

Severe droughts reduce estuarine primary productivity with cascading effects on higher trophic levels

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Abstract

Using a 10-yr time-series data set, we analyzed the effects of two severe droughts on water-quality and ecosystem processes in a temperate, eutrophic estuary (Neuse River Estuary, North Carolina). During the droughts, dissolved inorganic nitrogen concentrations were on average 46–68% lower than the long-term mean due to reduced riverine input. Phytoplankton productivity and biomass were slightly below average for most of the estuary during a spring–autumn drought in 2002, but were dramatically lower than average throughout the estuary during an autumn–winter drought in 2007–2008. Droughts affected upper trophic levels through alteration of both habitat condition (i.e., bottom-water dissolved oxygen levels) and food availability. Bottom-water dissolved oxygen levels were near or slightly above average during the 2002 drought and during summer 2007. Concomitant with these modest improvements in bottom-water oxygen condition, fish kills were greatly reduced relative to the long-term average. Low-oxygen bottom-water conditions were more pronounced during summer 2008 in the latter stages of the 2007–2008 drought, and mesozooplankton abundances were eight-fold lower in summer 2008 than during nondrought years. Below-average mesozooplankton abundances persisted for well over 1 yr beyond cessation of the drought. Significant fish kills were observed in summer 2008 and 2009, perhaps due to the synergistic effects of hypoxia and reduced food availability. These results indicate that droughts can exert both ephemeral and prolonged multiyear influence on estuarine ecosystem processes and provide a glimpse into the future, when many regions of the world are predicted to face increased drought frequency and severity due to climate change.

Estuaries are among the most productive and diverse aquatic ecosystems on Earth, providing food resources and habitat for many ecologically and economically important fish and shellfish species (Hobbie 2000; Bianchi 2007). Adequate freshwater delivery is vital to support the biodiversity, productivity, and fishery habitat of estuaries (Nixon and Buckley 2002). Estuaries also process terrigenous material transported by rivers and play a major role in regional and global biogeochemical cycles (Bianchi 2007).

Over the past century, natural cycles of freshwater delivery to the coastal zone have been altered due to human activity and climate change (Milliman et al. 2008). There is increasing concern that ongoing anthropogenic nutrient enrichment, human modification of hydrologic regimes, and climate change will drive estuaries to an unsustainable status through negative effects on water quality and habitat (Flemer and Champ 2006). One particularly worrisome climate-change scenario centers on droughts, which are predicted to increase in frequency and severity over the coming century in many world regions (Trenberth et al. 2003; Christensen et al. 2007). Through their potential to dramatically reduce freshwater delivery to estuaries, droughts represent an important driver of contemporane-

ous and future estuarine ecosystem functioning. Nonetheless, lack of sufficiently long time-series has left the scientific community with only a limited understanding of the full ecological effect that these climatic stressors have on estuaries and the coastal zone.

Among the critical needs in projecting estuarine ecosystem response to ongoing or impending environmental change is the development of mechanistic linkages between specific key features of climatic and anthropogenic drivers (e.g., nutrient loading, variable freshwater delivery) and relevant components of the afflicted ecosystem. Here, we examine a 10-yr time-series (2000–2009) of water quality, plankton, and biogeochemical measurements from North Carolina's Neuse River Estuary (NRE), a eutrophic estuary. During this time-series, two severe droughts occurred, allowing us to assess the ecosystem response to these features. Our guiding questions were: How is phytoplankton productivity affected by drought-induced reductions in freshwater and nutrient inputs? What are the consequences for upper trophic levels in terms of food availability and habitat condition? We hypothesized that because planktonic primary productivity is largely controlled by nutrient (mainly nitrogen) availability in this and many other estuaries (Rudek et al. 1991; Fisher et al. 1992), drought-induced reductions in river flow and nutrient loading would lead to reduced primary productivity.

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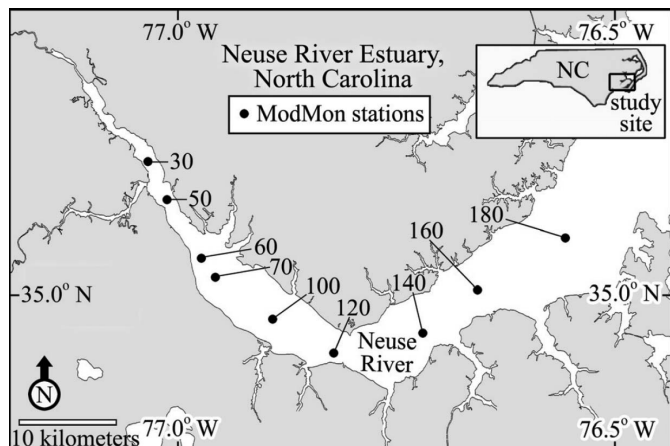


Fig. 1. Map of the Neuse River Estuary indicating ModMon sampling sites.

Methods

Study area—The NRE is a shallow (average 2.7 m) microtidal estuary that has experienced accelerated eutrophication, largely due to nonpoint-source input of nutrients from expanding urbanization, agricultural rowcrop, and livestock operations in its watershed (Stow et al. 2001). Water residence times range from several weeks during high freshwater discharge periods in winter to several months in summer, and the system regularly undergoes persistent vertical salinity stratification (Paerl et al. 1998). Water-quality measurements have been made biweekly since 1994 at fixed stations as part of the Neuse River Estuary Modeling and Monitoring program (ModMon; Fig. 1). The ModMon database served as the main source of water-quality data used in this study (01 Jan 2000 to 01 Dec 2009).

Environmental data—Monthly mean river flow was obtained from a U.S. Geological Survey gauging station (02089500) located near Kinston, North Carolina. Salinity and dissolved oxygen (DO; as % saturation) were measured at discrete depths in the water column using a Hydrolab Datasonde 3 (prior to 13 Sep 2000) or a Yellow Springs Instruments (YSI) 6600 multiparameter sonde. The diffuse light attenuation coefficient (K_d) was calculated from depth profiles of photosynthetically active radiation (PAR, 400–700 nm) measured using a LiCor underwater quantum sensor. Dissolved inorganic nutrient and chlorophyll *a* (Chl *a*) concentrations were estimated from discrete samples collected at the surface (~ 0.2 m). Dissolved inorganic nitrogen (DIN) concentration was calculated by summing nitrate (NO_3^-), nitrite (NO_2^-), and ammonium (NH_4^+). DIN and orthophosphate (PO_4^{3-}) samples were prepared by vacuum filtering (< 25 kPa) duplicate water samples from a site through precombusted Whatman glass microfiber filters (GF/F). The filtrate was stored frozen (-20°C) in high-density polyethylene bottles until analysis. $\text{NO}_3^- + \text{NO}_2^-$ concentration was determined using a Lachat QuickChem 8000 flow-injection autoanalyzer by method 31-107-04-1-C. Detection limits ranged from $0.08 \mu\text{mol L}^{-1}$

to $0.26 \mu\text{mol L}^{-1}$. NH_4^+ concentration was determined using method 31-107-06-1-A/B. Detection limits ranged from $0.31 \mu\text{mol L}^{-1}$ to $0.34 \mu\text{mol L}^{-1}$. PO_4^{3-} was determined using method 31-115-01-1-F/G. The detection limit was $< 0.02 \mu\text{mol L}^{-1}$.

Chl *a* was determined using the modified in vitro fluorescence technique, Environmental Protection Agency method 445.0, without acidification. Duplicate 50-mL samples from each site were vacuum-filtered (< 25 kPa) under subdued lighting through GF/F filters. The filters were blotted dry, wrapped in foil and frozen immediately at -20°C until analysis. Chl *a* was extracted using a tissue grinder and 10 mL of 90% acetone, then stored overnight at -20°C . Extracts were filter-clarified via centrifugation and analyzed on a Turner Designs 700 fluorometer that was configured for nonacidification. The fluorometer was calibrated with known concentrations of pure Chl *a* (Sigma Chem.). Primary productivity (PPR) was determined using an adaptation of the ^{14}C bicarbonate method (Paerl et al. 1998). Water samples from each site were stored in 10-liter high-density polyethylene containers overnight in an outdoor pond at the University of North Carolina-Chapel Hill Institute of Marine Sciences, Morehead City, North Carolina, that receives a constant flow of water from adjacent Bogue Sound, thereby simulating ambient water temperatures. The following morning, subsamples were added to triplicate clear plastic bottles and to one dark bottle for determination of CO_2 uptake. A solution of ^{14}C bicarbonate was added to each bottle, and they were subsequently incubated for 4 h in the outdoor pond. The light bottles were incubated underneath a field light simulator (FLS), while the dark bottles were incubated in a covered perforated bucket that was submerged in the pond. The FLS simulates the ambient light conditions that phytoplankton are exposed to via mixing in the estuary and is comprised of a rotating wheel with varying levels of screening. During the incubations, PAR was measured using a 2π LiCor spherical quantum sensor. At the conclusion of incubations, samples were gently mixed and the entire contents were vacuum filtered (< 25 kPa) through GF/F filters. Filters were exposed to concentrated HCl fumes for ~ 1 h to remove inorganic ^{14}C , then placed in 7-mL plastic scintillation vials to which 5 mL of liquid scintillation cocktail was added. Vials were capped, shaken, stored in the dark for 3–24 h and then assayed for radioactivity using a Beckman LS 6500 liquid scintillation spectrometer. In addition to the samples, triplicate voucher samples were used to quantify the radioactivity of added ^{14}C . Voucher samples consisted of 100 μL of ^{14}C and 100 μL of phenylethylamine, to which 5 mL of liquid scintillation cocktail were added.

From 2000 to 2002, mesozooplankton were collected during the summer at a single station in the NRE (located between Sta. 120 and 140; Fig. 1) using a Schindler–Patalas trap (30 liters collected). From 2007 to 2009, mesozooplankton were collected from discrete depths every 2–4 weeks throughout each year from all stations in the NRE via a pump (60 liters collected). Flow rates were calibrated prior to each cruise. Gear comparisons were completed and no differences were found in species counts or size

measurements for copepods or nauplii (J. C. Taylor unpubl. data). With both approaches, collected or pumped water was filtered through a 65- μm -mesh-size Nitex net. Captured organisms were preserved with 3% buffered formalin and stored in the dark until further analysis in the laboratory. Triplicate 10-mL subsamples were extracted using a Hensen–Stempel pipette, and mesozooplankton were counted using a Leica Zoom 2000 dissecting microscope equipped with a rotating counting wheel. Organisms were identified to genus and species when possible. Fish mortality data from the Craven and Pamlico County NRE sections were obtained from the North Carolina Division of Water Quality Environmental Sciences Section (<http://portal.ncdenr.org/web/wq/ess/fishkills>).

Data analysis—The 10-yr monthly average of each parameter was calculated, and the deviation (hereafter ‘anomaly’) of each parameter on a given month was calculated by subtracting the 10-yr monthly average from a parameter’s average during a given month.

Application of remote sensing—To support the development of satellite-based Chl *a* estimates for the NRE, data were initially collected using the National Aeronautics and Space Administration’s Advanced Visible-Infrared Imaging Spectrometer (AVIRIS). AVIRIS provided hyperspectral imagery at a 20-m ground sampling distance (GSD) that was used to simulate Medium Resolution Imaging Spectrometer (MERIS) imagery. Chl *a* concentrations were optimally estimated using AVIRIS bands centered at 673.6 nm and 692.7 nm. Ratios of AVIRIS bands centered at or near those corresponding to the MERIS sensor indicated that relatively good satellite-based estimates could be derived ($R^2 = 0.80$) for water-color constituents using a 665 : 709 nm reflectance ratio (Lunetta et al. 2009). From 2006 to 2009, MERIS provided water-color imagery that was used to produce Chl *a* concentration estimates across the entire NRE. MERIS top of atmosphere satellite radiance were calibrated using in situ ferry-based monitoring (FerryMon) Chl *a* data collected along a NRE transect ($n = 633$). This allowed for development of a semi-empirical model to predict Chl *a* concentrations across the entire NRE at a 300-m GSD.

Results

There are extensive records of spatially–temporally explicit water-quality data in the NRE from ModMon and other programs. Readers are encouraged to consult Christian et al. (1991) and Paerl et al. (2007) for typical ranges of nutrient concentrations, and Valdes-Weaver et al. (2006) and Paerl et al. (2007) for Chl *a* concentrations.

Ecological effects of 2002 and 2007–2008 droughts—2002: Sporadic low- to moderate-intensity drought conditions occurred in early 2001, but were not contiguous with more prolonged moderate-to-severe drought conditions that developed in the NRE watershed during late October 2001 (Fig. 2B; see also U.S. Drought Monitor, <http://www.drought.unl.edu/dm/archive.html>). The late 2001 drought

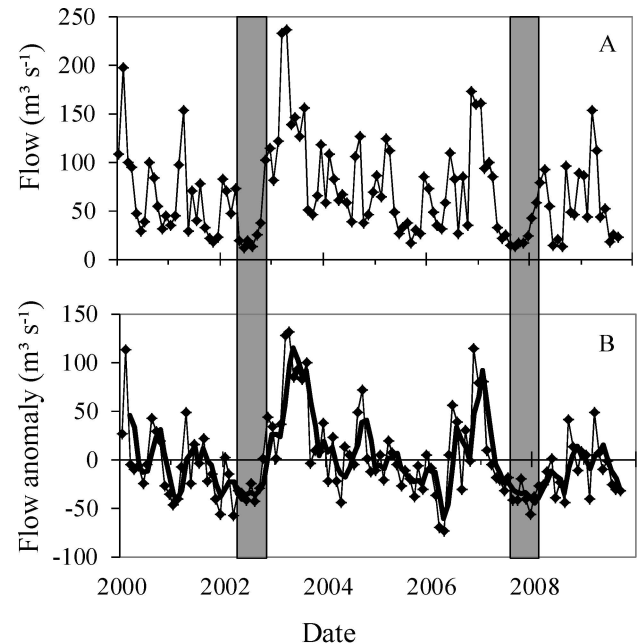


Fig. 2. (A) Mean monthly Neuse River flow rates, and (B) mean monthly river flow anomaly (thin line) with 3-month moving average (thick line) superimposed. Shaded bars highlight timing of severe droughts.

conditions were accompanied by below-average Neuse River flow rates (Fig. 2B) and above-average salinities throughout the NRE (Fig. 3). A brief return to average river flows in early 2002 was punctuated by development of even more extreme drought conditions throughout the NRE watershed during early spring (U.S. Drought Monitor). River flow remained below average through autumn of 2002 (Fig. 2B), and salinity was above average by ~ 3 –7 throughout the estuary until the end of 2002 (Fig. 3; Table 1). During the drought, K_d was also below average throughout most of the estuary by 0.1–0.3 m^{-1} , except at Sta. 30 (Table 1). DIN concentrations were below average by 0.2–8.3 $\mu\text{mol L}^{-1}$ or 16–71% (mean \pm SD = 46% \pm 18% [Fig. 4; Table 1]). PO_4^{3-} concentrations were above average by 0.3–0.6 $\mu\text{mol L}^{-1}$ at Sta. 30–70, but were near average in the lower estuary (data not shown).

The effects of the 2002 drought on phytoplankton biomass and productivity varied depending on location in the NRE. Sta. 30 exhibited above-average Chl *a* (by 15.5 $\mu\text{g L}^{-1}$) and PPR (by 31.3 $\text{mg C m}^{-3} \text{h}^{-1}$ [Figs. 5 and 6, respectively; Table 1]). Chl *a* was below average by 5.5–12.6 $\mu\text{g L}^{-1}$ at Sta. 100–160 (Fig. 5; Table 1). Primary productivity was below average at Sta. 50–140 by 1.4–6.2 $\text{mg C m}^{-3} \text{h}^{-1}$, but was above average at Sta. 160 and 180 by 3.4 $\text{mg C m}^{-3} \text{h}^{-1}$ and 9.8 $\text{mg C m}^{-3} \text{h}^{-1}$, respectively (Fig. 6; Table 1). At Sta. 30 and 50, bottom-water (~ 0.5 m above bottom) DO was less saturated than average by 9.5–23% (Fig. 7; Table 1). In contrast, bottom DO at Sta. 60 and 100–160 was slightly more saturated than average (by 2.4–14% [Fig. 7; Table 1]). There was no obvious effect of the 2002 drought on summertime zooplankton abundances relative to previous nondrought summers (Fig. 8). Fish mortalities ($\sim 32,000$ dead fish

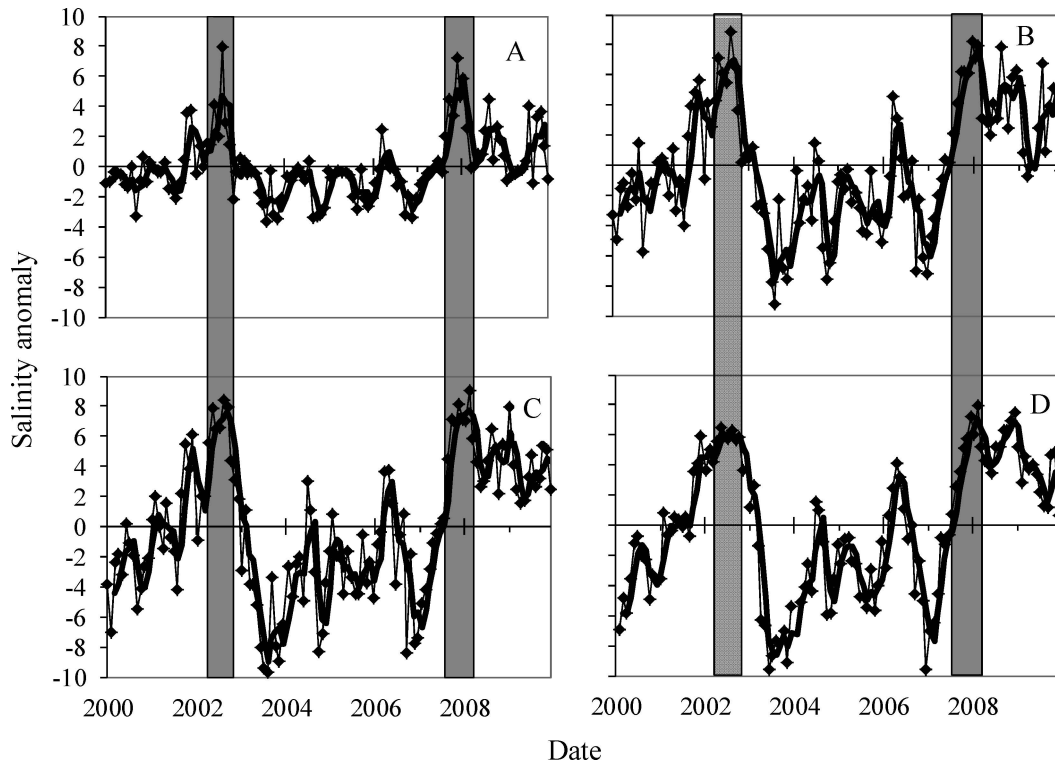


Fig. 3. Mean monthly salinity anomaly (thin line) with 3-month moving average (thick line) from January 2000 to December 2009 at Sta. (A) 30, (B) 70, (C) 120, and (D) 180. Shaded bars highlight timing of severe droughts.

total) were dramatically lower in 2002 than the 10-yr average by almost two orders of magnitude (Fig. 9).

2007–2008: Dry conditions were in place throughout the NRE watershed during much of spring (Mar to May) 2007. More severe dry conditions developed in late summer, and by September, ‘exceptional’ drought conditions were in place (U.S. Drought Monitor). Below-average Neuse River

flow rates developed in April 2007 (Fig. 2B), but above-average salinities did not develop until July (Fig. 3), owing to the fact that Neuse River flow rates in the previous winter were well above average, which depressed estuary-wide salinities (Figs. 2, 3). River flow remained below average through early spring 2008 (Fig. 2B), and salinity throughout the estuary was above average (by ~ 4 –7

Table 1. Mean anomalies for water-quality parameters in the Neuse River Estuary during the 2002 and 2007–2008 droughts. Bold values indicate that anomalies are statistically different than the mean anomaly from the same time frame of all other years of this study (repeated-measures analysis of variance, $p < 0.05$).

Date	Sta.	Salinity	K_d (m^{-1})	DIN ($\mu mol L^{-1}$)	Chl <i>a</i> ($\mu g L^{-1}$)	PPR ($mg C m^{-3} h^{-1}$)	Bottom DO (% saturation)
Apr 2002– Oct 2002	30	3.1	0.2	-8.3	15.5	31.3	-23.0
	50	3.9	-0.1	-5.2	0.8	-6.2	-9.5
	60	5.3	-0.2	-2.8	-0.4	-2.7	14.0
	70	6.0	-0.3	-4.2	2.2	-1.4	-0.2
	100	6.8	-0.3	-2.1	-5.5	-4.9	14.0
	120	6.8	-0.2	-1.4	-12.6	-4.3	2.4
	140	6.8	-0.2	-0.9	-6.1	-4.5	9.0
	160	6.7	-0.2	-0.6	-6.1	3.4	4.6
	180	5.9	-0.1	-0.2	0.2	9.8	-2.8
Aug 2007– Feb 2008	30	4.3	-0.5	-17.4	10.7	49.7	11.9
	50	6.0	-0.6	-17.5	5.0	7.0	13.5
	60	6.7	-0.6	-13.2	-13.9	-22.6	18.7
	70	6.6	-0.6	-11.1	-12.4	-25.1	13.2
	100	6.8	-0.6	-5.7	-14.5	-32.1	14.9
	120	7.1	-0.5	-4.2	-11.9	-32.2	12.8
	140	6.9	-0.4	-2.5	-13.2	-24.6	6.5
	160	5.9	-0.4	-1.1	-11.9	-19.2	10.2
	180	5.4	-0.3	-0.3	-8.1	-16.6	5.2

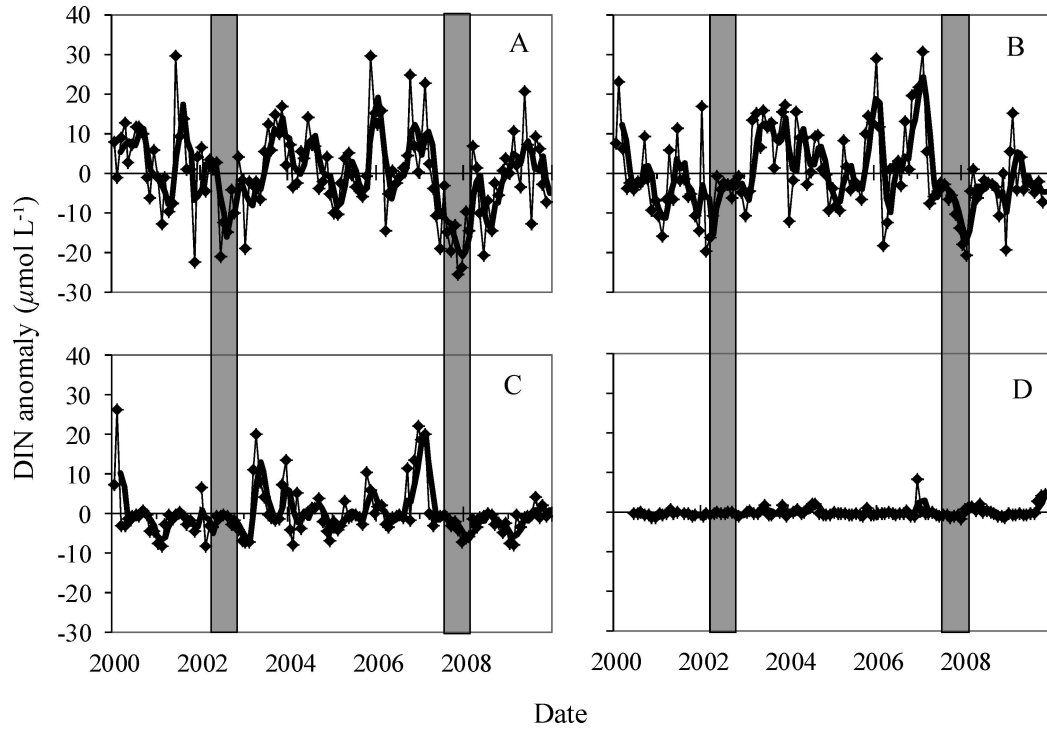


Fig. 4. Mean monthly dissolved inorganic nitrogen anomaly (thin line) with 3-month moving average (thick line) from January 2000 to December 2009 at Sta. (A) 30, (B) 70, (C) 120, and (D) 180. Shaded bars highlight timing of severe droughts.

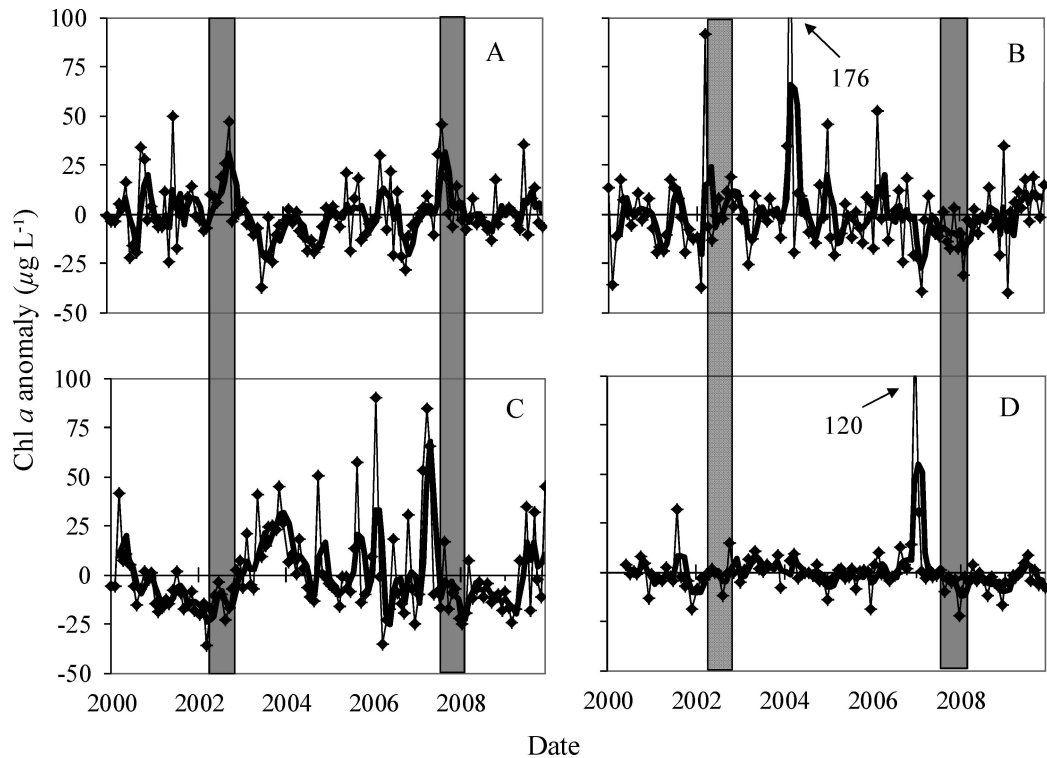


Fig. 5. Mean monthly Chl *a* anomaly (thin line) with 3-month moving average (thick line) from January 2000 to December 2009 at Sta. (A) 30, (B) 70, (C) 120, and (D) 180. Shaded bars highlight timing of severe droughts.

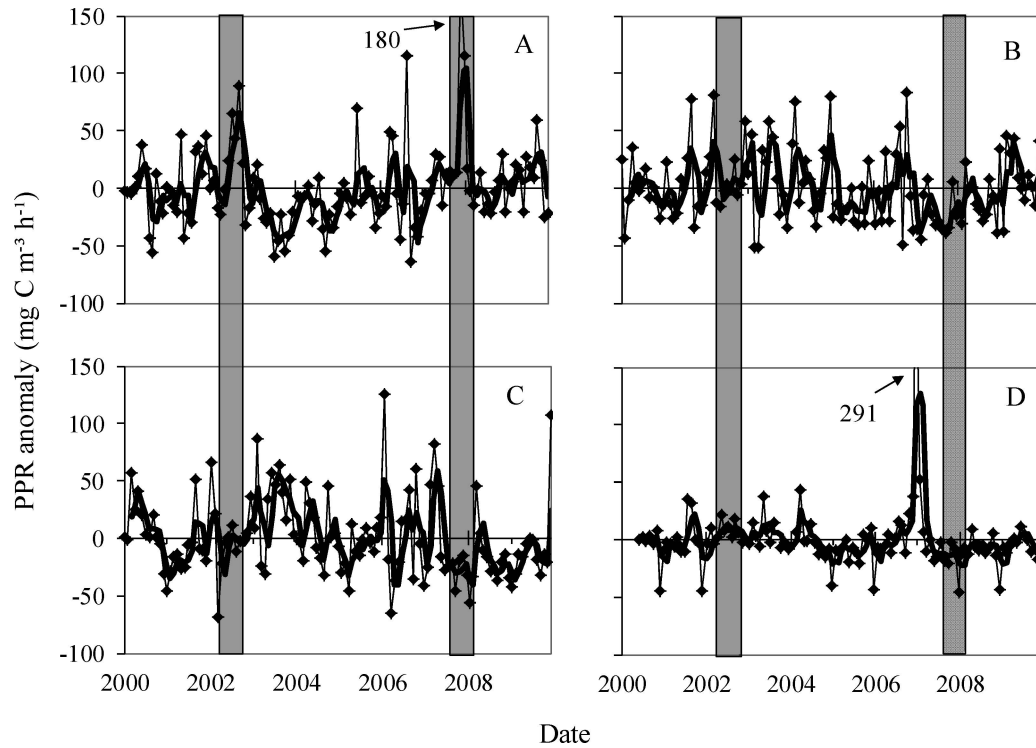


Fig. 6. Mean monthly primary productivity anomaly (thin line) with 3-month moving average (solid line) from January 2000 to December 2009 at Sta. (A) 30, (B) 70, (C) 120, and (D) 180. Shaded bars highlight timing of severe droughts.

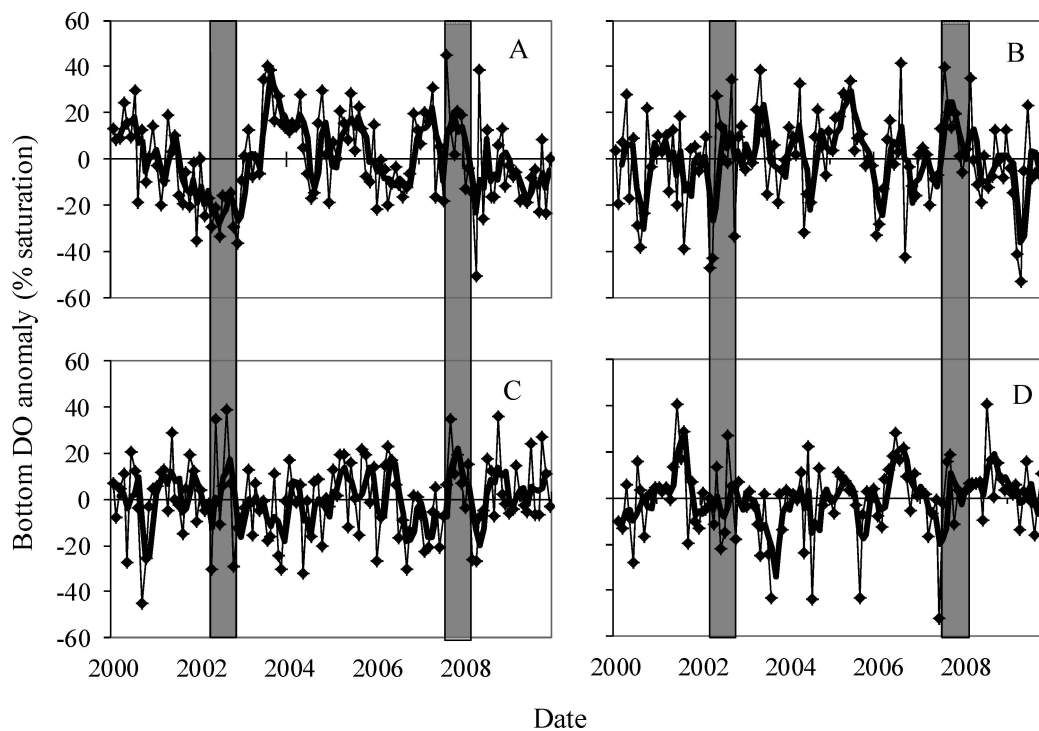


Fig. 7. Mean monthly bottom dissolved oxygen anomaly (thin line) with 3-month moving average (thick line) from January 2000 to December 2009 at Sta. (A) 30, (B) 70, (C) 120, and (D) 180. Shaded bars highlight timing of severe droughts.

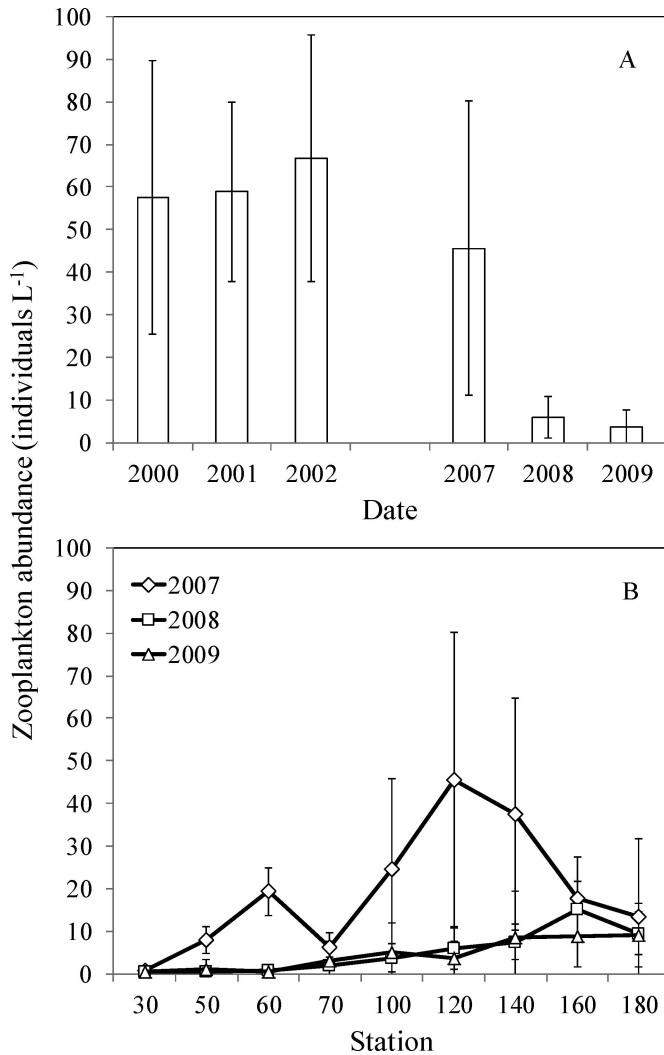


Fig. 8. (A) Mean combined summer (Jun, Jul, Aug) abundances of *Acartia* sp. and *Oithona* sp. from a location between Sta. 120 and 140 (2000–2002) and from Sta. 120 (2007–2009). (B) Mean combined summertime abundances of *Acartia* sp. and *Oithona* sp. at each station in 2007 (diamonds), 2008 (squares), and 2009 (triangles).

during the peak of the drought from August 2007 to February 2008 (Fig. 3; Table 1). During this time, K_d was well below average throughout the estuary by 0.3–0.6 m⁻¹ (Table 1). DIN concentrations were also below average by 0.3–17.5 $\mu\text{mol L}^{-1}$ or 22–92% (mean \pm SD = 68% \pm 23% [Fig. 4; Table 1]). PO_4^{3-} concentrations were above average by 0.1–0.5 $\mu\text{mol L}^{-1}$ at Sta. 30–100, but were slightly below average in the lower estuary (data not shown).

As with the 2002 drought, the effect of the 2007–2008 drought on phytoplankton biomass and productivity varied depending on location in the NRE. Sta. 30 and 50 exhibited above-average Chl *a* (by 10.7 $\mu\text{g L}^{-1}$ and 5.0 $\mu\text{g L}^{-1}$, respectively [Fig. 5; Table 1]) and PPR (by 49.7 mg C m⁻³ h⁻¹ and 7.0 mg C m⁻³ h⁻¹, respectively [Fig. 6; Table 1]). Chl *a* was below average by 8.1–14.5 $\mu\text{g L}^{-1}$ (Fig. 5; Table 1) and PPR by 16.6–32.2 mg C m⁻³ h⁻¹ (Fig. 6; Table 1) at Sta. 60–180. Chl *a* and PPR were below

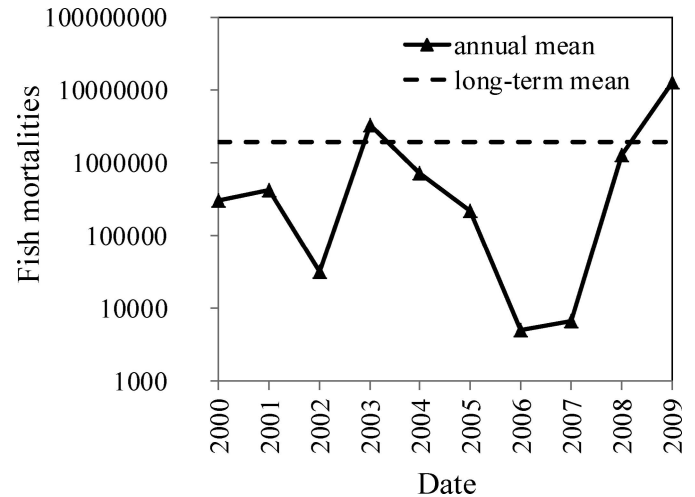


Fig. 9. Annual mean and long-term (2000–2009) mean fish mortality.

average by 29% \pm 43% and 29% \pm 60%, respectively, throughout the entire estuary, and by 50% \pm 7% and 56% \pm 8%, respectively, at Sta. 60–180. Bottom DO during autumn 2007–winter 2008 was more saturated than average by 5.2–18.7% (Fig. 7; Table 1).

Multiyear effects of the 2007–2008 drought—A brief cessation of the most severe 2007–2008 drought conditions resulted in a return to normal river flow rates from May to early June 2008. This was interrupted by continuation of moderate drought conditions that lasted from June to October 2008 (U.S. Drought Monitor; Fig. 2). Neuse River flow rates finally returned to near average in late 2008 (Fig. 2). Nonetheless, the 2007–2008 drought had effects on NRE water-quality parameters that lasted well into 2009. Salinity remained above average through early 2009 in the upper estuary (Sta. 30–100; Fig. 3), and through the end of 2009 at Sta. 120–180 (Fig. 3; data not shown for stations other than 120 and 180). K_d was near average in late spring to early summer 2008, but from July through December 2008 it was below average (by 0.3 \pm 0.1 m⁻¹) throughout the estuary (data not shown). K_d generally remained below average (by 0.2 \pm 0.2 m⁻¹) at Sta. 120–180 through the end of 2009, and was below average in mid to upper estuary from July through October 2009 (data not shown). DIN concentrations briefly returned to near average for parts of the estuary in spring 2008 (Fig. 4). From May through December 2008, DIN was again below average (by 3.5 \pm 4.5 $\mu\text{mol L}^{-1}$) throughout the estuary, and generally remained so at Sta. 100–180 through late summer 2009 (Fig. 4; data not shown for stations other than 120 and 180). In the mid to upper estuary, DIN concentrations were above average in winter 2009, but below average at those stations in summer through autumn 2009.

Perhaps the most striking effect of this extended period of drought was on downstream phytoplankton communities. For example, in January–February 2007 prior to the drought, large phytoplankton blooms exceeding 40 $\mu\text{g L}^{-1}$ Chl *a* were noted throughout the length of the estuary, but

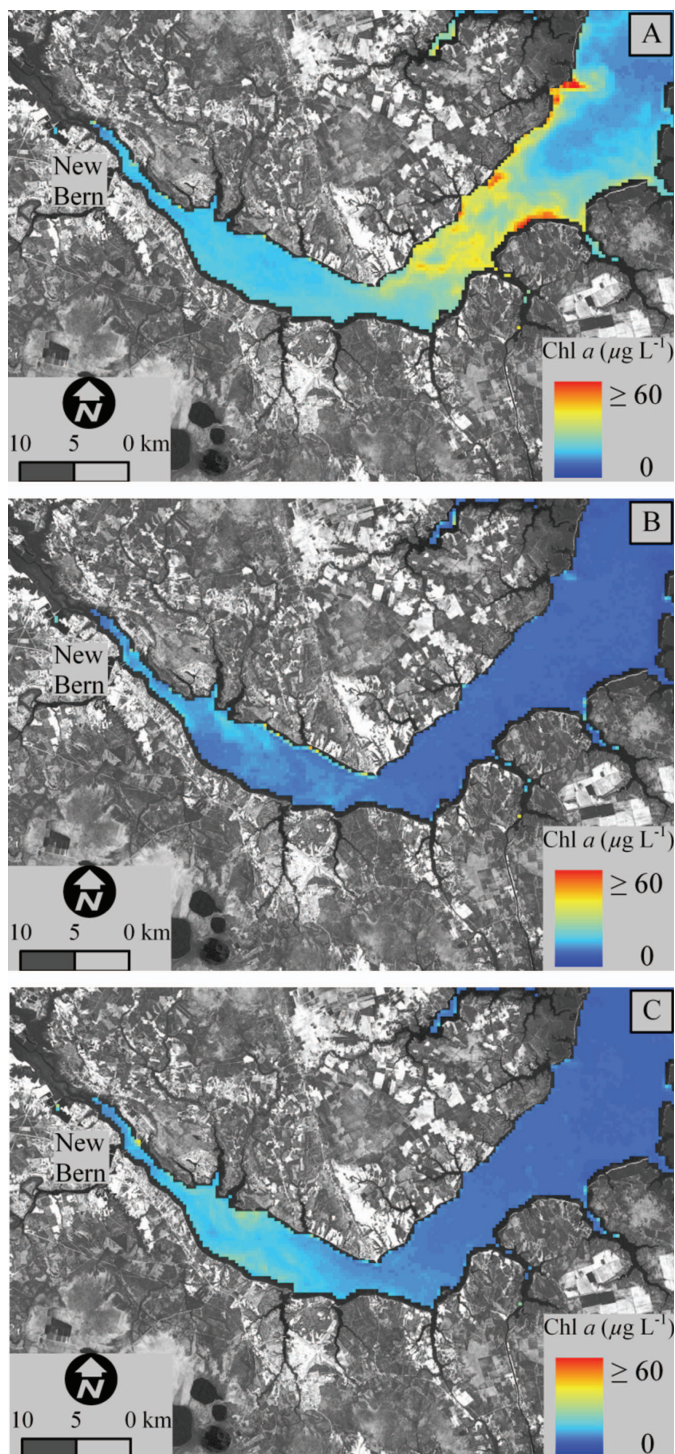


Fig. 10. MERIS-derived Chl *a* concentration for winter 2007–2009. Mean concentrations were calculated using the following imagery dates: (A) 2007 – 11 January, 29 January, and 23 February; (B), 2008 – 04 January and 08 February; (C) 2009 – 14 January, 12 February, 21 February, and 23 February. Note that a one pixel buffer (300-m GSD) was eliminated between the land–water interface to remove land-reflectance contamination.

were most concentrated in the lower estuary (Figs. 5, 10). However, during the peak of the drought in January–February 2008, phytoplankton biomass was well below average throughout the estuary and the downstream region was devoid of blooms (Figs. 5, 10). Chl *a* patterns were spatially–temporally variable in the mid to upper estuary during summer 2008, but were uniformly below average (by $10 \pm 6 \mu\text{g L}^{-1}$) in the lower estuary from summer 2008 through April 2009 (Fig. 5). During winter 2009, blooms ($\geq 20 \mu\text{g L}^{-1}$ Chl *a*) were again seen in the upper estuary, but the downstream region of the NRE remained devoid of blooms (Figs. 5, 10). PPR was spatially variable during spring 2008, but was well below average (by $20 \pm 10 \text{ mg C m}^{-3} \text{ h}^{-1}$) at all stations from June through September 2008 (Fig. 6). At Sta. 100–180, PPR remained below average (by $15 \pm 13 \text{ mg C m}^{-3} \text{ h}^{-1}$) through May 2009 (Fig. 6). During summer 2008, bottom DO was below average in most of the NRE during June and in the mid to upper estuary during September, but near or above average during July and August (Fig. 7). During summer 2009, bottom DO was below average for most stations in June, August, and September, but above average in July at most mid-estuary stations (60–120; Fig. 7). Mean summertime combined abundances of the two dominant mesozooplankton taxa, *Acartia* sp. and *Oithona* sp., were much lower in 2008 (6.0 ± 4.8 individuals L^{-1}) and 2009 (3.5 ± 4.0 individuals L^{-1}) than in 2007 (45.6 ± 34.4 individuals L^{-1}) at Sta. 120 (Fig. 8A), where mesozooplankton tend to be concentrated in the NRE (M. Wetz unpubl.). No upstream migration of the zone of maximum mesozooplankton abundance was observed during 2008 and 2009 compared to 2007 (Fig. 8B). Fish mortalities were near average in 2008 ($\sim 1,290,000$ dead fish total; Fig. 9), and even higher in 2009 ($\sim 12,700,000$ dead fish total; Fig. 9).

Discussion

Droughts represent a natural feature of regional climates, such as in the eastern United States, where numerous dry periods lasting 10 to < 100 yr have been identified in paleoclimate records of the past 1600 yr (Stahle et al. 1988; Cronin et al. 2000). Yet despite the fact that various world regions undergo regular drought cycles, their ecological effects have not been well-characterized to date. Results presented here indicate that droughts can exert both ephemeral and prolonged multiyear influences on estuarine ecosystem processes, and provide a glimpse into the future when many regions of the world are predicted to face increased drought frequency and severity due to not only natural drought cycles but also anthropogenic climate change (Trenberth et al. 2003; Christensen et al. 2007). The two droughts studied here clearly affected the physical–chemical properties of the NRE. Interestingly, the extent by which the droughts influenced nutrient loading, plankton productivity and biomass, water quality, and fishery habitat seemed to depend on their timing as well as the progression of regional climate patterns after they ceased. The 2002 drought was most severe during spring–summer, ended abruptly when an extended wet period began in the NRE watershed, and no long-term effects were

detected. In contrast, the 2007–2008 drought was most severe during autumn–winter. Although Neuse River flow rates returned to normal at the cessation of the drought, they were not substantially higher than average as following the 2002 drought and, thus, it took well over 1 yr for the NRE ecosystem to recover. We will first discuss in detail differences in ecological effects that can be attributed to droughts occurring at different times of year, then we will discuss long-term effects from the 2007–2008 drought.

Spatial–temporal aspects of drought effects—During spring–summer in the NRE, phytoplankton productivity is partly supported by episodic freshwater nutrient pulses, but mostly by recycled nutrients from within the water column and sediments (Christian et al. 1991; Twomey et al. 2005), consistent with observations from other temperate estuaries (Malone et al. 1988; Lewitus et al. 1998). In general the region of chlorophyll maxima (C_{MAX}) tends to be located in the oligo- and mesohaline zones (Valdes-Weaver et al. 2006). The 2002 drought brought exceptionally low spring–summer river flow to the NRE, and consequently the C_{MAX} was concentrated in the uppermost region of the estuary. Throughout the estuary, DIN concentrations were below average as a consequence of both enhanced upstream uptake (Sta. 30) and a general reduction in riverine nutrient loading. Despite this, the effect on phytoplankton biomass and productivity was small. Both parameters were reduced relative to the long-term average in the mid-estuary, but only minimally. Because productivity during this time of year is mostly driven by recycled nitrogen (Christian et al. 1991; Twomey et al. 2005), it is not surprising that the effect of reduced riverine nitrogen input was negligible. Nonetheless, accompanying the modest reduction in productivity were small increases in bottom DO relative to the long-term average at most mid-estuary stations. Bottom-water DO tends to undergo prolonged, frequent periods of hypoxia in the mid-estuary during summer as a consequence of microbial degradation of sinking phytodetritus (Paerl et al. 1998; Buzzelli et al. 2002). Hence, one would expect improved bottom DO conditions if surface phytoplankton bloom activity was reduced. The reduced freshwater inflow also led to a slight reduction in salinity stratification (M. Wetz unpubl.), which (stratification) along with degradation of phytodetritus largely controls bottom-water hypoxic conditions (Paerl et al. 1998). These modest improvements in bottom DO may have had a significant effect on fisheries habitat in the NRE, because fish kills were greatly reduced in 2002 relative to the long-term average. Although it is difficult to establish causality due to the complexity of factors controlling NRE fish kills and overall fishery response to hypoxia (Paerl et al. 1998; Eby et al. 2005), extensive bottom-water hypoxia is one of the main correlates of fish kills in the system (Paerl et al. 1998). It is important to note that a similar chain of events was observed in summer 2007, during the tempered ‘spin-up’ phase of the more severe autumn 2007–winter 2008 drought. Phytoplankton productivity was reduced, bottom DO was elevated, and fish kills were greatly reduced relative to the long-term average.

During autumn–winter in the NRE, phytoplankton productivity is strongly dependent on riverine nutrient supplies (Rudek et al. 1991), and productivity can be nitrogen-limited (primarily in the lower estuary) or nitrogen and phosphorus co-limited (in the upper estuary; Rudek et al. 1991). Large blooms of the dinoflagellate, *Heterocapsa triquetra*, are a common feature of the NRE and other adjacent estuaries in winter (Paerl et al. 1998; Pinckney et al. 1998; Litaker et al. 2002), and these blooms may contribute > 50% of total annual phytoplankton production to the system (Paerl et al. 1998; Pinckney et al. 1998). During the winter 2007–2008 drought, light attenuation and inorganic nitrogen concentrations were greatly reduced relative to the long-term average. A small C_{MAX} developed in the uppermost region of the estuary, possibly in response to enhanced light availability. However, both productivity and Chl *a* were well below average throughout the rest of the system, most likely due to reduced nutrient availability. Given both the contribution of winter blooms to system-wide annual primary productivity in the NRE and other temperate estuaries and the role that their sedimented biomass plays in benthic nutrient dynamics extending into warm summer months (Kemp and Boynton 1984; Paerl et al. 1998), failure of these phytoplankton blooms to develop may have profound but yet to be determined consequences for ecosystem function.

Multiyear effects of droughts—Ecological effects of the 2007–2008 drought persisted well into 2009. Compared to long-term averages, salinity remained above average and DIN below average throughout a large segment of the estuary. Consequently, Chl *a* and PPR remained well below average in the downstream region of the estuary through spring 2009. This region of the estuary is an important habitat for mesozooplankton growth and trophic transfer (Mallin 1991; Mallin and Paerl 1994; M. Wetz unpubl.). Mesozooplankton abundance was 8–13-fold higher in summer 2007 prior to the peak of the drought as compared to summer 2008 or 2009, indicating that the downstream reduction in primary production may have had a multiyear negative effect on these important intermediaries between phytoplankton and fish. Although the downstream region of the NRE remained mostly devoid of blooms into 2009, relatively large phytoplankton blooms were observed in the mid to upper estuary during summer 2008 and winter–spring of 2009 as normal river flow resumed. This, along with intensifying stratification due to freshwater inflow, inevitably led to development of hypoxic conditions in this region and consequently, significant fish kills were observed.

Effects of drought on water quality and higher trophic levels—Only recently have time-series of sufficient length been developed to discern the effect of large-scale climatic or anthropogenic change on estuarine and coastal ecosystems (Zingone et al. 2010). An emerging trend from many of these studies is that abnormally low river flow, from droughts or otherwise, consistently results in below-average estuarine phytoplankton productivity or biomass (Rask et al. 1999; Abreu et al. 2010; Philips et al. 2010). It is important to note, however, that both droughts in the

present study resulted in greater light penetration, due presumably to less phytoplankton and river-derived organic matter in the water column. Do droughts create conditions favorable for benthic microalgal or plant production, which may perhaps compensate for reduced phytoplankton production in the water column? During a severe drought in northern Europe, Rask et al. (1999) found that below-average phytoplankton biomass and light attenuation led to stimulation of eelgrass growth and enhanced bottom-water oxygen concentrations. In the NRE, Fear et al. (2004) estimated that a 15% reduction in phytoplankton biomass (due to nutrient-load reductions), within range of our observations, would lead to a 20% increase in sediment surface area that falls within the euphotic zone, implying that benthic microalgal production would increase as a result. These studies highlight the connectivity between benthic–pelagic processes in shallow coastal systems, and emphasize the necessity for consideration of both pelagic and benthic processes when assessing the ecological effects of large-scale climatic features such as drought.

Do the observed reductions in phytoplankton productivity lead to improved estuarine water quality, particularly in eutrophic systems? Paleocological records of much lower spatial–temporal resolution than the present study show a trend of more oxygenated estuarine waters during prolonged droughts (Cronin and Vann 2003). Our results, though generally compatible with the paleocological data, indicate that the relationship between drought and water quality is not straightforward, however. For instance, we found previously unexplored yet important spatial–temporal components to drought effects on estuarine phytoplankton communities. While phytoplankton productivity was below average and bottom DO above average over a substantial portion of the estuary during drought, phytoplankton productivity was actually enhanced and bottom DO below average in the upper estuary. Thus from an estuarine habitat-management perspective, water quality may improve in some areas of an estuary while deteriorating in others as a result of droughts, adding further complexity to management efforts in an era of dual anthropogenic–climatic change (Paerl 2006). We also found that the timing of the most severe stages of drought may determine its subsequent effect on phytoplankton communities and ultimately water quality. Notably, there was a small to moderate effect of the 2002 summer drought on phytoplankton, but a more substantial effect of the 2007–2008 autumn–winter drought. These differences may be a result of NRE phytoplankton–nutrient relationships, in that winter phytoplankton populations are much more reliant on riverine nutrients than those during summer (Paerl et al. 1998; Twomey et al. 2005).

In light of the consistent reductions in primary productivity during droughts, an emerging research and management focus from this work should be to better understand the effects of droughts and human-driven reductions in river flow on trophic transfer and fisheries in estuaries. Our results and those of others indicate that droughts may affect higher aquatic organisms through several pathways, namely alteration of food availability

and habitat condition (i.e., bottom DO). Abnormally low mesozooplankton abundances were noted in the NRE during summers of 2008 and 2009. Similarly, Reaugh et al. (2007) found lower mesozooplankton biomass in the Chesapeake Bay during years with reduced river flow vs. years with elevated flow. In terms of habitat, bottom waters were more oxygenated than average in the NRE during the 2002 drought and initial phase of the 2007–2008 drought (summer 2007), but not in summer 2008. Fish kills were relatively small in magnitude during both 2002 and 2007, but significant fish kills were noted during summer 2008, suggesting that lack of food availability (i.e., zooplankton) coupled with seasonal hypoxia affected fish health and population dynamics (Baptista et al. 2010; Martino and Houde 2010). In another example, Baptista et al. (2010) observed dramatic reductions in the biomass of estuarine resident and nonresident but estuarine-dependent fish species in a European estuary during a severe drought. Taken as a whole, the changes in zooplankton biomass and habitat condition, and their subsequent effects on fisheries, suggests that mechanisms by which variable freshwater delivery, including droughts, influence higher trophic levels are complex and require further study (Bennet et al. 1995; Livingston et al. 1997).

A recent synthesis of global ocean phytoplankton-biomass data concluded that in most of the world's oceans, phytoplankton biomass has declined dramatically over the past century due to ongoing climatic change (Boyce et al. 2010). As noted by the authors, this may have serious long-term implications for fisheries. Despite their small size, estuaries play a key role in global biogeochemical cycles and serve as critical habitat for many commercially important fish (Able 2005). Although droughts represent more of an acute climatic feature as opposed to the abovementioned chronic changes in oceanic condition, our results show that droughts can still elicit seasonal to multiannual reductions in planktonic biomass and likewise negatively affect resident fish populations. Further, considering that the estuarine-dwelling phase of many commercial fish species may be critically dependent on one particular season (Able and Fahay 1998), it is tempting to speculate that a single drought could have prolonged negative consequences on estuarine-dependent fish species if larval or juvenile growth is hampered (Baptista et al. 2010; Martino and Houde 2010). The ecological ramifications of a predicted increase in drought frequency and intensity as a result of ongoing climate change are indeed worrisome.

Droughts represent but one symptom of ongoing and impending global change that may influence estuarine ecosystems. The observed ecological changes resulting from drought may also reflect those that will occur in response to manmade reductions in freshwater delivery to the coastal zone, such as from damming, irrigation, and human consumption (Livingston et al. 1997; Milliman et al. 2008). Other symptoms of global change include warming, CO₂ accumulation and resultant changes to estuarine carbonate chemistry, and continuing human modification of nutrient cycling. Furthermore, computer models predict that many world regions will face more frequent and

intense precipitation extremes, including not only droughts but also flooding events (Trenberth et al. 2003; Christensen et al. 2007). Within the past several decades, including during the 10-yr data set presented here, several high river-flow periods have affected the NRE. The effects of these high-flow periods have been extensively studied and reported on for both the NRE and elsewhere (Paerl et al. 2007, 2010) and are not discussed here. Nonetheless, to better understand and predict how estuaries may change in the future, it will be necessary to examine and interrogate contemporaneous time-series to determine both the individual and interactive effects of these multiple symptoms of global change. As is hopefully obvious from results presented here, ongoing time-series should be careful to include observations at all trophic levels within a given system.

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