



Predator-mediated landscape structure: seasonal patterns of spatial expansion and prey control by *Chrysaora quinquecirrha* and *Mnemiopsis leidyi*

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ABSTRACT: The scyphomedusa *Chrysaora quinquecirrha* and lobate ctenophore *Mnemiopsis leidyi* are dominant consumers in the planktivorous food web in Chesapeake Bay, USA, and are important predators throughout much of their ranges. Our studies in the Patuxent River (a subestuary of Chesapeake Bay) and its tributary creeks suggest successive waves of population spread and trophic influence of these 2 gelatinous species in opposing directions across the aquatic landscape. In years when both species were abundant, *Mnemiopsis* appeared first in the main channel of the Patuxent River and initially was most abundant in the bottom layer of the water column. *Mnemiopsis* densities then rapidly increased in shallow tributaries and coves, with distributions likely caused by a combination of transport and temporally and spatially varying patterns of growth and reproduction. In contrast, densities of *Chrysaora* ephyrae were initially highest in small coves and tributary creeks, with densities of *Chrysaora* medusae spreading outward from these small systems to the main river as summer progressed. We found no conclusive evidence for tidally-cued vertical migrations of either species or directional swimming by *Chrysaora* that would create these differing spatio-temporal patterns. As *Chrysaora* increased and spread, it likely reduced or eliminated *Mnemiopsis* by direct predation, and possibly through the effect that partial predation could have on *Mnemiopsis* reproduction. Because of differences in diets and feeding rates, these shifting temporal and spatial patterns of medusa and ctenophore dominance potentially influence spatial distributions and temporal patterns of survival of ichthyoplankton, oyster larvae, and copepods.

KEY WORDS: Gelatinous zooplankton · Estuary · Food web · Spatial distributions · Chesapeake Bay

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INTRODUCTION

Studies of variation in ecological communities across heterogeneous landscapes have generated a rich theoretical literature (Leibold et al. 2004, Logue et al. 2011) as well as practical applications in the aquatic realm in the form of ecosystem-based management approaches and marine spatial planning (Conover et al. 2000, Mangel & Levin 2005, White et al. 2012). Understanding causes of this spatial variation may often require consideration of the trophic ecology of systems because effects of the physical environment on species of interest can be mediated

through direct environmental effects on predators, competitors, and prey. Predator-mediated landscape structure—whereby dominant consumers are influenced by physical habitat, and their distributions then influence or control the landscape patterns of habitat suitability and survival of both their prey and species influenced by their prey—may be an important feature of many ecological systems (Breitburg et al. 2010).

The Chesapeake Bay planktivorous food web is dominated by 2 native gelatinous zooplankton species, the semaestome scyphomedusa *Chrysaora quinquecirrha* (the sea nettle) and the lobate ctenophore

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Mnemiopsis leidyi. These species (referred to by genus names below) influence—and at times exert strong control over—ichthyoplankton, mesozooplankton, and larvae of the eastern oyster *Crassostrea virginica* (e.g. Nelson 1925, Purcell et al. 1991, 1994, Cowan & Houde 1993), which is considered to be a key ecosystem engineer because of its habitat creation and water filtration roles (Coen et al. 2007, Grabowski & Peterson 2007). The portion of the Chesapeake Bay food web dominated by these gelatinous species can be thought of as 3 overlapping intraguild predation webs (Fig. 1; see also Kolesar 2006) that vary in the extent of control over their common ichthyoplankton and zooplankton prey. The local and seasonal increases in *Chrysaora*, the main predator of *Mnemiopsis* in Chesapeake Bay (Purcell & Cowan 1995), potentially act as a switch between the *Chrysaora* and *Mnemiopsis*-dominated intraguild predation webs. Predator-prey interactions between the 2 gelatinous species are not restricted to adult stages; *Chrysaora* ephyrae have high clearance rates when feeding on *Mnemiopsis* larvae and *Mnemiopsis* larvae may be an important cause of high growth rates of *Chrysaora* in Chesapeake Bay (Olesen et al. 1996).

During 2003 to 2005, we conducted field sampling to investigate the temporal and spatial patterns of *Chrysaora* and *Mnemiopsis* abundances in the mainstem and adjacent tributaries (referred to as 'creeks') of the mesohaline Patuxent River, a subestuary of Chesapeake Bay (see Fig. 2). A number of factors,

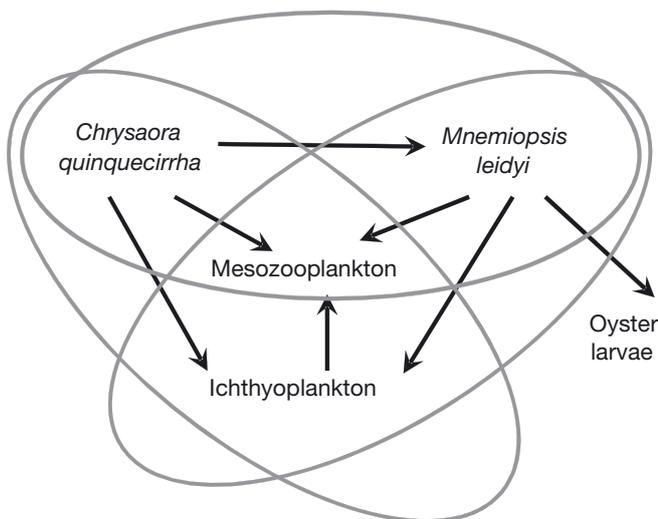


Fig. 1. Overlapping intraguild predation webs dominated by *Chrysaora* and *Mnemiopsis*. *Chrysaora* preys on *Mnemiopsis* and competes with it for mesozooplankton and ichthyoplankton prey. Both gelatinous species prey on fish larvae and compete with them for shared zooplankton prey

including water temperature (Costello et al. 2006), the location of seasonal refugia for overwintering populations (Costello et al. 2006, 2012, Beaulieu et al. 2013), predators (Riisgård et al. 2010), the locations of appropriate habitat for sessile stages (Lo & Chen 2008), flushing rates (Lo & Chen 2008), and currents that affect transport (Kremer & Nixon 1976) have been suggested to affect seasonal patterns of spatial distributions of gelatinous zooplankton. Population control of *Mnemiopsis leidyi* has been of special interest because it has been a voracious predator and competitor in some areas that it has invaded (Purcell et al. 2001, Costello et al. 2012). Predation by other gelatinous species, including the ctenophore *Beroe ovata* (Shiganova et al. 2004), the scyphomedusa *Aurelia aurita* (Riisgård et al. 2010) and possibly the scyphomedusa *Pelagia noctiluca* (Tilves et al. 2013) may reduce *Mnemiopsis* abundances in parts of its non-native range, and the lack of predator control has been suggested as a major factor facilitating the spread of *Mnemiopsis* (Purcell et al. 2001, Fuentes et al. 2010).

Our motivation for this study was the observation by earlier researchers (Cargo & Schultz 1966), local residents, and ourselves that *Chrysaora* appeared to be more abundant in coves and creeks than in the mainstem of large subestuaries or the mainstem Chesapeake Bay, and the possibility that the consequence was spatial and temporal variability in habitat suitability for prey across the estuarine landscape. Cargo & Schultz (1966) suggested that headwaters of tidal creeks were important nursery grounds for *Chrysaora*, and that ephyrae are either produced in high numbers or transported there. Highest published Chesapeake Bay *Chrysaora* densities from trawls in the Eastern Shore region of the Bay reported in previous studies are also from shallow (≤ 3 m depth) creeks—in this case creeks that flow into the Choptank River, a subestuary along the eastern shore of Chesapeake Bay (Purcell 1992). Maximum *Chrysaora* densities in that study were 18.6 medusae m^{-3} in the creeks, compared to 2.4 medusae m^{-3} at a shallow mainstem Chesapeake Bay station, and 0.1 medusae m^{-3} in deeper mainstem Bay stations. During 2 of the 3 sampling periods when both the creeks and the shallow mainstem Bay stations were examined, feeding rates were highest in one of the creek stations (Purcell 1992). High predation potential of other medusae species in shallow coves has also been noted elsewhere (e.g. Purcell & Grover 1990, Olesen 1995). Our sampling was designed to examine the roles of behavior, seasonal patterns of population spread, and locations of highest larval

densities in creating observed landscape patterns of abundance and trophic control by these 2 gelatinous species.

MATERIALS AND METHODS

Overwintering locations of *Mnemiopsis*

In order to examine large scale seasonal patterns and locations of overwintering *Mnemiopsis*, we analyzed data from the Maryland Chesapeake Bay Water Quality Monitoring Program: Mesozooplankton Component that was conducted at fixed stations in Maryland waters by Versar for Maryland Department of Natural Resources (MD-DNR) and the Chesapeake Bay Program (CBP 2007) between 1984 and 2002. Data were downloaded from the CBP website; all years and sites for which separate surface and bottom samples were available and that distinguished *Mnemiopsis leidyi* from other ctenophores were included in the analyses. Ctenophores were not identified to species prior to 1987 in Maryland waters, and in later years at some Virginia sites. Although the database also included medusae, we analyzed only *Mnemiopsis* densities. The small size and leading harness of the plankton net used for CBP sampling likely biased against capture of medium to large-sized *Chrysaora* medusae, and sample volumes were inadequate for typical *Chrysaora* densities.

CBP samples were collected by combining catches from duplicate 5 to 10 min stepped oblique tows from 1 net of a pair of 20 cm diam. 202 μm mesh bongo nets, and concentrating the net contents on a metal sieve. Total volume of each gelatinous species was determined in the field from unpreserved samples; total volume of water sampled by nets was estimated based on the net diameters and numbers of revolutions on calibrated flow meters.

Spatial distributions of *Mnemiopsis* and *Chrysaora* in the Patuxent River and its tributary creeks

In order to identify variation in spatial distributions of *Mnemiopsis* and *Chrysaora* during the late spring through early autumn period when both species rise to peak abundances, gelatinous zooplankton were sam-

pled at 8 (2003) to 12 (2004) sites in the Patuxent River and its tributaries with a 244 μm mesh, 6 m long, 1 m^2 Tucker trawl approximately weekly during late spring and summers of 2003 and 2004. Sampling sites were arranged in 3 clusters (St. Leonard, Hellen and St. John Creeks), each including a mainstem Patuxent River station in the deep central channel near the mouth of a tributary creek (Fig. 2, Sites 4, 8, 12), 2 stations within the creek—one near the confluence with the mainstem Patuxent or an adjacent creek (Fig. 2, Sites 3, 7, 11), and one as far up the creek as we could sample in approximately 1.2 m water depth (Fig. 2, Sites 2, 6, 10)—and one inlet or cove site with little freshwater inflow (Fig. 2, Sites 1, 5, 9). The selection of these 4 habitat types was intended to (1) determine whether the anecdotal and less targeted observations that *Chrysaora* densities in coves and inlets far exceeded densities in the mainstem portions of major tributaries were correct, and (2) if so, to test whether *Chrysaora* swimming behavior or larval distributions could be responsible for that pattern. We were also interested in determining (3) whether temporal patterns of *Mnemiopsis* distributions were similar to those of *Chrysaora*, and how the spatial distribution of potential *Chrysaora* control of *Mnemiopsis* varied within the season.

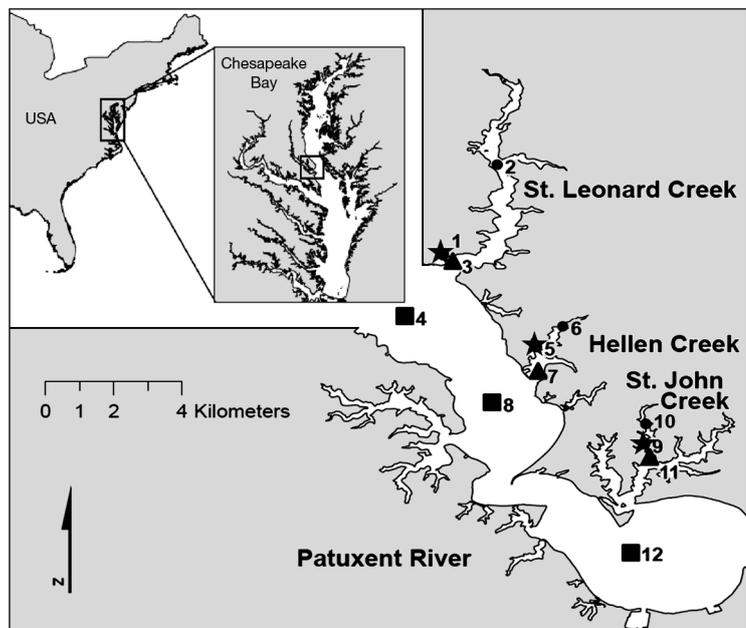


Fig. 2. Site map showing location of the Patuxent River within the Chesapeake Bay system, and the location of sampling sites within the Patuxent, its tributary creeks and small inlets and coves on those creeks. Habitat designations: cove and inlet stations (★, Sites 1, 5 and 9); upper creek stations (●, Sites 2, 6 and 10); lower creeks stations (▲, Sites 3, 7 and 11); mainstem stations (■, Sites 4, 8 and 12). Site 1 is Mackall Cove, which is mentioned by name in the text

Wheels (30 cm diam.) were attached to a metal rod added to the lower edge of the Tucker trawl frame so that tows could be taken very close to the substrate while minimizing sediment in the net. Duplicate tows of the surface layer and whole water column (2003) or surface and bottom layers (2004), each lasting 2 min and sampling an average of 53 m³, were taken at each site on each date. *Chrysaora* and *Mnemiopsis* in each tow were counted live onboard the ship in total or through a volumetric subsample containing at least 200 individuals. Total biovolume of each species was determined. Total length of up to 25 *Mnemiopsis* individuals and bell diameter of all *Chrysaora* medusae were measured to the nearest 0.5 cm.

***Mnemiopsis* larvae and *Chrysaora* ephyrae sampling in 2003 and 2004**

In order to examine the spatial patterns of early life stages, we sampled for larval *Mnemiopsis* and *Chrysaora* ephyrae using paired 30 cm diam. bongo nets fitted with 200 µm mesh, 1.5 m long nets. In 2003, we sampled all 6 habitats (mainstem river surface and whole water column, lower creek surface and whole water column, coves and upper creeks) in the St. Leonard and Hellen Creek clusters. In 2004, we allocated our sampling effort differently and sampled only surface waters in the mainstem river, coves, and lower creek sites for larval *Mnemiopsis* and *Chrysaora* ephyrae, but included all 3 creek clusters. In both years, we only used the contents of one net of each pair. In 2003, the entire contents of those bongo nets were examined immediately onboard ship with the aid of a dissecting microscope; *Mnemiopsis* larvae and *Chrysaora* ephyrae were identified and enumerated. In 2004, net contents were preserved in acid Lugol's (Sullivan & Gifford 2009), and *Mnemiopsis* larvae and *Chrysaora* ephyrae counted at a later date in the laboratory with the aid of a dissecting microscope.

Relationship between vertical distributions, swimming direction and tidal stage in 2005

Field sampling was conducted during summer 2005 to determine the relationship between vertical distributions of gelatinous zooplankton and tidal stage, and to quantify the relationship between *Chrysaora* swimming direction and tidal stage. The goal was to determine whether selective tidal-stream transport

(Forward & Tankersley 2001) or other active behaviors might influence transport from the mainstem to creeks, or retention in creek and cove parts of the system. These data also provided further information on the use of mainstem river, cove and lower creek habitats by *Chrysaora* and *Mnemiopsis*. We focused on St. Leonard Creek (furthest upriver Patuxent cluster) for this work because of its proximity of the Morgan State Laboratory, and availability of boat docking and launch facilities. Six 24 h cruises were completed to sample vertical distributions, densities and size distributions of *Chrysaora* and *Mnemiopsis* during day and night ebb and flood tides. Methods were similar to those described for Tucker trawl sampling during 2004.

We also videotaped the swimming direction of *Chrysaora* at the surface during daytime ebb and flood tides in Mackall Cove and lower St. Leonard Creek using a video camera suspended 1.5 m from the side of a 3 m boat. A compass was included in the view field of the video. *Mnemiopsis* were rarely seen at the surface during video sampling events and were not clearly seen in video footage, so were not targeted for swimming direction filming. To facilitate clear footage, filming only took place on clear, calm days. These conditions should maximize behavioral control of medusa over swimming direction, but could introduce unintended biases. The length of video for each individual was only a few seconds; our goal was to get a clear instantaneous image, not to integrate swimming direction over time. Medusae swimming direction was determined for each case in which both the medusa and compass images were clear enough to extract these data. Both video and trawl datasets were later corrected to replace predicted tides with actual tides, which in some cases required us to drop intended ebb-flood comparisons.

Environmental measurements

During all 3 yr of gelatinous zooplankton sampling, we concurrently measured dissolved oxygen, temperature, salinity, and depth at 1 m depth intervals with a YSI 600QS sonde. We also recorded Beaufort scale wind force, which is a measure of sea surface roughness related to wind speed. Beaufort scale was a better measure of the local effect of wind than regional wind speed measurements because sites varied in the degree to which the surrounding landscape reduced wind at the water surface.

Statistical analyses

Data are presented as means \pm SE in the text. Differences in log-transformed *Mnemiopsis* densities among sites and depths (above vs. below the pycnocline) in the CBP monitoring data were analyzed during spring prior to peak densities (March through May) and summer (June through August) as a fixed-effect factorial design ANOVA (Proc GLM, SAS ver. 9.2). Only the 10 stations at which *Mnemiopsis* were found were included in analyses. The effect of depth on densities during winter (December through February) was tested only for the 4 stations with year-round ctenophore presence in the samples. Sequential Bonferroni tests on LSmeans (least-square means) were used for post hoc comparisons of sites. In all analyses, non-significant interaction terms with $p > 0.20$ were dropped from statistical models.

Randomized block ANOVAs (Proc Mixed, SAS ver. 9.2) were run to test for differences in biovolumes and numerical densities among habitats for 2004 when we sampled all 3 creek clusters. Spatial patterns for other years were not analyzed because of low statistical power. Quantile regression (Proc Quantreg, SAS ver. 9.2) run on the mean biovolume and density collected with Tucker trawls at each site and date including all 3 yr of the study was used to test for a negative relationship between *Mnemiopsis* and *Chrysaora*. We selected this test rather than standard linear regression under the assumption that predators would limit the maximum density or biovolume of prey, but that many other factors (seasonality, prey, etc.) could also result in low abundances.

Differences in larval abundances among habitats were considered in 2 ways, reflecting the different ways we allocated sampling effort in 2003 and 2004. In 2003, when we sampled only 2 creek clusters and 6 habitats in each cluster, we addressed only the simple question of whether the total number of larvae collected that year, normalized by mean tow volume, differed among habitats. We tested the actual distribution against the null hypothesis that there would be equal numbers of larvae in all habitats by using chi-square tests (Proc Freq, SAS ver. 9.2), followed by pairwise comparisons using a sequential Bonferroni adjustment. For 2004 data, which included sampling of all 3 clusters but only 3 habitats per cluster, we also used a randomized block ANOVA (SAS Proc Mixed, habitat = fixed, date and cluster = random), followed by LSmeans comparisons using a sequential Bonferroni adjustment to test for differences in larval densities among habitats.

To examine the potential for behaviors that could enhance tidal-stream transport, we used general linear models (Proc GLM, SAS ver. 9.2) testing the relationship between the proportion of individuals in the surface layer of the water column and tidal stage (ebb or flood), Beaufort sea surface state (as recorded during surface tows), day vs. night, and bottom dissolved oxygen (tested separately as a continuous variable, and as above vs. below 2.0 mg l^{-1}). Variables with $p > 0.20$ were dropped from the model, and the model was then further simplified based on AIC criteria.

We calculated univariate summary statistics for each of the 5 site, date, and tide-stage combinations, and used Watson's U^2 tests to compare swim angles on different tidal stages within Mackall Cove (Oriana 4 software). Too few images were captured in the lower St. Leonard Creek during flood tide for formal statistical comparisons ($n = 4$).

RESULTS

Overwintering locations of *Mnemiopsis*

Mnemiopsis were found at 10 CBP monitoring stations, including 7 mesohaline sites and 3 stations located in oligohaline waters (salinity >5.0 to 18.0 and >0.5 to 5.0 , respectively, and based on CBP 2004 categories; Fig. 3). Peak spring/summer abundances occurred in June at the mesohaline sites and in July or later in oligohaline sites. Several locations had a second population peak in November or December. Sampling for this monitoring program did not include creek and cove habitats, but Stn LE2.2 coincided with our mainstem Patuxent River site for the St. Leonard Creek cluster. This site had the highest *Mnemiopsis* density recorded on a single date over the duration of the zooplankton monitoring program (296 ind. m^{-3} in June 1990).

Overwintering populations and year-round occurrences were recorded at 4 sites: 2 in the mesohaline portion of the Patuxent River (monitoring Stns LE 1.1 and LE2.2 in Fig. 3), and 2 in the mesohaline portion of the mainstem Chesapeake Bay (Stns CB4.3c and CB5.2). Even at these sites, mean densities during winter (December through February) tended to be quite low; only at Stn LE1.1 did mean densities approach or exceed $1 \text{ Mnemiopsis m}^{-3}$ every month of the year. Winter densities at the 4 sites with year-round populations did not differ among stations ($p = 0.17$), depths (i.e. above vs. below pycnocline samples; $p = 0.70$), or in the interaction between these factors ($p = 0.98$; overall model $F = 0.74$, $df = 5$, $p = 0.597$, $n = 542$ samples).

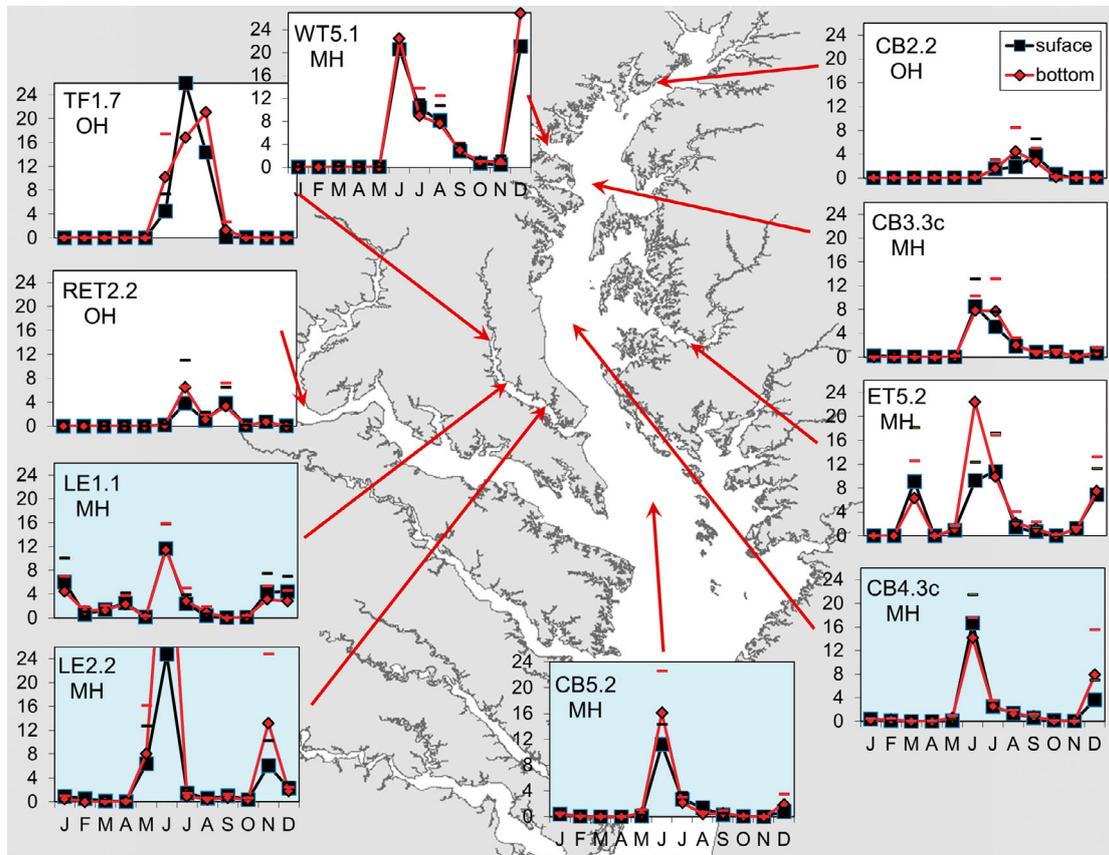


Fig. 3. *Mnemiopsis* biovolume densities (mean + SE, ml m⁻³) at the Chesapeake Bay Program (CBP) zooplankton monitoring program stations in the Maryland portion of Chesapeake Bay at which ctenophores were found. *Mnemiopsis* were found during all 12 months of the year, although not necessarily in the same year, at sites illustrated by graphs with shaded backgrounds. Standard errors (horizontal bars) not visible are obscured by symbols. Vertical axis scale was selected to illustrate seasonal pattern; maximum densities at several sites exceed densities shown (WT5.1 December: surface = 21.0 ± 19.3, bottom = 26.8 ± 24.3; TF1.7 July: surface 26.0 ± 21.0, bottom 20.5 ± 10.9; LE2.2 June: surface 24.7 ± 12.4, bottom 53.5 ± 40.7; ET5.2 June: bottom 22.4 ± 12.8). MH = mesohaline, OH = oligohaline. Prefixes in site names in graphs reflect salinity zones and habitats: CB = mainstem Chesapeake Bay; ET and RET = estuarine turbidity zone; LE = lower estuary; TF = tidal fresh (although site is oligohaline); WT = western shore tributary

Spring densities (March through May) differed among stations ($F = 15.91$, $df = 9$, $p < 0.0001$) but not depths ($p = 0.87$) or in the interaction between station and depth ($p = 1.0$; overall model $F = 7.59$, $df = 19$, $p < 0.0001$; $n = 510$ samples). Stn ET5.2 located in the mesohaline Choptank River, and Patuxent River Stn LE1.1 had significantly higher spring densities than all other sites. Patuxent River Stn LE2.2 also had higher spring densities than Stns TF1.7 (Patuxent River oligohaline zone) or WT5.1 (the Patapsco River).

Spatial distributions of *Mnemiopsis* and *Chrysaora* in the Patuxent River and its tributary creeks

The seasonal pattern of spatial distributions of *Mnemiopsis* and *Chrysaora* in the mesohaline Patux-

ent River can be thought of as opposing waves of high population densities that spread across the aquatic landscape (Figs. 4 & S1 in the Supplement at www.int-res.com/articles/suppl/m510p183_supp.pdf). *Mnemiopsis* became abundant first in the mainstem river, and then appeared and increased in abundance in the lower portions of creeks and the upper creeks and coves. *Chrysaora* followed the opposite pattern, with highest initial abundances in creeks and coves, and then generally increasing downstream and in the mainstem Patuxent River.

The pattern can be seen most clearly in 2004, when both gelatinous species were abundant and we sampled all 3 creek clusters. Highest *Mnemiopsis* biovolumes were initially found in the bottom water layer of the mainstem river (27 May), then spread to the surface layer of the mainstem (1 June), and then into the

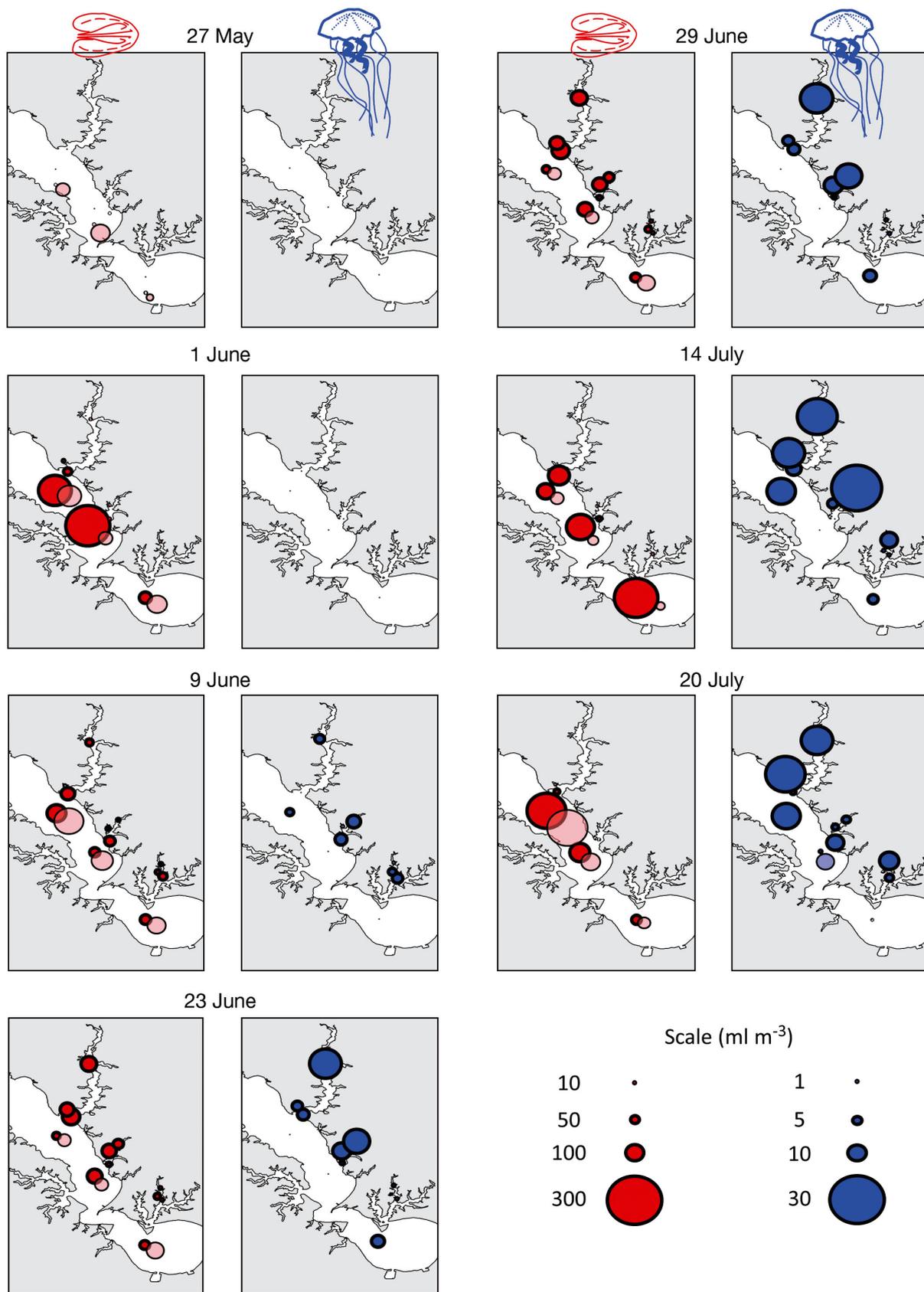


Fig. 4. (this page and the next page) Biovolumes (ml m^{-3}) of *Mnemiopsis* (red) and *Chrysaora* (blue) collected in Tucker trawls during May to September 2004. Note the order of magnitude difference in scales. Darker symbols are surface layer samples; lighter symbols are subpycnocline bottom layer samples, which were only collected at our deepest stations (the mainstem Patuxent River and lower St. Leonard Creek)

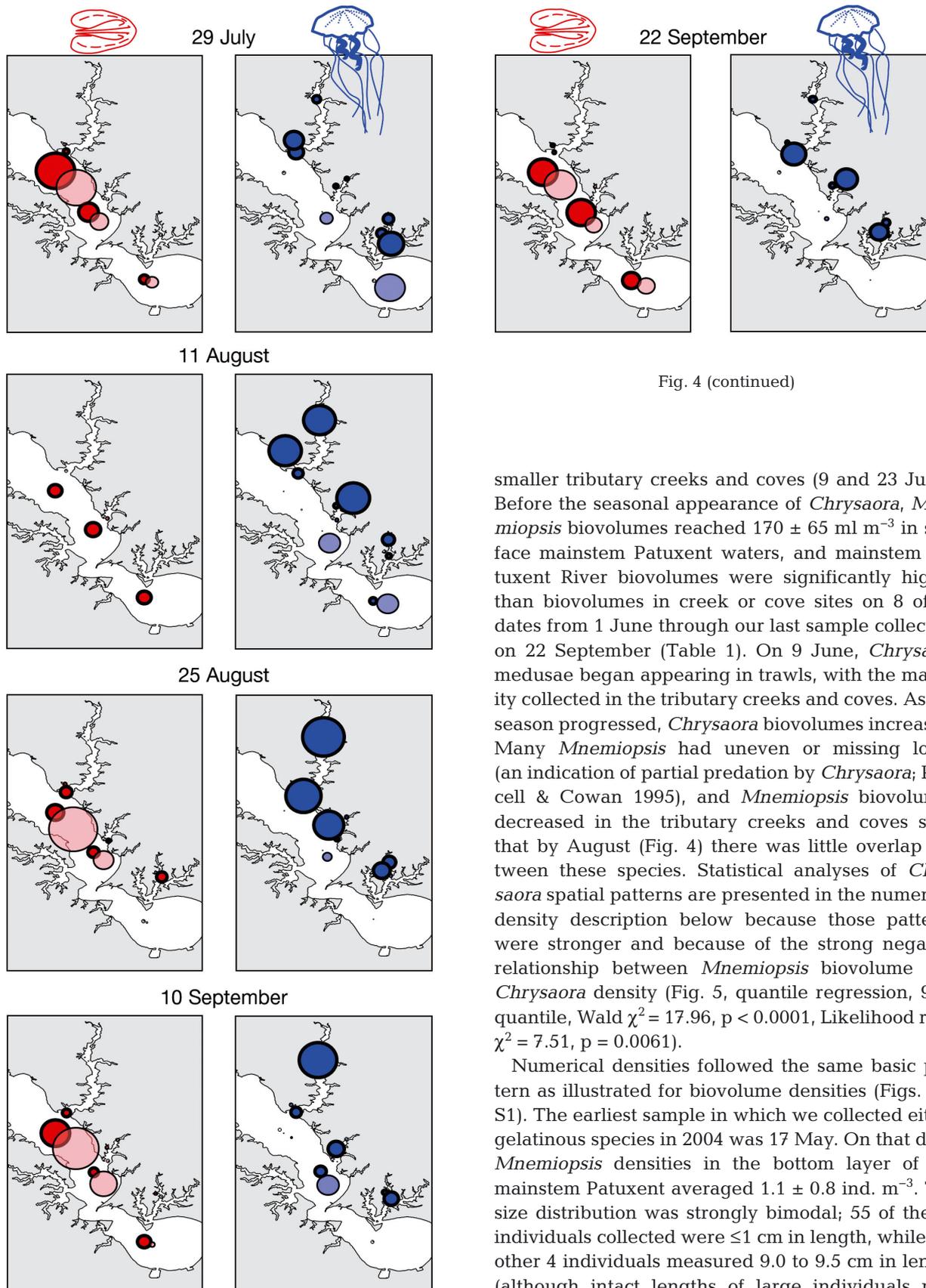


Fig. 4 (continued)

smaller tributary creeks and coves (9 and 23 June). Before the seasonal appearance of *Chrysaora*, *Mnemiopsis* biovolumes reached $170 \pm 65 \text{ ml m}^{-3}$ in surface mainstem Patuxent waters, and mainstem Patuxent River biovolumes were significantly higher than biovolumes in creek or cove sites on 8 of 11 dates from 1 June through our last sample collection on 22 September (Table 1). On 9 June, *Chrysaora* medusae began appearing in trawls, with the majority collected in the tributary creeks and coves. As the season progressed, *Chrysaora* biovolumes increased. Many *Mnemiopsis* had uneven or missing lobes (an indication of partial predation by *Chrysaora*; Purcell & Cowan 1995), and *Mnemiopsis* biovolumes decreased in the tributary creeks and coves such that by August (Fig. 4) there was little overlap between these species. Statistical analyses of *Chrysaora* spatial patterns are presented in the numerical density description below because those patterns were stronger and because of the strong negative relationship between *Mnemiopsis* biovolume and *Chrysaora* density (Fig. 5, quantile regression, 90th quantile, Wald $\chi^2 = 17.96$, $p < 0.0001$, Likelihood ratio $\chi^2 = 7.51$, $p = 0.0061$).

Numerical densities followed the same basic pattern as illustrated for biovolume densities (Figs. 4 & S1). The earliest sample in which we collected either gelatinous species in 2004 was 17 May. On that date, *Mnemiopsis* densities in the bottom layer of the mainstem Patuxent averaged $1.1 \pm 0.8 \text{ ind. m}^{-3}$. The size distribution was strongly bimodal; 55 of the 59 individuals collected were $\leq 1 \text{ cm}$ in length, while the other 4 individuals measured 9.0 to 9.5 cm in length (although intact lengths of large individuals may

Table 1. Results of statistical analyses testing effects of variation among habitats on biovolumes of *Mnemiopsis* and *Chrysaora* on each date sampled during 2004 when that species was present. Habitat differences show results of post-hoc LSmeans comparisons where $p < 0.05$ for the main ANOVA model

Date	Test for habitat effect		Habitat differences
	$F_{3,10}$	p	
<i>Mnemiopsis</i>			
17 May	0.55	0.662	
27 May	1.84	0.203	
1 June	9.61	0.003	Mainstem river > all others
9 June	8.72	0.004	Mainstem river > cove and upper creek
23 June	0.99	0.438	
29 June	12.39	0.001	Mainstem river > all others
14 July	2.53	0.117	
20 July	16.23	0.0004	Mainstem river > all others
29 July	13.33	0.0008	Mainstem river > all others
11 Aug	10.40	0.0002	Mainstem river > all others
25 Aug	2.14	0.159	
10 Sept	6.41	0.010	Mainstem river > all others
22 Sept	40.88	<0.0001	Mainstem river > all others
<i>Chrysaora</i>			
9 June	7.18	0.007	Cove > all others
23 June	3.90	0.044	No significant differences in post hoc comparisons
29 June	16.38	0.0003	Upper creek > all others; lower creek > mainstem river
14 July	8.88	0.004	Upper creek > lower creek and mainstem
20 July	7.15	0.008	Upper creek > mainstem
29 July	2.86	0.091	
11 Aug	6.61	0.010	Upper creek > mainstem
25 Aug	2.72	0.101	
10 Sept	0.73	0.556	
22 Sept	3.39	0.062	

have been exaggerated in our measurements because of damage from nets). In contrast to bottom mainstem river waters, on 17 May, *Mnemiopsis* densities averaged only 0.002 ± 0.002 ind. m^{-3} in mainstem river surface waters, 0.003 ± 0.004 ind. m^{-3} in the lower portion of the creeks, 0.003 ± 0.006 ind. m^{-3} in upper portions of creeks, and 0.005 ± 0.006 ind. m^{-3} in coves. On 9 June, the first date on which we collected more than 2 *Chrysaora* in any of the Tucker trawl samples, numerical densities of *Chrysaora* averaged 0.009 ± 0.009 ind. m^{-3} in mainstem river bottom waters, 0.004 ± 0.004 ind. m^{-3} in mainstem river surface waters, and an order of magnitude or more higher in creek and cove habitats (0.03 ± 0.01 ind. m^{-3} in the lower portion of the creeks, 0.03 ± 0.02 ind. m^{-3} in upper portions of creeks, and 0.12 ± 0.05 ind. m^{-3} in coves). Of the 60 *Chrysaora* collected

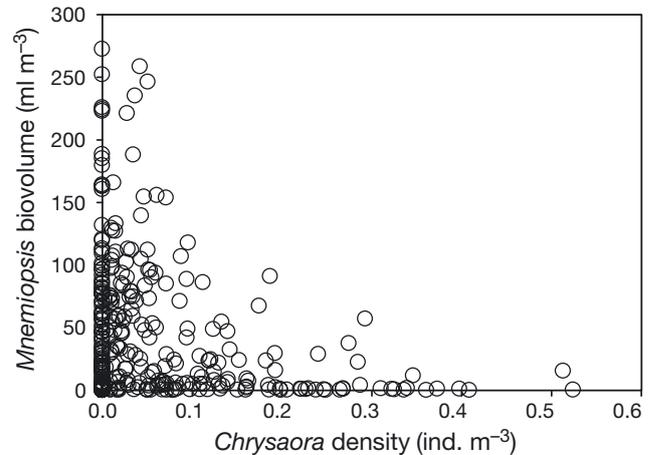


Fig. 5. Relationship between *Chrysaora* numerical density and *Mnemiopsis* biovolume during July and August 2004 at all sampled sites

on 9 June in Tucker trawls, 44 were ≤ 2 cm diam. During August in the upper creeks and coves, *Chrysaora* numerical densities averaged 0.18 ± 0.04 ind. m^{-3} and *Mnemiopsis* densities averaged 0.10 ± 0.05 ind. m^{-3} , but in the mainstem Patuxent the pattern was reversed; *Chrysaora* densities averaged 0.01 ± 0.007 ind. m^{-3} and *Mnemiopsis* densities averaged 2.95 ± 0.63 ind. m^{-3} in the surface layer and 0.03 ± 0.002 ind. m^{-3} and 6.41 ± 1.68 ind. m^{-3} , respectively, in the bottom layer of the water column. Randomized block ANOVA indicated that sea nettle density varied significantly among habitats on 6 dates; in those cases either the coves or upper creeks had significantly higher densities than the mainstem river, and on some dates, other habitats as well (Table 1).

Spatial and temporal patterns were initially similar in 2003 when we sampled only 2 site clusters (St. Leonard and Hellen Creeks; Fig. S1), but *Chrysaora* densities were lower, and generally remained below levels at which medusae predation would limit *Mnemiopsis* densities (i.e. 0.16 ind. m^{-3} ; Breitburg & Fulford 2006). Highest numerical densities of *Mnemiopsis* were found in the whole water column samples in the mainstem in May (0.002 ind. m^{-3}) and June (0.27 ind. m^{-3}), lower creeks in July (8.33 ind. m^{-3}), coves (45.07 ind. m^{-3}) and mainstem sites (36.03 ind. m^{-3}) in August, and in the mainstem whole water column (5.40 ind. m^{-3}) and surface layer samples (4.09 ind. m^{-3}) in October. No *Chrysaora* were found in May or June, but highest mean *Chrysaora* densities were in the upper creeks in July (but only 0.007 ind. m^{-3}), in the coves in August (0.037 ind. m^{-3}), and in the whole water column mainstem river samples in October (0.038 ind. m^{-3}). No sampling was conducted during September 2003.

Because our 2005 sampling goals were directed towards detecting relationships between tidal stage, vertical distributions, and swimming behaviors, we limited sampling to a single creek cluster (St. Leonard) and did not sample the upper creeks where *Chrysaora* were most abundant in 2004, but where shallow depths precluded depth-specific sampling with the 1 m² Tucker trawl (Fig. S1). Samples with the highest *Mnemiopsis* densities and biovolumes in 2005 were collected in the mainstem river, as in previous years. Samples with the highest *Chrysaora* densities were collected in the lower creek until late 10 August, when abundances in the mainstem river were particularly high. *Chrysaora* biovolumes were highest in the lower creek and bottom layer of the mainstem river, reflecting the capture of large individuals in trawls at these sites.

Larval gelatinous zooplankton samples

A total of 6875 *Mnemiopsis* larvae and 8 *Chrysaora* ephyrae were collected in 2860 m³ of water sampled on the 9 dates in 2003. All but 16 *Mnemiopsis* larvae were collected on the last 4 sampling dates, and all ephyrae were collected on the last 2 sampling dates.

Because of the small number of *Chrysaora* ephyrae collected, no statistical analyses were performed for that species in 2003. During 2004, we collected 15 576 *Mnemiopsis* larvae and 113 *Chrysaora* ephyrae in 537 m³ of water sampled. In both years, larval *Mnemiopsis* densities averaging <1.0 ind. m⁻³ were found in the mainstem river sites 1 to 2 wk earlier in the season than in other habitats sampled (Fig. 6). During May through August, both the bottom and surface waters of the mainstem river were significantly colder (by 1.0 to 5.2°C) than surface waters of the lower creeks or coves (Proc GLM 1-way ANOVA, 0.0001 < p < 0.0013 for all month comparisons).

In 2003, when *Chrysaora* densities were low, *Mnemiopsis* larvae reached their highest densities in coves; peak density reached 738 larvae m⁻³ in Mackall Cove on 6 August. The cumulative number of *Mnemiopsis* larvae (normalized to mean tow volume) collected in 2003 differed among habitats (i.e. upper creeks, lower creeks, coves and mainstem river sites; $\chi^2 = 2020.7$, df = 5, p < 0.0001), and post hoc pairwise comparisons of sampled habitats indicated that all habitats differed from each other (Table 2a). The rank order of cumulative abundance was cove > lower creek surface layer > lower creek whole water column > mainstem river surface

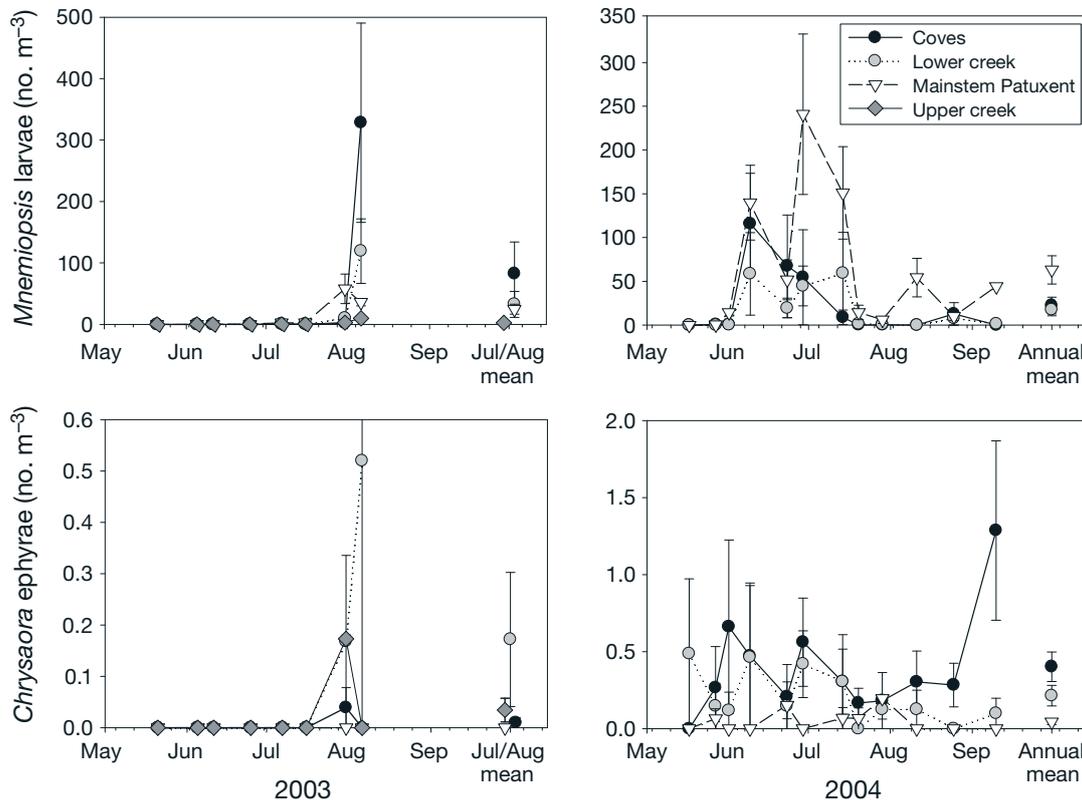


Fig. 6. Densities of *Mnemiopsis* (upper panels) and *Chrysaora* (lower panels) larvae collected during 2003 and 2004

Table 2. Statistical results for (a) pairwise χ^2 tests of differences in larval densities among habitats during 2003, and (b) LSmeans comparisons for 2004. Data in tables are χ^2 and p values (df = 1 for all tests). Comparisons in **bold** are significant based on post hoc comparisons with a sequential Bonferroni adjustment. Upper portion of table cells = larval *Mnemiopsis*; lower portion = *Chrysaora* ephyrae. No statistical tests were run for *Chrysaora* in 2003; only a total of 17 ephyrae were collected on the 10 dates sampled during that year

(a) 2003	Mainstem surface	Mainstem whole water column	Lower creek surface	Lower creek whole water column	Upper creek
Cove	350.83, <0.0001	684.82, <0.0001	115.21, <0.0001	468.09, <0.0001	1570.69, <0.0001
Mainstem surface		67.05, <0.0001	68.02, <0.0001	9.78, 0.002	631.08, <0.0001
Mainstem whole water column			262.06, <0.0001	25.99, <0.0001	343.46, <0.0001
Lower creek surface				127.99, <0.0001	993.10, <0.0001
Lower creek whole water column					513.14, <0.0001
(b) 2004					
	Cove	Mainstem surface	Lower creek surface		
Cove		1086.33, <0.0001	50.95, <0.0001		
Mainstem surface	16.29, <0.0001		1535.3, <0.0001		
Lower creek surface	3.56, 0.059	5.93, 0.015			

layer > mainstem river whole water column > upper creek.

In contrast, in 2004 when *Chrysaora* were more abundant, *Mnemiopsis* larvae densities averaged higher in surface waters of the mainstem Patuxent than in surface waters of the lower portion of creeks or in coves (randomized block ANOVA, SAS Proc Mixed; $F_{2,85} = 24.88$, $p < 0.0001$ and post hoc LSmeans comparisons). The highest density of *Mnemiopsis* larvae in 2004 was found on 29 June in the mainstem Patuxent near St. Leonard Creek (418 larvae m^{-3}). The cumulative number of *Mnemiopsis* larvae (normalized to mean tow volume) collected in 2004 differed among habitats ($\chi^2 = 1535.3$, $df = 5$, $p < 0.0001$), and post hoc pairwise comparisons of sampled habitats indicated that all habitats differed from each other (Table 2b).

Peak densities of *Chrysaora* ephyrae in surface waters in 2003 were only about one-third that in 2004, and abundances >0.1 ind. m^{-3} were found on only 2 sampling dates. In contrast, ephyra densities >0.1 ind. m^{-3} persisted for the full 4 mo sampling period during 2004. Ephyrae appeared first in lower creek sites, and the highest density of ephyrae (2.5 ephyrae m^{-3}) was found on 10 September 2004 in the cove site within the St. John Creek cluster—the creek cluster furthest downriver along the Patuxent. The cumulative number of *Chrysaora* ephyrae (normalized to mean tow volume) collected in 2004 differed among habitats (i.e. mainstem river, lower creek, upper creek and cove sites; $\chi^2 = 5.93$, $df = 5$,

$p < 0.015$). Post hoc pairwise comparisons of sampled habitats indicated that the cumulative number of ephyrae was significantly higher in coves than in the mainstem, significantly higher in the lower portion of creeks than in the mainstem, and tended to be higher in coves than in lower creeks (but $p = 0.059$; Table 2b).

Vertical distributions and swimming directions relative to tides

We found no evidence of tide-stage related vertical migration in our 2005 sampling within the St. Leonard Creek cluster. Of 16 paired ebb and flood samples that each contained at least 8 *Chrysaora*, a higher percentage of individuals was in the surface layer during ebb tide than flood tide in 8 pairs. Similarly, of 19 paired samples of *Mnemiopsis*, a higher percentage was in the surface layer during ebb tide than flood tide in 8 pairs. Regression models that included tidal stage, wind state, day vs. night, bottom dissolved oxygen, and site as a random variable indicated that the proportion of *Chrysaora* in the surface layer was best described by a model that included day vs. night ($F_{1,29} = 18.75$, $p = 0.0002$), mean Beaufort wind force ($F_{1,29} = 4.62$, $p = 0.040$), and the presence of hypoxia ($F_{1,29} = 4.68$, $p = 0.039$) as explanatory variables (SAS Proc mixed; Fig. 7). *Chrysaora* were more surface oriented at night, when bottom oxygen concentrations were <2.0 mg l^{-1} , and at

higher mean Beaufort wind force. However, it is important to note that we collected only 3 sample sets when mean Beaufort wind force was ≥ 3.0 because of the difficulty of handling our nets in high winds. The positive linear relationship between *Chrysaora* vertical distribution and wind force (Fig. 7) may not hold under more severe conditions. The best fit model for *Mnemiopsis* also included day vs. night ($F_{1,52} = 7.51$, $p = 0.048$) and mean Beaufort wind force ($F_{1,52} = 74.12$, $p = 0.048$) as explanatory variables for *Mnemiopsis* vertical distributions. Like *Chrysaora*, *Mnemiopsis* were significantly more surface oriented during night than day. The relationship between the proportion of *Mnemiopsis* in the surface layer and wind force was not significant when day vs. night was excluded from the model (Fig. 7).

Chrysaora tended to be most abundant in bottom layer samples (26 of 35 paired bottom and surface samples, $\chi^2 = 8.26$, $p = 0.004$; Fig. 8). In contrast, *Mnemiopsis* were more frequently most abundant in surface samples (37 of 55 sample pairs, $\chi^2 = 6.56$, $p =$

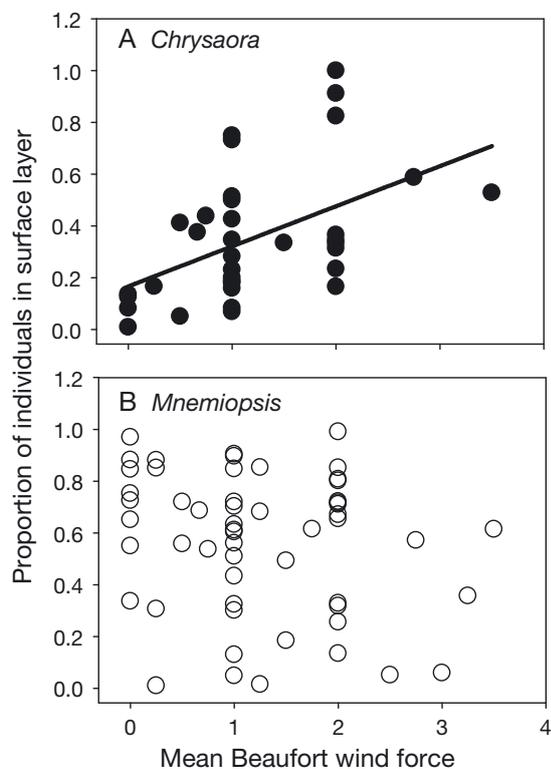


Fig. 7. Relationships between gelatinous species and Beaufort scale wind force. Within the range of wind forces during which we sampled, the proportion of *Chrysaora* in the surface layer increased with increasing wind force ($R^2 = 0.23$, $p = 0.0061$). The relationship between *Mnemiopsis* and wind force was not significant in this analysis ($R^2 = 0.05$, $p = 0.113$), but was significant when day vs. night was included in the model (see 'Results')

0.01). Vertical separation of *Chrysaora* and *Mnemiopsis* was more marked in Mackall Cove than in the lower creek or mainstem river sites in spite of the shallow water column and lack of strong density stratification in the cove. Surface water conditions in coves tended to be calmer than in other habitats samples, most likely because trees and hills sheltered the water surface from wind.

Surface current speeds measured in Mackall Cove tended to average $< 0.25 \text{ km h}^{-1}$ during flood and ebb tide observations (D. Breitbart unpubl. data). Therefore, swimming behavior of *Chrysaora* could conceivably influence retention within this cove if swimming direction tended to be oriented away from the creek mouth. However, video images of 57 *Chrysaora* individuals swimming within approximately 0.2 m of the surface of Mackall Creek did not provide strong evidence for this behavior. Surface swimming direction varied greatly among individuals, did not vary consistently with tidal stage, and was not tightly oriented away from the mouth of the cove (Table 3, Fig. 9). During flood tides on 26 July and 8 August, 53% of *Chrysaora* were oriented within $\leq 90^\circ$ of the cove origin (i.e. towards the junction of the cove and St. Leonard Creek; $n = 30$). During ebb tides on the same dates, only 25% were oriented in this same direction, but our sample size was much smaller ($n = 8$). U^2 tests (Oriana 4 software) showed no difference in swimming direction between ebb and flood tides for paired July samples ($U^2 = 0.072$, $p > 0.50$) or on both dates combined ($U^2 = 0.068$, $p > 0.50$) in Mackall Cove, reflecting the large variation among individuals in swimming direction (Table 3). In lower St. Leonard Creek, 3 of 4 individuals were oriented towards the creek mouth during flood tide, and 50% of *Chrysaora* individuals were oriented toward the creek mouth during ebb tide.

DISCUSSION

The spatial patterns of gelatinous zooplankton we documented during 2004 and 2005, when both *Chrysaora* and *Mnemiopsis* were abundant, can be viewed as waves of predation pressure by the 2 gelatinous species spreading in opposing directions through the landscape. *Mnemiopsis* appeared first in the subpycnocline mainstem Patuxent River, and then spread to the surface of the mainstem and into the creeks and coves. In contrast, sea nettle medusae and ephyrae were initially most abundant in the upper creeks or coves, with abundances increasing in the mainstem as the summer progressed.

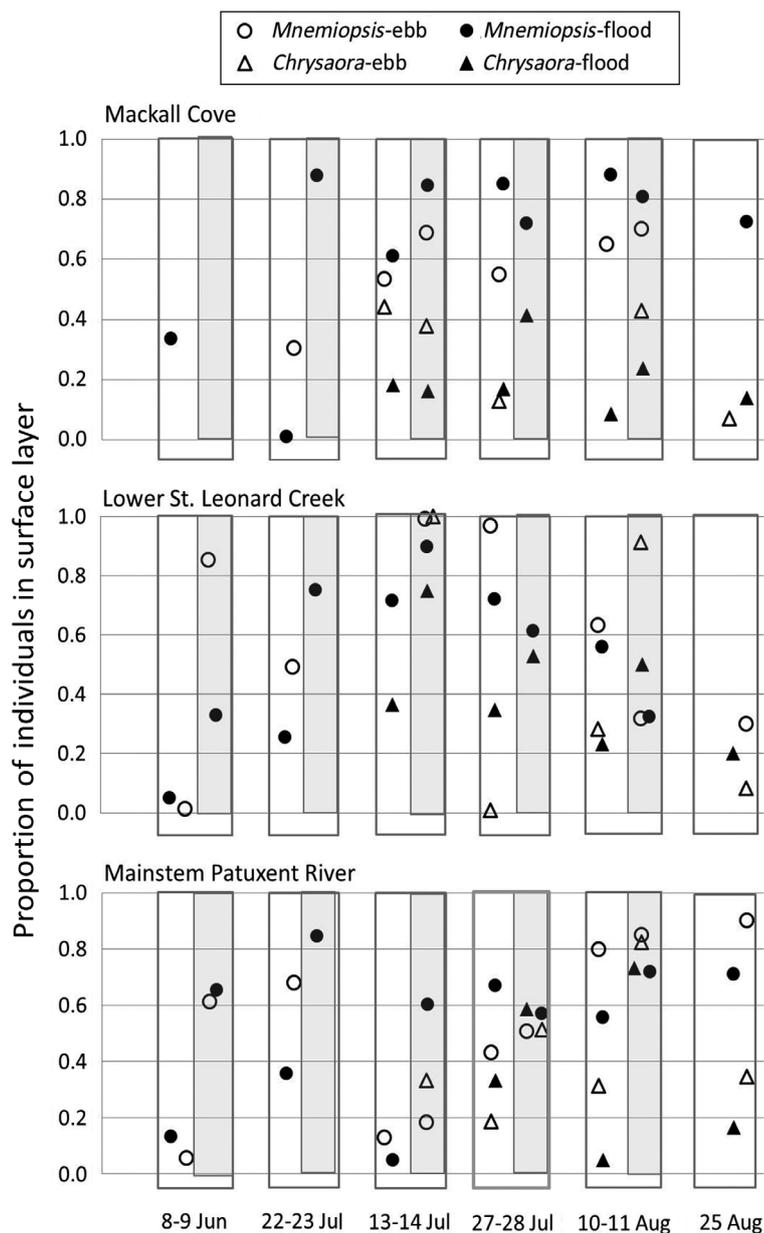


Fig. 8. Proportional densities of *Mnemiopsis* and *Chrysaora* in the surface layer at St. Leonard Creek cluster sites. Shaded bars indicate night samples

Table 3. Summary statistics for *Chrysaora* swim angles videotaped at the surface in Mackall Cove and lower St. Leonard Creek during 2005

Date	Site	Tide Stage	Mean direction	Circular standard deviation	N
26 Jul	Mackall Cove	Ebb	275.3°	73.5°	8
26 Jul	Mackall Cove	Flood	208.7°	71.2°	7
8 Aug	Mackall Cove	Flood	338.9°	142.4°	30
8 Aug	St. Leonard Creek	Ebb	93.5°	84.1°	8
8 Aug	St. Leonard Creek	Flood	175.8°	68.9°	4

Chrysaora predation likely eliminated *Mnemiopsis* in the upper creeks and coves by late summer in 2004 when they were abundant, but medusae never reached sufficient numbers in the mainstem Patuxent to eliminate ctenophores there in either year. Quantile regression indicated that *Chrysaora* limited maximum *Mnemiopsis* volume (ml m^{-3}) during July and August. When *Chrysaora* densities were above approximately 0.18 ind. m^{-3} , *Mnemiopsis* volume was at or near zero (Fig. 8). This *Chrysaora* density is similar to that estimated to control *Mnemiopsis* by Breitburg & Fulford (2006). In addition, as *Mnemiopsis* densities declined, many individuals had uneven lobes, indicative of *Chrysaora* predation (Purcell & Cowan 1995). Control of *Mnemiopsis* populations by *Chrysaora* predation is an important component of seasonal dynamics in Chesapeake Bay, as well as other mid-Atlantic estuaries in the US. It has been reported in New Jersey (Mansueti 1955), North Carolina (Miller 1974), and Virginia (Condon & Steinberg 2008), as well as in Maryland (Purcell & Cowan 1995) waters. More generally, predation by other gelatinous species is commonly cited as a major factor controlling ctenophore populations in estuaries and inland seas (e.g. Purcell et al. 2001, Shiganova et al. 2004).

These opposing waves of gelatinous zooplankton predation are likely to affect the spatial distribution and temporal patterns of survival of ichthyoplankton, copepods, and oyster larvae. Based on clearance rates for *Mnemiopsis* and *Chrysaora* in Purcell et al. (2001), during summer, *Mnemiopsis* consumption was sufficient to remove 100% of the bay anchovy eggs, zooplankton and oyster larvae (assuming clearance rates for oyster larvae are at least as high as for mesozooplankton) per day in the mainstem river. In contrast, during July and August 2004 when *Chrysaora* were abundant, *Mnemiopsis* would generally have been able to clear no more than 10% of zooplankton or fish eggs per day in the creeks and coves we sampled.

Because *Chrysaora* does not consume bivalve larvae (Purcell et al. 1991) but *Mnemiopsis* is a voracious predator on

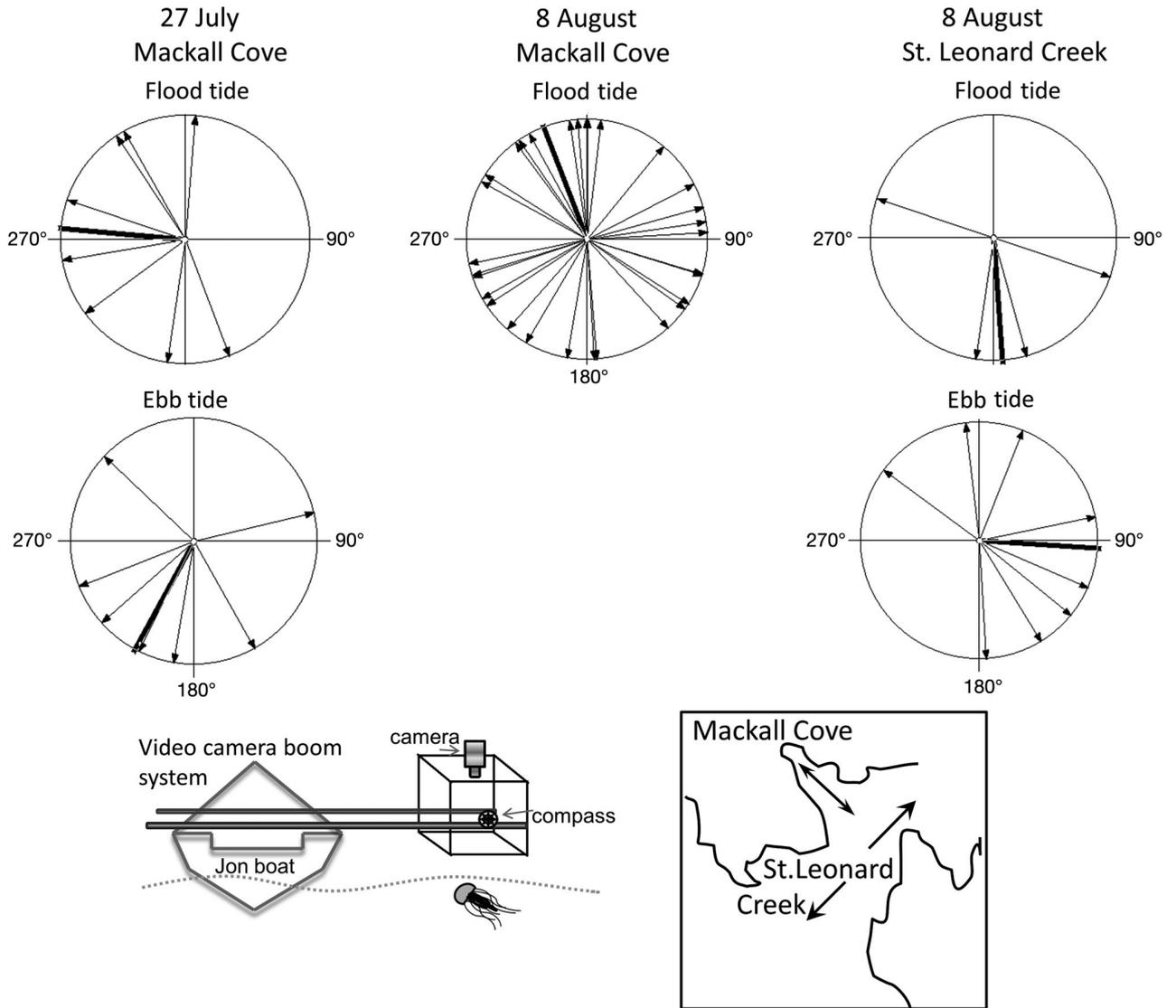


Fig. 9. Surface swimming direction of *Chrysaora* relative to tidal stage. Arrows indicate swimming directions of individuals; black bars are mean swimming directions. Swimming direction was recorded in Mackall Cove and lower St. Leonard Creek with a video camera suspended off the side of a small boat. Arrows in the map show the main axis of sampling areas that was compared with swimming directions

oyster larvae (Nelson 1925, Purcell et al. 1991), high medusae abundances in creeks and coves may indirectly facilitate oyster settlement in those areas by eliminating or greatly reducing an important larval predator. Consideration of these biological interactions when determining site selection for oyster restoration may be particularly important. Peak *Chrysaora* densities in Chesapeake Bay coincide with June to August occurrences of oyster larvae in Chesapeake Bay (Kennedy 1991). As a result, the landscape-level patterns of *Chrysaora* predation on *Mnemiopsis* may create landscape level patterns in the suitability of habitat for oyster recruitment and the establishment of sustainable oyster populations.

The presence of large *Mnemiopsis* individuals in the earliest mainstem Patuxent River samples in which ctenophores were present along with data from the Versar zooplankton monitoring program indicate the survival of overwintering adults in the mainstem Patuxent River. On the earliest date each year when more than a few scattered individuals were collected (in >1200 m³ [in 2003] to >1800 m³ [in 2004] of water sampled on each date), *Mnemiopsis* densities in the mainstem Patuxent bottom layer averaged 1 to 2 orders of magnitude higher than in other habitats. The combination of high egg production rates, short generation times and the capacity for self-fertilization would allow these overwintering

individuals to seed the rapidly increasing and spatially expanding populations we found in our field sampling (Baker & Reeve 1974, Kremer 1976, Costello et al. 2012). High densities of larvae and very small postlarval *Mnemiopsis* in the mainstem Patuxent River also suggest that this habitat is an important early-season source of summer populations within the broader Patuxent River system.

Although the general model of cold season refugia that serve as sources for population expansion as the water warms (Costello et al. 2006, Beaulieu et al. 2013) appears to be supported by our study, the specific characteristics of refugia sites may be quite different in Chesapeake and Narragansett Bays, and may reflect important differences between the systems. Residence time in Chesapeake Bay is nearly 10 times longer than in the central region of Narragansett Bay (Dettmann 2001). This would increase the potential for *Mnemiopsis* to be retained in mainstem Chesapeake Bay and large tributary main-channel habitats even during cold temperatures with no or low reproduction, when advective losses can eliminate local populations (Beaulieu et al. 2013). Creeks and embayments are important overwintering habitat in Narragansett Bay (Costello et al. 2006, Beaulieu et al. 2013). But high predation by *Chrysaora* may reduce numbers of potential overwintering *Mnemiopsis* in embayments and creeks in Chesapeake Bay, resulting in densities too low to serve as source populations the following spring, at least during years that *Chrysaora* populations persist into autumn. The latter point is difficult to assess because of the lack of sampling for gelatinous zooplankton during late fall and early spring in these habitats. A more directed comparison between the 2 systems could better characterize differences and similarities in overwintering habitat in mid-Atlantic and New England estuaries, and may be useful for identifying general system and habitat characteristics controlling *Mnemiopsis* populations year-round.

Locations of early season larval peak densities also differed between *Mnemiopsis* and *Chrysaora* species within the Patuxent River. However, the relative importance of the mainstem river and the shallower creeks and coves for *Chrysaora* asexual reproduction is unclear. There may be a substantial difference between total ephyrae production in a habitat (which would be strongly related to sustaining *Chrysaora* populations) and ephyrae densities (which are especially important in determining effects of *Chrysaora* predation on prey populations) because of differences in the bottom area:water volume ratio or the

effect of currents on accumulation of ephyra and medusa in the shallower subhabitats. Equal ephyrae production per m² of bottom would result in lower water column densities (no. m⁻³) and perhaps great export in the deeper, faster flowing mainstem than in shallower creeks and coves. A more detailed, targeted study of site-specific reproduction, including the role of stone revetment in enhancing natural habitat (Duarte et al. 2013) is required to resolve the question, first raised by Cargo & Schultz (1966) of whether headwaters of tidal creeks are the primary nursery habitat for *Chrysaora*. Our data (in Duarte et al. 2013, and H. Soulen et al. unpubl. data) indicate that subtidal stone revetment supports similar densities of *Chrysaora* polyps as does oyster shell, but the total surface area of subtidal rock plus oyster shell in different habitats is unknown.

Miller (1974) suggested that the bottom-oriented behavior of small *Mnemiopsis* may facilitate its retention in estuaries, but also found highest densities at the surface during the day. During 2005, when we sampled vertical distributions in finer detail than the other years of our study, both species tended to be more bottom-oriented during the day than at night; averaged across all samples, *Chrysaora* were more abundant in bottom layer samples and *Mnemiopsis* were more abundant in surface samples. In general, this pattern may increase retention of *Chrysaora* and downstream transport of *Mnemiopsis*, assuming that the strength of day and night tidal currents and river flow were similar.

The only samples in which *Chrysaora* densities were substantially higher in the surface layer than in bottom layer samples in the mainstem Patuxent were the night samples on 10 August, which were the only samples at that site in which bottom dissolved oxygen concentrations were <2.0 mg l⁻¹. On the same date and during one night sample on 13 July, bottom oxygen was <2 mg l⁻¹ in lower St. Leonard Creek, and again *Chrysaora* were more abundant near the surface than in the bottom layer. These results, along with results in Keister et al. (2000) and Kolesar et al. (2010) indicate that bottom layer oxygen depletion may reduce retention of *Chrysaora* by reducing their use of bottom waters. Similarly, when medusae are abundant, predation or predation threat by *Chrysaora* in the bottom layer could negatively affect retention of *Mnemiopsis*. The dominant use of the upper meter of the water column in Mackall Cove may have been facilitated by the typically calm wind conditions at the surface at that site. *Mnemiopsis* avoids surface waters at high levels of vertical shear (Mianzan et al. 2010).

We did not find the relationship between temperature and location of early season appearances of either species that has been found in several other studies, nor did we find a correspondence between spatial variation in temperature and location of *Mnemiopsis* blooms (Condon & Steinberg 2008). In our case, the highest densities of *Mnemiopsis* on the first sample date in which we collected more than a few scattered individuals was always in the bottom layer of the mainstem Patuxent River, which was consistently the coldest habitat sampled at that time of year. In July 2003, when highest *Mnemiopsis* densities were found in coves, surface layer temperatures at all sites and locations sampled were within 1°C on each date. *Chrysaora* ephyrae were first found in lower creeks or coves, where surface water temperatures on dates of first appearance were either the same (i.e. within 0.1°C; 2003) or 2°C (2004) warmer than mainstem river surface waters, but were well above the 17°C threshold for strobilation reported for *Chrysaora* (Cargo & Schultz 1967).

Our tidal sampling and measures of swimming direction do not provide strong evidence for tidally-cued directional swimming likely to result in retention in inlets and creeks. Swimming direction of *Chrysaora* varied among individuals within each of the 5 sample periods. Mean swimming direction did not vary systematically between flood and ebb tides in Mackall Cove where current speeds were low, and bore no consistent relation to current direction. In addition, both species had high densities in coves when they were not subject to substantial predation (i.e. *Chrysaora* in 2004 and 2005 and *Mnemiopsis* in 2003) in spite of substantial differences in swimming capabilities and vertical distributions. Our results, therefore, do not support a role for selective tidal stream transport in creating the spatial patterns we observed. Instead, it is likely that a combination of hydrodynamics favorable for retention, and habitat favorable for growth and reproduction result in high population densities of *Mnemiopsis* in years when *Chrysaora* densities are low, and high densities of *Chrysaora* in months and years when that species was abundant in coves and inlets. Our goal was not to examine causes of interannual variation in *Chrysaora* abundance, but the occurrence of interannual variation in *Chrysaora* during our study allowed us to examine spatial patterns of *Mnemiopsis* in years of high and low densities of their predator.

We also observed *Chrysaora* swimming behavior within Mackall Cove suggestive of mating behavior. Under calm conditions, many pairs of adult *Chrysaora* were seen circling each other in close proximity.

Although we cannot rule out other reasons for this behavior, such as frequent turning behaviors within high density prey patches (Matanoski et al. 2001), a high incidence of spawning in shallow subsystems would be consistent with our 2004 results for ephyra distributions. A clear next step would be to collect pairs of individuals to determine sex and reproductive state.

Spatial variation and patchiness of planktonic organisms is the rule rather than the exception. Previous work on gelatinous zooplankton, including the 2 species that were the focus of the current study, has shown variation in densities on scales of meters to 100s of kilometers related to temperature, salinity, hydrographic conditions, dissolved oxygen, and depth (Keister et al. 2000, Costello & Mianzan 2003, Purcell & Decker 2005, Costello et al. 2006, Decker et al. 2007, Condon & Steinberg 2008, Kolesar et al. 2010, Sexton et al. 2010). Although we were unable to identify the specific mechanisms responsible for these patterns, spatial variation in *Chrysaora* density in the Patuxent River system showed the same pattern of higher densities in creeks than in the mainstem river in studies spanning nearly 40 yr (Cargo & Schultz 1966, this study), and similar patterns have been found in both the eastern (Purcell 1992) and western shores of the Chesapeake Bay system. When spatial patterns of medusae and ctenophores are consistent relative to physical features of the landscape, these trophically important consumers can create repeatable spatial variation in habitat suitability and survival for their prey. In addition, spatial patterns of high density *Chrysaora* populations can potentially be used to inform decisions on siting of oyster restoration efforts, and where successful, these oyster restoration sites may enhance and reduce variability in *Chrysaora* ephyra production by creating habitat for the overwintering sessile stage of this species.

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