

PROJECTED RANGE SHIFT OF THE ATLANTIC SURFCLAM, SPISULA
SOLIDISSIMA, AND THE OCEAN QUAHOG, ARCTICA ISLANDICA, UNDER
CLIMATE-INDUCED BENTHIC WARMING: FORECASTING FISHERY
INFLUENCE IN THE MID-ATLANTIC BIGHT THROUGHOUT THE 21ST
CENTURY

by

Molly M. Spencer

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Committee:

Dr. Eric N. Powell., Committee Chair
Dr. Chet F. Rakocinski
Dr. John M. Klinck

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ABSTRACT

The Atlantic surfclam, *Spisula solidissima*, and ocean quahog, *Arctica islandica*, are biomass dominant bivalve species on the eastern North American continental shelf, both supporting lucrative commercial fisheries in the Mid-Atlantic with a combined value of \$53.6 million in ex-vessel revenue per year. Rapid climate change is expected to modify the geographic range of these bivalve populations across the Mid-Atlantic Bight (MAB), suggesting transformative consequences for the surfclam fishery. This study forecasted future distributions of the two species from years 2016 – 2095, based on projected bottom water temperatures and a temperature-dependent population dynamics model, to project subsequent fishery-based indicators using a Spatially Explicit, agent-based Fisheries and Economics Simulator (SEFES). Simulations showed a positive trend in Atlantic surfclam biomass throughout the next three-quarters of the century as the clam's range continues to shift offshore and northward into habitat previously occupied by the ocean quahog, restricting ocean quahog habitat to offshore Long Island by 2095. Regional surfclam populations expand into deeper waters off New Jersey, Long Island, and southern New England starting in the early 2050s, whereas Georges Bank and Delmarva populations begin to gradually decline. A general decrease in fishing mortality is projected, with a simultaneous increase in catch and LPUE (landings per unit effort), signaling future potential growth in the surfclam fishery. These results can inform industries dependent on this resource, and other competing coastal users, by providing a basis for the development of anticipatory management for the socio-ecological and economic impacts that may result from future changes in range distribution.

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DEDICATION

This accomplishment in my educational career is dedicated to those who supported me and were my cheerleaders when I couldn't find it in me. To my mother, who modeled what true determination and courage was, and what it could achieve. To my father, who was always by my side exploring the ocean's treasures with me, whether it was under the seaweed and rocks or on the dinner table. I also dedicate this to Maine, where my love for the coast and all that's connected to it began.

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LIST OF ABBREVIATIONS

<i>USM</i>	The University of Southern Mississippi
<i>MAB</i>	Middle Atlantic Bight
<i>NES</i>	Northeast Continental Shelf
<i>SEFES</i>	Spatially Explicit Fisheries Economics Simulator
<i>Delmarva</i>	Deleware, Maryland, Virginia
<i>TMS</i>	Ten-Minute Square
<i>NEFSC</i>	Northeast Fisheries Science Center
<i>ROMS</i>	Regional Oceanographic Model Simulator
<i>LPUE</i>	Landings Per Unit Effort
<i>VTR</i>	Vessel Trip Report
<i>LS-Means</i>	Least Squared Means
<i>MSY</i>	Maximum Sustainable Yield
<i>FMP</i>	Fisheries Management Plan
<i>ABC</i>	Allowable Biological Catch

CHAPTER I – INTRODUCTION

1.1 Background

The Northeast Continental Shelf (NES), a highly productive ecosystem that supports many lucrative fisheries and coastal operations, has undergone significant warming in recent decades, and is projected to continue warming throughout the remainder of the century (Saba et al., 2016, Pershing et al., 2015). Accelerated warming documented in the NES over the past decade has led to significant increases in bottom water temperatures, particularly in the Mid Atlantic Bight (MAB) (Forsyth et al., 2015; Kavanaugh et al., 2017;). This bottom-water warming has significant implications for the structural integrity of the MAB's unique thermal gradient that arises from the Mid-Atlantic Cold Pool, a seasonal, bottom-trapped hydrogeographic feature located on the mid-to-outer-shelf of the MAB, consisting of cold, lower-salinity water identifiable by summer/fall temperatures of 10°C or less (Sha et al., 2015; Forsyth et al., 2015; 2018; Lentz, 2008; 2017; Chen et al., 2018). Recent studies, however, have documented a degradation in the seasonal extent of the Cold Pool, as well as an increase in its thermal gradient, with recent years showing a 10% decrease in the geographic footprint of this feature (Horwitz et al., 2020; Friedland et al. 2022).

The importance of the hydrogeographic feature off the MAB cannot be overstated, as it strongly influences the geographic range of many species on the MAB and Georges Bank region, permitting populations to extend farther south and offshore where temperatures would otherwise be too warm for many economically important boreal species to survive (Miller et al., 2016; Kleisner et al., 2017; Friedland et al., 2020, 2022; Powell et al., 2020; Miles et al., 2021; Horwitz et al., 2022). This disruption in Cold Pool hydrodynamics from accelerated ocean warming has severe implications for commercially valuable sedentary

species, notably the Atlantic surfclam (*Spisula solidissima*) and the ocean quahog (*Arctica islandica*), where the inshore range boundary of the latter and the offshore range boundary of the former are determined by the inshore and southern boundaries of the Cold Pool. Historically, these two species have occupied separate ecotypes within the Mid-Atlantic Bight, with the Atlantic surfclam occupying the warmer, inshore coastal region from Georges Bank to Cape Hatteras at depths of 10-50 m (Merrill and Ropes, 1969; Ropes 1980, NEFSC 2017a; Stromp et al. 2023b) and the pan-boreal ocean quahog occupying habitat offshore of the surfclam, within the reach of the Cold Pool at depths of 30-60 m (Dahlgren et al., 2000; Merrill & Ropes, 1969; NEFSC 2017b). Degradation of the Cold Pool, and observations of the northern extent of the Cold Pool retreating at a rate 2.6 times faster than its southern counterpart, places prospective suitable habitat for the two clam species in a particularly critical state (Chen et al., 2018b).

Academics and industry alike have dedicated extensive research into the poleward and offshore distributional shifts of commercially exploited species in the NES (Nye et al., 2009; Pinsky & Fogarty, 2012; Mills et al., 2013; Pershing et al., 2015; Kleisner et al., 2017; Young et al., 2019; Rheuban et al., 2017), but among the most well documented and geographically extensive range shifts in the northwestern Atlantic thus far has been the Atlantic surfclam (*Spisula solidissima*) (Hofmann et al., 2018). The offshore range of the species has shifted north and farther offshore and the southern and inshore boundaries of the species' range have moved concordantly over much of the MAB (Weinberg, 2005; NEFSC, 2013, 2017; Hofmann et al., 2018; Timbs et al., 2019). Many studies have concluded that the species' change in geographic distribution and productivity is associated with its extreme vulnerability to temperatures above 20°C

(Weinberg et al., 2002; Kim & Powell, 2004; Weinberg et al., 2005, Weinberg, 2005; Munroe et al., 2013; Narváez et al., 2015). The Atlantic surfclam is a cool-temperate bivalve that has a narrow upper thermal range of roughly 19°C - 21°C, the upper limit primarily determined by the effect of temperature on filtration rate, and generally exhibits rapid physiological decline as temperatures rise above 21°C (Munroe et al., 2013). The range shift in Atlantic surfclams includes its progressive invasion into the habitat of the ocean quahog, *Arctica islandica*, generating an extraordinarily expansive ecotone (Stromp et al. 2022b), and with it, a growing concern for the Atlantic surfclam fishery.

Current fishery regulations prohibit mixed-catch landings of both Atlantic surfclams and ocean quahogs. This is largely a matter of efficiency given the time intensive on-board sorting required when fishing in the overlap region given the limited time vessels have at sea due to the spoilage rate of clams and the restricted number of crew (Stromp et al., 2023a). The ongoing evolution of this ecotone between the two bivalve species exacerbates the continued displacement of fishing effort in the fishery from the southern-most portion of the fishery (McCay et al., 2011; Hofmann et al, 2018), ultimately constricting fishing grounds both in and offshore, as well as south of Delmarva. As global ocean warming is projected to continue over the remainder of the century, forecasting future impacts on the health of fisheries' stocks, as well as the response of fishers and their fishery to climate-induced changes in species distributions, is a crucial matter of investigation.

1.2 Objectives

The objective of this thesis is to project the geographic range distribution of the Atlantic surfclam and the ocean quahog in the MAB under forecasted warming climate

conditions, from 2016 to 2095, and subsequently evaluate the anticipated response of the surfclam fishery to the changing footprint of the Atlantic surfclam. The first objective, covered in Chapter II, models forecasted species distributions of the Atlantic surfclam and ocean quahog on the MAB seafloor under future temperature conditions using a regionally-forced predictive hydrodynamic model developed by Curchitser et al. (personal communication) that generates predictions of bottom water temperatures through year 2095. These predicted bottom water temperatures lay the foundation for the employment of a range shift algorithm specifying the distribution of Atlantic surfclams and ocean quahogs based on physiological temperature constraints that subsequently feed into a population dynamics model belonging to SEFES (Spatially Explicit Fisheries Economic Simulator; Munroe et al. 2022). Together, these models simulate spatially resolved biological probabilities for growth and survival across the current and projected habitat range of the Atlantic surfclam to evaluate the projected spatial extent of the ecotone supporting both clam species and to estimate surfclam biomass.

The second objective of this thesis, covered in Chapter III, is to elaborate upon the projected changes in Atlantic surfclam spatial distributions and biomass presented in the previous chapter by assessing the potential fishery consequences of this geographically large-scale range shift. Results of projected biomass from the previous chapter are used to inform fishery dynamics of the Atlantic surfclam fishing industry, including its scope for future growth and sustainability of regional stocks over time under the impacts of climate-induced warming. Fishery response is examined under important economic metrics such as LPUE, time at sea, and trip duration, as well as important managerial metrics such as fishing mortality rate and catch.

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CHAPTER II – CLIMATE-INDUCED WARMING ON THE MID-ATLANTIC BIGHT
CONTINENTAL SHELF: PREDICTIONS OF THE FUTURE DISTRIBUTION AND
CARRYING CAPACITY OF THE ATLANTIC SURFCLAM (*SPISULA*
SOLIDISSIMA) AND THE EXPANDING ECOTONE WITH THE OCEAN QUAHOG
(*ARCTICA ISLANDICA*)

2.1 INTRODUCTION

The Northeast Continental Shelf (NES), a highly productive ecosystem that supports many lucrative fisheries and coastal operations, has undergone significant warming in recent decades, and is projected to continue warming throughout the remainder of the century (Pershing et al., 2015, Saba et al., 2016; NOAA, 2021). Friedland et al. (2020a) reported average rates of warming in the NES for the most recent decade of approximately 0.95°C per decade, and in the Mid Atlantic Bight (MAB), between 1.1 and 2.4°C per decade. The warming of the continental shelf has led to significant increases in bottom water temperatures, particularly in the Mid-Atlantic Bight (MAB) and Gulf of Maine (Forsyth et al., 2015, Kavanaugh et al., 2017). Temporal patterns in warming of bottom water temperatures in the MAB diverge from those observed in surface waters due to the Cold Pool, a unique lens of cold bottom water produced by thermohaline stratification during late spring to early fall (Lentz, 2008; Kavanaugh et al., 2017; Friedland et al., 2020a; Chen et al., 2021). The Cold Pool is located on the mid and outer continental shelf of the MAB from the southern flank of Georges Bank to near Cape Hatteras, and is composed of cold, lower-salinity seawater formed on the shelf during winter with an admixture of waters from the Gulf of Maine

and the Labrador Sea (Sha et al., 2015; Forsyth et al., 2015; 2018; Lentz, 2017; Chen et al., 2018). A number of Cold Pool indices have been described to measure the geographic extent of this cold-water mass (Chen & Curchitser 2020; du Pontavice et al. 2023).

Notably, accelerated warming documented in the NES over the past decade has not been observed solely through sea surface temperature. Seasonal evolution and persistence of the Cold Pool plays a central role in the creation of thermal habitat defining the range of cool-temperate and boreal species, with cold waters stretching farther south and offshore along the MAB continental shelf where temperatures would otherwise be too warm for many economically valuable boreal species to survive, such as yellowtail flounder (*Pleuronectes ferruginea*), the sea scallop (*Placopecten magellanicus*), and the ocean quahog (*Arctica islandica*) (Miller et al., 2016; Kleisner et al., 2017; Friedland et al., 2020a, 2022; Powell et al., 2020b; Miles et al., 2021; Horwitz et al., 2022). Poleward and offshore distributional shifts in mobile commercially-exploited species within the southern New England and MAB regions are well documented (Nye et al., 2009; Pinsky & Fogarty, 2012; Mills et al., 2013; Pershing et al., 2015; Kleisner et al., 2017). In recent years, growing concerns also have been directed towards sedentary species within the Mid-Atlantic, such as commercially valuable bivalve species, including the Atlantic surfclam (*Spisula solidissima*) and the ocean quahog (*Arctica islandica*), the inshore range boundary of the latter and the offshore range boundary of the former being determined by the inshore and southern boundaries of the Cold Pool. Studies document a degradation in the seasonal extent of the Cold Pool and an increase in the thermal gradient of the Cold Pool due to bottom temperature warming, with recent years showing a 10% decrease in the geographic footprint, an overall reduction greater

than 23,000 km² (Horwitz et al., 2020; Friedland et al. 2022). Similarly, Chen et al. (2018b) place prospective suitable habitat for these two sedentary species in a particularly critical state with observations of the northern extent of the Cold Pool retreating at a rate 2.6 times faster than its southern counterpart.

The Atlantic surfclam and ocean quahog fisheries are important to the economies of the Mid-Atlantic and southern New England regions, producing a combined total of \$1.3 billion in annual economic impact (Murray, 2016). Historically, these two species have occupied separate ecotypes within the Mid-Atlantic Bight, with the Atlantic surfclam occupying the warmer, inshore coastal region from Georges Bank to Cape Hatteras at depths of 10-50 m (Merrill and Ropes, 1969; Ropes 1980, NEFSC 2017a; Stromp et al. 2023b) and the pan-boreal ocean quahog occupying habitat offshore of the surfclam, within the reach of the Cold Pool at depths of 30-60 m (Dahlgren et al., 2000; Merrill & Ropes, 1969; NEFSC 2017b). One of the most geographically extensive and well documented range shifts recorded in the North Atlantic belongs to the Atlantic surfclam, a bellwether species for climate change, the range of which has shifted north and offshore most noticeably off the New Jersey and Delmarva coast (Hofmann et al. 2018). Inshore warming temperatures in this region accrue from local atmospheric heating and warm water incursions from the Gulf Stream (Flagg et al., 2006; Chen et al. 2014). The influence of the warming of inshore bottom waters on the surfclam demonstrates an extreme vulnerability of this species to temperatures exceeding 20°C with species relocation, extensive population die-offs, and reduced condition observed along the southern and inshore range boundary (Weinberg et al., 2002; Weinberg et al., 2005, Weinberg, 2005; Kim & Powell, 2004; Marzec et al., 2010; Narváez et al., 2015).

The ability of this species to rapidly change its geographic footprint on half-decadal time scales is clear, despite the apparent requirement of larval transport counter to the net downcoast drift and in most months net onshore transport of surface waters (Zhang et al., 2015, 2016).

In comparison, the ocean quahog has a near knife edge upper thermal limit of 15°C, and therefore the core of the range of this pan-boreal species is found within the extent of the Cold Pool. Research on previous biogeographic range shifts for ocean quahogs has focused on their historical distributions over the last 200 years during which they occupied regions farther inshore and south than their present-day range, likely due to the Cold Pool's inshore boundary reaching farther inshore in past cold periods (Powell et al. 2020b; Pace et al., 2018; LeClaire et al., 2022). Despite recent trends restricting the extent of the Cold Pool, the cross-shelf and downcoast range of the ocean quahog remains unphased, likely due to the species' ability to burrow for long periods of time to escape unsuitably warm temperatures in the fall (Strahl et al, 2011; Taylor, 1976). Indeed, LeClaire et al. (2023) suggest multi-decadal to half-century time scales for recession of the inshore range boundary, poorly resolved by the <40-yr federal survey time series.

The noteworthy outcome of the difference in the time dimension associated with the two species' range shifts, in response to warming temperatures, is the influence on the geographic relationship of the two species over the last two decades. A recent study by Timbs et al. (2019) estimates an overall shift in surfclam stock in recent decades of roughly 20 km offshore and 30-40 km north off Delmarva and New Jersey. As a consequence, the distinct boundary between these two bivalve species has degraded due

to accelerated climate-warming and the recession of the inshore thermal boundary of the Cold Pool, paving the way for an evolving geographically extensive ecotone between the two (Stromp et al., 2023b; Powell et al., 2020b). The term ecotone as used herein follows the definition originally developed by Alfred Russel Wallace to pertain to the boundary between two biomes in which two biological communities meet and overlap. The expanding ecotone has severe implications for the southern fishery in the loss of suitable fishing grounds. The surfclam fishery is constrained by the inability to land both surfclams and ocean quahogs simultaneously and the inordinate cost of sorting the two species at sea; the economic implications of this has been described in Stromp et al. (2023a). Whether the two species interact biologically remains unclear (Stromp et al. 2023b).

The complex dynamics of a rapidly warming northeast continental shelf, its effects on species habitat, and the subsequent impacts on fisheries management has led to an increased demand to employ regional, high-resolution climate and hydrodynamic models to better understand and diagnose future impacts on the health of fisheries' stocks (Rheuban et al., 2017; Gawarkiewicz et al., 2018; Hennen et al., 2018; Robson et al., 2018; Friedland et al., 2020b; Chen et al., 2021; Goncalves Neto et al., 2021). Projected changes in ocean conditions are anticipated to further change stock distributions, likely to a greater extent than observed over the past decades. The objective of this study is to use projected climate conditions in the MAB to simulate predicted geographic distributions of the Atlantic surfclam (*Spisula solidissima*) and ocean quahog (*Arctica islandica*) from present-day to 2095, and, using a population dynamics model, to extend these predictions to the effect of rising temperatures on the abundance and biomass of the Atlantic

surfclam. The study builds upon a predictive hydrodynamic model developed by Curchitser et al. (personal communications) and an analysis of the geographic distribution of the Atlantic surfclam and ocean quahog relative to bottom water temperature leading to the delineation of the determinants of the inshore and offshore boundaries of the two species. Documentation of anticipated response of these two species to changing bottom water temperature then leads to a consideration of the biological implications for the MAB benthos and management of the MAB shellfish fisheries.

2.2 METHODS

This study employs a regionally-forced hydrodynamics model generating predictions of bottom water temperatures through 2095, a range shift algorithm specifying the distribution of Atlantic surfclams and ocean quahogs based on temperature constraints, and a population dynamics model based on SEFES (Spatially Explicit Fisheries Economic Simulator; Munroe et al. 2022) to apply projected future temperature conditions onto the distribution of these species on the MAB seafloor. Together, these models simulate spatially resolved biological probabilities for growth and survival across the current and projected habitat range of the Atlantic surfclam to evaluate the projected spatial extent of the ecotone supporting both clam species and to estimate surfclam biomass.

2.2.1 SEFES Model

SEFES was designed to simulate the surfclam fishery in the MAB, including the fishing fleet behavior and processing plant economics (Powell et al., 2015; Kuykendall et al., 2017); and consequently was formulated to include Atlantic surfclam geographic distribution and population dynamics. The model was updated to include the expanding

overlap between this species and the colder-water ocean quahog (Stromp et al., 2023a). The presence of ocean quahog distributions in the model serves as an external force on surfclam fishing vessels and their fishing effort (a measure of fishing intensity) in certain fishing grounds based on regulations prohibiting commercial fishing vessels from landing both Atlantic surfclams and ocean quahogs as a mixed catch (Stromp et al., 2023a) and, thus, the degree of overlap between the two species is economically important. Biological interaction between the two species is not specified as no evidence presently exists supporting it (Stromp et al., 2023b).

The SEFES model covers a geographic range from Georges Bank to Chesapeake Bay, with a spatial domain described by a 54 by 33 grid consisting of 10 min of latitude by 10 min of longitude squares (TMS) (Fig. 1). This grid encompasses the survey regions used in the Northeast Fisheries Science Center stock assessment of Atlantic surfclam in the MAB with resolution consistent with the standard VTR (vessel trip report) data format for tracking the locations of harvest (NEFSC, 2022). Data input and verification of the population dynamics in the SEFES model came from NEFSC stock assessment surveys (Munroe et al., 2022) and a detailed survey of the species' overlap zone south of Hudson Canyon (Stromp et al., 2023b). Further information on the SEFES model is provided in Powell et al. (2015) and Munroe et al. (2022).

2.2.2 Modeled Population Dynamics of the Atlantic Surfclam

The Atlantic surfclam population dynamics model, simulated within SEFES, is based on federal survey data collected from 2016-2019 (NEFSC, 2022). The population model includes rates for mortality and growth calculated using shell length and wet weight data. The model incorporates 18 Atlantic surfclam shell-length classes, specified

at 10-mm intervals, between 20 mm and 200 mm. The allometric parameters relating wet weight to length, $a = 5.84 \times 10^{-6} \text{ g mm}^{-1}$ and $b = 3.098$, are specified in Marzec et al.

(2010):

$$W = aL^b \quad (1)$$

with the central length in each 10-mm size class used to calculate surfclam stock biomass. Growth rate is specified by a von Bertalanffy age-length relationship as described by Munroe et al. (2022). The calculated growth rate of Atlantic surfclams in each TMS was derived for each length interval by using the age of the Atlantic surfclam at the lower bound of its length class and the length of the surfclam one year younger (Munroe et al., 2022).

Recruitment of the Atlantic surfclam is assumed to occur everywhere on the continental shelf (Timbs et al., 2018; Zhang et al., 2016), with recruitment to the model's simulated population occurring once per year in October, 4.5 months post-spring spawning and 1-month post-fall spawning (Munroe et al. 2022). The stock-recruitment relationship is not established for this species, steepness is high, so a standard Beverton-Holt relationship is used in the model using a steepness of 0.8 following past studies (Myers et al., 1999; O'Leary et al., 2011). The model produces a patchy distribution of interannual recruitment across the domain by distributing recruits to the smallest length interval (20-30 mm) based on a random draw from a negative binomial distribution (Munroe et al., 2022). The decision to recruit individuals into this length interval is consistent with juvenile growth rates of newly-settled Atlantic surfclams during their first year (Chintala and Grassle, 1995; Ma, 2005; Acquafredda et al., 2019).

The natural mortality rate specified varies across the MAB shelf to resemble variability observed in the natural environment (Weinberg, 1998). TMSs with fishable surfclams (120+ mm) present were assigned specific mortality rates based on surfclam density and age data (Munroe et al., 2022). TMSs where no surfclams or only small surfclams were present were assigned a background mortality rate of 1 yr^{-1} , which limits the survival of surfclams to roughly 3 years, thereby limiting clams to sizes lower than the selectivity limit of the survey gear. For TMSs where surfclam density data were available for 2016-2019, Munroe et al. (2022) estimated mortality rate based on abundance ($Mortality_{abundance}$) by using a hyperbolic tangent function of the form:

$$Mortality_{abundance} = 0.5 \left(1 - \tanh \left(\frac{D_{TMS} - D_0}{D_r} \right) \right) + m_{base} \quad (2)$$

where D_{TMS} is the observed density of Atlantic surfclams in each TMS, D_0 is a target density (0.2 Atlantic surfclams m^{-2}), D_r is the density range that allows maximum density (0.1 Atlantic surfclams m^{-2}) and m_{base} is the average base mortality rate (0.15 yr^{-1}) used in the stock assessment (NEFSC, 2022). More details are provided by Munroe et al. (2022). For TMSs where age data were available for the 2010s, the specific mortality rate based on animal age ($Mortality_{age}$) was estimated from the Atlantic surfclam with the oldest age observed using the relationship given in Hoenig (1983) as:

$$Mortality_{age} = \frac{-\ln(age_{perc})}{age_{max}} \quad (3)$$

where age_{max} is the oldest observed surfclam in a TMS and age_{perc} is the fraction of the cohort that survives to that oldest age, assumed to be 1% following Hoenig (1983). More details are provided by Munroe et al. (2022). Estimates obtained from equations (2) and (3) were combined to obtain a mortality rate for each TMS as follows: 1) if both rates

were available for a given TMS square, the lower of the two rates was used; 2) if only one of the two was available, that value was used; and 3) if neither were available, an average mortality rate from neighboring TMSs was calculated. The same mortality rate was imposed for all size classes at the end of each simulation year. The average mortality rate across all TMSs with surfclams of fishable size was 0.17 yr^{-1} , very near the assumed value for the stock as a whole of 0.15 yr^{-1} (NEFSC 2022).

2.2.3 Hydrodynamics Model

Present-day bottom water temperatures for each TMS were extracted from the DOPPIO implementation (López et al., 2020) of the Regional Ocean Modeling System (ROMs) (Wilkin et al., 2018; Levin et al., 2018). Specifically, the DOPPIO model was used to specify bottom water temperatures in the 2016-2019 period to verify observed surfclam distributions with those estimated using temperature constraints, as defined subsequently, and to verify consistency with a forward projecting hydrodynamic model described immediately hereafter.

The hydrodynamic model employed to obtain bottom water temperatures for the MAB shelf in years 2016-2095 is described in detail by Alexander et al. (2020), Chen and Curchitser (2020) and Kang and Curchitser (2013, 2015). Briefly, the large-scale climate change signals were obtained using small ensemble of global climate and earth system models from the Climate Model Intercomparison Project version 6 (CMIP 6) archive. Simulations used to provide the climate change forcing to the regional, high-resolution, ROMS (Regional Ocean Modeling System – Shchepetkin and McWilliams, 2005) model boundary conditions for this project utilized the Representative Concentration Pathway (RCP) 8.5 scenarios, which project strong greenhouse gasses

loading into the atmosphere through the 21st century. Boundary conditions included the fluxes of heat, moisture, and momentum at the ocean surface and the advection of heat, salt, and biogeochemical fluxes (when available) along the ocean boundaries. Given that the biases in present day global climate/earth system models and their relatively coarse resolution (~80-220 km) may result in an unrealistic representation of the ocean climate and its response to an increase in greenhouse gasses, a high-resolution, bias-corrected ensemble of averaged physical projections for the Northeast U.S. was produced by combining dynamical downscaling with a generalized application of a delta approach for boundary conditions and forcing (similar to Auad et al, 2006; Liu et al. 2015; Alexander et al. 2020). The delta approach to downscaling superposes the future climate change signal, as derived from the CMIP models, on top of the bias-corrected present day circulation leading to a more realistic representation of future conditions at the high-resolution needed to resolve shelf and coastal features.

2.2.4 SEFES Projected Biological Habitat

In this study, Atlantic surfclam habitat is specified within SEFES using past and current known conditions relating bottom water temperatures to TMSs identified as surfclam habitat and/or ocean quahog habitat as previously described. To cast the distribution of these species into the future required specifying range boundaries based on bottom water temperatures available from the hydrodynamic model. To do so, present-day conditions, herein defined as years 2016-2019 to conform to the model verification period implemented by Munroe et al. (2022), were used to evaluate temperature-determined range boundaries. Biological temperature constraints derived from DOPPIO bottom water temperature estimates were obtained by extracting average monthly bottom

temperatures for each TMS in the model domain for years 2016-2019. Seasons were defined as: Winter (January, February, March); Spring (April, May, June); Summer (August, September, October); and Fall (October, November, December). The month of October is present in both Summer and Fall due to its uniquely unpredictable behavior relative to the time that Cold Pool thermal stratification breaks down (Sha et al., 2015; Lentz, 2017, Chen et al., 2018b), the timing and intensity of which is highly variable, and thus differentially influences both summer and fall conditions.

For ocean quahogs, only the high-temperature range boundary was required, as temperatures are not cold enough in the MAB to generate a cold-temperature range boundary for this species (e.g., Strahl et al., 2011; Mette et al., 2016; Ballesta-Artero et al., 2017). To identify the high-temperature range boundary, TMSs in which Atlantic surfclams and ocean quahogs co-existed were identified from NEFSC survey data, anecdotal information from a survey of captains (Stromp et al. 2023a), and a dedicated survey targeting this inshore boundary reported by Stromp et al. (2023b). The observed average seasonal bottom water temperatures (2016-2019) for these TMSs are shown in Table 2.1, identified to define only the inshore (warm temperature) range boundary of the ocean quahog. Seasonal averages were obtained by averaging monthly values for the 3 months in each season and the 4 years of record ($n = 12$). Guidance for evaluation comes from the known upper thermal limit for the species ($\sim 15^{\circ}\text{C}$) and due to the quahog's capability of burrowing and remaining burrowed for an extended period of time (Taylor, 1976; Oeschager, 1990; Strahl et al., 2011), thereby avoiding highest summer and fall bottom water temperatures. That is, ocean quahogs are expected to be found in bottom water temperatures somewhat warmer than would be anticipated from their physiological

thermal limit. TMSs with a 2016-2019 mean summer temperature less than or equal to 13.5°C were defined as habitable for ocean quahogs. Comparison of these TMSs agreed with observed TMSs marking the inshore range boundary in the cross-shelf survey analyzed by Stromp et al. (2023b), confirming a reliable designation of ocean quahog habitat using this temperature rule. Importantly, the distribution of ocean quahog habitat in the model, designated by 13.5°C temperature, extends laterally and south of the definition of the Mid-Atlantic Bight Cold Pool, and therefore we term this area of habitat the “cold water habitat” to delineate this region from the Cold Pool as defined by Cold Pool indices (Chen & Curchitser 2020; du Pontavice et al. 2023).

Criteria for Atlantic surfclams are more complex because designation of both the inshore (warm temperature) range boundary and the offshore (cold temperature) range boundary were required. The average seasonal bottom water temperatures for the Atlantic surfclam TMSs as defined in Munroe et al (2022) and updated using Stromp et al. (2023b) can be seen in Table 2.2. TMSs were originally identified using NMFS survey data (Munroe et al., 2022). Unlike Table 2.1, values in Table 2.2 cover the full range of the Atlantic surfclam and so describe the temperature dependency of the entire range. Guidance for the warm temperature boundary comes from the known thermal limits for the species wherein temperatures above 20°C result in physiological stress (e.g., Munroe et al., 2013; Narváez et al., 2015; Hornstein et al., 2018). Using Table 2.2, and a comparison of results with the observed inshore range boundary. resulted in a high temperature threshold for Atlantic surfclam habitat defined as summer average temperatures not exceeding 18.5°C. The cold temperature boundary is a more difficult challenge, as Atlantic surfclams readily survive winter temperatures of 4-5°C, yet are not

found in habitats with summer temperatures much below 12°C. Designation of offshore-range temperatures were guided by bottom water temperatures found in the surfclam-ocean quahog overlap zone as determined by Stromp et al. (2023b). These comparisons yielded three rules: A TMS is deemed habitable by Atlantic surfclams only if 1) summer average temperatures did not drop below 11.5°C, 2) fall average temperatures did not drop below 12°C, and 3) mean spring temperatures did not drop below 7.5°C. The distribution of TMSs so designated showed good agreement with NEFSC survey data and data in Stromp et al. (2023b). The physiological and/or ecological underpinnings, however, are not well defined, unlike the warm temperature range boundary, although the temperature dependency on growth rate offers some guidance (Powell et al., 2020a).

The described rules permitted designation of TMSs as Atlantic surfclam and/or ocean quahog habitat but did not provide sufficient information to parameterize population dynamics processes for Atlantic surfclams such as variation of the natural mortality rate within the occupiable range. As surfclam larvae are allowed to recruit throughout the model domain, consistent with Timbs et al. (2017), any TMS outside of surfclam habitat was given a mortality rate of 1 yr⁻¹. This limited surfclam survival to about 3 years in these TMSs.

Detailed analyses of the within-habitat distribution of Atlantic surfclams based on temperature from the DOPPIO model, depth, local (within TMS) variability in depth (Tozer et al., 2019), and bottom current speed from the DOPPIO model relative to the mortality rates derived from NEFSC survey data as previously described did not yield any significant statistical models, suggesting that either the patchy distribution obtained from the previously-described analysis was based on insufficient data to support a more

detailed habitat delineation or that the within-habitat distribution was based on the chance distribution of recruitment generating a patchy distribution, an inference that would be consistent with observations (Flowers, 1973; Weinberg et al., 2002; Timbs et al., 2018, 2019). Based on Munroe et al. (2022), emphasis in developing a patchy distribution of the surfclam stock within a newly determined range was placed on the mortality rate; consequently, TMSs designated as surfclam habitat were randomly assigned mortality rates between 0.12 and 0.8 yr⁻¹ based on the mortality rate distribution estimated originally by Munroe et al. (2022) from survey data. In the model, the random assignment of mortality rates to surfclam-habitable TMSs thus implemented generates a patchy distribution of surfclams similar to present-day distributions.

2.2.5 Simulation Structure

A SEFES simulation has a run time of 300 years, wherein no fishing activity occurs in the first 100 years of each simulation to allow for surfclam populations to reach carrying capacity based on specified growth, mortality, and recruitment rates: fishing begins in year 101 (Munroe et al. 2022). For this study, only the biological parameters influencing distribution and biomass are important, and therefore analysis focused on the last 50 years of the first 100 years during which the population oscillated about carrying capacity. For each case, a series of 200 simulations were conducted. Variability between simulations is provided by 1) the randomness of recruitment amongst TMSs introduced by the negative binomial draw and 2) the re-randomization of mortality rates within surfclam habitat for each simulation.

Simulation scenarios were generated for every TMS using averaged seasonal bottom temperatures for that TMS. The generated temperatures had an approximately

decadal time step from the late 2010s to the 2090s. Eleven cases, each of 200 simulations, were run (Table 2.3) based on four-year-averaged time segments within each decade (hereafter referred to as “cases”), with years 2016-2019 used as the base case for comparison. Several model configurations were employed and are listed as follows. The basic SEFES model (Munroe et al., 2022), identified herein as case B1619 with naming convention ‘B’ standing for “base case model” and ‘1619’ for the analyzed years of 2016-2019, utilized contemporary fishery-based and stock survey-based information with verification and simulation results already reported (Munroe et al., 2022; Scheld et al., 2022; Stomp et al., 2023a). Clam distributions in this case depend upon observed species distributions rather than temperature data. The comparison case, D1619, naming convention ‘D’ of which stands for “Doppio model”, used current oceanographic conditions from the Doppio model to extract bottom water temperatures for years 2016-2019 to produce a spatial distribution of Atlantic surfclams and ocean quahogs and Atlantic surfclam biomass. A last comparison case, C1619, the naming convention ‘C’ of which stands for “Curchitser model”, uses current oceanographic conditions from the Curchitser et al. (personal communications) model, hereafter termed the Curchitser model, to extract bottom water temperatures for years 2016-2019 to produce spatial distributions of both clam species and Atlantic surfclam biomass. Lastly, cases 2629, 3639, 4649, 5255, 6265, 7275, 8285 and 9295, each of which is named for a 4-year period providing averaged bottom water temperatures (e.g., 2629 defines the period 2026-2029; see Table 2.3), use projected bottom water temperatures obtained from the Curchitser model to estimate future spatial distributions of species and Atlantic surfclam biomass.

Each case consisted of 200 simulations, each with its own distribution of mortality rates within habitable TMSs and each with its own recruitment time series, with the exception of case B1619 which retained the empirically derived mortality rates. That is, with the exception of B1619, fluctuations in biomass occur over the final 50 years of the simulation as the model oscillates about carrying capacity based on variations in the distribution and intensity of recruitment and the distribution of mortality rates amongst the Atlantic-surflclam habitable TMSs. Metrics extracted from the fifty-year analysis include the calculated average and standard deviation of stock biomass in millions of metric tons (MMT), the average fishable stock biomass defined for this analysis as sizes ≥ 120 mm (MMT), and the spatial distribution of Atlantic surfclams and ocean quahogs within the MAB model domain, including the number of TMSs habitable by both species.

Results were analyzed using R, MATLAB, and Fortran programs, with most statistical analyses implemented in SAS 9.4. Statistical comparisons of biomass metrics were carried out using Wilcoxon signed rank tests for comparisons using the B1619 base case because mortality rates did not vary within TMSs amongst the 200 simulations in this case, and by Analysis of Variance (ANOVA) for all other comparisons.

ANOVAs were run with either Atlantic surfclam total stock biomass or fishable biomass (120+ mm) as the dependent variable, and the main effects tested being Year (the final 50-year portion of the simulation with years chosen at every turn of the decade to represent the simulation to minimize the effect of autocorrelation within the yearly time series (Table 2.3, six levels), case number (Table 2.3, nine levels), and when appropriate region that encompassed five distinct regional areas within the MAB that describe regionally specific Atlantic surfclam habitats (Table 2.3, 5 levels). A post-hoc

Least Square Means test (LS-Means) was employed to further investigate the origin of significance within the ANOVAs.

The five regions compared (Fig. 1) were regions previously used by NEFSC in stock assessments (e.g., Fig. A1 in NEFSC, 2007). Region one, the southern-most region, encompasses parts of northern Virginia, Delaware, and Maryland (known as Delmarva), and is partitioned from region two, New Jersey, at Delaware Bay. Region three comprises Long Island, NY, and is separated from region two at Hudson Canyon. Region four includes southern New England, partitioned from region three at Block Island. Lastly, region five encompasses Georges Bank, and is separated from region four by the Great South Channel.

A pairwise Chi-square test for independence was conducted to compare the geographic distribution of Atlantic surfclam and ocean quahog habitat among the cases and their temperature regimes (total of nine cases, each composed of four habitat types, producing 36 pairwise tests). The TMS squares for each case were assigned to four categories as follows: 1 = neither species present, 2 = ocean quahogs present, but no Atlantic surfclams, 3 = Atlantic surfclams present, but no ocean quahogs, and 4 = both Atlantic surfclams and ocean quahogs present. The sums produced a 2x4 chi-square matrix for each test.

2.3 MODEL VALIDATION

Validation of the forward projecting model was a two-step process. First, determining the predictive power of seasonally averaged bottom water temperatures to specify Atlantic surfclam and ocean quahog distributions was undertaken using the ROMs-based DOPPIO model for years 2016-2019. The DOPPIO simulation, case

D1619, dispersed surfclam mortality values among TMSs using the seasonal temperature rules and the bottom temperatures derived from DOPPIO for 2016-2019. The resulting species distributions predicted from the D1619 case were compared to the base case, B1619, which represents present-day species distributions based on 2016-2019 stock assessment and related survey data (Munroe et al., 2022; Stromp et al., 2023b). The B1619 base case was validated by Munroe et al. (2022), and therefore the comparison between simulations from B1619 and D1619 tests whether the bottom water temperatures rules applied to bottom-water temperatures from the DOPPIO model can accurately depict both the distribution and biomass of Atlantic surfclams in the MAB.

A Wilcoxon signed-rank test compared the whole-stock biomass and fishable biomass produced by these two models. Whole-stock biomass was significantly different between the two case models (Table 2.4), with the base case B1619 yielding a lower biomass than D1619 (Table 2.4). Despite the significant difference, the average (over 200 simulations) biomasses produced by both models, 0.949 MMT for D1619 and 0.870 MMT for the base case (Table 2.4), are very close and well within the range estimated for biomass directly from the federal surfclam survey (see Fig 4a in Munroe et al., 2022). Similarly, the results for fishable biomass, 0.682 MMT for D1619 and 0.632 MMT for the base case (Table 2.4), though significantly different, are also very close and well within the range of values estimated directly from the federal stock survey. Therefore, application of seasonal bottom water temperatures and species-specific thermal rules provide reliable predictions of Atlantic surfclam biomass.

The next step in model verification is to compare the validated temperature-driven DOPPIO case (D1619) to the bottom temperature data for the same years obtained from

the forward-projecting Curchitser model (C1619). Results of ANOVA indicate that the whole-stock biomass and fishable biomass from each model were significantly different between the two simulations (Table 2.4). Average whole-stock biomass was 0.949 MMT for D1619 and 1.03 MMT for C1619, but both values were well within the range of observed biomass in the federal surfclam survey (Fig. 4a in Munroe et al., 2022) and also similar to the base case based on the federal survey. Average fishable biomass was 0.682 MMT for D1619 and 0.743 MMT for C1619 (Table 2.4), likewise well within the range observed in the federal stock survey and similar to the base case based on the federal survey.

The incremental increase in biomass from the base case (B1619) to DOPPIO (D1619) to the Curchitser case (C1619) stems from two factors. First, the base case run has a few TMSs with low biomass due to poor survey coverage relative to recruitment events in several regions, particularly southern Delmarva from where surfclams presently are being landed by the fishery (Wisner et al., 2023). Second, the Curchitser model positions the Cold Pool further offshore, permitting a modicum of increased coverage of bottom water temperatures conducive to Atlantic surfclams.

Comparison of the number of TMSs assigned to the four categories (no clams, ocean quahogs but no surfclams, surfclams but no ocean quahogs, both species present) using a Chi-square test for independence identified a barely significant difference ($P < 0.025$) driven primarily by the presence of an increased number of uninhabitable TMSs in the DOPPIO dataset (Table 2.5), also a product of a slight offshore shift in bottom water temperatures between the two hydrodynamic realizations. The results show that the two hydrodynamic models differ in the location of cold-water habitat, such that the

Curchitser model produces a larger region occupiable by ocean quahogs, a similar region but more offshore occupiable by Atlantic surfclams, but a lesser region inshore where neither species would be found. The similar biomasses for Atlantic surfclams between the two hydrodynamically-determined temperature fields is due to the similar areal extent of temperature conditions conducive to Atlantic surfclams, this region simply being translated slightly inshore/offshore by the two hydrodynamic simulations. Collectively these comparisons show that the modeled Atlantic surfclam distributions and stock biomasses for the 2016-2019 period provide similar results, thereby supporting the conclusion that the Curchitser model provides seasonal bottom water temperatures that can be used to develop realistic distributions of Atlantic surfclams and ocean quahogs.

2.4 RESULTS

2.4.1 Projected Atlantic surfclam and ocean quahog distributions from 2016-2095

Clam distributions for each of the nine cases defining 4-year time periods (Table 2.5) demonstrated statistically significant differences in their Atlantic surfclam biomasses and species distributional patterns across the period of interest, 2016-2095 (Fig. 2). All pairwise comparisons of the number of TMSs habitable by Atlantic surfclams and ocean quahogs were significantly different (Table 2.6), as were all pairwise comparisons between cases for Atlantic surfclam biomass (LSmeans: all $P < 0.0001$). The clam habitat values show a gradual 88% increase in total surfclam habitat area, an increase from 43,156 km² in 2016-2019 to 81,012 km² in 2092-2095, with a simultaneous 57% decrease in total ocean quahog habitat, a decrease from 73,245 km² in 2016-2019 to 31,697 km² in 2092-2095 (Fig. 3, Table 2.5). The number of TMSs assigned with optimal temperatures for both species – the ecotone habitat value 4 – is altered significantly between cases

2016-2019 and 2052-2055 (Fig 3, Table 2.5) where the number of TMSs along the offshore and inshore boundaries of the cold-water habitat exploitable by both species gradually increase. Subsequently the ecotone expands by the steady erosion of the core of the Cold Pool through 2095 (Fig. 2).

The reduction in the total area of the cold-water habitat is a dominant feature of the simulations and is best tracked by the reduction in habitat 2, only ocean quahogs. A dramatic shrinkage of this habitat occurs between the 2040s and the 2050s and the habitat is effectively gone by the 2070s (Fig. 2, Table 2.5). Another dominant habitat transition is an increase in habitat 1, no clams, beginning in the 2040s and accelerating in the 2070s (Table 2.5). This region expands across the shelf, principally from the south and inshore off Delmarva and less so off New Jersey, while also expanding atop Georges Bank. On the other hand, the areal coverage of habitat 3, only surfclams, is stable from the 2030s through the 2080s as the cool temperate zone translates across the shelf following the recession of the inshore boundary of the cold-water habitat and also expanding along the offshore region of the continental shelf as erosion of the cold-water habitat also accelerates along the shelf edge.

2.4.2 Projected whole-stock biomass of Atlantic surfclams from 2016-2095

The Atlantic surfclam whole-stock biomass shows an increasing trend over the 79-year time-series (Fig. 4a), with the average whole-stock biomass of 1.386 MMT. Both case and simulation year differed significantly over the 79-year time-series, with all pairwise comparisons between cases producing statistically significant differences based on the post-hoc LSmeans test. Similarly, fishable biomass demonstrates an increasing

trend over the 79-year time series (Fig. 4b), with an average biomass of 1.021 MMT. Post-hoc pairwise comparisons provided equivalent results.

Although each simulation year within the 50-year time series produced a different biomass, these values fluctuated about a carrying capacity based on yearly variations in recruitment rate and significant differences arise transiently due to the timing of unusual recruitment events generated by the negative binomial draw and the lifespan of the clam which retains the signal introduced by a large cohort for decadal time periods. As biomass varied yearly, year was included as a main effect in most analyses; however, results were rarely significant so that, although the year effect is retained and reported in some subsequent analyses, it will not be further analyzed.

Years 2026-2029 (case 2629) demonstrated the lowest Atlantic surfclam biomass across all case scenarios (Fig. 4, Table 2.8), with an average whole stock biomass of 0.90 MMT, and an average fishable biomass of 0.644 MMT, whereas years 2072-2075 displayed the highest biomass, with an average whole stock biomass of 1.79 MMT, and an average fishable biomass of 1.34 MMT (Fig. 4, Table 2.8). The nadir in 2629 is well below present-day (2016-2019) values, but consistent with more recent survey data recording a continuing decline in Atlantic surfclam biomass (NEFSC, 2022). The largest shift in biomass occurred between cases 4649 and 7275, during which biomass increased by a factor of approximately 5 (Fig. 4, Table 2.8), and then remained relatively stable through 9295.

2.4.3 Projected regional biomass of Atlantic surfclams from 2016-2095

Atlantic surfclam biomass varied regionally, with biomass trending higher northward, averaged over the entire timeseries (Fig. 6, 7, Table 2.9); however Atlantic

surfclam biomass between the five regions and amongst the nine cases routinely differed significantly (ANOVA, $P < 0.0001$), indicating that the trends in biomass over time diverged significantly among the regions within the cases and among the cases within the regions. Post-hoc LSmeans tests indicated that most pairwise comparisons between cases within regions differed significantly ($P < 0.0001$) and most pairwise comparisons between regions within cases differed significantly ($P < 0.0001$) (Table 2.10).

In New Jersey, Long Island, and southern New England, biomass increased over the decades simulated from 2016 to 2095, whereas biomass declined off Delmarva and increased transiently before decreasing again on Georges Bank (Fig. 6). Across the five regions, case 5255 proved to be a critical transition period in biomass, where New Jersey, Long Island, and southern New England saw a significant increase in biomass (Fig. 6). This pattern was also evident in the transition from years 2046-2049 to years 2052-2055 which showed a significant increase in the habitable region for surfclams across New Jersey, Long Island, and southern New England, much of which is retained within an expanding ecotone with ocean quahogs (Fig 2, Table 2.5). Conversely, the habitable region for surfclams on Georges Bank rose initially, for the same reason, but by 2052-2055 had begun to decline (case 5255, Fig. 6), a trend that can also be observed in Fig. 2, during which the uninhabitable region at the top of Georges Bank began to expand (Table 2.5). Delmarva biomass declined over time, with the primary period of decline beginning later in the transition period, between cases 6265 to 7275 (Fig. 6), during which the uninhabitable region for surfclams expanded across the Delmarva continental shelf (Fig. 2; Table 2.6).

Comparing regions, Long Island displayed the highest variability across cases due to a dramatic increase in biomass in the 2070s (Fig. 6), whereas Delmarva showed the least variability in biomass over time (Fig. 6). Delmarva and Long Island had the lowest average biomass distribution compared to all regions, 0.178 MMT and 0.207 MMT, respectively, whereas southern New England and Georges Bank had the highest average biomass distribution, 0.370 MMT and 0.371 MMT, respectively (Table 2.8). Long Island provided the lowest biomass distribution among the five regions between cases 1619 and 4649, but gradually became one of the top contributors of regional biomass by case 9295 (Fig. 6) (Appendix A). This transition in Long Island biomass is seen in Fig. 2, where total surfclam biomass increased from years 2052 to 2095 due to the expansion of surfclams into ocean quahog habitat (Fig. 2, Table 2.5). Conversely, the first six decades of case scenarios consistently showed Georges Bank to have the highest biomass distributions compared to other regions, but by case 7275, biomass began falling behind all regional biomasses but Delmarva (Fig. 6, Appendix A) as the uninhabitable region atop the bank began to expand (Fig. 2, Table 2.5).

Relative trends in regional biomass between cases displayed a more consistent pattern (Fig. 7). Generally, Long Island retained the lowest biomass level and Georges Bank the highest prior to 2050. This relationship changed as Delmarva fell consistently behind and southern New England rose to prominence. Over the post-2050 period, Long Island biomass rose to compete with southern New England, while biomass on Georges Bank waned (Fig. 7). Over the entirety of the 2016-2095 time series, New Jersey retained a relatively consistent ranking of 3 or 4 amongst the 5 regions for highest biomass (Fig. 7).

Overall, the simulations illustrate the gradual geographical shift in Atlantic surfclam distribution throughout the MAB over the 2016-2019 to 2092-2095 period, wherein the species' range moves northward and offshore, with the core of the range shifting toward the middle of the MAB off the mid-to-northern coast of New Jersey and into southern New England off of Long Island (Fig. 2). The Atlantic surfclam range shifts westward and offshore in regions of Georges Bank and southern New England as surfclams recede from the eastern side of Georges Bank to the western side of Georges Bank and into the offshore of southern New England (Fig. 2). In addition, in the later years of the simulations, the range of the Atlantic surfclam also wraps around the receding cold-water habitat and begins to build onshore from the outer continental shelf inwards, with the most dramatic examples being the far offshore off New Jersey and Long Island. Ultimately, the final stronghold of the cold-water habitat, central Long Island, falls into the temperature range of the ecotone occupied by both species (Fig. 2).

2.5 DISCUSSION

2.5.1 Model limitations

The simulated range of Atlantic surfclams within the TMSs of the MAB domain is dictated by the mortality rates assigned to each TMS and the random negative binomial draw generating the recruitment patterns across the shelf, mimicking the natural patchy distribution of the species. These generate a range of outcomes amongst the 200 simulations within each case. The TMSs with mortality rates defining surfclam presence are determined by the temperature constraints assigned to each decadal case scenario, based on bottom water temperatures predicted by the hydrodynamic model, and which state that a TMS is deemed habitable by Atlantic surfclams only if summer average

bottom temperatures stayed between 18.5°C and 11.5°C, average Fall bottom temperatures do not drop below 12°C, and average spring bottom temperatures do not drop below 7.5°C. Similar, but simpler, constraints dictate the presence of ocean quahogs in the MAB domain such that a TMS cannot have an average summer temperature over 13.5°C.

In the natural environment, many biological habitat characteristics provide additional sources of limitation on species range that are not considered within the SEFES model. One such parameter is the food supply available for the clam species. SEFES assumes that clam distribution on the shelf is independent of depth, and therefore does not consider the potential for insufficient food at deeper depths, although a depth-dependent gradient in the amount of primary production reaching the bottom over the continental shelf is inconsistent with some reported cross-shelf biomass trends (Rowe et al., 1982, Aller et al., 2002) though consistent with some cross-shelf gradients in primary production (Yoder et al., 2002; Hofmann et al., 2008). Cross-shelf variability in food concentration, with lower densities expected as distance increases offshore, has been suggested to be a factor in declining surfclam health (Marzec et al., (2010) and an important contributor to observed changes in growth rates in ocean quahogs (LeClaire et al. 2023) and variations in surfclam size (Munroe et al., 2013). The uncertainty in the importance of variation in food supply is compounded by the limited information available concerning the influence of warming temperatures in the northwest Atlantic on primary production (Friedland et al., 2019). Consequently, SEFES simulations remain agnostic on the question of decadal and geographic variations in food supply.

Simulations suggest a substantial offshore occupation by Atlantic surfclams over the coming decades. SEFES simulations do not include a direct influence of depth in determining range boundaries as available evidence indicates that the distribution of Atlantic surfclams and ocean quahogs are not directly influenced by depth. Ocean quahog presence is associated with the presence of the Cold Pool, and as climate phenomena have influenced the Cold Pool's hydrogeography through the years of warming and cooling, dead ocean quahog shells can serve as indicators of not only temperature patterns, but also as indicators of past geographic distributions across the shelf (Powell et al., 2020b; LeClaire et al. 2022). Specifically, LeClaire et al. (2022) reported radiocarbon-dated ocean quahog shells back to Neoglacial times inshore of the present-day range and extension of the species' range into the shallow subtidal in northern climes is well documented (Fogarty, 1981; Zettler et al., 2001; Strahl et al., 2011). Within the MAB, ocean quahogs already are found near the shelf edge. Thus, depth, per se, is not a constraint for ocean quahogs. The distribution of Atlantic surfclams is known to extend into the shallow subtidal within the MAB (Ambrose et al., 1980; Chintala and Grassle, 2001; NEFSC, 2017a). SEFES simulations, however, posit surfclams to be abundant in future decades at depths much deeper than observed present-day. Evidence that Atlantic surfclams persisted at such depths in the past is provided by three surfclam shells collected off southern New Jersey during a survey reported by Stromp et al. (2023b) and radiocarbon-dated as described by LeClaire et al. (2022) to the Medieval Warm Period (Andres and Peltier, 2016). Longitudes and latitudes of collection, radiocarbon dates, and collection depths for these shells are: -74.075, 38.225, 917 cal BP, 62.8 m; -74.170, 38.25, 1,032 cal BP, 64.0 m; and -74.192, 38.825, 1042 cal BP, 36.6 m. During this time,

temperatures in the North Atlantic were likely to have been at least as warm as today, as inferred from Cronin et al. (2010), Sicre et al. (2021) and LeClaire et al. (2022). Water depths were near present day at this time (Engelhart et al., 2011), so recorded collection depths are near life depths for these individuals. Two of these specimens came from depths distinctly deeper than the present-day offshore range of the Atlantic surfclam (Stromp et al., 2023b). For this reason, the simulated offshore movement of Atlantic surfclams predicted in SEFES simulations is proposed to be within physiological tolerances for the species.

In addition to depth, another non-correlative pattern associated with variable surfclam distribution is benthic substrate type. Surfclams are permitted to exist wherever temperatures are favorable to their survival. The existence of unsuitable benthic substrate in this model has potentially permitted assignment of clam abundance to regions where their presence would otherwise be limited by substrate type, such as Georges Bank, where boulder fields and cobble-rich substrates would limit, but not exclude, their presence (Powell et al., 2017; 2019), thus leading to an overestimate of surfclam density in this region. Though substrate type is an important ecological feature for benthic macrofauna, surfclams inhabit a wide range of bottom types within the MAB from sands to muddy sands to sandy muds (Powell et al, 2020). Pure muds potentially excluding the species are not geographically extensive on the continental shelf in the MAB, an exception being the New England Mud Patch (Dalyander et al., 2013; Goff, 2019). Anecdotal information from the Atlantic surfclam fishery suggests that surfclams are frequently found at the apex of topographic highs or on the downslope. Bearing this in mind, data for bottom topography was derived from a 15-arc second data set from NOAA

(Tozer et al., 2019), sufficiently detailed for this analysis. Using these data, the variability in depth within each 10-minute square was examined for statistical significance with surfclam presence, but no significant trends were found.

Zhang et al. (2015, 2016) describes an average down-coast trend in larval transport in the MAB that varies seasonally inshore and offshore as determined by regional hydrodynamics, though no attempt was made to integrate these trends into the Atlantic surfclam population dynamics model; rather parameterization of recruitment relied on the evaluation by Timbs et al (2018) that recruitment potential is high throughout most of the MAB. Consequent of the wide range of habitable sediment types occupied and the limited coverage of habitat unavailable for occupation, surfclam recruitment and mortality were specified, therefore, using random processes for recruitment rates and, within temperature-dependent habitat regions, mortality rates in simulations reported herein.

Although the relationship of Atlantic surfclam growth with temperature on a decadal scale is well described from latitudinally defined data (Munroe et al., 2016), the cross-shelf variability in growth is not well described and the growth curves, determined from animals of differing age and therefore of differing temperature history, restrict a straightforward implementation of variability in growth within the biological domain of the model. As a consequence, a standard growth curve for the entire stock is implemented in SEFES, discounting the potential local variability in cross-shelf or latitudinal impacts on the growth curves. This includes the absence of variability that may occur in surfclam growth as they move into deeper offshore habitats, where colder temperatures and lower phytoplankton concentration may persist. Recent evidence (e.g., Powell et al., 2020a)

suggests that the addition of such details may be feasible as ongoing shifts in range offshore are increasingly monitored.

Finally, the case histories simulated, each defined by average temperature conditions for a 4-year period, are not influenced by the size-frequency and abundance from the immediately preceding time nor do they provide information to the immediately succeeding time, even though the lifespan of even the shorter-lived species, the Atlantic surfclam, easily transcends the decadal steps between simulations. Each simulation is based on an assumed long-term, greater than generational, time period of constant environmental conditions. Interpretation of geographic patterns thus resolved must be interpreted within the context of this limitation.

2.5.2 Key findings from climate-forced simulations

The nine climate-forced simulations identify an offshore and northern movement of Atlantic surfclams and a slower recession of ocean quahogs over a 79-year period of increasingly warming temperatures on the seafloor within the MAB. The interaction between the projected bottom temperatures and the physiological thermal rules described for each clam species anticipate an increasingly suitable habitat for the Atlantic surfclam, with a simultaneous, but not equivalent, shrinkage of ocean quahog habitat. Atlantic surfclam biomass increases with rising temperatures over the progression of the time-series, dictated by a gradual increase in surfclam habitat occupied exclusively by this species (habitat 3) and more importantly jointly occupied by this species and ocean quahogs as the ecotone expands (habitat 4) (Table 2.6, Fig. 2), an expansion not balanced by the retraction of the surfclam from the southern inshore portion of its range.

This ecological shift in species' habitats manifest severe implications concerning the evolution of the continental shelf's oceanography. Both species respond to a gradual erosion of the Cold Pool from the offshore, the inshore, and the south, a process already well documented using Cold Pool indices and hydrodynamic modelling. The response to the erosion of the Cold Pool extends outside the temperature boundaries typically defining this hydrogeographic feature. The ongoing erosion of the cold-water habitat to the south and inshore, gradually commencing also at the offshore boundary, effectively alters the structure of the benthic communities in the MAB by creating new thermal habitat warm enough for the Atlantic surfclam yet remaining cool enough for the ocean quahog, thus generating an intermediate ecotone of vast extent undocumented in years prior to the 2010s decade. LeClaire et al. (2023) illustrate the progression of the deterioration of the inshore boundary of the Cold Pool since the end of the Little Ice Age. Implications of this continuing gradual decline in the footprint of the Cold Pool documented in recent times by Friedland et al. (2020a, 2022) are hereby extended into the future as an increasingly dominant cold-temperate MAB displaces boreal waters leading to the thermal habitat relocation of the two clam species.

Regional patterns of significantly different biomass distributions are clearly linked to the differential levels of warming along the MAB shelf (Forsyth et al., 2015; Kavanaugh et al., 2017; Lentz, 2017; Chen et al., 2018a; Friedland et al., 2020b) relative to the thermal tolerances of the species. The southernmost region, Delmarva, becomes increasingly uninhabitable for either clam species. Expansion of this habitat type could be due to increasing incursion of warmer waters from the south, a region of particular sensitivity to heat waves due to the already warm temperatures, and the continuing

erosion of the southern end of the Cold Pool limiting cold-water habitat in the region (Friedland et al., 2020a, 2022). Historically for surfclams, the Delmarva region, once a prime producer for the fishery (Ropes, 1982), has been characterized by decreasing landings, smaller shell lengths, and higher mortality rates (Weinberg et al, 2002; Weinberg 2005; Munroe et al., 2013; Narvaez et al., 2015; Diaz et al., 2024), all indicating that this southernmost region has become increasingly sensitive to warming bottom temperatures (for a possible exception, see Wisner et al., 2023). Simulations of future conditions show continuation of this already well-documented habitat progression, as seen in Figures 2 and 6. Unlike the more northern regions, Delmarva is also characterized by the gradual disappearance of the ecotone as ocean quahog habitat slowly dissipates, continuing a recession since the Little Ice Age, well-documented by LeClaire et al (2023).

In offshore New Jersey, simulations identify a continuing increase in surfclam biomass due to the predicted offshore increase in surfclam habitat by 2052-2055 (Fig.5). This habitat expansion, however, becomes equally balanced by the inshore recession of surfclam habitat by years 2072-2075 (Fig. 2), thus limiting biomass in the region to less than 0.4 MMT (Fig. 6). The expansion of surfclams beyond the offshore boundary of the Cold Pool, clearly present by 2052 and expanding subsequently, co-occurs with the near absence of habitat solely occupied by ocean quahogs by 2052-2055 and the total loss by 2072-2075. Consequently, expansion of surfclam habitat includes the expansion of the ecotone between the two species all the way across the outer shelf over much of the region south of Hudson Canyon by 2052-2055.

Long Island and southern New England regions encompass the heart of the Cold Pool with habitat changes dictated by the multi-decadal trends in its seasonal evolution and breakdown (Fig. 2). Long Island regularly holds the coldest waters of the Cold Pool, due to local cooling over the shelf during the winter and reduced mixing in comparison to Georges Bank (Lentz, 2017; Chen et al., 2018b). Overall, the inshore extent of the cold-water influence across the MAB in these simulations was characterized by a gradual recession of the Cold Pool's inshore boundary, a trend well-documented by the expansion of the ecotone and becoming a dominant feature by 2052-2055 (Fig. 2). As a consequence, Long Island showed the highest amount of surfclam biomass variability compared to the rest of the MAB (Fig.9) due to expansion of the ecotone with the ocean quahog across much of the continental shelf in an area that, prior to 2026-2029, was characterized by limited surfclam biomass. The expansion of surfclam habitat in the ecotone after 2052-2055 culminates by 2092-2095 in the loss of habitat occupied exclusively by the ocean quahog. Thus, by the end of the 21st century, Long Island retains the last vestiges of the vast ocean quahog presence of the first half of the century.

Surfclam landings in southern New England historically have come from inshore waters east and south of Nantucket. Modeled biomasses are somewhat inflated as simulations do not exclude from available habitat the New England Mud Patch, which historically has been characterized by low densities of clams. On the other hand, the region simulated includes the inshore region off Nantucket, historically not included in the federal survey (Jacobson and Hennen, 2019; Powell et al., 2020a), and so biomass estimates are likely biased relative to survey datasets (e.g., NEFSC 2017a). Southern New England, initially characterized by relatively low biomass, performed consistently

throughout the second half of the modeled timeline, typically reaching the highest or the second highest biomass distribution across all region and cases post-2055 (Fig. 6).

Biomass did not continue to increase thereafter, however, due to inshore warming south of Cape Cod, limiting surfclam habitat (Fig. 2). Additionally, simulations show an increased inshore recession in viable surfclam habitat from 2052 through 2095 (Fig. 2).

The northeastern continental shelf, including southern New England, has been ranked in the top 1% of world oceans in the rate of warming (Mills et al., 2013; Pershing et al., 2015), with important habitat implications for the commercially valuable American lobster (Rheuban et al., 2017), the blue mussel (Powell et al., 2019), and the surfclam (Powell et al., 2020a). The rapid retreat of the cold-water habitat off Long Island and southern New England and the disappearance of the ecotone by 2092-2095 suggest the loss of a vibrant ocean quahog fishery in this region within this century.

Georges Bank presents an interesting comparison to the other four regions. This bank has an unusual thermal history since the Little Ice Age, based on ocean quahog growth rates (Hemeon et al., 2023; Sower et al., 2023) wherein it was warm relative to parts west early in the 1800s, but has not warmed as much over the succeeding years in comparison to offshore New Jersey and Long Island. Georges Bank contributed a sizable portion of regional biomass to the MAB stock early in the period of simulation and significant surfclam landings during the second half of the 2010s (DeGrasse et al., 2014, NEFSC, 2017a), but a turning point in biomass trend occurs in years 2046-2049 when biomass starts to wane (Fig. 6). Recent assessment results suggest that this process may already be ongoing (NEFSC, 2022). In the transition between the late 2040s and early 2050s, a seemingly noteworthy time period within the study's simulated time series,

southern New England starts to overtake Georges Bank in biomass (Fig. 6). A noted offshore trend in surfclam occupation recorded for Georges Bank in the 2010s (Timbs et al., 2019) presages a continued offshore trend predicted to occur in subsequent years (Fig. 2). Temperatures atop Georges Bank become too warm for surfclams by 2052-2055, and this trend expands down-bank, thereby causing a decrease in surfclam biomass (Fig. 6). This is also seen in the species habitat values in Fig. 2, where Georges Bank gradually starts to turn from overwhelmingly surfclam territory, years 2016-2019 through 2046-2049, to a slowly expanding patch of unsuitable habitat atop the bank through the end of the century, and a relatively narrow ecotone trending offshore and eventually shrinking to meager areal coverage by 2072-2075 and disappearing completely by 2092-2095.

The benthic warming of Georges bank has been documented in several studies (Lee & Brink, 2010; Gawarkiewicz et al., 2012; Kavanaugh et al., 2017), which determined that destabilization and shifts in the Gulf Stream's northern wall could be significantly obstructing Labrador Current flow around the southern edge of the bank and thus preventing transmission of cold waters to these regions, an event hypothesized to be linked to the 20th century slowdown in the AMOC (Gawarkiewicz et al., 2012; Saba et al., 2015; Andres, 2016; Brickman et al., 2018; Gonçalves Neto et al., 2021; Seidov et al., 2021). Furthermore, Georges Bank has been cited to warm faster compared to the southern MAB due to the seasonal degradation of the Cold Pool (Lentz, 2008; Lentz, 2017; Chen et al., 2018b), thereby exposing a potential poleward limit for species northern expansion toward cooler thermal refuge. One consequence is the expectation that Georges Bank is likely to cease contributing productively to the fishery by the end of the century.

2.5.3 Implications for future habitat scenarios

The expanding overlap in the cool-temperate and boreal thermal habitats within the MAB due to the continuing constriction of the Cold Pool over the 79-year time frame of the simulations prompts a further look at the developing ecotone between the ocean quahog and the Atlantic surfclam initially noted in the early 2010s and analyzed in detail by Stromp et al. (2023b). The overlap is not well predicted by the known thermal characteristics of their core habitats, likely due to the differential physiological and behavioral characteristics of the two species, specifically considering the behavioral repertoire of the two clam species is quite different (Ropes and Merrill, 1966; Taylor, 1976; Strahl et al., 2011; Morys et al., 2017). Although both are suspension-feeding bivalves that have potential to exploit the same food resource (Rosa et al., 2018; but see Comerford et al., 2020) leading to a competitive interaction, evidence for such has not yet been obtained. On the other hand, the burrowing ability of the ocean quahog permits their evasion from the highest summer and fall temperatures, thereby permitting them to exist in a different thermal regime than the surfclam during part of the year despite being present together in the same sedimentary habitat. LeClaire et al. (2024) argue that the differential rate of range shifting thereby created explains the expanding ecotone under a period of warming temperatures, in which the surfclam expands its range offshore on half-decadal time scales (e.g., Powell et al., 2020a) while the ocean quahogs inshore range regresses on, minimally, 20-year to half-century time scales. The result is the dramatic enlargement of the ecotone between the two species over the remainder of the 21st century, resulting “in its extremum” the region off Long Island where it is predicted to occupy the bulk of the continental shelf by the end of the century.

In largest measure, the evolving geographic footprints of the two species can be described as (1) an increasing area uninhabitable by both species inshore and on the top of Georges Bank, (2) a translation offshore of surfclam habitat, with little increase in total footprint inshore of the ecotone, (3) a dramatic expansion of the ecotone in which both species are found, and (4) the continuing restriction of habitat occupied solely by ocean quahogs. The offshore and poleward movement of the Atlantic surfclam as described here, clearly shows further disintegration of inshore surfclam habitat along the coast of Delmarva and New Jersey (Fig. 2), however, a recession of the species southern range boundary is not as clearly demonstrated. In fact, the southern range boundary of the species in the 2016-2019 simulation is still relatively intact by 2095, with the only movement being offshore into deeper, presumably cooler waters. The hydrogeographic layout of the MAB is unique in its thermal relationship with the Atlantic surfclam species range, where the extent and endurance of the cool waters epitomized by the Cold Pool facilitate species expansion following the recession of cold-water habitat both inshore and offshore (see Fig. 2 2052-2055, 2062-2065, 2082-2085).

What is unique to the simulations is the occupation of surfclams offshore of the cold-water habitat beginning between 2045-2049 and 2052-2055. A bimodal distribution of the species about a central colder-water mass has not been observed during the period of the federal survey beginning in the early 1980s, but is perhaps supported by the finding of surfclams on the outer shelf during the Medieval Warm Period. When the offshore waters warm due to increased mixing and erosion along the offshore boundary, the surfclam range is able to expand offshore and shoreward toward the center of the MAB, thereby compressing habitat occupied solely by ocean quahogs on all sides, as thermal

habitat becomes optimized for the Atlantic surfclam (see Fig. 2; 2072-2075, 2092-2095). The model depicts what could be for ocean quahogs stages 1 and 2 of what Bates et al. (2014) describe as the stages of geographic range contraction, and stages 2 and 3 of geographic range extension for Atlantic surfclams in the Mid-Atlantic Bight.

2.6 CONCLUSIONS

The geographic range shifts of the Atlantic surfclam have been documented extensively within the past two decades, with retrospective studies revealing the decline in their southern inshore population in the MAB to have begun in the 1970s (Hofmann et al., 2018) and a more comprehensive overview of the extent of historical geographic occupation presented by Powell et al. (2020b). Inshore recession of the surfclam range accelerated during the first of a sequence of heat waves coincident with the 2000 regime shift (Lucey and Nye, 2010) well documented in a number of studies at the time (Weinberg et al., 2002, 2005; Kim & Powell, 2004; Weinberg, 2005). Although by the mid-2000s, an expansion of the range of the surfclam offshore was noted (NEFSC, 2013; NEFSC, 2017a; Hofmann et al., 2018; Powell et al., 2020a), the dramatic development of the ecotonal boundary with the ocean quahog did not clearly manifest until the late 2010s (Stromp et al., 2023b). Model simulations show a continuing theme of offshore movement and colonization of Atlantic surfclams throughout the 79-year projection into the MAB region earlier occupied by a colder water mass containing at its core the Cold Pool, with populations rising in locations where historically it was too cold for establishment. Ocean quahogs are predicted to demonstrate an opposing, albeit slower, population decrease by at least 2062-2065 (Fig. 2), with clear contraction in the southern range boundary occurring by 2092-2095 (Fig. 2). Historical context for the projected shift

in ocean quahog distribution due to long-term climate trends are still being uncovered from carbon dating studies (LeClaire et al., 2022, 2024).

The simulations show that future Atlantic surfclam biomass and geographic distribution within the Mid-Atlantic Bight are likely to change dramatically based on future projected bottom water temperatures. Temperature is a critical niche dimension for the life history of marine organisms and a dominant determinant of provincial boundaries (Hutchins, 1947; Hale, 2010) and can subsequently cause variability in species biomass and habitat location based on shifts in thermal dependencies. Model projections anticipate a biogeographical shift over the northeast continental shelf, where two critical transition zones between thermal regimes will occur. One of these is the conversion of Virginian province habitat into one resembling the Carolinian province, therefore enabling the expansion of warm-temperate species northward in geographic distribution. This provincial boundary is anticipated to displace northward and offshore as a diagonal across the continental shelf. Atlantic surfclams can now be documented inhabiting the Acadian (boreal) province, but advance of this provincial boundary represents a complex movement inshore, offshore, northward, and westward depending on location due to the unstable presence of the Cold Pool. The geographic region occupied by the MAB Cold Pool, historically a primary boreal habitat for the ocean quahog, is projected to be colonized by the Atlantic surfclam over much of its present extent in the projected time series by 2052-2055, and through its entirety by the end of the 21st century.

Documentation of range shifts, by observation or modeling, in the marine realm has become a focus of recent investigation (Beaugrand et al., 2002; Lucey and Nye, 2010; Coro et al., 2016; McHenry et al., 2019; Weinert et al., 2021). The expectation

from model projections in this study (e.g., Fig. 2) is that the MAB continental shelf community structure will support one of the greatest biotic reorganizations to be observed on the northeast continental shelf in the 21st century.

The changing benthic thermal regime over the NES prompts fisheries and general ecologists to consider what a geographically large ecotone will look like between these two species of clam. While no competitive interactions have been observed between the two species given the burrowing behavior of ocean quahogs, research into their growing co-inhabitation and what the natural state or capacity of this ecotone can support is important to understand the entirety of this shifting ecosystem. Of particular note is the influence of the many other species associated with the temperate-boreal boundary, for which little distributional data are available, and for which present information is effectively absent as to the rate of response and between-species interaction (e.g., Merrill and Ropes, 1969; Pratt et al., 1973; Franz and Merrill, 1980; Theroux and Wigley, 1983; Friedland et al., 2021).

Simulations at approximately decadal intervals, a much lesser time interval compared to the lifespan of the Atlantic surfclam, suggest that the Atlantic surfclam stock is never at equilibrium, presenting serious implications for estimating Atlantic surfclam carrying capacity, a metric important for establishing reference points for fisheries management (Ricker, 1975; Hilborn and Walters, 1992; Martell et al., 2008). Most fisheries assessment models assume that population biomass is constantly in equilibrium, or reasonably stable, to calculate a stock status and maximum sustainable yield (MSY) reference points (Brander, 2010; Pinsky and Byler, 2015). For surfclams in the MAB, the first stock survey was established in the early 1980s, around the time that the

northwestern Atlantic region was coming out of a relatively long-term cooling period that commenced in the early 1950s (Drinkwater, 1996; Nixon et al., 2004; Free et al., 2019). A reasonable surmise is that the sharper boundary between surfclams and ocean quahogs at the time was due to the regression inshore of the surfclam consequent of these cooling temperatures and a more modest expansion inshore of the ocean quahog. This inference would be consistent with the two species' capabilities to modify range boundaries. Since then, populations have been relatively stable through the 2000s, permitting a relatively stable estimate of carrying capacity and the application of equilibrium-based fisheries models for determination of fisheries reference points and allowable quotas. Today and into the future, a reasonable conclusion from the results of simulations presented here is that species abundance and distribution will vary rapidly according to decadal shifts in climate in the future.

At the same time, remaining unchanged, is the system in which federal fisheries management relies on reference points derived from estimates of carrying capacity, derived by assuming a stable state of environmental conditions. For Atlantic surfclams, simulations project dramatic changes in carrying capacity of the Atlantic surfclam over the next three-quarters of a century, with biomass increasing by nearly a factor of 2 and with significant implications for most fisheries models that are based on that metric as an equilibrium condition. Simulations presented here suggest the need for minimally decadal adjustments in such basic management requirements as the development of MSY reference points and modifications to stock survey designs to maintain sampling sufficiency in the face of continually changing geographic distributions and carrying capacities; this being a necessary step in getting ahead of the climate crisis that is

currently outpacing management actions and is now and will continue to bring forth a substantive reorganization of the MAB benthos.

2.7 TABLES

Table 2.1 Ocean quahog biological habitat temperature rules in degrees Celsius (C°). Values are the averages of all appropriate TMSs, each value being the average over 3 months per season and 4 years (n = 12) for that TMS. Because the analysis focused on the region of overlap between Atlantic surfclams and ocean quahogs, the values should not be interpreted to specify the complete temperature range of the species. See the text for more details.

Variable	Mean	Lower Quartile	Upper Quartile	Minimum	Maximum	Median	N
Summer	12.1	11.5	12.6	10.8	13.3	12.2	57
Winter	8.4	7.6	9.2	6.3	9.6	8.7	57
Spring	7.9	7.5	8.3	7.0	9.1	7.8	57
Fall	13.3	12.9	13.9	11.3	14.3	13.6	57

Table 2.2 Atlantic surfclam biological habitat temperature rules. Values are the averages of all appropriate TMSs, each value being the average over 3 months per season and 4 years (n = 12) for that TMS. As the analysis focused on the entire region of occupation for the Atlantic surfclams, the values can be interpreted to represent the complete temperature range of the species. See the text for more details.

Variable	Mean	Lower Quartile	Upper Quartile	Minimum	Maximum	Median	N
Summer	15.1	13.8	16.7	11.5	18.4	15.4	162
Winter	7.0	6.2	8.0	4.1	9.9	6.6	162
Spring	8.6	8.0	9.0	7.5	10.9	8.5	162
Fall	13.5	12.7	14.2	12.0	15.4	13.6	162

Table 2.3 List of cases simulated within SEFES.

Case Names	Years Covered	Origin of Data
B1619	2016-2019	Federal survey
D1619	2016-2019	DOPPIO model
C1619	2016-2019	Curchitser model
2629	2026-2029	Curchitser model
3639	2036-2039	Curchitser model
4649	2046-2029	Curchitser model
5255	2052-2055	Curchitser model
6265	2062-2065	Curchitser model
7275	2072-2075	Curchitser model
8285	2082-2085	Curchitser model
9295	2092-2095	Curchitser model

Table 2.4 Wilcoxon Scores for Atlantic surfclam biomass between cases B1619 and D1619 (a) and cases D1619 and C1619 (b)

(a)

Case	N	Mean Biomass	p-value for Biomass	Mean Big Biomass	P-value for Big Biomass
D1619	50	0.949	<0.0001	0.682	<0.0001
B1619	50	0.870		0.632	

(b)

Case	N	Mean Biomass	p-value for Biomass	Mean Big Biomass	P-value for Big Biomass
D1619	50	0.949	<0.0001	0.682	<0.0001
C1619	50	1.030		0.743	

Table 2.5 Chi-square matrix of TMS counts for each habitat type throughout the 9 case scenarios and the Doppio simulation; Neither Species Present; Only Ocean Quahogs; Only Atlantic Surfclams; Both Species Present. Total number of TMS counts with ocean quahogs and total number of TMS counts with Atlantic surfclams are also described.

Case	Habitat Types					
	Neither Species Present	Only Ocean Quahogs	Only Atlantic Surfclams	Both Species Present	Total Ocean Quahog	Total Atlantic Surfclam
D1619	151	194	125	36	230	161
1619	115	228	115	48	276	163
2629	106	254	112	34	288	146
3639	113	224	125	44	268	169
4649	129	172	140	65	237	205
5255	134	95	156	121	216	277
6265	132	130	155	89	219	244
7275	168	26	177	135	161	312
8285	172	56	161	117	173	278
9295	178	22	209	97	119	306

Table 2.6 Chi-square contrasts between case-specific habitat TMS counts (Table 2.5). Asterisks denote P-levels between total habitat TMS counts per case scenario; “****” indicates a P-value of $P^{****} \leq 0.0001$, “***” indicates a P-value of $0.0001 < P^{***} \leq 0.001$, “**” indicates a P-value of $0.001 < P^{**} \leq 0.025$.

Total Habitat TMS Count Contrasts								
C1619	****	****	*	**	**	**	**	**
2629		**	**	**	**	**	**	**
3639			*	**	**	**	**	**
4649				**	*	**	**	**
5255					*	*	*	**
6265						**	**	**
7275							*	*
8285								**
	2629	3639	4649	5255	6265	7275	8285	9295

Table 2.7 ANOVA results for the effect of Simulation Year on Case.

Case	Source of Effect	Whole Stock Pr > F	Fishable Pr > F
C1619	Year	0.4250	0.2992
2629	Year	<.0001	0.0002
3639	Year	0.0827	0.1424
4649	Year	0.1084	0.0742
5255	Year	0.7259	0.8792
6265	Year	0.1248	0.1378
7275	Year	0.5418	0.4005
8285	Year	0.5930	0.5667
9295	Year	0.6488	0.6707

Table 2.8 Average whole stock biomass and fishable biomass per case (MMT).

Case	Avg. Whole Stock Biomass (MMT)	Avg. Fishable Biomass (MMT)
C1619	1.03	0.743
2629	0.90	0.644
3639	1.04	0.752
4649	1.25	0.914
5255	1.63	1.21
6265	1.45	1.06
7275	1.79	1.34
8285	1.62	1.20
9295	1.76	1.31

Table 2.9 Average regional whole stock and fishable biomass in MMT.

Region	Whole Stock (MMT)	Fishable stock (MMT)
1	0.178	0.130
2	0.267	0.198
3	0.207	0.148
4	0.370	0.271
5	0.371	0.273

Table 2.10 Least squares means post-hoc analysis on regional Atlantic surfclam biomass significance between case scenarios per region. Asterisks denote significance levels between case biomass values per region; “****” indicates a P-value of $P^{****} \leq 0.0001$, “***” indicates a P-value of $0.0001 < P^{**} \leq 0.001$, and “*” indicates a P-value of $0.001 < P^* \leq 0.01$, and “NS” indicates no significant difference.

Region 1								
C1619	***	***	***	*	***	***	***	***
2629		***	***	***	***	***	***	***
3639			*	***	***	***	***	***
4649				***	***	***	***	***
5255					***	***	***	***
6265						***	***	***
7275							***	***
8285								NS
	2629	3639	4649	5255	6265	7275	8285	9295

Region 2								
C1619	NS	***	***	***	***	***	***	***
2629		***	***	***	***	***	***	***
3639			*	***	***	***	***	***
4649				***	***	***	***	***
5255					***	***	***	***
6265						***	***	***
7275							***	*
8285								**
	2629	3639	4649	5255	6265	7275	8285	9295

Region 3								
C1619	***	NS	***	***	***	***	***	***
2629		***	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					***	***	***	***
6265						***	***	***
7275							***	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Table 2.10 (continued).

Region 4								
C1619	***	***	***	***	***	***	***	***
2629		***	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					***	***	***	***
6265						***	***	***
7275							***	**
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Region 5								
C1619	***	***	***	***	***	NS	***	***
2629		***	***	***	***	***	***	***
3639			***	NS	NS	***	***	***
4649				***	***	***	***	***
5255					NS	***	***	***
6265						***	***	***
7275							***	*
8285								NS
	2629	3639	4649	5255	6265	7275	8285	9295

2.8 FIGURES

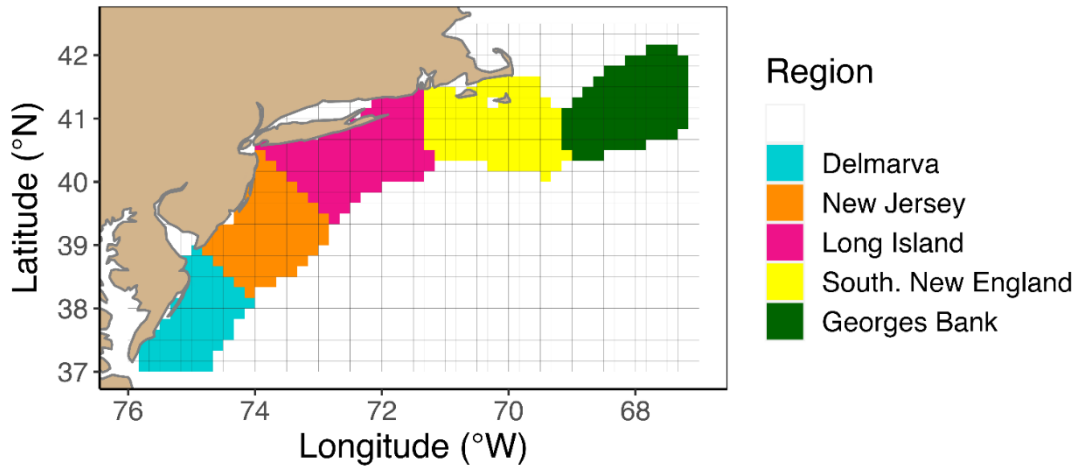


Figure 2.1 Regional map of the Mid-Atlantic Bight showing subregions historically used to evaluate the distributions of Atlantic surfclams and ocean quahogs; regions from southwest to northeast in the map are as follows: 1, Delmarva; 2, New Jersey; 3, Long Island, New York; 4, southern New England; 5, Georges Bank.

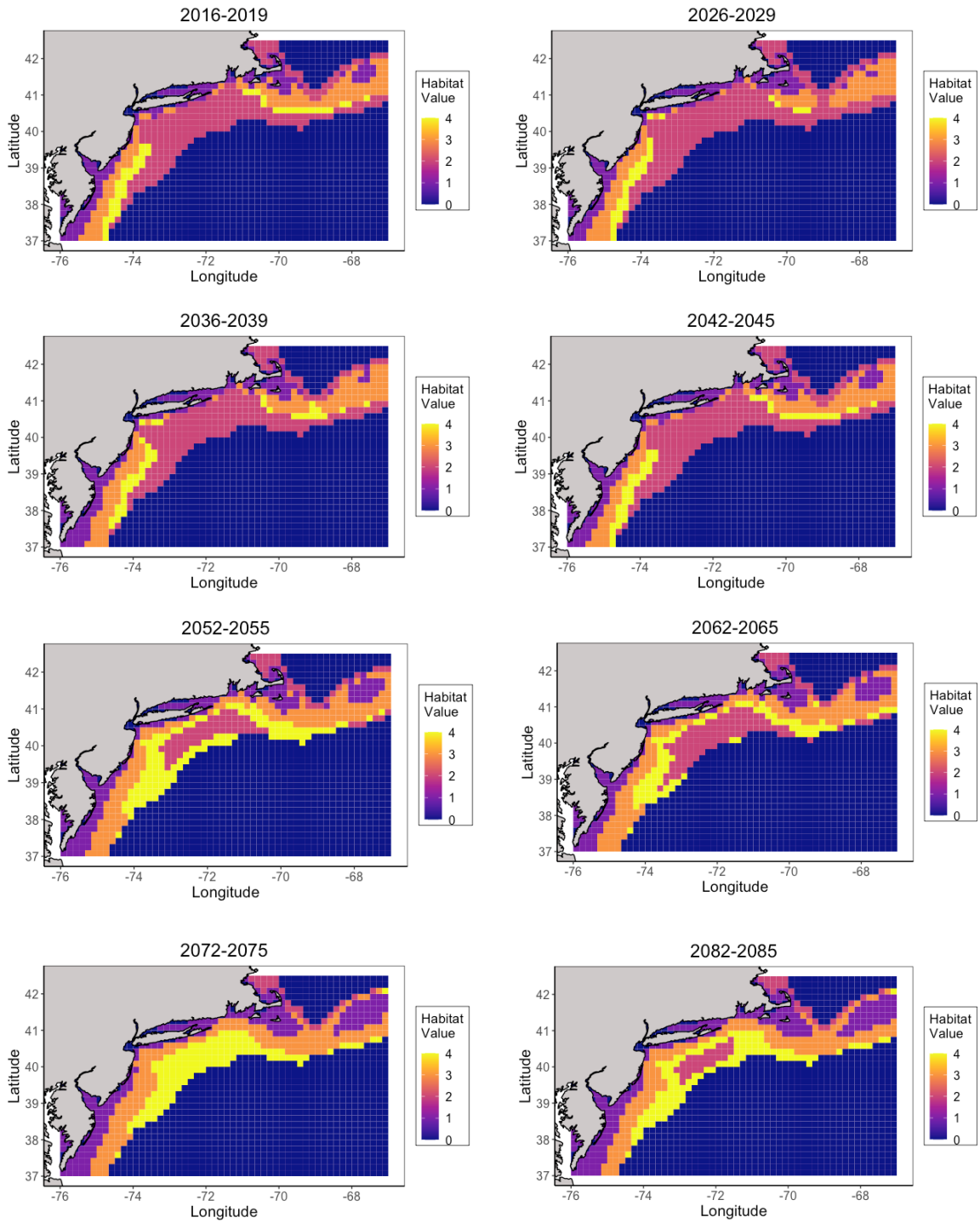


Figure 2.2 (continued).

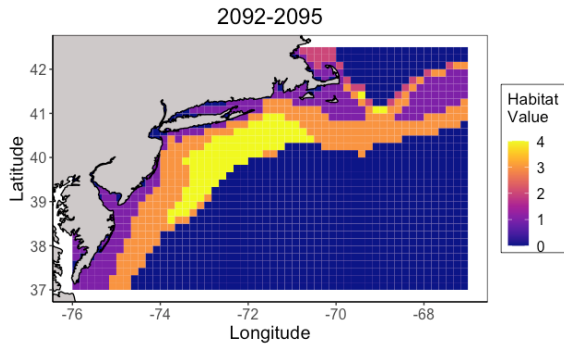


Figure 2.2 Distribution of Atlantic surfclams and ocean quahogs over the 2016-2095 time period. Habitat values are: 1, no ocean quahogs and no Atlantic surfclams (purple); 2, ocean quahogs, but no Atlantic surfclams (pink); 3, Atlantic surfclams, but no ocean quahogs (orange); 4, both ocean quahogs and Atlantic surfclams (yellow).

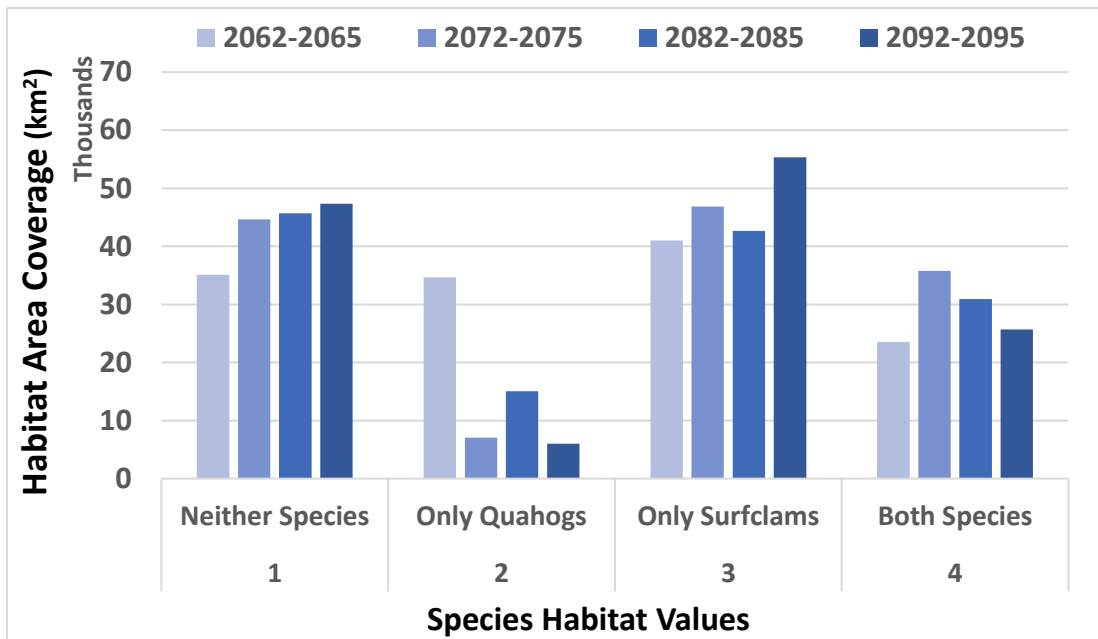
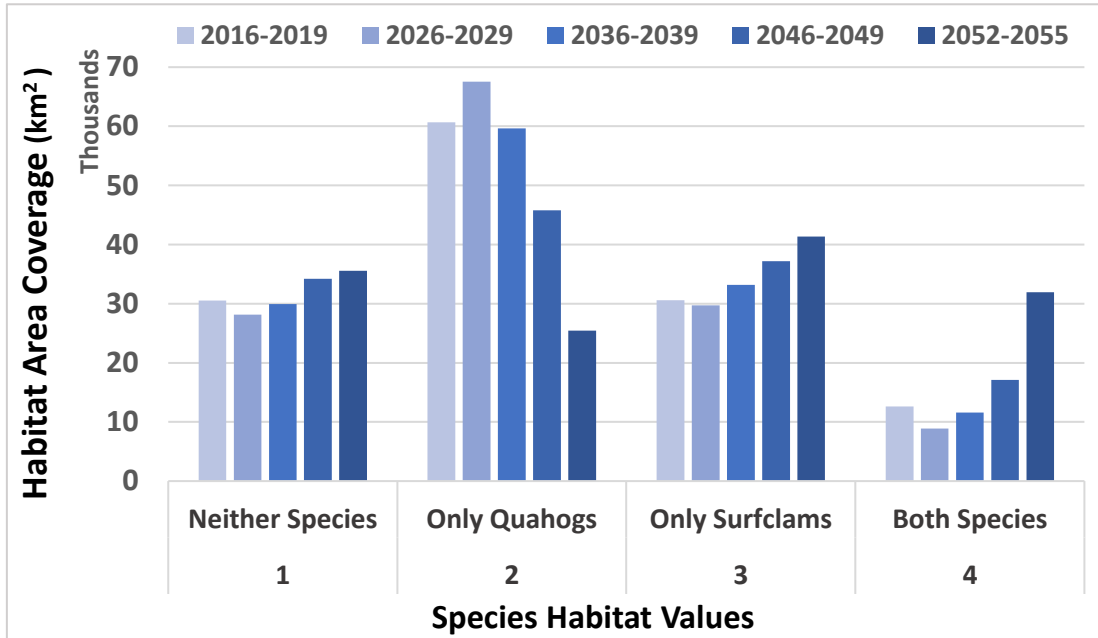
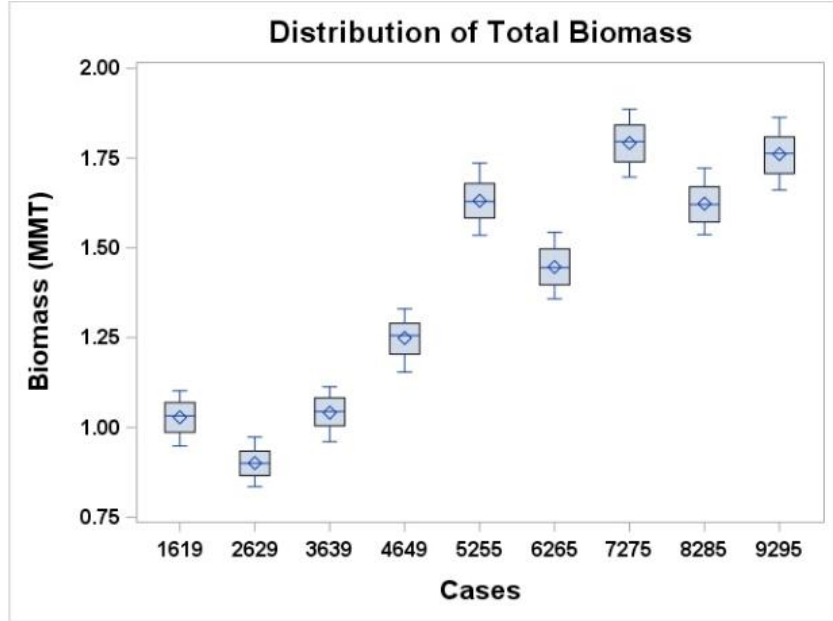


Figure 2.3 Atlantic surfclam and ocean quahog habitat area coverage (km² in thousands) in the Mid-Atlantic Bight from 2016-2095. Habitat types in Figure 2 and Table 2.5 correspond to species habitat values listed.

(a)



(b)

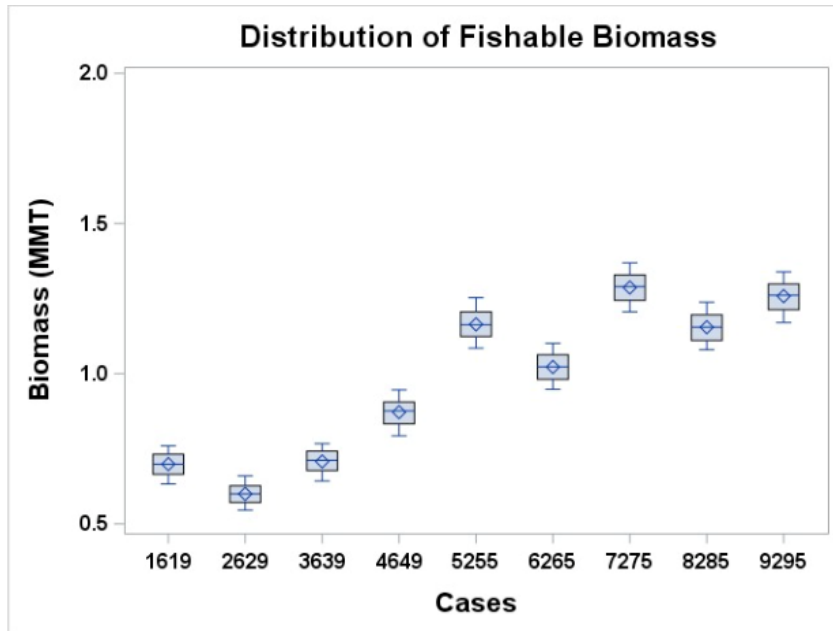


Figure 2.4 Distribution of total biomass (a) and of fishable biomass (b) (in Million Metric Tons) across case scenarios.

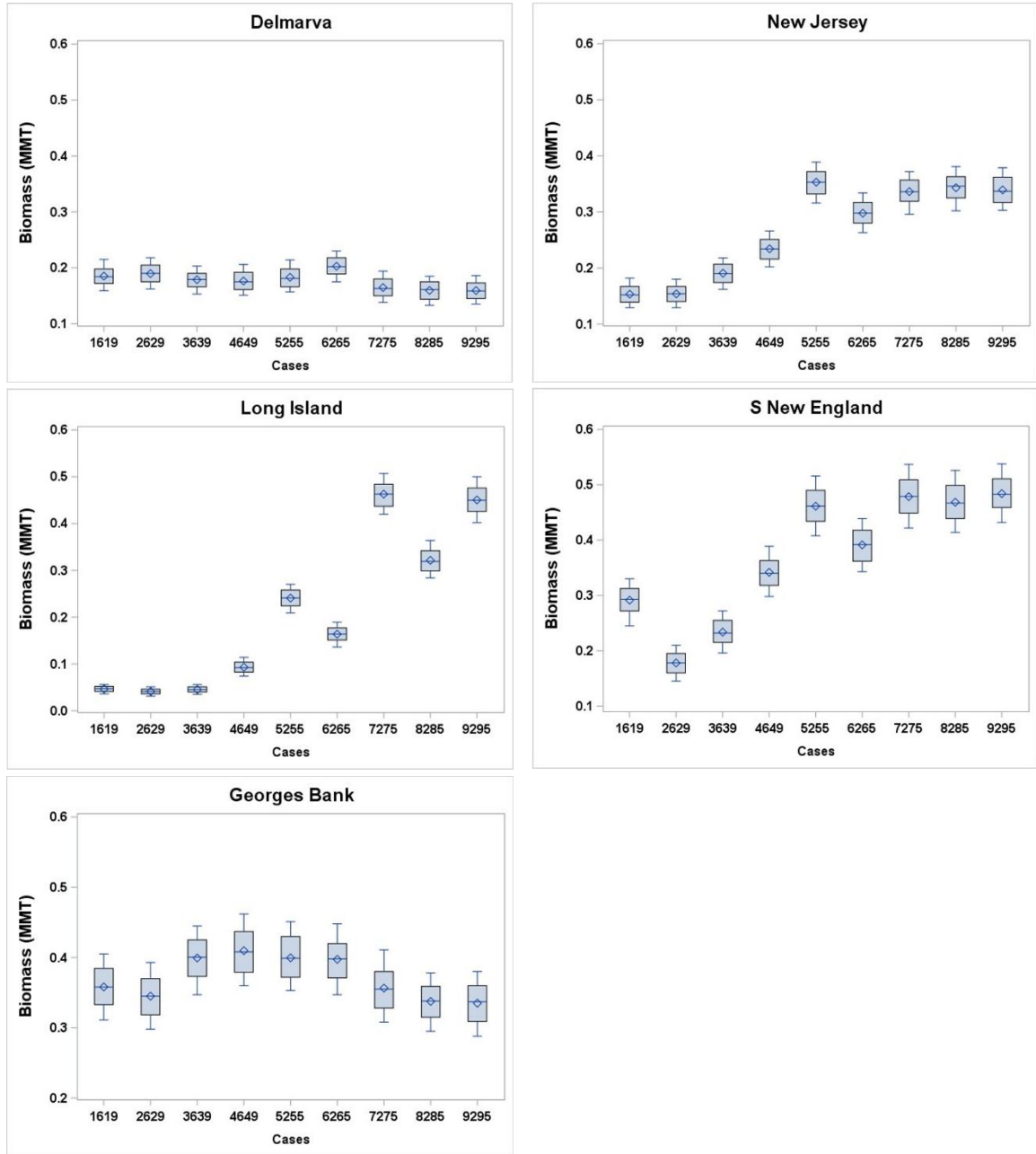


Figure 2.5 Regional biomass distribution (in Million Metric Tons) across cases per region.

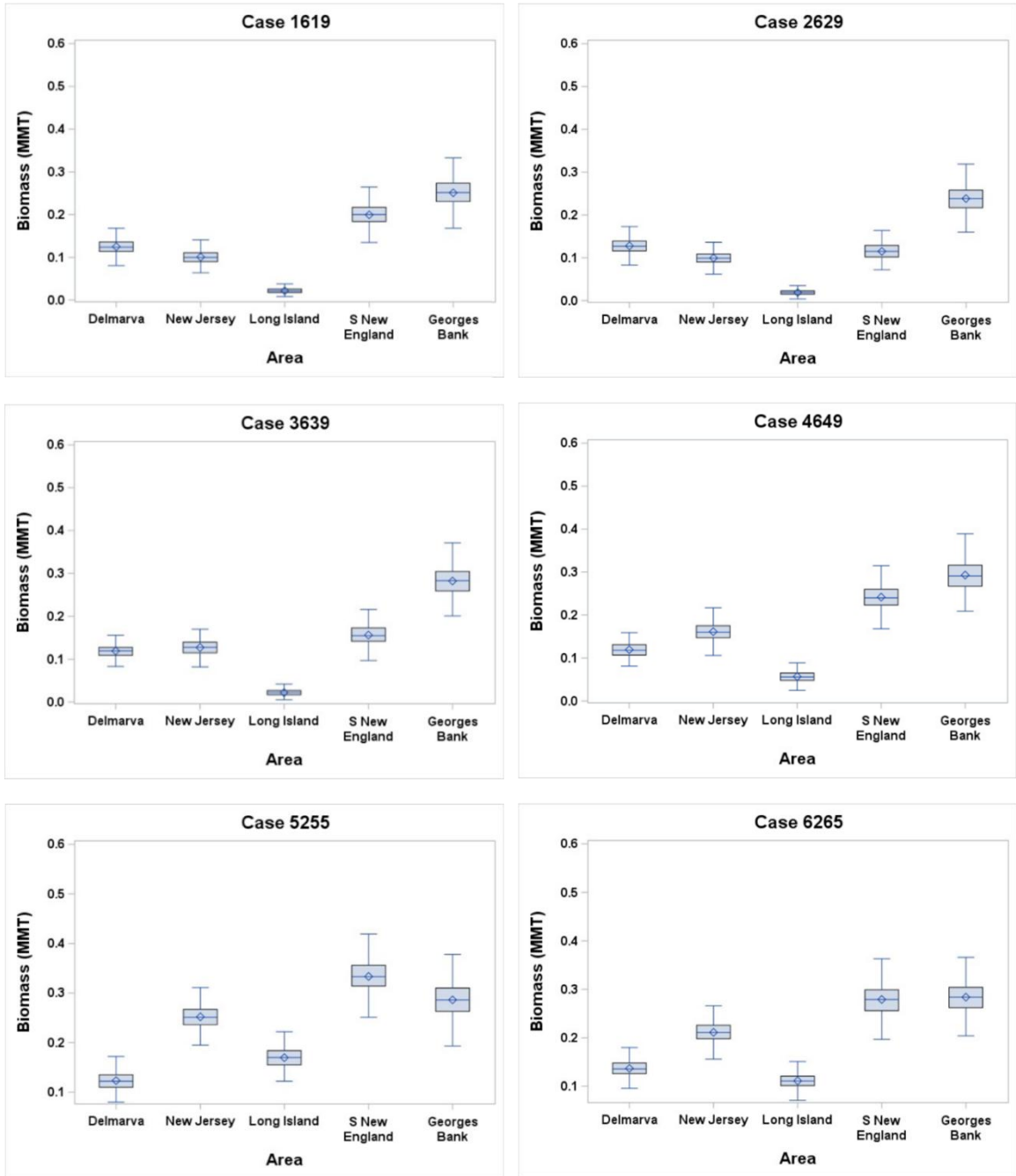


Figure 2.6 (continued).

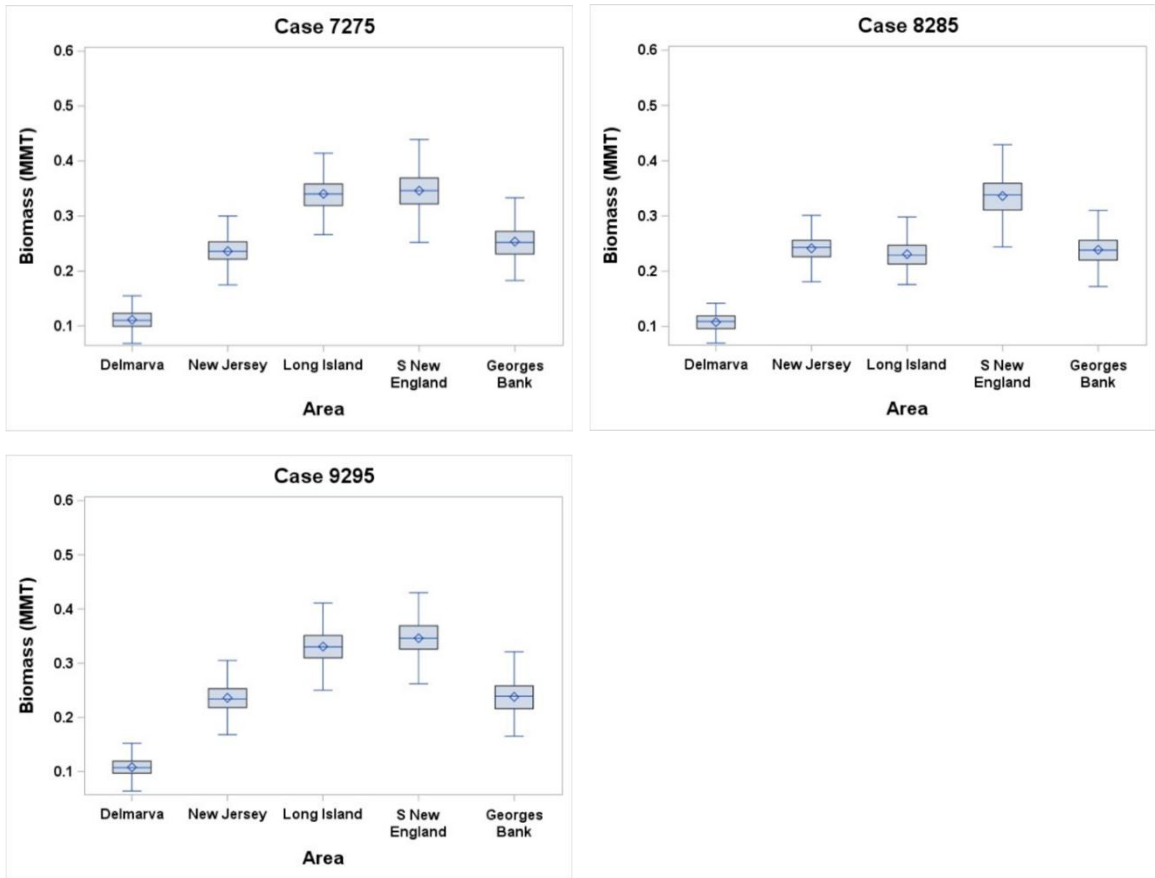


Figure 2.6 Regional biomass distributions by case simulation.

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CHAPTER III – WHAT IS THE FUTURE OF THE ATLANTIC SURFCLAM
(SPISULA SOLIDISSIMA) FISHERY UNDER CLIMATE-INDUCED WARMING ON
THE MID-ATLANTIC BIGHT CONTINENTAL SHELF: A MULTI-DECADAL
ASSESSMENT

3.1 INTRODUCTION

Fisheries are besieged by the rapidly evolving marine ecosystems fostered under intensifying climate change. Some fisheries on the Northeast continental shelf (NES), where warming has been most severe, have been in decline over recent decades as a consequence of climate-induced changes in the ecosystem (Lilly et al., 2013; Pershing et al., 2015; Tomasetti et al., 2023). In recent decades, species' range shifts have become a dominant feature of the NES (Lucey & Nye, 2010), examples including Atlantic cod (Drinkwater, 2005), American lobster (Pinsky & Fogarty, 2012; Wahle et al., 2015), and yellowtail flounder (Nye et al., 2009; Pinsky & Fogarty, 2012), but the most geographically extensive and well documented range shift in the northwestern Atlantic thus far has been the Atlantic surfclam (*Spisula solidissima*) (Hofmann et al., 2018).

The Atlantic surfclam has historically supported one of the largest commercial shellfish fisheries on the U.S. east coast since its rapid development in the 1940s (Yancey & Welch, 1968; Ropes, 1982), with fishing grounds situated between Georges Bank and Cape Hatteras, N.C. (Merrill & Ropes, 1969; Ropes, 1972, 1982). By the 1960s, a significant fishery had developed off the Delmarva Peninsula (a name combining coastal portions of Delaware, Maryland, and Virginia) and New Jersey (Yancey & Welch, 1968; Ropes, 1972, 1982), with landings also coming from the continental shelf off southern

New England. Over the last 30 years of the 20th century, the inshore fishery moved upcoast from Delmarva to New Jersey and thence to New York (Hofmann et al., 2018). The offshore range of the species has shifted north and farther offshore and the southern and inshore boundaries of the species' range have moved concordantly over much of the MAB (Hoffman et al., 2018; Weinberg, 2005; NEFSC, 2013, 2017). A well-documented mass mortality event off Delmarva circa 2000 (Kim & Powell, 2004; Weinberg et al., 2005) coincided with a widely observed regime shift in the North Atlantic (Lucey & Nye, 2010; Bjorndal et al., 2017; Perretti et al., 2017). In a recent study, Timbs et al. (2019) showed that the range of the Atlantic surfclam moved roughly 20 km offshore and 30-40 km north off Delmarva and New Jersey in recent decades, presumably due to the increased warming on the inner continental shelf of the MAB. Since the late 1990s, climate-induced warming has also led to geographic changes in the fishery such as vessels moving to more northern ports, re-location of processing plants, and geographic redistribution of fishing effort (McCay et al., 2011; DeGrasse et al., 2014).

Demographic variations, particularly but not exclusively along the southern and inshore range boundary of the Atlantic surfclam have been observed since the 1970s (Hoffman et al., 2018), including variations in growth rate and maximum size (Munroe et al., 2016; Diaz et al., 2024) and a reduction in population patchiness (Timbs et al., 2019), with severe implications for the fishery (Solinger et al., 2022), as surfclams are a low-value high-volume product requiring high LPUE for economic sustainability (Lipton & Strand, 1992; Weninger & Strand, 2003). Many studies have concluded that the species' change in geographic distribution and productivity is associated with its extreme vulnerability to temperatures above 20°C (Weinberg et al., 2002; Kim & Powell, 2004;

Weinberg et al., 2005, Weinberg, 2005; Munroe et al., 2013; Narváez et al., 2015). The Atlantic surfclam is a cool-temperate bivalve that has a narrow upper thermal range of roughly 19°C - 21°C, the upper limit primarily determined by the effect of temperature on filtration rate, and generally exhibits rapid physiological decline as temperatures rise above 21°C (Munroe et al., 2013).

This range shift in Atlantic surfclams has resulted in its progressive invasion into the habitat of the ocean quahog, *Arctica islandica*, another biomass dominant species on the northeast continental shelf. The increasing overlap between these cool temperate and boreal biomass dominants, generating an extraordinarily expansive ecotone (Stromp et al. 2022b), has severe consequences for the fishery given the current fishery regulations that prohibit mixed-catch landings of the two species. In addition, the time intensive on-board sorting required when fishing in the overlap region is prohibitive given the limited time vessels have at sea due to the spoilage rate of clams and the restricted number of crew: Stromp et al. (2023a) illustrate the economic implications for such a process. The primary consequence of the increasing overlap between Atlantic surfclams and ocean quahogs is the constriction of fishing grounds inshore due to the offshore shift in the surfclam's range and offshore due to the increased overlap of the two species. Though presently the southern component of the fishery is primarily threatened by this range shift, of much greater magnitude is the possible threat to the entire MAB surfclam fishery from the loss of fishing grounds as future climate projections suggest a dramatically increasing overlap between the two species (see Chapter II).

The evolution of the ecotone between the surfclam and ocean quahog under projected climate-induced benthic warming in the MAB was described in Chapter II,

wherein a regionally-forced hydrodynamics model generating predictions of bottom water temperatures through 2095 (Curchitser et al., personal communications) was combined with a clam habitat algorithm specifying the distribution of Atlantic surfclams and ocean quahogs based on bottom temperature constraints. Chapter II describes the projection of a continued offshore and northern movement of the Atlantic surfclam from 2016-2095 in addition to a dramatic colonization of the species across the MAB continental shelf as cool temperate conditions displace the boreal waters maintained by the Cold Pool (Kavanaugh et al., 2017; Chen & Curchitser 2020; Friedland et al., 2020; du Pontavice et al. 2023). The ocean quahog habitat external to the ecotone is predicted to degrade due to the projected warming, with habitat loss inshore, south, and offshore. Important changes in the spatial distributions of the surfclam were also projected, with Georges Bank becoming increasingly uninhabitable, as well as inshore off New Jersey and Delmarva, all three important fishing grounds for the surfclam fishery from its inception into the 2000s. The regional offshore habitat of New Jersey, Long Island, and southern New England, however, are projected to undergo an expansion in Atlantic surfclam biomass, and specifically within the region of Long Island where the surfclam is predicted to occupy the bulk of the continental shelf by the end of the century. The projections in Chapter II also indicate an increase in absolute biomass of the Atlantic surfclam in the MAB over much of the remainder of the 21st century. Altogether, the change in surfclam distribution, expansion of the two-species ecotone, and loss of fishable bottom inshore have important implications for the fishery and its current management.

Research focusing on the response of a fishery challenged by changing environmental (e.g., McCay et al., 2011), economic (e.g., Link et al., 2011; Chakraborty & Kar, 2012; Batsleer et al., 2015), and managerial (e.g., Hilborn, 2020; Miller & Brooks, 2021; Pentz & Klenk, 2022) conditions are numerous. Examples include reactions to habitat management constraints (Bohnsack, 2000; Walters, 2000; Bartholomew & Bohnsack, 2005), modifications to biological reference points (O’Leary et al., 2011), gear restrictions (Beard et al., 2003; Powell et al., 2004; King et al., 2009), and constraints on discarding (e.g., Gillis et al., 1995; O’Keefe & DeCelles, 2013). Also well recorded, are competitive use conflicts challenging historical fishery practices such as wind-energy development (Munroe et al., 2022; Scheld et al., 2022; Moya et al., in prep) and restrictions in access coincident with habitat management (Hicks et al., 2004; Kearney, 2013; Mann, 2021; Powell et al., 2021). Often, these examine the response of fishers individually or within the fishing fleet to such conditions (e.g., Béné, 1996; Dorn, 2001; Hutton et al., 2004; Millischer & Gasuel, 2006; Noveglio et al., 2022). Rarely, however, do such studies invoke the influence of climate change as a contributing factor (e.g., Hofmann & Powell, 1998; Brander, 2010; Young et al., 2019).

The Atlantic surfclam is an exemplar of the challenge imposed by climate change on the behavior of fishers and their fishery and is therefore an ideal and a quintessence for the study of such responses. This study’s purpose is to elaborate upon the projected changes in Atlantic surfclam spatial distributions and biomass presented in Chapter II by assessing the potential fishery consequences of this geographically large-scale range shift. Results of projected biomass in Chapter II are used in this study to inform fishery dynamics of the Atlantic surfclam fishing industry, including its scope for future growth

and sustainability of regional stocks over time under the impacts of climate-induced warming, the response in such important economic metrics as LPUE and time at sea, and such important managerial metrics as fishing mortality rate. Findings of this study provide insight into the potential challenges that the fishery could face under an evolving stock status and offer counsel on prospective management implementations to alleviate strain imposed on the fishery.

3.2 METHODS

3.2.1 SEFES (Spatially-Explicit Fishery Economic Simulator) Model

This study employs the model described in Chapter II, further detailed in Munroe et al. (2022), Kuykendall et al. (2019), and Powell et al. (2015), where the distribution of Atlantic surfclams and ocean quahogs are projected based on their species-specific temperature constraints using bottom water temperatures obtained using a high-resolution forward-projecting hydrodynamics model that includes predictions of bottom water temperatures (Curchitser et al., personal communications). The projected water temperatures used are obtained from the bottom-most layer of the simulated water column. The resulting projections of Atlantic surfclam and ocean quahog range boundaries and the Atlantic surfclam population dynamics as they evolve over time derived thusly are detailed in Chapter II.

SEFES was originally created to simulate the Atlantic surfclam population dynamics and fishery within the MAB, including the fishery's economic components (Powell et al., 2015; Kuykendall et al., 2017; Scheld et al., 2022). The addition of ocean quahog distributions described in Chapter II serves as an external force on surfclam fishing vessels and their fishing effort in certain fishery grounds based on regulations

prohibiting commercial fishing vessels from landing both Atlantic surfclams and ocean quahogs as a mixed catch (Stromp et al., 2023a) and, thus, the degree of overlap between the two species is economically important. Ocean quahog population dynamics, however, are not included nor is the ocean quahog fishery.

SEFES covers a geographic range from Georges Bank to Chesapeake Bay, with a spatial domain described by a 54 by 33 grid consisting of 10-min latitude by 10-min longitude ten-minute squares (TMS) (Fig. 1). This grid encompasses the survey regions used in the Northeast Fisheries Science Center stock assessment of Atlantic surfclam in the MAB with resolution consistent with the standard vessel trip report (VTR) data format for tracking the locations of harvest (NEFSC, 2022), but expands the domain east and south of Nantucket not covered by the federal survey (see Powell et al., 2019). The model incorporates a number of properties designed to provide a flexible decision-making process at the level of the vessel and homeport including a range of captain behaviors designed to simulate the decision-making process relative to trip initiation and destination, individually-specified vessel characteristics fully consistent with the present fishing fleet and constraining the ambit of the captains' decisions, and spatial dynamics of the Atlantic surfclam stock including variation in location and level of recruitment and post-settlement mortality. Verification of the surfclam population dynamics and the simulated fishery outcomes in the SEFES model were reported by Munroe et al. (2022).

3.2.2 Biological Habitat Conditions

Atlantic surfclam habitat is specified within SEFES using past and current known conditions relating bottom water temperatures to TMSs identified as surfclam habitat and/or ocean quahog habitat as described in Chapter II. Present-day conditions are herein

defined as years 2016-2019 to conform to the model verification period implemented by Munroe et al. (2022). Present-day bottom water conditions for each TMS were extracted from the DOPPIO implementation (López et al., 2020) of the Regional Ocean Modeling System (ROMs) (Wilkin et al., 2018; Levin et al., 2019). Validation by comparison of surfclam and ocean quahog range boundaries and surfclam population dynamics as derived from bottom water temperature estimates obtained from DOPPIO to federal survey data was described in Chapter II. Validation of surfclam and ocean quahog range boundaries and surfclam population dynamics obtained using bottom temperatures from the Curchitser et al. (personal communications) forward projection model was carried out by comparison to the DOPPIO-validated simulation for 2016-2019 (see Chapter II).

3.2.3 Fishing Fleet Simulations

The simulated MAB fishing fleet is based on specifications for each of the vessels in the fishery during 2016-2019. This simulated fleet comprises 33 vessels, each with a designated homeport, and equipped with specified landing capacities, dredge sizes, vessel speeds, fuel consumption rates, and allowed times at sea which restrict fishing ground access. Each vessel is randomly assigned a captain with a range of behavioral characteristics (total of 12 captain types), including their communication style with other fishery participants, their searching tendencies to identify new fishing grounds and their searching frequency; and their tendency to weigh the memories of past and recent catch histories to evaluate anticipated catch rates (Munroe et al., 2022; Powell et al., 2015; Scheld et al., 2022). Captains are re-randomized among vessels for each simulation; this, then, is an important source of variability between simulations for a particular time span

simulated. In the 2016-2019 MAB fishery, fishing vessels can switch ports, however, this is uncommon and is not allowed in model simulation.

Captains as simulated in the model fish in the TMS that provides the largest potential catch with the shortest time at sea, all of which is contingent on their assigned memory of past fishing history, communication with other fishers, and searching history. Weather restricts the decision to fish based on the known ability of vessels of varying size to fish in a range of sea states. Fishing is restricted by temperatures that affect spoilage rate of catch, and this constrains time at sea. Details are further provided in Munroe et al. (2022). Atlantic surfclam vessels are limited in their catch, and consequently by their time spent at sea to no more than two trips per week, in accordance with standard operating procedure restricting weekly landings. The presence of ocean quahogs limits the ambit of the fishery by requiring additional time at sea for on-deck sorting, thereby limiting LPUE. Based on reports from the fishery, a catch on deck in which ocean quahogs constituted more than 4% of the catch would dramatically reduce time fishing: thus, a 50% catch penalty is imposed in the model on vessels fishing in these mixed catch areas (Stromp et al., 2023a).

3.2.4 Simulation Structure

A SEFES simulation is run for 300 years, wherein no fishing activity occurs in the first 100 years of each simulation to allow for surfclam populations to reach carrying capacity under von Bertalanffy-defined growth rates, specified mortality rates, and Beverton-Holt-defined recruitment: fishing begins in year 101. In the following 50 years (101-150), the fishery fishes down the stock consistent with the fishing power of the fleet. However, due to the long generation time of surfclams, analysis of simulation output is

restricted to the last 50 years of the 200 years of fishing (years 250-300). A series of simulations were run, each defined by a period of years between 2016 and 2095. For each time period, a series of 200 simulations were conducted, each simulation producing a 50-year time series for analysis, totaling 10,000 annual observations. Metrics extracted from the fifty-year analysis include the average and standard deviation in fishable stock biomass (clams ≥ 120 mm) in millions of metric tons (MMT), LPUE (in cages per hour fished: 1 cage=32 surfclam bushels; 1 bushel = 53.2 L), catch (number of cages landed per year), fishing mortality rate (yr^{-1}), fishing vessel time at sea (accumulated hours converted to days yr^{-1}), fishing vessel time spent fishing (hours yr^{-1}), and the number of trips undertaken by the fleet per year. Catch and landings are equivalent, as discarding of the target species does not occur in the surfclam fishery. The term ‘fishable biomass’ is a historical convenience as the federal survey dredge reaches near-100% selectivity at 120 mm (NEFSC, 2017) and minimizes the influence of the smaller size classes rarely caught in commercial or survey operations.

Simulations were based on four-year averaged seasonal bottom water temperatures with an approximately decadal time step from late 2016 to 2095. Nine sets of simulations (hereafter termed cases), each comprising 200 simulations, and thus 10,000 annual observations, were run based on four-year averaged time segments within each decade, and referred to in shorthand as follows: 1619, 2629, 3639, 4649, 5255, 6265, 7275, 8285, and 9295 (where e.g., 1619 stands for 2016-2019) (Table 3.1). Variations between the 200 simulations were produced by randomized mortality rates within habitable TMSs that generated a varying map of clam patches, randomized recruitment time series contributing to the distribution of clam patches in space and over

time, and randomized captain behavioral repertoires relative to vessel configuration (Munroe et al., 2022; see Chapter II). An example of the variability of outcomes amongst 200 simulations within a case is shown in Figure 2.

Results were analyzed using R, MATLAB, and Fortran programs, with most statistical analyses implemented in SAS 9.4. An Analysis of Variance was run on fishable biomass, LPUE, catch, time at sea, time spent fishing, number of trips, and fishing mortality as the dependent variables, the main effects tested being Year with years chosen at every turn of the half-decade to represent the simulation in statistical analysis while minimizing the effect of autocorrelation within the yearly time series (six levels), case number (Table 3.1, nine levels), and, when appropriate, region that encompassed five distinct regional areas within the MAB that describe regionally specific Atlantic surfclam habitats (Fig. 1, five levels). A post-hoc Least Squares Means test (LS-Means) was employed to further investigate the origin of significance within the ANOVAs. Pairwise contrast matrixes from the LS-means tests are provided in Appendix B.

The five regions compared were previously used by the Northeast Fisheries Science Center (NEFSC) in stock assessments (e.g., Fig. A1 in NEFSC, 2007). Region one, the southern-most region, encompasses Delmarva, and is partitioned from region two, New Jersey, at Delaware Bay. Region three comprises Long Island, NY, and is separated from region two at Hudson Canyon. Region four includes southern New England, partitioned from region three at Block Island. Lastly, region five encompasses Georges Bank, and is separated from region four by the Great South Channel.

3.3 RESULTS

3.3.1 Trends in fishable biomass

Atlantic surfclam fishable biomass increased across the time series (Fig. 3), with the lowest biomass (0.600 MMT) in case 2629 and highest biomass (1.29 MMT) in case 7275 (Table 3.2). Biomass differed significantly by case ($P < 0.0001$) and did not differ by simulation years. All pairwise comparisons of biomass by a posteriori LS-means tests differed significantly (all $P < 0.0001$).

Fishable biomass increased in New Jersey, Long Island, and southern New England over the time series, with notable increases between cases 4649 and 5255 (Fig. 3); whereas fishable biomass in Delmarva and Georges Bank generally declined from case 5255 through 9295 (Fig. 3). Further details on the importance of this decadal transition in biomass are provided in Chapter II.

Fishable biomass differed significantly across cases, across regions, and by the interaction of case and region ($P < 0.0001$), thus indicating that biomass trends over time diverged significantly among the regions and the trends in biomass among regions differed significantly among cases. Results are supported by pairwise comparisons between cases within regions and between regions within cases.

3.3.2 Fishing metrics

Across all fishery parameters, all cases differed significantly from each other ($P < 0.0001$). Similarly, fishery metrics differed significantly among the five regions, all cases, and the interaction of region and cases ($P < 0.0001$), indicating that the trends over decades diverged significantly among the regions and that trends over decades among regions differed significantly among cases. Most pairwise comparisons between cases

within regions differed ($P < 0.0001$), and most pairwise comparisons between regions within cases differed ($P < 0.0001$). For all metrics, results for case comparisons among regions can be seen in Appendix B.

3.3.2.1 Trends in Atlantic surfclam catch

Total catch in the MAB averaged 85,703 cages per year over the time series, with minimum annual catch observed near the beginning of the time series (case 2629; 74,182 cages yr^{-1}) and maximum annual catch at the end of the time series (case 9295; 96,672 cages yr^{-1}) (Fig. 3, Table 3.2). Catch increases through the time series in New Jersey, Long Island, and southern New England (Fig. 4), whereas catch decreases in Delmarva and Georges Bank. Catch is lowest in Long Island, with catch in southern New England and Delmarva more than doubled that of Long Island. In contrast, catch is highest in New Jersey, followed by Georges Bank (Fig. 4).

The adjacent regions of Long Island and southern New England demonstrate the greatest increase in catch across the time series, wherein each region at least doubles the initial catch by the late 2040s and mid-2070s, respectively (Fig. 4). Long Island catch within the first three decades fell just under 1,000 cages (Table 3.3), but similar to southern New England, catch begins to increase after 3639 and continues to grow through the time series (Fig. 4). Catch in both southern New England and Georges Bank is relatively steady through 3639 but diverges in their respective trends after this with catch increasing in southern New England and decreasing in Georges Bank (Fig. 4; Table 3.3). In Delmarva and Georges Bank, catch drops after 6265, whereas catch increases in all other regions over the same time period (Fig. 4).

3.3.2.2 Trends in LPUE

LPUE gradually increases over the time series (Fig. 5), with average landings of 1.75 cages/hour (Table 3.2). Minimum average LPUE occurred near the beginning of the timeseries (case 2629; 1.61 cages/hour), whereas the maximum LPUE average was achieved at the end of the timeseries (case 9295; 1.93 cages/hour) (Table 3.2).

Average LPUE increased slightly in Delmarva across the time series, with the lowest LPUE (1.40 cages/hour) in 2629, and the highest LPUE (1.59 cages/hour) at the end of the time series in 9295 (Fig. 5). LPUE in New Jersey was the lowest among all regions, but steadily increased through the time series (Table 3.3). Long Island and southern New England demonstrated much larger variability in LPUE than more southern regions, most notably in the first four decades (2016-2049) (Fig. 5). LPUE in Long Island is relatively low (0.55 - 0.94 cages/hour) early in the time series (Fig. 4, Table 3.3), followed by an increase through the remaining time series until reaching maximum LPUE (1.64 cages/hour) in 9295 (Fig. 5, Table 3.3). In southern New England, LPUE initially declines from 2629 to 3639 before increasing throughout the rest of the time-series, reaching a maximum LPUE (3.07 cages/hour) in 9295 (Fig. 5). Lastly, LPUE in Georges Bank remains stable at around 3 cages/hour through the time series (Table 3.3). Most pairwise comparisons between cases within regions differed ($P < 0.0001$) as well as comparisons between regions within cases ($P < 0.0001$), but unlike most metrics and regions, LPUE for Georges Bank for nearly all cases were not significantly different from one another.

3.3.2.3 Trends in fishing mortality rate

Average fishing mortality rate declined across the time series, averaging 0.0177 yr⁻¹ (Fig. 6; Table 3.2). Peak mortality rate occurred near the beginning of the time series (case 2629; 0.024 yr⁻¹), whereas the lowest mortality rate was observed near the end of the time series (case 7275; 0.014 yr⁻¹) (Fig. 6).

Fishing mortality rates for three regions, Delmarva, southern New England, and Georges Bank, stayed stable across the time series (Fig. 6; Table 3.3), with Delmarva and New Jersey averaging larger rates compared to other regions. Despite similar average fishing mortality rates in southern New England and Long Island, Long Island trends demonstrated higher variability compared to southern New England's stable rate (~ 0.01 yr⁻¹) throughout the time series (Fig. 6; Table 3.3). Most pairwise comparisons between cases within regions and between regions within cases were significant at P < 0.0001 (Appendix B).

3.3.2.4 Trends in time spent fishing

Time spent fishing increased over the time series, averaging a total of 48,830 hours yr⁻¹ (Fig. 7; Table 3.2). The minimum average time fishing occurred in the beginning of the timeseries (case 1619; 45,895 hours yr⁻¹), and maximum time near the end of the timeseries (case 8285; 50,629 hours yr⁻¹).

Delmarva and Georges Bank fishing time declined across the time series starting in 3639, whereas fishing time in New Jersey, Long Island, and southern New England increased over the time series (Fig. 7; Table 3.3). Lowest time spent fishing occurred in Long Island, with considerable variation throughout the time series, the volatility being similar to that of the previously described trends observed in Long Island, whereas longer

fishing times were found to occur in New Jersey (Fig. 7; Table 3.3). Regional time spent fishing increased between 4649 and 5255 and was maintained throughout the time series in all regions except for Delmarva, which declined after 6265, and Georges Bank (Fig. 7). Trends in time spent fishing during the period between 4649 and 5255 mirror the increasing trends in fishable biomass, catch, and LPUE (Figs. 2 - 4).

3.3.2.5 Trends in time spent at sea

Time spent at sea increased across the time series (Fig. 8), averaging a total of 3,495 days yr⁻¹. Minimum averaged sea time was observed in the beginning of the time series (case 1619; 3,204 days yr⁻¹) and maximum averaged sea time at the end of the time series (case 9295; 3,744 days yr⁻¹) (Table 3.2).

Regional trends in time spent at sea largely mirror those observed in time spent fishing (Fig. 7, 8), with declining time observed in Delmarva and Georges Bank across the time series and increases within New Jersey, Long Island, and southern New England (Fig. 8). Highest average sea times were observed in both New Jersey and Delmarva and lowest in Long Island and southern New England (Fig. 8). Across all but Georges Bank, sea time increased between 4649 and 5255.

3.3.2.6 Trends in the number of trips taken

The number of trips taken per year by the fishing fleet increased over the time series, averaging 2,067 trips yr⁻¹ (Fig. 9; Table 3.2). The minimum number of trips occurred near the beginning of the time series (case 2629; 1,868 trips yr⁻¹) and the maximum number of trips at the end of the time series (case 9295; 2,234 trips yr⁻¹).

Average trip duration remained relatively consistent over the time series, but eventually

declined from a high of 1.72 days (~ 42 hours) in 2629 to a low of 1.67 days (~ 40 hours) in 9295 (Table 3.4).

Average trip duration increased over the time series for New Jersey, Long Island, and southern New England, with southern New England demonstrating the largest change in trip duration (Table 3.4). Trip duration did not change much within New Jersey and Long Island over time (Table 3.4). Trip duration decreased over time within Delmarva (1.71 days to 1.64 days per trip) and Georges Bank (2.90 days to 2.76 days per trip) (Table 3.4).

New Jersey, Long Island, and southern New England increased in the number of trips per year over the time series, with increases in both Long Island and southern New England starting between 3639 and 4649. New Jersey routinely had the highest number of trips taken, averaging around 700 trips yr⁻¹ until 6265, after which the number of trips increased through the remaining time series until reaching a maximum (909 trips yr⁻¹) in 9295 (Fig. 9; Table 3.3). In contrast, adjacent Long Island often had the least number of trips yr⁻¹ taken (Fig. 9). Delmarva had the second highest average number of trips per year, followed by southern New England and Georges Bank (Fig. 9).

The regional number of trips yr⁻¹ gradually declined in Delmarva and Georges Bank across the time series, however, this decline starts later for Georges Bank (between 4649 and 5255) compared to Delmarva (between 3639 and 4649) (Fig. 9). Across all regions but Georges Bank, the number of trips taken per year increased between 4649 and 5255, mirroring trends observed in all fishing metrics excluding fishing mortality rate (Fig. 3- 5, 7- 9).

3.4 DISCUSSION

3.4.1 Perspective

Evaluation of fisheries performance typically depends upon time series data on catch, stock size, fleet dynamics, economics and the like. Such data are often sufficient to describe the decision-making of captains, owners, and processors at the time of analysis as their decisions are already imbedded into the data obtained describing the fishery. Projections, particularly for conditions unobserved previously, however, require the ability to simulate the decision-making process under conditions where a track record of observations is not available. Of particular note is the need to simulate the performance of captains in planning and carrying out fishing trips, including the timing of the trip and target location given a range of uncertainties posed by time of year, weather, and imperfect knowledge of stock density.

Few models include the decision-making characteristics of captains (e.g., Bockstael & Opaluch, 1983; Holland & Sutinen, 2000; Dorn, 2001; Hutton et al., 2004; Millischer & Gasuel, 2006). The model used herein was specifically developed to simulate the responses of a fishery to new conditions not yet observed through the specification of a series of behaviors observed by captains during present-day operations and through extensive interviews with captains (Powell et al., 2015, 2016; Munroe et al., 2022). Additionally, the model has been used to examine options for area management (Kuykendall et al. 2017; 2019) and to determine the interaction of wind energy development on the continental shelf with the fishery (Munroe et al. ,2022; Scheld et al. 2022), both of which constitute situations not yet observed. Through these studies, however, the reliability of the formulated options for decision making by the captains has

been verified with specific attention to the reliability of estimated catch metrics, the dispersion of the fleet geographically and in time, and metrics defining details of fleet performance such as time at sea and LPUE as it varies between homeports, vessel sizes, and at-sea conditions imposed by weather and seasonal changes in temperature. Each of these metrics is directly dependent on the accuracy of formulated decision making by the simulated captains, a process of critical importance for any predictions applied to scenarios not yet observed. Thus, the simulations reported herein represent as reliable a view of anticipated fishery performance criteria as can be obtained today for future conditions anticipated with ongoing climate change.

3.4.2 Projected trends in fishery performance consequent of population range shifts

Simulations describe the expansion of the Atlantic surfclam fishery in the Mid-Atlantic Bight under increased bottom water temperatures over a 79-year decadal time series following an initial contraction (2016-2040s), a contraction already ongoing as documented by declining survey stock indices (NEFSC, 2022) and the constraint imposed by overlap of the surfclam with the ocean quahog (Stromp et al., 2023b). Following this near-term contraction, trends in Atlantic surfclam fishable biomass, catch, and LPUE are projected to increase steadily over the remainder of the 21st century, with gradual increases observed in time spent at sea, time spent fishing, and trips taken by the fleet. In each of these metrics, the increase is not due to declining LPUE requiring increased fishing effort to sustain catch; rather, the trends are outcomes of increasing biomass available to the fishery and decisions of the simulated captains to expand the fishing domain throughout the MAB and particularly in its central portion. The only parameter predicted to decrease over the simulations was fishing mortality rate, again an outcome of

increasing biomass. Increasing trends across catch, LPUE, and time indices describing the behavior of the Atlantic surfclam fishing fleet indicate an increase in accessible fishing grounds for the fleet to exploit over time, allowing more trips to be taken and more time spent fishing with increasing LPUE, as trips become more efficient and produce higher catch.

Regional differences are similarly resolved as the range of the surfclam changes over time. The Georges Bank and Delmarva fishery, historically important sources of landings (Loesch & Ropes, 1977; Weinberg, 1999; DeGrasse et al., 2014), are projected to be less resilient to the effects of warming bottom water temperatures, with declines in both fishable biomass and catch coupled with higher fishing mortality rates in Delmarva compared to adjacent regions. An important result in these regions is a relatively stable LPUE because captains both limit trips to those that minimize time at sea yet incur increased time steaming to reach fishing grounds with sufficient surfclam biomass to maintain LPUE, consequently limiting time spent fishing (Fig. 5).

The decrease in hours spent fishing, days at sea, and number of trips completed in the Delmarva and Georges Bank regions can likely be attributed to the geographic influence of warming on the dispersion of the surfclam stock in each region (Chapter II, see Fig. 2). For example, increasingly warmer waters are seen along the inner portion of the continental shelf off Delmarva, displacing the surfclam range and the fishery offshore resulting in longer travel times to fishing grounds, thereby constraining catch under the typical 36–40-hour time limit for a fishing trip. In contrast, on Georges Bank, warming waters develop from the middle of the bank and expand outward, causing surfclams to recede from the central and eastern side of Georges Bank to the western side and offshore

of southern New England. This removes from the captains' choice portfolio the need to access the Georges Bank fishing grounds as frequently as similar catch opportunities exist closer to the primary southern New England homeport of New Bedford. These range shifts, then, limit accessible fishing grounds at both geographic extremes of the stock, but for very different reasons.

A closer look at Georges Bank suggests that the fishery may peak between years 2036-2039 to 2052-2055, a period identified in Chapter II as a significant turning point in the range shift of the Atlantic surfclam as the stock begins to build out onto the Long Island continental shelf and off southern New England. For Georges Bank, fishable biomass and catch are at their highest during this time with an associated high LPUE of 3 cages per hour fished; however, after years 2052-2055, the fishable biomass and catch along with the at-sea time indices start to decline, while LPUE persists at around 3 cages per hour fished. This is in part due to the location of the largest vessels in the fleet, homeported in New Bedford, for only these vessels can effectively reach and fish Georges Bank, but as importantly, the expansion of fishable stock off Long Island and southern New England allows for a more economically favorable landing of clams into the proximate regional homeport of New Bedford, and therefore, along with a decline in biomass, explains the declining importance of Georges Bank.

On the other hand, the decline in catch off Delmarva in the second half of the 21st century is in part a result of the increasing distance of the stock from traditional homeports of Ocean City, Maryland, and Atlantic City, New Jersey, as the stock moves offshore. Note, however, that the model does not permit re-occupation of historically

important homeports south of Ocean City, Maryland (Ropes 1972, 1982) which may become viable to access the fishable stock farther offshore in this region.

Contrariwise, the region of New Jersey, a long-term prominent producer of surfclams and a region well-studied in the range shift response of the surfclam within it (Weinberg, 2005; Weinberg et al., 2005) reflects patterns demonstrated across the central regions of the MAB fishery, where fishable biomass, catch, and LPUE develop a steady increasing trend over time from about 2040 onwards. Simulations suggest that the New Jersey fishery is likely to grow as warming continues. A similar trend is observed in the Long Island and southern New England regions, with fishable biomass, catch, and LPUE increasing over time. These central regions participate strongly in the overall increase in landings seen in the second half of the 21st century and benefit from the more extensive continental shelf in this region providing more acreage for surfclam expansion.

The expansion in surfclam biomass by mid-century off southern New England also bodes well for its local ports as distance to fishing grounds decreases from the long steam to Georges Bank and this is seen in its increasing LPUE and associated fishery metrics. A similar trend is observed off Long Island, however muted in comparison to southern New England, for two reasons. Much of this region remains relatively far from homeports and, consequently, improved stocks closer to home limit captains' decisions to fish in the region. In addition, the inner-mid regional shelf is bordered by the inshore edge of the Cold Pool, where warming allows for the surfclam habitat to expand offshore where it was historically too cold for them to be found (Chapter II, see Fig. 2), but where much of the projected expansion is consumed by the extensive overlap of surfclams with ocean quahogs which limits exploitation relative to population expansion. Interestingly,

catch in the New Jersey and Long Island regions stabilize quicker than southern New England (Fig. 4), which may be attributed to the expanding range of surfclams in the southern New England region redirecting fishing from Georges Bank and the somewhat lesser overlap with ocean quahogs compared to Long Island.

3.4.3 Caveats

An inherent limitation of model projections is the static representations of the state of the MAB fishery and the surfclam stock over time. The approximately decadal time steps from late 2010 to the mid-2090s broken up into four-year average time segments, each defined by average temperature conditions, provide only a snapshot of what may be occurring regarding Atlantic surfclam population dynamics and subsequent fishery responses. The lifespan of the Atlantic surfclam transcends the decadal time steps between simulations; nonetheless, the nine cases presented are not influenced by size-frequencies or abundances from times immediately preceding a case simulation nor do they provide information to the immediately succeeding case simulation. Each simulation is based on an assumed long-term time period of constant environmental conditions, and thus interpretation of geographic patterns illustrated in this study must be interpreted within the context of this limitation. Chapter II discusses the assumptions underlying the population dynamics component of the model in more detail.

Importantly, the model's output is premised on the 2016-2019 regulations and management imposed upon the Atlantic surfclam fishery, particularly the fishing regulation that prevents vessels in the MAB from landing both Atlantic surfclams and ocean quahogs in the same catch (McCay et al., 1995). The regional fleets are subsequently limited in fishing ground accessibility in the model given the expanding

ecotone between the ocean quahog and Atlantic surfclam (see Chapter II; Stromp et al., 2023a, b) which progressively impairs fishing in areas newly occupied by surfclams as warming continues to impact species distributions on the continental shelf. Based on projections provided herein, one might assume that technological innovations and regulatory reform would be prioritized by the fishery at some future time. This expectation is not included in the model. Similarly, the model does not account for the possibility of changes occurring in the Atlantic surfclam fleet with respect to vessel size, vessel performance, homeport, or technological advances such as refrigeration, all of which have occurred historically since the 1970s as an outgrowth of ongoing climate change (McCay et al., 2011; DeGrasse et al., 2014).

Lastly, the model predicts an increase in catch over the nine-decade time series; however, based on demand limitations in the present market, whether landings can expand substantially without depressing price remains uncertain. An expanded marketability of surfclam products in addition to an increase in vessel capacity would be required to keep pace with this growth in biomass distribution if the fishery were to expand to its apparent potential. As the economic viability of vessel replacement, homeport change, relocation of processing plants, and product markets are not known, these options have not been included in the model.

3.4.4 Warming temperatures and management issues

Simulations in the projected geographic footprint of the Atlantic surfclam and ocean quahog in Chapter II (Fig. 2, 3) predict a drastic shrinkage in available fishing locations as the expanding ecotone limits fishing grounds where a mixed species catch is infeasible at this writing. Thus, catch efficiency can be expected to decline as vessels are

forced to steam out to fishing grounds further away, typically down or up coast, to avoid areas with mixed catch. The influence of such trends introduces a constraint on the fishery through year 2040 in these simulations, but not obviously thereafter. The reason is the substantive expansion of biomass, both in areas of species overlap and areas without species overlap, particularly in areas closer to homeports off southern New England and Long Island, thus limiting the influence of the overlapping species on the fishery. Nonetheless, the dramatic expansion of the overlap region suggests an increasing constraint on growth of the fishery, as discussed in Stromp et al (2023), as recession of the ocean quahog range will not likely encompass a vast region of the Mid-Atlantic Bight through the end of the 21st century. LeClaire et al. (2023) reflect on the ability of ocean quahogs to resist warming temperatures, thus slowing range recession as temperatures increase, and minimizing the recession of the warm-temperature boundary for this species. The uncertain future of the ocean quahog is one of the primary uncertainties in projecting the future of the surfclam fishery.

Aspects of the population dynamics of the Atlantic surfclam are poorly understood, specifically the stock-recruit relationship (Timbs et al., 2018; NEFSC, 2022) and the natural mortality rate. Both are likely to change dramatically over the next half-century. The projections of larval transport by Zhang et al. (2015, 2016) for example are likely to be substantively modified and the degree to which growth rates in the vast areas scheduled for occupation will remain similar to those observed today is highly uncertain (see Powell et al., 2020). Each of these will challenge estimation of the status of the stock. In addition, the estimation of a sustainable catch for this fishery is further challenged by the prevailing assumption that a commercial stock is always in equilibrium

under constant environmental conditions, leading to the estimation of a carrying capacity. Simulations reported here and in Chapter II suggest a rapid population expansion leading to a continually varying carrying capacity.

Rapid changes in carrying capacity under rapidly changing environmental regimes are not unanticipated (Scavia et al., 2002; Beaugrand et al., 2008), but pose challenges to adaptive management. Current management sets fishable biomass targets at half of the unfished population (Hennen et al., 2018). The present Atlantic surfclam fisheries management plan (FMP) includes a quota cap purposely maintained well below the ABC (allowable biological catch) (Borsetti et al., 2023). By 2040, this quota cap will increasingly impede fishery growth, presuming marketability constraints can be overcome, despite no previous history of overfishing occurring and no anticipation of it happening in the near future given the biomass results in this study. In addition, the present federal surfclam survey is conducted on a 6-year time schedule (Jacobson & Hennen 2017). Based on simulations presented here, the rate that climate-induced warming is impacting the Atlantic surfclam stock is on decadal or shorter time intervals. This will likely impose the need to reevaluate survey design and to assess the stock and its biological reference points on a decadal time scale to keep pace with the rapid climate-induced changes in the MAB. The simulations presented herein, however, do not vary the biological reference points or other management criteria: simulations assume, certainly incorrectly, a constant regulatory condition over the remainder of the century.

The history of the Atlantic surfclam fishery is one of arduous, but necessary, movement of vessels to more northern homeports, the need to develop refrigeration options to access fishing grounds further offshore, and the need to develop improved

processing capacity farther north. The movement of Atlantic surfclams offshore and north of their historical range projected by these simulations will impose additional pressures to optimize fleet distributions among potential homeports. However, the suggestion that the fishery will be constrained both at its most southern (Delmarva) and most eastern extent (Georges Bank) may ameliorate the need for redistribution of vessels and processing plants on the scale seen since the mid-1990s. In fact, given the suggested expansion of stock biomass from New Jersey to southern New England, a likely outcome will be the need to expand the fleet, as a potential doubling of catch, likely permitted sometime in the second half of the 21st century, will exceed the catching capacity of the present fleet. Whether current port capacity is sufficient to accommodate an expanded fleet size to take advantage of the increase in surfclam biomass projected in this region is unclear.

3.5 CONCLUSIONS

Consideration is typically given to the peril imposed by climate change on the future of key commercial fisheries (Brander, 2010; Perry et al., 2010; Brown et al., 2012; Pinsky & Byler, 2015; Young et al., 2019); case histories are well described (Pershing et al., 2015; Florko et al., 2021; Holland et al., 2022) and the importance of regime shifts well documented (Choi et al., 2004; Rocha et al., 2015; Sanchez-Rubio & Perry, 2015). The future of the Atlantic surfclam would appear to be demonstrably different, as projections of range shift within the MAB suggest increasing standing stock, increasing carrying capacity, and increasing potential fishery landings without substantial negative economic impacts, as metrics such as time at sea change consistent with increased landings, not increased effort to maintain present-day catch. The Atlantic surfclam fishery in the coming decades is identified as a fishery that may well benefit from future

warming temperatures as the geographic footprint of the species expands. The same cannot be said for ocean quahogs, unfortunately, regarded here as a species susceptible to significant anticipated loss under increasing temperatures, though more research needs to be conducted on this species to evaluate future outcomes.

Despite the possibility of surfclams being a winner under climate scenarios, challenges still exist for the fishery under this new paradigm, including the development of offshore windfarms in the MAB from off Delmarva to southern New England. Surfclam biomass is expected to increase over most of this region in the following decades (see Chapter II). Borsetti et al., (2023) discussed the potential fate of the Atlantic surfclam federal stock assessment under future windfarm scenarios. Evaluations of the interaction of the Atlantic surfclam fishery and the proposed windfarm footprint evaluated for the range of the surfclam today may well be inappropriate for future conditions (Moya et al., in prep).

Additionally, efficiency of fleet configurations and port sizes are unlikely to perform at optimum capacity under the anticipated expanding surfclam biomass in regions such as southern New England, Long Island, and New Jersey. Although projections in Chapter II suggest that the southern range of the Atlantic surfclam population remains stable in its southern boundary off Delmarva, albeit offshore from the present-day distribution, processing plants and homeports may be better suited well north of this border given the northern trend in fishable biomass. The projected increase in Atlantic surfclam biomass over the remainder of the 21st century, coupled with the expanding ecotone with the ocean quahog, emphasizes the need to re-assess the current management system as this species will be unlikely to establish a stable range within the

21st century, though opportunities for the fishery to expand harvesting without overfishing are suggested under climate-warming conditions.

3.6 Tables

Table 3.1 List of cases simulated with SEFES.

Case Names	Years Covered
1619	2016-2019
2629	2026-2029
3639	2036-2039
4649	2046-2029
5255	2052-2055
6265	2062-2065
7275	2072-2075
8285	2082-2085
9295	2092-2095

Table 3.2 Summary of average fishing parameters across all cases over the MAB.

Case Names	Biomass (MMT)	Catch (# cages yr ⁻¹)	Fishing Mortality rate (yr ⁻¹)	LPUE (# cages hr-fished ⁻¹)	Time Fishing (hours yr ⁻¹)	Time at Sea (days yr ⁻¹)	Number of Trips (yr ⁻¹)
1619	0.699	75,092	0.020	1.64	45,894	3,204	1,887
2629	0.600	74,182	0.024	1.61	46,075	3,213	1,869
3639	0.798	77,765	0.021	1.66	46915	3,288	1,938
4649	0.872	82,959	0.018	1.71	48,460	3,440	2,025
5255	1.16	89,873	0.015	1.78	50,497	3,612	2,147
6265	1.02	89,076	0.017	1.77	50,273	3,613	2,138
7275	1.29	93,730	0.014	1.86	50,543	3,701	2,198
8285	1.15	91,979	0.015	1.82	50,629	3,652	2,169
9295	1.26	96,672	0.015	1.93	50,187	3,733	2,235
Average	0.974	85,703	0.0177	1.75	48,830	3,495	2,067

Table 3.4 Average trip duration (in Days⁻¹) across all cases in the entire MAB and regionally

Case	Entire MAB	Delmarva	New Jersey	Long Island	Southern New England	Georges Bank
1619	1.70	1.71	1.43	1.78	1.30	2.90
2629	1.72	1.72	1.43	1.751	1.32	2.92
3639	1.70	1.70	1.43	1.77	1.26	2.87
4649	1.70	1.69	1.45	1.80	1.32	2.72
5255	1.68	1.69	1.44	1.77	1.37	2.74
6265	1.69	1.68	1.45	1.80	1.36	2.71
7275	1.68	1.66	1.44	1.80	1.52	2.70
8285	1.68	1.65	1.45	1.80	1.55	2.74
9295	1.67	1.64	1.44	1.77	1.62	2.76

3.7 FIGURES

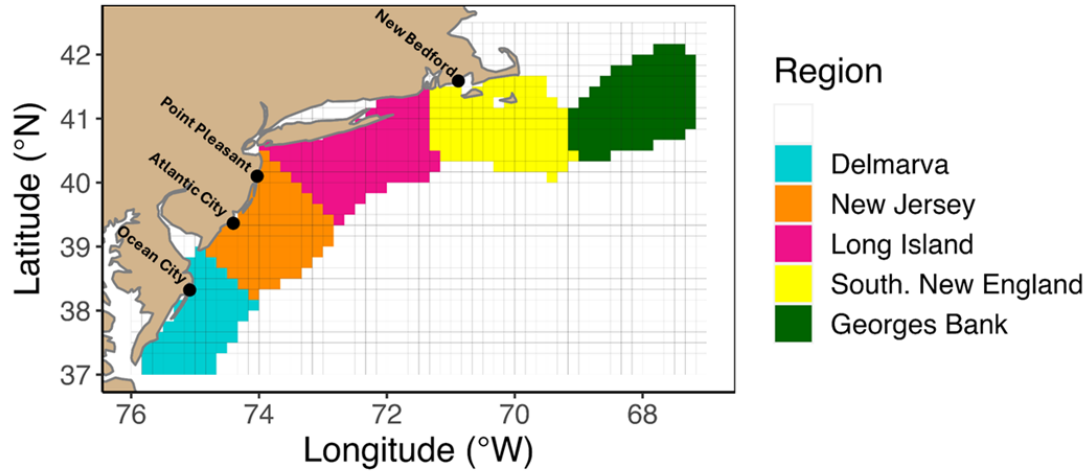


Figure 3.1 Mid-Atlantic Bight subregions historically used to evaluate the distributions of Atlantic surfclams and ocean quahogs. Starting from the southern-most region we have Delmarva, New Jersey, Long Island, Southern New England, and lastly the northern-most region Georges Bank.

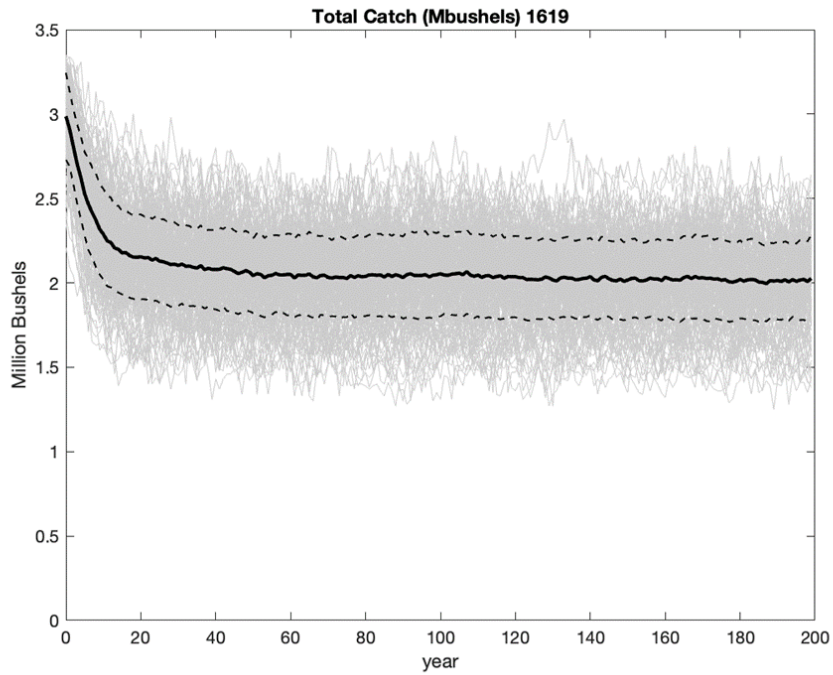


Figure 3.2 Example of the 200 simulations (grey lines) of catch estimates (in millions of bushels) (y-axis) for case 1619, produced over a run of 200 years (x-axis), that go into producing average Atlantic surfclam catch (black line).

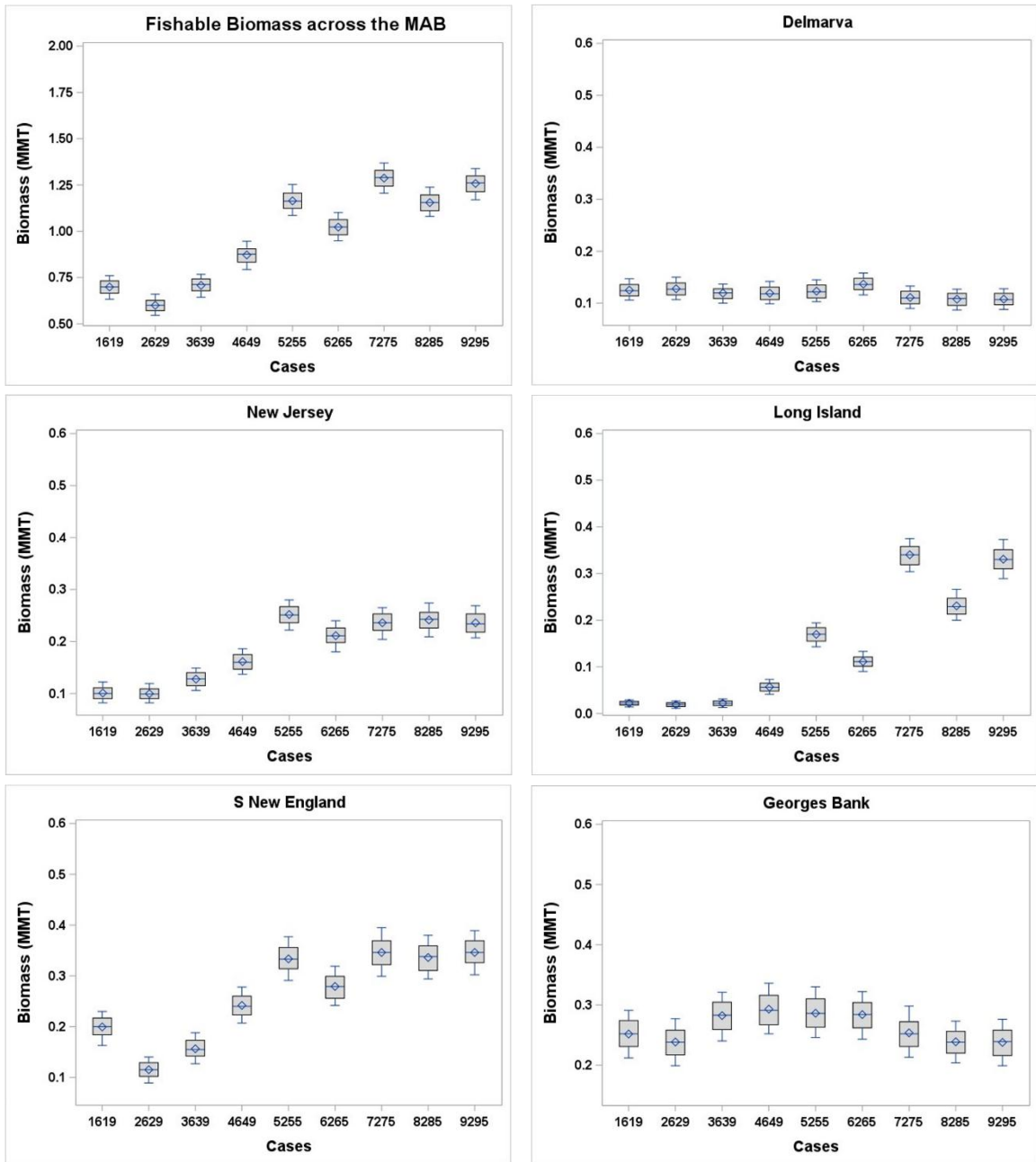


Figure 3.3 Average fishable biomass (in MMT) across all cases in the entire MAB and regionally. Graphic displays a series of boxplots across the nine-decade time series, 2016 – 2096, each containing the inner quartile range of Atlantic surfclam fishable biomass within a 4-year averaged decadal time-step (i.e. 1619, 2629, etc.), with middle bars in each boxplot displaying the median fishable biomass, the square inside the box indicating group mean, and whiskers calculated as the 10th percentile low and the 90th percentile high.

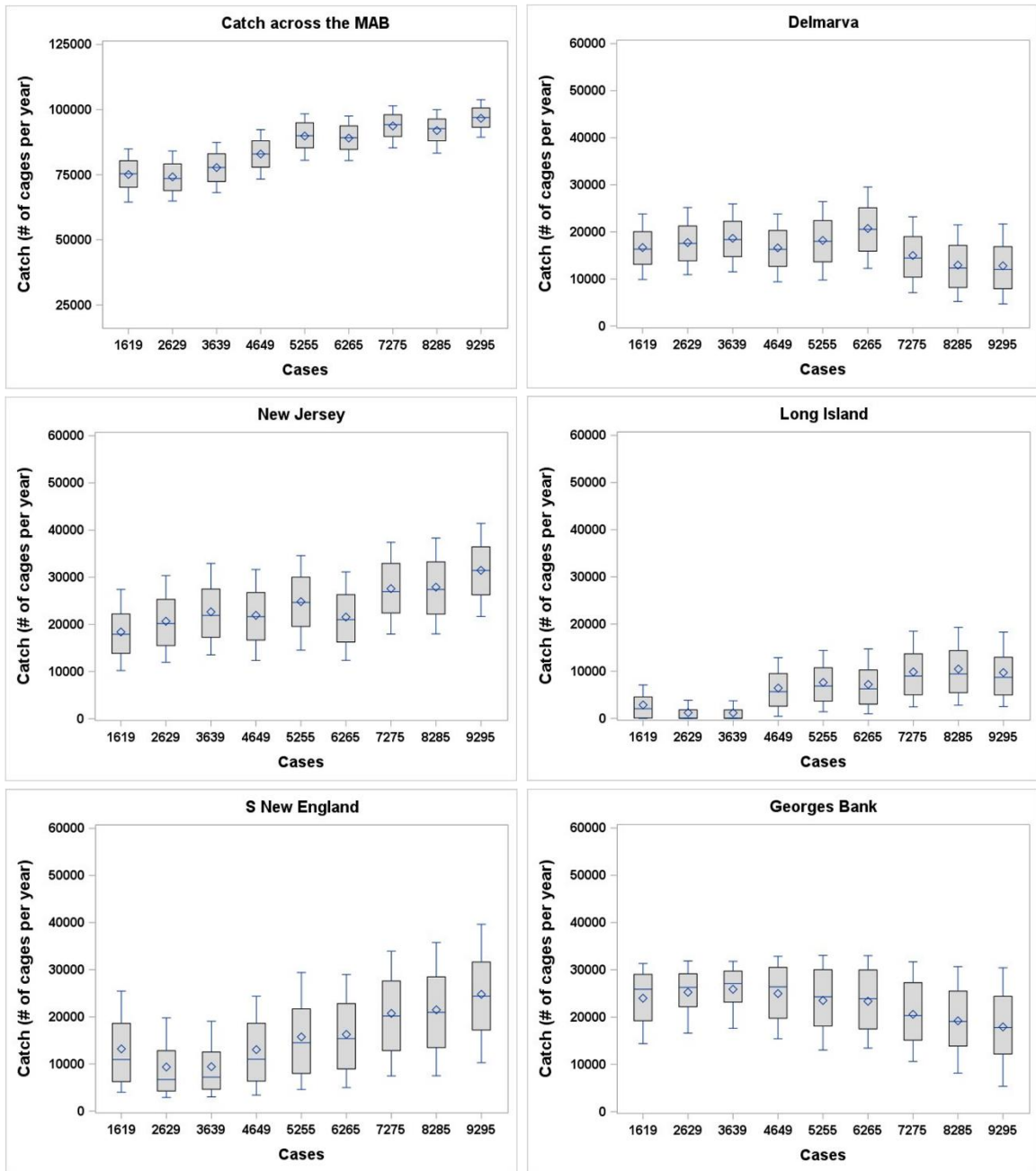


Figure 3.4. Average catch (in number of cages) across all cases in the entire MAB and regionally. Graphic displays a series of boxplots across the nine-decade time series, 2016 – 2096, each containing the inner quartile range of Atlantic surfclam catch within a 4-year averaged decadal time-step (i.e. 1619, 2629, etc.), with middle bars in each boxplot displaying the median catch, the square inside each box indicating group mean, and whiskers displaying the 10th percentile low and the 90th percentile high.

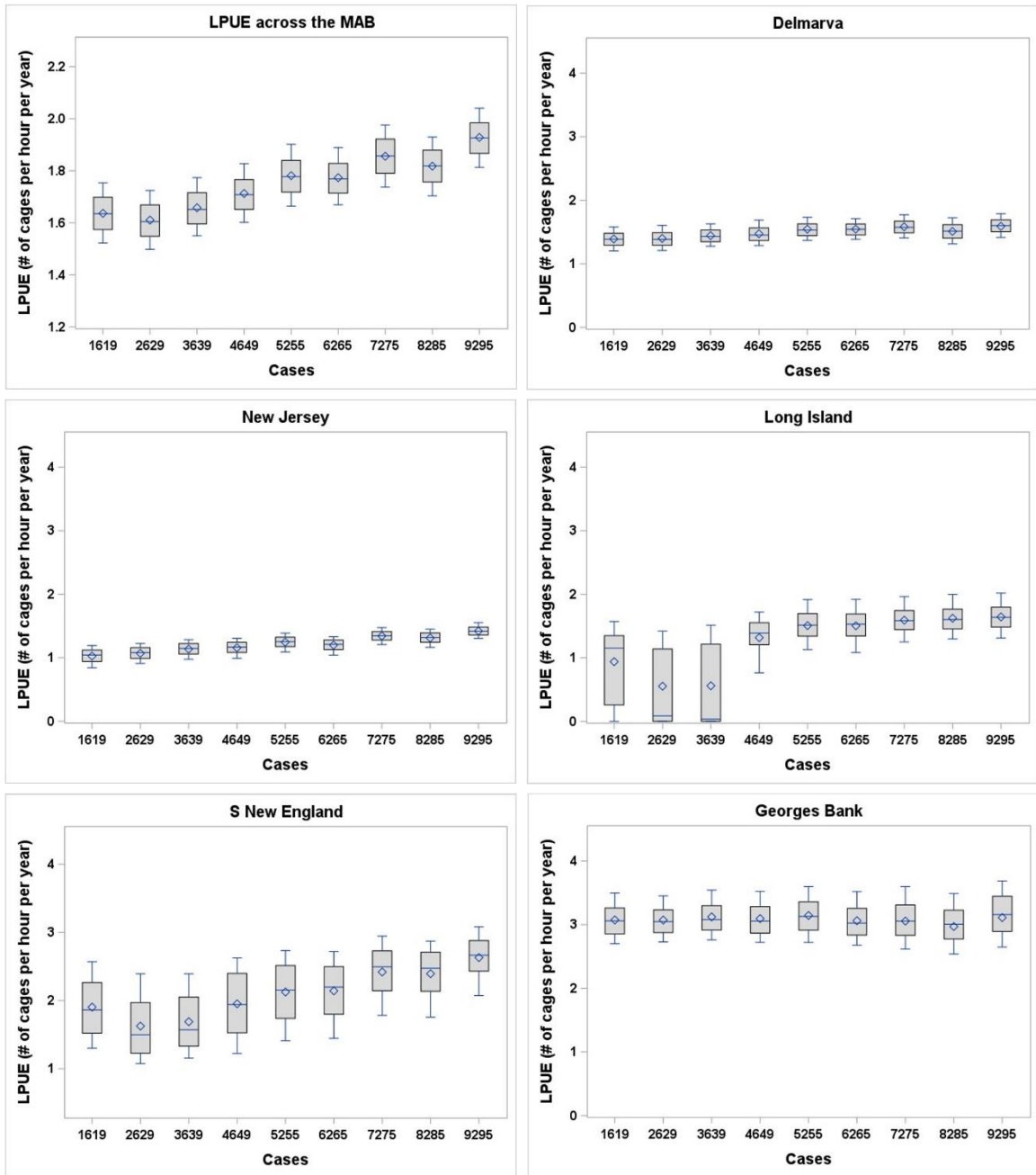


Figure 3.5. Average distribution of LPUE (landings per unit effort) across all cases in the entire MAB and regionally. Graphic displays a series of boxplots across the nine-decade time series, 2016 – 2096, each containing the inner quartile range of LPUE within a 4-year averaged decadal time-step (i.e. 1619, 2629, etc.), with middle bars in each boxplot displaying the median LPUE, the square inside each box indicating group mean, and whiskers displaying the 10th percentile low and the 90th percentile high.

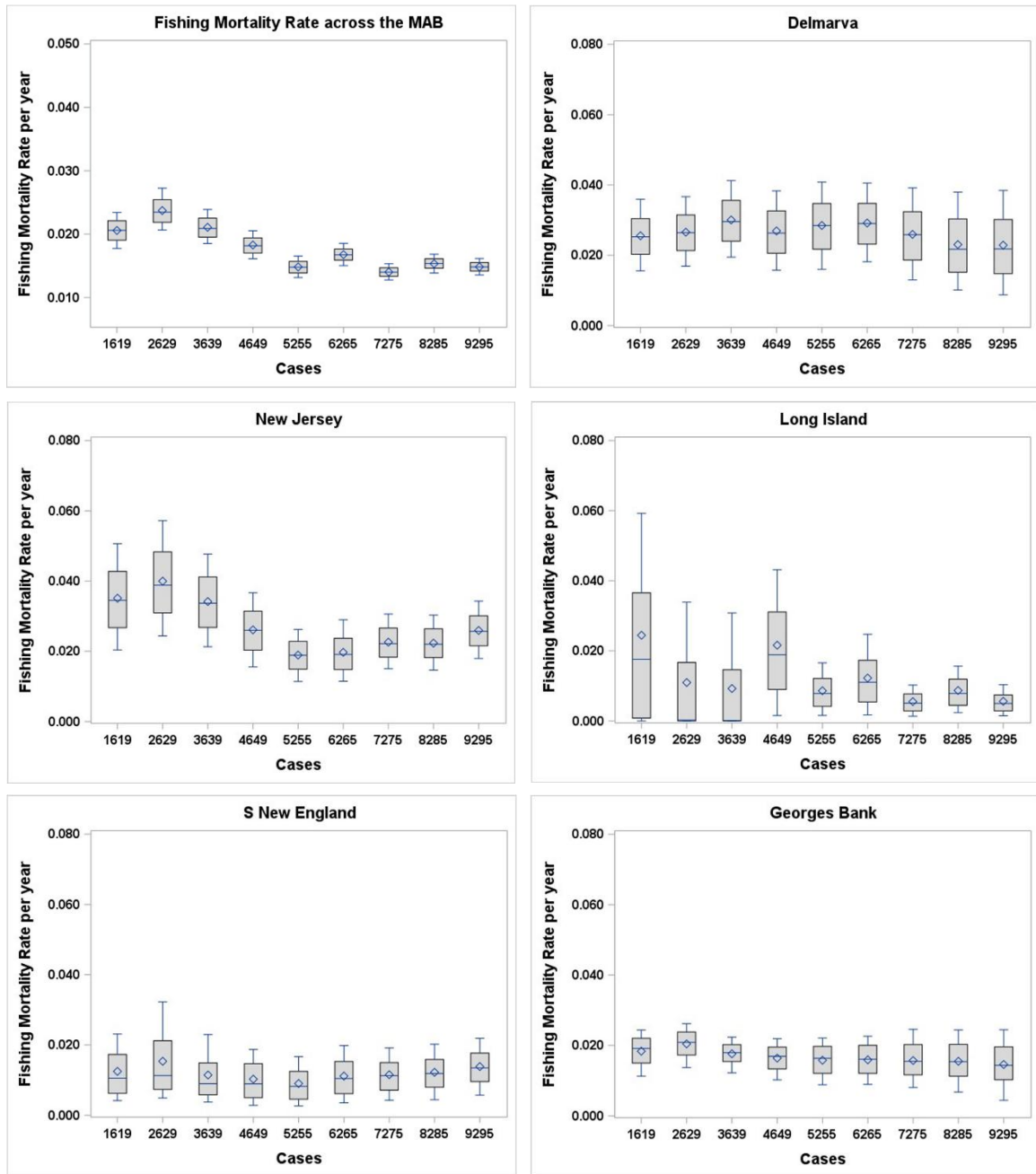


Figure 3.6. Average distribution of fishing mortality rate (yr^{-1}) across all cases in the entire MAB and regionally. Graphic displays a series of boxplots across the nine-decade time series, 2016 – 2096, each containing the inner quartile range of fishing mortality rates within a 4-year averaged decadal time-step (i.e. 1619, 2629, etc.), with middle bars in each boxplot displaying the median fishing mortality rate, the square inside each box indicating group mean, and whiskers displaying the 10th percentile low and the 90th percentile high.

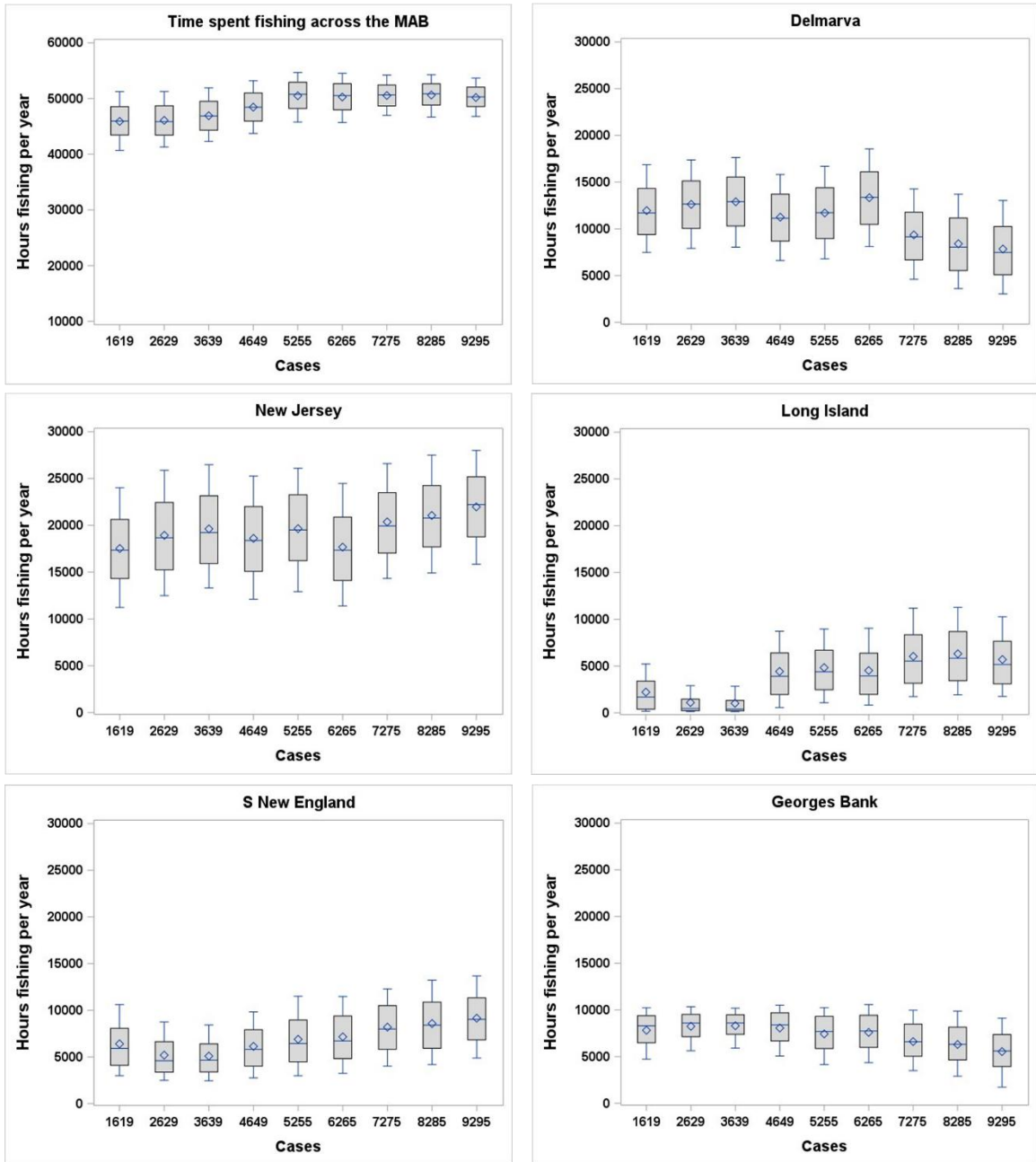


Figure 3.7 Average distribution of time spent fishing (hours yr⁻¹) across all cases in the entire MAB and regionally. Graphic displays a series of boxplots across the nine-decade time series, 2016 – 2096, each containing the inner quartile range of time spent fishing within a 4-year averaged decadal time-step (i.e. 1619, 2629, etc.), with middle bars in each boxplot displaying the median time spent fishing, the square inside each box indicating group mean, and whiskers displaying the 10th percentile low and the 90th percentile high.

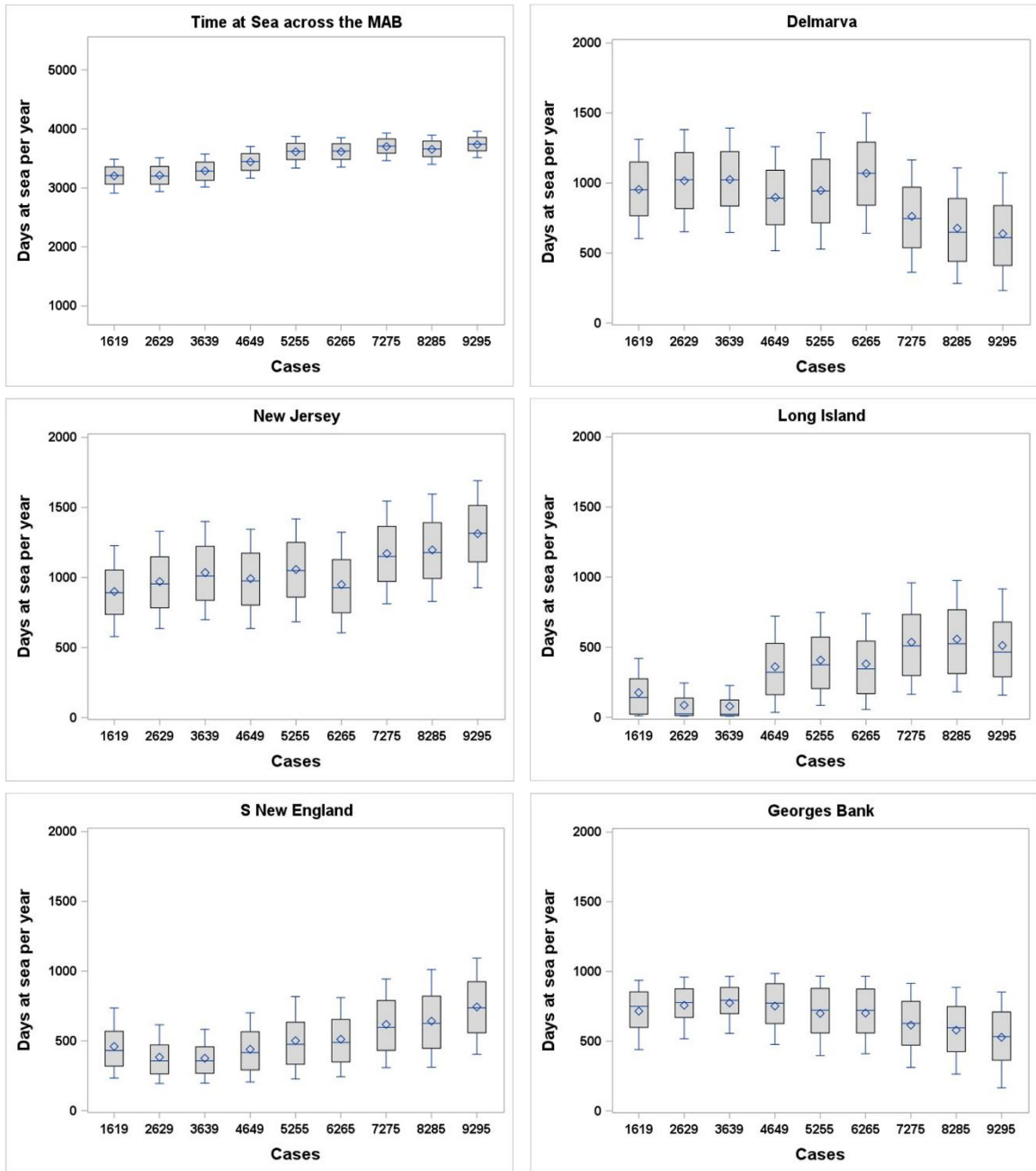


Figure 3.8 Average distribution of time spent at sea (days yr⁻¹) across all cases in the entire MAB and regionally. Graphic displays a series of boxplots across the nine-decade time series, 2016 – 2096, each containing the inner quartile range of time spent at sea within a 4-year averaged decadal time-step (cases 1619 – 9295), with middle bars in each boxplot displaying the median days at sea, the square inside each box indicating group mean, and whiskers displaying the 10th percentile low and the 90th percentile high.

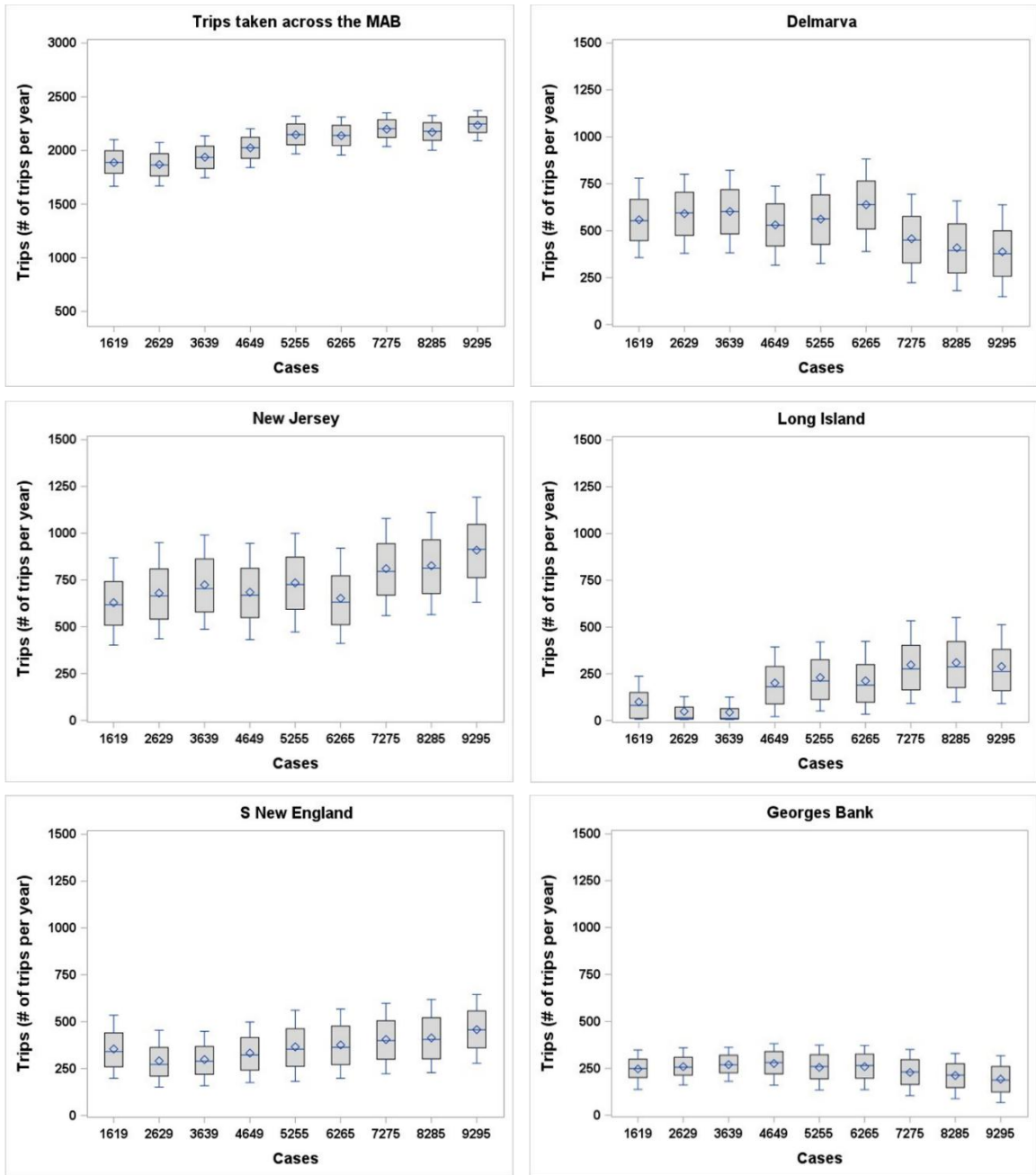


Figure 3.9 Average distribution of the number of trips (yr^{-1}) across all cases in the entire MAB and regionally. Graphic displays a series of boxplots across the nine-decade time series, 2016 – 2096, each containing the inner quartile range of trips taken within a 4-year averaged decadal time-step (cases 1619 – 9295), with middle bars in each boxplot displaying the median trips taken, the square inside each box indicating group mean, and whiskers displaying the 10th percentile low and the 90th percentile high.

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CHAPTER IV – CONCLUSIONS

Projected warming on the Northeast Continental Shelf is expected to continue over the remainder of the century, undoubtedly impacting many commercially valuable species and coastal communities that depend on this resource. Atlantic surfclams are known to be an ecosystem indicator species particularly sensitive to changes in the thermal environment and are therefore an important organism to study as climate change continues to shift marine ecosystem paradigms. Their noteworthy size, biomass dominance, and commercial value all conspire to elevate the species to a bellwether of climate change. Together with the ocean quahog, they establish a quintessential exemplar of how ecosystems are expected to change in the future over very large geographic regions due to climate-induced warming on the northeast continental shelf. In the case of the Atlantic surfclam, our study forecasts the continued offshore and northern movement of this species range over the next three-quarters of a century, eventually colonizing a majority of boreal ocean quahog habitat by the early 2050s. This projected expansion of Atlantic surfclam biomass alongside an opposing, but not equal, decline in ocean quahog habitat on the MAB continental shelf could support one of the greatest biotic reorganizations to be observed on the northeast continental shelf in the 21st century.

Modeled simulations of Atlantic surfclam biomass are estimated to increase by nearly a factor of 2 by the second half of the 21st century, suggesting the potential for an impressive growth in the Atlantic surfclam fishery in the

coming decades. Though our model projects the fishery to benefit from anticipated warming temperatures, with a majority of fishing grounds experiencing increasing standing stock, fishery landings, and time at sea without substantial negative economic impacts, this steady increase in biomass certainly presents serious implications for fisheries management in establishing reference points for the stock. Anticipated climate change impacts on the health of fisheries stock necessitate adjustments to be made on the development of MSY reference points in fisheries models as environmental conditions continue to change carrying capacities.

APPENDIX A– Regional Atlantic surfclam biomass by case

Table A.1 Average whole stock and fishable biomass per case across each region.

Case	Region	Average Whole Stock Biomass (MMT)	Average Fishable Biomass (MMT)
C1619	1	0.185	0.136
	2	0.153	0.110
	3	0.046	0.023
	4	0.291	0.210
	5	0.358	0.264
2629	1	0.190	0.140
	2	0.154	0.110
	3	0.041	0.019
	4	0.178	0.122
	5	0.345	0.253
3639	1	0.179	0.131
	2	0.191	0.139
	3	0.045	0.022
	4	0.234	0.164
	5	0.399	0.296
4649	1	0.176	0.129
	2	0.234	0.173
	3	0.093	0.060
	4	0.342	0.249
	5	0.410	0.304
5255	1	0.183	0.134
	2	0.353	0.265
	3	0.241	0.175
	4	0.461	0.343
	5	0.400	0.296
6265	1	0.203	0.150
	2	0.298	0.222
	3	0.163	0.114
	4	0.391	0.288
	5	0.397	0.294
7275	1	0.165	0.120
	2	0.336	0.252
	3	0.463	0.347
	4	0.479	0.356
	5	0.356	0.262

Table A.1 (continued).

8284	1	0.159	0.116
	2	0.343	0.258
	3	0.321	0.237
	4	0.468	0.348
	5	0.337	0.247
9295	1	0.159	0.116
	2	0.339	0.254
	3	0.450	0.338
	4	0.484	0.360
	5	0.335	0.245

APPENDIX B – Regional fishing metrics by case

Table B.1 Average regional fishing metrics across all cases.

Region	Case	Biomass (MMT)	Catch (# cages yr ⁻¹)	LPUE (# cages hr-fished ⁻¹)	Fishing Mortality rate (yr ⁻¹)	Time Spent Fishing (hours yr ⁻¹)	Time at Sea (Days yr ⁻¹)	Number of Trips (yr ⁻¹)
Delmarva	1619	0.125	16,667	1.39	0.025	11951	954	558
	2629	0.128	17,725	1.40	0.026	12622	1016	591
	3639	0.119	18,634	1.44	0.030	12896	1025	602
	4649	0.119	16,604	1.47	0.027	11245	897	531
	5255	0.123	18,191	1.54	0.028	11705	946	561
	6265	0.137	20,724	1.54	0.029	13335	1070	638
	7275	0.111	14,988	1.58	0.026	9350	761	457
	8285	0.108	12,934	1.51	0.023	8404	677	409
	9295	0.108	12,789	1.59	0.023	7840	638	388
	New Jersey	1619	0.101	18,389	1.02	0.035	17522	899
2629		0.0200	20,669	1.07	0.040	18933	970	679
3639		0.128	22,660	1.14	0.034	19623	1035	724
4649		0.161	21,920	1.16	0.026	18610	992	684
5255		0.252	24,815	1.25	0.019	19649	1057	734
6265		0.211	21,548	1.20	0.020	17678	949	652
7275		0.236	27,581	1.34	0.023	20371	1171	810
8285		0.241	27,897	1.31	0.022	21053	1197	826
9295		0.236	31,468	1.42	0.026	21974	1313	909
Long Island		1619	0.0220	2,849	0.939	0.024	2207	176
	2629	0.0189	1,200	0.553	0.011	1089	86	49
	3639	0.0220	1,163	0.559	0.009	1011	78	44
	4649	0.568	6,421	1.32	0.022	4412	361	201
	5255	0.170	7,614	1.51	0.009	4826	408	230
	6265	0.111	7,186	1.50	0.012	4516	381	212
	7275	0.340	9,849	1.59	0.005	6027	536	298
	8285	0.231	10,461	1.6	0.009	6303	558	309
	9295	0.331	9,710	1.64	0.006	5693	512	289

Appendix B.1 (continued).

Southern New England	1619	0.199	13,193	1.90	0.012	6395	460	354
	2629	0.115	9,346	1.62	0.015	5185	383	291
	3639	0.156	9,415	1.69	0.011	5083	375	298
	4649	0.242	13,034	1.95	0.010	6129	439	332
	5255	0.333	15,735	2.13	0.009	6883	501	365
	6265	0.279	16,262	2.14	0.011	7149	511	376
	7275	0.346	20,730	2.42	0.011	8185	618	405
	8285	0.336	21,487	2.39	0.012	8572	641	413
	9295	0.346	24,784	2.63	0.014	9143	743	458
Georges Bank	1619	0.252	23,994	3.07	0.018	7818	715	246
	2629	0.238	25,250	3.07	0.020	8244	757	259
	3639	0.282	25,893	3.12	0.018	8301	775	270
	4649	0.293	24,980	3.09	0.016	8062	752	276
	5255	0.286	23,517	3.14	0.016	7432	699	255
	6265	0.284	23,356	3.06	0.016	7593	701	259
	7275	0.253	20,581	3.06	0.016	6608	615	228
	8285	0.239	19,200	2.97	0.015	6296	579	211
	9295	0.238	17,921	3.11	0.014	5535	528	191

Table B.2 Least squares means post-hoc analysis on regional Atlantic surfclam fishable biomass significance between case scenarios per region. Asterisks denote significance levels between case biomass values per region; “****” indicates a P-value of $P^{****} \leq 0.0001$, “***” indicates a P-value of $0.0001 < P^{**} \leq 0.001$, and “**” indicates a P-value of $0.001 < P^* \leq 0.01$, and “NS” indicates no significant difference.

Delmarva								
1619	***	***	***	***	***	***	***	***
2629		***	***	***	***	***	***	***
3639			NS	***	***	***	***	***
4649				***	***	***	***	***
5255					***	***	***	***
6265						***	***	***
7275							***	***
8285								NS
	2629	3639	4649	5255	6265	7275	8285	9295

New Jersey								
1619	NS	***	***	***	***	***	***	***
2629		***	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					***	***	***	***
6265						***	***	***
7275							***	NS
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Long Island								
1619	***	NS	***	***	***	***	***	***
2629		***	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					***	***	***	***
6265						***	***	***
7275							***	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Table B.2 (continued)

Southern New England								
1619	***	***	***	***	***	***	***	***
2629		***	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					***	***	**	***
6265						***	***	***
7275							***	NS
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Georges Bank								
1619	***	***	***	***	***	NS	***	***
2629		***	***	***	***	***	NS	NS
3639			***	***	NS	***	***	***
4649				***	***	***	***	***
5255					NS	***	***	***
6265						***	***	***
7275							***	***
8285								NS
	2629	3639	4649	5255	6265	7275	8285	9295

Table B.3 Least squares means post-hoc analysis on regional Atlantic surfclam catch significance between case scenarios per region. Asterisks denote significance levels between case biomass values per region; “****” indicates a P-value of $P^{****} \leq 0.0001$, “***” indicates a P-value of $0.0001 < P^{**} \leq 0.001$, and “**” indicates a P-value of $0.001 < P^* \leq 0.01$, and “NS” indicates no significant difference.

Delmarva								
1619	***	***	NS	***	***	***	***	***
2629		***	***	NS	***	***	***	***
3639			***	NS	***	***	***	***
4649				***	***	***	***	***
5255					***	***	***	***
6265						***	***	***
7275							***	***
8285								NS
	2629	3639	4649	5255	6265	7275	8285	9295

New Jersey								
1619	***	***	***	***	***	***	***	***
2629		***	***	***	***	***	***	***
3639			***	***	**	***	***	***
4649				***	NS	***	***	***
5255					***	***	***	***
6265						***	***	***
7275							NS	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Long Island								
1619	***	***	***	***	***	***	***	***
2629		NS	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					*	***	***	***
6265						***	***	***
7275							***	NS
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Table B.3 (continued).

Southern New England								
1619	***	***	NS	***	***	***	***	***
2629		NS	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					NS	***	***	***
6265						***	***	***
7275							*	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Georges Bank								
1619	***	***	***	NS	*	***	***	***
2629		*	NS	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					NS	***	***	***
6265						***	***	***
7275							***	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Table B.4 Least squares means post-hoc analysis on regional LPUE significance between case scenarios per region. Asterisks denote significance levels between case biomass values per region; “****” indicates a P-value of $P^{****} \leq 0.0001$, “***” indicates a P-value of $0.0001 < P^{***} \leq 0.001$, and “**” indicates a P-value of $0.001 < P^{**} \leq 0.01$, and “NS” indicates no significant difference.

Delmarva								
1619	NS	***	***	***	***	***	***	***
2629		***	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					NS	***	***	***
6265						***	***	***
7275							***	NS
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

New Jersey								
1619	***	***	***	***	***	***	***	***
2629		***	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					***	***	***	***
6265						***	***	***
7275							***	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Long Island								
1619	***	***	***	***	***	***	***	***
2629		NS	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					NS	***	***	***
6265						***	***	***
7275							NS	**
8285								NS
	2629	3639	4649	5255	6265	7275	8285	9295

Table B.4 (continued).

Southern New England								
1619	***	***	**	***	***	***	***	***
2629		***	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					NS	***	***	***
6265						***	***	***
7275							NS	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Georges Bank								
1619	NS	**	NS	***	NS	NS	***	*
2629		**	NS	***	NS	NS	***	*
3639			NS	NS	***	***	***	NS
4649				**	NS	*	***	NS
5255					***	***	***	NS
6265						NS	***	**
7275							***	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Table B.5 Least squares means post-hoc analysis on regional fishing mortality rate significance between case scenarios per region. Asterisks denote significance levels between case biomass values per region; “****” indicates a P-value of $P^{****} \leq 0.0001$, “***” indicates a P-value of $0.0001 < P^{***} \leq 0.001$, and “**” indicates a P-value of $0.001 < P^{**} \leq 0.01$, and “NS” indicates no significant difference.

Delmarva								
1619	**	***	***	***	***	NS	***	***
2629		*	NS	***	***	NS	***	***
3639			***	***	*	***	***	***
4649				***	***	**	***	***
5255					NS	***	***	***
6265						***	***	***
7275							***	***
8285								NS
	2629	3639	4649	5255	6265	7275	8285	9295

New Jersey								
1619	***	**	***	***	***	***	***	***
2629		***	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	NS
5255					*	***	***	***
6265						***	***	***
7275							NS	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Long Island								
1619	***	***	***	***	***	***	***	***
2629		***	***	***	*	***	***	***
3639			***	NS	***	***	NS	***
4649				***	***	***	***	***
5255					***	***	NS	***
6265						***	***	***
7275							***	NS
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Table B.5 (continued).

Southern New England								
1619	***	***	***	***	***	***	NS	***
2629		***	***	***	***	***	***	***
3639			***	***	NS	NS	**	***
4649				***	***	***	***	***
5255					***	***	***	***
6265						NS	***	***
7275							*	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Georges Bank								
1619	***	***	***	***	***	***	***	***
2629		***	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				**	*	***	***	***
5255					NS	NS	NS	***
6265						NS	NS	***
7275							NS	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Table B.6 Least squares means post-hoc analysis on regional time spent fishing significance between case scenarios per region. Asterisks denote significance levels between case biomass values per region; “****” indicates a P-value of $P^{****} \leq 0.0001$, “***” indicates a P-value of $0.0001 < P^{***} \leq 0.001$, and “**” indicates a P-value of $0.001 < P^{**} \leq 0.01$, and “NS” indicates no significant difference.

Delmarva								
1619	***	***	***	NS	***	***	***	***
2629		NS	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					***	***	***	***
6265						***	***	***
7275							***	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

New Jersey								
1619	***	***	***	***	NS	***	***	***
2629		***	NS	***	***	***	***	***
3639			***	NS	***	***	***	***
4649				***	***	***	***	***
5255					***	***	***	***
6265						***	**	***
7275							***	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Long Island								
1619	***	***	***	***	***	***	***	***
2629		NS	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	NS	***	***	***
5255					**	***	***	***
6265						***	***	***
7275							*	**
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Table B.6 (continued).

Southern New England								
1619	***	***	*	***	***	***	***	***
2629		NS	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					*	***	***	***
6265						***	***	***
7275							***	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Georges Bank								
1619	***	***	**	***	*	***	***	***
2629		NS	*	***	***	***	***	***
3639			**	***	***	***	***	***
4649				***	***	***	***	***
5255					NS	***	***	***
6265						***	***	***
7275							***	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Table B.7 Least squares means post-hoc analysis on regional time at sea significance between case scenarios per region. Asterisks denote significance levels between case biomass values per region; “****” indicates a P-value of $P^{****} \leq 0.0001$, “***” indicates a P-value of $0.0001 < P^{***} \leq 0.001$, and “**” indicates a P-value of $0.001 < P^{**} \leq 0.01$, and “NS” indicates no significant difference.

Delmarva								
1619	***	***	***	NS	***	***	***	***
2629		NS	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					***	***	***	***
6265						***	***	***
7275							***	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

New Jersey								
1619	***	***	***	***	***	***	***	***
2629		***	NS	***	NS	***	***	***
3639			***	*	***	***	***	***
4649				***	***	***	***	***
5255					***	***	***	***
6265						***	***	***
7275							*	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Long Island								
1619	***	***	***	***	***	***	***	***
2629		NS	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	*	***	***	***
5255					**	***	***	***
6265						***	***	***
7275							*	*
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Table B.7 (continued).

Southern New England								
1619	***	***	*	***	***	***	***	***
2629		NS	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					NS	***	***	***
6265						***	***	***
7275							**	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Georges Bank								
1619	***	***	**	NS	NS	***	***	***
2629		*	NS	***	***	***	***	***
3639			**	***	***	***	***	***
4649				***	***	***	***	***
5255					NS	***	***	***
6265						***	***	***
7275							***	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Table B.8 Least squares means post-hoc analysis on regional number of trips significance between case scenarios per region. Asterisks denote significance levels between case biomass values per region; “****” indicates a P-value of $P^{****} \leq 0.0001$, “***” indicates a P-value of $0.0001 < P^{***} \leq 0.001$, and “**” indicates a P-value of $0.001 < P^{**} \leq 0.01$, and “NS” indicates no significant difference.

Delmarva								
1619	***	***	***	NS	***	***	***	***
2629		NS	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					***	***	***	***
6265						***	***	***
7275							***	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

New Jersey								
1619	***	***	***	***	***	***	***	***
2629		***	NS	***	***	***	***	***
3639			***	NS	***	***	***	***
4649				***	***	***	***	***
5255					***	***	***	***
6265						***	***	***
7275							*	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Long Island								
1619	***	***	***	***	***	***	***	***
2629		NS	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	*	***	***	***
5255					***	***	***	***
6265						***	***	***
7275							*	NS
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Table B.8 (continued).

Southern New England								
1619	***	***	***	*	***	***	***	***
2629		NS	***	***	***	***	***	***
3639			***	***	***	***	***	***
4649				***	***	***	***	***
5255					NS	***	***	***
6265						***	***	***
7275							NS	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295

Georges Bank								
1619	***	***	***	*	***	***	***	***
2629		***	***	NS	NS	***	***	***
3639			NS	***	***	***	***	***
4649				***	***	***	***	***
5255					NS	***	***	***
6265						***	***	***
7275							***	***
8285								***
	2629	3639	4649	5255	6265	7275	8285	9295