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The Pattern and Influence of Low Dissolved Oxygen in the Patuxent River, a Seasonally Hypoxic Estuary

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ABSTRACT: Increased nutrient loadings have resulted in low dissolved oxygen (DO) concentrations in bottom waters of the Patuxent River, a tributary of Chesapeake Bay. We synthesize existing and newly collected data to examine spatial and temporal variation in bottom DO, the prevalence of hypoxia-induced mortality of fishes, the tolerance of Patuxent River biota to low DO, and the influence of bottom DO on the vertical distributions and spatial overlap of larval fish and fish eggs with their gelatinous predators and zooplankton prey. We use this information, as well as output from watershed-quality and water-quality models, to configure a spatially-explicit individual-based model to predict how changing land use within the Patuxent watershed may affect survival of early life stages of summer breeding fishes through its effect on DO. Bottom waters in much of the mesohaline Patuxent River are below 50% DO saturation during summer. The system is characterized by high spatial and temporal variation in DO concentrations, and the current severity and extent of hypoxia are sufficient to alter distributions of organisms and trophic interactions in the river. Gelatinous zooplankton are among the most tolerant species of hypoxia, while several of the ecologically and economically important finfish are among the most sensitive. This variation in DO tolerances may make the Patuxent River, and similar estuaries, particularly susceptible to hypoxia-induced alterations in food web dynamics. Model simulations consistently predict high mortality of planktonic bay anchovy eggs (*Anchoa mitchilli*) under current DO, and increasing survival of fish eggs with increasing DO. Changes in land use that reduce nutrient loadings may either increase or decrease predation mortality of larval fish depending on the baseline DO conditions at any point in space and time. A precautionary approach towards fisheries and ecosystem management would recommend reducing nutrients to levels at which low oxygen effects on estuarine habitat are reduced and, where possible, eliminated.

Introduction

One of the most important consequences of high anthropogenic nutrient loadings to stratified coastal waters is low dissolved oxygen (DO) concentrations that reduce the extent and suitability of habitat for a wide range of organisms (e.g., Baden et al. 1990; Diaz and Rosenberg 1995, 2001; Rabalais et al. 2001; Breitburg 2002). Oxygen depletion occurs when nutrients stimulate primary production beyond levels that are used by consumers and increases biological oxygen demand within the bottom layer of the water column where density stratification limits reaeration. This process of eutrophication-induced bottom layer hypoxia or anoxia appears to be increasing worldwide in coastal systems (Diaz and Rosenberg 2001). As in many similar systems, nutrient overenrichment now results in bottom layer oxygen concentrations substantially below saturation during summer in the Patuxent River, as well as in the mainstem Chesapeake Bay and several of its other tributaries (see also D'Elia et al. 2003).

Low DO can reduce abundances, increase mortality, and alter growth and spatial distributions of fish and invertebrates (reviewed in Kramer 1987; Diaz and Rosenberg 1995; Breitburg 2002). Potential system-level and economic consequences include reduced production of commercially and recreationally important fish and shellfish species (Diaz and Rosenberg 1995; Breitburg 2002), changes in the relative importance of various tro-

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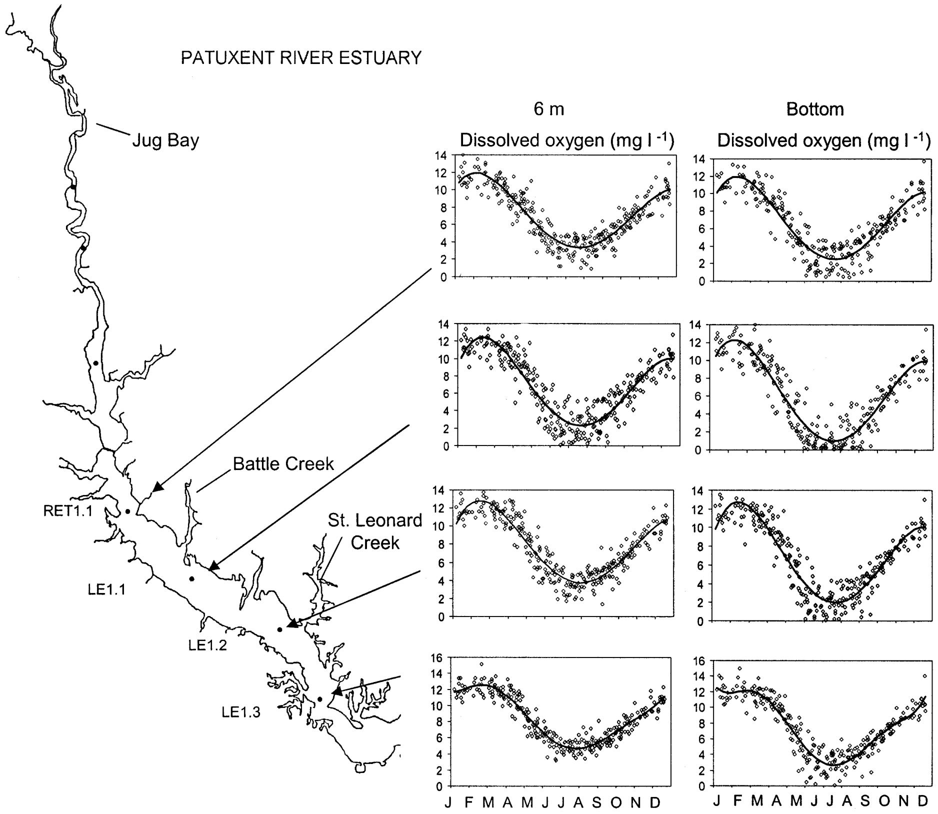

Fig. 1. Dissolved oxygen concentrations at 6 m and near-bottom in the mesohaline Patuxent River. Data include all observations for 1985–2001 from the Chesapeake Bay Water Quality Monitoring Program (CBP 2002). Fitted 2nd and 3rd order polynomial regressions (all $R^2 \geq 0.90$) show seasonal and depth-related patterns. The stretch of the river from monitoring station RET1.1 (estuarine turbidity zone) through LE1.2 (south of the mouth of St. Leonard Creek) experiences severe bottom-layer hypoxia. In this area, water deeper than 6 m is typically ≤ 50% saturation during summer, and near-bottom DO concentrations at or below 2 mg l^{-1} are common. The most severe oxygen depletion occurs in the area near Broomes Island (station LE1.1), south of the mouth of Battle Creek.

phic pathways within food webs (Breitburg et al. 1999), and a reduction in the economic value of commercial and recreational fisheries (Lipton et al. 2003; Mistiaen et al. 2003).

In this paper, we describe spatial and temporal patterns of low DO in the Patuxent River, examine effects of low oxygen on Patuxent River species and their interactions, and use a spatially-explicit, individual-based predation model to examine how current, worsened, and improved DO conditions may affect gelatinous zooplankton predation on estuarine fish eggs and larvae in the Patuxent River. Our analyses and model simulations include use of monitoring program data that has not been previously published in the peer-reviewed literature (DO measurements, fish-kill data, gelatinous zooplankton abundances), new data on lateral distributions of DO within the Patuxent River, experiments on tolerances of gelatinous zooplankton, and additional field sampling to test effects of DO on vertical distributions of biota. Our model simulations accomplish a direct link between land use within the watershed and subsequent consequences to water quality, and ultimately to effects on living resources. Our focus is on the mesohaline portion of the river (Fig. 1), which regularly experiences summer oxygen depletion under current nutrient loadings. Hypoxia will be defined as oxygen concentrations < 50% saturation (approximately 3.5–4.0 mg l^{-1} at Patuxent River summer temperatures and salinities) because such levels have been shown to negatively affect growth, predation rates, and habitat utilization by sensitive fish species (Breitburg 2002).

Temporal and Spatial Patterns of Low DO

Analysis of data collected 1985–2001 by the Chesapeake Bay Water Quality Monitoring Program (CBP) indicates that DO concentrations in the mesohaline Patuxent River create a spatial and temporal mosaic of habitats that vary in their suitability for growth and survival of fish and invertebrates. The mesohaline portion of the river typically stratifies during late spring through early autumn. During this period, subpycnocline waters are usually $< 50\%$ saturated, and can be severely hypoxic or anoxic in deep areas of the river that are most strongly stratified (Fig. 1). Bottom DO concentrations are typically at or below 2 mg l^{-1} near the bottom, and below 4 mg l^{-1} at 6 m depth, from the area near Sheridan Point (Chesapeake Bay Program monitoring station RET1.1) to below the mouth of St. Leonard Creek (monitoring station LE1.2). The depth of the upper bound of the pycnocline under conditions of strongest stratification ranges from about 4 m in the vicinity of Broomes Island to approximately 6 m near the river's mouth; depth of the pycnocline is shallowest during periods of the most severe low oxygen concentrations.

The most severe and persistent bottom layer hypoxia occurs near Broomes Island (Fig. 1, monitoring station LE1.1), where subpycnocline DO concentrations near 0 mg l^{-1} can occur during June through August. Because the Patuxent River's bathymetry includes broad shallow shoals, high oxygen concentrations occur both in the surface layer and along the benthos lateral to the deep central channel even during periods of severe hypoxia or anoxia in deep waters (Fig. 2a). These surface and shoal waters serve as potential spatial refuges for animals excluded from the deep bottom waters during all or part of the summer.

Unlike the more stable mainstem Chesapeake Bay, wind mixing associated with summer storms frequently disrupts the stratification in the mesohaline Patuxent River. The variability in DO concentrations shown in Fig. 1 reflects variation both among years and among sample dates within years.

In 1998, we sampled weekly on cross-river transects near Broomes Island (LE1.1) and St. Leonard Creek (LE1.2) from May through October. We conducted vertical profiles measuring DO, temperature, and salinity at 7 cross-river sites at Broomes Island and at 5 cross-river sites at St. Leonard Creek. These fixed stations spanned the river and included the deep central channel. More stations were sampled at Broomes Island than at St. Leonard Creek in order to position two stations in the broad, shallow eastern shoal area of the river at that site. Measurements were taken at 1-m depth intervals with a YSI Model 85 oxygen, temperature, and salinity meter. Examples of transect results from the Broomes Island transect are shown in Fig. 2 to illustrate DO stratification during severe hypoxia and temporal variation in DO. On July 22 (Fig. 2a), the water column was strongly stratified; pycnocline depth was approximately 4 m and DO concentration in the water column ≥ 6 m deep was ≤ 2 mg l^{-1}. Eleven days later on August 2 following a wind-mixing event, the water column was well mixed with DO concentrations ≥ 4 mg l^{-1} throughout (Fig. 2b).

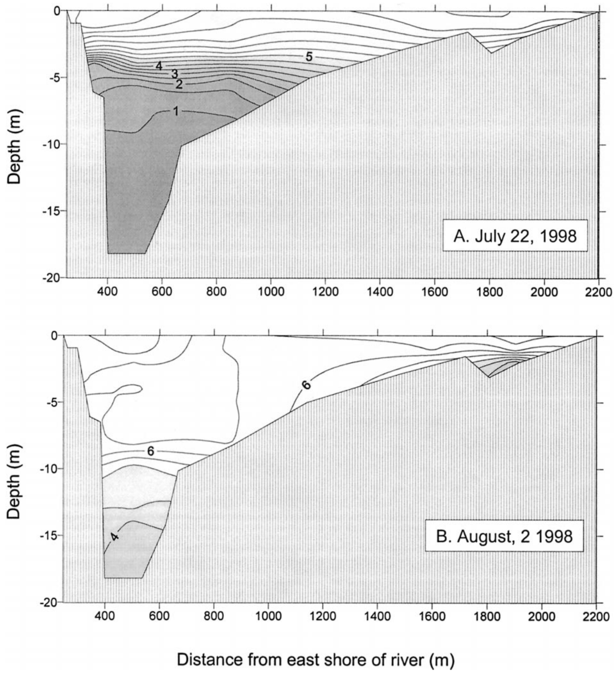

Fig. 2. Dissolved oxygen concentrations at a cross-river transect located at Patuxent River monitoring station LE1.1 during July and August 1998. Profiles taken on July 22 indicated strong stratification, a shallow pycnocline, and severe bottom layer hypoxia. On August 2, following wind mixing, oxygen concentrations were high throughout the water column.

The effect of short-term temporal variability in DO on higher trophic levels is not well understood. Most fish are able to move laterally and vertically to escape areas with declining DO concentrations (reviewed in Kramer 1987; Breitburg 2002). As oxygen concentrations improve, some fish may also temporarily increase the quantity and size of prey they consume by feeding on stressed benthic invertebrates that move onto or near the sediment surface and exhibit compromised escape responses (Pihl et al. 1991). However, in the Neuse River, North Carolina, caging experiments indicated that benthic invertebrate densities and fish growth rates decline in areas experiencing intermittent low DO, resulting in decreased growth rates of fish restricted to these areas (Eby 2001).

Very rapid declines in DO concentrations can result in high mortality of fish and mobile invertebrates that are unable to escape. In parts of the mainstem Chesapeake Bay, substantial mortality of demersal fishes and mobile epibenthic invertebrates, as well as some mid-water species, occurs when winds and internal lateral tides force oxygendepleted bottom water into nearshore shallow habitats (Breitburg 1992). These rapid drops in DO have not been reported for the Patuxent River.

Effects of Low Oxygen on Patuxent River Biota

Tests of DO Tolerances of Patuxent River Gelatinous Zooplankton

Field distributions and predation experiments indicated that the dominant gelatinous predators in the Patuxent River and the mesohaline Chesapeake Bay, the scyphozoan jellyfish *Chrysaora quinquecirrha* (the sea nettle) and the lobate ctenophore *Mnemiopsis leidyi,* might be highly tolerant of exposure to hypoxic conditions (Breitburg et al. 1997; Keister et al. 2000 and data from new field sampling described below; Kolesar unpublished data; Decker unpublished data). A second ctenophore, *Beroe ovata,* is abundant in the Patuxent River during late summer and early fall, and is an important predator on *Mnemiopsis.* To test the tolerance of *Mnemiopsis, Beroe,* and sea nettles to low DO, we held field-collected animals in 80-l aquaria (*Mnemiopsis, Beroe,* and small sea nettles) or cylinders filled to 90 l (large sea nettles) in which oxygen concentrations had been adjusted prior to the addition of animals by bubbling the water with nitrogen. All animals were collected from the mainstem Patuxent River or from Mackall Cove, which is located near the mouth of St. Leonard Creek, and held in the laboratory overnight. *Mnemiopsis* and sea nettles were fed brine shrimp (*Artemia* sp.) nauplii or live copepods during the morning prior to placing them in test aquaria; live copepods were added to test aquaria and cylinders daily to encourage active swimming. *Beroe* were fed live *Mnemiopsis* both prior to and during the exposure trial. DO was measured several times during each trial with a YSI Model 95 DO meter and adjusted, as needed, by gently bubbling water with nitrogen gas or air. Measured DO concentrations, number of animals per container, number of replicates per DO treatment, measured temperatures, and trial durations are listed in Table 1.

We determined 24-h survival for all species tested, but repeated or extended trials beyond 24 h if survival was 100% at the lowest DO concentration tested or if animals appeared near death at 24 h in one of the treatments. Following a preliminary 24-h trial in which *Mnemiopsis* had 100% survival at all oxygen concentrations tested (air-saturation and 2.5, 1.5, and 0.5 mg l^{-1}), we repeated the experiment with the exposure duration extended to 96 h. Individuals were 15 to 30 mm in total length; total biovolume in each aquarium was 6.5 to 7.5 ml. Small sea nettles (16–53 mm bell diameter) were tested at nominal DO concentrations of air

TABLE 1. Measured DO concentrations (mean (± 1 SE), number samples per replicate), temperatures (°C), and experiment durations (h) in tests of gelatinous zooplankton tolerance to hypoxia. Dissolved oxygen means are for individual experimental aquaria or cylinders for each target DO treatment. nt = not tested. Temperature ranges include minimum and maximum measurements across all dates, DO treatments, and treatment replicates. Temperatures were generally measured each time DO was determined. Number of animals per container varied with size of animals to avoid crowding.

				DO Concentration					
Species and Size Tested	Duration	No. ind. per Container	Replicates per DO Treatment	Air saturation	2.5 mg l^{-1}	1.5 mg l^{-1}	1.0 mg l^{-1}	0.5 mg l^{-1}	Temperature Range (°C)
Mnemiopsis leidyi	96	10	1	7.4 (0.02), 16	2.4 (0.05), 16	1.6 (0.03), 16	nt	0.6 (0.01), 16	22.4–24.2
Small *Chrysaora quinquecirrha*	48	5–7	2	7.5 (0.02), 8	nt	1.5 (0.05), 8	nt	0.6 (0.01), 8	23.4–25.1
				7.4 (0.03), 8		1.4 (0.05), 8		0.6 (0.04), 8	
Large *Chrysaora quinquecirrha*	50 (30 for 1 mg l^{-1} trt.)	3	2	6.9 (0.07), 7	nt	1.4 (0.04), 7	0.9 (0.05), 4	0.5, 2	21.0–21.8
				6.5 (0.07), 7		1.5 (0.03), 7	1.0 (0.05), 4	0.5 (0.01), 7	
Small *Beroe ovata*	24	5	2	7.4 (0.05), 5	2.1 (0.13), 5	1.5 (0.05), 5	nt	0.5 (0.09), 3	22.5–24.7
				7.4 (0.04), 4	2.4 (0.06), 4	1.5 (0.06), 4		0.5 (0.03), 3	
Large *Beroe ovata*	72	5	2	7.4 (0.05), 8	2.1 (0.13), 9	1.5 (0.05), 9	nt	0.5, 2	22.6–24.8
				7.4 (0.04), 8	2.4 (0.06), 9	1.5 (0.06), 9		0.5, 2	

saturation, 1.5, and 0.5 mg l^{-1} for 48 h. Large-sized (90–120 mm bell diameter) sea nettles were initially tested at the same DO concentrations used for small sea nettles. We added a 1.0 mg l^{-1} treatment 20 h after the start of the experiment in response to observed mortality at 0.5 mg l^{-1}. Total trial duration was 50 h. Small (1–5 ml biovolume each; approximately 3–4 cm) and large (8–17 ml biovolume each; length not estimated) *Beroe* were tested at air saturation, 2.5, 1.5, and 0.5 mg l^{-1}. Trial durations were 24 h for small *Beroe* and 72 h for large *Beroe.*

Mnemiopsis survival was 100% at all DO concentrations. *Mnemiopsis* that appeared inactive at 24 h responded to the addition of live copepods (*Acartia tonsa*) by moving up off the tank bottom and actively swimming throughout the tank. We did not observe any gross differences in behavior among treatments. In Fig. 3 we plot the 96 h LC$_{50}$ of *Mnemiopsis* as 0.5 mg l^{-1} because we lack data at lower DO concentrations. The true 96 h LC$_{50}$ value for this species is < 0.5 mg l^{-1}.

Survival of small sea nettles was 100% in all aquaria at all DO concentrations. Regardless of DO concentration, most sea nettles were on the tank bottom instead of actively swimming in the water column; bell contractions appeared normal in all individuals.

Survival of large sea nettles was 100% for all DO concentrations ≥ 1.0 mg l^{-1}. All three large-sized sea nettles died in one of the duplicate 0.5 mg l^{-1} cylinders within 16 h of adding them to test containers. One sea nettle died in the other 0.5 mg l^{-1} cylinder by 24 h, and a second sea nettle died after between 40 and 50 h of exposure. As with small sea nettles, most large-sized sea nettles were on the bottom of the tank, but all actively contracted their bell throughout the exposure trial. In Fig. 3 we plot the 24 h LC$_{50}$ for sea nettles as 0.5 mg l^{-1}. Our trials indicate that small individuals are somewhat more tolerant than that estimate, and large individuals are slightly less tolerant.

Beroe ctenophores were somewhat less tolerant of exposure to low oxygen than were the other two gelatinous species tested. In tests of both small and large *Beroe,* all individuals in the 0.5 mg l^{-1} treatment died in less than 19 h; trials were started in late afternoon and 100% mortality was noted during the first (0900) morning observation. Twenty-four to 28-h survival of all *Beroe* was 100% in treatments with nominal DO concentrations ≥ 1.5 mg l^{-1}.

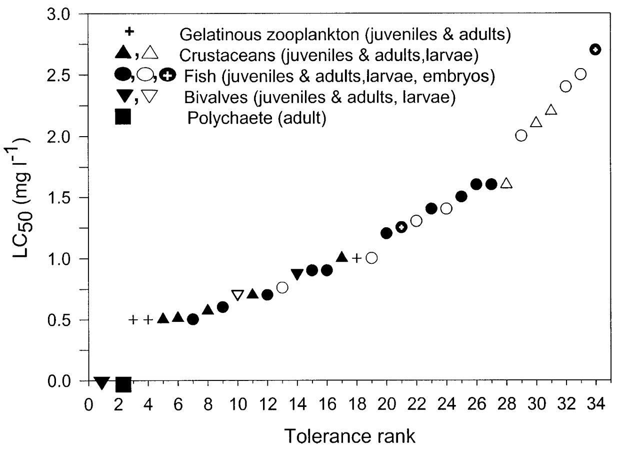

Fig. 3. Dissolved oxygen tolerances of Patuxent River fish and invertebrates. The ctenophore, *Mnemiopsis leidyi,* sea nettle, *Chrysaora quinquecirrha,* and some benthic invertebrates are the most tolerant species, while larval fish and larval crustaceans tend to be the most sensitive. LC$_{50}$ = concentration yielding 50% mortality. LT$_{50}$ = time to 50% mortality. Citations in the species list that follows are as follows: (a) = this paper; (b) = Poucher and Coiro 1997; (c) U.S.-Environmental Protection Agency 2000; (d) Pihl et al. 1991; (e) = Miller et al. 2002; (f) = Burton et al. 1980; (g) = Saksena and Joseph 1972; (h) = Breitburg 1994; (i) = Chesney and Houde 1989; (j) = Stickle et al. 1989; (k) = Llanso and Diaz 1994. Species (listed in the tolerance order shown on the graph), test duration or other explanation, and the source of data are as follows: (1) *Crassostrea virginica* adults (LT$_{50}$ under anoxia at 20°C and 10 psu = 20 d; j); (2) *Loimia medusa* (LT$_{50}$ under anoxia = approximately 72 h; k); (3) *M. leidyi* (24 and 96 h; a); (4) *C. quinquecirrha* (sea nettle; 24–72 h; a); (5) *Palaemonetes pugio* (grass shrimp; 24 h; b); (6) *Rithropanopeus harisii* (Harris mud crab; 96 h; c; < 0.55 mg l^{-1} in citation); (7) *Trinectes maculatus* (hogchoker; 24 h; d); (8) *Eurypanopeus depressus* (flat mud crab; 96 h; c); (9) *Prionotus carolinus* (northern sea robin; 96 h; e); (10) *Mercenaria mercenaria* (northern quahog; 24 h; c; < 0.71 mg l^{-1} in citation); (11) *Paleomonetes pugio* (grass shrimp; 96 h; e); (12) *Leiostomus xanthurus* (spot; 96 h; f); (13) *Cyprinodon variegatus* (sheepshead minnow; 96 h; b; < 0.76 mg l^{-1} in citation); (14) *Crassostrea virginica* (Eastern oyster; 96 h; c); (15) *Scopthalmus aquosus* (windowpane flounder; 24 h; e); (16) *Apeltes quadracus* (fourspine stickleback; 96 h; e); (17) *Paleomonetes vulgaris* (marsh grass shrimp; 96 h; e); (18) *Gobiesox strumosus* (skilletfish; 24 h; g); (19) *Brevoortia tyrannus* (Atlantic menhaden; 96 h; e); (20) *Menidia beryllina* (tidewater silverside; 96 h; c); (21) *Gobiosoma bosc* (naked goby; 24 h; g); (22) *Pleuronectes americanus* (winter flounder; 96 h; e); (23) *Menidia beryllina* (tidewater silverside; 24 h; e); (24) *Syngnathus fuscus* (pipe fish; 24 h; e); (25) *Morone saxatilis* (striped bass; 96 h; e); (26) *Paralichthys dentatus* (summer flounder; 24 h; e); (27) *Palaemonetes pugio* (grass shrimp; 24 h; e); (28) *Anchoa mitchilli* (bay anchovy; 24 h; h); (29) *Paleomonetes vulgaris* (grass shrimp; 48 h; e); (30) *Eurypanopeus depressus* (flat mud crab; 24 h; e); (31) *Morone saxatilis* (striped bass; 24 h; e); (32) *Chasmodes bosquianus* (striped blenny; 24 h; g); (33) *Anchoa mitchilli* (bay anchovy; 12 h; i). Sturgeon species are not included in Fig. 3 because experiments were not designed in a way that allows estimation of LC$_{50}$ values.

As with sea nettles, small *Beroe* individuals were more tolerant of low oxygen than were large individuals. Although ciliary action indicated that all individuals of both size classes were alive at 24 h in the 1.5 mg l^{-1} DO treatment, we noted opaque areas (i.e., degraded tissue) on some large individuals in that treatment by 24 h. We extended the duration of the large-sized *Beroe* trial. Mortality of large-sized *Beroe* in the 1.5 mg l^{-1} treatment averaged 30% by 44 h, 50% by 48 h, and 90% by 72 h. Survival to 72 h was 100% in the 2.5 mg l^{-1} and the air saturated treatments. In Fig. 3 we plot the 24 h LC_{50} of *Beroe* as 1.0 mg l^{-1}.

Variation in DO Tolerances of Patuxent River Species

The Patuxent River food web includes animals with a wide range of taxonomic affinities, behavioral capabilities, and physiological tolerances. Top consumers in the system include a scyphozoan jellyfish (the sea nettle) and ctenophore (*Mnemiopsis*) that are important predators of fish eggs and larvae, as well as piscivorous fishes that prey on ichthyoplankton and older fish life stages. Our tolerance experiments described above and published data on Patuxent River fish species indicate that the gelatinous zooplankton and trophically similar fish species are at opposite extremes of the ranges of tolerance to low DO (Fig. 3).

During periods of moderate to severe oxygen depletion during summer, DO concentrations in Patuxent River subpycnocline waters are lethal (if not avoided) to a large number of taxa (Fig. 3). Most species can survive exposure to DO concentrations of 2.5 mg l^{-1} for 24 h, but there is considerable variation among species. In general, early life history stages of fishes and crustaceans tend to be most sensitive to low DO, while gelatinous zooplankton and adults of some benthic fish and invertebrates tend to be more tolerant (Fig. 3).

The bay anchovy (*Anchoa mitchilli*) is the most abundant fish in the Chesapeake Bay system and the dominant zooplanktivorous fish in the food web (Houde and Zastrow 1991). Planktonic eggs of the bay anchovy are the most sensitive organisms currently inhabiting the mesohaline Patuxent River, and have a 12-h LC_{50} of 2.7 mg l^{-1} (Chesney and Houde 1989). Juveniles of Atlantic sturgeon (*Acipenser oxyrinchus*) and shortnose sturgeon (*Acipenser brevirostrum*), that are now extirpated from the system but are believed to have formerly been important components of the Patuxent River fish fauna, are the most sensitive Patuxent species that have been tested, and experience mortality at oxygen concentrations above 3 mg l^{-1} (Jenkins et al. 1994; Secor and Gunderson 1998). Striped bass (*Morone saxatilis*) larvae are also quite sensitive, with an LC_{50} value estimated at 2.4 mg l^{-1} (Miller et al. 2002).

In contrast to these sensitive fishes, sea nettles and *Mnemiopsis,* which are important zooplanktivores and consumers of ichthyoplankton (Purcell et al. 1994a,b), are among the most tolerant species in the system tested to date. The difference in tolerance to low DO of trophically-similar fish and gelatinous species may contribute to shifts in the relative importance of alternate pathways of carbon flow in the system, and contribute to the high abundances of *Mnemiopsis* and sea nettles observed in eutrophic hypoxic systems (Breitburg et al. 1997, 1999; Purcell et al. 2001). Many benthic invertebrate species are even more tolerant than sea nettles and *Mnemiopsis*. We plot adult Eastern oysters (*Crassostrea virginica*) and a polychaete (*Loimia medusa*) in Fig. 3 as examples of species that survive extended exposure to anoxia (Stickle et al. 1989; Llanso and Diaz 1994). Eastern oysters can survive > 28 d of anoxia at 10°C, and survive 3–8 d of anoxia at 30°C.

Fish Kills and Other Mortality

The extent to which subpycnocline hypoxia and anoxia cause mortality of biota in the Patuxent River depends both on the tolerances of the species exposed, and the ability of mobile animals to escape to well-oxygenated surface or shallow nearshore waters. Fish kills associated with low oxygen, in which mortality is obvious from the water's surface or shore, are not a regular feature of the Patuxent River, although they have been recorded. From 1987 to 2002, only 4 Patuxent River fish kills thought to be associated with low oxygen stress were identified in the Maryland State Fish Kill Database (Luckett personal communication). Three of the four incidents were in mesohaline portions of the Patuxent River or its feeder streams and primarily involved Atlantic menhaden (*Brevoortia tyrannus*). The fourth incident was in the tidal freshwater Jug Bay National Estuarine Research Reserve.

It is likely that substantial additional mortality goes undetected. Among the most vulnerable will be species or life stages with poor abilities to escape. The potential for high mortality of bay anchovy eggs is evaluated below using an individual-based model. Sensitive sessile benthic invertebrates that settle into deep areas during spring likely suffer extensive mortality during summer as oxygen concentrations decline to lethal levels. Benthic samples from the Patuxent River show a pattern of declining biomass with increasing depth (Fig. 4; data from Versar 2002). Although factors such as sediment quality, predation, and prey abundance strongly affect benthic invertebrate distribution and biomass, the pattern in the data is consistent with low DO negatively affecting recruitment, growth, or survival of Patuxent River benthos. Deepest areas experience the most severe and persistent oxygen depletion, and would be expected to be tolerated by the fewest species.

Habitat Use and Distributions

Distributions of mobile organisms within the Patuxent River may change markedly as animals

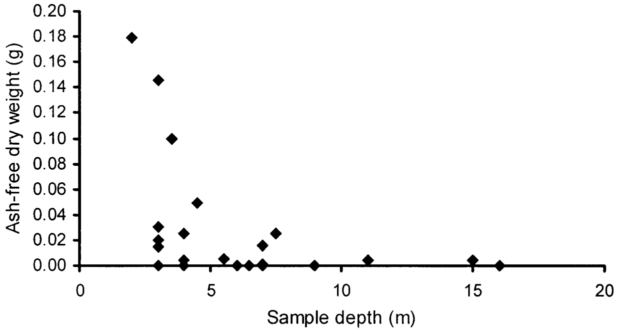

Fig. 4. Benthic biomass from fixed stations and random samples in the mesohaline Patuxent River. Data are from Versar 2002.

move vertically and shoreward to avoid lethal or stressful DO concentrations. All estuarine animals that have been tested show a behavioral avoidance response to low DO (e.g., fish: Deubler and Posner 1963; Breitburg 1994; Wannamaker and Rice 2000; copepods: Decker et al. In press; sea nettles and ctenophores: Breitburg unpublished data). Oxygen concentrations triggering such avoidance vary considerably among species depending on their own tolerances and those of their prey. The oxygen structure of the water column can have a strong effect on encounter rates between predators and their prey (Keister 1996); fish tend to avoid not only lethal oxygen concentrations, but also sublethal concentrations that result in reduced growth or feeding (Breitburg 2002). A study in North Carolina suggests, however, that use of suboptimal habitat by fish increases as the percent of total habitat with low oxygen concentrations increased (Eby 2001).

VERTICAL DISTRIBUTIONS

Previous field sampling in the Patuxent River in 1992–1993 indicated substantial shifts in the vertical distributions of zooplankton and fish larvae consistent with behavioral avoidance of hypoxic bottom waters (Keister et al. 2000). In order to increase sample size and to also sample during years with higher ctenophore abundances, we repeated the sampling procedure used by Keister et al. during two cruises in 1998 (June 22 and September 3: gelatinous zooplankton only), three cruises in 1999 (June 22, July 27, and August 24: gelatinous zooplankton, fish eggs, and fish larvae), and one cruise in 2001 (gelatinous zooplankton, fish eggs, and fish larvae). Mean *Mnemiopsis* biovolume in samples collected at LE1.1 during March–December was 2.3 and 3.9 ml m^{-3} during 1992 and 1993, respectively, and was 32.6, 24.9, and 12.1 ml m^{-3} during 1998 to 2000 (data from CBP 2002). Duplicate 1.5–2 min surface, pycnocline, and bottom layer discrete depth tows were taken with a 1-m^2 tucker trawl fitted with a 212-μm mesh net. The probe from a YSI Model 59 DO meter was attached to the trawl frame; DO readings were recorded when the trawl opened, and at 30-s intervals thereafter. The mean of these measurements was used as an estimate of the DO concentration of the water sampled by the net. We examined the mean DO values of each sample to confirm that our samples were assigned to the correct water layer. Ichthyoplankton and gelatinous zooplankton were separated onboard by rinsing samples through a coarse sieve, and then concentrating ichthyoplankton samples with a 200-μm mesh sieve. Ichthyoplankton samples were preserved in ethanol for later identification and measurement. Total sample biovolume, number per unit volume, and size of animals (length for ctenophores, bell diameter, and individual volumes for sea nettles) were determined for gelatinous zooplankton from unpreserved samples onboard the research vessel.

Combined results from Keister et al. (2000) and the more recent Patuxent cruises are shown in Fig. 5. There were three basic patterns of vertical distribution: bay anchovy eggs were distributed throughout the water column regardless of bottom DO concentration; *Mnemiopsis* preferentially used the bottom layer until bottom oxygen concentrations dropped below 1 mg l^{-1} and then were found only in the surface and pycnocline layers; and fish larvae (both bay anchovy and naked goby), copepods, and sea nettles showed a gradually increasing use of the bottom layer with increasing bottom DO, and no evidence of avoidance of DO $\geq$ 3.0 mg l^{-1}. Although we cannot rule out the possibility of direct hypoxia-induced mortality of motile species and life stages, laboratory experiments indicate that fish larvae (Breitburg 1994), copepods (Decker et al. In press), *Mnemiopsis,* and sea nettles (Breitburg and Morris unpublished data) all have the ability to respond to low DO in a stratified water column by moving vertically to more highly oxygenated depths. Our additional data re-emphasizes previous conclusions (Breitburg 1994; Keister et al. 2000) that, except for fish eggs, the strongest signals creating the observed vertical distributions in the field are active behaviors and depth-specific predation, not mortality resulting from direct exposure to hypoxia.

In order to examine how spatial overlap between predators and their prey varied with bottom layer DO, we estimated the proportion of individuals of each taxon that would occur in the surface, pycnocline, and bottom layers of the water column for different bottom DO concentrations. Predicted proportions in each layer were calculated based on

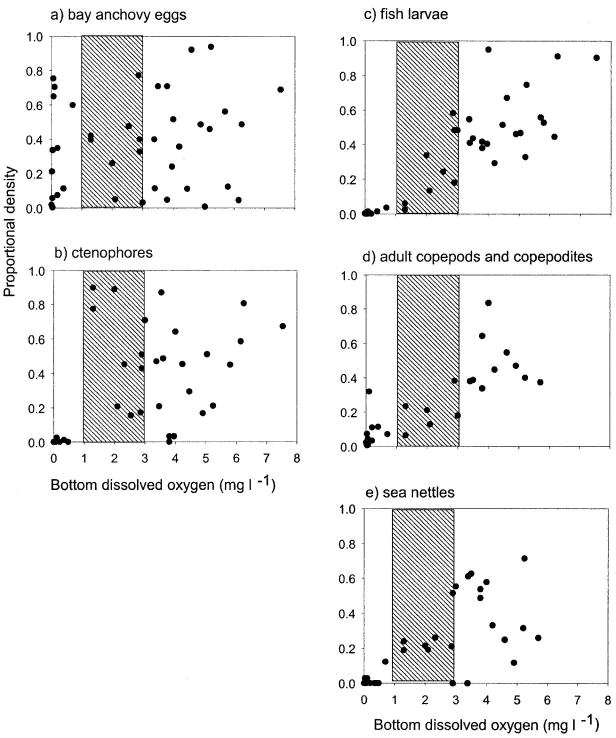

Fig. 5. Proportional density in the bottom layer of the water column for zooplankton and ichthyoplankton collected in depth stratified trawls and zooplankton pump samples from the Patuxent River between Broomes Island and Battle Creek, and near the mouth of St. Leonard Creek. Copepod data are from Keister et al. (2000); other data sets combine data from Keister et al. (2000) and new data collected at the same sites during 1998–2001. Proportional density is the proportion of individuals in a given layer of the water column assuming equal volumes in the surface, pycnocline, and bottom layers, and is used to illustrate the relationship between vertical distribution and bottom layer DO concentration. The vertical cross-hatched area highlights the 1–3 mg l^{-1} DO range in which species vary in their responses to low oxygen. The graph showing the distribution of fish larvae combines data for the two dominant ichthyoplankton species, bay anchovy, and naked goby, because their vertical distributions are similar. A proportional density of 0.33 would indicate no preference for or against the use of the bottom layer; 0 indicates that no individuals were in bottom layer samples, and 1.0 indicates individuals of that particular species were only found in the bottom layer in a particular matched set of surface, pycnocline and bottom-layer samples.

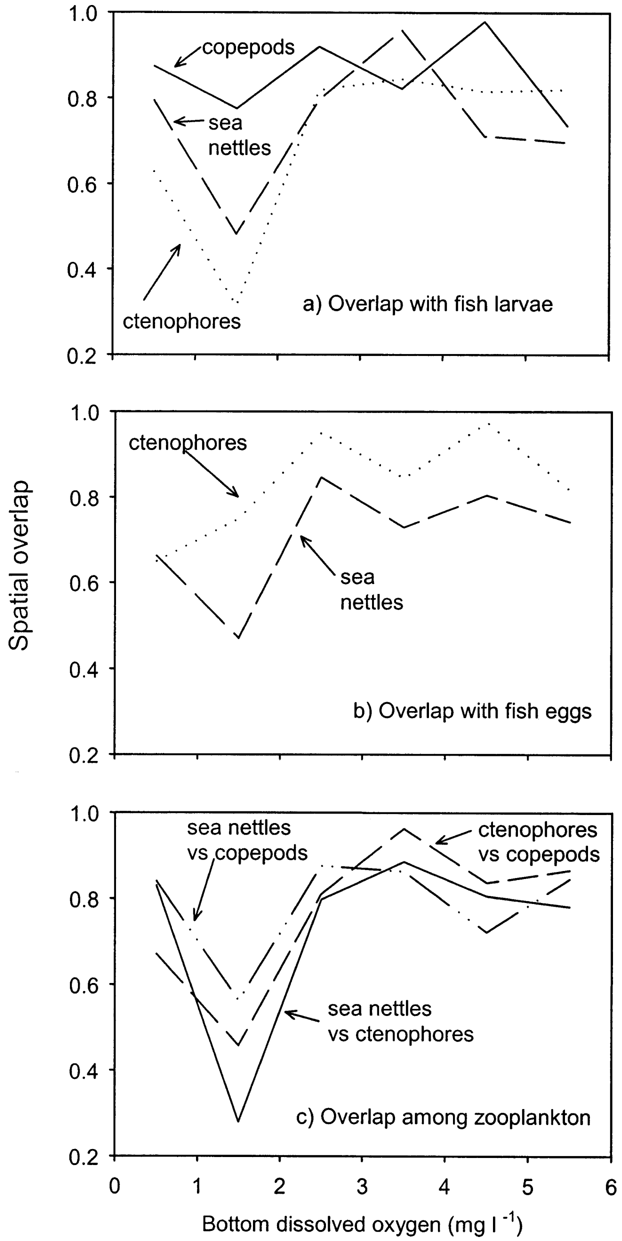

Fig. 6. Effect of bottom layer DO concentration on spatial overlap between predators and prey. Overlap was calculated for a 12-m water column with a 4 m deep, 2-m thick pycnocline using Schoener's index (Schoener 1970). A score of 1.0 would indicate that species had identical vertical distributions.

the total volume of each water layer and the relative densities calculated from field samples, and were calculated as the mean of each 1 mg l^{-1} bottom DO interval. We used Schoener's index of habitat overlap (Schoener 1970) to calculate spatial overlap for each DO interval. An overlap of 1.0 indicates identical use of all habitats, while an index of 0.0 indicates no overlap. Results are plotted in Fig. 6 for a 12-m water column with a 4-m thick surface layer, 2-m thick pycnocline, and 6-m thick bottom layer. Because vertical distributions are based on field samples, the resulting patterns include both DO avoidance and predation effects.

The pattern of spatial overlap varied somewhat with total water column depth (and therefore the percent of the water column in each layer), but several general patterns emerged. Overlap between fish larvae and their copepod prey remained high across the range of bottom DO concentrations (Fig. 6a). For most other predator-prey pairings, spatial overlap varied with bottom DO concentration. Lowest overlap most commonly occurred at oxygen concentrations of 1.0–1.99 mg l^{-1} (Fig. 6a–c), at which the bottom layer was preferentially used by *Mnemiopsis,* but avoided by most other species (Fig. 5). The differential use of the bottom layer led to strong differences among species in their use of the surface and pycnocline layers. Overlap between larvae and both gelatinous predators was lowest at 1.0–1.99 mg l^{-1}; spatial overlap between larvae and ctenophores was also reduced at oxygen concentrations < 1.0 mg l^{-1}. Oxygen concentrations < 2.0 mg l^{-1} reduced spatial overlap between the two gelatinous predators and bay anchovy eggs (Fig. 6b).

Fish eggs are unable to behaviorally avoid lethal DO concentrations. High abundances of bay anchovy eggs in bottom waters with lethal oxygen concentrations in these samples indicates the potential for subpycnocline oxygen depletion to represent a substantial source of mortality for fish eggs in weakly stratified tributaries. Approximately 60% of the volume of the Patuxent River from Broomes Island to midway between St. Leonard Creek and Pt. Patience is ≥ 7 m deep, and frequently has oxygen concentrations that would be lethal to bay anchovy embryos.

Modeling the Effect of Low Oxygen on Predation Mortality of Fish Eggs and Larvae

We used a spatially-explicit, individual-based model to predict how current, improved, and worsened DO affects larval fish and egg survival within the central portion of the mesohaline Patuxent River. Our modeled organisms are based on bay anchovy for the egg stage, and a composite of information on bay anchovy and naked goby for the larval stage. We performed two sets of simulations that expand upon the hypothetical single-site simulations described in Breitburg et al. (1999), and allow us to make quantitative predictions relevant to the Patuxent River. The first set of simulations uses as a baseline the 1985–2001 monthly mean DO concentrations measured by the Chesapeake Bay Water Quality Monitoring Program (CBP 2002), actual river bathymetry, and considers much of the lateral extent of the river in addition to the central channel. We compare fish egg and larval survival under these long-term mean baseline conditions to survival if DO increased or decreased by a fixed amount, or was high throughout the water column. Specifying constant DO concentrations within discrete mg l^{-1} intervals within water columns of fixed dimension permitted the isolation of the effects of known and constant DO concentrations on larval and egg survival, and allowed for easy interpretation of model predictions.

The second set of simulations used daily predictions from a water quality model (Lung and Bai 2003), and illustrates how changes in watershed management can be processed through watershed (Weller et al. 2003), water quality, and ecological models, culminating in a quantitative linkage between watershed actions and larval fish and egg survival. Rather than creating scenarios by altering DO by a fixed amount, we compared DO scenarios based on changes in DO predicted from land use within the watershed. The simulations that used the output from the water quality model were more realistic than the first set in the way that DO and water column dimensions were allowed to vary daily in response to watershed and hydrodynamic processes. There is a trade-off between realism and generality in that these simulations describe conditions and predictions for a single year, and are limited to the central channel of the river.

MODEL DESCRIPTION

The model tracks the daily location, encounters with gelatinous predators, and survival of individual fish eggs or fish larvae in a 3-layer (surface, pycnocline, and bottom) water column and is based on the models described in more detail in Cowan et al. (1996) and Breitburg et al. (1999). The water column is defined by the thickness of each of the 3 layers, the total volume of the modeled box, and the bottom-layer DO concentration. The numbers of individual fish eggs, fish larvae, sea nettles, and *Mnemiopsis* within the modeled box are generated at the beginning of each simulation from specified densities (number m^{-3}) based on field data (Table 2). The lengths of each individual larval prey (mm) and predator (body length for ctenophores; bell diameter for medusae) are generated from normal probability distributions. The length of each larva increases daily from its initial length based on an assigned growth rate; egg size (assumed to be 1 mm long) and predator lengths remain constant throughout the simulation. Growth and reproduction of gelatinous predators is reflected in the difference in predator numbers and sizes specified for each time period simulated, rather than as growth during the brief periods simulated.

On each day of the simulation, the number of encounters of each prey (larvae or eggs) with each predator is computed based on prey and predator swimming speeds and encounter radii (both functions of prey and predator lengths). Encounters only occur between prey and predator individuals that are located in the same layer. Whether an encounter leads to a successful capture is then evaluated for each encounter. All prey and predator individuals are randomly reassigned to a layer each

TABLE 2. Input values used for individual-based model simulations. Different *Mnemiopsis* (ctenophore) densities and sizes are used for the larval and egg simulations. Based on observations of laboratory feeding behavior (Kolesar unpublished data), we assume that all lobate individuals quantified in our field sampling (i.e., individuals ≥ 10 mm length) feed on eggs, but that only individuals ≥ 25 mm feed on larvae. We do not estimate the abundance or effect of ctenophores < 10 mm in length because these would have been lost from our samples in the process of separating fish larvae from gelatinous zooplankton. Field data and model include sea nettles ≥ 25 mm bell diameter. Lengths are total length for fish larvae and diameter for fish eggs. na = not applicable.

	Egg Predation			Larval Predation Mortality			Field Data (Combined Data from Keister et al. 2000 and 1998–2001 Patuxent Samples Described Here)		
Simulation duration		1 d			7 d				
Volume of simulated water column (m^3)		2000			2000			na na	
	June	July	August	June	July	August	June	July	August
Mean and standard deviation initial prey length (mm)	1.0, 0.0	1.0, 0.0	1.0, 0.0	2.8, 0.5	2.8, 0.5	2.8, 0.5	na	na	na
Minimum and maximum initial prey starting length (mm)	1.0, 1.0	1.0, 1.0	1.0, 1.0	2.3, 3.2	2.3, 3.2	2.3, 3.2	na	na	na
Ctenophore density (no. m^{-3} ≥ 10 mm length)	3.7	2.5	1.1	na	na	na	3.7	5.5	1.1
Ctenophore density (no. m^{-3} ≥ 25 mm length)	na	na	na	1	2.5	1.1	1.0	5.5	1.1
Ctenophore length ≥ 10 mm (mean, SD mm)	21, 12	58, 19	54, 14	na	na	na	20.6, 12.1	58,0, 19.0	54.0, 14.2
Ctenophore length ≥ 25 mm (mean, SD mm)	na	na	na	36, 13	59, 20	55, 15	35.8, 13.0	58.09, 19.0	54.0, 14.2
Minimum and maximum ctenophore length (mm)	10, 90	10, 106	10, 102	25, 90	25, 106	25, 102	10, 90	10, 106	10, 102
Sea nettle density (no. m^{-3})	0.0	0.05	0.08	0.0	0.05	0.08	0.0	0.10	0.08
Sea nettle bell diameter (mean, SD mm)	na	69, 37	84, 32	na	69, 37	84, 32	na	69.4, 36.7	84.2, 32.2
Minimum and maximum sea nettle bell diameter (mm)	na	25, 170	25, 190	na	25, 170	25, 190	na	25, 170	25, 190

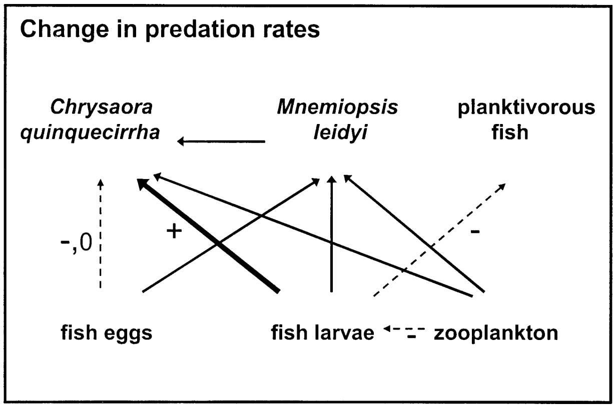

Fig. 7. Changes in predation rates at 1.5 and 2.5 mg l^{-1} relative to that at high oxygen concentrations. Sea nettle predation rate on fish eggs decreases at 1.5 mg l^{-1} but not at 2.5 mg l^{-1}; sea nettle predation on fish larvae increases at both low oxygen concentrations (Breitburg et al. 1997). Predation by naked goby larvae on zooplankton decreases at 2 mg l^{-1} (Houde and Zastrow unpublished data). Predation on naked goby larvae by juvenile striped bass decreases at oxygen concentrations ≤ 4 mg l^{-1} (Breitburg et al. 1997). Predation by *Mnemiopsis* on copepods (Decker unpublished data) and fish eggs and larvae (Kolesar unpublished data), and predation on *Mnemiopsis* by sea nettles (Breitburg and Morris unpublished data) were not affected by DO concentration.

day based on the proportional densities predicted from field data for each layer. The length of each larva is updated based on its assigned growth rate. The process is repeated for each day of the simulation, resulting in a prediction of the percent survival of larvae or eggs over the duration of the simulation.

Bottom layer DO concentrations (based on field data or water quality model output) were used to determine the proportional densities by layer. The DO concentration within each layer affects larval growth rate (slower with decreasing DO), capture success of some predators (Fig. 7), and the mortality rate of fish eggs. For all simulations, we divided the mesohaline portion of the Patuxent River into 7 segments from Broomes Island to below St. Leonard Creek, corresponding to river segments 30–36 in Lung and Bai (2003).

The model described in Breitburg et al. (1999) was modified to include ctenophores as predators and fish eggs as prey. Swimming speed, encounter radius, and capture success of ctenophores were added to the model based on their representation in a similar one-box version of the model by Cowan et al. (1996) and predation experiments conducted by Kolesar (unpublished data). Fish eggs were treated like 1-mm long fish larvae that did not

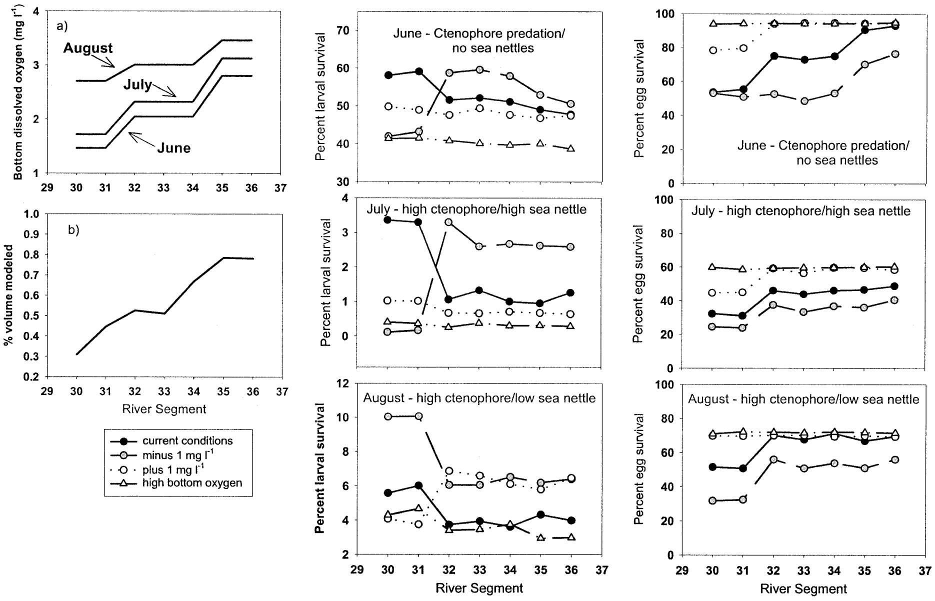

Fig. 8. DO conditions representative of June, July, and August and resulting model predictions of larval survival (7 d) and egg survival in 7 spatial segments of the mesohaline portion of the Patuxent River. Also shown is the percent of the river volume modeled in each of the segments. DO concentrations estimated from long-term monitoring data were considered baseline conditions. Predicted survival for each segment is the volume-weighted average of predicted survival rates for 3–4 depth zones in each segment (deep channel and 2–3 other depths). Larval and egg survival was predicted for the baseline conditions, for baseline bottom layer DO increased by 1 mg l^{-1} and decreased by 1 mg l^{-1}, and for high DO in all layers. (a) Bottom DO concentrations for June, July, and August in river segments, (b) percent of the total volume of each segment that was modeled. This percent includes all water layers within modeled areas, but only includes the portion of each river segment with at least 1 m of subpycnocline water. Larval survival for (c) June, (d) July, and (e) August and egg survival (f) June, (g) July, and (h) August. Note variation in scales used for larval survival required to illustrate variation among simulated DO condition effects.

grow or swim, and their capture success under all DO concentrations and for all predators was assumed to be 0.8. Laboratory experiments indicate that ctenophore predation rates on fish eggs and larvae at oxygen concentrations as low as 1.5 mg l^{-1} are similar to those at high oxygen concentrations (Kolesar unpublished data). Sea nettle capture success of fish eggs was not reduced by low DO because reduced predation and bell contraction rates only occur at oxygen concentrations that result in 100% mortality of eggs (Breitburg et al. 1994, 1997). Because eggs do not avoid lethal oxygen concentrations, we included a term for direct mortality of eggs. Chesney and Houde (1989) estimated the 12 h LC_{50} for bay anchovy eggs at 2.7 mg l^{-1}.

We do not include fish predators of eggs and larvae in these simulations as we had in Breitburg et al. (1999). The density, distribution, and importance of fish as ichthyoplankton predators in mesohaline portions of the Chesapeake Bay system are poorly understood. This omission may have its greatest effect on model results during June, when young-of-year striped bass are of an appropriate size to feed on fish larvae.

Patuxent River Model Simulations: Average Field Conditions

The first set of simulations was based on long-term average DO concentrations measured by the Chesapeake Bay Water Quality Monitoring Program and includes the portion of each river segment with at least 1 m of subpycnocline (i.e., potentially hypoxic) water (Fig. 8b). In addition to baseline conditions, we examined three hypothetical scenarios: increased (+1 mg l^{-1}) bottom DO, decreased (−1 mg l^{-1}) bottom DO, and high (above measurable biological effects) DO throughout the water column. Each bottom DO condition was simulated for three periods during the summer: June, July, and August. Because the proportion of the water column in the bottom layer can strongly affect results, we simulated 3 depth zones within each of the shallower segments (30, 31, 32, and 34) and 4 depth zones for the deeper segments (33, 35, and 36). Model boxes representing each depth zone were configured to that zone's mean depth (from nautical charts), and had a 2-m thick pycnocline. The mean pycnocline depth during strong stratification was determined from field data for station LE1.1 for segments 30–31

(4.0–5.9 m) and LE1.2 for segments 35–36 (6.0–7.9 m) (data from CBP 2002). The middle segments 32 through 34 were assumed to have a pycnocline extending from 5.0 to 6.9 m depth, i.e., intermediate between the upriver and downriver segments.

Field data were used to estimate average bottom DO concentration for each segment for each of the 3 time periods. DO concentrations were from field monitoring data taken biweekly during summer at stations LE1.1 and LE1.2 from 1985–2000 by the Chesapeake Bay Water Quality Monitoring Program (CBP 2002). As with pycnocline depths, we used data from LE1.1 for segments 30–31, data from LE1.2 for segments 35–36, and assumed that the middle segments had intermediate bottom DO concentrations (Fig. 8a). Average bottom layer DO was computed from all measurements taken in subpycnocline water during each time period, and was considered representative of current conditions. Constant DO values were simulated because the field data did not show any obvious trends in average bottom DO within each of the three time periods. Consistent with field data (Keister et al. 2000), DO concentration in the pycnocline layer was determined from the bottom DO value (3 mg l^{-1} if bottom DO was 0.0–0.99 mg l^{-1}, and 4 mg l^{-1} if bottom DO was $\geq$ 1 mg l^{-1}). DO concentrations in the surface layers were set to 5 mg l^{-1}, a level at which DO had no effects on growth, distributions, or predation rates, for all simulations.

Parameter values used in simulations are summarized in Table 2. Larval simulations were for 7 days to reflect a reasonable time period over which water column conditions would remain constant. Egg simulations were for one day to reflect their typical development rates. Initial larval and egg densities (200,000 individuals, equivalent to 100 m^{-3}) and larval lengths (mean = 2.8, SD = 0.5, min = 2.3, max = 3.2) and egg diameters (1.0 mm) were fixed at the same values for all simulations to permit easy comparisons. Because larvae and eggs do not affect the survival of other larvae or eggs, either directly or through predator behavior, their densities do not affect model simulations of survival rate. Larval and egg densities were set to high values to ensure accurate estimation of the percent surviving. Lower and more realistic larval densities would have to be used to predict the numbers surviving. Daily mortality of eggs due to low oxygen exposure was assumed to be 100% for DO < 2.0 mg l^{-1}, and 50% for eggs at 2.0–2.99 mg l^{-1}; larvae were assumed to avoid lethal oxygen concentrations.

We used Patuxent River field data from Keister et al. (2000) and the new sampling described above to estimate the densities and lengths of predators used in model simulations of each of the 3 time periods (Table 2). Predator densities and sizes remained constant within simulations, and were the same for all segments so that spatial variation in DO and bathymetry, rather than spatial variation in predators, would influence model results. Larval survival simulations used densities of ctenophores longer than 25 mm because smaller ctenophores have small lobes and are unlikely to capture larvae. Egg survival simulations used ctenophore densities that included the smallest ctenophores we quantified in our field samples (10 to 25 mm ctenophores, as well as larger individuals) because eggs are vulnerable to nearly all ctenophores (Kolesar unpublished data). Field densities of ctenophores and sea nettles were highest in July. We used only one-half the mean field density of ctenophores and sea nettles for July simulations to ensure at least minimal survival of larvae (Table 2: 4,982 ctenophores [= 2.5 m^{-3}] and 104 sea nettle medusae [0.05 m^{-3}]). We applied similar reductions to the ctenophore and sea nettle densities used for eggs in order to permit comparisons between larval and egg results. No sea nettles were present in June field data and so sea nettles were not included in June simulations.

All effects of DO in the field-based model simulations use DO specified at 1 mg l^{-1} intervals (i.e., 0.0–0.99, 1.0–1.99, 2.0–2.99, 3.0–3.99, and $\geq$ 4.0 mg l^{-1}). Predicted survival in each river segment was calculated by weighting the prediction for each depth zone by the proportion of the total modeled water volume in that segment made up by each depth zone. Volumes were calculated by digitizing a nautical chart. We report the results of a single set of simulations. Simulations repeated using 2 additional different random number sequences showed that differences in percent of larval survival of $\geq$ 3% in June and $\geq$ 1% in July and August, and differences in egg survival of $\geq$ 3% in all 3 time periods, were repeatable and therefore truly different.

PATUXENT RIVER MODEL SIMULATIONS: LINKAGE TO THE WATER QUALITY MODEL

The second set of simulations used simulated water column dimensions and DO output from a water quality model (Lung and Bai 2003). A watershed model (Weller et al. 2003) was first run for several land-use scenarios and output used as input to the water quality model. Output from the water quality model was then used as input to the individual-based larval and egg survival model. We considered effects of 3 land-use scenarios on predicted survival of early life stages of fish. The baseline watershed scenario modeled EPA-EMAP 1991 land use, nonpoint discharges measured by Jordan et al.

(2003) for July 1997–August 1998, and point source discharges and hydrographic information for the same time period (Weller et al. 2003). The water quality model then used the watershed model output with July 1997–August 1998 hydrographic information and point source discharges (Lung and Bai 2003). The two contrasting scenarios whose output we use here represent extremes of land-use changes: halved cropland, developed land, and point source flow; and doubled developed land and point source discharges. Both of these were also modeled using hydrographic data from July 1997–August 1998, a wetter-than-average year. Model simulations of larval and egg survival were for a 1-wk period in July (calendar days 181–187) for the main channel location in each of the segments.

We used the predictions of DO and water column dimensions from the water quality model as inputs to the individual-based model, rather than specifying DO concentrations in each layer of a fixed water column as we had in the field-based simulations. Water quality model predictions of daily DO by 1-m depth intervals were used to determine the thicknesses of the surface, pycnocline, and bottom layer each day, and the average DO in each layer each day, for each segment. The individual-based model then used these daily values of water column dimensions and average DO by layer, and combined with information on larvae and predators, predicted larval and egg survival. We used the same rules for vertically distributing the organisms, which is based on bottom DO only, because pycnocline and surface DO values from the water quality model were correlated to bottom DO values similarly to that assumed in vertical distribution rules. DO in each layer was used to impose the effects on larval growth rate, predator capture success, and DO-induced mortality of eggs.

There were two major differences between the simulations here that used the output from the water quality model and the simulations above that used specified DO values. Simulations based on the water quality model were for the main channel only; the simulations using field-based DO values were performed for locations across the river as well as the center of the main channel. Both DO and water column layer thicknesses were also allowed to vary daily in the simulations based on water quality model output. In the simulations with specified DO we controlled the DO values and therefore only needed DO effects on larval growth, vertical distributions, and predator capture success for DO intervals (0 to 0.99, 1.0 to 1.99, etc.). The water quality model based simulations used continuously varying DO, with DO in a layer often varying within one of the intervals over the 7 d. Representing DO effects as intervals resulted in artificially sharp changes in DO effects. To avoid threshold responses resulting from our discrete treatment of DO effects, we used linear interpolation to determine DO effects on larval growth rate, the vertical distributions of the larvae and predators, predator capture success, and DO mortality of eggs. We assumed effects occurred at the midpoints of each interval, and then linear interpolated effects for continuous values of DO. The other aspects of the water quality model-based simulations were the same as those used for July simulations using field-based DO values.

We report the larval survival and cumulative egg survival over the 7 d by segment for each scenario. Cumulative egg survival was computed as the sum of the daily number of eggs surviving divided by the total initial number of eggs. Because the individual-based model is stochastic and differences in predicted survival were small in some segments, we performed two replicate simulations using different random number sequences. The average of the two replicates is reported.

SIMULATION RESULTS: AVERAGE FIELD CONDITIONS

The most striking and common result of larval models using average field conditions as the baseline was that improving bottom DO would likely decrease, rather than increase, survival of fish larvae preyed upon by gelatinous zooplankton (Fig. 8c,d). This pattern was most consistent in late June and July, as well as in the upriver and middle segments modeled, when the times and locations of current DO concentrations are lowest. Across nearly all locations and simulation time periods, lowest larval survival occurred when the water column had high oxygen concentrations throughout, corresponding to conditions yielding high spatial overlap and fastest larval growth, both of which should increase encounter rates between predators and prey.

Variation among river segments and months in the effect of improved or worsened bottom DO on larval survival most strongly reflected variation in current DO concentrations. For example, in June and July, larval survival was highest in the upriver segments (30 and 31) under current conditions, whereas survival was highest under the -1 mg l^{-1} condition in the downriver segments (Fig. 8c,d). The -1 mg l^{-1} treatment makes bottom DO in the downriver segments equivalent to that under current conditions in the upriver segments; that is, 1.0–1.99 mg l^{-1}, the bottom DO range yielding the lowest overlap between larvae and their gelatinous predators (Fig. 6a). A reduction in bottom DO in the more severely hypoxic upriver segments resulted in higher predation mortality due to movement of the tolerant predators into the pycnocline and surface layers where larvae were located. Increased DO also resulted in higher predation mortality than current conditions because, under improved conditions, both larvae and their predators used the entire water column. Larval survival was constant and low under improved DO conditions (+1 mg l^{-1} and no effects) in all segments in June and July.

In August, effects of low oxygen on larval survival in the upriver segments also differed from effects in the downriver segments, but the pattern was different than in June and July. Bottom DO in August was moderate to high throughout the river, but was lower in segments 30 and 31 than in the downriver segments modeled (Fig. 8a). Current DO in the upriver segments is between 2.0 and 2.9 mg l^{-1} (Fig. 8a), a range of DO concentrations that results in high overlap of larvae and their gelatinous predators (Fig. 6a). Decreasing DO concentrations by 1 mg l^{-1} (i.e., the −1 mg l^{-1} simulation) resulted in the highest, or near highest, larval survival in all segments as vertical overlap between larvae and their predators decreased, but the magnitude of the effect was greatest in the upriver segments. The +1 mg l^{-1} condition resulted in low survival in the upriver segments but near the highest survival in the downriver segments, whereas the no effects condition resulted in low survival similar to current conditions in all segments. The reason for the differences between the +1 mg l^{-1} and no effects simulation results for downriver segments in August is unclear. Larval survival under the no effects condition was similar to that under current conditions.

Our results strongly suggest that gelatinous predators have the potential to significantly reduce local recruitment of larval fishes such as bay anchovy and naked goby in the Patuxent River. Predation rates on larvae exposed to gelatinous zooplankton were extremely high in July and August simulations, even with the relatively short 7-d simulations (typical larval stage duration is 30 d) and with July predator densities reduced by one-half. Larval survival in July and August under current conditions ranged from near zero to 6%.

The effect of changing DO concentrations on egg survival differed markedly from the effect on larval survival. In all months and almost all segments, highest egg survival occurred under improved DO conditions (+1 mg l^{-1} and no effects), and lowest survival occurred under the lowest DO (−1 mg l^{-1}) conditions. Increasing bottom DO greatly reduced, and often eliminated, low oxygen-induced mortality of eggs. Although, as with larvae, predation increased somewhat with increased DO conditions due to greater spatial overlap, direct mortality of eggs due to hypoxia decreased more strongly. Weighting all modeled river segments equally, as DO increased from −1 mg l^{-1}, to baseline, to +1 mg l^{-1}, to no effects, mortality due to predation was 25%, 27%, 37%, and 40% of all eggs, respectively (i.e., less than a 2-fold increase), while mortality due to hypoxia exposure was 41%, 31%, 7%, and 0% of the total egg population. The greater effect of reduced mortality associated with exposure to lethal oxygen conditions resulted in egg survival generally increasing with increasing bottom DO.

Our model predicts that nearly 20% of all bay anchovy eggs spawned in the modeled segments of the Patuxent River, including the shallow areas that were excluded from simulations, may currently be killed by low oxygen exposure. This estimate assumes that egg density in shallow shoals is the same as that measured in the center of the river, and that we modeled 60% of the river volume. The percentage of eggs killed by low oxygen exposure may also be higher, especially when and where predation is lower, since the model first subtracts predation mortality before calculating mortality due to hypoxia. Including egg sinking rates as an hourly rather than daily time step into model calculations might yield higher estimates of hypoxia-induced mortality. The vertical distribution of eggs used in our calculations was based on an average of all samples taken, including both day and night samples. If a high proportion of eggs sink into the bottom layer before they hatch, and if larvae that hatch in lethal conditions are unable to swim towards the surface, then mortality could be substantially higher than that predicted by this analysis.

Simulation Results: Linkage to Water Quality Model

Simulations using output of the water quality model indicated that changes in land use within the watershed can strongly affect survival of fish eggs and larvae, and alter the spatial arrangement of habitat quality in the river. Unlike results of simulations using field data for July baseline conditions, predicted larval survival was highest under reduced nutrient loading and lowest under increased nutrient loading in the upstream most segment 30, with differences among the land-use scenarios progressively diminishing downstream (Fig. 9c). Larval survival under baseline water quality model DO was near zero in upstream segments but was higher in downstream segments; improved water quality resulted in higher larval survival upstream than downstream. In both sets of simulations, worsened DO resulted in higher survival downriver than upriver, but only in the field-based simulations did worsened DO yield substantially

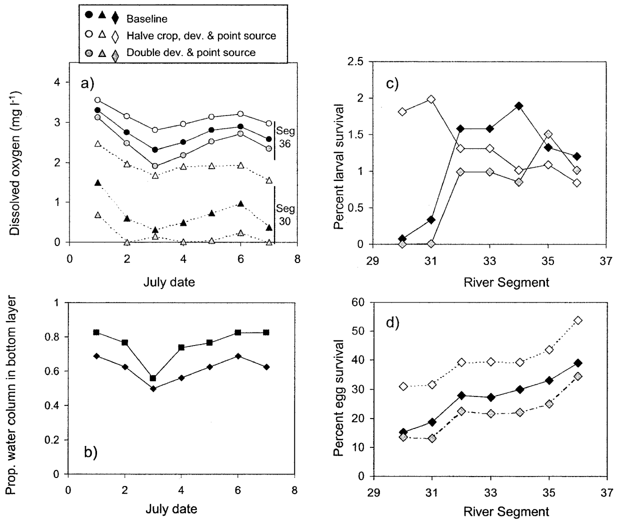

Fig. 9. Inputs to the individual-based model for July 1–7 and resulting predictions of larval and egg survival for each of the 7 spatial segments of the mesohaline portion of the Patuxent River. The inputs to the individual-based model are outputs from a water quality model, and are shown for the most upstream segment (30) and the most downstream segment (36). Model predictions of larval and egg survival are the total survival over the 7 d of the simulations. Values of the inputs and predicted survival are for 3 scenarios: baseline, increased nutrient loading (doubled developed land and point source loads), and reduced nutrient loading (halved cropland, developed land and point source loads). (a) Bottom DO concentrations for segments 30 and 36 (b) proportion of the water column within the bottom layers for segments 30 and 36, (c) larval survival for each of the segments, (d) egg survival for each of the segments.

higher survival in downriver segments than did other conditions.

The spatial pattern and the effects of changes in DO on fish egg survival were using water quality model DO similar to simulations using average field conditions. In the simulations that used water quality model output, survival of bay anchovy eggs was highest under reduced nutrient loading and lowest under increased nutrient loading for all segments (Fig. 9d). Survival also generally increased as one moved downstream from segment 30 to segment 36, as a result of increasing DO and increasing thickness of the bottom layer of the water column (shown by segments 30 and 36 in Fig. 9a,b). Egg survival averaged over the 7 cohorts was typically 10–15% higher under the reduced nutrient loadings and 0–5% lower under increased nutrient loadings along the length of the modeled river. The similarity in the predictions of the two sets of simulations, and the consistent differences among scenarios was due to the major role played by direct DO-induced mortality of eggs in all simulations.

The seemingly contradictory results for larval survival between the field-based and water quality model-based simulations are, in fact, consistent with each other, and illustrate the potential complexity of responses of biota to changing DO conditions. How increased or decreased DO will affect larval survival depends on both the absolute DO values and on how these values compare to the assumed baseline conditions. The differing predictions resulted from differences in baseline conditions used for the two sets of simulations and differences in the magnitude of change in DO modeled for the various scenarios. Larval survival in both the field-based and water quality model-based simulations was highly dependent on how DO concentrations affected the degree of spatial overlap between larvae and their predators.

In the upstream river segments (30 and 31), improved DO resulted in increased larval survival compared to baseline in the water quality model-based simulations, but resulted in reduced larval survival compared to baseline in the field-based simulations. These opposite results are consistent if one considers the lower bottom layer DO under baseline conditions in the water quality model-based analysis compared to the field-based analysis (generally < 1 mg l^{-1} versus about 1.8 mg l^{-1}). Under water quality model baseline conditions, both predators and prey were restricted to the pycnocline and surface layers. Improved DO in the water quality model-based simulation resulted in DO concentrations that allowed use of the bottom layer by some predators, but continued to restrict larvae to the surface and pycnocline. The higher baseline DO conditions in the field-based simulations were similar to those in the improved water quality model based simulations (yielding separation of larvae and *Mnemiopsis* predators), so that further increasing bottom DO by $+1$ mg l^{-1} resulted in a more uniform distribution of larvae and predators (greater spatial overlap) in the water column and caused reduced survival. Both the field-based and water quality model based baseline values are realistic and highlight the potential for strong interannual and spatial variation in DO effects on larval survival.

Conclusions

Field data, experiments, and modeling indicate that low DO in the Patuxent River creates temporal and spatial heterogeneity in the physical habitat, reduces habitat extent and suitability for fish and invertebrates, alters food web interactions, and affects survival of early life stages of ecologically important summer-breeding fishes. Because habitats throughout the river are connected by movement and transport of organisms, both the hypoxic and more highly oxygenated areas of the mesohaline river can be strongly affected.

Several features of the physical structure and biological composition of the Patuxent River may make it particularly sensitive to perturbations due to summer hypoxia. The Patuxent River is the deepest of the Chesapeake tributaries and has a shallow pycnocline relative to the mainstem Bay. Within the region of the Patuxent River that experiences hypoxia, a substantial portion of the total water volume lies below the pycnocline. The weak stratification or the shallow depth of the pycnocline (or both) in the Patuxent River allows large numbers of bay anchovy eggs to sink into the bottom layer, where they can be exposed to lethal DO concentrations. In the mesohaline mainstem Chesapeake Bay, most bay anchovy eggs are retained in the surface layer and pycnocline (North 2001; Breitburg unpublished data). Therefore, even though subpycnocline waters in the mesohaline mainstem Chesapeake have lower DO concentrations, low oxygen may be a more important source of egg mortality in the Patuxent River.

Another feature of the Patuxent River is that much of the bottom layer of the Patuxent River is moderately hypoxic (e.g., 1.0–2.9 mg l^{-1}), rather than severely hypoxic or anoxic, during the summer, and biota with a diverse range of tolerances to low DO coexist. The presence of trophically similar gelatinous zooplankton species that tolerate low oxygen concentrations, and fish that are sensitive to hypoxia, may make the Patuxent River and similar estuaries particularly susceptible to major alterations in food web dynamics, and increased dominance by gelatinous predators, when oxygen depletion occurs. Severe, persistent hypoxia and anoxia, characteristic of the mesohaline mainstem Chesapeake Bay during summer, may result in complete exclusion of fauna dependent on aerobic respiration. Moderately hypoxic areas that do not result in universal exclusion may instead have the greatest potential to cause differential shifts in spatial distributions, behaviors, and growth rates of exposed species. Organisms vary widely in their response to moderate hypoxia, reflecting interspecific and size-related and developmental stage-related variation in tolerances and behaviors. This variation in the intensity and pattern of responses among potentially interacting organisms may lead to important shifts in the relative importance of various ecological interactions. Our model results indicate that under current average densities of gelatinous zooplankton in the mesohaline Patuxent River, survival of larval fishes will be dependent on the presence of lower than average patches of gelatinous predators during certain key time periods. Our field results indicate that an important component of the spatial heterogeneity in gelatinous zooplankton densities in the Patuxent River is likely created by spatial variation in DO concentrations, and the behavioral responses of gelatinous zooplankton to low DO waters. Temporal variation in the abundance and predation rates of these hypoxia-tolerant gelatinous predators may also be influenced by temporal variation (both seasonal and higher frequency weather-related variation) in the extent and severity of bottom-layer hypoxia.

Mnemiopsis densities in the Patuxent River have increased in recent years as well as have shown substantial interannual variation. Average summer (June–August) biovolume from 1985–1993 was 7.5 ml m^{-3} (SE of annual means of 2.4; range of annual means of 0.04 to 22.2 ml m^{-3}) and increased to an average of 48.6 ml m^{-3} (SE of 12.2; range of 14.5 to 88.2 ml m^{-3}) during 1994–2000 (data from CBP 2002). This long-term pattern of increasing summer *Mnemiopsis* abundances has also been seen in Narragansett Bay, where it is thought to be related to rising water temperatures (Sullivan et al. 2001). Climate change, and as well as loss of oyster habitat used by the sessile stage of their sea nettle predators, could influence ctenophore abundance in the Chesapeake Bay system, including the Patuxent River. Our field data on vertical distributions indicate that during the past several decades the hypoxic bottom layer in the Patuxent River may have reduced predation mortality of *Mnemiopsis* by creating a spatial refuge from sea nettle predation (see Keister et al. 2000; D'Elia et al. 2003).

There may also be interannual variability in sea nettle predation that correlates with the extent or duration of hypoxia. Sea nettle densities tend to be inversely correlated with streamflow through streamflow's effect on salinity (Cargo and King 1990), while the severity and duration of hypoxia tend to be positively correlated with streamflow through streamflow's effect on density stratification (Boicourt 1992; Hagy 1996). The presence of a hypoxic bottom layer can either increase or decrease predation mortality due to sea nettles, depending on the local severity of oxygen depletion. Our model results predict that in the mesohaline Patuxent River, hypoxia generally decreases predation by sea nettles feeding on fish larvae. By most strongly decreasing predation rates in years when sea nettle densities are lowest, hypoxia may increase interannual variation in sea nettle-induced predation mortality of fish larvae.

Partially counterbalancing the factors that make the Patuxent River ecosystem susceptible to low oxygen effects, are behaviors by which mobile animals can avoid low oxygen, and the presence of highly oxygenated, productive shallow areas (Breitburg 2002). On a larger spatial scale, there is strong variation among tributaries and among regions of the mainstem Chesapeake in the duration, severity, and spatial extent of summer oxygen depletion. Although the entire Chesapeake Bay system is affected by nutrient overenrichment, the mesohaline portions of its tributaries and its mainstem most strongly experience the negative effects of low oxygen. The degree to which temporal and spatial heterogeneity in DO ameliorates its effects on coastal ecosystems is poorly understood. The net result of the numerous individual ecological effects of low DO is unknown. Models and other analysis techniques that can address broader spatial scales, longer time periods, and a more complete representation of the food web would make an important contribution towards understanding effects of low oxygen on coastal systems. In spite of these uncertainties, current understanding of the negative effects of low oxygen on habitat, individual organisms, and food webs, argues for a precautionary approach towards ecosystem management, that is, lowering nutrient loadings to levels at which low oxygen effects on estuarine habitat are reduced, and where possible, eliminated. Our model linking land use, water quality, and nekton strongly suggests that land use, through its influence on nutrient loading, can have a large effect on survival of early life stages of fishes.

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