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EVALUATION OF THE DEGREE OF CO-OCCURRENCE OF ATLANTIC SURFLCLAMS (*SPISULA SOLIDISSIMA*) AND OCEAN QUAHOGS (*ARCTICA ISLANDICA*) IN THE EXPANDING NORTHWESTERN ATLANTIC BOREAL/TEMPERATE ECOTONE: IMPLICATIONS FOR THEIR FISHERIES

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ABSTRACT Warming of the Mid-Atlantic continental shelf has resulted in a range shift of the Atlantic surfclam, *Spisula solidissima*, north and offshore into waters still occupied by ocean quahogs (*Arctica islandica*). An ecotone, a boundary transitioning between neighboring ecological systems over a wide range of space and time, now exists over much of the offshore range of the surfclam in which surfclams and ocean quahogs co-occur. Regulations prohibit fishers from landing both species in the same catch, limiting fishing to locations where the target species can be sorted on deck. An at-sea survey sampling 50+ stations in the overlap region was conducted in September 2021 with the purpose of mapping fishable concentrations of surfclams and ocean quahogs. Size frequency and density data of both species were assessed along with environmental parameters. Species overlap between surfclams and ocean quahogs was most prominent in the 40- to 55-m depth range. Density of surfclams shifted within this depth from surfclam dominant in less than 40 m to ocean quahog dominant in greater than 60 m. Atlantic surfclam length increased with increasing summer bottom water temperature, whereas densities remained stable, indicative of proportionately larger but fewer animals in warmer inshore waters. Ocean quahog size metrics and densities, on the other hand, remain relatively unresponsive to temperature and invading Atlantic surfclam populations and instead increase in size with higher latitude. Large ocean quahogs, in particular, exhibit a distinct correlation with high latitude but fail to do so with other environmental variables. This analysis emphasizes the potential for economic disruption of fisheries as climate change pushes surfclams further into the range of the ocean quahog and highlights the need for regulatory changes to allow mixed catches and landings. The study also emphasizes the importance of the relative rates of transgression and regression of range boundaries by abutting faunas in determining the degree of influence of the ecotone between them on the benthic community structure of the continental shelf.

KEY WORDS: *Spisula solidissima*, *Arctica islandica*, Atlantic surfclam, ocean quahog, range shift, ecotone, climate change, surfclam fishery, range boundary, species interaction

INTRODUCTION

The Northwest Atlantic Ocean is a bellwether of climate change, as its warming trends far exceed those observed throughout oceans around the world (Pershing et al. 2015, Kavanaugh et al. 2017, Seidov et al. 2021). Surface and bottom water temperatures in the Northwest Atlantic have risen on average 0.24°C per decade from 1968 to 2018 and 0.95°C per decade from 2004 to 2018 (Friedland et al. 2020). Rapidly rising temperatures are thought to stem from weakening of the Atlantic Meridional Overturning Circulation (AMOC) and a retreat of the Labrador Current, accompanied by a shift in the Gulf Stream, transporting warm, salty water northward, and thus, replacing cold Labrador Slope water along the continental shelf (Joyce & Zhang 2010, Zhang et al. 2011, Saba et al. 2016, Chen et al. 2021, Megann et al. 2021, Whitney et al. 2022). Modulation by the North Atlantic Oscillation (NAO), in which positive phases result in a northward shift of the Gulf Stream and westerly winds raising water temperatures in the Mid-Atlantic, is also well-described (Sha et al. 2015, Xu et al. 2015, Kavanaugh et al. 2017).

Two provincial boundaries exist on the northeast US continental shelf. Cool-temperate species inhabit the southern Virginian province, whereas boreal species are found in the northern Acadian province (Hale 2010). Acadian province

conditions advance southward into the Mid-Atlantic in the form of the Cold Pool, as a seasonal thermocline traps cold (<10°C) bottom water along the mid to outer continental shelf through much of the spring into the early fall (Houghton et al. 1982, Sha et al. 2015, Lentz 2017, Chen et al. 2018). The Cold Pool generates an unusual and extensive cross-latitude (N–S) provincial boundary distinctive from the typical cross longitude (E–W) boundary, the commonplace condition associated with most faunal provincial boundaries (Hutchins 1947, Briggs & Bowen 2012). Many demersal finfish and shellfish species and their fisheries are dependent on the setup of the Cold Pool (Colvocoresses & Musick 1984, Miles et al. 2021) for survival in the southernmost portion of their range.

The Atlantic surfclam (*Spisula solidissima*) is a biomass dominant, cool-temperate species of the northeast US continental shelf. Prior to the 1970s, the range of the surfclam extended from Cape Hatteras to Georges Bank at depths of 10–50 m (Merrill & Ropes 1969, Palmer 1991, Powell et al. 2017) but warming bottom water temperatures have caused the Atlantic surfclam to shift its range to cooler waters north and offshore. This range shift is one of the most geographically extensive range shifts recorded in the North Atlantic (Weinberg et al. 2005, Hennen et al. 2018, Hofmann et al. 2018, Hornstein et al. 2018, Timbs et al. 2019, Powell et al. 2019, 2020b). Temperature-induced mortality in surfclams at the southern and inshore portions of their range occurs as respiration rate exceeds assimilation rate and scope for growth declines, decreasing condition and compromising energetics until death (Kim & Powell 2004, Marzec et al. 2010,

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Munroe et al. 2016). This range shift is well-documented, beginning with the withdrawal of surfclams from shelf waters off Virginia and Maryland in the 1970s (Loesch & Ropes 1977, Powell 2003) and development of the surfclam fishery in New Jersey in the 1990s (NEFSC 2017a). A large mortality event occurred off the Delmarva Peninsula around 2000, followed by a decline in surfclams in New Jersey waters shortly thereafter (Kim & Powell 2004, NEFSC 2017a, Hofmann et al. 2018). Surfclam populations have expanded into federal waters off Long Island and Georges Bank (Powell et al. 2020b), but aggregate trends have resulted in a contraction of the range of the Atlantic surfclam.

Another biomass-dominant clam species of the North Atlantic is the ocean quahog (*Arctica islandica*). The ocean quahog is a boreal clam with a range extension into the Mid-Atlantic Bight (MAB) courtesy of the Cold Pool (Miles et al. 2021), which expands the range of the ocean quahog into lower latitudes than defined by the nearshore boreal-temperate provincial boundary (Engle & Summers 1999, Hale 2010). Ocean quahogs are most abundant at depths of 30–60 m in this region (Dahlgren et al. 2000) and have historically resided in waters offshore of those occupied by the Atlantic surfclam with relatively little overlap along the inshore range boundary (NEFSC 2017a, 2017b), presumably due to the stability of the temperature gradient maintained by the Cold Pool. Species' onshore and southern range limits often are temperature-determined, as many marine species live under conditions near their upper thermal limit (Brandt & Wadley 1981, Woodin et al. 2013, Pinsky et al. 2019; but see Sirén & Morelli 2020), as is the case with surfclams (Narváez et al. 2015) and would be presumed for ocean quahogs; however, the inshore boundary of ocean quahogs has remained relatively stable despite rapidly warming temperatures, presumably due to their ability to burrow and estivate for extended periods (Taylor 1976, Oeschager 1990, Strahl et al. 2011), thereby avoiding the high temperatures in early fall as the Cold Pool breaks down. LeClaire (2022) provides additional support in documenting the unusually slow rate of inshore range regression in ocean quahogs because the end of the Little Ice Age as a consequence of declining recruitment inshore but centurial survival of older animals under warming conditions.

An ecotone is defined as a boundary transitioning between neighboring ecological systems over a wide range of space and time (Gosz 1993). The historically narrow ecotone cross-shelf between Atlantic surfclams and ocean quahogs has broadened in scope in the past decades due to the offshore range expansion of the surfclam into the inshore portion of the range of the ocean quahog (Powell et al. 2020a) sans any obvious regression of the inshore boundary of the ocean quahog. Typically, three outcomes of range shift interaction between two species exist: the presence of transient multiple stable states (Powell et al. 2019), direct competition resolved by some limiting resource (Peterson & Andre 1980, Peterson 1982), and cases where no major interactions between the two species are observed. One might hypothesize that the third option is true for Atlantic surfclams and ocean quahogs, as both species inhabit overlapping portions of their respective ranges but are not known to interact.

Regulations currently prohibit commercial fishing vessels from landing Atlantic surfclams and ocean quahogs as a mixed catch. This regulation was promulgated after the

implementation of the Atlantic surfclam and ocean quahog individual transferrable quota (ITQ) system in 1990 (McCay et al. 1995). An amendment to the Atlantic surfclam and ocean quahog Fisheries Management Plan was made effective in April 1993, rendering any fishing or landing of surfclams and ocean quahogs on the same trip illegal (Anonymous 1993). The ruling also prohibits any commercial vessel from landing surfclams on a designated ocean quahog fishing trip, or landing ocean quahogs on a designated surfclam fishing trip. The amendment was proposed to simplify the tracking of landings and limit illegal harvesting but, as a consequence, the regulation also limits harvest from fishing locations to where surfclams and ocean quahogs can be sorted by hand on deck, with the nontarget species discarded. Industry guidance puts the amount of mixing deemed sortable on board at one individual of one species in every 25 total clams, or 4% of the total catch (Stromp et al. in press).

Warming of the Northwest Atlantic has required substantial adaptations by the regional fishing industries in such core characteristics as vessel homeport and vessel size distribution (Young et al. 2019). Atlantic surfclams and ocean quahogs are both vital species to the economic success of Mid-Atlantic fisheries, producing a combined \$53.6 million in ex-vessel annual revenue (Murray 2016) and are identified as species sensitive to climate change, with range contraction judged likely (Coro et al. 2016, Weinert et al. 2021). The minimal species overlap present throughout much of the history of the fishery produced a *de minimis* economic impact, whereas generating a fishery with a renowned low level of bycatch discards. This latter record has degraded dramatically in recent years as the continual range shift of Atlantic surfclams offshore jeopardizes both the profitability of the fishery by restricting access to a shrinking region of the Atlantic surfclam stock (Stromp et al. in press) and the record of minimal discarding.

This study examines the developing ecotone between Atlantic surfclams and ocean quahogs. A research survey sampled locations in the MAB in September 2021 and identified further areas of overlap between the two species, extending the known range of the ecotone. Results of the ecotone analysis reported here map offshore surfclam expansion, as evidenced by juveniles and small size class individuals and provide a detailed look at the differences in population demographics between these two species within what may be the most geographically extensive ecotone produced by global warming in the oceans.

MATERIALS AND METHODS

Sample Collection

Atlantic surfclam and ocean quahog abundance, density, and size data from this study were gathered from an at-sea survey of the Mid-Atlantic outer continental shelf on the *F/V E.S.S. Pursuit* in September 2021. The cruise plan was designed using information from surfclam and ocean quahog fishing-vessel captains who relayed locations of high overlapping densities of surfclams and ocean quahogs, augmented by recent (2016–2018) NMFS survey data (NEFSC 2022). This information suggested a central tendency for species overlap in the 40- to 50-m depth range, deeper in the south than in the north. The cruise track consisted of transects oriented perpendicular to the depth gradient from inshore (approximately 35 m) to offshore

(approximately 60m) so that the most inshore location had surfclams only and the most offshore stations had ocean quahogs only. The cruise track oriented the transects at an angle so that the boat zig-zagged through the region to limit time lost in steaming between stations.

A total of 117 tows at over 50 stations were taken on this cruise, with sampling locations ranging from offshore Ocean City, MD, to Hudson Canyon. A standard hydraulic clam dredge was used, the performance of which has been examined by Poussard et al. (2021). Further characteristics of this gear can be found in Parker (1971) and Meyer et al. (1981). Two tows were completed at most stations with differing bar spacing on the dredge. The surfclam dredge (indicated as the port dredge P in this analysis) operated with a bar spacing of 1.5" (3.8 cm) and a knife depth of 4.5" (11.4 cm). The ocean quahog dredge (identified herein as the starboard dredge S) used a slightly smaller bar spacing of 1.25" (3.2 cm) and a knife depth of 4" (10.2 cm). The use of two dredge designs permits a performance comparison between the two dredge's styles with respect to selectivity for Atlantic surfclams and ocean quahogs. On-board analysis included the number and size (in mm) of clams of the two target species, the GPS-measured tow length (decimal degrees, latitude, and longitude), and depth of each tow (m).

Statistical Analyses

Post-cruise, Atlantic surfclams, and ocean quahog catch data were sorted into size classes of 10-mm increments between 30 and 200 mm. Degree of species overlap was adjudged relative to the assumption that sorting between the two species during commercial operations is not feasible if more than 4%, or 1 clam of the mixing species in 25 total clams (e.g., >1 ocean quahog in every 25 clams), of the nontarget species was present in the dredge haul (Stromp et al. in press). Eleven summary statistics (referred to in analysis as size variables) were calculated for Atlantic surfclams and ocean quahogs in each tow and supplemented with environmental data (referred to in analysis as environmental variables) (Table 1). Temperature data were obtained from the Regional Ocean Modeling System (ROMS) implementation Doppio (López et al. 2020) and incorporated into the dataset as an average of mean September temperatures

from 2016 to 2019. Temperatures from 2020 to 2021 were not available at the time of writing. The clam densities for each tow were not corrected for dredge efficiency or dredge selectivity. An estimate of dredge efficiency is provided in Poussard et al. (2021) and estimates of dredge selectivity are provided in NEFSC (2017b) for the ocean quahog dredge. Estimated landings per unit effort (LPUE) are specified in cages h^{-1} , 1 cage = 32 surfclam bushels (1 bushel = 53.2 L) and are based on the following assumptions: tow speed 3.1 knots; dredge time on bottom 50 min h^{-1} ; dredge width 3.048 m; dredge efficiency 1.0 as density estimates were not corrected for dredge efficiency. Dredge efficiency is likely around 70% (Poussard et al. 2021).

Unless otherwise noted, evaluation of the distribution of Atlantic surfclams and ocean quahogs was performed using statistical software R (vers. 4.2.1). All statistical methods presented were completed separately for Atlantic surfclams and ocean quahogs. Type III SS analysis of variance (ANOVA) were used to analyze main effects and interaction effects for each size variable (as dependent variables) with the environmental variables (as continuous independent variables) in Table 1, totaling 22 ANOVA. Interaction terms Temperature $\times$ Depth, Depth $\times$ LPUE, and Temperature $\times$ Latitude were added. Dredge type was included as a factor.

Principal component analysis (PCA) was conducted for size and environmental variables for both species, totaling 4 PCAs. Each variable was scaled to a mean of zero and a standard deviation of 1, and the PCA displayed utilizing varimax rotation. A scree plot was used for each PCA to determine the number of significant axes (significance $\geq 10\%$ of variation). Significant PCA axes were then plotted against one another to determine how the variables are influenced by other variables of the same type (size or environmental). Factor scores of significant axes were subset from the PCA and applied to Type III SS ANOVA as independent variables, with a total of 14 ANOVA for each species (10 with size variables as dependent variables, 4 with environmental variables as dependent variables; density only included as an environmental variable). Dredge type was not included in the PCAs and ANOVA with PCA factors. Density and LPUE are perfectly collinear and thus, grouped together for this analysis. Pearson's correlation coefficients were calculated for all significant interactions between size and environmental PCA factors to determine the intensity of correlation between PCA factors.

Correspondence analysis (Clausen 1998) was used to compare both size and environmental variables for the two species. All continuous variables were classified into thirds by the 33rd and 67th percentile with lower values and higher latitude designated as 1, higher values and lower latitude as 3, and middle values and latitude as 2. Dredge type was included as a supplementary variable and did not influence the axes in the correspondence analysis.

RESULTS

Atlantic Surfclam and Ocean Quahog Overlap

Figures 1A, B display the estimated density of ocean quahogs and Atlantic surfclams, respectively, at each sampled station.¹ For context, see stock-wide distributional maps in NEFSC (2017a, 2017b). The two species occur in high densities

TABLE 1.

Size and environmental variables calculated for Atlantic surfclams and ocean quahogs in each tow.

Size variables	Environmental variables
Mean size	Depth (m)
Median size	Temperature (°C)
25 th percentile	Density (clams/m ²)
75 th percentile	LPUE (cages/h)
Range	Latitude (°)
Interquartile range	—
Maximum size	Dredge type (P/S)
Minimum size	—
Skewness	—
Kurtosis	—
Density	—

All size variables are in mm, with the exception of skewness and kurtosis (no units). P dredge, Atlantic surfclam dredge; S dredge, ocean quahog dredge.

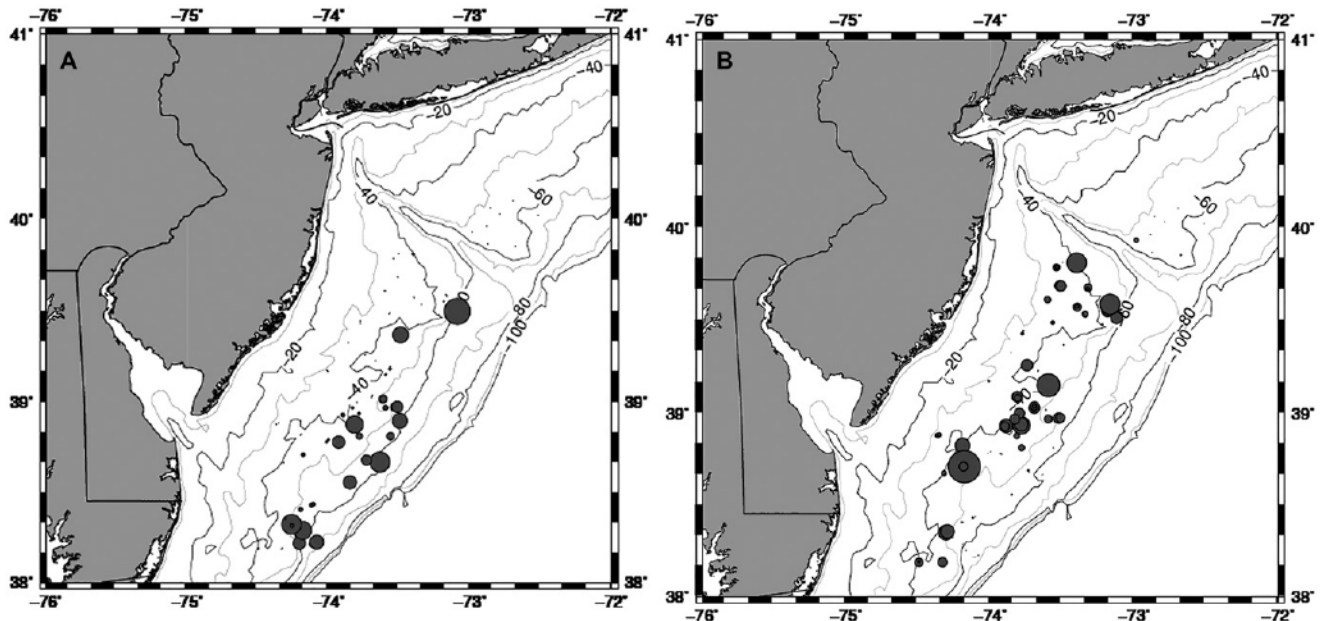


Figure 1. (A) Ocean quahog and (B) Atlantic surfclam catch. Circle diameters are proportional to numbers per square meter.

over much of the overlap zone. The largest catches of ocean quahogs occurred in deeper waters between 40 and 60 m. Atlantic surfclams were caught at depths of 30–60 m but were most abundant between 45 and 50 m.

Figure 2 shows the distribution of stations allocated to four groups defined by degree of overlap. Green boxes offshore indicate sampling sites, where more than 24 of every 25 total clams (<4% mixing) was an ocean quahog. In most cases, these tows exclusively caught ocean quahogs. Stations with majority ocean quahog catch occur in the 55- to 60-m depth range; ocean quahogs are found at deeper depths, but this depth range was not sampled in the survey. Pink boxes are inshore locations where more than 24 out of every 25 total clams (<4% mixing) were Atlantic surfclams, with most tows catching exclusively surfclams. Stations with majority Atlantic surfclam catch occur in the 30- to 40-m depth range; analogous to ocean quahogs, surfclams are found inshore of this depth range, but these shallower depths were not sampled on the survey. Yellow and brown boxes indicate regions of overlap between the two species. Yellow boxes are stations where between 1 and 12 of every 25 total clams (4%–50% mixing) was an ocean quahog, although the majority caught were surfclams. Brown boxes indicate stations where between 1 and 12 of every 25 total clams (4%–50% mixing) was an Atlantic surfclam, although the majority caught were ocean quahogs. Both of the station types yielding mixed catch occupy a substantial region between 40 and 55 m with the surfclam-rich stations lying somewhat inshore of the ocean quahog rich stations. For purposes of data presentation hereafter, the depth range of 40–55 m will be referred to as the region of overlap between Atlantic surfclams and ocean quahogs.

Stations were grouped together by tow depth in depth intervals of 2 m from less than 32–46 m and in intervals of 5 m at

deeper depths as fewer tows were taken at these deeper depths. The average density, LPUE, maximum size, and mean size of Atlantic surfclams and ocean quahogs was then calculated for each depth interval (Figs. 3A, B and 4A, B). Stations less than 40-m depth were dominated by Atlantic surfclams, whereas those 50+ m contained high densities of ocean quahogs (Fig. 3A). The highest ocean quahog LPUE (2.5–3 cages h⁻¹)

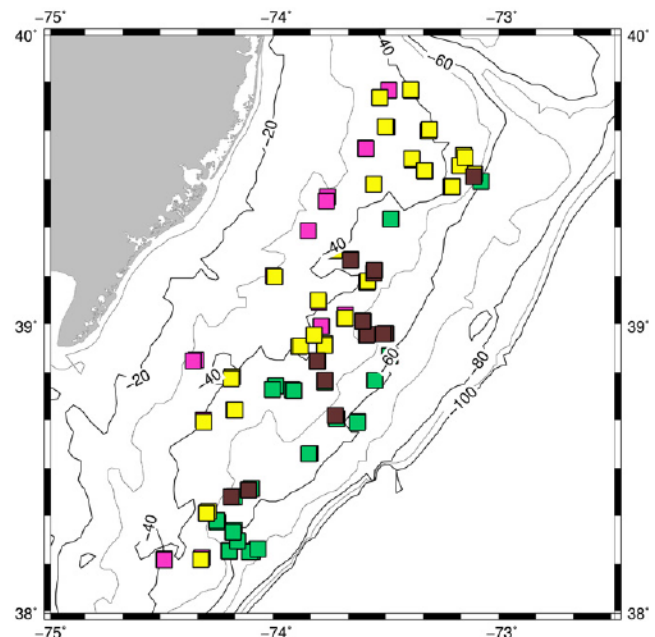


Figure 2. Locations sampled and catch characteristics. Dark pink boxes show locations where greater than 24 of 25 clams were surfclams. Green boxes show locations where greater than 24 of 25 clams were ocean quahogs. Yellow boxes show locations where at least 1 in 24 clams, but less than 12 in 24 were ocean quahogs. Brown boxes show locations where at least 1 in 24 clams, but less than 12 in 24 were surfclams.

¹ Post-cruise report and associated data are available at <https://scemfis.org/shellfish-publications/>

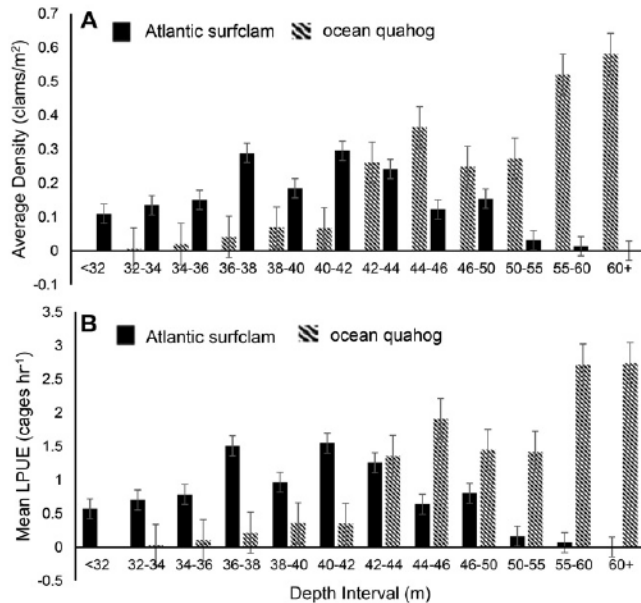


Figure 3. (A) Mean density and (B) mean LPUE [cages h⁻¹, 1 cage = 32 surfclam bushels (1 bushel = 53.2 L)] of Atlantic surfclams and ocean quahogs across the survey domain. Survey stations were grouped into intervals of 2 m based on the depth of each tow, with the exception of the deepest tows that were placed in 5-m intervals as a result of few numbers of tows in these intervals.

are found at the deepest sampled stations, whereas the highest values of LPUE for Atlantic surfclams (1.5 cages h⁻¹) occur at 35–50 m and decline with increasing depth (Fig. 3B). Clam densities and LPUE at depths of 40–55 m show a transition between surfclam-dominance and ocean quahog dominance, further defining the center of the species' overlap as located within the 40- to 55-m depth zone.

Maximum size for ocean quahogs remained constant at 110–120 mm across the sampled region, whereas the largest Atlantic surfclams declined from 170 mm at 32-m depth to 120 mm at 60-m depth (Fig. 4A). The maximum size in surfclams was reduced by 30 mm over the overlap depth of 40–55 m. Trends in mean size of both clam species were similar to the trends for maximum size. The mean size of ocean quahogs fluctuated little across depth intervals, from slightly below 90–110 mm (Fig. 4B). Mean surfclam size declined from 145 mm at 32-m depth to 90–100 mm at greater than 50 m. Surfclam size declines gradually down to 40 m, then more sharply down to 55 m, with a loss in size of 30 mm over the overlap region.

Sampled stations were also grouped together by their mean September monthly temperature from 2016 to 2019. September temperatures were used as the survey was completed in September 2021, however, temperature data from 2021 to 2020 were unavailable at the time of writing. Tows were divided into 0.25 °C intervals from less than 10.75 °C to 13.5 °C and into 0.5 °C intervals from 13.5 °C to greater than 15.0 °C, with the larger range being required by the fewer number of tows at higher temperatures. The mean density and size for Atlantic surfclams and ocean quahogs was calculated for each temperature interval (Fig. 5). Mean surfclam density varied minimally from 0.1 to 0.3 clams m⁻² across the temperature range, whereas ocean quahog density differed greatly between

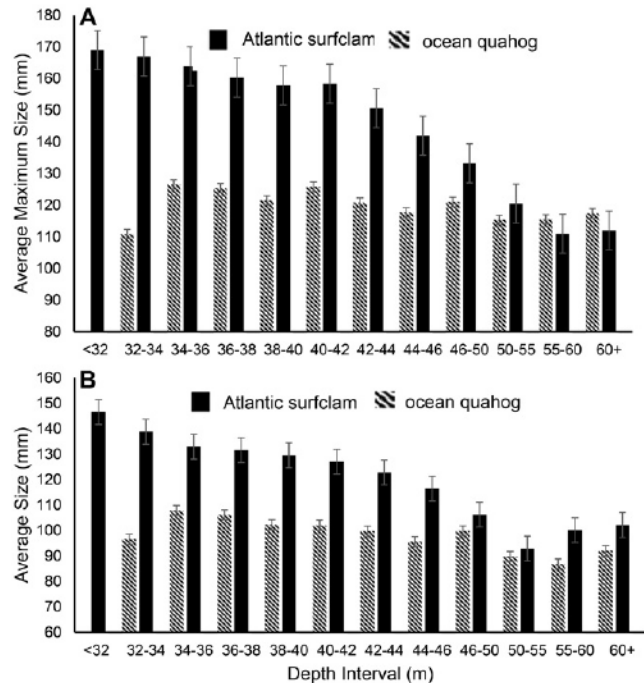


Figure 4. (A) Maximum size and (B) mean size of Atlantic surfclams and ocean quahogs across the survey domain. Survey stations were grouped into intervals of 2 m based on the depth of each tow, with the exception of the deepest tows that were placed in 5-m intervals as a result of few numbers of tows in these intervals.

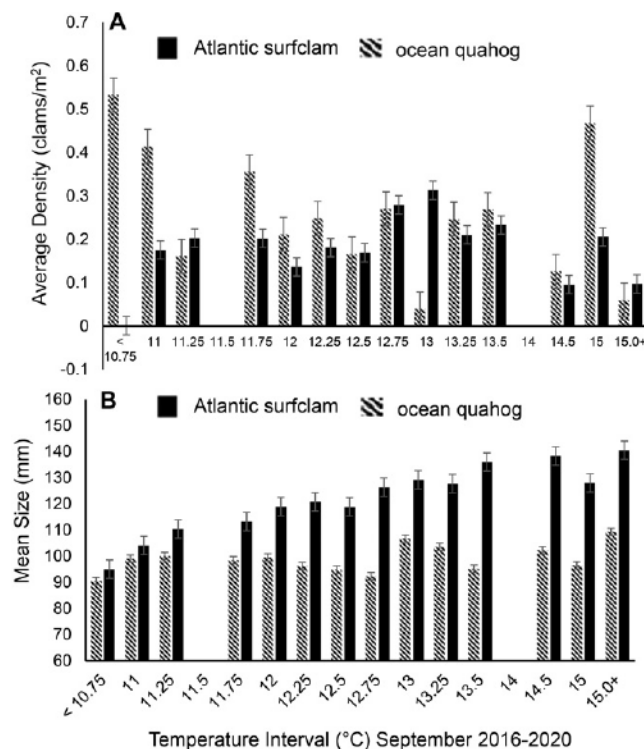


Figure 5. (A) Mean density and (B) mean size of Atlantic surfclams and ocean quahogs across the survey domain. Survey stations were grouped into intervals of 0.25 °C based on the average September temperature from 2016 to 2020, with the exception of the highest temperatures, which were placed in intervals of 0.5 °C as a result of few numbers of tows in these intervals.

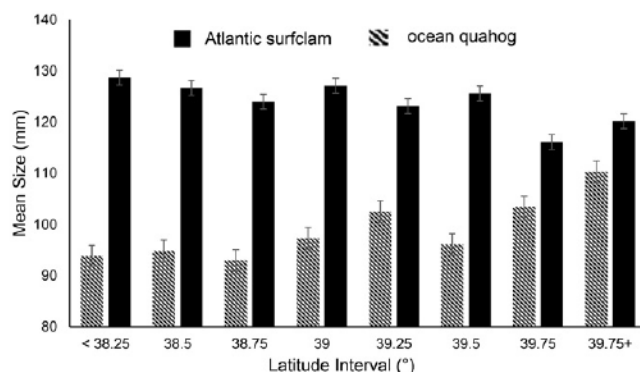


Figure 6. Mean size of Atlantic surfclams and ocean quahogs across the survey domain. Survey stations were grouped into intervals of 0.25° latitude.

intervals (Fig. 5A). The majority of high ocean quahog densities greater than 0.3 clams m^{-2} were found at temperatures below 12°C (with the exception of the 14.5°C–15°C interval). The majority of intermediate densities of approximately 0.2 clams m^{-2} were found between 12°C and 13.5°C and the majority of low densities 0.1 clams m^{-2} or less occurred at higher temperatures. Although Atlantic surfclam densities remained relatively constant across the temperature range, mean surfclam size increased with increasing temperature from 90 mm at less than 11°C to 140 mm at greater than 15°C (Fig. 5B). Mean ocean quahog size, unlike density, only differed from 90 to 110 mm across the entire temperature range and displayed no obvious pattern with increasing temperature.

Tows were also grouped by latitude in 0.25° intervals from less than 38.25° to 39.75°, spanning the entire geographic range of the survey (Fig. 6). Atlantic surfclam and ocean quahog mean sizes were calculated for each interval of latitude. Mean ocean quahog size increased with increasing latitude, from 90 mm at the most southerly latitude to 110 mm at the highest latitude. Atlantic surfclam mean size fluctuated from 115 mm to less than 130 mm across latitude, decreasing only slightly in the highest latitudinal intervals.

Analysis of Variance

Analysis of variance results show that the variance in size of Atlantic surfclams is primarily determined by depth followed by temperature, density/LPUE, and the depth × density interaction (Table 2). Depth is significant for all size variables with the exception of minimum size and kurtosis. Minimum size of surfclams did not show any significant trends among environmental variables or interaction terms. Variance in ocean quahog size is explained by temperature, latitude, and the temperature × latitude interaction (Table 3). Temperature, latitude, and the temperature × latitude interaction are significant for all size variables except the 75th percentile, skewness, and kurtosis (with the addition of maximum size for latitude). Skewness and kurtosis in ocean quahogs did not show any significant trends among environmental variables and interaction terms. Dredge type is significant in only two ANOVA: size range in surfclams and interquartile range in ocean quahogs. ANOVA using density as a dependent variable resolved a significance depth effect for both Atlantic surfclams and ocean quahogs, with a significant depth × temperature interaction also present for ocean quahogs.

Principal Component Analysis and Analysis of Variance with Principal Component Analysis Factors

Principal component analysis on Atlantic surfclam environmental variables yielded three factors that garnered 95.47% of the variation in the data (Table 4). Density/LPUE fell on factor 1, which explained 45.25% of the variability in the data. Temperature and depth fell on factor 2, explaining 34.95% and latitude on factor 3, accounting for an additional 15.27%. The Atlantic surfclam PCA for the size variables also resulted in three significant factors producing 92.01% of the variation (Table 5). Factor 1 contained variables of central tendency—mean and median size, 25th and 75th percentile, and skewness all explaining 59.69% of the variability in the data. Factor 2 is described by range variables—range, interquartile range, and minimum and maximum size accounting for 20.41% of the variation in the data. Factor 3 is defined exclusively by kurtosis encompassing 11.91% of the variation.

TABLE 2.

P values from Type III SS ANOVA conducted on Atlantic surfclam size variables as dependent variables and environmental variables and interaction terms as independent variables.

Size variables	Depth (m)	Temperature (°C)	Latitude (°)	Density/LPUE (clams/ m^2)	Dredge type	Temp. × depth	Temp. × Lat.	Depth × den./LPUE
Mean	0.00371	—	—	—	—	—	—	—
Median	0.00199	—	—	—	—	—	—	—
25 th Pct.	0.00756	—	—	—	—	—	—	—
75 th Pct.	0.00166	—	—	—	—	—	—	—
Range	0.00258	0.0415	—	0.0410	0.0375	—	—	0.0232
Interquartile range	4.06e-7	—	—	0.0174	—	—	—	0.0136
Minimum	—	—	—	—	—	—	—	—
Maximum	3.83e-5	0.0247	0.023	0.0431	—	0.00941	—	0.022
Skewness	1.40e-7	—	—	—	—	—	—	—
Kurtosis	—	0.00360	0.00582	—	—	—	0.00394	—
Density	0.02960	—	—	N/A	—	—	—	N/A

Only significant ($P < 0.05$) results are shown, nonsignificance is denoted by a dash (—).

TABLE 3.

P-values from Type III SS ANOVA conducted on ocean quahog size variables as dependent variables and environmental variables and interaction terms as independent variables.

Size variables	Depth (m)	Temperature (°C)	Latitude (°)	Density/LPUE (clams/m ²)	Dredge type	Temp. × depth	Temp. × Lat.	Depth × den./LPUE
Mean	—	0.0253	0.0126	2.14e-09	—	—	0.0247	—
Median	—	0.00108	0.00226	—	—	—	0.000782	—
25 th Pct.	—	0.00127	0.00069	—	—	—	0.00137	—
75 th Pct.	—	—	—	1.78e-7	—	—	—	—
Range	7.08e-8	7.17e-7	3.48e-5	—	—	2.64e-8	2.53e-6	—
Interquartile range	—	0.0131	0.0204	—	0.0182	—	0.0143	—
Minimum	—	5.60e-5	5.59e-5	—	—	—	7.00e-5	—
Maximum	1.47e-5	0.0104	—	—	—	1.76e-5	0.0197	—
Skewness	—	—	—	—	—	—	—	—
Kurtosis	—	—	—	—	—	—	—	—
Density	0.00196	—	—	N/A	—	0.0141	—	N/A

Only significant ($P < 0.05$) results are shown, nonsignificance is denoted by a dash (—).

Principal component analysis performed on ocean quahog environmental variables resulted in two factors that amassed 83.21% of variance in the data (Table 6). Factor 1 includes density/LPUE, depth, and temperature, explaining 62.49% of the variation. Factor 2 is described by latitude accounting for 20.72% of the variation. The ocean quahog PCA on size variables yielded three significant axes encompassing 90.37% of the variation (Table 7). The variables corresponding to each axis are identical to that of the PCA for Atlantic surfclam size variables, with factors 1–3 explaining 50.84%, 25.73%, and 13.80% of the variation, respectively.

Analysis of variance were conducted using PCA size factors as dependent variables and PCA environmental factors as independent variables. All three environmental factors (PC1, PC2, and PC3) were found to be significant for size factor 1 in Atlantic surfclams (Table 8). Factor 1 comprises sizes of central tendency: mean, median, 25th percentile, 75th percentile, and skewness and PCAs representing density, depth, temperature, and latitude all had significant explanatory power for the size metrics. Latitude (PC3) was the only significant environmental factor for size factors 2 and 3. Factor 2 includes size measures of range: interquartile range, range, and minimum

TABLE 4.

Significant factors from Atlantic surfclam PCA on environmental variables and related variables on each axis.

Factors (with eigenvalues)	Variables on axis
PC1 (2.2625)	Density/LPUE (1.7122)
PC2 (1.7473)	Temperature (1.5486), Depth (–1.2648)
PC3 (0.7636)	Latitude (–1.3446)

Factor load scores for environmental variables on each axis are included in parenthesis.

TABLE 5.

Significant factors from Atlantic surfclam PCA on size variables and related variables on each axis.

Factors (with eigenvalues)	Variables on axis
PC1 (5.9686)	Mean (–1.6582), Median (–1.664), 25 th Percentile (–1.5927), 75 th Percentile (–1.6961), Skewness (1.2114)
PC2 (2.0410)	Range (–1.0959), Interquartile Range (–1.1225), Minimum (1.6219), Maximum (–1.5955)
PC3 (1.1912)	Kurtosis (1.3822)

Factor load scores for size variables on each axis are included in parenthesis.

TABLE 6.

Significant factors from ocean quahog PCA on environmental variables and related variables on each axis.

Factors (with eigenvalues)	Variables on axis
PC1 (3.1243)	Density/LPUE (1.876), Depth (1.842), Temperature (–1.390)
PC2 (1.0361)	Latitude (–1.6304)

Factor load scores for environmental variables on each axis are included in parenthesis.

TABLE 7.

Significant factors from Atlantic surfclam PCA on size variables and related variables on each axis.

Factors (with eigenvalues)	Variables on axis
PC1 (5.0838)	Mean (–1.7445), Median (–1.7074), 25 th Percentile (–1.7194), 75 th Percentile (–1.6114), Skewness (1.0529)
PC2 (2.5729)	Range (1.6646), Interquartile Range (1.1045), Minimum (–1.2646), Maximum (1.1561)
PC3 (1.3802)	Kurtosis (–1.4441)

Factor load scores for size variables on each axis are included in parenthesis.

TABLE 8.
ANOVA results for Atlantic surfclam PCA factors.

PCA factor for size variables	Significant PCA factors—environmental variables (with Pearson's correlation coefficient and <i>P</i> values)
Factor 1 (Mean, Median, 25%, 75%, Skewness)	PC1 (Density/LPUE; -0.67 ; $P < 2.2e-16$) + PC2 (Depth/Temperature; -0.54 ; $P < 2.2e-16$) + PC3 (Latitude; -0.18 ; $P = 7.007e-4$)
Factor 2 (Range, ITQ, Range, Min, Max)	PC3 (Latitude; 0.24 ; $P = 0.02392$)
Factor 3 (Kurtosis)	PC3 (Latitude; 0.41 ; $P = 6.325e-5$)

Factors of size variables (listed in Table 5) were used as dependent variables in the ANOVA, and factors of environmental variables (listed in Table 4) as independent variables. Pearson's correlation coefficients between factors listed in parenthesis. *P*-values for significant environmental variables are noted in italics.

and maximum size. Factor 3 includes only kurtosis. Pearson's correlation coefficients were also calculated for each significant relationship between size and environmental factors. All environmental factors were negatively correlated with size variables in factor 1. Latitude was positively correlated with size variables in factors 2 and 3.

Ocean quahog environmental variables were divided between two factors: PC1 (density/LPUE, temperature, and depth) and PC2 (latitude). PCA factors for size variables comprised the same variables as Atlantic surfclams, described in the previous paragraph. PC1, representing density, depth, and temperature, was significant for size variable factors 1 and 2, with a positive Pearson's correlation for both (Table 9). PC2 was the only significant environmental variable for factor 3, with a weak negative correlation.

Size variables for central tendency were significantly related to density, depth, and temperature for both species. Kurtosis was significantly related only to latitude in both species. Size metrics relating to the range of sizes differed in their relationship to environmental variables for the two species, with latitude relevant for surfclams and density, depth, and temperature for ocean quahogs.

TABLE 9.
ANOVA results for ocean quahog PCA factors.

PCA factor for size variables	Significant PCA factors—environmental variables (with Pearson's correlation coefficient and <i>P</i> -values)
Factor 1 (Mean, Median, 25%, 75%, Skewness)	PC1 (Density/LPUE, Depth, Temperature; 0.56 ; $P = 1.285e-9$)
Factor 2 (Range, ITQ, Range, Min, Max)	PC1 (Density/LPUE, Depth, Temperature; 0.15 ; $P = 1.293e-3$)
Factor 3 (Kurtosis)	PC2 (Latitude; -0.07 ; $P = 0.01047$)

Factors of size variables (listed in Table 7) were used as dependent variables in the ANOVA, and factors of environmental variables (listed in Table 6) as independent variables. Pearson correlation coefficients between factors listed in parenthesis. *P*-values for significant environmental variables are noted in italics.

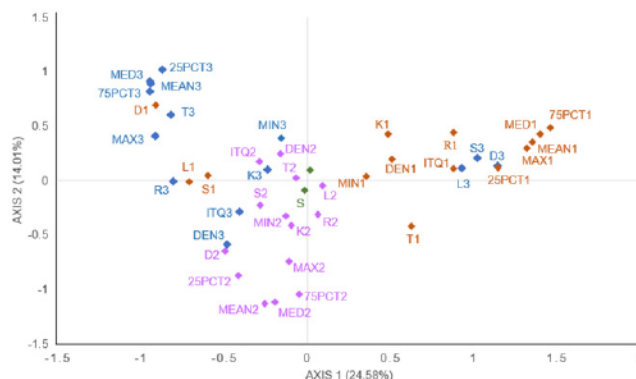


Figure 7. Correspondence analysis of Atlantic surfclam size and environmental variables. Individual values for each variable were categorized into thirds and designated 1 (orange), 2 (purple), or 3 (blue), with 1 being the smallest value (highest latitude) and 3 being the largest value (lowest latitude). Size variable abbreviations: MEAN = mean size, MED = median size, R = range, ITQ = interquartile range, 25PCT = 25th percentile, 75PCT = 75th percentile, MIN = minimum size, MAX = maximum size, and S = skewness, K = kurtosis. Environmental variable abbreviations: DEN = density, D = depth, T = temperature, and L = latitude. Dredge types (P, S) in green are included as supplementary variables and not used to set up the axes.

Correspondence Analysis

Correspondence analysis was conducted on Atlantic surfclam and ocean quahog datasets, including both size and environmental variables, to determine the relationships between and within variables. Many Atlantic surfclam categories with a 1 (smallest values) are grouped together on axis 1 in the upper right quadrant, including mean (MEAN1), median (MED1), maximum (MAX1), 25th (25PCT1) and 75th percentile (75PCT1), interquartile range (ITQ1), and range (R1) (Fig. 7). The smallest surfclam size categories are accompanied by categories of lowest latitude (L3) and deepest depth (D3), and to a lesser extent lowest density (DEN1). Intermediate surfclam sizes (2) align with axis 2, close to environmental categories of intermediate depth (D2), density (DEN2), latitude (L2), and temperature (T2). The largest size values for Atlantic surfclams lie between axes 1 and 2 in the upper left quadrant and are accompanied by categories of shallow depth (D1) and high temperature (T3).

Ocean quahog correspondence analysis places the largest clam sizes on axis 1 along with high latitude L1, but not with any categories of temperature, depth, or density (Fig. 8). The smallest ocean quahogs are located in the upper left quadrant and not found alongside any environmental variables. High density (DEN3), deepest depth (D3), and low latitude (L3), although not closely linked, are the nearest environmental variables to small clam sizes. Intermediate ocean quahog sizes lie on axis 2 between the lower two quadrants, aligned with low and intermediate temperatures (T1 and T2), intermediate latitude (L2), and density (DEN2). Low density (DEN1), shallow depth (D1), and high temperature (T3) correlate with small values of range (R1) and a large minimum size (MIN3). A key difference between the ocean quahog and surfclam correspondence analysis is the limited relationship of the environmental variables with metrics of the size–frequency distribution for ocean quahogs, compared with the much stronger association for surfclams.

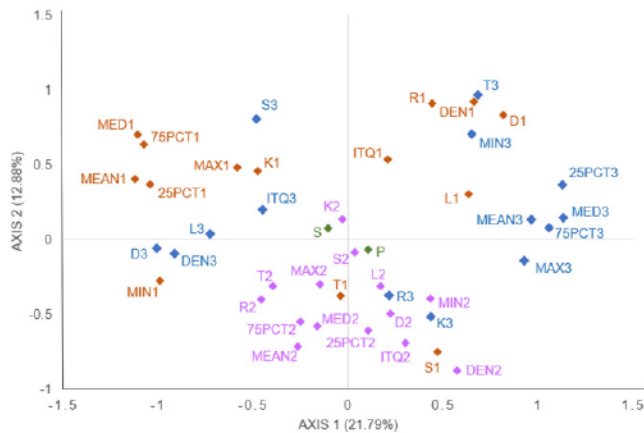


Figure 8. Correspondence analysis of ocean quahog size and environmental variables. Individual values for each variable were categorized into thirds and designated 1 (orange), 2 (purple), or 3 (blue), with 1 being the smallest value (highest latitude) and 3 being the largest value (lowest latitude). Size variable abbreviations: MEAN = mean size, MED = median size, R = range, ITQ = interquartile range, 25PCT = 25th percentile, 75PCT = 75th percentile, MIN = minimum size, MAX = maximum size, S = skewness, and K = kurtosis. Environmental variable abbreviations: DEN = density, D = depth, T = temperature, and L = latitude. Dredge types (P, S) in green are included as supplementary variables and not used to set up the axes.

In both correspondence analyses, the two dredge types fall close to 0 on both the x and y axes, indicating the limited impact of the differences in bar spacing and knife depth. The expectation that the differentials in dredge type might influence the catchability of small clams differentially is not well-supported by this analysis, nor the earlier described results of ANOVA.

DISCUSSION

Perspective

The Northwest Atlantic is warming faster than many of the oceans around the world (Pershing et al. 2015, Friedland et al. 2020, 2022). In response to increasing bottom water temperatures, Atlantic surfclam populations are shifting into cooler waters north and offshore of their historical range (Weinberg 2005, Hennen et al. 2018, Hofmann et al. 2018) into the present range of the ocean quahog. The Atlantic surfclam fishery has already responded to spatial shifts in the range of the surfclam by moving processing plants and vessels to northern locations and ports (McCay et al. 2011, DeGrasse et al. 2014) and opening up areas previously closed to fishing (DeGrasse et al. 2014), but future success of the fishery may depend on regulatory reform permitting mixed landing of clam species and improved sorting ability of surfclams and ocean quahogs on deck or in the processing plant. This study emphasizes the broad distribution of overlap between the two species and highlights depth, particularly between 40 and 55 m, as a limiting factor in Atlantic surfclam size and density. Distribution of ocean quahogs, meanwhile, is dependent more on temperature and latitude. The results described in this analysis may provide insight as to how the two species continue to respond to climate change and strengthen the need for regulatory reform.

The case history considered here also offers a unique perspective into the dynamics of ecotones and range boundaries on species' population dynamics during a period of rapid climate change. Range boundaries have received considerable attention observationally (Cook et al. 1998, Baker et al. 2007, Troost 2010, Thorson et al. 2016, Reise et al. 2017) and through modeling of dispersion and recruitment (Guo et al. 2005, Hughes et al. 2007, Berestycki et al. 2009), genetics (Ibrahim et al. 1996, Excoffier et al. 2009, Garnier & Lewis 2016), and bioenergetics (Parsons 1991, Thomas et al. 2016), but ecotones wherein species' range boundaries overlap have received much less consideration (Brandt & Wadley 1981, Zuschin & Piller 1997, Smith et al. 2000, Carney 2005), primarily due to the spatially limited region of overlap normally present between faunas. Rapid warming of the Northwestern Atlantic has provided unique examples of overlap between continental shelf faunas, presumably as a product of differential behaviors of species, permitting differential rates of range boundary shifts. Powell et al. (2019) provide one example, between blue mussels (*Mytilus edulis*) and Atlantic surfclams, where differential behaviors have created transient multiple stable points (see also a potential additional example for mussels (Jurgens & Gaylord 2016). Herein is examined a geographically much more extensive ecotone, occupied by two clam species belonging to the cool temperate and boreal faunas providing an unparalleled opportunity to study population dynamics within an ecotone consequent also of differential behaviors and thus, differential rates of range shifting by the two species.

The Developing Ecotone Between Atlantic Surfclams and Ocean Quahogs

The ranges of the Atlantic surfclam and ocean quahog overlap in the surveyed region of the Northwest Atlantic at depths between 30 and 60 m, with highest mixing at 40–55 m. Clam density within this depth range shifts from predominantly Atlantic surfclam at depths less than 40 m to ocean quahog dominated at depths greater than 45 m. Although ocean quahog size frequencies remain relatively constant between 40 and 55 m, metrics of the Atlantic surfclam size frequency begin to decrease around 40 mm. The size and density trends are indicative of larger surfclams at inshore sites and smaller surfclams offshore. Surfclam size increases with temperature, whereas density is stable.

The warm-temperature range boundary for surfclams is well-studied and clearly determined by the effect of high temperature on scope for growth (Munroe et al. 2013, Narváez et al. 2015, Hornstein et al. 2018). The determining factors controlling the cool temperature range boundary are much less well-defined. Statistical analysis lends weight to the expected importance of bottom water temperature as a determinant influencing the distribution of Atlantic surfclams and ocean quahogs along the ecotone boundary. Bottom water temperature (also determined by depth) is the primary factor in determining successful occupation by surfclams. Herein, the importance of depth *per se* is downgraded as both species live over a very wide depth range depending upon regional temperature gradients. Temperature was significant in ANOVA for 8 of 11 surfclam size variables (Table 2). Surfclam density and the density $\times$ depth interaction affect the size range, interquartile range, and maximum size of surfclams indicating biological modulation of the size-frequency distribution. Principal component analysis

further places density, depth, and temperature as explaining the majority of variation within sampled sites (Table 4) and correspondence analysis shows that smaller clams are found in areas of low latitude and greater depth consistent with cooler bottom water temperatures farther offshore, whereas larger clams inhabit shallower waters, where the temperature is higher (Fig. 7). The results shown in this study all support the expectation that range expansion at higher latitudes, lower temperatures, and greater depths should be characterized by a shift in the size frequency toward an increased presence of small surfclams.

The size differential across the shelf may accrue from differential age frequencies wherein an expectation of younger surfclams offshore due to more recent range expansion would be consistent with observation, but also feasible would be a slower growth rate due to cooler temperatures and lower food availability offshore. The two options cannot presently be discriminated and substantial information supportive of both interpretations is well-documented (Munroe et al. 2013, Powell et al. 2020b). What is clear is the absence of dispositive information determining the characteristics of the offshore range boundary of this species. Dispersal potential is clearly not a determining factor (Zhang et al. 2016, Timbs et al. 2019). Temperature clearly is, but whether temperature is a direct determinant (e.g., slow growth) or a time-dependent modulator (clam age determined by elapsed time because favorable temperatures for recruitment began) or both remains a conundrum.

Ocean quahog distribution is more influenced by temperature and latitude. Seven out of 11 ANOVA for ocean quahog size variables were significant for temperature, 6 for latitude, and 7 for the temperature $\times$ latitude interaction (Table 3). Large ocean quahogs exhibit a distinct correlation with high latitude, but not with other environmental variables (Fig. 8). Ocean quahog correspondence analysis places the largest clam sizes on axis 1 along with high latitude. Small ocean quahogs also show a lack of clear relationship to environmental variables, supported by weaker correlations (Pearson's correlation coefficients, Table 9) between PCA size and environmental variable factors. In correspondence analysis, the smallest ocean quahogs are located in the upper left quadrant well-separated from any environmental variable.

Two issues arise, an explanation for the position of the ocean quahog inshore boundary and an explanation for the latitudinal effect. Ocean quahog density decreases as temperatures reach 14 °C, but their size varies little. The temperature effect is consistent with the known upper thermal tolerance of the species, wherein continuous exposure to 16 °C or higher results in death. Temperatures this high are often observed in the fall when the Cold Pool breaks down, prior to winter cooling (Lentz 2017, Chen et al. 2018, Friedland et al. 2022). Ocean quahogs, given their ability to burrow into the sediment and estivate during warmer months (Taylor 1976, Ragnarsson & Thórarinsdóttir 2002, Strahl et al. 2011), escape warming temperatures and so are found in high densities with little variation in size within their historically (1982–present) occupied range. No evidence of range recession is observed because federal surveys began in 1982. Thus, surfclams and ocean quahogs differ substantially in their size frequencies within the ecotone when compared with their size frequencies in the core of their range. Moreover, ocean quahogs are found inshore of an expected range boundary determined by their known thermal tolerance.

Thus, the inshore boundary for this species is likely a complicated outcome of the interaction of physical environmental and behavioral processes.

The latitudinal effect on ocean quahog size presents an even greater enigma as growth rates are known to respond positively and substantively to warmer temperatures within the thermal limits of the species (Begum et al. 2010, Pace et al. 2018), providing an expectation of larger animals to the south, which is not observed. Ocean quahogs are long-lived and many of the individuals in the study were born in the 19th century, including prior to the ending of the Little Ice Age. As a result, these older animals grew slower early in life and thus, remain smaller than animals recruiting under the warmer conditions of the 20th century. Comparison of age frequencies from the Long Island continental shelf to southern New Jersey show that the age frequencies are enriched in older clams farther south, presumably due to differential recruitment trends during the 19th century (Pace et al. 2017, Hemeon et al. 2021, 2023, Sower et al. in press). As a consequence, a tendency exists for more small old animals to be present to the south.

Dredge Performance

Typically, the surfclam fishery uses a dredge with a wider bar spacing and a differential knife depth compared with the ocean quahog fishery. Presumably, this might influence the size frequency of the catch. This study deployed two dredge designs varying by bar spacing and knife depth identified herein as the P or surfclam dredge and the S or ocean quahog dredge. The P dredge had a slightly wider bar spacing than the S dredge, 1.5"–1.25". Dredge type was only significant in ANOVA for 2 of 20 size variables for both species, size range in Atlantic surfclams and interquartile range for ocean quahogs. For both clam species, minimum size and the 25th percentile were lowest in the S dredge, whereas the interquartile range was largest. The S dredge with narrower bar spacing, in conclusion, caught smaller individuals of both species and a greater range of sizes compared with the P dredge. The issue is important in that exclusion of small animals, recognizing the bias of small surfclams in the ecotone, would permit increased harvest of desired size classes, whereas minimizing sorting and discarding on the deck. The influence of dredge design on selectivity of surfclams and other clam species is well-known (Gaspar et al. 2003, Kim et al. 2005, Sala et al. 2007). The differential observed in this study is, however, not large; thus, the value of the differential between the two dredge designs tested in differentiating surfclams and ocean quahogs is limited.

Dredge efficiency did not vary between the two dredge styles, as inferred from the absence of a significant difference in density, nor was an influence of depth on dredge performance detected; both dredge types fell near the origin in correspondence analysis. A Wilcoxon signed rank test was performed comparing catch between paired tows, with the results ($P = 0.7894$) indicating the two dredges are not significantly different from each other. These results agree with Poussard et al. (2021) who found little effect of depth or species on dredge efficiency.

Mixed Landings: Is it Feasible?

The future of the Atlantic surfclam fishery rests on the extent of the ecotone between surfclams and ocean quahogs and how

the fishery can adapt to the increased probability of catching both species on the same tow. Both fisheries focus on aggregations of clams yielding 32 bushels/h or more. This is particularly important for surfclams, as ocean quahog densities are routinely well above this threshold, whereas this is increasingly not the case for surfclams (Timbs et al. 2019, Solinger et al. 2022). In this study, surfclam densities reaching this threshold were not at all uncommon in the overlap zone (Fig. 3B). Current industry advice puts the degree of mixing able to be sorted on deck at no more than 1 ocean quahog in 25 total clams, or 4% of the catch. Stromp et al. (in press) evaluated scenarios of increased sorting capability (>4%) that resulted in improved landings of 50,000–150,000 bushels of surfclams annually. Landing both species together would prevent a loss in fishing grounds and reduce discards; however, a regulatory change would be required.

In 2016, a request was made to the Mid-Atlantic Fishery Management Council (MAFMC) by clam companies to amend the Atlantic surfclam and ocean quahog Fishery Management Plan (FMP) (MAFMC 2016). The industry suggested a fixed number of clams other than the target species be allowed in a cage and raised questions as to how to handle the nontarget species. The MAFMC published a committee recommendations summary in December 2021 and were supportive of a management approach that would require manual on-board sorting and separation of clams by species into cages (MAFMC 2021). Long-term solutions, such as a research and development approach, would then be discussed by the Council. In October 2022, the MAFMC released a drafted amendment to the Atlantic surfclam and ocean quahog FMP that proposed modifications to regulations to allow for mixed catches on-board vessels. Four Alternatives were outlined, with the first as no action taken and no changes made to current regulations (MAFMC 2022). Alternative 2 proposed the creation of a new combined trip category allowing surfclams and ocean quahogs to be landed on the same trip, also requiring on-board sorting. Alternatives 3 and 4 also create the combined trip category, but would require mixing of clams within cages to be on only declared combined trips. Alternative 3 would require manually monitored landings and trips with the implementation of a new NOAA Fisheries sampling program, whereas Alternative 4 would require on-board electronic monitoring. A preferred Alternative has not been selected and reconsideration of options is ongoing at this writing.

The MAFMC organized public hearings in November 2022 to gather input on the proposed species separation amendment. No further information from the hearings or public comments nor updates from the MAFMC on the amendment were released at the time of this writing. A reasonable assumption is that changes to mixed landing regulations will occur, but many questions remain on the economic and biological impact of mixed landings. What this study shows is the magnitude of this problem. The overlap region, as defined in Figure 2, now covers a large fraction of the Mid-Atlantic continental shelf south of Hudson Canyon. Sufficient information is not available to permit a further evaluation to the northeast, though overlap regions almost certainly are present (Powell et al. 2020b) and comparison of the data presented herein with earlier survey data (e.g., NEFSC 2017a, 2017b) demonstrates the accelerating expansion of this ecotone throughout the Mid-Atlantic region over the last vicennium.

The ability to land both surfclams and ocean quahogs will certainly increase the fishable footprint in the Mid-Atlantic, however, the addition of other uses of the continental shelf must be considered. Atlantic surfclam fleets, in particular, may be displaced by growing wind energy leases (Munroe et al. 2022, Scheld et al. 2022, Borsetti et al. 2023, Stromp et al. in press) affecting profitability of the fishery. These leases are primarily, but not exclusively, inshore of the ecotone described herein so that the present surfclam fishable stock is being restricted both inshore and offshore by competition with other anthropogenic uses inshore and other biological realities offshore. This study attempts to provide understanding to future challenges of the Atlantic surfclam and ocean quahog fisheries in the face of climate change, by highlighting the extent of species overlap and emphasizing the priority for mixed landing reform.

CONCLUSIONS

Results of this study track the shift of Atlantic surfclams into deeper, cooler waters offshore and north of their historical range into areas currently occupied by ocean quahogs. Ocean quahogs, however, largely have not yet responded to warming temperatures or the introduction of surfclams, as inferred from an absence of a distinction in distribution between small and large ocean quahogs and their relationship to environmental variables, with the exception of latitude. An important question remains and that is to explain the cross-shelf extent of this ecotone. Historically, over the modern survey time period, which began circa 1982 (NEFSC 2017a, 2017b), these two species have had minimal overlap. Catching both species in quantity occurred rarely until well into the 2000s (e.g., NEFSC 1999, 2002). Why is the ecotone so expansive today; conversely, why was it so narrow previously?

The transgression of the range of the Atlantic surfclam has likely been occurring for 4–5 decades (Hofmann et al. 2018), but was not well-documented until after 2000 (Kim & Powell 2004). The life span of a surfclam can reach up to 30+ y, and most individuals spawn by age 1–2 (Chintala & Grassle 1995, Chute et al. 2016). Ocean quahogs are much longer lived (200+ y), take longer to reach maturity (Sower et al. 2022), but may recruit no less frequently (Weinberg 1999, Pace et al. 2017, Hemeon et al. 2021, 2023; but see Powell & Mann 2005). Individual ocean quahogs alive at the time of this study were likely to have been alive in the 1970s when the Atlantic surfclam began its range shift. Although surfclam populations can shrink and expand within years to shift the species range boundary, decades may be required for ocean quahogs to respond similarly. Ocean quahog past range shifts have been documented (Powell et al. 2017, LeClaire et al. 2022), particularly as a result of the regression of the Cold Pool at the end of the Little Ice Age. In particular, LeClaire et al. (in prep.) documented the offshore range recession of ocean quahogs after the Little Ice Age, during which they were found well inshore of their present-day depth range, with the largest, oldest animals surviving inshore longest. This process of departing the inshore region took place over a centurial time frame, presumably because large animals were able to survive apparently lethal temperatures through estivation and thus, live where they “should not be found.”

One might expect, as deduced from LeClaire et al. (2022), that ocean quahogs will slowly move offshore as the Northwest Atlantic continues to warm, but no response to temperature or

the presence of surfclams has been observed thus far. Possibly, the present situation is in fact the typical condition that has existed since the end of the Little Ice Age. The last warm period of the 20th century prior to initiation of the federal survey in 1982 occurred in the 1930s–1940s. The eastern United States was relatively cold beginning during the 1950s and extending through the 1980s, at the end of which the present warming trend began (Nixon et al. 2004, Ouellet-Bernier et al. 2020). A 30- to 40-y period of stable or decreasing temperatures could easily have limited surfclam expansion sufficiently to permit a relatively stable and narrow boundary to form between the two species, as observed in earlier stock surveys, as this time scale would be consistent with the slow establishment of a stable inshore range boundary by the ocean quahog, whereas limiting further recruitment by surfclams offshore. Under this hypothesis, the earlier adaptation of the fishery to the landing of the two species separately might be seen as a response to an unusual species distribution pattern rather than the commonplace and the present situation a more normal circumstance since the end of the Little Ice Age. One might consider that the apparent absence of obviously competitive interactions between the two species is consistent with the routine

extensive intermingling of these species fostered by the dramatic differential in rate of response to temperature change as the species march across the continental shelf consequent of climate change. The study emphasizes the importance of the relative rates of transgression and regression of range boundaries by abutting faunas in determining the degree of influence of the ecotone between them on the benthic community structure of the continental shelf.

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