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Environmental drivers of spatial variability in benthic macrofauna biomass and associated carbon fluxes in a large coastal-plain estuary

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Abstract

Extensive datasets document the distribution and composition of benthic macrofauna in some estuaries, yet their impact on carbon cycling remains poorly quantified. To address this, we investigated (1) how water chemistry and sediment composition correlate with benthic biomass distribution and (2) the contributions of benthic macrofaunal carbon fluxes to estuarine carbon budgets. We analyzed 8,128 benthic samples collected from Chesapeake Bay (1995–2022) and used generalized additive models to relate observed and modeled environmental variables to the biomass. We also estimated their associated carbon fluxes (calcification and respiration rates) using empirical relationships. The highest biomass was found in the upper Potomac River Estuary and Upper Bay; moderate dissolved oxygen, low salinity, and high nitrate concentrations were the clearest predictors of these zones (explaining 52% of the deviance in biomass). Low surface NO_3^- concentrations within the estuary coincide with high inputs of allochthonous particulate organic carbon (POC) from riverine sources; this POC be the primary food source supporting high biomass zones. In the oligohaline Upper Bay, benthic macrofauna respire 17-50% of total organic carbon available in that region, whereas their contribution is lower downstream. Moreover, the estimated benthic macrofaunal CO_2 production rates from respiration and calcification rates in the Upper Bay (205±70 g C m^{-2} yr^{-1}) exceeds estimated outgassing (74.5 g C m^{-2} yr^{-1}), suggesting benthic macrofauna contribute significantly to air-sea gas exchange. The explainable spatial distribution of biomass and major role in estuarine carbon cycling highlight the importance and feasibility of incorporating the impacts of benthic macrofauna into numerical models. Refining these models could improve predictions of estuarine responses to natural and anthropogenic changes.

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1. Introduction

Benthic macrofauna are vitally important to estuarine ecosystems because they can improve water quality, produce and consume organic matter, recycle nutrients, dilute or cycle pollutants, stabilize and transport sediment, and provide food to human populations and other estuarine organisms (Schratzberger & Ingels, 2018; Snelgrove, 1997; Wilson & Fleeger, 2023). As adults, benthic macrofauna often have limited mobility and, in some cases, long life spans, making them reliable indicators of local environmental variability caused by natural and anthropogenic stresses. Their relative abundance and diversity are often used as a proxy to describe the condition of estuaries (Dauer, 1993; Pearson & Rosenberg, 1978; Rosenberg, 1995; Weisberg et al., 1997).

1.1 Environmental drivers of benthic macrofauna distribution

Because benthic macrofauna are ecologically significant and sensitive to environmental conditions, numerous studies have examined the key factors influencing their distribution in estuaries. Here, we summarize key studies that have investigated how water quality and sediment composition influence benthic macrofauna distribution in estuaries.

Dissolved oxygen is one of the primary environmental variables affecting benthic composition; hypoxia (extremely low dissolved oxygen concentration events) significantly degrades the benthic habitat quality (Borja et al., 2008; Diaz et al., 1995; Murphy et al., 2011; Seitz et al., 2009; Woodland & Testa, 2020). Seitz et al., (2009) found that oxygen was the single best predictor of summer benthic biomass by depth in the Chesapeake Bay. In another study of the Chesapeake Bay, dissolved oxygen explains 42% of the variation in the benthic index of biotic integrity (B-IBI), a benthic habitat quality score compiled from multiple factors, including species composition, trophic composition, biomass and abundance, and diversity (Borja et al.,

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2008). Similarly in the Baltic Sea, near-bottom oxygen content was among the most important environmental variables shaping benthic communities (Rousi et al., 2019). Among aquatic organisms, benthic macrofauna are the most severely affected by low dissolved oxygen events because they are furthest from the atmosphere, immobile, and coastal sediments are often depleted in oxygen relative to the water column (Dauer & Alden, 1995; Vaquer-Sunyer & Duarte, 2008). Even within benthic communities, vulnerability to hypoxia can vary among taxonomic groups (Vaquer-Sunyer & Duarte, 2008). For example, bivalves are more tolerant of short-term hypoxic stress, which could increase their dominance among benthos as hypoxia increases (Seitz et al., 2009; Vaquer-Sunyer & Duarte, 2008; Woodland & Testa, 2020).

Salinity is also a very important control on benthic community structure (Dauer, 1993; Sturdivant et al., 2013) because different species have different physiological tolerances (Holland et al., 1987; Little et al., 2017; Seitz et al., 2009). In the Humber estuary in the United Kingdom, salinity was amongst the most important environmental variables that contributed to 80% of the biomass variation of the two most dominant bivalve species (Fujii & Raffaelli, 2008). In addition, it was predicted that a 0.3 m rise in sea level would result in a 6.9% loss of benthic macrofaunal biomass, partially due to salinity intrusion.

Ocean acidification, the decrease in seawater pH due to the uptake of atmospheric CO_2, has also negatively affected calcifying organisms in coastal systems. Mollusks (predominately bivalves) are the most strongly affected; ocean acidification decreases their ability to calcify and significantly reduces their survival, growth, development, and abundance (Kroeker et al., 2013). The mechanism of calcification in bivalves will make it difficult for them to adapt to ocean acidification in the future. Bivalves are weak acid-base regulators because they have poorly developed ion exchange mechanisms (Jakubowska & Normant-Saremba, 2015; Thomsen et al.,

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2015). They are also most susceptible to damage from ocean acidification in their early stages (Jansson et al., 2013). Among other benthic groups, there is a broad variation of sensitivity to variations in pH (Birchenough et al., 2015).

Very fine sediment grain size (i.e., high silt-clay fraction & low sand fraction) is associated with lower benthic biomass (Dauer & Alden, 1995; Seitz et al., 2009). A study off Siberia's coast found that sediment grain size is a key predictor of benthic macrofaunal composition, while organic carbon is a key indicator of benthic biomass (Grebmeier et al., 2015). In Chesapeake Bay, Woodland & Testa, (2020) found a negative correlation between accumulated organic matter and benthic biodiversity and a positive association between sediment sand percentage and benthic biodiversity.

Food availability has long been known as an important factor influencing benthic biomass (Ehrnsten et al., 2019; Pearson & Rosenberg, 1978). Food availability is driven by primary production in the Bay, which is dominated by phytoplankton in most estuaries (i.e. Chesapeake Bay, Hagy, 2002). A synthesis of shallow, normoxic estuaries worldwide found that as primary production increases, benthic biomass increases (Hagy, 2002; Kemp et al., 2005). However, the timing, size, and location of primary production could lead to hypoxia in the bottom waters, which could have a detrimental effect on the benthos (Dauer et al., 2000; Kemp et al., 2005). In a model of the Baltic Sea, Ehrnsten et al., (2020) predicted that climate change will cause benthic biomass to decrease. However, reduced nutrient loading (due to management efforts) was also predicted to cause the benthic biomass to decrease. Results from the (Ehrnsten et al., 2020) study suggest that the harmful effects of climate change can effectively cancel out the partially positive effects of moderate nutrient loading, perhaps due to increased primary production.

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In summary, studies theorize that dissolved oxygen, salinity, pH, sediment composition, and primary production are all significant predictors of benthic macrofauna biomass distribution in estuaries.

1.2 Impact of benthic macrofauna on carbon cycling

Benthic macrofauna biomass influences estuarine biogeochemical cycling, particularly carbon cycling through three major processes: secondary production, respiration, and calcification. Secondary production refers to the consumption of organic matter by benthos to produce soft tissue biomass (Diaz & Schaffner, 1990; Dolbeth et al., 2012; Sturdivant et al., 2013). Secondary production is an important pathway for trophic transfer, as the benthos are eventually consumed by predators or decomposers, with much of the organic carbon ultimately being removed from the estuarine system through advection into the open ocean or burial in sediment (Diaz & Schaffner, 1990; Wilson & Fleeger, 2023). The direct impact of secondary production on carbon cycling is more limited, as involves the transformation of organic matter into biomass rather than shifting carbon between organic and inorganic pools. Respiration is the process by which organic matter and oxygen are consumed, and CO_2, water, and energy are released. As a result, dissolved inorganic carbon (DIC) increases in the water column. During calcification, benthic calcifiers, such as bivalves, uptake bicarbonate and calcium to produce calcium carbonate shells. CO_2 and water are also released as byproducts. However, calcification decreases DIC because bicarbonate utilization exceeds CO_2 production. The removal of bicarbonate also decreases alkalinity (Waldbusser et al., 2013). Together, these processes play a significant role in the carbon budget, with respiration and calcification notably contributing to CO_2 generation (Chauvaud et al., 2003).

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Studies have quantified the relative contributions of respiration and calcification to estuarine carbon cycling. Respiration has been the most extensively studied. A compilation of data from 20 different estuaries estimated that 24% of total organic inputs to estuaries are respired by benthos, while plankton respiration is generally much lower (Hopkinson & Smith, 2004). Macrofauna account for 40% of all benthic respiration (Rodil et al., 2022). Given the high rates of benthic respiration observed in many estuaries, autochthonous primary production alone cannot account for the total organic matter being processed, indicating relatively high allochthonous inputs (Hopkinson & Smith, 2004; Kemp et al., 1997; Schwinghamer et al., 1986). Bivalves, in particular, substantially contribute to benthic respiration and have been thought to significantly decrease the phytoplankton and suspended particulate concentrations in estuaries (Galimany et al., 2020; Nakamura & Kerciku, 2000; Newell & Ott, 2011). Cerco & Noel, (2010) modeled the effect of bivalve filter feeders in the Chesapeake Bay and found that they removed 14% to 40% of the carbon load. Beyond respiration, the impact of benthic calcification on estuarine carbon cycling is underexplored (Waldbusser et al., 2013). However recent discoveries of large alkalinity sinks in estuarine tributaries could suggest a large role for bivalves (Najjar et al., 2020). The combined production of CO_2 from respiration and calcification may be a significant contributor to carbon cycling. In San Francisco Bay, this production is estimated to be twice the rate of CO_2 consumption by primary production (Chauvaud et al., 2003). A global extrapolation of the CO_2 generated from calcifying benthos in estuaries is comparable to the magnitude of the total CO_2 emissions from the world's lakes or planetary volcanism (Chauvaud et al., 2003).

The absolute fluxes of respiration, calcification, and secondary production can also be estimated from biomass. Multiple studies use empirical relationships to relate benthic biomass to

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secondary production based on the biomass, taxon, average body mass, water temperature, and other characteristics (Brey, 1990; Chauvaud et al., 2003; Dolbeth et al., 2012; Edgar, 1990; Schwinghamer et al., 1986; Sturdivant et al., 2013; Tumbiolo & Downing, 1994). Secondary production rates are often calculated indirectly because they can be expensive and time-consuming to measure (Sturdivant et al., 2013; Tumbiolo & Downing, 1994). Calcification and respiration rates can be estimated from secondary production using empirical relationships or simple proportional scaling (Chauvaud et al., 2003; Schwinghamer et al., 1986).

1.3 Focus of this Study

While numerous studies have examined the environmental drivers of benthic biomass in estuaries, most have focused on relatively small spatial and/or temporal scales. Benthic biomass, as opposed to other metrics such as diversity and abundance, is particularly important because it is most directly related to estuarine carbon cycling (Cerco & Noel, 2010; Snelgrove, 1999). Chesapeake Bay is of special interest because the carbon and alkalinity dynamics span the range observed in estuaries and there is extensive historical monitoring data (Najjar et al., 2020). To our knowledge, the most recent studies that specifically linked environmental variables with benthic biomass in the Chesapeake Bay were (Woodland et al., 2021), which focused on these relationships through the lens of forage for higher trophic levels and Seitz et al., (2009), which investigated benthic data from 1996–2004. Woodland & Testa, (2020) also explored the relationship between environmental variables and benthic species diversity in the Bay. However, benthic biomass and biodiversity are not correlated, so our study's results may differ significantly (Alden et al., 2002; Testa et al., 2020). Few studies have also looked at the effect of primary productivity on benthic biomass in the Bay (e.g., Hagy, 2002; Kemp et al., 2005), even

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though organic matter produced from primary production is considered the main food source for the benthos.

The resulting carbon fluxes from benthic macrofauna biomass have large implications for carbon cycling. Although numerous studies have quantified respiration rates in estuaries, very few have provided even rough estimates of calcification (Chauvaud et al., 2003; Waldbusser et al., 2013). Given the potentially important role calcification plays in carbon cycling, addressing this gap is essential for contextualizing the relative contribution of benthic calcification within the broader estuarine carbon budget.

In our study, we address the following research questions:

1) How do water chemistry and sediment composition variables predict the spatial distribution of benthic biomass?
2) What impact do benthic macrofaunal respiration and calcification have on the carbon budget in estuaries?

2. Methods

2.1 Overview

We examined historic benthic macrofauna biomass data collected annually by the Chesapeake Bay Long-Term Benthic Monitoring Program (BMP) (Dauer et al., 2000; Llansó & Zaveta, 2017) and time-averaged the data to emphasize the spatial distribution. To contextualize the benthic biomass data, we used measurements of bottom water temperature, salinity, dissolved oxygen, and sediment sand fraction measured by the BMP at the same time and location as the benthic biomass samples. In addition to these measured environmental variables, we utilized biogeochemical model output from ROMS-ECB, a fully coupled, three-dimensional, hydrodynamic, and estuarine carbon biogeochemistry (ECB) implementation of the Regional

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Ocean Modeling System (ROMS; Shchepetkin & McWilliams, 2005) developed for the Chesapeake Bay (St-Laurent & Friedrichs, 2024b). We identified correlations between these environmental variables (observed and modeled) and benthic macrofauna biomass using generalized additive models (GAMs). We reviewed the literature to identify empirical relationships between benthic biomass and secondary production, respiration, and calcification fluxes. We used these empirical relationships to quantify the impact of benthic macrofauna on carbon cycling in the Bay.

2.2 Benthic biomass data

Details of the BMP data we used in our study are described elsewhere (Dauer, 1993; Dauer et al., 2000; Dauer & Lane, 2010; Llansó & Scott, 2011; Llansó & Zaveta, 2017) and are summarized here. The program began in 1984, but consistency in sampling started in 1995, which is when we began our analysis. The sampling occurs mainly in the summer, between July 15 and September 30, at both fixed and random stations, with the latter changing location every year. The sampling is conducted by Maryland (Llansó & Zaveta, 2017) and Virginia (Dauer & Lane, 2010) separately, with slightly different protocols used in each state (see below). Our analysis spanned 1995 to 2022, the recent extent of available data, incorporating 28 years of data.

The Maryland monitoring program comprises 27 fixed and 150 random stations in the upper Chesapeake Bay. The Virginia monitoring program comprises 21 fixed and 100 random stations in the lower Chesapeake Bay. In Virginia, random stations were not sampled in 1995, and fixed stations were not sampled in 2017 or 2018. Water depths greater than 12 m in the mainstem part of the Bay in Maryland are not sampled because the bottom waters become anoxic in the summer, resulting in azoic sediments. The tributaries are sampled only in the tidal zone; areas with less than 1 m mean lower low water are considered non-tidal. Some locations, such as

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oyster reefs and other hard substrates, are also not sampled due to gear unsuitability in such habitats. To avoid seasonal biases, we excluded samples collected outside of the summer sampling window of July 15–September 30, as some earlier years included some sampling outside of this window. This selection resulted in a dataset of 8128 samples across both states, or an average of 290 samples per year, slightly less than the maximum of 298.

At each sampling station, the uppermost layers of sediment are collected. In Maryland, the sites introduced in 1995 (two fixed sites and all random sites) are sampled with a Young grab, which collects a surface area of 0.0440 m^2 to a depth of 0.10 m. For the other fixed sites in Maryland, nearshore shallow sandy habitats of the mainstem and tributaries are sampled with a modified box corer with a surface area of 0.0250 m^2 to a depth of 0.25 m. Muddy habitats and deep-water habitats in the mainstem and tributaries of Maryland are sampled with a Wildco box corer with a surface area of 0.0225 m^2 to a depth of 0.23 m. The fixed site in the Nanticoke River is sampled with a Petite Ponar grab with a surface area of 0.0250 m^2 to a depth of 0.07 m. In Virginia, fixed sites use a spade-type box-coring device with a surface area of 0.0182 m^2 to a depth of 0.02 m; random sites use a Young grab with a surface area of 0.0400 m^2 to a depth of 0.10 m.

For both monitoring programs, the sampling contents are sieved through a 0.5 mm screen to retain only benthic macrofauna. The macrofauna are identified at the lowest taxonomical level. The specimens are dried on a pan for at least 24 hours to a constant weight, then a final weight is measured. The specimens are then placed in a muffle furnace for 4 hours at 500°C for ashing, and the specimens are weighed again. The ash-free dry weight (AFDW) is the difference between the dry and ashed weight. We converted the AFDW in g per sample to biomass density B in units of g m^{-2} by dividing the AFDW by the area of the sampling device. The data used in

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our GAMs analysis include the biomass density of individually selected species and classes and the total biomass density.

To determine the long-term average spatial distribution, biomass densities from all 8128 biomass samples from 1995–2022 were time-averaged onto a grid with cells 0.04° in longitude and 0.03125° in latitude, making the cells nearly square, ~ 3.5 km per side. At least one biomass sample was collected in all 846 cells. Within those cells, the average number of samples per grid cell was 6.62 ± 10.13 (Fig A1). Tributaries and the upper Bay were sampled more densely than the mainstem.

2.3 Bottom water quality data

From the BMP, we used bottom temperature, salinity, and dissolved oxygen data, which are measured with a YSI 660 Sonde or Hydrolab DataSonde 4a in Maryland and a YSI 85 Model meter in Virginia one meter above the sediment surface. Extreme outliers, defined as data points that fall beyond three times the interquartile range from the first or third quartile, were removed. As a result, one value for dissolved oxygen and one for water temperature were excluded from the analysis. The salinity zones are also characterized at each site as tidal fresh (<0.5 ppt), oligohaline (0.5–5 ppt), low mesohaline (5–12 ppt), high mesohaline (12–18 ppt), and polyhaline (>18 ppt); these zones are relatively geographically fixed (with some changes in 2011 due to Hurricane Irene and Tropical Storm Lee) based on long-term averages of salinity (Llansó, 2002; Llansó & Zaveta, 2017). Sediment sand fraction was measured by first collecting two 120 ml benthic grab sub-samples. Sand particles are separated by wet-sieving through a 63-µm stainless steel sieve. Sand fraction is recorded after drying and weighing the samples. The bottom water quality and sediment composition data were time-averaged using the same scheme described earlier for the benthic biomass data.

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2.4 Biogeochemical model output

ROMS-ECB output was used to characterize environmental variables not measured by the BMP that could be relevant to predicting the benthic macrofauna biomass distribution. ROMS-ECB uses 20 terrain-following vertical levels and a uniform horizontal resolution of 600 m (St-Laurent & Friedrichs, 2024b). We compiled daily averaged output at various grid points from 1995 to 2022 corresponding to the locations of each of the 8128 benthic biomass samples. We selected the ROMS output at the nearest ROMS grid point to each BMP sample location for each variable of interest, described below. Some ROMS-ECB environmental variables are directly linked to primary production. Because the timing of primary production peaks does not always coincide with periods of high food availability for benthos, annual averages may obscure important seasonal patterns. To better capture these temporal mismatches, we calculated both seasonal and annual averages for each variable. For seasonal averages, spring was defined as March–May, summer as June–August, fall as September–October, and winter as December–February. The seasonal and annual averages were then time-averaged in the same scheme explained earlier, resulting in 846 gridded cells.

We used ROMS-ECB output, as opposed to Chesapeake Bay Water Quality Monitoring Program (WQMP) data. WQMP has also measured water quality variables since 1984 at over 100 tidal stations (Chesapeake Bay Program, n.d.). However, the stations are at different locations than the BMP stations, requiring interpolation to correlate these data with benthic biomass. Other studies have opted to use kriging, a method used to spatially interpolate surface water quality data, to increase the spatial resolution. It has been found to outperform the standard inverse distance weighting tools typically used in the Chesapeake Bay (Murphy et al., 2015). One study evaluated the kriging of surface WQMP data for July 2007 using 117–123 data points

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(Murphy et al., 2015). In cross-validation, one measured sample is removed, and the interpolation is then performed at that location; the interpolated value is then compared to the observed value. Cross-validation of temperature, salinity, and dissolved oxygen yielded root-mean-square errors (RMSE) of 0.75 °C, 1.1 ppt, and 1.2 mg L^{-1}, respectively. In contrast, ROMS-ECB output was evaluated with over 500,000 WQMP data points at multiple depths and locations from 1985 to 2021 (St-Laurent & Friedrichs, 2024a). The RMSEs for temperature, salinity, and dissolved oxygen were 1°C, 1.9 psu, and 1.5 mg L^{-1}, respectively. Although these RMSEs are slightly higher than those from kriging, the evaluation was much more robust, and the long time series evaluation is more relevant to our time-averaging technique over 28 years. In addition, we wanted to utilize bottom water quality data, as these variables are measured closer to the location of benthic macrofauna. However, cross-validation for kriging was only performed at the surface, presumably due to the challenges of accounting for bottom topography in spatial interpolation. For these reasons, ROMS-ECB output was used instead of interpolated WQMP data.

ROMS-ECB simulates many variables, and we considered the subset that might be good predictors of benthic biomass: bottom particulate organic carbon (POC) concentration, bottom total suspended solids (TSS), and surface nitrate (NO_3^-). POC was considered because a large fraction of POC represents food for benthic macrofauna. TSS was considered a metric of suspended inorganic material, which can inhibit filter-feeding organisms (Grant & Thorpe, 1991). Photosynthesis is largely limited by nitrate in the Chesapeake Bay (Zhang et al., 2021); because phytoplankton productivity and the subsequent sinking of POC is an important source of organic matter to the benthos, nitrate could be a predictor of benthic biomass. ROMS-ECB output was evaluated for robustness with WQMP data using Spearman's rank correlation

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coefficient, r_s, which measures the strength of the association between two variables (Hauke & Kossowski, 2011). In our analysis of benthic biomass predictors, we included only variables with r_s above 0.7, which generally indicates a strong association (Akoglu, 2018). NO_3^- was used as it had r_s = 0.77, whereas POC and TSS were not as they had r_s= 0.26 and 0.24, respectively (St-Laurent & Friedrichs, 2024a).

We also considered potentially good predictors that could be computed from ROMS-ECB output: surface oxygen supersaturation (ΔO_2) and bottom aragonite saturation state (Ω_{arag}). ΔO_2 can be used as a tracer for net ecosystem production (Herrmann et al., 2020) and hence may indicate organic matter availability to the benthos. Ω_{arag} could predict benthic biomass because bivalve calcification is expected to depend on this metric (Thomsen et al., 2015). $\Delta[O_2]$ is equal to O_2 minus the saturation concentration, which was computed (as in ROMS-ECB), from temperature and salinity (Garcia & Gordon, 1992). Ω_{arag} is the product of calcium ion concentration and the carbonate ion concentration divided by the solubility product for aragonite, which is a function of temperature, salinity, and pressure. PyCO2SYS (Humphreys et al., 2022) was used to derive the solubility product and carbonate ion concentration from alkalinity, DIC, temperature, salinity, and water depth. We retained ΔO_2 and Ω_{arag} in the analysis because the variables used to compute them can be evaluated with observation (temperature, salinity, DO, alkalinity, and DIC) all had r_s >0.7). Calcium measurements were not available for model evaluation, but calcium is highly correlated to salinity, though deviations may occur at low salinity (Beckwith et al., 2019).

2.5 Statistical modeling

We used GAMs to evaluate how the bottom water quality data and biogeochemical model output predict the spatial distribution of benthic macrofauna biomass. GAMs have been used

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extensively in ecological research since the late 1960s in coastal ecosystems (Guisan et al., 2002; Smith et al., 2023). GAMs have been shown to perform as well or better than other predictor models based on environmental conditions (Drexler & Ainsworth, 2013). They are data-driven statistical models that find the response to a suite of predictor variables (Grüss et al., 2014; Guisan et al., 2002; Hastie & Tibshirani, 1987; Wood, 2017). They examine how well the predictor (or explanatory) variables explain the ecological response, the strength of the association, and the relative contribution of the different predictors (Guisan et al., 2002). GAMs assume that the multiple functions describing the association between the predictor and response variables are additive and can be smoothed (Guisan et al., 2002). The GAMs package used here— the mgcv library in R with the restricted maximum likelihood (REML) optimization method (Wood, 2011; Wood, 2017)—automates the polynomial order used to fit the smooth function for each predictor variable. An intercept term and an error term are added to the associated smoothed functions for each predictor variable. Model diagnostics include the percentage of deviance explained, signifying how much of the variance in the response variable can be explained by the additive effects of all the smoothed functions associated with the predictor variables. We used GAMs because they are uniquely suited to model the non-linear and non-monotonic relationships between response and predictor variables in our dataset. GAMs require a relatively large amount of data, and with our extensive dataset, they can estimate spatial patterns across a broad geographic region (Grüss et al., 2014; Wood, 2011).

To ensure predictor variables in the GAMs analysis were not strongly correlated, we used six variables in the GAMs analysis: total depth, sand fraction, bottom water temperature, bottom salinity, bottom dissolved oxygen, and surface NO_3^- (Table 1). If predictor variables are highly correlated, they distort the GAMs results (Grüss et al., 2014; Grüss et al., 2018; Guisan et al.,

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2002). We used Pearson's correlation coefficients, a common approach for evaluating cross-correlation in GAMs, to evaluate the linear correlation between the predictor variables. If two predictor variables have correlations greater than 0.7, one of the variables was discarded (Dormann et al., 2013). As an alternate means of evaluating multicollinearity, concurvity was also analyzed after the smooth functions were applied to the predictor variables. High concurvity values (>0.8) indicated that the model might struggle to distinguish between the individual contributions of correlated smooth terms (Wood, 2017). However, applying the Pearson's correlation coefficient cut-off also eliminated high concurvity values (St-Laurent & Friedrichs, 2024a). Ω_{arag} and $\Delta[O_2]$ were not used as predictor variables because of their high correlation with other predictor variables.

Table 1: Predictor variables from the Chesapeake Bay Benthic Monitoring Program and ROMS-ECB. Information collected from 1995–2022 with annual averages giving every daily average value for the entire period. Seasonal averages were taken for spring (March–April), summer (July–August), fall (September–November), and winter (December–February)

Dataset	**Location**	**Variable**	**Units**	**Processing?**	**Used in GAMs?**
BMP	Bottom	DO	mmol m^{-3}	Removed extreme outliers	Yes
BMP	Bottom	Salinity	ppt	None	Yes
BMP	Bottom	Total depth	m	None	Yes
BMP	Bottom	Water temperature	^{o}C	Removed extreme outliers	Yes

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BMP	Bottom	Sand fraction	%	None	Yes
ROMS-ECB	Surface	NO_3^-	mmol m^{-3}	Annually and seasonally averaged	Yes
ROMS-ECB	Bottom	POC	mmol m^{-3}	Annually and seasonally averaged	No, model-data validation gave poor results
ROMS-ECB	Bottom	TSS	mg L^{-1}	Annually and seasonally averaged	No, model-data validation gave poor results
ROMS-ECB	Bottom	Ω_{arag}		Calculated from alkalinity, DIC, temperature, water depth, and salinity using PyCO2SYS. Annually and seasonally averaged	No, highly correlated with salinity
ROMS-ECB	Surface	$\Delta[O_2]$	mmol m^{-3}	Calculated from oxygen, salinity and temperature using Gracia & Gordon	No, highly correlated with salinity and NO_3^-

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				(1991, 1992). Annually and seasonally averaged	

We used Akaike's Information Criterion (AIC), a statistical measure that has been increasingly used in ecology, to evaluate which combination of parameters results in the best model fit (Symonds & Moussalli, 2011). AIC is calculated using the number of fitted parameters in the model, the maximum likelihood estimate, and the residual sum of squares (Symonds & Moussalli, 2011). The model with the lowest AIC value indicates the most parsimonious model with the minimum number of necessary parameters. We chose the predictor variables in our model by minimizing AIC. We generally used annually averaged predictor variables from the ROMS-ECB output because using seasonal averages had a negligible difference on the AIC. To assess the relative influence of each predictor variable, we used Akaike weights, which indicate the probability that a given model is the best among those considered. We ranked models by AIC and summed the Akaike weights for all models containing each predictor variable. Higher Akaike weights indicate stronger support for a variable's inclusion in the best-fitting models. Interaction terms between predictor variables were examined, but their inclusion did not significantly improve the AIC values.

We also evaluated the model fit by looking at the distribution of the residuals and a scatter plot of observed vs model response values. A good model would have relatively normally distributed residuals as well and a near 1:1 line in the observed vs model response values. Although GAMs can handle non-normal distributions of the response variable (Guisan et al., 2002), we found the best model fit by applying a natural logarithmic transformation to the biomass. A small constant (0.0001 g m^{-2}) was added to the biomass values before applying the

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natural logarithmic transformation to account for zeros in the data. The resulting biomass was normally distributed after applying the natural logarithm function, so the GAMs model was fitted with a Gaussian distribution with an identity link function.

2.6 Carbon Flux Estimations

To estimate the relative impact of benthic macrofauna on carbon cycling, we used empirical equations to quantify carbon fluxes, including secondary production, calcification, and respiration.

The first step involved converting biomass B (units of g m^{-2}) to a carbon-based biomass B_c (units of g C m^{-2}) using:

$$B_c = r_c B \quad (1)$$

where r_c is the ratio of carbon mass to total mass in benthic organic matter. In a study on the bivalve filter feeders *Rangia cuneata* and *Corbicula fluminea* that dominate in the tidal fresh and oligohaline waters of the Chesapeake Bay, r_c = 0.47 g C g^{-1} was used (Cerco & Noel, 2010). A slightly lower value of 0.41 g C g^{-1} was used in a study of native and introduced bivalves in six North American freshwater systems (Chauvaud et al., 2003). Uncertainties for B_c is derived from the two different r_c values:

$$\frac{\Delta B_c}{B_c} = \sqrt{\left(\frac{\Delta r_c}{r_c}\right)^2} \quad (2)$$

Δr_c=0.03 g C g^{-1}, half the range of possible r_c values.

We then converted biomass to secondary production rates S (units of g C m^{-2} yr^{-1}). Multiple approaches have been used for this conversion, and we used several to be able to broadly quantify uncertainty in our estimates. Some studies assume S is proportional to B_c:

$$S_1 = \alpha B_c \quad (3)$$

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where the constant of proportionality α is the specific growth rate. We found three studies that estimated α for benthic macrofauna. At the low end, a study of benthic macrofauna in the Chesapeake Bay used α = 1.06 yr^{-1} (Wilson & Fleeger, 2023). At the high end, a study of *C. fluminea* used α = 4.45 yr^{-1} (Chauvaud et al., 2003). An intermediate value of α = 2 yr^{-1} was based on monthly observations of benthic macrofauna dominated by the crustacean *Corophium volutator* and the bivalve *Limecola balthica* at an intertidal site in the upper Bay of Fundy (Schwinghamer et al., 1986). A mean value of 2.50 yr^{-1} was used in Eq. 3. The uncertainty for S_1 is derived from B_c and α:

$$\frac{\Delta S_1}{S} = \sqrt{\left(\frac{\Delta \alpha}{\alpha}\right)^2 + \left(\frac{\Delta B_c}{B_c}\right)^2} \quad (4)$$

$\Delta \alpha$ is half the range of possible α values and equals 1.695 yr^{-1}. Temperature dependence for bivalve secondary production was included by Edgar (1990):

$$S_2 = S_0 \left(\frac{B}{1\ \mathrm{g\ m^{-2}}}\right)^{0.87} \left(\frac{T}{1\ ^{o}\mathrm{C}}\right)^{0.46} \quad (5)$$

where S_0 = 0.40 g m^{-2} yr^{-1}. Note that the coefficient at the beginning of the equation differs from that of Edgar (1990) because of a change in units of B from mg to g m^{-2} and of S from mg C d^{-1} to g C m^{-2} yr^{-1}. This equation has been shown to agree well with direct secondary production and biomass measurements (Sturdivant et al., 2013). Tumbiolo & Downing (1994) developed Eq. 6, and the model was also validated with direct calculations of production in the Chesapeake Bay:

$$\log_{10}(S_3) = \beta_0 + b\ \log_{10}\left(\frac{B}{1\ \mathrm{g\ m^{-2}}}\right) - m\ \left(\frac{M}{1\ \mathrm{mg}}\right) + t\ \left(\frac{T}{1\ ^{o}\mathrm{C}}\right) - z\ \log_{10}\left(\frac{Z}{1\ \mathrm{m}} + 1\right) \quad (6)$$

where $\beta_0 = 0.24, b = 0.96, m = 0.21, t = 0.03, z = 0.16$. In this calculation, we used the AFDW of biomass for B. The bottom water temperature (T) was measured only in the summer on the same day the benthic samples were collected. This reliance on summer bottom water

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444 temperatures may be slightly inaccurate, as it reflects summer production scaled up to annual
445 values. For max individual body mass (M), we used the maximum weight of the bivalve *R.*
446 *cuneata* collected in a study in the Choptank River in the Chesapeake Bay, which was 5953 mg
447 (Hartwell et al., 1991). Z corresponds to the water depth. The Edgar (1990) and Tumbiolo &
448 Downing (1994) secondary production equations do not include explicit sources of uncertainty.
449 The mean S value was calculated from the three different secondary production equations (Eqs.
450 3, 5, and 6) and uncertainty arises from the multiple equations used:

451 $$\frac{\Delta S}{S} = \sqrt{w_3 \left(\frac{\Delta S_1}{S_1}\right)^2 + w_5 \varepsilon + w_6 \varepsilon} \quad (7)$$

452 where w corresponds to the weights associated with the uncertainty for each secondary
453 production calculation. The subscripts in w correspond to the secondary production equations
454 (Eqs. 3,5, and 6), with values of 0.1 for w_3, 0.45 for w_5, and 0.45 for w_6. Higher weights were
455 assigned to w_5 and w_6 since the associated secondary production equations have been more
456 extensively validated. Since there is no well-defined source of uncertainty in these two
457 equations, a small error term ε of 0.001 was included.

458 We then calculated calcification rates from secondary production rates. We relied on a
459 study by Chauvaud et al. 2003, which calculates the ratio of shell production (g $CaCO_3$ m^{-2} yr^{-1})
460 to tissue production (g C m^{-2} yr^{-1}):

461 $$C = \gamma_{CO_2} r_s S \quad (8)$$

462 where r_s is the ratio of shell production to tissue production. The study samples the bivalve
463 *Potamocorbula amurensis* in the northern San Francisco Bay. The ratio of shell production to
464 tissue production was 10. There was also a ratio of 15 cited for the bivalve *C. fluminea*, a more
465 relevant species to our study, but the reference is from unpublished data. Calcification C (units of

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g C m^{-2} yr^{-1}) is in terms of CO_2 produced as calcification shifts seawater equilibrium and produces dissolved CO_2. γ_{CO_2} corresponds to the ratio of the mass of CO_2 produced divided by the mass of calcium carbonate produced. Chauvaud et al., (2003) gives a ratio of 0.12 for the bivalve *C. fluminea* and 0.09 for the bivalve *P. amurensis*. For the two bivalve species, the product of the ratio of shell production to tissue production (r_s) and the ratio of mass of CO_2 produced divided by calcium carbonate produced (γ_{CO_2}) gives an average value of 1.35; this value was used in Eq. 8. Calcification uncertainty is derived from γ_{CO_2}, r_s, and S:

$$\frac{\Delta C}{C} = \sqrt{\left(\frac{\Delta k}{k}\right)^2 + \left(\frac{\Delta S}{S}\right)^2} \quad (9)$$

where k is the product of r_s and γ_{CO_2}, with one value for *C. fluminea* and one for *P. amurensis*. $\Delta k = 0.45$ and is half the range of possible k values.

We also calculated respiration rates from secondary production. A ratio of respiration rates to secondary production rates was derived from an empirical relationship between benthic macrofauna biomass and respiration rates in the Bay of Fundy study referenced earlier:

$$\log_{10}\left(\frac{\mathrm{R}}{1\ kcal\ \mathrm{m^{-2}\ yr^{-1}}}\right) = \alpha_0 + \mathrm{s}\log_{10}\left(\frac{\mathrm{S}}{1\ kcal\ \mathrm{m^{-2}\ yr^{-1}}}\right) \quad (10)$$

where $s = 0.993$ and $\alpha_0 = 0.367$. Kcal were converted to grams of carbon, using the ratio 1 g C=11.4 kcal (Chauvaud et al., 2003). The estimations for calcification and respiration rates have less data validation than secondary production. However, we are confident they can approximate the relative carbon flux impact of the benthic macrofauna. The uncertainty in respiration rates is derived solely from S:

$$\frac{\Delta R}{R} = \ln(10)\, S \frac{\Delta S}{S} \quad (11)$$

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Eq. 12 shows that the total CO_2 generated, TC, is the sum of the CO_2 generated from respiration and calcification (units of g C m^{-2} yr^{-1}) (Chauvaud et al., 2003).

$$TC = C + R \quad (12)$$

The uncertainties in TC are derived from C and R:

$$\Delta TC = \sqrt{(\Delta C)^2 + (\Delta R)^2} \quad (13)$$

We grouped the biomass measurements and associated carbon fluxes into 12 regions to highlight broader spatial differences. These regions were created by combining the 92 segments delineated by the Chesapeake Bay Program (CBP; 2004). The 12 regions were the Patuxent River, the Potomac River, the Rappahannock River, the York River, the James River, the Western Shore (the small western tributaries in Maryland), the Eastern Shore (all tributaries east of the mainstem), the Upper Bay (mainstem oligohaline zone and tidal fresh zones or CB1 and CB2), the Mid Bay (mainstem mesohaline zones or CB3, CB4, and CB5), and the Lower Bay (mainstem polyhaline zones or CB6, CB7, and CB8). Biomass density values were calculated for each region.

3. Results

3.1 Spatial distribution of benthic macrofauna biomass

Benthic macrofauna biomass exhibits strong spatial variability across the Chesapeake Bay, with higher concentrations in the tidal fresh and oligohaline zones, and lower concentrations in the Mid Bay and lower sections of many tributaries. Figure 1 shows the spatial distribution of the time-averaged (1995–2022) summer benthic macrofauna biomass. The arithmetic mean of all biomass measurements (based on the full data set, $N = 8128$) is 7.93 g m^{-2}, whereas the spatial mean is 6.31 g m^{-2} ($N = 846$). The sampling scheme oversamples tributaries (Fig. A1) where more biomass is concentrated, inflating the arithmetic mean. The standard

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deviation of the full dataset is 28.70 g m^{-2}, indicating that the distribution is heavily skewed to the right, with the highest sample reaching up to 722 g m^{-2}. The standard deviation of the time-averaged data is 17.02 g m^{-2}, considerably smaller than the full data set since it does not include temporal variability, but is nevertheless still skewed to the right, with the highest gridded value of 220.18 g m^{-2}. Most of the high biomass density zones (>30 g m^{-2}) are concentrated in the tidal fresh and oligohaline sections of the mainstem and Potomac River. The other tributaries have higher biomass in the tidal fresh and oligohaline and zones compared to the other salinity zones. In the Mid Bay and lower sections of many tributaries, biomass is very low.

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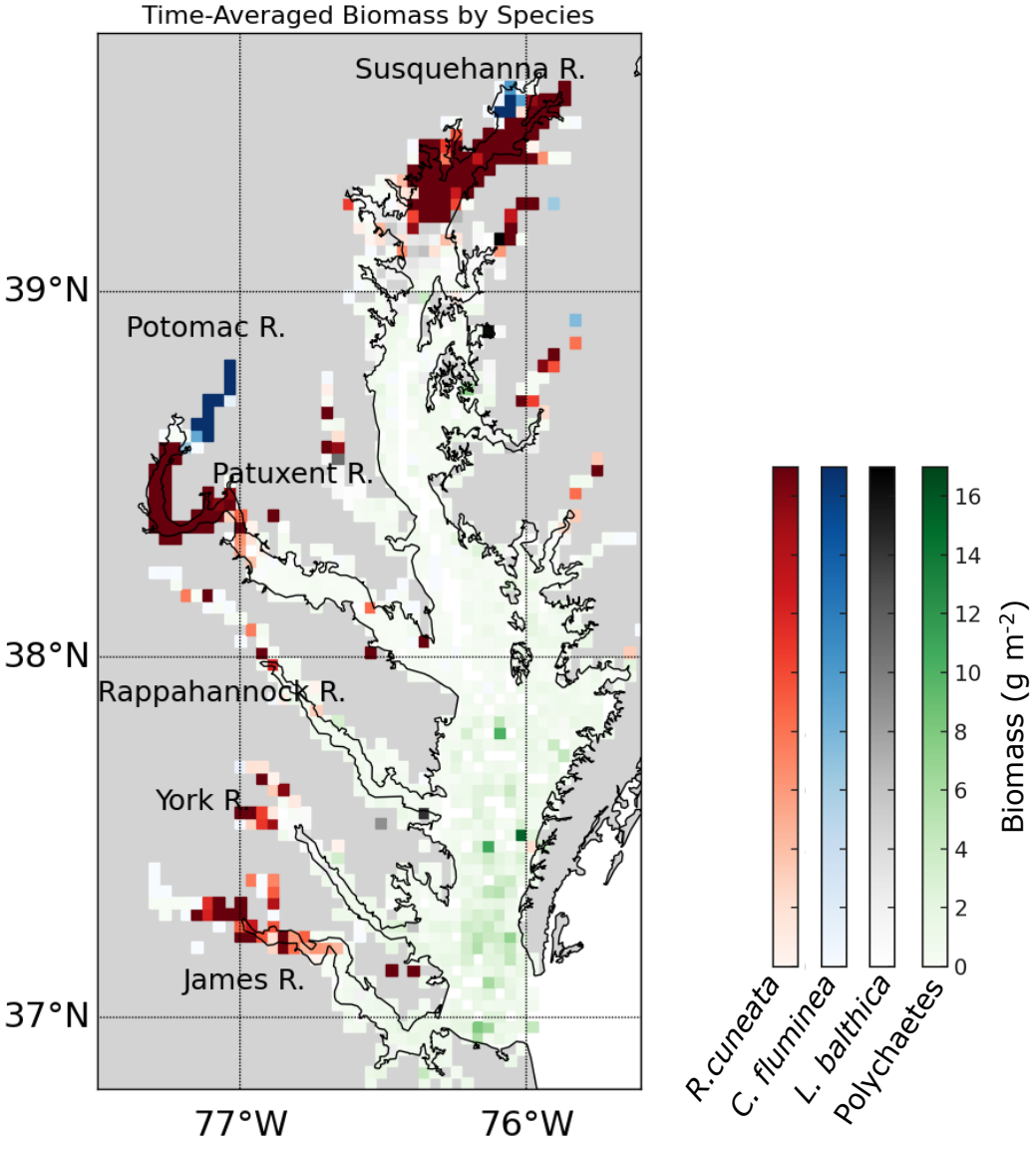

Figure 1: Average summer biomass density from 1995 to 2022 from the Maryland and Virginia Benthic Monitoring Program. Each color corresponds to a specific bivalve species (*M. balthica, C. fluminea, or R. cuneata*) or polychaetes. The color shown on the map is the species with the highest time-averaged biomass in that grid cell.

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In the high-biomass tidal fresh and oligohaline zones, bivalves dominate; whereas polychaetes are more prevalent in the lower-biomass mesohaline and polyhaline zones. The distribution of benthic biomass density into salinity zones for multiple taxonomic groups and species is shown in Fig. 2. Bivalves comprise 88.0% of the benthic biomass, and polychaetes comprise 7.3%. At a taxonomic species level, the bivalve *R. cuneata* comprises 66.1% of the biomass, followed by the bivalve *C. fluminea* (8.0%) and the bivalve *L. balthica* (7.5%). The high biomass zones in the Upper Bay, Potomac River, and James River are dominated by *R.* cuneata, mostly in the oligohaline zone (Fig. 2). *C. fluminea* also dominates in relatively higher quantities in the tidal fresh zone of the Potomac River and the tidal fresh zone of the Upper Bay (Fig. 2). In general, *R. cuneata* has a higher biomass density in the tidal fresh than *C. fluminea* because *R. cuneata* is present in all tidal fresh zones. *L. balthica* is distributed in multiple salinity zones; it is highest in the lower mesohaline and is the dominant species in the lower mesohaline zone of the Upper Bay and Patuxent River. The biomass density of *L. balthica* in the lower mesohaline (<2 g m^{-2}) is significantly lower than *C. fluminea* and *R. cuneata* in the tidal fresh and oligohaline zones. Polychaetes are the species that dominate over the largest geographic area, throughout the polyhaline and part of the higher mesohaline (Fig. 1 & 2). However, their biomass density is low relative to bivalves (<2 g/m^2). Bivalves are sparse throughout the higher mesohaline and polyhaline zones.

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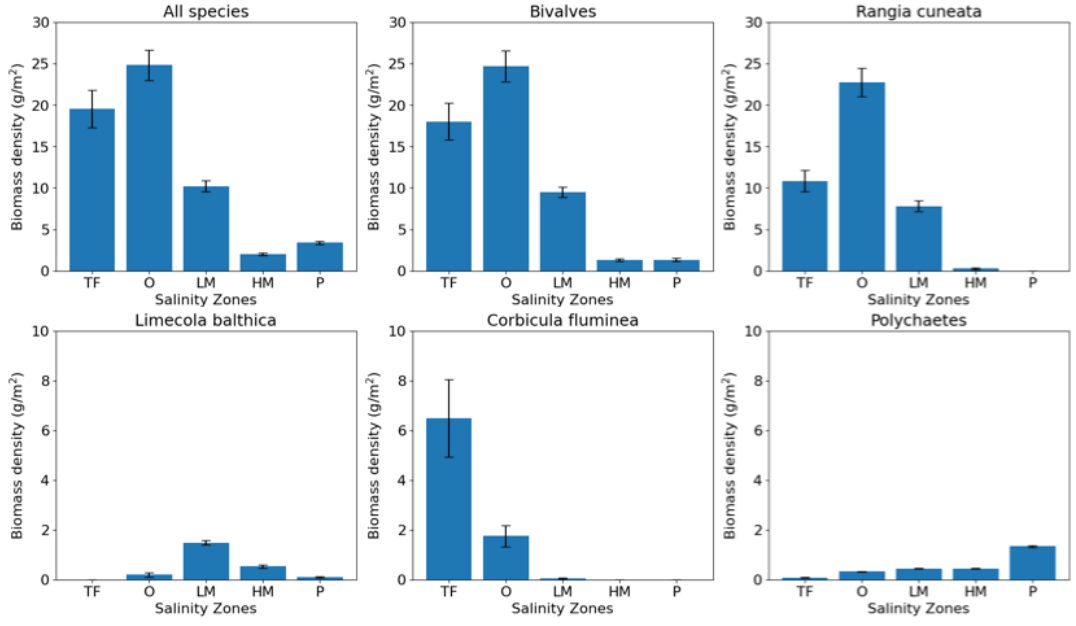

Figure 2: Average summer benthic biomass density of multiple classes and species in each salinity zone from 1995 to 2022. The salinity zones are determined by the BMP program based on the long-term average of salinity in each geographic zone: TF (Tidal Freshwater) 0–0.5 ppt, OH (Oligohaline) 0.5–5 ppt, LM (Low Mesohaline) 5–12 ppt, HM (High Mesohaline) 12–18 ppt, and Polyhaline (PO) ≥ 18 ppt. Averages and standard errors (bars) are computed using the full data set, not the gridded values. Note difference in vertical scale between upper row and lower row.

3.2 Correlation of environmental variables with biomass

The GAMs analysis revealed key drivers of benthic biomass both at the community level (all taxa combined) and for specific taxonomic groups and species. The results for total benthic biomass (all taxa), polychaetes, and the bivalve species *R. cuneata*, *C. fluminea*, and *L. balthica* are shown in Table 2. The bivalve group was excluded from the table because its results were nearly identical to total benthic biomass results. For total benthic biomass, the predictor variables

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555 explain 54.9% of the deviance in biomass. For individual taxa, the predictive capability of
556 GAMs increases, with 73.7% of *R. cuneata* biomass deviance explained by the predictor
557 variables. For total benthic biomass, dissolved oxygen was the most influential predictor variable
558 (highest summed Akaike weight), followed by total depth, salinity and NO_3^-. Although, water
559 temperature and sand fraction were included in the model, they had relatively little influence. For
560 individual taxa, dissolved oxygen became less influential, especially for *R. cuneata* and *C.*
561 *fluminea*. Salinity generally increased in influence as a predictor variable for species-specific
562 models most notably for *C. fluminea*. NO_3^- also generally increased in influence as a predictor
563 variable for species-specific models, with very high influence as a predictor of *C. fluminea*
564 biomass.
565 Table 2: This table presents the best-fitting generalized additive model (GAM) for each taxa
566 assemblage, determined by minimizing Akaike's Information Criterion (AIC). Summed Akaike
567 weights indicate the relative importance of each predictor variable across all models considered,
568 with higher values suggesting stronger support for a variable's inclusion in the best-fitting
569 models. "N/A" indicates that the variable was not included in the best model. Some variables
570 may have high summed Akaike weights even if they are not in the best-fitting model. For
571 example, in the R. cuneata model, DO has a summed Akaike weight of 0.571, while water
572 temperature has 0.032. In the C. fluminea model, DO has 0.384, and total depth has 0.24.

Taxa	**N**	**Deviance Explained**	**Summed Akaike Weight**					
			DO	Salinity	Total Depth	Water temperature	Sand fraction	NO_3^-

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All taxa	846	54.9%	0.536	0.032	0.400	0.000	0.000	0.031
Polychaetes	846	50.0%	0.457	0.173	0.266	N/A	0.000	0.104
R. cuneata	846	73.7%	N/A	0.161	0.183	N/A	0.024	0.059
C. fluminea	846	65.9%	N/A	0.212	N/A	0.122	0.078	0.132
L. balthica	846	58.4%	0.888	0.000	0.112	N/A	0.000	0.000

The relative effects of DO, salinity, NO_3^- and total depth on benthic biomass varied considerably. Figure 3 shows partial plots of the relative effect of these four significant predictor variables on total benthic biomass. Macrofauna biomass reaches its lowest values at low dissolved oxygen, the only section of all the partial plots that reach 0 g m^{-2}. Biomass is generally higher at shallower depths, although the effect is small. Biomass is highest at both low and high salinities and high surface NO_3^-. In summary, biomass is highest at moderate dissolved oxygen, shallow depths, low or high salinities, and high NO_3^-.

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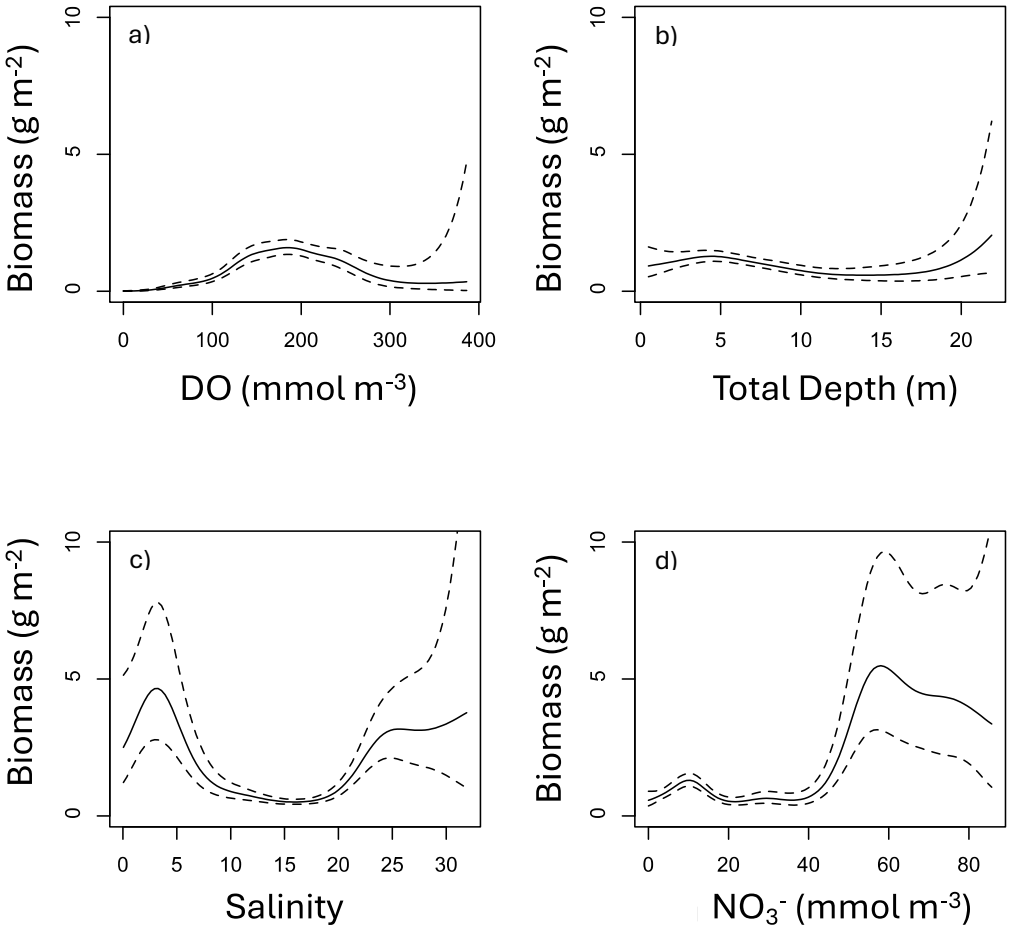

581

582 Figure 3: Partial plots of the effect of significant predictor variables on all-species biomass: (a)
583 bottom dissolved oxygen, (b) total depth, (c) bottom salinity, and (d) surface nitrate. Water
584 temperature and sand fraction were included in the model but omitted from display as they since
585 they did not significantly improve the model fit. The solid black line shows the response with the
586 dashed lines showing the 95% confidence interval. The natural log transformation was removed

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from biomass to enhance viewing of the partial plots. The x-axis was cut-off at the upper quartile plus three interquartile ranges in order to remove extreme outliers from the plots.

The model fit evaluation reveals some systemic biases examined in Fig. A2. The residuals (observed values minus model-fitted values) are slightly skewed to the left (Fig. A2b), meaning the model is more likely to overestimate biomass. The response vs. fitted value scatter plot shows a nearly linear relationship (Fig. A2a). The map of residuals (Fig. A2c) shows that the regions where the model is most likely to overestimate the biomass response are at the lowest biomass zones in the Mid Bay and the lower Potomac River. In these sections, the biomass is nearly zero. There is also an underestimation in the model fit at the high biomass zones, especially in the Upper Bay.

3.3 Carbon flux estimates

The biomass density and associated carbon fluxes vary across watershed regions, as shown in Fig. A3. The associated carbon fluxes scale proportionally to the biomass with large uncertainty. To evaluate our secondary production calculations, we examined the ratio of secondary production to biomass. The ratio of the secondary production (in g C m^{-2} yr^{-1}) to biomass (in g m^{-2} yr^{-1}) for the whole Bay was 1.6, with ratios ranging from 1.4 to 1.9 for the different regions. Secondary production calculations from the two observationally validated models, Dauer (1993), Edgar (1990), and Sturdivant et al., (2013) also found magnitudes within that range.

In multiple segments of the Bay, respiration fluxes are comparable to the available organic carbon supply. To assess the relative contribution of macrofaunal respiration, we compared estimated respiration rates from benthic biomass to previously reported values for

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primary production and other organic carbon inputs (Table 3). To estimate total organic carbon (TOC) and particulate organic carbon (POC) fluxes in the Upper Bay, we calculated the areal flux by distributing the total organic carbon load over the surface area of the tidal fresh and oligohaline zones of the mainstem, represented by the CBP segments CB1 and CB2. This approach assumes that the majority of the annual TOC load from the Susquehanna River remains concentrated in the Upper Bay and is respired rather than transported downstream, an assumption supported by Canuel & Hardison, (2016). In the Upper Bay, benthic macrofaunal respiration fluxes are within the range of gross primary production (GPP). To estimate the fraction of organic carbon load respired, we took the extreme ends of the uncertainty ranges of our respiration rates and divided them by the sum of the estimates of GPP and POC in the Upper Bay. The results suggest that 17 to 50% of available carbon in the Upper Bay is respired by benthic macrofauna. Potomac River respiration rates exceed organic carbon production from GPP. However, in the mainstem and the Bay as a whole, respiration fluxes are much lower than GPP. Our estimates suggest that benthic macrofauna respire between 1.8 and 5.0% of the available organic carbon in the mainstem.

Table 3: Primary production organic carbon, and respiration compiled from the listed studies compared with respiration from our study. All units were converted to g C m^{-2} yr^{-1}. The watershed region areas were determined by summing the areas of the Chesapeake Bay Program segments within each watershed. The Susquehanna River estimates assumed the entire load was concentrated in the Upper Bay.

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Region	**Carbon Flux**	**Value**	**Study**	**Region (our study)**	**Carbon Flux (our study)**	**Value (our study)**
Eastern North America	Estuarine GPP	309 g C m^{-2} yr^{-1}	Najjar et al., (2018)	Whole Bay	Respiration	25±12 g C m^{-2} yr^{-1}
Mid Atlantic Blight	TOC from tidal wetlands	6.8 g C m^{-2} yr^{-1}	Herrmann et al., 2015			
Mid Atlantic Blight	TOC from streamflow	14.4 g C m^{-2} yr^{-1}	Herrmann et al, 2015			
Mainstem	GPP	657.4 g C m^{-2} yr^{-1}	Kemp et al., 1997	Mainstem	Respiration	23±11 g C m^{-2} yr^{-1}
	Benthic Respiration	163.1 g C m^{-2} yr^{-1}	Kemp et al., 1997			
All Inputs	TOC	90 g C m^{-2} yr^{-1}	Kemp et al., 1997			
	POC	15.6 g C m^{-2} yr^{-1}	Zhang & Blomquist (2018)			

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Upper Bay	GPP	123.4 g C m^{-2} yr^{-1}	Kemp et al., 1997	Upper Bay	Respiration	128±63 g C m^{-2} yr^{-1}
	Benthic Respiration	44.3 g C m^{-2} yr^{-1}	Kemp et al., 1997			
Susquehanna River	TOC	354 g C m^{-2} yr^{-1}	Kemp et al., 1997			
	POC	257.7 g C m^{-2} yr^{-1}	Zhang & Blomquist (2018)			
Potomac River	POC	31.7 g C m^{-2} yr^{-1}	Zhang & Blomquist (2018)	Potomac	Respiration	57±29 g C m^{-2} yr^{-1}

Benthic macrofaunal calcification also represents a major flux within the Bay. Our study shows that calcification rates by benthic macrofauna analyzed in the BMP program far exceeds estimates of the Eastern oyster (*Crassostrea virginica*) calcification rates (Table 4). To calculate oyster calcification rates, we used Fulford et al., (2007) model estimates of oyster biomass in different CBP segments and we related the ash-free dry weight of oyster biomass to the live weight using a ratio of 10:1 (Mo & Neilson, 1994). We then calculated calcification rates using a ratio of 2 mg $CaCO_3$ per gram live mass per day of oyster (Waldbusser et al., 2013). To maintain consistency with our results, which frame fluxes in the context of carbon, we converted calcification rates to the equivalent amount of CO_2 generated. While this is a non-standard way

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of presenting calcification rates, it allows for direct comparison with other carbon fluxes and better integration into our broader analysis of estuarine carbon cycling. We estimated CO_2 generated (in g m^{-2} yr^{-1}) is about 12% of the $CaCO_3$ production (in g m^{-2} yr^{-1}) (Chauvaud et al., 2003). Using these values and CBP segment areas, we derived oyster calcification fluxes for the mainstem and Upper Bay. Remarkably, bivalve calcification rates from our study exceeds oyster calcification rates by over 80 times in the mainstem and by over 1000 times in the Upper Bay.

Table 4: Oyster calcification and riverine calcium input compiled from the listed studies compared with calcification from our study. Calcification calculated from the yearly Ca flux and oyster calcification from the listed studies. All units were converted to g C m^{-2} yr^{-1} with information about how the calculations were made in the text. The watershed region areas were determined by summing the areas of the Chesapeake Bay Program segments within each watershed. The Upper Bay calcification from yearly Ca flux assumed that the entire load from the Susquehanna River was concentrated in the Upper Bay.

Region	**Carbon Flux**	**Value**	**Study**	**Region (our study)**	**Carbon Flux (our study)**	**Value (our study)**
Mainstem	Oyster Calcification	0.17 g C m^{-2} yr^{-1}	Fulford et al., 2007/ Waldbusser et al., 2013	Mainstem	Calcification	14±5 g C m^{-2} yr^{-1}

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Upper Bay	Calcification from Yearly Ca Flux	557.6 g C m^{-2} yr^{-1}	USGS	Upper Bay	Calcification	78±31 g C m^{-2} yr^{-1}
	Oyster Calcification	0.07 g C m^{-2} yr^{-1}	Fulford et al., 2007/ Waldbusser et al., 2013			
Potomac River	Calcification from Yearly Ca Flux	77.9 g C m^{-2} yr^{-1}	USGS	Potomac	Calcification	35± 14 g C m^{-2} yr^{-1}

Evaluating the role of bivalve calcification in utilizing calcium further underscores its biogeochemical significance. If all the calcium used in bivalve calcification were sourced from rivers, bivalves would consume a significant fraction of the available calcium (Table 4). To quantify riverine calcium input, we used data from non-tidal USGS stations in the Susquehanna and Potomac Rivers from 1995 to 2022. Annual calcium fluxes were calculated using Weighted Regression on Time, Discharge, and Season (WRTDS; Hirsch et al., 2010). In calcification, one mole of $CaCO_3$ is produced for every mole of Ca consumed. To keep units consistent, we again estimated the CO_2 produced (in g m^{-2} yr^{-1}) from 12% of the $CaCO_3$ production (in g m^{-2} yr^{-1}). The Upper Bay calculation assesses how much CO_2 bivalves would generate if all the Susquehanna calcium input was used in calcification within the Upper Bay. Similarly, the Potomac River calculation estimates the rates of calcification that would occur if all of the calcium input into the Potomac River was utilized for calcification within the Potomac River.

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669 Relative to annual riverine calcium fluxes, benthic macrofauna would use ~14% of the available
670 calcium in the Upper Bay and 45% in the Potomac River.

671 The role of benthic macrofaunal metabolic processes in the carbon budget is particularly
672 pronounced when the effects of calcification and respiration are combined. Our estimates
673 indicate that calcification contributes 38% of the total CO_2 flux while respiration accounts for
674 62% (Table 5). This combined CO_2 flux exceeds the amount of outgassing estimated in the
675 Upper Bay and the mainstem overall (Table 5). Compared to other estuaries worldwide, the
676 Chesapeake Bay exhibits relatively modest levels of CO_2 outgassing (Table 5). In estuaries with
677 greater outgassing rates, the proportional contribution of calcification and respiration to total
678 CO_2 exchange might be lower, but would still be substantial.
679
680 Table 5: Air/sea gas exchange from the listed studies compared with total benthic CO2 flux in
681 our study, calculated as the sum of respiration and calcification fluxes. All units were converted
682 to g C m^{-2} yr^{-1} .

Region	**Carbon Flux**	**Value**	**Study**	**Region (our study)**	**Carbon Flux (our study)**	**Value (our study)**
Upper Bay (CB1,	Air/Sea CO_2 exchange	74.5 g C m^{-2} yr^{-1} (outgassing)	Herrmann et al., 2020	Upper Bay (CB1 & CB2)	Total CO_2 Flux	205±70 g C m^{-2} yr^{-1}

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CB2, & CB3)						
Mainstem	Air/Sea CO_2 exchange	14.5 g C m^{-2} yr^{-1} (outgassing)	Herrmann et al., 2020	Mainstem	Total CO_2 Flux	36±12 g C m^{-2} yr^{-1}
Global Estuaries	Air/Sea CO_2 exchange	92.5 g C m^{-2} yr^{-1} (outgassing)	Chen et al., 2013	Whole Bay	Total CO_2 Flux	40±14 g C m^{-2} yr^{-1}
Eastern North America	Air/Sea CO_2 exchange	108.1 g C m^{-2} yr^{-1} (outgassing)	Chen et al., 2013	Whole Bay		

4. Discussion

4.1. Environmental controls on benthic biomass distribution

Bivalve species distribution within the Bay is primarily driven by salinity tolerances. Both the GAMs analysis (Table 2) and the biomass densities associated with salinity zones (Fig. 2) showed that benthic biomass, dominated by bivalves, was much higher at lower salinities. The strong influence of salinity on benthic fauna distribution within estuaries has long been recognized (Cain, 1975; Hopkins et al., 1973). This relationship is illustrated in our study by the preference of the most abundant species, *R. Cuneata*, *L. balthica*, and *C. fluminea*, for less saline water. *R. Cuneata* is widely known to need less saline waters, optimally between 1 and 15 ppt, to survive (Hopkins et al., 1973). *C. fluminea* prefers freshwater environments (Phelps, 1994; Sousa

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et al., 2008). *L. balthica* has a range of tolerances but abundance declines below 5 ppt (Jansson et al., 2015). In our study, *L. balthica* is more concentrated between 5 and 13 ppt. While salinity determines which species dominate, other factors influence their relative abundances within these zones.

Within mesohaline zones, summer hypoxia appears to be driving extremely low benthic biomass. In our GAMs analysis, an association existed between biomass and extremely low bottom dissolved oxygen values. Among the different salinity zones, low biomass is associated with low dissolved oxygen in the high mesohaline, where we had the lowest biomass densities. Long-term exposure to hypoxia (<2 mg L^{-1} or 62.5 mmol m^{-3}) is fatal to benthic fauna (Diaz et al., 1995; Seitz et al., 2006; Seitz et al., 2009) and many benthic communities (approximately 50%) only recover on an annual timescale (Diaz et al., 1995). In other words, regions that suffer frequent hypoxia often see lower levels of benthic biomass even when hypoxic conditions are not occurring. In the Chesapeake Bay, hypoxia is most likely to occur in the deeper, mesohaline regions (Frankel et al., 2022; Zheng & DiGiacomo, 2020), providing evidence that our suppressed values of benthic fauna at this salinity zone could be due to mass mortality from hypoxia. This pattern is particularly evident where biomass is extremely low through the Mid Bay and lower Potomac, regions typically associated with summer hypoxia (Sturdivant et al., 2013).

Across the Bay, the relatively narrow range of summer bottom water temperatures likely explains why temperature has an insignificant effect on the spatial distribution of benthic biomass. In our GAMs analysis, summer bottom water temperature was not significantly correlated with benthic biomass. Water temperature has been considered an important driver of benthic biomass (Marsh & Tenore, 1990; Seitz et al., 2006; Seitz et al., 2009; Testa et al., 2020),

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with low temperature specifically creating mass mortality of *R. cuneata* during winter and spring (Tuszer-Kunc et al., 2020). Higher temperatures, however, will drive early and larger seasonal hypoxia in the Chesapeake Bay (Hinson et al., 2022; Irby et al., 2018; Ni et al., 2019). So, temperature could still indirectly affect benthic biomass through its effect on dissolved oxygen. Therefore, while temperature many not directly drive spatial patterns of biomass, it could be more relevant to temporal changes in biomass.

Although NO_3^- is a clear predictor of benthic biomass, the mechanisms driving this association are likely complex. NO_3^- is an important limiting nutrient for primary production, and high annually-averaged concentrations indicate an excess of NO_3^- not fully utilized by phytoplankton. Excess NO_3^- from the tributaries flows into the mainstem, fueling a spring phytoplankton bloom (Brush et al., 2020b). The highest primary production zones in the spring are in the mesohaline and fuel hypoxia where the Bay is deeper and stratified (Brush et al., 2020a), possibly explaining why long-term increases in phytoplankton biomass have not been linked with an increase in benthic biomass (Harding & Perry, 1997). In the tidal fresh and oligohaline zones, abundant NO_3^- is present, but high suspended solid loads limit light penetration, consequently inhibiting primary production (Brush et al., 2020b).

Given the complexity of explaining the relationship between NO_3^- and benthic biomass, further insights may come from examining the relationship between inorganic suspended solid loads and POC. A significant portion of suspended solids in the tidal fresh and oligohaline regions is POC, given previous studies have that suggest substantial inputs of POC are respired in the Upper Bay (Kemp et al., 1997; Testa et al., 2020). Canuel & Hardison, (2016) further demonstrated that above the Estuarine Turbidity Maximum (ETM), organic matter is dominated by allochthonous (terrigenous) sources, which could contribute to the high POC content in

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suspended solids. Further evidence for substantial allochthonous inputs of POC comes from the dissolved oxygen supersaturation ($\Delta[O_2]$) model-derived information (Fig. 4). As explained earlier, $\Delta[O_2]$ was not included as a predictor variable because it was highly correlated with NO_3^- and salinity, the two most influential predictors of the high biomass zones. Under steady-state conditions and ignoring advection and mixing, negative surface $\Delta[O_2]$ indicates net heterotrophy, where oxygen consumption from respiration exceeds oxygen production from photosynthesis. This imbalance leads to undersaturation and uptake from the atmosphere. Conversely, positive $\Delta[O_2]$ indicates net autotrophy, where oxygen production from photosynthesis exceeds oxygen consumption from respiration. The $\Delta[O_2]$ maps (Fig. 4) indicate high levels of heterotrophy year-round throughout the upper reaches of the tributaries and the Upper Bay, corresponding to the tidal fresh and oligohaline zones of the Bay. Autotrophy dominates year-round in the polyhaline Lower Bay. In the lower tributaries and Mid Bay (mesohaline zones), there are seasonal shifts, with heterotrophy in the summer and fall and autotrophy in the spring and winter. High levels of heterotrophy near the freshwater sources of the Bay could indicate substantial inputs of allochthonous organic matter being respired (Kemp et al., 1997).

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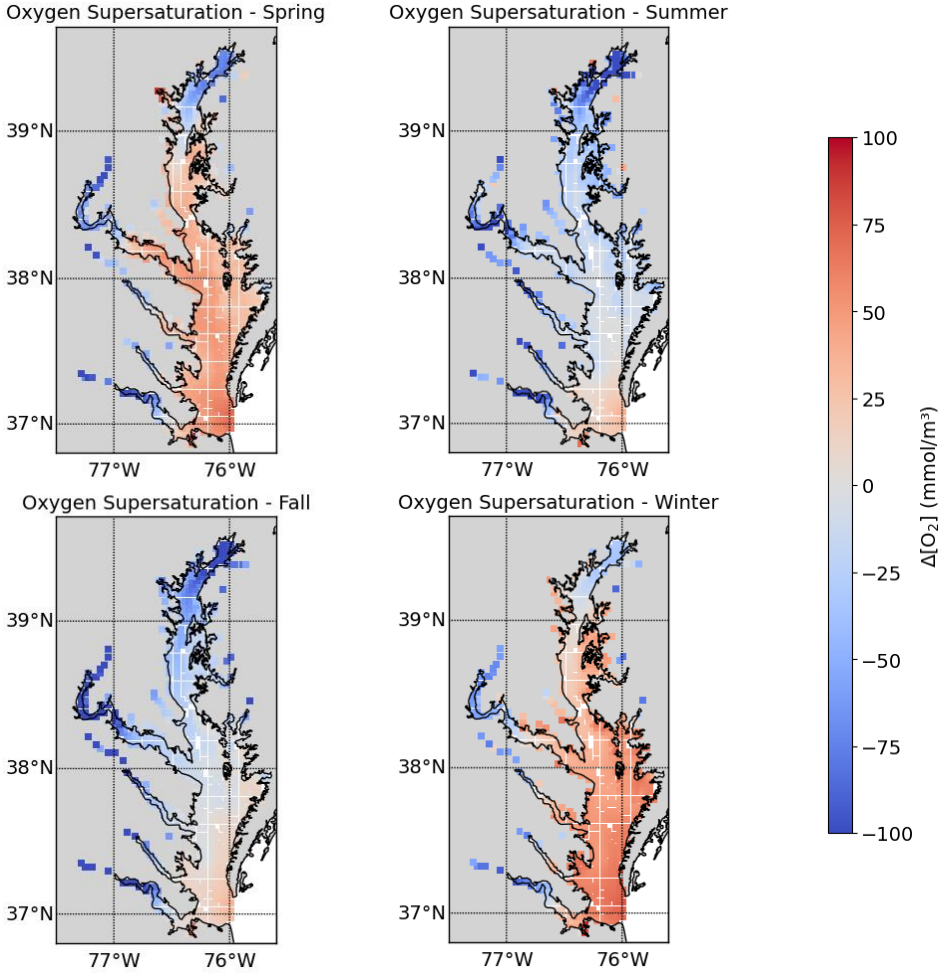

Figure 4: Surface oxygen supersaturation for each season in the Bay. Spring (March–April), Summer (July–August), Fall (September–November), and Winter (December–February). Method for calculating oxygen supersaturation is described in the text.

If the highest NO_3^- concentrations coincide with elevated suspended solid loads at and above the ETM, and if POC is substantially present in these loads, then annually averaged NO_3^- may act as a proxy for allochthonous POC. In contrast, below the ETM, NO_3^- is more readily

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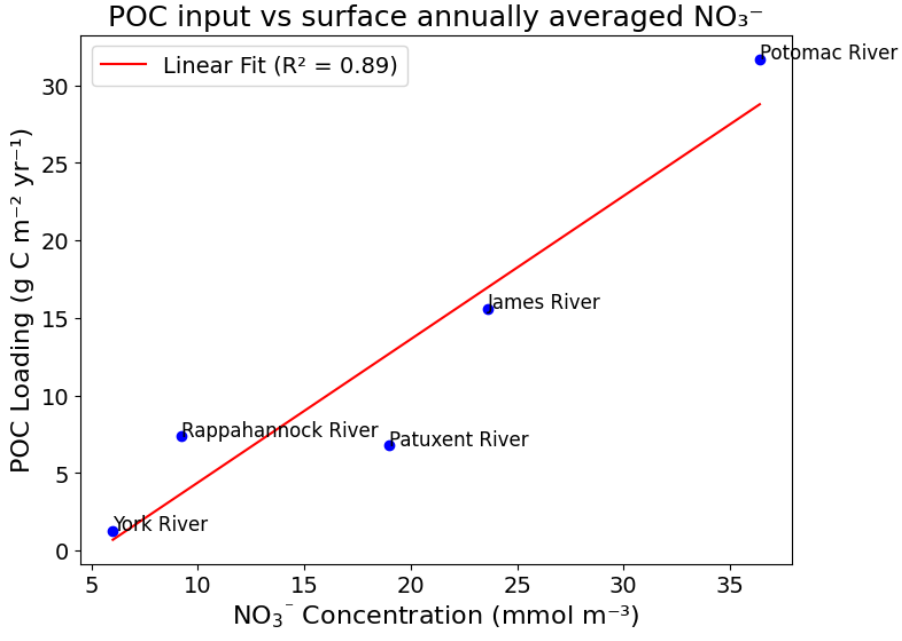
764 utilized in primary production, and most of the POC is autochthonous. Unfortunately, POC
765 modeled by ROMS-ECB can't be used to support our hypothesis, as model-data evaluation did
766 not meet our robustness threshold ($r_s < 0.7$). However, USGS data compiled by Zhang &
767 Blomquist (2018) give long-term averages (1985–2016) of POC input into various tributaries
768 measured at non-tidal gauging stations. Figure 5 compares the concentration of allochthonous
769 input of POC and the average surface nitrate NO_3^- in each tidal region. We calculated the POC
770 concentration using the average load of POC input into the tributary divided by the area of the
771 watershed region. Only the six largest tributaries had POC data reported. The Susquehanna River
772 data was excluded because it discharges directly into the mainstem, making it less comparable to
773 the other river estuaries. There was a substantial linear correlation between NO_3^- and POC.
774



775
776 Figure 5: Particulate organic carbon (POC) vs surface nitrate (NO_3^-) for five watershed regions.
777 POC fluxes were calculated using load data from USGS compiled by Zhang and Blomquist

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(2018). The watershed region areas were determined by summing the areas of the Chesapeake Bay Program segments within each watershed. NO_3^- concentrations were obtained from ROMS-ECB output and represent the annually averaged mean concentration in each watershed region.

Taken together, these data strongly support the hypothesis that the correlation between surface NO_3^- and benthic biomass is driven by allochthonous POC. This link is further reinforced by our dataset, where regions of high heterotrophy (Fig. 4) align with the highest benthic biomass (Fig. 1). If salinity dictates species distribution by limiting certain taxa to fresher zones and dissolved oxygen reduces benthic biomass in mesohaline zones, then the relative inputs of terrestrial organic matter could be controlling biomass variation in the fresher regions.

4.2. Benthic macrofaunal contributions to estuarine carbon budget

The higher benthic biomass in less saline waters suggests a significant role for respiration in the carbon budget in this region. The proportion of organic carbon respired by benthic macrofauna estimated in our study in the Upper Bay (17 to 50%) is remarkably similar to the 14 to 40% range estimated for bivalve filter feeders in tidal fresh and oligohaline waters by Cerco & Noel (2010). In the Upper Bay, where the benthic macrofauna respiration flux is comparable to the GPP flux, if all the GPP were respired solely by benthic macrofauna, net ecosystem production would be zero. However, given the consideration of additional respiration by other organisms (e.g., microbes and pelagic zooplankton) the allochthonous POC from the Susquehanna River must be a critical source of organic carbon driving net heterotrophy in this region. These findings reinforce the earlier conclusion that high biomass zones in the Upper Bay are sustained by allochthonous organic inputs. The Potomac River, however, presents a less conclusive case, partly due to the lack of available GPP estimates. In the Potomac, where benthic

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macrofaunal respiration rates exceed the estimated POC flux, additional carbon sources, such as autochthonous GPP or tidal wetland outwelling, may be contributing to carbon metabolism. Herrmann et al., (2015) estimated that wetland outwelling accounts for approximately half of the organic carbon exported by streamflow in Mid-Atlantic estuaries.

Benthic macrofaunal respiration plays a smaller role in the rest of the Bay, where autochthonous organic carbon dominates. For both the mainstem and the whole Bay, the estimated primary production far exceeds the average estimated respiration rates calculated from our benthic biomass data. Overall, the autochthonous organic carbon contribution from primary production is about 15 times greater than the allochthonous input from estuaries in the Mid-Atlantic Bight. This ratio is even more pronounced since only a fraction of the total organic carbon (TOC) is particulate (POC) and can be respired by the benthos (Kemp et al., 1997). Kemp et al., (1997) calculated benthic respiration from sulfate reduction and sediment oxygen consumption rates. Their estimates could highlight the relatively modest role of benthic macrofaunal respiration for the entire mainstem, given the lower biomass values in the Mid and Lower Bay, where autochthonous primary production and overall organic carbon flux to the sediments are higher. Their calculation may have underestimated benthic respiration rates, as our respiration rates estimates for benthic macrofaunal respiration are higher than their calculations. Our estimates of benthic macrofaunal respiration in the mainstem (1.8–5.0%) is significantly lower than estimates derived from the combined findings of Hopkinson & Smith, (2004) and Rodil et al., (2022). Hopkinson & Smith, (2004) estimated that approximately 24% of organic carbon is respired by the benthos, while Rodil et al., (2022) found that benthic macrofauna account for roughly 40% of total benthic respiration. Taken together, these studies suggest that around 10% of available organic carbon is expected to be respired by benthic macrofauna, more

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than double our findings. Although our estimates indicate that benthic macrofaunal respiration accounts for a relatively small fraction of total organic carbon metabolism at the scale of the entire Bay, this does not preclude the existence of localized hotspots where it plays a dominant role.

Unlike the extensive research on estuarine benthic respiration, little attention has been given to calcification, yet our findings suggest that benthic macrofaunal calcification could be important to the carbon budget. The relative importance of bivalve calcification in the Bay is illustrated in Table 4. Eastern oysters (*Crassostrea virginica*) have received significant attention due to their ecological and economic importance, but their populations in the Chesapeake Bay used to be at least two orders of magnitude higher than its present levels (Fulford et al., 2007; Newell, 1988). The bivalves sampled in the BMP program contribute substantially more to estuarine carbon cycling than present-day Eastern populations. Evaluating the role of bivalve calcification in utilizing calcium further underscores its biogeochemical significance. Our estimations assume that all calcium input is used in calcification; however, since calcium contributions from the ocean and groundwater may far exceed riverine inputs, this comparison does not represent a complete calcium budget but rather provides a useful context for understanding the scale of bivalve calcification.

Benthic macrofauna may play a major role in CO_2 outgassing, as indicated by our estimated high carbon fluxes in the Upper Bay and upper tributaries relative to air-sea gas exchange. Furthermore, our total CO_2 generation estimates for the Upper Bay (205±70 g C m^{-2} yr^{-1}), where bivalve biomass is concentrated, exceed those reported by Chauvaud et al., (2003), who estimated CO_2 production from calcification and respiration at 55±51 g C m^{-2} yr^{-1} for the bivalve *P. amurensis* in Northern San Francisco Bay. This further supports their hypothesis that

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benthic calcifiers can serve as major CO_2 generators in estuaries. Given the high heterotrophy in the Upper Bay and upper tributaries, as well as the balance between benthic macrofaunal respiration and organic carbon inputs in the Potomac River, it is conceivable that benthic macrofauna are major contributors to CO_2 outgassing in these regions.

Conclusion

This study examines how water chemistry and sediment composition influence the spatial distribution of benthic biomass and to assess the role macrofaunal respiration and calcification plays in estuarine carbon budgets. We found that benthic macrofauna, especially bivalves, were concentrated in the upper portions of the tributaries and mainstem Bay. High biomass zones generally had low salinity, high surface NO_3^-, moderate dissolved oxygen, and low depth. NO_3^- could behave as a proxy for POC, with high biomass being driven by allochthonous POC in the tidal fresh and oligohaline zones, areas with lower autochthonous primary production and high heterotrophy. Calcification from benthic macrofauna biomass could be a significant sink of calcium in the Bay, and the calcification rates from bivalves collected in the BMP program far exceeds Eastern oyster calcification rates. CO_2 generated from calcification and respiration could substantially contribute to outgassing in the tidal fresh and oligohaline zones. These findings highlight the significant role of benthic macrofauna in estuarine biogeochemical cycling, particularly in Chesapeake Bay.

Estuarine numerical models have historically focused on microbiota while overlooking the role of macrobiota in biogeochemical transformations (Ehrnsten et al., 2020; Ganju et al., 2016). However, our study demonstrates that benthic macrofauna can significantly influence carbon dynamics within the Chesapeake Bay and should be more consistently incorporated into numerical models. Additionally, we show that the spatial distribution of benthic macrofauna is

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highly predictable based on environmental variables already included in models, reducing the need for high-resolution benthic biomass data. Our findings provide a strong foundation for integrating benthic macrofauna into numerical models, highlight both the feasibility and necessity of doing so.

Several limitations in our study must also be acknowledged. One key limitation is the need for better empirical equations relating biomass to metabolic processes, particularly calcification. Our estimates relied heavily on Chauvaud et al., (2003), who assumes a direct proportionality between secondary production rates and calcification rates, but this relationship requires further validation across different estuarine systems. However, we attempted to account for this uncertainty by incorporating a range of estimates in our analysis. Additionally, our study was constrained by the interactions between highly correlated variables. As a result, we did not use our calculated values for Ω_{arag}, despite its potential importance for bivalves. The saturation state of aragonite could strongly influence calcification rates, but due to its correlation with other environmental variables, its independent effect was difficult to parse. Furthermore, while our model explained a little over half of the deviance in biomass from predictor variables, this predictive capability could be improved. In our study we emphasized bottom-up controls. Top-down controls such as predation could also play a significant role in biomass distributions.

Future research should focus on refining metabolic estimates and further investigating the factors driving temporal changes in biomass. Climate change, along with ongoing management efforts aimed at reducing nutrient loading, is expected to alter key water quality parameters. Understanding how these shifts will impact benthic biomass distribution and metabolism is critical for predicting their broader impacts on ecosystem functioning and biogeochemical cycling.

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Overall, our findings emphasize the predictability of benthic biomass distributions within estuaries and their importance to estuarine carbon budgets, underscoring their need for further integration into numerical models.

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Appendix A

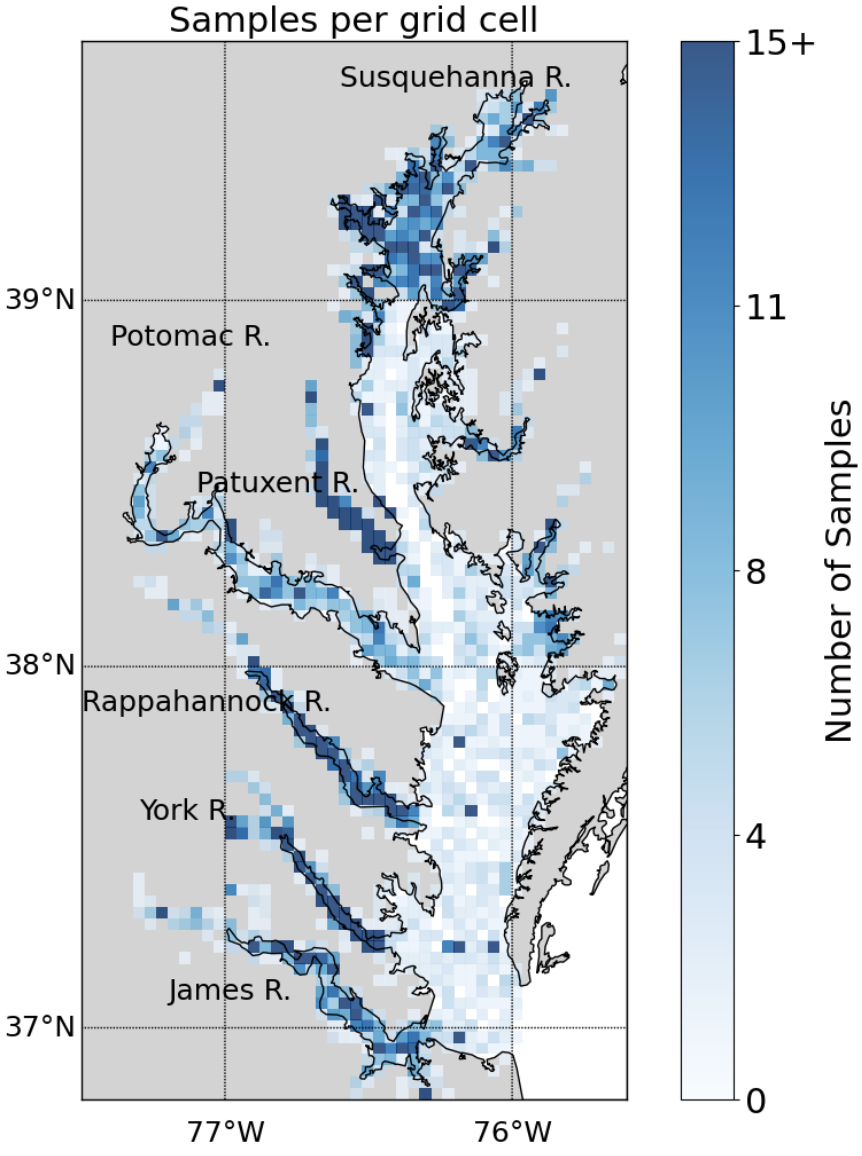

Figure A1: Number of benthic samples collected in each grid cell in the summer (July 15 to September 30) from 1995 to 2022 from the Maryland and Virginia Benthic Monitoring Program. The grids are approximately square, measuring 3.5 km by 3.5 km. Each grid cell contains a time-average of each measurement collected in the cell

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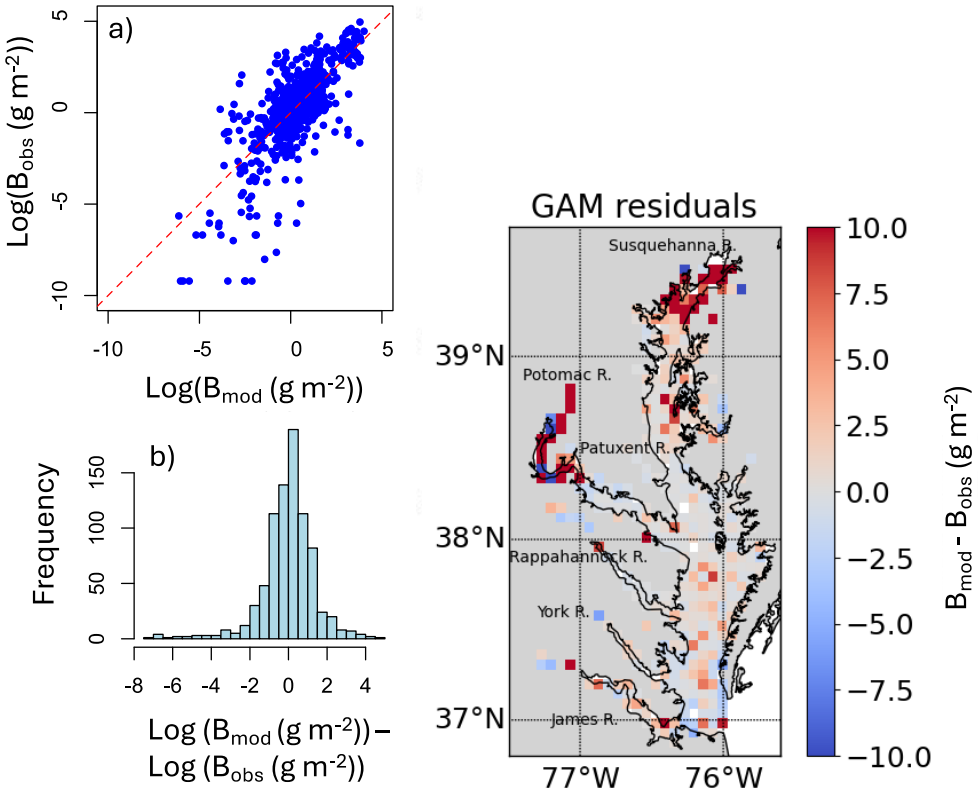

Figure A2: Evaluation of the total biomass GAM, which includes DO, salinity, total depth, , and NO_3^-, sand fraction, and water temperature as predictor variables. "Log" refers to the natural logarithm. (a) Modeled vs. observed values. (b) Histogram of biomass residuals (modeled minus observed values, $B_{mod} - B_{obs}$). (c) Spatial distribution of the residuals.

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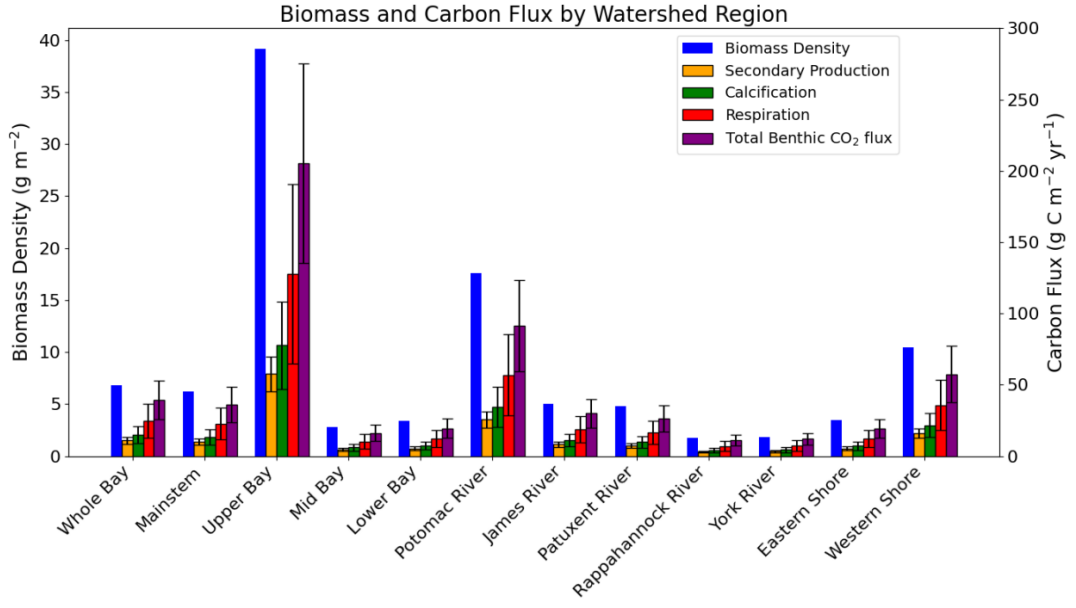

Figure A3: Biomass density and carbon fluxes for each watershed region in the Bay. The carbon fluxes are the mean value with associated total uncertainty range, as described in the text.

Data Availability

All data used in this study are publicly available and have been described in the Methods section. Water quality data were obtained from the *Chesapeake Bay Water Quality Monitoring Program* (https://datahub.chesapeakebay.net/WaterQuality), and benthic data were sourced from the *Chesapeake Bay Long-Term Benthic Monitoring Program* (https://www.baybenthos.versar.com/data.htm). Model output used in this study is publicly available at https://www.seanoe.org/data/00882/99441/.

Author Contribution

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SA led the research, conducted data analysis, interpreted results, and wrote the initial and subsequent drafts of the manuscript.
RN conceptualized the project, defined overarching research goals, secured financial support, and contributed substantially to manuscript drafts through critical reviews, commentary, and revisions.
ER provided significant insights from her expertise on the physiological responses of marine invertebrates to environmental variables, influencing the scope and direction of the study. She also substantially contributed to manuscript revisions through critical reviews and commentary.
RW contributed significant expertise on benthic biomass distribution in Chesapeake Bay and generalized additive modeling techniques, shaping the analytical framework of the study. He provided critical feedback and revisions during manuscript preparation.
MF provided ongoing feedback throughout the research process, particularly regarding the integration of modeling information and interpretation of results, and contributed critical commentary on multiple presentations of the work.
PS consistently provided feedback and contributed modeling expertise, assisting with data interpretation and manuscript revisions through critical reviews and commentary.
SD developed the original empirical models linking benthic macrofaunal biomass to carbon fluxes, laying foundational methodological contributions to the study.

Competing Interests

The authors declare that they have no conflict of interest.

Acknowledgements

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https://doi.org/10.5194/egusphere-2025-1315
Preprint. Discussion started: 8 April 2025

References

Akoglu, H. (2018). User's guide to correlation coefficients. *Turkish Journal of Emergency Medicine*, *18*(3), 91–93. https://doi.org/10.1016/j.tjem.2018.08.001

Alden, R. W., Dauer, D. M., Ranasinghe, J. A., Scott, L. C., & Llansó, R. J. (2002). Statistical verification of the Chesapeake Bay benthic index of biotic integrity. *Environmetrics: The Official Journal of the International Environmetrics Society*, *13*(5–6), 473–498. https://doi.org/10.1002/env.548

Beckwith, S. T., Byrne, R. H., & Hallock, P. (2019). Riverine calcium end-members improve coastal saturation state calculations and reveal regionally variable calcification potential. *Frontiers in Marine Science*, *6*(APR). https://doi.org/10.3389/fmars.2019.00169

Birchenough, S. N. R., Reiss, H., Degraer, S., Mieszkowska, N., Borja, Á., Buhl-Mortensen, L., Braeckman, U., Craeymeersch, J., De Mesel, I., Kerckhof, F., Kröncke, I., Parra, S., Rabaut, M., Schröder, A., Van Colen, C., Van Hoey, G., Vincx, M., & Wätjen, K. (2015). Climate change and marine benthos: a review of existing research and future directions in the North Atlantic. *Wiley Interdisciplinary Reviews: Climate Change*, *6*(2), 203–223. https://doi.org/10.1002/wcc.330

Borja, A., Dauer, D. M., Díaz, R., Llansó, R. J., Muxika, I., Rodríguez, J. G., & Schaffner, L. (2008). Assessing estuarine benthic quality conditions in Chesapeake Bay: a comparison of three indices. *Ecological Indicators*, *8*(4), 395–403. https://doi.org/10.1016/j.ecolind.2007.05.003

Brey, T. (1990). Confidence limits for secondary production estimates: application of the bootstrap to the increment summation method *. *Marine Biology*, *106*, 503–508.

Brush, M. J., Giani, M., Totti, C., Testa, J. M., Faganeli, J., Ogrinc, N., Michael Kemp, W., & Umani, S. F. (2020). Eutrophication, harmful algae, oxygen depletion, and acidification. In T. C. Malone, A. Malej, & J. Faganeli (Eds.), *Coastal ecosystems in transition: A comparative analysis of the Northern Adriatic and Chesapeake Bay* (pp. 75–104). Wiley. https://doi.org/10.1002/9781119543626.ch5

Brush, M. J., Mozetič, P., Francé, J., Aubry, F. B., Djakovac, T., Faganeli, J., Harris, L. A., & Niesen, M. (2020). Phytoplankton dynamics in a changing environment. In T. C. Malone, A. Malej, & J. Faganeli (Eds.), *Coastal ecosystems in transition: A comparative analysis of the Northern Adriatic and Chesapeake Bay* (pp. 49–74). Wiley. https://doi.org/10.1002/9781119543626.ch4

Cain, T. D. (1975). Reproduction and recruitment of the brackish water clam, Rangia cuneata in the James River, Virginia. *Fishery Bulletin*, *73*(2), 412. https://scholarworks.wm.edu/vimsarticles/2139

https://doi.org/10.5194/egusphere-2025-1315
Preprint. Discussion started: 8 April 2025

Canuel, E. A., & Hardison, A. K. (2016). Sources, ages, and alteration of organic matter in estuaries. *Annual Review of Marine Science*, *8*, 409–434. https://doi.org/10.1146/annurev-marine-122414-034058

Cerco, C. F., & Noel, M. R. (2010). Monitoring, modeling, and management impacts of bivalve filter feeders in the oligohaline and tidal fresh regions of the Chesapeake Bay system. *Ecological Modelling*, *221*(7), 1054–1064. https://doi.org/10.1016/j.ecolmodel.2009.07.024

Chauvaud, L., Thompson, J. K., Cloern, J. E., & Thouzeau, G. (2003). Clams as CO2 generators: The Potamocorbula amurensis example in San Francisco Bay. *Limnology and Oceanography*, *48*(6), 2086–2092. https://doi.org/10.4319/lo.2003.48.6.2086

Chesapeake Bay Program. (n.d.). *CBP Water Quality Database (1984-present)*.

Dauer, D. M. (1993). Biological criteria, environmental health and estuarine macrobenthic community structure. *Marine Pollution Bulletin*, *26*(5), 249–257. https://doi.org//10.1016/0025-326X(93)90063-P

Dauer, D. M., & Alden III, R. W. (1995). Long-term trends in the macrobenthos and water quality of the lower Chesapeake Bay (1985-1991). *Marine Pollution Bulletin*, *30*(12), 840–850.

Dauer, D. M., & Lane, M. F. (2010). *Quality assurance/quality control plan: Benthic biological monitoring program of the Lower Chesapeake Bay (July 1, 2010 to June 30, 2011)*.

Dauer, D. M., Ranasinghe, J. A., & Weisberg, S. B. (2000). Relationships between benthic community condition, water quality, sediment quality, nutrient loads, and land use patterns in Chesapeake Bay. *Estuaries*, *23*(1), 80–96.

Diaz, R. J., & Schaffner, L. C. (1990). *Perspectives on the Chesapeake Bay, 1990* (M. Haire & E. C. Krome, Eds.).

Diaz, R., Rosenberg, R., D Ansell R N Gibson, C. A., Barnes, M., & Diaz, R. J. (1995). Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology. An Annual Review*, *33*, 245–303. https://www.researchgate.net/publication/236628341

Dolbeth, M., Cusson, M., Sousa, R., & Pardal, M. A. (2012). Secondary production as a tool for better understanding of aquatic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(7), 1230–1253. https://doi.org/10.1139/F2012-050

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., García Marquéz, J. R., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46.

https://doi.org/10.5194/egusphere-2025-1315
Preprint. Discussion started: 8 April 2025

Drexler, M., & Ainsworth, C. H. (2013). Generalized Additive Models Used to Predict Species Abundance in the Gulf of Mexico: An Ecosystem Modeling Tool. *PLoS ONE*, *8*(5). https://doi.org/10.1371/journal.pone.0064458

Edgar, G. J. (1990). The use of the size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. *Journal of Experimental Marine Biology and Ecology*, *137*(3), 195–214.

Ehrnsten, E., Norkko, A., Müller-Karulis, B., Gustafsson, E., & Gustafsson, B. G. (2020). The meagre future of benthic fauna in a coastal sea—Benthic responses to recovery from eutrophication in a changing climate. *Global Change Biology*, *26*(4), 2235–2250. https://doi.org/10.1111/gcb.15014

Ehrnsten, E., Norkko, A., Timmermann, K., & Gustafsson, B. G. (2019). Benthic-pelagic coupling in coastal seas – Modelling macrofaunal biomass and carbon processing in response to organic matter supply. *Journal of Marine Systems*, *196*, 36–47. https://doi.org/10.1016/j.jmarsys.2019.04.003

Frankel, L. T., Friedrichs, M. A. M., St-Laurent, P., Bever, A. J., Lipcius, R. N., Bhatt, G., & Shenk, G. W. (2022). Nitrogen reductions have decreased hypoxia in the Chesapeake Bay: Evidence from empirical and numerical modeling. *Science of the Total Environment*, *814*. https://doi.org/10.1016/j.scitotenv.2021.152722

Fujii, T., & Raffaelli, D. (2008). Sea-level rise, expected environmental changes, and responses of intertidal benthic macrofauna in the Humber estuary, UK. *Marine Ecology Progress Series*, *371*, 23–35. https://doi.org/10.3354/meps07652

Fulford, R. S., Breitburg, D. L., Newell, R. I. E., Kemp, W. M., & Luckenbach, M. (2007). Effects of oyster population restoration strategies on phytoplankton biomass in Chesapeake Bay: a flexible modeling approach. *Marine Ecology Progress Series*, *336*, 43–1.

Galimany, E., Lunt, J., Freeman, C. J., Houk, J., Sauvage, T., Santos, L., Lunt, J., Kolmakova, M., Mossop, M., Domingos, A., Phlips, E. J., & Paul, V. J. (2020). Bivalve feeding responses to microalgal bloom species in the Indian River Lagoon: the potential for top-down control. *Estuaries and Coasts*, *43*(6), 1519–1532. https://doi.org/10.1007/s12237-020-00746-9

Ganju, N. K., Brush, M. J., Rashleigh, B., Aretxabaleta, A. L., del Barrio, P., Grear, J. S., Harris, L. A., Lake, S. J., McCardell, G., O'Donnell, J., Ralston, D. K., Signell, R. P., Testa, J. M., & Vaudrey, J. M. P. (2016). Progress and challenges in coupled hydrodynamic-ecological estuarine modeling. *Estuaries and Coasts*, *39*(2), 311–332. https://doi.org/10.1007/s12237-015-0011-y

https://doi.org/10.5194/egusphere-2025-1315
Preprint. Discussion started: 8 April 2025

Garcia, H. E., & Gordon, L. I. (1992). Oxygen solubility in seawater: Better fitting equations. *Limnology and Oceanography*, *37*(6), 1307–1312. https://doi.org/10.4319/lo.1992.37.6.1307

Grant, J., & Thorpe, B. (1991). Effects of suspended sediment on growth, respiration, and excretion of the soft-shell clam (Mya arenaria). *Canadian Journal of Fisheries and Aquatic Sciences*, *48*(7).

Grebmeier, J. M., Bluhm, B. A., Cooper, L. W., Denisenko, S. G., Iken, K., Kędra, M., & Serratos, C. (2015). Time-series benthic community composition and biomass and associated environmental characteristics in the Chukchi Sea during the RUSALCA 2004-2012 Program. *Oceanography*, *28*(3), 116–133. https://doi.org/10.2307/24861905

Grüss, A., Drexler, M., & Ainsworth, C. H. (2014). Using delta generalized additive models to produce distribution maps for spatially explicit ecosystem models. *Fisheries Research*, *159*, 11–24. https://doi.org/10.1016/j.fishres.2014.05.005

Guisan, A., Edwards, T. C., & Hastie, T. (2002). Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling*, *157*(2–3), 89. www.elsevier.com/locate/ecolmodel

Hagy, J. D. (2002). *Eutrophication, hypoxia and trophic transfer efficiency in Chesapeake Bay* [Doctoral dissertation, University of Maryland, College Park]. https://www.researchgate.net/publication/237005296

Harding, L. W., & Perry, E. S. (1997). Long-term increase of phytoplankton biomass in Chesapeake Bay, 1950-1994. *Marine Ecology Progress Series*, *157*, 39–52.

Hartwell, S. I., Wright, D. A., Takacs, R., & Hocutt, C. H. (1991). Relative respiration and feeding rates of oyster and brackish water clam in variously contaminated waters. *Marine Pollution Bulletin*, *22*(4), 191–197.

Hastie, T., & Tibshirani, R. (1987). Generalized additive models: some applications. *Journal of the American Statistical Association*, *82*(398).

Hauke, J., & Kossowski, T. (2011). Comparison of values of Pearson's and Spearman's correlation coefficients on the same sets of data. *Quaestiones Geographicae*, *30*(2), 87–93. https://doi.org/10.2478/v10117-011-0021-1

Herrmann, M., Najjar, R. G., Da, F., Friedman, J. R., Friedrichs, M. A. M., Goldberger, S., Menendez, A., Shadwick, E. H., Stets, E. G., & St-Laurent, P. (2020). Challenges in quantifying air-water carbon dioxide flux using estuarine water quality data: Case study for Chesapeake Bay. *Journal of Geophysical Research: Oceans*, *125*(7). https://doi.org/10.1029/2019JC015610

https://doi.org/10.5194/egusphere-2025-1315
Preprint. Discussion started: 8 April 2025

Herrmann, M., Najjar, R. G., Kemp, W. M., Alexander, R. B., Boyer, E. W., Cai, W. J., Griffith, P. C., Kroeger, K. D., McCallister, S. L., & Smith, R. A. (2015). Net ecosystem production and organic carbon balance of U.S. East Coast estuaries: A synthesis approach. *Global Biogeochemical Cycles*, *29*(1), 96–111. https://doi.org/10.1002/2013GB004736

Hinson, K. E., Friedrichs, M. A. M., St-Laurent, P., Da, F., & Najjar, R. G. (2022). Extent and causes of Chesapeake Bay warming. *Journal of the American Water Resources Association*, *58*(6), 805–825. https://doi.org/10.1111/1752-1688.12916

Hirsch, R. M., Moyer, D. L., & Archfield, S. A. (2010). Weighted regressions on time, discharge, and season (WRTDS), with an application to Chesapeake Bay river inputs. *Journal of the American Water Resources Association*, *46*(5), 857–880. https://doi.org/10.1111/j.1752-1688.2010.00482.x

Holland, A. F., Shaughnessy, A. T., & Hiegel, M. H. (1987). *Long-Term Variation in Mesohaline Chesapeake Macrobenthos: Spatial and Temporal Patterns Bay* (Vol. 10, Issue 3).

Hopkins, S. H., Anderson, J. W., & Horvath, K. (1973). *The brackish water calm Rangia cuneata as an indicator of ecological effects of salinity changes in coastal waters*.

Hopkinson, C. S., & Smith, E. M. (2004). Estuarine respiration: an overview of benthic, pelagic, and whole system respiration. *Respiration in Aquatic Ecosystems*, 122–146.

Humphreys, M. P., Lewis, E. R., Sharp, J. D., & Pierrot, D. (2022). PyCO2SYS v1.8: Marine carbonate system calculations in Python. *Geoscientific Model Development*, *15*(1), 15–43. https://doi.org/10.5194/gmd-15-15-2022

Irby, I. D., Friedrichs, M. A. M., Da, F., & Hinson, K. E. (2018). The competing impacts of climate change and nutrient reductions on dissolved oxygen in Chesapeake Bay. *Biogeosciences*, *15*(9), 2649–2668. https://doi.org/10.5194/bg-15-2649-2018

Jakubowska, M., & Normant-Saremba, M. (2015). The effect of CO2-induced seawater acidification on the behaviour and metabolic rate of the Baltic clam Macoma balthica. *Annales Zoologici Fennici*, *52*(5–6), 353–367. https://doi.org/10.5735/086.052.0509

Jansson, A., Norkko, J., Dupont, S., & Norkko, A. (2015). Growth and survival in a changing environment: Combined effects of moderate hypoxia and low pH on juvenile bivalve Macoma balthica. *Journal of Sea Research*, *102*, 41–47. https://doi.org/10.1016/j.seares.2015.04.006

Jansson, A., Norkko, J., & Norkko, A. (2013). Effects of reduced pH on Macoma balthica larvae from a system with naturally fluctuating pH-dynamics. *PLoS One*, *8*(6). https://doi.org/10.1371/journal.pone.0068198

Kemp, W. M., Boynton, W. R., Adolf, J. E., Boesch, D. F., Boicourt, W. C., Brush, G., Cornwell, J. C., Fisher, T. R., Glibert, P. M., Hagy, J. D., Harding, L. W., Houde, E. D., Kimmel, D.

https://doi.org/10.5194/egusphere-2025-1315
Preprint. Discussion started: 8 April 2025

G., Miller, W. D., Newell, R. I. E., Roman, M. R., Smith, E. M., & Stevenson, J. C. (2005). Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Marine Ecology Progress Series*, *303*, 1–29. www.int-res.com

Kemp, W. M., Smith, E. M., Marvin-DiPasquale, M., & Boynton, W. R. (1997). Organic carbon balance and net ecosystem metabolism in Chesapeake Bay. *Marine Ecology Progress Series*, *150*, 229–248.

Kroeker, K. J., Kordas, R. L., Crim, R., Hendriks, I. E., Ramajo, L., Singh, G. S., Duarte, C. M., & Gattuso, J. P. (2013). Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Global Change Biology*, *19*(6), 1884–1896. https://doi.org/10.1111/gcb.12179

Little, S., Wood, P. J., & Elliott, M. (2017). Quantifying salinity-induced changes on estuarine benthic fauna: The potential implications of climate change. *Estuarine, Coastal and Shelf Science*, *198*, 610–625. https://doi.org/10.1016/j.ecss.2016.07.020

Llansó, R. J. (2002). *Methods for calculating the Chesapeake Bay benthic index of biotic integrity*. http://www.baybenthos.versar.com

Llansó, R. J., & Scott, L. (2011). *Chesapeake Bay water quality monitoring program: Long-term benthic monitoring and assessment component, quality assurance project plan, 2011–2012*.

Llansó, R. J., & Zaveta, D. (2017). *Chesapeake Bay water quality monitoring program: Long-term benthic monitoring and assessment component level 1 comprehensive report, July 1984 – December 2016 (Volume 1)*.

Marsh, A. G., & Tenore, K. R. (1990). The role of nutrition in regulating the population dynamics of opportunistic, surface deposit feeders in a mesohaline community. *Limnology and Oceanography*, *35*(3), 710–724. https://doi.org/10.4319/lo.1990.35.3.0710

Mo, C., & Neilson, B. (1994). Standardization of oyster soft tissue dry weight measurements. *Water Research*, *28*(1), 243–246.

Murphy, R. R., Kemp, W. M., & Ball, W. P. (2011). Long-term trends in Chesapeake Bay seasonal hypoxia, stratification, and nutrient loading. *Estuaries and Coasts*, *34*(6), 1293–1309. https://doi.org/10.1007/s12237-011-9413-7

Murphy, R. R., Perlman, E., Ball, W. P., & Curriero, F. C. (2015). Water-distance-based kriging in Chesapeake Bay. *Journal of Hydrologic Engineering*, *20*(9). https://doi.org/10.1061/(asce)he.1943-5584.0001135

Najjar, R. G., Herrmann, M., Cintrón Del Valle, S. M., Friedman, J. R., Friedrichs, M. A. M., Harris, L. A., Shadwick, E. H., Stets, E. G., & Woodland, R. J. (2020). Alkalinity in tidal tributaries of the Chesapeake Bay. *Journal of Geophysical Research: Oceans*, *125*(1). https://doi.org/10.1029/2019JC015597

https://doi.org/10.5194/egusphere-2025-1315
Preprint. Discussion started: 8 April 2025

Nakamura, Y., & Kerciku, F. (2000). Effects of filter-feeding bivalves on the distribution of water quality and nutrient cycling in a eutrophic coastal lagoon. *Journal of Marine Systems*, *26*, 209–221. www.elsevier.nlrlocaterjmarsys

Newell, R. I. E. (1988). Ecological changes in Chesapeake Bay: are they the result of overharvesting the American oyster, Crassostrea virginica. *Understanding the Estuary: Advances in Chesapeake Bay Reserach*, *129*, 536–546.

Newell, R. I. E., & Ott, J. A. (2011). Macrobenthic communities and eutrophication. *Ecosystems at the Land-Sea Margin: Drainage Basin to Coastal Sea*, *55*, 265–293. https://doi.org/10.1029/ce055p0265

Ni, W., Li, M., Ross, A. C., & Najjar, R. G. (2019). Large projected decline in dissolved oxygen in a eutrophic estuary due to climate change. *Journal of Geophysical Research: Oceans*, *124*(11), 8271–8289. https://doi.org/10.1029/2019JC015274

Pearson, T. H., & Rosenberg, R. (1978). Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology: An Annual Review*, *16*, 229–311.

Phelps. (1994). *The Asiatic Clam (Corbicula fluminea) Invasion and System-Level Ecological Change in the Potomac River Estuary Near* (Vol. 17, Issue 3).

Rodil, I. F., Lohrer, A. M., Attard, K. M., Thrush, S. F., & Norkko, A. (2022). Positive contribution of macrofaunal biodiversity to secondary production and seagrass carbon metabolism. *Ecology*, *103*(4). https://doi.org/10.1002/ecy.3648

Rosenberg, R. (1995). Benthic marine fauna structured by hydrodynamic processes and food availibility. *Netherlands Journal of Sea Research*, *34*(4), 303–317.

Rousi, H., Korpinen, S., & Bonsdorff, E. (2019). Brackish-water benthic fauna under fluctuating environmental conditions: the role of eutrophication, hypoxia, and global change. *Frontiers in Marine Science*, *6*(JUL), 464. https://doi.org/10.3389/fmars.2019.00464

Schratzberger, M., & Ingels, J. (2018). Meiofauna matters: the roles of meiofauna in benthic ecosystems. *Journal of Experimental Marine Biology and Ecology*, *502*, 12–25. https://doi.org/10.1016/j.jembe.2017.01.007

Schwinghamer, P., Hargrave, B., Peer, D., & Hawkins, C. M. (1986). Partitioning of production and respiration among size groups of organisms in an intertidal benthic community. *Marine Ecology Progress Series*, *31*(2), 131–142.

Seitz, R. D., Dauer, D. M., Llansó, R. J., & Long, W. C. (2009). Broad-scale effects of hypoxia on benthic community structure in Chesapeake Bay, USA. *Journal of Experimental Marine Biology and Ecology*, *381*(SUPPL.). https://doi.org/10.1016/j.jembe.2009.07.004

https://doi.org/10.5194/egusphere-2025-1315
Preprint. Discussion started: 8 April 2025

Seitz, R., Lipcius, R. N., Olmstead, N. H., Seebo, M. S., & Lambert, D. M. (2006). Influence of shallow-water habitats and shoreline development on abundance, biomass, and diversity of benthic prey and predators in Chesapeake Bay. *Marine Ecology Progress Series*, *326*, 11–27.

Shchepetkin, A. F., & McWilliams, J. C. (2005). The regional oceanic modeling system (ROMS): A split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Modelling*, *9*(4), 347–404. https://doi.org/10.1016/j.ocemod.2004.08.002

Simon N. Wood. (2017). *Generalized Additive Models* (2nd ed.).

Smith, M., Paperno, R., Flaherty-Walia, K., & Markwith, S. (2023). Species Distributions in a Changing Estuary: Predictions Under Future Climate Change, Sea-Level Rise, and Watershed Restoration. *Estuaries and Coasts*, *46*(6). https://doi.org/10.1007/s12237-023-01219-5

Snelgrove, P. V. R. (1997). The importance of marine sediment biodiversity in ecosystem processes. *Ambio*, *26*(8), 578–583. https://doi.org/https://www.jstor.org/stable/4314672

Snelgrove, P. V. R. (1999). Snelgrove, P. V. (1999). Getting to the bottom of marine biodiversity: sedimentary habitats: ocean bottoms are the most widespread habitat on earth and support high biodiversity and key ecosystem services. *BioScience*, *42*(2), 129–138. www.jstor.org

Sousa, R., Antunes, C., & Guilhermino, L. (2008). Ecology of the invasive Asian clam Corbicula fluminea (Müller, 1774) in aquatic ecosystems: an overview. In *Annales de Limnologie-International Journal of Limnology* (Vol. 44, Issue 2, pp. 85–94). https://doi.org/10.1051/limn:2008017

St-Laurent, P., & Friedrichs, M. A. M. (2024a). An atlas for physical and biogeochemical conditions in the Chesapeake Bay. *SEANOE*.

St-Laurent, P., & Friedrichs, M. A. M. (2024b). On the sensitivity of coastal hypoxia to its external physical forcings. *Journal of Advances in Modeling Earth Systems*, *16*(1). https://doi.org/10.1029/2023MS003845

Sturdivant, S. K., Seitz, R. D., & Diaz, R. J. (2013). Effects of seasonal hypoxia on macrobenthic production and function in the Rappahannock River, Virginia, USA. *Marine Ecology Progress Series*, *490*, 53–68. https://doi.org/10.3354/meps10470

Testa, J. M., Faganeli, J., Giani, M., Brush, M. J., De Vittor, C., Boynton, W. R., Covelli, S., Woodland, R. J., Kovač, N., & Michael Kemp, W. (2020a). Advances in our understanding of Pelagic-Benthic Coupling. In T. C. Malone, A. Malej, & J. Faganeli (Eds.), *Coastal Ecosystems in Transition: A Comparative Analysis of the Northern Adriatic and Chesapeake Bay* (pp. 147–175). Wiley. https://doi.org/10.1002/9781119543626.ch8

https://doi.org/10.5194/egusphere-2025-1315
Preprint. Discussion started: 8 April 2025

Testa, J. M., Faganeli, J., Giani, M., Brush, M. J., De Vittor, C., Boynton, W. R., Covelli, S., Woodland, R. J., Kovač, N., & Michael Kemp, W. (2020b). Advances in our understanding of pelagic-benthic coupling. In T. C. Malone, A. Malej, & J. Faganeli (Eds.), *Coastal Ecosystems in Transition: A Comparative Analysis of the Northern Adriatic and Chesapeake Bay* (pp. 147–175). wiley. https://doi.org/10.1002/9781119543626.ch8

Thomsen, J., Haynert, K., Wegner, K. M., & Melzner, F. (2015). Impact of seawater carbonate chemistry on the calcification of marine bivalves. *Biogeosciences*, *12*(14), 4209–4220. https://doi.org/10.5194/bg-12-4209-2015

Tumbiolo, M. L., & Downing, J. A. (1994). An empirical model for the prediction of secondary production in marine benthic invertebrate populations. *Marine Ecology Progress Series*, *114*(1), 165–174.

Tuszer-Kunc, J., Normant-Saremba, M., & Rychter, A. (2020). The combination of low salinity and low temperature can limit the colonisation success of the non-native bivalve Rangia cuneata in brackish Baltic waters. *Journal of Experimental Marine Biology and Ecology*, *524*. https://doi.org/10.1016/j.jembe.2019.151228

Vaquer-Sunyer, R., & Duarte, C. M. (2008). Thresholds of hypoxia for marine biodiversity. *Proceeds of the National Academy of Sciences*, *105*(40), 15452–15457. www.pnas.org/cgi/content/full/

Waldbusser, G. G., Powell, E. N., & Mann, R. (2013). Ecosystem effects of shell aggregations and cycling in coastal waters: an example of Chesapeake Bay oyster reefs. *Ecology*, *94*(4), 895–903. https://doi.org/10.1890/12-1179.1

Weisberg, S., Ranasingiie, A., Schaffner Robert J Diaz, L. C., Dauer, D. M., & Frithsen, F. B. (1997). An estuarine benthic index of biotic integrity (B-IBI) for Chesapeake Bay. *Estuaries*, *20*(1), 149–158.

Wilson, J. G., & Fleeger, J. W. (2023). *Estuarine Ecology* (B. C. Crump, J. M. Testa, & K. H. Dunton, Eds.; 3rd ed.). Wiley.

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society Series B: Statistical Methodlogy*, *73*(1), 3–36. https://academic.oup.com/jrsssb/article/73/1/3/7034726

Woodland, R. J., Buchheister, A., Latour, R. J., Lozano, C., Houde, E., Sweetman, C. J., Fabrizio, M. C., & Tuckey, T. D. (2021). Environmental drivers of forage fishes and benthic invertebrates at multiple spatial scales in a large temperate estuary. *Estuaries and Coasts*, *44*(4), 921–938. https://doi.org/10.1007/s12237-020-00835-9

https://doi.org/10.5194/egusphere-2025-1315
Preprint. Discussion started: 8 April 2025

Woodland, R. J., & Testa, J. M. (2020). Response of Benthic Biodiversity to Climate-Sensitive Regional and Local Conditions in a Complex Estuarine System. In V. Lyubchich, Y. R. Gel, K. H. Kilbourne, T. J. Miller, N. K. Newlands, & A. B. Smith (Eds.), *Evaluating Climate Change IMpacts* (Vol. 1, pp. 87–22). CRC Press.

Zhang, Q., & Blomquist, J. D. (2018). Watershed export of fine sediment, organic carbon, and chlorophyll-a to Chesapeake Bay: Spatial and temporal patterns in 1984–2016. *Science of the Total Environment*, *619*, 1066–1078. https://doi.org/10.1016/j.scitotenv.2017.10.279

Zhang, Q., Fisher, T. R., Trentacoste, E. M., Buchanan, C., Gustafson, A. B., Karrh, R., Murphy, R. R., Keisman, J., Wu, C., Tian, R., Testa, J. M., & Tango, P. J. (2021). Nutrient limitation of phytoplankton in Chesapeake Bay: Development of an empirical approach for water-quality management. *Water Research*, *188*. https://doi.org/10.1016/j.watres.2020.116407

Zheng, G., & DiGiacomo, P. M. (2020). Linkages between phytoplankton and bottom oxygen in the Chesapeake Bay. *Journal of Geophysical Research: Oceans*, *125*(2). https://doi.org/10.1029/2019JC015650