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Spatial and temporal variability in factors affecting mesozooplankton dynamics in Chesapeake Bay: Evidence from biomass size spectra

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Abstract

Zooplankton biomass in Chesapeake Bay was estimated with an optical plankton counter mounted on a towed body (Scanfish). Normalized zooplankton biomass size spectra were calculated for three Bay regions three times a year across 4 yr. Zooplankton biomass was maximum during April, and the zooplankton size at peak biomass was large compared with July and October. The variability of the normalized zooplankton biomass size spectrum in April was related to freshwater input, a proxy for nutrient loading, lower temperatures, and salinities. The normalized zooplankton biomass size spectrum showed little interannual variability in July, and the curvature of the biomass size spectrum was reduced. The lack of variability in July normalized zooplankton biomass size spectra was related to gelatinous zooplankton and fish predators. Normalized zooplankton biomass size spectra in October were similar to April and had the lowest total zooplankton biomass. October normalized zooplankton biomass size spectra were affected by gelatinous predators in the upper Chesapeake Bay and by fish predators in the middle to lower Chesapeake Bay. Food limitation did not appear to affect normalized zooplankton biomass size spectra because measured particulate carbon concentrations were always in excess of estimated maintenance food concentrations. The ratio of phytoplankton biomass to zooplankton biomass was higher than in other aquatic systems and was consistent across the year. The zooplankton biomass–to–fish biomass ratio varied seasonally, with April samples having the highest ratios and October the lowest. The normalized zooplankton biomass size spectra in Chesapeake Bay have more negative, and a wider range of, linear regression slopes than other aquatic systems. Normalized zooplankton biomass size spectra in Chesapeake Bay were influenced by climatologically driven variation in the densities of predators and prey. The variability of the normalized zooplankton biomass size spectrum was indicative of a highly eutrophic ecosystem.

The biomass size spectrum has been used to assess the biological structure of pelagic ecosystems (Sheldon et al. 1972; Kerr and Dickie 2001). The biomass structure of the North Atlantic Ocean pelagic community was found to be flat or have a slope of zero; thus, biomass was evenly distributed from ''bacteria to whales'' (Sheldon et al. 1972). The slope estimate was later refined by normalizing the biomass size spectrum (expressing the biomass of each size class as a function of the width of the size class) and was predicted to be slightly less than −1 (Platt and Denman 1977, 1978). Subsequent research has supported this prediction (Rodriguez and Mullin 1986; Sprules and Munawar 1986; Quinones et al. 2003). The normalization of the biomass size spectrum allowed easy comparison across systems and was found to be a useful tool to assess simple, first-order system dynamics (Heath 1995) despite some disadvantages of a linear fit (Vidondo et al. 1997).

The biomass size spectrum has also been used to assess the nutrient state of pelagic ecosystems. Biomass size spectrum slopes of oligotrophic marine waters appear to be stable, whereas biomass size spectrum slopes of eutrophic systems appear to be more variable (Rodriguez and Mullin 1986; Quinones et al. 2003). The linear regression slope of biomass size spectra from the Great Lakes was found to vary with nutrient state. Eutrophic lakes had slopes more similar to −1, whereas the slope of oligotrophic lakes ranged from −1.16 to −1.14 (Sprules and Munawar 1986). An examination of biomass size spectra in seven marine and freshwater environments found that all had slight negative slopes that were not significantly different from one another (Boudreau and Dickie 1992); however, the intercepts varied considerably among systems. Boudreau and Dickie (1992) also reported the results of a fertilization experiment in Great Central Lake and reported a fivefold increase in the slope of the zooplankton biomass size spectrum; that is, it became less negative after the lake was fertilized.

The majority of biomass size spectrum studies have been

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conducted in oligotrophic lakes and open ocean gyre systems. Chesapeake Bay would be expected to have more variability in the characteristics of its biomass size spectrum because of dynamic hydrographic conditions. The aim of this study was to identify possible factors affecting the Chesapeake Bay normalized zooplankton biomass size spectrum and compare the size spectrum to spectra of other systems. Seasonal, interannual, and spatial fluctuations in zooplankton biomass have been demonstrated (Roman et al. 2005); thus, we hypothesize that the normalized zooplankton biomass size spectrum in Chesapeake Bay is highly variable. We also hypothesize that temporally and spatially variable external forcing factors, such as phytoplankton biomass, gelatinous zooplankton biovolume, and fish biomass, will influence the shape of the size spectrum through bottom-up and top-down controls. These variable, external forcing factors are related to variations in freshwater input that drive seasonal and interannual changes in biomass of phytoplankton (Harding 1994), abundance of zooplankton (Kimmel and Roman 2004), and fish community composition and biomass (Jung and Houde 2003). We expect the normalized zooplankton biomass size spectrum of the eutrophic Chesapeake Bay to have less negative linear regression slopes when compared with other systems (Sprules and Munawar 1986) and expect the ratio of prey (phytoplankton) biomass to predator (zooplankton) biomass to be elevated relative to other systems (Sprules et al. 1983).

Methods

We conducted continuous underway sampling with a towed body, the Scanfish (Geological & Marine Instrumentation), equipped with sensors for conductivity, temperature, depth, oxygen, and fluorescence and an optical plankton counter (OPC; Focal Technologies). The sampling program consisted of axial surveys along the 300-km length of Chesapeake Bay (Fig. 1) conducted in April, July, and October 1996–2000, with the exception of 1998 because of an OPC malfunction. Depth range of the Scanfish varied with sea state. In general, the Scanfish undulated from 2 m below the surface to 2 m above the bottom. Fluorescence readings were converted to chlorophyll *a* (Chl *a*) units by collecting samples for Chl *a* determination (Yentsch and Menzel 1963) and regressing the two variables. Scanfish and OPC data were recorded at a frequency of 2 Hz. The horizontal resolution of the Scanfish data was depth dependent, and we obtained approximately seven vertical profiles per kilometer.

The OPC detected and sized particles by measuring the amount of light blocked, which is proportional to the projected area of particles passing through the OPC sampling tunnel (Herman 1988). A semiempirical relationship was used to convert the amount of light blocked to the equivalent spherical diameter (ESD) for particles that are larger than 250 μm ESD (Herman 1992). Particle volume was calculated according to a spherical model with diameter = ESD. We used the following procedures to calculate particle abundance (numbers m^{-3}), biovolume concentration (mL m^{-3}), and average biomass (mg C m^{-3}) per size class. Zooplankton biovolume was converted to carbon with the relationship:

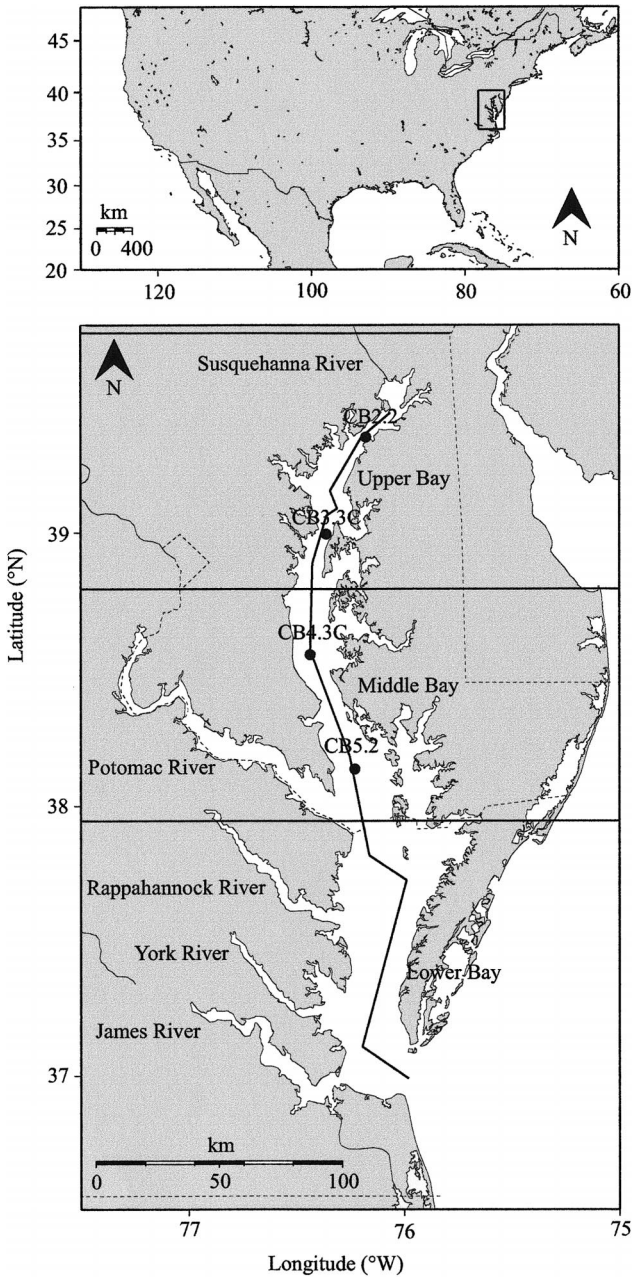

Fig. 1. Map of Chesapeake Bay. Scanfish sampling transect is shown along the axis of the Bay. Chesapeake Bay Program zooplankton monitoring stations (CB2.2, CB3.3C, CB4.3C, and CB5.2) are shown in the middle and upper Bay.

$\log DV = -1.429 + 0.808 \log C$, where DV is zooplankton biomass expressed as displacement volume (mL m^{-3}) and C is zooplankton biomass expressed as carbon (mg C m^{-3}; Wiebe et al. 1975). We calculated the velocity of water passing through the opening of the OPC sampling tunnel (2 × 7 cm) on the basis of the simultaneous rate of change of longitude, latitude, and the depth of the OPC. The flow rate (m^3 s^{-1}) of water passing through the OPC sampling tunnel was calculated on the basis of the cross-sectional area (m^2) of the OPC sampling tunnel and the velocity of water (m s^{-1}) passing through the OPC sampling tunnel. We calculat-

Table 1. Mean (SD) water column salinity, temperature (*T*), and dissolved oxygen concentration (DO) for each month, region, and year.

Month	Region	Year	Salinity	*T* (°C)	DO (mL L^{-1})
April	Upper	1996	4.86 (6.88)	9.95 (1.66)	No data
		1997	4.82 (6.66)	9.76 (0.07)	11.00 (4.84)
		1999	9.14 (3.56)	11.75 (0.14)	6.50 (1.43)
		2000	6.47 (6.64)	11.30 (0.21)	4.66 (3.95)
April	Middle	1996	12.94 (0.94)	8.62 (0.39)	6.62 (1.62)
		1997	12.15 (0.66)	9.47 (0.14)	9.46 (3.20)
		1999	15.55 (0.94)	12.20 (0.64)	7.10 (1.03)
		2000	15.46 (1.53)	11.36 (0.58)	7.27 (3.42)
April	Lower	1996	22.01 (6.43)	8.36 (0.12)	7.88 (0.72)
		1997	21.79 (6.13)	10.07 (0.06)	11.52 (1.78)
		1999	21.67 (3.26)	11.59 (0.47)	8.32 (0.63)
		2000	23.71 (4.03)	12.49 (0.81)	9.90 (1.51)
July	Upper	1996	5.89 (7.53)	24.30 (1.24)	0.64 (1.00)
		1997	8.86 (6.62)	24.81 (1.96)	3.31 (4.05)
		1999	11.01 (6.83)	26.37 (1.98)	8.05 (0.40)
		2000	8.34 (5.99)	23.77 (0.56)	5.73 (0.11)
July	Middle	1996	13.77 (0.85)	24.04 (0.51)	1.23 (1.78)
		1997	15.87 (0.88)	24.00 (0.55)	2.63 (3.97)
		1999	18.21 (1.01)	25.26 (0.55)	No data
		2000	15.50 (1.16)	24.35 (0.74)	2.46 (1.86)
July	Lower	1996	22.61 (4.59)	23.16 (2.25)	2.34 (1.55)
		1997	23.44 (3.46)	24.21 (2.15)	6.21 (3.87)
		1999	24.63 (3.53)	24.97 (1.45)	6.90 (2.87)
		2000	23.26 (3.55)	23.76 (1.20)	No data
October	Upper	1996	5.92 (4.29)	17.92 (0.88)	5.45 (1.96)
		1997	11.61 (8.00)	19.42 (1.45)	10.86 (1.52)
		1999	7.43(10.22)	19.77 (0.32)	6.38 (0.91)
		2000	10.81 (7.28)	17.05 (1.77)	5.94 (2.24)
October	Middle	1996	12.37 (1.67)	18.92 (0.81)	5.64 (1.53)
		1997	19.57 (0.44)	20.80 (0.42)	10.84 (1.31)
		1999	18.81 (0.90)	20.85 (0.42)	6.72 (0.39)
		2000	18.30 (0.33)	19.05 (0.14)	5.73 (1.59)
October	Lower	1996	21.55 (4.68)	17.96 (0.37)	6.57 (0.79)
		1997	25.04 (3.35)	18.92 (3.03)	10.60 (0.93)
		1999	24.94 (3.22)	20.58 (0.60)	7.25 (0.53)
		2000	23.44 (4.07)	18.11 (0.46)	7.31 (0.87)

ed the particle abundance and biovolume concentration by summing the number and biovolume of all particles in each size category that were detected during each sampling interval (0.5 s) and dividing by the water volume passing through the sample tunnel during each sampling interval: water volume (m^3) = flow rate ($m^3\ s^{-1}$) × sample interval (0.5 s). Zooplankton biomass (mg C m^{-3}) was averaged for each size class of particles from 250 to 2,000 μm ESD. Optical plankton counters give reasonable estimates of zooplankton abundance and biomass when compared with net-collected samples (Herman 1992; Woodd-Walker et al. 2000; Zhang et al. 2000). Zooplankton biomass estimates from OPC measurements were significantly correlated with biomass estimates from net-collected samples (Roman et al. 2005).

Zooplankton biomass estimates were used to generate normalized size spectra (Kerr and Dickie 2001). The arithmetic average zooplankton biomass for each size class (317 size classes ranging from 250 to 2,000 μm), as determined from OPC measurements, was calculated for each month and region of the Chesapeake Bay for the years 1996, 1997, 1999, and 2000. The Bay was divided into three geographic regions: upper (38.75–39.42°N), middle (37.92–38.75°N), and lower (37.08–37.92°N). The regions differ in depth, area, volume, and physiographic features. The upper Bay is shallow, has a smaller area and volume compared with the other regions, and is oligohaline. The middle Bay is deeper (because of the presence of the drowned Susquehanna River channel), broader in area and volume, and is mesohaline. The lower Bay is shallow, wider, has a larger volume than the other two regions, and is polyhaline.

The normalized biomass size spectrum was generated by taking the logarithm of zooplankton biomass divided by the difference in weight between each size class (Platt and Denman 1977, 1978) and plotting it against the logarithm of the modal weight for each size class. A quadratic regression line was fit to the data with S-PLUS statistical analysis software (Insightful). We used the quadratic regression equation $y =$

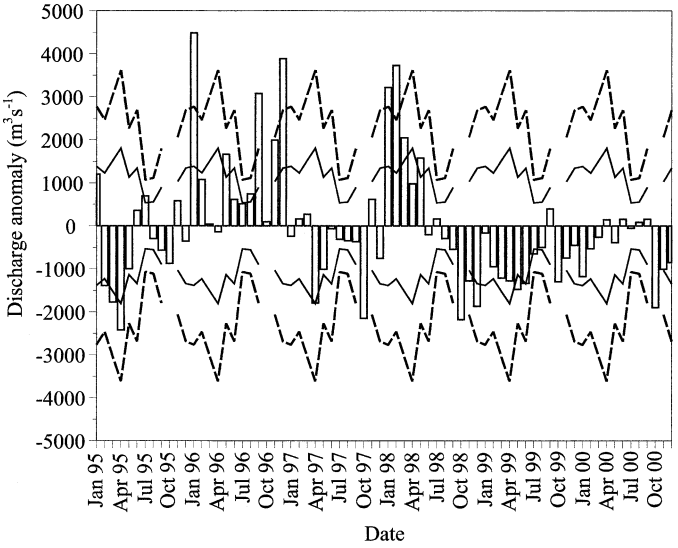

Fig. 2. Chesapeake Bay total monthly freshwater input anomalies calculated as divergence from monthly mean input 1951–2000. The solid line indicates 1 SD from the mean, and the dashed line indicates 2 SD from the mean.

$a + 0.5c(x - b)^2$, where c is the curvature of the parabola and a and b are the y- and x-coordinates of the vertex, respectively (Sprules and Goyke 1994). The regression coefficients and coefficient of determination were calculated for interannual comparisons. Zooplankton : phytoplankton biomass ratio estimates were calculated from data taken from Roman et al. (2005), and fish : zooplankton biomass ratio estimates were calculated from data taken from Jung and Houde (2003). We converted fish wet weight into carbon assuming 10% of fish wet weight consisted of carbon (Nixon et al. 1986).

Zooplankton species composition data were acquired from the Chesapeake Bay Program monitoring database (accessible at http://www.chesapeakebay.net). Species composition and size information was compiled for two stations in the upper and two stations in the middle Chesapeake Bay (Fig. 1) but was not available for the lower Chesapeake Bay because of zooplankton enumeration inconsistencies (Kimmel and Roman 2004). Gelatinous zooplankton biovolume estimates were calculated from Tucker trawl samples. A 1-m^2 Tucker trawl net with 280-μm mesh was towed for 2 min in the upper 1 m of the water column. Gelatinous zooplankton were identified to species, and biovolume was estimated with a graduated cylinder. A flowmeter (General Oceanics) was used to estimate the total amount of water passing through the net, and this value was used to estimate the abundance of gelatinous zooplankton species in the upper water column. Bay-wide estimates of phytoplankton and zooplankton biomass were acquired from Roman et al. (2005). Bay-wide estimates of fish biomass were acquired from Jung and Houde (2003). The estimates of freshwater input into the whole Bay were computed with a method developed by the U.S. Geological Survey (Bue 1968). Discharge data are available at http://md.water.usgs.gov/waterdata/. Freshwater discharge anomalies were calculated by computing the arithmetic mean monthly discharge for the period 1951–2000. Each monthly discharge estimate was subtracted from the long-term mean (1951–2000) discharge for each month to generate the anomaly.

Table 2. Normalized zooplankton biomass size spectra quadratic regression parameters for each month, region, and year. Quadratic regression equation is $y = a + 0.5c(x - b)^2$, where c is the curvature of the parabola and a and b are the y and x coordinates of the vertex, respectively.

Month	Region	Year	a	b	c	r^2
April	Upper	1996	—	—	—	—
		1997	6.21	0.75	−1.09	0.95
		1999	6.46	0.46	−1.69	0.98
		2000	6.51	0.21	−1.73	0.97
April	Middle	1996	6.63	0.18	−1.66	0.97
		1997	6.38	0.50	−1.39	0.98
		1999	6.46	0.31	−1.49	0.98
		2000	6.47	0.20	−1.64	0.98
April	Lower	1996	6.59	0.69	−2.16	0.98
		1997	6.60	0.68	−2.30	0.96
		1999	6.60	0.49	−2.45	0.98
		2000	6.40	0.36	−1.55	0.99
July	Upper	1996	6.33	0.20	−0.79	0.97
		1997	6.26	0.22	−0.88	0.96
		1999	6.31	0.11	−0.80	0.96
		2000	6.25	−0.02	−0.73	0.98
July	Middle	1996	6.53	−0.05	−1.25	0.99
		1997	6.51	−0.42	−0.84	0.98
		1999	—	—	—	—
		2000	6.81	−0.76	−0.88	0.95
July	Lower	1996	6.48	0.36	−1.80	0.98
		1997	7.07	−1.44	−0.49	0.97
		1999	6.52	−0.06	−1.16	0.97
		2000	—	—	—	—
October	Upper	1996	6.33	0.26	−1.45	0.99
		1997	6.42	−0.03	−1.07	0.97
		1999	6.49	−0.05	−1.37	0.98
		2000	6.20	0.12	−0.78	0.97
October	Middle	1996	6.95	−0.98	−0.69	0.97
		1997	6.47	0.01	−1.29	0.97
		1999	8.35	−2.62	−0.45	0.89
		2000	20.48	−18.05	−0.08	0.94
October	Lower	1996	7.69	−1.85	−0.56	0.95
		1997	6.73	−0.61	−0.69	0.86
		1999	6.73	−0.59	−0.84	0.94
		2000	6.93	−1.12	−0.62	0.97

Results

The year 1996 was wet, characterized by high freshwater input in January, above average freshwater input during July, and high freshwater discharge late in the year (Fig. 2). The magnitude of freshwater runoff into the Bay during 1996 caused salinity and temperature values to remain low during 1996 and into April of 1997, particularly in the upper and middle Bay (Table 1). Dissolved oxygen concentrations were lowest during July 1996, a period of widespread hypoxia in Chesapeake Bay (Table 1). After a brief wet period in early 1998, the Bay experienced a prolonged period of below average freshwater input (Fig. 2). The drought was most pro-

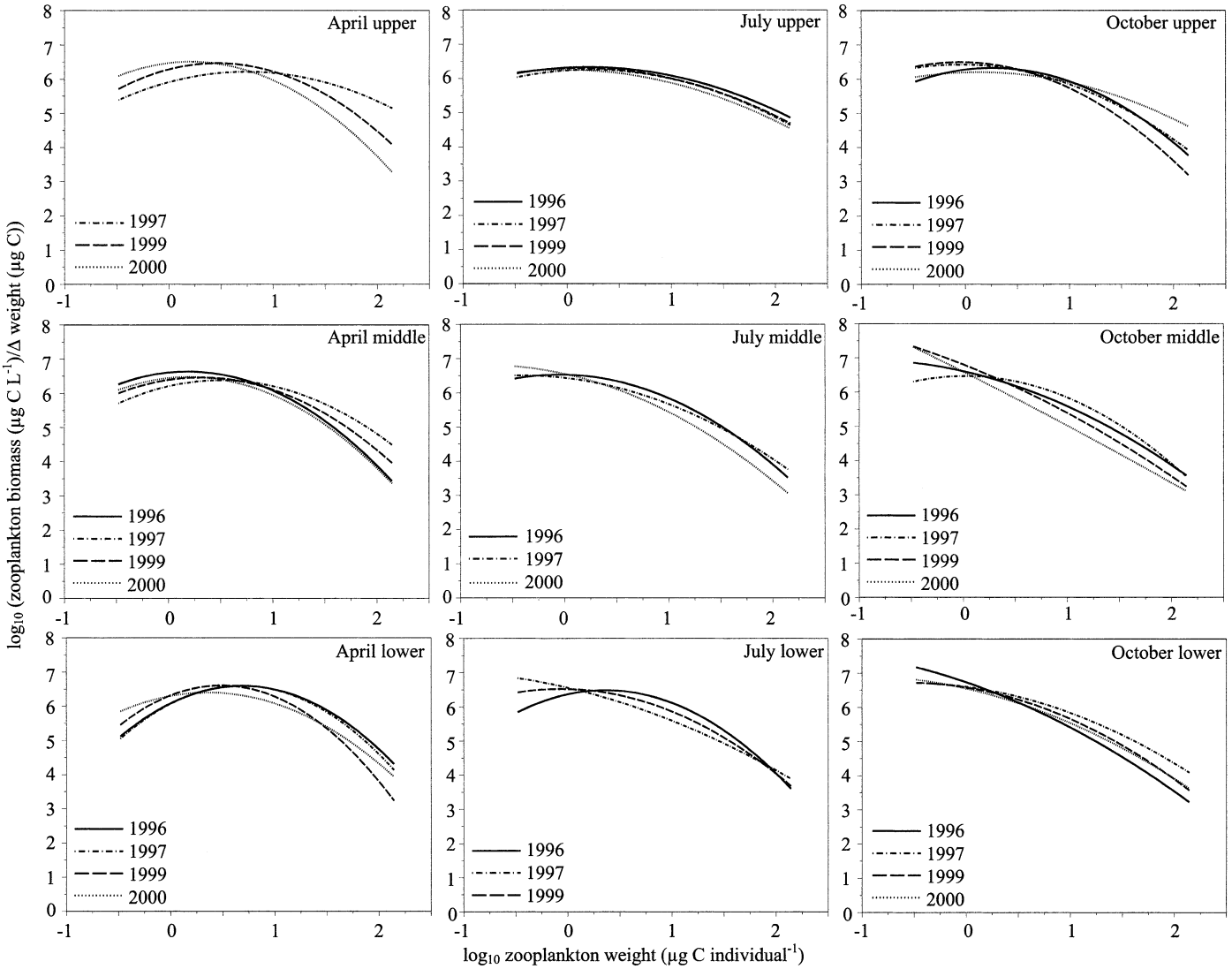

Fig. 3. April, July, and October normalized zooplankton biomass size spectra for the upper, middle, and lower Chesapeake Bay.

nounced during 1999, but below average freshwater inputs continued well into 2000. Salinity and temperature during the dry period were much higher compared with the prior low-salinity period in 1996–1997 (Table 1).

The April normalized zooplankton biomass size spectra showed variability across the entire range of size classes in Chesapeake Bay (Table 2; Fig. 3). The distribution of biomass across the size classes differed interannually, particularly in the upper and lower Chesapeake Bay (Fig. 3; Table 3). The greatest proportion of biomass was found in larger size classes during April 1997 in the upper Bay (Fig. 3). The middle Bay showed fewer interannual differences among size spectra (Fig. 3); however, the curvatures of the parabolae were variable (Table 2). Overall, a wide range of parabola curvatures (-1.09 to -2.45) were observed during April (Table 2). The *y*-coordinate vertex (*a*) showed little variability in April; however, the *x*-coordinate vertex (*b*) did vary with larger values in the upper and lower Bay (Table 2).

July size spectra showed little interannual variability during the study period (Fig. 3). The distribution of biomass across size classes was similar during July (Fig. 3; Table 3), with the exception of the middle Chesapeake Bay, in which less biomass was found in larger size classes. Parabolic curvatures were similar among the three regions (Table 2). The degree of curvature from the quadratic fits was less pronounced compared with April (Fig. 3; Table 1); thus, the biomass peak was found among smaller sized zooplankton. This can also be seen in the July values of the *x*-coordinate vertex (*b*) (Table 2). Biomass also tended to be more evenly distributed across the size classes (Fig. 3).

October size spectra were more variable than July, and the distribution of biomass appeared to be similar across the lower size classes but diverged significantly among the larger size classes (Fig. 3). The degree of curvature for October size spectra was similar in the mid and lower Bay (Table 2). Parameters values for the middle Bay in 2000 were different from those at other locations and in other years (Table 2). The *x*-coordinate vertex (*b*) further decreased in October (Table 2). The parabolic curve fit for this set of data was es-

Table 3. Bay-wide summary of phytoplankton biomass (PB), zooplankton biomass (ZB), fish biomass (FB), the phytoplankton biomass to zooplankton biomass ratio (P : Z), the zooplankton biomass to fish biomass ratio (Z : F), zooplankton size (equivalent spherical diameter) at peak biomass, and log of the individual zooplankton weight at peak biomass for each month and year.

Month	Year	PB (kg×10⁶ C)*	ZB (kg×10⁶ C)*	FB (kg×10⁶ C)†	P : Z	Z : F	Zooplankton at peak biomass (μm)	Log zooplankton weight at peak biomass (μg C)
April	1996	55.6	14.6	1.8	3.81	8.11	720	0.81
	1997	38.3	10.5	1.0	3.64	10.03	890	1.10
	1999	24.4	8.0	1.0	3.06	7.89	690	0.76
	2000	45.7	7.0	4.9	6.50	1.44	640	0.66
July	1996	34.5	7.6	1.5	4.51	5.21	580	0.53
	1997	22.6	4.1	3.0	5.48	1.37	470	0.27
	1999	18.9	6.1	1.7	3.09	3.60	590	0.56
	2000	24.5	4.9	2.7	4.98	1.82	410	0.08
October	1996	20.5	3.8	2.4	5.38	1.59	540	0.44
	1997	20.6	5.1	3.2	4.01	1.60	550	0.47
	1999	17.0	5.3	4.1	3.20	1.29	480	0.30
	2000	10.8	2.7	4.5	4.02	0.60	420	0.12

* Roman et al. (2005).
† Jung and Houde (2003).

sentially linear (curvature = −0.08), skewing the vertex *x*- and *y*-coordinates relative to the other spectra. This was the result of a biomass increase at larger size classes (Fig. 3). In other years, biomass tended to be concentrated among the smaller size classes, with larger zooplankton at the lowest levels in October (Fig. 3; Table 3).

Species composition was dominated by the calanoid copepods *Eurytemora affinis* and *Acartia tonsa.* April species composition in the upper Bay was dominated by *E. affinis* (Fig. 4). Chesapeake Bay Program (CBP) station CB2.2 had a higher proportion of adult *E. affinis,* and the proportion of adult *E. affinis* declined further south in the Bay. The latter 2 yr of data (1999 and 2000) had very low freshwater input and had different species composition and size distributions. These years were characterized by fewer adult *E. affinis* at station CB2.2 and more adult *A. tonsa* at the stations further south (CB3.3C, CB4.3C, CB5.2; Fig. 4). July species composition was dominated by *A. tonsa,* with the exception of the wet year 1996 (Fig. 4). Copepodites were found in larger numbers in the first 3 yr of the study period (1995–1997), and copepodites and adults were found in roughly equal proportions in the final 3 yr (1998–2000; Fig. 4). October species composition was also dominated by *A. tonsa* (Fig. 4). Copepodites were more abundant than adults in general, with the exception of 1997 and 1998 at stations CB3.3C and CB4.3 (Fig. 4).

Water column–averaged Chl *a* values were highest throughout the Bay during April (Fig. 5). The Chl *a* peak in April was representative of the spring phytoplankton bloom in Chesapeake Bay, a bloom that is largely driven by freshwater input, nutrients, and light availability (Harding 1994). In general, July and October Chl *a* levels were lower than April values. This was seen in the majority of the years, except the wet year 1996, which had similar Chl *a* levels throughout the year (Fig. 5). The upper and lower Bay appeared to have relatively constant Chl *a* concentrations during the year (Fig. 5).

Gelatinous zooplankton biovolume was highest during July (Fig. 6). Both the ctenophore *Mnemiopsis leidyi* and the sea nettle *Chrysaora quinquecirrha* were collected during

Table 4. Normalized biomass size spectra slopes, ranges of slopes and coefficients of determination (r^2) for linear fits from other studies.

Study area	*n*	Slope	Slope range	r^2	Reference
North Pacific Ocean*†	1	−1.13	—	0.85	Rodriguez and Mullin (1986)
Lake Superior‡	11	−1.10	−1.00 to −1.15	0.94–0.98	Sprules and Munawar (1986)
Lake Huron‡	8	−1.02	−0.90 to −1.18	0.59–0.94	Sprules and Munawar (1986)
Lake Ontario‡	4	−0.97	−0.90 to −1.04	0.82–0.90	Sprules and Munawar (1986)
Lake Erie‡	4	−0.99	−0.77 to −1.24	0.62–0.90	Sprules and Munawar (1986)
Lake St. Clair‡	14	−0.90	−0.76 to −1.05	0.68–0.89	Sprules and Munawar (1986)
Inland Lakes‡	25	−0.98	−0.92 to −1.05	0.93–0.98	Sprules and Munawar (1986)
Northwest Atlantic Ocean†‡§	214	−1.14	−1.09 to −1.17	0.99	Quinones et al. (2003)
Chesapeake Bay*†	33	−1.32	−0.45 to −1.70	0.87	This study

* Macrozooplankton only.
† Carbon units.
‡ Combined phytoplankton and zooplankton spectra.
§ Combined bacterio-, nano-, micro-, and mesozooplankton spectra.

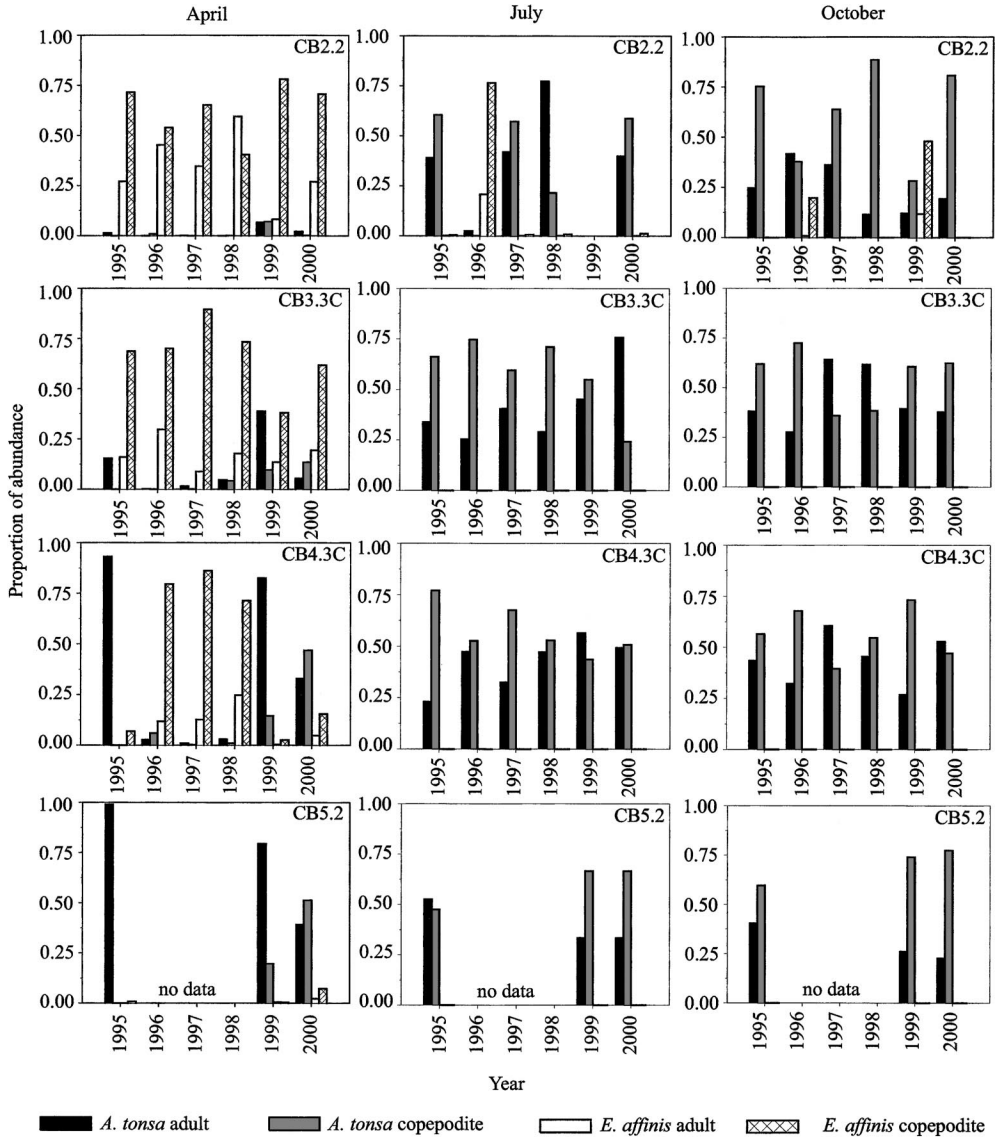

Fig. 4. Monthly and yearly proportion of *Eurytemora affinis* and *Acartia tonsa* adults and copepodites at the Chesapeake Bay Program monitoring stations.

July. *M. leidyi* was seen in April in the lower and middle Bay, but in low biovolume. *C. quinquecirrha* was not collected during the April cruises (Fig. 6). October gelatinous zooplankton species composition consisted of very low biovolumes of *M. leidyi* and moderate biovolumes of *C. quinquecirrha* in the upper Chesapeake Bay (Fig. 6). There was little interannual variability in *M. leidyi* biovolumes, with the exception of 1998 (Fig. 6). The highest abundances of both species appeared to have occurred in 1998, a year that we did not measure normalized zooplankton biomass size spectra. *Chrysaora* appeared to have more interannual variability, showing peaks in the early part of the data set and lower abundances during 1999–2000, particularly in the lower Chesapeake Bay (Fig. 6).

Trawlable fish biomass was dominated by the bay anchovy, *Anchoa mitchilli* (Jung and Houde 2003) and typically peaked during October (Fig. 7). The fish biomass reported was relative, minimal biomass, and only pelagic and benthopelagic species were included (Jung and Houde 2003). In general, fish biomass increased throughout the year (Fig. 7). The earlier years in the survey were characterized by lower overall fish biomass, with later years in the survey having higher biomass (Fig. 7). The shift in fish community composition and biomass was related to freshwater input (Jung and Houde 2003).

A summary of the interannual differences in Bay-wide normalized zooplankton biomass size spectra for each month is presented in Table 3. Zooplankton biomass was highly correlated to phytoplankton biomass (Spearman $\rho = 0.72$, $p < 0.001$). The phytoplankton-to-zooplankton biomass (P : Z) ratio was always >3, regardless of season or year (Table 3). The zooplankton-to-fish biomass ratio (Z : F) was highest in April and decreased in subsequent months. The curvatures of the normalized zooplankton biomass size spectra para-

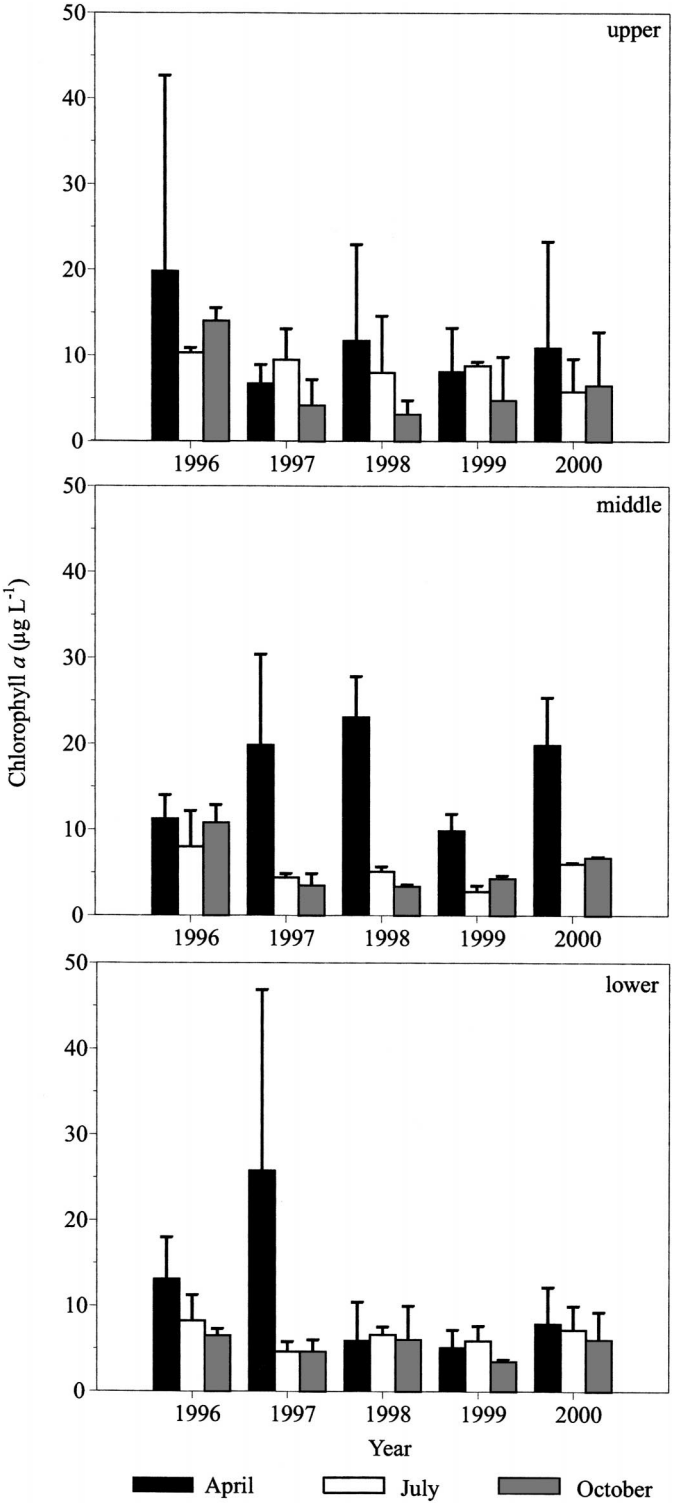

Fig. 5. Water column average Chl *a* concentration (μg L^{-1}) for each region, month, and year. Error bars represent 1 SD.

bolae were highest in April and decreased in subsequent months (Table 3). April also had the largest zooplankton size at peak biomass (Table 3). The normalized zooplankton biomass size spectra had less curvature during July and October, and the majority of zooplankton biomass during these months was typically found in the size range 400–600 μm (Table 3).

Discussion

The normalized zooplankton biomass size spectrum was variable in Chesapeake Bay. This variability was driven by a variety of climatic factors, such as nutrient loading, phytoplankton biomass, and predator biomass, all of which varied spatially and temporally in Chesapeake Bay. Local changes in the distribution of predators and prey determine the availability of a particular size of prey to a predator (Kerr and Dickie 2001). Therefore, the dynamic nature of Chesapeake Bay caused the configuration of predators and prey to constantly change; as a result, the normalized zooplankton biomass size spectrum was more variable than in other systems (Table 4). The normalized zooplankton biomass size spectrum undergoes changes related to multiple forcing factors, such as the April bloom of phytoplankton, the July peak of gelatinous zooplankton, and the October decrease in overall biomass, which coincides with increased fish biomass.

The dominant copepod in April was *E. affinis* (Fig. 4), which can reach extremely high numbers, particularly in wet years (Kimmel and Roman 2004). Chl *a* values in the upper Bay were low in 1997 (Fig. 5), a year of high *E. affinis* abundance and size at peak biomass (Table 3), suggesting an alternative food source for *E. affinis* in the upper Chesapeake Bay or carryover from October 1996 populations (Kimmel and Roman 2004). The alternative food source could be detritus (Heinle and Flemer 1975), particle-attached bacteria (Crump et al. 1998), or both. Indirect biomass flow through detritus might explain the variability in the size spectrum in the upper Bay during April. A similar pattern was seen in Mediterranean coastal waters following a winter production pulse in which chlorophyll biomass did not explain the amount of zooplankton present in the size spectrum (Rodriguez et al. 1987). We might have observed the propagation of the spring bloom through the zooplankton in the upper Chesapeake Bay, and this is manifested in larger sizes at peak biomass (Table 3). We recognized that detritus might affect the OPC signal in the upper Chesapeake Bay (Zhang et al. 2000); however, independent estimates of zooplankton abundance (CBP, www.chesapeakebay.net; Kimmel and Roman 2004) and net tows done during this study confirmed high zooplankton abundance in the upper Bay. The OPC has been shown to give accurate estimates of zooplankton biovolume in detritus-rich waters, particularly waters containing $<$100 particles L^{-1} detritus (Zhang et al. 2000).

More curvature in the normalized zooplankton biomass size spectrum was seen in the middle and lower Chesapeake Bay during April (Fig. 3), indicating less zooplankton biomass distributed across all size classes (Sprules and Goyke 1994). The normalized zooplankton biomass size spectra in July were relatively uniform during the study period (Fig. 3). Curvatures of the size spectra were reduced along with total biomass, suggesting that predation was occurring equally across the size spectrum (Quinones et al. 2003). Gelatinous zooplankton were found in high densities in July (Fig. 6), and the combination of ctenophores (*M. leidyi*) and sea

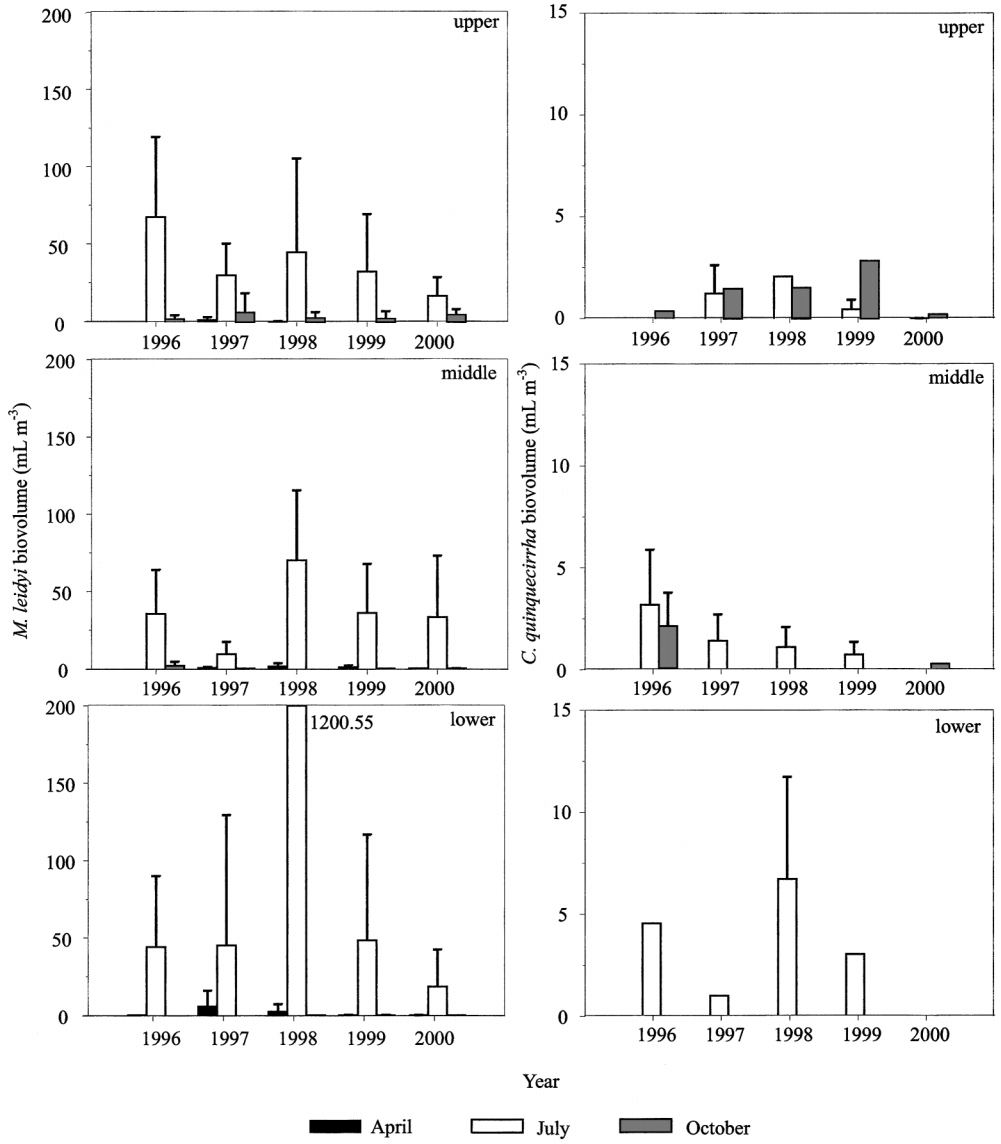

Fig. 6. Average surface, ctenophore (*Mnemiopsis leidyi*), and sea nettle (*Chrysaora quinquecirrha*) biovolume (mL m^{-3}) for each region, month, and year. Error bars represent 1 SD.

nettles (*C. quinquecirrha*) preyed heavily on zooplankton (Suchman and Sullivan 1988; Purcell 1992; Sullivan and Gifford 2004). Predation control of zooplankton populations by gelatinous zooplankton has been shown to be important in Chesapeake Bay (Heinle 1974; Lonsdale 1981; Feigenbaum and Kelly 1984). Bay anchovy, a major fish predator of *A. tonsa*, are also abundant during July in the middle to lower Chesapeake Bay (Rilling and Houde 1999). The most common prey for bay anchovy are *A. tonsa* copepodites and adults (40% of diet), and the size range of prey increases as larvae grow into juveniles (Detwyler and Houde 1970).

The Chesapeake Bay experiences prolonged periods of low dissolved oxygen concentration during July, particularly in the deeper, middle Chesapeake Bay (Hagy et al. 2004). Reductions in dissolved oxygen could have indirect effects on normalized zooplankton biomass size spectra by enhancing the susceptibility of zooplankton to gelatinous predators and creating a favorable habitat for gelatinous predators that are tolerant of low dissolved oxygen concentrations (Breitburg et al. 1997; Decker et al. 2004). Subpycnocline oxygen depletion might also reduce the available copepod habitat by disrupting the vertical migrations of *A. tonsa*. The inability of *A. tonsa* to migrate would increase their susceptibility to fish predation in the upper water column. Low dissolved oxygen might also contribute to lower abundances of juvenile copepod stages because of egg mortality (Roman et al. 1993). The lack of available habitat and increased susceptibility to predation likely caused the lack of interannual variability of normalized zooplankton biomass size spectra seen in our study (Fig. 3).

Another variable period for normalized zooplankton biomass size spectra was October (Fig. 3). The persistence of gelatinous predators appeared to shape zooplankton biomass size spectra in the upper Bay. Larger size classes of zoo-

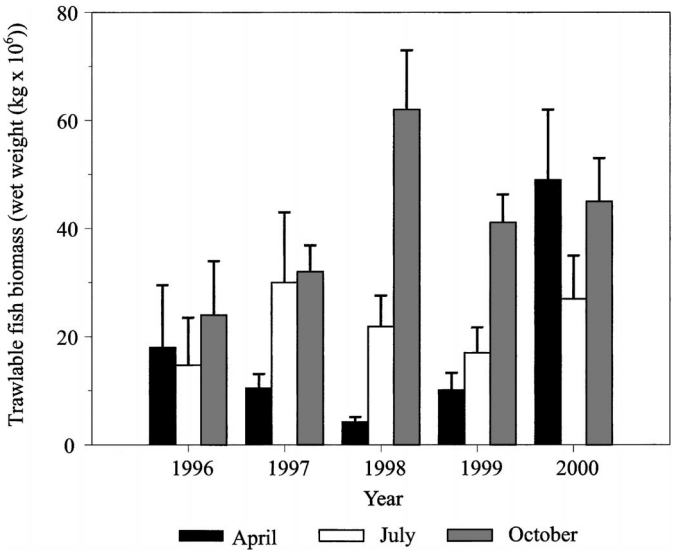

Fig. 7. Estimated, average trawlable fish biomass (wet weight; kg $\times$ 10^6 C) in Chesapeake Bay (after Jung and Houde 2003). Error bars represent 1 SEM.

plankton had lower biomass in years when gelatinous predators (particularly *C. quinquecirrha*) persisted into October (Figs. 3, 6). The effect of sea nettles, which selectively feed on adult *A. tonsa* (Suchman and Sullivan 1998), can be seen in the variability of the spectra in the larger size classes, particularly in 1999 (Fig. 3). The variability in October spectra in the middle and lower Chesapeake Bay is more difficult to explain. Gelatinous predators were not in high abundance, except in the upper Chesapeake Bay (Fig. 6). Food limitation could be important during October, particularly in the lower Chesapeake Bay, because *A. tonsa* requires high food concentrations to accumulate biomass (Paffenhöfer and Stearns 1988). However, measured food concentrations were always in excess of maintenance food concentrations, indicating that food was never limiting for *A. tonsa* (data not shown; Huntley and Boyd 1984). High fish biomass, which peaks during this period (Fig. 7), might account for the decrease in zooplankton biomass. Fish biomass was primarily represented by bay anchovy, and larger size bay anchovy were in higher abundance (Jung and Houde 2004). Luo and Brandt (1993) reported that average bay anchovy consumption did not affect zooplankton abundance; however, they did note that local reductions of zooplankton were possible because of predator–prey patchiness. Bay anchovy is a size-selective predator, eating primarily copepodites and adults (Detwyler and Houde 1970); thus, the very low values of biomass in larger size zooplankton in October could be related to increased bay anchovy predation.

Ratios of phytoplankton-to-zooplankton biomass in Chesapeake Bay during our study always exceeded 3.0, and one observation was in excess of 6.0 (Table 3). These values were higher than what has been predicted for marine systems (0.5–3.3, with a median of 1.0–1.2) and freshwater systems (0.3–3.5, with a median of 1.6; Sprules et al. 1983). Historical declines in Eastern oyster populations (*Crassostrea virginica*), a major filter feeder, combined with a long-term increase in nutrient input into the Chesapeake Bay, has resulted in a 50-yr increasing trend in phytoplankton biomass (Harding and Perry 1997). The large amount of phytoplankton biomass in the system is likely a direct result of human activity and not related to any changes in zooplankton community composition or size structure. Also of note was the small zooplankton size at peak biomass seen in the middle and lower Chesapeake Bay (Table 3), further suggesting the important role predation plays in structuring the zooplankton community.

We calculated linear regression parameters for the normalized zooplankton biomass size spectrum for interstudy comparison (Table 4). We recognized that a linear fit to a biomass size spectrum is biased (Vidondo et al. 1997) and did this only for the purpose of comparing our results to past studies. We observed a large range of linear slope values (-0.45 to -1.70) for zooplankton biomass size spectra in Chesapeake Bay. Similar variability was seen in the eutrophic Lake Erie (-0.77 to -1.24); however, the range of slope variability in Chesapeake Bay was larger than that of oligotrophic systems (Sprules and Munawar 1986). This variability was not unexpected because open ocean gyre systems are more stable (Rodriguez and Mullin 1986; Quinones et al. 2003). Similar studies on biomass size spectra (including other trophic levels in addition to zooplankton, e.g., phytoplankton, microzooplankton, fish, or a combination) found linear size spectrum slopes to be slightly less than -1 (Rodriguez and Mullin 1986; Sprules and Munawar 1986; Quinones et al. 2003). Chesapeake Bay linear regression slopes were more negative, on average, when compared with other studies (Table 4). We have no explanation for this phenomenon, except to suggest that gelatinous zooplankton and planktivorous fish might structure the normalized zooplankton biomass size spectra in Chesapeake Bay by removing larger zooplankton and creating a more negative slope. We recognize that the units of biomass used to calculate the slope of size spectra can affect the results (i.e., slopes based on carbon are slightly more negative than those based on biovolume), as was found in the northwest Atlantic (Quinones et al. 2003). However, our slopes, as calculated in carbon units, were still more negative when compared with other systems (Table 4). Overall, our normalized zooplankton biomass size spectra data support White and Roman's (1992) suggestion that the zooplankton population in the eutrophic Chesapeake Bay is controlled primarily by predation.

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