

The Atlantic surfclam fishery and offshore wind energy development: 1. Model development and verification

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Competing pressures imposed by climate-related warming and offshore development have created a need for quantitative approaches that anticipate fisheries responses to these challenges. This study used a spatially explicit, ecological-economic agent-based model integrating dynamics associated with Atlantic surfclam stock biology, decision-making behavior of fishing vessel captains, and fishing fleet behavior to simulate stock biomass, and fishing vessel catch, effort and landings. Simulations were implemented using contemporary Atlantic surfclam stock distributions and characteristics of the surfclam fishing fleet. Simulated distribution of fishable surfclam biomass was determined by a spatially varying mortality rate, fishing by the fleet was controlled by captain decisions based on previous knowledge, information sharing, and the ability to search and find fishing grounds. Quantitative and qualitative evaluation of simulation results showed that this modeling approach sufficiently represents Atlantic surfclam fishery dynamics. A fishing simulation showed that the captain's decision-making and stock knowledge, and the distribution of fishing grounds relative to home ports controlled the landed catch. The approach used herein serves as the basis for future studies examining response of the Atlantic surfclam fishery to a nexus of simultaneous, complex natural and anthropogenic pressures, and provides a framework for similar models for other resources facing similar pressures.

Keywords: Atlantic surfclam, agent-based model, Middle Atlantic Bight, ocean multi-use, spatial model.

Introduction

Increasing industrialization and expanded uses of the coastal ocean are producing challenges for established and new user communities because of overlapping and competing needs, such as conflicts between existing fisheries and developing offshore renewable energy and aquaculture industries (Arbo and Thy, 2016; Schupp *et al.*, 2019). This offshore development is coincident with a warming climate that is altering the coastal ocean habitat and distribution of commercial fish stocks, thereby posing a salient threat to the stability and productivity of marine fisheries (Kleisner *et al.*, 2017; Free *et al.*, 2019; Rogers *et al.*, 2019). Tools that can predict and proactively manage these complex and interconnected challenges to marine fisheries are an increasingly important approach for managers and planners to evaluate costs and benefits of strategies that allow for multiple users of the offshore environment.

The Atlantic surfclam (*Spisula solidissima*), a long-lived and large-bodied clam, supports a fishery that is a major economic driver for communities from Virginia to Massachusetts (Figure 1). Collectively, the Atlantic surfclam and ocean quahog (*Arctica islandica*) fisheries generate USD 1.3 Billion annually in total economic impacts (Murray, 2016) and the Atlantic surfclam fishery landings alone exceed \$30 Million USD (ex-vessel) in annual revenue. The distribution of the Atlantic surfclam population is confined to the inner and mid-shelf of the Middle Atlantic Bight (MAB, Figure 1); areas that have been designated for offshore wind energy development. More-

over, landings from the Atlantic surfclam fishery to the major ports (Atlantic City, NJ and New Bedford, MA, Figure 1) come from areas slated for development as offshore wind energy farms (Methratta *et al.*, 2020). The vessels and gear used to harvest Atlantic surfclams (large vessels with hydraulic dredges) make fishing in and around wind farm infrastructure, such as buried cables and support structures, highly uncertain, which exacerbates economic vulnerability of the fishery to wind farms (Kirkpatrick *et al.*, 2017).

The MAB (Figure 1), where the bulk of the Atlantic surfclam fishery operates, is warming in response to long-term climate change at rates faster than reported for other continental shelves (Saba *et al.*, 2016). The Atlantic surfclam has a limited thermal tolerance (Kim and Powell, 2004; Munroe *et al.*, 2013), making it vulnerable to warming bottom temperatures (Narváez *et al.*, 2015). The northward shift in the range occupied by this species has been attributed to warming bottom temperature over the past three to four decades (Hennen *et al.*, 2018; Hofmann *et al.*, 2018). This distribution change has affected Atlantic surfclam catch per unit effort with consequent economic effects on dependent communities (McCay *et al.*, 2011). Thus, the Atlantic surfclam fishery is simultaneously at risk from warming bottom temperatures and offshore wind energy development.

The interconnectivities of offshore wind energy development, warming temperatures, and Atlantic surfclam population distribution are complex, making evaluation of the

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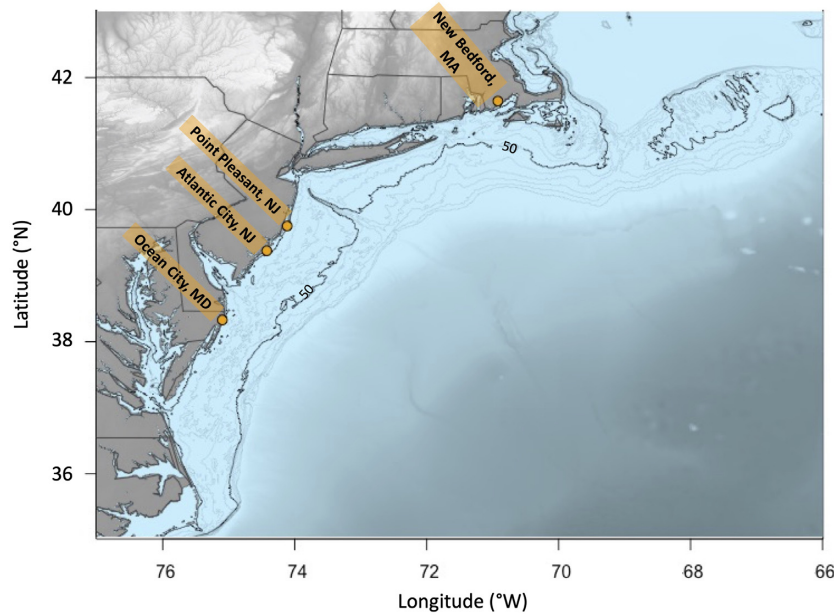


Figure 1. Map of the Middle Atlantic Bight showing locations of the major ports for the Atlantic surfclam fishing fleet (orange circles). Over much of the MAB, Atlantic surfclam habitat on the continental shelf is bounded inshore by the 10-m isobath and offshore by the 50-m isobath (black line).

fishery's exposure to these stressors difficult. Identifying and assessing potential outcomes and impacts, with associated costs and benefits, is integral to developing mitigation strategies that will afford some level of sustainability for the Atlantic surfclam fishery. Thus, quantitative evaluations of interactions between offshore wind energy development and warming bottom temperatures on the Atlantic surfclam fishery, with particular focus on economic impacts, are needed.

The spatially explicit, ecological-economic agent-based Atlantic surfclam fishery model used in this study provides the capability for quantitative evaluations of the fishery and its economics. The focus of this study is on simulation of fishing fleet behavior, and evaluation of the simulations with observations of fishing effort, distribution, and total landings. These analyses provide verification for establishing a reference simulation that is the basis for projections of the economic impacts of wind farm placement on the Atlantic surfclam fishery, which is the focus of a companion paper (Scheld *et al.*, 2022).

Materials and methods

Model overview

The model implemented in this study, Spatially Explicit Fishery Economics Simulator (*SEFES*), includes components that simulate Atlantic surfclam fishable stock, the economics of the processing plants, fishing fleet behavior and economics, and fishing behavior (Figure 2). The Fishable Stock is obtained from an Atlantic surfclam population dynamics model that includes growth, recruitment, and natural and fishery-based mortality to provide an estimate of biomass (yield) that is available to the fishery. Removal of the fishable biomass (Fishing) depends on the memory, searching, and communication skills of captain of individual fishing vessels. The individual fishing boats combine to form fishing fleets that are made up of specific vessel types, and home port locations (Fishing

Fleet). The fishing fleet disperses from its home port, providing spatial variability in the distribution of fishing effort and in the acquisition of the allowed fishing quota. The landed fishing quota determines the economics of individual processing plants (Processor). External forces that modify the individual components and between-component interaction are offshore wind energy development (Multiple Ocean Users), climate-related warming of bottom temperature and seasonal weather (Climate & Weather), species overlap with other clam stocks (Biological Interactions), which affects the ability to fish, and management decisions that modify the fishable quotas (Management). These components of *SEFES* are represented by detailed processes that govern interactions within a component and between components (Figure S1). Data from the Atlantic surfclam stock assessment surveys and management council, fishery-dependent data, and guidance from Atlantic surfclam industry and management representatives provided inputs for the development of implementation of *SEFES* as well as for verification of simulations.

The population dynamics model included in Fishable Biomass component simulates the change in number (surfclams m^{-2}) and size distribution (1-cm shell length intervals) of Atlantic surfclams. Spatially explicit growth and mortality rates (Figure 3a) estimated from stock assessment observations were imposed, allowing observed gradients in Atlantic surfclam size, growth rate, and abundance to emerge in the simulations. Recruitment is defined using Beverton–Holt stock recruit dynamics (Beverton and Holt, 1993) with parameters based on stock assessment observations (NEFSC, 2022) and detailed evaluations of recruitment as influenced by post-settlement mortality (Timbs *et al.*, 2019).

The active agents in *SEFES* are the captains (Fishing component) and fishing vessels (Fishing Fleet component). Each Atlantic surfclam fishing vessel (Fishing) is controlled by a captain with specified characteristics that determine where and how efficiently the vessel harvests the fishable Atlantic surfclam biomass (Figure 3b). The captain's memory, and communication and searching skills were specified using informa-

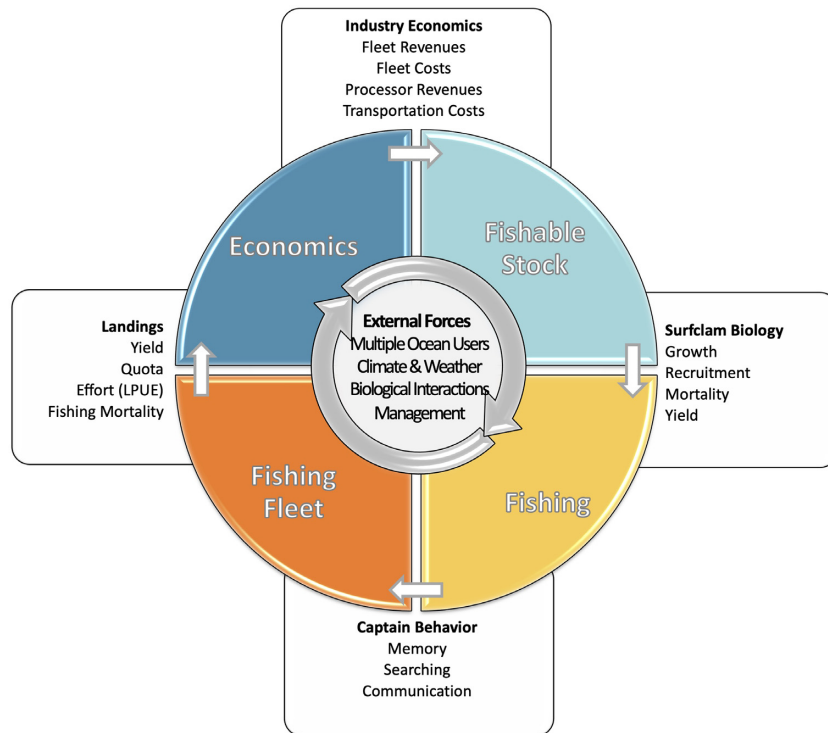


Figure 2. Components included in *SEFES* represent the Fishable Stock (light blue), Fishing (yellow), Fishing Fleet (orange), and Economics (dark blue). The primary processes that determine each component and links between components (outside boxes) and the external forces that affect all model components (inner circle) are shown. Details of *SEFES* used in this paper are provided in the text and in the description of the full *SEFES* model is provided in supplemental materials (Figure S1).

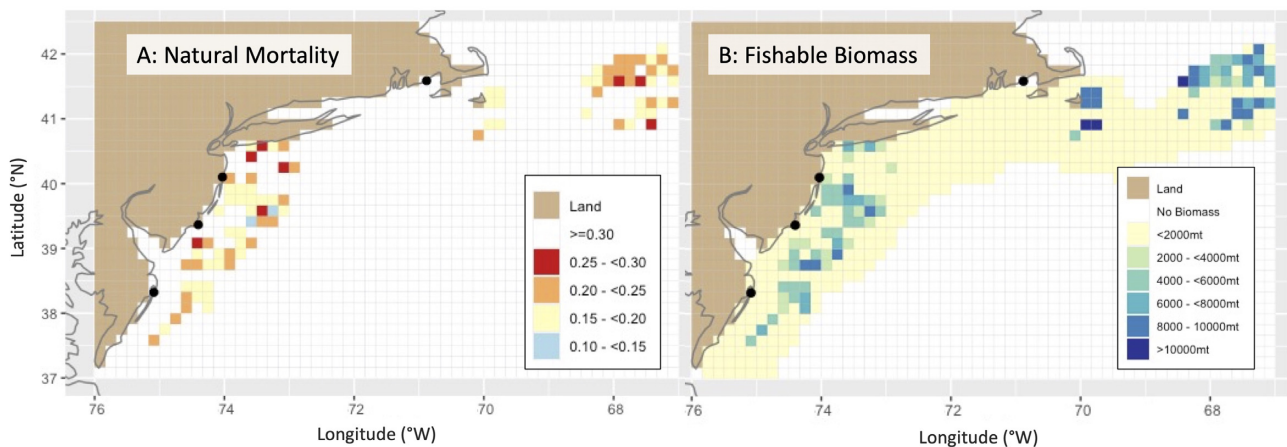


Figure 3. Map of the Middle Atlantic Bight showing the model domain and locations of ports for the Atlantic surfclam fishing fleet (black dots). The model domain is composed of 10' latitude by 10' longitude (about 10 NM on each side) rectangular squares, with 54 cells east-west across the shelf and 33 cells north-south. (A) Spatial distribution of natural specific mortality rate (yr^{-1}) input to the Atlantic surfclam spatially explicit population dynamics model. (B) Average annual distribution of fishable (> 120 mm shell length) Atlantic surfclam biomass (metric tons, mt) obtained from the population dynamics model included in the Fishable Biomass component of *SEFES* (Figure 2). The land areas (tan) and coastline (black line) are indicated.

tion provided by Atlantic surfclam fishing captains to ensure that the model decisions reflect those made in the real fishery (Smajgl and Barreteau, 2017).

The characteristics assigned to fishing vessels (Fishing Fleet) determine speed, Atlantic surfclam harvest rates, landing capacities, and costs and are based on those associated with vessels in the actual fishing fleet. Vessels move around the model domain and harvest Atlantic surfclams based on decisions by each captain that are constrained by the operating characteris-

tics of the vessel, such as speed, maximum time allowed at sea, and imposed harvest quota, as well as the knowledge base of the captain which integrates previous experience with natural fishing ability.

The simulated Atlantic surfclam harvest is purchased by specific processing plants (Industry Economics) associated with the home port of the fishing vessel. The processes and interactions of these components of *SEFES* are discussed in Scheld *et al.* (2022).

The *SEFES* framework was implemented in a model domain that extends from Georges Bank to Chesapeake Bay and consists of 10' latitude by 10' longitude squares (ten-minute squares, hereafter TMS, Figure 3). The model grid is consistent with the survey regions used for the Atlantic surfclam stock assessment along the MAB conducted by the Northeast Fisheries Science Center (e.g. NEFSC, 2022). The model domain includes relevant Atlantic surfclam fishing ports along the MAB (Figures 1 and 3). An overview of the processes included in Fishable Stock, Fishing and Fishing Fleet components of *SEFES* used to establish a reference simulation follows; the fleet, processor, and economics processes included in the Industry Economics component are described in Scheld *et al.* (2022).

Surfclam biology

The implementation of the Atlantic surfclam population dynamics model was based on data and observations that describe the current conditions, 2016 to 2019, of the stock and fishery. This restriction in time allows the model to reflect the contemporary stock and prevent bias by the shift in Atlantic surfclam range over recent decades (Hennen *et al.*, 2018; Hofmann *et al.*, 2018).

Atlantic surfclam length, wet weight, and growth

The Atlantic surfclam population dynamics model uses 18 length classes, specified at 10-mm intervals between 20 and 200 mm. The average length for a category is the average of the lengths on either edge of the length class, e.g. the first interval includes all Atlantic surfclams between 20 and 30 mm in length and has an average length of 25 mm.

The average wet weight (W , grams) for Atlantic surfclams is obtained from an allometric relationship of the form:

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

using the average length (L , mm) for each size category. The allometric parameters, $a = 5.84 \times 10^{-6} \text{ g mm}^{-1}$ and $b = 3.098$, are specified using values given in Marzec *et al.* (2010). The wet weights are used with the length data obtained from the simulated stock surveys to estimate Atlantic surfclam stock biomass.

A daily growth rate for each Atlantic surfclam size class was calculated from the von Bertalanffy age-length relationship (von Bertalanffy, 1938) given by:

$$L = L_{\infty} \left(1 - e^{-kA}\right) \quad (2)$$

where L is length (mm), L_{∞} is the largest length (mm), k is the specific growth rate (yr^{-1}), and A is age (years). The length, maximum length, and age data were obtained from the Atlantic surfclam stock assessment survey (NEFSC, 2022). Data provided by Mann (unpubl. data) and Munroe *et al.* (2013) were used to estimate growth rate (k) using a nonlinear curve fitting routine. The growth rate, as length change per time, was estimated for each length interval from the age of the Atlantic surfclam at the lower bound of the interval and the length of the surfclam one year younger for each TMS. The one-year length change (mm yr^{-1}) divided by the length change over the interval determines the rate at which Atlantic surfclams move to the next length interval. The von Bertalanffy parameters were adjusted so that the Atlantic surfclams reached the largest lengths routinely encountered (~ 190 mm) in some locations in the model domain. Smaller local maximum lengths

were obtained by varying the mortality rate, as described below.

Atlantic surfclam reproduction and recruitment

Atlantic surfclams recruit to the simulated population once per year on 1 October, about 4.5 months post-spawning in the spring, and 1-month post-spawning in the fall (Ropes, 1968). A stock-recruitment relationship is not available for Atlantic surfclams, so a standard Beverton-Holt relationship was used (Beverton and Holt, 1993). The total number of recruits was estimated from the total population biomass assuming a steepness of 0.8, following Myers *et al.* (1999) and O'Leary *et al.* (2011). Interannual recruitment variability was imposed by adding individuals (recruits) to the smallest length interval (20–30 mm) based on a random draw from a negative binomial distribution, which provides a patchy distribution among each TMS. The smallest length interval is consistent with juvenile growth rates that result in newly settled Atlantic surfclams reaching 20 mm by the end of the settlement year (Chintala and Grassle, 1995; Ma, 2005; Acquafredda *et al.*, 2019).

Atlantic surfclam mortality

Mortality rate varies along the MAB shelf (Weinberg, 1998), which imposes spatial variability on Atlantic surfclam abundances. Recruitment is assumed to occur everywhere in the model domain, which is consistent with the observed wider geographic distribution of recruits relative to adults (Timbs *et al.*, 2018) and with simulations from Atlantic surfclam larval transport models (Zhang *et al.*, 2016). However, fishable populations of Atlantic surfclams do not occur over much of the model domain (cf. Figure 3b) because the mortality rate is sufficiently high to prevent development of populations of harvestable size. This mortality gradient, which is driven by habitat suitability, was simulated by specifying a background mortality rate over the model domain that was then modified for each TMS. The background mortality was set at 1.5 year^{-1} (Weinberg, 1998), limiting Atlantic surfclam survival to about 3 years. For TMSs with high (fishable) Atlantic surfclam densities based on the federal stock assessment survey data, mortality rates lower than this background mortality rate were estimated based on abundance or age data from the stock assessment survey (NEFSC, 2022).

The specific mortality rate based on abundance ($Mortality_{abundance}$) was then obtained using a hyperbolic tangent (\tanh) function of the form:

$$Mortality_{abundance} = 0.5 \left(1 - \tanh\left(\frac{D_{TMS} - D_0}{D_r}\right)\right) + m_{base} \quad (3)$$

where D_{TMS} is the observed density of Atlantic surfclams in each TMS, D_0 is a target density ($0.2 \text{ Atlantic surfclams m}^{-2}$), D_r is the density range that allows maximum density ($0.1 \text{ Atlantic surfclams m}^{-2}$) and m_{base} is the average base mortality (0.15 yr^{-1}) used in the stock assessment (NEFSC, 2022).

The specific mortality rate based on animal age ($Mortality_{age}$) for an individual TMS was also estimated using the Atlantic surfclam with the oldest age, as determined from the stock assessment survey, from the relationship given in Hoenig (1983) as:

$$Mortality_{age} = \frac{-\ln(age_{perc})}{age_{max}} \quad (4)$$

Where age_{max} is the oldest observed surfclam in a TMS and age_{perc} is the % of the population that survives to that oldest age, which was assumed to be 1% following Hoenig (1983).

Abundance-based mortality estimates can overestimate mortality if recent recruitment is low, or the stock is under-sampled (Wang and Jiao, 2015). Age-based mortality estimates can be biased if certain ages are under-sampled relative to their frequency in the population (Ricker, 1969). Thus, the estimates obtained from equations (3) and (4) were combined to obtain a mortality rate for each TMS as follows. Abundance- or age-based estimates were used for TMS for which only one of the rates was available. The lower of the two rates was used for TMS for which both estimates were available. For TMS without abundance or age-based rates, mortality rate was calculated from an average of the rates in two or more neighboring TMS.

Surfclam natural mortality was imposed at the end of the simulation year and was the same across all length classes. Initial simulations that used a constant natural mortality of 0.17 yr^{-1} in each TMS resulted in unrealistically high Atlantic surfclam abundances across the model domain (Figure S2). Therefore, a spatially-varying mortality rate that ranged from ~ 0.25 to 0.12 yr^{-1} , with an average of about 0.17 yr^{-1} (Figure 3a), was imposed for the TMSs with Atlantic surfclams.

Atlantic surfclam meat yield

Meat yield depends on the time of year and the TMS. Yield is measured as usable meat and is about 75% of the total wet meat weight (Powell *et al.*, 2015). The actual yield depends on the time of year because Atlantic surfclam meats are heavier in late spring through early fall during the spawning season (Ropes, 1968; Jones, 1981; Spruck *et al.*, 1995). This seasonal variation in meat yield was imposed using a 5th-order polynomial of the form:

$$\begin{aligned} YieldScale_i = & -0.003411 + 1.18 \left(\frac{i}{365} \right) + 24.06 \left(\frac{i}{365} \right)^2 \\ & - 82.28 \left(\frac{i}{365} \right)^3 + 88.46 \left(\frac{i}{365} \right)^4 \\ & - 31.41 \left(\frac{i}{365} \right)^5 \end{aligned} \quad (5)$$

that scales meat yield by day of the year (i) to vary between 5 to 7 kg of Atlantic surfclam meat per bushel. The minimum and maximum yield estimates are based on ranges provided by the Atlantic surfclam industry. The yield curve is based on seasonal catch records provided by the Atlantic surfclam industry to allow incorporation of yield into economic planning. The weight of meat in a bushel that is landed is scaled by the yield curve so that seasonal changes in meat weights supplied to processors are included in the simulations.

Captain behavior

Characteristics associated with the captains of each simulated fishing vessel include searching behavior, differential use of information in older logbooks to inform fishing location decisions, skill at fishing, and a range of tendency to communicate with other captains. Relationships used to describe a captain's decision-making process when planning a fishing trip, con-

straints imposed by landing deadlines and weather, and the tendency to gain or share information about surfclam abundance were obtained from inputs provided by Atlantic surfclam fishery captains and other industry representatives (Smajgl and Barreteau, 2017). Details of these are provided in the following sections.

Captain memory

The captain controls when, where, and how a fishing vessel operates. Information on how a captain makes these decisions is based on memory of past fishing trips, which varies for individual captains. The simulated captain's memory log includes an expected landings per unit effort (LPUE), specified in cages of catch per hour for every fishable TMS in the model domain. At the beginning of a simulation, the distribution of fishable Atlantic surfclam abundance for each TMS is known by every captain (cf. Figure 3b). That is, initially, all captains have omniscient information. At the end of each fishing trip, the catch history in the captain's memory log is updated for the TMS that was fished. In reality, a captain of an Atlantic surfclam fishing vessel is not restricted to a single TMS and often fishes across more than one TMS on a single trip. This information was included in the simulated captain's memories by updating the memory log with the LPUE in a randomly selected TMS adjacent to the one that was fished for 80% of the captain's fishing trips. This approach ensures that the captain's memory of the entire domain is updated or outdated over time depending on the TMS that is fished and changes in the Atlantic surfclam population distribution. The captain uses memory of the LPUE across all TMSs in selecting areas to fish on subsequent trips. Final selection of the target TMS for fishing is obtained by minimizing the sum of fishing time required to fill the hold capacity of the fishing vessel and inbound travel time (steaming time).

Observations and information provided by captains of Atlantic surfclam fishing vessels indicated that captains keep detailed logs of their fishing activities, thereby providing an extensive history of fishing experiences that is used to make decisions about where to fish. The relevance of this information can be expected to decrease over time as fishing, recruitment, and natural mortality change the distribution and abundance of the surfclam stock. Nonetheless, a captain may still use older information to make decisions. This reduction in information relevance was included by assigning each simulated captain a memory weight factor that emphasizes new or old information in the memory record. After fishing in a certain TMS and returning to port, the LPUE for that fishing trip is used to update the information in the captain's memory record and a memory factor that specifies the weight to be placed on recent LPUE information is applied. The updated memory of LPUE (M_{LPUE}) in fished TMS is based on a memory factor (f), the previously remembered LPUE (Old_{LPUE}), and the new LPUE (New_{LPUE}) for that TMS as:

$$M_{LPUE} = fOld_{LPUE} + (1 - f)New_{LPUE} \quad (6)$$

A memory factor of 0.5 indicates that the memory retained is the average of the previously stored and new LPUEs. The captain's memory, but not the memory factor, varies over time during the simulation. In simulations, a captain memory can be assigned memory weight factors ranging from 0.2 to 0.99 which allow memories to be biased towards new or old in-

Table 1. Vessel characteristics by vessel category used for the simulated Atlantic surfclam fishing fleet.

Vessel Category	Hull Length (m)	Number of Vessels	Average Cage Capacity	Average Vessel Steaming Speed (m s ⁻¹)	Average Dredge Width (m)	Wind Conditions Preventing Fishing (m s ⁻¹)
Small	≤24	11	31	4.5	2.3	>5
Medium	24–29	10	54	4.6	3.3	>8
Large	29–33	8	66	4.9	3.7	>8
Jumbo	>33	4	140	5.1	4.6	>10

formation, respectively. Memory weights of 0.2 and 0.8 place emphasis of using information from the previous 1 to 6 weeks, respectively, to make decisions about fishing. Memory weights of 0.98 or 0.99 bases fishing decisions on performance over 7 months to over 1 year, respectively (Powell *et al.*, 2015).

Captain searching

Inputs from Atlantic surfclam fishery captains and other industry representatives about the frequency and nature of searching for new fishing grounds provided the basis for implementing options for the simulated fishing vessel captains to spend time at sea searching for new fishing locations. On a percentage of the fishing trips, a captain will search for new fishing grounds by targeting a random TMS within a 6-hour steam of the homeport that is independent of the captain's memory of past LPUE performance in that TMS. The percentage of trips during which a captain will search is defined for each captain for each simulation. Catch rate in the TMS that was searched is then updated in the captain's memory. The purpose of the random searching (for real captains and simulated captains) is to identify unknown areas containing surfclams. The random search only includes TMS grid cells that are defined as surfclam habitat. This constraint prevents the captains from searching in areas with unsuitable habitat or that are too deep.

Captain communication

Information sharing among surfclam fishing vessel captains affects time spent fishing, catch, and landings. The level of communication among fishing vessel captains can range from no information sharing to limited or total information sharing. Inputs from Atlantic surfclam fishery captains about how often, with whom, and the type of fishing information that is shared with other captains suggested that information sharing about fishing trips occurs primarily among captains from the same company and the same home port. Information sharing was less among captains from different companies but same home port and even less among captains from different companies and home ports. These inputs were incorporated into the captain's behavior using a probability distribution that allows captains from the same company and the same port to share 75% of information about fishing trips. Captains sharing the same home port, but from different companies, share 50% of information, and captains from different ports share only 25% of information. The relative contribution of information sharing was assessed with a simulation with no information sharing among fishing vessel captions. This simulation showed the simulated surfclam fishery to be relatively insensitive to the degree of information sharing, with the sharing of information only slightly reducing fishing performance (Figure S3). This provides support for the information sharing approach used in the reference simulation.

Fishing vessels

The simulated fishing fleet was specified to reflect the range of vessels and capacity in the present day Atlantic surfclam fishery using information provided by industry representatives, vessel owners, and operators. The simulated fleet consists of 33 fishing vessels, each with individual specifications for dredge width, catch capacity, steaming speed, fuel consumption, and home port location (Table 1). Most of the simulated fleet has a home port in Atlantic City, NJ (19 vessels) and New Bedford, MA (11 vessels). The remaining three vessels were assigned to Ocean City, MD (2 vessels) and Point Pleasant, NJ (1 vessel). The simulated fleet was grouped into vessel size classes based on hull length categorized as small (≤24 m: 11 vessels), medium (24–29 m: 10 vessels), large (>29–33 m: 8 vessels), and jumbo (>33 m: 4 vessels). Atlantic surfclams are caught with a hydraulic dredge at a rate (cages per hour, capped at 10 cages per hour) that scales with the density of market-size surfclams in the TMS. The simulated catch is apportioned into standardized cages, each of which holds 32 bushels of surfclams (1 bushel = 53.2 L). Each vessel has capacity to hold a specific number of cages when fully loaded (Table 1).

For the simulations, fishing vessel activity is configured such that individual vessels either wait at the homeport, steam to and from a fishing location, or actively fish for Atlantic surfclams. Processing plants distribute quota to each vessel on a weekly schedule that allows vessels to make 2 fishing trips per week. The choice of vessel activity is made each hour and continues for the remainder of the hour and total time spent in each activity is tracked in the simulations. Vessel movement is based on waypoints that prescribe a path to follow to each possible fishing location. The waypoint calculation includes information about the TMSs occupied by land, other obstructions (e.g. wind farms), ports, and Atlantic surfclam habitat. Paths from each port to each TMS with Atlantic surfclam habitat are calculated with the A* (A Star) path algorithm (Hart *et al.*, 1968), which finds the shortest path between two locations in two dimensions, avoiding squares where transit is not allowed (e.g. land, wind farms). A path-finding module in MATLAB (Premakumar, 2021) that includes TMS locations and a mask of no-transit TMSs, calculates a list of TMSs that define the path to follow between the two locations; defined paths are truncated to remove points connected by a straight line between two base points. The resultant waypoint file contains a set of points to traverse from each port to each TMS with Atlantic surfclam habitat. Pre-calculation of transit routes follows a minimum distance path, which reduces simulation time required to find an optimal fishing location.

Weather

Weather determines if and when Atlantic surfclam fishing is feasible and safe. Weather control on fishing is implemented using relationships between wind speed and boat size that pre-

vent a vessel from leaving port under certain weather conditions. Wind speed and direction were obtained for 2015–2019 from meteorological buoys deployed along the MAB (NOAA National Data Buoy Center) and used to calculate the probability of winds in specified speed ranges, a measure of weather conditions. Weather on a specific simulation day was related to conditions two days later by a random draw from the calculated wind speed probability for that day and season. This provides a forecast that is used to decide if a vessel should leave the dock. Wind forecasts of > 5 , > 8 , and $> 10 \text{ m s}^{-1}$ prevent small vessels, medium and large vessels, and jumbo vessels, respectively, from leaving port to fish for surfclams (Table 1). The same weather conditions were imposed to force boats to stop fishing and return to the dock, sometimes without acquiring a full load of Atlantic surfclam catch (Table 1).

A practice in the fishery is to stack live Atlantic surfclams on the deck (i.e. deck load) for transport to the home port rather than placing the catch into refrigeration units. The deck-loaded catch can spoil when air temperatures are high ($> 25^\circ\text{C}$) and transit time back to the dock after fishing begins is too long (> 30 hours). This effect was included in the simulations using a seasonally varying air temperature factor that forces fishing boats to avoid catch spoilage by returning to port earlier when air temperatures rise in the summer. Seasonally varying air temperature distribution was calculated from meteorological observations reported from airports nearest to each New Jersey port (Cape May International, Atlantic City International, Ocean County Airport); port locations for which spoilage of deck-loaded catch is a concern. The minimum (summer) and maximum (winter) trip duration scales with the monthly air temperature factor to constrain the trip length seasonally. Both weather and time limits on certain trips can cause vessels to return to port without filling to full capacity (Table 1).

Simulation implementation

Model domain

Each of the TMSs that make up the model domain have a north-south distance of 10 NM. The east-west distance of each square is fixed at the width determined by the central latitude of the grid. The TMS are categorized by depth which restricts access for some fishing vessels because of size and draft requirements (Table 1), i.e. regions too shallow for vessels or land areas. Large and jumbo vessels fishing out of New Bedford, MA are unable to fish on Nantucket Shoals because it is too shallow. Thus, the TMSs in this region were set to exclude the largest vessels in the fishing fleet. The location of ports and processing plants that are the primary landing sites for Atlantic surfclams are specified in the relevant land TMS (Figure 3).

Current federal regulations prohibit Atlantic surfclam fishing vessels from landing mixed-species catches, such as can happen in areas where Atlantic surfclams co-exist with ocean quahogs. In the overlap regions, the handling time of the catch is increased because fishers need to sort the catch, as a result fishing effort is typically relocated to avoid these areas. The areas where Atlantic surfclams and ocean quahogs overlap were identified using information provided by fishing vessel captains, and approximately follows the 40-m isobath. This overlap region was defined in the biological habitat of each TMS. The simulated vessels that fish in the overlap area accrue a penalty of lower catch efficiency. This penalty is subtracted

from the captain's skill while fishing in the overlap area, making that captain 50% less effective at capturing Atlantic surfclams in any TMS that overlaps with ocean quahogs.

Initial Atlantic surfclam distribution

Initial biomass distribution, given as Atlantic surfclams m^{-2} per length class, was specified using a total population biomass that was distributed into each TMS as a total Atlantic surfclam density (summed over lengths) using a negative binomial random distribution to create a patchy distribution. A spatially-varying length distribution was then used to distribute the Atlantic surfclam biomass in each TMS into length intervals. The patchiness structure is maintained subsequently by recruitment, as described previously.

Captain types

Each captain of the simulated vessels was allowed to randomly search the model domain for Atlantic surfclams on 0%, 5%, or 10% of the fishing trips, and was assigned memory weights of 0.2, 0.8, 0.98 or 0.99. This results in a total of 12 captain types, who were randomly assigned to each of the 33 fishing vessels for each simulation. The captain-vessel assignments were randomized, and simulations were repeated 200 times which allows variability to emerge in the simulations. The simulation outputs were averaged to obtain estimates of average annual fishery metrics.

The relative contribution of searching and captain memory was assessed with simulations with no searching and a constant captain memory weight of 0.8. These simulations showed the simulated surfclam fishery to be relatively insensitive to changes to random searching and captain memory weight that are within the known range of true behaviors (Figure S3), thereby supporting the approach used in the reference simulation.

Model implementation and validation

The population dynamics model was initialized with the Atlantic surfclam biomass distribution and run for 100 years without fishing to allow the population to come into equilibrium with the specified growth rates, mortality, and recruitment. This equilibrium simulation provided a reference simulation that reproduced the unfished spatial patterns in Atlantic surfclam distribution. Fishing was then allowed for the next 200 years of simulation so that the model reached equilibrium with the fishery dynamics and reproduced the contemporary spatial patterns in Atlantic surfclam distribution. The last 50 years of simulation with fishing were used for analysis. Quantitative and qualitative approaches were used to assess the reference simulation results. These were done with inputs from surfclam industry representatives to ensure that simulations represented the current state of the fishery as reflected by current knowledge.

Observed annual Atlantic surfclam catch for 2015 to 2019 is reported as part of the annual stock assessment (NEFSC, 2022). Data on fishing vessel trips for 2015 to 2019 for the 33 vessels (6830 total trips) that make up the actual Atlantic surfclam fishing fleet were obtained from the Greater Atlantic Regional Fisheries Office (GARFO, 2021). These data allow calculation of time at sea, catch in bushels, LPUE (cages per hour fished), and the fraction of cage capacity utilized for each fishing trip. Equivalent metrics were calculated from simulations for each simulated year and weekly vessel trips during the last 50 years of the 200 model runs

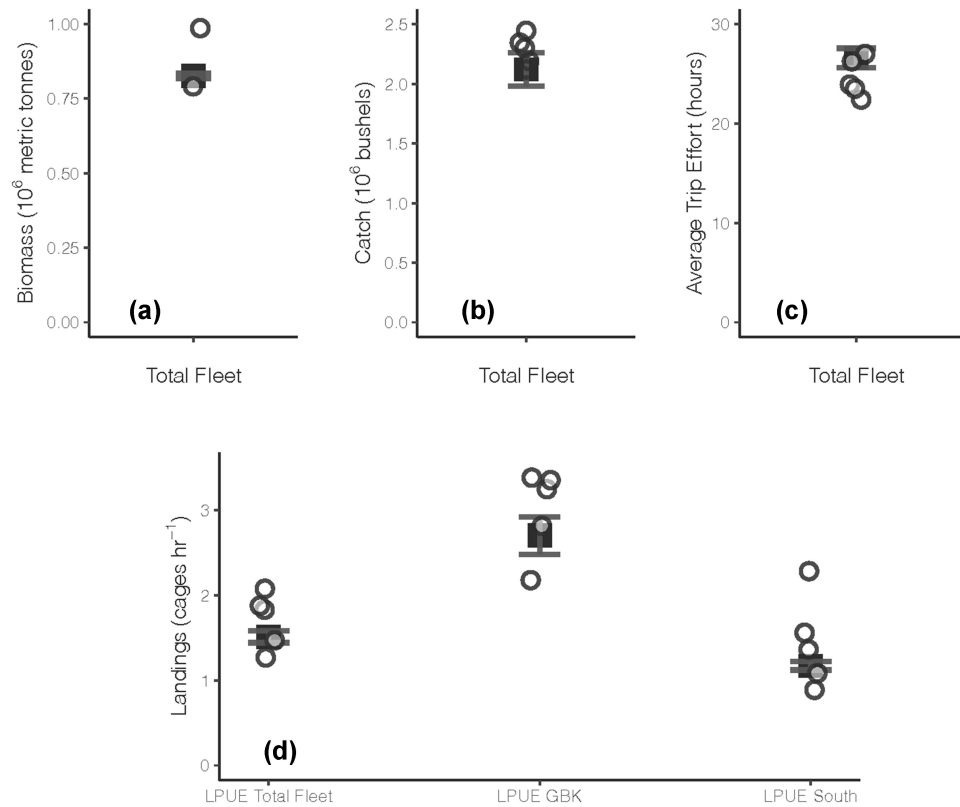


Figure 4. Average Atlantic surfclam. (A) biomass, and (B) catch for the total fishing fleet; (C) number of hours fishing per trip across the total fleet; (D) landings per unit effort (LPUE) for the total fleet (left), only vessels fishing on Georges Banks (center, GBK), and the rest of the fleet (right, south) calculated from the fishing simulation (filled black squares). Corresponding observed values from the 2015 to 2019 annual stock surveys are shown (open black circles). Only two survey-based estimates for biomass were made between 2015 and 2019 (A). Standard deviations for the simulated averages are shown.

($n = 10\,000$ years, and $n = 11623095$ weekly vessel observations). Quantitative comparisons of simulated and observed values were done using Mann-Whitney-Wilcoxon tests and boxplots to visually evaluate data overlap. Typically, the root mean square error (RMSE) is used as a measure of the differences between simulated and observed distributions (Willmott, 1981). However, the normalized root mean squared error (NRMSE), which is obtained by dividing simulated and observed values by observed trip-level averages, was used to calculate the fleet-, annual- and trip-level metric, which have varying units. Spatial patterns were also examined using qualitative comparisons of observed and simulated distributions of catch and effort; these qualitative features have been identified as important considerations that are often disregarded in favor of more quantitative analyses in these complex systems (Smajgl and Barreteau, 2017; Burgess *et al.*, 2020).

Results

Atlantic surfclam fishing simulation

Simulated Atlantic surfclam biomass from the fishing simulation was similar to biomass estimates from the federal stock assessment (Figure 4A; $p < i = 1 >$, $W = 50$). The NRMSE of 0.10 indicates that simulated biomass closely matches observed biomass. The simulated average biomass of 0.82 million metric tonnes was intermediate between the two observed

values of Atlantic surfclam biomass. The stock is not completely surveyed each year, which results in only two observed biomass values being available for 2015 to 2019.

Simulated annual catch in millions of metric tonnes was slightly lower than the catch reported for 2015 to 2019 (Figure 4B; $p = 0.005$, $W = 30$). However, two of five observed catch values were within the standard deviation of model variability and the NRMSE is 0.09. The spatial pattern of simulated catch, in bushels per TMS, relative to the observed fishery (Figure 5) showed that the footprint of the simulated fishing fleet was similar to the actual fishery. In particular, the regions of enhanced catch (hotspots) were similar in the simulated and observed spatial distributions (Figure 5).

Simulated annual average number of fishing hours per trip was slightly higher than hours fishing per trip reported as part of the stock assessment (Figure 4C; $p = 0.02$, $W = 203$), yet has a low NRMSE of 0.10. There was considerable overlap in hours at sea per trip between simulated and trip times reported in GARFO (2021) (Figure 6A) as well as good predictive accuracy of the simulation at the individual vessel level, as shown by a median (across vessels) NRMSE value of 0.20 (Figure 7).

Simulated and observed spatial patterns of fishing effort (hours fished) per TMS were similar (Figure 8). The simulated pattern placed more effort in some TMS compared to the observed pattern in the fishery, such as the Georges Bank region. Likewise, fishing effort showed a slightly greater spread over a larger area in the fishery compared to the simulated effort (Figure 8).

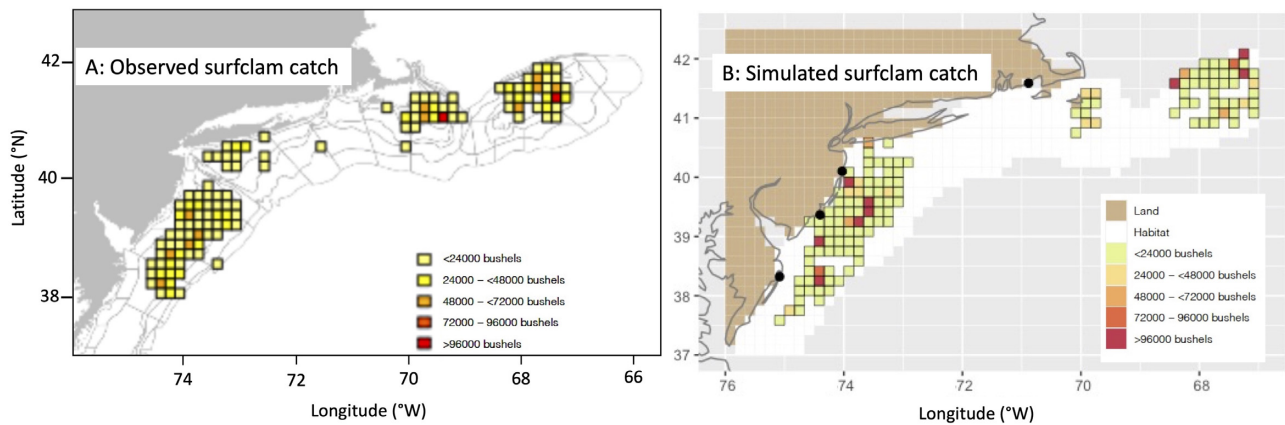


Figure 5. Spatial pattern of Atlantic average surfclam catch in bushels in each TMS per year obtained from the A) 2016 to 2019 stock assessment surveys and B) fishing simulation.

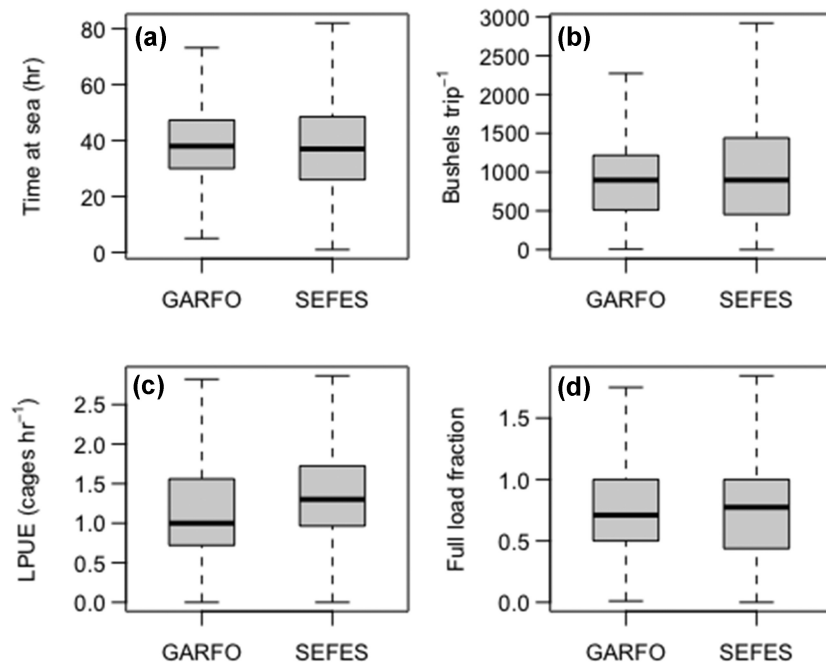


Figure 6. Comparison between observed (Greater Atlantic Fisheries Office, GARFO) and simulated average (A) dock-to-dock time at sea for fishing trips, (B) fraction of full load capacity of the fishing vessel for each trip, (C) catch in bushels per trip, and (D) landings per unit effort (LPUE) per trip. The observed values were obtained from GARFO (2021) trip data reports. Full-load fraction may exceed 1 as Atlantic surfclam fishing vessels occasionally have a large last haul and land more than the vessel cage capacity.

The simulated and observed catch, as bushels per trip, exhibited a similar, though broader, distribution compared to reported catch for fishing trips (GARFO, 2021; Figure 6B) and individual vessel behavior was well represented (median NRMSE = 0.24; Figure 7). The simulated and observed LPUE were also similar (Figure 4C) for the entire fleet ($p = 0.22$, $W = 83$; NRMSE = 0.20), the vessels only fishing in the south ($p = 0.37$, $W = 94$; NRMSE = 0.37), and the vessels fishing on Georges Bank ($p = 0.07$, $W = 64$; NRMSE = 0.18). Trip level LPUE values from the simulation were slightly higher on average but exhibited a range similar to reported values from fishing trips (Figure 6C). Individual vessel simulated LPUE was lower than reported values as indicated by a higher NRMSE (median NRMSE = 0.29; Figure 7), likely because LPUE depends both on simulated catch and effort. The fraction of a full load for a simulated fishing trip matched that calculated

from reported fishing trip loads (GARFO, 2021; Figure 6D) and individual vessel predictive accuracy for trip loads was strong (median NRMSE = 0.24; Figure 7).

Discussion

Simulation characteristics and evaluation

Estimates of Atlantic surfclam biomass are based on sampling strategies that can introduce error and variability and therefore biomass estimated by the stock assessments can vary from year-to-year. Atlantic surfclams are relatively long-lived (~30 years) and fishing mortality is relatively low (~3%, NEFSC, 2022), which gives the expectation that across the stock, overall biomass should remain relatively stable on short time scales despite localized changes in Atlantic surfclam abun-

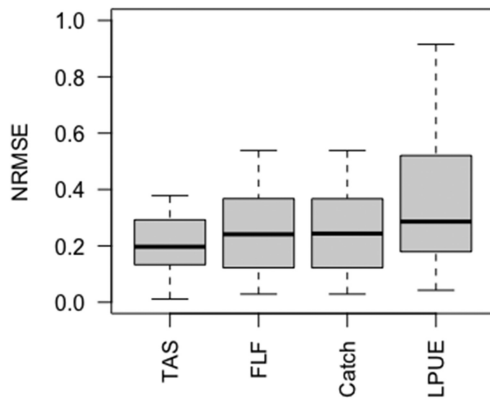


Figure 7. Normalized root mean squared error (NRMSE) for annual average time-at-sea (TAS), full load fraction (FLF), catch, and LPUE per trip calculated for each simulated vessel ($n = 33$).

dance from targeted fishing and patchy larval recruitment. Surfclams do not demonstrate a broodstock-recruitment relationship (Timbs *et al.*, 2018), and have relatively long larval lifespans that facilitate population connectivity via larval dispersal over large areas (Zhang *et al.*, 2015, 2016). The year-to-year random larval success across the MAB region and steepness of 0.8 used in the simulations provided variability to local surfclam density and maintained a relatively stable stock biomass that was representative of the average condition observed in the stock assessment surveys. Correspondence between the simulated and observed stock biomass and distribution implies that larval dispersal is widespread across the stock, is relatively independent of spawning stock biomass, and that variation among observed survey biomass estimates ($\sim 25\%$; NEFSC, 2022) is due to sampling error rather than true changes in stock biomass on inter-survey timescales (2 to 5 years).

The simulated spatial distribution of the unfished stock is determined primarily by a spatially varying natural mortality rate. The adult surfclam mortality rate of 0.15 yr^{-1} estimated from the stock survey (NEFSC, 2022) is based on the estimated mortality rate for an animal that lives ~ 30 years, which is a reasonable stock-wide rate applied to regions supporting the core of the stock. However, this rate does not ap-

ply across the entire geographic range of recruitment. Timbs *et al.* (2019) found that the geographic distribution of new recruits substantially exceeded that of older adults, implying that the mortality rate of recruits was noticeably higher outside the core of the surfclam range and is supported by the increase in the variance-to-mean ratio with increasing age in surfclams (Timbs *et al.*, 2018). This is further supported by the absence of a broodstock-recruitment relationship in most bivalves (Hancock, 1973) including surfclams (Timbs *et al.*, 2018; NEFSC, 2022), and the well-described tendency for species such as mussels to recruit to regions where survival is low (Wells and Gray, 1960; Morse and Hunt, 2013; Fuentes-Santos and Labarta, 2015). Thus, local variability in mortality rate is a likely source of adult patchiness and contributes to the location of hotspots.

The spatially varying mortality rate used in the simulations, based on known abundance (higher abundance implying lower mortality rate) and age distributions (older ages implying lower mortality rate), generated a patchy stock distribution consistent with observations (NEFSC, 2022) with a stock-wide mortality rate of $\sim 0.17 \text{ yr}^{-1}$, which agrees well with the 0.15 yr^{-1} used in the federal stock assessment (NEFSC, 2022) and rates estimated by Weinberg (1999). Whether the mortality rate is representative of the true population dynamics is unknown, though it is consistent with evidence supporting the importance of post-settlement mortality in determining post-settlement patterns of abundance (Keough and Downes, 1982; Ólafsson *et al.*, 1994; Hunt *et al.*, 2003; White *et al.*, 2014a). Also, implementation of the spatially-varying mortality rate produced simulated distributions of the Atlantic surfclam stock that are consistent with observed distributions, including hotspots that are targeted by captain decision making that lead to simulated vessel dispersion patterns that match observed patterns.

Catch reporting is required for the Atlantic surfclam fishery, similar to many managed commercial fisheries. Thus, catches are effectively a census and are known with more precision than fishery-independent estimates of absolute stock abundance (NRC, 2000). The simulated catch slightly underestimated the reported average annual catch for the whole Atlantic surfclam fishery. This discrepancy resulted from the composition of the simulated Atlantic surfclam fishing fleet. The simulated fishing fleet included only vessels owned by

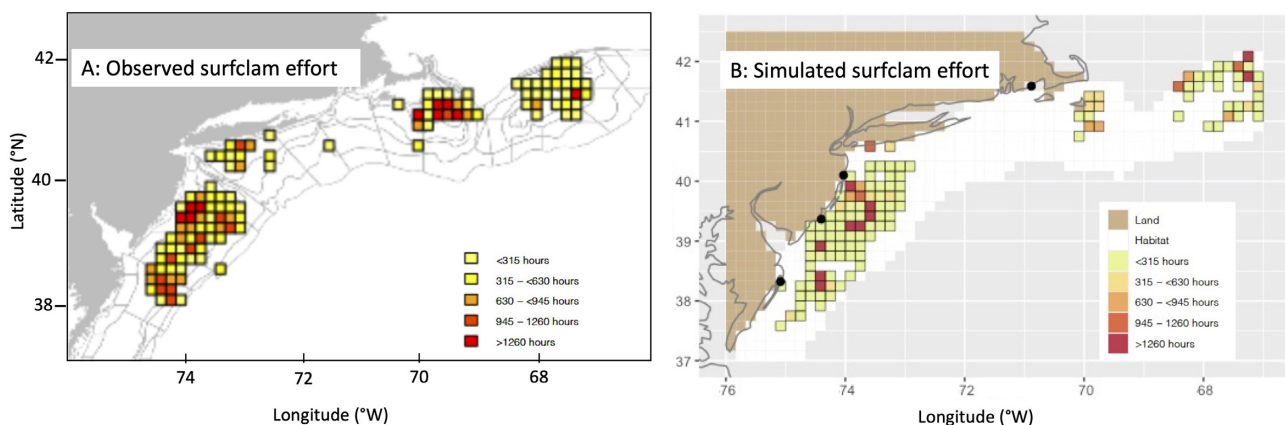


Figure 8. Spatial pattern of average Atlantic surfclam fishing effort in hours fished in each TMS per year obtained from the (A) 2016 to 2019 stock assessment surveys and (B) the fishing simulation.

companies with multiple vessels and those that participate exclusively in the federal Atlantic surfclam and ocean quahog fisheries. This allowed inclusion of vessels that distributed fishing trips between the two species as well as those dedicated to Atlantic surfclam fishing. Vessels that fish only part-time in the federal fishery, thus recording some state-water landings, were not included as part of the simulated fishing fleet. These vessels may have been important contributors to the fishery historically, but fleet consolidation has led to changes in fleet composition. The result is that the overall contribution from these fishing vessels to the Atlantic surfclam catch is small. The simulated annual average landings underestimated the observed annual landings in the past 5 years by ~5%, suggesting that the current consolidated, vertically integrated Atlantic surfclam fishing fleet accounts for around 95% of the annual landings in the fishery.

Average annual simulated trip characteristics, such as time fishing and LPUE, agree with those reported for the Atlantic surfclam fishery. However, considerable variability occurred among individual trip characteristics. For the simulations, each fishing trip was determined first by the captain's memory of catch in locations within a specified fishing distance from the dock. Once the simulated fishing vessel reached the fishing grounds, the trip characteristics were determined by the Atlantic surfclam abundance of catch at that location, which may differ from the captain's memory either because the biomass has been fished down, or recruitment has increased abundance. The agreement between characteristics of the simulated and observed trips suggests that the approach used to specify fishing trip attributes in the simulations reflects realistic system inertia wherein a captain's memory of the catch available on the fishing grounds is slightly out of phase with the actual Atlantic surfclam biomass on the grounds, which is a reflection of the long lifespan of surfclams (~30 years) and relatively low fishing mortality (~3%, NEFSC, 2022).

Simulated vessel activity, such as steaming, fishing, or remaining at port, is set each hour and that activity continues for the remainder of the hour. As a result, for some fishing trips the simulated fishing vessels return to port with greater than 100% full load capacity. The vessel may only have a small fraction of its total capacity remaining empty at the beginning of the hour, but fishing activity will continue for a full hour which, in some instances, puts a vessel over full capacity when it returns to the dock. The result of this extended fishing over the remaining part of the hour matches the behavior in the actual fishery in that vessels will on occasion return to port with their full capacity of cages filled with catch, plus additional catch in the dredge and hopper which is loaded into cages for tagging and transport after reaching the dock and unloading. Thus, the simulated catches above the full capacity of the vessel are consistent with the occasional over-full capacity of actual Atlantic surfclam fishing vessels.

External forcing by weather and season imposes constraints on the Atlantic surfclam fishery, which in turn affects the stock biomass and fishing fleet behavior. The Atlantic surfclam fishery is vulnerable to inclement weather that prevents fishing in certain conditions. Additionally, trip duration is constrained by air temperature that can cause product spoilage if vessels do not land catch in a timely manner, and refrigeration does not provide an adequate solution to this problem. Weather, as it interacts with vessel size and product spoilage, thus constrains fishing opportunity and location. The importance of

weather as a controlling factor on the Atlantic surfclam fishery is likely to increase with climate change, and as offshore development creates increasing risk to fishing vessels operating in inclement weather.

Co-production of information with experts is key to ensuring that agent-based models are representative of the system of interest and facilitates model acceptance and utility (Smajgl and Barreteau, 2017; Burgess *et al.*, 2020). Further, use of experts and any available data is key to evaluation of model results (Ahrweiler and Gilbert, 2005; Schulze *et al.*, 2017) and stakeholder participation in agent-based modeling helps ensure their use and value in management decision-making (Matthews *et al.*, 2007). In the development of *SEFES*, representatives from the Atlantic surfclam fishery, including fishing vessel captains, and the management sector were engaged from the start to ensure that representations of fleet behavior and captain decision-making were realistic. Also, development of metrics from the simulated Atlantic surfclam fishing fleet distributions that could be directly compared with observed metrics provided by the surfclam fishery, i.e. fishing trip duration, is an outcome of this co-development.

Stock assessment data provided by the federal surveys (NEFSC, 2022) provide aggregate biomass estimates over a region, which limits the statistical power of comparisons with simulated biomass. However, comparisons between simulated and observed Atlantic surfclam biomass are useful for constraining the simulations. The trip reports (GARFO, 2021) provide many observations that are compared against a large set of simulated data and thus even small differences in average values calculated from the simulations appear to be statistically different; a potential complication of comparing simulated and observed datasets with large numbers of observations (White *et al.*, 2014b). These statistical challenges encountered in comparing observations and simulation output were aided by inclusion of stakeholder input and review to provide additional evaluation of how well model output represents the dynamics in the fishery and the use of NRMSE.

Importance of captain decision making

Accurate simulation of the spatial pattern of Atlantic surfclam catch and effort that reflects the observed dispersion in the fishery requires variability in captain decision making. Fishing choices made by fishing vessel captains are intricate and often suboptimal for maximizing catch while minimizing effort (Bockstael and Opaluch, 1983; Holland and Sutinen, 2000; Hutton *et al.*, 2004; Monroy *et al.*, 2010). Captains of Atlantic surfclam fishing vessels identified behavioral tendencies, such as memory of past catch and communication with other captains, that influence decisions about where to fish. These behaviors were included in the simulations by randomly assigning captains with specific behavioral patterns to fishing vessels. This approach distributed captains with varying degrees of reliance on memory and willingness to search for fishing areas across the fishing fleet, thereby allowing for emergent behavior that varied fishing locations and, on some trips, produced suboptimal decisions (reliance on long-term memory and overemphasis on searching being two examples). Simulated fishing fleet dispersion matched that of the observed fleet dispersion, indicating that the Atlantic surfclam fishery, like many others (Carrella *et al.*, 2020), operates under conditions of imperfect decision making when targeting fishing locations.

The agent-based model used in this study included daily behavioral decision-making processes that captains use to operate their vessels. The benefit of this daily decision-making is that it allows the fishing behavior to respond to changes in the Atlantic surfclam stock, such as temporary localized depletion. Additionally, the ability of simulated captains to integrate information over time, via the captains' memory, provides flexibility in simulation of a spatiotemporally dynamic resource (Cabral *et al.*, 2010), such as the Atlantic surfclam. Agent-based models used for other systems show that an agent's memory is important in dynamic decision-making (Rouchier *et al.*, 2001). For the Atlantic surfclam fishing simulations, the approach used to specify the ability of the fishing vessel captains to recall catch rates from previous locations fished was based on information provided by Atlantic surfclam fishers. Inclusion of mixed memory in agent-based models has been used in studies of stock market volatility (LeBaron, 2001), habitat use by monarch butterflies (Grant *et al.*, 2018), and optimizing traffic route patterns (Levy and Ben-Elia, 2016). The Atlantic surfclam fishing simulation shows the importance of including mixed memory as a component of agent-based fisheries models.

An earlier version of *SEFES* was used to examine the sensitivity of simulated outcomes (LPUE, landings, fleet economics) to changes in captain behaviors (Powell *et al.*, 2015). These analyses showed that in general, fleet dispersion was influenced by captain behaviors but the simulations were robust to changes in captain behaviors (Powell *et al.*, 2015), with some exceptions. Searching takes time at sea and the degree of searching interacts with the volume landed such that some searching improves performance, but additional searching decreases performance (Powell *et al.*, 2015). Communication among captains does not improve the overall fleet performance when captains have varied characteristics, because both good and poor information is shared equally (Powell *et al.*, 2016). Importantly, in circumstances where the stock is changing rapidly, as would be the case with a climate-induced range shift or change in recruitment, memories more heavily weighted towards old information decreases the ability of a captain to fish.

Conclusion

As use of the coastal ocean expands, spatial overlap will create conflicts between fisheries and new users such as offshore renewable energy and aquaculture (Arbo and Thy, 2016; Schupp *et al.*, 2019) that may prohibit or limit the ability of fishing vessels to access fishing grounds. Additionally, the rate of warming of the northwest Atlantic Ocean and consequent ongoing shift in the range of the Atlantic surfclam into deeper water (Hofmann *et al.*, 2018; Powell *et al.*, 2020) creates great uncertainty about the future success of the fishery and its interaction with new ocean users. Tools that can be used to assess the impacts of these challenges and their influence on fisheries and dependent communities are sorely needed (Lindkvist *et al.*, 2020).

Implementation of a spatially-explicit agent-based fishery model that included interactions among stock dynamics, the fishery, and fishing fleet decision-making allowed investigation of the scale, variability, and change in spatial patterns of Atlantic surfclam stock biomass that resulted from the external factors imposed by catch, fishing effort, and behavior of fishing vessel captains. Evaluation of simulation results with

quantitative and qualitative analyses showed that this modeling approach has sufficient skill to represent the dynamics of Atlantic surfclam fishery. As such, the approach used in this study can serve as the basis for future studies designed to examine the response of the Atlantic surfclam fishery to a nexus of simultaneous and complex natural and anthropogenic pressures, as well as provide a framework for development of similar models for other resources facing similar pressures.

The byzantine structure of the Atlantic surfclam fishery, like many other fisheries (Garcia and Charles, 2008), requires an evaluation approach that includes the complexities of stock dynamics, fishery/fleet decision-making, and management and economic factors. It is through the ability to simulate emergent behaviors and properties that the challenge of anticipating the future of this fishery as it responds to increasing use of the coastal ocean and climate change can be realized. This in turn will inform the larger socio-economic-ecological fisheries system that will ultimately determine the future viability of the Atlantic surfclam fishery.

Supplementary Data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Data availability statement

The data underlying this article cannot be shared publicly due to private company confidentiality issues. The data will be shared on reasonable request to the corresponding author when possible.

Author contributions

DMM, ENP, JMK, AMS, and EEH conceived ideas and acquired funding; all authors developed methodology and contributed to model calibration and validation; JMK wrote and maintained *SEFES* model code; AMS and JB conducted economic analyses of model output; DMM drafted initial manuscript; all authors contributed to manuscript review and editing.

Conflict of interest

The authors have no competing interests to declare.

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