NOAA Technical Memorandum NMFS-NE-191

Essential Fish Habitat Source Document:

Northern Shortfin Squid, *Illex illecebrosus*, Life History and Habitat Characteristics

Second Edition

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

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NOAA Technical Memorandum NMFS-NE-191

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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]).

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[a]Robins, C.R. (chair); Bailey, R.M.; Bond, C.E.; Brooker, J.R.; Lachner, E.A.; Lea, R.N.; Scott, W.B. 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 EFH species reports (plus one consolidated methods report). The EFH species reports are a survey of the important literature as well as original analyses of fishery-independent data sets from NOAA Fisheries and several coastal states. The species reports are also the source for the current EFH designations by the New England and Mid-Atlantic Fishery Management Councils, and understandably have begun to be referred to as the "EFH source documents."

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

The initial series of EFH species source documents were published in 1999 in the *NOAA Technical Memorandum NMFS-NE* series. Updating and review of the EFH components of the councils' Fishery Management Plans is required at least every 5 years by the NOAA Fisheries Guidelines for meeting the Sustainable Fisheries Act/EFH Final Rule. The second editions of these species source documents were written to provide the updated information needed to meet these requirements. The second editions provide new information on life history, geographic distribution, and habitat requirements via recent literature, research, and fishery surveys, and incorporate updated and revised maps and graphs. This second edition of the northern shortfin squid EFH source document is based on the original by Luca M. Cargnelli, Sara J. Griesbach, and Christine A. Zetlin, with a foreword by Jeffrey N. Cross (Cargnelli *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 northern shortfin squid, *Illex illecebrosus* (Figure 1), is a highly migratory species of the family Ommastrephidae. Distributed across a broad geographic area, *I. illecebrosus* is found in the northwest Atlantic Ocean between the Sea of Labrador and the Florida Straits (66ºN to 29º30'N; Roper *et al.* 1998). Throughout its range of commercial exploitation, from Newfoundland to Cape Hatteras, North Carolina, the population is considered to constitute a single stock (Dawe and Hendrickson 1998). The southern stock component (inhabiting U.S. waters) is managed by the Mid-Atlantic Fishery Management Council, in accordance with the Atlantic Mackerel, Squid and Butterfish Fishery Management Plan (MAFMC 1998), and the northern stock component (inhabiting waters between Newfoundland and Nova Scotia) is assessed and managed by the Northwest Atlantic Fisheries Organization (Hendrickson *et al.* 2002). Both stock components are managed based on an annual quota.

This Essential Fish Habitat Source Document provides information on the life history and habitat characteristics of northern shortfin squid. Data sources and methodologies used to prepare this document are described in Reid *et al.* (1999).

LIFE HISTORY

The life history characteristics of northern shortfin squid have been reviewed by Black *et al*. (1987), Perez (1994), and O'Dor and Dawe (1998). Most of the supporting studies have been based on the northern component of the stock. Like many squid species, *I. illecebrosus* lives for less than one year, has a high natural mortality rate, and exhibits a protracted spawning season whereby overlapping "microcohorts" enter the population throughout the year and exhibit variable growth rates (Caddy 1991; Jackson 1994). The life cycle is comprised of oceanic and neritic components. During spring, squid migrate onto the continental shelf between Newfoundland and Cape Hatteras. During late autumn, squid migrate off the continental shelf, presumably to a winter spawning site (Black *et al*. 1987). The seasonal proportion of squid residing beyond the continental shelf is unknown because this habitat is not sampled during seasonal U.S. and Canadian bottom trawl surveys. Little is known about either the habitat of mature individuals (particularly females) or the winter habitat of the species.

The life cycle (Figure 2) proposed by Black *et al.* (1987) remains hypothetical because several aspects remain unknown. These include the location of the winter spawning site, migration patterns between northern and southern stock components, the autumn spawning migration route, and what fraction of the stock inhabits waters beyond the continental shelf.

New life history information regarding population structure, spawning location, lifespan, and age and size at maturity are described herein. This new information is based on data collected on the U.S. shelf during a stratified, random bottom trawl survey of the population (Hendrickson 2004).

EGGS AND PARALARVAE

Illex illecebrosus egg masses have never been collected in the wild (O'Dor and Dawe 1998) but have been described from laboratory spawning events. The gelatinous egg balloons are 0.5 to 1.0 m in diameter and contain between 10,000 and 100,000 eggs (Durward *et al.* 1980). Females can produce multiple egg masses (Durward *et al.* 1978). Mature eggs are ovoid, ranging from 0.9 x 0.6 to 1.0 to 0.8 mm in size, and weigh between 200 and 250 μg (Durward *et al.* 1980).

Laboratory studies indicate that hatching occurs in 16 days at 13°C, 12 days at 16°C, and 8 days at 21°C; normal embryonic development requires water temperatures of at least 12.5°C (O'Dor *et al*. 1982b). Paralarvae may remain within the remnants of the egg mass to utilize the nutrients as a food source (Durward *et al.* 1980). In the laboratory, paralarvae hatch at approximately 1.1 mm mantle length (ML) (Durward *et al.* 1980), then enter a transitional stage at approximately 5.0 mm ML, followed by a juvenile stage at about 7.0 mm ML (Hatanaka 1986).

Based on the distribution of paralarvae, it is hypothesized that the Gulf Stream serves as the primary transport mechanism for egg masses and paralarvae (O'Dor 1983; Rowell *et al.* 1985a). Paralarvae have been collected during all seasons (Roper and Lu 1979), from south of Cape Hatteras to as far north as the tail of the Grand Bank (Dawe and Beck 1985; Hatanaka *et al.* 1985). Paralarvae are most abundant in February and March, in the nutrient-rich waters of the Gulf Stream/Slope Water convergence zone; above the thermocline at temperatures greater than 13°C (Hatanaka *et al.* 1985).

I. illecebrosus paralarvae hatched in the laboratory were 1.10 to 1.25 mm ML (O'Dor *et al.* 1986). *Illex* sp. hatchlings have only been collected in waters south of Cape Hatteras (35.5ºN) and during February through March (Dawe and Beck 1985; Rowell *et al*. 1985a). However, species identification of *Illex* paralarvae is problematic, particularly if caught south of New Jersey, due to the difficulty in distinguishing between paralarvae of *I. illecebrosus* and two sympatric *Illex* species (Vecchione and Roper 1986).

JUVENILES AND ADULTS

Onset of the juvenile stage at 8 to 10 mm ML is indicated by a separation of the proboscis into a pair of tentacles (Roper and Lu 1979). Juveniles collected in surveys conducted in the Gulf Stream and continental slope waters during February through May ranged in size from 10 to 94 mm ML (O'Dor 1983). During late spring, juveniles migrate onto the continental shelf between Nova Scotia and Cape Hatteras (O'Dor 1983; Black *et al*. 1987).

Juveniles caught on the continental shelf in late May ranged in size from 34 to 68 mm ML. Gonadal development began at about 64 mm ML in males and at 74 mm ML in females. Males attained 50% maturity at a smaller size and older age than females, but these differences were not statistically significant. Size- and age-at-maturity increased with latitude and were correlated with decreases in water temperature (Hendrickson 2004). Mean size at maturity may also vary inter-annually (Coelho and O'Dor 1993). In inshore Newfoundland waters, the percentage of mature males and male gonadosomatic indices were significantly higher for squid hatched in May than during March or April. Although females do not become mature in inshore Newfoundland waters, those hatched in May were more mature than those hatched in March or April (Dawe and Beck 1997). Captive females matured within 40 to 60 days (O'Dor *et al*. 1977).

In Nova Scotian and Newfoundland waters, males mature at a faster rate than females and are believed to emigrate during autumn from continental shelf fishing areas before females (Black *et al.* 1987). Evidence for this phenomenon is a seasonal decline in the percentage of males collected on the Scotian Shelf during some years (Amaratunga 1980a). However, a reduction in the proportion of males, which tend to be small individuals, can also result from cannibalism by larger females (O'Dor and Dawe 1998). During late autumn, nearly-mature squid migrate from all continental shelf fishing areas (Hurley 1980; Black *et al.* 1987), presumably to spawn. Most mature females have been collected from the U.S. shelf (Hendrickson 2004), but four have also been recorded from waters off the coast of Newfoundland and Nova Scotia (Dawe and Drew 1981).

Age estimation, accomplished by counting daily growth increments in the statoliths, has been validated for *I. illecebrosus* (Dawe *et al*. 1985; Hurley *et al*. 1985). Increment counts of statoliths from mated females caught in the Mid-Atlantic Bight indicate a lifespan of about 115 to 215 days (Hendrickson 2004). Squid inhabiting warmer waters of the Mid-Atlantic Bight exhibit faster rates of growth and maturation, and possibly a shorter lifespan, than squid from the northern stock component (Hendrickson 2004). The species may achieve a maximum size of 35 cm ML and 700 g, with females achieving larger sizes than males (Hendrickson 1998; O'Dor and Dawe 1998).

The terms recruit and pre-recruit are used herein to describe geographical distributions and habitat characteristics for the exploited and unexploited portions of the stock, respectively. Exploitation occurs at a minimum mantle length of 10 cm ML, the approximate length at which individuals migrate onto the continental shelf (O'Dor 1983; Hendrickson *et al.* 1996). Pre-recruits and recruits are thus defined as individuals ≤ 10 cm ML and ≥ 11 cm ML, respectively.

REPRODUCTION

Mating and spawning have only been observed in captivity. *I. illecebrosus* is a semelparous, terminal spawner whereby spawning and death occur within several days of mating (O'Dor 1983). Mature females collected on the U.S. continental shelf had mated with as many as four males (Hendrickson 2004).

Until recently, few mature females and only two mated individuals have been recorded (Dawe and Drew 1981). However, back-calculations of hatch dates based on statolith age analyses indicate that spawning occurs during October through June (Dawe and Beck 1997; Hendrickson 2004).

A winter spawning area, located off the east coast of Florida in the vicinity of the Blake Plateau (Figure 2; Black *et al*. 1987), has been inferred based on: the presence of *Illex* sp. hatchlings along the north wall of the Gulf Stream during January and February (Dawe and Beck 1985; Rowell *et al*. 1985a; Vecchione and Roper 1986; Coelho and O'Dor 1993); the offshore migration of adults in late autumn (Black *et al*. 1987); and the presence of minimum water temperatures required for hatching (O'Dor *et al.* 1982b; Trites 1983; Rowell and Trites 1985).

The only confirmed spawning area is located in the Mid-Atlantic Bight, at depths of 113 to 377 m, where a large number of mated females were collected between 39º10´N and 35º50´N during late May (Figure 3; Hendrickson 2004). This spawning area overlaps spatially with the fishing grounds of the directed fishery (Hendrickson *et al.* 1996). Spawning may also occur offshore in the Gulf Stream/Slope Water frontal zone, where paralarvae have been collected (O'Dor and Balch 1985; Rowell *et al.* 1985a), or south of Cape Hatteras during winter where *Illex* sp. hatchlings have been collected (Dawe and Beck 1985). Previous reports of mated females consist of three individuals that were caught south of Georges Bank (Dawe and Drew 1981).

DIET

Trophic relationships between *I. illecebrosus* and other marine species are described by Dawe and Brodziak (1998). Northern shortfin squid feed primarily on fish and crustaceans, but cannibalism of small individuals (most likely males) by larger females also occurs, particularly during autumn (Squires 1957; Froerman 1984; Maurer and Bowman 1985; Dawe 1988). An ontogenetic shift in diet from a predominance of crustaceans to a predominance of fish and squid is evident in squid from both stock components (Maurer and Bowman 1985; Dawe 1988).

Fish prey consists of the early life history stages of Atlantic cod, Arctic cod and redfish (Squires 1957, Dawe *et al*. 1997), sand lance (Dawe *et al*. 1997), mackerel and Atlantic herring (O'Dor *et al*. 1980a; Dawe *et al*. 1997), and haddock and sculpin (Squires 1957). *Illex* also feed on adult capelin (Squires 1957; O'Dor *et al*. 1980a; Dawe *et al*. 1997) and longfin inshore squid, *Loligo pealeii* (Vinogradov 1984).

Illex exhibit diel vertical migrations (Roper and Young 1975; Brodziak and Hendrickson 1999) and both juveniles (Arkhipkin and Fedulov 1986) and adults feed primarily at night in the upper layers of the water column (Maurer and Bowman 1985). On the U.S. shelf in the spring, *I. illecebrosus* primarily consume euphausiids, whereas fish and squid were the dominant prey in the summer and fall. *I. illecebrosus* 6-10 cm and 26-30 cm in size eat mostly squid, while 11-15 cm *Illex* eat mostly crustaceans and fish, and individuals 16-20 cm eat mostly crustaceans (Maurer and Bowman 1985).

Illex gut content data collected during Northeast Fisheries Science Center (NEFSC) bottom trawl surveys (Link and Almeida 2000) were combined across seasons to compute the percent composition of major prey categories (Figure 4). For both pre-recruits (92%) and recruits (57%), a majority of the gut contents consisted of well-digested prey. Pre-recruit prey types that could be identified consisted of crustaceans (3%) and fish (3%). The diet of recruits consisted of cephalopods (30%), crustaceans (including euphausiids, 7%), and fish (6%).

PREDATION AND MORTALITY

Numerous species of pelagic and benthic fishes prey on *Illex*, including bluefin tuna (Butler 1971), silver hake and red hake (Vinogradov 1972). Other fish predators include bluefish (Maurer 1975; Buckel 1997), goosefish (Maurer 1975; Langton and Bowman 1977), fourspot flounder (Langton and Bowman 1977), Atlantic cod (Lilly and Osborne 1984), sea raven (Maurer 1975), spiny dogfish (Templeman 1944; Maurer 1975), and swordfish (Langton and Bowman 1977; Stillwell and Kohler 1985; Scott and Scott 1988). Mammalian predators include pilot whales (Squires 1957; Wigley 1982) and the common dolphin (Major 1986). Seabird predators include shearwaters, gannets, and fulmars (Brown *et al*. 1981). Northern shortfin squid are known to exhibit a variety of defense mechanisms that may reduce predation, such as camouflage coloration (O'Dor 1983), schooling behavior, jetting, and ink release (Major 1986).

MIGRATION

Northern shortfin squid are highly migratory. An individual tagged off Newfoundland was recaptured off the coast of Maryland, more than 1,000 miles away (Dawe *et al*. 1981b). A hypothetical, annual migration route (Figure 2, from Black *et al*. 1987) has been constructed based on seasonal squid distribution patterns observed in bottom trawl surveys of the U.S. and Canadian continental shelves, concentrations of hatchlings in offshore waters south of Cape Hatteras during winter (Dawe and Beck 1985; Hatanaka *et al*. 1985; Rowell *et al*. 1985a), and suggestions that the neutrally-buoyant egg masses and paralarvae are rapidly transported northeastward by the Gulf Stream current (Trites 1983).

Seasonal distribution patterns in *Illex* abundance suggest that annual migrations off the U.S. shelf in autumn and onto the shelf in spring occur simultaneously along the entire length of the shelf edge rather than over the shelf in a gauntlet pattern (Hendrickson 2004; also see Geographical Distribution below). Tagging studies have demonstrated a southeastward migration of individuals from Newfoundland during autumn (Dawe *et al*. 1981b). However, the migration patterns between northern and southern stock components remain unknown and the offshore fraction of the population is not well understood because NEFSC surveys do not extend beyond the edge of the continental shelf and few stations are sampled in the deepest survey strata (185 to 366 m).

GEOGRAPHICAL DISTRIBUTION

Illex illecebrosus utilizes oceanic and neritic habitats and adults are believed to undergo long-distance migrations between boreal, temperate and sub-tropical waters. Data from U.S. and Canadian seasonal bottom trawl surveys (1975 to 1994) indicate that northern shortfin squid are distributed on the continental shelf of the U.S. and Canada, between Newfoundland and Cape Hatteras, North Carolina (Figure 5). The species is present in the Gulf of St.

Lawrence, along the western edge of the Grand Bank, and along the western shore of Newfoundland, but are most abundant on the U.S. and Scotian Shelf. Paralarvae and juveniles inhabit the Gulf Stream-slope water interface, located off the continental shelf of the U.S. and Canada, and juveniles also occur on the U.S. continental shelf. Adults have primarily been collected on the shelf due to sampling depth limitations of U.S. and Canadian bottom trawl surveys.

The southernmost limit of the range of *I. illecebrosus* is difficult to identify because of its co-occurrence with *I. coindetii* and *I. oxygonius*. Distinguishing between the three species is difficult given the high degree of interspecific and intraspecific variability in morphological characters (Roper and Mangold 1998; Roper *et al*. 1998).

EGGS AND PARALARVAE

Egg masses have never been collected in nature (O'Dor and Dawe 1998). Paralarvae have been collected during all seasons (Roper and Lu 1979), but predominately during January and February in the nutrient-rich waters of the Slope Water-Gulf Stream frontal zone, from south of Cape Hatteras to as far north as the Grand Bank (Dawe and Beck 1985; Hatanaka *et al*. 1985). The Gulf Stream has been hypothesized as the primary mechanism for the transport of egg balloons and paralarvae toward the Grand Bank (Trites 1983) based on its northeastern trajectory and rapid current (about 100 km/day).

PRE-RECRUITS

NEFSC bottom trawl surveys [see Reid et al. (1999) for details] have captured pre-recruits during all seasons (Figure 6; note that winter and summer distributions are presented as presence/absence data, precluding a discussion of abundances). In winter, the occurrence of pre-recruits is very low and distributed along the shelf edge between Cape Hatteras and Georges Bank. In the spring, pre-recruits are concentrated in low densities along the shelf edge, including the southern Scotian Shelf; the highest densities are found off of Cape Hatteras. By summer, pre-recruits have migrated onto the continental shelf and are distributed throughout all depths, primarily in the Mid-Atlantic Bight and along the coast of Maine. In autumn, pre-recruits begin their return migration to waters off the shelf. During fall, pre-recruits are present at depths greater than 60 m, between Georges Bank and Cape Hatteras, and are most abundant along the shelf edge. Low densities are also present in the Gulf of Maine.

The autumn distribution and abundance of pre-recruits around coastal Massachusetts, based on Massachusetts inshore bottom trawl surveys [see Reid et al. (1999) for details], is shown in Figure 7. During all of the spring surveys conducted between 1978 and 2003, only 16 individuals were collected at five stations in Massachusetts coastal waters. During the fall surveys, pre-recruits were present at very low densities at 28 stations located primarily off Cape Ann and northern Cape Cod Bay (at depths of 20 to 60 m); a few higher concentrations were found east of Cape Cod and near Nantucket Island.

Few (N=30) northern shortfin squid were caught during seasonal surveys of Narragansett Bay between 1990 and 1996. *Illex* were captured only during the summer and at three stations. Individuals ranged in size from 4 to 11 cm ML.

ADULTS

NEFSC bottom trawl surveys indicate similar seasonal distributions of recruits and pre-recruits. (See Figure 8 for recruits; again note that winter and summer distributions are presented as presence/absence data, precluding a discussion of abundances). Recruit abundance during spring and autumn appears to be greater than that of pre-recruits, but this is partially due to differences in catchability between the two size groups. The occurrence of recruits on the U.S. continental shelf is lowest during winter and concentrated along the shelf edge (at depths around 366 m) between Georges Bank and Cape Hatteras. By spring, recruits are still only present at low densities and concentrated near the shelf edge, extending to south of Cape Hatteras, where some of the highest densities are found. Recruits occur both inshore and throughout the continental shelf during the summer between the Gulf of Maine and Cape Hatteras. During autumn, recruits begin to migrate back offshore and south, as indicated by their high concentrations at depths between 60 and 366 m.

Recruit abundance was low in Massachusetts coastal waters during 1978-2003, particularly during the spring, when only a few recruits were collected at four stations. During the fall, recruits were collected at more stations and at higher densities. Abundance was highest in the waters off Cape Ann and the northern portion of Cape Cod Bay (Figure 9).

HABITAT CHARACTERISTICS

Habitat characteristics of northern shortfin squid are summarized by life history stage in Table 1.

EGGS AND PARALARVAE

Based on lab studies, egg balloons probably occur at water temperatures between 12.5°C, the minimum temperature required for successful embryonic development (O'Dor *et al.* 1982b), and 26°C (Balch *et al.* 1985). Egg masses are neutrally-buoyant and probably occur in midwater near the pycnocline (O'Dor and Balch 1985).

Illex sp. paralarvae have been collected at water temperatures from 5 to 20°C (Vecchione 1979; O'Dor 1983; Dawe and Beck 1985; Hatanaka *et al.* 1985; Vecchione and Roper 1986), with maximum abundance, in the Gulf Stream, at temperatures greater than 16.5°C (Hatanaka *et al.* 1985) and salinities ranging from 35 to 37 ppt (Vecchione 1979; O'Dor 1983; Dawe and Beck 1985; Vecchione and Roper 1986). Paralarvae exhibit diel vertical migrations and are more abundant in the upper layer of the water at night and in deeper water during the day (Hatanaka *et al.* 1985).

JUVENILES

During the spring, epipelagic juveniles migrate from oceanic to neritic waters as they grow. Juveniles have been collected from continental slope waters at temperatures from 14.3 to 16.3°C (Fedulov and Froerman 1980; Perez 1994), at temperatures above 16°C in the Gulf Stream (Perez 1994), and at temperatures from 5 to 6°C on the Scotian Shelf in spring (Perez 1994). During late May, juveniles (34 to 68 mm ML) were collected along the southeast flank of Georges Bank, at depths of 140 to 260 m, where surface and bottom temperatures were 10.6°C and 9.9°C, respectively (Hendrickson 2004). Juveniles have been collected at salinities of 34 to 37 ppt (Vecchione 1979; Amaratunga *et al.* 1980b; Fedulov and Froerman 1980; Rowell *et al.* 1985a). South of Cape Hatteras, squid 7 to 10 cm ML are most abundant during spring (Whitaker 1980).

Distributions of pre-recruits relative to bottom water temperature, depth, and salinity based on spring and fall NEFSC bottom trawl surveys from the Gulf of Maine to Cape Hatteras are shown in Figure 10. During the spring surveys, pre-recruits occur in deep water and are most abundant at depths ranging from 101 to 300 m, bottom temperatures of 11 to 14ºC and at salinities of 35 to 36 ppt. During the fall surveys, pre-recruits occur in greater abundance across a broader depth range, and in a wider range of temperatures and salinities. During autumn, juveniles are most abundant at bottom temperatures of 10 to 13ºC and salinities of 32 to 35 ppt.

The spring and autumn distributions of pre-recruits in Massachusetts coastal waters relative to bottom water temperature and depth based on Massachusetts inshore bottom trawl surveys are shown in Figure 11. As observed in the NEFSC spring surveys, pre-recruits are distributed offshore during spring; only 16 individuals were collected at five stations in Massachusetts coastal waters (< 80 m deep), most at temperatures of 11ºC and at a depth of 11 to 15 m. During the fall, pre-recruits were present at very low densities at only 28 stations and were most abundant at depths of 31 to 55 m, and were found over at bottom temperatures of 6 to 10ºC.

ADULTS

Adults have been captured at temperatures ranging from -0.5 to 27.3°C (Whitaker 1980), salinities of 30 to 36.5 ppt (Palmer and O'Dor 1978), and at depths ranging from the surface to 1000 m or more (Whitaker 1980), depending on the time of year (see Migrations above). In summer, on the eastern U.S. continental shelf, adults are most abundant at depths of 100 to 200 m (Bowman 1977; Grinkov and Rikhter 1981) and are not generally found in waters shallower than 18 m. In the fall and winter, adults migrate offshore, and have been found at 100 to 945 m (Amaratunga *et al.* 1980a; Felley and Vecchione 1995). However, there is little information on the offshore component of the population, which may be found at depths greater than 1000 m (O'Dor and Dawe 1998).

Distributions of recruits relative to bottom water temperature, depth, and salinity based on NEFSC spring and fall bottom trawl surveys are shown in Figure 12. During the spring, recruits are found over a temperature range of 4 to 20°C, but are most abundant at 10 to 14°C. Recruits are found over a depth range of 11 to 500 m, but are most abundant at 121 to 400 m. The majority of recruits occur at a salinity of 35 ppt in the spring. In the autumn, recruits were found over a bottom temperature range of 4 to about 21°C, and are most abundant at 8 to 13°C. Recruit abundance increased with depth between 31 and 140 m and reached a secondary peak at 201 to 300 m. During autumn, recruits occur over a salinity range from 31 to 36 ppt.

The spring and autumn distributions of recruits in Massachusetts coastal waters relative to bottom water temperature and depth based on Massachusetts inshore bottom trawl surveys are shown in Figure 13. The few adults caught in the spring occurred at temperatures of 10 to 13°C and at depths of 11 to 15 m, 26 to 30 m, and 41 to 45 m. Recruits were caught at higher densities in the fall and were found over a temperature range of 4 to 15°C, with most recruits found between 7 and 9°C.

Recruits were caught over a depth range of 11 to 85 m, with most found between 41 and 75 m.

RESEARCH NEEDS

Additional research is needed to better understand the life cycle of this species. In particular, recruitment patterns and the exchange of squid between the northern and southern stock components remain unknown, along with the migration routes from fishing areas during autumn. U.S. research surveys do not include waters deeper than 366 m, so it remains unknown what fraction of the stock resides offshore and whether spawning occurs there. In addition, the location of the winter spawning area has not been confirmed.

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Table 1. Summary of life history and habitat parameters for northern shortfin squid *Illex illecebrosus*.

Life Stage	Size and Growth	Habitat	Substrate	Temperature	Salinity
Eggs [1]	Eggs protected in gelatinous masses ranging in diameter from 30 - 100 cm. In lab studies, females produced 10,000 - 400,000 eggs.	Egg masses have not been collected in the wild. It is hypothesized that egg masses are transported northeasterly in the Gulf Stream current based on distribution of paralarvae and temperatures required for hatching.	Egg masses are pelagic; do not attach to substrate (based on lab-induced spawning events).	Egg incubation lasts 16 days at 13°C, 12 days at 16°C and 8 days at 21°C; normal development requires at least 13°C.	Egg masses have greater density than seawater; possibly become neutrally - buoyant in colder, higher-density water (shown in lab studies).
Paralarvae [2] Hatchling: 1.0-1.1 mm Paralarvae: 1.2-5.0 mm Transitional: 5.1-6.9 mm	Size at hatch: 1.0-1.1 mm ML. Paralarvae have non-functional tentacles; body not yet elongated. Rhynchoteuthion (Type C[1]) larval stage ends when proboscis splits into 2 tentacles. Mantle length increases during migration from Gulf Stream to continental shelf. Only find hatchlings south of Cape Hatteras.	Offshore, along continental shelf edge from surface waters to 360 m. Hatching occurs at inshore boundary of Gulf Stream, 9 to 16 days after spawning. Paralarvae have been found during winter and spring off tail of Grand Bank. Abundant in late February-March in Gulf Stream/slope waters above the thermocline. The convergence of Gulf Stream and slope water creates an area of high productivity that is beneficial to young for feeding and growth. Undergo diel vertical migrations; greater abundance during the day at 50-100 m.		Found from 5-20°C; maximum abundance at temperatures > 16.5°C.	Found at salinities ranging from 35-37 ppt.
Pre-recruits [3] ≤ 10.0 cm	Separation of proboscis into tentacles indicates onset of juvenile stage. Larger juveniles found from east to west, indicating westward movement on continental shelf with growth. Growth is approximately 1.5 mm/day.	Winter: in Gulf Stream/slope water interface. Spring: begin migration onto U.S. continental shelf (Georges Bank to south of Cape Hatteras). Summer: occur throughout U.S. shelf (Georges Bank to Cape Hatteras). Fall: migrate off U.S. shelf (Georges Bank to south of Cape Hatteras). Undergo diel vertical migrations; greater abundance near the bottom during the day.		Gulf Stream: > 16°C; slope water: < 16°C; surface: 14-21°C; continental shelf: 5-6°C in spring. Pre-recruits on U.S. shelf most abundant at bottom temperatures > 10°C and surface temperatures 14.6-20.5°C.	Found at salinities ranging from 34-37 ppt.
Recruits [4] ≥ 11 cm	Can reach size of 35 cm ML. Life span less than a year; (215 days for squid in U.S. shelf waters). Males and females grow about 1 mm/day. Females generally larger than males.	Range from Labrador to south of Cape Hatteras; most abundant at depths of 100-150m. Winter: low abundance along edge of U.S. shelf; presumably in warmer waters offshore and south of Cape Hatteras. Spring: begin migration onto U.S. shelf (Georges Bank to south of Cape Hatteras) and Scotian Shelf. Summer: occur throughout U.S. shelf (Gulf of Maine to Cape Hatteras), Scotian Shelf and inshore Newfoundland waters. Fall: migrate off continental shelf of U.S. and Canada; presumably to spawn. Increase in squid size with depth in autumn.	Over various sediment types, including sand-silt or "Sambro sand" (sediment between banks and edges of basins on Scotian Shelf, as well as along edge of continental shelf, 100-300m). Avoid areas inhabited by anemones.	*Illex* ≥ 11 cm found at bottom temperatures ranging from 3.5-15.0°C (surface > 20°C), most abundant at bottom temperatures of 5-10.0°C. Maturation may be enhanced by high temperatures but not initiated by it.	Generally found at 30-36.5 ppt.

[1] Durward *et al*. (1978); O'Dor and Durward (1979); Durward *et al*. (1980); O'Dor *et al*. (1980b, 1982b, 1986); O'Dor (1983); O'Dor and Balch (1985); Rowell *et al*. (1985a); Perez (1994).
[2] Vecchione (1979); Amaratunga (1980a); Durward *et al*. (1980); O'Dor (1983); Trites (1983); Dawe and Beck (1985); Hatanaka *et al*. (1985); Rowell and Trites (1985); Rowell *et al*. (1985a); Vecchione and Roper (1986); Young and Harman (1988); Mann and Lazier (1991); Perez (1994).
[3] Squires (1957); Vecchione (1979); Amaratunga (1980a); Amaratunga *et al.* (1980b); Fedulov and Froerman (1980); Dawe *et al*. (1981a); Coelho (1985); Rowell *et al*. (1985a); Black *et al*. (1987); Nigmatullin (1987); Perez (1994); Dawe and Beck (1997); Brodziak and Hendrickson (1999).
[4] Frost and Thompson (1933); McLellan *et al*. (1953); Squires (1957, 1967); Templeman (1966); Mercer (1973a, b); Mercer and Paulmier (1974); Bowman (1977); Mesnil (1977); O'Dor *et al*. (1977, 1980a); Amaratunga *et al*. (1978, 1980a); Lange (1978); Lux *et al*. (1978); Palmer and O'Dor (1978); Amaratunga and McQuinn 1979; Fedulov and Froerman (1980); Hurley (1980); Whitaker (1980); Dawe and Drew (1981); Dawe *et al*. (1981b); Grinkov and Rikhter (1981); Lange and Johnson (1981); Scott (1982); Wigley (1982); Amaratunga 1983; Waldron (1983); Roper *et al*. (1984); Coelho (1985); Dawe and Beck (1985, 1997); Rowell *et al.* (1985b); Vecchione *et al*. (1989); Laptikhovsky and Nigmatullin (1993); Perez (1994); Felley and Vecchione (1995); Brodziak and Hendrickson (1999); Hendrickson (2004).

Table 1. Cont'd.

Life Stage	Prey	Predators	Spawning	Notes
Eggs [1]			Spawning has bee induced in the lab, but not observed in the wild. Lab studies indicate that egg masses are spawned pelagically.	Eggs that are presumably spawned in Gulf Stream waters can hatch in northern shelf waters > 12.5ºC (transported by Gulf Stream at rate of 7 km/hr); can also hatch in warm Gulf Stream waters.
Paralarvae [2] Hatchling: 1.0-1.1 mm Paralarvae: 1.2-5.0 mm Transitional: 5.1-6.9 mm	Hatchlings may spend early life in remains of egg mass to utilize the nutrients for food. Yolk-sac not especially large; food must be adequate to sustain hatchling during this stage of rapid growth and increased metabolism.			Gulf Stream may be important mode of transportation for paralarvae throughout range in NW Atlantic; initially flows northeastward along shelf, off Cape Hatteras, then flows easterly and creates eddies in which young are transported westward into slope waters.
Pre-recruits [3] ≤ 10.0 cm	Primarily feed on crustaceans (euphausiids) at night near the surface; also consume nematodes and fish.			Gulf Stream presumably transports juveniles northward; hydrographic variability in this system may explain annual abundance differences.
Recruits [4] ≥ 11 cm	Visual predators; feeding rate reduced in highly turbid waters. Feed primarily on fish and are cannibalistic (larger females cannibalize smaller males, increased in autumn). Fish prey includes juvenile Atlantic cod, mackerel, redfish, sand lance, Atlantic herring, and adult capelin. Seasonal/ontogenetic diet shifts, during spring (offshore): euphausiids; during summer-fall (inshore): fish and squid.	Many pelagic and benthic fishes feed heavily on *Illex*, including bluefin tuna and silver and red hakes. Other fish predators include shark and dogfish species, fourspot flounder, Atlantic cod, swordfish, bluefish, goosefish, and sea raven. Mammalian predators include common dolphin and pilot whales. Avian predators include shearwaters, gannets, and fulmars.	Spawning likely pelagic and occurs during October-July. Late May: mated females indicate spawning area (113-377 m) in Mid-Atlantic Bight; overlaps with fishing grounds. Winter: presumably spawn during December-March in the Gulf Stream and/or south of Cape Hatteras where *Illex* sp. hatchlings were collected. Lab studies indicate females mate, spawn once (may release multiple egg masses), then die within a week. Mated females collected in Mid-Atlantic Bight indicate females may mate with as many as four males.	Diel vertical migrations: more abundant on bottom at dawn/dusk and day than at night; feed primarily at night before sunrise near surface or mid-water. Migrate to bottom or deeper waters during daytime. Change color to camouflaged pattern when resting on bottom to reduce risk of predation by benthic species.

[1] O'Dor *et al*. (1980b, 1982a, 1986); O'Dor (1983); Rowell *et al*. (1985a); Perez (1994).
[2] Durward *et al*. (1980); Trites (1983); Rowell and Trites (1985); O'Dor *et al*. (1986); Vecchione and Roper (1986); Csanady and Hamilton (1988); Mann and Lazier (1991); Perez (1994).
[3] Amaratunga *et al*. (1980b); Dawe *et al*. (1981a); Coelho (1985); Arkhipkin and Fedulov (1986).
[4] Templeman (1944); Squires (1957, 1966, 1967); Vinogradov (1970, 1972, 1984); Butler (1971); Mercer and Paulmier (1974); Maurer (1975); Langton and Bowman (1977); Bennett (1978); Durward *et al*. (1978); Hirtle (1978); Ennis and Collins (1979); Froerman (1979); Vinogradov and Noskov (1979); Amaratunga (1980b, 1983); Amaratunga *et al*. (1980a); Fedulov and Froerman (1980); Hurley (1980); Lange and Sissenwine (1980); O'Dor *et al*. (1980a, b); Brown *et al*. (1981); DeMont (1981); Hirtle *et al.* (1981); Wigley (1982); O'Dor (1983); Lily and Osborne (1984); Dawe and Beck (1985, 1997); Maurer and Bowman (1985); Nicol and O'Dor (1985); O'Dor and Balch (1985); Rowell *et al*. (1985a); Stillwell and Kohler (1985); Major (1986); Scott and Scott (1988); Vecchione *et al*. (1989); Laptikhovsky and Nigmatullin (1993); Perez (1994); Dawe *et al*. (1997); Brodziak and Hendrickson (1999); Hendrickson (2004).

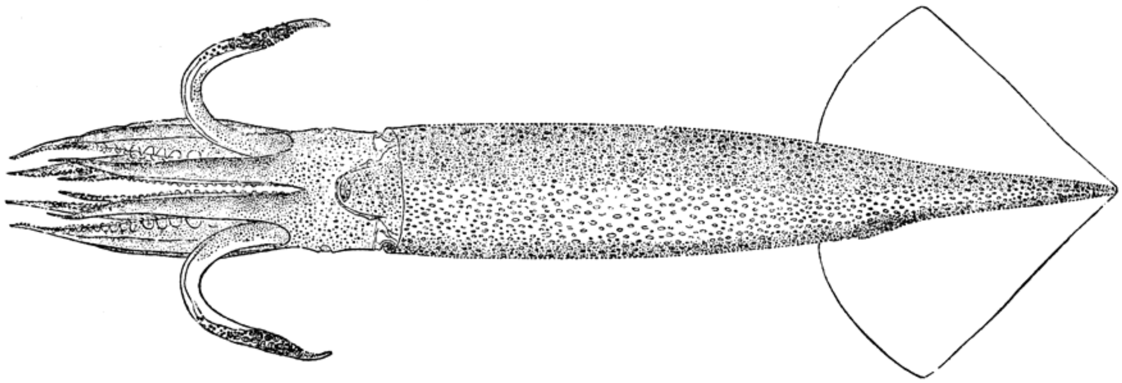


Figure 1. The northern shortfin squid, *Illex illecebrosus* (from Goode 1884).

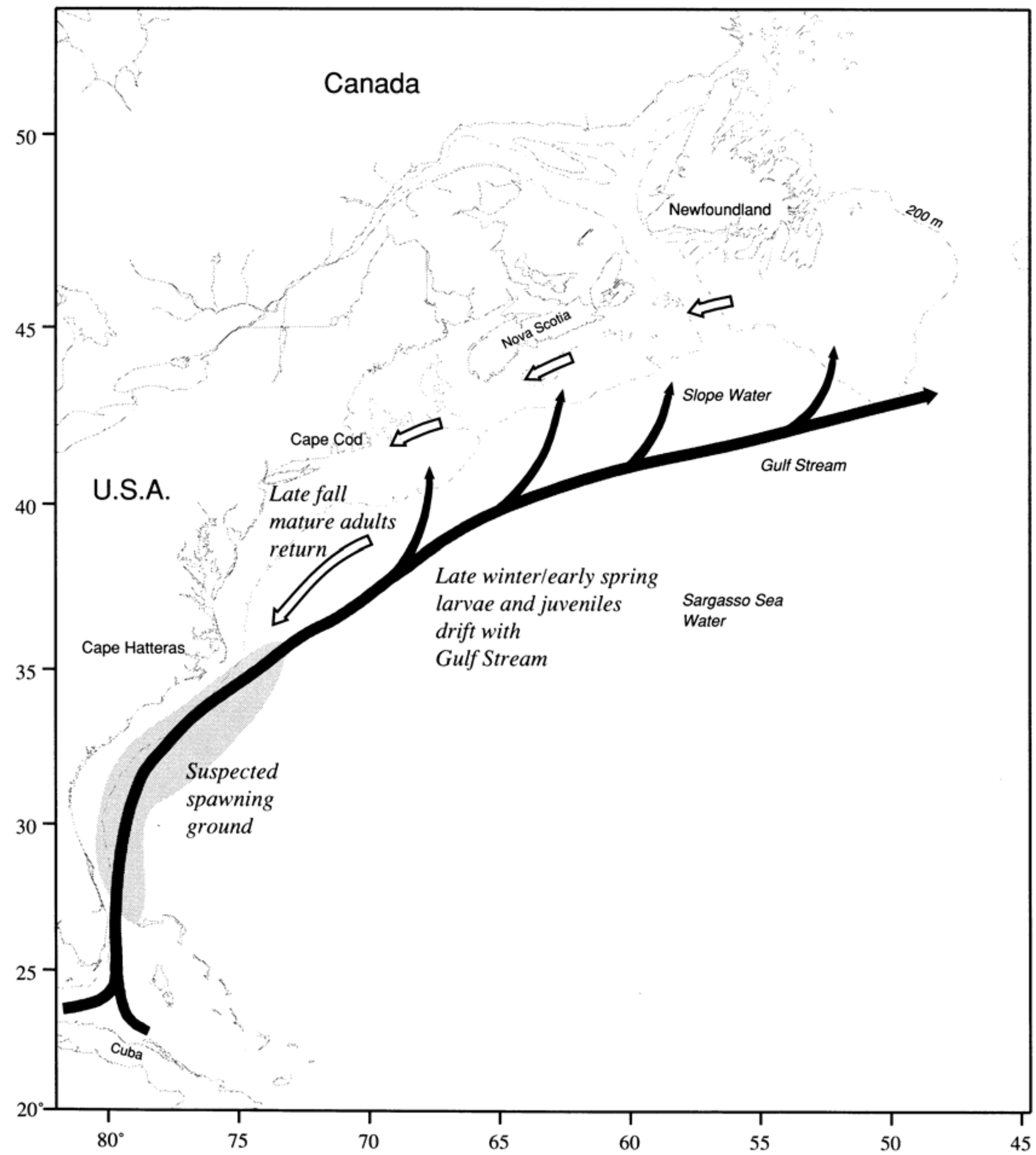


Figure 2. Hypothetical migration path of the northern shortfin squid, *Illex illecebrosus*. From Black *et al.* (1987).

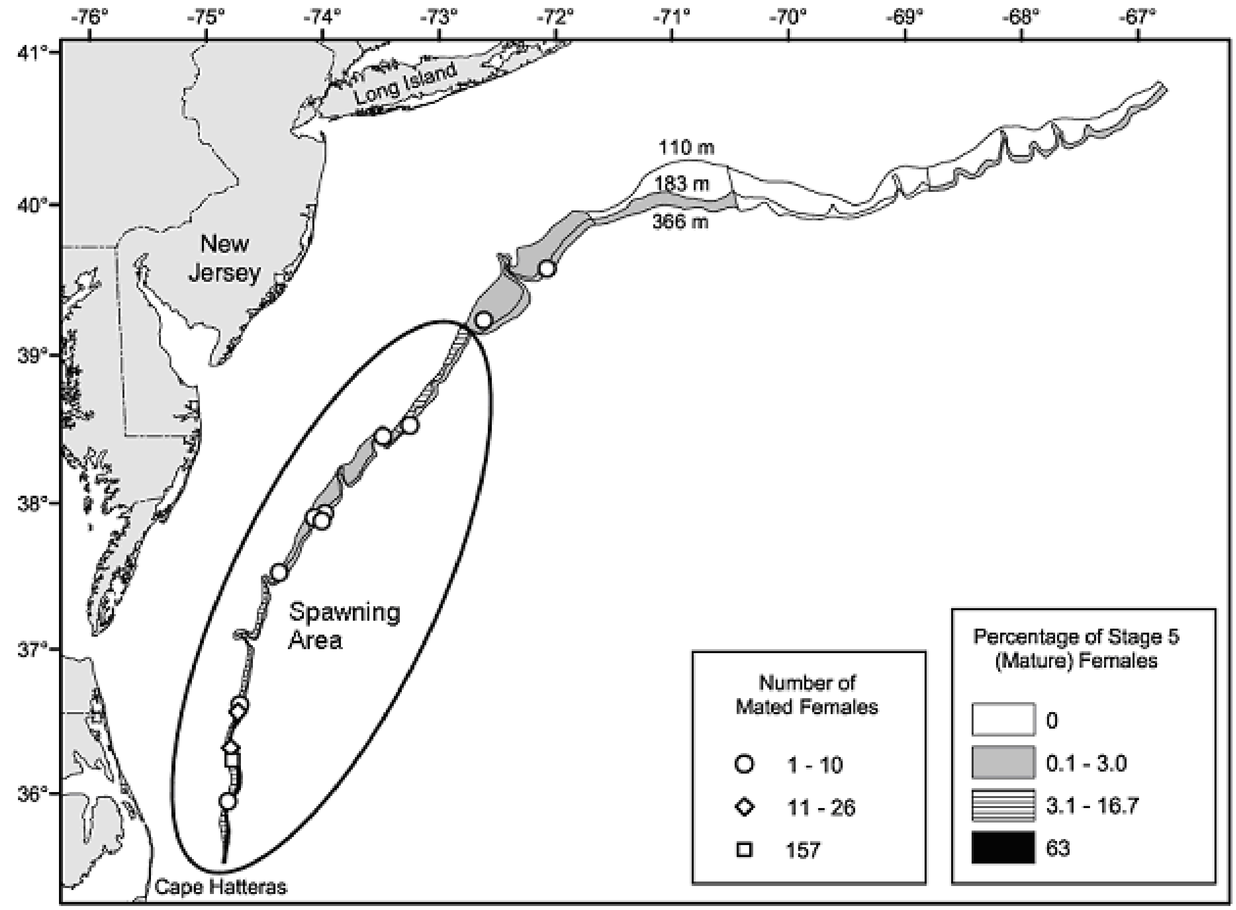


Figure 3. Spawning area of northern shortfin squid (encircled) during late May. Based on the distribution of mated females (Hendrickson 2004).

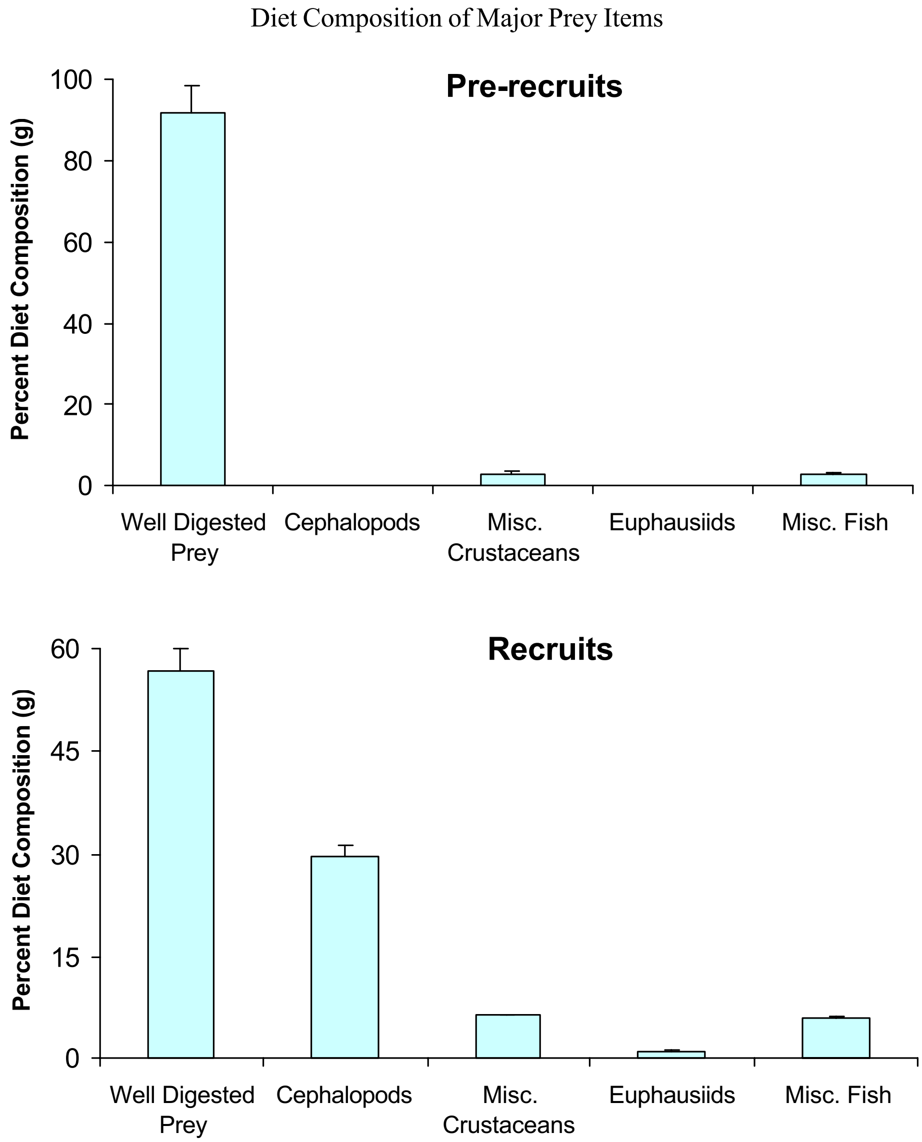
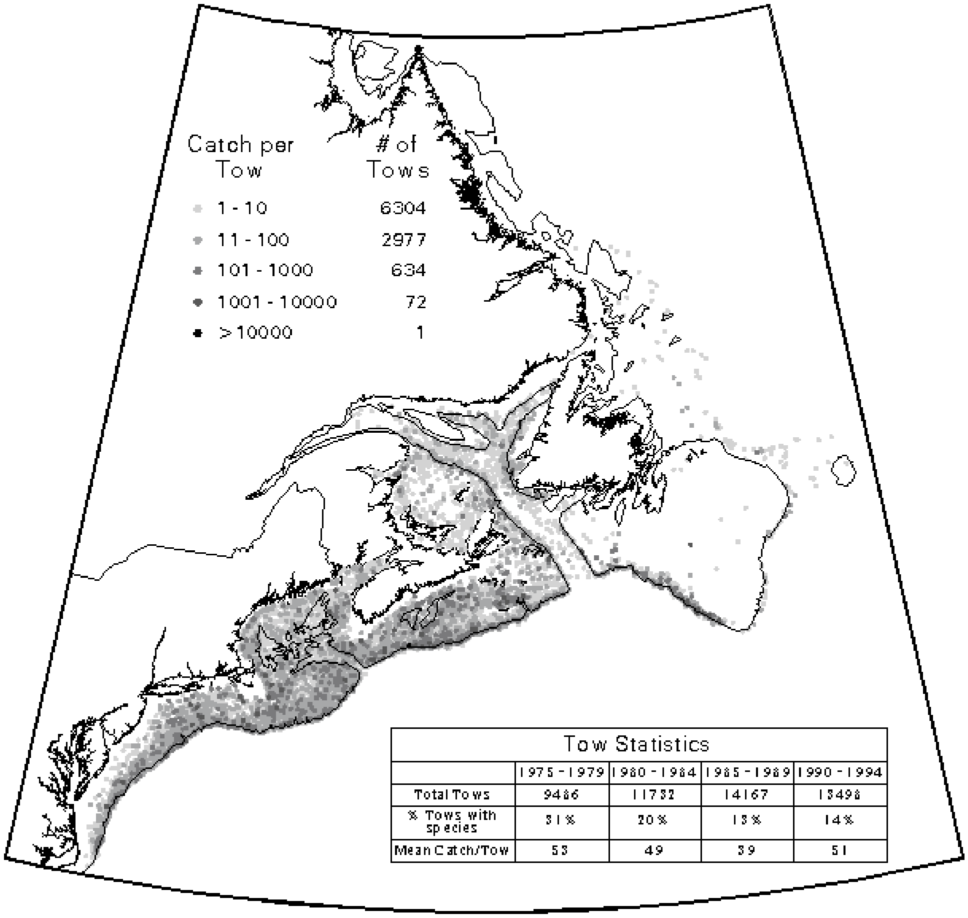


Figure 4. Percent by weight (g) of the major prey items in the diet of northern shortfin squid. From specimens collected during NEFSC bottom trawl surveys from 1973-2001 (all seasons). For details on NEFSC diet analysis, see Link and Almeida (2000).



Tow Statistics				
	1975 - 1979	1980 - 1984	1985 - 1989	1990 - 1994
Total Tows	9486	11732	14167	13498
% Tows with species	31%	20%	13%	14%
Mean Catch/Tow	53	49	39	51

Figure 5. Distribution and abundance of northern shortfin squid from Newfoundland to Cape Hatteras. Based on research trawl surveys conducted by Canada (DFO) and the United States (NMFS) from 1975-1994 (http://www-orca.nos.noaa.gov/projects/ecnasap/ecnasap_table1.html).

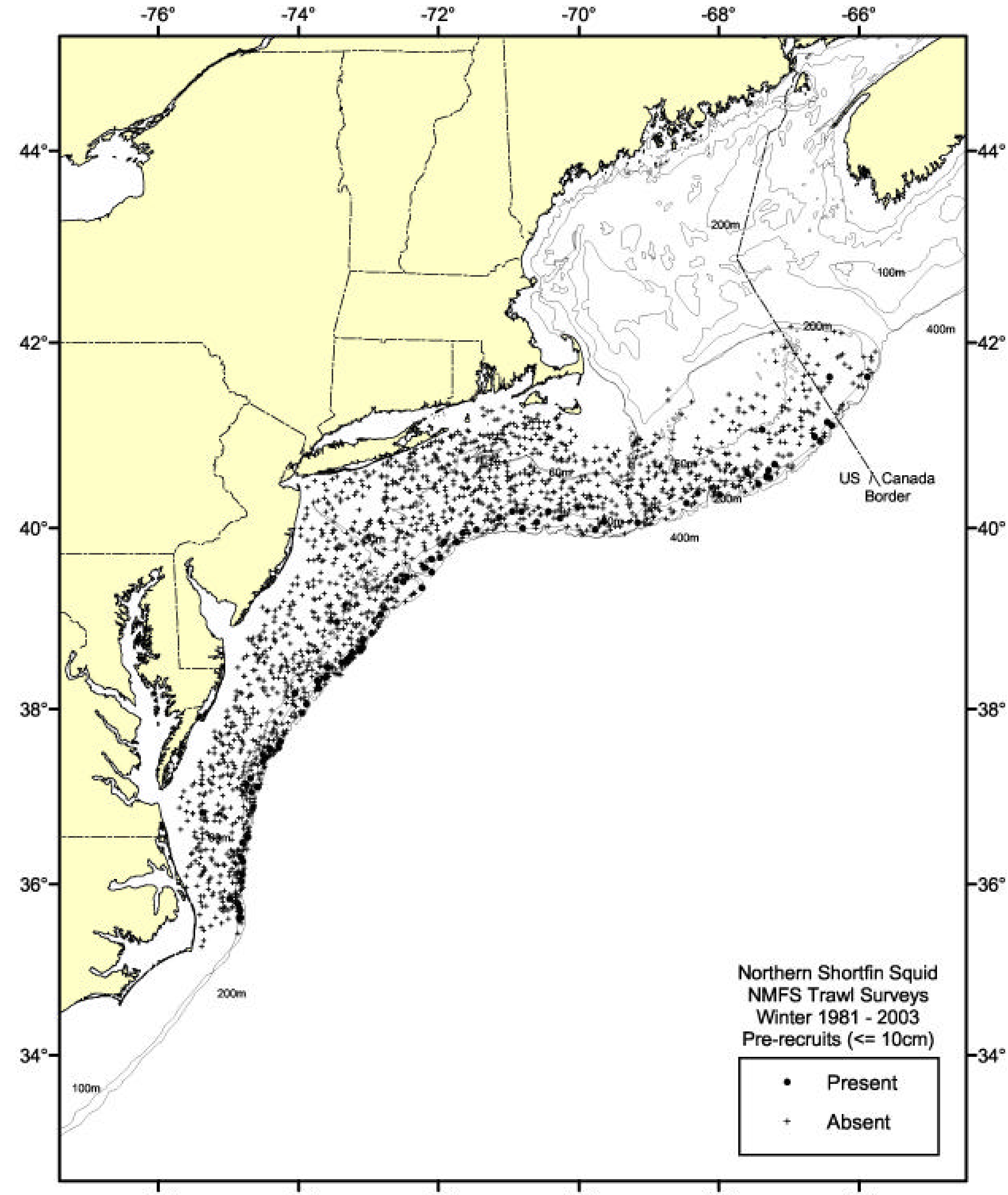


Figure 6. Seasonal distributions and abundances of pre-recruit northern shortfin squid collected during NEFSC bottom trawl surveys.
From NEFSC winter bottom trawl surveys (1981-2003, all years combined). Distributions are displayed as presence/absence only.

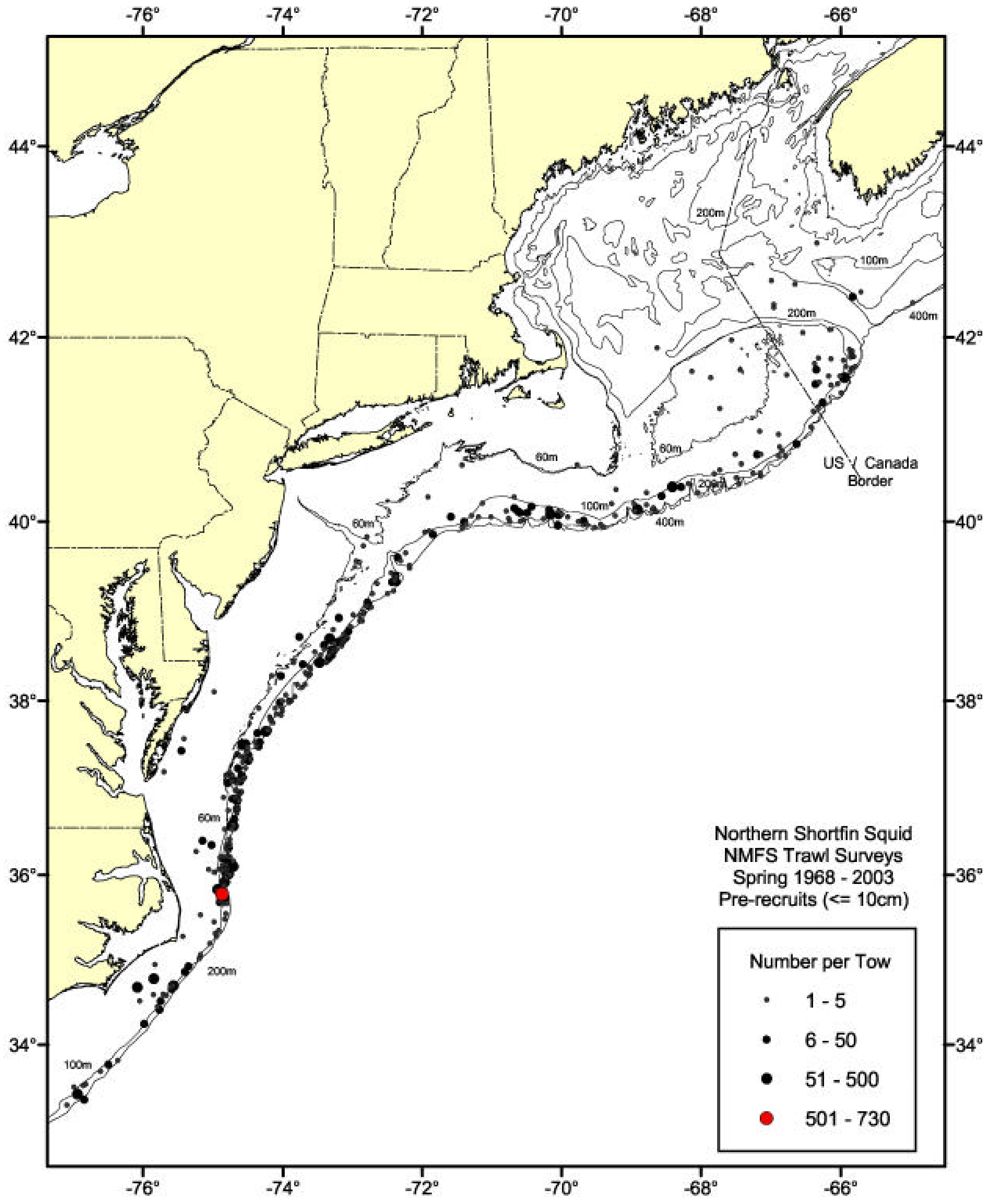


Figure 6. Cont'd.
From NEFSC spring bottom trawl surveys (1968-2003, all years combined). Survey stations where pre-recruits were not found are not shown.

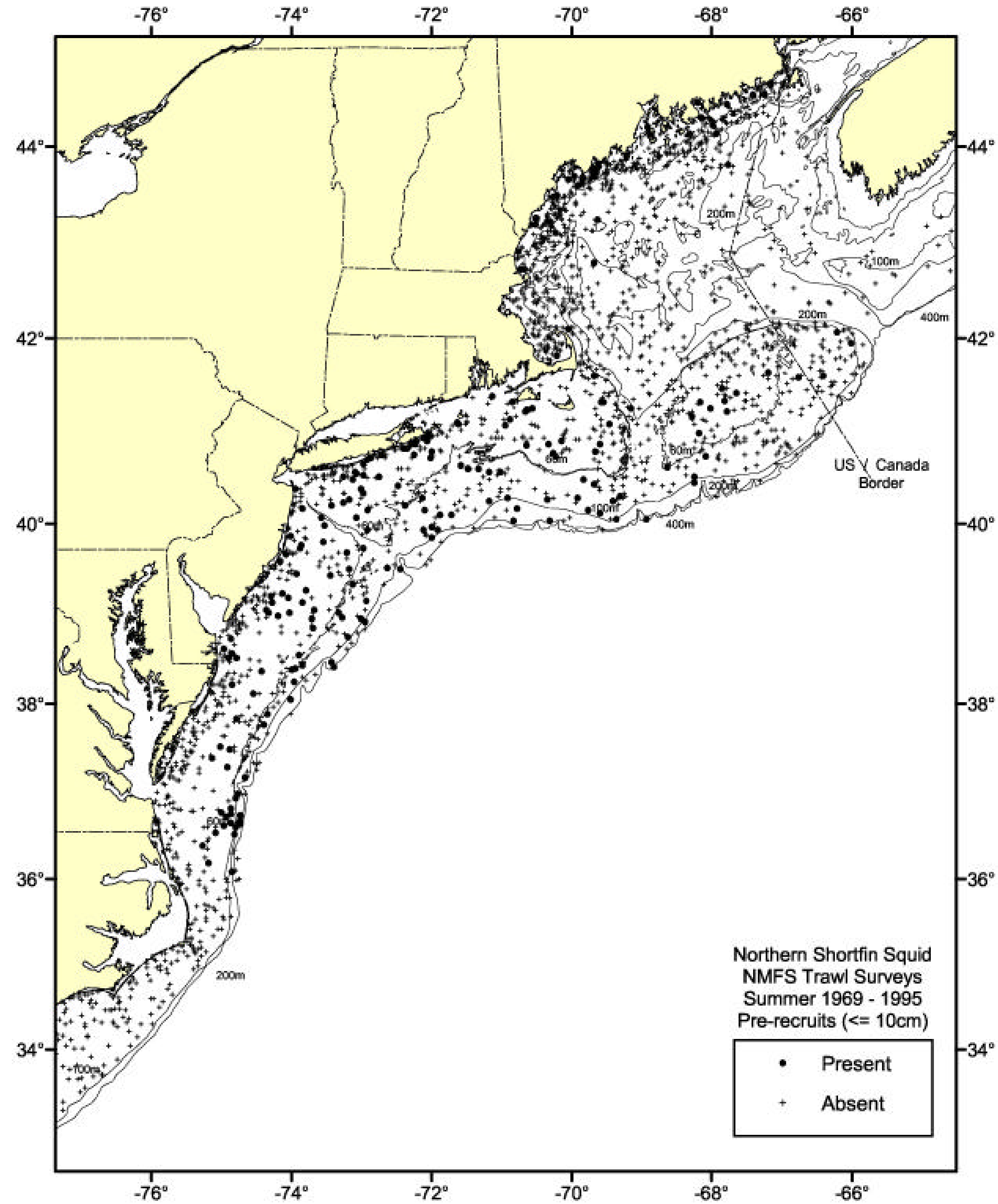


Figure 6. Cont'd.
From NEFSC summer bottom trawl surveys (1969-1995, all years combined). Distributions are displayed as presence/absence only.

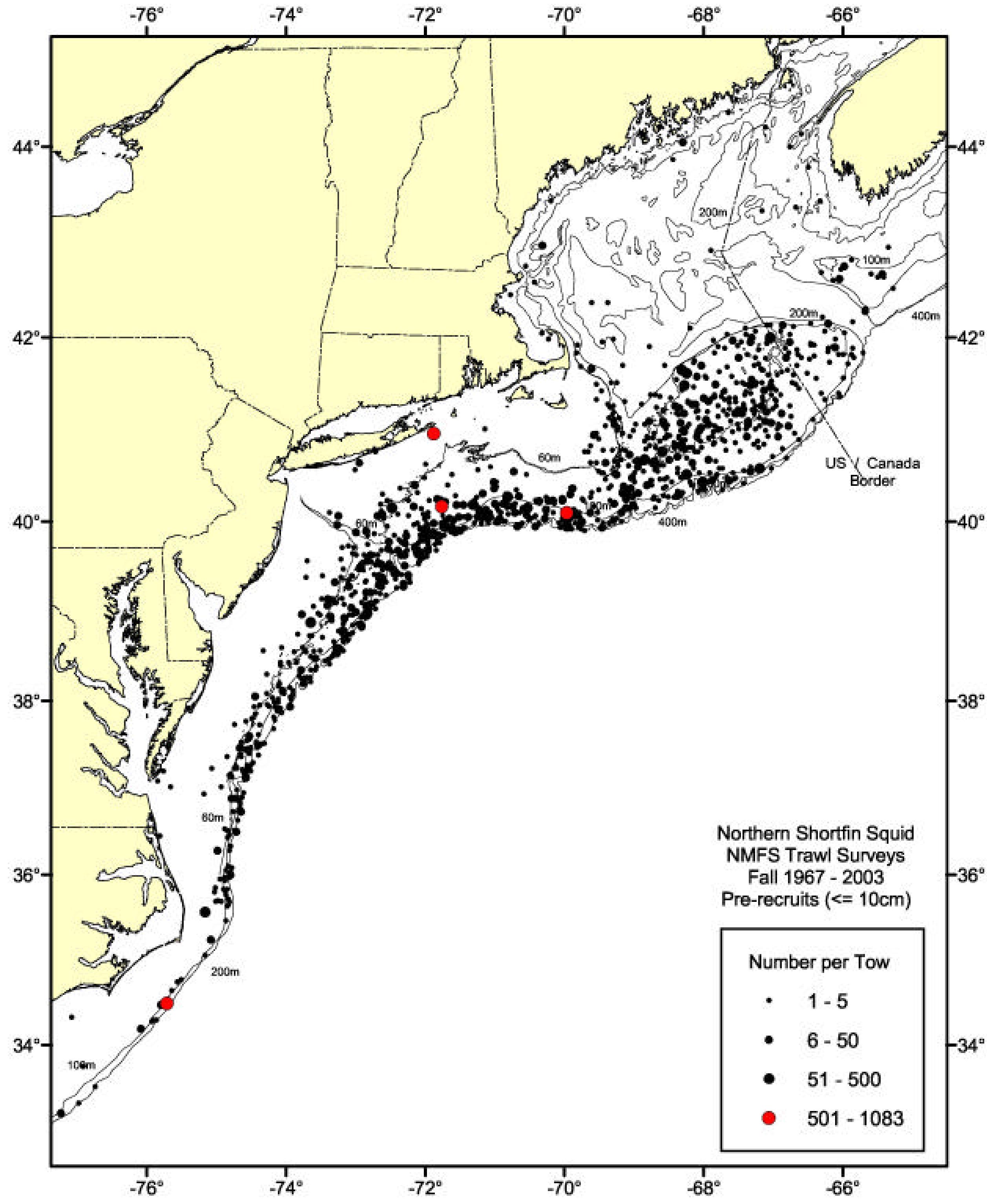


Figure 6. Cont'd.
From NEFSC fall bottom trawl surveys (1967-2003, all years combined). Survey stations where pre-recruits were not found are not shown.

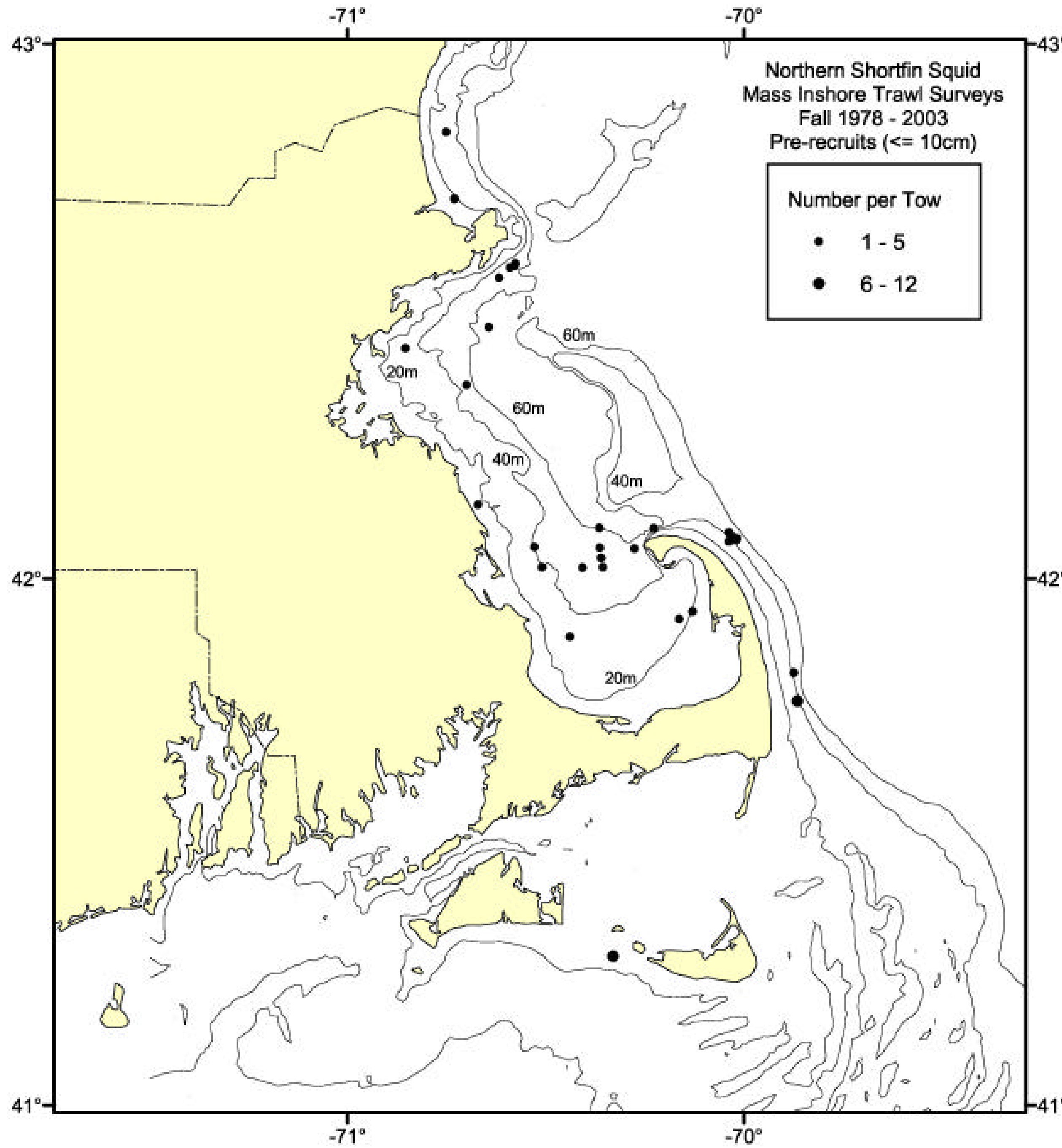


Figure 7. Distribution and abundance of pre-recruit northern shortfin squid in Massachusetts coastal waters. From fall Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Survey stations where pre-recruits were not found are not shown.

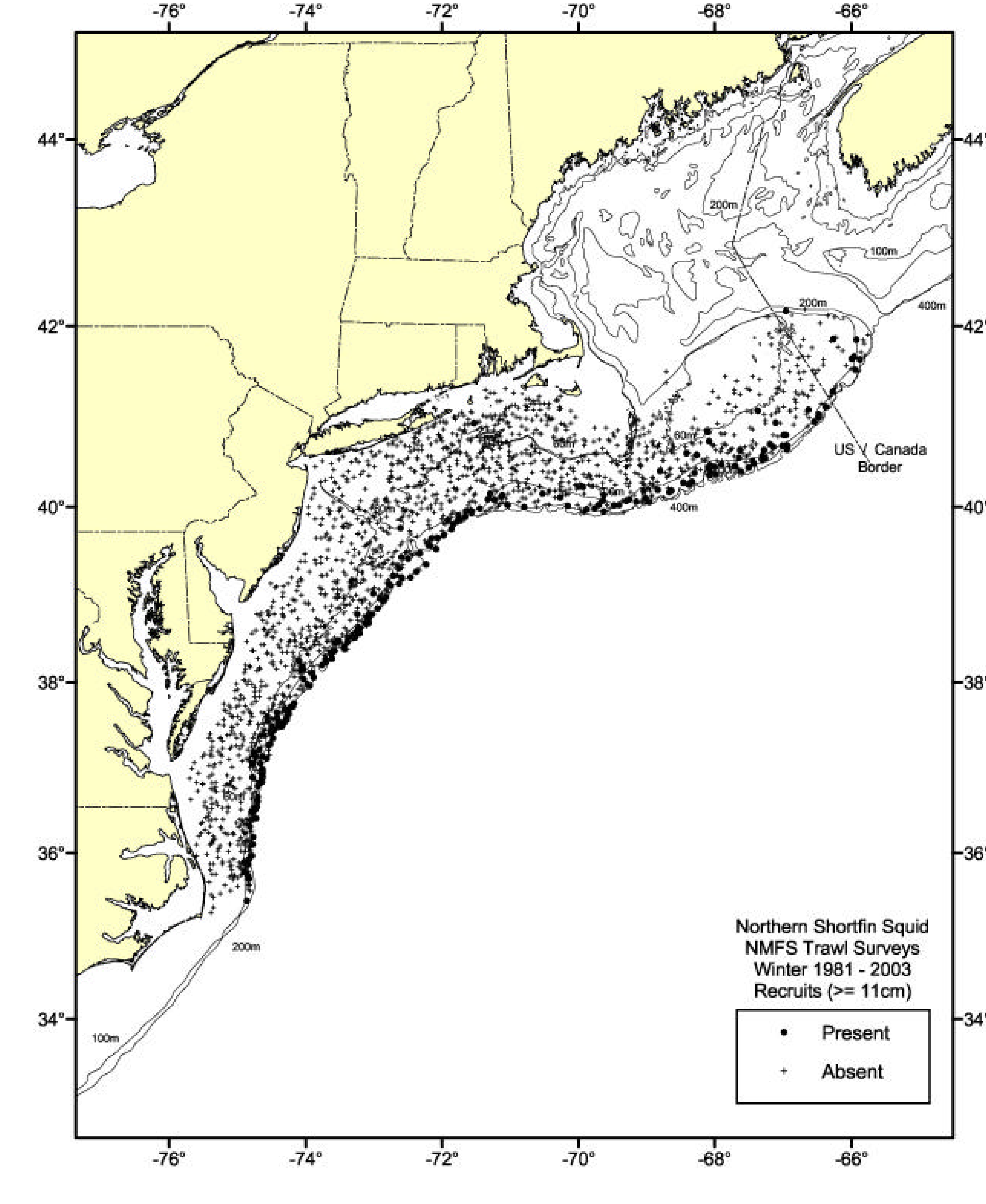


Figure 8. Seasonal distributions and abundances of recruit northern shortfin squid collected during NEFSC bottom trawl surveys.
From NEFSC winter bottom trawl surveys (1981-2003, all years combined). Distributions are displayed as presence/absence only.

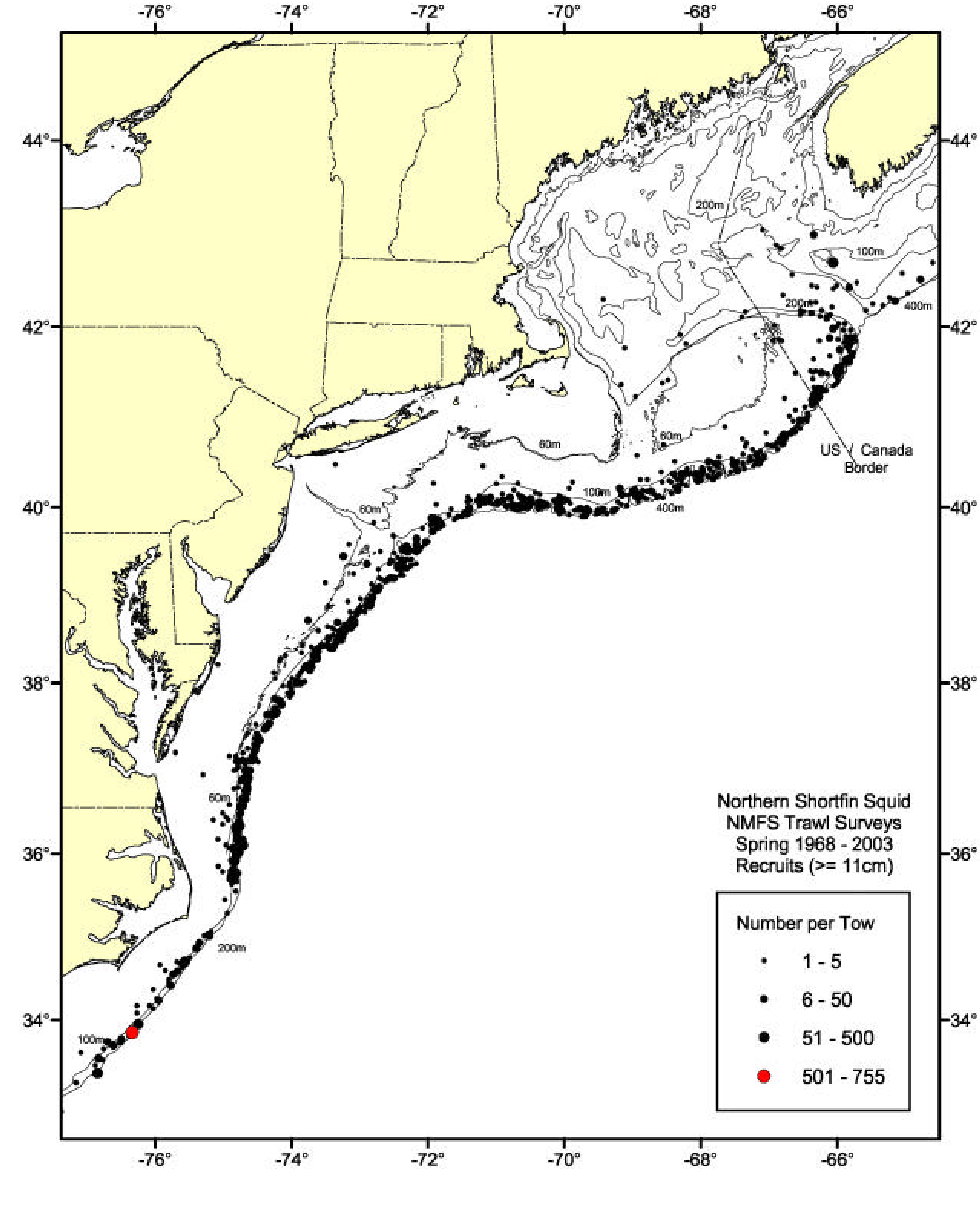


Figure 8. Cont'd.
From NEFSC spring bottom trawl surveys (1968-2003, all years combined). Survey stations where recruits were not found are not shown.

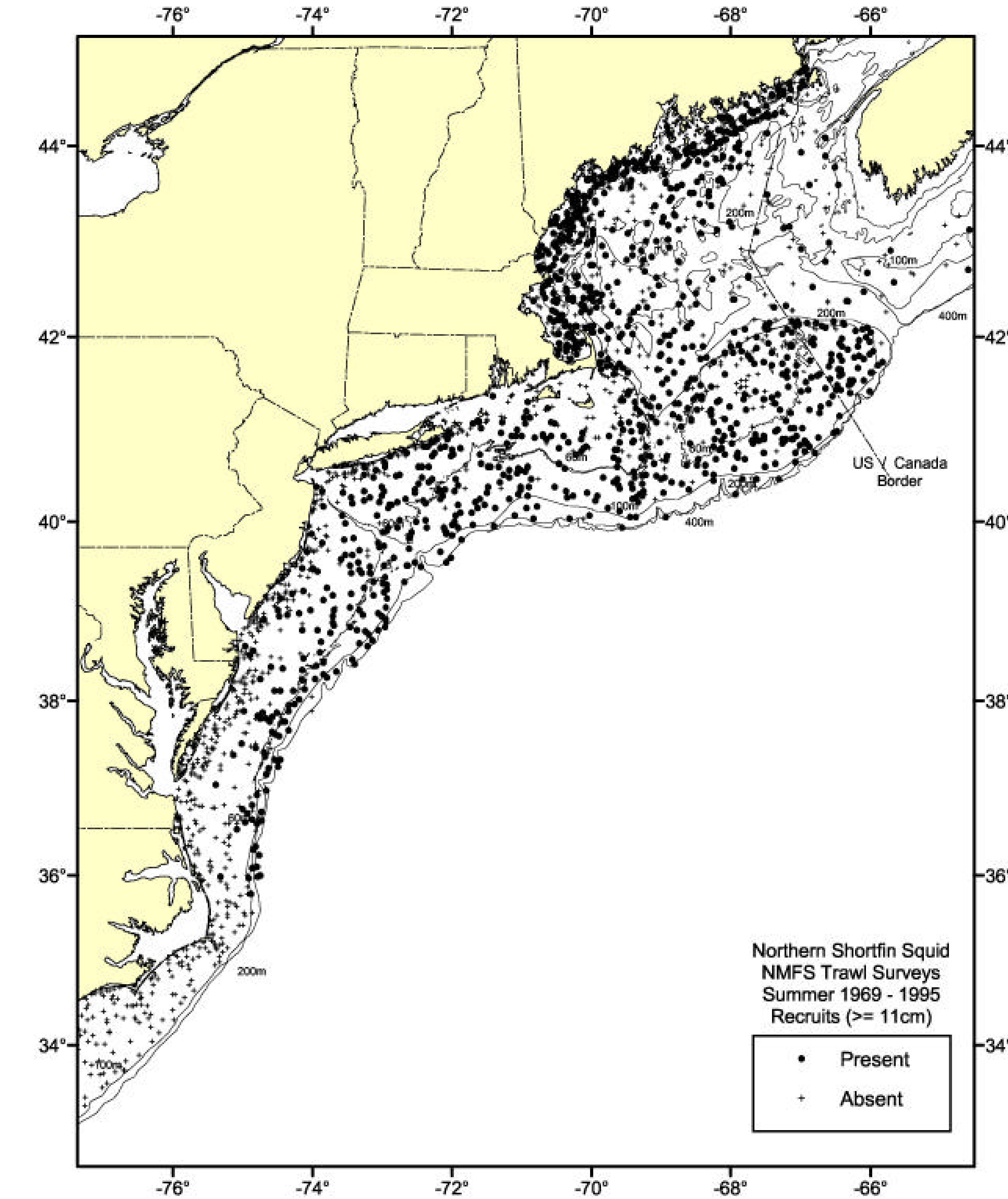


Figure 8. Cont'd.
From NEFSC summer bottom trawl surveys (1969-1995, all years combined). Distributions are displayed as presence absence only.

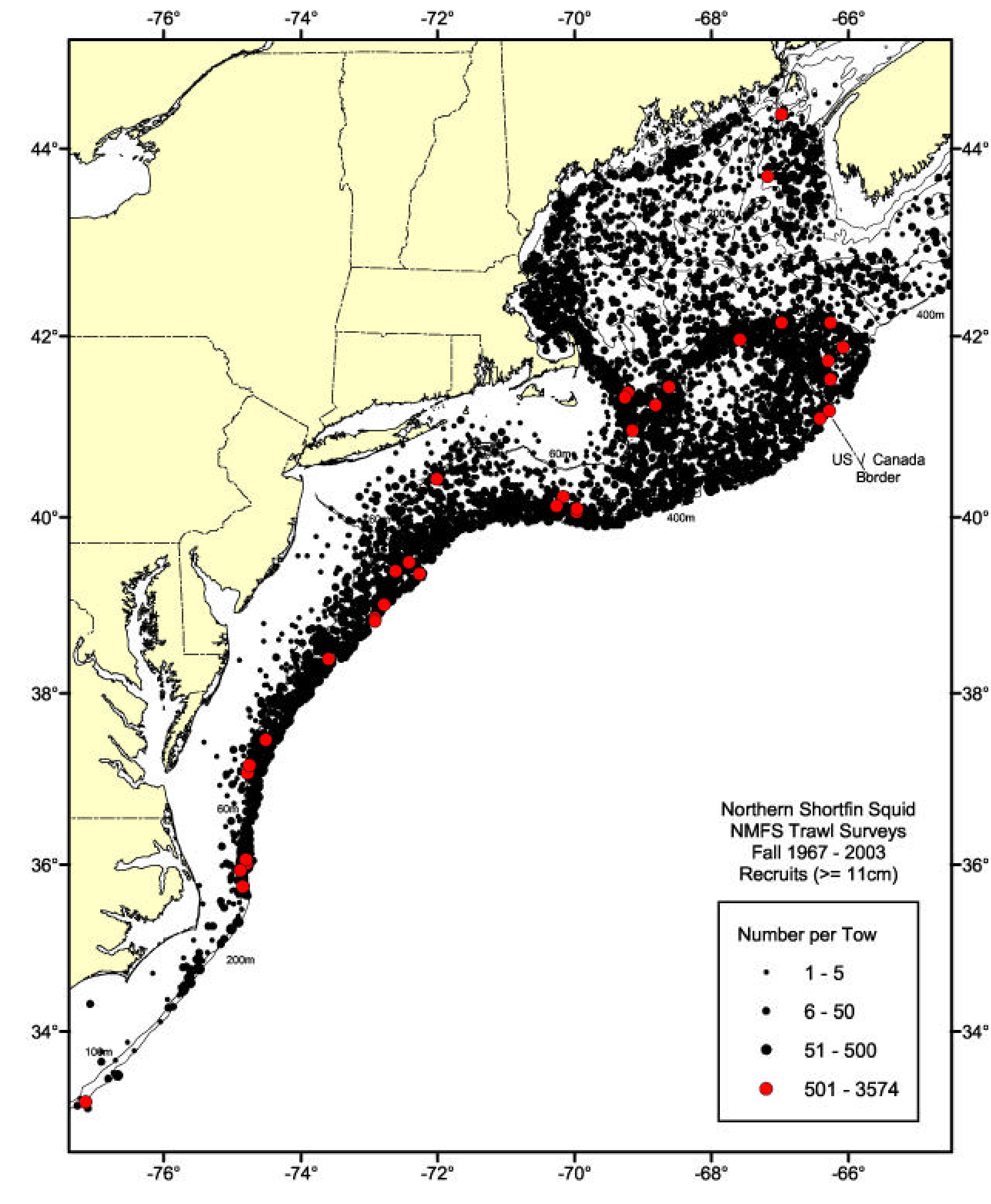


Figure 8. Cont'd.
From NEFSC fall bottom trawl surveys (1967-2003, all years combined). Survey stations where recruits were not found are not shown.

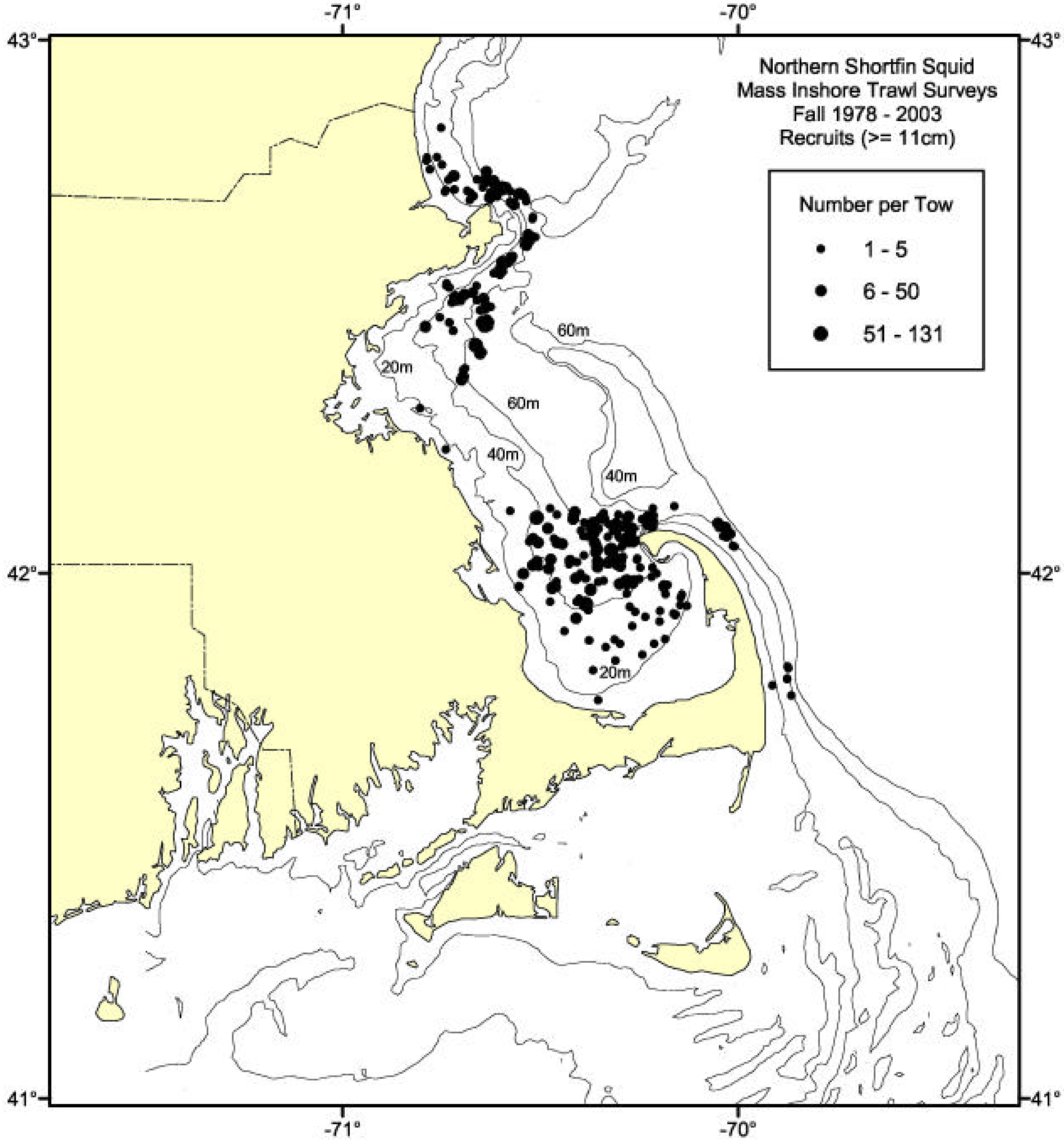


Figure 9. Distribution and abundance of recruit northern shortfin squid in Massachusetts coastal waters. From fall Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Survey stations where recruits were not found are not shown.

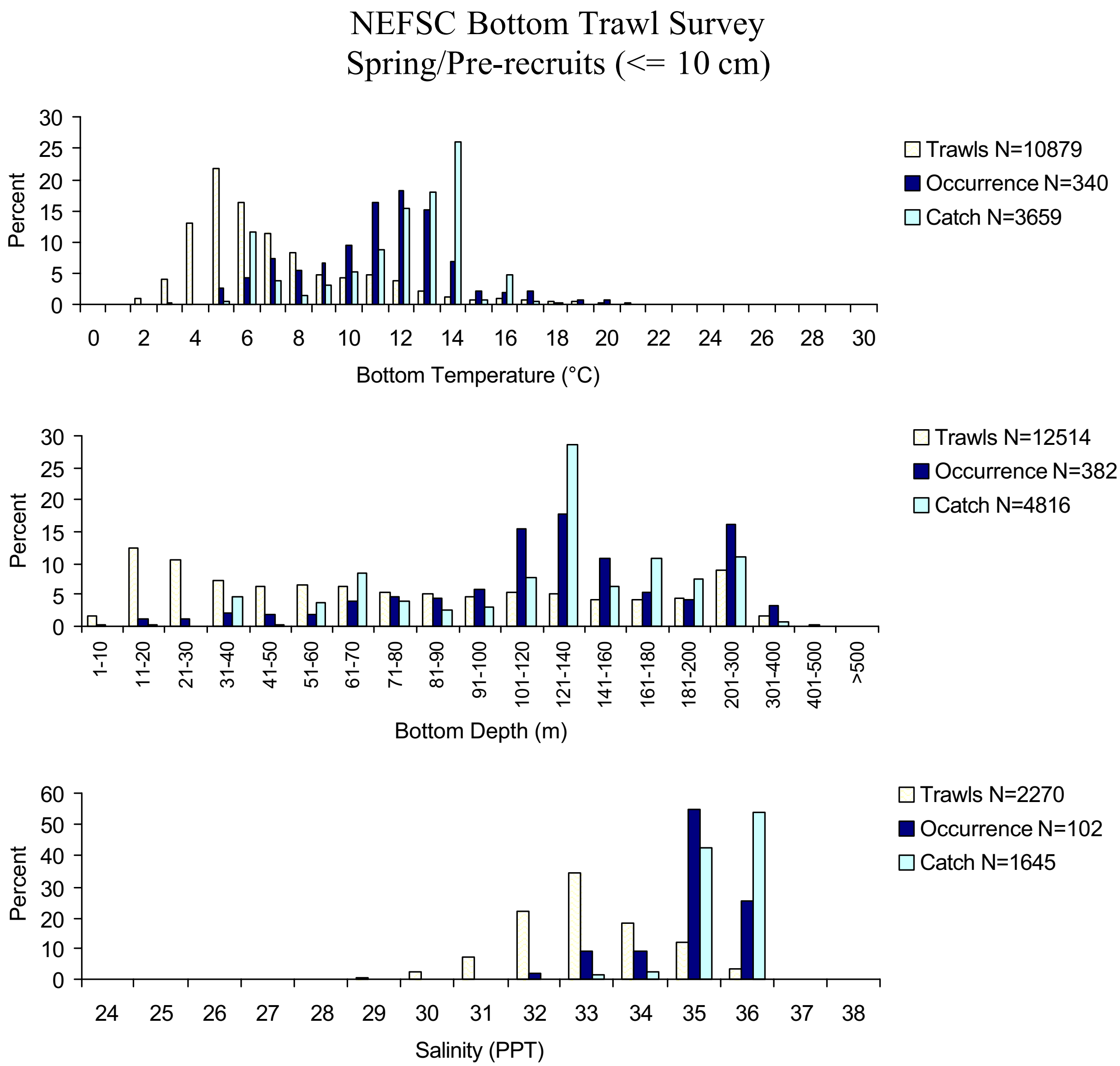


Figure 10. Distributions of pre-recruit northern shortfin squid and trawls from NEFSC bottom trawl surveys relative to bottom water temperature, depth, and salinity.
Based on NEFSC spring bottom trawl surveys (temperature and depth: 1968-2003, all years combined; salinity: 1991-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which northern shortfin squid occurred and medium bars show, within each interval, the percentage of the total number of northern shortfin squid caught. Note that the bottom depth interval changes with increasing depth.

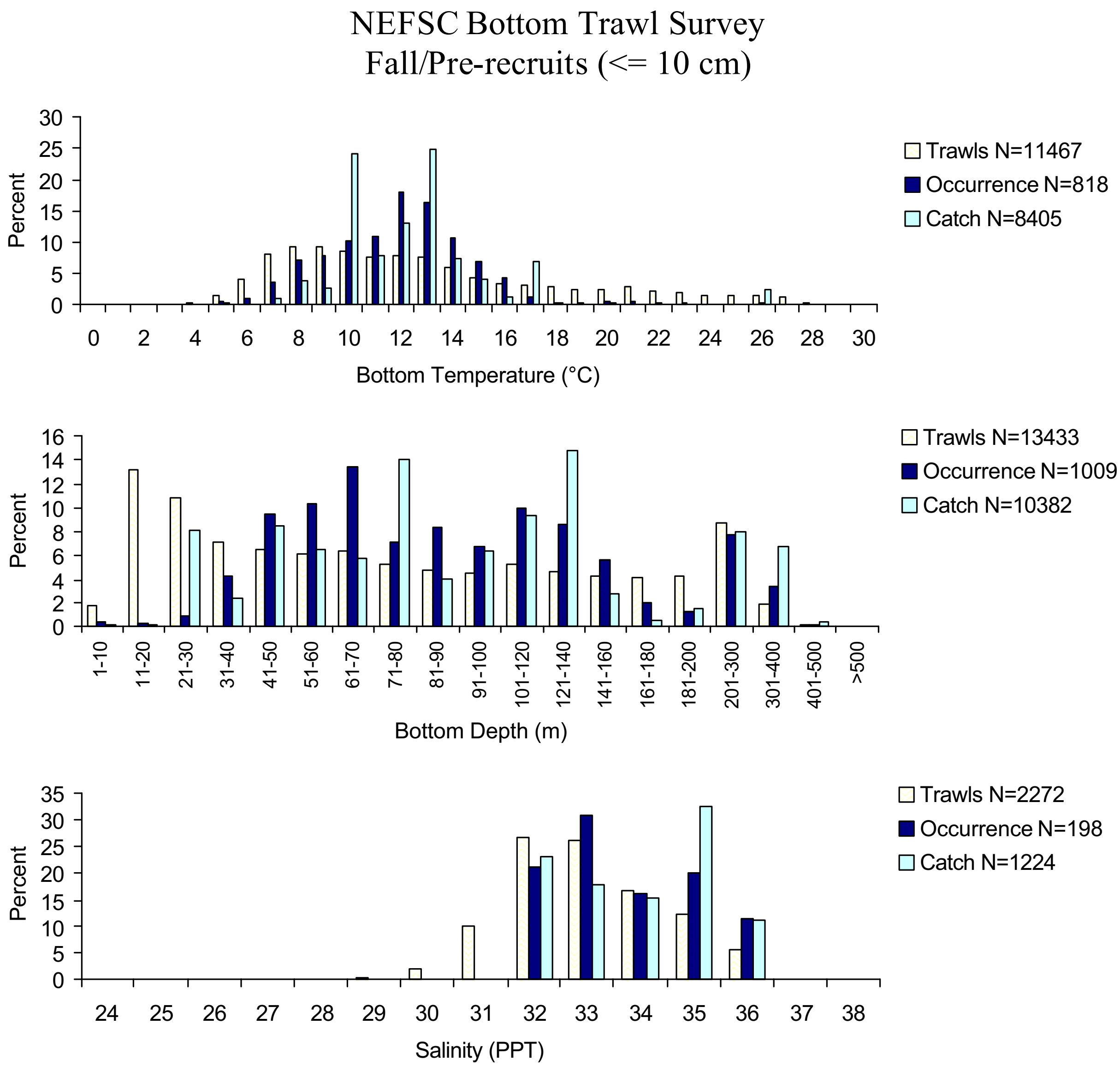


Figure 10. Cont'd.
Based on NEFSC fall bottom trawl surveys (temperature and depth: 1967-2003, all years combined; salinity: 1991-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which northern shortfin squid occurred and medium bars show, within each interval, the percentage of the total number of northern shortfin squid caught. Note that the bottom depth interval changes with increasing depth.

Massachusetts Inshore Bottom Trawl Survey
Spring/Pre-recruits (<= 10 cm)

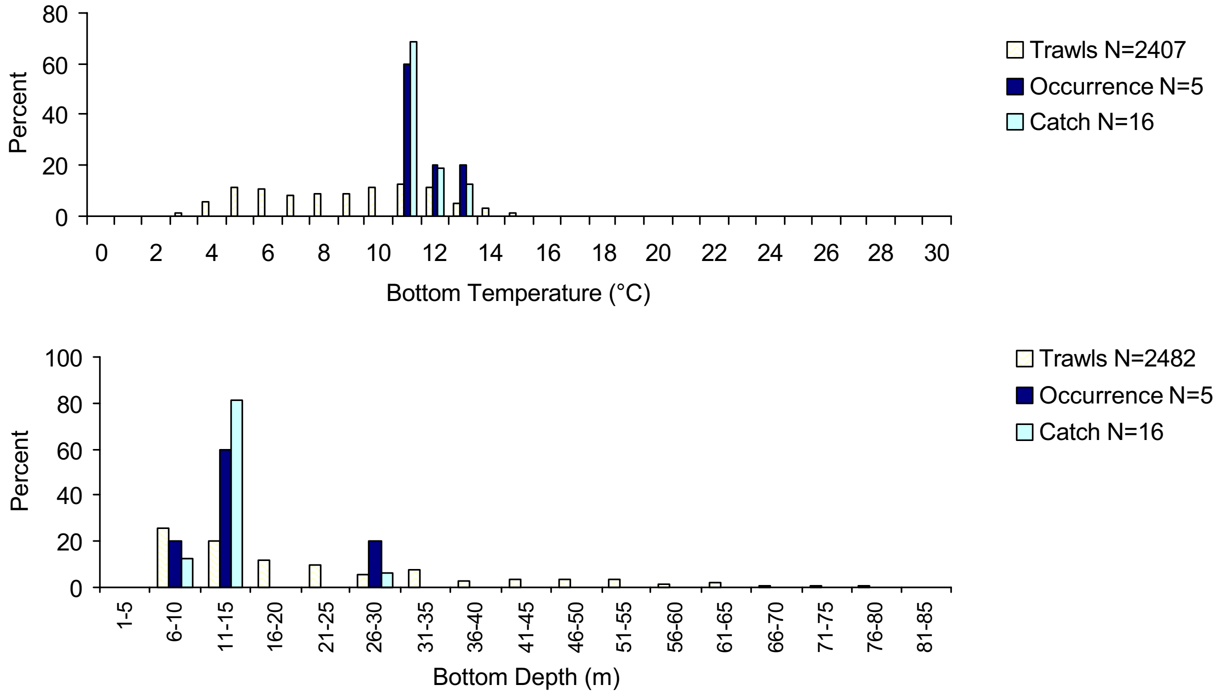


Figure 11. Distributions of pre-recruit northern shortfin squid and trawls in Massachusetts coastal waters relative to bottom water temperature and depth.
Based on spring Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which northern shortfin squid occurred and medium bars show, within each interval, the percentage of the total number of northern shortfin squid caught.

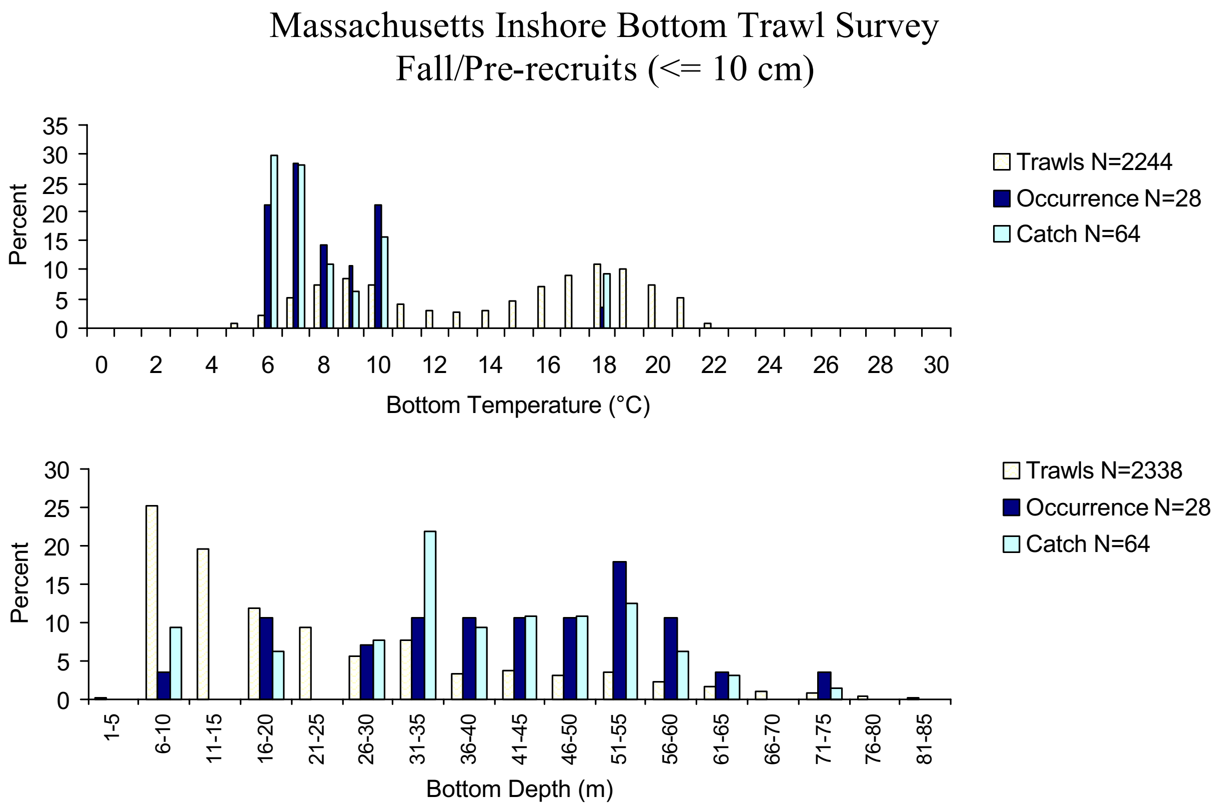


Figure 11. Cont'd.
Based on fall Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which northern shortfin squid occurred and medium bars show, within each interval, the percentage of the total number of northern shortfin squid caught.

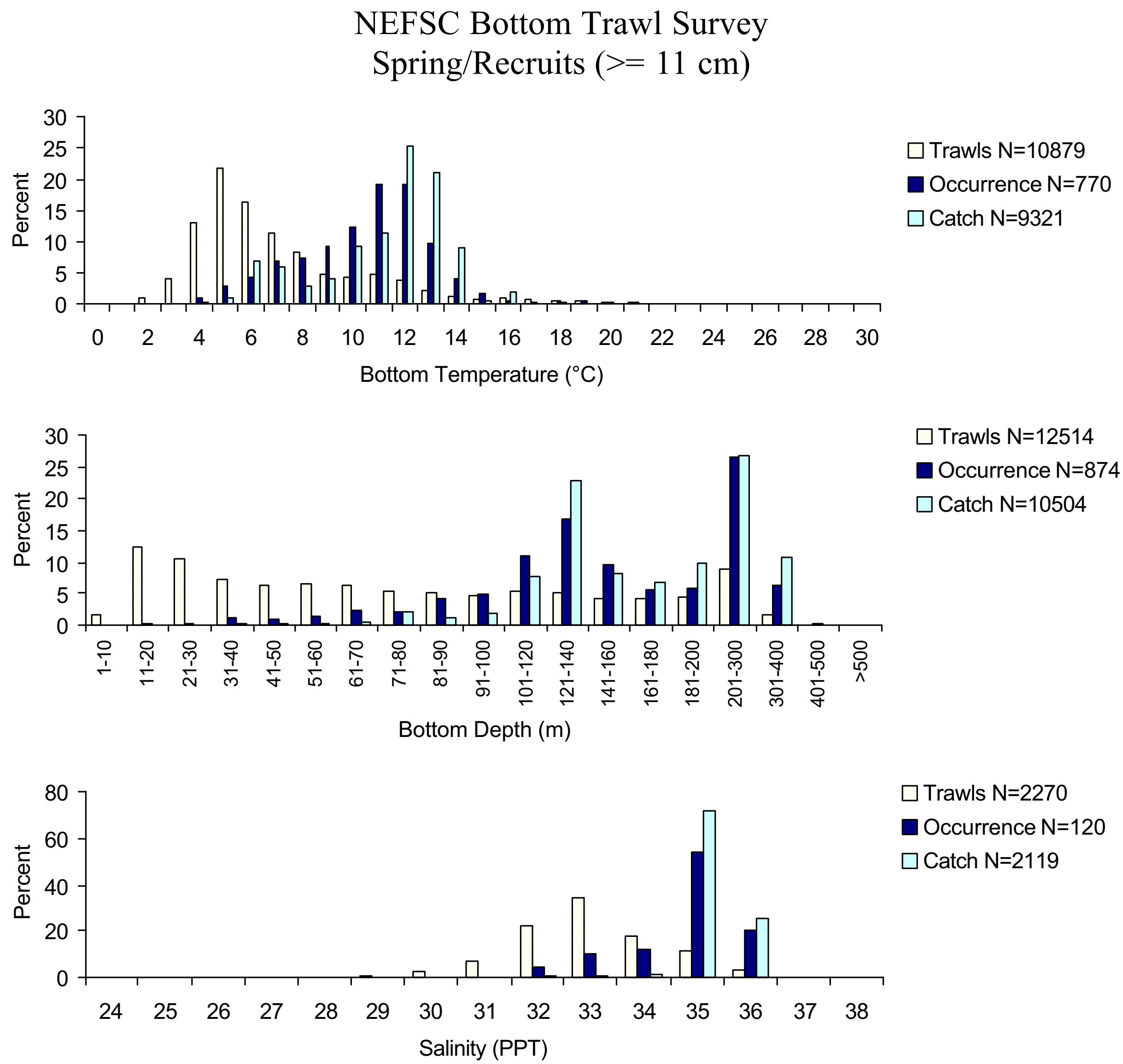


Figure 12. Distributions of recruit northern shortfin squid and trawls from NEFSC bottom trawl surveys relative to bottom water temperature, depth, and salinity.
Based on NEFSC spring bottom trawl surveys (temperature and depth: 1968-2003, all years combined; salinity: 1991-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which northern shortfin squid occurred and medium bars show, within each interval, the percentage of the total number of northern shortfin squid caught. Note that the bottom depth interval changes with increasing depth.

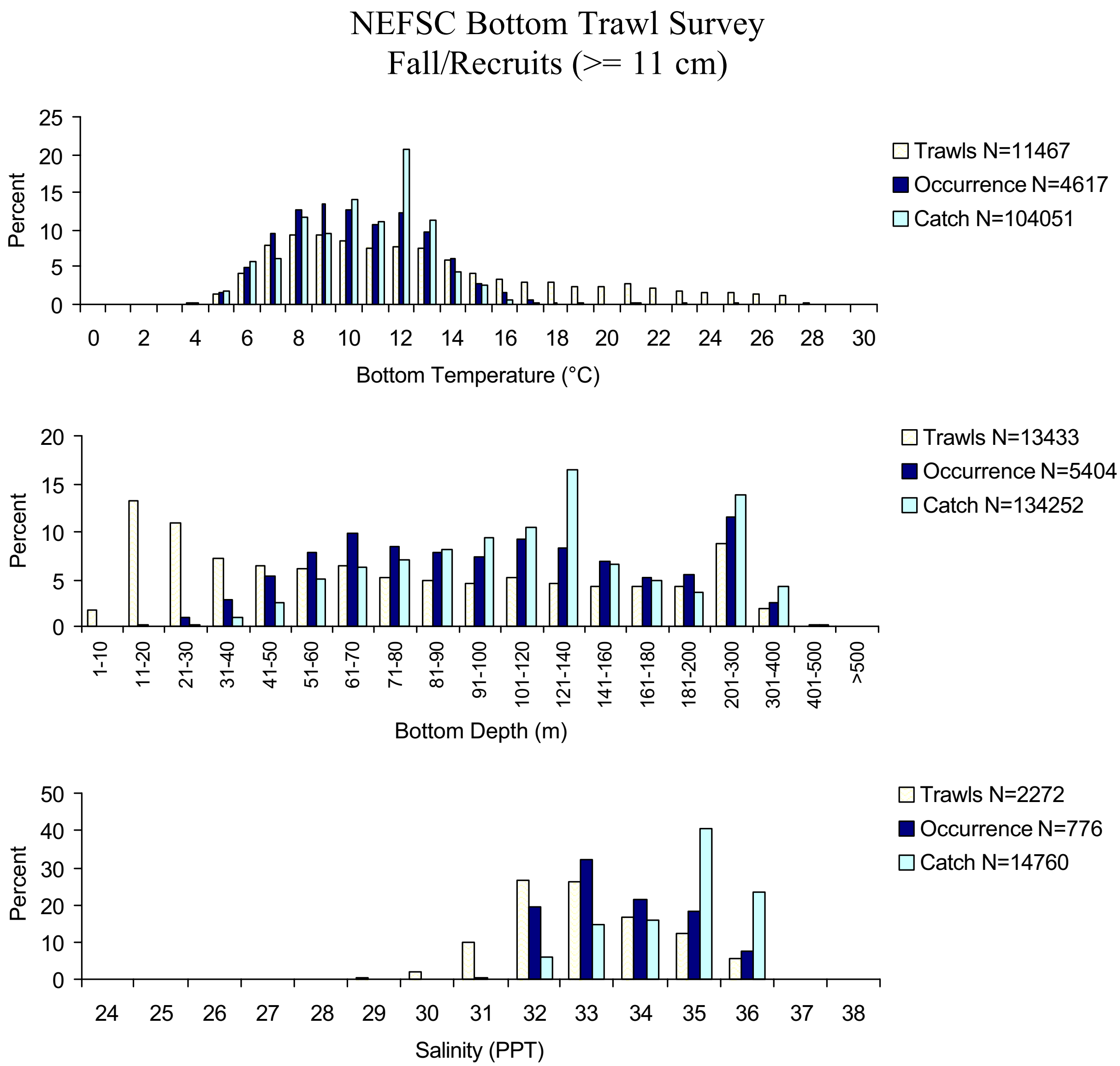


Figure 12. Cont'd.
Based on NEFSC fall bottom trawl surveys (temperature and depth: 1967-2003, all years combined; salinity: 1991-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which northern shortfin squid occurred and medium bars show, within each interval, the percentage of the total number of northern shortfin squid caught. Note that the bottom depth interval changes with increasing depth.

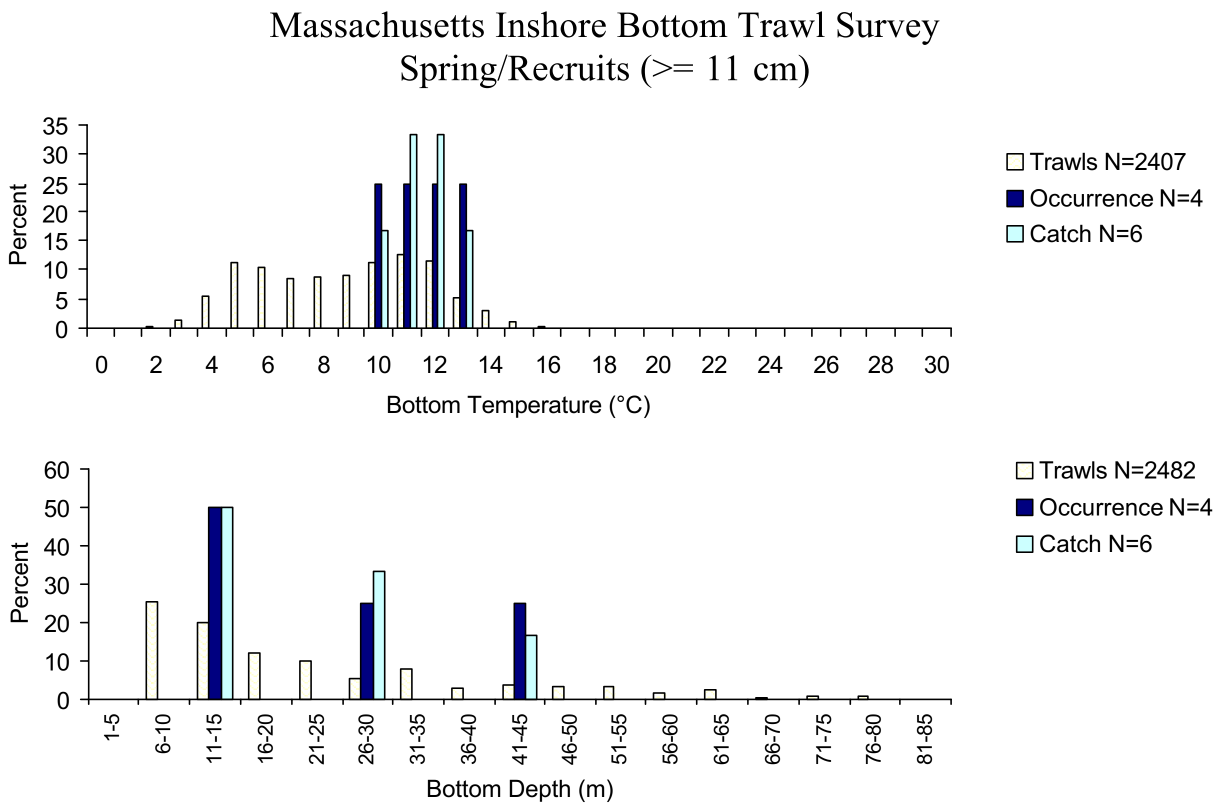


Figure 13. Distributions of recruit northern shortfin squid and trawls in Massachusetts coastal waters relative to bottom water temperature and depth.
Based on spring Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which northern shortfin squid occurred and medium bars show, within each interval, the percentage of the total number of northern shortfin squid caught.

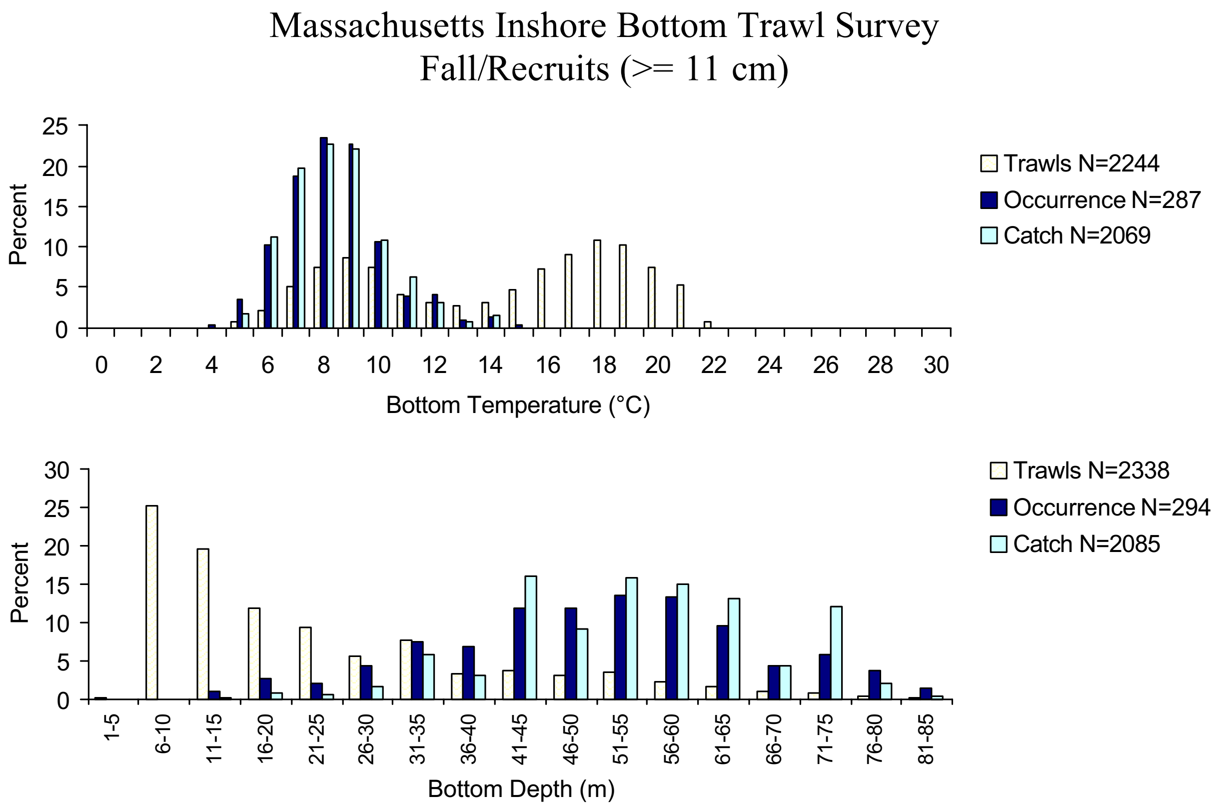


Figure 13. Cont'd.
Based on fall Massachusetts inshore bottom trawl surveys (1978-2003, all years combined). Light bars show the distribution of all the trawls, dark bars show the distribution of all trawls in which northern shortfin squid occurred and medium bars show, within each interval, the percentage of the total number of northern shortfin squid caught.

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Publications and Reports of the Northeast Fisheries Science Center

The mission of NOAA's National Marine Fisheries Service (NMFS) is "stewardship of living marine resources for the benefit of the nation through their science-based conservation and management and promotion of the health of their environment." As the research arm of the NMFS's Northeast Region, the Northeast Fisheries Science Center (NEFSC) supports the NMFS mission by "conducting ecosystem-based research and assessments of living marine resources, with a focus on the Northeast Shelf, to promote the recovery and long-term sustainability of these resources and to generate social and economic opportunities and benefits from their use." Results of NEFSC research are largely reported in primary scientific media (*e.g.*, anonymously-peer-reviewed scientific journals). However, to assist itself in providing data, information, and advice to its constituents, the NEFSC occasionally releases its results in its own media. Currently, there are three such media:

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