NOAA Technical Memorandum NMFS-NE-189

Essential Fish Habitat Source Document:

Sea Scallop, *Placopecten magellanicus*, Life History and Habitat Characteristics

Second Edition

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

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Editorial Notes on "Essential Fish Habitat Source Documents" Issued in the NOAA Technical Memorandum NMFS-NE Series

Editorial Production

For "Essential Fish Habitat Source Documents" issued in the *NOAA Technical Memorandum NMFS-NE* series, staff of the Northeast Fisheries Science Center's (NEFSC's) Ecosystems Processes Division largely assume 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 is performed by, and all credit for such production rightfully belongs to, the staff of the Ecosystems Processes Division.

Internet Availability and Information Updating

Each original issue of an "Essential Fish Habitat Source Document" is published both as a paper copy and as a Web posting. The Web posting, which is in "PDF" format, is available at: http://www.nefsc.noaa.gov/nefsc/habitat/efh.

Each issue is updated at least every five years. The updated edition will be published as a Web posting only; the replaced edition(s) will be maintained in an online archive for reference purposes.

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.* 1991a*, bb), mollusks (*i.e.*, Turgeon *et al.* 1998c), and decapod crustaceans (*i.e.*, Williams *et al.* 1989d), and to follow the Society for Marine Mammalogy's guidance on scientific and common names for marine mammals (*i.e.*, Rice 1998c). 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 1998f; McEachran and Dunn 1998g).

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

^bRobins, C.R. (chair); Bailey, R.M.; Bond, C.E.; Brooker, J.R.; Lachner, E.A.; Lea, R.N.; Scott, W.B. 1991b. World fishes important to North Americans. *Amer. Fish. Soc. Spec. Publ.* 21; 243 p.

^cTurgeon, 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.

^dWilliams, 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.

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

^fCooper, J.A.; Chapleau, F. 1998. Monophyly and interrelationships of the family Pleuronectidae (Pleuronectiformes), with a revised classification. *Fish. Bull. (Washington, DC)* 96:686-726.

^gMcEachran, J.D.; Dunn, K.A. 1998. Phylogenetic analysis of skates, a morphologically conservative clade of elasmobranchs (Chondrichthyes: Rajidae). *Copeia* 1998(2):271-290.

PREFACE TO SECOND EDITION

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 NOAA Fisheries to assist the regional fishery management councils in the implementation of EFH in their respective fishery management plans.

NOAA Fisheries 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 a series EFH species reports (plus one consolidated methods report). The EFH species reports are a survey of the important literature as well as original analyses of fishery-independent data sets from NOAA Fisheries 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 understandably have begun to be referred to as the "EFH source documents."

NOAA Fisheries 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.

The initial series of EFH species source documents were published in 1999 in the NOAA Technical Memorandum NMFS-NE series. Updating and review of the EFH components of the councils' Fishery Management Plans is required at least every 5 years by the NOAA Fisheries Guidelines for meeting the Sustainable Fisheries Act/EFH Final Rule. The second editions of these species source documents were written to provide the updated information needed to meet these requirements. The second editions provide new information on life history, geographic distribution, and habitat requirements via recent literature, research, and fishery surveys, and incorporate updated and revised maps and graphs. This second edition of the sea scallop EFH source document is based on the original by David B. Packer, Luca M. Cargnelli, Sara J. Griesbach, and Sandra E. Shumway, with a foreword by Jeffrey N. Cross (Packer et al. 1999).

Identifying and describing EFH are the first steps in the process of protecting, conserving, and enhancing essential habitats of the managed species. Ultimately, NOAA Fisheries, 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.

Contents

INTRODU	JCTION	1
	TORY	
	PHICAL DISTRIBUTION	
	CHARACTERISTICS	
	VLEDGEMENTS	
	NCES CITED	
KLILKLI	VCES CITED	0
	Tables	
Table 1.	Relative abundance of egg, larval, juvenile, and adult sea scallop, <i>Placopecten magellanicus</i> , in	1.0
T-1.1. 2	New England bays and estuaries by salinity zone.	
Table 2.	Summary of sea scallop habitat parameters based on the pertinent literature.	13
	Figures	
Figure 1.	The sea scallop, <i>Placopecten magellanicus</i> (photograph by Dann Blackwood, USGS)	
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	
Figure 4.	Distribution of sea scallop spawning beds off the northeast coast of North America.	
Figure 5.	Distribution and abundance of sea scallops collected during NEFSC scallop surveys during summer 1979-	
	1993	
Figure 6.	Distribution and abundance of sea scallops collected during NEFSC scallop surveys during summer 1994-	
	2003	21

INTRODUCTION

The Atlantic sea scallop, Placopecten magellanicus (Gmelin), is a bivalve mollusk of the family Pectinidae and order Ostreoida (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. The Atlantic sea scallop is one of the most economically important species in the northeast United States, and supports the most valuable wild scallop fishery in the world. The 2003 U.S. landings of 25,476 MT (meats) had an ex-vessel value of about \$229,000,000. The sea scallop fishery is managed under the New England Fishery Management Council's Sea Scallop Management Plan (NEFMC 2003). 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

Besides the account given here, the life history of the sea scallop is summarized in NEFSC (2004), Stewart and Arnold (1994), Mullen and Moring (1986), and Shumway *et al.* (in prep.). An overview of scallop biology and the early history of the fishery may be found in Bourne (1964). The life cycle of the sea scallop is depicted in Figure 2.

EGGS

Sea scallops are among the most fecund of bivalves, producing gametes starting in the first or second year and eventually producing up to 270 million eggs (Langton et~al.~1987). The average diameter of spawned eggs is $66.8\pm1.6~\mu m$ (Langton et~al.~1987). After fertilization, the eggs are slightly heavier than seawater and probably remain on the sea floor until they develop into the first free-swimming larval stages.

LARVAE

The first 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 move independently on a small scale. Veliger larvae have been observed to move vertically at

velocities of 1-1.5 mm s⁻¹, upward by ciliary action and downward by sinking with the valves closed (Manuel *et al.* 2000). 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. Manuel *et al.* (2000) observed that veligers were able to detect and react to small temperature gradients. In stratified areas, the veliger's position relative to the thermocline may be beneficial for dispersion, growth, and feeding.

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 previously been described (Tremblay *et al.* 1987) but the horizontal distribution of larval scallops is still largely unknown. Since scallop larvae are planktonic, larval transport is influenced by the flow of currents in and around spawning areas.

Sea scallops on Georges Bank are thought to be self-sustaining because many of the larvae from this region are retained in the Georges Bank gyre (see Figure 3) long enough for metamorphosis to be complete (Tremblay et al. 1994). Good year classes on Georges Bank are associated with tight autumnal gyres that tend to retain larvae on the Bank and poorer year classes are associated with loose gyres (Posgay 1950). McGarvey et al. (1993) found a correlation between egg production on the Northern Edge and Peak area of Georges Bank and recruitment on Georges Bank, possibly due to the high percentage of spawning stock biomass that was located in the Northern Edge and Peak during the study period.

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 by 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 occurred between Georges Bank and the Scotian Shelf.

SPAT

At the end of their pelagic existence, the larvae enter the pediveliger stage with the development of a foot and byssus gland which secretes threads that 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 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 on Georges Bank (Thouzeau *et al.* 1991a). The transition to the benthos of the free-swimming larvae occurs at a size of about 0.25 mm shell height and is accompanied by drastic changes in diet, morphology, and locomotory ability. Mortality during natural settlement may be as high as when spat are reared artificially (Bourne 1965; Culliney 1974).

When scallop spat settle, they are extremely delicate and do not survive on shifting sand bottoms (Merrill and Edwards 1976). Those that land on sedentary branching plants, animals or on any other hard surface that offers freedom of shell movement 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 scallop survival. Pediveligers 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 amphipod tubes (Larsen and Lee 1978). Spat settlement varies 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 exists between the bryozoan, *Eucratea loricata* (= *Gemelleria* of Baird 1953), and post-larval scallops. *Eucratea* may contain large numbers of 2-5 mm juvenile scallops (Baird 1953; Caddy 1972). The scallops detach themselves from the bryozoan when about 4-5 mm in shell height and then attach themselves to the shells of larger scallops (Dow 1956).

Pediveligers may delay metamorphosis for a considerable time until suitable physical substrates for settlement are encountered; however, the effects of this delay on the scallops are not known (Culliney 1974).

JUVENILES AND ADULTS

Juvenile scallops (5-12 mm shell height) leave the original substrate on which they have settled and attach themselves by byssus to shells and bottom debris (Dow and Baird 1960). As the young scallops grow older, they lose their byssal attachment (Caddy 1972). Scallops are relatively active until they are about 80 mm shell height, they swim to escape predation (Baird 1954) and disturbances such as commercial dredging (Caddy 1968). While swimming, young scallops can be carried long distances by currents (Baird 1954). The

maximum size for frequent swimming was found to be 110 mm (4-6 yrs old).

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 down-current 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 the color of the gonads (red for females, white for males) as they 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 observed in females as young as one year (Langton *et al.* 1987) and scallops have been reported to spawn during their second year (Naidu 1970; MacKenzie 1979). However, significant egg production may not occur until age 4.

Fecundity is directly related to shell height and maximum egg production is not reached until several years after maturity. It is estimated that female 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 typically greater and temperatures 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 differences in fecundity. MacDonald and Thompson (1988) found that scallops from New Jersey were 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 a latitudinal scale (MacDonald and Thompson 1985a, b; 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 underwent a period of recovery (December/January).

Spawning generally occurs synchronously when 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 (Langton *et al.* 1987).

A major annual spawning period occurs during late summer to fall (August to October) (Parsons et al. 1992a) although spring or early summer spawning can also occur, especially in the Mid-Atlantic (Barber et al. 1988; DuPaul et al. 1989; Schmitzer et al. 1991; Davidson et al. 1993; Almeida et al. 1994; Dibacco et al. 1995). The timing of spawning can vary with latitude, starting in summer in southern areas and in fall in the northern areas. 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 versus late (September-November August-early They found no clearly identifiable latitudinal trends in the timing of spawning. A biannual spawning cycle on the Mid-Atlantic shelf has been reported 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 spring spawning in the Mid-Atlantic is the more predictable and dominant spawning event, while fall spawning is minor, temporally irregular, and sometimes does not occur. 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; Almeida *et al.* 1994, 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" over an extended time period has been reported in scallops from Newfoundland coastal waters (Naidu 1970) and possibly in the Gulf of Maine (Langton *et al.* 1987) and in New Jersey in June and July (MacDonald and Thompson 1988). A rapid temperature change, the presence in the water of gametes from other scallops, agitation, or tides may trigger scallop spawning (Parsons *et al.* 1992a).

FOOD HABITS

Sea scallops are suspension filter feeders, using currents created by cilia on the gills to move and filter water containing suspended particulate material. Their diet primarily consists of phytoplankton and microzooplankton (such as ciliated protozoa), but particles of detritus can also be ingested, especially 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 as an additional minor source of nutrition, particularly for scallop larvae (Marshall and Lee 1991). Palp-pedal feeding (using the ciliated end of the foot to bring organic matter from biofilms to the labial palps) as well as DOM absorption may also be used by postsettlement scallops, during the time that feeding structures on the gill develop (Veniot et al. 2003).

Juvenile scallops can ingest up to 7 mg of food per liter filtered, but at very high concentrations of food or suspended detritus, the rate of feeding (clearance rate) is reduced (Bacon *et al.* 1998). Current velocities of more than 10 cm/sec also reduce feeding activity in juveniles (Wildish and Saulnier 1992). In adult scallops, feeding is inhibited at current velocities exceeding 25 cm/sec or more, and when scallops have been feeding heavily (Pilditch and Grant 1999a). Elevated concentrations of inorganic suspended material and clay-sized particles can interfere with 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 efficiently utilize phytoplankton cells (Cranford and Gordon 1992). Sea scallops have the ability to select higher-quality food particles for ingestion and create pseudofeces from rejected matter (Bacon *et al.* 1998).

Dietary components vary depending on geographic location. 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 appears necessary to meet scallop energetic demands, although seaweed detritus may be an important food supplement in nearshore environments (Grant and Cranford 1991).

Shumway et al. (1987) documented seasonal changes in the gut contents of sea scallops. scallop populations were compared, one in shallow water (20 m depths) and one 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 detrital material, and bacteria. Benthic and pelagic food species were equally represented in the shallow water population; however, benthic species outnumbered pelagic species in the deep-water scallops. In both populations, seasonal variations in food items occurred and coincided with bloom periods of individual algal species. The gut contents generally reflected the available organisms in the surrounding habitat, indicating that sea scallops are opportunistic filter feeders which take advantage of both benthic and pelagic food. Cranford and Hill (1999) report that ingestion rates of sea scallops in Nova Scotia are highest in spring and fall; spring and fall are the periods of highest and lowest food concentrations, respectively, during the year. These periods of maximum ingestion are driven by physiological needs of the scallops rather than the concentration of food particles in the water.

GROWTH

Larval growth rates of 3.1-3.5 µm/day (Gallager *et al.* 1996) and 4.3-4.8 µm/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). The growth rate of post-larval (< 2 mm) scallops in Passamaquoddy Bay was estimated to be 0.03-0.06 mm/d, with the growth rate increasing with size (Parsons *et al.* 1993b). A laboratory study of post-larval development at 14°C found growth rates between

0.008-0.028 mm/d, depending on diet (Milke *et al.* 2004). Wildish and Saulnier (1992) reported juvenile growth rates of 0.047-0.199 mm/d at 1.2-7.6°C, and adult growth rates of 0.02-0.121 mm/d in the laboratory.

Adult 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 generally decreases with depth (Schick et al. 1988; Thouzeau et al. 1991a). A study by Pilditch and Grant (1999b) indicated that food concentration was more important than temperature in controlling growth rates for 2-yearold scallops. Estimates of von Bertalanffy growth coefficients for Georges Bank sea scallops range from 141.8-152.5 mm for the mean maximum shell height L_{∞} , and 0.26-0.34/y for the growth coefficient K (Thouzeau et al. 1991a), while the only published Mid-Atlantic growth equation has parameters $L_{\infty} = 151.8$ and K = 0.30 (Serchuk *et al.* 1979).

PREDATION

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

Predation on juvenile and adult sea scallops decreases with shell height (Stokesbury and Himmelman 1995). Teleost predators of scallops include Atlantic cod (Medcof and Bourne 1964), wolffish (Medcof and Bourne 1964; Nelson and Ross 1992), eel pouts such as ocean pout (Klein-MacPhee and Collette 2002), sculpins (Caddy 1968, 1973), American plaice (Medcof and Bourne 1964; Naidu and Meron 1986; Robert *et al.* 1986), winter flounder (Caddy 1968, 1973), and yellowtail flounder (Naidu and Meron 1986).

Invertebrate predators include crabs (Cancer spp.) and lobsters (Homarus americanus) that crush or chip away the shells (Elner and Jamieson 1979; Stokesbury and Himmelman 1995; Nadeau and Cliche 1998; Wong and Barbeau 2003). Infestation by the boring polychaete Polydora websteri, abundant off eastern North America, can weaken the shell and increase vulnerability to lobsters (Bergman et al. 1982). A number of sea star species, including Leptasterias polaris, Astropecten americanus, Crossaster papposus, Asterias forbesi, and Asterias vulgaris, have been observed to consume sea scallops (Medcof and Bourne 1964; Naidu and Scalpen 1979; Franz and Worley 1982; Barbeau and Scheibling 1994a, b; Nadeau and Cliche 1998; Wong and Barbeau 2003). Medcof and Bourne (1964) reported that small juvenile scallops

were ingested whole by *Crossaster papposus*. *Astropecten americanus* is also holophagous (Franz and Worley 1982), and appears to be a predator of juvenile sea scallops in the Mid-Atlantic Bight. Naidu and Scalpen (1979) reported that juvenile *Asterias vulgaris* were the principal predators of scallop spat in spat traps in Newfoundland. A textured substrate such as shell or pebble significantly reduced the predation rate of *Asterias vulgaris* on 11-15 mm juvenile scallops in an experimental setting (Wong and Barbeau 2003).

GEOGRAPHICAL DISTRIBUTION

The sea scallop is distributed on the Atlantic continental shelf of North America from the Strait of Belle Isle, Newfoundland, to Cape Hatteras, North Carolina (Posgay 1957). In the United States, sea scallops are located on Georges Bank, in the Mid-Atlantic Bight, and in the Gulf of Maine.

Sea scallops typically occur at depths ranging from 18-110 m, but may also occur in waters as shallow as 2 m in estuaries and embayments along the Maine coast and in Canada (Serchuk *et al.* 1982; Naidu and Anderson 1984). In southern areas, scallops are primarily found at depths between 45-75 m, and are less common in shallower water (25-45 m) due to high temperature (Bourne 1965). Although sea scallops are not common at depths greater than about 110 m, some populations have been found as deep as 384 m (Merrill 1959), and deep-water populations at 170-180 m have been reported in the Gulf of Maine (Barber *et al.* 1988; Schick *et al.* 1988).

Sea scallops often occur in 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 were not enumerated by the Northeast Fisheries Science Center (NEFSC) Marine Resources Monitoring, Assessment and Prediction (MARMAP) program. 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 1; Jury *et al.* 1994).

JUVENILES AND ADULTS

Summer NEFSC sea scallop surveys sample from Georges Bank to Cape Hatteras (Figure 5 and Figure 6, NEFSC 2004). The Gulf of Maine is not routinely surveyed. In the Mid-Atlantic Bight, from Long Island to Cape Hatteras, scallops occur mostly between 40 and 70 m, with the densest concentrations near Hudson Canyon and off of Delaware Bay. Further north, the highest concentrations occur in the Great South Channel and in the eastern portion of Georges Bank, areas that traditionally have provided large harvests (MacKenzie *et al.* 1978; Serchuk *et al.* 1979; Posgay 1981).

In more recent years, scallop density has increased markedly in the three groundfish closed areas that have been closed to scallop fishing for most of the time since December, 1994 (Figure 6; Murawski *et al.* 2000, NEFSC 2004), and in the Mid-Atlantic Bight, especially off of New Jersey, Delaware, and Maryland. The increases in the Mid-Atlantic Bight are due to a combination of increased recruitment, reduced fishing mortality, and the rotational closure of an area south of Hudson Canyon for a three year (1998-2001) period (NEFSC 2004).

The NOAA ELMR program has identified the presence of juvenile and adult sea scallops in a number of New England bays and estuaries (Table 1; Jury *et al.* 1994).

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 on Jeffreys Basin, Cashes Ledge, Fippinnies Ledge, Jeffreys Ledge, near Three-Dory Ridge, Toothaker Ridge, off Jonesport and Machias bays, and on Stellwagen Bank (Serchuk and Rak 1983; Serchuk and Wigley 1984). The largest offshore catches in the Gulf of Maine have traditionally occurred on Jeffreys Ledge and Fippinnies Ledge (Serchuk and Rak 1983; Serchuk and Wigley 1984).

HABITAT CHARACTERISTICS

The habitat characteristics of sea scallops are summarized in Table 2.

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 were preferred (Culliney 1974). In nature, larvae initially settle on gravelly sand or shell fragments (Langton and Robinson 1990), or filamentous animals and plants, many of which colonize the backs of adult scallops (Stokesbury and Himmelman 1995). Settling larvae often actively select substrates covered with a biofilm (Parsons *et al.* 1993a). 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 nature juvenile scallops are mainly found on gravel, small rocks, shells and silt (Thouzeau et al. 1991a; Parsons et al. 1992b), or attached to branching bryozoans, hydroids or algae (Stokesbury Himmelman 1995). Gravel bottoms have higher juvenile and adult scallop abundances than other substrates (Thouzeau et al. 1991a; Kostylev et al. 2003). 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). Frenette and Parsons (2001) determined the best conditions for survival for juveniles < 35 mm were temperatures below 18°C and salinities > 25 ppt. The optimal current velocity for feeding and growth is 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 can be avoided by feeding during periods of slack water (i.e., low and high tide). Maximum densities of juveniles on Georges Bank have been found at depths of 62-91 m (Thouzeau et al. 1991a).

ADULTS

Adult sea scallops are generally found on firm sand, gravel, shells and rock (MacKenzie *et al.* 1978; Langton and Robinson 1990; Thouzeau *et al.* 1991a; Stewart and Arnold 1994). Other invertebrates associated with scallop beds include sponges, hydroids, anemones, bryozoans, polychaetes, mussels, moon snails, whelks, amphipods, crabs, lobsters, sea stars, sea cucumbers, and tunicates (Kenchington 2000).

Adult scallops 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). Adults prefer full strength seawater, and salinities of 16.5 ppt or lower are lethal (Stewart and Arnold 1994). Scallops require some water movement (optimal growth occurs at 10 cm/s) for feeding, oxygen uptake, and removal of waste (Wildish and Saulnier 1992; Stewart and Arnold 1994).

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Table 1. Relative abundance of egg, larval, juvenile, and adult sea scallop, *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 J		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	Α		R	A
Narraguagus Bay			A		R	A		R	Α		R	A
Blue Hill Bay			A		R	A		R	Α		R	A
Penobscot Bay		R	A		R	A		R	Α		R	A
Muscongus Bay			С			С			С			С
Damariscotta River			С			С			С			С
Sheepscot River			С			С			С			С
Kennebec/Androscoggin			R			R			R			R
Rivers												
Casco Bay			С			C			С			C
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.

Table 2. Summary of sea scallop habitat parameters based on the pertinent literature.

Life Stage	Size and Growth	Habitat	Substrate
Eggs 1	Average diameter of spawned eggs: $66.8\pm1.6~\mu m$. Average wet weight of spawned eggs: $1.6\times10^{-7}~g$.	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	Larval length 0.06-0.3 mm. Larvae grow through 4 larval stages in 4-6 weeks (on Georges Bank), then settle to the bottom (assumed to occur by mid-December); maximum larval settlement in Passamaquoddy Bay occurs in 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. Growth rates: 3.1-3.5 μm/day (Trinity Bay, Newfoundland), 4.3-4.8 μm/d (Passamaquoddy Bay and Georges Bank).	distributed evenly through water column; in stratified areas, larvae aggregated above pycnocline. Larvae capable of detecting and using thermocline. Vertical migration: in response to tidal, solar cues; Passamaquoddy Bay veligers generally found shallower than Georges Bank veligers.	Larvae settle in areas of gravelly sand, shell fragments or on hydroids, bryozoans and sponges; 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	Size ~1-80 mm shell height. Average shell height at age: 1-14.4 mm, 2-44.5 mm (50.8 at 66-70 m deep, 33.8 mm at 81-85 m). Average shell height decreases with increasing depth. Growth of Bay of Fundy scallops peaks in July and is best predicted by temperature. Growth rate in one study: 0.047-0.199 mm/day shell height.	Maximum density of 1 and 2 year old scallops (0.88-1.65 juveniles/m²) found on northeast 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 Passamaquoddy Bay study, 76% of the scallops moved an average of 3.3 m in 4 months.	Mainly found on gravel, small rocks, shells, and among branching animals and plants that permit attachment of juveniles.
Adults ⁴	6-112.0 mm, 7-121.0 mm. Growth rates of Bay of Fundy scallops in lab: 0.020-0.121 mm/d shell height.	Wide distribution on offshore banks and coastal waters from Newfoundland to Cape Hatteras; from low tide level to ~100 m line; generally shallower in northern populations. On Georges Bank, 4 spatially separated subpopulations (Northern Edge and Northeast Peak, Southeast Part, Great South Channel east, Great South Channel west) are linked by larval transport; largest concentrations on Northern Edge and Northeast Peak at 37-100 m. In Maine, mostly in shallow water (< 20m), but also on Fippenies Ledge and Jeffreys Ledge (56-84 m), and some also observed in very deep water (~175m). In Mid-Atlantic Bight, largest concentrations from Hudson Canyon south to off of Delaware Bay; collected at depths of 27-80 m (average 55 m).	Generally found in seabed areas with firm sand, gravel, shells and cobble substrate. 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 Passamaquoddy Bay). Scallops 50-90 mm (shell height) spawn first, followed by those > 90 mm (on Georges Bank). Reproductive effort increases with age and size.	See Adults.	See Adults.

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. (1993b); Stokesbury and Himmelman (1995); Gallager et al. (1996); Manuel et al. (1996a, b, 1997); Robinson et al. (1996); Manuel et al. (2000).

³ Thouzeau et al. (1991a); Parsons et al. (1992b); Wildish and Saulnier (1992); Stewart and Arnold (1994); Stokesbury and Himmelman (1995); 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); Barber *et al.* (1988); NEFSC (2004).

⁵ Posgay and Norman (1958); Mackenzie *et al.* (1978); MacDonald and Thompson (1988); Kirkley and DuPaul (1991); Schmitzer *et al.* (1991); McGarvey et al. (1992); Parsons et al. (1992a).

Table 2. 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 New Hampshire 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 Georges Bank peaks when thermal stratification is high.	although behavior was abnormal (lack of swimming). Swimming and other behaviors	strength, and weak cross-isobath flow. Differences in vertical distribution may be related to differences in horizontal transport by currents.	Feed on phytoplankton, 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. Optimum survival at temperatures less than 18°C. Consumption rate by predators, rate of scallop movement, and growth rate increases with temperature.	For optimum survival, salinities > 25 ppt.	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 and low tide). Juveniles from Georges Bank 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.	Feed on suspended particles, primarily phytoplankton. Newly settled juveniles may also feed on biofilms.
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 Georges Bank, 39% moved toward the southeast, 30% to the Northwest). A 1989 study showed southward drift of adults. Strong tidal currents (> 25 cm/s) inhibit feeding; fluctuations in scallop clearance rates are related to flow velocity.	Filter feeders on phytoplankton (mostly diatoms) 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. Georges Bank: typically 9-11.2°C. Isle of Shoals, New Hampshire: 14-16°C; spawning triggered in lab when temperature was raised abruptly from 5 to 10°C, or from 12 to 15°C. Mid-Atlantic Bight: 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, Virginia. Spawning may be delayed by low summer temperatures.		Tidally related spawning cue in Passamaquoddy Bay; spawning occurs just prior to spring tides.	

¹ Karney (1996).

² Culliney (1974); Tremblay and Sinclair (1986, 1990a, b, 1992); Thouzeau *et al.* (1991a); Tremblay *et al.* (1994); Manuel *et al.* (1996a, 1997).

² Culliney (19/4); Tremblay and Sinclair (1986, 1990a, b, 1992); Thouzeau *et al.* (1991a); Tremblay *et al.* (1994); Manuel *et al.* (1996, 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); Frenette and Parsons (2001).

⁴ Posgay (1981); Shumway *et al.* (1987); Thouzeau *et al.* (1991a); Wildish and Saulnier (1992); Stewart and Arnold (1994); Cranford *et al.* (1998); Pilditch and Grant (1999a).

⁵ Culliney (1974); MacKenzie et al. (1978); Schmitzer et al. (1991); Parsons et al. (1992a).

Table 2. 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 (trochophore and veliger) are pelagic, swim freely. Passamaquoddy Bay larvae reach the veliger stage faster than larvae on Georges Bank; a shortened trochophore stage may allow earlier vertical migration and control of horizontal movement (strong tides in this area make larvae vulnerable to being advected away). No large scale exchange between Georges Bank and the Scotian Shelf; self-seeding likely for the Great South Channel and Northeast Peak; simulations indicate significant larval exchange between Northeast Peak, Southern Flank, and Great South Channel.
Juveniles ³	Predators include Atlantic cod, American plaice, yellowtail and winter flounder, ocean pout, Atlantic wolffish, crabs, lobsters, and sea stars.		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	Predators of adults include Atlantic wolffish, lobsters, and sea stars. Adults damaged by dredging and trawling activity have been shown to fall prey to crabs, starfish, lobster, and groundfish (winter flounder and sculpins).	See spawning adults	Sea scallop populations on Georges Bank have traditionally been the largest, densest, and most intensively exploited of the species, though very high densities and catches have occurred recently in the Mid-Atlantic Bight. In a 1989 study, the Northern Edge (2.91 g/m²) and Northeast Peak (1.32 g/m²) have the highest biomass (meat weight) density (other areas on Georges Bank much lower, 0.29-0.44). By area, the Northeast Peak has the highest biomass (20599 mt) followed by the Northern Edge (4291 mt). Sex ratios: Georges Bank, 1:1; Mid-Atlantic Bight, 1.4:1 (male: female, 1975 studies).
Spawning Adults ⁵		Georges Bank: spawning in late Septearly Oct; reports of a semi-annual reproductive cycle on northeast Georges Bank: spring spawning in May-June and fall spawning in SeptOct.; fall is larger, more synchronized and consistent among years, spring is more protracted, erratic. Maine: in shallow sites, spawning in SeptOct.; deep water sites, possible minor spawning in May, and more abrupt spawning in Oct. (1 month later than in shallow sites). Passamaquoddy Bay: relatively consistent reproductive cycle with major spawning in late July-late Sept. (peaked Aug.); similar to spawning period in southeast Newfoundland and areas of Gulf of Maine. New Jersey: mostly SeptNov., some in June-July. Mid-Atlantic Bight: 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).	Gulf of Maine: deep-water scallops produced fewer eggs than shallow-water scallops;

¹ Langton et al. (1987); Stewart and Arnold (1994).

Langton *et al.* (1987); Stewart and Arriola (1994).

2 Tremblay and Sinclair (1986, 1992); Langton and Robinson (1990); Tremblay *et al.* (1994); Manuel *et al.* (1996a).

3 Elner and Jamieson (1979); Langton *et al.* (1987); Thouzeau *et al.* (1991a); Barbeau and Scheibling (1994a, b); Kleinman *et al.* (1996).

4 MacKenzie *et al.* (1978); McGarvey *et al.* (1992, 1993); Stewart and Arnold (1994); NEFSC (2004).

5 Posgay and Norman (1958); Culliney (1974); MacKenzie *et al.* (1978); Beninger (1987); Barber *et al.* (1988); MacDonald and Thompson (1988);

5 Postate de (1980); Visite and De Postate (1981); Schmitters *et al.* (1981); Dedeved and Parsone (1982); McGarvey *et al.* (1992); DiBarce *et al.* (1993); DuPaul et al. (1989); Kirkley and DuPaul (1991); Schmitzer et al. (1991); Dadswell and Parsons (1992); McGarvey et al. (1992); DiBacco et al. (1995).



Figure 1. The sea scallop, *Placopecten magellanicus* (photograph by Dann Blackwood, USGS).

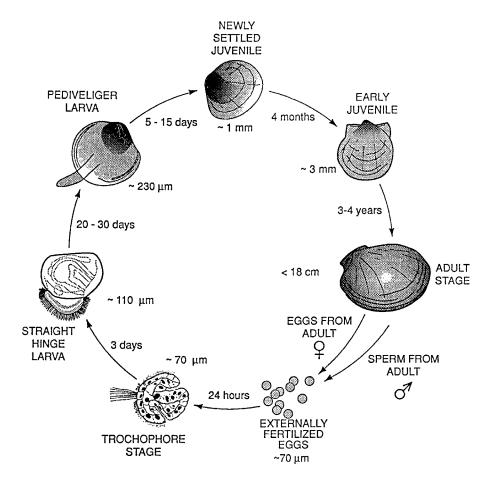


Figure 2. Generalized life cycle of the sea scallop, from Stewart and Arnold (1994).

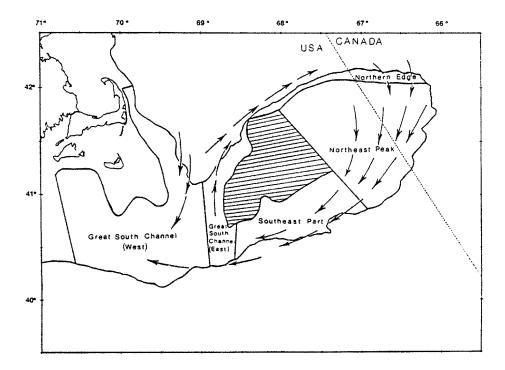


Figure 3. Map of Georges Bank indicating the five sub-regions and the clockwise flow of the residual current. From McGarvey *et al.* (1993).

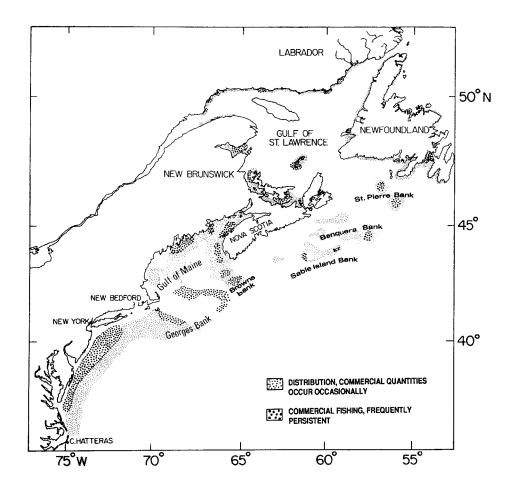


Figure 4. Distribution of sea scallop spawning beds off the northeast coast of North America. From Shumway *et al.*, in prep.

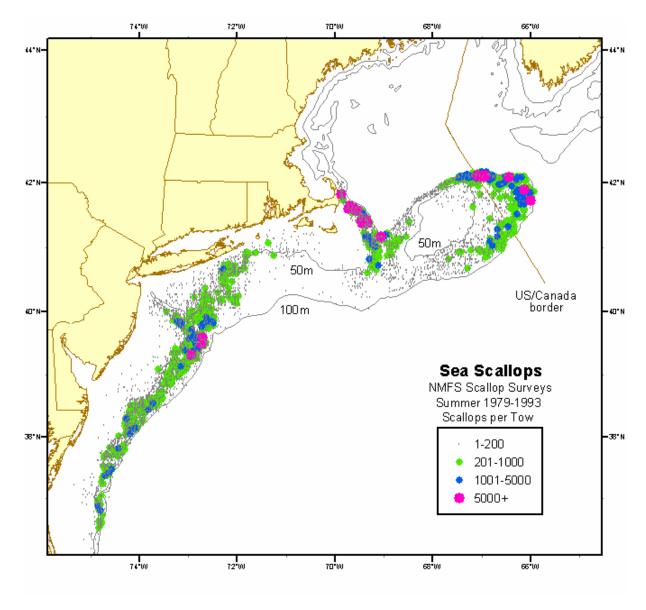


Figure 5. Distribution and abundance of sea scallops collected during NEFSC scallop surveys during summer 1979-1993.

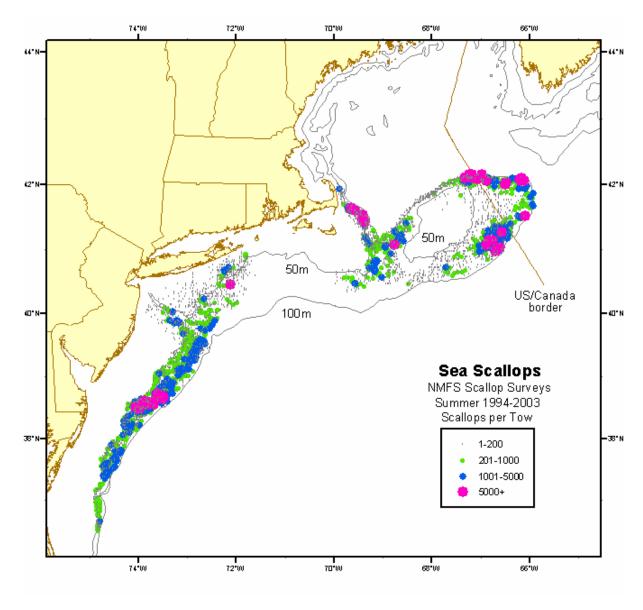


Figure 6. Distribution and abundance of sea scallops collected during NEFSC scallop surveys during summer 1994-2003.

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