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Environmental Factors Affecting Recent Summertime Eelgrass Diebacks in the Lower Chesapeake Bay: Implications for Long-term Persistence

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ABSTRACT

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We investigated the effects of several environmental factors on eelgrass abundance before, during, and after widespread eelgrass diebacks during the unusually hot summer of 2005 in the Chesapeake Bay National Estuarine Research Reserve in Virginia. Systematic sampling with fixed transects was used to investigate changes in eelgrass abundance at downriver and upriver regions of the York River Estuary. Concurrently, continuous and discreet measurements of water quality were made at fixed stations in each area within the eelgrass beds from 2004 through 2006. Results indicate nearly complete eelgrass vegetative dieback during the July–August period of 2005, in contrast to the more seasonal and typical declines in the summer of 2004. Losses were greatest in the deeper areas of the beds and at the upriver site where light availabilities were lowest. Recovery of eelgrass during 2006 was greater in the downriver area, especially at mid-bed depths. By the fall of 2006, no shoot vegetation remained at the upriver site. In 2005, the frequency and duration of water temperatures exceeding 30°C were significantly greater than that of 2004 and 2006. Additionally, the frequencies of low dissolved oxygen excursions of 1–3 mg L^{-1} during this period were greater in 2005 than 2004 or 2006. These results suggest that eelgrass populations in this estuary are growing near their physiological tolerances. Therefore, the combined effects of short-term exposures to very high summer temperatures, compounded by reduced oxygen and light conditions, may lead to long-term declines of this species from this system.

ADDITIONAL INDEX WORDS: *Submerged aquatic vegetation, anoxia, hypoxia, dissolved oxygen, turbidity, light attenuation, inorganic phosphorus, nitrate, ammonium, climate change, National Estuarine Research Reserve.*

INTRODUCTION

Within the Chesapeake Bay, beds of eelgrass (*Zostera marina* L.) have declined precipitously from historical abundances in many areas (ORTH and MOORE, 1983). In the York River, a major subestuary where the Chesapeake Bay National Estuarine Research Reserve in Virginia (CBNERRVA) is located (37°13.6′ N, 76°28.7′ W), these declines have been greatest in the most upriver regions of the former eelgrass distribution (ORTH and MOORE, 1983) where anthropogenic inputs from the watershed are typically greatest (MOORE *et al.,* 1997). Although eelgrass beds remain in lower estuary regions, they have been found growing at much shallower depths compared to historical records, and since the late 1990s, overall abundances in these areas have been declining (ORTH *et al.,* 2006).

The interactions of environmental factors can have important consequences for eelgrass growth and survival. The effective light requirements of eelgrass can vary as a function of temperature (BINTZ *et al.,* 2003; MOORE *et al.,* 1997), sediment characteristics (GOODMAN *et al.,* 1993), or other factors such as epiphytic fouling (KEMP *et al.,* 2004). In addition, since plant respiration in eelgrass is supported by internally derived oxygen during the day, as well as that supplied from the water column by diffusion at night, factors that affect the sources and sinks of oxygen to and from the plants can also be very important (HOLMER and BONDGAARD, 2001). For example, GREVE *et al.* (2005) have associated late summer diebacks of eelgrass in Danish coastal waters with periods of low water-column concentrations of oxygen. Low oxygen supply to belowground and meristematic tissues can be especially injurious to seagrass through the accumulation of anaerobic metabolites (SMITH *et al.,* 1988) or the accumulation of phytotoxins such as sulfide from the reducing sediments (BORUM *et al.,* 2005; PEDERSON *et al.,* 2004) that can negatively affect photosynthesis, nutrient uptake, and growth (GOODMAN *et al.,* 1993; HOMER and BONDGAARD, 2001; PREGNALL *et al.,* 1984).

Climate change can have significant impacts on eelgrass as well as other seagrass through temperature increases, atmospheric and weather changes, and sea level increases (SHORT and NECKLES, 1999). OVIATT (2004) hypothesized

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that declines of eelgrass populations along the western Atlantic during the past 100 years have been associated with periods of warming. A projected one degree centigrade increase in average temperature (NEFF *et al.,* 2000) has been associated with short-term pulses of high water temperatures and low oxygen levels (GARRETT, 1992; NEFF *et al.,* 2000), which can have adverse effects on seagrass survival (GREVE *et al.,* 2005). PRESTON (2004) has determined through trend analysis of historical monitoring data from the Chesapeake Bay that the estuary has warmed approximately 0.8–1.1°C since the mid-20th century. Increased storm frequency and increased rainfall patterns have been projected for the Chesapeake Bay region (NAJJAR *et al.,* 2000; POLSKY *et al.,* 2000) and elsewhere (LABAT *et al.,* 2004; ROGERS and MCCARTHY, 2000) as a result of climate changes during the next 30 to 100 years. Increased rainfall (NEFF *et al.,* 2000) will result in increased sediment and nutrient inputs (NAJJAR *et al.,* 2000; POLSKY *et al.,* 2000), further decreasing light availability for eelgrass populations in the Chesapeake Bay (MOORE *et al.,* 1996, 1997). Sea level rise associated with climate warming will be observed both globally (DOUGLAS, 1991; WARRICK *et al.,* 1996) and locally (GEHRELS *et al.,* 2005; TITUS and NARAYANAN, 1995). As shorelines in the Chesapeake Bay are hardened as a result of human occupation, landward transgression of intertidal and shallow subtidal regions will be likely reduced and water levels will increase (NAJJAR *et al.,* 2000), limiting seagrass and other littoral habitat. In the Chesapeake Bay, eelgrass is growing near the southern limits of its distribution along the western shore of the Atlantic (KOCH and ORTH, 2003). It could be expected that the effects of climate change on eelgrass populations might be first evident in areas such as this one that are near the limits of its growth. This might be especially true in regions such as the Chesapeake Bay where light and temperature conditions have been demonstrated to already significantly affect eelgrass growth and reproduction (MOORE *et al.,* 1996, 1997; SILBERHORN *et al.,* 1983).

The highest global surface temperature in more than a century of instrumented data was recorded in the 2005 calendar year (Goddard Institute for Space Studies, New York, NY). For the Chesapeake Bay region, unusually high summertime water temperatures in 2005 were combined with extremely low dissolved oxygen (DO) levels. For example, summertime anoxia of bay waters exceeded 2.5 km^3 (Chesapeake Bay Program, 2006). This was 40% greater than in 2004 and more than 100% greater than similar periods in 2006. During August at the peak of bay anoxia, the measured bay anoxia volume exceeded 5 km^3 (1985–2005 average of 2.3 km^3). In addition, historical analysis of wind data for the summers of 1997–2005 (CHESAPEAKE BAY PROGRAM, 2005) indicated that the region had below normal wind. The mean summer wind speed for 2005 was the lowest recorded during the 1997–2005 period, which may have compounded the effects of high temperatures and other factors on oxygen levels.

In shallow water areas it is possible that short-term high temperatures may compound the effects of other prolonged environmental stresses that are influencing eelgrass persistence (GREVE *et al.,* 2005; MOORE *et al.,* 1997). Evaluating and quantifying these effects requires nearly continuous measurements of habitat conditions, as well as concurrent measurements of seagrass response (MOORE, 2004). In 2004, the National Estuarine Research Reserve System (NERRS) began a program to monitor biological resources including, areas of seagrasses. The NERRS is a network of 27 areas representing different coastal, biogeographic regions of the United States that are protected for long-term research, water-quality monitoring, education, and coastal stewardship through federal-state partnerships (NATIONAL ESTUARINE RESEARCH RESERVE SYSTEM, 2008). In the Chesapeake Bay region, the CBNERRVA instituted a study with the objectives to quantify the local patterns of short-term and interannual variability of eelgrass beds in the reserve system in the lower Chesapeake Bay and to relate these patterns to environmental and water quality conditions over several years of varying climatic conditions. In this study, we investigate the relationships between water quality conditions before, during, and after the summer of 2005, when a large-scale dieback of eelgrass beds occurred in the lower Chesapeake Bay region. Our specific questions were twofold: (1) What are the interannual patterns of variability and distribution of eelgrass growing in varying depths at two sites located along a water quality gradient? (2) How do any patterns of change relate to environmental and water quality conditions at these sites?

METHODS

Study Sites

Two sites were chosen for investigation in the York River Estuary (Figure 1), which is a tributary of the Chesapeake Bay and the location of reserve sites for CBNERRVA. Each of the two sites was initially evaluated through review of historical yearly aerial photography and ground survey information so as to be representative of patterns of seagrass distribution and abundance for the region (ORTH *et al.,* 2006). The Goodwin Island (GI) site (37°13′ N, 76°23′ W) is an island complex located at the mouth of the York River. It is a CBNERRVA reserve site and is an area that has been surrounded with seagrass beds for at least the last 70 years (MOORE *et al.,* 2000; ORTH and MOORE, 1983; ORTH *et al.,* 2006). The Gloucester Point (GP) site (37°15′ N, 76°30′ W) is located approximately 10 km upriver. It is located near the current upriver limits of seagrass growth in the York system (ORTH *et al.,* 2006). Eelgrass beds declined precipitously in the region upriver of this site between 1972 and 1974 (ORTH and MOORE, 1983), and the abundance of vegetation in this area can vary from year to year (ORTH *et al.,* 2006). It is a site that has been characterized during at least the past several decades by higher levels of turbidity and nutrients than downriver regions of the York River Estuary (MOORE, 2004; MOORE *et al.,* 1996, 1997).

Biological Sampling

A systematic sampling design, consisting of fixed transects located perpendicular to the shoreline and extending channelward past the deepest end of the seagrass vegetation, was used to investigate changes in seagrass abundance across the depth gradients at each site. Three permanent transects at

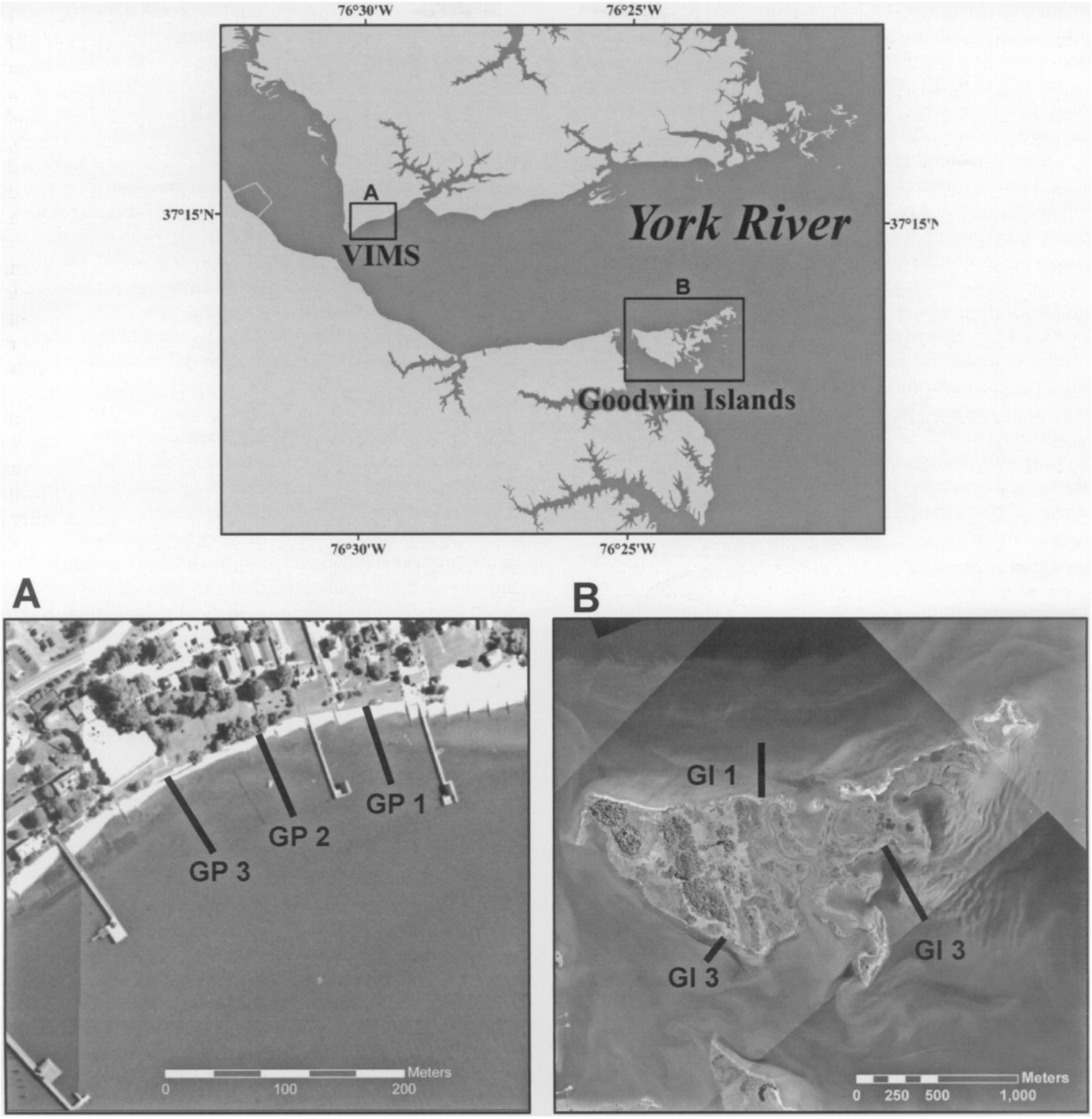

Figure 1. Locations of seagrass bed transects at the York River (A) Goodwin Island (GI) and (B) Gloucester Point (GP) study sites in the Chesapeake Bay National Estuarine Research Reserve in Virginia (CBNERVA).

Goodwin Island (Figure 1) were set at the approximate midpoints of the three shoreline reaches that encompass this reserve site. Three permanent transects were set at the Gloucester Point site (Figure 1). These were placed at approximately one-fourth, one-half, and three-fourths of the distance along the continuous band of eelgrass growing along that reach of shoreline.

Transects were sampled bimonthly to monthly over 5- to 10-m intervals by divers from the high tide shoreline to beyond the deepest channelward limits of seagrass growth using survey lines that were strung between permanent poles fixed at 50- to 100-m intervals. Sampling intervals were scaled to bed width. The shorter transects (GP1, GP2, GP3, GI1, and GI2) ranging from 80 m to 300 m were sampled at 5-m intervals for water depth and 10-m intervals for seagrass cover, density, and length. The longest transect (GI3) at 700 m in length was similarly sampled at 10-m and 20-m intervals. The individual relative depth data were normalized to

Mean Lower Low Water (MLLW), using concurrent water depth measurements at the Nation Ocean Survey, Yorktown, Virginia, U.S. Coast Guard Training Center tidal water level station located on the York River at a midpoint between the two sites (37°13.6′ N, 76°28.7′ W) as reference. At each 10- or 20-m sampling point, one observation of seagrass species bottom cover was made by divers over approximately a 2-m × 2-m area surrounding the transect sampling point. Next, a 0.5-m × 0.5-m quadrat was haphazardly tossed three times within the 2-m × 2-m sampling area, and seagrass cover by species was estimated within each tossed quadrate. The cover estimates were standardized to reference photographs of seagrass cover, and the visual census of seagrass cover was calibrated among individual divers in the field using a range of test quadrats to assure that they were the same (Short *et al.*, 2006). A small, 20-cm-diameter ring was placed over a representative vegetation patch within each quadrat, and all shoots were counted. The length of the longest shoot (cm) was also measured and recorded. Previous work in eelgrass beds in this region (Moore, 2004; Orth and Moore, 1988) has demonstrated that cover estimates by divers can provide good estimates of plant biomass.

Water-Quality Sampling

Fixed-station sampling of water quality, including temperature, salinity, DO, turbidity, chlorophyll fluorescence, and pH measurements was made at 15-minute intervals at fixed elevations of 0.25 m above the bottom using YSI 6600 EDS data sondes, following standard YSI (YSI, Inc., Yellow Springs, Ohio) and NERRS System-Wide Monitoring Program protocols (National Estuarine Research Reserve System, 2008). Measurements were made from January through December of 2004, 2005, and 2006 at the Goodwin Island site and from March through November of 2004, March through December of 2005, and January through December of 2006 at the Gloucester Point site. Mean water depths at both sites were approximately 0.5 m MLLW.

Triplicate subsurface water samples were taken approximately every 14 days at each of the fixed station sampling sites. All samples were obtained sequentially beginning with the most downriver site and stored in the dark on ice for up to 4 hours before filtering. Nutrients and chlorophyll samples were then frozen until analysis. Nitrite, nitrate, ammonium, and orthophosphate were analyzed by flow injection using a Lachet QuickChem 8000 Automated Ion Analyzer (Lachat Instruments, Loveland, Colorado). Suspended matter was collected on precombusted, Gelman Type A/E glass fiber filters, dried to constant weight at 55°C and combusted at 500°C for 5 hours. Chlorophyll *a* was collected on Whatman GF/F glass fiber filters, extracted in a solvent mixture of acetone, dimethyl sulfoxide, and 1% diethylamine (45 : 45 : 10 by volume) and determined fluorometrically (Shoaf and Lium, 1976). Chlorophyll concentrations were uncorrected for phaeopigments. Diffuse downwelling attenuation of photosynthetically available radiation (PAR) was determined by triplicate water column profiles of downwelling photosynthetic photon flux density measured with a LI-COR, LI-192, underwater cosine-corrected sensor (LI-COR Biosciences, Lincoln, Nebraska). These data were obtained concurrently with the water samples. The downwelling attenuation coefficient (K_d) was calculated as the decay constant of a negative exponential function according to the Lambert-Beer equation.

RESULTS

Eelgrass Distribution and Abundance

Bottom depth profiles across each transect were not found to vary markedly among the different sampling dates, and therefore a common depth profile for each transect is presented here (Figures 2A, 2B). Figure 3 presents the mean bed vegetative bottom cover across all three transects at each site for all sampling dates in 2004, 2005, and 2006. Overall, seagrass cover was greatest during July 2004 at both study areas when it reached 40% to 50%, then decreased by August and was low (~15%) in October. These low levels of abundance in October 2004 were followed by regrowth by April 2005 at the both the Goodwin Island and Gloucester Point areas, reaching seasonal maximum levels comparable to 2004 by July 2005. By October 2005, however, a precipitous decline in seagrass cover had occurred at all transects, with virtually no aboveground cover evident. Although comprehensive transect sampling was not conducted until October, qualitative observations by divers indicated that the dieback was complete in both areas by the beginning of September 2005. Regrowth from both seedlings and the re-emergence of vegetative shoots from living rhizomes were observed beginning in March 2006. By July 2006, the levels of abundance at Goodwin Island nearly reached levels of 2004 and 2005; however, mean overall cover at Gloucester Point did not exceed 15%. Regrowth from the seasonal summertime decline was observed at Goodwin Island beginning in October 2006. In contrast, there was no significant regrowth at Gloucester Point, and no shoots could be found after October 2006.

The detailed pattern of growth, decline, and recovery of eelgrass at Goodwin Island is illustrated in Figure 4 using the mean cover observations along transect GI2 for early season, midseason, and late season samplings in 2004, 2005, and 2006. Overall patterns at transect GI2 were similar for the other two transects in this study area. Eelgrass abundance was greatest in the shallow, nearshore region of the bed where water depths were approximately −0.4 m MLLW or greater. Abundance decreased as depths increased in channelward areas to −0.8 m MLLW. Maximum colonization depth was approximately −0.9 m to −1.0 m MLLW. Early season abundance in 2004 in the deepest region of the bed decreased by July 2004, with dieback of both the shallow and deep areas by October. Early season cover of the inshore section of the bed in April 2005 generally exceeded that of May 2004, but the offshore section at depths of −0.7 m MLLW was much less abundant. By September 2005 only a few small shoots of eelgrass were present throughout the entire area. Recovery and regrowth in 2006 were again significant, though largely concentrated in the intermediate regions where depths were −0.4 m to −0.5 m MLLW.

At Gloucester Point, the pattern of eelgrass growth across the depth distribution among all 3 years is illustrated using detailed data from the middle transect GP2 (Figure 5). Early

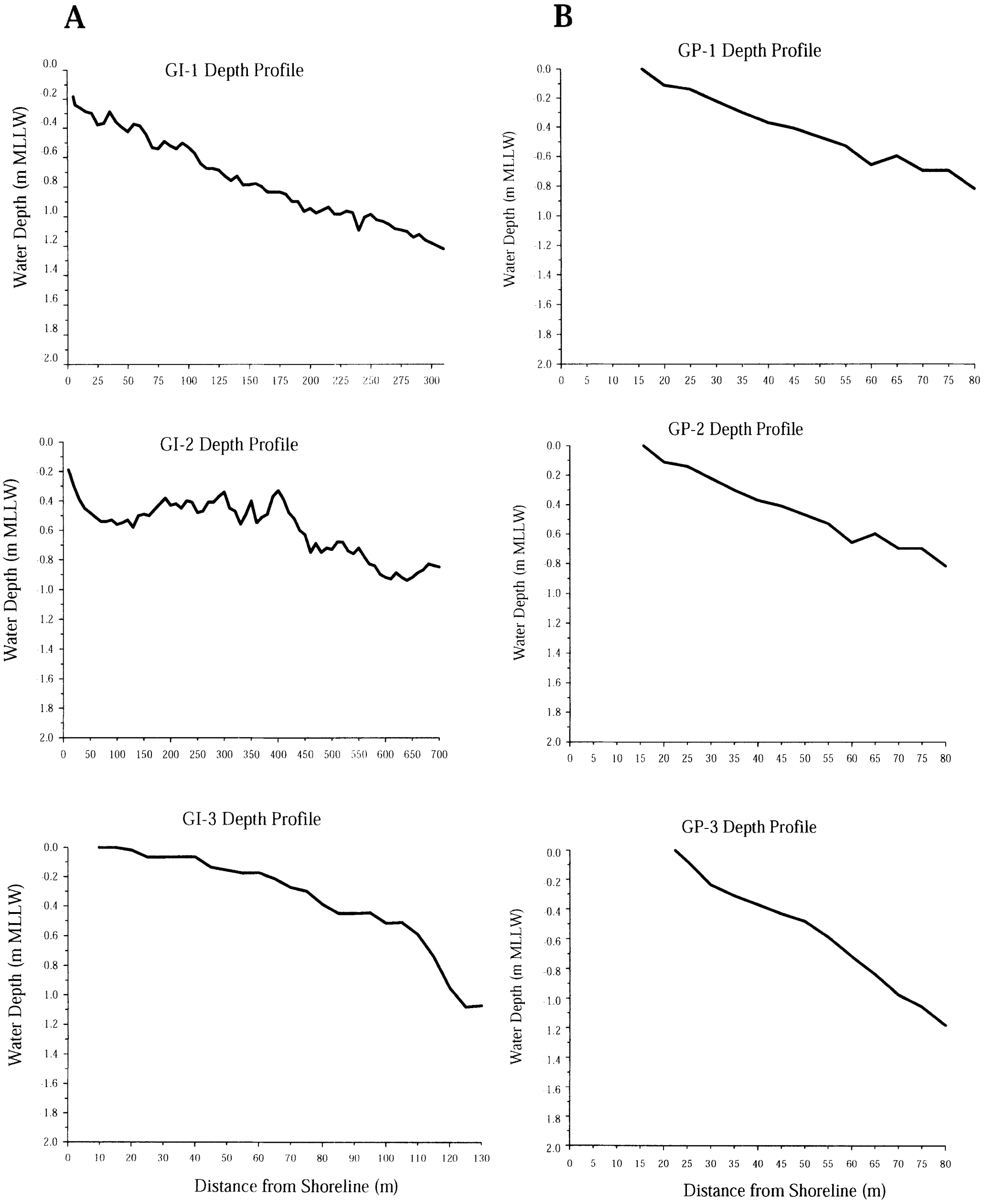

Figure 2. Bottom depth profiles across the eelgrass beds for all transects at (A) Goodwin Island and (B) Gloucester Point sites.

season eelgrass cover was nearly continuous and most abundant at depths from −0.3 to −0.7 m MLLW, with sparse patches of seedlings evident at depths shallower and deeper than this range. By the fall of 2004, cover had decreased one-third with the greatest loss of vegetation at the deepest depths. Recovery by early summer 2005 was primarily in the midbed region, with no recovery in the deepest areas greater than 0.7 m MLLW. No aboveground shoots were found by September 2005. Regrowth in early 2006 was much less than in either 2004 or 2005, and of all shoot vegetation present in July 2006, most plants growing at depths deeper than −0.5 m MLLW had died back by August. By September, the eelgrass mortality was complete throughout the depth range.

Water Quality Conditions

Daily mean water temperatures for the Goodwin Island (Figure 6A) and Gloucester Point (Figure 6B) sites had similar annual trends, but maximum seasonal temperatures during July and August were higher in 2005 (28–30°C) than those for similar periods in 2004 and 2006 (25–28°C), as well as the longer-term averages (1997–2003) that were available

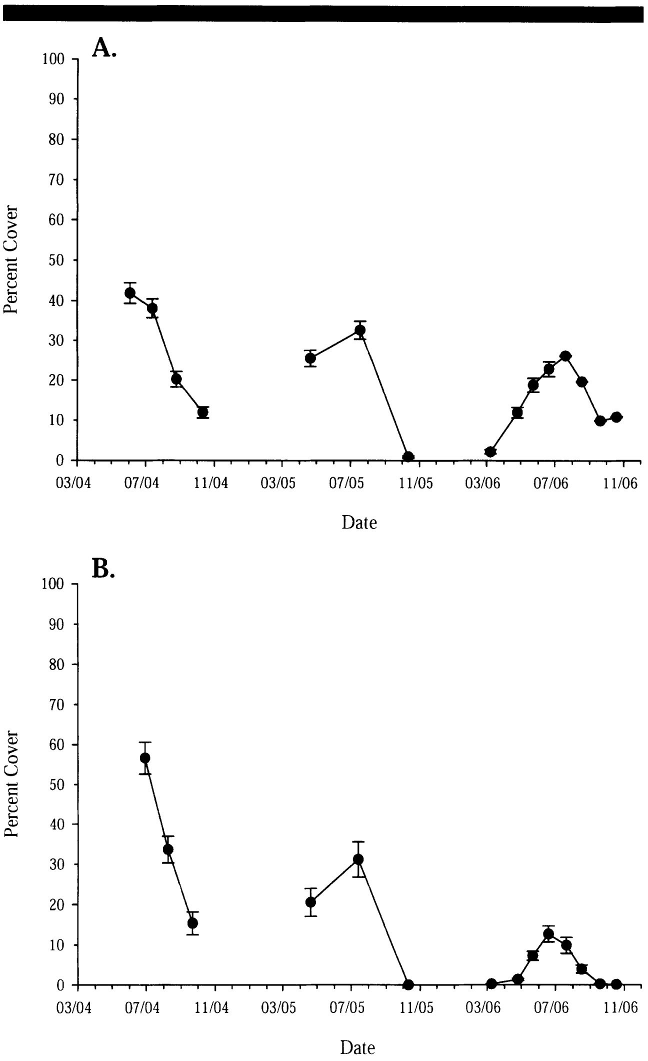

Figure 3. Integrative mean (±SE) bed vegetative bottom cover across all three transects at each site for all sampling dates. (A) Goodwin Island and (B) Gloucester Point.

for the Goodwin Island site. Short-term peaks in temperature were also greatest in 2005. Figure 7 presents the frequency distribution of 15-minute water temperature measurements during July and August of 2004, 2005, and 2006. A distinct shift to higher temperatures in July and August 2005 compared to 2004 was evident at both sites during the period when the dieback was observed. For example, water temperatures of 30°C were observed for approximately 13–14% of the July–August time period in 2005 compared to only 0–3% of the time in 2004. A temperature of 32°C was observed approximately 2% of the summertime period in 2005, but that level was never reached in 2004. The distribution of shallow water temperatures in the July–August period of 2006 was intermediate between the previous 2 years. Although summertime temperatures in 2006 were higher than in 2004, the highest proportion of July–August water temperatures was between 27°C and 28°C in 2006 compared to 28–29°C for 2005 (Figure 7). Analysis of the maximum difference in the cumulative frequency distributions of the July–August water temperatures for 2004, 2005, and 2006 (Kolmogorov-Smirnov Test; ZAR, 1984) revealed significantly higher water temperatures ($p < 0.05$, $n = 5952$) during the 2005 dieback period compared to either of the other 2 years.

Turbidity levels at the two shallow water study areas demonstrated considerable temporal variability among all years, with short bursts of high turbidity being common. The frequency distributions for 15-minute turbidity measurements at both sites during July and August of 2004, 2005, and 2006 (Figure 8) demonstrate distinctly higher turbidity at the Gloucester Point site compared to the Goodwin Island site during all years, but little difference among the 3 years at each individual site.

Generally lower levels of suspended sediments and PAR light attenuation (Table 1) characterized the water quality conditions at the downriver Goodwin Island site during the predominant *Z. marina* growing season of March through November than those at the upriver Gloucester Point site (Table 2). Geometric means of PAR light attenuation (K_d) at Gloucester Point for the March through November periods of 2004, 2005, and 2006 were -1.40, -1.34 and -1.24 m^{-1}, respectively. For the same periods at Goodwin Island, the light attenuation coefficients were -1.11, -1.14 and -1.08 m^{-1}. This light level is also equal to a turbidity of 10 NTU (Nephelometric Turbidity Unit), based on a regression of simultaneous measurements of light attenuation profiles and NTU turbidity measurements made monthly at the study areas for the 2004–2006 study period (MOORE and JARVIS, unpublished data). The cumulative frequency plots of turbidity (Figure 8) show that levels of turbidity were below this 10 NTU threshold for sustained eelgrass growth 80–100% of the time during July and August of all 3 years at Goodwin Island, but less than 40% of the time at Gloucester Point.

Summer nutrient concentrations were low (<1 μm) and comparable among the sites. Chlorophyll levels were also similar and ranged 10–30 μg L^{-1} during July and August. During the late summer of 2005, large blooms of the dinoflagellate, *Cochlodinium polykrikoides,* were observed throughout the York River. These blooms are evident in the elevated chlorophyll concentrations recorded at the Gloucester Point study area during August and September of 2005 but not at Goodwin Island (Tables 1 and 2).

Concentrations of daily mean DO demonstrated summertime depressions, with minimum daily seasonal concentrations during July through September when water temperatures exceeded 25°C. There was also considerable diurnal variability, with minimum levels of 1–2 mg L^{-1} recorded during predawn periods throughout July and August. Whereas hypoxic conditions (1–3 mg L^{-1}) were a small temporal component of these periods, the frequency of these low DO excursions was higher in 2005 at both sites than in either 2004 or 2006 (Figure 9).

DISCUSSION

The interannual patterns of change observed in eelgrass beds of the York River from 2004 through 2006 suggest that the significant shoot dieback during the summer of 2005 was

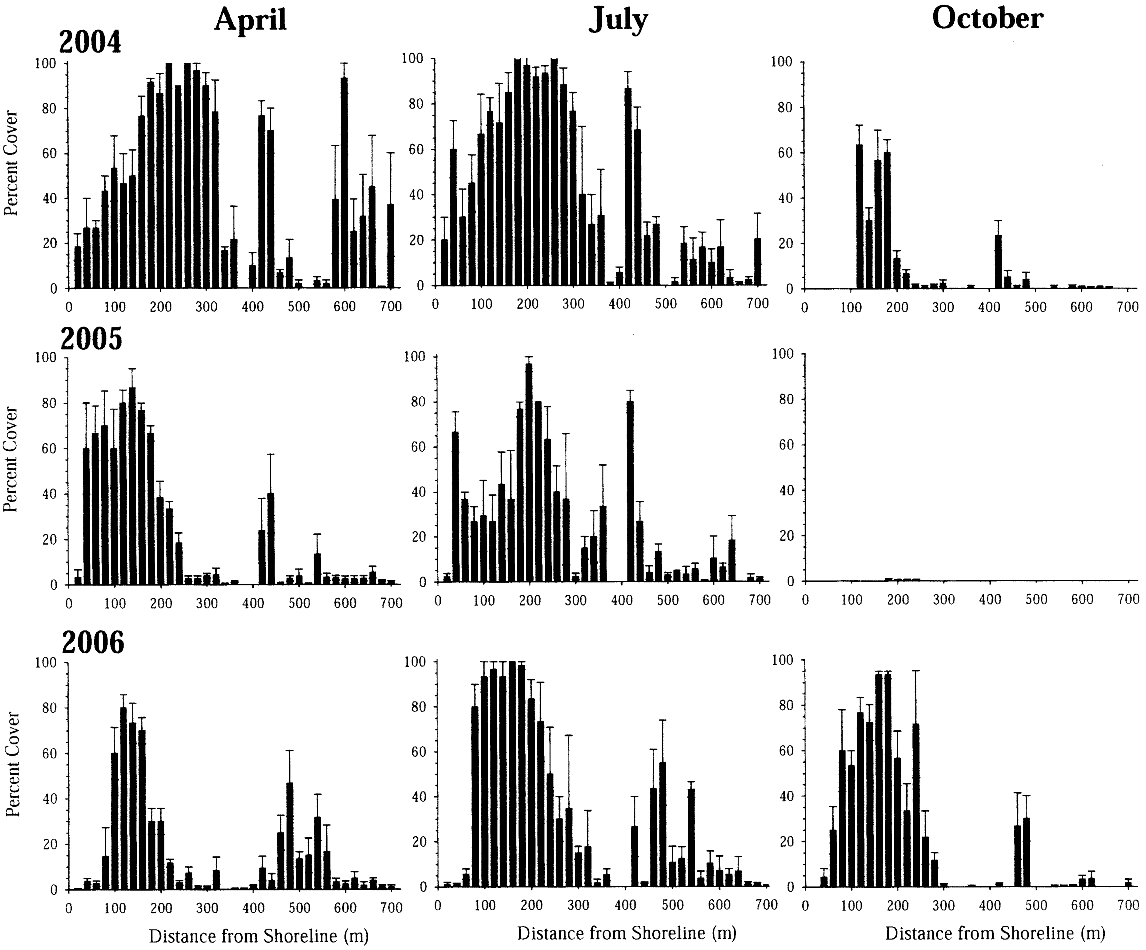

Figure 4. Detailed pattern of mean (±SE) eelgrass cover across Goodwin Island transect, GI2, for the April, July, and October sampling periods of 2004, 2005, and 2006.

precipitated by increased frequency and duration of high (>30°C) summertime water temperatures compared to the other years. Additionally, annual aerial photographic mapping of eelgrass populations in the Chesapeake Bay from the late spring of 2004 to 2006 demonstrate that the pattern of these York River mortalities were characteristic of many eelgrass bed mortalities throughout the lower Chesapeake Bay (ORTH *et al.,* 2006). Therefore the specific responses we measured here may be considered representative of the larger region. Whereas there were no distinct differences in turbidity evident among 3 years at either of the sites, markedly higher levels of turbidity and light attenuation in the upriver Gloucester Point region of the York, which corresponded to greater eelgrass decline and reduced regrowth, suggests that estuarine turbidity can compound the negative effects of high water temperatures on long-term eelgrass survival. Episodic oxygen reductions, which can compound the effects of elevated temperature (BORUM *et al.,* 2005), may also have provided an additional stressor affecting plant dieback.

We found recolonization of eelgrass from summertime mortality in 2005 to near predieback levels within 1 year at Goodwin Island. This is similar to that reported by others for eelgrass recolonization after massive mortalities (FREDERIKSEN *et al.,* 2004; GREVE *et al.,* 2005; PLUS *et al.,* 2003). However our work and that of others suggest that if environmental conditions are not improved during subsequent years, especially in areas where chronic stressors such as turbidity or eutrophication remain high such as the Gloucester Point site, the potential exists for persistent declines with limited recovery due both to limited propagule supply and fundamental habitat state change (FREDERIKSEN *et al.,* 2004; MOORE, 2004; MOORE *et al.,* 1996, 1997).

The magnitude of summertime temperature differences between years with eelgrass persistence and growth (2004 and 2006) and a year with massive dieback (2005) was small (1–2°C) and of limited duration (~5% to 15% difference in frequency). This suggests that populations here are growing near their upper temperature limit during July and August, and small temperature increases can have profound effects. Interestingly, eelgrass populations are found growing further south into North Carolina (34°32′ N, 77°21′ W; GREEN and SHORT, 2003) where the climate is much warmer and water

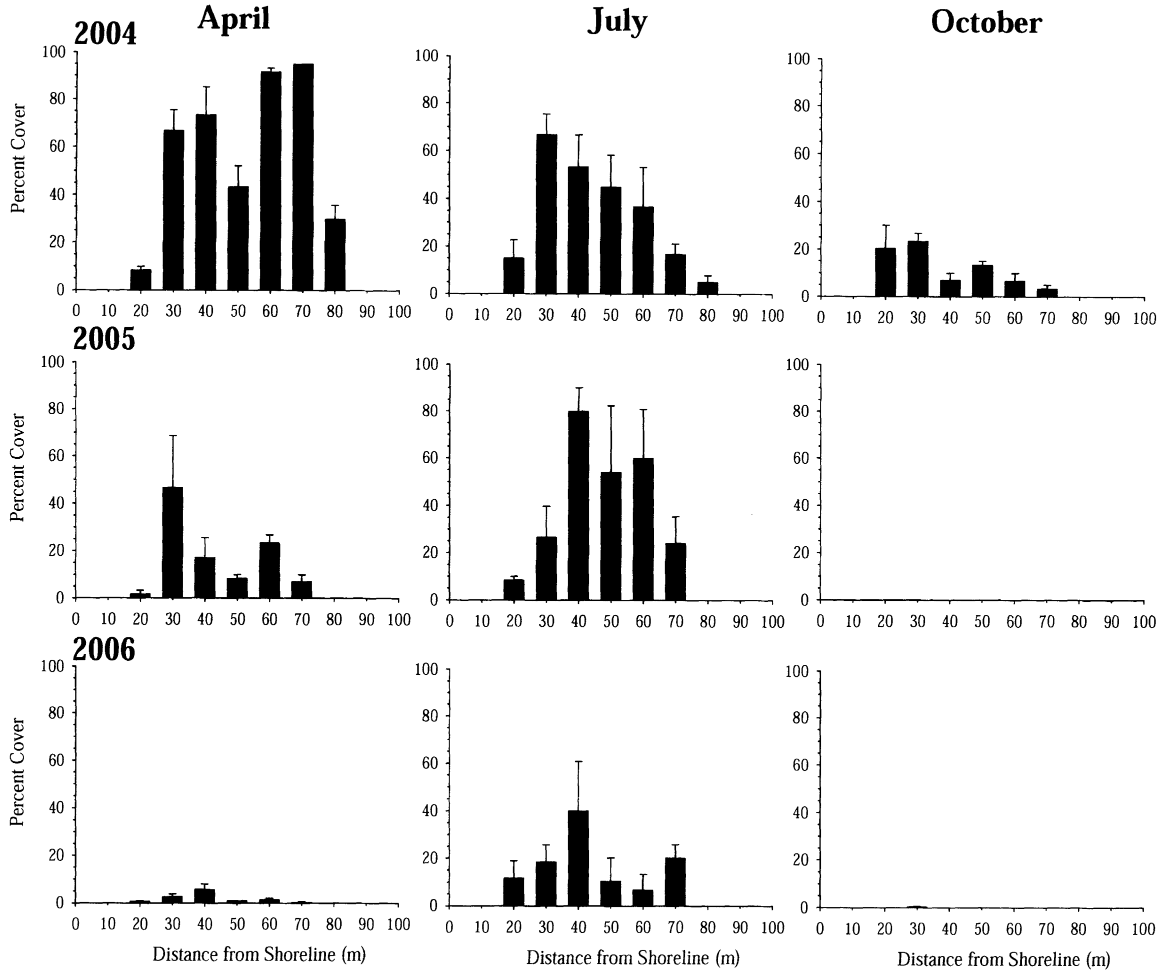

Figure 5. Detailed pattern of mean (±SE) eelgrass cover across Gloucester Point transect, GP2, for the April, July, and October sampling periods of 2004, 2005, and 2006.

temperatures can reach higher levels for longer durations than in some areas of the Chesapeake Bay (North Carolina National Estuarine Research Reserve, unpublished data). However, eelgrass populations in North Carolina are restricted to the coastal bays and lagoons where other stressors such as turbidity and eutrophication may be lower than the Chesapeake Bay, and periodic tidal flushing by oceanic waters may ameliorate temperature effects for many beds. During 2005, few large-scale declines of eelgrass populations were reported in the coastal bays along the western mid-Atlantic from New Jersey (Kennish *et al.* 2007) to Virginia (R. Orth, personal communication) and North Carolina (J. Kenworthy, personal communication). However, in one lagoon (Chincoteague Bay, Virginia) with restricted oceanic flushing and deteriorating water quality conditions (Boynton *et al.*, 1996), some large-scale diebacks were reported (R. Orth, personal communication). This suggests that an interaction of persistent and episodic stress factors (high temperatures, high turbidity, nutrient enrichment, and lower salinity) in the Chesapeake Bay and other areas near the southern limits of eelgrass growth in the western Atlantic may be interacting to affect eelgrass populations during the summer with a resultant increase in mortalities.

The specific mechanisms of the mortalities observed here can only be hypothesized, but the physiological response of the plants to the interaction of high temperatures with other stress factors remains a principal assumption. Occasionally, water temperatures here were measured as high as 33°C during July and August of 2005, suggesting that some maximum temperature threshold was exceeded. However, given the wider scale mortalities of eelgrass reported throughout the Chesapeake Bay by the end of the summer of 2005 (Orth *et al.*, 2006), it is unlikely that high temperatures alone resulted in the regional scale effects observed. Continuous monitoring data collected by the CBNERRVA (Virginia Estuarine and Coastal Observing System, 2008) from other areas indicate that water temperatures in other sites experiencing some eelgrass loss did not exceed 30°C in 2005. The losses of eelgrass plants at the deep edge and upper estuary locations of the beds and their subsequent poor recovery in these areas provide insight that light availability is an important additional contributor to eelgrass persistence during these epi-

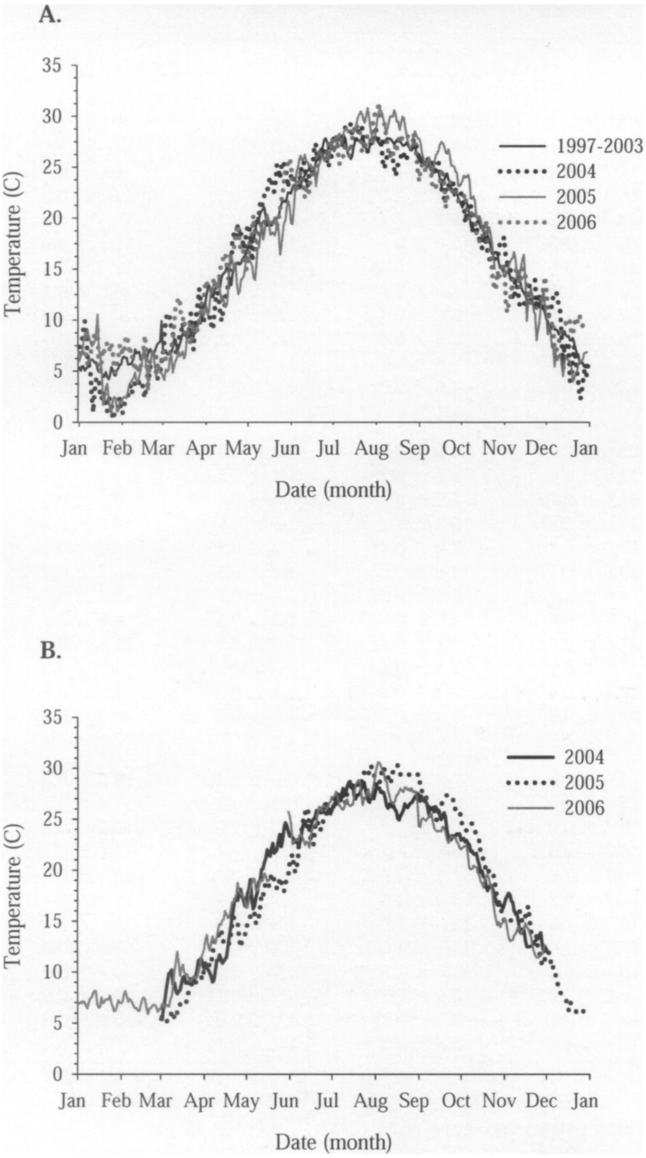

Figure 6. Daily mean water temperatures for (A) Goodwin Island and (B) Gloucester Point.

sodic warming periods. As the compensating light requirements of the eelgrass increase with temperature (Moore *et al.,* 1997), it would be expected that as temperatures increase, mortalities of eelgrass would be greatest in areas of lowest light availability; that is, at the deep edges and the upper estuary regions of its distribution. This hypothesis is consistent with our observations in this study.

Both low oxygen levels and high sulfide concentrations, which can covary with temperature, have also been demonstrated to be related to eelgrass summertime mortalities (Greve *et al.,* 2003; Homer and Bondgaard, 2001; Plus *et al.,* 2003). Greve *et al.* (2003) found in a laboratory study that under lighted conditions at water temperatures above 30°C eelgrass meristematic tissues became anoxic. In the dark, this occurred at temperatures of 25–30°C. Borum *et al.* (2005) found spontaneous increases in sulfide into the roots, rhizomes, and meristematic tissues of *in situ Thalassia testudinum* at low internal oxygen content. These increases were related to both reduced light availability and water column oxygen levels. Although the exact cause and effect mechanisms of low oxygen conditions on *Z. marina* remain unclear, the degradation of meristematic tissues due to oxygen deprivation and/or sulfide toxicity are suspected (Greve *et al.,* 2003). Furthermore the decreased capacity of eelgrass photosynthesis under increasing sulfide conditions (Goodman *et al.,* 1993) to provide internal oxygen to reduce this toxicity would further compound these physiological stresses. At salinities of approximately 20 and temperatures of 30°C measured in our study, we would expect tissue oxygen deprivation and sulfide intrusion to occur at water column DO concentrations of 1–3 mg L^{-1} (Borum *et al.,* 2005; Greve *et al.,*

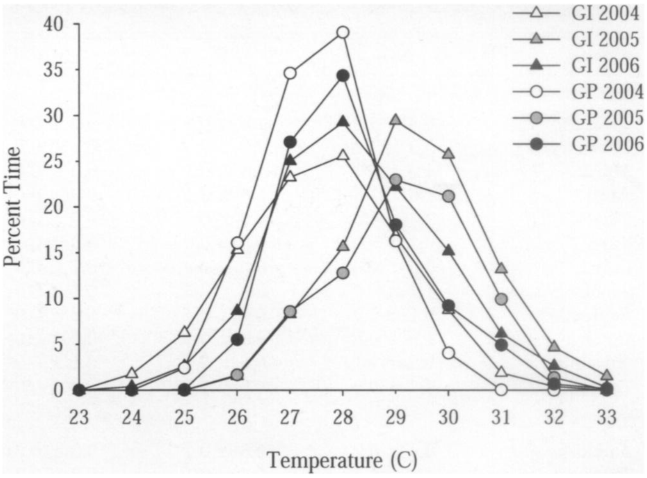

Figure 7. Frequency distribution of 15-minute water temperature measurements during July and August of 2004, 2005, and 2006.

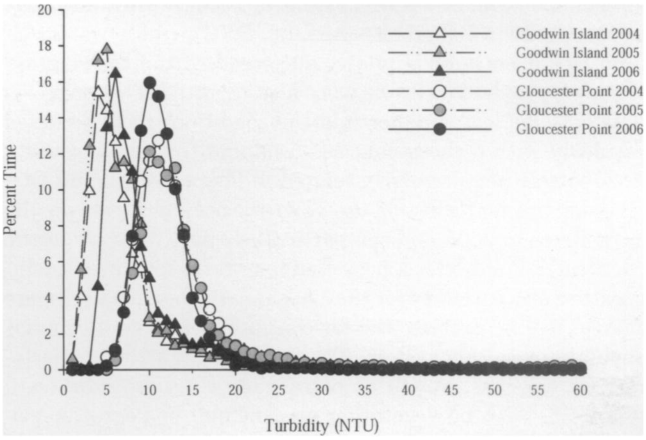

Figure 8. Frequency distribution of 15-minute water column turbidity measurements during July and August of 2004, 2005, and 2006.

Table 1. *Mean (±SE) monthly Goodwin Island water quality conditions. (N/A = not available,* NO_x *= μM nitrate+nitrite,* NH_4 *= μM ammonium, DIP = μM dissolved inorganic phosphate, CHL a = μg/l chlorophyll a, TSS = mg/l total suspended solids,* K_d *= downwelling light attenuation coefficient.)*

Date	NO_x	NH_4	DIP	CHL *a*	TSS	K_d	Salinity
2004							
January	0.8 ± 0.3	1.5 ± 0.5	0.0 ± 0.0	66.3±11.3	25.1 ± 3.3	1.2 ± 0.1	16.6 ± 0.3
February	5.8 ± 1.2	2.0 ± 0.5	0.1 ± 0.0	18.7 ± 2.1	18.7 ± 0.6	0.9 ± 0.1	14.7 ± 0.2
March	4.6 ± 0.7	0.4 ± 0.1	0.0 ± 0.0	14.7 ± 2.1	13.3 ± 1.6	0.8 ± 0.1	16.8 ± 0.5
April	7.6 ± 2.5	0.5 ± 0.1	0.0 ± 0.0	15.3 ± 2.4	17.2 ± 2.9	1.0 ± 0.1	17.0 ± 0.3
May	2.3 ± 1.0	0.6 ± 0.1	0.0 ± 0.0	29.2 ± 4.7	15.2 ± 1.4	1.5 ± 0.1	18.6 ± 0.2
June	0.1 ± 0.0	0.3 ± 0.0	0.0 ± 0.0	20.1 ± 1.3	14.5 ± 0.9	1.1 ± 0.1	18.1 ± 1.0
July	0.0 ± 0.0	0.5 ± 0.0	0.1 ± 0.0	21.5 ± 1.6	12.1 ± 0.5	1.0 ± 0.0	19.2 ± 0.3
August	1.2 ± 0.5	0.6 ± 0.1	0.1 ± 0.0	15.9 ± 0.8	11.5 ± 1.3	1.3 ± 0.1	18.5 ± 0.1
September	0.1 ± 0.0	0.4 ± 0.1	0.2 ± 0.0	27.4 ± 1.1	6.8 ± 0.4	1.2 ± 0.0	15.4 ± 0.0
October	1.6 ± 0.8	0.4 ± 0.1	0.0 ± 0.0	16.2 ± 1.3	7.8 ± 0.6	1.1 ± 0.1	15.5 ± 0.4
November	0.2 ± 0.1	0.6 ± 0.1	0.1 ± 0.0	22.1 ± 3.7	8.3 ± 2.2	1.0 ± 0.2	17.5 ± 0.1
December	4.7 ± 0.0	0.6 ± 0.1	0.0 ± 0.0	15.7 ± 0.5	4.8 ± 0.9	0.6 ± 0.1	16.4 ± 0.0
2005							
January	0.4 ± 0.2	0.6 ± 0.1	0.0 ± 0.0	22.8 ± 2.2	5.0 ± 0.3	1.3 ± 0.1	11.2 ± 2.2
February	4.6 ± 0.3	0.6 ± 0.1	0.0 ± 0.0	17.5 ± 1.0	3.9 ± 0.2	1.1 ± 0.1	17.0 ± 0.3
March	2.9 ± 1.4	0.3 ± 0.1	0.1 ± 0.0	31.8 ± 2.7	4.0 ± 0.3	0.9 ± 0.1	16.9 ± 0.5
April	0.1 ± 0.0	0.2 ± 0.0	0.0 ± 0.0	41.8 ± 3.6	6.3 ± 1.2	1.6 ± 0.2	16.3 ± 0.6
May	0.1 ± 0.0	0.2 ± 0.0	0.0 ± 0.0	17.0 ± 0.8	2.9 ± 0.4	1.2 ± 0.1	16.5 ± 0.1
June	0.1 ± 0.0	0.5 ± 0.1	0.0 ± 0.0	13.6 ± 0.7	4.8 ± 0.2	1.2 ± 0.1	16.2 ± 0.2
July	0.0 ± 0.0	0.7 ± 0.0	0.1 ± 0.0	14.8 ± 1.7	5.1 ± 0.5	1.1 ± 0.1	19.5 ± 0.0
August	0.0 ± 0.0	0.5 ± 0.1	0.1 ± 0.0	17.9 ± 0.6	4.5 ± 0.3	1.2 ± 0.1	19.9 ± 0.1
September	0.0 ± 0.0	0.3 ± 0.0	0.1 ± 0.0	11.7 ± 0.9	4.1 ± 0.4	1.0 ± 0.2	21.3 ± 0.0
October	15.7 ± 0.3	0.1 ± 0.0	0.3 ± 0.0	7.8 ± 0.0	2.7 ± 0.2	N/A	21.7 ± 0.0
November	1.6 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	18.4 ± 0.4	2.7 ± 0.5	1.1 ± 0.3	21.3 ± 0.0
December	0.9 ± 0.4	0.4 ± 0.1	0.0 ± 0.0	11.2 ± 0.8	3.4 ± 0.1	1.0 ± 0.2	20.4 ± 0.3
2006							
January	0.1 ± 0.0	0.3 ± 0.0	0.0 ± 0.0	16.5 ± 1.8	7.9 ± 2.0	0.8 ± 0.1	18.9 ± 0.3
February	0.1 ± 0.0	0.3 ± 0.0	0.0 ± 0.0	14.4 ± 1.9	3.3 ± 0.4	0.9 ± 0.1	17.9 ± 0.2
March	0.1 ± 0.0	0.3 ± 0.1	0.0 ± 0.0	6.4 ± 0.9	9.0 ± 1.0	0.7 ± 0.9	18.9 ± 0.1
April	0.1 ± 0.0	0.4 ± 0.1	0.0 ± 0.0	6.3 ± 0.8	9.5 ± 1.1	1.1 ± 0.1	19.1 ± 0.2
May	0.2 ± 0.0	0.2 ± 0.0	0.0 ± 0.0	8.7 ± 2.5	11.1 ± 1.5	1.3 ± 0.2	19.1 ± 0.4
June	0.1 ± 0.0	0.6 ± 0.2	0.0 ± 0.0	8.7 ± 0.2	13.6 ± 1.5	1.2 ± 0.1	20.7 ± 0.1
July	0.0 ± 0.0	0.4 ± 0.1	0.0 ± 0.0	13.8 ± 1.3	12.8 ± 1.9	1.3 ± 0.0	20.6 ± 0.0
August	0.3 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	16.7 ± 1.4	11.1 ± 1.0	1.2 ± 0.1	21.3 ± 0.6
September	0.6 ± 0.1	1.4 ± 0.3	0.0 ± 0.0	16.3 ± 0.4	11.5 ± 1.9	1.4 ± 0.0	20.4 ± 0.0
October	3.3 ± 0.3	3.9 ± 0.4	0.5 ± 0.1	6.9 ± 0.4	5.9 ± 0.5	0.8 ± 0.1	20.0 ± 0.2
November	1.9 ± 0.1	0.6 ± 0.0	0.1 ± 0.0	13.7 ± 0.1	2.1 ± 0.1	1.0 ± 0.0	20.0 ± 0.0
December	N/A	N/A	N/A	19.8 ± 4.3	3.5 ± 0.5	1.2 ± 0.1	17.3 ± 0.1

2003). In our study, these levels occurred in predawn and dawn hours approximately 3–5% of the time in July and August of 2005 and to a lesser extent in 2004. A previous study at the Goodwin Island site (MOORE, 2004), where water column DO levels were similarly measured within the eelgrass canopy, episodic low levels were also reported. This suggests that episodic low summertime DO conditions have occurred regularly within these eelgrass beds and that the mortality in 2005 was not singularly related to low water column DO.

Given the mortality of the eelgrass beds observed in the York River in 2005 and the particularly poor recovery at the Gloucester Point site, a projected long-term increase in temperature and turbidity for the Chesapeake Bay due to climate change will be problematic for continued success of eelgrass populations in this system. The 2004 through 2006 trajectories for eelgrass growth at both study sites are downward (Figure 3) with no vegetation present and no regrowth evident at Gloucester Point as of November 2006. These downward trends parallel similar downward trajectories observed for eelgrass populations baywide (ORTH *et al.,* 2006). The results presented here that relate continuous measures of water quality with concurrent measures of eelgrass bed responses suggest these eelgrass populations are near their limits for continued growth and survival and that episodic events can have significant long-term impacts. Increased frequency of these episodic stresses may result in the loss of this species in certain areas of the Chesapeake Bay.

Alternative strategies for seagrass populations in this region are few. Annual forms of eelgrass have been observed in other regions, and this strategy of reproduction, *i.e.,* seed production during the first year of growth followed by die off during the stressful summer, may be one. Little is yet known about why or how these annual form populations develop (KEDDY and PATRIQUIN, 1978; MELING-LOPEZ and IBARRA-OBANDO, 1999). In the Chesapeake Bay so far, no annual populations have been observed. Other species such as *Ruppia maritima* may expand and *Halodule wrightii* may become established; however, their lack of effective root structure and other aspects of their growth forms make their survival in many areas currently vegetated by eelgrass problematic.

Table 2. *Mean (±SE) monthly Gloucester Point water quality conditions. (N/A = not available, NO_x = µM nitrate+nitrite, NH_4 = µM ammonium, DIP = µM dissolved inorganic phosphate, CHL a = µg/l chlorophyll a, TSS = mg/l total suspended solids, K_d = downwelling light attenuation coefficient.)*

Date	NO_x	NH_4	DIP	CHL *a*	TSS	K_d	Salinity
2004							
January	3.2 ± 1.2	3.1 ± 1.0	0.0 ± 0.0	45.0 ± 9.7	17.3 ± 2.0	1.6 ± 0.0	16.9 ± 0.1
February	11.4 ± 0.8	2.9 ± 0.7	0.0 ± 0.0	21.1 ± 2.8	16.1 ± 0.8	1.0 ± 0.1	15.0 ± 0.2
March	5.3 ± 1.1	0.3 ± 0.0	0.0 ± 0.0	21.6 ± 1.3	15.3 ± 2.7	0.9 ± 0.1	16.6 ± 0.5
April	6.0 ± 0.9	1.1 ± 0.2	0.0 ± 0.0	14.4 ± 1.9	20.0 ± 3.1	1.3 ± 0.2	17.7 ± 0.6
May	2.6 ± 0.4	2.3 ± 0.2	0.1 ± 0.0	29.1 ± 5.6	17.3 ± 3.3	1.9 ± 0.3	18.3 ± 0.6
June	0.5 ± 0.2	0.4 ± 0.1	0.0 ± 0.0	21.6 ± 1.5	23.7 ± 3.1	1.4 ± 0.1	18.1 ± 0.5
July	0.4 ± 0.2	0.6 ± 0.1	0.1 ± 0.0	34.6 ± 1.4	18.8 ± 1.3	1.9 ± 0.1	19.0 ± 0.3
August	8.5 ± 0.9	3.1 ± 0.7	0.5 ± 0.0	14.8 ± 0.8	13.5 ± 1.0	1.8 ± 0.0	17.3 ± 0.2
September	0.6 ± 0.1	0.4 ± 0.0	0.3 ± 0.0	27.8 ± 0.7	8.8 ± 0.5	1.7 ± 0.0	13.2 ± 0.0
October	6.3 ± 0.4	3.0 ± 0.5	0.5 ± 0.1	14.9 ± 1.6	9.1 ± 0.7	1.4 ± 0.1	15.5 ± 0.2
November	8.1 ± 0.2	2.2 ± 0.1	0.1 ± 0.0	9.6 ± 1.1	6.2 ± 0.5	1.0 ± 0.1	16.4 ± 0.3
December	6.7 ± 0.2	2.0 ± 0.1	0.2 ± 0.0	5.5 ± 0.2	4.8 ± 0.4	0.6 ± 0.1	15.1 ± 0.0
2005							
January	0.1 ± 0.0	1.1 ± 0.1	0.0 ± 0.0	22.6 ± 1.7	20.2 ± 2.0	1.5 ± 0.2	16.4 ± 0.8
February	0.2 ± 0.0	1.9 ± 0.2	0.0 ± 0.0	16.1 ± 1.7	11.2 ± 0.7	1.4 ± 0.1	16.5 ± 0.5
March	1.7 ± 0.3	1.8 ± 0.8	0.0 ± 0.0	25.1 ± 2.2	9.5 ± 0.4	1.1 ± 0.0	17.6 ± 0.3
April	0.1 ± 0.0	0.2 ± 0.0	0.0 ± 0.0	26.4 ± 1.7	13.7 ± 1.3	1.5 ± 0.0	15.4 ± 0.5
May	1.0 ± 0.1	0.8 ± 0.2	0.01 ± 0.0	20.1 ± 0.9	9.6 ± 0.9	1.6 ± 0.1	16.6 ± 0.0
June	0.3 ± 0.2	0.5 ± 0.0	0.1 ± 0.0	17.1 ± 0.4	12.3 ± 0.2	1.5 ± 0.1	16.3 ± 0.4
July	0.1 ± 0.0	0.7 ± 0.5	0.3 ± 0.1	19.7 ± 1.5	20.6 ± 3.5	1.4 ± 0.1	19.4 ± 0.0
August	0.6 ± 0.2	0.6 ± 0.0	0.4 ± 0.1	54.3 ± 13.7	14.1 ± 1.3	1.7 ± 0.1	20.2 ± 0.0
September	0.0 ± 0.0	0.4 ± 0.1	0.5 ± 0.0	92.3 ± 25.1	24.5 ± 2.7	1.7 ± 0.2	21.0 ± 0.0
October	19.6 ± 1.9	1.3 ± 0.1	1.0 ± 0.0	8.8 ± 0.2	5.3 ± 0.8	0.8 ± 0.0	20.7 ± 0.0
November	7.3 ± 0.3	2.6 ± 0.1	0.2 ± 0.0	10.7 ± 0.7	8.5 ± 0.8	1.2 ± 0.1	21.6 ± 0.0
December	2.3 ± 0.7	1.4 ± 0.5	0.1 ± 0.0	11.9 ± 1.7	8.1 ± 0.9	1.0 ± 0.1	19.3 ± 0.4
2006							
January	0.1 ± 0.0	0.4 ± 0.1	0.0 ± 0.0	16.3 ± 0.5	7.7 ± 0.6	1.0 ± 0.1	18.6 ± 0.5
February	0.3 ± 0.1	0.3 ± 0.0	0.0 ± 0.0	17.0 ± 1.8	11.4 ± 0.7	1.1 ± 0.1	18.0 ± 0.2
March	0.1 ± 0.0	0.3 ± 0.1	0.0 ± 0.0	10.0 ± 1.7	10.2 ± 1.5	0.8 ± 0.1	20.1 ± 0.1
April	0.2 ± 0.0	0.4 ± 0.0	0.0 ± 0.0	9.8 ± 1.6	12.3 ± 1.6	1.1 ± 0.2	19.2 ± 0.2
May	0.6 ± 0.2	1.1 ± 0.4	0.0 ± 0.0	10.0 ± 1.2	10.3 ± 0.8	1.1 ± 0.1	18.7 ± 0.4
June	0.1 ± 0.0	0.4 ± 0.1	0.0 ± 0.0	12.9 ± 0.6	17.2 ± 4.3	1.5 ± 0.1	20.3 ± 0.2
July	0.2 ± 0.1	1.2 ± 0.5	0.3 ± 0.1	16.3 ± 1.1	10.7 ± 0.5	1.6 ± 0.1	20.2 ± 0.2
August	2.1 ± 0.9	0.1 ± 0.0	0.4 ± 0.1	19.1 ± 1.0	18.5 ± 3.7	1.7 ± 0.1	21.8 ± 0.3
September	6.1 ± 0.4	1.1 ± 0.1	0.3 ± 0.0	17.0 ± 0.3	14.5 ± 2.7	1.4 ± 0.0	19.8 ± 0.0
October	4.1 ± 0.3	6.5 ± 1.5	0.6 ± 0.2	9.1 ± 0.5	8.9 ± 1.3	1.3 ± 0.2	19.1 ± 0.1
November	2.9 ± 0.0	2.2 ± 0.1	0.3 ± 0.0	12.6 ± 0.5	6.2 ± 0.3	1.0 ± 0.0	19.4 ± 0.0
December	N/A	N/A	N/A	8.2 ± 1.1	5.8 ± 0.7	1.0 ± 0.1	17.1 ± 0.3

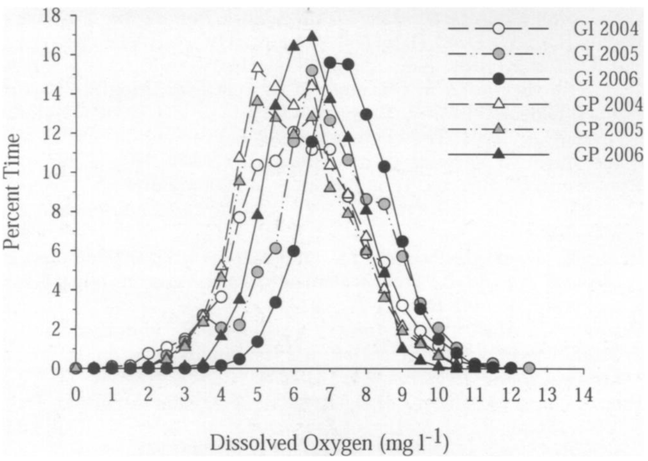

Figure 9. Frequency distribution of 15-minute water column dissolved measurements during July and August of 2004, 2005, and 2006.

Overall, a suggestion can be made that the predicted results of climate change for the Chesapeake Bay region may already be having negative effects on eelgrass populations. Continued temperature rise, increased runoff of sediments and nutrients, and increased hypoxia will all likely interact in a negative way to increase eelgrass mortality and decrease its success in the region.

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