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Spatial variability in plankton biomass and hydrographic variables along an axial transect in Chesapeake Bay

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[1] High-resolution, axial sampling surveys were conducted in Chesapeake Bay during April, July, and October from 1996 to 2000 using a towed sampling device equipped with sensors for depth, temperature, conductivity, oxygen, fluorescence, and an optical plankton counter (OPC). The results suggest that the axial distribution and variability of hydrographic and biological parameters in Chesapeake Bay were primarily influenced by the source and magnitude of freshwater input. Bay-wide spatial trends in the water column-averaged values of salinity were linear functions of distance from the main source of freshwater, the Susquehanna River, at the head of the bay. However, spatial trends in the water column-averaged values of temperature, dissolved oxygen, chlorophyll-a and zooplankton biomass were nonlinear along the axis of the bay. Autocorrelation analysis and the residuals of linear and quadratic regressions between each variable and latitude were used to quantify the patch sizes for each axial transect. The patch sizes of each variable depended on whether the data were detrended, and the detrending techniques applied. However, the patch size of each variable was generally larger using the original data compared to the detrended data. The patch sizes of salinity were larger than those for dissolved oxygen, chlorophyll-a and zooplankton biomass, suggesting that more localized processes influence the production and consumption of plankton. This high-resolution quantification of the zooplankton spatial variability and patch size can be used for more realistic assessments of the zooplankton forage base for larval fish species.

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1. Introduction

[2] Spatial patterns in the abundance of zooplankton have important consequences for understanding and predicting the food resources available for larval and juvenile fish [e.g., Lasker, 1975; Folt *et al.*, 1993] as well as the spatial variability in biogenic flux and biogeochemical cycles [e.g., Fowler and Knauer, 1986; Small *et al.*, 1989; Roman *et al.*, 2002]. The description of zooplankton patches and their relationship to hydrographic and phytoplankton variability has received considerable attention [e.g., Cushing and Tungate, 1963; Steele and Henderson, 1977; Mackas, 1984; Piontkovski *et al.*, 1997]. Early studies used traditional net sampling [e.g., Cushing and Tungate, 1963; Steele and Henderson, 1977] to describe the spatial variability in zooplankton abundance and biomass. Modified net systems such as the Longurst-Hardy Plankton Recorder [Longhurst *et al.*, 1966; Haury *et al.*, 1976] and multiple opening-

closing net systems [Wiebe *et al.*, 1976; Sameoto *et al.*, 1980] have been used to describe the horizontal variability of zooplankton [Harris *et al.*, 2000]. With the advent of acoustic [e.g., Holliday *et al.*, 1989; Wiebe *et al.*, 1997], optical [Herman, 1992], and video [Davis *et al.*, 1996] techniques to estimate zooplankton, investigators can obtain synoptic measurements of zooplankton and physical parameters at increased spatial resolution. These simultaneous measurements of physical and biological variables with high temporal and spatial resolution are essential for studying the scale-dependent interactions between physical processes and zooplankton distributions [Huntley *et al.*, 1995; Wieland *et al.*, 1997; Roman *et al.*, 2001, 2005]. Towed sensor packages equipped with an optical plankton counter (OPC) have become powerful tools for collecting high-resolution, two-dimensional hydrographic zooplankton data [Herman *et al.*, 1993; Huntley *et al.*, 1995; Stockwell and Sprules, 1995; Wieland *et al.*, 1997; Roman *et al.*, 2005].

[3] In general, the spatial variability of plankton is greater on the continental margins as compared to the open ocean [e.g., Haury *et al.*, 1978; Mackas, 1984; Piontkovski *et al.*, 1997; Fischer *et al.*, 2002]. There are a variety of physical mechanisms (i.e., changes in bathymetry, local wind-forcing, eddies, tidal fronts) [Walsh, 1988; Brink and Robinson, 1998] that potentially could contribute to the formation and dissipation of zooplankton aggregations on continental shelves and slope regions. Less attention has been given to

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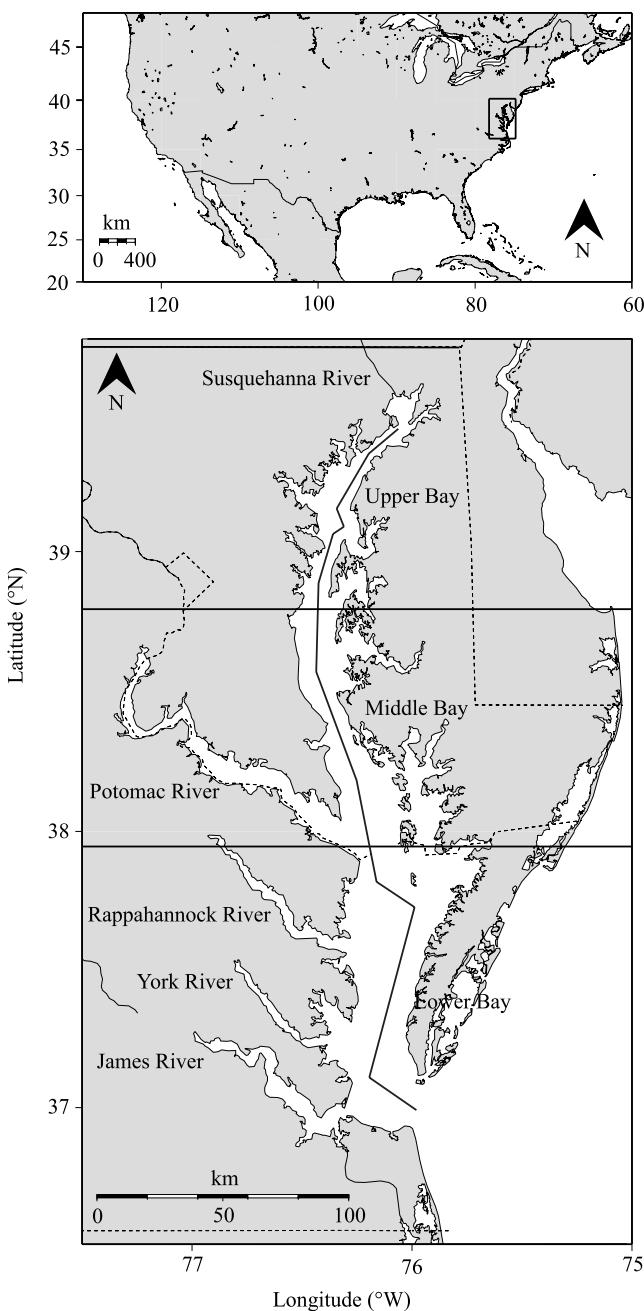


Figure 1. Map of Chesapeake Bay with Scanfish sampling transect.

describing the spatial heterogeneity of estuarine zooplankton (but see papers by *Dodson et al.* [1989] and *Roman et al.* [2005]). This is surprising in light of the important commercial fisheries that are supported by estuarine zooplankton [e.g., *Houde and Rutherford*, 1993].

[4] Estuaries contain a variety of physical discontinuities (tidal fronts, hydraulic control, river plumes, salt fronts [see *Largier*, 1993]) that could potentially aggregate zooplankton and generate patches. The number of these physical discontinuities in estuaries and the resulting zooplankton patches may be one reason that fish yield normalized to primary production is higher in estuaries as compared to open ocean, continental shelves and lakes

[*Nixon*, 1988]. In order to learn more about the mechanisms which generate spatial heterogeneity in estuarine zooplankton, we conducted a high-resolution sampling program in Chesapeake Bay.

[5] The Chesapeake Bay is the largest estuary in the United States, with an area of 6,500 km² and a mean depth of 8.4 m (Figure 1). Chesapeake Bay is shallow and oligohaline in the upper bay ($>38.8^{\circ}\text{N}$), deeper and mesohaline in the middle bay ($>37.8^{\circ}\text{N}$ and $<38.8^{\circ}\text{N}$), and shallow and polyhaline in the lower bay ($<37.8^{\circ}\text{N}$; Figure 1). There is a strong salinity gradient from the upper bay to the lower bay (0–30). Distributions of nutrients and organisms are associated with this salinity gradient [*Fisher et al.*, 1992; *Harding and Perry*, 1997]. In addition to the salinity gradient along the axis of the bay, the estuarine turbidity maximum zone, tidal fronts, and river plumes are common hydrodynamic structures found in Chesapeake Bay and other estuaries [*Legendre and Le Fevere*, 1989; *Largier*, 1993; *Hanson and Rattray*, 1966; *Valle-Levinson et al.*, 2003; *Roman et al.*, 2005]. Distributions of zooplankton and fish are associated with these hydrodynamic features on a variety of temporal and spatial scales [*Taggart et al.*, 1989; *Largier*, 1993; *North and Houde*, 2001; *Roman et al.*, 2001, 2005; *Jung and Houde*, 2003; *Valle-Levinson et al.*, 2003].

[6] The temporal and spatial variability of zooplankton aggregations are an important feature of Chesapeake Bay ecology. Zooplankton play a critical role in Chesapeake Bay as the food source for larval anadromous fish (striped bass, *Morone saxatilis* and white perch, *Morone americana*) [*Uphoff*, 1989; *Setzler-Hamilton*, 1987] and juvenile and adult bay anchovy (*Anchoa mitchilli*) [*Detwyler and Houde*, 1970]. The degree of aggregation, or patchiness, of the zooplankton food source is an important factor affecting the survival of early life stages of fish [*Houde*, 1987]. The degree of zooplankton patchiness can affect the predation rate of fish and change the impact of the fish predators on prey abundance and distribution [*Folt et al.*, 1993]. Fish that encounter patches of elevated zooplankton abundance often experience enhanced survival and growth [e.g., *Lasker*, 1975; *Wroblewski and Richman*, 1987; *Wroblewski et al.*, 1989]. Therefore knowledge of the patch size and spatial distribution of zooplankton patches are important to improve fisheries recruitment models for more accurate representations of the available prey fields.

[7] The goal of our study was to determine the spatial distribution and patch sizes of zooplankton and physical/biological variables in Chesapeake Bay. We made simultaneous observations of zooplankton, chlorophyll-a and hydrographic variables using a towed-sensor package (Scanfish, GMI) equipped with an OPC. We conducted axial surveys down the length of Chesapeake Bay in April, July and October from 1996 to 2000. These high-resolution data were used to quantify the spatial patterns of plankton and physical variables in Chesapeake Bay, bay-wide trends, and patch sizes.

2. Methods

[8] Sampling surveys were conducted in April, July, and October from 1995 to 2000 using a towed body (Scanfish, GMI) mounted with sensors of pressure, temperature, conductivity, oxygen, fluorescence, and an optical plankton

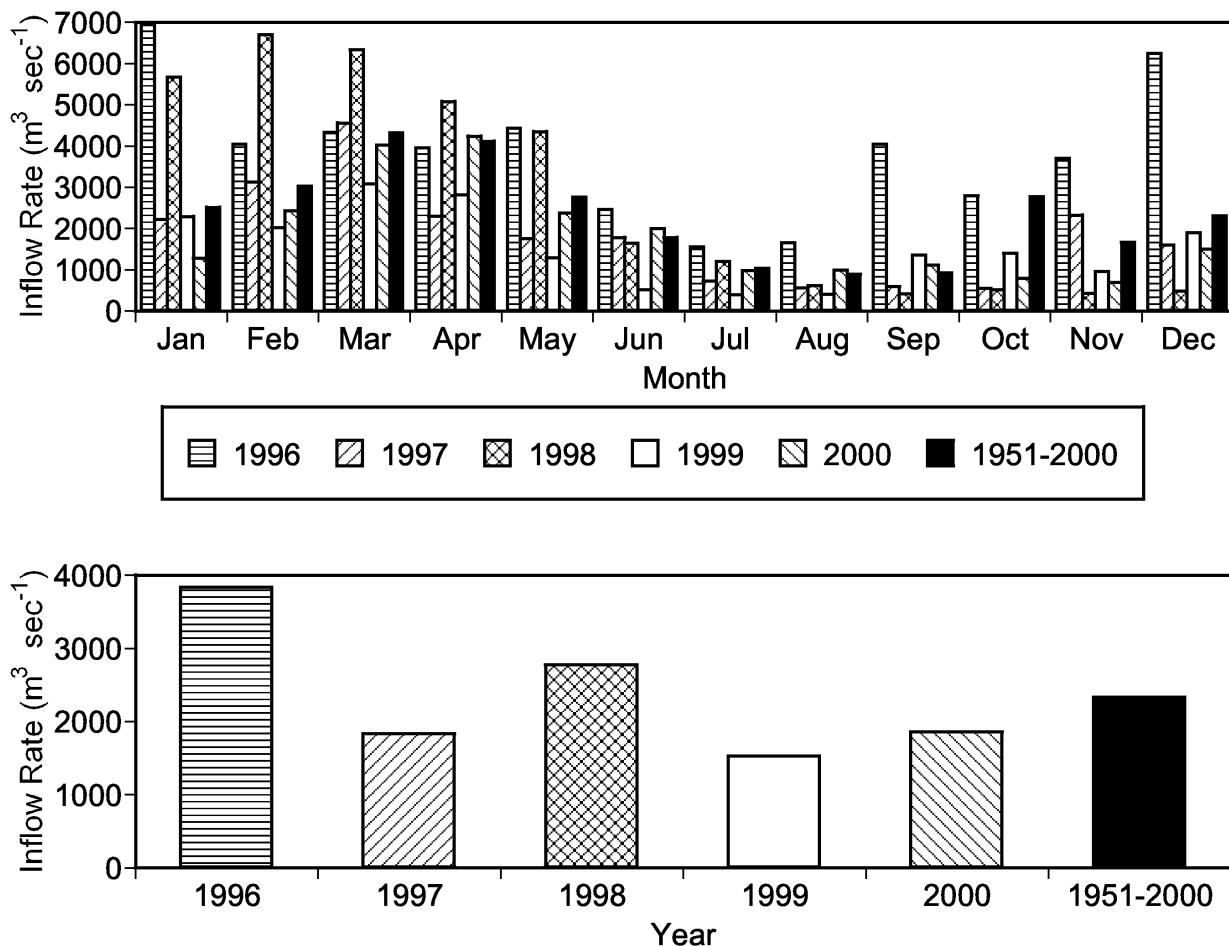


Figure 2. Monthly, yearly and 50-year climatological (1951–2000) averaged freshwater inflow rates to Chesapeake Bay from major rivers.

counter (OPC-1T with a sampling tunnel opening of 2×7 cm; Focal Technologies). Data were collected continuously throughout the water column along a 270 km axial transect of Chesapeake Bay over approximately 30 hours (Figure 1). The Scanfish undulated from approximately 2 m below the surface to 2 m above the bottom with a vertical data resolution of 1 m. The horizontal resolution of the Scanfish data was depth dependent. On average we obtained seven vertical profiles per km. The OPC experienced problems during 1995 and 1998 and zooplankton data were not collected. Fluorescence readings were converted to chlorophyll-a units by collecting samples for chlorophyll-a determination [Yentsch and Menzel, 1963] and regressing the two variables. Freshwater inflow rates to Chesapeake Bay from major rivers were acquired from the United States Geological Survey (www.chesapeake.usgs.gov).

[9] The OPC detects and sizes 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 is 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 using a spherical model (Particle volume = $1/6 \times \pi \times D^3$) with diameter (D) = ESD.

[10] We calculated the velocity of water passing through the OPC sampling tunnel based on the rate of change of longitude, latitude, and the depth of the Scanfish. Over the study we also employed a mechanical flow meter (General Oceanics) which was mounted on the OPC unit and a doppler current meter located in the OPC tunnel. Neither of these direct velocity measurements proved reliable over the entire study period. However, when we compared the direct velocity measurement (General Oceanics flowmeter) to the velocity estimates based distance/time we found that the two velocity estimates were highly correlated ($p < 0.05$) and were not significantly different (mean = 2.87 m s^{-1} , std dev 0.27 m s^{-1} for flowmeter; mean = 3.20 m s^{-1} , std dev 0.24 m s^{-1} for estimated velocity; $n = 38132$).

[11] The flow rate of water passing through the OPC sampling tunnel was based on the area of the OPC sampling tunnel opening and the velocity of water passing through the OPC sampling tunnel. We calculated the particle abundance and volume concentration of each size category by recording the flow rate and the number of particles of each size that were detected during each time interval (0.5 s).

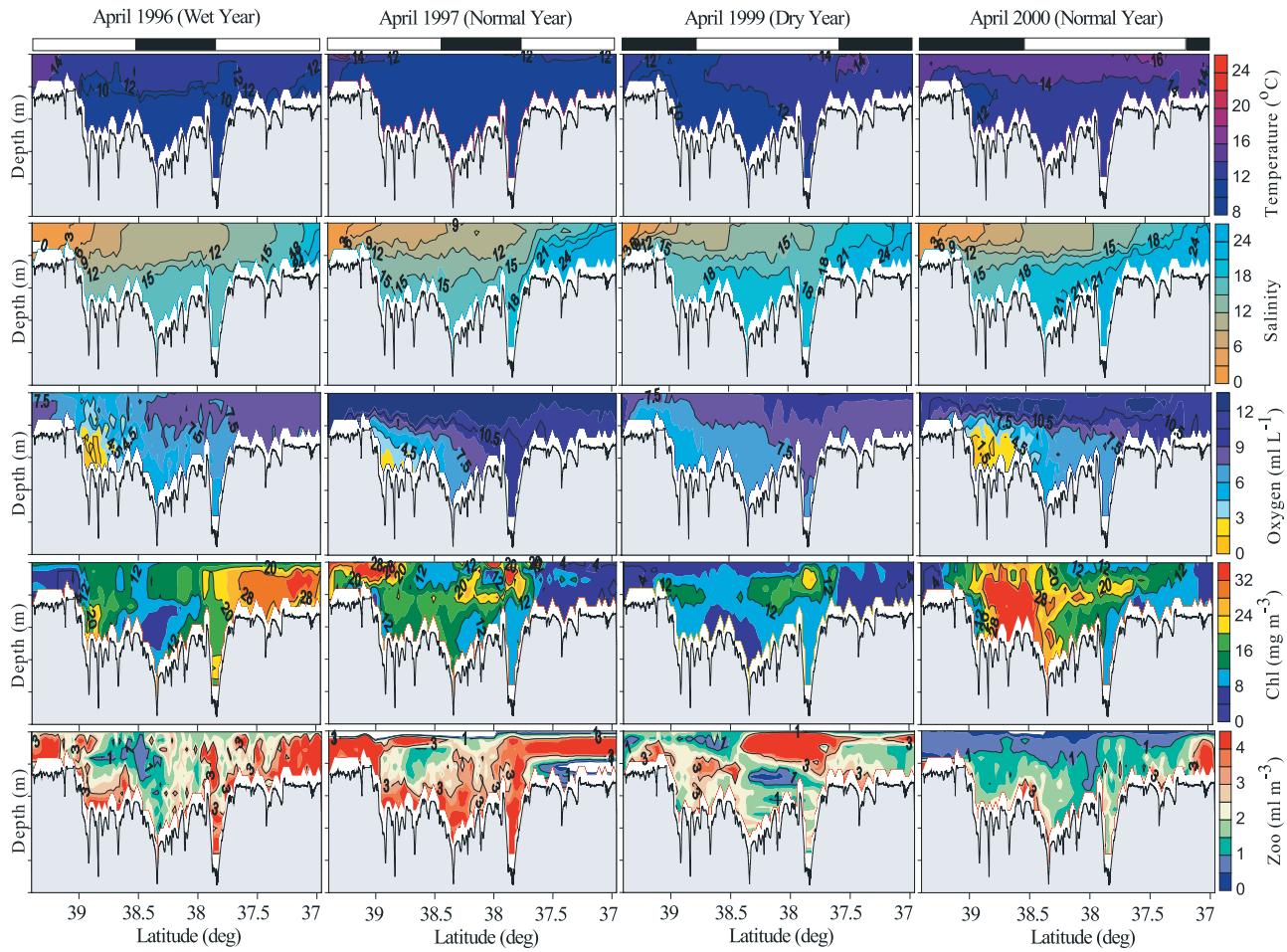


Figure 3. Distribution of temperature, salinity, dissolved oxygen concentration, chlorophyll-a, and zooplankton biomass along the axis of Chesapeake Bay in April. Night is represented by the black bar.

Zooplankton biomass was represented by the sum of all particles that were larger than $250 \mu\text{m}$ ESD.

[12] Other investigators have found that OPCs give reasonable estimates of zooplankton abundance and biomass when compared to net-collected samples [e.g., Herman, 1992; Huntley *et al.*, 1995; Sprules *et al.*, 1998, Zhang *et al.*, 2000; Roman *et al.*, 2005]. We compared estimates of zooplankton biomass measured from the Scanfish/OPC and net-collected samples. The result of the comparison has been published by Roman *et al.* [2005]. Briefly, the Scanfish was maintained in the surface 1–3 m approximately 20 m behind the stern of the research vessel. At the same time (5 min) we deployed a plankton net (200 μm) which had a mouth opening the exact size of the OPC sampling tunnel opening ($2 \times 7 \text{ cm}$). Upon collection, we filtered triplicate aliquots of the net sample onto preweighed GF/F filters for dry weight measurements. Zooplankton biomass estimated by the OPC and the zooplankton net were significantly correlated (zooplankton dry weight (mg m^{-3}) = $0.0053 \text{ OPC biomass (mm}^3 \text{ m}^{-3}\text{)} + 2.5332$; $r = 0.59$, $N = 30$).

[13] Although ctenophores, *Mnemiopsis leidyi*, and scyphomedusae, *Chrysaora quinquecirrha*, account for a significant amount of the zooplankton biomass in Chesapeake Bay during certain times of the year, because of their relative low densities compared to copepods, large size in relation to the mouth opening of the OPC sampling tunnel

and translucence to the OPC light beams, they are unlikely to be measured effectively by the OPC.

[14] A software integration program (*Surfer* by Golden Software) was used to generate contour maps by interpolating data collected along the axial transect in Chesapeake Bay. Contours were calculated using the Kriging point interpolation method with a linear variogram model using an anisotropy ratio of 1, anisotropy angle of 0, and a quadrant search type.

[15] Data were binned by latitude into 300 evenly spaced water columns and averaged over each water column along the axial transect of the bay (meridional distance = 270 km). Bay-wide trends of the water column-averaged values of each variable along the axial transect were quantified by fitting a linear regression function and a quadratic regression function between each variable (at each of the 300 evenly spaced water columns along the axis of the bay) and latitude for each cruise. The bay-wide linear or quadratic trends were removed (i.e. the difference between the water column-averaged values of each variable and the predicted values based on the derived linear or quadratic regression function). We tested for autocorrelation in the water column-averaged values of each variable along the axis of the bay and the residuals of the linear and quadratic regressions. The patch size of each variable was calculated using the lagged distance at which the autocorrelation coefficient first

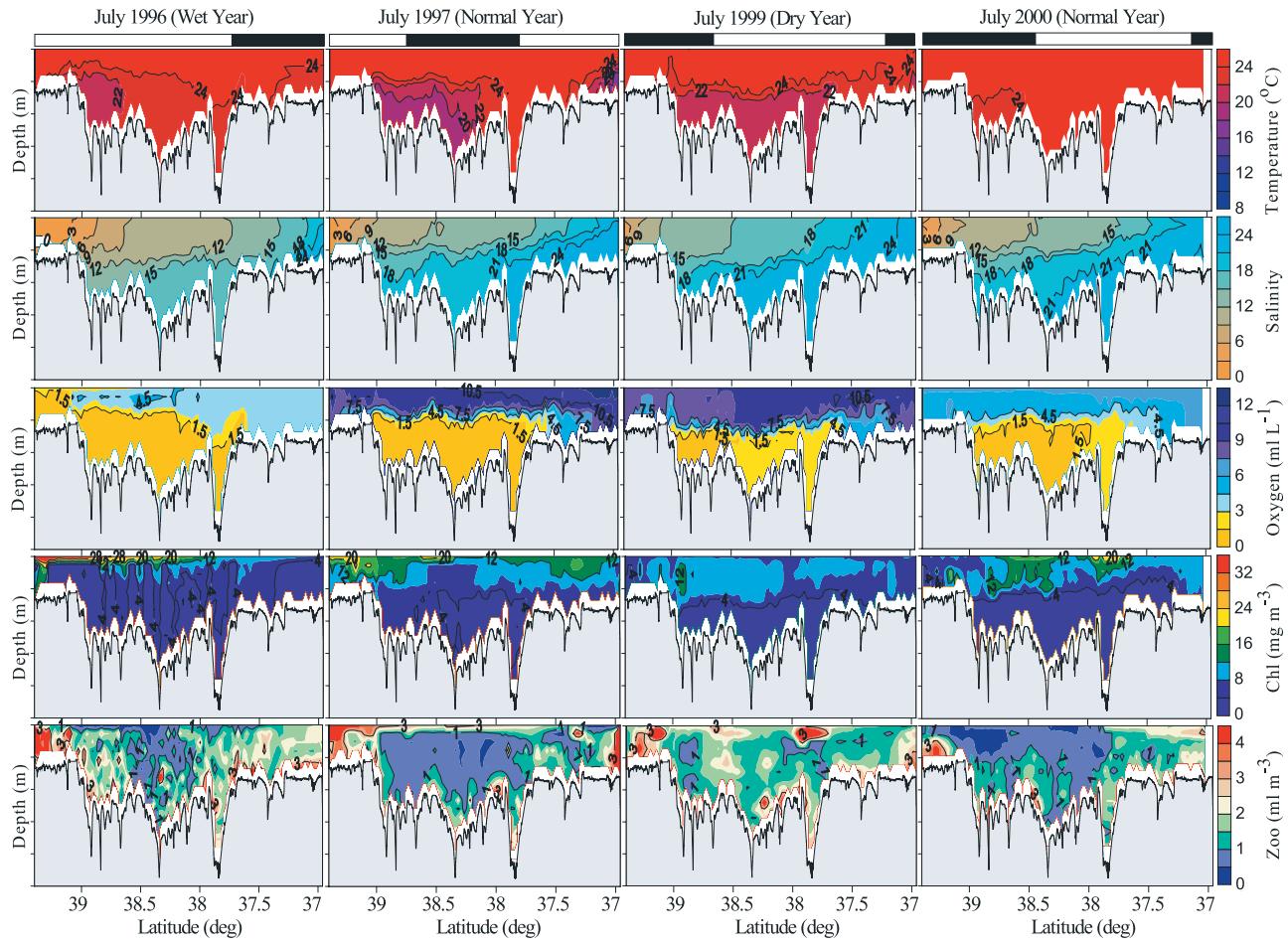


Figure 4. Distribution of temperature, salinity, dissolved oxygen concentration, chlorophyll-a, and zooplankton biomass along the axis of Chesapeake Bay in July. Night is represented by the black bar.

passes zero [Richerson *et al.*, 1978; Rowe and Epifanio, 1994].

3. Results

3.1. Freshwater Input

[16] Freshwater input to Chesapeake Bay normally is highest from late winter through early spring (January–April; Figure 2). Compared to the 50-year climatology, the average freshwater input during the late winter and early spring was 35% higher in 1996; 30% lower in 1999; and similar to the 50-year climatology in 1997 and 2000 (Figure 2). The average annual freshwater inflow rate was 73% higher in 1996; 31% lower than the mean inflow in 1999; and within 2% of the 50-year climatology in 1997 and 2000 (Figure 2). In order to contrast the inter-annual variation in freshwater input and the resultant spatial patterns of plankton and hydrographic variables in Chesapeake Bay, we will refer to 1996 as a “wet” year, 1999 as a “dry” year, and 1997 and 2000 as “normal” years.

3.2. Hydrographic Variables, Chlorophyll-a, and Zooplankton Biomass

3.2.1. April

[17] Annual differences in the axial distribution of temperatures in April, July, and October did not appear to be

influenced by freshwater input (Figures 3–5). However, salinity was lower in April 1996 (a wet year) when the 12 isohaline extended down the bay to 38°N and to 16–17 m depth (Figure 3). In contrast, salinity was higher in April 1999 (a dry year), when the 12 isohaline extended south to 38.5°N and to 8–9 m depth (Figure 3). Although the 12 isohaline extended to 38°N in 1997 and 2000 (normal years), 12 salt was confined to the surface 10 m (Figure 3). Salinity distributions showed fine-scale (meter) vertical variations that mirrored bathymetric features (Figure 3).

[18] Hypoxic water (dissolved oxygen concentration $<1.5 \text{ ml L}^{-1}$) generally begins to develop in May between 39 and 38.5°N (Chesapeake Bay Program Water Quality Monitoring Program, www.chesapeakebay.net). Under conditions that promote stratification (warmer temperatures, lower surface salinity) hypoxic bottom waters can develop earlier [Hagy *et al.*, 2004]. For example, hypoxia was observed between 39 and 38.5°N in April 2000 when water temperatures were elevated (Figure 3).

[19] Chlorophyll-a concentrations were high in the wet 1996, and an extensive April phytoplankton bloom developed which occupied almost the entire lower bay ($<37.8^{\circ}\text{N}$; Figure 3). Chlorophyll-a maxima in April 1997 and 2000 were further up-bay with peaks in biomass present around 38.9°N and 38.7°N in 1997 and 2000, respectively

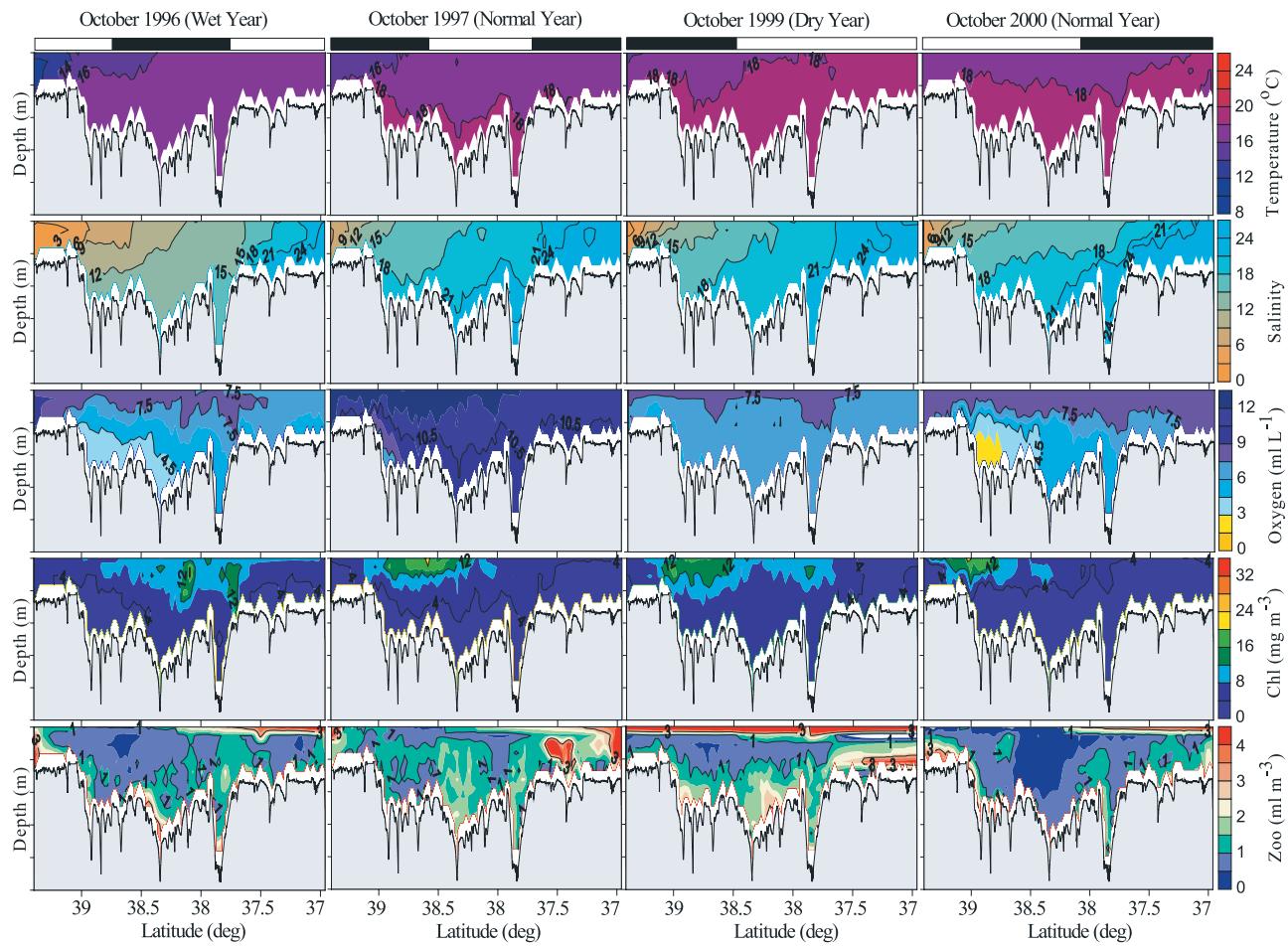


Figure 5. Distribution of temperature, salinity, dissolved oxygen concentration, chlorophyll-a, and zooplankton biomass along the axis of Chesapeake Bay in October. Night is represented by the black bar.

(Figure 3). Chlorophyll-a was low in the dry April 1999 and phytoplankton biomass peaked further north at 37.8°N (Figure 3).

[20] We did not detect diel vertical migration of zooplankton (i.e., higher zooplankton biomass in the surface waters at night and at depth during the day) during April of any years (Figure 3). High zooplankton biomass occurred in the upper and lower bay in 1996, with high zooplankton biomass closely matched with high chlorophyll-a concentrations only in the lower bay (Figure 3). Zooplankton biomass in the middle bay in 1999 was spatially coincident with chlorophyll-a concentrations (Figure 3). High zooplankton biomass in the upper and lower bay in 1997 was closely matched with high chlorophyll-a concentration in the upper bay, but not in the lower bay (Figure 3). Zooplankton biomass was low in April 2000 with maximum concentrations found in the lower bay (Figure 3).

3.2.2. July

[21] Salinity in July was higher than in April, and <12 salinity occupied a much smaller area of Chesapeake Bay in July as compared to April (Figures 3 and 4). The area of lowest oxygen concentration was generally found between 38 and 39°N (Figure 4). The horizontal and vertical extent of hypoxia was highest in July 1996 (a wet year), when hypoxic water occupied almost the entire bottom waters

(>10 m) in the middle bay as well as the entire upper bay (Figure 4). In contrast, the extent of hypoxia was low in July 1999 (a dry year), when hypoxic water occupied only >15-m bottom waters in the upper portion of the middle bay (Figure 4).

[22] Chlorophyll-a concentrations were lower in July as compared to April, with the highest values generally in the surface 15 m (Figure 4) and patches of high chlorophyll-a found in the hypoxic bottom waters. Similar to chlorophyll-a concentration, zooplankton biomass was lower in July than in April, and patches of elevated zooplankton biomass often existed in the upper and lower bay (Figures 3 and 4). There were no clear differences in the day/night vertical distribution of zooplankton biomass. The OPC sometimes recorded significant quantities of zooplankton biomass in low oxygen bottom waters of the middle bay region (Figure 4).

3.2.3. October

[23] Surface waters in the upper and middle bay were cooler than bottom waters (Figure 5). Salinities generally were higher in October as compared to surveys in April and July (Figures 3–5), and except for the wet 1996, salinity <12 occupied only a small portion of the upper bay (Figure 5). Bottom water oxygen concentrations were higher in October compared to July (Figures 4 and 5). In

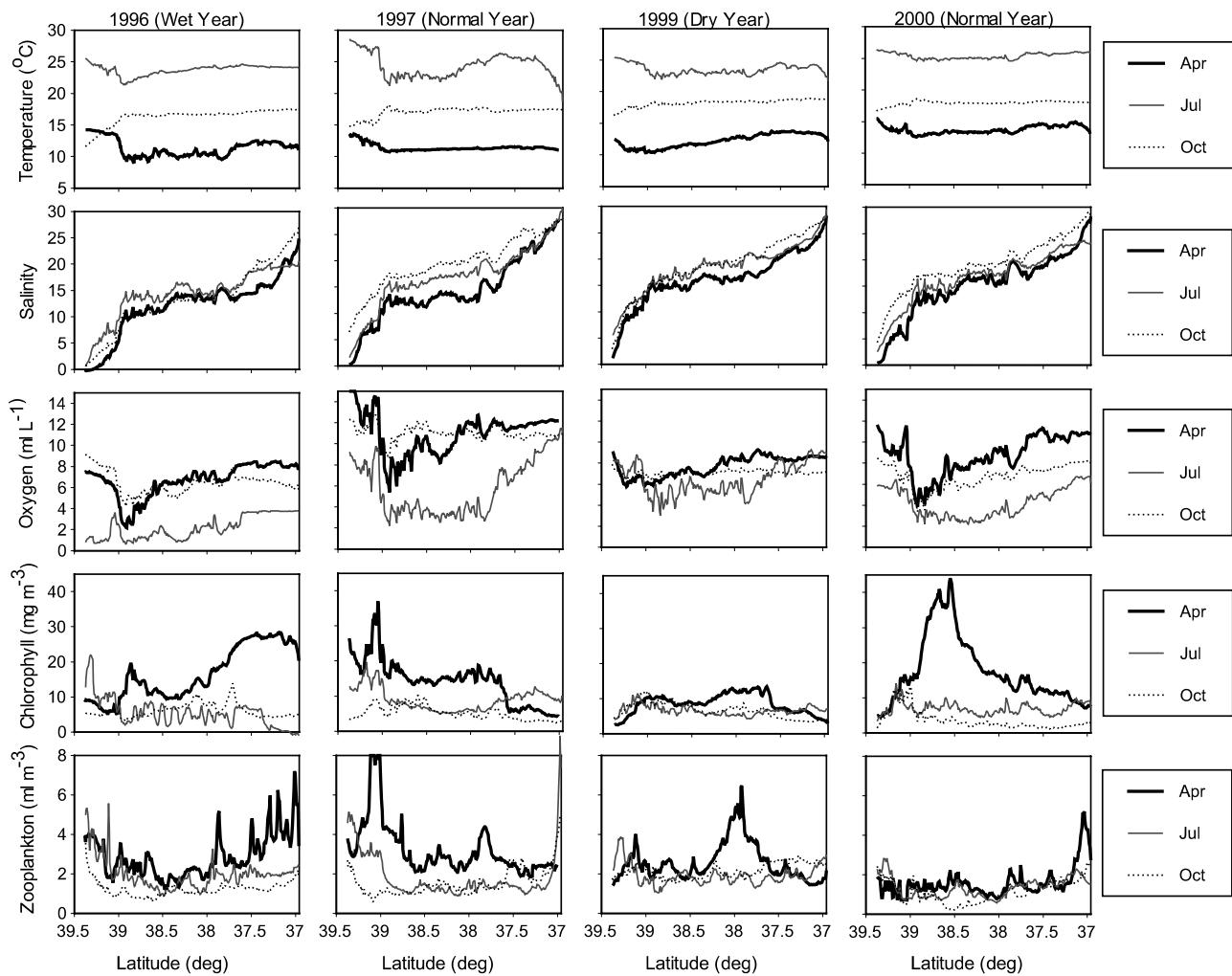


Figure 6. Distribution of water column-averaged temperature, salinity, dissolved oxygen, chlorophyll-a, and zooplankton biomass at each of the 300 evenly spaced water columns along the axis of Chesapeake Bay.

October of 1996 (high freshwater input) and 2000 (normal freshwater input and highest water temperatures) bottom water oxygen concentrations between 39 and 38.5°N were hypoxic (Figure 5). In general, the highest chlorophyll-a biomass was found in middle bay waters <10 m deep (Figure 5). However, the middle bay region did not have maximum zooplankton concentrations. Similar to the pattern found in July, patches of zooplankton biomass often existed in the upper and lower bay (Figures 4 and 5) during October.

3.3. Hydrographic Variables, Chlorophyll-a, and Zooplankton Biomass Averaged Over the Water Column

[24] Average water column temperatures were lowest in April and highest in July with little interannual variability (Figure 6). Temperatures were higher in the upper bay and lower in the middle bay in April and July, with the trend reversed in October (i.e., lower in the upper bay and higher in the middle bay; Figure 6).

[25] Average water column salinity was low in April, higher in July, and peaked in October (Figure 6). Along the axis of the bay, salinity was lower in the upper bay, did not

vary spatially in the middle bay (39–38°N), and was higher in the lower bay. In general, the salinity gradient was larger in the upper bay and smaller in the lower bay.

[26] Average water column dissolved oxygen concentration was lowest in July (Figure 6) with oxygen minima generally located between 39 and 38°N. Although dissolved oxygen in April and October did not vary greatly between 1996 and 1999, dissolved oxygen in July was much lower during the wet year as compared to the dry year (Figure 6). The dissolved oxygen minimum was often limited to the upper portion of the middle bay in April and October but expanded to the entire middle bay in July (Figure 6).

[27] Average water column chlorophyll-a concentrations were highest in April with annual differences in the axial location of maximum chlorophyll-a biomass (Figure 6). The location of peak chlorophyll-a concentrations was related to freshwater input; the maxima occurred farther down-bay during the wet 1996 and up-bay during the dry 1997 and 2000. The lowest chlorophyll-a values were recorded during the dry year 1999 (Figure 6). Chlorophyll-a concentrations in July and October did not vary greatly between 1996 and 1999, but chlorophyll-a in April was much higher during the wet year 1996 compared to the dry year 1999 (Figure 6).

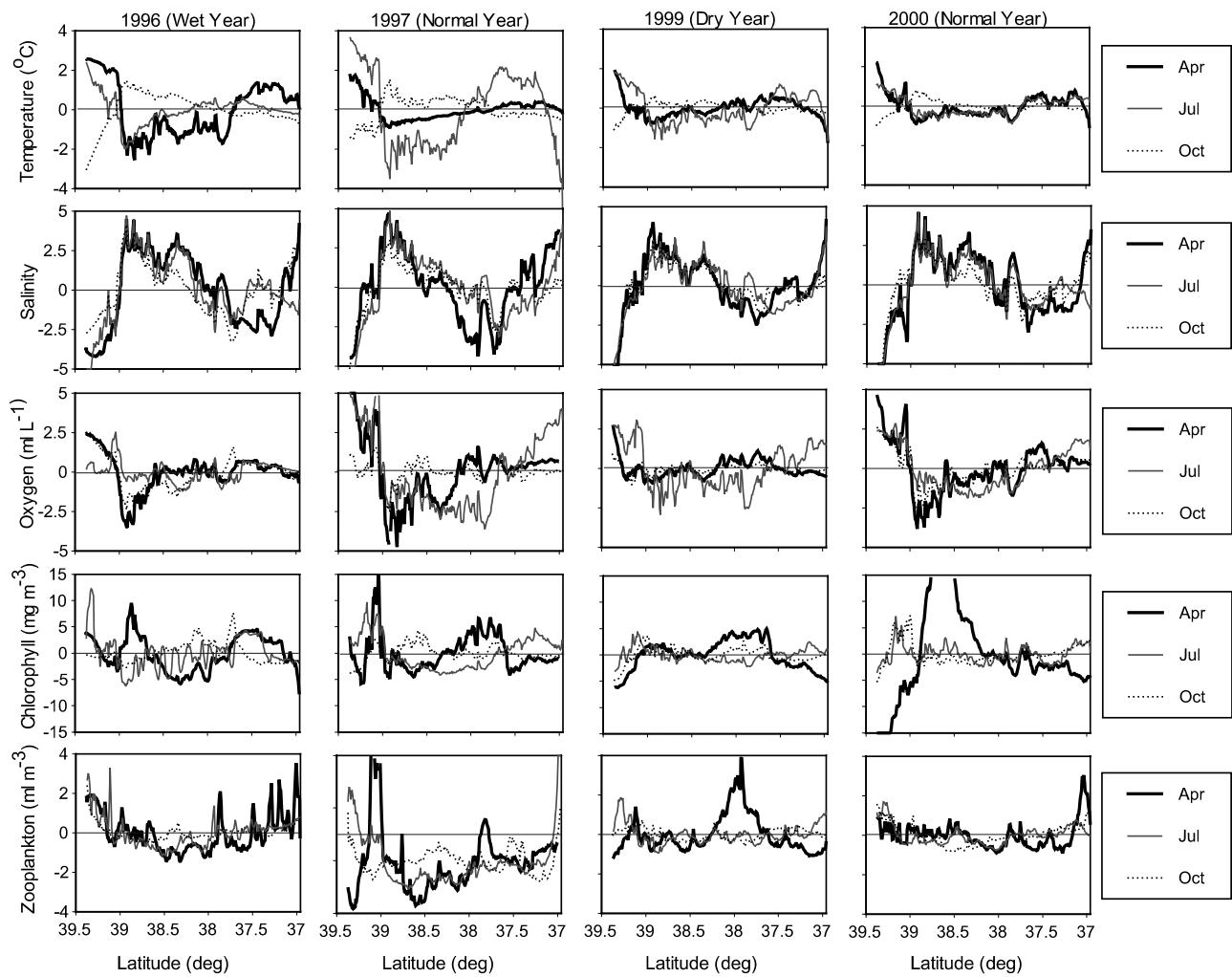


Figure 7. Distribution of the residuals of linear regression between water column-averaged temperature, salinity, dissolved oxygen concentration, chlorophyll-a, and zooplankton biomass at each of the 300 evenly spaced water columns along the axis of Chesapeake Bay and latitude. The residuals are equal to the observed water column-averaged values minus the predicted values based on the linear regression between each variable and latitude.

In general, chlorophyll-a concentrations in July and October did not vary greatly along the axis of the bay.

[28] Average water column zooplankton biomass was highest in April (Figure 6). Similar to chlorophyll-a, zooplankton biomass in July and October did not vary greatly between the wet, dry, and normal years (Figure 6). In general, zooplankton biomass distribution along the axis of the bay in April was similar to the distribution of chlorophyll-a except in April 2000 when a large chlorophyll-a maximum developed in the upper portion of the middle bay, but only a small zooplankton biomass maximum developed in the lower bay (Figure 6). The highest zooplankton concentrations in July and October were usually found in the upper and lower Chesapeake Bay (Figure 6).

3.4. Axial Trends in Plankton and Hydrographic Variables

[29] The spatial trend in the axial salinity distributions was effectively removed by either a linear or quadratic regression between the water column-averaged values at

each of the 300 evenly spaced water columns along the axis of the bay and latitude (Table 1). In contrast, a quadratic function provided a better description of the spatial patterns of the water column-averaged values of temperature, dissolved oxygen, chlorophyll-a, and zooplankton biomass along the axis of the bay and latitude (the coefficients of determination of linear regression were significantly smaller than the correspondent quadratic regression for each variable, especially for zooplankton biomass, t-test, $p < 0.05$, Table 1). The axial linear/quadratic description of the water column-averaged plankton and hydrographic values for each cruise were more significant for salinity compared to other variables (coefficients of determination of regressions, ANOVA, Tukey's HSD post-comparison test, $p < 0.05$, Table 1).

3.5. Patterns in the Residuals of the Linear and Quadratic Regressions

[30] Patterns in the residuals of the linear and quadratic regressions between the water column-averaged plankton and hydrographic values along the axis of the bay and

Table 1. Function Parameters and Coefficients of Determination of Linear and Quadratic Regressions (r^2) Between the Water Column-Averaged Values of Temperature, Salinity, Dissolved Oxygen, Chlorophyll-a, and Zooplankton at Each of the 300 Evenly Spaced Water Columns (Y) Along the Axis of Chesapeake Bay and Latitude (X) for Each Cruise^a

Variable	Cruise	Linear Regression			Quadratic Regression			
		a	b	r^2	α	β	γ	r^2
Temperature	Apr 1996	0.27	1.04	0.02	2.29	-174.69	3339.08	0.55
Temperature	Apr 1997	0.32	-0.63	0.14	0.76	-57.62	1104.59	0.47
Temperature	Apr 1999	-1.37	64.53	0.80	-0.01	-0.99	57.22	0.80
Temperature	Apr 2000	-0.39	28.64	0.19	0.76	-58.72	1141.42	0.49
Temperature	Jul 1996	-0.48	42.25	0.18	0.45	-34.61	693.25	0.24
Temperature	Jul 1997	0.43	8.13	0.02	1.31	-99.76	1919.45	0.12
Temperature	Jul 1999	1.11	19.25	0.01	1.12	-85.29	1648.43	0.38
Temperature	Jul 2000	-0.15	31.06	0.05	0.86	-66.03	1287.93	0.66
Temperature	Oct 1996	-1.40	69.89	0.58	-1.27	95.33	-1775.54	0.77
Temperature	Oct 1997	-0.68	43.11	0.39	-0.95	71.95	-1342.45	0.68
Temperature	Oct 1999	-0.69	44.67	0.76	-0.38	28.08	-504.36	0.84
Temperature	Oct 2000	-0.25	27.37	0.27	-0.26	19.56	-350.45	0.39
Mean (SD)				0.28 (0.29)				0.53 (0.23)
Salinity	Apr 1996	-7.05	281.31	0.81	-2.61	191.98	-3516.11	0.86
Salinity	Apr 1997	-8.20	327.39	0.87	1.51	-123.65	2533.15	0.88
Salinity	Apr 1999	-6.37	259.59	0.85	-0.72	48.76	-792.16	0.86
Salinity	Apr 2000	-7.87	315.75	0.87	-2.15	156.24	-2815.17	0.90
Salinity	Jul 1996	-5.67	230.59	0.78	-2.51	185.57	-3417.62	0.84
Salinity	Jul 1997	-7.53	304.57	0.87	-1.26	88.97	-1536.43	0.88
Salinity	Jul 1999	-5.98	246.50	0.88	-1.35	97.28	-1723.36	0.90
Salinity	Jul 2000	-6.57	267.30	0.87	-2.33	170.98	-3119.88	0.91
Salinity	Oct 1999	-8.35	332.17	0.92	0.22	-25.29	655.36	0.93
Salinity	Oct 1997	-6.58	270.78	0.92	-0.97	67.35	-1139.56	0.92
Salinity	Oct 1999	-7.13	290.86	0.92	-1.53	109.80	-1940.08	0.93
Salinity	Oct 2000	-6.68	273.88	0.90	-0.71	47.57	-760.93	0.90
Mean (SD)				0.87 (0.04)				0.89 (0.03)
Oxygen	Apr 1996	-1.40	60.10	0.41	0.80	-62.60	1227.73	0.47
Oxygen	Apr 1997	-0.44	27.71	0.02	2.34	-179.34	3441.31	0.30
Oxygen	Apr 1999	-1.11	49.88	0.65	-0.09	5.49	-75.86	0.65
Oxygen	Apr 2000	-1.47	65.05	0.30	1.88	-144.60	2795.59	0.49
Oxygen	Jul 1996	-1.29	51.47	0.68	0.67	-52.52	1028.75	0.75
Oxygen	Jul 1997	-1.43	60.20	0.15	5.01	-383.83	7355.51	0.86
Oxygen	Jul 1999	-0.80	36.85	0.14	2.45	-187.98	3607.84	0.66
Oxygen	Jul 2000	-0.62	27.80	0.10	2.81	-215.20	4121.45	0.86
Oxygen	Oct 1996	0.19	-0.71	0.02	1.06	-80.43	1537.33	0.23
Oxygen	Oct 1997	0.18	4.01	0.04	0.05	-3.96	82.98	0.04
Oxygen	Oct 1999	-0.11	11.34	0.08	-0.10	7.87	-140.94	0.11
Oxygen	Oct 2000	-0.75	35.52	0.22	1.35	-103.56	1996.75	0.50
Mean (SD)				0.23 (0.23)				0.49 (0.28)
Chlorophyll	Apr 1996	-9.52	380.01	0.80	2.42	-194.01	3900.07	0.82
Chlorophyll	Apr 1997	7.63	-277.00	0.69	-1.32	108.44	-2201.09	0.71
Chlorophyll	Apr 1999	0.18	1.60	0.00	-5.40	412.51	-7864.53	0.69
Chlorophyll	Apr 2000	4.59	-157.53	0.11	-12.79	981.08	-18786.52	0.46
Chlorophyll	Jul 1996	3.75	-137.88	0.42	1.53	-112.95	2088.63	0.44
Chlorophyll	Jul 1997	1.06	-31.62	0.06	5.43	-413.82	7883.19	0.63
Chlorophyll	Jul 1999	0.47	-11.20	0.06	1.32	-100.40	1913.09	0.25
Chlorophyll	Jul 2000	0.06	4.76	0.00	0.93	-70.68	1354.21	0.06
Chlorophyll	Oct 1996	-0.26	16.15	0.01	-2.65	201.89	-3840.38	0.36
Chlorophyll	Oct 1997	1.73	-60.76	0.39	-1.60	124.10	-2395.25	0.52
Chlorophyll	Oct 1999	2.25	-79.45	0.53	-1.47	114.79	-2226.53	0.62
Chlorophyll	Oct 2000	2.63	-96.83	0.46	1.93	-144.76	2715.07	0.56
Mean (SD)				0.29 (0.29)				0.51 (0.21)
Zooplankton	Apr 1996	-0.68	28.86	0.19	1.69	-129.66	2489.80	0.65
Zooplankton	Apr 1997	1.27	-45.16	0.27	0.75	-55.91	1046.15	0.31
Zooplankton	Apr 1999	-0.05	0.62	0.00	-1.15	88.06	-1678.45	0.27
Zooplankton	Apr 2000	-0.52	21.28	0.22	0.80	-61.54	1185.38	0.43
Zooplankton	Jul 1996	0.30	-9.63	0.08	1.19	-90.15	1716.00	0.53
Zooplankton	Jul 1997	0.43	-14.46	0.07	1.91	-145.74	2773.98	0.58
Zooplankton	Jul 1999	0.09	-1.49	0.02	0.70	-52.97	1010.70	0.37
Zooplankton	Jul 2000	0.17	7.79	0.06	0.77	-58.70	1124.41	0.50
Zooplankton	Oct 1996	-0.07	3.73	0.01	0.53	-40.27	770.68	0.38
Zooplankton	Oct 1997	-0.55	22.65	0.31	0.81	-62.21	1198.89	0.57
Zooplankton	Oct 1999	-0.32	14.48	0.38	0.35	-26.90	521.59	0.55
Zooplankton	Oct 2000	-0.26	10.97	0.11	1.00	-76.22	1460.20	0.73
Mean (SD)				0.14 (0.13)				0.49 (0.14)

^aLinear regression function is $Y = aX + b$. Quadratic regression function is $Y = \alpha X^2 + \beta X + \gamma$.

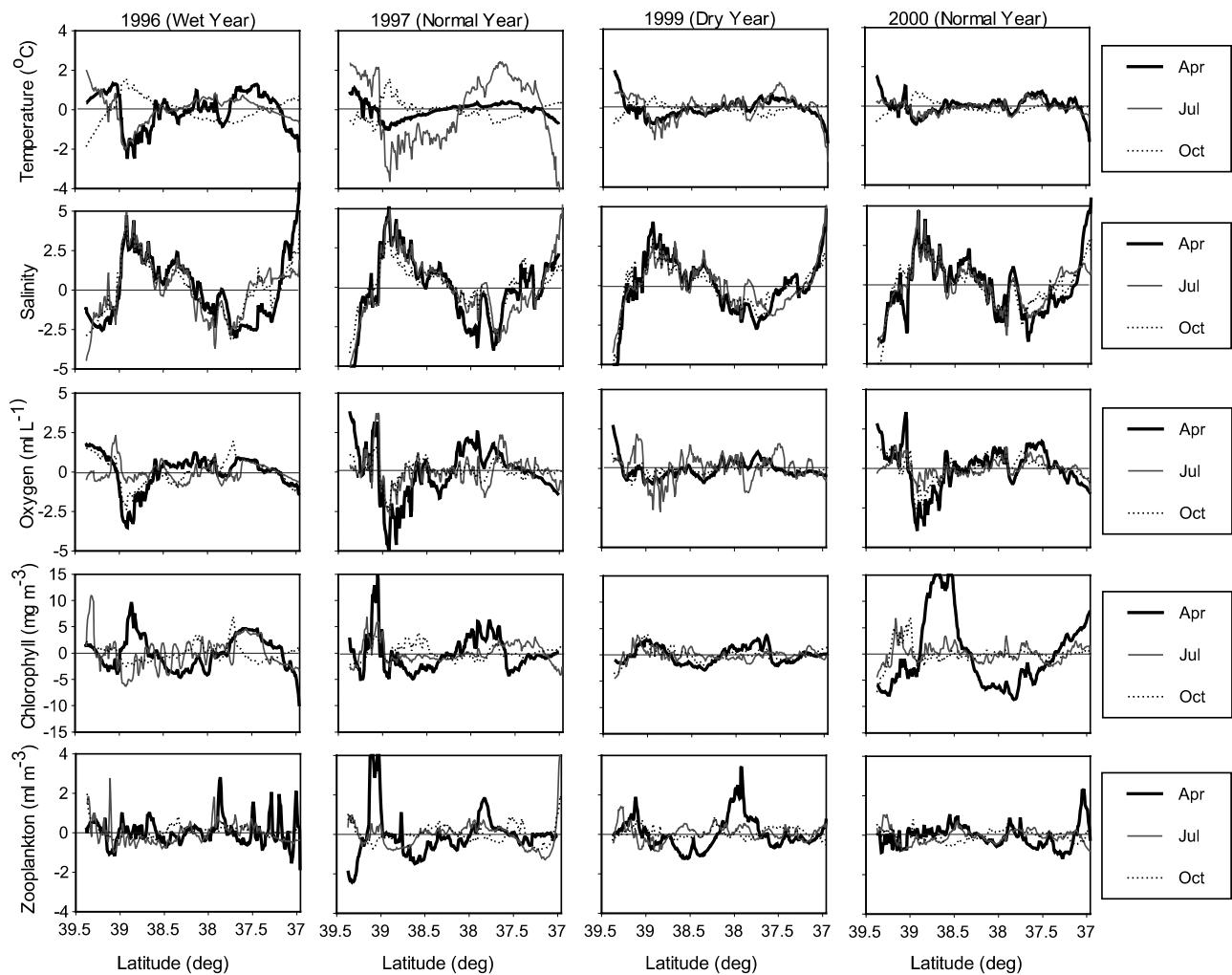


Figure 8. Distribution of the residuals of quadratic regression between water column-averaged temperature, salinity, dissolved oxygen concentration, chlorophyll-a, and zooplankton biomass at each of the 300 evenly spaced water columns along the axis of Chesapeake Bay and latitude. The residuals are equal to the observed water column-averaged values minus the predicted values based on the quadratic regression between each variable and latitude.

latitude, reflected the sources of freshwater input into Chesapeake Bay. The patterns in the residuals of linear and quadratic regressions for salinity were similar (Figures 7 and 8). Negative residuals for salinity were found in the upper part of the transect where the Susquehanna flow enters the bay and at 38°N near the Potomac River outflow, the second largest freshwater source for Chesapeake Bay (Figures 7 and 8). The magnitude of the variability in the residuals of the quadratic regressions for temperature, dissolved oxygen, chlorophyll-a, and zooplankton biomass generally was smaller than those of the linear regression (*t*-test, $p < 0.05$), but the spatial locations of the major positive/negative deviations generally were similar (Figures 7 and 8). There were often positive residuals for chlorophyll-a, and zooplankton biomass south of the negative salinity residuals as phytoplankton and zooplankton communities developed in the lower salinity plume waters (Figures 7 and 8). Negative residuals for oxygen developed around 39°N coincident with positive residuals for salinity (more bottom-layer salt and stratification)

and chlorophyll-a (more organic input to bottom waters; Figures 7 and 8).

3.6. Patch Sizes of Plankton and Hydrographic Variables

[31] Analysis showed that the water column-averaged values of each variable and the residuals of linear and quadratic regressions between the water column-averaged values and latitude were autocorrelated (Figures 9–11). The patch size of each variable depended on whether the data were detrended and the detrending technique applied. The mean patch size of water column-averaged hydrographic and plankton values was larger than the mean patch size of the residuals of linear and quadratic regressions but the differences between linear and quadratic regressions were not significant (ANOVA, Tukey's HSD postcomparison test, $p > 0.05$, Table 2). For all three autocorrelation analyses, the patch sizes of salinity were larger than those for temperature, dissolved oxygen, chlorophyll-a, and zooplankton biomass (ANOVA, Tukey's HSD post-comparison

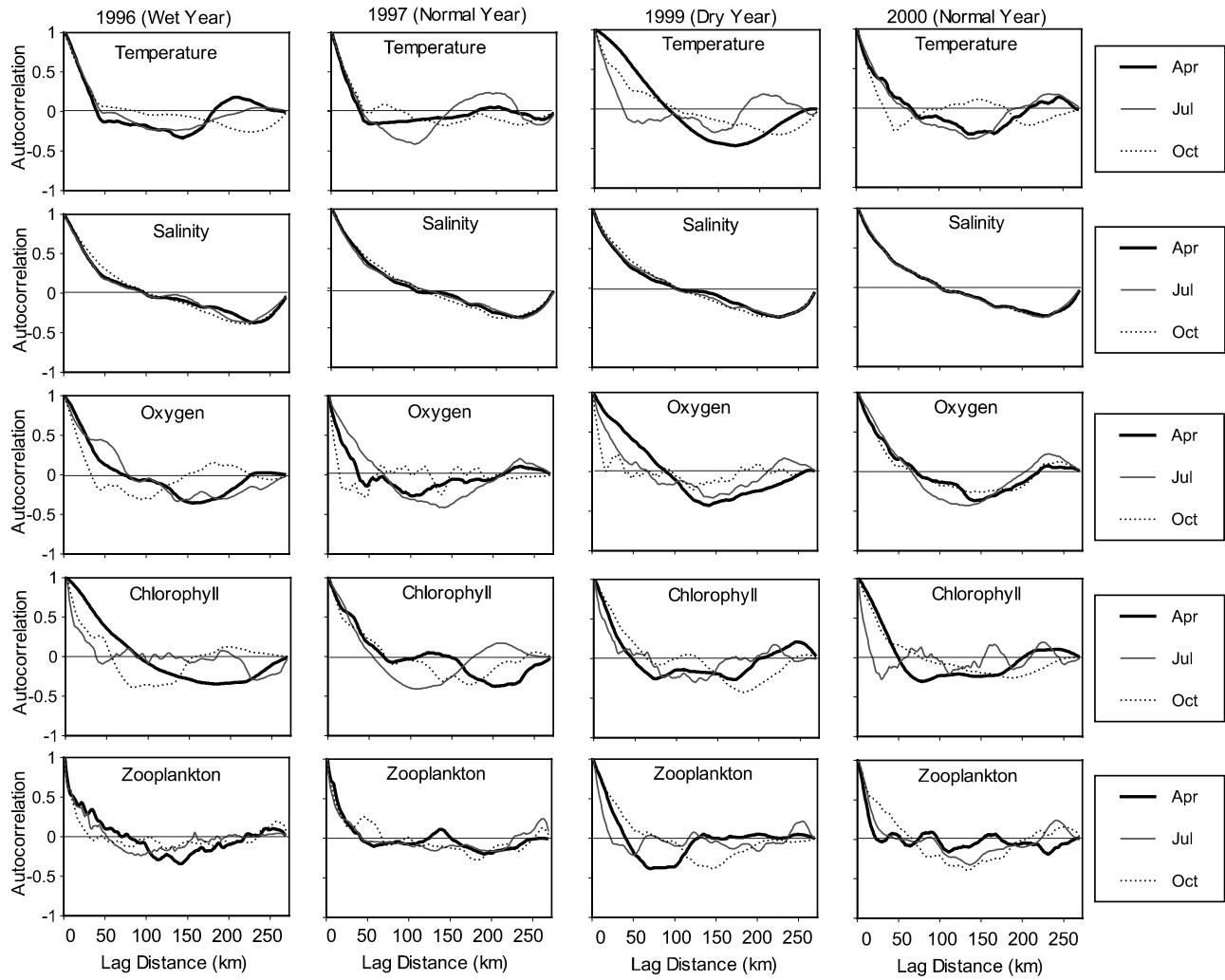


Figure 9. Autocorrelation function of the water column-averaged temperature, salinity, dissolved oxygen concentration, chlorophyll-a, and zooplankton biomass at each of the 300 evenly spaced water columns along the axis of Chesapeake Bay.

test, $p < 0.05$, Table 2). Seasonal variations in the patch sizes of each variable were not significant (ANOVA, $p > 0.05$, Table 2). The mean zooplankton patch size for all the cruises was 49, 36, and 21 km for the nondetrended, linear-detrended, and quadratic-detrended autocorrelation analysis (Table 2).

4. Discussion

[32] There were strong variations in freshwater input to Chesapeake Bay during the field program (Figure 2). Freshwater input is one of the most important physical forces for the Chesapeake Bay ecosystem affecting salinity distribution, water stratification and mixing, and nutrient levels [Boicourt, 1992; Boynton and Kemp, 2000; Langland et al., 2001]. As a consequence of water column structure and nutrient availability, dissolved oxygen, chlorophyll-a, and zooplankton biomass often co-vary with freshwater input [Malone et al., 1988; Hagy et al., 2004; Kimmel and Roman, 2004].

[33] The variability in salinity distribution was mainly influenced by freshwater input and showed strong seasonal

and interannual variability (Figures 2–6). The most striking example of this was the location of the 12 isohaline during April of 1996 and 1999 (Figure 3). Such large changes in the salinity distribution in the estuary influence the distribution of many organisms, in particular zooplankton (Figure 3) [Kimmel and Roman, 2004]. The majority (50%) of freshwater input into Chesapeake Bay is from the Susquehanna River at the head of the bay (Figure 1) [Schubel and Pritchard, 1986]. This major freshwater source is responsible for establishing the strong salinity gradient along the axis of the bay (Figures 3–6).

[34] The magnitude and location of the phytoplankton biomass maximum in April is largely determined by freshwater input during January to April [Malone et al., 1988; Harding, 1994]. The freshwater input was low from January to April in 1999 (Figure 2), and a small April phytoplankton bloom developed around 37.8°N (Figures 3 and 6). The freshwater input was high from January to April in 1996 (Figure 2), and an extensive April chlorophyll-a maximum developed in almost the entire lower bay ($<37.8^{\circ}\text{N}$; Figures 3 and 6). Although the accumulated freshwater input was similar between 1997 and 2000, the April

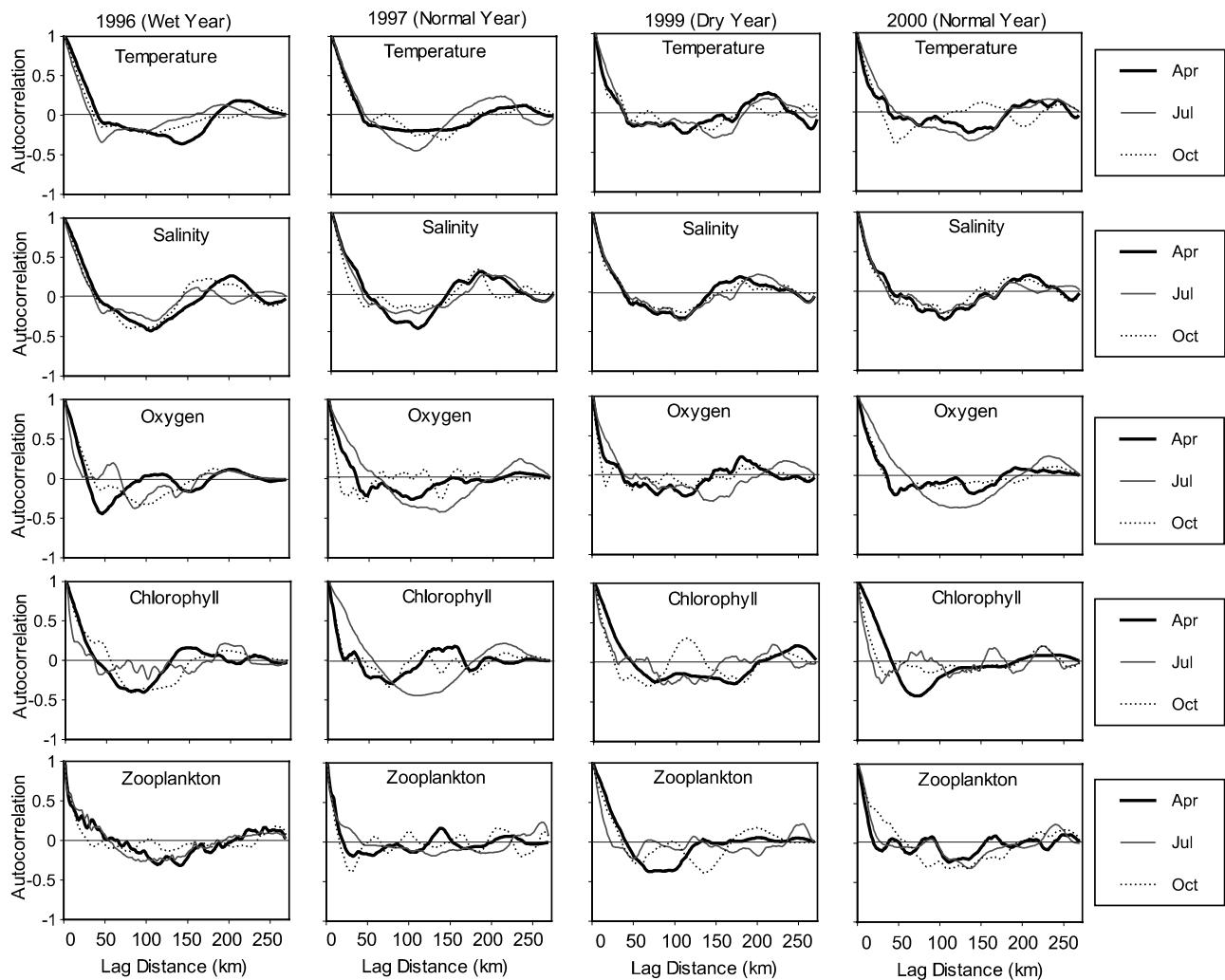


Figure 10. Autocorrelation function of the residuals of water column-averaged temperature, salinity, dissolved oxygen concentration, chlorophyll-a, and zooplankton biomass at each of the 300 evenly spaced water columns along the axis of Chesapeake Bay. The residuals are equal to the observed water column-averaged values minus the predicted values based on the linear regression between each variable and latitude.

freshwater input was lower in 1997 than in 2000 (Figure 2). Therefore the April chlorophyll-a maximum in 2000 was not only more extensive in magnitude, but also farther down the bay in location than in 1997 (Figure 6).

[35] In general, high zooplankton biomass occurred in the upper and lower bay regardless of season (Figures 3–6). In the upper bay this may be due to the physical trapping of zooplankton in the estuarine turbidity maximum (ETM). In most coastal plain estuaries, a zone of increased suspended particulate concentration, the ETM is associated with landward limit of salt intrusion. The estuarine gravitational circulation results in a near-bottom convergence at the salt limit, trapping settling particles and aggregating copepods and fish [Schubel, 1968; North and Houde, 2001, 2003; Roman et al., 2001, 2005; Jung and Houde, 2003]. The high zooplankton biomass in the lower bay may result from the combination of the intrusion of shelf water that can have high zooplankton concentrations relative to Chesapeake Bay water [Boicourt et al., 1987] and the cyclonic eddy in the lower bay that can accumulate passively drifting

particles by means of convergent flows and low flushing rates [Hood et al., 1999].

[36] The middle portion of Chesapeake Bay (38 to 39°N) was usually an area of low zooplankton biomass (particularly in July and October) despite the elevated concentrations of chlorophyll-a in the region (Figures 3–6). This area is the deepest portion of Chesapeake Bay and the bottom waters are hypoxic during the summer and fall (Figures 5 and 6) [Officer et al., 1984]. The low-oxygen waters can restrict the distribution of zooplankton and result in copepod egg mortality [Roman et al., 1993]. The middle portion of Chesapeake Bay is also an area of elevated concentrations of zooplankton predators: ctenophores, *Mnemiopsis leidyi*, scyphomedusae, *Chrysaora quinquecirrha* (Purcell et al. [1994], Kimmel and Roman [2004], and Chesapeake Bay Program Water Quality Monitoring Program, www.chesapeakebay.net), and juvenile bay anchovy, *Anchoa mitchilli* [Luo and Brandt, 1993; Rilling and Houde, 1999; Jung and Houde, 2003]. Thus both anoxia and predation can result in reduced copepod biomass in the middle portion of Ches-

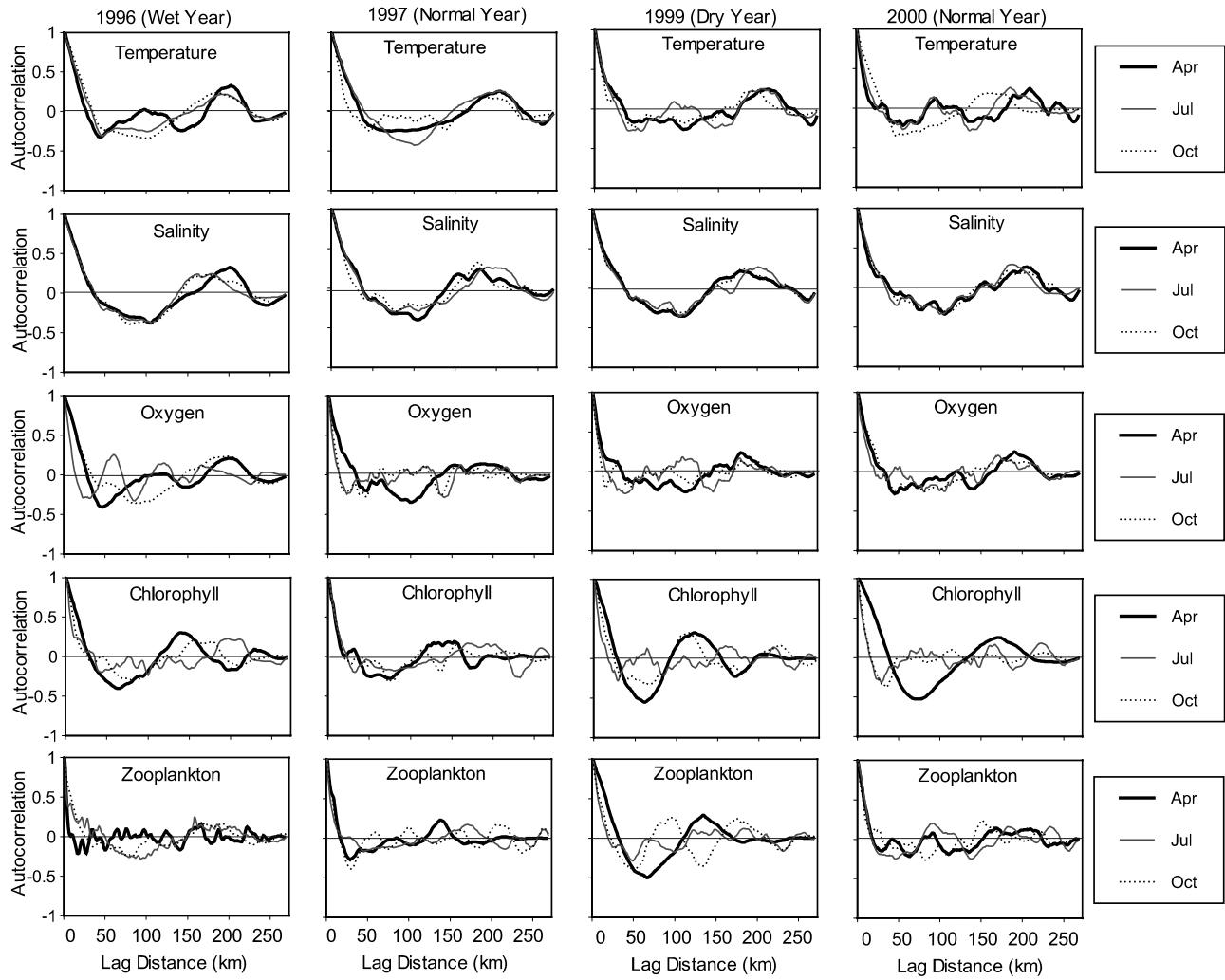


Figure 11. Autocorrelation function of the residuals of water column-averaged temperature, salinity, dissolved oxygen concentration, chlorophyll-a, and zooplankton biomass at each of the 300 evenly spaced water columns along the axis of Chesapeake Bay. The residuals are equal to the observed water column-averaged values minus the predicted values based on the quadratic regression between each variable and latitude.

apeake Bay. This negative impact would be expected to increase in the summers and falls of wet years as a result of increased hypoxic water [Officer *et al.*, 1984] as well as increased biomass of ctenophores [Kimmel and Roman, 2004]. In general, ctenophore biomass in Chesapeake Bay is highest in summers and falls following springs of average to above-average freshwater discharge [Kimmel and Roman, 2004]. Thus increased freshwater discharge can enhance both the food resources (chlorophyll-a) and predators (ctenophores) of zooplankton.

[37] Water column-averaged values of temperature, salinity, dissolved oxygen, chlorophyll-a, and zooplankton biomass showed strong bay-wide patterns (Figure 6) with a large proportion of the variance in these water column-averaged values accounted for by the linear/quadratic relationship between each variable and latitude (Table 1). The relationships between phytoplankton and zooplankton with latitude were weaker than that for salinity as a result of more localized physical and biological controls of the

plankton (Table 1). In contrast to the bay-wide linear/quadratic trends, the pattern of variability in the residuals of linear/quadratic regression, especially for the biological variables (Figures 7 and 8), is mostly likely a result of local processes such as convergence/divergence zones, biological processes (e.g., top-down and bottom-up controls [Daly and Smith, 1993; Folt and Burns, 1999; Roman *et al.*, 2005]), freshwater input from the subestuaries of Chesapeake Bay and inputs of plankton from shelf waters.

[38] Autocorrelation analysis has been used to asses patch sizes of plankton and larval fish [e.g., Richerson *et al.*, 1978; Rowe and Epifanio, 1994]. The autocorrelation function is often dominated by large-scale trends in the data [Warner, 1998]. Therefore in order to minimize the influence of these large-scale trends, data must be detrended before using autocorrelation analysis [Warner, 1998]. Although the bay-wide trends of the wafer column-averaged values varied considerably (Figure 6), the trends could be modeled by a linear or quadratic regression (Table 1). If

Table 2. Patch Sizes of Temperature, Salinity, Dissolved Oxygen, Chlorophyll-a, and Zooplankton for Each Cruise Along the Axis of Chesapeake Bay in the Water Column-Averaged Values at Each of the 300 Evenly Spaced Water Columns Along the Axis of Chesapeake Bay, the Residuals of Linear, and the Residuals of Quadratic Regressions, Respectively (See Text for Details)

Cruise	Patch Size, km														
	Temperature			Salinity			Oxygen			Chlorophyll			Zooplankton		
Avg	Lin	Quad	Avg	Lin	Quad	Avg	Lin	Quad	Avg	Lin	Quad	Avg	Lin	Quad	
Apr 1996	38	40	25	96	41	34	72	27	27	87	36	28	71	65	10
Apr 1997	34	32	33	96	36	36	36	37	32	67	34	34	41	53	15
Apr 1999	88	36	33	99	38	37	88	34	34	46	54	27	40	29	31
Apr 2000	66	36	21	98	41	37	70	34	32	46	37	37	23	20	17
Mean	56	37	28	97	40	36	67	33	31	61	40	32	45	36	18
SD	22	2	6	1	2	1	19	4	3	17	4	5	20	19	9
Jul 1996	44	41	32	95	36	36	77	62	13	36	54	33	51	41	31
Jul 1997	37	35	39	104	28	36	68	14	13	54	43	22	42	15	29
Jul 1999	34	34	26	99	37	36	66	36	15	67	46	15	22	41	18
Jul 2000	59	35	23	97	40	33	65	39	20	18	27	14	51	22	16
Mean	43	38	30	99	37	35	69	49	15	44	33	21	42	36	23
SD	9	6	7	3	2	1	5	12	3	18	14	9	12	12	7
Oct 1996	87	37	33	100	39	36	32	37	32	55	24	25	30	35	24
Oct 1997	41	39	22	103	41	30	14	35	13	68	41	17	67	19	14
Oct 1999	97	47	33	103	35	39	39	59	11	63	17	23	79	29	21
Oct 2000	32	30	32	102	37	38	71	32	28	77	24	15	66	59	28
Mean	64	34	30	102	35	36	39	29	21	66	36	20	60	34	22
SD	28	3	6	1	4	4	21	9	11	8	13	5	18	16	6
<i>All Cruises</i>															
Mean	55	37	29	99	37	36	58	37	22	57	36	24	49	36	21
SD	24	4	6	3	4	2	22	13	9	19	12	8	20	16	7

there were no linear/quadratic bay-wide trends, the detrending processes would have little or no effect on the subsequent autocorrelation analysis. If trends were present, the linear and quadratic detrending techniques would have a similar effect on the subsequent autocorrelation analysis (e.g., salinity, Tables 1 and 2). If there were quadratic bay-wide trends, then the quadratic regression would be more effective in trend removal than the linear regression (all variables except for salinity, Table 1), which in turn would affect the subsequent autocorrelation analysis (all variables except for salinity, Tables 2).

[39] The patch sizes of the hydrographic and plankton variables were undetrended data > linear detrended data > quadratic detrended data (Figures 9–11; Table 2). For each procedure, the patch size of salinity was larger than those for temperature, dissolved oxygen, chlorophyll-a and zooplankton biomass (Table 2).

[40] The mean zooplankton patch size for all the Chesapeake Bay axial cruises conducted with the Scanfish-OPC data was 49, 36, and 21 km for the nondetrended, linear detrended, and quadratic-detrended autocorrelation analysis (Table 2). Using different sampling systems and statistical techniques, investigators have found similar patch sizes of zooplankton biomass in shelf waters [e.g., Mackas, 1984; Huntley et al., 1995; Solow and Steele, 1995].

[41] Zooplankton patches affect the average and variance in individual larval fish growth rates [Letcher and Rice, 1997] and survival [Houde, 1987]. Both abundance and growth rates of bay anchovy (*Anchoa mitchilli*) larvae tend to be positively correlated with zooplankton concentrations in Chesapeake Bay [Rilling and Houde, 1999; Auth, 2003]. Bay anchovy egg concentrations also tend to be positively correlated with local zooplankton concentrations, suggesting that adult bay anchovy are spawning in areas where zooplankton concentrations are relatively high

(good for both feeding the adults and the newly hatched larvae [Dorsey et al., 1996]). Auth [2003] found a significant relationship between recruitment of bay anchovy (at about 100 days of age) in Chesapeake Bay and feeding incidence of larvae ($r = +0.93$), when larvae were about 10 days of age and feeding on zooplankton. This result suggests that zooplankton availability or abundance in the larval stage was important in controlling recruitment. Brandt [1993] used bioenergetics models to illustrate that the patchiness and availability of zooplankton must be considered in order to evaluate how fronts might affect planktivore fish growth and production. The two dominant fish planktivores in the lower bay, bay anchovy (*Anchoa mitchilli*) and Atlantic menhaden (*Brevoortia tyrannus*), can respond rapidly to both persistent and ephemeral fronts [Brandt, 1993]. Thus these fish species may have adapted to the more patchy distribution of zooplankton in the middle and lower bay (Figures 3–5). These zooplankton biomass patches may represent critical food concentrations for the enhanced growth and survival of fish larvae. Models of the effect of zooplankton patches on the growth rate of larval fish suggest that zooplankton patches enhance net growth of the fish larvae [Davis et al., 1991]. Zooplankton patches in Chesapeake Bay and their regular occurrence at bathymetric and frontal features [Roman et al., 2005] suggest that zooplankton patches could increase the growth of larval and juvenile fish. Thus knowledge of the size, persistence and location of zooplankton patches in Chesapeake Bay may allow better forecasting of fish recruitment.

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