Impacts of predators, habitat, recruitment, and disease on soft-shell clams *Mya arenaria* and stout razor clams *Tagelus plebeius* in Chesapeake Bay

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ABSTRACT

Soft-shelled clams, *Mya arenaria*, and razor clams, *Tagelus plebeius*, in Chesapeake Bay have been in decline since the 1970s, with severe declines since the early 1990s. These declines are likely caused by multiple factors including warming, predation, habitat loss, recruitment limitation, disease, and harvesting. A bivalve survey was conducted in Chesapeake Bay to examine influential factors on bivalve populations, focusing on predation (crab, fish, and cownose rays), habitat type (mud, sand, gravel, shell, or seagrass), environment (temperature, salinity, and dissolved oxygen), recruitment, and disease. *M. arenaria* and *T. plebeius* were found more often in more-complex habitats such as seagrass or shell than any other habitat. Pulses in bivalve density associated with recruitment were attenuated through the summer and fall when predators are most active, indicating that predators likely influence temporal dynamics in these species. *Mya arenaria*, which is near the southern extent of its range in Chesapeake Bay, was negatively associated with high water temperatures. Recruitment of *M. arenaria* in Rhode River, MD, declined steadily between 1980 and 2016. Infection by the parasitic protist *Perkinsus* sp. was associated with stressful environmental conditions, bivalve size, and environmental preferences of *Perkinsus* sp, but was not associated with bivalve densities. It is likely that habitat loss, low recruitment, and predators are major factors keeping *T. plebeius* and *M. arenaria* at low densities in Chesapeake Bay. Persistence at low densities may be facilitated by complex habitats, whereas further reductions in habitats such as seagrass could result in local extinction of these important bivalve species.

INTRODUCTION

The soft-shell clam *Mya arenaria* and the stout razor clam *Tagelus plebeius* are both large, deep-burrowing bivalves that are harvested in the Chesapeake Bay for human consumption and for bait (Dungan et al. 2002, Homer et al. 2011). *Mya arenaria*, in particular, supports a large commercial fishery in the U.S., and it accounted for 14% of domestic commercial bivalve dollar value in 2015 (NMFS 2016). In Chesapeake Bay, *M. arenaria* has supported a commercial hydraulic dredge fishery in Virginia and Maryland starting in the early 1950s with the invention of the hydraulic dredge. Commercial clammers also harvest *T. plebeius* for eel and crab bait (Dungan et al. 2002, Homer et al. 2011).

Historically, *M. arenaria* and *T. plebeius* served important roles as biomass dominants that contributed substantially to the food web and water quality of Chesapeake Bay (Abraham & Dillon 1986, Eggleston et al. 1992, Seitz et al. 2001). *Mya arenaria* and *T. plebeius* are key prey for numerous commercially and recreationally important fish and crab species (Eggleston et al. 1992, Seitz et al. 2005, Fisher 2010). These large-bodied filter-feeding clams likely played a large role in filtration of the water column when they were abundant; *M. arenaria* in the Baltic Sea can filter the entire water column in less than a day (Forster & Zettler 2004), and filtration by *M. arenaria* in the Gulf of Maine increased water clarity in some lagoons where their densities were high (Thiet et al. 2014). Non-oyster bivalves have recently gained attention for water filtration as an ecosystem service in Chesapeake Bay (Gedan et al. 2014), but the value of filtration by soft-shelled clams has not been assessed.

In Chesapeake Bay, *M. arenaria* has been in decline since the early 1970s, with more pronounced declines since the 1990s, and this species now exists in Chesapeake Bay at record

low levels (Fig. 1). Declines during and after 1972 are attributed to impacts from Tropical Storm Agnes, a 100-year storm that drastically reduced salinities and increased sedimentation throughout Chesapeake Bay (Hyer & Ruzecki 1976, Schubel 1976, Schubel et al. 1976), which resulted in a mass mortality event for *M. arenaria* (Cory & Redding 1976). Due to this storm, which followed declines in abundance of *M. arenaria* in the late 1960s, the commercial hydraulic dredge fishery for *M. arenaria* essentially ended in Virginia waters around 1968, and has failed to recover since then (Haven, 1970). More recent (post-1990) dramatic declines in abundance of *M. arenaria* have resulted in variable, low harvests in Maryland waters (Homer et al. 2011). Since 1980, commercial clammers have gradually switched to harvest of *T. plebeius* for eel and crab pot bait (Dungan et al. 2002, Homer et al. 2011). Like *M. arenaria*, *T. plebeius* populations have experienced declines in recent years, which were first documented in 2003 and resulted in the loss of 70-80% of the population in Maryland (Fig. 1; Homer et al. 2011). There are no historic landings records or long-term time series of *T. plebeius* abundance, so the history of decline and potential mechanisms for decline in this species are largely unknown.

Multiple factors have been blamed for the inability of *M. arenaria* to recover from Tropical Storm Agnes and the recent declines in *M. arenaria* and *T. plebeius* abundances, including predation, overfishing, low recruitment, rising temperatures, habitat loss, and disease mortalities. Although a fishery still exists in the upper Chesapeake Bay, these species have not been fished commercially in Virginia waters since the closure of the hydraulic dredge fishery in the 1970s. Recruitment of *M. arenaria* remains high in several tributaries of Chesapeake Bay (Lovall et al. 2017) though these individuals rarely survive to adulthood, except in habitats with sufficient structure to allow protection from predators (Seitz et al. 2005). This leads to the notion that populations are not limited by fishing pressure or recruitment, but rather by other factors

such as predation and lack of suitable habitat.

There is some evidence that habitat preferences, including environmental tolerances and availability of refuge habitat that allows clams to avoid predation, may influence population dynamics of *M. arenaria* and *T. plebeius*. *Mya arenaria* is near the southern extent of its geographic range in Virginia, and is not tolerant of temperatures above 28°C, a temperature that is frequently exceeded in Chesapeake Bay during summer months (Moore & Jarvis 2008). In contrast, *T. plebeius* is a warm-water species that is distributed into South America (Abrahao et al. 2010). Habitat type has been shown to influence the distribution and abundances of *M. arenaria*. Growth rates can be impacted by sediment type, with higher growth rates observed in sand than mud-gravel-shell mixtures (Newell 1982). Habitats with more structure, such as gravel, shell hash, or seagrass, can also provide refuge from predators (Sponaugle & Lawton 1990, Skilleter 1994, Seitz et al. 2001).

The availability of some refuge habitats, such as seagrass and oyster shell, is decreasing in the Chesapeake Bay (Rothschild et al. 1994, Lefcheck et al. 2017). The severe and persistent declines of Chesapeake Bay seagrass in the recent past have been attributed mostly to anthropogenic nutrient and sediment pollution, which decrease water clarity (Kemp et al. 2004). The dominant seagrass species in Chesapeake Bay, eelgrass *Zostera marina*, is also sensitive to warming, and the interaction between warming and poor water quality has resulted in recent declines of shallow beds (Lefcheck et al. 2017). In the past several years, seagrass die-offs induced by extreme high temperatures in Chesapeake Bay have resulted in the prediction that *Z. marina* may disappear from the Bay entirely (Moore & Jarvis 2008; though seagrass may be increasing in the coastal bays, see Orth & McGlathery 2012). Loss of oyster reefs in Chesapeake Bay due to overfishing and habitat destruction has resulted in the ecological extinction of oysters

in the Bay (Rothschild et al. 1994). As oysters have been lost, so has a major source of shell material in the Bay. Oyster shell is a limited resource, and shell half-life is estimated to be as little as 3-10 years in Delaware Bay (Mann & Powell 2007). Loss of this structural refuge may have implications for populations of deep-burrowing clams such as *M. arenaria* and *T. plebeius*.

The recent findings of high prevalences of the parasitic protist *Perkinsus chesapeaki* in *M. arenaria* and *T. plebeius* suggest that this could be a cause of the population declines of both bivalve species (Dungan et al. 2002, Reece et al. 2008). *Perkinsus chesapeaki* infections have reached epizootic levels in *M. arenaria* (Farley et al. 1991, Dungan et al. 2002, Reece et al. 2008). However, prevalence is not necessarily equal to pathogenicity, as seen in some disease-resistant oyster stocks in the Chesapeake Bay (Encomio et al. 2005). The cancer disseminated neoplasia also causes mortality of *M. arenaria*, but this disease is not as prevalent as *P. chesapeaki*, and is not reported to affect *T. plebeius* (Dungan et al. 2002); thus, this study focuses only on the impact of *P. chesapeaki* on *M. arenaria* and *T. plebeius.*

No single factor can likely be exclusively attributed to the declines of these two bivalve species; thus, multiple factors were considered to gain useful insight into the problem. The Chesapeake Bay provides an ideal location to study the effects of predators, habitat type, recruitment, disease, and physical factors on the distribution and abundance of *M. arenaria* and *T. plebeius.* The Bay offers a range of environmental conditions including temperature, salinity, dissolved oxygen, and availability of complex habitat. Lower Chesapeake Bay (the Virginia portion of Chesapeake Bay) is mostly polyhaline (except in the upper reaches of the tributaries). Upper Chesapeake Bay (the Maryland portion of the Bay) is mostly mesohaline. Bottom habitat type in the upper Bay is characterized by oyster shell hash, soft muds, fine sands, and gravel/pebbles (Smith et al. 2003). Bottom type in the lower Bay is similar to that of the upper

Bay (Wright et al. 1987), except shallow shoals in the lower Bay south of the Potomac River often have mixed beds of eelgrass *Z. marina* and widgeongrass *Ruppia maritima* (Orth et al. 2010). The entire Chesapeake Bay experiences seasonal hypoxia in deep channel water, which occasionally wells up onto the shoals with the tides and wind events (Sanford 1990, Kemp et al. 2005). Summer temperatures in the upper Bay are likely still hospitable for *M. arenaria*, while the lower Bay experiences periods when they are above the tolerance limit for the species. In Chesapeake Bay, the dominant predators of *M. arenaria* and *T. plebeius* include the blue crab *Callinectes sapidus*, horseshoe crabs *Limulus polyphemus* (Botton 1984, Lee 2010), and demersal fishes (de Goeij et al. 2001, Seitz et al. 2001) including cownose rays (Fisher 2010). Crabs forage for clams from the sediment and consume the entire clam (Beal 2006), whereas demersal fishes nip clam siphons, causing clams to reduce their burial depth and exposing them to increased predation by probing predators (de Goeij et al. 2001). High predation rates on infauna are also associated with seasonal migratory behavior of cownose rays *Rhinoptera bonasus* (Blaylock 1993), which are able to consume bivalves that would otherwise avoid predation by burrowing, armor, and/or size refuges (Fisher 2010).

In this study, we concurrently examined predation, habitat, recruitment, and disease prevalence/intensity to disentangle the relative effects of these factors on survival and persistence of *M. arenaria* and *T. plebeius*. We hypothesized that: (1) densities of *M. arenaria* and *T. plebeius* are positively associated with presence of complex habitat such as seagrass and shell, and negatively correlated with predator densities; (2) densities of *M. arenaria* are negatively correlated with temperature; and (3) intensity and prevalence of infection by presumed *Perkinsus chesapeaki* (hereafter, *Perkinsus* sp.) increase under stressful environmental conditions (i.e., positively correlated with temperature and river discharge, negatively correlated with salinity and

dissolved oxygen).

MATERIALS AND METHODS

Survey design

Clams were collected from three river systems of lower Chesapeake Bay (Lynnhaven River, York River, Mobjack Bay), and three river systems of upper Chesapeake Bay (Western Shore, Eastern Bay, Chester River) in fall 2011; spring/summer/fall 2012; and either spring/summer 2013 (for lower Bay) or summer/fall 2013 (for upper Bay; see Table 1 for sampling dates). Each sampling season, four to nine sites within each subestuary were sampled, with three to four replicate samples from each site (Table 1).

At each site in the lower Bay, bivalves were collected from shallow water of 1.5-2 m depth mean high water, using a suction sampling device that collects samples of 0.11 m^2 area and 40 cm depth. Three replicate sample locations in each site were selected by throwing the suction cylinder from the boat, and samples were sieved through 3-mm mesh. All samples were assigned a habitat category (mud, sand, gravel, shell, or seagrass) based on observations made in the field and the lab during sample processing. In the upper Bay, samples were collected using a commercial hydraulic escalator dredge targeting areas fished for *M. arenaria*. Habitats were categorized by the presence/absence of oyster shell hash retained on the escalator dredge, and by diver surveys conducted in 2012. All *M. arenaria* and *T. plebeius* were counted, and clam densities at each site were determined by sample area (in lower Bay) or dredge distance (in upper Bay). All clams were measured to the nearest 1 mm for shell length. Dissolved oxygen, salinity,

and temperature were also recorded at each site using a YSI (Model 85, Yellow Springs Instruments).

Between spring 2012 and summer 2013, blue crab abundance was quantified at each lower Bay site within a few days of bivalve suction sampling, using six replicate 20-m tows of a modified commercial crab scrape (usually used for harvesting soft-shell, peeler crabs in seagrass in lower Chesapeake Bay; 1 m width; Seitz et al., 2008). In Maryland, tows were conducted in the spring, summer, and fall of 2012 with two replicate 4.9 m-wide otter trawl tows for seven minutes each (approx.~ 500 m). Any fish caught in tows were counted and released. Some trawls occurred approximately a month before or after bivalve sampling, due to logistical constraints. In this case, an average of crab or fish abundance before and after the bivalve sampling was used in analyses. At each bivalve sampling site and for each season, the number of ray pits within 1 m to either side of a 50-m transect were counted, and are treated as a proxy of cownose ray *Rhinoptera bonasus* density (Hines et al. 1997). Ray pits were about 0.3 m in diameter and 10 cm deep, and could be easily seen in good visibility, or detected by sweeping the sediment with hands in poor visibility. Horseshoe crabs *Limulus polyphemus* were not quantified because they were not abundant enough in any of our samples. Fish and crab abundances per tow and ray pit counts were converted to density per 100 m^2 for analyses. Due to logistical constraints, certain data, such as environmental data and predator abundance, were missing from the survey dataset, especially for fall 2011, so models that included these missing variables were fit to data from spring 2012 through fall 2013. Environmental data from the CBIBS monitoring buoy at 38.963N 76.448W were used for Maryland western shore samples from summer and fall 2013.

We conducted a gear comparison of bivalve sampling methods by using suction samples collected in the same areas as hydraulic dredging in spring 2012. Site-average densities from

suction samples were regressed against site-average densities from hydraulic dredging for both *M. arenaria* and *T. plebeius*. *Mya arenaria* densities calculated using suction sampling were 3.58 times higher than those calculated from hydraulic dredge samples (R^2 = 0.95; Supplementary Fig. 1a); thus, suction sample densities for *M. arenaria* were reduced by a factor of 3.58 to allow both data sets to be analyzed together. Densities calculated for *T. plebeius* using both methods were in close agreement (slope = 1.10, R^2 = 0.90; Supplementary Fig. 1b), so the raw data sets were combined for analyses. Suction samples appeared to collect more small and large *Mya arenaria* (mean 42.33 mm, SD 13.73 mm; Supplementary Fig. 2a) than dredge sampling (mean 40.22 mm, SD 5.42 mm; Supplementary Fig. 2b), indicating that the discrepancy in densities was not an artifact of hydraulic dredge mesh size. Biomass of both *M. arenaria* and *T. plebeius* from the lower Bay was determined as ash free dry weight of bivalves dried in a drying oven for 24 hours, and ashed in a muffle furnace at 550 °C for five hours; bivalves in the upper Bay were not processed for biomass.

The long-term trend of *M. arenaria* recruitment in Maryland was evaluated using data from surveys conducted by SERC in the Rhode River, Maryland. Benthic core samples were collected approximately quarterly (typically March/April, June, October, December) at two sandy subtidal sites from 1981-2016. Cores were 10.2 cm in diameter and 35 cm long. Seven core samples were taken per site on each sample date and animals retained on a 500 µm sieve were preserved in 10% buffered formalin and stained with rose Bengal. All *M. arenaria* were measured for shell length and individuals <10 mm shell length were considered recruits. The total number of recruits in each year was calculated by site and then averaged across the two sites to provide an index of annual recruitment.

Disease

Whenever possible, 30 clams from each upper Bay site were held for 24-96 h in flow-through systems of ambient Rhode River or Tred Avon River waters before they were examined for *Perkinsus* sp. infections. Clams were dissected to secure labial palp tissues that were inoculated into tubes containing 3 ml of Ray's fluid thioglycollate medium (RFTM, Ray 1966), and then incubated in the dark at 28 °C for 4-7 d. After incubation in RFTM, individual clam tissues were macerated in pools of 25% Lugol's iodine before microscopic examinations at 40x magnification. *Perkinsus* sp. hypnospores were quantified in the most heavily infected palps of individual clams, and infections were assigned ordinal intensity ranks of 0-5.

Perkinsus sp. prevalence and intensity data for 2011-2013 were analyzed together with similar data collected 2000-2009. Only data from clams collected at the same geographic locations by both investigations were used for the time series. For samples collected during our 2011-2013 survey, infection intensity categories included the rank of 0.5 for infections of very low intensities (Ray 1954). In accordance with suggested methods for cross-calibrating such data (Dungan & Bushek 2015), infection intensity data for 2011-2013 were cross calibrated to those of 2000-2009 by pooling infection intensities of the lowest ranks (0.5, 1.0) (Dungan et al. 2002, Reece et al. 2008, Homer et al. 2011). Prevalences were estimated as the proportion of infected clams.

Clams tested for *Perkinsus* sp. infections were predominantly collected from upper Bay sites where hydraulic dredging was used to reliably collect adequate numbers of adult clams. Although hydraulic escalator dredging was unavailable in the lower Bay, 30 juvenile *M. arenaria* were collected by hand from Indian Field Creek, York River, VA, in April 2013, held

in flow-through tanks for several months until they were 20-30 mm in shell length, and were assayed for *Perkinsus* sp. infections in July 2013.

Statistical analyses

Both *M. arenaria* and *T. plebeius* exhibited many instances of zero catch, so two models were used to analyze the data: presence/absence was modeled with a binomial generalized additive model (GAM, logit link), and non-zero densities were modeled with a Gaussian GAM (identity link) on log-transformed data. GAMs for *T. plebeius* included the following as parametric predictors: temperature (°C), salinity, dissolved oxygen (mg L^{-1}), ray pit density (m^{-2}), crab density (m^{-2}), fish density (m^{-2}), and habitat (5 categories: gravel, mud, sand, shell, and seagrass). *Mya arenaria* were rarer and data contained many more zeroes than *T. plebeius*; to meet assumptions, habitat was reduced to two categories (simple, including mud, sand, and gravel; and complex, including seagrass and shell) in both presence/absence and non-zero density models, and the presence/absence model was run only on spring/summer data for 2012. *Perkinsus* sp. infection intensity rank-score was modeled as a log-transformed continuous variable using a Gaussian GAM (identity link). Disease GAMs for *M. arenaria* and *T. plebeius* included the following as parametric predictors: temperature (°C), salinity, dissolved oxygen (mg L^{-1}), bivalve length (mm), and bivalve density (m^{-2}). To account for trends in data across space, a two-dimensional spline (trend-surface) was fit on latitude and longitude for all GAMs (Cressie 1993). To account for trends in time, sampling day was fit in each model using a spline with a kernel smoothing function (Kohn et al. 2002). The number of knots (k) in each model was chosen automatically using a Generalized Cross-validation (GCV) optimizer, except for the

presence/absence model for *M. arenaria*, which was fit with a spline of order k = 2 because only two seasons were modeled, and the GCV optimizer produced a model with skewed residuals. For all GAMs, model assumptions were assessed visually using residual and quantile-quantile plots.

Time series (infection intensity, infection prevalence, and *M. arenaria* recruitment) were analyzed using automatic time series forecasting (ARIMA models; Hyndman & Khandakar 2008), and disease models included spring/summer temperature (April-August) obtained from the Chesapeake Bay Program Water Quality Database (http://www.chesapeakebay.net/data) for all tidal mainstem Chesapeake Bay stations, and annually averaged Susquehanna River discharge obtained from the USGS water quality monitoring station at Harrisburg, PA (National Water Information System at https://waterdata.usgs.gov/usa/nwis). No autocorrelation or non-stationarity was detected in ARIMA models of *Perkinsus* sp. infection intensities or prevalences ([p,d,q] = [0,0,0]), so analysis proceeded using linear models. For multiple comparisons, significant difference was determined using non-parametric bootstrap hypothesis testing with 10,000 simulations and $\alpha = 0.05$ (Efron & Tibshirani 1993), and Cohen's d was calculated as a measure of effect size for all two-group comparisons. All analyses were completed in R (R Core Team 2017).

RESULTS

Survey

Temperature over the course of the survey (fall 2011 – summer 2013) ranged 12.6 °C – 33.3 °C. Temperatures exceeding 28 °C and 30 °C were observed for 23.7% and 6.5% of all

samples collected, respectively. Salinity ranged from 5.3 in the upper York River site to 25.7 in the Lynnhaven Bay sites. The minimum dissolved oxygen level observed was 3.3 mg L^{-1} in Mobjack Bay, though the site means ranged 6.50 mg L^{-1} - 9.35 mg L^{-1} (Table 1). The maximum density of fish observed was 9.38 fish m^{-2} (mean: 0.47, sd: 1.18); the maximum density of ray pits observed was 0.46 pits m^{-2} (mean: 0.04, sd: 0.09); and the maximum density of blue crabs observed was 7.25 crabs m^{-2} (mean: 0.36, sd: 0.97). Several major storms occurred during the study period, including Hurricane Sandy, which made landfall in New Jersey on October 29, 2012 and caused major flooding throughout Chesapeake Bay (Kunz et al. 2013), and Hurricane Lee in 2011, which was a major inflow event (Hirsch 2012). These storms produced no noticeable mortality in our survey of *M. arenaria* and *T. plebeius* in the Chesapeake Bay.

Densities of *M. arenaria* were 2.75 times higher in the lower Bay than in the upper Bay ($p = 0.02$, $d = 0.01$). The maximum density observed was 53.33 m^{-2} *M. arenaria* near the mouth of the York River, VA, in spring 2012. Out of all samples collected, 54.73% of upper Bay and 89.82% of lower Bay samples did not contain *M. arenaria*. Despite repeated sampling, samples from four sites in Virginia contained no *M. arenaria* (two in Mobjack Bay and two in Lynnhaven). Bay-wide, densities of *Tagelus plebeius* were 13.07 times higher than *M. arenaria* densities ($p < 0.001$, $d = 0.02$, Fig. 2b). Densities of *Tagelus plebeius* were 8.37 times higher in the lower Bay than in the upper Bay ($p < 0.001$, $d = 0.04$). In the upper Bay, densities of *T. plebeius* were 6.58 times higher in the Eastern Bay and Chester River than on the Western Shore ($p < 0.001$, $d = 0.03$; Fig. 2a). The maximum density observed for *T. plebeius* was 218.18 m^{-2} in the lower Bay in Lynnhaven (Linkhorn Bay) in summer 2013. *Tagelus plebeius* were found at every lower Bay site, but were not found at two sites in the Eastern Bay of Maryland throughout

the study period. Trends in biomass of both *M. arenaria* and *T. plebeius* in the lower Bay closely matched trends in densities (Supplementary Figure 3).

Average shell length of *M. arenaria* was 1.43 times greater in the upper Bay than in the lower Bay ($p < 0.001$, $d = 0.07$; Fig. 3a). Similarly, *T. plebeius* in the upper Bay were 2.07 times larger than those in the lower Bay ($p < 0.001$, $d = 0.04$; Fig. 3b). Only 5.56% of *M. arenaria* collected in the lower Bay were greater than 50 mm in shell length, while 29.73% of upper Bay *M. arenaria* were 50 mm or larger.

The highest densities of *Mya arenaria* were in the spring, with declining density through the fall (Fig. 4a). *Tagelus plebeius* densities did not show consistent seasonal trends over the study period. In the lower Bay, *T. plebeius* densities were the lowest in spring 2012, increased through the summer and fall, and then remained high (generally 15-20 m^{-2}) and stable through 2013 (Fig. 4b). In contrast, in the upper Bay the clearest seasonal trend involved a pulse of *T. plebeius* in spring 2012 (~5 m^{-2}) which disappeared through the summer and fall (Fig. 4a).

Within each season, there were some differences in *M. arenaria* densities among habitats: *M. arenaria* were very rarely found in gravel, were found in mud and sand mainly in the spring, and had a tendency towards high but variable densities in seagrass throughout the seagrass growing season (Fig. 5a). The odds of finding *M. arenaria* in seagrass or shell were 392.04 times greater than in less-complex habitats such as mud, sand, and gravel. When *M. arenaria* were present, densities in seagrass or shell were 2.15 times greater than in less-complex habitats such as mud, sand, and gravel. The odds of finding *M. arenaria* decreased as temperature increased, and when they were present, *M. arenaria* density was negatively correlated with dissolved oxygen (Table 2). There was no significant relationship between *M. arenaria* density and predator density (Table 2).

Tagelus plebeius density in seagrass was higher than in less-complex habitats in most seasons (Fig. 5b). The odds of finding *T. plebeius* in seagrass were 11.65 times greater than in mud (significant at $\alpha = 0.10$), 3.95 times greater than in sand (significant at $\alpha = 0.10$), and 11.28 times greater than in shell (significant at $\alpha = 0.05$). When *T. plebeius* were present, densities in sand were 4.63 times greater than in gravel, 5.39 times greater than in seagrass, and 4.74 times greater than in shell. High densities in sand were only observed in the spring (Fig. 5b). High densities of *T. plebeius* were also observed in shell, though this was not significant in the models (Table 2). When they were present, *T. plebeius* density increased with salinity (Table 2). There was no significant relationship between *T. plebeius* density and predator densities (Table 2).

Mya arenaria recruitment in the Rhode River declined steadily between 1980 and 2016. Recruitment was characterized by an Autoregressive Integrated Moving Average (ARIMA[2, 1, 1]), with a negative trend (drift) of -0.03 million clams ha^{-1} y^{-1}. The survey captured no recruits post-2005 (Fig. 6).

Disease

Mean infection intensity for *Mya arenaria* was light throughout the upper Bay, with a mean of 0.48 on a 5-point scale (Fig. 7a). Infection intensity in *M. arenaria* increased 54.9% for each degree increase in temperature, and increased 6.7% for each mm in shell length (Table 2). *Mya arenaria* infection intensity was positively correlated with temperature, salinity, and dissolved oxygen (Table 2). Infection intensity for *M. arenaria* on the Western Shore of Maryland was 1.54 times higher than for *M. arenaria* on the Eastern Shore in Eastern Bay or the Chester River ($p = 0.03$, $d = 0.02$; Fig. 7a). The mean infection intensity for *T. plebeius* was light

to moderate and was 1.57 times greater than that for *M. arenaria* ($p < 0.001$, $d = 0.03$; Fig. 7b). Mean infection intensity for *T. plebeius* decreased by 16.3% with each unit increase in salinity, and increased 21.2% with each unit increase in temperature (Table 2). Infection intensity increased with *T. plebeius* size (3.6% for each mm of shell length; Table 2). Disease intensity for *T. plebeius* and *M. arenaria* did not increase with bivalve density (Table 2).

Perkinsus sp. infection prevalence was low for *M. arenaria*, averaging 29.21% over the course of the survey (2011-2013). Infection prevalence for *M. arenaria* was 1.19 times higher on the Western Shore of Maryland than on the Eastern Shore in Eastern Bay or Chester River ($p = 0.002$, $d = 0.03$; Fig. 7c). *Perkinsus* sp. infection prevalence during the survey (2011-2013) was 2.17 times higher in *T. plebeius* (Fig. 7c) than in *M. arenaria* (Fig. 7d; $p < 0.001$, $d = 0.06$). Mean infection prevalence for both bivalve species increased with temperature and dissolved oxygen, and prevalence also increased with salinity for *M. arenaria* (Table 2). Infection prevalence increased with bivalve size for *M. arenaria*, but not for *T. plebeius* (Table 2). Infection prevalence and intensity were not related to *M. arenaria* or *T. plebeius* densities (Table 2). In the lower Bay, where 30 juvenile *M. arenaria* were assayed, hypnospores were present in two individuals at very low infection intensities (ordinal rank 0.05).

Prevalence of infection was moderate to high between 2000 and 2013, with mean infection rates of 68.46% for *M. arenaria* and 81.86% for *T. plebeius* (Fig. 8a). Across all years in the time series, average prevalence of infection was similar between species ($d = 0.25$, $p = 0.16$), and average infection intensities were light and similar between *M. arenaria* and *T. plebeius* ($d = 0.04$, $p = 0.18$). Infection prevalence and intensity were negatively correlated with annual Susquehanna River discharge for *M. arenaria* (prevalence: coef. = $-1.25E^{-5}$, $t_9 = -3.40$, $p = 0.01$; intensity: coef. = $-2.28\ E^{-5}$, $t_9 = -2.31$, $p = 0.05$) but not for *T. plebeius* (prevalence: coef. =

$-6.99E^{-6}$, $t_8 = -1.60$, $p = 0.15$; intensity: coef. = $-1.17E^{-5}$, $t_8 = -1.28$, $p = 0.24$; Fig. 8c). Infection prevalence and intensity were not correlated with spring/summer temperature for *M. arenaria* (prevalence: coef. = $2.96E^{-2}$, $t_9 = -0.56$, $p = 0.59$; intensity: coef. = $6.23E^{-2}$, $t_9 = 0.44$, $p = 0.67$) or for *T. plebeius* (prevalence: coef. = $-2.51E^{-2}$, $t_8 = -0.40$, $p = 0.70$; intensity: coef. = $-9.95E^{-2}$, $t_8 = -0.76$, $p = 0.47$).

DISCUSSION

As we hypothesized, the distributions of thin-shelled commercial species *Mya arenaria* and *Tagelus plebeius* were positively associated with complex habitat. Densities of both *M. arenaria* and *T. plebeius* were associated with habitats with a high degree of complexity (seagrass and shell) as compared to some less-complex habitats (mud, sand, and gravel). Complex habitats may be more favorable for these species because they increase rates of larval settlement by baffling water currents (Heiss et al. 2010), provide increased food resources for both suspension and facultative deposit-feeding species (Peterson et al. 1984), and provide refuge from predators (Orth et al. 1984). However, this also implies that habitat loss may be an important factor in the decline of *M. arenaria* and *T. plebeius*, as both seagrass and oyster reef habitats are declining in Chesapeake Bay (Orth et al. 1984, 2006, Rothschild et al. 1994, Beck et al. 2011, Lefcheck et al. 2017).

In agreement with our hypotheses, densities of *M. arenaria* were negatively associated with increasing temperature. *Mya arenaria* is a cold-water species that is distributed from the sub-arctic regions to North Carolina along Atlantic coasts of North America (Abraham & Dillon 1986, Maximovich & Guerassimova 2003). Typically *M. arenaria* survives well in temperatures

from 2 to 28 °C (Cohen 2005), with mortality usually occurring above 30 °C (Kennedy & Mihursky 1971). It is expected that with global climate change, Chesapeake Bay may become inhospitable for this species. The upper tolerance range for *M. arenaria* is frequently surpassed in the summer in Chesapeake Bay, especially in shallow waters where this sampling effort took place. High summer temperatures in particular are likely a major factor in the decline of *M. arenaria* in lower Chesapeake Bay.

Bivalve presence/absence and density were not negatively associated with ray, blue crab, or fish densities for either species, in contrast to our hypothesis, and horseshoe crabs were not abundant enough to determine their relative contribution to bivalve mortality. However, the snapshot in time provided by our predator and bivalve sampling may not reflect the legacy of predator-prey interactions experienced by local clam populations (Thrush et al. 1997, Seitz & Lipcius 2001, Seitz et al. 2016). Our seasonal time series for *M. arenaria* abundance in particular seem to indicate that predation is an important factor in determining density. In both the upper and lower Bay, densities of *M. arenaria* decline throughout the summer months when predation peaks (Hines et al. 1990). Observed temporal trends also correspond with *M. arenaria* reproductive behavior in Chesapeake Bay, where the fall spawn is more successful than the spring spawn, due to decreased predation pressure in the winter months (Blundon & Kennedy 1982a, Baker & Mann 1991). Individuals spawned in the fall are able to settle and grow throughout the winter, when risk of predation is minimal, and this new generation manifests as a springtime spike in density. However, even the clams that survive until the spring are almost completely consumed by predators each year, essentially resulting in an “annual crop” rather than a stable population with a sustainable age distribution. The declines in *M. arenaria* in summer may be associated with increasing temperature as well as predation, and we have

insufficient evidence from our snapshot in time to distinguish between effects of the two. However, this effect persisted in both the upper and lower Bay, under different temperature regimes, indicating that predation is likely a major driver of observed trends in *M. arenaria* density.

Despite occupying a similar niche in Chesapeake Bay, *M. arenaria* and *T. plebeius* exhibited different seasonal trends in densities. *Tagelus plebeius* spawns in the spring (Holland & Dean 1977), and while a spring high-density event was noted in the upper Bay in 2012, the lower Bay had relatively steady densities that did not show a clear recruitment signal or summer crash. *Tagelus plebeius* in the lower Bay likely do not exhibit the same seasonal crashes in abundance observed for *M. arenaria* because a robust adult *T. plebeius* population remains in lower Chesapeake Bay throughout the seasons. This population allows for high densities of many different size classes to exist at any given time. However, in the upper Bay, where densities are much lower, seasonal spring recruitment was evident in time series, indicating very different population dynamics in these two regions of Chesapeake Bay. *Tagelus plebeius* in the upper Bay seem to exhibit annual population fluctuations more similar to those of *M. arenaria*. This may be because of density-dependent mortality sources specific to the upper Bay, including fishing pressure and disease, which work to keep upper Bay *T. plebeius* at low densities that are sensitive to annual recruitment and predation.

Predation and low fecundity likely drive patterns in recruitment of *M. arenaria* in Chesapeake Bay, which is characterized by very low recruitment with some pockets of locally high recruitment, though studies examining recruitment in more locations would be necessary to identify factors contributing to low recruitment. Although there are some cases of locally high recruitment of *M. arenaria* in Virginia (Lovall et al. 2017), recruitment in the Rhode River,

Maryland, declined drastically since the 1980s and now is essentially zero. Predation has been identified as the most important limiting factor in recruitment of *M. arenaria* in other regions (Beal et al. 2001, Hunt & Mullineaux 2002, Beal 2006), and likely plays an important role in Chesapeake Bay as well. In addition, low adult densities and small body sizes may limit recruitment. *Mya arenaria* are highly fecund, but clams ~32 mm shell length (the most common size encountered in the lower Bay during the survey) are rarely mature in the western Atlantic (Brousseau 1978, Brousseau & Baglivo 1988). Clams ~46 mm shell length (the mean size of clams in the upper Bay) are generally mature, though expected fecundity for clams of that size is less than half the fecundity of clams >60 mm shell length (Brousseau 1978, Brousseau & Baglivo 1988). Clams >60 mm shell length were rarely encountered in the upper Bay, and never encountered in the lower Bay, indicating fecundity may be limited by age, and therefore body size, in Chesapeake Bay *M. arenaria*.

In agreement with our hypothesis, *Perkinsus* sp. infection intensity and prevalence in both species was positively associated with high temperatures, conditions that were considered stressful for *M. arenaria* in particular. Impacts of dissolved oxygen on *Perkinsus* sp. infection was less clear, though dissolved oxygen was generally within the tolerable range for *M. arenaria* and *T. plebeius* and may not have been extreme enough to induce a stress response during the course of the survey. Disease intensity and prevalence in *M. arenaria* was positively correlated with salinity, and long-term intensities and prevalences of *Perkinsus* sp. infections in *M. arenaria* were negatively associated with Susquehanna River discharge, a proxy of salinity. Salinity preference of *Perkinsus* sp. may explain the long-term correlation between infection intensities/prevalences and river discharge/salinity. *Perkinsus* sp. survives and proliferates best at moderate to high salinities, depending on the species. At 28 °C, *Perkinsus chesapeaki* survival

and proliferation is optimal at moderate salinities 15-25‰ (La Peyre et al. 2006) or 14 ‰ (McLaughlin et al. 2000). In oysters, infection intensity and prevalence of a similar protist, *Perkinsus marinus*, were both greater in higher salinity waters (Burreson & Calvo 1996). Thus, it may be expected that *Perkinsus* sp. infection in *M. arenaria* would be greatest in high-salinity (low flow) years and locations.

It is possible that disease dynamics do not drive trends in *M. arenaria* and *T. plebeius* density in space and time, as intensities of infections were generally low for both species. In addition, infection intensity was associated with clam size (proxy of age), but not with clam densities. Previous studies have also failed to find an association between *P. chesapeaki* infection and mortality (Bushek et al. 2008). However, this study was unable to disentangle the impact of disease on mortality (which would manifest as a negative relationship between bivalve density and disease) from density-dependent disease dynamics (which would manifest as a positive relationship between bivalve density and disease). To our knowledge, this study documents the most complete record of *Perkinsus* sp. infection in *M. arenaria* and *T. plebeius* to date, but impacts of disease mortalities on depleted clam populations of Chesapeake Bay remain to be carefully evaluated by rigorous experimental investigations of disease pathogenesis and outcomes.

The lack of information on *T. plebeius* long-term abundances is an impediment to understanding the decline of this species and the consequences of this decline. Without landings records or fisheries-independent indices of *T. plebeius* abundance, it is difficult to assess the health of the population. In addition, basic population biology information for *T. plebeius* populations in the coastal U.S. is often lacking. Investigations of some populations of *T. plebeius* in Argentina (Lomovasky et al. 2016) and Brazil (da Silva et al. 2015) have established valuable

baselines for the species. The ecological and commercial importance of this species, as well as its role harboring *Perkinsus* sp., warrant future studies on growth, reproduction, tolerance to environmental conditions, disease-related mortality, and distribution within U.S. waters.

Conclusions

It is likely that habitat loss, low recruitment, and predators are major factors keeping *Mya arenaria* and *Tagelus plebeius* at low densities in Chesapeake Bay, though continued harvest, which was not addressed in this study, may play a role as well. We found no evidence suggesting densities of *M. arenaria* or *T. plebeius* are negatively impacted by *Perkinsus* sp. infection prevalence or intensity, though the direct effect of *Perkinsus* sp. infection on bivalve mortality remains to be addressed. Extremely low densities of *M. arenaria*, decimated after tropical storm Agnes in 1972 (Cory & Redding 1976, Haven et al. 1976), and a susceptibility of this thin-shelled species to predation by blue crabs, likely fuel a feedback loop that leads to high per-capita rates of predation, which works to keep *M. arenaria* populations at low levels. In recent years, similar dynamics may have been at work in the upper Chesapeake Bay, where populations of *T. plebeius* have reached low densities through fishing pressure or possibly disease. Since *M. arenaria* and *T. plebeius* are preferred prey items for major predators such as *Callinectes sapidus* and *Rhinoptera bonasus* (Blundon and Kennedy, 1982b; Fisher, 2010), it is unlikely that predator switching will provide much relief. However, both species appear able to take advantage of refuge provided by complex habitats. Habitats such as seagrass and shell allow both bivalve species to persist at a low-density refuge, which may be stable. Further work should focus on predator-prey interactions, elucidating the existence and stability of low-density refuge habitats,

the effect of population declines on exosystem services such as filtration, and the likelihood that thin-shelled bivalve species may persist, recover, and sustain commercial fisheries in Chesapeake Bay.

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TABLES

Table 1. Locations and dates of suction sampling in the lower Chesapeake Bay and hydraulic dredge sampling in the Upper Chesapeake Bay. Sites (latitude = Lat. and longitude = Lon.) were each sampled on multiple dates, listed here for each river. Means are shown for temperature (Temp., °C), salinity (Sal.) and dissolved oxygen (DO, mg L^{-1}).

Region	River	Lat.	Lon.	Temp.	Sal.	DO	Dates
Lower Bay	Lynnhaven River	36.88367	-76.01586	24.25	22.25	7.27	11/9/11
		36.89569	-76.08216	22.35	22.87	7.77	4/30/12 7/12/12
		36.89569	-76.10185	22.29	23.21	7.67	10/4/12
		36.89872	-76.04659	23.55	23.18	7.82	5/1/13 7/23/13
	Mobjack Bay	37.29100	-76.38210	21.20	19.06	8.99	11/3/11
		37.31217	-76.40636	21.62	18.82	8.53	4/20/12 7/30/12
		37.34371	-76.41560	21.76	18.84	8.63	10/17/12
		37.37065	-76.36165	21.54	19.36	8.53	4/30/13 7/15/13
	York River	37.26266	-76.39778	22.87	20.33	8.21	11/2/11
		37.28126	-76.58297	22.41	17.40	7.46	4/19/12 7/10/12
		37.41419	-76.67194	23.17	12.94	8.41	9/13/12
		37.43980	-76.70376	22.78	12.13	7.08	4/24/13 7/10/13
Upper Bay	Chester River	38.93225	-76.22830	23.8	12.36	9.35	10/25/11
		38.99975	-76.20897	22.20	11.80	8.60	4/20/12 7/26/12
		39.04367	-76.18493	22.71	11.71	7.70	10/23/12
		39.08914	-76.15221	22.35	10.80	6.80	6/11/13 9/18/13
	Eastern Bay	38.83910	-76.24934	22.97	13.33	8.43	10/18/11
		38.87986	-76.33017	22.66	13.34	8.14	5/31/12
		38.90133	-76.25754	22.22	13.23	8.28	7/31/12
		38.91160	-76.25772	23.63	12.94	7.70	6/18/13
		38.94111	-76.25729	23.65	12.54	7.75	9/20/13
	Western Shore	38.86741	-76.51770	22.49	11.73	7.06	11/1/11
		38.86819	-76.50999	21.68	11.21	7.01	4/20/12
		38.88224	-76.48127	22.04	12.33	6.96	8/2/12
		38.89855	-76.43542	26.80	13.20	8.60	10/24/12
		38.90902	-76.45731	21.71	11.84	7.11	7/11/13
		38.93742	-76.43924	24.01	11.76	6.50	9/25/13
		38.98781	-76.41432	22.78	12.95	7.94	
		38.9808	-76.44611	22.95	13.05	7.77	
		39.01121	-76.39606	22.82	12.65	7.58	

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Table 2. Generalized additive model (GAM) coefficients and standard deviations (in parentheses) for presence/absence (P/A), density, *Perkinsus* sp. infection intensity (average ordinal intensity rank of infected individuals) and prevalence (Dis. Prevalence) of infection (proportion of individuals infected) models for *Mya arenaria* and *Tagelus plebeius*. Transformations (either log or logit) are indicated next to the variable name and coefficients are not back transformed. Parametric predictor variables were temperature (temp., °C), salinity (Sal.), dissolved oxygen (DO, mg L^{-1}), ray pit density (rays m^{-2}), crab density (crabs m^{-2}), fish density (fish m^{-2}), and habitat (gravel [GR], mud [MU], sand [SA], shell [SH], and seagrass [included in the intercept, int.]). Disease GAMs also included bivalve length (mm), and bivalve density (m^{-2}). Coefficients significant at $\alpha = 0.05$ are bolded.

	Mya arenaria				*Tagelus plebeius*			
	logit(P/A)	log(Density)	log(Intensity)	Dis. Prevalence	logit(P/A)	log(Density)	log(Intensity)	Dis. Prevalence
Int.	147.01 (62.41)	6.11 (7.09)	**-21.90 (2.09)**	**-23.01 (2.10)**	12.14 (5.45)	-4.56 (4.22)	**-4.23 (1.73)**	-3.18 (1.70)
Temp.	-4.79 (2.34)	-0.27 (0.29)	**0.44 (0.12)**	**0.60 (0.07)**	-0.28 (0.16)	0.01 (0.11)	**0.19 (0.07)**	**0.14 (0.07)**
Sal.	-1.27 (0.75)	0.17 (0.17)	**0.27 (0.13)**	**0.48 (0.04)**	-0.29 (0.16)	0.31 (0.14)	**-0.18 (0.06)**	0.06 (0.05)
DO	-0.55 (0.78)	-0.32 (0.16)	**0.54 (0.06)**	**0.19 (0.03)**	0.22 (0.17)	-0.04 (0.1)	-0.03 (0.03)	**0.10 (0.03)**
Rays	-7.94 (15.51)	0.09 (1.76)	NA	NA	1.45 (2.89)	0.63 (1.25)	NA	NA
Crabs	0.34 (0.77)	-0.04 (0.37)	NA	NA	-0.09 (0.18)	-0.01 (0.15)	NA	NA
Fish	-0.37 (0.65)	0.10 (0.17)	NA	NA	-0.12 (0.15)	-0.15 (0.12)	NA	NA
Habitat	SG & SH v.	SG & SH v.	NA	NA	GR: -0.46 (1.32)	GR: 0.15 (0.97)	NA	NA
	MU, SA & GR	MU, SA & GR			MU: -2.46 (1.48)	MU: 1.27 (0.96)	NA	NA
	-5.97 (2.82)	-0.77 (0.38)			SA: -1.37 (0.81)	SA: 1.68 (0.65)	NA	NA
					SH: -2.42 (0.69)	SH: 0.13 (0.59)	NA	NA
Bivalve length	NA	NA	**0.06 (0.01)**	**$2.89E^{-2}$ ($4.01E^{-3}$)**	NA	NA	**0.04 (0.01)**	-0.02 (0.01)
Bivalve density	NA	NA	$8.13E^{-5}$ ($2.26E^{-3}$)	$4.11E^{-4}$ ($1.62E^{-3}$)	NA	NA	$1.78E^{-3}$ ($3.52E^{-3}$)	$1.04E^{-3}$ ($2.92E^{-3}$)

FIGURES

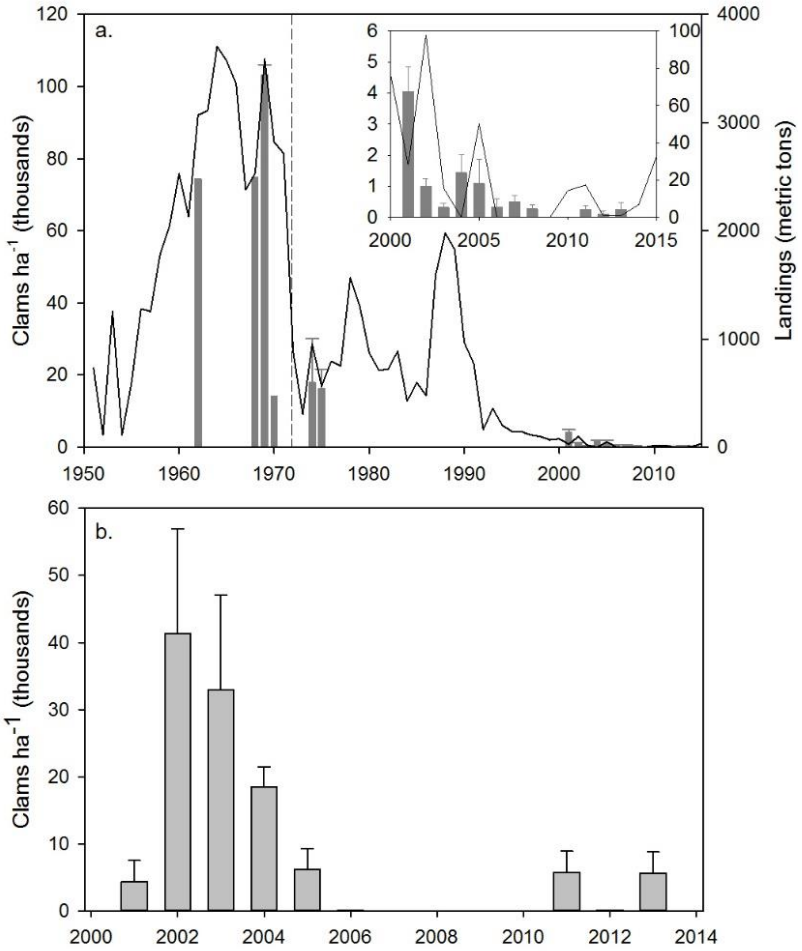


Figure 1. (a) *Mya arenaria* abundance (± S.E.) and fishery landings (solid line) for the period 1951-2015, with inset showing amplification of abundance and landings for 2000-2015. Abundance data (shaded bars) are from Maryland DNR (2001-2008) and SERC (2011-2013) fishery-independent escalator dredge sampling. Landings are for the Maryland and Virginia portions of Chesapeake Bay combined (NMFS Commercial Landings Database). Vertical dashed line represents Tropical Storm Agnes (1972). Data source: NMFS Commercial Landings Database. (b) *Tagelus plebeius* abundance (± S.E.) from Maryland DNR (2001-2008) and SERC (2011-2013) fishery-independent escalator dredge sampling. Note differences in y-axis ranges.

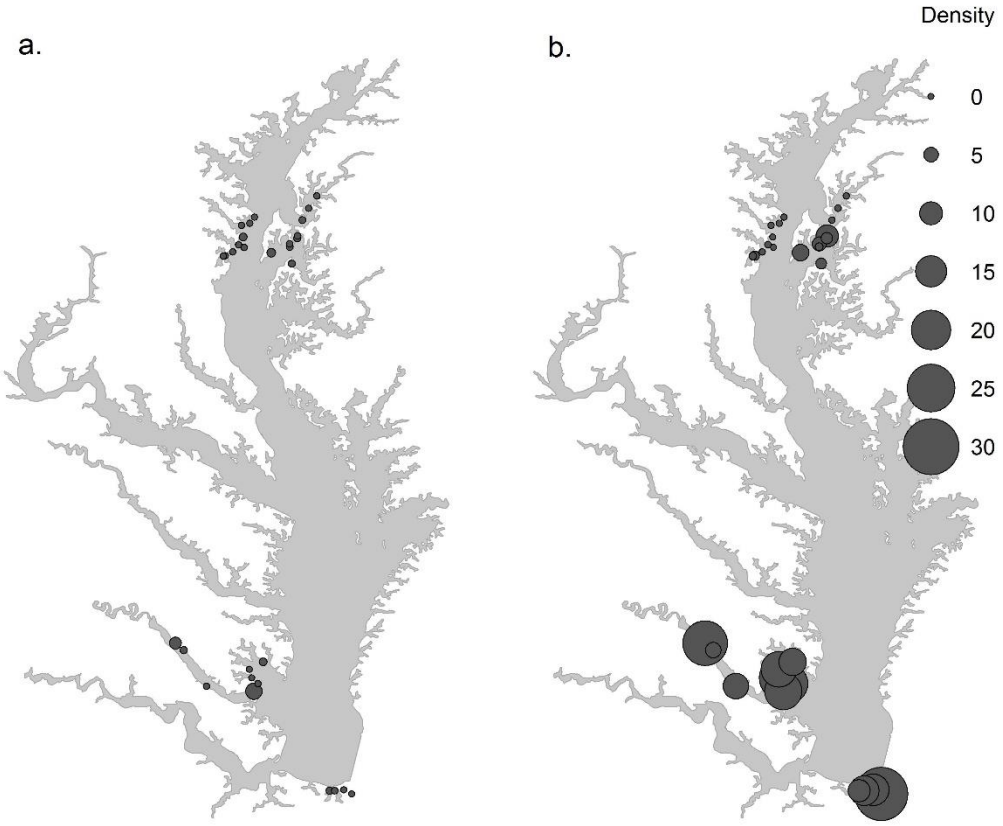


Figure 2. Mean density (m^{-2}) of (a) *Mya arenaria* and (b) *Tagelus plebeius* captured in suction and hydraulic dredge samples between fall 2011 and summer 2013. Point size is a linear function of mean density at each site: Radius = (0.25 x Density) + 1

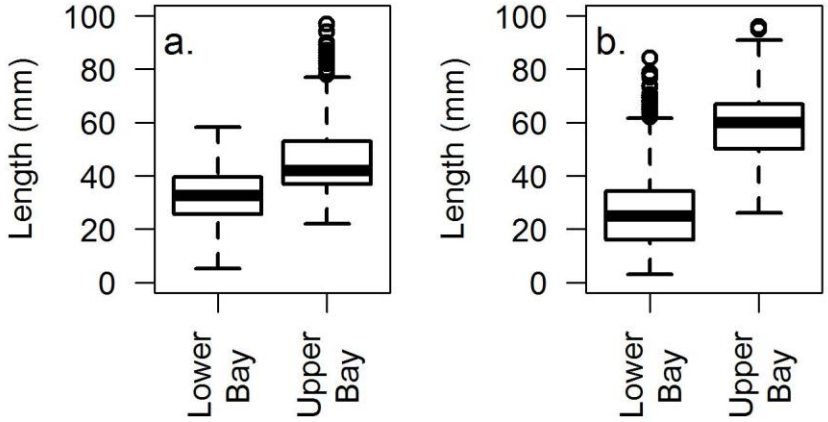


Figure 3. Average shell length in lower and upper Chesapeake Bay for (a) *Mya arenaria* and (b) *Tagelus plebeius*, with boxes from the first to third quartile and a horizontal line at the median. Whiskers extend from the lowest data point that is still within 1.5 inter-quartile range (IQR) of the lower quartile, to the highest data point still within 1.5 IQR of the upper quartile, and data outside this range are shown as circle symbols.

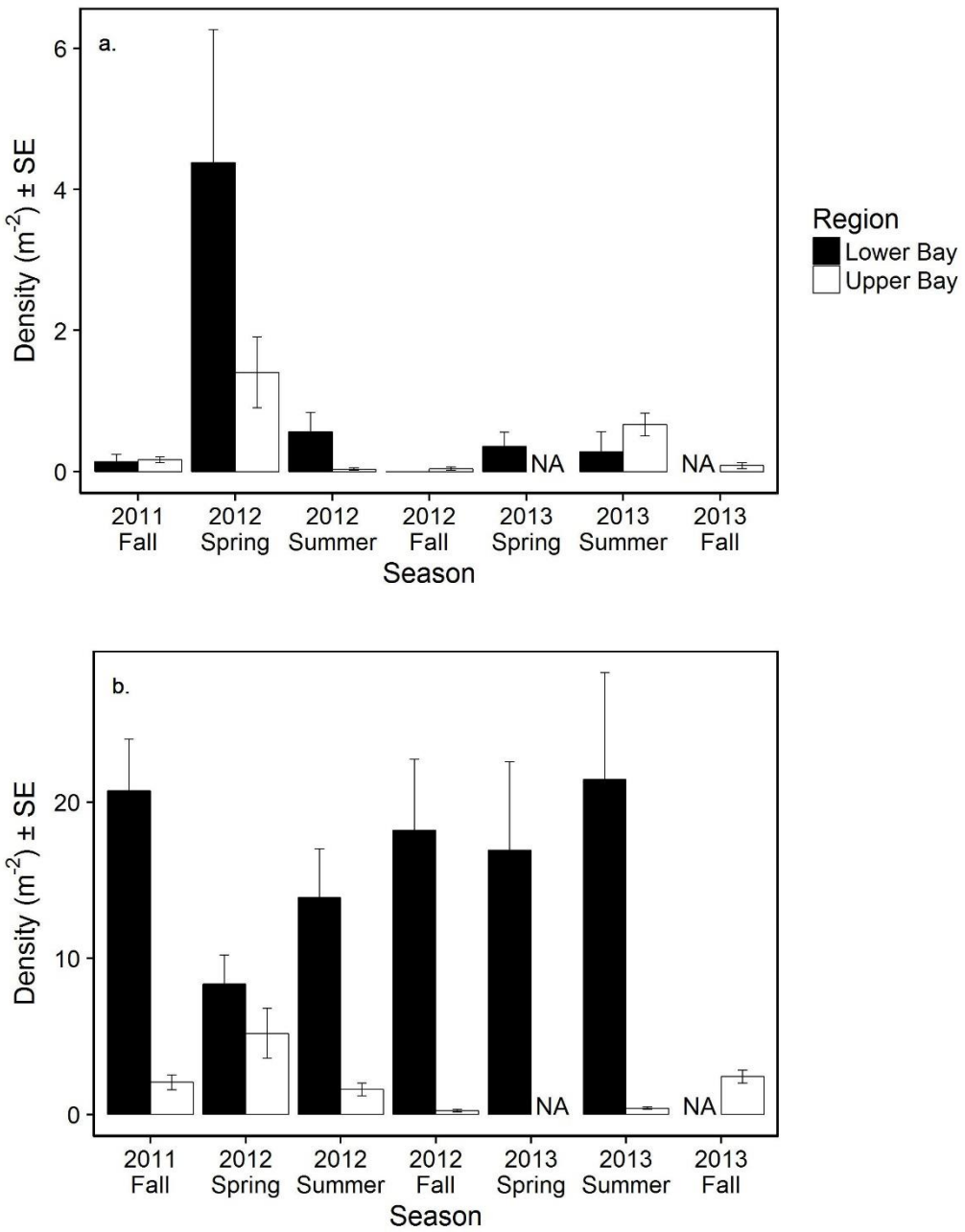


Figure 4. Mean densities and standard errors for (a) *Mya arenaria* and (b) *Tagelus plebeius* from fall 2011 through fall 2013 for the lower Bay (black) and upper Bay (white). NA = not available (not sampled). For the lower Bay, N = 36 for all seasons. For the upper Bay, N = 62, 51, 67, 59, NA, 43, 67.

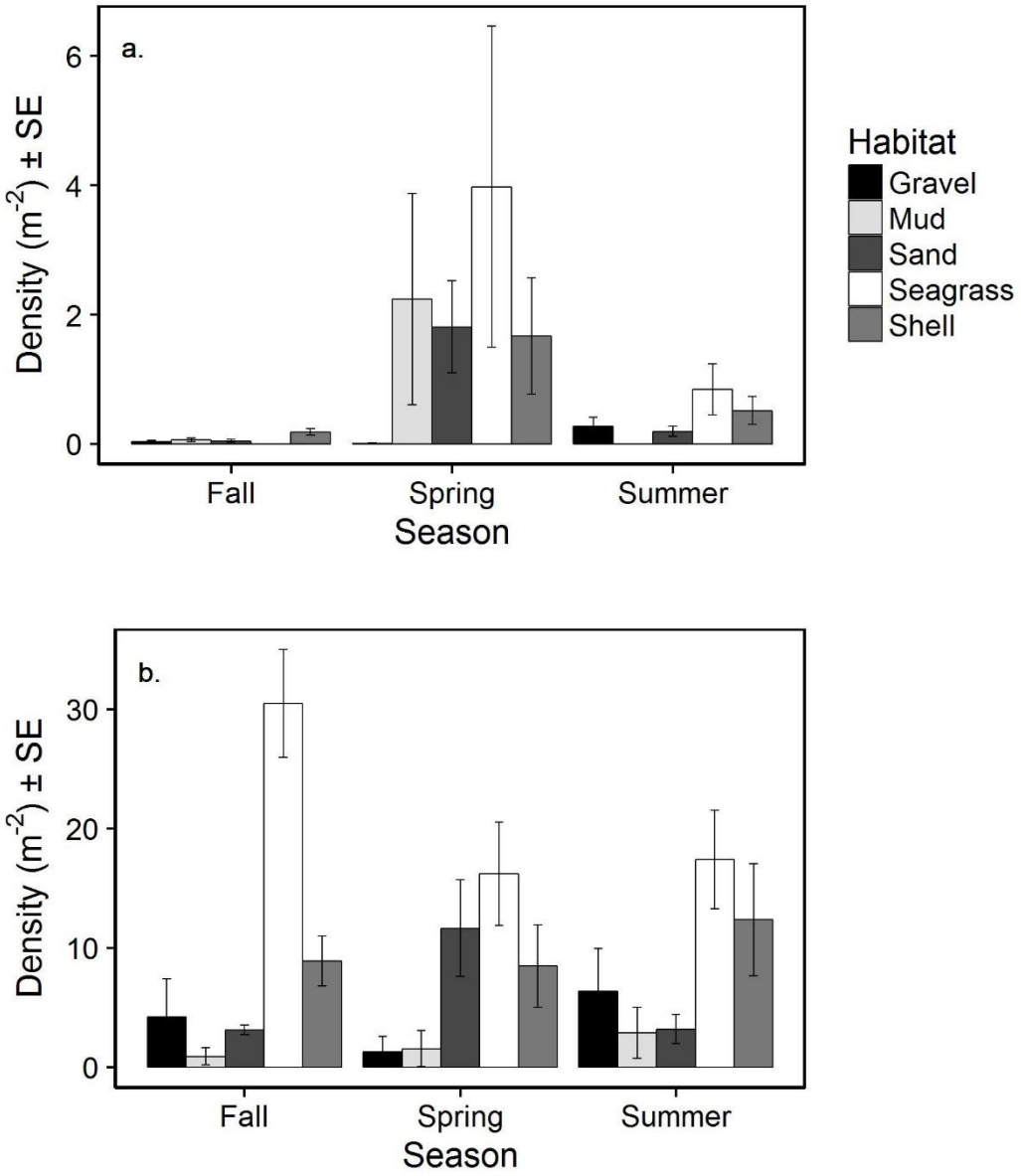


Figure 5. Seasonal trends in density for (a) *Mya arenaria* and (b) *Tagelus plebeius* in different substrates (shown in different color bars) and seasons. Error bars denote standard error. In the fall, N = 15, 25, 92, 17, 90. In the spring, N = 7, 6, 35, 23, 44. In the summer, N = 10, 26, 55, 24, 53.

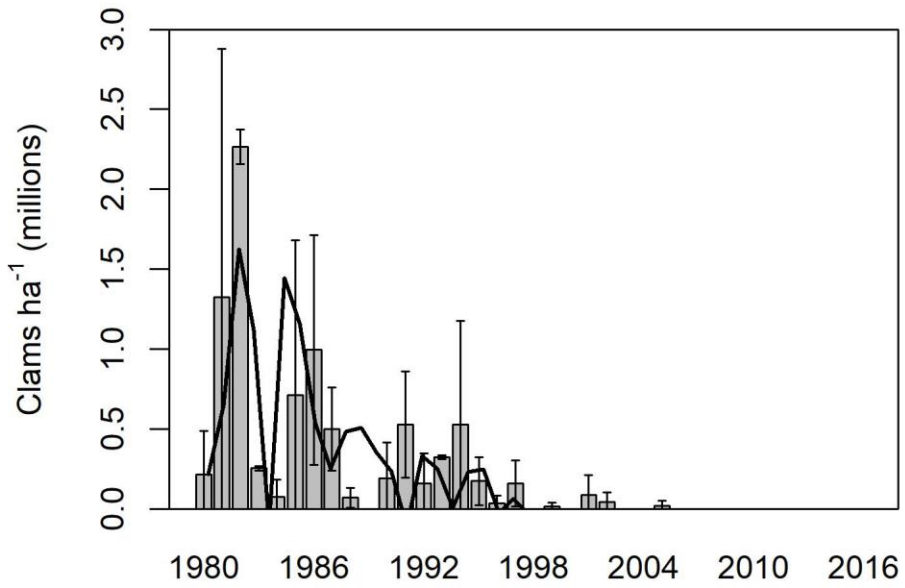


Figure 6. Mean annual *Mya arenaria* recruitment from fishery-independent core sampling in the Rhode River, Maryland (1980-2016). Recruitment data include only clams ≤ 10 mm shell length. Shown are means of two sampling sites (bars), standard deviation (error bars) and fit from ARIMA model (solid black line). No clams were captured in samples after 2005.

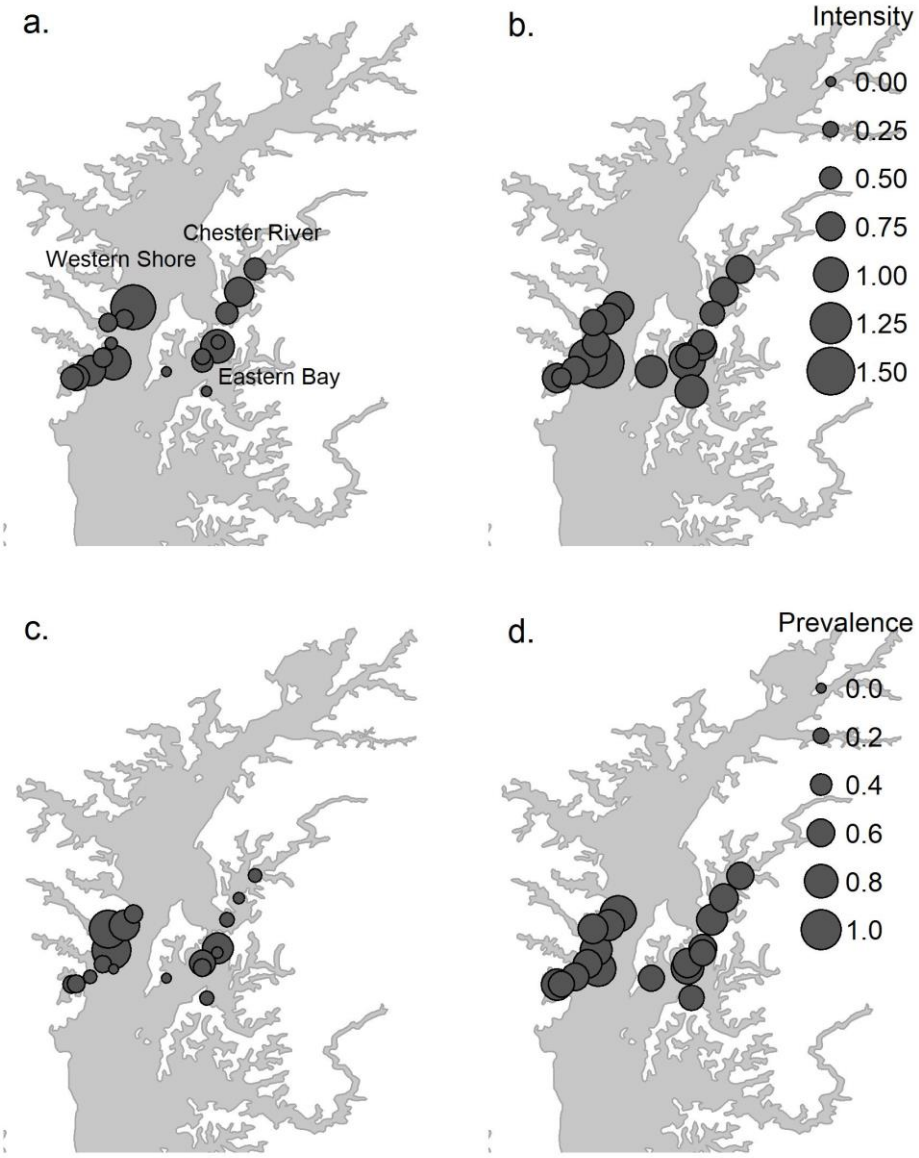


Figure 7. Average *Perkinsus* sp. (a) infection intensity (average ordinal intensity rank of individuals 0-5) for *Mya arenaria*, (b) infection intensity for *Tagelus plebeius*, (c) prevalence of infection (proportion of individuals infected) for *M. arenaria*, and (d) prevalence of infection for *T. plebeius* for the upper Chesapeake Bay from hydraulic dredge samples collected between fall 2011 and fall 2013. Point size is a linear function of mean disease intensity (Radius = [2.5 x Intensity] + 1) or mean disease prevalence (Radius = [3.0 x Prevalence] + 1) at each site.

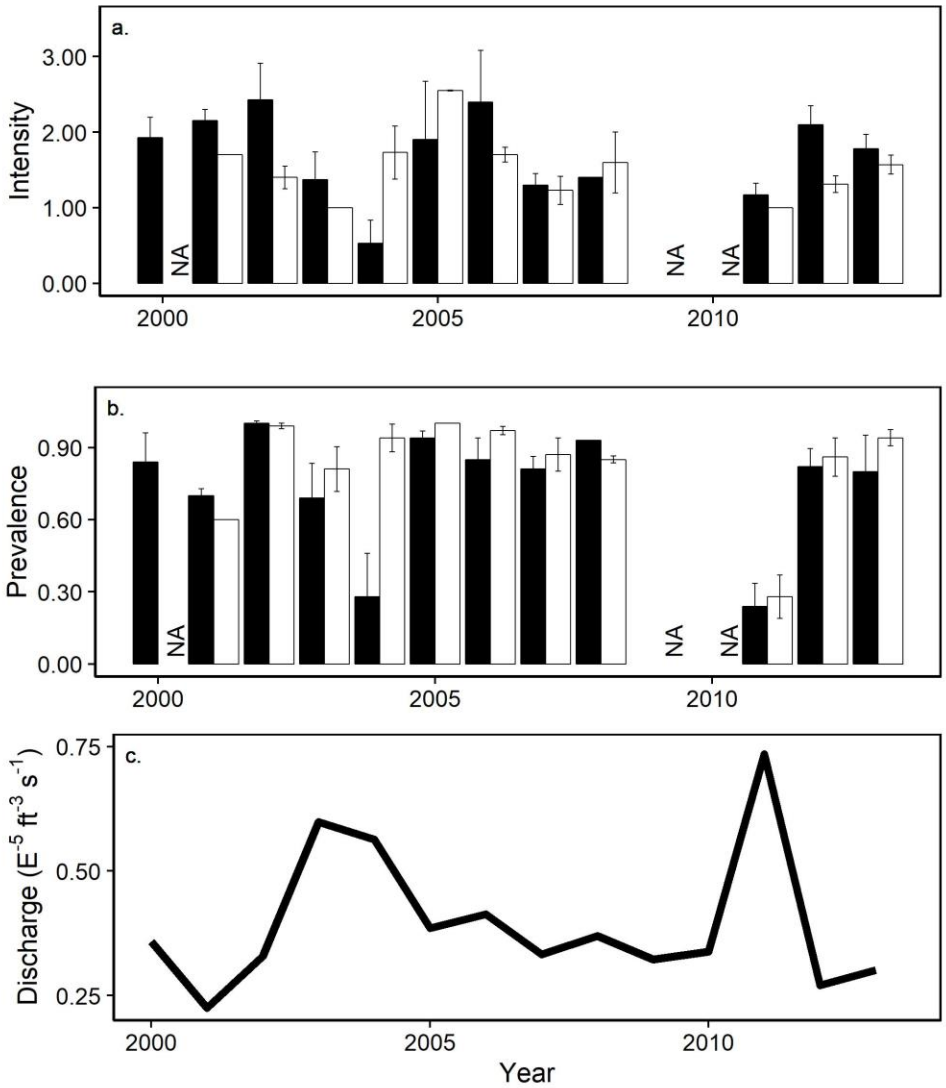
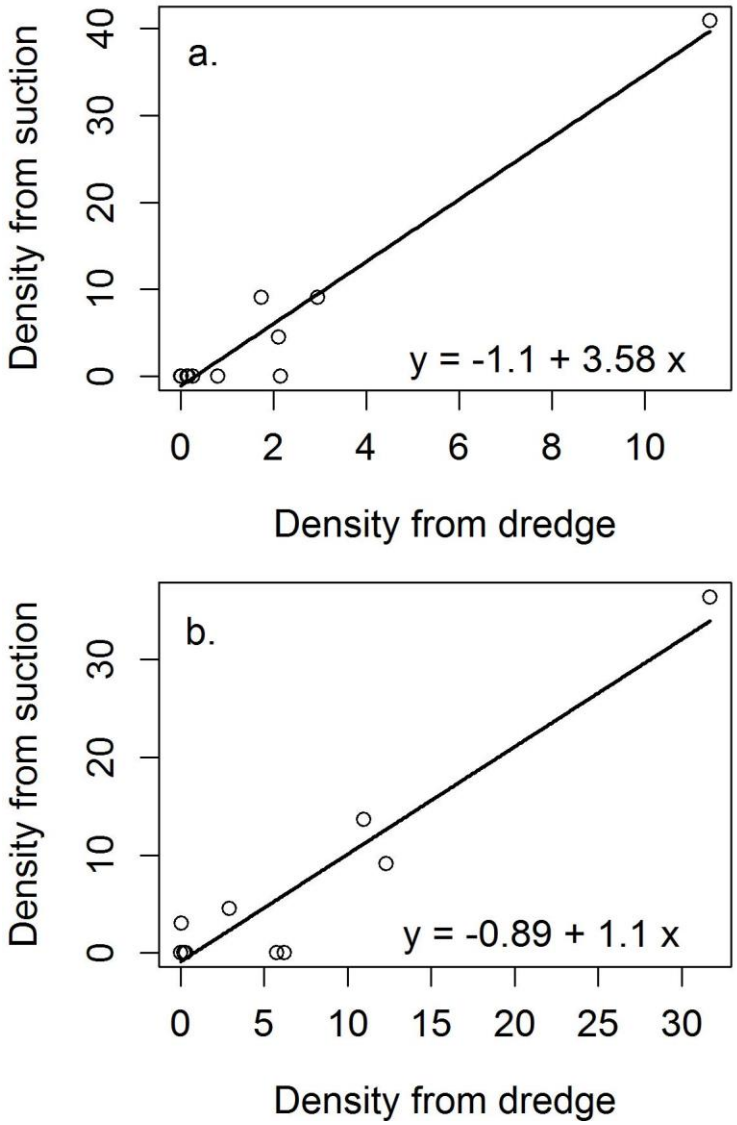
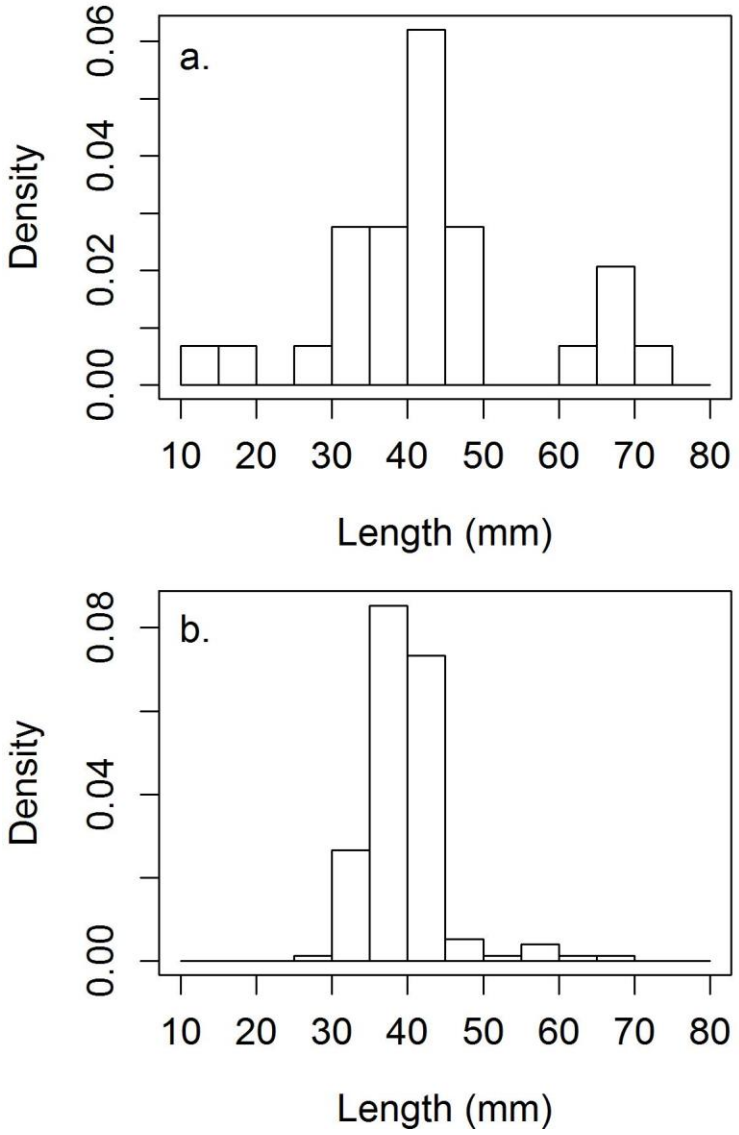


Figure 8. Time series of *Perkinsus* sp. (a) mean annual infection intensity (average ordinal intensity rank) and (b) mean annual prevalence (proportion of individuals infected) for *Mya arenaria* (black) and *Tagelus plebeius* (white) from 2000-2013. Error bars indicate standard error. Also shown is (c) average annual Susquehanna River discharge as a proxy for salinity (from the USGS National Water Information System). NA = not available (not sampled). See supplementary data files for sample sizes.

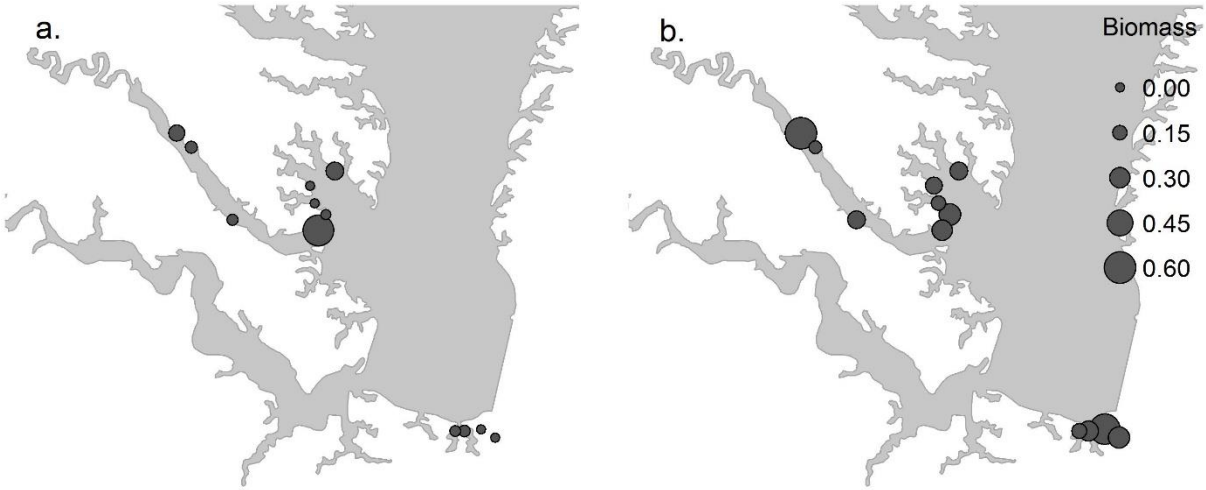
SUPPLEMENTARY FIGURES



Supplementary Figure 1. Relationship between density of (a) *Mya arenaria* and (b) *Tagelus plebeius* in suction samples and hydraulic dredge samples, including equations from simple linear regressions.



Supplementary Figure 2. Size (length) density histograms for *Mya arenaria* captured in (a) suction samples and (b) hydraulic dredge samples.



Supplemental Figure 3. Lower Chesapeake Bay biomass (ash-free dry weight) of (a) *Mya arenaria* and (b) *Tagelus plebeius* captured in suction samples between fall 2011 and summer 2013. Point size is a linear function of mean biomass at each site: Radius = (4.0 x Density) + 1.