

Warming temperatures alter the relative abundance and distribution of two co-occurring foundational seagrasses in Chesapeake Bay, USA

J. Paul Richardson^{1,*}, Jonathan S. Lefcheck^{1,2}, Robert J. Orth¹

¹Virginia Institute of Marine Science, College of William & Mary, PO Box 1346, Gloucester Point, VA 23062, USA

²Bigelow Laboratory for Ocean Science, 60 Bigelow Drive, East Boothbay, ME 04544, USA

ABSTRACT: Climate change has the potential to alter the abundance and distribution of coastal foundational species worldwide through range expansions. However, there is comparatively little evidence to show how climate change may alter interactions between foundational species that already co-occur. Here, we use long-term environmental monitoring data and non-parametric models to identify the factors driving the local cover of 2 co-existing foundational seagrasses, *Zostera marina* and *Ruppia maritima*, across 38 non-consecutive years in Chesapeake Bay, USA. We show, from an analysis of cover along permanent transects in the lower, polyhaline areas of the bay, an altered relationship between the abundance of these 2 species through time and space: mean cover on these transects of *Z. marina* was 47% in the 1990s, declined to 19% in the 2000s, and further declined to 17% in the 2010s, indicating a general decline of about 64% over the past 3 decades. In contrast, *R. maritima* cover was generally lower and less variable than *Z. marina* cover and increased from 6.8% in the 1990s to 7.5% in the 2000s and finally to 11.4% in the 2010s. Generalized additive models revealed that, after accounting for other environmental covariates, the cover of one species was strongly influenced by the cover of the other. The dominance of *Z. marina* over *R. maritima* was further modulated by rising temperatures. Thus, we propose that climate change may mediate the distributional patterns of these 2 species to the detriment of *Z. marina* and the benefit of *R. maritima*.

KEY WORDS: Eelgrass · Widgeongrass · Foundation species · Competition · Climate change

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INTRODUCTION

Coastal foundation species are heavily impacted by human activities, leading to precipitous global declines in coral reefs (Hoegh-Guldberg et al. 2007, T. P. Hughes et al. 2017), kelp forests (Wernberg et al. 2016), marshes (Deegan et al. 2012), and seagrasses (Waycott et al. 2009). In addition to direct losses, anthropogenic impacts have the potential to alter the range, distribution, and composition of foundational communities. Climate change, for example, has promoted the expansion of numerous marine algae, plants, invertebrates, and vertebrates, including a number of habitat-forming and keystone species

(reviewed in Sorte et al. 2010). Many studies of climate change effects on foundational species have also treated them as single taxonomic groups, even when they contain multiple individual species (e.g. mangroves, see Cavanaugh et al. 2014). How climate change affects individuals of habitat-forming species that already co-exist remains less studied, but has important ramifications for the future of key coastal ecosystems.

Niche theory predicts that co-existing species must compete for habitat (substrate) and resources (light and/or nutrients). The degree of competition depends on the resource pool and the intensity of environmental stressors, such as high temperatures or

*Corresponding author: jprichar@vims.edu

other physical forces (Menge & Sutherland 1987, Tylianakis et al. 2008). Changes in the abiotic environment brought on by climate change have been shown to alter interactions among communities of foundational species, leading to several outcomes for their structure and function (Doney et al. 2012). The null hypothesis is that foundational species are invariant to the observed degree of change, and therefore their interactions remain unchanged. For example, increased inundation due to moderate sea level rise has prompted the shoreward migration of marshes (Donnelly & Bertness 2001) and seagrasses (Short & Neckles 1999), resulting in no net change in community properties despite the added stress of rising tides.

Alternately, climate change can negatively affect all species in a community. Kelp forests, for example, are universally susceptible to heat waves, which have caused extensive contractions in their range on the west coast of Australia, allowing their replacement by seaweeds (Wernberg et al. 2010). Likewise, coral communities are susceptible to rising temperatures and ocean acidification brought on by increasing atmospheric carbon dioxide (Hoegh-Guldberg et al. 2007), driving these systems towards algal-dominated states (e.g. Diaz-Pulido et al. 2011). Oppositely, increasing environmental stress may lead to facilitation, where communities perform better than would otherwise be evident under ambient conditions. For example, the furoid alga *Ascophyllum nodosum* promoted the recruitment of intertidal barnacles only in warm months by shading the substrate and ameliorating heat stress (Leonard 2000). Similarly, the presence of competitors in warm southern New England salt marshes alleviated salinity stress and promoted community biomass but had the opposite effect at cool northern sites (Bertness & Ewanchuk 2002). Finally, environmental change may differentially affect species. In one extreme, warming may favor the dominant competitor and drive other species from the community, as has been shown in salt marshes (Gedan & Bertness 2009), or, it may favor weaker or weedy species, allowing them to persist even in the presence of superior competitors; high-temperature stress accompanied by high nutrients allowed the ephemeral macroalga *Enteromorpha compressa* to outcompete *Fucus* spp. on the coast of Norway (Steen 2004).

Evidence for these various scenarios suggests that the impacts of climate change on the interactions of foundational taxa can be difficult to predict, even in well-studied foundation communities such as salt marshes (Bertness & Ewanchuk 2002) or macroalgae

(Wernberg et al. 2016). One potential reason for such variable outcomes is that most studies have been conducted over one or a few growing seasons (e.g. Leonard 2000, Bertness & Ewanchuk 2002) or using experimentally simulated stressors that might otherwise take years or decades to manifest. Ideally, systems under the greatest risk of human impacts would be systematically followed for the long periods over which such changes would be expected to act (B. B. Hughes et al. 2017). To that end, we examine the role of a rapidly changing environment in mediating the interaction between 2 foundational seagrasses using 38 non-consecutive years of local monitoring along permanent transects across the lower, polyhaline areas of Chesapeake Bay, USA. The Chesapeake Bay experiences some of the most extreme temperature variations in the world and is expected to be a hotspot of climate change in the coming century, including associated changes in storm frequency and rainfall (Najjar et al. 2010). Furthermore, its watershed supports almost 18 million people with substantial nutrient and sediment runoff that reduces light availability through a number of different mechanisms (Lefcheck et al. 2017, 2018, Orth et al. 2017). Thus, the Chesapeake Bay represents an ideal location for questions pertaining to human impacts and ultimately how climate change will influence foundational species.

The 2 foundational seagrasses—eelgrass *Zostera marina* and widgeongrass *Ruppia maritima*—co-occur in polyhaline regions of the bay (Orth & Moore 1988) and provide habitat for a wide variety of invertebrate and vertebrate species, sequester carbon, and enhance nutrient cycling and water quality (Orth et al. 2006, Lefcheck et al. 2017). Historically, *Z. marina* has dominated cover in the lower bay, but large-scale declines in the 1970s and, more recently, in the 1990s and 2000s have prompted interest in larger-scale trends in the abundance of these 2 seagrasses and whether *R. maritima* can ultimately replace *Z. marina* (Moore et al. 2014, French 2015, Lefcheck et al. 2018). In the current study, we coupled intensive ground-based monitoring along a number of permanent transects with long-term abiotic data to ask: (1) What were the general trends in the abundance of *Z. marina* and *R. maritima*? and (2) What factors were associated with the relative abundance of these 2 foundational seagrasses? Based on a recent study, we expected to see a decline in *Z. marina* driven by a combination of reduced light availability and physiological stress introduced by rising temperatures (Lefcheck et al. 2017). In contrast, we expected the more thermally tolerant *R. maritima* to

persist or even increase in the face of climate change (Johnson et al. 2003, Moore et al. 2014).

MATERIALS AND METHODS

Seagrass data

Transect surveys of seagrass cover were initiated in 1978 at 17 sites throughout the lower Chesapeake Bay (Orth et al. 1979) and continued intermittently at a subset of sites through 2000 (i.e. 1 in 1990, 3 in 1993, 4 in 1994, 2 in 1995, 1 in 1996, 1 in 1997, 2 in 1998, 1 in 1999, and 4 in 2000). Following a heat-induced *Zostera marina* die-off in 2005 (Moore & Jarvis 2008), a concerted annual effort was initiated focusing on a more comprehensive set of sites (5 in 2006 and 2007, and then between 17 to 26 sites from 2009 to 2016) that comprise a more complete sample of submersed aquatic vegetation communities in the polyhaline region of the Chesapeake Bay (Fig. 1). All surveys were conducted during peak growth in late June or early July (Evans et al. 1986, Orth & Moore 1986). Transects were oriented perpendicular to the shoreline and encompassed the entire bed from the shoreline to the offshore edge of the bed. At each 10 m interval along a transect, snorkelers placed 1.0 m² PVC quadrats on the bed (0.25 m² in 1978, extrapolated to 1.0 m² for all analyses) and visually assessed cover of *Z. marina*, *Ruppia maritima*, or bare sediment. Cover was assessed in 10 % bins from 5 to 95 %. It is important to note that the percent cover estimates were scaled to the total area of bottom surveyed across each transect and not each other; thus, their sum can, but is not constrained to, equal 100 %. Once 3 successive 10 m intervals with no seagrass were encountered, the survey was terminated. Transects ranged in size from 180 to 1500 m, depending on the size of the bed.

Environmental data

Environmental data were acquired from the US Environmental Protection

Agency's Chesapeake Bay Program (CBP) database (www.chesapeakebay.net/data/downloads/cbp_water_quality_database_1984_present). These data are collected by the CBP for the long-term monitoring of the overall health of the estuary and are freely available. From these data, we identified the 7 monitoring stations most proximate to our survey sites, determined by a nearest neighbor analysis in Arc-Map (Supplement 1 at www.int-res.com/articles/suppl/m599p065_supp/). From these monitoring stations, we extracted the following data: water temperature, Secchi depth (water clarity), specific conductivity (salinity), and dissolved oxygen. Water samples were also collected at each station for later laboratory analysis of chl *a* concentrations, total



Fig. 1. Lower Chesapeake Bay, USA, showing the location of seagrass transects (dots with letters) and the Chesapeake Bay Program water quality monitoring stations (stars). Letters associated with the transects (A–Z) are the station locations represented in Fig. 3

nitrogen, and total phosphorus. To most closely reflect the conditions in the shallow-water seagrass beds, we used only the data from the surface (0.5 or 1.0 m) observations. Environmental data were summarized as yearly averages over the period from February to June, representing the growing season immediately preceding each survey (Orth et al. 2010, Lefcheck et al. 2017). The one exception was mean water temperature, whose values were averaged across the period from July to September of the previous year during which the seagrasses were most sensitive to extreme temperatures (following Lefcheck et al. 2017). Using the corresponding UTM coordinates, we additionally obtained depth estimates for each sample along each transect by employing the Virginia–Maryland bathymetric digital elevation model (NOAA, <http://estuarine-bathymetry.noaa.gov/>). Table S1 lists the exact locations and distances of all the sampling locations from the monitoring stations.

Statistical analysis

We restricted our modeling exercise of the drivers of cover to only the most recent samples from 2006 to 2016 due to the consistency of the data collection and sampling methodology. We calculated the response as the percent cover of each species along the entire transect to account for both differences in the size of quadrats through time and in the total length of the transect (which we also included as a covariate in all statistical

models). To model this response, we employed generalized additive models (GAMs). GAMs are non-parametric and therefore capture potentially non-linear relationships between seagrass cover and the suite of environmental variables under investigation, as have been observed in other studies (Lefcheck et al. 2017).

We fitted the following model to each species:

$$\sum_{k=1}^p f_k(x_{ij}) = f_1(\text{long, lat}) + f_2(\text{abundance}_{mj}) + f_3(\text{temp}_{i(j-1)}) + f_5(\text{nitrogen}_{ij}) + f_6(\text{phosphorus}_{ij}) + f_7(\text{salinity}_{ij}) + f_8(\text{chl } a_{ij}) + f_9(\text{secchi}_{ij}) + f_{10}(\text{depth}_i) + \text{Transect length}_{ij} + \epsilon \quad (1)$$

where x_{ij} is the percent cover of seagrass i in year j , $f_1(\text{long, lat})$ is the smoothed function based on the UTM coordinates of the transect to account for spatial autocorrelation, and $f_2(\text{abundance}_{mj})$ is the abundance of the other seagrass species m . Following are the smoothed functions for mean temperature, total nitrogen, total phosphorus, salinity, water column chl a , Secchi depth, and water depth. As noted in the model above, transect length was added as a parametric covariate. We additionally modeled an autoregressive correlation structure of order 1 to account for any temporal autocorrelation. We held an experiment-wide significance threshold at $\alpha = 0.05$. All models were fit using the gam function in the MASS package (Venables & Ripley 2002) in the R statistical program (version 3.2.4, R Development Core Team 2017). All data and code to conduct the analyses are included in Supplements 1–5 at www.int-res.com/articles/suppl/m599p065_supp/.

RESULTS

On average, across all transects and across the 38 years of the survey, *Zostera marina* percent cover ranged from a high of 60% in the early to mid-1990s to a low of just 2% in 2006 (Fig. 2), following a heat-induced die-off (Moore & Jarvis 2008). Low levels were also observed following the tropical storm Agnes in 1978. While *Z. marina* populations have periodically rebounded from these disturbances,

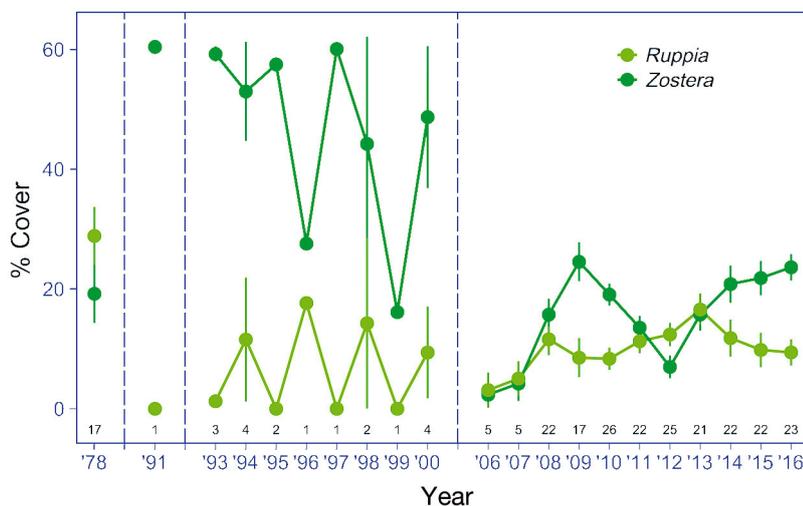


Fig. 2. Mean \pm 1 SE of percent cover summed across all quadrats for a given replicate transect of *Zostera marina* and *Ruppia maritima* across all locations. The number of replicate transects (n) are given along the bottom of the graph. The dashed lines indicate breaks in the time series

general trends reveal that mean cover declined from 47% in the 1990s to 19% in the 2000s and to 17% in the 2010s, indicating an overall decline of 64% over the past 3 decades. In contrast, *Ruppia maritima* cover was generally lower and less variable than *Z. marina* cover, ranging from 0 to 29% with a mean cover of 9.1%. Mean cover of *R. maritima* actually increased over the last 3 decades, from 6.8% in the 1990s to 7.5% in the 2000s and then to 11.4% in the 2010s.

In some cases, local-scale trends deviated significantly from the bay-wide averages, especially since the post-die-off period beginning in 2006 (Fig. 3). For instance, *Z. marina* cover ranged from 0 to 64% on any given transect, with Hungar's Creek South and Horn Point South having the highest observed cover of *Z. marina* (Fig. 3). Similarly, *R. maritima* cover ranged from 0 to 47% on any given transect, with Hungar's Creek North, Back River Shoal, and Ware Point South having the highest observed cover of *R. maritima* over the course of the survey (Fig. 3). Surprisingly, even areas in close proximity—e.g. Hungar's Creek North and South—demonstrated substantial differences in the identity of the dominant species. In all, 14 sites were dominated by *Z. marina* (>50% cover relative to *R. maritima*) and 2 sites by *R. maritima*, and 10 were relatively even mixes of the two.

Our GAMs revealed that the factors associated with *Z. marina* cover were the cover of *R. maritima* ($p = 0.002$), water temperature of the previous year ($p < 0.001$), total water column nitrogen concentration ($p = 0.01$), and chl *a* ($p = 0.02$, Fig. 4). The expected effect of the first 3 factors on *Z. marina* was negative, indicating that high cover of the competitor, warm temperatures, and high nutrients all acted to decrease *Z. marina* cover at the local scale (Fig. 4A,C,D). Oppositely, water column chl *a* showed a marginally positive relationship with *Z. marina* cover (Fig. 4B). As expected from examination of individual transects, we found a strong spatial component—as the smoothed combination of latitude and longitude—and depth in explaining cover. In all, the model explained 67.3% of the deviance in *Z. marina* cover.

We identified the cover of *Z. marina* ($p = 0.002$), water column chl *a* concentration ($p = 0.01$), salinity ($p < 0.001$), and water temperature ($p = 0.03$) as significant predictors of *R. maritima* cover (Fig. 5). All 3 predictors were expected to reduce cover (Fig. 5). The response of *R. maritima* to temperature was curvilinear and became positive when temperatures exceeded 27.5°C (Fig. 5D). Space and depth were

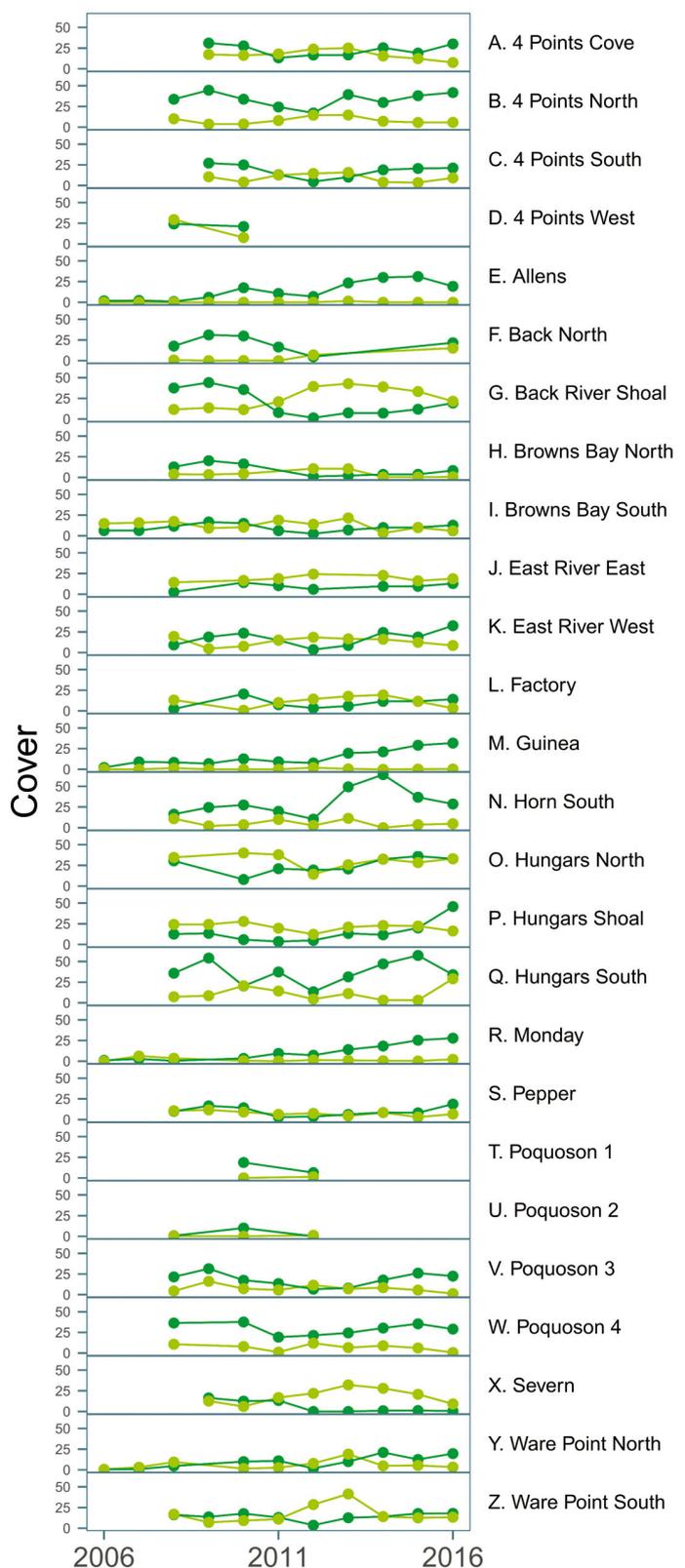


Fig. 3. Percent cover of *Zostera marina* (dark green) and *Ruppia maritima* (light green) through time for each of the 26 individual transects conducted from 2006 onward

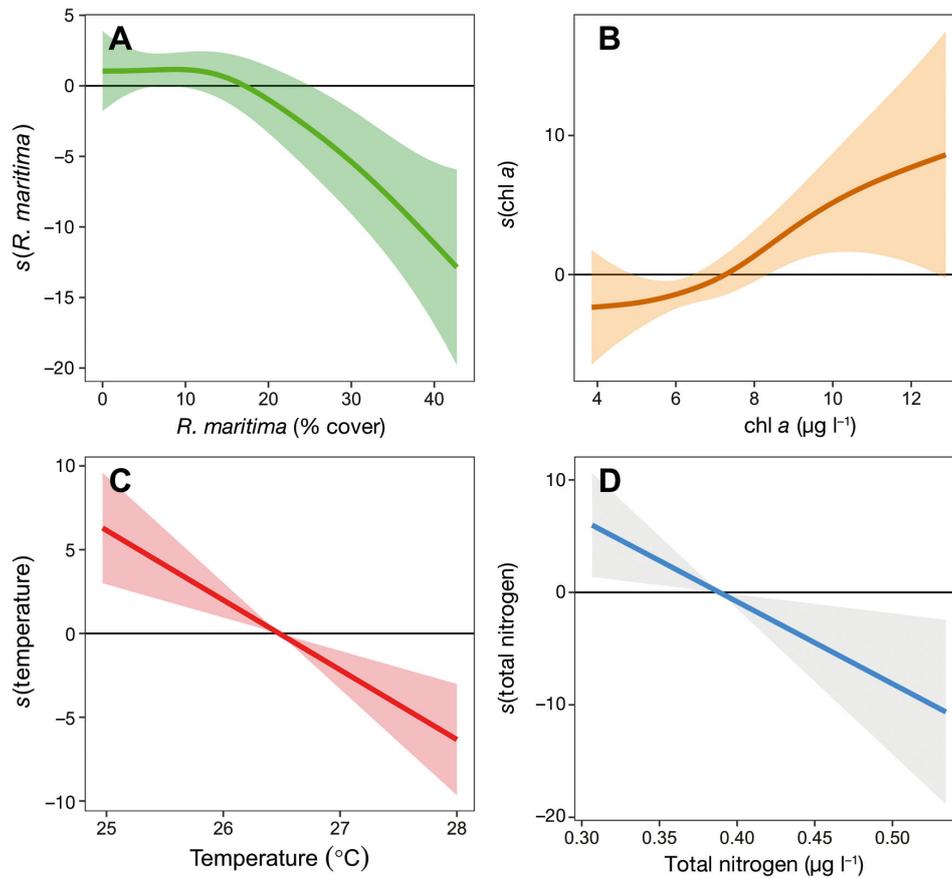


Fig. 4. Significant predictors ($p < 0.05$) of *Zostera marina* cover from a generalized additive model. Values on the x-axis are the raw values of the predictor, while values on the y-axis represent the predicted fit from the partial smoothed residuals accounting for the influence of the other predictors in the model (i.e. the independent relationship of the predictor to *Z. marina* cover). Shaded bounds indicate 95% CIs. Predicted *Z. marina* cover (A) decreases with increasing *Ruppia maritima* cover, (B) increases with increasing water column chl *a*, (C) decreases with increasing water temperature, and (D) decreases with increasing water column nitrogen

also highly significant covariates, and despite less clear trends than for *Z. marina*, the model for *R. maritima* actually explained a higher proportion of deviance: 74.3%. We obtained identical results for both species when excluding sites that had been surveyed fewer than 3 times from 2006 to 2016 (see codes in Supplements 4 & 5).

Given the known physiological intolerance of *Z. marina* to high temperatures (Moore et al. 2014, Lefcheck et al. 2018) and the die-backs of *Z. marina* after the summers of 2005 and 2010 (Fig. 2), coupled with the increase in *R. maritima* at the same time, we suspected temperature might be mediating the relationship between the 2 seagrasses. To explore this idea, we computed the difference in cover (*Z. marina* – *R. maritima*) and regressed these values against the significant predictors from the prior analysis: chl *a*, salinity, temperature, and nitrogen (Fig. 6). Only temperature showed a significant

and negative trend ($p < 0.001$, based on linear regression, Fig. 6C). The remaining predictors were all non-significantly related to the difference index ($p = 0.25, 0.15$, and 0.63 for chl *a*, salinity, and total nitrogen, respectively).

DISCUSSION

Through our statistical analysis, we have shown the relative difference in cover of these 2 seagrass species is most strongly correlated with temperature, suggesting that warming temperatures related to climate change may mediate the distributional patterns of these 2 species and, ultimately, could favor one over the other. One species, *Zostera marina*, has experienced significant decline in the Chesapeake Bay since the early 1990s as a function of increasing temperatures (Lefcheck et al. 2017), potentially

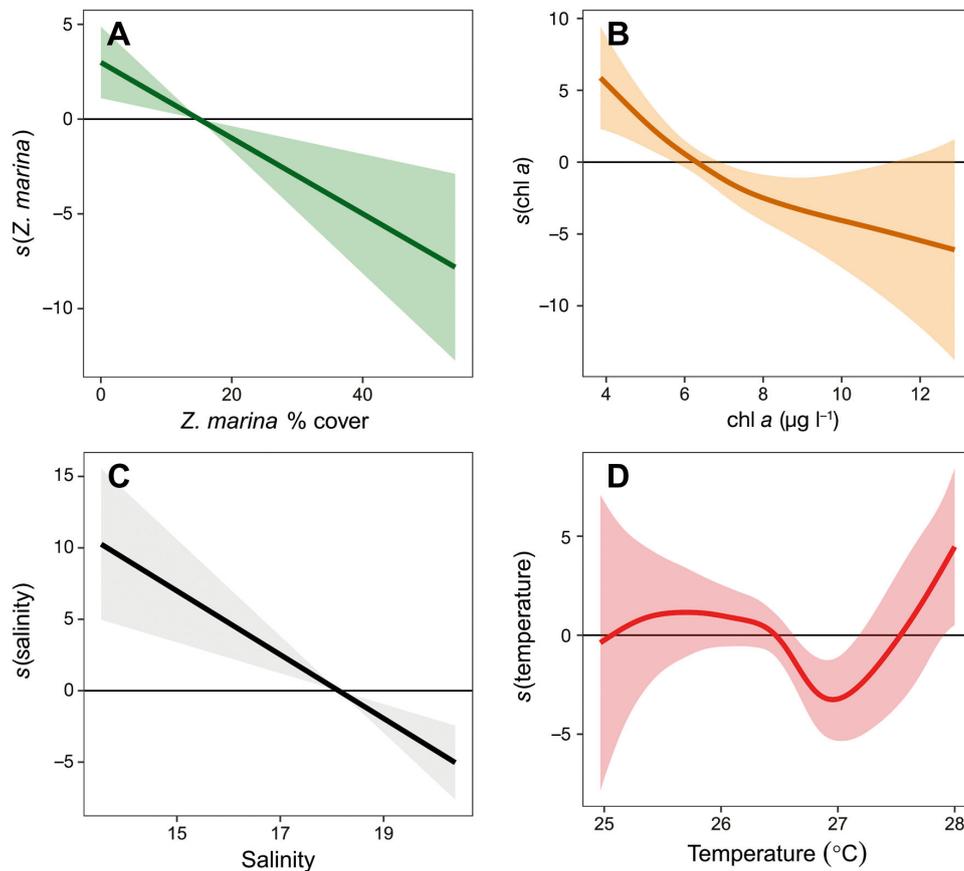


Fig. 5. Significant predictors ($p < 0.05$) of *Ruppia maritima* cover from a generalized additive model. Interpretation is the same as Fig. 4. Predicted *R. maritima* cover (A) decreases with increasing *Zostera marina* cover, (B) decreases with increasing water column chl *a*, (C) decreases with increasing salinity, and (D) has a non-linear relationship with water temperature

opening space for *Ruppia maritima* to overtake it as the dominant foundation species in the lower bay (Moore & Jarvis 2008). However, while *R. maritima* has experienced a slight increase in cover on average over the past decades, this amount is minimal relative to the much larger losses of *Z. marina*. Thus, it appears from our historical data that *R. maritima* has not yet supplanted *Z. marina* generally in the lower Chesapeake Bay.

Among these 2 species, competition is generally assumed to be for light and, to a lesser degree, space. It is known that *Z. marina* has greater tolerance for low light and, hence, why its historical distribution has extended to greater depths; in contrast, *R. maritima* has historically occupied only very shallow areas (Orth & Moore 1986). The high light requirements of *R. maritima* may also explain why we recovered a strong negative signal of water column chl *a* on this species in our analysis, indicating the presence of phytoplankton blooms that shade the water column. Historical partitioning along the depth gra-

dient has been altered, however, as a recent analysis has shown that high turbidity has all but eliminated *Z. marina* in deeper waters (>0.5 m) (Lefcheck et al. 2017). Thus, *Z. marina* is now found predominantly in shallower water locations, where water temperature is the primary driver of its continued growth and survival, and at the same depths that favor the growth of *R. maritima*.

We observed that warming affected *Z. marina* to a much greater degree than *R. maritima*, with growth ceasing around 26.5°C . Interestingly, this same threshold was identified using both large-scale aerial monitoring data (Lefcheck et al. 2018) and small-scale investigations in this system (Moore & Jarvis 2008) and in other regions where *Z. marina* is dominant (Reusch 2006, Beca-Carretero et al. 2018). However, given the strong negative effect of temperature on *Z. marina*, its removal relaxes the light limitation on *R. maritima* and may explain the shift towards dominance of *R. maritima* in some formerly mixed beds at high temperatures.

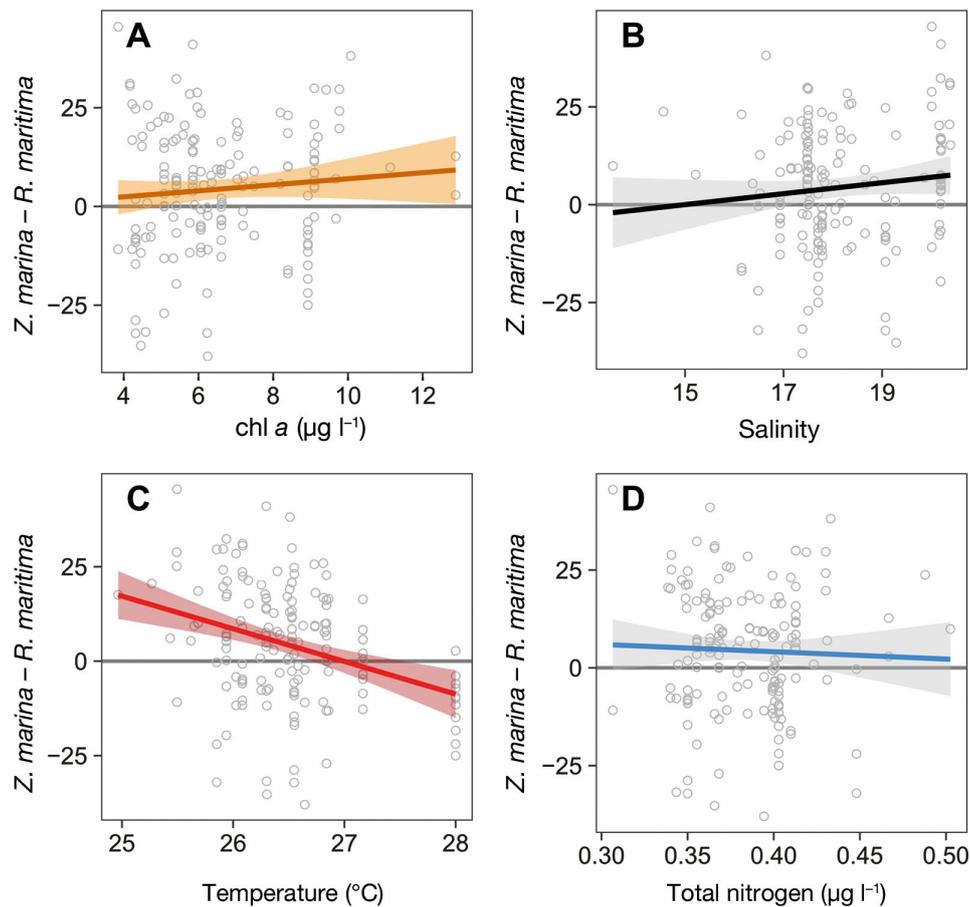


Fig. 6. Difference in total cover (*Zostera marina* – *Ruppia maritima*) against the significant predictors of their individual abundances (Figs. 4 & 5). Values >0 denote dominance by *Z. marina*, and values <0 indicate dominance by *R. maritima*. Lines are predicted fits from a simple linear regression $\pm 95\%$ CIs. There is no significant change in cover of the 2 seagrasses as (A) water column chl *a*, (B) salinity, and (D) total nitrogen increase. However, this difference does (C) decrease with increasing water temperature

The role of climate in mediating ecological interactions among marine foundational species has so far yielded inconsistent results across a range of systems (Doney et al. 2012). Our study is distinguished by being one of the few examples in seagrasses where climate change preferentially impacts the dominant competitor to the benefit of a weaker competitor (see also Micheli et al. 2008, Moore et al. 2014). Similar examples exist in marsh (Gedan & Bertness 2009) and macroalgal communities (Steen 2004). A key factor uniting these studies appears to be a large differential in stress tolerance (e.g. Bertness & Ewanchuk 2002). In the Chesapeake Bay, *Z. marina* exists near the southernmost extent of its range and is particularly susceptible to extreme temperature events (Moore et al. 2014), as opposed to *R. maritima*, which is distributed along the entire eastern US seaboard and worldwide and can tolerate much higher average temperatures (Evans et al. 1986).

While temperature appears to be the biggest control over the relative dominance of *Z. marina*, we also observed a reduction in *R. maritima* cover in response to increases in salinity. We believe the maintenance of *R. maritima* meadows is dependent on the interaction between salinity and their seed banks. *R. maritima* is highly fecund (Cho et al. 2009), with seed development continuing even when flowering shoots are detached from the parent plant, which would likely result in a significant persistent seed bank (Orth et al. 2000). Germination of *R. maritima* seeds, however, does require pulses of much lower springtime salinities than generally found at our sites (Ailstock et al. 2010). Overall, the increasing precipitation as a function of greater and more frequent storms in the Chesapeake Bay (Najjar et al. 2010) could lead to greater germination of *R. maritima* and the future persistence of this species in the lower bay.

We also identified a negative effect of nutrients (total nitrogen) on *Z. marina* which was not apparent from a larger-scale study using aerial imagery (Lefcheck et al. 2017). This result may have been due to our relatively smaller sample size or because the prior study discarded any beds not dominated by *Z. marina*. However, emerging evidence has demonstrated a key role for nutrient-induced eutrophication in explaining trends in cover of underwater grasses in most areas of the bay (Lefcheck et al. 2018). Given that *R. maritima* comprises almost 50% of total cover of underwater grasses in the mesohaline region of the bay (Orth et al. 2017), the focus of the current study on sites containing both *R. maritima* and *Z. marina* may have led to the divergence with previous work.

Our study is remarkably similar to another study by Micheli et al. (2008) that looked at long-term trends in *Z. marina* and a subtropical species of seagrass, *Halodule wrightii*, in North Carolina, USA. *H. wrightii* is morphologically similar to *R. maritima* and exhibits growth patterns similar to *R. maritima*. Decline of *Z. marina* over a 19 yr period in North Carolina was linked to increasing springtime water temperatures and water nutrient concentrations, whereas abundance of *H. wrightii* showed inconsistent temporal patterns (Micheli et al. 2008). Another similar study found that an increase in water temperature resulting from an El Niño-Southern Oscillation event in southern California, USA, resulted in a shift in dominance of *R. maritima* over *Z. marina* for similar reasons identified above (Johnson et al. 2003). These findings suggest possible generalities in the responses of seagrass communities to climate change, at least where the globally distributed species *Z. marina* is involved.

Though the long-term effects of climate change on these 2 foundational seagrasses remain uncertain, the evidence does not favor the long-term persistence of the historically dominant *Z. marina* at many locations in the Chesapeake Bay. The Intergovernmental Panel on Climate Change (Blunden & Arndt 2014) predicts increasing temperatures and more variable weather patterns that are already observable in the Bay (Kaushal et al. 2010, Lefcheck et al. 2017, Orth et al. 2017). If these conditions continue on their current trajectory, we would expect populations of heat-sensitive *Z. marina* to continue to decline unless mediated by improved light conditions (Lefcheck et al. 2017, Beca-Carretero et al. 2018). Replacement and expansion by *R. maritima* have not manifested, based on our data, but, as the result of converging environmental conditions may yet occur. It will, however, be dependent on pre-

dictable pulses of lower salinity water that allow *R. maritima* seeds to germinate and contribute to the population structure of established beds (Collier et al. 2014). This successful replacement might be a preferred scenario to the complete loss of seagrass and its accompanying functions. Our study also provides a template for understanding future changes in the composition and interactions among foundational species in the face of warming climate and other anthropogenic stressors.

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