



NOAA Technical Memorandum NMFS-NE-126

Essential Fish Habitat Source Document:
Atlantic Herring, *Clupea harengus*,
Life History and Habitat Characteristics

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

September 1999

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NOAA Technical Memorandum NMFS-NE-126

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Essential Fish Habitat Source Document:

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

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September 1999

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

Editorial Production

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

Special Acknowledgments

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

Internet Availability

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

Information Updating

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

Species Names

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

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

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

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

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

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

FOREWORD

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

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

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

NMFS Strategic Plan for Fisheries Research (February 1998)

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

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

The Northeast Fisheries Science Center compiled the available information on the distribution, abundance, and habitat requirements for each of the species managed by the New England and Mid-Atlantic Fishery Management Councils. That information is presented in this series of 30 EFH species reports (plus one consolidated methods report). The EFH species reports comprise a survey of the important literature as well as original analyses of fishery-

independent data sets from NMFS and several coastal states. The species reports are also the source for the current EFH designations by the New England and Mid-Atlantic Fishery Management Councils, and have understandably begun to be referred to as the “EFH source documents.”

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

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

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

JAMES J. HOWARD MARINE SCIENCES LABORATORY
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SEPTEMBER 1999

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INTRODUCTION

The Atlantic herring, *Clupea harengus* (Figure 1), is a schooling, coastal pelagic species that inhabits both sides of the North Atlantic Ocean. In the western North Atlantic they range from Labrador to Cape Hatteras where spring and autumn spawning populations support major commercial fisheries (Messieh 1988). Juveniles and adults undergo complex north-south and inshore-offshore migrations for feeding, spawning, and overwintering. In U.S. waters, herring from the Gulf of Maine and Georges Bank are assessed and managed as a single stock complex with two major spawning components (Atlantic States Marine Fisheries Commission 1995; Northeast Fisheries Science Center 1996).

This report provides information on the life history and habitat characteristics of Atlantic herring stocks that inhabit U.S. waters. This includes spawning populations of the Gulf of Maine and Georges Bank/Nantucket Shoals, as well as the southwestern Nova Scotia population that is believed to mix with the coastal Maine herring population (Stobo 1983).

LIFE HISTORY

This section provides a brief review of the biology of Gulf of Maine area Atlantic herring. More detailed reviews are provided by Bigelow and Schroeder (1953), Sindermann (1979), Kelly and Moring 1986, the Atlantic States Marine Fisheries Commission (1998), Munroe (in prep.), and Tupper *et al.* (in prep.).

EGGS

Herring deposit demersal eggs on a variety of substrates ranging from boulders, rocks, and gravel to sand, shell fragments, and macrophytes in 20 to 80 m of water in areas with strong tidal currents. The eggs are 1.0-1.4 mm in diameter (Bigelow and Schroeder 1953; Fahay 1983) and adhere to the bottom, forming extensive egg beds that are often many layers deep (Stevenson and Knowles 1988). Gravel is the preferred spawning substrate (Drapeau 1973), but eggs have been reported on aquatic macrophytes on Jeffreys Ledge (Cooper *et al.* 1975) and in the Gulf of St. Lawrence, (Messieh *et al.* 1985). The eggs hatch in 10-15 days (Bigelow and Schroeder 1953).

LARVAE

The larvae are pelagic, free-floating, and 4-9 mm long (Das 1972; Graham and Chenoweth 1973; Cooper *et al.* 1975). 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 other larvae are dispersed soon after hatching and drift with residual currents (Iles and Sinclair 1982; Townsend *et al.* 1986; Chenoweth *et al.* 1989; Smith and Morse 1993).

Larvae from Nantucket Shoals and Georges Bank tend to drift to the southwest (Lough *et al.* 1980; Grimm 1983). Larvae produced off southwestern Nova Scotia are retained initially near the spawning ground and then drift up into the Bay of Fundy (Iles 1971; Stephenson and Power 1988). Larvae produced in coastal Gulf of Maine generally remain inshore (Graham 1982; Townsend 1992) and disperse in a westerly direction and enter bays and estuaries where they overwinter (Graham *et al.* 1972; Chenoweth *et al.* 1989; Townsend 1992). In some years, late-hatched larvae from Jeffreys Ledge and Stellwagen Bank are transported eastward and overwinter in the Sheepscot River (Lazzari and Stevenson 1992). During the first winter after hatching, herring larvae 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 overwintering in nearshore and estuarine waters (Graham 1982) or in coastal waters (Townsend 1992).

Herring are 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 (Graham 1972; Stephenson and Power 1988).

JUVENILES

Larvae metamorphose into juveniles at 40-50 mm total length (TL) in early spring (April-May). Juveniles form large schools in coastal waters throughout the Gulf of Maine (Munroe, in prep.) and off southern New England, where they have been collected in surveys off Connecticut and southern Massachusetts in May and June (A.B. Howe, Massachusetts Division of Marine Fisheries, East Sandwich, MA, personal communication). In the summer and fall, juveniles move out of nearshore waters 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.

Juveniles (and adults) perform 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 (Johnson 1940; Brawn 1960a); activity is highest just after sunrise and just before sunset. Blaxter (1985) suggested that herring move away from the surface in daylight to avoid predation by diving birds.

ADULTS

Both males and females generally mature between 25-27 cm (O'Brien *et al.* 1993). 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 (Boyar 1968). Maximum size is about 39 cm TL and 0.68 kg, and maximum age is 15-18 years (Anthony 1972). Adults almost invariably occur in large schools. Vertical migrations linked to changing light intensity are pronounced and are probably related to movements of prey and avoidance of predatory seabirds (Blaxter 1985).

A reduction in mean weight at age of adults has occurred since 1983. The mean weight of fish averaged across ages 3 to 7 was 247 g in 1983, 160 g in 1988, 137 g in 1994, and 146 g in 1997. Changes in the seasonal distribution of fishing and changes in the contribution of faster-growing Georges Bank fish did not affect the reductions in mean weight because the fishery has occurred only in the Gulf of Maine since 1983 (D.K. Stevenson, Maine Department of Marine Resources, West Boothbay Harbor, ME, personal communication).

REPRODUCTION

In general, males and females mature at around 3-4 years old. Length at maturity of herring has remained fairly constant for 40 years (Table 1) in contrast with other New England marine fish species that have experienced significant declines in size at maturity in recent years. In this report, size at maturity follows O'Brien *et al.* (1993) and lengths were rounded to the nearest whole centimeter. Thus, herring ≥ 25 cm are considered adults.

Age at maturity may be density dependent; a higher percentage of age 3 fish mature when abundance is low (Tupper *et al.*, in prep.). Beginning in 1983, coincident with increasing population size (stock recovery), herring growth rates decreased and the percentage of fish maturing at age 3 declined, especially on Georges Bank and Nantucket Shoals (D.K. Stevenson, Maine Department of Marine Resources, West Boothbay Harbor, ME, personal communication). The percent of mature age 3 fish declined from 50-70% in the mid-1980s to 10-30% in 1990-1996.

Historically, three herring spawning stocks have been recognized in the U.S. fishery: southwestern Nova Scotia,

coastal Gulf of Maine, and Georges Bank/Nantucket Shoals (Figure 2). Spawning off Nova Scotia occurs in the Trinity Ledge/Lurcher Shoals/German Bank area (Stephenson and Power 1988). In the inshore coastal areas of the Gulf of Maine, spawning occurs in Scots Bay in the Bay of Fundy, off eastern Maine and the southwest shore of Grand Manan Island, off Penobscot Bay, and in the western gulf off Wood Island, Jeffreys Ledge, and Stellwagen Bank (Tupper *et al.*, in prep.). On Georges Bank, major spawning sites have historically been located near the Northeast Peak, Cultivator Shoals, and Nantucket Shoals (Boyar 1968; Anthony and Waring 1980; Grimm 1983; Lough *et al.* 1985) (Figure 3).

Gulf of Maine herring spawn in the fall, typically between July and November (Sinclair and Tremblay 1984). Spawning begins in the northern areas of the Gulf and occurs progressively later with decreasing latitude; spawning commences last on Nantucket Shoals (Bigelow and Schroeder 1953). Spawning off southwestern Nova Scotia occurs from July to November and peaks in September-October (Boyar 1968; Das 1968, 1972). In the coastal Gulf of Maine, spawning occurs from August to October (Kelly and Stevenson 1985), and peaks in mid-September to mid-October in eastern Maine and in October in western Maine (Graham *et al.* 1972). On Jeffreys Ledge, spawning occurs from September to November (Kelly and Stevenson 1985). On Georges Bank, spawning occurs from late August to December (Boyar 1968; Berenbeim and Sigaev 1978; Lough *et al.* 1980) with a peak in September-October (Boyar 1968; Pankratov and Sigaev 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).

There is some evidence of spring spawning. Approximately 2% of the fish sampled in the coastal Gulf of Maine and on the southwestern Scotian Shelf during spring were in spawning condition (Boyar 1968).

FOOD HABITS

Larvae begin exogenous feeding before the yolk sac is completely absorbed (Bigelow and Schroeder 1953). They feed opportunistically on whatever zooplankton of appropriate size are abundant (Sherman and Perkins 1971). Their primary prey are copepods (Bigelow and Schroeder 1953; Sherman and Honey 1971), in particular, *Pseudocalanus* sp., *Paracalanus 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, cirriped larvae, cladocerans, and pelecypod larvae (Sherman and Perkins 1971). Adults have a diet dominated by euphausiids, chaetognaths, and copepods (Bigelow and Schroeder 1953). Maurer (1976) reported that the most important prey items of adult herring collected on Georges Bank

were chaetognaths (*Sagitta elegans*, 43% by weight), euphausiids (*Meganctiphanes norvegica*, 23%; *Thysanoessa inermis*, 6.1%), pteropods (*Limacina retroversa*, 6.2%), and copepods (3%).

During 1973-1980, the diets of juveniles and adults collected in the Gulf of Maine during Northeast Fisheries Science Center (NEFSC) trawl surveys were dominated by euphausiids (47% by weight), of which more than 50% were *M. norvegica*, and copepods (26%) (Figure 4a). On the Scotian Shelf, euphausiids composed more than 50% of the herring diet. During 1981-1990, amphipods were the most common prey item on Georges Bank, followed by mysids (Figure 4b). Present in smaller amounts were euphausiids, copepods, chaetognaths, and unidentified fish larvae. Herring diets in southern New England and the Mid-Atlantic during 1981-1990 were more varied.

PREDATION

Juvenile and adult herring are preyed on by many marine species, including sand lance (*Ammodytes hexapterus*), cod (*Gadus morhua*), pollock (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*), silver hake, white hake (*Urophycis tenuis*), striped bass, mackerel, billfish, tuna, salmon, sculpins, winter flounder (*Pseudopleuronectes americanus*), dogfish, porbeagle shark, and skates (*Raja* spp.). Fish predation can be a significant source of mortality, especially at spawning time. Several fish species, as well as American lobster (*Homarus americanus*) and starfish, eat herring eggs. Sand lance may consume large quantities of eggs and larvae, which are sometimes cannibalized by adult herring as well. Jellyfish may also be an important predator on the early life stages. Large numbers of herring are also eaten by marine birds, northern shortfin squid, seals, porpoises, and whales (Munroe, in prep.).

MIGRATION

Adult herring make extensive feeding, spawning, and overwintering migrations. Schooling behavior begins at metamorphosis (Sindermann 1979). Schools are usually composed of fish of similar size (Bigelow and Schroeder 1953), and to a large extent, of the same year class (Munroe, in prep.). In the Gulf of Maine, juveniles spend the summer in inshore areas off Maine and New Brunswick. In autumn, they move south to waters off Massachusetts and Rhode Island; they return to Maine the following spring (Tupper *et al.*, in prep.). Some juveniles spend at least the spring and early summer off southern New England, especially off southern Massachusetts (through at least mid-June) before moving into the Gulf of Maine or offshore, presumably east of Cape Cod. Juveniles are sometimes abundant in winter and spring in the Hudson-Raritan estuary and in fall in Long Island

Sound. Young-of-the-year herring are not effectively retained by standard resource survey trawls, but in Long Island Sound, 15-min tows using a trawl with 0.25-inch codend liner have yielded up to 80,000 herring (Gottschall *et al.*, in review).

Adult herring are highly migratory and there is evidence of intermixing of adults from different spawning groups during the non-spawning phase of their seasonal cycle (Sinclair and Iles 1985). Three general migratory patterns are recognized off the northeast coast of the U.S. (NAFO regions 4X, 5, and 6) (Sindermann 1979; Figure 5). Herring that spend the summer and fall in southwest Nova Scotia overwinter in Chedabucto Bay in northeast Nova Scotia. The Georges Bank/Nantucket Shoals stock overwinters south of Cape Cod and along the mid-Atlantic coast. The stock moves 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. The migrations of coastal adults are less well known. Adults in the western Gulf of Maine may migrate southwest along the coast after spawning and overwinter at the western extreme of their migratory path, possibly south of Cape Cod. Adults in the eastern Gulf of Maine may migrate southwest and overwinter in Massachusetts Bay and southern New England.

STOCK STRUCTURE

Atlantic herring may have the most complex stock structure of any marine fish (Iles and Sinclair 1982) and attempts to define stock structure have a long history (Kornfield *et al.* 1982). Herring in the Gulf of Maine region have historically been considered three distinct spawning stocks: Nova Scotia, coastal Gulf of Maine, and Georges Bank/Nantucket Shoals (Iles 1972; Atlantic States Marine Fisheries Commission 1995) (Figure 2). In U.S. waters, they are treated as one coastal stock complex for assessment (Northeast Fisheries Science Center 1996). Evidence for and against the discreteness of local herring stocks includes spawning and larval distributions, tagging studies, morphometrics and meristics, genetics, and parasites.

Genetic studies indicate that herring spawning groups are not discrete, genetically distinct stocks. Safford and Booke (1992) did not find consistent differences between herring from two well-separated spawning areas, Jeffreys Ledge and Trinity Ledge, using traditional enzyme electrophoresis. Analysis of mitochondrial DNA also failed to distinguish between fish from these areas (Kornfield and Bogdanowicz 1987). Kornfield *et al.* (1982) found low levels of genetic heterogeneity among fall spawning herring in the Gulf of St. Lawrence and the Gulf of Maine, and concluded there is only one genetic population of fall spawners in the northwest Atlantic. They did, however, find that spring spawning herring

from the Gulf of St. Lawrence were genetically distinct from fall spawners in the Gulf of St. Lawrence and the Gulf of Maine.

There has been speculation that adult herring return to spawn at the spawning grounds where they were born, but this has only been demonstrated in one study. Herring off Newfoundland were shown to have a homing rate of 66-93% (Wheeler and Winters 1984). The inability to tag herring larvae has made it impossible to determine whether individuals are actually returning to the site where they were spawned. Results from an international herring tagging program and from the Canadian Department of Fisheries and Oceans (summarized in Stobo 1983) indicate that stocks are generally mixed throughout most of the year and that spatial and temporal isolation occurs chiefly during spawning. However, migration patterns of individual stocks persist among years and there is little straying of fish from a given stock. Tagging along the Maine and New Hampshire coasts by the Maine Department of Marine Resources showed consistency of migration patterns over time (Creaser and Libby 1988). Patterns were similar for juveniles and adults, but adults often covered greater distances; many adults tagged in summer in eastern Maine overwintered in Massachusetts Bay. There was some tendency for adults tagged in eastern Maine to be recovered in the southwestern Nova Scotian fishery.

Herring in the Gulf of Maine and on Georges Bank and the Scotian Shelf spawn in well-defined areas, although homing to natal spawning grounds has not been demonstrated. Distinct and spatially stable larval retention areas may also promote genetic isolation. Iles and Sinclair (1982) stated that larval herring were concentrated in such areas in the northwest Atlantic and hypothesized that the number of retention areas determined the number of genetically distinct stocks. However, Smith and Morse (1993) discussed evidence for larval drift in the region and questioned whether stocks could be separated through larval retention. Chenoweth *et al.* (1989) reported extensive westward transport of larvae from Gulf of Maine spawning sites and possible larval retention by a sharp oceanographic front near Grand Manan Island.

Pectoral fin ray counts were once considered the most promising meristic character for discriminating stocks. The number of pectoral fin rays is related to water temperatures and is determined at an early age. Adult herring from Georges Bank-Cape Cod have lower pectoral fin ray counts than adults from waters to the north, presumably due to warmer temperatures. In the 1958-1963 year-classes, herring from eastern Maine and Nova Scotia had the highest pectoral fin ray counts and fish from western Maine were intermediate in fin ray numbers. However, juvenile fish from Maine had counts similar to fish from Georges Bank-Cape Cod, indicating that they probably came from that area. It is likely that some of those juveniles subsequently entered the Georges

Bank fishery (Anthony 1981).

Significant phenotypic differences have been identified among herring spawning groups, but this may reflect different environmental histories rather than genetic differentiation. Safford and Booke (1992) found differences in several morphometric characters between herring from Jeffreys Ledge and Trinity Ledge, but overall results supported the single-population hypothesis. They postulate that either sufficient gene flow exists between spawning groups to prevent the evolution of genetically distinct stocks, or that genetic isolation is a recent phenomenon and genetic differences have not had time to evolve.

Parasites may be useful as biological indicators to differentiate between fish populations. Parasites of Georges Bank and Gulf of Maine herring have apparently not been studied, but Bay of Fundy, Scotian Shelf, and Gulf of St. Lawrence fish have been surveyed (McGladdery and Burt 1985). Seven of 18 parasite species identified were potential indicators. Patterns of occurrence of the parasites indicated movement of fish to and from the Bay of Fundy, and extensive mixing of stocks in feeding and nursery areas.

McQuinn (1997) reviewed arguments for a discrete versus dynamic balance population concept for Atlantic herring. He 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. Although the metapopulation (or stock complex) is the practical unit for management, local populations must be conserved to preserve spawning potential and viable coastal fisheries. The metapopulation may increase resilience of local populations because a strong year class may enhance several local populations (McQuinn 1997).

HABITAT CHARACTERISTICS

Information on the life history and habitat characteristics of Atlantic herring are presented here and are summarized in Tables 2-5. This information is limited to the Georges Bank, coastal Gulf of Maine, and Nova Scotia stocks, which occur in U.S. waters at some time during the year. Information for other stocks in the northwest and northeast Atlantic were not considered.

EGGS

Herring eggs are usually spawned on horizontal beds at depths of 40-80 m on Georges Bank, 20-50 m in coastal Gulf of Maine, and as shallow as 11-13 m off southwest Nova Scotia. Eggs are laid on gravel (the preferred substrate), sand, rocks, shell fragments, aquatic

macrophytes, and structures such as lobster pots. Spawning occurs in areas of well-mixed water with tidal currents of 1.5-3.0 knots. These high energy environments provide aeration and reduce siltation and accumulation of metabolites. Spawning occurs at temperatures of 12-15°C on Georges Bank, 6-13°C on Nantucket Shoals, and 8-12°C near Grand Manan Island, and at salinities of 31.9-33.0 ppt. Laboratory studies found normal egg development and hatching at 10 and 15°C, no development at 0 and 5°, and rapid initial development followed by 100% mortality at $\geq 20^\circ\text{C}$.

LARVAE

Larvae occur at temperatures of 9-16°C and salinities of 32 ppt in the Gulf of Maine. Survival and growth in winter may be enhanced in offshore waters, which are up to 5°C warmer than inshore waters. Larvae may acclimate to lower temperatures when the rate of temperature decline is slow; in the laboratory, survival was $\leq 30\%$ when the rate of change was 0.1-0.25°C/day, but up to 70% when the rate of change was $< 0.1^\circ/\text{day}$. Larvae occur at depths > 50 m on Georges Bank where they are retained in the clockwise current gyre for several months. Light, turbidity, and tidal currents may control their vertical migrations.

In the NEFSC Marine Resources Monitoring, Assessment and Prediction (MARMAP) survey, most larvae were collected at 8-14°C from September to November; maximum abundance was at 9-12°C (Figure 6). 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 (Figure 6).

JUVENILES

In the Sheepscot River, juveniles prefer temperatures of 10-16°C. They may overwinter in Passamaquoddy Bay until the temperature drops to 0°C. In the laboratory, the upper lethal temperature is 19.5-21.2°C, the lower lethal temperature is -1.1°C, and the preferred temperature is 8-12°C. Juveniles in the Gulf of Maine occur at average surface salinities of 31-32.4 ppt. In the Sheepscot River, they occur at 16-32 ppt, although most occur at 30-32 ppt. Laboratory studies indicate a general preference for 26-32 ppt. This salinity preference is temperature dependent; there is a preference for > 29 ppt at $< 10^\circ\text{C}$. There is a tendency to prefer higher salinities and to avoid brackish conditions with increasing fish age.

Juveniles caught during NEFSC bottom trawl surveys were most abundant at temperatures of 3-4°C and depths

of 30-90 m in spring, 6-9°C and 15-135 m in summer, 8°C and 30-60 m in fall, and 2-4°C and 30-60 m in winter (Figure 7a). There is a bimodal distribution in occurrence relative to temperature based on Massachusetts inshore trawl survey catches; relative abundance was highest at 4-7°C and 12°C in spring, and 7-12°C and 17°C in the fall (Figure 8). The bimodality may be related to temperature differences north relative to south of Cape Cod. Relative abundance was greatest at bottom depths of 5-30 m in spring and 5-75 m in the fall. In Narragansett Bay, juveniles were most abundant at 3-6°C in winter, 10-12°C in spring, 17-19°C in summer, and 18-20°C in fall (Figure 9a). Relative abundance was high at bottom depths of 100 ft (30 m) in all seasons and at 30 and 60 ft (9 and 18 m) in spring. In the Hudson-Raritan Estuary, herring were found at 2-6°C and 12-22°C but were most abundant at 4-6°C and at 15-18°C (Figure 10a). There were few differences in abundance over the range of depths and salinities sampled.

ADULTS

In the Gulf of Maine, herring spawn at 7-15°C. Spawning begins earlier in years when August water temperatures are warmer. Adults may overwinter at temperatures as low as 0°C in Passamaquoddy Bay. They generally occur at salinities > 28 ppt and spawn at 31.9-33.0 ppt (never in brackish water). The distribution of schools is often related to concentrations of their euphausiid prey; areas with phytoplankton blooms may be avoided.

Catches of adult herring in the NEFSC bottom trawl survey were greatest at 5°C and 30-50 m in spring, 6°C and 20-130 m in summer, 5-6°C and 60-170 m in fall, and 7-8°C and 70-100 m in winter (Figure 7b). In the Massachusetts inshore trawl survey, the largest catches occurred at 4-6°C in depths of 5-75 m in spring and at 7°C in depths of 50-80 m in the fall (Figure 8). Abundance in Narragansett Bay was highest at 3-6°C and 100 ft (30 m) in winter, 3-5°C and 100 ft in spring and 7-11°C, and 30 ft (9 m) in fall; no adults were caught in summer (Figure 9b). In Long Island Sound, springtime abundance was highest at 9-10°C, 10-30 m, and salinities of 25-28 ppt. The largest autumn catches occurred at 17-21°C, 10-18 m, and 27-28 ppt. In the Hudson-Raritan estuary, catches were highest at 3-6°C and 15-45 ft (4.5-13.5 m) (Figure 10b).

GEOGRAPHICAL DISTRIBUTION

EGGS

The eggs of herring are demersal and adhere to the substrate (Bigelow and Schroeder 1953; Fahay 1983) and were not usually collected during the NEFSC MARMAP

survey. The general location of herring spawning areas in the northwest Atlantic Ocean is presented in Figure 2.

LARVAE

The NEFSC MARMAP survey collected herring larvae from New Jersey to the Bay of Fundy inshore to the seaward limit of the survey (Figure 11). Larvae were collected in all months, even though herring in the Gulf of Maine do not spawn in the spring and larvae undergo metamorphosis in April and May. The highest mean monthly density (351 larvae/10 m²) occurred in September off southwestern Nova Scotia (Figure 11) 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); high larval densities occurred from the western Gulf of Maine and Massachusetts Bay to western Georges Bank and Nantucket Shoals indicating that spawning began earlier in the northeast (see also Bigelow and Schroeder 1953; Tupper *et al.*, in prep.). Mean densities were much lower (less than 6 larvae/10m²) from December through August. Herring spawn in the fall (Sinclair and Tremblay 1984) and with a peak from September to October (Boyar 1968).

The distribution of herring larvae changed considerably around Georges Bank from 1971 to 1990, a period of widely fluctuating adult spawning biomass (Figure 12; Smith and Morse 1993). In 1971, herring spawned throughout Georges Bank and Nantucket Shoals; the principal spawning ground was on the Northeast Peak of Georges Bank. Following the collapse of the Georges Bank fishery, spawning was restricted to Nantucket Shoals by 1976. By 1979, larvae were found only around Stellwagen Bank in Massachusetts Bay. The reappearance of larvae on Nantucket Shoals in 1985 indicates an increase in spawning stock distribution. By 1988, larvae were collected on Cultivator Shoals on Georges Bank, but were not found on the Northeast Peak through 1990.

JUVENILES AND ADULTS

NEFSC Bottom Trawl Survey

The seasonal distribution pattern and abundance of juvenile and adult herring were similar. Juveniles and adults range from south of Cape Hatteras to the Bay of Fundy and Browns Bank (Figure 13). In spring, juveniles and adults were most abundant on the inner shelf from North Carolina to New Jersey, shelf-wide from Long Island to Cape Cod, and in Massachusetts Bay, and moderately abundant on Georges Bank. Juveniles were also abundant along the coast of Maine. In summer, juveniles and adults occurred most frequently in the Gulf of Maine and to a lesser extent on Georges Bank.

Densities in autumn were highest in Massachusetts Bay, on northern Georges Bank, and Nantucket Shoals. In winter, herring were caught throughout the Middle Atlantic Bight and on southern Georges Bank; juveniles also occurred in the Gulf of Maine. These distributions show the overwintering migrations to areas south of Cape Cod (Tupper *et al.*, in prep.).

Massachusetts Inshore Trawl Survey

In spring, juvenile herring were most abundant northwest of Cape Ann, throughout Cape Cod Bay, along the northern shore of Nantucket Island and southern shore of Martha's Vineyard, and in Buzzards Bay (Figure 14). In the fall, the largest catches occurred around Cape Ann, in central and western Cape Cod Bay, off Buzzards Bay, and off the southern shore of Martha's Vineyard. Adults were most abundant in northern Cape Cod Bay and around Cape Ann in spring and fall.

Rhode Island Trawl Survey

Catches of juveniles were patchy in Narragansett Bay (Figure 15). 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 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.

Connecticut Fisheries Division Survey

In spring, herring were abundant in central Long Island Sound (Figure 16). Juveniles were not separated from adults, but most fish were 26-30 cm long (i.e., adults). Catches were much smaller in autumn and occurred mostly along the west-central coast. Most fish in autumn were 9-12 cm (Gottschall *et al.*, in review).

Hudson-Raritan Estuary Trawl Survey

Catches of all sizes of herring were distributed fairly evenly throughout the Hudson-Raritan estuary (Figure 17). Juveniles were most abundant in winter and spring throughout the lower estuary. They were sometimes common at the mouth of the estuary in summer, and were rare in fall. Adults were most common in winter, which is consistent with the fact that adults from the Gulf of Maine overwinter south of Cape Cod (Sindermann 1979; Tupper *et al.* in prep.). Adult herring were occasionally collected throughout the survey area in spring and fall, however none were caught in summer.

Estuarine Living Marine Resources

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 the New England (Jury *et al.* 1994) and the Middle Atlantic (Stone *et al.* 1994) (Table 6). Adults and juveniles were 'highly abundant' in the northernmost estuaries (Passamaquoddy Bay through Penobscot Bay). Larvae were 'highly abundant' from Englishman-Machias Bays through the Sheepscot River. Abundance of all life stages was lower in the Middle Atlantic estuaries; only adults were abundant in Narragansett Bay (Jan-Apr), Long Island Sound (Nov-May) and Great South Bay, Long Island (Nov-Feb). Herring occurred in all major estuaries south to Chesapeake Bay.

STATUS OF THE STOCKS

Atlantic herring were extremely abundant in northeastern U.S. waters during the 1960s and were fished intensively by a large foreign fleet. The Georges Bank-Nantucket Shoals fishery extracted a peak of 373,598 mt in 1968, and an average of 168,750 mt/year over a 16-year period before the stock collapsed in the early 1970s (Atlantic States Marine Fisheries Commission 1995). Landings remained low for about 10 years, but stock biomass is now high and apparently increasing (Figure 18; Northeast Fisheries Science Center 1996). The stock complex is under-utilized (Northeast Fisheries Science Center 1996), but the Gulf of Maine portion of the complex may be fully exploited (Atlantic States Marine Fisheries Commission, unpublished data).

RESEARCH NEEDS

Historically, Atlantic herring in the Gulf of Maine have supported large, economically important fisheries (Friedland 1995). Herring have a complex life history and many areas still require study. The Gulf of Maine Aquarium Development Corporation has identified several research needs for Gulf of Maine herring (Tupper *et al.*, in prep.):

- Identify discrete populations/metapopulations and major and minor spawning components in the Gulf of Maine/Bay of Fundy region and the degree of intermixing. Consider using scales, otolith structure, and possibly morphometrics. Concentrate on spawning grounds and tag ripe and running fish only. Perhaps combine with acoustic surveys.
- Explore new technologies (e.g., acoustics or laser illumination) for improving surveys of all life stages.
- Validate the current natural mortality estimate for Gulf of Maine/Bay of Fundy (18%). Synthesize

information on mammal, seabird, and other predation. Examine size/age-specific natural mortality. Identify oceanographic influences on larval survival, particularly effects of temperature, climate change, and plankton patch dynamics.

- Conduct surveys to provide an overview of larval abundance/distribution throughout the Gulf of Maine for a single year. Determining the fate of herring spawned on Jeffreys Ledge is a high priority.

Other research needs that became apparent during development of this report include:

- Sample the Northeast Peak of Georges Bank for larvae, which were present there 30 years ago but not in 1990.
- Conduct experimental studies of temperature and salinity preferences; most existing information is for European stocks.
- Prior attempts to discriminate stocks by analyzing otolith elemental composition have been unsuccessful, but given recent improvements in analytical techniques this line of research may now be more promising.
- Map the distribution of seabed habitat types, including determining the scale of detail needed for habitat mapping.
- Continue efforts to locate all significant herring spawning areas.
- Determine effects of bottom-tending fishing gears and natural processes on spawning grounds.
- Determine the value of marine protected areas for conserving and enhancing herring stocks. Identify how these areas would function as larval exporters and collectors.

ACKNOWLEDGMENTS

Bruce Collette provided the draft update to the Bigelow and Schroeder (1953) section on herring written by Thomas Munroe. Judy Berrien, Rande Ramsey-Cross, and Claire Steimle aided with the literature search. Sukwoo Chang assisted in generating the maps and histograms from NEFSC trawl surveys. Stuart Wilk, Robert Pikanowski, and Donald McMillan produced the maps and histograms for the Hudson-Raritan data and Jeffrey Cross produced the status of the stocks figure. Helpful comments on drafts of the document were provided by David Stevenson, Kevin Friedland and technical experts associated with the New England Fishery Management Council.

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Table 1. Size and age at sexual maturity for Atlantic herring, *Clupea harengus*.

Period	Age at Maturity (A ₅₀ , years)		Size at Maturity (L ₅₀ , cm)		Reference
	male	female	male	female	
1987-1989	2.9	3.0	25.3	25.4	O'Brien <i>et al.</i> (1993)
1966-1975	-	-	25.4-27.4		Sinclair <i>et al.</i> (1982)
1949-1952	-	-	26.9		Scattergood (1952)

Table 2. Summary of life history and habitat parameters for Atlantic herring, *Clupea harengus* – Georges Bank.

Life Stage	Size and Growth	Habitat	Substrate	Temperature	Salinity
Eggs ¹		Spawning beds level and horizontal with only occasional shallow depressions or ridges; at 40-80 m depth. Major spawning site on NE part of Georges Bank.	Herring spawn found only on gravel (2-10 mm diameter) associated with strong bottom currents. Although gravel substrate is extensive, egg beds are limited to small region on western edge of northeast area of the Bank.	Temperatures in the vicinity of the Georges Bank egg beds tend to be 12-15°C. Nantucket Shoals tends to be colder (6-13°C). There was an increase of 2-3°C on Georges/Gulf of Maine from the late 1960s to 1977.	High salinities of 32 ppt reported in surface waters around egg beds.
Larvae ²	Recently hatched: 4-9 mm TL, mean = 7 mm. Total size range: 4-45 mm. Growth = 0.2 mm/4 days.				
Adults ³	(age: avg. length, cm) III: 23.7 - 25.6 IV: 27.1 - 27.9 V: 28.9 - 29.4 VI: 30.6 - 30.8 VII: 31.4 - 32.1 VIII: 33.0 - 33.3		Spawn on gravel sea floors; attachment of eggs to stable material prevents translocation by strong currents.	Correlation has been demonstrated between summer thermal regime (i.e., temperature in August) and the date of peak spawning; a warm August results in an earlier spawning peak.	

¹ Boyar (1968), Caddy and Iles (1973), Drapeau (1973), Graham and Chenoweth (1973), Pankratov and Sigaev (1973), Berenbeim and Sigaev (1978), Lough *et al.* (1980, 1985), Grimm (1983), Valentine and Lough (1991)

² Boyar *et al.* (1973), Graham and Chenoweth (1973), Lough *et al.* (1980, 1985), Cohen and Lough (1983), Grimm (1983)

³ Boyar (1968), Drapeau (1973), Pankratov and Sigaev (1973), Maurer (1976), Berenbeim and Sigaev (1978)

Table 2. cont'd.

Life Stage	Currents	Prey	Predators	Notes
Eggs ¹	High energy environments; tidal action provides aeration, prevents siltation and accumulation of metabolites.	N/A	Increased abundance of other fish species in areas of spawn; 4 most common fish: red hake, sculpin, dogfish, skate; also increase in starfish and moon snails.	1-2 cm (7-14 layers) thick egg mat. Area of egg bed ranges from 4500 to 10000 km ² . Egg mortality varies: on north and south spawning beds, approx. 8% of spawn removed within 1-2 days of hatching. Surveys on eastern Georges Bank over 5 spawning seasons (1964-1970) show year to year decrease in area occupied by egg beds. Spawning time: late Aug - Oct; peaks in mid/late Sept - Oct.
Larvae ²	Clockwise current gyre; larvae generally dispersed in a SW direction (2-15 km/d), towards coastal Gulf of Maine.	Primary prey: juvenile stages and adults of seasonally dominant copepods. The 3 most important species were <i>Pseudocalanus</i> sp., <i>Paracalanus parvus</i> and <i>Centropages typicus</i> . Feeding activity peaked twice daily: shortly after sunrise and in mid-afternoon.		Northeast Georges Bank: highest larval abundance on Bank; maximum abundance mid-late Oct. Nantucket Shoals: maximum larval abundance late Oct - early Nov. > 80% larval production occurred on Nantucket Shoals in 1976-1978. Estimated larval mortality in NW in 5 day period = 75% (< 10 mm); winter mortality on Maine coast much lower.
Adults ³	High energy environments; tidal currents and storm waves.	Primary prey: the chaetognath <i>Sagitta elegans</i> (43% by weight); the euphausiids <i>Meganyctiphanes norvegica</i> (23.1%) and <i>Thysanoessa inermis</i> (6.1%), the pteropod <i>Limacina retroversa</i> (6.2%), copepods (3%). May avoid feeding in areas with phytoplankton blooms.		Mean size of spawning fish = 29.5 cm; sex ratio 1:1 (Aug - Sept).

¹ Boyar (1968), Caddy and Iles (1973), Drapeau (1973), Graham and Chenoweth (1973), Pankratov and Sigaev (1973), Berenbeim and Sigaev (1978), Lough *et al.* (1980, 1985), Grimm (1983), Valentine and Lough (1991)

² Boyar *et al.* (1973), Graham and Chenoweth (1973), Lough *et al.* (1980, 1985), Cohen and Lough (1983), Grimm (1983)

³ Boyar (1968), Drapeau (1973), Pankratov and Sigaev (1973), Maurer (1976), Berenbeim and Sigaev (1978)

Table 3. Summary of life history and habitat parameters for Atlantic herring, *Clupea harengus* – Coastal Gulf of Maine.

Life Stage	Size and Growth	Habitat	Substrate	Temperature	Salinity
Eggs ¹		Depths of egg beds varies from 20 to 50 m, averaging 45 m; deeper beds have been shown to be more successful: 35% greater egg density and 2X higher mean egg abundance.	Preferred substrate is gravel associated with strong bottom currents. Gravel often mixed with shell fragments and/or sand; can be almost 100% shell fragments. On Jeffreys Ledge, eggs spawned on boulders & rocks, gravel & coarse sand, and on red alga <i>Ptilota serrata</i> .	Hatching success temperature dependent. Lab results: 10°C and 15°C: egg development & hatching normal; 0 and 5°C: no development; 20, 25 and 30°C: rapid development began but 100% mortality. Field results: 9.6°C, average bottom temperature at spawning.	
Larvae ²	Newly hatched: 4-6 mm autumn: 7-10 mm winter: 21-30 mm spring: 31-40 mm			Larvae may be able to acclimate to lower winter temps. when T declines more slowly. Survival < 30% when T changes 0.1-0.25°C/d; more variable (20-70%) when < 0.1°C/d. Low temp. effects may be avoided through acclimation & occupancy of warmer coastal water.	Larvae that overwinter in estuaries typically experience reduced salinities.
Juveniles ³	4-23 cm	Tendency to move to surface at night results in increased vulnerability to fixed gear fishery during dark phases of the moon. One study has shown that juveniles overwinter with adults in Passamaquoddy Bay; they remain in the bay until temp. reaches 0°C.		Lab: upper lethal = 19.5-21.2°C, lower = -1.1°C, preferred = 8-12 °C. Field: preference for 10-16°C in Sheepscoot River; Sardine production positively correlated to stock size & temp., but density overrides temp. when abundance high. Highest catches in the nearshore weir/stop seine fisheries at 10-13°C; > 13°C activity declines. Juvenile schools disappear in colder months (Nov.-Mar.). Effects of temp. on determination of yr-class strength occurs during late larval/early juvenile phase.	Lab: preference for 26-32 ppt, can resist salinities as low as 5 ppt for brief periods; at < 10°C a preference for > 29 ppt; at > 10°C no salinity preference seen. Field: present in 16-32 ppt; highest abundance at 30-32 ppt. Older juveniles generally avoid brackish conditions.
Adults ⁴	(age: avg. length, cm) III: 23 - 26 IV: 27 - 28 V: 29 - 30 VI: 30 - 31 VII: 31.9 - 32 VIII: 33 - 33.4			One study has shown that adults overwinter (along with juveniles) in Passamaquoddy Bay; remain there down to 0°C. Spawning in Grand Manan and northern Gulf primarily at 8-12°C.	

¹ MacFarland (1931), Boyar (1968), Graham *et al.* (1972), Cooper *et al.* (1975), Kelly and Stevenson (1985), Townsend *et al.* (1986), Stevenson and Knowles (1988), Chenoweth *et al.* (1989), Stevenson (1989)

² Sherman and Honey (1971), Graham (1972), Boyar *et al.* (1973), Cooper *et al.* (1975), Graham and Townsend (1985), Chenoweth *et al.* (1989), Graham *et al.* (1990)

³ Brawn (1960a, b, c), Anthony (1971), Stickney (1969), Sherman and Perkins (1971), Recksiek and McCleave (1973), Sindermann (1979), Anthony and Fogarty (1985)

⁴ Bigelow and Schroeder (1953), Boyar (1968), Sherman and Perkins (1971), Cooper *et al.* (1975), Kelly and Stevenson (1985), Munroe (in prep.)

Table 3. cont'd.

Life Stage	Currents	Prey	Predators	Notes
Eggs ¹	Bottom currents at spawning beds 0 - 1.0 knots.	N/A	Level of egg predation varies. Most abundant predators on eggs: 1) cunner, <i>Tautogolabrus adspersus</i> , 2) cod, <i>Gadus morhua</i> .	1-3 cm thick egg mat (20-30 eggs deep) and low egg mortality (< 5%) reported. Egg beds elliptical to irregular in shape; 2/3 to 1 1/3 km ² in area. 90% of eggs on rock-gravel. Not known if Jeffreys herring spawn selectively over algal clumps or if algae function as egg traps. Hatching success (excluding predation) 99%. Spawning time: mid Aug - Nov; peaks Sept - Oct.
Larvae ²	Use tidal flows to migrate. On ebb, majority of larvae shallow; on flood, majority deep. More larvae at landward end of channel than seaward.	Seasonal differences in diet; prey principally on 5 groups of zooplankton: copepods, crustacean eggs, crustacean nauplii, cirriped larvae, and tintinnids. Prey volume (cc/10m ³): summer = 1.1, autumn = 0.5, winter = 0.2, spring = 0.8.	Low temp. may indirectly increase starvation & vulnerability to predation.	Selective tidal transport (larvae retained within estuary despite seaward flow). Mortality avg. 2%/d; growth 0.199 mm/d. No growth difference in early vs. late spawned cohorts. Mortality & G inversely correlated. Larvae drift from eastern Maine spawning ground to estuaries.
Juveniles ³		Opportunistic feeders. 15 groups of zooplankton eaten; only 5 by > 20% of fish: (1) copepods, (2) decapod larvae, (3) cirriped larvae, (4) cladocerans, (5) pelecypod larvae; copepods are the most important food item year round.		Diurnal vertical movements in response to changing light intensity. Regardless of year class, western Maine herring grow faster through age 3 than eastern Maine; at the end of age 2 avg. ~3 cm longer. Plankton less abundant, water temp. lower, salinity greater in eastern Maine than in central or western Maine.
Adults ⁴		Selective, opportunistic feeders. Primary prey: shrimp and copepods. Distribution of schools of large herring likely related to presence/absence of euphausiids.	Spawning adults preyed on by bluefish and pollock; ranging from 30-65 cm TL. Predation mostly at night.	Spawning areas from Jeffreys Ledge to eastern Maine should be considered as a single spawning population.

¹ MacFarland (1931), Boyar (1968), Graham *et al.* (1972), Cooper *et al.* (1975), Kelly and Stevenson (1985), Townsend *et al.* (1986), Stevenson and Knowles (1988), Chenoweth *et al.* (1989), Stevenson (1989)

² Sherman and Honey (1971), Graham (1972), Boyar *et al.* (1973), Cooper *et al.* (1975), Graham and Townsend (1985), Chenoweth *et al.* (1989), Graham *et al.* (1990)

³ Brawn (1960a, b, c), Stickney (1969), Anthony (1971), Sherman and Perkins (1971), Recksiek and McCleave (1973), Sindermann (1979), Anthony and Fogarty (1985)

⁴ Bigelow and Schroeder (1953), Boyar (1968), Sherman and Perkins (1971), Cooper *et al.* (1975), Kelly and Stevenson (1985), Munroe (in prep.)

Table 4. Summary of life history and habitat parameters for Atlantic herring, *Clupea harengus* – Nova Scotia.

Life Stage	Size and Growth	Habitat	Substrate	Temperature	Salinity	Currents	Prey	Predators	Notes
<i>Eggs</i> ¹		Spawning bed at Black Point, NS at depth of 11-13 m.	Egg beds on sand and small stones.	Temperature of water column in spawning area ranged from 9-15 °C.		Tidal currents at egg beds 1.5-2.0 knots.	N/A	Haddock is main egg predator.	3.25 cm thick egg bed reported. Spawning time: Aug - Oct; peaks late Aug - Sept.
<i>Larvae</i> ²	Recently hatched: 5-9 mm TL. Initial growth rate = 2 mm/week; late autumn/winter months ≤ 1 mm/week; spring/early summer = 2.5 mm/week.	Spawning site in SW Nova Scotia in an area of well mixed water.		Temperature of water column in spawning area ranged from 9-15 °C.	Salinity ranged very little from 32.09 - 32.56 ppt.				Semidiel pattern of vertical migration demonstrated; possibly linked to time of day (light) and/or tidal currents.
<i>Adults</i> ³	(age: average length, cm) III: 23.7 IV: 26.4 - 27.9 V: 28.9 - 29.6 VI: 30.7 - 30.9 VII: 32.0 - 32.1 VIII: 33.0 - 33.4								

¹ McKenzie (1964), Boyar (1968), Das (1968, 1972), Stephenson and Power (1988)² McKenzie (1964), Das (1972), Stephenson and Power (1988)³ Boyar (1968)

Table 5. Summary of life history and habitat parameters for Atlantic herring, *Clupea harengus* – No specific location given in literature.

Life Stage	Size and Growth	Habitat	Substrate	Temperature	Salinity
<i>Eggs</i> ¹	1.0-1.4 mm in diameter.	All spawning grounds in high energy environments, either nearshore shallows subject to wave/tidal flux, or deeper water with tidal action.	Spawning substrate varied (stones, gravel); free of fine sediments that might prevent gaseous exchange between eggs and environment.	Bottom temp. of 5-15°C required. Average incubation time for autumn spawned eggs is 10-15 days. Developmental rate inversely related to temp.: 40 d at 4-5°C, 15 d at 6-8°C, 11 d at 10-12°C, 6-8 d at 14.4-16°C.	
<i>Larvae</i> ²				Occur in 9-16°C in the Gulf of Maine. Offshore waters in winter generally have higher temperatures than inshore waters (up to 5°C difference); may favor a more rapid development in offshore waters, thereby reducing time of vulnerability to predation.	
<i>Juveniles</i> ³					Preference for higher salinities with increasing age.
<i>Adults</i> ⁴			Spawn on stable material: small stones, gravel.	Movements become sluggish at less than 4°C. Spawning occurs at temperatures of 7-15°C. Spawning in western Gulf of Maine occurs at warmer temperatures than east.	Enter bays and estuaries, but 28 ppt is lower limit of occurrence. Spawn at high salinities, ranging from 31.9 - 33.0 ppt; never brackish water.

¹ Bigelow and Schroeder (1953), Haegele and Schweigert (1985), Munroe (in prep.)² Colton and Byron (1977), Munroe (in prep.)³ Recksiek and McCleave (1973), Munroe (in prep.)⁴ Haegele and Schweigert (1985), Munroe (in prep.)

Table 5. cont'd.

Life Stage	Currents	Prey	Predators	Notes
<i>Eggs</i> ¹	Spawning generally occurs in areas with good tidal exchange: average 1.5-3 knots tidal current.	N/A	Predation by a variety of bottom predators (Winter Flounder major egg predator). Cannibalism by adult herring occurs.	Eggs are demersal, adhesive. Eggs laid in sheets in successive layers; rarely exceeds 2 cm in thickness. Egg mortality is primarily due to suffocation (from high egg densities and siltation) and predation. Spawning time: Sept - early Nov.
<i>Larvae</i> ²		Begin exogenous feeding before yolk sac disappears. Select the most abundant prey of a suitable size range; seasonal differences occur. Primary prey: copepod eggs, nauplii, copepods, mollusk larvae. As larvae grow, consume larger proportion of copepods.	Solitary and pelagic; vulnerable to planktonic predators: jellyfish, chaetognaths, larger copepods, euphausiids and pelagic fishes.	Larvae exhibit diurnal migratory behavior. Possible controlling mechanisms: light level, turbidity, shifts in prey location & tidal effects.
<i>Juveniles</i> ³		Selective, opportunistic feeders; predominantly copepod diet. In darkness: stop schooling behavior; swim in tight paths & feed only by filtering (unable to feed by biting). In the light: can feed by either particle biting or filtering.	Preyed upon by almost all pelagic predators, including fishes, marine birds, northern shortfin squid, and marine mammals.	Vertical diurnal movements occur in all seasons. Juveniles often active near/at the surface at night; generally move up water column at dusk.
<i>Adults</i> ⁴		Selective, opportunistic feeders; predominantly euphausiid diet, also chaetognaths and copepods.	Preyed upon by almost all pelagic predators, including fishes, marine birds, northern shortfin squid, and marine mammals. Predation by fish is intense during spawning.	

¹ Bigelow and Schroeder (1953), Haegele and Schweigert (1985), Munroe (in prep.)² Colton and Byron (1977), Munroe (in prep.)³ Recksiek and McCleave (1973), Munroe (in prep.)⁴ Haegele and Schweigert (1985), Munroe (in prep.)

Table 6. Relative abundance of eggs, larvae, and juvenile Atlantic herring (*Clupea harengus*) in New England and Mid-Atlantic estuaries by salinity zone, 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.

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

Table 6. cont'd. Relative abundance of spawning adult and adult Atlantic herring (*Clupea harengus*) in New England and Mid-Atlantic estuaries by salinity zone 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.

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

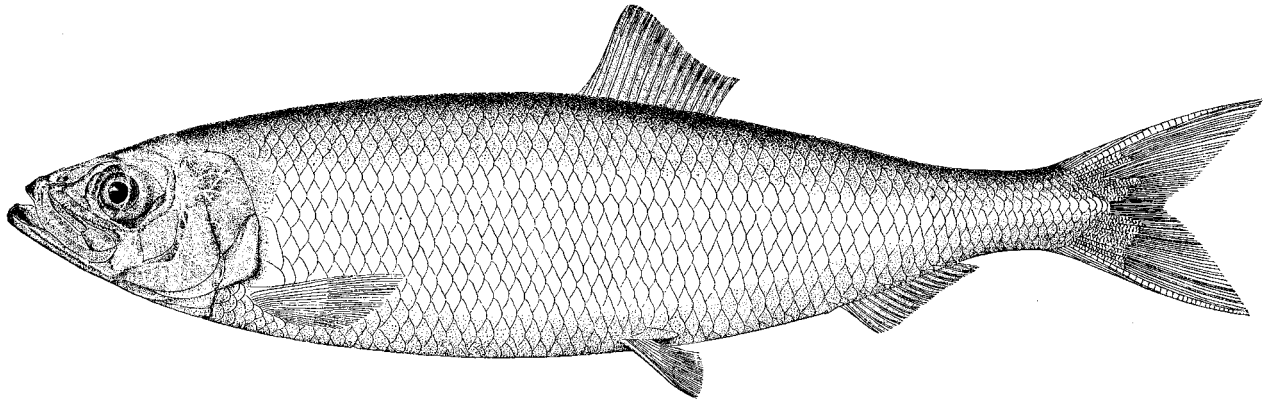


Figure 1. The Atlantic herring, *Clupea harengus* L. (from Goode 1884).

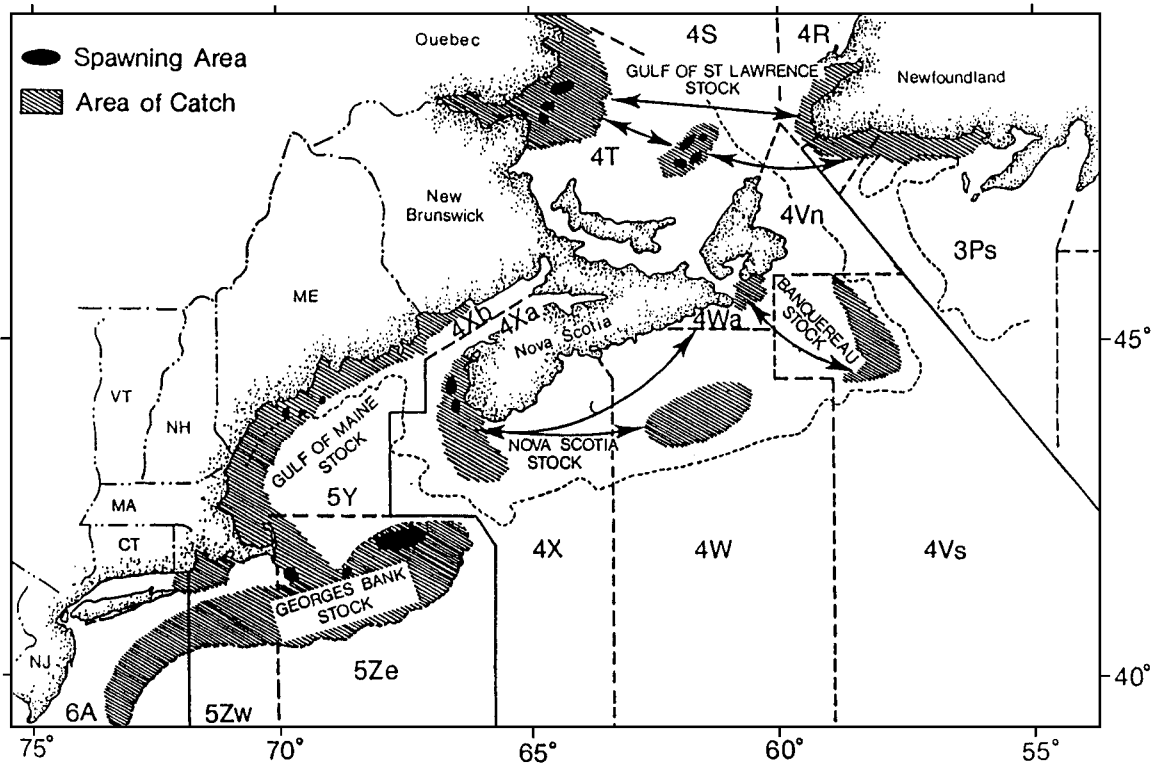


Figure 2. Location of Atlantic herring spawning populations within the Gulf of Maine area. Solid black represents spawning areas, while hatched lines represent areas of herring catch (from Iles 1972).

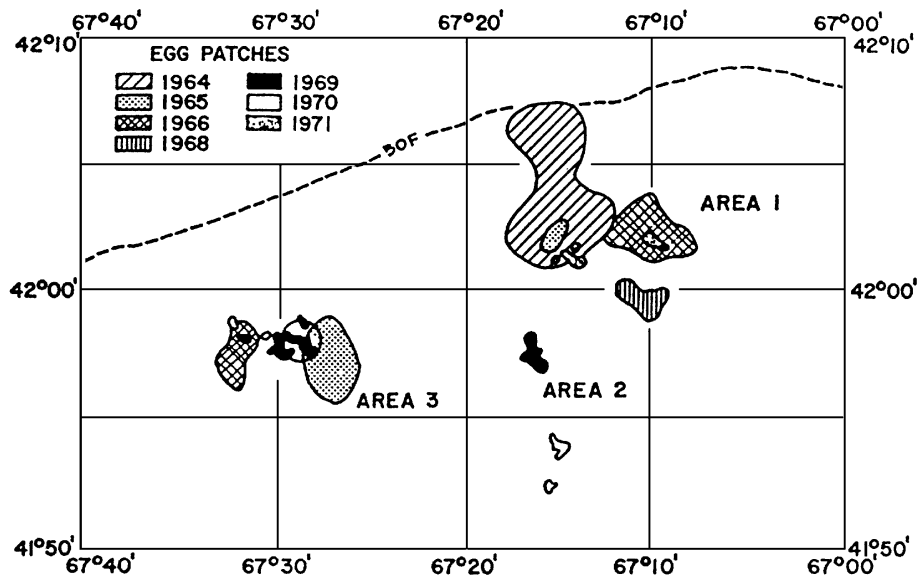


Figure 3. Principal spawning grounds on Georges Bank, 1964-1971 (excluding 1967), with a comparison of egg patch sizes among years (from Anthony and Waring 1980).

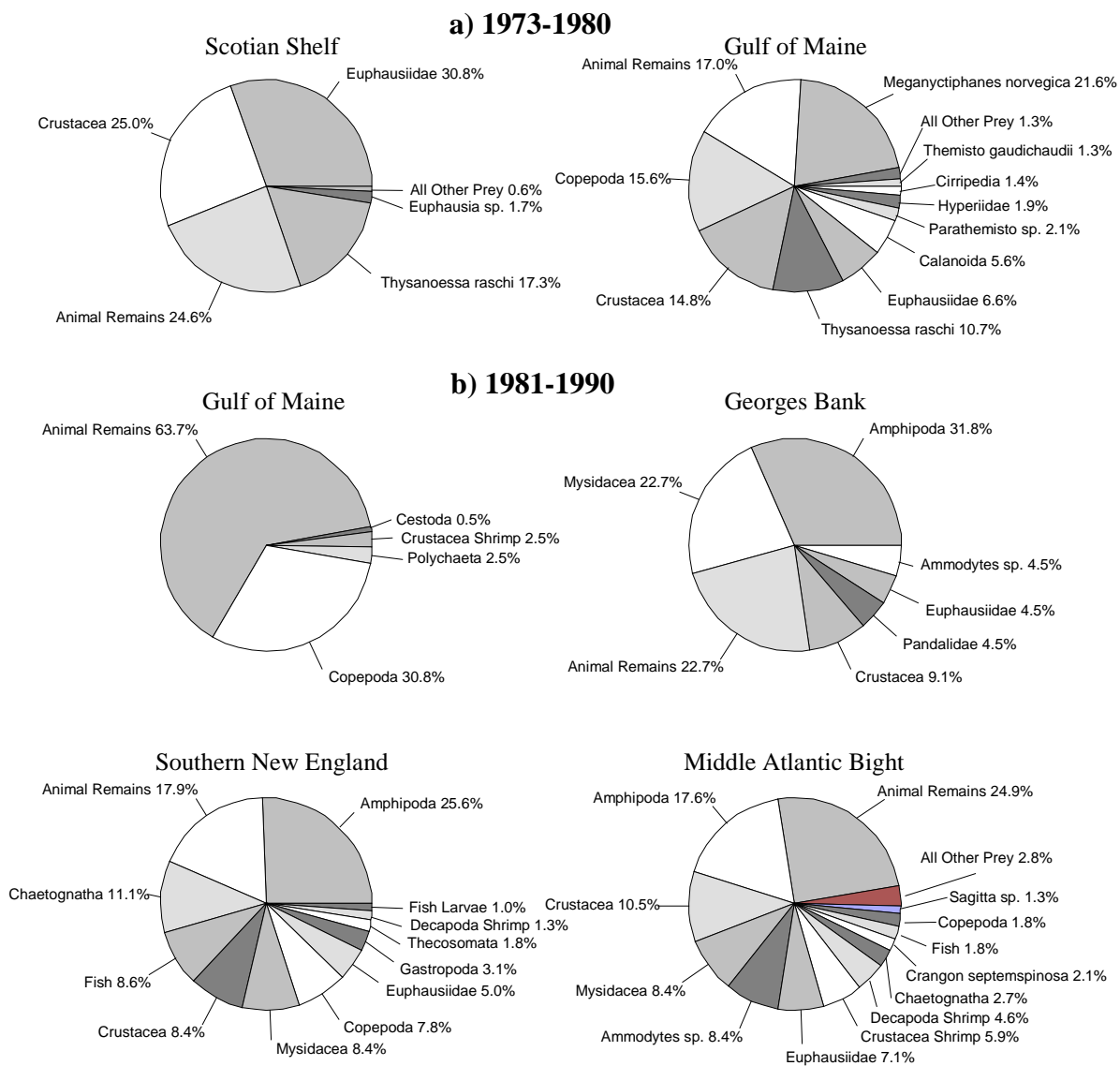


Figure 4. Abundance (percent of total prey volume) of the major prey items in the diet of Atlantic herring from the Scotian Shelf, the Gulf of Maine, Georges Bank, southern New England, and the Middle Atlantic based on NEFSC bottom trawl survey data on food habits, a) 1973-1980 and b) 1981-1990. Methods for sampling, processing, and analysis of samples differed between the time periods [see Reid *et al.* (1999) for details]. The category “animal remains” refers to unidentifiable animal matter.

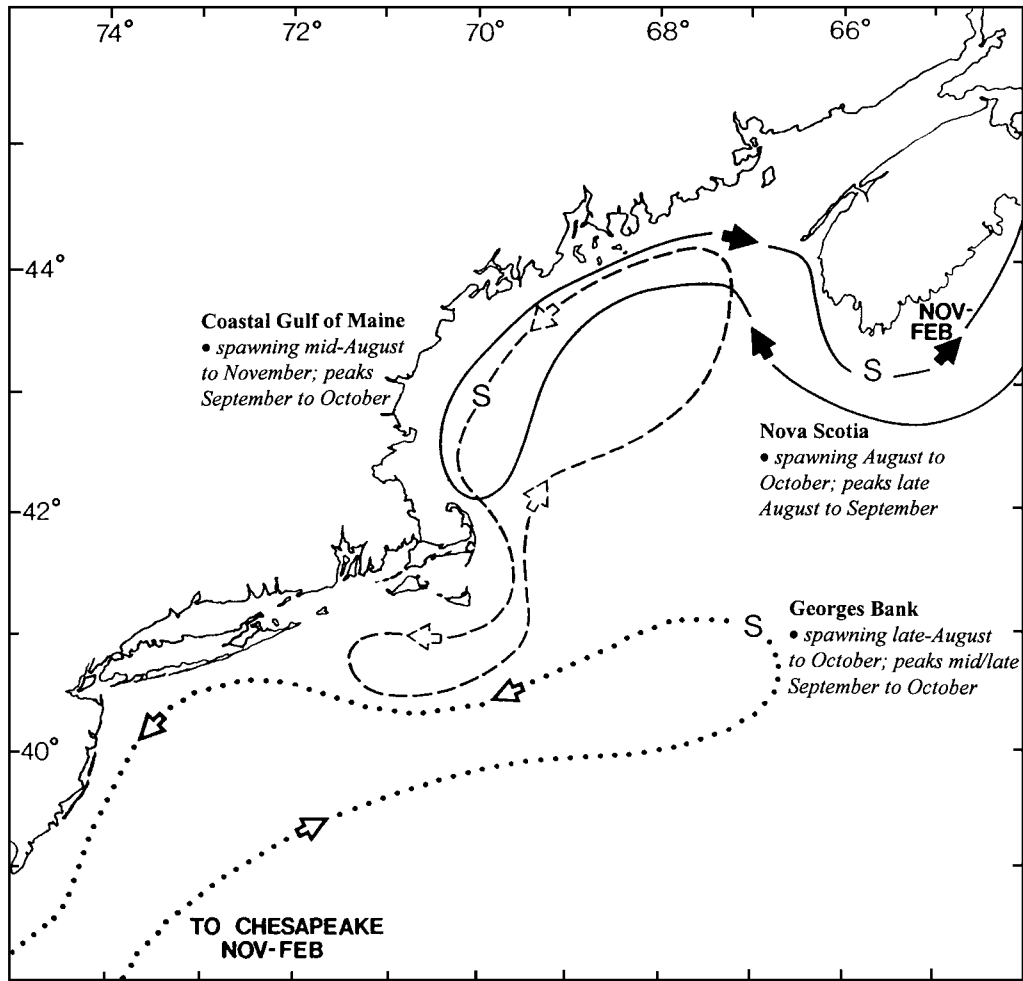


Figure 5. Hypothesized seasonal movements of three Atlantic herring spawning stocks inhabiting U.S. waters (modified from Sindermann 1979).

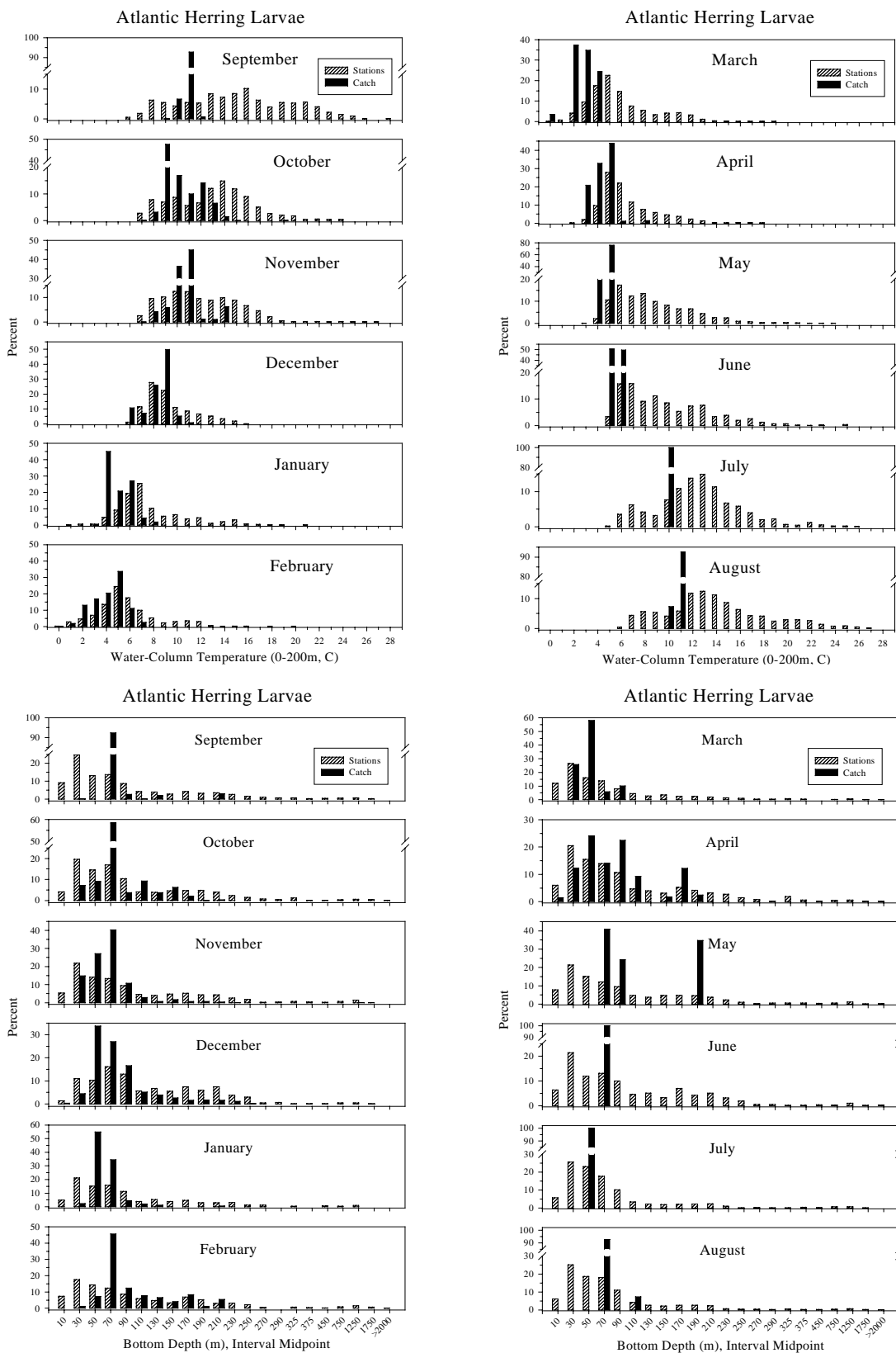


Figure 6. Mean water column temperature and bottom depth at stations where Atlantic herring larvae were collected (solid bars) and at all stations sampled (open bars) during NEFSC MARMAP ichthyoplankton surveys, 1977-1987.

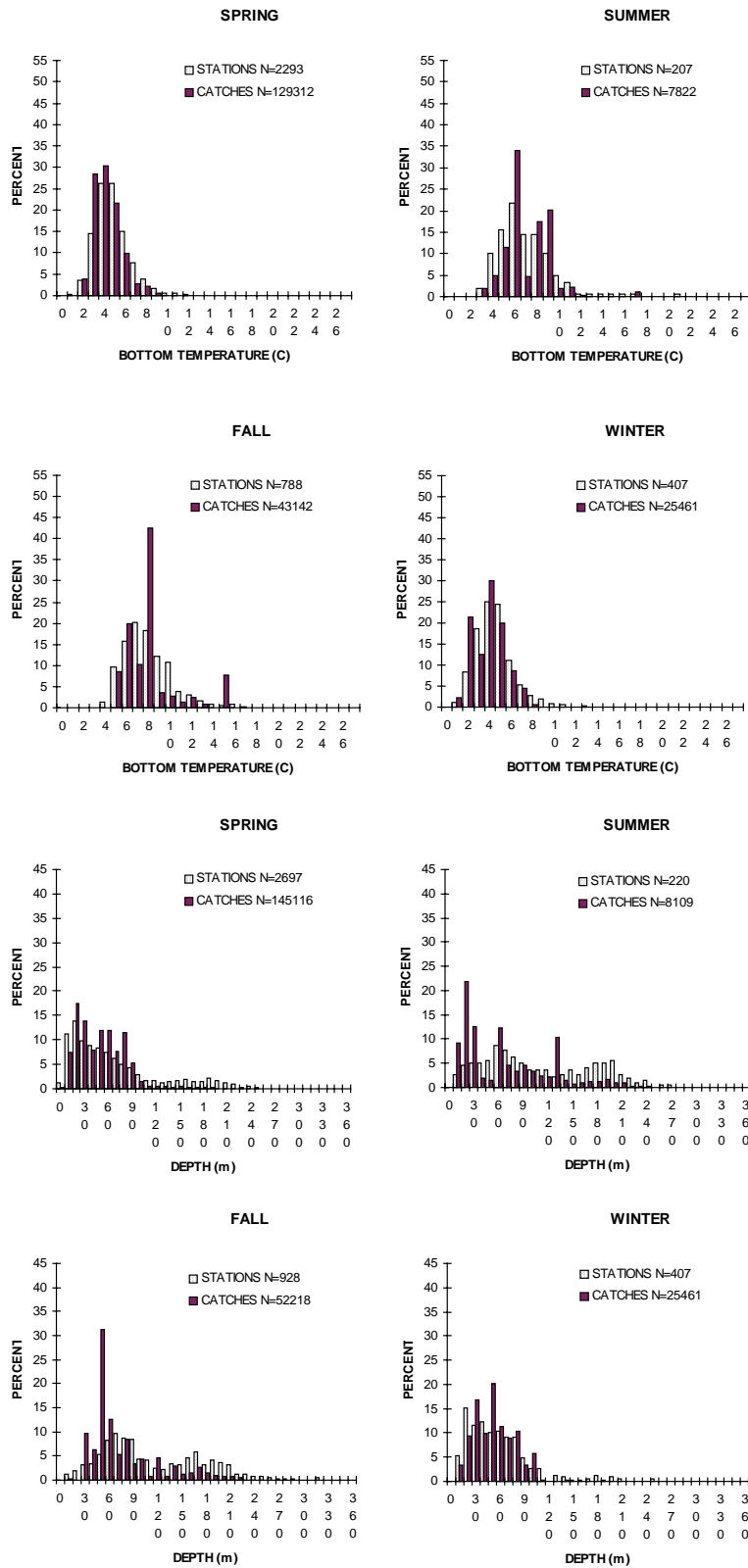


Figure 7a. Mean bottom water temperature and depth at stations where juvenile (< 25 cm TL) Atlantic herring were collected (solid bars) and at all stations sampled (open bars) during NEFSC bottom trawl surveys.

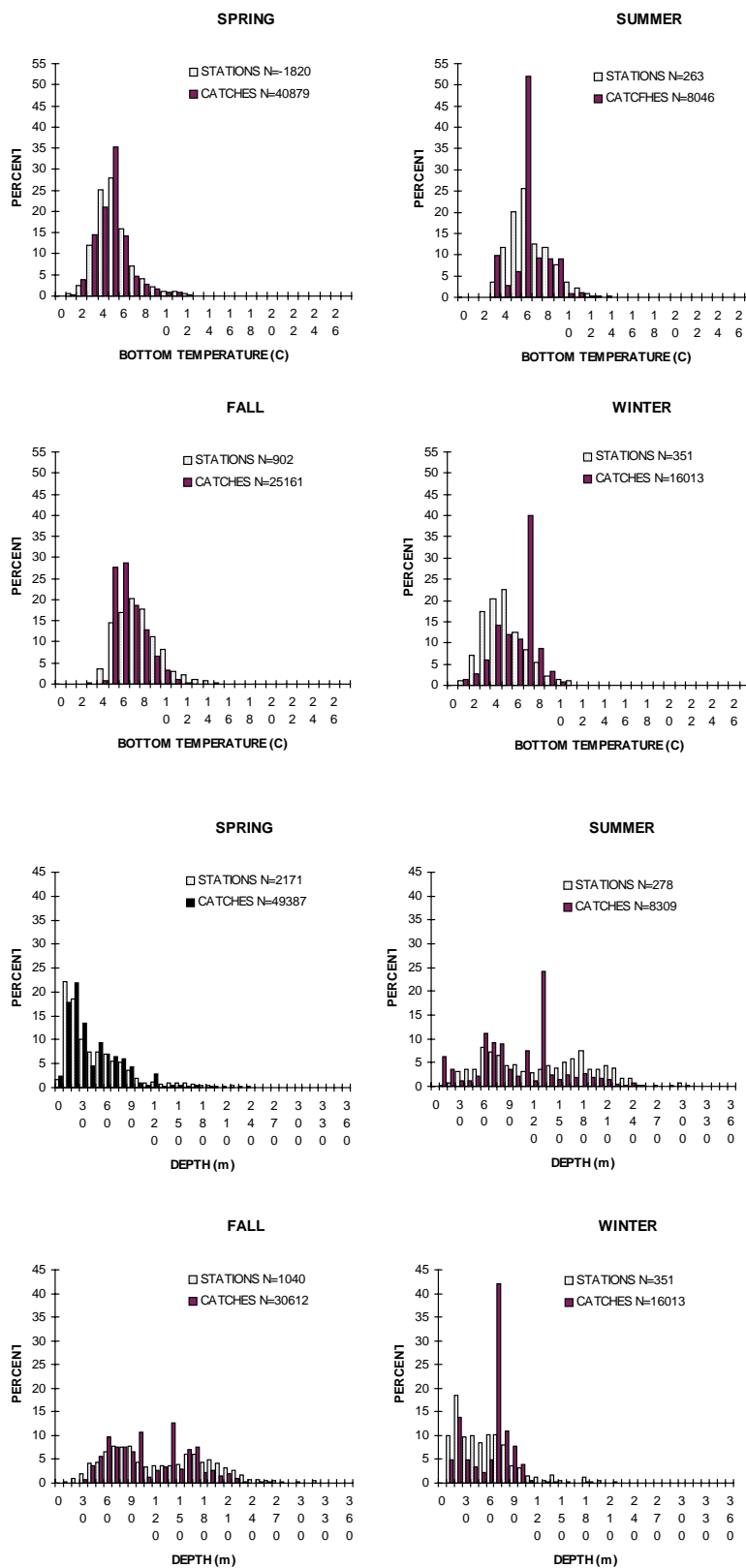


Figure 7b. Mean bottom water temperature and depth at stations where adult (≥ 25 cm TL) Atlantic herring were collected (solid bars) and at all stations (open bars) sampled during NEFSC bottom trawl surveys.

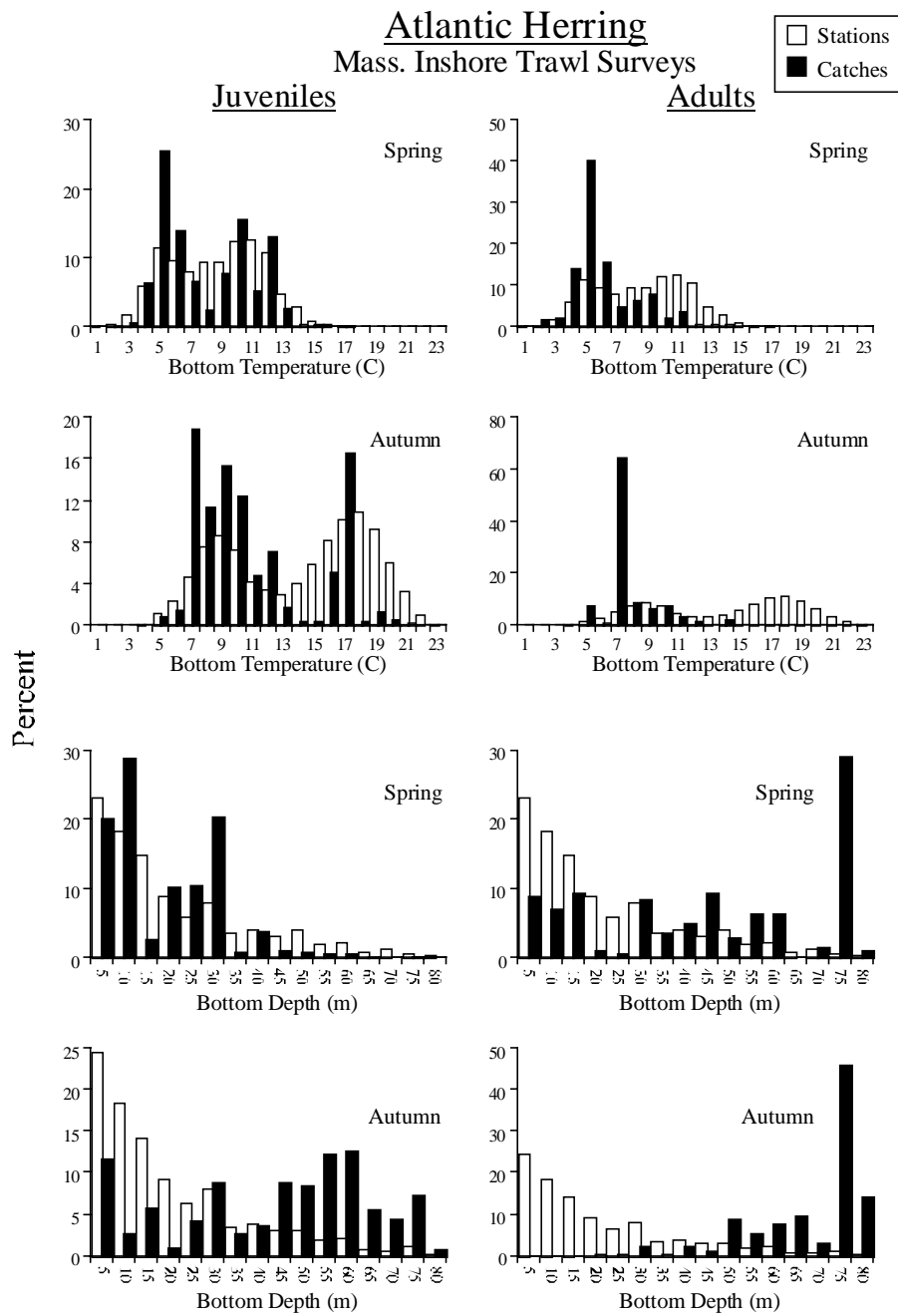


Figure 8. Mean bottom water temperature and depth at stations where juvenile and adult Atlantic herring were collected (solid bars) and at all stations sampled (open bars) during Massachusetts inshore bottom trawl surveys, 1978-1996.

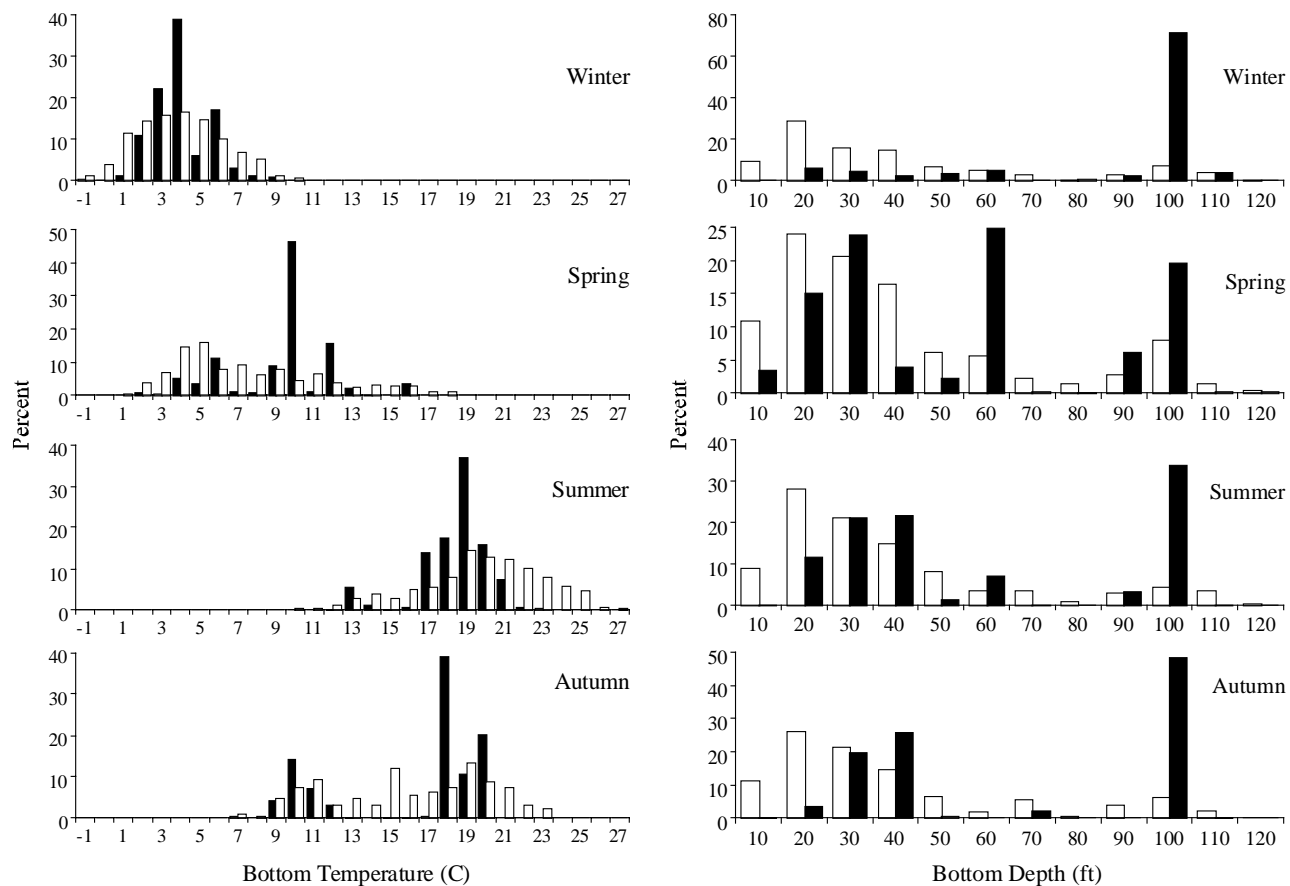


Figure 9a. Mean bottom water temperature and depth at stations where juvenile Atlantic herring were collected (solid bars) and at all stations sampled (open bars) during Rhode Island Narragansett Bay trawl surveys.

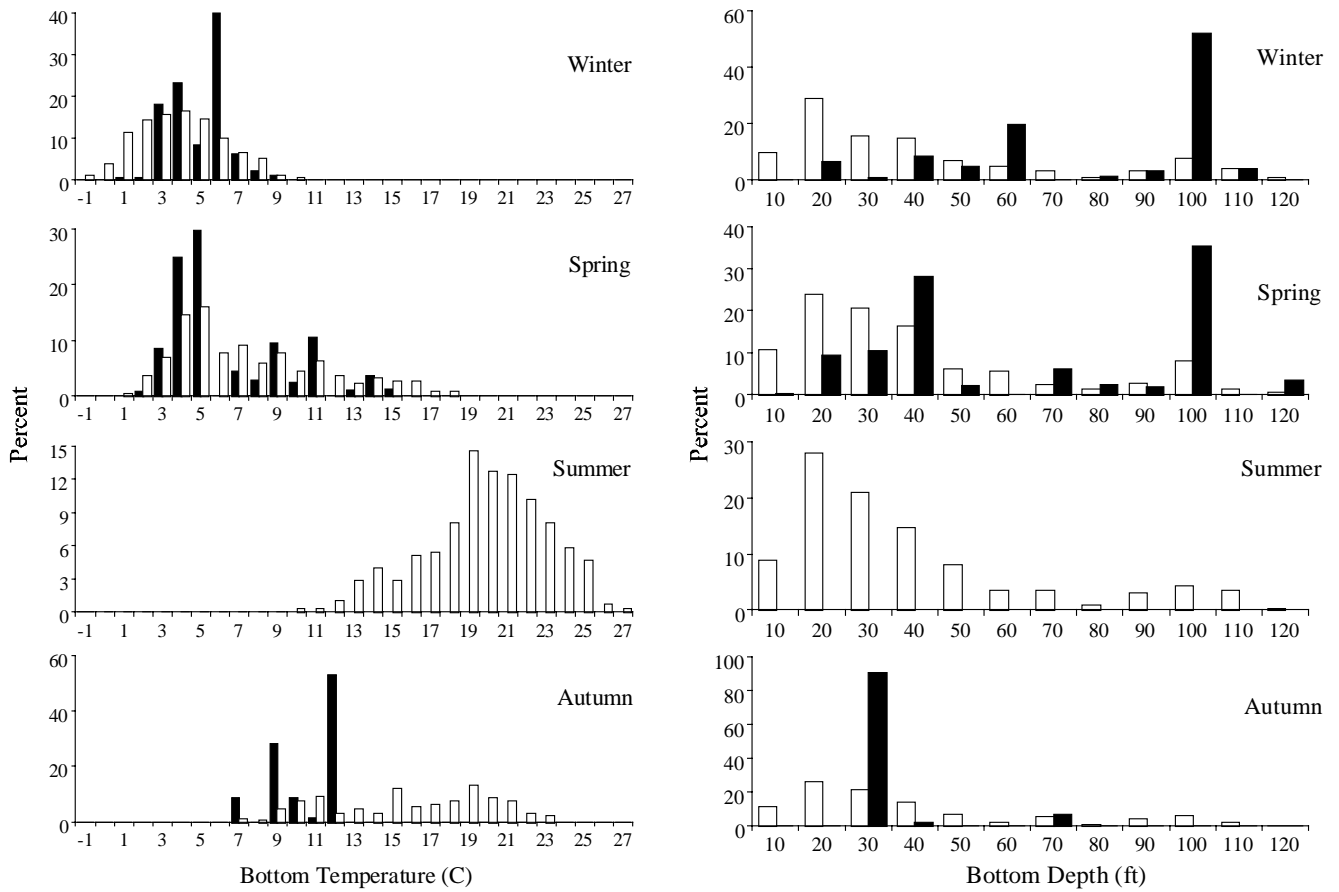


Figure 9b. Mean bottom water temperature and depth at stations where adult Atlantic herring were collected (solid bars) and at all stations sampled (open bars) during Rhode Island Narragansett Bay trawl surveys.

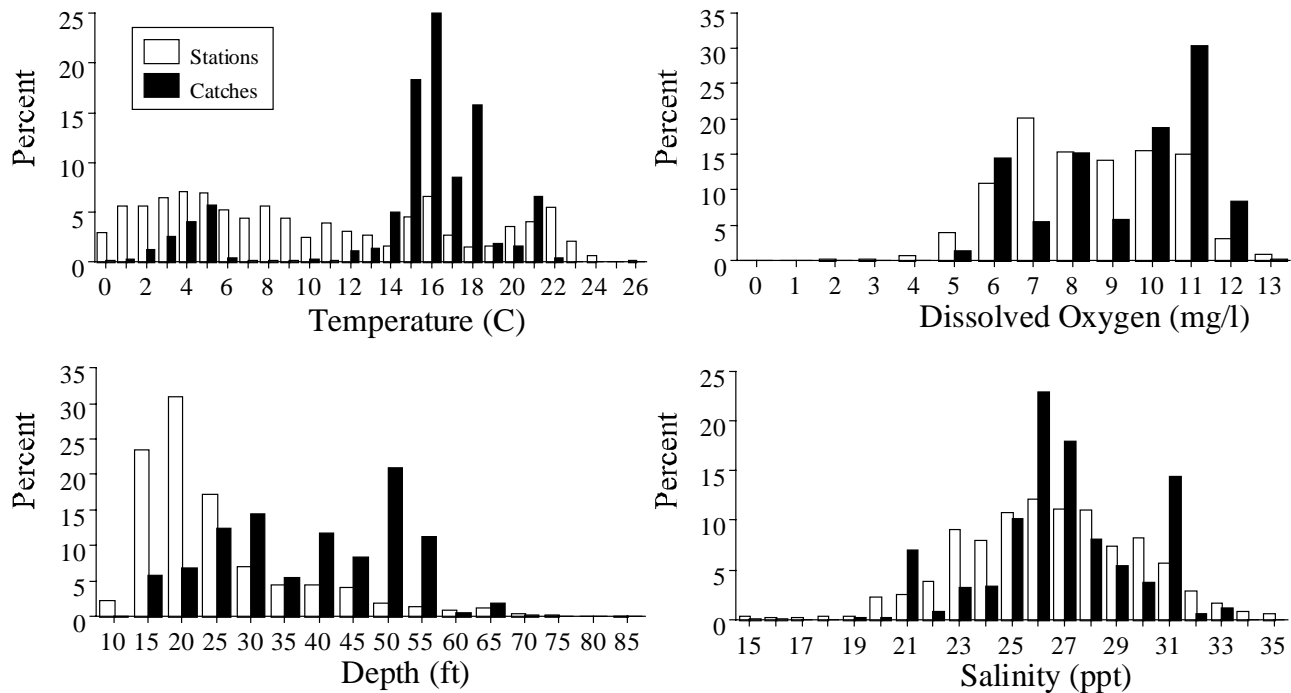


Figure 10a. Mean water temperature, depth, dissolved oxygen, and salinity at stations where juvenile Atlantic herring were collected (solid bars) and at all stations (open bars) during Hudson-Raritan trawl surveys.

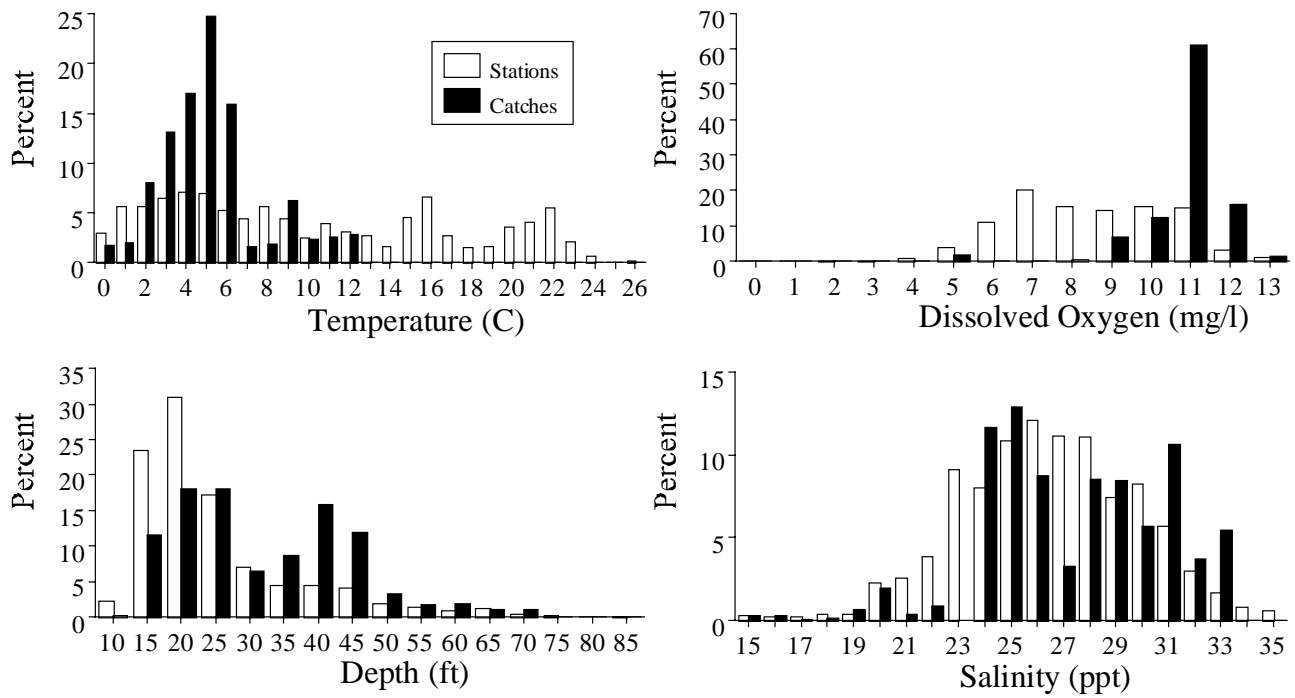


Figure 10b. Mean water temperature, depth, dissolved oxygen, and salinity at stations where adult Atlantic herring were collected (solid bars) and at all stations (open bars) during Hudson-Raritan trawl surveys.

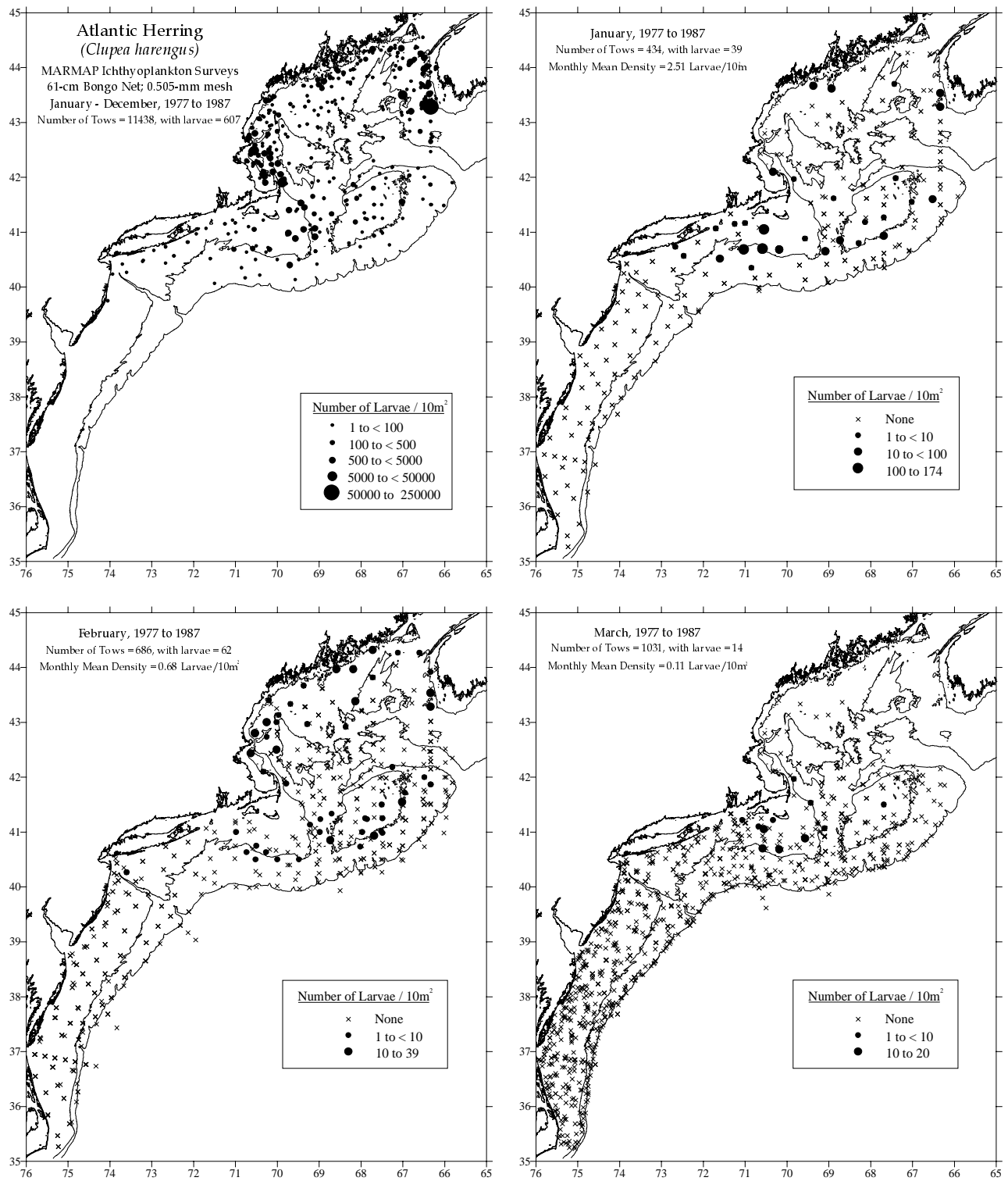


Figure 11. Distribution and abundance of Atlantic herring larvae collected during NEFSC MARMAP ichthyoplankton surveys, January to December, 1977-1987 [see Reid *et al.* (1999) for details].

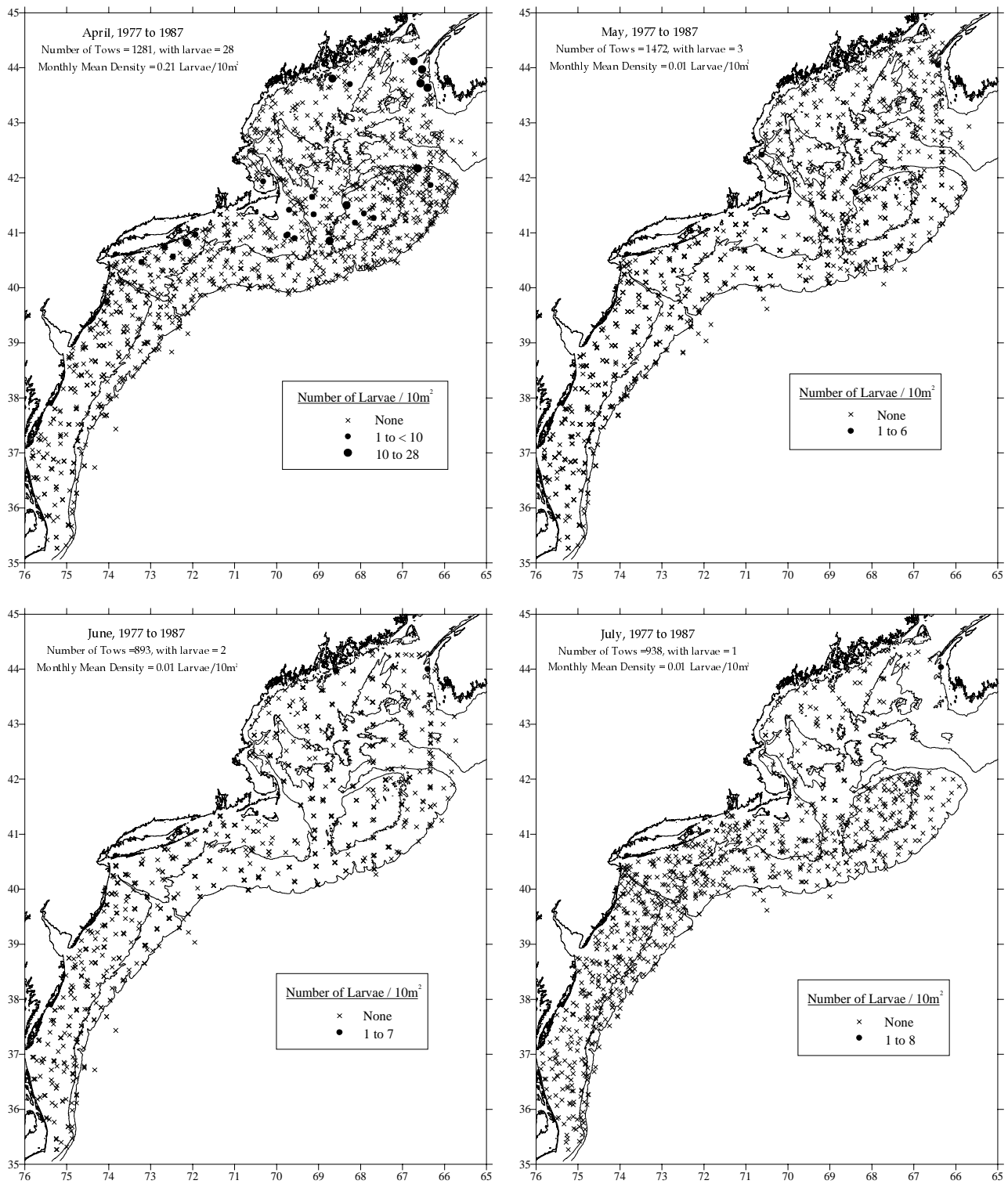


Figure 11. cont'd.

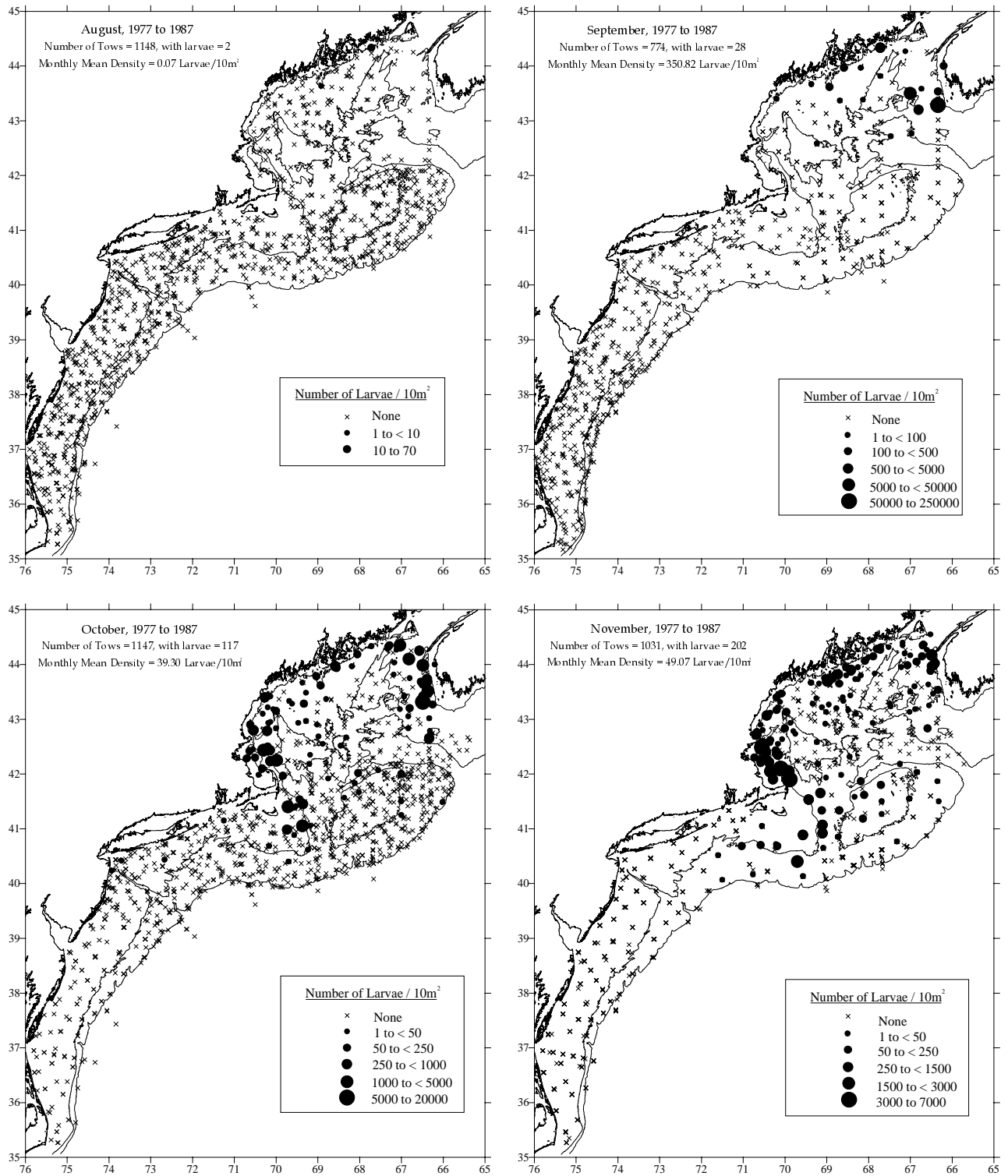


Figure 11. cont'd.

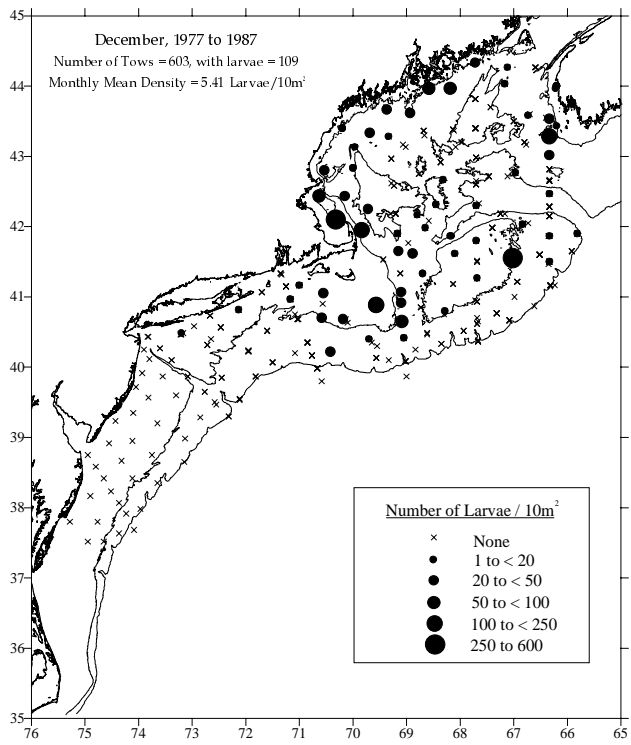


Figure 11. cont'd.

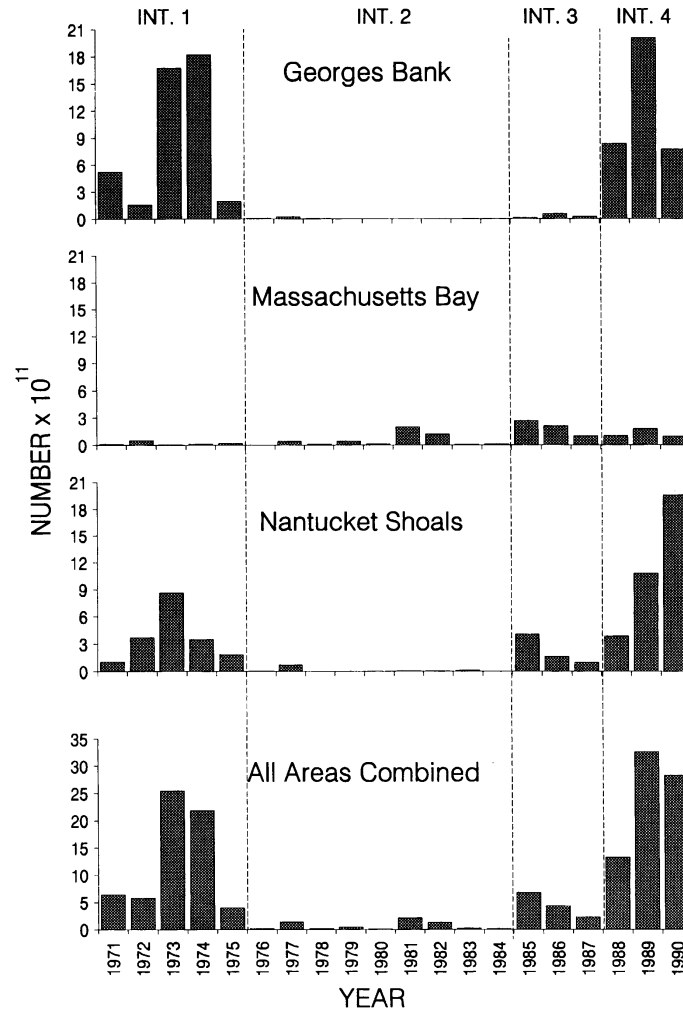


Figure 12. Changes in abundance of Atlantic herring larvae on Georges Bank, Nantucket Shoals, and in Massachusetts Bay from 1971-1990 (from Smith and Morse 1993). Intervals (Int.) denote periods of changing spawning patterns.

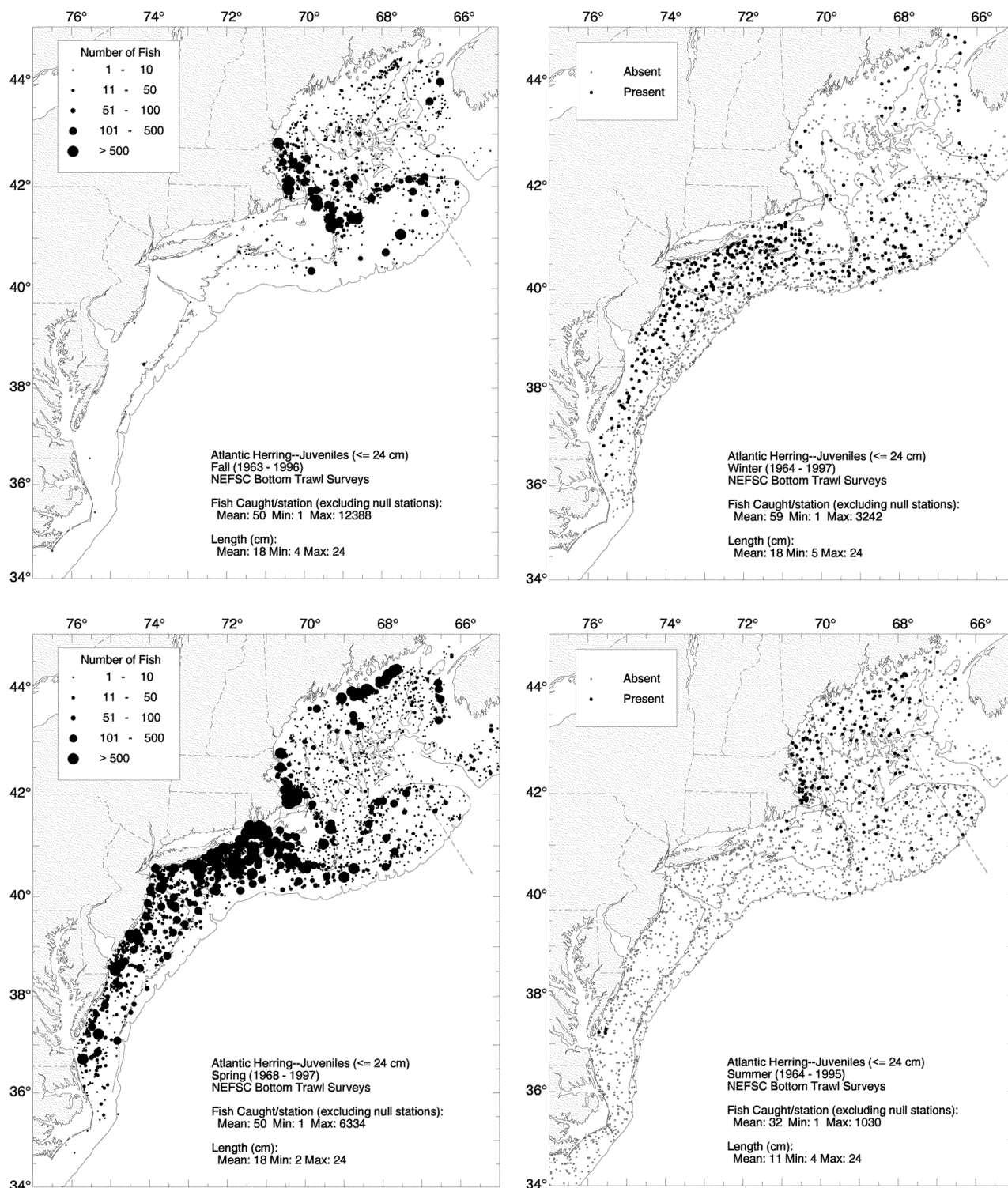


Figure 13. Distribution and abundance of juvenile (≤ 24 cm) and adult (≥ 25 cm) Atlantic herring collected during NEFSC bottom trawl surveys, 1963-1997. Densities are represented by dot size in spring and fall plots, while only presence and absence are represented in winter and summer plots [see Reid *et al.* (1999) for details].

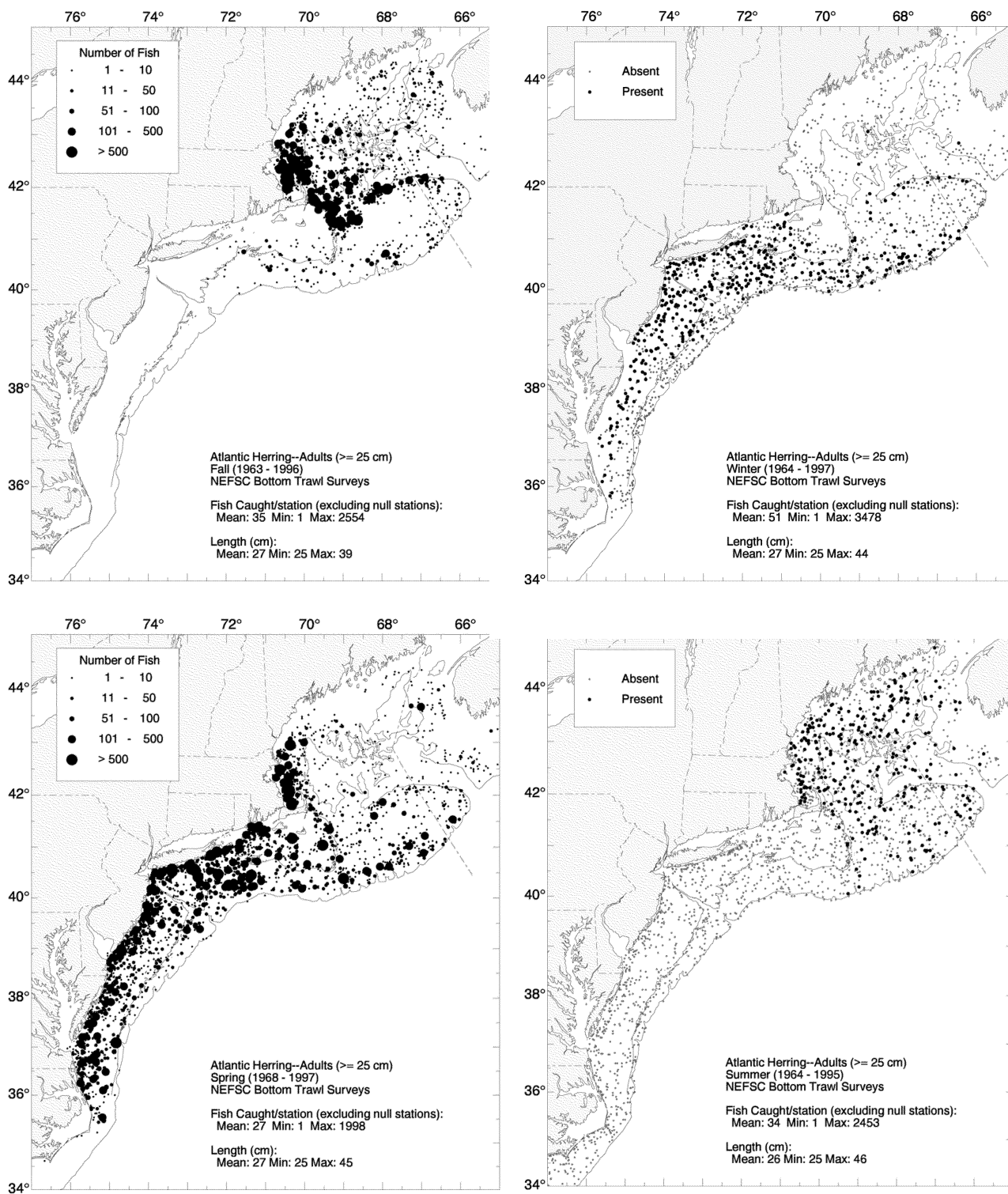


Figure 13. cont'd.

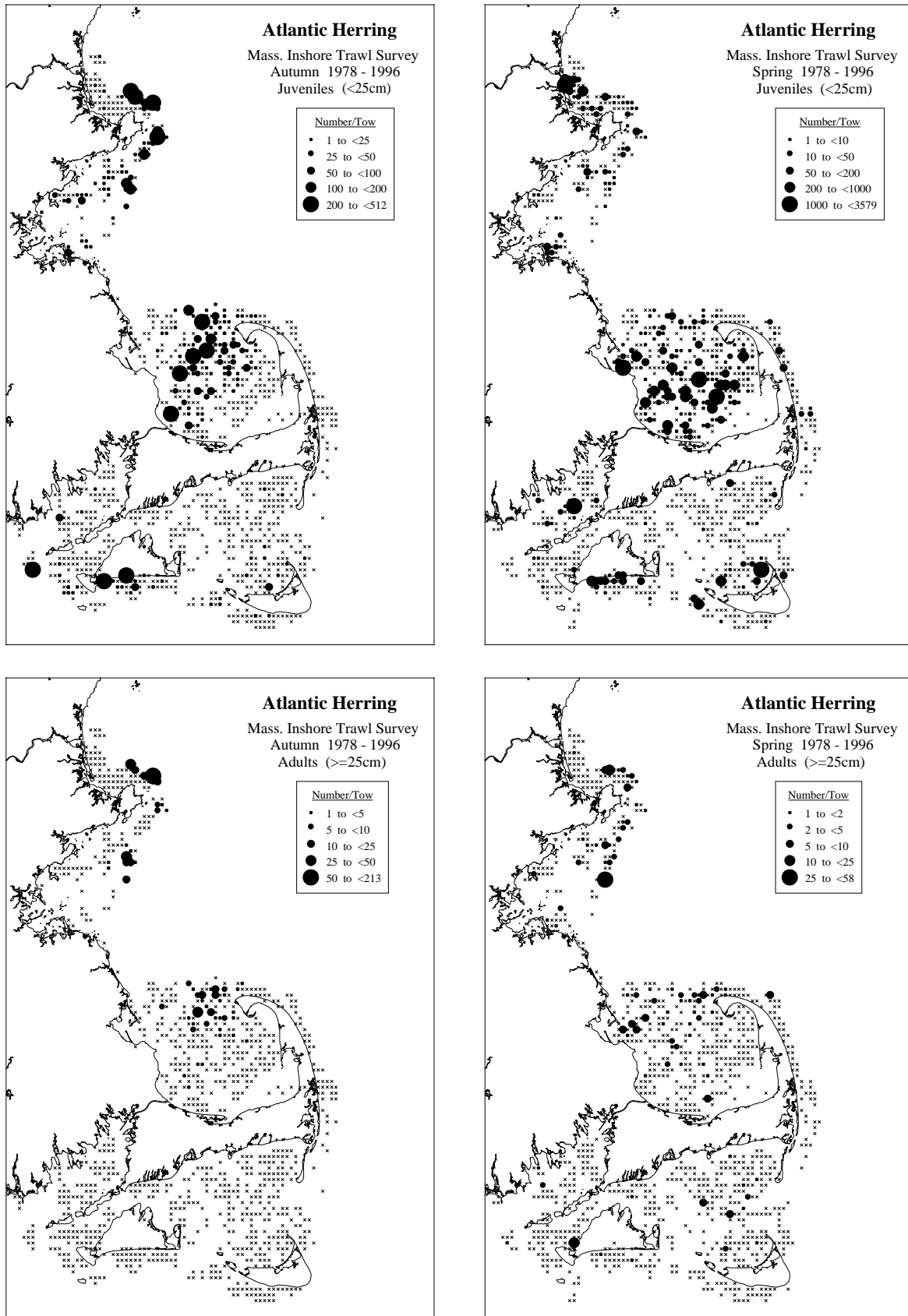


Figure 14. Distribution and abundance of juvenile (< 25 cm) and adult (≥ 25 cm) Atlantic herring collected in spring and autumn during Massachusetts inshore bottom trawl surveys (1978-1996) [see Reid *et al.* (1999) for details].

Juveniles (< 25 cm)

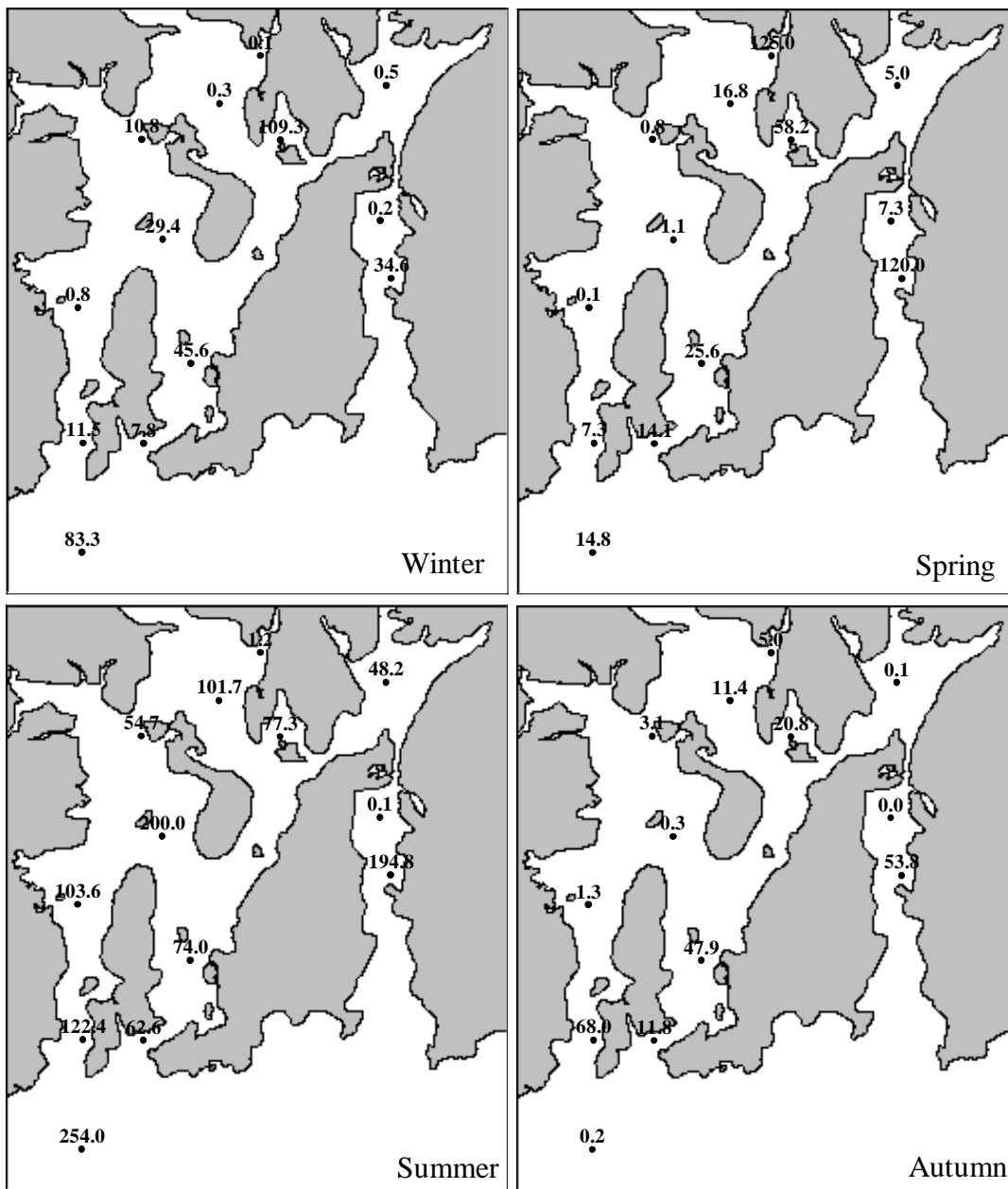


Figure 15. Distribution and abundance of juvenile (< 25 cm) and adult (≥ 25 cm) Atlantic herring collected in Narragansett Bay during the Rhode Island bottom trawl survey, 1990-1996. The numbers shown at each station are the average catch per tow rounded to one decimal place [see Reid *et al.* (1999) for details].

Adults (≥ 25 cm)

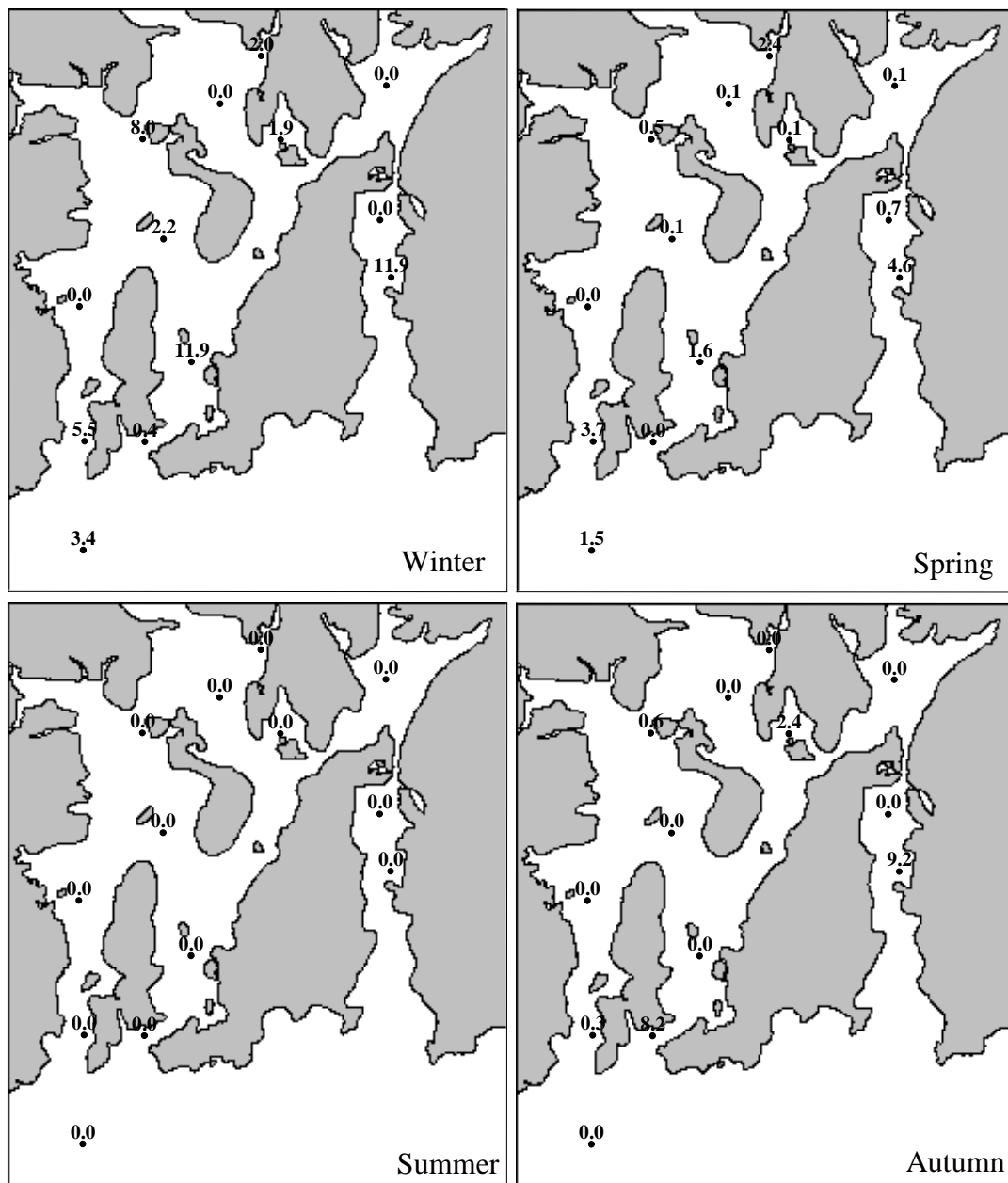


Figure 15. cont'd.

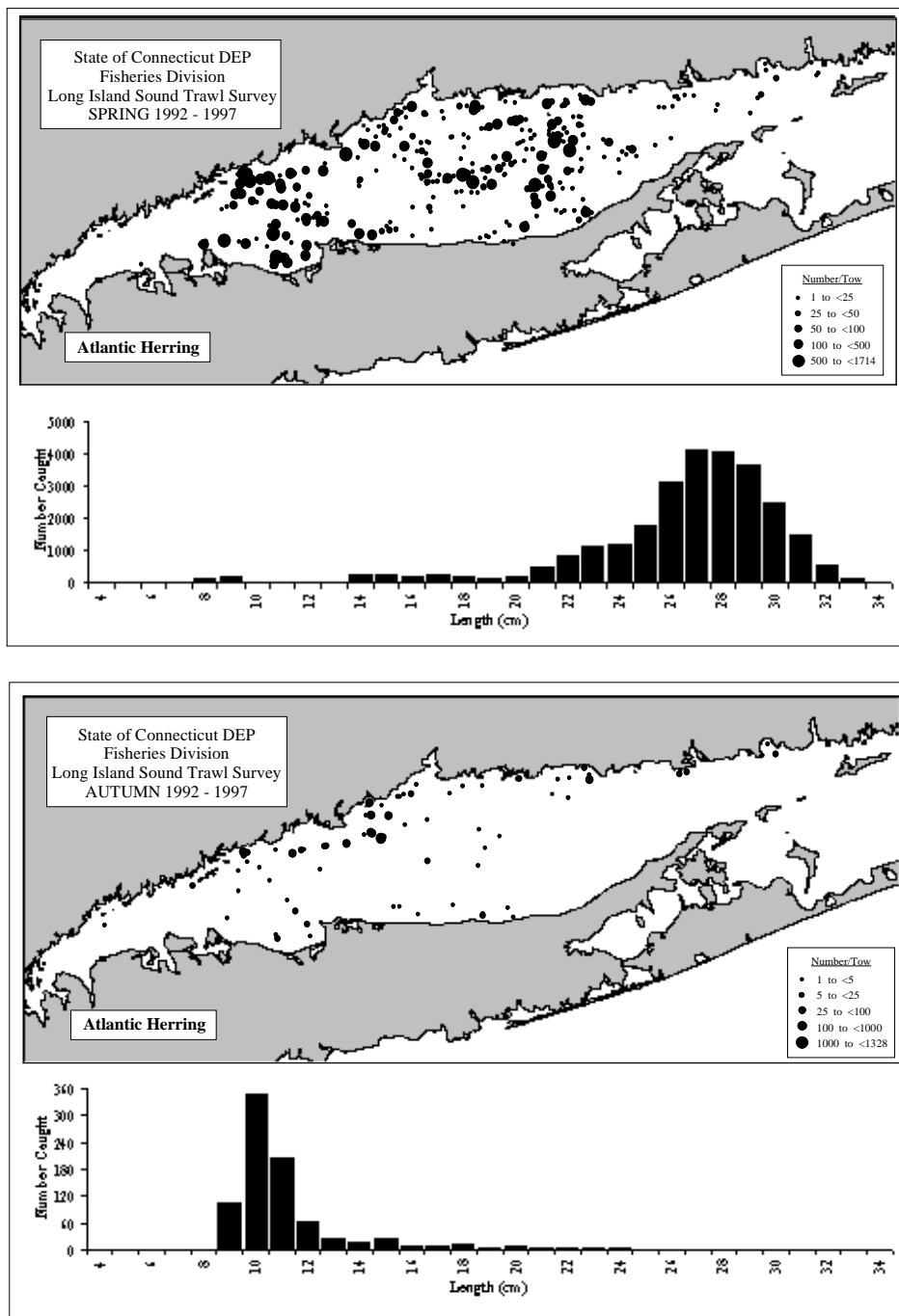


Figure 16. Distribution and abundance of Atlantic herring collected in Long Island Sound during spring and autumn Connecticut bottom trawl surveys, 1992-1997 [see Reid *et al.* (1999) for details]. Histograms show lengths of herring during spring and autumn from a subset of 1992-1997 and earlier collections.

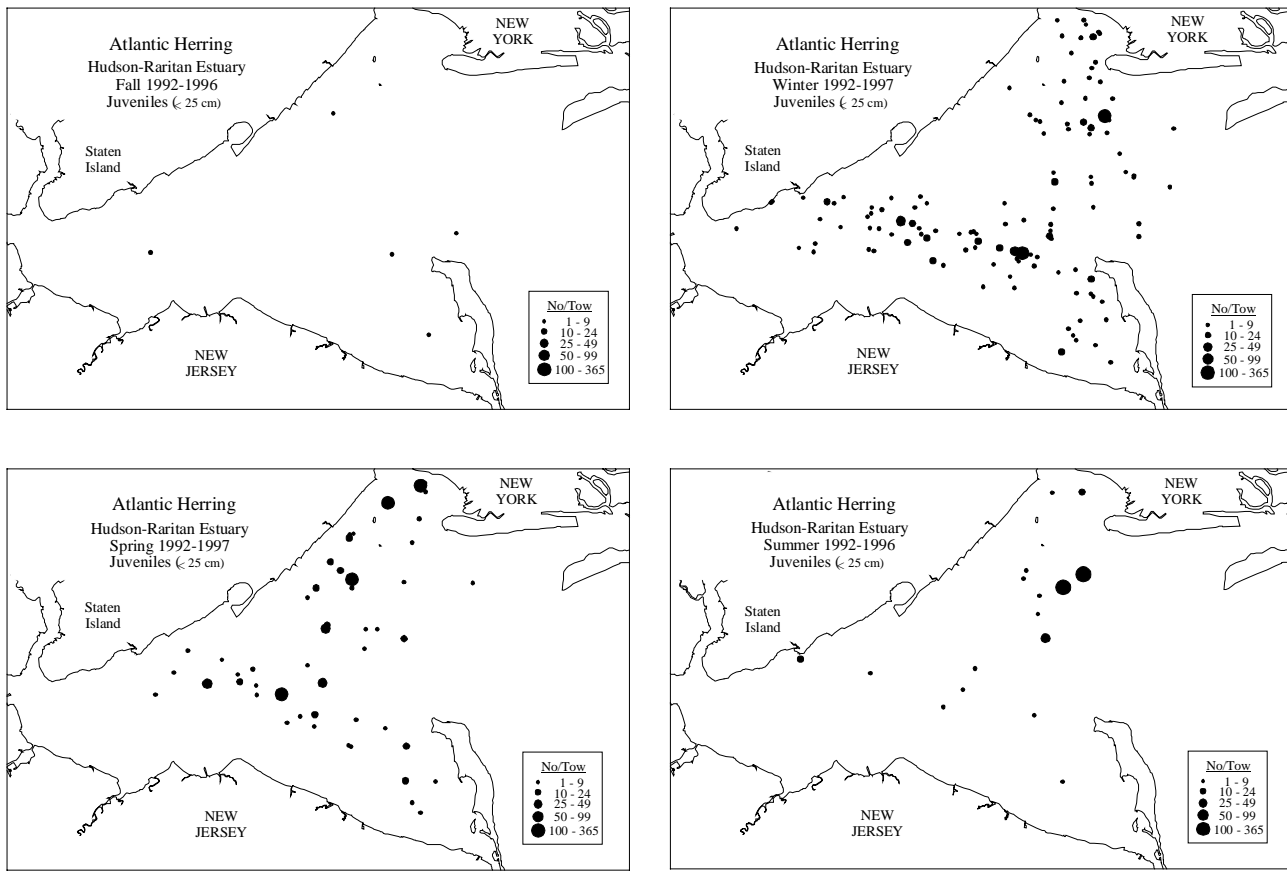


Figure 17. Distribution and abundance of juvenile (< 25 cm) and adult (\geq 25 cm) Atlantic herring collected in the Hudson-Raritan estuary during Hudson-Raritan trawl surveys, 1992-1997 [see Reid *et al.* (1999) for details].

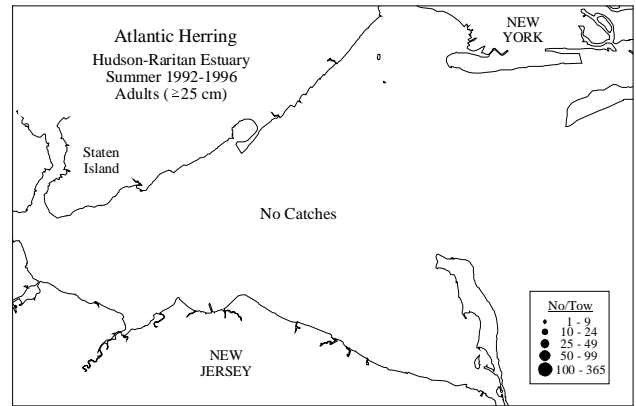
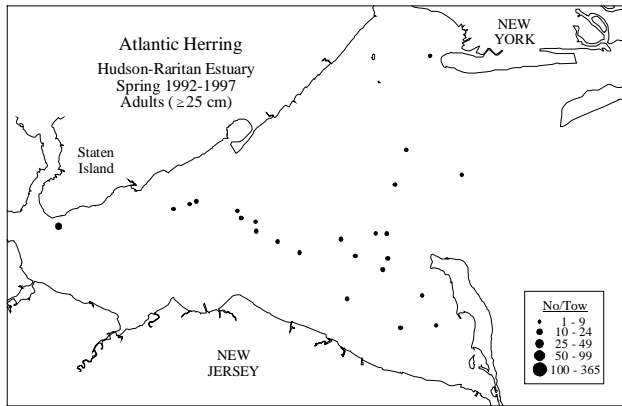
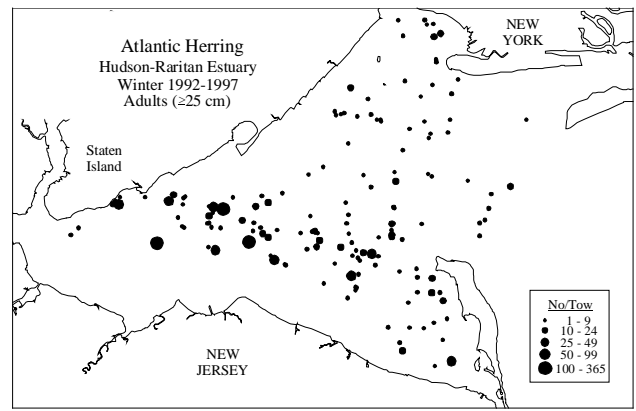
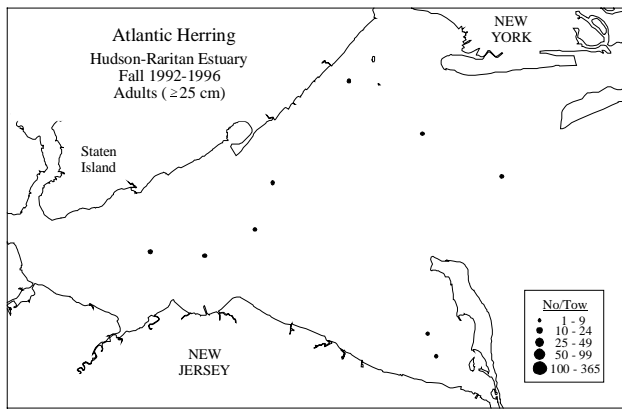


Figure 17. cont'd.

Coastal Stock Complex

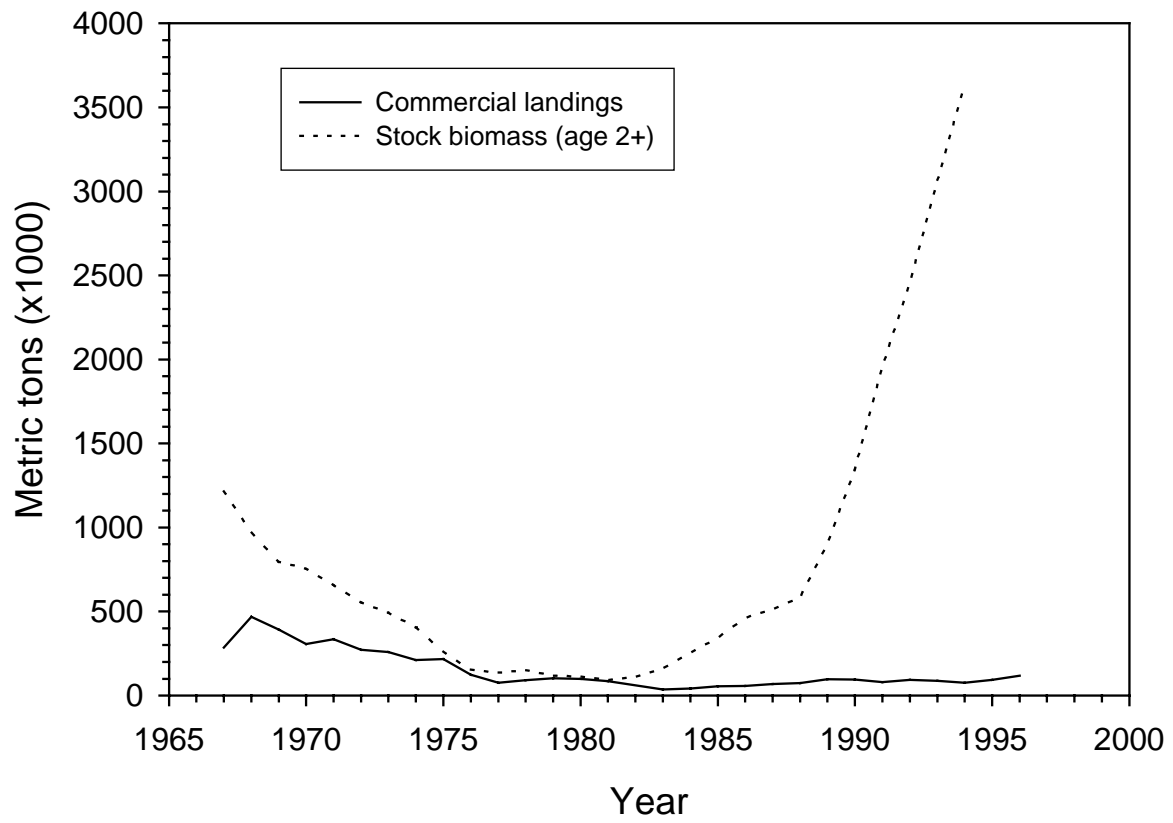


Figure 18. Commercial landings and estimated stock biomass index (ages 2+) of Atlantic herring, 1967-1992 (Friedland 1995, 1998).

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