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Spatial Distribution and Stock-Recruitment Analysis of the Atlantic Surfclam, *Spisula solidissima*, in the Mid-Atlantic Bight and on Georges Bank

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Spatial Distribution and Stock-Recruitment Analysis of the Atlantic
surfclam, *Spisula solidissima*, in the Mid-Atlantic Bight
and on Georges Bank

by

Jeremy R. Timbs

A Thesis

Submitted to the Graduate School,
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and the Department/ School of Ocean Science and Technology
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ABSTRACT

Atlantic surfclams, *Spisula solidissima*, are long-lived bivalve molluscs with dispersive larval stages. Surfclam patchiness throughout the U.S. Exclusive Economic Zone (EEZ) has declined from the 1980's to the present in all assessed regions (Delmarva, New Jersey, Long Island, Southern New England, and Georges Banks). Warming of Mid-Atlantic bottom waters is driving the surfclam stock into new habitat and extirpating the surfclams from nearshore areas. Based on a species distribution function model, the small surfclams appear to inhabit a greater area than the large market-size surfclams across the entire stock. The wider distribution of recent recruits relative to the fishable stock, however, positions the species well to respond to changing bottom water temperatures as Mid-Atlantic warming continues.

Atlantic surfclams support a major commercial fishery in the western North Atlantic Ocean. The stock is not and historically has not been overfished nor has overfishing occurred; however, in recent years landings per unit effort have declined. A species distribution function model was used to assess the effective area occupied by surfclams for 5 study regions. Three independent statistical analyses of the stock-recruitment relationship found little evidence of a significant association in any of the 5 regions, suggesting that factors besides spawning stock biomass are primary determinants of recruitment success. The recruitment index obtained from the NEFSC-NMFS survey across the range of the stock, as a consequence, is unlikely to usefully presage changes in abundance of the fishable stock due to a bias in mortality of juveniles inshore.

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CHAPTER I - BACKGROUND

Atlantic surfclams, *Spisula solidissima*, are long-lived bivalve molluscs with dispersive larval stages. Fertilized eggs develop into planktonic trochophore larvae and then to veliger larvae when the bivalve shell begins to develop (Cargnelli et al., 1999). Development of the foot begins at the pediveliger larval stage. Settlement occurs at the late pediveliger stage and is followed by metamorphosis to the benthic juvenile. (Fay et al., 1983). Surfclams were thought to be planktivorous feeders typically feeding on diatoms, ciliates, and other planktonic organisms (Cargnelli et al., 1999); however, Munroe et al. (2013) showed that planktonic production was insufficient to support the population and suggested that benthic primary production had to be an important additional food source. Surfclams burrow energetically in medium-grain sand at water depths from nearshore down to 60 meters. Surfclams are distributed from Cape Hatteras, North Carolina to the Gulf of St. Lawrence in Canada with high concentrations found offshore the Delmarva peninsula, offshore of New Jersey, and on Georges Bank (NEFSC, 2016). The surfclams at the southern portion of their range in the Delmarva region are slowly disappearing with movement offshore occurring as Mid-Atlantic bottom waters continue to warm (Weinberg, 2002; 2005). This reduction in the clams could be attributed to the detrimental physiological effects of warm temperatures as surfclams prefer water temperatures below 22 °C (Cargnelli, 2005; Weinberg, 2005).

A primary determinant of population dynamics in sessile invertebrates, such as the Atlantic surfclam, is larval transport and settlement (Thorson, 1966). All of the regions (Delmarva, New Jersey, Long Island, Southern New England, Georges Bank) where surfclams are extant are interconnected through larval dispersal with the possible

exception of the Georges Bank region (Zhang et al., 2015). Planktonic larval dispersal is determined by hydrodynamics, larval swimming behavior, and the length of planktonic development (Roegner, 2000). Larval dispersal depends mainly on hydrodynamic processes with larval swimming ability being limited to vertical positioning in the water column (Fraschetti et al., 2003; Zhang et al., 2015). Historically, surfclam population dynamics has been described by dividing the stock into the aforementioned regions. Each region is considered a source and sink of larvae (Zhang et al., 2016). Many environmental factors can affect the survival, settlement location, and successful metamorphosis of planktonic larvae. Ólafsson et al. (1994) emphasized the importance of post settlement processes in determining survival to a reproductive size. Post-settlement processes can include intra- and interspecific competition for space, bioturbation, predation, interaction between recruits and adults, food limitation, suboptimal environmental conditions, and physical disturbance (Fraschetti et al., 2003). Increasing bottom water temperatures is likely exerting an important negative effect on larvae at the southern end of their range (Weinberg, 2005; Zhang et al., 2015).

The Northeast Fisheries Science Center (NEFSC) clam survey used the *R/V Delaware II* equipped with a 5 ft wide dredge from 1982 to 2011. In 2012, the survey was switched to a commercial fishing vessel and modified commercial dredge (NEFSC, 2017). A general description of a hydraulic clam dredge is given in Wallace and Hoff (2005). The dredge is equipped with high pressure hydraulic jets that fluidize the sediment, thereby loosening the clams to be scooped up by a cutting blade into a cage for harvest. The bar spacing of the dredge cage insures that the dredge is size selective, excluding small clams and capturing with maximum efficiency clams of market size (\geq

120 mm). The Atlantic surfclam supports one of the largest fisheries in the northwest Atlantic Ocean. The assessment for Atlantic surfclams is in the U. S. EEZ and the stock is managed as a single unit, so the previously mentioned regions are combined for status determination (NEFSC, 2017). Based on current reference points, there is a very low probability that the stock is overfished or that overfishing is occurring, but a decline in landings per unit effort (LPUE) has been identified as an indicator of stock depletion at local levels (NEFSC, 2017). Depletion at local levels is not considered indicative of the stock as a whole due to limited coverage by the fishery.

Atlantic surfclams have a patchy distribution across their range. The origin of regional patchiness is not well understood and could be changing as increasing bottom water temperatures push the surfclam's range further north and offshore (Munroe et al., 2016; NEFSC, 2013). As this clam is a biomass dominant on the inner continental shelf of the northeastern U.S. coast, as well as supporting an important fishery, the response of this species to warming bottom water temperatures has received considerable attention (Kim and Powell, 2004; Weinberg, 2005; Weinberg et al., 2005; Narváez et al., 2015; Munroe et al., 2017). The objective of this thesis is to investigate the changes in the regional patchiness and distributional shift over time and to determine if a stock-recruitment relationship exists for the Atlantic surfclam.

CHAPTER II – ASSESSMENT OF THE SPATIAL DISTRIBUTION

Introduction

The Atlantic surfclam, *Spisula solidissima*, is a bivalve mollusc with a dispersive larval stage. The species is distributed from Cape Hatteras, North Carolina to the Gulf of St. Lawrence in Canada from nearshore down to depths of about 60 m wherever average bottom temperatures do not exceed 25°C (Cargnelli et al., 1999; Merrill and Ropes, 1969; Snelgrove et al., 1998) and edaphic requirements are met (Cargnelli et al., 1999). Surfclams burrow energetically (Ropes and Merrill, 1973) and are typically found in medium-grain sand (Cargnelli et al., 1999; Chintala and Grassle, 2001). High concentrations of surfclams are found offshore of the Delmarva Peninsula and New Jersey and on Georges Bank (NEFSC, 2013, 2017). Atlantic surfclams have a maximum life span of ~30 years and reach a maximum shell length of ~220 mm (Jones et al., 1978). That being said, over much of the United States Economic Exclusion Zone (EEZ), the maximum shell length has decreased 15 – 20 mm since 1982 (Munroe et al., 2016). Declining shell length is likely a manifestation of physiological constraints imposed by rising bottom water temperatures over that time period (see Munroe et al., 2013).

In marine ecosystems, many species with commercial importance have patchily distributed populations (Bascompte et al., 2002). These species commonly include sessile and sedentary marine invertebrates that are patchy at a local scale (Flowers, 1973; Jumars et al., 1977; Munroe and Noda, 2009; Kristensen et al., 2013) while frequently also being patchy at a larger geographic scale by being distributed in more or less isolated populations within the metapopulation (Borregaard and Rahbek, 2010; Pinsky et al., 2010). 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, absolute and gradients of temperature and salinity, and behavior of the larvae exert a strong influence on larval survival and transport from one patch to another (Gaylord and Gaines, 2000; Ma et al., 2006; Narváez et al., 2012; Zhang et al., 2016). Disagreement exists as to the determinant of the spatial and temporal variations seen in patchily distributed species. One school of thought contends that patchiness arises from variations in larval dispersal and recruitment of larvae (Gaines et al., 1985; Jackson, 1986; Underwood and 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 and Downes, 1982; Luckenbach, 1984; Ólafsson et al., 1994; Gosselin and Qian, 1997; Tezuka et al., 2012). Patchiness often arises in bivalve molluscs post-settlement for these reasons (Brand, 2006; Stokesbury, 2002; Dresler and Cory, 1980). At the largest of spatial scales, range boundaries may be established in either of these two ways, by dispersal dynamics or post-settlement survival (Hutchins 1947; Sexton et al., 2009; Woodin et al., 2013).

Atlantic surfclams have a patchy distribution across their range. The origin of regional patchiness is not well understood, although both recruitment (Chintala and Grassle, 2001; Ma et al., 2006; Zhang et al., 2016) and post-settlement (Weinberg et al., 1999; Narváez et al., 2015) processes seem to be involved. Regional patchiness could be changing as increasing bottom water temperatures push the surfclam's range further north and offshore (Munroe et al., 2016; NEFSC, 2013). A warm period in Delmarva between

1999 and 2002 resulted in thermal stress combined with poor physiological condition causing mortality and a shift of Delmarva surfclams into deeper water (compare Merrill and Ropes, 1969; Weinberg, 2005; see also Kim and Powell, 2004). Higher summer water temperatures off Delmarva have resulted in surfclams having relatively low growth rates and meat weights (Weinberg et al., 2002; Marzec et al., 2010; Narváez et al., 2015). Simulations predict that an increase in average bottom water temperatures will significantly reduce surfclam assimilation rate leading to starvation mortality and a reduction in the surfclam population (Narváez et al., 2015). 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 area of interest for the current study is the Mid-Atlantic Bight (MAB) and Georges Bank. This area has, in the context of historical surfclam distributions, been divided into five regions (Delmarva, New Jersey, Long Island, Southern New England, and Georges Bank) for stock assessment purposes (NEFSC, 2003, 2007). The objective of the current study is to examine the spatial distribution of the Atlantic surfclam to determine the following: (1) the degree of patchiness of the surfclam population across each of these assessment regions, (2) the presence of any change in patchiness of the population over the 30+ year history of surveys of the surfclam stock, and (3) if any shift in range has occurred over this time frame and specifically whether the center of distribution has shifted in any of the five study regions.

Methods

The Atlantic surfclam 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 years beginning in 1982 and continuing to 2011. Data after 2011 have been excluded from this analysis because a new dredge was employed for the survey after 2011 and gear calibration between the two dredges, though feasible (Hennen et al., 2012; NEFSC, 2017), would introduce challenges of interpretation for the analyses contemplated herein. Figure 1 shows the location of each tow across the entirety of the surfclam stock assessment from 1982 to 2011. For the current study, the survey data were divided by region (Delmarva, New Jersey, Long Island, Southern New England, Georges Bank) and size class (lower limit: 64, 80, 93, 104, 120-mm shell length or SL). The surfclams are considered a single stock in the U.S. EEZ 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) and 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 the Delmarva and New Jersey regions requires about five years to reach market size (≥ 120 -mm SL), with each larger size class decrementing one year of time to do so.

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). Temporal changes in patchiness and spatial distribution were evaluated by decade (1982 – 1989, 1992 – 1999, 2002 – 2011). The decadal divisions were chosen based on two criteria. The

separation of the 1980's and 1990's represents a distinctive boundary between relatively low and relatively high catch rates in the survey (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 the mortality rates off Delmarva contemporaneous with a regime shift in the North Atlantic propositionally due to a negative to positive excursion of the Atlantic Multidecadal Oscillation (Lucey and Nye, 2010; see also Powell et al., 2008). All tows that caught zero 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. The majority of these tows were in areas uninhabitable by surfclams at the time of sampling.

Patchiness was assessed using the variance-to-mean ratio (VtMR) of the density. The VtMR has been widely used for this purpose (Harte, et al., 2005; Maurer and Taper, 2002; Powell et al., 1987). 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) provides 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 one tow were excluded as a variance calculation was not possible. The mean and variance of the number of surfclams caught per tow were calculated for each size class over the three decades for each of the remaining survey strata. This provided one 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 year or region as necessary. A two-way ANOVA was conducted by region to examine the effect of decade and size class on the VtMR. A two-way ANOVA was also used to evaluate differences in the VtMR between regions and decade. Interaction terms were always included in the ANOVA. Post-hoc pairwise contrasts were obtained using Least Square Means for multiple comparisons.

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 over a series of population or metapopulation units (Taylor, 1961). Taylor's Power Law has received considerable study in the context of its explanatory power in describing the geographic characteristics of a species' distribution (Maurer and Taper, 2002; Kristensen et al., 2013; Pertoldi and Fourby, 2013). The TPL describes the relationship between the mean and variance among a series of sample sets taken from different locations within a population or metapopulation, expressed as:

$$\sigma = \alpha * \mu^{\beta}$$

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 (Elliot, 1977; Green, 1989; Kristensen et al., 2013; Taylor, 1961)). In practice, the parameters are derived after log transformation; thus α is the intercept and β is the slope of the linear model. An ANCOVA using the log-mean as the covariate and the log-variance as the dependent variable was used to assess if the dispersion parameter beta (β) changed over time or differed between size classes within each decade.

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 Spatial 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; then, spatial autocorrelation is employed over time to predict shifts in distribution and area coverage (Thorson et al., 2016). For the current study, the center of distribution for surfclams was derived from the 2-dimensional density maps produced by the 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 zero point, while Georges Bank used UTM 19.

Results

Aspatial analysis

The VtMR declined for each size class from the 1980s decade to the 2000s decade within all regions except for Long Island, that showed a decline in all size classes except market-size (≥ 120 -mm), and for the 104-mm size class in the Southern New England region which increased slightly (Figure 2). Frequently, the decline 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 (≥ 120 -mm) clams had a higher

VtMR within each decade than other size classes and the VtMR generally declined with decreasing size except for the 1980 decade in Delmarva in which the smaller size classes had a larger VtMR (Figure 2, Table 1). The VtMR were significantly higher in the 1980's and the VtMR in the Delmarva region were significantly higher than any of the other regions (Table 2). The VtMR during the 1980s decade for the Delmarva region was significantly higher than the VtMR for the 1990s and 2000s (Table 2). For the Long Island region, the VtMR for the market-size (≥ 120 -mm) clams was significantly higher than for any of the other size classes (Table 2). In the Southern New England region, the VtMR of the market-size (≥ 120 -mm) clams was significantly higher than the VtMR for the other size classes (Table 2). The VtMR for the market-size (≥ 120 -mm) clams was also significantly higher than for the other size classes for Georges Bank (Table 2). In the New Jersey region, the VtMR for the 2000s was significantly lower than for the other two decades and the VtMR of the 104-mm size class and market-size (≥ 120 -mm) clams were significantly higher than the VtMR of the smaller size classes (Table 2). A comparison across regions within decade shows that the VtMR for the Delmarva region is significantly higher than for the other regions in the 1980s (Table 3). After the 1980s the difference in VtMR between regions is no longer significant.

The mean number of surfclams per tow ranged from 0.5 to 1,500 while the variance ranged from 3.0×10^{-5} to 3.4×10^6 . Figure 3 shows the Taylor's Power Law relationships for the Delmarva sector. The exponent beta for Taylor's Power Law, a measure of the degree of patchiness, ranged from 2 to 4 for most size classes and decades within each region (Table 4). Although the VtMR frequently varies significantly (Table 2), the exponent (β) of the Taylor's Power Law did not change over time for any of the

regions (Figure 4; Table 5), indicating that the relationship between the differential in the VtMR occurred when both the variance and the mean varied concordantly along the power curve. The same was true for the size classes for three of the five regions. For New Jersey and Southern New England, however, the exponent beta changed significantly (Table 4; Table 5). In New Jersey, the power law exponent for the 64-mm size class was significantly higher than for the 104-mm and market-size (≥ 120 -mm) clams (Table 4; Table 5). For the Southern New England region, the power law exponent was significantly lower for the 80-mm size class than the 93-mm size class (Table 4; Table 5).

The exponent for Taylor's Power Law varied significantly between regions for the larger size classes (104 and ≥ 120 mm), 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, the power law exponents were higher for Delmarva, New Jersey, and Georges Bank, indicating that the larger size classes were more patchy with increasing mean abundances in these regions than in the intervening regions of Long Island and Southern New England.

Spatial analysis

The SDF model provided results consistent with the VtMR analysis. The density (kg of surfclams per km²) maps produced by the model show, for example, a reduction in patchiness in the Delmarva market-size (≥ 120 -mm) clams and also a shift northward and offshore from the 1980s to the 2000s (Figure 5). Figure 6 provides evidence of a shift in the center of distribution of market-size (≥ 120 -mm) clams off Delmarva northward and

offshore over three decades, but little change was seen in the 64-mm surfclams over the same time. The range shift for market-size (≥ 120 -mm) clams was on the order of 20 km east and 40 km north. The market-size (≥ 120 -mm) clams in New Jersey also shifted northward and offshore, about 20 km east and 30 km north, while again the center of distribution for the smaller surfclams remained relatively unchanged. The center of distribution for the smaller surfclams, however, is distinctly further offshore than for the market-size (≥ 120 -mm) clams (Figure 7).

Figure 8 compares the distribution pattern of the five size classes off New Jersey, demonstrating the significantly higher degree of aggregation in the market-size (≥ 120 -mm) clams and the consistent reduction in regional patchiness across the smaller size classes. Increased dispersion for the 64-mm clams explains the offshore trend in the range center relative to the market-size (≥ 120 -mm) clams, as the smaller sized clams are much more uniformly distributed across the continental shelf. The center of distribution for 64-mm surfclams on Georges Bank remained constant while the market-size (≥ 120 -mm) clams shifted slightly east and south (Figure 9). The density plot (kg per km² of surfclams) of Georges Bank illustrates the significantly higher aggregation in the market-size (≥ 120 -mm) 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 (Figure 10). The centers of distribution for Long Island and Southern New England surfclams fluctuated over time but do not reveal any substantial directional movements (Figure 11; Figure 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 survey (NEFSC, 2017).

Discussion

Aspatial analysis

The objective of the current study was to examine the dynamics of patchiness of Atlantic surfclams among size classes 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 surfclam population was patchy in each of the five geographic regions. Patchiness is not unexpected, as it is a rarity if marine species are other than significantly aggregated in their distributions. Much more surprising, though, is that patchiness has declined since the 1980s and this decline is universal over the entirety of the U.S. stock from the Delmarva continental shelf to Georges Bank (Table 1). However, the exponent of Taylor's Power Law did not change significantly over time; thus, the decline in the VtMR did not indicate an inherent change in the aggregative propensity of the surfclam. Rather, both the variance and the mean translated along one basic descriptive power curve.

Significant differences in the VtMR and the exponent of Taylor's Power Law were identified in size class and regional comparisons. Surfclams in the Delmarva region were routinely more patchy than in the other regions (Table 2). VtMR 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 higher VtMR. An alternative is to examine the exponent of Taylor's Power Law. In this case, although variable, most exponents fell within values between 2.2 and 3.0. Nonetheless, the power laws 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. Interestingly, these three regions support the bulk of the stock, suggesting that the patchy proclivities of the surfclam vary with the regional optimality of the habitat.

The exponent of Taylor's Power Law varies little amongst the size classes, the case of the Delmarva region being an exception, perhaps not surprisingly as this region represents the southern range boundary for the species. Nonetheless, the routine significant differences in VtMR between the size classes, with the ratio tending to increase with increasing size, perhaps 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 the power law.

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 (≥ 120 -mm), so that patchiness increases with clam size. Patchiness also has declined over time either because abundances in high-clam abundance areas have declined or areas of low clam abundance have increased in importance over time. The tendency towards patchiness, however, has

not changed over time, nor does it change with growth to market-size (≥ 120 -mm). 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 and the degree of aggregation increases disproportionately with the mean in comparison to the remainder of the range of the stock.

Changes in the dynamics of the range

The movement of surfclams offshore has been known for some time with warming of the Mid-Atlantic bottom waters (Kim et al., 2004; Weinberg, 2005; NEFSC, 2013). The ubiquity of this trend is shown by the SDF model which documents offshore translations of the range core in Delmarva and New Jersey, an extension into deeper waters on Georges Bank, and northward translations in the Delmarva and New Jersey region. The current study shows a 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 patches nearer the southern and inshore range boundary. The newly occupied areas tend to have surfclams more spread out because the smaller surfclams tend to be less patchy. The 64-mm surfclams in New Jersey are more broadly distributed offshore than the larger surfclams even though the

core of the distribution of market-size (≥ 120 -mm) clams has moved offshore slowly over the course of the survey (Figure 4). That is, recruitment offshore New Jersey predisposes the surfclam to an offshore translation. 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 boundary compounded possibly by slower growth along the leading edge of the range (e.g., Marzec et al., 2010).

The patterns observed off New Jersey and Delmarva are similar in suggesting that smaller surfclams are capable of recruiting offshore of the market-size (≥ 120 -mm) range core and, in this area, are less patchy. In both regions, the core of the range of market-size (≥ 120 -mm) clams has translated offshore, while the established areas containing the earlier patches of market-size (≥ 120 -mm) 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 near shore (Hansen et al., 2010; Orr et al., 2005; Poloczanska et al., 2013) and the predisposition for an offshore shift provided by recruitment offshore of the present range core of the market-size (≥ 120 -mm) clams. 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; McInerney 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 a more dispersed recruitment dynamics that sets up the opportunity for a translation of the range core.

The influence of fishing

The surfclam fishery targets patches, reducing the numbers of the larger surfclams (NEFSC, 2013; Weinberg et al., 2005; Powell et al., 2015, 2016). The fishery targeting patches is unlikely to be the cause of the observed shift in the surfclam distribution or the large reduction in patchiness. One reason for this is that fishing mortality is low across the stock. The fishing mortality rate has been between 0.01 and 0.06 over the history of this study period (NEFSC, 2013). Weinberg (2005) estimated that the natural mortality rate ($\geq 0.22 \text{ y}^{-1}$) for surfclams in the Delmarva region between 1999 and 2002 had a much greater impact on the biomass than the commercial fishery (fishing mortality $< 0.04 \text{ y}^{-1}$). Declining maximum size of surfclams over the last three decades is likely the result of environmental shifts and not fishing of the largest size classes (Munroe et al., 2016). In addition, 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 Taylor's Power Law occurred there as in the southern regions of 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.

Landings per unit effort (LPUE) have reached record lows in some regions and have been steadily declining across all regions except Georges Bank 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 in the local populations (Powell et al., 2015, 2016). Increased natural mortality caused by warming bottom water temperatures (Weinberg, 2005) is affecting 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. However, LPUE is not an ideal metric for the reason that surfclams are patchily distributed and the fishery focuses its efforts on high density patches. Thus, low LPUE may be a symptom of ongoing range shift, robbing the population of high-abundance patches in 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.

Surfclams were historically closer to shore off Delmarva before the NEFSC surveys began in the 1980's (e.g., Loesch and Ropes, 1977; Ropes, 1982; see also Hofmann et al., in press). The observation of surfclams historically closer to shore points towards a migration of surfclams 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 et al., 2010; Hare et al., 2016). Changes in climate could result in surfclams disappearing from the southern portion of their 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, unpubl. data).

As the surfclams continue 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 United States 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 and Fogarty, 2012). This trend is well-known for the surfclam fishery (McCay et al., 2011; Powell et al., 2016, Hofmann et al., in press). 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). On the other hand, declining VtMR may improve survey accuracy at a specified level of sample allocation (Powell and Mann, 2016; Powell et al., 2017), because survey bias tends to increase with increasing patchiness (Bros and Cowell, 1987).

A major concern is the unknown time required to reestablish dense patches of market-size (≥ 120 -mm) 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 surfclams 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 (≥ 120 -mm) stock. The degree of aggregation appears to be in part a function of the stage in translation 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 new core of the range.

CHAPTER III - STOCK AND RECRUITMENT ANALYSIS

Introduction

Atlantic surfclams, *Spisula solidissima*, support a major commercial fishery in the western North Atlantic Ocean. Around 20,000 metric tons (mt) of surfclam meat were landed in 2015 with landings consistently between 15,000 and 25,000 mt since 1982 (NEFSC, 2017). Recent stock assessments show that recruitment has been low in the southern portion of the surfclam's range post-2000 while Zhang et al. (2015) provide some support to suggest that larval supply is not a limiting factor. According to recent stock assessments, (NEFSC, 2017), the surfclam is not overfished and overfishing is not occurring; however, landings per unit effort (LPUE) have declined. That being said, LPUE is not necessarily a good measure of fishable biomass for patchily distributed sedentary species like the Atlantic surfclam as dense patches are targeted preferentially by the fishery (Powell et al., 2015, 2016; Kuykendall et al., 2017).

An important population dynamics relationship for the assessment of fisheries is the relationship between spawning stock biomass and recruitment. Many examples are available of fisheries being overfished to the point where recruitment declines and the stock collapses (Cushing, 1971; Hilborn and Walters, 1992; Myers et al., 1996). Shellfish are no exception (Jackson et al., 2001; Krauter et al., 2008; Tettelbach et al., 2013). For sessile and sedentary species, the potential of Allee effects cannot be discounted (Shepherd et al., 1998; Krauter et al., 2005; Tettelbach et al., 2015), although behavioral adaptations may mitigate the probability (Buroker, 1983; Krauter et al., 2008; Ambrogio and Pechenik, 2009; Tettelbach et al., 2017). An example is the hard clam, *Mercenaria*

mercenaria, where unsustainable fishing mortality led to recruitment overfishing in both North Carolina and New York (Peterson, 2002; Kraeuter et al., 2005).

A relationship between recruitment and spawning stock biomass (SSB) is consequential in determining the reference points supporting maximum sustainable yield (Brooks, 2013; Mangel et al., 2013; Powell et al., in press). One difficulty when dealing with bivalves is the rarity of a clear relationship between SSB and recruitment (Hancock, 1973; Peterson and Summerson, 1992; Kraeuter et al., 2005; Powell et al., 2009) and the relationship is inherently important in understanding the population dynamics of a species (e.g., McGarvey et al., 1993; Harris et al., 1998; Honkoop et al., 1998). A crucial reason for limited evidence of a broodstock-recruitment relationship in bivalves is the importance of recruit survival determining the degree and spatial distribution of recruitment (Powell et al., 1984; Guillou and Tartu, 1994; Ólafsson et al., 1994; Hunt et al., 2003). Not infrequently, recruitment occurs in locations inimical to growth to adulthood (e.g., Wells and Gray, 1960; Morse and Hunt, 2013; Fuentes-Santos and Labarta, 2015).

Surfclams could follow one of two life-history strategies. The first scenario is that surfclams are k-selected (Pianka, 1970; Stearns, 1976); such species have an expected relationship between SSB and recruitment (e.g., Adams, 1980; Goodwin et al., 2005). Surfclams have a long life span (Jones et al., 1978; Munroe et al., 2016) consistent with the k-selected end of the r-k continuum. The second scenario is that surfclams are bet-hedgers (Pianka, 1970; Stearns, 1976). These are species with long life spans that, nonetheless, produce large numbers of young yearly while generating substantive recruitment events much less frequently due to inimical conditions during the planktonic

or juvenile life span. Bet-hedging lowers the variance in fitness between good and poor environmental conditions in order to maximize long-term fitness (Olofsson et al., 2009). This provides the bet-hedger the opportunity to maintain its fitness in an unpredictable environment. An important outcome is the potential for decoupling of SSB from recruitment (Hornbach et al., 1981). One consequence of this decoupling is that predicting one variable based on the other becomes increasingly difficult. Surfclams produce large numbers of offspring, few of which survive to maturity. Surfclams also suffer high post-settlement mortality (MacKenzie et al., 1985; Quijón et al., 2007). These are characteristics of the bet-hedging mode of life.

Potentially confounding any relationship between SSB and recruitment is the fact juvenile surfclam distribution is significantly different from market-size clams, suggesting that many recruits fail to survive in suboptimal habitat (see Chapter II). The area of interest for this study is the Mid Atlantic Bight (MAB) and Georges Bank. The MAB with Georges Bank have historically been subdivided into five regions (Delmarva, New Jersey, Long Island, Southern New England, and Georges Bank) for stock assessment purposes. Surfclam larvae remain in the plankton for 20-30 days (Goldberg, 1989; Cargnelli et al., 1999; Zhang et al., 2015), much too short a time for the entirety of the Mid-Atlantic broodstock to participate in recruitment in all regions, and this possibility is further minimized by prevailing currents. Surfclam larvae are carried by southwesterly flowing currents in the MAB, with the exception of Georges Bank; thus, recruitment in any region may result from spawning activity therein or to the north and east (Zhang, 2015, 2016). One extreme consequence is larval drifting beyond the southern range boundary, these larvae being lost to the population. The dynamics of

recruitment, then, may preclude development of a useful recruitment index as an indicator of future adult biomass and distribution.

Determining how SSB and recruitment are related are additionally important because of the sensitivity of the Atlantic surfclam to climate change. Surfclams have a narrow upper temperature range between optimal and lethal which makes this species a bellwether species for climate change (Hofmann et al., in press). In particular, the surfclam stock has been shifting its range north and offshore over the course of many decades, with a distinct acceleration beginning circa 2000. The response of surfclams to warming bottom water temperatures has received considerable attention because it is both a biomass dominant on the inner continental shelf of the northeastern U.S. coast and supports an important fishery (Kim and Powell, 2004; Weinberg, 2005; Weinberg et al., 2005; Narváez et al., 2015; Munroe et al., 2017).

The objective of this study is to examine the relationship between SSB and recruitment to determine the following: (1) whether a quantitative relationship between SSB and recruitment can be identified using 30+ years of comprehensive NEFSC survey data, (2) whether the relationship between SSB and recruitment has changed over the past 30+ years during a period of climate change by incorporating larval dispersal model projections, and (3) if the effective area of recruits is consistent with the adult distribution.

Methods

Data for the Atlantic surfclam used in this study were collected by the National Marine Fisheries Service (NMFS) Northeast Fisheries Science Center (NEFSC) stock assessment surveys which took place every 2-3 years beginning in 1982 and continuing

to 2011 (all references to a survey hereafter refers to the NEFSC stock assessment survey). Surveys subsequent to 2011 used a larger dredge and different survey vessel and, consequently, have been excluded to eliminate the uncertainty imposed by conflation of data from gears of differential efficiency and selectivity. Figure 1 shows the location of each tow across the entirety of the surfclam survey domain from 1982 to 2011 and the subdivisions of the region (Delmarva, New Jersey, Long Island, Southern New England, and Georges Bank) historically used for assessment of the status of the stock (NEFSC, 2007) and used by Zhang et al., (2015, 2016) to examine larval transport dynamics throughout the MAB.

Surfclams are patchily distributed throughout the MAB and this distribution pattern has changed over time. Therefore, the estimated area coverage of surfclams used for calculation of SSB and recruits was derived from a Spatial Distribution Function (SDF) model developed by Thorson et al. (2016). The effective area is estimated as total km² occupied by surfclams in each region over time. This model uses survey data to estimate model parameters for expected densities within a spatial domain for each given location and employs spatial autocorrelation to predict changes in effective area over time (Thorson et al., 2016). Chapter II provides additional details.

The Atlantic surfclam survey has occurred every two to three years. A three parameter von Bertalanffy growth equation was used to predict the age at length of a surfclam in a given survey year:

$$shell\ length = L_{\infty}(1 - e^{-k(t-t_0)}) \quad (1)$$

where L_{∞} is the asymptotic shell length, k is the Brody growth constant, t is time, and t_0 is the age at which the organism would have a size of zero. The parameters needed for

this calculation were obtained from NEFSC (2013). Since the dredge used for the survey is size selective, surfclams smaller than 60 mm were excluded from this analysis.

Recruits were defined as animals of a given age that would have been spawned the year of the previous survey. Therefore, the number of recruits in a given year was calculated from the number of clams at a particular shell length observed in the subsequent survey based on the age at length obtained from the von Bertalanffy relationship:

$$R = A_R * \left(\frac{\sum (c_i / t_i)}{n} \right) \div e^{-m\tau} \quad (2)$$

where R is the number of recruits across the total area, A_R is the total area (km²) occupied by surfclams estimated by the SDF model, c_i is the number of surfclams caught for the i^{th} tow, t_i is the swept area (km²) for the i^{th} tow, and n is the total number of tows. This total number of recruits was then increased by back-calculating mortality (m) at a constant rate of 0.15, over the elapsed time τ between surveys to account for any loss in recruits due to natural mortality. Smaller clams very likely have a higher mortality rate than larger clams. Consequently, this back-calculation can be expected to yield an underestimate. However, no information on size-dependent trends in mortality presently exists; thus, we adopt the constant mortality assumption used in the surfclam assessment (NEFSC, 2017; see also Weinberg, 1999).

SSB (kg) was calculated using:

$$SSB = A_{SSB} \left(\frac{\sum (w_i / t_i)}{n} \right) \quad (3)$$

where A_{SSB} is the total estimated area (km²) occupied by the surfclams from the SDF model, w_i is the total summed weight (kg) of the surfclams for the i^{th} tow, t_i is the swept area (km²) for the i^{th} tow and n is the total number of tows. The effective area (A_R) from

the SDF model for the recruits was estimated using the data from the clam sizes predicted by the von Bertalanffy relationship to be the size range reached by recruits from a subsequent survey to a given survey (e.g., 64 – 80-mm shell length) while the effective area used for the SSB calculations was estimated using the data from all surfclams ≥ 60 -mm shell length for a given survey. Chintala et al. (1995) showed that surfclams mature at a size below 60 mm, but these clams are not efficiently caught by the survey dredge; hence, SSB is slightly underestimated by their exclusion. Not all strata were sampled in every survey leaving “holes” in the SSB calculation. These “holes” were filled by averaging the number of tows from the same stratum in the previous and/or next survey (NEFSC, 2013).

Zhang et al. (2015) showed that larvae potentially recruiting to a region were derived from that region and usually the adjacent region to the northeast. Zhang et al. (2015) used an individual-based larval model that included both growth and behavioral components coupled to the ROMS (Regional Ocean Modeling System), a free-surface, terrain-following, primitive equations ocean model widely applied by the scientific community for various applications in both deep ocean and coastal settings (e.g., Haidvogel et al., 2000; Powell et al., 2006; Budgell, 2005; Warner et al., 2005). The hydrodynamic model was to identify larval trajectories from release points in each region throughout the surfclam April-October spawning season. These connectivity data permitted allocation of a portion of the potential recruits from an upstream region into the regions downstream. The estimated SSB from each region was allocated into portions representing the percentage of said SSB responsible for larvae released into a downstream region or remaining in the origin region (Table 7) based on a larval

connectivity matrix provided by Zhang et al. (2015; see Zhang's figure 8-B). The allocated portion of SSB was then apportioned into the percentage of larvae that settled in the downstream region or region of origin (Table 7).

Spearman's correlation analysis was used to determine if any relationship existed between observed recruits in a given region and allocated SSB as defined by the Zhang et al. (2015) connectivity matrix. A Ricker SSB and recruitment model was fitted to the data. The Ricker model assumes that recruitment decreases relative to spawning stock at high spawning stock abundance (overcompensation), as might be the case in bivalves where competition for food may reduce fecundity disproportionately at high SSB:

$$R = \alpha S e^{-\beta S} \quad (4)$$

where R is the recruits, S is the SSB, α is the recruits per spawners at low stock sizes, and β is the shape of the curve (DeAlteris, 2000). The parameters α and β were estimated using a non-linear model in R (programming language) to best fit the data.

A potential relationship between SSB and recruitment was further investigated using quadrant plots defined by the medians of SSB and recruitment. Figure 13 presents the four quadrants defined as: 1, low recruit/low SSB; 2, high recruit/low SSB; 3, high recruit/high SSB; and 4, low recruit/high SSB (Rothschild and Mullen, 1985).

Consecutive survey year transitions were used to derive a transition matrix for calculation of mean first passage times following Redner (2001; see also Rothschild et al., 2005; Rothschild and Mullen, 1985). Mean first passage times are a measure of the number of years likely to elapse before the population with the x-y relationship characteristic for any one quadrant is described by the relationship characteristic of the same quadrant or

obtains the relationship characteristic of one of the three other quadrants (Powell et al., 2009).

Results

Area analysis

The Spatial Distribution Function (SDF) model estimated effective areas occupied by the recruits and the larger surfclams for each region. In all regions, the recruits covered a greater area than the larger surfclams. The effective area for both the recruits and larger surfclams in the Delmarva region fluctuated over time without a noticeable increase or decrease (Figure 14). This is consistent with the offshore shift in range in this region since circa 2000 which has debited the inshore range while expanding the offshore range. The effective area ranged between 8.1×10^3 and 2.2×10^4 km² excluding an outlier in 1984 for the recruits whereas the effective area for the larger surfclams ranged between 4.9×10^3 and 8.1×10^3 km² (Table 8). In Delmarva, the effective area, on average, was 55% less for the larger surfclams compared to the recruits. The effective area for both the recruits and larger surfclams in the New Jersey region increased over time from the 1980s to the 2000s (Figure 15). This is consistent with the expansion of the population offshore since circa 2000 (Weinberg et al., 2005), while the recession of the inshore boundary has impacted primarily state waters (Hofmann et al., in press) not considered in this analysis. The effective area for the recruits in the New Jersey region fluctuated over time ranging from 7.3×10^3 to 1.5×10^4 km² and the effective area for the large surfclams ranged from 5.4×10^3 to 1.1×10^4 km² with an average reduction of 21.5% in the effective area from the recruits to the large surfclams (Table 8). The effective area for the recruits in the Long Island region fluctuated over time while the effective area for the large surfclams

remained constant with a reduction of 53.1% in area from the recruits to the large clams (Figure 16). An offshore range expansion noted in the most recent surveys (NEFSC, 2017) is not recorded in the dataset used in this analysis. In the Long Island region, the effective area for the recruits ranged from 4.9×10^3 to 9.0×10^3 km² while the effective area for the large surfclams ranged from 3.0×10^3 to 3.6×10^3 km² (Table 8). The effective area in the Southern New England region for the recruits was much higher with some fluctuations over time than for the larger surfclams for which the effective area remained relatively constant (Figure 17). The effective area for the recruits and larger surfclams ranged from 7.3×10^3 to 1.1×10^4 and 1.8×10^3 to 2.2×10^3 km², respectively, in the Southern New England region (Table 8). The Southern New England region had a considerably larger reduction in area of 78.6% than the other regions between the recruits and larger surfclams. In the Georges Bank region, the effective area for the recruits remained relatively constant over time, excepting the 1986 outlier, whereas the effective area for the larger surfclams increased over time with some fluctuations (Figure 18). This is consistent with an expansion of the area occupied by surfclams on Georges Bank noted by NEFSC (2013, 2017; see also Chapter II). The effective area for the recruits on Georges Bank ranged from 1.6×10^3 to 2.0×10^4 km² with the effective area for the larger surfclams ranging from 3.0×10^3 to 9.9×10^3 km² (Table 8). A 59.3% reduction in area was observed from the recruits to the large clams.

Stock-Recruitment

The recruits and SSB for each survey year are provided in Table 9 and shown in Figures 8 and 9. Based on the Spearman's correlation results, the Delmarva, Long Island, and Southern New England regions exhibit no relationship between the recruits and SSB

whereas the New Jersey and Georges Bank regions exhibit a weak negative relationship between the recruits and SSB (Figure 21) which, however, are not significant. Ricker models highlight that no clear relationship exists between the recruits and SSB for any of the study regions (Figure 19 – 20).

The recruits and SSB for each survey year were allocated to one of four quadrants based on division of each by their respective median (Table 10). Chi-square tests found no significant differences between the number of stock-recruitment points falling into one of the quadrants relative to the others for any of the regions (Table 11). These results indicate the stock and recruitment observations are uniformly distributed among the four quadrants. No relationship exists between the stock and recruits based on this analysis.

Mean first passage times for the Delmarva region suggested similar transition times between all quadrant pairs (Table 12). In the New Jersey region, the first passage times estimated that transitioning to quadrant 2 from the other quadrants is more unlikely (Table 12). Quadrant 2 is characterized by high recruitment-low SSB. The first passage times for the Long Island region point towards a transition to quadrant 1, low recruitment-low SSB, from the other three quadrants being less likely to occur (Table 12). The Southern New England mean first passage times suggested the unlikely occurrence of a transition to state 4, low recruitment-high SSB, from the other quadrants whereas the Georges Bank region was characterized by the less likely transition to state 3, high recruitment-high SSB, from the other quadrants (Table 12).

Discussion

The objective of this study was to determine if a stock-recruitment relationship exists for the Atlantic surfclam. A number of challenges exist in making this

determination. Juvenile surfclams may be distributed significantly differently than market-size clams, suggesting that many recruits fail to survive in suboptimal habitat. The area of interest for this study is the Mid Atlantic Bight (MAB) and Georges Bank. This area historically has been subdivided into five regions (Delmarva, New Jersey, Long Island, Southern New England, and Georges Bank) for stock assessment purposes. Surfclam larvae remain in the plankton for 20-30 days (Goldberg, 1989; Cargnelli et al., 1999; Zhang et al., 2015), much too short a time for the entirety of the Mid-Atlantic broodstock to participate in recruitment in all regions, and this possibility is further minimized by prevailing currents. Surfclam larvae are carried by southwesterly flowing currents in the MAB, with the exception of Georges Bank; thus, recruitment in any region may result from spawning activity therein or to the north and east (Zhang, 2015, 2016) and the geographic scale of the contributing spawning stock is highly variable interannually (Zhang et al., 2016). One extreme consequence is larvae drifting beyond the southern range boundary; these larvae being lost to the population. The dynamics of recruitment, then, may complicate development of a useful recruitment index.

During the 1982-2011 period, warming of the Mid-Atlantic bottom waters has occurred, an important result of which has been a shift of the surfclam population offshore and north (Hofmann et al., in press). Rising temperatures can be expected to impact recruitment potential and long-lived species. This may introduce variability in the relationship between broodstock and recruitment (e.g., Rijnsdorp et al., 2009; Dutertre et al., 2010; Shepard et al., 2010). In particular, Perretti et al. (2017) recognized that recruitment success has varied approximately decadal over the 1980-2010 period for many northeast continental shelf stocks. The decline in surfclam recruitment noted in the

2000s is consistent with this trend. The triennial survey protocol limits the number of decadal observations and, consequently, identification of regime shifts, as they might influence the relationship of broodstock and recruitment in surfclams, is unlikely.

Nonetheless, the time series addressed in this study carries through the late 1990s through early 2000s period during which time a regime shift has been described for a number of western Atlantic and Gulf of Mexico species (Lucey and Nye, 2010; Powell, 2017), observed also in the eastern Atlantic (Chaalali et al., 2013; Beukema et al., 2017), and which likely would impact a long-term relationship between broodstock and recruitment in surfclams.

A series of statistical analyses were performed designed to reveal the relationship between the spawning stock and recruitment over the 1982 to 2011 period, should it exist. Each of these failed to provide unequivocal evidence. These included basic correlation analysis, a by-quadrant analysis with the expectation that quadrants 1 and 3 (Figure 13, Table 10) would be disproportionately represented, and an analysis of mean first passage times, with the expectation that certain transitions would be more likely than others (Powell et al., 2009). For the latter, unlikely transitions were observed, but they varied between regions; whether this be the provenance of chance within a group of unrelated pairwise relationships or indicative of underlying regional differences cannot be presently determined.

Assuming from these afore-listed analyses that a relationship between recruitment and broodstock does not exist; that is, that SSB is relatively inconsequential in determining the temporal dynamics of recruitment, and setting aside the expected stochastic variability that can be anticipated to exist in such a dataset, a number of

characteristics of surfclams may foster a limited influence of SSB on recruitment. The discrepancy between the effective area occupied by the recruits and the market-size (≥ 120 mm) clams is noteworthy. Based on the SDF model, the estimated effective areas of small surfclams covered a more substantial area than that for market-size clams in all 5 regions. Post-settlement mortality appears to be an important causative agent in determining the spatial distribution of market-size clams as it certainly is the basis for much of this discrepancy. Thus, surfclams recruit over wide expanses but only in some locations do these individuals survive in large numbers. The consequence of small clams succumbing to natural mortality before entering the fishery is a decoupling between the abundance of recruits and that of market-size surfclams.

The clear inference from the differential in effective area between the recruits and the market-size clams is that recruitment occurs in suboptimal habitat lying inshore and offshore of the range boundary established by the larger clams. Results described in Chapter II showed that much of this additional area was located offshore of the range core, likely because mortality of recruits inshore occurred so early in life that the juveniles did not grow large enough to recruit to the survey dredge, as recruitment inshore is well-documented (MacKenzie et al., 1985; Chintala and Grassle, 2001; Ma et al., 2006; Quijón et al., 2007). Zhang et al. (2015, 2016) showed that recruitment inshore was a preferential outcome based on the net across-shelf flow on the continental shelf wherein offshore larval transport occurred less frequently over the spawning season than inshore transport. By inference, then, life spans of the offshore recruits are somewhat longer than that of inshore recruits, allowing some of them to grow large enough to recruit to the survey dredge. What environmental changes limit survival offshore have

not been identified; however, large scale modulations of the cold pool, which occur aperiodically, may be responsible (Sha et al. 2015). The inner wall of the cold pool defines the offshore boundary of the surfclam's range core.

Zhang et al. (2016) identified important interannual variability in the potential for recruitment based on interannual variability in the hydrodynamic regime throughout the study domain. Such variability, coupled with post-settlement mortality as a dominant determinant of recruitment success, favors the bet-hedging mode of life. For surfclams, the fact that recruitment cannot be specified from a stock-recruitment relationship is anticipated to result from a bet-hedging strategy in which the variance in fitness imposed by the environment produces unpredictable levels of recruitment in any given year (e.g., Stearns, 1976; Olofsson et al., 2009; Lovich et al., 2015). In this, surfclams are typical iteroparous bivalves (e.g., van der Meer et al., 2003; Beukema et al., 2010; Adkins et al., 2014). Although a Ricker model theoretically should be the bivalve norm, as competition for food at high abundance is well documented and can be expected to limit growth and reproduction (Grizzle and Lutz, 1989; Beukema and Cadée, 1996; Knights, 2012), market-size abundance regionally does not seem to reach levels sufficient for that outcome (Munroe et al., 2017). Thus, the Ricker model fails to describe the number of recruits based on a spawning stock biomass and bet-hedging minimizes the relationship at SSB levels below those engendering competition for food.

These previous ruminations address mechanisms militating against a consistent relationship between SSB and recruitment as a function of the dynamics of the ecosystem, including hydrodynamics and agents of mortality. In possible contrast, the surfclam stock has been judged to be near carrying capacity (NEFSC, 2017) in that SSB

is near the value anticipated to occur as a consequence of the balance between recruitment, growth, and natural mortality. This SSB level appears to be below that resulting in competition for food, as no evidence of such exists: constraints on growth in contrast appear to be a function of the influence of temperature on physiological processes that maintain clam maximum size near that which can be sustained by the individual's filtration rate and local food supply (Munroe et al., 2013, 2016). In this scenario, the variations in SSB and recruitment observed in the survey dataset may result from limitations in survey station density introducing biased outcomes, be they overestimates or underestimates, in each survey event. Obtaining unbiased survey SSB estimates for biomass dominants such as surfclams is inherently problematic (Powell and Mann, 2016; Powell et al., 2017). To what extent stochasticity limiting detection and determinism limiting existence of a relationship between SSB and recruitment cannot presently be ascertained.

Mean first passage times may not be adequate to describe the relationship between stock and recruitment, but they may be informative to the point of identifying certain unlikely transitions. The New Jersey region, for instance, has some transitions that are predicted to take 16 surveys (i.e. quadrant 4 to quadrant 2) before they occur and with surveys typically being three years apart, that is a period of time that may not have occurred in the history of the surfclam fishery (Table 9). The first passage times for the Delmarva region on the other hand show no clear difference in transitions between states. The Delmarva region is different from the other regions in that it is primarily a sink for incoming larvae while the other four regions are sources and sinks (Zhang et al., 2015). Thus, the Delmarva region draws recruits from a large upstream region and spawns

larvae a large fraction of which are transported across the southern boundary where survival is highly unlikely. Both may enhance the chanciness of any particular recruitment event relative to the apparent SSB supporting it.

Any recruitment index derived from the current survey will be limited in use due to a bias in mortality of juveniles at and beyond the range boundaries and the inherent long-term and interannual variability in recruitment influenced by changing hydrodynamics and post-settlement mortality. Interannual variability in recruitment is an important source of uncertainty (Rothschild et al., 2005) and warming bottom waters driving the surfclams into new habitat may be making this interaction between recruits and spawning stock biomass more complex (Weinberg, 2005). What is apparent from this study is that an easily resolved relationship between SSB and recruitment does not exist and that its absence is readily understood by the dynamics of a stock that exists over a broad region of the continental shelf and for which bet-hedging is an evolutionary adaptation to the uncertainty in recruitment success imposed by the environment of the continental shelf. What can then be inferred is that a recruitment index obtained from a survey is unlikely to routinely provide a useful forecast of future market-size abundance.

Of perhaps greater interest is the much larger effective areas for the recruits relative to the adult population. This phenomenon may be typical of bivalves, but studies that examine a large geographic region which would be needed to address this possibility are rare. This larger footprint for the recruits would appear at first glance to waste larvae, although a surfeit of larvae almost certainly exists. In reality, it continuously positions the species advantageously in response to unpredictable environmental changes in time and space. One consequence is the relatively rapid shift in range that has been observed in

comparison to the species' life span, a shift promoted by the extended effective area of the recruits. Whereas, the broader footprint of the recruits assures that a prediction of SSB from recruitment is unlikely to be achieved, the distribution of the recruits provides important information on the resiliency of the stock to climate change by identifying the potential of outlying regions to support future expansions of the stock.

CHAPTER IV – CONCLUSIONS

While considerable research has been reported on the biology, distribution, and stock assessment of Atlantic surfclams, limited information is available on how the distribution has changed over time, the spatial differences between small versus market-size clams, and the predictability of future recruitment based on current stock. That surfclams have been shifting offshore over the past few decades is well-documented. Declines in the number of surfclams in the southern portion of the range have been attributed to climate change as the fishery does not assert enough pressure on the population as a whole to account for the long-term changes in distribution and abundance. By understanding the changes in the distribution over the history of the stock assessment as well as the relationship between the recruits and the spawning stock biomass, valuable information can be obtained to better inform management of this species.

Chapter II provides a comprehensive description of changes occurring across the range of the surfclam as warming continues to influence the species' distribution. The VtMR for surfclams have declined from the 1980's to the present in all assessed regions. In contrast, the VtMR rose with increasing clam size. A Taylor's Power Law analysis for each of the regions corroborated the results from the VtMR, establishing that surfclams are highly patchy across their range. The patchy proclivity of the clams varied significantly regionally, with regions supporting the bulk of the stock characterized by significantly higher degrees of patchiness as demonstrated by a higher exponent for the power law. A Spatial Distribution Function model also provided corroborative results of

declining patchiness over time and the model analysis supports previous inferences from survey data that the range of the surfclam is shifting offshore. Future climate predictions point towards an increase in bottom water temperatures that should continue to drive this trend (Saba et al., 2016). The Spatial Distribution Function model analysis buttresses the hypothesis that warming of Mid-Atlantic continental shelf bottom waters is driving the surfclam stock into new habitat and extirpating the surfclams from nearshore areas. The range core for the large surfclams has shifted offshore to a greater degree than that of the small surfclams in the Delmarva, New Jersey, and Georges Bank regions. This is primarily due to the extended footprint of the small clams which encompasses much of the continental shelf and within which the range core of the larger clams is repositioned. The decline in patchiness across the entire stock is informative when considering the decline in landings per unit effort (LPUE). Although the LPUE for local populations could be impacted by the fishery, the decline in LPUE for the entire stock is likely an effect of warming bottom waters as the VtMR has declined over the whole of the stock while some regions such as Georges Bank have been fished little or not at all. This decline in LPUE will result in a need for relocation of vessels and processing plants to counteract costs associated with travel time to fishing grounds. 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 new core of the range.

Chapter III examined the stock-recruitment relationship for the Atlantic surfclam. The effective area occupied by small surfclams was consistently much greater than that for large (≥ 120 mm) surfclams. Three independent statistical analyses of the stock-recruitment relationship found little evidence of a significant association in any of the 5

regions, suggesting that factors besides spawning stock biomass are primary determinants of recruitment success. The recruitment index obtained from the NEFSC survey is unlikely to be useful in evaluating the status of the stock due to a bias in mortality of juveniles inshore and the extended footprint of the recruits which assures that an indeterminate portion of them will survive to market size. Interannual variability in recruitment is an important source of uncertainty and warming bottom waters driving the surfclams into new habitat also obfuscates any underlying relationship between recruits and spawning stock biomass. The wider distribution of recruits relative to the fishable stock, however, positions the species well to respond to changing bottom water temperatures as Mid-Atlantic warming continues.

The research in this thesis provides substantial information about Atlantic surfclam spatial distribution, incorporating models to observe changes over time, and the relationship between recruits and spawning stock biomass that is essential to the management of the species. This migration of surfclams north and offshore could result in reaching a critical threshold in which the surfclams have nowhere to go due to uninhabitable areas seriously impacting the population. This in turn will impact the fisheries as the need to move the fishery and vessels further north to follow the migration of surfclams becomes increasingly difficult. Combining a spatial analysis with a stock recruitment analysis creates a unique framework in which to observe changes in the surfclam population and provides information for management of the species.

APPENDIX A - TABLES

Table 1

Variance-to-mean ratios for each decade by size class for each region.

Region	Decade	Size Class	Ratio	Region	Decade	Size Class	Ratio
Delmarva	1980	64	3201.99	Long Island	1980	64	12.35
		80	6207.03			80	5.62
		93	1488.18			93	5.05
		104	708.02			104	10.80
		120	420.17			120	34.54
	1990	64	32.36		1990	64	9.94
		80	75.66			80	3.93
		93	65.37			93	3.70
		104	507.36			104	15.63
		120	248.36			120	57.01
	2000	64	23.93		2000	64	3.64
		80	25.72			80	2.42
		93	20.09			93	1.57
		104	36.83			104	5.04
		120	65.30			120	82.80
New Jersey	1980	64	31.12	S. New England	1980	64	1.19
		80	32.70			80	2.65
		93	120.30			93	4.13
		104	562.80			104	4.58
		120	258.59			120	77.60
	1990	64	72.06		1990	64	4.46
		80	29.96			80	3.99
		93	39.02			93	3.44
		104	280.21			104	2.88
		120	255.38			120	69.30
	2000	64	8.03		2000	64	0.26
		80	8.18			80	1.58
		93	4.53			93	1.15
		104	8.85			104	7.83
		120	55.65			120	22.28
Georges Bank	1980	64	248.15				
		80	272.28				
		93	139.71				
		104	169.57				
		120	564.85				
	1990	64	16.43				
		80	82.15				
		93	154.90				
		104	204.50				
		120	360.98				
	2000	64	4.12				
		80	1.73				
		93	2.59				
		104	29.64				
		120	144.96				

Regions are Delmarva, New Jersey, Long Island, Southern New England, and Georges Bank. A ratio greater than 1 indicates a patchy distribution.

Table 2

ANOVA and post-hoc analyses for the variance-to-mean ratios by size class and decade for each region.

ANOVA				Pairwise Comparisons			
Region	Factor	DF	P-value	Region	Contrast	DF	P-value
Delmarva	Decade	2	0.011*	Delmarva	1980 - 1990	177	0.019*
	Class	4	0.956		1980 - 2000	177	0.006*
	Decade*Class	8	0.938		1990 - 2000	177	0.673
New Jersey	Decade	2	0.004*	New Jersey	1980 - 1990	347	0.355
	Class	4	<0.001*		1980 - 2000	347	0.017*
	Decade*Class	8	0.104		1990 - 2000	347	0.001*
Long Island	Decade	2	0.441	Long Island	64 - 80 mm	347	0.978
	Class	4	0.015*		64 - 93 mm	347	0.773
	Decade*Class	8	0.645		64 - 104 mm	347	0.009*
S. New England	Decade	2	0.701		64 - 120 mm	347	0.0001*
	Class	4	0.002*		80 - 93 mm	347	0.752
	Decade*Class	8	0.741		80 - 104 mm	347	0.009*
Georges Bank	Decade	2	0.082		80 - 120 mm	347	0.0001*
	Class	4	<0.001*		93 - 104 mm	347	0.024*
	Decade*Class	8	0.829		93 - 120 mm	347	0.0001*
					104 - 120 mm	347	0.052
				S. New England	64 - 80 mm	NA	NA
					64 - 93 mm	73	0.968
					64 - 104 mm	73	0.898
					64 - 120 mm	73	0.023*
					80 - 93 mm	NA	NA
					80 - 104 mm	NA	NA
					80 - 120 mm	NA	NA
					93 - 104 mm	73	0.864
					93 - 120 mm	73	0.018*
					104 - 120 mm	73	0.029*
				Georges Bank	64 - 80 mm	61	0.973
					64 - 93 mm	61	0.934
					64 - 104 mm	61	0.952
					64 - 120 mm	61	0.005*
					80 - 93 mm	61	0.907
					80 - 104 mm	61	0.926
					80 - 120 mm	61	0.005*
					93 - 104 mm	61	0.984
					93 - 120 mm	61	0.008*
					104 - 120 mm	61	0.010*
					64 - 80 mm	230	0.598
					64 - 93 mm	230	0.578
					64 - 104 mm	230	0.108
					64 - 120 mm	230	0.0001*
					80 - 93 mm	230	0.951
					80 - 104 mm	230	0.281
					80 - 120 mm	230	0.0002*
					93 - 104 mm	230	0.338
					93 - 120 mm	230	0.0004*
					104 - 120 mm	230	0.007*

Regions are Delmarva, New Jersey, Long Island, Southern New England and Georges Bank. ANOVA results indicate a significant effect across decades for the Delmarva and New Jersey regions and a significant effect for size classes of all regions except the Delmarva region. Pairwise comparisons represent Least Square Mean analyses demonstrating differences between size classes or decades within each region. NA's for pairwise comparisons for Long Island re due to limited data for the smaller size classes.

Table 3

ANOVA and post-hoc analyses for the variance-to-mean ratios by region and decade for all regions combined.

ANOVA				Pairwise Comparisons			
Region	Factor	DF	P-value	Region	Contrast	DF	P-value
All Regions	Region	4	0.0002*	All Regions			
	Decade	2	0.0005*		1980 - 1990	954	0.078
	Region*Decade	8	<0.001*		1980 - 2000	954	0.020*
					1990 - 2000	954	0.400
					DMV - LI	954	0.003*
					DMV - SNE	954	0.004*
					DMV - GBK	954	0.001*
					DMV - NJ	954	0.0003*
					LI - SNE	954	0.931
					LI - GBK	954	0.449
					LI - NJ	954	0.406
					SNE - GBK	954	0.512
					SNE - NJ	954	0.469
					GBK - NJ	954	0.958

Regions are Delmarva (DMV), New Jersey (NJ), Long Island (LI), Southern New England (SNE), and Georges Bank (GBK).

ANOVA results indicate a significant effect across decades and for regions including a significant interaction effect. Pairwise comparisons represent Least Square Mean analyses demonstrating differences between decades and regions.

Table 4

Exponents (beta) of the Taylor's Power Law listed by decade and size class for each region.

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

Regions are Delmarva, New Jersey, Long Island, Southern New England, and Georges Bank. A beta value greater than 1 indicates a patchy distribution. NA's indicate limited data for certain size classes and decades.

Table 5

ANCOVA and post-hoc analyses for cases with significant interaction terms comparing log-variance to log-mean by size class and decade for each region.

ANCOVA				Pairwise Comparisons			
Region	Factor	DF	P-value	Region	Contrast	DF	P-value
Delmarva	LogMean	1	<0.001*	New Jersey	64 - 80 mm	352	0.160
	Class	4	0.516		64 - 93 mm	352	0.120
	LogMean*Class	4	0.375		64 - 104 mm	352	0.041*
	LogMean	1	<0.001*		64 - 120 mm	352	0.025*
	Decade	2	0.351		80 - 93 mm	352	0.878
	LogMean*Decade	2	0.136		80 - 104 mm	352	0.545
New Jersey	LogMean	1	<0.001*	S. New England	80 - 120 mm	352	0.248
	Class	4	0.041*		93 - 104 mm	352	0.657
	LogMean*Class	4	0.001*		93 - 120 mm	352	0.299
	LogMean	1	<0.001*		104 - 120 mm	352	0.458
	Decade	2	0.060		64 - 80 mm	66	0.079
	LogMean*Decade	2	0.063		64 - 93 mm	66	0.919
Long Island	LogMean	1	0.009*		64 - 104 mm	66	0.260
	Class	4	0.069		64 - 120 mm	66	0.694
	LogMean*Class	4	0.066		80 - 93 mm	66	0.041*
	LogMean	1	<0.001*		80 - 104 mm	66	0.417
	Decade	2	0.186		80 - 120 mm	66	0.075
	LogMean*Decade	2	0.082		93 - 104 mm	66	0.172
S. New England	LogMean	1	<0.001*		93 - 120 mm	66	0.568
	Class	4	0.025*		104 - 120 mm	66	0.326
	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	0.120				
	LogMean	1	<0.001*				
	Decade	2	0.781				
	LogMean*Decade	2	0.825				

Regions are Delmarva, New Jersey, Long Island, Southern New England, and Georges Bank. Significant interaction terms indicate a change in the slope of the Taylor's Power Law and therefore the exponent beta (β) of the power law.

Table 6

ANCOVA and post-hoc analyses for cases with significant interaction terms comparing log-variance to log-mean by size class across regions.

ANCOVA				Pairwise Comparisons			
Size Class	Factor	DF	P-value	Size Class	Contrast	DF	P-value
64-mm	LogMean	1	<0.001*	104-mm			
	Region	4	0.969		DMV - GBK	176	0.960
	LogMean:Region	4	0.518		DMV - LI	176	0.003*
80-mm					DMV - NJ	176	0.238
	LogMean	1	<0.001*		DMV - SNE	176	0.025*
	Region	4	0.031*		GBK - LI	176	0.002*
	LogMean:Region	4	0.313		GBK - NJ	176	0.186
93-mm					GBK - SNE	176	0.020*
	LogMean	1	<0.001*		LI - NJ	176	0.016*
	Region	4	0.025*		LI - SNE	176	0.900
	LogMean:Region	4	0.184		NJ - SNE	176	0.091
104-mm				120-mm			
	LogMean	1	<0.001*		DMV - GBK	202	0.648
	Region	4	0.273		DMV - LI	202	0.001*
	LogMean:Region	4	0.024*		DMV - NJ	202	0.908
120-mm					DMV - SNE	202	0.104
	LogMean	1	<0.001*		GBK - LI	202	0.002*
	Region	4	0.184		GBK - NJ	202	0.488
	LogMean:Region	4	0.014*		GBK - SNE	202	0.192
					LI - NJ	202	0.0001*
					LI - SNE	202	0.094
					NJ - SNE	202	0.045

Regions are Delmarva, New Jersey, Long Island, Southern New England, and Georges Bank. Significant interaction terms indicate a change in the slope of the Taylor's power law and therefore the exponent beta (β) of the power law.

Table 7

The connectivity data estimated allocation percentages for each region.

Region	DMV		NJ		LI		SNE		GBK	
	R	S	R	S	R	S	R	S	R	S
Delmarva	0.3218	0.3138	-	-	-	-	-	-	-	-
New Jersey	0.4698	0.4698	0.4581	0.4702	-	-	-	-	-	-
Long Island	0.0625	0.0646	0.6607	0.5298	0.2768	0.9894	-	-	-	-
S. New England	-	-	-	-	0.3333	0.0106	0.6667	1.0000	-	-
Georges Bank	-	-	-	-	-	-	-	-	1.0000	1.0000

Regions are Delmarva (DMV), New Jersey (NJ), Long Island (LI), Southern New England (SNE), and Georges Bank (GBK). The estimated SSB (kg) from each region was allocated into portions representing the percentage of said SSB (kg) responsible for larvae released (R) into a downstream region or remaining in the origin region based on the larval connectivity matrix (see Zhang et al., 2015 figure 8-B). The allocated portion of SSB (kg) was then portioned into the percentage of larvae that settled (S) in the downstream region or origin region.

Table 8

Estimated effective area (km^2 ; $\times 1000$) for recruits and larger (spawning stock biomass or SSB) surfclams in each region.

Region	Size	Year												
		1982	1983	1984	1986	1989	1992	1994	1997	1999	2002	2005	2008	2011
DMV	Recruits	16.09	12.79	0.43	16.23	18.52	19.96	12.70	15.41	15.66	16.03	17.33	19.03	16.68
	SSB	7.96	6.62	5.99	5.49	7.23	7.29	7.12	5.81	7.56	7.82	7.08	6.33	7.58
NJ	Recruits	7.75	10.23	8.08	8.23	7.85	13.55	9.98	12.78	10.03	15.39	13.39	13.66	13.81
	SSB	5.71	6.79	6.57	8.01	7.49	8.67	8.23	9.70	11.20	10.46	10.47	11.06	9.27
LI	Recruits	7.37	7.37	6.63	8.57	6.98	7.79	8.88	7.65	4.75	6.49	6.77	6.59	9.35
	SSB	2.96	3.45	3.48	3.42	3.45	3.51	3.53	3.45	3.46	3.44	3.49	3.50	3.48
SNE	Recruits	9.91	8.28	7.91	10.50	7.61	8.13	8.82	7.83	9.78	9.42	7.90	8.48	9.81
	SSB	2.27	1.84	1.86	1.90	1.87	1.80	1.86	1.87	1.89	1.88	1.82	1.83	1.80
GBK	Recruits	17.55	19.54	19.87	1.65	19.46	17.70	18.82	15.31	17.59	18.94	19.72	19.38	16.61
	SSB	4.44	7.20	7.34	6.65	3.10	7.85	5.10	6.72	8.79	9.78	8.46	6.80	8.10

Regions are Delmarva (DMV), New Jersey (NJ), Long Island (LI), Southern New England (SNE), and Georges Bank (GBK).

Table 9

The number of recruits ($\times 10,000$) and the spawning stock biomass (SSB) (kg; $\times 10,000$)

for each region.

Year	DMV		NJ		LI		SNE		GBK	
	Recruits	SSB	Recruits	SSB	Recruits	SSB	Recruits	SSB	Recruits	SSB
1982	45,637	5,439	31,521	2,981	3,865	158	8,356	596	139,852	347
1983	28,946	5,093	34,191	3,065	3,915	24	5,927	1,321	443,142	60
1984	942	5,872	27,904	3,258	4,732	133	7,352	1,210	26,730	2,333
1986	19,452	7,027	23,940	4,160	21,897	113	16,522	542	2,890	5,983
1989	35,884	5,051	31,081	3,456	28,978	204	18,853	576	53,621	5,976
1992	267,394	5,810	99,447	3,815	7,656	202	3,895	468	60,886	4,641
1994	85,392	14,781	33,657	10,012	9,055	319	21,799	170	70,739	13,137
1997	27,529	17,192	19,673	11,584	22,430	213	11,465	1,346	37,683	13,196
1999	82,215	11,074	31,323	8,150	4,579	572	18,018	649	42,059	6,899
2002	15,839	7,841	12,715	5,274	5,264	128	1,947	495	29,082	3,639
2005	21,705	2,728	20,147	2,534	5,342	485	5,076	3	-	-
2008	129,253	2,662	43,082	2,135	8,592	192	3,110	368	22,059	12,543

Regions are Delmarva (DMV), New Jersey (NJ), Long Island (LI), Southern New England (SNE), and Georges Bank (GBK). The Georges Bank region was not sampled in 2005.

Table 10

Stock-recruitment observations classified into quadrants based on division by the median recruits and median spawning stock biomass.

Region	S1	S2	S3	S4
	low stock/ low recruitment	low stock/ high recruitment	high stock/ high recruitment	high stock/ low recruitment
Delmarva	2	4	2	4
New Jersey	3	3	3	3
Long Island	4	2	4	2
S. New England	4	2	4	2
Georges Bank	4	2	3	2

See Figure 13 for quadrant definitions.

Table 11

Chi-square test on stock-recruitment observations classified into quadrants.

Region	DF	P-value
Delmarva	3	0.721
New Jersey	3	1.000
Long Island	3	0.721
S. New England	3	0.721
Georges Bank	3	0.484

In no case was the distribution of observations between quadrants significantly different from the expectation that all observations are distributed uniformly between the four quadrants with no existing relationship between the stock and recruits. See Figure 13 and Table 10 for details on quadrant divisions.

Table 12

Mean first passage times for the Delmarva, New Jersey, Long Island, Southern New England and Georges Bank regions.

a. Delmarva				
Quadrant	1	2	3	4
Mean first passage time (survey)				
1 →	5.50	3.00	5.33	2.67
2 →	4.33	3.67	4.17	3.33
3 →	5.67	5.00	5.50	1.00
4 →	4.67	4.00	4.50	2.75
b. New Jersey				
Quadrant	1	2	3	4
Mean first passage time (survey)				
1 →	5.50	9.00	8.00	4.00
2 →	2.00	5.50	10.00	6.00
3 →	8.50	17.50	3.67	1.50
4 →	7.00	16.00	4.00	2.75
c. Long Island				
Quadrant	1	2	3	4
Mean first passage time (survey)				
1 →	5.75	3.33	4.33	4.50
2 →	12.00	7.67	1.00	5.00
3 →	11.00	6.67	1.92	4.00
4 →	7.00	2.67	3.67	5.75
d. S. New England				
Quadrant	1	2	3	4
Mean first passage time (survey)				
1 →	2.50	3.00	4.00	16.00
2 →	4.50	5.00	1.00	13.00
3 →	3.50	4.00	3.75	12.00
4 →	6.50	2.00	3.00	7.50
e. Georges Bank				
Quadrant	1	2	3	4
Mean first passage time (survey)				
1 →	4.67	5.00	14.00	1.00
2 →	4.33	3.50	9.00	3.00
3 →	4.67	5.00	14.00	1.00
4 →	3.67	4.00	13.00	2.33

The time it takes for one quadrant to transition to another quadrant are given in terms of surveys, not years. Surveys are typically 3 years apart. A high transition time for remaining in a quadrant (i.e. 1 to 1) indicates a higher probability of a transition to another quadrant than remaining in original quadrant. Arrows indicate trajectories between quadrants.

APPENDIX B – FIGURES

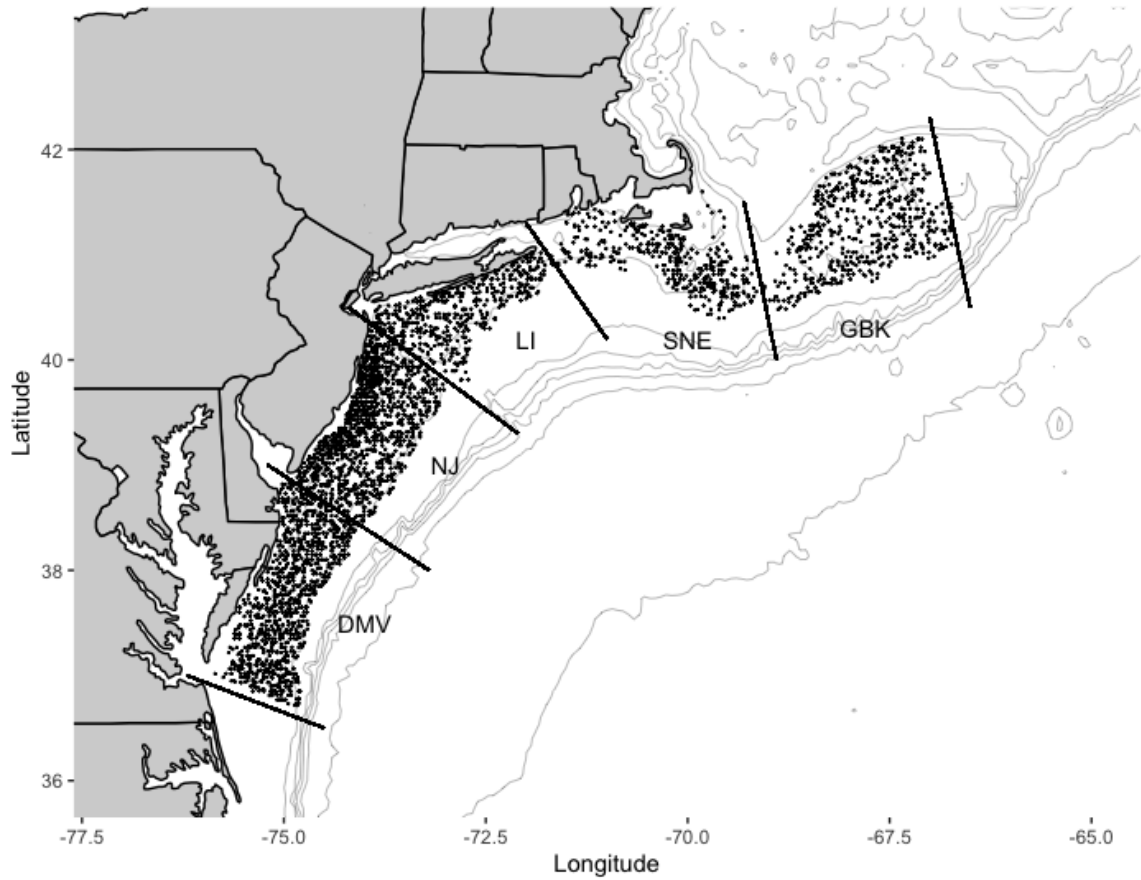


Figure 1. Tow locations for the Atlantic surfclam stock assessment survey from 1982 to 2011.

Solid lines delineate the regions of interest (DMV = Delmarva, NJ = New Jersey, LI = Long Island, SNE = Southern New England, GBK = Georges Bank).

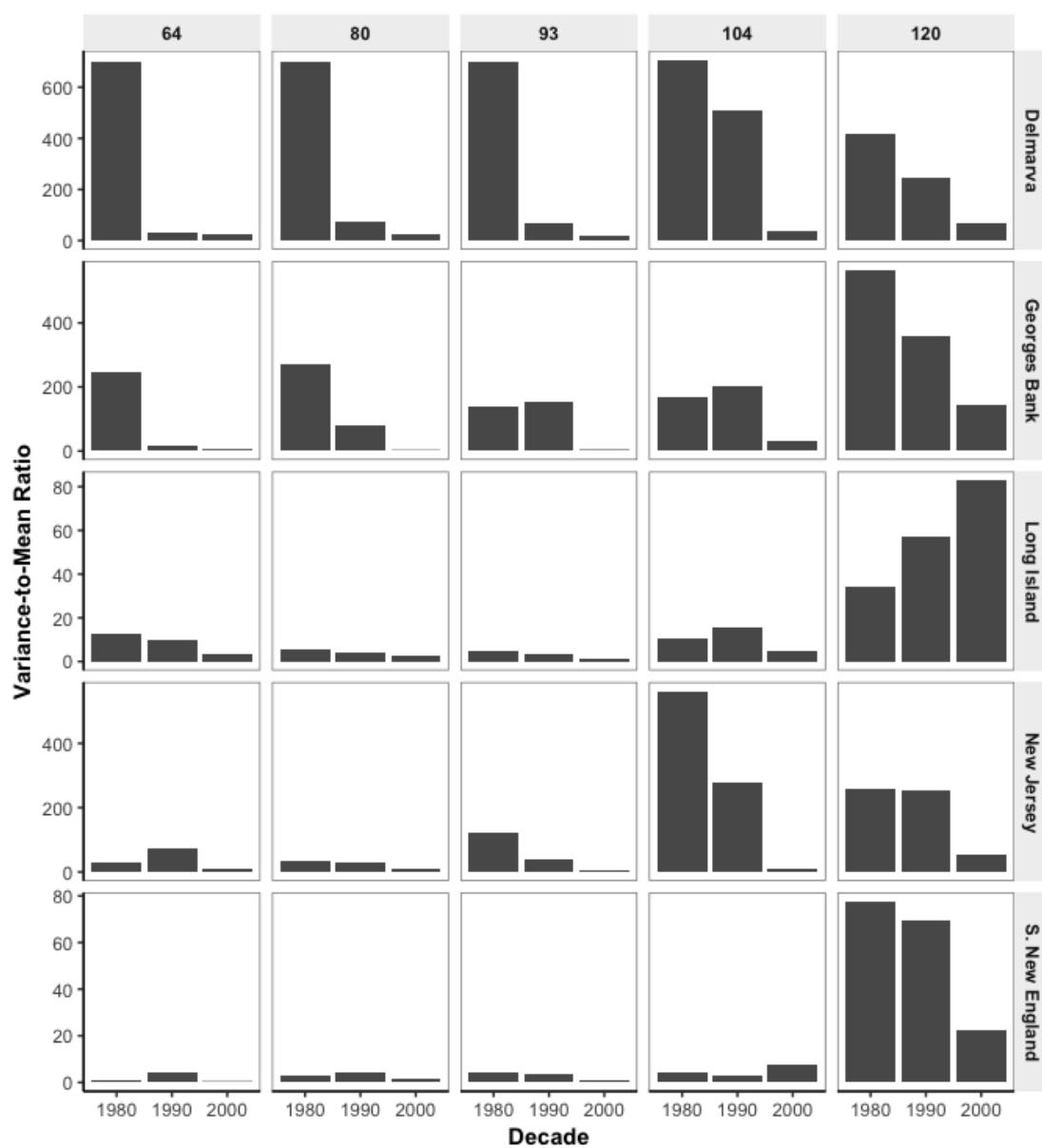


Figure 2. Variance-to-mean ratios for each size class by decade for each region.

Regions are Delmarva, New Jersey, Long Island, Southern New England, and Georges Bank. A ratio greater than 1 indicates a patchy distribution.

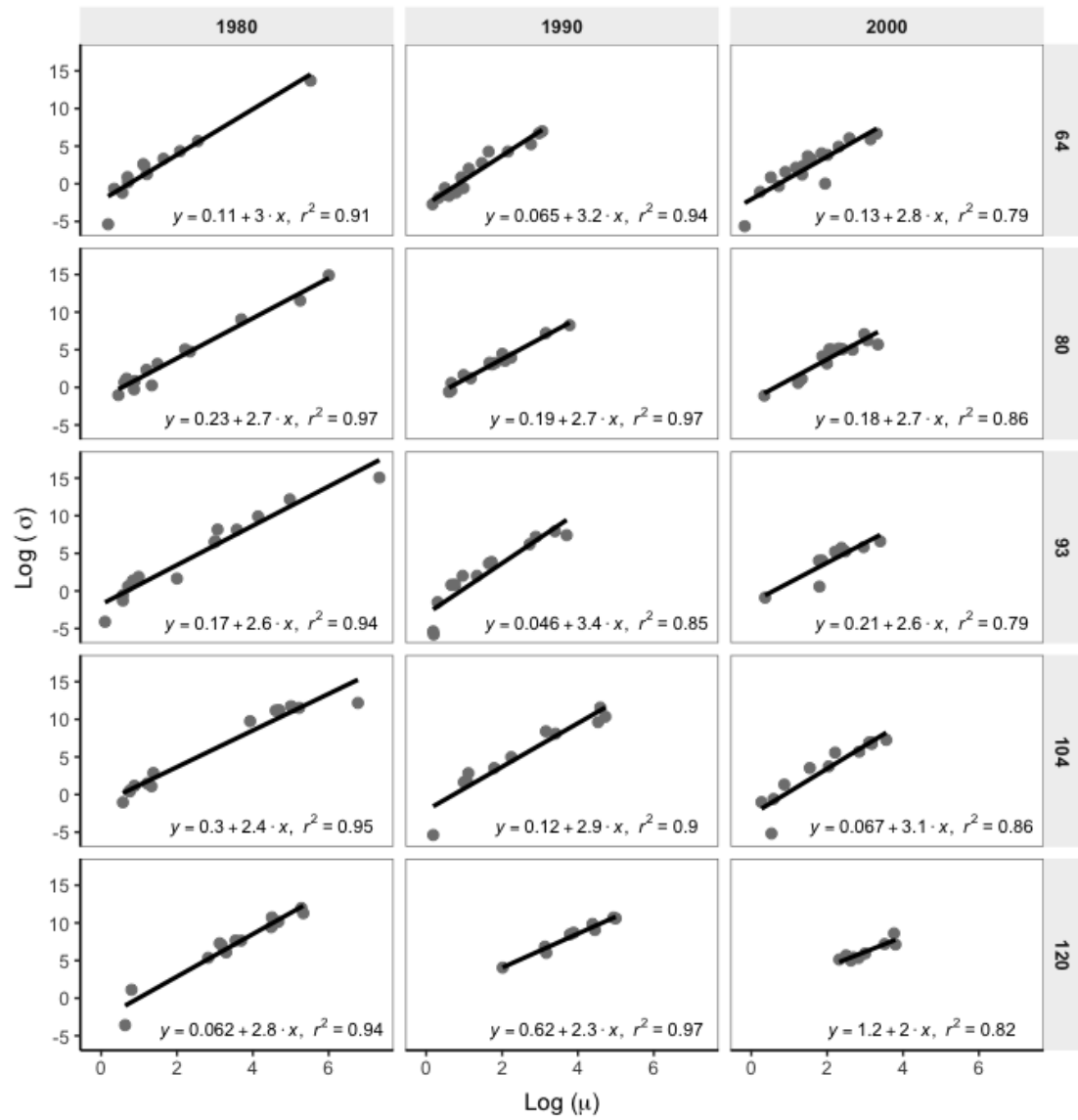


Figure 3. Examples of Taylor's Power Law relationship between log-variance (σ) and log-mean (μ) for the Delmarva region.

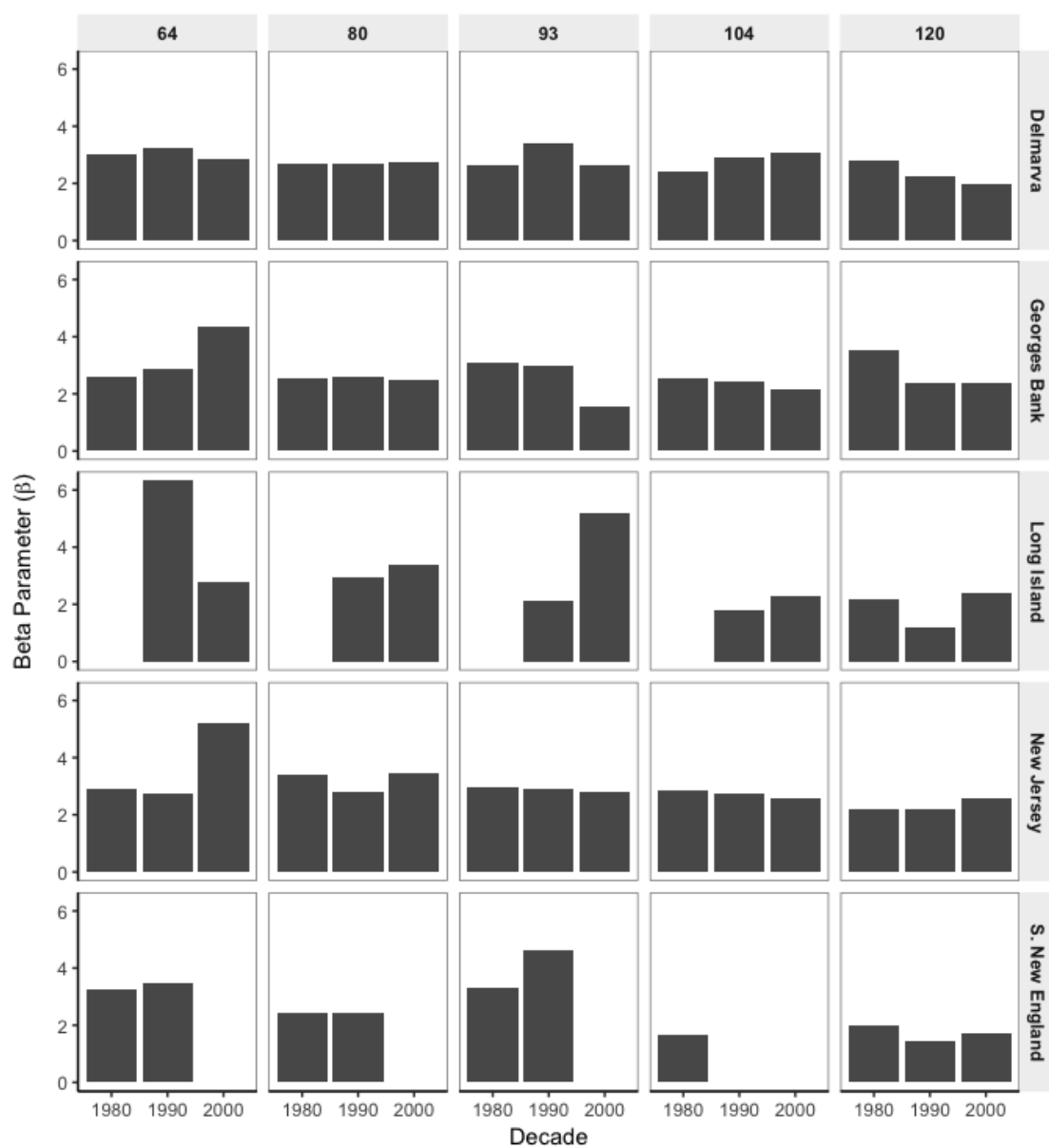


Figure 4. Taylor's power law beta parameters for each size class by decade for each region.

Regions are Delmarva, New Jersey, Long Island, Southern New England, and Georges Bank. A beta greater than 1 indicates a patchy distribution.

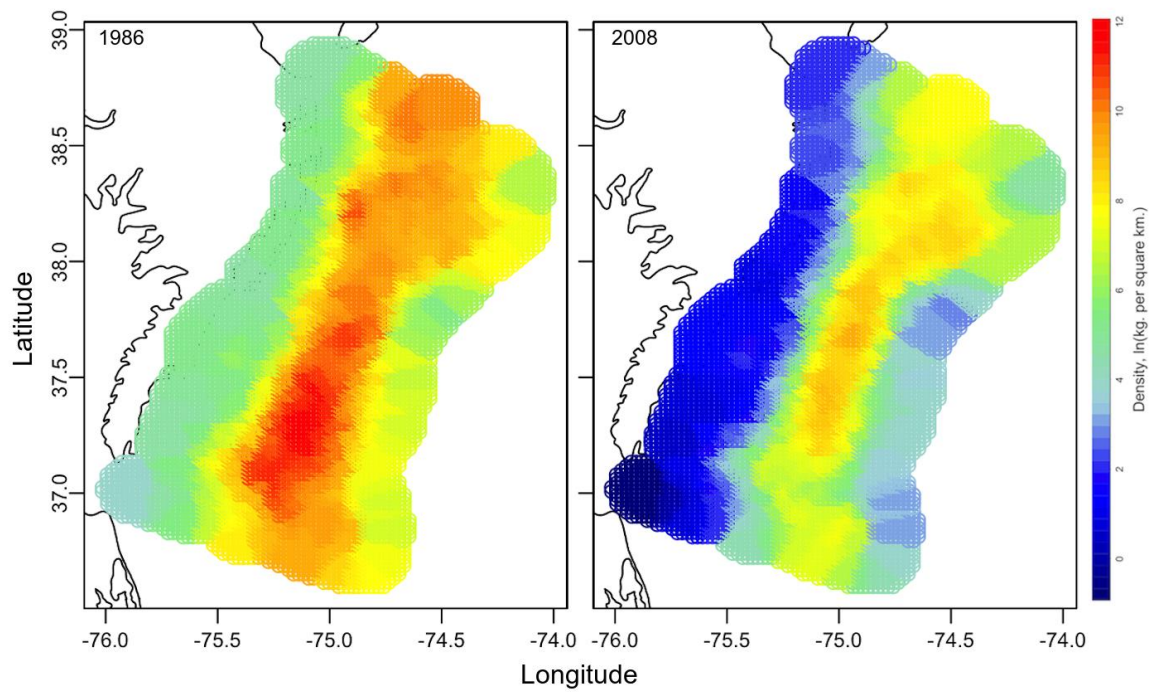


Figure 5. Density ($\log \text{ kg per km}^2$) of market-size ($\geq 120\text{-mm}$) clams in Delmarva for survey years 1986 and 2008.

The density is lower in 2008 than in 1986 over nearly the entirety of the Delmarva region indicative of a movement of the surfclam stock offshore and a reduction in patchiness.

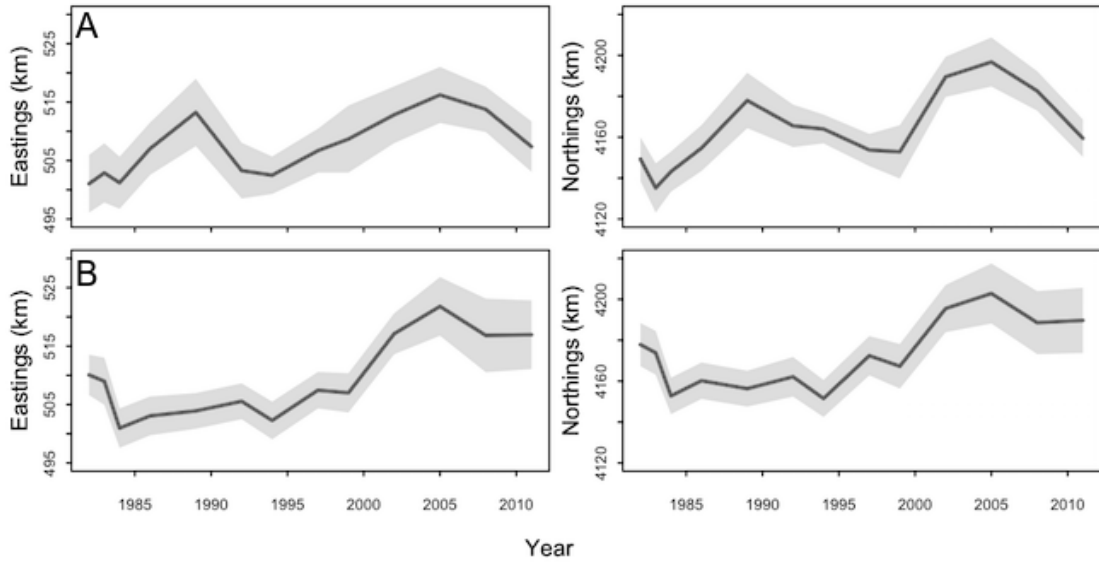


Figure 6. Center of distribution of the Atlantic surfclam population off Delmarva.

(A) The eastings and northings of 64-mm surfclams indicate a slight movement north and offshore. (B) The eastings and northings of the market-size (≥ 120 -mm) clams clearly indicate a shift north and offshore, the most rapid shift during the 1990s-2000s decadal transition. The black line is the maximum-likelihood estimate and the grey shaded area is ± 1 standard error.

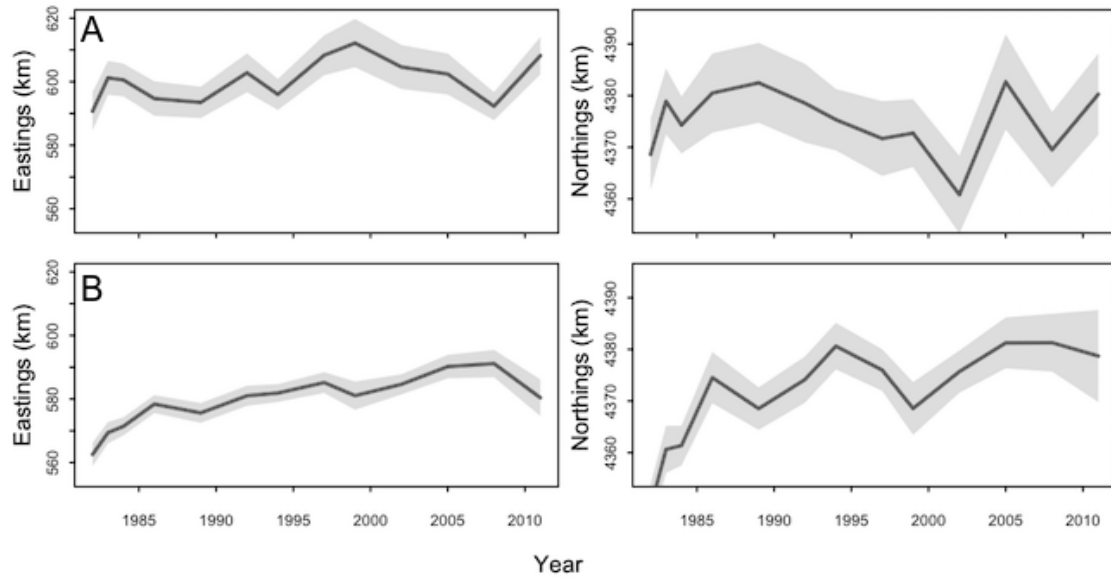


Figure 7. Center of distribution of the Atlantic surfclam population off New Jersey.

(A) The eastings and northings of 64-mm surfclams indicate relatively little change in range center over time. (B) The eastings and northings of the market-size (≥ 120 -mm) clams clearly indicate a significant shift north and offshore. The black line is the maximum-likelihood estimate and the grey shaded area is ± 1 standard error.

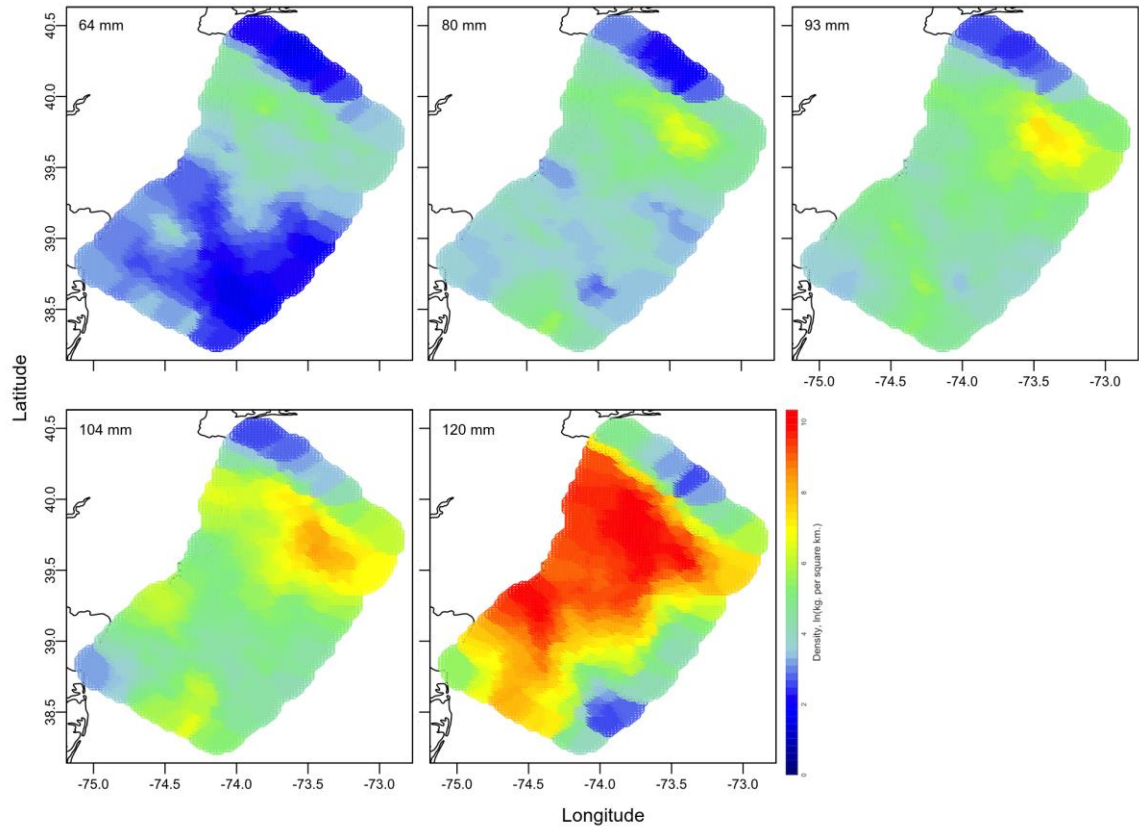


Figure 8. Density maps (log kg per km²) comparing the distribution of the size classes of surfclams off New Jersey during the 2000s.

This demonstrates a significantly higher aggregation (patchiness) in the market-size (≥ 120 -mm) clams.

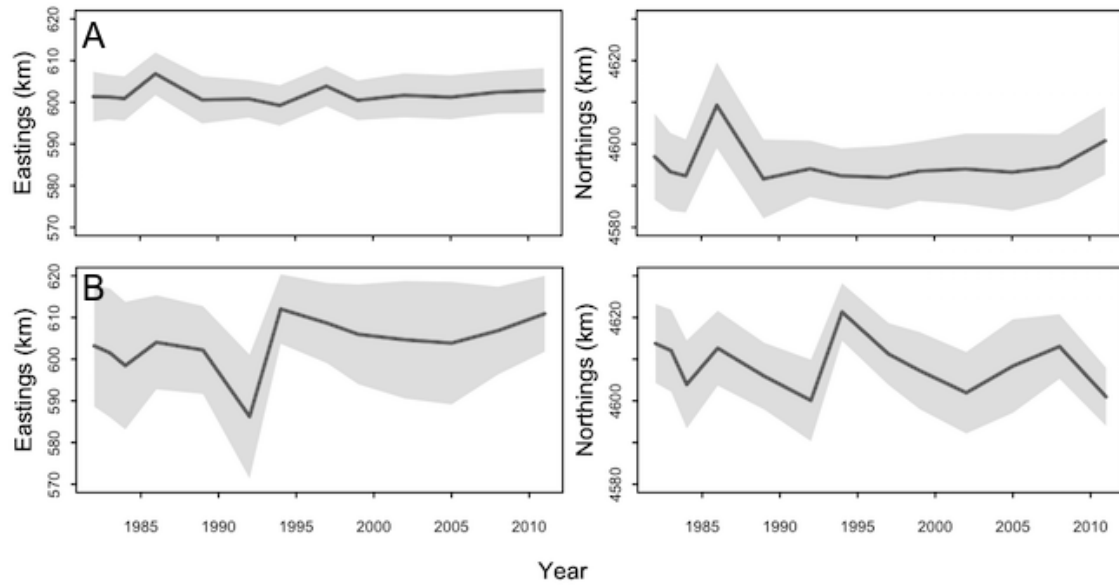


Figure 9. Center of distribution of Atlantic surfclams on Georges Bank.

(A) The eastings and northings of 64-mm surfclams. The distribution of the 64-mm surfclams has fluctuated about a single easterly and northerly axis. (B) The eastings and northings of the market-size (≥ 120 -mm) clams suggest a modest shift east and south. The black line is the maximum-likelihood estimate and the grey shaded area is ± 1 standard error.

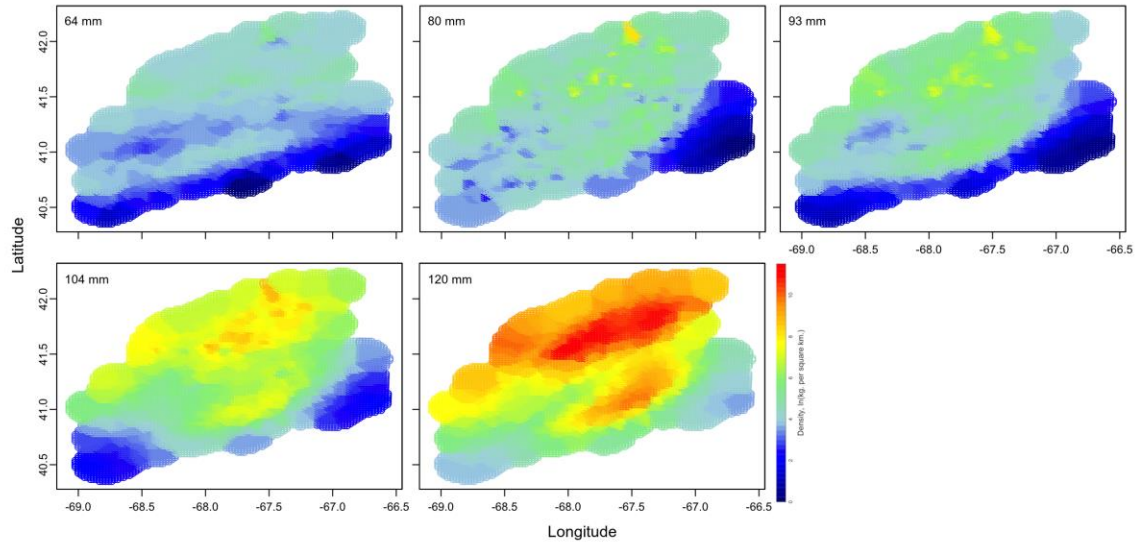


Figure 10. Density maps (log kg per km²) comparing the distribution of the five size classes of surfclams on Georges Bank during the 2000s.

This demonstrates a significantly higher patchiness in the market-size (≥ 120 -mm) clams. The southerly movement of the market-size (≥ 120 -mm) clams identified in Figure 9 is observed in the increased density of clams along the southeastern portion of the bank.

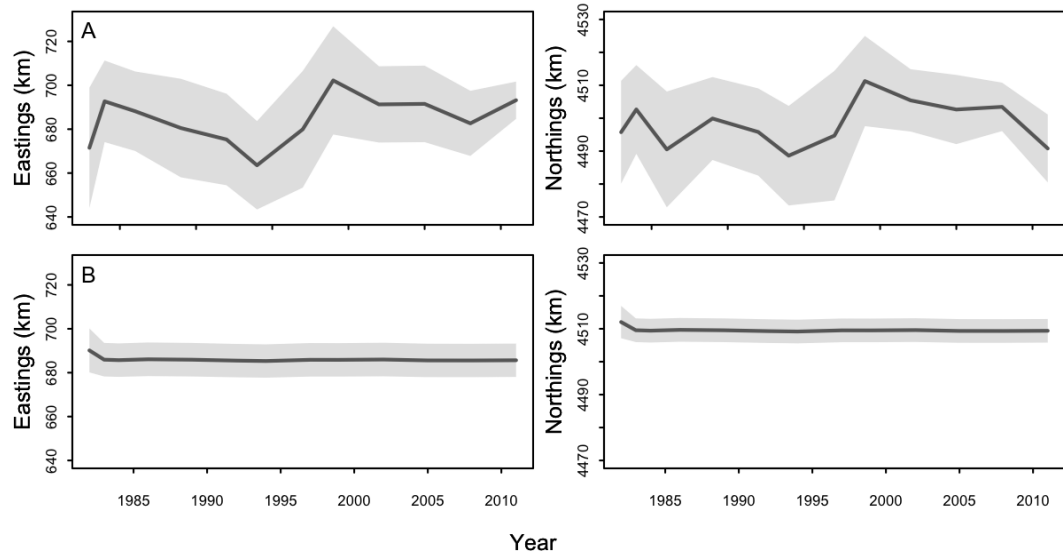


Figure 11. Center of distribution of Atlantic surfclams off Long Island.

(A) The eastings and 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). (B) The eastings and northings of the market-size (≥ 120 -mm) clams also showing a stable axis over time. The black line is the maximum-likelihood estimate and the grey shaded area is ± 1 standard error.

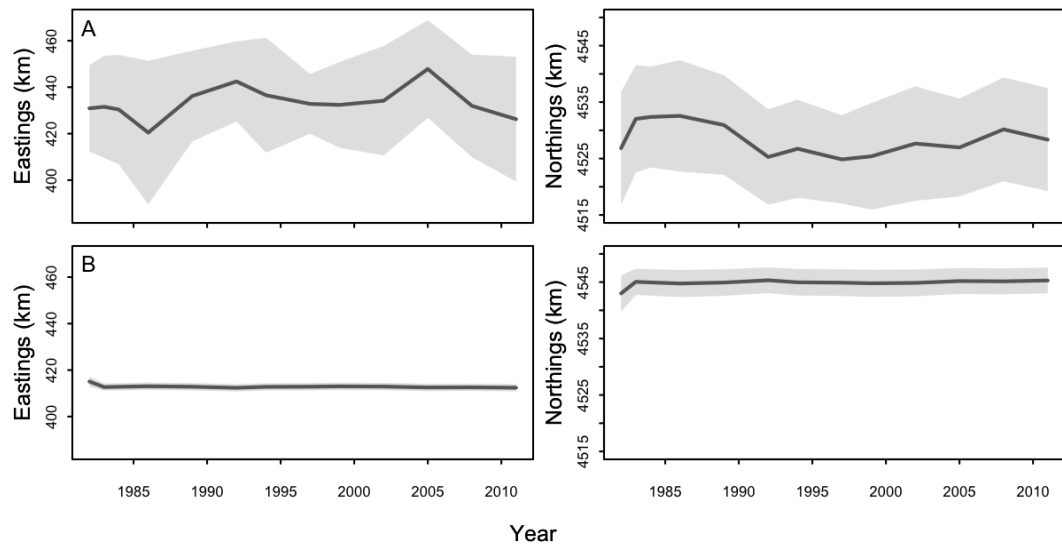


Figure 12. Center of distribution of Atlantic surfclams off Southern New England.

(A) The eastings and northings of 64-mm surfclams. The distribution of the 64-mm surfclams has fluctuated about a stable axis (B) The eastings and northings of the market-size (≥ 120 -mm) clams also indicate a stable range center. The black line is the maximum-likelihood estimate and the grey shaded area is ± 1 standard error.

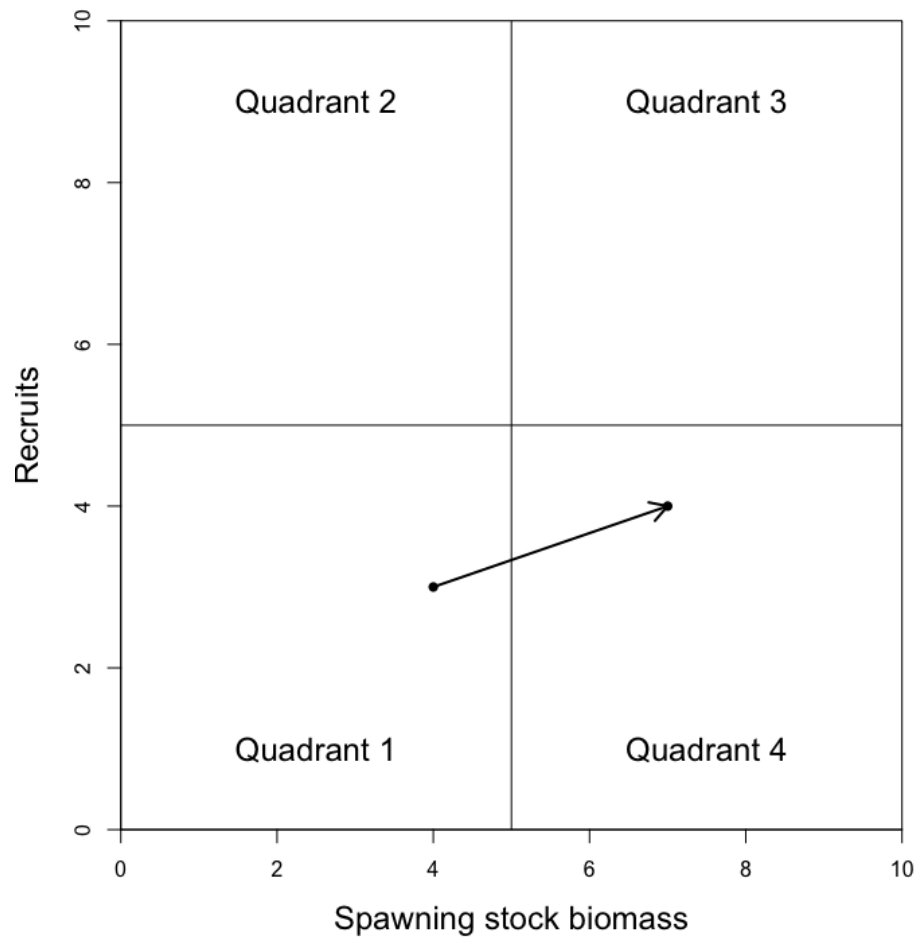


Figure 13. The four quadrants defined with respect to the medians of SSB (kg) and recruits.

The quadrants are defined as: 1, low recruit/low SSB (kg); 2, high recruit/low SSB (kg); 3, high recruit/high SSB (kg); 4, low recruit/high SSB (kg). The arrow represents an example transition between quadrants from 1 to 4.

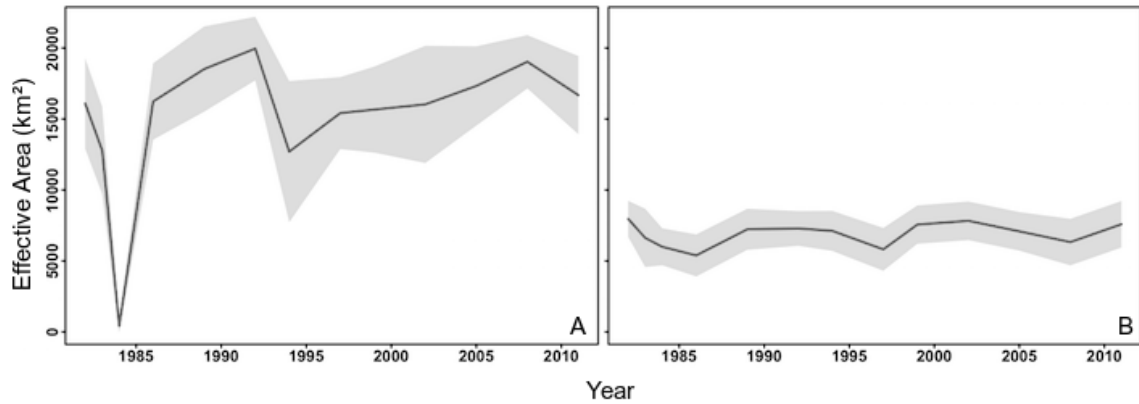


Figure 14. Estimated effective area (km²) for (A) recruits and (B) larger surfclams in the Delmarva region.

Both areas fluctuated slightly over time with a 55% reduction in area from the recruits to the large surfclams. The large drop in the area for the recruits in 1984 is an anomaly that is unrealistic in terms of the biology of the surfclam and does not appear in the area of the larger surfclams. The black line is the maximum-likelihood estimate and the grey shaded area is ± 1 standard error.

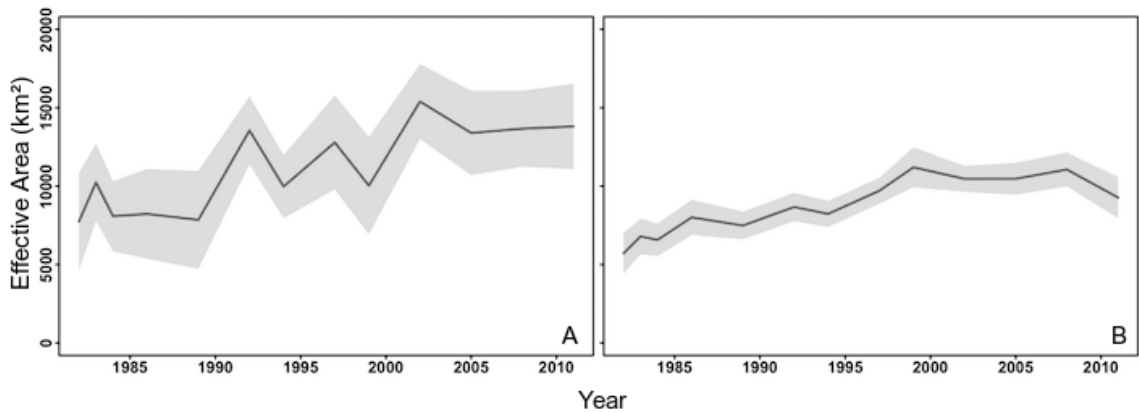


Figure 15. Estimated effective area (km²) for (A) recruits and (B) larger surfclams in the New Jersey region.

Areas for both size classes increased from 1982 to 2011 with a 21.5% reduction in area from the recruits to the large surfclams. The black line is the maximum-likelihood estimate and the grey shaded area is ± 1 standard error.

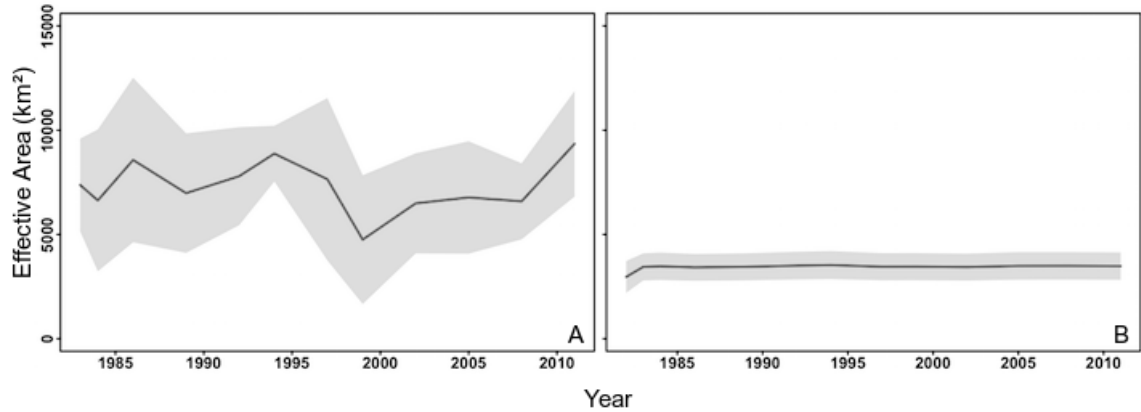


Figure 16. Estimated effective area (km²) for (A) recruits and (B) larger surfclams in the Long Island region.

The area for the recruits fluctuated over time with a slight increase and the area occupied by the large surfclams remained constant over time with a reduction of 53.1% in area from the recruits to the large clams. The black line is the maximum-likelihood estimate and the grey shaded area is ± 1 standard error.

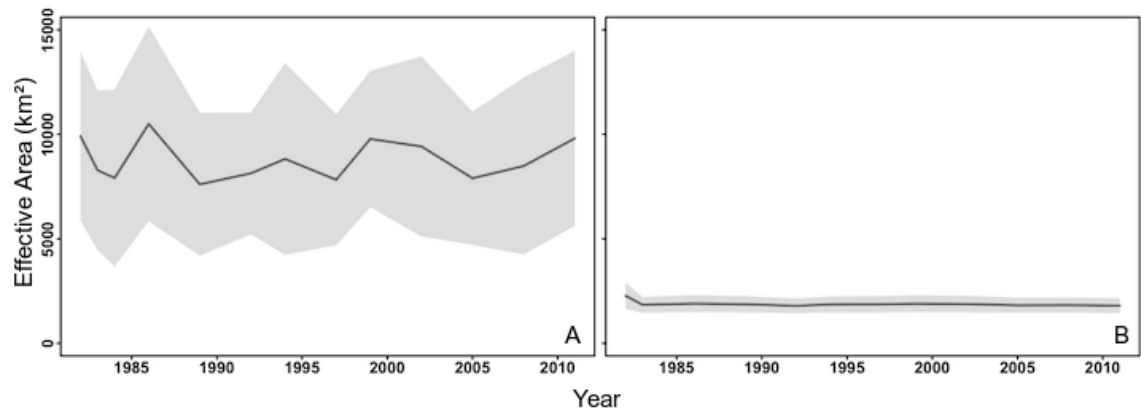


Figure 17. Estimated effective area (km²) for (A) recruits and (B) larger surfclams in the Southern New England region.

The area for the recruits fluctuated over time and the larger surfclams remained constant over time. The Southern New England region had a considerably larger reduction in area of 78.6% than the other regions between the recruits and larger surfclams. The black line is the maximum-likelihood estimate and the grey shaded area is ± 1 standard error.

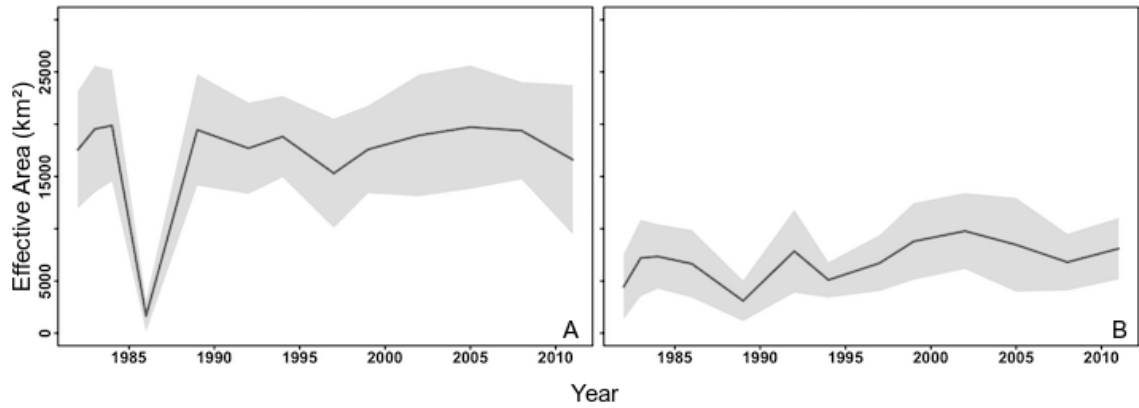


Figure 18. Estimated effective area (km²) for (A) recruits and (B) larger surfclams in the Georges Bank region.

The area for the recruits slightly fluctuated with a large drop in 1986 and the effective area of the larger surfclams fluctuated over time with a slight increase. A 59.3% reduction in area was observed from the recruits to the large clams. The large drop in the area for the recruits in 1986 is an anomaly that is unrealistic in terms of the biology of the surfclam and does not appear in the area of the larger surfclams. The black line is the maximum-likelihood estimate and the grey shaded area is ± 1 standard error.

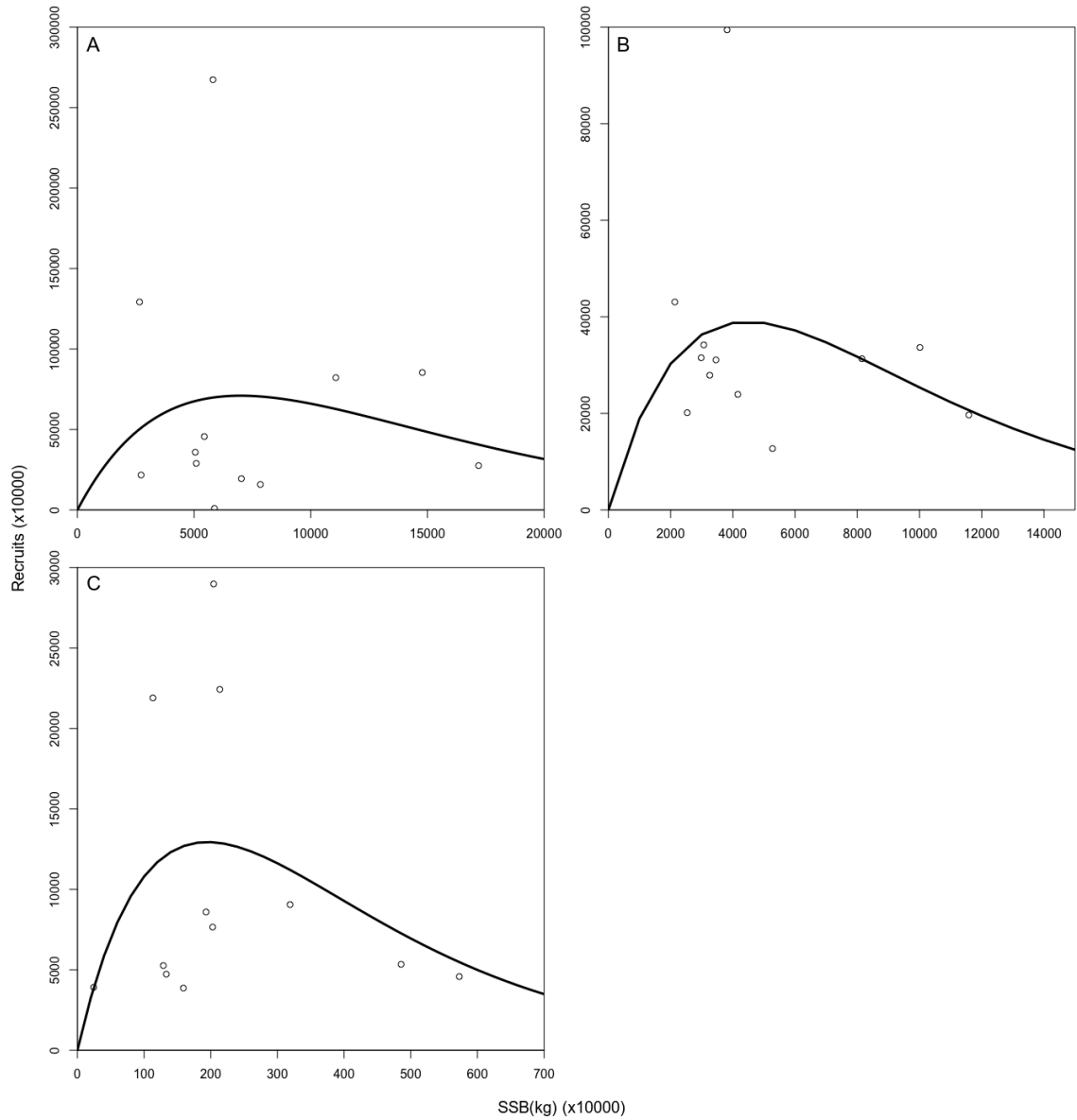


Figure 19. Spawning stock biomass versus recruits for the (A) Delmarva, (B) New Jersey, and (C) Long Island regions.

Ricker curve fitted to each SSB (kg) vs. recruit relationship.

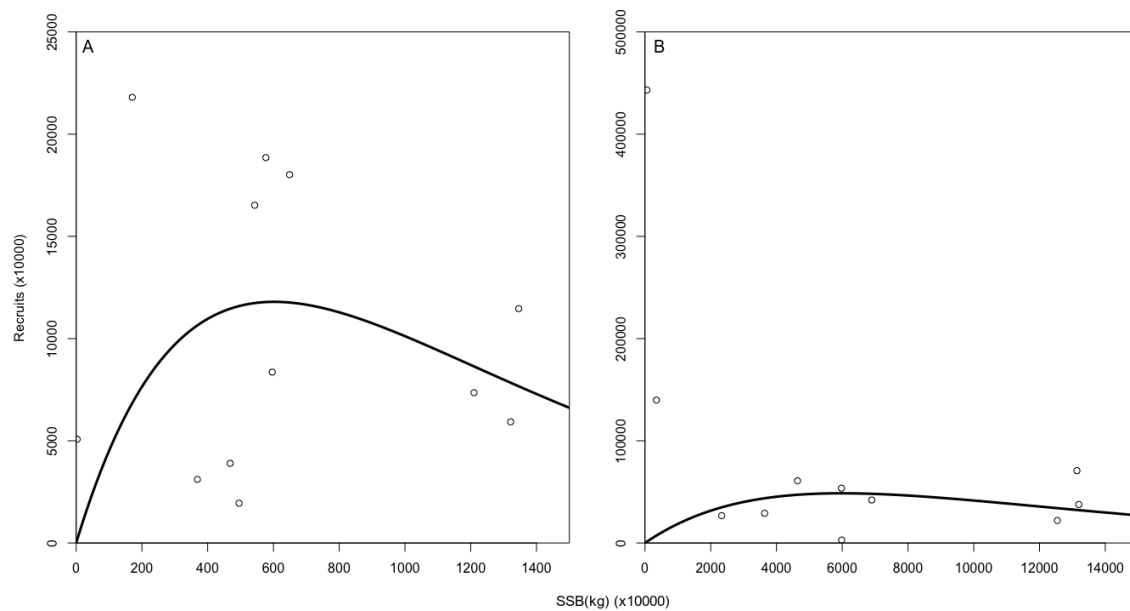


Figure 20. Spawning stock biomass versus recruits for the (A) Southern New England and (B) Georges Bank regions.

Ricker curve fitted to each SSB (kg) vs. recruit relationship.

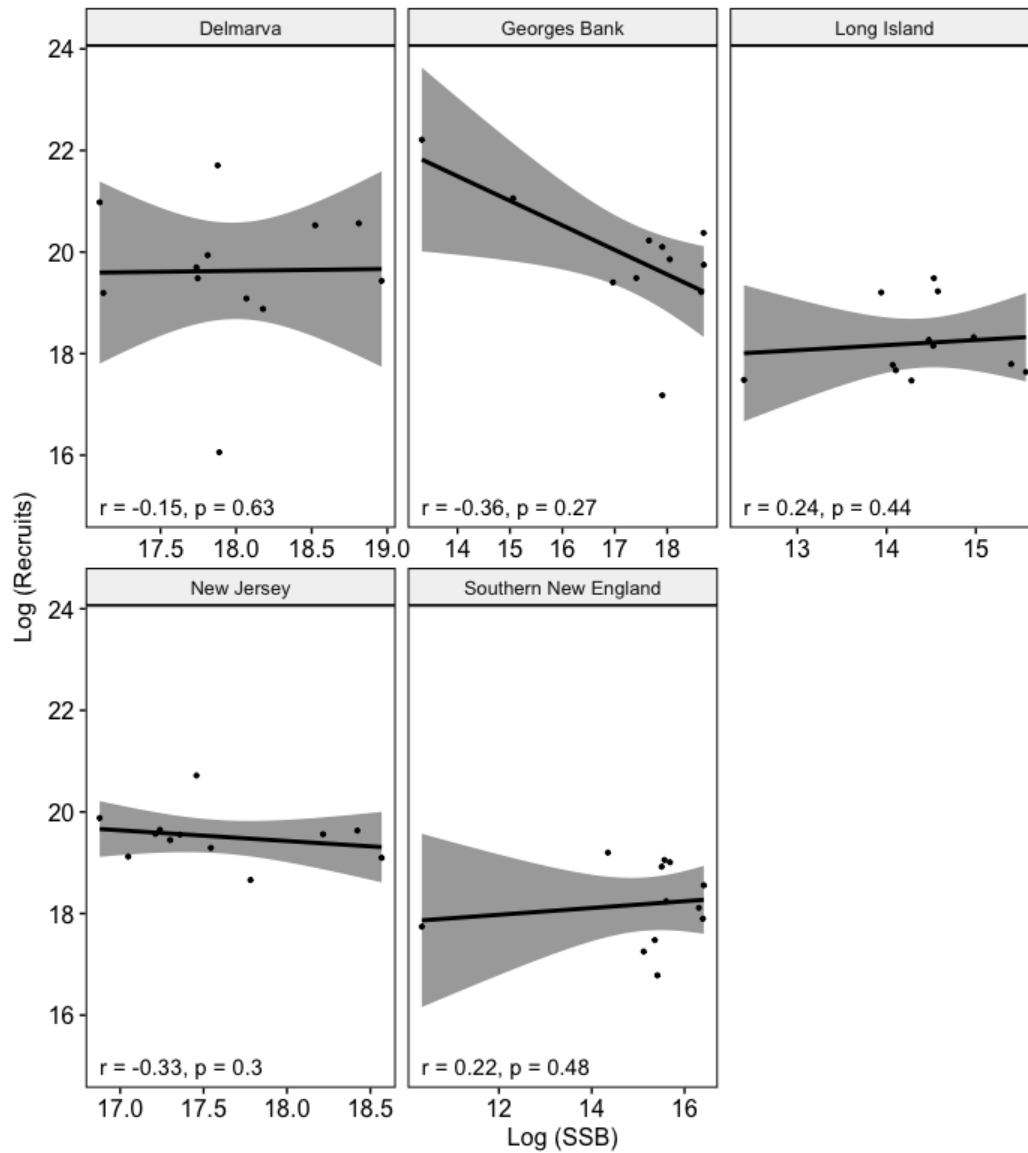


Figure 21. Spearman's correlation testing possible relationships between the recruits and spawning stock biomass (SSB, kg).

The grey area represents the confidence intervals around the line.

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