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Deployment of an imaging system to investigate fine-scale spatial distribution of early life stages of the ctenophore *Mnemiopsis leidyi* in Chesapeake Bay

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A high-resolution digital imaging system, the zooplankton visualization and imaging system (ZOOVIS) was deployed in the mid-region of Chesapeake Bay to investigate the fine-scale distribution of small individuals of the lobate ctenophore *Mnemiopsis leidyi*. Counts of individuals, mostly <5 mm, were enumerated from each frame of ZOOVIS and merged with data from a conductivity-temperature-depth to provide corresponding values of depth, temperature and salinity. *Mnemiopsis leidyi* rarely occurred below the pycnocline depth but commonly occurred in the upper water column. Where the water column was strongly stratified, *M. leidyi* tended to be more common near the pycnocline, but it was more abundant near the bottom at locations where the water column was well mixed. Horizontally, *M. leidyi* was more abundant on the shoulders of the middle Bay than in the deeper main channel. In this survey, *M. leidyi* occurred more frequently in relatively warm and low salinity water. Furthermore, small *M. leidyi* were patchily distributed and the patch size was <700 m in horizontal extent. A zero-inflated, general additive model successfully simulated the spatial distribution of *M. leidyi*, with temperature and salinity as predictors. The ZOOVIS system proved to be a valuable tool to study fine-scale distributions of small and delicate gelatinous zooplankton, even in the relatively turbid conditions that prevailed in this estuarine system.

KEYWORDS: ZOOVIS; zooplankton; *Mnemiopsis leidyi*; spatial distribution; zero-inflated general additive model; pycnocline depth

INTRODUCTION

Gelatinous organisms are increasingly recognized as key components of marine ecosystems. In some circumstances, they may strongly affect ecosystem structure and function (Malakoff, 2001; Daskalov, 2002; Richardson *et al.*, 2009; Condon *et al.*, 2011). Although historical data are insufficient to reach firm conclusions (Condon *et al.*, 2012), mounting evidence suggests that the structure of pelagic ecosystems can change rapidly from one dominated by fish to a less desirable state dominated by gelatinous zooplankton, with substantial ecological, economic and social consequences (Malakoff, 2001; Richardson *et al.*, 2009). The shift from fish-dominated to gelatinous-dominated systems can be caused by overexploitation of fish (Lynam *et al.*, 2006) and climate-related environmental change (Mills, 2001; Purcell and Decker, 2005; Richardson, 2008). Historically, the trophic role of gelatinous zooplankton had been characterized as a trophic dead end (Arai, 2001) but we now know that jellyfish are prey for many fishes (Link and Ford, 2006) and other predators (Houghton *et al.*, 2006).

The lobate ctenophore *M. leidyi* occurs over a wide latitudinal range, 40°N–46°S (Mianzan, 1999; Purcell *et al.*, 2001a). It is abundant within estuaries and coastal waters of the eastern USA (Kremer, 1994; Purcell, 2005) and is invasive in the Black and Baltic Seas (Shiganova, 1998; Javidpour *et al.*, 2006). This ctenophore has a relatively simple life cycle that is entirely planktonic. Hermaphroditic adults produce fertilized eggs that develop through a larval stage and gradually grow into an adult (Sullivan and Gifford, 2004). In the Chesapeake Bay, adult *M. leidyi* are euryhaline and their abundance is at least partly controlled by predators such as the scyphomedusa *Chrysaora quinquecirrha* (Breitburg *et al.*, 1997; Purcell and Decker, 2005; Kimmel *et al.*, 2009).

Understanding spatial and temporal variability of the *M. leidyi* population requires information on early life stages. The abundant early life stages, though little understood at present, must contribute importantly to the consumption of prey and population productivity. Spatial and temporal variability in early life stages, coupled with physical processes such as advection, likely determine adult abundance and distribution. A knowledge of environmental factors and processes that impart variability to abundance and distributions of early life

stages is critical to understanding *M. leidyi* population dynamics.

Small (<5 mm) gelatinous zooplankton remain poorly studied because they (i) break up in nets making them difficult to sample quantitatively (Reeve and Baker, 1975; Remsen *et al.*, 2004), (ii) are difficult to preserve or (iii) are so patchily distributed that they are poorly sampled using traditional methods (Mills, 2001). Recent advances in zooplankton and ichthyoplankton imaging systems make it feasible to quantitatively sample small individuals of gelatinous zooplankton and map their fine-scale spatial distributions (Jaffe, 2005; Benfield *et al.*, 2007). However, the application of imaging systems has been almost entirely restricted to relatively clear offshore waters (e.g. Benfield *et al.*, 1996; Remsen *et al.*, 2004; Cowen and Guigand, 2008). Their successful use in estuaries characterized by high turbidity attributable to high phytoplankton and particulate concentrations is a challenge.

Our study had two objectives: (i) to demonstrate the expediency of a recently developed imaging system, the ZOOVIS, for pelagic sampling in high-turbidity estuarine environments, especially for fragile gelatinous taxa; and (ii) to map and explain the spatial distribution of early life stages of a common ctenophore *M. leidyi* in the mid-region of Chesapeake Bay. Specifically, we analyzed the spatial distribution of early life stages of *M. leidyi* in relation to a frontal region where the outflow of the Patuxent River sub-estuary enters Chesapeake Bay.

METHOD

Study site and sampling

The Chesapeake Bay is the largest estuary in the USA, extending ~320 km from its head to its mouth near Virginia Beach, Virginia (Fig. 1). We deployed ZOOVIS in the region offshore of the Patuxent River mouth (Fig. 1) on 19 July 2011 between 8:30 and 11:30 a.m. local time. The Secchi depth, a measure of water transparency, was <2 m.

The imaging system, ZOOVIS, employs a high-resolution digital still camera with a 12 bit, 5.0 megapixel Charge Coupled Device (CCD) sensor (Fig. 2g). The camera is capable of acquiring full-frame images at 15 Hz. Specialized optics enable a highly collimated red

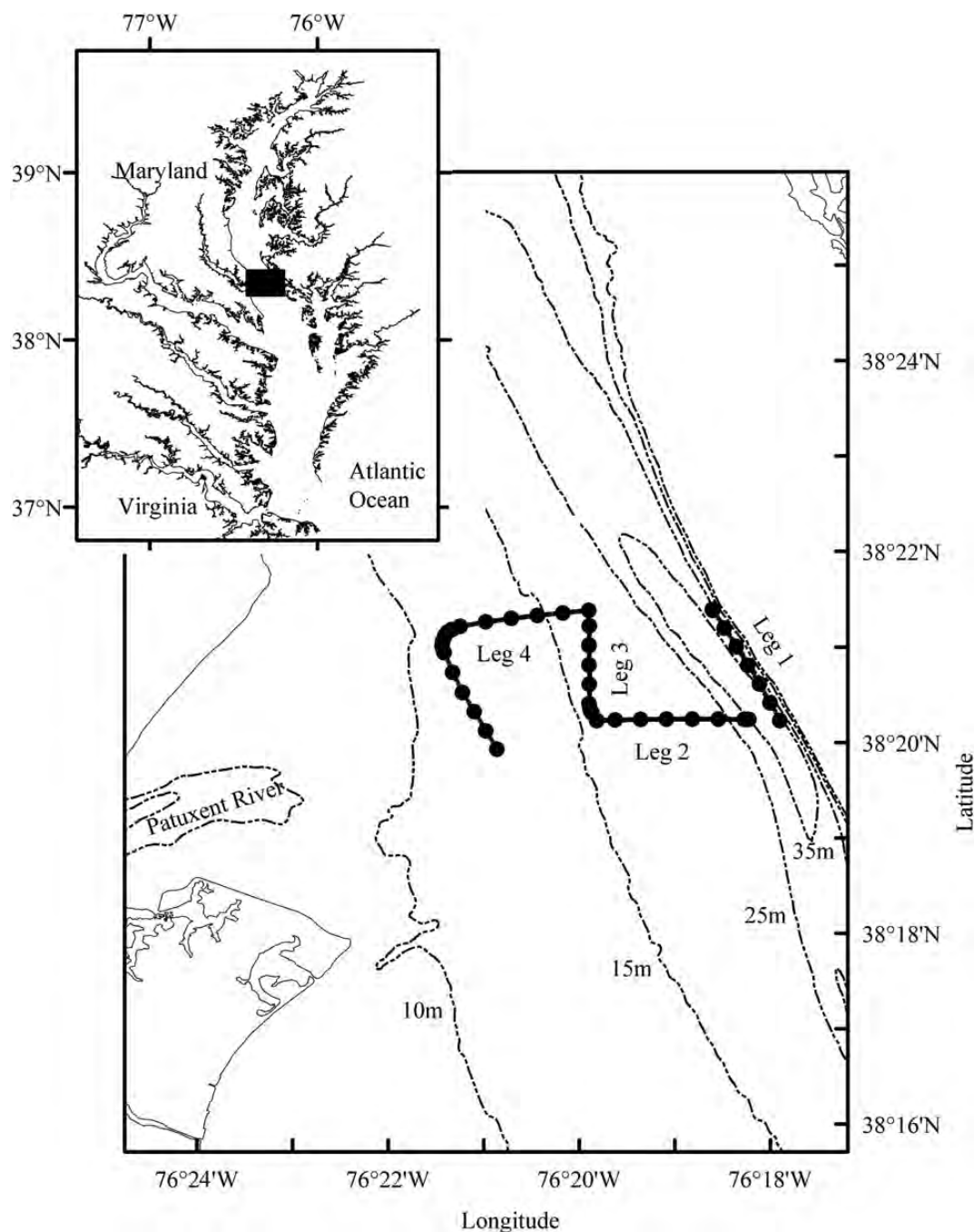


Fig. 1. Survey track lines and map of Chesapeake Bay (upper left).

(625 nm) beam produced by an LED to be pulsed at 5- μ s intervals. This beam passes directly through a relatively large volume of water between the illumination and camera pods. Within the camera pod, another set of lenses focuses the beam back on to the CCD. This shadowgraph illumination permits a long depth of field (currently 30 cm), within which, objects of 20–40 μ m

and larger can be resolved. The image volume is ~ 240 mL for each frame, which enables the system to quantify the contents of 3.6 L s^{-1} (216 L min^{-1}) at its maximum frame rate. The entire system is battery powered and records data internally. In the present study, the camera acquired images at 4 Hz, (0.96 L s^{-1} or 57.6 L min^{-1}).

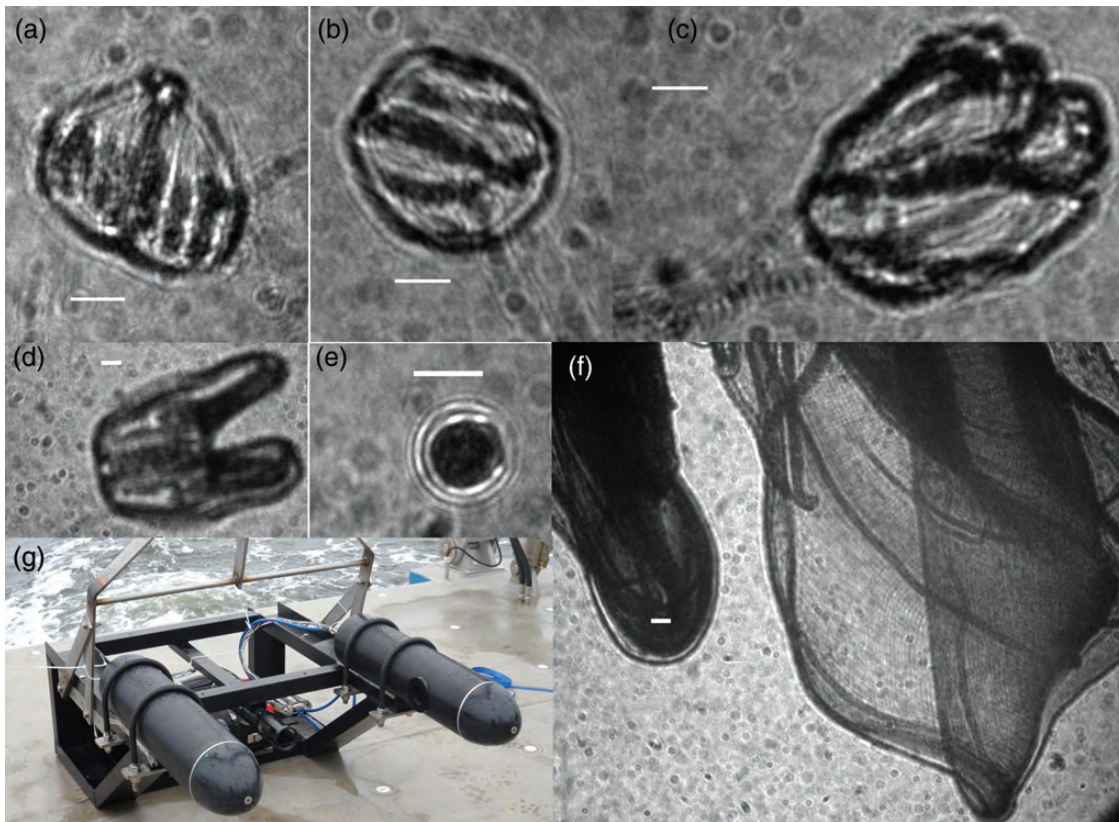


Fig. 2. Stages of *Mnemiopsis leidyi* and zooplankton sampled by the visualization system (ZOOVIS): (a) tentaculate-stage cydippid larva, (b) transition-stage larva with tentacles and small oral lobes, (c) lobate-stage larva, with developing auricles, (d) post-larval stage with completely developed auricles and oral lobes; (e) unidentified egg; (f) large fragment of *M. leidyi*; and (g) photograph of ZOOVIS. White bars in (a)–(f) represent 1 mm.

The imaging system was equipped with a conductivity-temperature-depth (CTD) (RBR Model XR-420) to record environmental data including water depth, temperature and salinity at 0.5 Hz. The vessel steamed at 1 m s^{-1} and a wire on the winch was paid out or hauled back at 0.15 m s^{-1} to deploy ZOOVIS along an undulating (tow-yo) trajectory. The mean horizontal and vertical tow speeds were 1 and 0.1 m s^{-1} , respectively. All tows were within 2 m of the bottom to avoid possible damage to ZOOVIS and within $\sim 1 \text{ m}$ of the surface to avoid imaging within the bubble field of the ship's wake. There were four survey legs that resulted in 52 paired up and down casts (Figs 1 and 3).

Each ZOOVIS image was visually examined for the presence of *M. leidyi*. Then, abundances were estimated for 2 s bins and merged with data from the CTD to provide a corresponding value of depth, temperature and salinity to accompany each estimate of abundance. The abundance of *M. leidyi* was estimated as the number of ctenophores encountered in 2 s divided by the volume sampled (1.92 L). The longitude and the latitude were derived from the vessel position and merged with the CTD data.

Data analysis

We examined the occurrence of *M. leidyi* in relation to water depth to determine the depth distribution with respect to variability in the physical environment. We then constructed temperature–salinity (T–S) diagrams to generate density surfaces and the occurrences of *M. leidyi* were overlaid on the density surface. T–S profiles from different segments of the survey area were examined to compare the variability in hydrographic conditions.

Spatial autocorrelation, the distances at which data are inter-dependent, can be analyzed to describe the patch size of an organism. To estimate the patch size of *M. leidyi*, the semi-variogram was calculated to estimate the spatial scale beyond which ctenophore densities were spatially unrelated. The semi-variance was calculated as $\gamma(h) = \frac{1}{2} \text{Var}[\mathcal{Z}(x) - \mathcal{Z}(x+h)]$, where $\mathcal{Z}(x)$ and $\mathcal{Z}(x+h)$ are the number of *M. leidyi* at any two spatial locations separated by a spatial distance h . Data were binned using $h = 221 \text{ m}$, such that there were from 125 to 146 paired spatial distances in each increment, which allowed reasonable estimation of the semi-variogram.

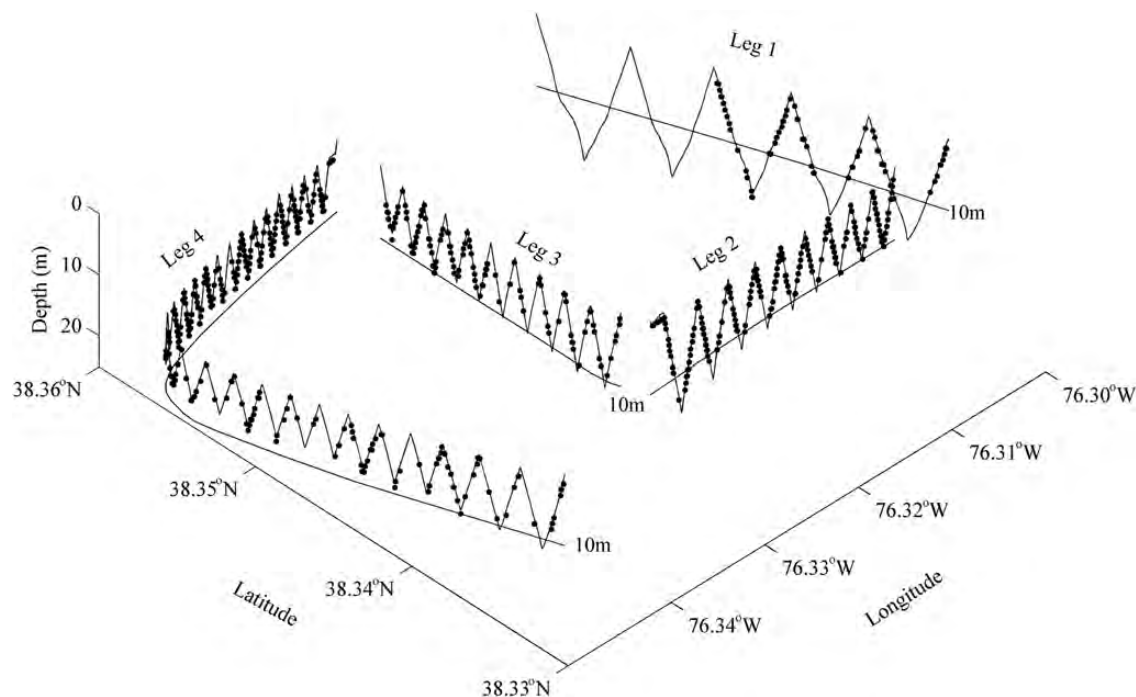


Fig. 3. The presence of small *Mnemiopsis leidyi* in the survey area. Black undulating lines indicate the track of the zooplankton visualization system in relation to the water depth. Black horizontal lines indicate a water depth of 10 m. Black dots represent the presence of ctenophores.

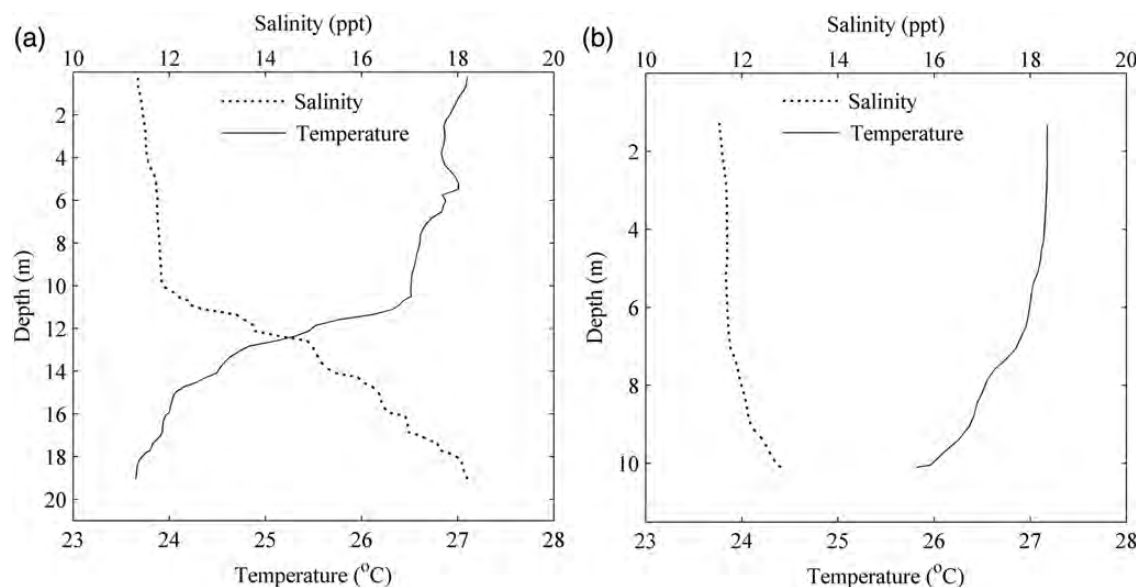


Fig. 4. Representative temperature and salinity for different parts of the survey areas. (a) Typical temperature and salinity profiles for survey leg 1 shown in Fig. 1 where the water column was stratified. (b) Typical temperature and salinity profiles for the survey legs 3 and 4 where the water column was well mixed.

Modeling the spatial distribution

To map the spatial patterns, a mean abundance of *M. leidyi* was calculated based on survey data (every 2 s) for each up-down cast, e.g. bottom to surface or surface to bottom. In total, 104 mean abundances were

estimated. A generalized additive model (GAM) was applied to model the spatial distribution. The distribution of abundance data for the early life stages approximately followed a negative binomial distribution. The GAM model was used to analyze the relationship

between the abundance of *M. leidy* and environmental factors. The Akaike information criterion was used to select the best combination of independent variables. Water T–S were retained in the final model after selection: $g(\mu) = \alpha + s(\text{temperature}, k_1) + s(\text{salinity}, k_2)$, where g is a log link, $g(\mu)$ is the expectation of observation (i.e. abundance), α is the intercept, s is a cubic spline smoothing function and k_1 and k_2 are the smoothing parameters that were selected by the generalized cross-validation method. The model coefficients were estimated based on the penalized likelihood maximization method.

RESULTS

ZOOVIS and hydrographic conditions

Approximately 50 000 images were acquired during the cruise in which various taxa including copepods (dominant species: *Acartia tonsa* and *Eurytemora affinis*), ctenophores (*M. leidy*), hydromedusae (e.g. *Liriope tetraphylla*) and chaetognaths (*Sagitta* spp) were recorded. For *M. leidy*, images of different developmental stages were acquired (Fig. 2a–f) and most individuals were <5 mm.

The bathymetry of the survey area was characterized by a relatively deep channel on the east side of the Bay and the Patuxent River outflow on the west side (Fig. 1). The buoyant river plume resided on top of relatively salty water that typically forms a lateral frontal zone (e.g. Fig. 2 in Roman *et al.*, 2005). The first survey leg was in the main channel where survey sampling depths ranged 0–20 m (Fig. 3). Temperature ranged 23.50–27.13°C and salinity from 11.30 to 19.35. T–S patterns indicated strong stratification (Fig. 4a). The second survey leg crossed the Bay where survey depths ranged 0–18.4 m, with the deepest casts near the main channel. T–S showed less vertical variation and less stratification (Fig. 4b) as the water depth shoaled. The third survey leg began in shallow water (~10-m survey depth) and gradually deepened. The vertical variation in T–S gradually increased as the water depth increased. The fourth survey leg was mostly in shallow water near the Patuxent River mouth. T–S showed relatively little variation and no strong stratification (Fig. 4b).

Distribution of *M. leidy*

The abundance of early life stages of *M. leidy* differed among transect legs: leg 1, 46 ± 48 individuals m^{-3} (mean \pm standard error, averaged over 2 s); leg 2, 177 ± 87 individuals m^{-3} ; leg 3, 100 ± 73 individuals m^{-3} and leg 4, 132 ± 99 m^{-3} . The overall vertical

pattern was clear: small early life stages of *M. leidy* were common in the upper water column but rare below the pycnocline. Where the water column was strongly stratified, e.g. survey leg 1, small *M. leidy* tended to be more common above the pycnocline, but under well-mixed conditions they tended to be more abundant near the bottom, e.g. the first part of leg 4 (Fig. 3). Small *M. leidy* were more abundant in shallow water near the Patuxent River mouth (legs 3 and 4) and less abundant in deeper waters of the main channel (leg 1) (Fig. 3).

When occurrences of small *M. leidy* were overlaid on a T–S diagram that defined water types (Fig. 5), *M. leidy* occurred most commonly at temperatures >25°C and at salinities <13. The T–S profiles indicated that the temperature was ~24°C and the salinity was ~12 at the pycnocline. Most small *M. leidy* were above the pycnocline in relatively warm, low-salinity water (Fig. 5).

Spatial pattern and autocorrelation

The spatial distribution showed that early life stages of *M. leidy* were not uniformly distributed in the study area (Fig. 3). Small individuals were least abundant in the main channel near the eastern shore, more abundant in the relatively shallow water toward the western shore. The semi-variance plot indicated that when the lag distance increased to ~700 m, the semi-variance of small *M. leidy* abundance increased by >50% (Fig. 6a). The semi-variance of temperature increased >400% when the lag distance increased to ~700 m and increased >400% when the lag distance increased to 2500 m (Fig. 6b). The changes in semi-variance of salinity were similar to those for temperature and the figure is not shown here. Overall, the patch size of small *M. leidy* was less than ~700 m in the surveyed area (~6000 \times 2000 m).

Modeling the spatial distribution of small *M. leidy*

The GAM with negative binomial distribution explained a large proportion of the deviance in the abundance of *M. leidy* in the survey area. Overall, both T–S had significant effects on the abundance of small *M. leidy* (temperature: $\chi^2 = 23.20$, $P < 0.01$; salinity: $\chi^2 = 25.98$, $P < 0.01$). Over the range of temperature observations, the surface water temperature showed a predominantly negative effect on abundance of small *M. leidy* (Fig. 7a). At temperatures <25.5°C, its effect on abundance increased quickly as the temperature increased. At <12.0, salinity increases had a positive effect on small *M. leidy* abundance (Fig. 7b). However, when the salinity was >13, it had no significant effect. The modeled

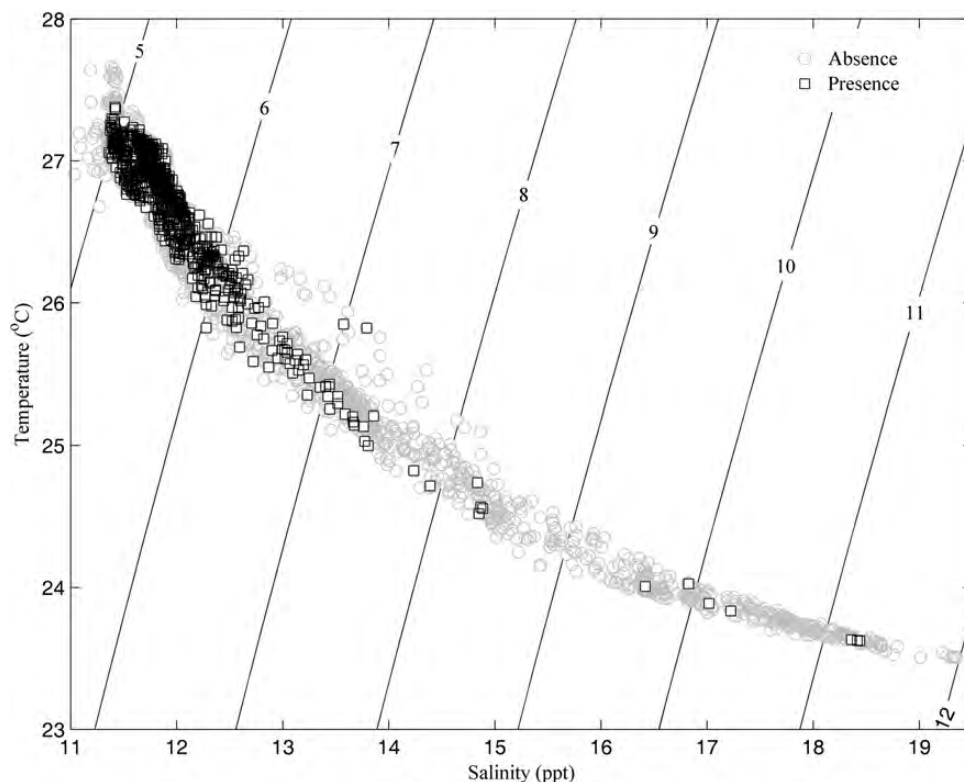


Fig. 5. The presence of <5 mm small *Mnemiopsis leidyi* in relation to temperature and salinity. The presence (black squares) and absence (gray circles) data were estimated for 2 s bins and merged with data from the CTD so that there was a corresponding value of depth, temperature and salinity to accompany each presence/absence data point. Solid lines indicate the iso-density lines. Black open circles indicate the absence of small *M. leidyi*. Solid blue squares indicate the presence of small *M. leidyi*.

abundance, while generally consistent with the observed abundance, tended to underestimate at high levels of abundance (Fig. 7c). The residuals did not show a clear pattern (Fig. 7d). T–S combined explained 51% of the variability in the observed abundance.

DISCUSSION

Estuaries are rich in physical features expressed over a range of spatial scales that are attributed to freshwater and saltwater mixing, tides, wind and other forces. The typically high turbidity and high concentration of particulates are impediments to the deployment of most currently available plankton imaging systems. The present study tested ZOOVIS in a frontal zone in Chesapeake Bay where low salinity water from the Patuxent River sub-estuary mixes with relatively high-salinity Bay water. ZOOVIS proved to be effective in this environment, providing high-quality data on zooplankton distributions in relation to hydrographic factors. In general, we believe that ZOOVIS can outperform other sampling instruments such as plankton nets, including multiple opening/closing nets, optical

plankton counters and acoustic samplers that have been deployed in Chesapeake Bay in the past because ZOOVIS (i) can provide data to document small-scale spatial distributions with reliable taxonomic resolution and (ii) can sample fragile species more effectively. Furthermore, studies in estuaries often use small vessels that are not equipped with winches capable of deploying imaging systems that require power from a fiber-optic link to the vessel. A battery-powered, self-contained imaging system, such as ZOOVIS, can be a useful tool for research on plankton distributions in estuaries.

Although ZOOVIS can provide information on diverse plankton taxa, the images alone, in general, do not provide adequate information at the species level for all organisms. In our case, the study was conducted in an area with ample historical data from a zooplankton monitoring program that provided taxonomic information (<http://www.chesapeakebay.net/data>). Additionally, we took plankton net samples which provide taxonomic information for the ZOOVIS images. The net collected large individuals of gelatinous zooplankton and confirmed that *M. leidyi* was the dominant ctenophore during the survey.

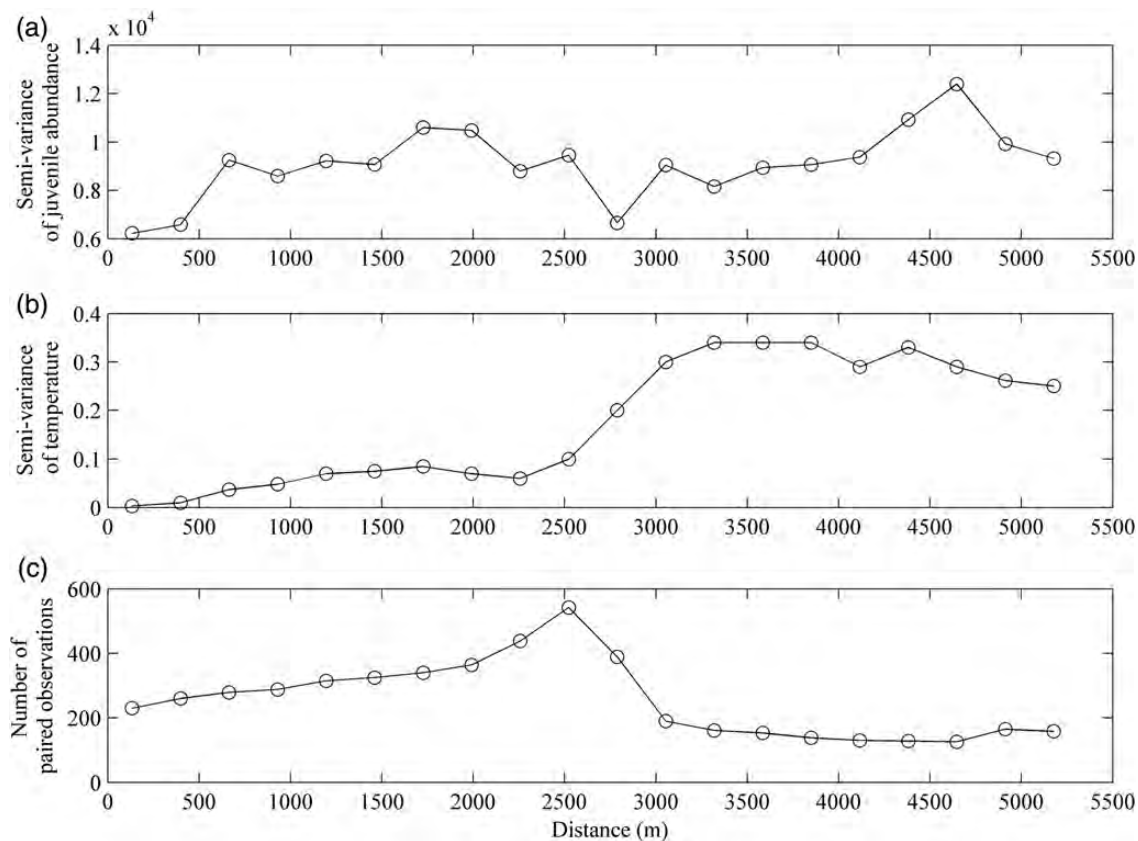


Fig. 6. (a) Semi-variance of small ctenophores (<5 mm) in the survey area. (b) Semi-variance of temperature. (c) The number of paired observations within each distance interval.

ZOOVIS provides useful information on the horizontal distribution of small *M. leidy*. MacGregor and Houde (MacGregor and Houde, 1996) surveyed the same area to investigate the distribution and abundance of bay anchovy *Anchoa mitchilli* eggs and larvae, gelatinous predators and zooplankton in relation to the Patuxent River plume. While they found no indication that anchovy eggs or larvae were concentrated in the frontal region, gelatinous predators, including *M. leidy*, and zooplankton, copepod nauplii in particular, tended to increase at the front. In the present study, we found that early life stages of *M. leidy* were also more abundant in the low-salinity plume of the Patuxent River, suggesting that the frontal region may be favorable for early life stages of *M. leidy* because of the relatively high abundance of potential prey such as copepod nauplii. Our estimated horizontal extent of the patch size for small *M. leidy* was ~ 700 m which is similar to the patch size of ~ 500 m reported by Sullivan *et al.* (Sullivan *et al.*, 2001) for adult *M. leidy* in Narragansett Bay. The horizontal distribution of small *M. leidy* in our

survey was likely due to their association with relatively low-salinity water masses.

ZOOVIS is a useful tool to investigate the vertical distribution of *M. leidy* in relation to the vertical structure of the water column. North and Houde (North and Houde, 2004) investigated the vertical distribution of bay anchovy eggs and larvae, gelatinous predators and zooplankton at a fixed station in the Bay's mid-region over a weekly period. They showed that *M. leidy* was present throughout the above-pycnocline layer and its abundance was negatively correlated with copepod nauplii and *Acartia tonsa* copepodite abundances. Purcell *et al.* (Purcell *et al.*, 1994, 2001b) also reported a negative relationship between *M. leidy* and copepods in Chesapeake Bay.

Javidpour *et al.* (Javidpour *et al.*, 2009) conducted a year-round investigation on the population dynamics and vertical distribution of *M. leidy* in the Baltic Sea, finding that during winter and spring, when the water column was well mixed, the bulk of the population was concentrated in the bottom waters. However, in

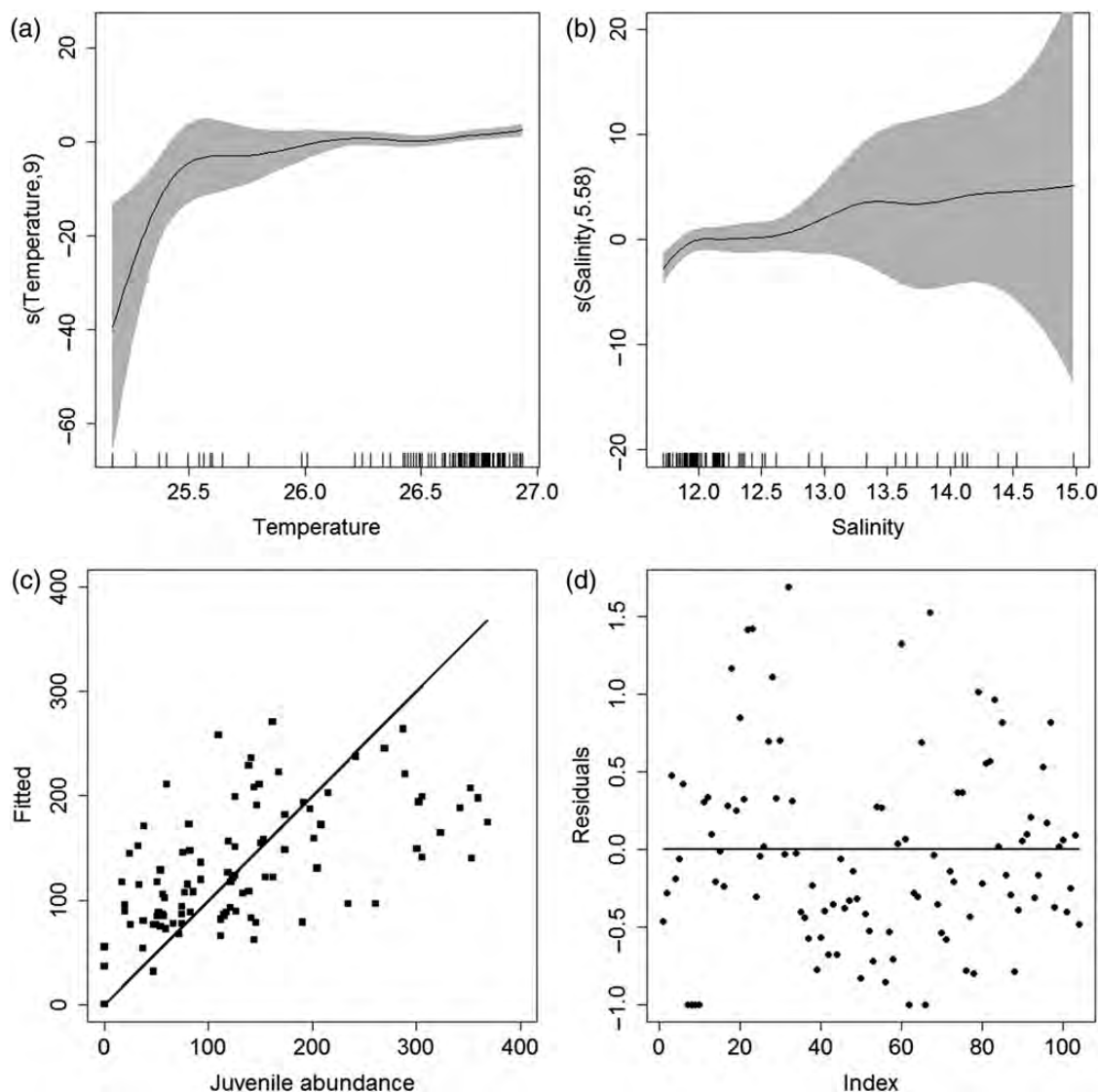


Fig. 7. Effects of predictor variables for the abundance of small *M. leidyi* from the general additive model: (a) temperature, (b) salinity, (c) the predicted values versus observed values and (d) the distribution of residuals. The shaded area represents the 95% confidence interval.

summer and fall, when the water column was stratified, the bulk of the population shifted to occupy the upper layers. Although our study is only a snapshot, it provides information complementary to that reported based on traditional sampling techniques. In our survey, *M. leidyi* rarely occurred below the pycnocline depth, ~ 10 m, but commonly occurred in the upper water column. Where the water column was strongly stratified in the main channel, *M. leidyi* tended to be more common near the pycnocline, but in the shallower, unstratified water on the shoulders of the channel it was more abundant near the bottom. The near-bottom distribution where the water column was well mixed is potentially related to the vertical

shear structure: when the surface vertical shear was high, ctenophores tended to occur deeper in the water column where shear levels were lower (Mianzan *et al.*, 2010).

ZOOVIS provides data on finer spatial scales than traditional plankton nets. ZOOVIS is designed to visualize small-scale distributions and abundance while nets are designed to estimate abundance integrated over wider spatial scales. However, our estimated abundances of early life stages of *M. leidyi* from ZOOVIS are comparable with abundances measured by Condon and Steinberg (Condon and Steinberg, 2008) in the York River sub-estuary of Chesapeake Bay, where they estimated a mean concentration of $128 \pm 81 \text{ ind m}^{-3}$ for

early life stage *M. leidyi* based on 104 vertical net tows. ZOOVIS is a useful alternative sampling method that can be adopted to study fine-scale distributions of zooplankton not easily accomplished with nets. Combining data from ZOOVIS with hydrographic measurements can lead to a much clearer understanding of factors that affect fine-scale spatial distributions of organisms in estuaries.

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