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Settlement and survival of *Chrysaora chesapeakei* polyps: implications for adult abundance

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ABSTRACT: Understanding the dynamics of pelagic scyphozoan blooms requires detailed knowledge of their source stages or sessile polyps. Results from a 2 yr *in situ* polyp settlement study of *Chrysaora chesapeakei* coupled with historical data and environmental conditions (temperature, salinity and water residence time) were analyzed to investigate the formation and distribution of polyp colonies at multiple spatial scales in Chesapeake Bay, USA. A spatially explicit generalized linear model suggested the importance of flushing rates in describing patterns of the spatial distribution of *C. chesapeakei* bay-wide. At smaller scales, seasonal variability of the pelagic stages of *C. chesapeakei* may be due to the survivability of *C. chesapeakei* polyps through harsh winter conditions within and between optimal habitat in sub-estuaries. Findings of this study reveal significant species- and stage-specific spatial and temporal patterns of *C. chesapeakei* within a local shallow habitat and affirm the importance of studying jellyfish species within a species-specific context.

KEY WORDS: *Chrysaora chesapeakei* · Polyps · Residence time · Spatial · Seasonality

INTRODUCTION

Although simple in body plan, jellyfish or gelatinous zooplankton represent a diverse array of species that span across phyla (i.e. Ctenophora vs. Cnidaria). Jellyfish adaptability, rapid reproductive response time, and stinging capabilities have large and seasonally consistent impacts on recreational and commercial enterprises (Purcell et al. 2007, Graham et al. 2014). The success of jellyfish in the fast-changing Anthropocene (i.e. they can tolerate a wide range of environmental conditions) make them formidable competitors and predators in the water column.

It has been suggested that their adaptability to environmental stressors may lead to a potential increase in abundance in parts of the world with degrading marine ecosystems (Mills 2001, Purcell et al. 2007, Richardson et al. 2009, Brotz et al. 2012, Purcell 2012, Graham et al. 2014). However, scyphozoan species are susceptible to hypoxia, variation in temperature and salinity as well as habitat loss (Breitburg et al. 2003, Wiegner et al. 2003, Breitburg & Fulford 2006, Lucas et al. 2012), making predictions in dynamic estuarine environments a difficult task. Researchers lack a strong understanding of jellyfish population dynamics because historical and current data are insufficient in drawing significant conclusions at a global scale (Condon et al. 2012, 2013). The uncertainty in jellyfish population dynamics is, in part, due to a lack of long-term monitoring data and limited sampling across different life stages (Gibbons & Richardson 2013, Brodeur et al. 2016). Furthermore, species diversity weakens broad-stroke generalizations of 'jellyfish population dynamics,' whereby research on jellyfish species outside the context of their life history can result in an underestimation of their effective impact on ecosystem function and structure (Lucas et al. 2014).

Many scyphozoan species have a complicated life history (Arai 2012) that contrasts with the simplicity of their morphological structure, i.e. they are metagenic species that exhibit alternation of generations.

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Dioecious male and female medusae of metagenic scyphozoans (marked 'A' in Fig. 1) produce planula larvae (B in Fig. 1) by way of proximity spawning (external fertilization). Planula larvae settle on hard substrate and grow into perennial polyps which form colonies through asexual reproduction (C–F in Fig. 1). Polyps survive harsh conditions in an encysted (quiescent) stage and inoculate the shallow habitat the following year via strobilation (transverse fission, see E in Fig. 1) and the release of juvenile jellyfish or ephyra after excystment from dormancy (F and G in Fig. 1).

Localized adaptations and subsequent success of jellyfish in their habitat may be controlled by water quality (Breitburg et al. 2003, Arai 2009, Lucas et al. 2012, Tills et al. 2016, Treible et al. 2018), food availability (Purcell et al. 1999, Arai 2009), temperature (Loeb 1972, Klein et al. 2016), habitat availability (Cargo & King 1990, Breitburg & Fulford 2006, Duarte et al. 2013), and the hydrodynamic environment. The hydrodynamic environment of a jellyfish is an important component of their success and dispersal to new habitat due to its role in food acquisition by polyps at a small (<1 mm) scale (Gili & Coma 1998), as well as transport and dispersal of pelagic stages including planula larvae, ephyrae and medusae at a larger (kilometer) scale (Cargo & King 1990).

On the Atlantic seaboard, there are 2 distinct species of the sea nettle: *Chrysaora quinquecirrha* and *C. chesapeakei*. *C. chesapeakei* (henceforth referred to as *Chrysaora*) is predominantly found in the Chesapeake Bay, USA, during summer months (Bayha et al. 2017), and was the target species of our study. This study aims to describe and analyze abundance patterns of *Chrysaora* in the Chesapeake Bay. Both polyps and medusae are expected to be found in higher abundances in sluggish headwaters with longer residence times (Cargo & King 1990, Purcell 1992, Breitburg & Burrell 2014). Shallow habitats are particularly vulnerable to consequences of climate change, including sea-level rise and increased precipitation, whereby the hydrographic state may be altered enough to affect dispersal of planktonic species that live within.

To better understand how components of the hydrodynamic environment such as the stability of the water column and residence time contribute to *Chrysaora* polyp survival and perennial reproductive success in Chesapeake Bay, we explored portions of the *Chrysaora* life cycle through field studies and spatially explicit modeling. We integrated *in situ* planula recruitment observations and historical datasets to explore *Chrysaora* population dynamics in Chesapeake Bay. Evidence gained from investigations of *Chrysaora* polyp populations in potential shallow habitat suggests that late summer/early fall planula recruitment is essential as a first step in the successful colonization of new habitat. However, we hypothesize that it is the overwintering survival of *Chrysaora* polyps within a shallow habitat that contributes to the occurrence of medusae blooms the following summer. We also tested the hypothesis that the spatial-temporal variability of water residence

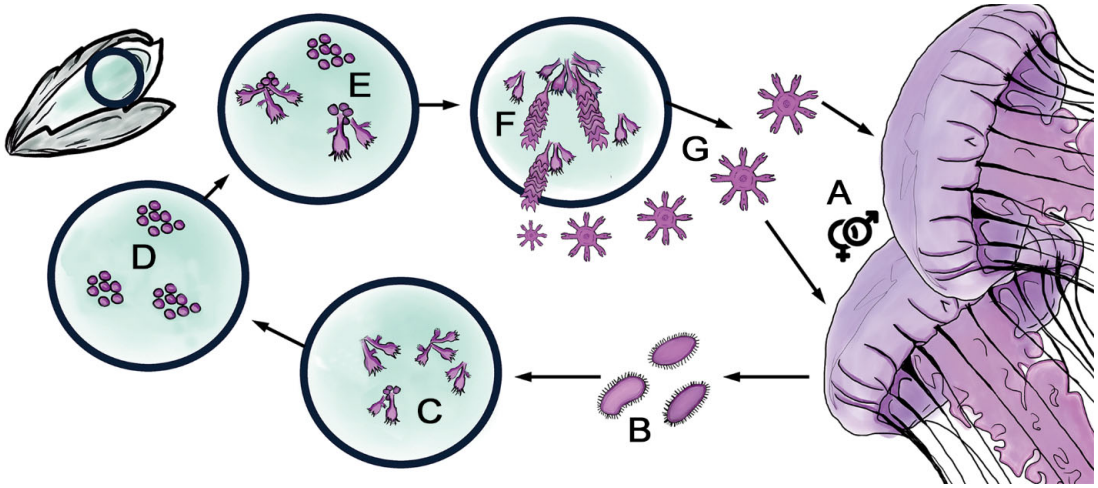

Fig. 1. Scyphozoan life cycle, adapted from descriptions and figures in Arai (2012). Life cycle was amended to include seasonality of *Chrysaora chesapeakei* polyps in Chesapeake Bay. Dioecious male and female medusae (A) reproduce via proximity spawning from summer/early fall, whereby planula larvae (B) get released. Planula larvae are cued to settle (C) on hard substrate and propagate via budding to increase densities before encystment in the late fall (D). Stages (C–F) occur attached to the underside of oyster shells, depicted top-left. If encysted polyps survive the winter, they excyst in the spring and begin to propagate via budding (E). With rising temperatures in the spring, excysted and newly budded polyps strobilate (F) and release juvenile ephyra into the water column (G)

time is a factor explaining patterns of recruitment success and overwintering survival in Chesapeake Bay. Understanding the environmental factors that contribute to the perennial success of *Chrysaora* provides insight into the localized adaptations that lead to jellyfish dispersal to new habitat within a temperate estuarine system threatened with change.

MATERIALS AND METHODS

Study sites

Chesapeake Bay is the most extensive estuary in the United States. The complex hydrodynamic state of Chesapeake Bay results from the bay's geomorphology, discharge, tidal influences and wind at varying scales. Together, these parameters govern water exchange between Chesapeake Bay and the coastal Atlantic, leading to interannual variation in residence times ranging from 110 to 264 d, and showcasing spatial trends through the seasons (Du & Shen 2016). Our 8 study sites (Fig. 2) of the polyp monitoring study spanned the middle and upper portions of the Chesapeake Bay on both the eastern and western shores. Selected sites were within salinity ranges consistent with polyp presence reported previously in Chesapeake Bay (Cargo & Schultz 1966). Salinity and temperature were monitored for our sites using 'Eyes on the Bay' data available through the Maryland Department of Natural Resources website (Table S1 in the Supplement at www.int-res.com/articles/suppl/m601p139_supp.pdf; buoy locations marked on Fig. 2; http://eyesonthebay.dnr.maryland.gov/).

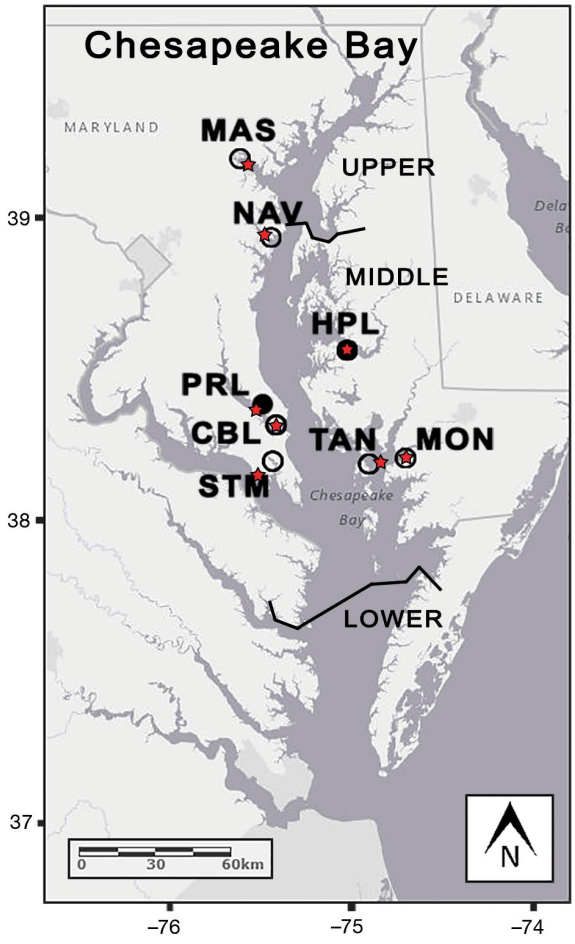

Fig. 2. Eight settlement tower study sites selected based on salinity (5–35 ppt) and accounting for spatial coverage of Chesapeake Bay, with sites on western and eastern shores: MAS: Masonville Cove, an adjacent creek of Patapsco River; NAV: Naval Academy, on Severn River channel; HPL: Horn Point Laboratory, on Choptank River channel; PRL: Patuxent River Environmental Research Lab, in an adjacent creek of Patuxent River; CBL: Chesapeake Biological Lab, at the mouth of Patuxent River; TAN: Karen Noonan Center, on Tangier Sound; MON: Monie Creek, a tributary of Tangier Sound; and STM: residential pier on St. Mary's River channel. Filled black circles: sites with observed *Chrysaora chesapeakei* polyps; unfilled circles: sites with no noted polyps; red stars: water quality monitoring stations (Table S1 in the Supplement, www.int-res.com/articles/suppl/m601p139_supp.pdf). Black lines divide the 3 portions of Chesapeake Bay (upper, middle and lower), with no sites selected in the lower portion of the bay

Field methods

Site-specific recruitment and overwinter success of *Chrysaora* polyps were estimated using polyp settlement towers (Fig. 3). Sections of half-inch diameter (1.3 cm) PVC pipe were joined together with marine-safe silicone glue to create settlement towers with 3 tiers (Fig. 3A). Each individual tier supported a plate created to simulate oyster boxes for planula settlement. One side of a plate was assembled by zip-tying cleaned and drilled oyster shells to PVC grate (Fig. 3A). The oyster-box plates were designed to allow for maximum flowthrough of water and to decrease predation. To ensure complete immersion of the towers, they were affixed to docks and piers, with each tower attached to a beam or post with steel cable and suspended 10–15 inches (25–38 cm) from the sea floor. The site locations were all approximately 3–5 m in depth, and towers were suspended in the water column, with no signs of contact with the sea floor or exposure during low tide. Each of the 8 sites contained 5 replicate towers, for a total of 40 towers placed throughout Chesapeake Bay (Figs. 2 & 3B,C).

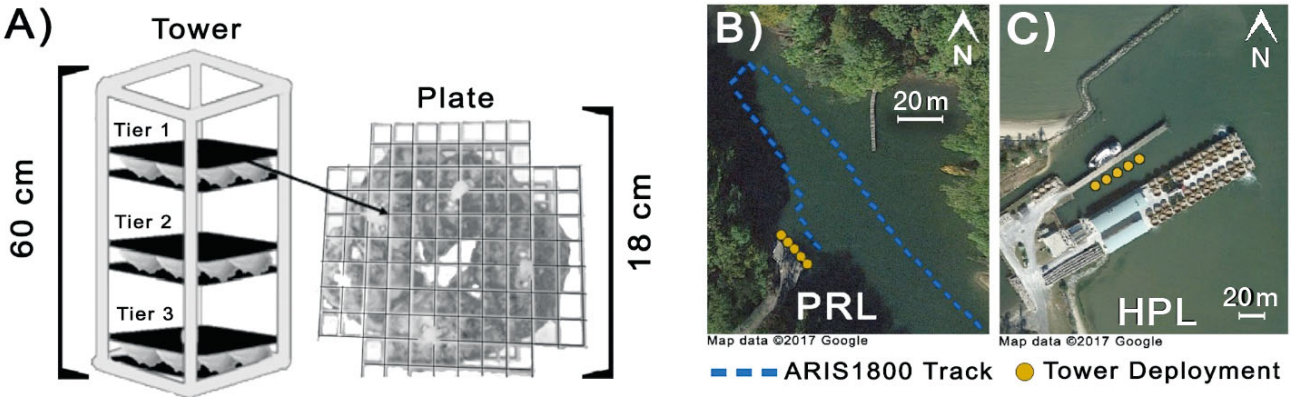

Fig. 3. (A) Polyp settlement tower for *Chrysaora chesapeakei* polyps and plates (N = 40). Each tower was designed with 3 tiers to account for varying immersion durations and repeated sampling events. Each tier supported an oyster-box plate, made by sandwiching 2 sections (18 × 18 cm) of PVC grate, fitted with zip-tied oysters. (B) Site PRL and (C) site HPL are 2 example sites. Yellow dots represent 5 replicate settlement towers and their typical deployment from docks and piers at all other sites. Blue dashed line: ARIS1800 sonar survey track lines carried out in summer 2016 at PRL used to estimate medusa abundance in Mackall Cove

Sampling events (see Table 1) for the polyp towers occurred 3 times: August 2015, September 2015, and March 2016. Each tower contained randomly generated immersion durations of 1 mo, 2 mo, and overwinter (October 2015 through March 2016). The tier sampling (immersion duration) was randomly generated at the start of the experiment to account for small-scale differences in depth between tiers (20–0 cm). Replacement of sample tiers (new plates) occurred in August 2015, which were sampled in September 2015, along with plates assigned 2 mo immersion durations. In 2016, we deployed 5 towers at Morgan State University's Patuxent River Environmental Research Lab (site PRL), Mackall Cove (Fig. 3B), for continued monitoring of polyp populations. We reduced immersion durations to 1–2 wk, and increased sampling frequency to 5 events.

During a sampling event, plates were removed from towers and placed in aerated seawater for transport to the laboratory and then replaced with new plates. Oyster shells were processed immediately by identifying and counting polyps under a dissecting microscope in the lab. Oyster surface area was calculated using ImageJ software to analyze photographs of all oyster shells from each sampled tier/plate. Dividing polyp count by the surface area of the exposed underside of oysters attached to the upper plate of an oyster box calculated polyp density. The density data were standardized to polyp count per 100 cm^2 oyster shell to account for the variability in oyster size.

To estimate *Chrysaora* medusa abundance, we used a sonar-based imaging system capable of retrieving high-resolution abundance data on medusae (Fig. 4). As part of a more extensive survey, Mackall Cove (Patuxent River) was surveyed from 26 May

Fig. 4. (A) Sonar camera deployment using (B) the ARIS1800. (C) Example data with 5 observed *Chrysaora chesapeakei* jelly fish (yellow number markers)

2015 to 11 October 2016 (Fig. 3B), providing both spatial and temporal overlap with the 2016 settlement tower study. The ARIS1800 (Fig. 4B; Sound Metrics) was mounted onto the gunwale of the research vessel and the camera submerged via a polearm (Fig. 4A) at a consistent depth (0.7 m from the surface) with a fixed field of view (7 m). A live feed of the sonar data was viewed and recorded with a laptop computer and ARISScope software (Sound Metrics), and a 120 V portable generator powered both the camera and computer. The data were processed with ARISFish software (Sound Metrics), whereby recorded sample footage was played back and each *Chrysaora* medusa (Fig. 4C) was manually located and marked (clicked) in the water column. Using the ARISFish software, we generated a list of geolocations and depth of each located medusa. Medusae with a bell diameter size of approximately 30 mm (~golf ball size) were detectable, although larger medusae were much more distinguishable. Volume estimation and density for recorded data was not variable due to the fixed field of view but changed based on the topography of the sea floor. Image analysis techniques (Shahrestani et al. 2017) were adapted to calculate changes in topography of the sea floor using Matlab (Mathworks) and used to calculate volume and estimate density and abundance of medusae in Mackall Cove. We standardized medusa abundance in the 2016 summer season by the estimated volume of Mackall Cove (~59 300 m^3).

Data and statistical analyses

A linear mixed-effects model (LMM) was used to investigate site-specific recruitment and overwintering success. Differences in polyp density between the sites at Horn Point Laboratory (HPL) and PRL and sample events (repeated measures, fixed effects), as well as differences between replicate towers, salinity and temperature (random effects) at each of the sites were used to explore patterns in recruitment. The LMM is robust in handling longitudinal data often needed to explore dynamic variables, including missing points as well as non-normality, which fits the *in situ* planula recruitment data well. R statistical software was used to perform all statistical procedures in this study. The LMM was developed using the R package 'nlme'.

Data from field sampling of polyps (planula recruitment) and medusae (density) as well as polyp density and strobilation density from Calder (1974) were used to compare patterns of seasonality and how they reflect variations across the *Chrysaora* life cycle. Data from Calder (1974) were standardized by the number of counted scyphistomae per sample and strobila densities as strobila per sample. The Calder (1974) dataset is valuable in that it monitors polyp and strobila density, capturing the seasonality of *Chrysaora* polyps from March 1972 to February 1973, with implications for periodicity in asexual reproduction (budding and strobilation). The 4 datasets were centered and scaled in R statistical software using the scale function. Data were first centered at 0 and then scaled by dividing the values in each variable by their standard deviations. Normalized values of abundance or density are not directly comparable between all datasets, but observed seasonal patterns of density within the datasets reveal valuable information.

A historical dataset (Cargo & Schultz 1966) and the results from our 2015 Chesapeake Bay field study (N = 8 study sites) were used to develop a generalized linear model (GLM) that predicted the probability of polyp presence in Chesapeake Bay using water residence time reported in Du & Shen (2016). We extracted values of residence time from rasters provided in Du & Shen (2016) for January and July with references to the Cargo & Schultz (1966) study sites. We performed a similar operation on salinity maps provided by the Chesapeake Bay Foundation (www.chesapeakebay.net/what/maps/keyword/salinity) averaged from 1985 to 2006. Multi-scale ultra-high resolution (MUR) average sea surface temperature (SST) from 2007 to 2017 were derived from NOAA's satellite data (https://coastwatch.chesapeakebay.noaa.gov/time_series_sst_gen.php?region=cd). To validate our extraction procedure of our residence time data, we calculated the mean average residence time using rasterized values in Chesapeake Bay (approximately 175 d), which was consistent with Du & Shen (2016). Latitude and longitude of the Cargo & Schultz (1966) study sites (N = 52) were derived from the site map and site information provided in their study, i.e. Hellen's Creek, Patuxent River, using Google Earth software. For comparative assessments of the presence/absence models, we tested the effects of salinity, SST, and residence time in January and July with different link functions (Probit, Logit, and cloglog; see Table 3). Model comparisons were made using the Akaike information criterion (AIC), visual observations of residual diagnostics and *k*-fold (10) cross-validation. A spatially explicit GLM was then constructed using our chosen model (see Table 3 for details) to predict and compare probabilities of *Chrysaora* polyp occurrence throughout the different areas of Chesapeake Bay.

Table 1. *Chrysaora chesapeakei* settlement-tower sampling design for study sites with observed polyps in 2015 and 2016, i.e. sites HPL and PRL (see Fig. 2). Polyp density is calculated as the average newly recruited polyps to 100 cm^2 oyster shell for 5 replicate towers placed at each site

Year	Site	Immersion duration	Time period	Polyp density
2015	HPL	1 mo	Aug	70
	HPL	1 mo	Sep	11
	HPL	2 mo	Aug & Sep	15
	HPL	6 mo	Oct 2015–Mar 2016	0
	HPL	8 mo	Aug 2015–Mar 2016	1
	PRL	1 mo	Aug	14
	PRL	1 mo	Sep	38
	PRL	2 mo	Aug & Sep	60
	PRL	6 mo	Oct 2015–Mar 2016	0
	PRL	8 mo	Aug 2015–Mar 2016	27
2016	PRL	1 wk	27 Jul–3 Aug	0
	PRL	1 wk	3–10 Aug	0
	PRL	2 wk	27 Jul–10 Aug	35
	PRL	2 wk	3–24 Aug	29
	PRL	2 wk	24 Aug–7 Sep	0
	PRL	6 wk	27 Jul–5 Oct	68

RESULTS

Site-specific recruitment and overwinter success

Planula recruitment to new shell only occurred at 2 sites, PRL and HPL (Table 1), based on observed polyps. Highest and lowest densities of newly recruited polyps occurred at HPL in August 2015 and September 2015 respectively, although results from the LMM revealed that overall planula recruitment and asexual propagation were not significantly different between sites (df = 15, $p > 0.05$). The LMM suggested significant variability in temporal patterns of within-season recruitment between sites, among 2 of the 3 sampling events, although temperature and salinity were not significant in describing the variance observed in the data. In August, density in HPL was significantly higher ($\beta = 57$, SE = 12, $p \leq 0.005$), and in September, polyp density was lower in HPL ($\beta = -44$, SE = 12, $p \leq 0.005$). There were no significant differences in polyp density between sites for the third sampling event, at a 5% alpha level ($\beta = 26$, SE = 12, $p = 0.06$). Standard deviation of residuals among tower replicates (random effect) was estimated at 20 polyps per 100 cm^2 oyster shell.

Newly recruited polyp colonies at PRL showed signs of asexual propagation, meaning the combined density of polyps with 1 mo immersion durations were less than the densities of plates with 2 mo immersion durations over the same period (Table 1). Although planula recruitment at HPL was highest in August 2015, there was a notable decrease in recruitment in September 2015. There were no signs of asexual propagation at HPL, whereby the combined densities of newly recruited polyps from August 2015 and September 2015 were less than polyp densities with 2 mo immersion durations from August 2015 through September 2015 (Fig. 5A). Densities of polyps from oyster shell immersed from August 2015 through March 2016 (overwintering) had significantly lower polyp densities than settlement towers immersed from August 2015 through September 2015. Overwintering success at HPL was much lower than that of PRL (Fig. 5A). Strobilation of polyps did not occur on oyster shell with newly recruited polyps, and no polyps were found on oyster shell with immersion durations from early October 2015 through March 2016.

When medusae began appearing in 2016, we deployed polyp towers for the second season in Mackall Cove, sampling at higher frequencies with shorter immersion durations (Table 1, Fig. 5B). Oyster shell with 1 wk immersion durations did not recruit polyps or they were not yet observable, which

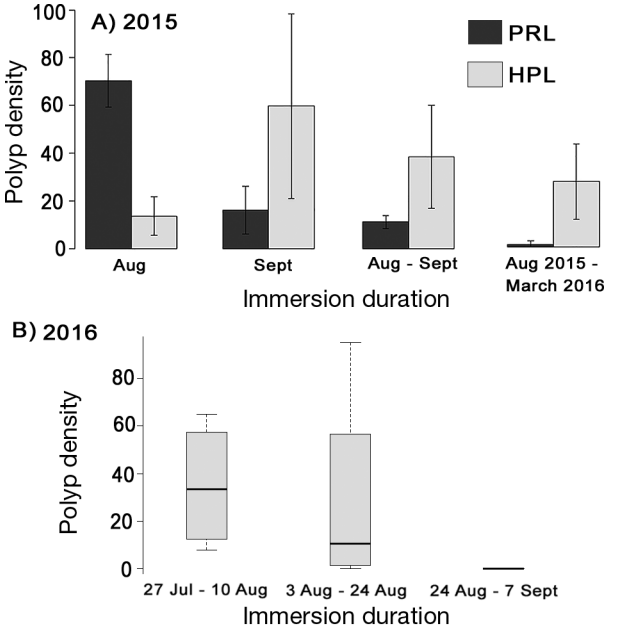

Fig. 5. Planula recruitment of *Chrysaora chesapeakei* represented by polyp density or newly recruited polyps to 100 cm^2 oyster shell. (A) 2015 polyp densities and estimated error bars (SD) for sites with observed polyps, which are limited to sites PRL and HPL. (B) Observed densities of oyster shell with 2 wk immersion durations during 27 Jul–7 Sep 2016 at PRL. Boxes are median and interquartile range, whiskers are minimum and maximum

led us to conclude early on that an immersion duration of 1 wk was not long enough. Two weeks was a sufficient immersion duration, as we found polyps on the first 2 of the 3 sampling events. However, medusa abundance went to zero rather quickly by mid-August 2016 before the replacement of oyster shell/plates for the final sampling event, i.e. there was no expectation of polyps for the third sampling event in 2016. Planula recruitment was highly variable, ranging from 0 to 95 polyps per 100 cm^2 oyster shell. Variability of polyp density occurred among sample replicates, although there were no significant differences between sample periods with similar polyp densities for the 2 wk immersion durations 27 July–10 August 2016 and 3–24 August 2016 (Fig. 5B; 29 vs. 35 polyps per 100 cm^2 oyster shell, respectively).

Table 2. Pearson's correlations of *Chrysaora chesapeakei* life stages. Strobilae and polyp data from Calder (1974), as well as medusa abundance from the 2016 sonar survey and planula recruitment from the 2016 settlement tower study, were centered and normalized along with other life stages, including strobilae, polyps and planula recruitment with a 1 mo lag. *Significance level, $\alpha \leq 0.05$

	Medusae		Polyps	
	Correlation	p	Correlation	p
Strobilae	0.31	0.55	0.84*	0.04
Planula recruitment	0.66	0.66	−0.99*	0.02
Polyps	−0.61	0.84		
Strobilae with 1 mo lag	0.99*	0.02		
Polyps with 1 mo lag	0.99*	0.04		
Planula recruitment with 1 mo lag	0.99*	0.02		

Seasonality of *Chrysaora* population dynamics

Polyp density reported in Calder (1974) collected from 1972–1973 revealed 2 peaks in density in May and then again in September. Polyps were lowest at the start of spring, which was consistent with our field sampling that suggests high overwintering mortality. Polyp density remained above zero into the fall, although in July, polyp densities decreased, with a lull in reproductive activity before an increase in abundance heading into winter (Fig. 6). Strobila density had a single peak from early May through the middle of June before it declined to zero in the late summer and early fall (Fig. 6). Strobilation and polyp densities are correlated through spring (Table 2, Fig. 6). Strobilation declined in July, when polyp densities were at their lowest, although polyp density began to increase due to planula recruitment (spawning medusae) and asexual propagation in late summer to early fall, which was also observed with polyps settled on towers in 2015 (Fig. 5A).

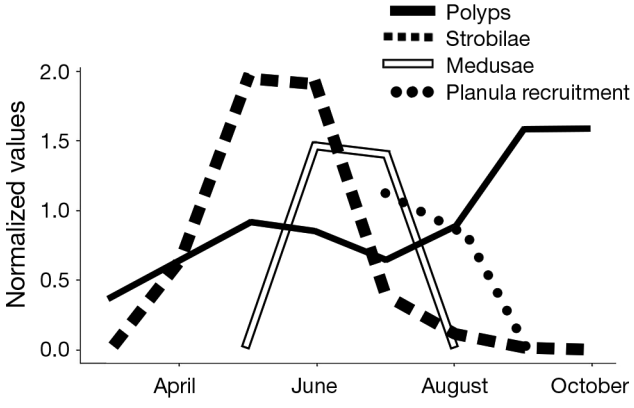

Fig. 6. Seasonality of *Chrysaora chesapeakei* population dynamics as described by the normalization of 4 datasets: polyp density and strobilae density reported in Calder (1974) collected from Sarah Creek, York River; medusa abundances observed in Mackall Cove, Patuxent River in 2016; planulae recruitment in 2016 collected from polyp settlement towers deployed at site PRL (see Fig. 2)

Small *Chrysaora* medusae (30 mm size) did not appear in Mackall Cove (or in other parts of the Patuxent River) until late June 2016. Highest abundances of medusae in Mackall Cove were observed on 28 June 2016 (388 medusae), with declining abundances through the season, ultimately reaching zero on 11 August 2016. Observed medusa abundance in Mackall Cove correlated with strobilae, polyp density, and planula recruitment when a 1 mo lag was applied to the data (Fig. 6), which suggests periodicity in the seasonal dynamics of *Chrysaora* in Chesapeake Bay, as also observed and noted in Calder (1974).

Bay-wide polyp distribution

Model selection implicated Model IV (Table 3) as the best GLM in describing the presence/absence of polyps in Chesapeake Bay. Model IV described the interaction between water residence time in July and January as significant in explaining polyp presence in Chesapeake Bay. The most suitable link function was determined to be 'Probit.' Model IV + Probit had the lowest AIC value (Bozdogan 1987). Comparisons of the models' (I–IV) predictive performance was carried out using k = 10-fold, cross-validation prediction

Table 3. Generalized linear model selection and validation for *Chrysaora chesapeakei* polyp presence/absence using a negative binomial distribution and explanatory variables including water residence time (RT) in July and January as well as their interactions. Akaike information criterion (AIC) was used to differentiate between models with 'Probit,' 'Logit' or 'cloglog' link functions. A $k = 10$ cross-validation error (CVE) was used to validate models and aid in model selection. Cells shaded in gray highlight the best performing model in predicting the probability of polyp presence in Chesapeake Bay. *Significance level, $\alpha \leq 0.05$

Model/Link	p			AIC	CVE
I RT Jul					
Probit	0.06			77.92	0.40
Logit	0.06			77.49	0.40
cloglog	0.10			78.32	0.39
II RT Jan					
Probit	0.04*			77.30	0.43
Logit	0.08			78.09	0.43
cloglog	0.07			77.79	0.43
III RT Jan + Jul					
Probit	RT Jan: 0.40	RT Jul: 0.75		79.20	0.45
Logit	RT Jan: 0.41	RT Jul: 0.74		79.39	0.45
cloglog	RT Jan: 0.42	RT Jul: 0.75		79.70	0.44
IV RT Jan × Jul					
Probit	RT Jan: 0.05*	RT Jul: 0.01*	RT Jan × RT Jul: 0.02*	71.17	0.33
Logit	RT Jan: 0.02*	RT Jul: 0.06	RT Jan × RT Jul: 0.02*	71.35	0.33
cloglog	RT Jan: 0.01*	RT Jul: 0.06	RT Jan × RT Jul: 0.02*	71.28	0.33

error (CVE) (a 'leave one out' process), with results (Table 3) suggesting Model IV was most robust in predicting the probability of *Chrysaora* polyps in Chesapeake Bay. Temperature was removed early on from the model, as it was not significant in explaining the patterns of the polyp data. Spatially explicit salinity and residence times were highly correlated in space and time (Table S2), and salinity alone was not significant in explaining polyp presence in Chesapeake Bay. Therefore, a spatial filter was applied to exclude areas with salinity less than the physiological tolerances of *Chrysaora* polyps in Chesapeake Bay (Cargo & Schultz 1966, Cargo & King 1990, Purcell et al. 1999).

Regarding the interaction of water residence time in January and in July, Model IV + Probit predicted localized areas with the highest residence time, in both summer and winter, with the most significant probabilities of polyp occurrence. Results of the model suggest that the mid-Chesapeake Bay may be most suitable for polyp settlement, while the Patuxent and Choptank rivers showed the highest predictions of polyps (Fig. 7). Limited areas of the lower bay tributaries revealed lower predictions of polyps in the headwaters of the bay (Fig. 7). Sampling in the lower bay was limited to the mainstem, but our model predicts polyp occurrence in localized areas of both the James and York rivers, 2 tributaries in the lower bay.

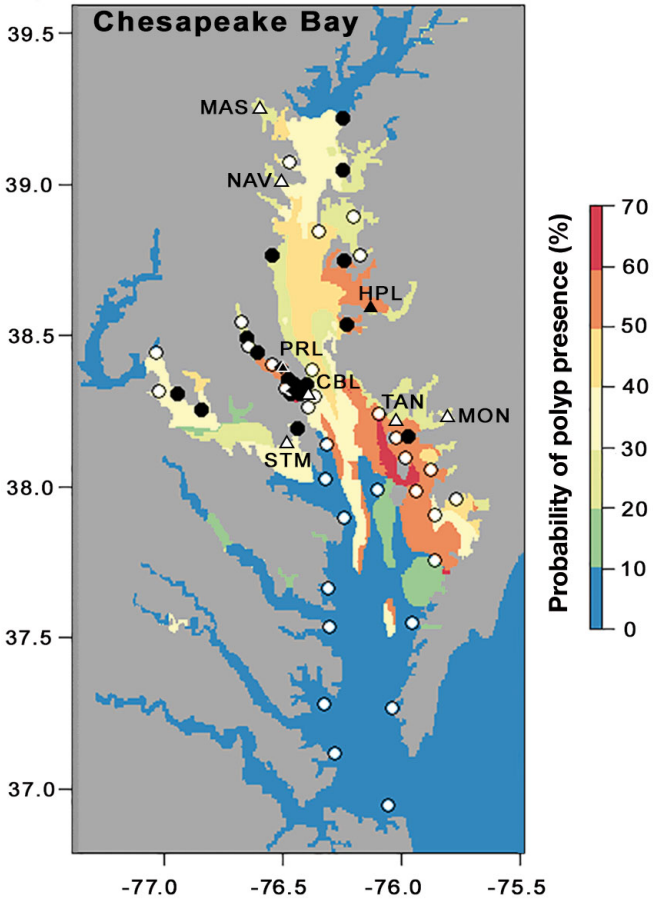

Fig. 7. Spatially explicit generalized linear model predictions of *Chrysaora chesapeakei* polyps using a binomial distribution and 'probit' link function as well as a salinity filter (<5 ppt). Probability is described by a cold (lower probability of polyp occurrence) to warm color (higher probability of polyp presence) gradient. Filled black circles: sites with observed polyp presence, and unfilled circles: sites with no polyps, both from Cargo & Schultz (1966). Filled black triangles: sites with polyps present, and unfilled triangles: sites with no observed polyps, both from our 2015 settlement tower study. See Fig. 2 for site abbreviations

DISCUSSION

The range and long-term survival of *Chrysaora* polyp colonies was characterized by both residence time (hydrological flushing) and environmental conditions within shallow habitat of Chesapeake Bay. Successful recruitment, overwintering success and inoculation of *Chrysaora* into shallow habitat each summer allows for a source of reproductive dispersal vectors (medusae) which spawn and produce newly recruited colonies of polyps. In contrast, tropical medusae and strobilae of the *Mastigias* spp. are found throughout the year in the jellyfish lakes of Palau (Dawson & Martin 2001), whereby the population dynamics of both *Mastigias* and *Chrysaora* spp. are governed by the physiological responses (i.e. senescence of medusae, strobilation) to the seasonality of their environmental conditions. In this study, we explored water residence time as a possible factor for describing *Chrysaora* polyp distribution in Chesapeake Bay, because it encompasses facets such as geomorphology, water exchange, salinity and the overall stability of the shallow habitat of *Chrysaora* as it varies with seasonality (Du & Shen 2016).

The spatial model used in the present study identified a significant interaction between July and January water residence time in predicting polyp distribution, which suggests that the variability in residence time across the seasons plays a significant role in polyp distribution, and not July residence time or January residence time alone. The success of planula larvae recruitment to hard substrate (i.e. a consequence of medusa dispersal and planula dispersal) could be affected by summer residence time, while winter residence time could explain the subsequent asexual propagation/overwintering success of newly recruited polyp colonies.

Although salinity and temperature are known variables in describing the distribution of many medusa species (Dawson et al. 2001, Purcell 2005, Zhang et al. 2012), including *Chrysaora* medusae in Chesapeake Bay (Brown et al. 2002, Decker et al. 2007), many of these studies examine medusae in dispersal habitat outside the range of optimal polyp habitat, which does little to explain polyp distribution in source creeks. However, when considering sites within the range of optimal habitat (i.e. appropriate salinity, temperature, and oxygen), the temperature and salinity between sites varies less than residence time between adjacent sites. For example, in the Patuxent River estuary, the river channel and an adjacent cove are a few kilometers apart with indistinguishable differences in salinity and temperature, but notable variability in residence time (Hagy et al. 2000). We suggest the patterns noted in polyp abundance were caused by differences in flushing rates (between adjacent sites), which contrasts with the homogeneity of salinity and temperature observed among adjacent sites during the same period.

The physiological limitations of medusa species that die off in the cold winter months of temperate zones, including *Chrysaora chesapeakei*, or *Cotylorhiza tuberculata* in the Mediterranean (Kikinger 1992), are different from the physiological limitations of polyps of the same species, which allows for their longevity in a dynamic habitat. Adaptations to environmental conditions, like temperature, salinity, hypoxia and hydrography, manifest across different life-stages of scyphozoan species and affect the appearance and abundance of jellyfish populations worldwide (Keister et al. 2000, Breitburg et al. 2003, Lucas et al. 2012, Purcell et al. 2013, Kolesar et al. 2017). Changes to the environmental features that characterize shallow estuarine habitats also make them especially vulnerable to the pressures of human activities in the rapidly changing Anthropocene, i.e. sea-level rise and increased temperatures and precipitation (Barbier et al. 2011, Kennedy & Turner 2011). While many species of jellyfish tolerate harsh conditions, there are no physiological defenses against habitat loss due to changes in hydrographic conditions, making jellyfish populations (especially those found in shallow habitat) more susceptible to climate change than once believed.

Data reported from the Cargo & Schultz (1966) study make it difficult to distinguish between source colonies (found in the spring) or newly recruited colonies (found in late summer/early fall), although distinguishing differences in polyp morphology can be observed (Loeb 1972). Regardless, closer evaluation of sample dates from the Calder (1974) study aided in distinguishing source colonies from newly recruited polyp colonies. We assumed that samples taken by Cargo & Schultz (1966) during May were from established colonies because medusae had not yet matured or spawned. Based on the corresponding site locations of polyps present in May, we conclude that the Patuxent River facilitated and continues to facilitate planula recruitment as well as overwintering success of *Chrysaora* polyps.

Using the Patuxent River (a tributary of mid-Chesapeake Bay) as an example when exploring patterns of residence time, it becomes apparent that areas of the tributary and its adjacent creeks experience high residence time through the year, with low variability between the summer and winter seasons

(comparing July to January residence time). Areas with low variability in residence time throughout the season may provide optimal habitat required for polyp settlement and survival, i.e. areas with stable laminar flow and less water exchange, in contrast to habitat with faster flushing times and high intra-seasonal variability in average residence time. In Calder's (1974) study, carried out in Sarah Creek in the New York River or Virginia, USA, polyps were present in high densities, corroborating predictions of the spatially explicit GLM, although the predicted probability of polyps (30–40%) is lower when compared to the Patuxent River (50–60%). Similarly, polyps reported by Cones & Haven (1969) settled approximately 10 km from the model's predicted areas of polyp presence. The York River in the lower bay experiences relatively low residence time in both the summer and winter months, which was a good validation point for the model.

Small-scale variability of polyp predictions throughout shallow habitats of Chesapeake Bay (i.e. differences between the upper and lower portions of the Patuxent River) may be indicative of the local features of a shallow habitat, which include wind, available substrate, depth, salinity, and flow rate among others. Many of these factors have been used to explain the variability of polyp settlement and hold merit in describing localized patterns of abundance. For example, Cones & Haven (1969) found polyps on oyster shell suspended in bags from docks in the York River, Virginia, USA, but not on oyster shell dredged kilometers away. Fine-scale variability in polyp presence could be indicative of failed planula recruitment to deeper oyster bars, although our study did not reveal differences comparing polyp density over depth differences between tiers of settlement towers (7–10 inches [18–25 cm] between each tier).

Other factors that affect planula recruitment vary with species and habitat, but may include biofilm development (Holst & Jarms 2007, Holst et al. 2007) and the presence of conspecifics (Gröndahl 1989). With regard to biofilm development and the subsequent settlement of conspecifics, hydrography is an important consideration due to the role of shear force and laminar flow in biofilm accumulation. Less turbulence may lead to higher rates of biofilm accumulation (Stoodley et al. 1998, Liu & Tay 2002). In short, if biofilm is required for settlement and biofilm accumulation is optimized in laminar flow, the mechanistic explanation for polyps preferring shallow sluggish waters may be a response to localized hydrographic conditions.

In temperate zones, observations of localized differences in habitat may also contribute to overwintering success or surviving dormancy, which became apparent in our study. Our model predicts similar recruitment success of planulae at 2 of our tower study sites (PRL and HPL). However, polyps did not survive the winter at HPL, perhaps due to variability between sites regarding the presence of overwintering refugia. For example, a sheltering riparian buffer present at PRL (Fig. 3B) was absent from HPL (Fig. 3C). Furthermore, the sample towers placed in the enclosed creek of the Patuxent River were in an area of higher water-residence time relative to the HPL polyp colonies that recruited to the towers placed in the Choptank River channel (Hagy et al. 2000).

For scyphozoan species that exist in temperate zones and contain a polyp stage, medusa densities should correlate with planula recruitment and subsequent populations of newly recruited polyp colonies, but these colonies do not contribute to the medusa population of that year. Typical consideration of the scyphozoan life cycle that does not incorporate seasonality ignores differences between source colonies excysted in the spring (in the case of summer-dominant species) and newly recruited colonies via planula recruitment in the late summer through fall. However, parsing out differences of behavior across multiple stages of polyps reveals valuable information regarding the within-season abundance of medusae. Not a single strobila observation occurred in our 2015–2016 settlement tower studies, which isn't surprising considering polyps never experienced springtime warming of water temperatures needed to induce strobilation. Our study suggests fall strobilation does not occur (regardless of the appropriate temperature range) because polyps recruited in summer and early fall do not experience the strobilation cue, i.e. water temperature increase only occurred in the spring. In the lab, newly recruited polyps do indeed strobilate when polyps are chilled at 20°C and then exposed to increasing temperatures up to 26°C (Loeb 1972), although strobilation of newly recruited polyps has not been observed *in situ*.

Including newly recruited polyps in population dynamics studies of scyphozoan species could bias estimates of within-season production of medusae because the recruits do not strobilate. We could not distinguish between source polyps and recruits with the results published in Cargo & Schultz (1966), so we made the safest assumption that polyp presence was an indication of successful planula recruitment alone and not overwinter survival (spring excystment). With this assumption, our spatial model may be overpredicting the range of source colonies if we

aim to consider habitat that facilitates both planula recruitment and overwintering success. For temperate scyphozoan species dominant in the summer, early-spring polyp sampling should give an accurate estimate of polyp source colonies and their impact on within-season medusa abundance because recruits have not yet appeared with the summertime spawning of medusae. The opposite should be true for species that are cued to excyst and strobilate with decreasing temperatures in the fall, i.e. *Cyanea capillata* in Chesapeake Bay and *Aurelia* spp. in many locations worldwide (Gröndahl 1988, Omori et al. 1995, Liu et al. 2009, Purcell et al. 2009), whereby early-fall polyp density and asexual reproduction should be considered for estimating abundance of medusae that winter.

The complexity of the *Chrysaora chesapeakei* life cycle as it unfolds in Chesapeake Bay exhibits their adaptability. Mechanisms at all life stages contribute to the success of the species within a complex and dynamic estuarine environment. Investigations of spatiotemporal distribution and abundance of jellyfish species are most revealing when they occur within the context of their life history. With regard to *C. chesapeakei*, small-scale features of polyp source habitat could explain differences in the success of planula recruitment and overwintering survival at a fine scale, while water residence time helps define the overall pattern of presence or absence absence of polyps within Chesapeake Bay at the sub-estuary scale. Springtime strobilation cues are only experienced by excysted spring polyps (*in situ*) that survive the winter, while planula recruitment and asexual reproduction in the fall ramps up polyp density to buffer against the harsh conditions of winter. The current and future changes to hydrographic conditions and temperature in shallow habitat at both large and small scales, like faster flushing rates, may lead to large shifts in the spatial and temporal distribution patterns of *Chrysaora* polyps inhabiting them. The success of polyp settlement and dormancy through harsh conditions is not only a necessary step in the life cycle of *C. chesapeakei*, but vital in other metagenic jellyfish species that require inoculation of medusae into the water column every year.

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