Limnol. Oceanogr., 48(1), 2003, 238–248

Microzooplankton grazing on *Prorocentrum minimum* and *Karlodinium micrum* in Chesapeake Bay

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Abstract

Potential grazing rates on the bloom forming dinoflagellates *Prorocentrum minimum* and *Karlodinium micrum* were measured in Chesapeake Bay during summer (2000). Cultured *P. minimum* and *K. micrum* cells were fluorescently labeled with 5-chloromethylfluoroscein diacetate and introduced to <200 μm filtered water. Microzooplankton grazing was assessed by measuring the disappearance of labeled prey over time. Grazing on *P. minimum* and *K. micrum* was highest between lower oligohaline to midmesohaline regions of the open bay, where microzooplankton biomass was greatest. In June, grazing rates on *P. minimum* were high at all stations, apparently because of naked (NHD) and thecate heterotrophic dinoflagellates. In July, grazing pressure on *P. minimum* was related to aloricate oligotrich and choreotrich biomass ($r^2 = 0.5107$, $p = 0.030$), whereas *g* for *K. micrum* was correlated with *Oxyrrhis marina* ($r^2 = 0.7217$, $p = 0.004$) abundance. In August, grazing on *P. minimum* was correlated with abundance of the NHD *Gyrodinium* spp. ($r^2 = 0.6621$, $p = 0.006$) and *Polykrikos kofoidii* ($r^2 = 0.6617$, $p = 0.010$) abundance. Microzooplankton biomass peaked within the mesohaline regions of Chesapeake Bay during all months, and these assemblages were dominated by heterotrophic dinoflagellates. On the basis of these results, microzooplankton grazing is an important loss to *P. minimum* and *K. micrum* populations in Chesapeake Bay.

Photosynthetic dinoflagellates are an important component of plankton assemblages in Chesapeake Bay, forming sporadic blooms throughout the year and contributing substantially to the overall summer primary productivity maximum (Malone et al. 1996; Sellner and Fonda Umani 1999). *Prorocentrum minimum* (Pavillard) Schiller [=*P. mariae lebouriae* (Parke and Ballintine) Faust] and *Karlodinium micrum* (Leadbeater and Dodge) J. Larsen *comb. nov.* [=*Gyrodinium galatheanum* (Braarud) Taylor], are widespread within the Chesapeake Bay system. Both species form annual blooms, under a broad range of salinity and temperature conditions. Red tides of *P. minimum* occur on an annual basis in the upper and middle regions of Chesapeake Bay, with cell concentrations sometimes approaching 1×10^5 cells ml^{-1} (www.dnr.state.md.us). *K. micrum* can also be abundant, with concentrations reaching >1,000 cells ml^{-1} in portions of middle and upper Chesapeake Bay between May and September (Li et al. 2000). However, the role of grazing in the regulation of these blooms in Chesapeake Bay is poorly understood.

Typically, blooms of phytoplankton occur as a result of net biomass production in response to favorable conditions and an uncoupling of losses to a population (e.g., grazing or advection). However, some taxa may also benefit from grazing inhibition by production of allelopathic compounds (Smayda 1997). In Chesapeake Bay, grazing pressure on some dinoflagellate blooms appears to be minor, and much of the biomass is believed to be remineralized within the surface layer as the blooms decline (Sellner and Brownlee 1990).

In general, there appear to be two major mechanisms that dissipate dinoflagellate blooms, direct losses (i.e., grazing), and meteorological forcing. In some situations dinoflagellate blooms have been reported to decline as a result of intense grazing pressure from microzooplankton (e.g., Nakamura et al. 1995; Matsuyama et al. 1999) or mesozooplankton (e.g., Watras et al. 1985). However, the persistence of many dinoflagellate blooms suggests that some species may be undesirable to grazers or have chemical or physical defensive capabilities (e.g., toxins or extrusosomes). Several studies have shown that some grazers avoid dinoflagellate blooms (Fiedler 1982) and that interaction with certain dinoflagellate species may be inhibitory or lethal to microzooplankton (Hansen 1995) and mesozooplankton (Delgado and Alcaraz 1999) predators.

In the present study, cells of *P. minimum* and *K. micrum* were labeled with a vital stain and added to natural planktonic assemblages (<200 μm) from Chesapeake Bay. By monitoring the disappearance rates of labeled cells, potential grazing pressure on both species were assessed and compared with biomass and abundance distributions of microzooplankton.

Materials and methods

Culture and staining of dinoflagellates—Cultures of *P. minimum* (strain PM-1) and *K. micrum* (strain GE or CCMP 1974) were obtained from Dr. A. Li and were originally isolated from the Choptank River, Maryland (spring 1995) and the mesohaline region of the Chesapeake Bay (May 1995),

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Acknowledgments

This work was supported by an ECOHAB NOAA grant NA86OP0493. An NSF Research Experience for Undergraduates grant supported the contributions of M.R. We thank Daniel E. Gustafson Jr. and Tim Deering for technical assistance, D. Wayne Coats for shipboard space during summer research cruises, and two anonymous reviewers for their suggestions to improve this manuscript. UMCES contribution 3590.

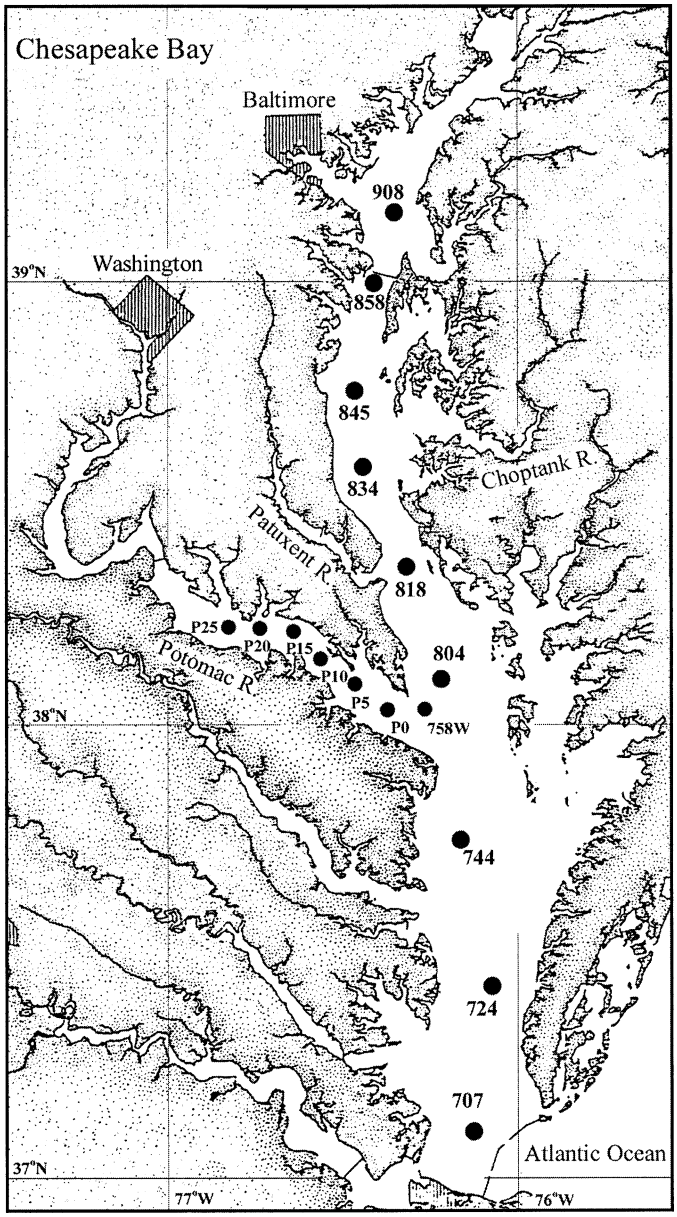

Fig. 1. Chesapeake Bay and Potomac River stations during summer 2000 cruises.

respectively. Cultures were maintained at 20°C in 15 psu, f/2-Si medium (Guillard 1975), with a light regimen of 12 h light : 12 h dark and a photon irradiance between 100 and 150 μmol m^{-2} s^{-1}.

Dinoflagellate cells were stained with the vital green fluorescent stain 5-chloromethylfluoroscein diacetate (CMFDA; Molecular Probes) using the protocol of Li et al. (1996). Stained cells appeared to behave normally and showed no indication of cytotoxic effects (Li et al. 1996; Kamiyama 2000; Stoecker et al. 2000). Furthermore, Kamiyama (2000) found no difference in grazing by tintinnid ciliates when offered stained or unstained *Heterocapsa cirularisquama* cells. Cultures were stained for 2 h with a final concentration of 3 μmol L^{-1} CMFDA and used for grazing experiments within 2 h. Grazing rates on *K. micrum* in June were not determined because of the poor staining of *K. micrum* cells during this cruise.

Table 1. Location and salinity of sampling sites where grazing experiments were conducted. NR, not recorded.

Station	Location	Salinity June	Salinity July	Salinity August
Main Bay Transect				
908	39°07.86′N, 076°20.04′W	4.7	7.0	8.6
858	38°58.15′N, 076°22.96′W	5.7	8.8	10.0
845	38°45.17′N, 076°25.96′W	9.5	10.1	12.3
834	38°33.96′N, 076°26.01′W	10.5	10.6	12.7
818	38°18.01′N, 076°17.04′W	11.7	11.9	13.2
804	38°03.93′N, 076°13.04′W	12.7	13.7	13.9
744	37°43.36′N, 076°11.80′W	15.2	15.3	14.9
724	37°24.06′N, 076°05.13′W	17.6	19.3	18.8
707	37°06.83′N, 076°07.05′W	23.1	22.6	21.2
Potomac River Transect				
758W	37°58.06′N, 076°16.81′W	—	12.9	—
P0	37°59.37′N, 076°17.70′W	—	12.9	—
P5	38°01.88′N, 076°23.25′W	—	12.5	—
P10	38°04.28′N, 076°28.63′W	—	11.7	—
P15	NR	—	10.7	—
P20	NR	—	10.5	—
P25	NR	—	9.1	—

Enumeration of dinoflagellates stained with CMFDA—To obtain cell concentrations of stained dinoflagellates, 3-ml fixed samples (gluteraldehyde 1% final concentration) were filtered (<15 mm Hg pressure) onto 2 μm pore size, black polycarbonate membrane filters and then mounted onto glass slides with immersion oil (Resolve) under a cover slip. Slides were counted with a standard Nikon Labophont epifluorescence microscope (filter sets B-2E/C; exciter filter 465–495 nm, dichromatic beam splitter 505 nm, barrier filter 515–555 nm). Slides made from grazing experiments were kept frozen (−20°C) until enumerated by epifluorescence microscopy, using a Nikon Eclipse standard microscope (Nikon filter set EF-4 B-2A; exciter filter 450–490 nm, dichromatic beam splitter 500 nm, barrier filter 515 nm) at ×400 magnification. With this filter set, *P. minimum* and *K. micrum* stained with CMFDA appeared bright green, with some red from chlorophyll fluorescence.

Determination of potential grazing on P. minimum *and* K. micrum—Grazing experiments were conducted at stations within the main stem of Chesapeake Bay and in the estuarine regions of the Potomac River (Fig. 1, Table 1). Samples were collected during monthly cruises between 19 and 23 June, July, and August 2000 on the RV *Cape Henlopen.* At each station, vertical profiles of salinity, temperature, and fluorescence were measured with a contuctivity-temperature-depth (CTD) probe. Surface samples for experiments were taken during daytime by bucket. The water was passed through a 200 μm mesh and stored in 1-liter polycarbonate bottles within coolers at ambient temperature before the start of experiments (within 2 h of collection). For each station, two

separate experiments were conducted with CMFDA-labeled *P. minimum* and *K. micrum*, and each experiment had two treatments that were applied in duplicate. The treatments consisted of incubating labeled culture in each of the following: water passed through a <200 μm screen and <1.2 μm water that was filtered through a GF/C glass fiber filter. Experiments were conducted in 250-ml narrow-mouthed polycarbonate bottles with 200 ml of water from the <200 or <1.2 μm treatments. Each treatment for both prey species had two replicate bottles. Experiment bottles were kept dark within coolers and indoors, to maintain water temperature close to in situ levels. At $t = 0$ stained *P. minimum* or *K. micrum* cells were added to a final concentration of ~500 cells ml^{-1}. After gently mixing the contents of each bottle by inverting them several times, a 20-ml aliquot was immediately removed and fixed with gluteraldehyde (final concentration, 1%). A final time point was taken after 5 h, and a 20-ml aliquot was again fixed with gluteraldehyde.

Apparent growth rates of the stained dinoflagellates in the <200 (K) and <1.2 μm (μ) treatments were calculated as $\mu = (\ln C_{t1} - \ln C_{t0}) \times (t_1 - t_0)^{-1}$ and $K = (\ln C'_{t1} - \ln C'_{t0}) \times (t_1 - t_0)^{-1}$, where C and C' are the concentrations of cells in the <1.2 and <200 μm treatments, respectively, at the end point (t1) and beginning of the experiment (t0) (Frost 1972). Three milliliters of fixed sample were filtered onto a 2.0 μm membrane (described above), to estimate apparent growth. To check whether grazing rates were significant, the slopes of the <200 and <1.2 μm treatments were compared for each station using a one-way analysis of variance (ANOVA) test. An estimate of the grazing coefficient, g, for each replicate was calculated by the following equation: $g = \mu - K$, using the average μ for the <1.2 μm treatment.

Enumeration of photosynthetic dinoflagellates—Cell abundance of photosynthetic dinoflagellates from various stations were enumerated as described above, using slides with 2–4 ml of filtered sample, from the $t = 0$ time points. The total number of dinoflagellate cells within two transects at ×400 were enumerated, providing an accurate assessment of only the most abundant taxa. Between 50 and 300 cells were counted, depending on their natural abundance. Because cells were counted on membrane filters using epifluorescence microscopy, identification beyond the level of genera was not possible for most dinoflagellates, except in the case of very common and distinct species.

Enumeration of microzooplankton and observations of grazers from experimental samples—One replicate from the $t = 5$ time point of the grazing experiments was used to enumerate microzooplankton at each station and to identify grazers of stained *P. minimum* and *K. micrum.* These samples were kept in the dark and at 4°C until analyzed. To count microzooplankton, 10 ml of fixed sample was settled in a Utermöhl chamber in the dark and examined using fluorescence microscopy, with a Nikon Eclipse inverted microscope (Nikon filter set B-2E/C; exciter filter 465–495 nm, dichromatic beam splitter 505 nm, barrier filter 515–555 nm). Four transects at ×200 magnification were counted for each slide. Between 50 and 650 total cells were counted on each slide, depending on the density of microzooplankton cells. The dimensions of microzooplankton taxa ($N = 10$ individuals for each species per sample, when possible) were measured with an ocular micrometer and converted to biovolume, using geometric formulae described by Edler (1979) and Hillebrand et al. (1999). Carbon contents were estimated from biovolume calculations using empirically derived estimates of 0.146 pg C μm^{-3} for dinoflagellates, 0.201 pg C μm^{-3} for aloricate ciliates, and 0.185 pg C μm^{-3} for loricate ciliates (Menden-Deuer and Lessard 2000).

Results

Environmental conditions and abundance of photosynthetic dinoflagellates—Salinity conditions are summarized in Table 1. Surface water temperature within the bay varied little throughout the study (23.4–25.9°C). Discrete chlorophyll samples were not taken during this study, but chlorophyll fluorescence was followed in situ by CTD (Table 2). Chlorophyll data taken from the Chesapeake Bay Program website (http://www.chesapeakebay.net) from stations within our sampling region during summer 2000 provide an estimate of chlorophyll levels: 5.3–22.6, 4.8–13.0, and 5.8–24.1 μg chlorophyll *a* L^{-1}, during June, July, and August, respectively.

Maximum abundances of photosynthetic dinoflagellates along the main bay axis were found within the oligohaline and upper mesohaline bay (Sta. 834–908) (Table 2). Values within the main bay ranged between <10 and 1,000 cells ml^{-1} and on average were highest in August. Small dinoflagellate cells dominated the upper bay in June, whereas larger species were found at Sta. 908 in July and August (data not shown). *K. micrum* and *P. minimum* were abundant (≥100 cells ml^{-1}) within the main bay in June and August but at relatively few stations.

In July, a small dinoflagellate bloom was encountered at Sta. 758W, with >2,000 cells ml^{-1}, composed mostly of *Gymnodinium* spp., a *Heterocapsa*-like species, and *Scrippsiella* spp. (Table 3). This bloom extended into the mouth of the Potomac River (Sta. PO), with levels of photosynthetic dinoflagellates reaching 3,500 cells ml^{-1}.

Surface microzooplankton abundance and distribution—Biomass of heterotrophic and mixotrophic ciliates and heterotrophic dinoflagellates along the main bay axis was highly variable (5–80 and 6–200 μg C L^{-1}, respectively) among stations and between months (Fig. 2). Both average abundance and biomass of heterotrophic ciliates and dinoflagellates increased over the summer, with maximum values found during the August cruise. Heterotrophic dinoflagellates comprised the majority of microzooplankton biomass throughout much of the mesohaline portion of Chesapeake Bay, whereas ciliates were generally greater in the polyhaline and euryhaline regions (Fig. 2). During the study, ciliate abundance was positively correlated to chlorophyll fluorescence in June (Pearson, $r = 0.885$, $p = 0.046$, $n = 5$) and August (Pearson, $r = 0.920$, $p = 0.0004$, $n = 9$), whereas no significant correlations were found for heterotrophic dinoflagellate abundance.

Aloricate oligotrich (Oligotrichida) and choreotrich (Cho-

Table 2. Chlorophyll fluorescence and photosynthetic dinoflagellate abundance for Chesapeake Bay surface stations. Chl Fluor, chlorophyll fluorescence (relative units); PD, total photosynthetic dinoflagellate abundance (cells ml^{-1}); % <25 μm, percentage of PD <25 μm. *Abundance (cells ml^{-1}) of common dinoflagellate taxa: Asan, *Akashiwo sanguinea*; Gym <30, *Gymnodinium* spp. (<30 μm); Gym >30, *Gymnodinium* spp. (> 30 μm); Gon/Scrip, *Gonyaulax*/*Scrippsiella* spp.; Het, *Heterocapsa* spp.; Kmic, *Karlodinium micrum*; Pmin, *Prorocentrum minimum*; Pmic, *P. micains.*

Station	Chl Fluor	PD	% <25 μm	Asan	Gym <30	Gym >30	Gon/Scrip	Het	Kmic	Pmin	Pmic
June											
908	1.3	425	>99	0*	0	0	0	237.9	0	187.2	0
858	2.1	—	—	—	—	—	—	—	—	—	—
845	2.9	987	96	0	25.4	0	5.9	592.8	362.7	0	0
834	1.6	—	—	—	—	—	—	—	—	—	—
818	1.0	178	93	0	0	0	7.8	107.3	50.7	7.8	0
804	1.2	—	—	—	—	—	—	—	—	—	—
744	1.0	86	77	0	0	0	0	58.5	3.9	3.9	2
724	0.5	—	—	—	—	—	—	—	—	—	—
707	0.5	22	18	0	0	0	0	0	3.9	0	2
July											
908	1.7	279	37	0	11.7	0	179.4	11.7	41	2	0
858	1.4	516	16	0	12.7	0	411.5	34.1	2	5.9	0
845	0.9	184	54	<1	2	0	109.2	30.2	15.6	3.9	0
834	1.0	251	56	4.9	24.4	2	34.1	57.5	3.9	9.8	2
818	0.6	121	93	4.9	<1	<1	17.6	54.6	0	2	<1
804	0.6	49	64	<1	2	<1	11.7	11.7	2	3.9	<1
744	0.7	264	>99	6.8	11.7	3.9	60.5	148.2	5.9	3.9	3.9
724	0.5	101	71	0	0	14.6	30.2	28.3	0	7.8	14.6
707	0.5	75	70	0	11.7	4.9	1.95	10.7	0	15.6	4.9
August											
908	0.9	702	10	<1	0	0	643.5	24.4	32.5	0	0
858	1.4	323	97	2.9	<1	0	56.9	48.8	211.3	0	0
845	2.8	437	>99	3.9	0	0	9.8	273	130	6.5	0
834	2.4	923	>99	27	2	0	89.4	726.4	48.8	9.8	0
818	1.1	166	98	7.8	<1	0	14.6	34.1	29.3	71.5	0
804	0.9	109	73	10.7	11.7	0	1.6	60.1	0	6.5	<1
744	0.9	195	65	<1	17.6	0	8.1	69.9	0	35.8	18.5
724	0.6	338	82	0	43.9	0	11.4	68.3	32.5	130	5.9
707	0.6	250	19	0	91.7	0	9.8	6.5	0	32.5	12.7

reotrichida) ciliates of the class Spirotrichea made up the greatest proportion of ciliate biomass on average throughout this study and were highest during the August cruise (Table 4). Tintinnid ciliates (Choreotrichida) also contributed substantially to overall ciliate biomass (Table 4), although large tintinnid cells were always rare. In August, the rise in tintinnid biomass at Sta. 707 near the mouth of the bay (Table 4) was due in part to presence of *Favella* sp. Other Spirotrichs, such as *Euplotes,* and haptorid ciliates (Litostomatea), such as *Mesodinium* spp., were also found to be abundant in mesohaline regions of the bay (Table 4).

Heterotrophic dinoflagellate biomass always peaked within the mesohaline region of Chesapeake Bay (Fig. 2) and was dominated by species within the genera, *Gyrodinium, Oxyrrhis,* and *Polykrikos* (Table 4). Small thecate heterotrophic dinoflagellates (THD) were the dominant component of dinoflagellate biomass throughout much of the bay in June (<1–57 μg C L^{-1}). In July and August, the majority of het-

Table 3. Chlorophyll fluorescence and photosynthetic dinoflagellate abundance for the July Potomac River surface stations. Abbreviations as in Table 2.

Station	Chl Fluor	PD	% <25 μm	Asan	Gym <30	Gym >30	Gon/Scrip	Het	Kmic	Pmin	Pmic
758W	4.8	2,005	36	29.3*	762.5	25.4	321.8	651	0	74.1	11.7
P0	1.7	3,474	35	226.2	561.6	54.6	1,287	1,151	0	62.4	23.4
P5	1.2	1,209	45	54.6	298.4	9.8	237.9	347.1	46.8	152.1	17.6
P10	1.1	561	22	42.9	107.3	11.7	218.4	93.6	3.9	23.4	13.7
P15	—	342	38	26.3	15.6	9.8	119.9	86.8	21.5	21.5	0.98
P20	—	372	36	15.6	33.2	27.3	143.3	95.6	21.5	11.7	1.95
P25	—	473	65	0	23.4	21.5	85.8	122.9	167.8	19.5	0

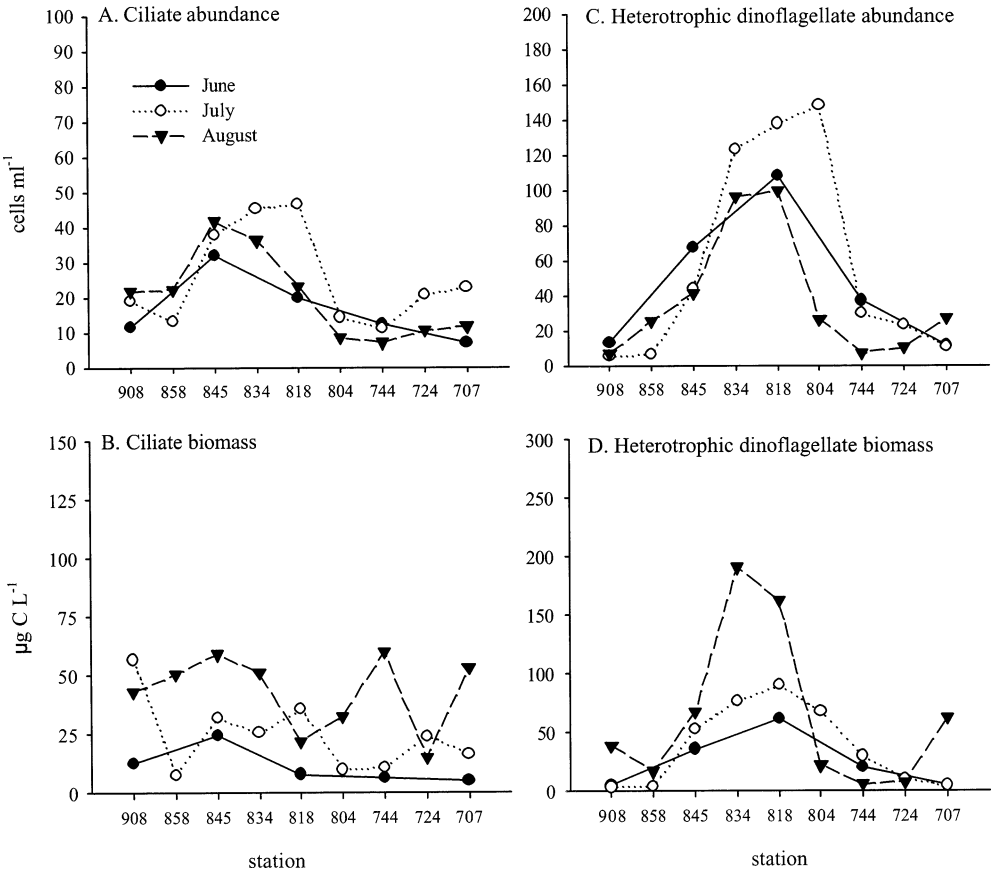

Fig. 2. Biomass and abundance of heterotrophic dinoflagellates and ciliates along the main transect of Chesapeake Bay. (A) Ciliate abundance, (B) ciliate biomass, (C) dinoflagellate abundance, and (D) dinoflagellate biomass.

erotrophic dinoflagellate diversity, abundance, and biomass were composed of nonthecate genera. In July, *Oxyrrhis marina* was abundant in the lower mesohaline bay, with cell densities >100 ml^{-1} (Table 4), whereas in August a *Gyrodinium* sp. (similar to *G. spirale*) was the most abundant heterotrophic dinoflagellate in the bay (5–67 cells ml^{-1}) (Table 4). However, high heterotrophic dinoflagellate biomass levels within the middle bay in August were largely due to *Polykrikos kofoidii* (Table 4).

High levels of heterotrophic dinoflagellates and ciliates (140 and 350 μg C L^{-1}, respectively) were encountered within the dinoflagellate bloom near the mouth of the Potomac River in July (Fig. 3). This region had a relatively high abundance of the large heterotrophic dinoflagellate, *P. kofoidii,* and an unidentified hypotrich ciliate (13 and 40 cells ml^{-1}, respectively) (Fig. 3, Table 4).

Grazing pressure on labeled P. minimum *and* K. micrum—Overall the mean *g* across all stations was higher for *P. minimum* in the main bay than for *K. micrum;* however, the relationship was not significant (NS, ANOVA, $\alpha = 0.05$) (Fig. 4). In July, potential grazing on *P. minimum* was nearly double that for *K. micrum* (NS), whereas in August the average main bay grazing coefficients were similar for both dinoflagellates. Average grazing on *K. micrum* throughout the main bay increased in August over July ($p = 0.022$, ANOVA), whereas grazing on *P. minimum* remained about the same during all 3 months.

Green fluorescent inclusions (GFI) were observed in various microzooplankton taxa from samples collected at experiment end points ($t = 5$ h), including *Gyrodinium* spp., *O. marina, P. kofoidii,* large (generally >2 × 10^4 μm^3) aloricate oligotrich and choreotrich ciliates, and the haptorid ciliate, *Mesodinium pulex.* Taxa that were observed to only ingest labeled *P. minimum* included an unidentified THD and mixotrophic *K. micrum,* whereas the tintinnid *Eutintinnis* sp. only ingested *K. micrum.* Copepod nauplii and rotifers were the only metazoan microzooplankton observed within treatment samples and were rarely found. When present, nauplii did appear to ingest labeled prey, whereas grazing by rotifers was uncertain because of their high background green fluorescence when fixed with gluteraldehyde. No relationships were found between overall abundance or biomass of microzooplankton and *g* for either *P. minimum* or *K. micrum* (Fig. 5A,B); however, significant regression coefficients (r^2) were found between *g* and abundance or biomass of specific grazer types during July and August (Fig. 5C,D, Table 5).

Discussion

Growth rates of *P. minimum* and *K. micrum* under in situ conditions were not measured; however, conservative com-

Table 4. Microzooplankton abundance (cells ml^{-1}) and biomass ($\mu g\ L^{-1}$) for Chesapeake Bay and Potomac River surface stations. Numbers in parentheses are biomass.

Station	Aloricate Olig./Chor.	Tintinnids	Other ciliates	*Gyrodinium* spp.	*Oxyrrhis marina*	*Polykrikos* sp.	THD
Bay stations							
June							
908	8.9 (8.3)	2 (4.1)	0.6 (0.3)	5.4 (2.7)	0.3 (0.2)	UD	0.9 (0.3)
845	22 (15)	1.4 (6.7)	8 (2.7)	8.1 (3.9)	0.4 (0.2)	UD	52 (30)
818	14 (2.5)	1.4 (3.1)	4.9 (2.5)	14 (6.8)	UD	UD	99 (58)
744	9.5 (4.8)	2.9 (1.7)	UD	UD	UD	UD	23 (13)
707	5.2 (5)	2 (0.2)	UD	UD	UD	UD	7.2 (4.2)
July							
908	18 (56)	UD	0.9 (0.8)	0.9 (0.7)	1.3 (0.5)	UD	UD
858	8.9 (21)	1.7 (0.5)	0.3 (0.7)	UD	UD	UD	UD
845	4.9 (21)	4 (2.1)	6.9 (7.5)	16 (13)	20 (7.5)	1.2 (27)	1.2 (2.4)
834	9.1 (27)	UD	40 (24)	25 (21)	63 (23)	0.6 (13)	UD
818	4.3 (1.3)	0.6 (0.2)	37 (33)	18 (15)	91 (34)	1.2 (27)	UD
804	3.2 (7.8)	UD	7.8 (7)	2.3 (1.9)	122 (45)	0.3 (6.7)	UD
744	2.6 (39)	0.9 (4.2)	3.5 (3.5)	2.6 (2.2)	16 (5.8)	0.9 (20)	UD
724	2 (5.2)	12 (12)	2.6 (2.6)	UD	13 (4.7)	UD	0.4 (0.9)
707	1.7 (0.7)	12 (8.4)	3.9 (3.9)	UD	5.6 (2.1)	UD	UD
August							
908	10 (12)	2.3 (13)	9.5 (18)	5.2 (4.5)	0.6 (0.2)	1.4 (34)	28 (ND)
858	8.9 (21)	2 (12)	12 (18)	15 (13)	11 (4.1)	UD	4.3 (ND)
845	4.9 (21)	1.7 (5.7)	35 (32)	23 (20)	17 (6.5)	1.7 (41)	1.2 (ND)
834	9.1 (27)	0.4 (0.1)	27 (24)	66 (58)	25 (9.5)	5.2 (123)	1.3 (ND)
818	4.3 (1.3)	UD	19 (21)	67 (58)	29 (11)	3.9 (93)	0.4 (ND)
804	3.2 (7.8)	5.2 (24)	0.3 (0.5)	24 (21)	2.9 (1.1)	UD	0.6 (ND)
744	2.6 (39)	4.6 (21)	UD	6.3 (5.5)	1.2 (0.4)	UD	0.6 (ND)
724	2 (5.2)	6.3 (5.4)	2.3 (4.4)	8.4 (7.3)	2 (0.8)	UD	1.4 (ND)
707	1.7 (0.7)	6.6 (59)	3.5 (5.3)	21 (21)	2 (0.8)	UD	0.9 (ND)
Potomac River Transect							
July							
758W	4.3 (5.1)	0.3 (1.4)	59 (124)	2.6 (2.2)	42 (16)	14 (313)	UD
PR0	6.1 (3.1)	1.3 (4.4)	43 (52)	8.7 (6.5)	33 (11)	8.2 (190)	7.4 (3.9)
PR5	5.2 (7.8)	1.3 (1.6)	21 (16)	9.1 (6.9)	48 (16)	3.9 (90)	16.6 (7.5)
PR10	14 (7.6)	3.5 (10)	16 (6.3)	11 (8.5)	28 (9.3)	1.7 (40)	11.7 (5)
PR15	4.3 (1.7)	13 (40)	14 (5.5)	10 (7.8)	19 (6.5)	UD	15.2 (6.4)
PR20	4.3 (10)	5.6 (15)	9.1 (2.4)	8.7 (6.5)	16 (5.3)	UD	13.4 (5.8)
PR25	12 (30)	0.4 (12)	14 (3.1)	22 (16)	23 (7.8)	UD	9.5 (4.8)

Olig., oligotrich; Chor., choreotrich; UD, undetected; ND = not determined.

parisons may be made between literature values of maximum growth rates (μ_{max}) and potential grazing rates found herein. Grazing coefficients in the main stem of Chesapeake Bay were $>\mu_{max}$ for *P. minimum* (1.38 d^{-1}; Furnas 1982) 57% of the time, whereas g was $>\mu_{max}$ for *K. micrum* (0.94 d^{-1}; Li et al. 1999) 50% of the time. Potential grazing pressure on *P. minimum* decreased as summer progressed within the main bay. Conversely, the number of stations where grazing coefficients for *K. micrum* were greater than the potential μ_{max} increased between July and August (22% and 78%). These data suggest that the net growth of these photosynthetic dinoflagellates may be limited in many bay regions because of high potential grazing rates. The highest observed grazing coefficient for *P. minimum* during our study was in June, at Sta. 908. This peak in grazing corresponded to the maximum observed abundance of *P. minimum* (~200 cells ml^{-1}) during the study. It is possible that grazing pressure measured at this station was due to the presence of a well-developed community of grazers acclimated to feeding on *P. minimum.*

It is likely that the variability observed in grazing coefficients during this study is attributable to the taxonomic composition of grazer communities at each station and chemical and/or physical characteristics of the prey cells. *P. minimum* has been shown to be a poor food source for the tintinnid *Favella ehrenbergii* and is avoided by the ciliate in cultures (Stoecker et al. 1981). *K. micrum* has been shown to have lipid-based toxins that are hemolytic to fish erythrocytes and cause death in fish larvae (Deeds et al. 2002); however, there are no reports on whether such toxins in *K. micrum* make them undesirable prey to protistian grazers. The strain of *K. micrum* used in this study has been found to produce low to intermediate toxin levels compared with other *K. micrum* isolates and with samples collected during

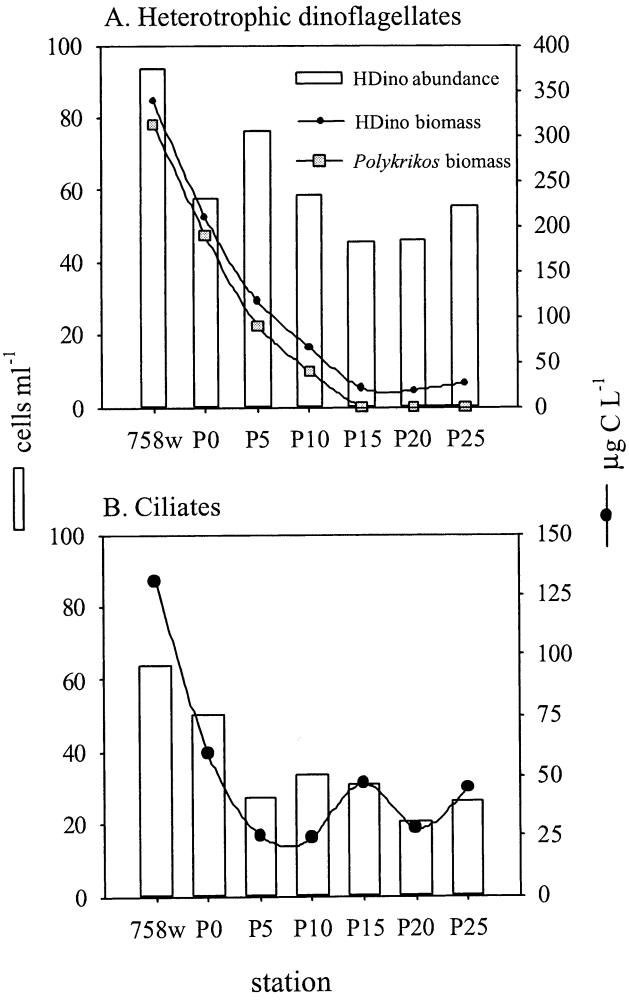

Fig. 3. Abundance and biomass of microzooplankton on the surface water of the Potomac River. (A) Total heterotrophic dinoflagellates and *Polykrikos kofoidii* and (B) total ciliates.

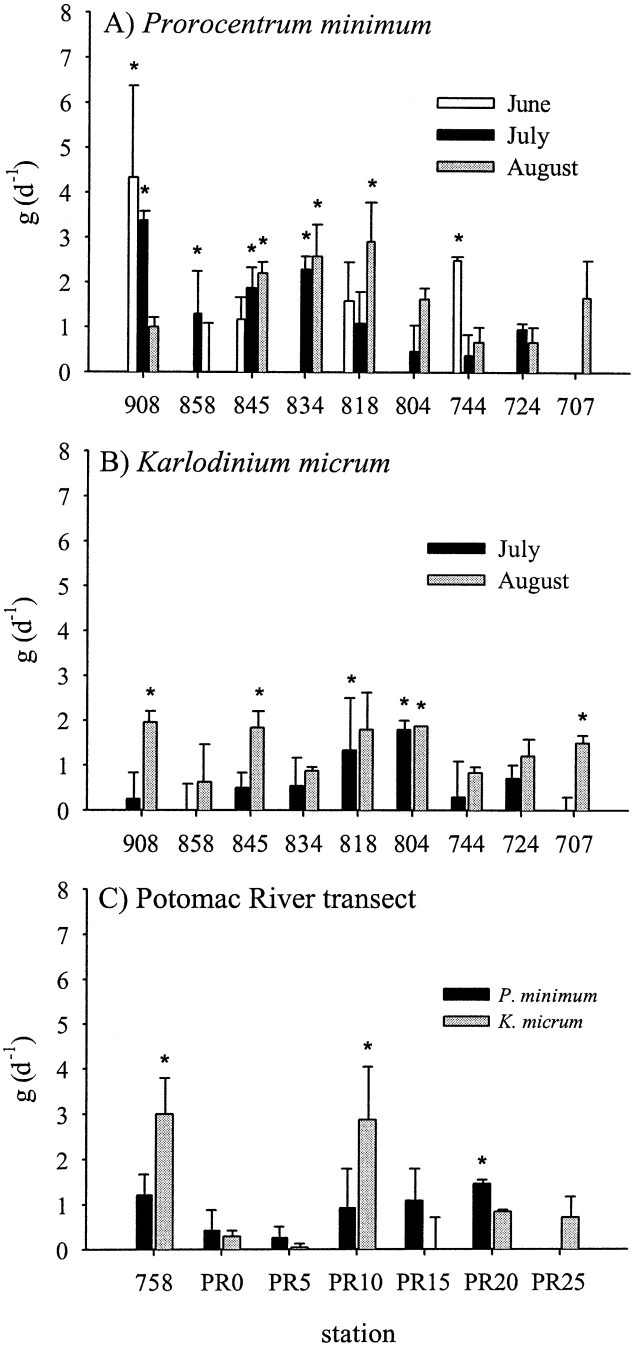

Fig. 4. Potential grazing rates on (A) *Prorocentrum minimum* and (B) *Karlodinium micrum* in Chesapeake Bay and (C) Potomac River estuary. Mean ± SD. *$p < 0.05$, slope of <200 μm versus <1.2 μm (GF/C) treatment (ANOVA).

fish kills in which high concentrations of *K. micrum* were present (Deeds et al. 2002; Kempton et al. 2002; Deeds and Place, pers. comm.). A closely related dinoflagellate, *G. aureolum*, has been shown to be toxic to *F. ehrenbergii* at high concentrations (Hansen 1995). Chronic cytotoxic responses that result in growth inhibition may be difficult to measure in short-term grazing studies. During this study, most microzooplankton grazers were observed to ingest *P. minimum* and *K. micrum* to different degrees. In general, large aloricate ciliates and *Gyrodinium* spp. ingested *P. minimum* more than did *K. micrum*, whereas *Oxyrrhis marina* were more frequently observed with ingested *K. micrum*. Although both dinoflagellates are similar in cell size, *P. minimum* is thecate and *K. micrum* is not. To better understand prey selection of microzooplankton, the effect of physical characteristics and production of toxic metabolites among photosynthetic dinoflagellates deserves further investigation.

Grazers of P. minimum *and* K. micrum—Our data on microzooplankton abundance and biomass are to be taken with some caution, because they are unreplicated estimations. Furthermore, the use of gluteraldehyde as a fixative may have underestimated the abundance and biomass of total and aloricate ciliates during this study by as much as 46% and 31%, respectively (Leakey et al. 1994). Overall abundance or biomass of microzooplankton in Chesapeake Bay is apparently a poor indicator for accessing species-specific grazing of dinoflagellate prey. This result is not surprising, because grazing by some microzooplankton on dinoflagellate prey is known to be selective (e.g., Stoecker et al. 1981).

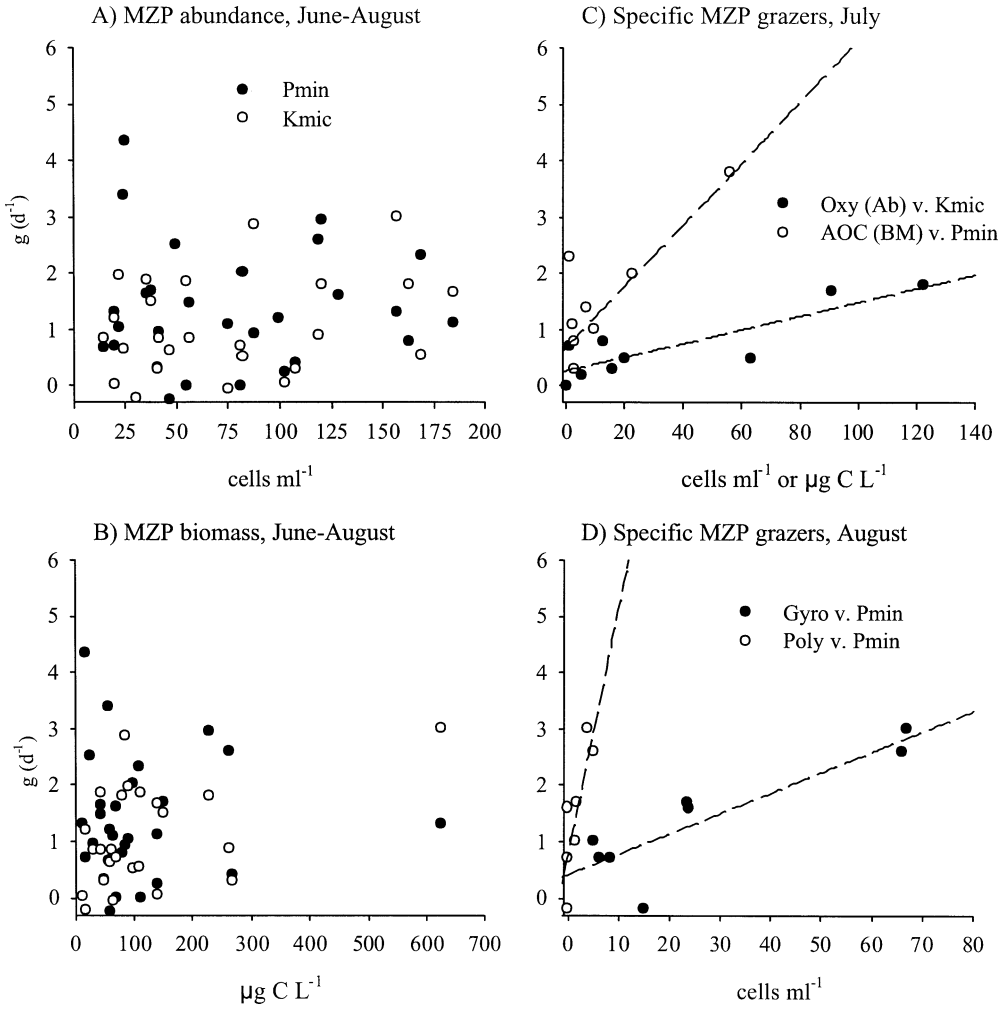

Fig. 5. Comparison of abundance and biomass of total microzooplankton (MZP) and specific MZP classes to grazing coefficients (*g*) on *Prorocentrum minimum* and *Karlodinium micrum* in Chesapeake Bay. Total MZP abundance (A) and biomass (B) versus all *g* values for *P. minimum* and *K. micrum*, June–August. Specific MZP grazer classes versus *g* of *K. micrum* or *P. minimum* in (C) July and (D) August. Pmin, *P. minimum;* Kmic, *K. micrum;* Oxy, *Oxyrrhis marina;* Ab, abundance; AOC, aloricate oligotrichs and choreotrichs; BM, biomass; Gyro, *Gyrodinium* spp.; and Poly, *Polykrikos* sp. Regression line indicates a significant relationship; see Table 5 for r^2 and *p* values of specific comparisons.

During this study, nonthecate heterotrophic dinoflagellates (NHD) were found to be abundant in July and August and frequently observed with fluorescent inclusions of labeled prey. There have been numerous reports of >20 μm *Gyrodinium* species attaining high cell densities and being important grazers during blooms of microphytoplankton in various regions (e.g., Hansen 1991; Archer at al. 1996; Tiselius and Kuylenstierna 1996). However, most reports of abundant *Gyrodinium* species have been made during periods of high diatom abundance (e.g., Tiselius and Kuylenstierna 1996), whereas fewer observations have been made during dinoflagellate blooms. Nakamura et al. (1995) reported high densities of *G. dominans* and *G. spirale* during a red tide of *Gymnodinium mikimotoi* in the Seto Sea, Japan. In the present study, heterotrophic *Gyrodinium* spp. (~30 μm) frequently ingested CMFDA-labeled *P. minimum*, and to a lesser extent *K. micrum*, and thus may be important grazers of some photosynthetic dinoflagellates in Chesapeake Bay. Other observations of red tides have documented the grazing potential of large NHD, such as *Noctiluca* or *Polykrikos*, and have implicated these genera in the cessation of blooms (Holmes et al. 1967; Matsuyama et al. 1999). Because of their small size, *P. minimum* and *K. micrum* are probably not important prey items for *Polykrikos* spp. (Jeong et al. 2001), and few GFI were observed within *Polykrikos* cells during this study. *O. marina* was abundant in this study during the July sampling period in mesohaline waters and is considered to be a common heterotrophic dinoflagellate in estuarine systems (Steidinger and Tangen 1996). *O. marina* were frequently observed in July to have GFI of labeled *K. micrum. O. marina* has been reported to feed on various nanoflagellates in culture (e.g., Barlow et al. 1989) and the heterotrophic dinoflagellate *Pfiesteria piscicida* in field experiments (Stoecker et al. 2000). THD were only abundant during the June sampling period, and although GFI were observed in many cells, their feeding mechanism was un-

Table 5. Linear regression (model 1) analysis of grazer groups versus grazing coefficients (g) in Chesapeake Bay and the Potomac River. Values are regression coefficients (r^2). PM, *Prorocentrum minimum*; KM, *Karlodinium micrum*; NHD, naked heterotrophic dinoflagellates; THD, thecate heterotrophic dinoflagellates; AOC, aloricate oligotrichs and choreotrichs; and HHC, heterotrophic haptorid ciliates. Significance is indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.005$.

	June Bay	July Bay		July Potomac		August Bay	
Grazer type	PM ($F_{1,3}$)	PM ($F_{1,7}$)	KM ($F_{1,7}$)	PM ($F_{1,3}$)	KM ($F_{1,4}$)	PM ($F_{1,7}$)	KM ($F_{1,7}$)
Heterotrophic dinoflagellates							
NHD (abundance)	0.4531	0.0006	0.6199**	0.1785	0.0823	0.640**	0.1187
Oxyrrhis marina (abundance)	ND	0.0044	0.7217***	0.2711	0.0005	0.4860*	0.0929
Gyrodinium spp. (abundance)	ND	0.1404	0.0689	0.0018	0.2842	0.6621**	0.1352
Polykrikos (abundance)	ND	0.0023	0.0992	0.1240	0.6787*	0.6617**	0.0046
THD (abundance)	0.0048	ND	ND	0.0804	0.0006	ND	ND
Ciliates							
AOC (abundance)	0.0130	0.2764	0.0128	0.1079	0.0624	0.0070	0.4532
AOC (biomass)	0.0122	0.5107*	0.0062	0.3846	0.0116	0.0609	0.2594
Tintinnids (abundance)	0.0409	0.2830	0.1505	0.0080	0.1127	0.1907	0.0146
Tintinnids (biomass)	0.1829	0.3022	0.1021	0.0005	0.1165	0.0152	0.0210
HHC (abundance)	0.0055	0.0165	0.0134	0.2329	0.0006	0.3612	0.0010

ND, not determined.

certain. During July and August, THD were rare in the bay and therefore do not appear to be important grazers of photosynthetic dinoflagellates in Chesapeake Bay during these months.

Throughout most of this study, choreotrich and oligotrich ciliates that appeared large enough to ingest *P. minimum* and *K. micrum* were rare. When large (40–100 μm) aloricate ciliates from these groups were detectable in the oligohaline and upper mesohaline stations in June and July, grazing coefficients were highest. Large aloricate oligotrichs and choreotrichs were observed with ingested fluorescently labeled prey more frequently than any other ciliate group (data not shown). Macrophagous (consumers of nanoplankton-sized or larger prey) ciliates were the dominant class of ciliates during this study and have previously been shown to account for ~73% of total ciliate biomass in Chesapeake Bay (Dolan 1991). Numerous studies have illustrated that ciliates have a greater clearance potential per cell volume than do heterotrophic or mixotrophic dinoflagellates (e.g., Jakobsen and Hansen 1997). Large planktonic tintinnid and oligotrich ciliates have ingestion and clearance rates that are 10 to >100 times greater than those of predatory dinoflagellates (e.g., Jeong et al. 1999). A large (5.6×10^5 μm^3) species of the oligotrich genera *Strombidinopsis* has been shown to have a ingestion rate of 267 ng C predator^{-1} d^{-1} and a clearance rate of 110 μl preditor^{-1} h^{-1} when offered *P. minimum* (Jeong et al. 1999). With such high grazing potential, it is not surprising that high grazing coefficients for *P. minimum* were observed during this study when large oligotrichs were present. *K. micrum*, however, had low grazing coefficients at these stations and was observed to be ingested by large oligotrichs less frequently. By applying a conservative clearance rate (0.03 ml ciliate^{-1} h^{-1}) estimated from rates previously determined for oligotrich and choreotrich grazers in the Chesapeake Bay region (Stoecker et al. 2000), an estimated grazing impact (EGI), synonymous to a potential g, can be calculated. In June grazing rates were high at Sta. 908, and the EGI (2.15 d^{-1}) was too low to explain observed g by microzooplankton grazing alone. However, in July, grazing at Sta. 908 was also high, as were levels of large (70–85 μm) oligotrichs (5.9 ml^{-1}), and the EGI (5.9 d^{-1}) was greater the than observed g. Throughout the mesohaline region during all months, heterotrophic dinoflagellate abundance was high, and, despite low estimated clearance rates (0.0005 μl grazer^{-1} h^{-1}), typical for dinoflagellates, the EGI by heterotrophic dinoflagellates alone could explain most of the observed grazing.

The potential role of microzooplankton grazing on dinoflagellate blooms in Chesapeake Bay—During summer months primary production in Chesapeake Bay reaches an annual maximum, whereas biomass levels are lower than the spring diatom dominated blooms (Boynton et al. 1982; Malone et al. 1988, 1996). This seasonal uncoupling of chlorophyll levels with rates of photosynthesis per unit of chlorophyll suggests that grazing is more important in controlling phytoplankton growth during summer months (Sellner and Kachur 1987; Malone et al. 1996). However, dinoflagellate blooms periodically occur throughout summer months in Chesapeake Bay, as observed during this study within the Potomac River estuary. Although stations within the bloom had high levels of microzooplankton biomass, grazing pressure on labeled photosynthetic dinoflagellates was low. This may have been due to feeding preferences of the grazer community or the ratio of labeled to free-living dinoflagellates. Although the dominant heterotrophic dinoflagellate within this bloom, *Polykrikos* sp., is known to consume large photosynthetic dinoflagellates, taxa representing most of the ciliate biomass (i.e., hypotrichs and *Didinium* sp.) were probably not directly consuming the bloom. It is possible that much of the ciliate production within the bloom was the result of enhanced microbial loop production.

During this study photosynthetic dinoflagellates were frequently abundant throughout the bay, especially in upper

mesohaline regions. The mesohaline region is enriched with nutrients from riverine flow and during summer receives high fluxes of recycled ammonium (NH_4) from benthic sediments (Malone et al. 1988). In all months during this study, a trend of decreasing abundance of photosynthetic dinoflagellates was observed in the mesohaline region, between Sta. 845 and 818. This decline was especially dramatic in June and August at Sta. 818, near the mouth to the Patuxent River. This region of decline corresponded to the peak in heterotrophic dinoflagellate biomass, high grazing coefficients on labeled *P. minimum* and *K. micrum*, and a decline in overall chlorophyll fluorescence during all months. These observations suggest that, within this region, photosynthetic and heterotrophic production are more closely coupled than in the upper mesohaline region during the summer. This decline in autotrophic biomass in the mesohaline and southern Chesapeake Bay has been observed previously (McManus and Ederington-Cantrell 1992). The observed rise in heterotrophic dinoflagellate biomass in lower mesohaline Chesapeake Bay may act to limit the accumulation of photosynthetic biomass within the open bay in this region.

The role of heterotrophic dinoflagellates in the microbial food web of Chesapeake Bay is perhaps underappreciated. Coats and Revelante (1999) previously noted that protozooplankton taxa, other than ciliates, have received little attention in Chesapeake Bay. Prior to this, few studies have sought to achieve qualitative or quantitative assessments of heterotrophic dinoflagellates in Chesapeake Bay. Our observations illustrate that heterotrophic dinoflagellates are an important component of microzooplankton in Chesapeake Bay and that some species can be important grazers of *P. minimum* and *K. micrum.*

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Received: 8 May 2002
Accepted: 9 September 2002
Amended: 26 September 2002