

1 **Acidification, warming, and nutrient management are projected to** 2 **cause reductions in shell and tissue weights of oysters in a coastal plain** 3 **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 growth model for Eastern oysters (*Crassostrea virginica*) was embedded in a 3-D
15 coupled hydrodynamic-biogeochemistry model implemented for two tributaries in the lower Chesapeake Bay. Model
16 simulations were forced with projected future conditions (mid-21st century atmospheric CO₂ and atmospheric temperature
17 under representative concentration pathway (RCP) 8.5, as well as managed nutrient reductions) and compared with a realistic
18 present-day reference run. Together, all three stressors are projected to reduce Ω_{Ca} and growth of oyster shell and tissue.
19 Increased atmospheric CO₂ and temperature are both projected to cause widespread reductions in Ω_{Ca} . The resulting reductions
20 in oyster shell and tissue growth will be most severe along the tributary shoals. Future warming during peak oyster growing
21 seasons is projected to have the strongest negative influence on tissue and shell growth, due to summer water temperatures
22 reducing filtration rates, enhancing shell dissolution and oyster respiration rates, and increasing organic matter remineralization
23 rates, thus reducing food availability. Nutrient reductions will exacerbate deficits in oyster food availability, contributing to
24 further reductions in growth. Quantifying the effects of these stressors provides insight on the areas in the lower bay where
25 oysters will be most vulnerable to mid 21st-century conditions.

26

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

31 1 Introduction

32 Anthropogenic climate change and its associated impacts on water quality may threaten marine organisms and
33 economic systems reliant on them. Oceanic uptake of increasing anthropogenic atmospheric carbon dioxide (CO₂) causes a
34 decrease in seawater pH and saturation states of calcium carbonate (e.g., Ω_{Ca}), a phenomenon known as ocean acidification
35 (Caldeira and Wickett, 2003; Doney et al., 2009). Globally, the ocean has absorbed about 30% of anthropogenic atmospheric
36 CO₂ since pre-industrial times (Gruber et al., 2019), and open-ocean surface pH is anticipated to decrease by 0.3 units on
37 average relative to the 2010s by the end of the century under ‘business-as-usual’ conditions (Riahi et al., 2011; IPCC, 2019).
38 The percent volume of ocean water undersaturated with calcite ($\Omega_{Ca} < 1$), a condition associated with elevated energetic costs
39 of shell-building for calcifying organisms, is predicted to expand to 91% by 2100 from 76% in the 1990s (Caldeira and Wickett,
40 2005; Gattuso et al., 2015). Concurrently, the global ocean has absorbed approximately 93% of the atmospheric heat produced
41 by anthropogenic activity, leading to a global sea surface temperature increase of 0.7°C since 1900 (Jewett and Romanou,
42 2017). Ocean warming is expected to continue, with global averages increasing by 2.7°C by 2100 and greater increases
43 expected in shallow coastal regions (Jewett and Romanou, 2017).

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

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
63 concentrations of CO₂ and H⁺ increase, and concentrations of carbonate ions ([CO₃²⁻]) decrease. A low ambient [CO₃²⁻] inhibits

64 calcifying organisms from forming CaCO_3 for their shells, as more energy is required to precipitate CO_3^{2-} from acidified waters
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
66 net dissolution of CaCO_3 , leading to weaker shells and greater juvenile susceptibility to predation (e.g., Waldbusser et al.,
67 2011; Amaral et al., 2012; Barclay et al., 2020). Acidification may further reduce shell growth through adverse physiological
68 effects that limit energy availability for calcification. Because acidification is often more extreme in estuaries, coastal bivalve
69 species experience stronger effects of climate change than organisms living in open-ocean environments (Poach et al., 2019;
70 Melzner et al., 2020; Cai et al., 2021). Oysters in particular are of high management and research interest due to their
71 commercial value in the United States (USDA, 2023). Prior experiments have revealed negative effects of acidification,
72 warming, and nutrient reductions on oyster biocalcification and growth (Beniash et al., 2010; Waldbusser et al., 2011; Gobler
73 and Talmage, 2014), but it is yet to be determined how the impacts of these stressors on oyster shell and tissue growth will
74 vary spatially in highly dynamic systems.

75 The Chesapeake Bay is an excellent study system for examining the interacting influences of acidification, warming,
76 and nutrient reductions (hereafter referred to collectively as “future stressors”) on estuarine biogeochemistry and the organisms
77 living there. The bay exhibits high temporal and spatial variability in pH due to seasonal phytoplankton blooms, eutrophication,
78 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
79 to mid-2010s, surface waters in the upper bay experienced pH increases between +0.2 and +0.4 pH units in early spring and
80 fall due to increased riverine TA from reduced acid mine drainage and lowered nitrate inputs, while surface waters in the
81 nitrogen-limited middle bay decreased up to -0.24 pH units during late spring and summer as a result of decreased primary
82 production (Da et al., 2021). Over the same time period, the bay warmed by $0.24 \pm 0.15^\circ\text{C}$ per decade (Hinson et al., 2022),
83 more than double the average rate of warming for the upper 75m of the global ocean (Rhein et al., 2013). Warming has also
84 led to more severe hypoxia (Irby et al., 2018; Ni et al., 2020; Frankel et al., 2022; Hinson et al., 2023; Hinson et al., 2024). In
85 2010, the Environmental Protection Agency mandated a Total Maximum Daily Load (TMDL) of pollutants from point and
86 non-point sources to be achieved by 2025 (EPA, 2010). As nutrient reductions negatively affect pH in surface waters of the
87 bay (Shen et al., 2020; Da et al., 2021), achieving the TMDLs may actually worsen acidification in shallow and near-shore
88 regions. Much of the research effort devoted to characterizing present-day carbonate chemistry and its historical trends has
89 focused on the mainstem and upper Chesapeake Bay (Cai et al., 2017; Shen et al., 2020; Su et al., 2020), and less is known
90 about these conditions throughout the tributaries of the lower bay (Shadwick et al., 2019).

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

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

This study addresses the following primary research question: How and where will carbonate chemistry and Eastern oyster growth in the lower Chesapeake Bay change in the future and which future stressors will drive these changes? A three-dimensional hydrodynamic-biogeochemical model is coupled with an oyster growth model and is applied to two major 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 interacting influences of future environmental change on carbonate chemistry and Eastern oysters. This study provides insight into which areas are most vulnerable to mid 21st-century acidification and how acidification, warming, and nutrient loading may each impact oyster growth in isolation as well as via simultaneous co-stressors.

2 Methods

2.1 Model description

2.1.1 Hydrodynamic model

This study uses the three-dimensional hydrodynamic Regional Ocean Modeling System (ROMS; Shchepetkin and 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 Rappahannock Rivers, as well as a portion of the mainstem shoal north of the Rappahannock. The model grid consists of 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 and two primary state variables: practical salinity and potential temperature. A wetting and drying scheme has been implemented to represent water levels and currents in coastal grid cells (Warner et al., 2013; St-Laurent and Friedrichs, 2024).

2.1.2 Carbon and biogeochemistry model

The Estuarine-Carbon-Biogeochemistry model (ECB) embedded in ROMS and used in this study has previously been 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

128 levels, represented by the following state variables: nitrate, ammonium, phytoplankton and zooplankton nitrogen, small and
129 large detrital nitrogen and carbon, semi-labile and refractory dissolved organic nitrogen and carbon, DIC, TA, and dissolved
130 oxygen (O₂). Phytoplankton and zooplankton carbon are calculated from fixed C:N ratios (Redfield, 1934; Hopkinson et al.,
131 1998). C:N ratios for dissolved organic matter in the estuary are allowed to freely evolve with time. Biogeochemical processes
132 include primary production, aggregation, sinking, basal metabolism, exudation, sloppy feeding, excretion, metabolism,
133 nitrification/denitrification, remineralization, grazing, and mortality. Biogeochemical sources and sinks are included in the
134 bottom vertical level (e.g., burial, resuspension, nitrification/denitrification, remineralization, sediment O₂ and CO₂ exchange).
135 Light attenuation throughout the water column is based on the diffuse attenuation coefficient (K_d), which is parameterized as
136 a function of surface total suspended solids (TSS; including inorganic and organic components) and salinity as a proxy for
137 colored dissolved organic matter (Feng et al., 2015; Turner et al., 2021). TSS is calculated within the model as the sum of the
138 four inorganic suspended sediment size classes and particulate organic matter. Particulate organic carbon (POC) is calculated
139 as the sum of phytoplankton carbon, zooplankton carbon, and small and large detrital carbon. The sediment transport module
140 within ECB accounts for sediment-water exchange processes, such as deposition and resuspension of inorganic sediment and
141 particulate organic matter, and is comprised of two vertical seabed layers that simulate four suspended sediment size classes
142 (Turner et al., 2021).

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

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

2.1.3 Oyster growth model

As part of this study, the oyster growth model EcoOyster (Brush and Kellogg, 2018; Kellogg et al., 2018) has been one-way coupled to ROMS-ECB in the deepest (bottom) level (see Supplementary Tables S1-S4 for EcoOyster equations). The one-way coupling means that environmental conditions from ROMS-ECB influence oyster growth in EcoOyster, but the oysters do not influence water quality conditions in ROMS-ECB. This allows the focus of our analysis to be on the effect of future climate change on oyster growth, rather than the effect of oyster growth on water quality, which has been previously studied in the Chesapeake Bay (e.g., Gawde et al., 2024). By focusing on the deepest vertical level of the model, the assumption is that oysters are growing on the bottom, and not inside floating cages. This is representative of conditions similar to on-bottom or bottom cage aquaculture methods that are common in Virginia. The coupled model, referred to hereafter as ROMS-ECBO, simulates daily somatic tissue dry weight, gonadal tissue dry weight, shell dry weight, and shell height of diploid and triploid oysters as a function of filtration, respiration, egestion, allocation to reproduction, calcification, and dissolution (Brush and Kellogg, 2018; Kellogg et al., 2018; Rivest et al., 2020). For the purpose of this study, only diploid oysters were included, as model equations were developed from a study on diploid oysters (Rivest et al., 2020), and triploid allometric equations are not as well constrained. Tissue growth rates depend on individual weight together with temperature, salinity, O₂, TSS, and POC from ROMS-ECB. Chla is required for the filtration function and is calculated from ROMS-ECB phytoplankton carbon and K_d, 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., 2020).

The *EcoOyster* equations were developed from a meta-analysis of existing oyster growth models and laboratory experiments with diploid oysters (Brush and Kellogg, 2018; Kellogg et al., 2018; Rivest et al., 2020). Allometric relationships between shell dry weight, tissue dry weight, and shell height used for initial conditions were derived from observational data in the Chesapeake Bay (VOSARA, 2024). Total dry tissue weight is calculated as the sum of somatic tissue weight and gonadal weight. Reproduction is simulated through gonadal weight, a function of growth of gonadal tissue, resorption of gonadal tissue, and spawning (Hofmann et al., 1994). Somatic tissue weight is a function of assimilation, respiration, growth of gonadal tissue, and resorption of gonadal tissue. Assimilation is a function of filtration and POC. Filtration is a function of a maximum filtration rate based on tissue weight, limited by sub-optimal temperature, salinity, TSS, O₂, and chl_a (Cerco and Noel, 2005; Fulford et al., 2007; Ehrich and Harris, 2015). The optimal temperature for oyster filtration (T_{opt}) is set to 27 °C (Jordan, 1987). Filtration is also multiplied by p , a tunable factor representing the proportion of computed filtration actually performed by oysters, which accounts for processes excluded from the model such as time spent filtering and is constrained by published growth rates. Respiration is a function of tissue weight, temperature, and assimilation. While filtration has a temperature limitation, respiration increases exponentially with temperature (Fig. S1). Tissue growth functions are not affected by

195 carbonate chemistry variables, as experimental studies have found that neither filtration (Lemasson et al., 2018) nor respiration
196 (Beniash et al., 2010; Matoo et al., 2013) of oysters are affected by pH changes; however, weight-specific net calcification is
197 a function of Ω_{Ca} and temperature (Rivest et al., 2020). Shell growth is a function of both total tissue weight and net
198 calcification.

199 **2.2 Present day reference simulation**

200 A realistic reference simulation was generated to represent 2017 conditions. The year 2017 was chosen for
201 atmospheric, terrestrial, and open-ocean boundary conditions as this represents a relatively typical hydrological year.
202 Atmospheric forcings (air temperature, long- and short-wave radiation, precipitation, winds, dewpoint temperature, and air
203 pressure) are obtained from the ERA5 atmospheric reanalysis (Copernicus Climate Change Service, 2017; Hersbach et al.,
204 2020). Surface atmospheric variables are available at 3-hourly intervals with a 0.25° resolution and are interpolated to a 0.2°
205 grid. Terrestrial inputs of freshwater, nitrogen, carbon, and sediment are derived from the Phase 6 CBP Watershed Model
206 (CBPWM; Bhatt et al., 2023) and USGS data. Daily estimates of freshwater discharge, water temperature, and loadings of
207 nitrate, ammonium, organic nitrogen, and four classes of sediment from the CBPWM were concatenated to 74 locations
208 throughout the model domain. To compute carbon loadings, constant carbon-to-nitrogen ratios are used, specifically 10:1 for
209 dissolved organic matter (Hopkinson et al., 1998) and 6.625:1 for particulate organic matter (Redfield, 1934). Riverine TA
210 concentrations are computed as in Da et al. (2024), using monthly-varying linear relationships between historical USGS
211 observations of discharge and USGS TA estimates determined using the Weighted Regression on Time, Discharge, and Season
212 (WRTDS; Hirsch et al., 2010) approach. Riverine DIC is calculated from daily riverine TA and daily DIC:TA ratios, linearly
213 interpolated from the monthly climatology of USGS WRTDS DIC:TA in each tributary. Open boundary conditions are derived
214 from a recent 600 m resolution whole-bay implementation of ROMS (St-Laurent and Friedrichs, 2024). Initial conditions for
215 the six-month spin-up were derived from Da et al., (2024).

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

222 **2.3 Comparison of reference simulation to in situ observations**

223 *In situ* water quality monitoring observations are available since 1984 throughout the Chesapeake Bay. Specifically,
224 the Chesapeake Bay Program's Water Quality Monitoring Program (CBP WQMP) conducts cruises in the Bay and its
225 tributaries. On average, stations are sampled once monthly, with the exception of June through August in the mainstem, when
226 sampling occurs twice. In this study, measurements of water temperature, salinity, O₂, pH (NBS scale), TSS, and POC are

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 meters of the water column. TSS and POC are obtained from bottle samples at the surface, bottom, and at deeper stations, two additional depths above and below the pycnocline. TSS is determined by filtering a known volume of water through a pre-weighted filter and then re-weighing the filter after filtration and drying. POC is determined through combustion of a filter using an elemental analyzer (Olsen, 2012).

Model skill was evaluated by comparing results from the reference simulation to the CBP WQMP observations 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, TSS, and POC, were compared with observations from the same station and time, within the bottom 10% of the water column (Table 1). Model bias and root-mean squared difference (RMSD) were computed for all aforementioned variables. Seasonal skill was also evaluated by comparing the 2017 reference run to CBP decadal averages. Decadal means were used for these comparisons, as once-monthly or once-seasonally sampling dates in 2017 bias outputs toward conditions on the time of the month when the measurements were taken in 2017, and the purpose of the comparison was to examine how the model reproduces average seasonal variability.

2.4 Future simulations

In addition to the reference run, this study generated five future simulations (Table 1) to investigate the change in carbonate chemistry conditions and oyster growth resulting from three drivers of future change in the bay: increased atmospheric CO₂ (*AtmCO₂*), 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 CO₂ concentration for the *AtmCO₂* 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). While it is reasonable to assume that warming temperatures will always accompany increases in atmospheric CO₂, separate experiments for each stressor were conducted. Isolating the physiological effects of each stressor helps us understand the mechanisms effecting the change in oyster growth and furthermore indicates the degree to which management strategies for offsetting acidification can reduce the effects of climate change on oysters. Future atmospheric temperature for the *Temp* and *Combined Future* simulations was obtained from the IPSL-CM5B-LR Earth System Model (Dufresne et al., 2013), statistically downscaled with the Multivariate Adaptive Constructed Analogs method (Abatzoglou and Brown, 2012). IPSL-CM5B-LR was selected as in Hinson et al. (2024), since it was deemed the most representative downscaled ESM of the 20 available (Hinson et al., 2023). As in Hinson et al. (2024), the delta method was used to calculate the daily average change in atmospheric temperatures between present-day and future conditions. To calculate this change, two 30-year climatologies, centered on 2000 and 2050 respectively, were computed and

260 daily averaged 50-year differences between the two climatologies (Fig. 2) were added to the atmospheric temperatures used
261 in the reference run. Future watershed inputs for the *TMDL* and *Combined Future* simulations included a climatology of nitrate,
262 ammonium, dissolved organic matter, and particulate organic matter concentrations, derived from a Phase 6 CBPWM 1991-
263 2000 run using reduced nutrient concentrations assuming the TMDLs had been successfully achieved (approximately a 20-
264 25% mean reduction in total nutrient loading; Bhatt et al., 2023). Freshwater discharge in this run was set to be identical to the
265 reference run, to isolate the effects of lowered nutrient concentrations on water chemistry and oyster growth. Since future
266 climate change is expected to impact terrestrial inputs much less than future management actions (Hinson et al., 2023), the
267 direct impact of climate change on the watershed is not considered in this analysis. A fifth simulation (*AtmCO₂ + Temp*) was
268 run to compare the influences of local management actions to the combined drivers of climate change, which includes both
269 future atmospheric CO₂ concentration and atmospheric temperature. Preliminary investigations revealed a minimal impact of
270 sea level rise on Ω_{Ca} in the bay; therefore, it was not included in the simulated climate change variables.

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

281 **3 Results**

282 **3.1 Model Skill Assessment**

283 When compared to 2017 WQMP observations and seasonal decadal averages, model skill of ROMS-ECB is
284 reasonably high (Table 2, Figs. 3, 4), and similar to other model implementations of the Chesapeake Bay (Irby et al., 2016).
285 Temperature and salinity are reproduced relatively well year-round (Fig. 3a,b) with annual biases of only 0.2°C and -1.5,
286 respectively (Table 2). Bottom O₂ and pH are slightly overestimated, exhibiting the greatest model-data misfit in the spring
287 and summer months in the tributary channels (Fig. 3c,d). pH is overestimated by 0.2 units, which is within the accuracy of the
288 electrode measurements. Observed POC concentrations in the York and upper Rappahannock are higher than simulated in the
289 model and exhibit very high spatial variability (Fig. 4a). Despite the high spatial variability of the TSS observations (Fig. 4b),
290 mean TSS ($45 \pm 54 \text{ mg L}^{-1}$) is captured within 1.1 mg L^{-1} by the model.

291 Growth rates determined using the *EcoOyster* equations and environmental outputs from ROMS-ECB were compared
292 with oyster data collected in the York River (Paynter et al., 2008; Liddel, 2008; Kingsley-Smith et al., 2009; Degremont et al.,
293 2012; Callam et al., 2016). Specifically, the tunable parameter (p) that limits oyster filtration was adjusted to provide a best
294 match between the modeled oyster growth rates and the published rates. Multiple p -values were tested, and a value of $p=0.15$
295 resulted in modeled oyster growth that best matched published growth rates. The resulting shell growth predicted by the model
296 was found to be close to the *in situ* data (52.0 ± 1.1 mm y^{-1} and 51.3 ± 2.9 mm y^{-1} for the model and observation means and
297 standard deviations, respectively).

298 3.2 Reference run results

299 In the present-day reference run, the environmental variables used as inputs to the oyster parameterizations exhibit
300 substantial seasonal (Fig. 5a-f) and spatial (Figs. 6, S3) variability. As expected, bottom temperature is highest in summer,
301 reaching an average of 29.3 °C in July when averaged across grid cells that support oyster growth (Fig. 5a). Temperature is
302 higher in the shallower parts of the tributaries compared to the channels (Fig. S3a). Bottom salinity exhibits higher values in
303 the fall and winter, reaching a maximum average of 17.7 in October, and drops in the spring and summer to reach a minimum
304 average of 12.3 in June (Fig. 5b). Annual average bottom salinity ranges from 0 to 26 throughout the model domain (Fig. S3b),
305 with the highest values in the southern areas in closest proximity to the open-ocean. The seasonal cycle for bottom POC is
306 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
307 also varies widely throughout the model domain (Fig. 6a), with relatively higher values in the Rappahannock compared to the
308 York River, along the shoals of the tributaries, and along the western shoals of the mainstem Bay north of the Rappahannock.
309 Ω_{Ca} exhibits an annual cycle similar to that of temperature and POC, reaching a maximum average of 3.2 in August and a
310 minimum average of 1.1 in January (Fig. 5d). Annual mean bottom Ω_{Ca} also varies widely throughout the model domain (Fig.
311 6d). Generally, bottom Ω_{Ca} increases with salinity, with low to zero values in the tidal fresh portions of the upper tributaries
312 and higher values along the western shoals of the mainstem Chesapeake Bay. The opposite temporal pattern is seen in bottom
313 O_2 , 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). O_2 concentrations are
314 highest along the shoals and lowest in the deep channels (Fig. S3c). Bottom TSS concentrations exhibit tidal variability
315 throughout the year and are highest in the York River with much lower concentrations observed in the other portions of the
316 model domain (Fig. S3d).

317 Tissue and shell weights increase modestly from July through April, and the highest rates of increase are seen in May
318 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
319 tissue weight are nearly identical (Fig. 7), as tissue growth largely drives shell growth (Table S4). Both shell and tissue weights
320 are highest along the shoals of the York and Rappahannock Rivers (Fig. 7a,d) and low in the deeper waters where TSS
321 concentrations are high (Fig. S3d). A wider region of high shell and tissue weight appears in the Rappahannock, while the
322 highest weights in the York are confined to a very narrow and shallow strip along the coastline. Shell and tissue weights are

323 higher along the southwestern than the northeastern coastlines of the tributaries, where the shoals are wider in both tributaries
324 (Fig. 1a).

325 3.3 Results of Combined Future simulation

326 All environmental variables examined exhibit change from the reference run in the *Combined Future* simulation.
327 Temperature and salinity are projected to increase across the entire model domain (Fig. S3a,b). When averaged over the model
328 domain, temperature is projected to increase by $1.5 \pm 0.26^\circ\text{C}$, and salinity is projected to increase by 0.21 ± 0.11 (Table S5).
329 Bottom POC is projected to decrease by $0.07 \pm 0.05 \text{ g C m}^{-3}$ (Table S5), with POC reductions predicted to be most pronounced
330 in the mid- to upper tributaries (Fig. 6c). Mid-century bottom Ω_{Ca} is projected to be lower throughout most of the region (Fig.
331 6f), with an average reduction of 0.8 ± 0.19 over the whole model domain (Table S5). The spatial distribution of future Ω_{Ca} is
332 generally consistent with present-day Ω_{Ca} patterns, and the greatest decreases are projected to occur in regions with the highest
333 present-day Ω_{Ca} (Fig. 6 d,e,f). An average reduction in O_2 of $0.3 \pm 0.08 \text{ mg L}^{-1}$ is predicted across the model domain (Table
334 S5), which will be mostly spatially uniform (Fig. S3c). TSS is projected to be reduced by $0.20 \pm 0.25 \text{ mg L}^{-1}$ with high spatial
335 variability in the projected change (Table S5; Fig. S3d).

336 Changes in environmental conditions do not occur uniformly throughout the year. Temporal changes in environmental
337 conditions averaged across grid cells that support oyster growth are provided in Figure 5. Annually averaged increases in
338 temperature and salinity are the same when averaged over only grid cells that support oyster growth as they are when averaged
339 across the entire model domain (Tables 3, S5). The greatest temperature increases are projected to occur in the warmer months,
340 with an average increase of 1.6°C predicted for June through August and an average increase of 1.2°C predicted for December
341 through February. Bottom temperatures are projected to surpass the optimal temperature for oyster filtration (27°C) primarily
342 in July and August (Fig. 5a). Salinity increases are projected to be greatest at the beginning of the year, with an average increase
343 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
344 grid cells that support oyster growth is expected to decrease slightly less than the average for the entire region (Tables 3, S5),
345 by an annual average of 0.09 g C m^{-3} , with the greatest reductions in the spring and summer and little to no change in the
346 winter (Fig. 5c). For Ω_{Ca} , O_2 , and TSS, projected reductions are slightly greater at oyster growth sites than for the entire domain.
347 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
348 to decrease year-round, though with slightly greater reductions in the winter (Fig. 5e) and an annual average reduction of 0.4
349 $\text{mg O}_2 \text{ L}^{-1}$ (Table 3). TSS is projected to decrease annually by 0.3 mg L^{-1} (Table 3), mostly in the spring, due to lowered POC
350 (Fig. 5f).

351 Modeled shell and tissue weights after one year of growth are projected to decline in all regions that exhibit present-
352 day growth, with the most severe reductions (up to 100%) occurring along the York and Rappahannock River shoals (Figs.
353 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
354 oyster growth (Table 4). Shell weight, which is largely driven by changes in tissue weight, is projected to be reduced by 11.4
355 g on average after one year of growth, representing a 68% reduction in average shell weight in regions that support oyster

356 growth (Table 4). The greatest reduction in shell and tissue growth rates will occur in the warmer months near the end of the
357 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
358 d^{-1} from December through February), as the least growth occurs during that time (Fig. 5g,h). Shell thickness, calculated as
359 the ratio of shell weight to shell height, will be reduced by 61% on average (0.11 g mm^{-1} ; Table 4).

360 Declines in year one shell weight will vary throughout the model domain (Fig. 8), following relative changes in
361 bottom POC and Ω_{Ca} (Fig. 9). The mainstem has the most moderate reduction in shell weight relative to reference shell weight,
362 with an average reduction of 31%, indicated by the slope of the scatterplot. Shell weights in the Rappahannock and York face
363 the steepest reductions relative to reference, with average reductions of 86% and 96%, respectively, and a large portion of
364 York oysters facing complete depletion of oyster tissue and shell in these locations (Fig. 9; indicated by proximity to 1:1 line).
365 Proportional shell weight reductions in the mainstem are projected to correlate with POC reductions (Fig. 9a). For Ω_{Ca} in the
366 mainstem, a group of sites face the greatest proportional reductions when Ω_{Ca} reductions are the greatest. However, for sites
367 with lower proportional shell loss, the opposite trend is observed (Fig 9d). In the Rappahannock, higher POC reductions
368 coincide with slightly lower proportional shell loss (Fig. 9b). Sites with the largest reductions in POC primarily occur in the
369 York (Fig. 9c; see dark blue symbols on the 1:1 line), and the greatest proportional shell weight reductions coincide with the
370 greatest POC and Ω_{Ca} reductions (Fig. 9c,f). Similar results are found for tissue weight (not shown).

371 3.4 Results of individual future sensitivity simulations

372 Four individual future sensitivity simulations were conducted to isolate the specific mechanisms (increased
373 atmospheric CO_2 , increased atmospheric temperature, and/or nutrient reductions) causing the projected changes described
374 above in the *Combined Future* simulation. The *AtmCO₂* sensitivity simulation produces substantial reductions in average
375 bottom Ω_{Ca} (Fig. 10d) and, as expected, is not projected to substantially impact bottom temperature, salinity, POC, O_2 , or TSS
376 (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
377 magnitude than the average reduction for the entire model domain (Table S5), as greater reductions are expected along the
378 shoals of the Rappahannock and mainstem shoal than the York and upper section of the Rappahannock (Fig. 10d). In this
379 *AtmCO₂* simulation, shell weight is predicted to be most steeply reduced in the Rappahannock, with less impact in the York
380 and mainstem regions (Fig. 11a). At grid cells with oyster growth, *AtmCO₂* produces a shell weight reduction of 6.3 g and a
381 shell thickness reduction of 0.06 g mm^{-1} in comparison to the reference simulation, but no change in tissue weight (Table 4).

382 The *Temp* sensitivity simulation produces changes in all environmental variables impacting oyster growth, with the
383 exception of Ω_{Ca} (Tables 3, S5). Average changes in temperature, salinity, and TSS will be identical to those from the
384 *Combined Future* simulation (Tables 3, S5). Predicted reductions in POC and O_2 will be smaller in magnitude than in
385 *Combined Future*, though more severe than any other single sensitivity experiment (Table 3, S5). Temperature and salinity
386 will increase across the entire model domain, with a greater salinity increase occurring in the Rappahannock and along the
387 mainstem shoal (Fig. S4a-c). TSS will decrease primarily in the channels of the lower York and Rappahannock and on the
388 mainstem shoal (Fig. S4d). POC reductions are expected to cover the majority of the model domain, with larger reductions in

389 the upper Rappahannock (Fig. 10b). Slight increases in Ω_{Ca} are observed in shallow tidal creeks (Fig. 10e); however, no
390 substantial change in average Ω_{Ca} is predicted (Table 3, S5). O_2 at oyster grid cells will exhibit a similar but slightly smaller
391 average reduction compared to *Combined Future* (Table 3). Patterns of change in shell weight in the *Temp* sensitivity
392 simulation resemble those in the *AtmCO₂* simulation (Figs. 7c, 11b), with additional reductions along the mainstem shoal and
393 a greater predicted mean reduction of 7.1 g, a 42% decrease at grid cells with oyster growth (Table 4). Unlike *AtmCO₂*, tissue
394 weight will decrease in *Temp*, by an average of 1 g, a 46% reduction (Table 4).

395 The *TMDL* sensitivity simulation produces a much smaller average change in environmental conditions than the
396 *AtmCO₂* or *Temp* simulations (Tables 3, S5). *TMDL* does not substantially influence temperature, salinity, or O_2 (Tables 3, S4,
397 S5), but produces POC and TSS reductions close to the averages for *Temp* (Tables 3, S5). While POC change in the *Temp*
398 simulation is concentrated in the deeper portions of the tributaries (Fig. 10b), the POC reductions in the *TMDL* simulation are
399 concentrated along the shoals of the tributaries, with the greatest reductions in the upper Rappahannock (Fig. 10c). TSS changes
400 in *TMDL* are limited to the tributaries, occurring along the shoals of the Rappahannock and in patches throughout the York
401 (Fig. S4d). Future change in Ω_{Ca} in this simulation is less than for *AtmCO₂* and is largely confined to the upper Rappahannock
402 shoals and in shallow tidal creeks throughout the study region (Fig. 10d, f). Patterns of change in shell weight will resemble
403 *AtmCO₂* and *Temp* in the tributaries, but no change is predicted along the mainstem shoal (Fig. 11a-c). The *TMDL* simulation
404 produces reduced shell (3.7 g) and tissue (0.5 g) weights, with a smaller negative influence on shell and tissue weight than
405 *Temp* (Table 4; Fig. 11b-f).

406 Environmental conditions in the *AtmCO₂* + *Temp* simulation are nearly identical to those in the *Temp* simulation
407 (Tables 3, S5), with the exception of Ω_{Ca} , which is lower due to the influence of heightened atmospheric CO_2 . As tissue growth
408 is unaffected by Ω_{Ca} , tissue weight in this simulation is identical to that of the *Temp* simulation (Table 4). Average shell weight
409 reduction in *AtmCO₂* + *Temp* is 10.2 g, greater than that from *AtmCO₂* alone, due to the combined influences of lowered tissue
410 growth and lower Ω_{Ca} (Table 4).

411 4 Discussion

412 This study provides high-resolution projections for oyster growing conditions and corresponding oyster growth in the
413 Chesapeake Bay, with a specific focus on two Virginia tributaries. A high-resolution hydrodynamic-biogeochemical model
414 was coupled with an Eastern oyster growth model and forced with future projections for atmospheric CO_2 , temperature, and
415 nutrient management. An overall reduction in Ω_{Ca} and oyster growth are predicted by mid-century throughout the study region
416 under the combined effects of all three future stressors. Specifically, the greatest reductions in oyster growth are projected to
417 occur in the York and Rappahannock Rivers, where unfavorable conditions for calcification will expand in the future and
418 where food availability will be strongly impacted by warming and nutrient reductions. Bottom conditions in the York and
419 Rappahannock rivers, particularly in the upper portions, will likely be unsuitable for aquaculture at mid-century on average,
420 indicating climate change preparedness is critical for the oyster aquaculture industry.

4.1 Future projections of Ω_{Ca}

The magnitude of future change in Ω_{Ca} varies with present-day Ω_{Ca} conditions (Fig. 6d-f). Regions with high present-day Ω_{Ca} , primarily the mainstem shoals, are projected to experience the greatest reductions because of their low partial pressure of CO_2 (pCO_2) relative to fresher waters. Biologically driven low pCO_2 water on mainstem shoals has a greater capacity for CO_2 uptake from the atmosphere than high pCO_2 water, which is causing the fresher tributaries to experience smaller increases in DIC and smaller reductions in Ω_{Ca} (Fig. 6f). Acidic freshwater input often causes pCO_2 in the upper tributaries to exceed atmospheric pCO_2 , causing outgassing (Cai et al., 2017; Shen et al., 2019b; St-Laurent et al., 2020; Cai et al., 2021). Despite the lower 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 Rappahannock than the lower York (Da et al. 2021), so the lower Rappahannock cannot resist changes in carbonate chemistry to the same degree as the York. As a result, we observe the Rappahannock changing faster than the York (Fig. 6f, Fig. 9). Since higher Ω_{Ca} regions will experience greater reductions than lower Ω_{Ca} regions (Fig. 6d-f), the overall spatial variability of Ω_{Ca} will be reduced by mid-century, and more areas will experience conditions that are unfavorable for oyster shell-building (Fig. 5).

Although future atmospheric CO_2 and reduced nutrient loading will both contribute to Ω_{Ca} reductions, the modeling experiments conducted here highlight that increasing atmospheric CO_2 is the largest contributor to decreases in Ω_{Ca} throughout the study region. Increased atmospheric CO_2 will cause reductions in Ω_{Ca} across the model domain, while nutrient reductions are expected to mainly influence Ω_{Ca} in shallow and fresh coastal areas, with little influence in oyster growing regions. The effects of warming on Ω_{Ca} may slightly offset the influence of atmospheric CO_2 in certain areas, but this will likely only occur in fresh tidal creeks where oysters do not currently reside (Fig. 10e). Given the importance of atmospheric CO_2 in shaping future Ω_{Ca} conditions in the lower bay, reductions in anthropogenic carbon emissions will be necessary to lessen the projected 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 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 California Current System between 2000 and 2100 under the same future emissions scenario used in our study, i.e., RCP8.5. Projections from the present work indicate a similar magnitude of reduction 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 relative differences in rates of acidification should be considered, however, in the context of present-day Ω_{Ca} . The Pacific 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., 2012). Therefore, while the Chesapeake Bay is acidifying faster, coastal Pacific waters may become undersaturated with calcite 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 the importance of climate change preparedness and resilience in the Chesapeake Bay region.

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

462 4.2 Future projections of oyster growth

463 Acidification, warming, and nutrient reductions are projected to affect shell and tissue growth of oysters in different
464 ways. Here, increased atmospheric CO₂ caused reductions in shell growth of Eastern oysters due to its negative effect on Ω_{Ca}
465 and thus calcification rates, which is consistent with experimental studies (Waldbusser et al., 2011; Gobler and Talmage, 2014;
466 Himes et al., 2024). Shell weight reductions from increased atmospheric CO₂ were driven by changes in calcification rate
467 alone, as tissue weight in *EcoOyster* is unaffected by Ω_{Ca} (Fig. 11d; Rivest et al., 2020). Experimental studies have identified
468 indirect physiological impacts of elevated CO₂ on juvenile/adult oyster metabolism, growth, and reproduction (Beniash et al.,
469 2010; Dickinson et al., 2012), suggesting that increased atmospheric CO₂ can sometimes influence tissue growth. Further
470 investigation is necessary in order to include the relationship between atmospheric CO₂ and oyster tissue growth in *EcoOyster*.
471 Biological and chemical reactions occur faster at higher temperatures, meaning calcification rates may be higher under future
472 warming conditions (Waldbusser et al., 2011), as long as Ω_{Ca} is still high enough to support calcification. Conversely, under
473 conditions of extreme low Ω_{Ca} , warming may exacerbate dissolution rates and shell weight reductions. Our results also show
474 that nutrient reductions will lead to reductions in shell weight, largely driven by a reduction in tissue weight resulting from
475 lower food availability (POC), rather than lower Ω_{Ca} .

476 While nutrient reductions are projected to have little influence on Ω_{Ca} in this study, their negative influence on food
477 availability may be detrimental to tissue growth in certain parts of the study region, particularly the York River. Our model
478 projections suggest that nutrient reductions may in some cases produce conditions that do not support any oyster growth along
479 the shoals of the York (Fig. 9c, f), a result of reductions in food availability that are predicted to be more substantial in the
480 tributaries than the mainstem region (Fig. 10c). Multiple studies have demonstrated that Eastern oysters and other calcifying
481 organisms perform better under acidification when they have sufficient food availability, as they are better able to keep up
482 with the energetic demands of environmental stress (Thomsen et al., 2015; Ramajo et al., 2016; Schwaner et al., 2023, Caillon
483 et al., 2025). Therefore, nutrient reductions will likely influence oyster growth under acidification stress by different
484 magnitudes in each tributary. When comparing the effects of local management actions to reduce nutrient runoff to the effects
485 of climate change (increased atmospheric CO₂ and warming), it is evident that, on average, climate change will have a much
486 greater negative influence on oyster growth (Table 4). However, the strong localized impacts of nutrient reductions in the York

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

489 Increased water temperatures are projected to slow oyster growth in the future. Specifically, large reductions in tissue
490 weight are underpinned by three primary mechanisms: limitations on filtration at high temperatures (Loosanoff, 1958),
491 increased respiration rates (Dame, 1972), and reduced food availability. In *EcoOyster*, the optimal temperature for Eastern
492 oyster filtration is 27°C (Cерco et al., 2005; Jordan, 1987), and under warming, the frequency at which ambient summer
493 temperatures will surpass this optimal temperature will be higher (Fig. 5a), therefore causing more frequent declines in
494 filtration rate (Cерco et al., 2005; Fulford et al., 2007). There is no clear optimal temperature for oyster respiration, and
495 therefore it is assumed to increase exponentially with temperature (Hochachka and Somero, 2002). Thus, as oyster filtration
496 rates begin to decline at high temperatures, respiration rates will continue to rise and decrease the potential for tissue
497 accumulation (Fig. S1). Previous studies on juvenile Eastern oysters do not support a consensus on the relationship between
498 warming and tissue growth. Some report that growth is inhibited at higher temperatures (31°C, Stevens and Gobler, 2018;
499 30°C, Speights et al., 2017). In contrast, Talmage and Gobler (2011) found no significant influence of high temperature (28°C)
500 alone on tissue growth. The optimal temperature for oyster filtration may also vary among oysters, based on observations of
501 maximum filtration rates of adult Eastern oysters occurring between 28.1°C– 32°C (Loosanoff, 1958). Variation in
502 experimental design may have contributed to the contrast in results summarized here, in addition to the influence of local
503 adaptation (Burford et al., 2014). Other studies that incorporate higher temperature thresholds into their models predict
504 increases in oyster biomass under warming in Chesapeake Bay (Allen et al., 2023), underscoring the importance of properly
505 parameterizing growth models. Additional modeling studies should be conducted to test the sensitivity of oyster growth
506 changes to optimal temperature parameterizations. Due to a lack of consensus on temperature limits of Eastern oyster filtration,
507 further research is also needed to more robustly represent oyster filtration in bioenergetics models and improve predictions of
508 impacts of warming on oysters and their ecosystem services in the region.

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

521 dependent on filtration. When food availability limits filtration, this critical temperature lowers, and the temperature threshold
522 for tissue loss is lowered. Experimental studies have demonstrated how organic carbon may be influenced by both warming
523 and acidification (Simone et al., 2021), but as these dynamics can differ based on nutrient availability, it is important to consider
524 how climate change will influence food webs and nutrient dynamics.

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

538 **4.3 Influence of future changes in oyster growth on aquaculture**

539 Understanding the relative impacts of global climate change and local nutrient management actions on oyster growth
540 and survival will allow aquaculture producers to anticipate how their oyster stock may respond to these anthropogenic changes.
541 As the effects of climate change are subject to natural interannual variability, the magnitude of acidification and warming in a
542 given year will likely differ (Cai et al., 2021; Moore-Maley et al., 2016; Li et al., 2016), influencing oyster growth through
543 differing mechanisms. Smaller oysters resulting from slower growing times in a particularly warm year may present a different
544 challenge to growers than weak-shelled oysters in a year with lower Ω_{Ca} and average temperatures. Mortality may also become
545 a more urgent challenge as summer temperatures warm. A previous study examining commercial performance of Pacific
546 oysters in Brazil found that interannual variability in temperature, *chl a* abundance, and climate events influenced survival and
547 growth phase timing (Mizuta et al., 2012). High temperatures inhibited survival of oyster seed in that study, which frequently
548 occurs in Pacific oysters (*Crassostrea gigas*) during the summer months in Europe and California (Goulletquer et al., 1998;
549 Burge et al., 2007; Malhan et al., 2009). A similar phenomenon has been observed in Eastern oysters; however, mortality
550 events in this species have not been conclusively linked to warmer water temperatures (Guevelou et al., 2019; Biranik and
551 Allam, 2023), and the cause is yet to be resolved for either species and remains an area of active research. Nonetheless, the
552 increasing occurrence of spring/summer mortality in Eastern oysters suggests that shifting the time of planting oysters on

553 leases later in the year may help mitigate the risk of widespread mortality, although the economic tradeoffs involved in shifting
554 the growing season for oysters should be taken into account.

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

569 Beyond reduced oyster growth, aquaculture operations may also be affected in the future by temporal changes in
570 optimal growing conditions. Due to the input of freshwater that lowers DIC and TA and increases pCO_2 (Cai et al., 2017; Cai
571 et al., 2021; Da et al., 2024), the greatest magnitude of Ω_{Ca} reductions occurs in spring. The majority of oyster growth is
572 projected to occur in the spring and summer (Fig. 5), so changes to growing conditions may be most consequential during
573 these warmer months. Deployment of oyster seed generally begins in the spring and continues into the summer, so it is
574 important for producers to be aware of ambient conditions being experienced by their newly deployed oysters. As spring
575 temperatures warm, phytoplankton blooms will likely occur earlier in the year, shifting the time when food availability is
576 highest (Da et al., 2021). Oysters deployed earlier in the year may benefit from greater food availability and perform better
577 than oysters deployed in July or August when waters are warmest. However, they may also face the challenge of spring/summer
578 mortality events, revealing the complexity of timing oyster deployment under worsening climate change conditions. For oyster
579 farms closer to freshwater sources, the combined effects of low Ω_{Ca} , low salinity, and high summer temperatures may severely
580 inhibit growth and extend time-to-market. This study focused on diploid oysters, since the laboratory experiments used to
581 develop the EcoOyster model parameterizations were conducted on diploids. Future laboratory experiments with triploids
582 would enhance our modeling efforts for triploid oysters, which are commonly used in aquaculture in the Chesapeake Bay
583 region.

584 4.4 Future work

585 Providing the aquaculture industry with the best existing estimates of climate change impacts to their operations will
586 allow them to make more informed decisions about their future practices. This study used a 120-meter horizontal resolution
587 model grid to examine near-lease-level effects of climate change and management actions on oyster growth in a section of the
588 lower Chesapeake Bay. Similar studies with high resolution model grids in other systems will strengthen our understanding of
589 how regional anthropogenic effects will influence the oyster aquaculture sector and could be used to identify areas of
590 opportunity for new aquaculture practices (Swam et al., 2022; Palmer et al., 2021; Lavaud et al., 2024). The present study
591 incorporated one Earth System Model and one emissions scenario; future work should quantify how these choices impact
592 estimates of future Ω_{Ca} and oyster growth (e.g., Hinson et al., 2023). Future modeling studies should also incorporate other
593 climate change impacts, such as sea level rise and increased storminess which are projected to influence conditions for oyster
594 growth in the Chesapeake Bay region (Seneviratne et al., 2012; Lowe et al., 2019, Rybovich et al., 2016, Jones et al., 2019).

595 To improve estimates of shell and tissue growth of oysters under climate change, additional experimental studies
596 should be conducted to reduce the data gaps that currently limit model formulations. Uncertainties in the functional
597 relationships and rate parameters used in these models may lead to an inaccurate influence of some environmental variables
598 on oyster growth. For example, results in this study may be particularly sensitive to the optimum temperature for filtration
599 rate. Reductions in tissue weight are particularly dramatic when average temperature conditions at oyster lease sites remain
600 above this optimal temperature from mid-June through late August, a vital time for oyster growth. Many physiological studies
601 of temperature impacts on oyster filtration date back to the mid-to-late-20th century, and present-day seasonal extremes that
602 coastal organisms experience may routinely exceed the maximum temperatures used in many of these earlier experimental
603 designs. For example, Jordan (1987) used a maximum temperature of 27 °C, which was the ambient temperature when samples
604 were collected in July from the Choptank River, MD. Between 1985 and 2014, bottom waters of the north mesohaline Bay
605 main stem (closest to the Choptank) warmed 1.01 ± 0.13 °C during May to October (Hinson et al., 2022), and the present study
606 predicts a 1.5 ± 0.26 °C increase across the entire model domain between 2017 and mid-century. To build stronger models of
607 future climate impacts, and to expand scientific understanding of physiological limits of the Eastern oyster, future studies
608 should re-examine temperature limitations on oyster filtration and respiration by using higher experimental temperatures.

609 As oyster growth is highly sensitive to food availability, improved measurements of particulate organic carbon in the
610 region would fortify projections of oyster production under future climate change and nutrient management. Here, it is assumed
611 that oysters feed on POC, a combination of plankton and detritus. However, average POC concentrations are highly
612 spatiotemporally variable in the Chesapeake Bay due to eutrophication and algal blooms. In this study, POC was
613 underestimated in the tributary channels; however, it is unclear how well POC was estimated in oyster growing areas, as *in*
614 *situ* measurements are currently limited to stations in the channels during monthly or semi-monthly sampling cruises. More
615 routine POC measurements, as well as measurements of POC in regions where oyster farming operations occur, are needed to

616 verify the spatiotemporal dynamics of food availability. Improved measurements of oyster food availability would allow for
617 stronger model skill assessment and improved projections of oyster production.

618 **5 Conclusions**

619 This study predicts widespread reductions in Ω_{Ca} in the lower Virginia tributaries of the Chesapeake Bay by mid-
620 century, highlighting the use of high-resolution model projections to better understand present-day carbonate chemistry
621 conditions and to predict the effects of climate change on a region of high interest for aquaculture production. While similar
622 modeling studies have projected acidification conditions in coastal regions with 3D coupled models (Siedlecki et al., 2021a,b;
623 Fujii et al., 2023) or modeled oyster growth with remote-sensing data and dynamic energy budget models (Palmer et al., 2020;
624 Palmer et al., 2021; Bertollini et al., 2021), the present study projects both carbonate chemistry conditions and oyster growth
625 in the Chesapeake Bay with the highest resolution thus far. Specifically, widespread reductions in Ω_{Ca} will negatively impact
626 oyster growth, with implications for aquaculture operations and local and regional economies. As bottom conditions worsen,
627 altered site-selection for oyster farms or other adaptive measures will become imperative to sustain production and reduce the
628 impacts of low Ω_{Ca} on farmed oysters.

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

640

641 **Code Availability**

642 Model code will be available upon request.

643

644 **Data Availability**

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

646

647 **Author Contribution**

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

652

653 **Competing Interests**

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

655

656 **Acknowledgements**

657 This paper is the result of research funded by the National Oceanic and Atmospheric Administration's Ocean Acidification
658 Program under award NA18OAR0170430 to the Virginia Institute of Marine Science (VIMS). We would like to thank the
659 VIMS and William & Mary (W&M) high performance computing group for their technical support and computing resources.
660 We also thank the NOAA Chesapeake Bay Program for providing us with watershed inputs from their Phase 6 Watershed
661 Model. This work was largely made possible by Sara Blachman's hard work on the EcoOyster model. We thank Bill Walton
662 for his aquaculture expertise and support throughout the project. The model results used for this manuscript are available at
663 W&M Scholarworks.

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1084

1085 Table 1. Experimental design for future simulations conducted for comparison to reference run. Model forcings include a
1086 combination of 2017 (reference) and 2067 (future) inputs of atmospheric CO₂, atmospheric temperature, and terrestrial nutrient
1087 loadings.

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

1088 ^aTMDL (Total Maximum Daily Load) forcing includes inputs of nitrate, ammonium, and dissolved and particulate organic
1089 matter under the assumption that the nutrient reduction goals (EPA, 2010) are met.

1090 Table 2. Model skill statistics (mean ± standard deviation) comparing bottom grid cells from the reference run to Chesapeake
 1091 Bay Program 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) n = 130	17.0 ± 9	16.7 ± 9	+ 0.2	0.7
Salinity n = 127	13.9 ± 7	15.4 ± 7	-1.5	2.7
Oxygen (mg O₂ L⁻¹) n = 130	8.0 ± 2.3	7.2 ± 2.9	+0.9	1.3
pH n = 74	7.8 ± 0.4	7.6 ± 0.4	+ 0.2	0.4
TSS (mg L⁻¹) n = 74	44 ± 34	45 ± 54	-1.1	48.3
POC (g C m⁻³) n = 74	0.7 ± 0.3	1.7 ± 2.1	-1.0	2.4

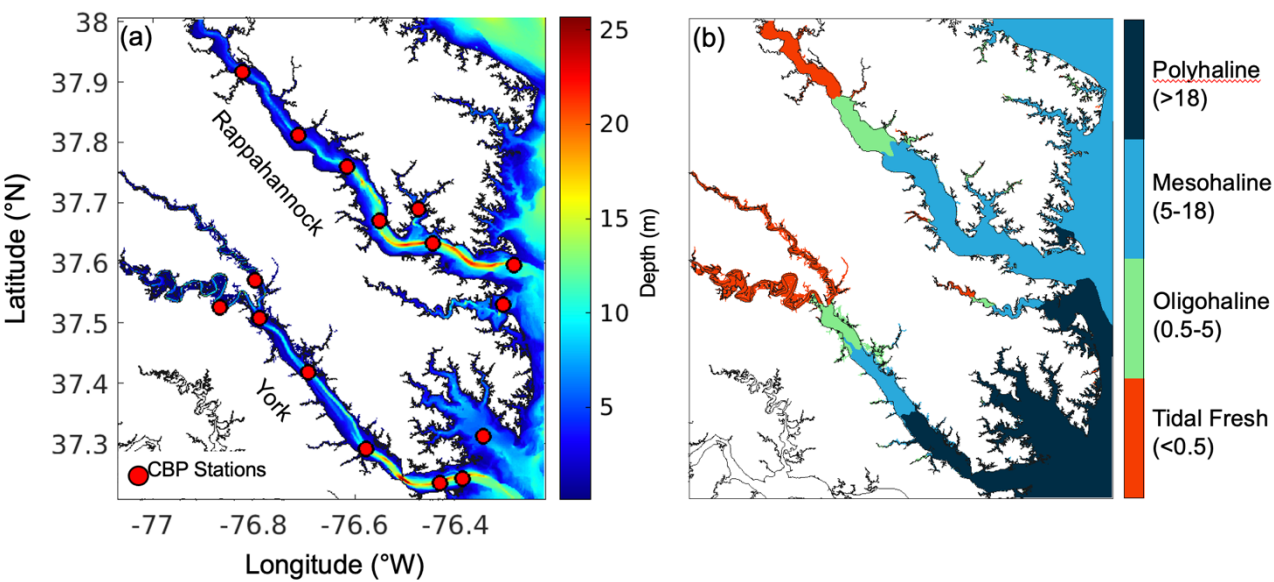
1092 ^aRMSD = root mean squared difference.

1093 Table 3. Bottom environmental variables for each model simulation (annual mean $\pm$ standard deviation) for grid cells that
 1094 support oyster growth in the reference run (defined as those with greater than 1g dry tissue weight after one year of growth;
 1095 Fig. S2). Analogous results averaged over all model grid cells are shown in Table S5.
 1096

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 $\pm$ 0.7	15.7 $\pm$ 2.1	1.12 $\pm$ 0.1	2.5 $\pm$ 0.49	9.1 $\pm$ 0.6	11.4 $\pm$ 5.8
Combined Future	18.5 $\pm$ 0.8	16.0 $\pm$ 2.1	1.03 $\pm$ 0.1	1.6 $\pm$ 0.35	8.7 $\pm$ 0.6	11.1 $\pm$ 5.9
AtmCO ₂	17.0 $\pm$ 0.7	15.7 $\pm$ 2.1	1.12 $\pm$ 0.1	1.6 $\pm$ 0.35	9.1 $\pm$ 0.6	11.4 $\pm$ 5.8
Temp	18.5 $\pm$ 0.8	16.0 $\pm$ 2.1	1.07 $\pm$ 0.1	2.5 $\pm$ 0.41	8.8 $\pm$ 0.6	11.1 $\pm$ 5.9
TMDL	17.0 $\pm$ 0.7	15.7 $\pm$ 2.1	1.08 $\pm$ 0.1	2.4 $\pm$ 0.53	9.1 $\pm$ 0.6	11.2 $\pm$ 5.9
Temp + CO ₂	18.5 $\pm$ 0.8	16.0 $\pm$ 2.1	1.07 $\pm$ 0.1	1.7 $\pm$ 0.33	8.8 $\pm$ 0.6	11.1 $\pm$ 5.9

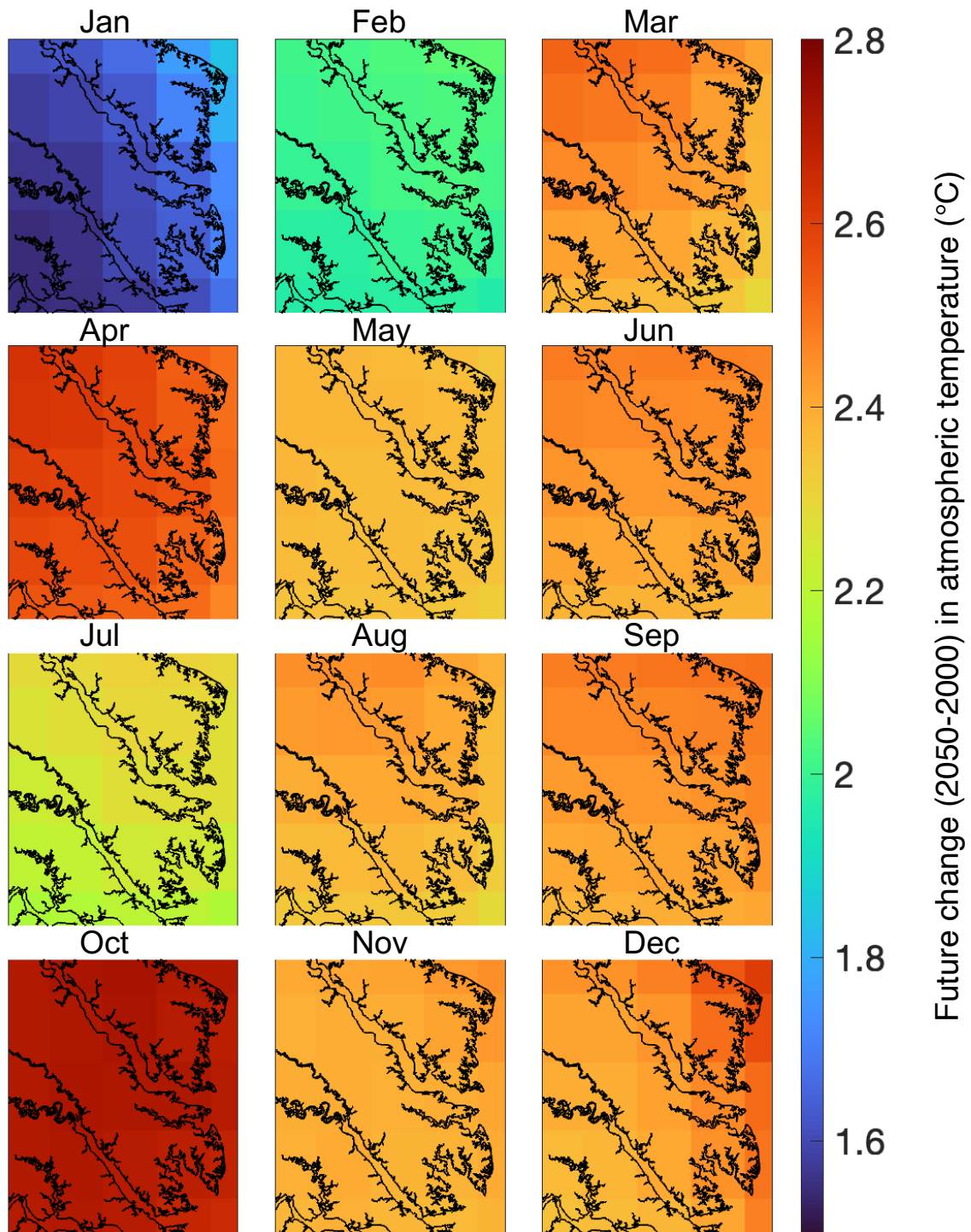
1097 Table 4. Modeled oyster characteristics from the end of each simulation (mean ± standard deviation) over grid cells that support
 1098 oyster growth in the reference run (defined as those with greater than 1g dry tissue weight after one year of growth; Fig. S2).
 1099

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
Temp	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



1101

1102 Figure 1. ROMS-ECBO model domain of Chesapeake Bay tributaries illustrating (a) bathymetry in meters and locations of
1103 Chesapeake Bay Program (CBP) water quality monitoring stations (red circles) and (b) bottom salinity zones.



1104 Figure 2. Monthly-averaged 50-year atmospheric temperature differences over the ROMS-ECBO model domain calculated as projections
 1105 from 2050 minus those from 2000.

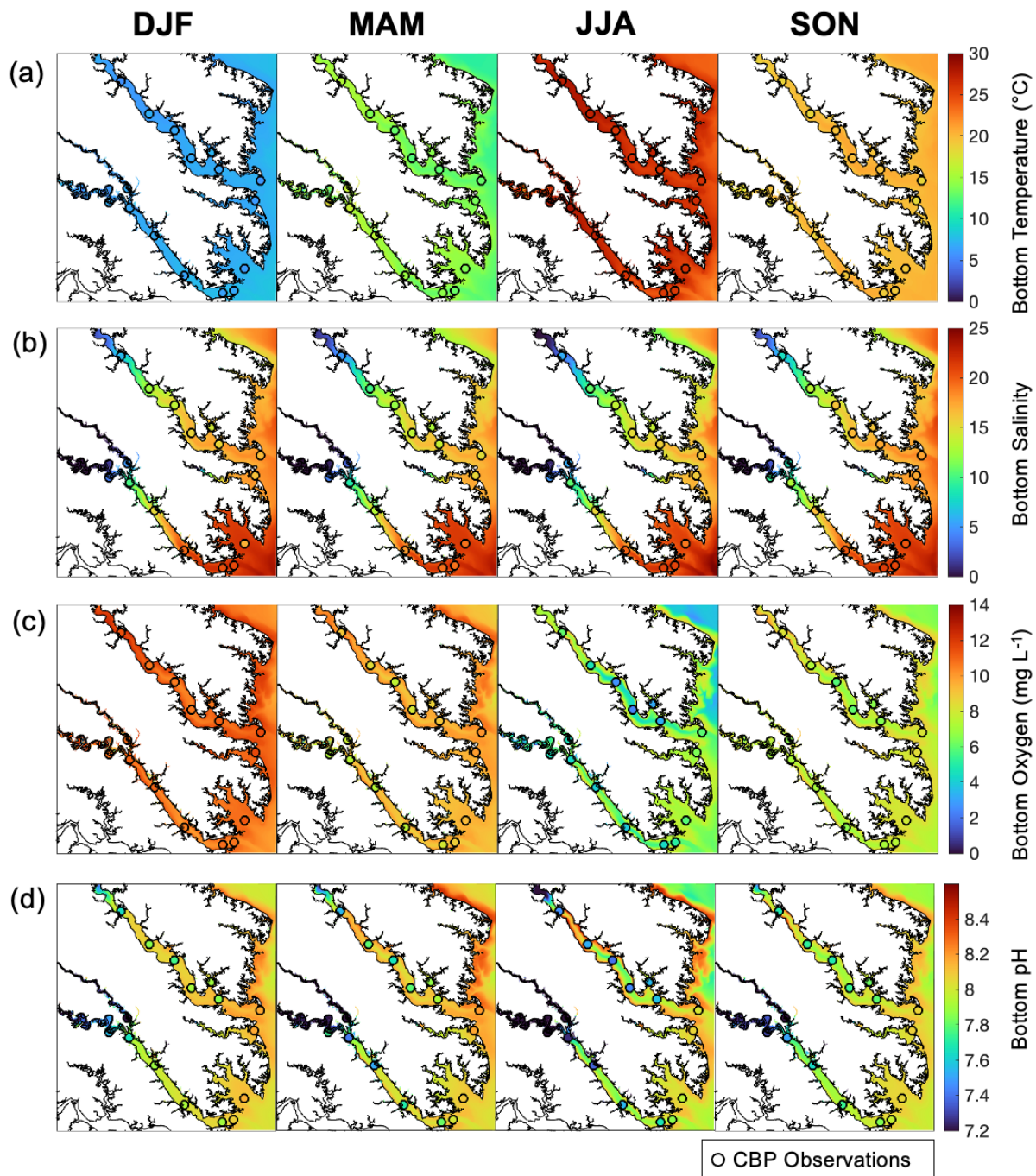
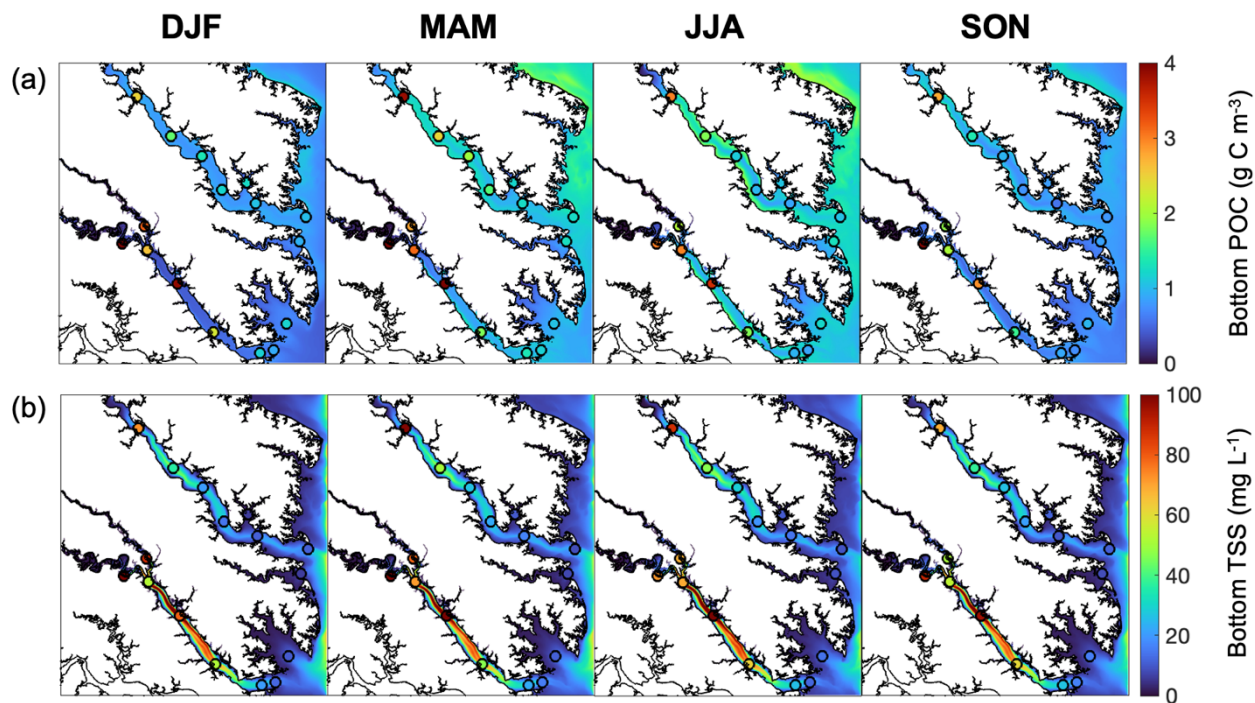
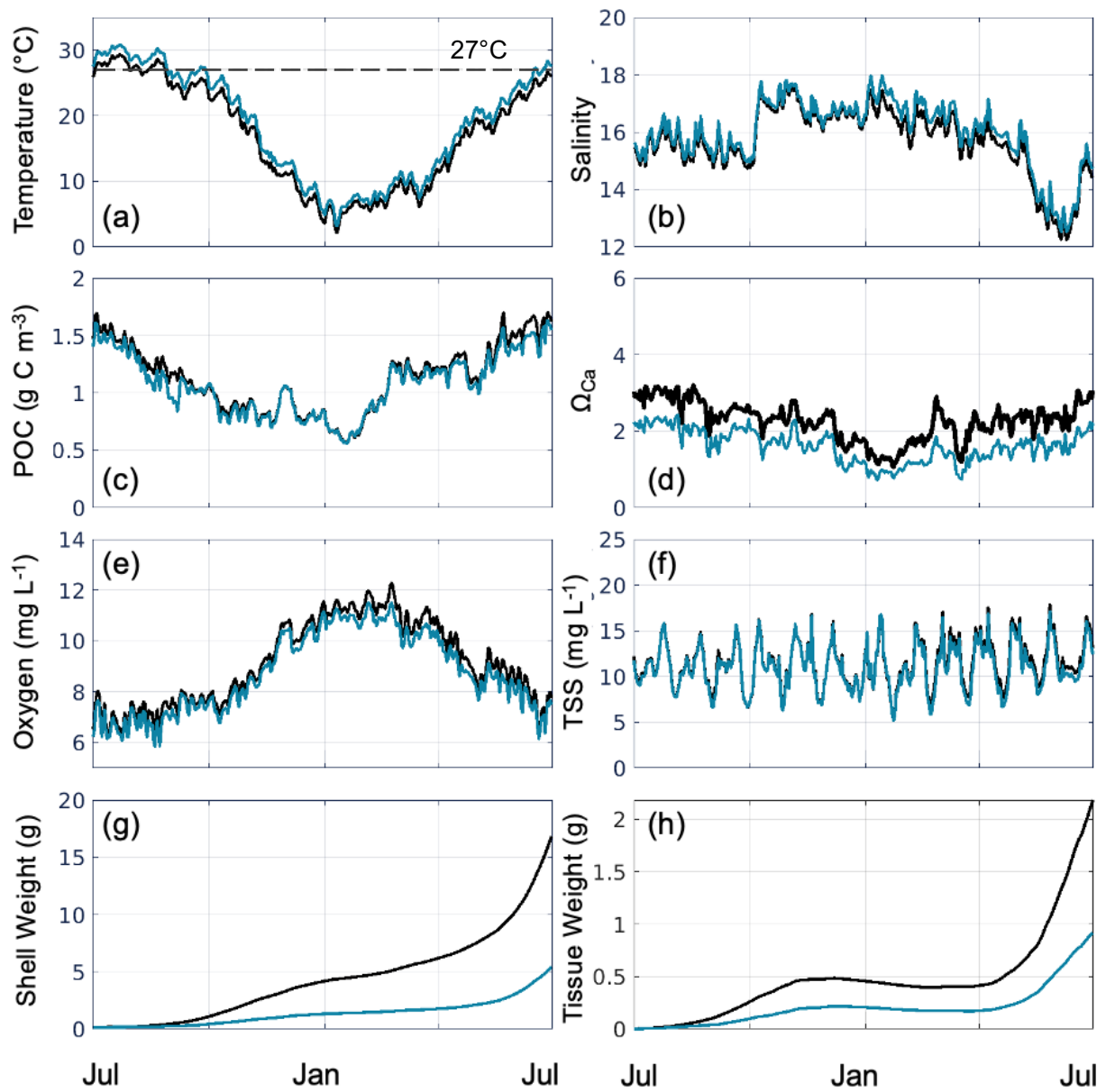


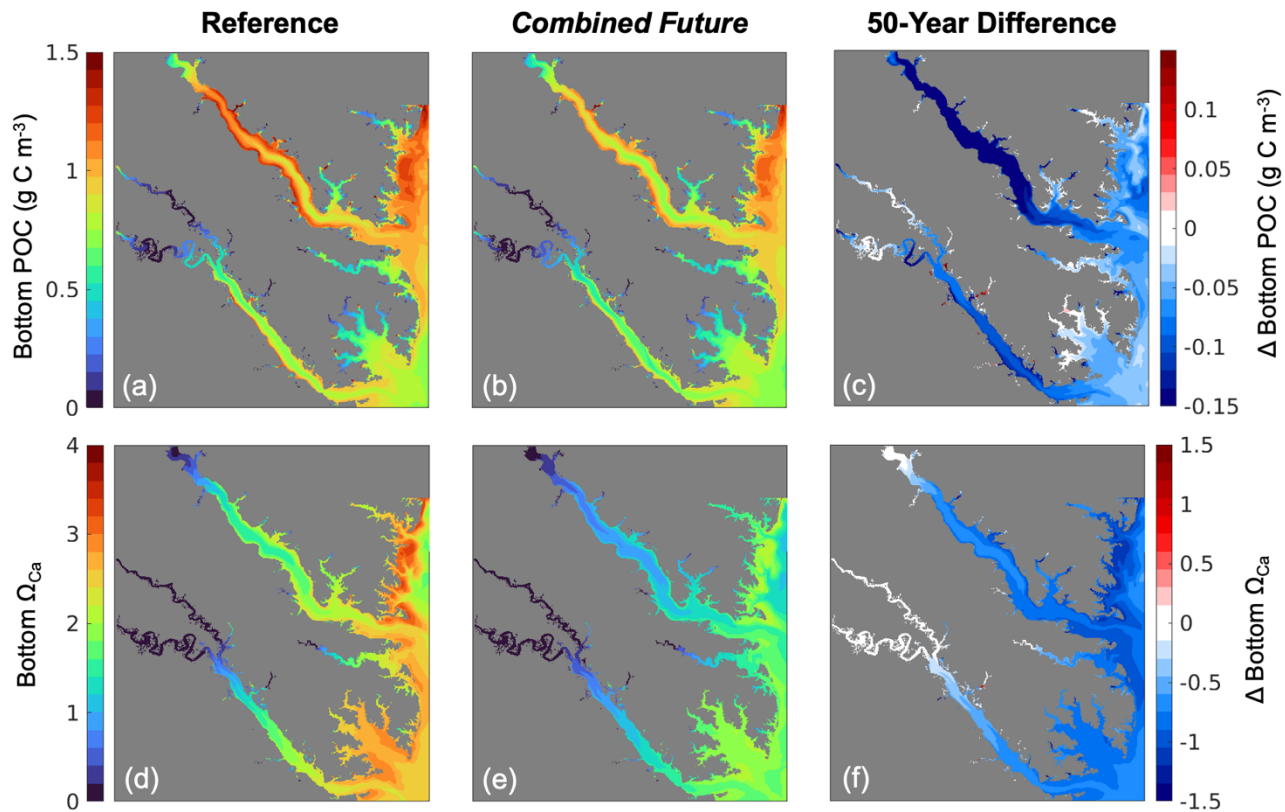
Figure 3. Seasonally-averaged bottom (a) temperature, (b) salinity, (c) dissolved oxygen, and (d) pH from the reference run. Circles represent seasonal decadal-averaged *in situ* observations at Chesapeake Bay Program stations (2010-2020). (DJF = winter, MAM = spring, JJA = summer, and SON = fall).



1109 Figure 4. Seasonally-averaged bottom (a) POC and (b) TSS from output of the reference run of the ROMS-ECBO model.
 1110 Circles represent seasonal decadal-averaged bottom measurements at Chesapeake Bay Program stations (2010-2020). (DJF =
 1111 winter, MAM = spring, JJA = summer, and SON = fall).

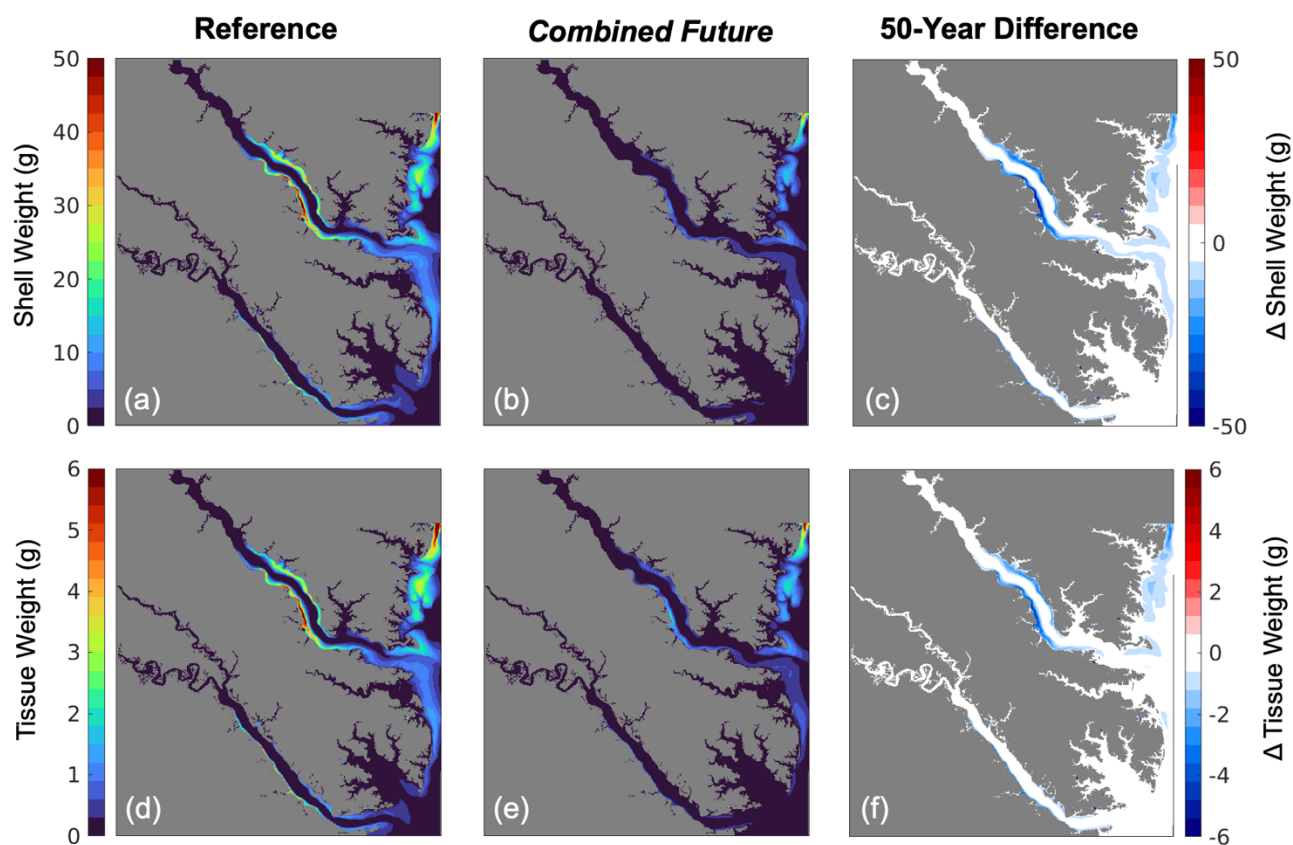


1112 Figure 5. Time series of daily bottom (a) temperature, (b) salinity, (c) POC, (d) Ω_{Ca} , (e) oxygen, (f) TSS, (g) shell weight, and
 1113 (h) tissue weight, averaged over grid cells that support oyster growth in the reference run, for the present-day reference run
 1114 (black line) and Combined Future simulation (blue line). The horizontal dashed line in (a) represents the optimal filtration
 1115 temperature in EcoOyster (27°C).

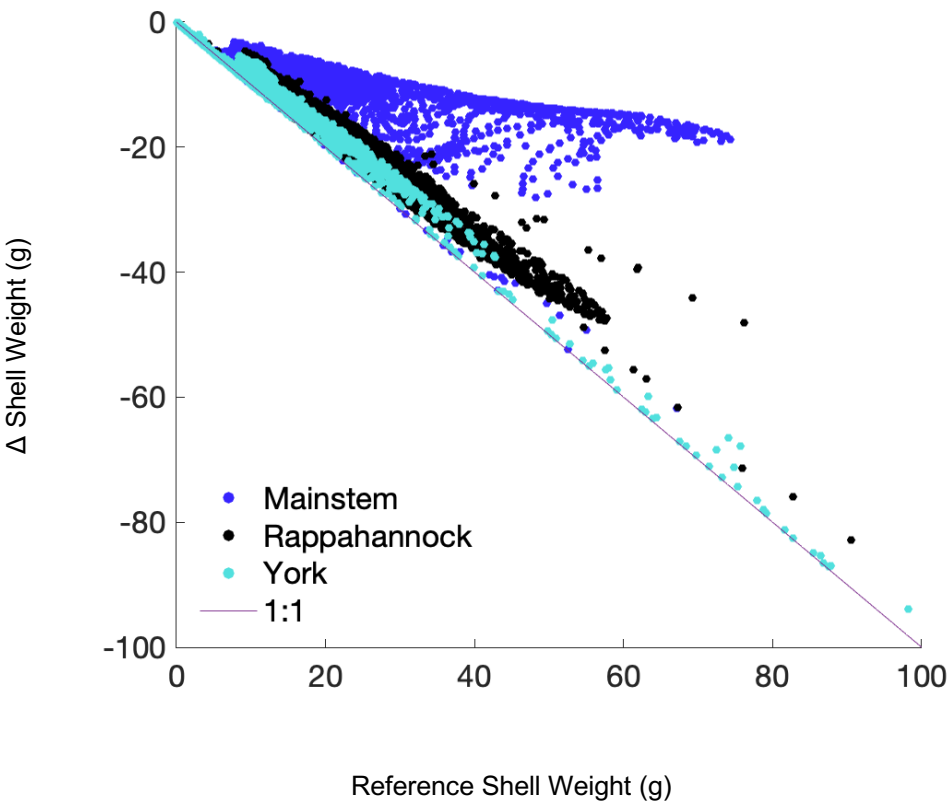


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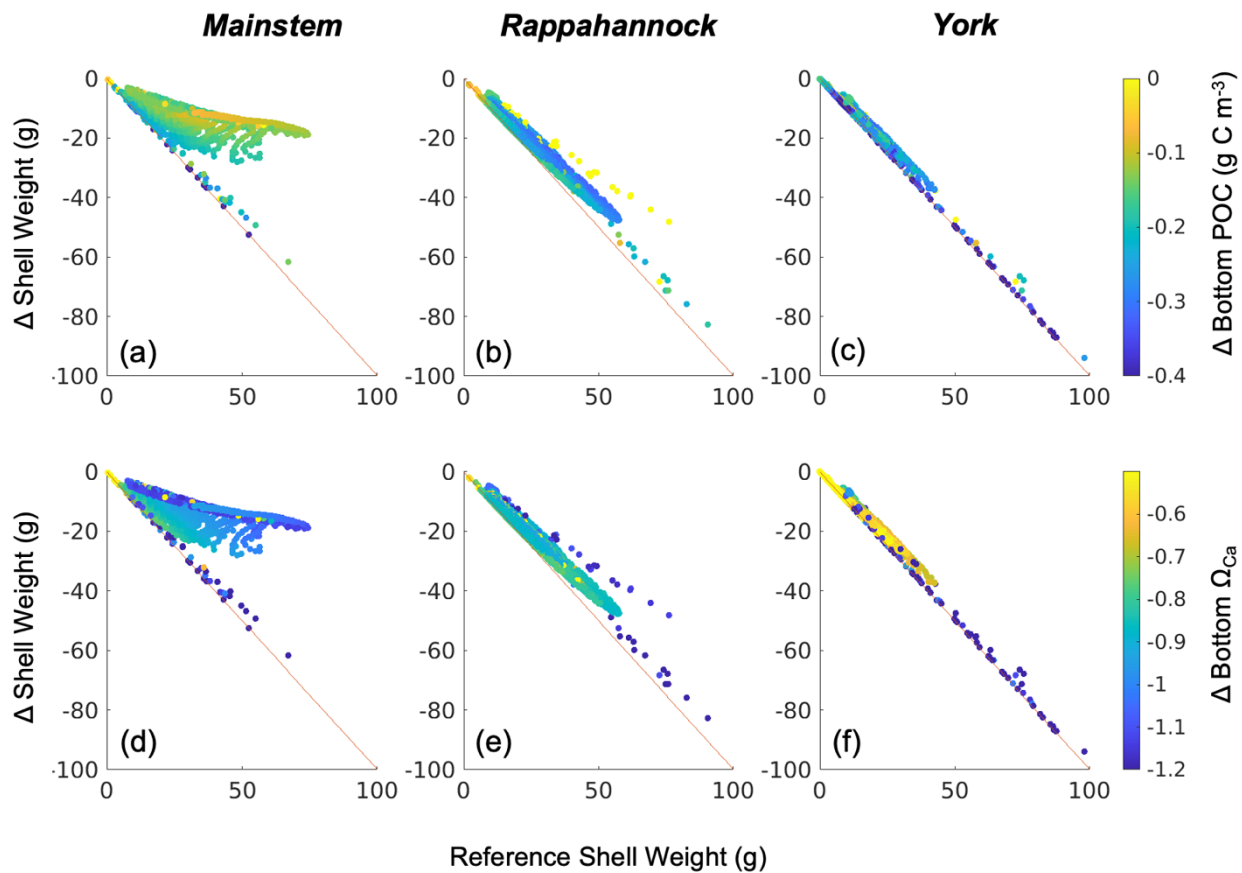
1117 Figure 6. Annual mean bottom (a-c) POC and (d-f) Ω_{Ca} from (a,d) the present-day reference run, (b,e) the *Combined Future*
 1118 simulation, and (c,f) the difference between (a) and (b), i.e., *Combined Future* minus reference.



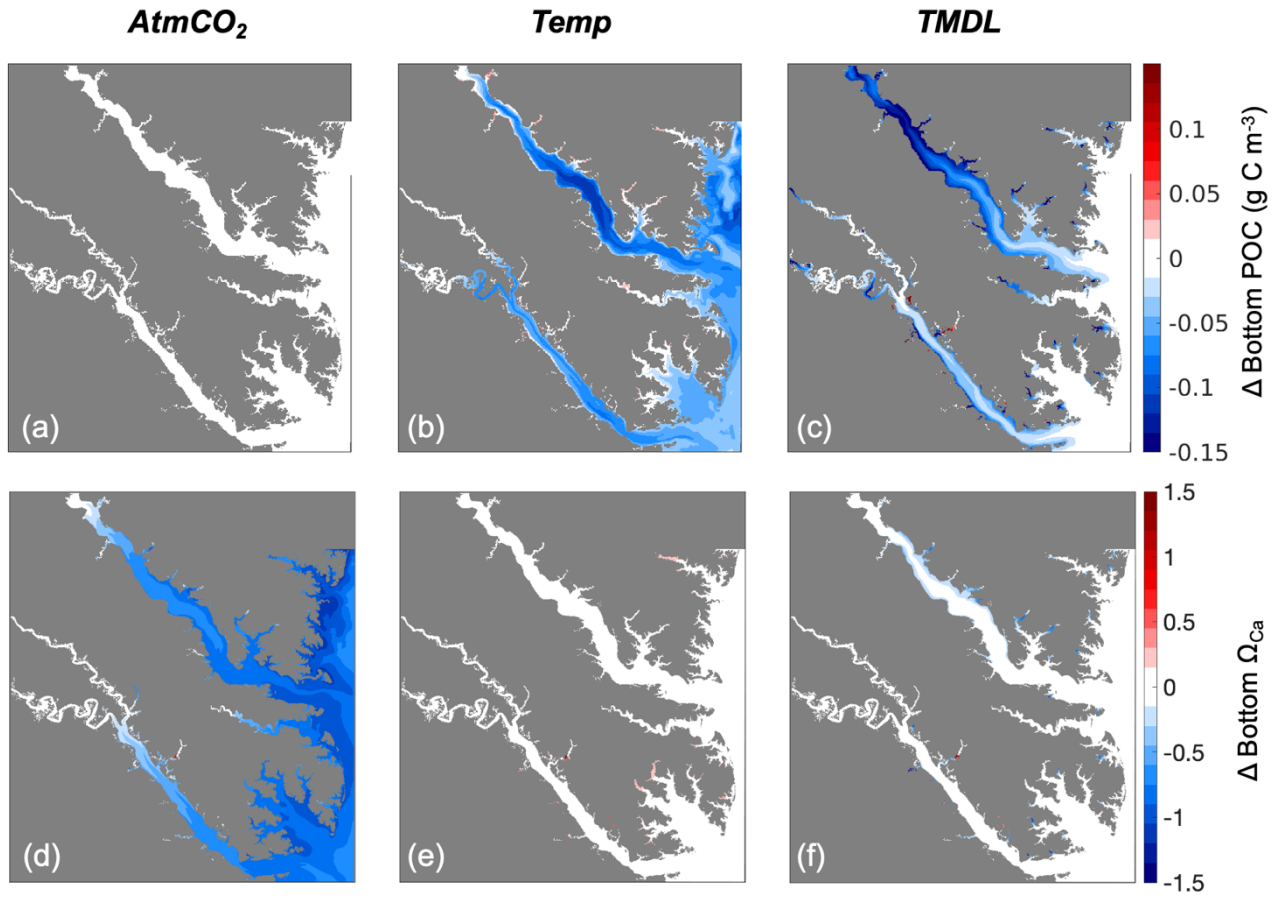
1119 Figure 7. (a-c) Shell weight and (d-f) tissue weight at the end of the one-year simulation from (a,d) the present-day reference
 1120 run, (b,e) the *Combined Future* run, and (c,f) their difference, i.e., *Combined Future* minus reference.



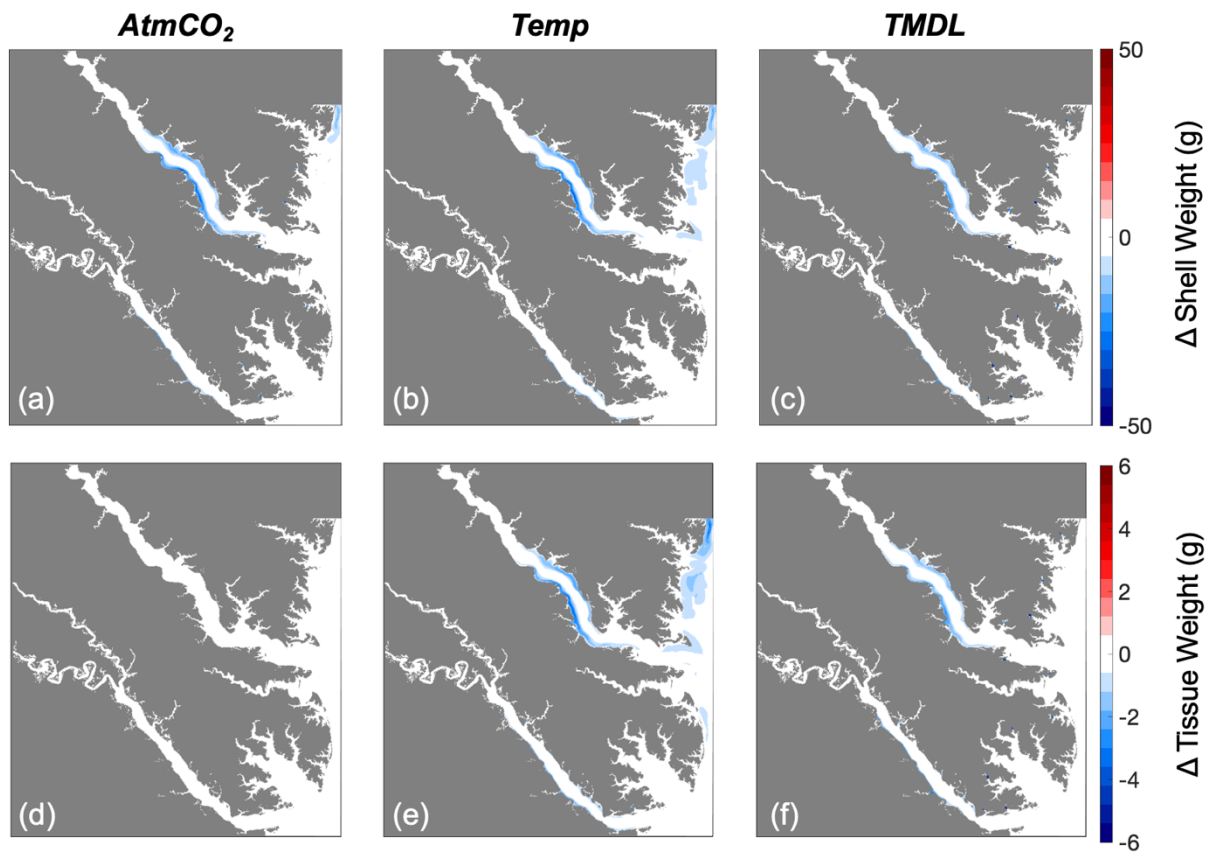
1122 Figure 8. Difference in shell weight at the end of the one-year simulation between the *Combined Future* run and the reference
1123 run, i.e., *Combined Future* minus reference, colored by region. Each point represents a grid cell where oyster growth occurs
1124 in the reference run.



1125
 1126 Figure 9. Difference in shell weight at the end of the one-year simulation between the *Combined Future* run and the reference
 1127 run colored by (a-c) change in bottom POC and (d-f) change in bottom Ω_{Ca} (i.e. *Combined Future* minus reference) for grid
 1128 cells that support oyster growth. Results are presented for (a,d) the mainstem shoal only, (b,e) the Rappahannock River only,
 1129 and (c,f) the York River only.



1130 Figure 10. Differences in annual averaged (a-c) bottom POC and (d-f) bottom Ω_{Ca} (d-f) for three sensitivity experiments: (a,d)
 1131 *AtmCO₂*, (b,e) *Temp*, and (c,f) *TMDL*. Differences represent future results minus those from the present-day reference run.



1132 Figure 11. Differences in (a-c) shell weight and (d-f) tissue weight at the end of the one-year simulation for three sensitivity
 1133 experiments: (a,d) *AtmCO₂*, (b,e) *Temp*, and (c,f) *TMDL*. Differences represent future results minus those from the present-
 1134 day reference run.

1135