NOAA Technical Memorandum NMFS-NE-147

Essential Fish Habitat Source Document:

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

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

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Essential Fish Habitat Source Document:

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

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

Editorial Production

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

Special Acknowledgments

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

Internet Availability

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

Information Updating

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

Species Names

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

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

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

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

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

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

FOREWORD

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

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

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

NMFS Strategic Plan for Fisheries Research (February 1998)

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

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

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

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

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

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

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

JEFFREY N. CROSS, CHIEF
ECOSYSTEMS PROCESSES DIVISION
NORTHEAST FISHERIES SCIENCE CENTER

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INTRODUCTION

The northern shortfin squid, *Illex illecebrosus* (Figure 1), is a pelagic species of the family Ommastrephidae, which consists primarily of the oceanic squids. Also referred to as the summer squid, it is distributed in the western North Atlantic from the Labrador Sea to the Florida Straits (Roper *et al.* 1998). Exploitation of the species is currently managed under the Mid-Atlantic Fishery Management Council's Atlantic Mackerel, Squid and Butterfish Fishery Management Plan (MAFMC 1995). Within the range of commercial exploitation, from Newfoundland to Cape Hatteras, the population is considered to be a single stock (Hendrickson 1998).

This Essential Fish Habitat Source Document provides information on the life history and habitat characteristics of northern shortfin squid inhabiting the western North Atlantic Ocean.

LIFE HISTORY

The life history characteristics of the northern shortfin squid have been reviewed by Black *et al.* (1987), Perez (1994), and O'Dor and Dawe (1998). However, it should be noted that the life cycle proposed by Black *et al.* (1987) remains hypothetical (Figure 2), as several aspects of the species' life cycle remain unknown. For example, the location of the spawning site(s), adult migration patterns, and the autumn spawning migration route are currently inferred from limited data (L. Hendrickson, NMFS, NEFSC, Woods Hole, MA, personal communication).

EGGS AND LARVAE

No *Illex illecebrosus* egg masses have ever been collected in the wild (O'Dor and Dawe 1998), and current descriptions are based on laboratory spawning events. The eggs are spawned in the water column, in a gelatinous mass, 0.5-1.0 m in diameter (Perez 1994), containing 10,000-100,000 eggs (Durward *et al.* 1980). Females can produce up to 400,000 eggs (Perez 1994). Finished eggs weigh 200-250 µg and are oval in shape, ranging from 0.9 x 0.6 to 1.0 to 0.8 mm in size (Durward *et al.* 1980; O'Dor and Dawe 1998). The egg masses are pelagic (Durward *et al.* 1978; O'Dor and Durward 1979), probably located at midwater near the pycnocline (O'Dor and Balch 1985). Eggs are laid, enter the Gulf Stream, become buoyant, and travel to the inshore boundary of the current and hatch in 9-16 days (Perez 1994). O'Dor *et al.* (1982b) found that egg incubation lasted 16 days at 13^{o}C, 12 days at 16^{o}C, and 8 days at 21^{o}C; normal development requires at least 13^{o}C. It is hypothesized that egg masses are transported to the north via the Gulf Stream current (O'Dor 1983; Rowell *et al.* 1985a), and hatching is thought to occur at the inshore boundary of the Gulf Stream (Perez 1994).

The resulting larvae may initially remain within the remnants of the egg mass to utilize the nutrients for food (Durward *et al.* 1980) and continue to be transported northward via the Gulf Stream during late winter and early spring (Dawe and Beck 1985; Perez 1994; MAFMC 1995). In the laboratory, larvae hatch at approximately 1.1 mm mantle length (ML) (Durward *et al.* 1980). They change from a paralarval stage to a transitional stage at approximately 5.0 mm ML, and to the juvenile stage at about 7.0 mm ML (Hatanaka 1986).

Larvae have been collected in 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). However, they are most abundant in late January to February in the nutrient rich waters of the Gulf Stream/Slope Water zone, in the warm water (> 13^{o}C) above the thermocline (Amaratunga 1980a; Hatanaka *et al.* 1985). The convergence of the Gulf Stream and Slope Water creates an area of high productivity that is beneficial to the young for feeding (Perez 1994). Hatchlings have only been collected south of Cape Hatteras (Dawe and Beck 1985; Rowell *et al.* 1985a), suggesting that this area may serve as the larval source for the entire stock (Hatanaka *et al.* 1985).

JUVENILES AND ADULTS

The onset of the juvenile stage is indicated by the separation of the proboscis into a pair of tentacles (Black *et al.* 1987). In late spring, at a size of about 10 cm ML, juveniles begin to move onto the continental shelf into shallow waters off northern New England, Nova Scotia and Newfoundland (O'Dor 1983; Black *et al.* 1987; Perez 1994) where they may form large surface schools (MAFMC 1995). This time is spent feeding, and growth is rapid, approximately 1.5 mm per day (Amaratunga 1980a). By late summer and early fall, juveniles attain sizes of 18-25 cm ML, and begin to show signs of maturity (Wigley 1982). The size at which 50% of individuals are mature (L_{50}) is 20 cm ML (Brodziak 1995), although mean size at sexual maturity varies latitudinally and inter-annually, ranging from 20 to 21.5 cm ML in U.S. EEZ waters (Coelho and O'Dor 1993).

Males undergo earlier maturation than females and appear to migrate south during the fall in advance of females (Black *et al.* 1987). Evidence for this includes a seasonal decline in the percentage of males collected on the continental shelf during autumn (Amaratunga 1980a; Lange and Sissenwine 1980), which may be attributed to earlier emigration of males than females. Off Newfoundland, mature squid begin to move offshore in October-November (Hurley 1980), moving southward to the spawning areas in the warmer waters of the Gulf Stream (Dawe *et al.* 1981b). Spawning occurs a few months after maturity is reached (Squires 1967).

The life span of *Illex illecebrosus* has been reported as ranging from 1-1.5 years (Squires 1967; Wigley 1982). However, several recent studies utilizing statolith aging (Dawe *et al.* 1985) have shown the life span to be less than 1 year for both the northern and southern portions of the stock (Dawe and Beck 1997; O'Dor and Dawe 1998). The species may achieve a maximum size of 33-35 cm ML and 700 g, with females achieving larger sizes than males (O'Dor and Dawe 1998; Hendrickson 1998).

REPRODUCTION

Illex illecebrosus is a semelparous, terminal spawner with a protracted spawning season. There have been no direct observations of spawning in nature, but speculation about the timing and location of spawning is based on squid size and timing of advanced male maturity stages (O'Dor and Dawe 1998), back-calculated hatch dates from aging studies, and the collection of hatchlings in the wild (L. Hendrickson, personal communication). Northern shortfin squid spawning takes place in the deep waters of the continental slope during winter (MAFMC 1995). Spawning likely occurs throughout the year (O'Dor and Dawe 1998), with the most intense spawning generally occurring during December to March (Lange and Sissenwine 1980), but this varies among years and locations. Between Cape Canaveral, Florida and Charleston, North Carolina, spawning occurs during December to January (Rowell *et al*. 1985a; MAFMC 1995), while off Newfoundland, spawning has been reported from December to June (Squires 1967; Dawe and Beck 1997).

The principal spawning area is believed to be south of Cape Hatteras over the Blake Plateau (Figure 2; Black *et al.* 1987), but other spawning is believed to occur between the Florida peninsula and central New Jersey at depths down to 300 m (Fedulov and Froerman 1980; MAFMC 1995). Spawning probably occurs in the northern part of the Gulf Stream/Slope Water frontal zone (Dawe and Beck 1985; O'Dor and Balch 1985; Rowell *et al.* 1985a).

DIET

Northern shortfin squid feed primarily on fish, cephalopods (i.e., squid) and crustaceans. Fish prey include 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; Wigley 1982; Dawe *et al.* 1997), haddock and sculpin (Squires 1957). *Illex* also feed on adult capelin (Squires 1957; O'Dor *et al.* 1980a; Dawe *et al.* 1997), smelt and mummichogs (O'Dor *et al.* 1980a), and longfin inshore squid, *Loligo pealeii* (Vinogradov 1984). Cannibalism is significant.

Maurer and Bowman (1985) have demonstrated a seasonal shift in diet based on gut content analysis from the Northeast Fisheries Science Center (NEFSC) bottom trawl survey collections. When *Illex* are offshore in the spring, they primarily consume euphausiids, whereas they consume mostly fish and squid when they are inshore in the summer and fall. Individuals 6-10 cm and 26-30 cm ate mostly squid, 11-15 cm *Illex* ate mostly crustaceans and fish, and those 16-20 cm ate mostly crustaceans. Perez (1994) also demonstrated an ontogenetic shift in diet, with northern shortfin squid consuming fewer crustaceans and more fish as they grow larger.

The most important prey items of northern shortfin squid from the NEFSC bottom trawl survey data on food habits were crustaceans, fish and cephalopods (Figure 3). During 1973-1980, the diet of pre-recruit northern shortfin squid (≤ 10 cm ML) was made up of crustaceans (13%), nematodes (10%) and fish (4.5%), and the diet of recruits (≥ 11 cm ML) was composed of crustaceans (17%), cestodes (11%), fish (11%) and cephalopods (8%). During 1981-1990, the diet of recruits was dominated by cephalopods (30%) and fish (23%).

PREDATION

Numerous species of pelagic and benthic fishes are known to prey extensively 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 which may reduce predation, such as camouflage coloration (O'Dor 1983), schooling behavior, direction changes, and ink release (Major 1986).

MIGRATION

Northern shortfin squid are highly migratory and are capable of long distance migrations of more than 1,000 miles (Brodziak 1995). The hypothetical migration path is summarized in Figure 2 (Black *et al.* 1987). The species is believed to live for less than 1 year (Dawe and Beck 1997; O'Dor and Dawe 1998), and in autumn, adults from as far north as Newfoundland are believed to migrate south and offshore to warmer, deeper waters off the southern United States (O'Dor and Dawe 1998). The basis for this belief includes the seasonal change in distribution observed from research surveys (Hendrickson *et al.* 1996), the concentration 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 planktonic paralarvae can be rapidly transported northeastward into northern areas by the Gulf Stream current (Trites 1983).

NEFSC surveys indicate that *Illex* squid migrate offshore in autumn, and are not observed on the shelf again until next spring (Hendrickson *et al.* 1996; also see Geographical Distribution below) and tagging studies in Canadian waters have demonstrated a southeastward migration of *Illex* squid (Amaratunga 1981; Dawe *et. al.* 1981b), although it is not known if this migration passes over the U.S. continental shelf. The offshore component of the migration is not well understood since research surveys generally do not extend beyond the edge of the continental shelf (L. Hendrickson, personal communication).

HABITAT CHARACTERISTICS

Illex illecebrosus utilizes oceanic and neritic habitats and adults are believed to undergo long-distance migrations between boreal, temperate and sub-tropical waters. The egg and larval stages occur beyond the continental shelf, in the Gulf Stream. This is followed by a period of feeding on the continental shelf, and a fall migration to an offshore area south of Cape Hatteras to spawn (Black *et al.* 1987).

The habitat characteristics and preferences of northern shortfin squid are summarized in Table 1.

The terms pre-recruit and recruit are used here in describing habitat characteristics and geographical distributions of juveniles and adults. These terms refer to the exploited and unexploited portions of the stock. This species is exploited at a minimum mantle length of 10 cm, the approximate length at which individuals migrate from offshore waters onto the continental shelf (O'Dor 1983; Hendrickson *et al.* 1996). Pre-recruits are ≤ 10 cm ML, and recruits are ≥ 11 cm ML.

EGGS AND LARVAE

No *Illex illecebrosus* egg masses have ever been found in nature (O'Dor and Dawe 1998), but lab studies indicate that the minimum temperature at which normally spawned eggs will develop is about 13°C (O'Dor *et al.* 1982b). Egg development occurs up to at least 26°C; at this temperature hatching occurs in only 6 days (Balch *et al.* 1985).

Larvae have been found in nature at 5-20°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 reported to be at temperatures greater than 16.5°C (Hatanaka *et al.* 1985) and salinities of 35-37 ppt (Vecchione 1979; O'Dor 1983; Dawe and Beck 1985; Vecchione and Roper 1986). Eggs in nature are most likely found at similar temperatures and salinities as larvae.

JUVENILES

Juveniles have been captured at temperatures of 14.3-16.3°C in waters of the continental slope (Fedulov and Froerman 1980; Perez 1994), at temperatures > 16°C in the Gulf Stream (Perez 1994), and at 5-6°C on the continental shelf in spring (Perez 1994). They have been taken at salinities of 34-37 ppt (Vecchione 1979; Amaratunga *et al.* 1980b; Fedulov and Foerman 1980; Rowell *et al.* 1985a), and to depths > 1000 m (O'Dor and Dawe 1998); depths less than approximately 20 m are not generally significant habitat for *Illex* pre-recruits (L. Hendrickson, personal communication). Brodziak and Hendrickson (1999) found that pre-recruit catch rates during NEFSC bottom trawl surveys peaked at 27-55 m, and at bottom temperatures > 10.2°C and surface temperatures of 14.6-20.5°C.

ADULTS

Adults have been captured at temperatures ranging from -0.5 to 27.3°C (Whitaker 1980), salinities of 30-36.5 ppt (Palmer and O'Dor 1978), and at depths ranging from the surface to 1000 m or more (O'Dor and Dawe 1998), depending on the time of year (see Migrations above). In summer on the continental shelf, they are most abundant at 100-200 m (Bowman 1977; Grinkov and Rikhter 1981) and are not generally found in water < 18 m deep. In the fall and winter, adults migrate offshore, and have been found at 100-945 m (Amaratunga *et al.* 1980a; Felley and Vecchione 1995). However, there is little information on the offshore component of the population, and they are probably found at depths > 1000 m (O'Dor and Dawe 1998). Brodziak and Hendrickson (1999) found that peak catches of recruits during NEFSC bottom trawl surveys were at 185-366 m and at bottom temperatures of 10.2-12.9°C and surface temperatures of 20.6°C.

GEOGRAPHICAL DISTRIBUTION

Until recently, *Illex illecebrosus* was believed to be distributed on both sides of the North Atlantic. However, a recent study indicates that the species does not inhabit the eastern Atlantic, as was once thought (Roper *et al.* 1998). This confusion seems to have been a result of misidentifications of the closely related species *I.*

coindetii (which does seem to be distributed on both sides of the Atlantic) as *I. illecebrosus*.

In the western Atlantic, *I. illecebrosus* ranges from the Sea of Labrador (66°N) to the Straits of Florida (approximately 29°N) (O'Dor and Dawe 1998; Roper *et al.* 1998). It is most abundant in the Newfoundland region, moderately abundant between Newfoundland and New Jersey (Wigley 1982), and is commercially exploited from Newfoundland to Cape Hatteras (Brodziak 1995). According to data from the NOAA/Canada DFO East Coast of North America Strategic Assessment Project, the areas of highest abundance of the species are the southern edge of the Grand Bank, the Scotian Shelf, Georges Bank, and the Middle Atlantic Bight (Figure 4).

There is overlap in the geographic distributions of *Illex* species in the northwest Atlantic Ocean. *I. illecebrosus* is the only species found north of New Jersey, but in the southern part of its range, it co-occurs with *I. coindetii* and *I. oxygonius* (Roper and Mangold 1998; Roper *et al.* 1998). The species are morphologically similar and are difficult to distinguish and identify.

EGGS AND LARVAE

The egg and larval stages of the northern shortfin squid were not sampled by NEFSC Marine Resources Monitoring, Assessment and Prediction (MARMAP) ichthyoplankton surveys [see Reid *et al*. (1999) for details]. Egg masses have never been collected in nature; however, the consistent occurrence of hatchlings during January to February in waters south of Cape Hatteras suggests that spawning occurs in the Gulf Stream between Florida and Cape Hatteras (Dawe and Beck 1985; Rowell *et al.* 1985a).

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, south of Cape Hatteras and as far north as the Grand Bank (Dawe and Beck 1985; Hatanaka *et al.* 1985). Based on the dynamics of the Gulf Stream current, a rapid transport of eggs and larvae (at about 100 km/day) northward toward the Grand Bank has been hypothesized (Trites 1983).

PRE-RECRUITS

NEFSC Bottom Trawl Surveys

The NEFSC bottom trawl surveys captured northern shortfin squid pre-recruits (≤ 10 cm ML) during all seasons (Figure 5). The distribution pattern corresponds well to the migrations described earlier. In winter, pre-recruits were distributed primarily offshore (e.g., in the Gulf Stream), in waters outside the range of the survey. Low catches were made from North Carolina to Georges Bank, but were highest in the Middle Atlantic region. In the spring, the larger catches along the shelf edge from south of Cape Lookout to the Scotian Shelf indicate that the inshore migration of juveniles onto the continental shelf had begun. The spring survey distribution suggests that the inshore migration occurs earliest to the south, presumably due to proximity to the site of spawning. By summer, pre-recruits were caught throughout the continental shelf, from the shoreline out to the 183 m (100 fathom) line, and from North Carolina to Georges Bank. The highest catches were made south of Cape Cod and Long Island. The autumn distribution indicates that pre-recruits had begun the return migration to warmer, offshore waters. In the Middle Atlantic almost all catches were made outside of the 55 m (30 fathom) line, and most were taken at the 183 m line. Low numbers were found from a number of areas in the Gulf of Maine, and many were taken from throughout Georges Bank.

Pre-recruits were taken at depths ranging from 10-450 m (Figure 6). In winter, > 70% of pre-recruits were found at 120 and 160 m, and in the spring most were caught at 30-230 m. In summer, they were found much shallower, from 10-120 m, with most between 20-80 m, and in autumn they were found from 30-450 m, with most between 20-120 m. *Illex illecebrosus* is generally not found in waters less than 55 m deep; thus, these depths may include some species misidentifications (L. Hendrickson, personal communication). Pre-recruits were found at temperatures ranging from 2-23°C (Figure 6). In winter, > 75% were caught at 12-13°C, in spring, about 70% were caught at 9-13°C, in summer about 80% were caught at 8-13°C, and in autumn about 70% were caught at 9-12°C.

Massachusetts Inshore Trawl Survey

Very few northern shortfin squid pre-recruits were taken in Massachusetts inshore waters during spring and autumn surveys from 1978-1996. They were only collected at a total of four stations during the spring and at only nine stations during autumn. Low numbers of pre-recruits were taken north of Nantucket in the spring, while in the autumn they were taken from west of Nantucket, east of Cape Cod, Cape Cod Bay, and Massachusetts Bay.

Rhode Island Narragansett Bay Survey

A total of only 30 northern shortfin squid were caught during all surveys of Narragansett Bay from 1990-1996. They were captured at only three stations, and only during the summer. They ranged in size from 4-11 cm ML, although 29/30 were ≤ 10 cm (i.e., pre-recruits).

RECRUITS

NEFSC Bottom Trawl Surveys

The seasonal distribution of *Illex illecebrosus* from NEFSC bottom trawl surveys indicates that recruits (≥ 11 cm ML) undergo seasonal migrations similar to pre-recruits (Figure 5). The abundance of recruits during spring, autumn, and winter seem to be greater than that of pre-recruits; however, this may at least partially reflect differences in catchability between the two size groups (L. Hendrickson, personal communication). In winter, recruits were distributed offshore, with only low numbers taken at the 183 m depth contour. The higher catches in the spring indicate the inshore migration onto the continental shelf; catches were much higher, but most were still at the edges of the shelf. In summer, recruits were caught throughout the continental shelf from the shoreline out to the 183 m line and from Pamlico Sound to Georges Bank and throughout the Gulf of Maine. Catches in autumn, at least in the Middle Atlantic, indicate that the return migration to deeper waters had begun. High numbers of recruits were taken from throughout Georges Bank, the Great South Channel, and the Gulf of Maine.

Recruits were taken at depths ranging from 10-420 m (Figure 6), and seem to inhabit shallower (i.e., inshore) waters in summer and autumn than in winter and spring. This corresponds with the seasonal migration patterns of the species. In winter, > 50% of recruits were found at 120 m and 210 m. In the spring, they were found at a wide range of depths, with most at 70-280 m. In summer, they were found much shallower, with most between 40-90 m, and in autumn, they were found from 30-370 m, but most were at depths of less than 130 m. Recruits were found at temperatures ranging from 4-19^{o}C (Figure 6). In winter, > 80% were caught at 11-13^{o}C, in spring, > 60% were caught at 9-12^{o}C, in summer > 70% were caught at 5-9^{o}C, and in autumn, > 70% were caught at 8-12^{o}C.

Massachusetts Inshore Trawl Survey

Northern shortfin squid recruits were taken in low numbers from throughout Massachusetts coastal waters in the spring, but were taken at only 9 stations in the fall (west of Nantucket, east of Cape Cod, Cape Cod Bay, and Massachusetts Bay). This distribution pattern corresponds well to the species' seasonal inshore-offshore migrations. The difference in spring inshore abundance between pre-recruits and recruits (i.e., recruits > pre-recruits) is probably due to size-related differences in the timing of migration, with larger individuals migrating inshore earlier in the spring.

STATUS OF THE STOCKS

In the U.S. Exclusive Economic Zone (EEZ), from Cape Hatteras to the Gulf of Maine, *Illex illecebrosus* is targeted primarily during June to September by small-mesh otter trawl fisheries near the edge of the continental shelf (Hendrickson 1998). This is a transboundary unit stock, with fisheries in the U.S. EEZ managed by the Mid-Atlantic Fishery Management Council, and fisheries in the Canadian EEZ managed by the Northwest Atlantic Fisheries Organization (NAFO) (Dawe and Hendrickson 1998).

Total landings (U.S. and Canada) of northern shortfin squid increased sharply from 1,600 mt in 1969 to 179,300 mt in 1979. During 1975-1982, 76% of the total landings were from Canadian waters. However, the northern fisheries collapsed following the peak in 1979. Landings from the U.S. EEZ peaked in 1976 at 25,000 mt. Since 1982, landings have been taken primarily by the U.S. fishery (Dawe and Hendrickson 1988; Hendrickson 1998). Directed foreign fishing was eliminated in 1987, and the fishery was restricted to the United States and Canada (Hendrickson *et al.* 1996). U.S. landings increased steadily since 1988 to 18,350 mt in 1994; landings in 1996 totaled 16,969 mt, 21% more than the 1995 total of 14,058 mt (Figure 7; Hendrickson 1998).

A recent assessment of the *Illex illecebrosus* stock within the United States EEZ, from Cape Hatteras to the Gulf of Maine, categorized the stock as almost fully exploited with a medium biomass level (Hendrickson *et al.* 1996). However, recruitment is highly variable and may vary with environmental conditions. Generally, patterns of *Illex illecebrosus* abundance seem to be cyclical, with alternating periods of extreme low and high abundance (MAFMC 1995). Stock biomass levels were lowest in 1982, highest in 1986 (Hendrickson *et al.* 1996) and have generally decreased to a medium level since 1989 (Hendrickson 1998).

RESEARCH NEEDS

Research is needed on a number of components of the life-cycle of this species. Currently the life cycle is hypothetical and based on limited information. In particular, the fall emigration routes, the location of the spawning areas (which are believed to be in the Gulf Stream from Florida to Cape Hatteras), and the egg and larval Gulf Stream migration need to be better understood. More information about the offshore component of the population, through directed sampling off of the continental shelf in fall and winter would provide information about these components of the annual cycle. Spawning by this species has never been observed in nature, and egg masses have never been captured.

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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 eggs may enter the Gulf Stream and travel northward at the inshore boundary of the current.	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).
Larvae [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 south of Cape Hatteras. Larvae have been found during winter and spring off tail of Grand Bank. Abundant in late Jan-Feb in Gulf Stream/slope water, in warm water above thermocline. The convergence of Gulf Stream and slope water creates an area of high productivity that is beneficial to young for feeding and growth. Greater abundance during the day at 50-100 m.		Found from 5-20°C; maximum abundance at > 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.	Late winter: in Gulf Stream Spring: open ocean, offshore, 50 to 500 m, begin migration onto continental shelf. Summer: after being transported northward via Gulf Stream, juveniles migrate onto continental shelf and into inshore waters near New England and Nova Scotia.		Gulf Stream: > 16°C; slope water: < 16°C; surface: 14-21°C; continental shelf: 5-6°C in spring. Pre-recruits on US 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 34-35 cm ML. Life span about 1 year; but may be somewhat variable. Recent statolith aging studies suggest life span of < 1 year. Males and females grow ~ 1 mm/day. Females grow faster than males but mature later.	Range from Labrador and Newfoundland to south of Cape Hatteras; most abundant at depths of 100-150m. Winter/spring: continental shelf to offshore, 100-945 m. Summer/fall: in bays, Gulf of Maine, Massachusetts Bay, and Georges Bank. Fall: migrate from inshore to Gulf Stream for spawning in winter. Larger *Illex* found at greater depths in autumn, indicating ontogenetic migration occurs when maturation begins.	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)

Table 1. cont'd.

Life Stage	Prey	Predators	Spawning	Notes
Eggs [1]			Spawning has never been observed in the wild. It is believed that most of the population spawns south of Cape Hatteras. Egg masses are spawned pelagically and masses that do not move with currents turn black on side towards bottom due to anoxia.	Eggs that are spawned in Gulf Stream waters can hatch in northern shelf waters (transported by Gulf Stream at rate of 7 km/hr); can also hatch in warm Gulf Stream waters.
Larvae [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 larvae throughout range in NW Atlantic; initially flows northeastward along shelf, off Cape Hatteras, flows easterly - creates an eddy in which young are transported westward into slope waters.
Pre-recruits [3] ≤ 10.0 cm				Diel vertical migrations; aggregated near bottom during daytime, migrate upwards at night. Gulf Stream provides mode of transportation northward for larvae and juveniles after spawning occurs in southern regions; hydrographic variability in this system may explain annual abundance differences.
Recruits [4] ≥ 11 cm	Visual predators; feeding rate reduced in highly turbid waters. Typically feed on squid, fish and crustaceans. Fish prey include juvenile Atlantic cod, mackerel, redfish, sand lance, Atlantic herring, adult capelin, smelt and mummichogs. Seasonal/ontogenetic diet shifts: spring (offshore): euphausiids; summer-fall (inshore): fish and squid. Cannibalism by large individuals on smaller ones (generally males), increases during autumn.	Many pelagic and benthic fishes feed heavily on *Illex*, including bluefin tuna and silver and red hakes. Other fish predators include shark and dogfish sp., 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 during Dec-March; probably in northern part of Gulf Stream or at boundary with slope water, possibly limited to south of Hatteras. Mature *Illex* migrate offshore in the late fall, spawn in waters > 366 m depth off the continental shelf. Adults spawn once, then die after spawning. Males may mate with more than one female of advanced sexual maturity (based on lab studies).	Diel vertical migrations: more abundant at dawn/dusk than day/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), 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)

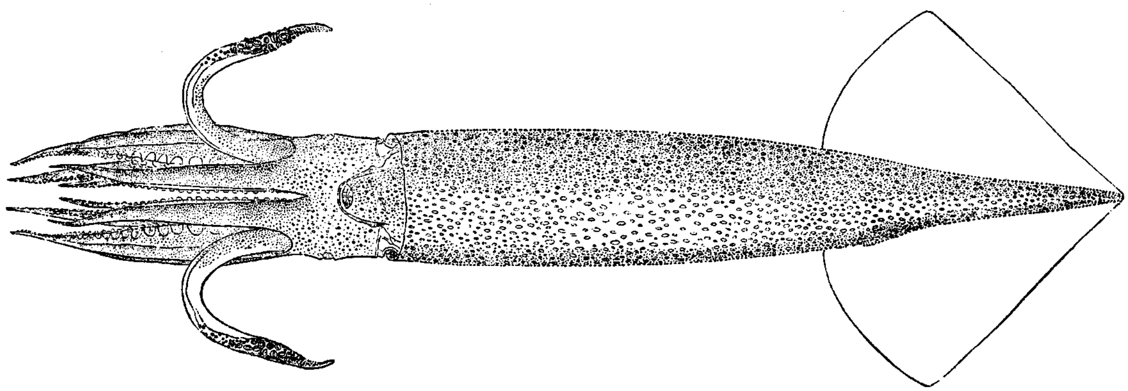


Figure 1. The northern shortfin squid, *Illex illecebrosus* (from Goode 1884).

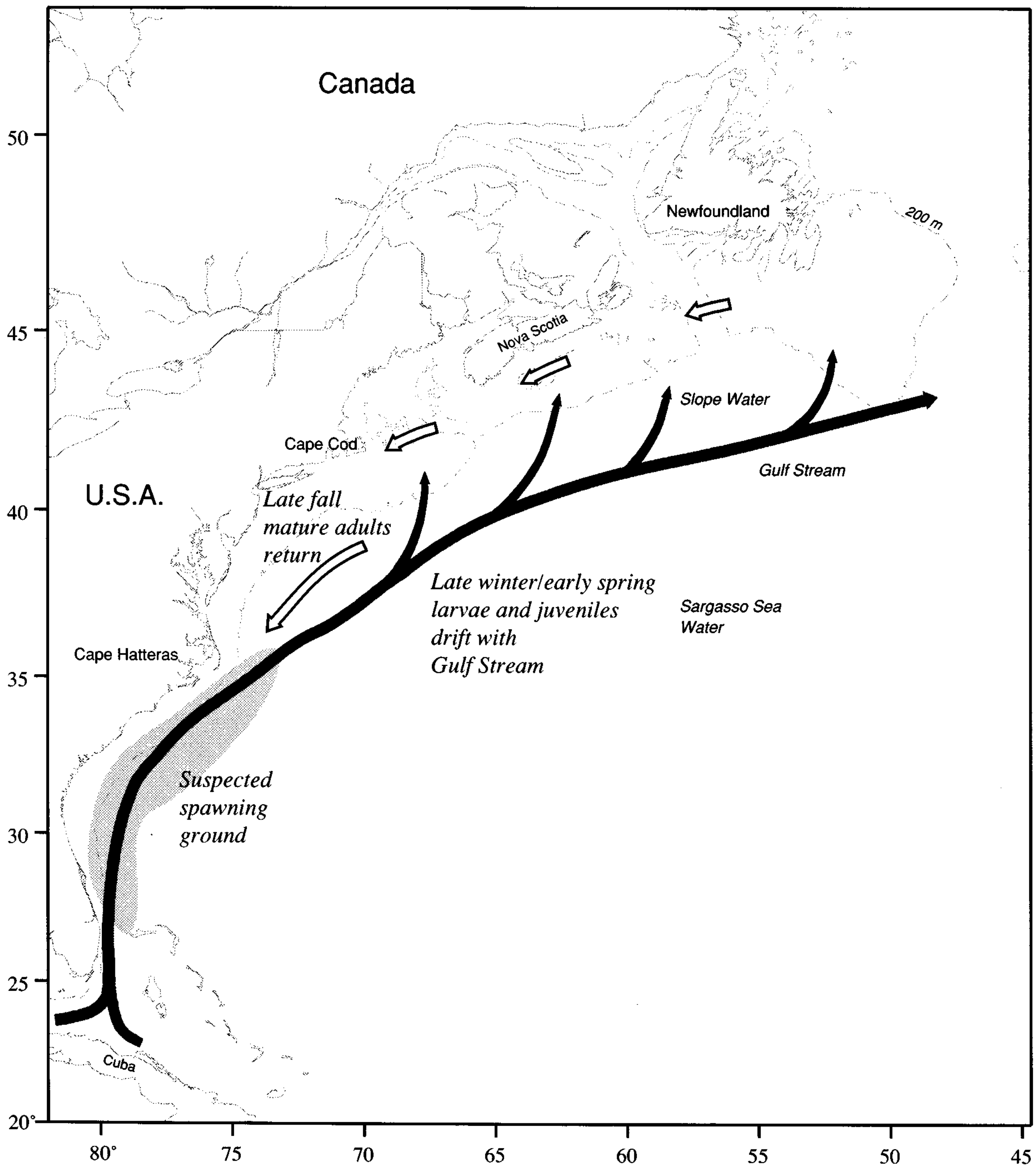


Figure 2. Hypothetical migration path of the northern shortfin squid, *Illex illecebrosus*. From Black *et al.* (1987).

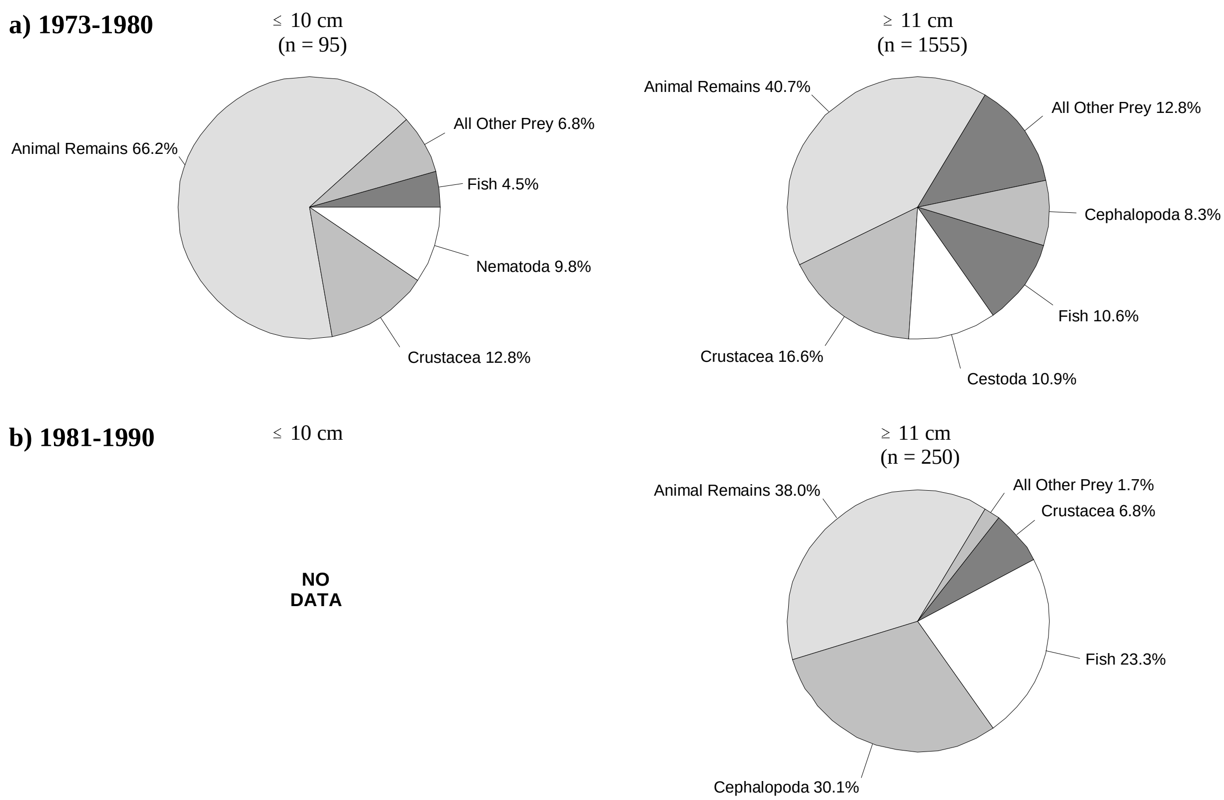


Figure 3. Abundance (% occurrence) of the major prey items in the diet of the northern shortfin squid during 1973-1980 and 1981-1990, from NEFSC bottom trawl surveys. The ≤ 10 cm size range corresponds to pre-recruits, and the ≥ 11 cm size class corresponds to recruits. The category “animal remains” refers to unidentifiable animal matter. Methods for sampling, processing, and analysis of samples differed between the time periods [see Reid *et al.* (1999) for details].

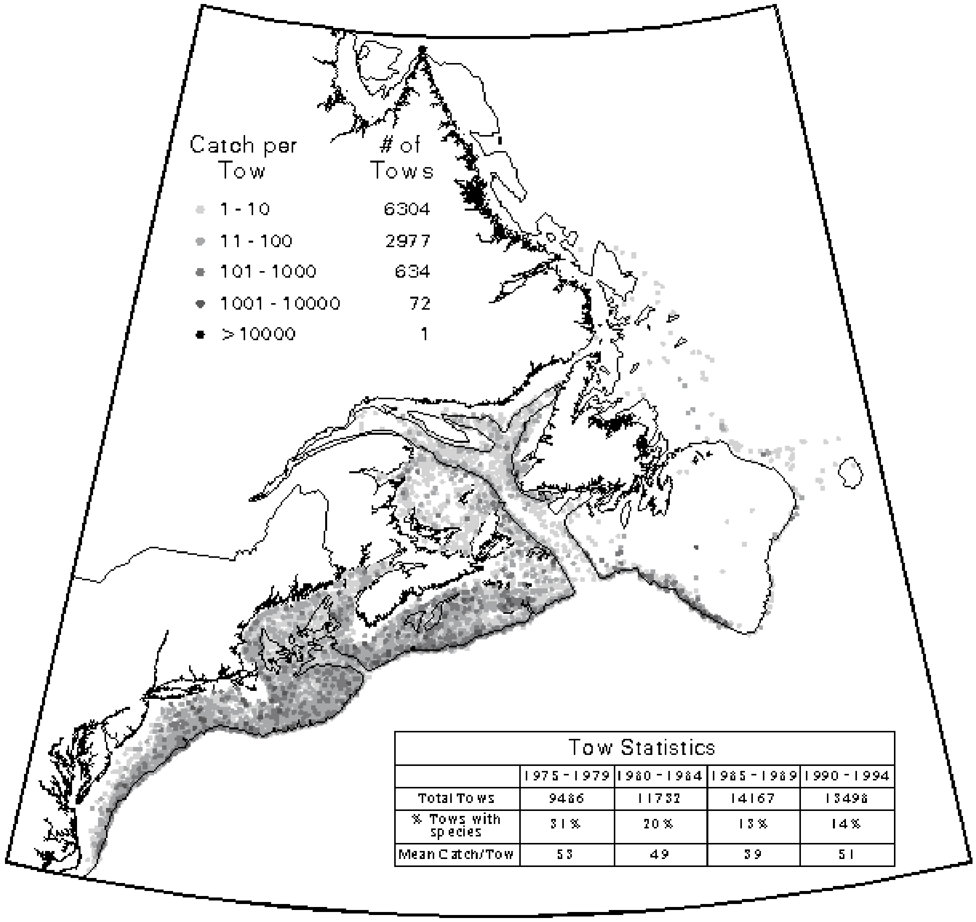


Figure 4. Distribution of northern shortfin squid from Newfoundland to Cape Hatteras during 1975-1994. Data are from the U.S. NOAA/Canada DFO East Coast of North America Strategic Assessment Project (http://www-orca.nos.noaa.gov/projects/ecnasap/ecnasap_table.html).

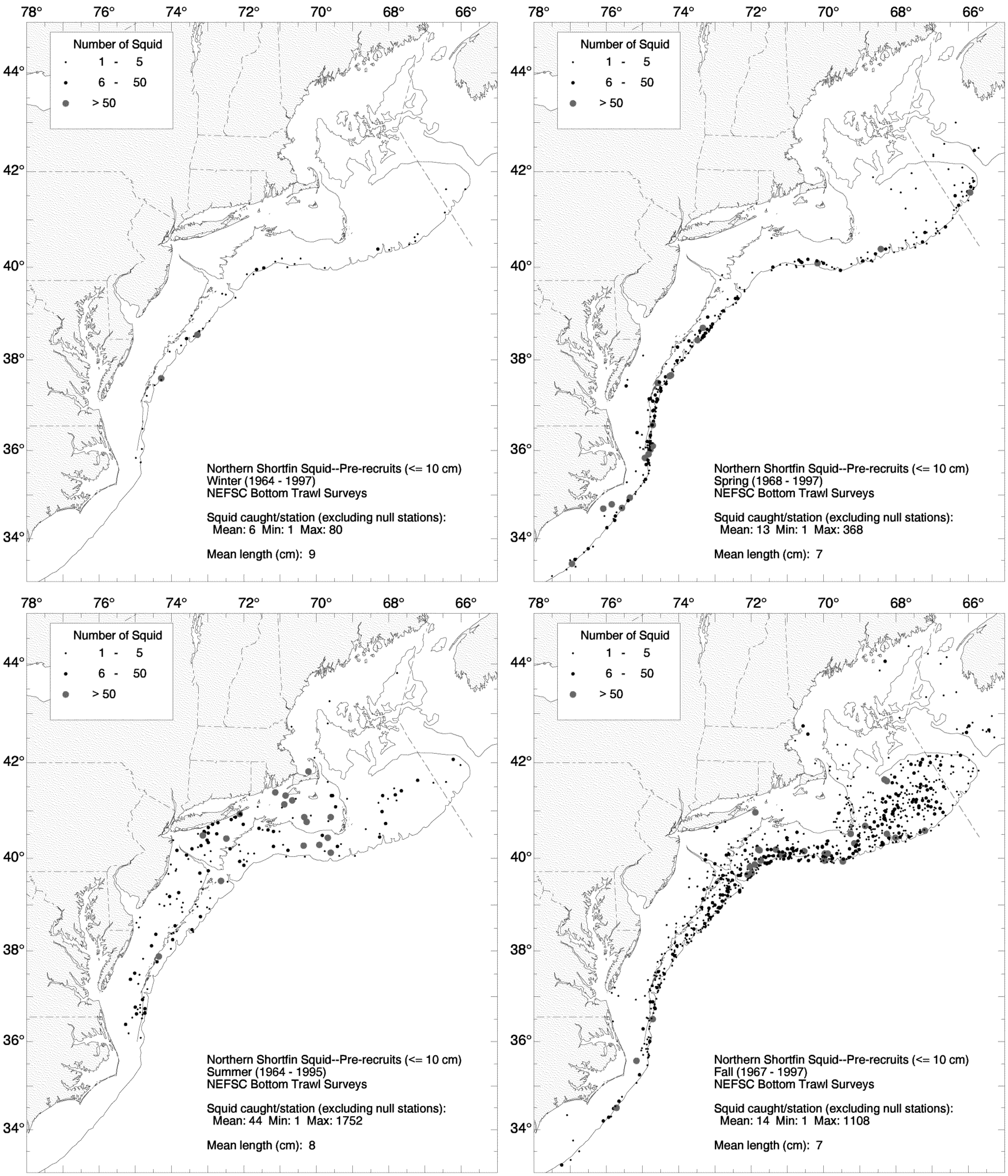


Figure 5. Distribution and abundance of northern shortfin squid pre-recruits (≤ 10 cm) and recruits (≥ 11 cm) collected during NEFSC bottom trawl surveys in winter (1964-1997), spring (1968-1997), summer (1964-1995), and autumn (1967-1997). Densities (number per tow) are represented by dot size [see Reid *et al.* (1999) for details].

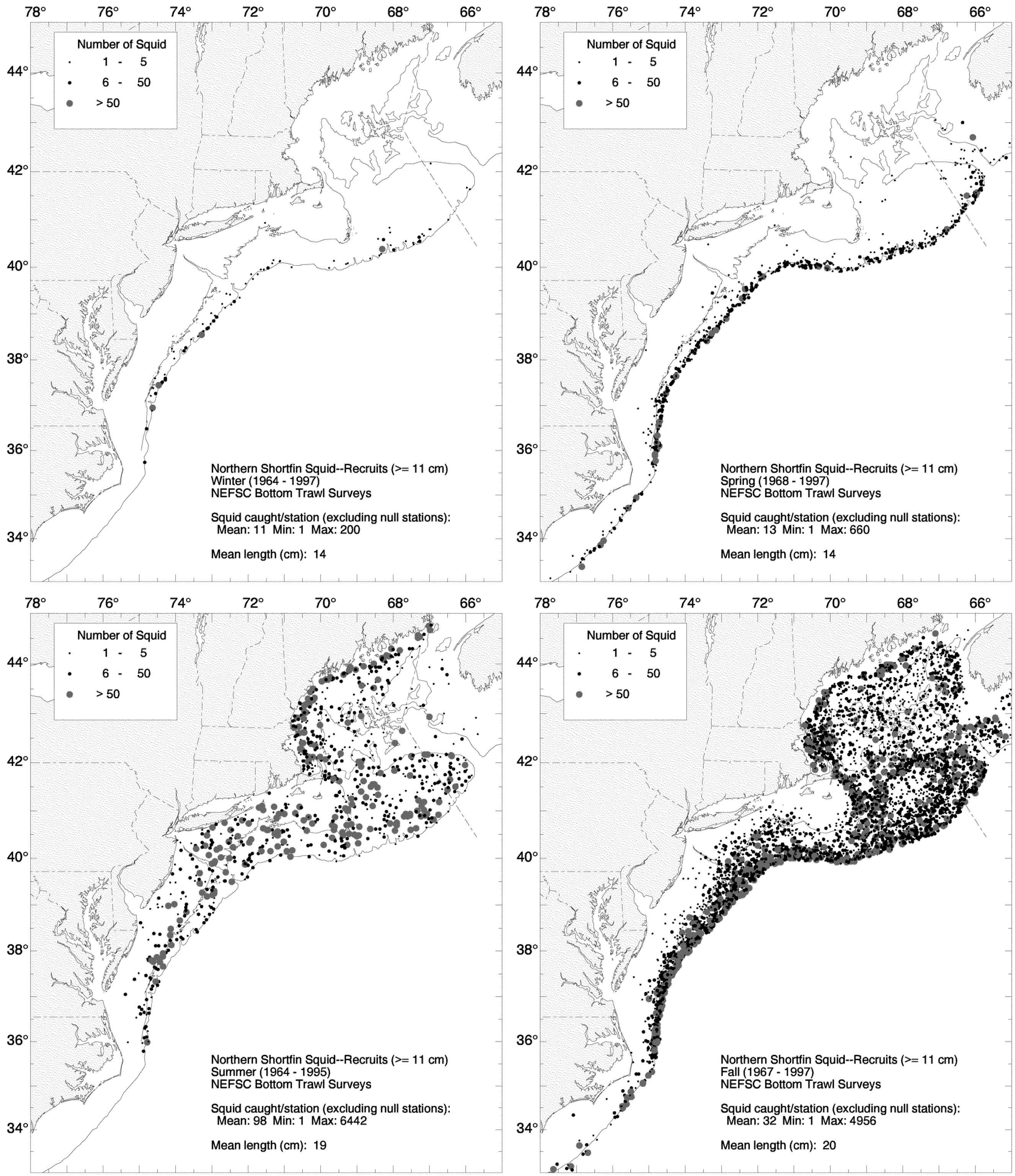


Figure 5. cont'd.

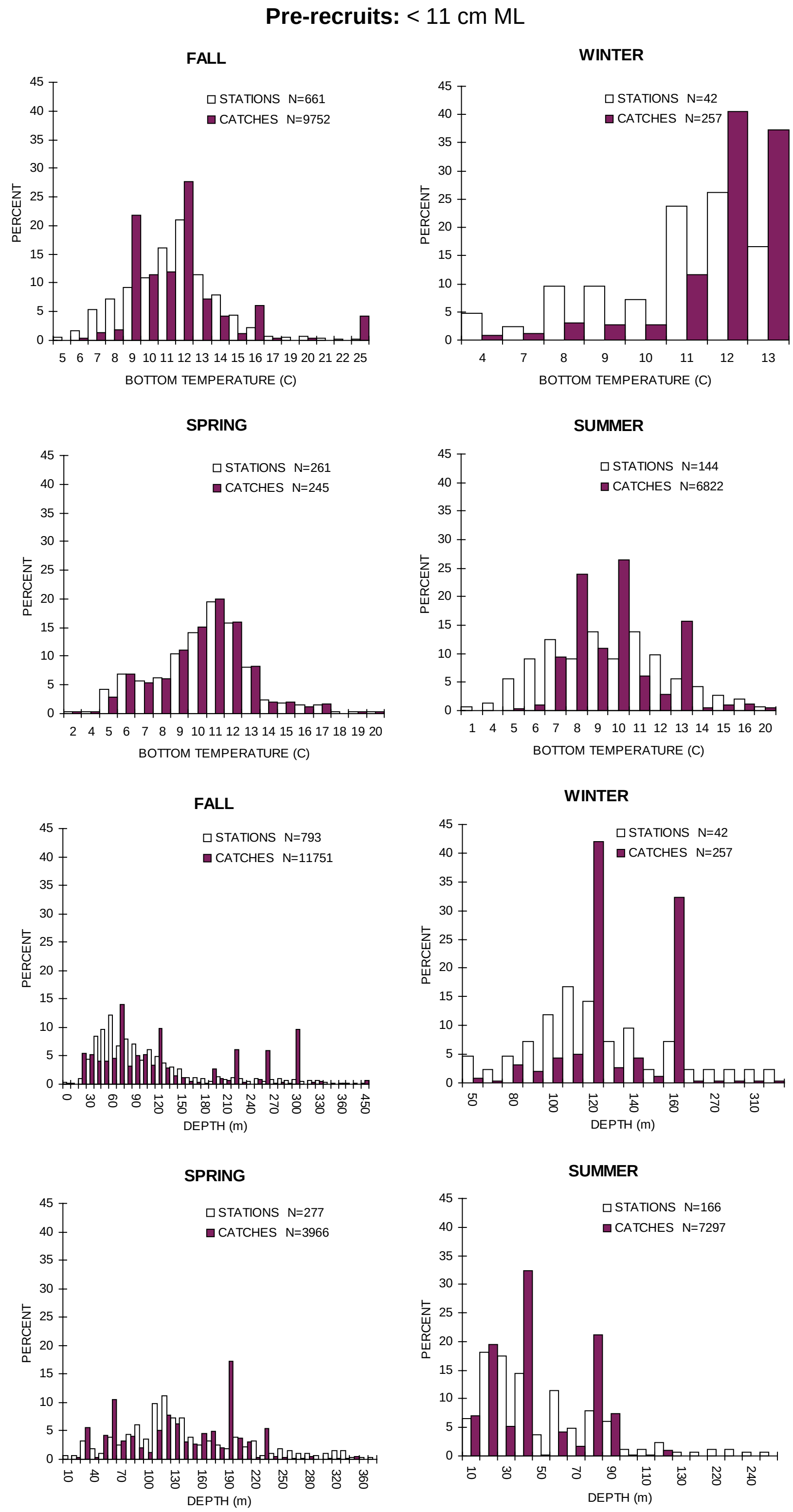
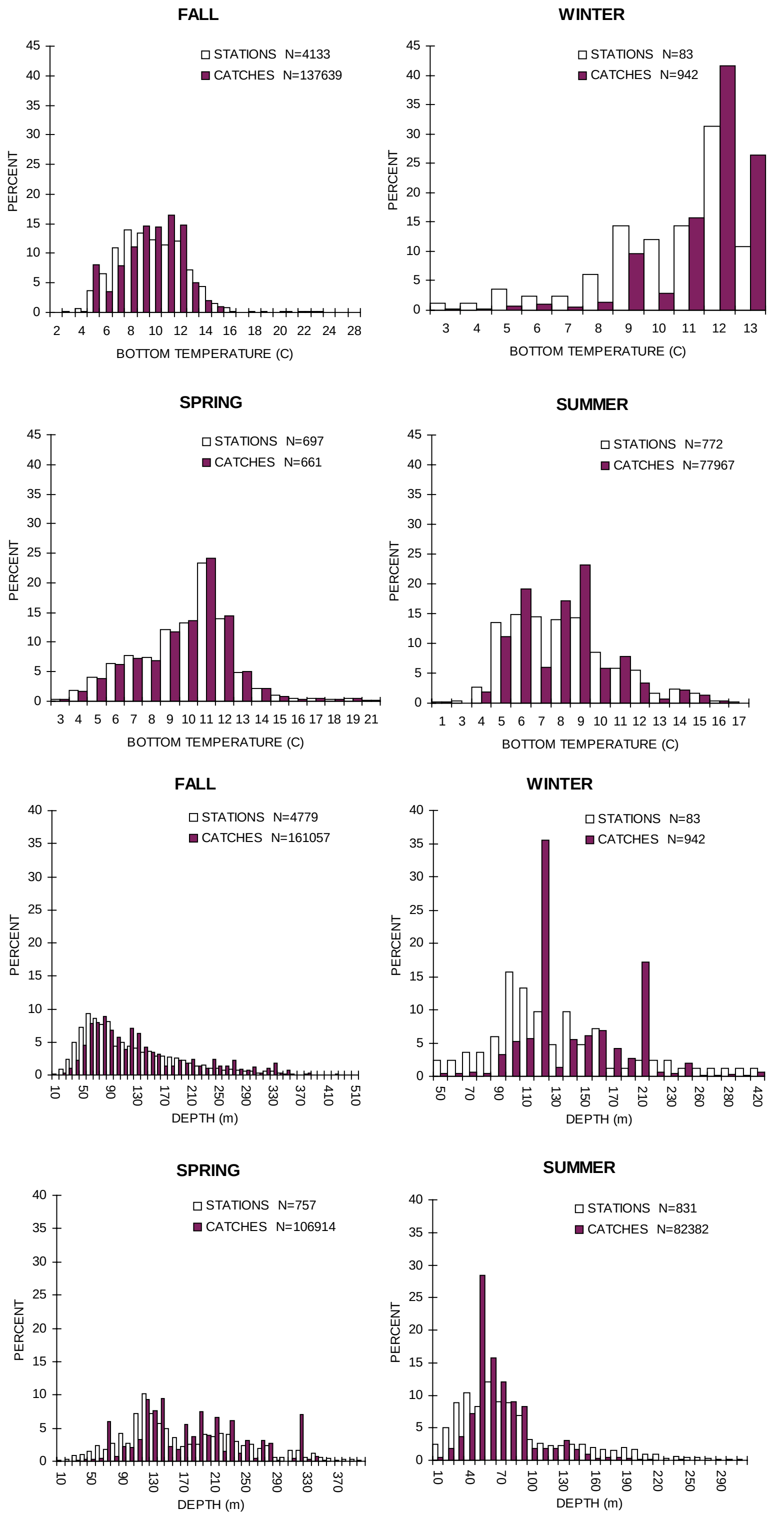


Figure 6. Seasonal abundance of northern shortfin squid pre-recruits (< 11 cm) and recruits (≥ 11 cm) relative to bottom water temperature and depth, based on NEFSC bottom trawl surveys (all years combined). Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).

Recruits: ≥ 11 cm ML



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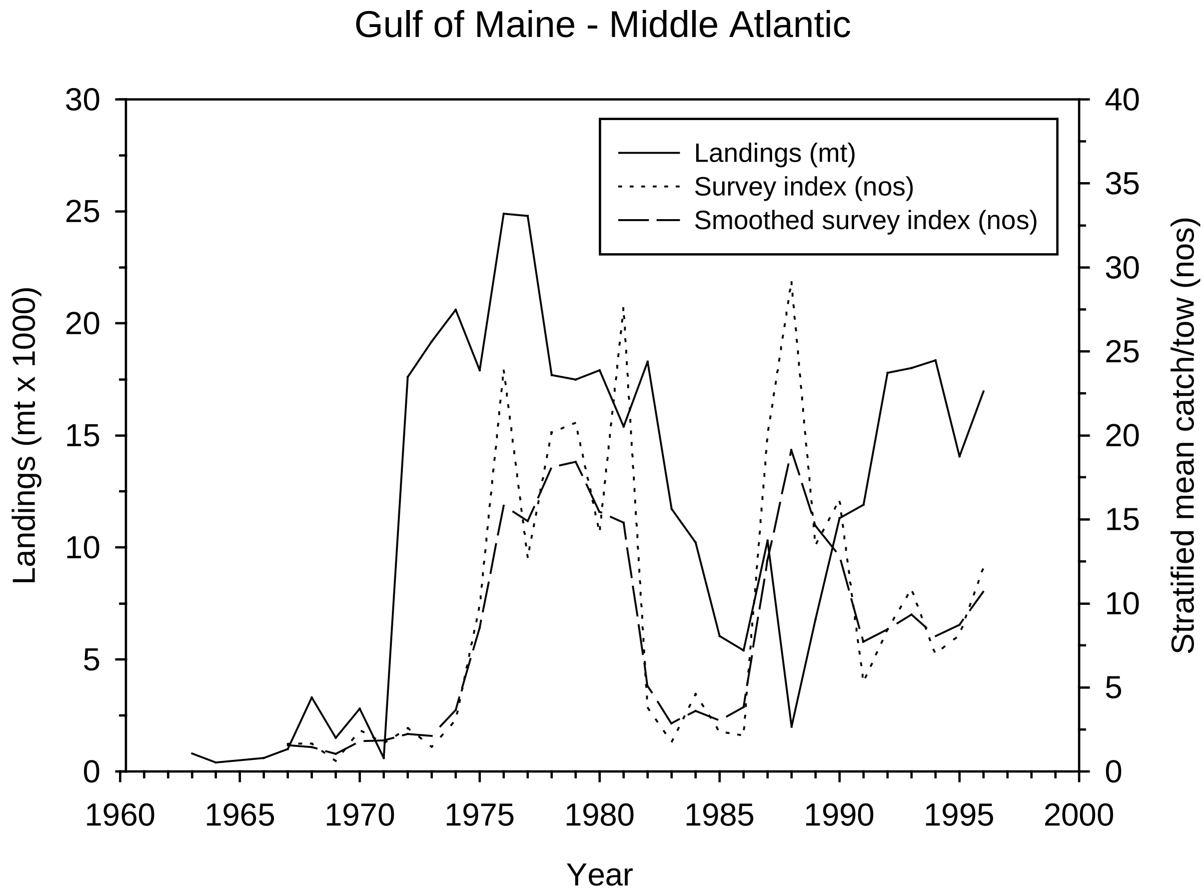

Figure 7. Commercial landings and survey indices for northern shortfin squid from the Gulf of Maine and Middle Atlantic regions, 1963-1996.

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