NOAA Technical Memorandum NMFS-NE-134

Essential Fish Habitat Source Document:

Sea Scallop, *Placopecten magellanicus*, 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
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Essential Fish Habitat Source Document:

Sea Scallop, *Placopecten magellanicus*, 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^c).

^aRobins, 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.

^bTurgeon, 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.

^eWilliams, 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.

^dRice, D.W. 1998. Marine mammals of the world: systematics and distribution. Soc. Mar. Mammal. Spec. Publ. 4; 231 p.

^eCooper, 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-

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

JEFFREY N. CROSS, CHIEF ECOSYSTEMS PROCESSES DIVISION NORTHEAST FISHERIES SCIENCE CENTER

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INTRODUCTION

The Atlantic sea scallop, *Placopecten magellanicus* (Gmelin), is a bivalve mollusk of the family Pectinidae (Figure 1). It occurs on the continental shelf of the northwest Atlantic, from the north shore of the Gulf of St. Lawrence south to Cape Hatteras, North Carolina. An economically important species, the sea scallop is managed under the New England Fishery Management Council's Sea Scallop Management Plan (NEFMC 1993). This Essential Fish Habitat source document provides information on the life history and habitat characteristics of sea scallops inhabiting U.S. waters in the Gulf of Maine, Georges Bank, and the Middle Atlantic Bight.

LIFE HISTORY

A brief synopsis of the life history characteristics of sea scallops is provided in Amendment #4 to the Sea Scallop Fishery Management Plan (NEFMC 1993). More detailed information is presented here and in reviews by Stewart and Arnold (1994) and Shumway *et al.* (in prep.). The life cycle of the sea scallop is summarized in Figure 2.

EGGS

The average diameter of spawned eggs is 66.8±1.6 µm (Langton *et al.* 1987). After fertilization, the eggs are slightly heavier than seawater and probably remain on the sea floor as they develop into the first free-swimming larval stages. The incubation period of eggs maintained in the laboratory at 13-17°C is 32 days (Langton *et al.* 1987).

LARVAE

The two larval stages of the sea scallop, trochophore and veliger, are pelagic. The larvae remain planktonic for over a month after hatching (Posgay 1982). The larvae drift with water currents, but can also swim freely, and appear to follow a daily vertical migration of up to several meters, occupying shallower depths at night (Tremblay and Sinclair 1988, 1990a; Gallager et al. 1996; Manuel et al. 1996b). They have been shown to migrate in response to both tidal and solar stimuli (Manuel et al. 1997). During the day larvae tend to aggregate at the thermocline (Gallager et al. 1996) and are seldom found below the thermocline until 21 days post-fertilization (Manuel et al. 1996b). Tremblay and Sinclair (1990b) found that in well-mixed areas, larvae were distributed evenly through the water column, while in stratified areas they aggregated above the pycnocline.

During the planktonic stage, the shell, eye spots, and foot develop (Naidu 1991). A description of larval

development in the laboratory has been published by Culliney (1974) and growth of larval scallops in the laboratory has been studied by Hurley *et al.* (1986). Duration of the larval stages is shorter at higher temperatures and where food is more plentiful.

Identification of planktonic sea scallop larvae in the wild has only recently been described (Tremblay *et al.* 1987) and the horizontal distribution of larval scallops is still largely unknown. Since scallop larvae are planktonic, speculation about their movement is based largely on the flow of currents in and around spawning areas.

The mechanism by which recruitment occurs in major production areas is conjectural at this point. The beds on Georges Bank, particularly in the vicinity of the Northern Edge, Northeast Peak, and Great South Channel, are thought to be self-sustaining at a fairly consistent and relatively high rate of recruitment. This is probably because the larvae are retained in the Georges Bank gyre (see Figure 3) long enough for metamorphosis to be complete. During the spawning season in September, the water currents form tight gyrals which confine the larvae to the Georges Bank area prior to settlement. Good year classes on Georges Bank are associated with tight autumnal gyrals and poorer year classes are associated with loose gyrals (Posgay 1950).

Tremblay and Sinclair (1986) reported on the horizontal distribution of larval scallops within the Bay of Fundy. They found that there was some transport of larvae within the Bay via the residual currents but that most of the larvae either remained in, or were returned to, the area of major spawning. They were further able to demonstrate that although there was larval dispersal beyond the Bay of Fundy, no large-scale exchange between Georges Bank and the Scotian Shelf occurred.

There is considerable uncertainty about the mechanisms involved in recruitment to the Mid-Atlantic region. Densities and distributions of scallops in the Hudson Canyon and sections off the Virginia Capes and Cape Hatteras are variable. It is thought that beds in productive areas, such as the New York Bight, may not be self-sustaining, but may supply recruits for beds located further down-current (i.e., to the south). The occasional heavy recruitment to the Middle Atlantic may be the result of periodically occurring optimal reproductive conditions, or augmented recruitment from spawning on Georges Bank, when years of loose gyrals may result in much of the spawn being swept away to these more southerly areas (Shumway et al., in prep.). Because of this variability and the fact that the spawn from southern populations is normally swept away from the parent population, these populations are not self-sustaining and the fishery in these areas varies from year to year.

It is not known if the beds on the coast of Maine or in deeper waters of the Gulf of Maine are self-sustaining.

SPAT

At the end of their pelagic existence, the larvae enter the pediveliger stage with the development of a foot and secreting threads (byssus) which are used to attach to hard surfaces (Culliney 1974). Spatfall (the settling of larval scallops to the bottom), and the period immediately following, is thought to be a time that is particularly important in the formation of scallop beds (Posgay 1953) and in determining year class size (Bourne 1965; Caddy 1975). Settlement is assumed to occur by mid-December (Thouzeau et al. 1991a). The transition from freeswimming to the benthos at a size of about 0.25 mm is accompanied by drastic changes in diet, morphology, and locomotory ability and it is conceivable that mortality may be as high during natural settlement as when spat are reared artificially (Bourne 1965; Culliney 1974).

Merrill and Edwards (1976) noted that when scallop spat settle they are extremely delicate and do not survive on shifting sand bottoms. Those that land on sedentary branching plants and animals or any other hard surface on or above the ocean floor which offers freedom of shell movement on all sides may have a distinct survival advantage (Larsen and Lee 1978).

The availability of suitable surfaces on which to settle seems to be a primary requirement for successful scallop reproduction. Larvae show a thigmotactic settling response to shell fragments and small pebbles; settlement occurs predominantly on the undersides of these objects (Caddy 1968; Culliney 1974). Spat also settle on navigation buoys (Merrill and Edwards 1976), on the red alga Rhodomela conferroides (Naidu 1970), on hydroids such as Hydrallmania, and on the tubes made by amphipods (Larsen and Lee 1978). Spat settlement varies significantly with depth and water turbulence: numbers of spat generally increase with increasing depth, but this relationship is less evident with increasing water turbulence (Pearce et al. 1998).

A close association between the bryozoan, *Eucratea loricata* (= *Gemelleria* of Baird 1953), and larval scallops has been reported. *Eucratea* attach to adult scallops, and have been found to contain large numbers of 2-5 mm immature scallops (Baird 1953; Caddy 1972). These scallops detach themselves from the bryozoan when about 4-5 mm and then attach themselves to the shells of larger scallops (Dow 1956).

Pediveligers appear to be able to delay metamorphosis for up to one month until suitable physical substrates for settlement are encountered; however, the effects of this delay on the scallops is not known (Culliney 1974).

JUVENILES AND ADULTS

During the second growing season, juvenile scallops (5-12 mm) leave the original substrate on which they

settled and attach themselves to shells and bottom debris by byssus (Dow and Baird 1960). As young sea scallops age, they become less mobile and show less tendency to attach to the bottom using byssal threads (Caddy 1972; MacKenzie 1979). The frequency of byssal thread production also decreases with age (Caddy 1972). The maximum size for frequent byssal attachment and swimming was found to be 110 mm (5-6 yrs old).

Scallops are relatively active until they are about 80 mm long, swimming in response to disturbances, such as predation (Baird 1954) and commercial dredging (Caddy 1968). While swimming, young scallops can also be carried long distances by currents (Baird 1954).

There is no evidence of mass migrations by scallops. The movements of sea scallops are usually localized and random or current-assisted. Numerous tagging experiments have shown that once aggregations of adults are formed, they remain fixed (Baird 1954; Dickie 1953; Naidu 1970; Schick 1979). Posgay (1981) reported that tagged scallops came primarily from downcurrent areas on Georges Bank. While 80% of the tagged returns had traveled < 3 km and 97% had traveled < 16 km, a few individuals were reported to have traveled more than 48 km in 2+ years. Melvin et al. (1985) reported primarily circular movements of tagged scallops on Georges Bank corresponding to the clockwise gyre on the Bank (Figure 3), and while 85% of the tagged returns had moved < 15 km, several had moved > 50 km.

REPRODUCTION

The sexes in sea scallops are separate and can be distinguished by their color as the gonads ripen prior to spawning. Hermaphroditism is known to occur, but is not common (e.g., Merrill and Burch 1960; Worms and Davidson 1986). Mature gametes have been seen in females as young as one year (Langton *et al.* 1987) and scallops have been reported to spawn after their first growth ring has formed (25-35 mm shell height) (Naidu 1970; MacKenzie 1979). However, most sea scallops do not become sexually mature until the spring of their third year (about 75 mm; Posgay 1982).

Egg number is directly related to shell height and maximum egg production is not reached until several years after maturity. It is estimated that scallops produce 1-270 million eggs per individual (Langton *et al.* 1987); by age 4 (85-90 mm) a female will release about two million eggs. Gonad output (egg number) is greater in scallops from shallow water (10-20 m), where the food supply is greater and temperatures are higher, than in scallops from deep water (170-180 m) (MacDonald and Thompson 1986; MacDonald *et al.* 1987; Barber *et al.* 1988). There is evidence of latitudinal differentiation in fecundity. For example, MacDonald and Thompson (1988) found that scallops from New Jersey are more fecund that those from locations further north, although

variation along a depth gradient on a microgeographic scale may be as great or greater than variation on latitudinal scale (MacDonald and Thompson 1985a; 1985b; 1988).

Shumway et al. (1988) summarized the gametogenic cycle of sea scallops from Maine as follows. During January, gametogenesis has already reached the early developmental stage; energy reserves are at their lowest level (Robinson et al. 1981), and energy must be mobilized from the accumulated reserves. During spring, gametogenesis is underway, gonad size increases, feeding begins with coincidental spring phytoplankton blooms and energy reserves begin to accumulate. During summer (June-August), food is plentiful, gametes are ripening and energy is derived from spring storage and from food intake (Robinson et al. 1981). Spawning takes place in September/October and the animals enter a reproductively quiescent or rest period. Barber et al. (1988) found that primary oogenesis in sea scallops from Boothbay Harbor, Maine, was initiated in February, secondary oogenesis in March and vitelogenesis after June. Spawning and reabsorption of mature ova was evident in September and to a greater extent in October, after which the animals were in a period of recovery (December/January).

Spawning generally occurs synchronously when the males extrude sperm and the females release eggs en masse into the water, but it may occur over a more protracted period of time depending on environmental conditions. It has been suggested that year-class strength may correlate with the degree of spawning synchrony, rather than fecundity per se (egg number) (Langton *et al.* 1987).

There is a major annual spawning period in the late summer to fall (August to October) (Parsons et al. 1992a) although spring or early summer (June-July) spawning also occurs at specific locations. The timing of spawning can vary with latitude, starting in summer in southern areas and in fall in the northern areas. For example, MacKenzie et al. (1978) reported that off the coast of North Carolina and Virginia, spawning generally occurred as early as July and that further north on the Mid-Atlantic shelf spawning occurred in August. However, there are exceptions to this pattern. MacDonald and Thompson (1988) report that scallops off of New Jersey spawned up to two months later than scallops from Newfoundland (September-November versus August-early late September). They found no clearly identifiable latitudinal trends in the timing of spawning.

More recently, however, researchers have discovered a biannual spawning cycle on the Mid-Atlantic shelf south of the Hudson Canyon, with spawning occurring both in the spring and fall (DuPaul *et al.* 1989; Schmitzer *et al.* 1991; Davidson *et al.* 1993). Kirkley and DuPaul (1991) found that the spring spawning event in the Mid-Atlantic is the more predictable and dominant spawning event, and that fall spawning is minor and temporally irregular, sometimes not occurring at all. Schmitzer *et al.* (1991)

also reported that the spring spawning was of longer duration and the scallops showed greater fecundity than in the fall

North of the Hudson Canyon there is generally a single annual spawning event starting in late summer or early fall. However, there are some reports of biannual spawning (spring and fall) in the Gulf of Maine and Georges Bank, with the fall spawning being dominant (Barber et al. 1988; DiBacco et al. 1995). On Georges Bank fall spawning generally occurs in late September or early October (Posgay and Norman 1958; MacKenzie et al. 1978; McGarvey et al. 1992; DiBacco et al. 1995). In Cape Cod Bay, spawning occurs in late September and early October (Posgay 1950). In the Gulf of Maine spawning occurs in August and September (Drew 1906; Welch 1950; Baird 1953; Culliney 1974; Robinson et al. 1981; Barber et al. 1988). In the Bay of Fundy the spawning period extends from late July to November (Stevenson 1936; Dickie 1955; Beninger 1987; MacDonald and Thompson 1988; Dadswell and Parsons 1992).

Scallops beds generally spawn synchronously in a short time, going from completely ripe to completely spent in less than a week (Posgay and Norman 1958; Posgay 1976). "Dribble spawning" (periodic pulsed spawning) has been reported in scallops from Newfoundland coastal waters (Naidu 1970) and possibly New Jersey in June and July (MacDonald and Thompson 1988). A rapid temperature change, the presence in the water of sperm from other scallops, agitation, or tides may trigger scallop spawning (Parsons *et al.* 1992a).

FOOD HABITS

Sea scallops are suspension or filter feeders, using currents created by short hairs (cilia) on the gills to move and filter water containing suspended particulate material. The principal food is phytoplankton, diatoms, and microscopic animals (such as peridinians, tintinnids, ciliate protozoa), but detrital particles (pieces of dead organic matter) and associated bacteria can also contribute to energy gain during periods of low phytoplankton concentrations (Bordon 1928; Stevenson 1936; Shumway et al. 1987; Grant and Cranford 1991). Dissolved organic matter (absorbed through the tissues) has been suggested to be an additional minor source of nutrition, particularly for scallop larvae (Marshall and Lee 1991).

Elevated concentrations of inorganic suspended material and clay-sized particles can interfere with scallop feeding, but the presence of low concentrations (< 0.5 mg/L) of inorganic particulate matter in the diet may be important in enabling sea scallops to utilize phytoplankton cells efficiently (Cranford and Gordon 1992).

Components of the diet vary in abundance depending on the geographic location of the bed. Sea scallops in coastal areas and bays encounter more seaweed and seagrass detritus and may be exposed periodically to significant amounts of resuspended inorganic material. Offshore scallops feed mainly on phytoplankton and resuspended organic material. Phytoplankton appear to be necessary for meeting scallop energy demands, although seaweed detritus may be an important food supplement in nearshore environments (Grant and Cranford 1991).

Shumway et al. (1987) reported on the seasonal changes in the gut contents of sea scallops. populations were compared, one in shallow water (20 m depths) and the other in deep water (180 m). A total of 27 species of algae, ranging in size from 10-350 µm were identified, plus a number of miscellaneous items including pollen grains, ciliates, zooplankton tests, and considerable detrital material and bacteria. The benthic and pelagic food species were equally represented in the shallow water population; however, benthic species outnumbered pelagic species in the deep water population. Seasonal variations in occurrence of food items were found and these coincided with bloom periods for the individual algal species. The gut contents generally reflected the available organisms in the surrounding habitat and it was concluded that sea scallops are opportunistic filter feeders which take advantage of both benthic and pelagic food.

GROWTH

Growth rates show considerable variation among populations. Some of the highest growth rates have been observed on Georges Bank and in Port-au-Port Bay (Stewart and Arnold 1994). Scallops from the Gulf of St. Lawrence generally have slower growth rates than Gulf of Maine and Bay of Fundy scallops (Chouinard and Mladenov 1991). Growth rates have been shown to be positively correlated to water temperature and food availability, and negatively related to depth, latitude, and age.

Larval growth rates of 3.1-3.5 μ m/day (Gallager *et al.* 1996) and 4.3-4.8 μ m/day (Manuel *et al.* 1996b) have been reported in mesocosm studies. Culliney (1974) reported that development to straight-hinge veliger took 4 days at 12-18°C, development to pediveliger took 28 days at 15°C, and settlement occurred in 35 days. The duration of the larval stage on Georges Bank is 40-60 days (Thouzeau *et al.* 1991a). Wildish and Saulnier (1992) reported juvenile growth rates of 0.047-0.199 mm/day at 1.2-7.6°C, and adult growth rates of 0.02-0.121 mm/day in the laboratory.

PREDATION

Scallop larvae are planktonic, thus they are potentially preyed upon by filter feeders and planktonic carnivores (Langton and Robinson 1990).

Teleost predators of juvenile scallops include cod

(Medcof and Bourne 1964), wolffish (Medcof and Bourne 1964; Nelson and Ross 1992), ocean pout (Bigelow and Schroeder 1953), sculpins (Caddy 1968; 1973), American plaice (Medcof and Bourne 1964; Naidu and Meron 1986; Robert *et al.* 1986), winter flounder (Caddy 1968, 1973), yellowtail flounder (Naidu and Meron 1986), and eel pout (Bigelow and Schroeder 1953). Crabs and lobsters may also prey on scallops (Elner and Jamieson 1979).

Medcof and Bourne (1964) reported that small juveniles were ingested whole by the sun starfish *Crossaster papposus*. Naidu and Scalpen (1976) reported that juvenile starfish, *Asterias vulgaris*, were the principal predators of scallop spat in spat traps in Newfoundland.

HABITAT CHARACTERISTICS

The habitat characteristics of sea scallops are summarized in Table 1. This information concentrates primarily on beds in U.S. water; most information on beds north of the Bay of Fundy was not considered.

LARVAE

In laboratory studies, larvae were viable at temperatures of 12-18°C (mass mortalities occurred at higher temperatures), and at salinities as low as 10.5 ppt, although salinities ranging from 16.9-30 ppt are preferred (Culliney 1974). In nature, larvae settle on gravelly sand which may contain shell fragments (Langton and Robinson 1990), and often actively select substrates covered with a biofilm (Parsons *et al.* 1993). Prior to settlement, larvae circulate with residual currents ranging from 6-25 cm/s and tend to concentrate in the upper 10 m of the water column (Tremblay and Sinclair 1990a; Parsons *et al.* 1992b).

JUVENILES

In laboratory studies, juveniles have been maintained successfully at 1.2-15°C (Manuel and Dadswell 1991; Wildish and Saulnier 1992; Barbeau and Scheibling 1994b; Kleinman *et al.* 1996). The optimal current velocity for feeding and growth has been shown to be 10 cm/s; currents stronger than 10 cm/s inhibit feeding (Wildish and Saulnier 1992). Stronger currents may be experienced in nature (e.g., up to 25 cm/s in Passamaquoddy Bay), but these can be avoided by feeding during periods of slack water (i.e., low and high tide). In nature juveniles are found mainly on gravel, small rocks, shells and silt (Thouzeau *et al.* 1991a; Parsons *et al.* 1992b), and maximum densities of juveniles on Georges Bank have been found at depths of 62-91 m (Thouzeau *et al.* 1991a).

ADULTS

Adults experience optimal growth at temperatures of 10-15°C; temperatures above 21°C are lethal (Stewart and Arnold 1994); spawning occurs at 9.0-11.2°C (MacKenzie et al. 1978). They prefer full strength seawater and salinities of 16.5 ppt or lower are lethal (Stewart and Arnold 1994). Adults are generally found on coarse substrate, usually gravel, shells and rock (MacKenzie et al. 1978; Langton and Robinson 1990; Thouzeau et al. 1991a; Stewart and Arnold 1994), in areas with at least some water movement (optimal growth occurs at 10 cm/s), which is critical for feeding, oxygen and removal of waste (Wildish and Saulnier 1992; Stewart and Arnold 1994). They are typically found at depths ranging from 18-110 m (MacKenzie et al. 1978; Serchuk et al. 1982; Naidu and Anderson 1984; Stewart and Arnold 1994), but tend to be found shallower in more northern populations (e.g., 2 m in estuaries and embayments along the coast of Maine).

GEOGRAPHICAL DISTRIBUTION

The sea scallop is distributed on the Atlantic continental shelf of North America from the north shore of the Gulf of St. Lawrence to Cape Hatteras, North Carolina (Stewart and Arnold 1994). In the United States, sea scallops are located on Georges Bank, in the Mid-Atlantic, and in the Gulf of Maine.

Sea scallops typically occur at depths ranging from 18-110 m, but they may also occur in waters as shallow as 2 m in estuaries and embayments along the Maine coast (Serchuk *et al.* 1982; Naidu and Anderson 1984). In southern areas they are rarely found at depths less than 55 m (Squires 1962), primarily due to temperature variation with depth (Bourne 1965). Although sea scallops are rarely found deeper than about 110 m, some deep-water populations have been found as deep as 384 m (Merrill 1959); deep-water populations at 170 to 180 m have been reported in the Gulf of Maine (Barber *et al.* 1988).

Sea scallops often occur in dense aggregations called beds. Beds may be sporadic (perhaps lasting for a few years) or essentially permanent (e.g., commercial beds supporting the Georges Bank fishery) (Figure 4). The highest concentration of many permanent beds appears to correspond to areas of suitable temperatures, food availability, substrate, and where physical oceanographic features such as fronts and gyres may keep larval stages in the vicinity of the spawning population (Thouzeau *et al.* 1991a, b; Tremblay and Sinclair 1992).

EGGS AND LARVAE

Eggs and larvae are not enumerated by the Northeast Fisheries Science Center (NEFSC) Marine Resources

Monitoring, Assessment and Prediction (MARMAP) program (P. Berrien, NMFS, NEFSC, Highlands, NJ, personal communication). Until recently sea scallop larvae could not even be identified in the wild (Tremblay *et al.* 1987).

However, the NOAA Estuarine Living Marine Resources (ELMR) program has identified the presence of eggs and larvae in a number of New England bays and estuaries (Table 2; Jury *et al.* 1994).

JUVENILES AND ADULTS

Summer NEFSC sea scallop surveys collected scallops from Georges Bank to Cape Hatteras (Figure 5). The Gulf of Maine was not surveyed. From New Jersey to Cape Hatteras scallops were concentrated along the edge of the continental shelf. Scallops were concentrated further inshore from the Hudson Canyon north to Long Island and in the Great South Channel. Scallops were found throughout Georges Bank; however, central Georges Bank near Cultivator Shoals (where density is known to be low) was not sampled. Highest densities were found in the northeastern area of Georges Bank, an area that traditionally provides the largest harvests and is the most valuable sea scallop fishery (MacKenzie *et al.* 1978; Serchuk *et al.* 1979; Posgay 1981).

The NOAA ELMR program has identified the presence of juvenile and adult sea scallops in a number of New England bays and estuaries (Table 2; Jury *et al.* 1994). They are listed as 'abundant' within the Gulf of Maine.

In the Gulf of Maine, non-stratified surveys and data from commercial catches indicate scallop beds occur in inshore areas from Penobscot Bay and eastward, as well as in Cape Cod Bay. Offshore beds occur at Jeffreys Basin, Cashes Ledge, Fippinnies Ledge, Jeffreys Ledge, near Three-Dory Ridge, Toothaker Ridge, off Jonesport and Machias bays, and Stellwagen Bank (Serchuk and Rak 1983; Serchuk and Wigley 1984). The largest catches in the Gulf of Maine have traditionally occurred on Jeffreys Ledge and Fippinnies Ledge (Serchuk and Rak 1983; Serchuk and Wigley 1984).

STATUS OF THE STOCKS

Total commercial sea scallop landings (U.S. and Canada) peaked at 26,671 metric tons (mt of meat) in 1978, declined to 9,781 mt in 1984, increased to 22,831 mt in 1991, but dropped back down to 9,822 mt in 1995 (Northeast Fisheries Science Center 1997). The total U.S. landings peaked in 1990 at 17,174 mt, but dropped to 7,300 mt in 1993, and have remained at comparable levels through 1995 (Murawski and Wigley 1995; Northeast Fisheries Science Center 1997).

Total landings from Georges Bank declined to 9,900

mt in 1993, 32% lower than the 1992 total of 14,600 (Murawski and Wigley 1995), and to 2,991 mt in 1995, the lowest in the 1957-1995 period (Northeast Fisheries Science Center 1997). U.S. Georges Bank landings decreased 90% from 1990 (9,982 mt) to 1994 (1,140 mt) as a result of several years of poor recruitment and redirection of vessel effort toward the Mid-Atlantic region (Northeast Fisheries Science Center 1997; Figure 6). In 1995, landings remained about the same as in 1994, due at least in part to area closures in December 1994 (Northeast Fisheries Science Center 1997), but landings increased to 2,180 mt in 1996, a 120% increase over 1995 (Lai and Rago 1998). Relative abundance indices dropped to their lowest level in 1993, but rebounded to median levels in 1996 (Northeast Fisheries Science Center 1997; Figure 6). This is probably a result of area closures on the Bank.

U.S. landings from the Gulf of Maine in 1993 were 800 mt, 10% higher than in 1991 (Murawski and Wigley 1995), dropped to 525 mt by 1994 and have increased to 715 mt in 1996 (Lai and Rago 1998; Figure 6).

U.S. landings from the Mid-Atlantic Bight averaged 6,000 mt in 1994 and 1995, about twice as high as 1993 landings, and were primarily driven by the strong 1990 and 1991 year classes (Northeast Fisheries Science Center 1997; Figure 6). Landings dropped to 4,677 mt in 1996, a 23% decrease from 1995 (Lai and Rago 1998). Relative abundance indices increased between 1992 and 1995 but decreased substantially from 1995 to 1996 (Northeast Fisheries Science Center 1997; Figure 6).

The September 1997 report to Congress, 'Status of Fisheries of the United States' (National Marine Fisheries Service 1997), states that the Atlantic sea scallop is currently in an overfished condition.

RESEARCH NEEDS

literature search uncovered substantial information on the biology of the giant sea scallop. However, more information on the genetic differentiation of scallop populations is needed to better understand recruitment and stock structure in the species. Previous of population discrimination have used morphometric or allozyme analyses; Zouros and Gartner-(1985)found no significant differentiation among 10 scallop populations near Nova However, current techniques for examining Scotia. genetic differentiation are much more powerful, and genetic markers which could potentially be very useful for studying the genetic structure of sea scallop populations have recently been developed (e.g., microsatellite DNA: Manuel et al. 1996a; Gjetvaj et al. 1997; Herbinger et al. 1998; random amplified polymorphic DNA: Patwary et al. 1994).

Existing information on recruitment processes (i.e., which beds are self-sustaining and which are not) is rather vague. Relatively little information exists since the

identification of planktonic sea scallop larvae in the wild was not possible until quite recently (Tremblay *et al.* 1987). New genetic techniques (see above) make it possible to track the movement of larvae, providing very detailed information about recruitment processes (e.g., Manuel *et al.* (1996a) used a microsatellite DNA probe to distinguish the population of origin of veliger larvae in a large mesocosm).

Better information on the effect of environmental variables on growth, survival, and production is needed. Current information is restricted for the most part to EFH levels 1 and 2, although some level 3 data exist, e.g., there is some evidence of fecundity and growth rate differences with depth (or temperature). There is almost no information on the scallop egg stage in the wild; what is known is restricted to morphometrics (i.e., egg sizes) and fecundity. More data on the duration of the egg stage, mortality rates, predation, and substrate effects are needed.

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Table 1. Summary of life history and habitat parameters for sea scallop, *Placopecten magellanicus*. Abbreviations: BOF = Bay of Fundy, GB = Georges Bank, MAB = Mid-Atlantic Bight, NB = New Brunswick, NF = Newfoundland, NH = New Hampshire, NJ = New Jersey, PB = Passamaquoddy Bay, SS = Scotian Shelf.

Life Stage	Size and Growth	Habitat	Substrate
Eggs ¹	Average diameter of spawned eggs: 66.8±1.6 μm. Average wet weight of spawned eggs: 1.6 x 10 ⁻⁷ g.	Fertilized eggs are slightly heavier than seawater and probably remain on the sea floor as they develop into the first free-swimming larval stages.	
Larvae ²	late September. Development times: 4 days to straight hinge veliger at 12-18°C; 28 days to pediveliger at 15°C, 40 days at 12-16°C; 35 days to settlement. Pediveligers delayed metamorphosis until suitable substrates were found.	Fall density on GB ranged 120-1500/m². Vertical distribution: in mixed areas, larvae distributed evenly through water column; in stratified areas, larvae aggregated above pycnocline. Vertical migration: in response to solar cues; shallower during night than day (in Grand Manan, NB, larvae concentrated in upper 10 m of water column; high concentration in upper 5 m only at night). Able to penetrate the thermocline at ~200 μm length. PB veligers generally found shallower than GB veligers.	Larvae settle in areas of gravelly sand with shell fragments; select substrates covered with a biofilm. In laboratory studies, larvae settle on undersides of pebbles, shell and glass fragments. Artificial substrates have been successful as settlement substrate.
Juveniles ³		Maximum density of 1 and 2 year old scallops (0.88-1.65 juveniles/m²) found on NE Georges Bank at depths of 62-91 m; age 1 were less dispersed than age 2 and mainly located on a gravel-pebble deposit in the northern half of the Bank. In a PB study, 76% of the scallops moved an average of 3.3 m in 4 months.	Mainly found on gravel, small rocks, shells and silt, which permit attachment of juveniles. The preferred substrates are associated with low concentrations of inorganics (optimal for feeding).
Adults ⁴	mm, 4 - 89.5 mm, 5 – 101.7 mm, 6 - 112.0 mm, 7 - 121.0 mm.	Wide distribution on offshore banks and coastal waters from NF to Cape Hatteras; from low tide level to ~100 m line; generally shallower in northern populations. On GB, 4 spatially separated sub-populations (Northern Edge & NE Peak, SE Part, Great South Channel east, Great South Channel west) are linked by larval transport; largest concentrations on N Edge and NE Peak at 37-100 m, intermediate in central area, at 70-110 m and low to the south. In Maine, more abundant on Fippenies Ledge (0.3±0.7 - 1.0±2.2 /m²) than on Jeffreys Ledge (0.2±0.5/m²); depths ranged from 56-84m. In MAB, largest concentrations south of Long Island and off coast of NJ; collected at depths of 31-80 m (average 55 m).	Generally found in seabed areas with coarse substrate, usually gravel, shells and rock. Typically abundant in areas with low levels of inorganic suspended particulates (fine clay size particles).
Spawning Adults ⁵	Some scallops mature as early as 30 mm, but most mature at 90 mm (in PB). Scallops 50-90 mm (shell height) spawn first, followed by those > 90 mm (on GB). Reproductive effort increases with age and size.	Spawning scallops are found at a variety of depths ranging from 13-180 m: Georges Bank, 60-68 m (egg production is highest on N Edge and NE Peak); Damariscotta River, shallowwater study site, 13-20 m; Gulf of Maine, deep-water study site, 170-180 m; Mid-Atlantic Bight (Long Island to Hatteras), 37-64 m.	Spawning more common on gravel than any other sediment type.

¹ Langton et al. (1987)

² Culliney (1974), Beninger (1987), Langton and Robinson (1990), Tremblay and Sinclair (1990a, b; 1992), Thouzeau et al. (1991a), McGarvey et al. (1992), Parsons et al. (1993), Gallager et al. (1996), Manuel et al. (1996a, b; 1997), Robinson et al. (1996)

³ Thouzeau et al. (1991a), Parsons et al. (1992b), Wildish and Saulnier (1992), Stewart and Arnold (1994), Kleinman et al. (1996)

⁴ Mackenzie et al. (1978), Langton and Robinson (1990), Thouzeau et al. (1991a), McGarvey et al. (1992, 1993), Wildish and Saulnier (1992), Stewart and Arnold (1994)

⁵ Posgay and Norman (1958), Mackenzie et al. (1978), Barber et al. (1988), MacDonald and Thompson (1988), Kirkley and Dupaul (1991), Schmitzer et al. (1991), McGarvey et al. (1992), Parsons et al. (1992a)

Table 1. cont'd.

Life Stage	Temperature	Salinity	Currents	Prey
Eggs ¹	Eggs maintained in the laboratory at 13-17°C hatched 32 days post fertilization.			
Larvae ²	Laboratory reared larvae from NH were viable at 12-18°C; mass mortalities when reared at 19°C. Duration of larval stages shorter at higher temperatures. One study shows that larval abundance on GB peaks when thermal stratification is high.	Laboratory reared larvae from NH viable at salinities as low as 10.5 ppt (at 15°C for 42 h), although behavior was abnormal (lack of swimming). Swimming and other behaviors appeared normal within 16.9-30 ppt.	Larvae circulate with residual currents ranging from 6-25 cm/s. In BOF there is some transport of larvae via residual currents, but most larvae remain near area of major spawning. Larval exchange influenced by duration and depth of planktonic drift, gyre strength and weak cross-isobath flow. Differences in vertical distribution may be related to differences in horizontal transport by currents.	Filter feeders, primarily on phytoplankton, diatoms and microscopic animals; also dissolved organic matter, detrital particles and bacteria.
Juveniles ³	Juveniles successfully maintained at temperatures of 1.2-15°C in laboratory. High exfoliation of epithelial cells at 21°C; damage to gills, mantles, and gonads at exposure to 14.7°C followed by 21°C. Consumption rate by predators, rate of scallop movement, and growth rate increases with temperature.		Optimum velocity for growth is 10 cm/s; > 10 cm/s can result in reduced feeding rate; but this can be avoided in areas with strong currents by feeding during periods of slack water (high & low tide). Juveniles from GB drift with currents to the south as they grow older. Byssal attachment by scallops < 12 mm shell height may be an adaptation to strong currents.	Opportunistic feeders on suspended particles, primarily phytoplankton.
Adults ⁴	Optimal growth at 10-15°C; lethal temperature: > 21°C.	Optimal survival at salinities approaching full-strength seawater; lower lethal threshold: 16.5 ppt.	Water movement critical for dispersal, replenishment of suspended food particles, supply of oxygen and removal of waste products. Adults drift with tidal currents (on GB, 39% moved toward the SE, 30% to the NW). A 1989 study showed southward drift of adults. Strong tidal currents (> 10 cm/s) inhibit feeding; fluctuations in scallop clearance rates are directly related to flow velocity; clearance rates significantly lower at low (< 4 cm/s) and high (> 9 cm/s) flow speeds.	Filter feeders on phytoplankton and other suspended organic particulates from the water; gut contents reflect available organisms in the immediate environment. Stomach contents of scallops (90-140 mm shell height) from shallow and deep study sites in Maine: 27 species of algae ranging in size from 10-350 µm, pollen grains, ciliates, zooplankton tests, detrital material and bacteria.
Spawning Adults ⁵	Spawning in nature occurs at temperatures ranging from 6.5-16°C. GB: typically 9-11.2°C. Isle of Shoals, NH: 14-16°C; spawning triggered in lab when temperature was raised abruptly from 5 to 10°C, or from 12 to 15°C. MAB: spawning coincided with decreasing and stable temperatures in winter/spring and increasing temperatures in fall; 6.5°C off Long Island; 11°C off Chincoteague, VA. Spawning may be delayed by low summer temperatures.		Tidally related spawning cue in PB; spawning occurs just prior to spring tides.	

Karney (1996)
 Culliney (1974), Tremblay and Sinclair (1986, 1990a, b; 1992), Thouzeau et al. (1991a), Tremblay et al. (1994), Manuel et al. (1996a, 1997)

³ Shumway et al. (1987), Manuel and Dadswell (1991), Thouzeau et al. (1991a), Wildish and Saulnier (1992), Manuel and Dadswell (1993), Barbeau and Scheibling (1994b), Stewart and Arnold (1994), Kleinman et al. (1996), Potter et al. (1997)

⁴ Posgay (1981), Shumway *et al.* (1987), Thouzeau *et al.* (1991a), Wildish and Saulnier (1992), Stewart and Arnold (1994), Cranford *et al.* (1998) ⁵ Culliney (1974), MacKenzie *et al.* (1978), Schmitzer *et al.* (1991), Parsons *et al.* (1992a)

Table 1. cont'd.

Life Stage	Predators	Spawning	Notes
Eggs ¹	Predation by a variety of bottom predators.	see spawning adults	Fecundity ranges from 1-270 million eggs/ individual. Egg production is positively correlated with age and shell height (exponentially).
Larvae ²	Scallop larvae potentially preyed on by filter feeders and larval and adult planktivores.		Early larval stages (trocophore and veliger) are pelagic, swim freely. PB larvae reach the veliger stage faster than larvae on GB; a shortened trocophore stage may allow earlier vertical migration and control of horizontal movement (strong tides in this area make larvae vulnerable to being washed away). No large scale exchange between GB and the SS; self-seeding likely for the Great South Channel & NE Peak; simulations indicate significant larval exchange between NE Peak, Southern Flank and Great South Channel.
Juveniles ³	Potential groundfish predators include cod, American plaice, Atlantic wolffish and winter flounder. Lab studies have shown that rock crabs, lobsters and sea stars are also potential predators (especially of smaller scallops). Larger predators had distinct preference for larger scallops; but scallops > 70 mm were rarely preyed upon.		The distribution of juveniles is determined by the hydrodynamic regime during the larval stage and by differential post-larval mortality at settlement. In laboratory studies, growth rate and metabolic condition increased with temperature; swimming frequency did not affect growth, but increased mass of adductor muscle. Somatic production (i.e., growth) increases to age 5 then levels off.
Adults ⁴	Adults damaged by dredging and trawling activity have been shown to be preyed upon by rock crabs starfish, lobster, and groundfish (winter flounder and sculpins).	see spawning adults	Sea scallop populations on GB are the largest, densest and most intensively exploited of the species. The Northern Edge (2.91 g/m²) and NE Peak (1.32 g/m²) have the highest biomass (meat weight) density (other areas on GB much lower, 0.29-0.44). By area, the NE Peak has the highest biomass (20599 mt) followed by the Northern Edge (4291 mt). Sex ratios: GB, 1:1; MAB, 1.4:1 (male: female, 1975 studies).
Spawning Adults ⁵		GB: spawning in late Sept-early Oct; reports of a semi-annual reproductive cycle on northeast GB: spring spawning in May-June and fall spawning in Sept-Oct; fall is larger, more synchronized and consistent among years, spring is more protracted, erratic. Maine: in shallow sites, spawning in Sept-Oct; deep water sites, possible minor spawning in May, more abrupt spawning in Oct (1 month later than in shallow sites). PB: relatively consistent reproductive cycle with major spawning in late July-late Sept (peaked Aug); similar to spawning period in southeast NF and areas of GOM. NJ: mostly Sept-Nov, some in June-July. MAB: Semi-annual gametogenic cycle; spring (May/June) and fall (Nov) spawning; spring spawning stronger, more predictable than fall (longer duration and greater fecundity in spring).	GOM: deep-water scallops produced fewer eggs than shallow-water scallops; lowered fecundity reduces the probability that the deep-water population is self-sustaining. MAB: the significance of the spring spawning event to recruitment processes uncertain. In spring, deep water scallops initiated gamete production about 1 month later than shallow water scallops. Reproduction and size attained by individuals are largely controlled by local environmental conditions. Fecundity and production greater, but longevity reduced in NJ scallops (avg. longevity 1-10 yrs), than in those from NB and NF (avg. 1-12 yrs).

Langton et al. (1987), Stewart and Arnold (1994)
 Tremblay and Sinclair (1986, 1992), Langton and Robinson (1990), Tremblay et al. (1994), Manuel et al. (1996a)
 Elner and Jamieson (1979), Langton et al. (1987), Thouzeau et al. (1991a), Barbeau and Scheibling (1994a, b), Kleinman et al. (1996)
 MacKenzie et al. (1978), McGarvey et al. (1992, 1993), Stewart and Arnold (1994)
 Posgay and Norman (1958), Culliney (1974), MacKenzie et al. (1978), Beninger (1987), Barber et al. (1988), MacDonald and Thompson (1988), DuPaul et al. (1989), Kirkley and DuPaul (1991), Schmitzer et al. (1991), Dadswell and Parsons (1992), McGarvey et al. (1992), DiBacco et al. (1995)

Table 2. Relative abundance of egg, larval, juvenile, and adult sea scallops, *Placopecten magellanicus*, in New England bays and estuaries by salinity zone, based on Estuarine Living Marine Resources (ELMR) data in Jury *et al.* (1994).

	Eggs		Larvae			Juveniles			Adults			
	<u>T</u>	<u>M</u>	<u>S</u>	<u>T</u>	<u>M</u>	<u>S</u>	<u>T</u>	<u>M</u>	<u>S</u>	<u>T</u>	<u>M</u>	<u>S</u>
Passamaquoddy Bay		R	A		R	A		R	A		R	A
Englishman/Machias Bays			A		R	A		R	A		R	A
Narraguagus Bay			A		R	A		R	A		R	A
Blue Hill Bay			A		R	A		R	A		R	A
Penobscot Bay		R	A		R	A		R	A		R	A
Muscongus Bay			С			С			С			С
Damariscotta River			С			С			С			С
Sheepscot River			С			С			С			С
Kennebec/Androscoggin Rivers			R			R			R			R
Casco Bay			С			С			С			С
Saco Bay			R			R			R			R
Wells Harbor												
Great Bay						R			С			С
Merrimack River												
Massachusetts Bay			С			С			С			С
Boston Harbor			na			na			R			R
Cape Cod Bay			A			A			A			A

Salinity zone: T = tidal fresh, M = mixing zone, S = seawater.

Relative abundance: H = highly abundant, A = abundant, C = common, R = rare, blank = not present, na = no data available.

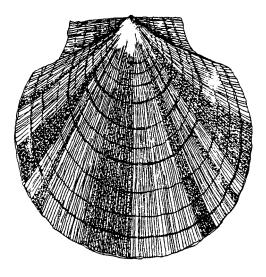


Figure 1. The sea scallop, *Placopecten magellanicus* (from Mullen and Moring 1986).

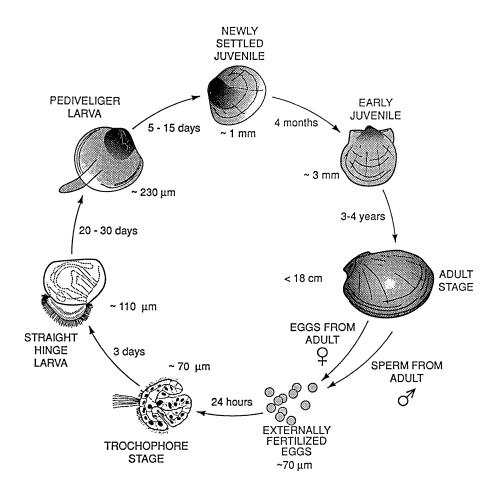


Figure 2. Generalized life cycle of the sea scallop (from Stewart and Arnold 1994).

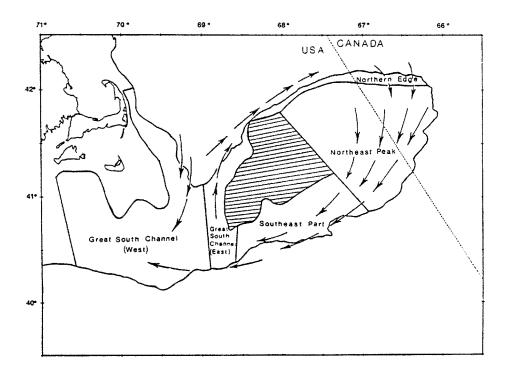


Figure 3. Map of Georges Bank indicating the five sub-regions and the clockwise flow of the residual current (from McGarvey *et al.* 1993).

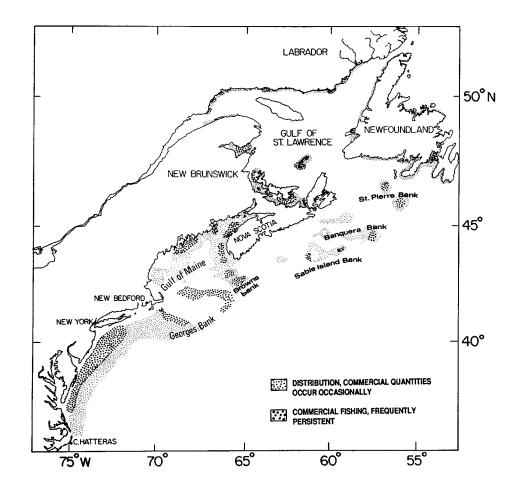


Figure 4. Distribution of sea scallop spawning beds off the northeast coast of North America (from Shumway *et al.*, in prep.).

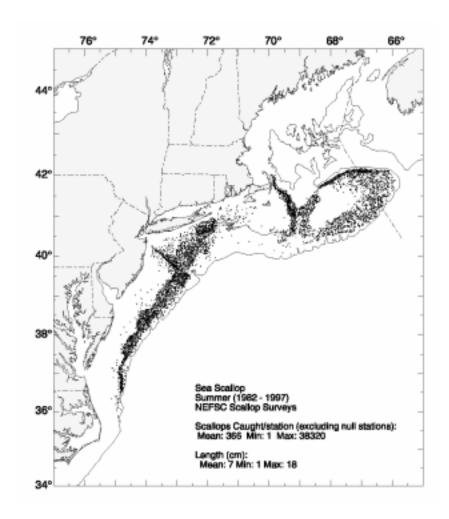


Figure 5. Distribution of sea scallops collected during NEFSC scallop surveys during summer 1982-1997. Dots represent stations where scallops were taken [see Reid *et al.* (1999) for details].

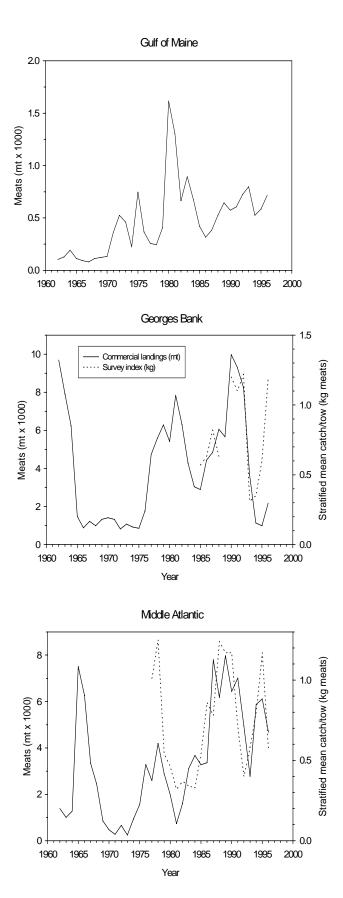


Figure 6. Commercial landings and survey indices of sea scallops for the Gulf of Maine, Georges Bank, and Mid-Atlantic.

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