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Fine-scale vertical distributions of *Mnemiopsis leidyi* ctenophores: predation on copepods relative to stratification and hypoxia

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ABSTRACT: Plankton concentrations near discontinuities in the water column (clines) are believed to be important for intensifying trophic interactions; however, evidence for increased feeding by predators at clines *in situ* is scarce. Here we demonstrate enhanced feeding near pycnoclines by a voracious planktivore, the ctenophore *Mnemiopsis leidyi*. To determine their feeding relative to stratification, we quantified temperature, salinity, dissolved oxygen concentration (DO), densities of ctenophores and copepods at 1 to 2 m depth intervals, and gut contents of ctenophores collected by depth layer at stations in a tributary and in the mainstem Chesapeake Bay during summer from 1999 to 2001. We tested the null hypotheses that patterns in the tributary and the bay were similar and that ctenophore vertical distributions and feeding were independent of the vertical distributions of the physical variables, stratification, and copepods. We rejected all null hypotheses. Ctenophores and copepods had peak densities below the pycnocline in the weakly stratified tributary, where DO was above 2 mg l^{-1} throughout the water column; by contrast, they were more concentrated above the strong pycnocline and near-anoxic waters at ~11 m in the bay. Predation on copepods by ctenophores was highest where both populations were concentrated. Our results illustrate the importance of stratification to planktonic trophic interactions for *M. leidyi*, which thrives in anthropogenically degraded waters and now is established throughout European seas, where it can negatively affect planktonic food webs and fisheries.

KEY WORDS: Jellyfish · Aggregation · Cline · *Acartia* · Zooplankton · Low dissolved oxygen · Feeding · Clearance · Chesapeake Bay (USA)

INTRODUCTION

The vertical layering of planktonic organisms has intrigued scientists for many decades (Barham 1963). Stratification of the water column and layering of the organisms have been studied extensively in the field with closing nets (e.g. Keister et al. 2000, Schaber et al. 2011) and at finer scales with acoustic, particle-counting, and camera systems (e.g. Cheriton et al. 2007, Möller et al. 2012, Bi et al. 2013). Concentration of organisms at water column discontinuities (clines) is hypothesized to enhance production, trophic interactions, and dispersion (reviewed by McManus & Woodson 2012). Evidence of behavioral concentra-

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tion of organisms and enhanced feeding at clines abounds in the laboratory (e.g. Woodson & McManus 2007, Woodson et al. 2007); however, evidence of increased feeding *in situ* is rare (see Möller et al. 2012).

Ctenophores, medusae, and copepods are known to accumulate at density discontinuities in the water column (Arai 1992, Graham et al. 2001, Malej et al. 2007, Jacobsen & Norrbin 2009, Frost et al. 2010). Arai (1992) concluded that *Sarsia tubulosa* hydromedusae behaviorally aggregate at salinity discontinuities. Similarly, hydromedusae of *Nemopsis bachei* remain in discontinuities created by salinity gradients with and without thin layers of algae and copepods (Frost et al. 2010). Most *Aurelia* spp. medusae occur at clines (Rakow & Graham 2006, Malej et al. 2007). *Acartia tonsa* copepods also aggregate in layers (Woodson et al. 2007). Thus, gelatinous predators and their prey actively aggregate at density discontinuities. Although medusae and their feeding increase at clines (Frost et al. 2010), we know of no previous studies on ctenophore feeding *in situ* in relation to stratification.

The mesohaline Chesapeake Bay (USA) and its tributaries can have high densities of mesozooplankton, *Mnemiopsis leidyi* ctenophores, and *Chrysaora quinquecirrha* scyphomedusae during summer. The eurythermal and euryhaline calanoid copepod *Acartia tonsa* is the most abundant component of the mesozooplanktonic assemblage, with cyclopoid copepods *Oithona colcarva* and meroplankton also abundant at times (Brownlee & Jacobs 1987). In Chesapeake Bay, copepods are the main prey of *M. leidyi* and *C. quinquecirrha*, whose diets contain varying proportions of other zooplankton and ichthyoplankton depending on their availability (Purcell 1992, Purcell et al. 1994a,b, 2001b). The medusae also are voracious predators of *M. leidyi* and, when abundant, can reduce ctenophore populations in the tributaries and mainstem bay (Purcell & Cowan 1995, Purcell & Decker 2005) and may affect their vertical distribution (e.g. Kolesar et al. 2010). In Chesapeake Bay, ctenophores can reduce copepod populations when the abundance of and predation by medusae are low (Purcell & Decker 2005).

Low dissolved oxygen (DO) in the water (hypoxia) has expanded exponentially in coastal waters globally since ~1950 and can severely damage ecosystem health (Diaz & Rosenberg 2008, Vaquer-Sunyer & Duarte 2008, Breitburg et al. 2009). Hypoxia is defined here as DO concentrations <2 mg O_2 l^{-1}. Hypoxic sub-pycnocline waters are a pervasive feature of the mesohaline region of Chesapeake Bay and many of its tributaries from June to October (Boicourt 1992). Seasonal stratification begins in March to April and, in the mesohaline portion of the mainstem bay, waters are severely hypoxic (<0.1 mg O_2 l^{-1}) below the abrupt pycnocline (1–2 m depth interval) by summer and this persists until October (Boicourt 1992). By contrast, in the Patuxent River tributary of Chesapeake Bay, the oxycline extends over several meters in depth, and episodes of hypoxia persist only hours or days depending on the strength of stratification, which is influenced by freshwater discharge and tidal and wind mixing (Boicourt 1992, Breitburg et al. 2003).

Vertical distributions of copepods, ctenophores, and medusae in the mainstem Chesapeake Bay and its tributaries are greatly affected by hypoxic bottom waters. *Acartia tonsa* copepods are restricted to the surface and pycnocline layers when bottom waters are hypoxic (Roman et al. 1993, Keister et al. 2000). Previous studies sampled *Chrysaora quinquecirrha* and *Mnemiopsis leidyi* with opening-closing nets in 2 or 3 layers (Purcell et al. 1994a, 1999, Keister et al. 2000, Breitburg et al. 2003, Purcell & Decker 2005, Kolesar et al. 2010). Densities of *C. quinquecirrha* and *M. leidyi* were greater above than below the pycnocline in the mainstem bay, where waters below ~11 m were anoxic (Purcell et al. 1994a). Sampling in the Patuxent River indicated that *C. quinquecirrha* did not use bottom waters when DO was <2.0 mg O_2 l^{-1}, but that *M. leidyi* could use bottom waters even at 1.0 mg O_2 l^{-1} (Keister et al. 2000, Breitburg et al. 2003, Kolesar et al. 2010).

When DO levels are not lethally low (reviewed by Marcus 2001, Breitburg 2002, 2009, Miller et al. 2002), they can affect the predatory and escape behaviors of various animals differently and alter trophic interactions in complex ways (Breitburg et al. 1997, 1999). Short-term (<24 h) laboratory and mesocosm experiments (Breitburg et al. 1994, 1997, Decker et al. 2004, Kolesar et al. 2010) on fish eggs, fish larvae, and copepods suggest that *Mnemiopsis leidyi* feeds better at low DO than *Chrysaora quinquecirrha* medusae and that ctenophores may be able take advantage of planktonic prey in hypoxic waters that medusae avoid (Breitburg et al. 1999).

Although the above general patterns are well documented, feeding relative to stratification or hypoxia at depth has not been measured previously in the field. In order to better understand how stratification and low oxygen may influence trophic interactions in eutrophic waters, we examined fine-scale vertical distributions of physical variables, ctenophores,

medusae, and copepods in the Patuxent River tributary and the mainstem Chesapeake Bay during summers in 1999 to 2001. Because medusa densities were low, our focus during this study was on ctenophores. We tested the null hypotheses that ctenophore vertical distributions and feeding were independent of the vertical distributions of temperature, salinity, stratification, DO, and their copepod prey (*Acartia tonsa*), and that vertical distribution patterns in the tributary and bay were similar.

MATERIALS AND METHODS

Sample collection and analyses

During 24 h periods on 22 June and 27 July 1999, we sampled at 2 of the deepest locations mid-channel in the Patuxent River, viz. the mouth of St. Leonard Creek (SL), Maryland (38° 21.41′ N, 76° 30.5′ W; average depth = 20 m), and south of the mouth of Battle Creek (BC; 38° 23.66′ N, 76° 33.08′ W; average depth = 16 m; Fig. 1). Those locations are known for chronic summertime hypoxia in previous years (Keister et al. 2000, Breitburg et al. 2003). During 24 h periods on 17 July and 8 August 2000, we sampled at deep stations in the mainstem Chesapeake Bay, off James Island (JI; 38° 23.5′ N, 76° 19.75′ W) and off a channel buoy (BY; 38° 28.2′ N, 76° 22.6′ W). During 24 h on 5 July 2001, we sampled at JI and SL (day) and BY and SL (night), and on 26 July 2001, we sampled at SL (day) and at BC (night). Data are presented as means ± standard error (SE). The same set of measurements and samples were collected at each sampling time, as follows (summarized in Table 1).

Temperature (T, in °C), salinity (S), and DO (mg O_2 l^{-1}) concentrations were measured at 1 to 2 m depth intervals from the surface to bottom with a YSI model 85 DO meter. Stratification intensity, delta sigma t ($\Delta\sigma_t$) in kg m^{-3}, was calculated as the difference between adjacent depths in seawater density (σ_t), as calculated from T and S using a seawater density calculator (Tomczak 2000), based on Fofonoff & Millard (1983). Although sampling was necessarily at discrete depths, all variables form continuous gradients in the field.

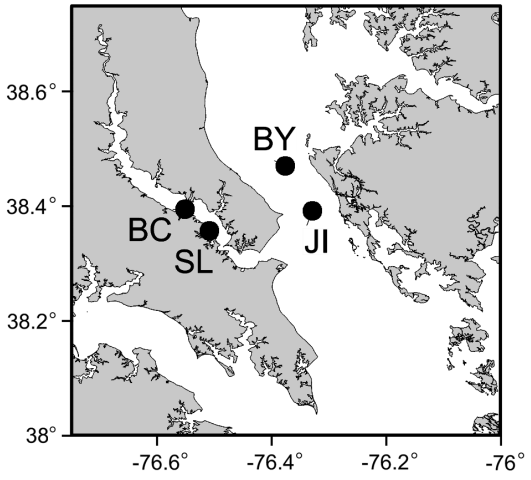

Fig. 1. Mid-Chesapeake Bay on the US east coast. Sampling stations in the mainstem bay were Buoy (BY) and James Island (JI). Stations in the Patuxent River tributary were Battle Creek (BC) and St. Leonard Creek (SL)

Mesozooplankton was collected at 2 m depth intervals with a submersible diaphragm pump; 20 l samples were filtered through a 35 µm mesh net onboard ship. Each sample was preserved in 5 % buffered formalin solution for later enumeration and identification with the aid of a dissecting microscope in the laboratory. Subsamples were taken with a Hensen stempel pipette until a total of at least 200 individu-

Table 1. Vertical samplings performed at stations in Chesapeake Bay during daytime and at night. SL: St. Leonard Creek, BC: Battle Creek, JI: James Island, BY: Buoy. Values are given as the number of profiles in daytime, nighttime and total number of profiles used in statistical analyses. Under each heading are the sampling depth intervals in parentheses. S: salinity, T: temperature, DO: dissolved oxygen, Zoopl: zooplankton. Su: surface, P: pycnocline, B: below pycnocline. Trawl samples were used only for ctenophore sizes and medusa densities

Location & date	Stn	Number of vertical profiles				
		S,T,DO (1–2 m)	Zoopl (2 m)	Video (1–2 m)	Trawls (Su,P,B)	Guts (Su,P,B)
Tributary						
22 June 1999	SL	1,1	1,1	1,1	2,2	0,0
	BC	1,1 [4]	1,1 [4]	1,1 [4]	1,2 [4]	0,0 [0]
27 July 1999	SL	1,1	1,1	1,1	2,2	1,0
	BC	1,1 [4]	1,1 [4]	1,1 [4]	2,2 [4]	1,0 [2]
5, 26 July 2001	SL	2,1	2,1	2,1	2,2	0,0
	BC	0,1 [4]	0,1 [4]	0,1 [4]	2,0 [3]	0,0 [0]
Mainstem bay						
17 July 2000	JI	1,1	1,1	1,1	2,1	1,0
	BY	1,1 [4]	1,1 [4]	1,1 [4]	2,2 [4]	1,0 [2]
8 Aug 2000	JI	1,1	1,1	1,1	2,2	1,0
	BY	1,1 [4]	1,1 [4]	1,1 [4]	2,2 [4]	1,0 [2]
5 July 2001	JI	1,0	1,0	1,0	2,0	0,0
	BY	1,0 [2]	1,0 [2]	1,0 [2]	2,0 [2]	0,0 [0]

als, or 25% of the whole sample, were counted and all zooplankton taxa identified. We present data only on the copepod *Acartia tonsa*, which was the predominant mesozooplankter in our study. Numbers of adults plus copepodites (hereafter referred to as copepods) were standardized to number l^{-1}.

Duplicate 1.5 to 2 min discrete-depth samples for *Mnemiopsis leidyi* and *Chrysaora quinquecirrha* were taken at a speed of ~2 knots in each of 3 layers (surface, pycnocline, bottom) using a Tucker trawl with a 1 m^2 mouth area and 212 to 224 µm mesh nets and a General Oceanics flowmeter attached in the mouth of the net. The surface layer was sampled with the top of the net skimming the water's surface. The upper and lower depths of the pycnocline at each station were first determined with a CTD cast. Geometric calculations using the lengths of towing cable and wire angles guided trawl deployment within the pycnocline and bottom layers. Sampling within the pycnocline was confirmed by a YSI model 52 DO meter probe attached to the frame of the trawl. Sampling within the bottom layer was from just above the sediment to the bottom of the pycnocline. Samples were sieved in colanders that retained gelatinous species but not mesozooplankton. Trawl samples were used here only for ctenophore sizes and medusa densities. Total wet volume of each species was measured to the nearest 50 ml in graduated pitchers. All medusae were counted from each sample. For large catches of ctenophores, a 1 to 2 l subsample was taken from each sieved sample, with larger subsamples used to measure larger, less numerous ctenophores. All ctenophores in each subsample were counted, and the average volume of individual ctenophores was calculated from the subsample volume divided by the number of ctenophores.

Vertical profiles to determine *Mnemiopsis leidyi* ctenophore and *Chrysaora quinquecirrha* medusa densities were made by videotaping at 1 to 2 m depth intervals throughout the water column. A black and white JAC M370 mono camera with a 3.6 mm 1:1.6 TV lens (Computar) in an underwater housing with red LED light were connected by an underwater cable to a Sony Video Hi8 EVO-250 NTSC video cassette recorder on deck. The camera and light were secured to a 0.25 m^2 frame with a model airplane propeller as a flow meter and a large vertical tail to orient the frame into the current. The video was monitored in real-time onboard ship, which ensured an adequate sample size of ctenophores at each depth (up to 81 ctenophores and an average of ~36 per depth). Recording was conducted for 5 min at each site and depth in 1999 (mean volume analyzed at each depth = 10.1 ± 0.6 m^3) and for 2 to 3 min at each site and depth in 2000 and 2001 (mean volume 6.0 ± 0.4 m^3). Videotapes automatically recorded date and time and were replayed in the laboratory on a Sony EV-S2000 NTSC Video Hi8 player. Ctenophores and medusae passing through the frame, as well as propeller revolutions, were counted while viewing the tapes on a Panasonic ct2084vy color high-resolution monitor. The linear relationship between water flow ('distance') and the number of propeller revolutions was determined in a flume at the Horn Point Laboratory. The volume of water passing through the frame equaled frame area × distance. Densities of ctenophores and medusae were standardized to numbers m^{-3}.

Ctenophores for gut content analysis were collected at 3 depths (surface, pycnocline, and bottom layers) in daytime by SCUBA divers with lights, which were needed to see the ctenophores in the turbid waters. Ctenophores were captured in 125 or 250 ml jars, into which ~10 ml of 37% buffered formaldehyde was injected to stop digestion of prey. Jars without ctenophores were collected and preserved concurrently as controls for mesozooplankton that might be collected inadvertently in the water with ctenophores. The formalin solution in diver-collected samples was brought to 5% onboard ship. All zooplankton in the samples were identified and counted from control and gut-content jars. The numbers of each zooplankton taxon in the control jars was subtracted from those in the gut content jars to correct for the possibility that the diving lights had increased zooplankton in the jars. We present data only for the copepod *Acartia tonsa*, which was the predominant mesozooplankter in the gut contents and in the plankton samples. Live ctenophore size (y, volume in ml) was estimated from the preserved length of each tentacle bulb (x, mm) according to the equation $y = 0.81 \times x^{1.913}$ (Purcell 1988). Ctenophore feeding was standardized to individual size by dividing the number of copepods eaten by ctenophore volume (ml).

Data analyses and statistics

We calculated several indices to evaluate the fine-scale vertical distributions of ctenophores and copepods relative to physical variables. At 1 to 2 m intervals, we calculated the mean weighted depth (MWD) of both species as $\Sigma(n_i z_i d_i)/\Sigma(n_i z_i)$, where d_i is the midpoint of the sample depth interval, z_i is the thickness of the stratum, and n_i is number of ind. m^{-3}

within depth layer *i*. For each profile at the MWD of copepods and ctenophores, we also determined the temperatures ($T_{MWDcope}$ and $T_{MWDcten}$) and salinities ($S_{MWDcope}$ and $S_{MWDcten}$). We also determined the depths of the maximum density changes for ctenophores (Δcteno $m^{-3}{}_{max}$) and copepods (Δcope $l^{-1}{}_{max}$) in the same way as $\Delta\sigma_{t\,max}$. We used Schoener's index of habitat overlap, the percent similarity index (PSI; Schoener 1970) to calculate vertical overlap between ctenophores and copepods. An overlap of 1.0 (100%) indicates identical use of all habitats, while an index of 0 indicates no overlap.

Several physical and biological indices were tested for differences: maximum $\Delta\sigma_t$ ($\Delta\sigma_{t\,max}$), depth of maximum $\Delta\sigma_t$ (depth $\Delta\sigma_{t\,max}$), minimum DO (DO_{min}), ctenophore MWD (MWD_{cten}), copepod MWD (MWD_{cope}), and PSI of copepods and ctenophores. PSI was logit transformed, as recommended by Warton & Hui (2011), before statistical analyses. Differences in each index were tested among stations and between day and night in 2-way ANOVA, with paired comparisons made by the Holm-Sidak method. Differences in each index also were tested among sampling dates for tributary and for bay stations by 1-way ANOVA, with paired-comparisons made by Dunn's Method. We tested for significant correlations between pairs of all indices with Pearson's correlation. To test whether the depth distributions of physical variables in the tributary and the bay differed from the depth distributions of ctenophores and copepods, we tested T, S, and DO at the MWD_{cten} and MWD_{cope} for all profiles in the tributary (12) and in the bay (10) by use of non-parametric Wilcoxon signed ranks paired *t*-tests. To determine whether animals were closer to stronger stratification, we tested the depths of the maximum density changes of ctenophores (Δcteno $m^{-3}{}_{max}$) and copepods (Δcope $l^{-1}{}_{max}$) by location (tributary versus bay) and day versus night with 1-way ANOVA for ctenophores; as copepod data did not meet assumptions of normality and equal variance, a non-parametric Kruskal-Wallis 1-way ANOVA was used.

Comparisons of feeding among depth layers in the tributary often did not meet assumptions of normality or equal variance and were analyzed with Kruskal-Wallis 1-way ANOVA on ranks and Mann-Whitney rank sum tests with the Holm-Sidak method for pairwise multiple comparisons, as appropriate. Our estimates of depth-specific feeding by ctenophores were limited by 3 factors. First, collections of ctenophores by SCUBA divers were possible only at some (4 tributary and 6 mainstem bay) of the total sampling stations and dates (12 tributary and 10 mainstem bay); second, due to limited visibility, ctenophores could be collected only at approximate depths; and third, divers collected larger ctenophores than did the trawls, which would bias (increase) the feeding rates. Therefore, we only compared gut contents among depth layers and did not use those data to estimate clearance rates.

We then estimated depth-specific clearance rates and predation effects of ctenophores with greater resolution and accuracy than possible from the gut content samples by calculating individual clearance rates (CR, in l ind^{-1} d^{-1}) from the regression $CR = 11.22\,V^{0.5413}$ linking individual ctenophore volume (V, in ml) to the volume of water they cleared of copepods (Purcell et al. 2001b, Purcell 2009). Mean individual ctenophore volumes were obtained from the Tucker trawls collected concurrently in the surface and pycnocline layers. The individual clearance rates were multiplied by the densities of ctenophores at each depth (from video profiles), which then were divided by copepod densities at each depth (from pump samples, converted to copepods m^{-3}) to estimate the percentage of the copepod standing stock consumed (predation effect in % d^{-1}). Predation effects in the oxic water column were calculated by first summing the depth-specific rates multiplied by the sampling depth interval (m) and then dividing by the water column depth, which was considered to be the greatest depth at which ctenophores were seen on the video (tributary stations 15.2 ± 1.2 m; bay stations 10.7 ± 1.0 m).

RESULTS

Physical stratification

Stratification was much stronger and deeper and bottom layer DO concentrations were much lower in both mainstem bay stations than in either tributary station (Figs. 2 & 3). All physical indices differed significantly between the tributary and the mainstem bay ($p \leq 0.01$; Table 2). Paired comparisons showed that the physical indices did not differ significantly between tributary stations (SL and BC) or between mainstem bay stations (JI and BY). Therefore, stations within each pair were not compared further, and we refer to the locations as 'tributary' and 'bay' rather than as individual stations. The mean maximum water density changes, $\Delta\sigma_{t\,max}$, were ≤0.54 in the tributary, but ≥1.54 in the bay where stratification was strong. The mean depths of $\Delta\sigma_{t\,max}$ were ≤6.8 m in the tributary, but ≥9.2 m in the bay. The mean DO

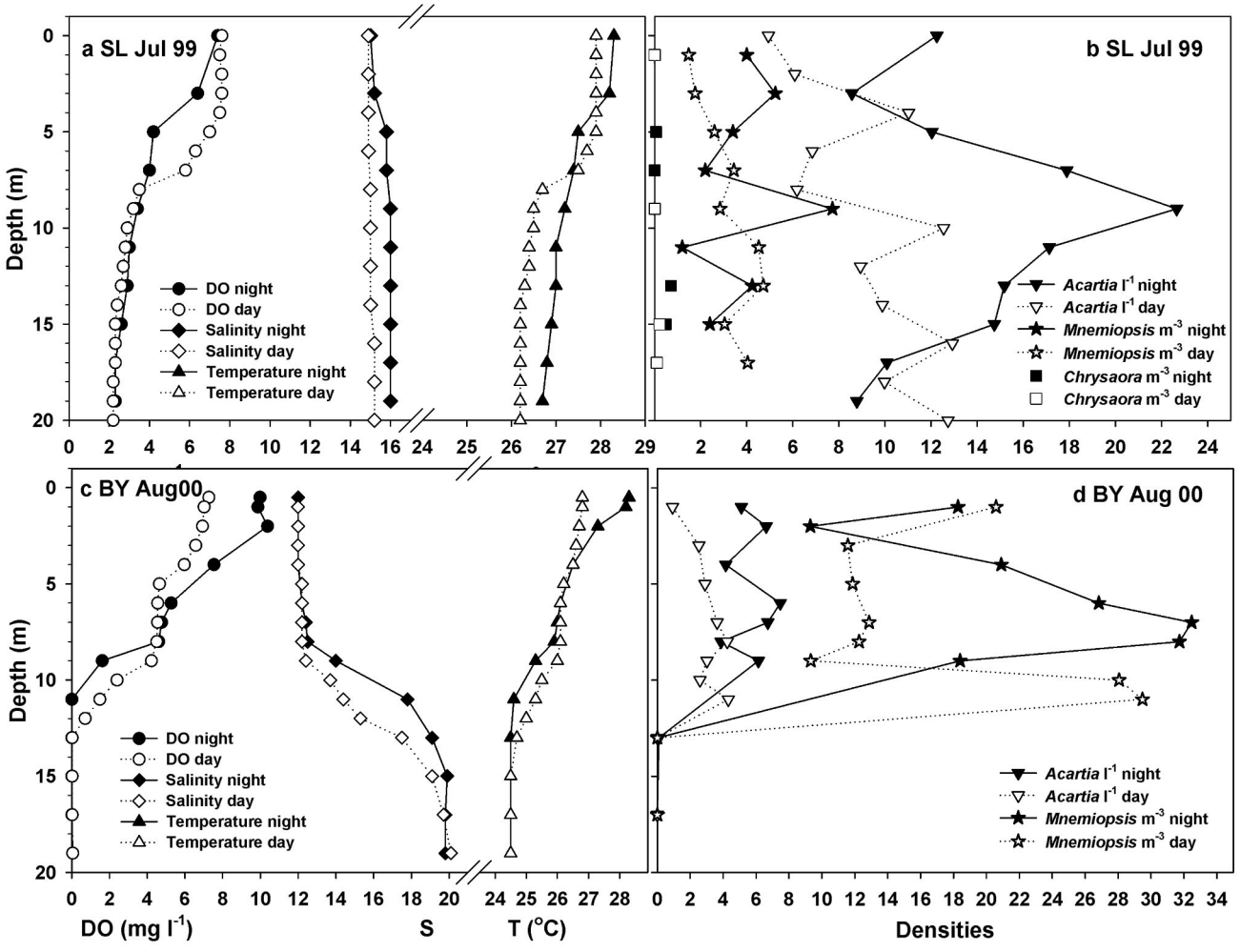

Fig. 2. Examples of vertical distributions of physical variables, ctenophores *Mnemiopsis leidyi*, copepods *Acartia tonsa*, and medusae *Chrysaora quinquecirrha* during day and night in (a,b) St. Leonard Creek (SL), a tributary of Chesapeake Bay, in July 1999, and (c,d) Buoy station (BY) in the mainstem bay in August 2000. DO: dissolved oxygen, S: salinity, T: temperature. Symbols mark each depth sampled

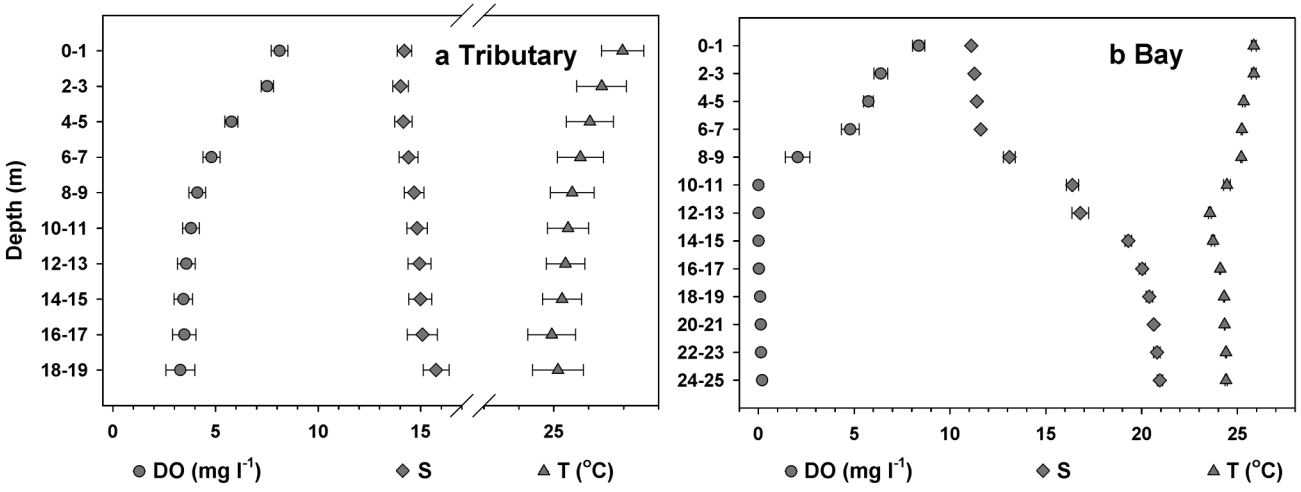

Fig. 3. Average vertical distributions of physical variables (DO: dissolved oxygen, S: salinity, and T: temperature) during day and night sampling in (a) 2 tributary stations and (b) 2 stations in the mainstem Chesapeake Bay. Symbols show means ± SE of profiles taken in the summers of 1999 to 2001. The locations, dates, and numbers of the profiles are given in Table 1

Table 2. Two-way ANOVA comparisons of the depth distributions of physical variables, ctenophores *Mnemiopsis leidyi*, and copepods *Acartia tonsa* in 1999 to 2001. Indices tested were the maximum change in stratification ($\Delta\sigma_{t\ max}$), depth (m) of $\Delta\sigma_{t\ max}$, lowest dissolved oxygen concentration (DO_{min}, mg l^{-1}), mean weighted depths (m) of ctenophores (MWD_{cten}) and copepods (MWD_{cope}), and the percent similarity index (PSI) of ctenophore and copepod densities. **Bold** text indicates significance ($p \leq 0.05$). The numbers of profiles tested for each station are given in Table 1. Trib: tributary, SL: St. Leonard Creek, BC: Battle Creek, Bay: mainstem Chesapeake Bay, JI: James Island, BY: Buoy. Station: effects due to station; D vs. N = day–night effects; NS: not significant. Different superscripts indicate statistically different pairwise comparison groups

Station	Test statistic	p
	$\Delta\sigma_{t\ max}$	
Trib SL[a]	Station: $F_{3,21} = 5.588$	**Station: 0.011**
Trib BC[a]	D vs. N $F_{1,21} = 0.003$	D vs. N: NS
Bay JI[b]	Interaction $F_{3,21} = 0.251$	Interaction: NS
Bay BY[b]		
	Depth $\Delta\sigma_{t\ max}$	
Trib SL[a]	Station $F_{3,21} = 14.120$	**Station: <0.001**
Trib BC[a]	D vs. N $F_{1,21} = 1.323$	D vs. N: NS
Bay JI[b]	Interaction $F_{3,21} = 1.435$	Interaction: NS
Bay BY[b]		
	DO_{min}	
Trib SL[a]	Station $F_{3,21} = 14.120$	**Station: <0.001**
Trib BC[a]	D vs. N $F_{1,21} = 1.323$	D vs. N: NS
Bay JI[b]	Interaction $F_{3,21} = 1.435$	Interaction: NS
Bay BY[b]		
	MWD_{cten}	
Trib SL[a]	Station $F_{3,21} = 7.774$	**Station: 0.003**
Trib BC[ab]	D vs. N $F_{1,21} = 1.096$	**D vs. N: 0.038**
Bay JI[b]	Interaction $F_{3,21} = 3.305$	Interaction: NS
Bay BY[b]		
	MWD_{cope}	
Trib SL[a]	Station $F_{3,21} = 12.415$	**Station: <0.001**
Trib BC[a]	D vs. N $F_{1,21} = 2.032$	D vs. N: NS
Bay JI[b]	Interaction $F_{3,21} = 0.957$	Interaction: NS
Bay BY[b]		
	PSI of copepods and ctenophores	
Trib SL	Station $F_{3,21} = 0.104$	Station: NS
Trib BC	D vs. N $F_{1,21} = 1.652$	D vs. N: NS
Bay JI	Interaction $F_{3,21} = 0.522$	Interaction: NS
Bay BY		

minima (DO_{min}) were ≥3.3 mg l^{-1} in the tributary, but ≤0.04 mg l^{-1} in the bay. Thus, depth distributions of physical variables were very different in the tributary than in the bay.

We found no significant day–night differences among physical indices (Table 2); therefore, daytime and nighttime samples were considered together in subsequent analyses. Averaged profiles illustrate the general differences between the tributary and bay water columns and the small variations among stations and dates, especially in the bay (Fig. 3).

Stratification and DO differed significantly among sampling dates (Table 3). Stratification was weaker in June than in July in the tributary. Increased wind and waves in July 2001 caused weaker stratification in the bay than on other dates. Depths of $\Delta\sigma_{t\ max}$ did not differ significantly among dates in either the tributary or in the bay. DO_{min} was significantly higher in June than in July in the tributary, but was ~0 mg l^{-1} on all sampling dates in the bay.

Physical indices were interrelated (Table 4). Because $\Delta\sigma_t$ was calculated from T and S, correlations of $\Delta\sigma_{t\ max}$ with T_{MWD} and S_{MWD} were expected. The depths of $\Delta\sigma_{t\ max}$ were strongly correlated with DO_{min} (Fig. 4). Because DO_{min} in the bay always was ~0 mg l^{-1}, correlations of other indices with DO_{min} were not meaningful there. Correlation between depth $\Delta\sigma_{t\ max}$ and DO_{min} was not significant in the tributary. Because the T_{MWD} and S_{MWD} of ctenophores and copepods were nearly perfectly correlated (R values >0.99), comparisons of T_{MWD} and S_{MWD} against other indices are shown only for copepods (Table 4).

Vertical distributions of ctenophores, medusae, and copepods relative to physical variables

The depth distributions of *Mnemiopsis leidyi* ctenophores and *Acartia tonsa* copepods differed greatly between the tributary and the bay (Figs. 2, 5, 6, Table 2). In the tributary, ctenophores and copepods occurred throughout the water column, but most were in or below the strongest stratification of the pycnocline (~5 m; Fig. 5). DO concentrations were ≥2 mg l^{-1} and not sufficiently low to exclude ctenophores, medusae, or copepods from tributary bottom waters during our study. By contrast, in the bay, ctenophores and copepods were always shallower than the depth $\Delta\sigma_{t\ max}$ (~10 m); below that depth, the water was virtually anoxic (Fig. 6).

Ctenophores and copepods were most closely associated with the strong pycnocline in the bay in daytime (Fig. 7). The distances between depths of maximum density changes of ctenophores and copepods (depth Δcteno $m^{-3}{}_{max}$ and depth Δcope $l^{-1}{}_{max}$, respectively) and the depths of maximum stratification (depth $\Delta\sigma_{t\ max}$) differed significantly between the weakly stratified tributary and the strongly stratified bay and between day and night (ctenophores $F_{3,17} = 13.024$, $p < 0.001$; copepods $H_3 = 10.877$, $p = 0.012$). In the bay, both ctenophores and copepods were closely associated with $\Delta\sigma_{t\ max}$ in the day (0.3 ± 0.2 m and 0.7 ± 1.4 m distance, respectively), but they moved towards the surface and farther from depth $\Delta\sigma_{t\ max}$ at

Table 3. One-way ANOVA comparisons among dates for the tributary (Trib) stations and the mainstem Chesapeake Bay (Bay) for vertical distributions of physical variables, ctenophores *Mnemiopsis leidyi*, and copepods *Acartia tonsa* in 1999 to 2001. Indices tested were the maximum change in stratification ($\Delta\sigma_{t\,max}$), depth (m) of $\Delta\sigma_{t\,max}$, lowest dissolved oxygen concentration (DO_{min}, mg l^{-1}), mean weighted depths (m) of ctenophores (MWD_{cten}) and copepods (MWD_{cope}), and the percent similarity index (PSI) of ctenophore and copepod densities. Different superscripts indicate statistically different pairwise comparison groups (Dunn's Method). Data are presented as means (SE); **bold** text indicates significance ($p \leq 0.05$). Numbers of profiles for each test are given in Table 1

Station	Date & index			ANOVA results Test statistic	p
Trib	June 1999	July 1999	July 2001		
Bay	July 2000	August 2000	July 2001		
		Mean $\Delta\sigma_{t\,max}$ (SE)			
Trib	0.060 (0.008)^{a}	0.357 (0.104)^{b}	0.415 (0.067)^{b}	$F_{2,10} = 5.165$	**0.036**
Bay	2.551 (0.392)^{a}	1.434 (0.261)^{ab}	0.793^{b}	$F_{2,9} = 5.157$	**0.032**
		Mean depth $\Delta\sigma_{t\,max}$ (SE)			
Trib	4.3 (0.9)	5.8 (0.8)	6.2 (1.5)	$F_{2,10} = 0.653$	0.546
Bay	9.5 (0.4)	11.1 (0.5)	10.2	$F_{2,9} = 3.484$	0.089
		Mean DO_{min} (SE)			
Trib	5.5 (0.1)^{a}	2.1 (0.8)^{b}	2.4 (0.2)^{b}	$F_{2,11} = 138.57$	**<0.001**
Bay	0.01 (0)	0.01 (0)	0.05	$H_2 = 4.0$	0.651
		Mean MWD_{cten} (SE)			
Trib	8.5 (1.5)	8.1 (0.8)	9.7 (1.6)	$F_{2,11} = 0.340$	0.721
Bay	5.3 (0.9)	5.3 (0.4)	8.1	$F_{2,9} = 3.234$	0.101
		Mean MWD_{cope} (SE)			
Trib	11.7 (0.5)^{a}	9.3 (0.8)^{b}	8.6 (0.8)^{b}	$F_{2,11} = 4.624$	**0.042**
Bay	5.0 (0.7)	5.7 (0.4)	7.5	$F_{2,9} = 3.445$	0.091
		Mean PSI of copepods and ctenophores (SE)			
Trib	0.658 (0.070)	0.793 (0.043)	0.639 (0.072)	$F_{2,11} = 2.031$	0.187
Bay	0.651 (0.074)	0.790 (0.016)	0.599	$F_{2,9} = 2.440$	0.157

night (3.2 ± 1.4 and 2.5 ± 0.5 m, respectively). In the tributary, depth $\Delta cteno\ m^{-3}{}_{max}$ was farther (3.6 ± 0.5 m) from depth $\Delta\sigma_{t\,max}$ in the day when the animals were deeper than at night (1.7 ± 0.8 m); however, depth $\Delta cope\ l^{-1}{}_{max}$ was closer to depth $\Delta\sigma_{t\,max}$ in the day (0.8 ± 2.2 m) than at night (2.8 ± 1.4 m). It was not possible to pinpoint the precise positions of the animals in the stratification, which changed continuously in a gradient.

The MWD of both ctenophores and copepods were correlated positively with DO_{min} in tributary and bay stations combined (Fig. 8a, Table 4). Because DO_{min}, depth $\Delta\sigma_{t\,max}$, T_{MWD}, and S_{MWD} were interrelated, it was not possible to conclude which of these variables influenced ctenophore or copepod vertical distributions; however, near-anoxic water excluded them from subpycnocline waters in the bay. We compared T, S, and DO at ctenophore and copepod MWDs at all stations. Differences were not significant for MWD_{cten} versus MWD_{cope} for any variable: T (25.7 ± 0.4°C versus 25.7 ± 0.3°C; W = 17.0, p = 0.52), S (13.6 ± 0.4 versus 13.5 ± 0.4; W = 17.0, p = 0.4), DO (4.7 ± 0.3 mg l^{-1} versus 4.7 ± 0.3 mg l^{-1}; W = 19.0; p = 0.60). Therefore, ctenophores and their copepod prey resided in the same physical conditions in the tributary and the bay, as also indicated by the near-perfect correlations of their T_{MWD} and S_{MWD} (Table 4).

Ctenophores occurred at similar depths as copepods in the tributary and in the bay (Figs. 2, 5, 6). Even though ctenophore and copepod MWD differed significantly between the tributary (≥6.4 m) and the bay (≤7.0 m; Table 2), MWD_{cten} and MWD_{cope} were strongly correlated in tributary and bay stations combined (Fig. 9, Table 4). Ctenophore and copepod distributions were somewhat shallower at night than in the day (Figs. 2 & 7), but day–night differences in the MWD were significant only for ctenophores (Table 2). MWD_{cten} did not differ significantly among dates in the tributary or in the bay (Table 3). MWD_{cope} were deepest in the tributary in June when stratification was weakest and bottom-water DO was

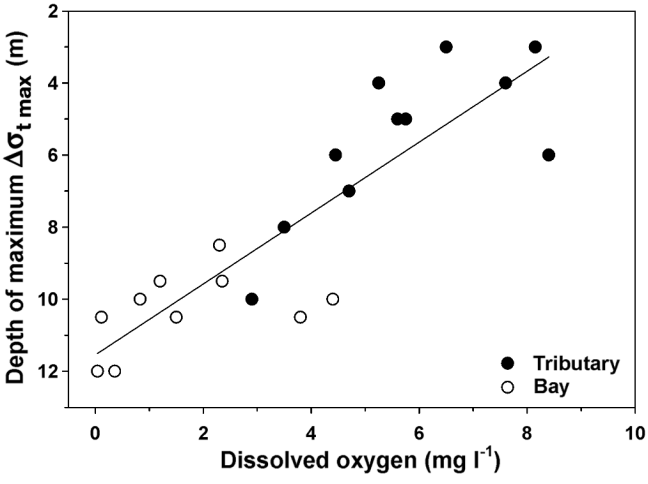

Fig. 4. Correlation between depth of maximum stratification ($\Delta\sigma_{t\,max}$) and dissolved oxygen (DO) concentrations in 2 tributary and 2 mainstem Chesapeake Bay stations, showing the greater pycnocline depth and lower DO in the bay

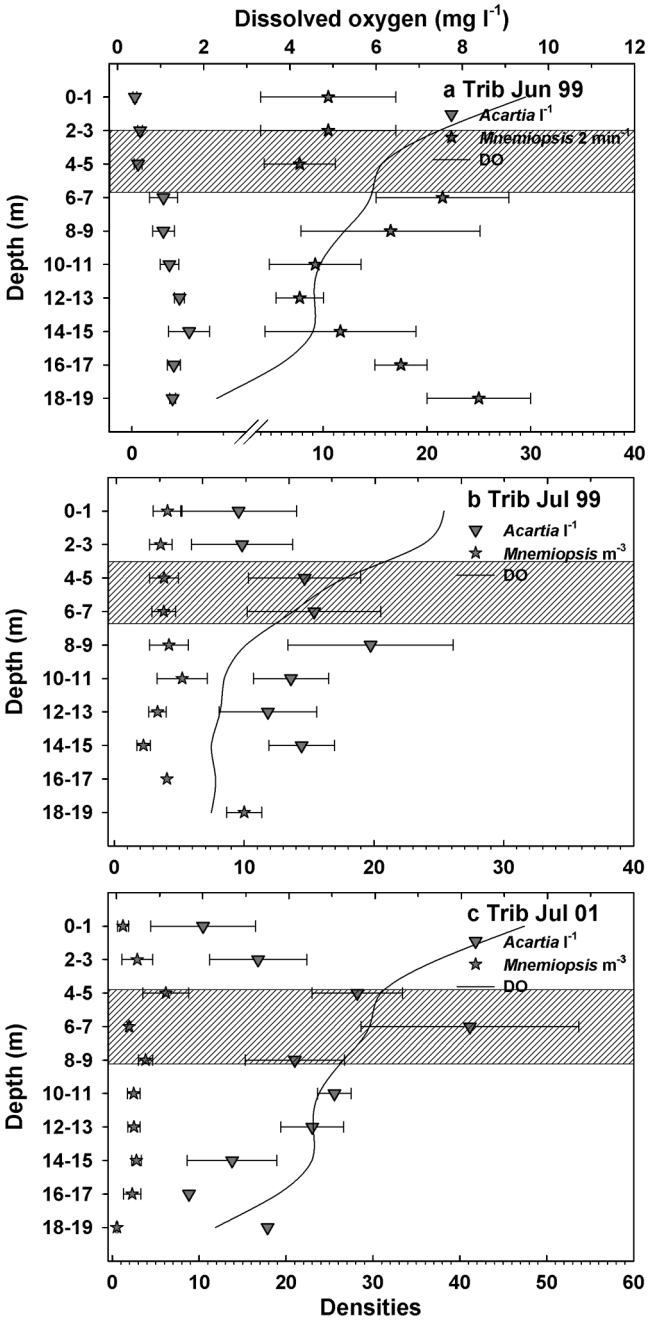

Fig. 5. *Mnemiopsis leidyi* and *Acartia tonsa*. Vertical distributions of ctenophores and copepods in day and night sampling at 2 stations in St. Leonard Creek tributary (Trib) of Chesapeake Bay. Symbols show means ± SE of 4 profiles each in (a) June 1999, (b) July 1999, and (c) July 2001. Note that abundances of *M. leidyi* in (a) are numbers per 2 min video recording. The mean vertical profiles of dissolved oxygen (DO) are also shown. Shading marks the approximate depths of strongest stratification ($\Delta\sigma_t$)

highest. The overlaps of ctenophore and copepod populations (PSIs) also did not differ significantly among stations or dates (Fig. 8b, Tables 2 & 3). PSIs were not significantly correlated with any physical index, including DO_{min} (Table 4). PSIs were slightly higher at night (73.7 ± 4.7%) than in the day (65.6 ± 4.3%), but the difference was not significant (Table 2).

Table 4. Pearson's correlations comparing the depth distributions of physical and biological indices at 4 stations in Chesapeake Bay (2 each in a tributary and in the mainstem bay): depth of maximum change in stratification (depth $\Delta\sigma_{t\,max}$, m), lowest dissolved oxygen concentration (DO_{min}, mg l^{-1}), mean weighted depths (m) of *Mnemiopsis leidyi* ctenophores (MWD_{cten}) and *Acartia tonsa* copepods (MWD_{cope}), temperature (T_{MWD}) and salinity (S_{MWD}) of copepods and ctenophores, and percent similarity index of copepod and ctenophore densities (PSI). **Bold** text indicates significance ($p \leq 0.05$). For each test, n = 21–22 profiles

Pair of indices	Pearson's correlation R	p
Physical		
Depth $\Delta\sigma_{t\,max}$ vs. DO_{min}	**–0.787**	**2.4×10^{-5}**
$T_{MWDcten}$ vs. $T_{MWDcope}$	**0.997**	**1.6×10^{-22}**
$S_{MWDcten}$ vs. $S_{MWDcope}$	**0.995**	**2.4×10^{-20}**
Depth $\Delta\sigma_{t\,max}$ vs. $T_{MWDcope}$	–0.037	0.878
$S_{MWDcope}$ vs. $T_{MWDcope}$	0.423	0.056
Depth $\Delta\sigma_{t\,max}$ vs. $S_{MWDcope}$	–0.436	0.055
DO_{min} vs. $T_{MWDcope}$	**–0.506**	**0.019**
DO_{min} vs. $S_{MWDcope}$	0.251	0.273
Physical against biological		
Depth $\Delta\sigma_{t\,max}$ vs. MWD_{cope}	**–0.619**	**0.003**
Depth $\Delta\sigma_{t\,max}$ vs. MWD_{cten}	–0.204	0.376
Depth $\Delta\sigma_{t\,max}$ vs. PSI	0.060	0.796
DO_{min} vs. MWD_{cope}	**0.829**	**1.8×10^{-6}**
DO_{min} vs. MWD_{cten}	0.419	0.052
DO_{min} vs. PSI	–0.0864	0.702
T_{MWD} vs. MWD_{cope}	–0.411	0.064
T_{MWD} vs. PSI	0.211	0.359
S_{MWD} vs. MWD_{cope}	**0.539**	**0.012**
$S_{MWDcope}$ vs. PSI	–0.015	0.948
Biological		
MWD_{cope} vs. MWD_{cten}	**0.683**	**4.6×10^{-4}**
PSI vs. MWD_{cope}	–0.077	0.732
PSI vs. MWD_{cten}	–0.343	0.118

Chrysaora quinquecirrha medusae were not abundant during our study. Too few were seen to permit statistical analysis of their fine-scale vertical distributions relative to copepods or ctenophores on any date (video: totals of 23 in the tributary and 0 in the bay, Tucker trawls: totals of 12 in the tributary and 2 in the bay). Video profiles showed that medusae co-occurred with ctenophores throughout the water column in the tributary, even when bottom DO was ~2 mg l^{-1} (Fig. 2). Daytime video recordings in July 1999 in both tributary stations showed that medusa MWDs (15.6 and 11.0 m) were deeper than the corre-

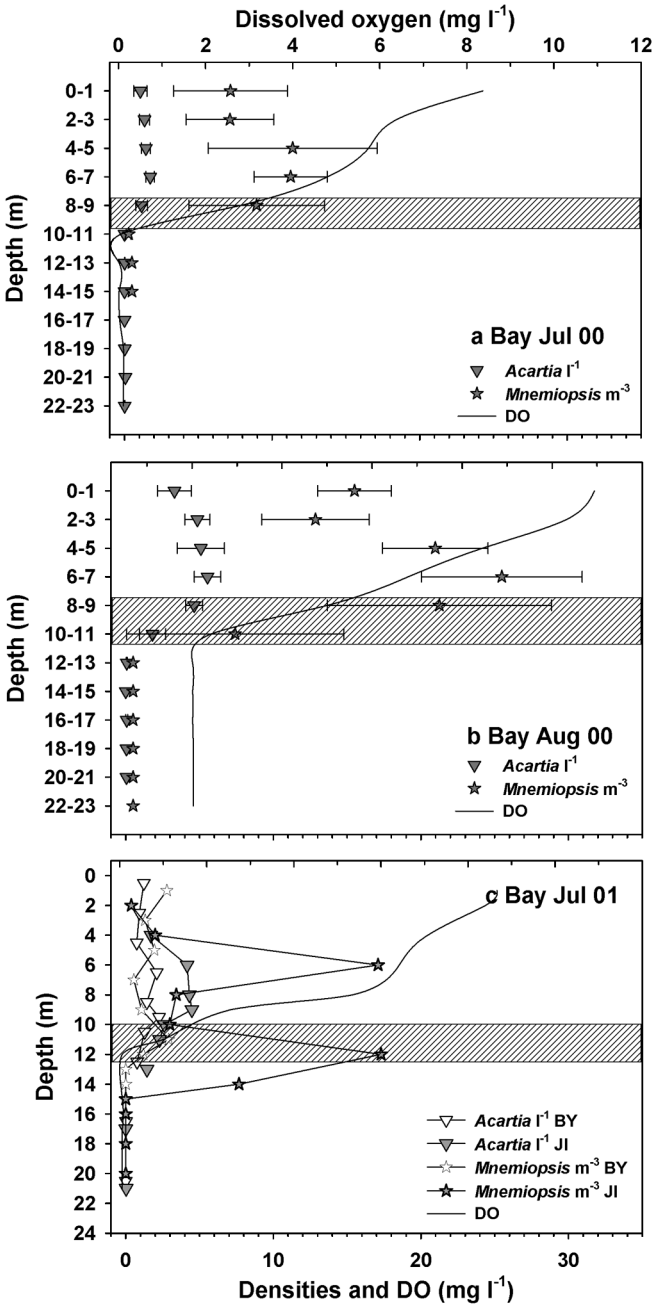

Fig. 6. *Mnemiopsis leidyi* and *Acartia tonsa*. Vertical distributions of ctenophores and copepods in day and night sampling at 2 stations in the mainstem Chesapeake Bay (Bay). Symbols show means ± SE of 4 profiles each in (a) July 2000 and (b) August 2000. (c) The 2 profiles in July 2001 could not be averaged; therefore, points were connected by lines to show individual profiles. BY: Buoy, JI: James Island. The mean vertical profiles of dissolved oxygen (DO) are also shown. Shading marks the approximate depths of strongest stratification ($\Delta\sigma_t$)

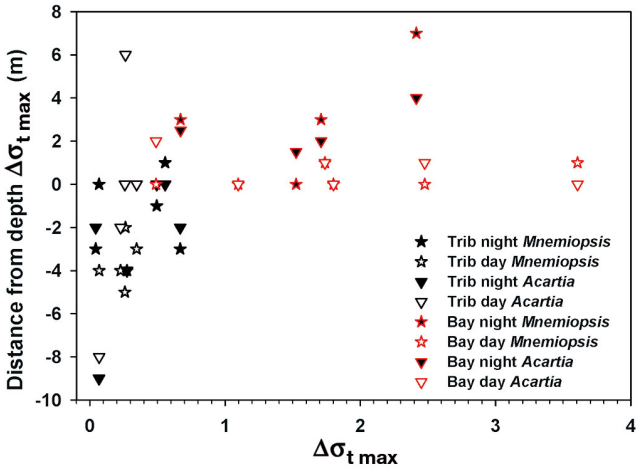

Fig. 7. *Mnemiopsis leidyi* and *Acartia tonsa*. Distances between the depths of maximum density changes of ctenophores (Δcteno m^{-3}_{max}) and copepods (Δcope l^{-1}_{max}) and the depth of maximum stratification (depth $\Delta\sigma_{t\ max}$) versus the strength of stratification ($\Delta\sigma_{t\ max}$, kg m^{-3}) in day and night sampling. Animals were closer to the depth $\Delta\sigma_{t\ max}$ in the strongly stratified bay. Each point represents one vertical profile; the numbers of profiles are given in Table 1. Symbols filled with black are during night; symbols with red are at bay stations

sponding MWD_{cope} (10.6 and 8.0 m) and MWD_{cten} (8.9 and 7.0 m); however, in July 2001, medusa MWDs were similar to those of copepods and ctenophores (~8 m). Therefore, our data for medusae were insufficient to gain insight into their possible effect on ctenophore vertical distribution.

Vertical distributions of ctenophore feeding

Ctenophores were collected by SCUBA divers at 3 depth strata in the tributary and near the surface and above the anoxic subpycnocline in the bay. Although 2 divers searched for ctenophores for 10 min on each dive in the anoxic subpycnocline water in the bay, none were found. Overall, *Acartia tonsa* copepodites and adults ('copepods') averaged 40% of the prey in ctenophore gut contents, copepod nauplii (probably *A. tonsa*) 37%, *Oithona colcarva* 6.7%, polychaete larvae 12.3%, and bivalve veligers 3.6%. In the available plankton overall, copepod nauplii (probably *A. tonsa*) averaged 65.1%, *A. tonsa* 16.3%, *O. colcarva* 1.8%, and polychaete larvae 9.7%; taxa not seen in ctenophore gut contents included *Eurytemora affinis* 2.5%, barnacle nauplii 3.4%, and gastropod veligers 2.0%. We focused on *A. tonsa* copepods, the predominant prey type and mesozooplankter available.

All comparisons of ctenophore feeding differed significantly between the tributary and the bay (Table 5). On average in the tributary, ctenophores contained more copepods (7.9) than in the bay (1.6), ctenophores were larger (21.5 versus 9.5 ml), and copepod

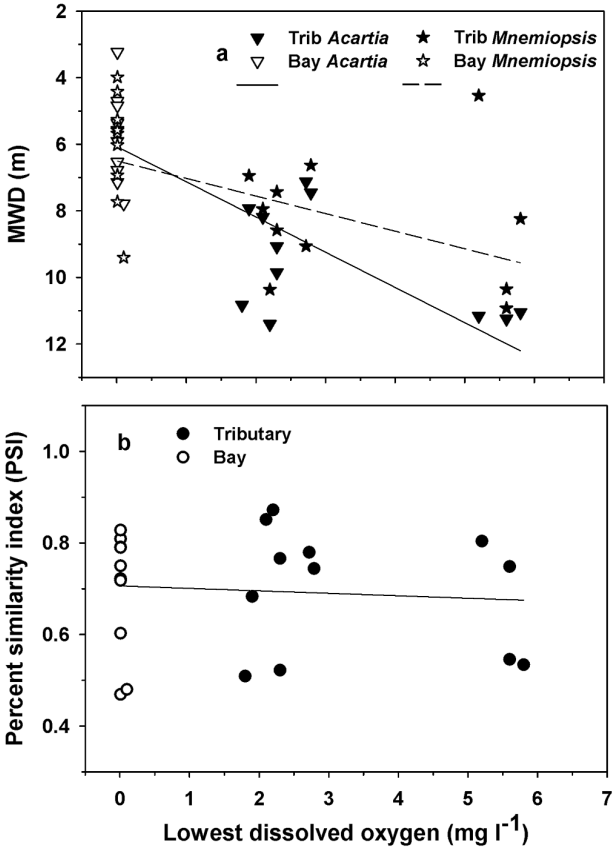

Fig. 8. *Mnemiopsis leidyi* and *Acartia tonsa.* (a) Correlations of ctenophore and copepod mean weighted depths (MWDs) in the mainstem Chesapeake Bay and in the tributary against dissolved oxygen (DO) concentrations; (b) ctenophore and copepod depth overlaps (percent similarity index, PSI) did not differ by location or with DO during day and night sampling. Each point represents 1 vertical profile at each of 2 tributary stations and 2 bay stations; the numbers of profiles are given in Table 1. The lines show the linear correlations

densities were higher (11.6 versus 2.3 l^{-1}). Both greater ctenophore size and prey density would contribute to more prey in the gut contents in the tributary than in the bay. Nevertheless, feeding standardized to ctenophore volume remained greater in the tributary than in the bay (0.5 versus 0.2 copepods ml^{-1} ctenophore), which indicated the importance of higher prey density in the tributary.

In the tributary, ctenophores in the bottom layer contained more copepods relative to the other layers; however, the difference was not significant when feeding was standardized to ctenophore volume (Table 5). Ctenophore sizes were consistent among the 3 depths, but copepod densities were higher in the pycnocline and bottom layers than in the surface layer. In the bay, although more copepods were in the ctenophore guts and in the water

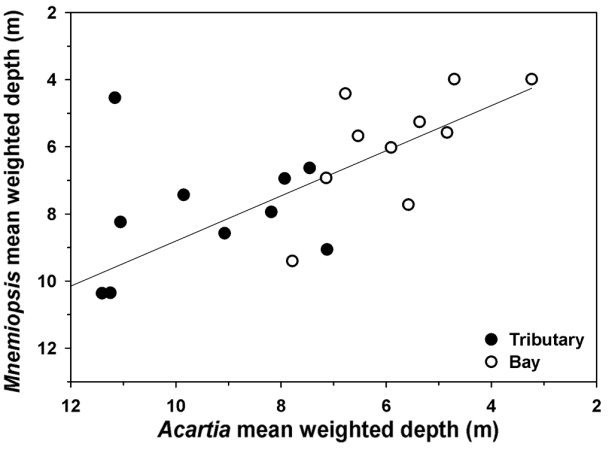

Fig. 9. *Mnemiopsis leidyi* and *Acartia tonsa.* Mean weighted depths (MWDs) of ctenophores were correlated with the MWDs of copepods during day and night sampling at 2 tributary stations and at 2 stations in the mainstem Chesapeake Bay. Each symbol represents one vertical profile; the numbers of profiles are given in Table 1

of the pycnocline, the differences between depths were not significant.

We calculated ctenophore predation effects from ctenophore sizes and densities and copepod densities and at each depth for each date and station (Figs. 10 & 11). The depth distributions of ctenophore predation effects mirrored ctenophore densities, with maxima near the pycnocline. The maximum predation effects on copepods were in or below the pycnocline in the tributary and in or above it in the bay.

We also averaged ctenophore predation effects for the oxic water column, to 15–17 m maximum depth in the tributary and to 8–14 m in the bay (Table 6). The average proportions of the water column cleared of prey were 13.6 to 25% d^{-1} in the tributary and 16.7 to 33% d^{-1} the bay on sampling days in July. The average predation effect during sampling in August was substantially greater in the bay (63%). Thus, ctenophores showed very high predation potentials for copepods during the summers in Chesapeake Bay.

DISCUSSION

Vertical distributions of ctenophores, medusae, and copepods relative to physical variables

Concentrations of *Mnemiopsis leidyi* ctenophores and *Acartia tonsa* copepods were most dramatic near the sharp pycnocline in the mainstem Chesapeake Bay stations and less defined, but still apparent, in the weakly stratified tributary stations. Because strat-

Table 5. *Acartia tonsa* and *Mnemiopsis leidyi.* Copepods in the gut contents of ctenophores at 3 depth layers (surface, pycnocline, bottom) at stations in Chesapeake Bay. No ctenophores or copepods were present in the anoxic bottom layer in the mainstem bay (NP = not present). Data are presented as mean (±SE) number of copepods per ctenophore and standardized to ctenophore volume (ml). The numbers of ctenophores collected appear in *italics* after (SE). The mean densities of copepods at each depth also are given; **bold** text indicates significance ($p \leq 0.05$). H = Kruskal-Wallis 1-way ANOVA on ranks; U = Mann-Whitney rank sum test. Comparisons were for 4 profiles in the tributary (Trib) and 6 in the Bay, as in Table 1. Superscripts indicate different pairwise multiple comparison groups

Location	Depth layer & variable				Test statistic	p
	Overall	Surface	Pycnocline	Bottom		
			Mean copepods ctenophore^{-1} (SE)			
Trib	7.9 (1.0) *56*	7.8 (1.7)^{a} *28*	5.4 (1.6)^{a} *18*	10.0 (1.2)^{b} *13*	$H_2 = 6.527$	**0.038**
Bay	1.6 (0.5) *64*	0.7 (0.3) *33*	2.4 (1.0) *31*	NP	$U = 446.0$	0.315
Trib vs. Bay					$U = 499.0$	**<0.001**
			Mean copepods ml^{-1} ctenophore (SE)			
Trib	0.5 (0.1) *52*	0.5 (0.2) *23*	0.4 (0.1) *17*	0.6 (0.1) *12*	$H_2 = 4.279$	0.118
Bay	0.2 (0.1) *60*	0.1 (0.04) *31*	0.4 (0.2) *29*	NP	$U = 395.0$	0.361
Trib vs. Bay					$U = 647.5$	**<0.001**
			Mean ctenophore volume (SE)			
Trib	21.5 (1.6)	21.1 (2.4)	22.3 (2.7)	21.8 (3.5)	$F_{2,52} = 0.056$	0.945
Bay	9.5 (0.8)	10.4 (1.1)	8.6 (1.1)	NP	$U = 557.5$	0.110
Trib vs. Bay					$U = 509.0$	**<0.001**
			Mean copepods l^{-1} (SE)			
Trib	11.6 (2.0)	4.1 (1.2)^{a}	11.9 (1.7)^{ab}	14.7 (3.7)^{b}	$F_{2,12} = 5.042$	**0.026**
Bay	2.3 (0.6)	1.9 (0.6)	2.8 (0.6)	~0	$t_7 = -1.075$	0.318
Trib vs. Bay					$t_8 = 4.442$	**<0.002**

ification, temperature (T), and salinity (S) were interrelated, it was not possible to distinguish which determined the vertical distributions of copepods and ctenophores. Because *M. leidyi* and *A. tonsa* are eurythermal and euryhaline, however, their distributions were unlikely to have been restricted by the moderate temperatures or salinities in our study. By contrast, low DO is well known to negatively affect the health, behavior, and vertical distributions of fish, zooplankton, ctenophores, and medusae (e.g. Keister et al. 2000, Breitburg et al. 2003, 2009, Grove & Breitburg 2005, Kolesar et al. 2010), and clearly excluded the animals from subpycnocline waters in the mainstem bay (Figs. 2b & 6). In the tributary, *M. leidyi* and *A. tonsa* were not restricted from bottom waters where DO ~2 mg l^{-1}, in agreement with previous research (Keister et al. 2000, Purcell et al. 2001a), and *M. leidyi* feeding remained high throughout the water column. Because concentrated ctenophores, copepods, and feeding existed in the tributary in the absence of hypoxia, we conclude that their depth distributions must have been in response to physical or biological factors related to stratification.

Because gelatinous zooplankton are known to concentrate at clines (e.g. Graham et al. 2001, Jacobsen & Norrbin 2009), the possible importance of density discontinuities and stratification per se must be considered. Both Arai (1992) and Frost et al. (2010) concluded that hydromedusae behaviorally aggregate at salinity discontinuities. *Aurelia* sp. medusae swam horizontally along regions of shear associated with vertical density gradients (Rakow & Graham 2006). Both a velocity gradient and phytoplankton exudates led *Acartia tonsa* copepods to spend increased time in the discontinuities (Woodson et al. 2007). Thus, gelatinous predators and their prey actively aggregate at density discontinuities, at least partly in response to the shear velocity gradients, and from enhanced feeding where their foods are concentrated.

The patterns of copepod and ctenophore vertical distributions in the Patuxent tributary observed in our study, which used fine-scale (1–2 m) depth intervals, matched well with previous coarse-scale results (3 depth layers; Keister et al. 2000, Breitburg et al. 2003, Kolesar et al. 2010). Breitburg et al. (2003) reported that *Mnemiopsis leidyi* was mostly in the bottom layer until bottom DO dropped below 1 mg l^{-1} when they then occurred only in the surface and pycnocline layers; bay anchovy and naked goby larvae, copepods, and medusae gradually increased in the bottom layer with increasing bottom DO, with no

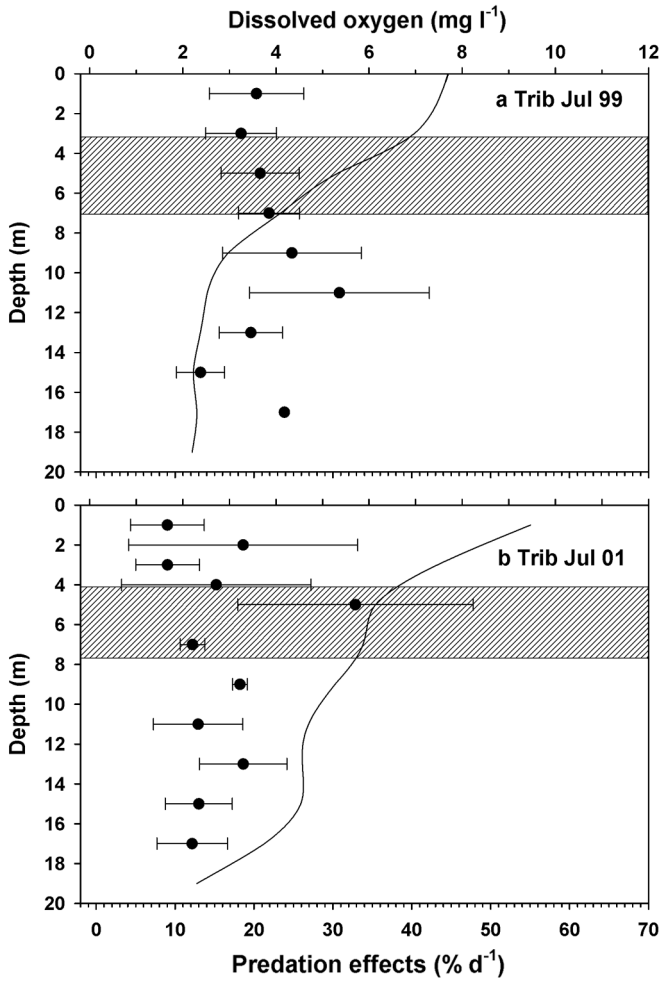

Fig. 10. *Mnemiopsis leidyi* and *Acartia tonsa.* Vertical distributions of predation effects (% d^{-1}) of ctenophores feeding on copepods in day and night sampling at 2 stations in St. Leonard Creek tributary of Chesapeake Bay. Symbols show means ± SE of 4 vertical profiles each in (a) July 1999 and (b) July 2001. The mean vertical profiles of dissolved oxygen (DO) are also shown. Shading marks the approximate depths of strongest stratification ($\Delta\sigma_t$)

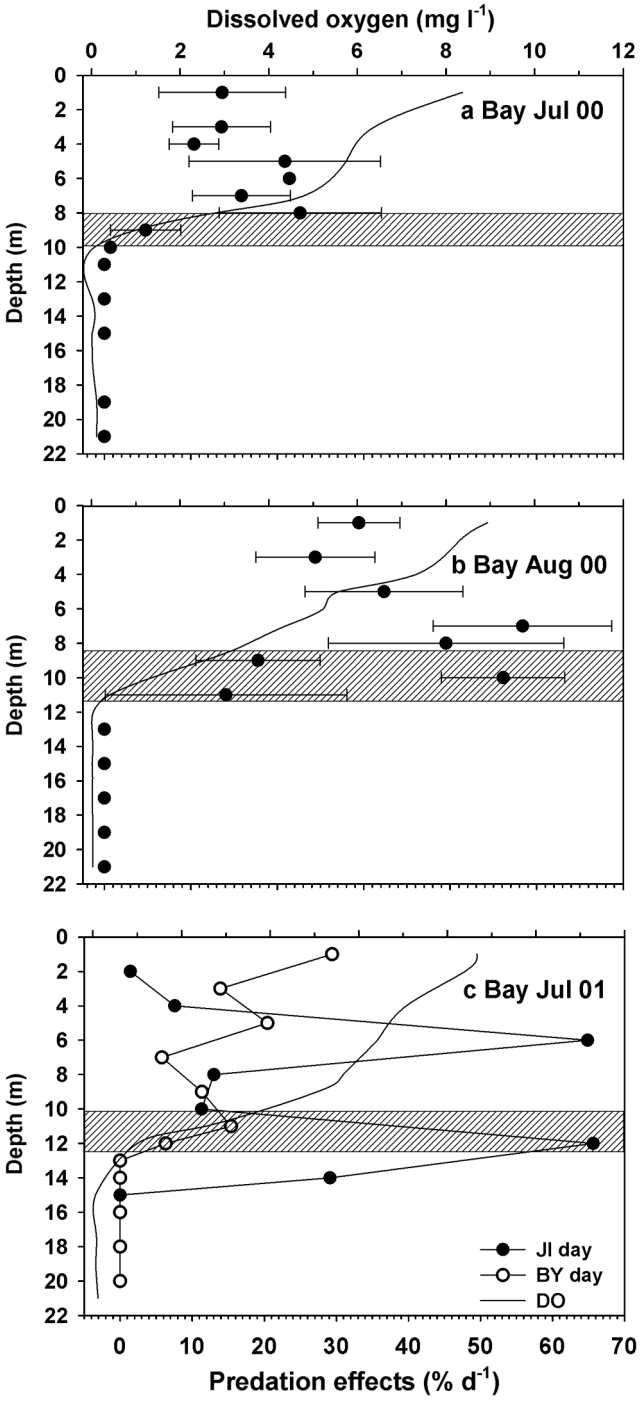

Fig. 11. *Mnemiopsis leidyi* and *Acartia tonsa.* Vertical distributions of predation effects (% d^{-1}) of ctenophores feeding on copepods in day and night sampling at 2 stations in the mainstem Chesapeake Bay. Symbols show means ± SE of 4 vertical profiles each in (a) July 2000 and (b) August 2000. (c) The 2 profiles in July 2001 could not be averaged; therefore, points were connected by lines to show individual profiles. The mean vertical profiles of dissolved oxygen (DO) are also shown. Shading marks the approximate depths of strongest stratification ($\Delta\sigma_t$)

avoidance of DO ≥3.0 mg l^{-1}. Ctenophores utilized the bottom layer waters of DO 1–2 mg l^{-1}, but most other species did not. Breitburg et al. (2003) concluded that the strongest factors contributing to the observed vertical distributions in the Patuxent River tributary were active behaviors and depth-specific predation, but not mortality due to direct exposure to hypoxia (except for fish eggs). The mean vertical overlap (PSI) of ctenophores and copepods sampled with Tucker trawls during 1992 to 1993 and 1999 to 2001 at tributary stations (SL and BC; 70%; n = 30; Kolesar et al. 2010) was virtually identical to our fine-scale estimates in 2000 to 2001 (69.6 ± 3.9; n = 12). The tributary sampling in 1999 to 2001 included only

Table 6. *Mnemiopsis leidyi* and *Acartia tonsa.* Mean volumes of individual ctenophores in Tucker trawls on different dates in the tributary (Trib) and mainstem Chesapeake Bay (Bay), ctenophore densities from video profiles, and copepod densities from plankton pump samples used to calculate the mean water column clearance of copepods by ctenophores. Water column depth = 15–17 m in the tributary and 8–14 m oxic depth in the bay. MWD: mean weighted depth. *H* = Kruskal-Wallis 1-way ANOVA on ranks. ND: no data. **Bold** text indicates significance ($p \leq 0.05$). The numbers of profiles for each test are given in Table 1. Superscripts indicate different pairwise multiple comparison groups

Station	Date & variable			Test statistic	p
Trib	June 1999	July 1999	July 2001		
Bay	July 2000	Aug 2000	July 2001		
	Mean ctenophore volume (ml) (SE)				
Trib	ND	26.4 (1.3)	17.3 (3.7)	$U = 720.0$	**<0.001**
Bay	12.3 (0.9)^a	7.3 (1.2)^b	13.7 (2.4)^a	$H_2 = 19.32$	**<0.001**
Trib vs. Bay				$U = 4581.0$	**<0.001**
	Mean ctenophores m^{-3} (SE)				
Trib	ND	3.6 (0.4)	2.6 (0.4)	$U = 380.080$	**0.005**
Bay	9.3 (1.2)^a	20.0 (1.8)^b	5.0 (1.8) ^{a}	$H_2 = 35.33$	**<0.001**
Trib vs. Bay				$U = 4581.0$	**<0.001**
	Mean copepods l^{-1} (SE)				
Trib	ND	12.0 (1.1)	21.3 (2.3)	$U = 993.5$	**<0.001**
Bay	1.3 (0.3)^a	4.5 (0.4)^b	2.1 (0.4)^a	$H_2 = 37.59$	**<0.001**
Trib vs. Bay				$U = 4712.0$	**<0.001**
	Mean water column predation effect (% d^{-1})				
Trib	ND	24.8 (2.3)	13.6 (4.4)	$t_6 = 2.266$	0.064
Bay	33.0 (5.5)^a	63.1 (10.4)^a	16.7 (7.4)^b	$F_{2,9} = 6.698$	**0.024**
Trib vs. Bay				$t_{16} = -2.517$	**0.023**
	Mean $MWD_{predation}$ (SE)				
Trib	ND	8.1 (0.8)	9.7 (1.6)	$t_6 = -0.819$	0.444
Bay	5.3 (0.9)	5.3 (0.4)	8.1	$F_{2,9} = 3.234$	0.101
Trib vs. Bay				$t_{17} = -2.276$	**0.036**

one incidence of bottom DO between 1 and 2 mg l^{-1}; therefore, we could not evaluate the effects of hypoxia on animal vertical distributions there.

Vertical migrations of ctenophores and copepods were apparent from greater distances of the populations towards the surface (positive) from the strongest stratification in both the tributary and the bay (Fig. 7), even though the day–night differences in MWD were not statistically significant (Table 2). Both species are known to migrate towards the surface at night in Chesapeake Bay (Roman et al. 1993, Keister et al. 2000, Kolesar et al. 2010). *Acartia tonsa* migrated further than *Mnemiopsis leidyi*, which resulted in somewhat reduced overlap (PSI) in their vertical distributions at night.

The vertical distribution of *Mnemiopsis leidyi* in other environments is also related to the vertical water column structure. Similar to our results, ctenophores were seen mostly within (3–6 m depth) or at the bottom of the pycnocline in a 7 to 13 m water column in the Gulf of Mexico where bottom layer DO was ~1 mg l^{-1} (Purcell et al. 2001a). When surface wind shear was >4.0 s^{-1}, ctenophore biomass was low above the thermocline at 20 to 30 m depth on the Patagonian shelf, Argentina, where hypoxia was not present (Mianzan et al. 2010). In 5 m deep water, they were concentrated near the bottom during the daytime (Costello & Mianzan 2003). In the Black Sea, *M. leidyi* was collected only above the steep thermocline at 20 to 30 m in summer; importantly, the oxycline was much deeper (50–100 m; Mutlu 1999), suggesting that low oxygen did not determine the ctenophore depth distribution there. In the central Baltic Sea, peak densities of *M. leidyi* were at 62.5 to 72.5 m, below the pycnocline at ~55 m during the day (Schaber et al. 2011); ctenophores may have avoided the cold waters (≤5°C) above the pycnocline, because DO (~2–6 ml l^{-1}) and salinities above (~8) and below (~16) the pycnocline should not have restricted them. Thus, various factors may affect the vertical distribution of *M. leidyi*.

Relationships of prey and predators with ctenophore vertical distributions

The MWD_{cope} and MWD_{cten} were strongly correlated ($p = 4.5 \times 10^{-4}$), and it is tempting to suggest that the ctenophores were tracking their prey. Some evidence suggests that medusae can sense concentrated food in the laboratory (Arai 1991), and the presence of prey doubles swimming speed to 1.5 cm s^{-1} and increases turning in *Chrysaora quinquecirrha* (Matanoski et al. 2001), which would concentrate the medusae where prey are abundant. Although the foraging speed of *Mnemiopsis leidyi* (0.6 cm s^{-1}) was reported by Kreps et al. (1997), their foraging patterns *in situ* are, to our knowledge, unknown. We believe it is likely that both sensitivity to physical gradients in the water column and behavioral responses to prey presence or capture contribute to their aggregations near the pycnocline.

Predators could also affect the vertical distribution of ctenophores and copepods. The ability of *Mnemiopsis leidyi* to sense the presence of a predator (*Beroe ovata*) was suggested by their lower position in a shallow (25 cm) aquarium (Titelman et al. 2012). Although *Chrysaora quinquecirrha* medusae were not abundant in our study (≤0.01 m^{-3}), they were of potential interest because they are known to affect the dynamics of *M. leidyi* ctenophores and copepods (e.g. Purcell & Decker 2005). Some studies suggest that *C. quinquecirrha* at densities ≥0.1 medusae m^{-3} may reduce *M. leidyi* populations in tributaries of Chesapeake Bay (Purcell & Cowan 1995, Breitburg & Fulford 2006). Medusae did not appear to reduce ctenophores in the mainstem mesohaline bay when medusa densities were <0.02 m^{-3} (Purcell et al. 1994a,b, Purcell & Decker 2005). Thus, at the low densities in our study, *C. quinquecirrha* should not have reduced *M. leidyi* populations in the tributary or the bay, and contacts and chemical cues from predators would also have been low. Therefore, we could evaluate the possible effects of environmental factors on ctenophore vertical distribution independently of the effects of *C. quinquecirrha* medusae.

A key difference between this and previous analyses (Keister et al. 2000, Breitburg et al. 2003, Kolesar et al. 2010) was that the densities (as estimated by the Tucker trawl) of *Chrysaora quinquecirrha* medusae in 1999–2001 in the tributary were one-tenth (0.012 ± 0.003 m^{-3}) of those in 1992 and 1993 (0.14 ± 0.02 m^{-3}). Kolesar et al. (2010) used data from 1992, 1993 (from Keister et al. 2000), 1999, and 2001 at our tributary stations and found that *C. quinquecirrha* medusae explained 63 to 86% of the variation in vertical overlap in addition to that explained by the abiotic factors.

Effects of vertical distributions on ctenophore feeding

Our study demonstrated, for the first time, depth-specific feeding by the ctenophore *Mnemiopsis leidyi* on its prey copepod *Acartia tonsa*. Depth-specific predation effects estimated from fine-scale densities of ctenophores (video data) and copepods (pump data) showed that maximum predation impacts were in or near the pycnocline. Importantly, the animals and feeding were concentrated at depth even without hypoxia in the tributary. Thus, to estimate feeding impacts, the relative depth distributions of the organisms must be determined. Also, gut content collection only from the surface would underestimate the actual predation rates.

A key important function of concentrations of planktonic organisms in the water column is enhancement of trophic interactions where concentrations occur. Feeding rates, especially for non-visual gelatinous predators, depend on encounters with the prey, which would increase with prey density (e.g. reviewed by Purcell 1997). Our results agreed with this expectation; specifically, ctenophore feeding was higher where copepods occurred at higher densities, in bottom waters of the tributary and near the pycnocline in the bay (Table 5).

Although most sampling in the tributary (1999) and the mainstem bay (2000) could not be conducted in the same year due to logistic constraints, direct comparisons between the tributary and bay stations were possible in July 2001 (Table 6). The tributary had fewer (2.6 ctenophores m^{-3}) but larger (17.3 ml) ctenophores than the bay (5.0 ctenophores m^{-3} of 13.7 ml volume), which resulted in only slightly lower predation effects in the tributary than in the bay (13.6 versus 16.7% d^{-1}). Because copepod densities were much higher in the tributary (21.3 versus 2.1 copepods l^{-1}), feeding on copepods was much greater there and ctenophores could grow larger. The higher animal densities were also distributed over greater depths at the tributary stations (16–20 m) than in the bay, where they were compressed into the ~10 m deep oxic layer. The greater availability of copepods in the tributary was reflected by the ctenophore gut contents, averaging 0.5 copepods ml^{-1} ctenophore there versus 0.2 copepods ml^{-1} ctenophore in the bay.

Interannual differences in predation effects can also be significant. Direct comparisons between years were possible for the tributary (July 1999 and 2001) and for the bay (July 2000 and 2001; Table 6). Ctenophores were larger and more abundant in the tributary in 1999 than 2001, leading to considerably higher predation effect (24.8 versus 13.6% d^{-1}) and possibly causing the lower copepod densities observed in 1999. In the bay, ctenophores were almost twice as numerous in 2000 as in 2001 but only slightly smaller. Consequently, predation effects in 2000 were almost twice that in 2001 in the bay (33.0 versus 16.7% d^{-1}). Thus, we observed substantial interannual differences in both the tributary and the bay.

Interannual differences were also seen by Purcell & Decker (2005), who compared the population predation effects of ctenophores among 10 yr at 3 mid-bay stations (38° 27′ – 34.2° N, 76° 22.8′ – 76° 28.2′ W) in Chesapeake Bay. Among summers comparable to the present study when densities of *Chrysaora quinquecirrha* medusae were low (1995–2000), 2000 was

an average year for densities of *Mnemiopsis leidyi* (6.4 ± 2.4 m^{-3}) and copepods (2.4 ± 0.7 l^{-1}). The average ctenophore predation effect calculated in their study on 28 July 2000 was lower (19.8 ± 6.9% d^{-1}) than in our study on 17 July 2000 (33.0 ± 5.5% d^{-1}), possibly due to spatial or temporal differences, or differences in sampling methods (Tucker trawl from pycnocline to surface versus video recordings at 7 to 8 depths above anoxic waters). Peak density of *M. leidyi* occurred in 1996 (19.8 ± 6.9 m^{-3}) and predation effects were about twice the average (Purcell & Decker 2005). Therefore, in years with such high ctenophore densities, predation effects could be even greater than estimated here (>33% d^{-1}). Our predation estimates were limited temporally and spatially, and were not intended to address the large-scale variation present in Chesapeake Bay.

Not only are *Mnemiopsis leidyi* important predators of copepods, they also are important predators of ichthyoplankton and bivalve larvae (Cowan & Houde 1993, Purcell et al. 1991, 1994a, McNamara et al. 2010). At our tributary sampling stations, the vertical habitat overlaps of ctenophores with fish eggs and larvae were 59 to 66%, only slightly lower than for copepods (70%; Kolesar et al. 2010). The vertical distributions of *M. leidyi, Acartia tonsa*, and bay anchovy *Anchoa mitchilli* eggs and larvae sampled at 5 m depth intervals tracked the pycnocline depth in the mainstem Chesapeake Bay (North & Houde 2004). Thus, *M. leidyi* feed directly on the planktonic stages of commercially-important species, including bay anchovy, menhaden, oysters, and clams in Chesapeake Bay, as well as the copepod prey of zooplanktivorous fish and their larvae.

CONCLUSIONS

Our study quantified for the first time the fine-scale vertical distributions of the ctenophore *Mnemiopsis leidyi*, its prey copepod *Acartia tonsa*, key environmental parameters, and *in situ* feeding rates. We found that ctenophores, copepods, and predation effects were concentrated near stratification in the water column. Only severe hypoxia (DO ~0 mg l^{-1}) and possibly low temperatures (≤5°C) restrict their vertical distribution. Because zoo- and ichthyoplankton prey, gelatinous predators, and their predation effects can be concentrated near stratification in the water columns, our results emphasize the importance of fine-scale vertical sampling to accurately estimate predation effects on prey populations and overall food web interactions.

Our results are relevant in coastal waters of eastern North and South America, Europe, and the Mediterranean Sea. *Mnemiopsis leidyi* is infamous because of its severe effects on zooplankton and ichthyoplankton in the Black Sea following its accidental introduction in the early 1980s (Shiganova 1998). Consequently, the effects of *M. leidyi* on planktonic communities in more recently invaded seas are of great concern (Shiganova et al. 2001, Tendal et al. 2007, Fuentes et al. 2010, Granhag et al. 2011, reviewed by Costello et al. 2012). The native populations of *M. leidyi* in the NW Atlantic also appear to be expanding temporally and spatially with ocean warming (Sullivan et al. 2001, Link & Ford 2006, Condon & Steinberg 2008). Thus, predation by *M. leidyi* may increase as populations expand in coastal waters severely degraded by human activities.

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