MICROBIAL FOOD WEB INTERACTIONS IN TWO LONG ISLAND EMBAYMENTS

by

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ABSTRACT: Phytoplankton mortality (herbivory) and bacterivory were examined experimentally in West Neck Bay and Coecles Harbor, Long Island, NY from April through September, 1998. Small algae (<5 μm diameter) dominated phytoplankton communities in both ecosystems throughout the summer, and zooplankton were also small (mostly <40 μm). Generally, plankton abundances were indicative of eutrophic ecosystems. Oscillations in standing stocks and mortality of prey indicated tight coupling of growth and grazing mortality in both bays. Phytoplankton mortality rates accounted for the removal of 14% to 65% of total phytoplankton standing stocks daily, while bacterivory accounted for the removal of 14% to 88% of total bacterial standing stocks daily. Estimates of carbon consumption revealed high energy flux through the nano- and microzooplankton assemblages of these estuarine environments.

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INTRODUCTION

The estuarine waters of Long Island, NY form a complex system of bays characterized by high standing stocks of microbial biomass and high rates of primary productivity (Ryther 1954, Bruno 1980, Lively et al. 1983, Cosper et al. 1989, Nuzzi & Waters 1989, Lonsdale et al. 1996). Seasonal maxima of chlorophyll concentration in excess of 60 $\mu g\ l^{-1}$ have been observed in these ecosystems, and rates of production have exceeded 400 mg C $m^{-2}\ h^{-1}$ (Cosper et al. 1989, Lonsdale et al. 1996). Maximal rates of primary productivity occur in these bays during summer, when high irradiance and high water temperatures favor algal growth.

West Neck Bay and Coecles Harbor form part of the Peconic Bays, a group of shallow, interconnected estuarine ecosystems in eastern Long Island. Phytoplankton communities in these bays traditionally have been dominated by picoplankton (0.2-2.0 μm) and nanoplankton (2-20 μm) species (Cosper et al. 1989, Kim 1993, Lonsdale et al. 1996). The Peconic Bays also have been affected sporadically since 1985 by harmful "brown tide" blooms of a picoplanktonic pelagophyte, *Aureococcus anophagefferens* (Cosper et al. 1987, Bricelj & Lonsdale 1997). Eutrophic West Neck Bay has repeatedly experienced high abundances of *A. anophagefferens,* typically in June or July. In contrast, the appearance of brown tides in Coecles Harbor has occurred only occasionally during the past 15 years when *A. anophagefferens* cells have reached bloom abundances throughout the entire Peconic Estuary System (SCDHS 1988-1989, Nuzzi & Waters 1989, Nuzzi 1995).

The dominance of the phytoplankton community by small algae in Long Island bays implies an important role for microbial consumers as conduits for energy and nutrient flow in these estuaries. The size range

of most algal prey in West Neck Bay and Coecles Harbor is below the optimal range for particle capture by mesozooplankton (Nival 1976, Bartram 1980). Studies in the Peconic Bays System during 1988-89 observed that grazers >64 μm in size did not contribute substantially to phytoplankton mortality during times when small algae comprised high percentages of the phytoplankton biomass (Kim 1993). Lonsdale et al. (1996) further showed that copepods depended on ciliate prey when picoplanktonic algae dominated the phytoplankton community in West Neck Bay. These observations support the supposition that protozoan assemblages play a major role in the removal of phytoplankton production in Long Island bays.

Bacteria also make up a significant component of total picoplankton biomass in most coastal plankton communities (Ducklow 1983, Cole et al. 1988, Ducklow & Carlson 1992). Long Island estuaries are no exception to this generality. High abundances of bacteria have been reported for a number of localities within the Peconic Bays System and other Long Island estuarine ecosystems (Caron et al. 1989). This finding implies a significant contribution of the microbial loop to energy flow in these environments. This aspect of the planktonic food web of Long Island estuaries, however, has not been studied previously.

I investigated the role of protozoan grazers in determining the fate of production in the Peconic Bays System. Bacterivory and herbivory experiments were conducted throughout the summer of 1998 in West Neck Bay and Coecles Harbor. Herbivory was determined using the dilution method. Bacterivory was estimated from the rate of disappearance of fluorescently labeled bacteria during 24 hour incubations. Our results indicate that major proportions of bacterial and primary production are

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channeled through the nano- and microzooplankton assemblages of these two estuaries.

MATERIALS AND METHODS

Field Sites and Sampling. West Neck Bay (WNB) and Coecles Harbor (CH) are part of the Peconic Bay Estuary located between the upper and lower forks of eastern Long Island, NY (Fig. 1). The Peconic Bay Estuary is a system of very shallow (average depth 4.7 m) interconnected bays with strong vertical mixing (Hardy 1976, Wilson 1995). WNB is situated on the southwest side of Shelter Island, NY, enclosed by an extension of land which restricts flow into and out of the bay. CH opens into the ocean side of the Peconic Bays on the eastern side of Shelter Island. CH has a less-enclosed mouth and therefore has more exchange with the surrounding estuarine system than WNB.

Water samples were collected throughout the summer of 1998 on 16 dates in WNB and 14 dates in CH (Tables 1, 2). Samples were hand-collected just below the water surface to 0.5 m using acid-washed, 30 l polyethylene carboys. An open carboy was inverted and lowered into the water with the spigot-end up and open to allow air to be pushed out of the carboy as it filled, minimizing bubbling and damage to delicate plankton. One carboy was filled to make diluent for both bacterivory and herbivory experiments. A second carboy was filled for preservation of microbial populations and for employment in the grazing experiments. Temperature and salinity measurements were made at each sampling.

Microbial Population Estimates. Samples for the enumeration of *A. anophagefferens,* nanoplankton and bacteria were preserved immediately with 1% gluteraldehyde (final concentration) and stored at

4°C in the dark. *A. anophagefferens* cells were probed and counted using the immunofluorescent technique of Anderson et al. (1989) using 0.8 μm blackened polycarbonate filters. Nanoplankton were stained with DAPI at 50 μg ml^{-1} final stain concentration, filtered onto 0.8 μm blackened polycarbonate filters, and counted using epiflourescence microscopy (Caron 1983, Sherr et al. 1993, Sherr & Sherr 1993a). Nanoplankton could not be processed consistently within 24 hours of collection and preservation because of the labor-intensive nature of the herbivory and bacterivory experiments. Therefore, heterotrophic and phototrophic nanoplankton were not distinguished in all samples, and counts are presented as total nanoplankton.

Samples for bacterial abundance were taken at the beginning of all grazing experiments in both WNB and CH, as well as on many of the intervening days throughout the course of the summer in order to obtain better resolution of the fluctuations in the abundance of this assemblage. Bacteria were stained with the nucleic acid dye Syto 13 (Molecular Probes®) and counted using a Becton Dickinson FacsCaliber flow cytometer (del Giorgio 1996). Bacterial carbon biomass was estimated from bacterial abundance using a conversion factor of 20 fg C $cell^{-1}$ (Lee & Fuhrman 1987).

Microplankton samples (20-200 μm) were preserved with Lugols preservative (10% final concentration) and stored in glass amber jars in the dark (Stoecker et al. 1994). Samples were settled in counting chambers and enumerated using inverted light microscopy. Microplankton were grouped into major taxa as follows: diatoms, *Prorocentrum* spp., other dinoflagellates, non-loricate ciliates, loricate ciliates, and other flagellates. Metazoa did not make up a significant fraction of microplankton abundances.

Chlorophyll analyses. Chlorophyll concentration was determined for all seawater samples and on seawater passing through 5 μm and 20 μm Nitex® screening. Subsamples were filtered onto Gelman GF/F glass fiber filters in triplicate. Chlorophyll was extracted in 100% acetone at -20°C overnight in the dark and measured using a Turner Designs fluorometer Model TD-700 (Strickland & Parsons 1972).

Chlorophyll concentrations were converted to phytoplankton carbon using a carbon to chlorophyll ratio of 60. This ratio was empirically determined on two dates in WNB during blooms of the dinoflagellate *Prorocentrum* spp. or the pelagophyte *A. anophagefferens*. The carbon:chlorophyll ratio (C:Chl) during the dinoflagellate bloom (May 11) was determined from the chlorophyll concentration and from phytoplankton biovolume converted to carbon using a conversion factor of 140 fg C μm^{-3} (Lessard 1991). The C:Chl ratio also was determined during the bloom of *A. anophagefferens* (June 30) using a conversion factor of approximately 2.1 fg C $cell^{-1}$ to estimate phytoplankton carbon biomass (Milligan & Cosper 1997). Carbon:chlorophyll ratios on both dates were 60. This ratio was applied to all samples taken during the study.

Phytoplankton mortality. Microbial herbivory was estimated using a refined dilution technique (Landry et al. 1995). All experimental containers, silicone transfer tubing, and filters were soaked in 10% HCl and rinsed in Milli Q water and/or filtered seawater prior to use. Filtrate was prepared by direct gravity flow of seawater through a 0.2 μm Gelman cartridge filter previously soaked in 10% HCl to remove dissolved organics. All work was performed with minimal bubbling. The dilution series consisted of 1200 ml clear polycarbonate bottles with 20, 40, 60, 80, and 100% unfiltered seawater, each in triplicate. A complete series of bottles were enriched with inorganic nutrients and trace metals (7.35 x

10^{-5} M $NaNO_3$; 3.02 x 10^{-6} M $NaH_2PO_4 \cdot H_2O$; 1ml of f/2 trace metals stock solution, Guillard 1975). An additional triplicate set of bottles with unfiltered seawater and without enrichment and a control diluent bottle were incubated along with the enriched dilution series. Chlorophyll concentrations in the diluent control bottles were near the limit of analytical detection and never showed measurable increases during any of the experiments. Incubations for both WNB experiments and CH experiments were conducted for 24 hours in CH. Bottles were strung on a line at a depth of approximately 30 cm below the water surface.

Replicate subsamples for chlorophyll analysis were taken at the end of the incubation from all experimental bottles. Subsamples were processed as described above (see **Chlorophyll analyses**). Apparent net growth rates were calculated from changes in chlorophyll *a* concentration over the length of the experiment as: $r = 1/t * \ln (Pt/Po)$ where t = time, Po = initial phytoplankton concentration, and Pt = final phytoplankton concentration. Mortality rates of phytoplankton were calculated by linear regression analysis of apparent net growth rates versus the relative grazing pressure (mortality estimate, m = regression slope).

Microbial bacterivory. Bacterial grazing rates were obtained by measuring the disappearance of fluorescently labeled bacteria (FLB) in unfiltered seawater samples during 24 hour incubations (Marrasé et al. 1992, Salat & Marrasé 1994). FLB were prepared from heat-killed and stained *Halomonas halodurans* (Sherr et al. 1987, Sherr & Sherr 1993b). Seawater subsamples from the 30 l carboys were dispensed into three 1200 ml polycarbonate bottles and FLB were added at concentrations that were 10 to 30% of the abundance of natural bacteria (5 x 10^5 - 2 x 10^6 FLB ml^{-1}). For each experiment, FLB were also added to three control bottles (0.2 µm filtered seawater) to monitor non-grazing related losses

of FLB. Bottles were incubated in CH as described above for dilution experiments. Samples were removed from each bottle at the beginning and end of the experiment, frozen and stored in liquid nitrogen until anlyzed. Abundances of FLB were determined on a Becton Dickinson FacScan flow cytometer.

Grazing rates on bacteria were estimated from the rates of loss of FLB assuming an exponential decrease during the incubation period. Grazing was calculated as: $g = -1/t * \ln (Ft/Fo)$ where t = time, Fo = initial concentration of FLB, Ft = final concentration of FLB. Two-sample t-tests were performed to test significant differences between loss of FLB in whole seawater treatments and loss of FLB in control treatments. Changes in the abundance of FLB in control treatments were never significantly different than zero ($p<0.01$).

RESULTS

Physical parameters

The restricted flow into and out of WNB relative to CH was reflected in higher temperatures and lower salinities in WNB (Figs. 2A, 2B). Temperature in both bays increased throughout May and June, peaked in July and August, and decreased in September. Overall average temperatures were 23.3°C ± 3.5 in WNB (range = 13.5°C - 27.3°C) and 22.4°C ± 3.5 in CH (range = 13.5°C - 26°C). Salinity increased slightly from June to July in both bays. Mean salinities were 1.9 ppt higher in CH than WNB, averaging 27.5 ppt ± 0.87 in CH and 25.6 ppt ± 0.95 in WNB.

Phytoplankton and protozoa

WNB had consistently higher microbial biomass than CH during this study. Chlorophyll values throughout the summer in WNB averaged 19.4 μg chl *a* l^{-1} (range = 4.9-30.5 μg chl *a* l^{-1}; Table 1). Chlorophyll concentrations were significantly lower in CH than WNB, averaging 5.6 μg chl *a* l^{-1} (range = 1.7-9.2 μg chl *a* l^{-1}; Table 2).

Size-fractionated chlorophyll analyses indicated that the phytoplankton communities of both bays were composed primarily of pico- and nanoplanktonic algae (Fig. 3). Most of the chlorophyll biomass in WNB occurred in the 5-20 μm size class on April 26 and May 11 (Fig. 3A). This bay was dominated by phytoplankton cells <5 μm in size during the remainder of the study period (70 to 100% of total phytoplankton biomass). The size structure of the phytoplankton community of CH was more heterogeneous. Phytoplankton <5, 5-20, and >20 μm each constituted more than 50% of the total phytoplankton biomass on several sampling dates (Fig. 3B).

Pico- and small nanoplanktonic phytoplankton (i.e. <5 μm) were composed of a variety of taxa including cyanobacteria, *A. anophagefferens* and a variety of other small eukaryotes. *A. anophagefferens* contributed significantly to this biomass in WNB from late May to late July (Fig. 2C). The highest cell abundances of the brown tide alga observed were near-bloom concentrations of 880,000 cells ml^{-1} on June 30. CH did not experience a brown tide bloom and *A. anophagefferens* cells were near the limit of detection throughout the study period (less than a few hundred cells ml^{-1}).

Differences in phytoplankton biomass between the two bays were reflected in differences in total nanoplankton and microplankton. Total (phototrophic and heterotrophic) nanoplankton cell concentrations were

generally six times as high in WNB than CH, averaging 2.76 X 10^5 cells ml^{-1} in WNB (excluding *A. anophagefferens*) and 4.42 X 10^4 cells ml^{-1} in CH (Fig. 4). Cell concentrations of microplankton were 2.7x higher in WNB (WNB avg = 4.44 x 10^4 cells l^{-1}, CH avg = 1.61 x 10^4 cells l^{-1}; Fig. 5). Microplankton in both bays were dominated by cells <40 μm in size.

A chlorophyll peak on May 11 in WNB corresponded with a brief *Prorocentrum* spp. bloom (1.64 x 10^6 cells l^{-1}). *Prorocentrum* spp. cell diameters were approximately 20 μm, and these cells were included with the microplankton in microscopical counts (Fig. 5A). However, the cells apparently passed through the 20 μm Nitex® screen and appeared largely in the 5-20 μm chlorophyll size class on May 11 (Fig. 3A).

Dinoflagellates other than *Prorocentrum* composed a large portion of the remainder of the microplankton community. In WNB, these dinoflagellates averaged 9.11 x 10^4 cells l^{-1}, with peaks in May and August. Dinoflagellates averaged 4.99 x 10^4 cells l^{-1} in CH during peak microplankton concentrations in July and August.

Ciliate assemblages were dominated by aloricate ciliates in both bays on most sampling dates (Fig. 5B,D). Aloricate ciliates averaged 4.17 x 10^4 cells l^{-1} in WNB and 2.75 x 10^4 cells l^{-1} in CH throughout the study. Loricate ciliates outnumbered aloricate ciliates only on two dates both of which coincided with high relative abundances of *Prorocentrum* spp. in WNB (June 2; Fig. 5B) and CH (July 6; Fig. 5D).

Phytoplankton mortality

Sixteen dilution experiments were performed in WNB from April 26 through September 23. Thirteen of these experiments yielded regressions that were significantly different than zero (Table 1). Fourteen

experiments were run in CH from May 12 through September 23 and thirteen of these experiments yielded significant regressions (Table 2). Averaged over all dates, phytoplankton mortality rates calculated from dilution experiments were surprisingly similar in WNB and CH. Average rates of mortality were 0.51 ±0.25 d^{-1} (±1 standard deviation) in WNB for the significant regressions (range = 0.15-1.05 d^{-1}) and 0.48 ±0.25 d^{-1} in CH (range = 0.19-1.04 d^{-1}). Seasonal trends in mortality rate were not apparent, although highest rates were observed during late June and early July in WNB and during August in CH. Peaks in phytoplankton mortality rates were often offset from peaks in standing stocks of phytoplankton in both bays, implying predator-prey oscillations (Figs. 6, 7).

The percentage of phytoplankton standing stocks removed d^{-1} were similar in both bays, averaging 38% in WNB (range = 14-65%) and 36% in CH (17-65%). Absolute rates of biomass removal, however, were quite different for the two bays because of differences in the standing stocks of phytoplankton. The absolute amount of phytoplankton biomass consumed averaged 400 μg C l^{-1} d^{-1} (7.85 μg chl *a* l^{-1} d^{-1}) in WNB and 138 μg C l^{-1} d^{-1} (2.43 μg chl *a* l^{-1} d^{-1}) in CH (Tables 1, 2). Maximal rates of phytoplankton biomass removal in WNB exceeded 1 mg C l^{-1} d^{-1} on two occasions.

Bacteria and bacterivory

Bacteria in WNB and CH were enumerated at the beginning of each experiment and on numerous other dates throughout the summer (Tables 3, 4; Figs. 8, 9). Bacterial abundances were more than twice as high in WNB, averaging 1.31 x 10^7 cells ml^{-1} in WNB and 5.6 x 10^6 cell ml^{-1} in CH.

Fluctuations in abundance were similar for both ecosystems (approximately a factor of five).

Bacterial grazing experiments were performed throughout the summer on the same days as phytoplankton mortality experiments. Rates of bacterivory averaged 0.57 ± 0.07 d^{-1} in WNB and 0.93 ± 0.31 d^{-1} in CH (Tables 3, 4). Rates of bacterivory in CH were significantly higher than in WNB ($p<0.01$, t-test). Bacterial standing stocks were removed at average rates of 41% d^{-1} in WNB and 55% d^{-1} in CH. However, the absolute amount of bacterial biomass consumed was greater in WNB than in CH because of higher abundances of bacteria in WNB. Removal of bacterial biomass averaged 99 μg C $l^{-1}d^{-1}$ (4.96 x 10^6 cells ml^{-1} d^{-1}) in WNB and 68 μg C $l^{-1}d^{-1}$ (3.39 x 10^6 cells ml^{-1} d^{-1}) in CH (Tables 3, 4). High rates of removal of bacterial biomass in WNB occurred throughout most of the mid-summer period, while peaks in the removal of bacterial biomass in CH corresponded to exceptionally high grazing rates on June 30 and August 17 (Figure 8, 9).

Discussion

Community Structure

Plankton abundances and biomasses in both WNB and CH were indicative of nutrient-rich, estuarine environments (Tables 1-4). However, hydrographic conditions were different at the two study sites, and these differences were reflected in higher values in WNB than in CH. Bacterial biomass and phytoplankton biomass estimates in WNB were comparable to those of other eutrophic estuaries on the east coast of the U.S. (Gallegos 1989, McManus & Ederington-Cantrell 1992).

The chlorophyll concentrations observed in the present study were typical of seasonal ranges of chlorophyll observed previously in the Peconic Bays System. Maximal chlorophyll concentrations of approximately 34 μg chl*a* l^{-1} in WNB during the present study (Table 1) were similar to published reports for this estuary (Cosper et al. 1989, Lonsdale et al. 1996). A site near the middle of the Peconic Bays System had a range of chlorophyll of 1-6.6 μg chl*a* l^{-1} (Bruno 1980), similar to the range observed in CH in the present study (Table 2).

Phytoplankton assemblages were composed of small algae throughout most of the summer in both WNB and CH. WNB was dominated by picoplanktonic eukaryotes, typically small chlorophytes or chrysophytes and *A. anophagefferens.* CH was characterized by a range of phytoplankton including small chlorophytes, chrysophytes, diatoms, and dinoflagellates. These results agree with previous studies that have investigated phytoplankton in the Peconic Bays. Studies in WNB have demonstrated the dominance of the phytoplankton community by algae <5 μm in size (Caron et al. 1989, Cosper et al. 1989, Nuzzi & Waters 1989, Lonsdale et al. 1996).

Densities of bacteria in both bays also indicated eutrophic conditions. Bacterial abundances in WNB were near the upper limit of published reports for natural marine ecosystems, ranging from 3.4 X 10^6 to 2.5 x 10^7 cells ml^{-1} (Sanders et al. 1992, Simon et al. 1992). These values are comparable to the range previously reported for this embayment (Caron et al. 1989). Abundances were lower but still substantial in CH, ranging from 3.2 x 10^6 to 1 x 10^7 cells ml^{-1}. Daily samplings of bacteria confirmed that abundances recorded on experimental days reflected the general trends observed throughout the

summer (Figs. 8, 9). However, occasional rapid changes in bacterial abundances illustrated that bacteria responded rapidly to environmental stimuli or removal processes.

Phagotrophic protists are believed to be a major source of mortality for bacteria and small algae (Fenchel 1982, Campbell & Carpenter 1986, McManus & Fuhrman 1988, Sherr & Sherr 1994). Protozoan assemblages in this study were largely composed of nanoflagellates, and heterotrophic dinoflagellates and aloricate ciliates <40 μm in diameter. Larger protozoa (>40μm) and metazoa made up an insignificant component of the microzooplankton assemblages of both bays. These results imply that small phagotrophic protists were responsible for the major grazing pressure observed in this study.

Results from a 1988 study in WNB support the idea that small protozoa are major consumers of bacteria and algae in Long Island bays (Caron et al. 1989). That study demonstrated consumption of both fluorescently labeled algae (FLA) and FLB by nanoflagellates, dinoflagellates, ebridians, aloricate choreotrich cilates, tintinnid ciliates and scuticociliates. While community grazing was not evaluated, estimates of ingestion rates indicated that individual protozoan taxa could negatively impact the prey populations.

Herbivory

Microzooplankton removed 14% to 65% of the daily standing stocks in experiments that yielded significant results (Tables 1, 2). Generally, the highest grazing rates occurred following peaks in algal biomass. This relationship implies grazer response to changes in phytoplankton abundance. Three-point regressions of the dilution curves in our study did

not indicate saturation of grazing in any of the experiments (Gallegos 1989).

Phytoplankton growth rates determined from dilution experiments yielded consistently negative net growth rates in this study. This result likely reflects a reduction in pigment content per cell due to photoadaptation (McManus 1995), and consequently growth rates are not presented. However, photoadaptation of the phytoplankton community should have affected pigment concentration similarly in all dilution bottles. Thus phytoplankton mortality rates should be unaffected.

Our phytoplankton mortality results are indicative of phytoplankton community grazing impacts similar to those reported in other productive coastal areas. Table 5 presents a summary of published reports of phytoplankton mortality based on the dilution technique and standing stocks of primary producers (i.e. chlorophyll) in a variety of coastal ecosystems. Removal of phytoplankton biomass ($\mu g\ C\ l^{-1}\ d^{-1}$) was calculated for those studies using the same C:Chl ratio (60) applied in the present study. Based on these calculations, reported rates of phytoplankton mortality in other coastal environments span a range of values that encompass the rates I observed. Highest rates were observed in the Estuary of Mundaka (Spain), Rhodes River (Chesapeake Bay, Maryland) and Atchafalaya River estuary (Louisiana) (3616, 10240 and 3270 ($\mu g\ C\ l^{-1}\ d^{-1}$, respectively). These latter values are well in excess of the removal rates observed in the present study. I observed maximal rates of phytoplankton removal of approximately 1260 and 290 $\mu g\ C\ l^{-1}\ d^{-1}$ in WNB and CH, respectively. Monthly averages of these removal rates were lower (49-815 $\mu g\ C\ l^{-1}\ d^{-1}$ in WNB and

47-217 μg C l^{-1} d^{-1} in CH; Table 5). Nevertheless, turnover rates for the phytoplankton assemblages (% standing stock of phytoplankton consumed per day) were similar in our study relative to those published reports (Table 5).

These studies indicate that nano- and microzooplankton control the fate of much of the primary production in eutrophic estuarine ecosystems. This result is a consequence of the dominance of these phytoplankton communities by pico- and/or nanophytoplankton during much of the growing season. High estimates of microbial grazing in these ecosystems implies that protozoan grazers constitute an important trophic link for carbon transfer in the pelagic food webs of these environments.

During the course of this study, the appearance of *A. anophagefferens* in WNB presented the opportunity to investigate the impact of this alga on phytoplankton mortality rates. *A. anophagefferens* has been reported to produce a dopamine-like compound that inhibits neurotransmission which reduces ciliary feeding action in bivalves (Gainey & Shumay 1991). Previous studies have suggested that *A. anophagefferens* may have similar effects on microzooplankton, inhibiting protozoan growth and grazing (Lonsdale et al. 1996, Mehran 1996). However, multiple regression analyses between *A. anophagefferens* and grazing mortality in our study did not reveal any obvious impact on protozoan grazing activity. Moreover, the phytoplankton mortality rate during peak *A. anophagefferens* population abundances on June 30 in WNB was 0.57 d^{-1}.

Bacterivory

Bacterial mortality due to protozoan grazing was measured by monitoring the rate of disappearance of FLB. Advantages of this method include the acquisition of absolute estimates of bacterial grazing,

minimal manipulation of samples, and fairly easy evaluation of samples using flow cytometry. One caveat of the method is the possibility of feeding selectivity by grazers, resulting in over- or underestimation of protozoan grazing activity. Heat-killing and labeling cells may affect acceptability of prey to some protozoa based on chemical cues (Landry et al. 1991). Yet, evidence indicates that many protozoa select and digest fluorescently labeled prey similarly to natural prey (Sherr et al. 1988, Dolan & Simek 1997). Overestimation of grazing may occur if bacterivores prefer larger cells (González et al. 1990), and thus I prepared FLB from late stationary phase cultures to generate cells that more closely resemble the size of natural bacteria.

Bacterivore populations exerted strong grazing pressure on bacterioplankton in both WNB and CH. Grazing rates were higher in CH (overall average = 0.93 d^{-1}) than in WNB (overall average = 0.57 d^{-1}), implying that turnover rates of the bacteria were more rapid in the less eutrophic environment. Bacterial abundances showed short-term (one to a few days) fluctuations, but were relatively stable over the course of the summer in both bays. This observation indicates that growth and grazing were in approximate balance throughout the course of the summer. A 1:1 correspondence between bacterial production and grazing in most pelagic ecosystems has been noted (Sanders et al. 1992). This situation in these two Long Island bays implies that growth rates of the bacterial assemblages must have been considerable in order to compensate for losses due to protistan mortality.

The rapid rates of bacterial removal observed in WNB and CH in this study, combined with the large standing stocks of bacteria in these ecosystems, resulted in considerable amounts of carbon flow through this aspect of the microbial community (Tables 3, 4). Overall averages for

daily carbon flux through bacterivores in the present study were 99 and 68 $\mu g\ C\ l^{-1}\ d^{-1}$ in WNB and CH, respectively. Removal rates of bacterial standing stocks in WNB and CH were similar to or greater than most rates published for other marine ecosystems (Coffin & Sharp 1987, Weisse 1989, Wikner et al. 1990, Wikner & Hagström 1991, Marrasé et al. 1992, Reckermann & Veldhuis 1997, Murrell & Hollibaugh 1998, Caron et al. 1999, Weisse 1999). Standing stocks of bacteria were twice as high in WNB compared to CH. Nevertheless, differences between estimates of carbon flow via bacterivory in the two bays differed only by a factor of ≈1.4 due to higher average mortality rates in CH (i.e. more rapid turnover of the bacterial assemblage).

Carbon flow

Ratios of bacterial biomass to phytoplankton biomass indicated that bacteria were an important reservoir of living carbon in these ecosystems. Average bacterial carbon was 31% of phytoplankton carbon in WNB and 45% of phytoplankton carbon in CH (Figure 10A, B). These ratios ranged from 8% to 101% in WNB and 19% to 128% in CH. The ratio of bacterial carbon to phytoplankton carbon increased slightly during the latter half of the summer in both bays.

Calculations of carbon consumption (herbivory and bacterivory) revealed that bacterivory constituted an important aspect of carbon flux through the microbial community in both bays. Carbon flux in WNB ranged from 5 to 1263 $\mu g\ C\ l^{-1}\ d^{-1}$ due to grazing on phytoplankton (overall average = 400), while carbon flux due to bacterivory ranged from 24 to 281 $\mu g\ C\ l^{-1}\ d^{-1}$ (overall average = 99). Average carbon flux due to bacterivory in this bay was approximately 25% of the carbon flux due to herbivory. The percentage of energy flux due to bacterial grazing

increased in August and September as phytoplankton biomass dropped (Figure 10C). Carbon flux in CH ranged from 36 to 291 μg C l^{-1} d^{-1} (overall average = 138) due to herbivory and from 17 to 162 μg C l^{-1} d^{-1} (overall average = 68) due to bacterivory. Average energy flux due to bacterivory was approximately one half of the flux due to herbivory, indicating that bacterivory was more important to energy flow in this bay (Figure 10D).

In summary, carbon flux due to herbivory and bacterivory was high in both the WNB and CH ecosystems in the present study. Our experimental results demonstrated that substantial percentages of primary and secondary (bacterial) production were consumed by phagotrophic protists in these bays. These protistan grazers presumably form an important trophic link between these prey assemblages and the metazoan zooplankton. Reports of significant grazing on ciliates by larger zooplankton in Long Island bays support the hypothesis that a major fraction of phytoplankton and bacterial production is transferred to higher trophic levels via nano- and microzooplanktonic consumers (Lonsdale et al. 1996).

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Table 1. West Neck Bay - Initial standing stocks of phytoplankton expressed as chlorophyll concentration and carbon biomass, phytoplankton mortality rates based on linear regression analyses, r^2 and significance of linear regression analysis (NS = non-significant), and daily removal of phytoplankton expressed as *µg chl. *a* $l^{-1}d^{-1}$, **µg C $l^{-1}d^{-1}$ and ***percentage standing stock d^{-1}.

Date	Initial Chlorophyll Concentration (µg chl *a* l^{-1})	Initial Phytoplankton Biomass (µg C l^{-1})	Phytoplankton Mortality Rate (d^{-1})	r^2	Significance (p-value)	µg chl *a* l^{-1} Consumed Daily*	µg C l^{-1} Consumed Daily**	% Standing Stock Consumed Daily***
26-Apr	4.8	290	0.66	0.60	<0.01	2.8	166	48
11-May	13.8	827	0.22	0.14	>0.05 NS	3.0	179	20
19-May	12.7	760	0.15	0.06	>0.05 NS	1.4	86	14
26-May	16.6	998	0.15	0.51	<0.01	2.1	125	14
2-Jun	30.3	1820	0.44	0.80	<0.01	12.1	723	36
6-Jun	34.4	2064	0.20	0.52	<0.01	6.3	378	18
18-Jun	22.1	1327	0.87	0.83	<0.01	18.1	1083	58
23-Jun	28.9	1735	0.42	0.64	<0.01	8.1	487	34
30-Jun	30.5	1829	0.57	0.84	<0.01	13.9	836	43
6-Jul	17.1	1025	1.05	0.84	<0.01	21.1	1263	65
20-Jul	22.0	1319	0.40	0.59	<0.01	6.1	367	33
3-Aug	6.5	391	0.38	0.57	<0.01	1.6	97	32
17-Aug	8.6	514	0.02	0.00	>0.05 NS	0.1	5	2
26-Aug	9.5	572	0.52	0.64	<0.01	3.5	208	41
9-Sep	8.3	499	0.63	0.73	<0.01	4.0	240	47
23-Sep	5.7	344	0.38	0.73	<0.01	2.5	151	32

Table 2. Coecles Harbor - Initial standing stocks of phytoplankton expressed as chlorophyll concentration and carbon biomass, phytoplankton mortality rates based on linear regression analyses, r^2 and significance of linear regression analysis (NS = non-significant), and daily removal of phytoplankton expressed as *µg chl. *a* $l^{-1}d^{-1}$, **µg C $l^{-1}d^{-1}$ and ***percentage standing stock d^{-1}.

Date	Initial Chlorophyll Concentration (µg chl *a* l^{-1})	Initial Phytoplankton Biomass (µg C l^{-1})	Phytoplankton Mortality Rate (d^{-1})	r^2	Significance (p-value)	µg chl. *a* l^{-1} Consumed Daily*	µg C l^{-1} Consumed Daily**	% Standing Stock Consumed Daily***
12-May	5.6	336	0.16	0.05	>0.05 NS	0.6	36	15
24-May	5.6	336	0.60	0.41	<0.01	4.8	290	45
4-Jun	2.5	147	0.53	0.43	<0.01	2.0	118	41
7-Jun	4.0	238	0.24	0.48	<0.01	0.9	56	21
18-Jun	5.7	344	0.32	0.76	<0.01	2.1	127	27
23-Jun	7.7	460	0.37	0.79	<0.01	2.7	164	31
30-Jun	9.1	544	0.40	0.76	<0.01	1.9	116	33
6-Jul	4.8	290	0.72	0.96	<0.01	4.9	291	51
20-Jul	9.2	550	0.44	0.67	<0.01	1.8	107	36
3-Aug	4.2	249	1.04	0.93	<0.01	4.1	247	65
17-Aug	5.8	350	0.78	0.82	<0.01	3.1	186	54
26-Aug	5.7	344	0.40	0.85	<0.01	1.7	101	33
9-Sep	2.9	176	0.19	0.31	<0.05	0.7	44	17
23-Sep	1.7	100	0.20	0.28	<0.05	0.8	50	18

Table 3. West Neck Bay - Initial standing stocks of bacteria expressed as cell concentration and carbon biomass, bacterial grazing rates based on removal of fluorescently labeled prey over 24 hours, and daily removal of bacteria expressed as *cells $ml^{-1}d^{-1}$, **$\mu g\ C\ l^{-1}d^{-1}$ and ***percentage standing stock d^{-1}.

Date	Initial Bacterial cell concentration (cells ml^{-1})	Initial Bacterial Biomass ($\mu g\ C\ l^{-1}$)	Grazing Rate (d^{-1})	Bacterial cells ml^{-1} Consumed Daily*	$\mu g\ C\ l^{-1}$ Consumed Daily**	% Standing Stock Consumed Daily***
26-Apr	4.38E+06	88	0.32	1.20E+06	24	27
11-May	3.41E+06	68	0.73	1.77E+06	35	52
19-May	5.16E+06	103	0.47	1.95E+06	39	38
26-May	8.34E+06	167	0.54	3.49E+06	70	42
2-Jun	1.33E+07	266	0.16	1.93E+06	39	14
6-Jun	1.28E+07	256	0.21	2.41E+06	48	19
18-Jun	1.28E+07	256	0.67	6.23E+06	125	49
23-Jun	1.54E+07	308	0.75	8.15E+06	163	53
30-Jun	1.70E+07	340	0.57	7.43E+06	149	44
6-Jul	1.56E+07	312	0.40	5.18E+06	104	33
20-Jul	1.04E+07	208	0.68	5.12E+06	102	49
3-Aug	1.98E+07	396	1.24	1.40E+07	281	71
17-Aug	1.16E+07	232	0.49	4.50E+06	90	39
26-Aug	1.31E+07	262	0.42	4.53E+06	91	35
9-Sep	1.42E+07	284	0.87	8.27E+06	165	58
23-Sep	7.81E+06	156	0.53	3.20E+06	64	41

Table 4. Coecles Harbor - Initial standing stocks of bacteria expressed as cell concentration and carbon biomass, bacterial grazing rates based on removal of fluorescently labeled prey over 24 hours, and daily removal of bacteria expressed as *cells $ml^{-1}d^{-1}$, **$\mu g\ C\ l^{-1}d^{-1}$ and ***percentage standing stock d^{-1}.

Date	Initial Bacterial cell concentration (cells ml^{-1})	Initial Bacterial Biomass ($\mu g\ C\ l^{-1}$)	Grazing Rate (d^{-1})	Bacterial cells ml^{-1} Consumed Daily*	$\mu g\ C\ l^{-1}$ Consumed Daily**	% Standing Stock Consumed Daily***
12-May	3.17E+06	63	0.32	8.60E+05	17	27
24-May	3.97E+06	79	0.35	1.18E+06	24	30
4-Jun	4.27E+06	85	0.75	2.26E+06	45	53
7-Jun	5.04E+06	101	0.75	2.65E+06	53	53
18-Jun	3.21E+06	64	1.48	2.48E+06	50	77
23-Jun	3.71E+06	74	1.32	2.72E+06	54	73
30-Jun	7.19E+06	144	2.12	6.33E+06	127	88
6-Jul	9.11E+06	182	0.43	3.17E+06	63	35
20-Jul	7.59E+06	152	1.14	5.17E+06	103	68
3-Aug	5.09E+06	102	0.86	2.93E+06	59	58
17-Aug	9.81E+06	196	1.76	8.12E+06	162	83
26-Aug	1.02E+07	203	0.84	5.79E+06	116	57
9-Sep	4.50E+06	90	0.41	1.53E+06	31	34
23-Sep	6.39E+06	128	0.44	2.28E+06	46	36

Table 5. Summary of dilution experiment results from various coastal bays. Initial chlorophyll concentrations and phytoplankton mortality rates for individual experiments are copied directly from reports, except as noted in table. Biomass consumed daily was calculated for each experiment as: $(e^{Uo}-e^{k})*Po$, where Uo=gross algal growth coefficient, k=net algal growth coefficient, Po=Initial phytoplankton standing stock. Biomass consumed daily is reported as chlorophyll removed (μg chl *a* $l^{-1}d^{-1}$) and carbon removed (μg C $l^{-1}d^{-1}$, determined using a carbon to chlorophyll ratio of 60). Percentage standing stock removed daily was calculated as: $((e^{Uo}-e^{k})/e^{Uo})*100$.

Reference (Notes)	Study Site	Date	Initial Chlorophyll Concentration (μg chl *a* l^{-1})	Phytoplankton Mortality Rate (d^{-1})	Biomass Consumed Daily (μg chl *a* $l^{-1}d^{-1}$)	Biomass Consumed Daily (μg C $l^{-1}d^{-1}$) (C:chl = 60)	% Standing Stock Consumed Daily
Present study (Monthly averages)	Coecles Harbor (Long Island, NY)	May-98	5.60	0.38	2.70	163	30
		Jun-98	5.80	0.37	1.92	116	31
		Jul-98	7.00	0.58	3.35	199	44
		Aug-98	5.00	0.91	3.60	217	60
		Sep-98	2.30	0.20	0.75	47	18
Present study (Monthly averages)	West Neck Bay (Long Island, NY)	Apr-98	4.80	0.66	2.80	166	48
		May-98	14.37	0.17	2.17	130	16
		Jun-98	29.24	0.50	11.70	701	38
		Jul-98	19.55	0.73	13.60	815	49
		Aug-98	8.20	0.31	1.73	103	25
		Sep-98	7.00	0.51	3.25	196	40
Burkhill et al. 1987	Carmarthen Bay Celtic Sea	Oct-84	4.69	0.36	2.01	121	30
		Jul-83	2.18	0.38	0.81	49	32
		Jul-83	0.72	0.55	0.42	25	42
		Oct-84	0.74	1.04	0.68	41	65
Landry and Hassett 1982	Washington coast	Oct-80	3.54	0.28	1.61	97	24
		Oct-80	2.03	0.07	0.20	12	6
		Oct-80	6.77	0.12	1.41	84	12
Gifford 1988	Halifax Harbour (Nova Scotia)	30-Aug-84	1.90	0.24	0.83	50	21
		13-Nov-84	2.20	0.02	0.07	4	2
		11-Mar-85	0.30	0.72	0.32	19	51
		15-Apr-85	1.80	0.24	0.62	37	21
		5-Jun-85	1.80	0.48	3.68	221	38
Murrell and Hollibaugh 1998	Tomales Bay (San Fransisco Bay, CA)	Jul-94	7.30	0.24	1.61	96	21
		Jul-94	5.30	1.14	5.54	333	68

Table 5, continued.

Reference (Notes)	Study Site	Date	Initial Chlorophyll Concentration (µg chl *a* l^{-1})	Phytoplankton Mortality Rate (day^{-1})	Biomass Consumed Daily (µg chl *a* $l^{-1}d^{-1}$)	Biomass Consumed Daily (µg C $l^{-1}d^{-1}$) (C:chl = 60)	% Standing Stock Consumed Daily
McManus and Ederington-Cantrell 1992 (Summer months)	Chesapeake Bay (Upper Bay)	16-May-90	2.18	0.76	9.96	598	53
		14-Aug-90	6.76	1.60	37.92	2275	80
	Chesapeake Bay (Mid-Bay)	17-May-90	19.47	0.43	10.25	615	35
		15-Aug-90	7.23	0.20	1.77	106	18
		16-Aug-90	11.31	0.25	2.94	176	22
Ruiz, Franco, Villate 1998 (Mean values for 3 salinity ranges)	Mundaka, Spain (<25 ppt)	Aug-90	62.00	0.54	128.13	7688	42
	(25-31 ppt)	Aug-90	6.37	0.80	21.43	1286	55
	(>31 ppt)	Aug-90	4.83	0.94	31.06	1864	61
Gallegos 1989	Rhode River, Maryland (Chesapeake Bay)	6-Jul-88	34.80	2.01	300.59	18036	87
		9-Aug-88	81.80	1.52	275.19	16511	78
		30-Aug-88	138.40	0.42	76.71	4602	34
		4-Oct-88	32.50	0.66	30.38	1823	48
Dagg 1995	Atchafalaya River Estuary	Jan-90	16.45	0.54	10.87	652	42
		Apr-90	14.31	0.32	6.44	386	28
		Sep-90	24.49	2.11	180.81	10849	87
		Sep-90	21.44	0.84	29.32	1759	51
		Aug-91	27.11	1.38	73.45	4407	81
		Aug-91	17.31	1.08	26.15	1569	71

FIGURE LEGENDS

Figure 1. Study site: Peconic Bays System, Long Island, NY. Experiments were carried out in West Neck Bay and Coecles Harbor.

Figure 2. (A) Water temperature, (B) Salinity, and (C) *Aureococcus anophagefferens* cell concentrations in West Neck Bay and Coecles Harbor.

Figure 3. Size fractionation of chlorophyll represented as % total chlorophyll for (A) West Neck Bay and (B) Coecles Harbor.

Figure 4. Total nanoplankton cell abundance for (A) West Neck Bay and (B) Coecles Harbor.

Figure 5. Microplankton abundances grouped as (A) *Prorocentrum* spp. and diatoms in WNB, (B) Other dinoflagellates and flagellates, and ciliates in WNB, (C) *Prorocentrum* spp. and diatoms in CH, (B) Other dinoflagellates and flagellates, and ciliates in CH.

Figure 6. Chlorophyll *a* concentration and phytoplankton mortality in West Neck Bay.

Figure 7. Chlorophyll *a* concentration and phytoplankton mortality in Coecles Harbor.

Figure 8. Bacterial abundances at time zero of grazing experiments and on multiple sampling dates throughout the summer, and bacterivory in West Neck Bay.

Figure 9. Bacterial abundances at time zero of grazing experiments and on multiple sampling dates throughout the summer, and bacterivory in Coecles Harbor.

Figure 10. Phytoplankton and bacterial carbon on the dates when herbivory and bacterivory experiments were conducted (A) in WNB and (B) in CH. Daily removal of phytoplankton and bacterial carbon on the dates when herbivory and bacterivory experiments were conducted (C) in WNB and (D) in CH.

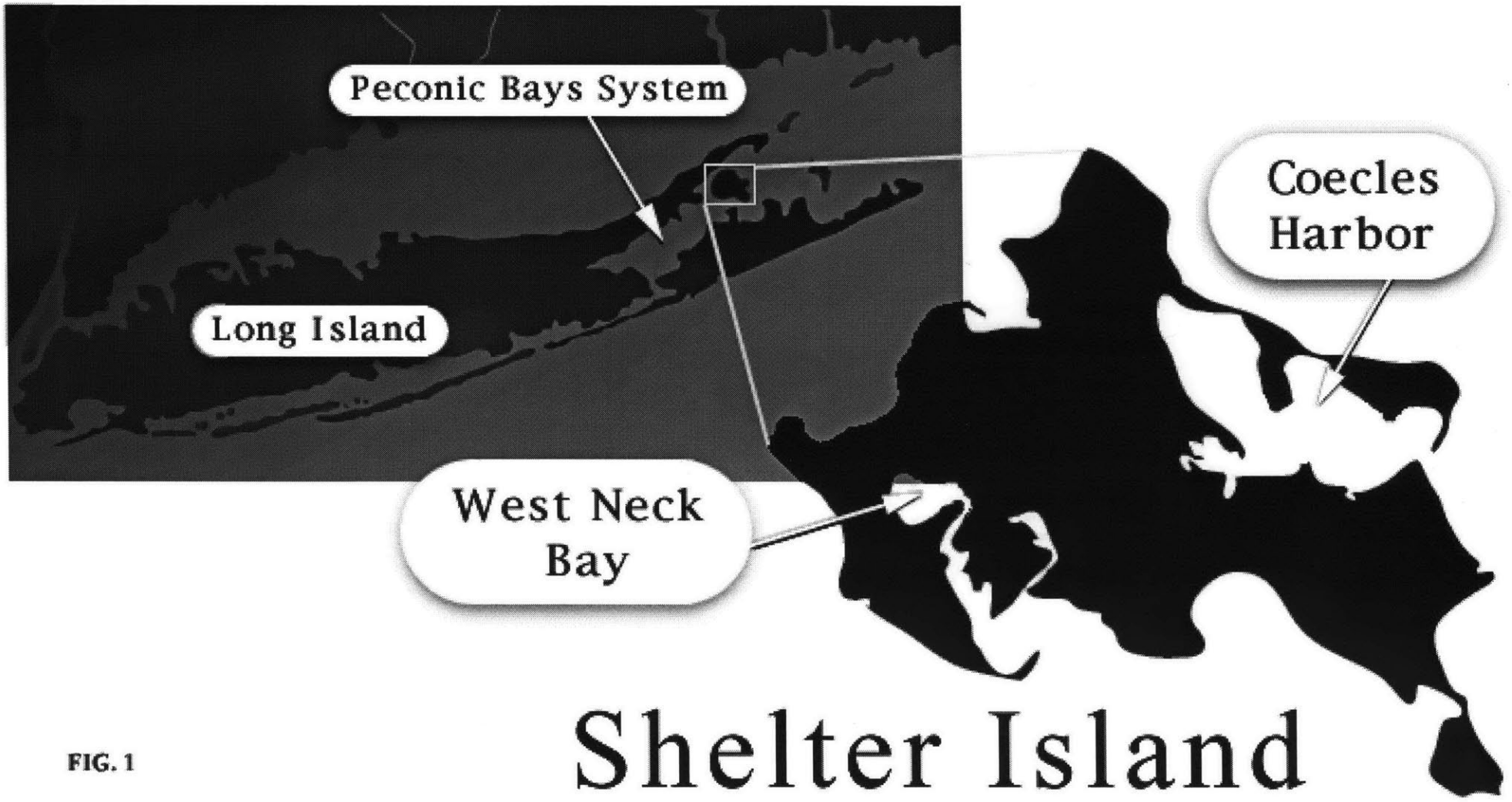

Peconic Bays System
Long Island
Coecles Harbor
West Neck Bay
Shelter Island

FIG. 1

FIG. 2

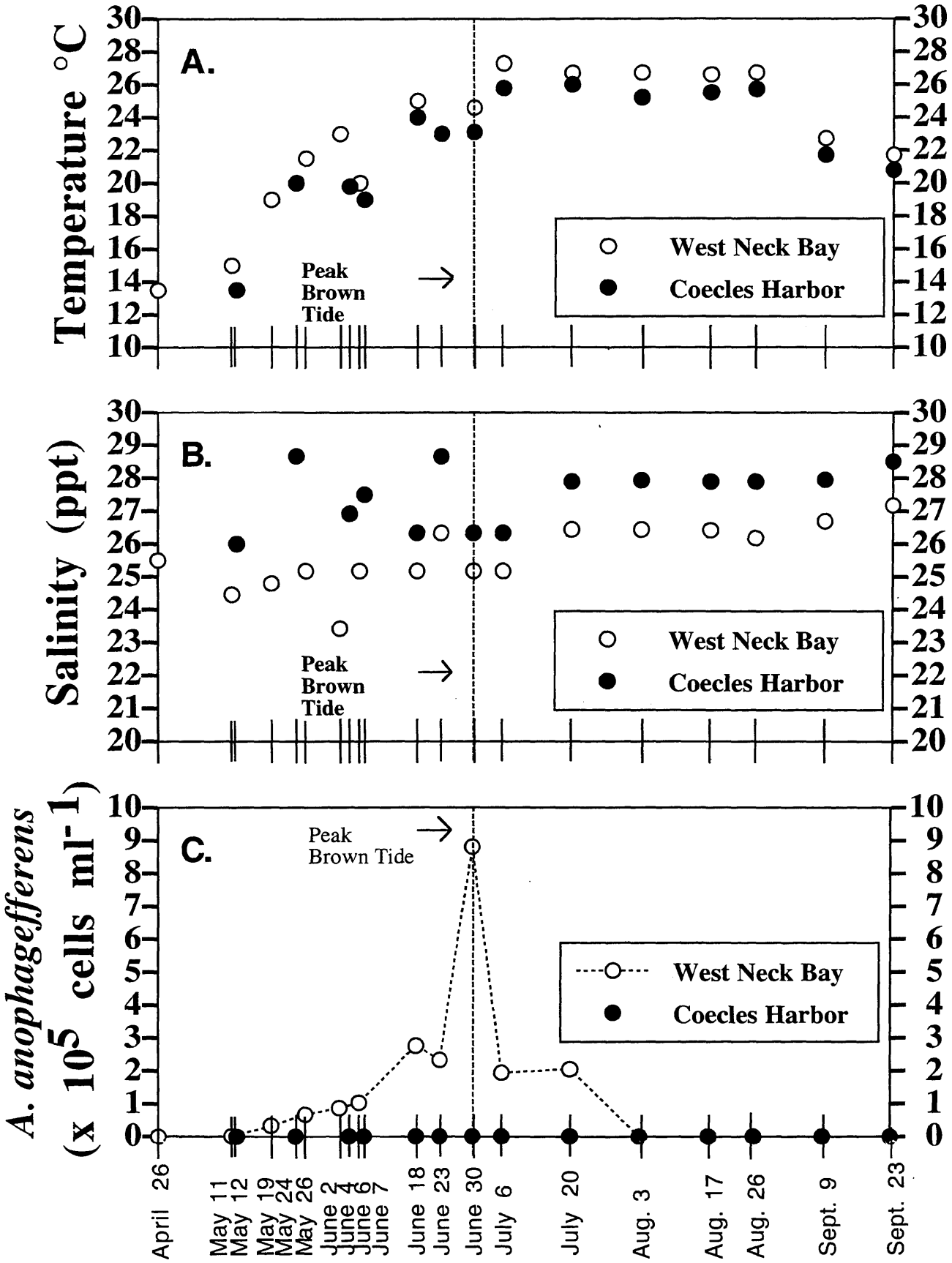
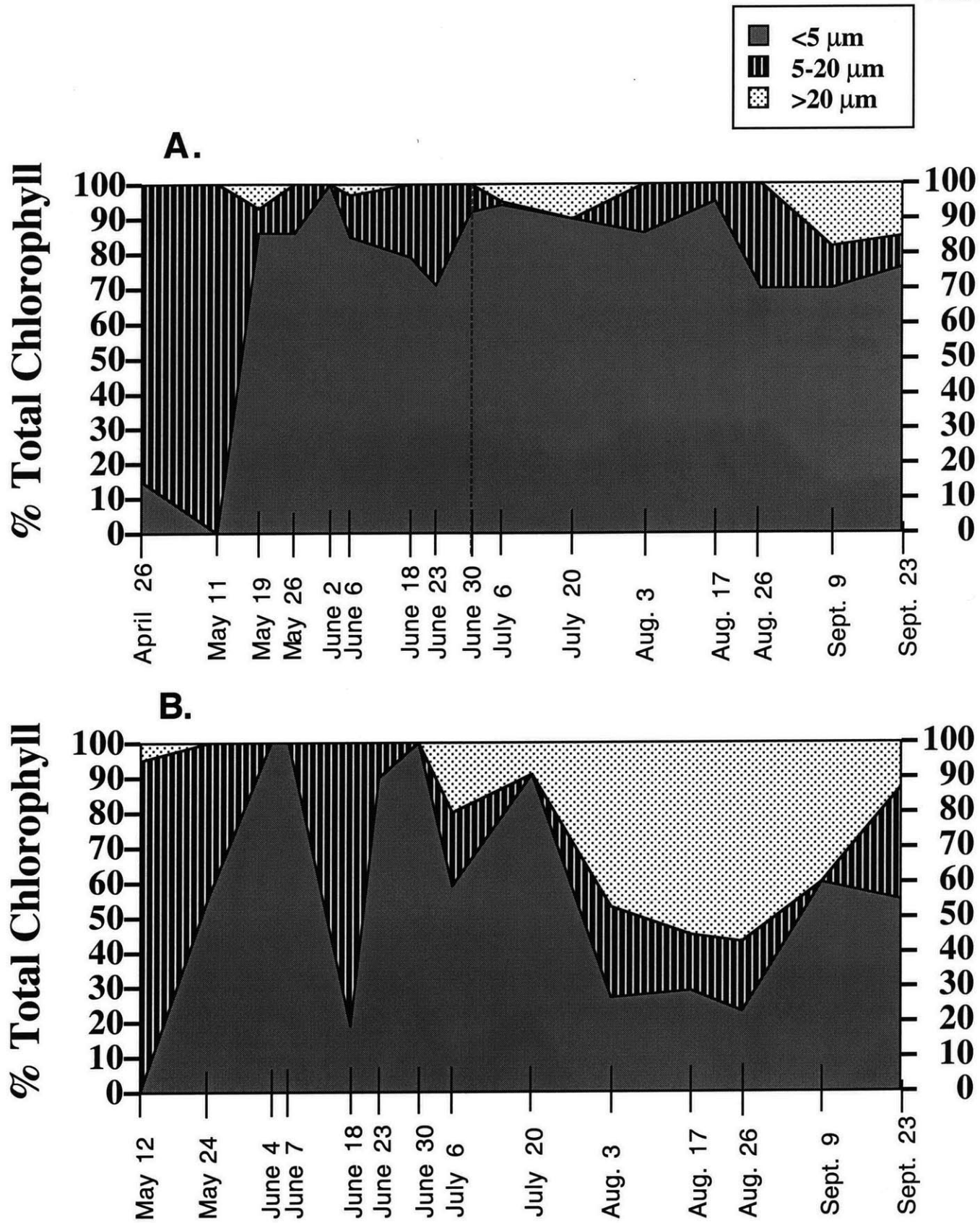

A.
Temperature °C
Peak Brown Tide
West Neck Bay
Coecles Harbor
B.
Salinity (ppt)
Peak Brown Tide
West Neck Bay
Coecles Harbor
C.
A. anophagefferens (x 10^5 cells ml^-1)
Peak Brown Tide
West Neck Bay
Coecles Harbor
April 26
May 11
May 12
May 19
May 24
May 26
June 2
June 4
June 6
June 7
June 18
June 23
June 30
July 6
July 20
Aug. 3
Aug. 17
Aug. 26
Sept. 9
Sept. 23

FIG. 3


<5 μm
5-20 μm
>20 μm
A.
% Total Chlorophyll
100
90
80
70
60
50
40
30
20
10
0
April 26
May 11
May 19
May 26
June 2
June 6
June 18
June 23
June 30
July 6
July 20
Aug. 3
Aug. 17
Aug. 26
Sept. 9
Sept. 23
B.
% Total Chlorophyll
May 12
May 24
June 4
June 7
June 18
June 23
June 30
July 6
July 20
Aug. 3
Aug. 17
Aug. 26
Sept. 9
Sept. 23

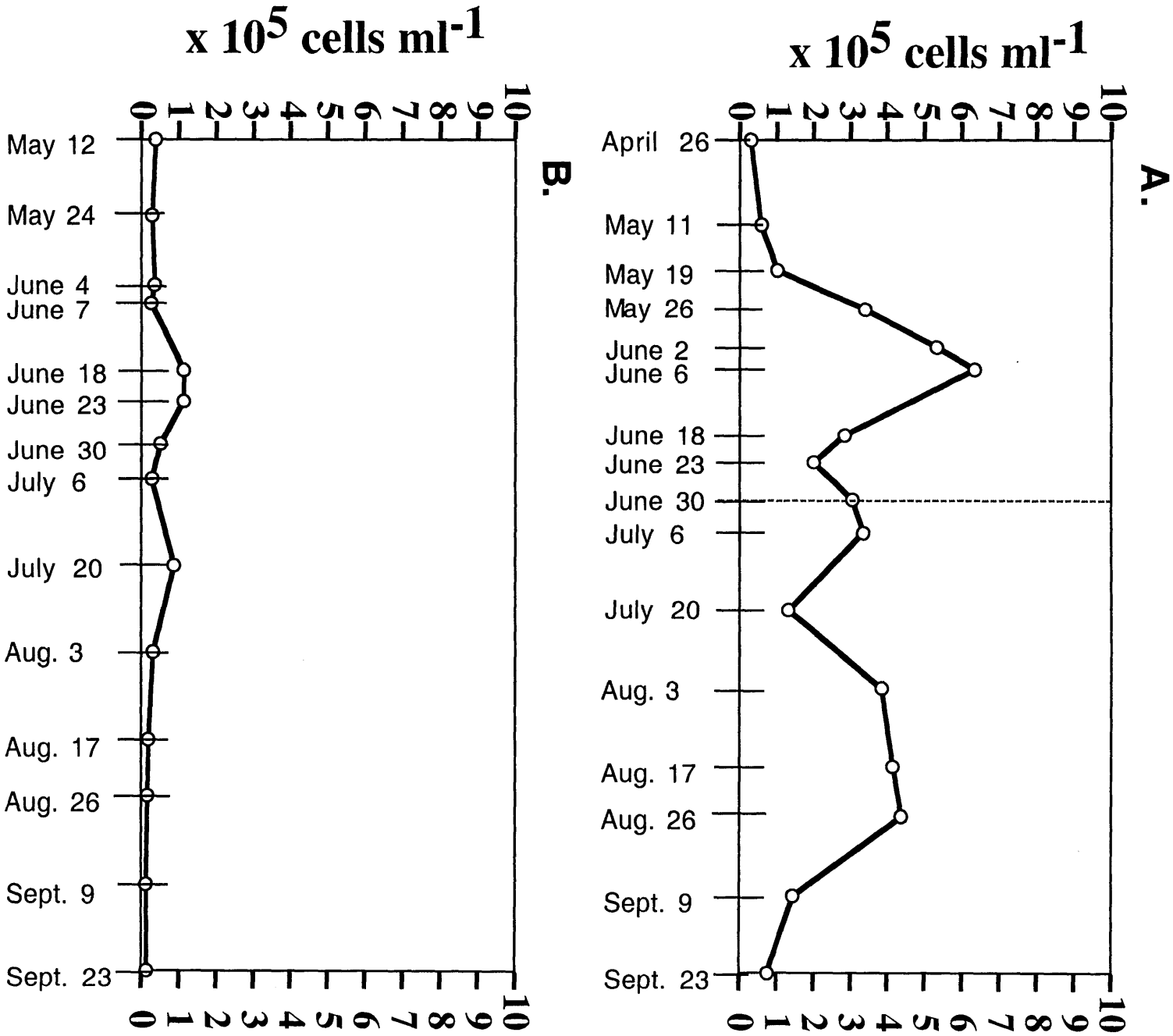

x 10^5 cells ml^-1
0 1 2 3 4 5 6 7 8 9 10
May 12
May 24
June 4
June 7
June 18
June 23
June 30
July 6
July 20
Aug. 3
Aug. 17
Aug. 26
Sept. 9
Sept. 23
B.
x 10^5 cells ml^-1
0 1 2 3 4 5 6 7 8 9 10
April 26
May 11
May 19
May 26
June 2
June 6
June 18
June 23
June 30
July 6
July 20
Aug. 3
Aug. 17
Aug. 26
Sept. 9
Sept. 23
A.

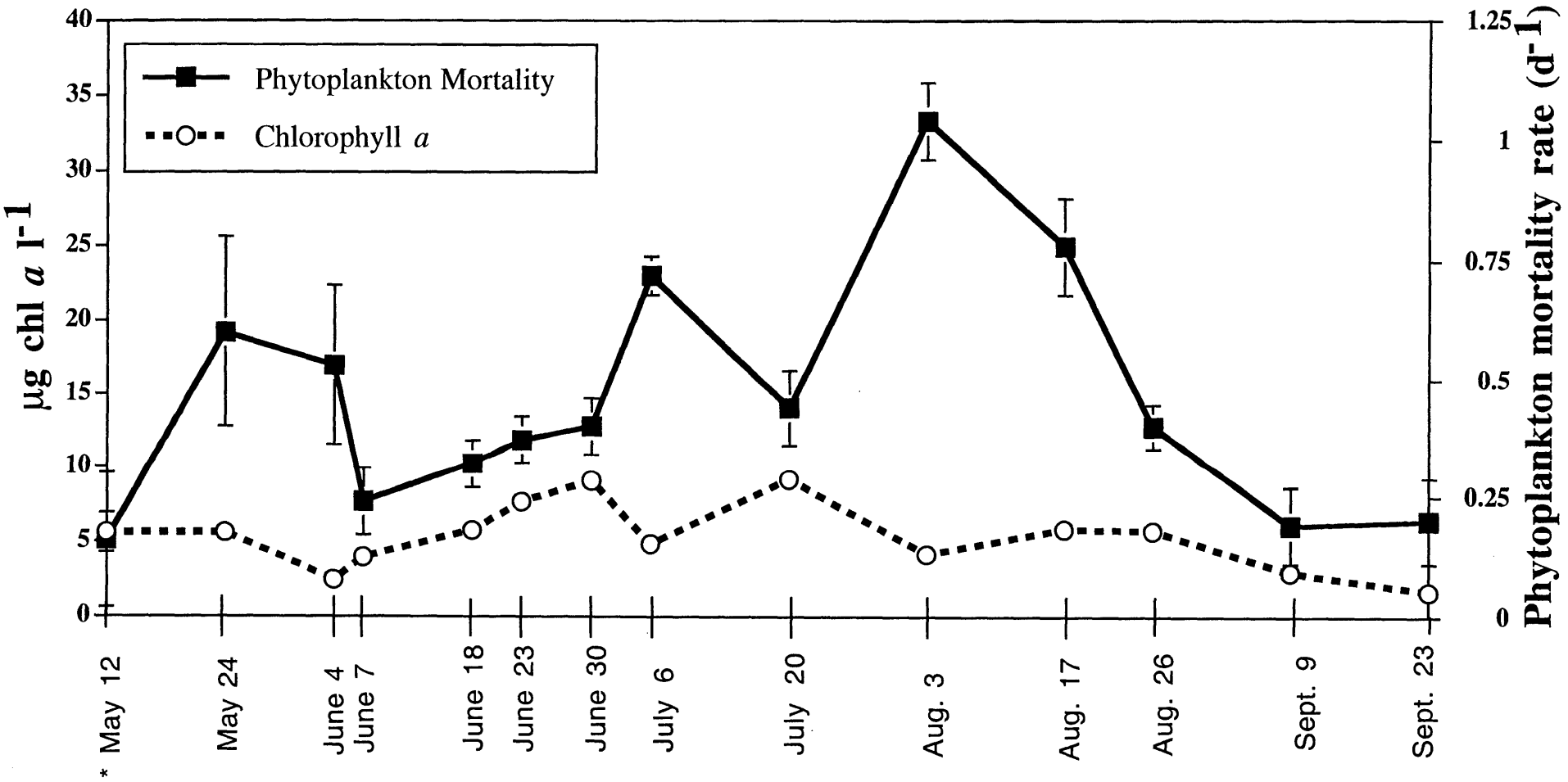
FIG. 4

A.
Prorocentrumspp.
Diatoms
x 10^5 cells l^-1
0
2
4
6
8
10
12
14
16
18
20
April 26
May 11
May 19
May 26
June 2
June 6
June 18
June 23
June 30
July 6
July 20
Aug. 3
Aug. 17
Aug. 26
Sept. 9
Sept. 23
B.
Other dinoflagellates
Aloricate ciliates
Loricate ciliates
Other flagellates
x 10^4 cells l^-1
0
5
10
15
20
25
30
35
40
45
50
April 26
May 11
May 19
May 26
June 2
June 6
June 18
June 23
June 30
July 6
July 20
Aug. 3
Aug. 17
Aug. 26
Sept. 9
Sept. 23
C.
Prorocentrumspp.
Diatoms
x 10^5 cells l^-1
0
2
4
6
8
10
12
14
16
18
20
May 12
May 24
June 4
June 7
June 18
June 23
June 30
July 6
July 20
Aug. 3
Aug. 17
Aug. 26
Sept. 9
Sept. 23
D.
Other dinoflagellates
Aloricate ciliates
Loricate ciliates
Other flagellates
x 10^4 cells l^-1
0
5
10
15
20
25
30
35
40
45
50
May 12
May 24
June 4
June 7
June 18
June 23
June 30
July 6
July 20
Aug. 3
Aug. 17
Aug. 26
Sept. 9
Sept. 23

FIG. 5

* Slope (m = mortality) not significant.

FIG. 6



* Slope (m = mortality) not significant.

FIG. 7

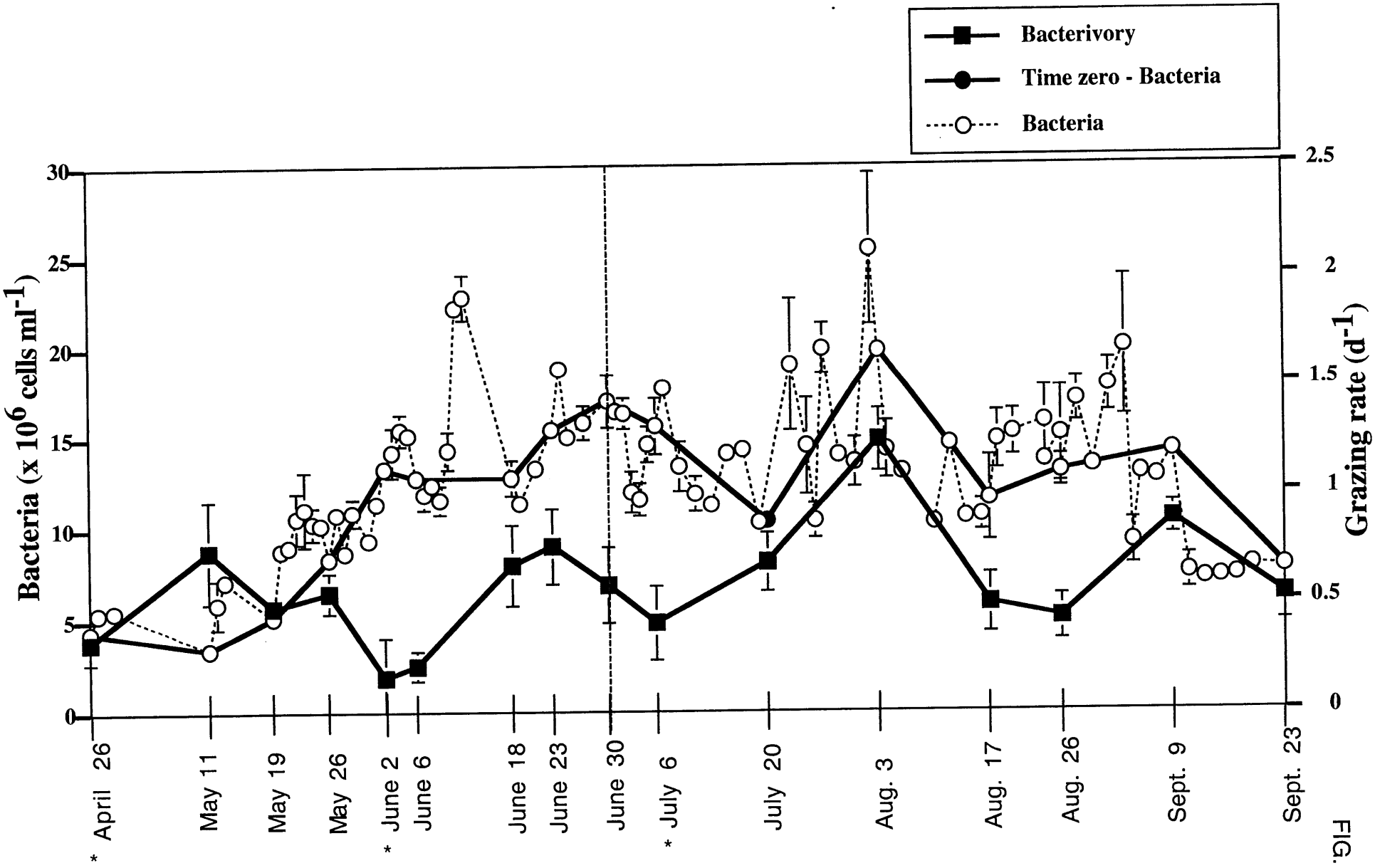


FIG. 8

*Grazing not significantly greater than zero ($p>0.05$).

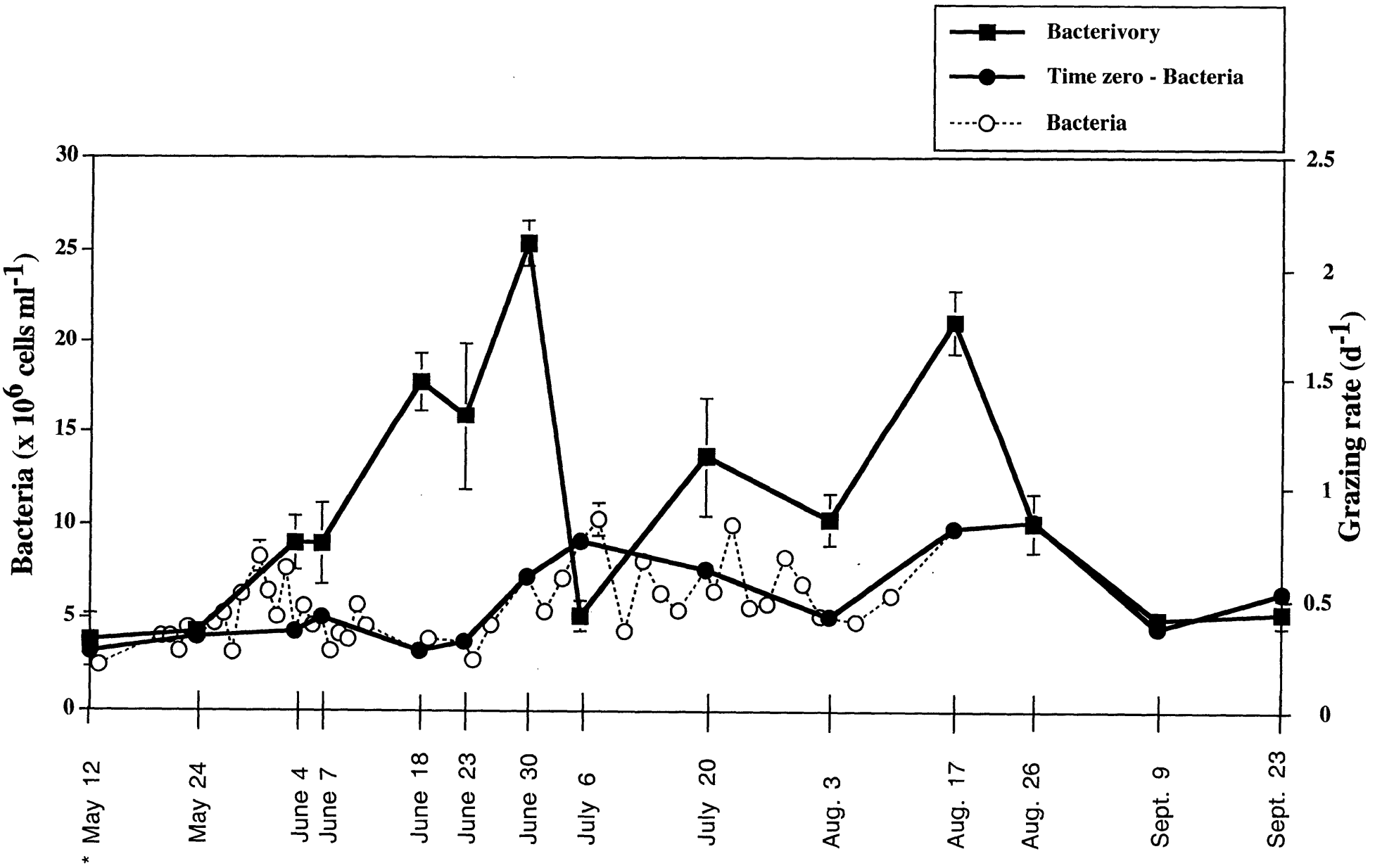


FIG. 9

* Grazing not significantly greater than zero ($p>0.05$).

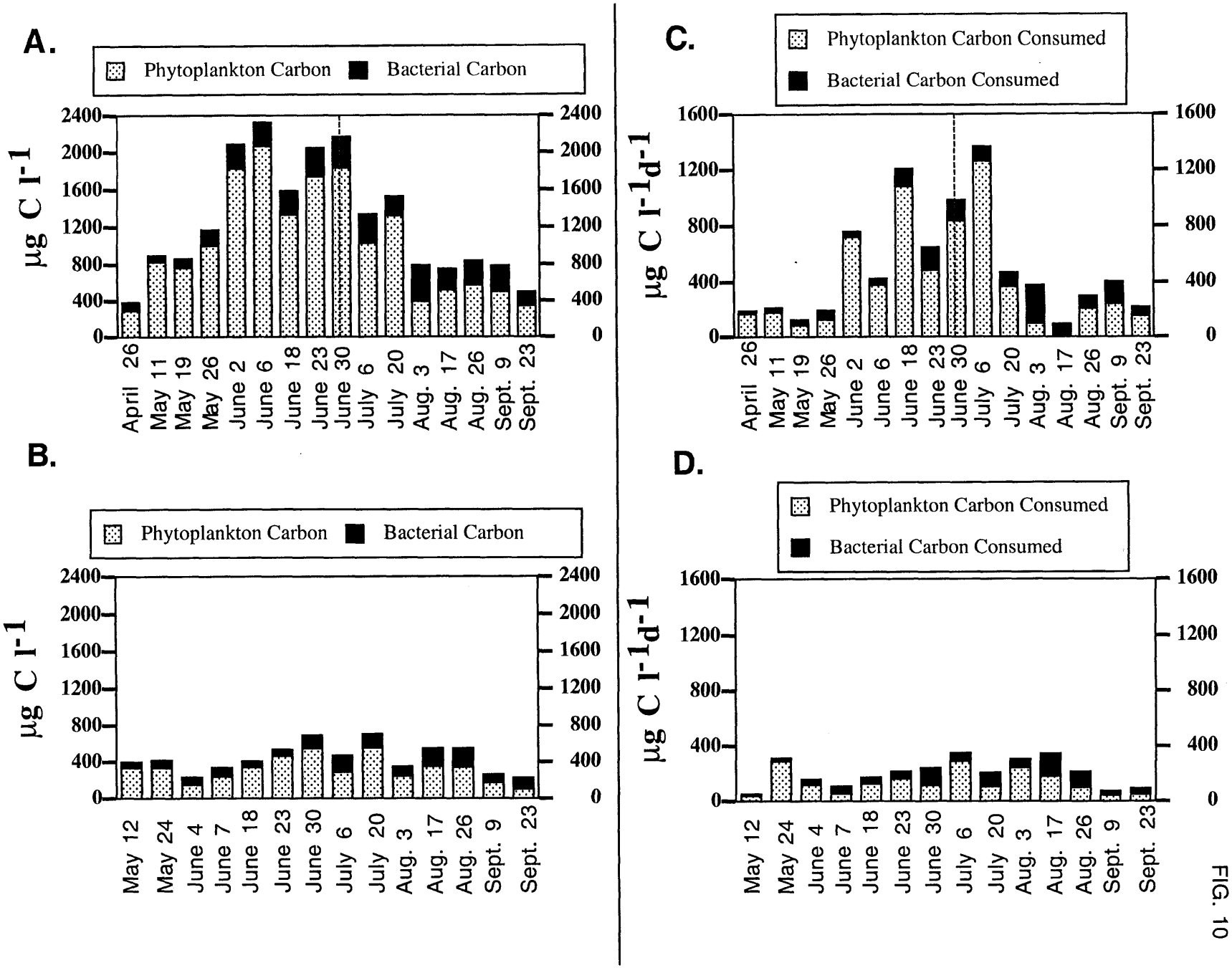

A.
Phytoplankton Carbon
Bacterial Carbon
µg C l-1
2400
2000
1600
1200
800
400
0
April 26
May 11
May 19
May 26
June 2
June 6
June 18
June 23
June 30
July 6
July 20
Aug. 3
Aug. 17
Aug. 26
Sept. 9
Sept. 23
B.
Phytoplankton Carbon
Bacterial Carbon
µg C l-1
May 12
May 24
June 4
June 7
June 18
June 23
June 30
July 6
July 20
Aug. 3
Aug. 17
Aug. 26
Sept. 9
Sept. 23
C.
Phytoplankton Carbon Consumed
Bacterial Carbon Consumed
µg C l-1d-1
1600
1200
800
400
0
April 26
May 11
May 19
May 26
June 2
June 6
June 18
June 23
June 30
July 6
July 20
Aug. 3
Aug. 17
Aug. 26
Sept. 9
Sept. 23
D.
Phytoplankton Carbon Consumed
Bacterial Carbon Consumed
µg C l-1d-1
May 12
May 24
June 4
June 7
June 18
June 23
June 30
July 6
July 20
Aug. 3
Aug. 17
Aug. 26
Sept. 9
Sept. 23

FIG. 10