NOAA Technical Memorandum NMFS-NE-124

Essential Fish Habitat Source Document:

Atlantic Cod, *Gadus morhua*, Life History and Habitat Characteristics

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

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Essential Fish Habitat Source Document:

Atlantic Cod, *Gadus morhua*, Life History and Habitat Characteristics

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Editorial Notes on Issues 122-152
in the
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Editorial Production

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

Special Acknowledgments

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

Internet Availability

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

Information Updating

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

Species Names

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

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

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

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

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

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

FOREWORD

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

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

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

NMFS Strategic Plan for Fisheries Research (February 1998)

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

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

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

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

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

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

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

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INTRODUCTION

The Atlantic cod (Figure 1) is distributed in the northwest Atlantic Ocean from Greenland to Cape Hatteras, North Carolina. Within the overall distribution, densities are highest off Newfoundland, in the Gulf of St. Lawrence and on the Scotian Shelf, while in U.S. waters, densities are highest on Georges Bank and the western Gulf of Maine. Atlantic cod are managed as two stocks in American waters: (1) Gulf of Maine and (2) Georges Bank and southward (Mayo 1995). Little interchange occurs between the two. It occurs from nearshore areas to depths exceeding 400 m (rarely). The greatest concentrations off the northeast coast of the U.S. are on rough bottoms in waters between 10 and 150 m and at temperatures between 0 and 10^{o}C.

A regular pattern of migrations, associated with reproduction and seasonal temperature change, has been observed in the Newfoundland stock (Rose 1993). Here, huge schools of cod leave wintering areas in deep oceanic waters and follow tongues of deep, relatively warm, oceanic waters ("highways") across the shelf to summer feeding areas nearshore. They then move northward along the Newfoundland coast in late summer, and eventually return to wintering areas. Spawning occurs in dense concentrations (> 1 fish/m^3) as they begin this mass movement, with multiple pairs of spawning fish observed in "columns" above the mass. As this huge mass of fish migrates inshore, it periodically encounters important prey aggregations (e.g., capelin and shrimp) and disperses. The mass is led by the largest size class (or "scouts") and the smallest fish are found at the rear. The author postulates that the youngest learn the route from the oldest, and that loss of the largest fish (through fishery pressure directed at them) could result in changes in this migration pattern. Similar changes have been observed in Norwegian herring stocks, but observations of such migrations are lacking in the two U.S. stocks. Off New England, Atlantic cod typically move into coastal waters during the fall and then retreat into deeper waters during spring. Another seasonal movement occurs in the Great South Channel area where they move southwesterly during autumn, spend the winter in southern New England and the Mid-Atlantic coast, and then return in the spring.

Atlantic cod attain ages of 20 years, although most enter fisheries at ages 2-5. They can grow to lengths of 130 cm and weights of 25-35 kg and average 26 cm by the end of their first year. Median age at sexual maturity is 1.7-2.3 years at lengths between 32 and 41 cm (O'Brien *et al.* 1993). Fecundity is high and a large female may produce between 3 and 9 million eggs. Spawning occurs near bottom during winter and early spring, usually in water temperatures between 5 and 7^{o}C. Eggs are pelagic and drift for 2-3 weeks before hatching. The larvae are also pelagic until they reach 4-6 cm in about 3 months, whence they descend to the bottom. Further details of the life history of Atlantic cod are summarized in the Final EIS for Amendment 5 (NEFMC 1993) for the multispecies complex, and certain data are updated in Amendment 7, Vol. 1 of the Multispecies FMP (NEFMC 1996). Generalizations contained in those summaries suffice to describe most biological and life history traits of cod occurring off the northeastern coast of the U.S. The present document examines dietary requirements and expands somewhat on spawning patterns, distributions and habitat characteristics of four life history stages (eggs, larvae, juveniles, adults).

LIFE HISTORY

EGGS

Atlantic cod eggs are pelagic, buoyant, spherical and transparent. Their diameter ranges from 1.2-1.7 mm. The chorion is smooth (unsculptured) and the yolk is homogeneous. There are no oil globules and the perivitelline space is narrow (Fahay 1983; Markle and Frost 1985). Hatching occurs after 8 to 60 days in varying temperatures (Hardy 1978) and averages 2-3 weeks in average spring conditions (Lough *et al.* 1989). Temperature, more than season, also exerts the most influence on egg and hatchling sizes (Miller *et al.* 1995).

LARVAE AND PELAGIC-JUVENILES

Larvae hatch at sizes between 3.3 and 5.7 mm, with pigmented eyes, but unformed mouth parts. The body is long and tapering and the vent opens laterally on the finfold, rather than at its margin. The preanus length is < 50% of the total length. Characteristic pigment includes pairs of bars on the dorsal and ventral edges of the body and individual melanophores under the notochord tip. Pollock (*Pollachius virens*) larvae are similar, but have five primary caudal rays on the superior hypural; Atlantic cod larvae have four (Fahay 1983). Some studies have found increased growth rates with warmer temperatures (e.g., Laurence 1978); others have correlated enhanced growth with concentrations of zooplankton prey (Suthers *et al.* 1989). Several studies have described developing larvae drifting in a clockwise pattern around Georges Bank with high concentrations over the southern flank between 50 and 100 m (e.g., Lough *et al.* 1989). Larvae occur from near-surface to depths of 75 m, and larvae move deeper with growth (Hardy 1978).

JUVENILES

Transformation to the juvenile stage occurs at sizes greater than 20 mm, when all fin rays are formed (Fahay 1983). Descent from the water column to bottom habitats occurs at sizes of 2.5-6 cm (Fahay 1983; Lough *et al.*

1989) or < 7 cm (Bailey 1975). Most remain on the bottom after this descent, and there is no evidence of a subsequent, diel, vertical migration (Bailey 1975). Coloration during this initial descent mimics the substrate, reducing predation (Lough *et al.* 1989). After descent to the bottom, juveniles are most dense in the following areas: off Cape Ann, MA, Massachusetts Bay, Vineyard Sound, Nantucket Shoals, and the Northeast Peak of Georges Bank (present report).

ADULTS

Adults are heavy-bodied and have a large head, blunt snout and a distinct barbel under the lower jaw tip. Color varies, but usually includes many small spots and a pale lateral line. Color can change depending on bottom habitats. There are three distinct dorsal fins and two distinct anal fins. Vertebrae number 50-59 and fin ray counts are: D_1: 13-16; D_2: 19-24; D_3: 18-21; A_1: 20-24; A_2: 17-22. Size averages 2.3-3.6 kg and the largest recorded was 95.9 kg (Scott and Scott 1988). They tend to move in schools, usually on the bottom, although they may also occur in the water column.

REPRODUCTION

Both size and age at maturity have declined in recent decades, likely in response to the fishery harvesting older and larger fish, or to a general decline in stock biomass due to intense exploitation. In a Scotian Shelf study (Beacham 1983), the median age at maturity declined about 50% between 1959 (when age at 50% maturity was 5.4 years in males, 6.3 years in females) and 1979 (when age at 50% maturity was 2.8 years in both sexes). Median lengths at maturity declined from 51 to 39 cm in males, 54 to 42 cm in females. This "smaller and younger at maturity" trend continued between 1972 and 1995 in all zones between Georges Bank and Labrador (Trippel *et al.* 1997). Presently, in U.S. waters, sexual maturity is reached at ages between 1.7 and 2.3 years (median) and lengths between 32 and 41 cm (average) (O'Brien *et al.* 1993). Age and length at 50% maturity for Georges Bank and Gulf of Maine stocks are shown in Table 1. In preparing the distribution maps for this report, a size of 35 cm was used as the division between juveniles and adults, based on data in Table 1 and Morse (1979).

On Georges Bank, an analysis of the Marine Resources Monitoring, Assessment and Prediction (MARMAP) data set indicates that 60% of spawning occurs between February 23 and April 6, based on the abundance of Stage III eggs, back-calculated to spawning date. Ninety percent occurs between mid-November and mid-May, with a median date of mid-March (Page *et al.* 1998; Colton *et al.* 1979). Spawning begins along the southern flank of Georges Bank and progresses toward the north and west. It ends latest in the year on the eastern side of the bank. Egg distributions indicate that the most intense spawning activity occurs on the Northeast Peak of Georges Bank (Page *et al.* 1998). The results of the present compilation of egg distributions indicate that most spawning occurs not only on the Northeast Peak of Georges Bank, but also around the perimeter of the Gulf of Maine, and over the inner half of the continental shelf off southern New England. It occurs year-round, with a peak in winter and spring. Peak spawning is related to environmental conditions. It is delayed until spring when winters are severe and peaks in winter when they are mild (Smith *et al.* 1979; Smith *et al.* 1981). Spawning peaks in April on Browns Bank (Hurley and Campana 1989). Reproduction also occurs in nearshore areas, such as Beverly-Salem Harbor, MA, where eggs are found November through July (with a peak in April) at temperatures between -2 and 20^{o}C (Elliott *et al.* 1979).

FOOD HABITS

The Atlantic cod has a varied diet. Reported food items vary by life history stage and study area (Table 2). During Northeast Fisheries Science Center (NEFSC) bottom trawl surveys, the most frequently observed food items were invertebrates, with fishes comprising only a minor component (Figure 2; Table 3). In another study, leading fish (also known as “scouts”) at the head of migrating shoals were larger, were more successful in feeding on preferred prey (fishes and pelagic invertebrates), and had a more varied diet than those following, which tended to feed mostly on benthic invertebrates (Deblois and Rose 1996). Although cannibalism is not often reported to occur in this species, recent studies suggest the importance of habitat segregation of Age 1 cod from older year classes in order to avoid it (Gotceitas *et al.* 1995, in prep.).

PREDATION

Yolk sac larvae are vulnerable to zooplankton predators including *Aurelia*, *Thysanoessa* and *Euchaeta* (Bailey 1984). Adults, because of their large size, have few enemies other than large sharks. Young stages, however, are preyed upon by spiny dogfish, winter skate, silver hake, sea raven, squid (northern shortfin), Atlantic halibut, fourspot flounder and adult cod.

MIGRATIONS

In the middle part of their range, cod are non-migratory in the strictest sense, only undertaking minor seasonal movements in reaction to changing temperatures. At the extremes of their range, however, cod migrate annually (see Introduction). In the extreme northern region (east coast of Labrador) cod are only present during summer and early fall. In the Middle Atlantic Bight as far south as Chesapeake Bay, cod only occur during winter and spring and retreat north and east to Nantucket Shoals as shallow waters in the southern part of the Bight exceed 20^{o}C (Heyerdahl and Livingstone 1982).

STOCK STRUCTURE

Several stocks have been recognized in Canadian and U.S. waters. In U.S. waters three (or four) stocks occur: (1) in the Gulf of Maine, north of Provincetown; (2) on Georges Bank; (3) in southern New England, south and west of Nantucket Shoals; and (4) along the Middle Atlantic Bight, although the latter three intermingle. In U.S. waters, cod are managed as two stocks, the Gulf of Maine, and the Georges Bank and southward stocks (Mayo 1995).

HABITAT CHARACTERISTICS

The results of a literature review directed at habitat requirements of four life history stages of Atlantic cod are presented in Appendix 1 and a synthesis of those data are presented in Table 4. These tables include data from U.S. (and certain non-U.S.) western Atlantic stocks, but excludes data from the eastern Atlantic. Data from Canadian waters were included only if the results could reasonably be applied to U.S. stocks. Specifics of some Canadian studies (e.g., distribution relative to temperatures within a distinct region) were not included since they have little applicability to U.S. waters.

In general, young stages of Atlantic cod tend to have restricted distributions near major spawning centers. With increasing age, they tend to be more widely distributed and occur in deeper, colder and more saline water (Tremblay and Sinclair 1985).

EGGS

An analysis of nearly 50 years of trawl data in Canadian waters concluded that spawning rarely occurs beyond the continental shelf, but rather occurs near where eggs and larvae are likely to be retained (Hutchings *et al.* 1993). These authors concluded that inshore spawning populations contribute more to recruitment than those farther offshore. In MARMAP sampling between 1979 and 1987, eggs were collected from virtually all depths sampled, but primarily from depths < 100 m (Berrien and Sibunka 1999). Many reports describe eggs occurring in the upper 10 m of the water column, although spring rainfalls can lower the salinity and they will then sink to lower depths. Although eggs are collected in a wide range of temperatures and salinities, several studies have found optimum conditions for incubation, hatching and development, depending on study site (Table 4). The present compilation of collections indicates that most eggs are found in water column temperatures of 4-8^{o}C (winter, spring, summer) or 7-14^{o}C (fall). A lab study found that egg mortality was independent of temperature, but that mortality increased at lower salinities within the range 26-36 ppt (Laurence and Rogers 1976).

LARVAE AND PELAGIC-JUVENILES

Several studies have found increased recruitment success when dispersion of larvae from spawning areas by currents is reduced (Table 4; Cong *et al.* 1996). Although larvae have been collected from a wide range of temperatures, most are found in temperatures < 8^{o}C, although growth rates may be enhanced in warmer temperatures (e.g., Lawrence 1978) and one study found no increased mortality when larvae were exposed to higher temperatures (Iversend and Danielssen 1984). Larvae can survive undercooling to -1.8^{o}C but if in direct contact with ice they froze at -1.36^{o}C (Valerio *et al.* 1992). When larvae are 3-8 days old, they are positively phototactic and are reported to occur from the surface to 75 m depths, moving deeper in the water column as they grow older (Hardy 1978).

JUVENILES

Juveniles may tolerate a wider range of temperatures than adults (Table 4; and Bigelow and Schroeder 1953). Several studies have stressed the importance of cobble substrates over finer grained bottoms after settlement (e.g., Bigelow and Schroeder 1953; Colton 1978), and some of these studies have related this preference to avoidance of predation by older year classes of cod (e.g., Gotceitas and Brown 1993 and others). Nearshore nurseries (including grass beds) may be significantly more important to survival of juveniles than offshore habitats (see Table 4).

ADULTS

Adult cod are typically found on or near bottom along rocky slopes and ledges. They prefer depths between 40 and 130 m, but are sometimes found in midwater. Cod rarely occur deeper than 200 m. Larger individuals remain closer to the bottom in deeper water, and many move to offshore banks during summer (Hardy 1978; Cohen *et al.* 1990). Several studies have ascertained a preference by adult cod for coarse sediments over finer mud and silt (Table 4; Scott 1982b). They engage in diel vertical migrations, where they make forays off the bottom and into the water column at night (several studies; e.g., Beamish 1966). Cod can occur in temperatures from near freezing to 20°C, and are usually found in temperatures < 10°C, except during fall when they can occur in warmer temperatures. Larger fish are generally found in colder waters (Cohen *et al.* 1990).

GEOGRAPHICAL DISTRIBUTION

Atlantic cod in the northwest Atlantic are distributed from Cape Chidley, Labrador to Cape Henry, VA (Figure 3). The areas of highest abundance are in Canadian waters and include the eastern coast of Labrador south of Cape Harrison, off eastern Newfoundland, the Flemish Cap, the Grand Bank, the Gulf of St. Lawrence, and the Scotian Shelf.

The estuarine occurrences of early life history stages between Maine and the Chesapeake Bay are shown in Table 5. These are expressed as relative abundance characterizations, based on the observations of biologists working in each of the systems listed, but they are not quantitative measurements and should be considered as presence or absence value only. Despite these limitations, it is apparent that no early life history stages are commonly collected south of Buzzards Bay, and north of there they are uncommon in systems comprised mostly of low salinity zones.

EGGS

During MARMAP sampling between the Gulf of Maine and Cape Hatteras, 1978-1987, eggs were distributed throughout the study area, with centers of abundance in western Gulf of Maine, Georges Bank and southern New England waters (Berrien and Sibunka 1999). Although they occurred year-round, densities were much lower during August and September. Maximum average densities of eggs occurred during March on Georges Bank. A downward trend in abundance was observed between 1979 and 1987 in this study area (Berrien and Sibunka 1999). Monthly distribution maps presented here (Figure 4) pertain to the same MARMAP collections. In general, eggs were most dense on the Northeast Peak of Georges Bank and around the perimeter of the Gulf of Maine, as well as lower densities in southern New England waters (Figure 4). Monthly densities reached a peak in March-April, declined through the summer, and began to increase again in the fall. Note the relative lack of sampling in the Gulf of Maine during March, when densities might be expected to be high.

Eggs usually occurred at temperatures between 4 and 8°C, although they also occurred at warmer temperatures, especially during the fall (Figure 5). Most eggs occurred over depths of 60-110 m, although they occurred in shallower waters during the winter (Figure 5).

There is no information on this life history stage from state surveys.

LARVAE AND PELAGIC-JUVENILES

Larvae also occurred in MARMAP samples year-round. They were most abundant in March-May over Georges Bank and southern New England (Figure 6), although sampling was light during March in the Gulf of Maine. Few larvae were collected between August and October. Most larvae were collected in temperatures between 4 and 10°C and over depths of 30-70 m (Figure 7).

There is no information on this life history stage from state surveys.

JUVENILES

The distribution of juveniles (< 35 cm) closely matches that of spawning activity, with centers of abundance on Georges Bank and the western part of the Gulf of Maine (Figure 8). [Also see the distribution of immature Atlantic cod, < 37 cm, resulting from NEFSC bottom trawl survey cruises, 1968-1986 in Wigley and Gabriel (1991)]. During spring trawl surveys, densities are highest in the area north and south of Cape Ann, Massachusetts. During summer (presence or absence data only) juveniles are mostly found along the western shore of Gulf of Maine, but also occur on the Northeast Peak of Georges Bank and on Browns Bank. Fall densities are highest in the areas of Massachusetts Bay, Nantucket Shoals and the Northeast Peak of Georges Bank. Winter distributions (presence or absence data only) are similar. During spring, juveniles are mostly found in temperatures of 4-7°C and depths of 25-75 m, while during fall, they occur mostly between 7 and 12°C, but in the same depths (Figure 9).

Juvenile cod (< 35 cm) occur in nearshore waters of Massachusetts during spring and fall (Figure 10). In the spring they are most dense around Cape Ann and the tip of Cape Cod, with scattered occurrences in Massachusetts Bay and Nantucket Sound. In the fall they occur densely around Cape Ann and throughout Cape Cod Bay, but are not found in Nantucket Sound. During spring surveys, their occurrences relative to temperature and depth closely match those sampled, but during fall surveys, they tend to occur at the coolest and deepest sampling stations (Figure 11).

In a trawl survey of Narragansett Bay undertaken by the Rhode Island Division of Fish and Wildlife, 1990-1996, very few juvenile cod were collected. They were collected in winter, spring and summer at stations with bottom temperatures between 5 and 22°C and depths of 10-110 ft. Too few were collected to draw conclusions regarding temperature or depth preferences.

See below for cod occurrences in Long Island Sound, and Hudson-Raritan Estuary/Sandy Hook Bay.

ADULTS

Spring densities of cod adults closely match those of the fall, with additional collections made throughout the central part of the Middle Atlantic Bight (Figure 8). Temperature and depth preferences are similar to those of juveniles except that the depth range of adults is greater than juveniles during the fall (Figure 9). During summer (presence or absence data only) adult cod are found throughout the Gulf of Maine and on Georges and Browns Banks (Figure 8). Fall densities are highest in the western part of Gulf of Maine, Nantucket Shoals and on the Northeast Peak of Georges Bank. Winter occurrences (presence or absence data only) are scattered over Georges Bank and southern New England with fewer occurrences in the western part of Gulf of Maine.

Adults occur more frequently in spring surveys than in fall surveys in nearshore Massachusetts. During the spring, they occur abundantly around Cape Ann, the tip of Cape Cod, and the western part of Cape Cod Bay (Figure 10). A few adults are found during fall surveys, and these are restricted to the Cape Ann and Cape Cod tip areas. Adults occur in the coolest stations sampled during spring and fall, occur at all depths sampled during spring, but only in the deepest stations sampled during fall (Figure 11).

Only one adult cod was collected in a survey of Narragansett Bay by the Rhode Island Division of Fish and Wildlife, 1990-1996. Cod do not regularly occur in Long Island Sound. In a survey of that body of water by the State of Connecticut, 1992-1997, only three (unmeasured) cod were collected, all near the eastern end of the sound, during the spring, at temperatures of 9-10^{o}C. A NEFSC trawl survey of the Hudson-Raritan Estuary/Sandy Hook Bay, 1992-1997, only collected two cod, both during winter (D. McMillan, National Marine Fisheries Service, Highlands, NJ, personal communication).

STATUS OF THE STOCKS

Combined commercial landings of the Gulf of Maine and Georges Bank stocks of cod are presently at their lowest level in 25 years (Mayo 1995 and Figure 12). Annual landings from the Gulf of Maine stock averaged 5,500 tons from 1960-1975; 12,000 tons from 1976-1985. A record high 18,000 tons was landed in 1991, but landings have declined since (Murawski *et al.* 1997). The relatively strong 1987 year-class no longer dominates catches, and recent landings are mostly comprised of weaker year classes deriving from 1988-1991 (Mayo 1995). The most recent year-classes have been among the weakest recorded. The Gulf of Maine stock is markedly depressed and remains overexploited.

Annual U.S. landings from the Georges Bank stock increased from 10,800 tons in 1960 to 40,000 tons in 1980, then declined to 18,000 in 1986 and 9,800 in 1994. Canadian landings from the same stock peaked at 14,300 tons in 1990, but have declined sharply since. The stock is currently dominated by the 1990 year-class. Subsequent year-classes have been much weaker and older fish are almost non-existent in this stock. This stock is presently at very low abundances, compared to historical levels (Murawski *et al.* 1997).

Based on landings (Gulf of Maine stock) or combined landings and estimates of spawning stock biomass (Georges Bank stock), 1979-1982 was selected as a period of relatively high abundance for cod, and 1993-1996 as a period of low abundance. The distributions of juveniles and adults during spring bottom trawl surveys were then plotted (Figure 13). Juveniles were relatively less dense in all areas where they occurred during the low-abundance period and are absent from certain areas (e.g., Long Island, Nantucket Shoals, Browns Bank) where they occurred during high-abundance periods. Distributions of adults during the two periods were similar. During the low-abundance period, densities were obviously lower throughout their range, and they did not occur in certain regions sampled (e.g., Browns Bank, much of southern New England) where they occurred during high-abundance periods.

RESEARCH NEEDS

Our knowledge of habitat requirements of Atlantic cod is scant beyond the distribution and relative abundance levels (EFH tiers 1 and 2). Scientists have only recently begun to investigate the early settlement stage and its associated substrate preferences (Lough *et al.* 1989) and the importance of certain bottom habitat types to the survival of young-of-the-year (e.g., Tupper and Boutilier 1995). Associated with these studies are those equating bottom habitats with the avoidance of predation, including cannibalism (e.g., Gotceitas *et al.* 1995, in prep.) or the importance of habitat segregation between year classes (e.g., Fraser *et al.* 1996). These kinds of studies are essential to improving our understanding of the importance of habitat at tiers 3 and 4 (effects of habitat variables on growth and/or survival).

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Table 1. Age and length at 50% maturity for two stocks of Atlantic cod, *Gadus morhua*. Data are from Mayo (1995). Similar results were obtained in a Canadian study for zones near U.S. waters (Trippel *et al.* 1997).

	Georges Bank	**Georges Bank**	**Gulf of Maine**	**Gulf of Maine**
	Males	Females	Males	Females
Age at 50% Maturity	1.9 years	1.7 years	2.3 years	2.1 years
Length at 50% Maturity	41 cm	39 cm	36 cm	32 cm

Table 2. Food habits of Atlantic cod, *Gadus morhua*.

Source	Study Area and Food Habits
	LARVAE
Marak 1960	Georges Bank, Gulf of Maine: Larvae eat most abundant prey. 4-18 mm eat mostly larval copepods; 18+ mm eat mostly adult copepods.
Bainbridge and McKay 1968	Greenland: Larvae (3-10 mm) mostly eat nauplii and copepodites of the copepods *Calanus* and *Temora*. Also euphausiids.
McLaren and Avendano 1995	Scotian Shelf (Western Bank): Larvae predominant prey: 2 species of the copepod *Pseudocalanus*.
	JUVENILES AND ADULTS
Bowman 1975	Gulf of Maine: Primary item: herring. Also redfish, mackerel, cod, and red and rock crabs.
Hacunda 1981	Central Maine coast ; Crustaceans most important, especially amphipods, *Unciola, Leptocheirus*, and decapods *Crangon, Cancer*.
Langton 1982	Northwest Atlantic: Initially crustaceans, switch to fishes with growth. Overlaps with white hake (*Urophycis tenuis*) and, at smaller sizes, with haddock (*Melanogrammus aeglefinus*).
Bigelow and Schroeder 1953	Gulf of Maine: Mollusks most important. Also other invertebrates.
Langton and Bowman 1980	Gulf of Maine: Diet by weight (%): Pisces 69.5; Clupeidae 23.3; Crustacea 26.1; other decapods 14.1; Mollusca 0.7; Echinodermata 0.4.
Tyler 1972	Passamaquoddy Bay: Winter - *Meganyctiphones, Mysis, Pandalus*; summer - *Meganyctiphones, Clupea, Pandalus.*
Keats *et al.* 1987	Conception Bay, Newfoundland: < 12.5 cm ate mostly small zooplankton; > 12.5 cm ate mostly benthic organisms, in areas with thick macroalgal cover. Latter not used as food source, however.
Whitehead *et al.* 1986	Northeastern Atlantic: Diet variable: (fishes) herring, capelin, haddock, codling; (invertebrates) euphausiids, hyperiids, amphipods, polychaetes.
Kohler and Fitzgerald 1969	Gulf of St. Lawrence, offshore Nova Scotian Banks: Small cod ate mostly crustaceans, switch to fish diet as they grow. Species taken depends on relative abundance of prey. Herring most important in GOSL, sand lance on Nova Scotian Banks. Some seasonal variation within areas and by depth.
Casas and Paz 1994	Flemish Cap: Invertebrates (crustaceans and polychaetes) dominant in juvenile diets; adults consume mostly fish, mainly redfish (*Sebastes* sp.).
Casas et al 1991	Flemish Cap: Hyperiid amphipods main item in juvenile cod; as size increases, shift to fish as food item. Most important fish prey juvenile redfish (*Sebastes* sp.). Rate of cannibalism very low.
Keats and Steele 1992	Newfoundland (eastern): Juveniles (Age 0 and 1) feed mostly during daylight and most prey was planktonic.
Witman and Sebens 1992	Gulf of Maine: Cod fed heavily on tethered brittle stars in this experiment.
Robichaud *et al.* 1991	Cape Breton I., Nova Scotia: Cod fed on snow crabs (*Chionecetes* sp.) and toad crabs (*Hyas* spp.), with the latter selected somewhat more often.
Methven and Piatt 1989	Newfoundland: Capelin very important diet item. When abundance is high, occurrences in cod stomachs high; when abundance low, occurrences in cod stomachs low.
Lilly and Parsons 1991	Northeast Newfoundland: Northern shrimp (*Pandalus borealis*) identified as important food item of cod throughout shrimp's range.
Minet and Perodou 1978	SW Newfoundland and NE Gulf of St. Lawrence: Capelin and crustaceans most important components. In some areas, larger cod ate more herring, redfish and plaice.

Table 3. Minor diet items of Atlantic cod (*Gadus morhua*) based on NEFSC Food Habits Study during bottom trawl surveys. Listed below are items occurring at 1-5 percent frequency. See Figure 1 for items occurring more frequently.

1973-1980: Diet Item	**Percent Frequency**	**1981-1990: Diet Item**	**Percent Frequency**
Polychaeta	4.70	Euphausiidae	4.68
Unciola irrorata	4.70	Decapoda (shrimp)	3.92
Eualus pusiolus	4.50	Paguridae	3.77
Trematoda	4.35	Ophiuroidea	3.64
Pagurus acadianus	3.49	*Cancer* sp.	3.24
Gastropoda	3.24	Bivalvia	2.81
Decapoda (crab)	3.03	*Cancer irroratus*	2.54
Ophiopholis aculeata	2.98	Gastropoda	2.26
Pandalidae	2.88	*Merluccius bilinearis*	2.26
Pandalus montagui	2.53	Gammaridea	2.11
Ammodytes sp.	2.53	Crustacea	1.63
Caprellidae	2.43	Mollusca	1.63
Cancridae	2.43	*Cancer borealis*	1.61
Decapoda	2.38	Isopoda	1.61
Paguridae	2.33	*Crangon septemspinosa*	1.56
Cephalapoda	2.22	Rock	1.45
Lysianassidae	2.18	Aphroditidae	1.44
Cancer borealis	2.18	Pectinidae	1.15
Ophiuroidea	2.12		
Aphroditidae	2.07		
Pagurus sp.	2.07		
Sand	2.07		
Aeginna longicornis	1.97		
Holothuroidea	1.87		
Pontogeneia inermis	1.82		
Cirolanidae	1.82		
Hyas sp.	1.72		
Axius serratus	1.52		
Bivalvia	1.52		
Politolana polita	1.47		
Pectinidae	1.47		
Pandalus borealis	1.32		
Neomysis americana	1.32		
Calanoida	1.32		
Gastropoda operculum	1.32		
Copepoda	1.26		
Anonyx sarsi	1.16		
Crangonidae	1.11		
Mollusca	1.11		
Clupeidae	1.11		
Syrrhoe crenulata	1.01		
Euphausiidae	1.01		

Table 4. Summary of life history and habitat parameters for Atlantic cod, *Gadus morhua*. Based on data contained in Appendix 1, Table of Habitat Parameters.

Life History Stage	Spatial and Temporal Distribution	Temperature	Salinity	Depth/ Substrate/ Vegetation	Diel/ Light/ Vertical	Predator/ Prey
Eggs [1]	Pelagic. Bays, harbors, offshore banks. Begins fall, peaks winter and spring.	Most 2.0-8.5°C for incubation. 12.0°C upper limit. Mortality independent of temp.	Most 32-33 ppt. Eggs sink in spring freshets. Inverse relationship with mortality, 26-36 ppt.	Usually < 70 m	Near surface unless salinities low. Eggs in poor condition may sink.	--
Larvae [2]	Pelagic. Most over Georges Bank, perimeter of Gulf of Maine, southern New England, continental shelf. Densest in spring.	Most 4-8°C (winter-spring), 7-12°C (summer-fall).	Most 32-33 ppt.	NA	Youngest from surface to 75 m. Move deeper with age. Migrate vertically in reaction to light.	Growth strongly correlated with zooplankton volume. Yolk sac larvae vulnerable to zooplankton predators.
Juveniles [3]	Mostly in shoal waters, coastal or offshore banks, summer. Deeper water winter.	6-20°C. More tolerant of extremes than adults. Temp. preferences differ winter-summer.	30-35 ppt.	'Cobble' preferred over finer grains. Uses vegetation for predator avoidance. Survival may be enhanced in structurally complex habitats.	Some changes in vertical distribution, day/night (see Appendix 1).	Avoid predation by seeking refuge in structured habitats.
Adults [4]	Seasonal migrations except in Gulf of Maine. Most dense Massachusetts Bay, NE Georges Bank, Nantucket Shoals.	Generally < 10°C. Varies seasonally.	Wide range of oceanic salinities. Mortality < 2.3 ppt.	Rocky, pebbly, gravelly. Avoid finer sediments.	Usually on bottom during day, may move up into water column at night.	Varied diet. Predation by large sharks, spiny dogfish, and, as juveniles, older cod.

[1] Bonnet 1939, Bigelow and Schroeder 1953, Laurence and Rogers 1976, Hardy 1978
[2] Rau 1974, Hardy 1978, Bailey 1984, Suthers *et al.* 1989
[3] Bigelow and Schroeder 1953, Hardy 1978, MacDonald *et al.* 1984, Clark and Green 1990, Gotceitas and Brown 1993
[4] Bigelow and Schroeder 1953, Beamish 1966, Odense *et al.* 1966, Hardy 1978, Scott 1982b, Cohen *et al.* 1990

Table 5. Distribution of life history stages of Atlantic cod (*Gadus morhua*) in representative estuaries between Maine and Chesapeake Bay. Occurrences are not quantitative and may be based on a single, or very few, specimens. Estimates of relative abundance after Jury *et al.* (1994), Stone *et al.* (1994).

Estuary	Eggs	Larvae	Juveniles	Adults
Passamaquoddy Bay	None	Common	Common	Common
Englishman, Machias Bays	Common	Common	Abundant	Common
Narraguagus Bay	Common	Common	Abundant	Common
Blue Hill Bay	Common	Common	Abundant	Common
Penobscot Bay	None	Common	Common	Common
Muscongus Bay	Rare	Rare	Common	Common
Damariscotta Bay	Rare	Rare	Common	Common
Sheepscot River	Abundant	Abundant	Common	Abundant
Kennebec/Androscoggin Rivers	None	None	Common	Common
Casco Bay	Common	Common	Common	Common
Saco Bay	Common	Common	Common	Common
Wells Harbor	Rare	Rare	Rare	None
Great Bay	Common	Common	Rare	Rare
Merrimack River	Rare	Rare	Rare	Rare
Massachusetts Bay	Common	Common	Common	Common
Boston Harbor	Common	Common	Common	Common
Cape Cod Bay	Common	Common	Common	Common
Waquoit Bay	Rare	Rare	Rare	None
Buzzards Bay	Common	Common	Common	Common
Narragansett Bay	Rare	Rare	Rare	Rare
Long Island Sound	Rare	Rare	Rare	Rare
Connecticut River	None	None	None	None
Gardiners Bay	Rare	Rare	Rare	Rare
Great South Bay	None	None	None	None
Hudson River/Raritan Bay	None	Rare	None	None
Barnegat Bay to Chesapeake Bay	None	None	None	None

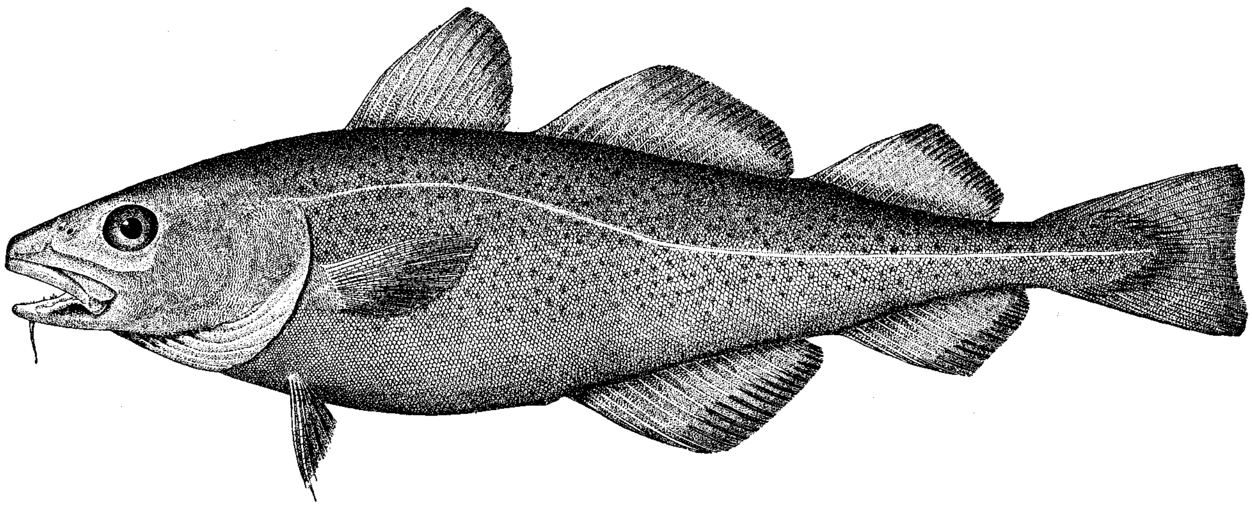


Figure 1. The Atlantic cod, *Gadus morhua* (from Goode 1884).

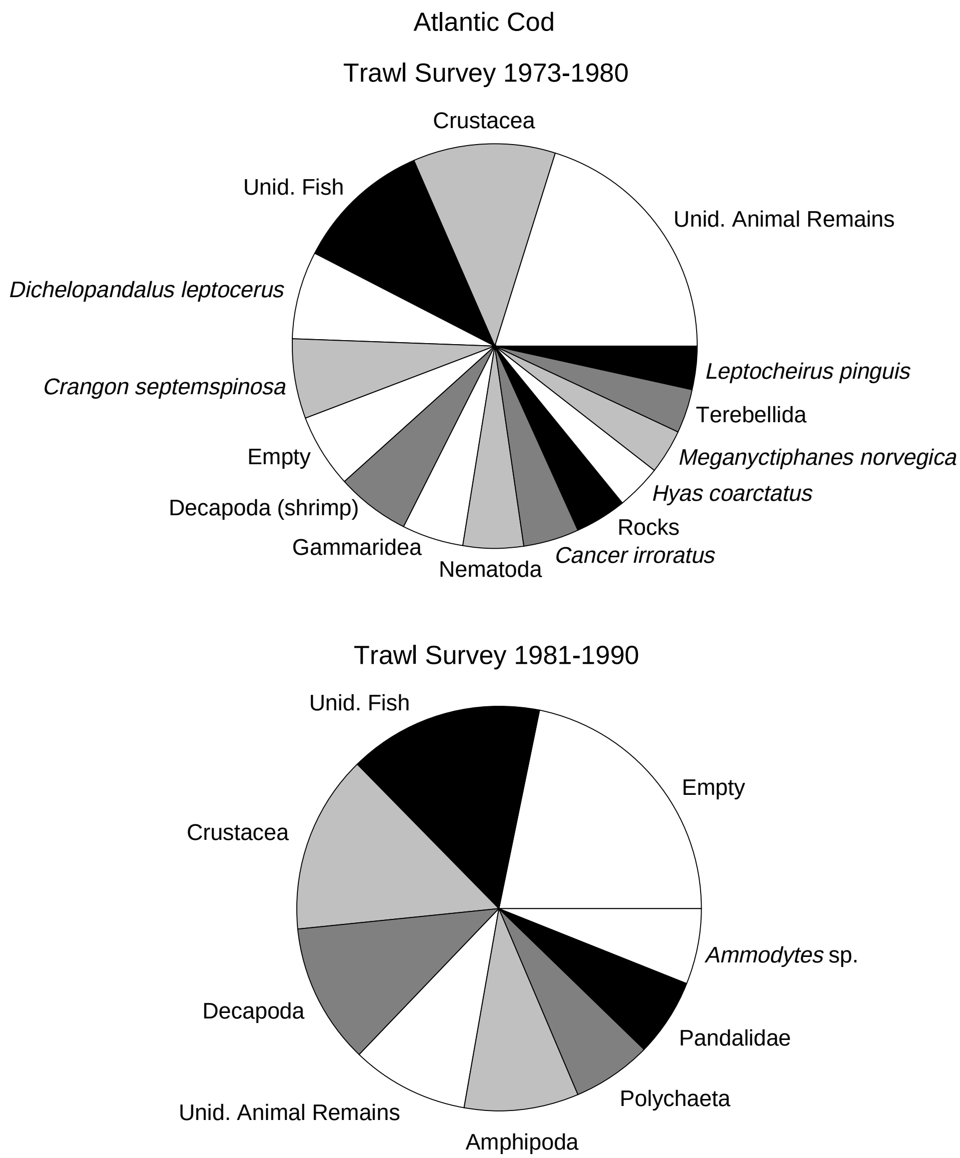


Figure 2. Abundance of the major prey items in the diet of Atlantic cod, based on NEFSC bottom trawl survey data on food habits collected during 1973-1980 and 1981-1990. Methods for sampling, processing, and analysis of samples differed between the time periods [see Reid *et al.* (1999) for details]. All other diet items less than 5 percent frequency are listed in Table 3. The category “animal remains” refers to unidentifiable animal matter.

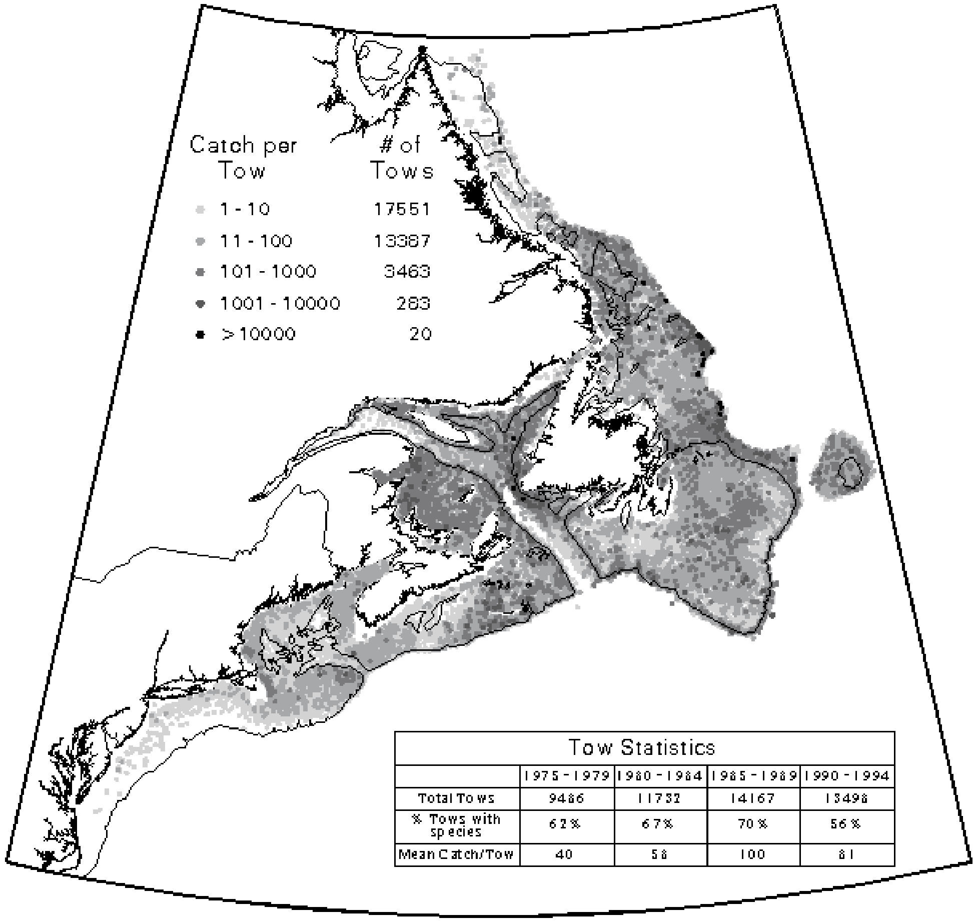


Figure 3. Distribution and abundance of Atlantic cod from Newfoundland to Cape Hatteras based on research trawl surveys conducted by Canada (DFO) and the United States (NMFS) from 1975-1994 (http://www-orca.nos.noaa.gov/projects/ecnasap/ecnasap_table1.html).

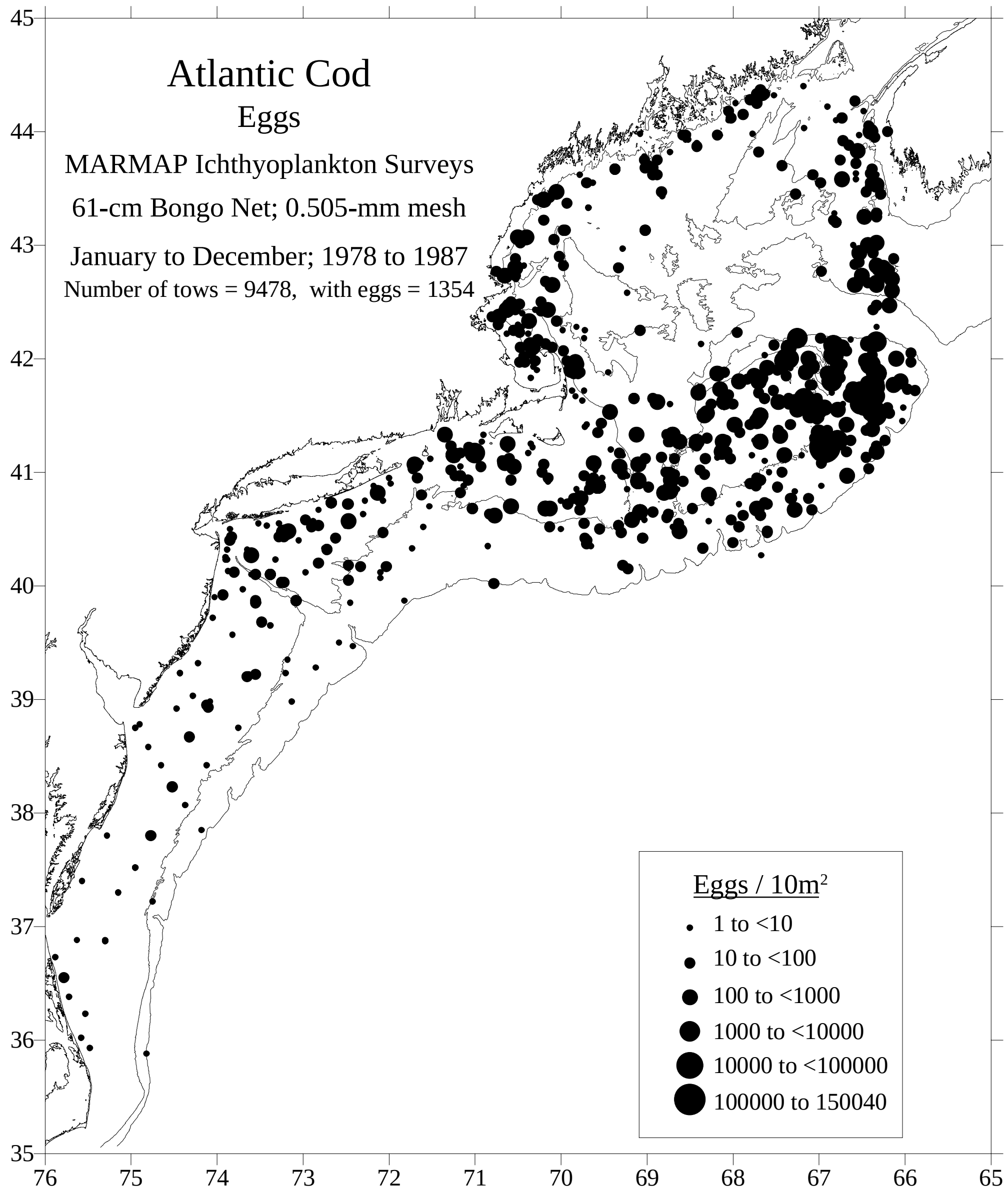
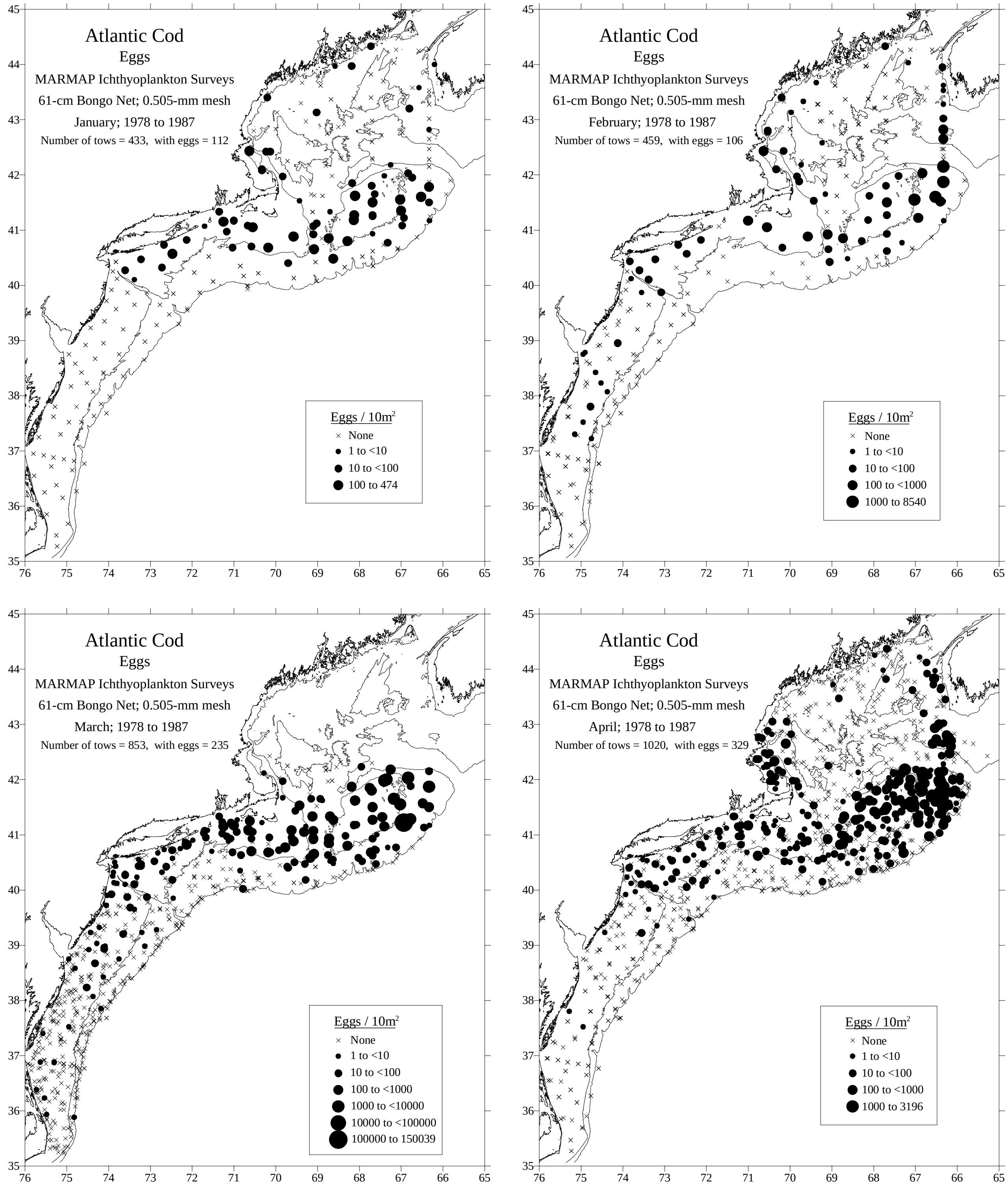


Figure 4. Distribution and abundance of Atlantic cod eggs collected during NEFSC MARMAP ichthyoplankton surveys, January to December, 1978-1987 [see Reid *et al.* (1999) for details]. Abundance is represented by dot size, and sampling effort is indicated by small x.



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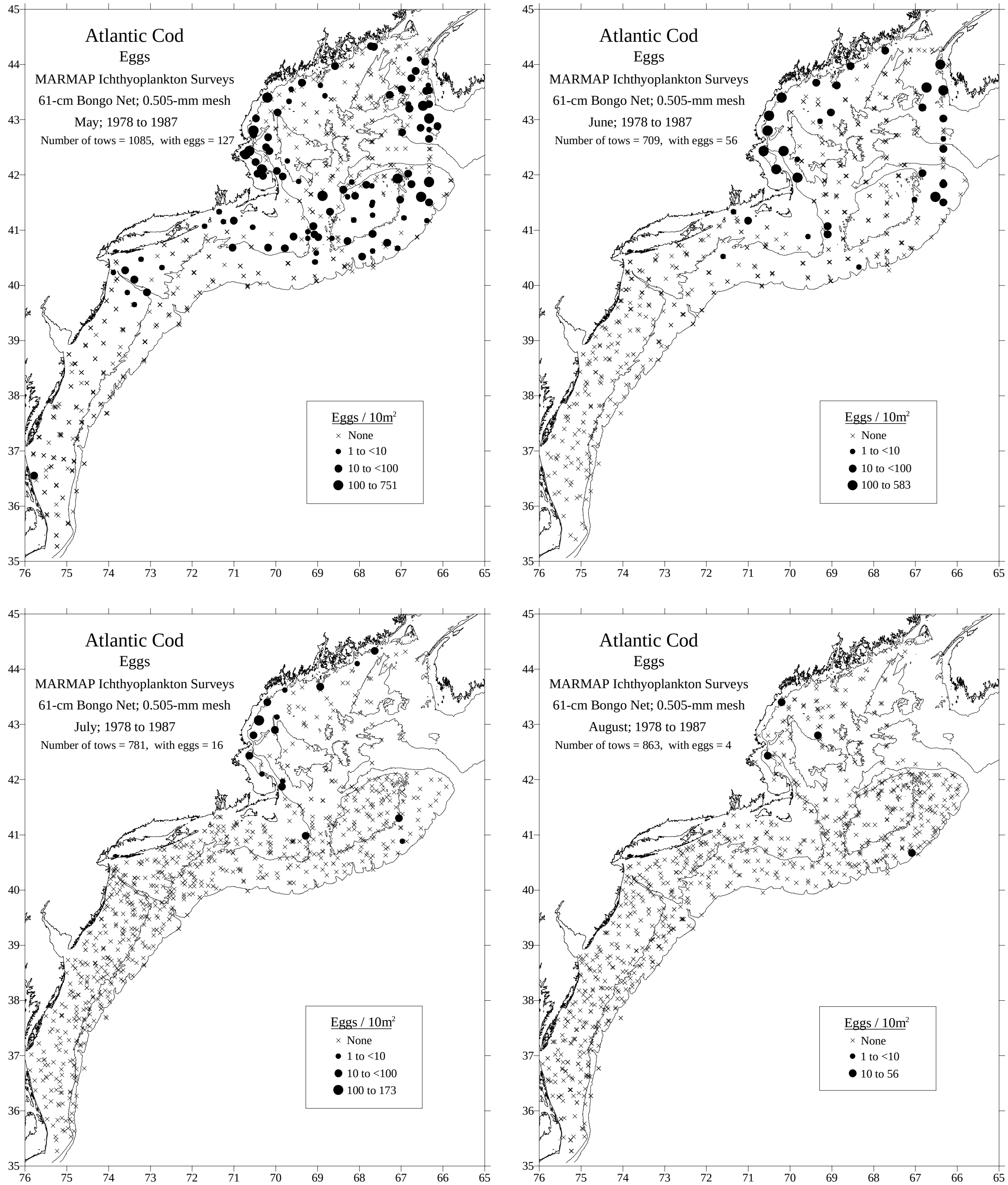

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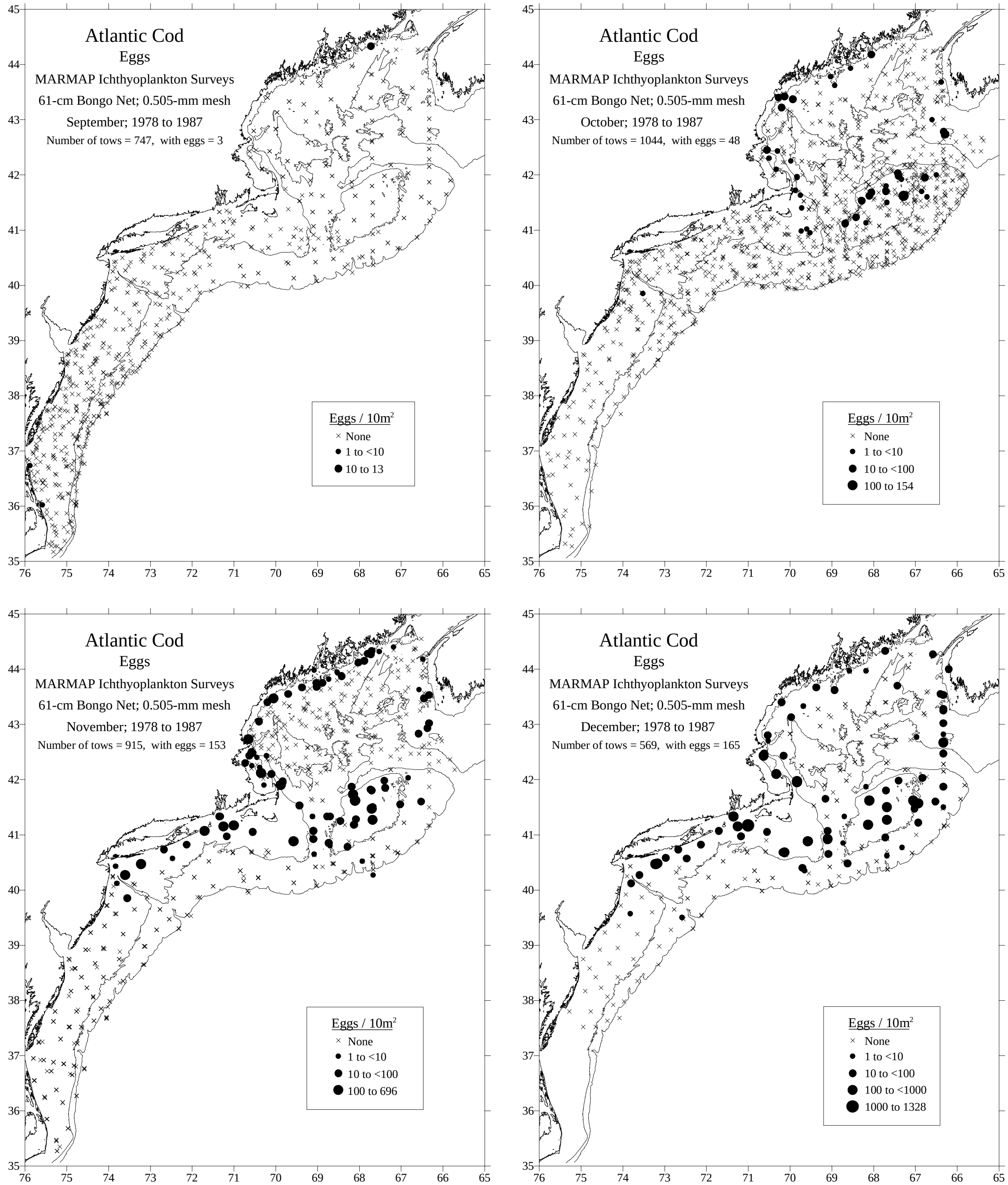

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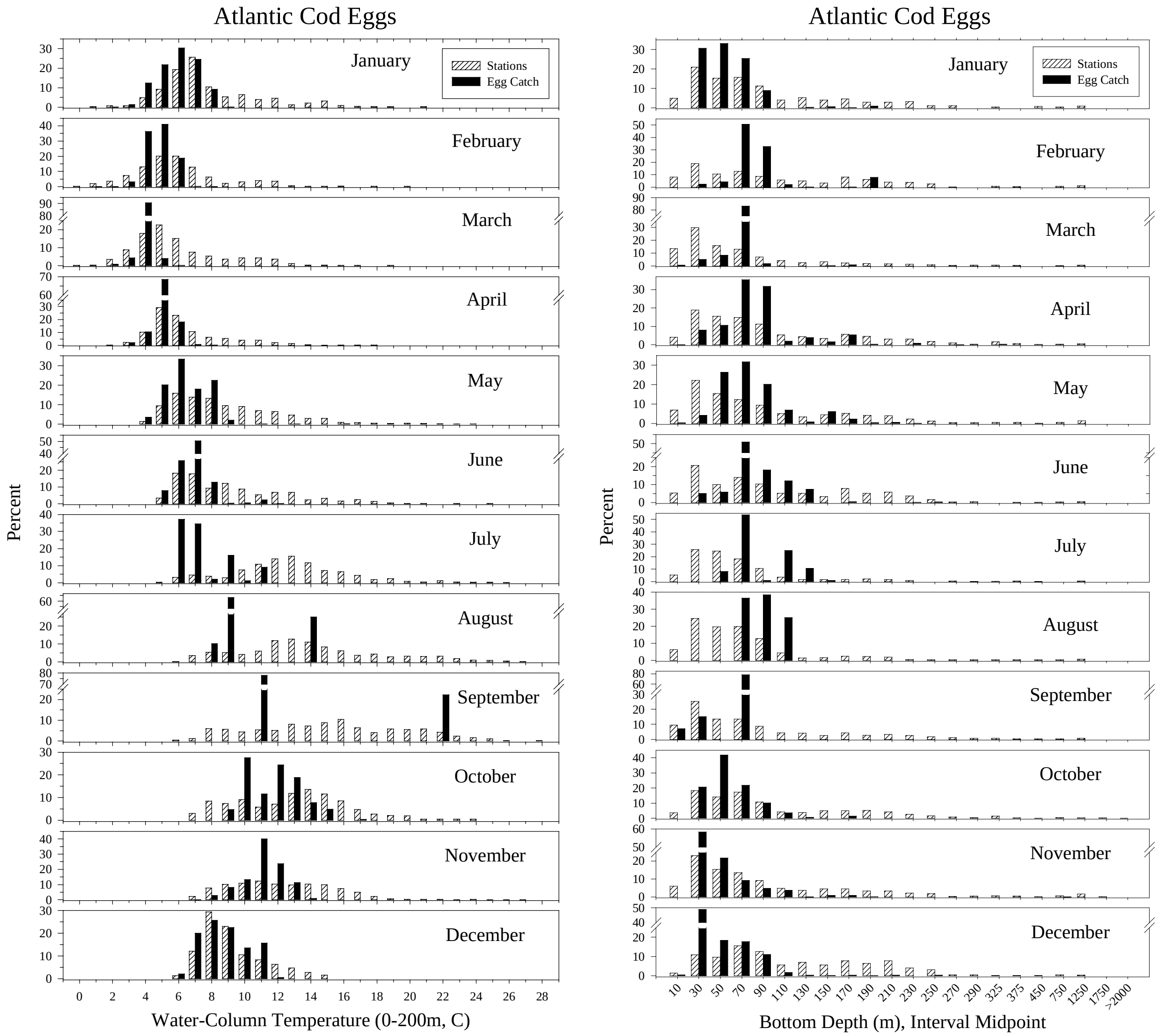


Figure 5. Mean water column temperature and bottom depth associated with collections of Atlantic cod eggs during NEFSC MARMAP ichthyoplankton surveys (1978-1987) by month for all years combined. Open bars represent the proportion of all stations which were surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).

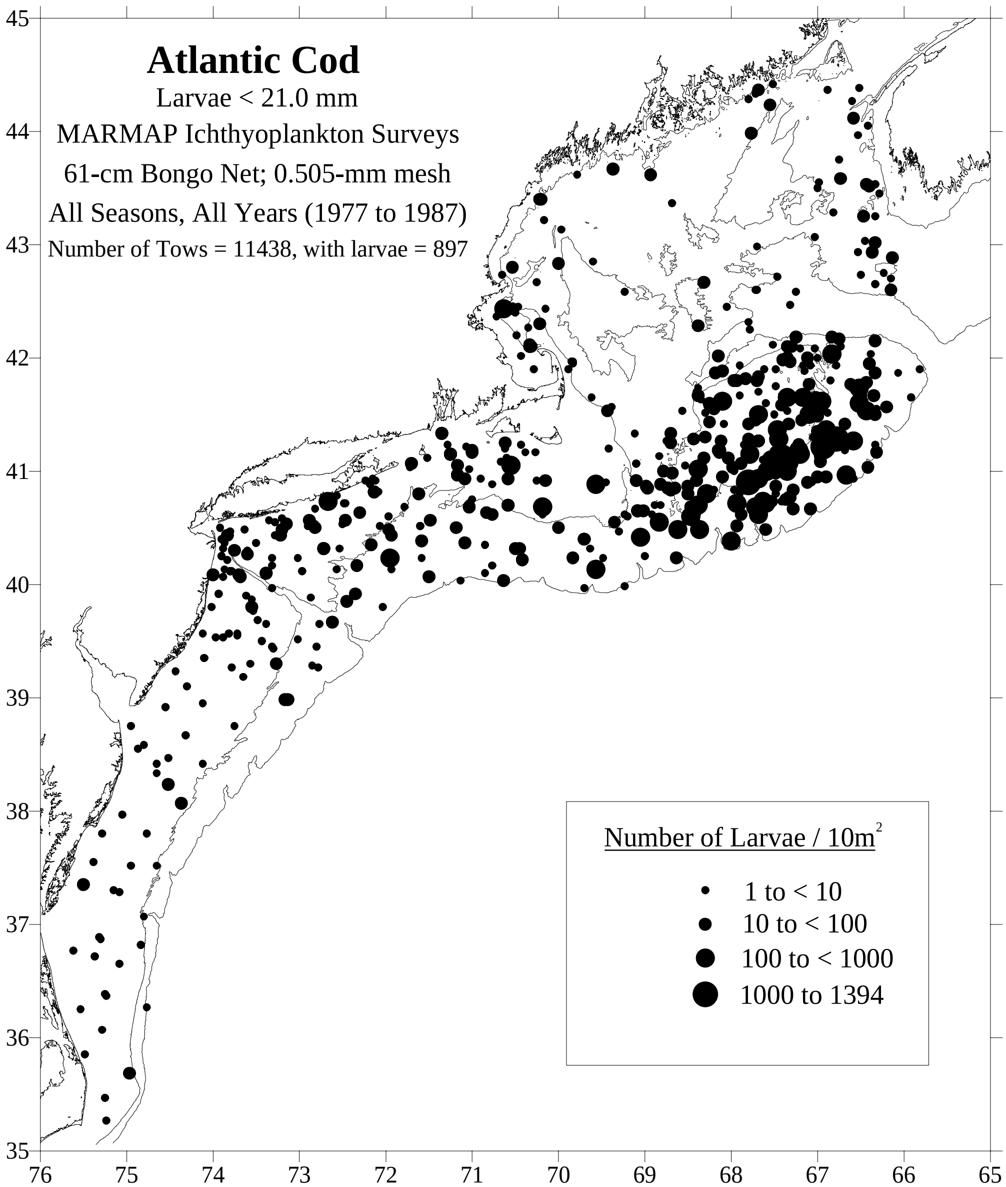
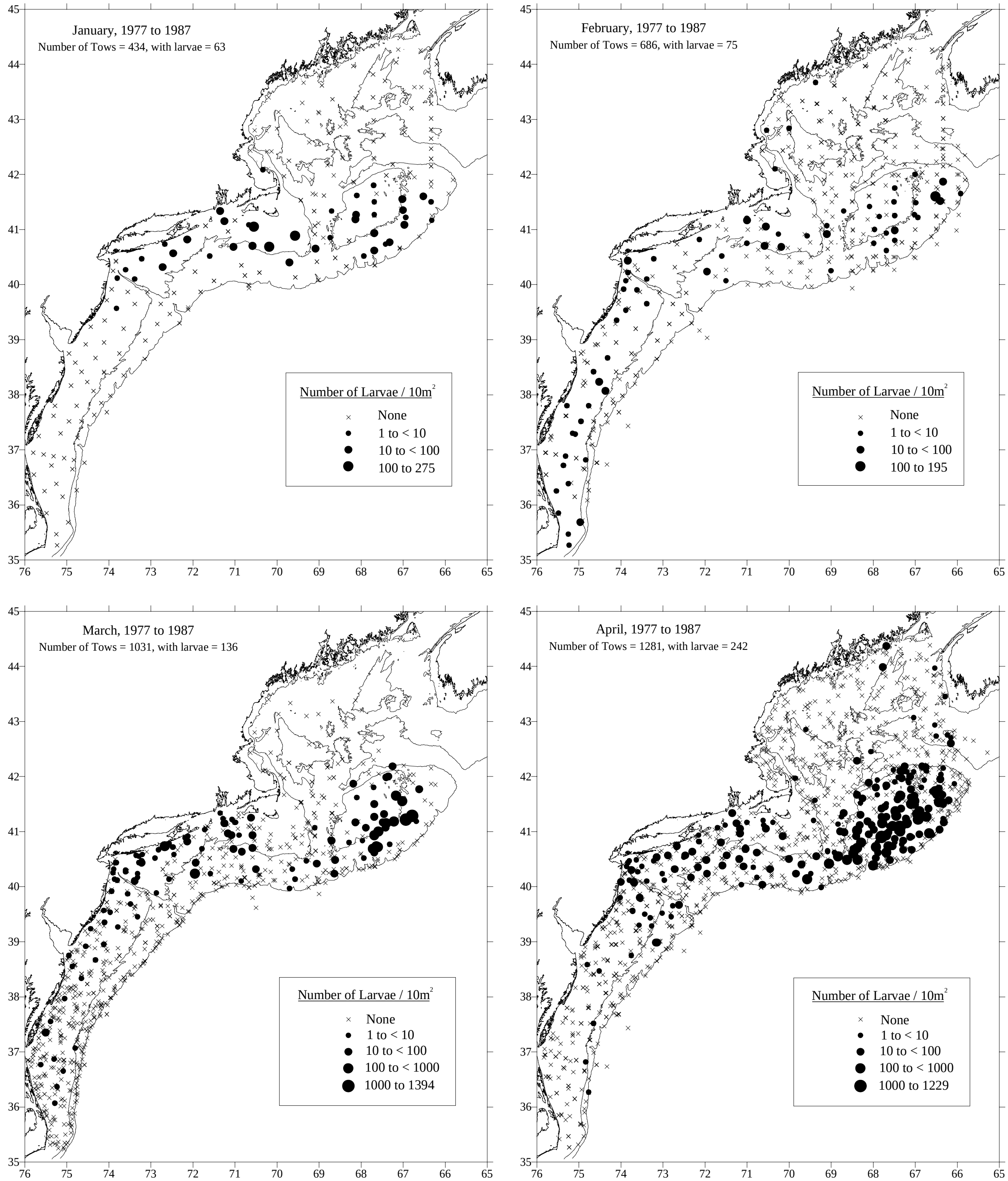


Figure 6. Distribution and abundance of Atlantic cod larvae collected during NEFSC MARMAP ichthyoplankton surveys, January to December, 1977-1987 [see Reid *et al.* (1999) for details]. Abundance is represented by dot size, and sampling effort is indicated by small x.



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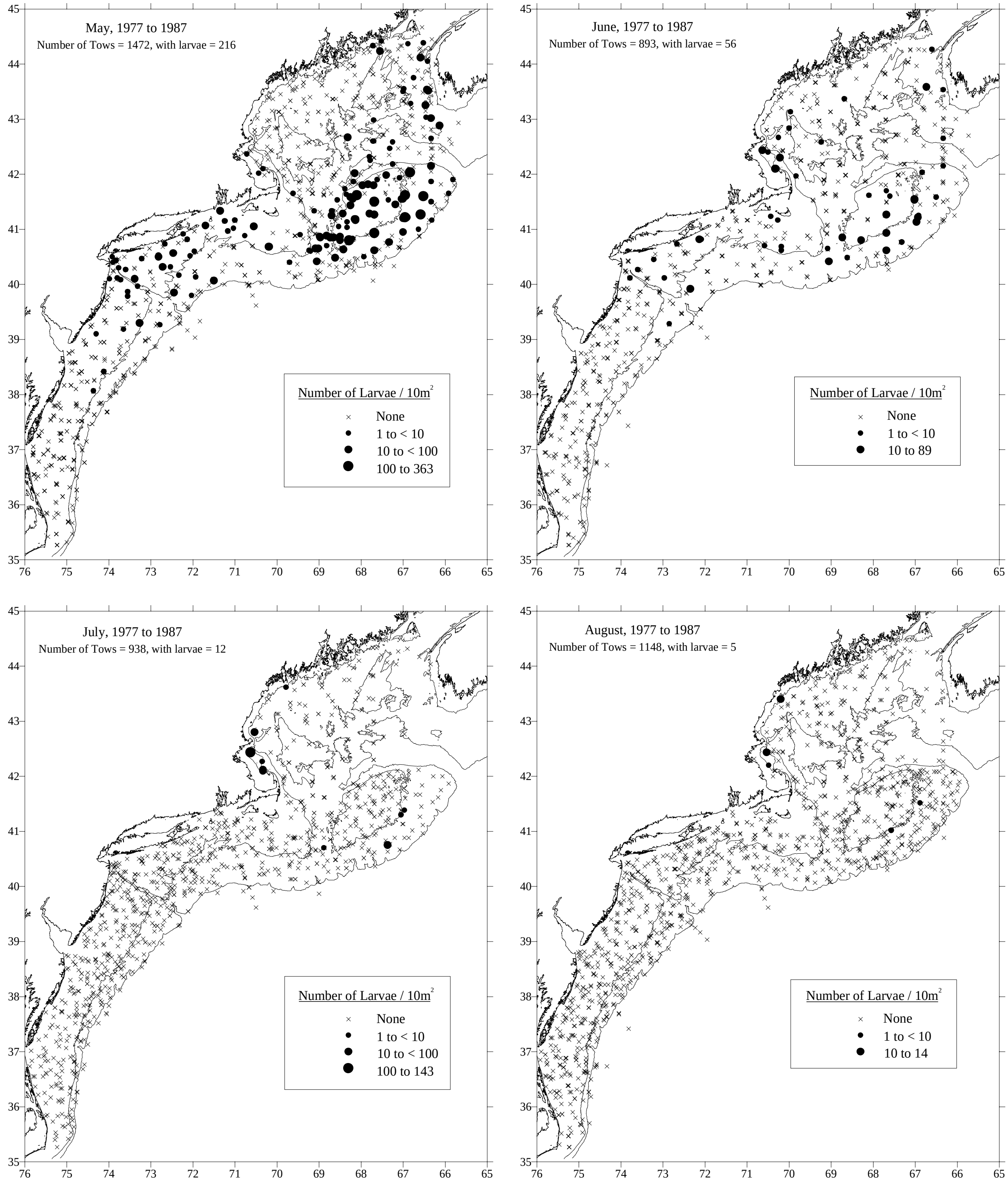

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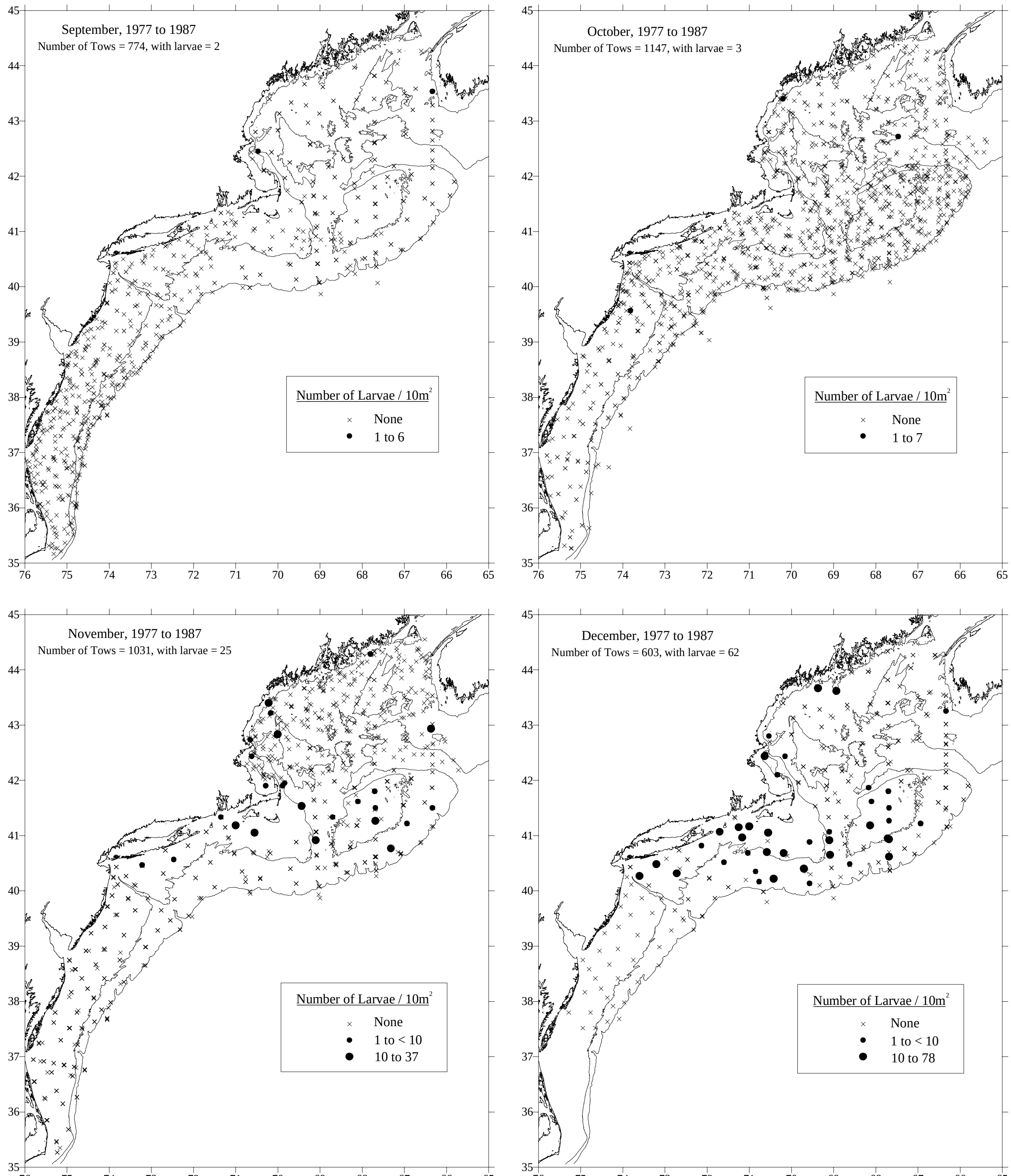

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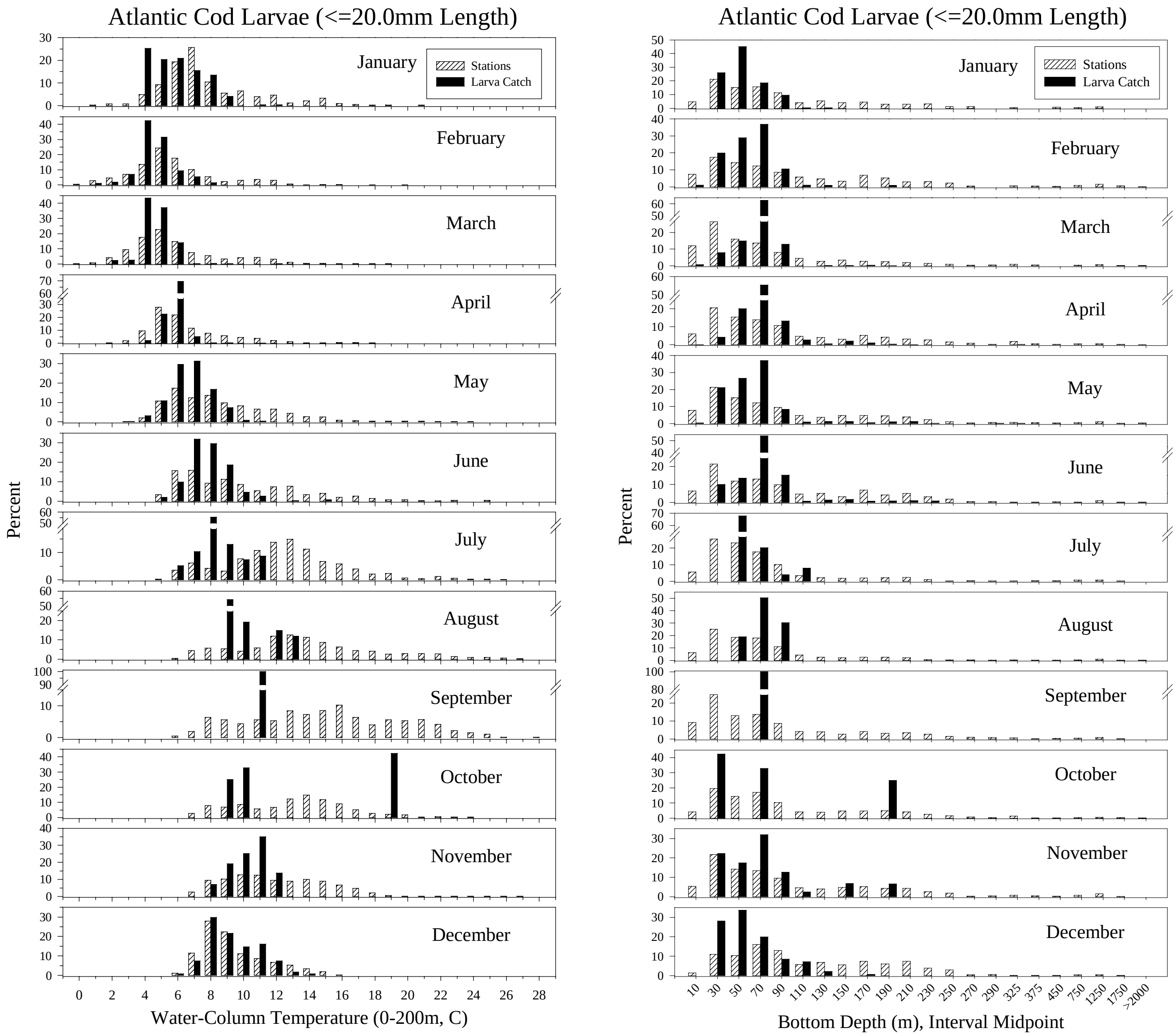


Figure 7. Mean water column temperature and bottom depth associated with collections of Atlantic cod larvae during NEFSC MARMAP ichthyoplankton surveys (1977-1987) by month for all years combined. Open bars represent the proportion of all stations which were surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).

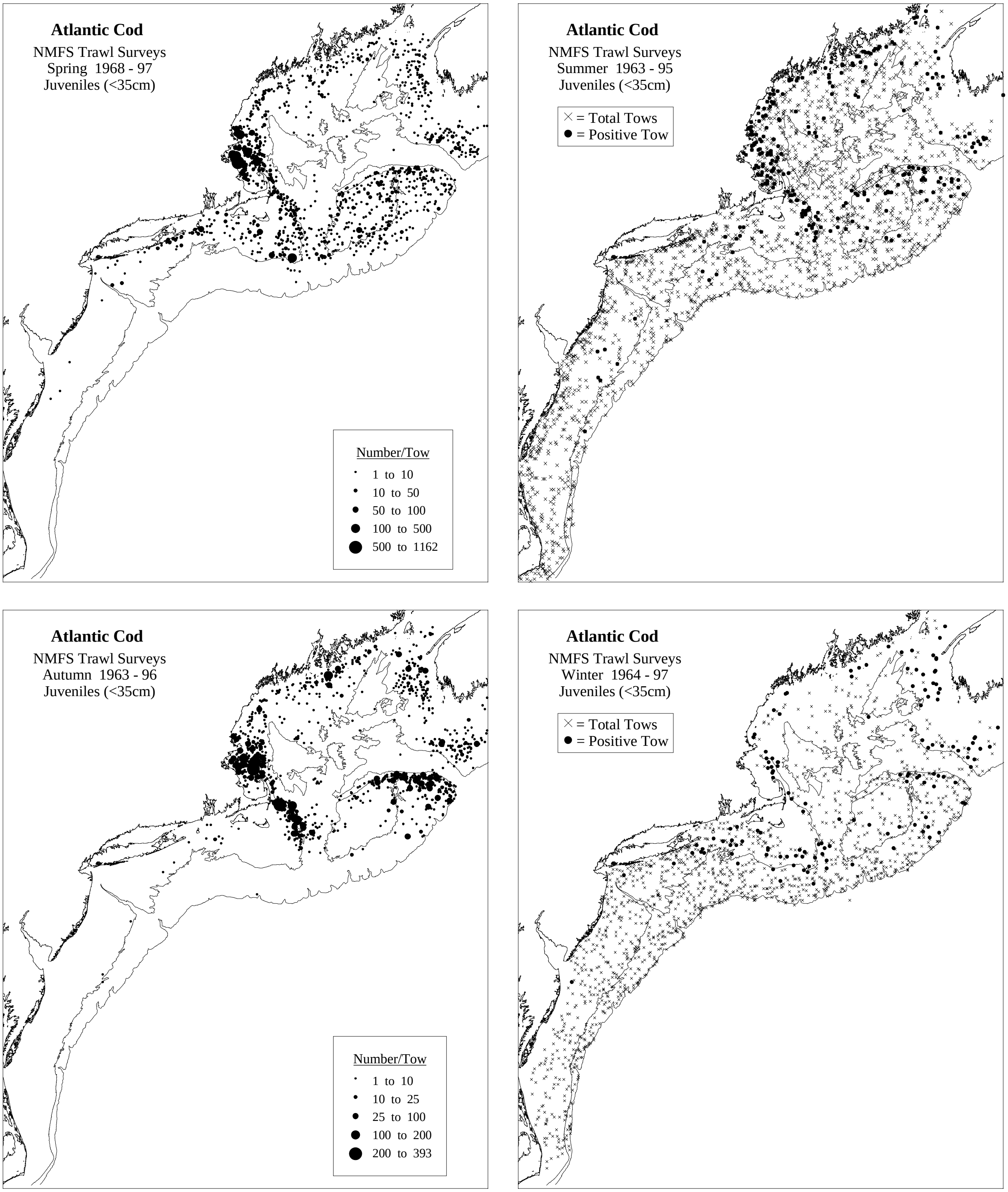
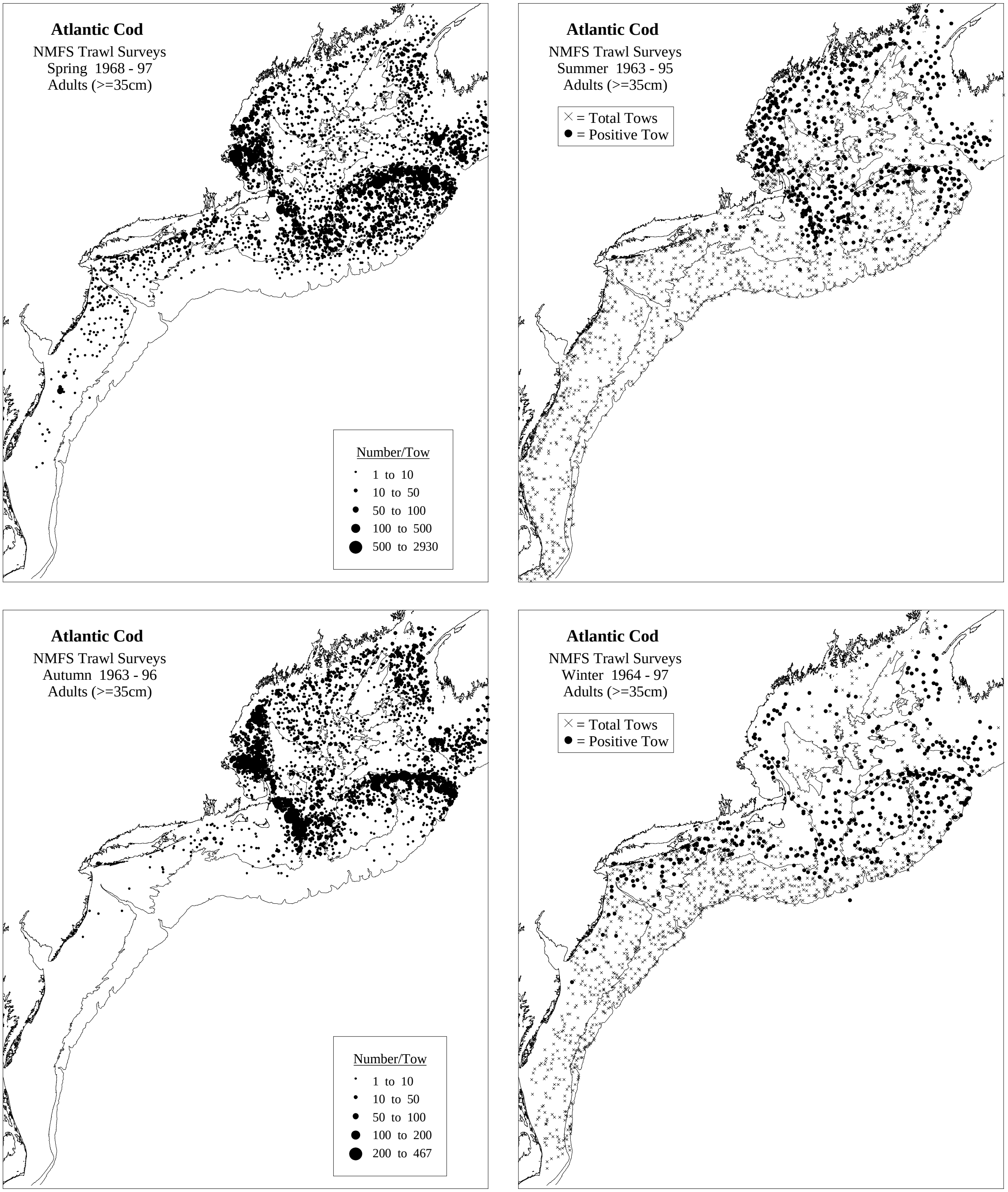


Figure 8. Distribution and abundance of juvenile (< 35 cm) and adult (≥ 35 cm) Atlantic cod from spring (1968-1997), summer (1963-1995), autumn (1963-1996), and winter (1964-1997) NEFSC bottom trawl surveys. Densities are represented by dot size in spring and fall plots, while only presence and absence are represented in winter and summer plots [see Reid *et al.* (1999) for details].



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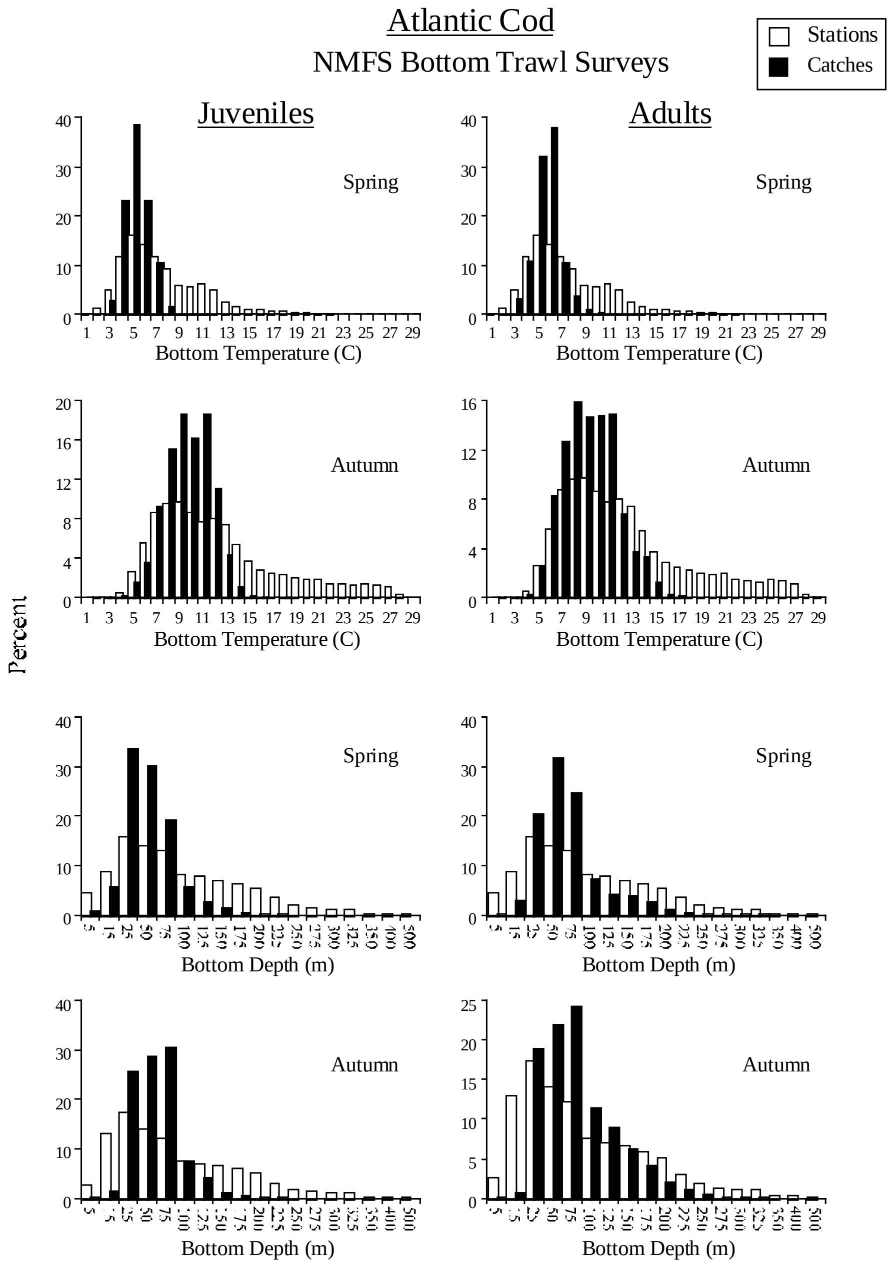

Figure 9. Distribution of juvenile and adult Atlantic cod in relation to bottom temperature and depth based on spring (1968-1997) and autumn (1963-1996) NEFSC bottom trawl surveys. Open bars represent the proportion of all stations which were surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).

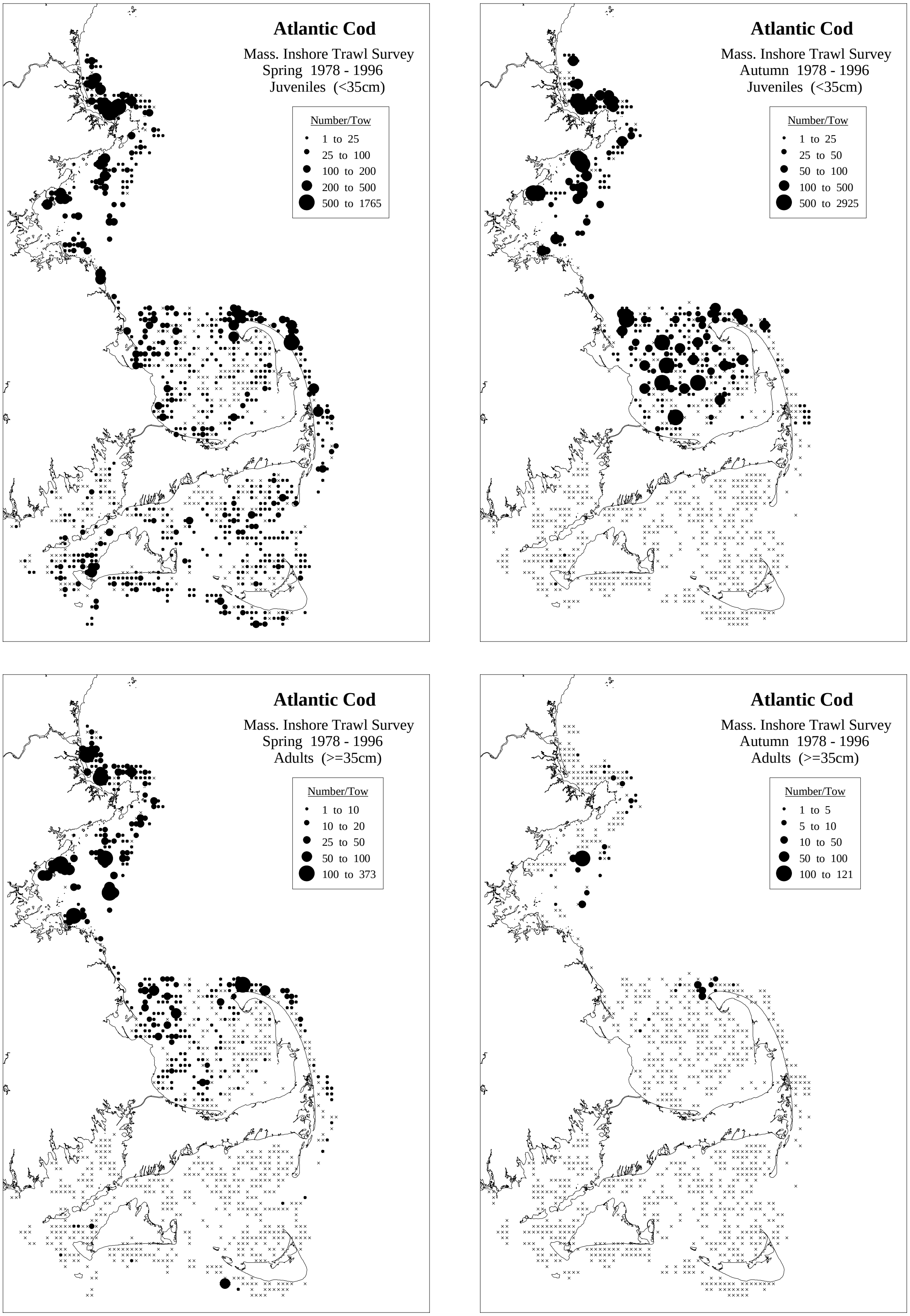

Figure 10. Distribution and abundance of juvenile (< 35 cm) and adult (≥ 35 cm) Atlantic cod collected during spring and autumn Massachusetts inshore bottom trawl surveys, 1978-1996 [see Reid *et al.* (1999) for details].

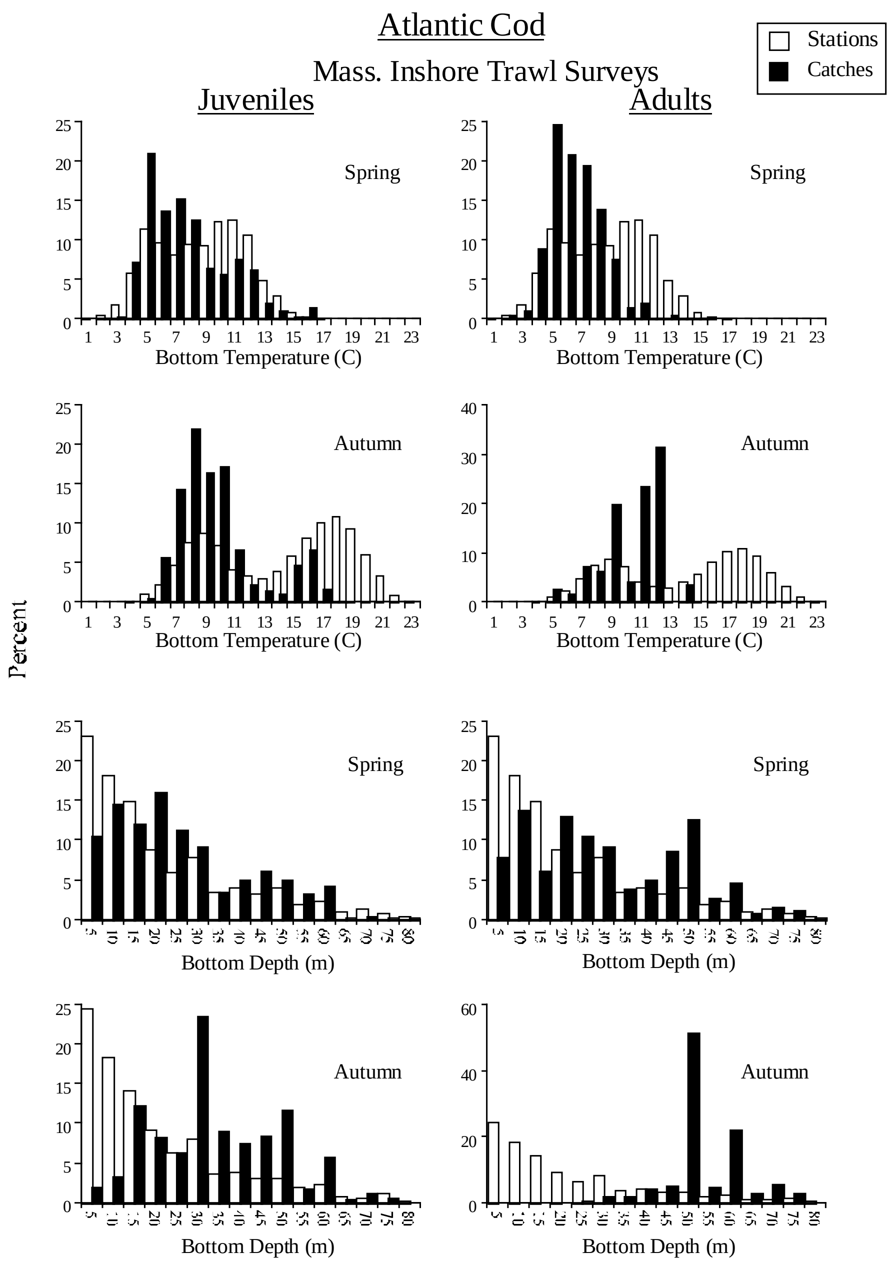

Figure 11. Distribution of juvenile and adult Atlantic cod in relation to bottom temperature and depth based on spring and autumn Massachusetts inshore bottom trawl surveys, 1978-1996. Open bars represent the proportion of all stations which were surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).

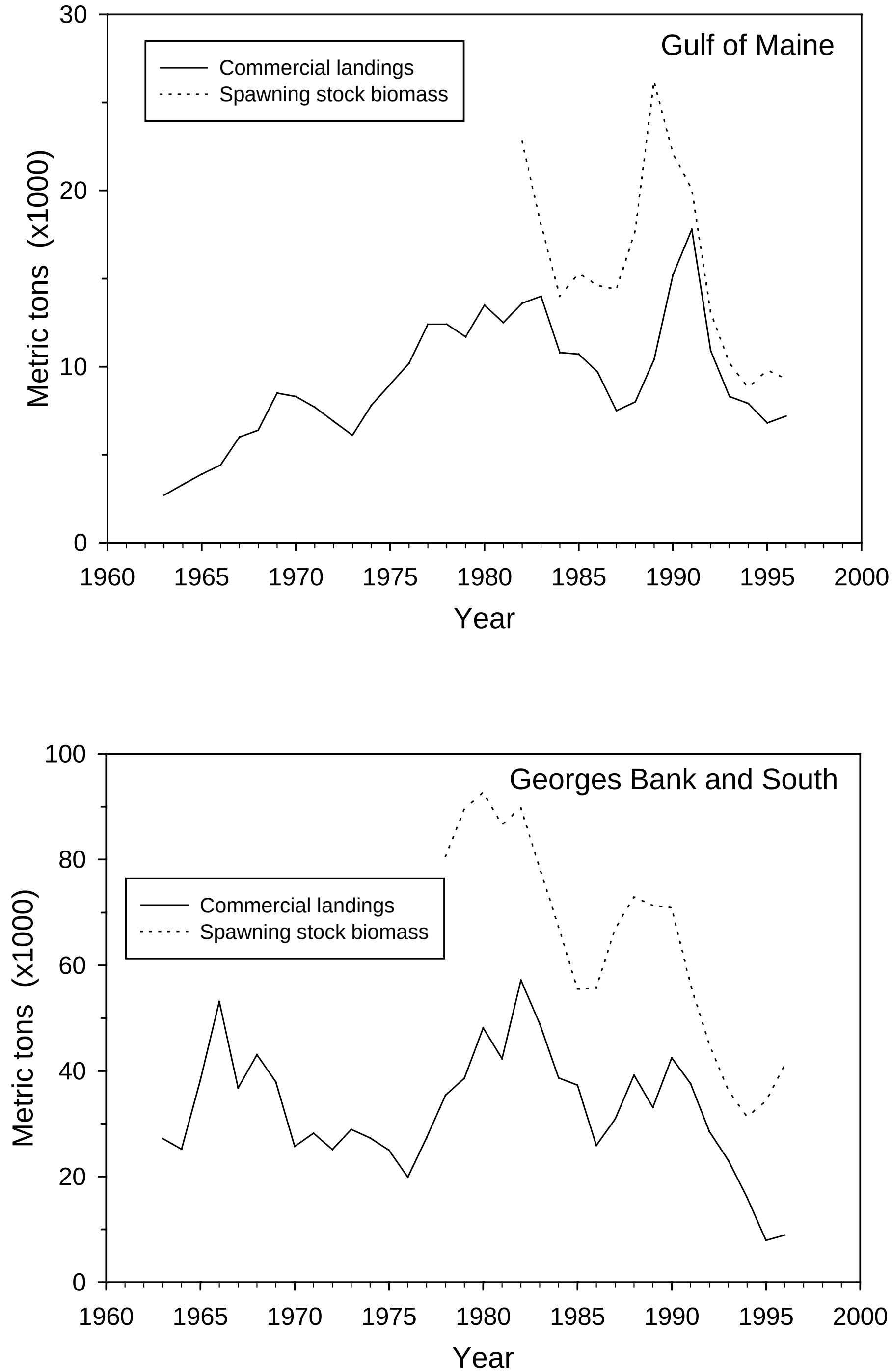

Figure 12. Annual commercial landings (including recreational catches) and estimates of spawning stock biomass (from the NEFSC bottom trawl surveys) for the Gulf of Maine and Georges Bank and south stocks of Atlantic cod.

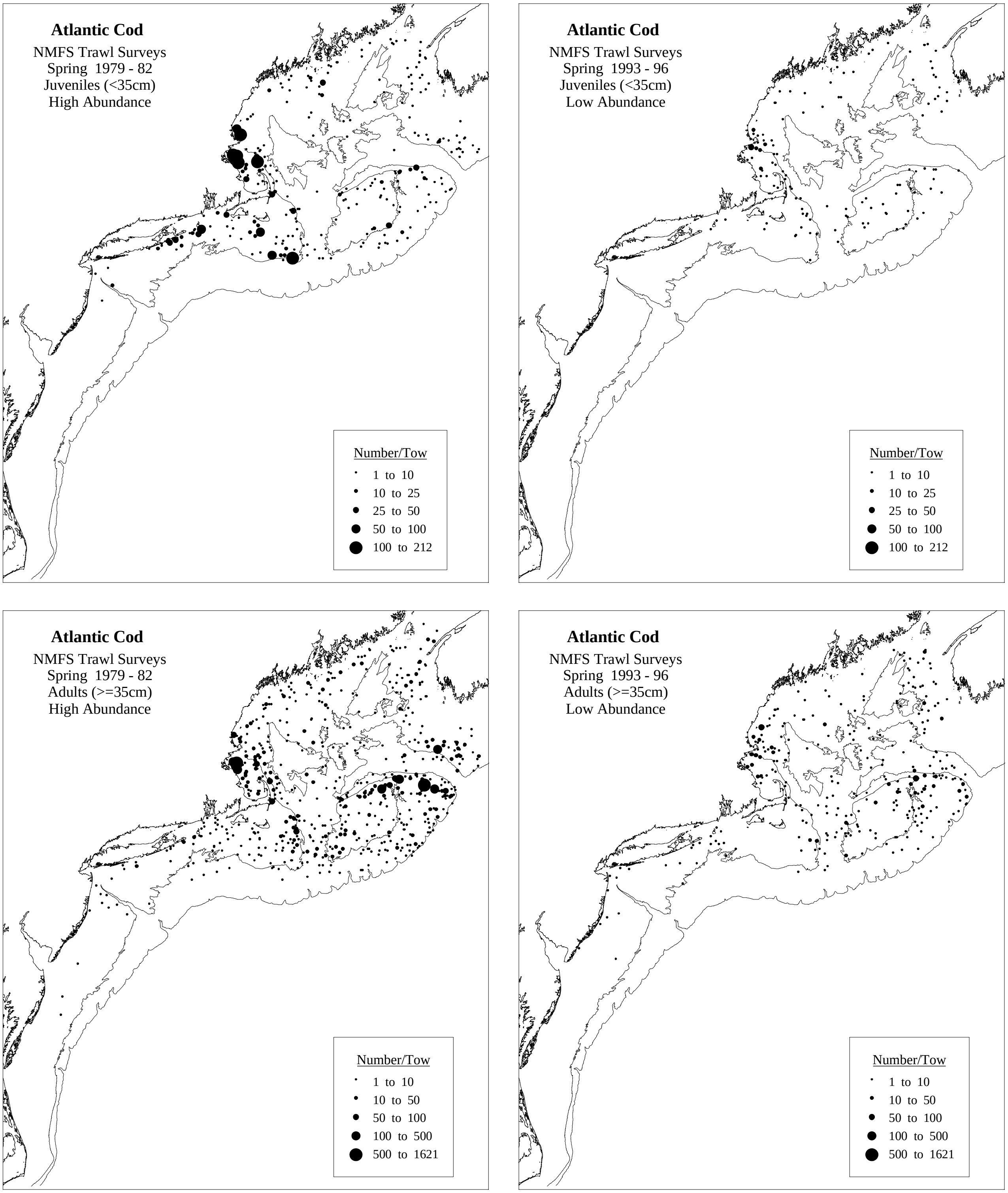

Figure 13. Distribution and abundance of juvenile (< 35 cm) and adult (≥ 35 cm) Atlantic cod during a period of relatively high abundance (1979-1982) and a period of relatively low abundance (1993-1996), from spring NEFSC bottom trawl surveys.

Appendix 1. Table of Habitat Parameters for Atlantic cod, *Gadus morhua*. This table is separated into four parts based on life history stage. "Present Study" refers to data presented herein. Abbreviations: GB = Georges Bank; GOM = Gulf of Maine; GOSL = Gulf of St. Lawrence; Mass Bay = Massachusetts Bay; Nfld. = Newfoundland; SNE = southern New England (Nantucket Shoals to Hudson Canyon); SS = Scotian Shelf.

SPAWNING/EGGS

Authors	**Study Area and Period**	**Habitat (Spatial and Temporal)**	**Temperature**	**Salinity**	**Currents/ Circulation**	**Light/Vertical**
Bigelow & Schroeder 1953	GOM	Pelagic. Spawn Mass Bay 3-10 miles from shore Nov-Apr.; Ipswich Bay Feb-May; West coast Maine Mar-May (into mid-summer). Also Isles of Shoals, Casco Bay, Sheepscot R. Always < 50 fm.	Bottom temps 0.6-8.9°C for spawning (2.2-5.6°C in Mass Bay). 5.0-8.3°C optimum for hatching. High mortalities at 0°C.	Sink in spring freshets	Drift southwest following coastline, 10-30 days	Near surface if salinities high
Hardy 1978	GB, GOM	Pelagic. Spawn in inlets, bays, harbors, coastal & offshore banks. Usually < 73 m.	0-6°C for spawning. 2.0-8.5°C optimum for incubation	Spawn salinity thru range: 10.0-35.5 ppt. Eggs sink in spring freshets. High mortality at low salinites (9.9-12.5 ppt)	---	Upper 10 m. Sink with age
Fish 1928	Mass Bay, SW GOM	Peak spawning, Mass Bay, January	10.1°C (Nov) to 0°C (January)	---	Advected out of Mass Bay by currents.	---
Bonnet 1939	Lab study	Ipswich Bay. Spawns at yearly minimum temp. (March)	0.5-3.0°C. 12°C upper limit for development	---	Eggs spawned in Ipswich bay would drift 120 miles before larvae settled to bottom	---
Colton 1978	GOM	Spawn Nantucket Shoals and Mass Bay, January-April (peak January). Also Georges and Browns banks, Ipswich Bay, SW GOM.	---	---	---	---
Cohen *et al.* 1990	North Atlantic	Most productive area in western North Atlantic is eastern half GB & Grand Banks, followed by SW GOM.	0-12°C with most 0-6°C. GOM stock spawns in colder water than others.	---	---	Spawn near bottom, unless temperatures unsuitable, then migrate into water column.
Rau 1974	Browns Bank, GB, Nantucket Shoals, Feb-Mar 1973	Most eggs found over central and northeast GB.	Most collected at 3-5°C	Most collected at 32-33 ppt	---	---
Anderson and de Young 1995	Northeastern Nfld. shelf	Studied vertical distribution and relative condition of eggs.	Temperature has effect on vertical distribution	Salinity (water density) has effect on vertical distribution	---	Eggs in poor condition found deeper in water column.
Miller *et al.* 1995	SS, October-May, 1991-1993	Peak spawn during fall.	Temperature (more than season) exerts most influence on egg size (and hatchling size).	---	---	---
Valerio *et al.* 1992	Nfld.	Studied freeze resistance of eggs & larvae. No antifreeze proteins detected.	If chorion intact, capable of undercooling to -4.0°C. Froze at -4.1 to -17.0°C.	---	---	---
Brander & Hurley 1992	SS	Spring spawning proceeds from SW to NE along shelf.	---	---	Spawning matches production of copepods.	---

Appendix 1. cont'd.

LARVAE

Authors	Study Area and Period	Habitat (Spatial and Temporal)	Temperature	Salinity	Currents/ Circulation	Light/ Vertical	Predators/ Prey (See Tables)
Rau 1974	Browns Bank, GB, Nantucket Shoals, Feb-Mar 1973	Most larvae (2-7 mm) between northeast GB and Nantucket Shoals.	Most collected 3-5°C	Most collected 32-33 ppt	---	---	---
Laurence 1978	Laboratory study	Growth rates increase with increasing temperatures.	4°C: 4.15%/d 7°C: 6.67%/d 10°C: 8.75%/d	---	---	---	---
Werner *et al.* 1993.	GB	Examined tidal currents, wind stress, Scotian Shelf inflow, advection and vertical distribution of larvae on Northeast Peak. Spawning shoalward of 50-m isobath enhances eventual retention of larvae on Georges Bank.	---	---	Larvae in surface layers subject to off-shelf advection via Ekman transport. Downwelling near shelf break allows larvae to avoid advection.	---	---
Suthers *et al.* 1989	SS	Recent growth in presumed inshore nursery area was less than in offshore waters, based on examination of birthdate distributions.	Temperature only rarely correlated with growth.	---	---	---	Growth rate strongly correlated with zooplankton biomass.
Perry & Neilson 1988	GB	Studied diel vertical distributions of cod and haddock late larvae in isothermal and stratified sites.	Thermocline may limit nightly upward migration.	---	---	Near bottom during day, in midwater at night. Migrations in reaction to light levels.	Late larval haddock did not change depth as much as cod larvae.
Myers & Drinkwater 1989	Middle Atlantic Bight, GB, Grand Banks	Examined effect of warm core ring activity on recruitment success in 17 groundfish stocks, 1973-1986.	---	---	Increased ring activity reduced recruitment in all stocks except GB cod.	Rings presumably entrained larvae of most stocks offshore.	---

Appendix 1. cont'd.

JUVENILES

Authors	Study Area and Period	Habitat (Spatial and Temporal)	Temperature	Salinity	Substrate/ Vegetation	Currents/ Circulation	Light/ Diel	Predators/ Prey
Gotceitas *et al.* 1994	Trinity Bay, Nfld. and laboratory studies, 1993	Nearshore bay, various substrates. July-mid-December.	---	---	Predator absent: preferred finer grains & avoided vegetation. Predator present: preferred cobble & hid in vegetation.	---	---	See Substrate/ Vegetation column
Gotceitas & Brown 1993	Laboratory Study	Studied substrate preference with and without a predator (e.g. a larger cod) present.	---	---	Cobble preferred over finer grained substrates when predator present. After predator leaves, larger juveniles return to fine grains, smaller remain in cobble.	---	---	Fewer juveniles succumb to predation in cobble than in finer grained substrates.
Hardy 1978	Northwest Atlantic	Coastal waters, rock pools, shallow inlets, river mouths, harbors. Leave coastal areas by mid-June (Massachusetts). 0+ average 35 m (range 8-42m); 1+ range 73-274 m.	Range 6-20°C	From < 31.3 to 35.0 ppt	---	---	---	---
Lough *et al.* 1989	GB	Descend to bottom @ 4-6 cm. 0+ (newly settled) fish dense on northeastern GB, 70-100 m depth, during summer.	---	---	Pebble-gravel deposit	Fall, transported southeast-ward by gyre	Migrate into lower water column at night to feed on inverte-brates	Coloration mimics substrate, reduces vulnerability to predation.
Tatyankin 1972	Barents Sea, 1967-1969 (laboratory study)	Determined preferred temperatures in gradient tank. In general, lower temperatures selected in winter, higher in summer. Older age classes preferred colder temperatures than younger.	Age 0+, summer: 7-11 °C. Age 1, winter: 3-6°C. Age 1+, fall: 5-8°C. Age 2, winter: 2-7°C	---	---	---	---	---

Appendix 1. cont'd.

JUVENILES

Authors	Study Area and Period	Habitat (Spatial and Temporal)	Temperature	Salinity	Substrate/ Vegetation	Currents/ Circulation	Light/ Diel	Predators/ Prey
MacDonald *et al.* 1984	Bay of Fundy and Passamaquoddy Bay	Juveniles in Passamaquoddy Bay in winter, close to beach in summer. (See "Adults")	0-6°C (winter); 8-13°C (summer)	30-31 ppt winter; 31-32 ppt summer	Mud, gravel, rock (winter); sand, mud, rock (summer)	---	---	---
Clark & Green 1990	Conception Bay, Nfld.	Studied diel, depth, seasonal movements in Broad Cove. Seasonal change in diel behavior due to disappearance of shallow (< 30m), summer thermocline.	Summer: day: 4.1-4.6°C; night: 10-12°C. Fall: stayed in warmer water.	---	Summer: wide-ranging (> 3km/day), between deep, cold & shallow, warmer water; Fall: small home ranges over sand in shallows; resting areas over rocks in shallows.	---	Summer: day, inactive; night, active. Fall: day, active; night, inactive.	Active periods coincide with feeding.
Keats *et al.* 1987	Conception Bay, Eastern Nfld.	Observations of juveniles in macroalgal habitat and adjacent sea-urchin dominated 'barrens'.	---	---	More abundant in macroalgal areas, used as cover, than in 'barrens'.	---	Diel not tested	Epiphytic food source not utilized.
Gotceitas *et al.* 1995	Nfld.	Studied reactions of 0+ cod to predator in combinations of substrates and artificial 'kelp'.	---	---	With no predator, 0+ prefer fine grain substrates, avoid 'kelp'. When predator present, 'kelp' provides protection from predation.	---	---	Juveniles select refuge type (cobble or 'kelp') when predator present.
Gotceitas *et al.* 1997	Nfld.	Studied vegetated and non-vegetated habitats, plus several bottom substrates with & without predator using SCUBA and seines.	---	---	Eelgrass used as nearshore nursery by 0+ cod. For refuge from predation & when combined with cobble, stem density was important.	---	---	Predator absent: 0+ used sand & gravel. Predator present: 0+ hid in cobble or eelgrass.

Appendix 1. cont'd.

JUVENILES

Authors	Study Area and Period	Habitat (Spatial and Temporal)	Temperature	Salinity	Substrate/ Vegetation	Currents/ Circulation	Light/ Diel	Predators/ Prey
Fraser *et al.* 1996	Laboratory Study	Studied interactions of 0+, 1+ and 3+ (predator) cod and their reactions to two different substrate types, sand/cobble & sand/gravel.	---	---	Some habitat segregation between Age 0+ and Age 1+, except when Age 3+ present, then both hid in cobble.	---	---	When predator present, 0+ and 1+ cod used same refuge (cobble).
Tupper & Boutilier 1995	St. Margaret's Bay, Nova Scotia	Studied survival and 0+ densities in 4 different bottom habitats (sand, seagrass, cobble, rock-reef).	---	---	Settlement equal among habitats, but subsequent densities highest in structurally complex habitat types.	---	---	Higher survival and densities appear to be related to shelter opportunities and reduced predation.
Keats 1990	Bonavista Bay, Nfld.	Examined diel depth distributions of juveniles.	---	---	---	---	Arrive in shallow water at dusk, remain until pre-dawn, then migrate into deeper water.	
Murawski & Finn 1988	GB	Evaluated species co-occurrences relative to temperature & depth preferences, spatial distribution by species & age. Overlap with silver hake, mostly in fall. See also "Adults"	YOY Means: winter: 2.9°C spring: 5.3°C summer: 9.9°C fall: 9.3°C	---	YOY Means: winter: 56 m spring: 60 m summer: 71 m fall: 71 m	---		---
Grant & Brown 1998a	Nfld.	Studied diel distribution in eelgrass habitat and diet differences between 0+ and 1+ cod.	---	---	After settlement in grass beds, Age 0+ change habits on diel basis.	---	Age 0+ in water column during day, disperse to bottom at night. Older yr. classes do opposite.	Age 0+ feed mostly on zooplankton during day; Age 1+ mostly on benthos and fish at night.
Grant & Brown 1998b	Nfld.	Studied encounters between just-settled juveniles and older cod (predators) in eelgrass and no-eelgrass habitats in Trinity Bay.	---	---	After settlement, juveniles display preference for eelgrass beds, but remain localized over grass and no-grass habitats for several weeks, perhaps through first winter.	---	Juveniles aggregate in grass beds during day, disperse at night. Different pattern by older cod results in reduced encounters.	Risk of cannibalism high in coastal habitats. Localized movements and preference for grass beds are mechanisms to avoid predation.

Appendix 1. cont'd.

ADULTS

Authors	Study Area and Period	Habitat (Spatial and Temporal)	Temperature	Salinity	Depth/ Substrate/ Vegetation	Currents/ Circulation	Light/ Diel/ Vertical	Predator/ Prey (See Tables)
Bigelow & Schroeder 1953	GOM	Non-migratory in GOM. Surface to 250 fm, but few > 100 fm. Most 5-75 fm. Usually within 1 fm of bottom. As shallow as 7 fm (summer), 3 fm (winter).	0-12.8°C. Prefer < 10.0 °C	---	Mostly rocky, pebbly, sandy or gravelly bottoms.	---	---	Large sharks and spiny dogfish.
Jean 1965	GOSL; SS	GOSL: 35-145 m (summer); 130-180 m (winter). SS: 65-110 m (summer); 90-135 m (winter).	GOSL: 0-6°C (summer); 1-3 °C (winter). SS: 1-8°C (summer); 2-4 °C (winter).	---	---	---	---	---
Odense *et al.* 1966	Bay of Chaleur (laboratory study)	Studied tolerance to low salinity	5-6°C (not manipulated)	First mortalities when reached 2.7 ppt; complete mortality at 2.3 ppt	---	---	---	---
MacDonald *et al.* 1984	Bay of Fundy and Passamaquoddy Bay	Adults in Passamaquoddy Bay summer, GOM, SS winter. (See "Juveniles")	8-13°C (summer); 4-8°C (winter)	31-32 ppt (summer); 31-32 ppt (winter)	Mud, rock (summer)	---	---	---
Scott 1982a	SS, Bay of Fundy	Determined preferred depths, temperatures & salinities for several groundfish species. Compared to other gadoids, cod prefers shallower, colder and less saline.	0-13°C (mean 4.9°C). Preferred temperature showed increase NE to SW, means 3.2 to 7.8°C.	31-34 ppt (mean 32.8 ppt)	27-366 + m, (mean 95 m). Preferred range 37-90 m.	---	---	---
Colvo-coresses and Musick 1984	Middle Atlantic Bight, continental shelf	Analyzed faunal associations, and zones occupied seasonally. Occurs with *Pseudo-pleuronectes americanus* and *Hemitripterus americanus*.	Boreal species, spring, < 10°C. "Relatively absent" during fall	---	< 100 m	---	---	---

Appendix 1. cont'd.

ADULTS

Authors	Study Area and Period	Habitat (Spatial and Temporal)	Temperature	Salinity	Depth/ Substrate/ Vegetation	Currents/ Circulation	Light/ Diel/ Vertical	Predators/ Prey (See Tables)
Tyler 1971	Passamaquoddy Bay, compared to bays south. Analyzed regular and periodic components in fish community.	Cod was member of 'regular' community (present throughout year), but most abundant March-April.	As annual temperature fluctuations increase (in southern bays), fewer 'regular' species.	29.5-29.6 ppt in Mar-Apr.; 32.3 ppt in September .	Sampled brown mud bottom, sloping from 38-55m.	---	---	---
Rose & Leggett 1988	GOSL	Onshore movements and inshore abundance of cod were affected by winds, upwellings, and downwellings.	Cod usually located where temps -0.5 to 8.5°C.	---	---	When alongshore winds create temperature changes, cod numbers decrease.	---	---
Rose & Leggett 1989	GOSL	Cod were aggregated within narrow temperature range, unless prey present, then found in wider range.	Without prey, usually between 0 & 5°C	---	---	---	---	When capelin present, range -0.5 to 8.5°C
Helser & Brodziak 1996	GOM, GB, SNE, Middle Atlantic Bight	Demonstrated seasonal differences in depth and bottom temperature preferences.	Spring: < 4.9 °C Fall: weaker association with temperatures	---	Spring: < 72 m Fall: weaker association with depth	---	---	---
Murawski & Finn 1988	GB	Evaluated species co-occurrences relative to temperature & depth preferences, spatial distribution by species & age. Overlap with silver hake, mostly in fall. Also see "Juveniles"	Age 1+ Means: winter: 4.2°C spring: 5.4°C summer: 8.0 °C fall: 9.3°C	---	Age 1+ Means: winter: 88 m spring: 67 m summer: 72 m fall: 84 m	---	---	---

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