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"Windows of opportunity" for dinoflagellate blooms: Reduced microzooplankton net growth coupled to eutrophication

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ABSTRACT

Links between eutrophication, plankton community structure, microzooplankton grazing and dinoflagellate abundance were investigated in two tributaries of the Chesapeake Bay, the Choptank and Patuxent Rivers (MD, USA). Sampling and experiments were conducted during the spring of consecutive dry (below average freshwater flow) and wet (above average freshwater flow) years. During the wet year (2003), dissolved inorganic nitrogen, phytoplankton, and copepod biomass, but not microzooplankton abundance, were greater than in the dry year. In 2003, but not 2002, small cell size photosynthetic dinoflagellates were abundant and blooms occurred in both rivers. Average potential microzooplankton grazing pressure on small dinoflagellates was spatially and temporally variable, but was not significantly different between years. Our data suggest that the variability in microzooplankton grazing pressure provided "windows of opportunity" for net growth of dinoflagellates in response to nutrient loading. The lack of net population growth of micrograzers in response to increases in dinoflagellate prey allowed dinoflagellate blooms to reach relatively high densities, however grazing also appeared to be important in limitation or demise of some blooms. We hypothesize that uncoupling of micrograzer–prey dynamics was partly due to strong top-down control by copepods of microzooplankton in the proportionately more eutrophic year, and perhaps also due to inhibition of microzooplankton grazing/growth once dinoflagellate densities are high.

1. Introduction

Nutrient enhanced eutrophication of estuaries and coastal waters due to sewage discharges, fertilizer applications, atmospheric deposition and changes in land use (Fisher et al., 2006) is thought to be linked to the increased frequency, intensity and duration of harmful algal blooms in estuaries and coastal waters (Anderson et al., 2002). Elevated nutrients are usually a necessary precondition for high biomass blooms, but loss factors also need to be considered. Blooms are only possible when "windows" or "loopholes" in grazing exist and algal population growth exceeds losses due to grazing (Stoecker et al., 2000; Irigoien et al., 2005). Nutrient enhanced eutrophication can cause changes in trophic structure that reduce total grazing pressure on selected groups or size classes of phytoplankton (Vadstein et al., 2004; Reaugh et al., 2007).

Trophic cascades are well documented in freshwater, but less well documented in estuarine and marine waters (Verity and Smetacek, 1996; Stibor et al., 2004; Vadstein et al., 2004). Small cell size bloom-forming dinoflagellates are very susceptible to microzooplankton grazing (Johnson et al., 2003; Calbet et al., 2003). Changes in trophic structure resulting in tight top-down control of microzooplankton, decreasing their grazing impact or numerical response to increases in prey populations, could create "windows of low grazing pressure" (Stoecker and Gustafson, 2002; Gobler et al., 2002; Buskey et al., 2003; Stoecker et al., 2000; Irigoien et al., 2005).

Both microzooplankton (defined here as <200 μm fraction) and mesozooplankton (0.2–20 mm size range) are important grazers on phytoplankton in estuaries and coastal waters, but the microzooplankton community grazing coefficient usually greatly exceeds the community grazing coefficient of the copepods on small dinoflagellates (<25 μm cell size) in estuarine and coastal waters (Stoecker and Gustafson, 2002; Calbet et al., 2003; Roman et al., 2006). High, but very spatially and temporally variable,

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microzooplankton community grazing coefficients on the small dinoflagellates *Karlodinium veneficum* (formerly *K. micrum*, *Gyrodinium galatheanum*), *Prorocentrum minimum*, and *Pfiesteria piscicida* have been measured in Chesapeake Bay and its estuaries, with potential grazing coefficients often equal to or exceeding the maximum growth coefficients of dinoflagellates (Stoecker et al., 2000; Stoecker and Gustafson, 2002; Johnson et al., 2003). The microzooplankton assemblage can remove a large fraction (sometimes 100%) of the standing stock daily. Heterotrophic dinoflagellates, and "oligotrichous" ciliates are usually the most important microzooplankton grazers of small photosynthetic dinoflagellates although rotifers and copepod nauplii can also be important (Sellner et al., 1991; Merrell and Stoecker, 1998; Stoecker et al., 2000; Calbet et al., 2003; Johnson et al., 2003). In contrast to copepods, which have generation times on the order of weeks to months, protistan microzooplankters have generation times on the order of hours to days, thus microzooplankton and their prey populations are usually tightly coupled (reviewed in Strom, 2002; Calbet and Landry, 2004).

In the Chesapeake Bay and many other estuaries, nutrient delivery (dissolved inorganic nitrogen, DIN), phytoplankton biomass and zooplankton populations are linked to freshwater flow (Cloern et al., 1983; Harding and Perry, 1997; Kimmerer, 2002; Kimmel and Roman, 2004; Roman et al., 2005). Reaugh et al. (2007) investigated the links between freshwater flow and community structure in two tributaries of the Chesapeake Bay (Choptank River and Patuxent River) during the spring of consecutive dry (2002, below average freshwater flow), wet (2003, above average freshwater flow) and average freshwater flow years. The biomass of phytoplankton and of copepods, but not microzooplankton, was significantly higher in the wet, eutrophic year. Because of the high copepod biomass, the estimated copepod community grazing impact on microzooplankton was often approximately equal to the estimated growth rate of microzooplankton in the wet year. These results suggest that under eutrophic conditions, top-down control of microzooplankton by copepods caused a trophic cascade which partially released small cell size phytoplankton from control by grazing (Reaugh et al., 2007).

Tributaries are important sites for the initiation of dinoflagellate blooms in the Chesapeake Bay region (Sellner et al., 1991; Li et al., 2000). In the Choptank and Patuxent Rivers, blooms of small cell size (<25 μm) photosynthetic dinoflagellates are common. *Heterocapsa rotundatum* (formerly *Katodinium rotundatum*) and *Heterocapsa triquetra* commonly form blooms in late winter–early spring and *P. minimum* commonly forms blooms in April–May (Sellner et al., 1991; Glibert et al., 2001; Tango et al., 2005; Lacouture et al., 2006). Recently, blooms of the toxic dinoflagellate, *K. veneficum* (formerly *K. micrum*, *G. galatheanum*) have occurred in late spring, summer and fall (Li et al., 2000; Goshorn et al., 2002).

Herein we address how differences observed by Reaugh et al. (2007) in trophic state and trophic structure in the Choptank and Patuxent Rivers during consecutive dry (2002) and wet (2003) years may have influenced top-down regulation of dinoflagellate blooms. We present data from both years on dissolved inorganic nutrients, photosynthetic dinoflagellate and micrograzer abundance, and potential microzooplankton grazing on two harmful algal bloom species, the dinoflagellates *P. minimum* and *K. veneficum*.

2. Materials and methods

2.1. Sampling and sample analysis

Sampling was conducted March, April and May in 2002 and 2003 on the Choptank and Patuxent Rivers, which are eastern and western shore tributaries of the Chesapeake Bay in Maryland, USA. Three locations (termed lower, middle and upper) were chosen for biological sampling on each river (Tables 1 and 2) because of their positions within distinct hydrological regions; the lower stations in the wind-driven circulation region, the middle stations in the two-layer gravitational circulation region, and the upper stations near the limit of salt intrusion in the upper estuary (Reaugh et al., 2007).

At each station, casts for conductivity, temperature and fluorescence were made using a CTD (Sea-Bird Electronics SBE SEALOG-

Table 1
Sampling in the Choptank River, spring of dry (2002) and wet (2003) years at the lower (L), middle (M) and upper stations (U).

Month	Station	*N*	Water temperature (°C)	Salinity	$NO_3^- + NO_2^-$ (μM)	NH_4^+ (μM)	PO_4^{-2} (μM)
2002							
Mar	L	3	7.3–8.4	16.0–17.1	1.4 (0.48)	0.8 (0.05)	0.08 (0.057)
	M	3	8.1–9.0	15.0–15.9	2.0 (2.77)	1.6 (2.01)	0.10 (0.010)
	U	3	8.9–9.7	13.0–13.5	2.7 (3.38)	4.9 (6.19)	0.26 (0.177)
Apr	L	4	9.6–16.2	13.8–16.4	2.9 (1.31)	1.1 (0.69)	0.22 (0.276)
	M	4	11.4–19.3	14.6–15.3	1.4 (1.52)	1.4 (1.30)	0.20 (0.028)
	U	4	11.6–20.9	11.0–12.8	18.6 (2.47)	5.7 (2.80)	0.12 (0.049)
May	L	4	16.3–21.0	9.1–14.4	1.3 (SL)	3.37 (SL)	0.01 (SL)
	M	4	18.1–22.5	12.7–13.9	1.0 (1.26)	1.2 (1.00)	0.01 (0.000)
	U	4	18.6–23.2	10.4–11.5	7.1 (5.42)	0.8 (0.49)	0.12 (0.163)
2003							
Mar	L	1	Nd[a]	Nd[a]	9.5	1.2	0.06
	M	2	6.5[a]	12.2[a]	32.8 (7.21)	1.2 (0.77)	0.16 (0.150)
	U	2	7.1[a]	8.4[a]	96.1 (36.63)	5.8 (6.99)	0.16 (0.035)
Apr	L	4	7.4–14.1	9.3–11.3	32.5 (6.00)	2.2 (0.26)	0.08 (0.015)
	M	4	9.0–14.7	8.6–11.2	34.1 (20.50)	11.4 (14.70)	0.26 (0.403)
	U	4	10.6–16.4	3.9–6.4	77.0 (48.67)	23.6 (12.41)	0.73 (0.440)
May	L	3	15.6–16.9	10.0–10.8	11.8 (7.81)	1.5 (0.96)	0.08 (0.120)
	M	5	16.6–19.4	7.9–8.9	17.4 (6.92)	3.0 (4.17)	0.14 (0.250)
	U	4	10.6–19.4	3.9–5.7	54.8 (19.70)	5.5 (4.23)	0.39 (0.464)

Choptank station coordinates are L = 38°39.12N, 76°18.36W; M = 38°36.14N, 76°06.89W; U = 38°36.66N, 75°58.94W. *N* is number of samples per month. Observed range of mixed layer water temperature and salinity for each station and month is presented. Inorganic nutrients, mean (S.D.). Nd = no data. SL = sample lost.

[a] Data from one cruise not available due to equipment failure.