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Microbial food web interactions in two Long Island embayments

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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 much of the summer, and most microzooplankton (<200 µm) were also small (<40 µm) for that category. 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. Carbon consumption was estimated from phytoplankton and bacterial removal rates and from conversion to carbon from chlorophyll (phytoplankton) or cell number (bacteria). These calculations indicated that carbon consumption due to bacterivory constituted an average of 21 and 47% of carbon consumption due to herbivory in West Neck Bay and Coecles Harbor, respectively. Total carbon consumption (bacterivory + herbivory) revealed high energy flux through the nano- and microzooplankton assemblages of these estuarine environments.

KEY WORDS: Bacterivory · Herbivory · Microbial ecology · Bacteria · Phytoplankton · Zooplankton · Protozoa · Long Island Bays · Peconic Bay · Estuary

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 et al. 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 µg 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 well-mixed bays during summer, when high irradiance and high water temperatures favor algal growth.

West Neck Bay (WNB) and Coecles Harbor (CH) form part of the Peconic Estuary System, a group of shallow (average depth 4.7 m), strongly mixed, interconnected estuarine ecosystems in eastern Long Island (Hardy 1976, Wilson 1995). Phytoplankton communities in these bays typically have been dominated by picoplankton (0.2 to 2.0 µm) and nanoplankton (2 to 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 tides'

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caused by a picoplanktonic pelagophyte, *Aureococcus anophagefferens* (Cosper et al. 1987, Bricelj & Lonsdale 1997). Eutrophic WNB has repeatedly experienced high abundances of *A. anophagefferens*, typically in June or July. In contrast, the appearance of brown tides in CH has occurred only occasionally during the past 15 yr 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 carbon, energy and nutrient flow in these estuaries. The size range of much of the algal community in WNB and CH is below the optimal range for particle capture by mesozooplankton (Nival & Nival 1976, Bartram 1980). Accordingly, studies in the Peconic Estuary 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 WNB. These observations support the supposition that phagotrophic protistan assemblages play a major role in the removal of phytoplankton production in Long Island bays.

Bacteria also make up a significant component of total picoplanktonic 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 Estuary System and other Long Island estuaries (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.

We investigated the role of protistan grazers in determining the fate of production in the Peconic Estuary System. Bacterivory and phytoplankton mortality (herbivory) were measured throughout the summer of 1998 in WNB and CH. Herbivory was determined using the dilution method. Bacterivory was estimated from the rate of disappearance of fluorescently labeled bacteria (FLB) during 24 h incubations. Our results indicate that major proportions of bacterial and primary production are channeled through the nano- and microzooplankton in these 2 bays.

Fig. 1. Study site: Peconic Bays System, Long Island, NY. Water samples were collected at the northeastern shore of West Neck Bay and the western shore of Coecles Harbor. All incubations were performed at the study site in Coecles Harbor

MATERIALS AND METHODS

Field sites and sampling. WNB and CH are part of the Peconic Estuary System located on Shelter Island between the upper and lower forks of eastern Long Island, NY (Fig. 1). WNB is situated on the southwest side of Shelter Island, enclosed by an extension of land that restricts flow into and out of the bay. CH opens into the ocean side of the Peconic system on the eastern side of Shelter Island. CH has somewhat more exchange with the surrounding estuarine system than WNB, but CH is also a larger body of water. These 2 estuaries were chosen because they represent different levels of eutrophication and different historical patterns in the occurrence of *Aureococcus anophagefferens*. Both were also close to our field laboratory.

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 were measured at each sampling.

Microbial population estimates. Samples for the enumeration of *Aureococcus anophagefferens*, nanoplankton and bacteria were preserved immediately with 1% glutaraldehyde (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

Table 1. Phytoplankton biomass, growth and mortality rates in West Neck Bay. Initial standing stocks of phytoplankton are expressed as chlorophyll (chl) concentration and carbon biomass (using a C:chl ratio of 60). Phytoplankton mortality rates were calculated from linear regression analyses of the nutrient-enriched dilution series (along with r^2 and significance values for the regressions; NS: not significant). Daily removal of phytoplankton, expressed as *µg chl *a* l^{-1} d^{-1} and **percentage of standing stock d^{-1}, were calculated using phytoplankton mortality rates and standing stocks derived from chlorophyll and a C:chl ratio of 60

Date (1998)	Initial chl concentration (µg chl *a* l^{-1})	Initial phytoplankton biomass (µg C l^{-1})	Unenriched growth rate; μ_0 (d^{-1})	Enriched growth rate; μ_n (d^{-1})	Net growth rate $k = \mu_0 - m$ (d^{-1})	Mortality rate, m (d^{-1})	r^2	Significance (p-value)	µg chl *a* l^{-1} consumed daily*	% standing stock consumed daily**
26 Apr	4.8	290	0.17	0.35	−0.49	0.66	0.60	<0.01	2.8	48
11 May	13.8	827	0.09	0.17	−0.13	0.22	0.14	>0.05 NS	–	–
19 May	12.7	760	−0.21	0.55	−0.36	0.15	0.06	>0.05 NS	–	–
26 May	16.6	998	1.30	0.93	1.1	0.15	0.51	<0.01	2.1	14
2 Jun	30.3	1820	0.11	1.1	−0.33	0.44	0.80	<0.01	12.1	36
6 Jun	34.4	2060	0.02	1.0	−0.19	0.20	0.52	<0.01	6.3	18
18 Jun	22.1	1330	0.34	1.4	−0.53	0.87	0.83	<0.01	18.1	58
23 Jun	28.9	1740	−0.20	0.46	−0.62	0.42	0.64	<0.01	8.1	34
30 Jun	30.5	1830	0.04	0.76	−0.52	0.57	0.84	<0.01	13.9	43
6 Jul	17.1	1020	0.64	2.0	−0.41	1.0	0.84	<0.01	21.1	65
20 Jul	22.0	1320	−0.17	1.5	−0.57	0.40	0.59	<0.01	6.1	33
3 Aug	6.5	391	−0.31	2.6	−0.62	0.38	0.57	<0.01	1.6	32
17 Aug	8.6	514	−0.74	1.5	−0.74	0.02	0.00	>0.05 NS	–	–
26 Aug	9.5	572	−0.09	1.0	−0.63	0.52	0.64	<0.01	3.5	41
9 Sep	8.3	499	0.04	1.2	−0.60	0.63	0.73	<0.01	4.0	47
23 Sep	5.7	344	0.32	0.68	−0.05	0.38	0.73	<0.01	2.5	32

Table 2. Phytoplankton biomass, growth and mortality rates in Coecles Harbor. Initial standing stocks of phytoplankton are expressed as chlorophyll (chl) concentration and carbon biomass (using a C:chl ratio of 60). Phytoplankton mortality rates were calculated from linear regression analyses of the nutrient-enriched dilution series (along with r^2 and significance values for the regressions; NS: not significant). Daily removal of phytoplankton, expressed as *µg chl *a* l^{-1} d^{-1} and **percentage of standing stock d^{-1}, were calculated using phytoplankton mortality rates and standing stocks derived from chl and a C:chl ratio of 60

Date (1998)	Initial chl concentration (µg chl *a* l^{-1})	Initial phytoplankton biomass (µg C l^{-1})	Unenriched growth rate; μ_0 (d^{-1})	Enriched growth rate; μ_n (d^{-1})	Net growth rate $k = \mu_0 - m$ (d^{-1})	Mortality rate, m (d^{-1})	r^2	Significance (p-value)	µg chl *a* l^{-1} consumed daily*	% standing stock consumed daily**
12 May	5.6	336	−0.37	0.15	−0.48	0.16	0.05	>0.05 NS	–	–
24 May	5.6	336	0.65	0.50	0.05	0.60	0.41	<0.01	4.8	45
4 Jun	2.5	147	0.68	1.4	0.14	0.53	0.43	<0.01	2.0	41
7 Jun	4.0	238	0.11	0.95	−0.14	0.24	0.48	<0.01	0.9	21
18 Jun	5.7	344	0.31	1.7	−0.02	0.32	0.76	<0.01	2.1	27
23 Jun	7.7	460	0.14	1.2	−0.23	0.37	0.79	<0.01	2.7	31
30 Jun	9.1	544	−0.43	1.2	−0.84	0.40	0.76	<0.01	1.9	33
6 Jul	4.8	290	0.67	2.4	−0.05	0.72	0.96	<0.01	4.9	51
20 Jul	9.2	550	−0.61	0.86	−1.0	0.44	0.67	<0.01	1.8	36
3 Aug	4.2	249	0.44	3.3	−0.61	1.0	0.93	<0.01	4.1	65
17 Aug	5.8	350	−0.02	2.6	−0.80	0.78	0.82	<0.01	3.1	54
26 Aug	5.7	344	−0.12	2.3	−0.50	0.40	0.85	<0.01	1.7	33
9 Sep	2.9	176	0.38	1.2	0.18	0.19	0.31	<0.05	0.7	17
23 Sep	1.7	100	1.1	1.3	0.82	0.20	0.28	<0.05	0.8	18

0.8 µm blackened polycarbonate filters. Nanoplankton were stained with 4',6-diamidino-2-phenylindole (DAPI) at 25 to 50 µg ml^{-1} final stain concentration, which stains protists effectively, filtered onto 0.8 µm blackened polycarbonate filters and counted using epiflourescence microscopy (Caron 1983, Sherr & Sherr 1993a, Sherr et al. 1993). Nanoplankton could not be processed consistently within 24 h 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 the determination of 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 short-term fluctuations in the abundance of this assemblage. Bacteria were stained with the nucleic acid dye Syto 13 (Molecular Probes®, Eugene, OR, USA) and counted using a Becton Dickinson FACSCalibur flow cytometer (BD Bioscience, Mansfield, MA, USA; del Giorgio et al. 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 to 200 µm) were preserved with Lugol's preservative (10% final concentration) and stored in glass amber jars in the dark until processed (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* sp., other dinoflagellates, non-loricate ciliates, tintinnids and other flagellates. Metazoa did not make up a significant fraction of microplankton abundances.

Chlorophyll analyses. Chlorophyll concentrations were determined fluorometrically (Strickland & Parsons 1972) for all seawater samples, and on seawater passing through 5 µm and 20 µm Nitex® screening (Sefar America, Kansas City, MO, USA). Subsamples were filtered onto Gelman GF/F glass fiber filters (Gelman Science, Ann Arbor, MI, USA) 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 (Turner Designs, Sunnyvale, CA, USA).

Chlorophyll concentrations were converted to phytoplankton carbon using a carbon to chlorophyll (C:chl) ratio of 60. This ratio was empirically determined on 2 dates in WNB during blooms of the dinoflagellate *Prorocentrum* sp. or the pelagophyte *Aureococcus anophagefferens*. The C:chl ratio during the dinoflagellate bloom (11 May) 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* (30 June) by assuming that this alga dominated the chlorophyll biomass at the time, using a conversion factor of approximately 2.1 pg C $cell^{-1}$ to estimate phytoplankton carbon biomass (Milligan & Cosper 1997). C:chl ratios on both dates were ~60. A ratio of 60 was applied to all samples taken during the study.

Phytoplankton growth and mortality rates. Phytoplankton growth rates and rates of phytoplankton mortality (microbial herbivory) were estimated using the refined dilution technique (Landry et al. 1995) but fluorescently labeled prey were not added. This method relies on dilution of herbivorous zooplankton with filtered seawater in the sample to create a gradient of phytoplankton mortality. Phytoplankton growth and mortality rates are determined from changes in apparent phytoplankton growth rate along the dilution gradient. 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 (73.5 µM $NaNO_3$; 3.02 µM $NaH_2PO_4 \cdot H_2O$; 1 ml 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 h in CH. Bottles were strung on a line at a depth of approximately 30 cm below the water surface. This incubation depth corresponded to ~1/5 (CH) and 1/3 (WNB) the depth of the entire water column at the sampling locations.

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 of the phytoplankton in each bottle were calculated from changes in chlorophyll *a* (chl *a*) concentration over the length of the experiment as $r = 1/t \times \ln(P_t/P_0)$, where t is time, P_0 is initial phytoplankton concentration and P_t is final phytoplankton concentration. Growth rates of the phytoplankton assem-

blages in the nutrient-enriched bottles (μ_n) were determined from the *y*-intercepts of the regressions of apparent growth rate in the bottles versus dilution. Phytoplankton mortality rates (*m*) were calculated from the slopes of the regressions. Phytoplankton growth rates in the unenriched bottles (μ_0) were obtained from net (apparent) growth rates of the phytoplankton in the unenriched, undiluted treatment (k) and the mortality rates ($\mu_0 = k + m$). This terminology is consistent with that of Landry et al. (1995).

Microbial bacterivory. Bacterial grazing rates were obtained by measuring the disappearance of FLB in unfiltered seawater samples during 24 h 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). The bacterium is rod-shaped, approximately 0.4 × 0.8 µm when grown to starvation conditions. 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 (5×10^5 to 2×10^6 FLB ml^{-1}). For each experiment, FLB were also added to 3 control bottles (0.2 µm filtered seawater) to monitor non-grazing related losses of FLB (e.g., adherence to the container walls). Bottles were incubated at approximately 0.5 m in CH as described above for the dilution experiments. Samples were removed from each bottle at the beginning and end of the experiment, and frozen and stored in liquid nitrogen until analyzed. Abundances of FLB were determined on a Becton Dickinson FACScan flow cytometer (BD Bioscience).

Grazing rates on bacteria were estimated from the rates of loss of FLB during the 24 h incubations, assuming an exponential decrease during the incubation period and assuming no significant changes in the abundances of total bacteria during the incubation. Grazing was calculated as $g = -1/t \times \ln(F_t/F_0)$, where t is time, F_0 is initial concentration of FLB and F_t is 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 from zero ($p < 0.01$).

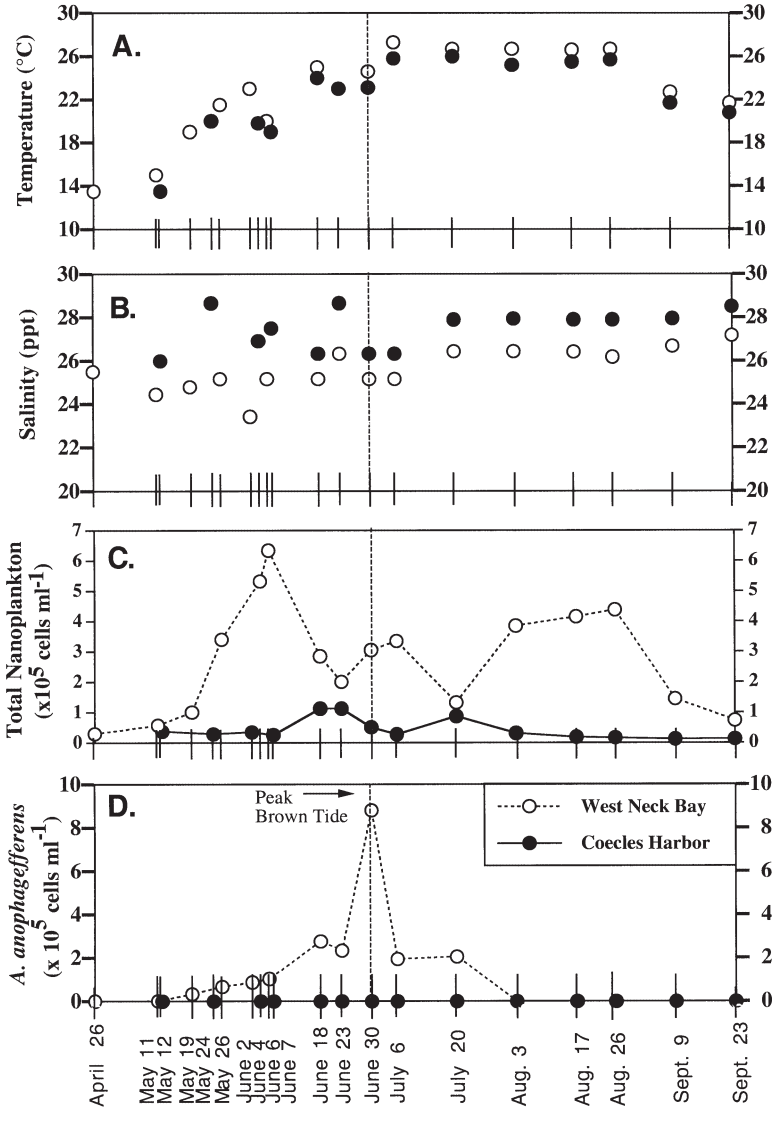

Fig. 2. (A) Water temperature, (B) salinity, (C) total nanoplankton abundance and (D) *Aureococcus anophagefferens* abundance in West Neck Bay and Coecles Harbor during 1998. The vertical dashed line indicates the sampling date with the highest observed abundance of *A. anophagefferens*

RESULTS

Physical parameters

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

were 1.9‰ higher in CH than WNB, averaging 27.5 ± 0.87‰ in CH and 25.6 ± 0.95‰ in WNB during the study period.

Phytoplankton and protozoa

WNB had consistently higher protistan abundance or biomass than CH during this study. Chlorophyll values throughout the summer in WNB averaged 17.0 µg chl *a* l^{-1} (range 4.8 to 34.4 µg chl *a* l^{-1}; Table 1). Chlorophyll concentrations were significantly lower in CH than WNB, averaging 5.3 µg chl *a* l^{-1} (range 1.7 to 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- (<2.0 µm) or nanoplanktonic (2 to 20 µm) algae, except in late summer in CH when microplanktonic forms (i.e., >20 µm) constituted a significant fraction of the total chlorophyll (Fig. 3). Most of the chlorophyll biomass in WNB occurred in the 5 to 20 µm size class on 26 April and 11 May (Fig. 3A). This bay was dominated by flagellated species of 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 to 20 and >20 µm in size each constituted more than 50% of the total phytoplankton biomass on several sampling dates (Fig. 3B).

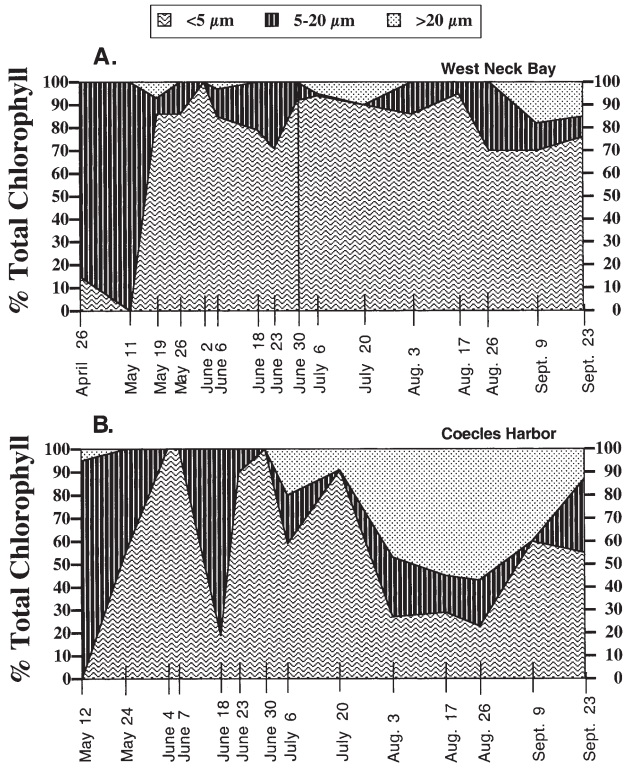

Fig. 3. Size-fractionated chlorophyll concentration (expressed as a percentage of the total chlorophyll) for (A) West Neck Bay and (B) Coecles Harbor. Total chlorophyll concentrations are given in Tables 1 & 2. The vertical dashed line in A indicates the sampling date with the highest observed abundance of *Aureococcus anophagefferens*

Differences in phytoplankton (i.e., chlorophyll) biomass between the 2 bays were reflected in differences in the abundances of nano- and microplankton. Total (phototrophic and heterotrophic) nanoplankton abundances were generally 6 times higher in WNB than CH, averaging 2.76×10^5 cells ml^{-1} in WNB (excluding *Aureococcus anophagefferens*) and 4.42×10^4 cells ml^{-1} in CH (Fig. 2C). 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 very significantly to abundance in this size fraction in WNB from late May to late July (Fig. 2D). The highest cell abundances of the brown tide alga observed were near-bloom concentrations of 8.80×10^5 cells ml^{-1} on 30 June. CH did not experience any significant buildup of *A. anophagefferens.* The latter cells were near the limit of detection throughout the study (less than a few hundred cells ml^{-1}).

Cell concentrations of microplankton were 2.7× higher in WNB (WNB average of 4.44×10^4 cells l^{-1}, CH average of 1.61×10^4 cells l^{-1}; Fig. 4). Microplankton in both bays were dominated by cells <40 µm in size. A brief bloom (1.64×10^6 cells l^{-1}) of *Prorocentrum* sp. was observed on 11 May in WNB. *Prorocentrum* sp. cell diameters were approximately 20 µm, and these cells were included with the microplankton in microscopical counts of these samples (Fig. 4A). However, the cells apparently passed through the 20 µm Nitex® screening and appeared largely in the 5 to 20 µm chlorophyll size class on 11 May (Fig. 3A). Dinoflagellates (heterotrophic and phototrophic) other than *Prorocentrum* composed a large portion of the remainder of the microplankton community in the bays. In WNB, these dinoflagellates averaged 9.11×10^4 cells l^{-1}, with peaks in May and August. Dinoflagellates averaged 4.99×10^4 cells l^{-1} in CH and exhibited peak concentrations in July and August.

Ciliate assemblages were dominated by aloricate ciliates in both bays on most sampling dates (Fig. 4B,D). Aloricate ciliates averaged 4.17×10^4 cells l^{-1} in WNB and 2.75×10^4 cells l^{-1} in CH throughout the study. Tintinnids outnumbered aloricate ciliates on only 2 dates, both of which coincided with high relative abundances of *Prorocentrum* sp. in WNB (11 May; Fig. 4B) and CH (6 July; Fig. 4D).

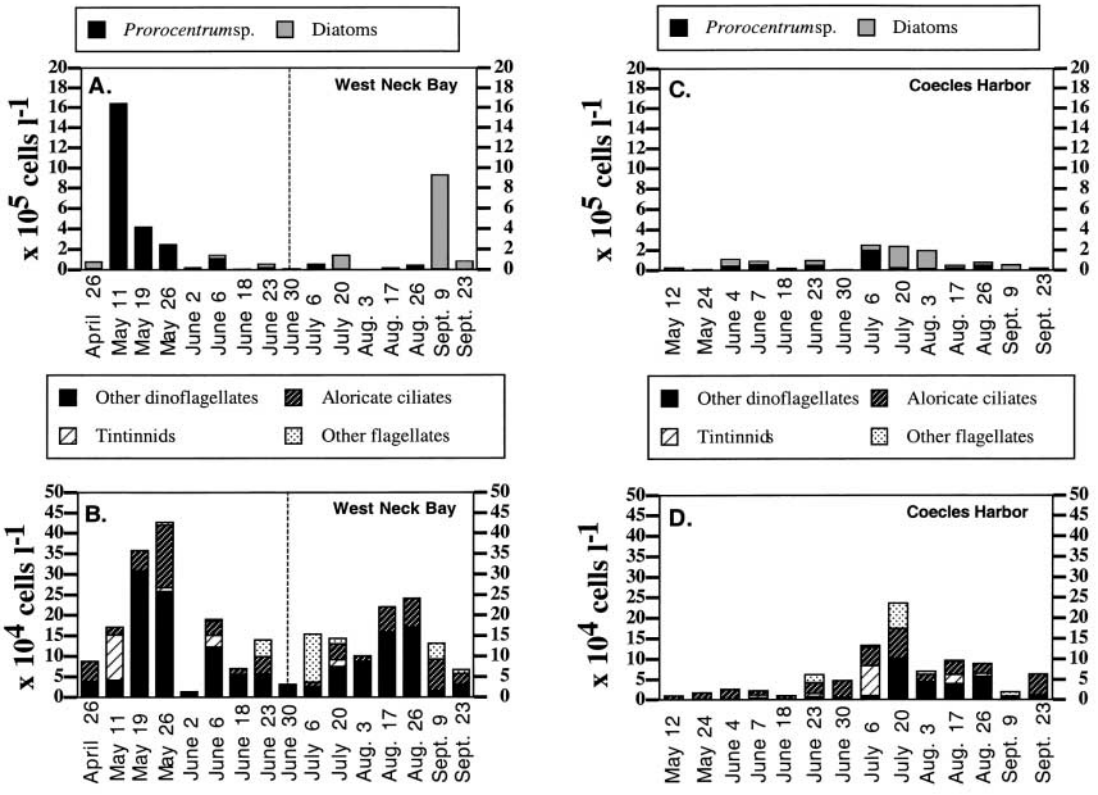

Fig. 4. Microplankton abundances in (A,B) West Neck Bay and (C,D) Coecles Harbor in 1998 grouped as (A,C) *Prorocentrum* sp. and diatoms, and (B,D) other flagellates and ciliates. The vertical dashed line in (A) and (B) indicates the sampling date with the highest observed abundance of *Aureococcus anophagefferens*

Phytoplankton growth and mortality

Sixteen dilution experiments were performed in WNB from 26 April through 23 September, and 14 experiments were conducted in CH from 12 May through 23 September to examine phytoplankton growth and mortality rates (Tables 1 & 2). Thirteen of 16 experiments in WNB and 13 of 14 experiments in CH had regressions that were significantly different from 0. Net phytoplankton growth rates (k, based on net changes in chlorophyll concentration in the unenriched, undiluted treatment) were very low for nearly all experiments and actually negative for most experiments (15 of 16 in WNB and 10 of 14 in CH). Overall average net growth rates were –0.35 d^{-1} for WNB and –0.25 d^{-1} for CH. In contrast, growth rates in the enriched bottles of the dilution series (μ_n) were positive and, in most cases, rapid (overall averages of 1.2 d^{-1} in WNB and 1.6 d^{-1} in CH for regressions yielding significant slopes). The highest growth rates in both estuaries were obtained in the nutrient-enriched treatments during the mid- to late summer. Gross phytoplankton growth rates in the absence of nutrient enrichment ($\mu_0 = k + m$) were variable during the study period (ranges –0.21 to 1.3 d^{-1} for WNB and –0.61 to 1.1 d^{-1} for CH for experiments with significant regressions). Overall averages for μ_0 in these experiments were modest (0.17 d^{-1} for WNB and 0.25 d^{-1} for CH).

Phytoplankton mortality rates determined by the dilution method were surprisingly similar in WNB and CH (Tables 1 & 2). Average rates of mortality were 0.51 ± 0.25 d^{-1} (±1 standard deviation) in WNB for the significant regressions (range 0.15 to 1.0 d^{-1}) and 0.48 ± 0.25 d^{-1} in CH (range 0.19 to 1.0 d^{-1}). These average rates were 0.41 d^{-1} (WNB) and 0.44 d^{-1} (CH) if non-significant regressions were included as mortality rates of 0. Seasonal trends in mortality rate were not apparent, although the highest rates were observed during late June and early July in WNB and during August in CH (Figs 5 & 6). Peaks in phytoplankton mortality rates were often offset from peaks in standing stocks of phytoplankton in both bays, implying predator-prey oscillations.

The average percentages of phytoplankton standing stocks removed per day were similar in both bays, owing to the similarity in mortality rates observed in the study. Removal rates averaged 38%

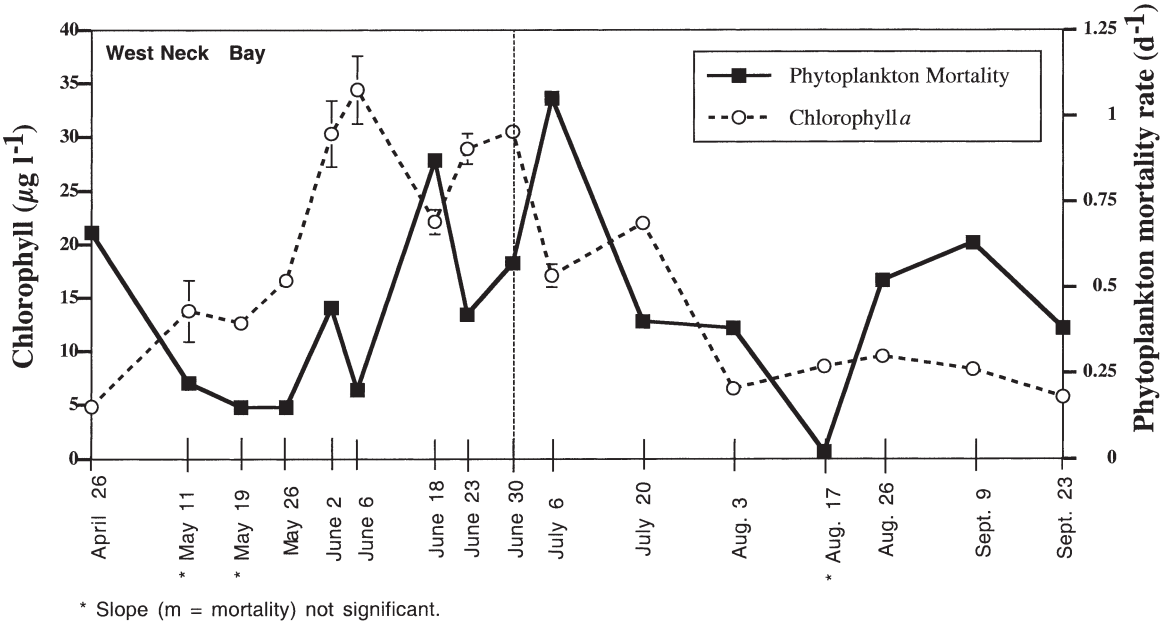

Fig. 5. Initial chlorophyll *a* concentrations and phytoplankton mortality rates determined from dilution experiments in West Neck Bay during 1998. Error bars for the chlorophyll concentrations are ±1 standard deviation of the mean. The vertical dashed line indicates the sampling date with the highest observed abundance of *Aureococcus anophagefferens*

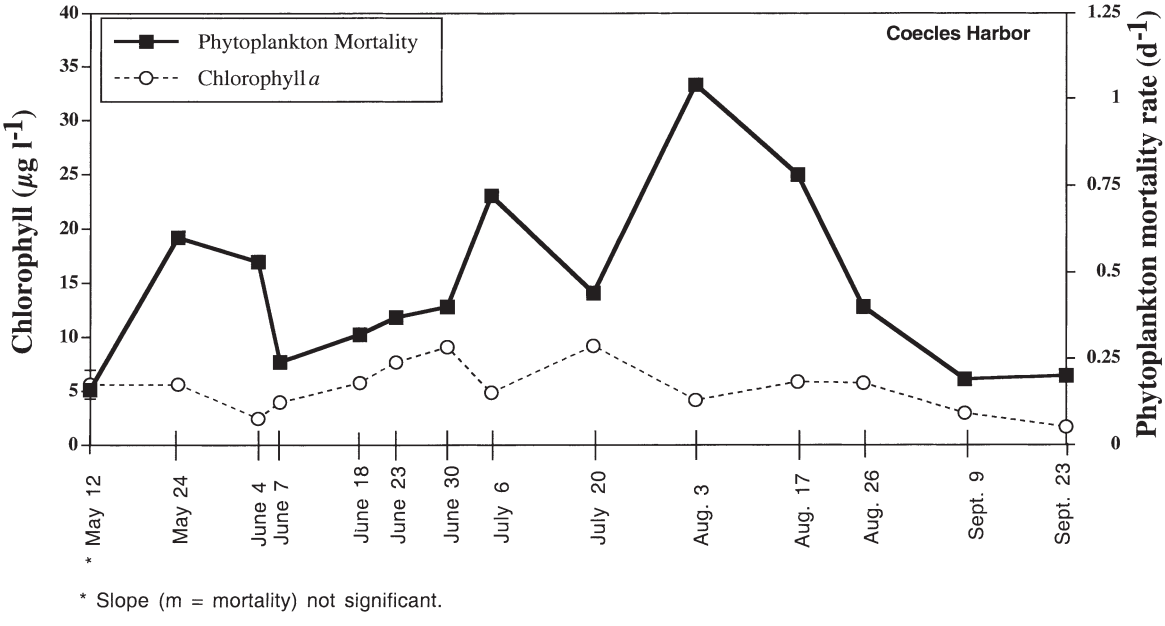

Fig. 6. Initial chlorophyll *a* concentrations and phytoplankton mortality rates determined from dilution experiments in Coecles Harbor during 1998. Error bars for the chlorophyll concentrations are ±1 standard deviation of the mean

in WNB (range 14 to 65%) and 36% in CH (17 to 65%). However, absolute rates of biomass removal (μg C l^{-1} d^{-1}) were quite different for the 2 bays because of differences in the standing stocks of phytoplankton. The average absolute amounts of phytoplankton biomass consumed were estimated to be 471 μg C l^{-1} d^{-1} (7.85 μg chl *a* l^{-1} d^{-1}) in WNB and 146 μg C l^{-1} d^{-1} (2.43 μg chl *a* l^{-1} d^{-1}) in CH using a C:chl ratio of 60 to convert chlorophyll to phytoplankton carbon (Tables 1 & 2). Maximal rates of phytoplankton biomass removal in WNB exceeded 1 mg C l^{-1} d^{-1} on 2 occasions.

Table 3. Bacterial standing stocks and grazing rates in West Neck Bay. Standing stocks of bacteria are expressed as cell concentration and carbon biomass (assuming 20 fg C cell^{-1}). Bacterial grazing rates were calculated from the rate of loss of fluorescently labeled prey during 24 h incubations. Daily removal of bacteria, expressed as *cells ml^{-1} d^{-1} and **percentage of standing stock d^{-1}, were estimated from grazing rates and standing stocks

Date (1998)	Initial bacterial cell concentration ($\times 10^6$ cells ml^{-1})	Initial bacterial biomass (µg C l^{-1})	Grazing rate (d^{-1})	Bacterial cells ml^{-1} consumed daily* ($\times 10^6$)	% standing stock consumed daily**
26 Apr	4.38	88	0.32	1.20	27
11 May	3.41	68	0.73	1.77	52
19 May	5.16	103	0.47	1.95	38
26 May	8.34	167	0.54	3.49	42
2 Jun	13.3	266	0.16	1.93	14
6 Jun	12.8	256	0.21	2.41	19
18 Jun	12.8	256	0.67	6.23	49
23 Jun	15.4	308	0.75	8.15	53
30 Jun	17.0	340	0.57	7.43	44
6 Jul	15.6	312	0.40	5.18	33
20 Jul	10.4	208	0.68	5.12	49
3 Aug	19.8	396	1.2	14.0	71
17 Aug	11.6	232	0.49	4.50	39
26 Aug	13.1	262	0.42	4.53	35
9 Sep	14.2	284	0.87	8.27	58
23 Sep	7.81	156	0.53	3.20	41

Table 4. Bacterial standing stocks and grazing rates in Coecles Harbor. Standing stocks of bacteria are expressed as cell concentration and carbon biomass (assuming 20 fg C cell^{-1}). Bacterial grazing rates were calculated from the rate of loss of fluorescently labeled prey during 24 h incubations. Daily removal of bacteria, expressed as *cells ml^{-1} d^{-1} and **percentage of standing stock d^{-1}, were estimated from grazing rates and standing stocks

Date (1998)	Initial bacterial cell concentration ($\times 10^6$ cells ml^{-1})	Initial bacterial biomass (µg C l^{-1})	Grazing rate (d^{-1})	Bacterial cells ml^{-1} consumed daily* ($\times 10^6$)	% standing stock consumed daily**
12 May	3.17	63	0.32	0.86	27
24 May	3.97	79	0.35	1.18	30
4 Jun	4.27	85	0.75	2.26	53
7 Jun	5.04	101	0.75	2.65	53
18 Jun	3.21	64	1.5	2.48	77
23 Jun	3.71	74	1.3	2.72	73
30 Jun	7.19	144	2.1	6.33	88
6 Jul	9.11	182	0.43	3.17	35
20 Jul	7.59	152	1.1	5.17	68
3 Aug	5.09	102	0.86	2.93	58
17 Aug	9.81	196	1.8	8.12	83
26 Aug	10.2	203	0.84	5.79	57
9 Sep	4.50	90	0.41	1.53	34
23 Sep	6.39	128	0.44	2.28	36

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 7 & 8). Bacterial abundances typically were more than twice as great in WNB than in CH, averaging 1.31×10^7 cells ml^{-1} in WNB and 5.6×10^6 cell ml^{-1} in CH. Fluctuations in abundance were similar for both ecosystems (a factor of approximately 5).

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 the higher

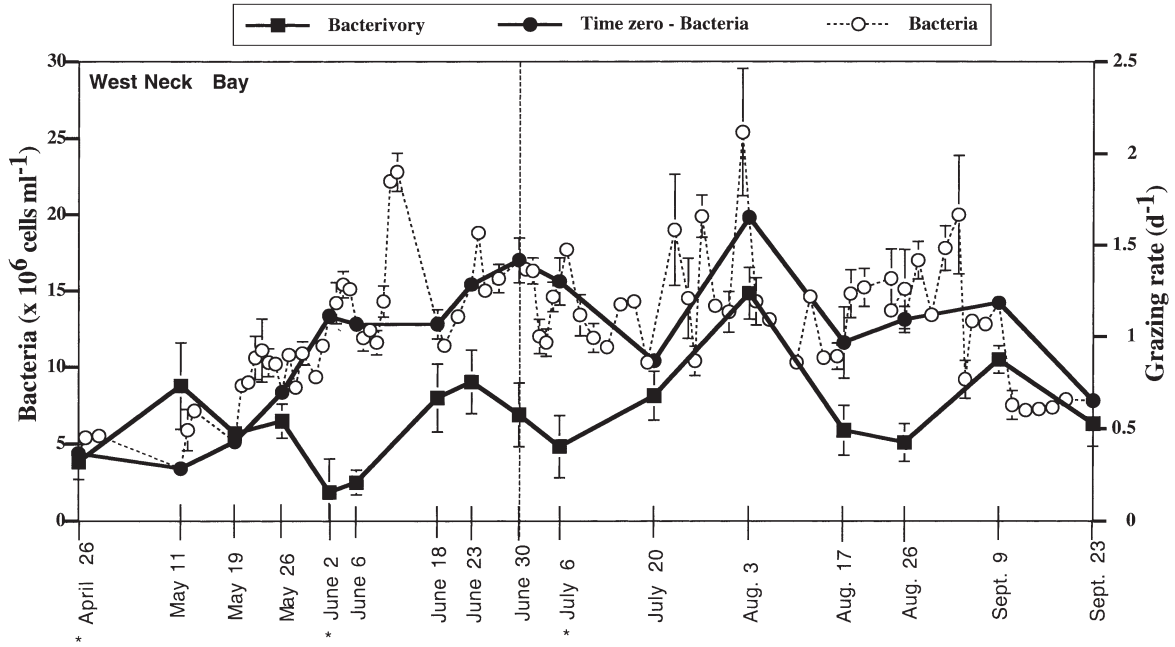

Fig. 7. Bacterial abundances and rates of bacterivory in West Neck Bay during 1998. Bacterial abundances were determined at time 0 for grazing experiments (solid circles) and on multiple sampling dates throughout the summer (open circles). Rates of bacterivory (solid squares) are the means of triplicate bottles. All error bars are ±1 standard deviation of the mean. The vertical dashed line indicates the sampling date with the highest observed abundance of *Aureococcus anophagefferens*

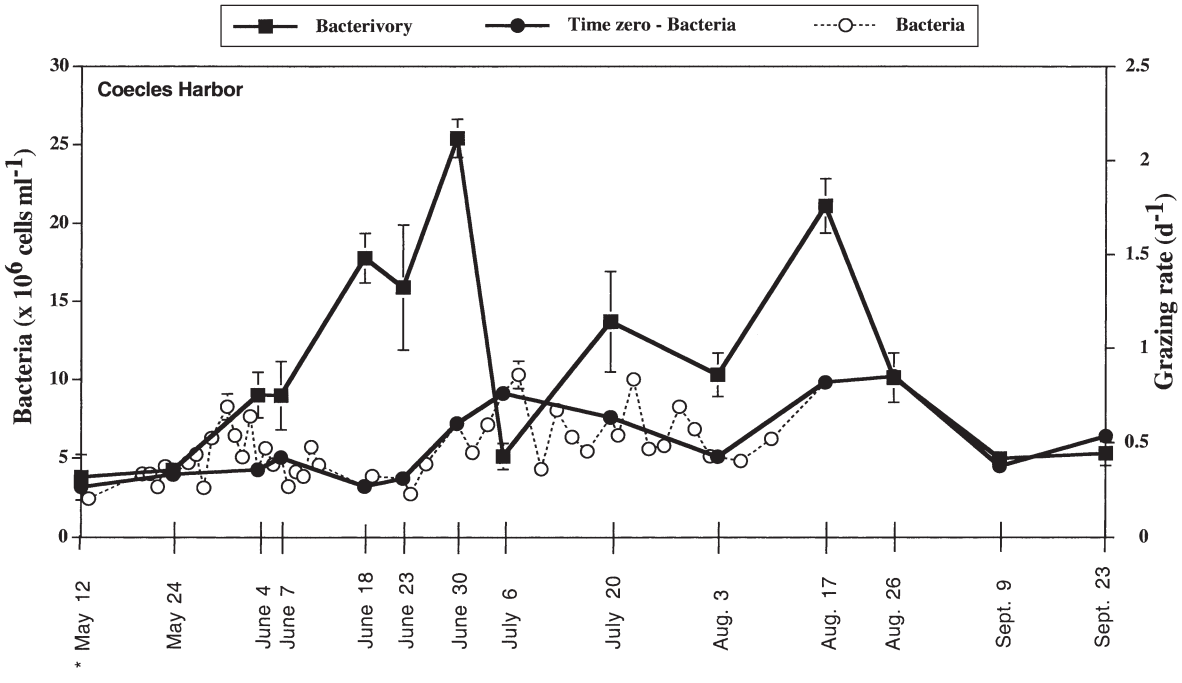

Fig. 8. Bacterial abundances and rates of bacterivory in Coecles Harbor during 1998. Bacterial abundances were determined at time 0 for grazing experiments (solid circles) and on multiple sampling dates throughout the summer (open circles). Rates of bacterivory (solid squares) are the means of triplicate bottles. All error bars are ±1 standard deviation of the mean

abundances of bacteria present in WNB. Removal of bacterial biomass averaged 99 µg C $l^{-1}d^{-1}$ (4.96×10^6 cells ml^{-1} d^{-1}) in WNB and 68 µg C $l^{-1}d^{-1}$ (3.39×10^6 cells ml^{-1} d^{-1}) in CH (Tables 3 & 4). This comparison does not take into account differences in average bacterial size between the 2 environments. 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 30 June and 17 August (Figs 7 & 8).

DISCUSSION

Community structure

Plankton abundances and biomasses in both WNB and CH were indicative of nutrient-rich, estuarine environments (Tables 1 to 4). However, hydrographic conditions, land runoff and groundwater intrusion presumably were different at the 2 study sites, and these differences were reflected in greater biological standing stocks 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 USA (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 Estuary 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 in central Peconic Bay had a range of chlorophyll of 1 to 6.6 µg chl *a* l^{-1} (Bruno et al. 1980), similar to the range observed in CH in the present study (Table 2).

Phytoplankton assemblages were composed of small algae throughout much of the summer in both WNB and CH (Fig. 3). WNB was dominated by picoplanktonic eukaryotes, typically small chlorophytes or chrysophytes and *Aureococcus anophagefferens*, while 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). CH displayed more variability in the dominant size class of algae, but small nanoplankton and picoplankton contributed significantly to phytoplankton standing stocks in this bay (Fig. 3B).

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 3.4×10^6 to 2.5×10^7 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 3.2×10^6 to 1×10^7 cells ml^{-1}. Daily samplings of bacteria confirmed that abundances recorded on experimental days reflected the general trends observed throughout the summer (Figs 7 & 8). However, occasional rapid changes in bacterial abundances illustrated that bacteria responded rapidly to environmental stimuli or removal processes (open circles and dotted lines in Figs 7 & 8).

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). Heterotrophic (apochlorotic) protistan assemblages in this study were largely composed of nanoflagellates, and heterotrophic dinoflagellates and aloricate ciliates <40 µm in diameter. Larger heterotrophic protists (>40 µm) and metazoa were minor components of the microzooplankton assemblages of both bays. These results imply that small phagotrophic protists probably were responsible for most of the grazing observed in this study.

Results from a 1988 study in WNB support the idea that small phagotrophic protists 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, tintinnids and scuticociliates. While community grazing was not evaluated, estimates of ingestion rates indicated that protistan taxa could constitute a significant source of mortality for these bacterial and algal populations.

Phytoplankton growth and mortality

Gross phytoplankton growth rates in the dilution bottles with nutrient additions (μ_n in Tables 1 & 2) were generally much greater than gross growth rates in the absence of nutrient additions (μ_0 in Tables 1 & 2). Differences in these rates were particularly striking for experiments performed in mid- to late summer. This finding implies that phytoplankton growth rates during many of the dilution experiments in this study could be increased by supplementing the assemblages with high concentrations of inorganic nutrients. Phytoplankton growth rates were increased 6- to 7-fold by

the addition of nutrients (from 0.17 to 1.2 d^{-1} in WNB and from 0.25 to 1.6 d^{-1} in CH when averaged over all experiments yielding significant regressions).

Gross phytoplankton growth rates in the absence of nutrient enrichment (μ_0) were generally low relative to rates of mortality. The overall result was that most of the net phytoplankton growth rates observed in the unenriched dilution bottles were negative (k in Tables 1 & 2). This result would imply that phytoplankton mortality rates exceeded phytoplankton growth rates on most of the sampling dates. However, phytoplankton standing stock actually remained constant or increased between many of the experimental dates. We speculate that this contradiction is a consequence of photoadaptation of the phytoplankton assemblages at the high irradiances employed in the dilution experiments. We chose 0.3 m for the depth of incubation because it represented a substantial fraction of the total water column depth at our sampling sites in both environments (~1.0 m in WNB and ~1.5 m in CH). We employed that depth in all incubations, and we performed all incubations in CH. However, we suspect that high intensity at 0.3 m in CH was sufficient to result in reductions in pigment content per cell due to photoadaptation. A reduction in chlorophyll per cell during the incubation would result in an underestimation of the actual growth rates of the phytoplankton assemblage (McManus 1995). Our contention is supported by the results of several experiments in which phytoplankton growth rates in the absence of grazing mortality were negative (μ_0 in Tables 1 & 2). In the absence of grazing mortality, these rates should be ≥ 0 assuming no reduction in per cell pigment content of the phytoplankton. Variable irradiance due to weather conditions among the days when experiments were performed would presumably result in variability in the degree of photoadaptation, and could help explain why only some of the experiments yielded negative values of μ_0.

Significant rates of phytoplankton mortality were observed in 26 out of 30 dilution experiments in this study. Non-significant regressions may indicate that mortality rates are indistinguishable from zero or that one or more assumptions of the method have been violated. It should be noted that while photoadaptation of the phytoplankton community during incubation will result in underestimation of phytoplankton growth rates in dilution experiments, phytoplankton mortality rates should be unaffected as long as the adaptation is similar in all dilution bottles. This requirement was probably met in our experiments because significant self-shading in 1 l bottles is highly unlikely. Ultraviolet light also should not have been a factor in these experiments (the incubation bottles absorb UV light), although adverse effects of high light intensity in the visible spectrum on protistan grazing activities cannot be ruled out in this study. Either of these perturbations (self-shading or light effects on phagotrophic protists) would presumably act to reduce the apparent mortality rates, and only during the daylight portion of the experiments. Thus, the rates observed in this study should represent at least lower limit estimates of microbial mortality.

Microzooplankton removed 14 to 65% of the daily standing stock in experiments yielding significant regressions (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).

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) from a variety of coastal ecosystems. Removal of phytoplankton biomass (µg C l^{-1} d^{-1}) was calculated for those studies using the same C:chl ratio (60) as that 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 we observed. The highest rates were observed in the Estuary of Mundaka (Spain), Rhodes River (Chesapeake Bay, Maryland) and Atchafalaya River estuary (Louisiana) (averages for these studies were 3610, 10 200 and 3270 µg C l^{-1} d^{-1}, respectively). These latter values are well in excess of the removal rates observed in the present study. We observed maximal rates of phytoplankton removal of approximately 1260 and 290 µg C l^{-1} d^{-1} in WNB and CH, respectively. Monthly averages of these removal rates were lower (49 to 815 µg C l^{-1} d^{-1} in WNB and 47 to 217 µg C l^{-1} d^{-1} in CH; Table 5). Nevertheless, turnover rates for the phytoplankton assemblages (percentage standing stock of phytoplankton consumed per day) were similar in our study relative to those published reports (Table 5).

The choice of a C:chl ratio of 60 was based on calculations performed on 2 experimental dates in our study. Use of a different C:chl ratio would affect our estimates of carbon flow. C:chl ratios reported in the literature vary greatly (~20 to >100) for natural populations (Caron et al. 1995). The value employed in this study should provide a fairly conservative estimate of phytoplankton carbon consumption given that the phytoplankton assemblage showed evidence of nutrient limitation on most of the sampling dates (see above) and

Table 5. Summary of dilution experiments from the 2 coastal bays examined in this study and from other marine environments. Initial chlorophyll (chl) concentrations and phytoplankton mortality rates for individual experiments are copied from reports, except as noted. Biomass consumed daily was calculated for each experiment as $(e^{\mu_0} - e^{k}) \times P_0$, where μ_0 is gross algal growth coefficient, k is net algal growth coefficient and P_0 is 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 C:chl ratio of 60). Percentage of standing stock removed daily was calculated as $[(e^{\mu_0} - e^{k})/e^{\mu_0}] \times 100$

Source	Study site	Date	Initial chl conc. (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)	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)	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
Burkill 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 & 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 & Hollibaugh (1998)	Tomales Bay (San Fransisco Bay)	Jul 94	7.30	0.24	1.61	96	21
		Jul 94	5.30	1.14	5.54	333	68
McManus & 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 et al. (1998) (mean values for 3 salinity ranges)	Mundaka, Spain (<25‰)	Aug 90	62.00	0.54	128.13	7688	42
	(25–31‰)	Aug 90	6.37	0.80	21.43	1286	55
	(>31‰)	Aug 90	4.83	0.94	31.06	1864	61
Gallegos (1989)	Rhode River, MD (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

given that C:chl ratio typically increases with increasing nutrient limitation.

Collectively, these studies indicate that nano- and microzooplankton control the fate of much of the primary production in eutrophic estuarine ecosystems. This result is presumably a consequence of the dominance of these phytoplankton communities by pico- or nanophytoplankton during much of the growing season. However, microbial grazing during periods when microplanktonic phytoplankton (i.e., >20 µm) dominated the phytoplankton assemblages was also evident (Fig. 3B). Presumably, phagotrophic dinoflagellates, tintinnids and non-loricate ciliates accounted for this activity. High estimates of microbial grazing in

these ecosystems implies that phagotrophic protists constitute an important trophic link for carbon transfer in the pelagic food webs of these environments.

During this study, the appearance of *Aureococcus 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 growth and grazing by phagotrophic protists (Lonsdale et al. 1996, Mehran 1996). Nonetheless, multiple regression analyses between *A. anophagefferens* and grazing mortality in our study did not reveal any obvious impact of this alga on grazing activity. The phytoplankton mortality rate during peak *A. anophagefferens* population abundance on 30 June in WNB was 0.57 d^{-1}. Moreover, we have successfully cultured several species of protozoa that are capable of consuming and growing on *A. anophagefferens* in the laboratory (Caron & Bossoinneault-Cellineri unpubl. data). We speculate that the contradictory nature of these past and present findings may relate to the absolute (or relative) abundance of *A. anophagefferens* in the water, aspects of the physiological state of *A. anophagefferens* or the presence of microbial consumers that can feed on the alga.

Bacterivory

Bacterial mortality due to protistan 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. Several caveats also exist regarding the applicability and accuracy of this method. Feeding selectivity by grazers, resulting in over- or underestimation of bacterivore grazing activity, can occur. Heat-killing and labeling cells may affect acceptability of prey to some protists based on chemical cues (Landry et al. 1991), although evidence indicates that many phagotrophic protists select and digest fluorescently labeled prey similarly to natural prey (Sherr et al. 1988, Dolan & Simek 1997). Grazing may be overestimated if bacterivores prefer larger cells (González et al. 1990). For this reason we prepared FLB from late stationary phase cultures to generate cells that more closely resembled the size of natural bacteria from these estuarine ecosystems.

Bacterivore populations exerted strong grazing pressure on bacterioplankton in both WNB and CH. Grazing rates were higher in CH (overall average of 0.93 d^{-1}) than in WNB (overall average of 0.57 d^{-1}), indicating that turnover rates of the bacteria as a consequence of bacterivory were more rapid in the less eutrophic environment. We speculate that the faster turnover rate of the bacterial assemblage in CH may be related to assessibility of these cells (WNB had a much higher load of particulate material that might facilitate bacterial attachment or provide refuge from grazing). Alternatively, our rates do not include losses due to viral lysis, and this process may be more important in WNB because of higher bacterial abundances in that bay.

Bacterial abundances showed low amplitude, 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 2 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 µg 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 as in CH. Nevertheless, differences between estimates of carbon flow via bacterivory in the 2 bays differed by a factor of only ~1.4 due to higher average mortality rates in CH (i.e., more rapid turnover of the bacterial assemblage).

It is important to note, however, that this comparison assumes a constant bacterial cell carbon content of 20 fg C for both ecosystems. While this number facilitates calculation of carbon from cell number, it is undoubtedly inappropriate to some degree for either environment. Cell volume was not determined in this study but microscopical examinations indicated that cell sizes of the bacteria in WNB were quite large at some times. Thus, 1.4 should be considered a minimal difference in carbon flow via bacterivory between the 2 environments.

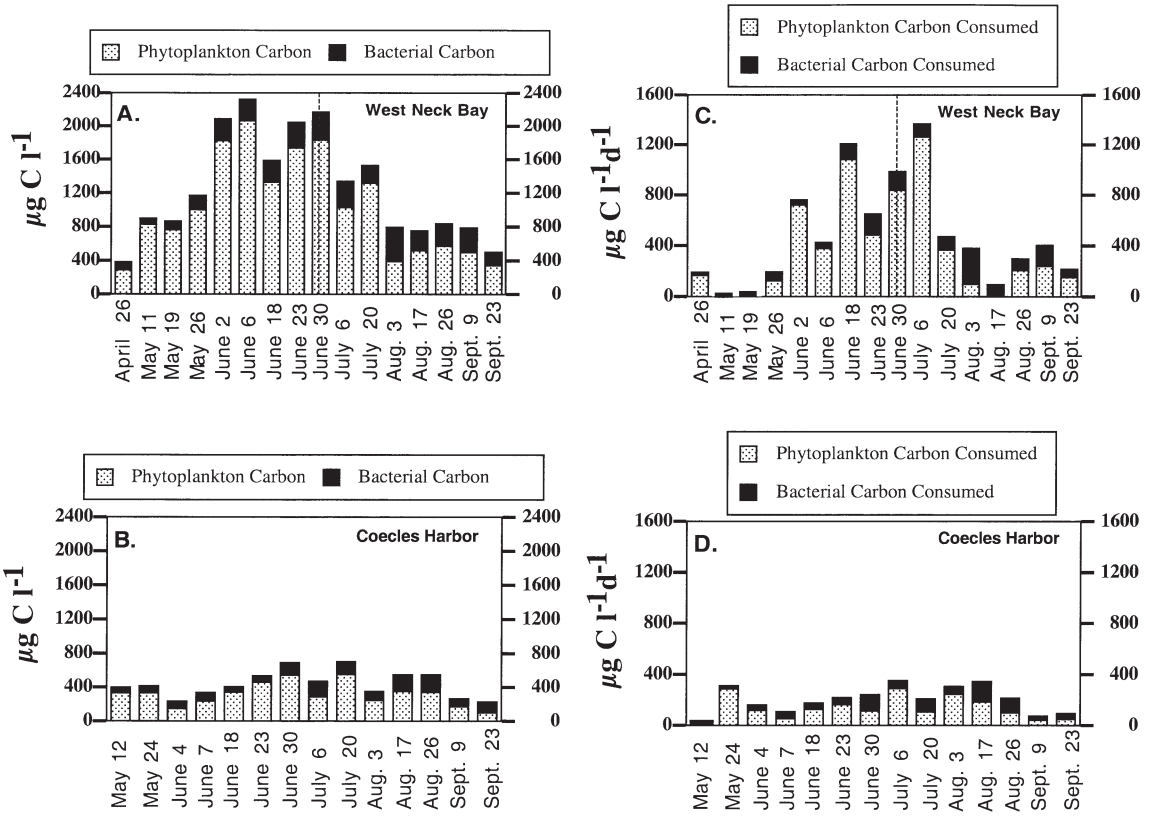

Fig. 9. Phytoplankton and bacterial carbon standing stocks on the dates when herbivory and bacterivory experiments were conducted in (A) West Neck Bay and (B) Coecles Harbor during 1998. Phytoplankton carbon was estimated from chlorophyll (chl) concentration and assuming a C:chl ratio of 60. Bacterial carbon was estimated from cell number and assuming a carbon content of 20 fg C cell^{-1}. Daily removal rates of phytoplankton and bacterial carbon are shown for the dates when herbivory and bacterivory experiments were conducted in (C) West Neck Bay and (D) Coecles Harbor. Removal rates are based on standing stocks (A,B) and mortality rates (Tables 1 to 4). The vertical dashed line in (A) and (C) indicates the sampling date with the highest observed abundance of *Aureococcus anophagefferens*

Carbon flow

Ratios of bacterial biomass to phytoplankton biomass in WNB and CH 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 (Fig. 9A,B). Ratios of bacterial carbon to phytoplankton carbon ranged from 0.08 to 1.01 in WNB and 0.19 to 1.28 in CH. The ratio of bacterial carbon to phytoplankton carbon increased slightly during the latter half of the summer in both bays, indicating a slight shift toward a more heterotrophic pelagic food web during the mid- to late summer.

Calculations of carbon consumption (herbivory and bacterivory) revealed that bacterivory constituted an important aspect of carbon flux through the microbial community in both bays (Fig. 9C,D). Carbon flux in WNB ranged from undetectable (i.e., slopes of regressions not significantly different from 0) to 1260 µg C l^{-1} d^{-1} due to grazing on phytoplankton (overall average of 471), while carbon flux due to bacterivory ranged from 24 to 281 µg C l^{-1} d^{-1} (overall average of 99). Thus, average carbon flux due to bacterivory in this bay was approximately 21% 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 (Fig. 9C). Carbon flux in CH ranged from undetectable to 291 µg C l^{-1} d^{-1} (overall average of 146) due to herbivory and from 17 to 162 µg C l^{-1} d^{-1} (overall average of 68) due to bacterivory. Average carbon flux due to bacterivory was approximately 47% of the flux due to herbivory, indicating that bacterivory was proportionally more important to energy flow in this bay relative to WNB (Fig. 9D). These comparisons are, of course, dependent on the specific conversion factors used to obtain phytoplankton carbon from chlorophyll concentration (C:chl = 60) and bacterial carbon from cell number (20 fg cell^{-1}). Nevertheless, our concurrent measure-

ments of microbial herbivory and bacterivory provide a means of directly comparing carbon flow via the consumption of phytoplankton and bacteria. A direct comparison of these trophic activities has rarely been reported.

In summary, carbon flux due to herbivory and bacterivory by microbial consumers was high in both the WNB and CH ecosystems in the present study. Our experimental results demonstrated that substantial percentages of phytoplankton and bacterial standing stocks 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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