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A Model of Carrying Capacity and Ecosystem Impacts in a Large-Scale, Bivalve-Dominated Agro-Ecosystem: Hard Clam Aquaculture in Cherrystone Inlet, VA

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A model of carrying capacity and ecosystem impacts in a large-scale, bivalve-
dominated agro-ecosystem:
hard clam aquaculture in Cherrystone Inlet, VA

A Thesis
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
of the Requirements for the Degree of
Master of Science

by
Michael A. Kushner
2015

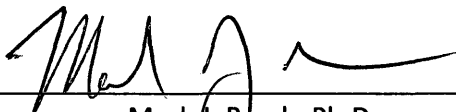
APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of
Masters of Science




Michael A. Kushner

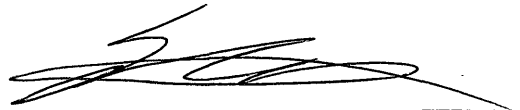
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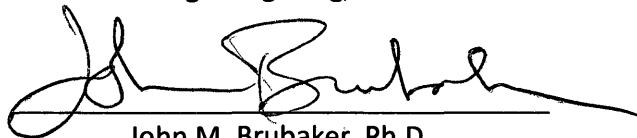
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DEDICATION

This thesis is dedicated to my father

Bruce Charles Kushner

“Never give up, never give in, and always give your best”

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ABSTRACT

With the recent growth of the hard clam aquaculture industry, sites of intensive aquaculture have emerged as large-scale agro-ecosystems where the success of aquaculture production is dynamically linked to ecosystem function. Large scale clam aquaculture operations are associated with a range of potential positive and negative feedbacks related to nutrient dynamics, water and sediment quality, proliferation of macroalgae, and carrying capacity. Quantitative modeling tools are needed to support system-level planning related to site selection, scale of operations, production capacity and ecosystem function. The purpose of this study was to develop a model for Cherrystone Inlet, VA, where one-third (1.9 km²) of the sub-tidal bottom area is held as 37 separate, private shellfish leases with an estimated 100-150 million cultured clams. A reduced complexity estuarine ecosystem model was coupled with a hard clam energetics and growth model and a watershed loading model. The linked models facilitate ecosystem-based management and enable regional spatial planning in a full ecosystem context, through coupled simulations of aquaculture activities, land use changes, nutrient loading, climate change, and estuarine response. Modeled output for hard clam growth and water column chlorophyll-*a*, dissolved oxygen, and dissolved inorganic nitrogen and phosphorous reproduced *in situ* data. Simulations with increasing clam numbers up to 500 million resulted in diminishing returns in terms of reduced growth rates, increased time to harvestable size, and reduced harvestable biomass, confirming observations by Cherrystone farmers of reduced clam growth rates above 200 million cultured clams. Modeled hard clam production capacity decreased in the absence of benthic microalgal resuspension (6%) and without the input of external production from the Chesapeake Bay (41%), and increased in simulations with increased water column chlorophyll-*a* (11%) and the removal of predator exclusion nets (13%). Simulations to optimize siting indicated that the highest hard clam growth rates occurred up-estuary. Model simulations with changes in land use and climate indicated that clam growth is most sensitive to increasing temperature, with rates decreasing by 37% when temperatures were increased by 5°C, while changes in land use, sea level rise and salinity did not result in large changes in hard clam production. At the system scale hard clam aquaculture was predicted to account for 14% of total nitrogen inputs to the water column between sediment recycling of clam feces (13%) and direct clam excretion (1%). The Cherrystone ecosystem model fills a critical gap on the Eastern Shore of Virginia and in similar coastal systems, providing resource managers with the most current available science in a decision-support framework to promote effective regional spatial planning and sustainability of hard clam operations and the surrounding coastal ecosystems.

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1.0 INTRODUCTION

Global aquaculture in marine and estuarine waters has grown by an average of 8.8% in the last three decades (FAO 2012). This large growth in global production of farmed fish has been driven by demand from human consumption, in a time when global wild catch is declining largely due to an increasing percentage of overexploited fish stocks and a decreasing percentage of healthy stocks. Bivalve aquaculture makes up 20% of the total farmed fish product in North America and increased from 2M to 12M tons per year worldwide since 1980 (FAO 2012).

Hard clam (*Mercenaria mercenaria*) harvest in North America has existed since pre-colonial times and has grown substantially within the last century, largely attributed to stability of the hard clam fishery due to the longevity and relatively slow growth rate of the species (MacKenzie et al. 2001). Commercial aquaculture operations of the hard clam in the Chesapeake Bay region were not fully established until the 1950s, when the previously dominant fishery of the Eastern oyster (*Crassostrea virginica*) collapsed due to extensive overfishing and disease. Hard clam aquaculture thrives in the relatively saline waters along the Delmarva (Delaware-Maryland-Virginia) Peninsula, with the Virginia hard clam aquaculture industry now generating between \$22M and \$34M in annual revenues (Hudson and Murray 2014).

Hard clam aquaculture on the Eastern Shore of Virginia is dominated by large-scale industry operations occupying many of the bay-side tributaries and ocean-side

lagoons. Clams are planted and grown to market size (~40 - 60 mm shell length) on the estuarine sediment surface in privately leased plots under predator exclusion nets to avoid predation by crabs, rays, birds, and other large marine species. This study is focused on Cherrystone Inlet, VA, a tidal tributary of the Chesapeake Bay on the western side of the Delmarva Peninsula (Figure 1), where over one third of the sub-tidal bottom is covered with over 800 privately leased clam beds which are planted at densities of 600-800 clams per m².

Critical evaluation of the sustainability of the hard clam industry requires quantitative assessment of multiple factors including clam carrying capacity at the system scale, nutrient dynamics within and adjacent to the clam beds, effects relating to predator exclusion methods, and disease dynamics (NRC (National Research Council) 2010). In recent years, the industry has reported slower growth rates in some grow-out areas, which translates to a longer time for the clams to reach market size (Condon 2005). Condon (2005) developed a carrying capacity model to predict that system-level clam production in Cherrystone Inlet was near exploitation carrying capacity with clam growth potentially food limited for part of the growing season. Additionally, the predator exclusion nets, which are designed to protect growing clams from predation mortality, were reported to have negative effects on clam feeding rates by reducing suspended particulates available to the clams (Condon 2005). These predator exclusion nets may have a detrimental effect on clam feeding, either by interfering with clam suspension feeding directly, or by indirectly modifying the benthic environment and negatively affecting clam growth.

Feedbacks associated with the benthic environment, particularly nutrient and oxygen dynamics, can indirectly affect hard clam growth at the clam bed scale. Large-scale aquaculture operations promote enhanced biodeposition and excretion from hard clams which have the ability to alter nitrogen cycling processes at the sediment-water interface (Bartoli et al. 2003, Viaroli et al. 2010, Kellogg et al. 2013). With increasing hard clam densities and restricted water flow from the presence of predator exclusion nets, alterations in nitrogen cycling processes have the ability to promote retention of nitrogen within the system, further promoting growth of macroalgae (*Ulva* and *Gracilaria*) (Bartoli et al. 2003), which have been suggested to further reduce clam growth rates (Newell et al. 2002, Viaroli et al. 2010). Secrist (2013) found that macroalgal proliferation associated with predator exclusion nets can potentially affect the availability of food sources to the cultured clams by acting as a barrier restricting water flow. Since the dominant primary producers within shallow coastal systems can vary spatially and temporally (Viaroli et al. 2010), it is also important to consider multiple sources of food (phytoplankton, benthic microalgae (BMA), and macroalgae) that may be available for clam production throughout the year.

Holistic assessment of hard clam aquaculture sustainability in coastal systems must also take into consideration effects of watershed nutrient loading and climate change (Najjar et al. 2010, Kremer and Pinckney 2011, Ingram et al. 2013). Increased nutrient loading from the watershed has the ability to impact aquaculture operations indirectly by increasing the rate of supply of organic matter to coastal systems, defined as coastal eutrophication (Nixon et al. 1995, Nixon 2009), which presumably increases

the food supply for cultured clams. Alternatively, decreases in allochthonous inputs of nutrients could reduce the organic matter supply, a process defined as oligotrophication, which may ultimately reduce the food supply to the benthos including filter feeding bivalves (Nixon et al. 2009). In addition to these bottom-up effects of watershed loading, large scale aquaculture operations may have the ability to exert a top-down control on eutrophication by utilizing the increased primary production as a food source, effectively increasing water clarity (Cloern 1982, Cloern 2001, Grall and Chauvaud 2002). Moreover, this filtration of phytoplankton may alter the relative presence of primary producers in the system by creating adequate water quality conditions to promote enhanced benthic primary production by BMA and macroalgae (Cloern 2001, Bartoli et al. 2003, Viaroli et al. 2010). However, some studies have postulated that shellfish species, especially clams, may actually increase ecosystem deterioration through localized eutrophication by not only enhancing inorganic nutrient regeneration through the decomposition of clam biodeposits, but also by providing a hard substrate to which macroalgae can attach (Bartoli et al. 2003, Condon 2005, Viaroli et al. 2010).

Ongoing climate change as manifested by increases in temperature and sea level (and in turn salinity) (Najjar et al. 2010) will further alter primary production and therefore clam food supply, clam physiology, and feedbacks associated with biogeochemical buffers (Ingram et al. 2013). Lake and Brush (in press) found that modeled primary production and ecosystem metabolism in the polyhaline York River estuary, VA decreased in the summer and fall in simulations with increased

temperatures, suggesting a decrease in food availability for clams with warming. Increased water temperatures are expected to have a large effect on the physiology of shellfish species, leading to changes in metabolism, reproduction, and species distribution within marine and estuarine environments (Ingram et al. 2013). Sea level rise is expected to have the greatest impact on aquaculture in shallow coastal estuaries such as Cherrystone Inlet by shifting the distribution of established oyster reefs and the productivity and accessibility of privately leased aquaculture operations (Ingram et al. 2013). Changes in sea level rise are also expected to increase salinity and modify estuarine salinity gradients (Najjar et al. 2010), potentially altering shellfish species distribution and estuarine circulation (Hilton et al. 2008). Climate change is also expected to alter the timing and magnitude of freshwater delivery to coastal systems, which could further alter rates of watershed loading, salinity gradients, and flushing time (Herman et al. 2007, Najjar et al. 2010).

To holistically assess the production capacity of hard clam aquaculture operations at the ecosystem level as a function of density, land use, and climate change, this work developed and implemented a reduced complexity ecosystem model (Brush 2002, 2004, 2013, Lake and Brush in press) coupled with a hard clam bioenergetics and growth model (Hofmann et al. 2006, Wiseman 2010) and a watershed nitrogen loading model (Giordano et al. 2011). The linked model was used to address the following objectives: (1) to evaluate the sustainability of the hard clam aquaculture industry in Cherrystone Inlet, and (2) to assess the resiliency of hard clam growth metrics and ecosystem function. These objectives were addressed through simulations with

increasing clam populations under changes in system food availability, land use and climate. The estuarine ecosystem model used in this study will ultimately be served as a dynamic online interface to assist managers, planners, and industry personnel in fostering a sustainable aquaculture industry within a resilient ecosystem.

2.0 METHODS

2.1 Site Description

Cherrystone Inlet is a shallow tidal system in lower Chesapeake Bay (Figure 1). One-third (1.9 km²) of its sub-tidal bottom area is reserved as 37 separate private shellfish leases with an estimated 100-200 million cultured clams (Anderson and Brush 2012). Cherrystone Inlet is composed of a central basin and five principal creeks covering an area of 5.6 km², with an average depth of 1.1 m at mean sea level. The basin volume at high tide is $8.8 \times 10^6 \text{ m}^3$ and the volume of the time-averaged tidal prism is $4.4 \times 10^6 \text{ m}^3$. The inlet is a well-mixed, polyhaline system, with water column salinities ranging from 16.5 to 27.3 based on monitoring data from the Virginia Department of Environmental Quality (VA DEQ). The mean range of tide (MN, mean high – mean low water) for the most recent 19-year tidal epoch at the nearest NOAA monitoring station in Kiptopeke, VA is 0.792 m (tidesandcurrents.noaa.gov).

Cherrystone Inlet Flushing Time Calculations

Flushing times for shallow coastal systems can vary greatly based on seasonality as a function of freshwater input, sustained winds, and topography. Mean flushing times in Cherrystone Inlet were estimated by three approaches. The tidal prism method

(Monsen et al. 2002) is a common estimate of flushing time in tidal systems which converts the tidal prism volume (the volume of water between high and low tide marks) into a volumetric flow rate modified by a return flow factor (b), which is the fraction of ebbing water that re-enters the estuary during the following flood tide:

$$T_f = \frac{VT}{(1-b)P}$$

where the volume of water at mean sea level (V) is multiplied by the tidal period (T) and divided by the tidal prism volume (P). Estimates generated from this method resulted in flushing times for the entire Cherrystone basin for a range of return flow factors (10-90%) from <1 to 7 days (Figure 3). Past estimates of flushing time in Cherrystone Inlet used a return flow factor of 30% (Kou et al. 1998).

Flushing times were also computed using the fraction of freshwater method (Officer 1980), which incorporates the input of freshwater, estimated from the Chesapeake Bay Program (CBP) Phase 5.3 Watershed Model (USEPA 2010), and observed salinity distributions based on interpolations from VA DEQ monitoring data (see below):

$$T_f = \frac{V}{R} * ((S_o - S_i) / S_o)$$

This equation calculates the volume of fresh water in the estuary, where the total volume of the basin (V) is divided by the river flow (R) and multiplied by the difference between the salinity downstream from the system (S_o) and within the estuary (S_i). This

method resulted in large variations in estimated flushing time, ranging from <1 to >200 days with an annual mean of 7.5 days (Figure 3).

Finally, Herman et al. (2007) computed a flushing time for Cherrystone Inlet using a “simple equation” which was estimated to be between 2-3 days (Figure 3):

$$T_f = \frac{V}{Q_b}$$

This “simple equation” divides the mean volume of water (V) in the basin by the quantity of mixed water that leaves the bay on the ebb tide (Q_b).

2.2 Estuarine Ecosystem Model

A reduced complexity estuarine ecosystem model (Brush 2002, 2004, 2013, Lake and Brush in press) was implemented in seven spatial elements (boxes; Table 1) within Cherrystone Inlet defined by geomorphic constrictions and fed by inputs of nutrients, sediments, and freshwater from the associated watersheds (Figure 1). Bathymetric soundings were obtained from CBP bathymetric grids for the Chesapeake Bay and tidal tributaries and were interpolated using ESRI® ArcMAP 10.1. The surface area and volume within each box was calculated from mean sea level (MSL) to the estuary bottom (Table 1). Watershed areas were delineated using the ESRI® ArcMAP 10.1 watershed delineation tool by calculating flow vectors based on topography. The model was implemented using STELLA software (www.iseesystems.com) with a time step (DT) of 0.125 days.

The model includes only state variables and rate processes that are of direct importance to the processes associated with shallow coastal systems, and integrates

robust empirical relationships that have been shown to apply across multiple temperate estuaries to predict key rate processes (Table 3: Brush et al. 2002, Brush and Brawley 2009). State variables include the biomass of phytoplankton (PHYTO) and benthic microalgae (BMA), simulated in units of carbon (C) with chlorophyll-*a* (Chl-*a*), nitrogen (N), and phosphorus (P) computed stoichiometrically, hard clam biomass as individual dry weight in three size classes (CLAM), dissolved inorganic nitrogen (DIN) and phosphorus (DIP), dissolved oxygen (O₂), and labile organic carbon in the water column (C_{WC}) sediments (C_{SED}), with the associated N and P computed stoichiometrically (Figure 2). Given the shallow depths within Cherrystone Inlet and an active BMA community, a newly developed BMA sub-model (Brush 2013, Lake and Brush in press) was coupled to the ecosystem model (Table 3). BMA production and respiration were simulated in 0.5 meter depth intervals within each box, as a function of irradiance at depth and temperature. During calibration of the model, water column chlorophyll-*a* was consistently underestimated compared to VA DEQ monitoring data. Secrist (2013) reported high abundance of pennate diatoms in the water column of Cherrystone Inlet, which suggests the importance of BMA resuspension. A temperature (T)-dependent (Logan 1988), seasonal BMA resuspension term was therefore added to the model to resuspend a fraction of the BMA biomass (BMA_{STOCK}) (BMA_{RESUSP}, g C m⁻² d⁻¹):

$$BMA_{RESUSP} = BMA_{STOCK} * k_7 \left[\left(\frac{k_1(T-k_2)^{k_3}}{(k_4^{k_3})+(T-k_2)^{k_3}} \right) - EXP \left(k_7 - \left(\frac{k_5-(T-k_2)}{(k_5-k_6)} \right) \right) \right]$$

where T is the daily average temperature forced in the model, k_1 scales the amount of resuspended BMA over yearly temperature cycles, k_2 is the lower temperature

threshold at which BMA resuspension does not occur, k_3 drives the slope of BMA resuspension, k_4 is the temperature at which BMA resuspension is half of its maximum value, k_5 is the maximum temperature at which BMA resuspension occurs, k_6 is the temperature at which the value of BMA resuspension is maximal, and k_7 is the amount of BMA stock allotted for BMA resuspension (Haefner 2005). Parameter values used in the BMA resuspension term are reported in Table 2.

Water exchange within the ecosystem model is driven by a tidal prism approach, which computes volumetric exchanges among the seven spatial elements as a function of the tidal prism volume. Each box within the model is treated as a single vertical layer, as Cherrystone Inlet is considered a well-mixed estuary. While this approach loses spatial resolution due to the use of homogeneous aggregated spatial elements compared to higher resolution 3-D hydrodynamic circulation models, the type of reduced complexity model used in this study is able to reproduce the correct magnitude of state variables and typical down-estuary gradients, operates at the scale of available monitoring data, and enables fast run times (seconds to minutes) on personal computers. These fast run times make possible multiple runs required for adequate calibration and sensitivity analysis, and enable ready translation to user-friendly, online decision-support tools directly usable by managers and industry personnel. Recent work has confirmed the utility of boxed approaches (Menesguen et al. 2007, Testa and Kemp 2008, Kremer et al. 2010).

2.3 Forcing Data and Site-Specific Functions

VA DEQ collected monthly monitoring data at three stations in Cherrystone Inlet from January 2001 to December 2002 (Figure 1); this is the most complete set of monitoring data for this system so the model was calibrated to this time period. DEQ data for temperature, salinity, total suspended solids (TSS), water column chlorophyll-*a* (WC Chl-*a*), dissolved oxygen (O₂), and dissolved inorganic nitrogen (DIN) and phosphorus (DIP) were downloaded from the Chesapeake Bay Program (CBP) website (www.chesapeakebay.net). Surface temperature, salinity, and TSS data were linearly interpolated between sampling dates and forced into boxes 2 and 3 of the model; for the remaining Cherrystone boxes (which did not have associated DEQ sampling stations) the nearest respective DEQ data were used. Boundary conditions for salinity, water column Chl-*a*, O₂, DIN, and DIP were specified using long-term monitoring data from the CBP at the nearest monitoring station (CB7.3E), which is located 6.5 km southwest of Cherrystone Inlet. All boundary data were linearly interpolated and forced into the model.

Chlorophyll-*a* was converted to carbon biomass using a carbon to chlorophyll-*a* ratio of 45.1 g g⁻¹, which was determined using the spring and summer regressions between C:Chl and light attenuation (K_D) in Cerco & Noel (2004). Light attenuation (k_D) within the model was computed from modeled water column Chl-*a* and forced TSS using the baywide regression of Xu et al. (2005).

Photosynthetically active radiation (PAR) data from T. Fisher at the Horn Point Laboratory, MD (January 2001 - December 2002; Fisher et al. 2003) were forced into the

model as this was the most complete dataset available. Mean daily wind speed data from the meteorological station at Kiptopeke, VA (January 2001 – December 2002) were downloaded from NOAA (tidesandcurrents.noaa.gov). Watershed loading of total nitrogen was estimated using a Nitrogen Loading Model (NLM, see below); the load of phosphorus was computed stoichiometrically.

2.4 Model Calibration and Skill Assessment

The Cherrystone Ecosystem Model was calibrated to VA DEQ data for water column Chl-*a*, O₂, DIN, and DIP from January 2001 to December 2002 (Figure 4). Following the calibration to 2001-2002 data, the model was updated for the period January 2011 – December 2013 and verified against water quality and rate process data (i.e., phytoplankton net primary production, BMA gross primary production, water column and sediment respiration, and the rate of denitrification) measured in Cherrystone from a preliminary one-year dataset of baseline conditions and mid-summer nutrient fluxes from Virginia Sea Grant (VASG) project R/715157.

A detailed skill assessment was conducted on Cherrystone Ecosystem Model output for water column Chl-*a*, O₂, DIN, and DIP. Absolute (ABS Error), percent (% Error), and root mean square error (RMS Error), as well as the Nash-Sutcliffe efficiency and regressions of observations against predictions were calculated for each parameter (Fitzpatrick 2009, Stow et al. 2009). Skill metrics were computed by comparing observations and predictions on the same day of the observations, and within 1 and 2

weeks of the observations. The utility of these single metrics for assessing model-data misfit is enhanced when multiple quantitative measures are evaluated in combination.

2.5 Nitrogen Loading Model (NLM) for Cherrystone Inlet

Watershed loading of total nitrogen (TN) to Cherrystone Inlet was computed with the Nitrogen Loading Model (NLM), a lumped parameter, spatially-aggregated spreadsheet model. The NLM was originally developed for Cape Cod (Valiela et al. 1997), and has been subsequently adapted for the Delmarva Peninsula (Cole 2005, Giordano et al. 2011). The original formulations of the NLM were generated in Waquoit Bay, MA which is characterized by sandy sediments which tend to transport N in a conservative fashion. The Delmarva Peninsula is characterized by finer sediments and likely mixes N non-conservatively. This distinction in sediment type with respect to transport of N through the sediments is not accounted for within the model formulations in the Cherrystone NLM; nevertheless the NLM accurately reproduces measured TN loads across the Delmarva (Giordano et al. 2011: Brush, unpublished data). The NLM model was initially calibrated by Giordano and Brush (see Brush 2010) to 14 Virginia watersheds monitored by Stanhope (2009) and successfully predicts annual TN loads in the region, with only a few values falling outside the estimated 38% accuracy of the model (Valiela et al. 1997).

The model computes TN inputs from atmospheric deposition, fertilizer application (agricultural and residential), poultry waste, and human waste through septic systems, and accounts for inputs onto four land use categories: natural

vegetation, residential turf, impervious surfaces, and agriculture computed based on the 2005 Mid-Atlantic Regional Earth Science Applications Center land use – land cover dataset (RESAC 2005). Each land use category is subject to an annual rate of atmospheric N deposition of $6.2 \text{ kg N ha}^{-1} \text{ y}^{-1}$, obtained from Stanhope et al. (2009) who based the N deposition calculation on long-term measurements of both wet (National Atmospheric Deposition Program) and dry (EPA CASTNet) deposition on the Virginia Eastern Shore.

Extensive row crop agriculture on the Delmarva Peninsula require further breakdown of the agriculture land use term into main crops of the region which include corn, soybeans, winter wheat, hay, and tomato plasticulture. Values for the model crop parameters were compiled by Giordano et al. (2011) and include fertilization rate (less volatilization), N content, and crop yield specific to Virginia and adjusted to 2007 Census of Agriculture data specific for Northampton County, VA (USDA 2007). Poultry waste is estimated in the NLM by the number of birds in the watershed (a function of the number houses, stocking densities, and rotation schedules) and an individual poultry N release per year; only waste in excess of the required fertilizer is leached to the groundwater. Cherrystone Inlet did not have any poultry operations during the time of this study.

Residential inputs of N enter the model through fertilization of lawns (less volatilization) and septic field leaching, computed for the septic population (100% of residents in the watershed) using US Census Bureau data (TIGER 2010) and assuming a

release of 4.8 kg N person⁻¹ y⁻¹ (Valiela et al. 1997). The model attenuates each of these N sources to account for plant uptake and losses/immobilization in the vadose zone and aquifer (Valiela et al. 1997). Finally, the Cherrystone watershed is characterized by a number of retention ponds. Losses of N in these ponds are included in the original NLM (Valiela et al. 1997) but not in Giordano et al.'s (2011) version; they were added to the current version of the model using Valiela et al.'s (1997) formulations.

2.6 Hard Clam Bioenergetics and Growth Model

Hard clam (*Mercenaria mercenaria*) bioenergetics were simulated with an individual-based model originally developed by Hofmann et al. (2006) and modified by Wiseman (2010). The model computes individual clam dry weight (W) as a balance between ingestion, respiration, and reproduction, which are in turn functions of temperature, salinity, TSS, Chl-*a*, and individual weight.

For the current application, the following modifications were made to Wiseman's (2010) model. The dry weight (W, g) to shell length (SL, mm) relationship was replaced with a regression developed for clams in Cherrystone Inlet (Arnold, unpublished):

$$W = (2 * 10^{-6}) * (SL)^{3.394}$$

Wiseman's (2010) parameters for time open (t_{open} , time clams spend feeding) and algae lost to pseudofeces (P) were removed since they were found to double count the effects of temperature and TSS.

The effect of temperature on filtration was reset to Hofmann et al.'s (2006) original function, as it yielded output closer to observed weight and growth rates for clams in Cherrystone Inlet (Condon 2005). Similarly, the base respiration rate ($a_r - \mu L O_2 h^{-1} g^{-1} dw$) was changed back to the original value of 52.1 published by Hofmann et al. (2006). Finally, assimilation efficiency (AE) was set at a fixed value of 0.75, based on other bivalve studies (Tenore and Dunstan 1973), as this produced more realistic weights and growth rates than Hofmann et al.'s (2006) weight-dependent function.

Empirical data from Cherrystone Inlet were used when available to aid in parameterization and calibration of the hard clam model. Hard clam numbers in Cherrystone Inlet in 2003-2004 were estimated at 101,079,410 from data collected by Cherrystone Aqua-Farm personnel (Condon 2005, Arnold personal comm.). This estimate was used for model calibration in 2001-2002 since hard clam numbers likely did not vary considerably between the two time periods (M. Pierson, personal comm.). Further model verification of key rate process data using VASG project data (2011-2013) used estimated clam numbers in Cherrystone Inlet in 2012 of 144,263,376, with clam densities of 797 clams m^{-2} (Emery in prep).

Hard clam aquaculture operations in Cherrystone Inlet are characterized by a range of clam sizes from juveniles to market size (<40.04 mm SL) growing in aquaculture beds throughout the year to allow for a near constant harvest cycle. Since clams typically reach market size in approximately three years, the hard clam model simulated three clam size classes. The initial weight for the first size class was set to 0.19 mg in weight. Initial *in situ* weights for the youngest size class are variable and more data is

needed to determine site specific first size class initial weights. Subsequently, Initial hard clam weight (W , mg) for the second and third size class was calibrated so that final weights after the first year of growth equaled the initial values for the next size class.

The hard clam model was coupled to the ecosystem model through clam filtration of phytoplankton and resuspended BMA, respiratory consumption of oxygen and associated remineralization of nutrients, and deposition of feces into the sediment carbon pool. The hard clam model accounts for the effects of macroalgal growth on predator exclusion nets by reducing the amount of food (phytoplankton and resuspended BMA) available to the clams for filtration by 33% (Condon 2005).

2.7 Model Simulations

Once the ecosystem and hard clam models were calibrated, the coupled models were used to evaluate the effect of clam numbers, food availability, land use, and climate change on water quality and system-level parameters including clam growth, time to market size, and harvestable biomass at 1096 days (3 years being the ideal harvest growth cycle for Cherrystone Aqua-Farms). Hard clam growth scenarios were run with system-wide clam numbers that increased by 25 million from 25 to 200 million and then by 50 million up to 500 million during the standard run (2001-2002); this output was used as a baseline for comparison to all subsequent simulations. All other hard clam growth scenarios, as well as land use and climate change simulations were run up to 300 million clams. Clam population simulations were conducted by changing the quantity of predator exclusion nets (72 m^2) within each box using a clam density of 797 clams m^{-2} and assuming an equal number of clams in each size class. 57% of hard

clams in each scenario were placed in Box 2 and 43% in Box 3 based on calculation of suitable shoreline length (i.e., shoreline where the adjacent shallow water substrate is suitable for clam aquaculture operations) using Arc GIS (Table 6).

Food Availability Scenarios

All simulations specific to clam food availability were conducted under calibration conditions (2001-2002). Scenarios were conducted with the entire clam population placed in Box 1, 2, or 3 (Figure 1), in-order to assess spatial differences in clam food availability and growth along the estuarine gradient and optimal planting locations. The importance of BMA resuspension and availability as a food source to clams was assessed by a scenario without BMA resuspension. The effect of food reduction under predator exclusion nets was assessed by running a simulation without this reduction. Based on results from the skill assessment (Table 8), modeled chlorophyll-*a* is underestimated by approximately 34% even with the addition of BMA resuspension; the impact of this underestimation was quantified in a model simulation where water column chlorophyll was increased by this amount. Lastly, model simulations were conducted to determine the relative influence of internal versus external primary production on clam growth by removing the input of Chesapeake Bay chlorophyll-*a*, along with an additional simulation simultaneously removing the input of Chesapeake Bay nutrients.

Land Use Change Scenario

External factors influencing clam production were evaluated through land use and climate change scenarios. In order to evaluate the influence of watershed nutrient loading due to potential changes in land use, the NLM was used to determine an extreme case of nutrient loading. Agricultural land use in the region results in the most elevated rates of nutrient loading (Giordano et al. 2011), so a simulation was conducted where all land use in the watershed was converted into agricultural use, changing the export rate of nitrogen from $9.0 \text{ kg ha}^{-1} \text{ y}^{-1}$ to $16.2 \text{ kg ha}^{-1} \text{ y}^{-1}$ (Table 12).

Climate Change Scenarios

Potential changes in water temperature due to climate change were evaluated through scenarios with increased temperatures of 1, 2, 3, 4, and 5 ° C, bracketing projections for Chesapeake Bay by 2100 (Najjar et al. 2010). Separate climate change scenarios were run to assess the impacts of increases in sea level and associated increases in salinity within the Chesapeake Bay. Potential changes in sea level were evaluated through scenarios of increased mean sea level of 0.4, 0.7, 1.0, 1.3, and 1.6 m, bracketing projections for the Chesapeake Bay by 2100 (Hilton et al. 2008). Increases in salinity associated with sea level rise in the Chesapeake Bay were previously computed with regressions based on hydrodynamic model simulations (Hilton et al. 2008). Thus, for this study, scenarios of increasing salinity of 0.8, 1.4, 2.0, 2.6, and 3.2 were run concurrently with sea level rise scenarios (Table 14; Hilton et al. 2008).

3.0 RESULTS

3.1 Nitrogen Loading Model Calibration

The NLM estimated a watershed TN load to Cherrystone Inlet of 33,759 kg N γ^{-1} (9.0 kg N ha⁻¹ watershed γ^{-1}) (Table 4). The modeled TN yield was lower than the modeled export rate for all of Northampton County generated by the CBP Phase 5.3 Model (USEPA 2010), which includes more urban development and poultry houses than that found in the Cherrystone watershed (Table 4). The modeled TN yield fell within the measured range on the seaside of the Virginia Eastern Shore by Stanhope et al. (2009), measured during a drought period, for all watersheds and for those with the most similar land use characteristics (Table 4).

Agricultural fertilization was estimated to contribute 80% to the annual watershed TN load while inputs from direct atmospheric deposition to the surface of Cherrystone Inlet contributed 11%. Contributions from residential sources were relatively small with waste water contributing just over 3% and urban drainage contributing less than 1%. NLM results were further broken down to annual TN load from watershed areas that directly drain into the estuary, as well as sub-watersheds that first drain into ponds that retain approximately 56% of the N inputs as described in Valiela et al. (1997). Roughly one third of the total N loading to the Cherrystone Inlet had been attenuated by these ponds in the watershed. Loads and relative contributions of nitrogen sources were different within each watershed box, reflecting differences in land use patterns, indicating the ability of the NLM to predict differences over relatively small spatial scales (Table 5).

3.2 Model Calibration and Skill Assessment

Overall modeled water quality followed observed VA DEQ data, with generally low absolute, percent, and root mean squared errors; errors were further reduced when observed and predicted values were compared within one week of each other (Figure 4; Table 7-8). Modeled water column chlorophyll-*a* matched the observes throughout the fall, winter, and spring in both calibration years (2001-2002) (Figure 4a,b). However, the model failed to capture the highest chlorophyll-*a* concentrations during summer of both years. Percent error between observations and predictions for the standard run with respect to chlorophyll-*a* was 31.9% (\pm one week mean comparison); this error decreased when clams were not included in the standard run (24.8%) (Table 7). The standard run illustrates that 33.7% of observed VA DEQ chlorophyll-*a* was not accounted for in the model predictions (Table 8). Modeled BMA biomass was within the range of observations near the clam beds (Anderson and Murphy, unpublished data; Table 10).

The model does particularly well capturing the seasonal cycle of dissolved oxygen (Figure 4c,d). Percent error between observations and predictions for dissolved oxygen were the lowest of all the parameters (3.1%; Table 7). Modeled nutrient concentrations (DIN and DIP) were within the range of measured concentrations and followed the expected seasonal cycles (Figure 4e,f,g,h). During the end of the second standard run year (2002), observed VA DEQ DIN and DIP data are marked by a distinct elevation in concentrations that is not represented by the model. While the mean percent error for DIN and DIP were relatively large (26.2% and 25.5%, respectively) due

to differences in the second calibration year, the absolute error was less at 0.32 and 0.04 μM for DIN and DIP, respectively (Table 7).

3.3 Hard Clam Growth Scenarios

3.3.1 Standard Run

Initial clam weights were calibrated to ensure a continuous transition between size classes and reach harvestable size after three years (Figure 5). The standard run of the model with 100 million clams, which reflects the estimated size of the population in 2001-02, produced hard clam growth rates of 13.4 mm y^{-1} in Box 2, 12.9 mm y^{-1} in Box 3, and 13.2 mm y^{-1} averaged over the system, compared to an observed growth rate of 13.6 mm y^{-1} (Condon 2005, Figure 6a). Further comparison of clam growth rates by size class indicate a close correspondence between modeled and observed rates for the youngest size class, while the model underestimated growth rates for size classes 2 and 3 (Table 9). This underestimation of growth rates in the older size classes may be due to the underestimation of modeled chlorophyll-*a* in the summer.

Model simulations across a range of clam population sizes illustrated an inverse relationship between clam growth rates and total clam numbers ranging from 15.5 to 12.4 mm y^{-1} (Figure 6a). Increasing clam numbers also resulted in increases in days until clams are of a harvestable size and system wide harvestable biomass at three years, ranging from 741 to 867 days and 7.4 to 79.1 kg dry weight, respectively (Figure 6b,c). Increasing clam populations resulted in a decrease of average annual water column chlorophyll-*a* in the system from 4.4 to 2.4 mg m^{-3} (Figure 7). With increasing clam

populations chlorophyll-*a* was drawn below that in the incoming Chesapeake Bay water by 200M clams (Figure 7).

3.3.2 Location/Siting

Siting all clams in Box 1 resulted in an increase in growth rates by 22.8% and 15.4% as compared to the standard run in simulations with 100M and 150M clams, respectively (Table 11). Days until the clams reach harvestable size was reduced by 306 and 261 days and the overall harvestable biomass increased by 69.4% and 57% for 100M and 150M clams, respectively (Table 11). System-wide water column chlorophyll-*a* concentrations increased minimally by 7.3% and 8.8% for the 100M and 150M clam simulations, respectively (Table 11).

Siting all clams in Box 2 resulted in minimal differences compared to the standard run (Table 11), as a majority (57%) of the privately leased aquaculture plots in the standard run are within this box (Table 6). However, when clam operations were relocated solely to Box 3, there was a negative effect on all clam growth parameters with a slight reduction in growth rates, increase in days until harvest, and reduction in harvestable biomass at three years (Table 11). System-wide water column chlorophyll-*a* values decreased by 12.3% and 11.8% for the two simulations (Table 11).

3.3.3 Benthic Microalgal Resuspension

Removal of BMA resuspension decreased clam growth rates by an average 6.8% ranging from 12.6 to 11.52 mm y^{-1} (Figure 8a). This scenario resulted in an average increase of 153 days until harvest (Figure 8b), and total system-wide harvestable

biomass at three years decreased by an average of 64% (Figure 8c). Average annual water column chlorophyll-*a* concentration decreased in this scenario by an average of 20.5% (Figure 9).

3.3.4 Removal of Predator Exclusion Nets

When the reduction in chlorophyll-*a* due to predator exclusion nets was removed from the model, hard clam growth rates increased by an average of 13.3% ranging from 15.8 to 13.7 mm y⁻¹ (Figure 10a). Removal of the nets resulted in an average decrease in time to harvest of 24.5%, translating to a decrease of 194 days (Figure 10b), and total system-wide harvestable biomass after three years increased by an average of 54.5% (Figure 10c). Average annual water column chlorophyll-*a* concentration in this scenario decreased minimally by an average of 6.4% (Figure 11).

3.3.5 Increase in Water-Column Chlorophyll-*a*

Increasing the concentration of water column chlorophyll-*a* to better match DEQ observations resulted in increased system-wide growth rates by an average of 11.3% compared to the standard run (Figure 12a). Increased chlorophyll-*a* further resulted in an average reduction of 161 days until the hard clams reach harvestable size (Figure 12b), and total system-wide harvestable biomass at the three year harvest date increased by an average of 47.5% (Figure 12c). Average annual water column chlorophyll-*a* increased in these scenarios by an average of 32.4% (Figure 13).

3.3.6 Importance of Chesapeake Bay Chlorophyll-*a*

Removing the input of nutrients and chlorophyll-*a* from Chesapeake Bay reduced hard clam growth rates by an average of 41.1% (Figure 14a). Under this scenario, hard clams did not reach marketable size after three years, and total system-wide harvestable biomass after three years decreased by an average of 87.9% (Figure 14b). Average annual water column chlorophyll-*a* concentration decreased by an average of 70.1% in this scenario (Figure 15).

3.4 Watershed Nutrient Load Simulation

Running the NLM under the extreme case with 100% agricultural land use more than doubled the predicted export of nitrogen to Cherrystone Inlet from 9.0 kg N ha⁻¹ y⁻¹ to 16.2 kg N ha⁻¹ y⁻¹ (Table 12). Based on watershed export rates elsewhere on the Eastern Shore of Virginia, this yield lies at the high end of current loading rates (Table 4). Increased watershed nutrient loading had minimal effects on all hard clam metrics (Figure 16) and mean water column chlorophyll-*a* concentrations (Figure 17).

3.5 Climate Change Scenarios

3.5.1 Temperature Scenarios

Temperature time series from the climate simulations are shown in Figure 18. Hard clam growth rates consistently decreased as temperatures increased with rates decreasing by 0.3% to 37.6% in the 100M clam scenario and from 0.4% to 37.3% in the 150M clam scenario (Figure 19a). The amount of days until harvest increased continually as temperature increased, and after an increase of 3 °C clams did not reach harvestable size in three years. As a result, total system-wide harvestable biomass after

three years decreased by an average of 47% and 47.2% respectively for the 100M and 150M scenarios (Figure 19b). Average annual water column chlorophyll-*a* concentrations also decreased throughout the temperature simulations by an average of 6.5% and 8.9%, respectively for the 100M and 150M clam scenarios compared to an average concentration of 4.5 mg m⁻³ in the absence of clams (Figure 20).

3.5.2 Sea Level Rise and Salinity Scenario

Sea level rise and increase in salinity for the climate simulations are shown in Table 14. Hard clam growth rates displayed a unimodal response to increases in sea level and salinity reaching an intermediate maximum; overall growth increased an average of 0.6% and only in the most extreme simulation did growth decrease below that in the standard run (Figure 21a). The number of days until the clams reached harvestable size reduced minimally by an average of 1.2% and 4.3% (Figure 21b), and as a result harvestable biomass after three years also exhibited a unimodal relationship and increased by an average of 6.7% and 6.4% for the 100M and 150M clam scenarios, respectively (Figure 21c). The average annual water column chlorophyll-*a* concentration decreased throughout the sea level and salinity simulations by an average of 7.9% and 11% for the 100M and 150M clam scenarios, respectively, compared to an average of 4.3 mg m⁻³ without clams (Figure 22).

4.0 DISCUSSION

4.1 Model Calibration

The model correctly simulated both the magnitude and seasonal variations of water quality variables in Boxes 2 and 3 where VA DEQ data were available for calibration (Figure 4; Tables 7-8). Similarly, the model accurately reproduced observed BMA biomass (Table 10) and predicted hard clam growth rates close to observed values (Figure 6a; Table 9), although the latter were underestimated particularly for the second size class. We attribute this underestimation to a tendency of the model to underestimate concentrations of water column chlorophyll during the summer (Figure 4a,b; Table 8), even with the inclusion of BMA resuspension. The effect of this underestimation in summer chlorophyll was addressed through the simulation with increased chlorophyll (Section 3.3.5), which resulted in hard clam growth that exceeded observations (Figure 12). This illustrates first that hard clam growth is quite sensitive to food supply in this system, and second that the model is able to bracket observed rates of hard clam growth in Cherrystone Inlet (Figure 6a). Modeled clam growth rates for the second and third size classes, while underestimates, were also calibrated to obtain harvestable sizes within the typical three year rotation employed by Cherrystone farmers. Improvement of modeled growth rates would be aided by data associated with initial planting sizes and specific planting and harvest schedules in Cherrystone Inlet but this information is currently unavailable. Nevertheless, the overall quality of the calibration indicates that the model is suitable for conducting scenario analysis.

4.2 Standard Run

The standard run of the model demonstrated that increasing clam numbers were associated with diminishing returns in terms of clam growth rates, time to harvest size (≥ 40 mm SL), and harvestable biomass (Figure 6). As expected water column chlorophyll-*a* concentrations decreased with increasing clam numbers (Figure 7). Notable in this simulation is that as clam numbers approached 200M the chlorophyll-*a* concentration approached the average annual concentration, 3.7 mg m^{-3} , in the lower Chesapeake Bay that exchanges with Cherrystone on every flood tide. Cherrystone clam farmers have reported reduced growth rates and increased time until the clams reach harvestable size at numbers approaching 200M (M. Pierson , personal comm.).

4.3 Siting / Location

Optimal site selection for hard clam grow out areas requires the assessment of the supply and exchange of phytoplankton throughout the estuary (Grant 1996, Condon 2005), which our model is able to provide at the scale of individual boxes. The upper estuary (Box 1) was predicted to provide the best conditions with the most available food for hard clam production, with diminishing returns moving down the estuarine gradient to Box 3 at the mouth of the system (Table 11). Siting clams in the upper estuary allowed for increased utilization of the elevated phytoplankton biomass and internal primary production in Box 1, and the absence of grazing down-estuary resulted in an increase in overall water column chlorophyll throughout the system. Alternatively, siting clams in Box 3 resulted in depletion of chlorophyll-*a* to concentrations below that of the incoming Chesapeake Bay water (Figure 7), which not only consumes the external

food supply but also reduces internal primary production by removing flooding phytoplankton before they can grow within Cherrystone Inlet. We note, however, that this analysis only accounts for food supply while many other factors are important in siting of aquaculture operations, including bottom substrate, area available for nets, and access by land or water.

4.4 Importance of Tides and BMA Resuspension

The tidal regime in Cherrystone Inlet plays an integral role in the growth and production of the hard clams. Physical factors and large scale influences on local seston and water quality characteristics impact clearance rates in Cherrystone Inlet (Condon 2005) and in other systems dominated by bivalve aquaculture (Prins et al. 1998, Newell 2004). The tides have a two-fold influence on seston availability for clams in Cherrystone, resulting in both an influx of chlorophyll-*a* from the Chesapeake Bay and increased benthic microalgal and detrital resuspension to the water column, and thereby provide an important 'auxiliary energy source' supporting benthic production in this system (Nixon et al. 1971).

The short flushing time of Cherrystone Inlet, largely driven by the expansive shallow shoals and wide estuary mouth, has been postulated to cause extensive resuspension of benthic microalgae (Condon 2005). Benthic microalgae are often overlooked in hard clam production capacity modeling studies, however they have been identified as an adequate supplement to phytoplankton for hard clam growth (Grant 1996; Secrist 2013). In this study, the benthic microalgal resuspension term was critical for matching modeled water column chlorophyll-*a* to observed values, and the

simulation without BMA resuspension illustrates the importance of BMA as a food source for clams (Figure 8). This simulation focused solely on an increased quantity of organic matter; however, the quality of different sources of organic matter may also play a role in hard clam growth (Secrist 2013) and warrants further investigation.

4.5 Removal of Predator Exclusion Nets and Potential Importance of Macroalgae

Reduced seston concentrations as a result of biofouling and macroalgal growth on the predator exclusion nets was found to limit hard clam growth and decrease overall harvestable biomass (Figure 10). Condon (2005) and Secrist (2010) recognized that macroalgal growth on the nets in Cherrystone Inlet significantly depleted local seston concentrations available to the hard clams and this has similarly been observed in other bivalve aquaculture operations (Muschenheim and Newell 1992). The effect of macroalgal growth and reduced filtration on bivalve growth has been observed in many systems (Bartoli et al. 2001, Marinov et al. 2008, Viaroli et al. 2010). Cherrystone growers recognize that the proliferation of macroalgae is an issue impacting the growth of the hard clams, and they actively clean the nets of the macroalgae in an effort to improve filtration capacity (Anderson and Brush 2012).

Alternatively, the macroalgal growth on the predator exclusion nets has been considered as a viable food source for the clams (Condon 2005, Secrist 2013, Hondula and Pace 2014). This study did not incorporate macroalgal production within the model given the lack of data on the amount and availability of macroalgal detritus in the water column and below the nets. It is possible that this macroalgal detritus is at least partially reflected in the observed water column chlorophyll-*a* concentrations from VA

DEQ, which the model underestimates in summer. As noted above, the simulation with increased chlorophyll-*a* biomass resulted in increased clam growth rates (Figure 12) and this simulation combined with the standard run bracket the observed clam growth in Cherrystone (Condon 2005). While this scenario partially demonstrates the role of macroalgae in this system, future versions of the model should more explicitly evaluate macroalgae as both a food source and a sink for regenerated nutrients derived from the clam beds.

4.6 Internal vs. external production

The importance of horizontal hydrological exchange and influx of allochthonous chlorophyll has been documented in shallow estuaries (Grant 1996). Condon (2005) reported a positive correlation between chlorophyll and salinity in Cherrystone, indicating that the major source of chlorophyll comes from the mainstem Chesapeake Bay. Our study highlights the importance of this external source to clam production in Cherrystone Inlet (Figure 14). Further analysis of simulation results with 100M clams indicated that 59% of clam growth was supported by the input of organic matter from Chesapeake Bay; in fact, 52% of modeled water column primary production within Cherrystone was derived from the input of Chesapeake Bay phytoplankton (64% in Boxes 2-3). To assess the relative importance of the external supply of nutrients versus chlorophyll from the Chesapeake Bay, the simulation was run with and without the input of nutrients which had a negligible impact on internal production, thus the input of Bay phytoplankton was the more important driver of internal production.

The hard clam aquaculture industries along the Delmarva Peninsula should monitor future changes in quality and quantity of chlorophyll originating from the main stem Chesapeake Bay as this may significantly impact future clam aquaculture production. The capacity of the model to differentiate between allochthonous and autochthonous sources of primary production available for hard clam growth provides a useful quantitative tool to predict aquaculture production within Cherrystone Inlet and address regional food resources supporting the industry. Growth impacts on bivalve aquaculture (Bartoli et al. 2001), as well as on wild hard clams (Henry and Nixon 2008), to changes in the quantity and quality of both allochthonous and autochthonous sources of organic matter have been documented in other temperate estuaries. Nutrient reduction efforts in the lower Chesapeake Bay (and in similar estuaries worldwide) aimed at reducing eutrophication could have negative consequences for hard clam production. The biomass of benthic infauna in Chesapeake Bay is directly related to water column primary production (Hagy 2002, Kemp et al. 2005), and the recent loss of the winter-spring phytoplankton bloom in Narragansett Bay has reduced the supply of organic matter to the benthos, which potential negative consequences for benthic secondary production (Nixon et al. 2009). Future changes to the quantity and quality of organic matter in the lower Chesapeake Bay have been predicted to alter internal production in other neighboring tidal tributaries (Havens et al. 2001, Lake and Brush in press), and may present future concerns for both bivalve aquaculture and restoration. These results underline the utility of modeling efforts to assess the supply and movement of organic matter through varying hydrological dynamics for managing

the sustainability of aquaculture operations (Luckenback and Wang 2004, Marinov et al. 2008).

4.7 System-Level Effects of Clams

Numerous studies have highlighted the impact that suspension feeding bivalves have on controlling phytoplankton biomass through feeding (Officer 1980, Cloern 1982, Cohen et al. 1984, Prins et al. 1998, Henry and Nixon 2008). In an aquaculture setting, the nutrients assimilated within the tissues of the clams are also permanently removed from the system upon harvest potentially preventing further eutrophication.

Additionally, under certain environmental conditions, cultured bivalves may promote nutrient cycling processes such as sedimentary denitrification, a microbial process that converts bioavailable nitrogen to N_2 gas (Kellogg et al. 2013). The removal of bioavailable nitrogen through bivalve-promoted nutrient cycling has been postulated as an approach to mitigating eutrophication within estuaries (Lindahl et al. 2005; Rose et al. 2012; Bricker et al. 2014; Petersen et al. 2014).

At the system level, 100M cultured clams in Cherrystone were computed to reduce water column chlorophyll by 9%, indicating a limited ability to drive 'top-down' control on the ecosystem (Figure 7). The presence of 100M clams increased DIN and DIP concentrations by 3% system-wide and had no change on water column dissolved oxygen concentrations. Despite these relatively small impacts on system-level water quality, clams were computed to have a much larger impact on the overall nitrogen budget of the system (Table 13). Annual remineralization of hard clam feces far outweighed the release of nutrients from bare sediments, and the amount of

bioavailable nitrogen released to the water column attributed to hard clams (through excretion and remineralization of feces) was comparable to the inputs from the watershed and atmosphere.

Cultured clams can also exert numerous impacts at the smaller, farm-scale not currently resolved by the model. For example, clams may influence local 'bottom-up' effects on production by enhancing nutrient recycling at the sediment-water interface (Newell et al. 2002, Nizzoli et al. 2006, Nizzoli et al. 2011, Murphy et al. in press). Thus, Cherrystone clams may have the effect of decreasing or increasing localized eutrophication, depending on environmental conditions and specific culture densities (Hondula and Pace 2014; Murphy et al. in press). Commercial-scale bivalve aquaculture has been shown to reduce sediment and water quality and cause local nutrient enrichment, which has been linked to changes in the quantity and quality of organic carbon production further altering industry bivalve growth standards (Prin et al. 1998; Bartoli et al. 2001). Increased localized eutrophication originating from the growth of macroalgae on the predator exclusion nets in Cherrystone Inlet (dominated by the opportunistic *Gracilaria* spp.) may be a result of the high capacity of macroalgae to intercept recycled nutrients from the clams and sediments under the nets. In Cherrystone Inlet, Murphy et al. (*in press*) showed that sediments under the clam nets were reduced via high rates of biodeposition, and in the presence of sulphide the nitrogen removal process of nitrification-denitrification was inhibited and dissimilatory nitrate reduction to ammonium (DNRA) promoted the retention of bioavailable ammonium (NH_4^+) within the system, further fueling macroalgal production. Murphy et

al. (in press) estimated that the macroalgae in Cherrystone Inlet on the clam nets reduced benthic ammonium effluxes by 20-77%. The enhanced nutrient recycling within clam sediments observed in Cherrystone Inlet suggests that the aquaculture operations serve as an important autochthonous source of nutrients to primary producers within the system.

4.8 Land Use Scenarios

Changes in land use and climate are important factors to consider when predicting the production of hard clams in the Chesapeake Bay. In this model, we evaluated the potential effects of land use changes to more extensive agricultural use by investigating the impacts of increased nitrogen and phosphorus loads (Table 12). Export rates derived from the Nitrogen Loading Model under this scenario were still within the range of nutrient loads found on the Eastern Shore (Table 4). While this scenario is extreme, even under this unlikely scenario the watershed load and resulting effects on water quality are small. Nutrient loads from the watershed of Cherrystone Inlet, and other locations on the Delmarva Peninsula with land uses primarily associated with forested land, are primarily derived from ground water and the attenuation of nutrients through the aquifer, as well as in freshwater ponds, results in relatively minimal export of nutrient loads to the estuary (Stanhope et al. 2009, Giordano et al. 2012). Additionally these watersheds are small in area; for example, the ratio of watershed to open water area for Cherrystone is 5.9 compared to a value of 14 for the Chesapeake Bay (Kemp et al. 2005).

Changes in hard clam production due to changes in land use and watershed nutrient loading were small (Figure 16). However, ecosystem response and aquaculture production due to changes in land use characteristics were simulated under current hydrologic patterns, where the system is well-flushed and any enhanced primary production as a result of increased nutrient loading was likely flushed out of the system before causing adverse effects. Future land use planning should continue to utilize quantitative ecosystem modeling efforts to test the effects of land use changes. While many systems along the Delmarva Peninsula have minimal watershed loading rates (Giordano et al. 2011), other regions have larger watershed areas relative to open water and changes to land use and nutrient loading may have greater implications for ecosystem function and bivalve growth (Carmichael et al. 2012).

4.9 Climate Change

Temperature simulations

Changes in the global climate are likely to have a major impact on marine ecosystems, affecting both biodiversity and productivity (Najjar et al. 2010). These changes will in turn have large impacts on marine industries, including bivalve aquaculture (Kimmel and Newell 2007, Viaroli et al. 2010). Model simulations of changing climate with respect to temperature, salinity and sea level provided potentially important implications for the hard clam aquaculture industry. Under the enhanced temperature scenarios both clam growth rates and harvestable biomass dramatically decreased (Figure 19). Warmer water temperatures are expected to have negative effects on the physiology of bivalves, leading to impacts on metabolism and

reproduction (Grant et al. 1996; Ingram et al. 2013). A comparison of net clam production (growth – respiration) from the scenarios indicated that under the most extreme case of increased temperatures (+5°C) with 150M clams, net production was reduced by 94% and 51% in Boxes 2 and 3, respectively, compared to the standard run. The large differences in net production between Boxes 2 and 3 are indicative of internal variability in temperatures along the estuarine gradient and suggest that cooler temperatures from the Chesapeake Bay closer to the mouth of the system reduce the impact of simulated warming on clam production. The reduction in net clam production likely resulted in increases to overall water column chlorophyll (Figure 20). Increased temperatures are also likely to enhance macroalgal growth on predatory exclusion nets, and could lead to a negative feedback loop associated with increased hypoxia, reduced sediment quality, alterations to sediment nutrient cycling, and decreased water quality (Viaroli et al. 2010).

Sea Level Rise and Salinity Simulations

Increases in sea level have been predicted to have the greatest impacts on aquaculture operations in shallow water estuaries, as distribution of suitable benthic habitat for clam growth could shift and affect the productivity and accessibility of privately leased clam farms (Ingram et al. 2013). While our model does not have the capability to assess shifts in accessibility to leased clam operations, the model does indicate that changes in salinity and sea level do have adverse effects on clam production (Figure 21). Notable however, is the fact that with a moderate increase in salinity and sea level (salinity of 1.4 and 0.7 m increase in sea level) there was an

increase in clam production (Figure 21). Through further simulations which imposed increased depth and salinity independently, it was determined that this unimodal relationship in clam industry metrics (Figure 21) was best explained by increased water depth, whereas salinity had minimal effects on clam growth. It may be the case that deeper waters initially provided for more water column primary production which increased food availability to the hard clams, while at increased depths above 0.7 m, decreased water column light availability may limit system primary production. A comprehensive understanding of future adaptations to clam aquaculture and availability of suitable estuary bottom is imperative for the sustainability of the industry.

While this study addresses some of the major predicted changes to the Chesapeake Bay with climate change (Najjar et al. 2010), changes in precipitation, frequency and intensity of storms, and therefore freshwater delivery are also likely to have a major impact on ecosystem state and hard clam production (Ingram et al. 2013); however the model used here was not designed to address these changes.

4.10 Utility of the Model

The utility of the Cherrystone Ecosystem Model for addressing hard clam production capacity, system-level impacts of clam culture, and the effects of land use and climate change makes it relevant for both resource management and aquaculture industry planning. The implementation of integrative modeling approaches, such as that used in this study, for developing sustainable management strategies in large-scale bivalve aquaculture systems has been highlighted in previous studies (Luckenback and Wang 2004, Ferreira et al. 2009, Marinov et al. 2007, Byron et al. 2011). The standard

model run presented in this study gives managers and industry personnel a baseline to evaluate and plan for the sustainability of the hard clam aquaculture operations in Cherrystone Inlet. Largely due to the current water quality (Figure 4) and hydrological regime of Cherrystone Inlet (Figure 3), clam farmers have been able to harness the ability of the ecosystem to support a relatively large hard clam production. However, industry farmers in Cherrystone Inlet have proactively addressed reduced hard clam growth rates, through trial and error, by limiting the quantity of clam beds so that system wide production does not exceed 200 million clams (M. Pierson : personal comm.). This ecosystem model gives resource managers and industry personnel a method to quantitatively develop a sustainable aquaculture strategy in light of future land use and climate change.

4.11 Concluding Remarks

Currently the ecosystem function of Cherrystone Inlet enables the production and harvest of hard clams without large negative impacts to estuary; however the industry should continue to manage resources to maintain sustainability long-term under changing climatic conditions. Maintaining the function of coastal ecosystems in the face of changing land use, climate, and the increasing demand for growth in hard clam aquaculture was assessed with the use of a quantitative, system-level decision support modeling tool. The Cherrystone Ecosystem Model provides an important tool for the Virginia Eastern Shore and similar coastal systems, to aid in ecosystem-based management, support regional spatial planning, and ensure the sustainability of the aquaculture industry.

TABLES

Table 1. Box dimensions for watershed area, water-body surface area, average depth (mean sea level; MSL), water volume, and tidal prism volume in the Cherrystone Ecosystem Model.

Box Dimensions					
Box	Watershed Surface Area (m ²)	Water Surface Area (m ²)	Average Depth (m)	Water Volume (m ³)	Tidal Prism Volume (m ³)
1	13,977,837	851,958	0.62	528,214	675,160
2	2,483,365	2,240,587	1.10	2,464,646	1,775,620
3	1,551,553	1,862,973	1.55	2,887,608	1,476,369
4	1,481,263	103,171	0.52	53,649	81,761
5	819,318	87,302	0.52	45,397	69,185
6	7,414,246	264,463	0.57	150,744	209,581
7	5,361,076	219,201	0.52	113,985	173,712

Table 2. Coefficients and values associated with benthic microalgal resuspension term used in the benthic microalgae sub-model.

BMA Resuspension Term	
Coefficients	Values
k1	1
k2	0
k3	3
k4	38.7
k5	40
k6	30
k7	0.1

Table 3. Values, units, definitions of parameters and coefficients used in the ecosystem model.

Parameter	Definition	Units	Value
<i>Phytoplankton Sub Model</i>			
Phyto C:Chl	Carbon to chlorophyll ratio	gC gChl ⁻¹	45.12
Phyto C:N	Carbon to nitrogen ratio	molar ratio	6.625
Phyto C:P	Carbon to phosphorous ratio	molar ratio	106
Phyto C:dw	Carbon to dry weight ratio	gC gdw ⁻¹	0.4
mBZI	Slope, phytoplankton production equation	n/a	0.76
Phyto PQ	Photosynthetic quotient	molar ratio (O ₂ :CO ₂)	1
Phyto RQ	Respiratory quotient	molar ratio (CO ₂ :O ₂)	1
wtrclm Rf0	0 ° intercept for wtrclm respiration	d ⁻¹	0.05
wtrclm RfQ10	Exponent for wtrclm respiration	°C ⁻¹	0.71
<i>Benthic Chlorophyll Sub Model</i>			
alpha intercept	Intercept for initial slope of the PI Curve	mg O ₂ mg ⁻¹ chl a h ⁻¹ (µE m ⁻² s ⁻¹) ⁻¹	0.0259
alpha exponent	Exponent for initial slope of the PI Curve	°C ⁻¹	-0.044
Gmax slope	Slope of regression between G _{max} and T	°C ⁻¹ d ⁻¹	0.0047
Gmax intercept	Intercept of regression between G _{max} and T	d ⁻¹	0.2464
BMA PQ	Photosynthetic quotient	molar ratio (O ₂ :CO ₂)	1
BMA RQ	Respiratory quotient	molar ratio (CO ₂ :O ₂)	1
BMA Rf0	20 ° intercept for respiration	d ⁻¹	0.045
BMA RfQ10	Exponent for respiration	°C ⁻¹	0.069
BMA β ₁ ⁻¹	First mortality coefficient	m ² gC ⁻¹ d ⁻¹	0.075
BMA β ₂ ⁻¹	Second mortality coefficient	d ⁻¹	0.085
BMA β ₃ ⁻¹	Third mortality coefficient	d ⁻¹	0.02
BMA C:Chl	Carbon to chlorophyll ratio	gC gChl ⁻¹	45.12
BMA C:N	Carbon to nitrogen ratio	molar ratio	9
BMA C:P	Carbon to phosphorous ratio	molar ratio	144
<i>Hard Clam Sub Model</i>			
AE	Assimilation efficiency	-	0.75
Clam RQ	Respiratory quotient	molar ratio (CO ₂ :O ₂)	1
Clam C:N	Carbon to nitrogen ratio	molar ratio	6.62
Clam C:P	Carbon to phosphorous ratio	molar ratio	116.25
<i>Watershed Nutrient Loading Model</i>			

Load P:N	Phosphorous to nitrogen ratio	molar ratio	0.0625
Natm	Atmospheric N deposition	gN m ⁻² d ⁻¹	0.0017
<i>Sediment Sub Model</i>			
SED Rf0	0 ° intercept for respiration	d ⁻¹	0.5
SED RFQ10	Exponent for respiration	°C ⁻¹	0.08
SED RQ	Sediment respiratory quotient	molar ratio (CO ₂ :O ₂)	1
DNF0	0 ° intercept for denitrification	d ⁻¹	0.005
DNFQ10	Exponent for denitrification	°C ⁻¹	0.04

$$^1 \text{BMA_mortality} = (\text{BMA_}\beta_1 * \text{BMA_BIOMASS}^2) + (\text{BMA_}\beta_2 * \text{BMA_BIOMASS}) + (\text{BMA_}\beta_3 * \text{BMA_BIOMASS})$$

Table 4. Modeled watershed yields of total nitrogen (TN) from the Cherrystone Inlet watershed and other lower Delmarva watersheds.

Estuary (Source)	Export TN (kg N ha ⁻¹ y ⁻¹)
Cherrystone (this study)	9.0
Northampton County, VA (CBP Phase 5.3 Watershed Model USEPA 2010)	16.1
14 VA Eastern Shore watersheds (Stanhope 2009)	0.1 - 12.9
4 VA Eastern Shore watersheds with land use most similar to Cherrystone (Stanhope 2009)	4.7 - 10.1

Table 5. Modeled watershed total nitrogen (TN) export ($\text{kg N ha}^{-1} \text{y}^{-1}$), load (kg N y^{-1}) and % load for each Cherrystone Inlet sub-watershed.

Spatial Element	TN Export ($\text{kg N ha}^{-1} \text{y}^{-1}$)	TN Load (kg N y^{-1})	% Load
Box 1	8.9	12,382	41.5
Box 2	11.6	2,887	9.7
Box 3	14.1	2,194	7.3
Box 4	13.2	1,954	6.5
Box 5	11.4	937	3.1
Box 6	7.6	5,626	18.8
Box 7	7.2	3,881	13.0
System	9.0	29,915	100

Table 6. Number of predator exclusion nets for the total estuary and for each size class in each spatial element based on model scenario (using a net area of 72 m² and hard clam planting density of 797 clams m⁻²).

Hard Clam Numbers	Net Numbers (Estuary)	Nets Numbers (size class ⁻¹)	
		Box 2	Box 3
25M	436	83	62
50M	871	166	125
75M	1307	248	187
100M	1761	335	252
125M	2178	414	312
150M	2514	478	360
175M	3050	579	437
200M	3485	662	500
250M	4357	828	624
300M	5228	993	749
350M	6099	1159	874
400M	6971	1324	999
450M	7842	1490	1124
500M	8713	1656	1249

Table 7. Skill assessment of the standard run under calibration conditions (100M clams during 2001-2002) compared to VA DEQ water column monitoring data. Skill metrics are shown for mean and median absolute error (ABS Error), percent error (% Error), root mean square error (RMS Error), and Nash-Sutcliffe modeling efficiency comparing model predictions to observations on the same day and within one and two weeks of data collection. Output for chl-*a* is also shown for a simulation without clams.

Temporal Comparison	Error Type	Measure	Chl- <i>a</i> Standard Run (mg m ⁻³)	Chl - <i>a</i> No Clams (mg m ⁻³)	DIN (uM)	DIP (uM)	DO (mg L ⁻¹)
Same Day	ABS Error	Mean	3.61	3.00	2.03	0.14	1.18
	ABS Error	Median	2.23	1.88	0.61	0.11	1.06
1 week	ABS Error	Mean	2.09	1.50	0.32	0.04	0.25
	ABS Error	Median	2.15	1.12	0.23	0.02	0.20
2 weeks	ABS Error	Mean	2.18	1.67	0.35	0.05	0.39
	ABS Error	Median	1.99	1.39	0.28	0.03	0.34
Same Day	% Error	Mean	45.2	59.7	52.7	60.0	13.3
	% Error	Median	43.1	30.9	50.9	58.3	12.9
1 week	% Error	Mean	31.9	24.8	26.2	25.5	3.1
	% Error	Median	33.0	17.5	19.6	23.5	2.5
2 weeks	% Error	Mean	32.3	29.1	27.5	28.9	5.0
	% Error	Median	32.6	19.8	22.2	25.8	4.6
Same Day	RMS Error	n/a	5.65	4.72	3.54	0.20	1.41
1 week	RMS Error	n/a	2.46	2.03	0.40	0.05	0.34
2 weeks	RMS Error	n/a	2.65	2.16	0.44	0.06	0.49
Same Day	Nash-Sutcliffe	n/a	-0.09	0.24	0.17	-0.45	0.21
1 week	Nash-Sutcliffe	n/a	-0.31	0.48	0.87	0.80	0.92
2 weeks	Nash-Sutcliffe	n/a	-0.25	0.50	0.85	0.67	0.84

Table 8. Slope and r^2 from regressions of model output (y) vs. VA DEQ water column monitoring data (x) for the standard run under calibration conditions (100M clams during 2001-02). Regressions compare model predictions to observations on the same day and within one week of data collection. Output for chl-*a* is also shown for a simulation without clams where all other parameters include clams.

Temporal Comparison		Chl- <i>a</i>	Chl- <i>a</i>	DIN (μM)	DIP (μM)	DO (mg L^{-1})
		Standard Run (mg m^{-3})	No Clams (mg m^{-3})			
Same Day	Slope	0.18	0.26	0.22	0.17	0.59
	r^2	0.28	0.27	0.71	0.08	0.63
1 week	Slope	0.66	1.02	0.84	0.83	0.91
	r^2	0.62	0.66	0.88	0.82	0.94

Table 9. Hard clam growth rates (mm y^{-1}) per size class from 25 million to 500 million clams computed in the standard model simulations compared to measured growth rates at 100 million clams in Cherrystone Inlet (Condon 2005).

Number of Clams	Size Class 1	Size Class 2	Size Class 3
Measured growth with 100M (Condon 2005)	25.47	13.04	8.02
25M	25.87	8.16	6.57
50M	25.69	8.01	6.46
75M	25.45	7.94	6.43
100M	25.30	7.82	6.30
125M	25.13	7.71	6.25
150M	24.99	7.67	6.23
175M	24.76	7.54	6.13
200M	24.62	7.47	6.04
250M	24.31	7.30	5.95
300M	24.12	7.14	5.86
350M	23.88	7.01	5.76
400M	23.64	6.88	5.65
450M	23.43	6.80	5.57
500M	23.23	6.67	5.48

Table 10. Mean and standard error of modeled benthic chlorophyll-*a* (mg m^{-2}) in the top 3 mm of sediment in the 0 – 0.5 m depth segment for Boxes 2 and 3, compared to data collected at approximately 0.5 m in Cherrystone Inlet (Anderson and Murphy, unpublished).

Benthic Chl- <i>a</i>	Mean	Standard Error
Box 2 Model Output	38.2	18.8
Box 3 Model Output	43.2	14.7
Observed, March 2013	39.7	20.6
Observed, July 2013	50.3	6.6
Observed, November 2013	35.0	14.3

Table 11. Simulation results in which hard clams were placed entirely within Box 1, Box 2, or Box 3, including the percent (%) difference from the standard run with corresponding clam numbers.

Simulation	Growth Rates, mm y ⁻¹		Time To Harvest, days		Harvestable Biomass, kg dry weight		Chl- <i>a</i> , mg m ⁻³	
	100M Clams	150M Clams	100M Clams	150M Clams	100M Clams	150M Clams	100M Clams	150M Clams
	Standard Run	13.1	13.0	767	803	29.9	40.8	4.0
BOX1	16.1	15.0	461	542	56.7	64.1	4.3	4.2
%difference	22.8	15.4	-39.9	-32.5	89.4	57.0	7.3	8.8
BOX2	13.2	12.9	757	806	30.8	41.1	4.3	4.1
%difference	0.4	-0.3	-1.3	0.4	2.9	0.8	7.8	5.9
BOX3	12.8	12.7	838	849	26.5	36.5	3.5	3.4
%difference	-2.4	-2.1	9.3	5.7	-11.4	-10.5	-12.3	-11.8

Table 12. Modeled watershed total nitrogen load (kg N y^{-1}) and export ($\text{kg N ha}^{-1} \text{y}^{-1}$) under calibration conditions (2001-2002) and for an increased load simulation (Total Ag Sim) in which all watershed land use was converted to agriculture.

Watershed Nitrogen Exchange	Calibration Conditions	Increased Watershed Exchange Sim
Load (kg N y^{-1})	29,838	53,583
Export ($\text{kg N ha}^{-1} \text{y}^{-1}$)	9.0	16.2

Table 13. Computed nitrogen inputs to Cherrystone Inlet ($\times 10^6$ g N y^{-1}) under the standard run with 100M clams.

Cherrystone Inlet Nitrogen Budget	$\times 10^6$ gN y^{-1}
Watershed Load	29.8
Direct Atmospheric Deposition	34.2
Input Across Mouth	55.1
Sediment Remineralization	11.2
Hard Clam Feces Remineralization	19.7
Hard Clam Excretion	2.0

Table 14. Increased sea level and salinity values for each simulation represented in Figures 21-22.

Simulation	0	1	2	3	4	5
Sea-Level Change	0m	0.4m	0.7m	1.0m	1.3m	1.6m
Salinity Change	0	0.8	1.4	2	2.6	3.2

FIGURES

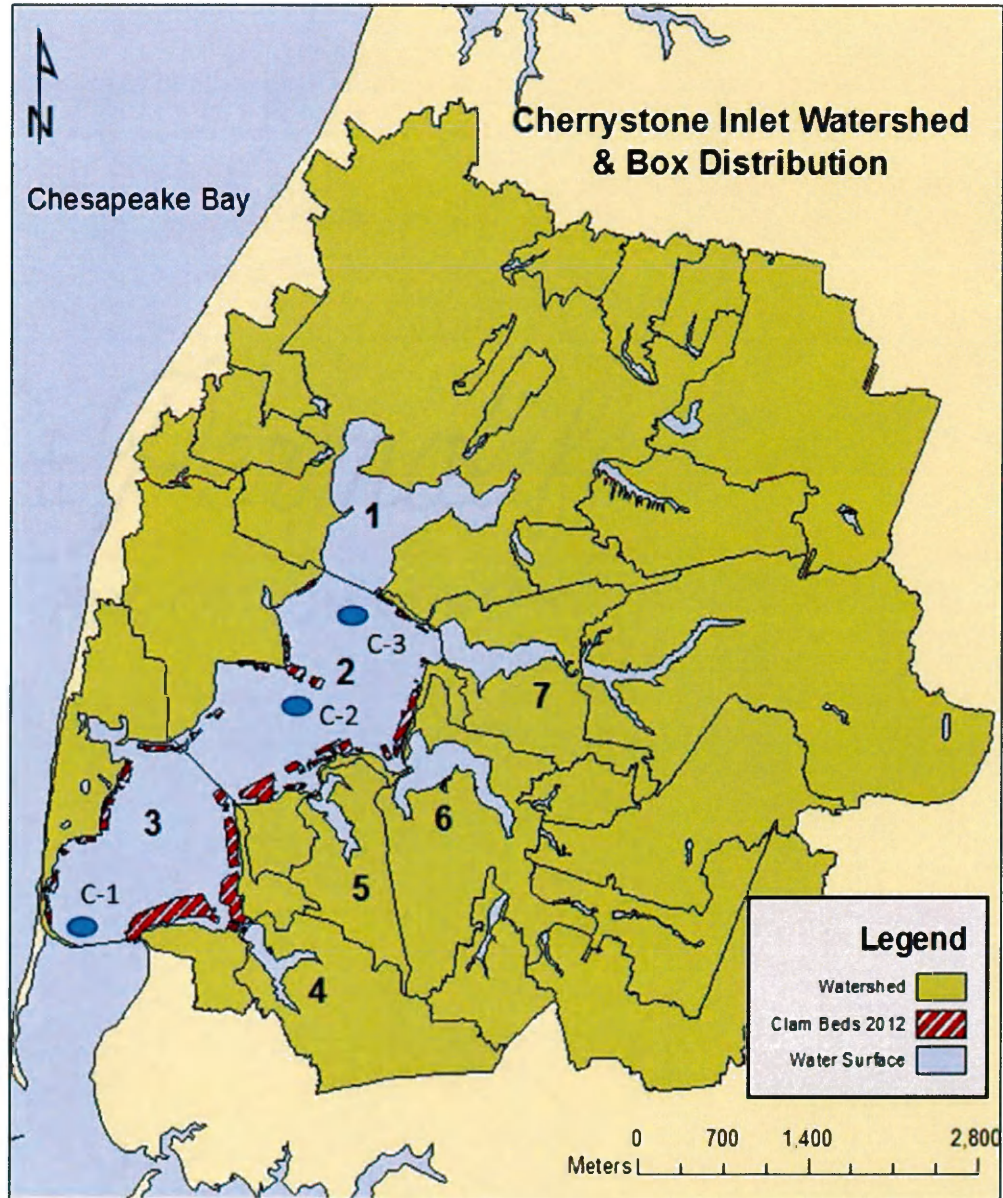


Figure 1. Cherrystone Inlet spatially separated into 7 boxes (labeled 1-7) within the ecosystem model, the adjacent watershed, the area of cultured clam beds in 2012 (Manley 2014), and Virginia Department of Environmental Quality stations.

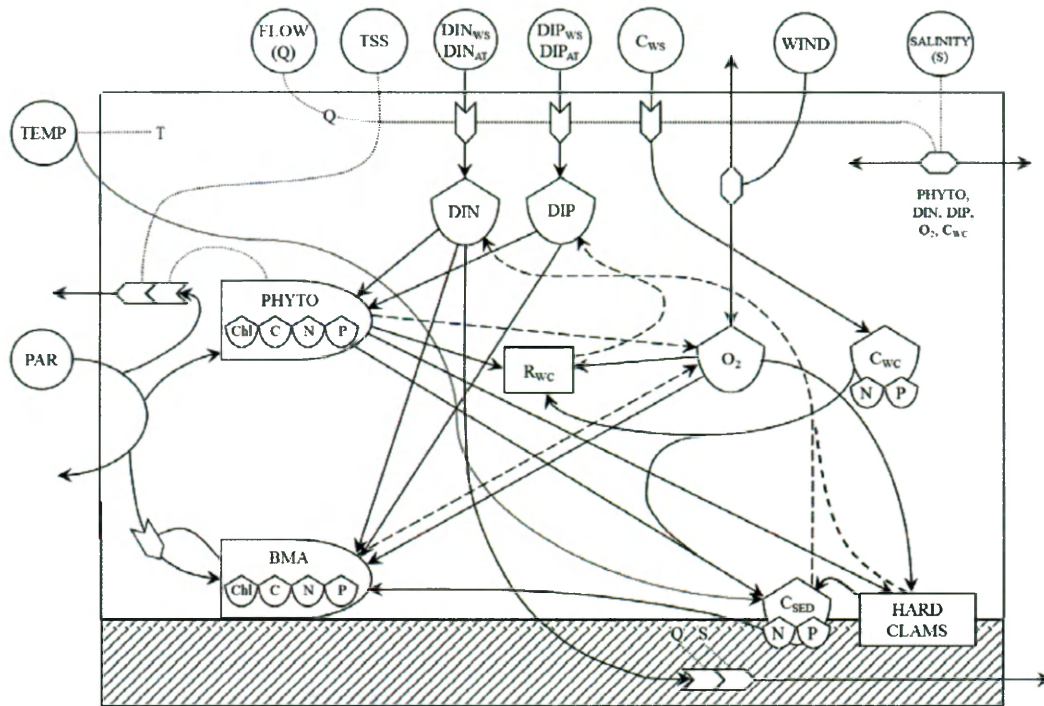


Figure 2. Cherrystone Ecosystem Model diagram depicting the mechanistic connections between key state variables (phytoplankton (PHYTO), benthic microalgae (BMA), DIN, DIP, O₂, water column and sediment organic carbon (C_{WC} and C_{SED}, respectively), and three size classes of hard clams, as well as the influence of major forcing functions (i.e., river flow, total suspended solids, watershed loads of DIN and DIP, wind, temperature, salinity, photosynthetically active radiation (PAR), and the exchange due to tides). Flows that consume material (e.g. nutrient uptake, oxygen consumption, loss of biomass) are shown with solid lines. Flows which produce material (e.g. remineralization, photosynthetic oxygen production) are shown with broken lines. To reduce the complexity of the figure, all respiratory demands are shown as being integrated into an estimate of total water column respiration (R_{WC}), which draws from the oxygen pool and remineralizes N and P. The effect of temperature (T) on most state variables and flows has likewise been excluded. All other terms are defined in the text.

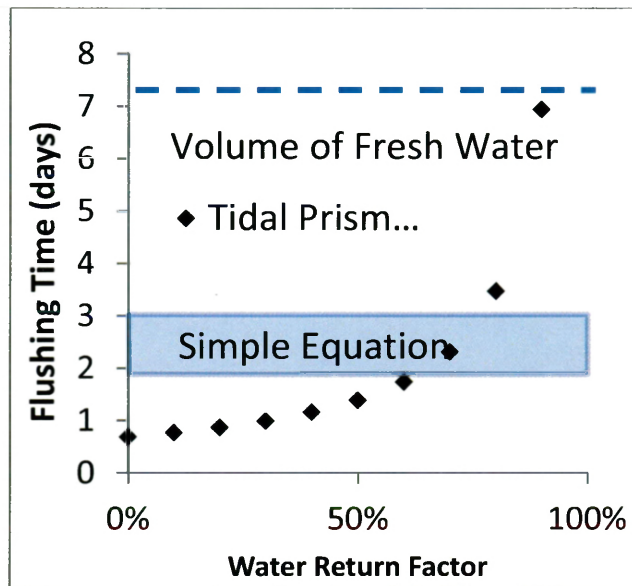


Figure 3. Flushing times for Cherrystone Inlet computed with the estuarine model via the tidal prism method (Monsen et al. 2002) with varying amounts of water that returns to the estuary after every ebb tide. In comparison, the simple equation (Herman et al. 2007) and the volume of freshwater method (Officer et al. 1980) resulted in annual average residence times of 2-3 days and ~7 days respectively.

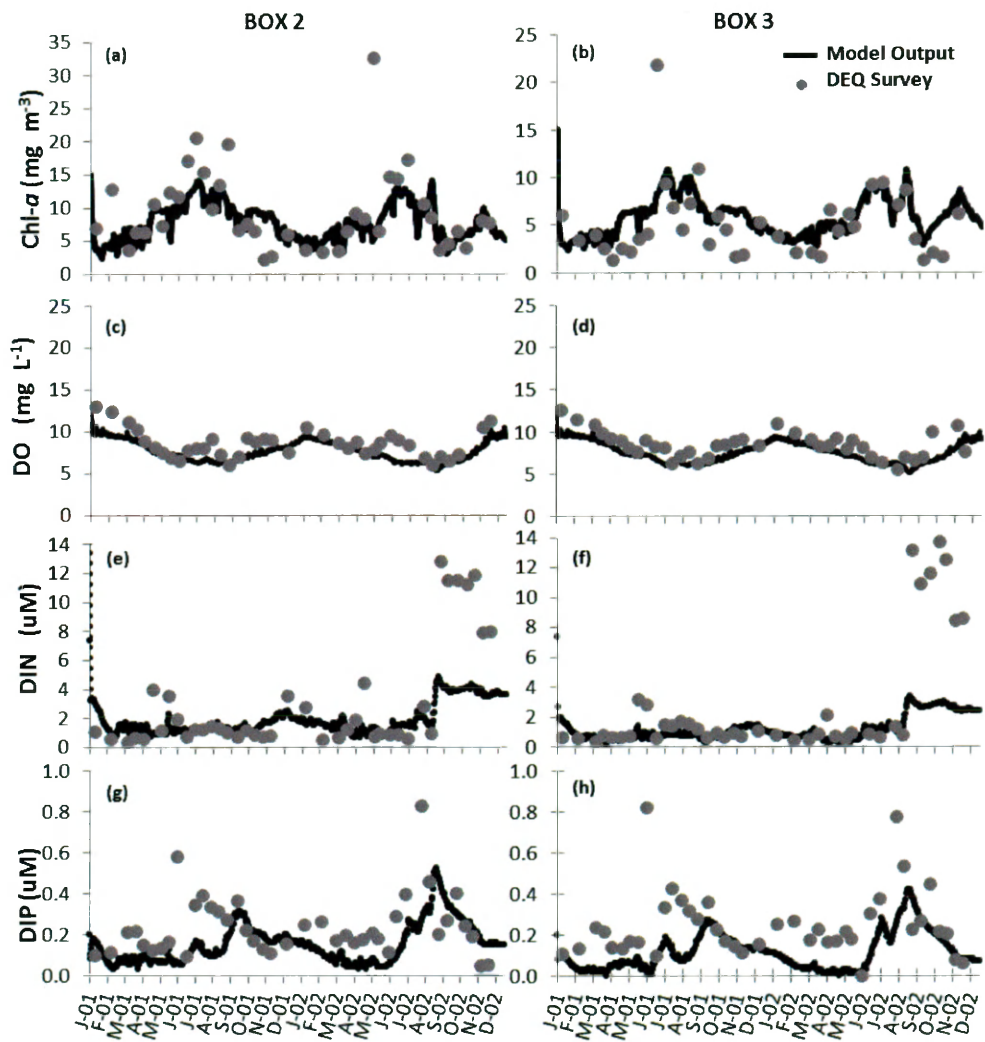


Figure 4. Model calibration plots for Cherrystone Inlet in Box 2 (with average DEQ survey data from stations C-2 & C-3) and Box 3 (with DEQ survey data from station C-1). Results are shown for water column chlorophyll-*a* (a, b), dissolved oxygen (c, d), dissolved inorganic nitrogen (e, f), and dissolved inorganic phosphorus (g, h).

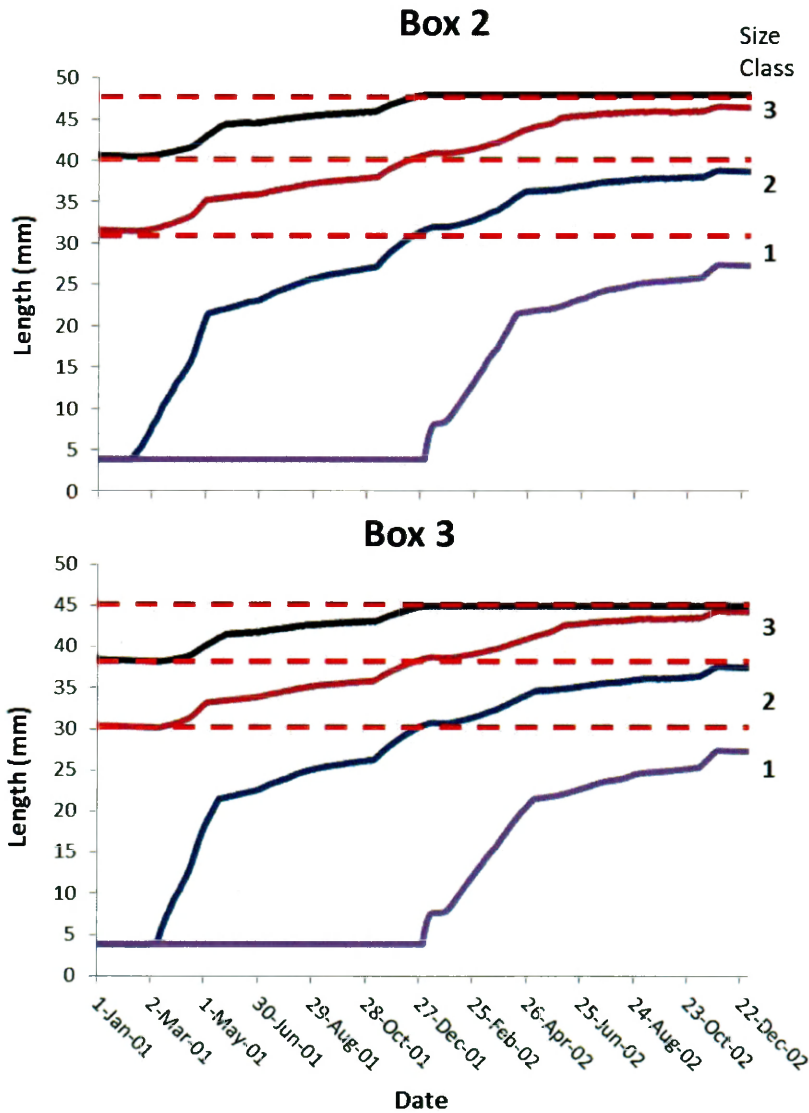


Figure 5. Modeled hard clam length (mm) over the two year model run for Boxes 2 and 3. Size classes are separated by dashed lines and size class number. Clams in a given size class transition into the next class in the second year of the simulation; clams in size class 3 in the first year of the simulation drop out of the model in the second year, and a new group of clams enters the model in size class 1.

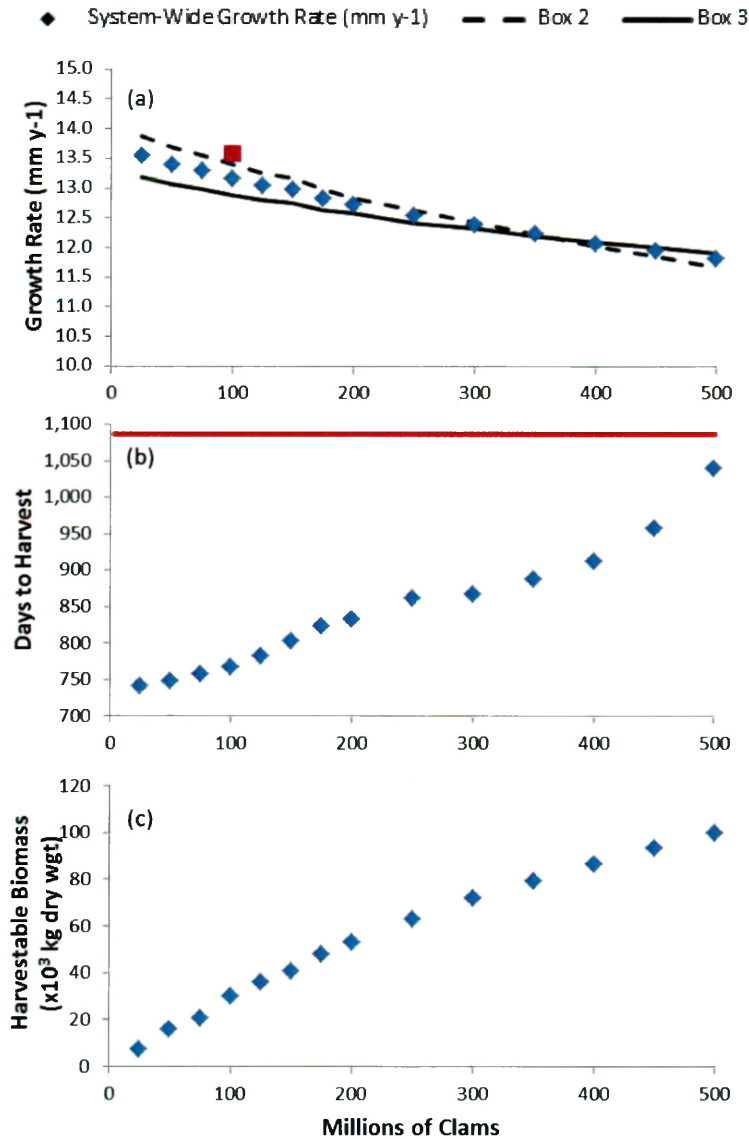


Figure 6. Modeled hard clam growth metrics under simulations of increasing numbers of clams. (a) Growth rate (mm y-1) in Boxes 2 (dashed line) and 3 (solid line), averaged between Boxes 2 and 3 (diamonds), and measured growth rate for Cherrystone Inlet with 100M clams (red square, Condon 2005). (b) Days to harvest compared to a standard harvest time for Cherrystone farmers of 3 years (1095 days, solid red line). (c) Harvestable biomass ($\times 10^3$ kg dry weight) after 1095 days.

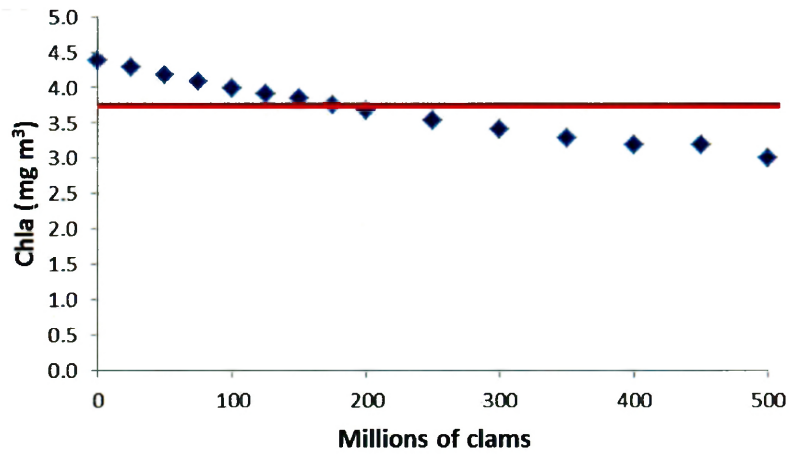


Figure 7. Modeled system-wide, average annual water column chlorophyll-*a* (mg m^{-3}) under simulations with increasing numbers of clams, compared to the annual mean concentration in incoming Chesapeake Bay water (CBP station 7.3E, red line).

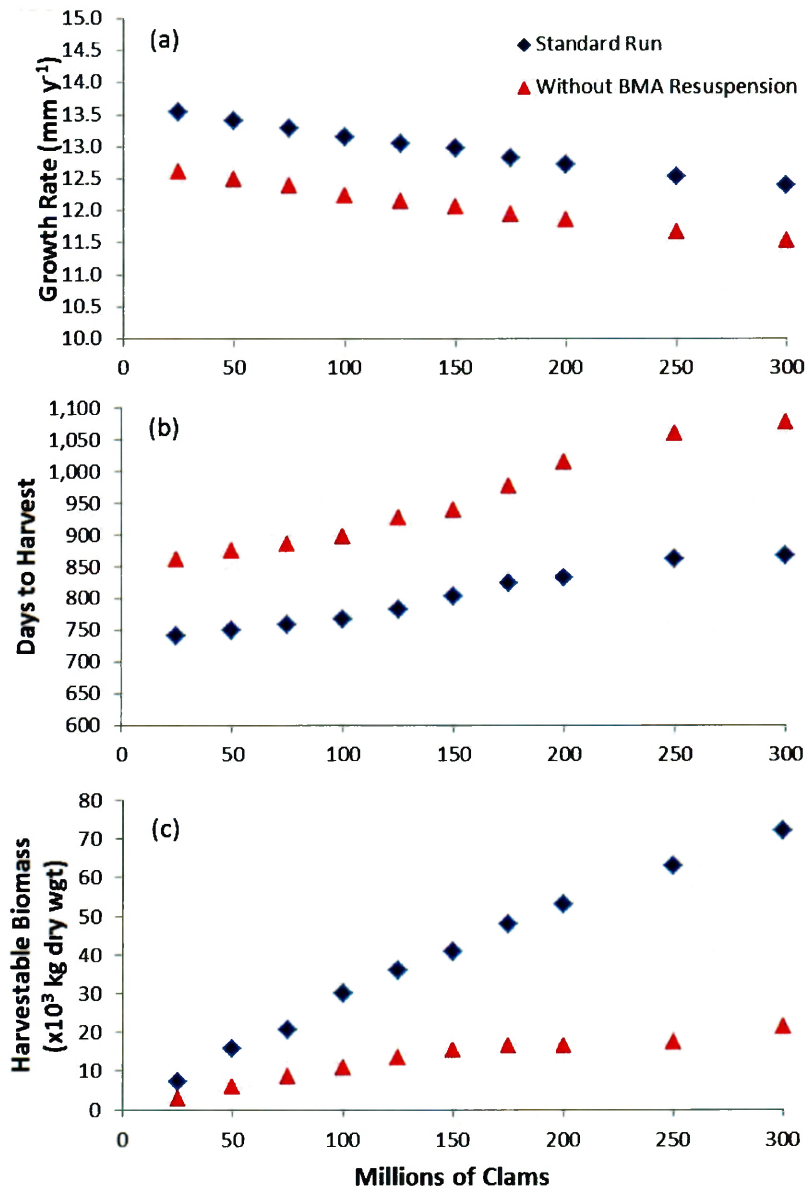


Figure 8. Modeled hard clam growth metrics without BMA resuspension (red triangles) with increasing numbers of clams compared to the standard run (blue diamonds). Formatting matches that in Fig. 6.

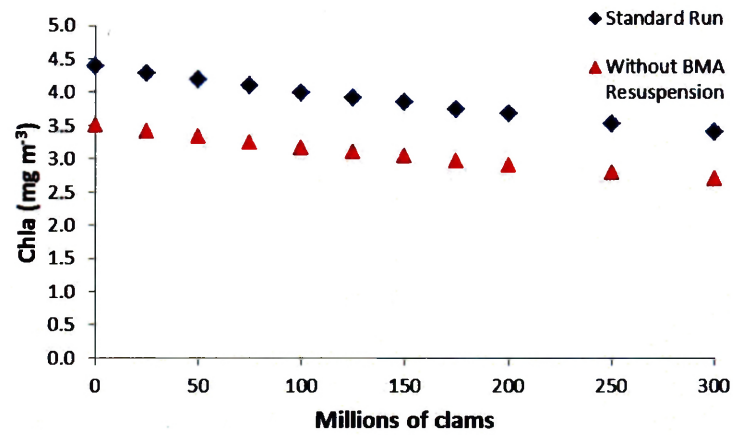


Figure 9. Modeled system-wide, average annual water column chlorophyll-*a* (mg m^{-3}) without BMA resuspension (red triangles) under increasing numbers of clams compared to the standard run (blue diamonds).

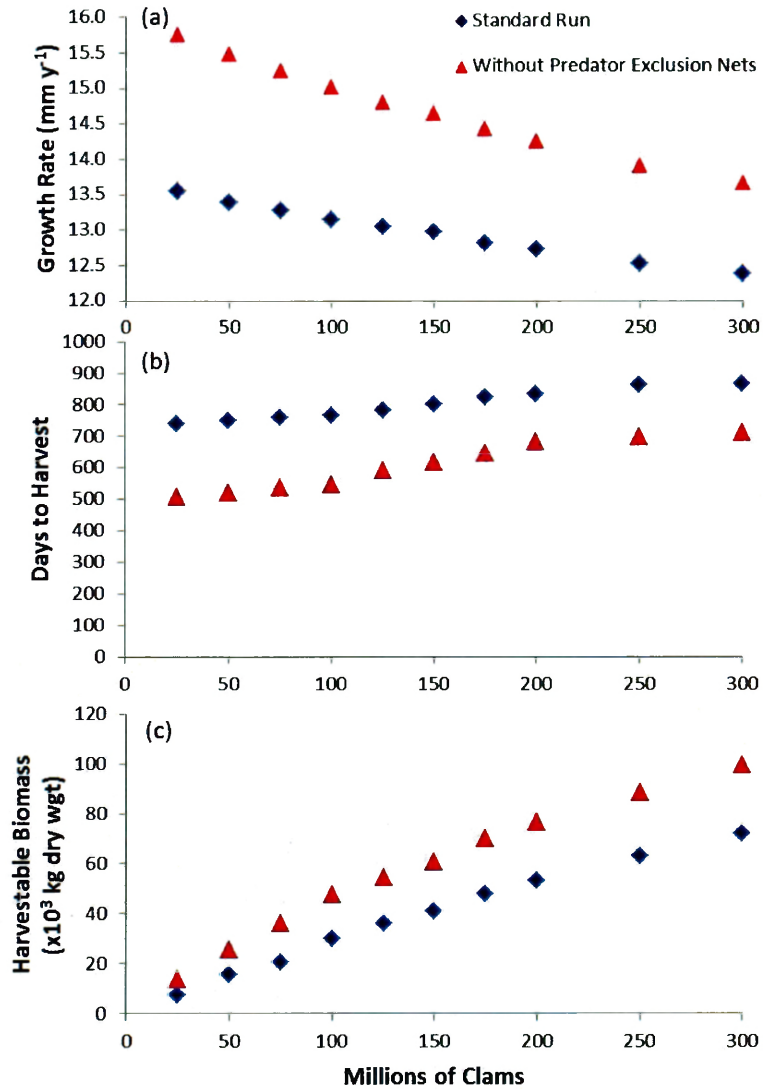


Figure 10. Modeled hard clam growth metrics with the scenario of no predator exclusion nets (red triangles) with increasing numbers of clams compared to the standard run (blue diamonds). Formatting matches that in Fig. 6.

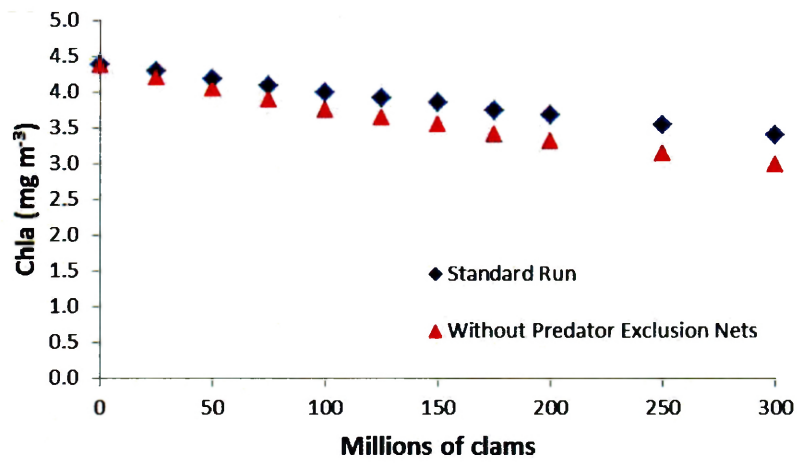


Figure 11. Modeled system-wide, average annual water column chlorophyll-*a* (mg m^{-3}) without the effect of predator exclusion nets on filtration (red triangles) under increasing number of clams compared to the standard run (blue diamonds).

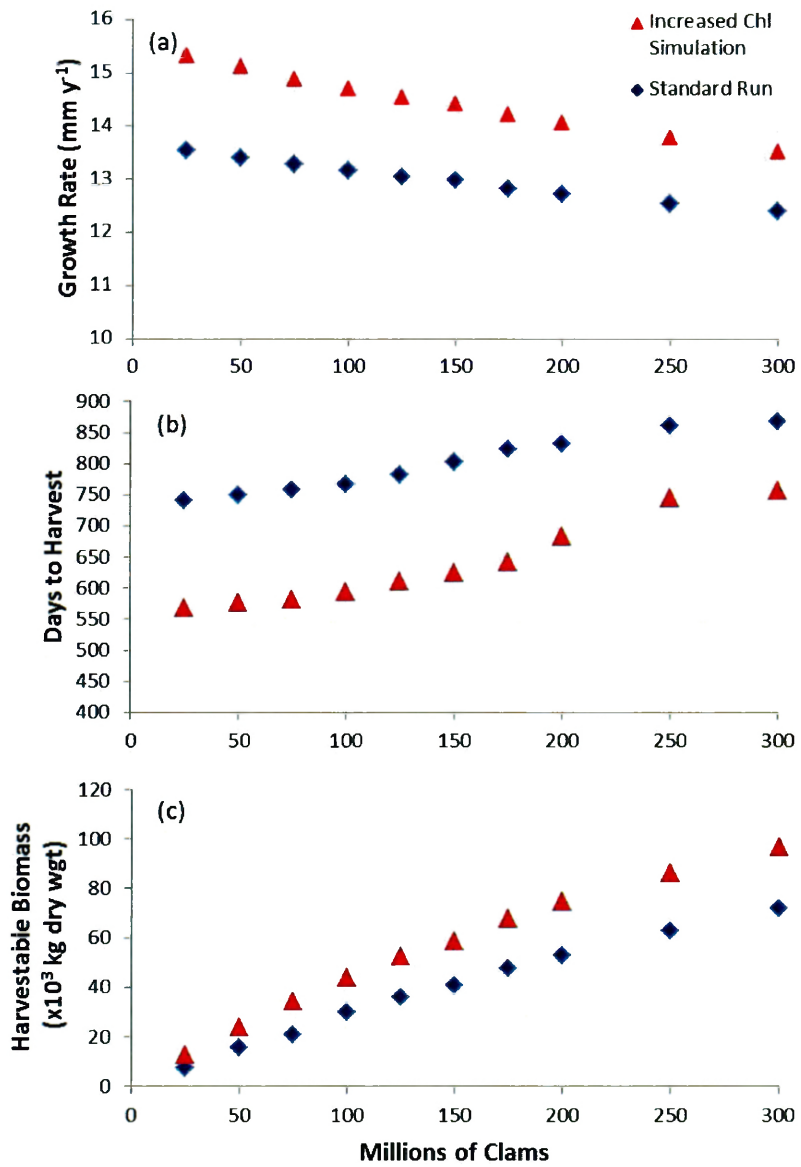


Figure 12. Modeled hard clam growth metrics of simulated increased water-column chlorophyll-*a* (red triangles) with increasing numbers of clams compared to the standard run (blue diamonds). Formatting matches that in Fig. 6.

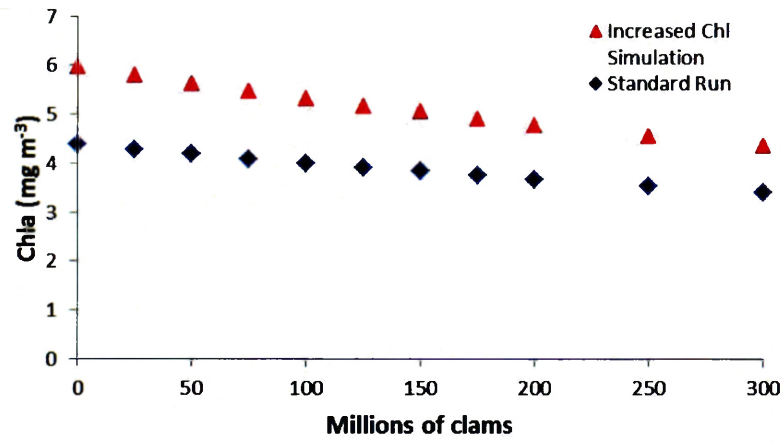


Figure 13. Modeled system-wide, average annual water column chlorophyll-*a* (mg m^{-3}) of simulated increased chlorophyll-*a* (red triangles) under increasing number of clams compared to the standard run (blue diamonds).

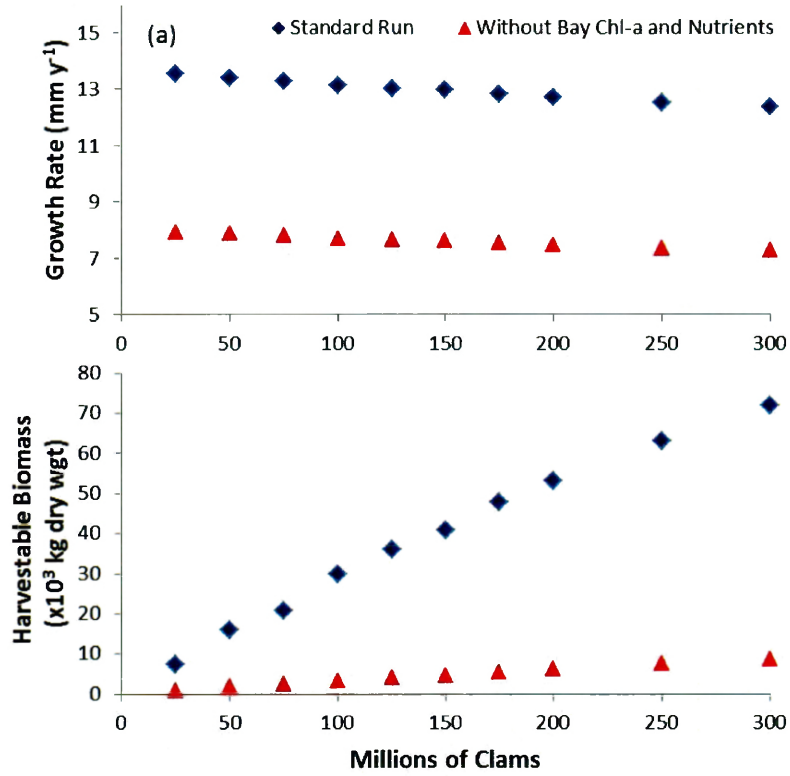


Figure 14. Modeled hard clam growth metrics with the scenario of no Chesapeake Bay chlorophyll or nutrient input to Cherrystone Inlet (red triangles) with increasing numbers of clams compared to the standard run (blue diamonds). Formatting matches that in Fig. 6.

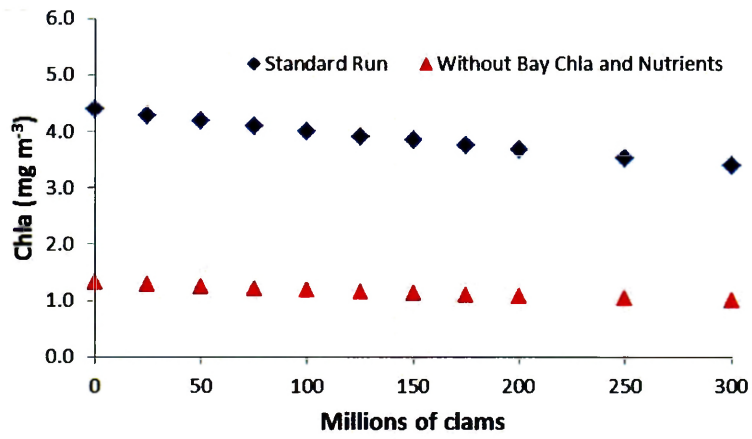


Figure 15. Modeled system-wide, average annual water column chlorophyll-*a* (mg m^{-3}) without Chesapeake Bay chlorophyll-*a* or nutrients (red triangles) under increasing number of dams compared to the standard run (blue diamonds).

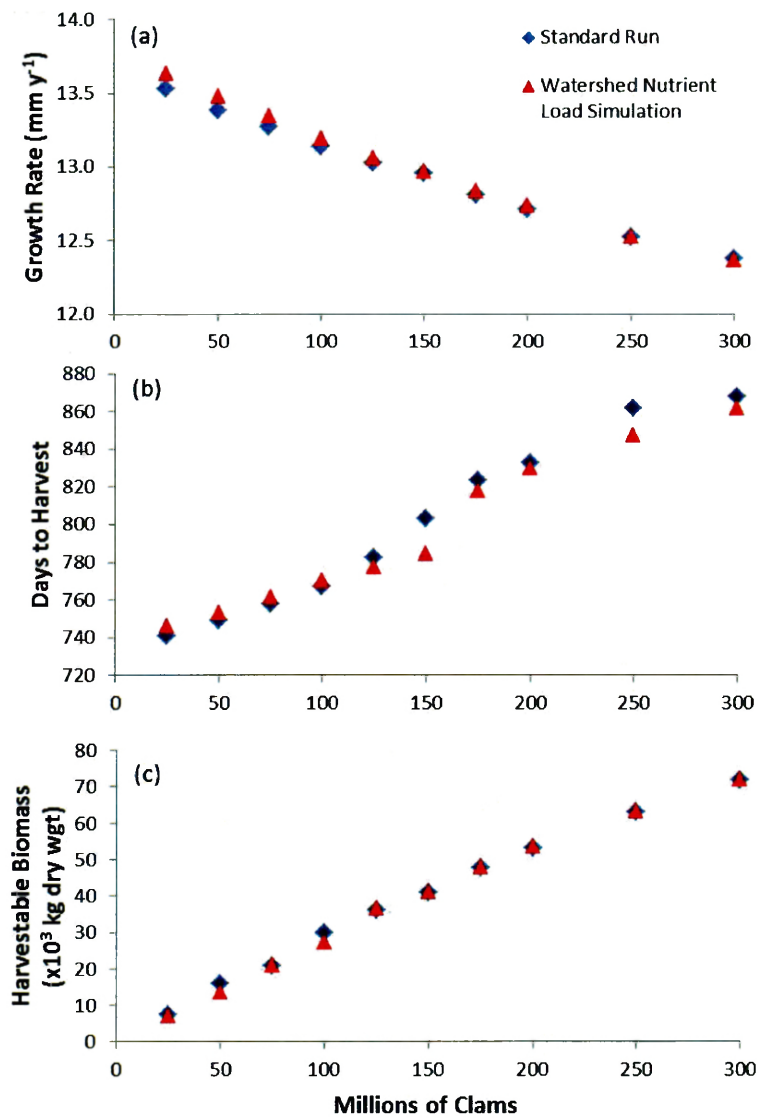


Figure 16. Modeled hard clam growth metrics with the scenario of increased watershed nutrient loading (red triangles; Table 12) with increasing numbers of clams compared to the standard run (blue diamonds). Formatting matches that in Fig. 6.

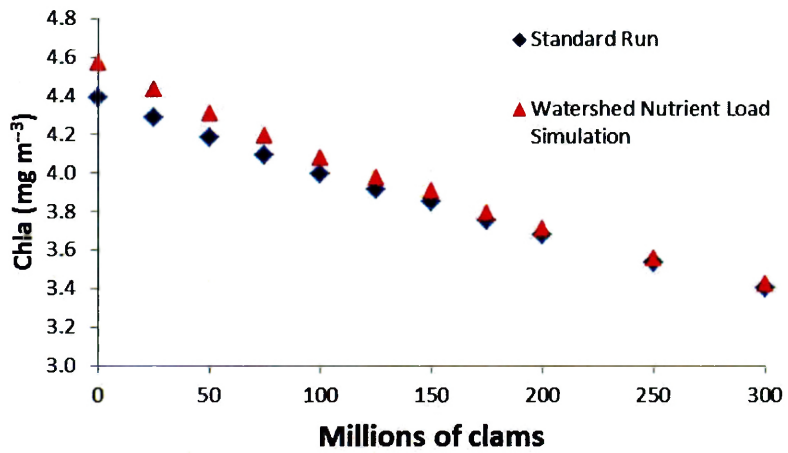


Figure 17. Modeled system-wide, average annual water column chlorophyll-*a* (mg m^{-3}) with an increased watershed nutrient load (red triangles; Table 12) under increasing number of clams compared to the standard run (blue diamonds).

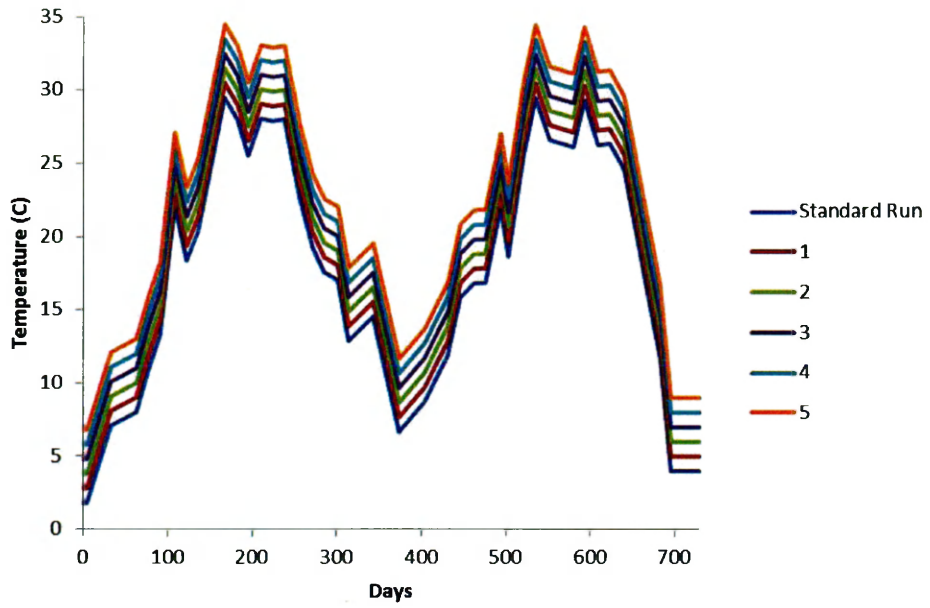


Figure 18. Forced seasonal cycles of temperature (°C) under the standard run (bottom line) and increasing in 1°C increments up to 5°C.

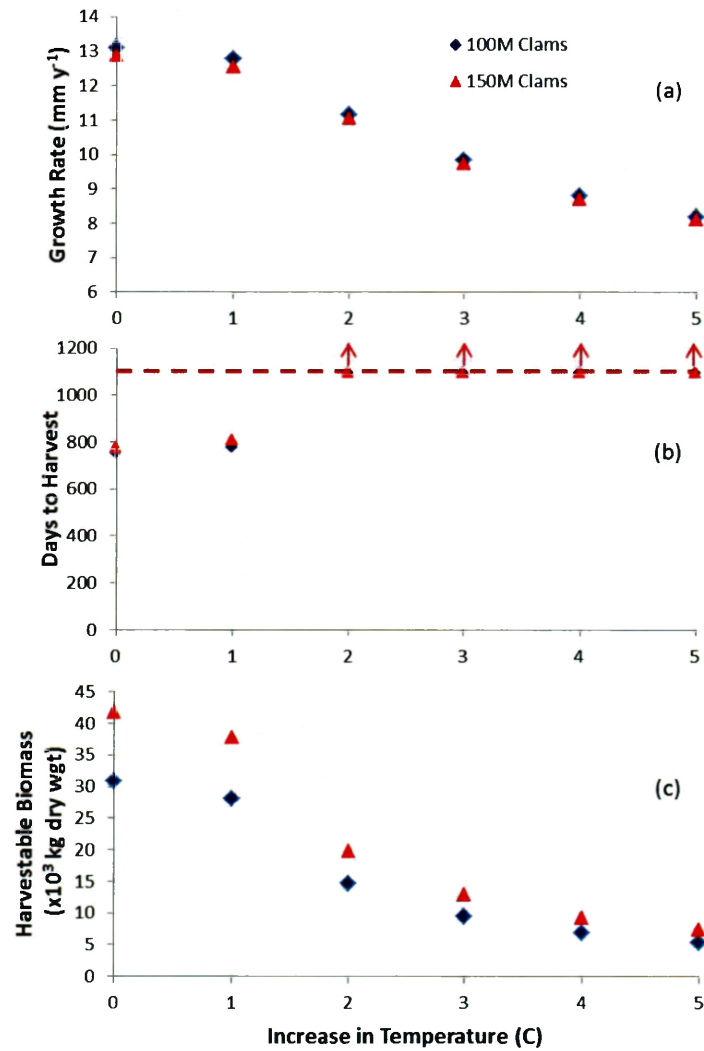


Figure 19. Modeled hard clam growth metrics with the scenario of increased water column temperatures (°C) for 100M (red triangles) and 150M clams (blue diamonds) with measured hard clam growth rates at 100M clams (black square; Condon 2005). Formatting matches that in Fig. 6.

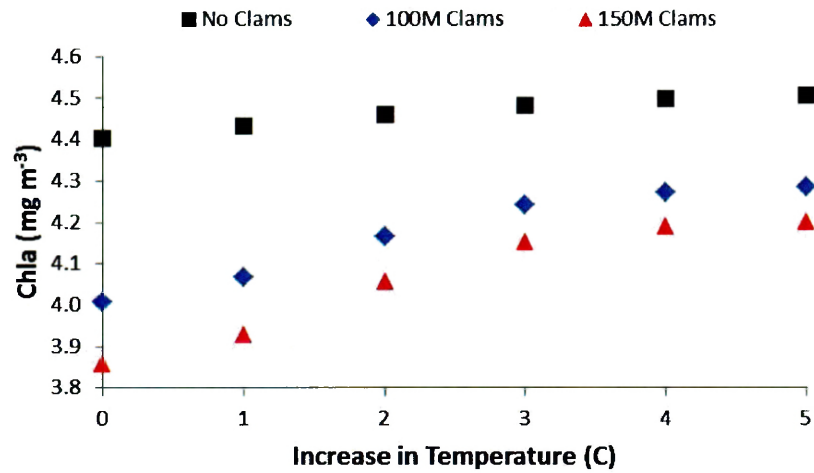


Figure 20. Modeled system-wide, average annual water column chlorophyll-*a* (mg m⁻³) with increasing water column temperatures °C for 100M (blue diamonds) and 150M clams (red triangles), compared to the model run with 0 clams (blue diamonds).

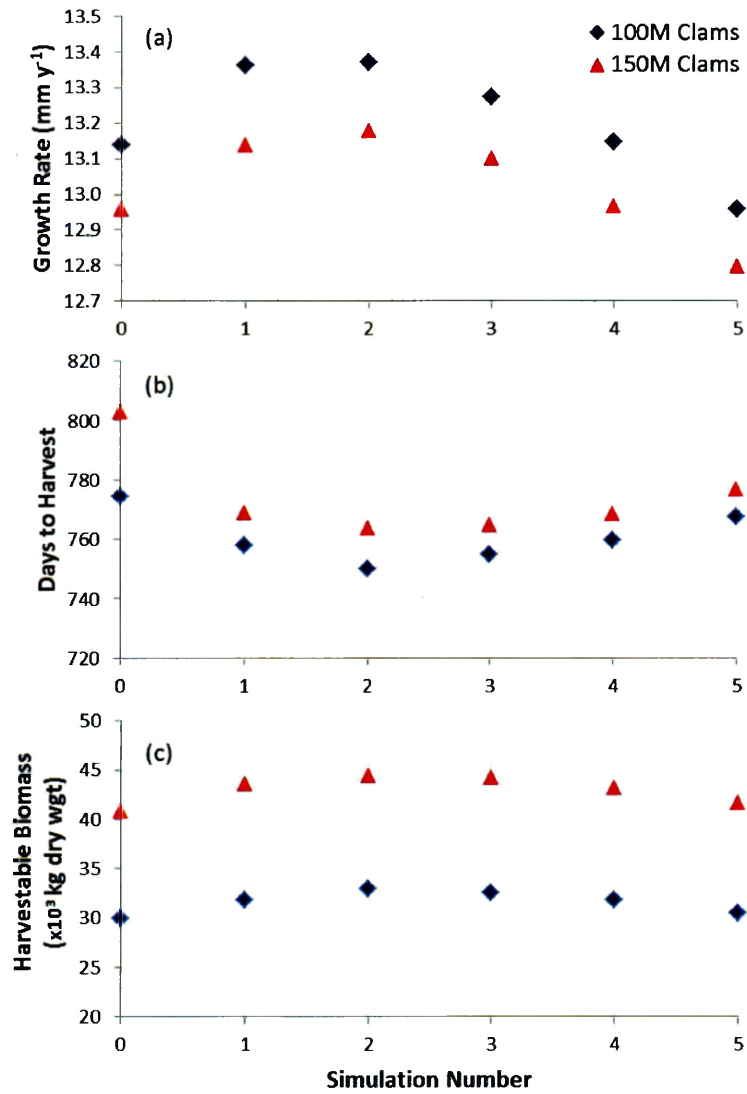


Figure 21. Modeled hard clam growth metrics with the scenario of increased sea level and salinity (Table 14) for 100M (red triangles) and 150M clams (blue diamonds) compared to the standard run simulation number (0). Formatting matches that in Fig. 6.

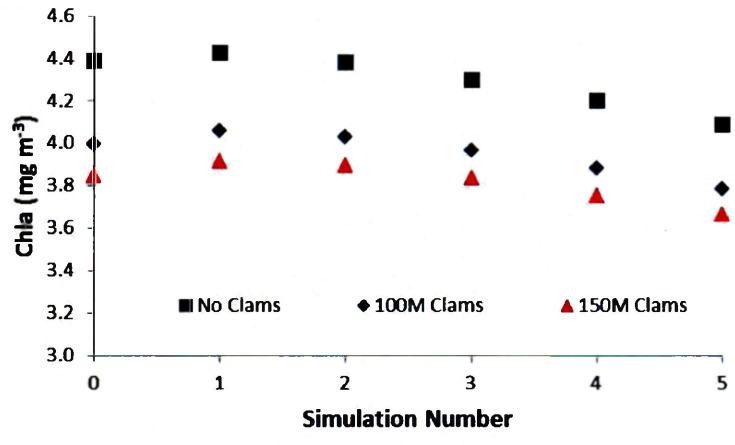


Figure 22. Modeled system-wide, average annual water column chlorophyll-*a* (mg m⁻³) with increasing sea level and salinity (Table 14) for 100M (blue diamonds) and 150M clams (red triangles) compared to the model run with 0 clams (blue diamonds).

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