Effects of hypoxia on *Mnemiopsis leidyi*, ichthyoplankton and copepods: clearance rates and vertical habitat overlap

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ABSTRACT: Differences in predator and prey tolerances to low dissolved oxygen (DO) concentrations influence planktonic food web interactions in seasonally hypoxic environments. We examined low-DO effects on predation by hypoxia-tolerant ctenophores, *Mnemiopsis leidyi*, on less hypoxia-tolerant ichthyoplankton prey in laboratory experiments. We also examined the relationship between bottom DO concentrations and vertical distributions, and considered potential effects of biotic (predators and competitors) versus abiotic factors (low DO concentration, temperature, salinity, time of day) on vertical habitat overlaps between gelatinous zooplankton and their prey during summer in a Chesapeake Bay subestuary. Laboratory clearance rates of *M. leidyi* feeding on bay anchovy (*Anchoa mitchilli*) eggs and yolk sac larvae, and naked goby (*Gobiosoma bosc*) larvae were as high at low DO (1.5 mg l^{-1}) as at high DO concentrations (7 mg l^{-1}). Multiple years of field sampling at 2 sites revealed that the proportions of motile species in the bottom layer of the water column, especially fish larvae and copepods, increased with increasing bottom DO concentrations during both day and night. Ctenophore densities remained high in the bottom layer even at low DO concentrations. Vertical habitat overlaps among 4 motile predator–prey pairs (*M. leidyi*–copepods, *M. leidyi*–naked goby larvae, bay anchovy larvae–copepods, and naked goby larvae–copepods) increased with increasing bottom DO concentrations (1st- or 2nd-order regression models). Vertical overlap between *M. leidyi* and fish eggs was significantly higher during the day than at night. Statistical models suggest that both bottom DO concentration and scyphomedusan predators influenced *M. leidyi*–fish egg nighttime and *M. leidyi*–copepod combined day–night overlaps. Hypoxia influences food web interactions more through altered habitat use and encounter rates than by directly affecting predation. Strong behavioral responses of larval fish and copepods to low bottom DO concentrations may decrease habitat overlap between *M. leidyi* predators and their prey.

KEY WORDS: Bay anchovy · Naked goby · Fish egg · Fish larva · Ctenophore · Predation · Food web · Chesapeake Bay · Eutrophication · Gelatinous zooplankton

INTRODUCTION

Hypoxia, or low dissolved oxygen (DO) concentrations, can cause mortality or sublethal effects on aquatic organisms that depend on aerobic respiration (Kra-mer 1987, Wannamaker & Rice 2000, Miller et al. 2002, Breitburg et al. 2009, Levin et al. 2009). Sublethal consequences of hypoxia include reduced growth rate, altered behavior, decreased foraging ability, and increased susceptibility to predation (Breitburg 1992,

1994, Howell & Simpson 1994, Petersen & Pihl 1995, Crocker & Cech 1997). Subtle shifts in trophic interactions caused by hypoxia may have a large effect on interactions among species (Rahel & Kolar 1990, Kolar & Rahel 1993, Rahel & Nutzman 1994). For example, sublethal oxygen concentrations may increase predation risk as predators opportunistically feed on prey species that are made vulnerable by low-DO stress (Pihl et al. 1992). In addition, low DO concentrations in aquatic ecosystems can compress organisms into reduced volumes of higher-DO water (Coutant 1985), thereby increasing predator and prey encounter rates (Breitburg et al. 1997), increasing the risk of fisheries exploitation (Craig & Crowder 2005), enhancing potential growth rates (Costantini et al. 2008), and increasing competition for limited prey (Eby et al. 2005).

Gelatinous zooplankton (e.g. scyphomedusae and ctenophores) tend to be more tolerant of low DO concentrations than trophically similar finfish (Purcell et al. 2001a). Hypoxia-tolerant gelatinous zooplankton can regulate oxygen consumption at oxygen concentrations that are lethal to co-occurring fishes (Rutherford & Thuesen 2005) and are abundant in eutrophic systems with seasonal hypoxia (Grove & Breitburg 2005, Purcell et al. 2001a, 2007). This can result in hypoxia increasing the predation rates of gelatinous zooplankton on DO-sensitive prey by increasing encounter rates or decreasing prey escape (Breitburg et al. 1997, Decker et al. 2004, Shoji et al. 2005a).

Prey behavioral responses to a biological threat (e.g. predation) may change in the presence of suboptimal but nonlethal physical conditions, such as mild to moderate hypoxia. Larval pike predation on zooplankton was lower in low-DO water with predator chemical cues present than in water with either low DO concentration or predator chemicals alone (Engström-Öst & Isaksson 2006). Young fish showed context-dependent behavioral responses in areas with both hypoxia and species interactions in the Neuse River estuary (Eby & Crowder 2002). Habitat selection and species overlap were mitigated by both biotic and abiotic factors, with the importance of each factor being dependent on the extent and severity of environmental conditions at the time. Two studies by Shoji et al. (2005a,b) detailed how the interactions of low DO concentration with larval fish age and predator sensitivity to hypoxia can alter predation vulnerability. Predation by *Aurelia aurita* medusae was equally high at DO = 1–2 mg l^{-1} for both younger and older red sea bream larvae, remained high for younger fish larvae at all DO levels tested, but declined at higher DO concentrations for older larvae —a result that Shoji et al. (2005a) attributed to better swimming and escape abilities of older larvae at high DO concentrations. Moreover, predation on larvae was higher at low DO concentration for a DO-tolerant

predator (*A. aurita*) than for a DO-sensitive predator (Spanish mackerel) (Shoji et al. 2005b).

Increased anthropogenic nutrient loading has led to frequent and widespread occurrences of low DO concentrations in a variety of environments ranging from enclosed seas and bays to open continental shelf areas (Diaz & Rosenberg 2008). In particular, changes in land use patterns have modified the Chesapeake Bay ecosystem, which is the largest semi-enclosed estuary in the United States. Conversion of forests and farms to urban areas, increased population, and increased fertilizer use have altered runoff patterns and increased nutrient inputs into the bay, which in turn has elevated algal production and biomass, and increased the intensity and extent of summer oxygen depletion (Cooper & Brush 1993, Boynton 1997, Karlsen et al. 2000, Hagy et al. 2005). Because Chesapeake Bay is strongly stratified during late spring and summer, the effects of eutrophication are manifested in seasonal bottom-water hypoxia or even anoxia (complete absence of DO).

One of the key species whose interactions within the Chesapeake Bay food web may be affected by changes in DO concentration is the lobate ctenophore *Mnemiopsis leidyi*. This species is an important predator on both zooplankton and the early life stages of fish (Reeve & Walter 1978, Kremer 1979, Purcell et al. 2001b), and can therefore act as both a predator and a competitor of fish larvae (Purcell & Arai 2001). All stages of ichthyoplankton, including eggs, yolk sac larvae, and older feeding larvae, are exploited by *M. leidyi*. *M. leidyi* is a year-round inhabitant of Chesapeake Bay that reaches peak abundance during early summer (Kremer 1994, Purcell et al. 2001b), and declines during late summer in some years, coincident with the decline of their copepod prey and the peak abundance of the scyphomedusa *Chrysaora quinquecirrha*, which can control their abundance (Purcell & Cowan 1995, Purcell et al. 2001b, Purcell & Decker 2005).

Predation can be a major source of mortality for ichthyoplankton (Bailey & Houde 1989). It is the result of many small-scale processes, including encounter, escape, and capture (Larson 1987, Purcell 1997, Costello et al. 1999, Waggett & Costello 1999), all of which are directly related to the swimming speeds of both predators and their prey (Gerritsen & Strickler 1977), and are affected by DO concentration (Kolesar 2006). The high abundance of *Mnemiopsis leidyi* during summertime in Chesapeake Bay and its tidal tributaries makes this ctenophore a potentially important predator of dominant mesohaline ichthyoplankton, such as naked goby (*Gobiosoma bosc*) larvae and bay anchovy (*Anchoa mitchilli*) eggs and larvae. Because of its abundance, high feeding rates, and temporal coincidence with fish spawning, *M. leidyi* can consume

large portions of crustacean zooplankton and ichthyo-plankton (Monteleone & Duguay 1988, Cowan & Houde 1993, Purcell et al. 1994a,b, Purcell & Decker 2005).

The vertical distributions of *Mnemiopsis leidyi*, ichthyoplankton, and crustacean zooplankton can shift with declining DO concentrations (Keister et al. 2000). The available habitat volume shrinks as DO concentrations below the pycnocline decrease because many organisms avoid low DO concentrations (Breitburg 2002, Robb & Abrahams 2002). *Mnemiopsis leidyi* remains below the pycnocline until DO declines to ~1 mg l^{-1} in the bottom layer of the water column (Breitburg et al. 2003); however, sensitive organisms (e.g. the early life stages of fish) tend to avoid oxygen concentrations <2 mg l^{-1} (Breitburg 1994, Keister et al. 2000, Breitburg et al. 2003), and encounter rates between predators and prey with different tolerances to DO may change as bottom DO concentrations decline. Eutrophication and the resulting hypoxia in the Chesapeake Bay system seem to favor gelatinous zooplankton over finfish (Breitburg 1992, Breitburg et al. 1997, 2009, Purcell et al. 2001a, 2007).

We conducted laboratory experiments to determine if DO concentration affects clearance rates of *Mnemiopsis leidyi* feeding on ichthyoplankton, and field sampling to quantify vertical habitat overlap between gelatinous predators and their prey at different bottom DO concentrations. We sampled co-occurring *M. leidyi,* ichthyoplankton, and a shared copepod prey species (*Acartia tonsa*). A predator (the scyphomedusa *Chrysaora quinquecirrha*) that feeds on all of the other organisms, and abiotic water column parameters were also sampled to test other factors that could influence the vertical habitat overlap between *M. leidyi* and ichthyoplankton. Our field sampling builds on data collected during a previous study (Keister et al. 2000); thus, we sampled the same 2 sites in the Patuxent River that exhibit chronic bottom layer hypoxia. *M. leidyi* densities were very low during the previous study (mean density ± SE = 0.07 ± 0.02 ind. m^{-3} in 1992), which coincided with high *C. quinquecirrha* densities (Keister et al. 2000). The current study was during a period of low *C. quinquecirrha* density, which enabled us to separate the effects of *C. quinquecirrha* and DO concentration on *M. leidyi* vertical distribution and overlap with prey.

MATERIALS AND METHODS

Organism collection and rearing. Laboratory experiments were conducted to examine the effects of oxygen concentration on clearance rates of *Mnemiopsis leidyi* on early life stages of Chesapeake Bay fishes: (1)

bay anchovy eggs, (2) bay anchovy yolk sac larvae, and (3) 1 and 4 d post hatch (dph) naked goby larvae, which feed exogenously. We chose these prey because they are the most abundant ichthyoplankton species in the mesohaline Chesapeake Bay during summer when *M. leidyi* is abundant (Keister et al. 2000), and because bay anchovy and naked goby larvae have similar oxygen tolerances (Breitburg 1994).

Prior to each experiment, organisms were collected from the mesohaline Patuxent River, which is a tributary of Chesapeake Bay. *Mnemiopsis leidyi* were dip-netted from the surface and kept no longer than 1 wk at ambient temperature (22 to 24°C) and salinity (12 to 15) in 80 l aquaria with small paddlewheels that provided gentle surface water movement. Ctenophores were fed with brine shrimp nauplii (*Artemia* spp.) or natural zooplankton (when available), and 50% of the aquarium water was replaced every other day. Bay anchovy eggs were collected with a 500 µm mesh plankton net that was towed at ~1 knot for 2 min in the surface layer during midnight to 07:00 h of the peak spawning period (MacGregor & Houde 1996). Fish eggs were placed in aerated buckets of water and brought to the laboratory as soon as sufficient numbers were collected. Target numbers of 32 to 200 fish eggs (dependent on availability) were immediately counted into 2 l glass dishes and then either placed directly into experimental tanks (for egg experiments) or maintained in the dishes for ~20 h until hatching (yolk sac larvae experiments). Fish eggs and yolk sac larvae that died before the start of experiments were replaced.

Naked goby eggs were collected from nesting trays that were deployed at several sites along the Patuxent River (Breitburg 1992, 1994). Nests with the guarding male were brought to the laboratory for egg hatching and larval rearing. After developing for up to 1 wk, eggs were placed under a directed light source to trigger hatching, and larvae were then transferred to 80 l rearing aquaria (25 larvae l^{-1}) that were filled with 5 µm filtered Patuxent River water at ambient temperature (22 to 24°C) and salinity (12 to 15). We maintained larval rearing tanks with constant gentle bubbling and 50% water changes every 2 to 3 d. Larvae were fed with laboratory reared rotifers (*Brachionus plicatus*) at densities of ~4000 l^{-1} and used in predation experiments when they were <7 dph.

Predation experiments. Clearance rates of *Mnemiopsis leidyi* on ichthyoplankton were compared at 3 different DO concentrations (Table 1). Experiments were conducted as a randomized complete block design with date as the blocking factor and DO level as the treatment. We selected 2 low DO concentrations (1.5 and 2.5 mg l^{-1}) that would not cause direct mortality of organisms during the experiments, but that resulted in different vertical distributions of fish larvae in

Table 1. Conditions for *Mnemiopsis leidyi* predation experiments in 100 l tanks. Clearance rate trials for each ichthyoplankton stage were conducted with a number of available prey (N_1) being added to predation tanks (plus 1 no-predator control tank each day) on 2 separate dates for specified durations (h) and number of replicates (N_2) at 3 target concentrations of dissolved oxygen (DO). The number of *M. leidyi* tank^{-1} (N_3) and the grand mean volume for each date are reported, as well as naked goby larvae age (days post hatch, dph)

| Prey type | Date (h) | Mean DO concentration ± SE (mg l^{-1}) (N_2) | | | *Mnemiopsis leidyi* |
		Low	Mid	High	Grand mean vol ± SE (ml) (N_3)
Bay anchovy (N_1):					
Eggs (200)	8 Jul 99 (4)	1.55 ± 0.03	2.37 ± 0.12	7.65 ± 0.03 (3)	87.56 ± 3.44 (10)
Eggs (100)	15 Jul 99 (4)	1.55 ± 0.10	2.48 ± 0.07	7.65 ± 0.03 (3)	211.44 ± 9.19 (10–11)
Yolk sac larvae (35–47)	12 Jul 01 (2)	1.59 ± 0.02	2.59 ± 0.04	6.67 ± 0.15 (3)	113.89 ± 3.33 (8)
Yolk sac larvae (32)	8 Aug 01 (2)	1.81	2.62	6.79 (1)	237.67 ± 6.89 (10)
Naked goby (age; N_1):					
Larvae (4 dph; 200)	2 Jun 99 (6)	1.72 ± 0.04	2.67 ± 0.043	7.22 ± 0.24 (3)	163.67 ± 6.19 (12–13)
Larvae (1 dph; 200)	15 Jun 99 (6)	1.72 ± 0.07	2.57 ± 0.07	7.32 ± 0.03 (3)	215.11 ± 7.74 (11–13)

the laboratory (Breitburg 1994) and in the field (Keister et al. 2000, Breitburg et al. 2003). We also estimated *M. leidyi* clearance rates on prey at an air-saturated control DO concentration of ~7 mg l^{-1}. We conducted trials on 2 d for each of the ichthyoplankton prey in 100 l tanks with 1 to 3 replicates DO treatment^{-1} d^{-1}; treatments were randomly assigned to tanks. In addition, 1 predator-free tank at each of the 3 DO treatments provided a baseline retrieval rate each day to assess prey mortality due to handling and DO stress.

Target DO concentrations in the tanks were reached by bubbling with nitrogen gas, and measured with a DO meter (YSI model 52 or 85). We then placed either 100–200 bay anchovy eggs, 32–47 yolk sac larvae, or 200 naked goby larvae into each tank for 30 min until they appeared to behave normally under experimental conditions. This was followed by the addition of 8 to 13 *Mnemiopsis leidyi* (average total volume 163.29 ± 8.16 ml) (Table 1) into small vessels within the experimental tanks for acclimation. Each experiment was initiated 30 min later upon release of the predators into the prey tanks. Tanks were sealed and small amounts of nitrogen gas, or air for DO control tanks, were fed into the headspaces to maintain DO conditions for the duration of each experiment. Tanks were maintained in low light at water temperatures (22 to –24°C) and salinities (11 to 16) that were similar to surface layer conditions of the summertime mesohaline estuary. Larger ctenophores were more prevalent as the summer progressed; consequently, total predator volume was made larger during the second than during the first set of experiments (Table 1). Experimental durations and predator numbers were adjusted for the different prey types to avoid prey depletion and to account for differing availability of organisms (Table 1). Rotifers were made available and added to all containers as alternative prey (~450 rotifers l^{-1}) to encourage naked goby larvae and ctenophores to swim and feed normally. Sinking was not a problem in egg experi-

ments because tanks were unstratified, sinking is independent of DO concentration, and eggs and ctenophores were observed throughout the tanks during experiments.

At the end of each trial, DO concentration was remeasured and ctenophores were removed with a dip net. Water was slowly siphoned through 65 to 100 μm mesh bags to collect remaining ichthyoplankton. Collection bags were immersed in MS-222 to euthanize larvae before preservation in 75% ethanol (larvae and eggs) or 5% buffered formalin (yolk sac larvae). The number of eggs or larvae collected from each trial day was enumerated with a dissecting microscope to determine N_o (the number of prey retrieved from the predator-free control tanks), which was averaged for all trials, and N_p (the number of prey retrieved from predation tanks), which was averaged by day. We also calculated percent predation, PP, for each prey type as:

$$PP = (N_o - N_p) / N_o \times 100 \qquad (1)$$

Mnemiopsis leidyi predation was expressed as clearance rate per individual volume; following the methods of Cowan & Houde (1993), we calculated instantaneous predation mortality, Z as:

$$Z = (\ln N_o - \ln N_p) / t \qquad (2)$$

where t = trial duration in hours. We also calculated instantaneous mortality per predator, Z_i as:

$$Z_i = Z / C \qquad (3)$$

where C = the number of *M. leidyi* in each trial tank. We then calculated Z_p, which is the instantaneous mortality per predator standardized for *M. leidyi* volume in the different trials (equation modified from de Lafontaine & Leggett 1988), as:

$$Z_p = (Z_i \times (\Sigma P_v / n)) / m \qquad (4)$$

where $\Sigma P_v / n$ = grand mean predator volume (ml) from all predator tanks on each day and m = mean *M. leidyi*

volume in each tank. Finally, we calculated volume-specific clearance rate, F_s (l ml ctenophore^{-1} h^{-1}) for each prey type as:

$$F_s = V \times Z_p / (\Sigma P_v / n) \qquad (5)$$

where V = volume of the tank in liters.

Field sampling. *Mnemiopsis leidyi*, *Chrysaora quinquecirrha*, ichthyoplankton, and crustacean zooplankton were collected from June to August in the mesohaline Patuxent River in 1992 and 1993 by Keister et al. (2000) and in 1999 and 2001 for the present study. Details of samples collected in 1992 and 1993 are in Keister et al. (2000); 1999 and 2001 methods followed the same general protocol. Two sites in the mid-channel Patuxent River were chosen based on a history of chronic summertime hypoxia: south of the mouth of Battle Creek (38° 25′ 30.0″ N, 76° 36′ 16.9″ W; average depth = 16 m) and the mouth of St. Leonard Creek (38° 22′ 34.1″ N, 76° 30′ 39.5″ W; average depth = 20 m) (Breitburg et al. 2003) (Fig. 1). Sampling was conducted by Keister et al. (2000) during day and night at both stations during cruises on July 24, 29, and August 4, 1992 and on July 6, 12, and 16, 1993. We also sampled during day and night at both stations during approximately monthly cruises on June 22, July 27, and August 24, 1999, and only at night at St. Leonard Creek on July 5, 2001 (Table 2).

Vertical profiles of water column temperature, DO concentration, and salinity were taken at each site using a DO meter (YSI model 85). The pycnocline was approximated from these measurements as the generally aligned depth range in which the greatest changes

Table 2. Bottom layer dissolved oxygen (DO) during 1992, 1993, 1999 and 2001 for 2 stations in the Patuxent River, Maryland: St. Leonard's Creek (20 m) and Battle Creek (16 m). Values represent day and night bottom DO measurements (mg l^{-1}), taken with a DO meter that was attached to the frame of the Tucker Trawl net. Duplicate samples are reported where available. ns: no sample taken

| Date | Bottom DO (mg l^{-1}) | | | |
| | St. Leonard's Creek | | Battle Creek | |
	Day	Night	Day	Night
24 Jul 92	4.2	3.5	0.7	0.4
29 Jul 92	5.2	4.6	4.0	4.9
4 Aug 92	3.4	5.7	3.8	3.8
7 Jul 93	2.0, 2.9	2.1	1.3, 1.3	3.0
13 Jul 93	0.03, 0.03	0.00	0.2, 0.2	0.1
17 Jul 93	0.04, 0.03	0.04	0.06, 0.02	0.07
22 Jun 99	6.1, 6.3	5.8[a]	7.5	6.0, 6.2
27 Jul 99	2.3, 2.5	3.3, 3.4	2.9, 2.8	2.7, 2.9
24 Aug 99	3.8, 4.0	4.5, 5.1	4.5	5.4, 5.3
5 Jul 01	ns	2.3, 1.7	ns	ns

[a]DO from CTD profile

in temperature, DO concentration, and salinity occurred, with preference for the oxycline. The surface layer was oxygenated; the pycnocline had decreasing temperatures, salinities, and DO concentrations; and the bottom layer had a lower rate of change in physical parameters than the pycnocline. Tidal stage and trawl time were also recorded.

Crustacean zooplankton was sampled every 1 to 2 m throughout the water column by pumping 50 l of water at 20 l min^{-1} for ~2 min through a 2.5 cm diameter hose
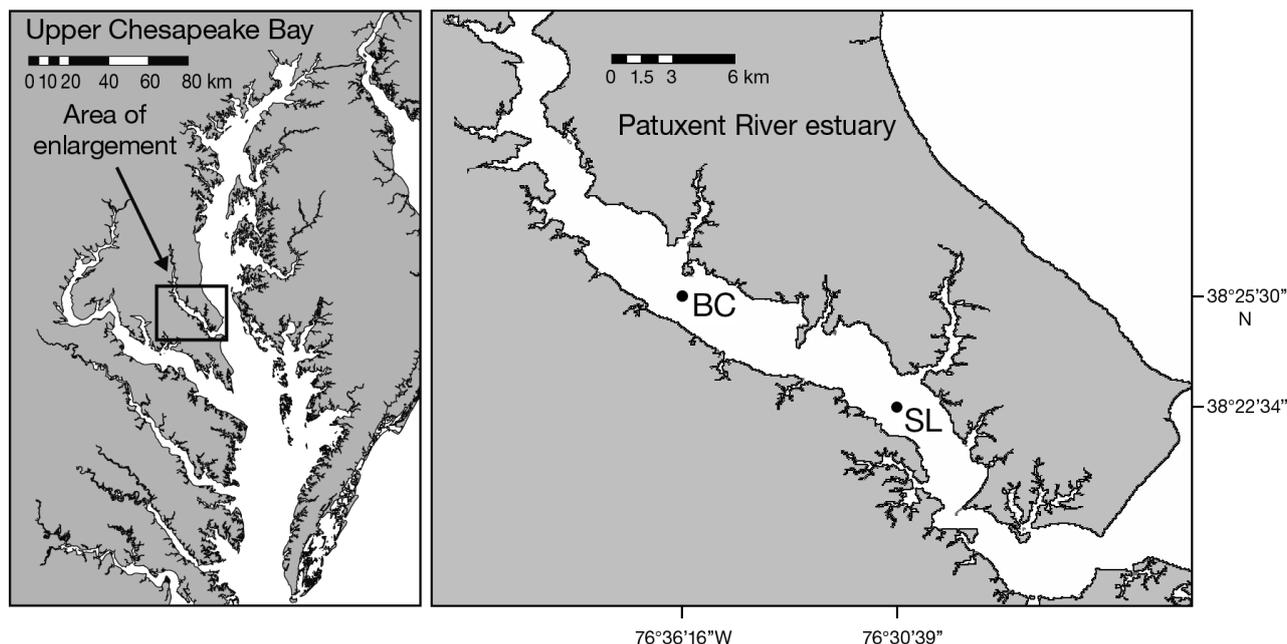

Fig. 1. Patuxent River Estuary, Chesapeake Bay. Sampling sites: BC = Battle Creek, SL = St. Leonard's Creek

(cleared for ~45 s before sample collection) into a 35 μm plankton net, and then preserved in 5% buffered formalin for later enumeration and identification using a dissecting microscope in the laboratory. Crustacean zooplankton was counted from stempel pipette aliquots of samples (totaling at least 200 ind. or $\frac{1}{4}$ of the whole preserved sample), identified to genus, and separated by life stage. Crustacean zooplankton was assigned to water column layers (surface, pycnocline, or bottom) according to their sampling depth and the concurrently measured physical profile of the water column.

Duplicate 1.5 to 2 min discrete-depth samples of *Mnemiopsis leidyi*, *Chrysaora quinquecirrha*, and ichthyoplankton were taken from each of 3 layers (surface, pycnocline, and bottom) using a trawl (Tucker) with a 1 m² mouth area and 212 to 224 μm mesh nets with a flowmeter (General Oceanics) attached to the mouth of the net (average tow volume ± SE = 87.9 ± 4.2 m³, n = 111). The surface layer was sampled by skimming the water surface with the top of the net; sampling within the pycnocline was ensured by attaching a DO meter (YSI model 52) on the frame of the net; and sampling depth within the bottom layer from just above the sediment to the pycnocline was calculated geometrically from cable length and wire angle. Total length of live ctenophores and scyphomedusa diameter were measured to the nearest 5 mm, while live volumes were measured to the nearest 1 ml in graduated cylinders. Whole sample biovolumes for both species were measured to the nearest 50 ml in graduated pitchers. Ichthyoplankton were removed and preserved in 75% ethanol, counted, and identified to genus (species level when possible) for whole preserved samples.

Statistical analysis: predation experiments. Analyses were performed on volume-specific clearance rates (l ml ctenophore^{-1} h^{-1}) to determine the effect of DO concentration on predation on each of the 3 prey types (bay anchovy eggs, bay anchovy yolk sac larvae, and naked goby larvae). *Mnemiopsis leidyi* clearance rates on naked goby larvae and bay anchovy yolk sac larvae were untransformed, but clearance rates on bay anchovy eggs were log$_{10}$ transformed to correct normality of residuals. We performed randomized complete block design ANOVA, including replication within blocks (date), for clearance rates on each prey type (except yolk sac larvae on the second date that had only 1 tank treatment^{-1}). For all statistics, significance was set at $\alpha < 0.05$, with observations in the range $0.05 \leq \alpha < 0.10$ being noted as an insignificant trend. All data are presented as means ± 1 SE.

Statistical analysis: field data. Schoener's Index of habitat overlap (Schoener 1970) was computed to determine the effect of low DO concentration on vertical overlap between species within the water column. Here we present a more detailed analysis of species

overlap than the general summaries provided by Breitburg et al. (2003). Overlap values (as proportions) ranged from 0 (no overlap in habitat use) to 1 (complete overlap). Vertical overlap was determined among 5 predator and prey groups: (1) numbers of adult and juvenile copepods (mostly *Acartia tonsa*) l^{-1}, (2) numbers of fish eggs m^{-3} (predominantly bay anchovy eggs, but other species were present in small numbers), (3) numbers of bay anchovy larvae (<15 mm standard length) m^{-3}, (4) numbers of naked goby larvae m^{-3}, and (5) numbers and volumes of *Mnemiopsis leidyi* m^{-3}. *Chrysaora quinquecirrha* numbers and volumes m^{-3} were included as secondary contributing factors in stepwise regressions, but were not considered to be the primary predators of concern in this *M. leidyi* focused study. We used both numbers and volumes of gelatinous species because numbers reflect behavioral responses while volume more accurately describes their consumption potential. To reduce error in overlap estimates for very small sample sizes, we compromised between the undue influence of small samples and having a representative estimate of overlap; specifically, if the total number of individuals of a species in the surface, pycnocline, and bottom layers at a station, time, and date was <8, data for that species were omitted from analyses (a cutoff of either 7 or 9 would have changed the number of included samples by only 1). Gelatinous zooplankton were the only organisms affected by this criterion. Remaining samples represent the minimum sample size for 3 layers and eliminated samples had station totals ≤0.1 *M. leidyi* or *C. quinquecirrha* m^{-3}; samples with 0 total *M. leidyi* or *C. quinquecirrha* collected at a station totaled ~$\frac{1}{3}$ of all eliminated samples. Approximately 20% of *M. leidyi* and *C. quinquecirrha* samples were excluded.

The vertical overlap between each predator–prey pair was calculated as: Schoener's Index = $1 - 0.5 \times (|\text{Ppred}_{SURF} - \text{Pprey}_{SURF}| + |\text{Ppred}_{PYCN} - \text{Pprey}_{PYCN}| + |\text{Ppred}_{BOTT} - \text{Pprey}_{BOTT}|)$, where Ppred_{LAYER} and Pprey_{LAYER} represent the proportions of predators or prey in each layer of the water column (surface, pycnocline, or bottom). The proportions of gelatinous zooplankton and ichthyoplankton were calculated from densities in pooled duplicate samples for each combination of date, station, and time. We used mean zooplankton densities for the depth interval corresponding to each layer (N = 43). The proportion of each species was calculated according to the thickness of each layer relative to the average depth of each sampling site and the DO profiles for each date and time (the oxycline and pycnocline always coincided vertically). The CV is presented along with mean vertical overlaps.

To test for relationships between species overlap and bottom DO concentration, we performed simple re-

gression analyses (which test for a nonzero slope) on the arcsine transformed overlap between 10 predator–prey pairs, including all pairs of ctenophores, fish larvae, fish eggs, and copepods in the water column against bottom DO concentrations. Scyphomedusae were not included as predators in this analysis due to their low densities in 1999 and 2001. As an exploratory technique, linear, 2nd order, or 3rd order regression models were fitted. The model or models that best explained the relationship between species overlap and bottom DO concentration were selected based on a combination of lowest Akaike's Information Criterion (AIC), p-values, and parsimony. The relationships of vertical overlap with tidal stage and with time (day or night) were analyzed using analysis of covariance (ANCOVA). ANCOVA indicated that differences between day and night were not significant; therefore, we analyzed vertical overlap with time periods being combined.

We used stepwise regressions (forward entry, backward elimination) to determine if biotic components of the food web with the potential to directly influence the predators and prey contributed to the degree of vertical habitat overlap in addition to bottom DO concentration (an abiotic factor). A typical model included bottom DO concentration (BOTDO), as well as predator, prey, and competitor species abundances. Temperature (TEMP) and salinity (SAL) were also included in stepwise regression models. We performed principal components analysis (PCA) to determine multicollinearity among factors in the stepwise regression. There was high collinearity between bay anchovy and naked goby larvae; hence, we used combined 'fish larvae' instead of individual species in the stepwise models. Likewise, either number or volume (not both) for each gelatinous predator was included in the model. As an example, the stepwise regression model for overlap between *Mnemiopsis leidyi* number (CTN) and number of combined fish larvae (LRV) was represented as OVERLAP = BOTDO + TEMP + SAL + CTN + MED + COP + LRV, where MED = number of *Chrysaora quinquecirrha* predators m^{-3} and COP = number of copepod prey l^{-1}. Models that included bottom DO concentration (along with other abiotic and biotic factors) and had $\alpha < 0.05$ were reported as significant.

RESULTS

Laboratory predation experiments

During all experiments, oxygen levels for both low DO concentrations were maintained within ~0.3 mg l^{-1} of target concentrations, while the air-saturated controls fell within a ~0.1 mg l^{-1} range (Table 1). Mean prey retrieval rates in tanks without *Mnemiopsis leidyi*

predators were 97% (range = 91 to 101%) for bay anchovy eggs and naked goby larvae, and 88% (range = 78 to 94%) for yolk sac larvae. Retrieval rates were lower for yolk sac larvae likely due to their fragility, which may have caused them to be damaged either during addition or retrieval. Predation calculations were adjusted based on retrieval rates. Overall, percent predation (± SE) was lowest for bay anchovy eggs (26.9 ± 0.02%), intermediate for naked goby larvae (39.7 ± 0.03%), and highest for bay anchovy yolk sac larvae (49.3 ± 0.04%). The DO concentrations tested did not significantly affect volume-specific clearance rates of *M. leidyi* feeding on bay anchovy eggs (ANOVA, p = 0.18, $F_{2,14} = 1.93$), bay anchovy yolk sac larvae (ANOVA, p = 0.41, $F_{2,8} = 1.00$), or naked goby larvae (ANOVA, p = 0.81, $F_{2,14} = 0.21$). Clearance rates for all 3 DO treatments varied within similar narrow ranges for bay anchovy eggs and naked goby larvae, but were an order of magnitude larger for yolk sac larvae (Fig. 2).

Field sampling

Addition of 1999 and 2001 field data to the 1992–1993 data (Keister et al. 2000) allowed us to examine the effect of DO concentration on vertical distributions and overlap over a wider range of DO concentrations and organism density conditions (Table 3). On average, all species had higher numerical densities in 1992–1993 than in 1999 and 2001. The exception was very low *Mnemiopsis leidyi* densities in 1992, resulting in smaller observed average volumes of ctenophores in 1992–1993 samples than in later years. No fish eggs were present in 2001 samples, and fish egg abundance was low in 1999 compared with abundances sampled in earlier years. Densities of bay anchovy larvae were almost identical in 1993 and 1999, but were an order of magnitude higher in 1992.

Both bottom DO concentration and time of day (day versus night) influenced the proportional densities of organisms in each layer within the water column, but not all species examined were affected by both factors (Fig. 3). The vertical distribution of fish eggs, which do not have any behavioral response to DO, was independent of bottom DO concentration (mean proportions ± SE of eggs in bottom layer during the day and at night were 0.52 ± 0.05 (N = 24) and 0.47 ± 0.09 (N = 19) respectively (Fig. 3a). The nighttime samples that had a high mean proportional density of fish eggs in the surface layer (0.30 ± 0.08, N = 19) (Fig. 3a) were taken near or after midnight and reflect a predominance of newly spawned eggs.

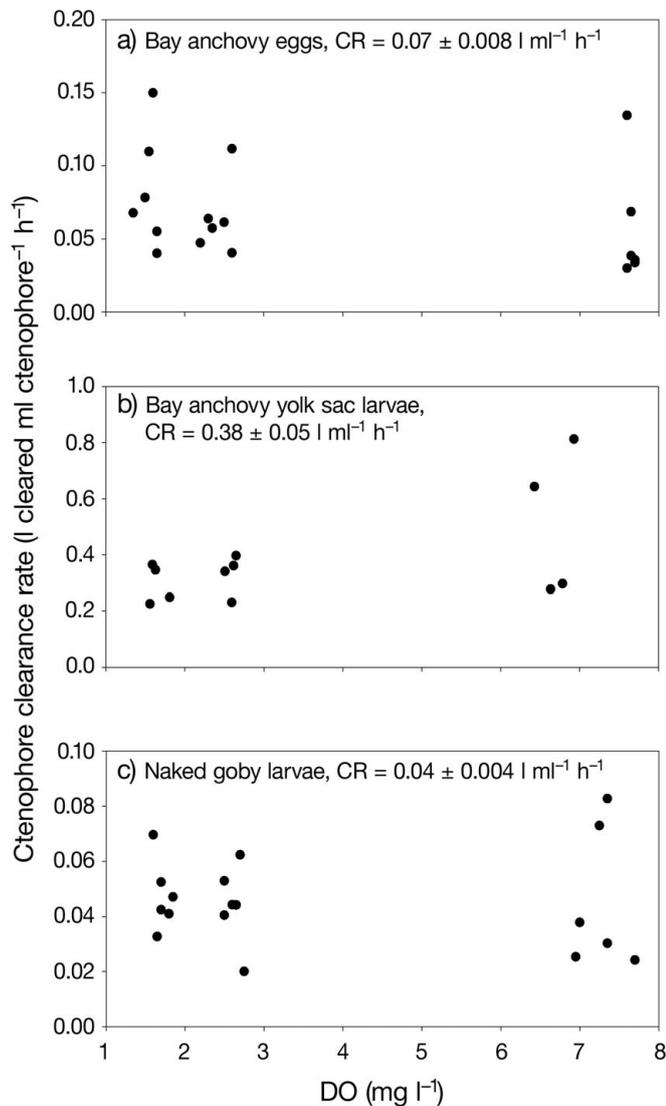When bottom DO concentrations were <1 mg l^{-1}, bay anchovy larvae occurred in either the pycnocline or the

Fig. 2. *Mnemiopsis leidyi*. Clearance rates (CR, l cleared ml ctenophore^{-1} h^{-1}) versus dissolved oxygen (DO) in laboratory experiments using 3 prey types: (a) bay anchovy eggs, (b) bay anchovy yolk sac larvae, and (c) naked goby larvae. CRs were adjusted for prey retrieval. Mean ± SE CRs for all DO treatments also are reported. Note different y-axis scales for each prey type

surface layer during both day and night and appeared to strongly avoid the bottom layer (Fig. 3b). When bottom layer DO concentration was >1 mg l^{-1}, bay anchovy larvae showed a strong pattern of increasing proportional densities in the bottom layer with increasing DO concentrations at night, and correspondingly decreased in the surface layer (Fig. 3b, Table 4); the same patterns occurred during the day, although they were not as clear due to increased proportional densities in bottom samples at 1 to 2 mg l^{-1} (Fig. 3b, Table 4).

Naked goby larvae were most abundant in the pycnocline when bottom DO concentration was <2 mg l^{-1} during both day and night; however, when bottom DO concentrations were ≥2 mg l^{-1}, they were most abundant in the bottom layer, especially at night (Fig. 3c). Abundances in the pycnocline and surface layers decreased during both day and night as DO concentrations increased in the bottom layer, and naked goby larvae proportions in the bottom layer increased in a linear fashion with increasing DO concentrations during both day and night (Fig. 3c, Table 4).

The vertical distributions of copepods also changed with bottom DO concentrations, exhibiting a general linear increase in the bottom layer with increasing DO concentrations during both day and night (Fig. 3d, Table 4). When bottom DO concentration was very low, the highest densities of copepods tended to occur in the pycnocline, especially during the day.

The relationship between vertical distributions of *Mnemiopsis leidyi* and bottom DO concentrations was not as clear as in most of the other species but followed the same general pattern (Fig. 3e). When bottom DO concentrations were <1 mg l^{-1}, *M. leidyi* densities were highest in the pycnocline during the day and in the pycnocline and surface layers at night. At higher DO concentrations, densities tended to be greatest in the bottom layer during both day and night, with densities in the pycnocline and surface layers being similar to each other (Fig. 3e). A significant linear relationship between *M. leidyi* distribution and bottom DO concentration was only observed for the proportion in the bottom layer at night (Table 4).

Table 3. Mean field densities of ctenophores (*Mnemiopsis leidyi*), ichthyoplankton, copepods, and scyphomedusae (*Chrysaora quinquecirrha*) at 2 stations in the Patuxent River, Maryland. Means ± SE reported are for all depths and times in 1992, 1993, 1999 and 2001. Data from 1992 and 1993 were reanalyzed from Keister et al. (2000)

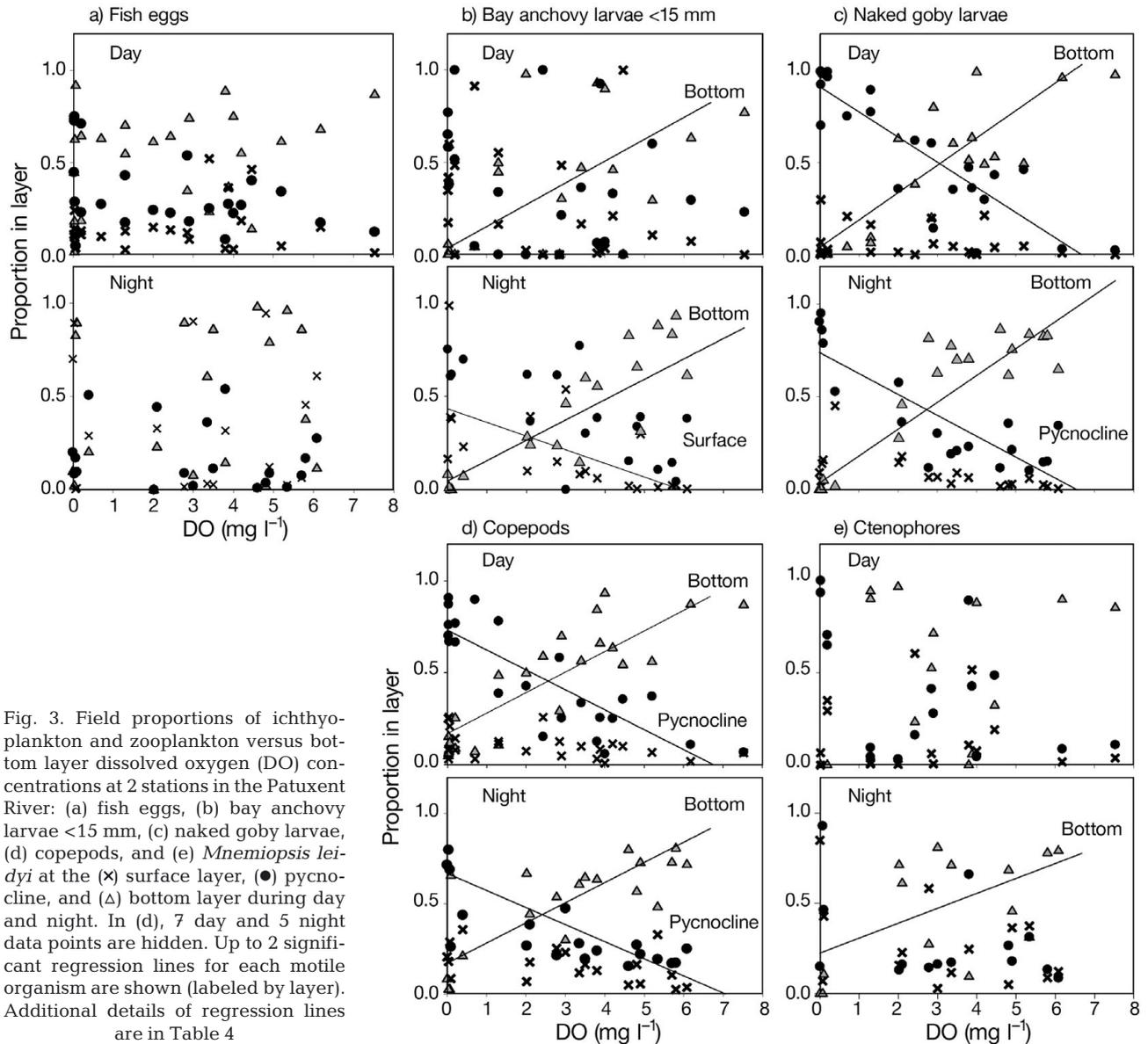| Year	Samples (n)	——*M. leidyi*—— (ml m^{-3})	(ind. m^{-3})	Fish eggs (ind. m^{-3})	Bay anchovy (larvae m^{-3})	Naked goby (larvae m^{-3})	Copepods (10^3 ind. m^{-3})	*C. quinquecirrha* (ml m^{-3})	(ind. m^{-3})
1992	36	0.4 ± 0.1	0.03 ± 0.008	41.3 ± 13.8	3.0 ± 0.7	9.8 ± 1.5	47.3 ± 5.6	5.1 ± 0.9	0.2 ± 0.02
1993	54	21.8 ± 6.5	8.5 ± 2.7	37.6 ± 14.1	0.3 ± 0.07	4.3 ± 0.8	19.7 ± 2.9	6.6 ± 1.0	0.1 ± 0.01
1999	36	23.6 ± 4.0	2.6 ± 0.5	11.3 ± 3.7	0.3 ± 0.1	1.3 ± 0.2	9.7 ± 1.5	0.4 ± 0.1	0.008 ± 0.002
2001	3	24.3 ± 4.1	6.8 ± 1.6	0	0.04 ± 0.02	3.6 ± 1.8	20.2 ± 5.2	2.1 ± 1.1	0.01 ± 0.003

Fig. 3. Field proportions of ichthyoplankton and zooplankton versus bottom layer dissolved oxygen (DO) concentrations at 2 stations in the Patuxent River: (a) fish eggs, (b) bay anchovy larvae <15 mm, (c) naked goby larvae, (d) copepods, and (e) *Mnemiopsis leidyi* at the (×) surface layer, (●) pycnocline, and (△) bottom layer during day and night. In (d), 7 day and 5 night data points are hidden. Up to 2 significant regression lines for each motile organism are shown (labeled by layer). Additional details of regression lines are in Table 4

The Schoener's Index calculated for vertical overlap including data for all DO concentrations ranged from a low of 0.59 for overlap between *Mnemiopsis leidyi* number and fish egg density to a high of 0.82 for naked goby larvae and copepod densities (Table 5). Values for Schoener's Index can range from 1 to 0, with the overlap value for a random distribution being 0.33. In our study, the values were relatively high, which implies a high degree of vertical overlap between predator–prey pairs. Schoener's vertical overlap between predators and their prey generally increased with increasing bottom DO concentrations (Fig. 4).

We performed ANCOVA to determine if the effect of DO concentration on predator and prey vertical overlap differed between day and night. Although the vertical distributions of many organisms differed between

day and night, time of day significantly modified the effect of DO concentration on predator and prey overlap for the overlaps between *Mnemiopsis leidyi* volume and number and fish eggs. The test for coincidence, which is a simultaneous test of both intercept and slope, indicated a significant effect of DO concentration on the overlap between *M. leidyi* volume and fish eggs ($F_{2,25} = 3.55$, p = 0.04), and a trend toward a DO effect on the overlap between *M. leidyi* number and fish eggs ($F_{2,25} = 3.03$, p = 0.07). All other ANCOVAs yielded p-values that were >0.05. Overlap values for vertical distributions of *M. leidyi* and fish eggs were smaller and more variable at night than during the day. During the day, overlap increased with increasing bottom DO concentrations, while no clear pattern of vertical overlap with bottom DO concentrations was

Table 4. Simple linear regression results of the vertical distributions (bottom, pycnocline, or surface) of motile organisms (*Mnemiopsis leidyi*, fish larvae, and copepods) versus bottom layer dissolved oxygen (DO) during both day and night at 2 stations in the Patuxent River, Maryland. Results correspond to significant regression lines in Fig. 3

Organism	Layer	Slope	R^2	F (df)	p
Day					
Bay anchovy larvae	Bottom	0.10	0.34	11.2 (1, 22)	0.003
Naked goby larvae	Pycnocline	−0.15	0.78	76.6 (1, 22)	<0.0001
Naked goby larvae	Bottom	0.16	0.78	78.4 (1, 22)	<0.0001
Copepods	Surface	−0.02	0.18	4.88 (1, 22)	0.04
Copepods	Pycnocline	−0.12	0.72	57.7 (1, 22)	<0.0001
Copepods	Bottom	0.09	0.79	80.8 (1, 22)	<0.0001
Night					
Bay anchovy larvae	Surface	−0.07	0.40	11.2 (1,17)	0.004
Bay anchovy larvae	Pycnocline	−0.06	0.29	7.00 (1,17)	0.02
Bay anchovy larvae	Bottom	0.14	0.84	90.3 (1,17)	<0.0001
Naked goby larvae	Surface	−0.03	0.32	8.01 (1,17)	0.01
Naked goby larvae	Pycnocline	−0.11	0.68	36.5 (1,17)	<0.0001
Naked goby larvae	Bottom	0.13	0.76	55.2 (1,17)	<0.0001
M. leidyi	Bottom	0.08	0.30	5.09 (1,12)	0.04
Copepods	Pycnocline	−0.07	0.57	22.8 (1,17)	0.0002
Copepods	Bottom	0.14	0.53	19.0 (1,17)	0.0004

Table 5. Schoener's Index of habitat overlap (mean ± SE) for vertical distributions of ctenophores (*Mnemiopsis leidyi*), ichthyoplankton, and copepods at 2 stations in the Patuxent River, Maryland. Untransformed values for Schoener's Index of habitat overlap for all predator–prey pairs were averaged over dissolved oxygen concentrations and time of day. n: number of samples

Predator – prey pair	Vertical overlap (n)
M. leidyi vol – fish eggs	0.60 ± 0.05 (29)
M. leidyi no. – fish eggs	0.59 ± 0.05 (29)
M. leidyi vol – copepods	0.71 ± 0.04 (30)
M. leidyi no. – copepods	0.70 ± 0.04 (30)
M. leidyi vol – bay anchovy larvae	0.63 ± 0.05 (26)
M. leidyi no. – bay anchovy larvae	0.63 ± 0.04 (26)
M. leidyi vol – naked goby larvae	0.65 ± 0.04 (30)
M. leidyi no. – naked goby larvae	0.66 ± 0.04 (30)
Bay anchovy larvae – copepods	0.70 ± 0.03 (39)
Naked goby larvae – copepods	0.82 ± 0.02 (43)

observed at night. Vertical overlap values (means ± SE) between *M. leidyi* and fish eggs respectively averaged 0.72 ± 0.05 (CV = 29.7) and 0.70 ± 0.05 (CV = 30.8) for *M. leidyi* volume and number during daytime, and 0.46 ± 0.08 (CV = 65.4) and 0.47 ± 0.08 (CV = 60.5) at night. The small nighttime overlap values reflected the small numbers of eggs and large numbers of *M. leidyi* in the bottom and pycnocline layers in some nighttime samples, probably due to time of sampling and sinking of eggs rather than a DO effect (Fig. 3a & e).

Because ANCOVA and regression revealed no significant differences in vertical overlap values of motile

predator–prey pairs relative to bottom DO concentrations in day versus night comparisons, we combined daytime and nighttime overlaps (total N = 43) in order to conduct regression analysis with a larger data set. The combined day–night regressions indicated that bottom DO concentrations significantly affected the vertical overlaps of 4 predator–prey pairs: (1) *Mnemiopsis leidyi* volume with copepods (both the linear and 2nd-order models had equally robust AICs), (2) *M. leidyi* number with copepods (both the linear and 2nd-order models; the 3rd-order regression had an insignificant trend, and all had equally robust AICs), (3) *M. leidyi* volume with naked goby larvae (both the linear and 2nd-order models had equally robust AICs), and (4) naked goby larvae with copepods (all 3 models were significant, but the linear model had the lowest AIC) (Fig. 4, Table 6). In addition, anchovy larvae and copepod overlap values tended to increase with increasing bottom DO concentrations ($0.05 ≤ α < 0.10$) (Fig. 4, Table 6). For all pairs of motile predator and prey, overlap increased with increasing DO concentrations, i.e. all regression analyses yielded net positive slopes (Table 6), although the relationship was not statistically significant; however, the percentage of variation in vertical overlap that was explained by bottom DO concentration was low even in cases where the relationship was statistically significant (Table 6). Tidal stage was not a significant indicator of vertical overlap for any predator–prey pair (ANCOVA, all p > 0.05).

Stepwise regressions were used to determine if predator and prey abundances (biotic factors) could explain the variation in vertical overlap in addition to that explained by bottom DO concentration, temperature and salinity (abiotic factors). For nighttime overlap between *Mnemiopsis leidyi* and fish eggs, *Chrysaora quinquecirrha* volume and bottom DO concentration explained 63 and 37 % of vertical overlap respectively, in the stepwise regression model (p = 0.05, $R^2 = 0.45$, $F_{2,10} = 4.1$). There were 2 stepwise regression models for combined day–night data that explained a higher percentage of the variation in predator–prey vertical overlap by improving the model fit over simple regressions: (1) *C. quinquecirrha* volume and bottom DO concentration in the model of *M. leidyi* volume and copepod overlap (p = 0.001, $R^2 = 0.39$, $F_{2,27} = 8.6$), in which *C. quinquecirrha* volume and bottom DO concentration explained 86 and 14 % of the variation in overlap respectively, and (2) *C. quinquecirrha* number and bottom DO concentration in the model of *M. leidyi* number and copepod overlap (p = 0.005, $R^2 = 0.33$, $F_{2,27} = 6.5$), in
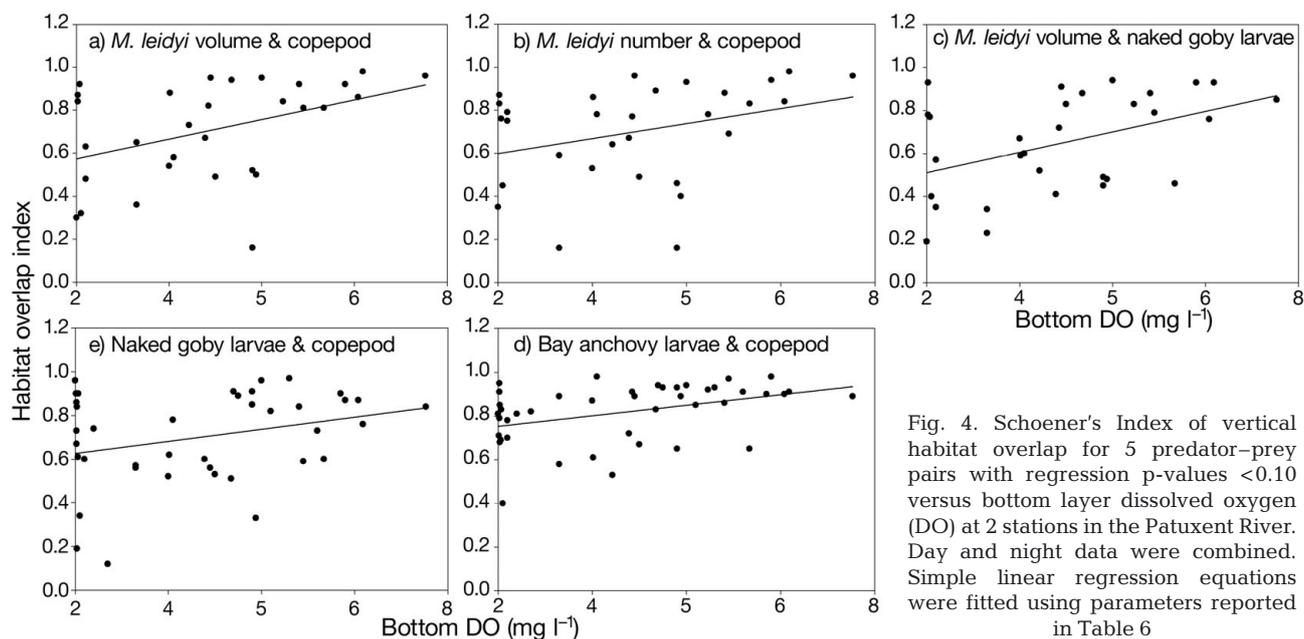
Fig. 4. Schoener's Index of vertical habitat overlap for 5 predator–prey pairs with regression p-values <0.10 versus bottom layer dissolved oxygen (DO) at 2 stations in the Patuxent River. Day and night data were combined. Simple linear regression equations were fitted using parameters reported in Table 6

which *C. quinquecirrha* number and bottom DO concentration explained 76 and 24% of the variation in overlap respectively. In addition, the stepwise model of overlap between bay anchovy larvae and copepods was significant for another abiotic factor (salinity, 21%), in addition to bottom DO concentration (14.5%) and biotic factors (anchovy larvae = 49% and *M. leidyi* number = 15%) (p < 0.0001, R^2 = 0.22, $F_{4,93}$ = 6.7).

DISCUSSION

There were no significant DO effects on *Mnemiopsis leidyi* clearance rates on bay anchovy eggs, bay anchovy yolk sac larvae, or naked goby larvae in the laboratory. This result was unexpected as we anticipated DO concentration to affect clearance rates based on significant effects of DO concentration on *Chrysaora quinquecirrha* predation on naked goby larvae (Breitburg et al. 1994), and *M. leidyi* predation on copepods (Decker et al. 2004). However, bottom layer DO concentrations affected the distributions of motile organisms in the water column. The proportions of fish larvae and copepods strongly increased in the bottom layer with increasing DO concentrations during both day and night, while *M. leidyi* proportions in the bottom layer increased with increasing bottom DO concentrations only at night. Increased abundance in the bottom layer and decreased abundance in the pycnocline (and to a lesser extent, the surface layer) resulted in a general increase in overlap between motile predators and prey with increasing bottom DO concentrations. Time of day significantly affected only the overlap between *M. leidyi* and fish eggs, which was greatest during the day regardless of DO concentration.

Mnemiopsis leidyi clearance rates in our experiments were highest for bay anchovy yolk sac larvae, intermediate for bay anchovy eggs, and lowest for naked goby larvae, similar to the pattern found by Monteleone & Duguay (1988). Clearance rates in our laboratory experiments were comparable to those in other studies (Monteleone & Duguay 1988, Cowan & Houde 1993, Purcell & Decker 2005), especially at our control DO concentrations.

Differences in *Mnemiopsis leidyi* clearance rates on the 3 ichthyoplankton prey may reflect ontogenetic changes in prey swimming speeds (which affect encounter probabilities) as well as prey escape ability (which affect escape probabilities). Fish eggs do not swim, are smaller than all but newly hatched fish larvae, and have no escape ability; these lead to lower encounter rates with *M. leidyi* compared with larval fish, but higher capture rates after encounter. The combination of these factors apparently results in lower clearance rates for fish eggs than for yolk sac larvae. Yolk sac larvae have limited swimming and escape abilities compared with older larvae (Bailey & Batty 1984, Purcell et al. 1987). The opposing effects of the well developed swimming and escape abilities of naked goby larvae probably explain the low clearance rates by *M. leidyi* in Monteleone & Duguay (1988) and in our study.

We expected that the combination of high tolerance to low DO concentration of *Mnemiopsis leidyi* and the low tolerance of their prey (Breitburg et al. 2003, Decker et al. 2003) would result in effects of low DO concentration on clearance rates on the motile prey

Table 6. Effects of bottom layer dissolved oxygen (BOTDO) on arcsine square root transformed Schoener's Index of vertical overlap in 8 pairs of motile predators (*Mnemiopsis leidyi* and fish larvae) and prey (fish larvae and copepods) at 2 stations in the Patuxent River, Maryland. Parameter estimates for the intercept and slopes from 1st-, 2nd-, and 3rd-order simple regression models are presented for combined day and night samples (total N = 43). Predators are listed first and their prey listed second. Models are arranged based on the smallest to the largest Akaike's Information Criterion (AIC). The order of the model is indicated by the number of slope parameters fit (e.g. a 2nd-order model has parameter estimates for $BOTDO^1$ and $BOTDO^2$, but "." indicates no slope parameter for $BOTDO^3$). Regressions with p-values <0.10 are presented in Fig. 4

Predator – prey	Intercept	$BOTDO^1$	$BOTDO^2$	$BOTDO^3$	AIC	δ AIC	R^2	F (df)	p
M. leidyi vol – copepods	0.86	0.06	.	.	−81.46	0.00	0.20	6.83 (1, 29)	0.01
	0.92	−0.01	0.01	.	−80.77	−0.69	0.23	4.04 (2, 29)	0.03
	0.93	−0.04	0.02	0.00	−78.84	−2.62	0.23	2.62 (3, 29)	0.07
M. leidyi no. – copepods	0.97	−0.06	0.02	.	−81.19	0.00	0.22	3.72 (2, 29)	0.04
	0.88	0.05	.	.	−80.21	−0.97	0.13	4.35 (1, 29)	0.05
	0.98	−0.09	0.03	0.00	−79.27	−1.91	0.22	2.42 (3, 29)	0.09
M. leidyi vol – bay anchovy larvae	1.03	−0.12	0.02	.	−63.73	0.00	0.12	1.63 (2, 25)	0.22
	0.92	0.01	.	.	−62.37	−1.36	0.00	0.08 (1, 25)	0.78
	1.03	−0.12	0.02	0.00	−61.73	−2.00	0.12	1.04 (3, 25)	0.39
M. leidyi no. – bay anchovy larvae	0.96	−0.08	0.02	.	−69.15	0.00	0.11	1.48 (2, 25)	0.25
	0.88	0.02	.	.	−68.74	−0.40	0.03	0.70 (1, 25)	0.41
	0.96	−0.08	0.02	0.00	−67.15	−2.00	0.11	0.94 (3, 25)	0.44
M. leidyi vol – naked goby larvae	0.80	0.05	.	.	−84.91	0.00	0.20	7.01 (1, 29)	0.01
	0.82	0.03	0.00	.	−83.15	−1.76	0.21	3.51 (2, 29)	0.04
	0.86	−0.09	0.05	0.00	−82.12	−2.80	0.23	2.61 (3, 29)	0.07
M. leidyi no. – naked goby larvae	0.95	−0.06	0.01	.	−77.82	0.00	0.14	2.11 (2, 29)	0.14
	0.88	0.03	.	.	−77.62	−0.20	0.07	2.10 (1, 29)	0.16
	1.00	−0.21	0.08	−0.01	−77.33	−0.48	0.18	1.88 (3, 29)	0.16
Bay anchovy larvae – copepods	0.93	0.03	.	.	−109.24	0.00	0.08	3.28 (1, 38)	0.08
	0.99	−0.19	0.08	−0.01	−108.47	−0.77	0.15	2.13 (3, 38)	0.11
	0.95	−0.01	0.01	.	−107.82	−1.42	0.10	1.89 (2, 38)	0.17
Naked goby larvae – copepods	1.07	0.03	.	.	−156.38	0.00	0.17	8.50 (1, 42)	0.006
	1.06	0.03	0.00	.	−154.38	−2.00	0.17	4.15 (2, 42)	0.02
	1.08	−0.04	0.03	0.00	−153.37	−3.01	0.19	3.06 (3, 42)	0.04

tested. However, despite a high tolerance to low DO concentrations, sustained swimming speeds of *M. leidyi* were slower at low DO (18.2 ± 1.0 mm s^{-1} at 1.7 mg l^{-1}) than at intermediate DO concentrations (22.5 ± 1.2 mm s^{-1} at 2.6 mg l^{-1}) (Kolesar 2006). In contrast, sustained swimming speeds of the hypoxia-sensitive fish larvae used here were not significantly affected by DO concentrations between 1.7 and 7.7 mg l^{-1} (Kolesar 2006), which suggests no differences in encounter rates at the DO concentrations tested. Experiments conducted under comparable conditions indicated that *Chrysaora quinquecirrha* predation on naked goby larvae (Breitburg et al. 1994, 1997) and clearance rates of larger-sized *M. leidyi* on copepods (Decker et al. 2004) were higher at low and intermediate DO than at high DO concentrations. Burst swimming speeds of fish larvae may be more important than sustained swimming speeds for avoiding entrainment by swimming scyphomedusae.

The unstratified water column used in our laboratory experiments eliminated the natural variation in physical habitats found in the field. Without an oxygen gradient, there were no areas of higher DO concentrations that were available to organisms as refuges from either low-DO stress or predation (Tyler & Targett 2007). A lack of refuges may be especially important for motile organisms such as fish larvae (Breitburg 1994) and copepods (Decker et al. 2003), which actively avoid nonlethal oxygen concentrations that are physiologically stressful (Miller et al. 2002).

The responses of organisms to low DO concentrations influence how they utilize the water column (Eby & Crowder 2002, Eby et al. 2005, Kreiner et al. 2009). Bottom layer DO concentration affected the vertical distribution of all motile species sampled, with proportions of motile organisms increasing in the bottom layer and decreasing in the surface and pycnocline layers as a function of bottom layer DO concentration. Bay anchovy larval distributions suggested a threshold response to DO concentration; however, sigmoid curves that were fitted to the relationship between bottom DO concentration and proportional densities of bay anchovy larvae (R^2 = 0.85, $F_{2,16}$ = 44.1, p < 0.0001 at night; R^2 = 0.39, $F_{2,21}$ = 6.8, p = 0.005 during the day)

had R^2 values that were nearly the same as in the linear models (Table 4). Because we lacked nighttime samples in the 1–2 mg l^{-1} bottom DO range, it was not possible to distinguish between linear and threshold responses for night samples. The same 2 factors made it impossible to distinguish between linear and threshold responses for naked goby larvae (bottom layer sigmoid R^2 = 0.86, $F_{2,16}$ = 48.4, p < 0.0001 at night; bottom layer sigmoid R^2 = 0.83, $F_{2,21}$ = 49.5, p < 0.0001 during the day; linear regressions in Table 4). The possibility of nonlinear relationships should not eclipse the strong positive correspondence of fish larvae and copepod distribution in the bottom layer with increasing bottom DO concentrations. Further, increasing the number of field samples at bottom DO concentrations between 1 to 2 mg l^{-1}, especially at night, may clarify species' responses to declining bottom DO conditions.

Increased overlap between predators and prey can lead to increased predation. Significant linear increases in bottom layer proportions of motile species with increased bottom DO concentrations (fish larvae and copepods during day and night, and *Mnemiopsis leidyi* at night) led to increased vertical overlaps between predators and prey that were well described by simple linear models, or by multivariate models including both DO and the abundance of a predator or competitor species. Moreover, although increased overlap can lead to increased predation, the ANCOVA result of day and night differences in vertical overlap between fish eggs and *M. leidyi* should not differentially affect predation because ctenophores are nonvisual predators that feed both during the day and at night.

In the present study, there were not only insignificant DO effects on predation rates by *Mnemiopsis leidyi* on ichthyoplankton, but also reduced the overlap between *M. leidyi* and its prey at very low bottom DO concentrations. Use of the bottom layer at low oxygen concentrations that elicit avoidance by its ichthyoplankton and mesozooplankton prey suggests that *M. leidyi* is responding to factors other than the vertical distributions of its prey. Comparison with studies on *Chrysaora quinquecirrha* (Breitburg et al. 1997, Breitburg et al. 1999) indicates that the relative importance of the 2 gelatinous predators can depend on bottom layer DO concentration. At moderately low bottom DO concentrations, *C. quinquecirrha*–fish larvae overlap and predation increased throughout the water column (Breitburg et al. 1997, Breitburg et al. 1999); *C. quinquecirrha* appeared to follow the vertical distribution of its more hypoxia-sensitive prey and avoided the bottom layer at oxygen concentrations that were unlikely to substantially reduce growth or survival (Grove & Breitburg 2005). In contrast, *M. leidyi*–fish larvae overlap (and predicted resulting predation) was highest at high bottom DO concentrations.

Other studies of hypoxia and habitat report higher species co-occurrence as species are forced to utilize smaller volumes due to declining DO concentrations (Vanderploeg et al. 2009, Zhang et al. 2009), resulting in habitat compression. Predator and prey in our study have very different tolerances to low DO concentrations, and declining DO concentrations elicited different responses of predator and prey, resulting instead in vertical habitat separation at low DO concentrations. Lower vertical overlaps between most of the predator–prey pairs in this study with decreasing bottom DO concentrations indicate the potential for decreased encounters in the field when DO concentrations are low in the bottom layer. Some predators and prey are also more active at high than at low DO concentrations (Decker et al. 2004), increasing encounter potential as DO returns to normal conditions. These potential increases can be offset if prey escape ability is also greater when DO concentrations are high (Domenici et al. 2007). As a result, there could be confounding interactions between increasing encounter rates (due to both increased vertical overlap and faster predator and prey swimming speeds) and increasing escape abilities of prey at high DO concentrations, such that predation rates may not necessarily increase despite likely increases in encounters at higher bottom DO concentrations.

An important factor determining the effect of DO on predator–prey overlaps appears to be the use of low DO bottom waters by *Mnemiopsis leidyi*. *M. leidyi* predators were more abundant than their prey in the bottom layer at lower DO concentrations, while the densities of both predator and prey increased in the bottom layer with increasing DO concentrations. The vertical overlap between *M. leidyi* and its prey tended to decrease as *M. leidyi* number or volume increased, with the only exception being one large overlap value between ctenophores and bay anchovy larvae at the greatest *M. leidyi* density. Overlap between both species of fish larvae and copepods was consistently high as these organisms have a similar response of avoiding low DO bottom waters and steadily increasing their densities in the bottom layer with increasing DO concentrations. For all significant predator–prey overlap pairs, the variance around the mean was inversely related to bottom DO concentrations, indicating that the environment may affect the variability of ecological responses.

The fit of simple regression models between organism overlap and bottom DO concentrations were often improved by including predator and competitor abundances. In particular, a large percentage of predator–prey overlaps were explained by including C*hrysaora quinquecirrha* terms in stepwise regression models, indicating that biotic components of the food web (*C. quinquecirrha* as a predator or competitor) influ-

enced habitat utilization and overlap between predators and prey along with an abiotic factor (bottom DO concentration). Previous studies have demonstrated that *C. quinquecirrha* predation on copepods and fish larvae increases with decreasing DO concentration (to 1.5 mg l^{-1}) in the laboratory (Breitburg et al. 1997), and that *C. quinquecirrha* displays similar vertical distribution responses to low DO concentrations in the field as its fish larvae and mesozooplankton prey (Keister et al. 2000). These patterns highlight the ability of *C. quinquecirrha* to both directly and indirectly affect trophic processes.

CONCLUSIONS

Vertical distribution in the water column can affect spatial overlap between predators and prey, potentially altering predation rates. Our data suggest that it is the influence of DO on vertical position within the water column, rather than the direct impacts of DO on predation rates, that are likely to be most important in the interactions between ctenophores and their prey in the field. Our laboratory predation experiments resulted in similar predation by *Mnemiopsis leidyi* on the early life stages of fishes regardless of DO concentrations. Because overlap declined with declining DO concentrations, our results suggest that predation on ichthyoplankton by *M. leidyi* would be higher in areas with high bottom oxygen concentrations than in areas with a hypoxic bottom layer.

Vertical stratification (as well as other forms of patchiness) has important implications for all aquatic environments. In Chesapeake Bay in particular, Govoni & Olney (1991) suggested that the non-uniform distribution of *Mnemiopsis leidyi* could potentially affect predation on ichthyoplankton. Biodiversity, conservation and cross-scale processes can all be affected by spatial distributions of organisms in a 3-dimensional environment (Resetarits 2005). The spatial structure of consumers in an ecosystem affects food web stability (McCann et al. 2005, Seitz et al. 2003), and mobile omnivores (McCann & Hastings 1997) such as ctenophores can be especially important to trophic dynamics in aquatic environments. The spatial heterogeneity of species serving as both consumers and prey (e.g. zooplankton) in aquatic systems can also shape food web interactions (Pinel-Alloul 1995).

Examining abiotic factors (e.g. DO concentration) in the water column in conjunction with density, distribution, and abundance of organisms is necessary to determine the importance of habitat and habitat degradation to predator–prey interactions. While our laboratory experiments showed that DO concentration did not directly affect predation rates of *Mnemiopsis*

leidyi feeding on ichthyoplankton, the effects of DO concentration on swimming speeds, behavior, and vertical distributions of species are important to food web dynamics in seasonally oxygen-stratified estuarine systems. Potentially stressful abiotic conditions such as low DO concentrations may serve to spatially separate predator and prey, possibly benefiting hypoxia-sensitive prey. Combining laboratory and field sampling as in this study to further examine species' responses to DO concentration at the level of the individual, as well as effects on interspecific interactions, will provide important answers to basic questions about the effects of species' behaviors and spatial distributions on food web dynamics.

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