



Acidification and nutrient management are projected to cause reductions in shell and tissue weights of oysters in a coastal plain estuary

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9 Abstract. Coastal acidification, warming, and nutrient management actions all alter water quality conditions that marine 10 species experience, with potential impacts to their physiological processes. Decreases in calcite saturation state (Ω_{Ca}) and food 11 availability, combined with warming water temperatures, pose a threat to calcifying organisms; however, the magnitude of 12 future changes in estuarine systems is challenging to predict and is not well known. This study aims to determine how and 13 where oysters will be affected by future acidification, warming, and nutrient reductions, and the relative effects of these 14 stressors. To address these goals, an oyster bioenergetics model for Eastern oysters (Crassostrea virginica) was embedded in a 3-D coupled hydrodynamic-biogeochemistry model implemented for two tributaries in the lower Chesapeake Bay. Model 15 16 simulations were forced with projected future conditions (mid-21st century atmospheric CO₂, atmospheric temperature, and 17 managed nutrient reductions) and compared with a realistic present-day reference run. Together, all three stressors are projected to reduce Ω_{Ca} and growth of ovster shell and tissue. Increased atmospheric CO₂ and temperature are both projected 18 19 to cause widespread reductions in Ω_{Ca} . The resulting reductions in oyster shell and tissue growth will be most severe along the 20 tributary shoals. Future warming during peak oyster growing seasons is projected to have the strongest negative influence on 21 tissue and shell growth, due to summer water temperatures reducing filtration rates, enhancing shell dissolution and oyster 22 respiration rates, and increasing organic matter remineralization rates, thus reducing food availability. Nutrient reductions will 23 exacerbate deficits in oyster food availability, contributing to further reductions in growth. Quantifying the effects of these 24 stressors provides insight on the areas in the lower bay where oysters will be most vulnerable to mid 21st-century conditions.

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Short summary. Under future acidification, warming, and nutrient management, substantial reductions in shell and tissue weights of Eastern oysters are projected for the Chesapeake Bay. Lower oyster growth rates will be largely driven by reduced calcium carbonate saturation states and reduced food availability. Oyster aquaculture practices in the region will likely be affected, with site selection becoming increasingly important as impacts will be highly spatially variable.





30 1 Introduction

31 Anthropogenic climate change and its associated impacts on water quality may threaten marine organisms and 32 economic systems reliant on them. Oceanic uptake of increasing anthropogenic atmospheric carbon dioxide (CO₂) causes a 33 decrease in seawater pH and saturation states of calcium carbonate, a phenomenon known as ocean acidification (Caldeira and Wickett, 2003; Doney et al., 2009). Globally, the ocean has absorbed about 30% of anthropogenic atmospheric CO₂ since pre-34 35 industrial times (Gruber et al., 2019), and open-ocean surface pH is anticipated to decrease by 0.3 units on average relative to 36 the 2010s by the end of the century under 'business-as-usual' conditions (Riahi et al., 2011; IPCC, 2019). The percent volume of ocean water undersaturated with calcite ($\Omega_{Ca} < 1$) is predicted to expand to 91% by 2100 from 76% in the 1990s (Caldeira 37 38 and Wicket, 2005; Gattuso et al., 2015).

39 Since estuaries have lower and more variable pH than the open-ocean, the effects of increased CO₂ on estuarine water quality and biota are often amplified. In coastal and estuarine systems, acidification may be exacerbated by local-level 40 41 processes, such as the input of acidic freshwater and nutrient runoff from precipitation, a process termed coastal acidification 42 (Salisbury et al., 2008; Wallace et al., 2014; Carstensen and Duarte, 2019). Freshwater has relatively low total alkalinity (TA), 43 or buffering capacity, so areas in estuaries with greater relative freshwater influence cannot resist changes to pH as easily as 44 more saline or open-ocean waters (Hasler et al., 2018; Pacella et al., 2024). Eutrophication, the increased rate of organic matter 45 input to a system (Nixon, 1995), may drive large variations in local pH and overall water quality. Elevated nutrient inputs 46 cause pH to increase in surface waters due to higher primary productivity, which will reduce surface acidification; however, 47 pH will decrease in deeper bottom waters as the additional organic matter sinks and is remineralized (Cai et al., 2021). Management actions to reduce eutrophication and improve water quality in bottom waters have been successful but may also 48 49 enhance acidification in shallow surface waters by lowering primary productivity (Borges and Gypens, 2010). The overall 50 effect of future changes in nutrient inputs on coastal biogeochemistry is thus unclear.

51 Warming, another driver of biogeochemical change in coastal waters, may compound or offset the effects of increased 52 atmospheric CO₂ on coastal ecosystems. The global ocean has absorbed approximately 93% of the atmospheric heat produced 53 by anthropogenic activity, leading to a global sea surface temperature increase of 0.7°C since 1900 (Jewett and Romanou, 54 2017). Ocean warming is expected to continue, with global averages increasing by 2.7°C by 2100 and greater increases expected in shallow coastal regions (Jewett and Romanou, 2017). Coastal acidification may accelerate as warming of coastal 55 56 waters increases rates of biogeochemical processes; increased respiration rates may drive larger diel variations in pH, dissolved 57 oxygen, and associated water quality (Du et al., 2018; Tian et al., 2021). Therefore, it is vital to understand how warming will interact with acidification to predict local changes in water quality and health of coastal organisms. 58

59 Characterizing spatiotemporal patterns of acidification in estuarine waters is important, as negative impacts of 60 acidification on the biology of marine organisms may be substantial. Acidification disrupts the formation of calcium carbonate 61 (CaCO₃) during shell-building, i.e., biocalcification, which is a vital process for growth and survival of many aquatic 62 invertebrate species (e.g., Orr et al., 2005; Gazeau et al., 2007; Dong et al., 2023). Under acidified conditions, water





concentrations of CO₂ and H⁺ increase, and concentrations of carbonate ions ([CO₃²⁻]) decrease. A low ambient [CO₃²⁻] inhibits 63 calcifying organisms from forming CaCO₃ for their shells, as more energy is required to precipitate CO₃²⁻ from acidified waters 64 65 (e.g., Guinotte and Fabry, 2008; Lutier et al., 2022; Matoo et al., 2020; Mederios and Souza, 2023). Low Ω_{Ca} may also lead to net dissolution of CaCO₃, leading to weaker shells and greater juvenile susceptibility to predation (e.g., Waldbusser et al., 66 67 2011; Amaral et al., 2012; Barclay et al., 2020). Acidification may further reduce shell growth through adverse physiological effects that limit energy availability for calcification. Because acidification is often more extreme in estuaries, ovsters and 68 69 other commercially valuable coastal bivalve species experience stronger effects of climate change than organisms living in 70 open-ocean environments (Poach et al., 2019; Melzner et al., 2020; Cai et al., 2021;). Prior experiments have revealed negative effects of acidification, warming, and nutrient reductions on oyster biocalcification and growth (Beniash et al., 2010; 71 72 Waldbusser et al., 2011; Gobler and Talmage, 2014), but it is yet to be determined how the impacts of these stressors on oyster 73 shell and tissue growth will vary spatially in highly dynamic systems.

74 The Chesapeake Bay is an excellent study system for examining the interacting influences of acidification, warming, and nutrient reductions (hereafter referred to collectively as "future stressors") on estuarine biogeochemistry and the organisms 75 76 living there. The bay exhibits high temporal and spatial variability in pH due to seasonal phytoplankton blooms, eutrophication, and acidic freshwater input (Da et al., 2021; St-Laurent et al., 2020; Kemp et al., 2005; Cai et al., 2021). From the mid-1980s 77 78 to mid-2010s, surface waters in the upper bay experienced pH increases between +0.2 and +0.4 pH units in early spring and 79 fall due to increased riverine TA from reduced acid mine drainage and lowered nitrate inputs, while surface waters in the 80 nitrogen-limited middle bay decreased up to -0.24 pH units during late spring and summer as a result of decreased primary 81 production (Da et al., 2021). Over the same time period, the bay warmed by 0.24 ± 0.15 °C per decade (Hinson et al., 2022), 82 more than double the average rate of warming for the upper 75m of the global ocean (Rhein et al., 2013). Warming has also led to more severe hypoxia (Irby et al., 2018; Ni et al., 2020; Frankel et al., 2022; Hinson et al., 2023). In 2010, the 83 84 Environmental Protection Agency mandated a Total Maximum Daily Load (TMDL) of pollutants from point and non-point 85 sources to be achieved by 2025 (EPA, 2010). As nutrient reductions negatively affect pH in surface waters of the bay (Shen et 86 al., 2020; Da et al., 2021), achieving the TMDLs may actually worsen acidification in shallow and near-shore regions. Much 87 of the research effort devoted to characterizing present-day carbonate chemistry and its historical trends has focused on the 88 mainstem and upper Chesapeake Bay (Cai et al., 2017; Shen et al., 2020, Su et al., 2020), and less is known about these 89 conditions throughout the tributaries of the lower bay (Shadwick et al., 2019).

The combined effects of future stressors will impact calcifying organisms in the lower Chesapeake Bay as well as the economic systems reliant upon them. The Eastern oyster *Crassostrea virginica* (Gmelin, 1791) is a foundation species native to the bay (Dayton, 1972). Eastern oyster aquaculture in this region has grown rapidly in the past few decades, with Virginia becoming the third most productive oyster fishery in 2018 (Hudson, 2019), largely a result of the development of diseaseresistant oyster strains (Frank-Lawale et al., 2014). Negative impacts of acidification on aquaculture practices in other parts of the world (Barton et al., 2015) have already stirred concern over the vulnerability of oysters in the Chesapeake Bay. For example, in the Pacific Northwest, major larval mortality occurred at a shellfish hatchery following an upwelling event that





97 lowered pH and Ω of aragonite, which had cascading impacts on the oyster industry all along the West Coast (Barton et al., 98 2015). While most effects of acidification on aquaculture have been observed in oyster larvae in hatcheries, fewer studies have 99 examined acidification's influence on adult oysters when deployed in the field. Water quality conditions within oyster farms 100 can be highly spatially variable, so the impacts of acidification may vary with growing conditions (Saavedra et al., 2024; 101 Simpson et al., 2024). To support the future of the oyster aquaculture industry in Chesapeake Bay, it is critical to identify 102 which areas in the bay will be most vulnerable to acidification at mid-century and how each driver of change contributes to 103 acidification and its impacts on growth.

104 This study addresses the following primary research question: How and where will carbonate chemistry and Eastern 105 oyster growth in the lower Chesapeake Bay change in the future and which future stressors will drive these changes? A three-106 dimensional hydrodynamic-biogeochemical model is coupled with an oyster bioenergetics model and is applied to two major 107 Virginia tributaries of the Chesapeake Bay. The model provides detailed information on present-day environmental conditions, and when combined with climate projections from Earth System Models, allows for simulations of the independent and 108 interacting influences of future environmental change on carbonate chemistry and Eastern oysters. This study provides insight 109 110 into which areas are most vulnerable to mid 21st-century acidification and how acidification, warming, and nutrient loading 111 may each impact oyster growth in isolation as well as via simultaneous co-stressors.

112 2 Methods

113 2.1 Model description

114 2.1.1 Hydrodynamic model

115 This study uses the three-dimensional hydrodynamic Regional Ocean Modeling System (ROMS; Shchepetkin and 116 McWilliams, 2005), implemented similarly to St-Laurent and Friedrichs (2024) but on a higher resolution grid focused on two of the lower Virginia Chesapeake Bay tributaries (Fig. 1). The model domain (Da et al., 2024) includes the York and 117 Rappahannock Rivers, as well as a portion of the mainstem shoal north of the Rappahannock. The model grid consists of 118 119 620x740 horizontal grid cells with a horizontal resolution of 120 m, allowing for greater resolution of coastlines than many other Chesapeake Bay model grids (Irby et al., 2016). The hydrodynamic model includes 20 terrain-following vertical levels 120 and two primary state variables: practical salinity and potential temperature. A wetting and drying scheme has been 121 122 implemented to represent water levels and currents in coastal grid cells (Warner et al., 2013; St-Laurent and Friedrichs, 2024).









126 2.1.2 Carbon and biogeochemistry model

127 The Estuarine-Carbon-Biogeochemistry model (ECB) embedded in ROMS and used in this study has previously been 128 implemented in the Chesapeake Bay (Feng et al., 2015; St-Laurent et al., 2020; Frankel et al., 2022; Hinson et al., 2023) as well as in the lower Virginia tributaries (Da et al., 2024). ECB simulates full carbon and nitrogen cycles of the lower trophic 129 levels, represented by the following state variables: nitrate, ammonium, phytoplankton and zooplankton nitrogen, small and 130 large detrital nitrogen and carbon, semi-labile and refractory dissolved organic nitrogen, DIC, TA, and dissolved oxygen (O₂). 131 132 Phytoplankton and zooplankton carbon and dissolved organic carbon (DOC) are calculated from established C:N ratios 133 (Redfield, 1934; Hopkinson et al., 1998). Biogeochemical processes include primary production, aggregation, sinking, basal metabolism, exudation, sloppy feeding, excretion, metabolism, nitrification/denitrification, remineralization, grazing, and 134 135 mortality. Additional biogeochemical sources and sinks are included in the bottom vertical level (e.g., burial, resuspension, 136 nitrification/denitrification, remineralization, sediment O2 and CO2 exchange). Light attenuation throughout the water column 137 is based on the diffuse attenuation coefficient (Kd), which is parameterized as a function of surface total suspended solids 138 (TSS; including inorganic and organic components) and salinity as a proxy for colored dissolved organic matter (Feng et al., 139 2015; Turner et al., 2021). The sediment transport module within ECB is comprised of two vertical seabed layers that simulate 140 four suspended sediment size classes (Turner et al., 2021).





141 The carbon module within ECB has been fine-tuned in this implementation of the model, allowing for greater performance in carbonate system simulations (Da et al., 2024). The model grid includes tidal wetlands along the York River 142 143 based on estimated wetland areas (Mitchell et al., 2017), which further contribute to TA fluxes through sulfate reduction in 144 sediments (Raymond et al., 2000; Najjar et al., 2020). Ω_{Ca} is calculated from DIC, TA, temperature, and salinity using CO2SYS (van Heuven et al., 2011) using the equilibrium constants of Cai and Wang (1998) as they are suitable for both fresh and 145 estuarine waters (Dinauer and Mucci, 2017; Herrmann et al., 2020). Although submerged aquatic vegetation is a possible 146 147 source of CaCO₃ (Mazarrasa et al., 2015; Su et al., 2020), CaCO₃ precipitation and dissolution are not simulated in ECB due 148 to both insufficient observations and low submerged aquatic vegetation presence throughout the model domain (Orth et al., 149 1998; Moore et al., 2009).

150 Several updates have been made in this implementation of ROMS-ECB to better represent oxygen and primary production dynamics in the lower Virginia tributaries. The minimum phytoplankton growth rate has been increased to 2.15 d-151 152 ¹, and the growth rate is limited in the fresh portion of the tributaries using a Michaelis-Menten function of salinity and a halfsaturation of 1.5 (Da et al., 2024). The sediment bed climatology from Moriarty et al. (2021) has been adjusted to better 153 154 represent the sand class distributions published in Nichols (1991) and observations taken by the USGS (Reid et al., 2005). 155 Specifically, the changes include a greater percentage of small clay-rich flocs throughout the main stem of the York River as 156 well as more sand and large silt-rich flocs in the Rappahannock River. Previously, the sediment module assumed the same 157 critical shear stress for large silt-rich flocs, small clay-rich flocs, and unaggregated mud; here, the critical shear stress of smaller particles is lower than larger particles, meaning smaller particles resuspend more easily. The updated critical shear stress 158 159 coefficient for erosion and deposition is 0.5 Pa for large silt-rich flocs and 0.4 Pa for both small clay-rich flocs and unaggregated mud, which represent a small portion of the sediment bed. The ballasting formulation of Turner et al. (2021) has 160 also been added to simulate the increase in particle sinking rates due to the aggregation of particles in turbid waters. 161

162 2.1.3 Oyster bioenergetics model

163 As part of this study, the oyster bioenergetics model EcoOyster (Brush and Kellogg, 2018; Kellogg et al., 2018) has 164 been one-way coupled to ROMS-ECB in the deepest (bottom) level (see Supplementary Tables S1-S4 for EcoOyster 165 equations). The one-way coupling allows the focus in this analysis to be on the effect of future climate change on oyster 166 growth, rather than the effect of oyster growth on water quality, which has been previously studied in the Chesapeake Bay 167 (e.g., Gawde et al., 2024). By focusing on the deepest vertical level of the model, the assumption is that ovsters are growing on the bottom, and not inside floating cages. The coupled model, referred to hereafter as ROMS-ECBO, simulates daily somatic 168 169 tissue dry weight, gonadal tissue dry weight, shell dry weight, and shell height of diploid and triploid oysters as a function of 170 filtration, respiration, egestion, allocation to reproduction, calcification, and dissolution (Brush and Kellogg, 2018; Kellogg et 171 al., 2018; Rivest et al., 2023). For the purpose of this study, only diploid oysters were included, as the triploid allometric 172 equations are not as well constrained. Tissue growth rates depend on individual weight together with temperature, salinity, O₂, TSS, and particulate organic carbon (POC) from ROMS-ECB. Chla is required for the filtration function and is calculated 173





from ROMS-ECB phytoplankton carbon and Kd, in combination with seasonal carbon:chl*a* ratios that are computed using equations from Cerco and Noel (2004). The calcification function includes a threshold value of $\Omega_{Ca} = 0.93$, determined through laboratory experiments with Eastern oysters (Rivest et al., 2023).

177 The EcoOyster equations were developed from a meta-analysis of existing oyster bioenergetics models and laboratory experiments with diploid oysters (Brush and Kellogg, 2018; Kellogg et al., 2018; Rivest et al., 2023). Allometric relationships 178 179 between shell dry weight, tissue dry weight, and shell height used for initial conditions were derived from observational data 180 in the Chesapeake Bay (VOSARA, 2024). Total dry tissue weight is calculated as the sum of somatic tissue weight and gonadal 181 weight. Reproduction is simulated through gonadal weight, a function of growth of gonadal tissue, resorption of gonadal tissue, 182 and spawning (Hofmann et al., 1994). Somatic tissue weight is a function of assimilation, respiration, growth of gonadal tissue, 183 and resorption of gonadal tissue. Assimilation is a function of filtration and POC. Filtration is a function of a maximum 184 filtration rate based on tissue weight, limited by sub-optimal temperature, salinity, TSS, O₂, and chla (Cerco and Noel, 2005; Fulford et al., 2007; Ehrich and Harris, 2015). The optimal temperature for oyster filtration (Topt) is set to 27 °C (Jordan, 1987). 185 Filtration is also multiplied by p, a tunable factor representing the proportion of computed filtration actually performed by 186 187 oysters, which accounts for processes excluded from the model such as time spent filtering and is constrained by published 188 growth rates. Respiration is a function of tissue weight, temperature, and assimilation. While filtration has a temperature 189 limitation, respiration increases exponentially with temperature (Fig. S1). Tissue growth functions are not affected by 190 carbonate chemistry variables, as experimental studies have found that neither filtration (Lemasson et al., 2018) nor respiration 191 (Beniash et al., 2010; Matoo et al., 2013) of oysters are affected by pH changes; however, weight-specific net calcification is a function of Ω_{Ca} and temperature (Rivest et al., 2023). Shell growth is a function of both total tissue weight and net 192 193 calcification.

194 2.2 Present day reference simulation

195 A realistic reference simulation was generated to represent 2017 conditions. The year 2017 was chosen for 196 atmospheric, terrestrial, and open-ocean boundary conditions as this represents a relatively typical hydrological year. 197 Atmospheric forcings (air temperature, long- and short-wave radiation, precipitation, winds, dewpoint temperature, and air 198 pressure) are obtained from the ERA5 atmospheric reanalysis (Copernicus Climate Change Service, 2017; Hersbach et al., 199 2020). Surface atmospheric variables are available at 3-hourly intervals with a 0.25° resolution and are interpolated to a 0.2° grid. Terrestrial inputs of freshwater, nitrogen, carbon, and sediment are derived from the Phase 6 CBP Watershed Model 200 201 (CBPWM; Bhatt et al., 2023) and USGS data. Daily estimates of freshwater discharge, water temperature, and loadings of 202 nitrate, ammonium, organic nitrogen, and four classes of sediment from the CBPWM were concatenated to 74 locations throughout the model domain. To compute carbon loadings, constant carbon-to-nitrogen ratios are used, specifically 10:1 for 203 204 dissolved organic matter (Hopkinson et al., 1998) and 6.625:1 for particulate organic matter (Redfield, 1934). Riverine TA concentrations are computed as in Da (2023), using monthly-varying linear relationships between historical USGS 205 observations of discharge and USGS TA estimates determined using the Weighted Regression on Time, Discharge, and Season 206





(WRTDS; Hirsch et al., 2010) approach. Riverine DIC is calculated from daily riverine TA and daily DIC:TA ratios, linearly
interpolated from the monthly climatology of USGS WRTDS DIC:TA in each tributary. As in Da (2023), open boundary
conditions are derived from a recent 600 m resolution whole-bay implementation of ROMS (St-Laurent and Friedrichs, 2024).
Initial conditions for the six-month spin-up were derived from previous model results (Da et al., 2024).

Since spring-spawned oysters are typically deployed in late spring through summer on oyster farms, the reference run was started on July 1st and spanned one full year, ending June 30th of the following year. Oyster sizes were initialized based on shell height approximations of a typical spring-spawned oyster at deployment in July (i.e., a few months old). Starting dry tissue weight was assumed to be 0.001 g for all oysters, back-calculated from the approximate height of an oyster at the time of deployment. Starting shell dry weights and heights were calculated from allometric relationships to be 0.144 g and 11.6 mm, respectively.

217 **2.3** Comparison of reference simulation to in situ observations

In situ water quality monitoring observations are available since 1984 throughout the Chesapeake Bay. Specifically, 218 219 the Chesapeake Bay Program's Water Quality Monitoring Program (CBP WQMP) conducts cruises in the Bay and its tributaries. On average, stations are sampled once monthly, with the exception of June through August in the mainstem, when 220 sampling occurs twice. In this study, measurements of water temperature, salinity, O₂, pH (NBS scale), TSS, and POC are 221 222 used from 16 CBP stations throughout the model domain, with depths ranging from 5 to 16 m (Fig. 1a; CBP, 2024). For all variables except TSS and POC, measurements are taken in situ using a YSI or Hydrolab® sonde roughly every one to two 223 224 meters of the water column. TSS and POC are obtained from bottle samples at the surface, bottom, and at deeper stations, two 225 additional depths above and below the pycnocline. TSS is determined by filtering a known volume of water through a preweighted filter and then re-weighing the filter after filtration and drying. POC is determined through combustion of a filter 226 227 using an elemental analyzer (Olsen, 2012).

228 Model skill was evaluated by comparing results from the reference simulation to the CBP WOMP observations 229 described above. Hourly outputs from the four closest grid cells to each CBP station were spatially interpolated to obtain results at each respective station. Multiple variables in ECB at the bottom level of the model, including temperature, salinity, O₂, pH, 230 TSS, and POC, were compared with observations from the same station and time, within the bottom 10% of the water column 231 232 (Table 1). Model bias and root-mean squared difference (RMSD) were computed for all aforementioned variables. Seasonal 233 skill was also evaluated by comparing the 2017 reference run to CBP decadal averages (Figs. 2, 3). Decadal means were used 234 for these comparisons, as once-monthly or once-seasonally sampling dates in 2017 bias outputs toward conditions on the time 235 of the month when the measurements were taken in 2017, and the purpose of the comparison was to examine how the model 236 reproduces average seasonal variability.

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Figure 2. Seasonally-averaged bottom (a) temperature, (b) salinity, (c) dissolved oxygen, and (d) pH from the reference run. Circles represent seasonal decadal-averaged *in situ* observations at Chesapeake Bay Program stations (2010-2020). (DJF = winter, MAM = spring, JJA = summer, and SON = fall). Figure 1 ROMS-ECBO model domain of Chesapeake Bay tributaries illustrating (a) bathymetry in meters and locations of Chesapeake Bay Program water quality monitoring stations (red circles) and (b) bottom salinity zones.

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Figure 3. Seasonally-averaged bottom (a) POC and (b) TSS from output of the reference run of the ROMS-ECBO model. Circles represent seasonal decadal-averaged bottom measurements at Chesapeake Bay Program stations (2010-2020). (DJF = winter, MAM espring, JJA = summer, and SON = fall).

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When compared to 2017 WQMP observations and seasonal decadal averages, model skill of ROMS-ECBO is reasonably high (Table 1, Figs. 2, 3), and similar to other model implementations of the Chesapeake Bay (Irby et al., 2016). Temperature and salinity are reproduced relatively well year-round (Fig. 2a,b) with annual biases of only 0.2° C and -1.5, respectively (Table 1). Bottom O₂ and pH are slightly overestimated, exhibiting the greatest model-data misfit in the spring and summer months in the tributary channels (Fig. 2c,d). pH is overestimated by 0.2 units, which is within the accuracy of the electrode measurements. Observed POC concentrations in the York and upper Rappahannock are higher than simulated in the





model and exhibit very high spatial variability (Fig. 3a). Despite the high spatial variability of the TSS observations (Fig. 3b), mean TSS ($45 \pm 54 \text{ mg L}^{-1}$) is captured within 1.1 mg L⁻¹ by the model.

Growth rates determined using the *EcoOyster* equations and environmental outputs from ROMS-ECB were compared with oyster data collected in the York River (Paynter et al., 2008; Liddel, 2008; Kingsley-Smith et al., 2009; Degremont et al., 2012; Callam et al., 2016). Specifically, the tunable parameter (*p*) that limits oyster filtration was adjusted to provide a best match between the modeled oyster growth rates and the published rates. Multiple *p*-values were tested, and a value of *p*=0.15 resulted in modeled oyster growth that best matched published growth rates. The resulting shell growth predicted by the model was found to be close to the *in situ* data ($52.0 \pm 1.1 \text{ mm y}^{-1}$ and $51.3 \pm 2.9 \text{ mm y}^{-1}$ for the model and observation means and

265 standard deviations, respectively).

266Table 1. Model skill statistics (mean ± standard deviation) comparing bottom grid cells from the reference run to Chesapeake Bay267Program observations from the same station location and time, within the bottom 10% of the water column.

Variable	Model	Observation	Model Bias	RMSD ^a
Temperature (°C)	17.0 ± 9	16.7 ± 9	+ 0.2	0.7
n = 130				
Salinity	13.9 ± 7	15.4 ± 7	-1.5	2.7
n = 127				
Oxygen (mg O ₂ L ⁻¹)	8.0 ± 2.3	7.2 ± 2.9	+0.9	1.3
n = 130				
рН	7.8 ± 0.4	7.6 ± 0.4	+ 0.2	0.4
n = 74				
TSS (mg L ⁻¹)	44 ± 34	45 ± 54	-1.1	48.3
n = 74				
POC (g C m ⁻³)	0.7 ± 0.3	1.7 ± 2.1	-1.0	2.4
n = 74				

^aRMSD = root mean squared difference

269 2.4 Future simulations

In addition to the reference run, this study generated five future simulations (Table 2) to investigate the change in carbonate chemistry conditions and oyster growth resulting from three drivers of future change in the bay: increased atmospheric CO_2 (*AtmCO*₂), atmospheric warming (*Temp*), and reduced nutrient loading (*TMDL*). Model forcings were modified for each simulation to represent mid-century conditions. A *Combined Future* simulation was run including forcings of all future stressors, in addition to three sensitivity simulations to isolate the impacts of each stressor on oyster growth. Atmospheric CO_2 concentration for the *AtmCO*₂ and *Combined Future* simulations was set to 655 ppm, derived from the Coupled Model Intercomparison Project Phase 5 report RCP8.5 (business-as-usual) scenario projected for 50 years in the





future relative to the reference run (Meinshausen et al., 2011). Future atmospheric temperature for the Temp and Combined 277 278 Future simulations was obtained from the IPSL-CM5A-LR Earth System Model (Dufresne et al., 2013), statistically 279 downscaled with the Multivariate Adaptive Constructed Analogs method (Abatzoglou and Brown, 2012). IPSL-CM5A-LR 280 was selected as in Hinson et al. (2023), since it was deemed the most representative downscaled ESM of the 20 available. As in Hinson et al. (2023), the delta method was used to calculate the daily average change in atmospheric temperatures between 281 282 present-day and future conditions. To calculate this change, two 30-year climatologies, centered on 2000 and 2050 283 respectively, were computed and daily averaged 50-year differences between the two climatologies (Fig. 4) were added to the atmospheric temperatures used in the reference run. Future watershed inputs for the TMDL and Combined Future simulations 284 285 included a climatology of nitrate, ammonium, dissolved organic matter, and particulate organic matter concentrations, derived from a Phase 6 CBPWM 1991-2000 run using reduced nutrient concentrations assuming the TMDLs had been successfully 286 287 achieved (Bhatt et al., 2023). Freshwater discharge in this run was set to be identical to the reference run, to isolate the effects of lowered nutrient concentrations on water chemistry and oyster growth. Since future climate change is expected to impact 288 terrestrial inputs much less than future management actions (Irby et al., 2018), the direct impact of climate change on the 289 290 watershed is not considered in this analysis. A fifth simulation ($AtmCO_2 + Temp$) was run to compare the influences of local management actions to the combined drivers of climate change, which includes both future atmospheric CO2 concentration 291 292 and atmospheric temperature. Preliminary investigations revealed a minimal impact of sea level rise on Ω_{Ca} in the bay; 293 therefore, it was not included in the simulated climate change variables.

294

295	Table 2. Experimental design for future simulations conducted for comparison to reference run. Model forcings include a
296	combination of 2017 (reference) and 2067 (future) inputs of atmospheric CO2, atmospheric temperature, and terrestrial nutrient
297	loadings.

Future Simulation Name	Atmospheric CO ₂	Atmospheric Temperature	Terrestrial inputs
Combined Future	Future	Future	TMDL ^a
AtmCO ₂	Future	Reference	Reference
Тетр	Reference	Future	Reference
TMDL	Reference	Reference	TMDL
AtmCO ₂ + Temp	Future	Future	Reference

298 ^aTMDL (Total Maximum Daily Load) forcing includes inputs of nitrate, ammonium, and dissolved and particulate organic 299 matter under the assumption that the nutrient reduction goals (EPA, 2010) are met.







300Figure 4. Monthly-averaged 50-year atmospheric temperature differences over the ROMS-ECBO model domain calculated as301projections from 2050 minus those from 2000.





302 To generate open boundary conditions for each future simulation, a full bay model (St-Laurent and Friedrichs, 2024) 303 was run with the same atmospheric and river forcings as in this 120-meter model implementation. As in the reference run, all 304 future simulations were spun up for six months (January 1 – June 30) before beginning on July 1, but represent 50 years in the 305 future from the reference simulation (i.e., July 1, 2067). Initial conditions for all spin-ups are identical to the reference simulation. Analysis confirmed the effects of initial conditions are negligible by July 1. To examine results most relevant to 306 307 oysters, model output was extracted at locations that support oyster production, defined as all grid cells in which tissue weight 308 exceeded 1 g at the end of the reference run (i.e., one year of growth; Fig. S2). All results shown are from the bottom level of 309 the model, representing conditions similar to on-bottom or bottom cage aquaculture methods that are common in Virginia. 310 Spatial variation in model outputs across grid cells in the model domain is reported using standard deviation.

311 3 Results

312 **3.1 Reference run results**

313 In the present-day reference run, the environmental variables used as inputs to the oyster parameterizations exhibit 314 substantial seasonal (Fig. 5a-f) and spatial (Figs. 6, S3) variability. As expected, bottom temperature is highest in summer, reaching an average of 29.3 °C in July when averaged across grid cells that support oyster growth (Fig. 5a). Temperature is 315 higher in the shallower parts of the tributaries compared to the channels (Fig. S3a). Bottom salinity exhibits higher values in 316 317 the fall and winter, reaching a maximum average of 17.7 in October, and drops in the spring and summer to reach a minimum average of 12.3 in June (Fig. 5b). Annual average bottom salinity ranges from 0 to 26 throughout the model domain (Fig. S3b), 318 319 with the highest values in the southern areas in closest proximity to the open-ocean. The seasonal cycle for bottom POC is similar to that of temperature, peaking at 1.7 g C m⁻³ in June and dropping to 0.57 g C m⁻³ in January (Fig. 5c). Bottom POC 320 also varies widely throughout the model domain (Fig. 6a), with relatively higher values in the Rappahannock compared to the 321 322 York River, along the shoals of the tributaries, and along the western shoals of the mainstem Bay north of the Rappahannock. Ω_{Ca} exhibits an annual cycle similar to that of temperature and POC, reaching a maximum average of 3.2 in August and a 323 minimum average of 1.1 in January. Annual mean bottom Ω_{Ca} also varies widely throughout the model domain (Fig. 6d). 324 325 Generally, bottom Ω_{Ca} increases with salinity, with low to zero values in the tidal fresh portions of the upper tributaries and 326 higher values along the western shoals of the mainstem Chesapeake Bay. The opposite temporal pattern is seen in bottom O₂, which peaks at 12.3 mg L^{-1} in February and drops to an average of 6.3 mg L^{-1} in August (Fig. 5e). O₂ concentrations are highest 327 328 along the shoals and lowest in the deep channels (Fig. S3c). Bottom TSS concentrations exhibit tidal variability throughout 329 the year and are highest in the York River with much lower concentrations observed in the other portions of the model domain (Fig. S3d). Environmental conditions averaged annually across grid cells that support oyster growth are provided in Table 3, 330 331 and conditions averaged annually across all grid cells in the model domain are provided in Table S5.







332

Figure 5. Time series of daily bottom (a) temperature, (b) salinity, c) POC, (d) ΩCa, (e) shell weight, and (f) tissue weight, averaged
 over grid cells that support oyster growth in the reference run, for the present-day reference run (black line) and Combined Future
 simulation (blue line).

336









Figure 6. Annual mean bottom (a-c) POC and (d-f) Ω_{Ca} from (a,d) the present-day reference run, (b,e) the *Combined Future* simulation, and (c,f) the difference between (a) and (b), i.e., *Combined Future* minus reference.

340

341 Tissue and shell weights increase modestly from July through April, and the highest rates of increase are seen in May and June near the end of the one-year reference run (Fig. 5g,h). At the end of the reference run, the spatial patterns of shell and 342 343 tissue weight are nearly identical (Fig. 7), as tissue growth largely drives shell growth (Table S4). Both shell and tissue weights 344 are highest along the shoals of the York and Rappahannock Rivers (Fig. 7a,d) and low in the deeper waters where TSS 345 concentrations are high (Fig. S3d). A wider region of high shell and tissue weight appears in the Rappahannock, while the highest weights in the York are confined to a very narrow and shallow strip along the coastline. Shell and tissue weights are 346 higher along the southwestern than the northeastern coastlines of the tributaries, where the shoals are wider in both tributaries 347 (Fig. 1a). Oyster growth metrics averaged across grid cells that support oyster growth are provided in Table 4. 348





Table 3. Bottom environmental variables for each model simulation (annual mean ± standard deviation) for grid cells that support oyster growth in the reference run (defined as those with greater than 1g dry tissue weight after one year of growth; Fig. S2). Analogous results averaged over all model grid cells are shown in Table S5.

Model Simulation	Temperature (°C)	Salinity	POC (g C m ⁻³)	Ω_{Ca}	Dissolved Oxygen (mg O ₂ L ⁻¹)	TSS (mg L ⁻¹)
Reference	17.0 ± 0.7	15.7 ± 2.1	1.12 ± 0.1	2.5 ± 0.49	9.1 ± 0.6	11.4 ± 5.8
Combined	18.5 ± 0.8	16.0 ± 2.1	1.03 ± 0.1	1.6 ± 0.35	8.7 ± 0.6	11.1 ± 5.9
Future						
AtmCO ₂	17.0 ± 0.7	15.7 ± 2.1	1.12 ± 0.1	1.6 ± 0.35	9.1 ± 0.6	11.4 ± 5.8
Temp	18.5 ± 0.8	16.0 ± 2.1	1.07 ± 0.1	2.5 ± 0.41	8.8 ± 0.6	11.1 ± 5.9
TMDL	17.0 ± 0.7	15.7 ± 2.1	1.08 ± 0.1	2.4 ± 0.53	9.1 ± 0.6	11.2 ± 5.9
Temp + CO ₂	18.5 ± 0.8	16.0 ± 2.1	1.07 ± 0.1	1.7 ± 0.33	8.8 ± 0.6	11.1 ± 5.9

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Table 4. Modeled oyster characteristics from the end of each simulation (mean ± standard deviation) over grid cells that support oyster growth in the reference run (defined as those with greater than 1g dry tissue weight after one year of growth; Fig. S2).

Model Simulation	Shell Weight (g)	Tissue Weight (g)	Shell Thickness (g mm ⁻¹)
Reference	16.8 ± 10.9	2.2 ± 1.5	0.18 ± 0.08
Combined Future	5.4 ± 5.7	0.9 ± 0.8	0.07 ± 0.05
AtmCO ₂	10.5 ± 8.0	2.2 ± 1.5	0.12 ± 0.06
Тетр	9.7 ± 9.1	1.2 ± 1.1	0.10 ± 0.07
TMDL	13.1 ± 8.2	1.7 ± 1.2	0.15 ± 0.06
Temp + CO ₂	6.6 ± 7.1	1.2 ± 1.1	0.08 ± 0.06







Figure 7. (a-c) Shell weight and (d-f) tissue weight at the end of the one-year simulation from (a,d) the present-day reference run, (b,e) the *Combined Future* run, and (c,f) their difference, i.e., *Combined Future* minus reference.

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358 3.2 Results of Combined Future simulation
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All environmental variables examined exhibit change from the reference run in the *Combined Future* simulation. Temperature and salinity are projected to increase across the entire model domain (Fig. S3a,b). When averaged over the model domain, temperature is projected to increase by 1.5 ± 0.26 °C, and salinity is projected to increase by 0.21 ± 0.11 (Table S5). Bottom POC is projected to decrease by 0.07 ± 0.05 g C m³ (Table S5), with POC reductions predicted to be most pronounced in the mid- to upper tributaries (Fig. 6c). Mid-century bottom Ω_{Ca} is projected to be lower throughout most of the region, with an average reduction of 0.8 ± 0.19 over the whole model domain (Table S5). The spatial distribution of future Ω_{Ca} is generally consistent with present-day Ω_{Ca} patterns, and the greatest decreases are projected to occur in regions with the highest present-





day Ω_{ca} (Fig. 6 d,e,f). An average reduction in O₂ of 0.3 ± 0.08 mg L⁻¹ is predicted across the model domain (Table S5), which will be mostly spatially uniform (Fig. S3c). TSS is projected to be reduced by 0.20 ± 0.25 mg L⁻¹ with high spatial variability in the projected change (Fig. S3d).

369 Changes in environmental conditions do not occur uniformly throughout the year. Temporal changes in environmental conditions averaged across grid cells that support oyster growth are provided in Figure 5. Annually averaged increases in 370 371 temperature and salinity are the same when averaged over only grid cells that support oyster growth as they are when averaged 372 across the entire model domain (Tables 3, S5). The greatest temperature increases are projected to occur in the warmer months, 373 with an average increase of 1.6 °C predicted for June through August and an average increase of 1.2 °C predicted for December 374 through February. Bottom temperatures are projected to surpass the optimal temperature for oyster filtration (27 °C) primarily in July and August (Fig. 5a). Salinity increases are projected to be greatest at the beginning of the year, with an average increase 375 376 of 0.44 between January and March and an average increase of 0.20 for the remainder of the year (Fig. 5b). Bottom POC at grid cells that support oyster growth is expected to decrease slightly less than the average for the entire region (Tables 3, S5), 377 with the greatest reductions in the spring and summer and little to no change in the winter (Fig. 5c). For Ω_{Ca} , O₂, and TSS, 378 379 projected reductions are slightly greater at oyster growth sites than for the entire domain. Ω_{Ca} is projected to decrease by 0.9, with the greatest reductions expected to occur the warmer months (Fig. 5d). O_2 is projected to decrease year-round, though 380 with slightly greater reductions in the winter (Fig. 5e) and an annual average reduction of 0.4 mg O₂ L⁻¹ (Table 3). TSS is 381 382 projected to decrease annually by 0.3 mg L^{-1} (Table 3), mostly in the spring, due to lowered POC (Fig. 5f).

383 Modeled shell and tissue weights after one year of growth are projected to decline in all regions that exhibit present-384 day growth, with the most severe reductions (up to 100%) occurring along the York and Rappahannock River shoals (Figs. 7c,f, 8). One-year tissue weight will be reduced by 1.3 g, on average, representing a 60% reduction across grid cells that support 385 ovster growth (Table 4). Shell weight, which is largely driven by changes in tissue weight, is projected to be reduced by 11.4 386 387 g on average after one year of growth, representing a 68% reduction in average shell weight in regions that support oyster growth (Table 4). The greatest reduction in shell and tissue growth rates will occur in the warmer months near the end of the 388 389 one-year simulation (-0.1 g d⁻¹ from May through June), whereas the smallest change will occur in the winter months (-0.02 g 390 d⁻¹ from December through February), as the least growth occurs during that time (Fig. 5g,h). Shell thickness, calculated as the ratio of shell weight to shell height, will be reduced by 61% on average (0.11 g mm⁻¹; Table 4). 391

392 Declines in year one shell weight will vary throughout the model domain (Fig. 8), following relative changes in 393 bottom POC and Ω_{Ca} (Fig. 9). The mainstem has the most moderate reduction in shell weight relative to reference shell weight, with an average reduction of 31%, indicated by the slope of the scatterplot. Shell weights in the Rappahannock and York face 394 395 the steepest reductions relative to reference, with average reductions of 86% and 96%, respectively, and a large portion of 396 York oysters facing complete depletion of oyster tissue and shell in these locations (Fig. 9; indicated by proximity to 1:1 line). Proportional shell weight reductions in the mainstem are projected to correlate with POC reductions (Fig. 9a). For Ω_{Ca} in the 397 398 mainstem, a group of sites face the greatest proportional reductions when Ω_{Ca} reductions are the greatest. However, for sites 399 with lower proportional shell loss, the opposite trend is observed (Fig 9d). In the Rappahannock, higher POC reductions





400 coincide with slightly lower proportional shell loss (Fig. 9b). Sites with the largest reductions in POC primarily occur in the 401 York (Fig. 9c; see dark blue symbols on the 1:1 line), and the greatest proportional shell weight reductions coincide with the 402 greatest POC and Ω_{Ca} reductions (Fig. 9c,f). Similar results are found for tissue weight (not shown).



403

Figure 8. Difference in shell weight at the end of the one-year simulation between the *Combined Future* run and the reference run, i.e., *Combined Future* minus reference, colored by region. Each point represents a grid cell where oyster growth occurs in the

405i.e., Combined406reference run.







Reference Shell Weight (g)

Figure 9. Difference in shell weight at the end of the one-year simulation between the *Combined Future* run and the reference run colored by (a-c) change in POC and (d-f) change in bottom Ω_{Ca} (i.e. *Combined Future* minus reference) for grid cells that support oyster growth. Results are presented for (a,d) the mainstem shoal only, (b,e) the Rappahannock River only, and (c,f) the York River only.

411 **3.3 Results of individual future sensitivity simulations**

Four individual future sensitivity simulations were conducted to isolate the specific mechanisms (increased atmospheric CO₂, increased atmospheric temperature, and/or nutrient reductions) causing the projected changes described above in the *Combined Future* simulation. The *AtmCO*₂ sensitivity simulation produces substantial reductions in average bottom Ω_{Ca} (Fig. 10d) and, as expected, is not projected to substantially impact bottom temperature, salinity, POC, O₂, or TSS (Table 3; Figs. 10a, S4). The projected reduction in Ω_{Ca} is 0.9 when averaged over oyster growth sites (Table 3), 0.1 greater in magnitude than the average reduction for the entire model domain (Table S5), as greater reductions are expected along the shoals of the Rappahannock and mainstem shoal than the York and upper section of the Rappahannock (Fig. 10d). In this





419 AtmCO₂ simulation, shell weight is predicted to be most steeply reduced in the Rappahannock, with less impact in the York 420 and mainstem regions (Fig. 11a). At grid cells with oyster growth, AtmCO₂ produces a shell weight reduction of 6.3 g in 421 comparison to the reference simulation, but no change in tissue weight (Table 4). 422



Temp





Figure 10. Differences in annual averaged (a-c) bottom POC and (d-f) bottom Ω_{Ca} (d-f) for three sensitivity experiments: (a) AtmCO₂, (b) Temp, and (c) TMDL. Differences represent future results minus those from the present-day reference run.

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Figure 11 Differences in (a-c) shell weight and (d-f) tissue weight at the end of the one-year simulation for three sensitivity experiments: (a) AtmCO₂, (b) Temp, and (c) TMDL. Differences represent future results minus those from the present-day reference run.

429 The Temp sensitivity simulation produces changes in all environmental variables impacting oyster growth, with the exception of Ω_{Ca} (Tables 3, S5). Average changes in temperature, salinity, and TSS will be identical to those from the 430 431 Combined Future simulation (Tables S5, 3). Predicted reductions in POC and O₂ will be smaller in magnitude than in 432 Combined Future, though more severe than any other single sensitivity experiment (Table 3). Temperature and salinity will 433 increase across the entire model domain, with a greater salinity increase occurring in the Rappahannock and along the mainstem 434 shoal (Fig. S4a-c). TSS will decrease primarily in the channels of the lower York and Rappahannock and on the mainstem 435 shoal (Fig. S4d). POC reductions are expected to cover the majority of the model domain, with larger reductions in the upper Rappahannock (Fig. 10b). Slight increases in Ω_{Ca} are observed in shallow tidal creeks (Fig. 10e); however, no substantial 436





437 change in average Ω_{Ca} is predicted (Table 3, S5). O₂ at oyster grid cells will exhibit a similar but slightly smaller average 438 reduction compared to *Combined Future* (Table 3). Patterns of change in shell weight in the *Temp* sensitivity simulation 439 resemble those in the *AtmCO*₂ simulation (Fig. 11b), with additional reductions along the mainstem shoal and a greater 440 predicted mean reduction of 7.1 g, a 42% decrease at grid cells with oyster growth (Table 4). Unlike *AtmCO*₂, tissue weight 441 will decrease in *Temp*, by an average of 1 g, a 46% reduction (Table 4).

442 The TMDL sensitivity simulation produces a much smaller average change in environmental conditions than the 443 AtmCO₂ or Temp simulations (Tables S5, 3). TMDL does not substantially influence temperature, salinity, or O₂ (Tables S5, 444 3, Fig. S4), but produces POC and TSS reductions close to the averages for Temp (Tables S5, 3). While POC change in the 445 Temp simulation is concentrated in the deeper portions of the tributaries (Fig. 10b), the POC reductions in the TMDL simulation are concentrated along the shoals of the tributaries, with the greatest reductions in the upper Rappahannock (Fig. 10c). TSS 446 447 changes in TMDL are limited to the tributaries, occurring along the shoals of the Rappahannock and in patches throughout the York (Fig. S4d). Future change in Ω_{Ca} in this simulation is less than for AtmCO₂ and is largely confined to the upper 448 Rappahannock shoals and in shallow tidal creeks throughout the study region (Fig. 10f). Patterns of change in shell weight 449 450 will resemble AtmCO₂ and Temp in the tributaries, but no change is predicted along the mainstem shoal (Fig. 11c). The TMDL simulation produces reduced shell (3.7 g) and tissue (0.5 g) weights, with a smaller negative influence on shell and tissue 451 452 weight than *Temp* (Table 4; Fig. 11c, d).

Environmental conditions in the $AtmCO_2 + Temp$ simulation are nearly identical to those in the *Combined Future* simulation (Tables 3, S5), with the exception of Ω_{Ca} , which is slightly higher due to the absence of *TMDL*'s influence. As tissue growth is unaffected by Ω_{Ca} , tissue weight in this simulation is identical to that of the *Temp* simulation. Average shell weight reduction in $AtmCO_2 + Temp$ is 10.2 g, slightly greater than from $AtmCO_2$ alone, due to the combined influences of lowered tissue growth and lower Ω_{Ca} .

458 4 Discussion

459 This study provides high-resolution projections for oyster growing conditions and corresponding oyster growth in the 460 Chesapeake Bay, with a specific focus on two Virginia tributaries. A high-resolution hydrodynamic-biogeochemical model was coupled with an Eastern oyster bioenergetics model and forced with future projections for atmospheric CO₂, temperature, 461 462 and nutrient management. An overall reduction in Ω_{Ca} and oyster growth are predicted by mid-century throughout the study 463 region under the combined effects of all three future stressors. Specifically, the greatest reductions in oyster growth are 464 projected to occur in the York and Rappahannock Rivers, where unfavorable conditions for calcification will expand in the 465 future and where food availability will be strongly impacted by warming and nutrient reductions. Bottom conditions in the York and Rappahannock rivers, particularly in the upper portions, will likely be unsuitable for aquaculture at mid-century on 466 467 average, indicating climate change preparedness is critical for the oyster aquaculture industry.





468 4.1 Future projections of Ω_{Ca}

469 The magnitude of future change in Ω_{Ca} varies with present-day Ω_{Ca} conditions. Regions with high present-day Ω_{Ca} . 470 primarily the mainstem shoals, are projected to experience the greatest reductions because of their low partial pressure of CO₂ (pCO_2) relative to fresher waters. Biologically driven low pCO_2 water on mainstem shoals has a greater capacity for CO_2 471 472 uptake from the atmosphere than high pCO_2 water, which is causing the fresher tributaries to experience smaller increases in 473 DIC and smaller reductions in Ω_{Ca} . Acidic freshwater input often causes pCO₂ in the upper tributaries to exceed atmospheric 474 pCO₂, causing outgassing (Cai et al., 2017; Shen et al., 2019b; St-Laurent et al., 2020; Cai et al., 2021). Despite the lower 475 Rappahannock having a lower salinity than the lower York, it also has a lower DIC to TA ratio, so the rate at which the lower Rappahannock absorbs pCO_2 is higher (Da et al., 2021). Total alkalinity, or buffering capacity, is also lower in the lower 476 Rappahannock than the lower York, so the lower Rappahannock cannot resist changes in carbonate chemistry to the same 477 478 degree as the York. As a result, we observe the Rappahannock changing faster than the York. Since higher Ω_{Ca} regions will 479 experience greater reductions than lower Ω_{Ca} regions (Fig. 5), the overall spatial variability of Ω_{Ca} will be reduced by mid-480 century, and more areas will experience conditions that are unfavorable for oyster shell-building.

481 Although future atmospheric CO₂ and reduced nutrient loading will both contribute to Ω_{Ca} reductions, the modeling 482 experiments conducted here highlight that increasing atmospheric CO₂ is the largest contributor to decreases in Ω_{Ca} throughout 483 the study region. Increased atmospheric CO₂ will cause reductions in Ω_{Ca} across the model domain, while nutrient reductions 484 are expected to mainly influence Ω_{Ca} in shallow and fresh coastal areas, with little influence in oyster growing regions. The 485 effects of warming on Ω_{Ca} may slightly offset the influence of atmospheric CO₂ in certain areas, but this will likely only occur 486 in fresh tidal creeks where oysters do not currently reside (Fig. 10e). Given the importance of atmospheric CO_2 in shaping 487 future Ω_{Ca} conditions in the lower bay, reductions in anthropogenic carbon emissions will be necessary to lessen the projected 488 impacts on carbonate chemistry in the Chesapeake Bay and globally.

Comparing our results to other studies examining the effects of acidification reveals that the Chesapeake Bay will 489 490 likely acidify faster than the US West Coast. Siedlecki et al. (2021a) projected a decrease of 0.8-1.0 in Ω_{Ca} in the Northern 491 California Current System between 2000 and 2100. Projections from the present work indicate a similar magnitude of reduction 492 in the lower Chesapeake Bay over a shorter time period (50 years), suggesting a faster rate of acidification in the lower bay. Feely et al. (2009) also reported that projections for Ω_{Ca} reductions are slightly greater in the Atlantic than in the Pacific. The 493 494 relative differences in rates of acidification should be considered, however, in the context of present-day Ω_{Ca} . The Pacific 495 Ocean has a higher ratio of DIC:TA than the Atlantic, so present-day Pacific Ω_{Ca} is lower (Feely et al., 2004; Dunne et al., 496 2012). Therefore, while the Chesapeake Bay is acidifying faster, coastal Pacific waters may become undersaturated with calcite 497 and aragonite sooner than in Chesapeake Bay. US West Coast shellfish mortality events associated with acidification or other climate change stressors may place increased pressure on US Atlantic fisheries to provide shellfish to the nation, highlighting 498 499 the importance of climate change preparedness and resilience in the Chesapeake Bay region.





500 While atmospheric CO₂ is primarily responsible for changes in Ω_{Ca} , nutrient reductions are also projected to worsen 501 carbonate chemistry conditions. Eutrophication can suppress acidification by increasing primary production (Borges and 502 Gypens, 2010; Shen et al., 2019; Da et al., 2021), and when simulating a reduction in eutrophication via nutrient management 503 in our modeling study, the countering effect occurred. While the reduction in Ω_{Ca} from nutrient management is minor compared 504 to the projected impacts of CO₂-driven acidification, its small contribution may shift Ω_{Ca} conditions from favoring net 505 calcification to favoring net dissolution, demonstrating the importance of considering multiple drivers when predicting 506 exposure to ecologically relevant conditions of coastal acidification.

507 4.2 Future projections of oyster growth

508 Acidification, warming, and nutrient reductions are projected to affect shell and tissue growth of oysters in different 509 ways. Here, increased atmospheric CO₂ caused reductions in shell growth of Eastern oysters due to its negative effect on Ω_{Ca} 510 and thus calcification rates, which is consistent with experimental studies (Waldbusser et al., 2011; Gobler and Talmage, 2014; 511 Himes et al., 2024). Shell weight reductions from increased atmospheric CO_2 were driven by changes in calcification rate 512 alone, as tissue weight in *EcoOyster* is unaffected by Ω_{Ca} (Fig. 11d; Rivest et al., 2023). Experimental studies have identified indirect physiological impacts of elevated CO₂ on juvenile/adult oyster metabolism, growth, and reproduction (Beniash et al., 513 514 2010; Dickinson et al., 2012), suggesting that increased atmospheric CO₂ can sometimes influence tissue growth. Further 515 investigation is necessary in order to include the relationship between atmospheric CO₂ and oyster tissue growth in *EcoOyster*. Biological and chemical reactions occur faster at higher temperatures, meaning calcification rates may be higher under future 516 517 warming conditions (Waldbusser et al., 2011), as long as Ω_{Ca} is still high enough to support calcification. Conversely, under conditions of extreme low Ω_{Ca} , warming may exacerbate dissolution rates and shell weight reductions. Our results also show 518 519 that nutrient reductions will lead to reductions in shell weight, largely driven by a reduction in tissue weight resulting from 520 lower food availability (POC), rather than lower Ω_{Ca} .

521 While nutrient reductions are projected to have little influence on Ω_{Ca} in this study, their negative influence on food 522 availability may be detrimental to tissue growth in certain parts of the study region, particularly the York River. Our model 523 projections suggest that nutrient reductions may in some cases produce conditions that do not support any oyster growth along the shoals of the York (Fig. 9c; 10c), a result of reductions in food availability that are predicted to be more substantial in the 524 525 tributaries than the mainstem region (Fig. 6c). Multiple studies have demonstrated that Eastern oysters and other calcifying 526 organisms perform better under acidification when they have sufficient food availability, as they are better able to keep up with the energetic demands of environmental stress (Thomsen et al., 2015; Ramajo et al., 2016; Schwaner et al., 2023). 527 528 Therefore, nutrient reductions will likely influence oyster growth under acidification stress by different magnitudes in each 529 tributary. When comparing the effects of local management actions to reduce nutrient runoff to the effects of climate change 530 (increased atmospheric CO₂ and warming), it is evident that, on average, climate change will have a much greater negative 531 influence on oyster growth (Table 4). However, the strong localized impacts of nutrient reductions in the York highlight the





532 importance of examining the spatial variability of future changes in oyster growth. It is important for managers to consider 533 local conditions when assessing the effects of nutrient reductions on oyster production.

534 Increased water temperatures are projected to slow oyster growth in the future. Specifically, large reductions in tissue 535 weight are underpinned by three primary mechanisms: limitations on filtration at high temperatures (Loosanoff, 1958), increased respiration rates (Dame, 1972), and reduced food availability. In EcoOvster, the optimal temperature for Eastern 536 537 oyster filtration is 27°C (Cerco et al., 2005; Jordan, 1987), and under warming, the frequency at which ambient summer 538 temperatures will surpass this optimal temperature will be higher (Fig. 7a), therefore causing more frequent declines in 539 filtration rate (Cerco et al., 2005; Fulford et al., 2007). There is no clear optimal temperature for oyster respiration, and 540 therefore it is assumed to increase exponentially with temperature (Hochachka and Somero, 2002). Thus, as oyster filtration 541 rates begin to decline at high temperatures, respiration rates will continue to rise and decrease the potential for tissue 542 accumulation (Fig. S1). Previous studies on juvenile Eastern oysters do not support a consensus on the relationship between 543 warming and tissue growth. Some report that growth is inhibited at higher temperatures (31°C, Stevens and Gobler, 2018; 544 30°C, Speights et al., 2017). In contrast, Talmage and Gobler (2011) found no significant influence of high temperature (28°C) 545 alone on tissue growth. The optimal temperature for oyster filtration may also vary among oysters, based on observations of maximum filtration rates of adult Eastern oysters occurring between 28.1°C- 32°C (Loosanoff, 1958). Variation in 546 experimental design may have contributed to the contrast in results summarized here, in addition to the influence of local 547 548 adaptation (Burford et al., 2014). Other studies that incorporate higher temperature thresholds into their models predict 549 increases in oyster biomass under warming in Chesapeake Bay (Allen et al., 2023), underscoring the importance of properly 550 parameterizing growth models. Due to a lack of consensus on temperature limits of Eastern oyster filtration, further research 551 is needed to more robustly represent oyster filtration in bioenergetics models and improve predictions of impacts of warming on oysters and their ecosystem services in the region. 552

553 Warming will likely have a negative effect on food availability for oysters. Compared to the effects of nutrient reductions, warming will have a much more widespread influence on POC, causing reductions throughout the model domain 554 555 (Fig. 10b,c). Despite warming increasing rates of POC production via increased phytoplankton growth rates, factors such as nutrient limitation and increased respiration rates will result in a net decrease in POC availability. In the tributaries, reductions 556 in food availability will be most widespread due to warming, but less extreme than those from nutrient reductions in the shallow 557 parts of the tributaries where ovsters are affected. Remineralization of organic carbon in marine systems is temperature-558 559 dependent (López-Urrutia et al., 2006), and as warming occurs, remineralization of detrital carbon to DIC in bottom waters will occur at higher rates. As much of the lower bay is nutrient-limited (Zhang et al., 2021), phytoplankton growth rates will 560 not increase much from warming alone; therefore, increased remineralization will likely reduce the overall amount of food 561 562 available to oysters. Despite a similar average reduction in food availability being predicted for the future warming simulation 563 and managed nutrient reductions simulation, the influence of warmer temperatures will amplify the negative effects of reduced food availability on growth. In this study, the critical temperature at which respiration rates exceed assimilation rates is 564 dependent on filtration. When food availability limits filtration, this critical temperature lowers, and the temperature threshold 565





for tissue loss is lowered. Experimental studies have demonstrated how organic carbon may be influenced by both warming and acidification (Simone et al., 2021), but as these dynamics can differ based on nutrient availability, it is important to consider how climate change will influence food webs and nutrient dynamics.

569 The projected mid-century reductions in oyster growth obtained from this analysis are consistent with the results of other studies that examine oyster growth under projected climate change conditions. A study modeling oyster responses in 570 571 Barataria Bay, LA, for example, predicts that under a warming and high flow scenario (though without the effects of future 572 nutrient reductions or atmospheric CO₂), oysters will experience widespread mortality in fresher parts of the bay by the end of the century (Lavaud et al., 2021). Experimental studies have shown similar negative effects of acidification, warming, lower 573 574 food availability, and increased freshwater flow on oyster survival (La Peyre et al., 2013; Rybovich et al., 2016; Lowe et al., 2019; Jones et al., 2019). Da (2023) found that the reductions in salinity and Ω_{Ca} that result from high discharge events in the 575 576 York River will increase in extent as climate change progresses and increasingly threaten aquaculture production. In the Chesapeake Bay, extreme precipitation events are predicted to occur more frequently with future climate change, however an 577 overall decline in annual average precipitation is also predicted (St. Laurent et al., 2021). As a result, the overall impact of 578 579 freshwater from the land is not projected to change significantly in the future (Hinson et al., 2023). Changes in precipitation 580 were thus not simulated in this study, but future work could examine the dynamics of climate change, salinity, Ω_{Ca} , and oyster growth in a year with more heavy rainfall events but lower annual rainfall. 581

582 **4.3 Influence of future changes in oyster growth on aquaculture**

583 Understanding the relative impacts of global climate change and local nutrient management actions on oyster growth 584 and survival will allow aquaculture producers to anticipate how their oyster stock may respond to these anthropogenic changes. As the effects of climate change are subject to natural interannual variability, the magnitude of acidification and warming in a 585 586 given year will likely differ (Cai et al., 2021; Moore-Maley et al., 2016; Li et al., 2016), influencing oyster growth through differing mechanisms. Smaller oysters resulting from slower growing times in a particularly warm year may present a different 587 588 challenge to growers than weak-shelled oysters in a year with lower Ω_{Ca} and average temperatures. Mortality may also become 589 a more urgent challenge as summer temperatures warm. A previous study examining commercial performance of Pacific oysters in Brazil found that interannual variability in temperature, chla abundance, and climate events influenced survival and 590 591 growth phase timing (Mizuta et al., 2012). High temperatures inhibited survival of oyster seed in that study, which frequently 592 occurs in Pacific oysters (Crassostrea gigas) during the summer months in Europe and California (Goulletquer et al., 1998; Burge et al., 2007; Malhan et al., 2009). A similar phenomenon has been observed in Eastern oysters; however, mortality 593 594 events in this species have not been conclusively linked to warmer water temperatures (Guevelou et al., 2019; Biranik and Allam, 2023), and the cause is yet to be resolved for either species. Nonetheless, the increasing occurrence of spring/summer 595 596 mortality in Eastern oysters suggests that shifting the time of planting oysters on leases later in the year may help mitigate the 597 risk of widespread mortality, although the economic tradeoffs involved in shifting the growing season for oysters should be 598 taken into account.





599 Future climate change and nutrient management are projected to worsen conditions for oyster growth, and the spatial 600 variation in these changes may unevenly influence aquaculture production. While reductions in shell and tissue growth are 601 predicted for nearly all regions where oysters grow, these changes will likely differ based on present-day environmental 602 conditions. Under present day conditions, the most oyster growth is projected to occur in regions with some of the highest present-day Ω_{Ca} and the greatest projected Ω_{Ca} reductions, i.e., in the Rappahannock River and mainstem shoals. Some of the 603 604 most dramatic tissue and shell reductions are projected to occur in the York and upper Rappahannock, where reduced food 605 availability and low Ω_{Ca} will limit oyster filtration and shell growth. Oysters in parts of both the Rappahannock and York Rivers will likely face mortality (represented by near complete depletion of oyster shell and tissue) by mid-century (Figs. 8, 606 607 9). However, these reductions will not be spatially uniform, underscoring the importance of oyster farm site selection within a tributary. In contrast, oysters grown outside the tributaries are projected to exhibit a smaller decline in growth, indicating 608 609 greater future opportunity for oyster farming in these locations. Under the business-as-usual climate change trajectory analyzed here, bottom conditions in the tributaries will be less suitable for oyster aquaculture by mid-century, and producers might 610 consider alternate farm locations or shifting production methods toward floating culture to avoid exposure to low Ω_{Ca} 611 612 conditions and access greater food availability.

613 Beyond reduced oyster growth, aquaculture operations may also be affected in the future by temporal changes in optimal growing conditions. Due to the input of freshwater that lowers DIC and TA and increases pCO₂ (Cai et al., 2017; Cai 614 615 et al., 2021; Da et al., 2024), the greatest magnitude of Ω_{Ca} reductions occurs in spring. The majority of oyster growth is projected to occur in the spring and summer (Fig. 7), so changes to growing conditions may be most consequential during 616 617 these warmer months. Deployment of oyster seed generally begins in the spring and continues into the summer, so it is 618 important for producers to be aware of ambient conditions being experienced by their newly deployed oysters. As spring 619 temperatures warm, phytoplankton blooms will likely occur earlier in the year, shifting the time when food availability is 620 highest (Da et al., 2021). Oysters deployed earlier in the year may benefit from greater food availability and perform better 621 than oysters deployed in July or August when waters are warmest. However, they may also face the challenge of spring/summer 622 mortality events, revealing the complexity of timing oyster deployment under worsening climate change conditions. For oyster farms closer to freshwater sources, the combined effects of low Ω_{Ca} , low salinity, and high summer temperatures may severely 623 inhibit growth and extend time-to-market. 624

625 4.4 Future work

Providing the aquaculture industry with the best existing estimates of climate change impacts to their operations will allow them to make more informed decisions about their future practices. This study used a 120-meter horizontal resolution model grid to examine near-lease-level effects of climate change and management actions on oyster growth in a section of the lower Chesapeake Bay. Similar studies with high resolution model grids in other systems will strengthen our understanding of how regional anthropogenic effects will influence the oyster aquaculture sector and could be used to identify areas of opportunity for new aquaculture practices (Swam et al., 2022; Palmer et al., 2021; Lavaud et al., 2024). The present study





incorporated one Earth System Model and one emissions scenario; future work should quantify how these choices impact estimates of future Ω_{Ca} and oyster growth (e.g., Hinson et al., 2023). Future modeling studies should also incorporate other climate change impacts, such as sea level rise and increased storminess which are projected to influence conditions for oyster growth in the Chesapeake Bay region (Seneviratne et al., 2012; Lowe et al., 2019, Rybovich et al., 2016, Jones et al., 2019).

To improve estimates of shell and tissue growth of oysters under climate change, additional experimental studies 636 637 should be conducted to reduce the data gaps that currently limit model formulations. Uncertainties in the functional 638 relationships and rate parameters used in these models may lead to an inaccurate influence of some environmental variables 639 on oyster growth. For example, results in this study may be particularly sensitive to the optimum temperature for filtration 640 rate. Reductions in tissue weight are particularly dramatic when average temperature conditions at oyster lease sites remain 641 above this optimal temperature from mid-June through late August, a vital time for oyster growth. As a result, growth in the 642 model is sensitive to the simulation start date, and future studies should compare the influence of warming on growth in simulations that start at different times in the year. Many physiological studies of temperature impacts on oyster filtration date 643 back to the mid-to-late-20th century, and present-day seasonal extremes that coastal organisms experience may routinely exceed 644 645 the maximum temperatures used in many of these earlier experimental designs. For example, Jordan (1987) used a maximum temperature of 27 °C, which was the ambient temperature when samples were collected in July from the Choptank River, MD. 646 Between 1985 and 2014, bottom waters of the north mesohaline Bay main stem (closest to the Choptank) warmed 1.01 ± 0.13 647 $^{\circ}$ C during May to October (Hinson et al., 2022), and the present study predicts a 1.5 ± 0.26 $^{\circ}$ C increase across the entire model 648 649 domain between 2017 and mid-century. To build stronger models of future climate impacts, and to expand scientific 650 understanding of physiological limits of the Eastern oyster, future studies should re-examine temperature limitations on oyster 651 filtration and respiration by using higher experimental temperatures.

652 As ovster growth is highly sensitive to food availability, improved measurements of particulate organic carbon in the region would fortify projections of oyster production under future climate change and nutrient management. Here, it is assumed 653 that oysters feed on POC, a combination of plankton and detritus. However, average POC concentrations are highly 654 655 spatiotemporally variable in the Chesapeake Bay due to eutrophication and algal blooms. In this study, POC was underestimated in the tributary channels; however, it is unclear how well POC was estimated in oyster growing areas, as in 656 situ measurements are currently limited to stations in the channels during monthly or semi-monthly sampling cruises. More 657 routine POC measurements, as well as measurements of POC in regions where oyster farming operations occur, are needed to 658 659 verify the spatiotemporal dynamics of food availability. Improved measurements of oyster food availability would allow for 660 stronger model skill assessment and improved projections of oyster production.

661 5 Conclusions

662 This study predicts widespread reductions in Ω_{Ca} in the lower Virginia tributaries of the Chesapeake Bay by mid-663 century, highlighting the use of high-resolution model projections to better understand present-day carbonate chemistry 664 conditions and to predict the effects of climate change on a region of high interest for aquaculture production. While similar





modeling studies have projected acidification conditions in coastal regions with 3D coupled models (Siedlecki et al., 2021a,b; Fujii et al., 2023) or modeled oyster growth with remote-sensing data and dynamic energy budget models (Palmer et al., 2020; Palmer et al., 2021; Bertollini et al., 2021), the present study projects both carbonate chemistry conditions and oyster bioenergetics in the Chesapeake Bay with the highest resolution thus far. Specifically, widespread reductions in Ω_{Ca} will negatively impact oyster growth, with implications for aquaculture operations and local and regional economies. As bottom conditions worsen, altered site-selection for oyster farms or other adaptive measures will become imperative to sustain production and reduce the impacts of low Ω_{Ca} on farmed oysters.

672 Increased atmospheric CO₂ and nutrient reductions are projected to inhibit oyster calcification, while warming and 673 nutrient reductions will reduce oyster tissue and shell growth due to limitations on filtration and lowered food availability. 674 While the effects of global climate change on oyster growth are projected to be much stronger overall than the effects of local 675 nutrient management, lowered food availability from nutrient reductions may have a strong influence on oyster growth in certain parts of the study region. As a result, all areas will not be equally vulnerable to future changes in the atmosphere and 676 watershed. Understanding how individual drivers influence oyster growth is important for predicting effects on aquaculture 677 678 production in the context of interannual variability of climate change and nutrient management outcomes. While the negative 679 effects of temperature on growth were strong in this study, additional studies on Eastern oyster temperature limits are needed to improve projections, particularly as summer mortality of oysters is already common. Increased in situ measurements of 680 681 biogeochemical variables and experimental studies on oyster physiology and bioenergetics will allow for improved projections of mid-century conditions and their potential impacts on oyster growth and the aquaculture industry. 682

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684 Code Availability

685 Model code will be available upon request.

686

687 Data Availability

688 Model output will be available with a DOI on William & Mary ScholarWorks.

689

690 Author Contribution

MAMF, EBR, MJB, and PS wrote the proposal and acquired the funding for the project; MAMF, PS, and FD developed the ROMS-ECB code; MJB developed the EcoOyster code; CC, MAMF, and EBR designed the experiment; CC ran model simulations, analyzed the output, created the figures, and wrote the manuscript draft; MAMF, EBR, MJB, PS, and FD reviewed and edited the manuscript.

695

696 Competing Interests

697 The authors declare that they have no conflict of interest.

698





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707 References

- Abatzoglou, J. T. and Brown, T. J.: A comparison of statistical downscaling methods suited for wildfire applications, Int. J.
 Clim., 32, 772–780, https://doi.org/10.1002/joc.2312, 2012.
- 710 Allen, K. L., Ihde, T., Knoche, S., Townsend, H., & Lewis, K. A.: Simulated climate change impacts on striped bass, blue crab
- 711 and Eastern oyster in oyster sanctuary habitats of Chesapeake Bay. Estuar. Coast. Shelf Sci., 292, 108465,
- 712 https://doi.org/10.1016/j.ecss.2023.108465, 2023.
- 713 Amaral, V., Cabral, H. N., and Bishop, M. J.: Effects of estuarine acidification on predator-prey interactions. Mar. Eco. Prog.
- 714 Ser., 445, 117-127, https://doi.org/10.3354/meps09487, 2012.
- 715 Barclay, K.M., Gingras, M.K., Packer, S.T. and Leighton, L.R.: The role of gastropod shell composition and microstructure in
- resisting dissolution caused by ocean acidification, Mar. Environ. Res., 162, 105105,
 https://doi.org/10.1016/j.marenvres.2020.105105, 2020.
- 718 Barton, S. and Yvon-Durocher, G.: Quantifying the temperature dependence of growth rate in marine phytoplankton within
- 719 and across species, Limnol. Oceanogr., 64, 2081–2091, https://doi.org/10.1002/lno.11170, 2019.
- 720 Beniash, E., Ivanina, A., Lieb, N., Kurochkin, I., and Sokolova, I.: Elevated level of carbon dioxide affects metabolism and
- 721 shell formation in oysters Crassostrea virginica (Gmelin), Mar. Ecol. Prog. Ser., 419, 95–108, 722 https://doi.org/10.3354/meps08841, 2010.
- 723 Bertolini, C., Brigolin, D., Porporato, E. M. D., Hattab, J., Pastres, R., and Tiscar, P. G.: Testing a Model of Pacific Oysters'
- 724 (Crassostrea gigas) Growth in the Adriatic Sea: Implications for Aquaculture Spatial Planning, Sustainability, 13, 3309,
- 725 https://doi.org/10.3390/su13063309, 2021.
- 726 Bhatt, G., Linker, L., Shenk, G., Bertani, I., Tian, R., Rigelman, J., Hinson, K., and Claggett, P.: Water quality impacts of
- r27 climate change, land use, and population growth in the Chesapeake Bay watershed, JAWRA J. Am. Water Resour. Assoc., 59,
- 728 1313–1341, https://doi.org/10.1111/1752-1688.13144, 2023.
- 729 Borges, A. V. and Gypens, N.: Carbonate chemistry in the coastal zone responds more strongly to eutrophication than to ocean
- 730 acidification, Limnol. Oceanogr., 55, 346–353, https://doi.org/10.4319/lo.2010.55.1.0346, 2010.





- 731 Boulais, M., Chenevert, K. J., Demey, A. T., Darrow, E. S., Robison, M. R., Roberts, J. P., and Volety, A.: Oyster reproduction
- is compromised by acidification experienced seasonally in coastal regions, Sci. Rep., 7, 13276, https://doi.org/10.1038/s41598-
- 733 017-13480-3, 2017.
- 734 Brianik, C. J. and Allam, B.: The need for more information on the resistance to biological and environmental stressors in
- 735 triploid oysters, Aquaculture, 577, 739913, https://doi.org/10.1016/j.aquaculture.2023.739913, 2023.
- 736 Bukaveckas, P. A.: Carbon dynamics at the river-estuarine transition: a comparison among tributaries of Chesapeake Bay,
- 737 Biogeosciences, 19, 4209–4226, https://doi.org/10.5194/bg-19-4209-2022, 2022.
- 738 Brush, M.J., and M.L. Kellogg: Harris Creek Oyster Restoration Model v2. Virginia Institute of Marine Science, Gloucester
- 739 Point, VA, https://www.vims.edu/research/departments/bio/programs/semp/models/index.php, 2018.
- 740 Burford, M., Scarpa, J., Cook, B., and Hare, M.: Local adaptation of a marine invertebrate with a high dispersal potential:
- revidence from a reciprocal transplant experiment of the eastern oyster Crassostrea virginica, Mar. Ecol. Prog. Ser., 505, 161–
- 742 175, https://doi.org/10.3354/meps10796, 2014.
- 743 Burge, C. A., Judah, L. R., Conquest, L. L., Griffin, F. J., Cheney, D. P., Suhrbier, A., Vadopalas, B., Olin, P. G., Renault, T.,
- and Friedman, C. S.: Summer seed mortality of the pacific oyster, Crassostrea gigas (Thunberg) grown in Tomales Bay,
- 745 California, USA: the influence of oyster stock, planting time, pathogens, and environmental stressors, J. Shellfish Res,
- 746 https://doi.org/10.2983/0730-8000, 2007.
- 747 Cai, W., Feely, R. A., Testa, J. M., Li, M., Evans, W., Alin, S. R., Xu, Y.-Y., Pelletier, G., Ahmed, A., Greeley, D. J., Newton,
- J. A., and Bednaršek, N.: Natural and Anthropogenic Drivers of Acidification in Large Estuaries, Annu. Rev. Mar. Sci.,
 https://doi.org/10.1146/annurev-marine-010419-011004, 2021.
- 750 Cai, W.J., Huang, W.-J., Luther, G. W., Pierrot, D., Li, M., Testa, J., Xue, M., Joesoef, A., Mann, R., Brodeur, J., Xu, Y.-Y.,
- Chen, B., Hussain, N., Waldbusser, G. G., Cornwell, J., and Kemp, W. M.: Redox reactions and weak buffering capacity lead
 to acidification in the Chesapeake Bay, Nat. Commun., 8, 369, https://doi.org/10.1038/s41467-017-00417-7, 2017.
- 753 Cai, W.J., Xu, Y.-Y., Feely, R. A., Wanninkhof, R., Jönsson, B., Alin, S. R., Barbero, L., Cross, J. N., Azetsu-Scott, K.,
- 754 Fassbender, A. J., Carter, B. R., Jiang, L.-Q., Pepin, P., Chen, B., Hussain, N., Reimer, J. J., Xue, L., Salisbury, J. E.,
- 755 Hernández-Ayón, J. M., Langdon, C., Li, Q., Sutton, A. J., Chen, C.-T. A., and Gledhill, D. K.: Controls on surface water
- rth American ocean margins, Nat. Commun., 11, 2691, https://doi.org/10.1038/s41467-020-
- 757 16530-z, 2020.
- Cai, W. J., and Wang, Y.: The chemistry, fluxes, and sources of carbon dioxide in the estuarine waters of the Satilla and
 Altamaha Rivers, Georgia. Limnol. Oceanogr., 43(4), 657-668, https://doi.org/10.4319/lo.1998.43.4.0657, 1998.
- Caldeira, K. and Wickett, M. E.: Anthropogenic carbon and ocean pH, Nature, 425, 365–365, https://doi.org/10.1038/425365a,
 2003.
- 762 Caldeira, K. and Wickett, M. E.: Ocean model predictions of chemistry changes from carbon dioxide emissions to the
- 763 atmosphere and ocean, J. Geophys. Res.: Oceans, 110, https://doi.org/10.1029/2004jc002671, 2005.





- Callam, B. R., Allen, S. K., and Frank-Lawale, A.: Genetic and environmental influence on triploid Crassostrea virginica
 grown in Chesapeake Bay: Growth, Aquaculture, 452, 97–106, https://doi.org/10.1016/j.aquaculture.2015.10.027, 2016.
- 766 Carstensen, J. and Duarte, C. M.: Drivers of pH Variability in Coastal Ecosystems, Environ. Sci. Technol., 53, 4020-4029,
- 767 https://doi.org/10.1021/acs.est.8b03655, 2019.
- Cerco, C. and Noel, M.: Process-based primary production modeling in Chesapeake Bay, Mar. Ecol. Prog. Ser., 282, 45–58,
 https://doi.org/10.3354/meps282045, 2004.
- 770 Cerco, C. F. and Noel, M. R.: Nonnative Oysters in the Chesapeake Bay, 2005.
- 771 Cerco, C. F., Noel, M. R., and Wang, P.: The Shallow-Water Component of the Chesapeake Bay Environmental Model
- 772 Package, JAWRA J. Am. Water Resour. Assoc., 49, 1091–1102, https://doi.org/10.1111/jawr.12106, 2013.
- 773 Chesapeake Bay Program DataHub: https://datahub.chesapeakebay.net/, last access: 28 January 2024
- 774 Comeau, L. A., Mayrand, É., and Mallet, A.: Winter quiescence and spring awakening of the Eastern oyster Crassostrea
- 775 virginica at its northernmost distribution limit, Mar. Biol., 159, 2269–2279, https://doi.org/10.1007/s00227-012-2012-8, 2012.
- 776 Copernicus Climate Change Service: ERA5: Fifth Generation of ECMWF Atmospheric Reanalyses of the Global Climate,
- 777 Copernicus Climate Change Service Climate Data Store (CDS). https://cds.climate.copernicus.eu/cdsapp#!/home, 2017.
- 778 Da, F., Friedrichs, M. A. M., St-Laurent, P., Shadwick, E. H., Najjar, R. G., and Hinson, K. E.: Mechanisms Driving Decadal
- 779 Changes in the Carbonate System of a Coastal Plain Estuary, J. Geophys. Res.: Oceans, 126, 780 https://doi.org/10.1029/2021jc017239, 2021.
- 781 Da, F: Chesapeake Bay Carbon Cycle: Past, Present, Future, PhD. Dissertation, Virginia Institute of Marine Science, William
- 782 & Mary, Virginia, USA, https://dx.doi.org/10.25773/v5-46f7-e286, 2023.
- Da, F., Friedrichs, M. A. M., St-Laurent, P., Najjar, R. G., Shadwick, E. H., and Stets, E. G.: Influence of Rivers, Tides, and
 Tidal Wetlands on Estuarine Carbonate System Dynamics, Estuaries Coasts, 1-23, https://doi.org/10.1007/s12237-024-01421z, 2024.
- 786 Dame, R.F.: The ecological energies of growth, respiration and assimilation in the intertidal American oyster Crassostrea
- 787 virginica, Mar. Biol., 17, 43-250, 1972.
- Dayton, P.K.: Toward an understanding of community resilience and the potential effects of enrichments to the benthos at
 McMurdo Sound, Antarctica, Proceedings of the colloquium on conservation problems in Antarctica, 81-96, 1972.
- Dégremont, L., Garcia, C., Frank-Lawale, A., and Allen, S. K.: Triploid Oysters in the Chesapeake Bay: Comparison of Diploid
 and Triploid Crassostrea virginica, J. Shellfish Res., 31, 21–31, https://doi.org/10.2983/035.031.0103, 2012.
- 792 Dickinson, G. H., Ivanina, A. V., Matoo, O. B., Pörtner, H. O., Lannig, G., Bock, C., Beniash, E., and Sokolova, I. M.:
- 793 Interactive effects of salinity and elevated CO₂ levels on juvenile eastern oysters, Crassostrea virginica, J. Exp. Biol., 215, 29–
- 794 43, https://doi.org/10.1242/jeb.061481, 2011.
- 795 Dinauer, A. and Mucci, A.: Spatial variability in surface-water pCO 2 and gas exchange in the world's largest semi-enclosed
- restuarine system: St. Lawrence Estuary (Canada), Biogeosciences, 14, 3221-3237, https://doi.org/10.5194/bg-14-3221-2017,
- 797 2017.





- Doney, S. C., Fabry, V. J., Feely, R. A., and Kleypas, J. A.: Ocean acidification: the other CO₂ problem., Annu. Rev. Mar.
 Sci., 1, 169–92, https://doi.org/10.1146/annurev.marine.010908.163834, 2009.
- 800 Dong, S., Lei, Y., Li, T., Cao, Y., and Xu, K.: Biocalcification crisis in the continental shelf under ocean acidification. Geosci.
- 801 Front., 14(6), 101622, https://doi.org/10.1016/j.gsf.2023.101622, 2023.
- 802 Du, J., Shen, J., Park, K., Wang, Y. P., and Yu, X.: Worsened physical condition due to climate change contributes to the
- increasing hypoxia in Chesapeake Bay, Sci. Total Environ., 630, 707–717, https://doi.org/10.1016/j.scitotenv.2018.02.265,
 2018.
- 805 Duarte, C. M., Hendriks, I. E., Moore, T. S., Olsen, Y. S., Steckbauer, A., Ramajo, L., Carstensen, J., Trotter, J. A., and
- McCulloch, M.: Is Ocean Acidification an Open-Ocean Syndrome? Understanding Anthropogenic Impacts on Seawater pH,
 Estuaries Coasts, 36, 221–236, https://doi.org/10.1007/s12237-013-9594-3, 2013.
- 808 Dufresne, J.-L., Foujols, M.-A., Denvil, S., Caubel, A., Marti, O., Aumont, O., Balkanski, Y., Bekki, S., Bellenger, H.,
- 809 Benshila, R., Bony, S., Bopp, L., Braconnot, P., Brockmann, P., Cadule, P., Cheruy, F., Codron, F., Cozic, A., Cugnet, D.,
- 810 Noblet, N. de, Duvel, J.-P., Ethé, C., Fairhead, L., Fichefet, T., Flavoni, S., Friedlingstein, P., Grandpeix, J.-Y., Guez, L.,
- 811 Guilyardi, E., Hauglustaine, D., Hourdin, F., Idelkadi, A., Ghattas, J., Joussaume, S., Kageyama, M., Krinner, G., Labetoulle,
- 812 S., Lahellec, A., Lefebvre, M.-P., Lefevre, F., Levy, C., Li, Z. X., Lloyd, J., Lott, F., Madec, G., Mancip, M., Marchand, M.,
- 813 Masson, S., Meurdesoif, Y., Mignot, J., Musat, I., Parouty, S., Polcher, J., Rio, C., Schulz, M., Swingedouw, D., Szopa, S.,
- 814 Talandier, C., Terray, P., Viovy, N., and Vuichard, N.: Climate change projections using the IPSL-CM5 Earth System Model:
- 815 from CMIP3 to CMIP5, Clim. Dyn., 40, 2123–2165, https://doi.org/10.1007/s00382-012-1636-1, 2013.
- 816 Dunne, J. P., John, J. G., Adcroft, A. J., Griffies, S. M., Hallberg, R. W., Shevliakova, E., Stouffer, R. J., Cooke, W., Dunne,
- 817 K. A., Harrison, M. J., Krasting, J. P., Malyshev, S. L., Milly, P. C. D., Phillipps, P. J., Sentman, L. T., Samuels, B. L., Spelman,
- 818 M. J., Winton, M., Wittenberg, A. T., and Zadeh, N.: GFDL's ESM2 Global Coupled Climate–Carbon Earth System Models.
- 819 Part I: Physical Formulation and Baseline Simulation Characteristics, J. Clim., 25, 6646–6665, https://doi.org/10.1175/jcli-d-
- 820 11-00560.1, 2012.
- EPA, Chesapeake Bay Total Maximum Daily Load for Nitrogen, Phosphorus, and Sediment, United States Environmental
 Protection Agency, 2010.
- 823 Guinotte, J. M. and Fabry, V. J.: Ocean Acidification and Its Potential Effects on Marine Ecosystems, Ann. N. York Acad.
- 824 Sci., 1134, 320–342, https://doi.org/10.1196/annals.1439.013, 2008.
- Ehrich, M. K. and Harris, L. A.: A review of existing eastern oyster filtration rate models, Ecol. Model., 297, 201–212,
 https://doi.org/10.1016/j.ecolmodel.2014.11.023, 2015.
- 827 Feely, R. A., Sabine, C. L., Lee, K., Berelson, W., Kleypas, J., Fabry, V. J., and Millero, F. J.: Impact of Anthropogenic CO2
- 828 on the CaCO3 System in the Oceans, Science, 305, 362–366, https://doi.org/10.1126/science.1097329, 2004.
- 829 Feely, R. A., Doney, S. C., and Cooley, S. R.: Ocean Acidification: Present Conditions and Future Changes in a High-CO2
- 830 World, Oceanography, 22, 36–47, https://doi.org/10.5670/oceanog.2009.95, 2009.





- Feng, Y., Friedrichs, M. A. M., Wilkin, J., Tian, H., Yang, Q., Hofmann, E. E., Wiggert, J. D., and Hood, R. R.: Chesapeake
 Bay nitrogen fluxes derived from a land-estuarine ocean biogeochemical modeling system: Model description, evaluation, and
- 833 nitrogen budgets, J. Geophys. Res.: Biogeosciences, 120, 1666–1695, https://doi.org/10.1002/2015jg002931, 2015.
- 834 Fitzer, S. C., Torres Gabarda, S., Daly, L., Hughes, B., Dove, M., O'Connor, W., Potts, J., Scanes, P., and Byrne, M.: Coastal
- 835 acidification impacts on shell mineral structure of bivalve mollusks. Ecol. Evol., 8(17), 8973-8984,
- 836 https://doi.org/10.1002/ece3.4416, 2018.
- 837 Frankel, L. T., Friedrichs, M. A. M., St-Laurent, P., Bever, A. J., Lipcius, R. N., Bhatt, G., and Shenk, G. W.: Nitrogen
- 838 reductions have decreased hypoxia in the Chesapeake Bay: Evidence from empirical and numerical modeling, Sci. Total
- 839 Environ., 814, 152722, https://doi.org/10.1016/j.scitotenv.2021.152722, 2022.
- 840 Frank-Lawale, A., Allen, S. K., and Dgremont, L.: Breeding and Domestication of Eastern Oyster (Crassostrea virginica) Lines
- 841 for Culture in the Mid-Atlantic, Usa: Line Development and Mass Selection for Disease Resistance, J. Shellfish Res., 33, 153-
- 842 165, https://doi.org/10.2983/035.033.0115, 2014.
- 843 Fujii, M., Hamanoue, R., Bernardo, L. P. C., Ono, T., Dazai, A., Oomoto, S., Wakita, M., and Tanaka, T.: Assessing impacts
- 844 of coastal warming, acidification, and deoxygenation on Pacific oyster (Crassostrea gigas) farming: a case study in the Hinase
- area, Okayama Prefecture, and Shizugawa Bay, Miyagi Prefecture, Japan, Biogeosciences, 20, 4527–4549,
 https://doi.org/10.5194/bg-20-4527-2023, 2023.
- Fulford, R., Breitburg, D., Newell, R., Kemp, W., and Luckenbach, M.: Effects of oyster population restoration strategies on
 phytoplankton biomass in Chesapeake Bay: a flexible modeling approach, Mar. Ecol. Prog. Ser., 336, 43–61,
 https://doi.org/10.3354/meps336043, 2007.
- Gattuso, Strong, A. L., Kroeker, K. J., Teneva, L. T., Mease, L. A., and Kelly, R. P.: Ocean Acidification 2.0: Managing our
 Changing Coastal Ocean Chemistry, BioScience, 64, 581–592, https://doi.org/10.1093/biosci/biu072, 2014.
- 852 Gawde, R. K., North, E. W., Hood, R. R., Long, W., Wang, H., and Wilberg, M. J.: A high resolution hydrodynamic-
- 853 biogeochemical-oyster-filtration model predicts that the presence of oysters (Crassostrea virginica) can improve, or reduce,
- water quality depending upon oyster abundance and location. Ecol. Model., 496, 110833,
 https://doi.org/10.1016/j.ecolmodel.2024.110833, 2024.
- B56 Gazeau, F., Quiblier, C., Jansen, J. M., Gattuso, J. P., Middelburg, J. J., and Heip, C. H.: Impact of elevated CO₂ on shellfish
- 857 calcification. Geophys. Res. Lett., 34, 7, https://doi.org/10.1029/2006GL028554, 2007.
- 858 Gobler, C. J. and Talmage, S. C.: Physiological response and resilience of early life-stage Eastern oysters (Crassostrea 859 virginica) to past, present and future ocean acidification, Conserv. Physiol., 2, cou004, https://doi.org/10.1093/conphys/cou004, 2014. 860
- 861 Goulletquer, P., Soletchnik, P., Le Moine, O., Razet, D., Geairon, P., and Faury, N.: Summer mortality of the Pacific cupped
- 862 oyster Crassostrea gigas in the Bay of Marennes-Oléron (France), CIEM Conseil International pour l'Exploration de la Mer,
- 863 1998.
- 864 Gmelin, J. F.: Caroli a Linnaei Systema Naturae per Regna Tria Naturae, Systema Naturae, Linneaeus, 13, 3021-3910, 1791.





- 865 Gruber, N., Clement, D., Carter, B. R., Feely, R. A., Heuven, S. van, Hoppema, M., Ishii, M., Key, R. M., Kozyr, A., Lauvset,
- S. K., Monaco, C. L., Mathis, J. T., Murata, A., Olsen, A., Perez, F. F., Sabine, C. L., Tanhua, T., and Wanninkhof, R.: The
 oceanic sink for anthropogenic CO₂ from 1994 to 2007, Science, 363, 1193–1199, https://doi.org/10.1126/science.aau5153,
- 868 2019.
- 869 Guévélou, E., Carnegie, R. B., Small, J. M., Hudson, K., Reece, K. S., and Rybovich, M. M.: Tracking Triploid Mortalities
- of Eastern Oysters Crassostrea virginica in the Virginia Portion of the Chesapeake Bay, J. Shellfish Res., 38, 101–113,
 https://doi.org/10.2983/035.038.0110, 2019.
- 872 Hasler, C. T., Jeffrey, J. D., Schneider, E. V. C., Hannan, K. D., Tix, J. A., and Suski, C. D.: Biological consequences of weak
- 873 acidification caused by elevated carbon dioxide in freshwater ecosystems, Hydrobiologia, 806, 1–12, 874 https://doi.org/10.1007/s10750-017-3332-y, 2018.
- 875 Herrmann, M., Najjar, R. G., Da, F., Friedman, J. R., Friedrichs, M. A. M., Goldberger, S., Menendez, A., Shadwick, E. H.,
- 876 Stets, E. G., and St-Laurent, P.: Challenges in Quantifying Air-Water Carbon Dioxide Flux Using Estuarine Water Quality
- Data: Case Study for Chesapeake Bay, J. Geophys. Res.: Oceans, 125, e2019JC015610, https://doi.org/10.1029/2019jc015610,
- 878 2020.
- 879 Hersbach, H., Bell, B., Berrisford, P., Hirahara, S., Horányi, A., Muñoz-Sabater, J., Nicolas, J., Peubey, C., Radu, R., Schepers,
- 880 D., Simmons, A., Soci, C., Abdalla, S., Abellan, X., Balsamo, G., Bechtold, P., Biavati, G., Bidlot, J., Bonavita, M., Chiara,
- 881 G., Dahlgren, P., Dee, D., Diamantakis, M., Dragani, R., Flemming, J., Forbes, R., Fuentes, M., Geer, A., Haimberger, L.,
- 882 Healy, S., Hogan, R. J., Hólm, E., Janisková, M., Keeley, S., Laloyaux, P., Lopez, P., Lupu, C., Radnoti, G., Rosnay, P.,
- 883 Rozum, I., Vamborg, F., Villaume, S., and Thépaut, J.: The ERA5 global reanalysis, Q. J. R. Meteorol. Soc., 146, 1999–2049,
- 884 https://doi.org/10.1002/qj.3803, 2020.
- Hinson, K. E., Friedrichs, M. A. M., St-Laurent, P., Da, F., and Najjar, R. G.: Extent and Causes of Chesapeake Bay Warming,
 JAWRA J. Am. Water Resour. Assoc., 58, 805–825, https://doi.org/10.1111/1752-1688.12916, 2022.
- 887 Hinson, K. E., Friedrichs, M. A. M., Najjar, R. G., Herrmann, M., Bian, Z., Bhatt, G., St-Laurent, P., Tian, H., and Shenk, G.:
- 888 Impacts and uncertainties of climate-induced changes in watershed inputs on estuarine hypoxia, Biogeosciences, 20, 1937–
- 889 1961, https://doi.org/10.5194/bg-20-1937-2023, 2023.
- 890 Himes, A.R., Schatz, A. and Rivest, E.B.: Differences in larval acidification tolerance among populations of the eastern oyster,
- 891 Crassostrea virginica. J. Exp. Mar. Biol. Ecol., 577, 152023, https://doi.org/10.1016/j.jembe.2024.152023, 2024.
- Hochachka, P. W. and Somero, G. N.: Biochemical Adaptation: Mechanism and Processing Physiological Evolution. Oxford
 University Press, 2002.
- 894 Hofmann, G. E. and Hand, S. C.: Global arrest of translation during invertebrate quiescence., Proc. Natl. Acad. Sci., 91, 8492-
- 895 8496, https://doi.org/10.1073/pnas.91.18.8492, 1994.
- 896 Hopkinson, C. S., Buffam, I., Hobbie, J., Vallino, J., Perdue, M., Eversmeyer, B., Prahl, F., Covert, J., Hodson, R., Moran, M.
- 897 A., Smith, E., Baross, J., Crump, B., Findlay, S., and Foreman, K.: Terrestrial inputs of organic matter to coastal ecosystems:





- An intercomparison of chemical characteristics and bioavailability, Biogeochemistry, 43, 211–234,
 https://doi.org/10.1023/a:1006016030299, 1998.
- 900 Hudson, K.: Virginia Shellfish Aquaculture Situation and Outlook Report: Results of the 2018 Virginia Shellfish Aquaculture
- 901 Crop Reporting Survey, 2019.
- 902 Intergovernmental Panel on Climate Change: IPCC Special Report on the Ocean and Cryosphere in a Changing Climate [H.-
- 903 O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai,
- A. Okem, J. Petzold, B. Rama, N.M. Weyer (eds.)]. Cambridge University Press, Cambridge, UK and New York, NY, USA,
- 905 755 pp. <u>https://doi.org/10.1017/9781009157964</u>, 2019.
- 906IntergovernmentalPanelonClimateChange:ThePhysicalScienceBasis,673–816,907https://doi.org/10.1017/9781009157896.007, 2021.
- 908 Irby, I. D., Friedrichs, M. A. M., Friedrichs, C. T., Bever, A. J., Hood, R. R., Lanerolle, L. W. J., Li, M., Linker, L., Scully,
- 909 M. E., Sellner, K., Shen, J., Testa, J., Wang, H., Wang, P., and Xia, M.: Challenges associated with modeling low-oxygen
- waters in Chesapeake Bay: a multiple model comparison, Biogeosciences, 13, 2011–2028, https://doi.org/10.5194/bg-132011-2016, 2016.
- 912 Irby, I. D., Friedrichs, M. A. M., Da, F., and Hinson, K. E.: The competing impacts of climate change and nutrient reductions
- 913 on dissolved oxygen in Chesapeake Bay, Biogeosciences, 15, 2649–2668, https://doi.org/10.5194/bg-15-2649-2018, 2018.
- 914 Jewett, L. and Romanou, A: Ocean acidification and other ocean changes. In: Climate Science Special Report: Fourth National
- 915 Climate Assessment, Volume I [Wuebbles, D.J., D.W. Fahey, K.A. Hibbard, D.J. Dokken, B.C. Stewart, and T.K. Maycock
- 916 (eds.)]. U.S. Global Change Research Program, Washington, DC, USA, pp. 364-392, doi: 10.7930/J0QV3JQB, 2017.
- Jones, H. R., Johnson, K. M., and Kelly, M. W.: Synergistic Effects of Temperature and Salinity on the Gene Expression and
 Physiology of Crassostrea virginica, Integr. Comp. Biol., 59, 306–319, https://doi.org/10.1093/icb/icz035, 2019.
- 919 Jordan, S. J.: Sedimentation and remineralization associated with biodeposition by the American oyster Crassostrea virginica
- 920 (Gmelin). University of Maryland, College Park, 1987.
- Kellogg, M. L., Brush, M., and Cornwell, J. C.: An updated model for estimating the TMDL- related benefits of oyster reef
 restoration, A final report to The Nature Conservancy and Oyster Recovery Partnership, 2018.
- 923 Kelly, C. J., Laramore, S. E., Scarpa, J., and Newell, R. I. E.: Seasonal Comparison of Physiological Adaptation and Growth
- 924 of Suminoe (Crassostrea ariakensis) and Eastern (Crassostrea virginica) Oysters, J. Shellfish Res., 30, 737–749, 925 https://doi.org/10.2983/035.030.0314, 2011.
- 926 Kemp, W., Boynton, W., Adolf, J., Boesch, D., Boicourt, W., Brush, G., Cornwell, J., Fisher, T., Glibert, P., Hagy, J., Harding,
- 927 L., Houde, E., Kimmel, D., Miller, W., Newell, R., Roman, M., Smith, E., and Stevenson, J.: Eutrophication of Chesapeake
- Bay: historical trends and ecological interactions, Mar. Ecol. Prog. Ser., 303, 1–29, https://doi.org/10.3354/meps303001, 2005.
- 929 Kingsley-Smith, P. R., Harwell, H. D., Kellogg, M. L., Allen, S. M., Allen, S. K., Meritt, D. W., Paynter, K. T., and
- 930 Luckenbach, M. W.: Survival and Growth of Triploid Crassostrea virginica (Gmelin, 1791) and C. ariakensis (Fujita, 1913) in





- Bottom Environments of Chesapeake Bay: Implications for an Introduction, J. Shellfish Res., 28, 169–184,
 https://doi.org/10.2983/035.028.0201, 2009.
- 933 La Peyre, M.K., Eberline, B.S., Soniat, T.M. and La Peyre, J.F.: Differences in extreme low salinity timing and duration
- 934 differentially affect eastern oyster (Crassostrea virginica) size class growth and mortality in Breton Sound, LA, Estuar. Coast.
- 935 Shelf Sci., 135, 146-157, 2013.
- 936 Lake, S. and Brush, M.: Modeling estuarine response to load reductions in a warmer climate: York River Estuary, Virginia,
- 937 USA, Mar. Ecol. Prog. Ser., 538, 81–98, https://doi.org/10.3354/meps11448, 2015.
- 938 Lavaud, R., Peyre, M. K. L., Justic, D., and Peyre, J. F. L.: Dynamic Energy Budget modelling to predict eastern oyster growth,
- 939 reproduction, and mortality under river management and climate change scenarios, Estuar., Coast. Shelf Sci., 251, 107188,
- 940 https://doi.org/10.1016/j.ecss.2021.107188, 2021.
- 941 Lavaud, R., Peyre, M. K. L., Couvillion, B., Pollack, J. B., Brown, V., Palmer, T. A., and Keim, B.: Predicting restoration and
- 942 aquaculture potential of eastern oysters through an eco-physiological mechanistic model, Ecol. Model., 489, 110603,
- 943 https://doi.org/10.1016/j.ecolmodel.2023.110603, 2024.
- Lemasson, A. J., Hall-Spencer, J. M., Fletcher, S., Provstgaard-Morys, S., and Knights, A. M.: Indications of future
 performance of native and non-native adult oysters under acidification and warming, Mar. Environ. Res., 142, 178–189,
 https://doi.org/10.1016/j.marenvres.2018.10.003, 2018.
- Li, M., Lee, Y. J., Testa, J. M., Li, Y., Ni, W., Kemp, W. M., and Toro, D. M. D.: What drives interannual variability of
 hypoxia in Chesapeake Bay: Climate forcing versus nutrient loading?, Geophys. Res. Lett., 43, 2127–2134,
 https://doi.org/10.1002/2015gl067334, 2016.
- Liddel, M. K.: A von Bertalanffy based model for the estimation of oyster (Crassostrea virginica) growth on restored oyster
 reefs in Chesapeake Bay, 2008.
- Liu, Z., Zhou, Z., Zhang, Y., Wang, L., Song, X., Wang, W., Zheng, Y., Zong, Y., Lv, Z., and Song, L.: Ocean acidification
- inhibits initial shell formation of oyster larvae by suppressing the biosynthesis of serotonin and dopamine. Sci. Total Environ.,
 735, 139469, https://doi.org/10.1016/j.scitotenv.2020.139469, 2020.
- 955 Loosanoff, V. L.: Some aspects of behavior of oysters at different temperatures, Biol. Bull., 114, 57–70, 956 https://doi.org/10.2307/1538965, 1958.
- 957 López-Urrutia, Á., Martin, E. S., Harris, R. P., and Irigoien, X.: Scaling the metabolic balance of the oceans, Proc. Natl. Acad.
- 958 Sci., 103, 8739–8744, https://doi.org/10.1073/pnas.0601137103, 2006.
- 959 Lowe, A. T., Kobelt, J., Horwith, M., and Ruesink, J.: Ability of Eelgrass to Alter Oyster Growth and Physiology Is Spatially
- 960 Limited and Offset by Increasing Predation Risk, Estuaries Coasts, 42, 743–754, https://doi.org/10.1007/s12237-018-00488961 9, 2019.
- 962 Lutier, M., Di Poi, C., Gazeau, F., Appolis, A., Le Luyer, J., and Pernet, F.: Revisiting tolerance to ocean acidification: insights
- 963 from a new framework combining physiological and molecular tipping points of Pacific oyster. Glob. Change Bio., 28(10),
- 964 3333-3348, https://doi.org/10.1111/gcb.16101, 2022.





- Mazarrasa, I., Marbà, N., Lovelock, C. E., Serrano, O., Lavery, P. S., Fourqurean, J. W., Kennedy, H., Mateo, M. A., KrauseJensen, D., Steven, A. D. L., and Duarte, C. M.: Seagrass meadows as a globally significant carbonate reservoir,
 Biogeosciences, 12, 4993–5003, https://doi.org/10.5194/bg-12-4993-2015, 2015.
- Matoo, O. B., Lannig, G., Bock, C., and Sokolova, I. M.: Temperature but not ocean acidification affects energy metabolism of and enzyme activities in the blue mussel. Mutilus edulis Ecol. Evol. 11(7), 3366-3379. https://doi.org/10.1002/ace3.7289
- and enzyme activities in the blue mussel, Mytilus edulis. Ecol. Evol., 11(7), 3366-3379, https://doi.org/10.1002/ece3.7289,
 2021.
- 971 Medeiros, I. P. M., and Souza, M. M.: Acid times in physiology: a systematic review of the effects of ocean acidification on
- 972 calcifying invertebrates. Environmental Research, 116019, https://doi.org/10.1016/j.envres.2023.116019, 2023
- 973 Melzner, F., Mark, F.C., Seibel, B.A. and Tomanek, L.: Ocean acidification and coastal marine invertebrates: tracking CO2
- effects from seawater to the cell. Annu. Rev. Mar. Sci., 12, pp.499-523, https://doi.org/10.1146/annurev-marine-010419010658, 2020.
- Mitchell, M., Herman, J., Bilkovic, D. M., and Hershner, C.: Marsh persistence under sea-level rise is controlled by multiple,
 geologically variable stressors, Ecosyst. Heal. Sustain., 3, 1379888, https://doi.org/10.1080/20964129.2017.1396009, 2017.
- 978 Mizuta, D. D., Silveira, N., Fischer, C. E., and Lemos, D.: Interannual variation in commercial oyster (Crassostrea gigas)
- farming in the sea (Florianópolis, Brazil, 27°44′ S; 48°33′ W) in relation to temperature, chlorophyll a and associated oceanographic conditions, Aquaculture, 366, 105–114, https://doi.org/10.1016/j.aquaculture.2012.09.011, 2012.
- 981 Mizuta, D. D. and Wikfors, G. H.: Seeking the perfect oyster shell: a brief review of current knowledge, Rev. Aquac., 11, 586–
- 982 602, https://doi.org/10.1111/raq.12247, 2019.
- 983 Moore, K. A., Orth, R. J., and Wilcox, D. J.: Assessment of the Abundance of Submersed Aquatic Vegetation (SAV)
- Communities in the Chesapeake Bay and its Use in SAV Management, in: Remote Sensing and Geospatial Technologies for
 Coastal Ecosystem Assessment and Management, https://doi.org/10.1007/978-3-540-88183-4, 2009.
- 986 Moore-Maley, B. L., Allen, S. E., and Ianson, D.: Locally driven interannual variability of near-surface pH and ΩA in the 987 Strait of Georgia, J. Geophys. Res.: Oceans, 121, 1600–1625, https://doi.org/10.1002/2015jc011118, 2016.
- 988 Moriarty, J. M., Friedrichs, M. A. M., and Harris, C. K.: Seabed Resuspension in the Chesapeake Bay: Implications for
- Biogeochemical Cycling and Hypoxia, Estuaries Coasts, 44, 103–122, https://doi.org/10.1007/s12237-020-00763-8, 2021.
- 990 Najjar, R. G., Herrmann, M., Valle, S. M. C. D., Friedman, J. R., Friedrichs, M. A. M., Harris, L. A., Shadwick, E. H., Stets,
- E. G., and Woodland, R. J.: Alkalinity in Tidal Tributaries of the Chesapeake Bay, J. Geophys. Res.: Oceans, 125, https://doi.org/10.1029/2019jc015597, 2020.
- 993 Newell, R. I. E. and Koch, E. W.: Modeling seagrass density and distribution in response to changes in turbidity stemming
- from bivalve filtration and seagrass sediment stabilization, Estuaries, 27, 793–806, https://doi.org/10.1007/bf02912041, 2004.
- 995 Ni, W., Li, M., and Testa, J. M.: Discerning effects of warming, sea level rise and nutrient management on long-term hypoxia
- 996 trends in Chesapeake Bay, Sci. Total Environ., 737, 139717, https://doi.org/10.1016/j.scitotenv.2020.139717, 2020.
- 997 Olson, M.: Guide to Using Chesapeake Bay Program Water Quality Monitoring Data, Chesapeake Bay Program, Annapolis,
 998 MD, 2012.





- 999 Nichols, M.M., Kim, S.C. and Brouwer, C.M.: Sediment Characterization of Chesaapeake Bay and Its Tributaries, 1991.
- 1000 Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A., Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F. and
- 1001 Key, R.M.: Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms,
- 1002 Nature, 437, 681-686, https://doi.org/10.1038/nature04095, 2005.
- 1003 Orth, R. J., Nowak, J. F., Wilcox, D. J., Whiting, J. R., and Nagey, L. S.: Distribution of Submerged Aquatic Vegetation in the
- 1004 Chesapeake Bay and Tributaries and the Coastal Bays, Am. Zoöl., 3, 315–317, https://doi.org/10.1093/icb/3.3.315, 1998.
- 1005 Pacella, S.R., Brown, C.A., Kaldy, J.E., Labiosa, R.G., Hales, B., Mochon Collura, T.C. and Waldbusser, G.G.: Quantifying
- 1006 the combined impacts of anthropogenic CO2 emissions and watershed alteration on estuary acidification at biologically-
- 1007 relevant time scales: a case study from Tillamook Bay, OR, USA. Front. Mar. Sci., 11, 1293955, 1008 https://doi.org/10.3389/fmars.2024.1293955, 2024.
- 1009 Palmer, S. C. J., Gernez, P. M., Thomas, Y., Simis, S., Miller, P. I., Glize, P., and Barillé, L.: Remote Sensing-Driven Pacific
- 1010 Oyster (Crassostrea gigas) Growth Modeling to Inform Offshore Aquaculture Site Selection, Front. Mar. Sci., 6, 802, 1011 https://doi.org/10.3389/fmars.2019.00802, 2020.
- 1012 Palmer, S. C. J., Barillé, L., Kay, S., Ciavatta, S., Buck, B., and Gernez, P.: Pacific oyster (Crassostrea gigas) growth modelling
- 1013 and indicators for offshore aquaculture in Europe under climate change uncertainty, Aquaculture, 532, 736116,
 1014 https://doi.org/10.1016/j.aquaculture.2020.736116, 2021.
- Paynter, K. T., Goodwin, J. D., Chen, M. E., Ward, N. J., Sherman, M. W., Meritt, D. W., and Allen, S. K.: *Crassostrea ariakensis* in Chesapeake Bay: Growth, Disease and Mortality in Shallow Subtidal Environments, J. Shellfish Res., 27, 509–515, https://doi.org/10.2983/0730-8000(2008)27[509:caicbg]2.0.co;2, 2008.
- 1018 Peyre, M. K. L., Eberline, B. S., Soniat, T. M., and Peyre, J. F. L.: Differences in extreme low salinity timing and duration
- 1019 differentially affect eastern oyster (Crassostrea virginica) size class growth and mortality in Breton Sound, LA, Estuar., Coast.
- 1020 Shelf Sci., 135, 146–157, https://doi.org/10.1016/j.ecss.2013.10.001, 2013.
- 1021 Planton, S., Déqué, M., Chauvin, F., and Terray, L.: Expected impacts of climate change on extreme climate events, C. R.
- 1022 Geosci., 340, 564–574, https://doi.org/10.1016/j.crte.2008.07.009, 2008.
- Poach, M., Munroe, D., Vasslides, J., Abrahamsen, I. and Coffey, N.: Monitoring coastal acidification along the US East coast:
 concerns for shellfish production. Bull. Jap. Fish. Res. Edu. Agen. No, 49, 53-64, 2019.
- 1025 Ramajo, L., Pérez-León, E., Hendriks, I. E., Marbà, N., Krause-Jensen, D., Sejr, M. K., Blicher, M. E., Lagos, N. A., Olsen,
- 1026 Y. S., and Duarte, C. M.: Food supply confers calcifiers resistance to ocean acidification, Sci. Rep., 6, 19374, 1027 https://doi.org/10.1038/srep19374, 2016.
- 1028 Raymond, P. A., Bauer, J. E., and Cole, J. J.: Atmospheric CO₂ evasion, dissolved inorganic carbon production, and net
- 1029 heterotrophy in the York River estuary, Limnol. Oceanogr., 45, 1707–1717, https://doi.org/10.4319/lo.2000.45.8.1707, 2000.
- 1030 Riahi, K., Rao, S., Krey, V., Cho, C., Chirkov, V., Fischer, G., Kindermann, G., Nakicenovic, N., and Rafaj, P.: RCP 8.5-A
- 1031 scenario of comparatively high greenhouse gas emissions, Clim. Chang., 109, 33, https://doi.org/10.1007/s10584-011-0149-
- 1032 y, 2011.





- 1033 Redfield, A.C.: On the proportions of organic derivatives in sea water and their relation to the composition of plankton,
- 1034 University Press of Liverpool, Liverpool, UK, 1934.
- 1035 Reid, J.M., Reid, J.A., Jenkins, C.J., Hastings, M.E., Williams, S.J. and Poppe, L.J.: usSEABED: Atlantic coast offshore
- 1036 surficial sediment data release, US Geological Survey Data Series, 118, 2005.
- 1037 Rivest, E.B., Brush, M., Zimmerman, R., Hill., V," Can Meadows of Submerged Aquatic Vegetation (SAV) Mitigate Ocean
- 1038 Acidification Thresholds for Eastern Oysters in the Chesapeake Bay? Final report, NOAA Ocean Acidification Program.
- 1039 Award number NA18NOS4780177, 2023.
- 1040 Roden, E. and Tuttle, J.: Inorganic sulfur cycling in mid and lower Chesapeake Bay sediments, Mar. Ecol. Prog. Ser., 93, 101-
- 1041 118, https://doi.org/10.3354/meps093101, 1993.
- 1042 Rybovich, M., Peyre, M. K. L., Hall, S. G., and Peyre, J. F. L.: Increased Temperatures Combined with Lowered Salinities
- 1043 Differentially Impact Oyster Size Class Growth and Mortality, J. Shellfish Res., 35, 101–113, 1044 https://doi.org/10.2983/035.035.0112, 2016.
- Saavedra, L., Bastías, M., Mendoza, P., Lagos, N. A., García-Herrera, C., Ponce, V., Alvarez, F., and Llanos-Rivera, A.:
 Environmental correlates of oyster farming in an upwelling system: Implication upon growth, biomass production, shell
 strength and organic composition, Mar. Environ. Res., https://doi.org/10.1016/j.marenvres.2024.106489, 2024.
- 1048 Salisbury, J., Green, M., Hunt, C., and Campbell, J.: Coastal Acidification by Rivers: A Threat to Shellfish?, Eos, Trans. Am.
- 1049 Geophys. Union, 89, 513–513, https://doi.org/10.1029/2008eo500001, 2008.
- 1050 Schwaner, C., Barbosa, M., Schwemmer, T. G., Espinosa, E. P., and Allam, B.: Increased Food Resources Help Eastern Oyster
- 1051 Mitigate the Negative Impacts of Coastal Acidification, Animals, 13, 1161, https://doi.org/10.3390/ani13071161, 2023.
- 1052 Simone, M. N., Schulz, K. G., Oakes, J. M., and Eyre, B. D.: Warming and ocean acidification may decrease estuarine
- dissolved organic carbon export to the ocean, Biogeosciences, 18, 1823–1838, https://doi.org/10.5194/bg-18-1823-2021, 2021.
- 1054 Nixon, S.W.: Coastal marine eutrophication: A definition, social causes, and future concerns, Ophelia, 41, 199-219,
- 1055 htpps://doi.org/10.1080/00785236.1995.10422044, 1995.
- 1056 Shadwick, E. H., Friedrichs, M. A. M., Najjar, R. G., Meo, O. A. D., Friedman, J. R., Da, F., and Reay, W. G.: High-Frequency
- 1057 CO₂ System Variability Over the Winter-to-Spring Transition in a Coastal Plain Estuary, J. Geophys. Res.: Oceans, 124, 7626–
- 1058 7642, https://doi.org/10.1029/2019jc015246, 2019.
- 1059 Shchepetkin, A. F. and McWilliams, J. C.: The regional oceanic modeling system (ROMS): a split-explicit, free-surface,
- topography-following-coordinate oceanic model, Ocean Model., 9, 347–404, https://doi.org/10.1016/j.ocemod.2004.08.002,
 2005.
- 1062 Shen, C., Testa, J. M., Li, M., Cai, W., Waldbusser, G. G., Ni, W., Kemp, W. M., Cornwell, J., Chen, B., Brodeur, J., and Su,
- 1063 J.: Controls on Carbonate System Dynamics in a Coastal Plain Estuary: A Modeling Study, J. Geophys. Res.: Biogeosciences,
- 1064 124, 61-78, https://doi.org/10.1029/2018jg004802, 2019a.





- 1065 Shen, C., Testa, J. M., Ni, W., Cai, W., Li, M., and Kemp, W. M.: Ecosystem Metabolism and Carbon Balance in Chesapeake
- Bay: A 30-Year Analysis Using a Coupled Hydrodynamic-Biogeochemical Model, J. Geophys. Res.: Oceans, 124, 6141–
 6153, https://doi.org/10.1029/2019jc015296, 2019b.
- 1068 Shen, C., Testa, J. M., Li, M., and Cai, W.: Understanding Anthropogenic Impacts on pH and Aragonite Saturation State in
 - 1069 Chesapeake Bay: Insights From a 30-Year Model Study, J. Geophys. Res.: Biogeosciences, 125, 1070 https://doi.org/10.1029/2019jg005620, 2020.
 - 1071 Siedlecki, S. A., Pilcher, D., Howard, E. M., Deutsch, C., MacCready, P., Norton, E. L., Frenzel, H., Newton, J., Feely, R. A.,
 - 1072 Alin, S. R., and Klinger, T.: Coastal processes modify projections of some climate-driven stressors in the California Current
 - 1073 System, Biogeosciences, 18, 2871–2890, https://doi.org/10.5194/bg-18-2871-2021, 2021a.
 - 1074 Siedlecki, S., Salisbury, J., Gledhill, D., Bastidas, C., Meseck, S., McGarry, K., Hunt, C., Alexander, M., Lavoie, D., Wang,
 - 1075 Z., Scott, J., Brady, D., Mlsna, I., Azetsu-Scott, K., Liberti, C., Melrose, D., White, M., Pershing, A., Vandemark, D.,
 - 1076 Townsend, D., Chen, C., Mook, W., and Morrison, R.: Projecting ocean acidification impacts for the Gulf of Maine to 2050,
 - 1077 Elem.: Sci. Anthr., 9, https://doi.org/10.1525/elementa.2020.00062, 2021b.
 - 1078 Speights, C. J., Silliman, B. R., and McCoy, M. W.: The effects of elevated temperature and dissolved ρ CO₂ on a marine 1079 foundation species, Ecol. Evol., 7, 3808–3814, https://doi.org/10.1002/ece3.2969, 2017.
 - 1080 Simpson, E., Ianson, D., Kohfeld, K. E., Franco, A. C., Covert, P. A., Davelaar, M., and Perreault, Y.: Variability and drivers
 - 1081 of carbonate chemistry at shellfish aquaculture sites in the Salish Sea, British Columbia. Biogeosciences, 21, 1323-1353,
 - 1082 https://doi.org/10.5194/bg-21-1323-2024, 2024.
 - 1083 Stevens, A. and Gobler, C.: Interactive effects of acidification, hypoxia, and thermal stress on growth, respiration, and survival
 - 1084 of four North Atlantic bivalves, Mar. Ecol. Prog. Ser., 604, 143–161, https://doi.org/10.3354/meps12725, 2018.
 - 1085 St-Laurent, P. and Friedrichs, M. A. M.: On the Sensitivity of Coastal Hypoxia to Its External Physical Forcings, J. Adv.
 - 1086 Model. Earth Syst., 16, https://doi.org/10.1029/2023ms003845, 2024.
 - 1087 St-Laurent, P., Friedrichs, M. A. M., Najjar, R. G., Shadwick, E. H., Tian, H., and Yao, Y.: Relative impacts of global changes
 - and regional watershed changes on the inorganic carbon balance of the Chesapeake Bay, Biogeosciences, 17, 3779–3796,
 - 1089 https://doi.org/10.5194/bg-17-3779-2020, 2020.
 - 1090 Su, J., Cai, W.-J., Brodeur, J., Chen, B., Hussain, N., Yao, Y., Ni, C., Testa, J. M., Li, M., Xie, X., Ni, W., Scaboo, K. M., Xu,
 - 1091 Y., Cornwell, J., Gurbisz, C., Owens, M. S., Waldbusser, G. G., Dai, M., and Kemp, W. M.: Chesapeake Bay acidification
 - 1092 buffered by spatially decoupled carbonate mineral cycling, Nat. Geosci., 13, 441–447, https://doi.org/10.1038/s41561-020-1093 0584-3, 2020.
 - 1094 Swam, L. M., Couvillion, B., Callam, B., Peyre, J. F. L., and Peyre, M. K. L.: Defining oyster resource zones across coastal 1095 Louisiana for restoration and aquaculture, Ocean Coast. Manag., 225, 106178,
 - 1096 https://doi.org/10.1016/j.ocecoaman.2022.106178, 2022.





- 1097 Talmage, S. C. and Gobler, C. J.: Effects of Elevated Temperature and Carbon Dioxide on the Growth and Survival of Larvae 1098 of and Juveniles Three Species of Northwest Atlantic Bivalves, PLoS ONE. 6. e26941. 1099 https://doi.org/10.1371/journal.pone.0026941, 2011.
- 1100 Tian, R., Cerco, C. F., Bhatt, G., Linker, L. C., and Shenk, G. W.: Mechanisms Controlling Climate Warming Impact on the
- 1101 Occurrence of Hypoxia in Chesapeake Bay, JAWRA J. Am. Water Resour. Assoc., 58, 855-875, https://doi.org/10.1111/1752-
- 1102 1688.12907, 2022.
- 1103 Thomsen, J., Haynert, K., Wegner, K. M., and Melzner, F.: Impact of seawater carbonate chemistry on the calcification of
- 1104 marine bivalves, Biogeosciences, 12, 4209-4220, https://doi.org/10.5194/bg-12-4209-2015, 2015.
- Turner, J. S., St-Laurent, P., Friedrichs, M. A. M., and Friedrichs, C. T.: Effects of reduced shoreline erosion on Chesapeake 1105
- 1106 Bay water clarity, Sci. Total Environ., 769, 145157, https://doi.org/10.1016/j.scitotenv.2021.145157, 2021.
- van Heuven, S., D. Pierrot, J.W.B. Lewis, R.E., and Wallace, D.W.R.: MATLAB Program Developed for CO₂ System 1107
- 1108 Calculations. ORNL/CDIAC-105b. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S.
- 1109 Department of Energy, Oak Ridge, Tennessee. https://doi.org/10.3334/CDIAC/otg.CO2SYS_MATLAB_v1.1, 2011.
- 1110 VOSARA: https://cmap22.vims.edu/VOSARA/,last access: 28 January 2024.
- Waldbusser, G. G., Voigt, E. P., Bergschneider, H., Green, M. A., and Newell, R. I. E.: Biocalcification in the Eastern Oyster 1111
- 1112 (Crassostrea virginica) in Relation to Long-term Trends in Chesapeake Bay pH, Estuaries Coasts, 34, 221-231,
- 1113 https://doi.org/10.1007/s12237-010-9307-0, 2011.
- 1114 Wallace, R. B., Baumann, H., Grear, J. S., Aller, R. C., and Gobler, C. J.: Coastal ocean acidification: The other eutrophication
- 1115 problem, Estuar., Coast. Shelf Sci., 148, 1-13, https://doi.org/10.1016/j.ecss.2014.05.027, 2014.
- Warner, J. C., Defne, Z., Haas, K., and Arango, H. G.: A wetting and drying scheme for ROMS, Comput. Geosci., 58, 54-61, 1116 https://doi.org/10.1016/j.cageo.2013.05.004, 2013.
- 1117
- 1118 Zhang, Q., Fisher, T. R., Trentacoste, E. M., Buchanan, C., Gustafson, A. B., Karrh, R., Murphy, R. R., Keisman, J., Wu, C.,
- 1119 Tian, R., Testa, J. M., and Tango, P. J.: Nutrient limitation of phytoplankton in Chesapeake Bay: Development of an empirical
- approach for water-quality management, Water Res., 188, 116407, https://doi.org/10.1016/j.watres.2020.116407, 2021. 1120