NOAA Technical Memorandum NMFS-NE-142

Essential Fish Habitat Source Document:

Atlantic Surfclam, *Spisula solidissima*, Life History and Habitat Characteristics

U. S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northeast Region
Northeast Fisheries Science Center
Woods Hole, Massachusetts

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Essential Fish Habitat Source Document:

Atlantic Surfclam, *Spisula solidissima*, Life History and Habitat Characteristics

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Editorial Notes on Issues 122-152 in the *NOAA Technical Memorandum NMFS-NE* Series

Editorial Production

For Issues 122-152, staff of the Northeast Fisheries Science Center's (NEFSC's) Ecosystems Processes Division have largely assumed the role of staff of the NEFSC's Editorial Office for technical and copy editing, type composition, and page layout. Other than the four covers (inside and outside, front and back) and first two preliminary pages, all preprinting editorial production has been performed by, and all credit for such production rightfully belongs to, the authors and acknowledgees of each issue, as well as those noted below in "Special Acknowledgments."

Special Acknowledgments

David B. Packer, Sara J. Griesbach, and Luca M. Cargnelli coordinated virtually all aspects of the preprinting editorial production, as well as performed virtually all technical and copy editing, type composition, and page layout, of Issues 122-152. Rande R. Cross, Claire L. Steimle, and Judy D. Berrien conducted the literature searching, citation checking, and bibliographic styling for Issues 122-152. Joseph J. Vitaliano produced all of the food habits figures in Issues 122-152.

Internet Availability

Issues 122-152 are being copublished, *i.e.*, both as paper copies and as web postings. All web postings are, or will soon be, available at: *www.nefsc.nmfs.gov/nefsc/habitat/efh*. Also, all web postings will be in "PDF" format.

Information Updating

By federal regulation, all information specific to Issues 122-152 must be updated at least every five years. All official updates will appear in the web postings. Paper copies will be reissued only when and if new information associated with Issues 122-152 is significant enough to warrant a reprinting of a given issue. All updated and/or reprinted issues will retain the original issue number, but bear a "Revised (Month Year)" label.

Species Names

The NMFS Northeast Region's policy on the use of species names in all technical communications is generally to follow the American Fisheries Society's lists of scientific and common names for fishes (*i.e.*, Robins *et al.* 1991[a]), mollusks (*i.e.*, Turgeon *et al.* 1998[b]), and decapod crustaceans (*i.e.*, Williams *et al.* 1989[c]), and to follow the Society for Marine Mammalogy's guidance on scientific and common names for marine mammals (*i.e.*, Rice 1998[d]). Exceptions to this policy occur when there are subsequent compelling revisions in the classifications of species, resulting in changes in the names of species (*e.g.*, Cooper and Chapleau 1998[e]).

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[a]Robins, C.R. (chair); Bailey, R.M.; Bond, C.E.; Brooker, J.R.; Lachner, E.A.; Lea, R.N.; Scott, W.B. 1991. Common and scientific names of fishes from the United States and Canada. 5th ed. *Amer. Fish. Soc. Spec. Publ.* 20; 183 p.

[b]Turgeon, D.D. (chair); Quinn, J.F., Jr.; Bogan, A.E.; Coan, E.V.; Hochberg, F.G.; Lyons, W.G.; Mikkelsen, P.M.; Neves, R.J.; Roper, C.F.E.; Rosenberg, G.; Roth, B.; Scheltema, A.; Thompson, F.G.; Vecchione, M.; Williams, J.D. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks. 2nd ed. *Amer. Fish. Soc. Spec. Publ.* 26; 526 p.

[c]Williams, A.B. (chair); Abele, L.G.; Felder, D.L.; Hobbs, H.H., Jr.; Manning, R.B.; McLaughlin, P.A.; Pérez Farfante, I. 1989. Common and scientific names of aquatic invertebrates from the United States and Canada: decapod crustaceans. *Amer. Fish. Soc. Spec. Publ.* 17; 77 p.

[d]Rice, D.W. 1998. Marine mammals of the world: systematics and distribution. *Soc. Mar. Mammal. Spec. Publ.* 4; 231 p.

[e]Cooper, J.A.; Chapleau, F. 1998. Monophyly and interrelationships of the family Pleuronectidae (Pleuronectiformes), with a revised classification. *Fish. Bull. (U.S.)* 96:686-726.

FOREWORD

One of the greatest long-term threats to the viability of commercial and recreational fisheries is the continuing loss of marine, estuarine, and other aquatic habitats.

Magnuson-Stevens Fishery Conservation and Management Act (October 11, 1996)

The long-term viability of living marine resources depends on protection of their habitat.

NMFS Strategic Plan for Fisheries Research (February 1998)

The Magnuson-Stevens Fishery Conservation and Management Act (MSFCMA), which was reauthorized and amended by the Sustainable Fisheries Act (1996), requires the eight regional fishery management councils to describe and identify essential fish habitat (EFH) in their respective regions, to specify actions to conserve and enhance that EFH, and to minimize the adverse effects of fishing on EFH. Congress defined EFH as "those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity." The MSFCMA requires NMFS to assist the regional fishery management councils in the implementation of EFH in their respective fishery management plans.

NMFS has taken a broad view of habitat as the area used by fish throughout their life cycle. Fish use habitat for spawning, feeding, nursery, migration, and shelter, but most habitats provide only a subset of these functions. Fish may change habitats with changes in life history stage, seasonal and geographic distributions, abundance, and interactions with other species. The type of habitat, as well as its attributes and functions, are important for sustaining the production of managed species.

The Northeast Fisheries Science Center compiled the available information on the distribution, abundance, and habitat requirements for each of the species managed by the New England and Mid-Atlantic Fishery Management Councils. That information is presented in this series of 30 EFH species reports (plus one consolidated methods report). The EFH species reports comprise a survey of the important literature as well as original analyses of fishery-independent data sets from NMFS and several coastal states. The species reports are also the source for the current EFH designations by the New England and Mid-Atlantic Fishery Management Councils, and have understandably begun to be referred to as the "EFH source documents."

NMFS provided guidance to the regional fishery management councils for identifying and describing EFH of their managed species. Consistent with this guidance, the species reports present information on current and historic stock sizes, geographic range, and the period and location of major life history stages. The habitats of managed species are described by the physical, chemical, and biological components of the ecosystem where the species occur. Information on the habitat requirements is provided for each life history stage, and it includes, where available, habitat and environmental variables that control or limit distribution, abundance, growth, reproduction, mortality, and productivity.

Identifying and describing EFH are the first steps in the process of protecting, conserving, and enhancing essential habitats of the managed species. Ultimately, NMFS, the regional fishery management councils, fishing participants, Federal and state agencies, and other organizations will have to cooperate to achieve the habitat goals established by the MSFCMA.

A historical note: the EFH species reports effectively recommence a series of reports published by the NMFS Sandy Hook (New Jersey) Laboratory (now formally known as the James J. Howard Marine Sciences Laboratory) from 1977 to 1982. These reports, which were formally labeled as *Sandy Hook Laboratory Technical Series Reports,* but informally known as "Sandy Hook Bluebooks," summarized biological and fisheries data for 18 economically important species. The fact that the bluebooks continue to be used two decades after their publication persuaded us to make their successors – the 30 EFH source documents – available to the public through publication in the *NOAA Technical Memorandum NMFS-NE* series.

JAMES J. HOWARD MARINE SCIENCES LABORATORY
HIGHLANDS, NEW JERSEY
SEPTEMBER 1999

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ECOSYSTEMS PROCESSES DIVISION
NORTHEAST FISHERIES SCIENCE CENTER

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INTRODUCTION

The Atlantic surfclam, *Spisula solidissima* (Figure 1), is a bivalve mollusk that inhabits sandy continental shelf habitats from the southern Gulf of St. Lawrence to Cape Hatteras, North Carolina (Merrill and Ropes 1969). Atlantic surfclams are managed under the Mid-Atlantic Fishery Management Council Atlantic Surfclam and Ocean Quahog Fishery Management Plan (MAFMC 1997).

This Essential Fish Habitat source document provides information on the life history and habitat requirements of Atlantic surfclams inhabiting United States waters in the Gulf of Maine, Georges Bank, and the Mid-Atlantic Bight.

LIFE HISTORY

A brief synopsis of the life history characteristics of Atlantic surfclams is provided in Amendment #10 of the Fishery Management Plan for Atlantic Surfclam and Ocean Quahog Fisheries (MAFMC 1997). More detailed information is provided here and in reviews by Ropes (1980) and Fay *et al.* (1983).

EGGS

Unfertilized Atlantic surfclam eggs are 56 µm in diameter, unpigmented, and relatively free of yolk (Allen 1951, 1953) -- characters that are generally associated with planktotrophic eggs. Fertilization occurs in the water column above the beds of spawning clams (Ropes 1980). In the laboratory, the optimal concentration of gametes for fertilization is 0.8-4 x 10^6 sperm/ml and 5-30 x 10^3 eggs/ml (Clotteau and Dubé 1993). No information on fecundity in *S. solidissima* is available (Fay *et al.* 1983), however, fecundity of the southern subspecies *S. solidissima similis* ranges from 0.14-13 million eggs in individuals 26-50 mm shell height (Walker *et al.* 1996).

LARVAE

Fertilized eggs develop into pyramid-shaped, planktonic trochophore larvae approximately 9 h after fertilization at 21.7°C (Ropes 1980) and 40 h at 14°C (Loosanoff and Davis 1963). Veliger larvae, the first larval stage to possess a bivalved shell, appear in 72 h at 14°C and 28 h at 22°C (Loosanoff and Davis 1963). The pediveliger stage, a transitional "swimming-crawling" larval stage with development of a foot for burrowing (Fay *et al.* 1983), occurs 18 d after fertilization at 21.7°C (Ropes 1980). Metamorphosis to juveniles, which consists of complete absorption of the velum and settlement to the substrate, occurs anywhere from 19 to 35 d after fertilization depending on temperature (Fay *et al.* 1983). Size at metamorphosis is 230-250 µm shell length; however Ropes (1980) noted that larvae metamorphosed at 303 µm.

JUVENILES AND ADULTS

The size and age of sexual maturity is variable. Off New Jersey, Atlantic surfclams may reach maturity as early as 3 months after settlement and at lengths of less than 5 mm (Chintala and Grassle 1995; Chintala 1997). At the other extreme, clams from Prince Edward Island, Canada, may not reach maturity until 4 yrs of age and 80-95 mm shell length (Sephton 1987; Sephton and Bryan 1990). In Virginia, the minimum length at maturity is 45 mm; size rather than age is more important in determining sexual maturity (Ropes 1979). Because of the wide variability in age at maturity, juveniles and adults will be discussed together in this report.

Atlantic surfclams may reach a maximum size of 226 mm (Ropes 1980) and a maximum age of 31 yrs (Jones *et al.* 1978). Growth appears to be similar among different localities during the first 3-5 yrs of life (Ambrose *et al.* 1980; Sephton and Bryan 1990). However, after the first 5 yrs, clams offshore grow faster and attain a larger maximum size than clams inshore (Jones *et al.* 1978; Ambrose *et al.* 1980; Jones 1980; Wagner 1984). High clam density may negatively affect growth rate and maximum size (Fogarty and Murawski 1986; Cerrato and Keith 1992); density effects on growth have been detected at relatively low densities (> 50 clams per 352 m^2) (Weinberg 1998b). Growth lines in Atlantic surfclams are deposited at times of spawning and high temperature, but there is a question as to whether lines are annual (Jones *et al.* 1978; Jones 1980; Wagner 1984; Walker and Heffernan 1994). Growth is not uniform over the year; temperature significantly affects Atlantic surfclam growth, physiology, and behavior (Ambrose *et al.* 1980; Davis *et al.* 1997).

Atlantic surfclams are susceptible to several parasites, including the thigmotrich *Sphenophyra dosinae*, the cyclopoid copepod *Myocheres major*, a cestode of the genus *Echeneribothrium*, a nematode tentatively identified as *Paranisakiopsis pectinis*, and the hyperparasite haplosporidian *Urosporidium spisuli* (Ropes 1980; see also Perkins *et al.* 1975 and Payne *et al.* 1980). Payne *et al.* (1980) found an anisakine nematode of the genus *Sulcascaris* in clams from New Jersey to Virginia. Yancey and Welch (1968) noted the presence of trematodes in Atlantic surfclams, but their effects are unclear.

REPRODUCTION

Atlantic surfclams spawn in the summer and early fall. In New Jersey, spawning occurs from late June to early August (Ropes 1968a), although spawning may begin as early as late May or early June closer inshore (Tarnowski 1982; J.P. Grassle, Rutgers University, New Brunswick, NJ, unpublished data). Spawning begins and ends earlier in the south; in Virginia, it may begin in May and end in July (Ropes 1979). The southern subspecies *Spisula solidissima similis* spawns in the spring to early summer (Kanti *et al.* 1993).

Spawning is not associated with a particular temperature or abrupt temperature changes (Ropes 1968a), but usually occurs when temperatures are greater than 15^{o}C. There may be a second, minor spawning in October, caused by breakdown of the thermocline; in extremely cold years, this second spawning may not occur (Ropes 1968a). Little is known about the effects of other environmental factors, such as salinity and dissolved oxygen, on Atlantic surfclam spawning.

FOOD HABITS

Atlantic surfclams are planktivorous siphon feeders. Leidy (1878) noted the presence of many genera and species of diatoms in Atlantic surfclam guts. Ciliates were also a common component of the diet in the field. Riisgård (1988) showed that Atlantic surfclams retained particles as small as 4 µm in diameter. High concentrations of suspended clay particles may decrease the amount of algae ingested and digested (Robinson *et al.* 1984).

PREDATION

Atlantic surfclams have many predators, including the naticid snails *Euspira heros* and *Neverita duplicata* (Franz 1977; Dietl and Alexander 1997), the sea star *Asterias forbesi* (Meyer *et al.* 1981), lady crabs (*Ovalipes ocellatus*), Jonah crabs (*Cancer borealis*) (Stehlik 1993), and horseshoe crabs (*Limulus polyphemus*) (Botton and Haskin 1984). Fish predators include haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) (Ropes 1980). The sevenspine bay shrimp, (*Crangon septemspinosa*) preys on recently settled clams (Viscido 1994). In the New York Bight, crabs accounted for 48.3-100% of Atlantic surfclam mortality while naticid moon snails accounted for 2.1% of mortality (MacKenzie *et al.* 1985).

HABITAT CHARACTERISTICS

Information on the habitat characteristics of the Atlantic surfclam is summarized in Table 1. This information focuses primarily on Atlantic surfclam beds in U.S. waters; most of the information is from the Middle Atlantic Bight.

EGGS

Fertilization of Atlantic surfclam eggs is optimal at 6-24^{o}C, 20-35 ppt salinity, and a pH of 7.8-10 (Allen 1953; Castagna and Chanley 1973; Clotteau and Dubé 1993). Eggs and sperm can withstand salinities as low as seawater diluted to 40% for 2-3 h (Schechter 1956).

LARVAE

Larvae tolerate temperatures of 14-30^{o}C, with an optimum at 22^{o}C (Fay *et al.* 1983). High temperatures can be lethal to developing larvae. Substantial mortality occurs in early cleavage stages exposed to 29.5^{o}C water for 10 min, in trochophores exposed to 31.5^{o}C water for 1 hr, and in straight-hinge veligers exposed to 34^{o}C for 3 h (Wright *et al.* 1983; Roosenberg *et al.* 1984). Larvae are capable of growing in salinities as low as 16 ppt (Castagna and Chanley 1973), and can survive in salinities of 8 ppt at 7.7^{o}C (Yancey and Welch 1968). In the laboratory, larvae did not cross salinity discontinuities greater than 15 ppt, and remained in the high-salinity end of a salinity gradient (Mann *et al.* 1991).

Few studies have examined Atlantic surfclam larvae in the field. In New England, Mann (1985) reported high larval concentrations (up to 823 larvae/m^3) associated with 14-18^{o}C water masses and relatively low chlorophyll *a* concentrations. In New Jersey, Tarnowski (1982) noted high concentrations of Atlantic surfclam larvae in the spring and fall. Spring larvae were derived from inshore clams, while fall larvae were from offshore clams. Dispersal by currents occurs during the larval stage (Fay *et al.* 1983) and larval settlement may coincide with the relaxation of upwelling events (Ma 1997). Franz (1976) hypothesized that a convergence of tidal and longshore currents trap Atlantic surfclam larvae off western Long Island, although this theory is based on juvenile and adult distributions rather than larval samples.

JUVENILES AND ADULTS

The greatest concentrations of Atlantic surfclams are usually found in well-sorted, medium sand (Dames and Moore 1993), but they may also occur in fine sand (MacKenzie *et al.* 1985) and silty-fine sand (Meyer *et al.* 1981). Ambrose *et al.* (1980) noted a positive correlation between growth rate and mean sediment grain size when other variables were controlled, although Goldberg and Walker (1990) found that substrate type did not affect the growth rate of clams in the laboratory and field, although clams did not burrow in mud. Atlantic surfclams are most common at depths of 8-66 m in the turbulent areas beyond the breaker zone (Fay *et al.* 1983).

Henderson (1929) determined the upper lethal temperature of Atlantic surfclams to be 37^{o}C, however, this was based on only five individuals. Mid-Atlantic surfclams reared in a laboratory in Georgia did not survive temperatures above 28^{o}C (Spruck *et al.* 1995). Atlantic surfclams rarely encounter such temperatures in the wild and are usually found in areas where the bottom temperature rarely exceeds 25^{o}C. The minimum temperatures experienced by Atlantic surfclams are probably not < 1^{o}C. Spawning in nature occurs at temperatures > 15^{o}C and is typically heaviest when temperatures are at their highest (Jones 1981b; Sephton 1987).

Growth is not uniform over the year. Ambrose *et al.* (1980) noted that growth of Atlantic surfclams in the Middle Atlantic Bight was positively correlated with temperature and negatively correlated with variation in temperature. Davis *et al.* (1997) found that growth in the coastal Gulf of Maine was higher at warmer temperatures and at higher chlorophyll *a* concentrations. Stable oxygen isotopes revealed that shell growth in New Jersey waters reflects seawater temperature; growth is most rapid in spring and early summer, slow in late-summer and fall, and extremely slow or non-existent in winter (Jones *et al.* 1983). In Delaware waters, Atlantic surfclam production is highest in August and September when temperatures are high (Howe *et al.* 1988). In the laboratory, Atlantic surfclam heart rate increased with increasing temperature from 5-15^{o}C (deFur and Mangum 1979). Savage (1976) found that clams burrowed fastest at 16-26^{o}C, and were unable to burrow at 30^{o}C. Prior *et al.* (1979) noted no uniform effect of temperature on the leaping escape response of Atlantic surfclams, but did note that clams seemed to be more active above 15^{o}C.

Although Atlantic surfclams are found only at salinities higher than 28 ppt in the field, they are capable of surviving salinities as low as 12.5 ppt for 2 d (Castagna and Chanley 1973). This suggests that something other than salinity is controlling the distribution of Atlantic surfclams. In the laboratory, Atlantic surfclam heart rate increased as salinity dropped from 30 ppt to 20 ppt (deFur and Mangum 1979).

Atlantic surfclams are susceptible to low levels of dissolved oxygen (DO). Severe hypoxic events (DO < 3 ppm) in New Jersey have killed Atlantic surfclams several times (Ogren and Chess 1969; Garlo *et al.* 1979; Ropes *et al.* 1979). Weinberg and Helser (1996) showed spatial and temporal changes in growth rate and maximum size and hypothesized these changes may be related to low dissolved oxygen levels. Positive effects of hypoxia include the decimation of Atlantic surfclam predators, allowing successful recruitment of recently-settled clams (Garlo 1982). In the laboratory, Thurberg and Goodlett (1979) noted that a dissolved oxygen level < 1.4 ml/L was nearly always fatal, although clams could survive at levels as low as 0.7 ml/L if acclimated slowly. Atlantic surfclam heart rate remained relatively constant over a wide range of oxygen concentrations (deFur and Mangum 1979). Supersaturation of oxygen may also negatively affect clams. In the laboratory, significant Atlantic surfclam mortality occurred at 114% O_2 saturation (Goldberg 1978). Sublethal effects at lower O_2 levels included tissue blisters and secretion of shell material surrounding air bubbles.

There has been little work on the effects of currents on Atlantic surfclams, particularly on feeding and bedload transport of small clams. The dynamic environments in which Atlantic surfclams live may substantially affect flux of food and population distribution. For example, oceanic storms can displace adults a considerable distance from their burrows (Fay *et al.* 1983).

GEOGRAPHICAL DISTRIBUTION

Atlantic surfclams are distributed in western North Atlantic continental shelf waters from the southern Gulf of St. Lawrence to Cape Hatteras, North Carolina (Merrill and Ropes 1969; Weinberg 1998a). In United States waters, major concentrations of Atlantic surfclams are found on Georges Bank, south of Cape Cod, off Long Island, southern New Jersey, and the Delmarva Peninsula (Merrill and Ropes 1969; Ropes 1978). Although Atlantic surfclams can inhabit waters from the surf zone to a depth of 128 m, most are found at depths of less than 73 m (Ropes 1978). Along Long Island and New Jersey, the highest concentrations occur at < 18 m, whereas off the Delmarva Peninsula, the greatest concentrations occur from 18 to 36 m (Ropes 1978).

A southern subspecies, *Spisula solidissima similis*, occurs south of Cape Hatteras (Walker and Heffernan 1994). *Spisula raveneli* occurs in the southern part of the range of *S. solidissima*. The distinction of the species, based on distribution and morphology (Jacobson and Old 1966; Porter and Schwartz 1981), is controversial (Vecchione and Griffis 1996).

EGGS AND LARVAE

The eggs and larvae of Atlantic surfclam were not counted during the Northeast Fisheries Science Center (NEFSC) Marine Resources Monitoring, Assessment and Prediction (MARMAP) program (P. Berrien, NMFS, NEFSC, James J. Howard Marine Sciences Laboratory, Highlands, NJ, personal communication).

PRE-RECRUITS AND RECRUITS

The terms pre-recruit and recruit are used here to describe Atlantic surfclam distribution. They refer to the exploited and unexploited portions of the stock. Atlantic surfclams are exploited at a minimum size of 12 cm; pre-recruits are ≤ 11 cm and recruits are ≥ 12 cm.

The NEFSC clam surveys [see Reid *et al*. (1999) for survey methods] collected Atlantic surfclams from Georges Bank to just north of Cape Hatteras (Figure 2). Pre-recruits and recruits had similar distributions, although recruits were not collected quite as far to the south. The greatest number of catches of pre-recruits and recruits were made from the Hudson Canyon to Cape Hatteras inshore of the 60 m contour. The Gulf of Maine was not surveyed, although Atlantic surfclams are found there in areas containing suitable substrate (sand).

STATUS OF THE STOCKS

The total commercial landings of Atlantic surfclam peaked during 1973-1975, with an average meat weight of 40,100 metric tons (mt). This was followed by a decline to an historic low of 15,800 mt by 1979. Landings increased to more than 30,000 mt in 1984 and have remained at comparable levels ever since. Landings in 1996 were 28,800 mt, almost identical to 1995 and 7% below landings in 1994 (Figure 3; Weinberg 1998a). Biomass indices from research vessel surveys generally parallel trends in landings. The results of the 1997 surveys indicate that the majority of the Atlantic surfclam resource is concentrated in northern New Jersey, the Delmarva Peninsula, and Georges Bank (Northeast Fisheries Science Center 1998). Gulf of Maine Atlantic surfclams are currently not harvested commercially (Davis *et al.* 1997).

The EEZ Atlantic surfclam resource is currently at a medium level of biomass and appears under-exploited overall (Northeast Fisheries Science Center 1998). The September 1997 report to Congress, 'Status of Fisheries of the United States' (National Marine Fisheries Service 1997), states that Atlantic surfclams are presently not overfished, nor approaching an overfished condition.

RESEARCH NEEDS

- Accurate estimates of population sizes are needed. Efforts to refine estimates of population abundance in different regions, and to understand factors affecting dredge efficiency, need to be continued. In addition to assessment surveys, total population densities and age structure should be assessed using depletion experiments by commercial vessels, complemented by quantitative techniques.
- The implications of density effects on growth and size for harvesting and optimal yield should be determined. High population density may negatively affect growth rate, size at age, and meat weight, but there is insufficient information to determine optimal densities for management purposes. Region-specific studies on the effects of population density on age-specific growth are needed.
- The genetic structure of populations of *Spisula solidissima* over the geographic range of the species should be determined. Molecular techniques can be used to determine the relationship between *S. solidissima*, the southern subspecies *S. s. similis*, and the named species *S. raveneli*, whose systematic status is uncertain. If the Atlantic surfclam population consists of independent genetic units, this would have important implications for management.
- The effects of dredging on settlement and recently settled clams needs to be examined. While the effects of dredging on juvenile and adult clams have been studied, there are no data on the effects of dredging on the youngest clams. Because of their small size, settling and recently settled clams may be adversely affected by dredging.
- Region-specific studies on the correlation between environmental parameters (e.g., bottom temperature), spawning, and recruitment are needed. Physical data are often available from other research programs on the continental shelf, and these can be correlated with yearly changes in spawning times and subsequent settlement intensity and recruitment.

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Table 1. Summary of life history and habitat characteristics for the Atlantic surfclam, *Spisula solidissima*.

Life Stage	Size and Growth	Habitat	Substrate	Temperature	Salinity
Eggs [1]	Unfertilized eggs are 56 µm in diameter.			6-24^{o}C optimal for fertilization.	Sperm and eggs can withstand salinities as low as 40% diluted seawater for 2-3 h. 20-35 ppt optimal for fertilization; fertilized eggs do not develop at 22 ppt or lower. Hypo- or hypertonicity may cause parthenogenesis (hermaphroditism).
Larvae [2]	At 22^{o}C: 28 hr to straight hinge veligers. At 21.7^{o}C: trochophore larvae 9 h post-fertilization, veligers 19-20 h, pediveligers at 18 d. At 14^{o}C: 40 hr to trochophore, 72 hr to straight hinge veligers. Metamorphosis: 35 d at 14^{o}C, 19 d at 22^{o}C. Most larvae metamorphose at 230-250 µm, although one study reports 303 µm.	One study in Massachusetts found the highest concentration of larvae (823 larvae/m^3) at 30 m in early October. High concentrations of larvae in NJ occur from May-June and Sept-Oct; minor peaks sometimes occur in July. Spring larvae were derived from inshore clams, while fall larvae were derived from offshore clams.		Larvae tolerate 14-30^{o}C; optimum 22^{o}C, mortality > 30^{o}C. Larvae reared at lower temperatures were smaller than those at warmer temperatures. In New England, high larval concentrations are associated with 14-18^{o}C water.	Larvae in the lab can survive and grow at 16 ppt; with acclimation as low as 8 ppt. Larvae starting at 30 ppt crossed a salinity gradient of 5 ppt and 10 ppt, but not 15 ppt. Upward swimming rate increased with salinity, larvae stayed in high salinity.
Juveniles/ Adults [3]	Growth rates are similar for the first 3-5 years of life, then offshore clams grow more rapidly than inshore clams. High population density reduces growth rate and maximum length. Clams may reach lengths of 226 mm and 37 yrs of age.	Range from the Gulf of Maine south to Cape Hatteras, NC. Oceanic, most common in turbulent areas beyond breaker zone, from 8-66 m. Distribution of beds ranges from even aggregations to localized or patchy dense beds.	Adults burrow in medium to coarse sand and gravel substrates, also found in silty to fine sand, do not burrow in mud. Substrate type does not affect growth rate.	37^{o}C is lethal in the lab. Clams survive temperatures as low as 2^{o}C in the field; clams more active > 15^{o}C. Burrowing is fastest at 16-26^{o}C; inhibited ≥ 30^{o}C. Growth rate is positively correlated with temperature, growth most rapid in spring/early summer.	Adults in lab tolerated 14-52 ppt. Atlantic surfclams at 28 ppt in the field survived in the lab at 12.5 ppt for several days, suggesting that a variable other than salinity controls distribution.
Spawning Adults [4]				Spawning occurs from 19.5-30^{o}C; detrimental > 30^{o}C. Laboratory: burrowing increased up to 20^{o}C, but decreased > 20^{o}C. Temperature important for initiation and timing of both gonadal development and spawning. Off NJ, spawning heaviest in summer/fall when temperatures are at their highest; may be a minor Oct spawning, brought about by breakdown of thermocline. Delayed spawning and single annual cycle may be related to cold temperatures. Abrupt temperature changes not a clear cause of spawning in nature.	

[1] Allen (1953), Schechter (1956), Yancey and Welch (1968), Castagna and Chanley (1973), Wright *et al.* (1983), Roosenberg *et al.* (1984), Clotteau and Dubé (1993)
[2] Loosanoff and Davis (1963), Yancey and Welch (1968), Ropes (1980), Tarnowski (1982), Fay *et al.* (1983), Wright *et al.* (1983), Roosenberg *et al.* (1984), Mann (1985), Mann *et al.* (1991), Ma (1997)
[3] Henderson (1929), Clarke (1954), Yancey and Welch (1968), Merrill and Ropes (1969), Ogren and Chess (1969), Ropes and Merrill (1970), Castagna and Chanley (1973), Flowers (1973), Franz (1976), Savage (1976), Loesch and Ropes (1977), Ropes and Ward (1977), Goldberg (1978), Jones *et al.* (1978, 1983), Ropes (1978, 1980), Boesch (1979), Prior *et al.* (1979), Ambrose *et al.* (1980), Garlo (1980), Jones (1980, 1981a), Meyer *et al.* (1981), Fay *et al.* (1983), Wagner (1984), MacKenzie *et al.* (1985), Fogarty and Murawski (1986), Howe *et al.* (1988), Murawski and Serchuk (1989), Goldberg and Walker (1990), Sephton and Bryan (1990), Walker and Heffernan (1990, 1994), Cerrato and Keith (1992), Dames and Moore (1993), Weinberg and Helser (1996), Chintala (1997), Weinberg (1998a, b)
[4] Loosanoff and Davis (1963), Ropes (1968a, b, 1980, 1982), Jones (1981b), Fay *et al.* (1983), Sephton (1987), Kanti *et al.* (1993), Chintala and Grassle (1995)

Table 1. cont'd.

Life Stage	Dissolved Oxygen	Currents	Prey	Predators	Spawning	Notes
Eggs [1]					see spawning adults	Fertilization occurs in water column above spawning beds; pH 7.8-10 optimal for fertilization.
Larvae [2]		Larval settlement coincides with relaxation of upwelling events. Dispersal via water currents, swimming and crawling occur during larval stages. Convergence of tidal and longshore currents may trap larvae off western Long Island.	Larvae are planktotrophic.			Larval stages: trochophore (planktonic), veliger (bivalve shell present), pediveliger (transitional swimming-crawling stage).
Juveniles/ Adults [3]	Hypoxia may be lethal, or lower growth rate and maximum size in the field. In the lab, burrowing time was slower at 1.45 mg/L than at higher DO levels. Clams died after 5 d at a DO of 0.9 mg/L. Anoxic event in 1976 off NJ and Long Island killed 62% of NJ Atlantic surfclam resource; lower lethal limit of 2 ppm DO assumed.	Currents important in determining eventual patterns of distribution and settlement of developing juveniles. Oceanic storms and currents may displace adults considerable distance from burrows; survivors reburrow at new site.	Planktivorous siphon feeders. Food varies with season, geographic location and depth of bed; feed primarily on phytoplankton, especially diatoms and ciliates. Retain particles $\geq 4 \mu m$ diameter.	Primarily moon snails, also sea stars, horseshoe crabs, lady crabs, Jonah crabs, sea gulls, and shrimp. Predation rate of moon snails lowered by low temperatures and salinities, ceased feeding at < 2 and 5^oC respectively, and < 10 and 6 ppt salinity respectively. Haddock and cod prey on injured clams after storms.		Metamorphosis to juveniles and settlement to substrate ranges from 18-35 d (varies with temperature). The age of maturity ranges from 3 months to 4 years post-settlement. Without examining the gonads of small clams, one can't assume level of maturity. Longevity up to 25 years; largest individual recorded 226 mm.
Spawning Adults [4]					Atlantic surfclams can reach sexual maturity and spawn as early as 3 months post-settlement. Off NJ: major spawning early July to mid-Aug; in some years second minor spawning occurs mid-Oct. Spawning is earlier in more southern areas.	Rate of temperature change may be a more important stimulus for spawning than ambient temperature.

[1] Allen (1953), Fay *et al.* (1983), Clotteau and Dubé (1993)
[2] Ropes (1980), Mann (1985), Ma (1997)
[3] Leidy (1878), Ropes and Merrill (1966, 1973), Yancey and Welch (1968), Ogren and Chess (1969), Jacobson (1972), Savage (1976), Franz (1977), Goldberg (1978), Garlo *et al.* (1979), Prior *et al.* (1979), Ropes *et al.* (1979), Thurberg and Goodlett (1979), Garlo (1980, 1982), Ropes (1980), Fay *et al.* (1983), Botton and Haskin (1984), Robinson *et al.* (1984), MacKenzie *et al.* (1985), Howe *et al.* (1988), Riisgård (1988), Walker and Heffernan (1990), Stehlik (1993), Viscido (1994), Chintala and Grassle (1995), Weinberg and Helser (1996), Dietl and Alexander (1997)
[4] Allen (1951), Loosanoff and Davis (1963), Ropes (1968a, b, 1979, 1980, 1982), Yancey and Welch (1968), Jones (1981b), Meyer *et al.* (1981), Tarnowski (1982), Fay *et al.* (1983), Mann (1985), Sephton (1987), Kanti *et al.* (1993), Chintala and Grassle (1995)

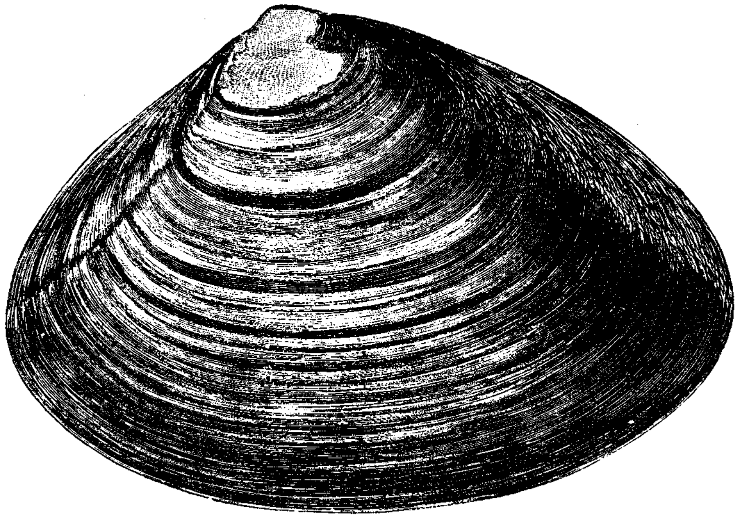

Figure 1. The Atlantic surfclam, *Spisula solidissima* (from Goode 1884).

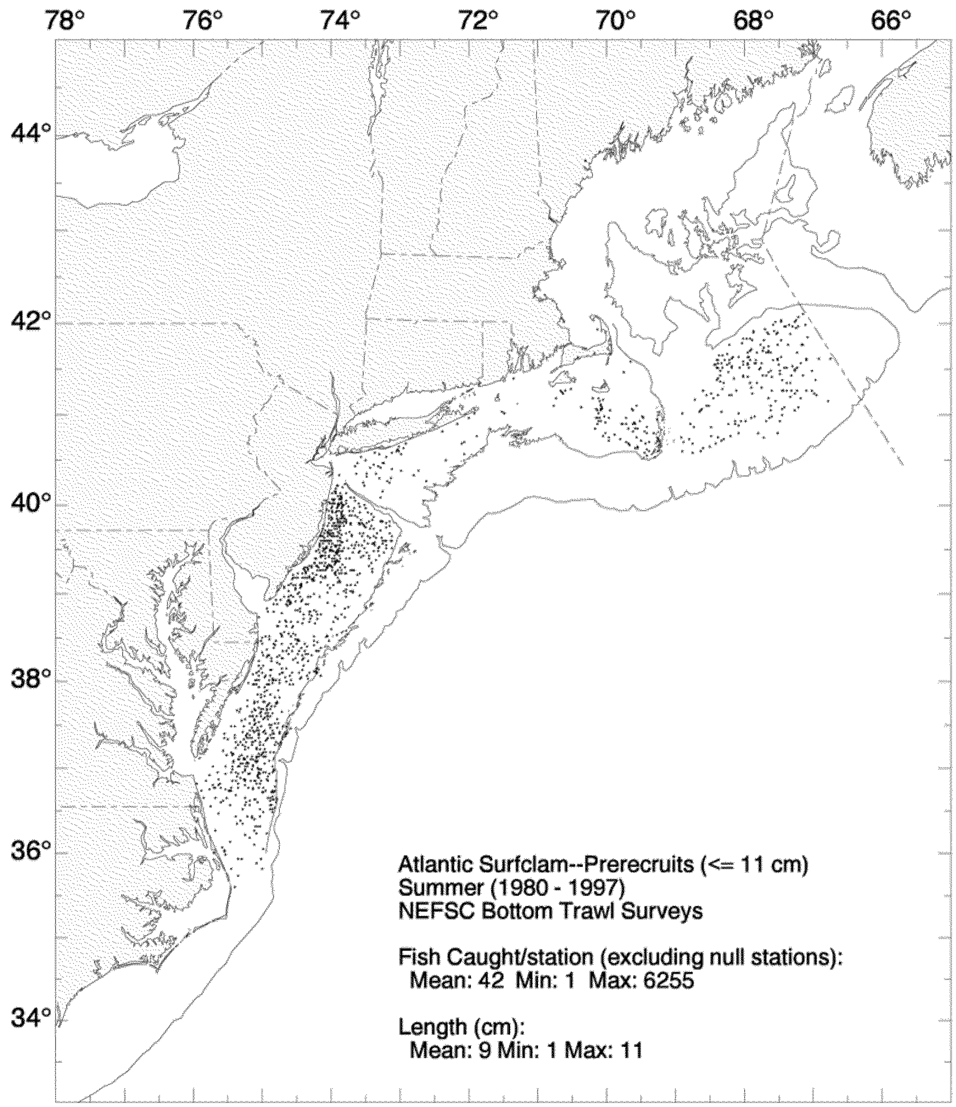

Figure 2. Distribution of Atlantic surfclam pre-recruits (≤ 11 cm) and recruits (≥ 12 cm) collected during NEFSC summer clam surveys from 1980-1997 [see Reid *et al.* (1999) for details]. Black dots represent stations where Atlantic surfclams were taken.

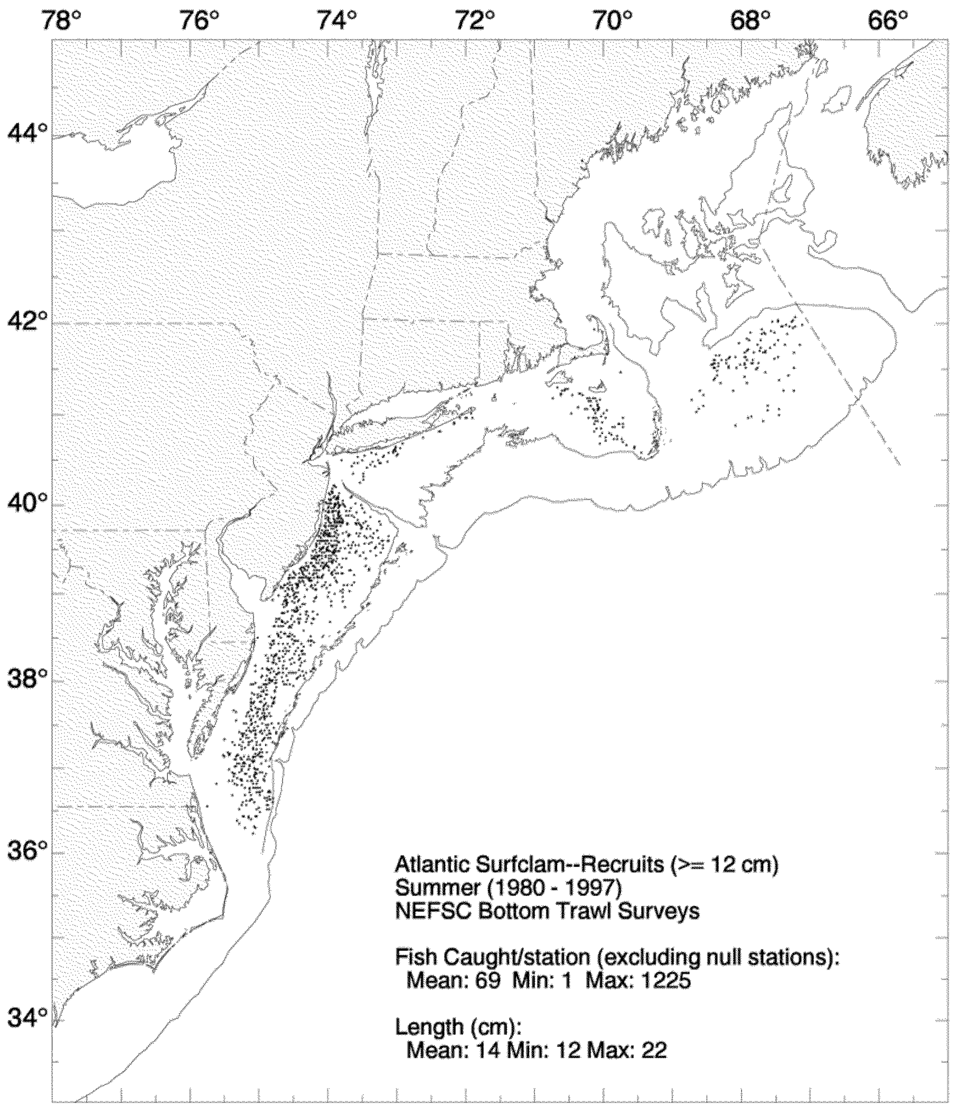

Figure 2. cont'd.

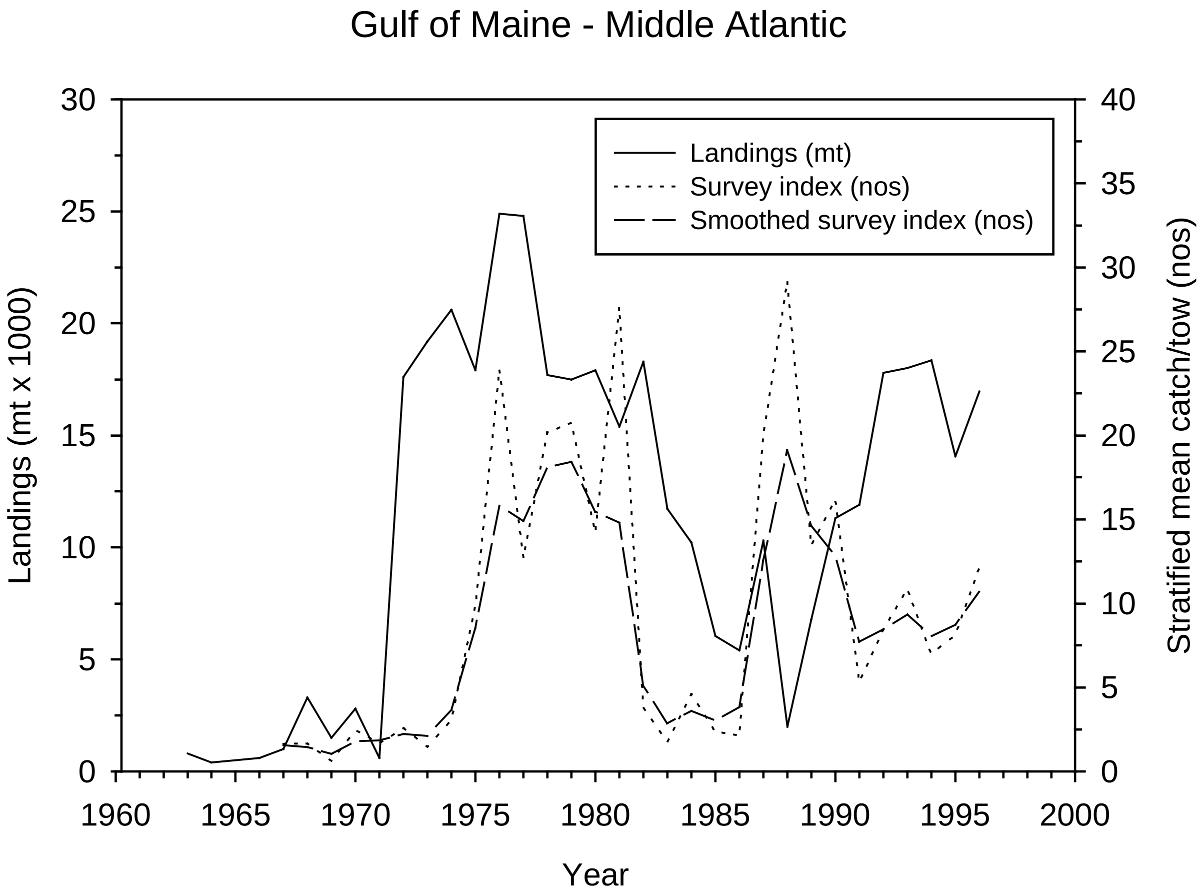

Figure 3. Commercial landings and survey indices (from the NEFSC surveys) for Atlantic surfclam from the Gulf of Maine and Middle Atlantic Bight regions.

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Publications and Reports of the Northeast Fisheries Science Center

The mission of NOAA's National Marine Fisheries Service (NMFS) is "stewardship of living marine resources for the benefit of the nation through their science-based conservation and management and promotion of the health of their environment." As the research arm of the NMFS's Northeast Region, the Northeast Fisheries Science Center (NEFSC) supports the NMFS mission by "planning, developing, and managing multidisciplinary programs of basic and applied research to: 1) better understand the living marine resources (including marine mammals) of the Northwest Atlantic, and the environmental quality essential for their existence and continued productivity; and 2) describe and provide to management, industry, and the public, options for the utilization and conservation of living marine resources and maintenance of environmental quality which are consistent with national and regional goals and needs, and with international commitments." Results of NEFSC research are largely reported in primary scientific media (*e.g.*, anonymously-peer-reviewed scientific journals). However, to assist itself in providing data, information, and advice to its constituents, the NEFSC occasionally releases its results in its own media. Those media are in three categories:

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