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Essential Fish Habitat Source Document:

Winter Flounder, *Pseudopleuronectes americanus*, 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:

Winter Flounder, *Pseudopleuronectes americanus*, Life History and Habitat Characteristics

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September 1999

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

Editorial Production

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

Special Acknowledgments

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

Internet Availability

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

Information Updating

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

Species Names

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

---

[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
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INTRODUCTION

The winter flounder, *Pseudopleuronectes americanus*, a small-mouthed, right-eyed flounder (Figure 1), is a valuable commercial and recreational species. It is distributed along the northwest Atlantic coast as far north as Labrador (Kendall 1909; Backus 1957) and as far south as North Carolina and Georgia (Hildebrand and Schroeder 1928; Klein-MacPhee, in prep.). One of the more familiar fishes in the Gulf of Maine (Klein-MacPhee, in prep.), winter flounder are common on Georges Bank and in shelf waters as far south as Chesapeake Bay and are ubiquitous in inshore areas from Massachusetts to New Jersey.

The species is managed as three separate stocks: the Gulf of Maine, southern New England and the Middle Atlantic, and Georges Bank (Brown and Gabriel 1998). However, there have been questions as to whether the population on Georges Bank, where fish tend to grow larger and have different meristic characteristics and movement patterns than those residing inshore (Lux *et al* 1970; Howe and Coates 1975; Pierce and Howe 1977), is in fact a separate species. It has been concluded that many of these differences could be attributed to temperature (Lux *et al* 1970)

Except for the Georges Bank population, adult winter flounder migrate inshore in the fall and early winter and spawn in late winter and early spring throughout most of their range (Perlmutter 1947; Bigelow and Schroeder 1953; Pearcy 1962; Dovel 1967; Scarlett 1991). In northern waters, spawning occurs somewhat later: April in Passamaquoddy Bay (Tyler 1971a) and May and June in Newfoundland (Kennedy and Steele 1971; Van Guelpen and Davis 1979). After spawning, adults typically leave inshore areas although some remain inshore year-round.

This Essential Fish Habitat source document will focus on specific habitat requirements of the various life history stages of winter flounder as well as their historical and current geographical distributions.

LIFE HISTORY

The life history of winter flounder has been well studied (see Howell *et al.* 1992) and only a brief outline will be given here. Howell *et al.* (1992) also includes an excellent review of diseases and effects of pollutants. Further information on pollution effects is provided by Gould *et al* (1994).

EGGS

The eggs of winter flounder are demersal, adhesive, and stick together in clusters. They range in size from 0.74-0.85 mm in diameter. Although Breder (1923) reported that winter flounder eggs develop a "small sphere similar to oil globules in pelagic ova" which disappears with further development, Martin and Drewry (1978) make no mention of this structure. It is possible that the structure reported by Breder (1923) was an artifact. Hatching occurs in 2 to 3 weeks, depending on temperature, and at sizes as small as 2.4 mm in the northwest Atlantic (Fahay 1983) and up to 3.0-3.5 mm in the Gulf of Maine (Bigelow and Schroeder 1953).

LARVAE

Larvae are initially planktonic but become increasingly bottom-oriented as metamorphosis approaches. Settlement occurs at 9-13 mm standard length (SL) (Pearcy 1962; Witting 1995). Metamorphosis, when the left eye migrates to the right side of the body and the larvae become "flounder-like", begins around 5 to 6 weeks after hatching, and is completed by the time the larvae are 8-9 mm in length at about 8 weeks after hatching (Bigelow and Schroeder 1953). Variation in age at metamorphosis is greater than for size (Chambers and Leggett 1987), with age variation influenced by temperature (Laurence 1975; see also Able and Fahay 1998).

JUVENILES

Off southern New England, newly metamorphosed young-of-the-year (YOY) winter flounder take up residence in shallow water where they may grow to about 100 mm within the first year (Bigelow and Schroeder 1953). Growth rates in the Mystic River, Connecticut estuary averaged 0.28-0.35 mm per day in summer and fall with monthly mortality during the first year averaging 31% and total mortality during larval (and juvenile stages) reaching over 99% (Pearcy 1962). Average density of settled juveniles in this system was higher than $1/m^2$ (Pearcy 1962).

Growth rates may be somewhat faster in more southern waters (Chesapeake Bay) where fish up to 110-180 mm are collected in late winter. In a southern New Jersey system, growth ranged from 0.23-0.47 mm per day (Witting 1995). In this system, settlement appeared to be localized in a small cove, with very high densities (averages reaching as high as 4.1 individuals/m^2) (Witting 1995). In several caging studies at other coastal New Jersey locations, growth rates ranged even higher (Sogard 1992, 0.95 mm per day; Phelan *et al*, in press, 0.68 mm per day) and settlement appeared more widespread (B A. Phelan, National Marine Fisheries Service, Highlands, NJ, unpublished data). Although juveniles presumably overwinter in the estuary (Bigelow and Schroeder 1953), large numbers are also found on the shelf (Phelan 1992) and outside southern New Jersey estuaries (Able and

Hagan 1995; Able and Fahay 1998).

ADULTS

Winter flounder may grow up to 58 cm total length (TL) and attain 15+ years of age. Growth varies among geographical areas, with slower growth in the north than in the south Growth in the Gulf of Maine ($k = 0.41$, $L_\infty = 39\ 8$ cm for males, $k = 0\ 27$, $L_\infty = 49.0$ cm for females) was somewhat lower than on Georges Bank ($k = 0.37$, $L_\infty = 55\ 0$ cm for males, $k = 0.31$, $L_\infty = 63\ 0$ for females) (see Mayo 1994).

REPRODUCTION

Winter flounder spawn from winter through spring, with peak spawning occurring during February and March in Massachusetts Bay and south of Cape Cod and somewhat later along the coast of Maine continuing into May (Bigelow and Schroeder 1953). Spawning occurs earlier (November to April) in the southern part of the range (Klein-MacPhee, in prep.) Major egg production occurs in New England waters before temperatures reach 3.3°C with an upper limit of about 4 4-5.6°C in the inner parts of the Gulf of Maine (Bigelow and Schroeder 1953). Spawning can occur at depths of less than 5 m to more than 45 m on Georges Bank, and at salinities of 11 ppt inshore near Woods Hole to 31-33 ppt offshore.

Winter flounder maturity comparisons are complicated by the complex stock structure of this species (O'Brien *et al* 1993). Based on the Northeast Fisheries Science Center (NEFSC) trawl surveys, the median length at maturity (L_{50}) for male and female winter flounder from Georges Bank was 25 6 and 24.9 cm respectively; median age at maturity (A_{50}) was 1 9 years for both males and females (O'Brien *et al.* 1993) For inshore stocks north of Cape Cod, values of L_{50} were 29.7 cm for females and 27 6 cm for males; for stocks south of Cape Cod, L_{50} was 27.6 cm for females and 29.0 cm for males. Median age at maturity was 3.5 years for females and 3.3 years for males north of Cape Cod; 3.0 years for females and 3.3 years for males south of the Cape (O'Brien *et al* 1993).

Other studies report different values. In Long Island Sound, maturity occurred at 2 to 3 years and 20 to 25 cm (Perlmutter 1947); in Newfoundland, L_{50} was 25 cm for females, 21 cm for males, with ages for full maturity reaching 7 years for females and 6 years for males (Kennedy and Steele 1971) indicating that maturity was related to size, not age However, Beacham (1982) found that maturity of fish from the Scotian Shelf and southern Gulf of St. Lawrence was highly variable from year to year. Burton and Idler (1984) found a 2 to 3 year cycle in oocyte maturation and large numbers of non-reproductive individuals in any given year. Thus, interpretations of winter flounder maturity data should be treated cautiously (O'Brien *et al* 1993).

Fecundity measurements indicate that in Newfoundland, 220-440 mm females produced from 99,000 to over 2 million eggs (Kennedy and Steele 1971); in Rhode Island, 250-450 mm females produced from 93,000 to over 1.3 million eggs (Saila 1962); and in coastal Massachusetts, 300-450 mm females produced from 435,000 to over 3.3 million eggs (Topp 1968).

Recent laboratory studies have shown that when held at 4°C, winter flounder spawned over a two month period with females and males averaging 40 and 147 spawns, respectively (Stoner *et al* 1999). Spawning was concentrated between sunset and midnight, with the majority of spawning events involving more than one male, which potentially maximizes fertilization success.

FOOD HABITS

Pearcy (1962) investigated the food habits of winter flounder larvae from hatching through metamorphosis. A large percentage of the stomach contents were unidentifiable but nauplii, harpacticoids, calanoids, polychaetes, invertebrate eggs, and phytoplankton were all present. Food item preference changed with larval size: smaller larvae (3-6 mm) ate more invertebrate eggs and nauplii while larger larvae (6-8 mm) preferred polychaetes and copepods. Plant material was found in larval stomachs but usually with other food items and was probably incidentally ingested (Pearcy 1962).

Pearcy (1962) found that copepods and harpacticoids were important foods for metamorphosing and recently metamorphosed winter flounder Amphipods and polychaetes gradually become more important for both YOY and yearling flounder (Pearcy 1962). Franz and Tanacredi (1992) found that the amphipod, *Ampelisca abdita,* made up the majority of the diet of young flounder in Jamaica Bay, New York Stehlik and Meise (in press) found clear ontogenetic patterns in diet, with calanoid copepods disappearing from the diet as fish grew > 50 mm TL and an increase in the number of taxa in diet with growth.

Winter flounder have been described as omnivorous or opportunistic feeders, consuming a wide variety of prey (see Figure 2). Polychaetes and crustaceans (mostly amphipods) generally make up the bulk of the diet (Hacunda 1981; Macdonald 1983; Steimle *et al.* 1993; Martell and McClelland 1994; Carlson *et al.* 1997). Linton (1921) examined the stomachs of 398 winter flounder ranging in size from 25-225 mm. Annelids and amphipods dominate the diet in almost all size classes (Linton 1921). Winter flounder may modify their diet based on availability of prey. They feed on bivalves (Medcoff and MacPhail 1952; Macdonald and Green 1986, Stehlik and Meise, in press), capelin eggs (Kennedy and Steele 1971; Frank and Leggett 1983) and fish

(Kennedy and Steele 1971).

Adult winter flounder are sight feeders, using their dorsal fins to raise their heads off the bottom with eye turrets extended for a better view (Olla *et al.* 1969). Prey are then taken in a 10 to 15 cm lunge. (Olla *et al.* 1969). If no prey are spotted, the fish change location and resume the feeding posture. A fish might change location and direction four to five times a minute. These movements involve a combination of swimming and "shambling" (Kruuk 1963; Macdonald 1983) or literally crawling across the bottom on the tips of the fin rays Fish were able to maintain this feeding posture in currents exceeding 20 cm/sec by pushing the edges of the fins into the substrate (Olla *et al.* 1969) This same feeding method is used by young-of-the-year and juvenile flounder as well (J. Pereira, National Marine Fisheries Service, Milford, CT, unpublished observation). Increases in turbidity or current speed could interfere with feeding success.

The importance of adequate light for feeding in flounder is demonstrated in a study by Able *et al.* (1999) and Duffy-Anderson and Able (1999). Young-of-the-year flounder held in cages underneath piers in the lower Hudson River lost weight when compared to fish caged in open areas between the piers. One of the contributing factors could have been an inability to feed due to lack of light (Able *et al* 1999; Duffy-Anderson and Able 1999). Macdonald (1983) noted that flounder were more attracted to moving rather than stationary prey and reemphasized the flounder's dependence on sight for feeding. Frame (1971) noted that the amount and duration of feeding behavior varied with light levels, being reduced on cloudy and winter days and increased on sunny days. Van Guelpen and Davis (1979) found that winter flounder moved out of shallow water during storm events to avoid turbulence. They noted that Gibson (1973) observed similar behavior in other flatfish species particularly for plaice, *Pleuronectes platessa*. It is possible that the suspended sediment caused by turbulence interferes with feeding.

Field observations by Olla *et al.* (1969) show that adult winter flounder are inactive at night. Stomach samples taken from fish during the day almost always contained food while those taken before sunrise were almost always empty indicating that adult flounder do not feed at night (Olla *et al* 1969). However, fish in the laboratory were nocturnal during the reproductive season, only becoming active during the day during the post-spawning periods under increasing temperature and photoperiod (Stoner *et al.* 1999). Young-of-the-year winter flounder are also more nocturnal during the summer (Manderson *et al.*, in review; B.A. Phelan, National Marine Fisheries Service, Highlands, NJ, unpublished observation).

Winter flounder have been reported to cease feeding during the winter months (Kennedy and Steele 1971, Van Guelpen and Davis 1979; Martell and McClelland 1994). Other authors simply report a reduction in feeding in the winter (Frame 1971; Levings 1974). Recent field studies in a New Jersey estuary before, during and after the spawning season indicated that females began feeding, primarily on siphons of the clam, *Mya arenaria,* and ampeliscid amphipods earlier than males (Stoner *et al* 1999). In the laboratory, males fed only after most spawning had ended (Stoner *et al.* 1999)

Degradation or improvement of environmental conditions causing shifts in benthic invertebrate populations may also cause shifts in prey selection such as eating the pollution-tolerant annelid *Capitella* (Haedrich and Haedrich 1974; Steimle *et al.* 1993) or eating the pollution-sensitive amphipod, *Unciola irrorata,* once environmental conditions have improved (Steimle *et al.* 1993).

PREDATION

Pearcy (1962) reported that the small medusae, *Sarsia tubulosa*, prey upon winter flounder larvae, and that all other potential predators of larvae were numerically unimportant when compared to *Sarsia* medusae. The predatory amphipod, *Calliopius laeviusculus*, was shown to prey upon larval winter flounder in the laboratory (Williams and Brown 1992). Klein-MacPhee *et al.* (1993) suggests the mud anemone, *Ceriantheopsis americana,* as a potential predator on winter flounder larvae. Pepin *et al.* (1987) reported that Atlantic mackerel, *Scomber scombrus,* selectively prey on larval fish between 3 and 10 mm in length. Mackerel would co-occur with winter flounder larvae in early spring. Since winter flounder are 3.5 mm in length at hatch they are certainly vulnerable to predation by mackerel.

Howe *et al.* (1976) found that injured juvenile winter flounder were more common when large numbers of "snapper" bluefish, *Pomatomus saltatrix*, were present in their study area, suggesting that young bluefish are an important predator on young winter flounder Gulls and cormorants were also suggested as important predators (Howe *et al.* 1976). Witting and Able (1995) have documented in the laboratory the ability of the sevenspine bay shrimp, *Crangon septemspinosa*, to prey on YOY winter flounder ranging in length from newly settled, 10 mm individuals to those up to 20 mm long. Juvenile winter flounder, particularly as they get larger, are probably also preyed upon by the same predators that prey on adults. Summer flounder, *Paralicthys dentatus,* sea robins (*Prionotus evolans*), and windowpane (*Scophthalmus aquosus*) also prey on YOY and juvenile winter flounder (Poole 1964; Richards *et al* 1979; Manderson *et al.* 1999, in review). As many as 12 winter flounder have been found in a single searobin stomach (P.E. Clark, National Marine Fisheries Service, Milford, CT, unpublished observation)

Adult winter flounder are preyed upon by a wide variety of predators including striped bass (*Morone saxatilis*), bluefish, spiny dogfish (*Squalus acanthias*), goosefish (*Lophius americanus*), oyster toadfish (*Opsanus tau*), and sea raven (*Hemitripterus americanus*), (Lux and Mahoney 1972; Azarovitz 1982). Cormorants, blue herons, seals, and ospreys have also been cited as predators (Pearcy 1962; Tyler 1971b) Payne and Selzer (1989) found that seals ate 5 different species of flounder including winter flounder, but that the flounder group as a whole made up only 10 % of the diet

MIGRATION

With the exception of the Georges Bank population, adult winter flounder migrate inshore in the fall and early winter and spawn in late winter and early spring. Following spawning, adults typically leave inshore areas when water temperatures exceed 15°C (McCracken 1963; Howe and Coates 1975); however, these movements may not be totally controlled by temperature Winter flounder may remain inshore year-round if temperatures remain at 15°C or lower and if enough food is available (Kennedy and Steele 1971) In the more northern latitudes, they may be driven out by turbulence or ice formation (Van Guelpen and Davis 1979).

Powell (1989) reviewed tagging studies of winter flounder conducted by Perlmutter (1947), Saila (1961, 1962), McCracken (1963), Poole (1969), Howe and Coates (1975), Van Guelpen and Davis (1979), Danila and Kennish (1982), Scarlett (1983), Weber and Zawacki (1983), Northeast Utilities Service Company (1984), and Weber (1984), and compared them to his own studies in Rhode Island. He concluded that, with the exception of Georges Bank, there were two distinctive patterns of movement. While all studies showed a winter congregation on inshore, shoal spawning grounds and summer dispersal to deeper cooler waters, the extent and the timing of these movements varied with location. Winter flounder distributions in NEFSC bottom trawl surveys (Figure 3), Massachusetts inshore trawl surveys (Figure 4), and Hudson-Raritan trawl surveys (Figure 5) confirm this general pattern of movement.

Howe and Coates (1975) tagged fish during the winter and early spring while they were concentrated near spawning grounds in areas both north and south of Cape Cod and on Georges Bank. Fish tagged north of Cape Cod tended to make shorter post-spawn migrations (average distance traveled from tagging location = 14.3 km or less) probably because of the close proximity of cooler bottom temperatures (Howe and Coates 1975). Studies conducted even further to the north in Nova Scotia (McCracken 1963) and Newfoundland (Van Guelpen and Davis 1979) also showed short onshore-offshore migrations associated with spawning. Most fish tagged on Georges Bank tended to stay on the Bank and there was very little exchange (less than 1% in either direction) with fish on Nantucket Shoals (Howe and Coates 1975). Fish tagged south of Cape Cod migrated farther than their counterparts north of the Cape (average distance traveled up to 61.2 km). Mixing was minimal; only nine fish (0.66% of the tag recoveries) tagged north of the Cape were recovered south and east of the peninsula and only 61 fish (2.50% of recovered tags) tagged south of Cape Cod were recaptured to the north Tag returns in the fall showed return of fish to inshore, shoal areas when water temperatures had reached 15°C (Howe and Coates 1975).

Studies conducted further south in Connecticut (Northeast Utilities Service Company 1984), New York (Poole 1969; Weber and Zawacki 1983; Weber 1984), and New Jersey (Danila and Kennish 1982; Scarlett 1983) also showed longer onshore-offshore migrations. Powell (1989) also noted that in the tagging studies south of Cape Cod, all post-spawn, summer migrations were to the east, i.e., offshore. This adult migration is shown by seasonal trawl survey catches, especially off New Jersey and southern New England (Figures 3 and 4) as well as by more recent studies. For example, Pereira *et al.* (1994) found that some fish move as far as 113 km to the east during the post-spawn period. Phelan (1992) tagged fish in the New York Bight area and recovered one fish from Nantucket, a distance of 328 km from the tagging site Timing of these spawning and post-spawning movements varied along the coast, occurring earlier farther south and later farther north.

There are exceptions to these general patterns, and migrations may also be related to food availability Kennedy and Steele (1971) reported that winter flounder left Long Pond, Canada and were found in Conception Bay, Canada even though water temperatures in both locations were around 11°C. They attribute the exodus to a lack of food in Long Pond. Van Guelpen and Davis (1979) reported emigration from the study area in July even though water temperatures remained within the winter flounder's acceptable range. They believe this was a feeding migration similar to that reported by Kennedy and Steele (1971). When winter flounder disappeared from study areas again in August, they were found in nearby Horse Cove where they had been feeding heavily on capelin eggs (Van Guelpen and Davis 1979). Feeding migrations by winter flounder have also been documented by Tyler (1971b) who found that adult winter flounder move into the intertidal zone on the high tide to feed. It would seem that if water temperatures are not limiting over a wide area, winter flounder will move in response to availability of food Howe and Coates (1975), who noted similar movements in the Cape Cod area, doubt that these movements are solely in response to availability of food Howe *et al.* 1976 and studies in Raritan Bay (Figure 5) provide evidence that some adult fish may remain inshore throughout the summer.

STOCK STRUCTURE

This species is currently managed as three stocks (one north of Cape Cod, one south of the Cape and the third on Georges Bank) which were first differentiated based on differences in fin ray counts and movement patterns (Lux *et al.* 1970; Howe and Coates 1975; Pierce and Howe 1977). The Georges Bank stock not only differed in fin ray count, but has a much higher growth rate (Lux 1973). Some researchers feel that three "stock complexes" are being managed and that there may be one or more stocks in Canadian waters, based on differences in age at maturity (Kennedy and Steele 1971) and migratory habits (Van Guelpen and Davis 1979). Other stocks may exist north of the Massachusetts border along the coast of New Hampshire and Maine.

HABITAT CHARACTERISTICS

A summary of the habitat characteristics of the various life history stages of winter flounder is provided in Table 1.

EGGS

Collection of winter flounder eggs from the wild is difficult because of their adhesive and demersal nature. It is these same characteristics, however, that make them valuable in pinpointing spawning grounds. With the exception of Georges Bank and Nantucket Shoals, winter flounder eggs are generally collected from very shallow waters (less than about 5 m), at water temperatures of 10°C or less, and salinities ranging from 10 to 30 ppt. These shallow water, nearshore habitats are of critical importance because they are most likely to be impacted by human activities. The type of substrate where eggs are found varies, having been reported as sand, muddy sand, mud and gravel, although sand seems to be the most common. Vegetation may or may not be a factor. Spawning areas also occur where hydrodynamics function to keep the hatched larvae from being dispersed (Pearcy 1962; Crawford and Carey 1985; Monteleone 1992). This is true even on Georges Bank where different water masses function to keep larvae on the Bank (Backus and Bourne 1987).

Scott (1929) collected winter flounder eggs near St. Andrews, New Brunswick, with a plankton net in one foot of water along the flats on mud bottom. Surface temperatures in the area ranged from 9.25-10.0°C, but bottom temperatures to which the eggs were exposed were probably lower.

Pearcy (1962) working in the Mystic River, Connecticut, began his sampling in February when water temperatures were around 2-5°C. Specific gravity of seawater where eggs were collected was reported to be 1.01-1.024 (corresponding roughly to a salinity range of 10 to 25 ppt) at 5°C. Crawford and Carey (1985) collected winter flounder eggs using a benthic sled in Point Judith Pond, Rhode Island The greatest concentration of eggs was found in the vicinity of a tidally submerged gravel bar with eggs clumped on the gravel substrate or attached to fronds of algae. Crawford and Carey (1985) began their sampling only after water temperatures had reached 3°C. It has also been reported that winter flounder eggs collected by divers were attached to vegetation (Anonymous 1972). Scarlett and Allen (1989) found that winter flounder eggs constituted the vast majority of all the eggs found in collections made in the Manasquan River in New Jersey in February and March of 1985. Eggs were found at salinities ranging from 14 to 32 ppt, temperatures of 0.9 to 10°C, and depths of 2-4.5 m. In a subsequent study, Scarlett (1991) used an epibenthic sled for sampling winter flounder eggs in the Shrewsbury and Navesink rivers in New Jersey to identify spawning areas He collected eggs in water temperatures ranging from 4 to 7.5°C, at salinities of 14 to 22 ppt, and at depths of 2 to 4 m.

More recently, Monteleone (1992) collected winter flounder eggs in a plankton net towed horizontally just under the surface of the water in a relatively shallow (average depth 1.3 m) The turbulence caused by the sampling gear was probably responsible for these demersal eggs finding their way into the net. Like Scott (1929), Monteleone (1992) reported a surface water temperature of 9.1°C during the collection of winter flounder eggs.

Hughes (in prep.) used a benthic sled to collect winter flounder eggs in Point Judith and Ninigret coastal salt ponds in Rhode Island in the vicinity of the *North Cape* oil spill. Samples were taken in March. Depths in the sample areas ranged from 1 to 3 m Lee *et al.* (1997) measured temperature and salinity near Hughes (in prep.) sample sites at various times between 1985 and 1994. Samples taken in March of various years showed a mean temperature of 6±1.94°C and a mean salinity of 23±8.01 ppt.

Temperature and depth measurements taken in conjunction with the plankton samplings conducted by the NEFSC Marine Resources Monitoring, Assessment and Prediction (MARMAP) program on Georges Bank showed that the eggs were collected at water temperatures between 3 and 8°C and at depths of 90 m or less (Figure 6). These results confirmed the report by Bigelow and Schroeder (1953) that winter flounder spawn on sandy bottom, often in water as shallow as one to three fathoms but as deep as 25 to 40 fathoms (13-22 m) on Georges Bank and, most probably, on Nantucket Shoals.

While evidence from eggs collected in the field provides information about the conditions under which winter flounder prefer to spawn, laboratory studies provide information about how winter flounder eggs might fare in marginal environments. One parameter

typically studied in the laboratory is the number of days required for hatching. Time to hatch is controlled by temperature. Human activities could change ambient temperatures directly by discharge of heated cooling water or indirectly by changing the hydrodynamics and therefore, the water turnover rate of an area

Scott (1929) collected winter flounder eggs in the field, and in the laboratory determined the number of days for all the eggs to hatch or die, as well as hatching success. He found that 4-5°C produced the best hatch success, averaging 73% The average time for all the eggs to hatch or die was 26 days At 0°C, only 50% of the eggs had hatched or died in an average of 21 days and the hatch success was poor, averaging only about 9%. Williams (1975) reported an average of 38.6 days to hatch or die for eggs held at 0°C. Williams (1975) also reported an average hatch time of 21 5 days for eggs held at 3.5°C, very close to the value reported by Scott (1929) for eggs held at 4–5°C. Eggs held at 12 to 17°C hatched sooner (mean 18 days), but the percent hatch only averaged about 52%. An earlier, similar study by Brice (1898) found that eggs hatched in 17-18 days at 3°C Neither Brice (1898) nor Scott (1929) determined the developmental stage of the field-collected embryos when they were brought into the laboratory or what percent were even fertilized. This may explain some of the variability apparent in the reported time to hatch in these studies.

Rogers (1976) tested the effects of various combinations of temperature (3-15°C) and salinity (0.5 to 45 ppt) on the viability and incubation times of winter flounder embryos and she concluded that winter flounder embryos are euryhaline and hatch at salinities of 5 to 40 ppt. Salinity extremes tended to induce abnormal development, however, and the best survival occurred between 10 and 30 ppt. She concluded that optimal conditions for winter flounder embryo development and survival appear to be 15 to 35 ppt salinity at 3°C and 15 to 25 ppt for temperatures above 3°C. These results agree well with the results of Williams (1975), who reported a minimum mortality range of 0 to 10°C and an upper lethal limit of 15°C.

Rogers (1976) also found that incubation times (days for 50% of the embryos to hatch) were inversely related to temperature: 19 to 31 days at 3°C and 10 ppt salinity, and 5 to 10 days at 14°C, regardless of salinity tested. Buckley (1982) also reported similar results, noting that the time required for 50% hatch of embryos held in the laboratory was 8 days at 10°C and 23 days at 2°C. Increased mortality was noted in developing embryos held at 2°C. These results agreed more closely with the statements of Bigelow and Schroeder (1953), who report that hatching occurred in 12-15 days at a temperature of 2 8 to 3.3°C.

This inverse relationship between incubation time and temperature may provide a mechanism for the phenomenon observed by Frank and Leggett (1983) They found that several species of fish which laid demersal eggs (capelin, sea snail, radiated shanny, and winter flounder) seemed to time their hatching to the advent of favorable environmental conditions. Hatching occurs simultaneous to the onset of onshore winds which cause the replacement of cooler, predator-laden, food-poor, up-welling waters with warmer, predator-poor, food-rich, surface water over the shallow spawning areas. The synchronous hatching is thought to have the effect of swamping predators and enhancing survival of winter flounder because the capelin are so much more numerous than the other species Crawford and Carey (1985) described a similar phenomenon when they reported that a mid-February pulse of warm weather seemed to stimulate winter flounder spawning in Point Judith Pond, Rhode Island

LARVAE

Pearcy (1962) concluded that because winter flounder spawn in coves and inlets and the young stages are non-dispersive, breeding and nursery grounds would be close together. This view had been previously expressed by Perlmutter (1947) Thus, larvae (and later juveniles) may offer an important clue to the location of spawning grounds, and are the link between spawning grounds and nursery areas. Data from the NEFSC MARMAP ichthyoplankton surveys show that, with the exception of Georges Bank and Nantucket Shoals, most winter flounder larvae are found inshore and that spawning progresses from the southern end of its range northward (see Geographical Distribution below)

Pearcy (1962) collected winter flounder larvae from the Mystic River, Connecticut. Comparing the number of larvae in surface tows to those collected by bottom tows he found that the bottom tows contained the majority of the larvae. He also knew from laboratory observations that winter flounder larvae are negatively buoyant and sink when they stop swimming. His hydrographic survey of the estuary revealed that in the surface waters the net movement over a tidal cycle was seaward while in the bottom waters it was landward. The natural tendency of the larvae to sink would explain why most were caught near the bottom and would also function to retain the larvae within the estuary rather than get washed out in the surface waters In fact, he calculated that only about 3% of the larval population was dispersed seaward per tidal cycle.

Crawford and Carey (1985) believe that spawning areas and nursery areas are close together, after locating both eggs and larvae in Point Judith Pond in Rhode Island They concluded that winter flounder larvae could have been retained in the estuary by the mechanism proposed by Pearcy (1962) but that the hydrodynamics of the area also played a role. They further suggested that winter flounder, when they spawn, take advantage of the hydrodynamic characteristics of small, narrow estuaries

that restrict water flow in order to help retain the larvae in suitable nursery areas. Monteleone (1992) noted the highest concentrations of winter flounder larvae in Great South Bay, New York at stations with low current speeds and turnover rates.

Winter flounder larvae were collected in the higher salinity regions of Miramichi Bay (New Brunswick, Canada) in early to mid-June where bottom salinities ranged from 6 to 26 ppt, and temperatures ranged from 12.5 to 20.5°C (Locke and Courtenay 1995). Scarlett (1991) collected winter flounder larvae in the Navesink and Shrewsbury Rivers in New Jersey from February through April where bottom salinities ranged from 10 to 22 ppt, bottom temperatures ranged from 2 to 19.5°C and depths ranged from 2 to 6 m. Pearcy (1962) found that winter flounder larvae were common in the upper Mystic River Estuary from May to June when temperatures ranged from 3 to 15°C. Average bottom salinities for the upper estuary ranged from 18 to 22 ppt. Scarlett and Allen (1989) collected winter flounder larvae in the Manasquan River in New Jersey at salinities ranging from 4 to 30 ppt and temperatures ranging from 0.9 to 15°C. NEFSC MARMAP surveys collected larvae from March through July, and in September (Figure 7). Most were caught at temperatures of 6-10°C (those caught in September were at 18°C) and depths of 10-70 m.

Winter flounder larvae are surprisingly tolerant of short-term temperature shock. In laboratory studies, Itzkowitz and Schubel (1983) found that mortality in five-day-old winter flounder larvae was minimal when the temperature was increased from the acclimation temperature of 5 to 27°C (a change in temperature of 22°C) so long as the duration was kept to less than 32 minutes. At longer durations, mortality increased rapidly. Similar results were obtained for changes in temperature of 24°C if duration was 16 minutes or less. At changes in temperature ≥ 28°C mortality was virtually total and immediate (Itzkowitz and Schubel 1983).

YOUNG-OF-THE-YEAR, YEARLINGS AND JUVENILES

Winter flounder less than one year old (or young-of-the-year, YOY) are treated separately here because their habitat requirements are so different from that of the larger juveniles (fish 1 year old or more). Yearling is a term used for fish which are between one and two years of age, their behavior being transitional between YOY and older juveniles.

Winter flounder spend their first year in very shallow inshore waters. Although temperature tolerance of YOY is higher than for yearlings or adults, Pearcy (1962) concluded that temperatures of 30°C might be too high. He found that an area that had produced fish previously failed to do so when the temperature reached 30°C, but that the fish returned when temperatures were lower. This upper limit is in agreement with studies by Huntsman and Sparks (1924) and Battle (1926) who also noted higher lethal temperatures for smaller flounder than for larger ones, and with McCracken (1963) who determined an upper incipient lethal temperature of 27°C. Pearcy (1962) reported a minimum lethal temperature between -1.5 and -1.0°C. Juvenile winter flounder captured in offshore areas by NEFSC bottom trawl surveys were found at temperatures well outside of these lethal limits. The majority of juveniles were at 4-7°C in the spring and 11-15°C in autumn (Figure 8).

Laboratory studies by Casterlin and Reynolds (1982) on yearling flounder indicated that flounder selected temperatures in the range of 8-27°C, with a mode of 18.5°C. They also noted that in the laboratory, these fish were more active at night.

Young-of-the-year flounder also tolerate lower salinities (5 ppt) than do yearling flounder (10 ppt) (Reynolds and Thomson 1974). Pearcy (1962) reported that the minimum salinity tolerance varied between 1 and 5 ppt for flounder as small as 7-10 mm. Bigelow and Schroeder (1953) reported that winter flounder are commonly found in salinities ranging from 35 ppt to water that was fresh enough to drink. They were probably including all life history stages in that statement.

Ziskowski *et al.* (1991) investigated low dissolved oxygen tolerance and behavior of yearling winter flounder in the laboratory. Mortality occurred when flounder were exposed to 1.1 to 1.5 mg/l dissolved oxygen. Flounder were able to withstand an 8-hr exposure to dissolved oxygen levels in the 1.2 to 1.4 mg/l range. Low oxygen tolerance is not without a price, however. Bejda *et al.* (1992) found that growth of juvenile winter flounder was significantly reduced when dissolved oxygen levels were maintained at 2 2 mg/l or varied diurnally between 2.5 and 6.4 mg/l for periods of up to 11 weeks.

Pearcy (1962) conducted tag-recapture studies that indicate a relatively stable population of juvenile winter flounder within the Mystic River estuary over the summer and much lower numbers of juveniles beyond the mouth. Other investigations confirm that YOY winter flounder remain in the nearshore zone and migrate very little during their first summer (McCracken 1963; Saucerman 1990; Saucerman and Deegan 1991). In winter however, Pearcy (1962) found that catches increased outside of the estuary while densities within the estuary dropped, implying an outward winter migration. Warfel and Merriman (1944) made similar observations. Richards (1963) found increased numbers of juveniles in offshore locations in the winter. Laboratory experiments by McCracken (1963) and Pearcy (1962) showed that YOY winter flounder were less photonegative than yearling flounder. Pearcy (1962) further showed that YOY winter flounder became more photonegative in the winter. Thus it seems that photoresponse and temperature preferences drive the YOY flounder from the shallows in the late fall and early winter of their first year and keep older

juveniles in deeper, cooler water much of the year.

Several investigators have reported that the highest densities of newly settled winter flounder are found on muddy substrates (Saucerman 1990; Howell and Molnar 1995; O'Connor 1997; Phelan *et al*, in prep). Paradoxically, Saucerman (1990) also found that growth rates were slowest in these areas. She attributed this difference to increased competition for food caused by the high density of fish and possibly the detrimental effects of low oxygen levels later in the summer. Both Saucerman (1990) and O'Connor (1997) felt that smaller juveniles prefer finer sediments to bury into as was suggested by Gibson and Robb (1992) for the European flounder, *Pleuronectes platessa* In laboratory experiments, young-of-the-year winter flounder < 40 mm SL consistently preferred fine-grained sediments (Phelan *et al*, in prep.)

Since winter flounder metamorphose at a smaller size than other flatfishes (Bigelow and Schroeder 1953), it seems unlikely that a newly metamorphosed, 8 to 9 mm long flounder actively seeks out these soft muddy areas. It is more likely that they are simply deposited there by currents. Howell and Molnar (1995) reported that the highest catches of YOY winter flounder occurred on muddy substrates or muddy substrates covered by leaf litter or bivalve beds.

Witting (1995) and Able and Fahay (1998) have shown that specific areas, i e, small coves inside Little Egg Inlet in New Jersey, by virtue of location, proximity to currents or other factors, may serve as critical habitat, supporting high densities of recently settled individuals. What these areas have in common is that they are depositional areas probably with low current speeds. We have already seen that spawning winter flounder take advantage of areas of appropriate hydrodynamics and current speeds to insure that larvae are retained in the nursery areas Perlmutter (1947) and Pearcy (1962) both concluded that because eggs and larvae are non-dispersive that the nursery grounds will be close to the spawning grounds In a sense, it is the spawning adults that choose the habitat for YOY winter flounder. Recent studies by Pereira *et al.* (1994) and Curran *et al.* (1996) support this idea.

Sogard and Able (1991) and Sogard (1992) found that YOY winter flounder in Great Bay-Little Egg Harbor in New Jersey were more abundant on unvegetated substrates Their ability to bury in the sediment and change color to match it frees them from dependence on vegetation for refuge from predators. In this system, Able and Fahay (1998) indicate that juveniles larger than 25 mm are found in a variety of habitats types, regardless of sediment and structure. These habitats include macroalgae (Able *et al.* 1989), marsh creeks (Rountree and Able 1992) and to a lesser extent eelgrass (Goldberg *et al*, in prep.). Recent comparisons of habitat-specific patterns of abundance and distribution of YOY winter flounder in this system, as well in the Hudson-Raritan estuary and Long Island Sound, support the conclusion that habitat utilization by YOY winter flounder is not consistent across habitat types and is highly variable among systems and from year to year (Goldberg *et al.*, in prep).

The shallow inshore areas where YOY flounder spend their first 5 or 6 months of life are susceptible to anthropogenic impacts. Briggs and O'Connor (1971) compared the abundance of 40 different species of fish collected from undisturbed areas with natural vegetation with those collected where dredge spoil material (mostly sand) had been deposited. Species diversity was consistently higher over the undisturbed bottoms. Most species, including winter flounder, preferred the undisturbed bottom.

There have been a few attempts to relate juvenile habitat area to winter flounder production. Saila *et al.* (1965) calculated the theoretical biomass of juveniles needed to support the adult fishery. His studies led him to conclude that about 30% of the equilibrium yield weight is present in juveniles at 5 months of age and that efforts to enhance the fishery would be better aimed at culture and release of juveniles rather than larvae (Saila *et al.* 1965).

Howe *et al* (1976) used tagging methodologies to investigate the contribution of the Waquoit Bay-Eel Pond spawning/nursery areas to the offshore trawl fishery. This fishery includes NMFS statistical subareas number 538 (southern Massachusetts), 521 (west side of South Channel), and 526 (Nantucket Shoals and Lightship Grounds) By accounting for natural mortality and calculating the number of new recruits emigrating from these nursery areas and becoming available to the offshore fishery, they were able to calculate that Waquoit Bay-Eel Pond contributed 0.16% of the recruitment required to maintain an equilibrium catch.

ADULTS

Laboratory experiments by Reynolds (1977) established a preferred habitat temperature for adult winter flounder of 13.5°C. This concurs with the findings of McCracken (1963) who concluded, based on a review of field studies of winter flounder distribution and water temperatures, that adults have a preferred temperature range of 12-15°C. Results from several experimental trawl surveys tend to agree with these results. NEFSC trawl surveys captured adults at temperatures of 4-6°C in spring and 10-15°C in the fall (Figure 8). In the inshore waters of Massachusetts, adults were captured at 5-13°C in spring and 9-13°C in the fall (Figure 9). In the Hudson-Raritan estuary, most adults were captured at 4-12°C (Figure 10).

In contrast, Olla *et al.* (1969) observed actively feeding winter flounder where bottom temperatures always exceeded 17.2°C. They found active feeding at temperatures up to 22.2°C; but at 23°C feeding ceased and

the flounder buried themselves in the substrate, where temperatures 5 or 6 cm below the surface of the sediment were 19.8 to 20°C. They concluded that winter flounder escape short-term thermal stress by burying in the cooler sediments. Although this research seems to be at odds with the findings of McCracken (1963) and Reynolds (1977), Olla *et al* (1969) did not report the size of the flounder they observed at these high temperatures In another part of the study these authors reported stomach contents of fish ranging in size from 15 to 36 cm. If the fish observed during the high temperature period were toward the smaller end of the range reported for the feeding portion of their study (i.e., closer to the 15 cm end of the range of fish studied), that would likely make them yearlings. Reynolds (1977) determined that yearlings prefer a temperature of 18 5°C and may be able to tolerate these higher temperatures. Larger fish may have left the area because many have a lower temperature tolerance than smaller fish (McCracken 1963).

Acclimation is another important factor in determining temperature tolerance. Laboratory manipulation of acclimation temperature from 4 to 23°C increased the critical thermal maximum from 26 to 32°C (Everich and González 1977). If the temperature increase was gradual enough, acclimation could have occurred in the fish studied by Olla *et al.* (1969), thereby resulting in a higher temperature tolerance.

Pearcy (1962) reported that catches of adults in the upper estuary of the Mystic River, Connecticut, increased in February, peaked in March, and continued to be relatively high into April. Bottom temperatures during this period range from 1-10°C. He reported that peak spawning occurred when temperatures were between 2 and 5°C. Kennedy and Steele (1971) reported that peak spawning of winter flounder in Long Pond, Conception Bay, Canada occurred in May and early June. Water temperatures in May when the bulk of the spawning occurred were 8°C (Kennedy and Steele 1971). Van Guelpen and Davis (1979) reported that peak spawning in Conception Bay occurred in June in 1979 when water temperatures were 6°C.

McCracken (1963) found that winter flounder survived in salinities as low as 15 ppt, confirming earlier work done by Sumner (1907) Although Bigelow and Schroeder (1953) reported that winter flounder commonly live in areas where salinities are so low that the water was fresh enough to drink to areas where salinity was 35 ppt, McCracken (1963) found that winter flounder died in 72 to 96 hours when exposed to salinities of 8 ppt. It is difficult to assess the significance of these studies by McCracken (1963) since he did not always make it clear what size fish he used in these experiments. Bigelow and Schroeder (1953) probably are including all age groups in the salinity range that they cite and salinity tolerance is known to be age dependent Adults captured in the Hudson-Raritan estuary were found at salinities as low as 15 ppt, although most were found at > 22 ppt (Figure 10).

Since adult winter flounder prefer to live in cooler waters, they do not often encounter low oxygen events However, these do occur from time to time in response to high nutrient loading. Howell and Simpson (1994) described the distribution and abundance of finfish and lobsters in Long Island Sound in relation to near-bottom dissolved oxygen levels. Winter flounder abundance was significantly lower when dissolved oxygen was below 2.0 to 2.9 mg/l. Also significant was the decline in mean length of winter flounder as dissolved oxygen levels declined. Since the catch included fish ranging in size from 7 to 35 cm, it is probable that the decline in size of fish results from larger fish leaving the area before smaller fish which are more tolerant of low dissolved oxygen conditions (see above) Howell and Simpson (1994) also raised the possibility that the mean length difference was caused by slower growth rates caused by low dissolved oxygen (Bejda *et al* 1992). This may be possible if low oxygen events are of long duration or periodic in nature.

With the exception of Georges Bank and Nantucket Shoals (see Figure 3), mature winter flounder are found in very shallow waters during the spawning season Bigelow and Schroeder (1953) reported that winter flounder spawn on sandy bottom, often in water as shoal as one to three fathoms but as deep as 25 to 40 fathoms on Georges Bank. Kennedy and Steele (1971), working in Conception Bay, Newfoundland found that winter flounder spawn in May and June on sandy bottoms at depths less than 6 m McCracken (1963) reported that spawning in Passamaquoddy Bay, New Brunswick occurred at depths of 0 to 9 m. Pearcy (1962) reported that winter flounder spawn in the Mystic River, Connecticut at depths of 5 m or less.

After spawning, adults may remain in the spawning areas before moving to deeper waters when water temperatures reach 15°C (McCracken 1963). Kennedy and Steele (1971) found them at depths of 7-10 m in the post-spawning period. McCracken (1963) found that winter flounder remained in Passamaquoddy Bay after spawning, but in deeper water (around 20 m). Trawl surveys conducted by NEFSC show the bulk of the adult catch occurred in water 25 m or less in the spring (during and just after spawning) and 25 m or deeper in the fall (prior to spawning) (Figure 8). The Massachusetts survey shows similar results (Figure 9). Post-spawning migrations of winter flounder along the New Jersey coast appear to be limited by the 40 m contour (Danila and Kennish 1982; Scarlett 1983). Migration of flounder from shoal areas south and east of Cape Cod appears to be limited by the 55 m contour (Howe and Coates 1975).

Laboratory experiments by McCracken (1963) demonstrated that adult winter flounder are less sensitive to light than YOY and juvenile winter flounder Small flounder (6-9 cm) tended to be photophilic while intermediate fish (12-18 cm) were photophobic Large fish (28-33 cm) responded negatively to bright lights but

not to lower levels of illumination. Casterlin and Reynolds (1982) showed that the locomotor activity patterns of sixteen 12 to 13 cm flounder they examined in the laboratory were decidedly nocturnal. The spatial distribution of flounder observed in the field (YOY in the nearshore zone, older juveniles further offshore) may in part be due to these differences.

GEOGRAPHICAL DISTRIBUTION

Winter flounder are distributed from the Strait of Belle Isle, off northwest Newfoundland, to Cape Charles, Virginia (Figure 11). The area of highest abundance is the Gulf of St. Lawrence, off New Brunswick and northern Nova Scotia

EGGS AND LARVAE

The geographical distribution of winter flounder eggs and larvae matches that reported for the adults. Eggs and larvae have been collected from Canadian waters (Scott 1929; Locke and Courtenay 1995) to Chesapeake Bay (Dovel 1967). Govoni (1973) studied the icthyoplankton communities of the Acushnet and Westport Rivers in Massachusetts and found winter flounder larvae in his collections. Collection of winter flounder eggs in benthic sled samples show that coastal salt ponds in Rhode Island play host to much of the spawning activity in Rhode Island waters (Crawford and Carey 1985; Hughes, in prep.). The Pettaquamscut River and Narragansett Bay also support winter flounder spawning (Anonymous 1972; Bourne and Govoni 1988).

Collection of eggs and larvae by Pearcy (1962) and Monteleone (1992) confirm that the waters of Connecticut and Great South Bay, New York also serve as spawning areas for winter flounder. Winter flounder were the most common larva collected by Croker (1965) in the Sandy Hook estuary in New Jersey. The Navesink, the Shrewsbury, (Scarlett 1991), and the Manasquan rivers (Scarlett and Allen 1989) in New Jersey all harbor winter flounder larvae during the spawning season. Both the Indian River and Rehoboth Bay in Delaware also serve as spawning areas for winter flounder (Daiber *et al* 1976).

Eggs and larvae of winter flounder have been reported from several areas (the Magothy and Patuxent Rivers and the upper bay near the Susquehanna River) at the northern end of Chesapeake Bay (Dovel 1967, 1971) It seems unlikely, at first, to find winter flounder spawning so far south, in Chesapeake Bay. However, Chesapeake Bay runs almost north and south, and the Magothy River is located at the same latitude as the important spawning areas mentioned above in Delaware Bay, the Indian River and Rehoboth bays located a short distance to the east.

Winter flounder eggs and larvae have also been collected in standard plankton tows utilizing bongo nets by the NEFSC MARMAP survey (Figures 12 and 13). In some cases this was probably due to the nets accidentally hitting the bottom, but this explanation is not sufficient to explain the large numbers of eggs collected on Georges Bank and Nantucket Shoals. The large numbers of eggs collected on Georges Bank are probably due to the unique hydrodynamic conditions found there. The water mass on central Georges Bank is characterized by lack of stratification at any time of year due to good vertical mixing (Backus and Bourne 1987). These same forces probably lift demersal eggs up into the water column and make them available to sampling by bongo net.

YOUNG-OF-THE-YEAR AND JUVENILES

Young winter flounder are ubiquitous along the east coast of the United States from Canada (McCracken 1963) to Virginia's eastern shore where Richards and Castagna (1970) found that of seventy species collected, winter flounder was the tenth most numerous. Saco Bay in Maine has young winter flounder (Casterlin and Reynolds 1982) and there was a hatchery for winter flounder for many years in Boothbay (Bigelow and Schroeder 1953). Massachusetts (Pierce and Howe 1977; Heck *et al.* 1989; Saucerman 1990), Rhode Island (Saila *et al* 1965; Oviatt and Nixon 1977) and Connecticut (Pearcy 1962; Richards 1963; Howell and Simpson 1994; Carlson *et al.* 1997; Gottschall *et al.*, in review) are all home to young winter flounder. Briggs and O'Connor (1971) documented the presence of young winter flounder on the south shore of Long Island, New York, while Franz and Tanacredi (1992) described the food habits of young winter flounder in Jamaica Bay, New York. Juvenile winter flounder are a year-round resident of the New York Bight (Figure 5). Juveniles are common in the inshore waters of New Jersey (Rountree and Able 1992; Sogard 1992) and Delaware (Daiber *et al.* 1976). Offshore, the presence of winter flounder juveniles has been demonstrated by numerous surveys conducted by the Northeast Fisheries Science Center (Figure 3).

ADULTS

Winter flounder have been captured as far north as Ungava Bay in Labrador (Kendall 1909) and as far south as Georgia (Hildebrand and Schroeder 1928). In bottom-trawl surveys conducted by the NEFSC, winter flounder adults and juveniles are common on Georges Bank and in shelf waters as far south as the mouth of Chesapeake Bay during all seasons (Figure 3). Inshore trawl surveys in Massachusetts (Figure 4), Rhode Island (Saila 1961, Jeffries and Terceiro 1985) and Long Island Sound (Simpson *et al.* 1994) show them to be ubiquitous in those areas as well. Winter flounder are also common in the

lower reaches of the Hudson River (Boyce Thompson Institute for Plant Research, Estuarine Study Group 1977; Able *et al.* 1999) and the New York Bight/Hudson-Raritan estuary (Phelan 1992; Figure 5). They also use other protected bays and coastal ponds along the New Jersey coast (Tatham *et al.* 1984).

STATUS OF THE STOCKS

HISTORICAL PERSPECTIVE

Commercial fisheries for winter flounder flourished prior to 1980, even in the southern end of the range. Winter flounder was one of the dominant species in the Indian River and Rehoboth Bays in Delaware in the 1960's, but catches have since declined (Daiber *et al* 1976). The commercial landings of winter flounder in 1970 in Delaware totaled only 2,300 pounds, but a moderate sport fishing effort persisted at that time especially in Indian River Bay (Daiber *et al.* 1976). Hildebrand and Schroeder (1928) reported the existence of a winter commercial fishery for winter flounder in Chesapeake Bay in the 1920s; it was the principal fish caught in fyke nets in the winter (Hildebrand and Schroeder 1928). The bulk of the landings were in Maryland, and the rest in Virginia. The Maryland landings would seem to support the statement made by Hildebrand and Schroeder (1928) that winter flounder are more common in Maryland waters than in the lower (more southern) areas of Chesapeake Bay. Although Hildebrand and Schroeder (1928) reported the presence of winter flounder as far south as Georgia, they also note that they were not taken in commercial numbers south of Chesapeake Bay. Commercial landings of winter flounder peaked in the 1980s throughout its range (Brown and Gabriel 1998) and have since declined.

CURRENT STATUS OF THE STOCKS

Winter flounder are currently managed as three stocks, Gulf of Maine, southern New England-Middle Atlantic, and Georges Bank (Brown and Gabriel 1998). Both the Gulf of Maine Stock and the southern New England-Middle Atlantic stocks are considered over-exploited. Although there is some evidence that stock rebuilding has begun on Georges Bank, stock levels remain well below the historic average (Brown and Gabriel 1998).

Biomass in the Gulf of Maine stock declined from 19,600 mt in 1979 to a low of 6,000 mt in 1991 (Brown and Gabriel 1998) (Figure 14). The current biomass estimate for 1997 stands at 8,900 mt less than half of the 1979 value (Brown and Gabriel 1998). In the southern New England-Middle Atlantic stock, stock biomass declined from 39,000 mt in 1981 to a record low of 8,500 mt in 1992 (Brown and Gabriel 1998; Figure 14). Contributions from strong year classes in 1992 and 1994 have rebuilt the stock biomass to 18,000 mt in 1996 but the stock remains overexploited (Brown and Gabriel 1998). The NEFSC autumn bottom trawl survey biomass index declined from the mid-1970's until 1991 when it reached a record low of 0.14 kg per tow (Brown and Gabriel 1998; Figure 14). Although it has increased somewhat since then (1.76 kg per tow in 1996) it remains significantly below former levels (Brown and Gabriel 1998).

RESEARCH NEEDS

Although we know more about winter flounder than many other species, there are many more questions waiting to be answered. The driving forces behind winter flounder movements are still poorly understood. Temperature certainly plays a role, but does not explain all movements. The role of light intensity, food availability, and predators needs further attention.

Although we speak about spawning habitat and juvenile habitat as if they are separate things it is clear that they must be linked somehow. If spawning habitat is lost through man's activities, is the adjacent juvenile habitat lost as well for lack of juveniles to fill it? Pinpointing and mapping of habitats through the use of GIS technology on a large scale and over different ontogenetic stages will help us to maintain a more holistic outlook on habitat

The utilization of shallow bays and estuaries by winter flounder for spawning and nursery areas has been well documented. Less well studied is the utilization of nearby coastal waters. Lux and Kelly (1982) found winter flounder eggs at 13 coastal stations and 3 offshore stations and larvae at 17 coastal stations and 7 offshore stations between Provincetown to Cape Ann. A similar study by Howe (1973) also collected winter flounder eggs and larvae. Both studies generally collected relatively low densities of eggs and larvae but Howe (1973) showed that larval densities were highest at the mouths of estuaries. These collections probably represent eggs and larvae washed out of the estuaries by tidal flushing. Subsequent beam trawling in these areas failed to collect substantial numbers of YOY flounder indicating a low survival rate.

In contrast, Marine Research, Inc. (1986) reported good growth in winter flounder larvae that had been washed out of the Plymouth Harbor-Duxbury Bay estuary. Epibenthic sled collections of winter flounder eggs outside the estuary along the coast showed that spawning occurred there as well. The relative contribution of this coastal spawning to winter flounder recruitment needs further study.

The different components of these "stock complexes" need to be better described and their habitat preferences and needs documented. An attempt was made in 1980 to

separate stocks using eye lens proteins (Schenck and Saila 1982) but this effort only covered a small area near the Millstone Point area. The study showed that even in this small area there was a significant mixing of different stocks. A more comprehensive effort, spanning the entire range of the species needs to be done utilizing more modern techniques such as mitochondrial DNA

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Table 1. Summary of life history and habitat parameters for winter flounder, *Pseudopleuronectes americanus*.

Life Stage	Temperature	Salinity	Dissolved Oxygen
Eggs [1]	Spawning initiated at about 3°C, highest percent hatch at 3-5°C; 18°C lethal.	Found from 10-32 ppt; salinity has little effect on survival or hatch.	Found at 11.1-14 2 mg/l
Larvae [2]	No feeding or metamorphosis at 2°C, hatch from 1-12°C, larvae most abundant at 2-15°C.	Found at 3.2-30 ppt; higher on Georges Bank.	Found at 10 0-16 1 mg/l.
YOY [3]	Found at 2-29.4°C; Laboratory study suggests preferred temperature is 19.5°C, 30°C may be lethal.	Found at 23-33 ppt; 5 ppt suggested by laboratory study as lower avoidance salinity.	Constant 2.2 mg/l or diurnal variation from 2 6-6.4 mg/l adversely affects growth.
Juveniles [4]	Commonly found at 10-25°C during summer and fall.	Collected 19-21 ppt, 10 ppt suggested as lower avoidance level.	
Adults [5]	0.6-23°C, 12-15°C suggested as preferred; upper incipient lethal limit is 27°C.	Found at 15-33 ppt.	Lower dissolved oxygen associated with lower mean length of catch suggesting avoidance by larger fish or reduced growth

[1] Breder 1923, Scott 1929, Bigelow and Schroeder 1953, Pearcy 1962, Williams 1975, Rogers 1976, Buckley 1982, Crawford and Carey 1985, Scarlett and Allen 1989, Monteleone 1992

[2] Bigelow and Schroeder 1953, Pearcy 1962, Dovel 1967, 1971, Buckley 1982, Frank and Leggett 1983, Scarlett and Allen 1989, Monteleone 1992

[3] Pearcy 1962, Richards and Castagna 1970, Briggs and O'Connor 1971, Oviatt and Nixon 1977, Pierce and Howe 1977, Reynolds and Casterlin 1985, Heck *et al* 1989, Bejda *et al* 1992, Rountree and Able 1992

[4] Pearcy 1962, Oviatt and Nixon 1977, Casterlin and Reynolds 1982, Reynolds and Casterlin 1985, Carlson *et al* 1997

[5] Breder 1923, McCracken 1963, Olla *et al* 1969, Richards and Castagna 1970, Haedrich and Haedrich 1974, Howe and Coates 1975, Tyler and Dunn 1976, Oviatt and Nixon 1977, Van Guelpen and Davis 1979, Jeffries and Terceiro 1985, Reynolds and Casterlin 1985, Howell and Simpson 1994, Carlson *et al* 1997

Table 1. cont'd.

Life Stage	Depth	Substrate	Vegetation	Currents
Eggs [1]	Found at 0.3-4.5 m (inshore), 90 m or less on Georges Bank.	Mud to sand or gravel.	Diatom mats, drifting macroalgae.	
Larvae [2]	1-4 5 m inshore.	Fine sand, gravel.		Hydrodynamics work to retain larvae in nursery areas.
YOY [3]	0.5-12 m inshore.	Mud to sand with shell or leaf litter.	*Ulva*, eelgrass and unvegetated adjacent areas.	
Juveniles [4]	Peak abundance of flounder less than 200 mm occurs in 18-27 m of water in Long Island Sound in April and May In Canadian waters, juveniles were most abundant at 11-18 m Less than 100 m offshore.	Equally abundant on mud or sand shell.		
Adults [5]	Most 1-30 m inshore, shallowest during spawning, less than 100 m offshore.	Mud, sand, cobble, rocks, boulders.		

[1] Scott 1929; Bigelow and Schroeder 1953, Pearcy 1962, Anonymous 1972, Crawford and Carey 1985, Scarlett and Allen 1989, Monteleone 1992
[2] Pearcy 1962, Frank and Leggett 1983, Crawford and Carey 1985, Scarlett and Allen 1989, Monteleone 1992
[3] Briggs and O'Connor 1971, Heck *et al* 1989, Saucerman 1990, Sogard 1992, Howell and Molnar 1995, Gottschall *et al*, in review
[4] McCracken 1963, Richards 1963
[5] Breder 1923, Mansueti 1962, McCracken 1963, Olla *et al* 1969, Kennedy and Steele 1971, Van Guelpen and Davis 1979, Macdonald and Green 1986, Steimle *et al* 1993

Table 1 cont'd.

Life Stage	Predators	Prey	Migration
Eggs [1]			
Larvae [2]	Mackerel, *Sarsia tubulosa*	Nauplii, invertebrate eggs, protozoans, polychaetes	
YOY [3]	*Crangon* sp., summer flounder, striped searobin (*Prionotus evolans*)	Amphipods, copepods, polychaetes, bivalve siphons	Limited; deeper for first winter.
Juveniles [4]	Cormorants, snapper bluefish, gulls	Sand dollars, bivalve siphons, polychaetes, amphipods, *Crangon* sp.	Movement to deeper waters as size increases.
Adults [5]	Goosefish, spiny dogfish, sea ravens, striped bass, seals, sculpins	Amphipods, polychaetes, bivalves or siphons, capelin eggs, crustaceans	Inshore in fall, offshore in spring, long post-spawn migrations in some fish.

[2] Pearcy 1962, Dovel 1971, Frank and Leggett 1983
[3] Linton 1921, Poole 1964, Saucerman 1990, Saucerman and Deegan 1991, Witting and Able 1993, Howell and Molnar 1995, Witting and Able 1995, Manderson *et al* 1999, Stehlik and Meise, in press
[4] Linton 1921, Howe *et al* 1976, Reynolds and Casterlin 1985, Franz and Tanacredi 1992, Carlson *et al* 1997, Stehlik and Meise, in press
[5] Medcoff and MacPhail 1952, Bigelow and Schroeder 1953, Dickie and McCracken 1955, Fisher and Mackenzie 1955, Saila 1961, Mansfield 1967, Olla *et al* 1969, Kennedy and Steele 1971, Tyler 1971a, Haedrich and Haedrich 1974, Howe and Coates 1975, Tyler and Dunn 1976, Van Guelpen and Davis 1979, Azarovitz 1982, Macdonald 1983, Jeffries and Terceiro 1985, Macdonald and Green 1986, Phelan 1992, Martell and McClelland 1994, Steimle *et al* 1993, Carlson *et al* 1997

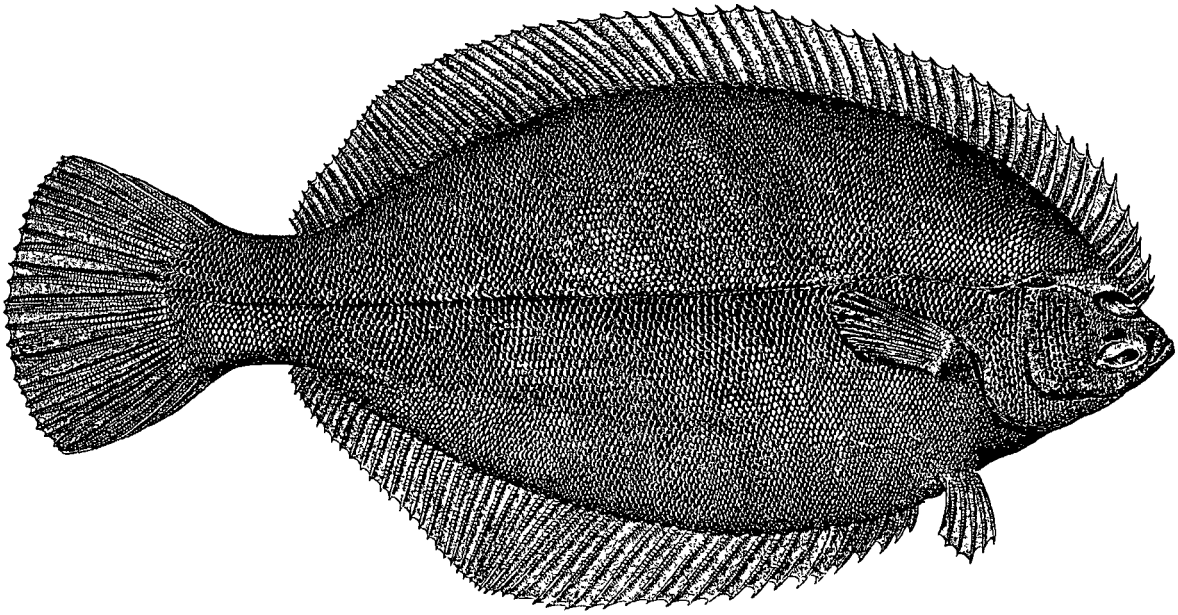


Figure 1. The winter flounder, *Pseudopleuronectes americanus* (Walbaum) (from Goode 1884).

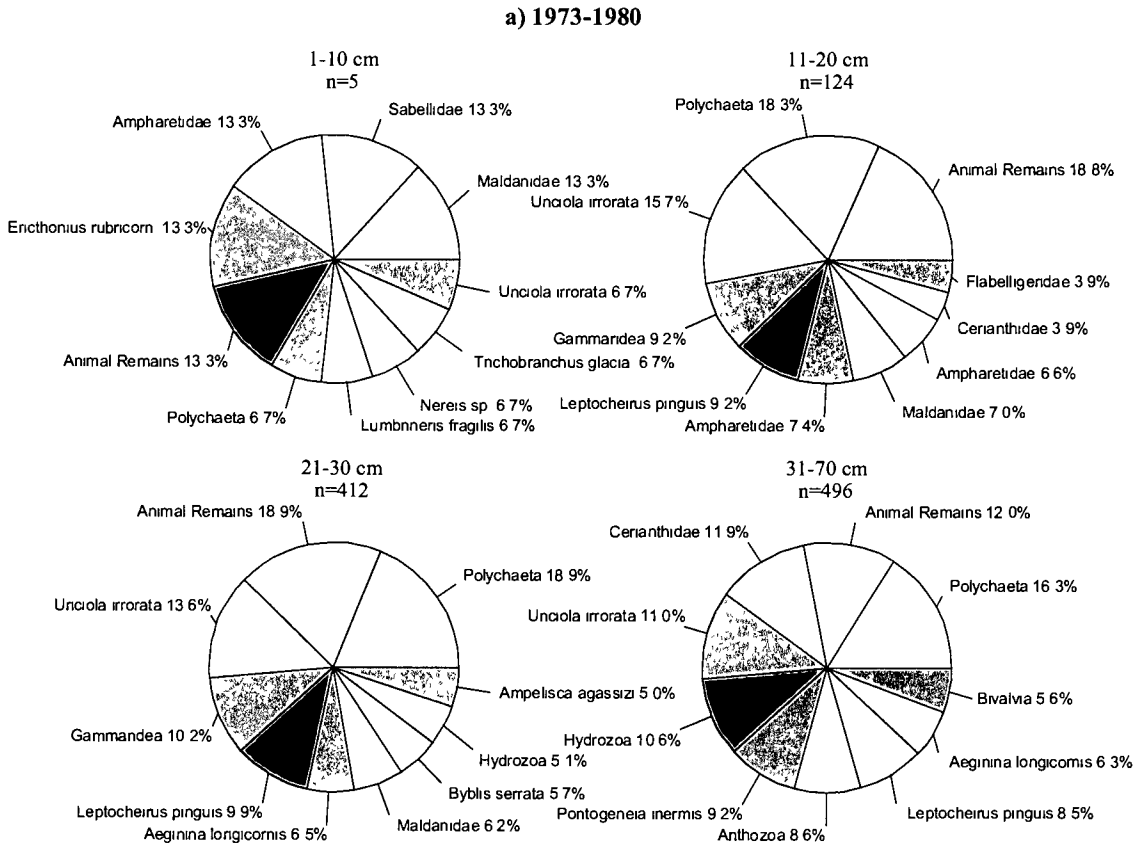


Figure 2. Abundance (percent occurrence of 10 most common prey items) of the major prey items of winter flounder, by size class, collected during NEFSC bottom trawl surveys from 1973-1980 and 1981-1990. The category "animal remains" refers to unidentifiable animal matter. Methods for sampling, processing, and analysis of samples differed between the time periods [see Reid *et al* (1999) for details].

b) 1981-1990

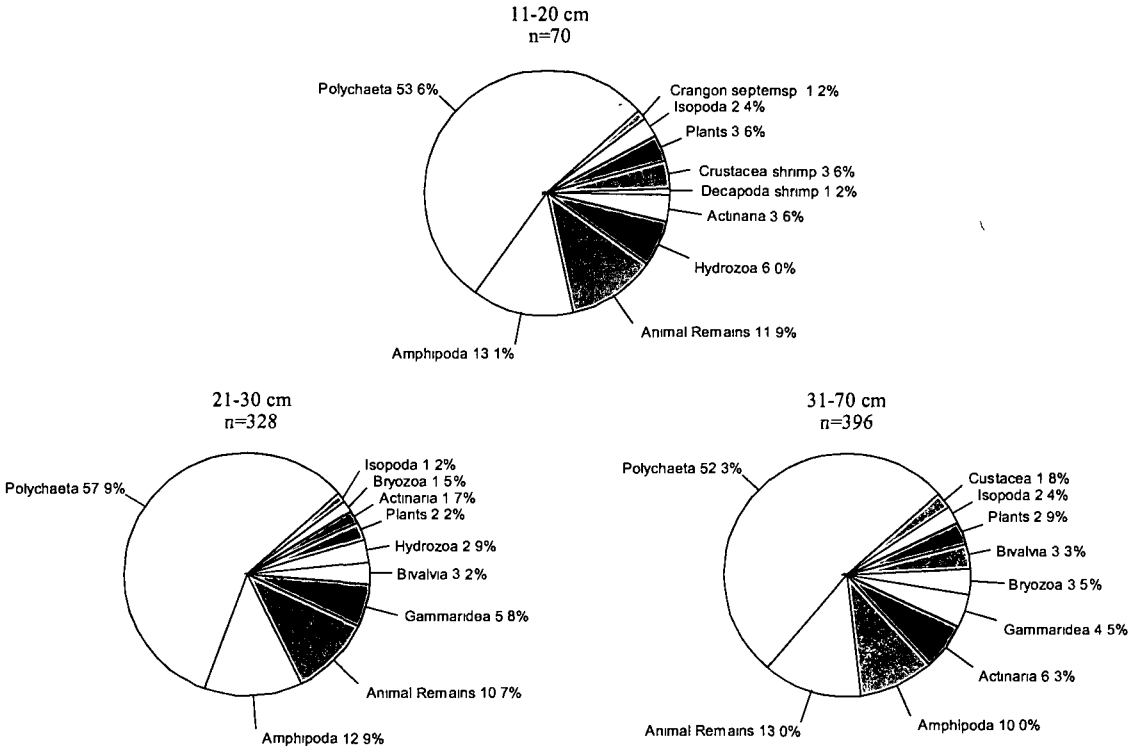


Figure 2. cont'd

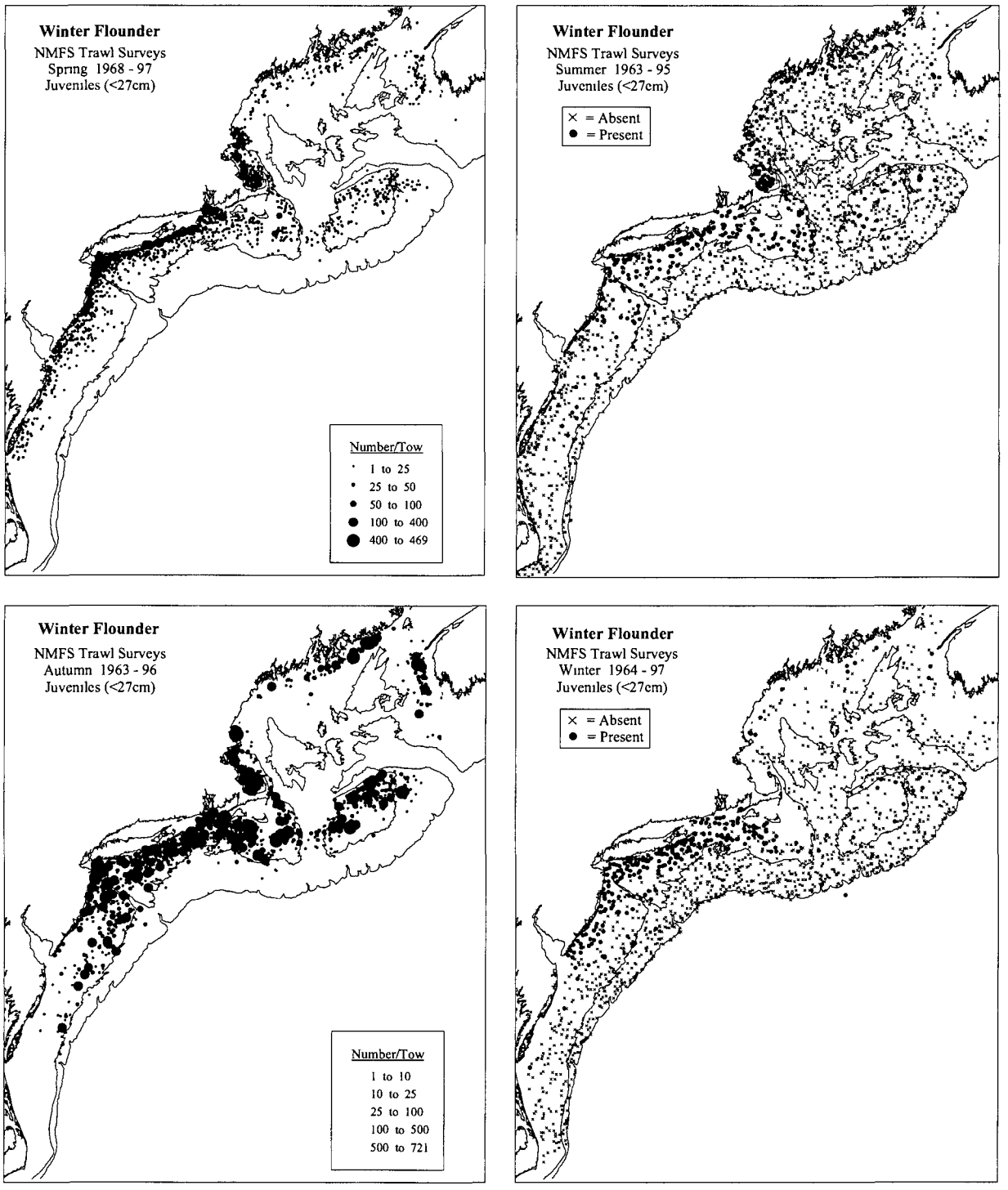
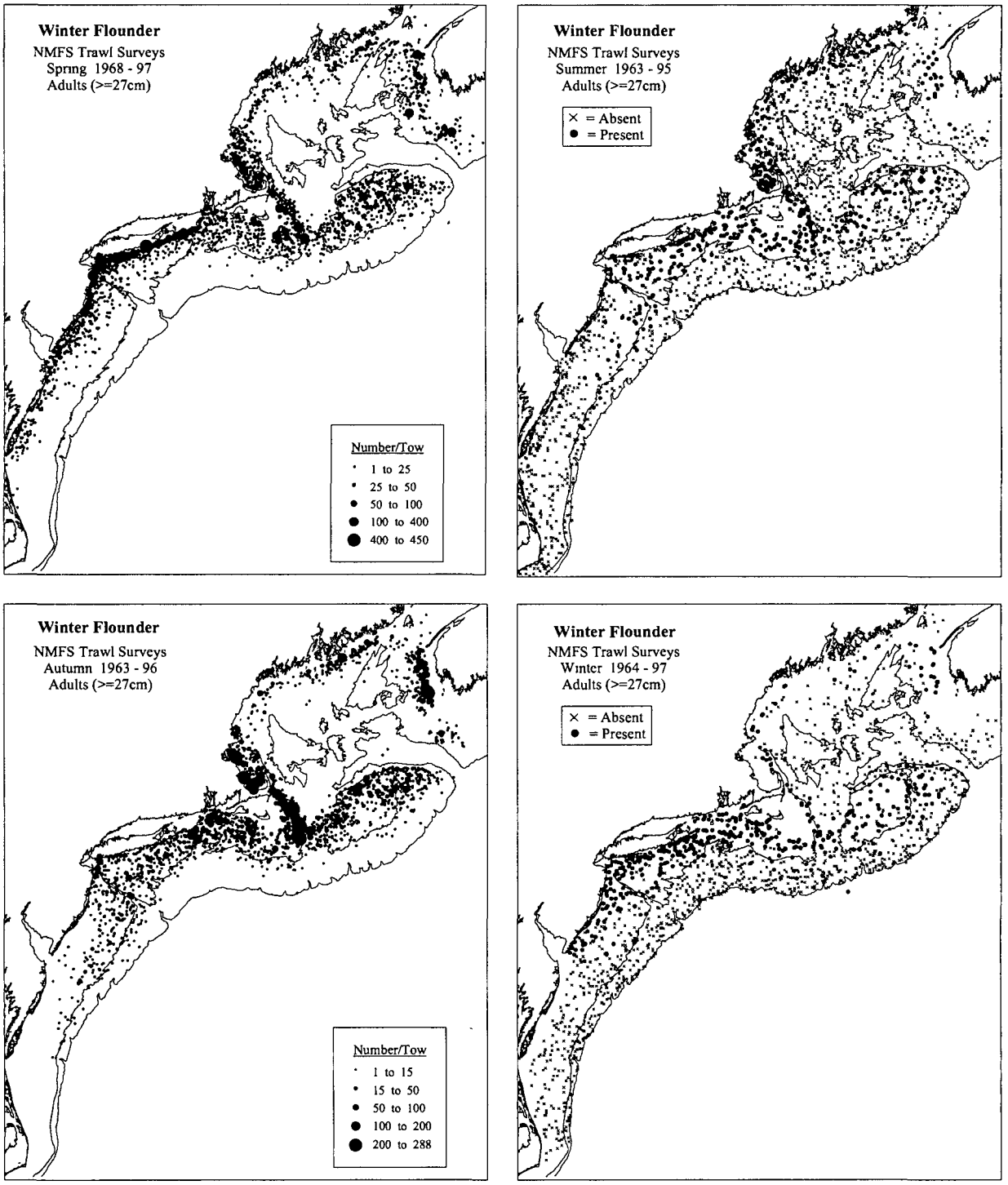


Figure 3. Distribution and abundance of juvenile and adult winter flounder collected during NEFSC bottom trawl surveys during all seasons from 1963-1997. Densities are represented by dot size in spring and fall plots, while only presence and absence are represented in winter and summer plots [see Reid *et al.* (1999) for details].



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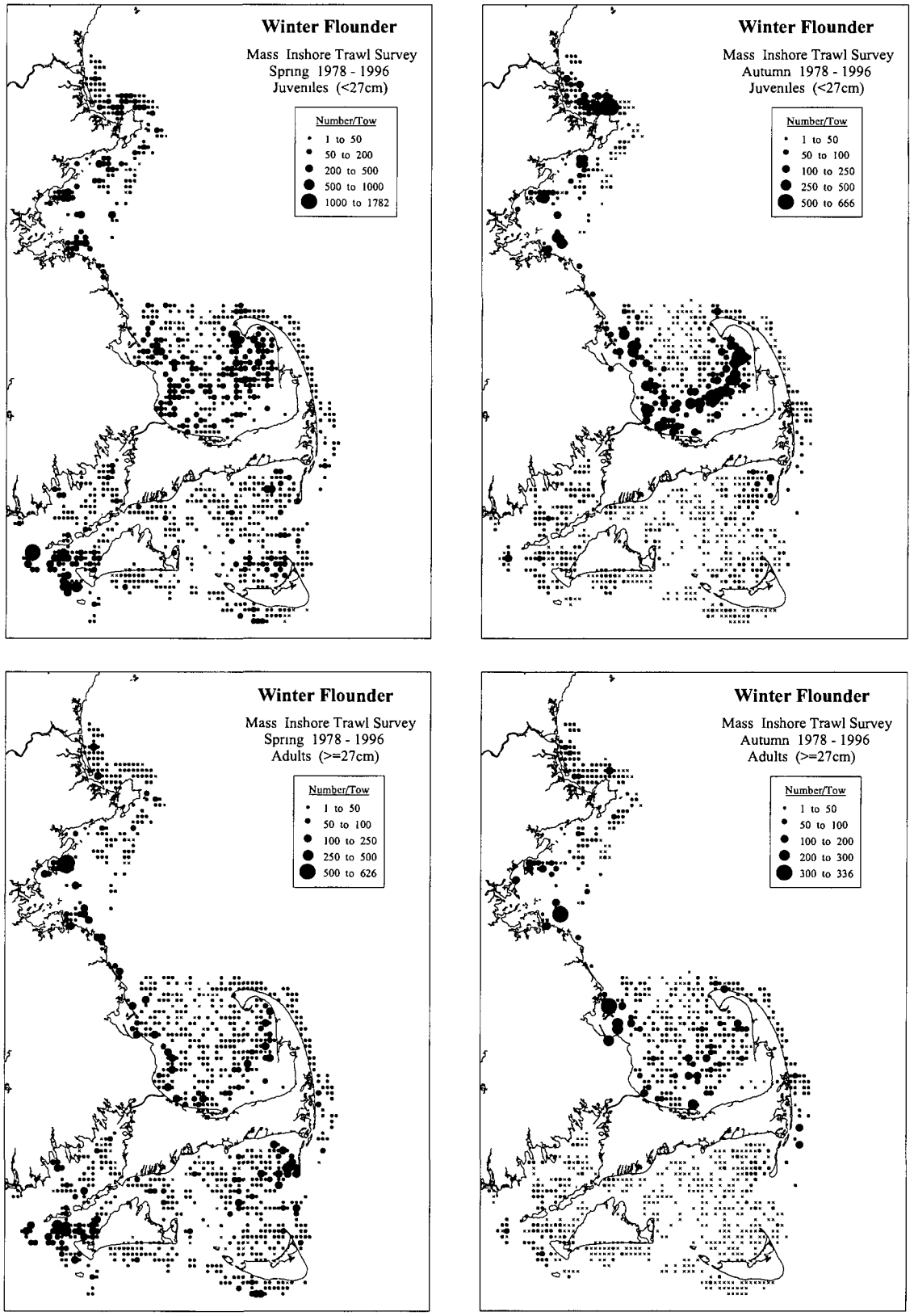


Figure 4. Distribution and abundance of juvenile and adult winter flounder in Massachusetts coastal waters collected during the spring and autumn Massachusetts trawl surveys, 1978-1996 [see Reid *et al.* (1999) for details].

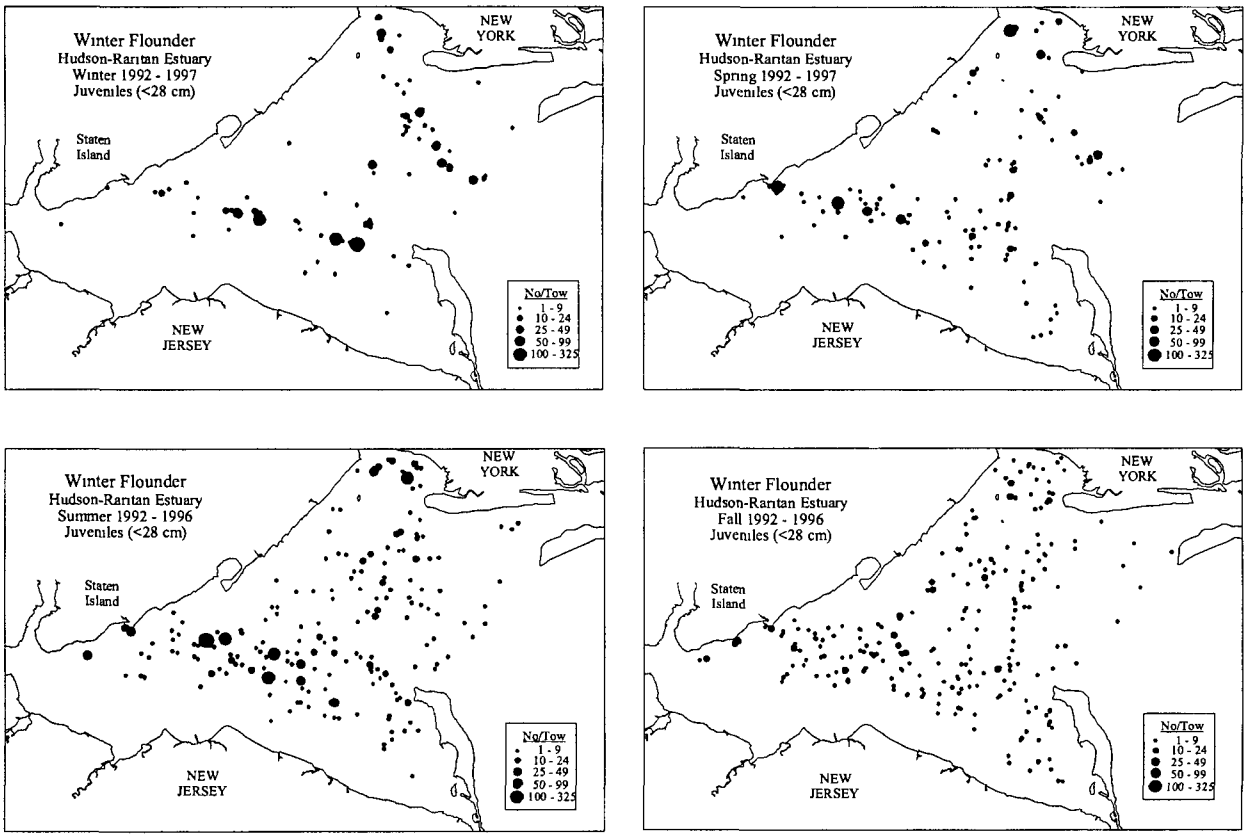
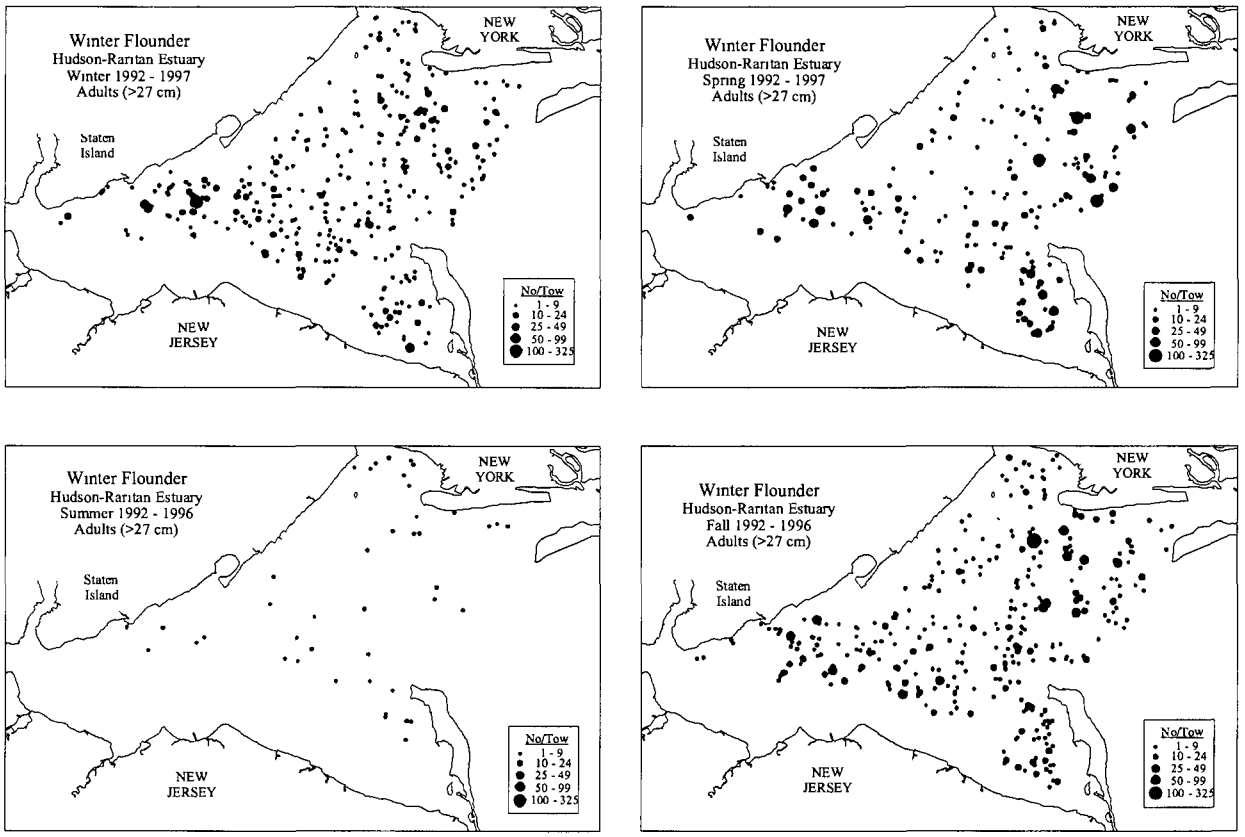


Figure 5. Distribution and abundance of juvenile and adult winter flounder collected in the Hudson-Raritan estuary, based on Hudson-Raritan trawl surveys during winter (January-March), spring (April and June), summer (July–August), and fall (October-December) from January 1992 to June 1997 [see Reid *et al.* (1999) for details].



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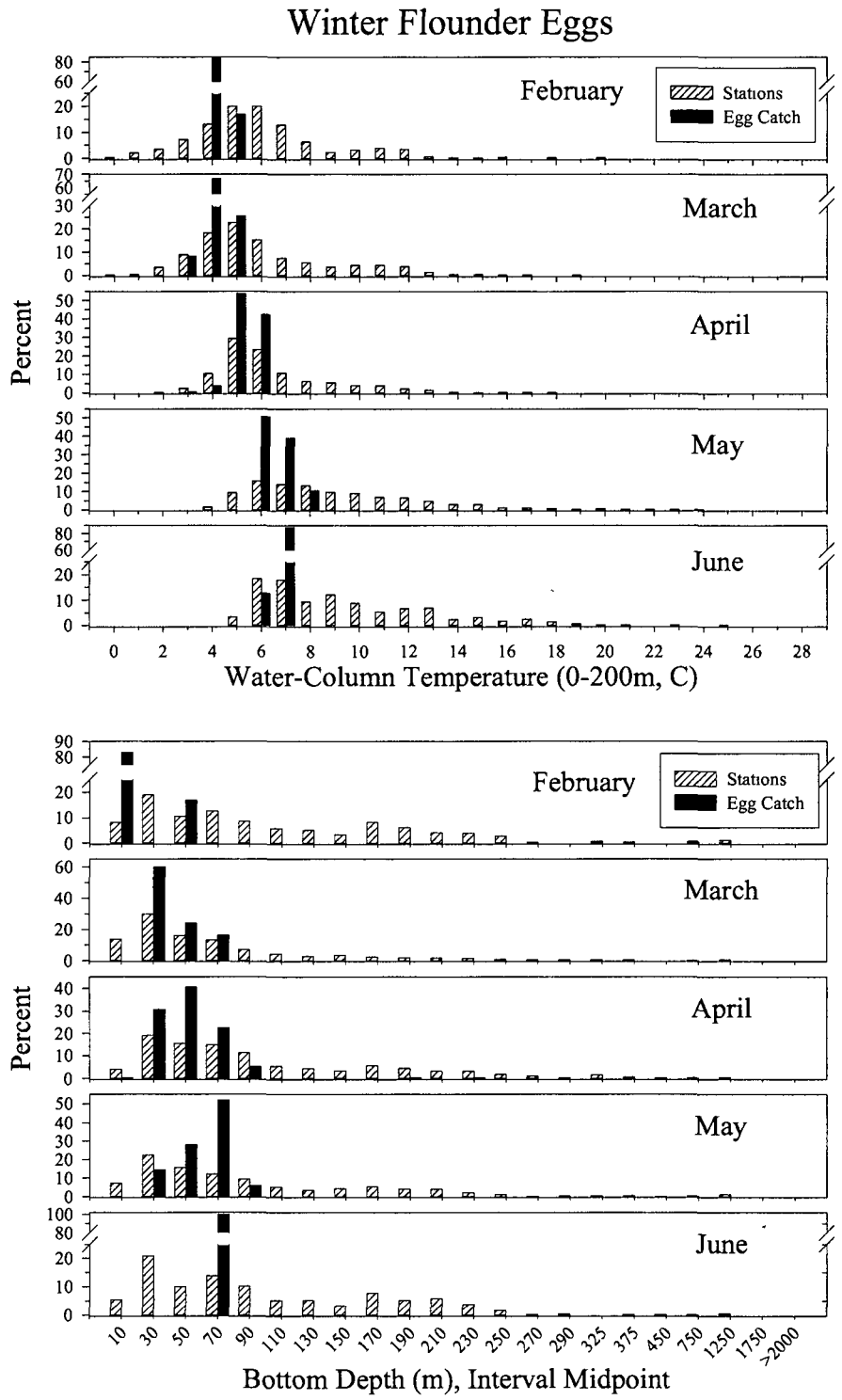


Figure 6. Abundance of winter flounder eggs relative to water column temperature (to a maximum of 200 m) and bottom depth from NEFSC MARMAP ichthyoplankton surveys, February to June, 1978-1987 (all years combined. Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2)

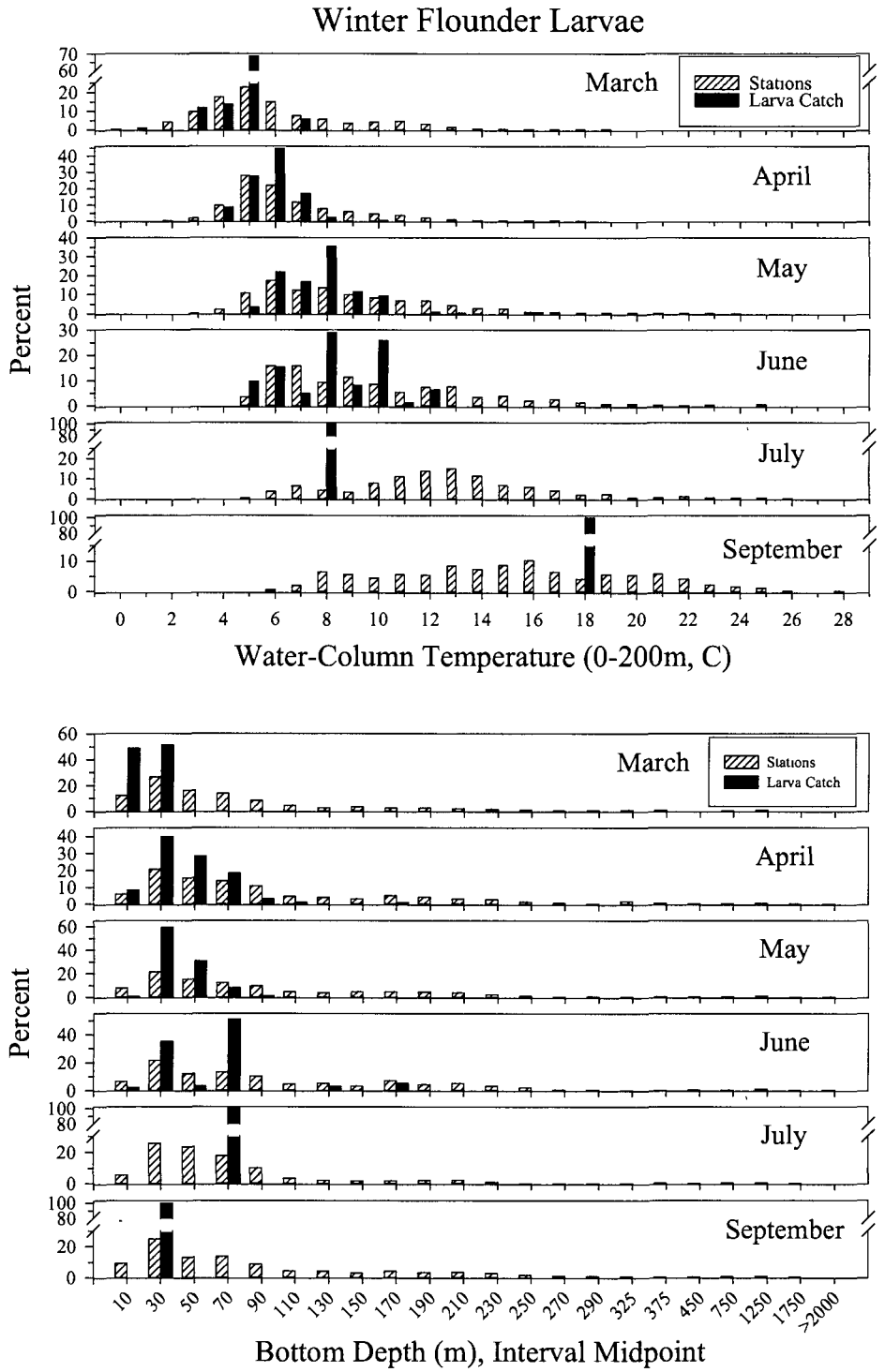


Figure 7. Abundance of winter flounder larvae relative to water column temperature (to a maximum of 200 m) and bottom depth from NEFSC MARMAP ichthyoplankton surveys, March to September, 1977-1987 (all years combined. Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).

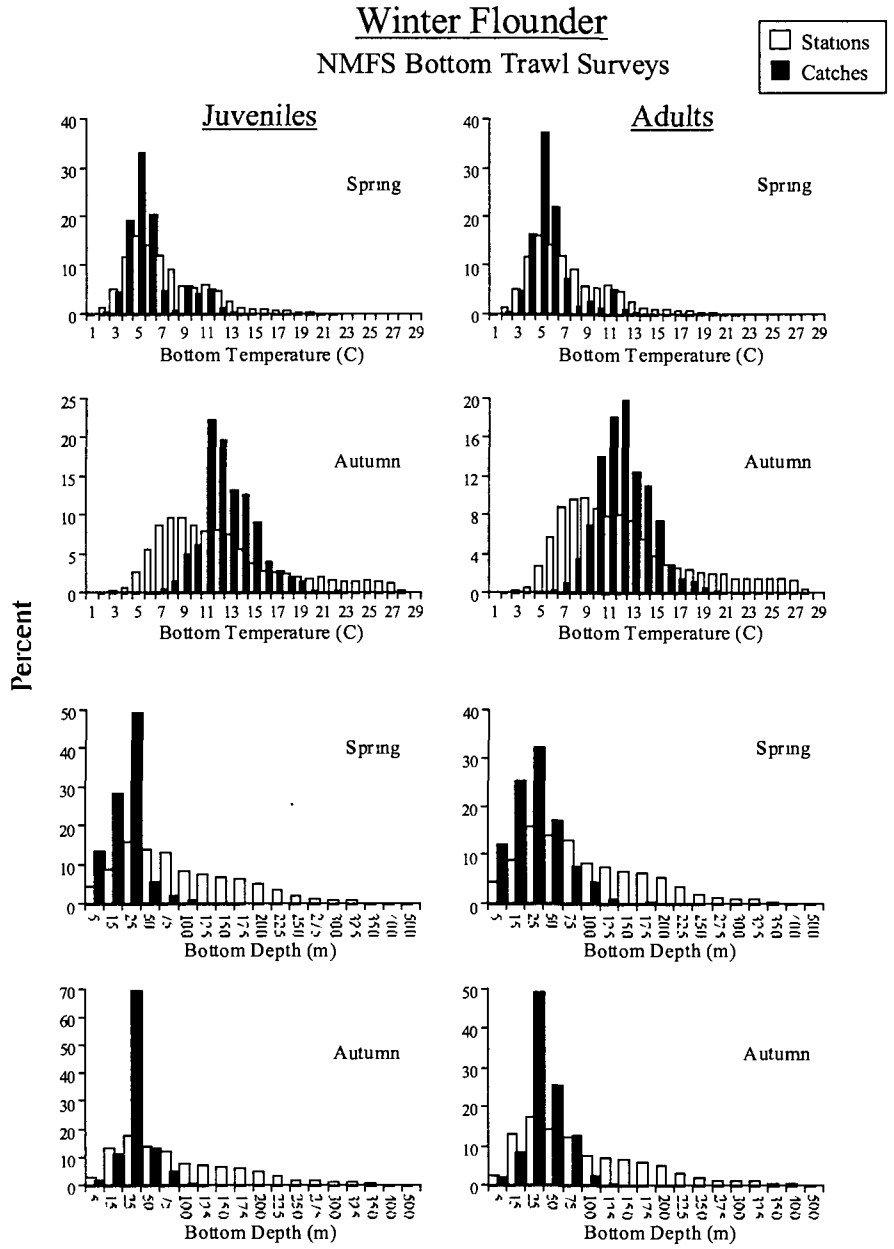


Figure 8. Abundance of juvenile and adult winter flounder relative to bottom water temperature and depth based on spring and autumn NEFSC bottom trawl surveys Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).

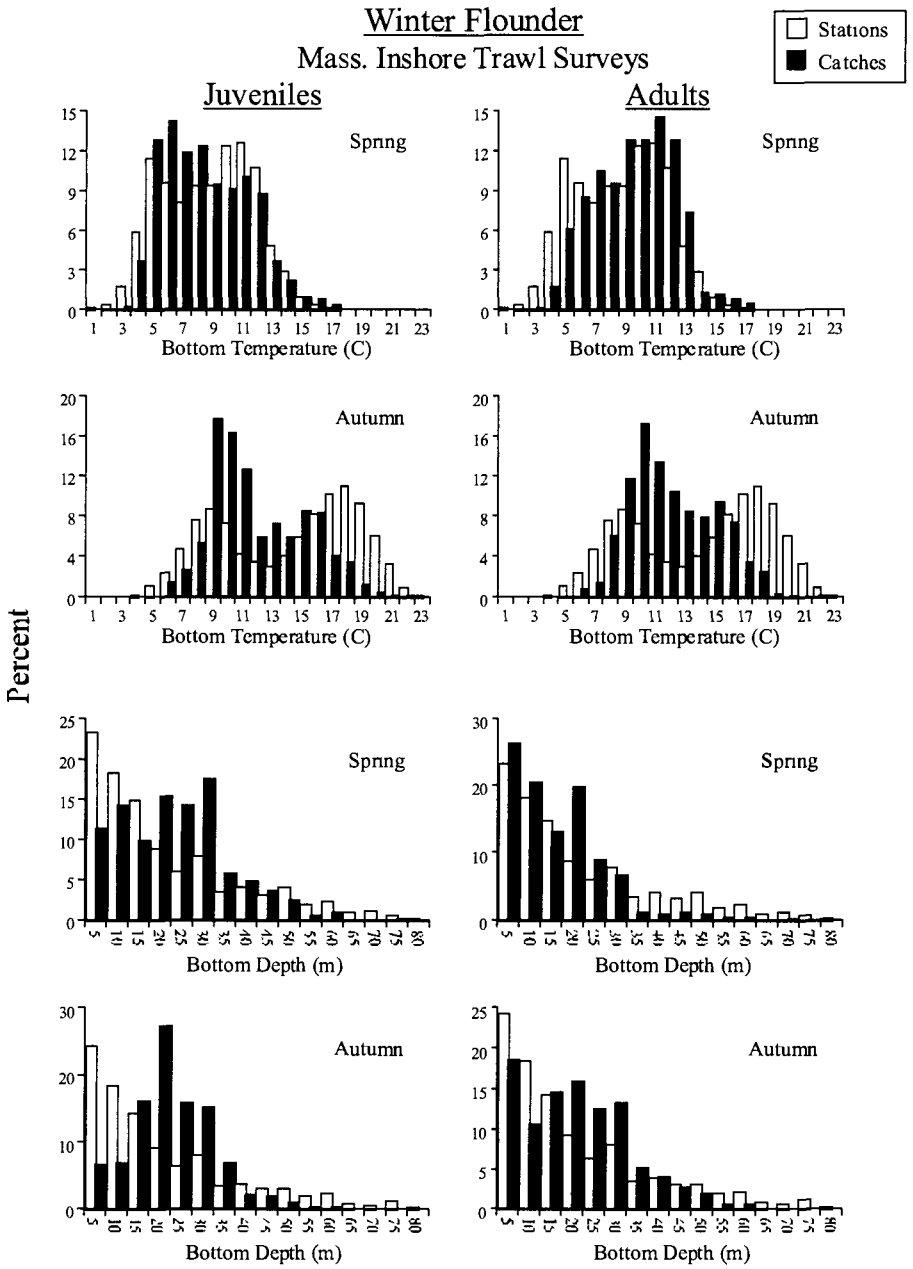


Figure 9. Abundance of juvenile and adult winter flounder relative to bottom water temperature and depth based on Massachusetts inshore bottom trawl surveys (spring and autumn 1978-1996, all years combined) Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).

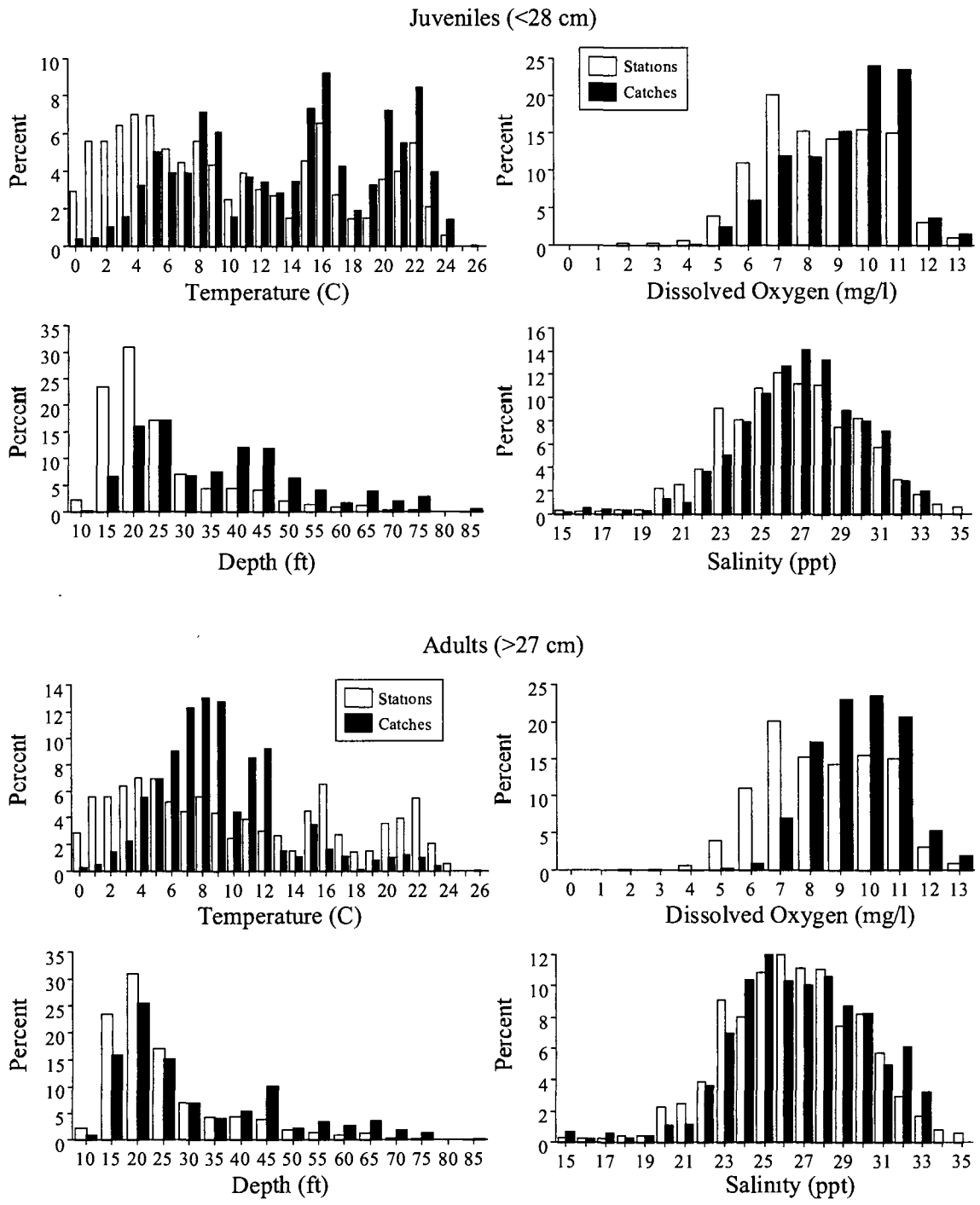
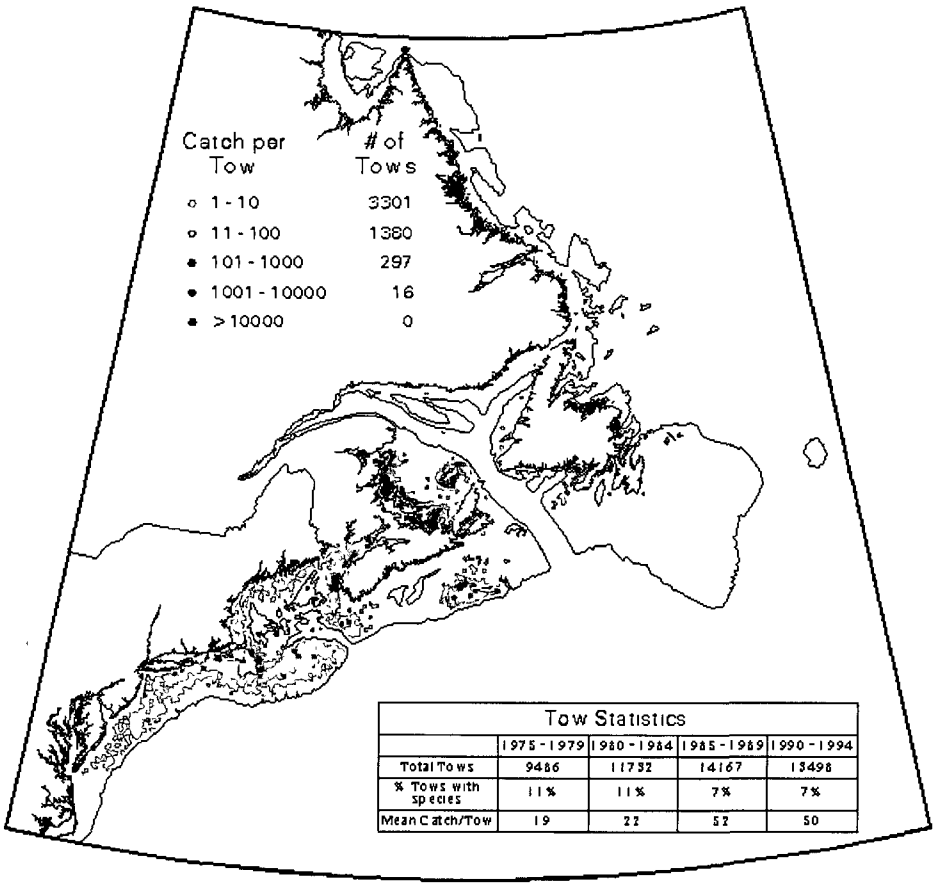


Figure 10. Abundance of juvenile and adult winter flounder relative to bottom water temperature, dissolved oxygen, depth, and salinity from Hudson-Raritan estuary trawl surveys (January 1992 - June 1997, all years combined).



Tow Statistics

	1975 - 1979	1980 - 1984	1985 - 1989	1990 - 1994
Total Tows	9486	11732	14167	13498
% Tows with species	11%	11%	7%	7%
Mean Catch/Tow	19	22	52	50

Figure 11. Distribution and abundance of winter flounder 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).

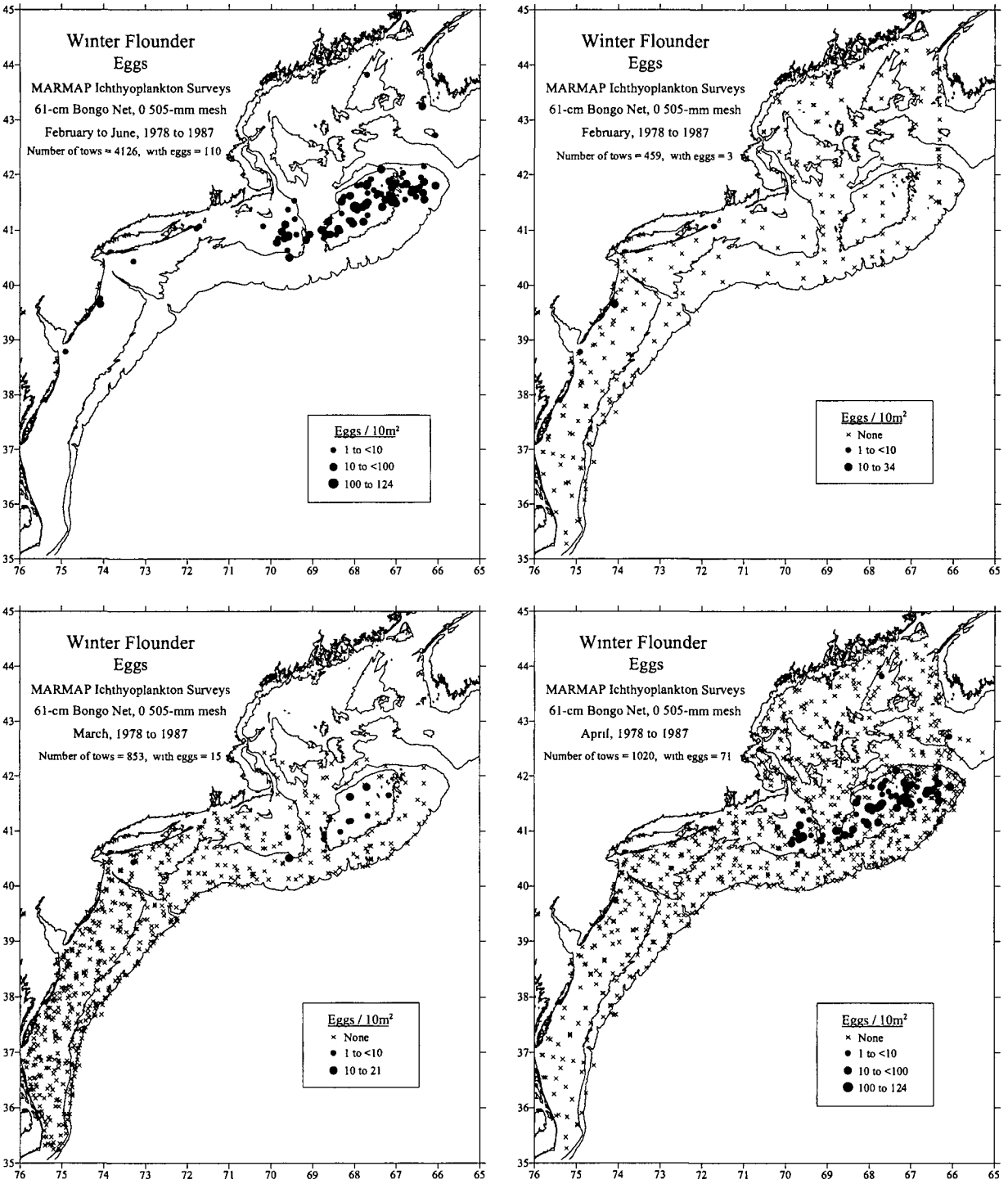


Figure 12. Distribution and abundance of winter flounder eggs collected during NEFSC MARMAP ichthyoplankton surveys from February to June, 1978-1987 [see Reid *et al.* (1999) for details].

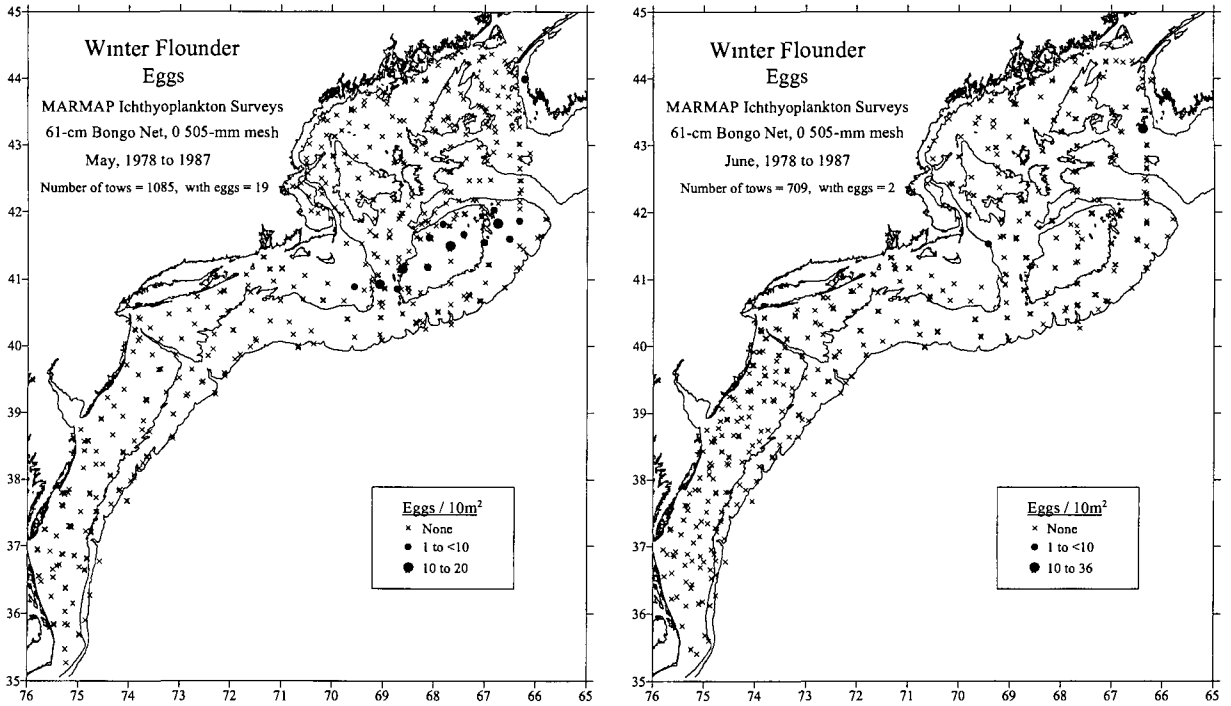


Figure 12. cont'd.

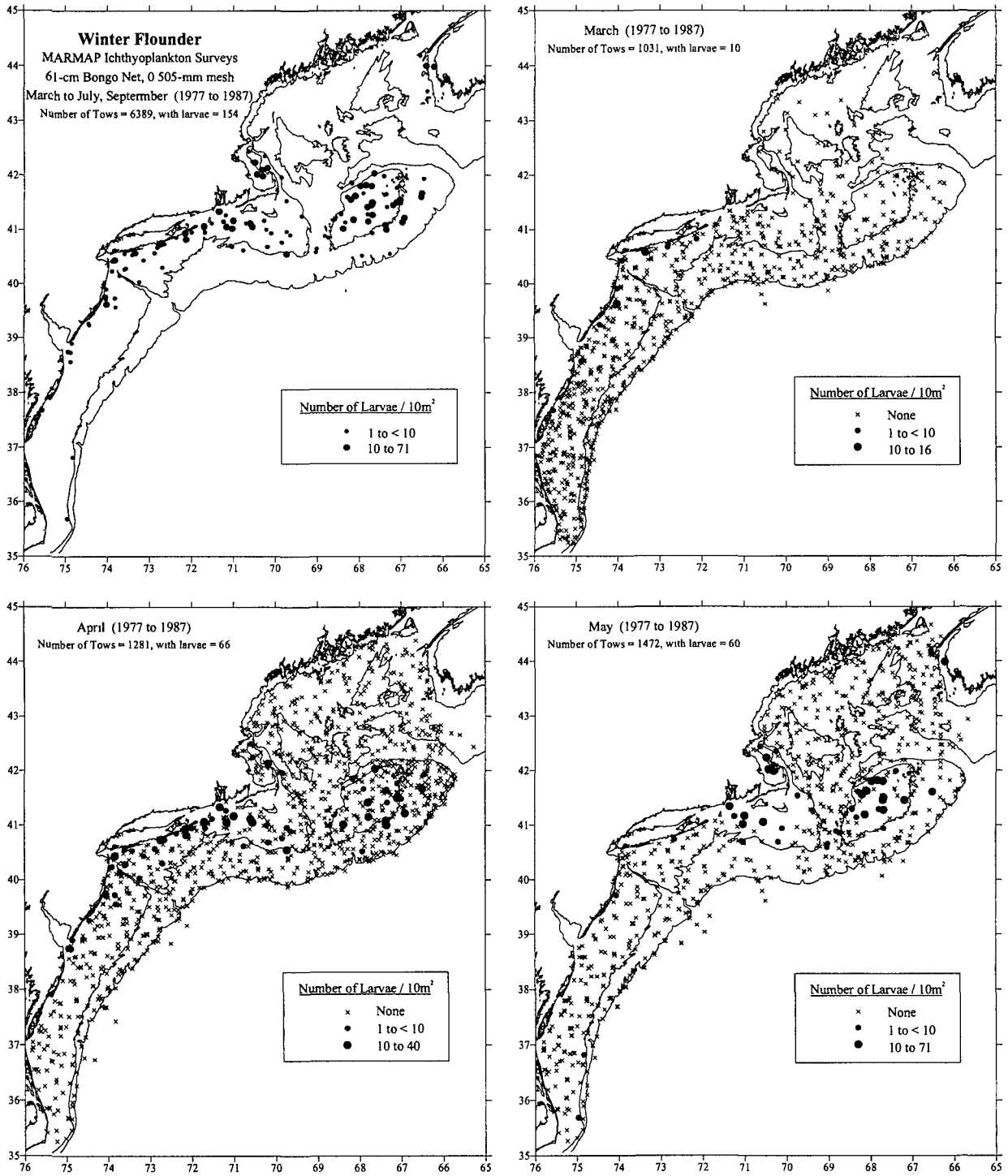


Figure 13. Distribution and abundance of winter flounder larvae collected during NEFSC MARMAP ichthyoplankton surveys from March to July, and September, 1977-1987 [see Reid *et al.* (1999) for details].

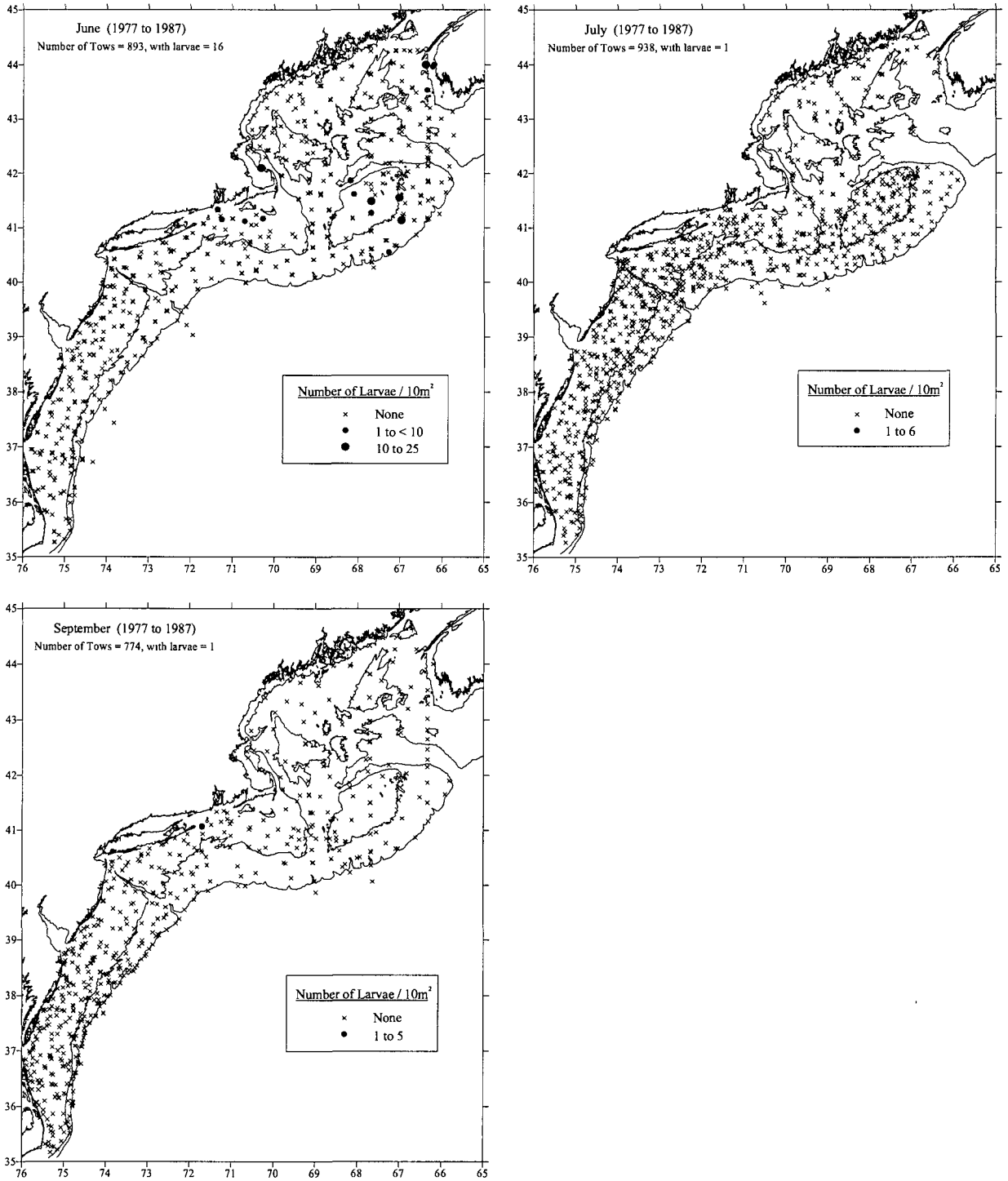


Figure 13. cont'd

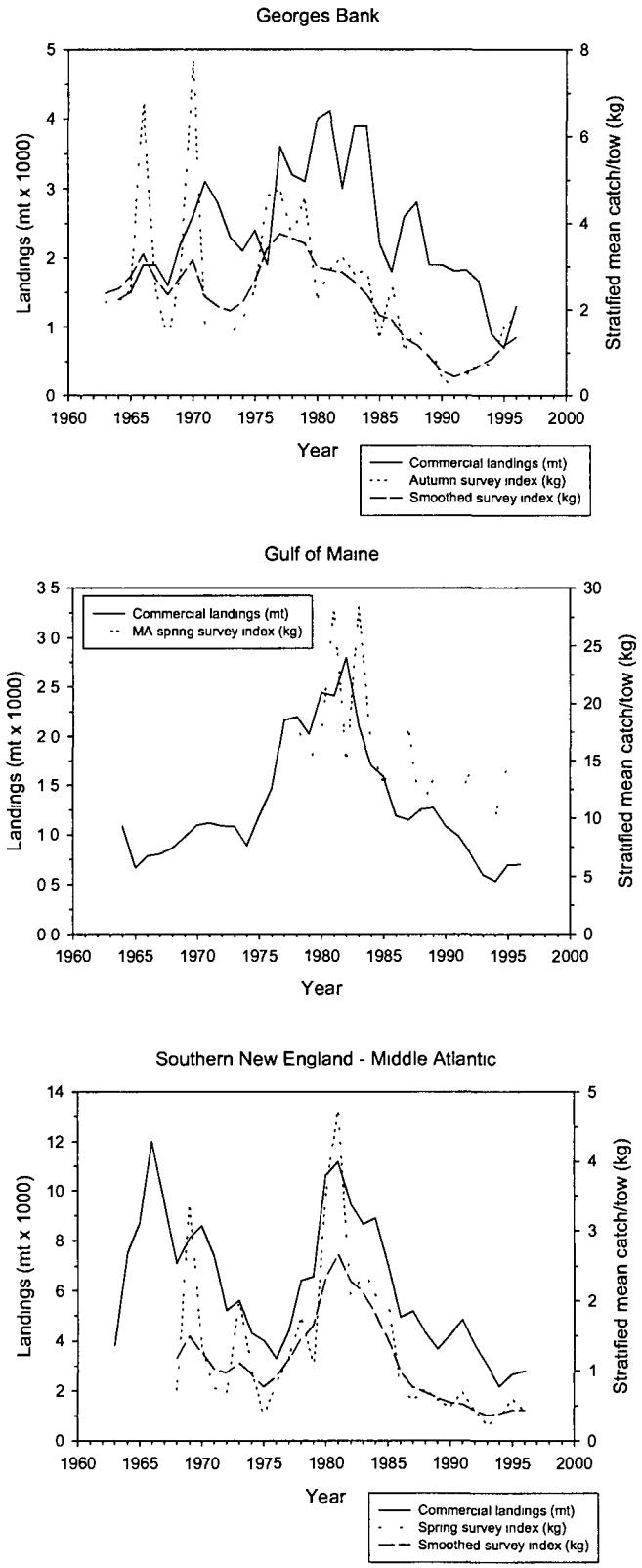


Figure 14. Commercial landings and survey indices (from the NEFSC bottom trawl surveys) for winter flounder stocks from Georges Bank, the Gulf of Maine, and southern New England-Middle Atlantic Bight.

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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 "planning, developing, and managing multidisciplinary programs of basic and applied research to: 1) better understand the living marine resources (including marine mammals) of the Northwest Atlantic, and the environmental quality essential for their existence and continued productivity; and 2) describe and provide to management, industry, and the public, options for the utilization and conservation of living marine resources and maintenance of environmental quality which are consistent with national and regional goals and needs, and with international commitments." 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. Those media are in three categories:

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