Large projected population loss of a salt marsh bivalve (*Geukensia demissa*) from sea level rise

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ABSTRACT

Salt marshes and their inhabitants are being displaced by climate change and human development along the coastline. One inhabitant, the ribbed mussel (*Geukensia demissa*), forms a mutualistic relationship with smooth cordgrass, *Sporobolus alterniflorus*, along the US Atlantic Coast. Ribbed mussels stabilize the marsh, remove particulate matter from the water column, and promote denitrification, thereby improving local water quality. To quantify the potential effects of SLR on ribbed mussel abundance and resulting impacts on water quality functions, we compared the current and projected future (2050) spatial distributions of ribbed mussels in Chesapeake Bay assuming an intermediate SLR for the region. We found that ribbed mussel abundance was reduced by more than half due to a combination of drowning marshes, coastal squeeze, and a shift from higher to lower quality habitat. Mussel losses were greatest along the mainstem of the Chesapeake Bay, with modest gains in the headwaters. Our results highlight the importance of permeable land cover (including living shorelines) in the future tidal extent to promote marsh transgression for future mussel populations. The projected mussel abundance reductions will result in a > 50% reduction in mussel-mediated filtration and nitrogen processing, ultimately reducing the resilience of marshes in the system.

INTRODUCTION

Along the salt marshes of the United States Atlantic Coast, ribbed mussels, *Geukensia demissa* (Dillwyn 1817), form a mutualistic relationship with *Sporobolus alterniflorus* (Loisel.; henceforth cordgrass). Cordgrass provides habitat for the ribbed mussel in several ways. First, cordgrass stems promote particle trapping by acting as baffles in the water (Leonard and Croft 2006). Ribbed mussel larvae are sufficiently small (Loosanoff and Davis 1963, Baker and Mann 2003) to be influenced by the viscosity dynamics that dominate the behavior and transport of particles with low Reynolds numbers (i.e., particle sizes at which a fluid becomes viscous) in water (Scheltema 1986, Vogel 1994). Like large sediment grains, ribbed mussel settlement is facilitated by the low-flow environment created by cordgrass marshes. Once settled, the shade provided by an extensive canopy of cordgrass reduces thermal and desiccation stress, which enhances mussel metamorphosis and survival (Bertness 1984). Ribbed mussels burrow into the sediment of salt marshes where they attach to the roots, rhizomes, and stems of the cordgrass with their byssal threads, which binds the sediment, reduces erosion, and increases the stability of the marsh (Bertness 1984, Bertness and Leonard 1997). The mussels filter considerable amounts of water (Wright et al. 1982, Kreeger and Newell 2001, Moody and Kreeger 2020a), excrete ammonium, and deposit nutrients on the surface and subsurface of the marsh in their feces and pseudofeces (Jordan and Valiela 1982). These excretions fertilize the sediment and promote vegetation growth in a positive feedback loop, increasing shade and particle trapping, and thus mussel recruitment and marsh accretion.

Within salt marshes, ribbed mussels are capable of providing a wealth of ecosystem services. These filter feeders are capable of clearance rates ($L \cdot h^{-1}$)) on par with oysters (Kreeger and Newell 2001), and effectively remove a wide size-range of particulate matter. Compared to oysters, ribbed mussels are exceptional in their ability to filter bacteria from the water column, making them especially valuable for improving water quality issues (Wright et al. 1982, Kreeger and Newell 2001). Through the process of filtration, ribbed mussels ingest particulate nitrogen (N), which they subsequently assimilate to their tissues, and deposit excess particulates and waste on the surface and subsurface of the marsh (Jordan and Valiela 1982). Mussels also enhance denitrification when they co-occur with cordgrass, resulting in higher N removal from the system than either could achieve separately (Bilkovic et al. 2017). Stabilizing and fertilizing the sediment increases the resilience of the marsh (Angelini et al. 2015, 2016) by reducing erosion and promoting shoot growth (Bertness 1984), thereby enhancing the marsh's ability to protect the upland during storm events (Schuerch et al. 2013). Mussels, however, are not homogeneously distributed across the marsh surface (Bertness 1984, Franz 2001, Julien et al. 2019, Moody and Kreeger 2020b). Throughout much of their region, mussels are densest on the front (waterward) edge of the marsh where they can achieve numbers in excess of 5,000 individuals per m^2 (Bertness and Grosholz 1985, Bilkovic et al. 2017). We have previously developed a mussel distribution model that identified the primary factors influencing abundance and distribution along the front edge of cordgrass marshes (Isdell et al. 2018). These factors included cordgrass stem density, wave exposure, and forested and agricultural land covers. High exposure marsh edges with dense cordgrass and minimal nearby forest were identified as high-quality mussel habitat.

Marshes around the world are rapidly changing in response to sea level rise (SLR), erosion, and human development. As the planet continues to warm as a result of anthropogenic releases of greenhouse gasses, melting land ice, thermal expansion, glacioisostatic rebound, and other local factors are raising the sea level (IPCC 2014). As SLR continues and accelerates

(Boon 2012), salt marshes will struggle to maintain their vertical position within the tidal frame (Mitchell et al. 2017). While there are mechanisms for marshes to keep apace of SLR, in many regions, the rate of SLR is expected to exceed the rate that marshes can sustainably accrete, resulting in marsh loss (Mitchell et al. 2017). Erosion is also playing a key role in the transformation of marshes through coastal squeeze—the process by which the front edge of the marsh is receding at a greater rate than the back (landward) edge is moving inland due to sea level rise (Pontee 2013). Coastal squeeze can be the result of both natural and human causes (Doody and Williams 2004, Torio and Chmura 2013). Natural causes include an increasing slope at the landward edge of the marsh, which decreases the potential rate of inland migration (Fagherazzi et al. 2019). Humans can also engineer sudden changes in slope/elevation at the back of a marsh by building shoreline protection structures such as riprap or bulkhead. These structures are designed to reduce erosion, but also create a physical barrier that impedes landward migration of the marshes. Eventually, marshes caught between these structures and a rising sea are likely to disappear entirely.

Like many urban estuaries around the world, the Chesapeake Bay has long been plagued by water quality issues caused by human disturbances and activities (Kemp et al. 2005). Decades of intense agricultural and urban runoff into the numerous tributaries of the Chesapeake Bay resulted in a highly eutrophic system and the development of an annual dead zone (Diaz and Rosenberg 2008). The loss of wildlife and commercially valuable species, in addition to the poor water quality, led to the establishment of several agreements between the states within the Chesapeake Bay watershed and the US Environmental Protection Agency (EPA) to reduce the input of nutrients from a variety of sources (Linker et al. 2013). Due, in part, to the limited success of these agreements and the continued water quality issues of the Bay, in 2010, the EPA established Total Maximum Daily Loads (TMDLs) for each sector of the Bay which requires states to meet the goals in accordance with the Clean Water Act (US Environmental Protection Agency 2010).

Accounting for the water quality improvement capacity of wild populations of shellfish is important for accurate assessments and planning to meet water quality goals. To date, very few management plans have incorporated standing or projected stocks of wild shellfish as water quality mediators despite their proven potential (for example, see USACE 2014). Oysters have long been promoted for their water quality improvement potential (Kellogg et al. 2014), and numerous studies have documented their ability to remove particulate organic and inorganic matter from the water column, improving visibility and reducing nutrients (Grabowski et al. 2012, Ermgassen et al. 2013). Ribbed mussels, in contrast, have received limited attention for their ability to remove nutrients and improve water quality on a large scale (Galimany et al. 2017, Kreeger et al. 2018). One of the limiting factors for this is the lack of understanding of the spatial distribution of ribbed mussels within estuaries. With only a handful of published estimates of ribbed mussel abundance in any large system (i.e., beyond the scale of a marsh; see Honig et al. 2015, Bilkovic et al. 2017, and Moody and Kreeger 2020b), their overall contribution to water quality is largely unknown. As such, we have the following objectives for this study: 1) to simulate future mussel abundance and distribution under projected sea level rise in the lower Chesapeake Bay, 2) to compare current and modeled future mussel distribution, and 3) to estimate changes to mussel-mediated nutrient removal and water filtration because of mussel population shifts, and the implications for water quality in the Bay. We hypothesize that ribbed mussel abundance in the Chesapeake Bay is likely to decrease as marshes are also expected to decrease in the future due to drowning and coastal squeeze (Mitchell et al. 2017). We expect these losses to be greatest in urban areas where extensive armoring and high exposure have accentuated the conditions necessary for coastal squeeze, and that ribbed mussel-mediated ecosystem services will also be similarly impacted.

METHODS

Study area and site selection

The study area included cordgrass-dominated marshes along ~6,700 km of shoreline (Center for Coastal Resources Management (CCRM) 2018) within Virginia's microtidal (~ 1 m; Boon and Mitchell 2015) waters of the Chesapeake Bay that fell within the physiological salinity tolerances of ribbed mussels (≥ 8‰; Lent 1969, Julien et al. 2019).

Mussel model

The current distribution and abundance of mussels along the front edge of the marsh (first two meters perpendicular to the water) was taken from Isdell et al. (2018), while the future mussel abundance was estimated using the Mussel Distribution Model (MDM) described within. The specific model is provided below (Eq. 1):

$$\log(y_i) = 0.5337 + 0.0363x_{1i} + 0.0125x_{2i} - 0.0133x_{3i} + 0.0009x_{4i} \qquad \text{Eq. 1}$$

where y_i is the density of mussels (individuals·m^{-2}), x_{1i} is the cordgrass stem density (stems·m^{-2}), x_{2i} is the percent water within a 300-m radius of a point along the shoreline (used as a proxy for exposure; referred to as exposure henceforth), x_{3i} is the percent forest within a 60-m radius of a point along the shoreline, and x_{4i} is the percent agriculture within a 300-m radius of a point along the shoreline.

Several surveys have suggested that the vast majority (~85%) of mussel biomass within a marsh resides in the front edge of the marsh (Bertness 1984, Franz 2001, Bilkovic et al. 2017, Isdell et al. 2018), and modeling the edge will provide the greatest insight into potential changes in mussel distribution. Spatial application of the MDM was completed in ArcMap v. 10.4.1 (ESRI 2017) using the raster calculator tool. Land use/land cover (LULC) data were derived from the VGIN 1 m Land Cover dataset (2016; https://bit.ly/2HwWWcy) and resampled to 5-m resolution using the "Resample" tool and majority technique. Moving window analyses were run using the "Focal Statistics" tool at the corresponding scale (e.g., forest at 60 m) for each LULC type. Cordgrass stem density was held constant at a mean density (224 stems m^{-2}; derived from surveys conducted in Isdell et al. 2018) to allow for spatial application throughout the study area.

Future marsh and mussel extent

Future marsh extent was derived from work done by Mitchell et al. (this issue). To set a timeframe for shifts in elevation in the tidal frame, a sea level rise projection curve based on data from the Sewell's Point, Virginia tide gauge was used, which suggests a 0.58-m increase in sea level by 2050 (Boon et al. 2018). Sea level rise projections vary minimally across the Virginia portion of the Chesapeake Bay (Ezer and Atkinson 2015), and Sewell's Point is considered representative of overall trends (Boon et al. 2018). The vegetated tidal marsh frame in the Chesapeake Bay falls in the elevation range between mean sea level to highest astronomical tide, considered to be a 0.61-m envelope in this analysis across the Chesapeake Bay, Virginia (Mitchell et al. this issue). Appropriate elevations encompassed in the tidal marsh frame projected for 2050 were selected from a LiDAR-based digital elevation model (DEM; https://goo.gl/2djptg). Land use data in the projected 2050 tidal frame were selected from the VGIN 1 m Land Cover dataset (2016). To approximate future mussel habitats, marsh migration was permitted into all pervious surfaces other than actively managed forests or turf on the assumption that these areas would be protected with some form of structure to prevent loss. Further, marsh migration was restricted from moving beyond existing barriers such as shoreline armoring. Erosion was incorporated into the future extent by multiplying spatially explicit known average annual erosion rates reported in Hardaway et al. (2017) by 32 (the number of years between 2018 and 2050) to estimate where the shoreline would be in 2050. The annual erosion rates reported in Hardaway et al. (2017) were calculated as the horizontal change in shoreline location divided by the number of years between the imagery on which the shorelines were based. Given that many locations had a timespan > 10 years between measurements, these rates incorporate the stochastic processes that result in variable erosion rates.

Mussel abundances in 2050 were estimated by adjusting predictive factors to reflect future conditions and applying the MDM to the projected future marsh distribution under sea level rise. The water layer was recreated to incorporate the erosion and landward migration of the marshes. The other predictors (cordgrass density, agriculture, and forest) were held constant because there are no available spatially-explicit estimates of how these factors will change by 2050. All area below the future tidal envelope estimated by Mitchell et al. (this issue) was considered to become subtidal and categorized as water. Segments of estimated 2050 shoreline that were > 175 m inland from their current position were excluded from the analysis due to erosion rates in excess of 5 m y^{-1} being too great to support a viable edge population of mussels (Isdell, unpublished data).

Zone of inference

We selected 12-digit hydrologic unit codes (HUCs; Henley 2006) as our zones for spatial inference (Figure 1). The 12-digit HUCs provide small-scale delineations of watersheds primarily at the level of small rivers or large tidal creeks, rather than political boundaries. This allows for a large, yet still localized approach to our analysis. We modified the shapefile provided by USGS (Henley 2006) by splitting HUCs that spanned both shores of the major rivers

(James, York, and Rappahannock Rivers) down the center of the channel. Our modeled estimates of mussel distribution fell within 80 HUCs, which were selected for further summaries. Within each HUC, we summarized the LULC data for agriculture, forest, impervious surface, and wetlands that fell within the 2050 tidal envelope, as well as the whole HUC. The total abundance of mussels in 2018 and 2050, as well as the total area of marsh edge habitat at each time were summarized for each HUC using QGIS 3.8.3 (QGIS Development Team 2019).

Statistical analyses

Watersheds were categorized by loss vs. gain for summary statistics. Land cover characteristics were used to develop a recursive regression tree (package ‘rpart’; Therneau et al. 2018) which was pruned to keep only nodes with a complexity parameter > 0.1. All statistical analyses were completed using R (R Development Core Team 2018).

Filtration and Nitrogen Processing Calculations

We used literature derived estimates for mussel filtration, biodeposition, and denitrification rates (Table 1). We assumed 12 hours per day for filtration and biodeposition on the basis of average marsh edge inundation frequency (mussels at the front of the marsh are approximately at mean sea level, and the Chesapeake Bay has a semi-diurnal tidal cycle), and 24 hours per day for denitrification. All rates were dependent on biomass (g dry tissue weight). For our calculations, we used the median dry tissue weight per mussel (0.26 g) derived from >1,000 mussels collected around the study area by Isdell et al. (2018), multiplied by the predicted number of mussels per m^2. The use of a static feeding time and single median biomass without taking population-level size demographics into consideration is a limitation of the approach, but unfortunately necessary given that we do not have population-level size demographics for ribbed mussels in the Chesapeake Bay, nor do we have how demographics vary throughout the Bay.

This information would provide significant improvements to the estimates, but was unavailable at the time of this publication. All rates were transformed to the expected annual contribution per watershed. We compared our estimates of service changes and nitrogen removal capacity with the established targets of the TMDLs set forth by the EPA.

RESULTS

Among the 80 watersheds examined, total mussel abundance decreased from 805 million in 2018 to 314 million in 2050. Losses were observed in 67 of the watersheds (mean = -7.70 ± 1.18 million mussels) and gains were observed in 13 (mean = 2.76 ± 1.04 million mussels), with a system-wide range of -47 – +14 million mussels (Figure 2). Increases primarily occurred where creeks widened as a result of coastal squeeze reducing extensive marsh areal extent, but still had enough permeable land cover in the uplands to support a greater length of fringing-marsh edge (Figure 3), with minor contributions coming from the conversion of formerly-interior high marsh fragmenting into high-quality low marsh edge habitat.

Spatially, relative decreases were greatest in the southern and northeastern portions of the Bay (Figure 4), while increases were diffuse among the upper reaches of the tributaries. The distributions of relative and absolute differences were similar overall, with the ultimate result being low abundances of mussels (< 5 million per HUC) through almost the entire study area. The largest absolute losses were in HUCs with large, extensive marsh complexes where drowning led to edge retreat in excess of 5 $m \cdot y^{-1}$ (see bright red HUCs in Figure 4A). The primary exception to the overall trend of loss was within the HUC encompassing Jamestown Island, which saw an increase of 14 million mussels by 2050—an approximately 100% increase over current numbers. This HUC has an upland in close proximity to the current shoreline with considerably greater complexity (i.e., linear distance) than the comparatively simple marshes that currently line the waterways (Figure 3). The regression tree identified 3 primary nodes to explain the relative change in ribbed mussel abundance (Figure 5). Watersheds with < 28% forested land cover in the future intertidal zone had the largest loss of mussels (-58% ± 17%), while watersheds with > 28% forested, 1% agricultural, and 36% marsh land cover in the future intertidal zone had the greatest potential for gains (69% ± 72%).

Given that filtration rates and nitrogen processing are directly tied to ribbed mussel biomass, we also expected a net loss of services throughout Virginia. On average, regions that gain mussels will filter an additional 6.3 ± 2.4 gigaliters (GL)$\cdot$y^{-1} (range < 0.1 – 32.6 GL$\cdot$y^{-1}), produce 173.2 ± 65.3 kg N$\cdot$y^{-1} (range 0.5 – 900.7 kg N$\cdot$y^{-1}) of additional biodeposits, and remove an additional 81.3 ± 30.7 kg N$\cdot$y^{-1} (range 0.2 – 422.9 kg N$\cdot$y^{-1}) via denitrification (Figure 6). In contrast, regions that lose mussels will filter 17.9 ± 2.8 GL$\cdot$y^{-1} (range -106.2 – -0.1 GL$\cdot$y^{-1}) less water, produce 493.2 ± 76.1 kg N$\cdot$y^{-1} (range -2,928.5 – -1.8 kg N$\cdot$y^{-1}) fewer via biodeposits, and remove 231.6 ± 35.7 kg N$\cdot$y^{-1} (range -1.374.9 – -0.9 kg N$\cdot$y^{-1}) via denitrification. The direct link between mussel abundance and services provided means that the spatial redistribution of those services follows suit.

We compared changes in nitrogen processing capacity between the present and future mussel populations to the TMDL targets for the Commonwealth of Virginia (Northam and Strickler 2019). Compared to the 2025 TMDL goal for N inputs (25.28 x 10^6 kg), we estimate that mussels along the edge of marshes are currently able to process 0.18% (46.27 x 10^3 kg) of nitrogen loading in Virginia through biodeposition and denitrification each year. However, by 2050, mussels along the marsh edge will only be able to process 0.07% (18.03 x 10^3 kg) of the annual N inputs in Virginia.

DISCUSSION

Ribbed mussel populations are likely to drop precipitously in the Chesapeake Bay as a result of SLR. As relative sea level rise (RSLR) continues to accelerate (Mitchell et al. 2018), many marshes will be unable to vertically accrete to maintain their current areal extent. The resulting drowning and erosion will result in marshes that change too quickly to support adult populations of ribbed mussels and/or shift toward lower-quality habitat for ribbed mussels throughout the Bay. While some of the effects will be tempered by marsh migration, the data do not support this mechanism to be a viable option for long-term sustainment of the ribbed mussel population as coastal squeeze will intensify as marshes continue to migrate landward. The reduction in the ribbed mussel population will result in proportional reductions in the ecosystem services they provide, such as nutrient removal, water filtration, and marsh stabilization.

Losing nearly 500 million ribbed mussels throughout Virginia's Chesapeake Bay will negatively impact the resilience of the system in the face of climate change. Even if marshes are able to maintain their acreage by migrating into the adjacent uplands, the rate of change along the edge of the marsh where mussels are densest is likely to exceed what mussels are able to keep up with, particularly in watersheds with extensive marsh complexes. We noted projected erosion/transgression rates in excess of 5 $m \cdot y^{-1}$ in several of the regions with extensive marsh complexes where the topography was exceptionally flat. These also tended to be the same regions where current mussel populations are at their highest due to the large amount of high-quality habitat. Given that mussels are densest along the edges of marshes, with about 85% of the population occurring within the first two meters of the marsh in Virginia (Bilkovic 2017, Isdell et al. 2018), erosion rates that exceed 5 $m \cdot y^{-1}$ will prevent the vast majority of new recruits from reaching maturity, which takes at least one year (Franz 1996). Even assuming an annual recruitment rate of 100%, this is not a sustainable rate of change, and will rapidly reduce the adult population that exists beyond the first 5 m to a point where they may not be able to produce enough larvae to maintain the population. We argue that simply using change in marsh acreage as a metric of how a region is responding to sea level rise is inadequate to capture the importance of edge habitats and processes, in which ribbed mussels play an integral role.

This study highlighted the importance of permeable land cover within the tidal frame for facilitating the inland migration of marshes and the perpetuation of ribbed mussel habitat. Greater quantities of forested, agricultural, and marsh land cover within the future tidal frame were important for mitigating the loss or even increasing the population of ribbed mussels within the Chesapeake Bay. Numerous other studies have documented the importance of permeable land cover for the inland migration of marshes (Mitchell et al. 2017, Scheider et al. 2017). While impervious surfaces weren't to blame for the substantial predicted losses in watersheds with expansive marsh complexes, they are a limiting factor in more urbanized settings. Coastal squeeze ultimately results in the loss of marsh habitat (Pontee 2013) and is exacerbated by human development. To sustain marshes and ribbed mussel habitat in urban areas, large-scale implementation of green infrastructure, such as living shorelines, coupled with managed retreat for inland marsh migration may be helpful. Local extirpation of an important bivalve will lead to lower water quality and ecological resilience in already heavily impacted areas. Note, however, that even these strategies will face the same stresses as natural marshes in the face of accelerating SLR, and may require regular maintenance and interventions (such as additions of sediment to increase marsh elevations) to sustain the marshes.

The projected changes in ecosystem services may have significant effects on the attainment of water quality goals at local scales. Despite a removal capacity of < 1% of the total nitrogen inputs to Virginia as a whole, the first two meters of a marsh represent a very small amount of the area in these watersheds. This results in a dense concentration of N removal potential and filtration capacity, making the ribbed mussel/cordgrass partnership along the marsh edge highly valuable per unit area for these services. Further, watersheds that currently have large abundances of mussels could be meeting much larger proportions of their TMDL targets via ribbed-mussel-mediated ecosystem services than the overall state average. For example, ribbed mussels in Accomack County (NE corner of the study area) are currently removing enough N to account for 10% of their 2025 TMDL target. By 2050, we expect that the ribbed mussel population will only be able to remove 4% of N inputs to the system. This reduction in ribbed mussel-mediated N-removal means greater reliance on implementing additional best management practices, increasing set-back distances, and improved ground water, surface water, storm water, and sewage management to compensate for the lost ecosystem services provided by ribbed mussels. Successful strategies for achieving these goals should include consideration of the natural capital available in the form of bivalve filter feeders, and ribbed mussels in particular.

The assumptions that we made for this study are most likely to result in an underestimate of mussel change by 2050. By assuming that all pervious surfaces that will be within the future tidal envelope will be suitable habitat for ribbed mussels almost certainly overestimates how much habitat will be available in the future. We also had to hold several of the factors in the model constant (cordgrass stem density, percent agriculture, and percent forest) for the future given that we didn't have projections of how they were likely to change. Given that the only one of those factors had a large impact on mussel density (cordgrass stem density), we don't expect that minor to moderate changes in either forested or agricultural land cover in the proximal upland are likely to have substantial effects on the density of ribbed mussels in the future.

Further, our necessary assumption of zero shoreline armoring growth fails to account for the additional coastal squeeze resulting in marsh loss that armoring growth will cause. This will be especially true in areas of greater exposure, making the loss of these habitats even more acutely felt given the greater densities of mussels found in higher exposure settings. Shorelines in densely populated areas are also most likely to be armored for property protection (Kittinger and Ayers 2010), making the loss of mussels even greater in urban areas, which have historically struggled to reduce nutrient inputs to healthy levels in adjacent waters. Conversely, this work also assumes a "bathtub" approach to SLR and marsh loss, which is often criticized for its assumption of no vertical marsh accretion and therefore a greater estimate of marsh loss than may be realistic (Passeri et al. 2015, Kirwan et al. 2016). Given that our approach to mussel population change is focused on the waterward edge of the marsh and not on total areal extent, we feel that our estimates of mussel population change may only be slightly tempered by this assumption. The Chesapeake Bay is a microtidal, sediment-limited estuary with the second highest rate of SLR in the country (Mitchell et al. 2017). Marshes in the Chesapeake Bay are already well below the theoretical limits of marsh accretion that would allow them to keep up with SLR as a result of current rates of SLR and low levels of suspended sediment (Kirwan et al. 2010), making it unlikely that marsh accretion will have substantial moderating effects on marsh and mussel loss throughout the lower Chesapeake Bay. Therefore, it is likely that our assumptions have resulted in a fairly conservative estimate of change, and expect that the actual change may be considerably larger.

CONCLUSIONS

Ribbed mussels are an integral part of the US Atlantic coast saltmarsh ecosystem. The mutualistic relationship between ribbed mussels and cordgrass promotes the stability and functionality of these ecosystem service-rich habitats. Given their aggregation along the front edge of the marsh, where SLR and erosion will have their biggest impacts, understanding where and how mussel populations are most likely to change in the future provides key insights into their resulting loss or gain of services. In systems like the Chesapeake Bay where water quality is poor due to anthropogenic inputs, and relative SLR is high, these changes in mussel abundance and distribution are likely to have noticeable impacts on the surrounding environment. Our study has demonstrated that the ribbed mussel population will not respond homogeneously throughout the Chesapeake Bay, with clear areas of gains and losses. Preparing for and adapting to the impacts of climate change and sea level rise must involve a comprehensive understanding of how changes in existing natural capital will impact our ecosystem restoration goals.

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TABLE HEADINGS

Table 1 – Ecosystem service rates used for mussel service contributions. In the "Rate" column, Sp is the Spring rate, Su is Summer, and F is Fall/Autumn.

Table 1 -

Service	Source		Rate	Units
Filtration	Kreeger *et al.* (2018)		5.01	$L \cdot h^{-1} \cdot g^{-1}$
Biodeposition	Jordan and Valiela (1982)	Sp	$29.8(wt)^{0.839}$	$\mu g\ N \cdot h^{-1} \cdot g^{-1}$
		Su	$78.0(wt)^{0.856}$	$\mu g\ N \cdot h^{-1} \cdot g^{-1}$
		F	$24.5(wt)^{0.770}$	$\mu g\ N \cdot h^{-1} \cdot g^{-1}$
Denitrification	Bilkovic *et al.* (2017)		12.92	$\mu g\ N \cdot h^{-1} \cdot g^{-1}$

FIGURE CAPTIONS

Figure 1- The study area was located in Virginia's portion of the Chesapeake Bay. Watershed boundaries used for this study are outlined in black. State boundaries are indicated by a broken black line.

Figure 2 – The total number of mussels (millions, M) within a given watershed in 2018 (A) and 2050 (B). Abundance estimates were derived from the spatial application of the mussel distribution model (MDM) which links landscape features to mussel densities.

Figure 3 – The front edge of the marsh throughout some sections of the study area is currently (A) primarily restricted to bordering narrow creek channels. Future projections (B) open up the narrow channel and expand the potential edge to the highly crenulated upland boundary. Future projections include the marsh loss resulting from SLR, and the mussel distribution model applied to the projected water-ward edge of the marsh in 2050.

Figure 4 – Absolute (A, in millions [M]) and relative (B) change in mussel populations by watershed from 2018 to 2050. Losses are in red, gains are in blue.

Figure 5 – Recursive regression tree illustrating the importance of soft features in the future tidal extent to mitigate the impacts of sea level rise on ribbed mussels. Watersheds with < 28% forested land cover in the future intertidal zone had the largest loss of mussels (-58% ± 17%; top-left), while watersheds with > 28% forested, 1% agricultural, and 36% marsh land cover in the future intertidal zone had the greatest potential for gains (69% ± 72%; bottom-right).

Figure 6 – Bar plot of ribbed mussel filtration and nutrient processing, summarized by watersheds with mussel gains vs. losses.

Figure 1

Click here to access/download;Colour Figure;Figure1.tif

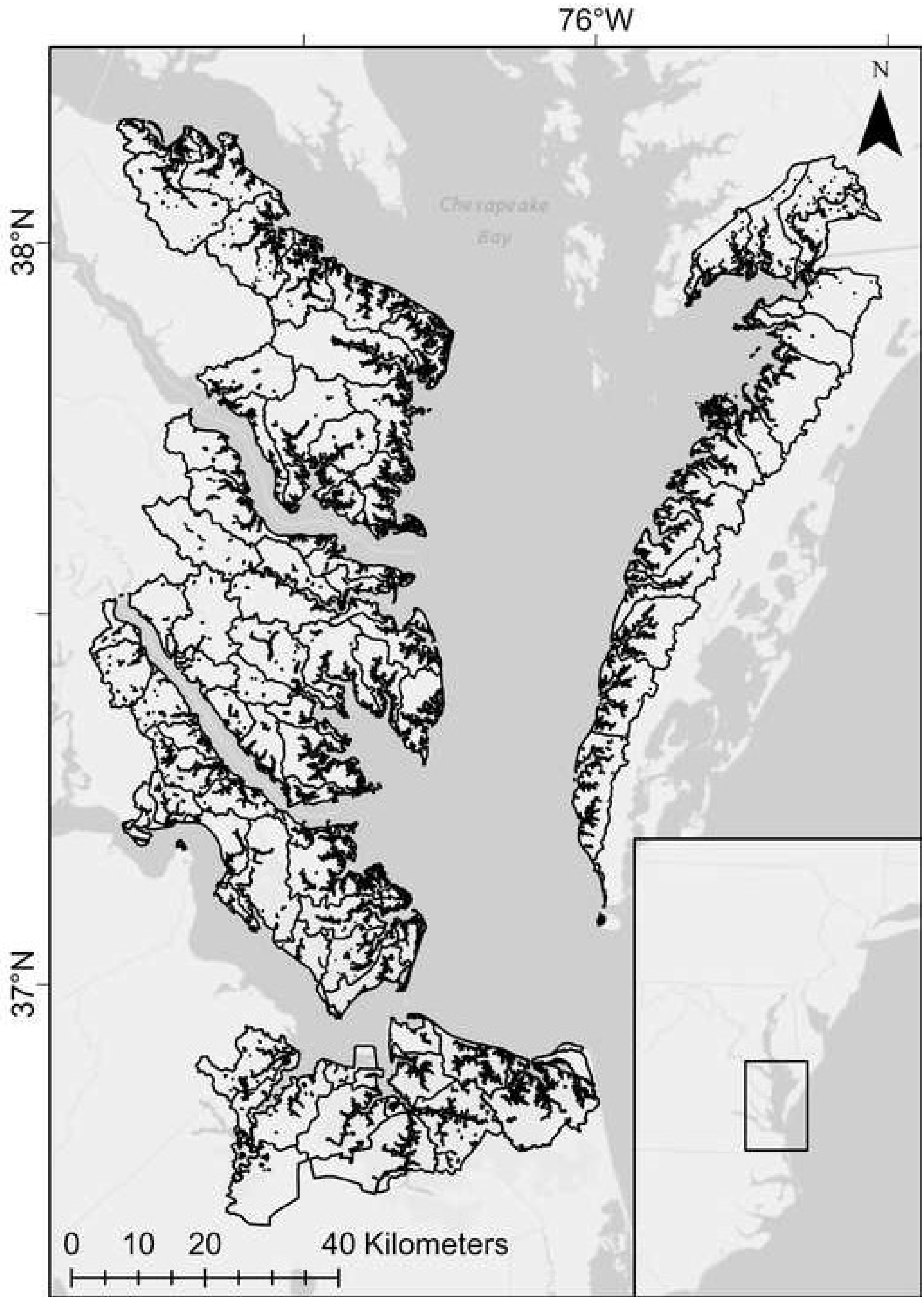


Figure 2

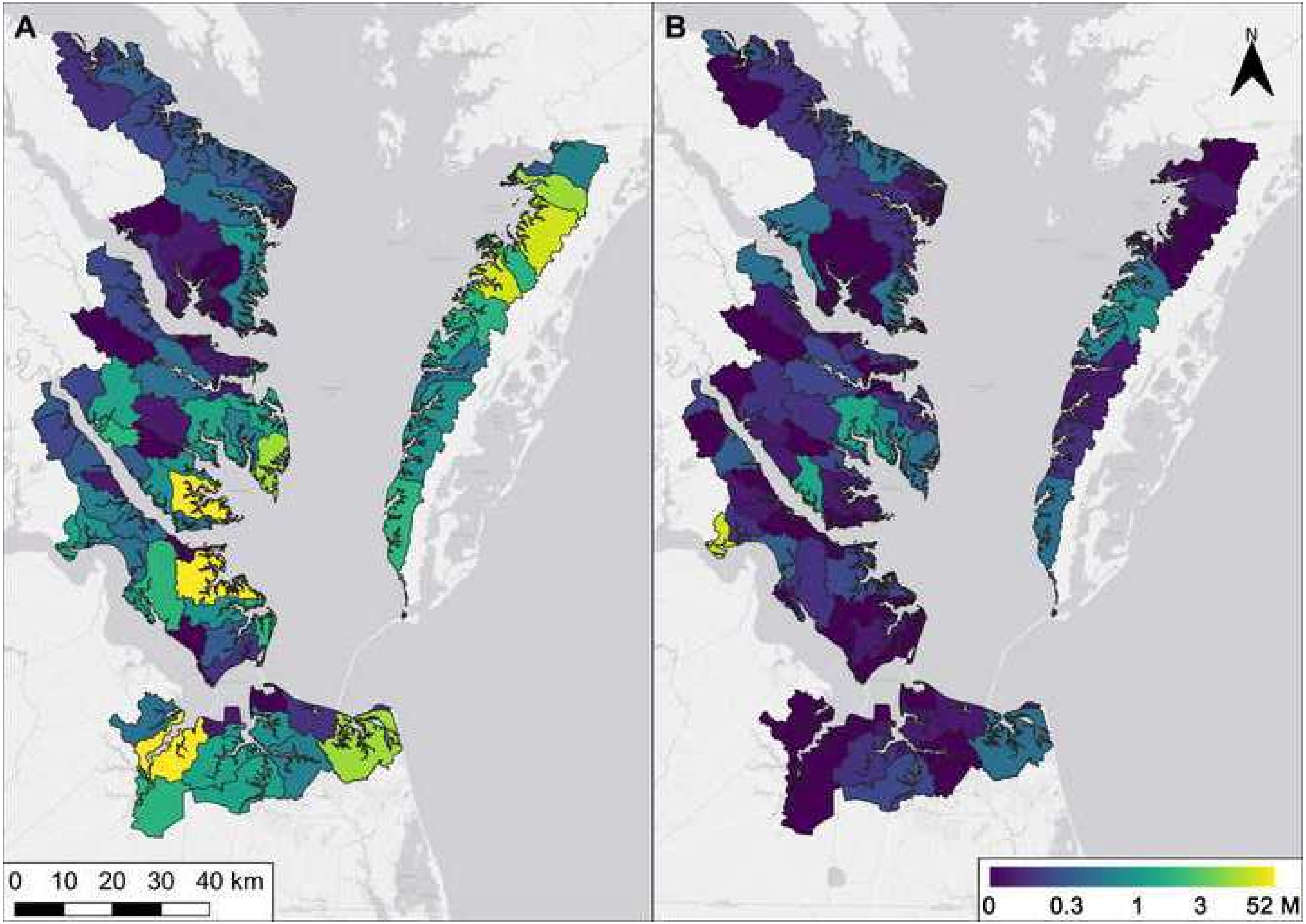


Figure 3

Figure 4

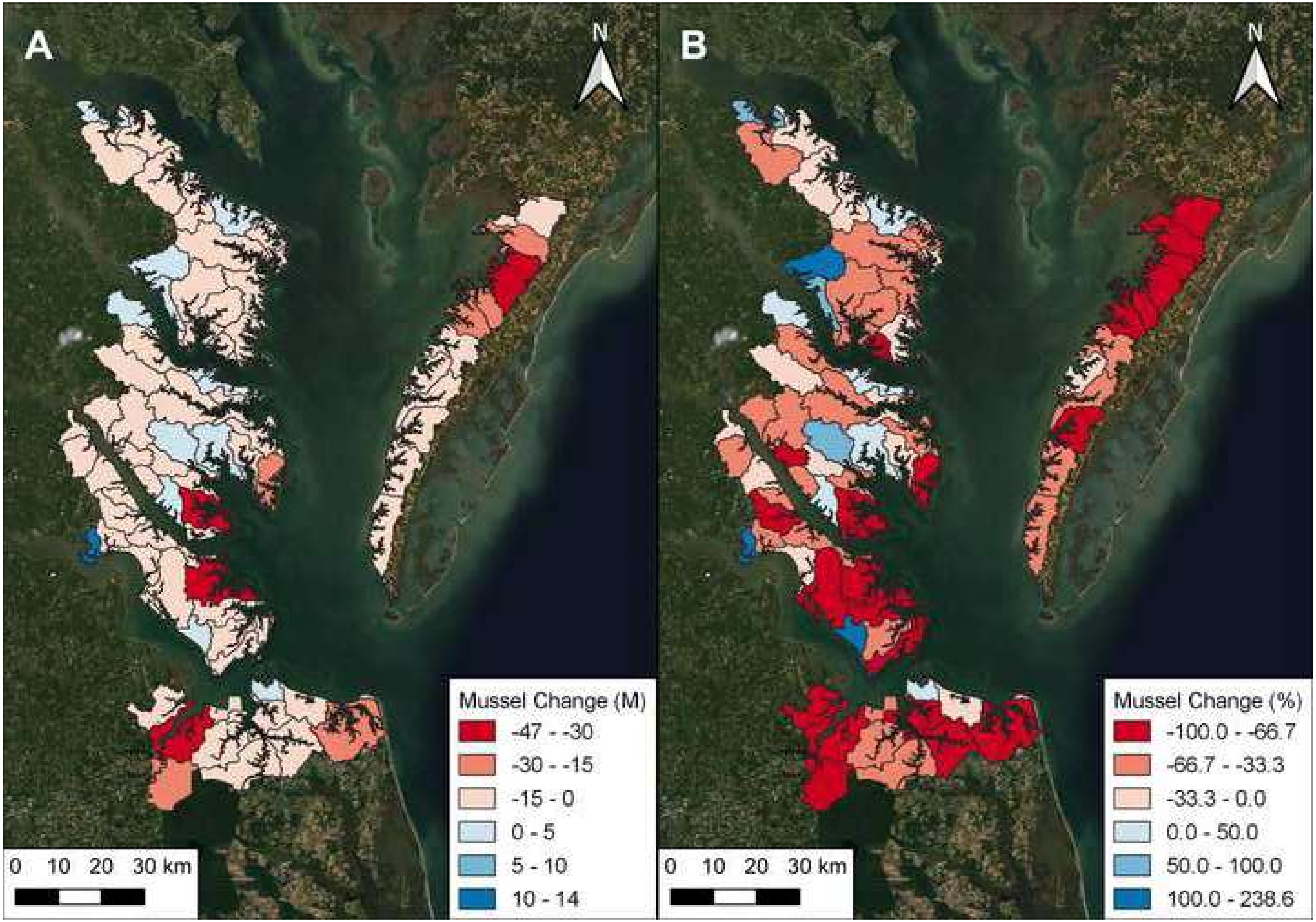

A
N
Mussel Change (M)
-47 - -30
-30 - -15
-15 - 0
0 - 5
5 - 10
10 - 14
0 10 20 30 km
B
N
Mussel Change (%)
-100.0 - -66.7
-66.7 - -33.3
-33.3 - 0.0
0.0 - 50.0
50.0 - 100.0
100.0 - 238.6
0 10 20 30 km

Figure 5

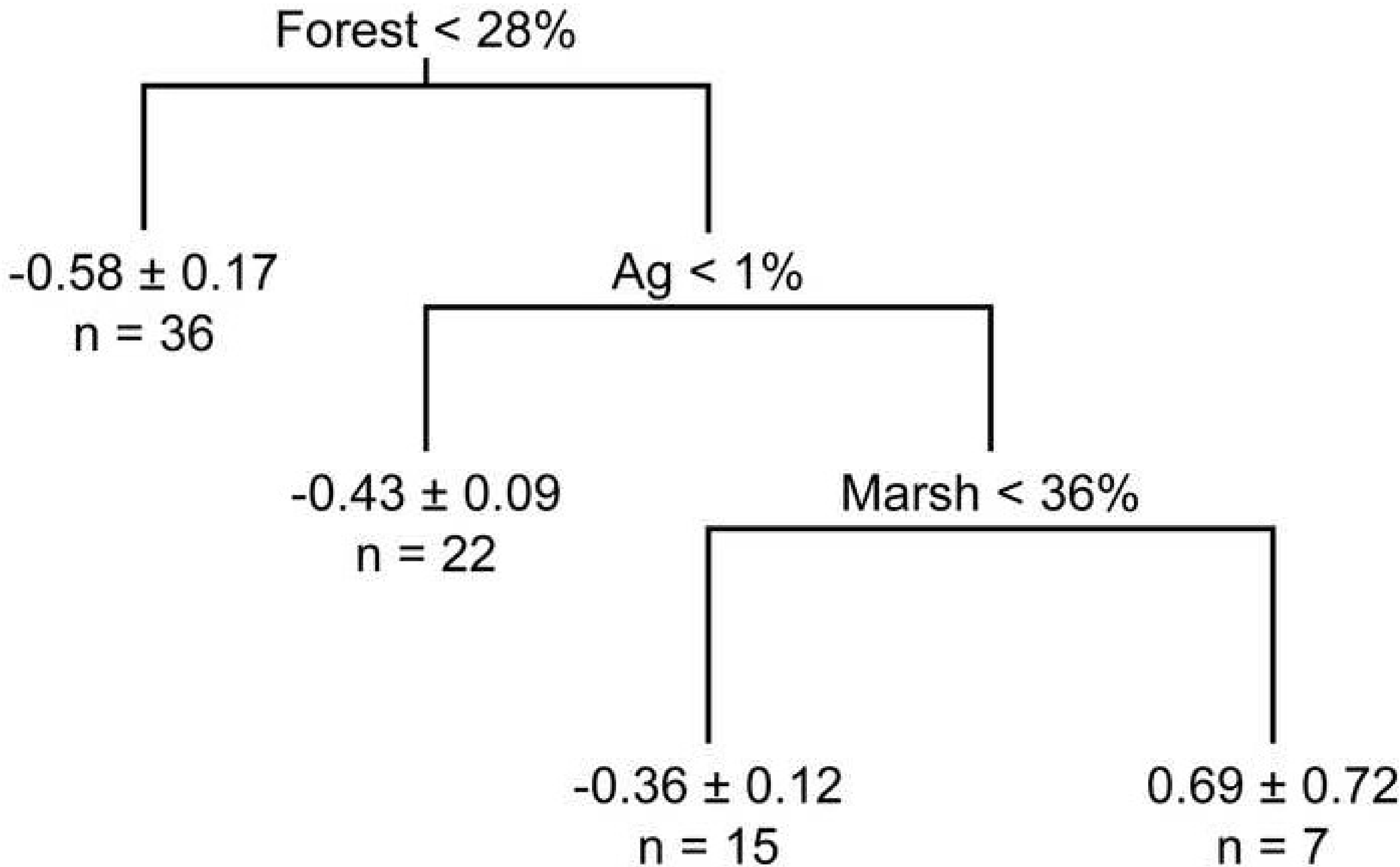
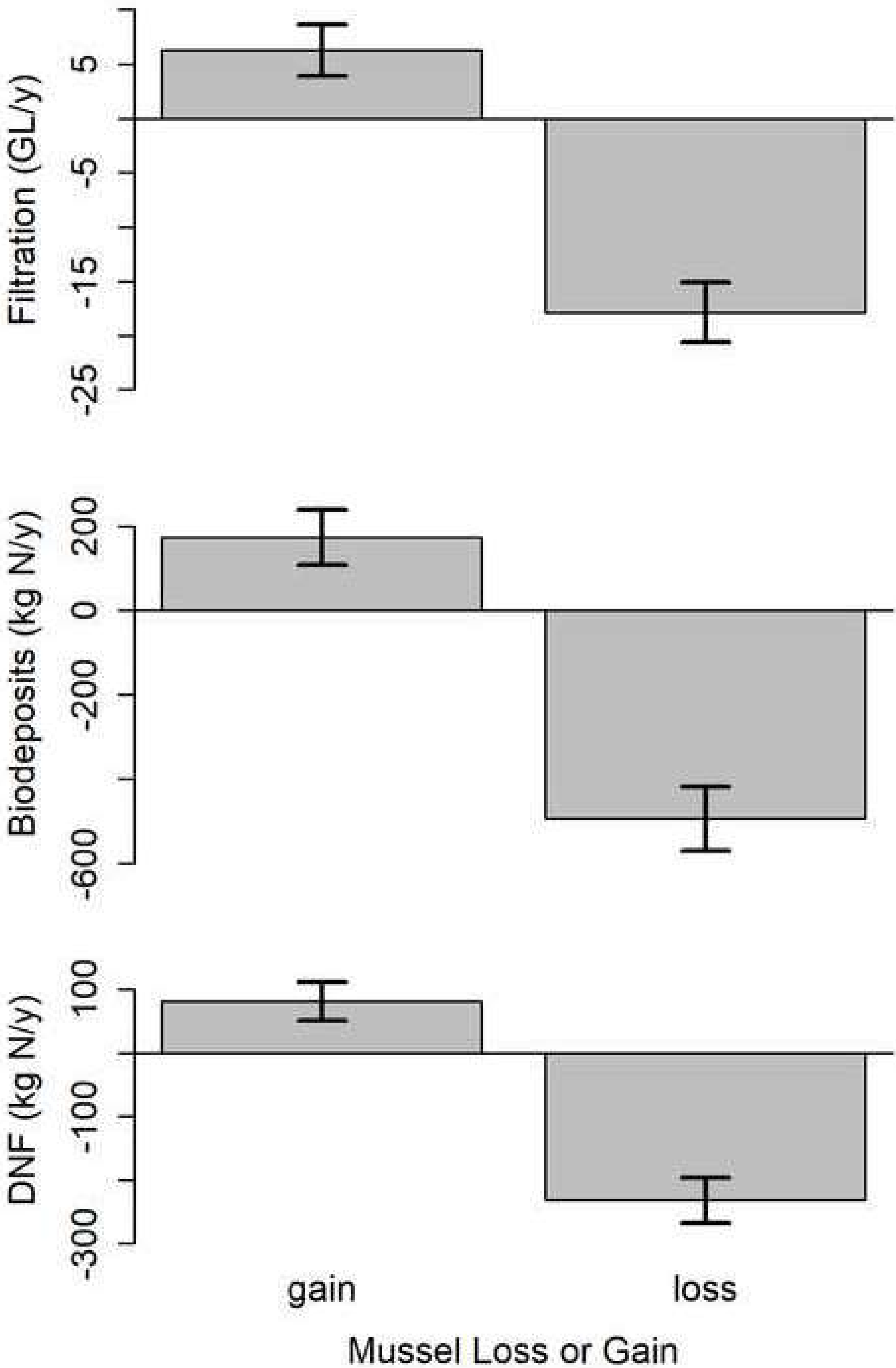

Forest < 28%
-0.58 ± 0.17
n = 36
Ag < 1%
-0.43 ± 0.09
n = 22
Marsh < 36%
-0.36 ± 0.12
n = 15
0.69 ± 0.72
n = 7

Figure 6



Filtration (GL/y)
5
-5
-15
-25
Biodeposits (kg N/y)
200
0
-200
-600
DNF (kg N/y)
100
-100
-300
gain
loss
Mussel Loss or Gain