 0.47 d^{-1}; Table 1). Microzooplankton grazing on eukaryotic phytoplankton ranged from 0.61 ± 0.20 d^{-1} (site 2) to 1.2 ± 0.46 d^{-1} (site 7) and averaged 0.79 ± 0.29 d^{-1}. Grazing on the total phytoplankton population (chl *a*) was highest at site 7 (1.2 ± 0.24 $d^{-1)}$ and lowest at site 8 (0.25 ± 0.12 d^{-1}) and averaged 0.66 ± 0.31 d^{-1}. Bacterivory rates were high in the west (0.94 ± 0.05 d^{-1} at site 1 and 0.78 ± 0.13 d^{-1} at site 2) and low or non-detectable in the central Florida Bay cyanobacteria bloom: 0.21 ± 0.05 d^{-1} at site 3, undetectable at site 4, and 0.26 ± 0.06 d^{-1} at site 5 (Table 1).

Winter - Although bacterivory was quantified at all locations during the winter, microzooplankton grazing on other prey was detectable in fewer than half of experiments conducted with bloom levels of cyanobacteria (7 of 15 experiments; Table

1). Bacterivory rates were generally low within cyanobacteria blooms (0.43 ± 0.32 d^{-1}) and higher elsewhere (1.2 ± 0.23 d^{-1}). Mean microzooplankton grazing rates on eukaryotic algae, cyanobacteria, and the total phytoplankton community during winter were 0.32 ± 0.13 d^{-1}, 0.31 ± 0.12 d^{-1}, and 0.36 ± 0.23 d^{-1}, respectively (Table 1).

Spring - During the spring, there was consistent bacterivory and detectable grazing on cyanobacteria 75% of the time (Table 1). As was found during prior seasons, grazing rates on cyanobacteria were undetectable at sites which had a sizeable cyanobacterial population (> 3 x 10^5 cells ml^{-1}; sites 2 and 9). Rates of bacterivory were high at most stations (1.8 ± 0.22 d^{-1}) but were lower at sites with cyanobacteria blooms (0.81 ± 0.29 d^{-1}). In contrast to the prokaryotes, microzooplankton grazing was undetectable during 50% of spring experiments for eukaryotic populations (chl *a*, eukaryotes; Table 1). Grazing rates on the total phytoplankton population and eukaryotic algae were similar to rates recorded during winter, averaging 0.36 ± 0.23 d^{-1} and 0.32 ± 0.13 d^{-1}, respectively (Table 1).

Mesozooplankton enrichment experiments

Enriching densities of mesozooplankton 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) during 86% of experiments conducted during this study. In July 2006, there was a significant, linear growth response from microbial prey items resulting from mesozooplankton enrichment in most of experiments, the majority of which yielded negative net growth rates (Table

2). During the fall, winter, and spring, statistically significant linear responses among all prey groups were somewhat less common (40% of experiments; Table 2). 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. 6). When cyanobacterial densities were low, enriching mesozooplankton densities, on average, lead to positive growth rates of all microbial prey (Fig. 6). In contrast, during bloom events, enrichment of mesozooplankton yielded progressively larger and more negative net growth rates of microbial prey (Fig. 6).

Effects of nutrient enrichment on microbial net growth rates

Nutrient enrichment had a large effect on the total phytoplankton community (chlorophyll *a*) with nutrients increasing net growth rates by an average of 0.44 ± 0.07 d^{-1}, an increase which was significantly larger than those displayed by all other plankton groups (Tukey test; $p < 0.05$, Fig. 8). 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 d^{-1} and 0.12 ± 0.04 d^{-1}, respectively. On average, nutrient addition elicited almost no change in the net growth rates of cyanobacteria with an average of 0.01 ± 0.07 d^{-1}. The response of each group's net growth rate to nutrient loading were not significantly different between bloom and non-bloom conditions.

DISCUSSION

During this study, we observed the occurrence of cyanobacteria blooms, microbial communities, and zooplankton grazing through an annual cycle in Florida Bay. Blooms of picocyanobacteria persisted during all four seasons within both the eastern and central regions of Florida Bay, expanding during the fall and winter and retracting during the spring. To our knowledge, this is the first report of dense cyanobacterial 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 associated with a microbial consortium comprised of high levels of chlorophyll *a*, heterotrophic bacteria, phototrophic nanoflagellates, and microflagellates. While there were high rates of microzooplankton grazing on all members of the picoplankton community when cyanobacteria densities were low, grazing rates were frequently undetectable during bloom events and quantifiable grazing rates on cyanobacteria and heterotrophic bacteria were substantially lower than regions without blooms. Together, these results provide new insight regarding the role of decreased zooplankton grazing pressure 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 in Florida Bay. When cyanobacteria cell densities were low ($< 3.0 \times 10^5$ cells ml^{-1}), cyanobacteria abundances were positively correlated with the densities of ciliates ($p < 0.001$; $R=0.65$) and heterotrophic nanoflagellates ($p < 0.0001$; $R=0.83$), two common grazers of picoplanktonic prey (Christaki *et al.*, 1999; Caron *et al.*, 1991; Jurgans and Massana, 2000). However, during cyanobacteria blooms in Florida Bay, the microbial consortium associated with cyanobacteria changed. For example,

during cyanobacteria blooms, densities of cyanobacteria became significantly correlated with chlorophyll *a* concentrations, heterotrophic bacteria, phototrophic nanoflagellates and 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). However, during blooms, cyanobacteria densities were no longer correlated with any known group of zooplankton including ciliates and heterotrophic nanoflagellates, indicating the grazers whose abundances paralleled cyanobacteria abundance at low densities did not increase in abundance correspondingly with cyanobacteria blooms in Florida Bay. It is possible that the absence of high levels of grazers allowed for the concurrent increase in other potential autrotrophic and picoplanktonic prey such as heterotrophic bacteria, phototrophic nanoflagellates and microflagellates which were all well correlated with cyanobacterial densities at stations with cyanobacteria blooms.

These observed changes in the microbial food web occurred in concert with altered grazing pressure on microbial populations. During non-bloom conditions, there was detectable microzooplankton grazing on at least one prey group in every experiment conducted (Table 1) and measurable grazing on cyanobacteria, eukaryotic algae, and the total phytoplankton community in 76, 67, and 71% of experiments, respectively (Table 1). With the onset of bloom conditions, microzooplankton grazing was less frequently detected on cyanobacteria (29%), eukaryotic algae (50%), and the total phytoplankton community (57%; Table 1). When microzooplankton grazing was detected, the grazing rates on prokaryotic prey during cyanobacterial blooms were three-fold lower than rates quantified in regions with low levels of cyanobacteria (t-tests, $p<0.001$; Fig. 7). In contrast, the absolute rates of grazing on eukaryotic algae and the total phytoplankton

community did not change during cyanobacteria blooms (Fig. 7). Microzooplankton grazing rates on autotrophic prey items in regions of Florida Bay without cyanobacteria blooms were generally equal to or slightly greater than the rates previously reported as typical of tropical regions and estuaries (~ 0.5 d^{-1}; Calbet and Landry, 2004). The grazing rates on cyanobacteria during bloom events were markedly lower (0.3 d^{-1}; Fig. 7).

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 densities to increase in parallel with cell densities, 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 genera of cyanobacteria which blooms in Florida Bay (Phlips *et al*., 1999; Lynch and Phlips, 2000) produces microcystin (Carmichael and Li, 2006), a well-established zooplankton grazing deterrent (de Bernardi and Giussani, 1990; Boon *et al.,* 1994; Christoffersen, 1996). In addition, the extracellular polysaccharides produced by *Synechococcus* within Florida Bay (Phlips *et al*., 1989) have been shown to reduce grazing on other bloom-forming harmful algae (Buskey *et al.,* 1997; Liu and Buskey, 2000). Regardless of the precise mechanism, low zooplankton grazing pressure on bloom forming phytoplankton may be a primary cause of ecosystem disruptive algal blooms (EDABs) such as *Synechococcus* in Florida Bay (Sunda *et al.,* 2006).

The trophic impact of mesozooplankton on microbial prey items also changed with the onset of cyanobacteria blooms in Florida Bay. When densities of cyanobacteria

were low in Florida Bay, enriching densities of mesozooplankton yielded increased net growth rates for picoplanktonic prey (Fig. 6). In this case, consumption of a picoplankton predator, such as microzooplankton, by the mesozooplankton may have released the picoplanktonic prey from predation pressure (Calbet and Landry, 1999; Deonarine *et al*., 2006). However, under bloom conditions, enhancing mesozooplankton densities had an anticipated predatory affect on microbial prey, with net growth rates of each population decreasing significantly and linearly with increasing mesozooplankton levels (Fig. 6). This could have been due to direct predation by mesozooplankton on these prey items or due to a trophic cascade (Calbet and Landry 1999; Deonarine *et al*., 2006). Increased grazing on microzooplankton might partly be facilitated by the onset of the bloom which leads to a decrease in the availability of autotrophic prey of a suitable size for mesozooplankton (Calbet and Landry, 1999; Jurgans and Massana, 2000). The observed change during blooms indicates a shift in trophic structure where bloom sites had an even number of trophic levels from mesozooplankton to the picoplanktonic prey (two or four levels) and non-bloom sites had an odd number trophic levels (likely three levels). The quantitative impact of mesozooplankton grazing on cyanobacteria was positively correlated with multiple plankton groups in Florida Bay including phototrophic nanoflagellates and dinoflagellates ($p<0.05$, $R=0.87$; $p<0.001$, $R=0.96$, respectively). Higher abundances of microzooplakton such as dinoflagellates might lead to enhanced mesozooplankton grazing on this group, allowing other groups such as cyanobacteria and phototrophic nanoflagellates to be released from grazing pressure. This supports the notion that cyanobacteria blooms may also be promoted via trophic cascades, specifically higher grazing on microzooplankton releases cyanobacteria from grazing pressure. 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, could be due to higher mesozooplankton grazing on these groups during blooms and thus is consistent with this hypothesis.

Traditionally, the occurrence of algal blooms has been associated with eutrophication (Anderson *et al*., 2002, Berman *et al.,* 2002) and it has been previously hypothesized that cyanobacteria blooms in Florida Bay are due to nutrient loading to this estuary (Phlips and Badylak, 1996; Phlips *et al.,* 1999). Comparisons of net growth rates of each plankton group with and without nutrient-enrichment demonstrated that total phytoplankton community (chlorophyll *a*) were most affected by nutrients, with net growth rates increasing by an average of 0.44 ± 0.07 d^{-1} (Fig. 8). Nutrient enrichment also significantly increased the growth rates of eukaryotic algae and heterotrophic bacteria, raising their net growth rates by 0.16 ± 0.06 d^{-1} and 0.12 ± 0.04 d^{-1}, respectively (t-test; $p < 0.05$; Fig 8). Conversely, nutrient enrichment had no effect on cyanobacterial net growth rates in Florida Bay (0.01 ± 0.07 d^{-1}, Fig. 8). 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 other eukaryotic phytoplankton. A similar conclusion has been reached for other HAB and EDAB species (Gobler *et al*., 2004, 2005). In parallel with those 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 thus are more likely to dominate under low inorganic nutrient conditions. This finding suggests that nutrient loading is unlikely to promote cyanobacteria blooms in Florida Bay and 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 blooms.

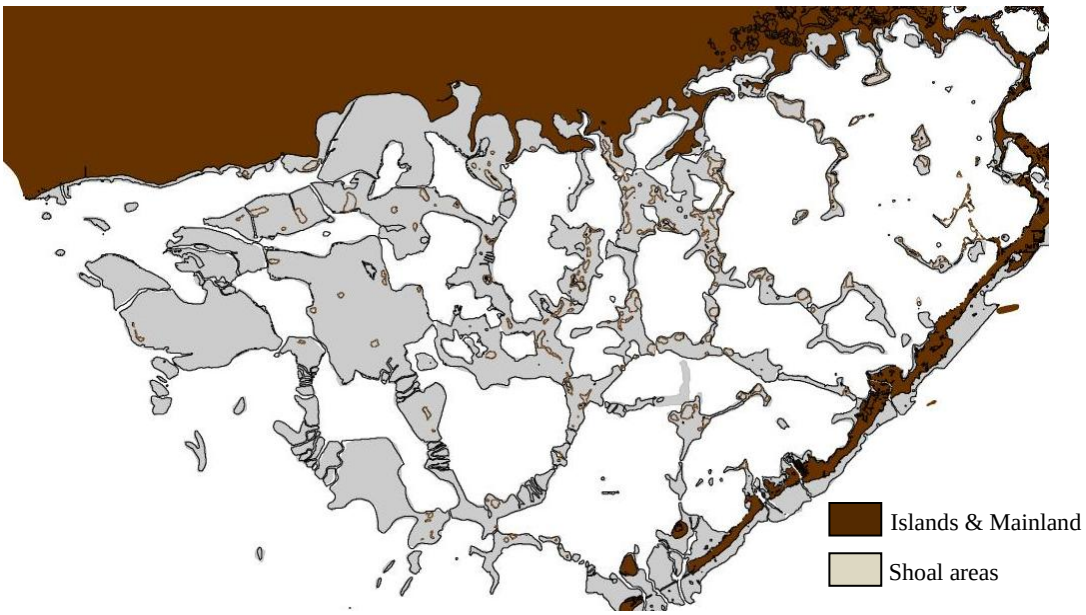

Figure 1. Study sites in Florida Bay, Florida, USA in the western (25.12ºN, 80.97ºW; 25.00ºN, 80.93ºW; sites 1 and 2), north-central (25.13ºN, 80.80ºW; 25.12ºN, 80.72ºW; sites 4 and 5), southern (24.98ºN, 80.80ºW; 24.97ºN, 80.70ºW; sites 3 and 6), and eastern basins (25.08ºN, 80.55ºW; 25.17ºN, 80.52ºW;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

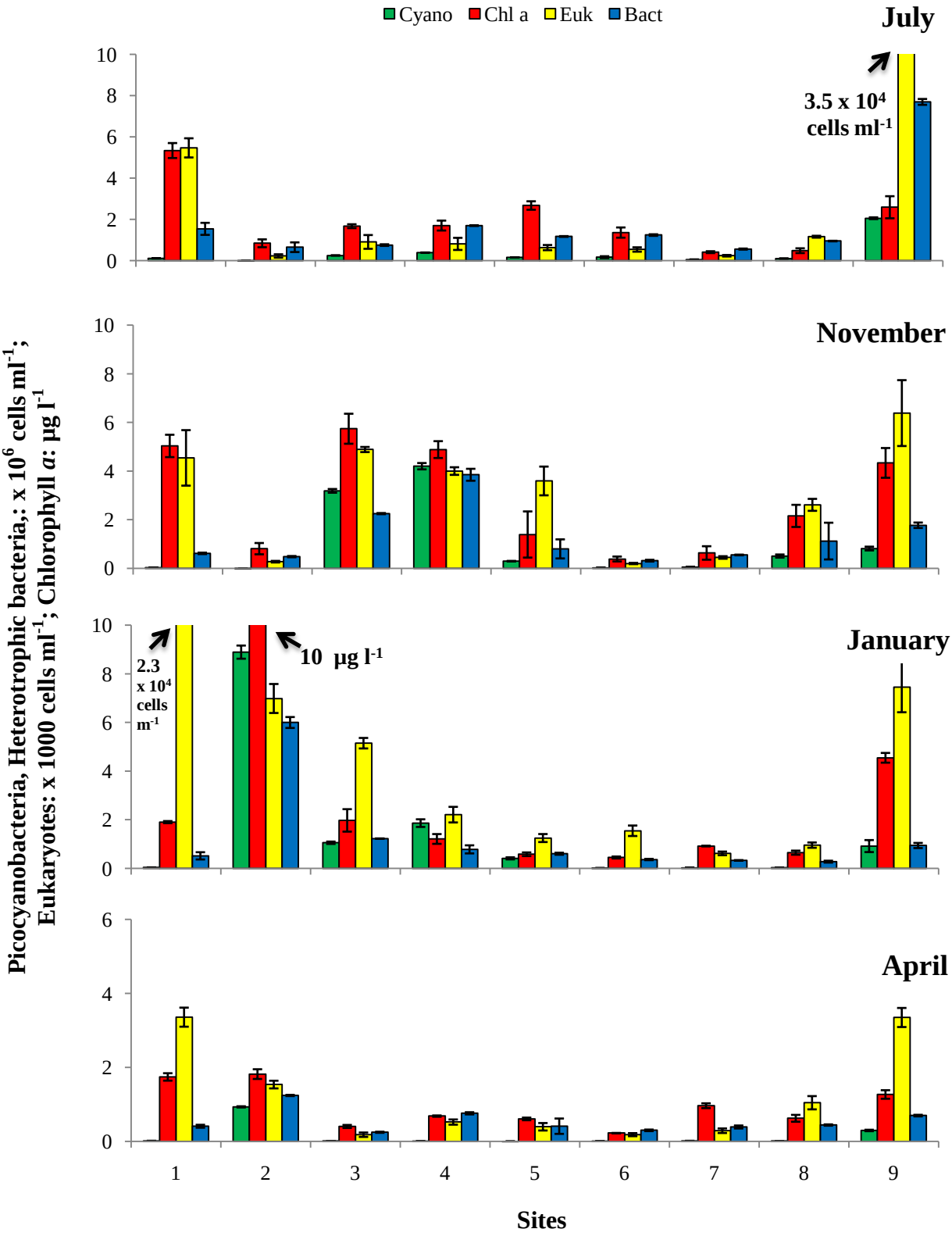

Figure 2. Densities of cyanobacteria (Cyano), eukaryotic algae (Euk), heterotrophic bacteria (Bact) and chlorophyll *a* (Chl *a*) in July 2006, November 2006, January 2007 and April 2007. Bars are means ± SD of triplicate measurements.

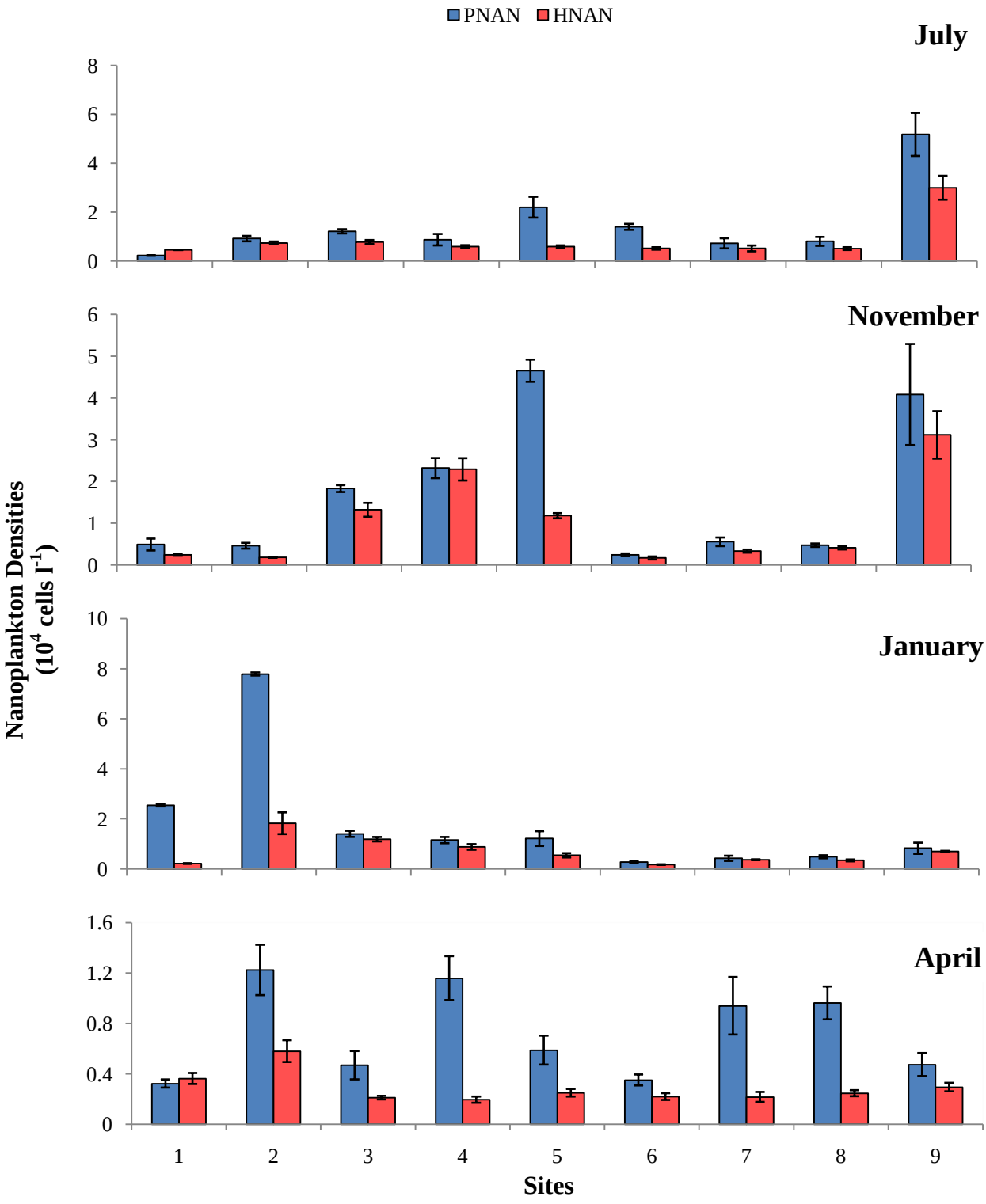

Figure 3. Phototrophic (PNAN) and heterotrophic (HNAN) nanoplankton abundances in July 2006, November 2006, January 2007 and April 2007. Error bars represent S.D. of multiple counts.

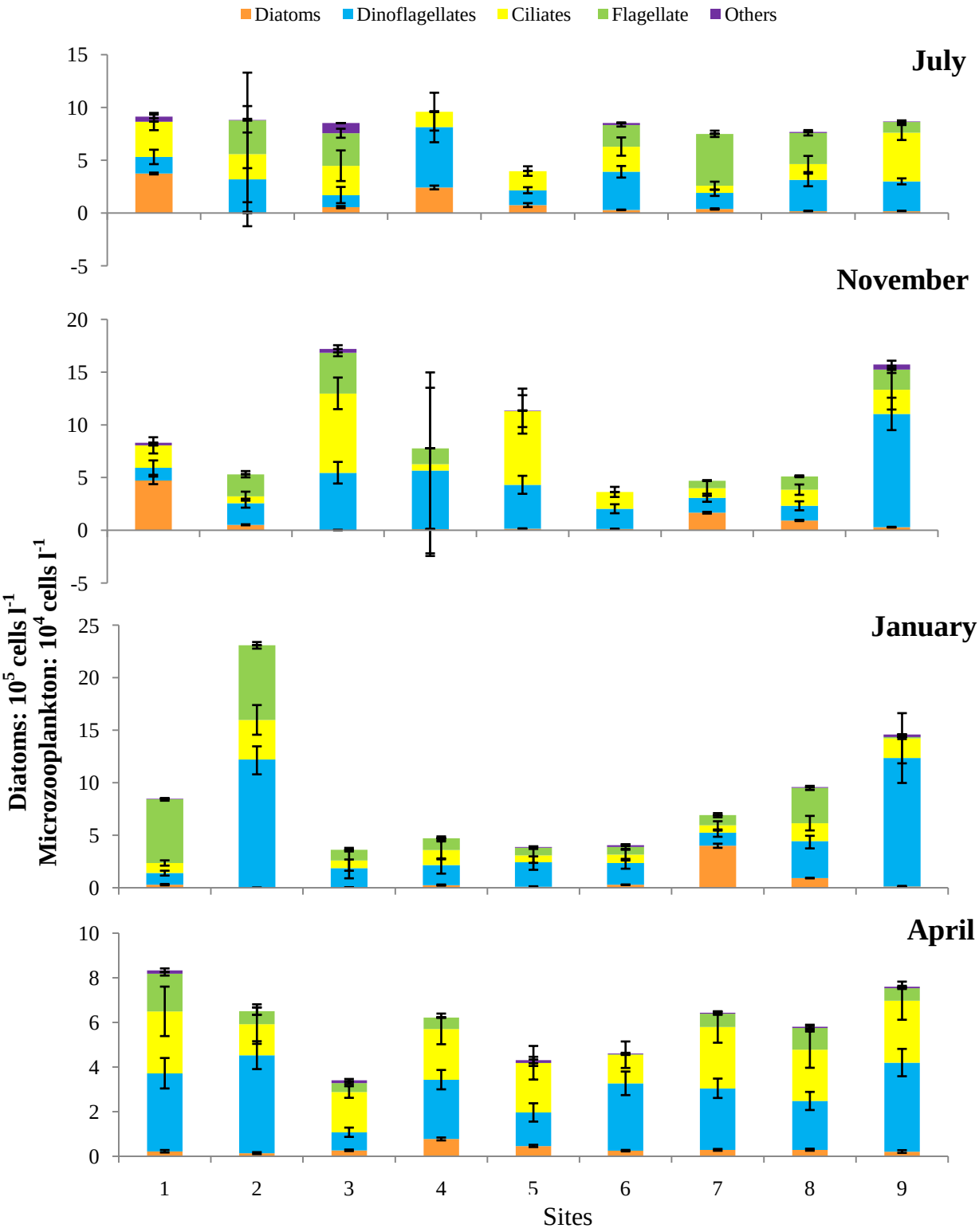

Figure 4. Microzooplankton abundance and composition in July 2006, November 2006, January 2007 and April 2007. Other microzooplankton includes rotifers and larvae. Error bars represent S.D. of multiple counts.

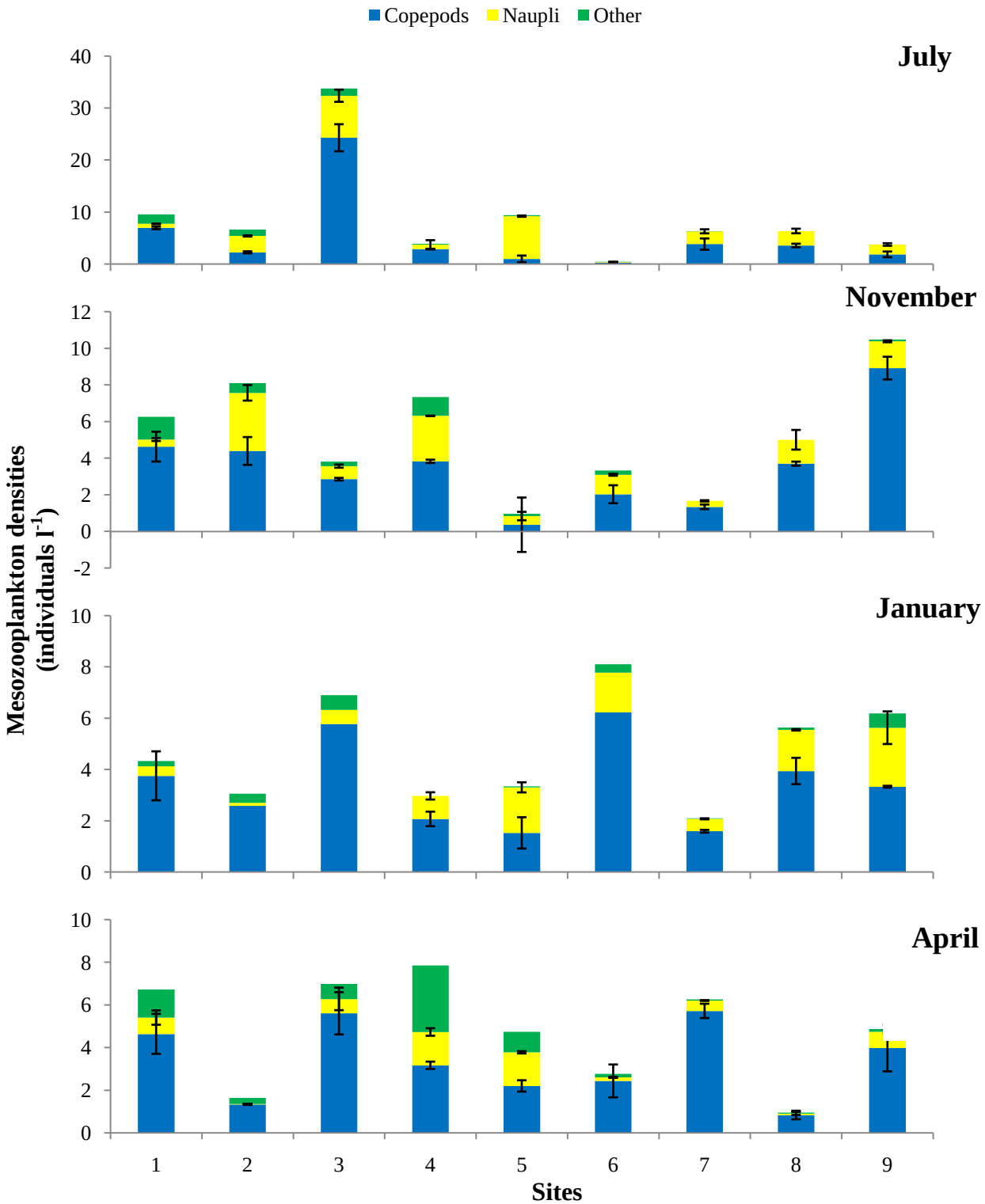

Figure 5. Mesozooplankton abundance and composition in July 2006, November 2006, January 2007 and April 2007. Other mesozooplankton includes larvae, mysids, and foraminifera. Error bars represent S.D. of multiple counts.

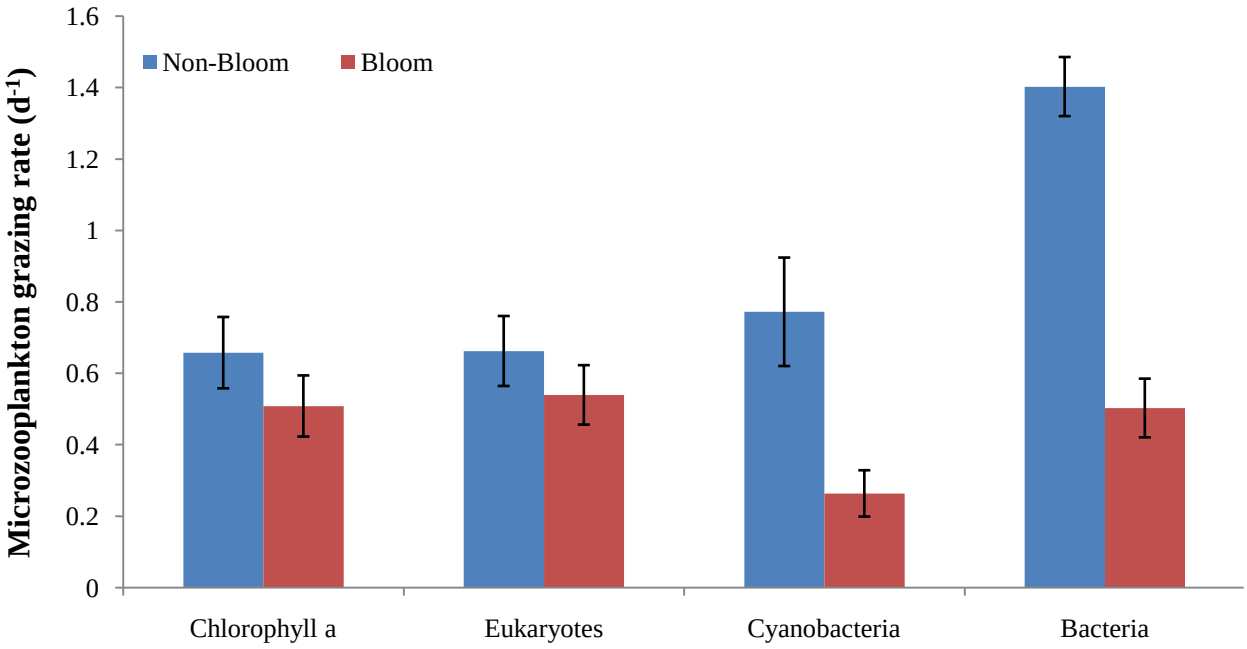

Figure 6. Average microzooplankton grazing rates per day on various prey items for July 2006, November 2006, January 2007 and April 2007. Error bars represent standard error.

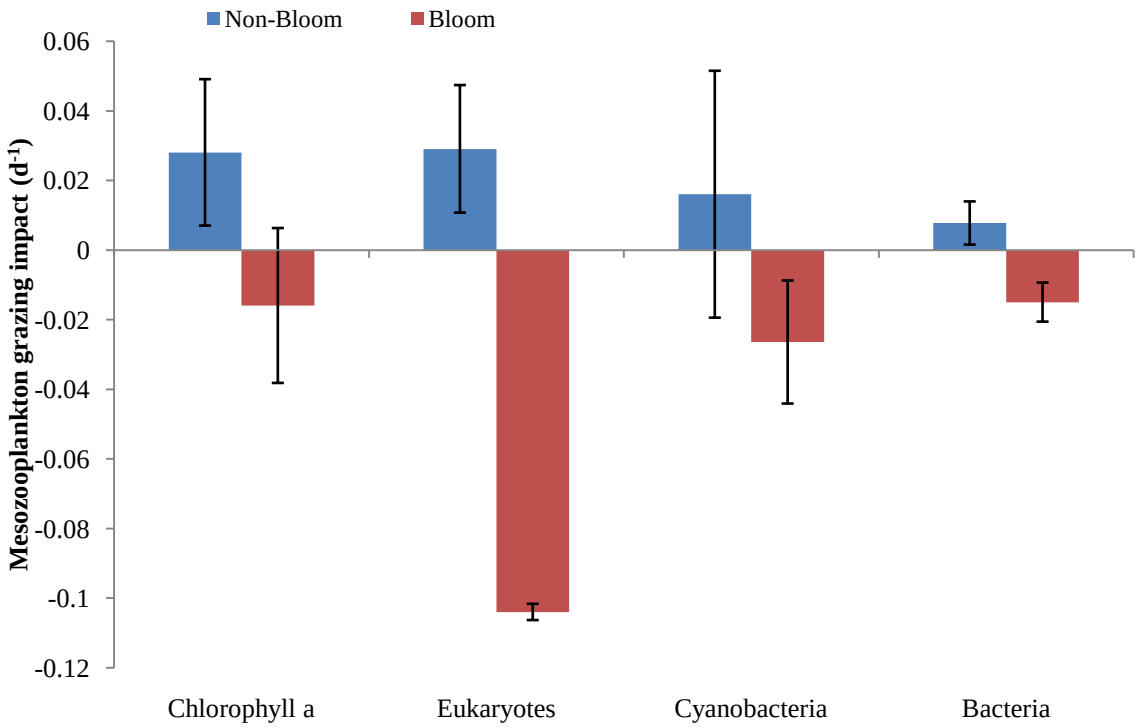

Figure 7. Average mesozooplankton grazing rates per day on various prey items for July 2006, November 2006, January 2007 and April 2007. Error bars represent standard error.

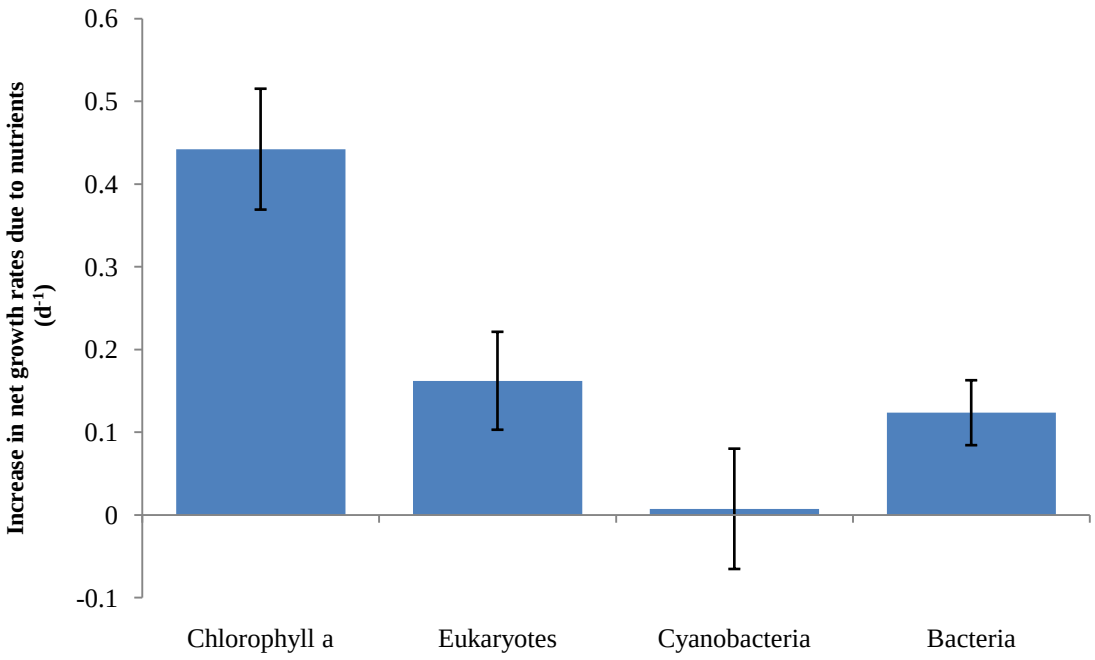

Figure 8. Average increase in net growth rates per day on various prey items due to nutrients for July 2006, November 2006, January 2007 and April 2007. Error bars represent standard error.

Date	Site	Chlorophyll a	Eukaryotes	Cyanobacteria	Bacteria
7/19/2006	1	1.6 ± 0.37	1.2 ± 0.17	1.7 ± 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**	**0.88 ± 0.23**	**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	0.16 ± 0.08	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	1.1 ± 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**	**0.63 ± 0.29**	**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 ± 0.06**
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**	**0.21 ± 0.08**	**0.15 ± 0.06**
1/8/2007	**3**	**0.25 ± 0.11**	**ND**	**ND**	**0.27 ± 0.06**
1/13/2007	**4**	**0.36 ± 0.13**	**0.38 ± 0.19**	**ND**	**0.37 ± 0.10**
1/13/2007	**5**	**ND**	**0.21 ± 0.09**	**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**	**0.29 ± 0.09**	**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**

Table 1. Microzooplankton grazing rates per day ± standard error. Non-detectable grazing was noted by ND. Bloom events are shown in bold.

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**

Table 2. Mesozooplankton grazing rates per day ± standard error. A non-linear response between the enrichment of mesozooplankton and microbial net growth rates was noted by ND. Bloom events are shown in bold.

Bibliography:

Anderson, D.M., Glibert, P.M., & Burkholder, J.M. (2002). Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. *Estuaries,* 25, 704-726.

Berman, J.M., Arrigo, K.R., & Matson, P.A. (2005). Agricultural runoff fuels large phytoplankton blooms in vulnerable areas of the ocean. *Nature,* 434, 211-214.

Boesch, D.F., Armstrong, N.E., D'Elia, C.F., Maynard, N.G., Paerl, H.N., & Williams, S.L. (1993). Deterioration of the Florida Bay ecosystem: an evaluation of the scientific evidence. Report to the Interagency Working Group on Florida Bay, Department of the Interior, National Park Service, Washington, D.C.

Boon, P.I., Bunn, S.E., Green, J.D. & Shiel, R.J. (1994). Consumption of cyanobacteria by freshwater zooplankton: Implications for the success of 'top-down' control of cyanobacterial blooms in Australia. *Australian Journal of Marine and Freshwater Research,* 45, 875–887.

Boyer, J. N., Dailey, S. K., Gibson, P. J., Rogers, M. T., & Mir-Gonzalez, D. (2006). The role of dissolved organic matter bioavailability in promoting phytoplankton blooms in Florida Bay. *Hydrobiologia,* 569, 71-85.

Buskey E.J., Montagna P.A., Amos A.F., & Whitledge T.E. (1997). Disruption of grazer populations as a contributing factor to the initiation of the Texas brown tide algal bloom. *Limnology and Oceanography*, 42, 1215-1222.

Butler, M.J. IV, Herrnkind, W.F., & Hunt, J.H. (1994). Sponge mass mortality and Hurricane Andrew: catastrophe for juvenile spiny lobsters in south Florida? *Bulletin of Marine Science,* 54, 1073.

Butler, M.J. IV, Hunt, J.H., Herrnkind, W.F., Childress, M.J., Bertelsen, R., Sharp, W., Matthews, T., Field, J.M., & Marshall, H.G. (1995). Cascading disturbances in Florida Bay, USA: cyanobacteria blooms, sponge mortality and implications for juvenile spiny lobsters *Panulirus argus*. *Marine Ecology Progress Series,* 129, 119-125.

Calbet, A. & Landry, M.R. (1999). Mesozooplankton influences on the microbial food web: Direct and indirect trophic interactions in the oligotrophic open ocean. *Limnology and Oceanography,* 44, 1370-1380.

Calbet, A. & Landry, M. R. (2004). Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnology and Oceanography,* 49, 51-57.

Carrick, H.J., Fahnenstiel, G.L., Stoermer, E.F., & Wetzel, R.G. (1991). The importance of zooplankton-protozoan couplings in Lake Michigan. *Limnology and*

Oceanography, 36, 1335-1345.

Carmichael, W. W. & Li, R. (2006). Cyanobacteria toxins in the Salton Sea. *Saline Systems*, 2, 5-17.

Caron, D. A., Lim, E. L., Miceli, G., Waterbury, J. B., & Valois, F. W. (1991). Grazing and utilization of chroococcoid cyanobacteria and heterotrophic bacteria by protozoa in laboratory culture and a coastal plankton community. *Marine Ecology Progress Series,*76, 205-217.

Chasar, L.C., Chanton, J.P., Koenig, C.C., & Coleman, F.C. (2005). Evaluating the effect of environmental disturbance on the trophic structure of Florida Bay, USA: Multiple stable isotope analyses of contemporary and historical specimens. *Limnology and Oceanography*, 50, 1059-1072.

Christaki, U., Jacquet, S., Dolan, J. R., Vaulot, D., & Rassoulzadegan, F. (1999). Growth and grazing on *Procholorococcus* and *Synechococcus* by two marine ciliates. *Limnology and Oceanography*, 44, 52-61.

Christoffersen, K. (1996). Ecological implications of cyanobacterial toxins in aquatic ecosystems. *Phycologia* , 36, 42-50.

Davis, G.E. & Dodrill, J.W. (1989). Recreational fishery and populations of spiny lobsters, *Panularis argus*, in Florida Bay, Everglades National Park, 1977-1980. *Bulletin of Marine Science*, 44, 78-88.

De Bernardi, R. & Giussani, G. (1990). Are blue-green algae a suitable food for zooplankton? An overview. *Hydrobiologia*, 200-201, 29-41.

Deonarine, S. N., Gobler, C. J, Lonsdale, D. J., & Caron, D. A. (2006). Role of zooplankton in the onset and demise of harmful brown tide blooms *(Aureococcus anophagefferens)* in US mid-Atlantic estuaries. *Microbial Aquatic Ecology*, 44, 181-195.

Draper, C., Gainey, L. Shumway, S. & Shapiro, L. (1990). Effects of *Aureococcus anophagefferens* ("Brown Tide") on the lateral cilia of 5 species of bivalve molluscs. In E. Graneli, B. Sundstrom, L. Elder & D. M. Anderson (Eds.) *Toxic Marine Phytoplankton* (pp. 128-l 31). New York: Elsevier Academic Press.

Fourqurean, J.W. & Robblee, M.B. (1999). Florida Bay: a history of recent environmental changes. *Estuaries*, 22, 345-357.

Gainey, L.F., Jr., & Shumway, S.E. (1991). The physiological effect of *Aureococcus anophagefferens* ("brown tide") on the lateral cilia of bivalve mollusks. *Biological Bulletin*, 181, 298-306.

Gallegos, C.L. 1989. Microzooplankton grazing on phytoplankton in the Rhode River, Maryland: non-linear feeding kinetics. *Marine Ecology Progress Series*, 57, 23-33

Glibert, P. M., Heil, C. A., Hollander, D., Revilla, M., Hoare, A., Alexander, J., & Murasko, S. (2004). Evidence for dissolved organic nitrogen and phosphorus uptake during a cyanobacterial bloom in Florida Bay. *Marine Ecology Progress Series*, 280, 73-83.

Gobler, C. J., Boneillo, G.E., Debenham C., & Caron, D.A. (2004). Nutrient limitation, organic matter cycling, and plankton dynamics during an *Aureococcus anophagefferens* bloom. *Aquatic Microbial Ecology*, 35, 31-43.

Gobler, C. J., Lonsdale, D. J., & Boyer, G. L. (2005). A review of the causes, effects, and potential management of harmful brown tide blooms caused by *Aureococcus anophagefferens* (Hargraves et sieburth). *Estuaries and Coasts*, 28, 726-749.

Hall, M.O., Durako, M.D., Fourqurean, J.W., & Zieman, J.C. (1999). Decadal changes in seagrass distribution and abundance in Florida Bay. *Estuaries*, 22, 445-459.

Harris, R.P., Wiebe, P.H., Lenz, J., Skjoldal, H.R., & Huntley, M. (Eds.). (2000). *ICES Zooplankton Methodology Manual*. London, UK: Elsevier Academic Press.

Hasle, G.R. (1978). The inverted microscope method. *Monographs on Oceanographic Methodology*, 6, 88-96.

Jeong, H. J. (1999). The ecological roles of heterotrophic dinoflagellates in marine planktonic community 1. *Journal of Eukaryotic Microbiology*, 46, 90-396.

Jeong, H. J., Kim, S. K., Kim, J. S., Kim, S. T., Yoo, Y. D., & Yoon, J. Y. (2001). Growth and grazing rates of the heterotrophic dinoflagellate *Polykrikos kofoidii* on red-tide and toxic dinoflagellates**.** *Journal of Eukaryotic Microbiology*, 48, 298-308.

Jeong, H. J., Kang, H., Shim, J. H., Park, J. K., Kim, J. S., Song, J. Y., & Choi, H. (2001). Interactions among the toxic dinoflagellate *Amphidinium carterae*, the heterotrophic dinoflagellate *Oxyrrhis marina*, and the calanoid copepods *Acartia* spp. *Marine Ecology Progress Serie*s, 218, 77-86.

Jeong, H.J., Yoon, J.Y., Kim, J.S., Yoo, Y.D., & Seong K.A. (2002). Growth and grazing rates of the prostomatid ciliate *Tiarina fusus* on red-tide and toxic algae. *Aquatic Microbial Ecology*, 28, 289-297.

Jeong, H.J., Yoo, Y.D., Kim, S.T., & Kang, N.S. (2004). Feeding by the heterotrophic dinoflagellate *Protoperidinium bipes* on the diatom *Skeletonema costatum. AquaticMicrobial Ecology*, 36, 171-179.

Jeong, H.J., Yoo, Y.D., Park, J.Y., Song, J.Y., Kim, S.T., Lee, S.H., Kim, K.Y., & Yih,W.H. (2005). Feeding by phototrophic red-tide dinoflagellates: five species newly revealed and six species previously known to be mixotrophic. *Aquatic Microbial Ecology,* 40, 133-150.

Jochem, F. J. (2001). Morphology and DNA content of bacterioplankton in the northern Gulf of Mexico: analysis by epifluorescence microscopy and flow cytometry. *AquaticMicrobial Ecology,* 25, 179-194.

Jurgens, K. & Massana, R. (2000). Protistan grazing on marine bacterioplankton. In Kirschman, D. (Ed.), *Microbial Ecology in the Oceans* (pp 383-442). New York: Wiley.

Landry, M.R. Kirshtein, J., & Constantinou, J. (1995). A refined dilution technique for measuring the community grazing impact of microzooplankton, with experimental test in the central equatorial Pacific. *Marine Ecology Progress Series,* 120, 53-63.

Landry, M. R., Barber, R. T., Bidigare, R. R., Chai, F., Coale, K. H., Dam, H. G., Lewis, M. R., Lindley, S. T., McCarthy, J. J., Roman, M. R., Stoecker, D. K., Verity, P. G., & White, J. R. (1997). Iron and grazing constraints on primary production in the central equatorial Pacific: An EqPac sysnthesis. *Limnology and Oceanography,* 42, 405-418.

Lehman, J.T. & Sandgren, C.D. (1982). Phosphorus dynamics of the prokaryotic nanoplankton of a Michigan Lake. *Limnology and Oceanography,* 27, 828-838.

Liu, H. & Buskey, E. J. (2000). The exopolymer secretions (EPS) layer surrounding *Aureoumbra laguenesis* cells affects growth, grazing, and behavior of protozoa. *Limnology and Oceanography,* 45, 1187-1191.

Lynch, T.C. & Phlips, E.J. (2000). Filtration of the bloom-forming cyanobacteria *Synechococcus* by three sponge species from Florida Bay, USA. *Bulletin of Marine Science,* 67, 923-936.

Mitsui, A., Rosner, D., Goodman, A., Reyes-Vasquez, G., Kusumi, T., Kodama, T., & Nomoto, K. (1989). Hemolytic toxins in marine cyanobacterium *Synechococcus* sp. In Okaichi, E., Anderson, P., & Nomoto, K. (eds.) *Red tides: biology, environmental science, and toxicology* (pp. 367-370). New York: ElsevierScience Publishing.

Olson, R.J., Zettler, E.R., Chisholm, S.W., & Dusenberry, J.A. (1991). Advances in oceanography through flow cytometry. In Demers, S. (Ed.), *Particle Analysis in Oceanography* (pp. 351-399). Berlin: Springer-Verlag.

Omori, M. & Ikeda, T. (1984). *Methods in marine zooplankton ecology*. New York:

J. Wiley & Sons.

Parsons, T.R., Maita, Y., & Lalli, C.M. (1984). *A manual of chemical and biological methods for seawater analysis*. New York: Pergomon Press.

Peterson, B.J., Chester, C. M., Jochem, F. J., & Fourqurean, J.W. (2006). Potential role of sponge communities controling phytoplankton blooms in Florida Bay. *Marine Ecology Progress Series*, 328, 93-103.

Phlips, E.J., Zeman, C. & Hansen, P. (1989). Growth, photosynethesis, nitrogen fixation and carbohydrate production by a unicellular cyanobacterium, *Synechococcus* sp. (Cyanophyta). *Journal of Applied Phycology*, 1, 137-145.

Phlips, E.J., Lynch, T.C., & Badylak, S. (1995). Chlorophyll *a*, tripton, color, and light availability in a shallow tropical inner-shelf lagoon, Florida Bay, USA. *Marine Ecology Progress Series*, 127, 223-234.

Phlips, E.J., & Badylak, S. (1996). Spatial variability in phytoplankton standing crop and composition in a shallow inner-shelf lagoon, Florida Bay, Florida. *Bulletin of Marine Science*, 58, 203-216.

Phlips, E.J., Badylak, S., & Lynch, T.C. (1999). Blooms of the picoplanktonic Cyanobacterium *Synechococcus* in Florida Bay, a subtropical inner-shelf lagoon. *Limnology and Oceanography*, 44, 1166-1175.

Raven, J. A. & Kubler, J. E. (2002). New light on the scaling of metabolic rate with the size of algae. *Journal of Phycology*, 38, 11-16.

Sherr, E.B., Caron, D.A., & Sherr, B.F. (1993). Staining of heterotrophic protests for visualization via epifluorescence microscopy. In Kemp, P.F., Sherr, B. F., Sherr, E. B.,& Cole, J.J. (Eds.) *Handbook of Methods in Aquatic Microbial Ecology* (pp. 213–227, pp. 187– 197). London: Lewis Publishers.

Sherr, E.B. & Sherr, B.F. (2002). Significance of predation by protists in aquatic microbial food webs. *Antonie van Leeuwenhoek*, 81, 293–308.

Stevely, J.M., & Sweat, D.E. (1998). Survey of recovery of Florida Keys sponge populations following a widespread sponge mortality. Contract Final Report for FDEP No. MR252.

Sunda, W. G., Graneli, E. & Gobler, C.J. (2006). Positive feedback and the development and persistence of ecosystem disruptive algal blooms. *Journal of Phycology*, 42, 963-974.

Tilmant, J.T. (1989). A history and overview of recent trends in the fisheries of Florida Bay. *Bulletin of Marine Science*, 44, 3-33.

Walters C., Gunderson, L., & Holling, C.S. (1992). Experimental policies for water management in the Everglades. *Ecological Applications,* 2, 189-202.