NOAA Technical Memorandum NMFS-NE-192

Essential Fish Habitat Source Document:

Atlantic Herring, *Clupea harengus*, 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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NOAA Technical Memorandum NMFS-NE-192

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Essential Fish Habitat Source Document:

Atlantic Herring, *Clupea harengus*, Life History and Habitat Characteristics

Second Edition

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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.*, Nelson *et al.* 2004^a; Robins *et al.* 1991^b), mollusks (*i.e.*, Turgeon *et al.* 1998^c), and decapod crustaceans (*i.e.*, Williams *et al.* 1989^d), and to follow the Society for Marine Mammalogy's guidance on scientific and common names for marine mammals (*i.e.*, Rice 1998^c). Exceptions to this policy occur when there are subsequent compelling revisions in the classifications of species, resulting in changes in the names of species.

^aNelson, J.S.; Crossman, E.J.; Espinosa-Pérez, H.; Findley, L.T.; Gilbert, C.R.; Lea, R.N.; Williams, J.D. 2004. Common and scientific names of fishes from the United States, Canada, and Mexico. 6th ed. *Amer. Fish. Soc. Spec. Publ.* 29; 386 p.

^bRobins, C.R. (chair); Bailey, R.M.; Bond, C.E.; Brooker, J.R.; Lachner, E.A.; Lea, R.N.; Scott, W.B. 1991. 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.

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 are 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 Atlantic herring EFH source document is based on the original by Robert N. Reid, Luca M. Cargnelli, Sara J. Griesbach, David B. Packer, Donna L. Johnson, Christine A. Zetlin, Wallace W. Morse, and Peter L. Berrien, with a foreword by Jeffrey N. Cross (Reid et al. 1999a).

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.

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INTRODUCTION

The Atlantic herring, Clupea harengus (Figure 1), is a pelagic, schooling, plankton-feeding species that inhabits both sides of the North Atlantic Ocean. In the western North Atlantic this species ranges from Labrador to Cape Hatteras and supports major commercial fisheries. Adult herring undergo complex north-south migrations for feeding, spawning, and overwintering. Herring produce demersal eggs and spawn during the summer and fall in the Gulf of Maine – Georges Bank region. Larvae overwinter offshore and in coastal waters and metamorphose into juveniles in the spring. Juveniles and adults are heavily preyed upon by a variety of marine fish, marine mammals, and seabirds.

Herring are assessed and managed in U.S. waters as a single stock complex with two major spawning components, one in the Gulf of Maine and another on Georges Bank and Nantucket Shoals. Herring that spawn in the Bay of Fundy and off southwest Nova Scotia are assessed and managed by Canada. The U.S. stock complex has fully recovered from the effects of over-exploitation during the 1960s and 1970s and is currently under-utilized, although there is concern that exploitation rates in the Gulf of Maine may be too high.

This report provides information on the life history, stock status, geographical distribution, and habitat characteristics of different life stages of Atlantic herring in U.S. and Canadian waters of the northwest Atlantic from Cape Hatteras to the Gulf of Maine (Figure 2).

LIFE HISTORY

This section provides a brief review of the biology and life history of Atlantic herring in U.S. and Canadian waters of the northwest Atlantic. More detailed reviews are provided by Bigelow and Schroeder (1953), Sindermann (1979), Kelly and Moring (1986), Tupper *et al.* (1998), and Munroe (2002).

EGGS

Atlantic herring deposit demersal eggs in 5-90 m of water in areas with strong tidal currents on a variety of substrates ranging from boulders, rocks, and gravel, to sand, shell fragments, and macrophytes. The eggs are 1.0-1.4 mm in diameter (Fahay 1983) and are adhesive, adhering to the bottom and forming extensive egg beds that are often many layers deep. They remain attached to the bottom throughout the incubation period, which

varies from 10-15 days in the Gulf of Maine region during the fall spawning season.

LARVAE

The larvae are 4-10 mm long at hatching (Able and Fahay 1998) and retain a yolk-sac for the first few days after hatching. The duration of the yolk-sac stage varies with temperature, from 2.5 days at 14.5°C to 6 days at 8°C (Mansueti and Hardy 1967; Lough et al. 1982). The volk sac is absorbed by the time the larvae reach 8-12 mm SL (Blaxter and Holliday 1963). While they have a yolk sac, they are negatively buoyant and remain in deep water on or near the bottom. Divers observed yolk-sac larvae among the branches of a benthic red alga (Ptiloda serrata) at a spawning site on Jeffreys Ledge for several days after hatching (Cooper et al. 1975) and observations made from a submersible on Georges Bank revealed a dense aggregation of yolksac larvae being carried by the current 15 cm above the bottom (Caddy and Iles 1973).

The larval stage of fall-spawned herring in the Gulf of Maine lasts 4-8 months, depending on the timing of spawning. The larval stage is shortest for early-spawned (August) larvae, and longest for late-spawned (December) herring. Currents affect the pelagic larvae; however, they may or may not disperse randomly from the spawning grounds. Some larvae are retained for several months after hatching on or near the spawning site, while others are dispersed soon after hatching and drift with residual currents (Iles and Sinclair 1982; Sinclair and Iles 1985; Townsend *et al.* 1986; Chenoweth *et al.* 1989; Smith and Morse 1993).

Larvae produced off southwestern Nova Scotia are retained initially near the spawning ground and then drift into the Bay of Fundy (Iles 1971; Stephenson and Power 1988). Larvae produced in coastal Gulf of Maine waters generally remain inshore (Graham 1982) and disperse in a westerly direction, entering bays and estuaries where they over-winter (Graham et al. 1972a; Graham and Townsend 1985). Some larvae are transported offshore, away from the coast (Townsend 1992). Larvae that hatch on Jeffreys Ledge are dispersed shoreward (Boyar et al. 1973). Some larvae from the southwestern Gulf of Maine are transported eastward into estuaries in the mid-coast region of Maine (Lazzari and Stevenson 1992), despite the fact that the surface currents flow in the opposite direction. During the winter, herring larvae in inshore waters are exposed to extremely low temperatures and food levels (Townsend and Graham 1981; Graham et al. 1990). It is not clear if larval survival is enhanced as a result of over-wintering in nearshore and estuarine waters or in coastal waters. Larvae from Nantucket Shoals and Georges Bank tend to drift to the southwest (Lough et al. 1980; Grimm 1983) and are transported as far south

as southern New Jersey, where they have been collected in the Great Bay – Little Egg Harbor estuary during the winter and spring (Able and Fahay 1998) and in Delaware Bay and its tributaries (NEFMC 1999). The NOAA Estuarine Living Marine Resources Program (ELMR) compiled information on the distribution and abundance of all life stages of Atlantic herring in estuaries in New England (Jury *et al.* 1994) and the Middle Atlantic (Stone *et al.* 1994). Larvae were 'highly abundant' from Englishman-Machias Bays (eastern Maine) to the Sheepscot River (central Maine). Larvae were rare or absent in estuaries south of Raritan Bay (Table 1).

The Atlantic herring is one of the few species that perform extensive vertical migrations as larvae. They make diel or semi-diel vertical migrations throughout the water column that may be linked to time of day or turbidity (related to light level), tidal currents, or shifts in prey abundance (Lough and Cohen 1982). Vertical movements may be a larval retention mechanism enabling them to control their displacement by tidal currents and move into estuaries (Graham 1972; Fortier and Leggett 1983; Stephenson and Power 1988; Lazzari et al. 1993).

Larvae in coastal Maine waters grow at a rate of about 2 mm a week between October and early January and from late February to March, but grow very little, if at all, in mid-winter (Townsend and Graham 1981). Lough *et al.* (1982) reported larval growth rates in the Gulf of Maine – Georges Bank area of 1.75 and 2.1 mm per week in the fall and less than 1 mm per week in the winter.

JUVENILES

Larvae metamorphose into juveniles at 40-55 mm standard length (SL) in the spring (April-May) (Sindermann 1979; Lough et al. 1982). Growth is rapid, with juveniles in coastal Maine waters reaching lengths of 90-125 mm by the end of their first year of life (Anthony 1972). Schooling behavior begins during metamorphosis and is well established by the time the larvae have made the transition to the juvenile life stage (Gallego and Heath 1994). In the Gulf of Maine, oneyear-old juveniles move out of nearshore waters in the summer and fall to overwinter in deep bays or near the bottom in offshore areas (Boyar 1968). Two-year old juveniles return inshore the following spring when they are fully recruited to the coastal fishery. Juvenile herring do not make seasonal north-south migrations. Herring tagged as overwintering one-year-old juveniles in eastern and western Maine remained in close proximity to the area where they were tagged throughout the following summer (Creaser and Libby 1986). Some summer-feeding two-year-old juveniles tagged in southwestern Maine overwintered in

Massachusetts Bay, but juveniles in eastern Maine had a greater tendency to remain there (Creaser and Libby 1988).

One and two-year-old juveniles form large schools in coastal waters throughout the Gulf of Maine in the spring and summer (Bigelow and Schroeder 1953). They are abundant or common in estuaries and embayments from Buzzards Bay to Delaware Bay, primarily in the spring, and have been reported in Narragansett Bay and Long Island Sound during all months of the year (Table 2). They are abundant or highly abundant in most estuaries and embayments north of Cape Cod and are particularly numerous between Penobscot Bay and Passamaquoddy Bay in the summer.

Juvenile herring perform diurnal vertical migrations that are linked to changing light intensity, most likely in response to movements of their prey (Blaxter 1985). They move up in the water column at twilight and remain near the surface when light intensity is low; activity is highest just after sunrise and just before sunset (Brawn 1960a; Tibbo 1964; Stickney 1972). Juvenile and adult herring feed on a variety of planktonic organisms (see "Feeding").

ADULTS

Like juveniles, adult herring are pelagic and form large schools, feeding on planktonic organisms. Adults in the Gulf of Maine region occupy inshore and offshore waters to depths of 200 m and make extensive seasonal migrations between summer and fall spawning grounds on Georges Bank and in the Gulf of Maine and overwintering areas in southern New England and the Mid-Atlantic region (see "Migrations"). Thermal oceanic fronts between colder and less saline continental shelf water and warmer, more saline continental slope water provide an abundance of plankton and other food sources and greatly influence the migratory behavior and spatial distribution patterns of this species (see "Habitat Characteristics").

Adults occur in estuaries and embayments from Passamaquoddy Bay (Bay of Fundy) to Long Island Sound (Table 3). They are abundant or highly abundant from April to November in estuaries and embayments north of Muscongus Bay, in mid-coast Maine. Adults generally are common or rare south of Long Island Sound. Adult herring behavior is affected by temperature changes. Herring probably have characteristic temperature ranges and tolerances during particular times of year (Blaxter and Holliday 1963) and can perceive temperature changes which are smaller than 0.1°C (Laevastu 1993). Vertical migrations linked to changing light intensity are pronounced. Observations during the summer in the North Sea have shown that adult herring remain below

the thermocline in the daytime, migrate upwards during sunset to form loose aggregations above the thermocline, disperse between the surface and the thermocline during the night, and aggregate close to the bottom during sunrise (Laevastu and Hayes 1981; Blaxter and Holliday 1963).

Median sizes and ages at maturity for male and female Atlantic herring during 1987-1989 autumn trawl surveys were 25.3 cm TL and age 2.9 years for males and 25.4 cm TL and 3.0 years for females (O'Brien et al. 1993). Boyar (1968) concluded that herring from the Gulf of Maine, Georges Bank, and southern Nova Scotia during the 1960s matured at age 4 and an average total length of 27.5 cm. Fewer herring matured at age 3 and at sizes around 26 cm. Growth and maturation rates appear to be density-dependant. Sinclair et al. (1982) correlated increased sizes at maturity in Nova Scotia with faster juvenile growth rates and Winters (1976) correlated decreased age at maturity with decreased adult biomass in the Gulf of St. Lawrence. Mean size at age of adult herring in U.S. waters of the northwest Atlantic has decreased steadily since 1983 as stock size has increased (Overholtz et al. 2004). Growth rates have been shown to increase progressively from Nova Scotia to Georges Bank, with intermediate growth rates in the western Gulf of Maine (Sindermann 1979). Mean lengths of herring on Georges Bank ranged from 23.7-25.6 cm at age 3 to 33.0-33.3 cm at age 7 during the 1960s (Boyar 1968). Atlantic herring can reach a maximum size of about 39 cm TL and 0.68 kg, and a maximum age of 15-18 years (Anthony 1972). However, herring caught in the U.S. commercial fishery seldom exceed 35 cm in length and 12 years of age (Overholtz et al. 2004).

REPRODUCTION

Most Atlantic herring in the Gulf of Maine region mature at 3 years of age and a total length of about 25 cm (O'Brien *et al.* 1993). In this report herring \geq 25 cm were considered to be adults. Predicted fecundities range from 44,000 eggs for small (25 cm) females to about 250,000 for large (36 cm) females (Morse and Morris 1981; Kelly and Stevenson 1985).

In the northwest Atlantic, herring spawn from Labrador to Nantucket Shoals. Spawning occurs in the spring, summer, and fall in more northern latitudes, but summer and fall spawning predominates in the Gulf of Maine-Georges Bank region (Haegele and Schweigert 1985). Small spring spawning stocks used to exist in the Bay of Fundy (Bigelow and Schroeder 1953). Herring spawning grounds are located in high-energy environments with strong tidal currents (Iles and Sinclair 1982) and, based on information from egg and larval surveys and the distribution of sexually mature

adults, are depicted - in very general terms - in Figure 3

Historically, three primary herring spawning stocks have been recognized in the Gulf of Maine region: southwestern Nova Scotia, coastal Gulf of Maine, and Georges Bank/Nantucket Shoals. These larger stocks may be composed of a number of smaller stocks that occupy discrete, localized spawning locations within the larger spawning grounds. This has been confirmed off southwestern Nova Scotia, where spawning occurs on or near a series of offshore banks and ledges (Stephenson *et al.* 2001).

In U.S. waters of the Gulf of Maine, herring eggs have been observed along the eastern Maine coast, at several other locations along the Maine coast (e.g., outer Penobscot Bay and near Boothbay), on Jeffreys Ledge and Stellwagen Bank, and on eastern Georges Bank (see Geographic Distribution: Eggs, and Figure 6). Nantucket Shoals is known to be an important spawning ground based on the concentrations of recently-hatched larvae that were repeatedly collected there during the 1970s and 1980s (Grimm 1983; Smith and Morse 1993). High concentrations of recentlyhatched larvae have also been collected in the vicinity of Cultivator Shoals on western Georges Bank, in the vicinity of Stellwagen Bank and Jeffreys Ledge, and on the outer continental shelf in southern New England (Grimm 1983; Smith and Morse 1993). High densities of recently-hatched larvae have also been observed in Saco Bay and Casco Bay on the southern Maine coast (Graham et al. 1972b, et al. 1973).

The spawning season in the Gulf of Maine-Georges Bank region begins in July and lasts until December. Spawning begins earlier in the northern areas of the Gulf. Off southwestern Nova Scotia, spawning occurs from July to November and peaks in September-October (Boyar 1968; Das 1968, 1972) Spawning in eastern Maine coastal waters during 1983-1988 extended from late July through early October, with peak spawning in late August (Stevenson 1989), but more recent egg bed surveys (1997-2002) in the same area indicated that spawning did not start until late August and lasted until October 21 (Neal and Brehme 2001; Neal 2003). Based on larval surveys, Graham et al. (1972b) concluded that spawning peaks in mid-September to mid-October in eastern Maine and in October in western Maine. Boyar et al. (1973) reported that spawning on Jeffreys Ledge in 1972 started in early September and peaked during the first three weeks of October. On Georges Bank, spawning occurs from late August to December (Boyar 1968; Berenbeim and Sigajev 1978; Lough et al. 1980) with a peak in September-October (Boyar 1968; Pankratov and Sigajev 1973; Grimm 1983). On Nantucket Shoals, spawning peaks from October to early November, 1-2 weeks later than on Georges Bank (Lough et al. 1980; Grimm 1983). Larval surveys conducted during 1971-1975 indicated that spawning on Georges Bank started on the northeast peak of the bank in September and

extended southwest to Nantucket Shoals in October, declined in November and was absent in December (Grimm 1983).

During spawning, it has been reported that the females first deposit ribbons of eggs on the substrate and then the males swim above them and release milt into the water (Blaxter and Holliday 1963). However, Messieh (1988) observed that females spawning in shallow water in the Gulf of St. Lawrence did not release their eggs until there was milt in the water and swam 30 cm above the bottom for four hours before spawning at night. A single school of spring-spawning herring in a bay in southwestern Norway was observed to separate into a pelagic component (a tight "ball") of fully-mature non-spawning fish and a demersal component of spawners that spread out in a flat layer at the bottom (Axelsen et al. 2000). Post-spawners seemed to return to the pelagic school. After spawning the two components rejoined each other in a loose, uneven layer at the surface. The majority of the herring in the school completed spawning within three days. A school of herring in eastern Maine was observed to remain near the site where they spawned for about a week; eggs were deposited on the bottom overnight and the next day the spent fish had dispersed from the spawning site (Stevenson and Knowles 1988).

In some cases egg masses are composed entirely of eggs that were all spawned at the same time (Caddy and Iles 1973; Stevenson and Knowles 1988), while in other cases several layers of eggs in different stages of development indicate that successive spawnings have occurred at the same site within a few days of each other (Pankratov and Sigajev 1973). Spawning often occurs repeatedly at the same site. Stevenson (1989) reported 49 spawning events at 24 different locations along the eastern Maine coast during 1983-1988. In a few cases, eggs were deposited at the same site twice in the same year.

Egg developmental rates are inversely related to temperature, varying from 40 days at 4-5°C to 6-8 days at 14.4-16°C, with an average incubation period of 10-15 days at temperatures (8-13°C) which prevail during the summer-fall spawning season in the Gulf of Maine (Bigelow and Schroeder 1953; Messieh 1988). In the Gulf of Maine, Atlantic herring spawn in fully saline seawater (32-33 ppt) (Munroe 2002).

FOOD HABITS

Atlantic herring prey upon a variety of planktivorous organisms. They are visual particulate feeders with diverse feeding behaviors, often switching between filtering and biting in response to light intensity and the size of available food (Bigelow and Schroeder 1953; Battle 1934; Blaxter 1966; Batty *et al.* 1990). All life stages of herring are opportunistic

feeders, and will take advantage of whatever prey of the appropriate size is available. As they grow and the size of their jaws increases, they consume larger organisms. Their diet therefore varies with season, their age and size, and location.

Larvae begin exogenous feeding before the yolk sac is completely absorbed (Munroe 2002). Newly-hatched larvae (7-20 mm) in coastal waters of central Maine feed primarily on the small, early developmental stages of copepods; during the winter, larger larvae (21-30 mm) feed on the adult stages of small copepods as well (Sherman and Honey 1971). During the spring, when a wider variety of planktonic organisms are available and the larvae are larger, their diet includes organisms such as barnacle larvae, crustacean eggs, copepods, and free-swimming ciliate protozoans (tintinnids) (Sherman and Honey 1971). Three copepod species preyed upon by larval herring on Georges Bank are *Pseudocalamus* sp., *Paracalamus parvus*, and *Centropages typicus* (Cohen and Lough 1983).

Juveniles feed on up to 15 different groups of zooplankton; the most common are copepods, decapod larvae, barnacle larvae, cladocerans, and molluscan larvae (Sherman and Perkins 1971). Adults have a diet dominated by euphausiids, chaetognaths, and copepods (Bigelow and Schroeder 1953; Maurer and Bowman 1975). Maurer (1976) reported that the most important prey items of adult herring collected on Georges Bank were chaetognaths (Sagitta elegans, 43% by weight), euphausiids (Meganyctiphanes norvegica, Thysanoessa inermis, 6.1%), pteropods (Limacina retroversa, 6.2%), and copepods (3%). The copepod Calanus finmarchicus is a common prey item. In addition, adults also consume fish eggs and larvae, including larval herring, sand lance, and silversides (Munroe 2002).

Spring and summer are the most intense feeding times for both juvenile and adult herring (Munroe 2002). Although it has been observed that adult herring on Georges Bank stop feeding prior to spawning (Pankratov and Sigajev 1973), there are also studies showing that they continue feeding before spawning (Bradford and Iles 1992; Axelsen *et al.* 2000). Feeding occurs primarily at dawn and dusk in the upper water layers due to the diurnal vertical migrations of herring in response to changes in light intensity; they rise to the surface to feed at dusk and then sink toward the seabed at dawn (Brawn 1960a; Tibbo 1964; Stickney 1972; Blaxter 1985).

Food habits data collected during Northeast Fisheries Science Center (NEFSC) bottom trawl surveys [see Reid *et al.* (1999b) and Link and Almeida (2000)] reveal that the most abundant identifiable prey items (percent by weight) for Atlantic herring include amphipods, copepods, and euphasiids (Figure 4).

PREDATION AND MORTALITY

Herring is an important species in the food web of the northwest Atlantic. Demersal fish species that have been observed feeding on herring eggs include cod, haddock, cunner, and red hake; invertebrates that probably consume herring eggs include moon snails, hermit crabs, and starfish (McKenzie 1964; Caddy and Iles 1973; Cooper et al. 1975). Herring eggs and larvae are consumed by sand lance (Rankine and Morrison 1989). Herring larvae are also eaten by jellyfish (Aurelia aurita), Atlantic mackerel, and adult Atlantic herring (Bailey 1984; Bailey and Batty 1984; Moller 1984; Lett and Kohler (1976). Juvenile herring, especially "brit" (age-1 juveniles) are heavily preyed upon due to their abundance, small size, and schooling behavior (Munroe 2002).

Atlantic herring is an important prey species for a large number of piscivorous fish, elasmobranchs (sharks and skates), marine mammals, and seabirds in the northwest Atlantic. Unlike other pelagic fishes such as Atlantic mackerel, herring are smaller and vulnerable to predation over most, if not all, of their life (Overholtz et al. 2000). According to the diet composition data in Table 4, the principal finfish and elasmobranch species that feed on Atlantic herring (or on clupeid species as a group) are Atlantic cod, silver hake, thorny skate, bluefish, goosefish, weakfish, summer flounder, white hake, and - in certain locations and times of year -Atlantic bluefin tuna. Other species that feed on herring are spiny dogfish, Atlantic halibut, red hake, striped bass, dusky shark, and black sea bass. Shortfinned squid (Illex illecebrosus) have also been observed feeding on juvenile herring (Bigelow and Schroeder 1953). The spiny dogfish is a much more important predator on Atlantic herring than is indicated by diet composition data. Link et al. (2002a) estimated that spiny dogfish consumed an average of 67,660 metric tons (mt) of Atlantic herring a year during 1977-1998, with a range of 15,526 to 148,197 mt. Thus, in some years, spiny dogfish may consume a greater quantity of herring biomass than is taken in the commercial fishery.

For many of the predator species listed in Table 4, herring made up a larger percentage of the diets of the larger size classes. This was the case for silver hake, summer flounder, white hake, bluefish, and goosefish. Link and Garrison (2002) reported that the percentages of herring in the stomachs of Atlantic cod increased from about 13% in 51-60 cm cod to 28% in 81-90 cm cod and then declined again to 6% in 111-120 cm cod. They also showed that herring made up a larger percentage of the diet of Atlantic cod in the Gulf of Maine than on Georges Bank or in southern New England. Garrison and Link (2000) reported higher percentages of Atlantic herring in the diet of silver hake on Georges Bank than in the Gulf of Maine or in southern New England. Bowman *et al.* (2000) reported

similar results for silver hake and Atlantic cod. Chase (2002) reported very high percentages of Atlantic herring in bluefin tuna diets on Jeffreys Ledge and in the Great South Channel, but very low percentages in three other locations. Less dramatic spatial variations were reported for striped bass by Nelson *et al.* (2003).

Overholtz et al. (2000) estimated the consumption of Atlantic herring by 10 species of predatory fish in northeastern U.S. waters from 1977-1997, and found that the amount of herring consumed varied in response to changes in the abundance of herring and the abundance of predator populations in the late 1980s and throughout the 1990s. Consumption of Atlantic herring by these predatory fish peaked at over 200,000 metric tons (mt) during 1992 and 1993, declining to less than 100,000 mt in 1997 (Table 5). By far the most important predator on herring was spiny dogfish, followed by silver hake, cod, white hake, and bluefish. The declines in consumption of herring in the late 1990s were coincident with the declines in the abundance of these five species.

Read and Brownstein (2003) used survey-based estimates of abundance for eight species of marine mammals between 1991 and 1997 to estimate the total annual consumption of Atlantic herring by these Their estimates of marine mammal consumption ranged from about 94,000-190,000 mt of herring per year. Their results show that minke whales, harbor porpoises, and white-sided dolphins are major predators on Atlantic herring because of high proportions of herring (34-51%) in their diets, whereas fin and humpback whales consume large quantities of herring to sustain their large body mass. Despite a three-fold increase in the harbor seal population in the Gulf of Maine between 1981 and 1997, herring only make up 13% of their diet. Consequently, the mean consumption estimate for harbor seals is below 5,000 mt a year.

Read and Brownstein's (2003) mean (or "best") estimate of Atlantic herring consumed annually by marine mammals during 1991-1997 was about 140,000 mt, with a range of 93,000-200,000 mt. Adding these estimates to the most current (1997) estimate of 100,000 mt of Atlantic herring consumed by fish and elasmobranch predators reported by Overholtz *et al.* (2000) produces a total mean estimate of 240,000 mt, with a range of 193,000-300,000 mt. During the 1990s, the total amount of herring consumed by all predators could have been as high as 400-450,000 mt.

MIGRATION

Adult herring make extensive seasonal migrations between summer spawning grounds on Georges Bank and in the Gulf of Maine and overwintering areas in southern New England and the Mid-Atlantic region. They seldom migrate seaward beyond a depth of about 100 m and usually inhabit waters closer to the surface than the bottom, except in midwinter (Hildebrand 1963). Adults from different spawning groups intermingle during the non-spawning phase of their seasonal cycle (Sinclair and Iles 1985). Juvenile herring make seasonal inshore-offshore movements, but do not make extensive north-south migrations (see Life History: Juveniles).

Three general migratory patterns are recognized off the northeast coast of the U.S., one for each of the three primary spawning stocks, based on the results of tagging studies (e.g., Stobo 1983 and Creaser et al. 1984) and observations from the commercial fishery (Sindermann 1979; Figure 5). Herring that spawn off southwest Nova Scotia move north along the eastern Scotian shelf after spawning, but some also move south to overwinter in the Gulf of Maine. Adults belonging to the Georges Bank/Nantucket Shoals stock overwinter south of Cape Cod and along the Mid-Atlantic coast. They move north onto Georges Bank and into the Gulf of Maine in the spring before congregating on spawning grounds southeast of Nantucket and on Georges Bank in the fall. Adults that spawn in the Gulf of Maine migrate southwest along the coast after spawning. Some of them overwinter south of Cape Cod and some remain in the southwestern region of the gulf. Thermal oceanic fronts between colder, and less saline continental shelf water and, warmer, more saline continental slope water provide an abundance of plankton and other food sources and greatly influence the migratory behavior of this species (see Habitat Characteristics: Adults).

STATUS OF THE STOCKS

Adult herring segregate into discrete spawning stocks in the summer and fall - on Georges Bank and Nantucket Shoals, in coastal waters of the Gulf of Maine, and off southwest Nova Scotia and in the Bay of Fundy. Each of the major spawning areas in the Gulf of Maine region consists of a number of smaller, discrete, spawning sites. Some degree of stock differentiation was achieved with early enzyme electrophoresis research (Ridgway et al. 1970, 1971), but more recent attempts to differentiate geographically isolated fall spawning stocks in eastern Canada and the northeast U.S. on the basis of more specific genetic characteristics have been unsuccessful (Kornfield et al. 1982; Kornfield and Bogdanowicz 1987; Safford and Booke 1992). Evidence for separate stocks is based on discrete larval distribution patterns (Iles and Sinclair 1982), differences in spawning times and locations (Boyar et al. 1973; Haegele and Schweigert 1985), distinct biological characteristics - such as growth rates (Anthony and Waring 1980) and meristic and

morphometric characteristics (Anthony 1981; Safford 1985) - and the incidence of parasites (McGladdery and Burt 1985). McQuinn (1997) reviewed arguments for a discrete versus dynamic balance population concept for Atlantic herring and proposed that the population structure and dynamics of herring fit well within a metapopulation model. This model allows for significant mixing and gene flow among units that still retain considerable persistence and discreteness due to behaviorally-induced homing to spawning grounds.

The most compelling evidence supporting the existence of separate Gulf of Maine and Georges Bank-Nantucket Shoals stocks was the collapse of the large Georges Bank-Nantucket Shoals stock in the early 1970s after several years of heavy exploitation by foreign fishing fleets (Overholtz and Friedland 2002). This stock remained in a depleted state for 10-15 years, during which time the smaller Gulf of Maine stock continued to support a strong coastal fishery.

Trawl and larval survey data show that the Georges Bank stock has fully recovered and support the view that herring recolonized the bank in stages from the Gulf of Maine and Nantucket Shoals during the late 1980s (Smith and Morse 1993; Overholtz and Friedland 2002). Analysis of trawl survey shows that the geographic range of herring in U.S. waters of the northwest Atlantic was greatly reduced during the period of stock depletion and was more widely dispersed by the mid 1990s (Overholtz 2002; Overholtz and Friedland 2002). During 1968-1970 the springtime center of distribution was south and west of Cape Cod and then gradually shifted northwards and As abundance eastwards as stock size declined. increased in the late 1980s, the center of the spring distribution moved southwards and westwards as adults that spawn on Georges Bank and on Nantucket Shoals migrated south and re-occupied the mid-Atlantic shelf.

The Bay of Fundy-southwest Nova Scotia stock is assessed by Canada as a component of a larger management unit that also includes coastal and outer shelf waters east of Nova Scotia. Biomass estimates derived from acoustic survey data indicate that the overall abundance of spawning herring declined from about 570,000 mt in 1997 to about 460,000 mt in 2000 and 2001, but increased in 2002 and 2003 (Melvin et al. 2004). Despite recent increases in spawning stock biomass (SSB), there are concerns that the stock is deteriorating: the total catch increased in 2003, but there are fewer adults in the population and SSB for two spawning components remains well below historical levels (Power et al. 2004). The abundance of herring that spawn at individual sites off southwest Nova Scotia varies from site to site in response to the amount of fishing that occurs at each site (Stephenson et al. 1999; Melvin et al. 2001). These observations support the view that each of these spawning aggregations constitutes a separate sub-stock of herring (Stephenson et al 2001). Some of these discrete

spawning sites are located within 10-15 miles of each other.

Herring that spawn on Georges Bank, Nantucket Shoals, and in coastal waters of the Gulf of Maine are currently assessed in the U.S. as a single coastal stock complex. According to a recent U.S. assessment, spawning stock biomass for the stock complex was about 1.4 million metric tons (mt) in 2001 while a Canadian assessment shows it to be about 600,000 mt (Overholtz et al. 2004). They both show the same downward trend in spawning stock size from about one million metric tons in the late 1960s to 100,000 mt between 1975 and 1985, but the U.S. assessment indicates a much more dramatic recovery during the last 20 years. Maximum sustainable yield (MSY) estimates from the U.S. assessment were 222,000 mt or 243,000 mt, based on two different model formulations (Overholtz et al. 2004). According to the U.S. assessment, current fishing mortality rates in the fishery are below 10%, indicating that the resource is significantly under-utilized. There is concern, however, that the inshore (Gulf of Maine) component of the stock, which is heavily exploited, is being overharvested.

GEOGRAPHICAL DISTRIBUTION

EGGS

Atlantic herring eggs are demersal and adhere to the substrate and were not usually collected during the NEFSC Marine Resources Monitoring, Assessment and Prediction (MARMAP) ichthyoplankton surveys. A few in situ surveys of herring spawning locations have been conducted in the Gulf of Maine - Georges Bank region during the past 40 years using divers, remotelyoperated underwater vehicles equipped with video cameras, submersibles, dredges and grab samplers. Information obtained from these surveys is summarized in Table 6. Geo-referenced spawning site locations are shown in Figure 6, Figure 7, and Figure 8. Spawning location information in this document is based on the presence of herring eggs on the bottom. More general information on herring spawning grounds based on catches of fully mature adults or the abundance and distribution of recently-hatched larvae is summarized in Life History: Reproduction.

LARVAE

Herring larvae were collected during the 1977-1987 NEFSC MARMAP surveys from New Jersey to the Bay of Fundy and from nearshore waters to the

seaward limit of the survey area (Figure 9). Larvae were collected in all months, but were most abundant in the fall (September - December). The highest mean monthly density (351 larvae/10 m²) occurred in September when larvae were restricted to the northeastern Gulf of Maine. Larvae were relatively abundant in October (39 larvae/10 m²) and November (49 larvae/10 m²). The appearance of larvae off Nova Scotia and eastern Maine in September, followed by more widespread larval production throughout the Gulf of Maine and on Nantucket Shoals and Georges Bank in October and November, indicates that spawning begins earlier in the northeast (see also Bigelow and Schroeder 1953; Tupper et al. 1998). Mean densities were much lower (less than 6 larvae/10m²) from December through August. The MARMAP surveys were conducted during the time when the abundance of the Georges Bank - Nantucket Shoals spawning stock of herring was very low.

The abundance and distribution of herring larvae on Georges Bank and Nantucket Shoals changed considerably between 1971 and 1990, as the number of herring spawning in these two areas declined in response to heavy fishing pressure and then increased beginning in the mid-1980s. By the end of the 1980s, larval abundance had increased to 1973-1974 levels on Georges Bank and exceeded the previous abundance levels on Nantucket Shoals (Figure 10). According to U.S. larval survey data compiled by Smith and Morse (1993), herring spawned on the northeast peak of Georges Bank and on Nantucket Shoals during 1971-75 (Figure 11). During 1976-1987, spawning was limited to a small area on Nantucket Shoals and in Massachusetts Bay. During 1988-1990, spawning spread over a larger area that included the western portion of Georges Bank (Cultivator Shoals), but not the northeast peak. More recent Canadian surveys have documented larval production in U.S. and Canadian waters on eastern Georges Bank, including - in 1994 the northeast peak (Figure 12; Melvin et al. 1996).

JUVENILES AND ADULTS

NEFSC bottom trawl surveys show that the distributions of juvenile (Figure 13) and adult (Figure 14) herring overlap during the summer, fall, and winter and are very similar in the spring. (Note that winter and summer distributions are presented as presence/absence data, precluding a discussion of abundances.) In the summer and fall, herring are distributed throughout the Gulf of Maine and in the deeper waters of Georges Bank and the Great South Channel, with a few in offshore waters of southern New England. In the winter, their distribution shifts southward, extending from Georges Bank to Cape Hatteras, primarily in offshore waters. A few remain in the Gulf of Maine,

which is not sampled very heavily in the winter (Reid *et al.* 1999b). In the spring, juvenile herring occupy the entire region. The spring adult distribution extends from Cape Hatteras to Georges Bank and the southwestern and central Gulf of Maine and the Scotian shelf, but there are only a few along the Maine coast. Herring are more concentrated in nearshore waters of the Mid-Atlantic, southern New England, and Massachusetts Bay in the spring than they are in the winter.

The distributions and abundances of Atlantic herring along the coasts of Maine and New Hampshire, based on spring and fall 2000-2003 Maine-New Hampshire inshore groundfish surveys (Sherman *et al.* 2004), are shown in Figure 15. Most of these were juveniles (Figure 16).

The distributions and abundances of juveniles and adults in Massachusetts coastal waters, based upon the spring and fall 1978-2003 Massachusetts inshore trawl surveys, are shown in Figure 17 (juveniles) and Figure 18 (adults). In the spring, the largest catches of juvenile herring occurred along the northern shore of Nantucket Island and southern shore of Martha's Vineyard, as well as in Buzzards Bay north of Cape Ann. In the fall, large catches were found in Cape Cod Bay (Figure 17). The few adults found in the spring and fall were most abundant in near Cape Ann (Figure 18).

The seasonal distributions and abundances of juveniles and adults in Narragansett Bay, based upon the 1990-1996 Rhode Island bottom trawl surveys, are shown in Figure 19 (juveniles) and Figure 20 (adults). Catches of juveniles were patchy in Narragansett Bay (Figure 19). Catches were highest in summer when the largest mean catch (254 fish/tow) occurred at the station farthest offshore and five of the 12 stations in the bay had > 100 per tow. Abundance was lower during the remaining seasons. Adults (Figure 20) were scarce in winter when the highest mean catch was 12 per tow. Catches were smaller in other months and no adults were caught in summer.

The distributions and abundances of both juvenile and adult Atlantic herring in Long Island Sound from April to November 1984-1994, based on the Connecticut Fisheries Division bottom trawl surveys, are shown in Figure 21, Figure 22, and Figure 23. The following description of their distributions relative to depth and bottom type is taken verbatim from Gottschall *et al.* (2000).

Atlantic herring taken in the survey ranged from 3-33 cm (Figure 23). The percentage of adults was 81% and 94% in April and May respectively, but declined to 0% by October. Although herring were not measured in November, recorded observations indicated that most were adults (Gottschall *et al.* 2000).

Atlantic herring abundance in the Connecticut survey was highest during April and May (Figure 22) when adults were most abundant in Long Island Sound. In the spring sampling period they were widely distributed, but were especially abundant in the Western

and Central Basins over mud bottom (Figure 21 and Figure 22B). Adult abundance declined through the spring months to very low abundance in the summer and fall periods, when most of the herring taken in the survey were juveniles. Although the survey did not effectively retain young-of-the-year, they were very abundant in the Sound during the summer months – in a separate sampling program, up to 80,000 per 15 minute tow were caught with an otter trawl equipped with a 6 mm codend liner [see reference in Gottschall et al. (2000)]. During the fall period, most herring were taken along the Connecticut side of the Sound in depths < 18 m, especially south of Milford (Figure 21 and Figure 22F). Abundance increased in November when adult fish were again taken. During November, abundance increased slightly with decreasing depth, and the largest catches occurred in the Central Basin (Gottschall et al. 2000).

Surveys of the Hudson-Raritan estuary show that juveniles were most abundant in winter and spring throughout the (Figure 24). Some were caught at the mouth of the estuary in summer, but they were rare in the fall. Adults (Figure 25) were common in winter, but not at any other time of year.

The Virginia Institute of Marine Science (VIMS) trawl surveys (1988-1999) and beach seine surveys (1994-1999) of Chesapeake Bay show that, although Atlantic herring were not often caught, nearly 90% of the catches were juveniles, with only three adults found from the seine surveys (Geer 2002). Juveniles were caught in the trawl survey during late winter and early spring, with peaks in April and May (Figure 26). During the winter juveniles were caught mostly in the tributaries but were distributed throughout the lower Chesapeake Bay in the spring (Figure 27). In the summer a few juveniles were found at the mouth of the Bay, and in the fall they were found in the mainstem of the Bay. Adults were only caught in the trawl survey during the winter (Figure 26 and Figure 28). Of the 9,321 herring captured during the beach seine surveys, over 86% came from a single sample in May 1996 (Geer 2002). They were found at the Bay mouth or along the Atlantic coast beaches (Figure 29).

HABITAT CHARACTERISTICS

Information on the habitat characteristics of Atlantic herring are presented here and summarized in Table 6 and Table 7.

EGGS

Atlantic herring eggs are spawned on the bottom in discrete beds in coastal and offshore waters of the Gulf of Maine, Georges Bank, and Nantucket Shoals. Depths reported during *in situ* egg bed surveys ranged from 5 m at Grand Manan Island to 73 m at a spawning site in eastern Maine (Table 6). Eggs have been reported on Jeffreys Ledge between depths of 53 and 59 m. Pre-spawning aggregations of adult herring have been observed on the northern edge of Georges Bank in depths of 50-100 m (Pankratov and Sigajev 1973). Munroe (2002) reported the maximum spawning depth in the Gulf of Maine region to be about 90 m.

Eggs have been observed on a variety of substrates that include rocks (ranging from pebbles to boulders), gravel, shell fragments, sand, and benthic macroalgae and epifauna attached to hard substrates (Table 6). Spawning sites have also been located by interviewing lobster fishermen who have seen eggs attached to their traps (Stevenson 1989). Gravel and shell fragments have been identified as the preferred substrate for herring eggs in nearshore spawning areas in eastern Maine, gravel and rocks with an attached red alga on Jeffreys Ledge, and gravel on Georges Bank. Fine sand and mud are not good substrates for herring eggs and often define the edges of egg beds. Fine sediments do not provide a stable substrate for attached eggs (Drapeau 1973) and are not characteristic of relatively shallow, tidally-energetic benthic habitats where herring spawn (Iles and Sinclair 1982). Egg beds on the northern edge of eastern Georges Bank surveyed by U.S. and Soviet scientists between 1964 and 1970 were all located in elongated ridges of gravel at depths of 40-50 m between gravelly sand and large sand ridges 10-20 m in height (Valentine and Lough 1991).

In the Gulf of Maine region, herring eggs have been observed as individual eggs, clumps, or patches and in cohesive mats up to 5 cm thick (Table 6). In some cases egg beds are quite uniform in thickness and in others they vary considerably, from several centimeters deep to individual eggs at the edges of the egg bed (Table 6). Egg mortality is directly related to current speed and the amount of oxygen that is available to eggs in the lower layers. Stevenson and Knowles (1988) observed that eggs throughout an egg mass 3 cm thick developed at the same rate and that in most samples collected from the egg mat, less than 1% of the eggs were dead (egg mortality was less than 5% in all samples). In contrast, Cooper et al. (1975) observed 50-70% egg mortality in the lower portion of an egg mat 4-5 cm thick.

The sizes of egg beds that have been surveyed in the Gulf of Maine and on Georges Bank have varied from 0.07-1.39 km² (Table 6). Egg beds on the eastern Maine coast are typically longer than they are wide, following depth contours that parallel the shoreline (Figure 7). Egg beds that were surveyed on offshore

banks (Georges Bank and Trinity Ledge) were more irregular in shape (McKenzie 1964; Pankratov and Sigajev 1973). Eggs on Georges Bank, Trinity Ledge, and eastern Maine were all deposited in fairly flat or gradually sloping bottom areas. Eggs at one site on Jeffreys Ledge were found on top of an underwater "hill" and down a 20-40 degree rocky slope to talus material at the base of the hill and beyond (Cooper *et al.* 1975).

Herring spawning sites are characterized by strong bottom currents. Tidal currents up to two knots in velocity have been measured during egg bed surveys in the Gulf of Maine and on Georges Bank (Table 6). Strong currents prevent siltation (which would impede egg adherence to the substrate and smother eggs), supply oxygen to the developing eggs, and remove metabolites (Drapeau 1973).

Bottom temperatures measured during herring egg bed surveys in the Gulf of Maine region have ranged from a low of 7°C to a high of 15°C (Table 6). The temperature range for normal egg development and survival is not known with certainty. Bigelow and Schroeder (1953) reported that temperatures above 20°C and below 5°C were lethal, but experiments in Europe have shown that egg development was normal between 1°C and 22°C, with mortality at -0.8°C (Blaxter and Holliday 1963). Slightly lower minimum temperatures have ranged from -1.2 to 0°C for herring stocks off northern Europe (Kelly and Moring 1986).

Atlantic herring in the Gulf of Maine spawn in fully saline seawater (32-33 ppt) (Munroe 2002). However, laboratory experiments show fertilization, egg development, and hatching can succeed in salinities of 5.9-52.5 ppt, with maximum fertilization at 25 ppt or more and maximum hatching success at 20-35 ppt (Holliday and Blaxter 1960). Hatching success is low at dissolved oxygen concentrations below 20% saturation (Bishai 1960). Eggs covered with 1 cm of sediment do not survive (100% mortality) while a thin film of sediment causes 85% mortality, but there was no effect of suspended sediments at any concentration up to 7,000 mg/l on hatching success (Messieh et al. 1981). Eggs incubated in 30 micrograms/l copper during incubation had relatively high mortality rates and premature hatching, with 70% of the larvae being deformed (Blaxter 1977).

LARVAE

Once the yolk-sac is absorbed (within a few days after hatching), herring larvae are pelagic and begin to feed on planktonic organisms. They are transported away from spawning areas and overwinter in inshore bays and estuaries, or in offshore coastal waters, for 4-8 months before metamorphosing to juveniles in the spring. Herring larvae are tolerant of wide ranges of

and salinity, and low temperature concentrations. In laboratory experiments, upper and lower temperature tolerances of newly hatched herring larvae were 22-24°C and -0.75 to -1.8°C (Blaxter and Holliday 1963). Larvae tolerated salinities of 1.4-60 ppt for 24 hours and 2.5-52.5 ppt for 7 days (Blaxter and Holliday 1963; Blaxter and Hunter 1982). De Silva and Tytler (1973) reported 50% mortality of larvae exposed to oxygen concentrations of 1.9-3.6 mg/l at 10°C after 96 hours. Eggs and larvae held under films of crude oil in concentrations of 1 ml or 20 ml/l or in emulsions experienced toxicities that varied with the origin of the oil (Kühnhold 1969, as cited in Blaxter and Hunter 1982). Fractions with lower boiling points seemed more harmful. Larvae swim into oil dispersants and are narcotized (Wilson 1974). High mortality of newly hatched larvae has been observed at copper concentrations of 1,000 micrograms/l; larvae were more resistant than eggs (Blaxter 1977).

In the NEFSC MARMAP survey, most larvae were collected at 8-14°C from September to November; maximum abundance was at 9-12°C (Figure 30). In December, larvae occurred at 6-11°C with the majority collected at 8-9°C. Temperatures at the time of collection decreased each month from January to March and increased from April to August. Larvae were collected at stations with bottom depths ranging from 10-250 m, although most were collected at stations with depths of 50-90 m.

JUVENILES

Laboratory experiments have shown that juvenile herring tolerate higher and lower temperatures than adults. The preferred temperature range for juveniles is 8-12°C and physiological stress has been observed at temperatures below 4°C and above 16°C (Stickney 1969). Brawn (1960b) reported that 50% of juvenile herring exposed to temperatures between 19.5 and 21.2°C died within 48 hours and that they survived at temperatures as low as -1.1°C. The blood of Atlantic herring contains antifreeze proteins (AFP) which allows them to survive in icy seawater. Plasma-freezing points are significantly lower and AFP activity significantly higher in juveniles than in adults (Chadwick *et al.* 1990).

Salinity is probably not as important a factor as temperature in affecting the distribution and movements of Atlantic herring (Munroe 2002). There is a tendency for herring to prefer higher salinities and to avoid brackish conditions with increasing age. Laboratory studies indicate that juveniles prefer salinities of 28-32 ppt (Stickney 1969), and can tolerate salinities as low as 5 ppt for brief periods of time (Brawn 1960c). Their salinity preference is temperature dependent. Stickney (1969) reported that juveniles preferred salinities above

29 ppt at temperatures below 10°C, but there was no salinity preference at temperatures above 10°C. Juveniles occupy inshore coves and estuaries with low salinities in the spring and summer of their first year of growth (Townsend 1992), whereas older juveniles avoid brackish estuarine conditions (Recksieck and McCleave 1973).

The spring and fall distributions of juvenile Atlantic herring relative to bottom water temperature, depth, and salinity based on NEFSC bottom trawl surveys from the Gulf of Maine to Cape Hatteras are shown in Figure 31. In the spring, juveniles were found between 2-12°C, with most between 3-7°C. During autumn, they were found between 5-17°C, with the majority between 6-10°C. They occurred on the outer continental shelf to a maximum depth of 300 m in the spring and fall. In the spring, the majority were found in depths < 100 m. They were caught in a salinity range of 30-35 ppt in the spring and 32-35 ppt in the autumn, with the majority found at 32-33 ppt during spring and 33-34 ppt in the autumn.

The spring and autumn distributions of juvenile Atlantic herring in Massachusetts coastal waters relative to bottom water temperature and depth based on 1978-2003 Massachusetts inshore trawl surveys are shown in Figure 32. Juveniles were collected at temperatures ranging from 1-16°C during the spring and 4-21°C during the autumn. Catch rates were high at 11°C in the spring and at 8°C in the fall. In the spring, they were found over depths ranging from 6-85 m, with higher catches between 11-20 m. During autumn they were found from 1-85 m, with a very high catch at 21-25 m.

In the Narragansett Bay bottom trawl survey, most juveniles were caught at 17-21°C in the summer, and 10-11°C and 18-20°C in the fall, 2-6°C in the winter, and 10 and 12°C in the spring (Figure 33). Most were caught between depths of 11-40 ft (3-12 m) in the spring, summer, and fall surveys. Catch rates were high at bottom depths of 91-100 ft (27-30 m) in all seasons and also at 51-60 ft (15-18 m) in spring.

The distributions and abundances of both juvenile and adult Atlantic herring in Long Island Sound relative to depth and bottom type were discussed previously under Geographic Distribution: Juveniles and Adults (Figure 22; Gottschall *et al.* [2000]).

In the Hudson-Raritan estuary, most juvenile herring were caught during winter, spring, and summer bottom trawl surveys at 3-5°C and 14-21°C, but they were most abundant at 15-18°C (Figure 34). Most were caught between 15 ft and 55 ft (4-16 m), dissolved oxygen (DO) concentrations of 6-12 mg/l, and salinities of 21-31 ppt. Catch rates were highest in depths of 30-55 ft (9-16 m), DO levels of 10 and 11 mg/l, and salinities of 21, 26, 27 and 31 ppt. Most juveniles were caught in the winter and spring surveys, with some in the summer and very few in the fall (Figure 34).

The hydrographic preferences of juvenile Atlantic herring in Chesapeake Bay from the 1988-1999 VIMS trawl surveys are shown in Figure 35 (all years and months combined). Geer (2002) states that the juveniles are found primarily at temperatures between 10-16°C and at salinities > 14 ppt. It appears they prefer dissolved oxygen levels of 9 mg/l and depths of < 10 m (Figure 35).

ADULTS

Like juvenile herring, adults utilize pelagic habitats, only using the bottom for spawning. Observations of seasonal distribution on Georges Bank suggested a preferred temperature range of 5-9°C (Zinkevich 1967). Adults regularly enter bays and estuaries, but are rarely found in low salinities (Hildebrand 1963; Munroe 2002). Bigelow and Schroeder (1953) reported that the lower limit of salinity for adult Atlantic herring in the Gulf of Maine was probably 28 ppt.

Factors which may affect herring distribution include currents and frontal zones (Sutcliffe et al. 1977; Sinclair and Iles 1985). Jakobsson (1980) reported that the densest concentrations of herring in Icelandic waters were in waters just at or just inside the edge of the continental shelf in boundary areas of warm and Depth, substrate type, and cold water masses. zooplankton abundance were significant factors affecting the presence and relative abundance of adult herring in the northern North Sea in 1992, 1994, and 1995 (Maravelias 1999). Herring were more abundant in depths < 150 m, on plankton "patches" or on their edges, and on gravel-sand seabeds where they spawned 1-2 months later. These relationships were stable over time, despite a substantial reduction in stock size (Maravelias et al. 2000b). Further analysis showed that there were more herring in areas where sea surface temperatures were between 11°C and 14°C, the thermocline was 25-45 m deep, and the difference between surface and bottom waters was only 3°C (Maravelias et al. 2000a). In more stratified waters (with colder bottom water), herring abundance decreased. This research supports the hypothesis that well-mixed waters and transition zones between wellmixed and stratified waters are preferred habitats for adult herring. Furthermore, as stock size decreased, herring aggregated in fewer, more distinct regions with these habitat characteristics. Schools were also found preferentially over areas of hard substrate and there was a strong relationship with particular topographic features within the survey area; i.e., a low ridge and two escarpments (Reid and Maravelias 2001).

Fronts created by currents and eddies act as distribution boundaries for herring through their direct effects on the fish themselves, and also indirectly by aggregating planktonic food organisms and increasing the production of zooplankton. Mixing, such as occurs

in the frontal zones at the edge of the continental shelf or as a result of increased current flow and turbulence on the edges of offshore banks causes elevated nutrient levels, increased primary production, and increased zooplankton abundance.

The spring and fall distributions of adult Atlantic herring relative to bottom water temperature, depth, and salinity based on NEFSC bottom trawl surveys from the Gulf of Maine to Cape Hatteras are shown in Figure 36. In the spring, adults were found between 2-13°C, with most between 4-7°C. During autumn, they were found between 4-16°C, with the majority between 6-10°C. They occurred on the outer continental shelf to a maximum depth of 300 m in the spring and the fall. In the fall, most were found > 80 m, while in the spring, the majority were found at shallower depths. They were caught in a salinity range of 27-35 ppt in the spring and 32-35 ppt in the autumn, with the majority found at 33 ppt during spring and 33-34 in the autumn.

The spring and autumn distributions of adult Atlantic herring in Massachusetts coastal waters relative to bottom water temperature and depth based on Massachusetts inshore trawl surveys are shown in Figure 37. Adults were collected at temperatures ranging from 2-13°C during the spring and 4-14°C during the autumn. Most were found at 4-5°C in the spring and at 6-10°C in the fall; the catch was high at 7°C in the fall. In the spring, they were found over depths ranging from 6-85 m, with higher catches between 46-50 m and 76-80 m. During autumn they were found from 21-85 m, with most at depths > 50 m.

In Narragansett Bay during the winter, most adults were caught in bottom temperatures of 3-7°C and depths of 20, 40-60, and 100 ft (6-30 m), while in the spring, most were caught at 3-5°C and 7-11°C and depths of 20-40, 70 and 100 ft in the spring (Figure 38). High catch rates occurred at 6°C in winter and 4-5°C in spring and at 100 ft at both times of year. In the fall, high catches occurred at 12°C and at 30 ft. Most adults were caught in the winter and spring surveys: none were caught in the summer.

In the Hudson-Raritan estuary, most adults were caught at bottom temperatures of 2-6°C, depths of 15-45 ft (4-14 m), dissolved oxygen (DO) concentrations of 9-12 mg/l, and salinities of 24-33 ppt. Catches were highest at 3-6°C, depths of 15-25 ft (10-14 m), DO levels of 11 mg/l, and salinities of 24-25 and 28-31 ppt. Most adults were caught in the winter (Figure 39).

The hydrographic preferences of the few adult Atlantic herring caught in Chesapeake Bay during the 1988-1999 VIMS trawl surveys are shown in Figure 40 (all years and months combined). Adults were found in only during the winter at greater depths and colder waters than the juveniles (Geer 2002). They preferred dissolved oxygen levels of 11 mg/l and salinities > 14 ppt.

RESEARCH NEEDS

The following research needs are based in part on a summary provided by Tupper *et al.* 1998.

Discrete populations/metapopulations within the Atlantic coastal stock complex need to be identified. This would involve identifying the major and minor spawning components within the Gulf of Maine -Georges Bank region and the degree to which they intermix at different times of year. Research methods that should be considered include the examination of environmentally-induced traits (scales, otoliths, and possibly morphometrics), and tagging studies. Tagging studies could be conducted in conjunction with other surveys (e.g., acoustic surveys during the summer and fall spawning seasons). Modern genetic techniques cDNA fingerprinting) and physiological performance indices might be useful for stock differentiation purposes and should be evaluated. Pertinent questions that should be addressed include:

- During the winter, what is the degree of mixing among adults that spawn on Georges Bank, Nantucket Shoals, and in the Gulf of Maine and migrate to southern New England and the mid-Atlantic region?
- During the summer and fall, what is the degree of mixing between adults that spawn in different locations?

Given the concerns that have been expressed regarding the status of the Gulf of Maine spawning stock (see Status of The Stocks), stock assessment surveys or analyses that would indicate trends in population size in the Gulf of Maine are badly needed. Procedures used to estimate population size or resource status for the different components of the coastal stock complex are complicated by the fact that adults from each spawning group mix to an unknown degree in different geographical areas and at different times of year. A large-scale larval herring survey, conducted repeatedly (e.g., at two-week intervals) throughout the spawning season on all known spawning grounds, would provide useful information for comparing the relative intensity of spawning by the different components of the resource and for evaluating to what extent larval production (and spawning stock size) on Georges Bank, Nantucket Shoals, and the southwest Gulf of Maine has changed since the last large-scale larval herring survey was done in these areas in 1990.

Existing surveys of pre-spawning aggregations of adult herring should be continued: currently, acoustic surveys are conducted in the Gulf of Maine and on the northern edge of Georges Bank (See Overholtz *et al.* 2004). New technologies, such as multi-beam acoustic equipment, towed-array video, and laser illumination, could provide surveying tools. The applicability of

alternative assessment models that have been used with other pelagic resource species (*e.g.*, surplus production, multi-species virtual population analyses, ecosystem-level models such as ECOSIM and ECOPATH) should be evaluated. The natural mortality rate that is routinely applied in stock assessment models (18% a year) needs to be validated and the degree to which it varies for different age groups of herring, and in response to annual changes in the population abundance of herring, herring predators, and other prey species, should be determined. Also, stock assessment information could possibly be improved by developing a direct method for estimating annual changes in the abundance of juvenile herring that recruit to exploited stocks.

More information is needed concerning the physical characteristics of benthic herring egg habitats and their vulnerability to disturbance by mobile, bottom-tending fishing gear, by natural disturbance, and, especially in nearshore spawning areas, to other habitat impacts related to human activities that are not associated with fishing.

In the pelagic realm, more information is needed regarding oceanographic features that affect the abundance and distribution of larval, juvenile, and adult herring. Research in the northern North Sea (see Habitat Characteristics: Adults) has demonstrated that the abundance of pre-spawning adults is higher in oceanographic fronts between well-mixed and stratified water masses (such as exist along the edges of offshore banks) where the abundance of their zooplanktonic food supply is high. Given the relatively large amount of information that is available for this species, its importance as a prey species, and the fact that the juveniles and adults are amenable to acoustic survey procedures, the Atlantic herring is an excellent subject for pelagic habitat research. Most pelagic fisheriesrelated research in the Gulf of Maine region has been directed at factors affecting the distribution, growth, and survival of larvae, but not juvenile and adult fish.

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Table 1. Relative abundance of Atlantic herring life stages in New England and Mid-Atlantic estuaries and embayments by salinity zone.

		Eggs			Larvae			Juvenile	s
	<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					С	A		A	Н
Englishman/Machias Bays			С		A	Н		С	Н
Narraguagus Bay					A	Н		С	Н
Blue Hill Bay					A	Н		С	Н
Penobscot Bay					Н	Н		С	Н
Muscongus Bay					A	Н		A	A
Damariscotta River				A	Н		С	A	
Sheepscot River				A	Н		С	A	
Kennebec/Androscoggin Rivers				С	С		С	С	
Casco Bay			R		A	A		С	A
Saco Bay					С	A		С	A
Wells Harbor	•			•	С	A	•	A	Н
Great Bay					С	С		С	С
Merrimack River		•		С	•		C	•	
Massachusetts Bay	•	•		•	•	A	•	•	A
Boston Harbor	•			•	R	A	•	С	A
Cape Cod Bay	•		R	•		С	•	С	A
Waquoit Bay						R		R	R
Buzzards Bay						R		С	С
Narragansett Bay						С		С	С
Long Island Sound					R	R		С	С
Connecticut River			•			•		R	•
Gardiners Bay	•			•			•	R	С
Great South Bay, NY	•			•			•		С
Hudson River/Raritan Bay					С	С		С	С
Barnegat Bay, NJ					R	R		С	С
New Jersey Inland Bays					R	R		С	С
Delaware Bay					R	R		С	С
Delaware Inland Bays	•			•			•		R
Chincoteague Bay	•	•		•	•		•	•	R
Chesapeake Bay Mainstem									R
Chester River			•			•			•
Choptank River			•			•			•
Patuxent River			•			•			•
Potomac River			•			•			•
Tangier/Pocomoke Sound	•		•	•		•	•	1	•
Rappahannock River			•			•			•
York River, VA			•			•			•
James River, VA			•	1	1	•	<u> </u>	1	•

Based on Estuarine Living Marine Resources (ELMR) data in Jury *et al.* (1994) and Stone *et al.* (1994). Salinity zone: T = tidal fresh, M = mixing zone, S = seawater, • = salinity zone not present.

Relative abundance: H = highly abundant, A = abundant, C = common, R = rare, blank = not present.

Table 1. Cont'd.

	Spav	vning A	lults		Adult	s
	<u>T</u>	<u>M</u>	<u>S</u>	<u>T</u>	<u>M</u>	<u>S</u>
Passamaquoddy Bay					A	Н
Englishman/Machias Bays			С		С	Н
Narraguagus Bay					С	Н
Blue Hill Bay					С	Н
Penobscot Bay					С	Н
Muscongus Bay					С	A
Damariscotta River					С	A
Sheepscot River					С	A
Kennebec/Androscoggin Rivers					С	С
Casco Bay				R		R
Saco Bay						R
Wells Harbor	•			•	R	С
Great Bay					R	С
Merrimack River			•		R	•
Massachusetts Bay	•	•		•	•	A
Boston Harbor	•			•	С	A
Cape Cod Bay	•		R	•	С	A
Waquoit Bay	•			•		R
Buzzards Bay	•			•	С	С
Narragansett Bay					С	A
Long Island Sound					С	A
Connecticut River			•		R	•
Gardiners Bay	•			•	R	С
Great South Bay, NY	•			•		A
Hudson River/Raritan Bay					С	С
Barnegat Bay, NJ					С	С
New Jersey Inland Bays					С	С
Delaware Bay					R	С
Delaware Inland Bays	•			•		R
Chincoteague Bay	•	•		•	•	
Chesapeake Bay Mainstem					R	С
Chester River			•			•
Choptank River			•			•
Patuxent River			•			•
Potomac River			•			•
Tangier/Pocomoke Sound	•		•	•		•
Rappahannock River			•		R	•
York River, VA			•		R	•
James River, VA			+-		R	•

Salinity zone: T = tidal fresh, M = mixing zone, S = seawater, $\bullet = salinity$ zone not present. Relative abundance: H = highly abundant, A = abundant, C = common, R = rare, blank = not present.

Table 2. Distribution and abundance of juvenile Atlantic herring in New England and Mid-Atlantic estuaries and embayments.

Month:	_	_							_			_
Bay/River/Estuary:	J	F	M	A	M	J	J	A	S	O	N	D
Passamaquoddy Bay	A	A	A	A	Н	Н	Н	Н	Н	Н	A	A
Englishman/Machias Bays	A	A	A	A	Н	Н	Н	Н	Н	A	A	A
Narraguagus Bay	A	A	Α	A	Н	Н	Н	Н	Н	A	A	A
Blue Hill Bay	A	A	Α	A	Н	Н	Н	Н	Н	A	A	A
Penobscot Bay	С	С	С	A	Н	Н	Н	Н	Н	Н	A	С
Muscongus Bay				R	A	A	A	A	A	A	С	R
Damariscotta River				R	A	A	A	A	С	С	С	R
Sheepscot River				R	A	A	A	A	С	С	С	R
Kennebec/Androscoggin Rivers				R	С	С	С	С	С	С	С	R
Casco Bay				R	A	A	A	A	A	С	С	R
Saco Bay				R	A	A	A	A	A	С	С	R
Wells Harbor				С	Н	Н	Н	Н	Н	A	A	R
Great Bay				С	С	С	С	С	С	С	С	R
Merrimack River				R	С	С	С	С	С	С	С	
Massachusetts Bay	A	A	Α	A	A	С	С	С	A	A	A	A
Boston Harbor	A	A	Α	A	A	С	С	С	A	A	A	A
Cape Cod Bay	A	A	Α	A	A	С	С	С	С	A	A	A
Buzzards Bay	С	С	С	С	С	R	R	R	R	С	С	С
Narragansett Bay	С	С	С	С	С	С	С	С	С	С	С	С
Long Island Sound	С	С	С	С	С	С	С	С	С	С	С	С
Gardiners Bay	R	R	R	R	С	С	С	С	R	R	R	R
Great South Bay	R	R	С	С	С	С	R	R	R	R	С	С
Hudson River/ Raritan Bay	С	С	С	С	С	R	R	R	R	R	R	R
Barnegat Bay	R	R	R	С	С	С	R	R	R	R	R	R
New Jersey Inland Bays	R	R	R	С	С	С	R	R	R	R	R	R
Delaware Bay				С	С	R	R	R	R	R		
Chincoteague Bay			R	R	R							
Chesapeake Bay			R	R	R							

Based on Estuarine Living Marine Resources (ELMR) data in Jury *et al.* (1994) and Stone *et al.* (1994). Relative abundance: H = highly abundant, A = abundant, C = common, R = rare, blank = not present.

Table 3. Distribution and abundance of adult Atlantic herring in New England and Mid-Atlantic estuaries and embayments.

Month:	J	F	M	A	M	J	J	A	S	О	N	D
Bay/River/Estuary:												
Passamaquoddy Bay	A	A	Α	A	Н	Н	Н	Н	Н	Н	A	A
Englishman/Machias Bays	С	С	С	A	Н	Н	Н	Н	Н	A	A	С
Narraguagus Bay	С	С	С	A	Н	Н	Н	Н	Н	A	A	С
Blue Hill Bay	С	С	С	A	Н	Н	Н	Н	Н	A	A	С
Penobscot Bay	С	С	С	A	Н	Н	Н	Н	Н	Н	A	С
Muscongus Bay				R	С	С	С	С	A	A	С	R
Damariscotta River				R	С	С	С	С	A	A	С	R
Sheepscot River				R	С	С	С	С	A	A	С	R
Kennebec/Androscoggin Rivers				R	С	С	С	С	С	С	С	R
Casco Bay				R	С	С	С	С	С	С	С	R
Saco Bay				R	С	С	С	С	С	С	С	R
Wells Harbor				R	С	С	С	С	С	С	С	R
Great Bay				R	R	R	R	R	С	С	С	R
Merrimack River					R	R	R	R	R	R	R	
Massachusetts Bay	A	A	A	A	С	R	R	R	С	С	A	A
Boston Harbor	A	A	Α	A	A	R	R	R	С	С	С	A
Cape Cod Bay	A	A	A	A	С	R	R	R	С	С	A	A
Buzzards Bay	С	С	С	С	С	R	R	R	R	С	С	С
Narragansett Bay	A	A	Α	A	С	С	С	С	С	С	С	С
Long Island Sound	A	A	Α	A	A	С	С	С	С	С	A	A
Gardiners Bay	R	R	R	R	С	С	С	С	R	R	R	R
Great South Bay	A	A	С	R	R	R	R	R	R	R	A	A
Hudson River/ Raritan Bay	С	С	С	С	С	R	R	R	R	R	R	R
Barnegat Bay	С	R									С	С
New Jersey Inland Bays	С	R	R	R	R	R	R	R	R	R	С	С
Delaware Bay	С	R	R	R	R	R	R	R	R	R	С	С

Based on Estuarine Living Marine Resources (ELMR) data in Jury et al. (1994) and Stone et al. (1994). Relative abundance: H = highly abundant, A = abundant, C = common, R = rare, blank = not present.

Table 4. Percentage of Atlantic herring in the diets of 15 predators in the northeast U.S. Atlantic coast ecosystem.

Predator species	Size	Percent in d		Years	Location	Number stomachs		Taxon		Source	
redator species	(cm)	By wt	By vol	Tears	Location	examined	C. harengus	Herrings	Clupeidae	Source	
Atlantic cod		15		1973-1975		8,176		✓			
		17		1976-1980		over		✓			
	51-120+	2		1981-1985		entire		✓		Link and Garrison	
		11		1986-1990		time		√		(2002)	
		25		1991-1998	NE shelf	period		√			
	61-70	4.4		1,7,1 1,7,0		86			√		
	71-80	9.7		1977-1980		52			√	Bowman <i>et al.</i> (2000)	
	81-90	6.5		1777 1700		91			· ✓	Bownian et al. (2000)	
Silver hake	< 20	0.5	4			8,722	√		<i>√</i>		
Silver liake	-		9	1973-1997			√		√	Garrison and Link	
	20-50			19/3-199/		26,070	√		√	(2000)	
	> 50	4.0	25		NIE -1, -16	1,037	✓		✓		
	26-30	4.0			NE shelf	323			V		
	31-35	11.1		1977-1980		373	√			Bowman et al. (2000)	
	41-45	20.5				72	√		✓	, , ,	
	> 45	23.3				75	✓		✓		
Summer flounder	41-45	5.5		1977-1980		80			✓	Bowman <i>et al.</i> (2000)	
	56-60	13.4		1577 1500	NE shelf	44			✓	, , ,	
	Mean = 36	8		1990-2000		na		✓		Link et al. (2002b)	
Atlantic halibut	41-50	11.1		1977-1980	NE abolf	26			✓	Bowman et al. (2000)	
	Mean = 58	4		1973-1998	NE shelf	155		✓		Link et al. (2002b)	
Spiny dogfish	51-60	2.5				235			✓	, ,	
-F,B	61-70	1.6				207			√		
	71-80	8.3		1977-1980	NE shelf	697	√		√	Bowman <i>et al.</i> (2000)	
	81-90	0.3		1777 1700	1 (2 011011	368	•		<i>'</i>	2000)	
	91-100	1.3				423	√		•		
White hake		1.3	20	1001 1007			√		√		
white nake	20-50+		20	1991-1997		na 5 241	✓		√	0 1 1711	
	20-50		2	1973-1997	NE shelf	5,341	✓		✓ ✓	Garrison and Link	
	> 50		13			6,049	√			(2000)	
Red hake	> 50		2	1973-1997		1,713			✓		
Bluefin tuna	Mean = 221	87.2			Jeffreys Ledge	147	✓				
	Mean = 221	48.4			Great South Channel	210	✓				
	Mean = 240	6		1988-1992	Stellwagen Bank	111	✓			Chase (2002)	
	Mean = 251	3.1			Cape Cod Bay	273	✓				
	Mean = 124	2.5			South of Martha's Vineyard	57	✓				
Bluefish	"Adults"	11.3		1994		50	✓			Buckel et al. (1999)	
	Adults	17.6		1995	Georges Bank	44	✓			Бискет <i>ет ат.</i> (1999)	
	21-30	2.7			NT 4 42	239			✓		
	31-40	2.3		1977-1980	NE shelf	71	✓			Bowman et al. (2000)	
Striped bass	30-120	3.4			North shore MA	1,536	✓				
pea oass	25-120	0.2		1997-2000	Cape Cod Bay	1,019	· ✓			Nelson et al. (2003)	
	30-120	0.2		1,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	Nantucket Sound	451	✓				
Dugley about-	91-100			1077 1000	NE shelf				√		
Dusky shark		1.5		1977-1980	INE SHEII	18	-		Y		
Thorny skate	61-70	36.5		1077 1000	NIT2 -1- 10	36	√			Bowman et al. (2000)	
	71-80	25.5	 	1977-1980	NE shelf	42	√			-	
	> 90	20.8				18	✓				
Goosefish	51-60	1.9		104				✓			
	81-90	1.2		1977-1980	NE shelf	86			✓	Bowman et al. (2000)	
	> 90	15.0				103	✓		✓		
Black sea bass	21-25	2.3		1977-1980	NE shelf	188	✓	-		Bowman et al. (2000)	
Weakfish	21-30	11.2		1977-1980	NE shelf	196	T	I	✓	Bowman et al. (2000)	

Table 5. Annual consumption (metric tons) of Atlantic herring by various predators.

Fish and	Elasmobranch Predators	Marine Mar	mmal Predators
Species	Estimated Annual Consumption, 1977-1997	Species	Estimated Annual Consumption, 1991-1997
Spiny Dogfish	36,000-214,000	Fin Whale	16,081-62,362
Silver Hake	11,500-36,000	Minke Whale	11,648-22,108
Georges Bank Cod	1,900-13,000	Humpback Whale	31,046-35,507
White Hake	500-20,000	Pilot Whale	149-512
Bluefish	500-13,600	Harbor Porpoise	20,863-27,655
Fluke	200-3,100	White-sided Dolphin	7,852-35,591
Pollock	200-3,100	Harbor Seal	4,853
Red Hake	200-3,100	Gray Seal	1,310
Goosefish	200-3,100		
Winter Skate	200-3,100		
Gulf of Maine Cod	200-3,100		
	Estimated Annual Consumption, 1977-1998		
Spiny Dogfish	15,526-148,197 (mean = 67,660)		
Winter Skate	20-2,329 (mean = 928)		

Sources: Overholtz *et al.* (2000) (finfish and elasmobranchs, 1977-1997); Link *et al.* (2002a) (finfish and elasmobranchs, 1977-1998); Read and Brownstein (2003) (marine mammals).

Table 6. Atlantic herring spawning site survey data and habitat parameters.

Authors	Observation or sampling method	Location	Date of survey	Size of egg beds (km²)	Depth (m)
McKenzie (1964)	Biological dredge	Trinity Ledge, southwest Nova Scotia	Sept 1961	.067	11-13
Caddy and Iles (1973)	Submersible	Northern edge of eastern Georges Bank	Sept/Oct 1970	1.1 a 0.53 a 0.3 a	50
Boyar et al. (1973)	Dredge	Jeffreys Ledge	Oct 1972		53-59
Cooper <i>et al</i> . (1975)	SCUBA divers, grab samples	Jeffreys Ledge	Oct 1974	0.78 1.39	35-55
Stevenson and Knowles (1988)	ROV, grab samples, and SCUBA	Eastern Maine	Sept 1985, 1986	0.8	20-50
Neal and Brehme (2001); Neal (2003)	Small benthic sampler	Eastern Maine	1997-2002		28-73
Neal and Brehme (2001)	Small benthic sampler	Grand Manan	Sept 2000		5-12
P. Valentine, U.S. Geological Survey, Woods Hole Field Center, 384 Woods Hole Road, Quissett Campus, Woods Hole, MA 02543, pers. comm.	Underwater video, grab sample	Stellwagen Bank	Oct 1996		34

 ^a Egg bed sizes reported by Pankratov and Sigajev (1973).
 ^b Temperatures reported by Graham and Chenoweth (1973).

Table 6. Cont'd.

Authors	Substrate	Bottom temp.	Bottom current	Other
		(°C)	(knots)	
McKenzie (1964)	Flat, sandy bottom with few small stones, no vegetation; eggs also attached to an alga (<i>Desmarestia aculeata</i>) in a nearby site that was not surveyed.	11.3-12	1.5-2	Egg mat 3.25 cm thick at deepest point, tapering to individual eggs spaced 2-6 mm apart; herring eggs in haddock stomachs.
Caddy and Iles (1973) ^a	Pebbles 2-10 mm in diameter, boulders embedded in gravel, and on epifaunal growth; eggs thin or absent on sand.	13-15 ^b	1-2	Eggs 1-2 cm thick in discrete bed. Predators (red hake, sculpin, dogfish, skate, hermit crabs, starfish, moon snails) left steep sided craters in egg layer – 8% eggs removed by predators.
Boyar <i>et al</i> . (1973)	Boulders, rocks, and gravel	7-8.5		Eggs collected in clumps, layers up to 5 mm thick.
Cooper <i>et al</i> . (1975)	80-90% eggs in <i>Ptiloda serrata</i> attached to rocks, few on non-algal covered rock surfaces at one site. At another, bedrock, boulder, rock, gravel, shell, 10% <i>Ptiloda</i> on bedrock. 90% eggs on rock-gravel. Deeper than 55 m, fine sand, no eggs.	9.5	0-1	Cunner most abundant predator observed feeding on eggs; red alga (<i>Ptiloda</i>) and eggs in cod stomachs. Hatching success > 99% at one site where egg cover was sparse. 50-70% egg mortality at bottom of 4-5 cm thick egg mass.
Stevenson and Knowles (1988)	Egg cover thickest on gravel and shell fragments, very few or no eggs on rocks or fine sand/shells at edges of egg beds.			Eggs at two sites in continuous "carpet" 1-3 cm thick, in clumps and patches at two other sites. Egg mortality negligible, no signs of predation, egg development uniform throughout egg mass.
Neal and Brehme (2001); Neal (2003)	Egg mats predominantly on gravel, eggs also observed on shell fragments and rocks			
P. Valentine, pers. comm.	Coarse sand			

Table 7. Summary of habitat characteristics and requirements for Atlantic herring in the northwest Atlantic continental shelf ecosystem.

Eggs

Habitat	Discrete, demersal, egg "beds" in coastal waters and on offshore banks and ledges in the Gulf of Maine and
Habitat	
	on Georges Bank with strong bottom currents and coarse substrate.
Depth	5-90 m.
Substrate	Boulders, rocks, gravel, coarse sand, shell fragments, macrophytes, and on a variety of benthic organisms
	and man-made structures (e.g., lobster traps); not on mud or fine sand.
Temperature	Bottom temperatures over egg beds ranged from 7-15°C; egg development normal 1-22°C; development
	rates/incubation times inversely related to temperature (10-15 days at 8-13°C).
Salinity	32-33 ppt in situ, maximum hatching success 20-35 ppt (lab studies).
Other	Low hatching success at dissolved oxygen concentrations < 20% saturation; 100% mortality of eggs under 1
	cm of sediment, 85% mortality under thin film of sediment.
Predators	Cod, haddock, cunner, red hake, sand lance, probably moon snails, hermit crabs and starfish.
Prey	Not applicable.

Larvae

Habitat	Pelagic, in estuaries, coastal, and offshore waters between Bay of Fundy and New Jersey; remain on or near
парнаі	
	bottom for first few days after hatching, until yolk-sac is absorbed, then rise to surface and are dispersed by
	currents.
Depth	Collected from very shallow water to 200 m, most 50-90 m.
Substrate	Not applicable.
Temperature	Lab study shows larvae tolerate wide temperature range (-1.8 to 24°C).
Salinity	Lab study shows larvae tolerate wide salinity range (2.5-52.5 ppt for 7 days).
Other	50% mortality in dissolved oxygen concentrations of 1.9-3.6 mg/l at 10°C after 96 hours; crude oil in
	concentrations of 1-20 ml/l is toxic; narcotized by oil dispersants (lab studies).
Predators	Sand lance, jellyfish, Atlantic mackerel, Atlantic herring.
Prey	Developmental stages of copepods (7-20 mm larvae, in fall); small adult copepods (21-30 mm, in winter);
•	wide variety of planktonic organisms (> 30 mm, in spring).

Juveniles

Juvennes	
Habitat	Pelagic; one-year-olds in nearshore waters during summer and fall, overwinter in deeper, coastal waters; two-year-olds in inshore/offshore continental shelf waters of Gulf of Maine, deeper waters of Georges Bank in summer and fall, Cape Hatteras to deeper parts of Georges Bank in winter, widespread from Cape Hatteras to Bay of Fundy in spring.
Depth	Collected in bottom trawl surveys to edge of continental shelf (300 m), mostly < 100 m in spring; migrate up in water column at dusk and down at dawn.
Substrate	Not applicable.
Temperature	Lab studies show that juveniles prefer 8-12°C, physiological stress < 4°C and > 16° C, can survive -1.1°C, 50% juveniles exposed to 19.5-21.2°C died within 48 hrs; most caught 3-7°C in spring and 6-10°C in fall NEFSC bottom trawl surveys.
Salinity	Lab studies show that juveniles prefer 28-32 ppt, can tolerate as low as 5 ppt for a short time, salinity preference is temperature-dependant (> 29 ppt below 10°C, no preference > 10°C); one-year-olds in coves/estuaries with low salinities, two-year-olds avoid brackish water.
Other	Spatial distribution affected by currents, frontal zones, and availability of zooplanktonic food organisms (see adults).
Predators	Heavily preyed upon by a variety of marine fish, marine mammals, and seabirds (see adults).
Prey	Feed on up to 15 types of zooplankton; most common are copepods, decapod larvae, barnacle larvae, cladocerans, and molluscan larvae.

Table 7. Cont'd.

Adults

Habitat	Pelagic, but spawn on bottom; inshore/offshore continental shelf waters of the Gulf of Maine and deeper parts of Georges Bank in summer and fall, Cape Hatteras to deeper parts of Georges Bank in winter, distributed across shelf in mid-Atlantic, southern New England, deeper waters of Georges Bank, and the southwest portion of the Gulf of Maine in spring.
Depth	Collected in bottom trawl surveys to edge of continental shelf (300 m), mostly < 80 m in fall and at shallower depths in spring; diel vertical migrations similar to juveniles; more abundant < 150 m in northern North Sea in summer.
Substrate	Pre-spawning aggregations more abundant over gravel/sand in northern North Sea.
Temperature	Field observations suggest adults prefer 5-9°C on Georges Bank in summer/fall; most caught 4-7°C in spring and 6-10°C in fall NEFSC trawl surveys; adults more abundant in areas of northern North Sea where summer sea surface temperatures are 11-14°C, thermocline 25-45 m deep, and difference between surface and bottom water temperatures was only 3°C.
Salinity	Adults most abundant 27-35 ppt in spring NEFSC trawl surveys, 32-34 ppt at other times of year.
Other	Well-mixed (unstratified) waters and transition zones (fronts) between well-mixed and stratified waters are preferred habitats for adults; also more abundant in or on edges of plankton "patches."
Predators	Important forage species in NW Atlantic ecosystem; principal finfish and elasmobranch predators are cod, silver hake, thorny skate, bluefish, monkfish, weakfish, summer flounder, white hake, and spiny dogfish – also, at certain locations and times of year – Atlantic bluefin tuna; principal marine mammal predators are minke whales, harbor porpoise, white-sided dolphins, fin and humpback whales.
Prey	Principal zooplankton prey organisms are euphausiids, amphipods, copepods, chateognaths, pteropods, mysids, and pandalid shrimp; adults also consume fish eggs and larvae (including their own).

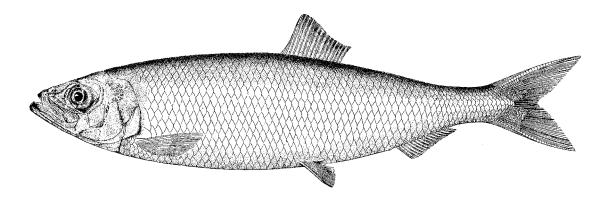


Figure 1. The Atlantic herring, Clupea harengus L. (from Goode 1884).

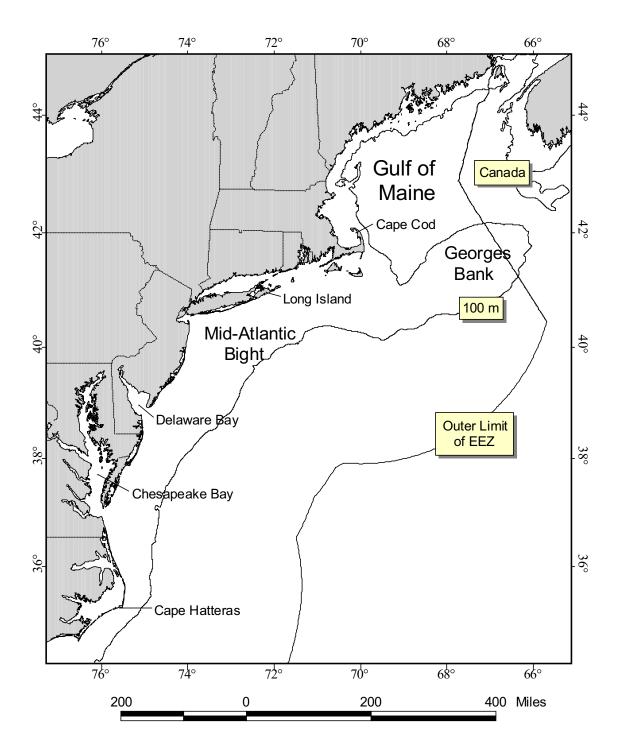


Figure 2. Northeast U.S. Atlantic coast ecosystem.

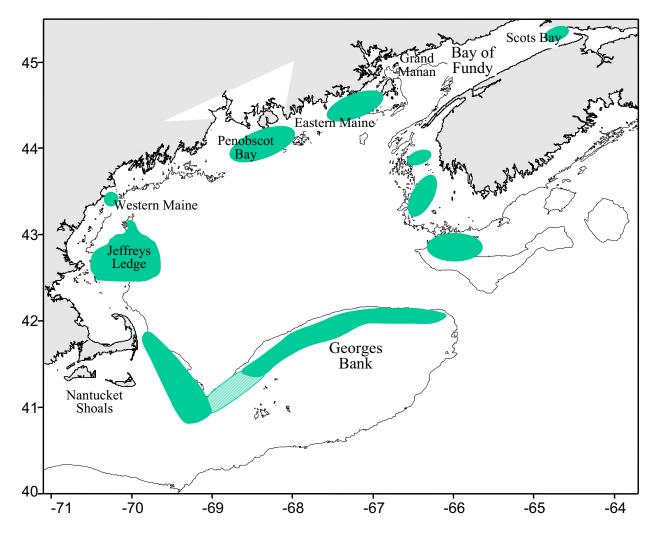


Figure 3. Generalized view of principal Atlantic herring spawning areas in the Gulf of Maine and on Georges Bank. Source: Overholtz *et al.* 2004.

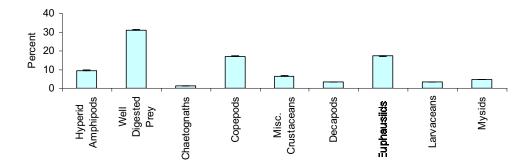


Figure 4. Percent by weight of the major prey items in the diet of Atlantic herring. Specimens were collected during NEFSC bottom trawl surveys from 1973-2001 (all seasons). For details on NEFSC diet analysis, see Link and Almeida (2000).

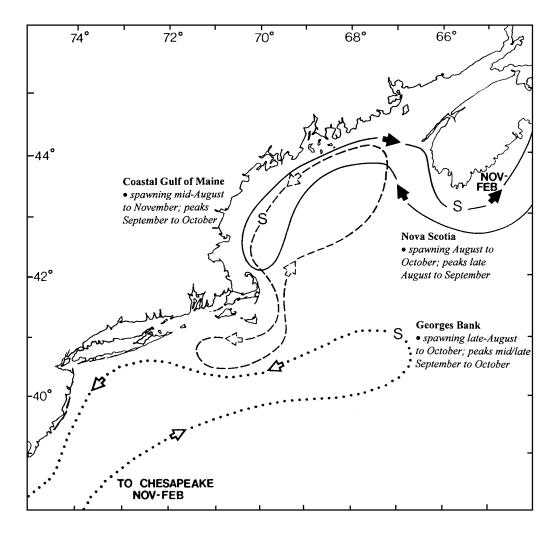


Figure 5. Hypothesized seasonal movements of three Atlantic herring spawning stocks inhabiting U.S. waters, based on Sindermann (1979).

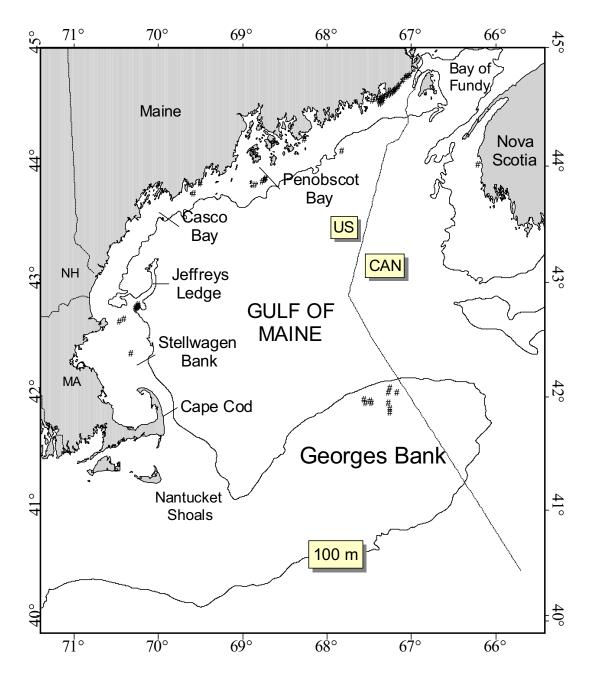


Figure 6. Geo-referenced in situ observations of Atlantic herring eggs (see Table 6).

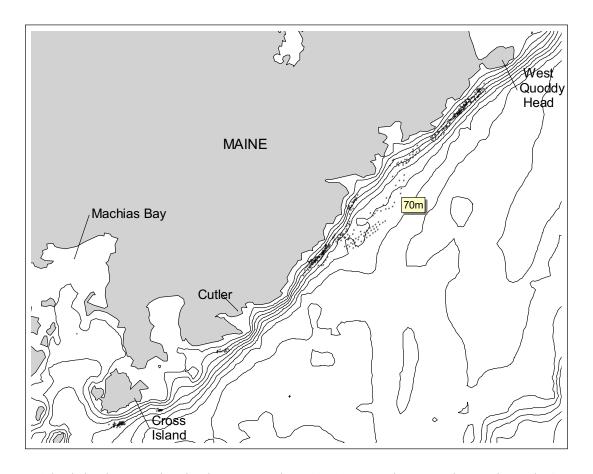


Figure 7. Atlantic herring spawning sites in eastern Maine, 1997-2002. Depth contours in 10 m intervals. Source: Island Institute, Rockland, ME [see Neal and Brehme (2001) and Neal (2003)].

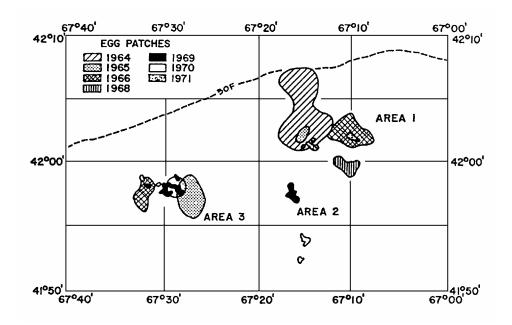


Figure 8. Principal spawning grounds of Atlantic herring on Georges Bank, 1964-1971 (excluding 1967), with a comparison of egg patch sizes among years. Source: Anthony and Waring (1980).

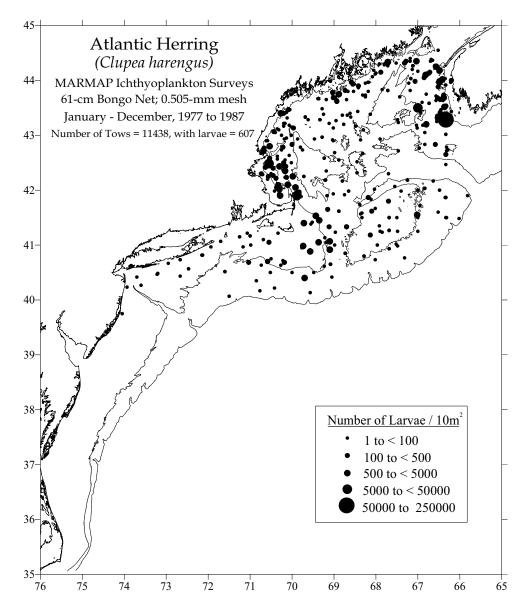


Figure 9. Distributions and abundances of Atlantic herring larvae collected during NEFSC MARMAP ichthyoplankton surveys.

For all available months and years from 1977 to 1987 combined.

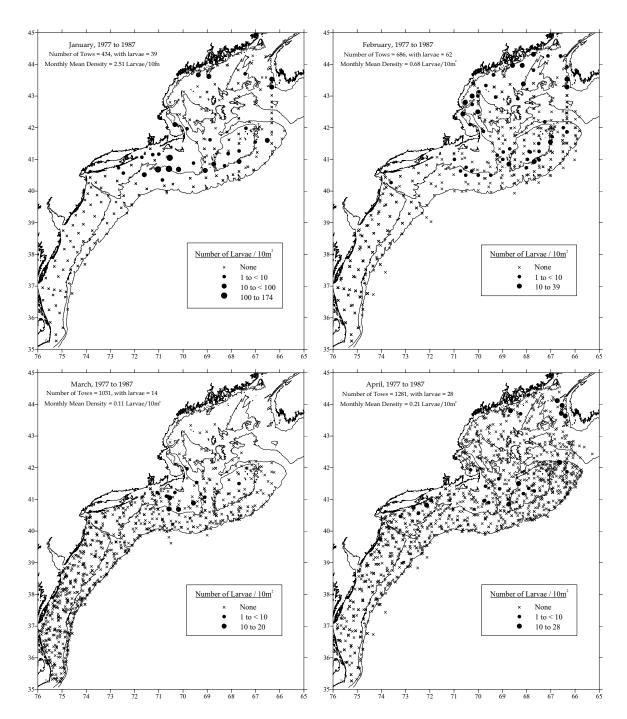


Figure 9. Cont'd. From MARMAP ichthyoplankton surveys, January through April, 1977-1987.

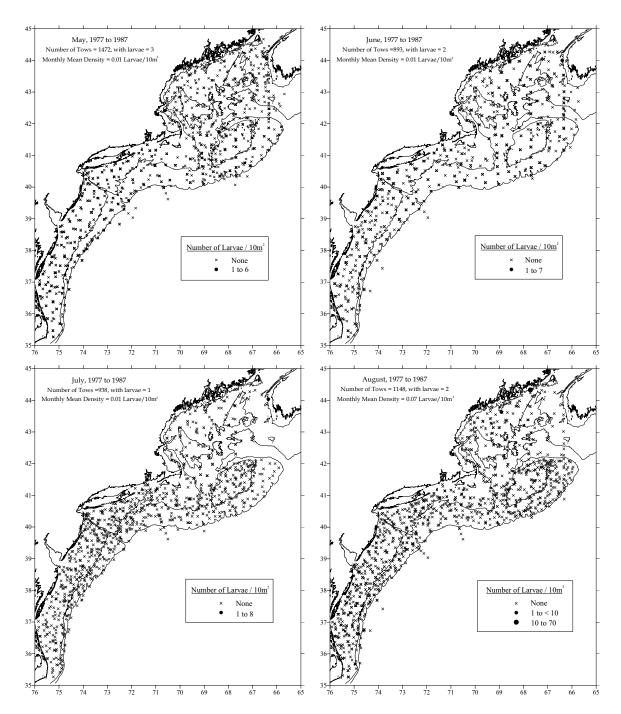


Figure 9. Cont'd. From MARMAP ichthyoplankton surveys, May through August, 1977-1987.

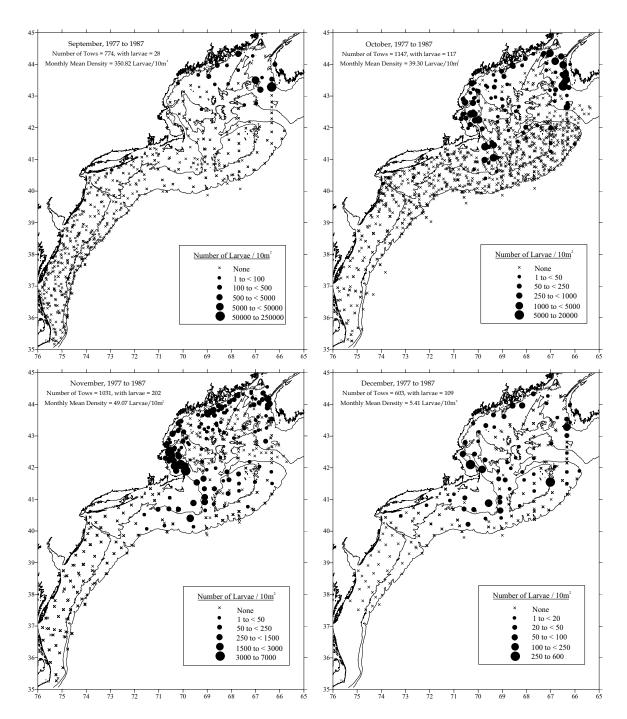


Figure 9. Cont'd. From MARMAP ichthyoplankton surveys, September through December, 1977-1987.

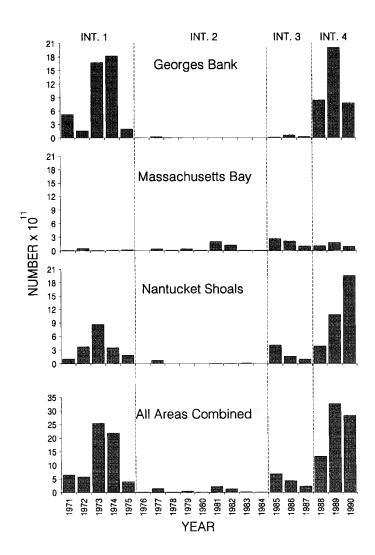


Figure 10. Changes in abundance of Atlantic herring larvae on Georges Bank, Nantucket Shoals, and in Massachusetts Bay from 1971-1990.

Source: Smith and Morse (1993). Intervals (Int.) denote periods of changing spawning patterns.

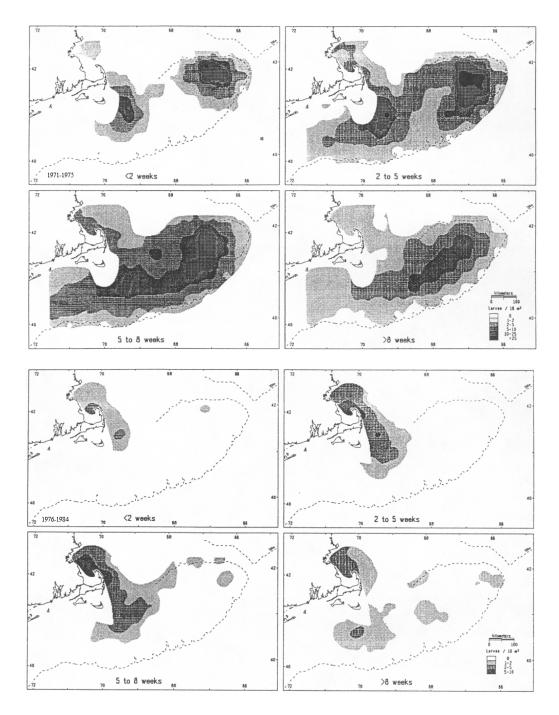


Figure 11. Distribution of Atlantic herring larvae by age in the Georges Bank area, 1971-1990. Source: Smith and Morse (1993).

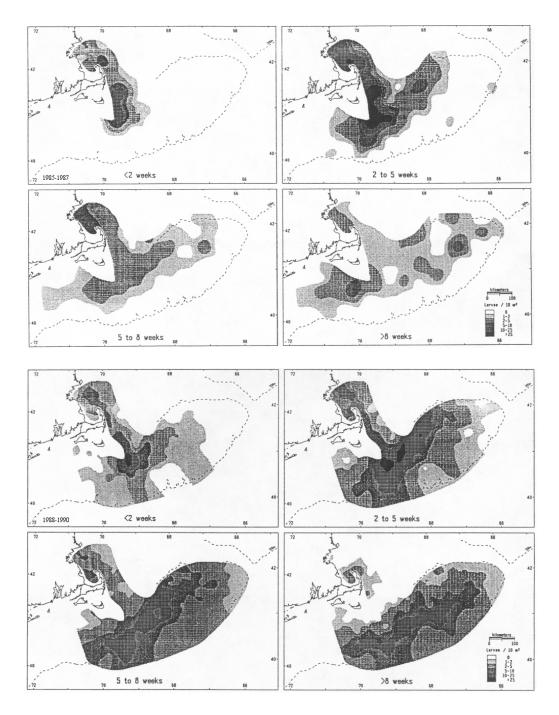


Figure 11. Cont'd.

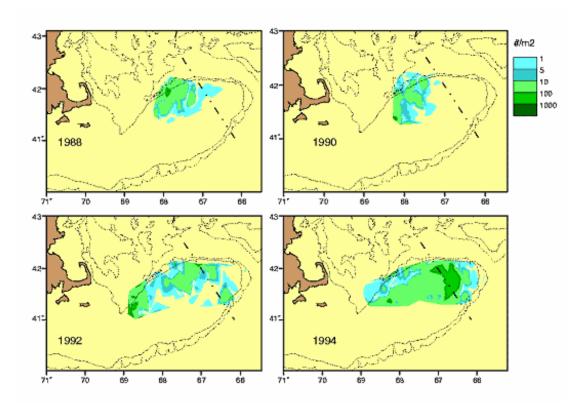


Figure 12. Distribution of recently-hatched Atlantic herring larvae on Georges Bank, 1988-1994. Source: Melvin *et al.* (1996).

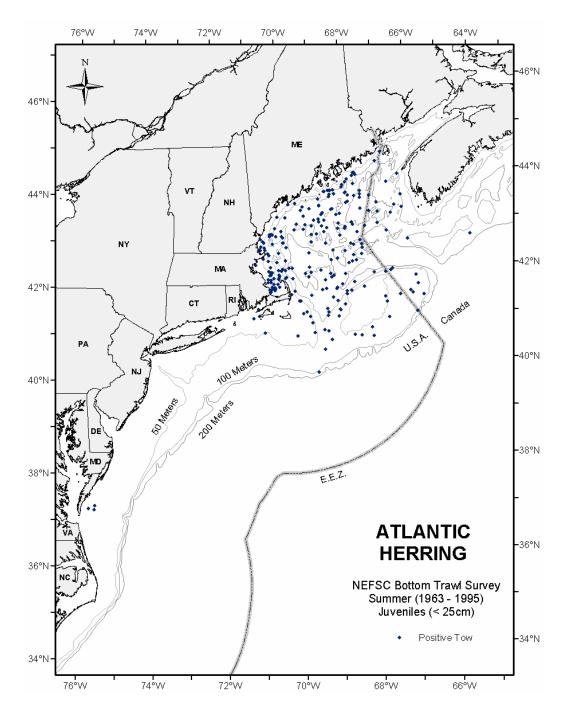


Figure 13. Seasonal distributions and abundances of juvenile Atlantic herring collected during NEFSC bottom trawl surveys.

From NEFSC summer bottom trawl surveys (1963-1995, all years combined). Distributions are displayed as presence/absence only.

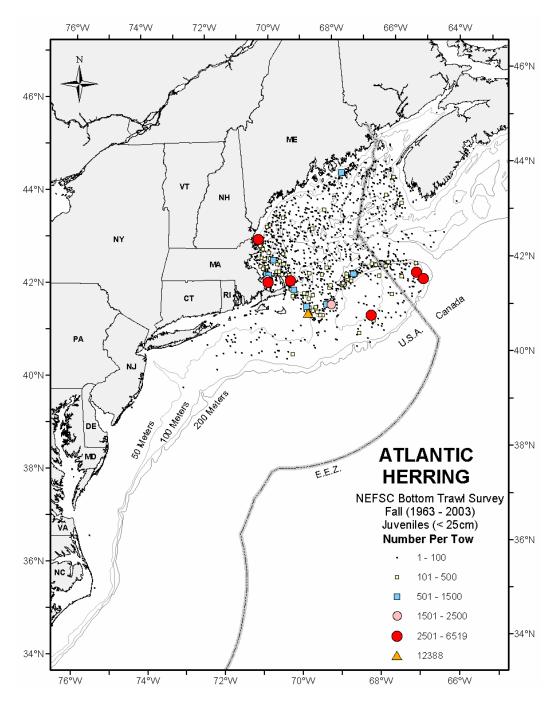


Figure 13. Cont'd.
From NEFSC fall bottom trawl surveys (1963-2003, all years combined). Survey stations where juveniles were not found are not shown.

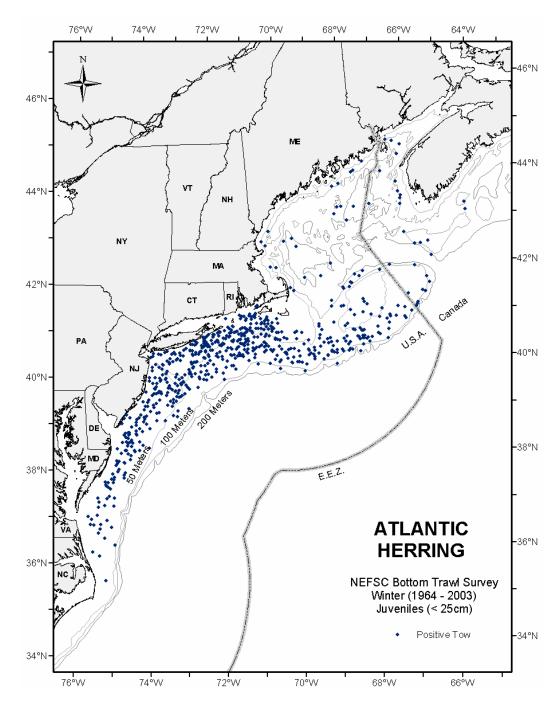


Figure 13. Cont'd. From NEFSC winter bottom trawl surveys (1964-2003, all years combined). Distributions are displayed as presence/absence only.

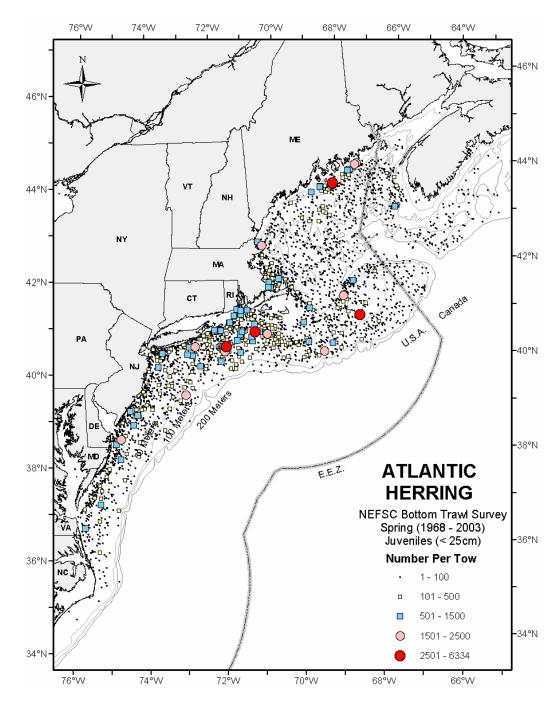


Figure 13. Cont'd. From NEFSC spring bottom trawl surveys (1968-2003, all years combined). Survey stations where juveniles were not found are not shown.

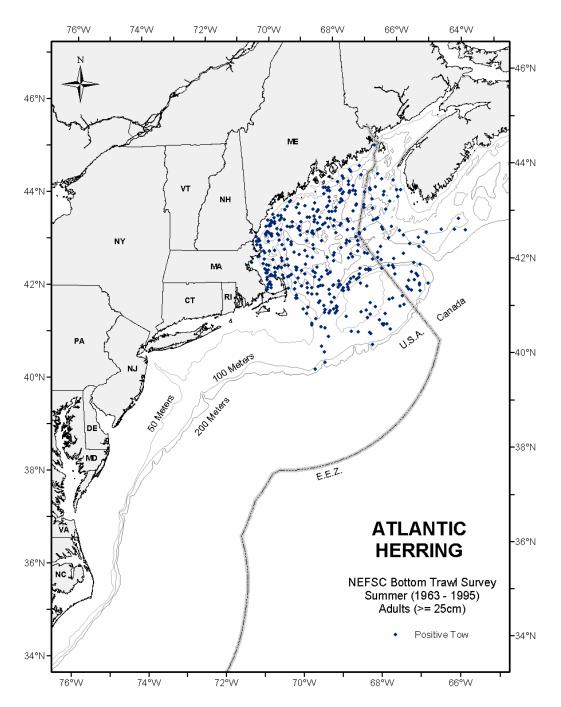


Figure 14. Seasonal distributions and abundances of adult Atlantic herring collected during NEFSC bottom trawl surveys.

From NEFSC summer bottom trawl surveys (1963-1995, all years combined). Distributions are displayed as presence/absence only.

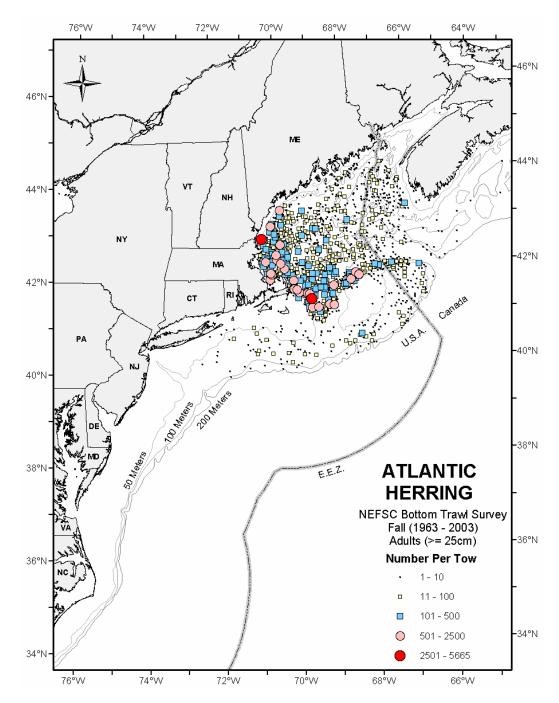


Figure 14. Cont'd.
From NEFSC fall bottom trawl surveys (1963-2003, all years combined). Survey stations where adults were not found are not shown.

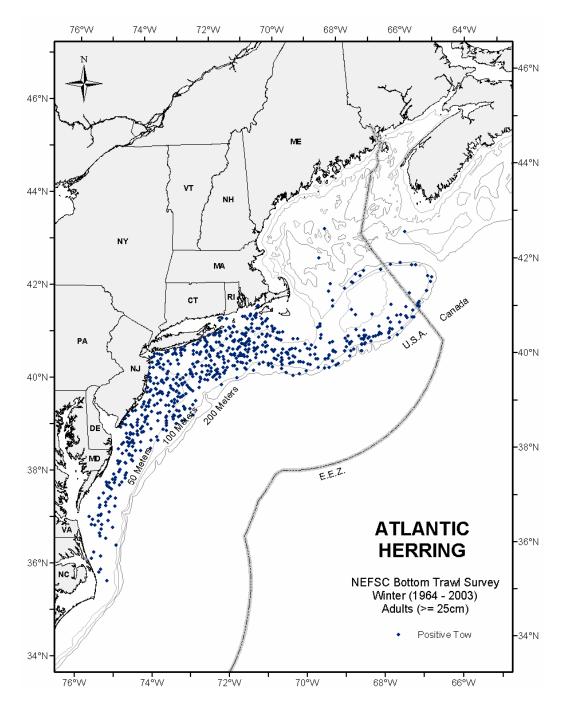


Figure 14. Cont'd. From NEFSC winter bottom trawl surveys (1964-2003, all years combined). Distributions are displayed as presence/absence only.

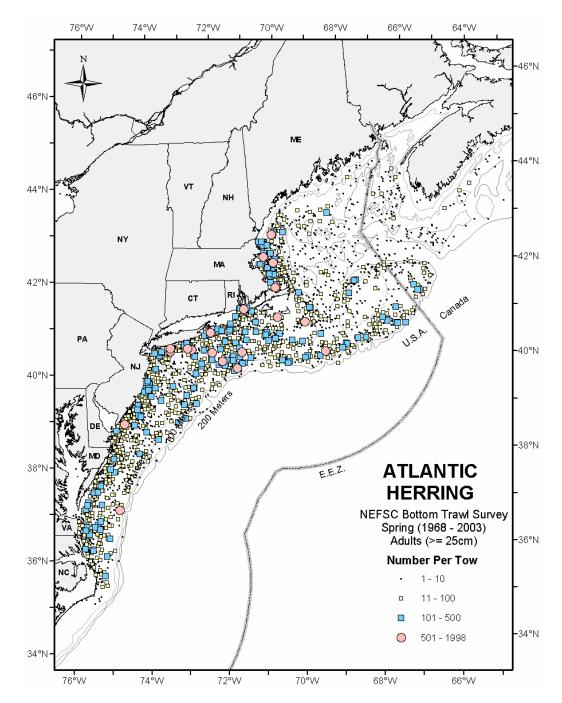


Figure 14. Cont'd.
From NEFSC spring bottom trawl surveys (1968-2003, all years combined). Survey stations where adults were not found are not shown.

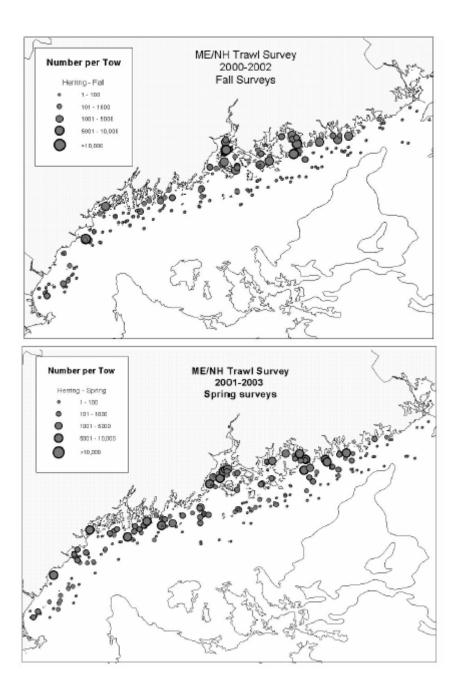


Figure 15. Distribution and abundance of Atlantic herring along the coasts of Maine and New Hampshire during spring of 2001-2003 and fall 2000-2002, from the Maine – New Hampshire inshore groundfish trawl survey. For details on the survey, see Sherman *et al.* (2004).

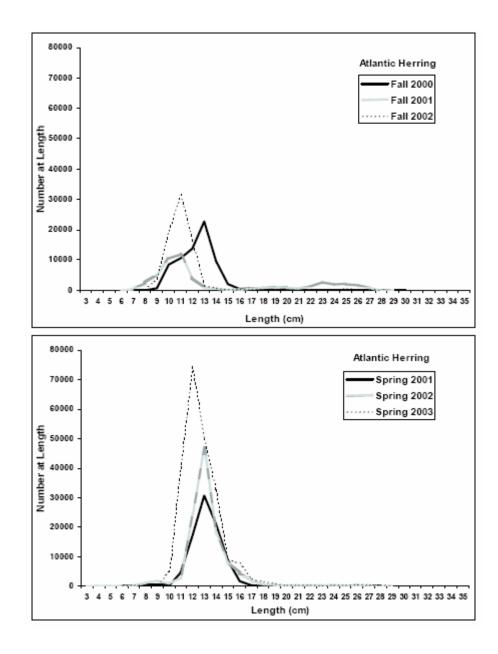


Figure 16. Length frequency plots for Atlantic herring caught along the Maine and New Hampshire coasts, by season/year. Based on the Maine – New Hampshire inshore groundfish trawl survey for spring 2001-2003 and fall 2000-2002. Source: Sherman *et al.* (2004).

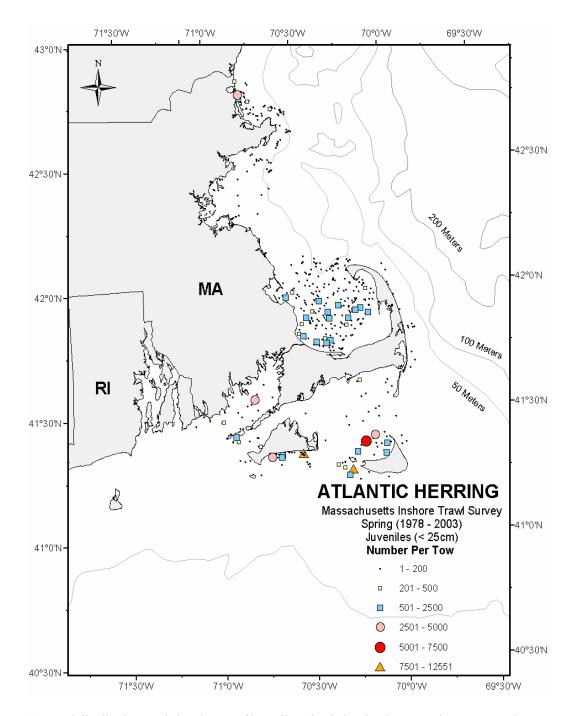


Figure 17. Seasonal distributions and abundances of juvenile Atlantic herring in Massachusetts coastal waters. From spring Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Survey stations where juveniles were not found are not shown.

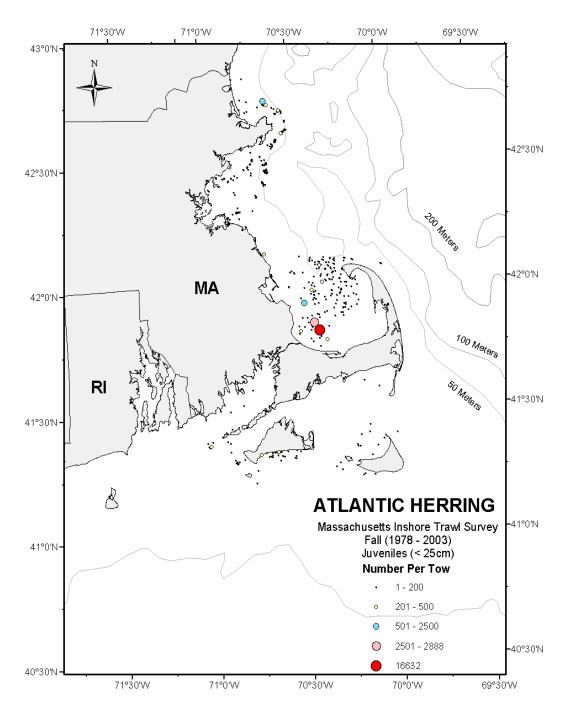


Figure 17. Cont'd.
From fall Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Survey stations where juveniles were not found are not shown.

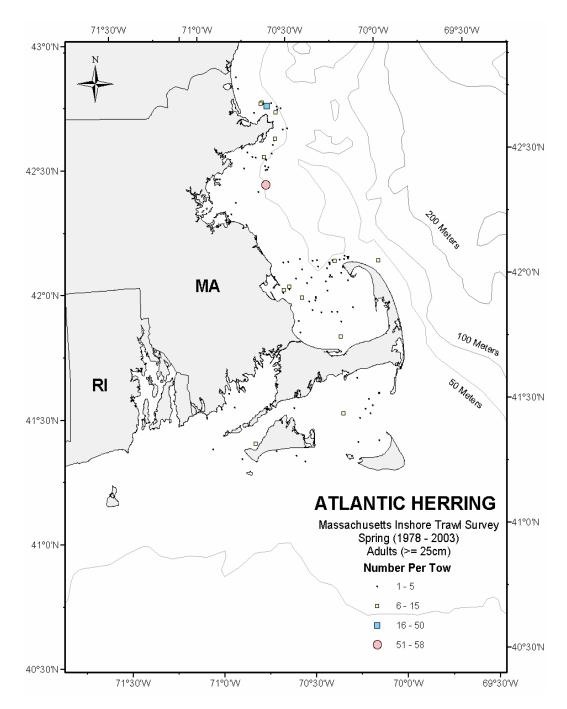


Figure 18. Seasonal distributions and abundances of adult Atlantic herring in Massachusetts coastal waters. From spring Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Survey stations where adults were not found are not shown.

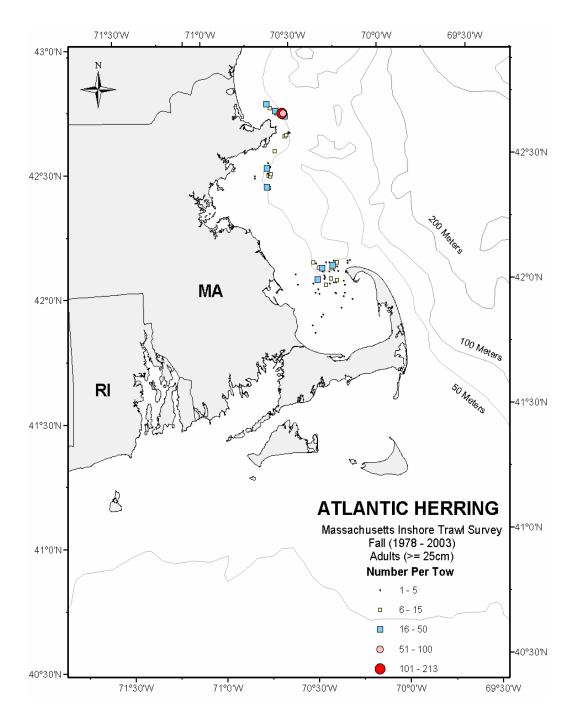


Figure 18. Cont'd. From fall Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Survey stations where adults were not found are not shown.

Autumn

Juveniles (< 25 cm) 0.5 83.3 14.8 Winter Spring 0.2 254.0

Figure 19. Seasonal distribution and abundance of juvenile Atlantic herring in Narragansett Bay. Based upon the Rhode Island bottom trawl surveys, 1990-1996. The numbers shown at each station are the average catch per tow rounded to one decimal place [see Reid *et al.* (1999b) for details].

Summer

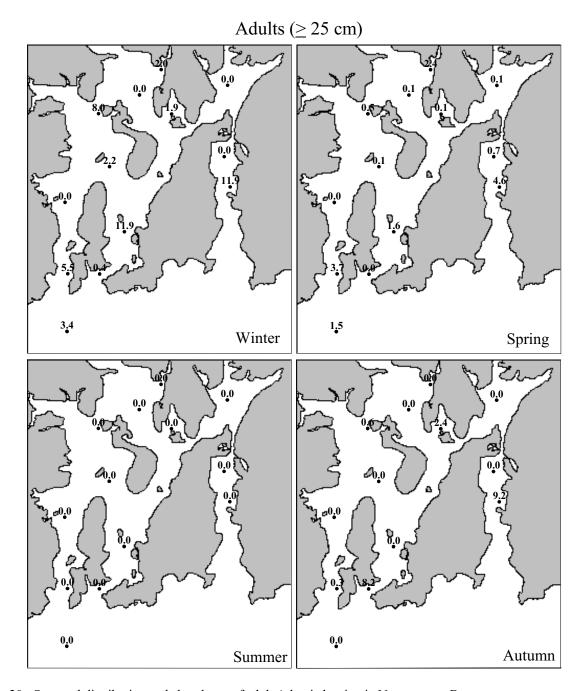


Figure 20. Seasonal distribution and abundance of adult Atlantic herring in Narragansett Bay. Based upon the Rhode Island bottom trawl surveys, 1990-1996. The numbers shown at each station are the average catch per tow rounded to one decimal place [see Reid *et al.* (1999b) for details].

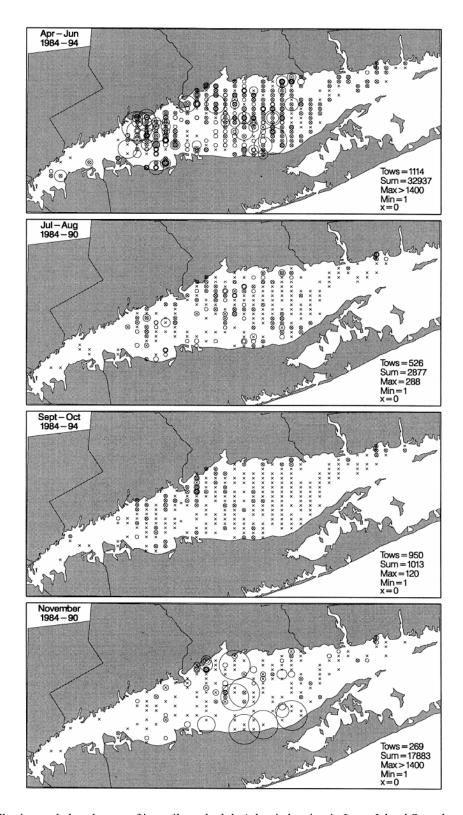


Figure 21. Distribution and abundances of juvenile and adult Atlantic herring in Long Island Sound. Based on the finfish surveys of the Connecticut Fisheries Division, 1984-1994 [from Gottschall *et al.* (2000)]. Circle diameter is proportional to the number of fish caught, and is scaled to the maximum catch (indicated by "max=" or "max>"). Collections were made with a 14 m otter trawl at about 40 stations chosen by stratified random design.

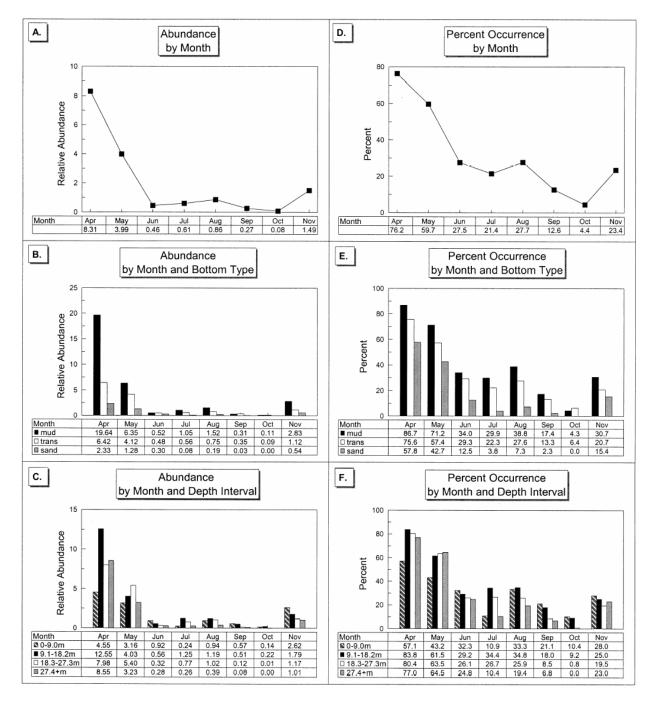


Figure 22. Relative abundance (geometric mean catch/tow) catch/tow and percent occurrence (proportion of samples in which at least one individual was observed) for juvenile and adult Atlantic herring in Long Island Sound. By month, month and bottom type, and month and depth interval. From Gottschall *et al.* (2000).

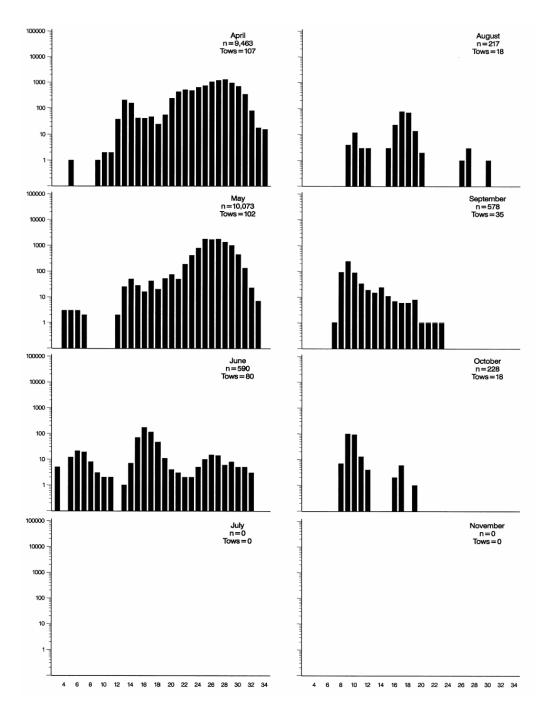


Figure 23. Monthly \log_{10} length frequencies (cm) of juvenile and adult Atlantic herring collected in Long Island Sound. Based on 21,149 fish taken in 360 tows between 1989 and 1994. From Gottschall *et al.* (2000).

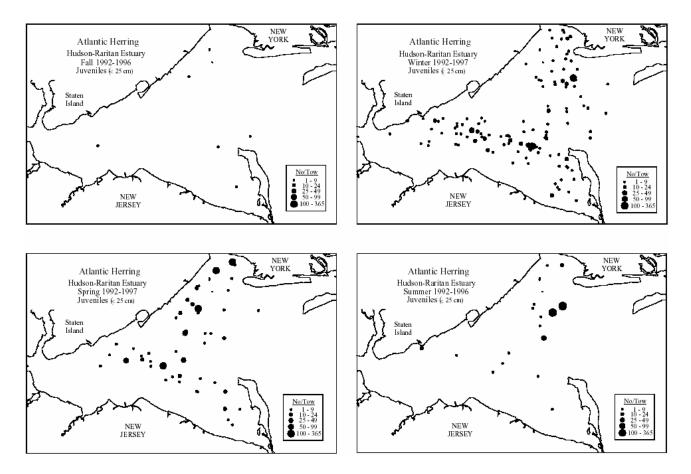


Figure 24. Seasonal distribution and abundance of juvenile Atlantic herring in the Hudson-Raritan Estuary. Based on Hudson-Raritan trawl surveys, January 1992 – June 1997 [see Reid *et al.* (1999b) for details].

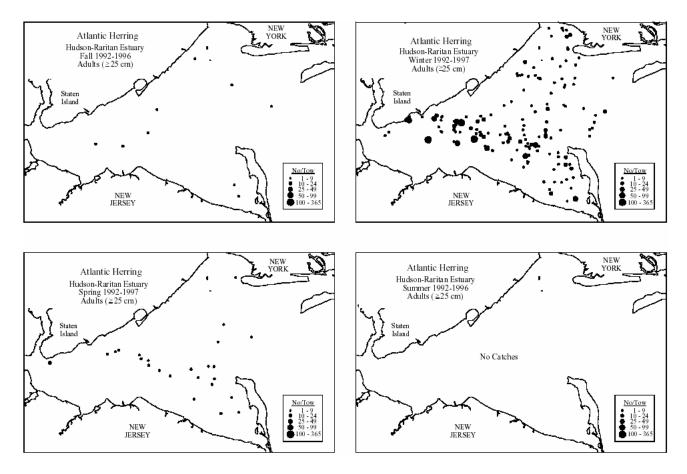


Figure 25. Seasonal distribution and abundance of adult Atlantic herring in the Hudson-Raritan Estuary. Based on Hudson-Raritan trawl surveys, January 1992 – June 1997 [see Reid *et al.* (1999b) for details].

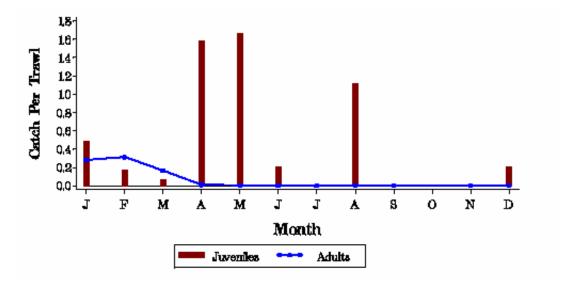


Figure 26. Catch per unit effort for total catch of juvenile and adult Atlantic herring in Chesapeake Bay, from the Virginia Institute of Marine Science's (VIMS) trawl surveys, 1988-1999 (all years combined). Monthly surveys were conducted using a random stratified design of the main stem of the Bay using a 9.1 m semi-balloon otter trawl with 38 mm mesh and 6.4 mm cod end with a tow duration of five minutes. Source: Geer (2002).

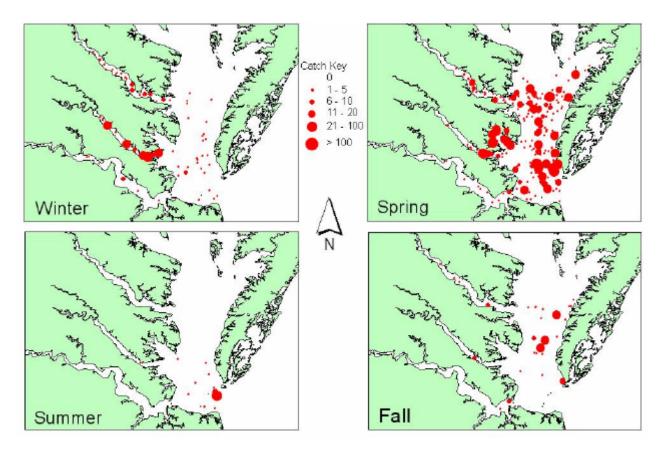


Figure 27. Seasonal distribution and abundance of juvenile Atlantic herring in Chesapeake Bay, from the VIMS trawl surveys, 1988-1999 (all years combined). Source: Geer (2002).

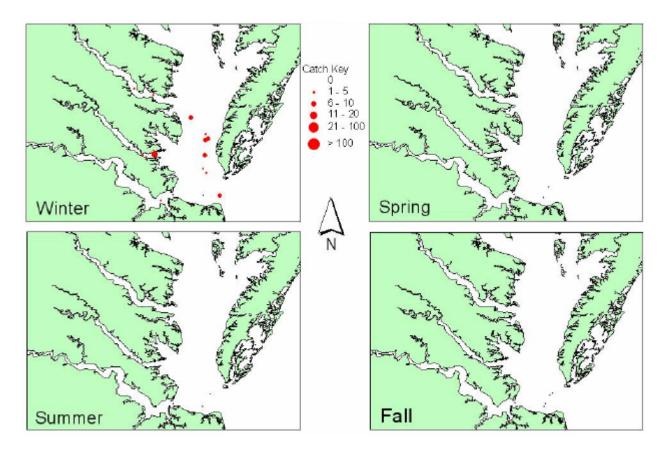


Figure 28. Seasonal distribution and abundance of adult Atlantic herring in Chesapeake Bay, from the VIMS trawl surveys, 1988-1999 (all years combined). Source: Geer (2002).

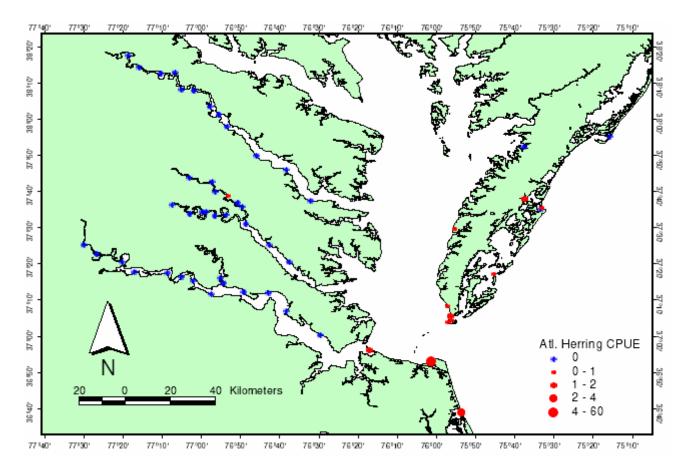


Figure 29. Atlantic herring catch per unit effort by site from the VIMS beach seine surveys, 1994-1999 (all years combined). Source: Geer (2002).

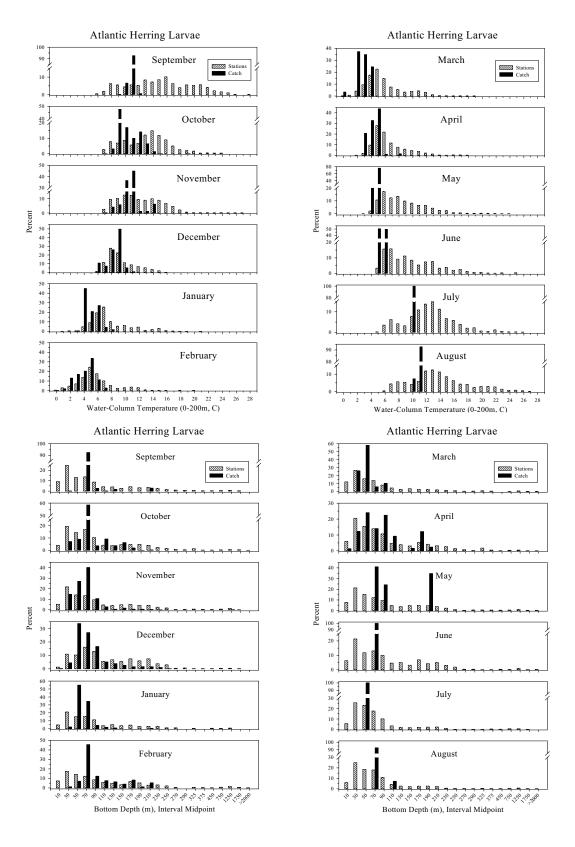


Figure 30. Distributions of Atlantic herring larvae collected during NEFSC MARMAP icthyoplankton surveys relative to water column temperature and bottom depth.

For the years 1977-1987, by month for all years combined. Open bars represent the proportion of all stations which were surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m²). Note that the bottom depth interval changes with increasing depth.

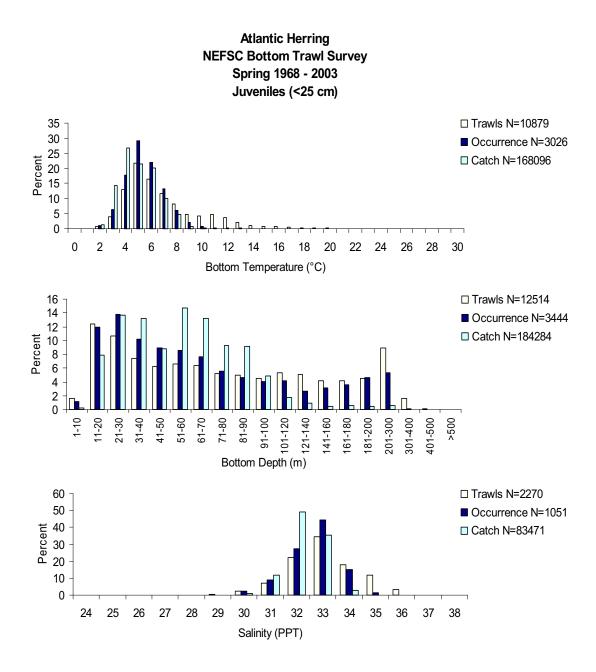


Figure 31. Distributions of juvenile Atlantic herring and trawls from NEFSC bottom trawl surveys relative to bottom water temperature, depth, and salinity.

Based on NEFSC spring bottom trawl surveys (temperature and depth: 1968-2003, all years combined; salinity: 1991-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which Atlantic herring occurred and medium bars show, within each interval, the percentage of the total number of Atlantic herring caught. Note that the bottom depth interval changes with increasing depth.

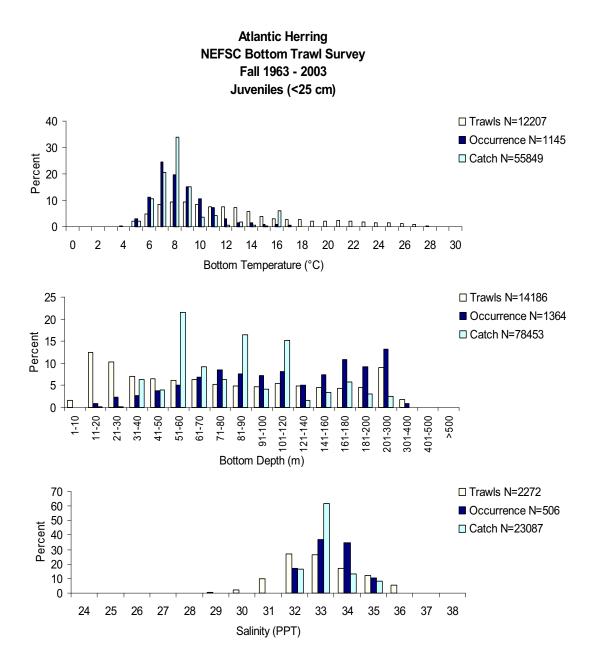


Figure 31. Cont'd.

Based on NEFSC fall bottom trawl surveys (temperature and depth: 1963-2003, all years combined; salinity: 1991-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which Atlantic herring occurred and medium bars show, within each interval, the percentage of the total number of Atlantic herring caught. Note that the bottom depth interval changes with increasing depth.

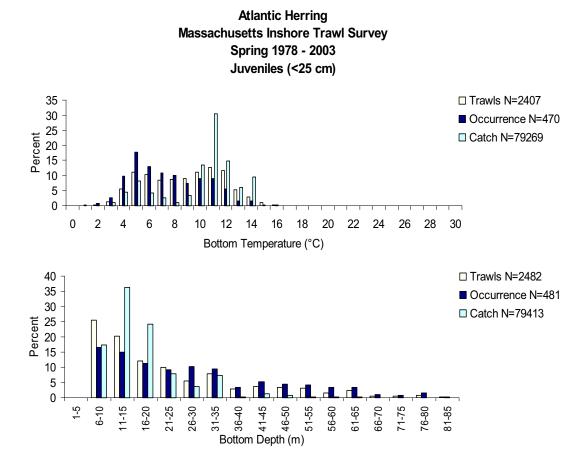


Figure 32. Distributions of juvenile Atlantic herring and trawls in Massachusetts coastal waters relative to bottom water temperature and depth.

Based on spring Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which Atlantic herring occurred and medium bars show, within each interval, the percentage of the total number of Atlantic herring caught.

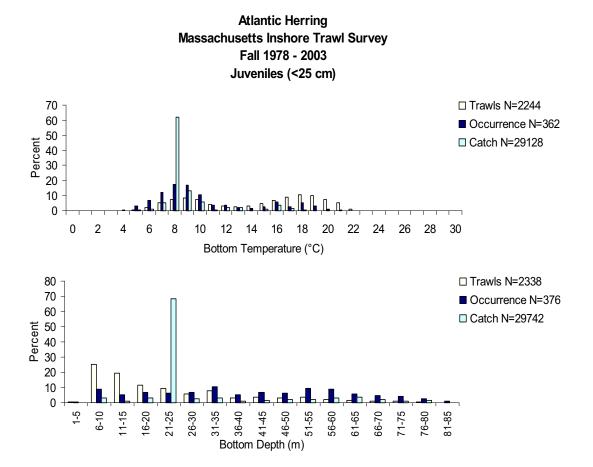


Figure 32. Cont'd.

Based on fall Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which Atlantic herring occurred and medium bars show, within each interval, the percentage of the total number of Atlantic herring caught.

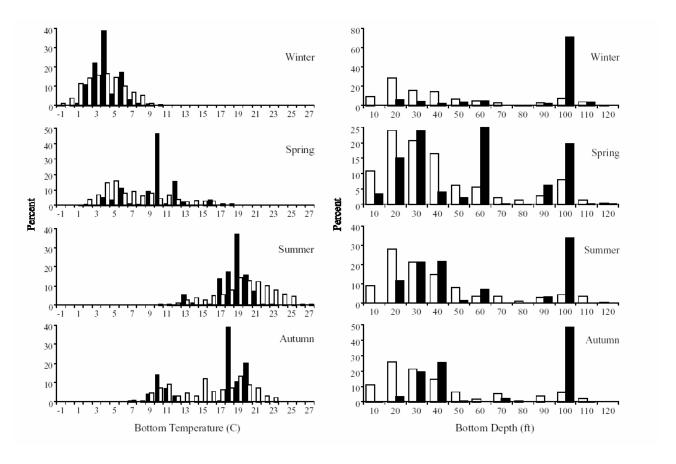


Figure 33. Distributions of juvenile Atlantic herring in Narragansett Bay relative to mean bottom temperature and bottom depth.

Based on the Rhode Island bottom trawl survey, 1990-1996. Open bars represent stations surveyed and closed bars represent fish collected.

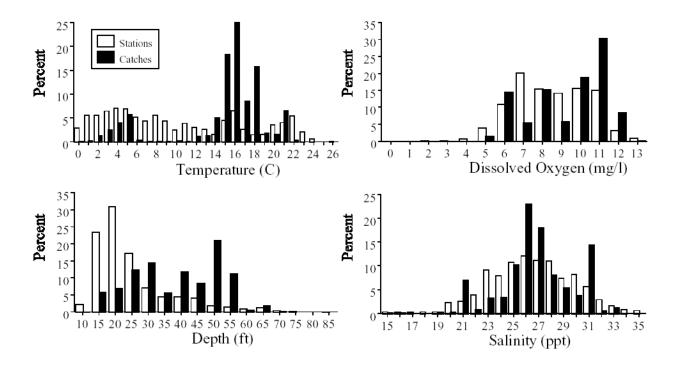


Figure 34. Distributions of juvenile Atlantic herring in the Hudson-Raritan Estuary relative to mean water temperature, depth, dissolved oxygen, and salinity.

Based on the Hudson-Raritan trawl surveys, 1992-1997. Open bars represent stations surveyed and closed bars represent

Based on the Hudson-Raritan trawl surveys, 1992-1997. Open bars represent stations surveyed and closed bars represent stations surveyed and closed bars represent stations.

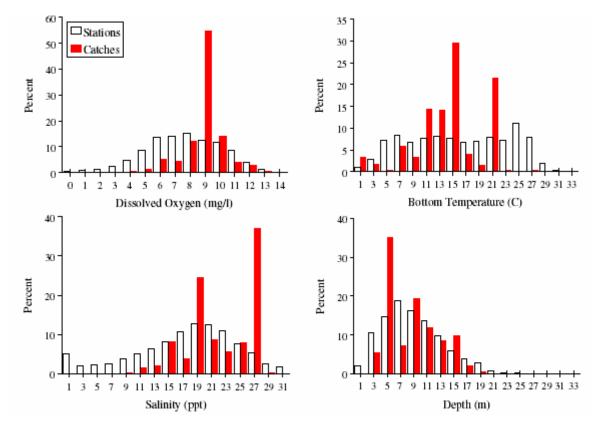


Figure 35. Hydrographic preferences for juvenile Atlantic herring in Chesapeake Bay, from the VIMS trawl surveys, 1988-1999 (all years combined). Source: Geer (2002).

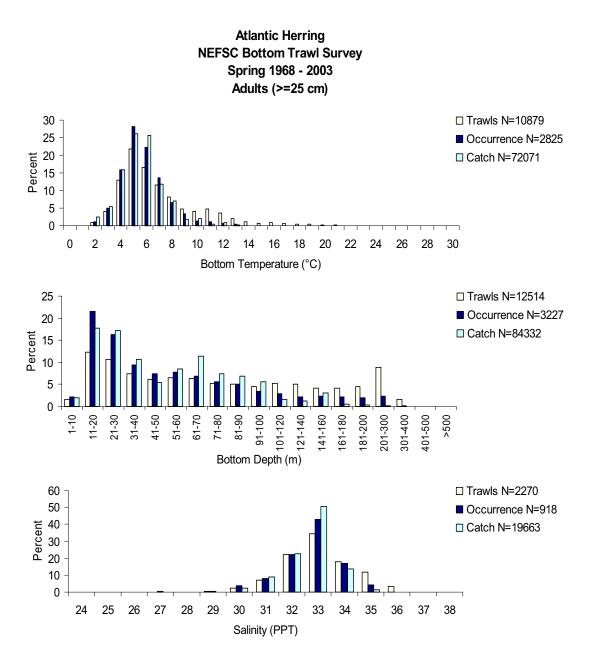


Figure 36. Distributions of adult Atlantic herring and trawls from NEFSC bottom trawl surveys relative to bottom water temperature, depth, and salinity.

Based on NEFSC spring bottom trawl surveys (temperature and depth: 1968-2003, all years combined; salinity: 1991-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which Atlantic herring occurred and medium bars show, within each interval, the percentage of the total number of Atlantic herring caught. Note that the bottom depth interval changes with increasing depth.

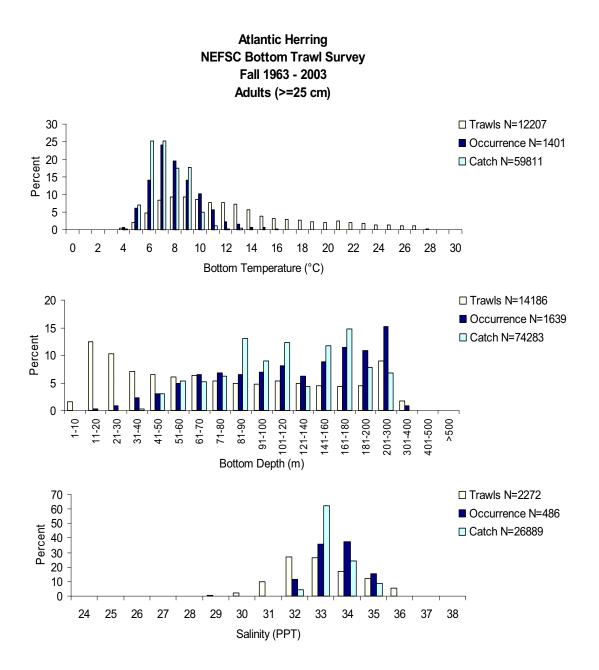


Figure 36. Cont'd.

Based on NEFSC fall bottom trawl surveys (temperature and depth: 1963-2003, all years combined; salinity: 1991-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which Atlantic herring occurred and medium bars show, within each interval, the percentage of the total number of Atlantic herring caught. Note that the bottom depth interval changes with increasing depth.

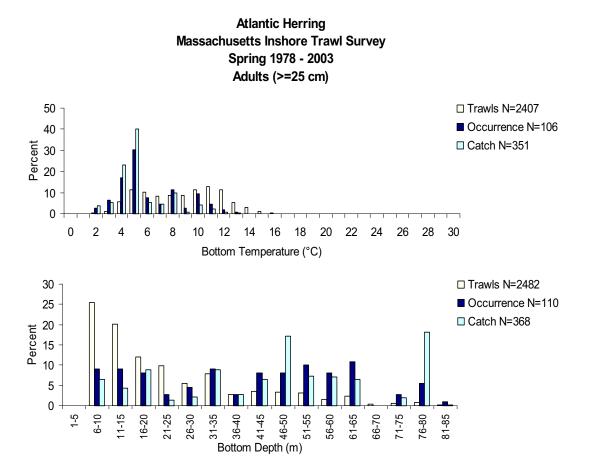


Figure 37. Distributions of adult Atlantic herring and trawls in Massachusetts coastal waters relative to bottom water temperature and depth.

Based on spring Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which Atlantic herring occurred and medium bars show, within each interval, the percentage of the total number of Atlantic herring caught.

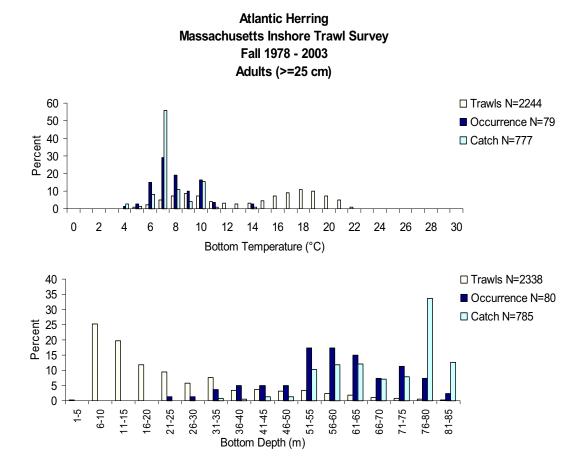


Figure 37. Cont'd.

Based on fall Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which Atlantic herring occurred and medium bars show, within each interval, the percentage of the total number of Atlantic herring caught.

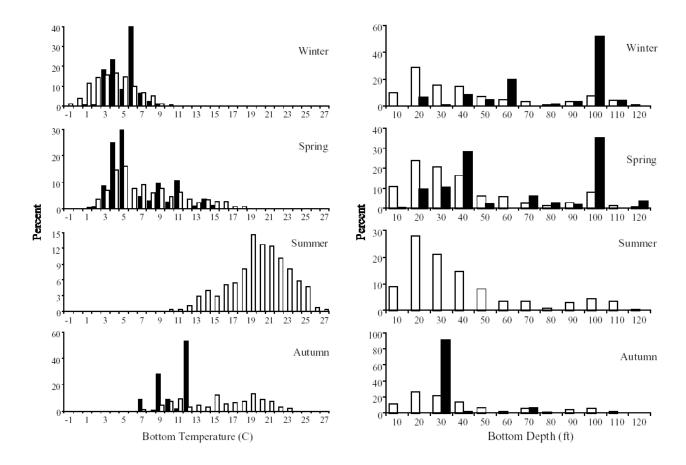


Figure 38. Distributions of adult Atlantic herring in Narragansett Bay relative to mean bottom temperature and bottom depth.

Based on the Rhode Island bottom trawl survey, 1990-1996. Open bars represent stations surveyed and closed bars represent fish collected.

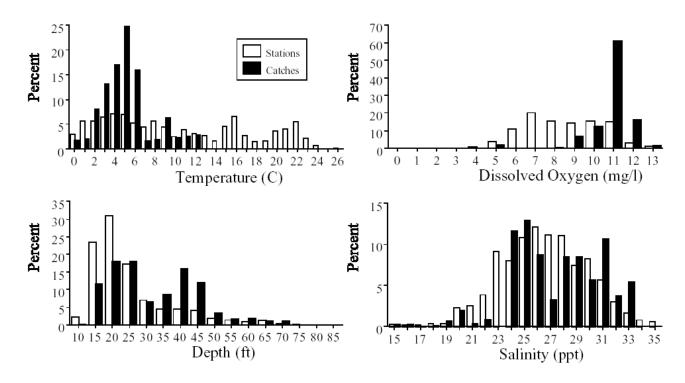


Figure 39. Distributions of adult Atlantic herring in the Hudson-Raritan Estuary relative to mean water temperature, depth, dissolved oxygen, and salinity.

Based on the Hudson-Raritan trawl surveys, 1992-1997. Open bars represent stations surveyed and closed bars represent fish collected.

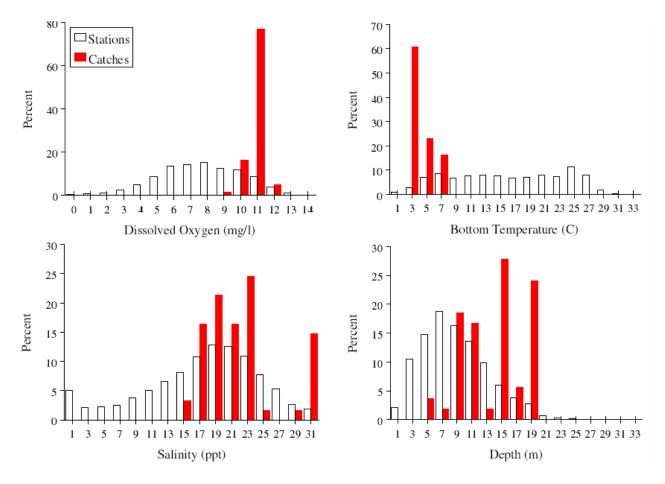


Figure 40. Hydrographic preferences for adult Atlantic herring in Chesapeake Bay, from the VIMS trawl surveys, 1988-1999 (all years combined). Source: Geer (2002).

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