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Simulated climate change impacts on striped bass, blue crab and Eastern oyster in oyster sanctuary habitats of Chesapeake Bay

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ABSTRACT

Oyster reefs and the species that inhabit them will likely be impacted by shifts in environmental conditions due to climate change. This study examined the potential impact of long-term shifts in water temperature and salinity as a result of climate change on the biomasses of important fisheries species within oyster sanctuary sites in the Choptank and Little Choptank river complex (CLC) in Chesapeake Bay using an Ecopath with Ecosim food web model. The model was used to evaluate changes in the oyster reef food web, with particular emphasis on impacts to striped bass (*Morone saxatilis*), blue crab (*Callinectes sapidus*), and Eastern oysters (*Crassostrea virginica*). Eight different climate change scenarios were used to vary water temperature and salinity within Chesapeake Bay up to the year 2100 based on projections given by previous studies. Simulations used a 4 °C increase in temperature along with an increase (+12 or +10) or decrease (−2) in salinity at annual time steps. The rate of change in species biomasses across scenarios ranged from −0.0052 to 0.0008 t/km^2/month for striped bass, −0.0021 to 0.0026 t/km^2/month for blue crab and −0.0018 to 0.0026 t/km^2/month for oysters. Across the majority of scenarios, the biomasses of striped bass and blue crab decreased, while oyster biomass increased. These results begin to offer insight on the interaction between oyster reef restoration benefits and climate change. The modeling framework utilized by this study may be adapted to other systems to assess the effects of climate change on other coastal restoration habitats.

1. Introduction

Estuarine systems are vulnerable to the effects of a warming climate through changes in both freshwater and saltwater environments. Such disturbances include sea level rise, changes in precipitation patterns, and increasing atmospheric and water temperatures (Najjar et al., 2010; Trenberth, 2011; Hoegh-Guldberg et al., 2014). These environmental shifts can impact the health of estuarine systems and the ecosystem services (i.e., benefits nature provides to people) estuaries provide, such as provision of nursery habitat (Beck et al., 2001; Sheaves et al., 2007; Chevillot et al., 2019; Leal Filho et al., 2022), water filtration (Whitehead et al., 2009; Barbier et al., 2011) and supporting commercial and recreational fishery populations (Kennedy, 1990; Roessig et al., 2004; Barbier et al., 2011; Leal Filho et al., 2022; Gillanders et al., 2022).

Chesapeake Bay, one of the most productive estuaries in North America, provides ecosystem services particularly through a historically high abundance of Eastern oyster (*Crassostrea virginica*) reef habitats (Wood et al., 2002; Peterson et al., 2003; Grabowski et al., 2012; Smaal et al., 2019). Oyster reefs improve water quality (Nelson et al., 2004; Grabowski and Peterson, 2007; Kellogg et al., 2018), aid in the efficient transfer of nutrients across the food web (Dame, 1993; Coen et al., 2007; Kellogg et al., 2013; Kesler, 2015), and provide protection from shoreline erosion (Scyphers et al., 2011; Grabowski et al., 2012; La Peyre et al., 2015; Gilby et al., 2018). Oyster reefs also serve as foraging, refuge, and nursery habitats for many economically and culturally important fisheries species in Chesapeake Bay at different points in their life histories, such as striped bass (*Morone saxatilis;* Harding and Mann, 2003; Hicks et al., 2004; Rodney and Paynter, 2006; Kellogg et al., 2016) and blue crab (*Callinectes sapidus;* Harding and Mann, 2010; Kellogg et al., 2016; Knoche et al., 2020; Longmire et al., 2021).

Chesapeake Bay is already experiencing the effects of climate change through sea level rise and the increasing intensity of storm events (Wood

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et al., 2002; Najjar et al., 2010; Teodoro and Nairn, 2020). Sea level rise and more intense storm events are expected to continue (and worsen) throughout the coming decades and likely affect oyster populations and the fishery species supported by oyster reef habitats (Teodoro and Nairn, 2020). For instance, climate change will result in an increase in water temperature in the mainstem Chesapeake Bay and likely more variable salinity patterns due to increased precipitation and freshwater input, sea level rise and increased drought conditions across the Chesapeake Bay watershed (Hilton et al., 2008; Kang and Sridhar, 2018; Teodoro and Nairn, 2020). Species such as oysters, striped bass and blue crab are limited by salinity or temperature tolerances at one or more stages in their life history. Rising water temperatures typically increase mortality of both small (<35 mm) and large (>35 mm) oysters (Southworth et al., 2017), decrease juvenile blue crab carapace thickness and adult size at maturity (Cunningham and Darnell, 2015; Glandon et al., 2018) and increase adult striped bass emigration due to a preference for cooler waters (Wood et al., 2002). Salinity increases are also associated with higher levels of oyster and blue crab mortality due to greater disease prevalence and predation (Hofmann et al., 2018; Huchin-Mian et al., 2018; Pusack et al., 2019). With these reported trends in the effects of temperature and salinity shifts on oysters, blue crab and striped bass, climate change is likely to negatively impact these species populations in Chesapeake Bay.

In the late 1800s, the Chesapeake Bay oyster fishery was once the largest in the world, but since 1980 overall Chesapeake Bay oyster abundance has declined to 1% of what it once was (Wilberg et al., 2011). From 1980 to 2009, oyster abundance in the upper portion (Maryland and the Potomac River) of Chesapeake Bay has declined by over 90% and habitat area has declined by 70% due to multiple stressors such as overfishing and disease (Wilberg et al., 2011). Previous studies suggest shifts in water temperature and salinity due to climate change could worsen this decline (Kimmel and Newell, 2007; Reeves et al., 2020). The past and predicted future status of Chesapeake Bay oyster populations highlighted the need for increasing oyster reef restoration efforts as well as clear success metrics and monitoring protocols to better assess restoration progress (Oyster Metrics Workgroup, 2011).

Since the 2009 "Chesapeake Bay Protection and Restoration" Executive Order, the Chesapeake Bay Program has been working to restore oyster populations in ten Chesapeake Bay tributaries by 2025 (Bruce et al., 2021). Harris Creek, Tred Avon River and Little Choptank River (all in Maryland) were selected as the first sites for large-scale oyster restoration based on optimal environmental conditions and historical recruitment (Maryland Oyster Restoration Interagency Workgroup of the Chesapeake Bay Program's Sustainable Fisheries Goal Implementation Team, 2013). These three sites lie within the Choptank and Little Choptank river complex (CLC). The oyster sanctuary sites were established in 2010 and restoration work was completed in 2015 for Harris Creek, 2020 for Little Choptank River and 2021 for Tred Avon River Maryland Oyster Restoration Interagency Workgroup of the Chesapeake Bay Program's Sustainable Fisheries Goal Implementation Team, 2021). Continual post-restoration monitoring at one-, three- and six-year assessments have shown that the oyster reefs in the Harris Creek and Little Choptank River sites are meeting the threshold success criteria for oyster density and biomass (Maryland Oyster Restoration Interagency Workgroup of the Chesapeake Bay Program's Sustainable Fisheries Goal Implementation Team, 2021), meaning the oyster populations have a mean density of at least 15 oysters and 15 g m^{-2} biomass covering at least 30% of the target restoration site (Oyster Metrics Workgroup, 2011). Restoration of oyster reefs across Chesapeake Bay has been found to enhance the ecosystem benefits provided by these areas, such as water filtration, greater habitat availability for many fish and invertebrate species and improvement of fishery landings (Hicks et al., 2004; Cerco and Noel, 2005; Rodney and Paynter, 2006; Coen et al., 2007; Knoche et al., 2020; Bruce et al., 2021).

Though oyster reef restoration in Chesapeake Bay has largely been successful (Maryland Oyster Restoration Interagency Workgroup of the Chesapeake Bay Program's Sustainable Fisheries Goal Implementation Team, 2021), it is unclear how the progress and benefits of oyster restoration may be affected by climate change. With the first Chesapeake Bay restoration site being completed in 2015, long term (10+ years) monitoring data is yet to be available to assess how climate change may impact the recently restored oyster sanctuaries. The authors of this current study previously developed a coupled food web and economic model to investigate changes in commercial fisheries harvest and regional economic impacts in response to different oyster reef restoration simulations (Knoche et al., 2020). Five different 15-year future scenarios were simulated, representing 1) young oyster reef habitat (2015 oyster biomass levels) in current sanctuaries, 2) mature oyster reef habitat (15.4% increase in oyster biomass per year) in sanctuaries, 3) mature oyster reef habitat and increase in other filter feeder biomasses, 4) oyster reefs open to harvest with a 10% decrease in oyster biomass over 15 years, and 5) scenario 4 conditions with an added decreases in other filter feeder bivalve biomasses (Knoche et al., 2020). That study found the presence of mature, restored oyster reefs increased harvested finfish and shellfish biomass (particularly in regard to blue crab harvest) by 80–110% and increased total dockside sales by more than $4.5 million relative to 2015 conditions (Knoche et al., 2020). While these results suggest overall positive outcomes for the fishing industry and food web dynamics, the forecasted impacts of climate change on Chesapeake Bay were beyond the scope of the original study. Therefore, to further leverage this modeling effort, and to provide more insight to managers about the direct and indirect impacts to the restored oyster reefs and their associated food web, this new study presents results evaluating how climate change may affect the ecosystem services provided by restored oyster reefs.

Given the physiological influence of temperature and salinity on oyster reef habitats and associated species, as well as the uncertain outcome of restoration efforts in the face of climate change, this study evaluated potential ecological impacts of shifts in these environmental conditions on the broader food web, with particular focus on oysters and two demersal Chesapeake Bay fisheries species (striped bass and blue crab). While many studies offer predictions on how the populations of Eastern oysters, striped bass and blue crab in Chesapeake Bay may respond to climate induced changes in water temperature and salinity individually (Najjar et al., 2010; Peer and Miller, 2014; Southworth et al., 2017; Huchin-Mian et al., 2018), there is a lack of research examining the concurrent effects of climate change on the three populations in association with an interconnected oyster sanctuary food web, while taking into consideration how changes to the trophic interactions mitigate or enhance these responses. In order to predict how the oyster reef food web and heavily sought-after fishery species populations could be affected by climate change, this study used a previously developed food web model of the CLC oyster sanctuary areas (Knoche et al., 2020) to simulate eight temperature and salinity change scenarios to examine the response of adult species biomasses up until the year 2100. The changes in temperature and salinity were simulated annually based on climate change projections for Chesapeake Bay (Najjar et al., 2000, 2010; Hilton et al., 2008). Examining changes in adult striped bass, blue crab and oyster populations is informative for assessing potential climate change effects on fisheries and different trophic guilds of an estuarine food web. The overarching objective of this study is to suggest a flexible framework for application in other systems, providing managers a range of potential outcomes when considering the development of future oyster restoration sites in the context of a changing climate.

2. Methods

To evaluate how climate induced changes to environmental drivers impact the food web in an oyster reef sanctuary, this study used an Ecopath with Ecosim food web model previously developed by the authors of this study (Knoche et al., 2020). For this study, an additional year of data was added to represent the trophic structure and food web dynamics of the CLC from the years 2006–2016 (as opposed to 2006–2015 in Knoche et al., 2020). Functional groups of species in the food web model were linked to annual time series of fishing effort and environmental data (see *2.3 Model Development: Ecosim*) to drive changes in species biomass over time. Species biomasses and their trophic interactions respond to simulated changes in water temperature and salinity in the Chesapeake Bay up until the year 2100 (see *2.4 Climate Change Scenarios*). The model generated predicted biomass time series data (2017–2100) for all functional groups in the model in response to the different climate change scenarios.

2.1. Study site

Regional analysis for this study focuses on the Harris Creek, Tred Avon River and Little Choptank River oyster sanctuary sites within the CLC (Fig. 1), an estuarine tidal embayment habitat (McCarty et al., 2008). Depth of the oyster sanctuary areas typically ranged between one and 6 m (Maryland Oyster Restoration Interagency Workgroup of the Chesapeake Bay Program's Sustainable Fisheries Goal Implementation Team, 2013; Maryland Oyster Restoration Interagency Workgroup of the Chesapeake Bay Program's Sustainable Fisheries Goal Implementation Team, 2015a; Maryland Oyster Restoration Interagency Workgroup of the Chesapeake Bay Program's Sustainable Fisheries Goal Implementation Team, 2015b). The total modeled area encompasses approximately 445 km^2 of Chesapeake Bay along the eastern shore of Maryland and includes all major features of the CLC region such as hard and soft bottom areas, oyster sanctuary sites and fished areas (Knoche et al., 2020).

2.2. Model Development: ecopath

The authors of this current study previously developed a food web model representative of the CLC using the Ecopath with Ecosim (EwE; www.ecopath.org, version 6.6.14980.0) modeling software (Knoche et al., 2020). The same model domain and parameterized Ecopath base model developed in Knoche et al. (2020) were also used in this study (i.e., no changes were made to the baseline food web model). The EwE modeling suite was developed approximately 35 years ago as a tool to describe the trophic interactions of aquatic ecosystems and has since become the most widely used modeling software in the world (Polovina, 1984; Colléter et al., 2015; Heymans et al., 2016; www.ecopath.org). Nodes in the food web model are represented as individual species or functional groups that are then mass-balanced. The process of mass-balancing the model describes the process whereby the user makes adjustments to input parameters to ensure no species is being overconsumed in the system. Ecopath uses two master equations to determine the production and energy balance of functional groups in the model. These equations, along with others that contribute to the core algorithms of EwE, are discussed in more detail in several published papers pertaining to the development and use of EwE (Christensen and Walters, 2004; Christensen, 2013; Heymans et al., 2016). In short, to develop a mass-balanced Ecopath model, three out of four parameters for the master equations must be provided for each functional group in the model. These parameters are initial biomass (B; t/km^2), production to biomass ratio (P/B; the rate of potential change in biomass of each species or group, approximated by the total mortality rate), consumption to biomass ratio (Q/B, the number of times a species or group consumes itself in a year), and ecotrophic efficiency (EE; the proportion of production utilized in the system; Christensen and Walters, 2004; Christensen, 2013). In this model application, biomass, the P/B ratio, and the Q/B ratio were provided as initial conditions, and set Ecopath to calculate the fourth required parameter, EE, using the first master equation (Christensen and Walters, 2004).

The food web model was designed to incorporate species considered to be commercially important and those important for ecosystem

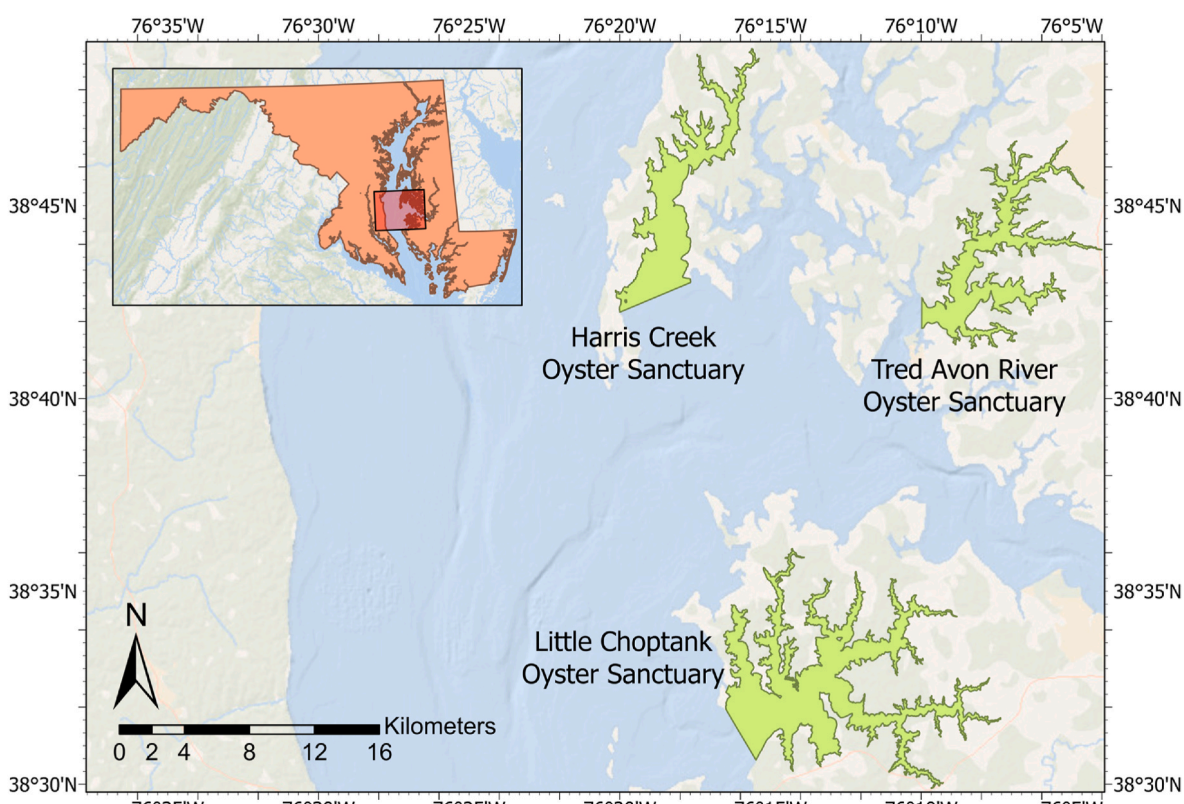

Fig. 1. The Harris Creek, Tred Avon River and Little Choptank River Oyster Sanctuary sites within the Choptank and Little Choptank river complex (CLC) of Chesapeake Bay, Maryland.

function (Knoche et al., 2020). A total of 38 functional groups were represented in the model (Appendix A). To better represent ontogenetic shifts some groups, including oysters, blue crab and striped bass, were split into adult and juvenile components, which were parameterized using Von Bertalanffy Growth Function *K* and age at maturity values (Christensen et al., 2009; Madeo, 2012; Ihde et al., 2016; Kellogg et al., 2016; D. Bruce, *unpublished data*; L. Kellogg, *unpublished data*; www.fishbase.org). As represented in Ecopath, these groups are not size-structured and represent a generalized average individual of the representative life stage. This study focuses on the predicted changes to the overall food web and to the adult groups of oysters (≥14 months), blue crab (≥11 months), and striped bass (≥37 months). Initial biomass measurements were estimated from a variety of sources, including field data for the region, existing models of Chesapeake Bay and a literature review (described in Knoche et al., 2020). Species biomasses are calculated as whole animal mass (t) per area surveyed (km^2). The biomass values included as initial conditions for the model were averaged across the year 2006, accounting for spatial heterogeneity in the system (Knoche et al., 2020). To represent the trophic dynamics between species in the model, a diet matrix was constructed using field data specific to the region and information from published literature (Appendix B; Knoche et al., 2020). Fishing fleets included in the model were represented by gear type, which included trotline, hook and line, eel pots, fish pots, pound net, haul seine, gill net, fyke net, oyster harvest, clamming. Recreational fishing and duck hunting were also included as artificial placeholders to constrain certain prey groups (Knoche et al., 2020). Landing amounts specific to the CLC were sourced from the Maryland Department of Natural Resources (MD DNR; Appendix C) and the initial landing amounts used were representative of the year 2006 (Knoche et al., 2020).

Completion of a mass-balanced model ensures the energy input is equal to energy output for the system (Christensen and Walters, 2004; Heymans et al., 2016). To determine if a model is mass-balanced, a user evaluates if the EE values are between 0 and 1, indicating balanced trophic exchanges. Adjustments using a 0.1 coefficient of variation (based on the Ecosim Monte Carlo routine described in *2.5 Sensitivity Analysis*) were made to species biomasses, P/B values and diet proportions to achieve EE values within the 0 to 1 range that were reflective of a species' trophic position. The fully mass-balanced model parameters can be found in Appendix A and a more detailed description of the model this study was based on can be found in Knoche et al. (2020).

2.3. Model Development: ecosim

Ecosim, the time-dynamic module of EwE, was used to calibrate the model and create the future scenario evaluations. Ecosim is able to define changes in species biomass over time using a series of differential equations that incorporate species growth, consumption, predation, and mortality (Christensen and Walters, 2004). This allows for the inclusion of different species life histories and generation times when simulating changes in population biomasses over time. Calibration of the food web model over time relies on time series of species biomass, fishery landings and environmental conditions. An additional year of data was added to the time series of species biomass, fishing effort and environmental conditions used in Knoche et al. (2020) to reflect observed conditions from 2006 to 2016. These data were used in the fit-to-time series application in Ecosim (Christensen and Walters, 2004). The fit-to-time series routine uses historical data to hindcast the model and determine how well it captures natural variability. The routine adjusts the vulnerability of groups to predation and fishing and determines the lowest sum of squares (SS) for each iteration (Christensen and Walters, 2004). The calibrated model with the lowest total SS represents the model version that best captures natural availability and is used for further simulations.

For the species in the model to respond to environmental changes over time, individual functional groups must be linked to the time series of environmental data input into the model. This step is completed using the habitat capacity model function within EwE (Christensen et al., 2014). The capacity model works by connecting the time series data of temperature, salinity, and dissolved oxygen to a habitat capacity value between 0 and 1 for each species. The capacity model can be applied to one or all species in the model using as many abiotic variables as needed. Species and age stanza-specific functional response curves for each environmental variable are used to apply the habitat capacity model. The functional response curves represent the optimal range of environmental conditions for species in the model. The response curves used in this study for the three focal species (adult striped bass, adult blue crab and adult oysters) represent each species' tolerance to temperature, salinity, and dissolved oxygen and were derived from those used in Knoche et al. (2020) and supplemented with additional information from previous studies (Hill et al., 1989a; Hill et al., 1989b; Secor et al., 1995; Fisher, 1999; Secor et al., 2000; Jensen et al., 2005; Rome et al., 2005; Eastern Oyster Biological Review Team, 2007, Fig. 2). Each response curve depicts the capacity values associated with a range of environmental values. The capacity value acts as a modifier to a species' consumption rate, which alters the output of the Ecopath master equations determining the production and energy balance of each functional group (Christensen et al., 2014). A lower habitat capacity value for a species results in decreased consumption by that species, further driving proportional changes in biomass (Christensen et al., 2014). This approach allows for the incorporation of optimal (or sub-optimal) species growth, as well as factors that would exclude species from the model domain (i.e., death or emigration).

2.4. Climate change scenarios

Annual time series data for temperature, salinity and dissolved oxygen were derived from the Chesapeake Bay Program environmental monitoring program stations within the CLC from 2006 to 2016 (station latitude and longitudes: 38° 31′ 33.6″, −76° 18′ 14.4"; 38° 34′ 51.6″, −76° 3′ 32.3994"; 38° 39′ 18″, −76° 15′ 50.3994"; CBP Water Quality Database). These time series were adapted from the 2006 to 2015 time series data used in Knoche et al. (2020) with the addition of newly available data for 2016. Salinity and temperature forcing functions were used to drive environmental variability at yearly time steps in the food web model. Future scenarios were characterized by either no change in current environmental conditions or a future that is influenced by climate change based on a range of projections for the Mid-Atlantic and Chesapeake Bay regions given by previous studies (Table 1). All future scenarios were simulated up until the year 2100, with forcing functions depicting annual changes in water temperature and/or salinity (Figs. 3 and 4).

The No Change scenario was characterized by a continuation of annual measures of salinity and water temperature (based on environmental data collected from 2006 to 2016) extended until the year 2100 (Figs. 3 and 4). This scenario is indicative of climate change mitigation efforts that would result in no net change in salinity or water temperature across the 94-year run, in contrast to the other seven scenarios where salinity and/or water temperature change over time.

Seven other scenarios were used to represent varying effects of climate change. These scenarios incorporated net changes in either water temperature, salinity, or both across the 94-year simulation. Projected changes in water temperature and salinity were appended to the observed data to create forcing functions representative of different climate change conditions. The climate change forcing functions pertained to published projected shifts in water temperature and salinity to the mainstem Chesapeake Bay region as a result of climate change by the year 2100, as discussed in Najjar et al. (2000), Hilton et al. (2008), and Najjar et al. (2010; Table 1). A single temperature change time series (High Temp; increase of 4 °C by 2100) was created to represent the predicted increase in Chesapeake Bay water temperature (Najjar et al., 2000, Fig. 3A). The temperature change forcing function applied a

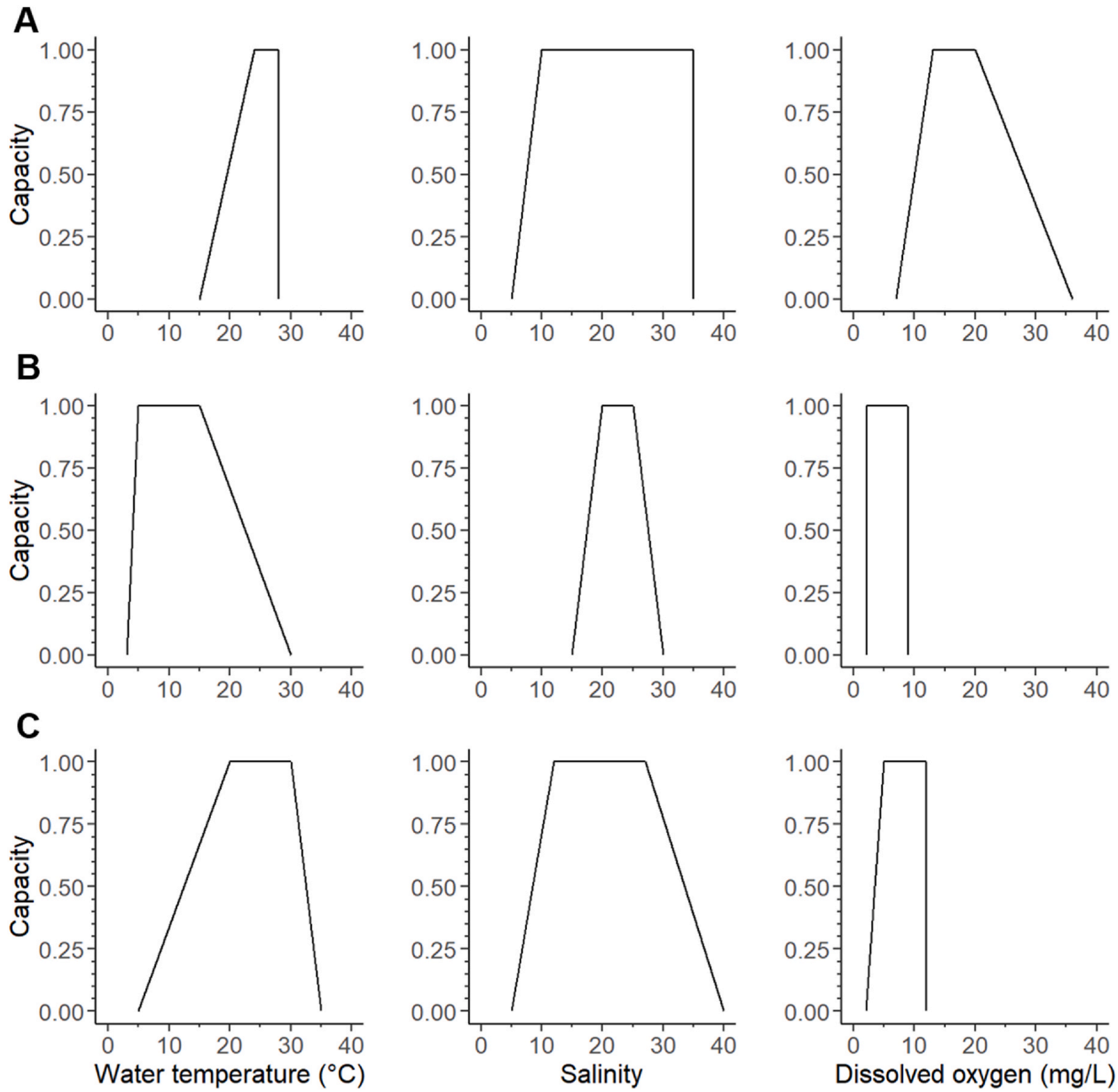

Fig. 2. Functional response curves indicative of the temperature (°C), salinity and dissolved oxygen (mg/L) tolerance capacities for adult striped bass (A), blue crab (B), and oysters (C; Knoche et al., 2020; Hill et al., 1989a; Hill et al., 1989b; Secor et al., 1995; Fisher, 1999; Secor et al., 2000; Jensen et al., 2005; Rome et al., 2005; Eastern Oyster Biological Review Team, 2007). The environmental parameter values encompassed by each curve represent the overall environmental tolerance range for each species, and the values under the flat line at the top of each curve are the optimum conditions.

gradual increase of 0.048 °C each year in order to achieve a total temperature increase of 4 °C (final temperature value of 19.57 °C) by 2100. Due to the high variability in predicted salinity changes to Chesapeake Bay, two salinity forcing functions were created; one reflecting the most drastic predicted increase (High Sal; increase of 12 by 2100; Fig. 3B; Hilton et al., 2008), and another reflecting the largest predicted decrease (Low Sal; decrease of 2 by 2100; Fig. 3B; Najjar et al., 2010). The salinity forcing functions also applied gradual yearly changes (+0.145 each year for the High Sal scenario and −0.024 each year for the Low Sal scenario) so that the final salinity values of 20.78 and 6.75 were reached by 2100.

Each climate change forcing function was applied individually, and later in combination with other forcing functions (Table 1). The two salinity forcing functions were sometimes applied together (Mod Sal; resulting in a net salinity increase of 10) to account for the potential effects of both increased sea level rise and increased freshwater input to the Chesapeake Bay to occur simultaneously (Table 1). For scenarios where an individual climate change forcing function was applied (i.e., salinity alone or temperature alone), a “No Change” forcing function (time series) was used to represent no significant change in the other environmental variable (Table 1). In each scenario run (Table 1), Ecosim uses the functional response curves (Fig. 2) to consider the optimum environmental conditions for each species and reflect shifts in relative biomass over time as a result of environmental changes.

While the main focus of this study was the influence of changes in water temperature and salinity on the three focal species, there are two other factors that impacted the model outcomes. Dissolved oxygen is also an important factor that can drive changes in species biomass (Breitburg et al., 1997). A “No Change” forcing function was created to reflect a continuation in the recorded pattern of dissolved oxygen observed in the CLC region up until the year 2100 (Fig. 3C), with changes in species biomass dictated through the functional response curves (Fig. 2). The dissolved oxygen forcing function was applied across all scenarios to ensure its influence on species biomass remained constant between the different simulations. Fishing effort was another factor affecting species biomasses. Similar to dissolved oxygen, fishing effort was represented as a constant variable, with time series of yearly average fishing effort for each fleet in the model based on 2006 to 2016 effort data (derived from MD DNR) applied in continuous 11-year

Table 1
Water temperature and salinity change scenarios run based on climate change projections for the year 2100. Environmental drivers were selected from the sources given. The salinity change in the Mod Sal and High Temp & Mod Sal scenarios is representative of the simultaneous application of the Low Sal and High Sal scenarios to account for the effects of both increased freshwater input and sea level rise in the Chesapeake Bay region.

Scenario	Water temperature change (°C)	Salinity change
No Change	None[a]	None[a]
High Temp	+4[b]	None[a]
Low Sal	None[a]	−2[c]
High Sal	None[a]	+12[d]
High Temp & Low Sal	+4[b]	−2[c]
High Temp & High Sal	+4[b]	+12[d]
Mod Sal	None[a]	+10[c,d]
High Temp & Mod Sal	+4[b]	+10[c,d]

[a] CBP Water Quality Database.
[b] Najjar et al. (2000).
[c] Najjar et al. (2010).
[d] Hilton et al. (2008).

periods up until the year 2100.

2.5. Sensitivity Analysis

The Monte Carlo routine in Ecosim tests the sensitivity of the model output to model input by randomly sampling input parameters from a uniform distribution centered on the initial input values with a coefficient of variation equal to 0.1 (Christensen and Walters, 2004). The Monte Carlo routine was initiated for 20 iterations for each scenario to determine input parameters that result in the lowest sum of squared deviations (SS) for the model.

2.6. Statistical analysis

Seasonal Kendall tests (SK tests) were performed to determine whether the changes in biomass over time for each species exhibited a significant trend during each scenario. The SK test is a variant of the standard Mann-Kendall Trend Test, which tests for a monotonic trend of a variable, but the SK test can account for seasonal fluctuations in the measured variable (Hirsch and Slack, 1984). The SK test was chosen for analysis in this study because species biomasses exhibit seasonal fluctuations during each year. Seasonal Kendall tests were run on the biomass trends output by Ecosim across the entire model run period (2006–2100) for each of the three focal species within each climate change scenario. The Kendall Tau value was used to determine the direction (positive or negative) and strength of each biomass trend. The slope value estimates the overall slope over time (t/km^2/month) by calculating the median of all slopes between each data point. The Z test statistic indicated whether each trend was significant. All analysis were performed using R statistical software (www.r-project.org; version 3.6.1).

3. Results

Changes in biomass over time for adult striped bass, blue crab and oysters were compared between eight environmental change scenarios using Ecosim. Values from 2006 through 2016 represent the calibrated portion of the model run, while those in 2017 and onward are the future predictions provided by the model. Seasonal Kendall tests measured the general trend in species biomasses across the entire model run period (2006–2100). Two scenarios resulted in a decreasing biomass trend for striped bass, blue crab and oysters (Low Sal and Mod Sal), while one scenario showed an increasing trend for the three species (High Sal). Across all scenarios, final relative biomass for 2100 varied by 80.92% for striped bass and 68.39% for blue crab and oysters.

The Monte Carlo routine created a balanced model for all iterations by varying the input parameters within a 10% confidence interval. The range of SS values for each scenario varied by 24–65% (Table 2).

Striped bass relative biomass averaged across 2006 to 2016 was 0.67 t km^{-2} (range of 0.29–1.09 t km^{-2}) and final annual average relative biomass values for 2100 varied between 0.39 and 0.92 t km^{-2} across scenarios (Fig. 4A). Seasonal Kendall test results indicated that striped bass biomass trends were significant ($z < 0.05$) across all scenarios and the majority exhibited a decreasing trend (Fig. 4A, Table 3). Biomass decreased over time in six out of the eight scenarios. An increase in biomass occurred in the No Change and High Sal scenarios. The strongest negative trend in striped bass biomass was seen in the High Temp & Low Sal scenario (tau = −0.5756, slope = −0.0052) and the strongest positive trend occurred in the High Sal scenario (tau = 0.2223, slope = 0.0005).

Blue crab initial average (2006–2016) relative biomass was 0.88 t km^{-2} (range of 0.26–1.99 t km^{-2}) and final average relative biomass values were between 0.51 and 1.04 t km^{-2} (Fig. 4B). For blue crab, the trends in biomass were significant for all scenarios except the No Change scenario (Fig. 4B, Table 3). Of the scenarios with significant trends in biomass, four out of seven exhibited negative trends. Positive trends in biomass occurred in the High Sal, High Temp & Low Sal and High Temp & High Sal scenarios. The strongest positive trend was observed in the High Temp & High Sal scenario (tau = 0.8861, slope = 0.0026) and the strongest negative trend was observed in the High Temp (tau = −0.5003, slope = −0.0020) and High Temp & Mod Sal (tau = −0.5003) scenarios.

Annual average oyster relative biomass was 0.68 t km^{-2} (range of 0.38–1.31 t km^{-2}) for the initial time period and between 0.51 and 1.04 t km^{-2} for the final scenario values (Fig. 4C). Trends in oyster biomass were significant for all scenarios (Fig. 4C, Table 3). Six out of the eight scenarios displayed an increase in oyster biomass over time. The negative trends occurred in the Low Sal and Mod Sal scenarios. The strongest negative trend occurred in the Low Sal scenario (tau = −0.6404, slope = −0.0018) while the strongest positive trend occurred in the High Temp & High Sal scenario (tau = 0.8861, slope = 0.0026).

4. Discussion

Chesapeake Bay is expected to experience shifts in water temperature and salinity over the coming decades as a result of climate change (Najjar et al., 2000, 2010; Wood et al., 2002; Teodoro and Nairn, 2020). This study investigated changes in the biomasses of three commercially important Chesapeake Bay species (adult striped bass, adult blue crab and adult oysters) in response to simulated environmental shifts within the CLC. The responses of each species varied across temperature and salinity climate change scenarios. The varied responses of striped bass, blue crab and oysters to the scenarios can be better understood in the context of each species' sensitivity to different environmental parameters. The CLC is both an important oyster restoration and commercial fishing area (Knoche et al., 2020), so the effects of climate change-induced shifts in water temperature and salinity on the three species of focus in this study have implications for future fisheries management and species restoration efforts.

4.1. Striped bass

Striped bass in Chesapeake Bay are likely to be negatively affected by climate change. Previous studies identify temperature as a major factor in driving striped bass abundance in upper and mainstem Chesapeake Bay, with adult striped bass exhibiting a preference for cooler temperatures (Wood et al., 2002; Peer and Miller, 2014). Chesapeake Bay striped bass are generally assumed to have a broad salinity tolerance range because of their anadromous nature (Hill et al., 1989a), though growth rate may be reduced when salinity increases or decreases from around 7 (Secor et al., 2000). Climate change impacts on striped bass vary in other estuarine habitats across the United States. Warming

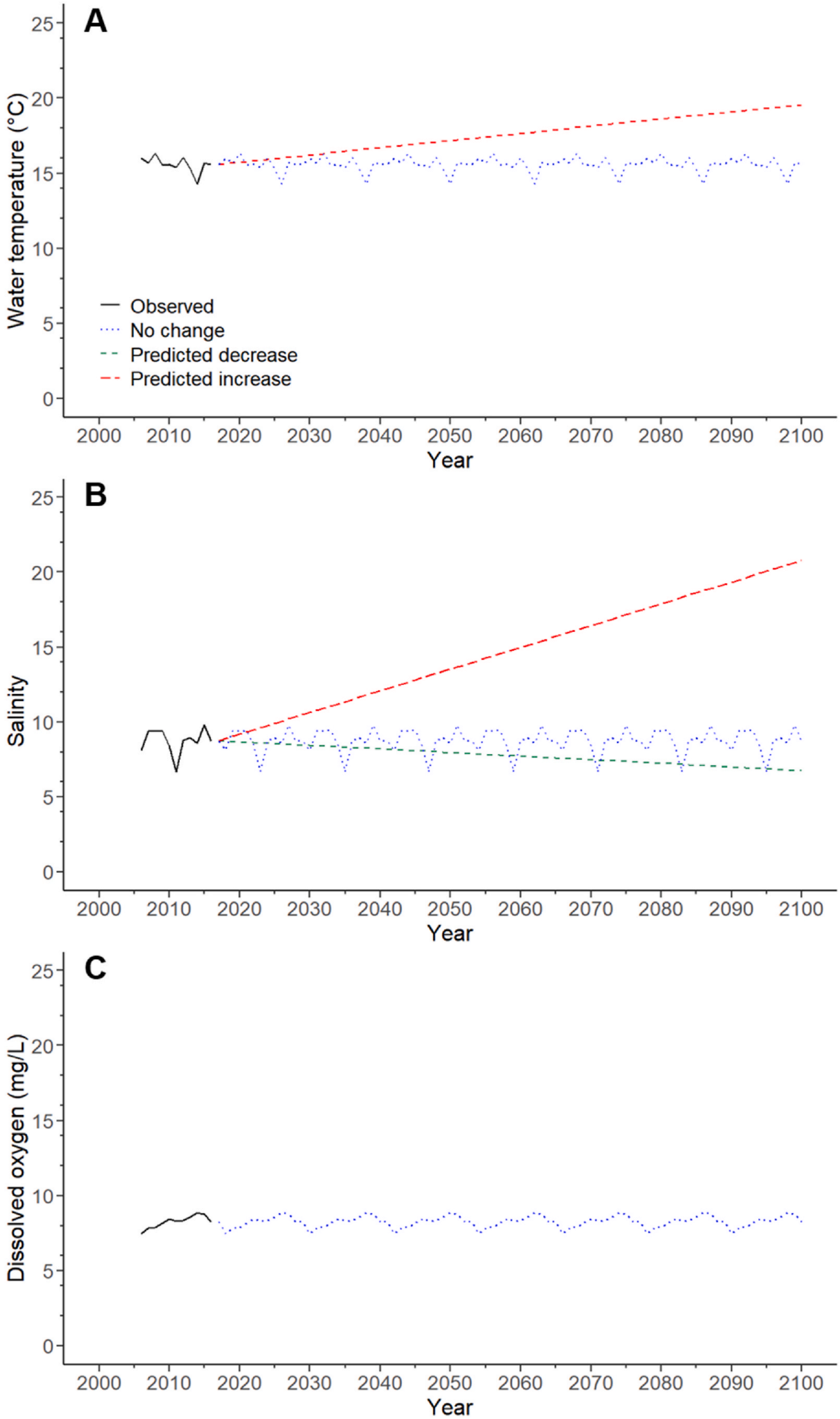

Fig. 3. Water temperature (°C; A), salinity (B) and dissolved oxygen (mg/L; C) forcing functions extending to the year 2100. Observed values span 2006 to 2016 and status quo values represent a continuation of the observed pattern up to 2100. The predicted increase in water temperature represents an overall increase of 4 °C between 2017 and 2100, based on climate change projections by Najjar et al. (2000), with an increase of 0.048 °C applied each year. The predicted increase in salinity represents an overall increase of 12 between 2017 and 2100, based on climate change projections by Hilton et al. (2008), with an increase of 0.145 applied each year. The predicted decrease in salinity represents an overall decrease of 2 between 2017 and 2100, based on climate change projections by Najjar et al. (2010), with a decrease of 0.024 applied each year.

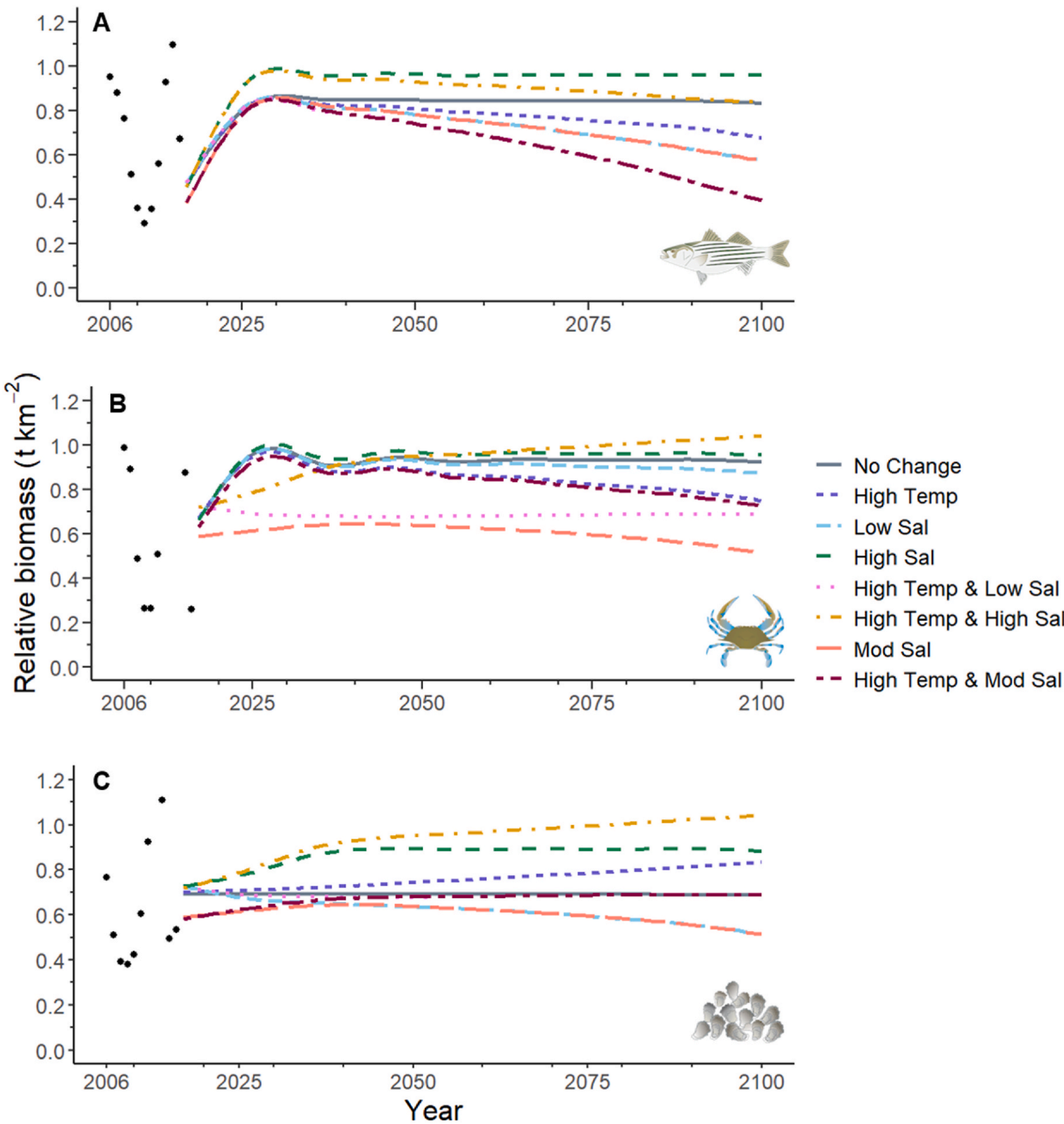

Fig. 4. Relative biomass of striped bass (A), blue crab (B) and oysters (C) as output by Ecosim. Points represent observed biomass from 2006 to 2016 and lines indicate simulated biomass over time in response to different climate change scenarios from 2017 to 2100. Species images sourced from University of Maryland Center for Environmental Science Media Library. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Results of the Ecosim Monte Carlo routine to determine the lowest SS for each scenario.

Scenario	Low SS	High SS	% Difference
No Change	154.7	202.6	24
High Temp	142.3	222.7	37
Low Sal	141.7	194.2	28
High Sal	145.6	203.0	29
High Temp & Low Sal	140.6	204.9	32
High Temp & High Sal	146.5	197.4	26
Mod Sal	135.5	201.4	33
High Temp & Mod Sal	151.8	429.9	65

temperatures have been found to result in earlier migration of striped bass to freshwater habitats to spawn in the San Francisco Bay-Delta (California; Goertler et al., 2021) and Hudson River Estuary (New York; Nack et al., 2019). Increasing salinities are associated with lower survival rates of juvenile striped bass in the Savannah River Estuary (Georgia-South Carolina; Reinert and Peterson, 2008). This study indicated decreases in striped bass biomass within the CLC primarily due to temperature. Striped bass biomass declined over time for most of the simulated climate change scenarios (Fig. 4A, Table 3). Biomass exhibited an increase (+0.0008 t/km^2/month) under the No Change scenario (Table 3), indicating that a continuation of environmental conditions from the 2006–2016 period within the CLC may be beneficial to the species. Biomass also increased (+0.0005 t/km^2/month) during the High Sal scenario (Table 3), so the model population of striped bass appears to tolerate a large increase in salinity. An increase in water temperature appears to be a major factor driving declines in striped bass

Table 3
Seasonal Kendall test results for striped bass, blue crab and oyster biomass trends over time. Tau values represent the direction and strength of each trend and the Z test statistic indicates whether the trend was significant (Z < 0.05, indicated by an asterisk). Slope values are an estimate of the overall slope (t/km^2/month) of the time series.

	No Change	High Temp	Low Sal	High Sal	High Temp & Low Sal	High Temp & High Sal	Mod Sal	High Temp & Mod Sal
Striped bass								
Tau	0.1685	−0.1587	−0.4636	0.2223	−0.5756	−0.2120	−0.3867	−0.5034
Z	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*
Slope	0.0008	−0.0011	−0.0032	0.0005	−0.0052	−0.0010	−0.0031	−0.0051
Blue crab								
Tau	0.0337	−0.5003	−0.2351	0.1176	0.2749	0.8861	−0.3462	−0.5003
Z	0.0942	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*
Slope	0.0001	−0.002	−0.0006	0.0002	0.0001	0.0026	−0.0011	−0.0021
Oysters								
Tau	0.051	0.4058	−0.6404	0.4206	0.2749	0.8861	−0.3462	0.7348
Z	0.0112*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*	<0.0001*
Slope	0.0001	0.0019	−0.0018	0.0012	0.0001	0.0026	−0.0011	0.0006

biomass in the model, as all scenarios that incorporated a temperature change resulted in decreasing biomass trends, while the responses to salinity changes were more variable. These results can be attributed to the environmental tolerances represented by the functional response curves for striped bass. The salinity response curve indicates a broad tolerance range, while the range of the temperature response curve is much narrower (Fig. 2).

The mostly negative effects of climate change on modeled striped bass biomass would affect the striped bass fishery and stock status. The population of striped bass in Chesapeake Bay has historically suffered because of overexploitation and poor water quality (Richards and Rago, 1999). While the population made a full recovery by 1995, abundance began declining again in 2005 (Fabrizio et al., 2017). The general Chesapeake Bay striped bass fishery remains successful as of 2020, ranking number six in terms of total dollar value harvested in Maryland and Virginia (Commercial Fisheries Landings database). The CLC is an important commercial fishing area for finfish such as striped bass and contributed $807,000 in finfish dockside value in 2015 (Knoche et al., 2020). If the CLC striped bass population follows the pattern indicated by these study results, the commercial benefits of the region would be hindered. The distribution and abundance patterns of striped bass would likely shift to favor areas of Chesapeake Bay with more optimal habitat conditions, resulting in a shift in fishing efforts as well.

4.2. Blue crab

Changes in water temperature and salinity have varying impacts on blue crab. An increase in temperature has been found to result in decreased carapace thickness and reduced size at maturity for blue crabs in Chesapeake Bay (Hines et al., 2010; Glandon et al., 2018), though less severe winters due to warming temperatures may promote greater survival rates of overwintering juvenile blue crabs (Bauer and Miller, 2010). In southeastern U.S. river-dominated estuaries, predation mortality of juvenile blue crabs is reportedly lower in less saline (<10) regions (Posey et al., 2005). Chesapeake Bay adult female blue crabs have been found to move to higher salinity areas of an estuary after mating and before spawning however (Aguilar et al., 2008), so blue crab presence may decrease in habitats that have higher salinity within Chesapeake Bay. This study showed varying potential impacts on adult blue crab biomass as a result of shifts in water temperature and salinity within the CLC. Negative biomass trends occurred in four out the seven statistically significant scenarios (Table 3). There was no significant trend in biomass over time for the No Change scenario, indicating that a modeled continuation of environmental conditions from the initial 2006 to 2016 period would be expected to sustain current levels of blue crab populations. While the trends across the other climate change scenarios were significant, the outputs lacked a discernible pattern of response to changes in environmental variables. The only notable pattern was that blue crab biomass is predicted to increase during scenarios with a 12 increase in salinity and decrease when scenarios incorporate a 10 increase (Table 3). Climate change scenarios incorporating the 12 increase in salinity result in a final salinity of approximately 20 in 2100 (Table 2), which coincides with the optimal salinity level for blue crab as represented by the salinity response curve (Fig. 2). The other salinity changes used in this study would fail to reach the optimal threshold for blue crab, potentially contributing to decreases in biomass displayed across some of the other climate change scenarios. The final temperature value (approximately 20 °C) in 2100 is not within the optimal temperature range of the response curve for blue crab (though still within the overall tolerance range), so the sub-optimal temperature conditions at the end of the century could contribute to the decreases in blue crab biomass exhibited by some scenarios. With the variable changes in blue crab biomasses across climate change scenarios simulated by this study, it is difficult to draw conclusions on the primary drivers of increases or decreases in blue crab biomass across climate change scenarios. Further study, particularly regarding changes in spatial distributions of blue crab in response to environmental changes, would be beneficial for assessing the impact of climate change on blue crab populations within the CLC and greater Chesapeake Bay (see *4.5 Future Directions*).

The modeled trends in blue crab biomass would imply an uncertain future for the CLC and greater Chesapeake Bay blue crab fishery in the face of climate change. Over the past few decades, Chesapeake Bay blue crab stock has declined due to overfishing and environmental degradation (Miller et al., 2005). During 2020 through 2020 there were some increases in blue crab abundance due to cleaner waters, an increase in seagrass and oyster reef habitat and responsible catch limits (Virginia Resources Commission, 2020). As of 2022 however, the estimated total abundance has again dropped to a record low (Chesapeake Bay Stock Assessment Committee, 2022). Blue crab remains the top fishery in Chesapeake Bay in terms of total value, bringing in approximately $70 million worth of landings during 2020 (Commercial Fisheries Landings database). In 2015, the CLC contributed $8.7 million in dockside value of blue crab harvest (Knoche et al., 2020). Several of the climate change scenarios in this study resulted in decreases in blue crab biomass over the next century, while other scenarios showed potential increases in blue crab biomass. With the CLC being an important blue crab fishing area, these biomass trends imply varying impacts to the greater Chesapeake Bay blue crab fishery depending on the type of environmental changes that occur. Blue crabs are also able to migrate in or out of the CLC based on the favorability of environmental conditions, which would lead to changes in fishing efforts as well. More information on the influence of multiple environmental factors on blue crab productivity in

Chesapeake Bay would be beneficial for informing stock assessment and fishery management decisions (Chesapeake Bay Stock Assessment Committee, 2021).

4.3. Oysters

The predicted trends in oyster biomass exhibited by this study present a more positive outcome compared to other studies investigating the effects of temperature and salinity changes on estuarine oyster populations. Studies on juvenile and adult estuarine oysters in the Gulf of Mexico report increasing oyster mortality rates due to disease, physiological effects and predation as a result of salinity fluctuations outside of the normal range for the habitat (Petes et al., 2012; La Peyre et al., 2016; Rybovich et al., 2016). Elevated water temperatures (generally above 25 °C) have also been found to increase oyster mortality due to similar factors in this region (La Peyre et al., 2013; Rybovich et al., 2016). In Chesapeake Bay, climate-induced variation in water temperature and salinity is strongly related to greater interannual variability in oyster spatfall (Kimmel and Newell, 2007). These study results showed an increasing trend in oyster biomass within the CLC over time for most climate change scenarios (Fig. 4C, Table 3), though the simulated environmental conditions were less extreme than those investigated by other studies. Only two climate change scenarios exhibited decreasing biomass trends (Fig. 4C, Table 3), and both were characterized by changes in salinity and no change in temperature (Low Sal and Mod Sal scenarios). Increasing temperature was likely the primary driver of increases in oyster biomass across the other scenarios, as the warmer temperatures fall within the optimal tolerance range as represented by the temperature response curve for oysters (Fig. 2).

The predicted increases in oyster biomass under climate change conditions offer a potential positive outlook for Chesapeake Bay oyster populations. As the CLC contains the first Maryland oyster restoration sites from the Chesapeake Bay Watershed Agreement (Maryland Oyster Restoration Interagency Workgroup of the Chesapeake Bay Program's Sustainable Fisheries Goal Implementation Team, 2013), the oyster biomass trends reported by this study serve as a possible example for what could happen in other Chesapeake Bay oyster restoration sites with similar depth, hydrographic and water quality characteristics. A continual increase in oyster biomass would benefit the gradually improving oyster reef restoration efforts (National Oceanic and Atmospheric Administration, 2017) as well as the highly valued oyster fishery (Commercial Fisheries Landings database). It should be noted that these study results are only indicative of oyster populations not subject to oyster fishing effort. The Harris Creek, Little Choptank River and Tred Avon oyster sanctuaries are closed to oyster harvest, and this protection from fishing likely contributed to the positive trends in oyster biomass over time. If the areas were to no longer be designated as oyster sanctuaries, oyster harvest would need to be regulated to ensure the sustainability of the population over time.

4.4. Oyster reef benefits to blue crab and striped bass

Increases in oyster biomass can be beneficial to striped bass and blue crab populations. Of the six scenarios that exhibited an increase in oyster biomass, three also resulted in an increase in blue crab biomass and two an increase in striped bass biomass (Table 3). An increase in blue crab population abundance over time has been associated with continued presence of mature oyster reefs in Chesapeake Bay oyster sanctuaries (Knoche et al., 2020). Striped bass also tend to be in higher abundance in restored oyster reef areas (Hicks et al., 2004). Oysters are a large component of blue crab diet in Chesapeake Bay (Eggleston, 1990), so increasing oyster biomass would contribute to an increase in blue crab biomass through greater prey availability. Blue crab is a component in the diet of adult striped bass (Walter and Austin, 2003), so it follows that an increase in blue crab biomass could contribute to an increase in striped bass biomass. Examining the trophic dynamics between oysters, blue crab, and striped bass, it appears the predicted trends in oyster biomass in this study may have played a role in driving the biomass patterns of the other two species. The results also exhibited bottom-up forcing that showed decreases in biomass for blue crab and striped bass across the other scenarios, suggesting the negative impacts of changes in temperature and salinity to these species may outweigh the benefits of increased oyster biomass in some cases. These results are specific to the generalized species age ranges and habitat area represented by the CLC model and do not account for changes in predation by adult striped bass and blue crab that may occur as these species shift their distributions to other areas of Chesapeake Bay. A loss of striped bass and blue crab biomass within the CLC area however would lessen the ecosystem services provided by the oyster sanctuaries; an effect that may translate to similar oyster restoration sites across Chesapeake Bay.

4.5. Future directions

The future directions of this work can help address some of the limitations of this study. For example, the temperature and salinity forcing functions used reflect very linear changes in the variables over time. This pattern, while able to isolate patterns between multiple variables, is not representative of real-life conditions, which would likely involve more fluctuation in environmental variables from year to year. The linear changes in temperature and salinity resulted in relatively smooth trends in species biomass across the future scenarios, which contrasted with the larger spread of biomass values in the observed data. The simulated future measures of adult striped bass, blue crab and oyster biomasses largely fell within the range of natural variability observed from 2006 to 2016. In reality, future shifts in water temperature and salinity, and thereby species biomasses, due to climate change will likely be much more variable, potentially amplifying the biomass trends exhibited in this study. Despite the modeled results falling within the range of natural variability, the SK tests still indicated significant positive or negative monotonic trends for certain scenarios, which is indicative of a general increase or decrease in species biomass across the entire time period (2006–2100). The future salinity and temperature projections utilized by the climate change scenarios are also metrics that pertain to the mainstem Chesapeake Bay (Najjar et al., 2000, 2010; Hilton et al., 2008). The hydrological characteristics of a more closed, tributary habitat such as the CLC would result in different variations in environmental conditions compared to the mainstem Chesapeake Bay. There is a need for more data at a localized scale in different Chesapeake Bay habitats to better evaluate future climate change scenarios (Teodoro and Nairn, 2020).

The scenarios used in this study also fail to consider some of the other potential effects of climate change on the Chesapeake Bay region, such as changes in nutrient concentrations and dissolved oxygen (Breitburg et al., 1997, 2003; Irby et al., 2018). Increased precipitation because of climate change could result in an increased load of sediments and nutrients in Chesapeake Bay through land runoff and these eutrophic conditions could likely result in reduced availability of dissolved oxygen in the water column (Irby et al., 2018). Warmer water temperatures also decrease oxygen solubility (Irby et al., 2018), so these climate impacts can lead to a higher prevalence of hypoxic (DO $<$ 2 mg/L) conditions in Chesapeake Bay (Breitburg et al., 2003; Hagy et al., 2004; Irby et al., 2018). Dissolved oxygen levels that fall below the tolerance range for a given species cause physiological stress, particularly for benthic species such as oysters and blue crab, though blue crabs are able to relocate to more favorable habitats (Pihl et al., 1991; Breitburg et al., 1997, 2003; Mistiaen et al., 2003). Due to a greater amount of uncertainty regarding quantifiable climate change-driven shifts in dissolved oxygen, a repeating pattern in dissolved oxygen levels was used from 2006 to 2016 across the 94-year simulation period. Further analysis incorporating shifts in dissolved oxygen over time as a result of climate change would provide additional information on how species biomasses may change over time.

Analysis of the spatial dynamics of environmental changes and species responses would provide additional information on climate change impacts to species populations. Ecosim is unable to account for spatial dynamics of environmental conditions and species in the system. Factors such as oceanography, tidal and wind mixing and bathymetry cause variation in temperature and salinity across different habitat areas. Changes in the spatial variation of environmental conditions could alter the distributions of migratory species such as striped bass and blue crab through effects on spawning. Striped bass and blue crab spawn in the Spring and Summer months in Chesapeake Bay, so shorter winters may result in an earlier Spring migration of their populations (Aguilar et al., 2008; Peer and Miller, 2014). Ecospace is an additional spatial-temporal component of EwE that can be used to display variation in environmental factors and species dispersal rates, as well as reflect spatial changes in fishing patterns (Christensen and Walters, 2004) and would therefore be a better module to analyze changes in species biomass distributions across a larger area.

Other factors indirectly related to climate change worth considering include species mortality due to disease and parasitic infection. Warming temperatures and/or higher salinities have been associated with greater striped bass mortality due to mycobacteriosis (Groner et al., 2018), greater blue crab mortality due to *Callinectes sapidus* reovirus 1 (CsRV1; Zhao et al., 2020) and increased prevalence of the lethal oyster diseases Dermo (*Perkinsus marinus*; Hofmann et al., 2018) and MSX (*Haplosporidium nelsoni*; Hofmann et al., 2001). Greater blue crab mortality due to parasitic infection by *Hematodinium perezi* has also been reported in elevated temperatures and salinities (Huchin-Mian et al., 2018). Neither disease or parasitic-related mortality were included in the food web model for this study, but the relationship between these factors and climate change would have consequences for the three focal species going forward. Further analysis incorporating these indirect consequences would give a more detailed picture of the changes in species biomasses over time.

4.6. Conclusions

The predictive trophic model used in this study incorporated the interactions of multiple species and environmental variables to demonstrate the effects of different future climate change scenarios on populations of adult striped bass, blue crab, and oysters within oyster sanctuary areas of the CLC. Trends in the biomass of the three species in response to simulated climate induced shifts in water temperature and salinity were highly variable, indicating the uncertain impacts of climate change on the oyster reef food web. Striped bass and blue crab biomass declined throughout most climate change scenarios. Oysters exhibited a promising increase in biomass across most scenarios, though this pattern may be dependent on a continuation of sanctuary status and does not reflect a potential increase in disease-related mortality associated with warmer temperatures and higher salinity. Consideration of the potential impacts of climate change on commercially and ecologically important species, along with the role of oyster sanctuaries in supporting these species, is important for maintaining healthy communities, harvest levels, and overall ecosystem productivity in Chesapeake Bay. Future studies that capture the spatial-temporal impacts of this changing system will be critical to effective and ongoing management. The methods used by this study offer an adaptable approach that can be applied to assess the effects of climate change on other coastal habitat restoration areas and the implications for future management actions.

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CRediT authorship contribution statement

Kira L. Allen: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation. **Thomas Ihde:** Writing – review & editing, Investigation, Data curation, Conceptualization. **Scott Knoche:** Writing – review & editing, Funding acquisition. **Howard Townsend:** Writing – review & editing, Methodology, Funding acquisition. **Kristy A. Lewis:** Writing – review & editing, Writing – original draft, Software, Resources, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Initial conditions of mass-balanced Ecopath model for the CLC. B = biomass, Z = total mortality, P/B = production to biomass ratio, Q/B = consumption to biomass ratio, EE = ecotrophic efficiency.

Group name	Trophic level	B (t/km^2)	Z (/year)	P/B (/year)	Q/B (/year)	EE
StripedBassJuv	3.61	0.643	1.500		8.000	0.581
StripedBassAdult	3.61	1.750	0.450		2.512	0.162
Weakfish	3.87	0.800		0.350	2.000	0.172
DivingDucks	3.18	0.043		0.511	120.000	0.000
CownoseRay	3.13	0.200		0.160	0.938	0.000
Catfish	3.57	4.934		0.228	1.000	0.800
ReefFish	3.52	2.037		0.510	4.050	0.900
OysterToadfish	3.69	6.800		1.000	5.000	0.697
AmericanEel	3.44	2.550		0.400	2.500	0.164
Panfish	2.55	5.000		1.750	6.500	0.507
WhitePerch	3.53	4.531		0.500	3.800	0.258
AtlCroaker	3.23	1.000		1.000	8.000	0.252
GizzardShad	2.01	0.884		0.700	3.000	0.750

(*continued on next page*)

(*continued*)

Group name	Trophic level	B (t/km^2)	Z (/year)	P/B (/year)	Q/B (/year)	EE
Peprilus spp.	3.74	3.900		4.100	14.000	0.989
AtlMenhaden	2.54	0.574		2.000	11.000	0.800
ForageReefFish	3.26	15.000		1.500	5.000	0.508
BlueCrabJuv	3.39	4.000	2.000		11.007	0.612
BlueCrabAdult	3.46	18.732	1.500		5.182	0.161
MudCrabs	2.94	15.000		3.500	13.000	0.868
Iso_cope_amph	2.34	40.000		3.800	19.000	0.440
Mysids	2.50	40.000		3.500	12.000	0.596
Ctenophores	2.92	17.000		8.800	35.000	0.510
SeaNettles	3.11	15.000		5.000	20.000	0.203
SeaAnemone	3.18	4.000		2.000	6.000	0.385
HookedMussel	2.15	60.000		2.250	10.000	0.244
LgClam	2.08	25.000		2.000	10.000	0.629
SmBivalves	2.21	30.000		3.500	14.500	0.839
Barnacles	2.42	8.000		4.700	13.000	0.754
OysterJuv	2.21	18.707	5.000		15.000	0.737
OysterAdult	2.27	42.000	1.000		3.962	0.533
Bryozoans	2.31	2.500		3.750	10.000	0.553
Tunicates	2.44	40.000		1.000	4.000	0.270
Annelids	2.03	50.000		4.500	22.000	0.337
Zooplankton	2.05	40.000		90.000	216.000	0.789
Dinoflagellates	1.63	20.000		140.000	360.000	0.520
Phytoplankton (Lg)	1.00	180.000		101.000		0.370
Phytoplankton (Sm)	1.00	72.000		125.000		0.730
Detritus	1.00	100.000				0.169

Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2023.108465.

Appendix C. Fishing effort and landing data for the CLC food web model.

C.1. Fishing effort observed from the years 2006–2016.

Year	Trotline	H&L	Eel Pots	Fish Pots	Pound net	Haul seine	Gill net	Fyke net	Oyster Harvest	Clamming (bait)	Duck Hunt	Rec Fishery	All fleets
2006	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.083	1.000	1.000	1.000
2007	0.639	1.299	0.685	0.618	1.422	0.166	1.551	1.806	0.424	1.083	1.000	1.000	1.000
2008	1.109	0.580	1.078	0.829	1.299	0.010	0.993	1.742	0.186	1.083	1.000	1.000	1.000
2009	1.007	1.250	0.951	1.087	2.750	0.367	1.010	1.188	0.072	1.083	1.000	1.000	1.000
2010	1.629	1.530	0.431	1.358	0.176	1.706	0.985	0.719	0.105	1.000	1.000	1.000	1.000
2011	2.202	1.667	1.666	1.204	0.448	0.690	3.276	0.727	0.137	0.109	1.000	1.000	1.000
2012	2.173	1.610	1.289	2.001	0.088	3.356	2.567	0.974	0.836	0.145	1.000	1.000	1.000
2013	1.058	1.029	1.341	1.783	0.109	0.879	1.379	1.228	0.948	1.791	1.000	1.000	1.000
2014	1.156	0.619	0.908	1.006	0.143	5.783	2.004	1.413	0.993	1.236	1.000	1.000	1.000
2015	1.696	0.292	1.081	0.651	0.087	10.712	1.583	1.271	1.044	2.218	1.000	1.000	1.000
2016	1.367	1.088	1.043	1.154	0.752	2.467	1.635	1.207	0.574	1.083	1.000	1.000	1.000

C.2 Landing data observed for the year 2006. Landing values given in t/km^2/year.

Group name	Trotline	H&L	EelPots	FishPots	Poundnet	Haulseine	Gillnet	Fykenet	OysterHarvest	Clamming (bait)	DuckHunt	RecFishery	Total
StripedBassJuv	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
StripedBassAdult	0.000	0.013	0.000	0.000	0.019	0.000	0.083	0.000	0.000	0.000	0.000	0.012	0.127
Weakfish	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
DivingDucks	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
CownoseRay	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Catfish	0.000	0.000	0.000	0.173	0.006	0.023	0.002	0.020	0.000	0.000	0.000	0.000	0.224
ReefFish	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.275	0.000	0.000	0.000	0.000	0.275
OysterToadfish	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
AmericanEel	0.000	0.000	0.063	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.072
Panfish	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
WhitePerch	0.000	0.000	0.000	0.003	0.004	0.000	0.129	0.020	0.000	0.000	0.000	0.016	0.172
AtlCroaker	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002
GizzardShad	0.000	0.000	0.000	0.043	0.005	0.037	0.020	0.001	0.000	0.000	0.000	0.000	0.105
Peprilus spp.	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
AtlMenhaden	0.000	0.000	0.000	0.002	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010
ForageReefFish	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
BlueCrabJuv	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
BlueCrabAdult	2.233	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	2.233

(*continued on next page*)

(*continued*)

Group name	Trotline	H&L	EelPots	FishPots	Poundnet	Haulseine	Gillnet	Fykenet	OysterHarvest	Clamming (bait)	DuckHunt	RecFishery	Total
MudCrabs	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Iso_cope_amph	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Mysids	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Ctenophores	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SeaNettles	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SeaAnemone	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
HookedMussel	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
LgClam	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.001
SmBivalves	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Barnacles	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
OysterJuv	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
OysterAdult	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.744	0.000	0.000	0.000	0.744
Bryozoans	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Tunicates	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Annelids	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Zooplankton	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Dinoflagellates	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Phytoplankton (Lg)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Phytoplankton (Sm)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Detritus	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sum	2.233	0.013	0.064	0.230	0.043	0.059	0.235	0.316	0.744	0.001	0.000	0.027	3.964

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