NOAA Technical Memorandum NMFS-NE-190

Essential Fish Habitat Source Document:

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

Second Edition

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

November 2004

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This series represents a secondary level of scientific publishing. All issues employ thorough internal scientific review; some issues employ external scientific review. Reviews are -- by design -- transparent collegial reviews, not anonymous peer reviews. All issues may be cited in formal scientific communications.

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Second Edition

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

Editorial Production

For "Essential Fish Habitat Source Documents" issued in the *NOAA Technical Memorandum NMFS-NE* series, staff of the Northeast Fisheries Science Center's (NEFSC's) Ecosystems Processes Division largely assume the role of staff of the NEFSC's Editorial Office for technical and copy editing, type composition, and page layout. Other than the four covers (inside and outside, front and back) and first two preliminary pages, all preprinting editorial production is performed by, and all credit for such production rightfully belongs to, the staff of the Ecosystems Processes Division.

Internet Availability and Information Updating

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

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

Species Names

The NMFS Northeast Region's policy on the use of species names in all technical communications is generally to follow the American Fisheries Society's lists of scientific and common names for fishes (*i.e.*, Robins *et al.* 1991a[a], b[b]), mollusks (*i.e.*, Turgeon *et al.* 1998[c]), and decapod crustaceans (*i.e.*, Williams *et al.* 1989[d]), and to follow the Society for Marine Mammalogy's guidance on scientific and common names for marine mammals (*i.e.*, Rice 1998[e]). 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[f]; McEachran and Dunn 1998[g]).

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

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

[c]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.

[d]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.

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

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

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

PREFACE TO SECOND EDITION

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

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

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

NMFS Strategic Plan for Fisheries Research (February 1998)

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

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

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

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

The initial series of EFH species source documents were published in 1999 in the *NOAA Technical Memorandum NMFS-NE* series. Updating and review of the EFH components of the councils' Fishery Management Plans is required at least every 5 years by the NOAA Fisheries Guidelines for meeting the Sustainable Fisheries Act/EFH Final Rule. The second editions of these species source documents were written to provide the updated information needed to meet these requirements. The second editions provide new information on life history, geographic distribution, and habitat requirements via recent literature, research, and fishery surveys, and incorporate updated and revised maps and graphs. This second edition of the Atlantic cod EFH source document is based on the original by Michael P. Fahay, Peter L. Berrien, Donna L. Johnson, and Wallace W. Morse, with a foreword by Jeffrey N. Cross (Fahay *et al*. 1999).

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

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INTRODUCTION

The Atlantic cod (Figure 1) is a demersal gadoid distributed in the northwest Atlantic Ocean from Greenland to Cape Hatteras, North Carolina (Figure 2). 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. The Georges Bank cod stock is the most southerly cod stock in the world (Wise 1958). 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 areas. Cod 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°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. Fahay (NOAA Fisheries, NEFSC, James J. Howard Marine Sciences Laboratory, Highlands, NJ, pers. comm.) 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. 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°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, when 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); see also Amendment 13, Vol. II of the Multispecies FMP (NEFMC 2003). 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. This document examines dietary requirements and expands somewhat on spawning patterns, distributions and habitat characteristics of four life history stages (eggs, larvae, juveniles, adults).

This document is mostly concerned with the northwest Atlantic stocks. New research applications have involved the development of circulation models to simulate the potential transport pathways of eggs and larvae from spawning sites under realistic conditions, and the use of genetic markers to identify stocks and potential intermixing. Also, there is a considerable body of literature on hypotheses for the collapse of the northern Atlantic cod off Newfoundland by the early 1990's. While not immediately relevant to the Georges Bank/Gulf of Maine stocks, they explore the interplay of over-fishing and environmental change, the relative contributions of inshore and offshore stocks, and the causes and effects of the contraction of spawning stock. Since December 1994 there has been a year-round closure to commercial fishing of a large part of Georges Bank to rebuild the spawning stock. Fortunately, a major field program (U.S. GLOBEC) conducted monthly (January-July) ichthyoplankton surveys on Georges Bank from 1995 to 1999. The resulting cod egg and larval data are presented in the same format so that a comparison can be made with the prior Northeast Fisheries Science Center (NEFSC) Marine Resources Monitoring, Assessment and Prediction (MARMAP) ichthyoplankton survey data from 1977-1987.

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 typical 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

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 at depths between 50 and 100 m (e.g., Lough *et al.* 1989; Lough and Manning 2001). Larvae occur from near-surface to depths of 75 m, and larvae move deeper with growth (Hardy 1978; Lough and Potter 1993).

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). By the end of their first year, juvenile cod reach a mean length of 26 cm (Penttila and Gifford 1976).

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 and 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 and 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). As of 1994, in U.S. waters, sexual maturity was reached at ages between 1.7 and 2.3 years (median) and lengths between 32 and 41 cm (average) (O'Brien *et al.* 1993). Presently (2000-2002), age and length at maturity have increased slightly for both Georges Bank and Gulf of Maine stocks (O'Brien 1999). Age and length at 50% maturity for Georges Bank and Gulf of Maine stocks are shown in Table 1. Gulf of Maine cod attain sexual maturity at a later age than Georges Bank cod which is related to differences in growth rates between the two stocks. The recently developed maturation reaction-norm analyses (Barot *et al*. 2004a, b) also indicated a shift towards lower ages and sizes of maturation for Georges Bank and Gulf of Maine cod stocks. The trend for Georges Bank cod to mature earlier than the Gulf of Maine cod was thought to be due mostly to environmental differences. Georges Bank is a highly productive and warmer shallow bank compared to the deeper Gulf of Maine. The reaction-norm approach supports the hypothesis that the Georges Bank and Gulf of Maine cod stocks have changed genetically in response to fishing.

On Georges Bank, an analysis of the MARMAP ichthyoplankton 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 (Colton *et al.* 1979; Page *et al.* 1998). 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. Historically, cod have spawned on both eastern and western Georges Bank. During the MARMAP period (1978-1987), spawning could either be split between eastern and western Georges Bank, or occur predominantly on one side or the other (Lough *et al.* 2002). Composite egg distributions indicate that the most intense spawning activity occurs on the Northeast Peak of Georges Bank (Page *et al.* 1998). Data from the more recent U.S. GLOBEC Georges Bank surveys (1995-1999) also indicated peak spawning occurs during the February-March period and mostly on the Northeast Peak (Mountain *et al*. 2003). 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). Within the Gulf of Maine, cod generally spawn throughout the winter and early spring in most locations, but the period of peak spawning varies depending on location (Schroeder 1930). In general, spawning occurs later in the year in the more northerly regions. Within Massachusetts Bay, Fish (1928) reported peak spawning activity during January and February. Bigelow and Welsh (1924) noted that north of Cape Ann, Massachusetts, most spawning occurred between February and April and further north, between Cape Elizabeth and Mt. Desert Island, Maine, the peak spawning period was between March and May. It has also been noted that cod spawning occurs mostly at night and may be crepuscular (Klein-MacPhee 2002). 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°C (Elliott *et al.* 1979).

Hanke *et al*. (2000) recently summarized all the available ichthyoplankton survey data from the Scotian Shelf, eastern Gulf of Maine, and the Bay of Fundy region, from 1975-1997, and provided evidence for a spring and fall spawning, but with regional differences. In March-April spawning was observed off southwestern Nova Scotia including Browns Bank, Georges Bank, and the Emerald/Western/Sable Island Bank area. Spawning occurs again in November and December on Georges Bank and the entire Nova Scotia coast, west of Grand Manan and on Western/Sable Island/ Banquereau Bank.

Ames (2004) characterized the Gulf of Maine historical Atlantic cod fishing and spawning grounds during the 1920's when stocks were high, compared with our present day knowledge. Four subpopulations were identified: Bay of Fundy, Downeast, Midcoast, and Western, each with 3-6 spawning components. Inshore cod feeding grounds were generally rocky bottoms along the 100 m isobath. Spawning occurred in channels and basins bordering the rocky, shallow, historic fishing grounds. Compared with recent survey data of cod eggs (Berrien and Sibunka 1999), it appears that more than half of the historic spawning grounds are inactive and show no evidence of spawning. Ames cites three factors that contributed to the collapse of the spawning components: (1) directed fishing with otter trawls and gillnets on coastal spawning aggregations, (2) pollution of coastal nursery grounds, and (3) destruction of anadromous forage stock by the construction of dams.

FOOD HABITS

The Atlantic cod has a varied diet. Reported food items vary by life history stage and study area (Table 2). The most frequently observed food items from the 1973-2001 NEFSC food habits database [see Link and Almeida (2000) for details on methodology] for cod ≤ 50 cm were crustaceans; cod ≥ 51 cm ate mostly fishes (Table 3;Figure 3). A comprehensive analysis and summary of cod trophic patterns on the northeastern U.S. continental shelf has been made by Link and Garrison (2002) based on a 25-year time series from the NEFSC food habits database. Early juveniles consumed more pelagic than benthic invertebrates, medium cod consumed benthic invertebrates and fish, and larger cod consumed larger amounts of fish. Cannibalism increased with size. Diets shifted significantly over 3 decades concurrent with shifts in forage species. Cod are opportunistic feeders, preferring sand lance, *Cancer* crabs, and herring.

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.* 1997).

PREDATION AND MORTALITY

Yolk sac larvae are vulnerable to zooplankton predators including *Aurelia, Thysanoessa*, and *Euchaeta* (Bailey 1984). Planktivorous fish can be important predators of larval fish, especially Atlantic herring and Atlantic mackerel as they migrate northward in the spring and overlap with patches of larvae on the southern flank of Georges Bank (Garrison *et al*. 2000). Juvenile cod are preyed upon by many piscivorous fish, such as dogfish, silver hake, larger cod, and sculpin (Edwards and Bowman 1979).

Because of their large size, adults 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.

MIGRATION

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°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 stock, and the Georges Bank and southward stock (Mayo 1995). The inshore Gulf of Maine stock appears to be relatively distinct from the offshore cod stocks on the banks of the Scotian Shelf and Georges Bank based on tagging studies (McKenzie 1956; Wise 1963; Hunt *et al*. 1999) and parasitic copepods (Sherman and Wise 1961). Although there is some mixing of the Gulf of Maine and Georges Bank stocks, their life history parameters, growth, and maturity, are basically different (Pentilla and Gifford 1976, Serchuck *et al*. 1994, O'Brien 1999). Part of the difference in growth between stocks may be attributed to genetic variations (Imsland and Jónsdóttir 2003). General conclusions by Imsland and Jónsdóttir (2003) from basin-scale genetic studies suggest that distinct subpopulations occur between most inshore and offshore areas, and among offshore areas themselves, and that the likelihood of inshore spawning stock contributing to offshore recovery is low (Beacham *et al*. 2002). Recent genetic studies by Lage *et al*. (2004) suggest that Nantucket Shoals cod are distinct from Georges Bank cod. Whereas Lage *et al*. (2004) did not find any significant genetic differences between Georges Bank and Browns Bank, Ruzzante *et al*. (1998) did. The degree of stock separation may be related to the isolation of spawning locations and times, and different circulation patterns. On Georges Bank, a clockwise gyre circulation pattern tends to retain and isolate the eggs and larvae spawned there (Lough and Bolz 1989; Werner *et al*. 1993; Lough and Manning 2001). Model simulations by Page *et al*. (1999) suggest that cod spawning occurs in areas and times of the year that have the longest residence times (> 35 days). However, advective losses can occur sporadically off the northeast peak and southern flank of Georges Bank (Lough *et al*. 1994). While significant numbers of larvae can be advected across the Great South Channel to Nantucket shoals, the southwest residual flow in the Nantucket Shoals area would tend to keep the early life stages from returning to Georges Bank. However, based on biophysical modeling of a related species, haddock, by Brickman (2003), there is a high probability of significant crossover events from Browns Bank to Georges Bank by two pathways, directly across the Northeast Channel, and from the Gulf of Maine. While crossover events are episodic in nature (Smith *et al*. 2003), the study indicates that Browns Bank can be a significant source of larvae for Georges Bank cod stocks, and similarly, Western Bank can be an upstream source for larvae found on Browns Bank.

GEOGRAPHICAL DISTRIBUTION

Atlantic cod in the northwest Atlantic are distributed from Cape Chidley, Labrador to Cape Henry, VA (Figure 4). 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 4. 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 indicators 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 5) 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 5). Monthly densities peaked 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.

Model simulations for the MARMAP years (Lough *et al*. 2002) show how variable spawning within a bank gyre system can have different consequences for transport and survival of eggs and larvae. Particles released from the Northeast Peak usually had higher retention than releases from western Georges Bank; however, the western Georges Bank releases could contribute significantly to retention, especially during the winter period when there is wind loss of particles from the Northeast Peak.

O'Brien *et al*. (2003) found a significant correlation between egg abundance and spawning stock biomass for Georges Bank cod. While there was considerable variability in egg survival that was unrelated to recruitment, there was a strong positive correlation between the abundance of small and large larvae and 0-group juveniles and that of recruits at age 1 (Lough *et al.* 2002). Variability in egg survival could be explained partially by the age diversity of repeat spawners, bottom temperature, and the spatial distribution of the eggs (O'Brien *et al*. 2003). The proportion of egg mortality that can be attributed to egg quality, advective loss, or predation has not been quantified.

During the GLOBEC years, 1995-1999, when sampling was only conducted from January through July on Georges Bank, the composite egg plots (Figure 6) show eggs to be broadly distributed across Georges Bank with higher concentrations on the eastern part, peaking in February and March. However, the station abundance estimates were about an order of magnitude lower than during the MARMAP period.

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 7), although sampling was light during March in the Gulf of Maine. Few larvae were collected between August and October.

During the GLOBEC years, 1995-1999, when sampling was only conducted from January through July on Georges Bank, the composite larval plots (Figure 8) show larvae to be wide spread across the Bank from January through May. Highest station abundance occurred along the deeper flank waters during March and April, but at about an order of magnitude lower than observed during the MARMAP period.

Prior to settling to the bottom in early summer, pelagic juveniles (20-50 mm) are broadly distributed over the entire Georges Bank (Lough *et al*. 1989).

JUVENILES

By July, juvenile pelagic fish on Georges Bank have reached a length of 4-6 cm and become more associated with the bottom and begin the changeover to a demersal feeding life style. Submersible studies on eastern Georges Bank (Lough *et al*. 1989) have observed from data collected during five years (1984-1987, 1989) that the recently-settled juveniles are widely dispersed over the Bank and are present on a range of sediment types from sand to gravelly sand to gravel pavement (Figure 9). However, by late July and August, the juveniles are present predominantly on the gravel pavement habitat on the northeastern part of the Bank and are absent from the sandy bottoms (Figure 10). The gravel pavement extends along the northern edge and Northeast Peak for 150 km and covers an area of more than 3000 km^2. The gravel habitat appears to favor the survival of recently-settled juveniles through predator avoidance and/or increased food availability associated with the frontal system. Several studies have stressed the importance of cobble substrates over finer grained bottoms after settlement (e.g., Bigelow and Schroeder 1953; Colton 1978; Klein-MacPhee 2002). By day, the young cod remain on the bottom, but at night they rise several meters into the water column and drift in the tidal current while feeding. During late summer, as the juveniles continue to grow, they are carried to the east and southeast in the residual bottom current, and by fall they are more widely dispersed and are no longer confined to the gravel pavement habitat. When predators are present, juvenile cod take refuge in a wide variety of complex substrates and vegetation and their diel activity patterns reported in the literature vary considerably (Keats *et al*. 1987; Keats 1990; Keats and Steele 1992; Gotceitas and Brown 1993; Gotceitas *et al*. 1994, 1995, 1997; Gregory and Anderson 1997a, b; Grant and Brown 1998a, b; Lindholm *et al*. 1999; Laurel *et al*. 2003, 2004). Nearshore nurseries (including grass beds) may be significantly more important to survival of juveniles than offshore habitats (for examples, see studies cited in Appendix 1: Juveniles).

The distribution of older juveniles (≤ 34 cm TL) from the NEFSC bottom trawl surveys closely matches that of spawning activity, with centers of abundance on Georges Bank and the western part of the Gulf of Maine [Figure 11; note that winter and summer distributions are presented as presence data only, precluding a discussion of abundances, for details see Reid *et al*. (1999). Also see the distribution of immature Atlantic cod, < 37 cm, resulting from NEFSC bottom trawl survey cruises, 1968-1986 in Wigley and Gabriel (1991)]. In winter they are concentrated near Massachusetts Bay, on the Northeast Peak of Georges Bank, and in southern New England near the 50 m isobath. During spring trawl surveys, densities are highest in the area north and south of Cape Ann, Massachusetts. During summer, juveniles are mostly found along the western shore of the Gulf of Maine, but also occur on the Northeast Peak of Georges Bank, on Browns Bank, and along the 50 m isobath south of Cape Cod. Large numbers of juveniles are concentrated around Cape Ann/Massachusetts Bay and south/southeast of Cape Cod in the fall.

The distributions and abundances of Atlantic cod along the coasts of Maine and New Hampshire, based on spring and fall 2000-2004 Maine-New Hampshire inshore groundfish surveys (Sherman *et al*. 2005), are shown in Figure 12. Cod were patchy in occurrence, and the majority were juveniles (Figure 13). Cod abundance was low compared to some of the other species in the survey, with a slight increase in numbers in the spring of 2004 (Figure 14), although Sherman *et al*. (2005) state that no real trends can be seen in overall abundance.

The spring and fall 1978-2003 Massachusetts inshore trawl surveys [Figure 15; see Reid *et al*. (1999) for details] show that in the spring, very high numbers are found in Massachusetts Bay, with large numbers of juveniles also found north of Cape Ann, on the outside of Cape Cod, and near Martha's Vineyard. High concentrations are also found in Massachusetts Bay and Nantucket Sound. In the fall, large numbers occur around Cape Ann and throughout Cape Cod Bay, but they are absent in Nantucket Sound.

Very few juvenile cod were collected during 1990-1996 trawl surveys of Narragansett Bay undertaken by the Rhode Island Division of Fish and Wildlife. See below for cod occurrences in Long Island Sound and Hudson-Raritan Estuary/Sandy Hook Bay.

ADULTS

NEFSC bottom trawl surveys (Figure 16; again, winter and summer distributions are presented as presence data only, precluding a discussion of abundances) show that during winter adults are scattered over Georges Bank, southern New England, and the central/northern Mid-Atlantic Bight, as well as in the western part of the Gulf of Maine. In spring, densities are highest in the western part of the Gulf of Maine (Massachusetts Bay and Cape Ann), south of Cape Cod, and especially on the Northeast Peak of Georges Bank, with additional collections made throughout southern New England and the central/northern part of the nearshore Middle Atlantic Bight. During summer, adult cod are concentrated along the coastal Gulf of Maine and south/southeast of Cape Cod and the Northeast Peak of Georges Bank, as well as being scattered throughout the Gulf and on Browns Banks; they are mostly absent from southern New England and south. In the fall, the highest densities are again found in the western part of the Gulf of Maine (Massachusetts Bay and Cape Ann), south of Cape Cod near the Great South Channel, and on the Northeast Peak/northern edge of Georges Bank; adults are generally absent south of southern New England.

The distributions of the adults in both the spring and fall 1978-2003 Massachusetts inshore trawl surveys are shown in Figure 17. More adults are caught in the spring, where they occur abundantly around Cape Ann, in Massachusetts Bay, and around the tip and eastern side of Cape Cod. Most of the adults caught during the fall are restricted to south of Cape Ann and the tip of Cape Cod.

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°C. A NEFSC trawl survey of the Hudson-Raritan Estuary/Sandy Hook Bay during 1992-1997 collected only two cod, both during winter.

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 some of those data are presented in Table 5. These tables include data from U.S. (and certain non-U.S.) western Atlantic stocks, but exclude 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, distributions of young stages of Atlantic cod tend to be restricted to the vicinity of 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).

Regime shifts, or rapid, large-scale changes in fish populations and other communities in marine ecosystems, are driven by both environmental forcing and fishing (Rothschild and Shannon 2004). Latitudinal shifts for groundfish in the Gulf of Maine have been observed in response to temperature changes (Mountain and Murawski 1992). Growth of cod depends on temperature, and mean bottom temperature accounts for most of the observed differences in growth rates in Atlantic cod stocks (Brander 1995). Physiologically, growth performance of cod is optimal near 10°C (Pörtner *et al*. 2001), so that global warming would lead to a northward shift in populations. Temperature also affects maturation and spawning times (Hutchings and Myers 1994). Changes in spawning times and locations have different consequences for recruitment. Temperature and salinity records for the Gulf of Maine/Scotian Shelf region show alternating cold and warm periods which can be broadly related to the NAO index (Werner *et al*. 1999). The cooling of the shelf waters in the 1960s was largely due to the increased flow of the Labrador Slope water penetrating into the shelf. From the 1970s to the mid-1990s, there has been a general, but more variable, warming on the shelf. Scotian Shelf cold and warm anomalies generally precede those in Georges Bank by 2-3 years. More recently in 1997-1998, cold and fresh Labrador Slope water has been observed to again be penetrating the Scotian Shelf and Gulf of Maine. All cod stocks in this region declined by the late 1960s with the intensive fishery effort, and in the 1970s all stocks showed some improved recruitment, but declined to very low levels in the early 1990s. Failure of these cod stocks to recover despite restricted fishing since the mid-1990s has been termed “the cod recruitment dilemma” and Swain and Sinclair (2000) have implicated the increased abundance of herring and mackerel in the southern Gulf of St. Lawrence to have had a negative effect on cod recruitment by preying on and competing with the young stages. Choi *et al*. (2004) continues on the theme of the alternation of the pelagic and demersal species but shows how interacting factors may have led to the restructuring of the Scotian Shelf ecosystem over the past four decades. While ground fish have historically dominated the Scotian Shelf, their continual removal has allowed the pelagic biomass to increase since the mid-1980s at the same time that environmental conditions began to favor the pelagics (increased water-column stratification) and limit the demersals (cold bottom water). The present “pelagic regime” appears to have decoupled the benthic-pelagic systems where less energy is passing from primary production to benthic prey for the demersals.

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; see also Figure 18). 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 5).

Data from the NEFSC MARMAP ichthyoplankton surveys and the GLOBEC Georges Bank survey were used to determine the relationships between cod egg abundances and bottom depth or water column temperature. During the MARMAP surveys from January to July, eggs were mostly collected at temperatures of 4-8°C (Figure 18). From August thru November, they were found at higher temperatures of approximately 9-14°C, while in December they were caught at temperature range of 6-12°C. Most eggs were found over a depth range of 30-110 m, occurring in the shallower end of the range from October thru January (Figure 18). During the GLOBEC Georges Bank survey from January to July, the majority of eggs were found in a narrow temperature range of about 4-8°C (Figure 19). Their depth range on Georges Bank during that same period was centered around 70-90 m (Figure 20).

A lab study by Laurence and Rogers (1976) found that egg mortality was independent of temperature, but that mortality increased at lower salinities within the range of 26-36 ppt.

LARVAE AND PELAGIC JUVENILES

Several studies have found increased recruitment success when dispersion of larvae from spawning areas by currents is reduced (Cong *et al.* 1996). Although larvae have been collected from a wide range of temperatures, most are found in temperatures < 8°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°C but if in direct contact with ice they froze at -1.36°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, Lough and Potter 1993).

During the MARMAP surveys (Figure 21), larvae were mostly found in a temperature range of about 4-5°C from February to March, at temperatures of 5-6°C in April, 6-8°C in May, and 7-9°C in June, and 8-9°C in July. Thereafter they were found in increasingly warmer temperatures of about 9-11°C thru November; in December they were caught mostly at temperatures of 8-11°C and in January they were found in lower temperatures of about 4-8°C. The majority of larvae were found over a depth range of 30-70 m throughout the MARMAP survey period (Figure 21). During the GLOBEC Georges Bank survey most larvae were caught at temperatures of 4-6°C from February to April and 6-7°C from May to June (Figure 22). Most were found at depths of 50-70 m in February, 70-90 m in March and April, 70 m in May, and 210 m in June (Figure 23).

JUVENILES

The substrate preferences of juvenile cod have already been discussed under Geographic Distribution.

The spring and fall distributions of juvenile Atlantic cod relative to bottom water temperature, depth, and salinity based on NEFSC bottom trawl surveys from the Gulf of Maine to Cape Hatteras are shown in Figure 24. In spring, they were found in waters between 2-10ºC, with the majority at 4-5ºC. During that season they were found over a depth range of 11-300 m, with most spread between about 21-120 m. Juveniles were found at salinities between 31-35 ppt, with almost all of them found between 32-33 ppt. During autumn, juveniles were found over a temperature range of 3-17°C, with most spread between about 8-10°C. During this time, they were found over depths ranging from 11-400 m; the majority were spread over depths roughly from 31-120 m. They were found at salinities ranging from about 31-35 ppt, with the majority between 32-33 ppt.

The spring and autumn distributions of juvenile Atlantic cod in Massachusetts coastal waters relative to bottom water temperature and depth based on Massachusetts inshore trawl surveys are shown in Figure 25. During the spring, juveniles were found in waters ranging from 2-16°C with the majority spread between about 5-12ºC. Their depth range was from 6-85 m, with the majority between about 6-25 m. In the autumn they were found in temperatures ranging from 5-18ºC, with most spread between 6-10ºC. Juveniles were found over a depth range of 6-85 m, with the majority found between about 16-65 m.

ADULTS

Adult cod are typically found on or near the 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 (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).

The spring and fall distributions of adult Atlantic cod relative to bottom water temperature, depth, and salinity based on NEFSC bottom trawl surveys from the Gulf of Maine to Cape Hatteras are shown in Figure 26. In spring, they were found in waters between 2-12ºC, with the majority at 4-6ºC. They were found over a depth range of 1-300 m. Adults were found at salinities between 30-35 ppt, with > 50% at 33 ppt. During autumn, adults were found over a temperature range of 3-17°C, with the majority spread between 6-11°C. During this season they were found over depths ranging from 11-400 m. They were found at salinities ranging from about 31-35 ppt, with the majority between 32-34 ppt.

The spring and autumn distributions of adult Atlantic cod in Massachusetts coastal waters relative to bottom water temperature and depth based on Massachusetts inshore trawl surveys are shown in Figure 27. During the spring, adults were found in waters ranging from 1-14°C, with the majority spread between 4-8ºC. Their depth range was from 6-85 m, with the majority < 56 m. In the autumn they were found in temperatures ranging from 4-13ºC, with most spread between 7-10ºC and at 12ºC. Adults were found over a depth range of 26-85 m, with peaks between 51-65 m.

RESEARCH NEEDS

Essential fish habitat is defined as those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity. 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.* 1997) 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). However, recent studies have documented regime shifts on decadal time scales over large areas of the continental shelf as a result of complex interaction of environmental factors and biological processes. Ecosystem based studies such as Choi *et al*. (2004), with continued monitoring of the environment, are needed to better understand the long-term changes in stocks.

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Table 1. Age and length at 50% maturity for two stocks of Atlantic cod, *Gadus morhua*..
Data for 1994 are from Mayo (1995). Similar results were obtained in a Canadian study for zones near U.S. waters (Trippel *et al.* 1997). Recent data are from L. O'Brien, (NOAA Fisheries, NEFSC, Woods Hole Laboratory, Woods Hole, MA, pers.comm.), pooled for the period 2000-2002.

1994	**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

2000-2002	**Georges Bank**	**Georges Bank**	**Gulf of Maine**	**Gulf of Maine**
	Males	Females	Males	Females
Age at 50% Maturity	2.1 years	2.1years	2.9 years	2.6 years
Length at 50% Maturity	42.2 cm	43.3cm	44.0 cm	43.3 cm

Table 2. Food habits of Atlantic cod.

Source	Study Area and Food Habits
	LARVAE
Bainbridge and McKay (1968)	Greenland: Larvae (3-10 mm) mostly eat nauplii and copepodites of the copepods *Calanus* and *Temora*. Also euphausiids.
Kane (1984)	Georges Bank: Larvae eat nauplii and copepodites of *Pseudocalanus* mostly; some *Calanus* eggs and nauplii.; some *Oithona* copepodites.
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.
McLaren and Avendano (1995)	Scotian Shelf (Western Bank): Larvae predominant prey: 2 species of the copepod *Pseudocalanus*.
McLaren *et al*. (1997)	Scotian Shelf (Western Bank): Early larvae feed predominantly on nauplii and copepodites of *Pseudocalanus* (mostly *P. newmani*); fewer *Centropages*, *Oithona,* and *Paracalanus*.
Lough and Mountain (1996)	Georges Bank: Primarily nauplii and copepodites of *Pseudocalanus* and *Oithona*; some *Calanus* nauplii.
Lough *et al*. (1996)	Georges Bank: Early larvae prey on nauplii and copepodites of *Pseudocalanus*.
Sherman *et al*. (1981)	Georges Bank: Larvae eat nauplii and copepodites of *Pseudocalanus* mostly; some *Calanus* nauplii.
	JUVENILES AND ADULTS
Bowman (1975)	Gulf of Maine: Primary item: herring. Also redfish, mackerel, cod, and red and rock crabs.
Bigelow and Schroeder (1953); Klein-MacPhee 2002	Gulf of Maine: Mollusks most important. Also other invertebrates.
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 are juvenile redfish (*Sebastes* sp.). Rate of cannibalism very low.
Hacunda (1981)	Central Maine coast: Crustaceans most important, especially amphipods, *Unciola, Leptocheirus*, and decapods *Crangon, Cancer*.
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.
Keats and Steele (1992)	Newfoundland (eastern): Juveniles (Age 0 and 1) feed mostly during daylight and most prey was planktonic.
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.
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*).
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.

Table 2 Cont'd.

Source	Study Area and Food Habits
	JUVENILES AND ADULTS (cont'd.)
Lilly and Parsons (1991)	Northeast Newfoundland: Northern shrimp (*Pandalus borealis*) identified as important food item of cod throughout shrimp's range.
Link and Garrison (2002)	Northeast U.S. Continental Shelf: Summary of 25 year time series of food habits data. Cod have omnivorous diet, prefer sand lance, *Cancer* crabs, and herring.
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.
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 American plaice.
Perry and Neilson (1988)	Georges Bank: Late pelagic juveniles. Calanoid copepods numerically most abundant, mysiid *Neomysis americana* biomass most important; harpacticoid *Tisb*e, some *Pagurus* larvae.
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.
Sameoto *et al*. (1994)	Scotian Shelf: Late pelagic juveniles. *C. finmarchicus* copepodite IV-V, *Pseudocalanus* female, and *Temora* male preferred prey. (Emerald and Lahave Basin). Small euphausiids (*Meganytiphanes norvegica*) significant part of diet at night, 20 m.
Tyler (1972)	Passamaquoddy Bay: Winter - *Meganyctiphones, Mysis, Pandalus*; summer - *Meganyctiphones, Clupea, Pandalus.*
Whitehead *et al.* (1986)	Northeastern Atlantic: Diet variable: fishes - herring, capelin, haddock, codling; invertebrates - euphausiids, hyperiids, amphipods, polychaetes.
Witman and Sebens (1992)	Gulf of Maine: Cod fed heavily on tethered brittle stars in this experiment.

Table 3. Minor diet items of Atlantic cod.
Based on the NEFSC Food Habits database from 1973-1990. Listed below are items occurring at 1-5 percent frequency. See Figure 3 for items occurring more frequently. Methods for sampling, processing, and analysis of samples differed between the time periods [see Reid *et al.* (1999) for details].

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		

Table 3 Cont'd.

1973-1980: Diet Item	Percent Frequency	1981-1990: Diet Item	Percent Frequency
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. Distribution of life history stages of Atlantic cod 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 from Jury *et al.* (1994) and 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

Table 5. Summary of life history and habitat parameters for Atlantic cod.
Based partially on data contained in Appendix 1, Table of Habitat Parameters. This table is the same as that in the first Atlantic cod EFH source document (Fahay *et al*. 1999); more recent studies were reviewed (see Appendix 1), but no new information of relevance to this table was found.

Life History Stage	Spatial and Temporal Distribution	Temperature	Salinity	Depth/ Substrate/ Vegetation	Diel/ Light/ Vertical	Predator/ Prey
Eggs [1]	Pelagic. Bays, harbors, offshore banks. Spawning begins in fall, peaks winter and spring.	Most 2.0-8.5°C for incubation. 12.0°C upper limit. Mortality independent of temperature.	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 in winter-spring, 7-12°C in summer-fall.	Most 32-33 ppt.	--	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, during summer. Deeper water in winter.	6-20°C. More tolerant of extremes than adults. Temperature 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, northeast 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).

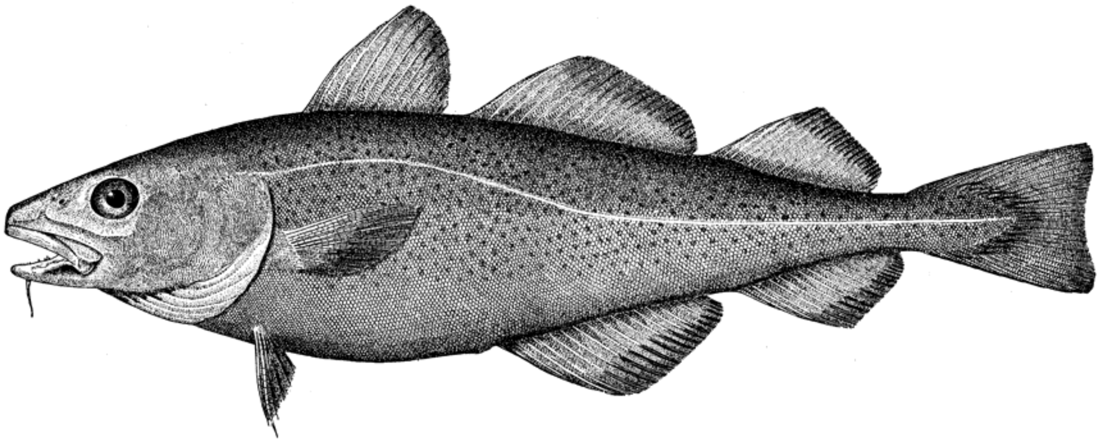
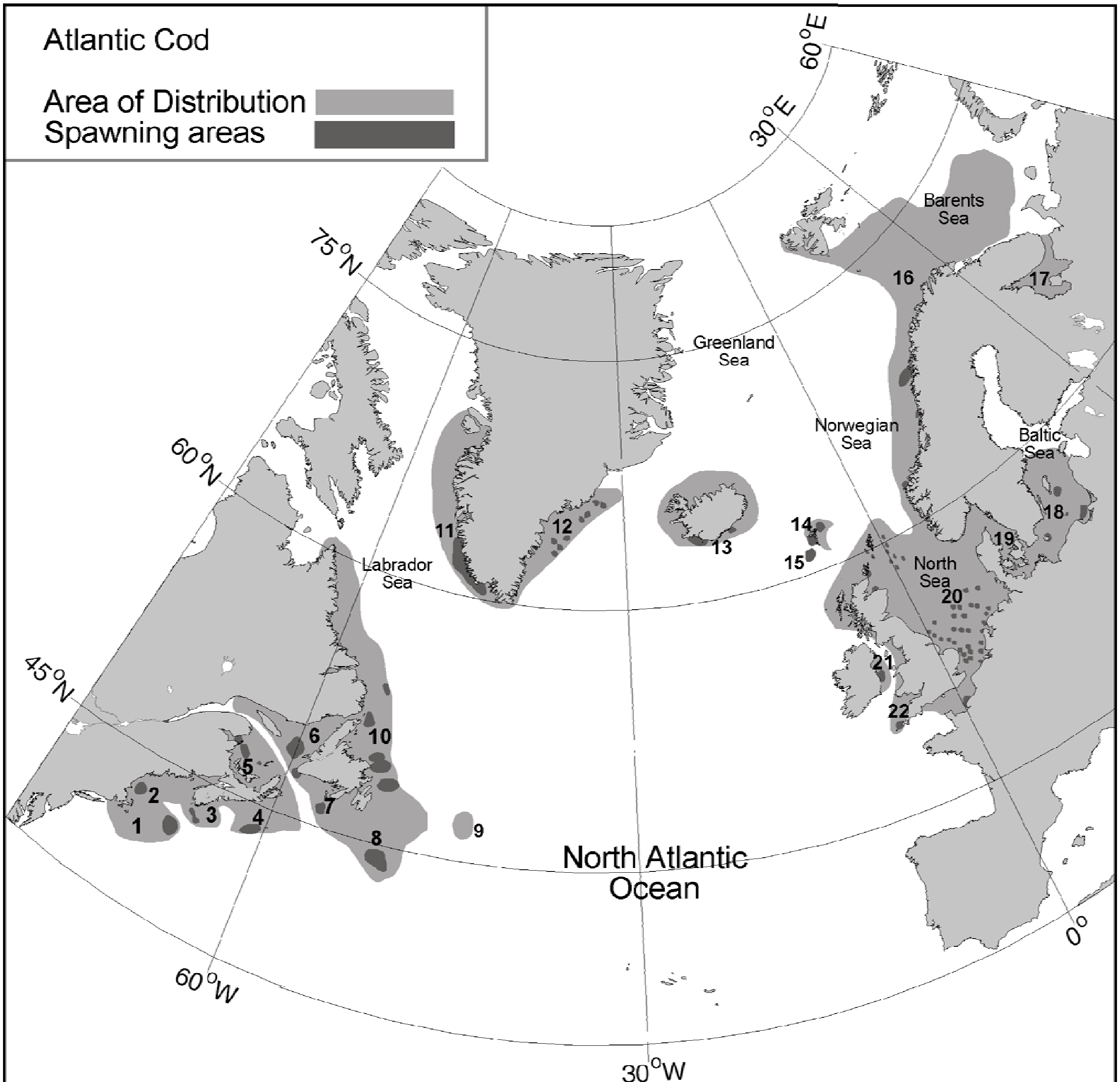


Figure 1. The Atlantic cod, *Gadus morhua* (from Goode 1884).



1 Georges Bank	9 Flemish Cap	16 North East Arctic
2 Gulf of Maine	10 Northern Newfoundland / Southern Labrador	17 White Sea
3 Western Scotian Shelf	11 West Greenland	18 Baltic Sea
4 Eastern Scotian Shelf	12 East Greenland	19 Kattegat
5 Southern Gulf of St. Lawrence	13 Iceland	20 North Sea-West Scotland -English Channel
6 Northern Gulf of St. Lawrence	14 Faroe Plateau	21 Irish Sea
7 Southern Newfoundland	15 Faroe Bank	22 Celtic Sea
8 Grand Bank		

Figure 2. Distribution of Atlantic cod stocks in the North Atlantic showing principle spawning sites.
Source: Brander (1994).

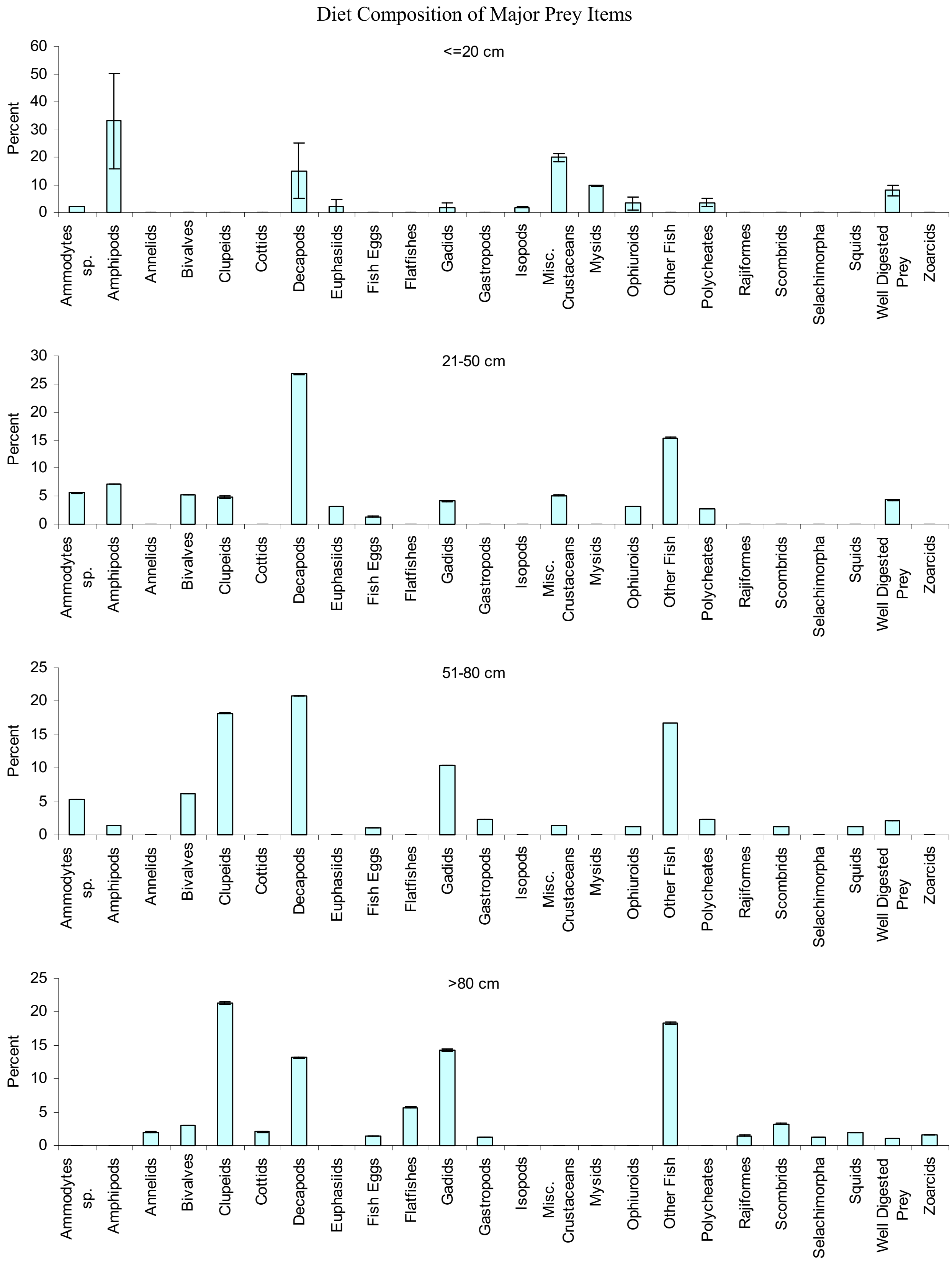
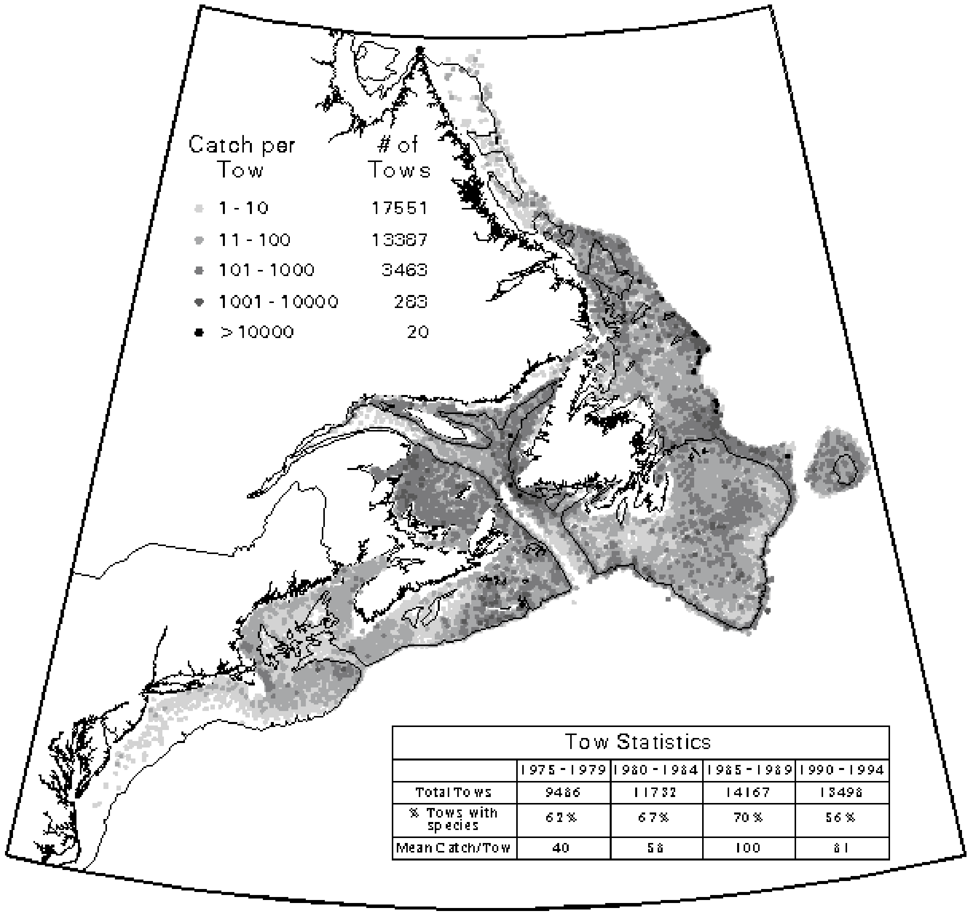


Figure 3. Percent by weight of the major prey items in the diet of three size categories of Atlantic cod.
From specimens collected during NEFSC bottom trawl surveys from 1973-2001 (all seasons). For details on NEFSC diet analysis, see Link and Almeida (2000).



Tow Statistics				
	1975 - 1979	1980 - 1984	1985 - 1989	1990 - 1994
Total Tows	9486	11732	14167	13498
% Tows with species	62%	67%	70%	56%
Mean Catch/Tow	40	58	100	81

Figure 4. Overall distribution and abundance of Atlantic cod in the northwest Atlantic Ocean. 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).

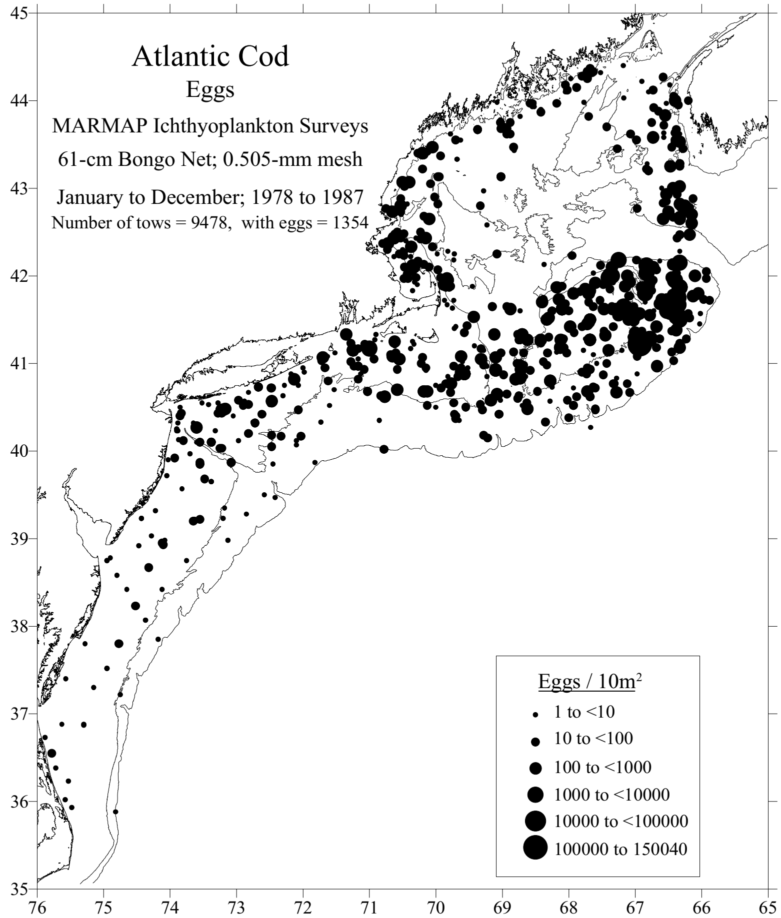


Figure 5. Distributions and abundances of Atlantic cod eggs collected during NEFSC MARMAP ichthyoplankton surveys.
For all available months and years from 1978 to 1987 combined.

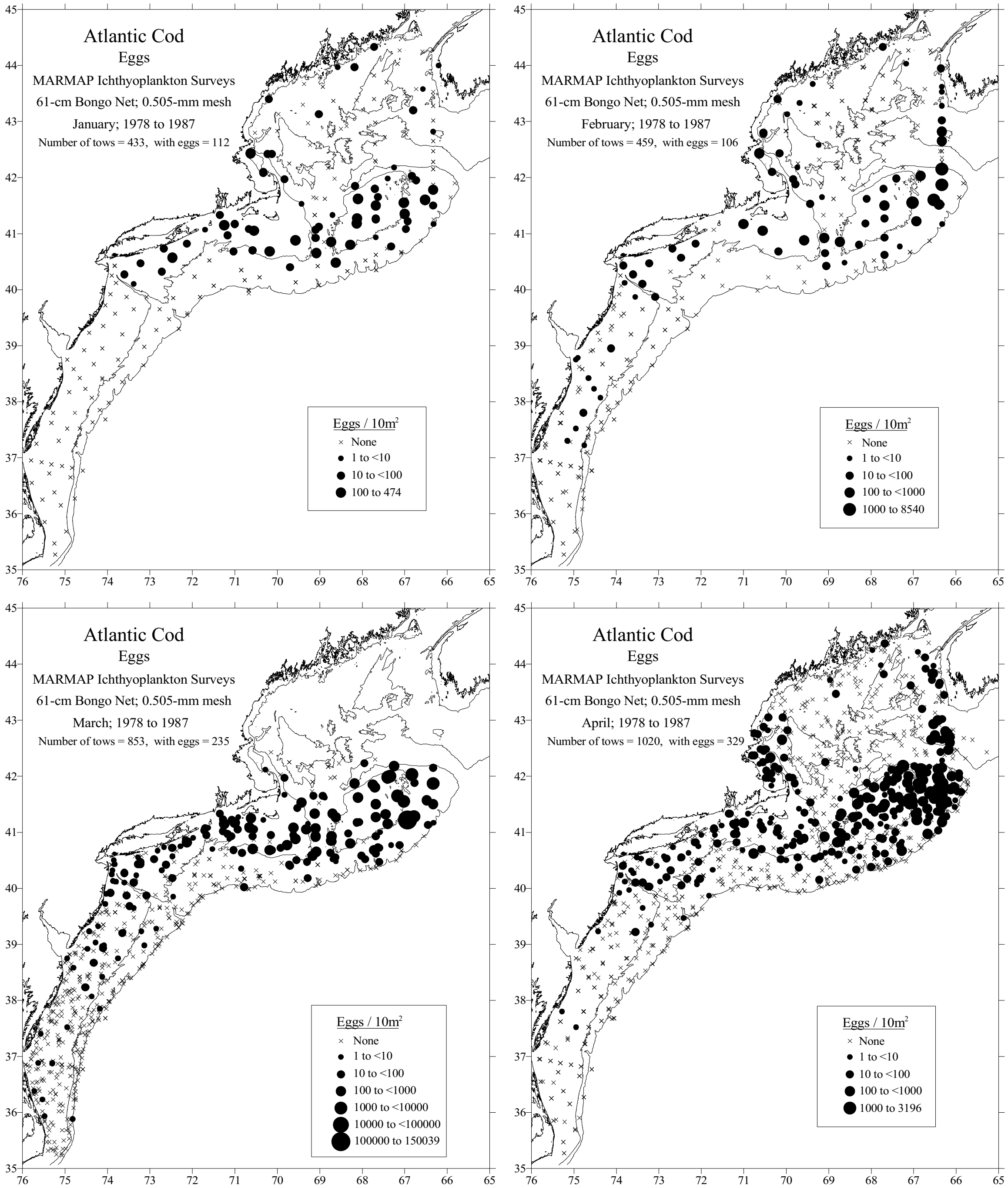
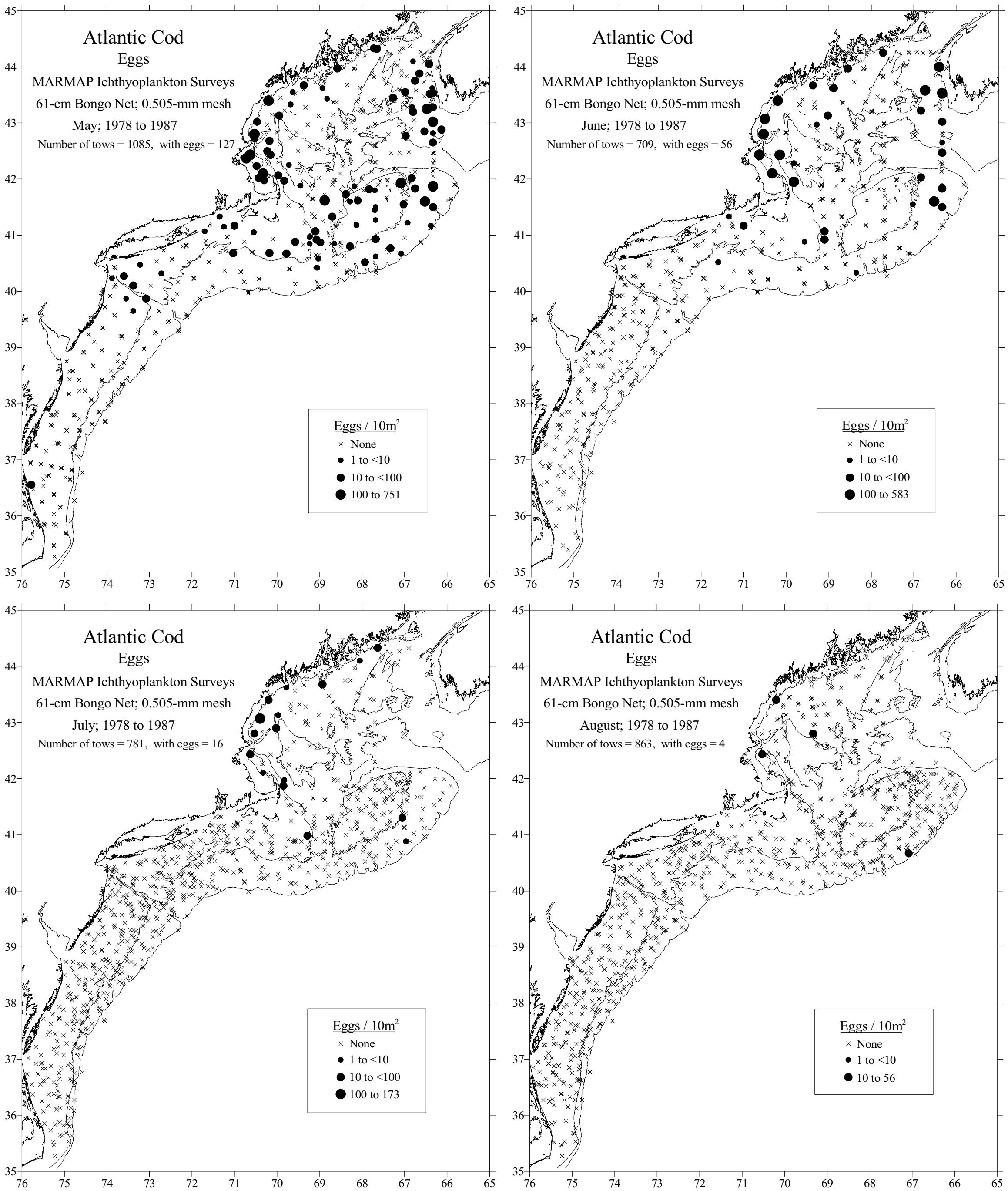


Figure 5. Cont'd.
From MARMAP ichthyoplankton surveys, January through April, 1978-1987.



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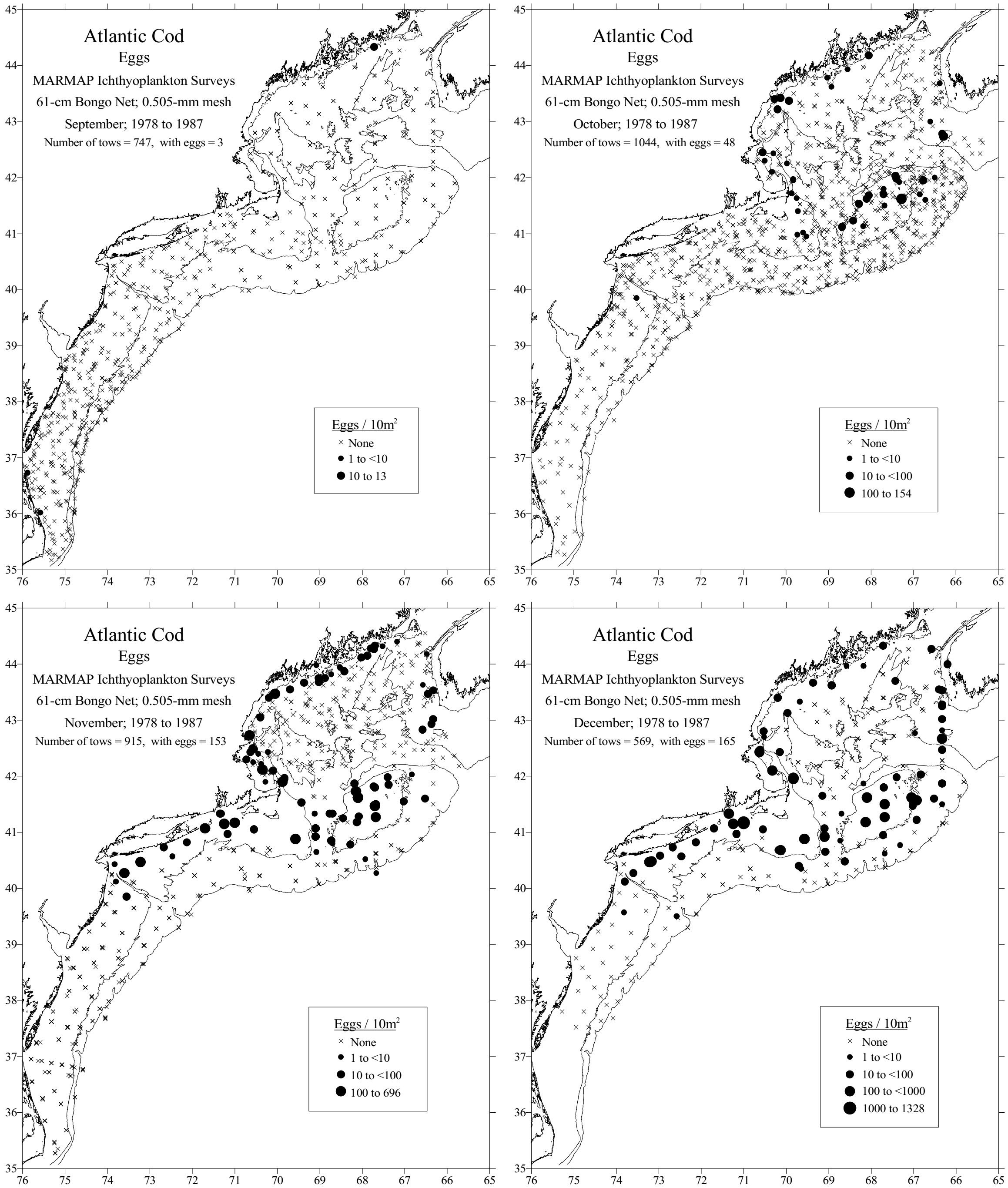
From MARMAP ichthyoplankton surveys, May through August, 1978-1987.



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From MARMAP ichthyoplankton surveys, September through December, 1978-1987

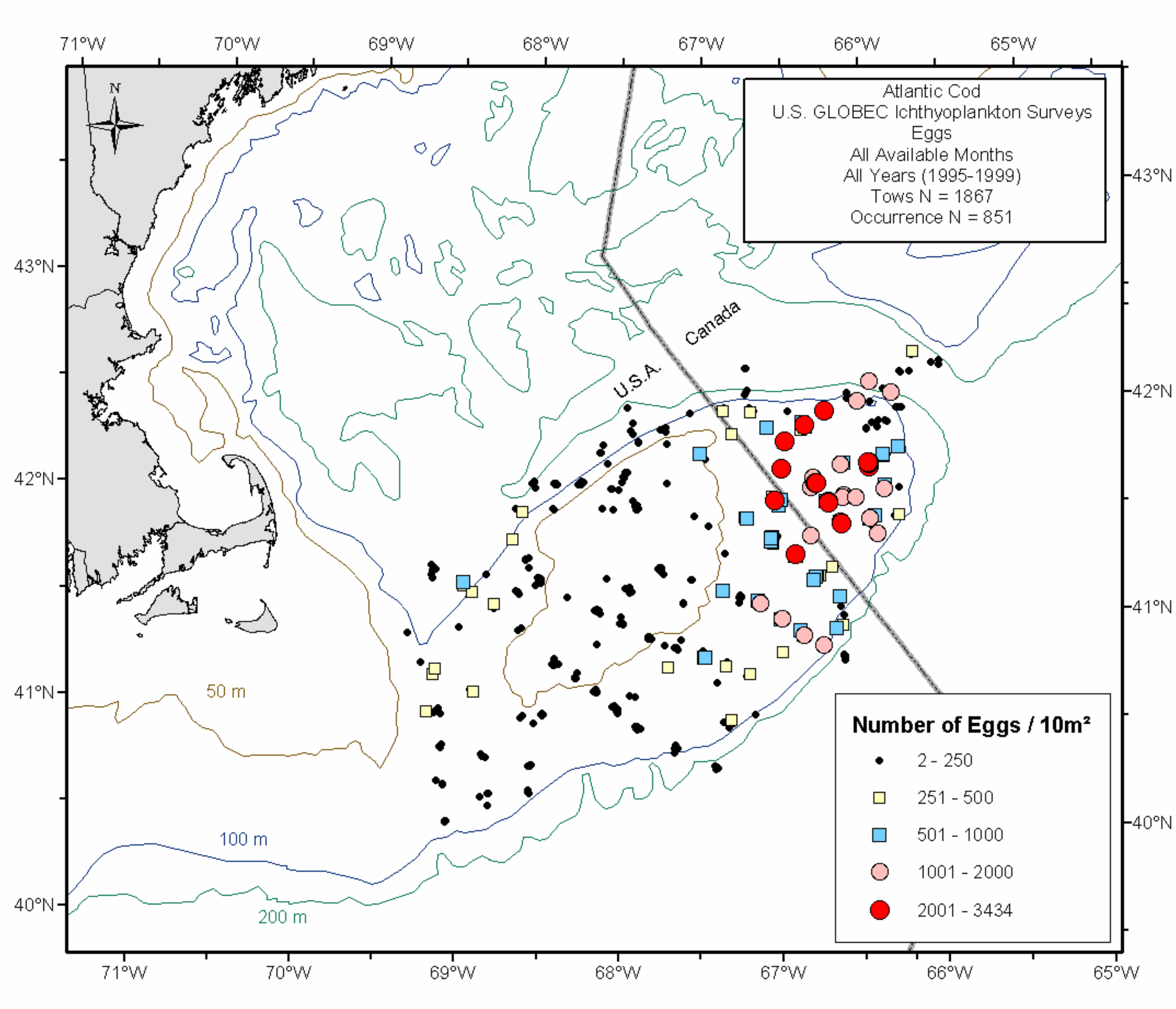
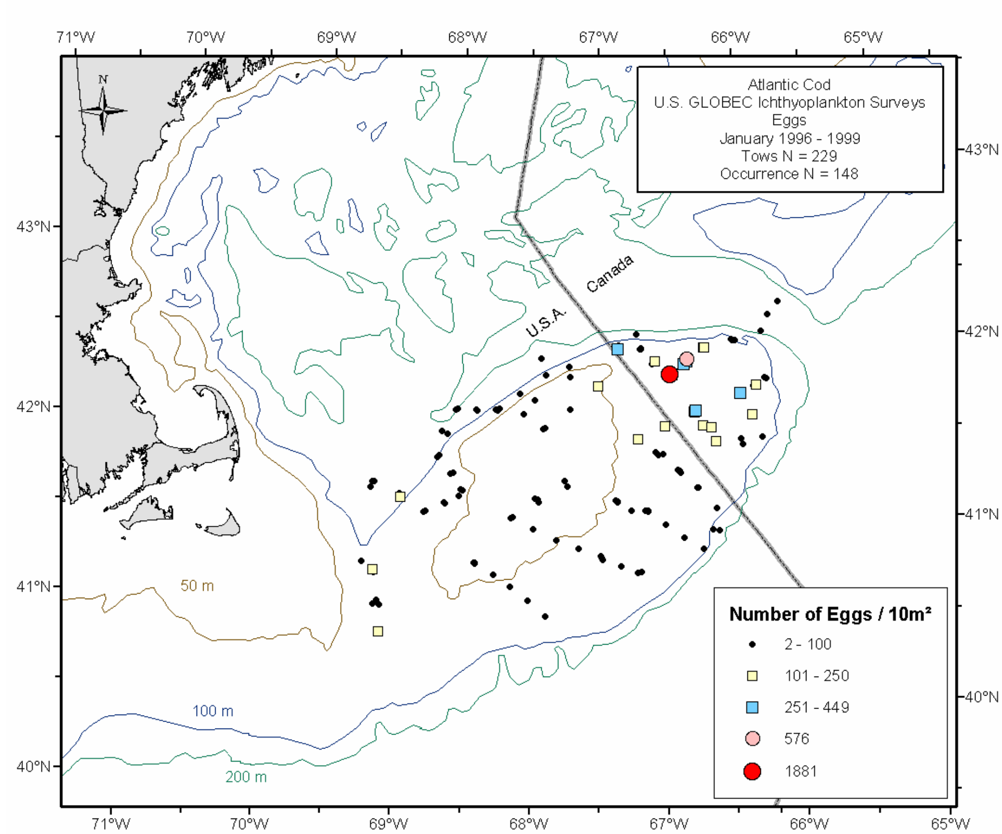


Figure 6. Distributions and abundances of Atlantic cod eggs collected during GLOBEC Georges Bank ichthyoplankton surveys.
For all available years (February-July, 1995; January-June, 1996-1999) combined.



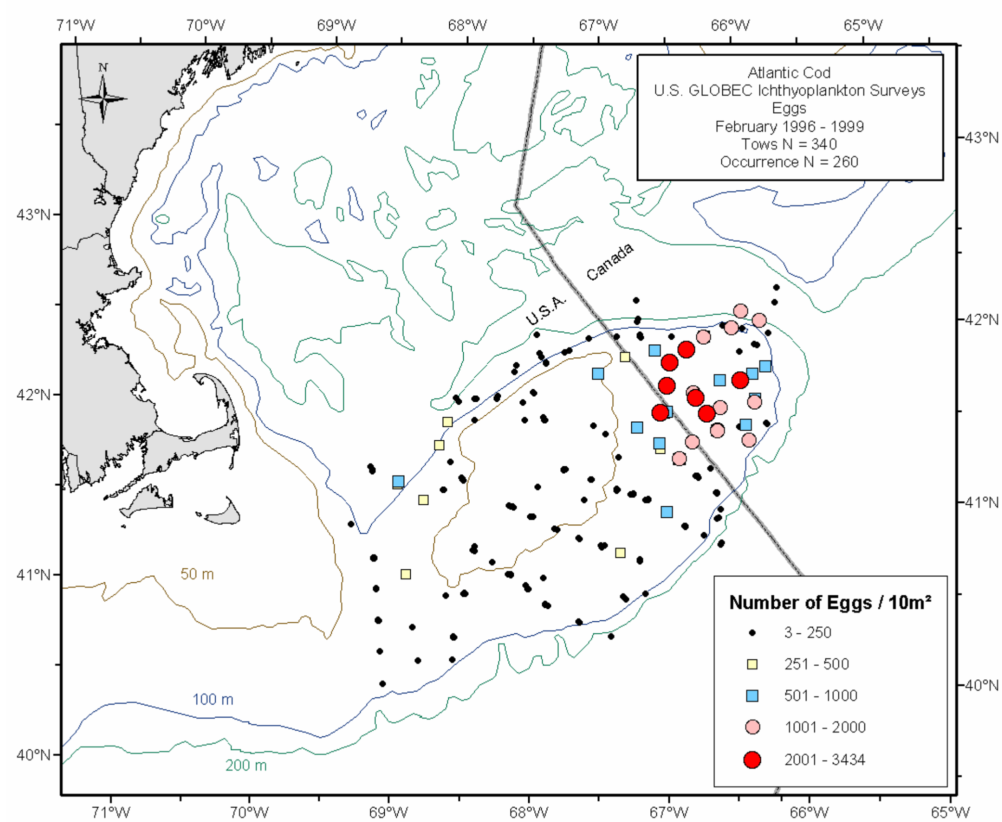
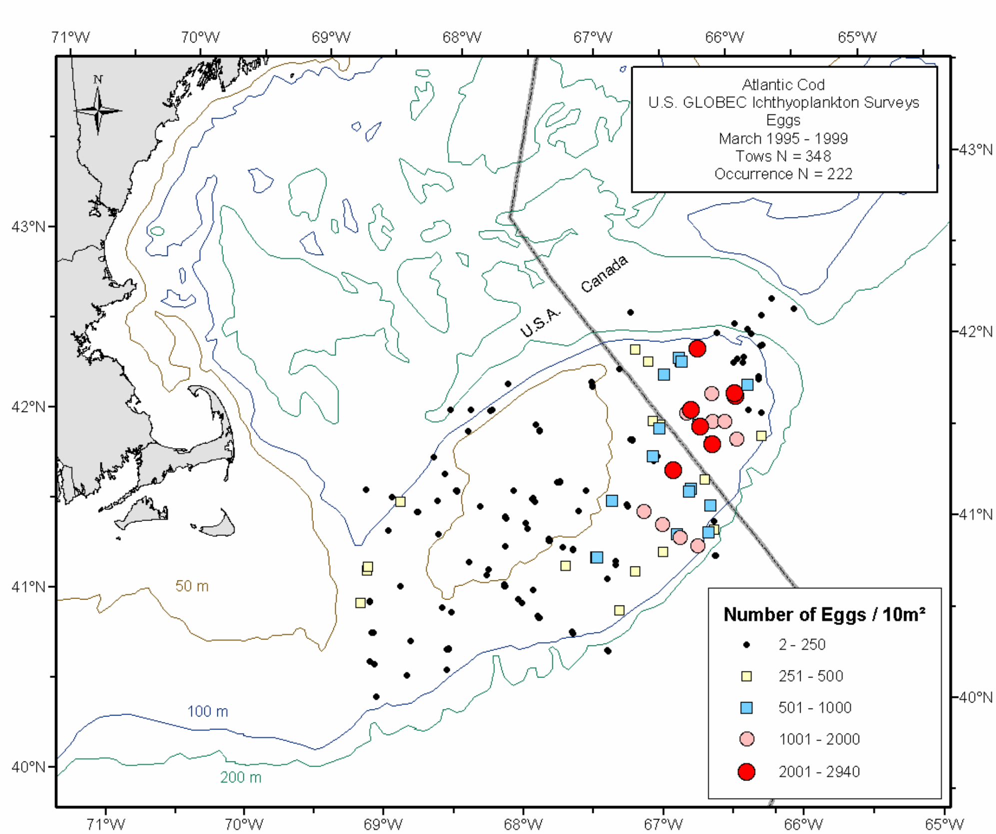


Figure 6. Cont'd.
From GLOBEC ichthyoplankton surveys, January and February, for all available years combined.



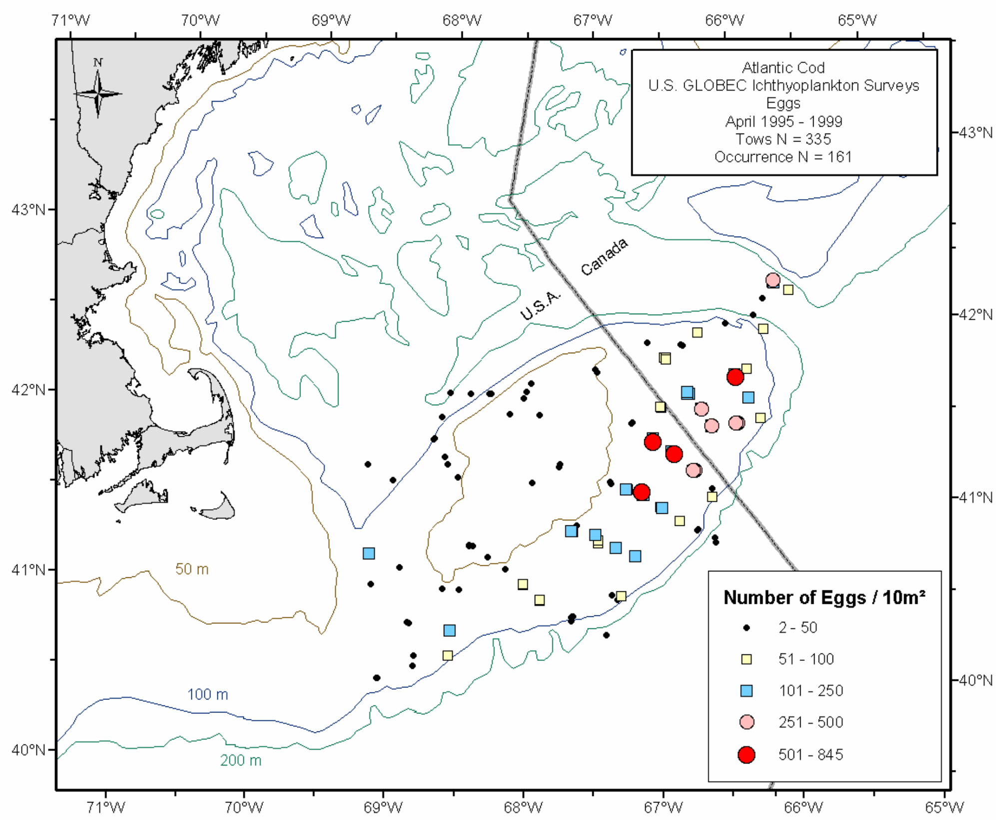


Figure 6. Cont'd.
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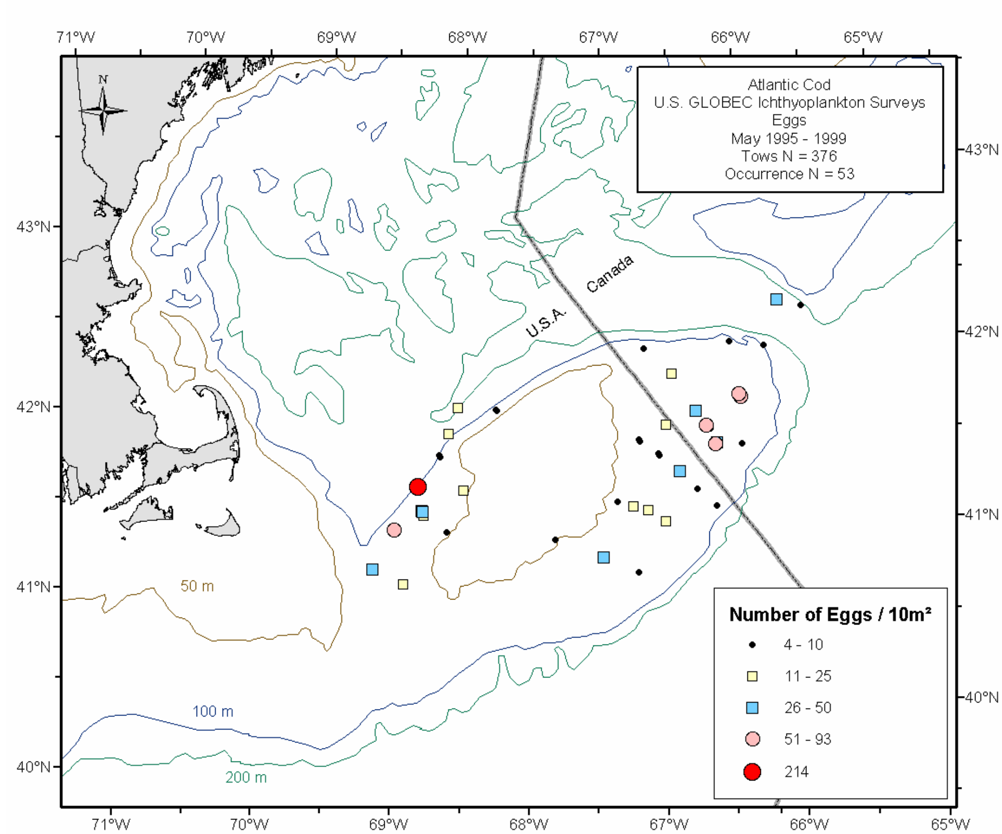

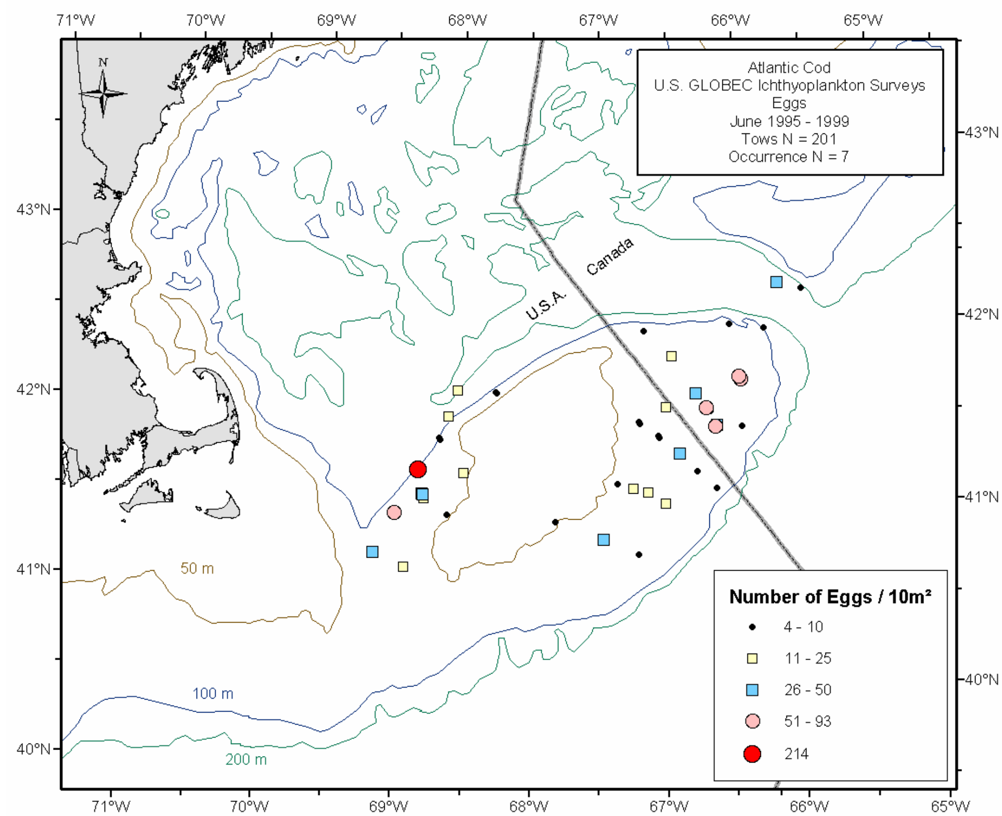

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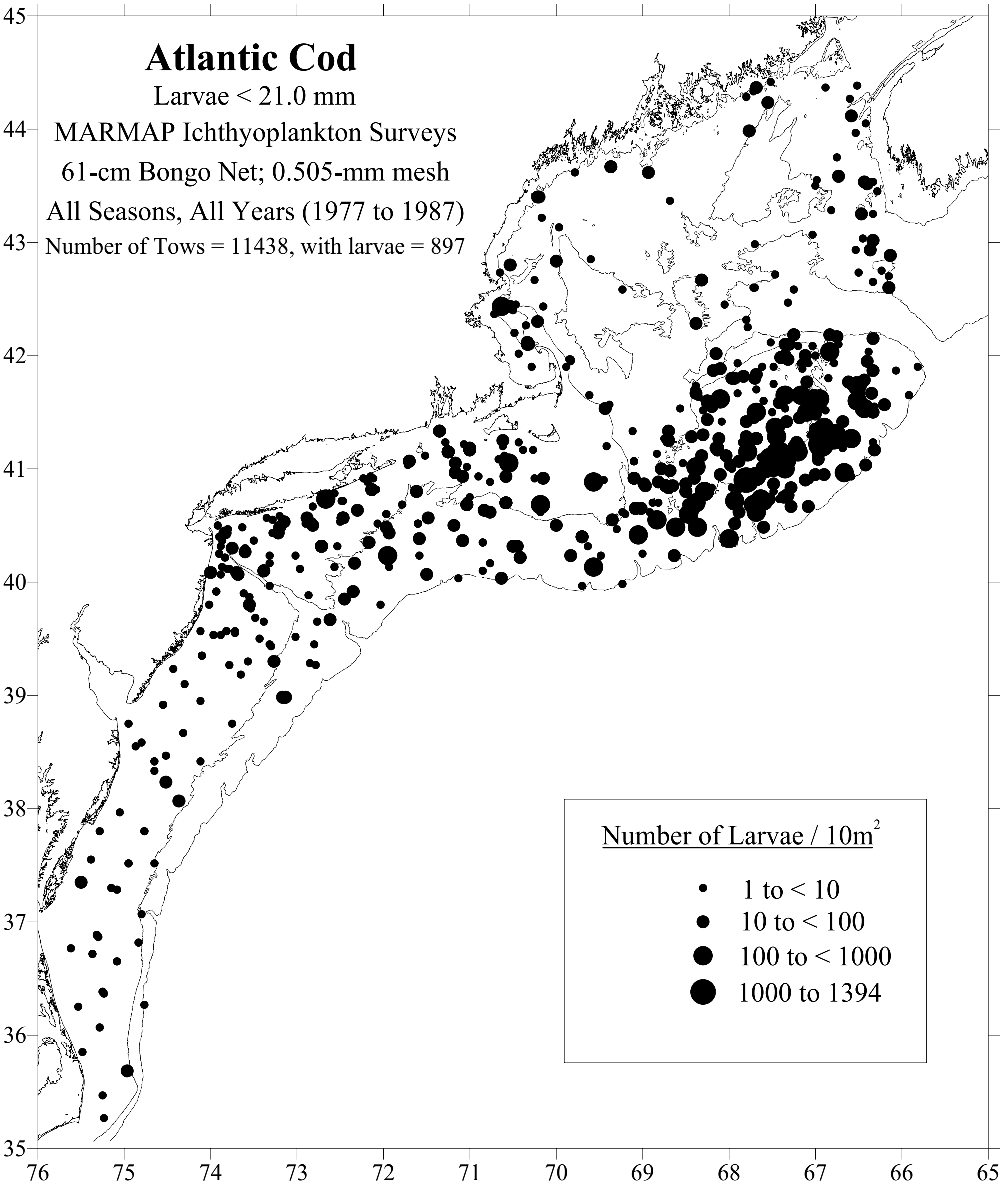


Figure 7. Distributions and abundances of Atlantic cod larvae collected during NEFSC MARMAP ichthyoplankton surveys.
For all available months and years from 1977 to 1987 combined.

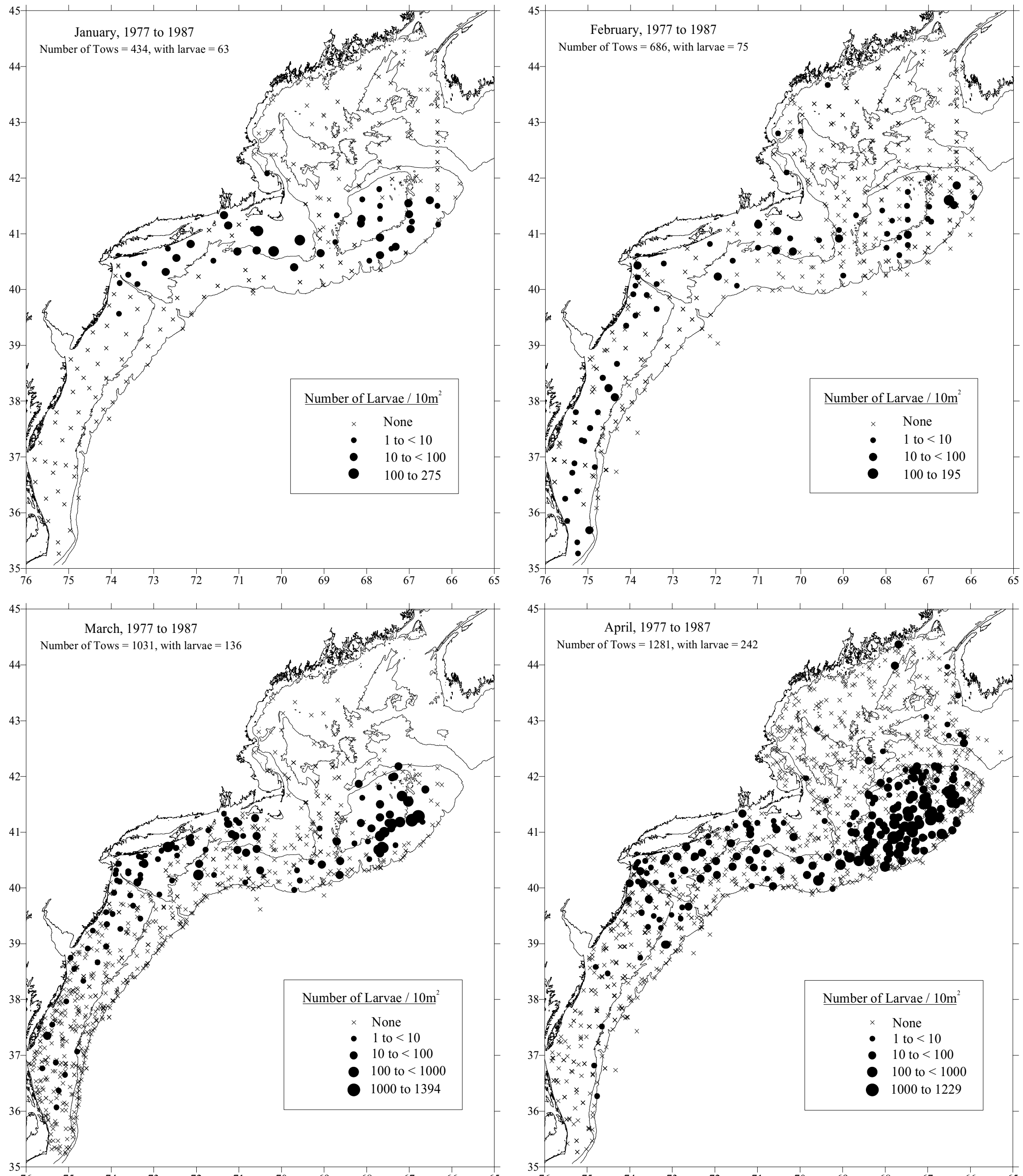
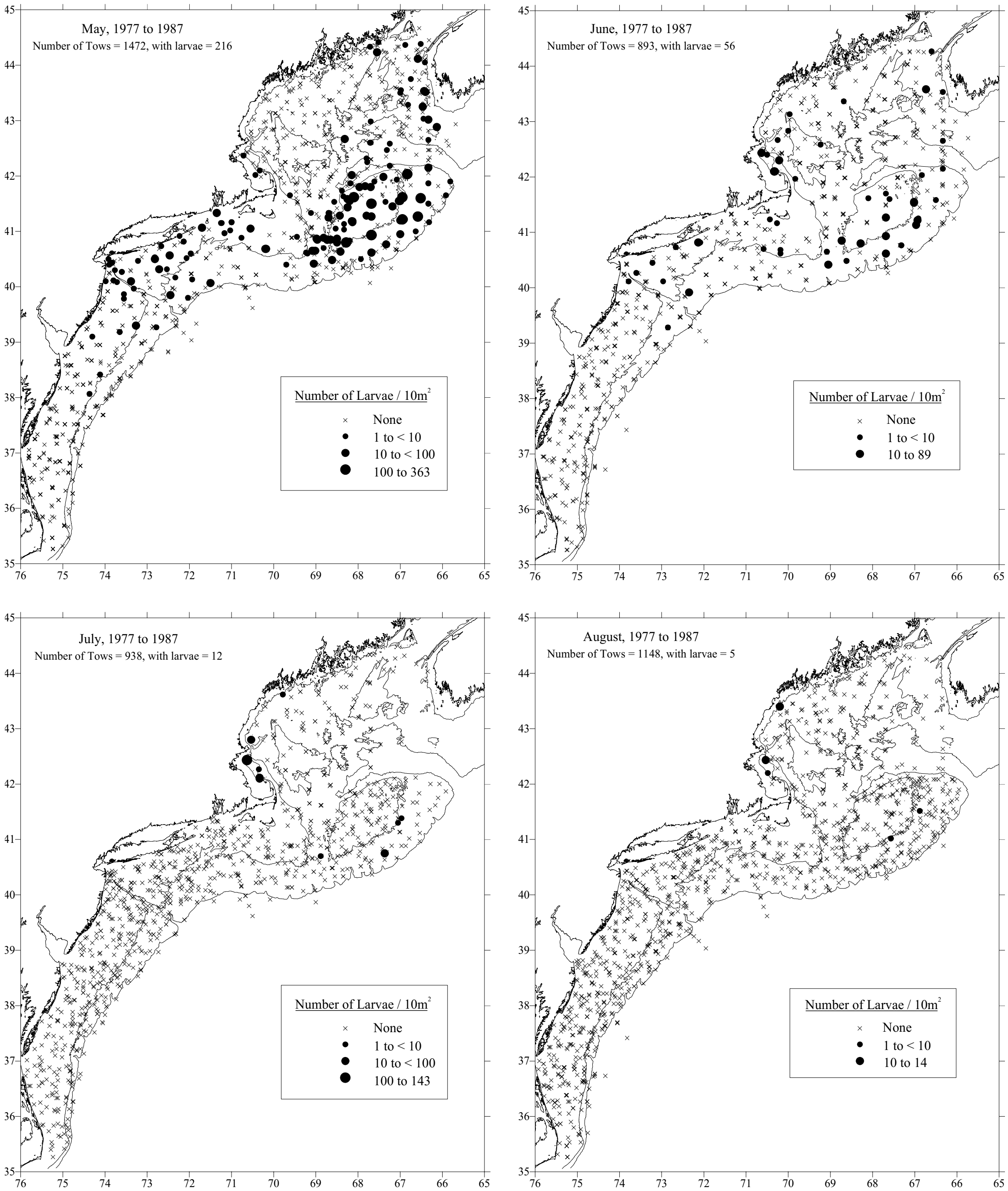


Figure 7. Cont'd.
From MARMAP ichthyoplankton surveys, January through April, 1977-1987.



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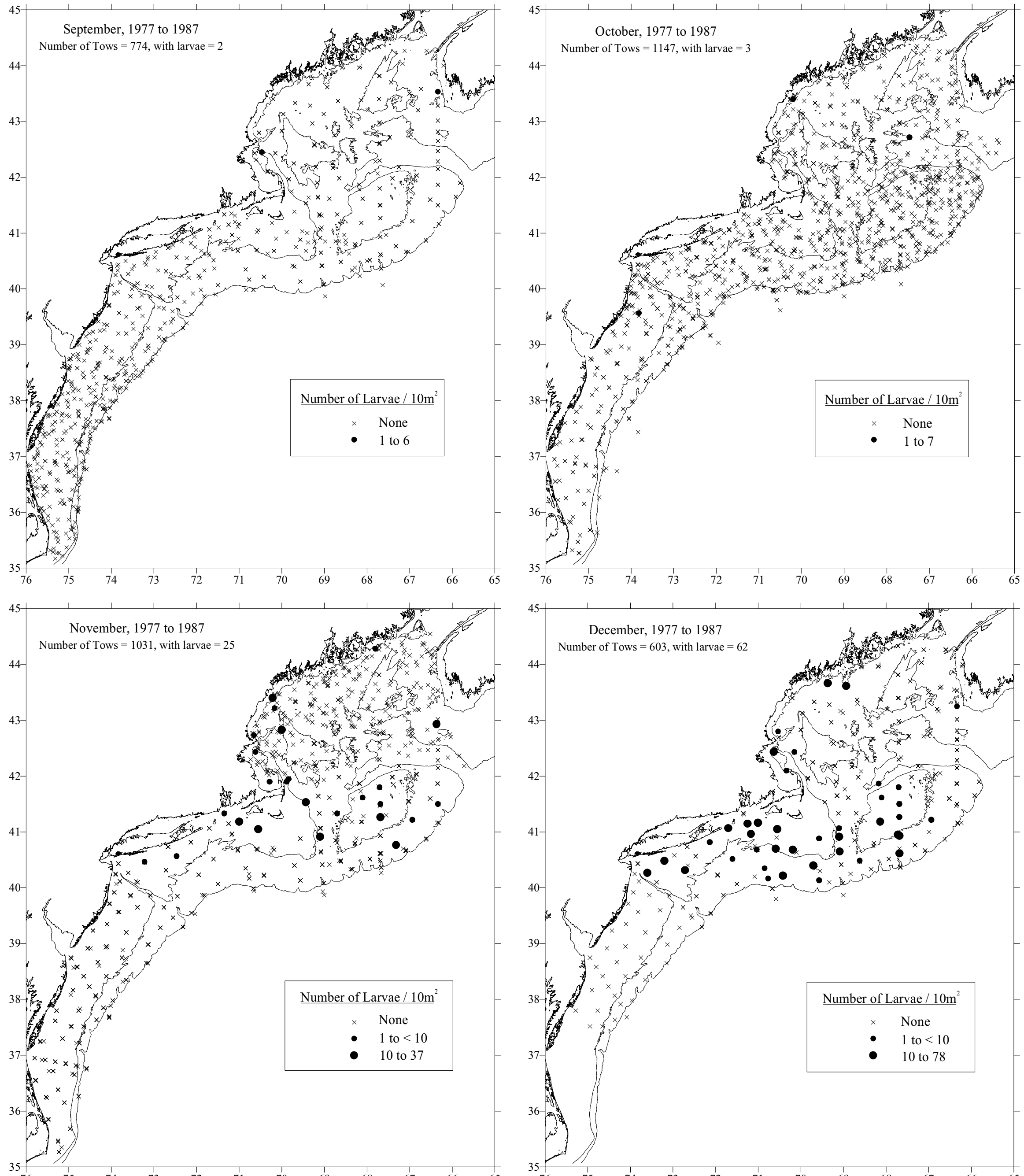

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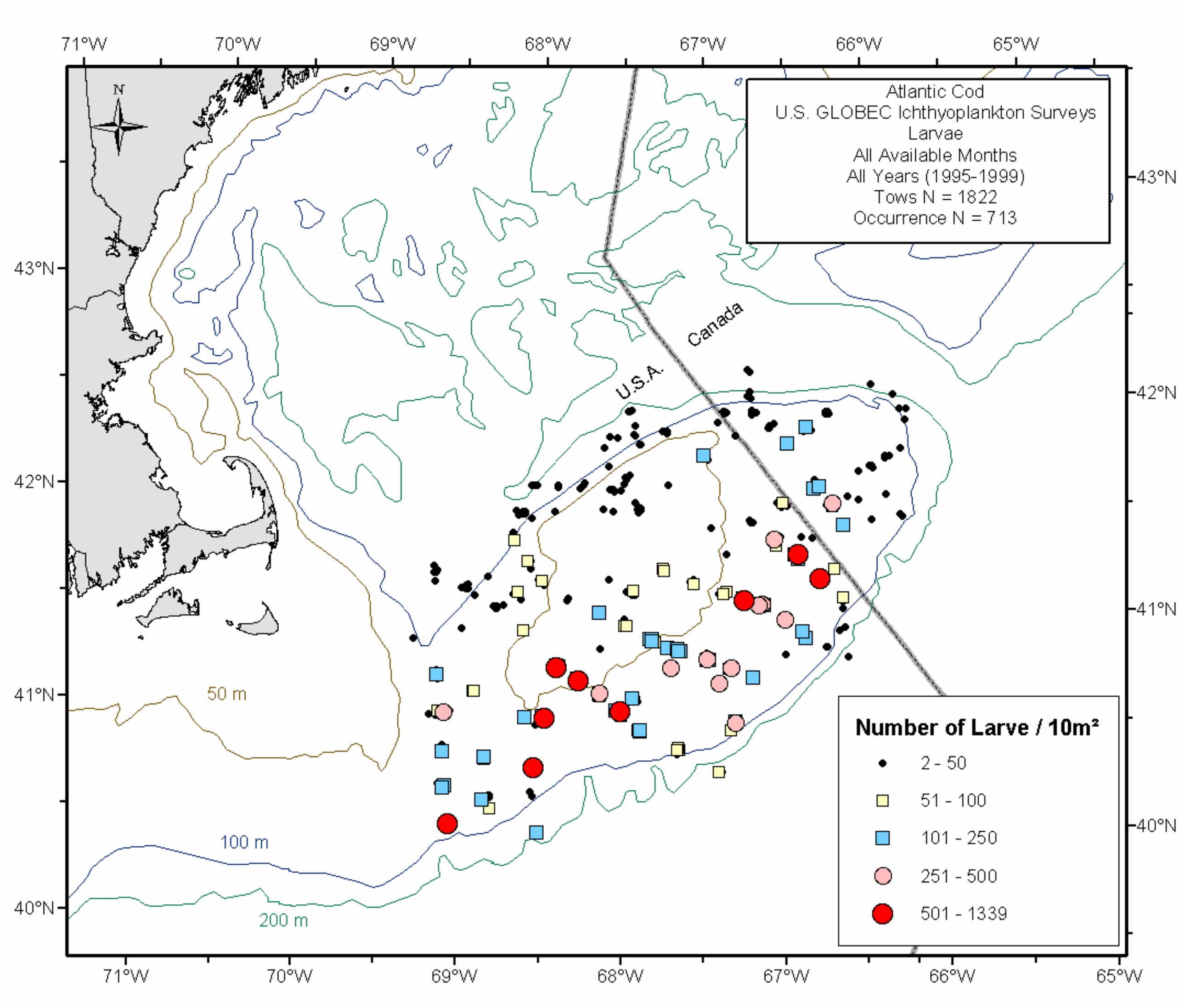
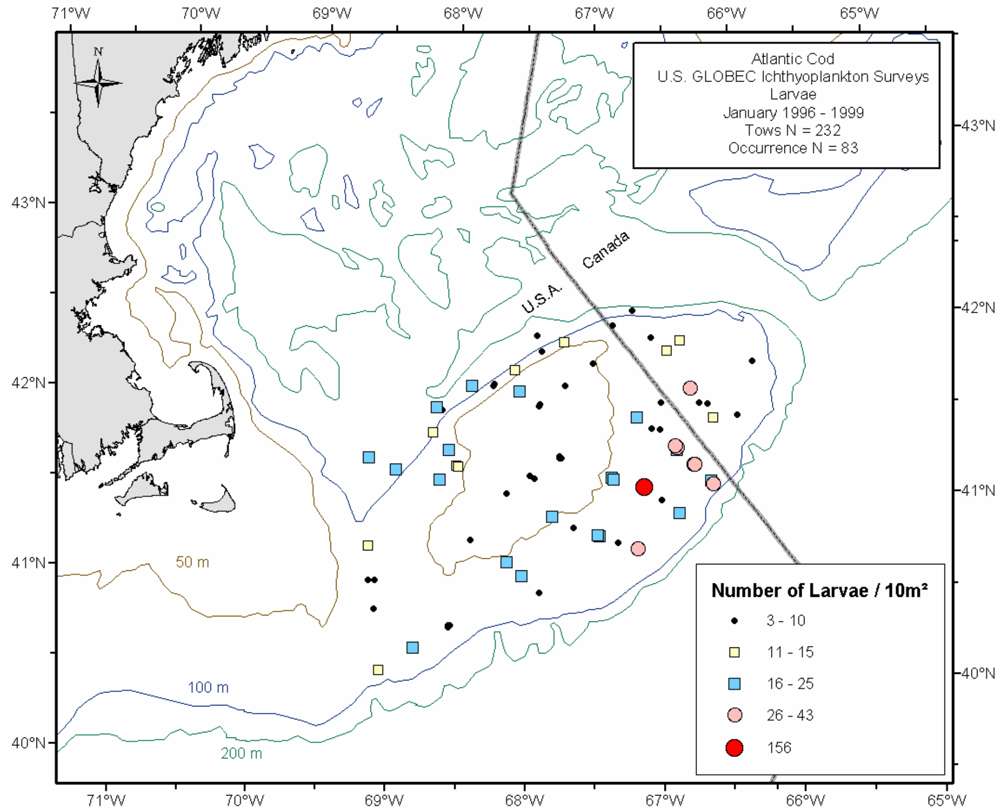


Figure 8. Distributions and abundances of Atlantic cod larvae collected during GLOBEC Georges Bank ichthyoplankton surveys.
For all available years (February-July, 1995; January-June, 1996-1999) combined.



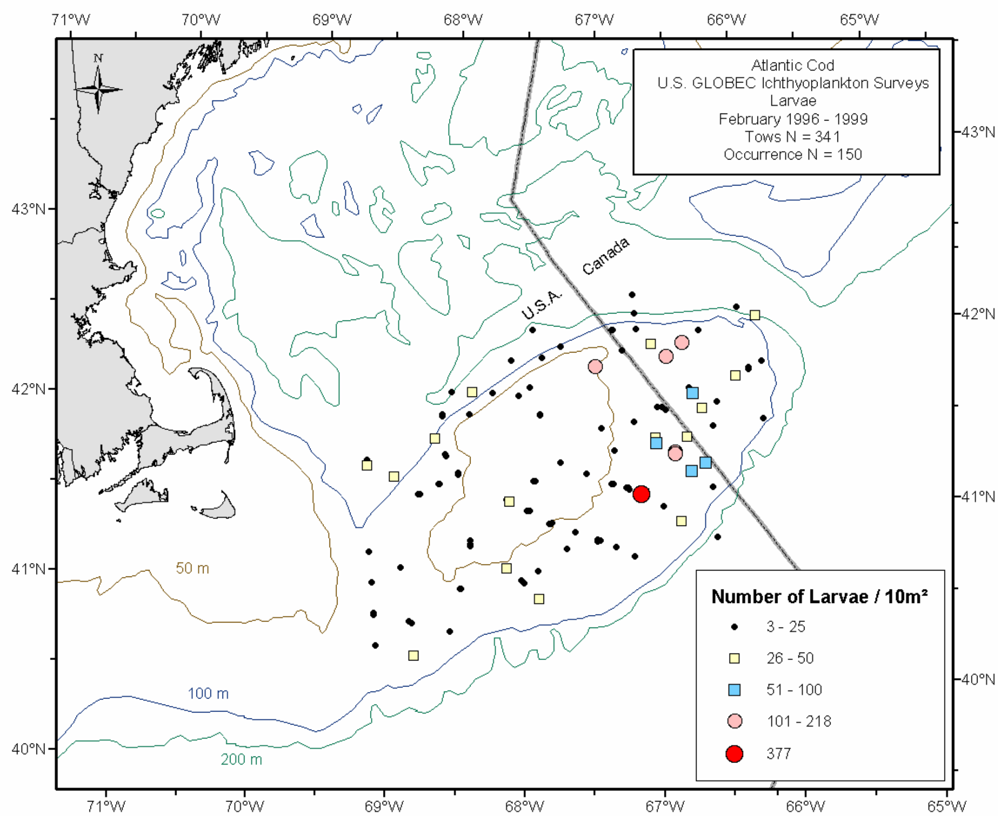
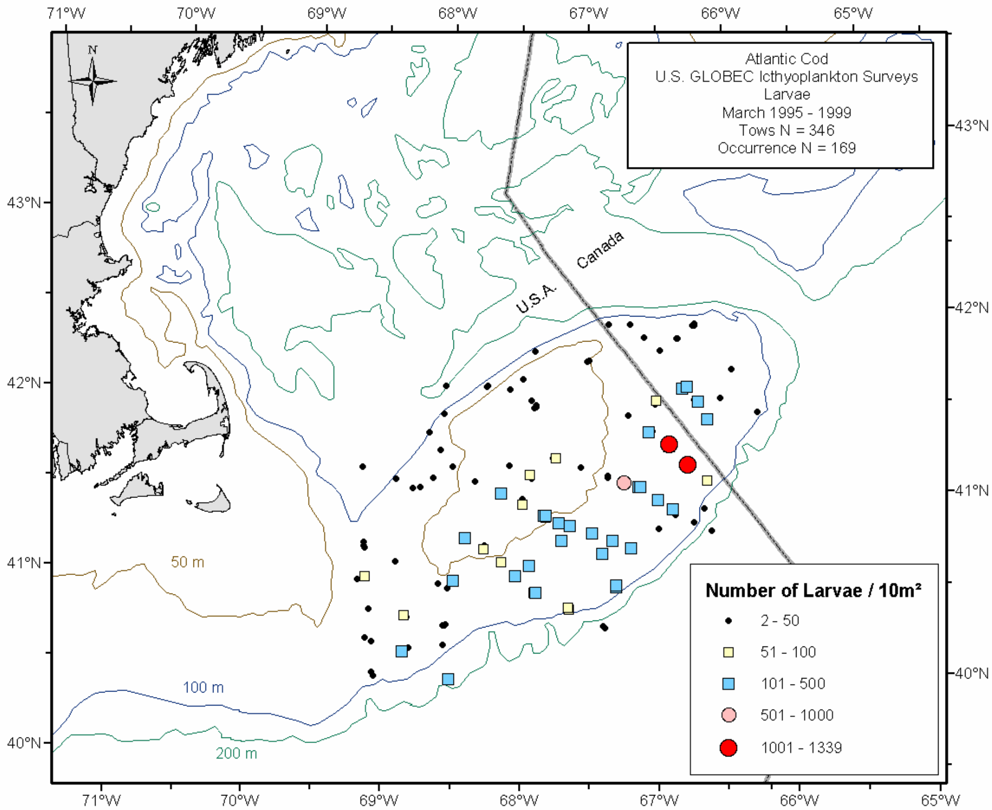


Figure 8. Cont'd.
From GLOBEC ichthyoplankton surveys, January and February, for all available years combined.



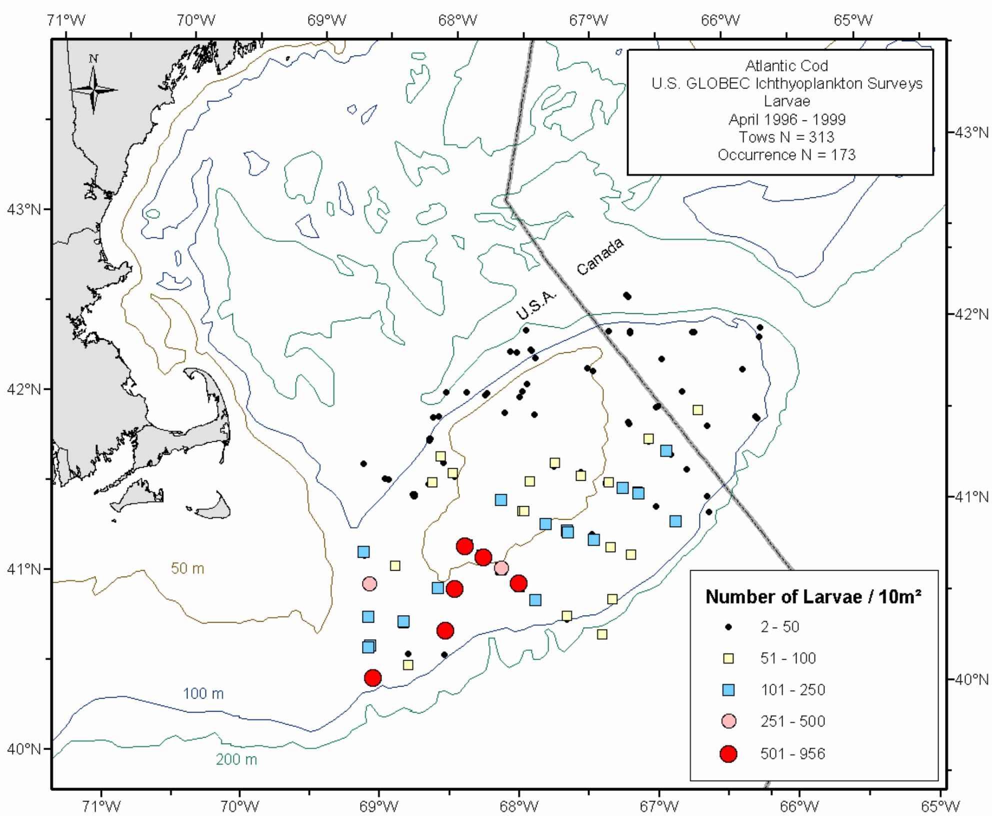


Figure 8. Cont'd.
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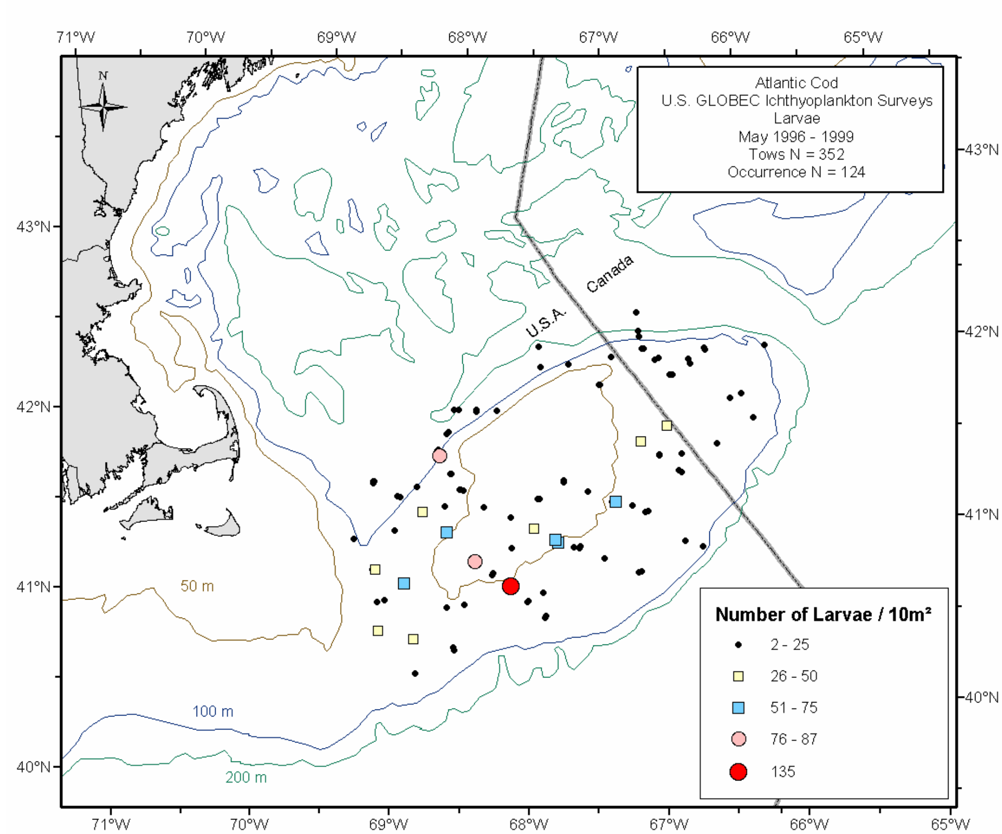

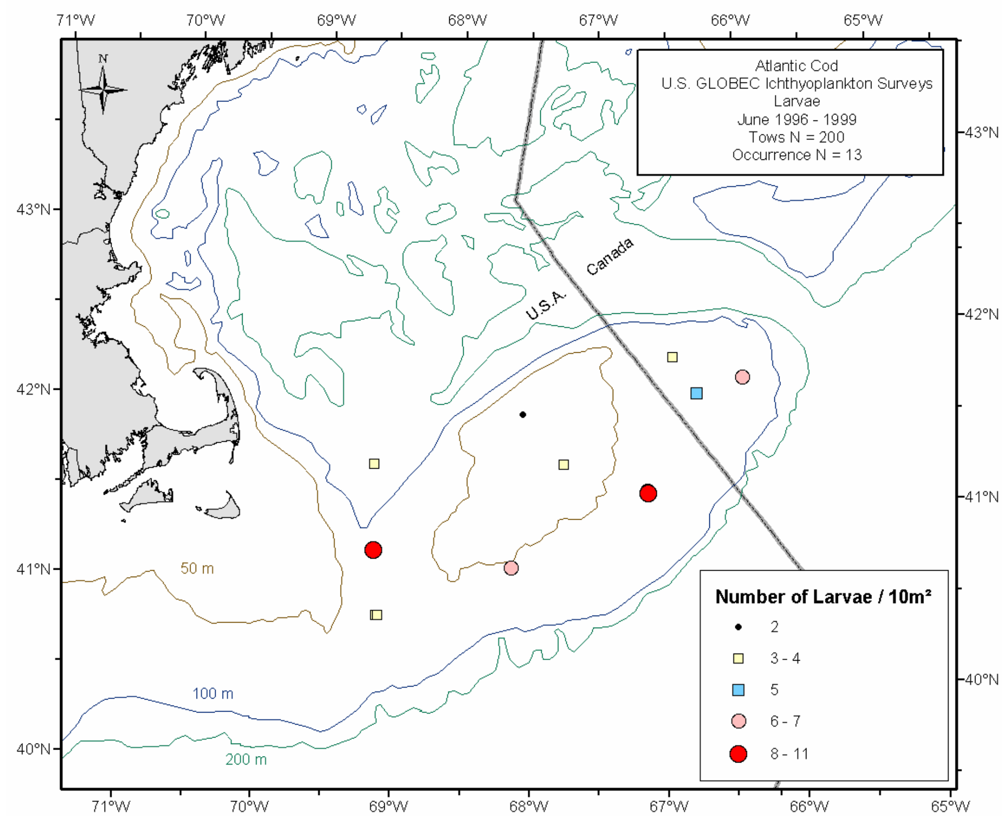

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From GLOBEC ichthyoplankton surveys, May and June, for all available years combined.

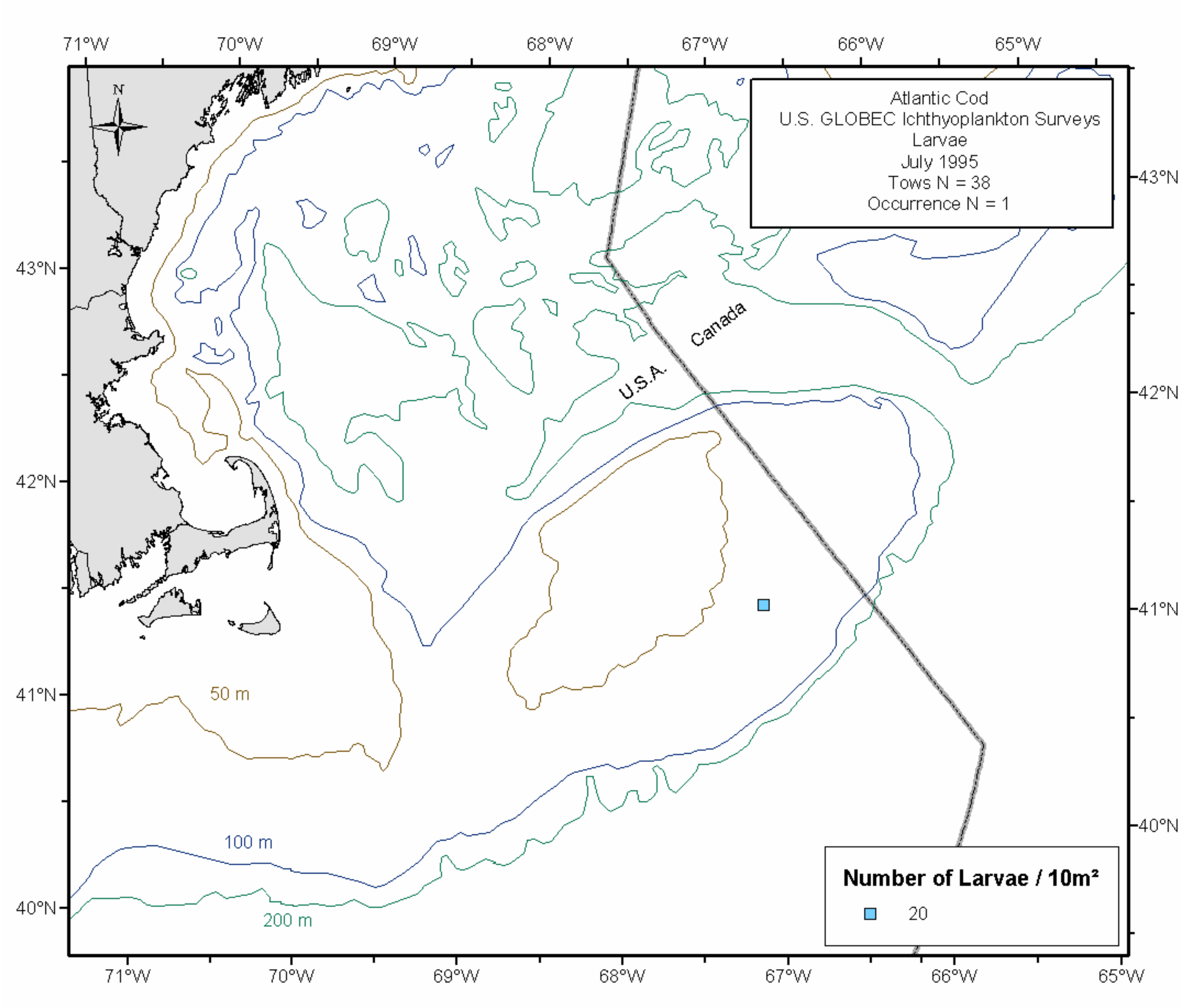

Figure 8. Cont'd.
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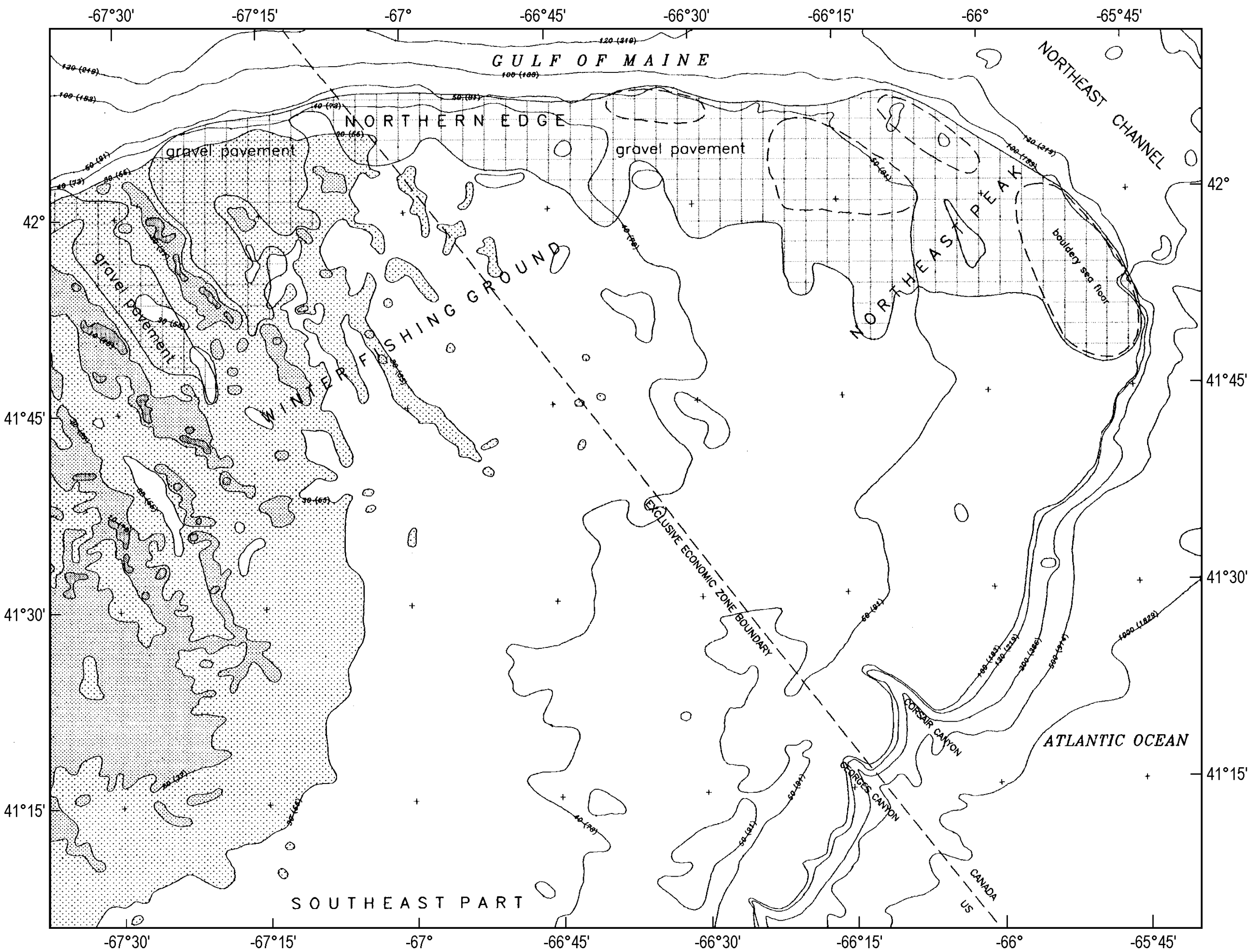


Figure 9. Topographic map of Georges Bank showing gravel distribution, from Valentine and Lough (1991).

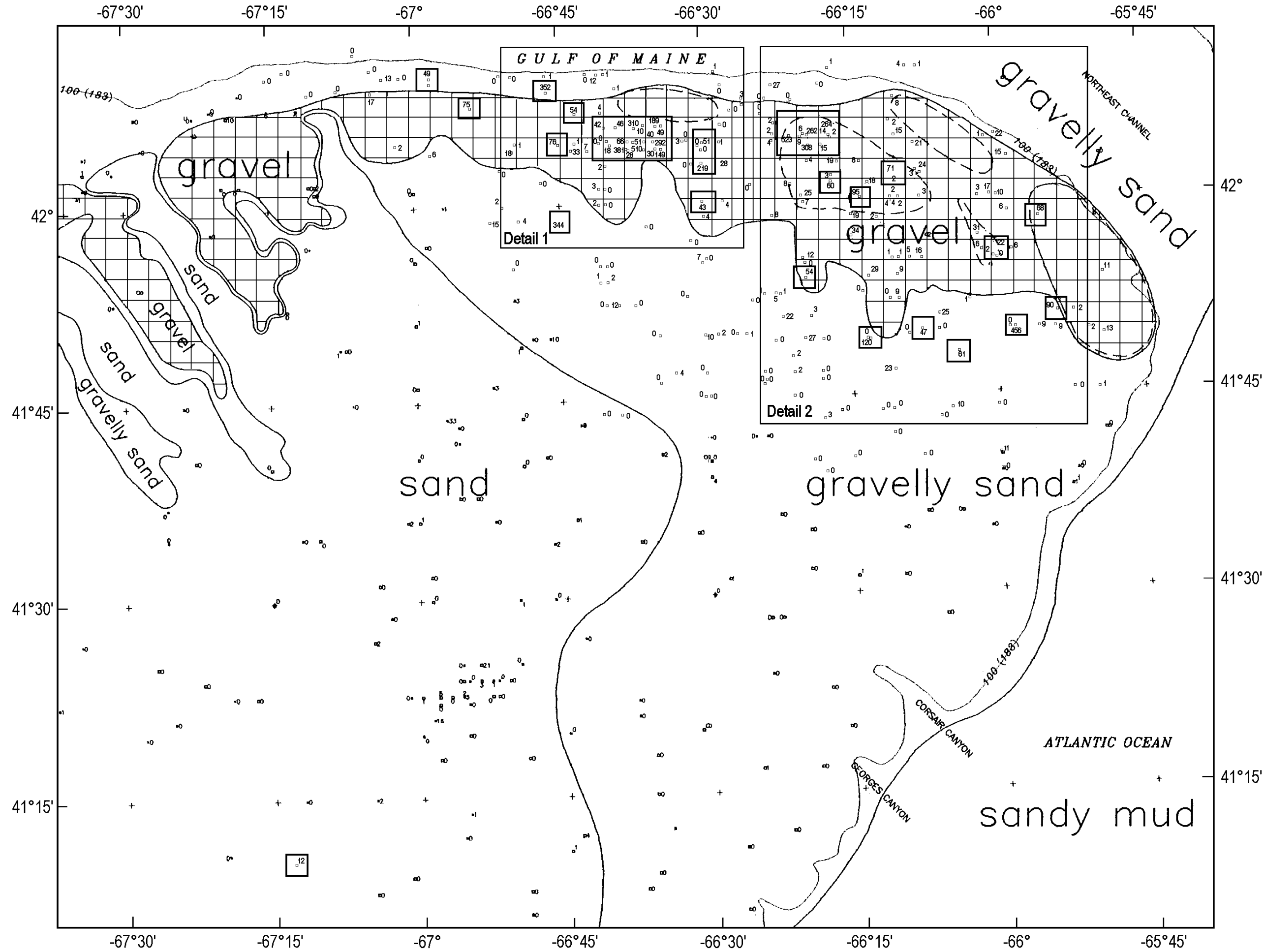
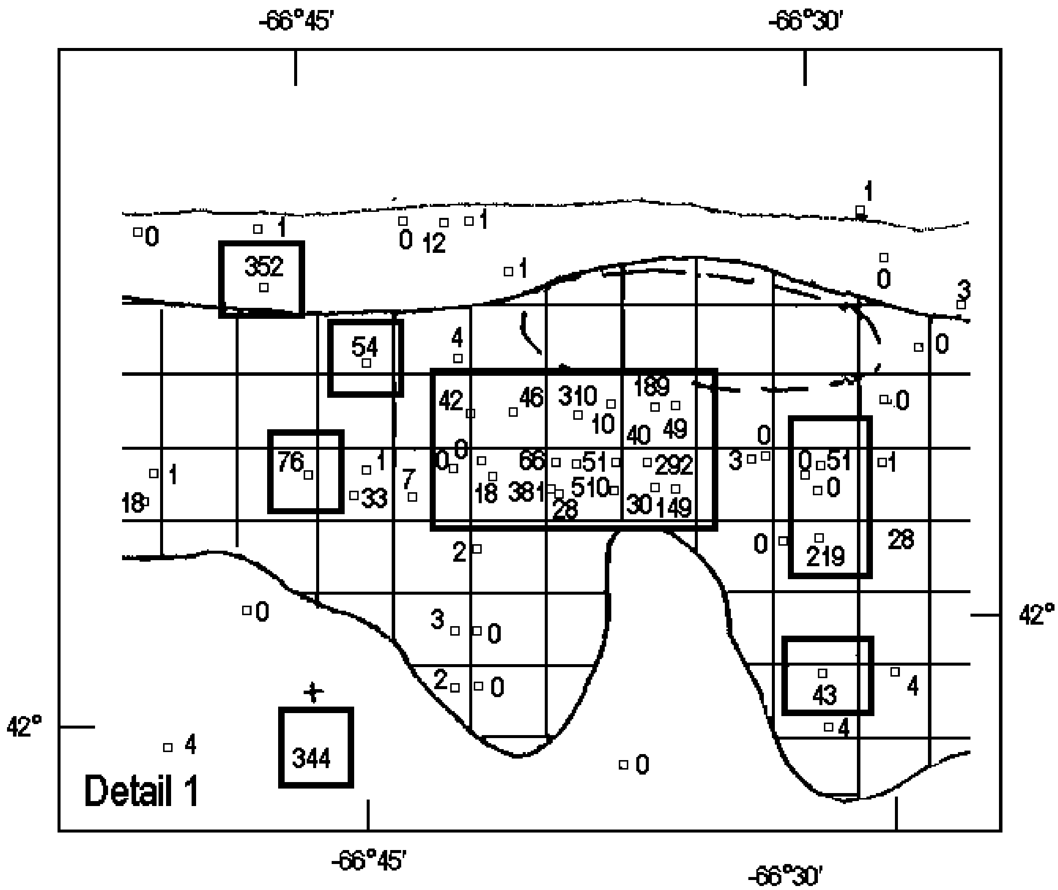


Figure 10. Distribution and abundance of recently-settled juvenile cod on eastern Georges Bank in relation to sediments. Source: Valentine and Lough (1991).



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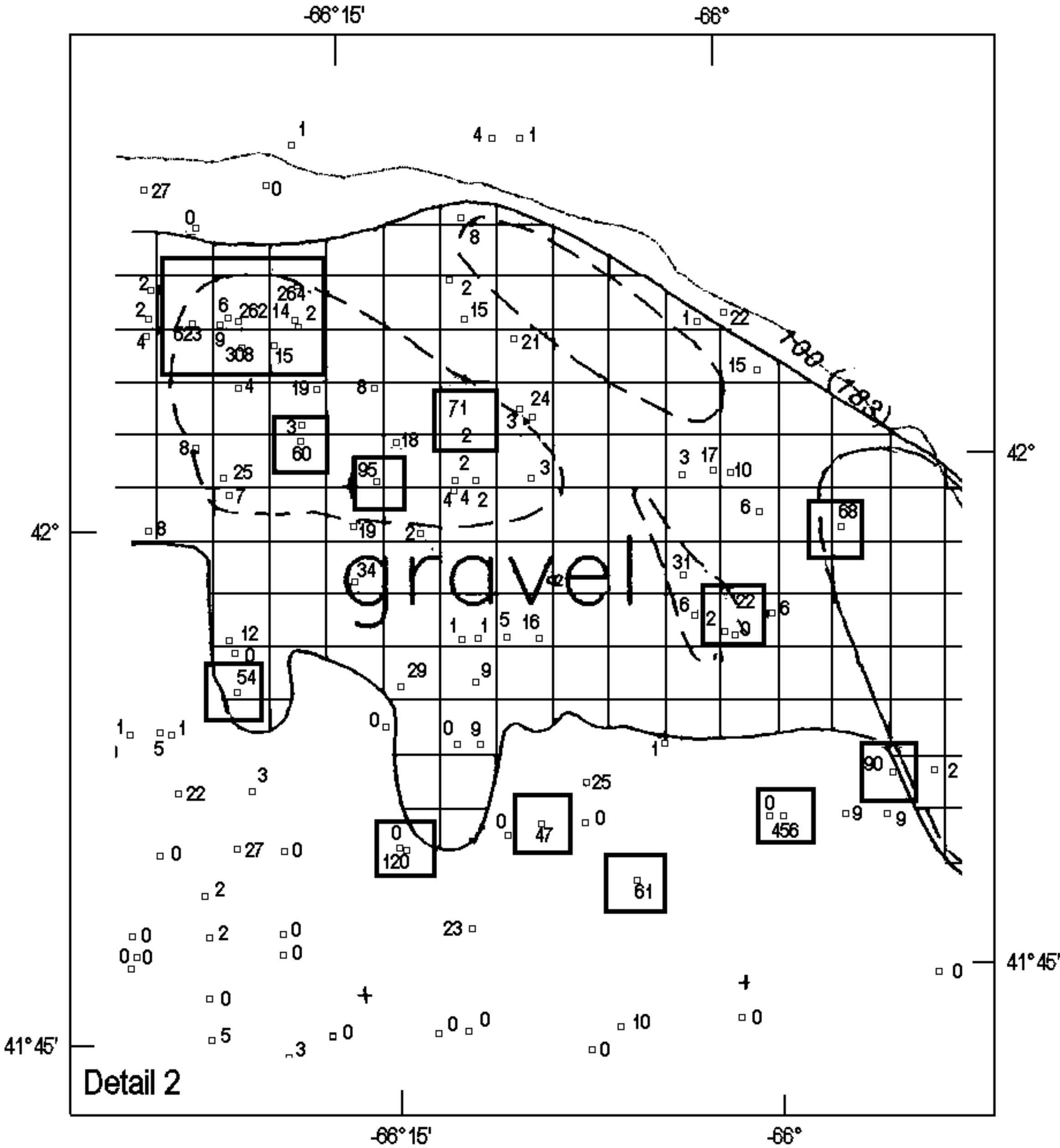

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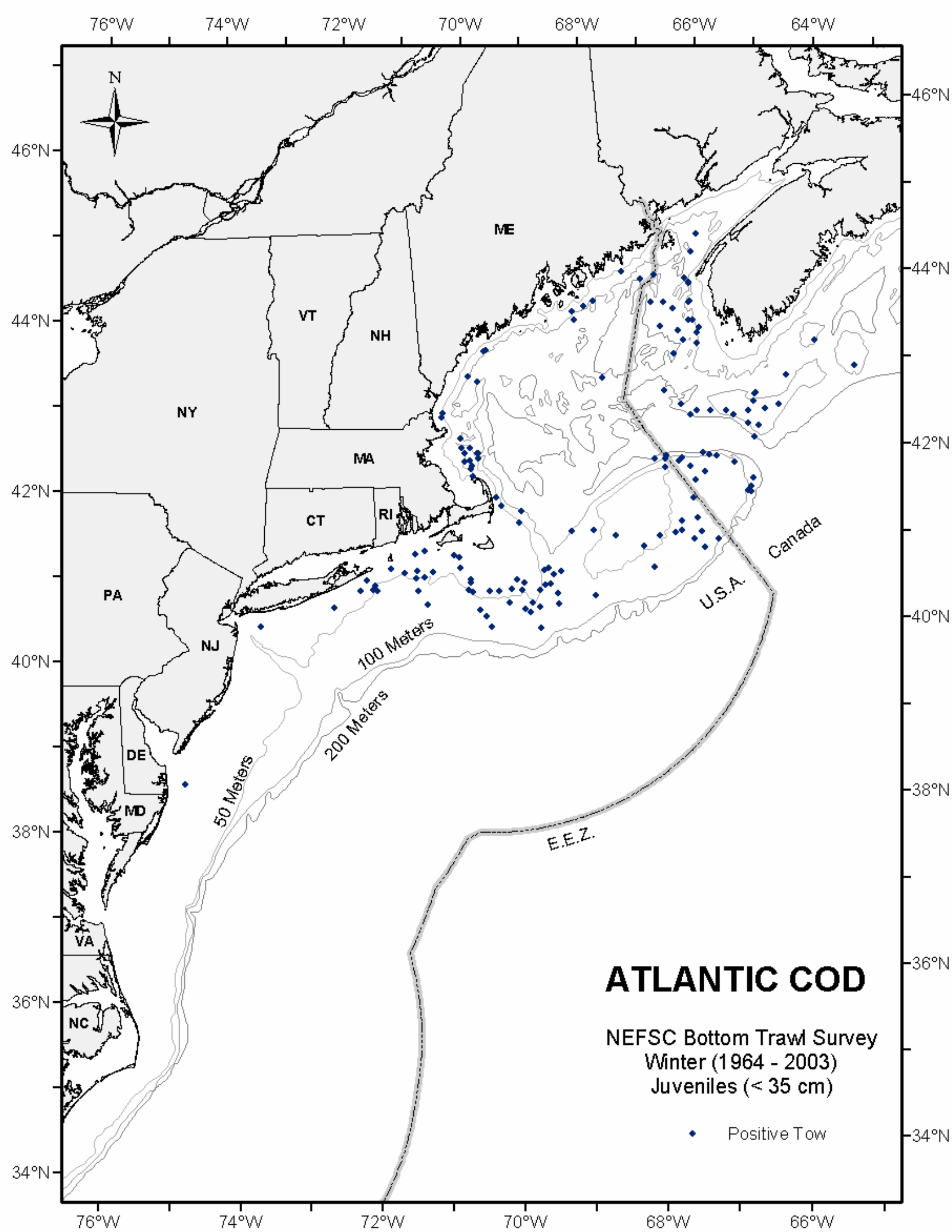


Figure 11. Seasonal distributions and abundances of juvenile Atlantic cod collected during NEFSC bottom trawl surveys.
From NEFSC winter bottom trawl surveys (1964-2003, all years combined). Distributions are displayed as presence only.

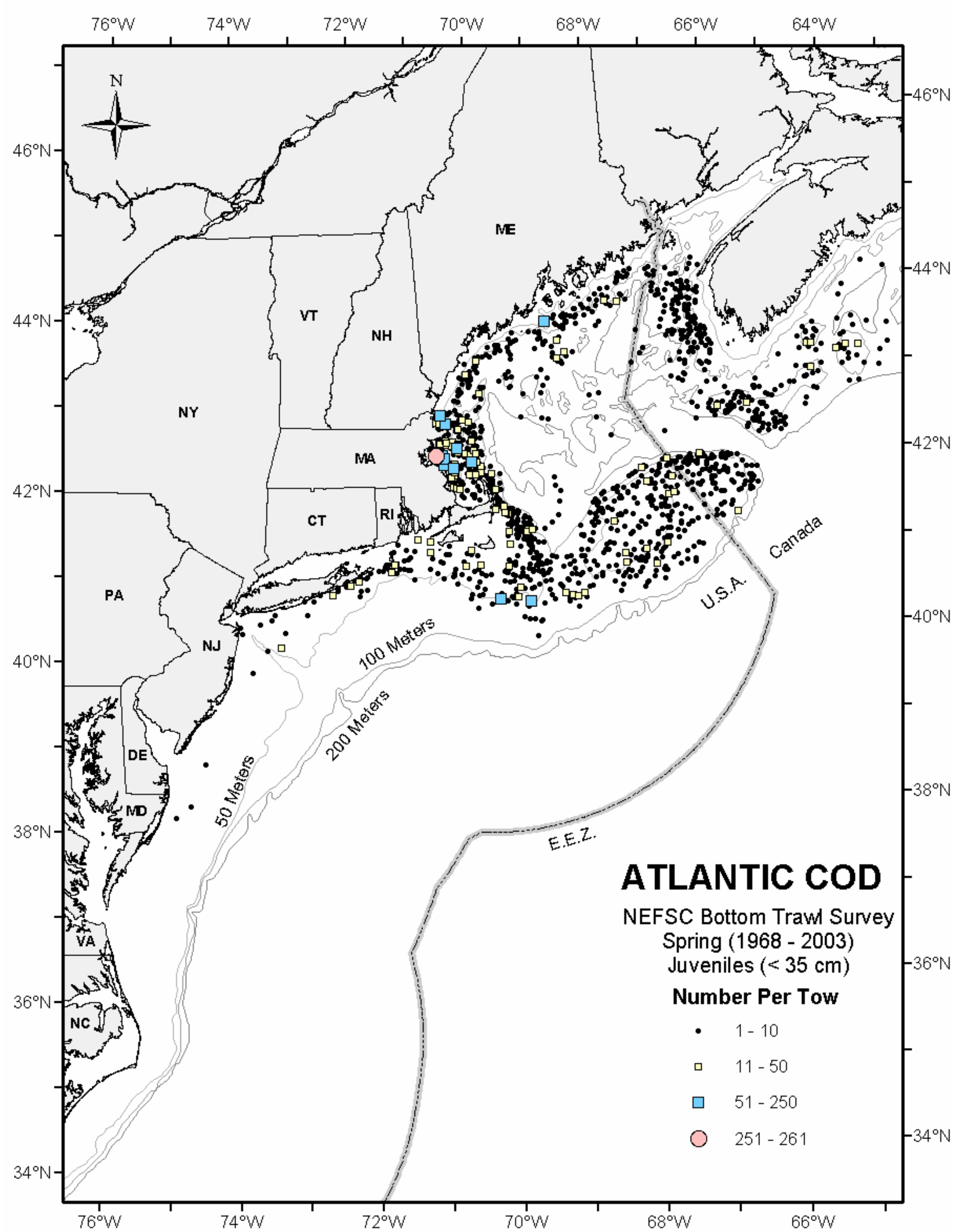


Figure 11. Cont'd.
From NEFSC spring bottom trawl surveys (1968-2003, all years combined). Survey stations where juveniles were not found are not shown.

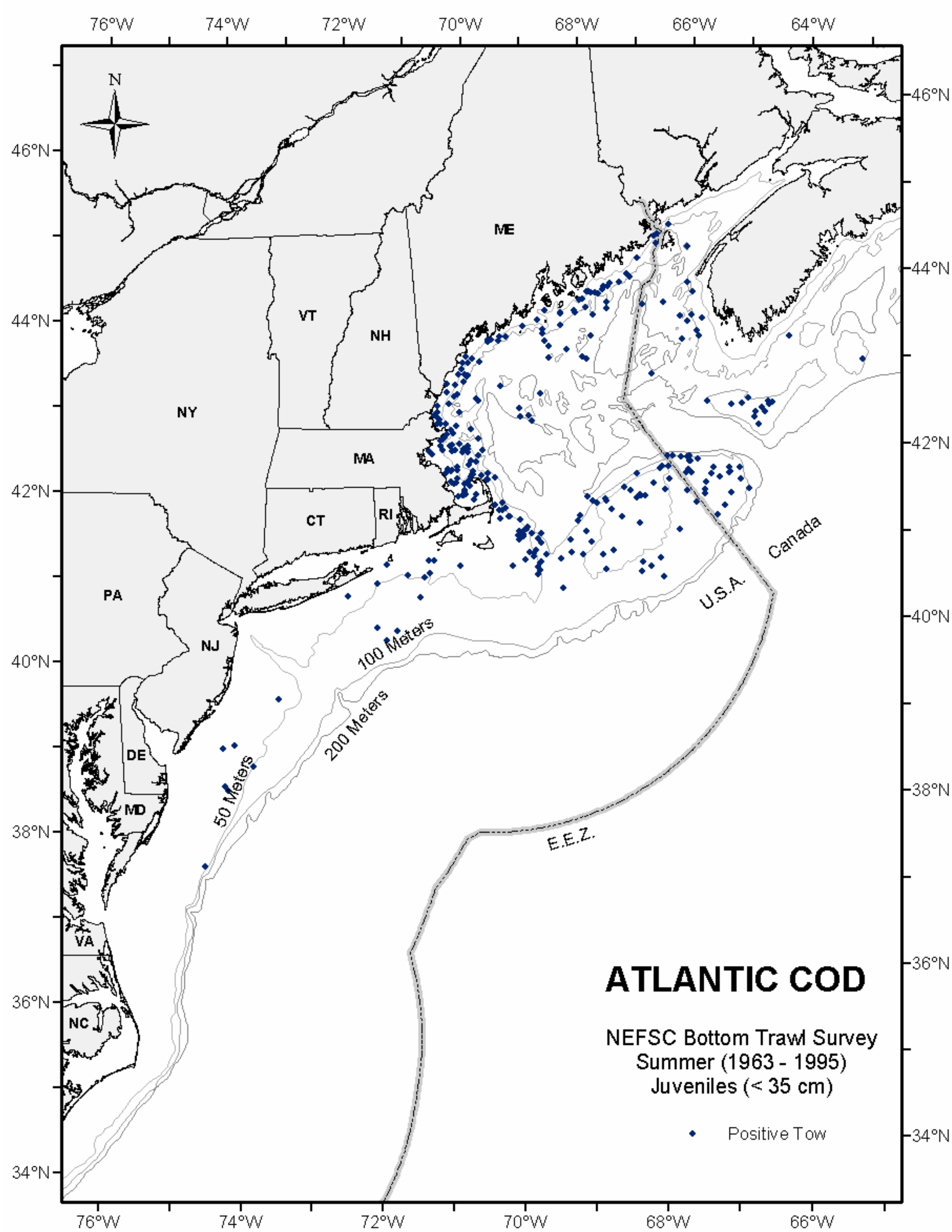


Figure 11. Cont'd.
From NEFSC summer bottom trawl surveys (1963-1995, all years combined). Distributions are displayed as presence only.

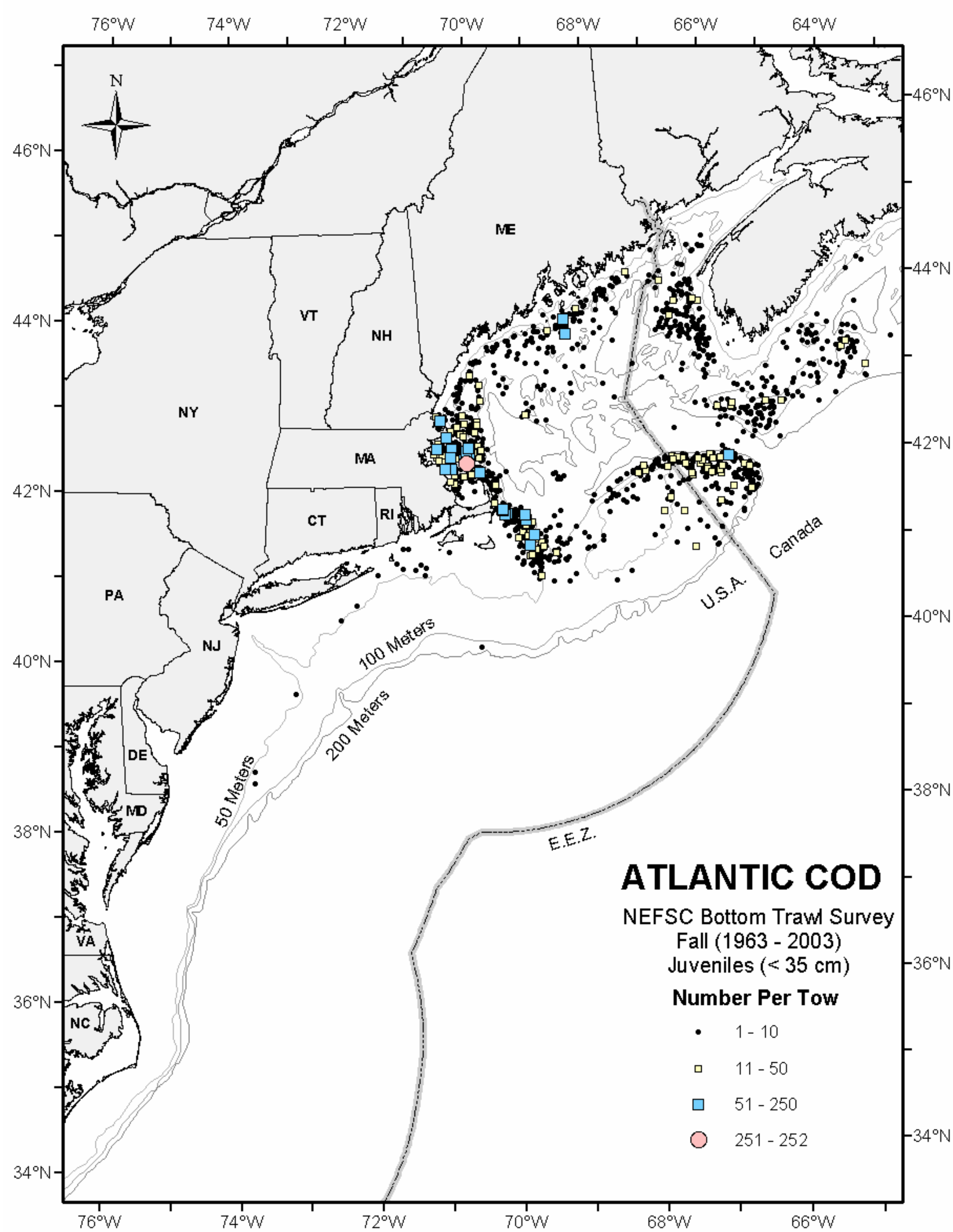
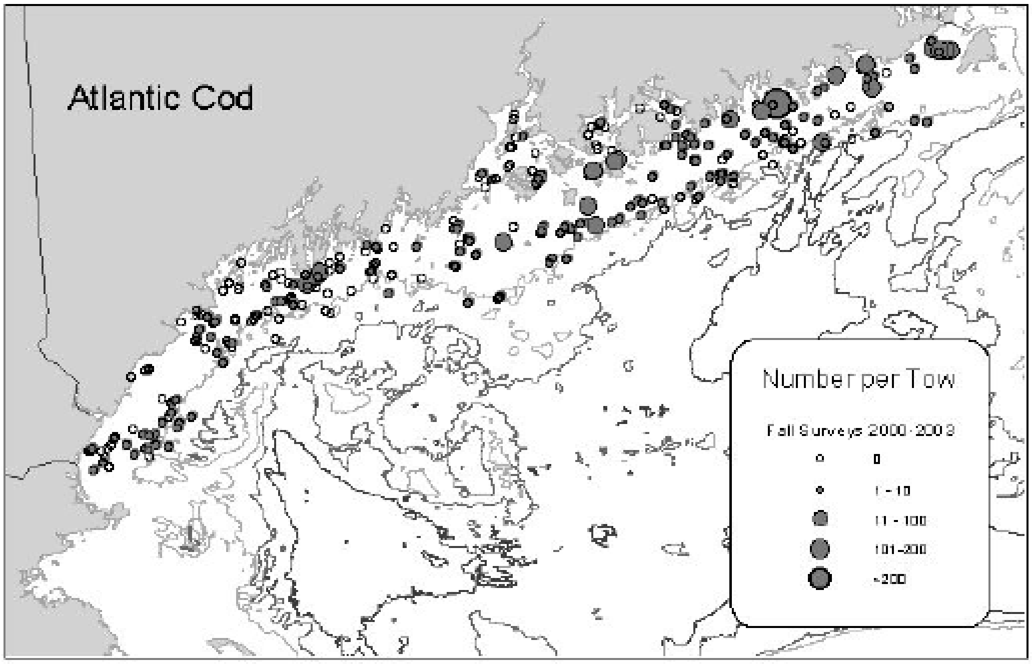


Figure 11. Cont'd.
From NEFSC fall bottom trawl surveys (1963-2003, all years combined). Survey stations where juveniles were not found are not shown.



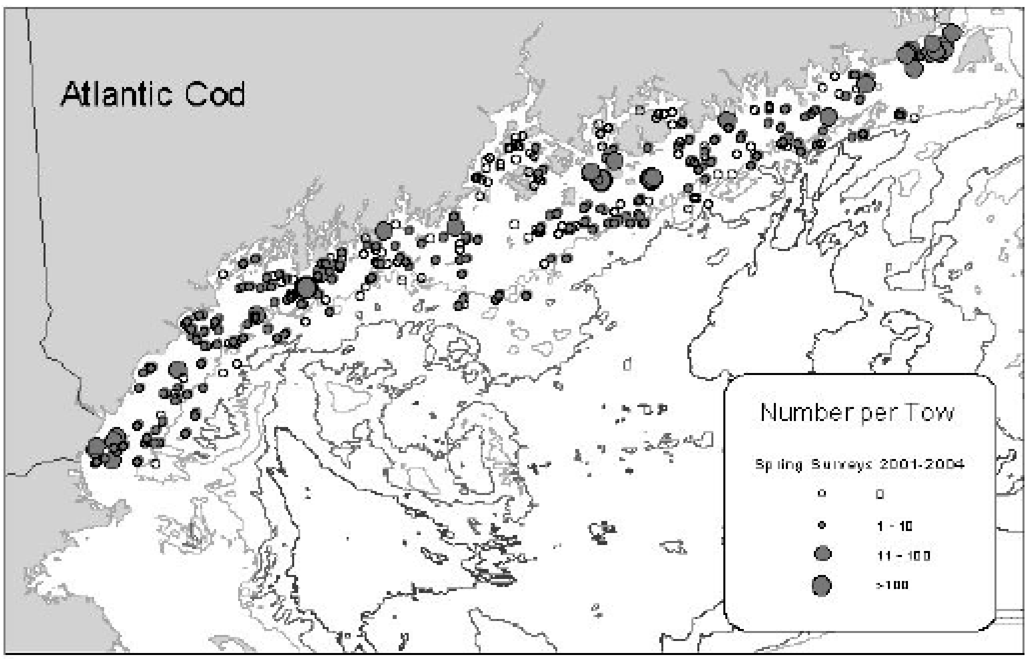
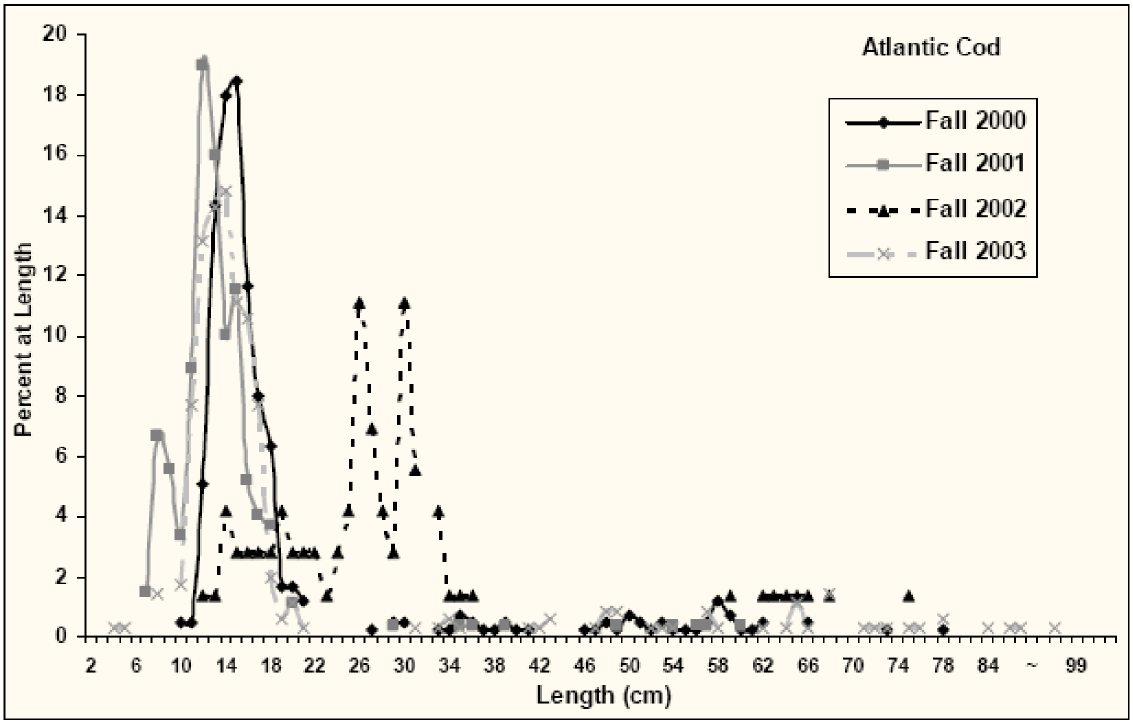


Figure 12. Distribution and abundance of Atlantic cod along the coasts of Maine and New Hampshire. From the Maine – New Hampshire spring 2001-2004 and fall 2000-2003 inshore groundfish trawl surveys. For details on the survey, see Sherman *et al*. (2005).



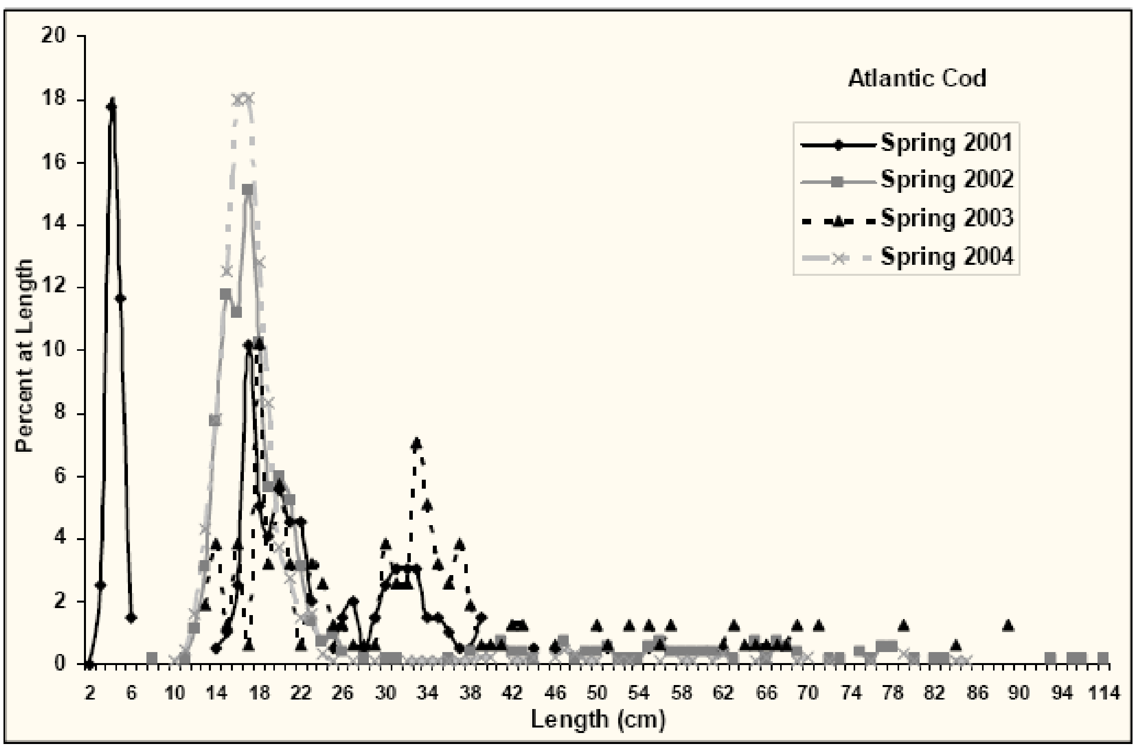
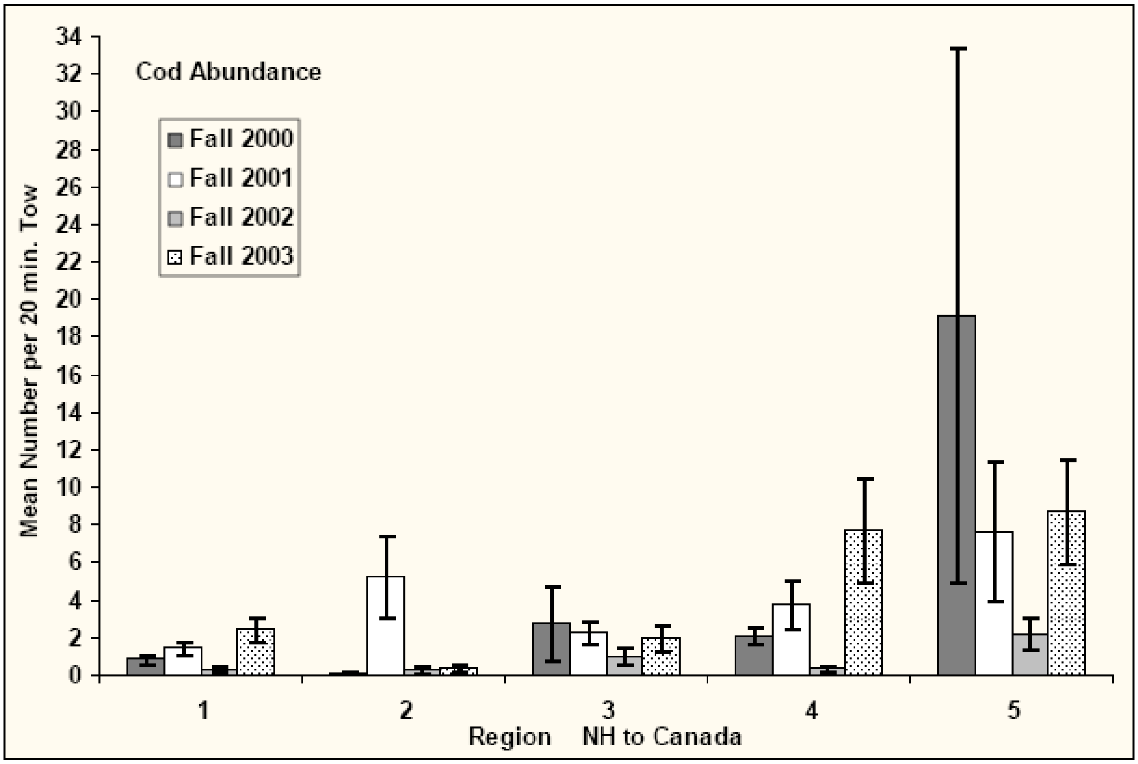


Figure 13. Length frequency plots for Atlantic cod caught along the Maine and New Hampshire coasts, by season/year. Based on the Maine – New Hampshire inshore groundfish trawl survey for spring 2001-2004 and fall 2000-2003. Source: Sherman *et al*. (2005).



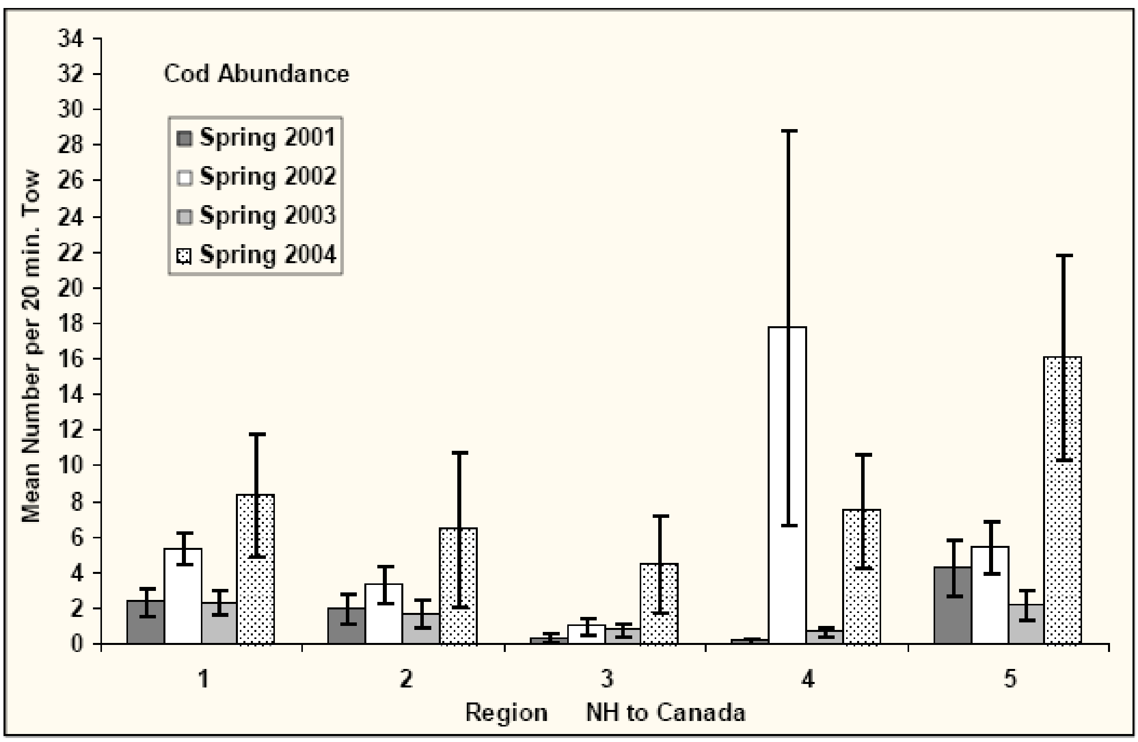


Figure 14. Regional catch-per-unit-effort of Atlantic cod caught along the Maine and New Hampshire coasts, by season/year.
Based on the Maine – New Hampshire inshore groundfish trawl survey for spring 2001-2004 and fall 2000-2003. Region 1 = NH–Southern ME; Region 2 = Casco Bay–Midcoast ME; Region 3 = Penobscot Bay, ME; Region 4 = Jerico–Frenchmens Bay, ME; Region 5 = Downeast ME. Source: Sherman *et al*. (2005).

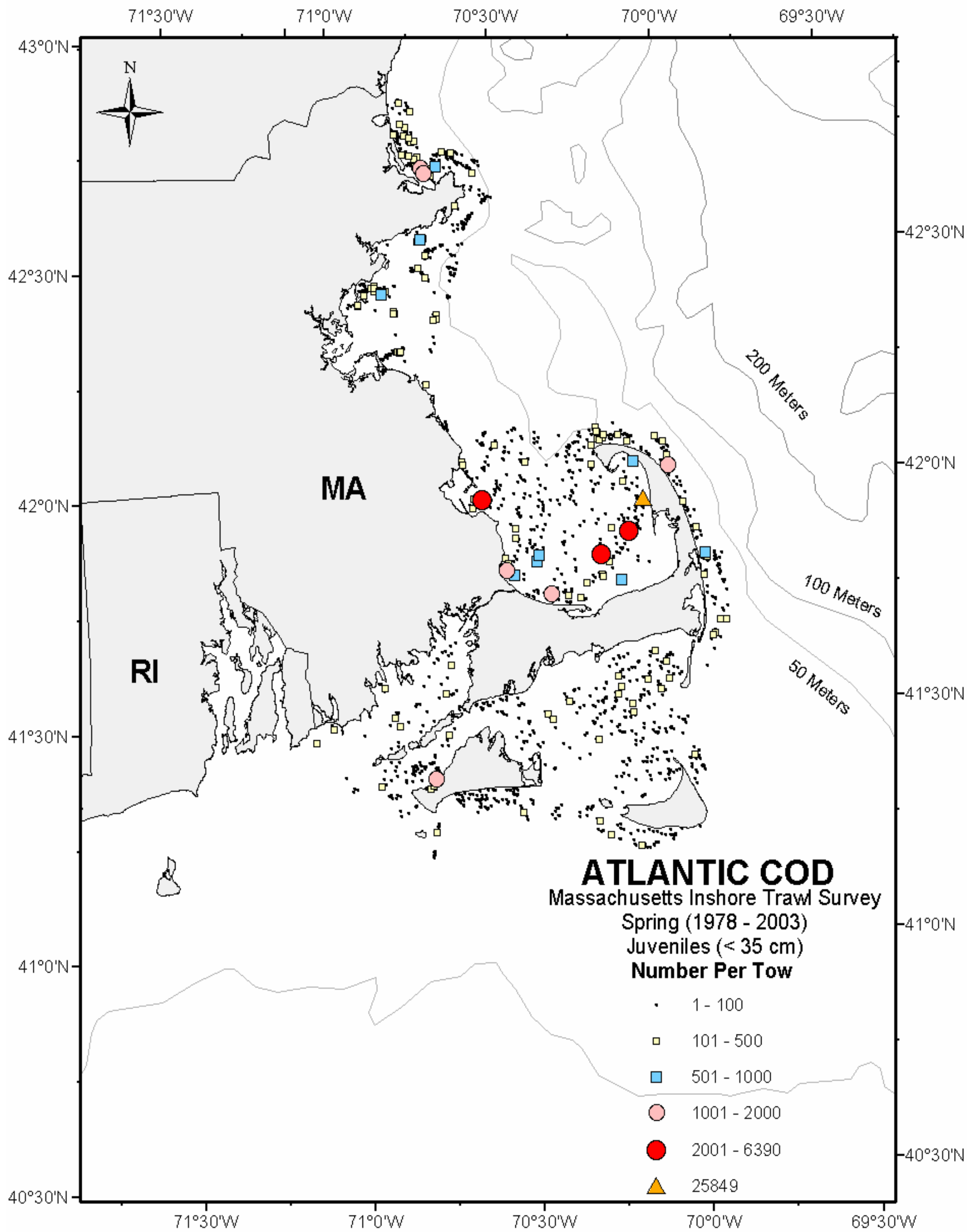


Figure 15. Seasonal distributions and abundances of juvenile Atlantic cod in Massachusetts coastal waters. From spring Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Survey stations where juveniles were not found are not shown.

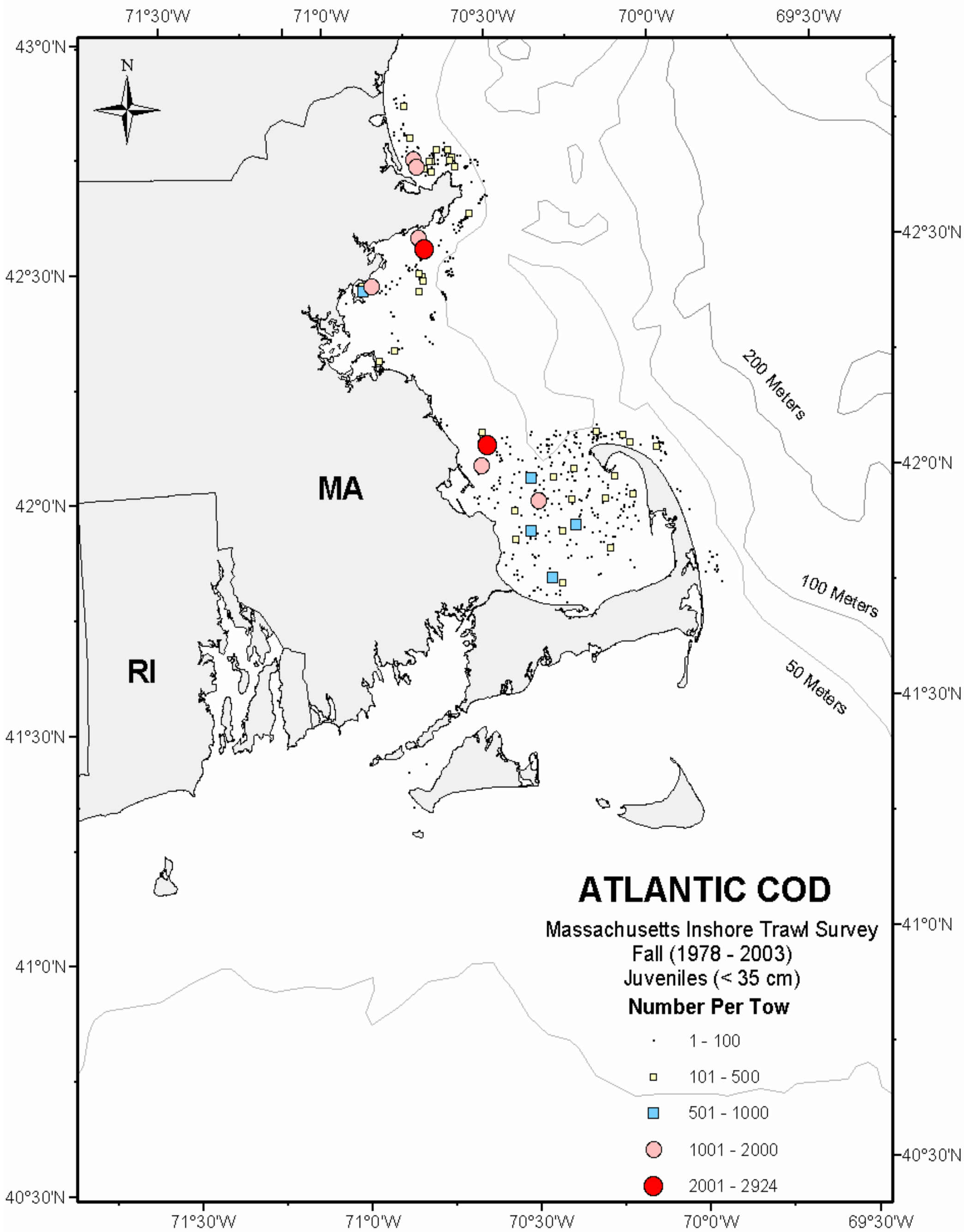


Figure 15. Cont'd.
From fall Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Survey stations where juveniles were not found are not shown.

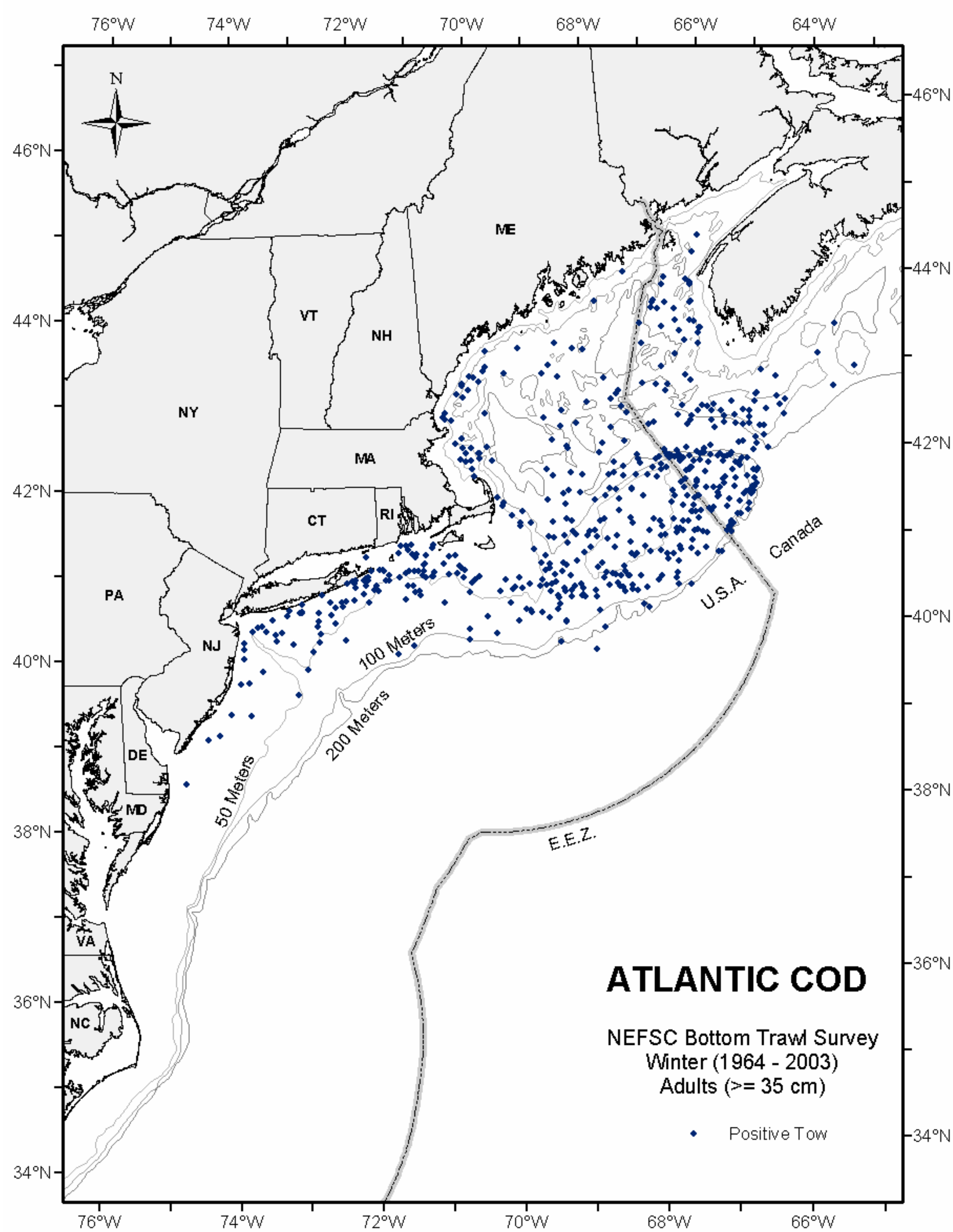


Figure 16. Seasonal distributions and abundances of adult Atlantic cod collected during NEFSC bottom trawl surveys. From NEFSC winter bottom trawl surveys (1964-2003, all years combined). Distributions are displayed as presence only.

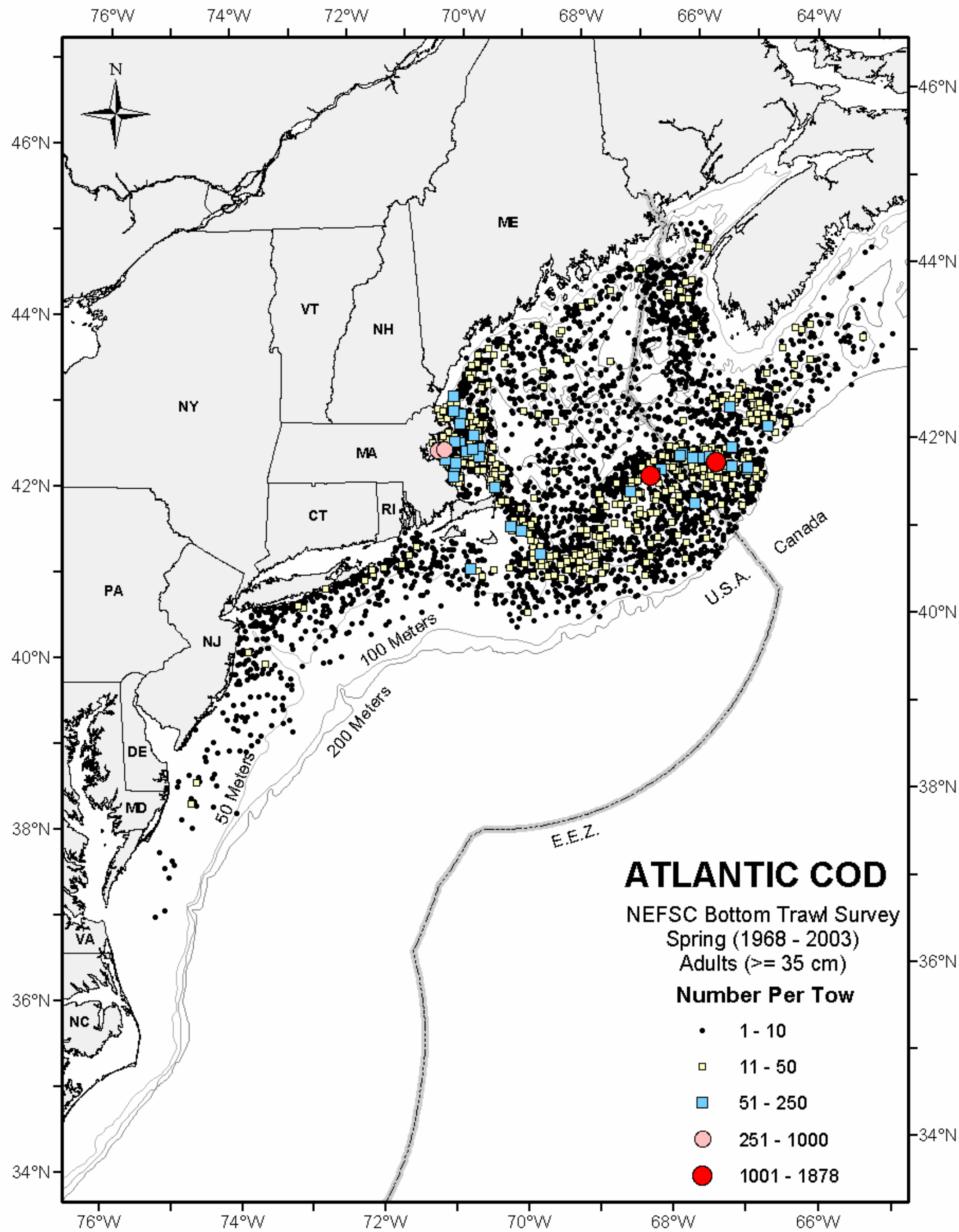


Figure 16. Cont'd.
From NEFSC spring bottom trawl surveys (1968-2003, all years combined). Survey stations where adults were not found are not shown.

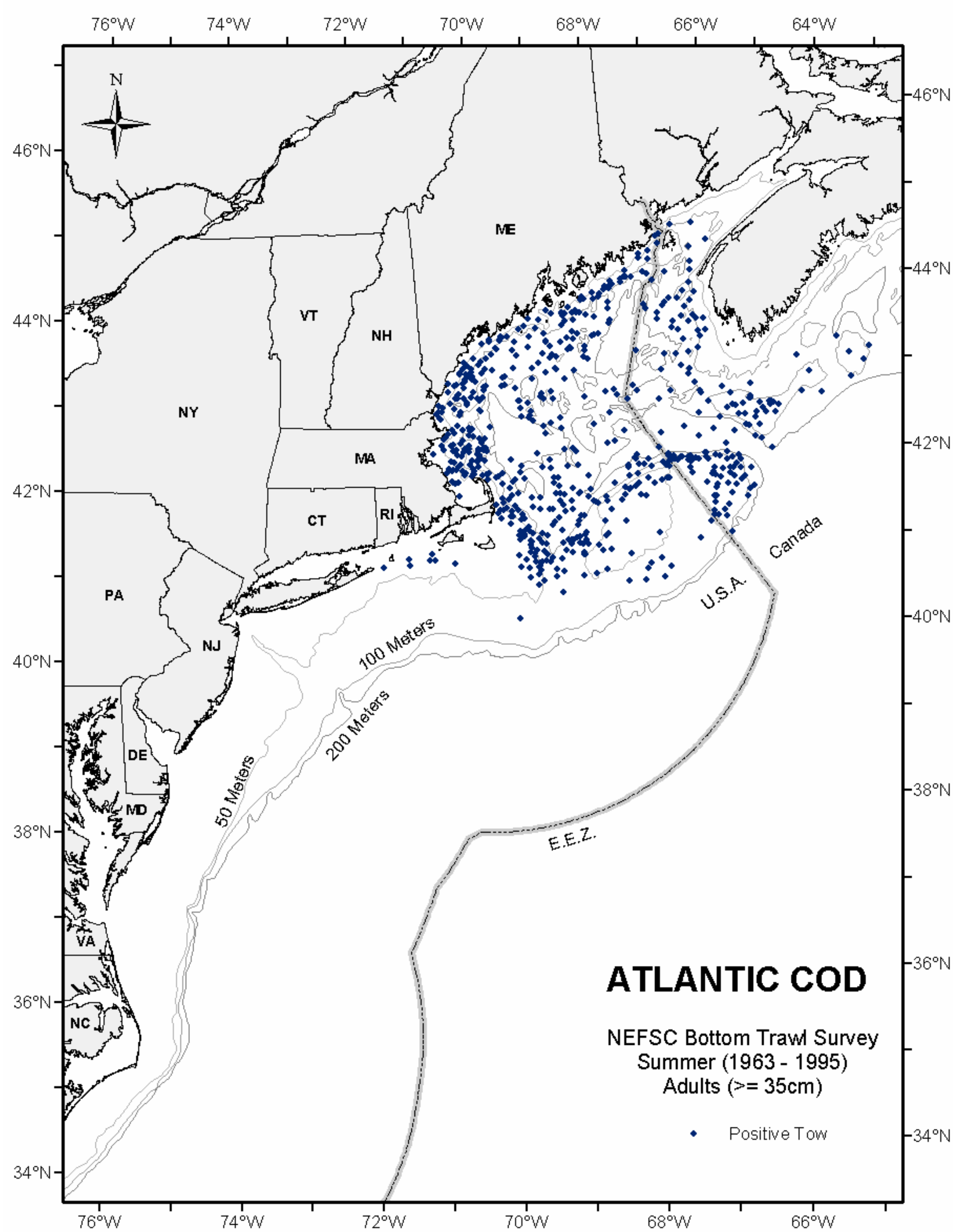


Figure 16. Cont'd.
From NEFSC summer bottom trawl surveys (1963-1995, all years combined). Distributions are displayed as presence only.

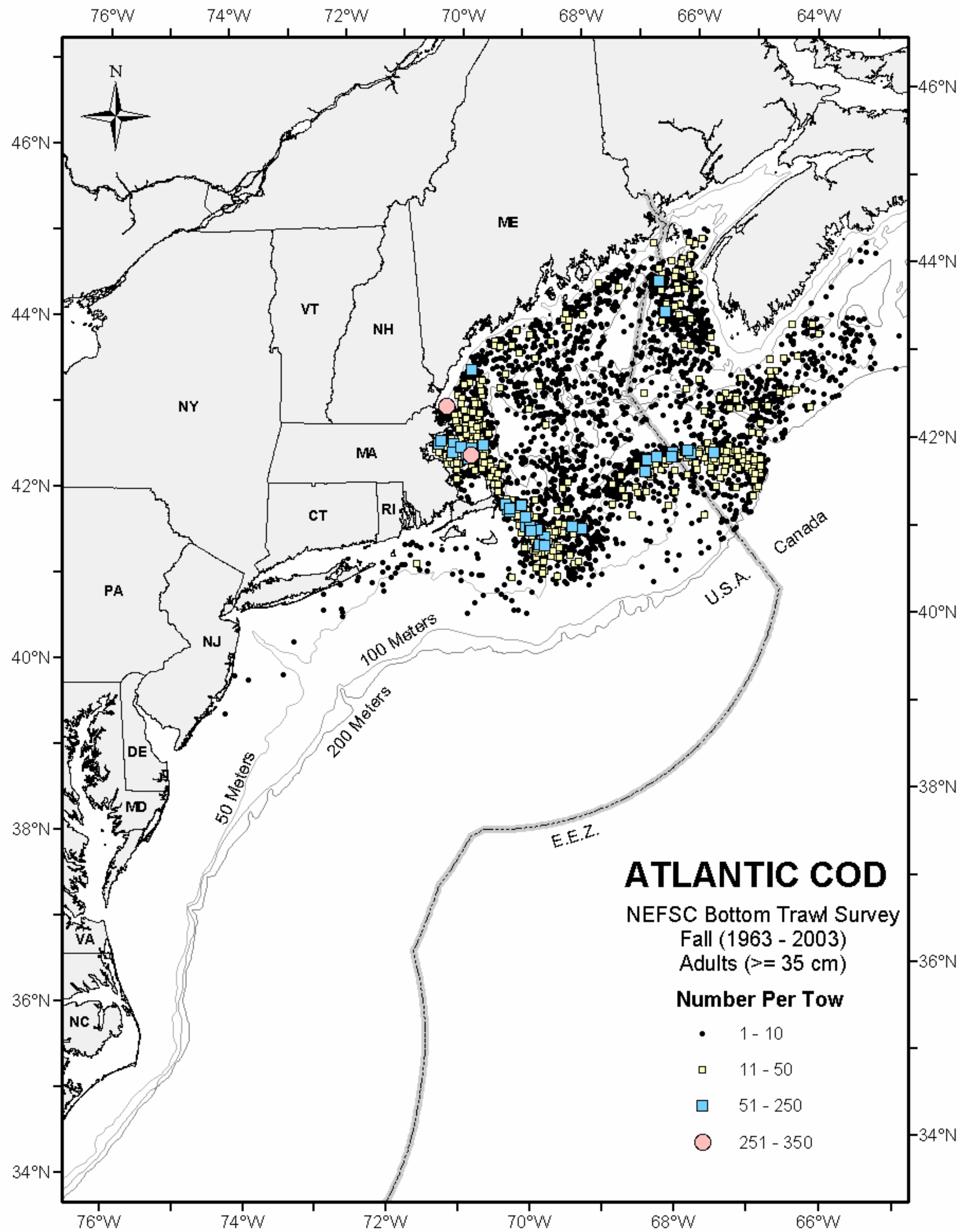


Figure 16. Cont'd.
From NEFSC fall bottom trawl surveys (1963-2003, all years combined). Survey stations where adults were not found are not shown.

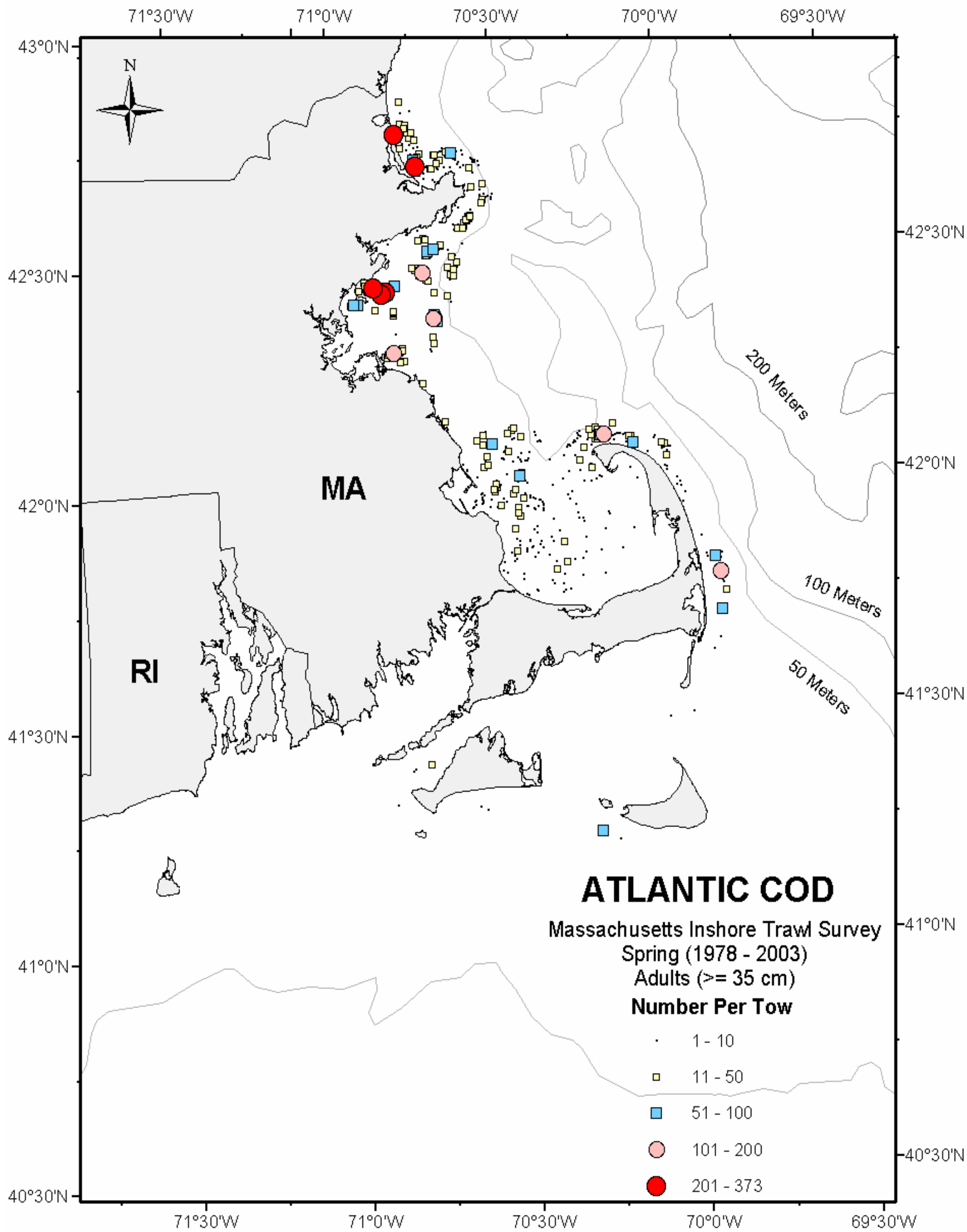


Figure 17. Seasonal distributions and abundances of adult Atlantic cod in Massachusetts coastal waters. From spring Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Survey stations where adults were not found are not shown.

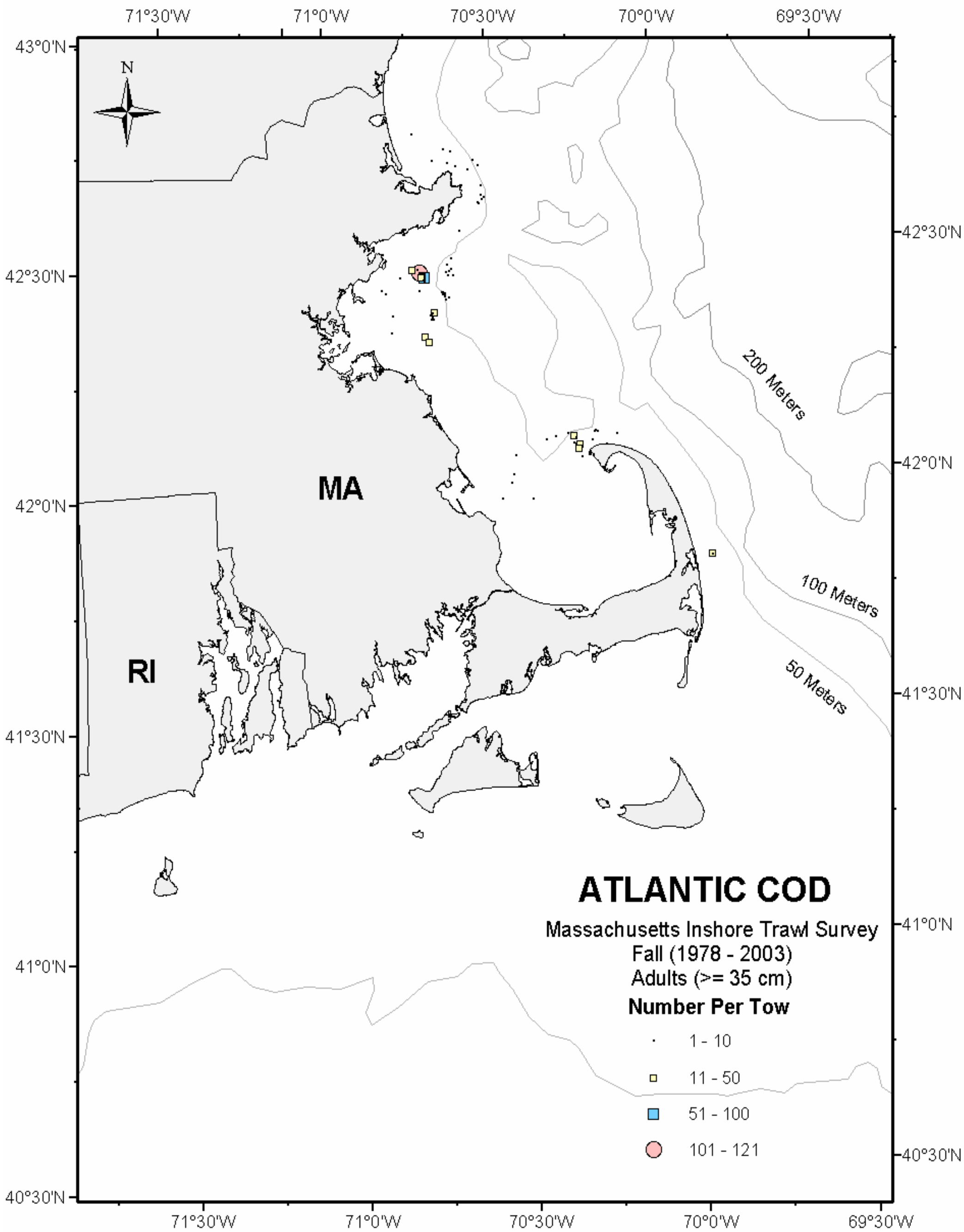


Figure 17. Cont'd.
From fall Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Survey stations where adults were not found are not shown.

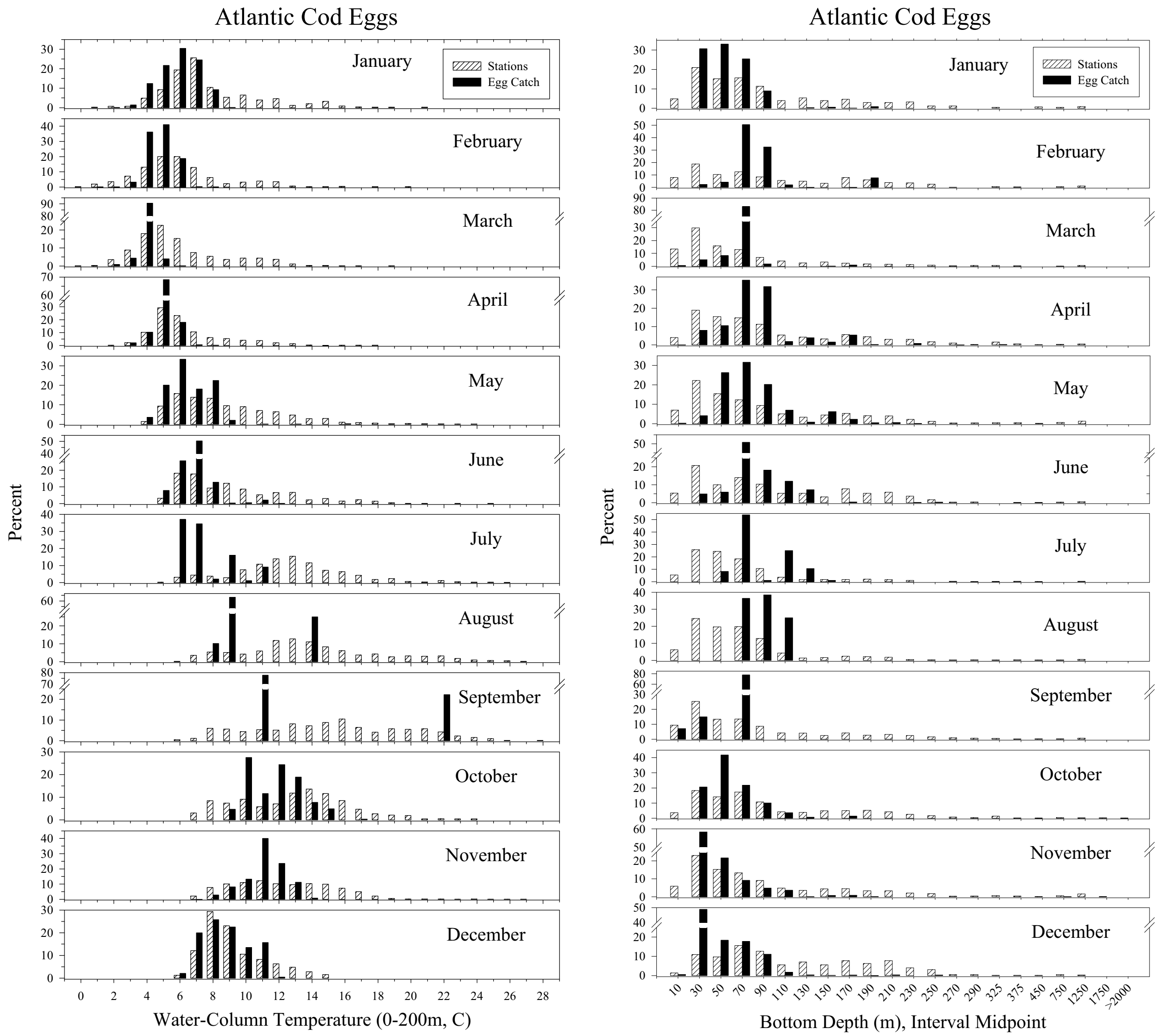


Figure 18. Monthly distributions of Atlantic cod eggs collected during NEFSC MARMAP ichthyoplankton surveys relative to water column temperature and bottom depth.
For all available months and years from 1978-1987combined. Open bars represent the proportion of all stations which were surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2). Note that the bottom depth interval changes with increasing depth.

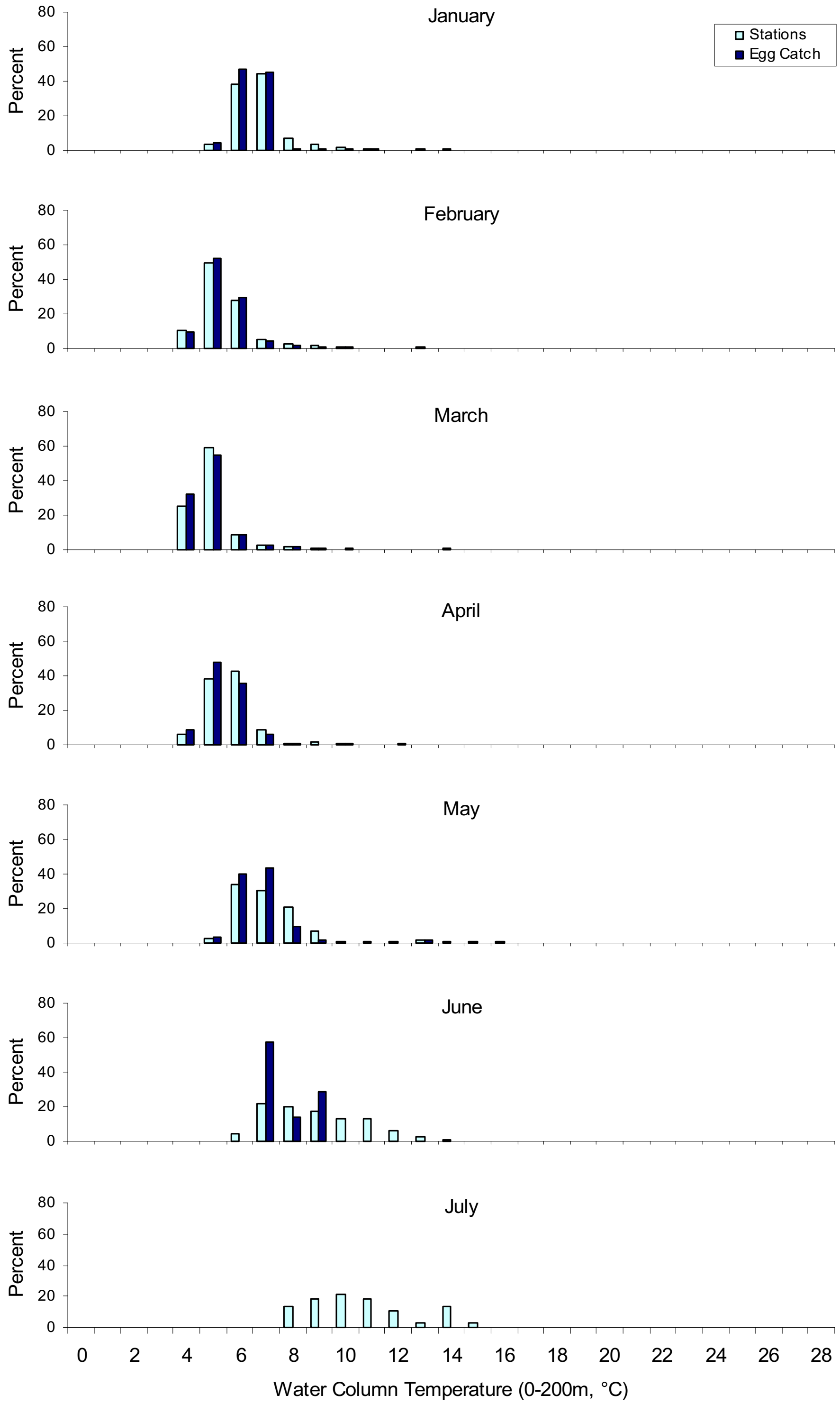


Figure 19. Distributions of Atlantic cod eggs collected during GLOBEC ichthyoplankton surveys relative to water column temperature.
From GLOBEC Georges Bank surveys (February-July, 1995; January-June, 1996-1999) by month for all available years combined. Light bars represent the proportion of all stations surveyed, while dark bars represent the proportion of the sum of all standardized catches (number/10m^2).

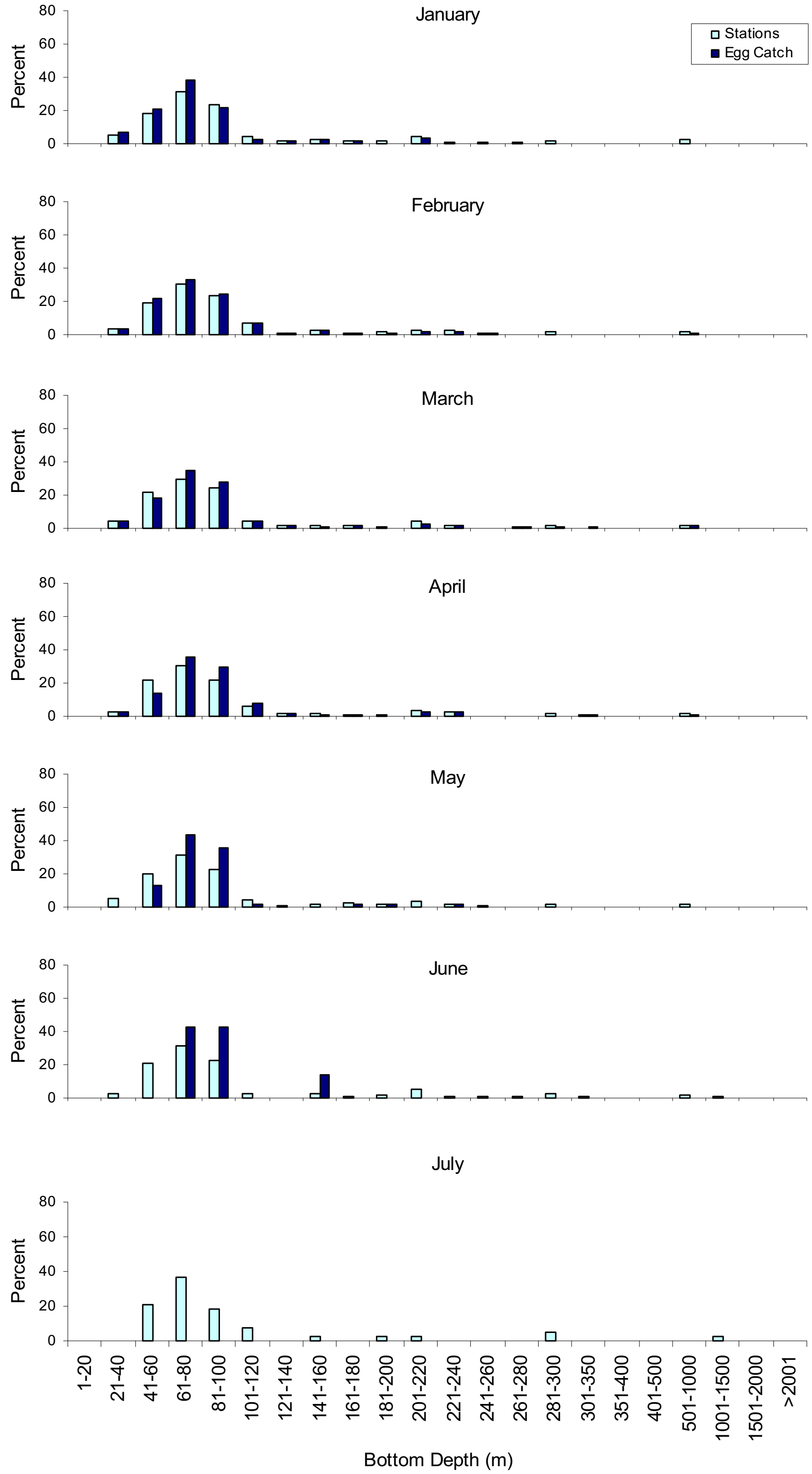


Figure 20. Distributions of Atlantic cod eggs collected during GLOBEC ichthyoplankton surveys relative to bottom depth.
From GLOBEC Georges Bank surveys (February-July, 1995; January-June, 1996-1999) by month for all available years combined. Light bars represent the proportion of all stations surveyed, while dark bars represent the proportion of the sum of all standardized catches (number/10m^2). Note that the bottom depth intervals change with depth.

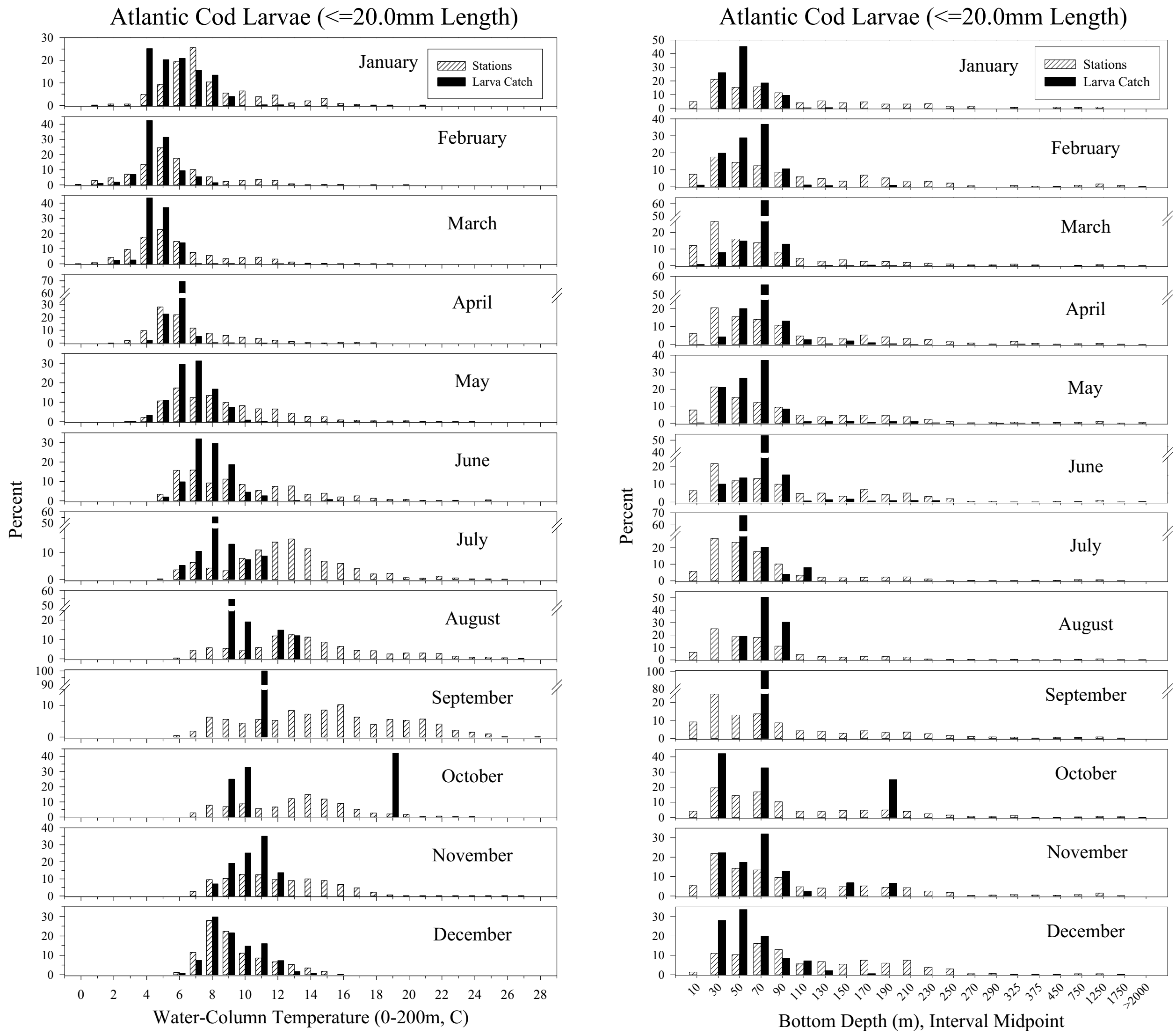


Figure 21. Monthly distributions of Atlantic cod larvae collected during NEFSC MARMAP ichthyoplankton surveys relative to water column temperature and bottom depth.
For all available months and years from 1977-1987combined. Open bars represent the proportion of all stations which were surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2). Note that the bottom depth interval changes with increasing depth.

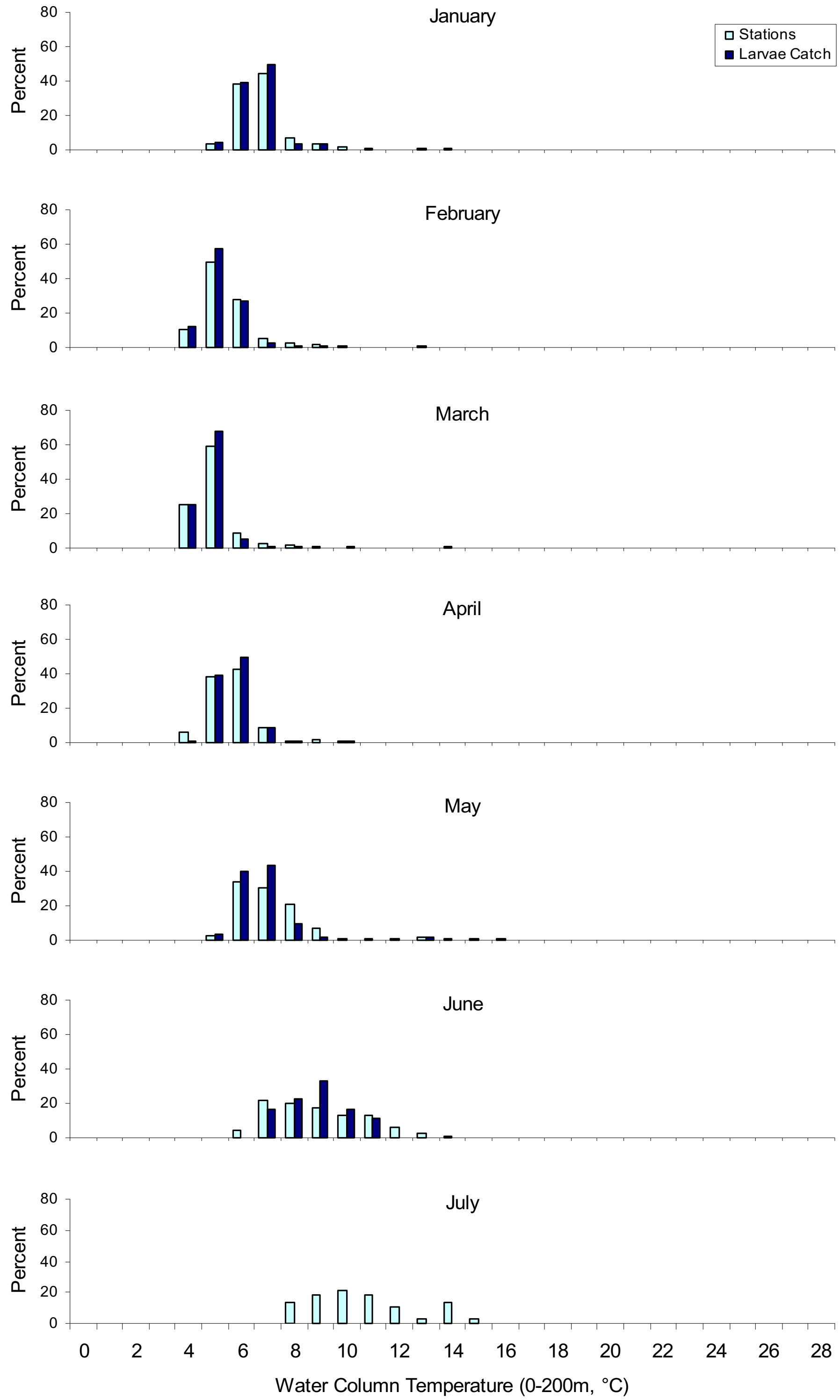


Figure 22. Distributions of Atlantic cod larvae collected during GLOBEC ichthyoplankton surveys relative to water column temperature.
From GLOBEC Georges Bank surveys (February-July, 1995; January-June, 1996-1999) by month for all available years combined. Light bars represent the proportion of all stations surveyed, while dark bars represent the proportion of the sum of all standardized catches (number/10m^2).

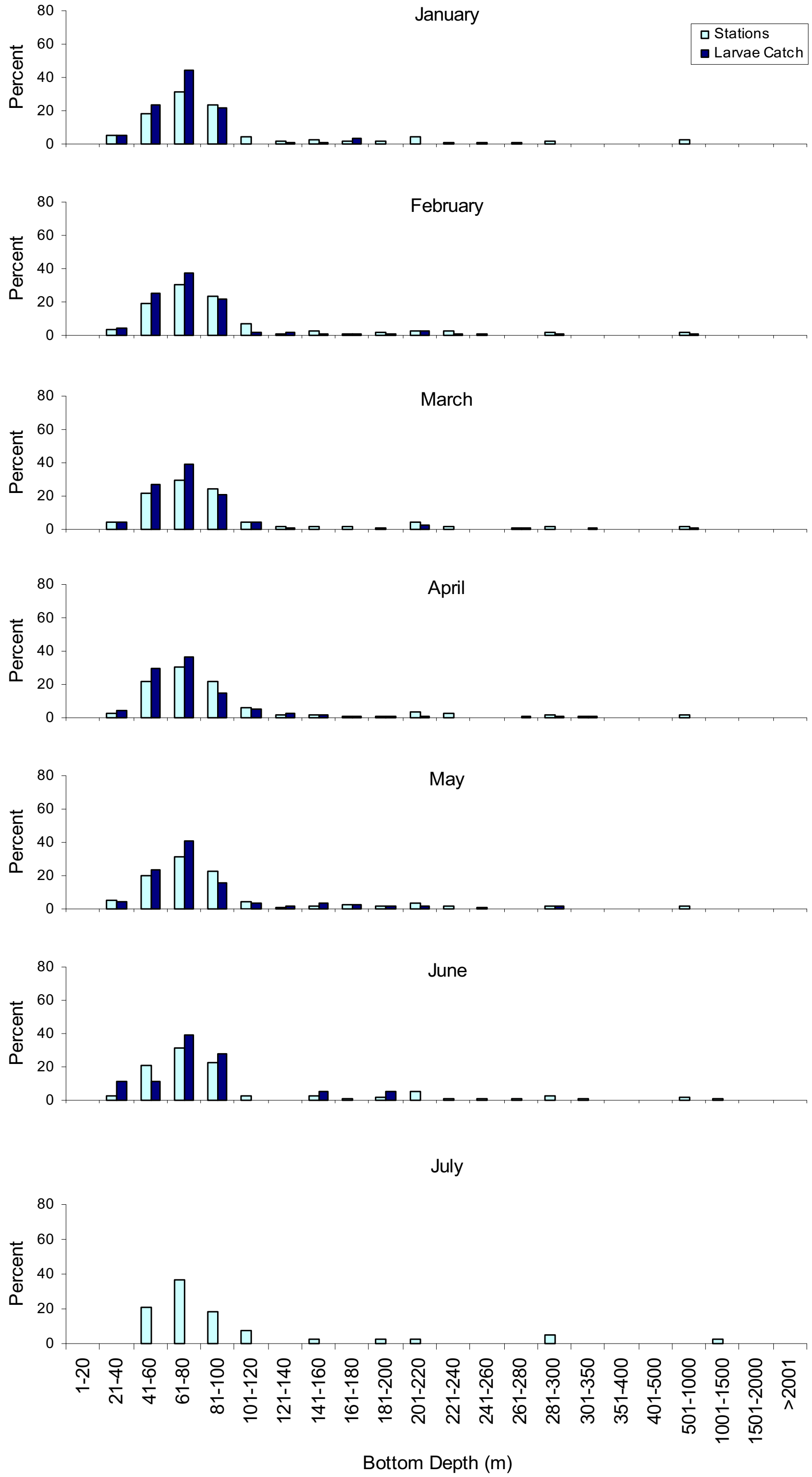


Figure 23. Distributions of Atlantic cod larvae collected during GLOBEC ichthyoplankton surveys relative to bottom depth.
From GLOBEC Georges Bank surveys (February-July, 1995; January-June 1996-1999) by month for all available years combined. Light bars represent the proportion of all stations surveyed, while dark bars represent the proportion of the sum of all standardized catches (number/10m^2). Note that the bottom depth intervals change with depth.

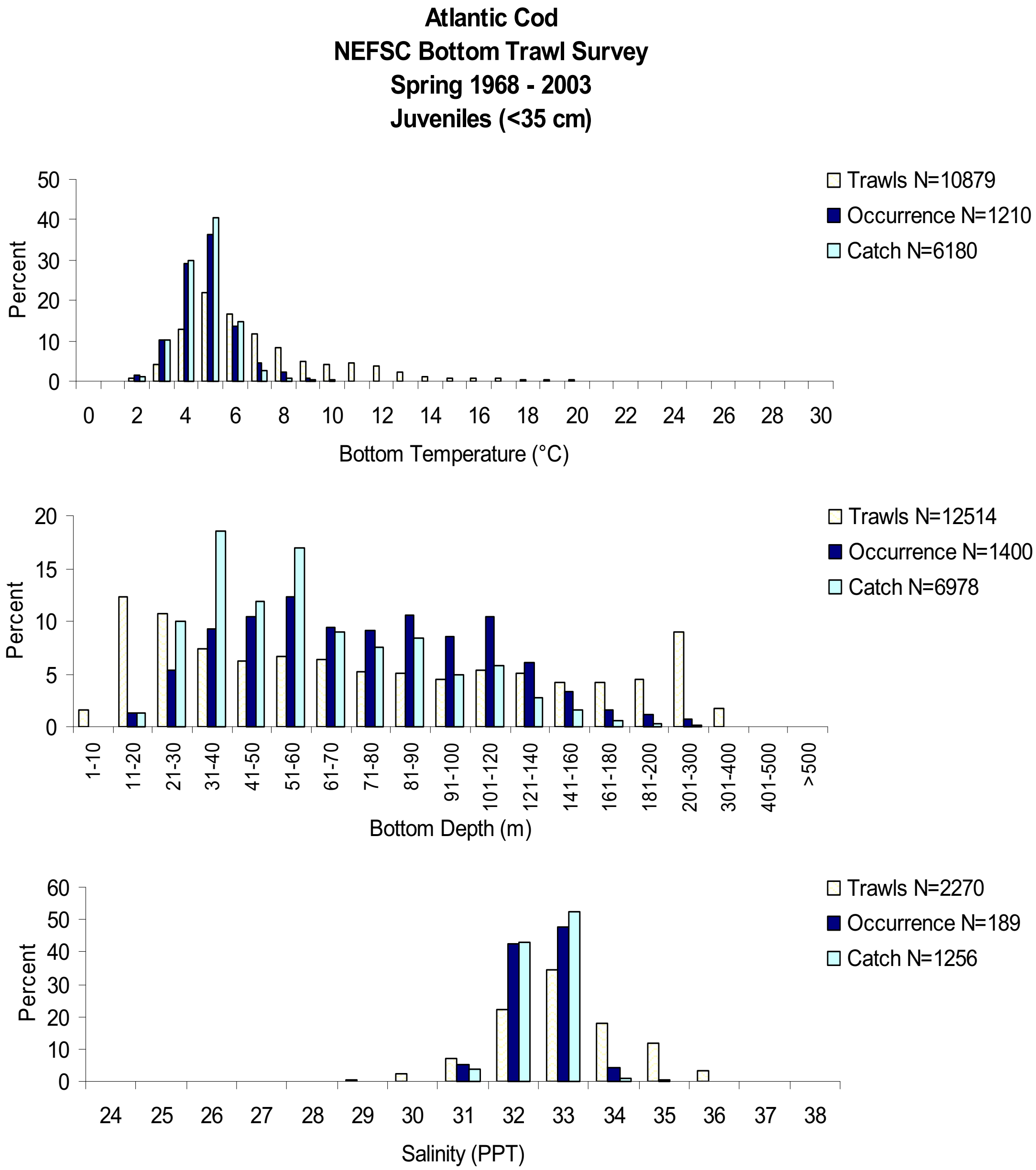


Figure 24. Distributions of juvenile Atlantic cod and trawls from NEFSC bottom trawl surveys relative to bottom water temperature, depth, and salinity.
Based on NEFSC spring bottom trawl surveys (temperature and depth: 1968-2003, all years combined; salinity: 1991-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which Atlantic cod occurred and medium bars show, within each interval, the percentage of the total number of Atlantic cod caught. Note that the bottom depth interval changes with increasing depth.

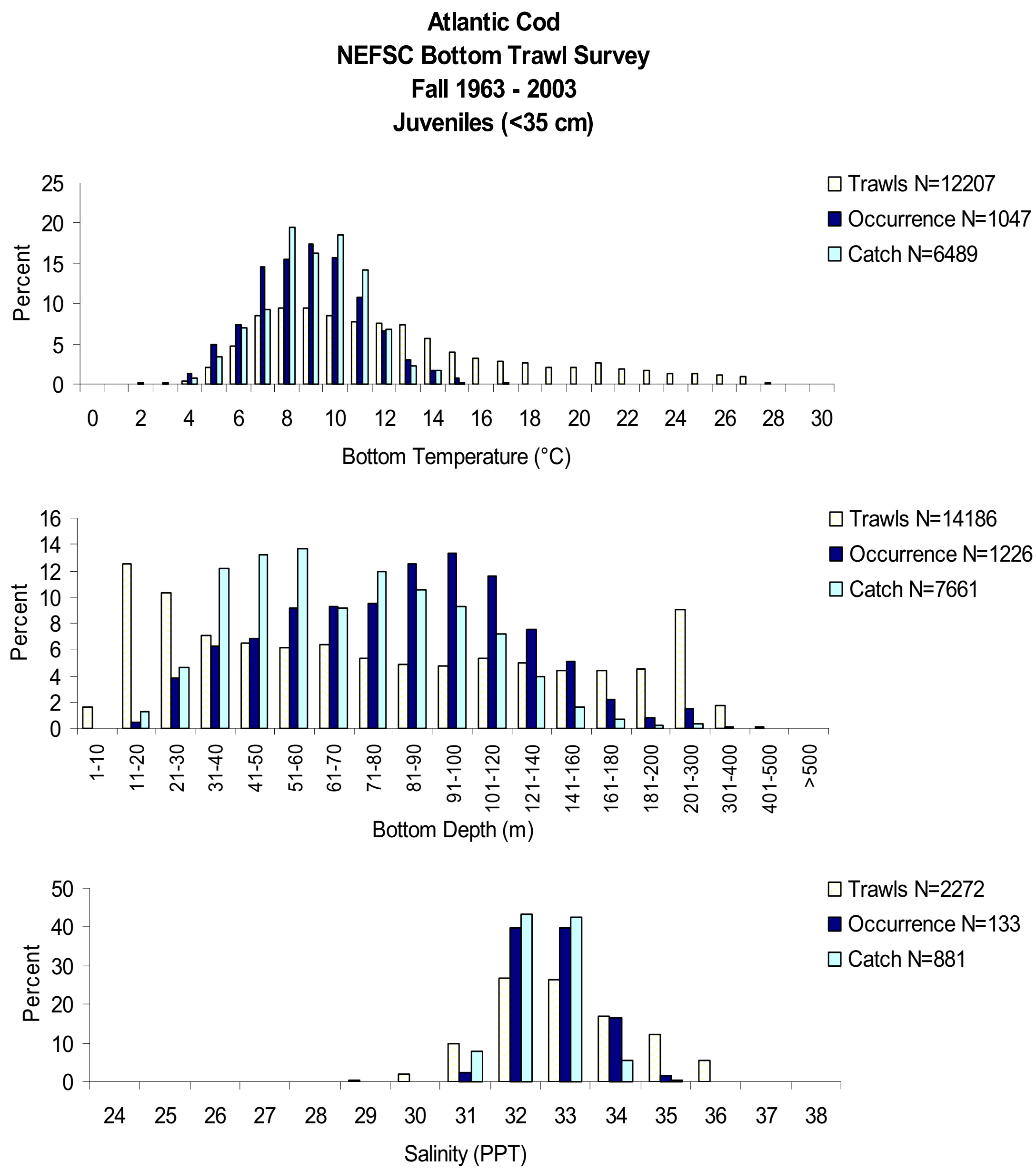


Figure 24. Cont'd.
Based on NEFSC fall bottom trawl surveys (temperature and depth: 1963-2003, all years combined; salinity: 1991-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which Atlantic cod occurred and medium bars show, within each interval, the percentage of the total number of Atlantic cod caught. Note that the bottom depth interval changes with increasing depth.

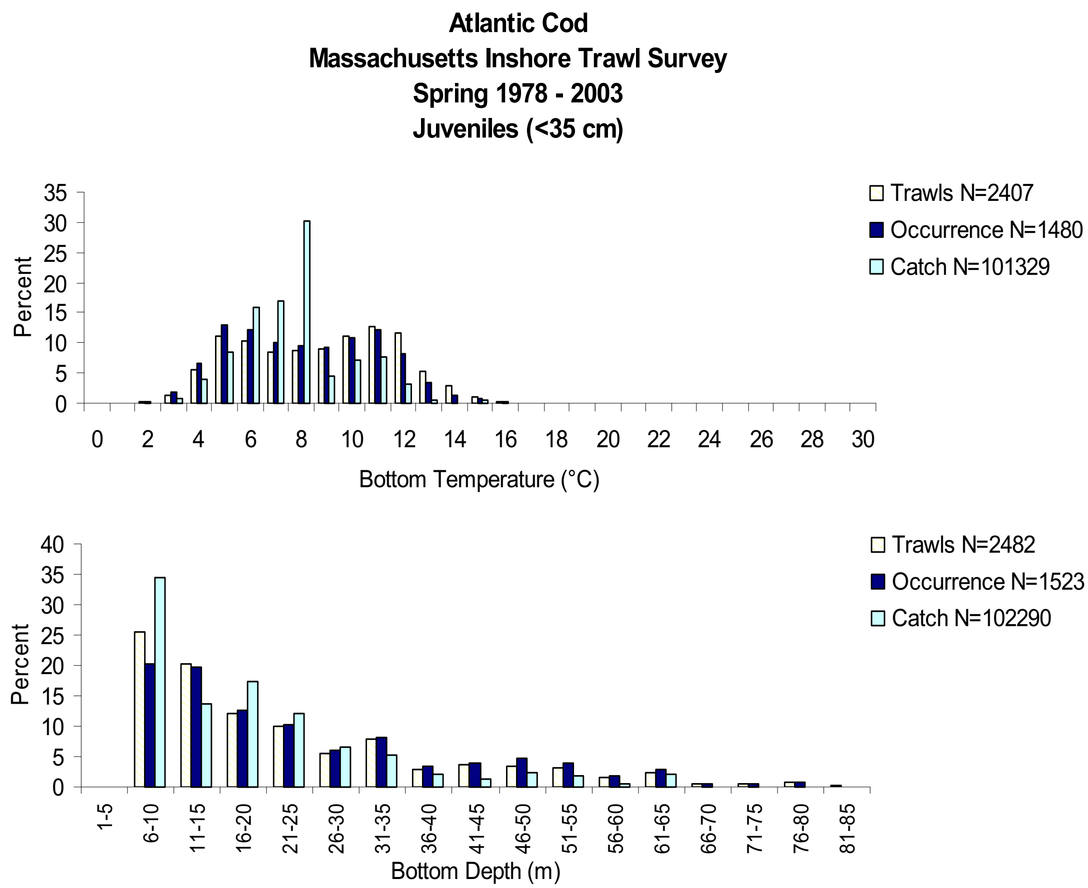


Figure 25. Distributions of juvenile Atlantic cod and trawls in Massachusetts coastal waters relative to bottom water temperature and depth.
Based on spring Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which Atlantic cod occurred and medium bars show, within each interval, the percentage of the total number of Atlantic cod caught.

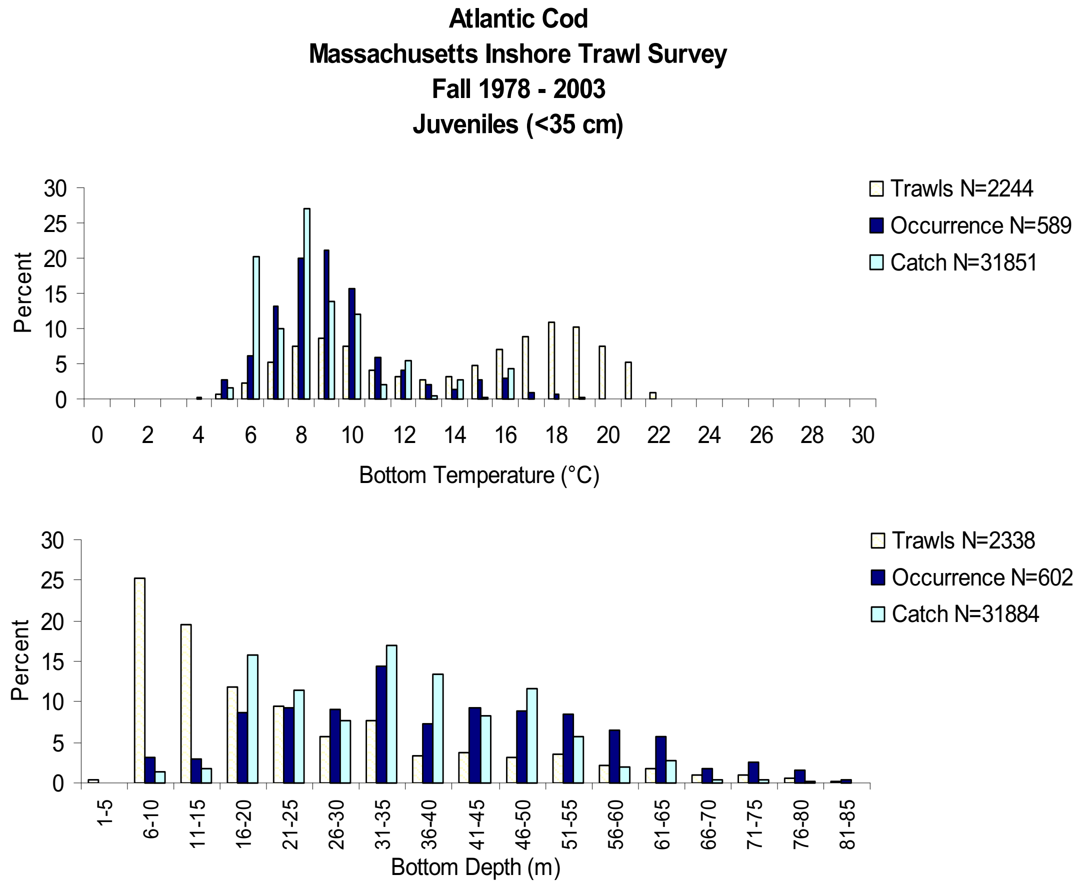


Figure 25. Cont'd.
Based on fall Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which Atlantic cod occurred and medium bars show, within each interval, the percentage of the total number of Atlantic cod caught.

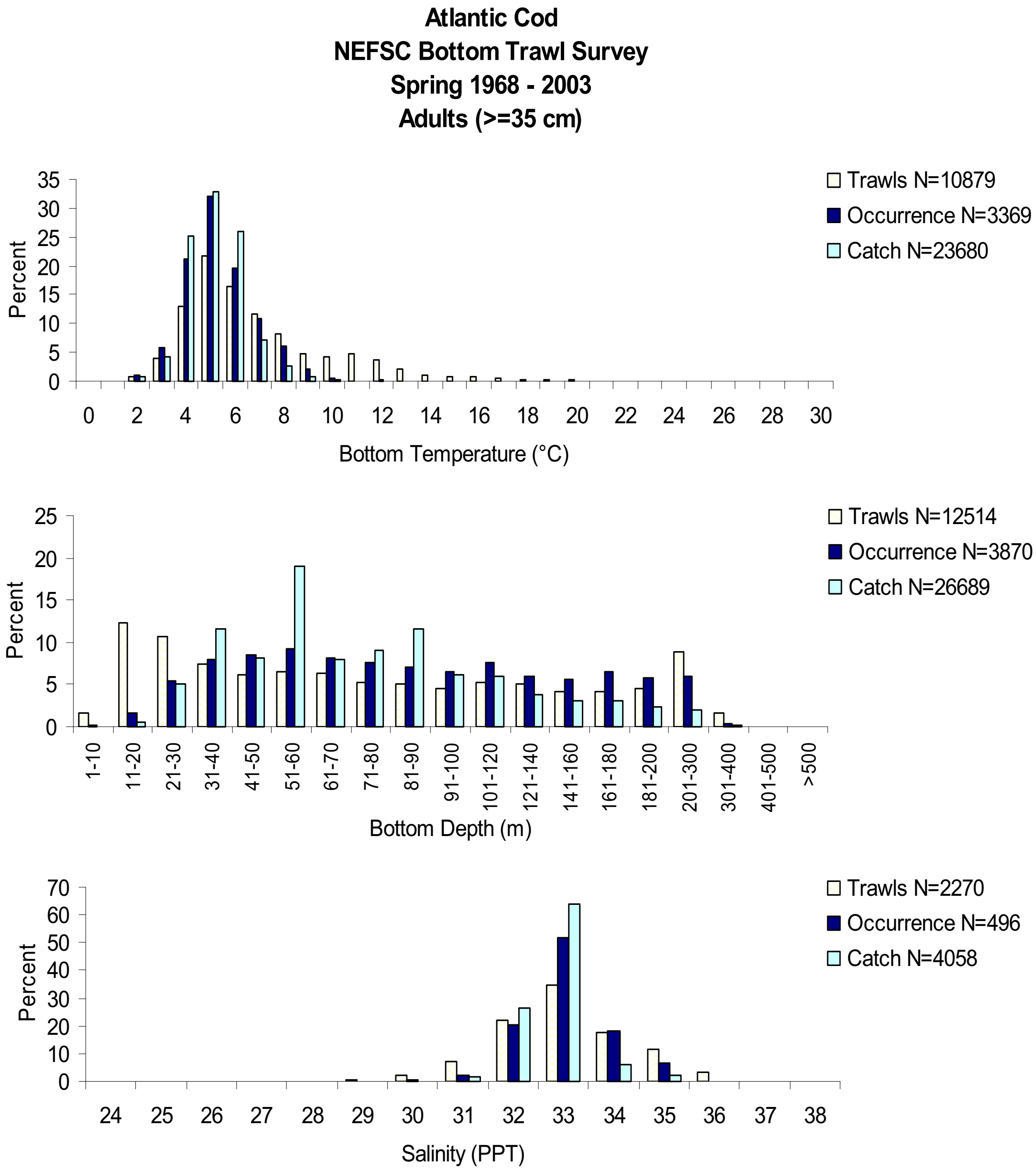


Figure 26. Distributions of adult Atlantic cod and trawls from NEFSC bottom trawl surveys relative to bottom water temperature, depth, and salinity.
Based on NEFSC spring bottom trawl surveys (temperature and depth: 1968-2003, all years combined; salinity: 1991-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which Atlantic cod occurred and medium bars show, within each interval, the percentage of the total number of Atlantic cod caught. Note that the bottom depth interval changes with increasing depth.

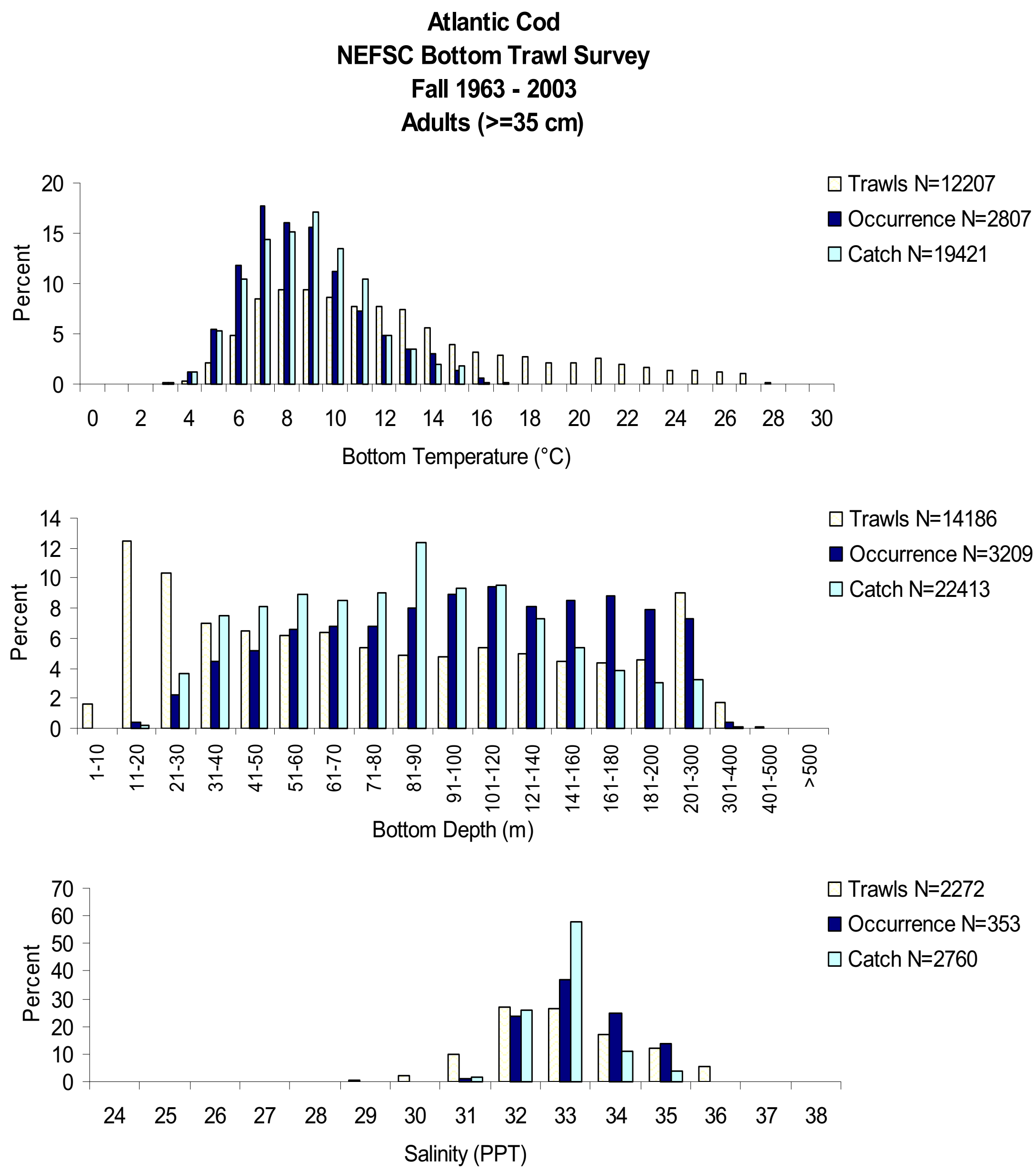


Figure 26. Cont'd.
Based on NEFSC fall bottom trawl surveys (temperature and depth: 1963-2003, all years combined; salinity: 1991-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which Atlantic cod occurred and medium bars show, within each interval, the percentage of the total number of Atlantic cod caught. Note that the bottom depth interval changes with increasing depth.

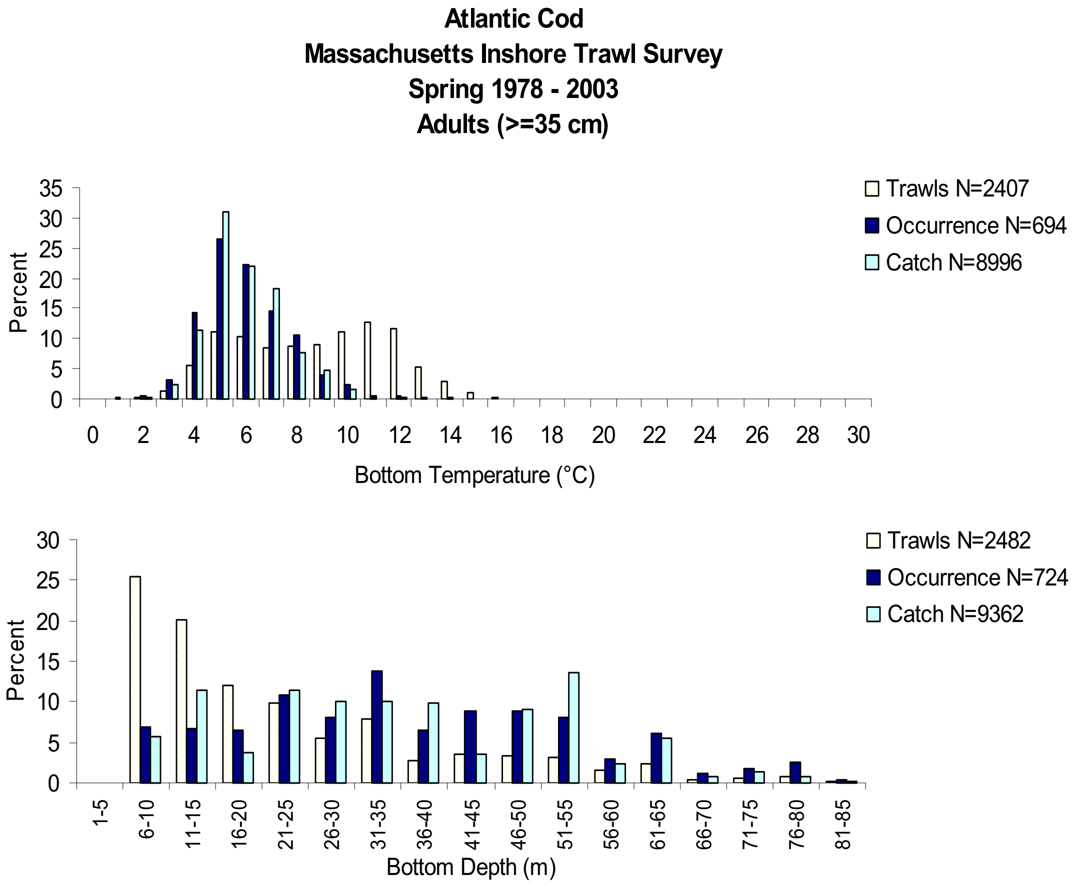


Figure 27. Distributions of adult Atlantic cod and trawls in Massachusetts coastal waters relative to bottom water temperature and depth.
Based on spring Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which Atlantic cod occurred and medium bars show, within each interval, the percentage of the total number of Atlantic cod caught.

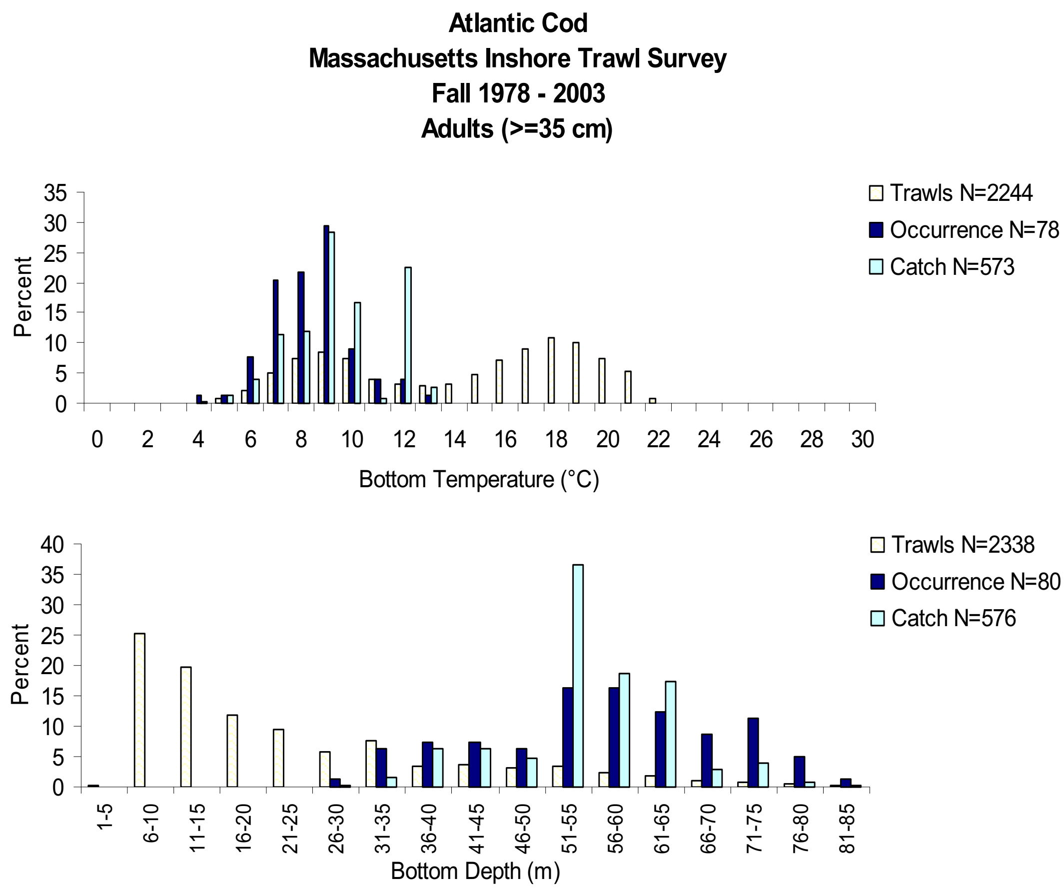


Figure 27. Cont'd.
Based on fall Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which Atlantic cod occurred and medium bars show, within each interval, the percentage of the total number of Atlantic cod caught.

Appendix 1. Table of habitat parameters for Atlantic cod, *Gadus morhua*.

This table is separated into four parts based on life history stage. Abbreviations: SS = Scotian Shelf; Nfld = Newfoundland; GOSL = Gulf of St. Lawrence; PB = Passamaquoddy Bay; GOM = Gulf of Maine; GB = Georges Bank; Mass Bay = Massachusetts Bay; SNE = southern New England (Nantucket Shoals to Hudson Canyon); MAB = Mid-Atlantic Bight.

SPAWNING/EGGS

Authors	Study Area and Period	Habitat (Spatial and Temporal)	Temperature	Salinity	Currents/ Circulation	Light/Vertical
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.
Bigelow and 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 River. Always < 50 fm.	Bottom temperatures 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
Bonnet (1939)	Lab study	Ipswich Bay. Spawns at yearly minimum temperature (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.	---
Brander and Hurley (1992)	SS	Spring spawning proceeds from southwest to northeast along shelf.	---	---	Spawning matches production of copepods.	---
Cohen *et al.* (1990)	North Atlantic	Most productive area in western North Atlantic is eastern half of GB and Grand Banks, followed by southwest 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.
Colton (1978)	GOM	Spawn in Nantucket Shoals and Mass Bay, Jan.-Apr. (peak Jan.). Also Georges and Browns Banks, Ipswich Bay, southwest GOM.	---	---	---	---
Fish (1928)	Mass Bay, southwest GOM	Peak spawning in Mass Bay in January	10.1°C (Nov.) to 0°C (Jan.).	---	Advected out of Mass Bay by currents.	---
Hanke *et al.* (2000)	SS, eastern GOM, Bay of Fundy; 1975-1997	Evidence for a spring and fall spawning, but with regional differences. In March-April spawning observed off southwestern Nova Scotia including Browns Bank, GB, and the Emerald/Western/Sable Island Bank area. Spawning occurs again in November/December on GB and entire Nova Scotia coast, west of Grand Manan and on Western/Sable Island/ Banquereau Bank.	---	---	---	---

Appendix 1. cont'd.

SPAWNING/EGGS

Authors	Study Area and Period	Habitat (Spatial and Temporal)	Temperature	Salinity	Currents/ Circulation	Light/Vertical
Hardy (1978)	GB, GOM	Pelagic. Spawn in inlets, bays, harbors, coastal and offshore banks. Usually < 73 m.	0-6°C for spawning. 2.0-8.5°C optimum for incubation	Spawning 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.
Lough *et al*. (1994)	GB, January-June 1982 vs. 1985	Particles tracked from Northeast Peak spawning in monthly mean flow fields and the 1982 and 1985 wind stresses from Feb through May.	---	---	Greater losses of particles in surface layers < 25 m along southern flank and Northeast Peak when wind stress along-shelf to the northeast. Results consistent with greater losses in 1982 associated with strong northeast wind in April.	Particles released in six horizontal layers.
Lough *et al*. (1996)	GB, May 1992	Vertical distribution of eggs at mixed and stratified sites on southern flank.	Mixed site: 4-7°C. Stratified site: 4-10°C.	---	Inferred southwest transport along southern flank.	At shoal site, eggs distributed through water column. At stratified site, eggs most abundant in surface 20 m with maximum density just above base of thermocline at 20-10 m.
Lough *et al*. (2002)	GB, January-May 1977-1987	Modeling specific year, weekly transport and retention of eggs from Northeast Peak and Western GB spawning areas.	---	---	Specific year flow fields estimated from January to July.	Considerable wind loss of particles at surface; retention consistent at depth (30 m). High recruitment occurred during years of high retention.
Miller *et al*. (1995)	SS, Oct.-May, 1991-1993	Peak spawning during fall.	Temperature (more than season) exerts most influence on egg size (and hatchling size).	---	---	---
Mountain *et al*. (2003)	GB, monthly surveys January-July 1995, 1996	Peak egg abundance in Februrary-March on Northeast Peak of GB	---	---	Advection of egg cohorts consistent with mean climatological pattern. Seasonal egg mortality rates 12-14% d^{-1}.	---

Appendix 1. cont'd.

SPAWNING/EGGS

Authors	Study Area and Period	Habitat (Spatial and Temporal)	Temperature	Salinity	Currents/ Circulation	Light/Vertical
O'Brien *et al*. (2003)	GB, 1978-2000	Egg survivorship was significantly related to age diversity of repeat spawners, spatial distribution of eggs, and bottom temperature.	---	---	---	---
Page *et al*. (1999)	GB, bi-monthly	Inferred mean spawning locations compared with patterns in particle residence times and locations.	---	---	Spawning occurs at times and locations characterized by model residence times >35 days: Northeast Peak during March-April.	Particles released at 1, 10, 20, 30, 40, 50 m depth in mean climatological bi-monthly flow fields.
Rau (1974)	Browns Bank, GB, Nantucket Shoals, February-March 1973	Most eggs found over central and northeast GB.	Most collected at 3-5°C.	Most collected at 32-33 ppt.	---	---
Valerio *et al.* (1992)	Nfld	Studied freezing resistance of eggs and larvae. No antifreeze proteins detected.	If chorion intact, capable of undercooling to -4.0°C. Froze at -4.1 to -17.0°C.	---	---	---
Werner *et al*. (1993)	GB, March-April	Modeling mean March-April transport of eggs from Northeast Peak.	---	---	Eggs in surface advected off bank, but below surface transported to southwest and retained on-bank if shoalward of 70-m isobath.	Vertical position of eggs specified in simulations based on day and night field observations.

Appendix 1. cont'd.

LARVAE

Authors	Study Area and Period	Habitat (Spatial and Temporal)	Temperature	Salinity	Currents/ Circulation	Light/ Vertical	Predators/ Prey (See Food Habits tables also)
Garrison *et al*. (2000)	GB, April-May 1990, 1994, 1995.	Spatial overlap of cod larvae and herring and mackerel predators on southern flank determined.	Larvae occurred mostly in well-mixed water where mean temperature < 7°C.	Mean range: 32.2-32.7 psu	Intrusions of Scotian Shelf water and Slope water increased spatial overlap of predators.	---	Atlantic herring and Atlantic mackerel as they migrate northward in the spring and overlap with patches of larvae on the southern flank of GB.
Hanke *et al*. (2000)	SS, 1975-1982.	Composite data from several programs. Fall and spring spawning populations observed, progressively older larvae found on western SS.	---	---	---	---	---
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.	---	---	---	---
Lough and Bolz (1989)	GB, April, May 1981, May 1983	Consistent cross-shelf age gradient with older larvae found nearer the shoals.	---	---	Average shoalward age gradient consistent with near-bottom cross-isobath current of ca. 1 cm s^{-1}.	Retention of larvae on the shoals enhanced by residing nearer to bottom in waters < 70 m.	---
Lough and Potter (1993)	GB, spring and summer 1981-1986	Vertical distribution patterns of eggs, larvae, and juveniles described from spawning to settlement.	Range: 4-14°C.	Range: 32.5-33.2 ppt	---	Larvae distributed throughout mixed water column, but concentrated within or above thermocline when strongly stratified. Older larvae deeper by day and shoaler by night indicating diel vertical migration.	---

Appendix 1. cont'd.

LARVAE

Authors	**Study Area and Period**	**Habitat (Spatial and Temporal)**	**Temperature**	**Salinity**	**Currents/ Circulation**	**Light/ Vertical**	**Predators/ Prey (See Food Habits tables also)**
Lough and Manning (2001)	GB, May 1997	Model simulation of larvae near the developing tidal front on southern flank.	Surface signature of tidal front 7^{o}C.	Sigma-t values given.	Complex frontal circulation of converging and diverging cells.	Vertical positioning important. Larvae caught in near surface jet transported southwest along flank, while larvae near bottom advected shoalward across the front.	---
Lough and Mountain (1996)	GB, April-May 1981; May 1983.	Effects of small-scale turbulence on larval feeding in well-mixed and stratified water on southern flank.	Turbulence minimal at or below pycnocline (ca. 25 m).	---	Higher turbulence near surface due to wind mixing and at depth due to shear in the tidal current near bottom.	Maximum feeding occurs at low to intermediate turbulence levels where prey is >10-20 prey l^{-1}; i.e., near pycnocline.	See Food Habits table.
Lough *et al*. (1994)	GB, January-June 1982 vs. 1985	Particles tracked from Northeast Peak spawning in monthly mean flow fields and the 1982 and 1985 wind stresses from Feb through May.	---	---	Greater losses of particles in surface layers < 25 m along southern flank and Northeast Peak when wind stress along-shelf to the northeast. Results consistent with greater losses in 1982 associated with strong northeast wind in April.	Particles released in six horizontal layers.	---
Lough *et al*. (1996)	GB, May 1992	Vertical distribution of larvae at mixed and stratified sites on southern flank.	Mixed site: 4-7^{o}C. Stratified site: 4-10^{o}C.	---	Inferred southwest transport along southern flank.	At shoal site, larvae distributed through water column. At stratified site, larvae most abundant in surface 20 m with maximum density just above base of thermocline at 20-10 m.	---

Appendix 1. cont'd.

LARVAE

Authors	**Study Area and Period**	**Habitat (Spatial and Temporal)**	**Temperature**	**Salinity**	**Currents/ Circulation**	**Light/ Vertical**	**Predators/ Prey (See Food Habits tables also)**
Lough *et al*. (2005)	GB, May 1993, 1994	Biophysical 1-D growth model used to compare field derived growth rates (RNA-DNA based) at stratified sites on southern flank. Model includes effect of light on larval feeding response.	Thermocline near 20 m. Temperatures above 20 m, 7-9^{o}C; below 20 m, 6-7^{o}C.	---	Higher turbulence near surface due to wind mixing and at depth due to shear in the tidal current near bottom.	Vertical growth profiles resulted from depth-dependent food limitation and prey selectivity coupled with greater metabolic costs induced by higher temperatures in May 1994. Minimum light level for feeding typically near 60 m depth, so that most of water column had non-limiting feeding. Possible feeding inhibition in surface 10 m due to high light levels.	---
Mountain *et al*. (2003)	GB, monthly surveys January-July 1995, 1996.	Peak abundance in March-April on southern flank GB.	---	---	Movement of larval cohorts between surveys consistent with mid-depth climatological flow fields around GB.	Larvae concentrated in middle and upper part of water column.	---
Myers and Drinkwater (1989)	MAB, 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.

LARVAE

Authors	Study Area and Period	Habitat (Spatial and Temporal)	Temperature	Salinity	Currents/ Circulation	Light/ Vertical	Predators/ Prey (See Food Habits tables also)
Perry and 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.	---
Rau (1974)	Browns Bank, GB, Nantucket Shoals, February-March 1973	Most larvae (2-7 mm) between northeast GB and Nantucket Shoals.	Most collected 3-5°C.	Most collected 32-33 ppt.	---	---	---
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.
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 70 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.	---	---

Appendix 1. cont'd.

JUVENILES

Authors	Study Area and Period	Habitat (Spatial and Temporal)	Temperature	Salinity	Substrate/ Vegetation	Currents/ Circulation	Light/Diel	Predators/ Prey (See Food Habits tables also)
Clark and Green (1990)	Conception Bay, Nfld	Studied diel, depth, seasonal movements in Broad Cove. Seasonal change in diel behavior due to disappearance of shallow (< 30 m) summer thermocline.	Summer: day: 4.1-4.6°C; night: 10-12°C. Fall: stayed in warmer water.	---	Summer: wide-ranging (> 3 km/day), between deep, cold and 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.
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 and 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).
Gotceitas and 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.
Gotceitas *et al.* (1994)	Trinity Bay, Nfld and laboratory studies, 1993	Nearshore bay, various substrates. July-mid-December.	---	---	Predator absent: preferred finer grains and avoided vegetation. Predator present: preferred cobble and hide in vegetation.	---	---	See Substrate/ Vegetation column
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 and without predator using SCUBA and seines.	---	---	Eelgrass used as nearshore nursery by 0+ cod. For refuge from predation and when combined with cobble, stem density was important.	---	---	Predator absent: 0+ used sand and gravel. Predator present: 0+ hid in cobble or eelgrass.
Grant and 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 year classes do opposite.	Age 0+ feed mostly on zooplankton during day; Age 1+ mostly on benthos and fish at night.

Appendix 1. cont'd.

JUVENILES

Authors	Study Area and Period	Habitat (Spatial and Temporal)	Temperature	Salinity	Substrate/ Vegetation	Currents/ Circulation	Light/Diel	Predators/ Prey (See Food Habits tables also)
Grant and 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.
Gregory and Anderson (1997a)	Placentia Bay, Nfld. April, October / November 1995	Submersible and QTC View acoustical seabed classification system for habitat use by age 1-4 juveniles. Occurred most abundantly at 60-120 m.	5.5°C at surface, declining to minus 1.0°C at 75 m.	---	Substrate selection was age specific. Age 1 cod found primarily in areas with gravel substrate and low relief. Age 2-4 cod found mostly associated with coarse substrate and high relief. Macroalgae cover substrate not selected by either group.	Slight tidal current (max 0.1 to 0.2 m s^{-1}).	Suggest diel movements do not occur among juveniles at spring water temperatures (~-1.0°C).	Predator avoidance behavior indicates young mottled individuals rely on crypsis, whereas older uniform-colored individuals associated with a specific physical feature.
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 8-42 m); 1+ range 73-274 m.	Range 6-20°C	From < 31.3 to 35.0 ppt.	---	---	---	---
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.	
Keats and Steele (1992)	Bonavista Bay, Nfld. May-August 1986	Described in Keats (1990).	---	---	---	---	Juveniles move into shallow water at night and mostly rest near bottom.	Diet consists mostly of planktonic prey taken during daytime.
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.

Appendix 1. cont'd.

JUVENILES

Authors	Study Area and Period	Habitat (Spatial and Temporal)	Temperature	Salinity	Substrate/ Vegetation	Currents/ Circulation	Light/Diel	Predators/ Prey (See Food Habits tables also)
Laurel *et al*. (2003)	Bonavista Bay, Nfld. Summer/autumn 1999 and 2000	Various sizes of artificial eelgrass mats deployed with tethered age 0-yr cod to monitor local predation rates.	---	---	Artificial eelgrass mats of 5 sizes.	---	---	Predation rates negatively correlated with patch size, suggesting that larger patches reduced predator foraging ability. However, high predator densities in largest eelgrass mat resulted in higher rates of predation than expected.
Laural *et al*. (2004)	Bonavista Bay, Nfld 1996, 1998-2001.	Shallow coastal areas < 6 m depth with substrate varying from mud to bedrock, often associated with vegetative cover, eelgrass being the most common. Bi-weekly seine surveys, mark-recapture and lab experiments conducted.	---	---	Cod initially settle in August/September, and again in October, mostly associated with eelgrass but periodically over sand as density in eelgrass increased. Cod formed tighter aggregations over sand than eelgrass. Mark-recapture experiments indicated movement between sites. Habitat suitability dynamic rather than fixed variable.	---	---	Eelgrass supports higher densities of prey such as pelagic and epiphytic zooplankton.
Lindholm *et al*. (1999)	Aquarium experiments on predation of 0-year juveniles by 3+ cod over 5 seafloor habitats.	Habitats vary in complexity to mimic the range of impacts of mobile fishing gear given a gradient in fishing effort.	Aquarium maintained at 8-10^{o}C.	---	Experimental habitats: sand, cobble, minimum density short sponge, maximum density short sponge, and tall sponge. Significant decrease in 0-yr mortality with epifaunal density compared to flat sand. Epifaunal density found to be more significant than epifaunal height in reducing 0-yr mortality.	---	12 h light/dark regime.	---
Lough *et al.* (1989)	GB	Descend to bottom at 4-6 cm. 0+ (newly settled) fish dense on northeastern GB, 70-100 m depth during summer.	---	---	Pebble-gravel deposits.	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.

Appendix 1. cont'd.

JUVENILES

Authors	Study Area and Period	Habitat (Spatial and Temporal)	Temperature	Salinity	Substrate/ Vegetation	Currents/ Circulation	Light/Diel	Predators/ Prey (See Food Habits tables also)
MacDonald *et al.* (1984)	Bay of Fundy and PB	Juveniles in PB in winter, close to beach in summer. (See "Adults")	0-6°C in winter; 8-13°C in summer.	30-31 ppt winter; 31-32 ppt summer.	Mud, gravel, rock in winter; sand, mud, rock in summer.	---	---	---
Murawski and Finn (1988)	GB	Evaluated species co-occurrences relative to temperature and depth preferences and spatial distribution by species and 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.	---		---
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.	---	---	---	---	---
Tupper and Boutilier (1995)	St. Margaret's Bay, Nova Scotia	Studied survival and 0+ densities in four 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.

Appendix 1. cont'd.

JUVENILES

Authors	Study Area and Period	Habitat (Spatial and Temporal)	Temperature	Salinity	Substrate/ Vegetation	Currents/ Circulation	Light/Diel	Predators/ Prey (See Food Habits tables also)
Wigley and Serchuk (1992)	GB, SNE. 1982-1986. Commercial landings data and spring and fall research-vessel data.	Ages 1-4 distributed at different depths in spring (57, 58, 68, 86 m, respectively). During autumn age 3 fish co-occurred with age 1-2 fish at 86 m. 0-group fish mean depth at 69 m. Seasonal shift in age 2 fish. Both the Nantucket Shoals and GB populations move to deeper water in the summer/fall along the 100 m contour, the western side of the Great South Channel, and the Northern Edge and Northeast Peak areas. Distribution patterns delineated more by depth than temperature. 0-group in autumn distinct from all other age-groups with respect to temperature and depth.	Mean temperatures for all age groups 5.3°C in spring and 9.2°C in autumn. Mean temperature for 0-group 10.0°C. Seasonal shifts most likely associated with temperature.	---	---	---	---	Fall occurrence of some age-3 fish with ages 1-2 may be related to diet.

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 Food Habits tables also)
Bigelow and 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 in summer, 3 fm in winter.	0-12.8°C. Prefer < 10.0 °C.	---	Mostly rocky, pebbly, sandy, or gravelly bottoms.	---	---	Large sharks and spiny dogfish.
Colvo-coresses and Musick (1984)	MAB, 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.	---	---	---
Helser and Brodziak (1996)	GOM, GB, SNE, MAB	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	---	---	---
Jean (1965)	GOSL; SS	GOSL: 35-145 m in summer; 130-180 m in winter. SS: 65-110 m in summer; 90-135 m in winter.	GOSL: 0-6°C in summer; 1-3 °C in winter. SS: 1-8°C in summer; 2-4 °C in winter.	---	---	---	---	---
Link and Garrison (2002)	SS, GOM, GB, SNE, MAB. Spring and fall research survey cruises 1973-1998. 25-yr time series of food habits data.	Omnivorous diet shifted significantly over 3 decades concurrent with forage species abundance and distribution.	---	---	---	---	---	Cod are opportunistic feeders, prefer sand lance, Cancer spp., crabs and herring, regardless of abundance or overlap. Early juveniles consumed more pelagic than benthic invertebrates, medium cod consumed benthic invertebrates and fish, and larger cod consumed larger amounts of fish. Cannibalism increased with size.

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 Food Habits tables also)
MacDonald *et al.* (1984)	Bay of Fundy and PB	Adults in PB summer; GOM, SS winter. (See "Juveniles").	8-13°C summer; 4-8°C winter.	31-32 ppt in summer; 31-32 ppt in winter.	Mud, rock in summer.	---	---	---
Mountain and Murawski (1992)	SS, GOM, GB, SNE, MAB. Spring NEFSC research survey cruises 1963-1990.	Significant correlation between GB weighted mean catch and areal average temperature, but unable to determine if distributional change either a north-south shift or change in water depth.	Significant decadal changes in spring temperatures from cold 1960's to warmer 1970's and intermediate 1980's. Interannual variations of ±2-4°C observed in all shelf regions.	---	---	---	---	---
Murawski and Finn (1988)	GB	Evaluated species co-occurrences relative to temperature and depth preferences and spatial distribution by species and age. Overlap with silver hake, mostly in fall. Also see "Juveniles"	Age 1+ means in winter: 4.2°C; spring: 5.4°C; summer: 8.0 °C; fall: 9.3°C.	---	Age 1+ means in winter: 88 m; spring: 67 m; summer: 72 m; fall: 84 m.	---	---	---
Odense *et al.* (1966)	Bay of Chaleur (laboratory study)	Studied tolerance to low salinity.	5-6°C (not manipulated).	First mortalities when salinities reached 2.7 ppt; complete mortality at 2.3 ppt.	---	---	---	---
Rose and 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 and Leggett (1989)	GOSL	Cod were aggregated within narrow temperature range, unless prey present, then found in wider range.	Without prey, usually between 0 and 5°C.	---	---	---	---	When capelin present, range -0.5 to 8.5°C.
Scott (1982a)	SS, Bay of Fundy	Determined preferred depths, temperatures, and salinities for several groundfish species. Compared to other gadoids, cod prefers shallower, colder, less saline waters.	0-13°C (mean 4.9°C). Preferred temperature showed increase northeast to southwest, 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.	---	---	---
Tyler (1971)	PB 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 Sept.	Sampled brown mud bottom, sloping from 38-55 m.	---	---	---

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