Changes in the spatial distribution and anatomy of a range shift for the Atlantic surfclam *Spisula solidissima* in the Mid-Atlantic Bight and on Georges Bank

Jeremy R. Timbs[1],*, Eric N. Powell[1], Roger Mann[2]

[1]**Gulf Coast Research Laboratory, The University of Southern Mississippi, Ocean Springs, MS 39564, USA**
[2]**Virginia Institute of Marine Sciences, The College of William and Mary, Gloucester Point, VA 23062-1346, USA**

ABSTRACT: The Atlantic surfclam *Spisula solidissima* supports one of the largest fisheries on the US northeast coast. Using ~30 yr of data from surfclam stock surveys, variance-to-mean ratios (VtMRs) were calculated both temporally and spatially for a range of surfclam size classes to determine the degree of patchiness. The VtMR declined from the 1980s to present in all regions (offshore Delmarva, New Jersey, Long Island, Southern New England, Georges Bank); however, VtMR rose with increasing clam size. Taylor's power law (TPL) analysis corroborated the VtMR; the surfclam is highly patchy across its range. The surfclam's proclivity for a patchy distribution varied regionally. Regions supporting the bulk of the stock were characterized by significantly higher degrees of patchiness and exhibited a higher exponent for the TPL. A species distribution function model corroborated findings of declining patchiness over time, supporting the hypothesis that warming of Mid-Atlantic continental shelf bottom waters is both driving the surfclam into new habitat and extirpating it from nearshore and southern areas. Size-dependent and temporal trends in VtMRs and temporal relative stability in TPL suggest that range expansion is conduced by regional settlement of larvae, followed by biased mortality in suboptimal habitats. This biased mortality ultimately re-establishes the increased patchiness characteristic of larger animals but also predisposes the species to a rapid range shift. Declining VtMRs over time may be a symptom of range expansion along the leading range boundary that has increased the proportion of newly occupied habitat without mature patch characteristics while, at the same time, range recession has removed the older mature patches along the range's trailing edge.

KEY WORDS: Patchy distribution · Larval transport · Ocean warming · Larval connectivity · Range shift

1. INTRODUCTION

Ecological impacts of climate change have been observed in many species across an array of biomes (e.g. Beaugrand et al. 2002, Walther et al. 2002, Brander 2010, Chen et al. 2011). An indicative response to climate change is a distributional shift that can be reflected by a change in the center of the distribution or in a contraction or expansion of a species' range (Nye et al. 2009). These responses have been reported for terrestrial species (Parmesan et al. 1999, Davis & Shaw 2001, Kelly & Goulden 2008, Sekercioglu et al. 2008, Chen et al. 2011), freshwater species (Woodward et al. 2010, Bond et al. 2011, Wenger et al. 2011), and marine species (Perry et al. 2005, Harley et al. 2006, Johnson et al. 2011), including some in the Mid-Atlantic Bight (Hare & Able 2007, Nye et al. 2009, Friedland et al. 2018). Increases in

bottom-water temperatures typically shift species to higher latitudes or deeper depths (e.g. Pershing et al. 2015, Friedland et al. 2018, Powell et al. 2019a). Sagarin et al. (1999), for example, observed a change in benthic invertebrate communities caused by increasing bottom-water temperatures, with southern species increasing in abundance while northern species decreased in abundance. Species with a narrow thermal tolerance, such as the Atlantic surfclam *Spisula solidissima*, can be expected to shift into higher latitudes and increased depths as water temperatures rise; evidence of an ongoing range shift for the surfclam as anticipated is well described (Hofmann et al. 2018).

In marine ecosystems, many species with commercial importance have patchily distributed populations (Bascompte et al. 2002). The term 'patchiness' is used to describe spatial distributions over a wide range of spatial scales, from small-scale within-habitat to geographic. The majority of sessile and sedentary marine invertebrates are distributed patchily at a local or within-habitat scale (e.g. Flowers 1973, Jumars et al. 1977, Munroe & Noda 2009, Kristensen et al. 2013, Beninger & Boldina 2014) while frequently also being patchy at a larger geographic scale by being distributed in more or less isolated populations within the metapopulation (e.g. Maurer & Taper 2002, Hummel 2003, Borregaard & Rahbek 2010, Pinsky et al. 2012). These various scales of patchiness often grade into one another (e.g. Munguia 2004, Harte et al. 2005, Kristensen et al. 2013). The present study addresses the subject of patchiness of the Atlantic surfclam on the continental shelf at a geographic scale that encompasses the distribution of the species across the continental shelf and latitudinally across its habitable range.

Typically, connectivity over the metapopulation is maintained by dispersal of planktonic larvae (Scheltema 1986, Condie et al. 2005, López-Duarte et al. 2012, Munroe et al. 2012, Zhang et al. 2015). The physical environment, including hydrodynamics, temperature, salinity, and gradients thereof, and behavior of the larvae exert a strong influence on larval survival and transport from one habitable location to another (Gaylord & Gaines 2000, Ma et al. 2006, Narváez et al. 2012, Zhang et al. 2016). Disagreement exists as to the determinant of spatial and temporal variations seen in patchily distributed species both within and between habitats. One school of thought contends that patchiness arises from variations in larval dispersal and recruitment of larvae (Gaines et al. 1985, Jackson 1986, Underwood & Fairweather 1989, David et al. 1997, Ayata et al. 2009).

The other school of thought invokes post-settlement mortality in which larvae settle relatively ubiquitously over the bottom and succumb to differential spatial gradients in predation or poor edaphic or environmental choice (Keough & Downes 1982, Luckenbach 1984, Ólafsson et al. 1994, Gosselin & Qian 1997, Tezuka et al. 2012). Patchiness often arises in bivalve mollusks post-settlement for these reasons (Dresler & Cory 1980, Stokesbury 2002, Brand 2006). At the largest of spatial scales, range boundaries may be established in either of these 2 ways, i.e. by dispersal dynamics or post-settlement survival (Hutchins 1947, Sexton et al. 2009, Woodin et al. 2013).

The Atlantic surfclam has a patchy distribution across its range at various spatial scales (compare Powell et al. 2017a to the present analysis). The determinant of regional patchiness in this species is not well understood, although both recruitment (Chintala & Grassle 2001, Ma et al. 2006, Zhang et al. 2016) and post-settlement (Weinberg 1999, Narváez et al. 2015) processes seem to be involved. The geographic distribution of this species is changing, however, as increasing bottom-water temperatures push its range farther north and offshore (NEFSC 2013, Munroe et al. 2016, Hofmann et al. 2018). Clear evidence was provided by a warm period off Delmarva[1] between 1999 and 2002 that resulted in thermal stress combined with poor physiological condition causing mortality and a shift of the surfclam into deeper water (compare Merrill & Ropes 1969, Weinberg 2005; see also Kim & Powell 2004). Higher summer water temperatures resulted in relatively low growth rates and meat weights (Weinberg et al. 2002, Marzec et al. 2010, Narváez et al. 2015). Simulations indicated that an increase in average bottom-water temperature as observed off Delmarva circa 2000 will significantly reduce surfclam assimilation rate, leading to starvation mortality and a reduction in the surfclam population (Narváez et al. 2015), supporting observational inferences made by Kim & Powell (2004).

Arguably, the distribution of a species within the metapopulation as measured by metrics of patchiness may remain unchanged even as the geographic

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[1]For convenience, in the following presentation, reference will be made to subsections of the surveyed stock's range as historically used in assessment reports (e.g. NEFSC 2003, 2007) (Fig. 1). These regions are termed Delmarva, a region extending from the Chesapeake Bay mouth to the Delaware Bay mouth; New Jersey, ranging from the mouth of Delaware Bay to Hudson Canyon; Long Island, encompassing the region from Hudson Canyon to Rhode Island; Southern New England, effectively the continental shelf south of Massachusetts; and Georges Bank.

footprint of the species shifts. Alternatively, a consequence may be a change in patchiness on a geographic scale with implications for the population dynamics of the species throughout its new range. How range shifts generating differential patterns in recruitment and survival may affect local and regional species patchiness has been considered (Holt et al. 2005, Hughes et al. 2007, Berestycki et al. 2009, Woodin et al. 2013) but remains poorly understood because geographically expansive and lengthy time series are rare. The availability of a geographically expansive and lengthy dataset for the Atlantic surfclam creates an opportunity to examine the relationship between changes in the species' spatial distribution and the degree of patchiness in the metapopulation.

The objective of this study was to examine the dynamics of patchiness of the Atlantic surfclam, including differences among size classes, over an expansive geographic scale and to determine if the degree of patchiness has been stable over time, with the goal of identifying any effects of a well-documented shift in range on these population characteristics. The area of interest for the current study is the Mid-Atlantic Bight and Georges Bank. This region encompasses nearly the entirety of the Atlantic surfclam's range (Hofmann et al. 2018). Specific analyses of the spatial distribution of the Atlantic surfclam that follow are designed to (1) determine the degree of patchiness of the surfclam population in each of 5 regional subdivisions historically used to assess the status of the stock, (2) identify any change in patchiness of the population over the 30+ yr history of surveys of the surfclam stock, (3) establish the geographic extent of a shift in the center of distribution throughout the 5 study regions and over what time frame that shift has occurred, and (4) evaluate the influence of a shift in range on the distribution of the species as measured by a series of metrics describing the degree of patchiness in the metapopulation.

2. METHODS

The data used in the current study were collected by the National Marine Fisheries Service (NMFS) Northeast Fisheries Science Center (NEFSC) stock assessment surveys that were conducted every 2–3 yr beginning in 1982 and continuing to 2011. Data after 2011 were excluded from this analysis because a new dredge was employed for the survey after 2011, and gear calibration between the 2 dredges, though feasible (Hennen et al. 2012, NEFSC 2017), would introduce challenges of interpretation for the analyses contemplated herein. Fig. 1 shows the location of each tow across the entirety of the surfclam-surveyed range from 1982 to 2011. With the exception of surfclam populations in state waters and a sliver of range off Nantucket up the Great South Channel into the Gulf of Maine, this dataset covers the entirety of the surfclam's range. For the current study, the survey data were divided by region (Delmarva, New Jersey, Long Island, Southern New England, Georges Bank; Fig. 1) and size class (64–79, 80–92, 93–103, 104–119, and ≥120 mm shell length, SL), referred to hereafter by the lower size boundary (i.e. 64, 80, 93, 104, and 120). Surfclam populations are considered a single stock in the US exclusive economic zone from Georges Bank to southern Virginia (NEFSC 2017). The historical allocation by region arises from regional differences in environment that influence biological properties (e.g. growth rate, Munroe et al. 2013, 2016; mortality, Weinberg 1999, 2005). The aforementioned size classes were chosen based on Kuykendall et al. (2017), who showed that a 64 mm SL surfclam, averaged across
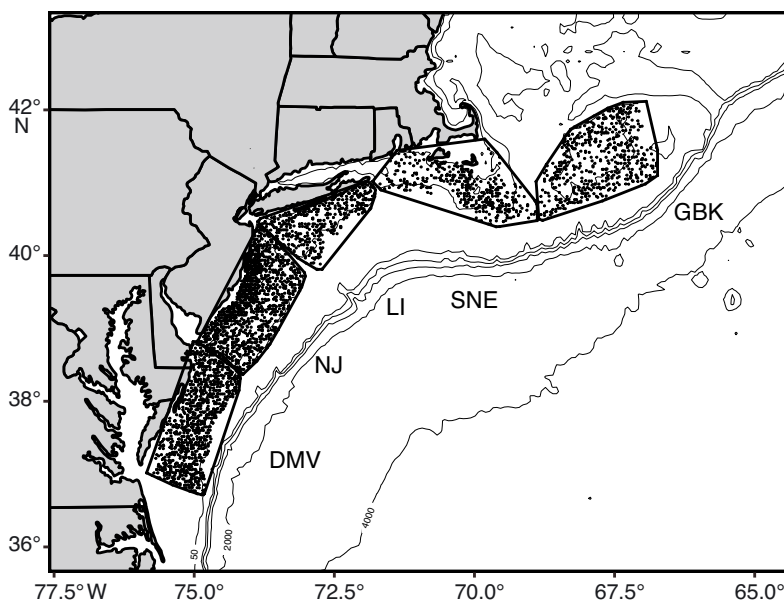

Fig. 1. Tow locations (dots) for the Atlantic surfclam stock assessment surveys from 1982 to 2011. Solid lines delineate the regions of interest (DMV: Delmarva; NJ: New Jersey; LI: Long Island; SNE: Southern New England; GBK: Georges Bank). Depths in m

the Delmarva and New Jersey regions, requires about 4 yr to reach market size, with each larger size class decrementing 1 yr of time to do so. These sizes, therefore, approximate the sizes that will recruit to the fishery (≥120 mm clams) in 4, 3, 2, and 1 yr.

The NEFSC survey data used were the number of surfclams caught per tow adjusted for nominal tow distance and selectivity by size class (NEFSC 2013). Biomass was obtained by applying a generalized linear mixed model using lengths and weights derived from selected measurements of individuals taken during the survey that covered the range of sizes in the catch. Details are provided in NEFSC (2013). Temporal changes in patchiness and spatial distribution were evaluated by decade (1982–1989, 1992–1999, 2002–2011, hereafter referred to as the 1980s, 1990s, and 2000s, respectively). The decadal divisions were chosen based on 2 criteria. The separation of the 1980s and 1990s represents a distinctive boundary between relatively low and relatively high survey biomass indices (NEFSC 2013) and coincides with a change in the rate of warming in the Mid-Atlantic region (Cook et al. 1998, Nixon et al. 2004, Oviatt 2004). The division at 2000 coincides with an increase in surfclam mortality rates off Delmarva contemporaneous with a regime shift in the North Atlantic, possibly due to a negative to positive excursion of the Atlantic Multidecadal Oscillation (Lucey & Nye 2010).

Only positive tows, i.e. tows catching at least 1 surfclam, were used. The NEFSC survey is a stratified random survey with strata based on depth and latitude rather than surfclam spatial distribution (Jacobsen & Hennen 2019). As such, in any year, an unknown proportion of tows within a stratum may have been sited in locations uninhabitable for the surfclam. Such tows would change the mean and variance in the stratum arbitrarily. Accordingly, all tows that caught 0 surfclams were removed from the analysis to eliminate the need to allocate, often arbitrarily, such tows to tows within and outside of viable surfclam habitat based on little or no information supporting the delineation.

Patchiness was assessed using the variance-to-mean ratio (VtMR) of the density. The VtMR has been widely used for this purpose (e.g. Powell et al. 1987a, Maurer & Taper 2002, Harte et al. 2005). As the organism's distribution becomes patchier, the variance increases relative to a given mean. A VtMR significantly above 1 indicates a patchy distribution; a VtMR significantly below 1 indicates a uniform distribution. Elliott (1977) provided statistical tests to identify cases where the ratio differs significantly from 1.

The NEFSC stock survey is a stratified random survey (NEFSC 2017). Each stratum in each survey year was considered a spatial unit for analysis. Strata containing only 1 tow were excluded, as a variance calculation was not possible. Most of these strata were narrow strata abutting the 3 mile (~5 km) state statutory limit. NEFSC (1999, 2002) provided examples of the distribution of tows among strata. Further details are given in NEFSC (2017). The mean and variance of the number of surfclams caught per tow were calculated for each size class over the 3 decades for each of the remaining survey strata. This provided 1 VtMR for each stratum, for each year, for each size class. The individual strata VtMRs for each survey year were allocated to each of 3 decades (1980, 1990, 2000) and each of 5 regions, with averages computed by decadal period or region as appropriate. A 2-way ANOVA was conducted by region to examine the effect of decade and size class on the VtMR. A 2-way ANOVA was also used to evaluate differences in the VtMR between regions by decade. Interaction terms were always included in the ANOVA. Post hoc pairwise contrasts were obtained using least square means tests for multiple comparisons. All aspatial statistics used the 'car' and 'lsmeans' packages in R (R Core Team, www.r-project.org).

The VtMR determines the degree of dispersion among a set of samples, typically obtained from a defined circumscribed area, in this case the survey stratum. An independent method for estimating the degree of patchiness within a metapopulation uses Taylor's power law (TPL). TPL relates the relationship of the mean and variance of a series of sample sets obtained from a series of population or metapopulation units (Taylor 1961). Accordingly, TPL provides a scale of comparison distinctly larger in geographic scale than individual VtMRs as computed herein and also provides a relational comparison across a range of VtMRs rather than conflating them into higher-order means.

TPL is expressed as:

$$\sigma = \alpha \times \mu^{\beta} \qquad (1)$$

where σ is the variance of a sample set, α is a scaling factor, μ is the mean of the sample set, and β is an index of dispersion (patchiness) that ranges from 0 for a regular distribution to infinity for a highly patchy distribution (Taylor 1961, Elliott 1977, Green 1989, Kristensen et al. 2013). In practice, the parameters are derived after log transformation; thus $\log(\alpha)$ is the intercept, and β is the slope of the linear model. Each stratum in each survey year provided 1 VtMR. Parameters of the power law were obtained for each

size class across years and regions using the appropriate suite of VtMRs. An ANCOVA using the log-mean as the covariate and the log-variance as the dependent variable was used to assess if β differed by region, changed over time, or differed between size classes.

TPL has been studied extensively in the context of its explanatory power in describing the geographic characteristics of a species' distribution (Maurer & Taper 2002, Kristensen et al. 2013, Pertoldi & Faurby 2013). Because the power law considers the relationship of the mean and variance over a range of means and variances, the average VtMR can vary without changing the power law. This might happen, for example, if sites yielding the highest mean and variance disappeared without influencing the relationship of the variance to the mean over the remainder of the metrics' ranges. The average VtMR would then decline, but the power law would remain unchanged. As a consequence, the VtMR and TPL provide fundamentally different evaluations of patchiness.

Patchiness can be evaluated aspatially and spatially (e.g. Powell et al. 1987a,b). For comparison to aspatial methods based on the relationship between the variance and the mean, an alternative spatial analysis was used to investigate shifts in surfclam distribution and changes in patchiness using a species distribution function (SDF) model developed by Thorson et al. (2016). The SDF model estimates expected densities within a spatial domain for a given location using model parameters estimated from catch data; spatial autocorrelation is then employed over time to predict shifts in distribution and areal coverage (Thorson et al. 2016, Timbs et al. 2018). For the current study, the center of distribution for the surfclam was derived from the 2-dimensional density maps produced by the SDF model. When calculated sequentially by survey year, changes in the location of the center of distribution can be identified. Similarly, the differential in spatial distribution between size classes can be compared. The distribution center is specified in terms of location latitudinally (northings) and longitudinally (eastings). Northings are defined in terms of distance (km) from the equator. Eastings are based on the Universal Transverse Mercator (UTM) coordinate system. All regions except Georges Bank used UTM 18 as the 0 point. Georges Bank used UTM 19. Timbs et al. (2018) provided an example of the application of this model to surfclam distributional patterns in investigating reasons for the absence of a broodstock–recruitment relationship in the Atlantic surfclam.

3. RESULTS

3.1. Aspatial analysis

The VtMR declined for each size class from the decade of the 1980s to the decade of the 2000s within all regions except for Long Island, which showed a decline in all size classes except market size (≥120 mm), and Southern New England, in which the VtMR for the 104 mm size class increased slightly (Fig. 2). Frequently, the decline in VtMR was monotonic over the decades, although for a subset, the VtMR rose in the 1990s before declining below the 1980s value in the 2000s. For all regions, market-size clams had a higher VtMR within each decade than other size classes, and the VtMR generally declined with decreasing size, except for in the 1980s in Delmarva, in which the smaller size classes had a larger VtMR (Fig. 2, Table 1), and the 1980s–1990s period in New Jersey, where the largest submarket size class (104 mm) had a larger VtMR than market-size clams.

The VtMR was significantly higher in the 1980s, and the VtMR in the Delmarva region was significantly higher than in any of the other regions (Table 2). The VtMR for the Delmarva region was significantly higher during the 1980s than in the 1990s and 2000s (Table 2). For the Long Island region, the VtMR for market-size clams was significantly higher than for any of the other size classes (Table 2). In the Southern New England region and Georges Bank, the VtMR of the market-size clams was significantly higher than that of the other size classes (Table 2). In the New Jersey region, the VtMR for the 2000s was significantly lower than for the other 2 decades, and the VtMRs of 104 mm size and market-size clams were significantly higher than those of the smaller size classes (Table 2). A comparison across regions within decade shows that the VtMR for the Delmarva region was significantly higher than for the other regions in the 1980s (Table 3). After the 1980s, the difference in VtMR between regions was no longer significant.

The mean number of individuals per tow ranged from 0.5 to 1500, while σ ranged from 3.0×10^{-5} to 3.4×10^6. Fig. 3 shows the TPL relationships for the Delmarva sector as an example. β ranged from 2 to 4 for most size classes and decades within each region (Table 4). Although the VtMR frequently varied significantly (Table 2), β did not change over time for any of the regions (Fig. 4, Table 5), indicating that the relationship between the differential in the VtMR occurred when both the σ and μ varied concordantly along the power curve. The same was true for the size classes for 3 of the 5 regions. For New Jersey and
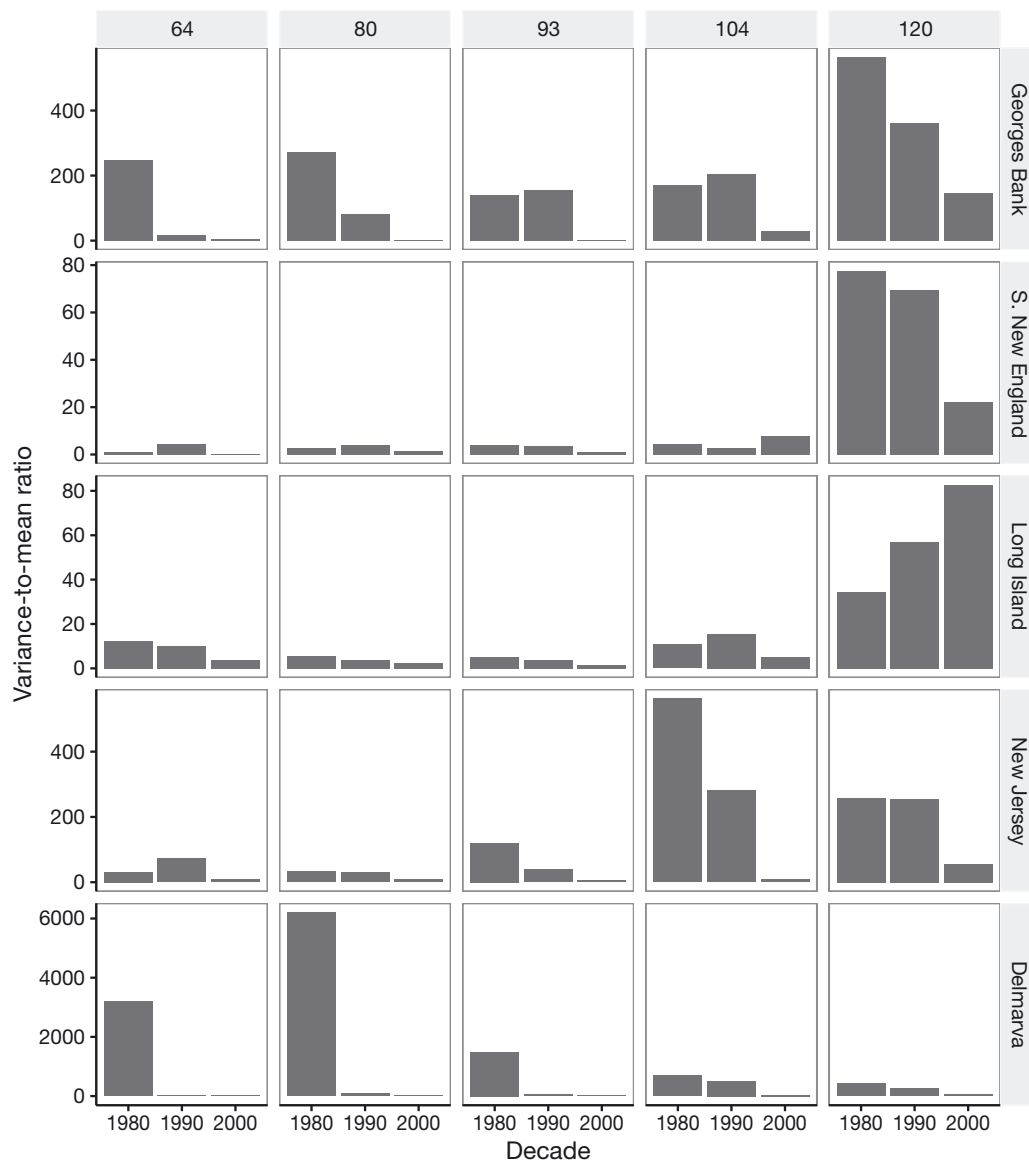
Fig. 2. Variance-to-mean ratios for each surfclam size class (columns; size classes as defined in Section 2) by decade for the Delmarva, New Jersey, Long Island, and Southern New England regions, and for Georges Bank. A ratio >1 indicates a patchy distribution. Values are provided in Table 1. Note the different *y*-axis scales

Southern New England, however, β changed significantly (Tables 4 & 5). In New Jersey, β for 64 mm clams was significantly higher than for the 104 mm and market-size clams (Tables 4 & 5). For the Southern New England region, β was significantly lower for the 80 mm than the 93 mm clams (Tables 4 & 5).

β varied significantly between regions for the larger size classes (104 and market size), but not for the smaller size classes (Table 6). Differences generally were significant between the southern regions (Delmarva and New Jersey) and the northern regions (Long Island and Southern New England), with Georges Bank similar to Delmarva and often different

from intervening regions. Overall, values of β were higher for Delmarva, New Jersey, and Georges Bank, indicating that the larger size classes were more patchy as mean abundance increased in these regions than in the intervening regions of lower abundance off Long Island and Southern New England.

3.2. Spatial analysis

The SDF model provided results consistent with the VtMR analysis. For example, the density (kg of surfclam km^{-2}) maps produced by the model show a

Table 1. Variance-to-mean ratios for each decade by surfclam size class for the Delmarva, New Jersey, Long Island, and Southern New England regions, and for Georges Bank. A ratio >1 indicates a patchy distribution. SD: standard deviation around the variance used to calculate the ratios. The number of tows per region and stratum is provided in NEFSC (2017, see their Table 10). Size classes (shell length in mm) are defined as 64: 64−79; 80: 80−92, 93: 93−103; 104: 104−119, and 120: ≥120 (market size)

Region Decade	64 mm Ratio	SD	80 mm Ratio	SD	93 mm Ratio	SD	104 mm Ratio	SD	120 mm Ratio	SD
Delmarva										
1980	3201.99	382.64	6207.03	734.03	1488.18	327.21	708.02	253.56	420.17	169.95
1990	32.36	18.62	75.66	33.84	65.37	34.46	507.36	170.33	248.36	143.47
2000	23.93	14.96	25.72	17.57	20.09	15.36	36.83	23.14	65.30	42.16
New Jersey										
1980	31.12	13.99	32.70	17.80	120.30	41.95	562.80	142.57	258.59	141.02
1990	72.06	25.65	29.96	17.05	39.02	19.97	280.21	85.25	255.38	169.33
2000	8.03	5.76	8.18	6.19	4.53	4.36	8.85	7.07	55.65	44.18
Georges Bank										
1980	248.15	58.79	272.28	63.58	139.71	39.94	169.57	55.58	564.85	210.81
1990	16.43	10.93	82.15	39.50	154.90	64.61	204.50	100.03	360.98	185.48
2000	4.12	3.20	1.73	2.25	2.59	3.06	29.64	20.04	144.96	105.12
Long Island										
1980	12.35	6.71	5.62	3.60	5.05	4.28	10.80	6.60	34.54	26.46
1990	9.94	5.44	3.93	3.24	3.70	3.75	15.63	12.76	57.01	41.98
2000	3.64	3.32	2.42	2.78	1.57	2.07	5.04	4.86	82.80	62.64
S. New England										
1980	1.19	1.62	2.65	2.54	4.13	3.23	4.58	3.92	77.60	60.58
1990	4.46	3.65	3.99	3.42	3.44	3.00	2.88	3.61	69.30	55.00
2000	0.26	0.59	1.58	1.68	1.15	1.22	7.83	5.74	22.28	21.44

reduction in patchiness in the Delmarva market-size clams and also a shift northward and offshore from the decade of the 1980s to the decade of the 2000s (Fig. 5). Fig. 6 provides evidence of a shift in the center of distribution of market-size clams off Delmarva northward and offshore over 3 decades, but little change was seen in the 64 mm size class over the same time. The range shift for market-size clams was on the order of 20 km east and 40 km north. The market-size clams off New Jersey also shifted northward and offshore, about 20 km east and 30 km north, while again the center of distribution for the smaller clams remained relatively unchanged. These analyses are consistent with Weinberg et al. (2005) and NEFSC (2017). The center of distribution for the smaller surfclams, however, is distinctly further offshore than for the market-size clams (Fig. 7).

Fig. 8 compares the distributional pattern of the 5 size classes off New Jersey, demonstrating the significantly higher degree of aggregation in the market-size clams and the consistent reduction in regional patchiness across the smaller size classes. Increased dispersion for the 64 mm size class explains the offshore trend in the range center relative to the market-size clams, as the smaller clams are much more uniformly distributed across the continental shelf. The center of distribution for the 64 mm size class on

Georges Bank remained constant while the market-size clams shifted slightly east and south (Fig. 9). The density plot (kg km^{-2}) for Georges Bank illustrates the significantly higher aggregation in the market-size clams compared to the other size classes and also shows the increased aggregation along the southeastern margin of the Bank that underpins the shift of the range center for these large clams in the southeasterly direction (Fig. 10). The centers of distribution for Long Island and Southern New England surfclams fluctuated over time but do not reveal any substantial directional movements (Figs. 11 & 12). The modest southerly shift of the range center off Long Island observed in 2011, however, foretells additional evidence for an offshore range expansion in that region observed in the most recent surveys (NEFSC 2017).

4. DISCUSSION

4.1. Aspatial analysis

The objective of the current study was to examine the dynamics of patchiness of the Atlantic surfclam among size classes over expansive geographic scales and to determine if the degree of patchiness has been stable over time, with the goal of identifying any

Table 2. (a) ANOVA and (b) post hoc analyses for the variance-to-mean ratios by surfclam size class (as defined in Section 2) and decade for the Delmarva, New Jersey, Long Island, and Southern New England regions, and for Georges Bank. Pairwise comparisons represent least square means analyses demonstrating differences between size classes or decades within each region. NA: not assessed (due to limited data for the smaller size classes for Long Island). *p < 0.05

(a) ANOVA Region	Factor	df	p
Delmarva	Decade	2	0.011*
	Class	4	0.956
	Decade × Class	8	0.938
New Jersey	Decade	2	0.004*
	Class	4	<0.001*
	Decade × Class	8	0.104
Long Island	Decade	2	0.441
	Class	4	0.015*
	Decade × Class	8	0.645
S. New England	Decade	2	0.701
	Class	4	0.002*
	Decade × Class	8	0.741
Georges Bank	Decade	2	0.082
	Class	4	<0.001*
	Decade × Class	8	0.829

(b) Pairwise comparison Region	Contrast	df	p
Delmarva	1980 vs. 1990	177	0.019*
	1980 vs. 2000	177	0.006*
	1990 vs. 2000	177	0.673
New Jersey	1980 vs. 1990	347	0.355
	1980 vs. 2000	347	0.017*
	1990 vs. 2000	347	0.001*
	64 vs. 80 mm	347	0.978
	64 vs. 93 mm	347	0.773
	64 vs. 104 mm	347	0.009*
	64 vs. 120 mm	347	0.0001*
	80 vs. 93 mm	347	0.752
	80 vs. 104 mm	347	0.009*
	80 vs. 120 mm	347	0.0001*
	93 vs. 104 mm	347	0.024*
	93 vs. 120 mm	347	0.0001*
	104 vs. 120 mm	347	0.052
Long Island	64 vs. 80 mm	NA	NA
	64 vs. 93 mm	73	0.968
	64 vs. 104 mm	73	0.898
	64 vs. 120 mm	73	0.023*
	80 vs. 93 mm	NA	NA
	80 vs. 104 mm	NA	NA
	80 vs. 120 mm	NA	NA
	93 vs. 104 mm	73	0.864
	93 vs. 120 mm	73	0.018*
	104 vs. 120 mm	73	0.029*
S. New England	64 vs. 80 mm	61	0.973
	64 vs. 93 mm	61	0.934
	64 vs. 104 mm	61	0.952
	64 vs. 120 mm	61	0.005*
	80 vs. 93 mm	61	0.907
	80 vs. 104 mm	61	0.926
	80 vs. 120 mm	61	0.005*
	93 vs. 104 mm	61	0.984
	93 vs. 120 mm	61	0.008*
	104 vs. 120 mm	61	0.010*
Georges Bank	64 vs. 80 mm	230	0.598
	64 vs. 93 mm	230	0.578
	64 vs. 104 mm	230	0.108
	64 vs. 120 mm	230	0.0001*
	80 vs. 93 mm	230	0.951
	80 vs. 104 mm	230	0.281
	80 vs. 120 mm	230	0.0002*
	93 vs. 104 mm	230	0.338
	93 vs. 120 mm	230	0.0004*
	104 vs. 120 mm	230	0.007*

effects of a well-documented shift in range on these population characteristics. The surfclam population was patchy in each of the 5 geographic regions. Patchiness is not unexpected, as it is a rarity if marine species are other than significantly aggregated in their distributions across their range (Guo et al. 2005, Borregaard & Rahbek 2010). Much more surprising is that patchiness has declined since the 1980s, and this decline is universal over the entire US stock from the Delmarva continental shelf to Georges Bank (Table 1). However, the exponent of TPL (β) did not change significantly over time; thus, the decline in the VtMR did not foretell a change in the inherent relationship between the variance and the mean over a range of population densities as expressed by their variances and means. Thus, the decline in VtMR indicates that fewer strata were characterized by high means and variances in the 2000s compared to the 1980s, whereas the conservatism of the TPL indicates that a change in the aggregative propensity of the Atlantic surfclam did not simultaneously occur. Rather, both the variance and the mean translated along one basic descriptive power curve describing the propensity of this species to become decreasingly patchy at ever lower densities.

Significant differences in the VtMR and β were identified in certain size classes and regional comparisons, however. Surfclams in the Delmarva region were routinely more patchy than in the other regions (Table 2). VtMRs were generally higher in contrast to the populations off Long Island and Southern New England, with the New Jersey and Georges Bank populations falling in between (Table 2). Variances routinely scale with the mean, and the fact that the surfclam population densities are higher in the Delmarva, New Jersey, and Georges Bank regions would inherently augur for a higher VtMR. An alter-

Table 3. (a) ANOVA and (b) post hoc analyses for the variance-to-mean ratios by region and decade for all regions combined (DMV: Delmarva; NJ: New Jersey; LI: Long Island; SNE: Southern New England; GBK: Georges Bank). ANOVA results indicate a significant effect across decades and for regions including a significant interaction effect. Pairwise comparisons represent least square means analyses demonstrating differences between decades or regions. *p < 0.05

(a) ANOVA			
Region	Factor	df	p
All regions	Region	4	0.0002*
	Decade	2	0.0005*
	Region × Decade	8	<0.001*

(b) Pairwise comparison			
Region	Contrast	df	p
All regions	1980 vs. 1990	954	0.078
	1980 vs. 2000	954	0.020*
	1990 vs.2000	954	0.400
	DMV vs. LI	954	0.003*
	DMV vs. SNE	954	0.004*
	DMV vs. GBK	954	0.001*
	DMV vs. NJ	954	0.0003*
	LI vs. SNE	954	0.931
	LI vs. GBK	954	0.449
	LI vs. NJ	954	0.406
	SNE vs. GBK	954	0.512
	SNE vs. NJ	954	0.469
	GBK vs. NJ	954	0.958

native is to examine β. In this case, although variable, most values of β fell between 2.2 and 3.0. Nonetheless, TPLs varied significantly by region for the larger, but not the smaller, size classes. Thus, over the stock, the patchy behavior of the clam varied. Patchiness tended to be higher off Delmarva and New Jersey and on Georges Bank than elsewhere. Inter-
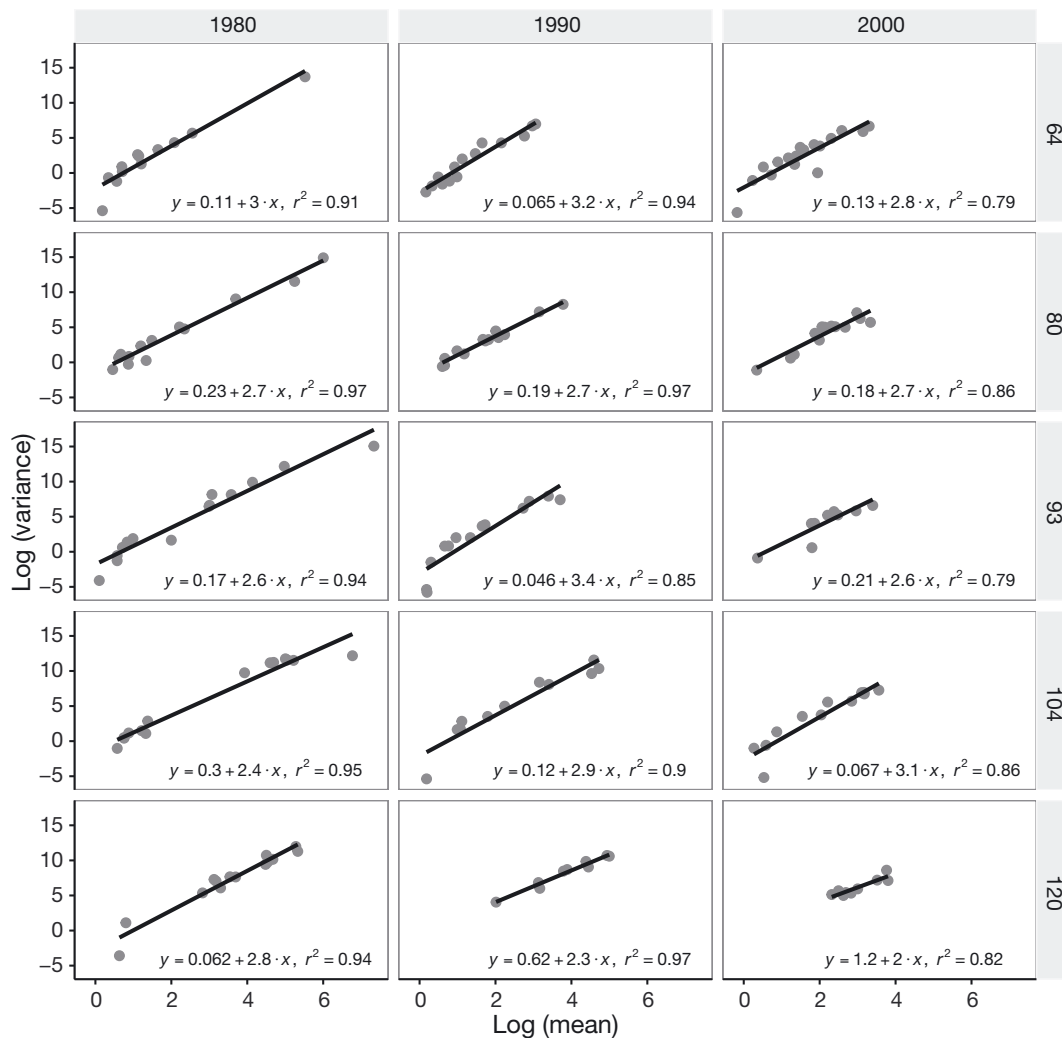

Fig. 3. Examples of Taylor's power law relationship between log variance and log mean for Delmarva. Each column represents a decade while each row represents a surfclam size class (as defined in Section 2)

Table 4. Exponents (β) of Taylor's power law listed by decade and surfclam size class (as defined in Section 2) for the Delmarva, New Jersey, Long Island, and Southern New England regions, and for Georges Bank. β > 1 indicates a patchy distribution. NA: not assessed due to limited data for certain size classes and decades

Region Decade	64 mm	80 mm	93 mm	104 mm	120 mm
Delmarva					
1980	3.04	2.66	2.61	2.43	2.82
1990	3.24	2.71	3.38	2.90	2.26
2000	2.84	2.72	2.65	3.07	1.99
New Jersey					
1980	2.92	3.38	2.98	2.87	2.19
1990	2.75	2.78	2.92	2.76	2.20
2000	5.20	3.45	2.81	2.60	2.60
Georges Bank					
1980	2.57	2.54	3.08	2.53	3.56
1990	2.86	2.61	3.00	2.44	2.38
2000	4.33	2.47	1.55	2.18	2.35
Long Island					
1980	NA	NA	NA	NA	2.16
1990	6.33	2.93	2.13	1.81	1.19
2000	2.81	3.38	5.19	2.31	2.37
S. New England					
1980	3.27	2.41	3.32	1.65	2.00
1990	3.45	2.41	4.63	NA	1.45
2000	NA	NA	NA	NA	1.73

estingly, these 3 regions support the bulk of the surf-clam resource, suggesting that the patchy proclivities of the surfclam vary with the regional optimality of the habitat.

β varies little among the size classes. Nonetheless, the routine significant differences in VtMRs between the size classes, with the ratio tending to increase with increasing size, indicates differential mortality between areas occupied and uninhabited by the larger clams. The strong suggestion is that many juveniles recruited at relatively low abundance into regions not supporting growth to adulthood — the lower variance in these areas being consistent with the lower mean — condensation of the stock through mortality then occurred with the result of a higher VtMR without a change in TPL. Timbs et al. (2018) provided corroborative evidence for this size-dependent contraction in cross-shelf distribution over the entirety of the surveyed (latitudinal) range.

A consideration of patchiness in the surfclam stock as revealed through aspatial analyses suggests that recruitment occurs over a wide area, much of which results in low abundance of small clams that fail to grow to market size, so that patchiness increases with clam size. Timbs et al. (2018) provided analyses that show the expanded geographic footprint of the smaller size classes in each of the 5 assessment regions

Table 5. (a) ANCOVA and (b) post hoc analyses for cases with significant interaction terms comparing log-variance to log-mean by surfclam size class (as defined in Section 2) and decade for the Delmarva, New Jersey, Long Island, and Southern New England regions, and for Georges Bank. Significant interaction terms indicate a change in the slope of Taylor's power law and therefore the exponent β of the power law. $^*p < 0.05$

(a) ANCOVA Region	Factor	df	p
Delmarva	LogMean	1	<0.001*
	Class	4	0.516
	LogMean × Class	4	0.375
	LogMean	1	<0.001*
	Decade	2	0.351
	LogMean × Decade	2	0.136
New Jersey	LogMean	1	<0.001*
	Class	4	0.041*
	LogMean × Class	4	0.001*
	LogMean	1	<0.001*
	Decade	2	0.06
	LogMean × Decade	2	0.063
Long Island	LogMean	1	0.009*
	Class	4	0.069
	LogMean × Class	4	0.066
	LogMean	1	<0.001*
	Decade	2	0.186
	LogMean × Decade	2	0.082
S. New England	LogMean	1	<0.001*
	Class	4	0.025*
	LogMean × Class	4	0.023*
	LogMean	1	<0.001*
	Decade	2	0.545
	LogMean × Decade	2	0.957
Georges Bank	LogMean	1	<0.001*
	Class	4	0.147
	LogMean × Class	4	0.12
	LogMean	1	<0.001*
	Decade	2	0.781
	LogMean × Decade	2	0.825

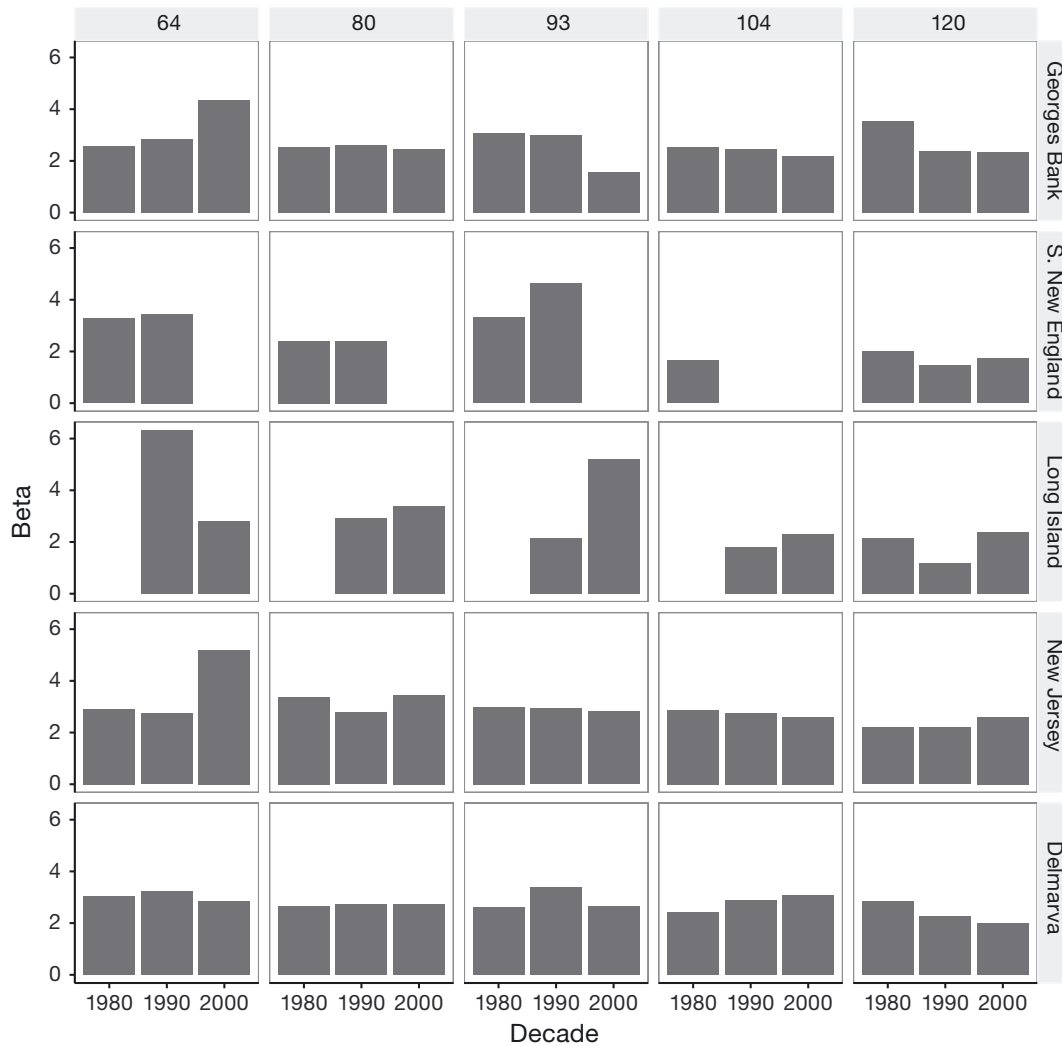| (b) Pairwise comparison Region	Contrast	df	p
New Jersey	64 vs. 80 mm	352	0.160
	64 vs. 93 mm	352	0.120
	64 vs. 104 mm	352	0.041*
	64 vs. 120 mm	352	0.025*
	80 vs. 93 mm	352	0.878
	80 vs. 104 mm	352	0.545
	80 vs. 120 mm	352	0.248
	93 vs. 104 mm	352	0.657
	93 vs. 120 mm	352	0.299
	104 vs. 120 mm	352	0.458
S. New England	64 vs. 80 mm	66	0.079
	64 vs. 93 mm	66	0.919
	64 vs. 104 mm	66	0.260
	64 vs. 120 mm	66	0.694
	80 vs. 93 mm	66	0.041*
	80 vs. 104 mm	66	0.417
	80 vs. 120 mm	66	0.075
	93 vs. 104 mm	66	0.172
	93 vs. 120 mm	66	0.568
	104 vs. 120 mm	66	0.326

Fig. 4. Beta values for Taylor's power law for each surfclam size class (columns; size classes as defined in Section 2) by decade in the Delmarva, New Jersey, Long Island, and Southern New England regions, and for Georges Bank. β > 1 indicates a patchy distribution. Values are provided in Table 4

relative to the market-size portion of the stock, confirming inferences from this study that the geographic scale of recruitment is substantively larger than the geographic footprint of the surviving market-size individuals. Patchiness has declined over time either because abundance in high-abundance areas declined or areas of low abundance increased in importance over time. The tendency towards patchiness, however, has not changed over time, nor does it change with growth to market size, as documented by the fact that β rarely changed significantly even though average VtMR declined over decadal time periods. What does vary is the relationship of patchiness and clam abundance regionally. Here, regions supporting the majority of the stock, arguably then supporting the majority of optimal habitat, demonstrate a significantly greater tendency towards

aggregation. The average VtMRs are higher, and the β values show that the degree of aggregation increases disproportionately with the mean in comparison to the remainder of the range of the stock.

4.2. Changes in the dynamics of the range

The movement of surfclams offshore with warming of the Mid-Atlantic bottom waters has been known for some time (Kim & Powell 2004, Weinberg 2005, NEFSC 2013). The ubiquity of this trend is shown by the SDF model, which documents offshore translations of the range core off Delmarva and New Jersey, northward translations in the Delmarva and New Jersey regions, and a southern extension into deeper water on Georges Bank. The current study shows a

Table 6. (a) ANCOVA and (b) post hoc analyses for cases with significant interaction terms comparing log-variance to log-mean by surfclam size class (as defined in Section 2) for the Delmarva (DMV), New Jersey (NJ), Long Island (LI), and Southern New England (SNE) regions, and for Georges Bank (GBK). Significant interaction terms indicate a change in the slope of Taylor's power law and therefore the exponent β of the power law. *$p < 0.05$

(a) ANCOVA Size class (mm)	Factor	df	p
64	LogMean	1	<0.001*
	Region	4	0.969
	LogMean × Region	4	0.518
80	LogMean	1	<0.001*
	Region	4	0.031
	LogMean × Region	4	0.313
93	LogMean	1	<0.001*
	Region	4	0.025*
	LogMean × Region	4	0.184
104	LogMean	1	<0.001*
	Region	4	0.273
	LogMean × Region	4	0.024*
120	LogMean	1	<0.001*
	Region	4	0.184
	LogMean × Region	4	0.014*

(b) Pairwise comparisons Size class (mm)	Contrast	df	p
104	DMV vs. GBK	176	0.960
	DMV vs. LI	176	0.003*
	DMV vs. NJ	176	0.238
	DMV vs. SNE	176	0.025*
	GBK vs. LI	176	0.002*
	GBK vs. NJ	176	0.186
	GBK vs. SNE	176	0.020*
	LI vs. NJ	176	0.016*
	LI vs. SNE	176	0.900
	NJ vs. SNE	176	0.091
120	DMV vs. GBK	202	0.648
	DMV vs. LI	202	0.001*
	DMV vs. NJ	202	0.908
	DMV vs. SNE	202	0.104
	GBK vs. LI	202	0.002*
	GBK vs. NJ	202	0.488
	GBK vs. SNE	202	0.192
	LI vs. NJ	202	0.0001*
	LI vs. SNE	202	0.094
	NJ vs. SNE	202	0.045*

contemporaneous reduction in the VtMR over time in each region. The information available does not permit an unequivocal answer to the question of the origin of the observed simultaneity of the decline in VtMR and the shift in the range cores. However, one possible hypothesis can be proposed based on the tendency for the smaller size classes to be distributed more broadly at lower abundances.

We propose the hypothesis that patchiness develops in the core of the distribution over time, and a range shift, caused by increasing bottom-water

temperature, generates mortality biased against the long-established high-density patches nearer the southern and inshore range boundary. Kim & Powell (2004) and Weinberg (2005) provide a well-documented example. The newly occupied areas tend to have surfclams more spread out because the smaller clams tend to be less patchy. As an example, the 64 mm size class in New Jersey is more broadly distributed offshore than the larger classes, even though the core of the distribution of market-size clams has moved offshore slowly over the course of the survey (Fig. 4; see also Timbs et al. 2018). That is, recruitment offshore New Jersey predisposes the surfclam to an offshore range expansion. Zhang et al. (2015, 2016) found that surfclam recruitment was likely biased inshore during certain parts of the year and offshore during other parts of the year, depending upon the prevailing cross-shelf hydrodynamics. Hence, the observed offshore bias in the range of smaller clams should not be taken as indicative of a bias in settlement; rather this is likely a result of post-settlement mortality heavily biased along the inshore range bound-
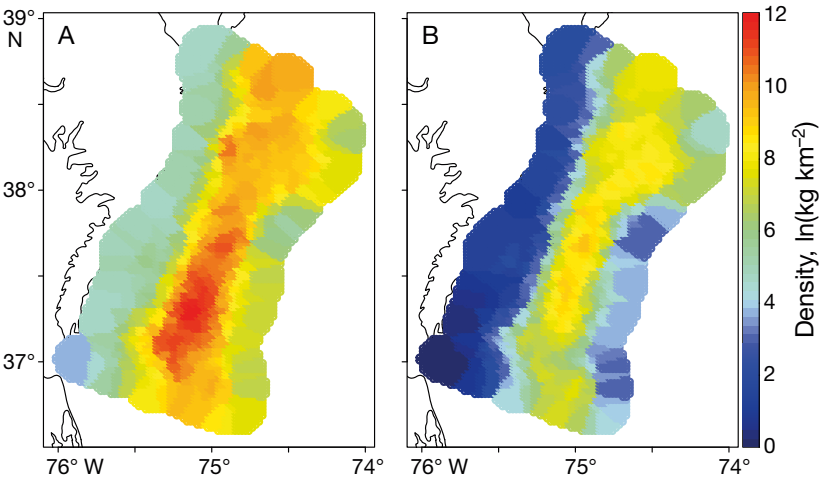

Fig. 5. Density of market-size surfclams in Delmarva for survey years (A) 1986 and (B) 2008. The density is lower in 2008 than in 1986 over nearly the entire Delmarva region. Note the movement of the surfclam stock offshore, as manifested by the dramatic reduction in surfclam density over the inner portion of the continental shelf. See Fig. 6 for temporal trends
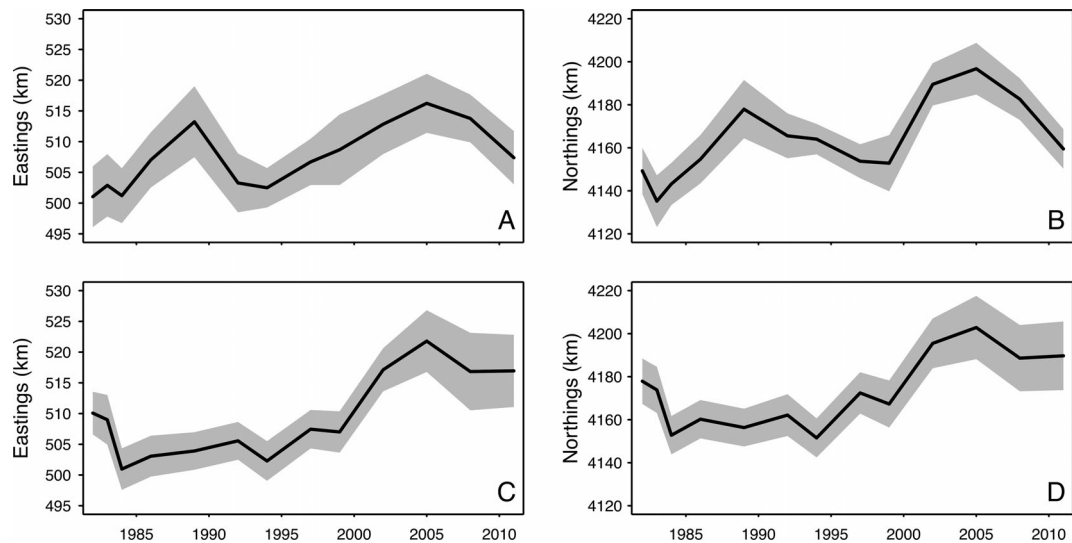
Fig. 6. Center of distribution of the Atlantic surfclam population off Delmarva. (A) Eastings and (B) northings of 64 mm surf-clams indicate a slight movement north and offshore. (C) Eastings and (D) northings of market-size clams clearly indicate a shift north and offshore, the most rapid shift coming during the 1990s to 2000s decadal transition. Black solid line is the maximum likelihood estimate, and the grey shaded area is ±1 SE
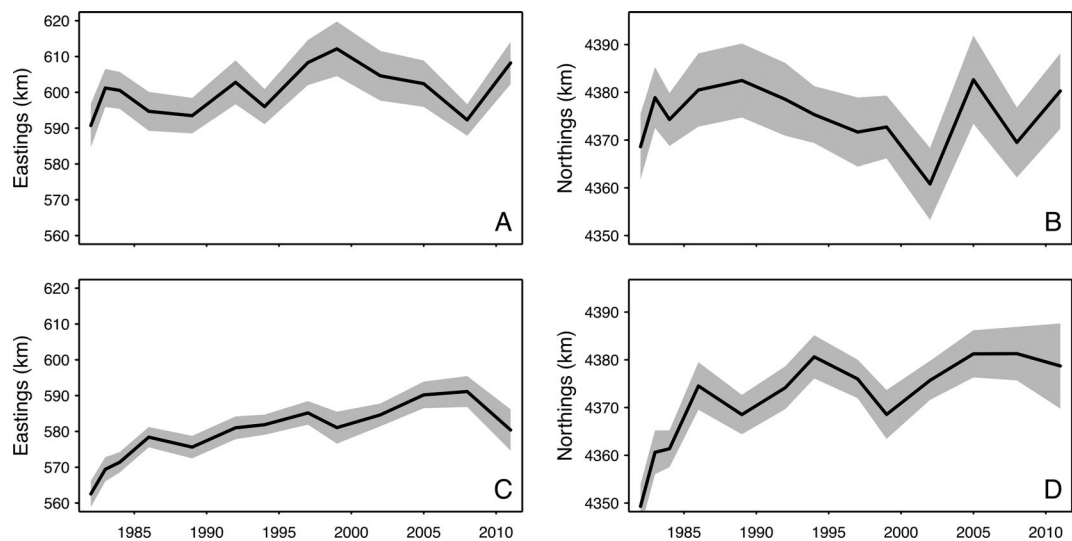

Fig. 7. Center of distribution of the Atlantic surfclam population off New Jersey. (A) Eastings and (B) northings of 64 mm surf-clams indicate relatively little change in the range center over time. (C) Eastings and (D) northings of market-size clams clearly indicate a significant shift north and offshore. Line and shading as in Fig. 6

ary compounded possibly by slower growth along the leading edge of the range (e.g. Marzec et al. 2010, Timbs et al. 2018, Powell et al. 2019b).

The differential distributions of the size classes observed in all 3 decades off New Jersey and during the 1900s and 2000s off Delmarva are similar in suggesting that smaller surfclams are capable of recruiting offshore of the market-size range core and, in these areas, are less patchy (Figs. 5–8, Table 1). In both regions, the core of the range of market-size clams has shifted offshore, while the established areas containing the older patches of market-size clams are disappearing. The observed shift off Delmarva and New Jersey likely is an additive effect of warming bottom waters preventing new recruits from establishing themselves nearshore (for further information on climate change, see Orr et al. 2005, Hansen et al. 2010, Poloczanska et al. 2013) and the
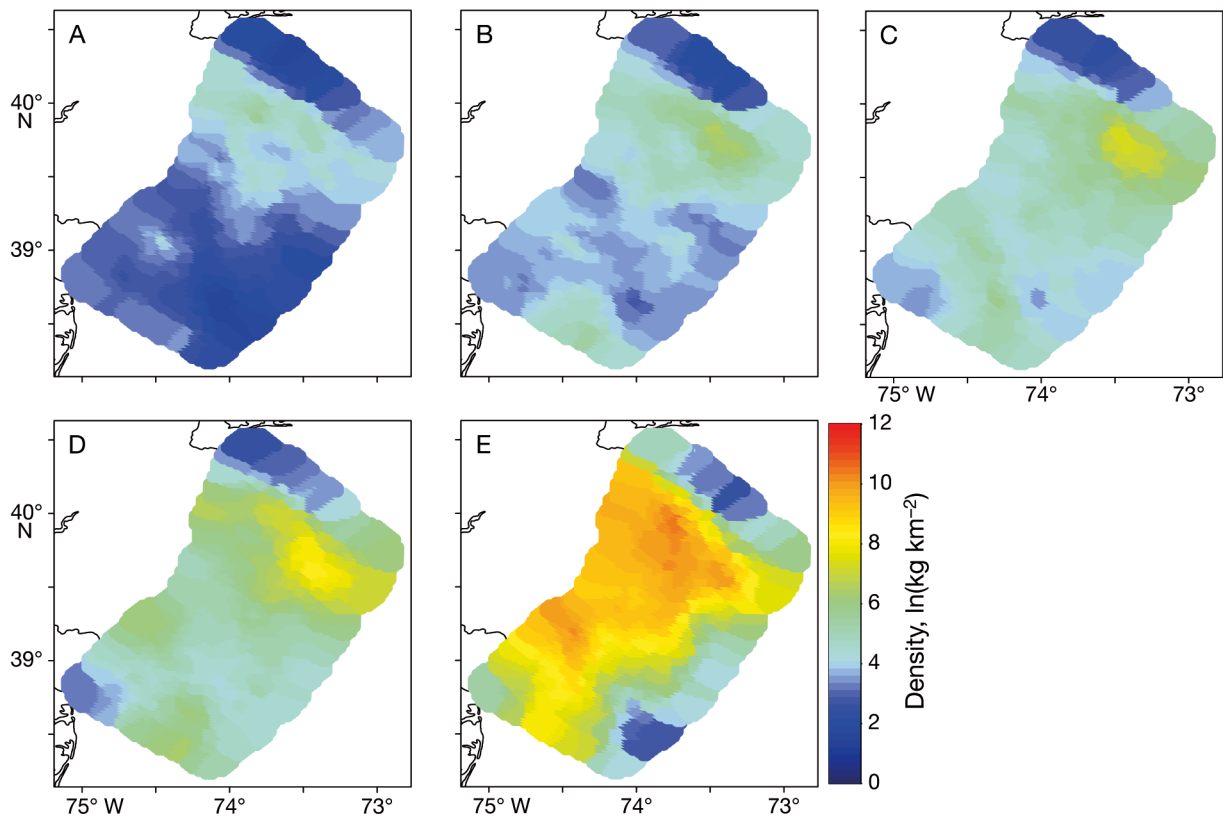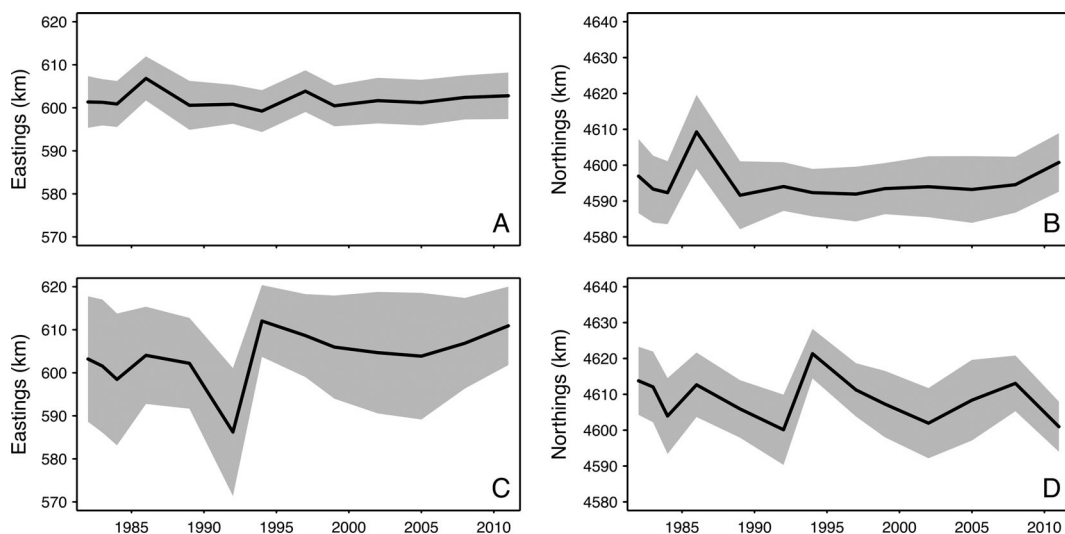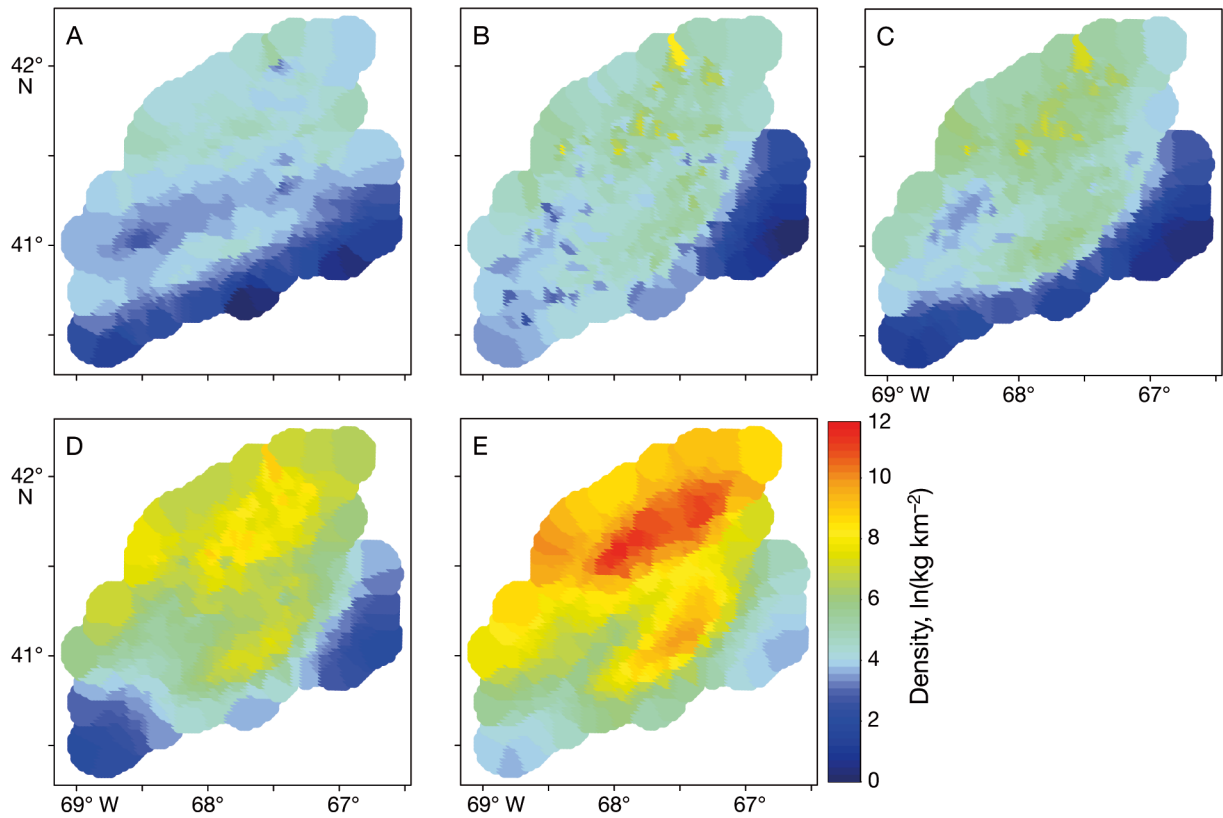
Fig. 8. Density maps comparing the distribution of size classes of surfclams off New Jersey during the 2000s. (A) 64, (B) 80, (C) 93, (D) 104, (E) 120 mm (size classes as defined in Section 2). Note the significantly higher degree of aggregation (patchiness) in the market-size clams (E), as evidenced by the much larger differential in density across the domain in comparison to the smaller size classes. Note also the intermediate level of aggregation in the larger submarket size classes (C and D). See Fig. 7 for additional temporal analyses
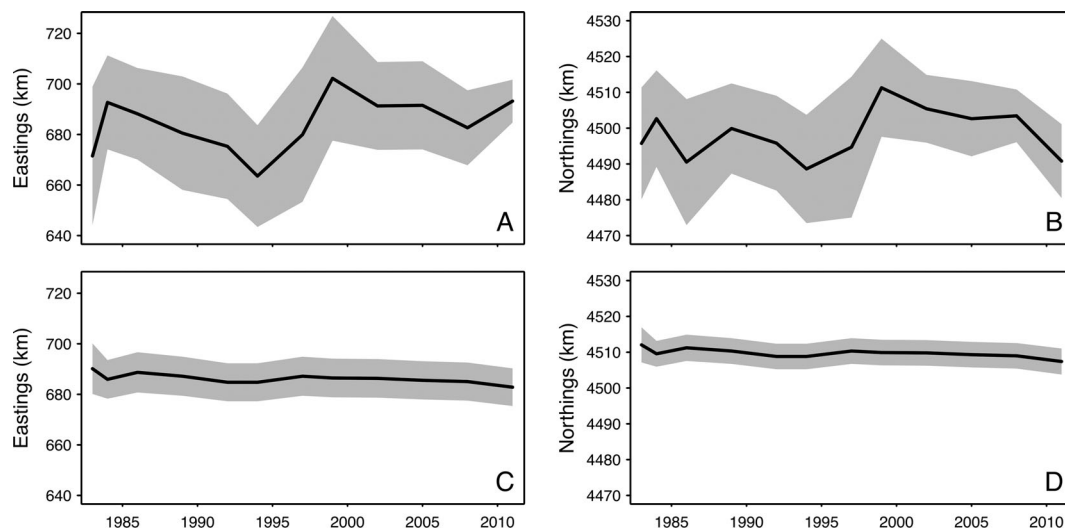

Fig. 9. Center of distribution of the Atlantic surfclam population on Georges Bank. (A) Eastings and (B) northings of 64 mm surfclams. The distribution of the 64 mm surfclams has fluctuated about a single easterly and northerly axis. (C) Eastings and (D) northings of the market-size clams suggest a modest shift east and south. Line and shading as in Fig. 6

Fig. 10. Density maps comparing the distribution of the 5 size classes of surfclams on Georges Bank during the 2000s. (A) 64, (B) 80, (C) 93, (D) 104, (E) 120 mm (size classes as defined in Section 2). The distributions demonstrate the significantly higher degree of aggregation in the market-size clams. The southerly movement of the market-size clams identified in Fig. 9 is observed in the increased density of (E) market and (D) near-market-size clams along the southeastern portion of the bank. See Fig. 9 for additional temporal analyses

Fig. 11. Center of distribution of the Atlantic surfclam population off Long Island. (A) Eastings and (B) northings of 64 mm surfclams. The distribution of the 64 mm surfclams has fluctuated about a stable axis until very recently, when a tendency for a southern shift foretells more recent survey evidence (NEFSC 2017). (C) Eastings and (D) northings of the market-size clams also show a stable axis over time. Line and shading as in Fig. 6
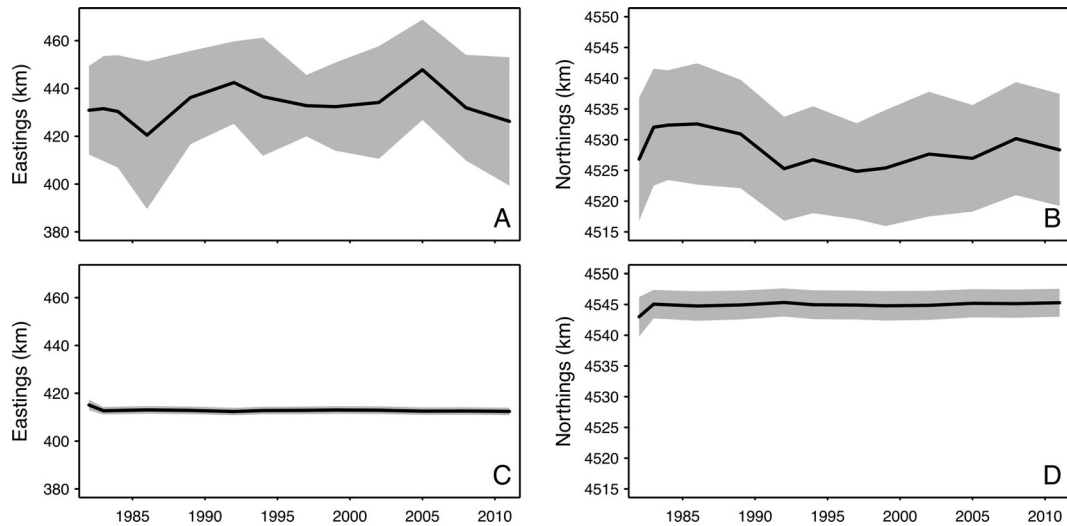
Fig. 12. Center of distribution of the Atlantic surfclam population off Southern New England. (A) Eastings and (B) northings of 64 mm surfclams. The distribution of the 64 mm surfclams has fluctuated about a stable axis. (C) Eastings and (D) northings of the market-size clams also indicate a stable range center. Line and shading as in Fig. 6

predisposition for an offshore shift provided by recruitment offshore of the present range core of the market-size clams (Timbs et al. 2018). Most models examining the characteristics of range shifts do not address the dynamics imposed by the intersection of changing environmental gradients with the dispersal gradients of the recruits (e.g. Holt et al. 2005, Hughes et al. 2007, McInerny et al. 2009, Sexton et al. 2009). Whether such dynamic interactions, in this case driven by warming bottom waters and cross-shelf dispersion dynamics, are typical for range shifts on the continental shelf is unknown; however, the evidence does not support patchy recruitment dynamics at the offshore range edge. Rather, the evidence supports more dispersed recruitment dynamics that sets up the opportunity for a translation of the range core and the subsequent maturing of the population into a more patchy state.

Patchiness in benthic species may arise from differentials in recruitment or post-settlement mortality. References cited earlier demonstrate the impressive degree of attention given to this dichotomy and the continuing uncertainty as to the dominance of 1 of the 2 alternatives. For the Atlantic surfclam, settlement likely varies spatially and between years over the geographic range of the stock, as variations in the hydrodynamics continuously modulate source and sink dynamics (Zhang et al. 2015, 2016). Nonetheless, settlement routinely occurs within the range core of the adults, but also inshore and offshore of the range core in what normally are marginal habitats, and this settlement is relatively non-patchy, as indicated by consistently low VtMRs. Differential survival establishes the core of the range and the degree of patchiness of the species, not differential settlement. The difference is important because the surfclam continuously positions itself for a rapid shift in range by 'wasting' larvae in marginal habitats in most years. Powell et al. (2019b) documented a revealing case history of a range shift that occurred on a subdecadal time scale in response to warming temperatures off Nantucket. This is likely an evolutionary adaptation to continuously changing, but unpredictable, environmental conditions, as surfclams over the Holocene have migrated across the continental shelf, potentially many times, as they are doing today (Powell et al. 2017b, 2019a)

4.3. Influence of fishing

The surfclam fishery targets patches, reducing the numbers of the larger individuals (Weinberg et al. 2005, NEFSC 2013, Powell et al. 2015, 2016) and thus might be an alternative explanation for the observed variations in VtMR. The fact that the fishery targets patches is unlikely to be the cause of the observed shift in the surfclam distribution or the large reduction in population patchiness, however. First, fishing mortality is low across the stock. The fishing mortality rate has varied between 0.01 and 0.06 yr^{-1} over the study period (NEFSC 2013). Weinberg (2005) estimated that the natural mortality rate (≥ 0.22 yr^{-1}) for surfclams in the Delmarva region between 1999

and 2002 had a much greater impact on the biomass than the commercial fishery (fishing mortality <0.04 yr⁻¹). Declining maximum size of surfclams over the last 3 decades, well documented by Munroe et al. (2016), is also a phenomenon often associated with fishing (Rice 2000, Planque et al. 2010, Brown et al. 2012). However, Munroe et al. (2016) demonstrated that in this case, declining maximum size is likely the result of environmental shifts and not size-frequency truncation by fishing of the largest size classes. Second and importantly, Georges Bank was closed to fishing between 1989 and 2010 due to the presence of paralytic shellfish poisoning (NEFSC 2013). Fishing on Georges Bank began in earnest in 2012 (NEFSC 2017). Nonetheless, a reduction in VtMR (Table 1), and therefore patchiness, occurred over the study period on Georges Bank and much the same trends in TPL occurred there as in the southern regions off Delmarva and New Jersey. This similarity indicates that the increasing bottom-water temperatures in the Mid-Atlantic Bight, and not the fishery, play the impactful role in determining the distributional dynamics of this species and the characteristics of the range shift offshore.

4.4. Influence on the fishery

Landings per unit effort (LPUE) have declined across all fished regions since the year 2000 (NEFSC 2013). On the local scale, the fishery targets the largest patches, fishing them down and decreasing patchiness, which in turn lowers LPUE locally (Powell et al. 2015, 2016). Increased natural mortality caused by warming bottom-water temperatures (Weinberg 2005) affects LPUE on a larger scale by decreasing abundance along the inshore and southern portion of the range. Based on the results of the SDF model and the VtMR analyses, the range shift coupled with natural mortality may be having a more dramatic effect on LPUE than the fishery, except at the most local level, and certainly exacerbates the decline of LPUE in areas such as Delmarva and New Jersey where more fishing effort occurs. Thus, low LPUE may be a symptom of an ongoing range shift, robbing the population of high-abundance patches in the trailing edge portion of the range core while adding to the population a more dispersed and lower-density portion of the stock at the leading edge boundary. The possibility exists that, as new patches are established in new habitat, these patches will grow over time and produce surfclams at a high density, thereby returning LPUE to historic levels.

The Atlantic surfclam was historically closer to shore off Delmarva before the NEFSC surveys began in the 1980s (e.g. Loesch & Ropes 1977, Ropes 1982, see also Hofmann et al. 2018). The observation of surfclams historically closer to shore points towards a migration northward and offshore in the Delmarva region that began well before the start of the survey dataset analyzed in the current study which then has progressed over time. Future climate predictions point towards an increase in bottom-water temperatures that should continue the movement offshore (Saba et al. 2016). The impact of climate change on fisheries is becoming well-documented (Perry et al. 2005, Brander 2010, Hare et al. 2016). Changes in climate could result in the Atlantic surfclam disappearing from the southern portion of its range (i.e. Delmarva and New Jersey). Indeed, most recent surveys identify the initiation of an offshore stock expansion off Long Island and eastward of Nantucket to the Great South Channel (NEFSC 2017, Powell et al. 2019b).

An unchanging survey design may foreshadow an increasing decline in survey accuracy as changes in population distributions continue to shift relative to stratum boundaries and sample allocations (NEFSC 2013, Jacobsen & Hennen 2019). On the other hand, declining VtMR may improve survey accuracy at a specified level of sample allocation (Powell & Mann 2016, Powell et al. 2017a), because survey bias tends to increase with increasing patchiness (Bros & Cowell 1987). Changes in station allocation amongst strata, accordingly, may be necessary to take advantage of declining patchiness in certain regions of the stock while limiting the added uncertainty posed by a shift in range.

As the surfclam continues to progress further north and offshore, a need will arise for relocation of vessels and processing plants to counteract costs associated with travel time to fishing grounds and harvest time as LPUE declines (Narváez et al. 2015). Generally, fisheries in the northeastern USA have shifted north in response to northward-shifting populations, but at a much slower rate, with regulatory and economic factors preventing them from keeping pace with their target species (Pinsky & Fogarty 2012). This trend is well known for the surfclam fishery (McCay et al. 2011, Powell et al. 2016, Hofmann et al. 2018).

A major uncertainty is the unknown time required to reestablish dense patches of market-size clams in newly occupied areas. This study represents the first in-depth examination of the impact of climate change and a shifting range on the spatial dynamics of surfclams. Is it even possible for the patches to return to

historic levels with the continual warming of Mid-Atlantic bottom waters driving the surfclam further northward and offshore? No clear answer arises from this analysis. What is clear is that the dynamics of recruitment demonstrate that continued progression of the range is not prohibited; rather, the distribution of juveniles may presage the directional movement of the market-size stock (Timbs et al. 2018). The degree of aggregation appears to be in part a function of the stage in relocation of the range core and in part the optimality of habitat where the stock resides, and this also can be expected to change as warming continues. As a consequence, the future of the fishery, dependent on the accessibility of large patches, may well depend on the rate of range shifting relative to the rate of maturing of the patchiness structure of the new core of the range.

LITERATURE CITED

Ayata SD, Ellien C, Dumas F, Dubois S, Thiébaut E (2009) Modelling larval dispersal and settlement of the reef-building polychaete *Sabellaria alveolata*: rate of hydroclimatic processes on the sustainability of biogenic reefs. Cont Shelf Res 29:1605–1623

Bascompte J, Possingham H, Roughgarden J (2002) Patchy populations in stochastic environments: critical number of patches for persistence. Am Nat 159:128–137

Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296:1692–1694

Beninger PG, Boldina I (2014) Fine-scale spatial distribution of the temperate infaunal bivalve, *Tapes* (=*Ruditapes*) *philippinarum* (Adams and Reeve) on fished and unfished intertidal mud flats. J Exp Mar Biol Ecol 457: 128–134

Berestycki H, Diekmann O, Nagelkerke CJ, Zegeling PA (2009) Can a species keep pace with a shifting climate? Bull Math Biol 71:399–429

Bond N, Thomson J, Reich P, Stein J (2011) Using species distribution models to infer potential climate change-induced range shifts of freshwater fish in south-eastern Australia. Mar Freshw Res 62:1043–1061

Borregaard MK, Rahbek C (2010) Causality of the relationship between geographic distribution and species abundance. Q Rev Biol 85:3–25

Brand AR (2006) Scallop ecology: distribution and behavior. In: Shumway SE, Parsons GJ (eds) Scallops: biology, ecology and aquaculture, 2nd edn. Elsevier, Oxford, p 991–1035

Brander K (2010) Impacts of climate change on fisheries. J Mar Syst 79:389–402

Bros WE, Cowell BC (1987) A technique for optimizing sample size (replication). J Exp Mar Biol Ecol 114:63–71

Brown CJ, Fulton EA, Possingham HP, Richardson AJ (2012) How long can fisheries management delay action in response to ecosystem and climate change? Ecol Appl 22:298–310

Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026

Chintala MM, Grassle JP (2001) Comparison of recruitment frequency and growth of surfclams, *Spisula solidissima* (Dillwyn, 1817), in different inner-shelf habitats of New Jersey. J Shellfish Res 20:1177–1186

Condie SA, Waring J, Mansbridge JV, Cahill ML (2005) Marine connectivity patterns around the Australian continent. Environ Model Softw 20:1149–1157

Cook T, Folli M, Klinck J, Ford S, Miller J (1998) The relationship between increasing sea-surface temperature and the northward spread of *Perkinsus marinus* (Dermo) disease epizootics in oysters. Estuar Coast Shelf Sci 46: 587–597

David P, Berthou P, Noel P, Jarne P (1997) Patchy recruitment patterns in marine invertebrates: a spatial test of the density-dependent hypothesis in the bivalve *Spisula ovalis.* Oecologia 111:331–340

Davis MB, Shaw RG (2001) Range shifts and adaptive responses to quaternary climate change. Science 292: 673–679

Dresler PV, Cory RL (1980) The Asiatic clam, *Corbicula fluminea* (Müller), in the tidal Potomac River, Maryland. Estuaries 3:150–151

Elliott JM (1977) Some methods for the statistical analysis of samples of benthic invertebrates, 2nd edn. Scientific Publication 25. Freshwater Biological Association, Ambleside

Flowers JM (1973) Pattern of distribution of the surf clam (*Spisula solidissima*) in the Point Judith, Rhode Island harbor of refuge. Proc Natl Shellfish Assoc 63:107–112

Friedland KD, McManus MC, Morse RE, Link JS (2018) Event scale and persistent drivers of fish and macroinvertebrate distributions on the northeast US shelf. ICES J Mar Sci, doi:10.1093/icesjms/fsy167

Gaines S, Brown S, Roughgarden J (1985) Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula.* Oecologia 67:267–272

Gaylord B, Gaines SD (2000) Temperature or transport? Range limits in marine species mediated solely by flow. Am Nat 155:769–789

Gosselin LA, Qian PY (1997) Juvenile mortality in benthic marine invertebrates. Mar Ecol Prog Ser 146:265–282

Green RH (1989) Power analysis and practical strategies for environmental monitoring. Environ Res 50:195–205

Guo Q, Taper M, Schoenberger M, Brandle J (2005) Spatial-temporal population dynamics across species range: from central to margin. Oikos 108:47–57

Hansen J, Ruedy R, Sato M, Lo K (2010) Global surface temperature change. Rev Geophys 48:1–29

Hare JA, Able KW (2007) Mechanistic links between climate

and fisheries along the east coast of the United States: explaining population outbursts of Atlantic croaker (*Micropogonias undulatus*). Fish Oceanogr 16:31–45

Hare JA, Morrison WE, Nelson MW, Stachura MM and others (2016) A vulnerability assessment of fish and invertebrates to climate change on the northeast U.S. continental shelf. PLOS ONE 11:e0146756

Harley CDG, Hughes AR, Hultgren KM, Miner BG and others (2006) The impacts of climate change on coastal marine systems. Ecol Lett 9:228–241

Harte J, Conlisk E, Ostling A, Green JL, Smith AB (2005) A theory of spatial structure in ecological communities at multiple spatial scales. Ecol Monogr 75:179–197

Hennen DR, Jacobson LD, Tang J (2012) Accuracy of the Patch model used to estimate density and capture efficiency in depletion experiments for sessile invertebrates and fish. ICES J Mar Sci 69:240–249

Hofmann EE, Powell EN, Klinck JM, Munroe DM and others (2018) An overview of factors affecting distribution of the Atlantic surfclam (*Spisula solidissima*), a continental shelf biomass dominant, during a period of climate change. J Shellfish Res 37:821–831

Holt RD, Keitt TH, Lewis MA, Maurer BA, Taper ML (2005) Theoretical models of species' borders: single species approaches. Oikos 108:18–27

Hughes CL, Dytham C, Hill JK (2007) Modelling and analysing evolution of dispersal in populations at expanding range boundaries. Ecol Entomol 32:437–445

Hummel H (2003) Geographic patterns of dominant bivalves and a polychaete in Europe: no metapopulations in the marine coastal zone? Helgol Mar Res 56:247–251

Hutchins LW (1947) The bases for temperature zonations in geographical distribution. Ecol Monogr 17:325–335

Jackson GA (1986) Interaction of physical and biological processes in the settlement of planktonic larvae. Bull Mar Sci 39:202–212

Jacobson L, Hennen D (2019) Improving the NEFSC clam survey for Atlantic surfclams and ocean quahogs. NEFSC Ref Doc 19-06. https://www.nefsc.noaa.gov/publications/crd/crd1906/

Johnson CR, Banks SC, Barrett NS, Cazassus F and others (2011) Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. J Exp Mar Biol Ecol 400:17–32

Jumars PA, Thistle D, Jones ML (1977) Detecting two-dimensional spatial structures in biological data. Oecologia 28:109–123

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. Proc Natl Acad Sci USA 105:11823–11826

Keough MJ, Downes BJ (1982) Recruitment of marine invertebrates: the role of active larval choices and early mortality. Oecologia 54:348–352

Kim Y, Powell EN (2004) Surfclam histopathology survey along the Delmarva mortality line. J Shellfish Res 23:429–441

Kristensen E, Delefosse M, Quintana CO, Banta GT, Petersen HC, Jørgensen B (2013) Distribution pattern of benthic invertebrates in Danish estuaries: the use of Taylor's power law as a species-specific indicator of dispersion and behavior. J Sea Res 77:70–78

Kuykendall KM, Powell EN, Klinck JM, Moreno PT, Leaf RT (2017) Management strategy evaluation for the Atlantic surfclam (*Spisula solidissima*) using a spatially explicit, vessel-based fisheries model. Fish Bull 115:300–325

Loesch JG, Ropes JW (1977) Assessments of surf clam stocks in nearshore waters along the Delmarva Peninsula and in the fishery south of Cape Henry. Proc Natl Shellfish Assoc 67:29–34

López-Duarte PC, Carson HS, Cook GS, Fodrie FJ, Becker BJ, Bacco CD, Levin LA (2012) What controls connectivity? An empirical, multi-species approach. Integr Comp Biol 52:511–524

Lucey SM, Nye JA (2010) Shifting species assemblages in the Northeast US Continental Shelf Large Marine Ecosystem. Mar Ecol Prog Ser 415:23–33

Luckenbach MW (1984) Settlement and early post-settlement survival in the recruitment of *Mulinia lateralis* (Bivalvia). Mar Ecol Prog Ser 17:245–250

Ma H, Grassle JP, Rosario JM (2006) Initial recruitment and growth of surfclams (*Spisula solidissima* Dillwyn) on the inner continental shelf of New Jersey. J Shellfish Res 25:481–489

Marzec RJ, Kim Y, Powell EN (2010) Geographic trends in weight and condition index of surfclams (*Spisula solidissima*) in the Mid-Atlantic Bight. J Shellfish Res 29:117–128

Maurer BA, Taper ML (2002) Connecting geographical distributions with population processes. Ecol Lett 5:223–231

McCay BJ, Brandt S, Creed CF (2011) Human dimensions of climate change and fisheries in a coupled system: the Atlantic surfclam case. ICES J Mar Sci 68:1354–1367

McInerny GJ, Turner JRG, Wang HY, Travis JMJ, Benton TG (2009) How range shifts induced by climate change affect neutral evolution. Proc R Soc B 276:1527–1534

Merrill AS, Ropes JW (1969) The general distribution of the surf clam and ocean quahog. Proc Natl Shellfish Assoc 59:40–45

Munguia P (2004) Successional patterns on pen shell communities at local and regional scales. J Anim Ecol 73:64–74

Munroe DM, Noda T (2009) Spatial pattern of rocky intertidal barnacle recruitment: comparison over multiple tidal levels and years. J Mar Biol Assoc UK 89:345–355

Munroe DM, Klinck JM, Hofmann EE, Powell EN (2012) The role of larval dispersal in metapopulation gene flow: local population dynamics matter. J Mar Res 70:441–467

Munroe DM, Powell EN, Mann R, Klinck JM, Hofmann EE (2013) Underestimation of primary productivity on continental shelves: evidence from maximum size of extant surfclam (*Spisula solidissima*) populations. Fish Oceanogr 22:220–233

Munroe DM, Narváez DA, Hennen D, Jacobson L and others (2016) Fishing and bottom water temperature as drivers of change in maximum shell length in Atlantic surfclams (*Spisula solidissima*). Estuar Coast Shelf Sci 170:112–122

Narváez DA, Klinck JM, Powell EN, Hofmann EE, Wilkin J, Haidvogel DB (2012) Modeling the dispersal of eastern oyster (*Crassostrea virginica*) larvae in Delaware Bay. J Mar Res 70:381–409

Narváez DA, Munroe DM, Hofmann EE, Klinck JM, Powell EN, Mann R, Curchitser E (2015) Long-term dynamics in Atlantic surfclam (*Spisula solidissima*) populations: the role of bottom water temperature. J Mar Syst 141:136–148

NEFSC (1999) Fishermen's report surfclam/ocean quahog Cape Hatteras-Gulf of Maine June 3-July 21, 1999. NMFS-NEFSC, Woods Hole, MA

NEFSC (2002) Fishermen's report surfclam/ocean quahog

Delmarva Peninsula-Georges Bank June 3-July 12, 2002. NMFS-NEFSC, Woods Hole, MA

NEFSC (2003) 37th Northeast Regional Stock Assessment Workshop (37th SAW) consensus summary of assessments. NEFSC Ref Doc 03-16. https://www.nefsc.noaa.gov/publications/crd/crd0316/

NEFSC (2007) 44th Northeast Regional Stock Assessment Workshop (44th SAW) assessment report. NEFSC Ref Doc 07-10. https://www.nefsc.noaa.gov/publications/crd/crd0710/

NEFSC (2013) 56th Northeast Regional Stock Assessment Workshop (56th SAW) assessment report. NEFSC Ref Doc 13-10. https://www.nefsc.noaa.gov/publications/crd/crd1310/

NEFSC (2017) 61st Northeast Regional Stock Assessment Workshop (61st SAW) assessment report. NEFSC Ref Doc 17-05. https://www.nefsc.noaa.gov/publications/crd/crd1705/

Nixon SW, Granger S, Buckley BA, Lamont M, Rowell B (2004) A one hundred and seventeen-year coastal water temperature record from Woods Hole, Massachusetts. Estuaries 27:397–404

Nye JA, Link JS, Hare JA, Overholtz WJ (2009) Changing spatial distribution of fish stocks in relation to climate and population size on the northeast United States continental shelf. Mar Ecol Prog Ser 393:111–129

Ólafsson EB, Peterson CH, Ambrose WG (1994) Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. Oceanogr Mar Biol Annu Rev 32:65–109

Orr JC, Fabry VJ, Aumont O, Bopp L and others (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437:681–686

Oviatt CA (2004) The changing ecology of temperate coastal waters during a warming trend. Estuaries 27:895–904

Parmesan C, Ryrholm N, Stefanescu C, Hill JK and others (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579–583

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308:1912–1915

Pershing AJ, Alexander MA, Hernandez CM, Kerr LA and others (2015) Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. Science 350:809–812

Pertoldi C, Faurby S (2013) Consequences of environmental fluctuations on Taylor's Power Law and implications for the dynamics and persistence of populations. Acta Biotheor 61:173–180

Pinsky ML, Fogarty M (2012) Lagged social-ecological response to climate and range shifts in fisheries. Clim Change 115:883–891

Pinsky ML, Palumbi SR, Andréfouët S, Purkis SJ (2012) Open and closed seascapes: Where does habitat patchiness create populations with high fractions of self-recruitment? Ecol Appl 22:1257–1267

Planque B, Fromentin JM, Cury P, Drinkwater KF, Jennings S, Perry RI, Kifani S (2010) How does fishing alter marine populations and ecosystems sensitivity to climate? J Mar Syst 79:403–417

Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W and others (2013) Global imprint of climate change on marine life. Nat Clim Chang 3:919–925

Powell EN, Mann R (2016) How well do we know the infaunal biomass of the continental shelf? Cont Shelf Res 115:27–32

Powell EN, White ME, Wilson EA, Ray SM (1987a) Small-scale spatial distribution of a pyramidellid snail ectoparasite, Boonea impressa, in relation to its host, Crassostrea virginica, on oyster reefs. Mar Ecol 8:107–130

Powell EN, White ME, Wilson EA, Ray SM (1987b) Small-scale spatial distribution of oysters (Crassostrea virginica) on oyster reefs. Bull Mar Sci 41:835–855

Powell EN, Ashton-Alcox KA, Kraeuter JN, Ford SE, Bushek D (2008) Long-term trends in oyster population dynamics in Delaware Bay: regime shifts and response to disease. J Shellfish Res 27:729–755

Powell EN, Klinck JM, Munroe DM, Hofmann EE, Moreno P, Mann R (2015) The value of captains' behavioral choices in the success of the surfclam (Spisula solidissima) fishery on the U.S. Mid-Atlantic coast: a model evaluation. J Northwest Atl Fish Sci 47:1–27

Powell EN, Klinck JM, Hofmann EE, Moreno P, Kuykendall KM, Munroe DM, Mann R (2016) Captains' response to a declining stock as anticipated in the surfclam (Spisula solidissima) fishery on the U.S. Mid-Atlantic coast by model evaluation. Ocean Coast Manag 134:52–68

Powell EN, Mann R, Ashton-Alcox KA, Kuykendall KM, Long MC (2017a) Can we estimate molluscan abundance and biomass on the continental shelf? Estuar Coast Shelf Sci 198:213–224

Powell EN, Kuykendall KM, Moreno P (2017b) The death assemblage as a marker for habitat and an indicator of climate change: Georges Bank, surfclams and ocean quahogs. Cont Shelf Res 142:14–31

Powell EN, Ewing AM, Kuykendall KM (2019a) Ocean quahogs (Arctica islandica) and Atlantic surfclams (Spisula solidissima) on the Mid-Atlantic Bight continental shelf and Georges Bank: the death assemblage as a recorder of climate change and the reorganization of the continental shelf benthos. Palaeogeogr Palaeoclimatol Palaeoecol, doi:10.1016/j.palaeo.2019.05.027

Powell EN, Mann R, Kuykendall KM, Long MC, Timbs JR (2019b) The intermingling of communities during a period of shifting range: the 'East of Nantucket' Atlantic surfclam survey. Mar Ecol (in press), doi: 10.1111/maec.12546

Rice JC (2000) Evaluating fishery impacts using metrics of community structure. ICES J Mar Sci 57:682–688

Ropes JW (1982) The Atlantic coast surf clam fishery, 1965–1974. Mar Fish Rev 44:1–14

Saba VS, Griffies SM, Anderson WG, Winton M and others (2016) Enhanced warming of the Northwest Atlantic Ocean under climate change. J Geophys Res Oceans 121:118–132

Sagarin RD, Barry JP, Gilman SE, Baxter CH (1999) Climate-related change in an intertidal community over short and long time scales. Ecol Monogr 69:465–490

Scheltema RS (1986) On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. Bull Mar Sci 39:290–322

Sekercioglu CH, Schneider SH, Fay JP, Loarie SR (2008) Climate change, elevational range shifts, and bird extinctions. Conserv Biol 22:140–150

Sexton JP, McIntyre PJ, Angert AL, Rice KJ (2009) Evolution and ecology of species range limits. Annu Rev Ecol Evol Syst 40:415–436

Stokesbury KD (2002) Estimation of sea scallop abundance in closed areas of Georges Bank, USA. Trans Am Fish Soc 131:1081–1092

Taylor LR (1961) Aggregation, variance and the mean. Nature 189:732–735

Tezuka N, Kamimura S, Hamaguchi M, Saito H and others (2012) Settlement, mortality and growth of the asari clam (*Ruditapes phiiippinarum*) for a collapsed population on a tidal flat in Nakatsu, Japan. J Sea Res 69:23–35

Thorson JT, Pinsky ML, Ward EJ (2016) Model-based inference for estimating shifts in species distribution, area occupied, and center of gravity. Methods Ecol Evol 7: 990–1008

Timbs JR, Powell EN, Mann R (2018) Assessment of the relationship of stock and recruitment in the Atlantic surfclam *Spisula solidissima* in the northwestern Atlantic Ocean. J Shellfish Res 37:965–978

Underwood AJ, Fairweather PG (1989) Supply-side ecology and benthic marine assemblages. Trends Ecol Evol 4: 16–20

Walther GR, Post E, Convey P, Menzel A and others (2002) Ecological responses to recent climate change. Nature 416:389–395

Weinberg JR (1999) Age-structure, recruitment, and adult mortality in populations of the Atlantic surfclam, *Spisula solidissima*, from 1978-1997. Mar Biol 134:113–125

Weinberg JR (2005) Bathymetric shift in the distribution of Atlantic surfclams: response to warmer ocean temperature. ICES J Mar Sci 62:1444–1453

Weinberg JR, Dahlgren TG, Halanych KM (2002) Influence of rising sea temperature on commercial bivalve species of the U.S. Atlantic coast. Am Fish Soc Symp 32:131–140

Weinberg JR, Powell EN, Pickett C, Nordahl VA Jr, Jacobson LD (2005) Results from the 2004 cooperative survey of Atlantic surfclams. NEFSC Ref Doc 05-01. https://www.nefsc.noaa.gov/publications/crd/crd0501/

Wenger SJ, Isaak DJ, Luce CH, Neville HM and others (2011) Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. Proc Natl Acad Sci USA 108:14175–14180

Woodin SA, Hilbish TJ, Helmuth B, Jones SJ, Wethey DS (2013) Climate change, species distribution models, and physiological performance metrics: predicting when biogeographic models are likely to fail. Ecol Evol 3: 3334–3346

Woodward G, Perkins DM, Brown LE (2010) Climate change and freshwater ecosystems: impacts across multiple levels of organization. Philos Trans R Soc B 365:2093–2106

Zhang X, Haidvogel D, Munroe D, Powell EN, Klinck J, Mann R, Castruccio FS (2015) Modeling larval connectivity of the Atlantic surfclams within the Middle Atlantic Bight: model development, larval dispersal and metapopulation connectivity. Estuar Coast Shelf Sci 153: 38–53

Zhang X, Munroe D, Haidvogel D, Powell EN (2016) Atlantic surfclam connectivity within the Middle Atlantic Bight: mechanisms underlying variation in larval transport and settlement. Estuar Coast Shelf Sci 173:65–78