ICES Journal of Marine Science, 62: 1444–1453 (2005)
doi:10.1016/j.icesjms.2005.04.020

Bathymetric shift in the distribution of Atlantic surfclams: response to warmer ocean temperature

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Weinberg, J. R. 2005. Bathymetric shift in the distribution of Atlantic surfclams: response to warmer ocean temperature. – ICES Journal of Marine Science, 62: 1444–1453.

Standard research vessel surveys during the 1980s and early 1990s demonstrated that Atlantic surfclams (*Spisula solidissima solidissima*) were common in the southern portion of their range (37–38°N) along the east coast of North America in the Delmarva region. Based on data from these surveys, the probability of capturing surfclams in shallow water (i.e. 20 m) tows of the Delmarva region was 75–85% in 1994 and 1997. In 1999 and 2002, this probability declined to 40–55%. The probability of capturing surfclams in survey tows from deeper waters (40–50 m) also declined, but this change was relatively small compared with that in shallower water. These changes were not the result of commercial clam fishing. Unusually warm water, which induces thermal stress in *S. s. solidissima*, was prevalent within the period from 1999 to 2002 over the Delmarva continental shelf during fall when annual bottom temperature was peaking. The combined effects of poor physiological condition and thermal stress likely resulted in mortality of Atlantic surfclams in shallow water habitats in the Delmarva region. This resulted in a shift in the bathymetric distribution of the population to deeper water. Between 1982 and 1997, most of the surfclams in the Delmarva region occurred at depths between 25 and 35 m, whereas in 1999 and 2002, most of the Delmarva population occurred at 35–40 m.

Published by Elsevier Ltd on behalf of International Council for the Exploration of the Sea.

Keywords: Atlantic surfclams, bivalve, climate change, distribution, ocean temperature, spisula, thermal stress.

Received 29 June 2004; accepted 27 April 2005.

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Introduction

Spisula solidissima solidissima (Dillwyn, 1817) is a filter-feeding bivalve common in sandy sediments along the northeast coast of the USA. In the USA, a multimillion dollar commercial fishery is based on this species. The species range extends from Canada to approximately Cape Hatteras (Abbott, 1974), located near 36°N. *S. s. solidissima* occurs primarily from 10 m to 50 m (Ropes, 1980; NEFSC, 2003). At these relatively shallow depths on the continental shelf, water temperature is influenced by fluctuations in air temperature and by circulation and convection of the ocean (Mountain, 2003).

The southern geographical boundary of *S. s. solidissima* is determined by water temperature (Goldberg and Walker, 1990). In the laboratory, the optimal temperature for growth and survival of *S. s. solidissima* is 20°C (Goldberg, 1980, 1989). The burrowing rate of *S. s. solidissima* declines exponentially due to physiological stress as temperatures rise above 20°C (Savage, 1976). Temperatures above 27–28°C are lethal to all stages of *S. s. solidissima* and growth ceases above 23.9°C (Saila and Pratt, 1973; Goldberg and Walker, 1990; Walker and Heffernan, 1994; Spruck *et al.*, 1995; O'Beirn *et al.*, 1997). South of Cape Hatteras, inshore seawater temperatures in the summer can exceed 30°C (Goldberg and Walker, 1990).

Temperature also controls the distributions of other bivalves in this region (Dahlgren *et al.*, 2000). For example, the ocean quahog, *Arctica islandica* Linné, inhabits deeper waters than *S. s. solidissima*, yet the southern limit of both species occurs near Cape Hatteras. Near its southern boundary, *A. islandica* is distributed farther offshore, where water is cooler (NEFSC, 2000b). This type of distributional response to temperature has been termed "submergence" (Franz and Merrill, 1980; Mann and Wolf, 1983). *Spisula solidissima similis* (Say, 1822), a southern species better able to tolerate warmer water compared to *S. s. solidissima* (Walker and Heffernan, 1994; O'Beirn *et al.*, 1997; Hare and Weinberg, 2005), primarily occurs south of Cape Hatteras.

For many years, high densities of *S. s. solidissima* occurred off the coast of the Delmarva Peninsula, close to the southern limit of the species range (Merrill and Ropes, 1969; Murawski and Serchuk, 1989; NEFSC, 2003). However, during the 1980s and 1990s, surfclams in this region became stressed physiologically, as indicated by significantly lower growth rate and tissue weight compared with individuals living farther north, near the centre of the range of this species (NEFSC, 1998). The stress may have been partially due to competition for resources brought on by high intraspecific density (Weinberg, 1998; Weinberg *et al.*, 2002a). Little commercial harvesting of surfclams from the Delmarva region occurred during 1987–2002 because of the low tissue weights (NEFSC, 2003).

Based on the most recent stock assessment (NEFSC, 2003), the biomass of *S. s. solidissima* in the Delmarva region declined substantially sometime between 1999 and 2002. Therefore, we examined environmental factors that may have changed in intensity around 1999. Long-term data sets from the Mid-Atlantic region, spanning multiple decades, suggest that some of the warmest bottom temperatures in the region occurred during 1999–2002 (Link and Brodziak, 2002; Jossi and Benway, 2003). In addition, seawater temperatures along the Atlantic coast of North America increased by 2–3°C during the twentieth century (Drinkwater, 1996; Levitus *et al.*, 2000; Austin, 2002; Stevenson *et al.*, 2002).

Weinberg *et al.* (2002a) noted that ocean temperatures along parts of the Atlantic coast had become warm enough to stress *S. s. solidissima* and possibly cause mortality and a bathymetric shift of the species to deeper water. The purpose of the present study is to: (i) describe a recent change in the bathymetric distribution of surfclams; (ii) identify factors that were likely to cause the change; and (iii) compare the condition of surfclams from the Delmarva region with those in other regions.

Methods

The US National Marine Fisheries Service (NMFS) has conducted clam resource surveys in federal ($\geq$5.5 km from shore) Mid-Atlantic waters every 1–3 years since 1982. The surveys, conducted using a stratified random sampling design and hydraulic clam dredge, took place in the months of June and July. One tow was made at every survey station. In every survey, surfclams were counted and lengths measured to the nearest millimetre. In 1997 and 2002, data were specifically collected to ascertain the relationship between individual shell length and total fresh tissue weight, in grams. Shell length was measured in the anterior–posterior direction. Detailed descriptions of the NMFS survey and sampling gear are given in Smolowitz and Nulk (1982), Weinberg *et al.* (2002b), and NEFSC (2003).

The absolute number of clams captured per tow is sensitive to dredge efficiency, which can vary among NMFS clam surveys (NEFSC, 2003). In contrast, the probability of capturing at least one individual per tow is relatively insensitive to changes in gear efficiency because a large area is sampled during each dredge haul (i.e. $\geq 353\ m^2$ per station; Weinberg *et al.*, 2002b). Because the presence/absence of any surfclams in a survey tow is a more robust statistic than clam density, presence/absence was used as the response variable in logistic regression analyses (Hosmer and Lemeshow, 1989) to examine whether the depth distribution of surfclams changed over time. The regression models were based on two explanatory variables: Year, which was categorical; and Depth, which was continuous. To select the best model, models of varying complexity were tested in a forward stepwise manner using the likelihood ratio G-statistic and following procedures in Hosmer and Lemeshow (1989). Model fit was tested with the Deciles of Risk statistic (Hosmer and Lemeshow, 1989). These analyses were carried out in SYSTAT 10.2 (SYSTAT, 2002) using the binary logit procedure. Predicted values from the models were in the form of logits, L. A logit is defined as

$$L = \ln(P/(1 - P)),$$

where P is the probability of capturing at least one surfclam per tow.

Thus,

$$P = \exp(L)/(1 + \exp(L)).$$

The logistic regression analysis of surfclam survey data included all random stations in NMFS survey stratum 9 (Figure 1). This is the largest survey stratum (6496 km^2) in the Delmarva region. It ranges in depth from approximately 20 m to 50 m; surfclams were common in this stratum throughout the 1980s and 1990s (Weinberg, 1999). Having random survey samples from this large area and broad depth range made it possible to examine whether the depth distribution of surfclams changed over time.

Owing to the size of the mesh in the NMFS clam dredge, small surfclams (<88 mm in length) are not captured consistently by this survey gear (NEFSC, 2000a). Unless otherwise stated, clams <88 mm in length were excluded from maps and analyses. Results and conclusions of this paper are not sensitive to the exclusion of these small clams as these individuals typically accounted for a small fraction (0–15%) of the survey catch in numbers from survey tows in the Delmarva region.

The goal of the analysis was to determine whether the distribution of surfclams changed within the last decade, and to examine whether this was due to recent harvesting or thermal stress. Given the focus of this paper on recent environmental effects on surfclams, data from the four most recent NMFS clam surveys (1994, 1997, 1999, and 2002) were analysed.

Commercial surfclam fishers are required by law to report the location and catch from each fishing trip. Catch

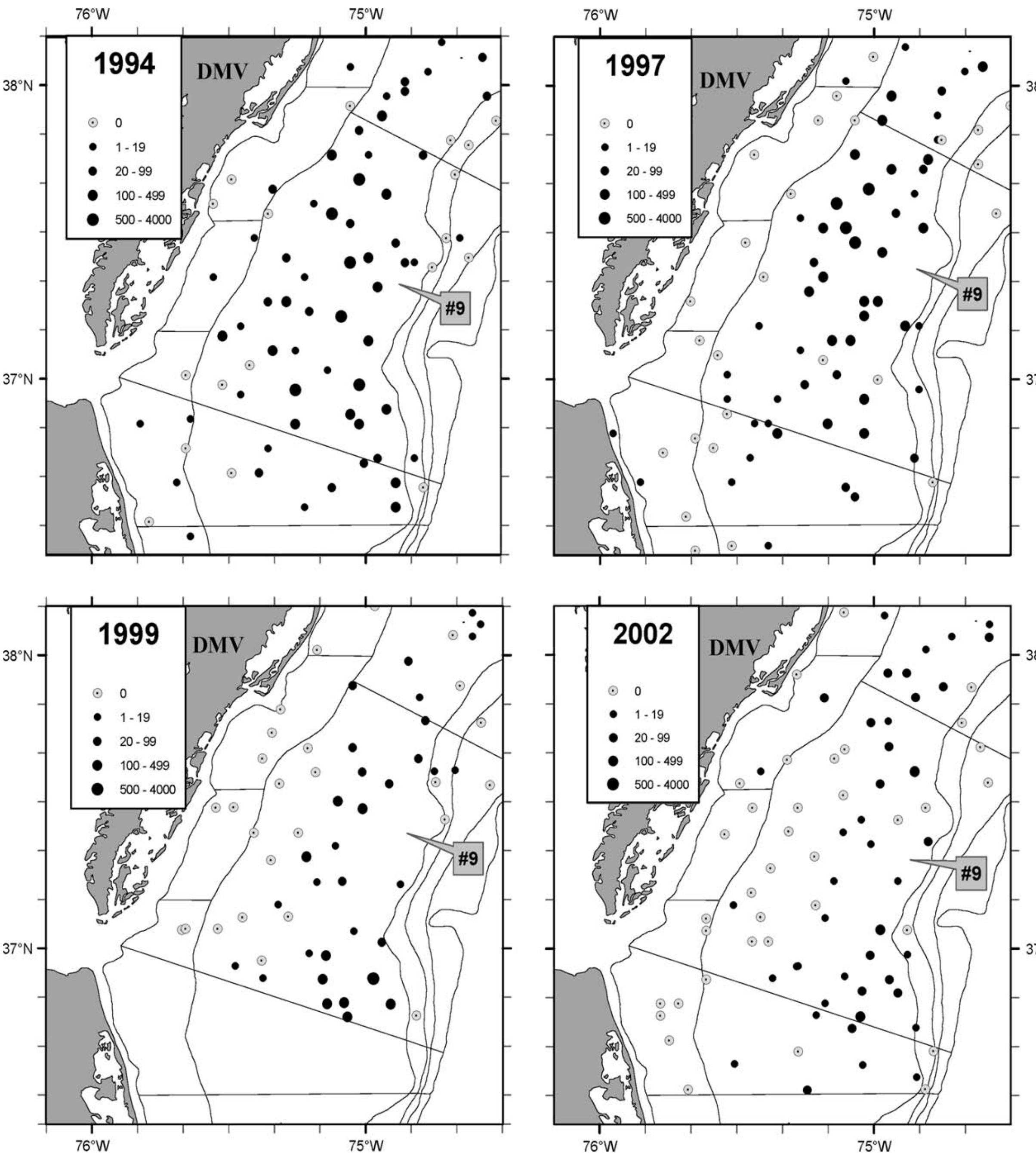

Figure 1. Spatial distribution of *Spisula solidissima solidissima* ($\geq$88 mm length) abundance per tow from NMFS research vessel surfclam surveys off the Mid-Atlantic coast of the USA, near the Delmarva Peninsula (DMV) in 1994, 1997, 1999, and 2002. The north–south lines bordering stratum 9 follow the bathymetry of the bottom. Stratum 9 ranges from approximately 20 m to 50 m in depth.

per trip is reported in units of "industry" bushels (0.0532 m^3). Fishing location is reported by ten-minute square of latitude and longitude, and often more precisely. A bushel of surfclams is assumed to yield 7.711 kg of tissue on average (NEFSC, 2003). Landings data are electronically archived in the NMFS Commercial Fisheries Database System (CFDBS).

Bottom water temperatures have been measured during NMFS semi-annual bottom trawl surveys since 1963. Temperature has been measured with a Seabird (SBE)

Model 19 profiling CTD (Taylor and Bascuñán, 2001). The data are archived in the NMFS/NEFSC Oceanography Database (OCDBS). Most of the temperature measurements in the Delmarva region from the bottom trawl surveys are obtained in March and September. In this paper, temperature records from September were analysed because September is closer to late October, the time of maximum bottom temperature in the Delmarva region (Mountain and Holzwarth, 1990). Maps depicting surfclam survey data, commercial catches, and bottom water temperatures were made using ArcMap 8.2 (ESRI Inc, 2002).

Results

During each of the four surfclam surveys conducted between 1994 and 2002, 38–39 tows were collected from random locations in NMFS stratum 9 (Table 1, Figure 1). The proportion of tows that captured at least one surfclam declined from 0.90 in 1994 to 0.64 in 2002 (Table 1). Because no small (<88 mm) individuals were captured, these proportions remain the same whether or not small surfclams are included.

Based on the log-likelihood model selection procedure, the best logistic regression included two main effects, Year and station Depth (Table 2, Model 3). The fit of the data to this model was very good (Deciles of Risk $\chi^2 = 4.64$, d.f. = 8, p = 0.79, n.s.). The probability of catching at least one surfclam per station declined over time, and this probability increased with station depth (Table 1, Figure 2). The Depth × Year interaction term was not statistically significant (Table 2), indicating that the direction and magnitude of the depth effect on the response variable was similar in all years.

Although the interaction term in the logistic regression model was not statistically significant (Table 2), there was a greater temporal decline in the probability of capturing at least one surfclam per tow in the shallower parts of stratum 9 than in the deeper waters. For example, based on predicted values from Model 3 (Figure 2), there was a strong temporal decline (50% between 1994 and 2002) in the probability of catching at least one surfclam per tow in 20 m of water: 0.84 (year = 1994), 0.76 (1997), 0.53 (1999), and 0.42 (2002). A smaller reduction in the probability of capture occurred in 40 m of water: 0.96 (1994), 0.93 (1997), 0.83 (1999), and 0.76 (2002).

Table 1. Summary of *Spisula solidissima* presence/absence data from NMFS survey stations in stratum 9, by year. Probabilities ("p") apply to surfclams ≥88 mm in shell length (see text for comments on smaller clams; these probabilities are not affected).

	Year			
	1994	1997	1999	2002
Total number of tows	39	39	38	39
Tows without surfclams	4	5	11	14
p{tow has no surfclams}	0.10	0.13	0.29	0.36
p{tow has surfclams}	0.90	0.87	0.71	0.64

Presence of a Year × Depth interaction is also suggested by the distribution of surfclam survey catches in and around stratum 9 (Figure 1). The number of random tows in stratum 9 that caught no surfclams increased over time, and these tows were primarily from shallower locations on the western side of the stratum.

NMFS survey data from 1982 to 2002 permit a longer-term examination of the depth distribution of surfclams in stratum 9 (Figure 3). Because the station locations were assigned randomly within stratum 9 in every survey, the expected sampling effort (i.e. number of stations) in each depth zone was the same in every survey, and it was proportional to the area covered by each depth zone. Thus, resulting size frequency distributions (Figure 3) are weighted by the areas of the 5-m depth intervals. During 1982–1997, the majority of surfclams captured in the stratum were from 25 m to 35 m. In 1999 and 2002, more surfclams were collected from 35 m to 40 m than from any other depth interval. Thus, in 1999 and 2002 a larger fraction of the population was found in deeper water than in any survey during the previous 18 years.

Tissue weight of surfclams in the Delmarva region continues to be low, relative to surfclams from the New Jersey and Georges Bank regions (Table 3, Figure 4). At a shell length of 120 mm, when surfclams have recruited to the fishery, the equation-predicted tissue weight of a Delmarva surfclam was 70.8 g in 1997 and 65.7 g in 2002. For comparison, the predicted weights of surfclams of this length from the New Jersey region were 87.4 g in 1997 and 77.4 g in 2002. Tissue weights of surfclams of this length from Georges Bank were 91.4 g in 1997 and 81.4 g in 2002. Thus, there has been approximately a −20% difference in surfclam tissue weight between Delmarva and the other regions since at least 1997.

A major change in the distribution of warm bottom water occurred in the Delmarva region during the last decade (Figure 5). During September 1996–1998, warm water (20–26°C) remained near the coast, at depths <20 m. In contrast, within the period 1999–2002 in September, warm bottom water extended over stratum 9 to depths of 42 m. Long-term historical data demonstrated that September is not the warmest month of the year in this region. Unfortunately, during the present study there were insufficient temperature measurements from October and November, when maximum bottom temperatures normally occur, to analyse for this effect. There were also too few temperature measurements from other months of the year to construct the annual temperature cycle for any single year of the present study.

During 1996–2002, the commercial surfclam fishery was concentrated off the coast of New Jersey, and commercial landings from the Delmarva region were relatively minor

Table 2. Forward stepwise model selection based on log-likelihoods (LL) from logistic regressions examining Atlantic surfclam presence/absence data from NMFS surveys of stratum 9 from 1994 to 2002. Terms in models: Intercept (u), Year (Y), Depth (D), interaction term (D × Y). Levels of statistical significance: "n.s.": ($p > 0.05$), "**": ($0.01 < p < 0.025$), "***": ($p < 0.01$). "G^2 ": likelihood ratio statistic. If a test is statistically significant, it means that the "Effect" being tested improves model fit and should be included in the model.

Model		−LL	Models compared	Effect tested	Change in LL between models	G^2 based on change in LL	d.f. for G^2	Significance
0	u	81.295						
1	u + Y	74.279	1:0	Y	7.016	14.032	3	***
2	u + D	78.355	2:0	D	2.940	5.880	1	**
3	u + D + Y	71.423	3:0	D + Y	9.872	19.744	4	***
			3:1	D given Y	2.856	5.712	1	**
			3:2	Y given D	6.932	13.864	3	***
4	u + D + Y + (D × Y)	70.851	4:3	D × Y	0.572	1.144	3	n.s.

(Figure 6). Landings from stratum 9 were only 0.4% of the total harvest (by tissue weight) during 1996−1998 and only 3.9% during 1999−2002. There was minimal spatial overlap between the area where harvesting occurred (Figure 6) and the area where survey catches of surfclams declined, farther to the south (Figure 1). Observed changes in the surfclam population in this stratum cannot be explained by commercial clam harvesting.

Discussion

South of Cape Hatteras, bottom water temperatures are too high in late summer and fall for *S. s. solidissima* to survive (Saila and Pratt, 1973; Savage, 1976; Goldberg, 1980, 1989; Goldberg and Walker, 1990; Walker and Heffernan, 1994; Spruck *et al.*, 1995; O'Beirn *et al.*, 1997). Although *S. s. solidissima* has been abundant in the Delmarva region for decades (Merrill and Ropes, 1969; Murawski and Serchuk, 1989), it has not been targeted by the commercial fishery since the late 1980s (NEFSC, 2003) because of low tissue weights and slow growth rates (Weinberg and Helser, 1996; Weinberg, 1998). The poor condition of these clams has probably been due to intraspecific competition for resources and stress associated with life near the southern limit of the range (Weinberg *et al.*, 2002a). In fish, poor condition has been associated with delayed maturity and low individual fitness (Morgan, 2004), which, at the population level, can reduce stock biomass.

The present study indicates that warmer water extended out over the Delmarva continental shelf during the fall seasons within the period 1999−2002. It would be useful to acquire additional and more complete data sets in the future, if they exist, to identify which of these years were the warmest. The combined effects of poor physiological condition and thermal stress are likely to have caused mortality of Atlantic surfclams in shallow water, resulting in a bathymetric shift of the population to deeper water. These results are consistent with a study of the bivalve *Macoma balthica* from the Atlantic coast of Europe (Hummel *et al.*, 1995), in which individuals from the southern limit of their range had higher sensitivity to stress. Lack of food, as well as exposure to copper, caused higher mortality in *M. balthica* from the southern part of the range compared with individuals from more northern locations.

Although the interaction term in the "best fit" logistic regression model was not statistically significant, three other types of analyses suggested that there was a greater decline of surfclams in shallow water than in deeper water. These included the bathymetric distribution of survey catches of surfclams over time (Figure 1), the presence/

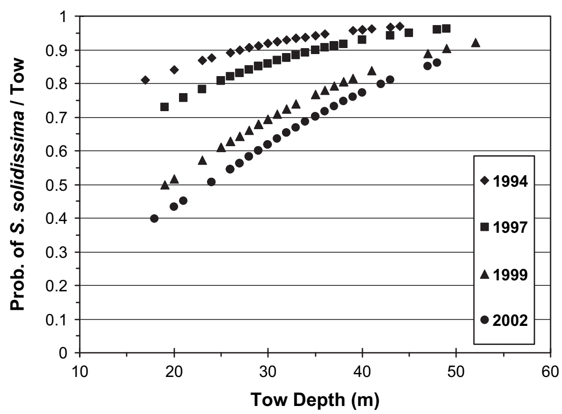

Figure 2. The probability of capturing *Spisula solidissima solidissima* (≥88 mm length) in a NMFS research vessel surfclam survey tow as a function of station depth and survey year. Results are from the logistic regression Model 3 (see Methods for additional explanation).

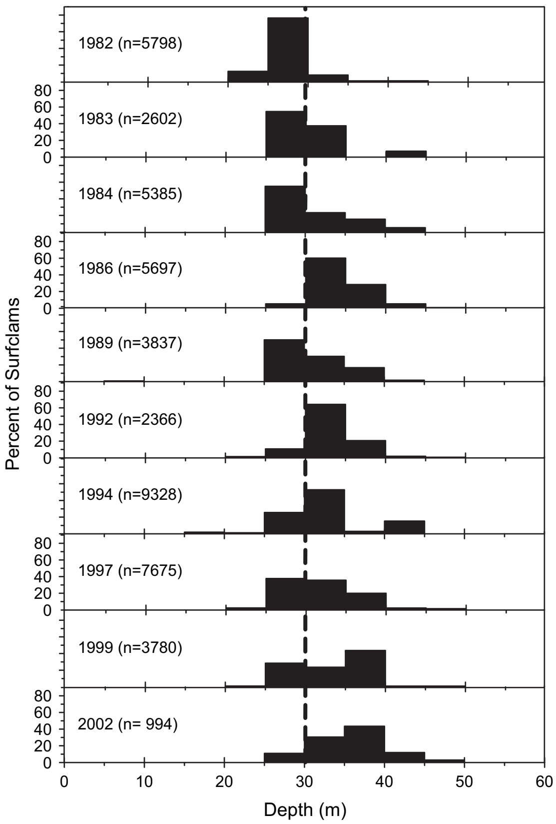

Figure 3. The percentage of *Spisula solidissima solidissima* (≥88 mm length) captured at various depths in stratum 9 during NMFS surfclam surveys, 1982–2002. Depth intervals of 5 m were used. "n": Total number of surfclams captured.

absence probabilities of capturing surfclams in stratum 9 plotted against depth (Figure 2), and the per cent size frequency of surfclams vs. depth in surveys conducted during 1982–2002 (Figure 3).

Bottom water temperatures in September in the Delmarva region were warmer after 1998. Data collected in September

Table 3. Parameter estimates for the relationship between Atlantic surfclam shell length (L), in millimetres, and fresh tissue weight (W), in grammes: $W = (e^{Alpha}) \times (L^{Beta})$. Sample sizes (n), collection dates, and locations are also listed. Regions: Georges Bank (GBK), New Jersey (NJ), Delmarva (DMV). These curves are plotted in Figure 4.

Year	Month	Region	Alpha	Beta	n
1997	July	GBK	−8.55829	2.73074	116
	May	NJ	−9.41163	2.89971	149
	June	DMV	−9.92060	2.96191	702
2002	July	GBK	−10.27049	3.06418	54
	June	NJ	−9.68603	2.93156	233
	June	DMV	−10.83117	3.13644	294

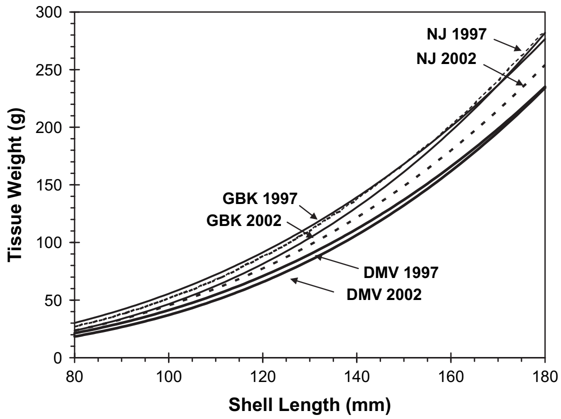

Figure 4. Fitted curves for the relationship between shell length (mm) and fresh tissue weight (g) in *Spisula solidissima solidissima*, by region and year. "GBK": Georges Bank, "NJ": New Jersey, "DMV": Delmarva. See Table 3 for the equation, parameter estimates, and sample sizes.

underestimate the maximum temperature reached during a year because observations made during NMFS bottom trawl surveys generally do not detect infrequent temperature spikes that could be most harmful to surfclams. Furthermore, September surveys are conducted 4–6 weeks prior to the annual average peak in bottom water temperature in the region (Mountain and Holzwarth, 1990). Bottom temperatures in the Delmarva region can rise an additional 1–4°C from mid-September to the late October maximum (Mountain and Holzwarth, 1990). Even with these data limitations, the September survey temperature measurements recorded within the period 1999–2002 ranged from 21°C to 24°C, temperatures high enough to induce some stress in surfclams in the laboratory (Savage, 1976; Goldberg, 1980, 1989).

It would be interesting to know how the timing of the fall bottom trawl surveys related to the annual cycle of bottom temperature in Delmarva for each year of the present study. This difference in timing between the two events might explain why some years might appear warmer than others. Unfortunately, too few measurements of bottom temperature in the NMFS OCDBS data set were made throughout the year to determine the annual temperature cycles. Rather, most of the measurements in this bottom temperature data set from the Delmarva region were made in September and March.

Consistent with the temperature data presented earlier, two published studies from the Mid-Atlantic region indicate that bottom temperatures during 1999–2002 were among the warmest in decades. Based on a 38-year time-series (1963–2000), 1999 and 2000 were the second and third warmest years, respectively, on the Mid-Atlantic continental shelf (Link and Brodziak, 2002). Based on a 25-year time-series (1978–2002) from the southern Mid-Atlantic Bight, all 4 years from 1999 to 2002 were ranked among

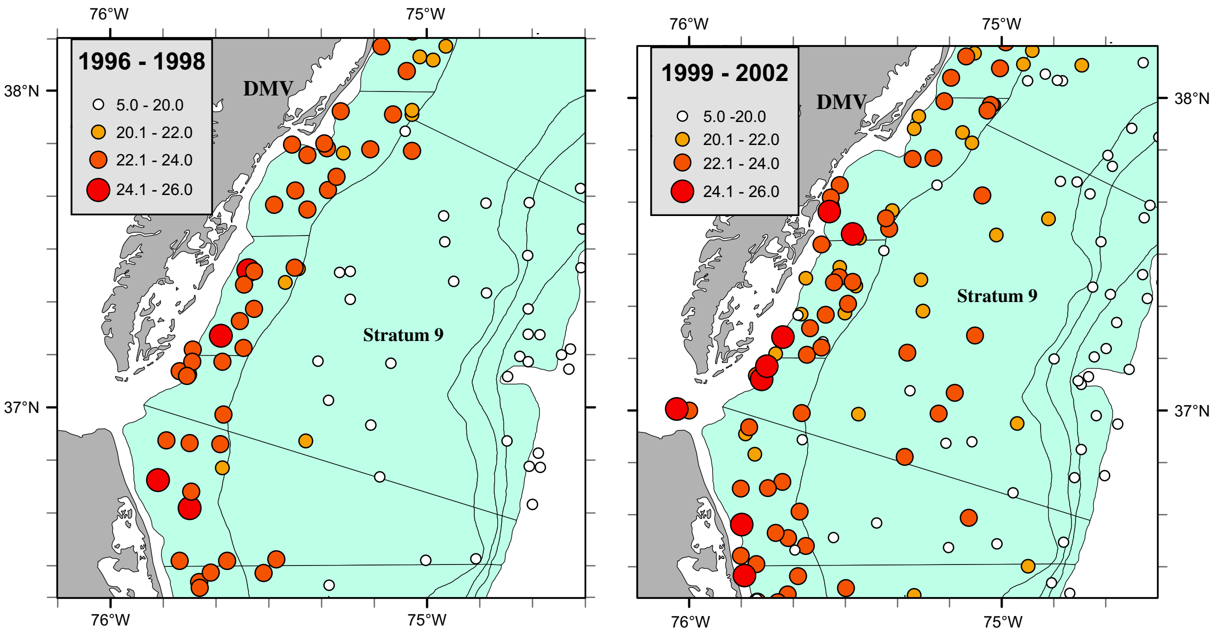

Figure 5. Bottom water temperatures (°C) in the Delmarva region, measured during NMFS research vessel bottom trawl surveys in September, 1996–1998 and 1999–2002. Optimal temperature for *Spisula solidissima solidissima* is 20°C.

the top five warmest years (Jossi and Benway, 2003). The highest value in the 25-year time-series occurred in 1999, with a value approximately 4°C above the long-term mean (Jossi and Benway, 2003).

Given the likely negative effect of recent temperature on surfclams in shallow water, how much did the biomass of surfclams decline in the Delmarva region? Estimates of surfclam biomass in this region are available for 1997 (292 000 t), 1999 (317 000 t), and 2002 (143 000 t) from an efficiency-corrected swept area biomass model (NEFSC, 2003). These estimates are uncertain because they rely on point estimates and variances of several parameters including survey-specific dredge efficiency, average area sampled by each survey tow, area and percentage suitable habitat in the region, and estimates of tissue weight derived from shell length measurements. No estimate of biomass is available for 1994 because dredge efficiency was not measured that year. These estimates suggest that there was little change in biomass from 1997 to 1999, followed by a substantial decline between 1999 and 2002.

The population dynamics equation

$$B_{1999} = B_{2002}(\exp((-M - F)t))$$

can be used to estimate M, the instantaneous natural mortality rate y^{-1}. Apart from M, terms in the equation include B = biomass of large surfclams in thousands of tonnes, F = instantaneous fishing mortality rate y^{-1}, and t = elapsed time in years. During 1997–2002, the instantaneous fishing mortality rate in this region was estimated to be $<0.04\ y^{-1}$ (NEFSC, 2003). Clam surveys were conducted every 3 years, which limits the choices of t, which represents the mortality period. Given the estimates of B, F, and t ($B_{1999} = 317$, $B_{2002} = 143$, $F \leq 0.04$, $t = 3$) from the 2003 stock assessment (NEFSC, 2003), M is estimated to be $\geq 0.22\ y^{-1}$. If this equation was made more realistic by including the small amount of recruitment that took place in this region after the 1999 survey (NEFSC, 2003), then the estimate of M would increase slightly. Based on this calculation, natural sources of mortality (e.g. temperature) during 1999–2002 had a much greater impact on biomass in this region than removals by commercial surfclam harvesting.

Although the increase in natural mortality had a detectable impact on the surfclam population in the Delmarva region, thus far the effect has been much less obvious than the hypoxic event that caused mass mortality of surfclams and other invertebrates off the New Jersey coast in 1976 (Swanson and Sindermann, 1979). The present study demonstrates that fairly subtle changes in climate can quickly alter the bathymetric distribution of a commercial species. Because surfclams burrow into the sediment and extend their siphons to suspension feed, their fitness can be controlled by short-term changes in the local environment. Such a clear response to environmental change is less likely in mobile animals such as fish.

Based on NMFS survey data (NEFSC, 2003), the bathymetric shift of surfclams in the Delmarva region was primarily due to a decline in abundance in shallower water, and not the result of better recruitment in deeper

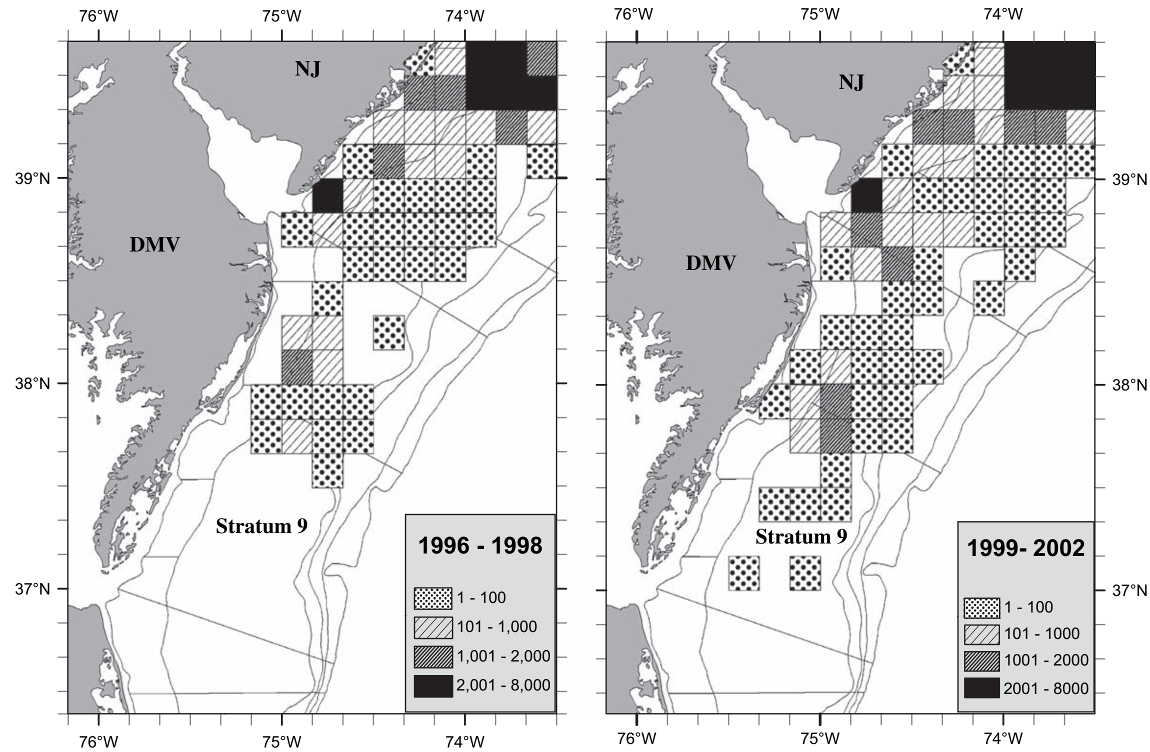

Figure 6. Spatial distribution of commercial landings (metric tons of tissue) of *Spisula solidissima solidissima* off the Atlantic coast of the USA, from 1996 to 1998 and from 1999 to 2002. Landings were aggregated by ten-minute square. "NJ": New Jersey, "DMV": Delmarva.

water than in shallower water. While temperature is likely to be one factor that caused surfclam abundance to decline, it is not known whether other environmental factors which have not been examined in detail (e.g. diseases and algal blooms) were also involved. A recent study (Kim and Powell, 2004) did not find evidence that diseases or parasites were responsible for the recent mortality in Atlantic surfclams in the Delmarva region.

A full explanation of what caused the temperature to rise is complex and beyond the scope of this paper. Properties of bottom water on the shelf of the Mid-Atlantic Bight are controlled by local as well as by more distant factors. For example, variations in bottom water temperature, volume, and salinity are due in part to advection of water masses that were formed well to the north in the Gulf of Maine (Mountain, 2003).

Individuals living near the geographical limit of their species range, especially in the lower latitudes, are more likely to experience temperatures that are close to the upper limit for the species. Unless these organisms are locally adapted to withstand higher temperatures, these organisms are more likely to be stressed by rising temperature (Hummel *et al.*, 1995). This may result in latitudinal changes in species distributions. For example, cold stenothermal species of endemic mysids in the Mediterranean Sea have recently been replaced by congeners with higher thermal tolerances (Chevaldonne and Lejeusne, 2003). If long-term warming continues along the Mid-Atlantic coast of the USA, replacement of *S. s. solidissima* by the more warm-water-tolerant southern species, *S. s. similis*, (Walker and Heffernan, 1994; O'Beirn *et al.*, 1997) may occur at certain inshore locations. *S. s. similis* is known in shallow coastal waters as far north as Cape Cod, Massachusetts, but further study will be required to document its precise distribution along the Mid-Atlantic coast (Hare and Weinberg, 2005). There is insufficient data at this time to predict whether this "southern" surfclam will increase its population size, spread into deeper water, and potentially compete with *S. s. solidissima* for food or space. Continued warming in this region might also result in northward contraction of the southern limit of *Arctica islandica* (Dahlgren *et al.*, 2000; Weinberg *et al.*, 2002a).

The northernmost reported population of *S. s. solidissima* is in the Gulf of St. Lawrence, Canada at 46°N (Caddy and Billard, 1976). If warming continues, expansion of the northern range limit is a possibility, but this would be mediated by availability of suitable sandy benthic habitat. Along the Atlantic coast of the USA there appears to be little sand habitat north of 43°N, so surfclams are unlikely to occur there. As species ranges shift, new interspecific interactions will take place. The number of endemic species replaced by species with higher thermal tolerances will depend on the strength of these interactions, on habitat suitability, and on future trends in sea temperature along marine coastlines (O'Hara, 2002).

Acknowledgements

I am grateful to B. Holmes and C. Pickett for generous help with computer graphics, and to P. Rago for statistical advice. I thank F. Serchuk, R. Mayo, R. Mann, and one other reviewer for their constructive editorial suggestions. This study would not have been possible without the efforts of the captains, crews, and scientists aboard the NOAA vessels RV "Delaware II" and "Albatross IV". I am grateful to Steve Lentz for sharing his knowledge about changes in sea temperature.

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