NOAA Technical Memorandum NMFS-NE-151

Essential Fish Habitat Source Document:

Summer Flounder, *Paralichthys dentatus*, 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

September 1999

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NOAA Technical Memorandum NMFS-NE-151

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Essential Fish Habitat Source Document:

Summer Flounder, *Paralichthys dentatus*, 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]).

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

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

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

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

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

FOREWORD

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

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

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

NMFS Strategic Plan for Fisheries Research (February 1998)

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

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

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

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

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

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

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

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INTRODUCTION

The geographical range of the summer flounder or fluke, *Paralichthys dentatus* (Figure 1), encompasses the shallow estuarine waters and outer continental shelf from Nova Scotia to Florida (Ginsburg 1952; Bigelow and Schroeder 1953; Anderson and Gehringer 1965; Leim and Scott 1966; Gutherz 1967; Gilbert 1986; Grimes *et al*. 1989), although Briggs (1958) gives their southern range as extending into the northern Gulf of Mexico. The center of its abundance lies within the Middle Atlantic Bight from Cape Cod, Massachusetts, to Cape Hatteras, North Carolina (Figure 2; Hildebrand and Schroeder 1928). North of Cape Cod and south of Cape Fear, North Carolina, summer flounder numbers begin to diminish rapidly (Grosslein and Azarovitz 1982). South of Virginia, two closely related species, the southern flounder (*Paralichthys lethostigma*) and the gulf flounder (*Paralichthys albigutta*) occur and sometimes are not distinguished from summer flounder (Hildebrand and Cable 1930; Byrne and Azarovitz 1982). For more detailed discussions of the summer flounder's distribution on the shelf and in the various estuaries, see the Life History and Geographical Distribution section.

Summer flounder exhibit strong seasonal inshore-offshore movements, although their movements are often not as extensive as compared to other highly migratory species. Adult and juvenile summer flounder normally inhabit shallow coastal and estuarine waters during the warmer months of the year and remain offshore during the fall and winter (Figure 3). Complete descriptions of the inshore-offshore migratory patterns of the summer flounder are in the Life History and Geographical Distribution section of this paper.

LIFE HISTORY AND GEOGRAPHICAL DISTRIBUTION

STOCK STRUCTURE

Several stocks of summer flounder may exist throughout its range, and numerous attempts have been made to identify them. Since a genetically distinct stock can have unique rates of recruitment, growth, and mortality (Cushing 1981), identification of the various stocks or subpopulations of summer flounder and their stock-specific biological traits, as well as their habitat distribution and overlap, is necessary for proper management. Previous stock identification studies suggested that significant differences exist between summer flounder north and south of Cape Hatteras; i.e., between those in the Mid-Atlantic Bight and South Atlantic Bight (Wilk *et al*. 1980; Fogarty *et al*. 1983; Able *et al*. 1990; Wenner *et al*. 1990a). Summer flounder north and south of the Cape were statistically separable on the basis of morphometric characters, with apparent intermixing of northern and southern contingents in the vicinity of Cape Hatteras [tagging studies by Desfosse (1995) also indicated that there was some exchange of summer flounder between the north and south of Cape Hatteras during winter]. Thus, it was suggested that the Cape Hatteras region may form a zoogeographical barrier between the Middle and South Atlantic Bights which results in the reproductive isolation of the adjacent stocks of summer flounder (Wilk *et al*. 1980; Fogarty *et al*. 1983). This was also suggested by tagging studies in the nearshore waters and sounds north of North Carolina which showed that fish tagged north of Cape Hatteras moved northward, while fish tagged south of Hatteras moved southward (Monaghan 1992, 1996). An alternative hypothesis by Wenner *et al*. (1990a) suggested that, rather than two separate populations, the South Atlantic Bight may serve as a nursery area for summer flounder in the Mid-Atlantic Bight.

However, Jones and Quattro (1999) analyzed the genetic diversity revealed in the mitochondrial DNA (mtDNA) in samples of juveniles and adult summer flounder collected from coastal sites from Buzzard's Bay, Massachusetts to Charleston, South Carolina during 1992 to 1996. In contrast to the previous morphological studies, analyses of mtDNA variation revealed no significant population subdivision centered around Cape Hatteras; i.e., summer flounder populations are not genetically different north and south of Cape Hatteras. Jones and Quattro (1999) suggest that the phenotypic divergence seen among geographic samples of summer flounder (Wilk *et al*. 1980; Fogarty *et al*. 1983) may reflect differential environmental influences.

Within the Middle Atlantic Bight, Fogarty *et al*. (1983) reported that a summer flounder discrimination workshop was unable to examine adequately the hypothesis of multiple stocks. Although Smith (1973) identified concentrations of summer flounder eggs off Long Island, Delaware-Virginia, and North Carolina, the workshop concluded that the distribution of summer flounder eggs and larvae was continuous throughout the Middle Atlantic Bight and that the apparent concentrations identified by Smith (1973) were not the result of multiple stocks, but may have been due to sampling variability. However, Jones and Quattro (1999) did detect population genetic structure in their samples of summer flounder from the northern portion of its range; i.e., a small but significant portion of the total genetic variance could be attributed to differences between their Massachusetts and Rhode Island samples and all the other samples. Furthermore, tagging studies by Desfosse *et al*. (1988) and Desfosse (1995) indicate that there may be two subpopulations of summer flounder in Virginia inshore waters, and studies by Van Housen (1984), Delaney (1986), and Holland (1991), as well as such supplemental observations as by Ross *et al*. (1990) off of North Carolina, suggest that inshore populations from Virginia to North Carolina may form a separate population from those to the north and offshore (a trans-Hatteras stock). Further studies from these regions will be necessary to confirm these observations.

Nonetheless, it is important to note that throughout the

U.S. EEZ, summer flounder is managed and assessed as a single stock by the Mid-Atlantic Fishery Management Council (NMFS 1997).

ADULTS

As stated above, summer flounder exhibit strong seasonal inshore-offshore movements (Figure 3). Adult flounder normally inhabit shallow coastal and estuarine waters during the warmer months of the year and remain offshore during the colder months on the outer continental shelf at depths down to 150 m (Figure 4; Bigelow and Schroeder 1953; Grosslein and Azarovitz 1982). Some evidence suggests that older adults may remain offshore all year (Festa 1977). However, due to overfishing, most of the adults are ≤ 3 years of age and they return to the inner continental shelf and estuaries during the summer [Able and Kaiser 1994; Terceiro 1995; Northeast Fisheries Science Center 1997; in addition, Desfosse's (1995) study in Virginia waters notes that the majority of fish sampled from 1987-1989 were from 0-3 years of age, and over 90% of the summer flounder survey catch in Delaware Bay for 1996 was also less than age 3 (Michels 1997)]. The southern population may undertake less extensive offshore migrations (Fogarty *et al*. 1983). Tagging studies indicate that fish which spend their summer in a particular bay tend largely to return to the same bay in the subsequent year or to move to the north and east (Westman and Neville 1946; Hamer and Lux 1962; Poole 1962; Murawski 1970; Lux and Nichy 1981; Monaghan 1992; Desfosse 1995). For example, tagging studies indicate that the majority of summer flounder from inshore New Jersey return to inshore New Jersey the following year. This homing is also evident in summer flounder which return to New York waters, with some movement to waters off Connecticut, Rhode Island and Massachusetts (Poole 1962). Once inshore during the summer months, there appears to be very little movement of inshore fish to offshore waters (Westman and Neville 1946; Poole 1962; Desfosse 1995).

Tagging studies conducted by Poole (1962) and Lux and Nichy (1981) on flounder released off Long Island and southern New England revealed that fish usually began seaward migrations in September or October. Their wintering grounds are located primarily between Norfolk and Veatch Canyons east of Virginia and Rhode Island, respectively, although they are known to migrate as far northeastward as Georges Bank. Fish that move as far north as the wintering grounds north of Hudson Canyon may become rather permanent residents of the northern segment of the Mid-Atlantic Bight (Lux and Nichy 1981). New York and New Jersey fish may move farther south in the winter months and generally may not move as far north in the summer as New England flounder (Poole 1962).

The presence, distribution, and abundance of the adults nearshore and in the estuaries has been documented by both fishery dependent and independent data and each States' flounder experts (Table 1). For example, summer flounder in Massachusetts migrate inshore in early May and occur along the entire shoal area south of Cape Cod and Buzzards Bay, Vineyard Sound, Nantucket Sound, and the coastal waters around Martha's Vineyard (Figure 5; Howe *et al*. 1997). They also occur in the shoal waters in Cape Cod Bay (A.B. Howe, Massachusetts Div. of Mar. Fish., Sandwich, MA, personal communication). In some years summer flounder are found along the eastern side of Cape Cod and as far north as Provincetown by early May. The Massachusetts Division of Marine Fisheries considers the shoal waters of Cape Cod Bay and the region east and south of Cape Cod, including all estuaries, bays and harbors thereof, as critically important habitat (Howe, personal communication). Summer flounder begin moving offshore in late September and October and Howe (personal communication) believes that spawning occurs within territorial waters south of Cape Cod because occasional ripe and running fish have been taken there. Summer flounder are regularly taken in southern Massachusetts waters as late as December, presumably as fish are dispersing to offshore wintering grounds, which, in most years are well out on the continental shelf from approximately Veatch Canyon to Baltimore Canyon.

T.R. Lynch (Rhode Island Dept. of Environ. Mgmt., Wickford, RI, personal communication) states that the coastal waters of Rhode Island, the immediate waters surrounding Block Island, and the waters of Little Narragansett Bay and all of Narragansett Bay are habitat for both adults and juveniles. Based on collections from the 1990-1996 Rhode Island Narragansett Bay survey, adults were distributed throughout the Bay and captured in all seasons except winter and most were caught in summer and autumn (Figure 6). The length frequencies show that similar sizes were captured in each season and lengths ranged from about 25-71 cm with most occurring from 30-50 cm (Figure 7). Abundance in relation to bottom depth shows a preference for depths greater than 12.2-15.2 m (40-50 ft) and that few were captured in depths less than 9.1 m (30 ft) (Figure 8).

In Connecticut, E. Smith (Connecticut Dept. of Environ. Prot., Hartford, CT, personal communication) states that the flounder migrate to inshore waters in late April and early May, and are present in Long Island Sound throughout the April-November trawl survey period, and probably occur in limited numbers in winter as well (Figure 9 -- these figures include juveniles and adults, see Figure 10). August through October are often the months of highest relative abundance (Simpson *et al*. 1990a, b, 1991; Gottschall *et al*., in review). Although they occur on all bottom types, their abundance does vary by area and depth (Gottschall *et al*., in review). In April, abundance is similar at all depths, but from May through August abundance is highest in shallow water, especially in depths less than 9 m along the Connecticut shore from New Haven to Niantic Bay, and near Mattituck, New York (Figure 9; Gottschall *et al*., in review). In September, when abundance peaks,

summer flounder are again distributed in all depths throughout the sound. After September, their abundance decreases, and the remaining fish are more common in deeper water. Abundance is highest in depths between 18-27 m in October and depths > 27 m in November (Gottschall *et al.*, in review). Abundance indices within the Sound are generally highest in the central Sound (Connecticut to Housatonic Rivers) and lowest west of the Housatonic River (Simpson *et al*. 1990a, b, 1991). Salinity range appears to be at least 15 ppt and greater. The trawl survey usually takes 400-700 fish in 320 tows per year. In 1989, only 47 fish were taken (D.G. Simpson, Connecticut Dept. of Environ. Prot., Waterford, CT, personal communication). From the Marine Angler Survey, about two-thirds of the sport flounder catch is from east of the Connecticut River, while the trawl survey catches indicate that the greater New Haven area is also important.

In the Hudson-Raritan estuary, New York and New Jersey, summer flounder was the 13th most abundant species in the Wilk *et al*. (1977) survey and it occurred in 21% of all trawls and had a mean annual density in the Lower Bay complex of 1.2/15 min tow (see also reviews by Gaertner 1976 and Berg and Levinton 1985). The 1992-1997 Hudson-Raritan surveys show the adults to be present in moderate numbers throughout the estuary in all seasons except winter (Figure 11). In the fall, they tend to be found in greater numbers in the deeper waters of the Raritan Channel (Figure 11). In the spring, the greatest numbers occurred in Sandy Hook Bay. The greatest densities of summer flounder adults occurred in the summer, particularly in the deeper Raritan and Chapel Hill channels and Raritan and Sandy Hook Bays. This species was not reported in any trawls in the Arthur Kill-Hackensack River estuary. However, it has been collected in Newark Bay from April-October (Wilk *et al*. 1997; Figure 12). Great South Bay, on the south shore of Long Island, supports an important recreational fishery, particularly around Fire Island inlet (Neville *et al*. 1939; Schreiber 1973).

Tagging studies by Murawski (1970) provided recaptured summer flounder from the entire New Jersey coastline. Summer flounder overwinter offshore of New Jersey in 30-183 m of water. Allen *et al*. (1978) collected both adult and juvenile summer flounder in Hereford Inlet near Cape May. They occurred in all of the major waterways, but were more abundant in the upper embayment from May to July and in the lower embayment from August to October. The majority were 200-400 mm and were caught on the slopes of the channels. In Barnegat Bay, an ichthyofauna survey by Vouglitois (1983) from 1976-1980 found a wide range of sizes of summer flounder, but in low numbers. This study was conducted along the western shoreline of the Bay, where muddy sediments predominate, and Vouglitois (1983) suggests that the scarcity of summer flounder is due to their apparent preference for sandy substrates. A hard sandy bottom does predominate in the eastern portion of the Bay and this is where most summer flounder have been caught.

Delaware Bay is an important nursery and summering area for adults as well as a nursery area for juveniles (R. Smith, Delaware Dept. of Nat. Res. and Environ. Control, Dover, DE, personal communication). They are abundant in the lower and middle portions of the estuary, and rare in the upper estuary (Ichthyological Associates, Inc. 1980; Seagraves 1981; Weisberg *et al*. 1996; Michels 1997). Smith and Daiber (1977) caught adults from the shoreline to a maximum depth of 25 m, mostly from May through September, while R. Smith (personal communication) states that adults have been captured in Delaware Bay during all months of the year, but appear to be most common from April to November. The Delaware Bay Coastal Finfish Assessment Survey for 1996 found adults throughout the April to December sampling period, with the highest catch rate in April and greatest occurrences at mid-bay stations (Michels 1997). Delaware's coastal bays are also used by summer flounder as nursery and summering areas [e.g., Indian River and Rehobeth Bays (Michels 1997)].

In Virginia adult flounder use the Eastern Shore seaside lagoons and inlets and the lower Chesapeake Bay as summer feeding areas (Schwartz 1961; J.A. Musick, Virginia Inst. Mar. Sci., Gloucester Point, VA, personal communication). These fish usually concentrate in shallow warm water at the upper reaches of the channels and larger tidal creeks on the Eastern Shore in April, then move toward the inlets as spring and summer progress. They are most abundant in the ocean near inlets by July and August. Tagging studies by Desfosse (1995) revealed that fall migration begins out of Chesapeake Bay in October and is completed by December where most recaptures of fish were from the nearshore fishery from Cape Henry south to Cape Hatteras. The majority of tagged returns during January through March came from offshore from the Cigar north to Wilmington Canyon, and were concentrated east of Cape Henry from the Cigar to Norfolk Canyon. A second group came from inshore waters near Oregon Inlet, south to Cape Hatteras. Movement inshore started in March or perhaps as early as February, and continued from April till June.

Virginia's artificial reefs also provide additional habitat for summer flounder (J. Travelstead, Virginia Mar. Res. Comm., Hampton, VA, personal communication; see also Lucy and Barr 1994). Reef materials include discarded vessels, automobile tires, and fabricated concrete structures.

Both adults and juveniles occur in Pamlico Sound and adjacent estuaries (Figure 13), although it appears that juveniles are usually the more abundant, confirming the significant role of these estuaries as a nursery area for this species (Powell and Schwartz 1977). They occur in areas of intermediate or high salinities, often close to inlets, and prefer a sandy or sand/shell substrate (Powell and Schwartz 1977).

Several surveys have shown that both adult and juvenile summer flounder occur in small numbers in the waters of South Carolina (e.g., Bearden and Farmer 1972; Hicks 1972; Wenner *et al*. 1981, 1986; Stender and Martore 1990; Wenner *et al*. 1990a, b). Artificial reefs also provide habitat

for summer flounder off of South Carolina (Parker *et al*. 1979).

Dahlberg (1972) surveyed the North and South Newport Rivers, Sapelo Sound, and the St. Catherines Sound estuarine complex in Georgia. Adult and juvenile summer flounder were most abundant in the lower reaches of the estuaries and were rarely trawled in the middle reaches.

REPRODUCTION

In the Middle Atlantic Bight, Morse (1981) estimated the length at which 50% of the fish are mature (L_{50}) is 24.6 cm for males and 32.2 cm for females. The smallest mature male was 19.1 cm and the largest immature male was 39.9 cm. Females began maturing at 24.9 cm and the largest immature female was 43.9 cm. The range of L_{50} for males and females indicates sexual maturity is attained by age 2 (Morse 1981; however see below). Adult females are 60 mm total length (TL) longer on average than males at first attainment of sexual maturity. The L_{50} also varied during the six years of Morse's (1981) study. No consistent general trend in L_{50} was evident as males and females appeared to exhibit independent changes. Murawski and Festa (1976) reported that the minimum size at maturity of female summer flounder sampled from off New Jersey during 1963-1964 was 37.0 cm TL, while Smith and Daiber (1977) reported that the minimum size at maturity of fish from Delaware Bay was 30.5 cm and 36.0 cm TL for males and females, respectively. Desfosse (1995) reported the minimum size at maturity of fish sampled from 1987-1989 in Virginia waters was 22-23 cm TL for males and 23-24 cm TL for females. The L_{50} for males was 26.1-27.0 cm TL and 36.1-37.0 cm TL for females. Powell (1974) noted that the minimum size at maturity of summer flounder from Pamlico Sound, North Carolina was 35.0 cm TL. In the South Atlantic Bight, Wenner *et al*. (1990a) estimated the L_{50} to be 28.9 cm TL for males and 30.7 cm TL for females, corresponding to fish approaching age 2. Based on the study by O'Brien *et al*. (1993) on the L_{50} of summer flounder sampled from 1985-1989 from Nova Scotia to Cape Hatteras, this report will use the female size of 28 cm (age 2.5) as the divide between all juvenile and adult individuals. The median length at maturity for males in the O'Brien *et al*. (1993) study was 24.9 cm (age 2). However, as O'Brien *et al*. (1993) notes, a revision to aging convention (Smith *et al*. 1981; Almeida *et al*. 1992) has resulted in median lengths being attained a year earlier than those reported above; thus, for example, the ages of O'Brien *et al*. (1993) are also off by a year (i.e., the age 2.5 female fish are now age 1.5). These conclusions have been supported by more recent growth studies (Able *et al*. 1990; Szedlmayer *et al*. 1992).

Fecundity and length exhibit a curvilinear relationship, but with logarithmic transformations, Morse (1981) expressed the relationship as:

$$\log_{10} \text{Fecundity} = \log_{10} a + b\,(\log_{10} \text{length})$$

where the intercept (a) = -3.098 and the slope (b) = 3.402. The relationship between fecundity and weight and ovary weight were expressed by Morse (1981) as:

$$\text{Fecundity} = a + bX$$

where the intercept (a_{weight}) = -101,865.5 and the slope (b_{weight}) = 908.864, and the intercept ($a_{ovary\ weight}$) = 52,515.161 and the slope ($b_{ovary\ weight}$) = 10,998.048.

Powell (1974) estimated that females ranging from 50.6-68.2 cm TL have 1.67-1.70 million ova per fish, while Morse (1981) reported fish between 36.6 and 68.0 cm TL have 0.46-4.19 million ova. The relative fecundity, number of eggs produced per gram of total weight of spawning female, ranged from 1,077-1,265 in Morse's (1981) study. The increase in variability in fecundity estimates as weight increases tends to obscure the true relationship. The high egg production to body weight is maintained by serial spawning. In fact, the weight of annual egg production, assuming an average egg diameter of 0.98 mm and 1.0 specific gravity, equals approximately 40-50% of the biomass of spawning females (Morse 1981).

Morse (1981) calculated the percent of ovary weight to total fish weight as an index for maturity. The mean maturity index increased rapidly from August to September, peaked in October-November, then gradually decreased to a low in July. The wide range in the maturity indices during the spawning season indicates nonsynchronous maturation of females and a relatively extended spawning season. The length and peak spawning time as indicated by the maturity index agree with results determined by egg and larval occurrence (Herman 1963; Smith 1973).

Spawning occurs over the open ocean areas of the shelf (Figure 14). Summer flounder spawn during the fall and winter while the fish are moving offshore or onto their wintering grounds; the offshore migration is presumably keyed to declining water temperature and decreasing photoperiod during the autumn. The spawning migration begins near the peak of the summer flounder`s gonadal development cycle, with the oldest and largest fish migrating first each year (Smith 1973).

The seasonal migratory/spawning pattern varies with latitude (Smith 1973); i.e., gonadal development, spawning and offshore movements occur earlier in the northern part of their range (Rogers and Van Den Avyle 1983). For example, in Delaware Bay, gonads of summer flounder appear to ripen from mid-August through November (Smith and Daiber 1977), while peak gonadal development occurs during December and January for fish around Cape Hatteras (Powell 1974). Spawning begins in September in the inshore waters of southern New England and the Mid-Atlantic. As the season progresses, spawning moves onto Georges Bank as well as southward and eastward into deeper waters across the entire breadth of the shelf (Berrien and Sibunka 1999).

Spawning continues through December in the northern sections of the Middle Atlantic Bight, and through February/March in the southern sections (Smith 1973; Morse 1981; Almeida *et al*. 1992). Spawning peaks in October north of Chesapeake Bay and November south of the Bay (Smith 1973; Able *et al*. 1990; note that the latter statement on spawning south of the Bay in November appears to contradict the published information above concerning peak gonadal development occurring December-January near Cape Hatteras). The half year spawning season reduces larval crowding and decreases the impact of predators and adverse environmental conditions on egg and larval survival (Morse 1981). In the South Atlantic Bight, maturity observations by Wenner *et al*. (1990a) suggest that spawning begins as early as October, and may continue through February and possibly early March.

EGGS

Eggs of summer flounder are pelagic and buoyant. They are spherical with a transparent, rigid shell; yolk occupies about 95% of the egg volume. Mean diameter of mature unfertilized eggs is 0.98 mm.

Eggs are most abundant between Cape Cod/Long Island and Cape Hatteras (Figures 14 and 15); the heaviest concentrations have been reported within 45 km of shore off New Jersey and New York during 1965-1966 (Smith 1973), and from New York to Massachusetts during 1980-1986 (Able *et al*. 1990). Able *et al*. (1990) discovered that the highest frequency of occurrence and greatest abundances of eggs in the northwest Atlantic occurs in October and November (Figure 15), although, due to limited sampling in December south of New England, December could be under represented. Festa (1974) also notes an October-November spawning period off New Jersey. Keller *et al*. (1999) found eggs (maximum density 19.5/100 m^3) from February to June in Narragansett Bay during a December 1989 to November 1990 sampling period. In southern areas, eggs have been collected as late as January-May (Figure 14; Smith 1973; Able *et al*. 1990).

The eggs have been collected mostly at depths of 30-70 m in the fall, as far down as 110 m in the winter, and from 10-30 m in the spring (Figure 16).

LARVAE

Planktonic larvae (2-13 mm) are often most abundant 19-83 km from shore at depths of around 10-70 m, and are found in the northern part of the Middle Atlantic Bight from September to February, and in the southern part from November to May, with peak abundances occurring in November (Smith 1973; Able *et al*. 1990; Figures 17, 18, 19). The smallest larvae (< 6 mm) were most abundant in the Mid-Atlantic Bight from October-December, while the largest larvae (≥ 11 mm) were abundant November-May with peaks in November-December and March-May (Able *et al*. 1990). Off eastern Long Island and Georges Bank, the earliest spawning and subsequent larval development occurs as early as September (Able and Kaiser 1994). By October, the larvae are primarily found on the inner continental shelf between Chesapeake Bay and Georges Bank. During November and December they are evenly distributed over both the inner and outer portions of the shelf. By January and February the remaining larvae are primarily found on the middle and outer portions of the shelf. By April, the remaining larvae are concentrated off North Carolina (Able and Kaiser 1994).

From October to May larvae and postlarvae migrate inshore, entering coastal and estuarine nursery areas to complete transformation (Table 1; Merriman and Sclar 1952; Olney 1983; Olney and Boehlert 1988; Able *et al*. 1990; Szedlmayer *et al*. 1992). Larval to juvenile metamorphosis, which involves the migration of the right eye across the top of the head, occurs over the approximate range of 8-18 mm SL (Burke *et al*. 1991; Keefe and Able 1993; Able and Kaiser 1994; Figure 20). They then leave the water column and settle to the bottom where they begin to bury in the sediment and complete development to the juvenile stage, although they may not exhibit complete burial behavior until mid-late metamorphosis when eye migration is complete, often at sizes as large as 27 mm SL (Keefe and Able 1993, 1994). However, burying behavior of metamorphic summer flounder is also significantly affected by substrate type, water temperature, time of day, tide, salinity, and presence and types of predators and prey (Keefe and Able 1994).

Keller *et al*. (1999) found larvae (maximum density 1.4/100 m^3) from September to December in Narragansett Bay during a December 1989 to November 1990 sampling period. Able *et al*. (1990) and Keefe and Able (1993) discovered that some transforming larvae (10-16 mm) entered New Jersey estuaries primarily during October-December, with continued ingress through April; Allen *et al*. (1978) collected larvae (12-15 mm) in February and April in Hereford Inlet near Cape May. Dovel (1981) recorded 9 larvae in the lower Hudson River estuary, New York in 1972. In North Carolina, the highest densities of larvae are found in Oregon Inlet in April, while farther south in Ocracoke Inlet, the highest densities occur in February (Hettler and Barker 1993). J.P. Monaghan, Jr. (North Carolina Dept. of Nat. Res. and Commer. Dev., Morehead City, NC, personal communication) mentions that for the years 1986-1988, peak immigration periods of larvae through Beaufort Inlet and into North Carolina estuaries were from late February through March. In the Cape Fear River Estuary, North Carolina, it has been reported that postlarvae first enter the marshes in March and April and are 9-16 mm SL during peak recruitment (Weinstein 1979; Weinstein *et al*. 1980b). Schwartz *et al*. (1979a, b) also notes that age 0 flounder appear in the Cape Fear River between March and May, depending on the year. Warlen and Burke (1990) found larvae (mean 13.1 mm SL) in the

Newport River estuary just inside Beaufort Inlet from February-April, 1986, with peak abundance in early March. Powell and Robbins (1998) reported larval summer flounder adjacent to live-bottom habitats (rock outcroppings containing rich invertebrate communities and many species of tropical and subtropical fishes) in Onslow Bay (near Cape Lookout) in November (at stations of 17-22 m depth), February (28-30 m depth), and May (14-16 m and 17-22 m depth). Burke *et al*. (1998) conducted night-time sampling for transforming larvae and juveniles in Onslow Bay, Beaufort Inlet, and the Newport River estuary in February-March 1995. Although flounders were captured both in Onslow Bay and in the surf zone during the immigration period, densities were low and all were transforming larvae (7-15 mm SL). After the immigration period, flounders were absent, as juveniles were not caught. Within the Newport River estuary, flounders were locally very abundant as compared to within Onslow Bay and initial settlement was concentrated in the intertidal zone. During February most were transforming larvae, in March some were completely settled juveniles (11-21 mm SL). In South Carolina, Burns (1974) captured summer flounder larvae (14.9-17.5 mm) in New Bridge Creek, North Inlet estuary in February-March, while Bearden and Farmer (1972) recorded larvae and postlarvae in Port Royal Sound estuary from January-March. During 1986-1988, Wenner *et al*. (1990a) found that ingress of recently transformed larval and juvenile summer flounder (10-20 mm TL) into Charleston Harbor, South Carolina estuarine marsh creeks began in January and continued through April (Figure 21). Larvae and postlarvae were also found during this period in the Chainey Creek area (Wenner *et al*. 1986).

JUVENILES

As stated above, juveniles are distributed inshore (e.g., Figure 22) and in many estuaries throughout the range of the species during spring, summer, and fall (Table 1; Deubler 1958; Pearcy and Richards 1962; Poole 1966; Miller and Jorgenson 1969; Powell and Schwartz 1977; Fogarty 1981; Rountree and Able 1992a, b, 1997; Able and Kaiser 1994; Walsh *et al*. 1999). During the colder months in the north there is some movement to deeper waters offshore with the adults (Figure 3; Figure 23), although many juvenile summer flounder will remain inshore through the winter months while some juveniles in southern waters may generally overwinter in bays and sounds (Smith and Daiber 1977; Wilk *et al*. 1977; Able and Kaiser 1994). In estuaries north of Chesapeake Bay, some juveniles remain in their estuarine habitat for about 10 to 12 months before migrating offshore their second fall and winter; in North Carolina sounds, they often remain for 18 to 20 months (Powell and Schwartz 1977). The offshore juveniles return to the coast and bays in the spring and generally stay the entire summer.

Fogarty (1981) examined the distribution patterns of prerecruit (≤ 30.5 cm) summer flounder caught during the 1968-1979 spring surveys and found a striking absence of small fish in northern areas. Both spring and autumn bottom trawl survey data indicated that the concentration of young-of-year summer flounder was south of 39^{o} latitude. The importance of the Chesapeake Bight to this species is demonstrated by the fact that almost all of the young-of-year caught during those spring surveys were from this area.

In Mid-Atlantic estuaries, first year summer flounder can grow rapidly and attain lengths of up to at least 30.0 cm (Poole 1961; Almeida *et al*. 1992; Szedlmayer *et al*. 1992). Young-of-the-year summer flounder in New Jersey marsh creeks have average growth rates of 1.3-1.9 mm/d, and increase from about 16.0 cm TL at first appearance in late July to around 26.0 cm by September (Rountree and Able 1992b; Szedlmayer *et al*. 1992). First year fish from Pamlico Sound, North Carolina obtained mean lengths of 16.7 cm for males and 17.1 cm for females (Powell 1982). In Charleston Harbor and other South Carolina estuaries from 1986-1988, Wenner *et al*. (1990a) found transforming larvae were recruited into the estuarine creeks when 1-2 cm TL. Growth accelerated in May and June when they reached modal sizes of 8 and 14 cm TL, respectively. By September, modal size was 16 cm TL and reached from 23-25 cm TL through October and November. Modal lengths of yearlings ranged from 23-25 cm in January through June and generally reached 28 cm by October. In Georgia, lab studies by Reichert and van der Veer (1991) found that juveniles from Duplin River of 28-46 mm SL had a maximum growth rate of about 1.3-1.4 mm/d at laboratory temperatures of 23.7-24.8°C.

Juvenile summer flounder make use of several different estuarine habitats. Estuarine marsh creeks are important as nursery habitat, as has been shown in New Jersey (Rountree and Able 1992b, 1997; Szedlmayer *et al*. 1992; Szedlmayer and Able 1993), Delaware (Malloy and Targett 1991), Virginia (Wyanski 1990), North Carolina (Burke *et al*. 1991) and South Carolina (Bozeman and Dean 1980; McGovern and Wenner 1990; Wenner *et al*. 1990a, b). Other portions of the estuary that are used include seagrass beds, mud flats and open bay areas (Lascara 1981; Wyanski 1990; Szedlmayer *et al*. 1992; Walsh *et al*. 1999).

Patterns of estuarine use by the juveniles can vary with latitude. In New Jersey, nursery habitat includes estuaries and marsh creeks from Sandy Hook to Delaware Bay (Allen *et al*. 1978; Rountree and Able 1992a, b, 1997; Szedlmayer *et al*. 1992; Szedlmayer and Able 1993; B.L. Freeman, New Jersey Dept. of Environ. Prot., Trenton, NJ, personal communication). The juveniles often make extensive use of creek mouths (Szedlmayer *et al*. 1992; Szedlmayer and Able 1993; Rountree and Able 1997). In the Hudson-Raritan estuary, New York and New Jersey, 1992-1997 surveys show the juveniles to be present in small numbers throughout the estuary in all seasons, with slightly higher numbers seen in the spring (Figure 24). In Great Bay, young-of-the-year stay for most of the summer, leaving as early as August and continuing until November-December (Able *et al*. 1990; Rountree and Able 1992a; Szedlmayer

and Able 1992; Szedlmayer *et al.* 1992). As stated previously, Allen *et al.* (1978) collected both adult and juvenile summer flounder (200-400 mm) in Hereford Inlet near Cape May where they occurred in all of the major waterways, but were more abundant in the upper embayment from May to July and in the lower embayment from August to October. Most were caught on the channel slopes.

Smith and Daiber (1977) report that in Delaware Bay, most summer flounder were collected May through September but a few juveniles have been caught in the deeper parts of the Bay in every winter month. The Delaware Bay Coastal Finfish Assessment Survey for 1996 found juveniles throughout their April to October sampling period (Michels 1997).

In Maryland, J.F. Casey (Maryland Dept. of Nat. Res., Ocean City, MD, personal communication) indicated that although the coastal bays are excellent habitat for both adults and juveniles (Schwartz 1961), in areas of significant pollution, a lack of proper food sources precludes the presence of summer flounder. Other areas which lack sufficient water circulation also appear to have considerably reduced populations. Shore-side development and resultant runoff also appear to have reduced some local populations (Casey, personal communication). Since the 1970's, Maryland has been conducting trawl and seine surveys around Ocean City inlet. Casey (personal communication) reported sharp declines in young-of-the-year flounder in the coastal bay trawl samples. The majority of the summer flounder taken in this sampling were between 76 and 102 mm, with larger fish basically absent. Summer flounder were also sometimes found in Maryland's portion of the Chesapeake Bay with the majority of these fish in the 200-300 mm range.

In Virginia, Musick (personal communication) states that the most important nursery areas for summer flounder appear to be in the lagoon system behind the barrier islands on the seaside of the Eastern Shore (Schwartz 1961), and the shoal water flat areas of higher salinity (> 18 ppt) in lower Chesapeake Bay. Young-of-the-year enter these nursery areas in early spring (March and April) and remain there until fall when water temperatures drop. Then these yearlings move into the deeper channel areas and down to the lower Bay and coastal areas. In most winters these age 1+ fish migrate out in the ocean but in warmer winters some may remain in deep water in lower Chesapeake Bay (Musick, personal communication). However, the Virginia Institute of Marine Science juvenile finfish survey for 1995 shows juvenile (as well as some adult) flounder occurring throughout most of the main stem of Chesapeake Bay and the major Virginia tributaries (Rappahannock, York, and James Rivers) over most of the year (Geer and Austin 1996; Figure 25; see also Wagner and Austin 1999). Lower numbers occurred from December-March (Figure 26). Wyanski (1990) found recruitment to occur from November to April on both sides of Virginia's Eastern Shore and from February to April on the western side of Chesapeake Bay. Peak recruitment occurred in November-December on the Eastern Shore, compared to March-April on the western side of the Bay. Wyanski (1990) and Norcross and Wyanski (1988) also found that young-of-the-year occur in a variety of habitats, including shallow, mud bottomed marsh creeks, shallow sand substrates (including seagrass beds), deep sand substrate, and deep fine-sand substrates.

Tagged summer flounder have been recaptured from inshore areas to the northeast of their release sites in subsequent summers, leading to the hypothesis that their major nursery areas are the inshore waters of Virginia and North Carolina, and as they grow older and larger, they would return inshore to areas farther north and east of these nursery grounds (Poole 1966; Murawski 1970; Lux and Nichy 1981). However, tagging studies by Desfosse (1995) indicate that it is not the older and larger fish, but rather the smaller fish (length at tagging) which return to inshore areas north of Virginia. Summer flounder that were recaptured north of their release site in subsequent years were smaller (length at tagging) than those recaptured at their release sites, or to the south, in later years. Desfosse (1995) suggests that while Virginia waters do indeed form part of the nursery grounds for fish which move north in subsequent years, they are primarily a nursery area for fish which will return to these same waters as they grow older and larger.

The estuarine waters of North Carolina, particularly those west and northwest of Cape Hatteras (Monaghan 1996) and in high salinity bays and tidal creeks of Core Sound (Noble and Monroe 1991), provide substantial habitat and serve as significant nursery areas for juvenile Mid-Atlantic Bight summer flounder. Powell and Schwartz (1977) found that juvenile summer flounder were most abundant in the relatively high salinities of the eastern and central parts of Pamlico Sound, all of Croatan Sound (Figure 13), and around inlets. Young-of-the-year disappeared from the catch during late summer, suggesting that the fish are leaving the estuaries at that time (Powell and Schwartz 1977). Upon leaving the estuaries, the juveniles enter the north-south, inshore-offshore migration of Mid-Atlantic Bight summer flounder (Monaghan 1996). Although North Carolina also provides habitat for summer flounder from the South Atlantic Bight, these fish do not exhibit the same inshore-offshore and north-south migration patterns as do Mid-Atlantic Bight fish (Monaghan 1996). Summer flounder > 30 cm are rarely found in the estuaries of North Carolina, although larger fish are found around inlets and along coastal beaches. Powell and Schwartz (1977) also noted that juvenile summer flounder were most abundant in areas with a predominantly sandy or sand/shell substrate, or where there was a transition from fine sand to silt and clay.

Surveys by Hoffman (1991) in marsh creeks in Charleston Harbor, South Carolina showed that recently settled summer flounder were abundant over a wide variety of substrates including mud, sand, shell hash, and oyster bars.

HABITAT CHARACTERISTICS

EGGS

Temperature

Smith (1973) found that eggs were most abundant in the water column where bottom temperatures were between 12 and 19°C; however, eggs were found in temperatures as cold as 9°C and as warm as 23°C. The Northeast Fisheries Science Center (NEFSC) Marine Resources Monitoring, Assessment, and Prediction (MARMAP) ichthyoplankton data from 1978-1987 also shows that the eggs occur at water column temperatures around 11-23°C with peak abundances in the fall at temperatures of around 14-17°C (Figure 27). A temperature increase of 20°C above an acclimation temperature of about 15°C caused no mortality in early embryo stage eggs, but an increase of 16°C for 16 minutes or an increase of 18°C for 2 minutes caused mortality in late embryo stage eggs (Itzkowitz *et al*. 1983). The rate of development is dependent on temperature, with development rate increasing as temperature increases. Embryos held at 16°C developed slower than those at 21°C (Johns and Howell 1980). The incubation period from fertilization to hatching was estimated by Smith (1973) and Smith and Fahay (1970) to vary with temperature as follows: about 142 hours at 9°C; 72-75 hours at 18°C; and 56 hours at 23°C. Other incubation times under experimental conditions were 48-72 hours at 16-21°C and 216 hours at 5°C (Johns and Howell 1980; Johns *et al*. 1981). In another study, summer flounder eggs required 72-96 hours to hatch while incubated at temperatures ranging from 15-18°C (Smigielski 1975). Eggs from Narragansett Bay and Long Island Sound broodstocks incubated at 12.5°C started hatching 85 hours after fertilization, while those incubated at 21°C hatched 60 hours after fertilization (Bisbal and Bengtson 1995c).

Watanabe *et al*. (1999) studied the combined effects of temperature and salinity on eggs from captive summer flounder broodstock in the laboratory, and also showed that higher temperatures and salinities accelerated the rate of embryonic development through hatching. At 16°C and 20°C, the hatching rate was moderate to high at all experimental salinities (22, 27, and 33 ppt). At a higher temperature of 24 °C, hatching rate was high at 33 ppt, but at lower salinities of 22 and 27 ppt, embryonic development and hatching was impaired, indicating a high-temperature–low-salinity inhibition.

Salinity

The studies of Watanabe *et al*. (1998, 1999; see also previous section) suggest that whereas temperature produces marked differences in developmental rates and median hatching time of summer flounder embryos, the effects of salinity on median hatching time are relatively small.

Dissolved Oxygen

No information is available.

Light

Watanabe *et al*. (1998) studied the effects of light on eggs from captive summer flounder broodstock in the laboratory. Although the rate of embryonic development appeared to be faster at higher light intensities, hatching rate was not influenced by light intensity within the range of 0-2,000 lx.

Water Currents

No information is available.

Predation

No information is available.

LARVAE/JUVENILES

Temperature

Larvae have been found in temperatures ranging from 0-23°C, but are most abundant between 9 and 18°C. NEFSC MARMAP ichthyoplankton data from 1977-1987 shows a seasonal shift in offshore larval occurrence with water column temperatures (Figure 28): most larvae are caught at temperatures ≥ 12°C in the fall, from 4-10°C in the winter and from 9-14°C in the spring. Sissenwine *et al*. (1979) found prerecruit summer flounder in the Mid-Atlantic Bight are often most abundant at temperatures in excess of 15°C during the spring, summer and fall, and usually at depths of 40-60 m. Larval flounder have been collected inshore earlier in years with mild winters than in years with severe winters (Cain and Dean 1976; Bozeman and Dean 1980). In the estuaries, transforming larvae (11-17 mm TL) have been collected over a temperature range from -2.0-14°C in Great Bay/Little Egg Harbor in New Jersey (Szedlmayer *et al*. 1992; Able and Kaiser 1994); from 2.1-17.6°C in the lower Chesapeake and Eastern Shore, Virginia (Wyanski 1990); from 2-22°C in North Carolina (Williams and Deubler 1968b); and from 8.4-23.4°C in South Carolina (McGovern and Wenner 1990). Hettler *et al*. (1997) also reported an increase in summer larval abundance with increasing temperatures (7-18°C) in Beaufort Inlet, North Carolina; however, they suggest that unknown factors are probably more important in causing peaks in the abundances of immigrating larvae (see also Hettler and Hare 1998).

Johns and Howell (1980) and Johns *et al*. (1981)

performed experiments on yolk utilization and growth to yolk-sac absorption in summer flounder embryos and larvae. Notochord lengths at hatching were 2.83-3.16 mm SL, with yolk-sac absorption completed at about 3.6 mm SL. For embryos and larvae reared at 21°C, total yolk-sac absorption was complete by 120 h post-fertilization, at 16°C, complete absorption did not occur until 168-182 h, while at 11°C absorption did not occur until 287 h post-fertilization; these development times are similar to those reported by Watanabe *et al*. (1998) for larvae at 19°C. After hatching, total yolk-absorption at 21°C was complete in 67 h, at 16°C it took 105 h, and at 11°C it took 137 h. Larvae reared in cyclic temperature regimes exhibited development rates intermediate to those at temperature extremes of the cycle. All larvae reared at 5°C and in the 5-11°C cycle regime died prior to total yolk-sac absorption. Although incubation temperature had a significant effect on the larval length at hatching, there were no significant differences in the notochord length or yolk utilization efficiency of the larvae at the time of yolk-sac absorption. The similarity in growth and yolk utilization efficiency for larvae reared under these temperature regimes suggests that the physiological mechanisms involved are able to compensate for temperature changes encountered in nature. Larvae are able to acclimate to new temperatures in less than one day (Clements and Hoss 1977).

Watanabe *et al*. (1999), using larvae hatched from eggs obtained from captive broodstock in the laboratory, also showed that development of yolk-sac larvae through first feeding was accelerated by higher temperatures within the range of 16-24°C, consistent with what was previously reported by Johns and Howell (1980) and Johns *et al.* (1981). In all three studies the rate of yolk disappearance (yolk utilization efficiency) was faster at higher temperatures. Watanabe *et al*. (1999) showed that the average time from the first-feeding to when 97% of the yolk-sac was absorbed in unfed larvae ranged from 2.4 to 4.3 times longer at 16°C (18.3 h) than at 20°C (4.3 h) or 24°C (7.7 h). Thus, larvae in 16°C waters may have considerably more time to initiate exogenous feeding before yolk reserves are exhausted [see also the discussion of the Bisbal and Bengtson's (1995c) study, below].

However, contrary to the Johns and Howell (1980) and Johns *et al.* (1981) studies, lower temperatures in the Watanabe *et al*. (1999) study produced larger larvae at the first-feeding and 97% yolk-sac absorption stages. Watanabe *et al*. (1999) state that these dissimilar results are attributable to the modifying influence of salinity, which differed between these studies (see the Salinity section, below). In their study, Watanabe *et al*. (1999) noted a high-temperature–low-salinity inhibition on growth and yolk utilization efficiency, but at a salinity of 33 ppt, there were no temperature-related differences in yolk utilization efficiency. Watanabe *et al*. (1999) suggest this may be consistent with what was observed in the Johns and Howell (1980) and Johns *et al.* (1981) studies, which used seawater of an unspecified salinity.

Further interactions of temperature and salinity in the Watanabe *et al*. (1999) study will be discussed in the Salinity section, below.

Bisbal and Bengtson (1995c) show the interdependence of temperature and food availability (i.e., delay of initial feeding) and their effects on survival and growth of summer flounder larvae hatched from Narragansett Bay and Long Island Sound broodstock. Their laboratory observations occurred from the time of hatching throughout the period of feeding on rotifers. The larvae withstood starvation for longer times at lower temperatures. They possessed sufficient reserves to survive starvation for 11 to 12 days when temperatures were maintained close to the experimentally determined lower tolerance limit (12.5°C; Johns *et al*. 1981). At temperatures close to the highest thermal limit reported to occur in their environment (21°C; Smith 1973), larvae only survived for 6 to 7 days. At either temperature, best survival occurred when the larvae began to feed at the time of mouth opening, thus survival is also significantly affected by the time at which they first have access to exogenous food. At 12.5°C, every treatment group was represented by a low number of survivors which did not grow significantly from the initial figures at mouth opening. Growth of the larvae at 21°C was inversely proportional to the duration of early starvation; the size distribution of the survivors of the 21°C experiment showed an increase in mean size and weight when the initial feeding delay was shorter.

The prevailing temperature conditions influence the duration of metamorphosis of pelagic larvae, with increasing temperatures resulting in a shorter metamorphic period. For example, Keefe and Able (1993) found the time to completion of metamorphosis in wild-caught New Jersey flounder maintained in the laboratory was clearly temperature dependent. While laboratory-reared summer flounder averaged 24.5 days (range 20-32 days) to complete metamorphosis (stage F- to stage I) at ambient spring temperatures of around 16.6°C, wild-caught flounder held in heated water (daily average 14.5°C) advanced metamorphosis over controls kept at ambient winter temperatures (daily average 6.6°C). Total time required to complete metamorphosis in the heated water averaged 46.5 days (range 31-62 days); ambient winter temperature treatments resulted in delayed metamorphosis such that partial metamorphosis (stage H- to stage I) required as much as 92.9 days (range 67-99 days). Burke (1991) found that settling behavior of fish raised at 18-20°C occurred 28 days after hatching, although some took as long as 70 days.

Keefe and Able (1993) also found that mortality during metamorphosis in the laboratory ranged from 17-83% among treatment groups, and was significantly greater in flounder maintained at approximately 4°C relative to those maintained at ambient New Jersey estuarine temperatures of around 10.1°C. They found no apparent effect of starvation on either mortality or time to completion of metamorphosis at cool water temperatures (< 10°C). Szedlmayer *et al*. (1992) examined the temperature-induced mortality of

young-of-the-year, early postmetamorphic (11-15 mm TL) summer flounder collected in New Jersey estuaries from November to May over a temperature range of 0-13°C. Survival of metamorphosing larvae in the laboratory decreased drastically relative to controls when temperatures dropped below 2°C. In trial 1, temperatures dropped steadily from 15-1°C over a 14-day period. Relatively little mortality (2%) occurred up to day 12. However, on days 13 and 14, temperatures dropped below 2°C causing 58% mortality. Temperatures then increased and fluctuated around 5°C but did not drop below 3°C, and during this period, mortality was lower (14%), for a total ambient temperature mortality of 74%. Only 3% total mortality occurred due to rearing environment in the control group, heated to 15°C. During trial 2, in which controls were absent and ambient temperatures did not drop below 2°C, overall mortalities were lower (31% total) and these occurred sporadically.

Malloy and Targett (1991) conducted laboratory experiments on juvenile summer flounder (41-80 mm TL) collected from Delaware to determine low temperature tolerance (2-3°C) and to measure feeding rate, assimilation efficiency, growth rate and growth efficiency at various temperatures. Above 3°C, all the juveniles survived. Mortality was 42% after 16 days at 2-3°C, and was highest in fish < 50 mm TL (1g). Mean specific growth rates were not significantly different between 2 and 10°C, and these rates were not significantly different from zero. Additional mortality probably resulted from low growth rates caused by sub-optimal temperatures (< 10°C). Malloy and Targett (1994a) also demonstrate that mortality of juveniles depends more on the rate of temperature decline than on the final exposure temperature: increased rate of temperature decline leads to decreased survival (lower LT_{50}'s). Their study showed that juveniles from Delaware had greater tolerances for low temperatures (1-4°C) than juveniles from North Carolina.

Malloy and Targett (1994a) showed that under maximum-feeding conditions, juvenile summer flounder (18-80 mm TL) from both Delaware and North Carolina do not exhibit positive growth rates at temperatures < 7-9°C. [They consider this a more precise estimate of maintenance temperature than that reported in their earlier study (Malloy and Targett 1991).] Similarly, Peters and Angelovic (1971) in their laboratory studies of North Carolina juveniles reported predicted growth rates of close to zero at 10°C. Growth rates of juvenile flounder at temperatures above 10°C are similar in studies on Delaware fish by Malloy and Targett (1991) and on North Carolina fish by Peters and Angelovic (1971). Malloy and Targett (1991) showed that mean growth rate increased to 2.4% per day at 14°C and 3.8% per day at 18°C and Peters and Angelovic (1971) demonstrated that specific growth rates of North Carolina juveniles were 5% and 10% per day, at 15 and 20°C, respectively. Both studies showed that feeding rates increased with temperature, ranging from 1.04% body weight per day at 2°C to 23-24% body weight per day at 18°C. Peters and Angelovic (1971) reported an increase in feeding and growth efficiency rates with increasing temperatures to an optimum; beyond that optimum increasing temperatures are detrimental. The optimal temperature in their experiments was 21°C. Mean assimilation efficiency (60.1%) was not affected by temperature in the Malloy and Targett (1991) study. Mean growth efficiency (K_1) for Delaware juveniles was significantly lower at 6°C (-23.1%) than at 14 and 18°C (18.4 and 22.1% respectively) and was highly variable. Malloy and Targett (1994a, b) conclude that North Carolina juveniles had higher maximum growth rates and gross growth efficiencies than Delaware juveniles at temperatures between 6 and 18°C. Growth efficiency accounted for most of these differences in growth rates, because there were no differences in feeding rate or assimilation efficiency. Newly settled juveniles likely remain at settlement sizes for up to 6 months until temperatures are conducive for positive growth (Able *et al*. 1990; Malloy and Targett 1991, 1994b).

Malloy and Targett (1994a) also reported that juveniles from North Carolina and Delaware can survive at least 14 d without food at the 10-16°C temperatures typically found after settlement. However, growth rates are dependent on feeding rate at all temperatures they examined. Growth rates under starvation conditions and maintenance rations do not change between 10-16°C; however, scope for growth increases with temperature. Scope for growth of the North Carolina juveniles was higher than that of the Delaware juveniles between 10-16°C. In another study, Malloy and Targett (1994b) showed that juveniles (18-80 mm TL) from both Delaware and a North Carolina sandy marsh were severely growth limited (< 20% of maximum growth) in May and June when temperatures were 13-20°C. Malloy and Targett (1994a, b) conclude that prey availability is very important to the growth and condition of early juveniles during the months immediately following settlement, and changes in prey abundance may explain the patterns in growth limitation.

Mortality resulting from acute exposure to low temperatures in Mid-Atlantic Bight estuaries probably occurs during a 2 to 4 week period each winter. Szedlmayer *et al*. (1992) hypothesized that year class strength may be affected by winter temperature in New Jersey estuaries, as has been suggested for juveniles by Malloy and Targett (1991) for the Mid-Atlantic Bight as a whole. Recruitment success may be lower in years with late winter cold periods (i.e., March vs. December) due to increased numbers of fish inshore at that time of the year being exposed to lethal low temperatures (Malloy and Targett 1991). Thus, the timing of ingress is critical. However, because Malloy and Targett (1991) found that there was 100% survival at temperatures above 3°C, juveniles are probably able to survive most winter water temperatures encountered throughout Mid-Atlantic Bight estuaries. However, Malloy and Targett (1994a) state that the magnitude of the variability in low temperatures may also be more important to prerecruit mortality than the magnitude of the temperature itself. The

low feeding rates observed at low temperatures in the laboratory and the apparent lack of a starvation effect on low-temperature tolerance suggest that food limitation during winter is less important than the magnitude and variability of temperature minima. They conclude that although low temperatures may contribute to prerecruit mortality south of Cape Hatteras, they are probably more important in more northern nurseries because they persist longer there. In New Jersey, the most probable factors affecting survival of metamorphic summer flounder are the prevailing environmental conditions, especially the timing of ingress relative to estuarine water temperatures and predation (Szedlmayer *et al*. 1992; Keefe and Able 1993; Witting and Able 1993).

Tracking studies by Szedlmayer and Able (1993) in Schooner Creek, near Great Bay and Little Egg Inlet, New Jersey, suggest that tidal movements of juveniles (210-254 mm TL) may be in response to a preferred range of environmental parameters. Although they were collected in a wide range of habitats during their first year (Szedlmayer *et al*. 1992), during the August to September study period, they were found within a narrow range of water temperature (mean 23.5^{o}C) and also dissolved oxygen. Small changes in these parameters may force the fish to move.

Several studies indicate that juvenile summer flounder in Chesapeake Bay may succumb to infections of the hemoflagellate *Trypanoplasma bullocki* at low temperatures (Burreson and Zwerner 1982, 1984; Sypek and Burreson 1983). Effective immune response to the parasite was not noted in natural infections below 10^{o}C (Sypek and Burreson 1983). Therefore, because *T. bullocki* causes mortality of juvenile summer flounder during winter, suggesting that this mortality is temperature dependent, and since no fish with symptoms of the disease have been observed south of Cape Hatteras, Burreson and Zwerner (1984) hypothesize that the presence of the symptoms of this disease in juvenile summer flounder can be used as a measure of mortality north of Cape Hatteras. In addition, increased antibody production in early spring eliminates the infection in the flounder and the recovered fish are immune for at least one year, even if challenged at temperatures as low as 9^{o}C (Burreson and Frizzell 1986).

NEFSC groundfish data shows a seasonal shift in offshore juvenile summer flounder occurrence with bottom temperatures (Figure 29): most juveniles are caught over a range of temperatures from 10-27^{o}C in the fall, from 3-13^{o}C in the winter, from 3-17^{o}C in the spring, and from 10-27^{o}C in the summer. Massachusetts inshore trawl survey data also shows a seasonal shift in juvenile occurrence with bottom temperature (Figure 30). In the spring, most juveniles occur at a range of temperatures from 9-14^{o}C, while in the fall they occur at temperatures from 15-21^{o}C.

Salinity

Watanabe *et al*. (1998) studied the effects of salinity and light intensity on yolk-sac larvae hatched from captive summer flounder broodstock in the laboratory. Significant effects of both salinity and light intensity on larval size were evident at hatching: larvae hatched under 500 lx and salinities of approximately 35 ppt showed maximum values, a trend observed at the first feeding stage. However, in a later study by Watanabe *et al*. (1999), salinity did not influence development and growth rates of yolk sac larvae through the first feeding stage. Watanabe *et al*. (1998) suggest that the differences among the two studies may be attributed to the lower salinity range (22-33 ppt) used in this later study.

Also in the Watanabe *et al*. (1999) study, a high temperature of 24^{o}C, although not greatly influencing larval survival at 33 ppt, markedly impaired survival at the 97% yolk-sac absorption stage when salinities were at 22 and 27 ppt, indicating high-temperature–low-salinity inhibition. Conversely, a low temperature of 16^{o}C enhanced larval survival at these reduced salinities, indicating a low-temperature–low salinity synergistic effect. Watanabe *et al*. (1999) therefore hypothesize that moderate to high survival under all salinities at 16^{o}C reflects an adaptability of the yolk sac larvae to inshore movement during the pelagic larval phase, whereas simultaneous exposure to higher temperatures and reduced salinities may increase mortality and affect year-class strength.

Transforming larvae and juveniles are most often captured in the higher salinity portions of estuaries. In New Jersey, Festa (1974) captured larval summer flounder in salinities of 26.6-35.6 ppt, while in two marsh creeks, larvae occurred at salinities ranging from 20-33 ppt (Able and Kaiser 1994). In the lower Chesapeake Bay, Virginia, young-of-the-year were common in creeks with salinities > 15 ppt and were most abundant at the highest salinities, but were absent in a small tributary of the Poropotank River with salinities 3-11 ppt (Able and Kaiser 1994). In North Carolina, Williams and Deubler (1968a) found postlarval summer flounder in waters ranging from 0.02-35 ppt, with optimal conditions at 18 ppt. In addition, postlarval summer flounder (10-18 mm SL) were captured most frequently at salinities exceeding 7.4 ppt in the Cape Fear River Estuary, North Carolina (Weinstein *et al*. 1980b). However, Turner and Johnson (1973) reported that summer flounder of all ages occurred in the Newport River, North Carolina, at salinities of 3-33 ppt. Data from 1987-1991 trawl surveys from Pamlico Sound show that almost all individuals were collected in the sound while few were found in the adjacent subestuaries with lower salinities such as the Pamlico and Neuse Rivers (Able and Kaiser 1994). M. Street (North Carolina Dept. of Nat. Res. and Commer. Dev., Morehead City, NC, personal communication) mentioned that summer flounder distribution in Pamlico Sound varied in response to salinity changes. In dry years the area of higher salinity

greatly expands in Pamlico Sound, and nursery areas similarly expand. In South Carolina, larvae have been collected at salinities from 0-24.7 ppt (McGovern and Wenner 1990). Recently settled individuals (< 50 cm TL) in the Charleston Harbor estuary occur at both very low and very high salinities from February to March (Figure 31). However by May, individuals 20-100 mm TL are found at higher salinities of > 10 ppt. This suggests that as the flounder disperse in this estuary, they may move up into nearly fresh water, but as they grow they concentrate in the higher salinities of the lower estuary (Wenner *et al*. 1990a; Hoffman 1991; Able and Kaiser 1994).

In an estuarine complex in Georgia, Dahlberg (1972) noted that adult and juvenile summer flounder were most abundant in the higher salinity zones.

Malloy and Targett (1991) found that salinities of 10-30 ppt had no significant effect on feeding, growth, or survival of juvenile summer flounder (41-80 mm TL) in Delaware. However, there was a slight interaction of temperature and salinity on growth rate, suggesting that fish have higher growth rates at high salinities and at high temperatures. This agrees with other laboratory studies which show that larval and juvenile growth rate and growth efficiency are greatest at salinities > 10 ppt (Deubler and White 1962; Peters and Angelovic 1971; Watanabe *et al*. 1998, 1999), although Malloy and Targett (1991) suggest that there appears to be no significant physiological advantage or greater capacity for growth in waters of higher salinities, except at high temperatures. In other laboratory experiments, however, summer flounder grew best at higher salinities and more moderate temperatures, typical of habitats close to the mouths of estuaries (Peters 1971). This could explain why Powell and Schwartz (1977) captured juveniles in the central portions and around inlets of North Carolina estuaries at intermediate to high salinities of 12-35 ppt. Burke (1991) and Burke *et al*. (1991) also found newly settled summer flounder concentrated on tidal flats in the middle reaches of a North Carolina estuary. In the spring, older juveniles moved to high salinity salt marsh habitats. Young-of-the-year in spring were also significantly correlated with salinity (around 22-23 ppt) in eelgrass (*Zostera marina*) beds in the shallow water (1.2 m), high salinity area near Hog Island in Pamlico Sound (Ross and Epperly 1985; it is unclear if this applies to the larger juveniles and adults caught in the study with sizes up to 320 mm). Walsh *et al*. (1999), sampling in the Newport River and Back Sound estuaries adjacent to Beaufort Inlet from April-October 1994, also found that during the spring, larger juveniles (e.g.; 57, 60, 78 mm mean SL) occurred in the high salinities of the lower estuary on sand flats and in channels and along marsh edges.

But Burke (1991) and Burke *et al*. (1991) make it clear that the summer flounder's distribution is due to substrate preference and is not affected by salinity. Malloy and Targett (1991) also suggest that reported distributions of juvenile summer flounder at salinities > 12 ppt are probably the result of substrate and prey availability. In addition, the data of Walsh *et al*. (1999) from the Newport River and Back Sound estuaries suggest that temperature, salinity, turbidity, and substrate type are related to juvenile summer flounder distribution and area of settlement, though they were unable to separate the independent effect of these variables.

Dissolved Oxygen

Klein-MacPhee (1979) measured oxygen consumption rhythms in juvenile summer flounder over a 24 hour period in a flow-through metabolic chamber. The flounder showed a standard metabolic rate cycle, as manifested by oxygen consumption, with maximum consumption occurring between the hours of 2300 and 0100, and a minimum between 1130 and 1300. Oxygen consumption varied inversely with the size of the fish. Mean oxygen consumption was 33.5 mg/kg body weight per hour for 120 g fish; 31.1 mg/kg body weight per hour for 165 g fish; and 22.9 mg/kg per hour for 250 g fish. Comparisons of metabolic rate cycles with activity cycles showed that the pattern was the same (high activity, high oxygen consumption in the dark) but the peaks of the two cycles did not always coincide, and there was less day to day variation in the oxygen consumption cycle.

As reported previously under the temperature section, tracking studies by Szedlmayer and Able (1993) in Schooner Creek, near Great Bay and Little Egg Inlet, New Jersey suggest that tidal movements of juveniles (210-254 mm TL) may be in response to a preferred range of environmental parameters. They were found within a narrow range of water temperature and dissolved oxygen (mean 6.4 ppm), and small changes in these parameters may force the fish to move.

Postlarvae of the closely related southern flounder (*Paralichthys lethostigma*) responded negatively to water with dissolved oxygen concentrations < 3.7 ml/l (or 5.3 mg/l) (Deubler and Posner 1963). The southern flounders also showed no difference in sensitivity to oxygen depletion when subjected to temperatures of 6.1, 14.4 and 25.3^{o}C. Growth rates of young-of-the-year winter flounder (*Pseudopleuronectes americanus*) were significantly reduced for fish exposed to low (2.3 ppm) and diurnally fluctuating (2.5-6.5 ppm; avg. 5.1 ppm) levels of dissolved oxygen (Bejda *et al*. 1992).

Light

As stated previously, Watanabe *et al*. (1998) studied the effects of light intensity and salinity on yolk-sac larvae hatched from captive summer flounder broodstock in the laboratory. Significant effects of both salinity and light intensity on larval size were evident at hatching: larvae hatched under 500 lx and salinities of approximately 35 ppt showed maximum values, a trend observed at the first

feeding stage. Shorter notochord lengths of larvae grown under a light intensity of 2,000 lx compared with 0-1,000 lx is presumably related to higher light-induced activity and energy metabolism. 500 lx appears to be the optimal intensity for culture of eggs and yolk-sac larvae.

Hettler *et al*. (1997) found that larvae inside Beaufort Inlet, North Carolina were more abundant in catches made later in the night, suggesting that they disperse into the water column from the edges and bottom. Night-time sampling by Rountree and Able (1997) at the mouths of marsh creeks in Little Egg Harbor estuary, New Jersey, suggests that young-of-the-year (range 138-390 mm SL) summer flounder make extensive use of these shallow habitats during night-time hours.

White and Stickney (1973) found that late larval and early postlarval summer flounder reared in the laboratory feed well with a surface light intensity of 300-500 foot candles (1 foot candle = 10.76 meter candles). Other laboratory studies by Keefe and Able (1994) in New Jersey suggest that metamorphic flounder exhibit a diel pattern in burying behavior with a higher incidence of burying occurring during the day, with swimming in the water column at night. Klein-MacPhee (1979) showed that, under 12 h light/12 h dark photoperiods, maximum activity by juveniles occurred in the dark and had a bimodal distribution. Peaks occurred at 1900 and 0400 h. Under constant dark regimes, peak activity occurred at 2000 and 0100 with a minor peak at 1200. The free running period was 26 hours. In natural light, major activity occurred at 0300 with minor peaks at 1200 and 1800 h. In constant light, activity was reduced and found to be acyclic. Activity patterns of laboratory juveniles were different from wild adults, the latter being light active. Laboratory studies by Lascara (1981) on juveniles and adults from lower Chesapeake Bay showed that peak feeding activity (search-pursuits/unit time) generally occurred during daylight hours between 0800 and 1200.

Grover (1998) studied the incidence of feeding of oceanic larval summer flounder collected north and east of Hudson Canyon. The incidence of feeding was defined as the percentage of frequency of larvae with prey in their guts, in relation to the total number of specimens examined in a time block. Pelagic larvae began feeding near sunrise; the presence of prey in the guts reached its lowest point at 0400-0599, then dramatically increased at 0600-0759. At 0800-0959, the incidence of feeding was 100%, and throughout daylight remained high until 2000. Full guts were not observed until 1200-1359. Maximum gut fullness was at 1200-1559 and 2000-2159. The only time block in which all larvae contained prey in their guts was at 0800-0959. These observations confirm the visual nature of oceanic larval feeding. The incidence of feeding in estuarine larvae was significantly lower than oceanic larvae at 1800-1959 and 2000-2159.

Surveys in the lower Chesapeake Bay, Virginia (Orth and Heck 1980; see also Lascara 1981) and near Beaufort Inlet, North Carolina (Adams 1976a) show that during daylight hours, juveniles tend to occupy areas in the estuaries that have submerged aquatic vegetation.

Water Currents

Smith (1973) found that larvae did not drift far from spawning areas, and were taken near the eggs. Williams and Deubler (1968a) stated that larvae shorter than 7 mm SL depend on currents for dispersal; however, there are no data that describe relationships between recruitment to nursery areas and wind-driven (Ekman) transport or prevailing directions of water flow. Greater densities of young fish were found in or near inlets, and greater numbers were captured during periods of the full moon (Williams and Deubler 1968a). Young-of-the-year summer flounder have been found in high concentrations around the mouths of tidal creeks (Szedlmayer *et al*. 1992; Szedlmayer and Able 1993; Rountree and Able 1997). This could serve to maximize energy efficiency, as the creek mouths are often areas of reduced current speed.

Laboratory experiments by Keefe and Able (1994) in New Jersey indicated an increase in burying behavior by early metamorphic summer flounder on a flood tide. Although this may represent a mechanism that allows the flounder to remain in favorable habitats, field studies by Burke *et al*. (1998) showed that during flood tides in Beaufort Inlet, North Carolina, the highest densities of transforming larvae occurred at mid-depths within the water column, while during ebb tide, the highest densities were at the bottom. Their position in the water column was dependent on tidal stage, and there was a shift in their distribution and abundance which was associated with the shift in tidal stage. However, the increase in the numbers of flounders in the water column occurred around slack tide, and preceded the rise in salinity which followed the onset of flood tide (Burke *et al*. 1998).

Dispersal in areas having strong tidal currents may be accomplished by diel vertical migrations that result in tidal transport (Weinstein *et al*. 1980a; Burke 1991; Burke *et al*. 1991; Burke *et al*. 1998). The shift in vertical distribution with tidal stage observed by Burke *et al*. (1998) in Beaufort Inlet indicates that flounders in Onslow Bay enter the estuary by tidal stream transport. In the laboratory, Burke *et al*. (1998) discovered that wild-caught G-H stage larvae had a regular pattern of activity correlated with the tidal cycle, and peak activity was associated with the time of ebb tide. Interestingly, laboratory-reared flounder had no clear pattern of activity. The observed tidal rhythm of activity of the wild-caught flounder, coupled with field observations that they appear to make the vertical shift into the water column during slack tide (see previous paragraph) when current velocities are low, suggests that there is a behavioral component to their tidal stream transport (Burke *et al*. 1998). The high activity during ebb tide seen in the laboratory suggests that the most active behavioral component of tidal stream transport involves avoidance of

advection by the ebbing tide rather than movement into the water column and transport by the flood tide (Burke *et al*. 1998). Burke *et al*. (1998) also hypothesize that a change in behavior necessary for development of a tidal rhythm occurs during the eye migration phase of metamorphosis. The lack of a tidal activity pattern seen in laboratory-reared flounder suggests that development of a tidal rhythm is dependent on exposure to physical variables that are correlated with the tide.

Tidal transport of young-of-year summer flounder has also been shown to occur in a New Jersey marsh creek (Szedlmayer and Able 1993). Fish moved up the creek on flood tides and down the creek with ebb tides. Rountree and Able (1992b) and Szedlmayer and Able (1993) hypothesize that tidal movements of summer flounder in marsh creeks are the result of both foraging behavior and behavioral homeostasis (e.g., behavioral thermoregulation). Stomach fullness of fish captured leaving the creeks on ebb tides was significantly greater than that of fish captured entering the creeks on flood tides, suggesting that summer flounder undergo tidal movements to take advantage of high concentrations of prey available in the creeks. Although the flounder were found in a wide range of temperatures, salinities and dissolved oxygen concentrations, they generally stayed within narrow limits of these parameters. Thus, movements may be related to the avoidance of environmental extremes.

Substrate/Shelter

Powell and Schwartz (1977) state that benthic substrate appears to influence juvenile summer flounder and southern flounder distributions in Pamlico Sound and adjacent estuaries, North Carolina. Summer flounder were dominant in sandy substrates or where there was a transition from fine sand to silt and clay, while southern flounder were dominant in muddy substrates. Turner and Johnson (1973) also note juvenile summer flounder occur more frequently over sandy substrates than mud or silt bottoms in Pamlico Sound. Burke (1991) and Burke *et al*. (1991) demonstrated in their North Carolina study that it is salinity which affects the distribution of southern flounder while the most important factor affecting the distribution of summer flounder is substrate type. Their data indicated that the highest probability of encountering juvenile summer flounder occurred on mixed to sandy substrates.

Walsh *et al*. (1999), who collected juveniles only during the spring and summer in estuaries adjacent to Beaufort Inlet from April-October 1994, also noted the same species-specific preferences in the type of marsh edge habitat occupied. Juvenile southern flounder were more abundant in the low salinity upper estuary on muddier substrates, while summer flounder juveniles were more abundant at higher salinities and on sandier substrates. However, regarding juvenile summer flounder abundances alone, they found no significant differences across the various habitat types within the estuaries. Indeed, during both seasons, but particularly in the spring, higher abundances of recently recruited juveniles were found along marsh edges in mud substrate. Lower numbers were found on sand flats and channels in the lower estuary. There was, however, evidence of size-specific habitat segregation during the spring, with the larger juveniles (e.g.; 57, 60, 78 mm mean SL) occurring in those sand flats and channels in the lower estuary. As stated above, although the data of Walsh *et al*. (1999) suggest substrate type, along with temperature, salinity, and turbidity are related to juvenile distribution and area of settlement, they were unable to separate the independent effect of these variables.

Juveniles make extensive use of marsh creeks (Wyanski 1990; Burke *et al*. 1991; Malloy and Targett 1991; Rountree and Able 1992b, 1997; Szedlmayer *et al*. 1992; Szedlmayer and Able 1993) as well as other estuarine habitats. For example, as stated previously, surveys by Hoffman (1991) in marsh creeks in Charleston Harbor, South Carolina also showed that recently settled summer flounder were abundant over a wide variety of substrates including mud, sand, shell hash, and oyster bars. In Virginia, Wyanski (1990) and Norcross and Wyanski (1988) found newly recruited juvenile summer flounder in shallow, mud bottomed marsh creek habitat until they were 60-80 mm TL in late spring, at which time they were on shallow sand substrates (including seagrass beds), deep sand substrate, and deep fine-sand substrates. Although Keefe and Able (1994) found that metamorphic and juvenile summer flounder collected from Great Bay-Little Egg Harbor estuary in southern New Jersey showed a preference for sandy substrates in the laboratory, studies by Szedlmayer *et al*. (1992) and Rountree and Able (1992a, 1997) show that in southern New Jersey they also occur abundantly in marsh creeks with soft mud bottoms and shell hash.

Substrate preferences of metamorphic and juvenile summer flounder, as well as burying behavior, may be correlated to the presence and types of predators and prey (Keefe and Able 1994). For example, in North Carolina estuaries, Burke (1991) suggests the preferred habitat of summer flounder appears to be in the mid-estuary, which also appears to correspond to high densities of their principal prey. This in spite of the fact that Burke (1991) also demonstrated that metamorphosing larvae raised in the lab exhibit substrate preferences that correspond to the habitat of older flounders in the wild, preferring sand whether benthic prey species were present or excluded from test substrates. Timmons (1995) also reported a preference for sand by juvenile (7.6-24.9 cm TL) summer flounder from the south shores of Rehobeth and Indian River Bays, Delaware, but in addition the flounder were captured near large aggregations of the macroalgae *Agardhiella tenera* only when large numbers of their principal prey, the grass shrimp *Palaemonetes vulgaris*, were present. Timmons (1995) suggests that the summer flounder are attracted to the algae because of the presence of the shrimp, but remain near the sand to avoid predation (“edge effect”). Indeed, in her

laboratory experiments, the juvenile summer flounder did not show a preference for the macroalgae, and in caging experiments, blue crabs were least able to prey on the flounder in cages with sand bottoms only, but had an advantage in capturing the flounder in cages containing macroalgae. Similar results have been reported in laboratory experiments by Lascara (1981) on larger juveniles and adults from lower Chesapeake Bay. Flounder appeared to utilize submerged aquatic vegetation (eelgrass) as a "blind", they lie-in-wait along the vegetative perimeter, effectively capturing prey (in this case, juvenile spot, *Leiostomus xanthurus*) which moved from within the grass. In the absence of the eelgrass, the spot visually detected and avoided the flounder; the flounder therefore consumed fewer spot on average in the non-vegetated treatment than in the vegetated treatments. Therefore, Lascara (1981) concludes that the ambush tactics of summer flounder are especially effective when the flounder are in patchy habitats where they remain in the bare substrate (sand) between eelgrass patches. Lascara (1981) also noted that if flounder remained within densely vegetated areas, they would probably be conspicuous to prey. As the flounder moved through the vegetation in his laboratory experiments, the grass blades were matted down and essentially "traced out" their body shape. The flounder might also be conspicuous to potential predators as well, again suggesting the "edge effect" hypothesis of Timmons (1995). Thus, flounder remain near the sand to both avoid predation and conceal themselves from prey.

Other studies have shown that summer flounder use vegetated habitats. Adams (1976a) reported the occurrence of juvenile summer flounder in eelgrass meadows near Beaufort, North Carolina during the summer; YOY juveniles in spring also appeared to favor the eelgrass beds in the shallow water (1.2 m), high salinity (means 22-28 ppt) area near Hog Island in Pamlico Sound (Ross and Epperly 1985). *Paralichthys* spp. in the eelgrass communities near Beaufort, North Carolina collectively accounted for about 1% of the annual production and respiration of the fish assemblage (Thayer and Adams 1975; Adams 1976b). Hettler (1989) also reported juveniles in North Carolina salt marsh cordgrass habitat during flood tides. Orth and Heck (1980) and Heck and Thoman (1984) indicated that summer flounder used similar shallow vegetated areas during daylight in Chesapeake Bay; Lascara (1981) reports that juvenile and adult flounder entered and fed in these same areas. In a Virginia tidal marsh creek prior to late summer, juveniles were randomly distributed, but in late summer and early fall, they were more abundant in the adjacent seagrass beds (Weinstein and Brooks 1983). These data indicate that grass bed habitats are important to summer flounder, and any loss of these areas along the Atlantic seaboard may affect flounder stocks (Rogers and Van Den Avyle 1983). In the inland bays of Delaware, Timmons (1995) suggests that macroalgal systems appear to act as ecological surrogates to seagrass beds and seagrass/macroalgal systems as described by various authors. As with seagrass systems that attract juveniles when the submerged aquatic vegetation (SAV) increases from June to September, so does the macroalgae attract summer flounder, because, as stated previously, the macroalgae attracts their prey. This may also be true for Great Bay and Little Egg Harbor in southern New Jersey. Szedlmayer and Able (1996) report that juvenile and adult summer flounder (140-416 mm SL) were associated with the station considered to be a sea lettuce (*Ulva lactuca*) macroalgae habitat.

Conversely, also in Great Bay-Little Egg Harbor, Keefe and Able (1992) determined habitat quality as measured by relative growth of juvenile summer flounder (17-41 mm SL). Growth did not appear to be related to the habitats tested, including eelgrass and adjacent unvegetated substrate, macroalgae (*Ulva*) and adjacent unvegetated substrate, and marsh creek. The fastest growth occurred in shallow bays and marsh creeks. However, Malloy and Targett (1994b) suggest that juvenile growth is related to substrate or habitat in the Newport River estuary, North Carolina because of the presence of specific prey items. The growth limitation of juveniles (18-80 mm TL) in one sandy-marsh habitat could be explained by the low abundance of mysids from May into summer, while the increasing abundance of other prey (polychaetes and amphipods) during that same month at a muddier site may account for favorable growth seen there. Other diet studies in this estuary (Burke 1991, 1995; Burke *et al*. 1991) suggest that polychaetes are actually the preferred prey for juveniles of this size (see the Food Habits section below).

Food Habits

The timing of peak spawning in October/November coincides with the breakdown of thermal stratification on the continental shelf and the maximum production of autumn plankton which is characteristic of temperate ocean waters of the northern hemisphere, thus assuring a high probability of adequate larval food supply (Morse 1981).

Initiation of feeding is a function of the rate and efficiency at which yolk-sac material is consumed, which in turn is dependent on incubation temperature. As reported previously by Johns and Howell (1980) and Johns *et al*. (1981), total yolk-absorption was complete in 67 h and 105 h at 21^{o}C and 16^{o}C, respectively. Within those 3 to 4 days from hatching, summer flounder larvae complete the morphological differentiation of the digestive tract, jaw suspension, and accessory organs necessary for independent exogeneous feeding (Bisbal and Bengtson 1995b).

To repeat the results of the Bisbal and Bengtson (1995c) study: they show the interdependence of temperature and food availability (i.e., delay of initial feeding) and their effects on survival and growth of summer flounder larvae hatched from Narragansett Bay and Long Island Sound broodstock. Their laboratory observations occurred from the time of hatching throughout the period of feeding on rotifers. The larvae withstood starvation for

longer times at lower temperatures. They possessed sufficient reserves to survive starvation for 11 to 12 days when temperatures were maintained close to the experimentally determined lower tolerance limit (12.5°C; Johns *et al*. 1981). At temperatures close to the highest thermal limit reported to occur in their environment (21°C; Smith 1973), larvae only survived for 6 to 7 days. At either temperature, best survival occurred when the larvae began to feed at the time of mouth opening, thus survival is also significantly affected by the time at which they first have access to exogenous food. At 12.5°C, every treatment group was represented by a low number of survivors which did not grow significantly from the initial figures at mouth opening. Growth of the larvae at 21°C was inversely proportional to the duration of early starvation; the size distribution of the survivors of the 21°C experiment showed an increase in mean size and weight when the initial feeding delay was shorter.

Bisbal and Bengtson (1995a) also determined the nutritional status of lab raised larvae and juveniles from the same areas. Mortality due to starvation occurs later in the older ontogenetic states; i.e., 60 h in 6 day old larvae, 72 h in 16 day old larvae, 8 d in 33 day old larvae, and 10 d in 60 day old juveniles at a temperature of around 19°C.

In the laboratory, Peters and Angelovic (1971) reared postlarvae on a diet of zooplankton (mostly copepods) and *Artemia* nauplii; Buckley and Dillmann (1982) also used *Artemia* for their larval feeding experiments. The larvae exhibited an exponential increase in daily ration with age and a linear increase with weight (Buckley and Dillmann 1982). Other investigators have raised larvae on rotifers (e.g., Bisbal and Bengtson 1995c).

Previous studies have inferred that larval and postlarval summer flounder initially feed on zooplankton and small crustaceans (Peters and Angelovic 1971; Powell 1974; Morse 1981; Timmons 1995). Grover (1998) studied the food habits of oceanic larval flounder collected north and east of Hudson Canyon. The diets of all stages of larvae were dominated by immature copepodites. The size of other prey was directly related to larval size. Preflexion larvae (1.9-6.9 mm SL) fed on, in order of importance: immature copepodites, copepod nauplii, and tintinnids, as well as bivalve larvae and copepod eggs. Flexion larvae (3.7-7.2 mm SL) fed on immature copepodites (mostly calanoids) and adult calanoid copepods. Premetamorphic (4.8-7.6 mm SL) and metamorphic (5.8-9.0 mm SL) larvae also fed on immature copepodites, but adult calanoid copepods (mostly *Centropages typicus*) and appendicularians were also prey items.

Studies on the food habits of late larval and juvenile estuarine summer flounder reveal that while they are opportunistic feeders and differences in diet are often related to the availability of prey, there also appears to be ontogenetic changes in diet. Smaller flounder (usually < 100 mm) seem to focus on crustaceans and polychaetes while fish become a little more important in the diets of the larger juveniles. In Great Bay-Little Egg Harbor estuary, New Jersey, Grover (1998) found that the primary prey of metamorphic (8.1-14.6 mm SL) summer flounder was the calanoid copepod *Temora longicornis*, indicating pelagic feeding. Evidence of benthic feeding was observed only in late-stage metamorphic flounder (H+ and I), where the prey included polychaete tentacles, harpacticoid copepods, and a mysid. Incidence of feeding, defined as the percentage of frequency of larvae with prey in their guts, in relation to the total number of specimens examined in a time block, declined as metamorphosis progressed, from 19.1% at stage G to 2.9% at stage I. Rountree and Able (1992b) also discovered that young-of-year summer flounder in Great Bay-Little Egg Harbor marsh creeks preyed on creek fauna in order of abundance (Rountree and Able 1992a): Atlantic silversides (*Menidia menidia*), mummichogs (*Fundulus heteroclitus*), grass shrimp (*Palaemonetes vulgaris*), and sand shrimp (*Crangon septemspinosa*) contributed most importantly to their diets. Seasonal shifts in diet reflected seasonal changes in creek faunal composition, and Rountree and Able (1992a) note that the maximum abundance of young-of-year summer flounder in August coincided with the peak in Atlantic silverside abundances. In Little Egg Harbor estuary, New Jersey, Festa (1979) reported that fish, including anchovies, sticklebacks and Atlantic silversides, comprised 32.6% of the diet volume of 6-24 cm summer flounder. The fish component was supplemented by mysid and caridean shrimp, of which the sand shrimp *Crangon septemspinosa* was of somewhat more importance.

Timmons (1995) reported that juvenile (7.6-24.9 cm TL) summer flounder from Rehobeth Bay, Delaware, fed mostly on the shrimp *Palaemonetes vulgaris* as well as porturid and blue crabs. Flounder from Indian River Bay fed mostly on mysids.

Postlarvae (10.5-14.2 mm SL) in Chesapeake Bay have been found with guts full of the mysid *Neomysis americana* (Olney 1983). In Magothy Bay, Virginia, small summer flounder (4.2-19.8 cm) also fed mainly on *Neomysis americana*, but in addition, consumed larger proportions of amphipods, small fishes, small gastropod mollusks, and plant material than the larger fish (Kimmel 1973). Wyanski (1990) found that mysids were also the dominant prey of 100-200 mm TL summer flounder in the lower Chesapeake Bay and Eastern Shore of Virginia. Lascara (1981) reported that larger juveniles and adults (avg. length 27.4 cm SL) from lower Chesapeake Bay fed on juvenile spot (*Leiostomus xanthurus*), pipefish (*Syngnathus fuscus*), the mysid *Neomysis americana*, and shrimps (*P. vulgaris*, *C. septemspinosa*).

Burke (1991, 1995) in his North Carolina field surveys in the Newport and North Rivers discovered that late larval and early juvenile summer flounder are active infaunal predators. Prey of summer flounder during the immigration period (11-22 mm SL) consisted of common estuarine crustaceans including harpactacoid copepods, polychaetes, and parts of infaunal animals such as polychaete tentacles (primarily from the dominant spionid *Streblospio benedicti*) gills and clam siphons (Figure 32). The appendages of

benthic animals appear to be the most important prey item for postlarval flounders. The increasing importance of polychaetes and clam siphons was suggested with development, while feeding on harpactacoid copepods and amphipods was independent of stage. For juveniles 20-60 mm SL, polychaetes, primarily spionids (*S. benedicti*), were the most important part of the diet (Figure 32). Burke (1991, 1995) suggests that the distribution of these dominant polychaetes may influence the distribution of summer flounder in this estuary and could explain the movement of juvenile summer flounder into marsh habitat [Burke *et al*. 1991; note the Malloy and Targett (1994b) study mentioned in the Substrate section, above]. Other prey items for this size class of summer flounder included invertebrate parts, primarily clam siphons; shrimp, consisting of the mysids *Neomysis americana* and palmonid shrimp; calanoid copepods, primarily *Paracalanus*; amphipods of the genus *Gammarus*; crabs, primarily *Callinectes sapidus*; and fish. Powell and Schwartz (1979) reported that larger juvenile (100-200 mm TL) summer flounder feed mainly on mysids (mostly *Neomysis americana*) and fishes throughout the year in Pamlico Sound, North Carolina (Figure 33). Mysids were found in relatively greater quantities in the smaller flounder, but as their size increased, the diet consisted of shrimps and fishes in similar quantities.

In South Carolina, Wenner *et al*. (1990a) reported that juveniles between 50-125 mm TL consumed only mysids and caridean shrimps (*Palaemonetes* sp., *P. pugio*, *P. vulgaris*). The importance of fish (mostly bay anchovy, *Anchoa mitchilli*, and mummichogs) in the diet increased as summer flounder size increased.

In Georgia, Reichert and van der Veer (1991) found that juveniles from the Duplin River of around < 40 mm SL fed principally on harpacticoid copepods; they also report that *Paralichthys* species > 25 mm fed on increasing numbers of other crustaceans including mysids, crabs, *Palaemonetes*, as well as polychaetes. Summer flounder > 100 mm also fed on fish.

Co-occurring Species and Predation

In Great Bay-Little Egg Harbor estuary in southern New Jersey, a survey by Witting *et al*. (1999) from 1989-1994 showed that the fall larval fish assemblage was more diverse than any of the other seasonal assemblages, with strong representation by summer flounder, Atlantic menhaden (*Brevoortia tyrannus*), Atlantic croaker (*Micropogonias undulatus*), bay anchovy, and a few other species.

Larval and juvenile summer flounder undoubtedly are preyed upon until they grow large enough to fend for themselves. Results of food habit studies by NEFSC from 1969-1972 showed that Pleuronectiformes occurred in the stomachs of the following piscivores: spiny dogfish, goosefish, cod, silver hake, red hake, spotted hake, sea raven, longhorn sculpin, and fourspot flounder (Bowman *et al*. 1976). These data do not indicate the proportion of summer flounder among the flatfish prey taken, but it is likely that they are represented.

Following a thermal shock of 10^{o}C above an acclimation temperature of 15^{o}C, larvae were actually less susceptible to predation by striped killifish (*Fundulus majalis*) than control larvae (Deacutis 1978).

Witting and Able (1993), working in the laboratory with 11-16 mm TL transforming larvae from Great Bay-Little Egg Harbor, New Jersey, suggest that these small summer flounder are vulnerable to predation by a large size range of *Crangon septemspinosa* (around 10-50 mm TL) in New Jersey's estuaries. Laboratory experiments by Keefe and Able (1994) in New Jersey demonstrated that predation on metamorphic summer flounder influences burying behavior and perhaps substrate preference. The type and abundance of predators could determine whether a metamorphic summer flounder stays in the substrate or the water column. For example, Keefe and Able's (1994) experiments showed that buried *C. septemspinosa* may reduce burying by the flounder, while pelagic mummichogs may cause more burying by the flounder during the day.

Timmons (1995) reports a preference for sand by juvenile (7.6-24.9 cm TL) summer flounder from the south shores of Rehobeth Bay and Indian River Bay, Delaware. In her study, the flounder were captured near large aggregations of the macroalgae *Agardhiella tenera* only when large numbers of their principal prey, the shrimp *Palaemonetes vulgaris*, were present. Timmons (1995) suggests that the summer flounder are attracted to the algae because of the presence of the shrimp, but the flounder remain near the sand to avoid predation ("edge effect"). Indeed, in her laboratory experiments, the juvenile summer flounder did not show a preference for the macroalgae, and in caging experiments, blue crabs were least able to prey on the flounder in cages with sand bottoms only, but had an advantage in capturing the flounder in cages containing macroalgae. Laboratory studies by Lascara (1981) on flounder from lower Chesapeake Bay also suggest that in patchy seagrass/sand habitats, the flounder may avoid predation by staying in the sand near the seagrass beds, rather than in the grass beds themselves.

Lab studies in Georgia by Reichert and van der Veer (1991) on juveniles from the Duplin River found potential predators to be blue crabs (*Callinectes* spp.) and sea robins (*Prionotus* spp.).

ADULTS

Temperature

NEFSC groundfish data shows a seasonal shift in offshore adult summer flounder occurrence with bottom temperatures (Figure 34): most adults are caught over a range of temperatures from 9-26^{o}C in the fall, from 4-13^{o}C

in the winter, from 2-20°C in the spring, and from 9-27°C in the summer. Massachusetts inshore trawl survey data also shows a seasonal shift in adult occurrence with bottom temperature (Figure 30). In the spring, most adults occur at a range of temperatures from 6-17°C, while in the fall they occur at temperatures from 14-21°C. Prior to 1979, Sissenwine *et al*. (1979) reported that NEFSC trawl surveys on the continental shelf showed that the distribution of summer flounder by depth was related to their temperature distribution. During spring they were distributed widely over the continental shelf, from 0-360 m depth (compare with Figure 4), and primarily in waters between 8-16°C. During summer the flounder were primarily captured in depths of less than 100 m, and in waters between 15-28°C. The autumn distribution was also at depths of less than 100 m and temperatures between 12-28°C. During winter, they generally were found at depths greater than 70 m, and at temperatures between 5-11°C (Sissenwine *et al*. 1979).

Based on collections from the 1990-1996 Rhode Island Narragansett Bay survey, adults were distributed throughout the Bay and captured in all seasons except winter; in spring they were found in bottom temperatures above 6°C and below 15°C in autumn (Figure 35). By summer the adults occurred at nearly all temperatures and in autumn they were concentrated where temperatures exceeded 17°C.

In the Mid-Atlantic Bight north of Chesapeake Bay, spawning and the offshore limits of migration coincide with the inshore edge of the mass of cold bottom water that disappears along with the thermocline in November (Smith 1973).

A study by Stolen *et al*. (1984a) compared the effect of temperature on the humoral antibody formation in the summer and winter flounder at 8, 12 and 17°C during the same time of the year. Summer flounder showed only a delay in the appearance of circulating antibody at lower temperatures while winter flounder showed both a delay and a marked suppression at lower temperatures. Summer flounder produced a high titered antibody that persisted over a long period of time and over a wide temperature range, while in winter flounder antibody levels began decreasing after one month.

A similar study on the kinetics of the primary immune response in summer flounder was also studied by Stolen *et al*. (1984b). The flounder produced antibody over a wide range of environmental temperatures ranging from 7.5-27°C. At the lower environmental temperatures, a corresponding delay in the appearance of circulation antibody occurred, although the magnitude and duration of the response was not appreciably affected. After immunizing at 12°C, lowering the environmental temperature gradually to 8°C did not appear to inhibit an ongoing primary response. Typical secondary responses were seen in fishes kept at warmer temperatures, but when the temperature was lowered to 8°C, no anamnestic response was seen. Individual variation was most noticeable at middle temperature ranges.

Salinity

Adult summer flounder return inshore to coastal waters in April through June, and are often found in the high salinity portions of estuaries [e.g., Abbe (1967) in Delaware, Tagatz and Dudley (1961) and Powell and Schwartz (1977) in North Carolina; Dahlberg (1972) in Georgia]. However, the adult summer flounder's distribution may be due more to substrate preference than salinity preference.

Dissolved Oxygen

Effects of dissolved oxygen concentration on summer flounder adults has not been investigated (Rogers and Van Den Avyle 1983). Festa (1977) reported that the high variability in catch rates of summer flounder off of New Jersey in the summer of 1976 appeared to be directly related to the movement of an anoxic water mass present that year. Large numbers of summer flounder were forced into inlets and bays where they were more concentrated and vulnerable to the sport fishery (Freeman and Turner 1977).

Light

Laboratory studies (Olla *et al*. 1972; Lascara 1981) and field collections (Orth and Heck 1980) indicate that adult summer flounder are active primarily during daylight hours. To repeat what was stated above for juveniles: laboratory studies by Lascara (1981) on juveniles and adults from lower Chesapeake Bay showed that peak feeding activity (search-pursuits/unit time) generally occurred during daylight hours between 0800 and 1200.

Water Currents

No information is available.

Substrate/Shelter

Adults have often been reported as preferring sandy habitats (Bigelow and Schroeder 1953; Schwartz 1964; Smith 1969). For example, in Pamlico Sound, North Carolina, Powell and Schwartz (1977) found that summer flounder were most abundant at stations where quartz sand or coarse sand and shell predominated. In Barnegat Bay, New Jersey, Vouglitois (1983) suggests that both juvenile and adult summer flounder are found in greater numbers in the eastern portion of the Bay, where sandy sediments predominate. However, adults can camouflage themselves via pigment changes to reflect the substrate (Mast 1916). Thus, they can be found in a variety of habitats with both mud and sand substrates, including marsh creeks, seagrass

beds, and sand flats (Bigelow and Schroeder 1953; Dahlberg 1972; Orth and Heck 1980; Lascara 1981; Rountree and Able 1992a).

As previously explained above in the Section on juveniles, laboratory experiments by Lascara (1981) on larger juveniles and adults from lower Chesapeake Bay found that flounders appear to utilize eelgrass beds as 'blinds'; i.e., they lie-in-wait along the vegetative perimeter, effectively capturing prey which move from within the grass. Lascara (1981) concludes that the ambush tactics of summer flounder are especially effective when the flounder are in patchy habitats where they remain in the bare substrate (sand) between eelgrass patches. Lascara (1981) also noted that if flounder remained within densely vegetated areas, they would probably be conspicuous to prey because, in his laboratory experiments, as the flounder moved through the vegetation, the grass blades were matted down and essentially "traced out" their body shape. The flounder might also be conspicuous to potential predators as well, suggesting the "edge effect" hypothesis of Timmons (1995). Thus, the flounder remain near the sand to both avoid predation and conceal themselves from prey.

Food Habits

Adult summer flounder are opportunistic feeders with fish and crustaceans making up a significant portion of their diet (Figure 36). Differences in diet between habitats or locations may be due to prey availability. The flounder are most active during daylight hours and may be found well up in the water column as well as on the bottom (Olla *et al*. 1972). Included in their diet are: windowpane (Carlson 1991), winter flounder, northern pipefish, Atlantic menhaden, bay anchovy, red hake, silver hake, scup, Atlantic silverside, American sand lance, bluefish, weakfish, mummichog, rock crabs, squids, shrimps, small bivalve and gastropod mollusks, small crustaceans, marine worms and sand dollars (Hildebrand and Schroeder 1928; Ginsburg 1952; Bigelow and Schroeder 1953; Poole 1964; Smith and Daiber 1977; Allen *et al*., 1978; Langton and Bowman 1981; Curran and Able 1998).

In Little Egg Harbor estuary, New Jersey, Festa (1979) reports that at least seven species of fish occurred in the stomachs of 25-65 cm summer flounder. These included Atlantic silversides, anchovies, sticklebacks, silver perch, sea robins, winter flounder and pipefish. Fish remains comprised 74.3% of the diet volume. Brachyuran crabs, primarily *Callinectes*, were of secondary importance in the diet. In Hereford Inlet near Cape May, New Jersey, Allen *et al*. (1978) found that adult and juvenile summer flounder (200-400 mm) fed mostly on *Crangon septemspinosa*, mysids and fish.

Smith and Daiber (1977) reported that Delaware Bay adults < 45 cm TL fed on invertebrates, while those > 45 cm TL ate more fish. Food items found, in order of percent frequency of occurrence, included decapod shrimp (*Crangon septemspinosa*), weakfish (*Cynoscion regalis*), mysids (*Neomysis americana),* anchovies (*Anchoa* sp.*),* squids (*Loligo* sp.*),* Atlantic silversides (*Menidia menidia*), herrings (*Alosa* sp.), hermit crabs (*Pagurus longicarpus*), and isopods (*Olencira praegustator*).

In Magothy Bay, Virginia, large summer flounder (20.1-47.6 cm) fed mainly on *Neomysis americana*, as well as large crustaceans such as *Squilla empusa*, xanthid crabs, and squids. The fish from this area are not mainly piscivorous, but the larger specimens (> 40.0 cm) did contain a higher percentage of fishes than did the smaller ones (Kimmel 1973). Lascara (1981) reports that larger juveniles and adults (avg. length 27.4 cm SL) from lower Chesapeake Bay fed on juvenile spot (*Leiostomus xanthurus*), pipefish (*Syngnathus fuscus*), the mysid *Neomysis americana*, and shrimps (*P. vulgaris*, *C. septemspinosa*).

In South Carolina, Wenner *et al*. (1990a) showed that flounder 50-313 mm TL consumed mostly decapod crustaceans, especially caridean shrimps (*Palaemonetes* sp., *P. pugio*, *P. vulgaris*). The importance of fish (mostly bay anchovy, *Anchoa mitchilli*, and mummichogs) in the diet increased as summer flounder size increased.

Co-Occurring Species and Predation

Spatial co-occurrence and dietary overlap among summer flounder, scup, and black sea bass have been previously documented (Musick and Mercer 1977; Gabriel 1989; Shepherd and Terceiro 1994). For example, the composition and distribution of fish assemblages in the Middle Atlantic Bight was described by Colvocoresses and Musick (1979) by subjecting NEFSC bottom trawl survey data to the statistical technique of cluster analyses. Summer flounder, scup, northern sea robin, and black sea bass, all warm temperate species, were regularly classified in the same group during spring and fall. In the spring this group was distributed in the warmer waters on the southern shelf and along the shelf break at depths of approximately 152 m. During the fall this group was distributed primarily on the inner shelf at depths of less than 61 m where they were often joined by smooth dogfish.

All of the natural predators of adult summer flounder are not fully documented, but larger predators such as large sharks, rays, and goosefish probably include summer flounder in their diets.

Laboratory studies by Lascara (1981) on flounder from lower Chesapeake Bay suggest that in patchy seagrass/sand habitats, the flounder may avoid predation by staying in the sand near the seagrass beds, rather than in the grass beds themselves.

INSHORE SUMMER FLOUNDER HABITAT CHARACTERISTICS

Habitat information is meaningful because habitat differences can be important in determining local abundances of summer flounder (Cadrin *et al*. 1995). Because most of the summer flounder habitat research occurs inshore, Tables 2-4 present the inshore habitat parameters or requirements for summer flounder found in nearshore New Jersey, Delaware, and North Carolina, respectively. Those States were chosen because of the amount of the high quality, habitat related research on summer flounder occurring there [by highest quality we mean Level 3 information as defined in the EFH Technical Manual (National Marine Fisheries Service, Office of Habitat Conservation 1998) and Interim Final Rule (Department of Commerce, National Oceanic and Atmospheric Administration 1997)]. Thus, we have also chosen to concentrate on studies (experimental or otherwise) which focus on the habitat parameter preferences, and are from published, peer-reviewed literature sources, rather than on information that merely attempts to correlate environmental variables with fish densities, such as that which often appears in general fisheries surveys. We heed the advice of Hettler *et al*. (1997), who suggest caution when interpreting correlations of environmental variables with fish abundances. For example, they reported an increase in summer flounder larval abundance with increasing temperatures in Beaufort Inlet, North Carolina. This could be caused by winter spawning and the larvae arriving at the inlet after a two to three month cross-shelf transport time, resulting in a higher larval abundance corresponding with rising temperatures. Their statistical analyses suggest that unknown factors are probably more important in causing peaks in the abundances of immigrating larvae (see also Hettler and Hare 1998).

Table 5 is a summation and synthesis of Tables 2-4, and should provide an overall, yet more succinct view of current habitat requirements information on inshore summer flounder. The habitat parameter headings for all the tables are based upon those used in the Habitat Characteristics section, above.

STATUS OF THE STOCKS

The following section is based on Terceiro (1995) and the Northeast Fisheries Science Center (1997). The coverage is from New England to Cape Hatteras.

The stock is at a medium level of historical (1968-1996) abundance and is over-exploited. The age structure of the spawning stock has begun to expand, with 34% of the biomass at ages 2 and older in 1996, although under equilibrium conditions about 85% of the spawning stock biomass would be expected to be ages 2 and older. The 1995 year class is about average (1982-1996), but the 1996 year class is estimated to be the smallest since the poor year class of 1988.

Commercial landings of summer flounder averaged 13,200 mt during 1980-1988, reaching a high of 17,100 mt in 1984 (Figure 37). The recreational fishery for summer flounder harvests a significant proportion of the total catch, and in some years recreational landings have exceeded the commercial landings. Recreational landings have historically constituted about 40% of the total landings. Recreational landings averaged 9,800 mt during 1980-1988, and peaked in 1983 at 12,700 mt. During the late 1980s and into 1990, landings declined dramatically, reaching 4,200 mt in the commercial fishery in 1990 and 1,400 mt in the recreational fishery in 1989 (Table 6). Reported 1996 landings in the commercial fishery used in the assessment were 5,770 mt and estimated 1996 landings in the recreational fishery were 4,704 mt (Table 6).

Spawning stock biomass declined 72% from 1983 to 1989 (18,900 mt to 5,200 mt), but has since increased with improved recruitment to 17,400 mt in 1996 (Figure 37**;** Table 6). The age structure of the stock is improving, with 34% of the spawning biomass in 1996 composed of fish of ages 2 and older, compared to only 17% in 1992.

Figure 38 shows the contrast between the distribution of summer flounder from periods of high abundances in the past (1974-1978) to recent periods of low abundances (1989-1993), for both adults and juveniles in the fall and spring.

RESEARCH NEEDS

Obviously, there are many gaps in our understanding of the autecology of summer flounder. Because it is such a highly migratory species and occurs everywhere throughout its range, knowledge of its life history and habitat requirements can vary regionally, and what affects them in one area can easily cause repercussions in the population in another area. Even though summer flounder is managed and assessed as one stock throughout the U.S. EEZ, the question of multiple stocks, particularly in the Mid-Atlantic Bight, still needs to be settled from a scientific standpoint. There is a lack of knowledge concerning the habitat requirements for all life history stages, especially the offshore eggs and larvae, but even for the adults within our own estuaries, since much of the current habitat research has focused on estuarine larvae and juveniles (note Tables 2-5). Of course, more habitat information is needed on the inshore transforming larval and early juvenile stages, especially because their health affects the future growth and survival of the population. Finally, critical habitat preferences must be defined. For example, while it is likely that temperature may drive the seasonal movements of juveniles and adults in and out of the estuaries, it may have less effect on their choice of specific habitats within those estuaries, where substrate, salinity, etc. may be the overriding factors. Once their habitat preferences are defined, their critical habitats can be more thoroughly delineated and mapped.

ACKNOWLEDGMENTS

This paper was originally presented as a rewrite of the habitat section of the summer flounder FMP with amendments [Mid-Atlantic Fishery Management Council (MAFMC) 1987, 1991].

The authors wish to thank Mark Terceiro, Anne Studholme, and Jeff Cross for reviews and editorial assistance, and Rande Ramsey-Cross, Judy Berrien, Claire Steimle, and Ferdinand Triolo for library assistance. Mark Terceiro provided the status of the stocks report. Rodney Rountree provided the original food habits data from the NEFSC trawl surveys with which Joe Vitaliano generated the pie charts. Frank Almeida provided much NMFS data and associated methodology and assisted with the figure captions.

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Table 1. Presence of summer flounder inshore, by State, as documented by authors cited in the text and personal communications from each States' flounder experts.

Author	Location	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Notes
	MA													
Howe personal communication	shoals s. of Cape Cod & Cape Cod Bay					**A** II				EE	EEEEEEE	EEEEEEE	EEEEEEE	
	CT													
Smith personal communication	Long Island Sound	**A**				III II				**A: peak**				
	NY													
Poole 62	Great South Bay, Long Island									**A** EEEEEEE	EEEEEEE			mean length 38cm
	NJ													
Szedlmayer *et al*. 92	Great Bay, Little Egg Harbor	TL IIIIIIIIIII	IIIIIIIIIII	IIIIIIIIIII	IIIIIIIIIII	IIIIIIIIIII	**J**			EE		TL IIIIIIIIIII	IIIIIIIIIII	TL: 11-17mm, J: YOY, 60-326mm
Allen *et al*. 78	Hereford Inlet, near Cape May		**TL**			**J, A**								TL: 12-15mm J/ A: 200-400m
Murawski 70	Sandy Hook & Cape May				**A** IIIIIIIIIII	IIIIIIIIIII				EEEEEEE				A: 230-700mm
Festa 74	NJ estuaries; Sandy Hook to Great Bay	L/TL IIIIIIIIIII	IIIIIIIIIII	IIIIIIIIIII							**L/TL** IIIIIIIIIII	IIIIIIIIIII	IIIIIIIIIII	L/TL 5-21mm; enter est. early Oct-late Jan most yrs, as late as March
Keefe and Able 93	NJ estuaries	**TL** IIIIIIIIIII	IIIIIIIIIII	IIIIIIIIIII	IIIIIIIIIII						**TL** IIIIIIIIIII	IIIIIIIIIII	IIIIIIIIIII	TL: 10-15mm, most abundant Oct-Dec
Able *et al*. 90	NJ estuaries							**J: peak**	EEEEEEE	EEEEEEE	EEEEEEE	EEEEEEE	EEEEEEE	J: YOY, 160-320mm TL

———	presence	**L**	larvae
———	peak abundance	**TL**	transforming larvae
- - -	limited numbers	**J**	juveniles
IIIIIIIII	peak ingress	**A**	adults
IIIIIIIII	ingress		
EEEEEE	egress		

Table 1. cont'd.

Author	Location	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Notes
	DE													
Smith personal communication	Delaware Bay	**A**			**A: peak**									some adults present all year
Smith and Daiber 77	Delaware Bay					**J/A: peak**								some juveniles present in deep parts of bay every winter month
	VA													
Musick personal communication	Eastern Shore & lower Chesapeake Bay	**J**		IIIIIIIIIIII	IIIIIIIIIIII						EEEEEEE	EEEEEEE		In milder winters some age 1+ fish remain in bay
	Eastern Shore, seaside inlets/lagoons				**A** IIIIIIIIIIII				EEEEEEE					
	lower Chesapeake Bay				**A** IIIIIII					EEE	EEE			
Wyanski 90	both sides of Eastern Shore	**J** IIIIIIIIIIII	IIIIIIIIIIII	IIIIIIIIIIII	IIIIIIIIIIII							IIIIIIIIIII	IIIIIIIIIII	peak recruitment Nov-Dec
	western Chesapeake Bay		**J** IIIIIIIIIII	IIIIIIIIII	IIIIIIIIII									peak recruitment March-April

———	presence	**L**	larvae
———	peak abundance	**TL**	transforming larvae
- - -	limited numbers	**J**	juveniles
IIIIIIIII	peak ingress	**A**	adults
IIIIIIIIII	ingress		
EEEEEE	egress		

Table 1. cont'd.

Author	Location	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Notes
	NC													
Hettler and Barker 93	Oregon Inlet, Ocracoke Inlet		TL IIIIIIIIIII		IIIIIIIIIII TL									TL: peak ingress
Powell and Schwartz 77	Pamlico sound	J IIIIIIII	IIIIIIII						*E					J=YOY, present ~18-20 mos. from mid winter recruitment to ~Aug of 2nd yr. *
Burke *et al.* 91	Newport River, North River estuaries	TL IIIIIIIIIII	IIIIIIIIIII	IIIIIIIIIII	IIIIIIIIIII									TL = 11-17mm SL
Monaghan personal communication	Beaufort Inlet		TL III	IIIIIIIIII										TL: peak ingress
Tagatz and Dudley 61	Beaufort Inlet			TL/J										TL/J = 11-180mm
Weinstein 79	Cape Fear River			TL IIIIIIIIIII	IIIIIIIIIII									TL = 9-16mm SL
	SC													
Wenner *et al.* 90a	Charleston Harbor & vicinity	TL/J IIIIIIIIIII	IIIIIIIIIII	IIIIIIIIIII	IIIIIIIIIII									TL/J = 10-20mm TL

———	presence	**L**	larvae
═══	peak abundance	**TL**	transforming larvae
- - - -	limited numbers	**J**	juveniles
IIIIIIIII	peak ingress	**A**	adults
IIIIIIIII	ingress		
EEEEEE	egress		

Table 2. Habitat parameters for summer flounder, *Paralichthys dentatus*: inshore New Jersey.

Life Stage	Authors	Size Range	Geographic Location	Time Period	Habitat	Substrate	Temperature
TRANSFORMING LARVAE	Grover 1998	8.1-14.6 mm SL (metamorphic)	Great Bay, Little Egg Harbor	Fall, winter, spring 89-95	Little Sheepshead Creek		
	Keefe and Able 1993, 1994	10-15.6 mm SL, mean 12.8 (metamorphic)	Great Bay, Little Egg Harbor	Nov 90-Nov 91 Nov 90-Mar 91	Little Sheepshead Creek	Sand preference by both metamorphs and juveniles. [1]	Increased temps. = shorter metamorphic period. Greater mortality at 4°C. No effect of starvation on mortality or time to completion of metamorphosis at temps. < 10°C. [1]
	Szedlmayer *et al*. 1992	11-17 mm TL (metamorphic)	Great Bay, Little Egg Harbor	Nov 88-Apr 89			0-13°C, mortality < 2°C [1]
	Witting and Able 1993	11-16 mm TL (metamorphic)	Great Bay, Little Egg Harbor	Jan-Feb 90			9-12°C [1]
JUVENILES	Rountree and Able 1992a	mean 132 mm SL (YOY), range ca. 16-245 mm	Great Bay, Little Egg Harbor	Apr-Nov 88 Apr-Oct 89	Schooner, New, Foxboro creeks	mud	mean 19°C
	Rountree and Able 1992b	mean 238 mm TL (YOY), range 156-312 mm	Great Bay, Little Egg Harbor	1987-1990	Schooner, New, Foxboro, Stoney creeks	mud	mean 22°C, range 15-27°C
	Rountree and Able 1997	mean 192 mm SL, range 138-390 mm, mostly YOY	Little Egg Harbor	May/July-Nov 90	Foxboro, Stonely Island creeks. Marsh creeks and deeper (4-9 m) bay shoals.	mud	
	Szedlmayer *et al*. 1992	60-326 mm TL (YOY)	Great Bay, Little Egg Harbor	June-Sept 89	**June**: mesohaline subtidal creeks **July**: shallow mudflats/dredged channels **Aug-Sep**t: marsh creeks	subtidal creeks 90-98% mud	
	Szedlmayer and Able 1993	210-254 mm TL (age 0)	Great Bay, Little Egg Harbor	Aug-Sept 90	Schooner Creek		mean 23.5°C (optimum?)

[1] Laboratory study
Adults: no pertinent information

Table 2. cont'd.

Life Stage	Authors	Salinity	Dissolved Oxygen	Light	Currents	Prey	Predators	Notes
TRANSFORMING LARVAE	Grover 1998					Primary prey: calanoid copepod *Temora longicornis*, indicating pelagic feeding. Evidence of benthic feeding observed only in late-stage metamorphs (stage H+ and I), where prey included polychaete tentacles, harpacticoid copepods.		
	Keefe and Able 1993, 1994			Prefer burying during daylight. [1]	Increased burial at flood tide. [1]		Less burying in presence of decapod shrimp *Crangon*, increased burying in presence of mummichog *Fundulus*. [1]	Time to completion of metamorphosis temperature dependent.
	Szedlmayer *et al*. 1992							
	Witting and Able 1993						11-16 mm TL transforming larvae are vulnerable to predation by a large size range of shrimp (*Crangon septemspinosa*, ~ 10-50 mm TL) in NJ estuaries. [1]	
JUVENILES	Rountree and Able 1992a	mean 29 ppt						Found mostly during summer. Abundance varied significantly between years. Maximum abundance of fluke during peak in *Menidia menidia* abundances.
	Rountree and 1992b	mean 27ppt, range 23.5-30 ppt			Moving with the tides. Tidal movements associated with foraging - stomachs fuller on ebb tide.	In order of abundance: Atlantic silversides *Menidia menidia*, mummichogs *Fundulus heteroclitus*, shrimps *Palaemonetes vulgaris* and *Crangon septemspinosa*.		Creeks are foraging habitat. Prey composition exhibits a seasonal influence. Frequency of *Menidia* declines during Aug, Sept, Oct while *Crangon* rises.
	Rountree and Able 1997	range 22-33 ppt		Nocturnal sampling: extensive use of shallow habitats during night-time.	Mostly caught on ebb tides (sampling during night hours).			Preference for creek mouths and tidal creeks rather than bay shoals. Peak catch in late July/Oct.
	Szedlmayer *et al*. 1992	subtidal creeks avg. 20 ppt						High use of creek mouths.
	Szedlmayer and Able 1993	mean 29 ppt (optimum?)	mean 6.4 ppm (optimum?)		selective tidal stream transport			Selective tidal transport, feeding, optimal environmental conditions cause movement. High use of creek mouths.

[1] Laboratory study
Adults: no pertinent information

Table 3. Habitat parameters for summer flounder, *Paralichthys dentatus*: inshore Delaware.

Life Stage	Authors	Size Range	Geographic Location	Time Period	Habitat	Substrate
JUVENILES	Malloy and Targett 1991	Collected 41-80 mm TL for experiment.	Roosevelt Inlet and Indian River Bay	Inlet: Nov 89-Apr 90 Bay: Feb-June 89-90	Estuarine marsh creeks 0.5-1.5 m in depth.	
	Malloy and Targett 1994a	18-80 mm TL	Indian River Bay	Jan-June 91/92		
	Malloy and Targett 1994b	18-80 mm TL	Indian River Bay	Jan-June 92	Protected beach close to muddy channel.	Intermediate size grains with ephemeral macroalgal cover.
	Timmons 1995	7.6-24.9 cm TL	Rehoboth Bay, Indian River Bay	June 92, Aug 92, Nov 92, Mar 93	Attracted to the algae *Agardhiella tenera* because of the presence of prey, but remain in nearby sand to avoid predation. Collected in water depths between 0.5-5.5 m.	Prefer sand to shell rubble or algae. [1] Captured in sand and mud.
ADULTS	Smith and Daiber 1977	> ~ 28 cm TL	Delaware Bay	Aug 66-Nov 71. Most captured May-Sept, a few [juveniles] have been caught in the deeper parts of the Bay in every winter month.	Captured from the shoreline to 25 m deep.	

[1] Laboratory study
Transforming larvae: no pertinent information
D.O., Currents, Light: no pertinent information

Table 3. cont'd.

Life Stage	Authors	Temperature	Salinity	Prey	Predator	Notes
JUVENILES	Malloy and Targett 1991	Mortality was 42% after 16 days at 2-3°C; > 3°C, all fish survived. Mortality highest in fish < 50 mm TL in < 3°C water; all fish > 65 mm survived < 2.5°C for 2 weeks. Growth rates were the same between 2 and 10°C. Mean growth rate increased to 2.4% per day at 14°C and 3.8% per day at 18°C. [1]	Collected at 24-30 ppt. Experimental salinity variation (10-30 ppt) had no effect on feeding, growth or survival. [1]	Fed locally caught mysid shrimp *Neomysis americana* in experiment. [1]	The extended period of time spent at small sizes may increase vulnerability to predation.	Juveniles that arrive in northern Mid-Atlantic Bight estuaries in the fall, in advance of winter temperature minima, may be able to grow past a lower critical size, thus increasing survival.
	Malloy and Targett 1994a	Mortality of juveniles depends more on rate of temperature decline than on final exposure temperature. No growth at temperatures < 9°C. DE fish more tolerant of low temperatures (1-4°C) than NC fish. [1]		Can survive 14 days with no food at 10-16°C (typical temperature at settlement). Prey availability is important to growth. Fed locally caught mysid shrimp *N. americana* in experiment. [1]		
	Malloy and Targett 1994b	2.6-20°C		Low densities of mysids (one of the dominant prey items) until June.	Extended period of time spent at small sizes (13-25mm TL) could increase vulnerability to predation.	< 50% maximum growth in May/early June.
	Timmons 1995	June: 22-28°C, August: 17-25°C, November: 7-12°C, March: 9-13°C	Range: 12-28 ppt. Salinities were constantly lower in Indian River Bay compared to Rehoboth Bay.	Rehoboth flounder fed on shrimp *Paleomonetes vulgaris*, plus porturid and blue crabs. Indian River fish fed on mysids.	In caging experiments, blue crabs were least able to prey on the flounder in cages with sand bottoms only, but had an advantage in capturing the flounder in cages containing macroalgae.[1]	Suggests that macroalgal systems appear to act as an ecological surrogate to seagrass beds and seagrass/macro-algal systems.
ADULTS	Smith and Daiber 1977			< 45 cm fed on invertebrates, > 45 cm TL ate more fish. In order of % frequency of occurrence: shrimp (*C. septemspinosa*), weakfish, mysids (*N. americana*), anchovies, squids, Atlantic silversides, herrings, hermit crabs (*P. longicarpus*), isopods (*O. praegusta*).		Appear to migrate little and may be permanent residents.

[1] Laboratory study
Transforming larvae: no pertinent information
D.O., Currents, Light: no pertinent information

Table 4. Habitat parameters for summer flounder, *Paralichthys dentatus*: inshore North Carolina.

Life Stage	Authors	Size Range	Geographic Location	Time Period	Habitat	Substrate	Temperature
TRANS-FORMING LARVAE	Burke 1991	mean 14.7 mm SL	Newport River Estuary	Feb-Mar 87-89		Wild caught and lab reared larvae: preferred sand over mud even when prey not present. Implies search for food to some extent restricted to sandy substrate in settling fish. [1]	6-20°C[1]
	Burke 1995	11-20 mm SL	Newport and North River	Jan-Apr 88	Tidal flats, channels.		10-13°C
	Burke *et al*. 1991	11-17 mm SL	Newport and North Rivers	Nov-Apr 86-89	Larvae concentrate on shallow tidal flats (< 1 m), middle reaches of estuary. Fewer catches in 1.5-3 m. In spring juveniles migrate to higher salinity salt marsh.	Substrate type can affect distribution. Higher probability on sand than mud.	
	Burke *et al*. 1998	Onslow Bay: 9-15 mm SL, transforming larvae. Beaufort Inlet: 11-15 mm SL, all at stages G - I_2. Newport River estuary: 11-21 mm SL.	Onslow Bay, includes nearshore waters; Beaufort Inlet and Newport River estuary.	Feb/Mar 1995	Onslow Bay: concentrate in estuarine areas. Outside the estuary in the surf zone and in deeper habitats of the Bay, larvae were present only during the immigration season. Within the Newport estuary initial settlement appears to be concentrated in the intertidal zone rather than in adjacent deeper areas.		
	Deubler and White 1962	12-15 mm SL	Bogue Sound	Feb-61			
	Hettler *et al*. 1997	12-15 mm SL	Beaufort Inlet	Nov 91-Apr 92, nightly	Tidal channel, 6m deep.		7-18°C, higher abundance with increased temperatures.
	Weinstein *et al*. 1980a	7-34 mm SL	Cape Fear River Estuary	Mar-Apr	Tidal salt marsh and creeks, shallow open water.		
	Weinstein *et al*. 1980b	mean 13.6 mm	Cape Fear River Estuary	Sept 77-Aug 78	Tidal creeks, shallow marsh.	Grain size variation among sites: fine sand (58-93%), medium sand (7-41%), mud (1-14%).	16.8-21.1°C
	Williams and Deubler 1968b		Pamlico Sound, Neuse River	1957-1966, biweekly, at night			2-22°C, most abundant at 8-16°C.

[1] Laboratory study
Adults: no pertinent information
D.O.: no pertinent information

Table 4. cont'd.

Life Stage	Authors	Size Range	Geographic Location	Time Period	Habitat	Substrate	Temperature
JUVENILES	Burke 1991, 1995	20-60 mm SL	Newport and North Rivers	Jan-Apr 88	Tidal flats and channels, juveniles migrate to salt marsh. Shallow: < 1 m mean low tide.		10-13^{o}C
	Malloy and Targett 1994a	18-80 mm TL	lower Newport River	Jan-June 91-92			2-20^{o}C: Increase in temperature = increase in feeding rate, maximum growth rate, gross growth efficiencies. Increased rate of temperature decline = decreased survival. < 7-9^{o}C no positive growth rates. [1]
	Malloy and Targett 1994b	18-80 mm TL	Newport River Estuary	Jan-June 92	Sandy salt marsh (adjacent to *Spartina alterniflora* marshes) and muddy beach.	Predicted growth rates higher at muddy beach site in May. [1]	8-23^{o}C (Feb-June)
	Peters and Angelovic 1971						10-30^{o}C, increase in temperature = increase in ad libitum feeding rate and growth efficiency. Little growth at low temperatures, fastest growth rate at 20-25^{o}C. Specific growth rate = 5% at 15^{o}C, 10% at 20^{o}C.[1]
	Powell 1982	18-224 mm TL, mean at end of 1st yr: males 167 mm, females 171 mm TL	Pamlico Sound	May 71-July 72			Migration to estuary in February: body weight increases 5%/day. After February increase in temperature = a decrease in growth rates. Late fall growth negligible. June: 2% increase body weight /day, August: 1%.
	Powell and Schwartz 1977	Range 70-250 mm TL. 8-16 mm when entering estuary, 90-100 mm at first spring, 1st yr. juveniles 170 mm by Dec.	Pamlico Sound	Aug 71-July 72	Most abundant in eastern and central Pamlico Sound (relatively high salinity), close to inlets.	Greater abundance with sand, or sand/shell, scarce where mud predominates.	Warm temperatures and intermediate/high salinities = increased growth rate.
	Powell and Schwartz 1979	100-400 mm TL (84% of captures 100-200 mm TL)	Pamlico Sound and adjacent estuary	Aug 71-July 72, monthly, daylight sampling	Dominant in lower estuary.		Increased temperatures = increased food consumption for overwintering juveniles.
	Ross and Epperly 1985	21-320 mm SL	Pamlico Sound	Mar 81-Nov 82	YOY on seagrass bed.	fine sand	

[1] Laboratory study
Adults: no pertinent information
D.O.: no pertinent information

Table 4. cont'd.

Life Stage	Authors	Salinity	Light	Currents	Prey	Predators	Notes
TRANS-FORMING LARVAE	Burke 1991	16-34 ppt [1]					Sand preference of metamorphosing larvae in laboratory corresponds to older fish in wild.
	Burke 1995	21-32 ppt			Polychaete tentacles most important, plus polychaetes and harpactacoid copepods. Increasing importance of polychaetes and clam siphons with increasing development.		
	Burke *et al*. 1991	19-31 ppt				Predator avoidance by burying in sandy substrate.	
	Burke *et al*. 1998	~31-34 ppt		During flood tides, highest larval densities at mid-depths within water column; during ebb tide, highest densities at bottom. Position in water column dependent on tidal stage; shift in distribution/abundance associated with shift in tidal stage, indicating flounders enter Onslow Bay by tidal stream transport. Wild-caught larvae had regular pattern of activity correlated with tidal cycle; peak activity associated with ebb tide[1]. Lab-reared flounder: no clear pattern of activity[1].			Observations of tidal rhythm of activity of wild-caught flounder[1] and vertical shift into water column during slack tide suggests behavioral component to tidal stream transport. High activity during ebb tide[1] suggests most active behavioral component of TST involves avoidance of advection by ebbing tide rather than movement into water column and transport by flood tide. Lack of tidal activity pattern in lab-reared flounder[1] suggests development of tidal rhythm dependent on exposure to physical variables that are correlated with the tide.
	Deubler and White 1962	10-30 ppt: increase in salinity = increase in body wt; 40 ppt = decrease in body wt. [1]					Salinities commonly found in lower estuary allows optimal growth.
	Hettler *et al*. 1997	24-36 ppt	More abundant in catches later at night.				mean density = 2 larvae/100m^3 (Dec 31-Apr 15)
	Weinstein *et al*. 1980a		Night catches > day catches. At night concentration at surface > concentration at other depths.	Marsh migration aided by surface movement on flood tides at night, settle to bottom on ebb.			Despite intensive tidal flows maintain preferred position in estuary by specific behavioral responses.
	Weinstein *et al*. 1980b	1.7-24.9 ppt; greater occurrence in mid/higher salinities.					Distribution influenced by salinity gradients and to lesser extent by substrate characteristics.
	Williams and Deubler 1968a	.02-35 ppt, 18 ppt optimum					

[1] Laboratory study
Adults: no pertinent information
D.O.: no pertinent information

Table 4. cont'd.

Life Stage	Authors	Salinity	Light	Currents	Prey	Predators	Notes
JUVENILES	Burke 1991, 1995	21-32 ppt	Visual predators. Feeding largely restricted to daylight.		Active predator; ate primarily infaunal crustaceans, polychaetes, invertebrate parts. Polychaetes (primarily spionids) most important.		Diets of summer and southern flounder similar during settlement when distributions overlapped. Diets diverged prior to segregated distribution. Spionid prey *Streblospio benedicti* abundant in marsh; may explain juvenile migration to marsh.
	Malloy and Targett 1994a	30 ppt			Winter food limitation less important than variability of temperature minima.		NC juveniles higher maximum growth rates and growth efficiencies than DE fish at temperatures from 6-18^{o}C. NC fish less tolerant of low temperatures (1-4^{o}C) than DE fish. [1]
	Malloy and Targett 1994b				Low abundance of NC mysids from May into summer might explain growth limitation in marsh juveniles during May. Increasing abundance of other prey (polychaetes, amphipods) may account for favorable juvenile growth in muddier site during May.		Predicted growth rates = 2-5%/d Feb-April. Marsh juveniles severely growth limited after April with temperatures 18-20^{o}C.
	Peters and Angelovic 1971	5-35 ppt; relatively little effect on ad libitum feeding rate. [1]					Maximum caloric growth efficiency predicted at 21^{o}C, 24 ppt salinity and 78% ad libitum feeding. All body processes including feeding increases with temperature to an optimum; > optimum, increasing temperature becomes detrimental.
	Powell 1982						Decrease in growth with increase in temperature probably due to intrinsic (not environmental) factors.
	Powell and Schwartz 1977	Most abundant moderate/high salinities 18-35 ppt. Spatial segregation with southern flounder: increase in salinity = increase in summer flounder abundance.		Shallow waters near inlets (fast flowing).			Juveniles overwinter in estuary (adults migrate to ocean). Distribution governed primarily by benthic substrate and salinity. Pamlico Sound unusual: solar-lunar tides immeasurable; salinities uniform in much of sound.
	Powell and Schwartz 1979	Dominant in higher salinities.			Young flounder fed mostly on mysids and fishes throughout the year. As size increases diet consisted of shrimps and fishes in similar quantities. Feeding rate decreases in winter.		Southern flounder diet compared: reverse importance was found - fishes, then mysids.
	Ross and Epperly 1985	Distribution significantly correlated with salinity, range 22-28 ppt, optimal 22-23 ppt.					

[1] Laboratory study
Adults: no pertinent information
D.O.: no pertinent information

Table 5. Summary of life history and habitat parameters for summer flounder, *Paralichthys dentatus*: inshore New Jersey, Delaware and North Carolina.

Life Stage	Size	Geographic Location	Habitat	Substrate	Temperature
TRANSFORMING LARVAE (No pertinent information for DE)	~ > 8 - < 18 mm SL	**NJ**: Great Bay, Little Egg Harbor; **NC**: Pamlico Sound and Cape Fear estuaries.	Shallow tidal flats and marsh creeks.	Sand preference [1]	Time to completion of metamorphosis temperature dependent. Increased temperatures = shorter metamorphosis. Mortality from < 2-4°C. No effect of starvation on mortality or time to completion of metamorphosis at temperatures < 10°C.[1]
JUVENILES	~ > 20 mm - ~ < 28 cm TL	**NJ**: Great Bay, Little Egg Harbor; **DE**: Delaware and Indian Rivers, Rehobeth Bays; **NC**: Pamlico Sound, Cape Fear, and adjacent estuaries.	Lower estuary: flats, channels, salt marsh creeks, eelgrass beds. Possible preference for creek mouths **(NJ)** and inlets **(NC)**. Creeks are foraging habitat. **DE**: Attracted to macroalgae because of the presence of prey, but remain in nearby sand to avoid predation.	**NJ**: found on muddy bottoms. **NC**: often greater abundances on sand or mixed substrates. Scarcer on mud. **DE**: Sand preference.[1] Captured on sand and mud. Substrate preference possibly overrides salinity preference.	**DE**: > 3°C, all fish survived. **NC**: Feeding rate, growth rate and efficiencies increase with increasing temperatures. < 7-9°C = no positive growth rates (both **DE**, **NC** fish); 20-25°C = fastest growth rates. **NC** fish higher maximum growth rates/growth efficiencies at 6-18°C than **DE** fish.[1] **DE** juveniles show greater tolerances for low temperatures than **NC** juveniles. Mortality of juveniles depends more on rate of temperature decline than on final exposure temperatures.[1]
ADULTS (No pertinent information for NJ, NC)	~ > 28 cm TL	Delaware Bay	Captured from the shoreline to 25 m.		

[1] Laboratory study
D.O.: no pertinent information

References
New Jersey: Rountree and Able (1992a,b, 1997), Szedlmayer *et al.* (1992), Keefe and Able (1993, 1994), Szedlmayer and Able (1993), Witting and Able (1993), Grover (1998)
Delaware: Smith and Daiber (1977), Malloy and Targett (1991), Malloy and Targett (1994a,b), Timmons (1995)
North Carolina: Deubler and White (1962), Williams and Deubler (1968b), Peters and Angelovic (1971), Powell and Schwartz (1977, 1979), Weinstein *et al.* (1980a,b), Powell (1982), Ross and Epperly (1985), Burke (1991), Burke *et al.* (1991, 1998), Malloy and Targett (1994a,b), Burke (1995), Hettler *et al.* (1997), Walsh *et al.* (1999)

Table 5. cont'd.

Life Stage	Salinity	Light	Currents	Prey	Predators
TRANSFORMING LARVAE (No pertinent information for DE)	Salinities found in lower estuaries optimal for growth: 10-30 ppt.; Increasing salinity = increased body weight [Weinstein *et al*. 80b: Distribution possibly influenced more by salinity than by substrate.]	Prefer burying during daylight.[1] Night active.	**NJ**: Increased burial at flood tide;[1] however, **NC**: possible surface or mid-depth movement on flood, settlement on ebb. Position in water column dependent on tidal stage, flounders utilize tidal stream transport (behavioral component suggested). Peak activity associated with ebb tide[1].	Calanoid copepod *Temora longicornis* -- indicates pelagic feeding. Benthic feeding in late-stage metamorphs, prey includes polychaete tentacles, harpactacoid copepods, polychaetes.	Burying behavior determined by presence of particular predator.[1] **NJ**: 11-16 mm transforming larvae vulnerable to predation by large size range of shrimp *C. septemspinosa* (~ 11-50 mm TL) [1]
JUVENILES	More abundant in higher salinities of 18-35 ppt. Possible preference, but interactions with substrate preferences. **DE**: Experimental salinity variation (10-30 ppt) had no effect on feeding, growth or survival.[1]	Visual predators, feeding restricted to daylight, but **NJ** study (Rountree and Able 97) shows increased night-time catches in marsh creeks. **DE**: No pertinent information.	Selective tidal stream transport. Feeding, optimal environmental conditions cause movement. **DE**: No pertinent information.	Smaller juveniles: infauna (e.g., polychaetes). Larger juveniles (~ > 100 mm TL): fish, shrimps, crabs; often tied to abundance in environment.	**DE**: In caging experiments, blue crabs were least able to prey on the flounder in cages with sand bottoms only, but had an advantage in capturing the flounder in cages containing macroalgae.[1] **NJ, NC**: No pertinent information.
ADULTS (No pertinent information for NJ, NC)				< 45 cm fed on invertebrates, > 45 cm TL ate more fish. In order of % frequency of occurrence: shrimp (*C. septemspinosa*), weakfish, mysids (*N. americana*), anchovies, squids, Atlantic silversides, herrings, hermit crabs (*P. longicarpus*), isopods (*O. praegusta*).	

[1] Laboratory study
D.O.: no pertinent information

References

New Jersey: Rountree and Able (1992a,b, 1997), Szedlmayer *et al.* (1992), Keefe and Able (1993,1994), Szedlmayer and Able (1993), Witting and Able (1993), Grover (1998)
Delaware: Smith and Daiber (1977), Malloy and Targett (1991), Malloy and Targett (1994a,b), Timmons (1995)
North Carolina: Deubler and White (1962), Williams and Deubler (1968b), Peters and Angelovic (1971), Powell and Schwartz (1977, 1979), Weinstein *et al.* (1980a,b), Powell (1982), Ross and Epperly (1985), Burke (1991), Burke *et al.* (1991, 1998), Malloy and Targett (1994a,b), Burke (1995), Hettler *et al.* (1997), Walsh *et al.* (1999)

Table 6. Summer flounder catch and status (weights in '000 mt, recruitment in millions, arithmetic means).

Year	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**Max[2]**	**Min[2]**	**Mean[2]**
Commercial landings	8.1	4.2	6.2	7.6	5.7	6.6	7.0	5.8	17.1	4.2	9.7
Commercial discards	0.7	1.2	1.1	0.7	0.8	0.9	0.3	0.5	1.2	0.3	0.8
Recreational landings	1.4	2.3	3.6	3.2	3.5	4.1	2.5	4.7	12.7	1.4	5.4
Recreational discards	0.1	0.6	1.1	0.9	1.8	1.4	1.8	1.6	1.8	0.1	1.1
Catch used in assessment	10.4	8.3	12.0	12.3	11.9	13.0	9.5	10.5	27.0	8.3	16.6
Spawning stock biomass[1]	5.2	7.5	5.8	7.3	9.3	12.4	17.3	17.4	18.9	5.2	12.4

[1]At the peak of the spawning season (i.e., November 1). [2]Over period 1982-1996.

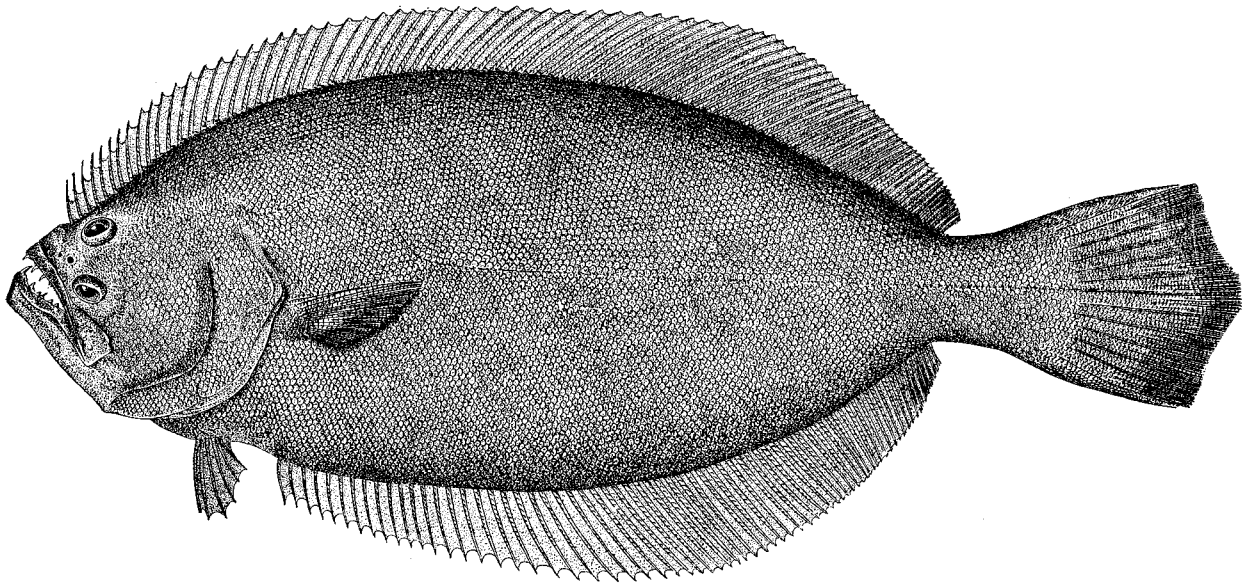


Figure 1. The summer flounder, *Paralichthys dentatus* (from Goode 1884).

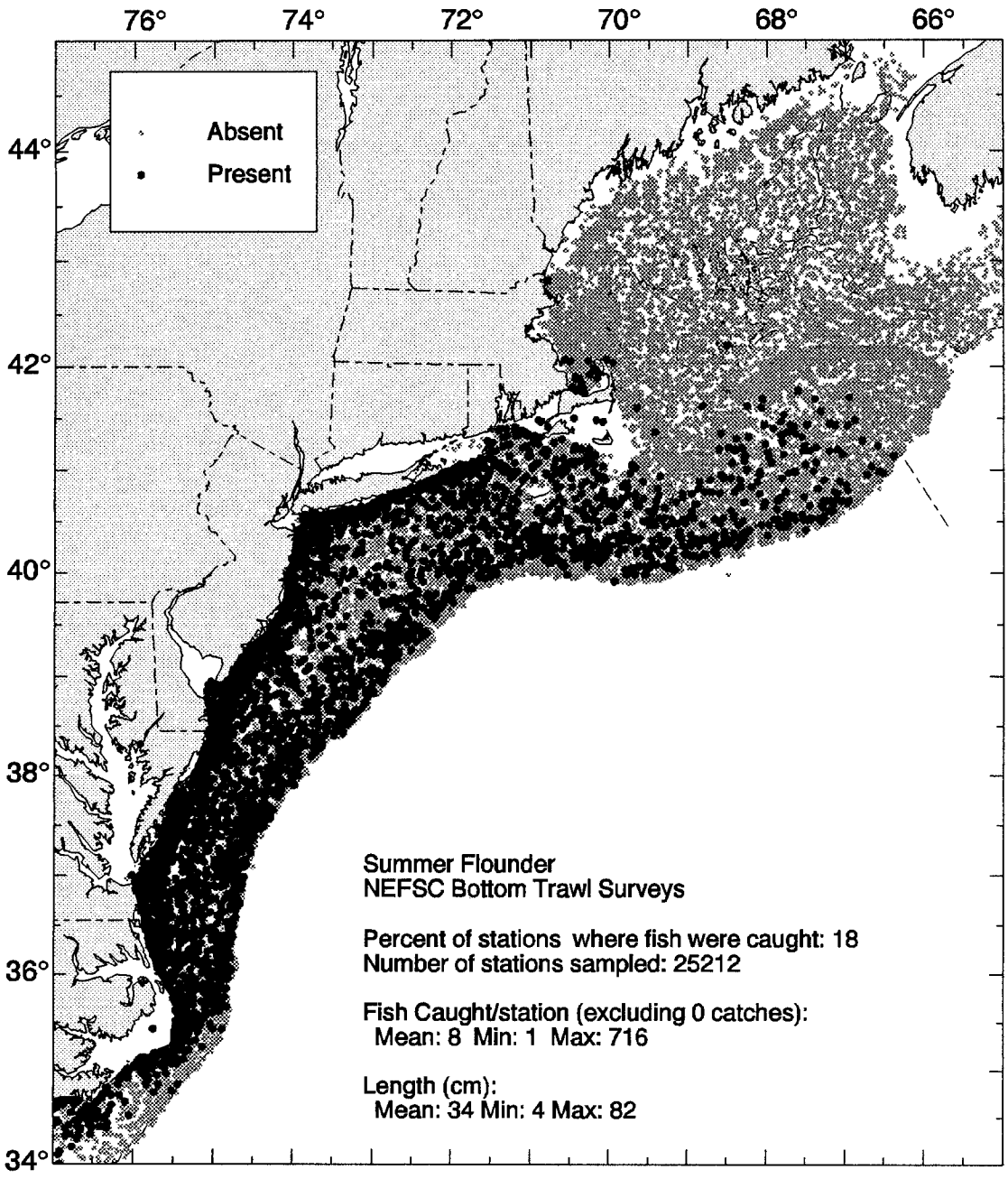


Figure 2. Overall distribution of adult and juvenile summer flounder in NEFSC bottom trawl surveys in autumn (1963-1996), winter (1964-1997), spring (1968-1997), and summer (1964-1995) [see Reid *et al.* (1999) for details].

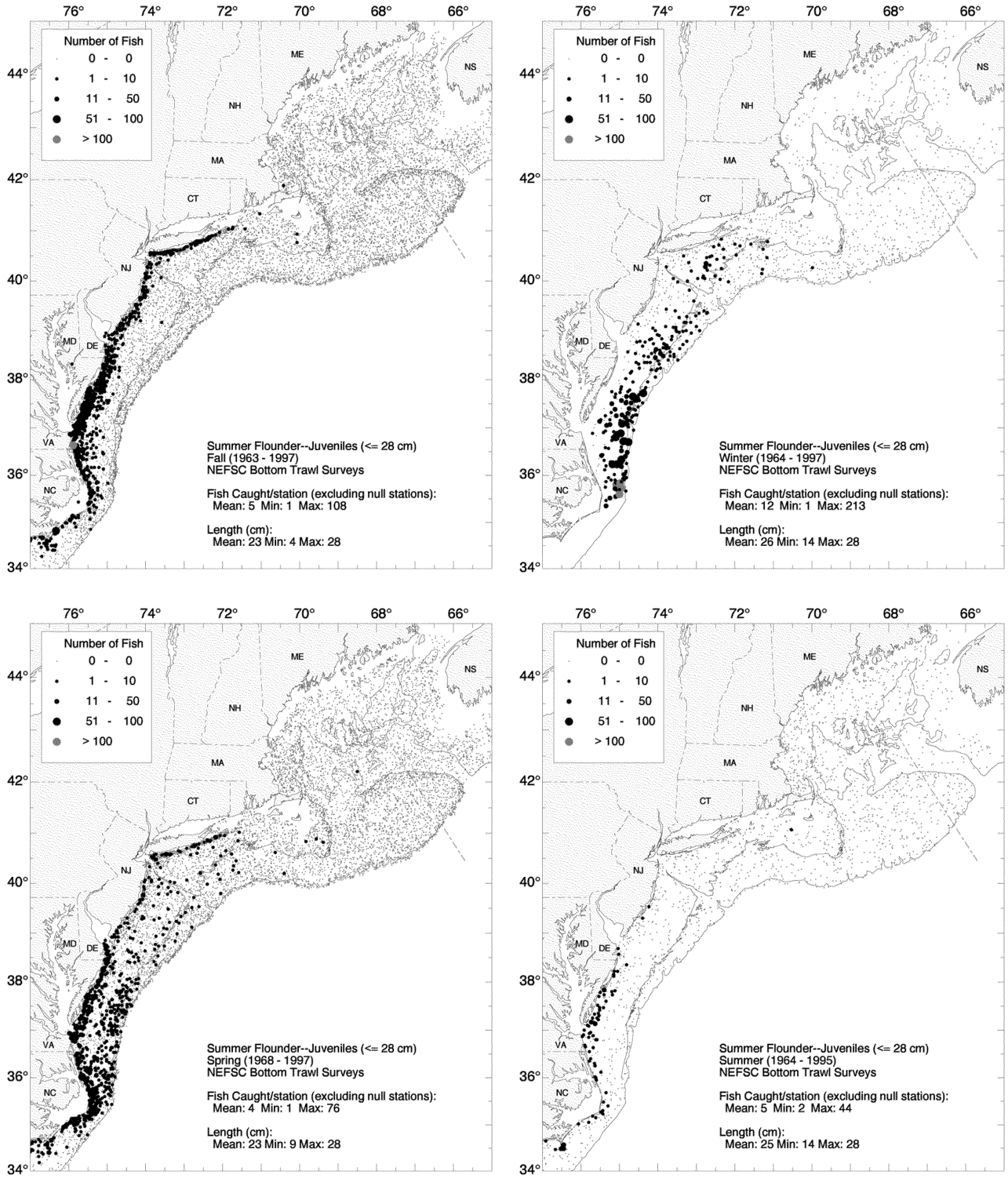


Figure 3. Distribution and abundance of juvenile (≤ 28 cm TL) and adult (> 28 cm TL) summer flounder by season, collected during NEFSC bottom trawl surveys during autumn (1963-1996), winter (1964-1997), spring (1968-1997) and summer (1964-1995) [see Reid *et al.* (1999) for details].

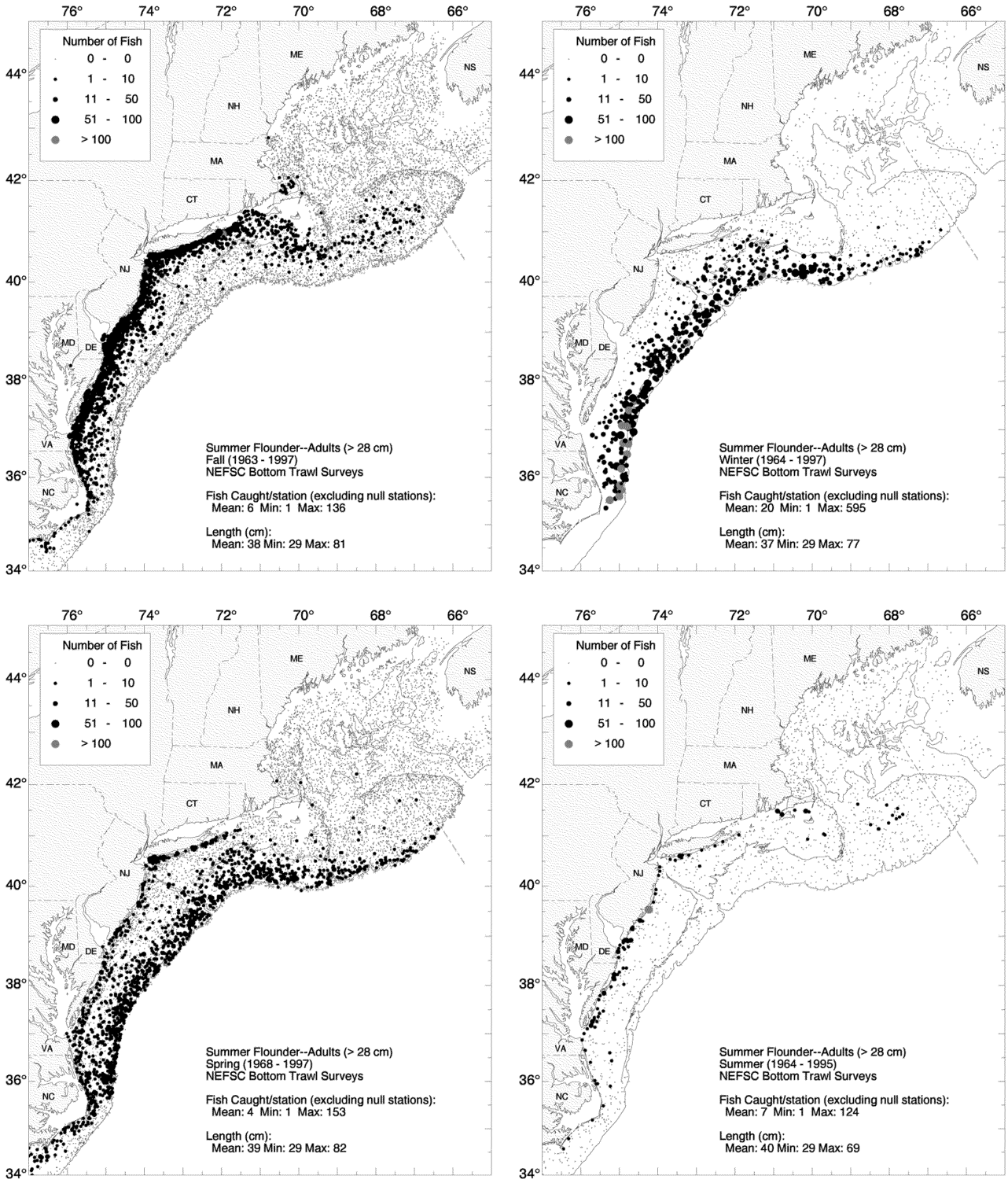


Figure 3. cont'd.

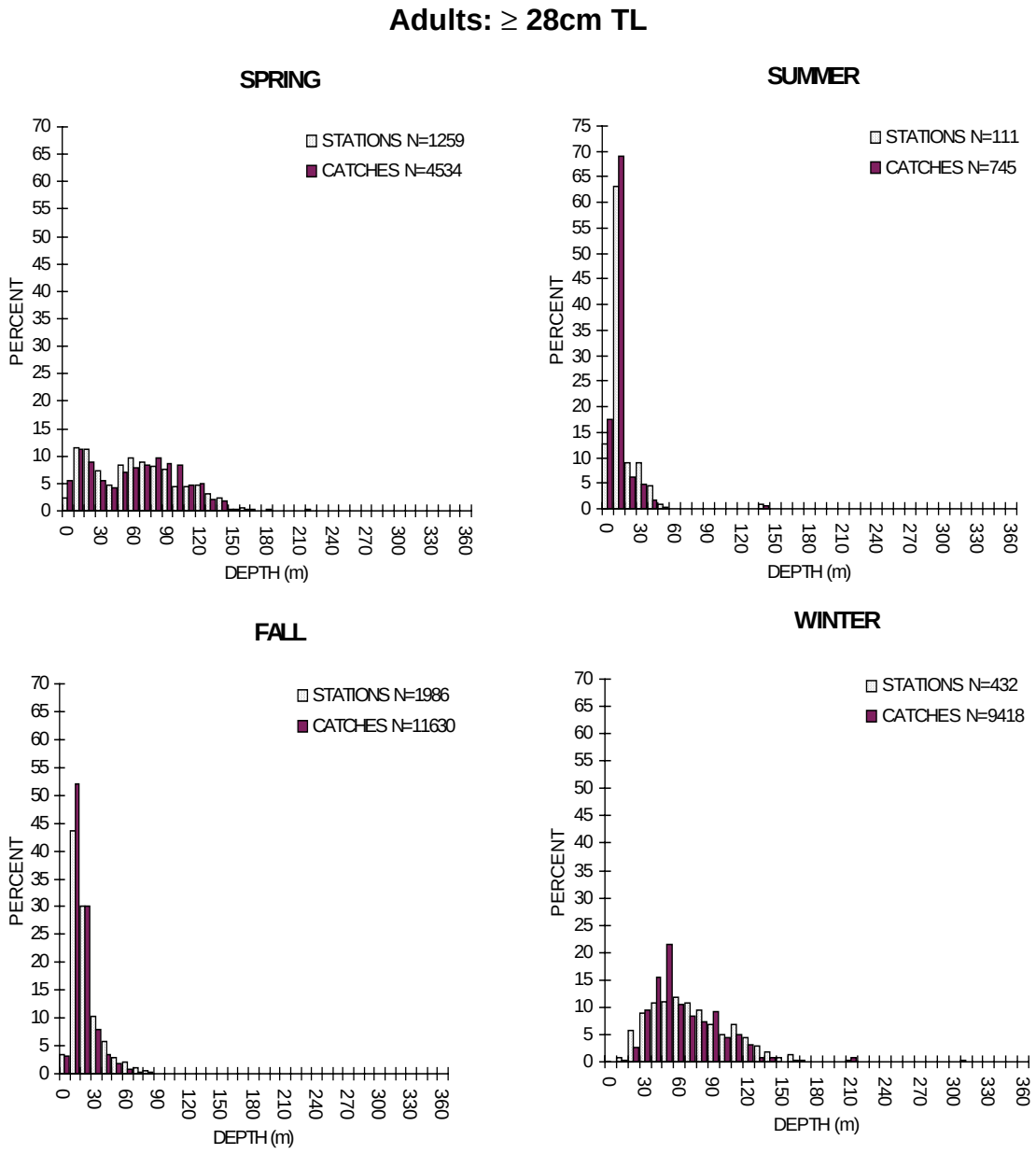


Figure 4. Seasonal abundance of adult summer flounder relative to water depth based on NEFSC bottom trawl surveys [1963-1997, all years combined; see Reid *et al.* (1999) for details]. Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).

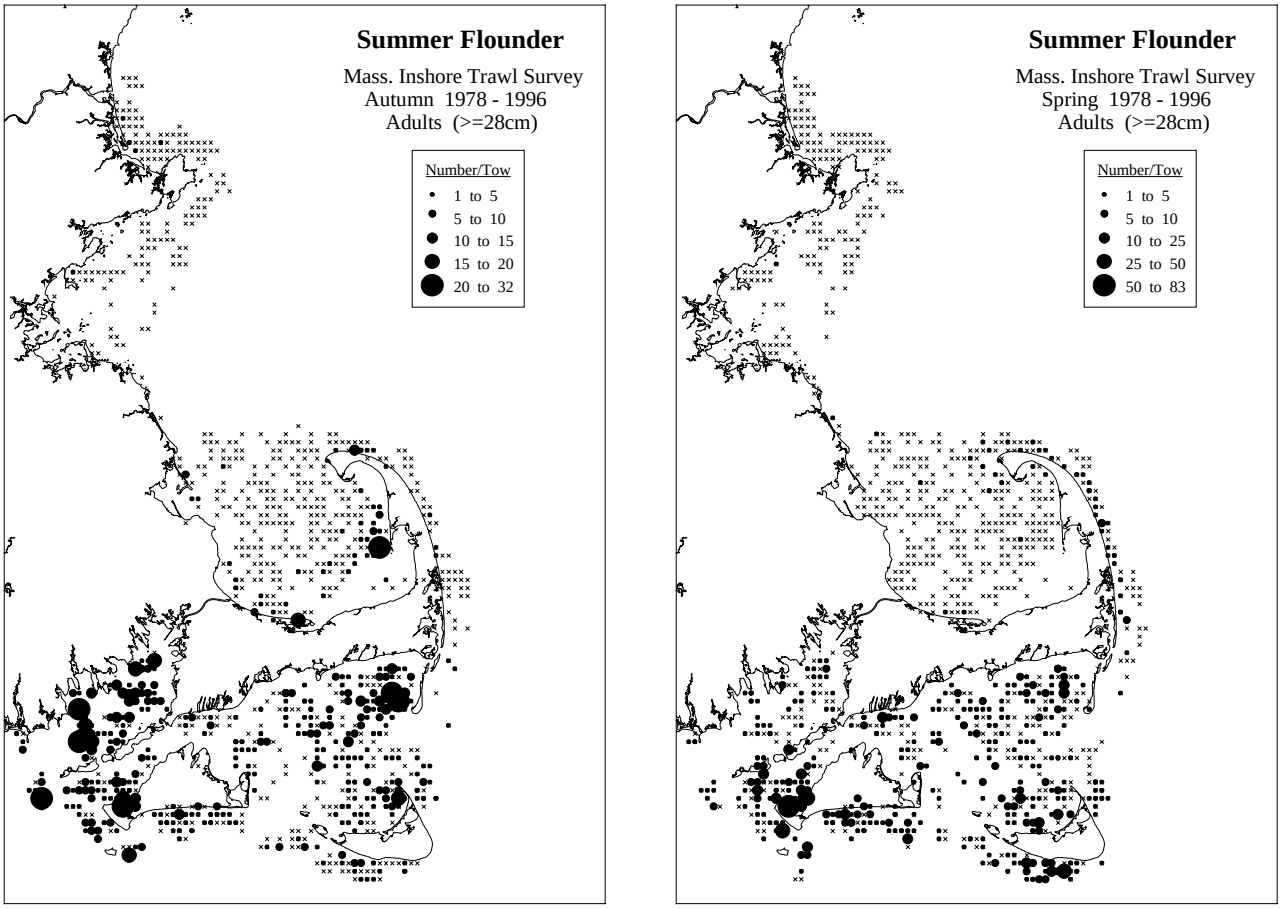


Figure 5. Distribution and abundance of adult summer flounder in Massachusetts coastal waters from shore out to 3 miles during fall (typically September) and spring (typically May), based on bottom trawl surveys by the Massachusetts Division of Marine Fisheries from 1978-1996 (Howe *et al.* 1997; Reid *et al.* 1999). Collections where no adults were caught are shown as small x's.

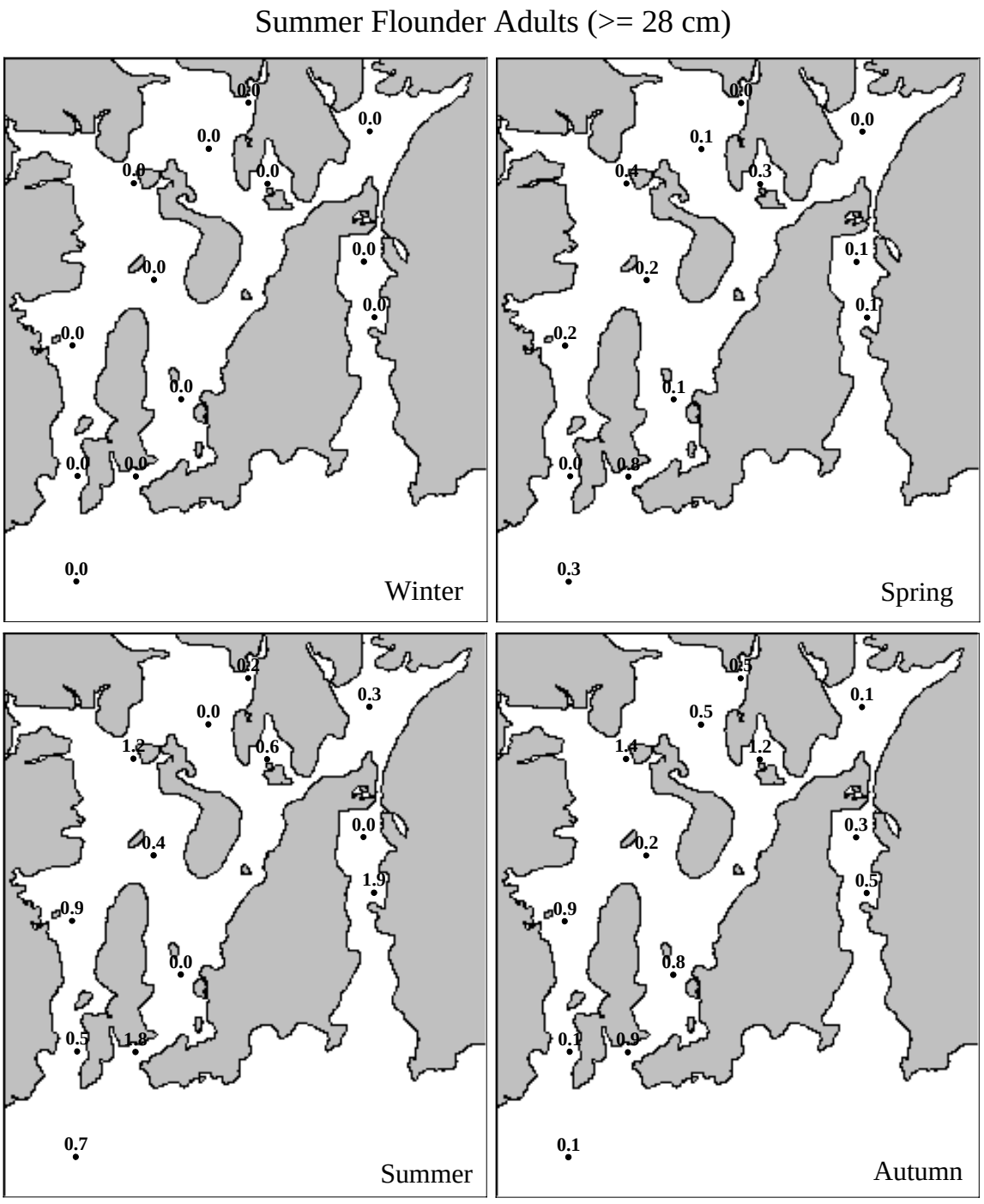


Figure 6. Seasonal distribution and relative abundance of adult summer flounder collected in Narragansett Bay during 1990-1996 Rhode Island Division of Fish and Wildlife bottom trawl surveys of Narragansett Bay. The numbers shown at each station are the average catch per tow rounded to one decimal place [see Reid *et al.* (1999) for details].

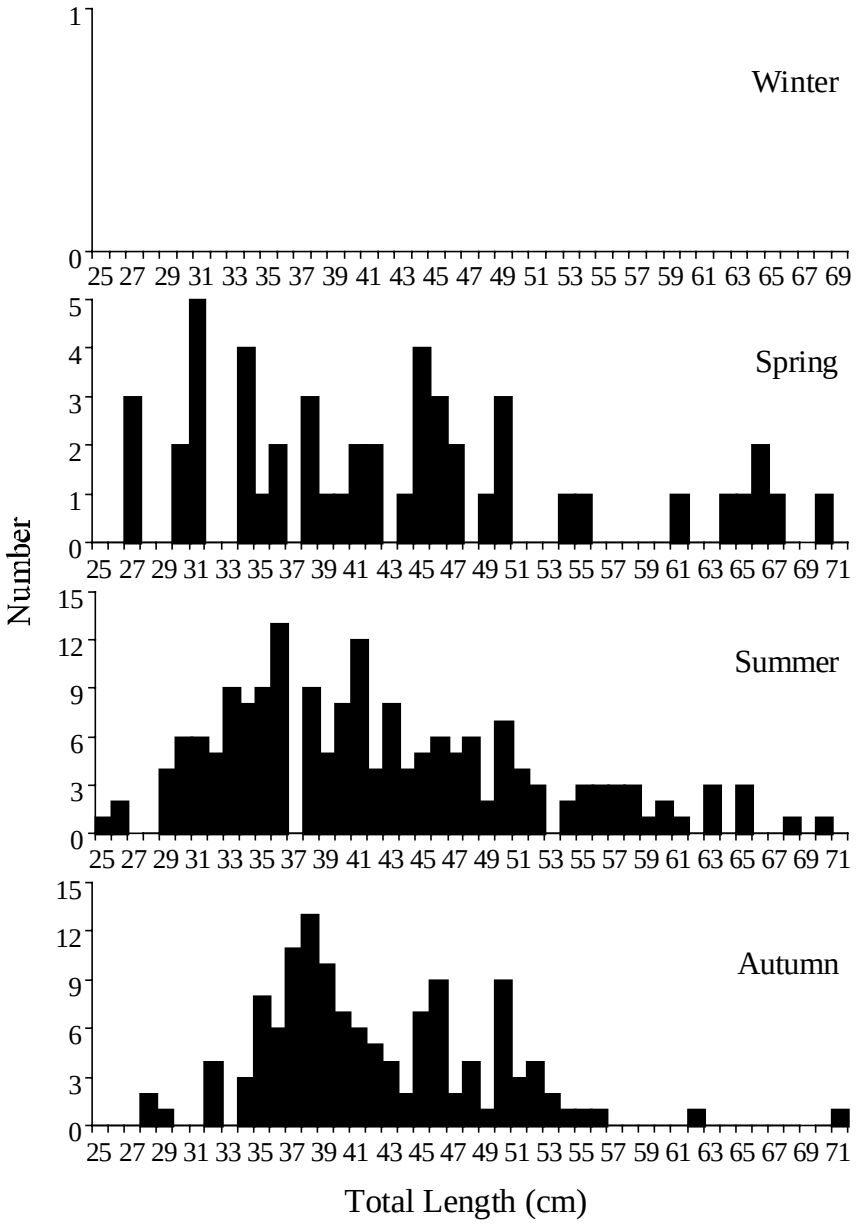


Figure 7. Seasonal length frequencies of summer flounder caught in Narragansett Bay during 1990-1996, from the Rhode Island Division of Fish and Wildlife Narragansett Bay bottom trawl surveys of 1990-1996.

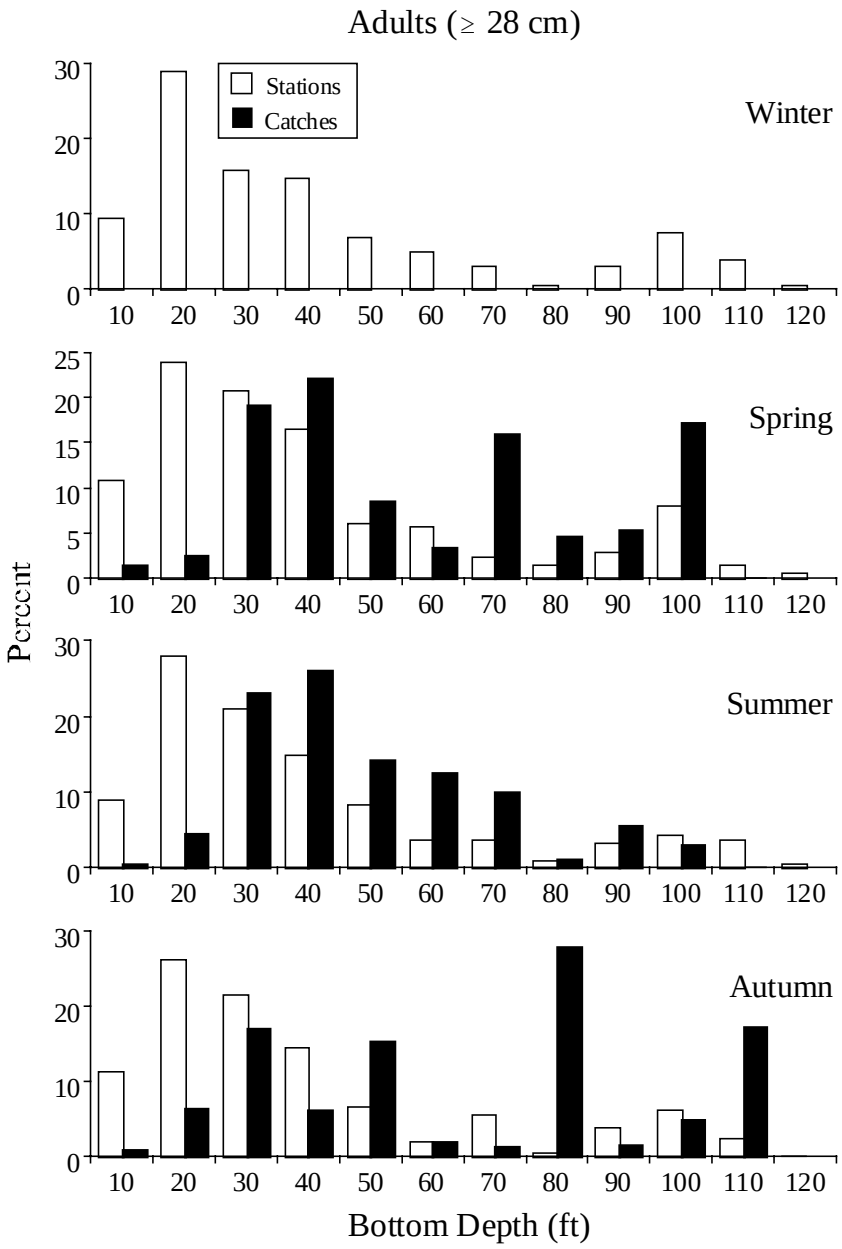


Figure 8. Seasonal abundance of adult summer flounder relative to bottom depth based on Rhode Island Division of Fish and Wildlife bottom trawl surveys of Narragansett Bay, 1990-1996. Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all catches.

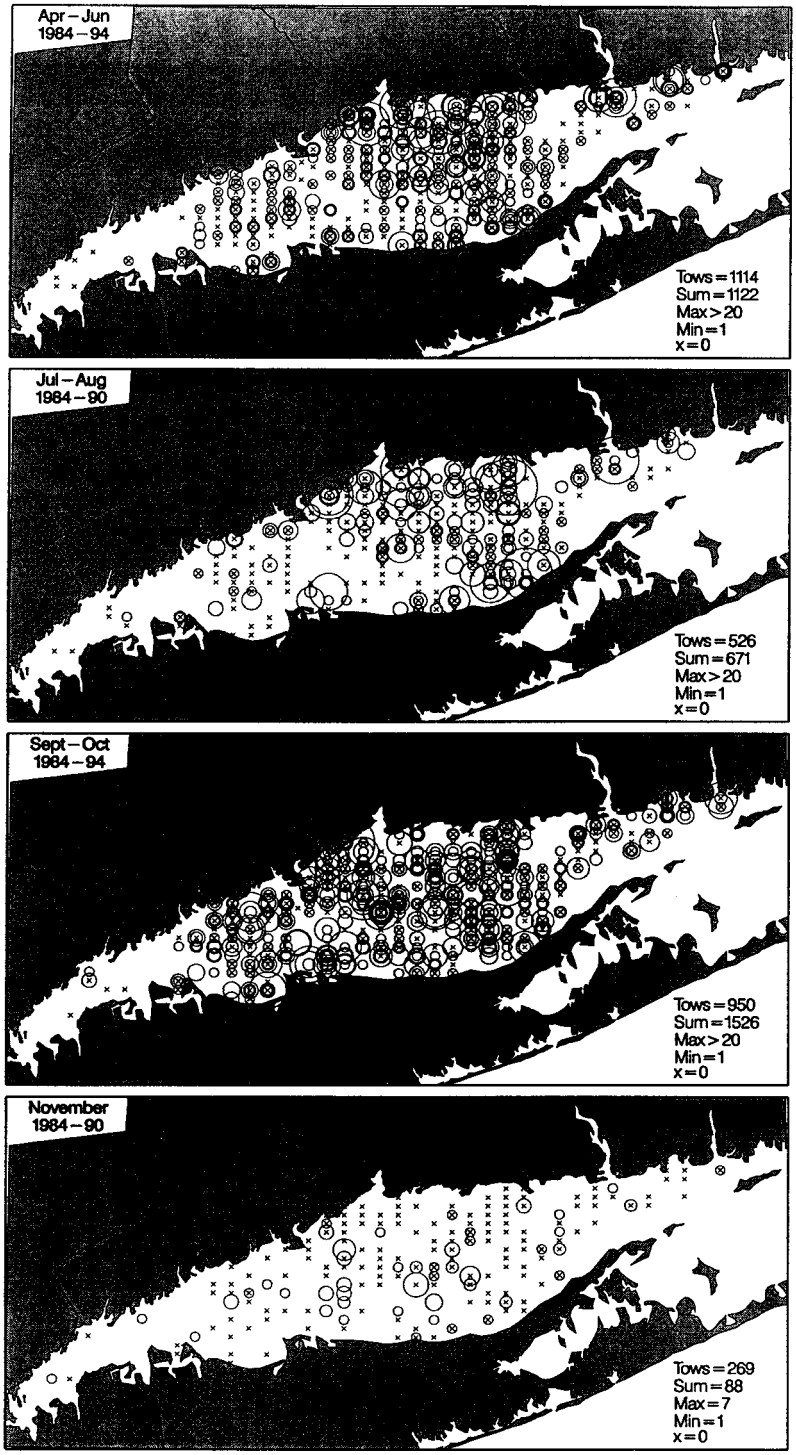


Figure 9. Distribution and abundance of juvenile and adult summer flounder (12-76 cm TL) collected in Long Island Sound, based on the finfish surveys of the Connecticut Fisheries Division, 1984-1994 (from Gottschall *et al.*, in review). Circle diameter is proportional to the number of fish caught, and is scaled to the maximum catch (indicated by "max=" or "max>"). Collections were made with a 14 m otter trawl at about 40 stations chosen by stratified random design.

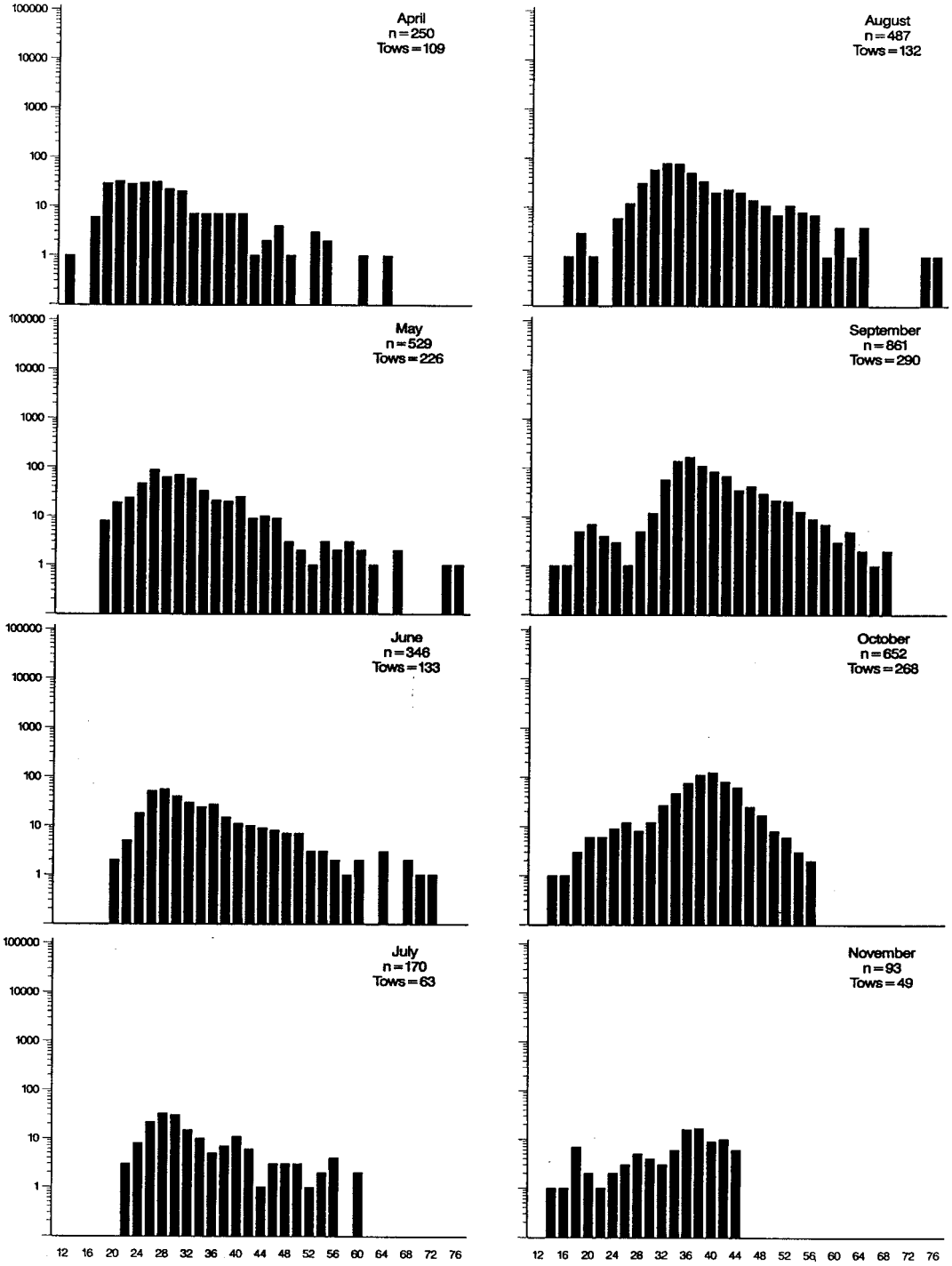


Figure 10. Length frequency distribution (cm) of juvenile and adult summer flounder collected in Long Island Sound, based on the finfish surveys of the Connecticut Fisheries Division, 1984-1994 (from Gottschall *et al.*, in review).

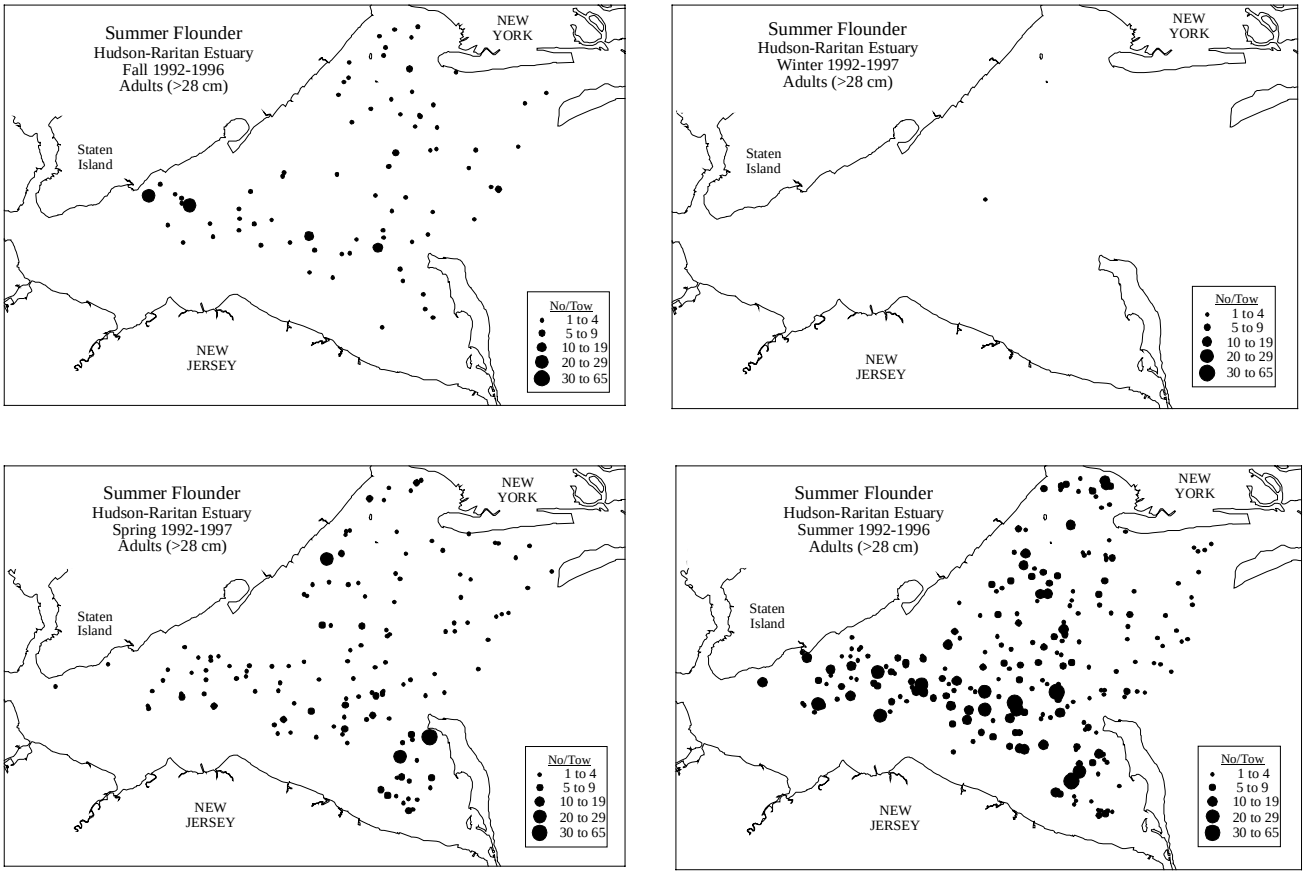


Figure 11. Distribution and relative abundance of adult summer flounder collected in the Hudson-Raritan estuary during Hudson-Raritan trawl surveys in fall (October-December, 1992-1996), winter (January-March, 1992-1997), spring (April and June, 1992-1996), and summer (July and August, 1992-1996) [see Reid *et al.* (1999) for details].

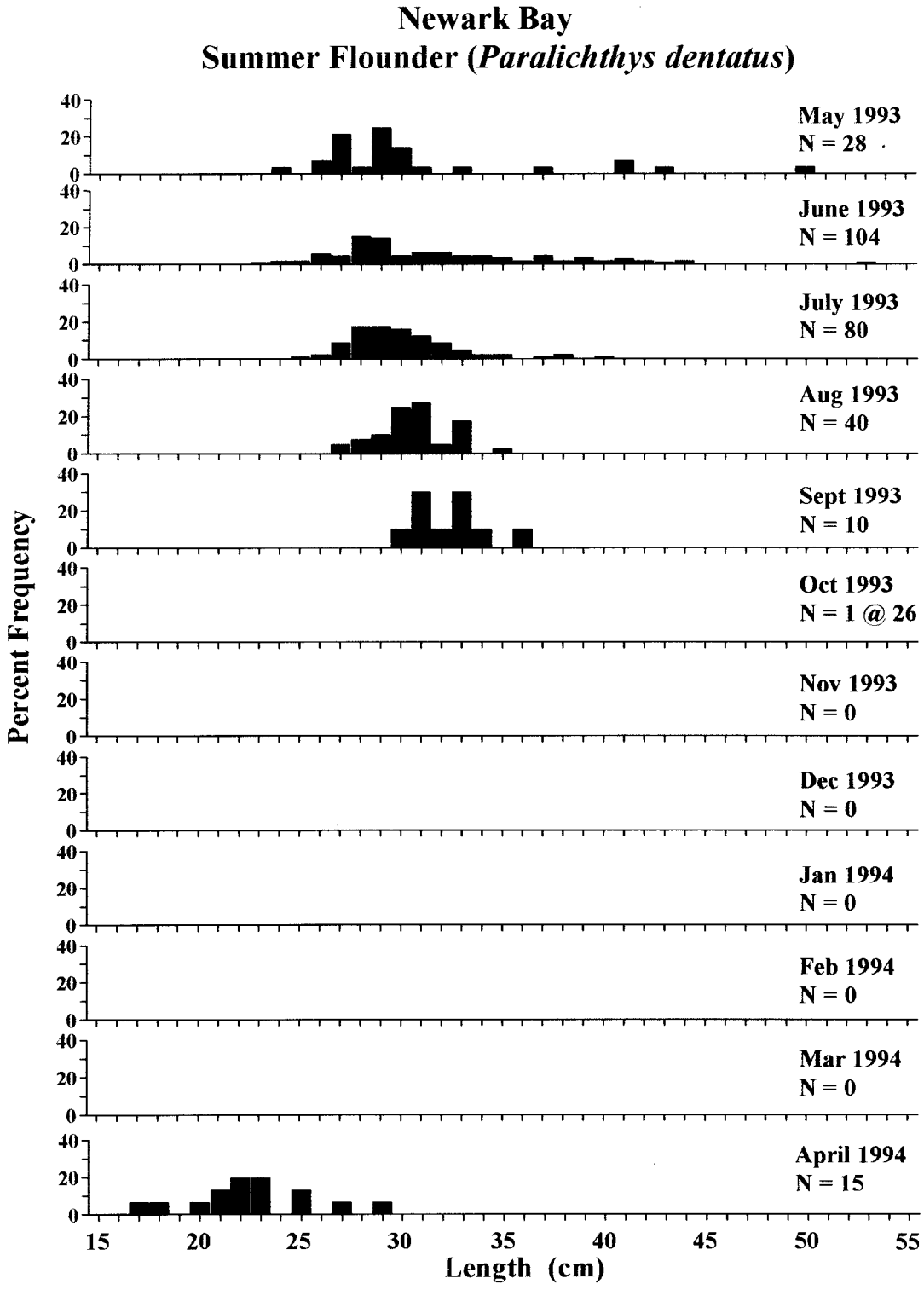


Figure 12. Length-frequency distributions of juvenile and adult summer flounder from Newark Bay, New Jersey. Collected using an 8.5 m otter trawl from May 1993-April 1994 (Wilk *et al*. 1997).

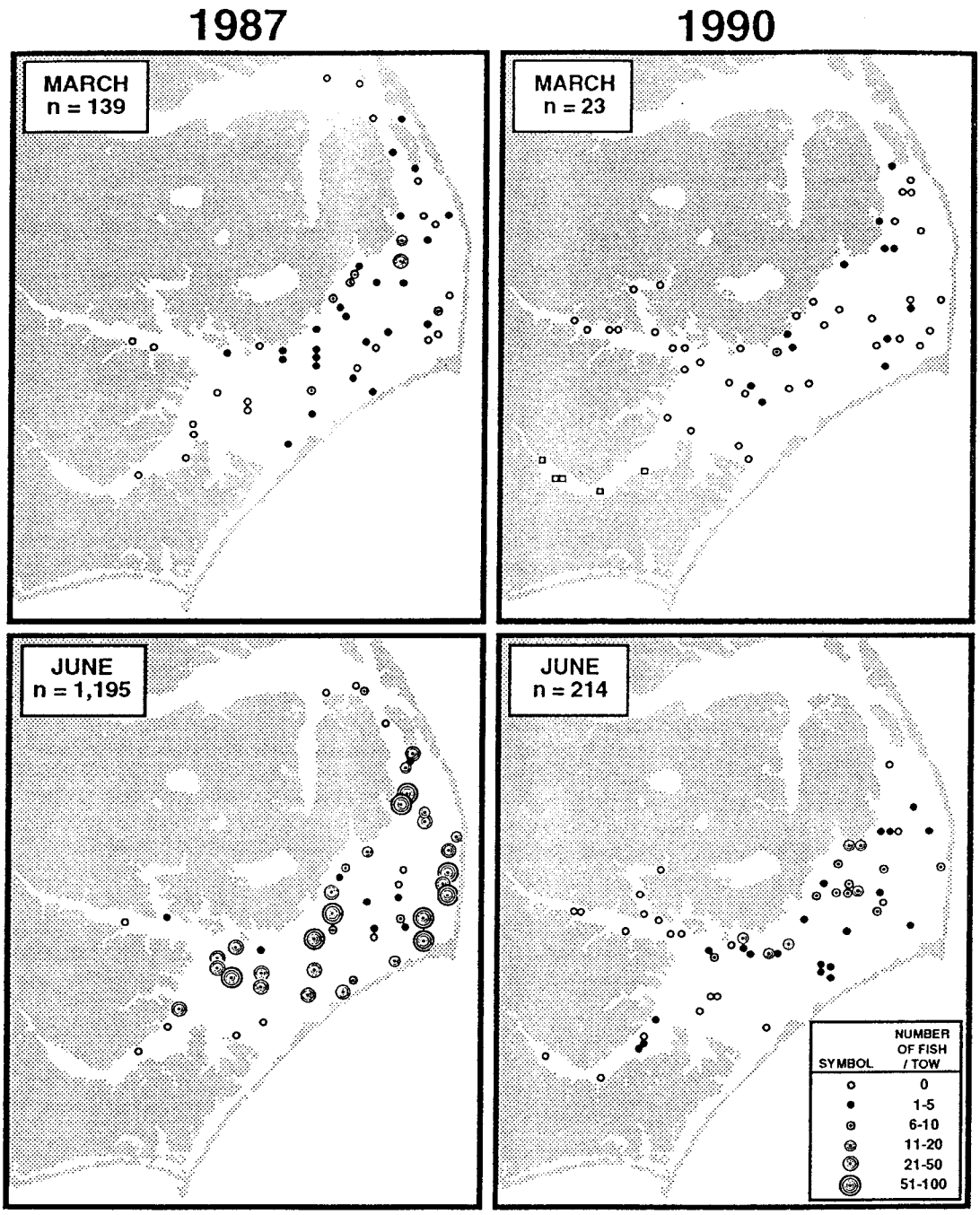


Figure 13. Distribution and abundance of juvenile and adult summer flounder in Pamlico Sound, North Carolina and adjacent estuaries during years of high (1987) and low (1990) abundance. Collections were made by Mongoose trawl at stations chosen by stratified random design. Data based on North Carolina Division of Marine Fisheries trawl surveys, 1987-1991. Adapted from Able and Kaiser (1994).

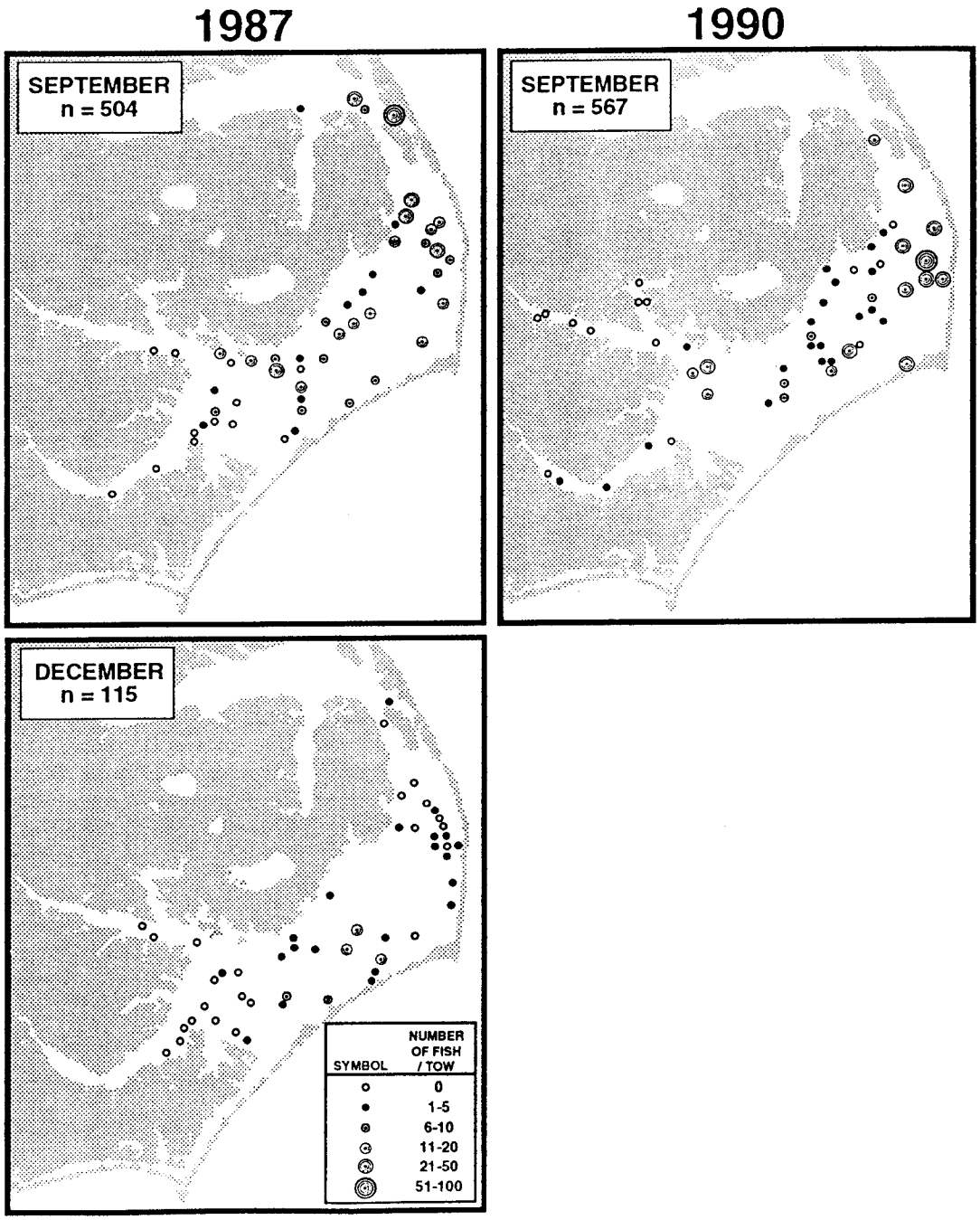


Figure 13. cont'd.

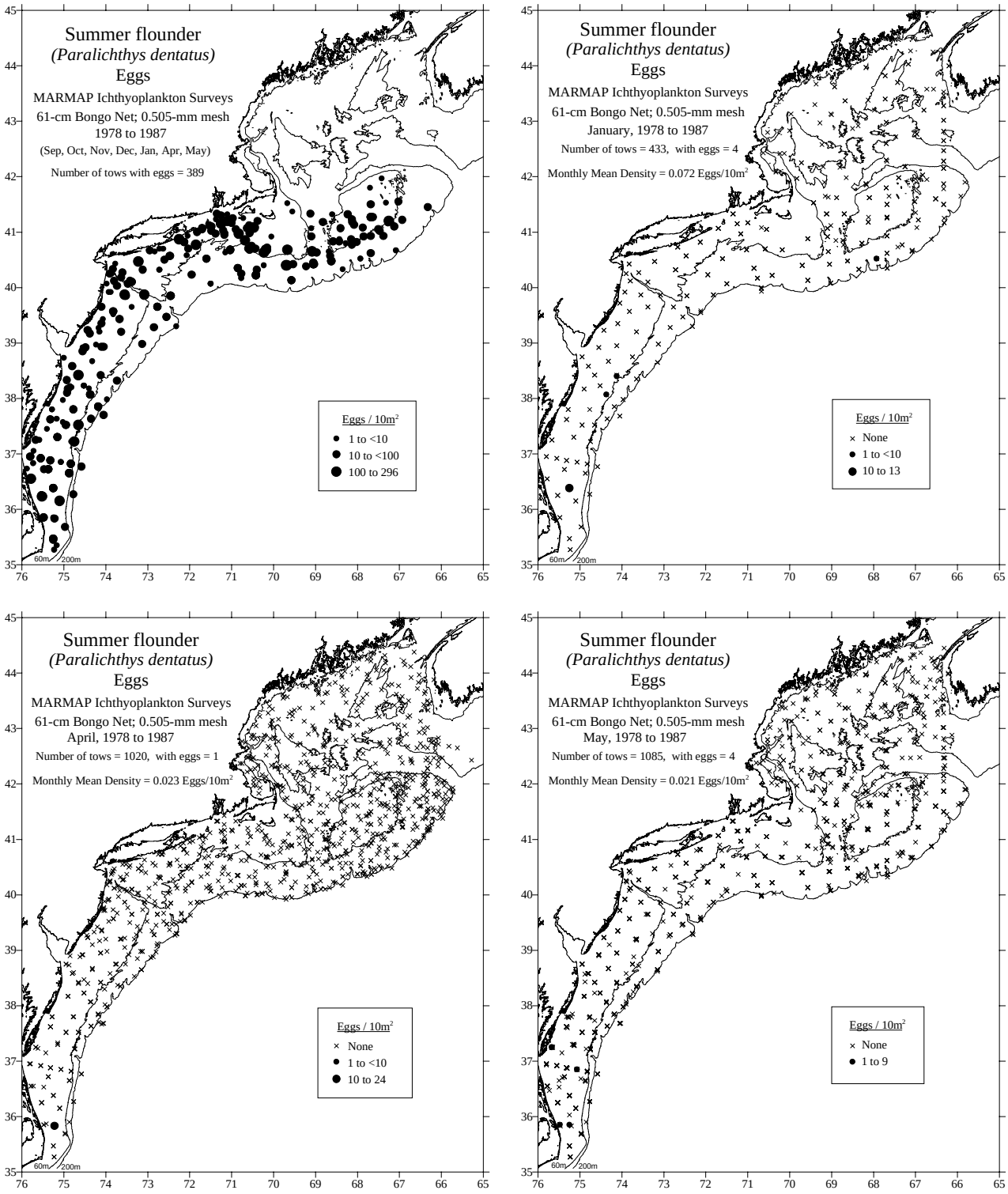
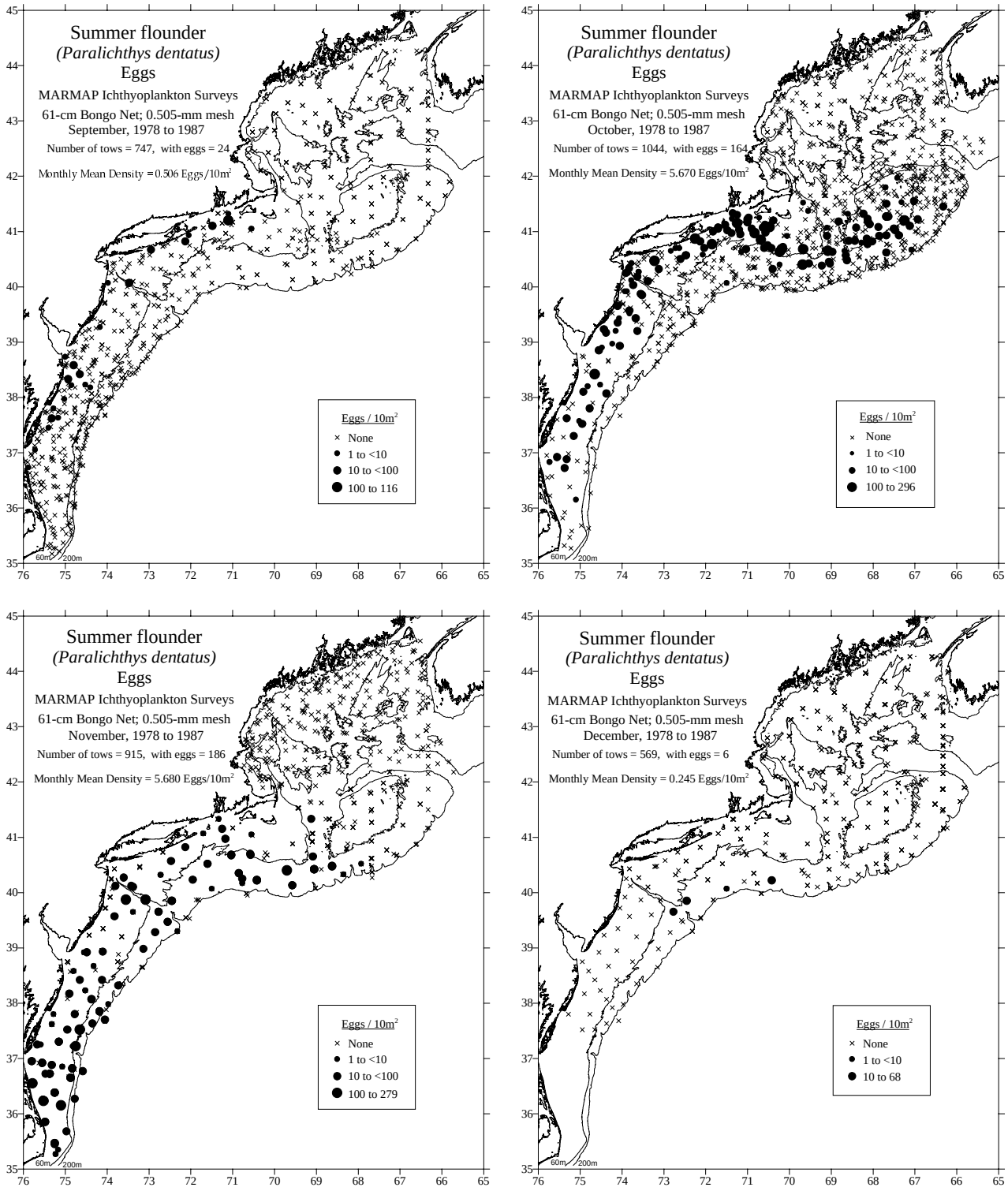


Figure 14. Distribution and abundance of summer flounder eggs collected during NEFSC MARMAP offshore ichthyoplankton surveys from Cape Sable to Cape Hatteras during 1978-1987 [see Reid *et al.* (1999) for details].



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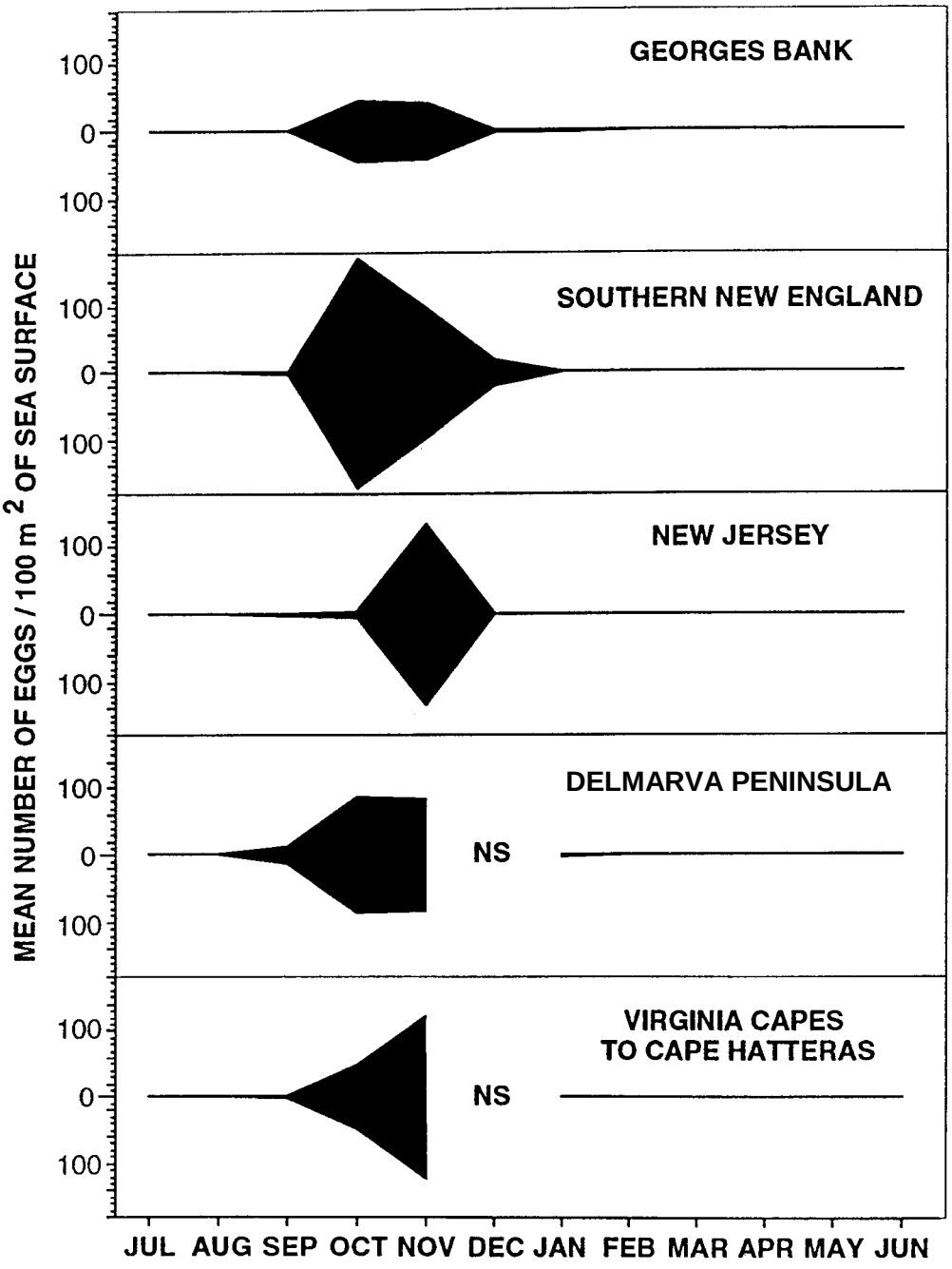


Figure 15. Monthly abundance of summer flounder eggs by region from NEFSC MARMAP offshore ichthyoplankton surveys from Cape Sable to Cape Hatteras during 1979-1981, 1984, and 1985 [see Reid *et al.* (1999) for details]. NS = no samples. Adapted from Able and Kaiser (1994).

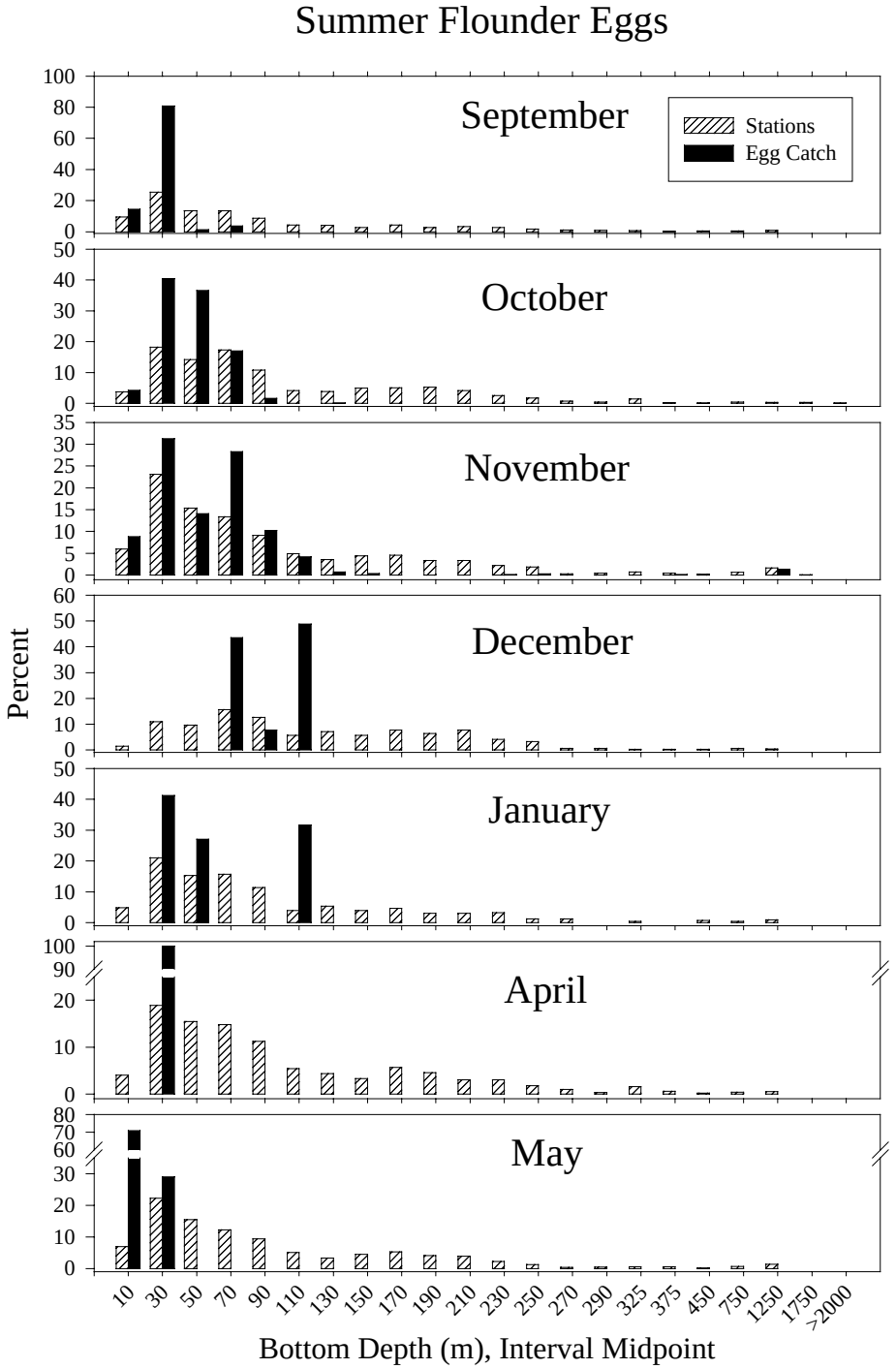


Figure 16. Abundance of summer flounder eggs relative to water depth based on NEFSC MARMAP offshore ichthyoplankton surveys [1978-1987, all years combined; see Reid *et al.* (1999) for details]. Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).

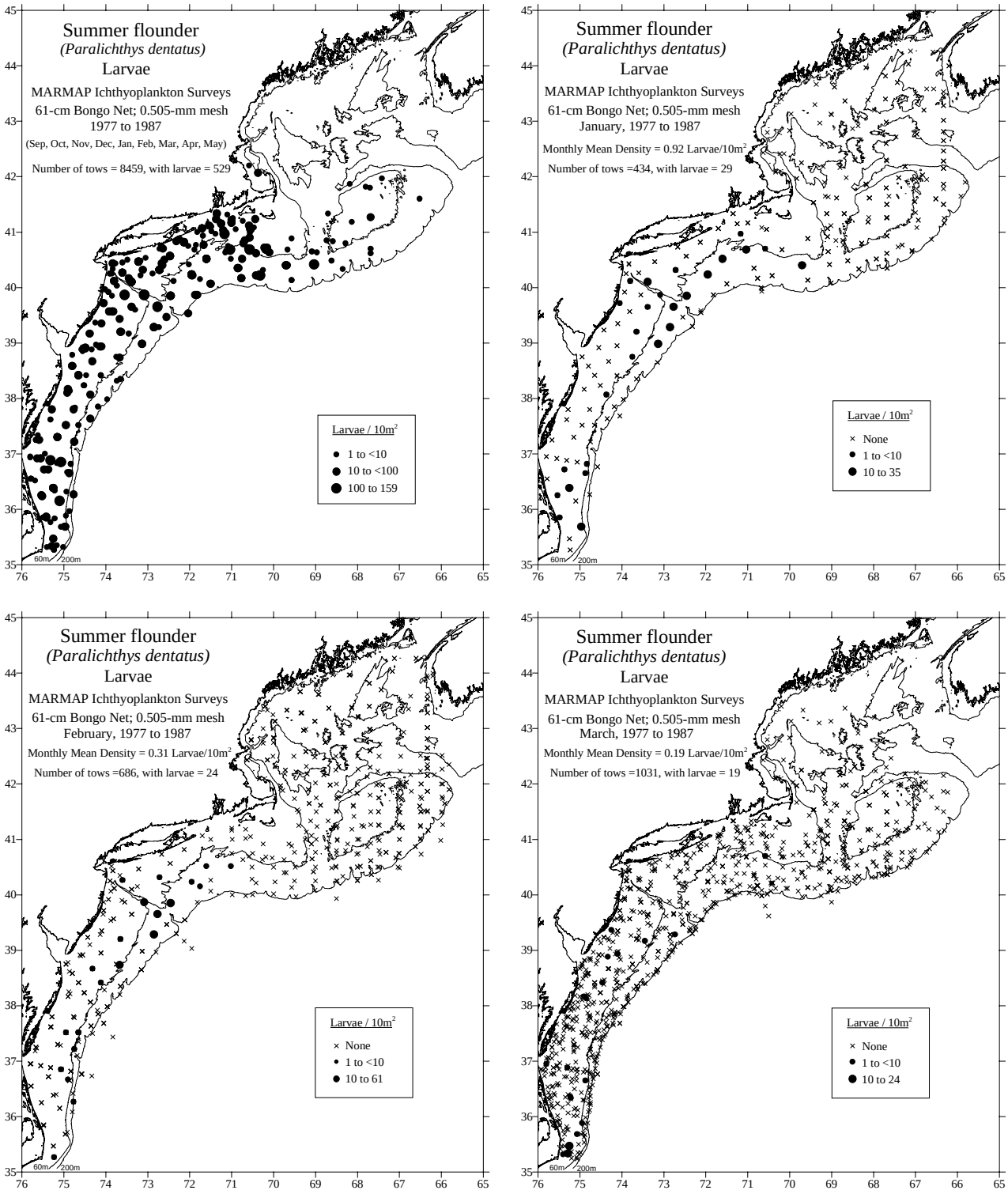


Figure 17. Distribution and abundance of summer flounder larvae collected during NEFSC MARMAP offshore ichthyoplankton surveys from Cape Sable to Cape Hatteras during 1977-1987 [see Reid *et al.* (1999) for details].

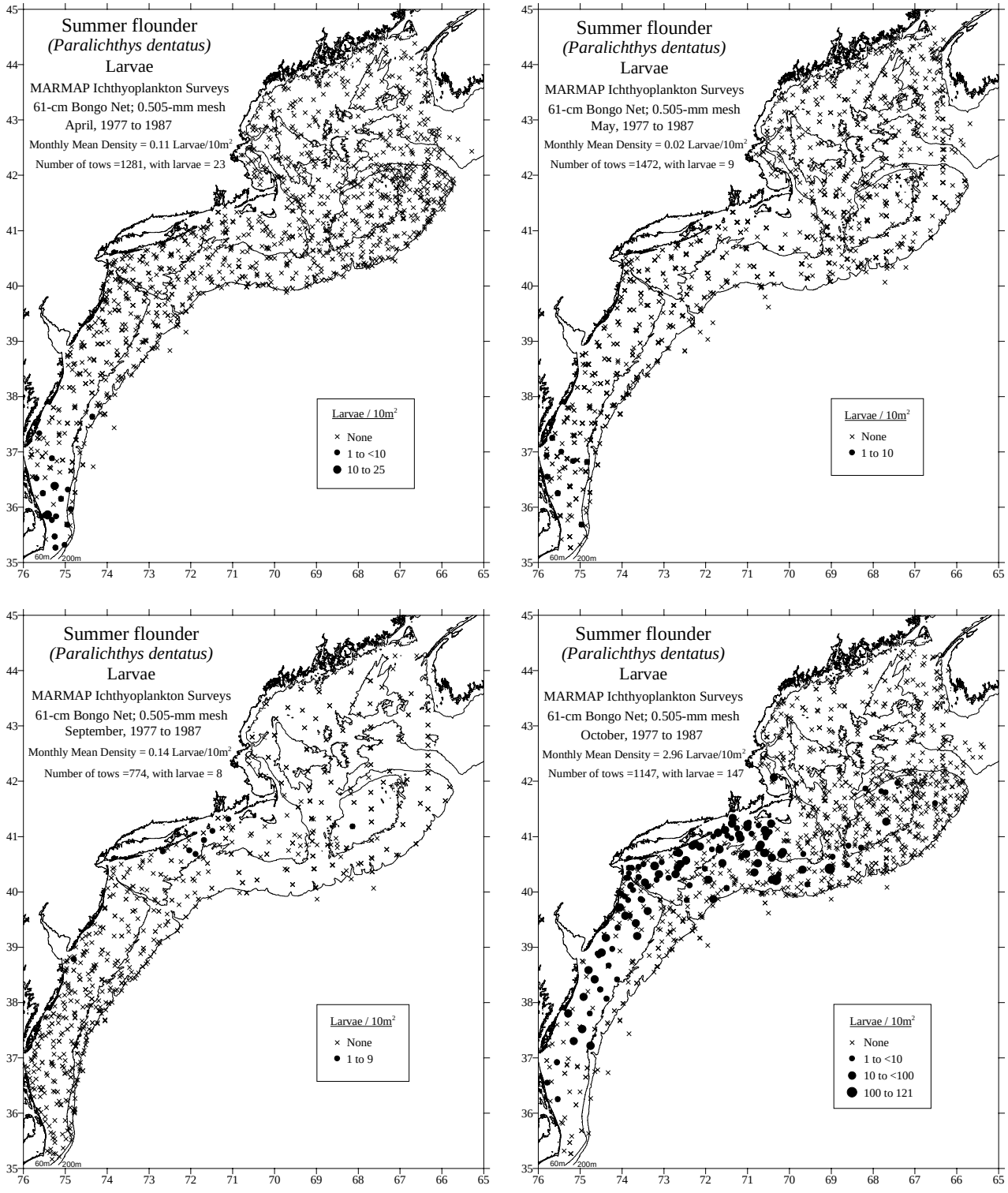


Figure 17. cont'd.

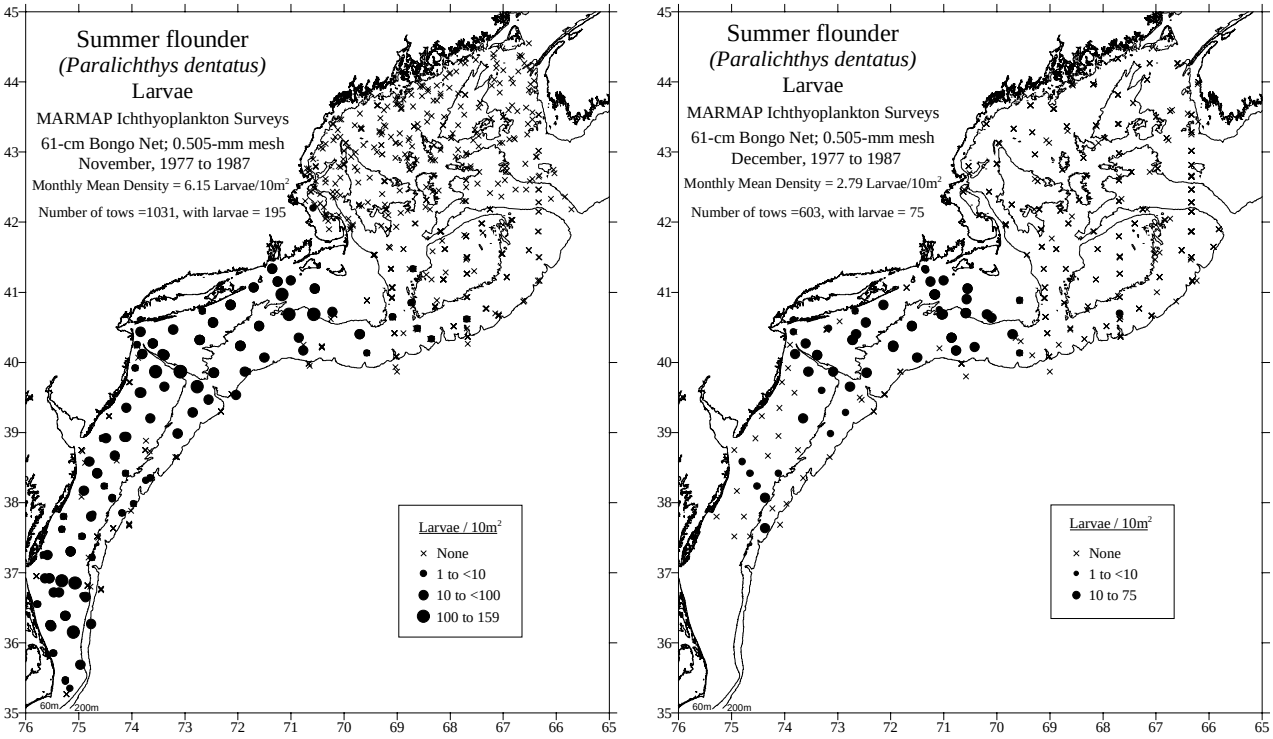


Figure 17. cont'd.

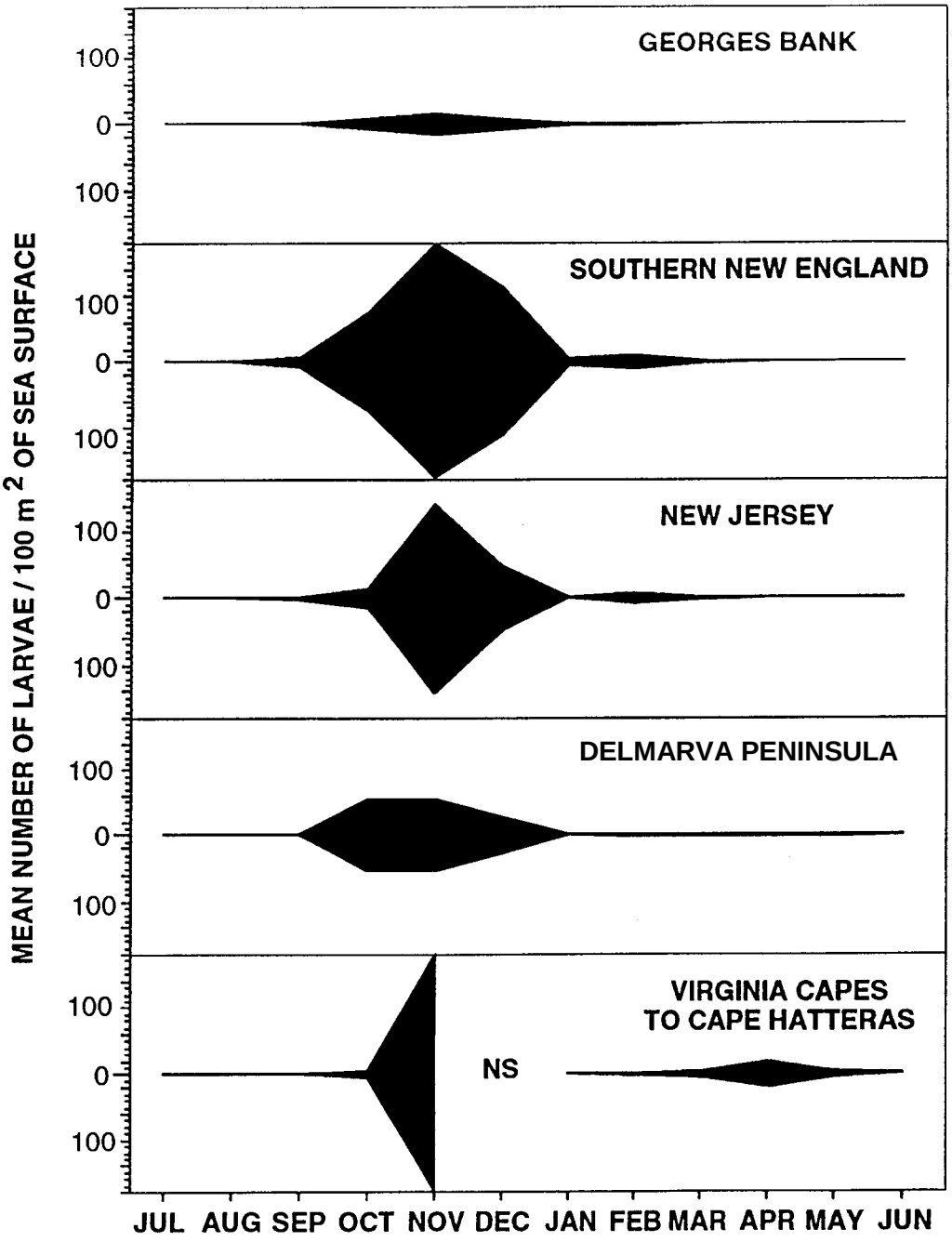


Figure 18. Monthly abundance of summer flounder larvae by region from NEFSC MARMAP offshore ichthyoplankton surveys from Cape Sable to Cape Hatteras during 1979-81, 1984, and 1985 [see Reid *et al.* (1999) for details]. NS = no samples. Adapted from Able and Kaiser (1994).

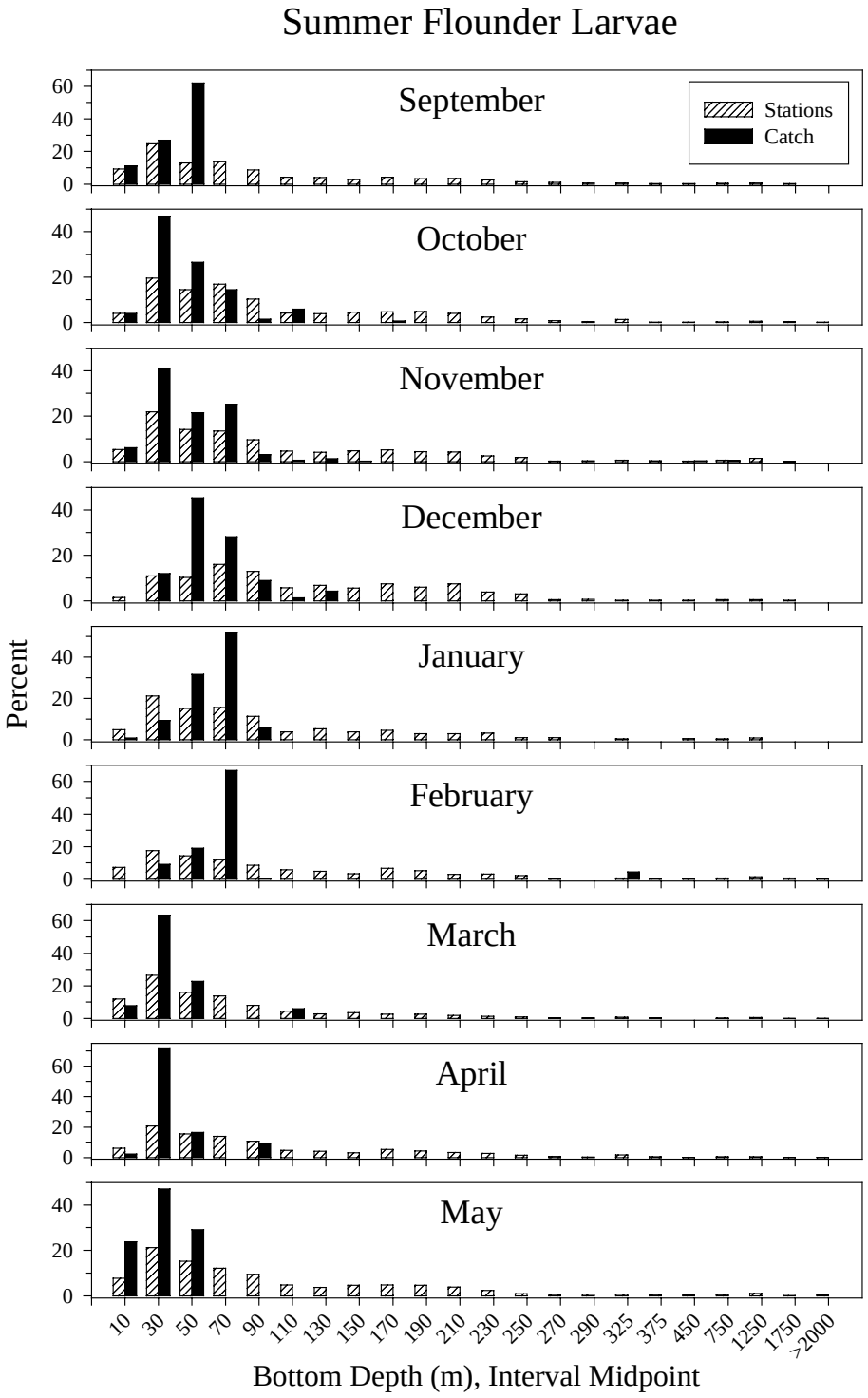


Figure 19. Abundance of summer flounder larvae relative to water depth based on NEFSC MARMAP offshore ichthyoplankton surveys [1977-1987, all years combined; see Reid *et al*. (1999) for details]. Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).

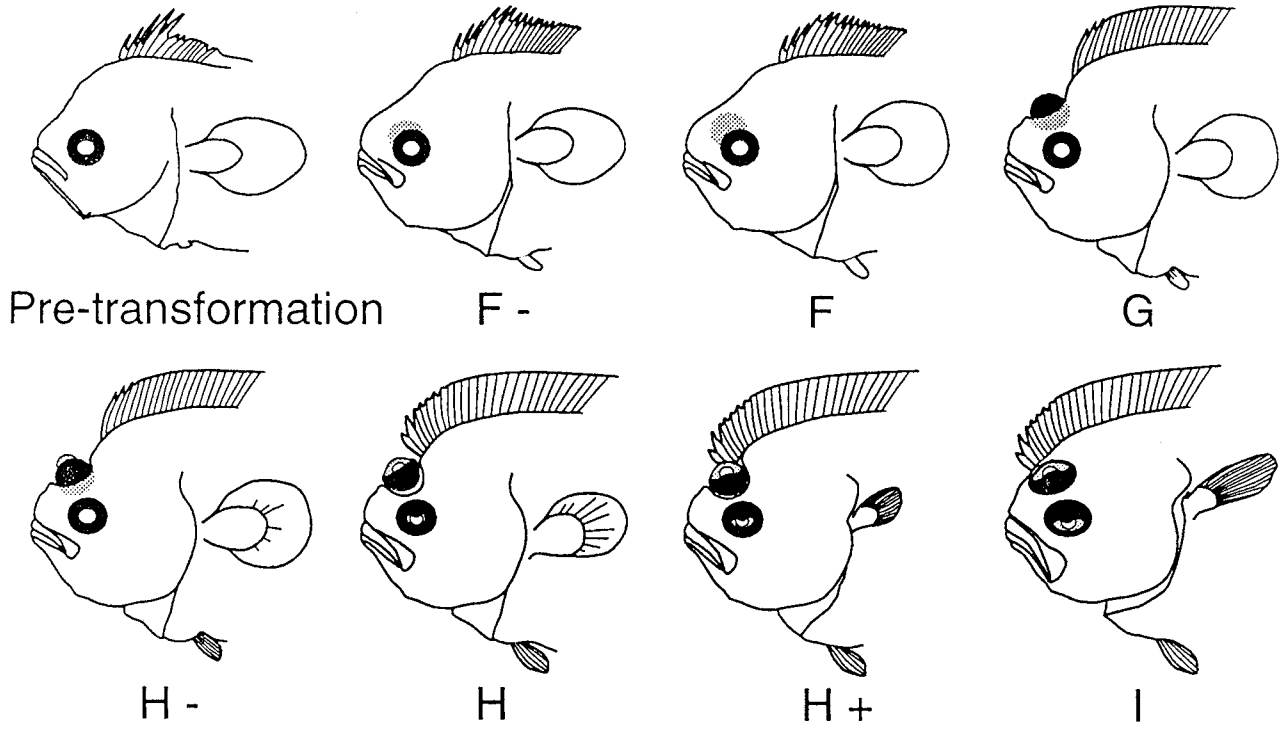


Figure 20. Classification of the transformation stages of summer flounder based on degree of eye migration [adapted from Keefe and Able (1993) and Able and Kaiser (1994)]. The right and left eyes are bilateral and symmetrical in pre-transformation individuals. At the first stage of transformation, F -, the eyes are bilateral but asymmetrical with the right eye just dorsal to the left eye. By stage G, the right eye is visible from the left side of the fish. Stage H - differs from G in that the cornea of the eye is visible from the left side of the fish. At Stage H, the right eye has reached the dorsal midline. By Stage H +, the right eye has reached the left side of the head but has not yet reached its final resting place. At Stage I, the eye is set in the socket and the dorsal canal is closed.

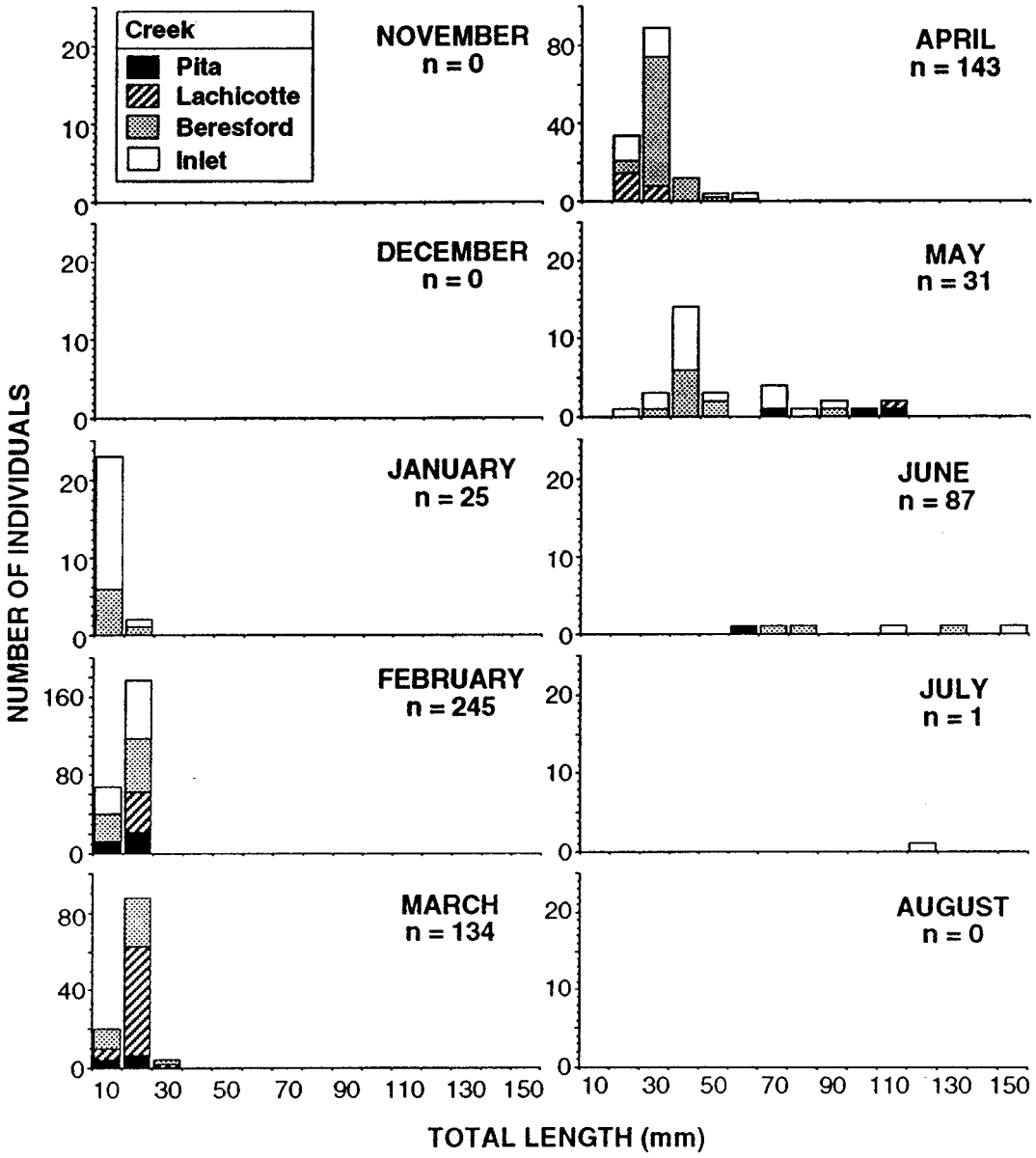
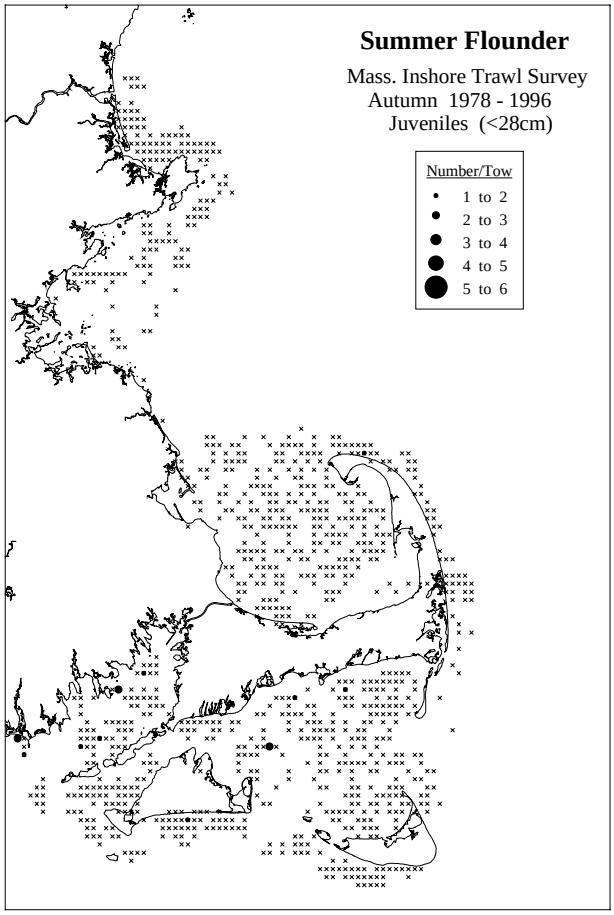


Figure 21. Length frequency distributions for transforming larval and juvenile summer flounder collected during 1986-1987 from estuarine marsh creeks in Charleston Harbor, South Carolina, using a rotenone/block net method (Wenner *et al.* 1990a). Adapted from Able and Kaiser (1994).



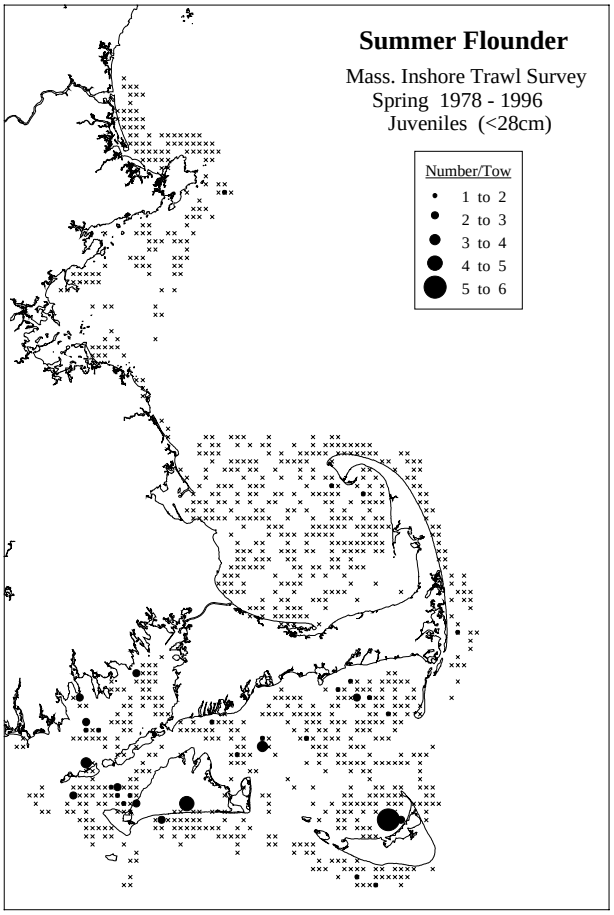


Figure 22. Distribution and abundance of juvenile summer flounder in Massachusetts coastal waters from shore out to 3 miles during fall (typically September) and spring (typically May), based on bottom trawl surveys by the Massachusetts Division of Marine Fisheries from 1978-1996 (Howe *et al.* 1997; Reid *et al.* 1999). Collections where no juveniles were caught are shown as small x's.

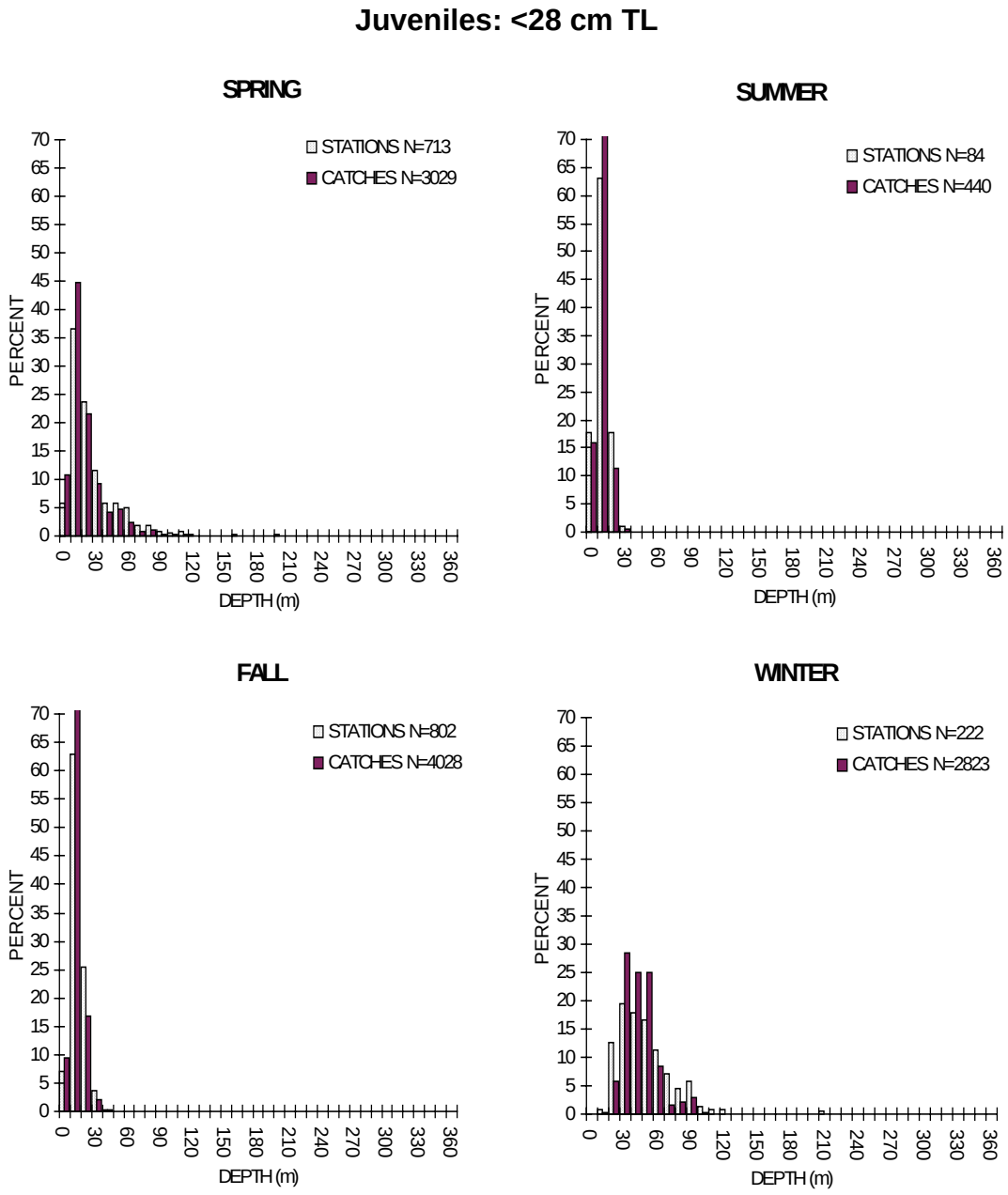


Figure 23. Seasonal abundance of juvenile summer flounder relative to water depth based on NEFSC bottom trawl surveys [1963-1997, all years combined; see Reid *et al.* (1999) for details]. Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).

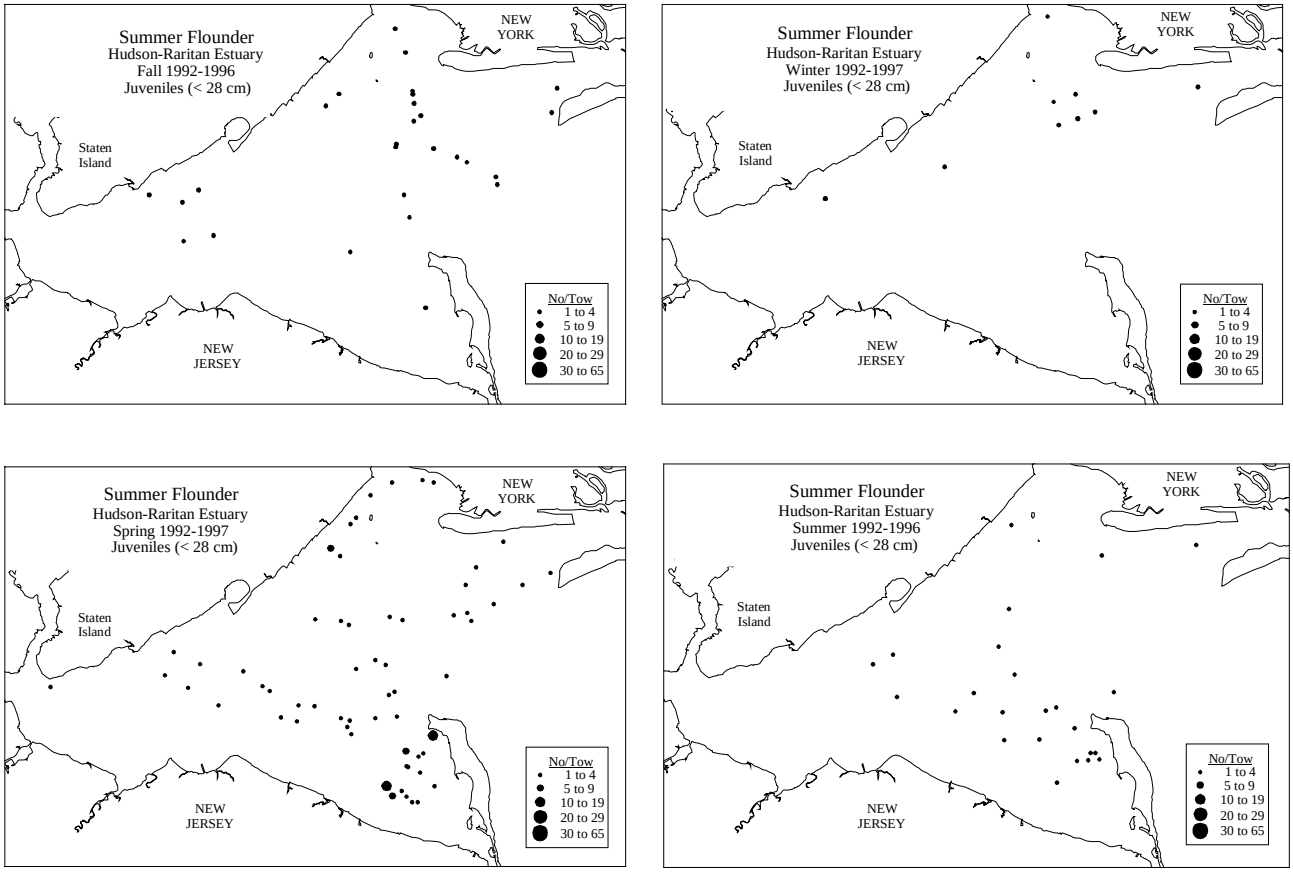


Figure 24. Distribution and relative abundance of juvenile summer flounder collected in the Hudson-Raritan estuary during Hudson-Raritan trawl surveys in fall (October-December, 1992-1996), winter (January-March, 1992-1997), spring (April and June, 1992-1996), and summer (July and August, 1992-1996) [see Reid *et al.* (1999) for details].

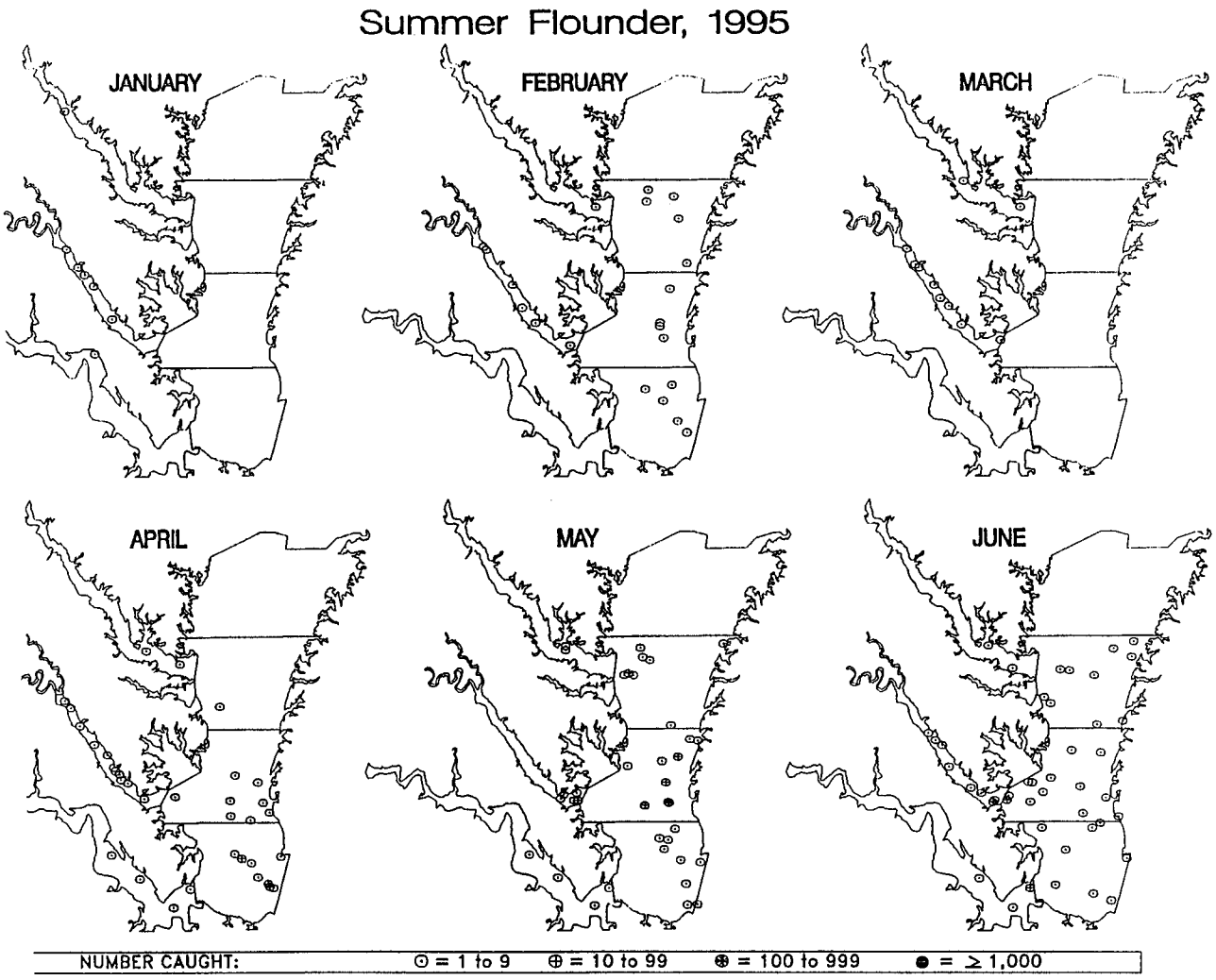


Figure 25. Monthly distribution of summer flounder in the main stem of Chesapeake Bay and in the major Virginia tributaries (from north to south: Rappahannock, York, James Rivers) from January-December 1995. Density values are the total number of individuals caught in a 9.1 m semi-balloon otter trawl with 38 mm mesh and 6.4 mm codend. Adapted from Geer and Austin (1996).

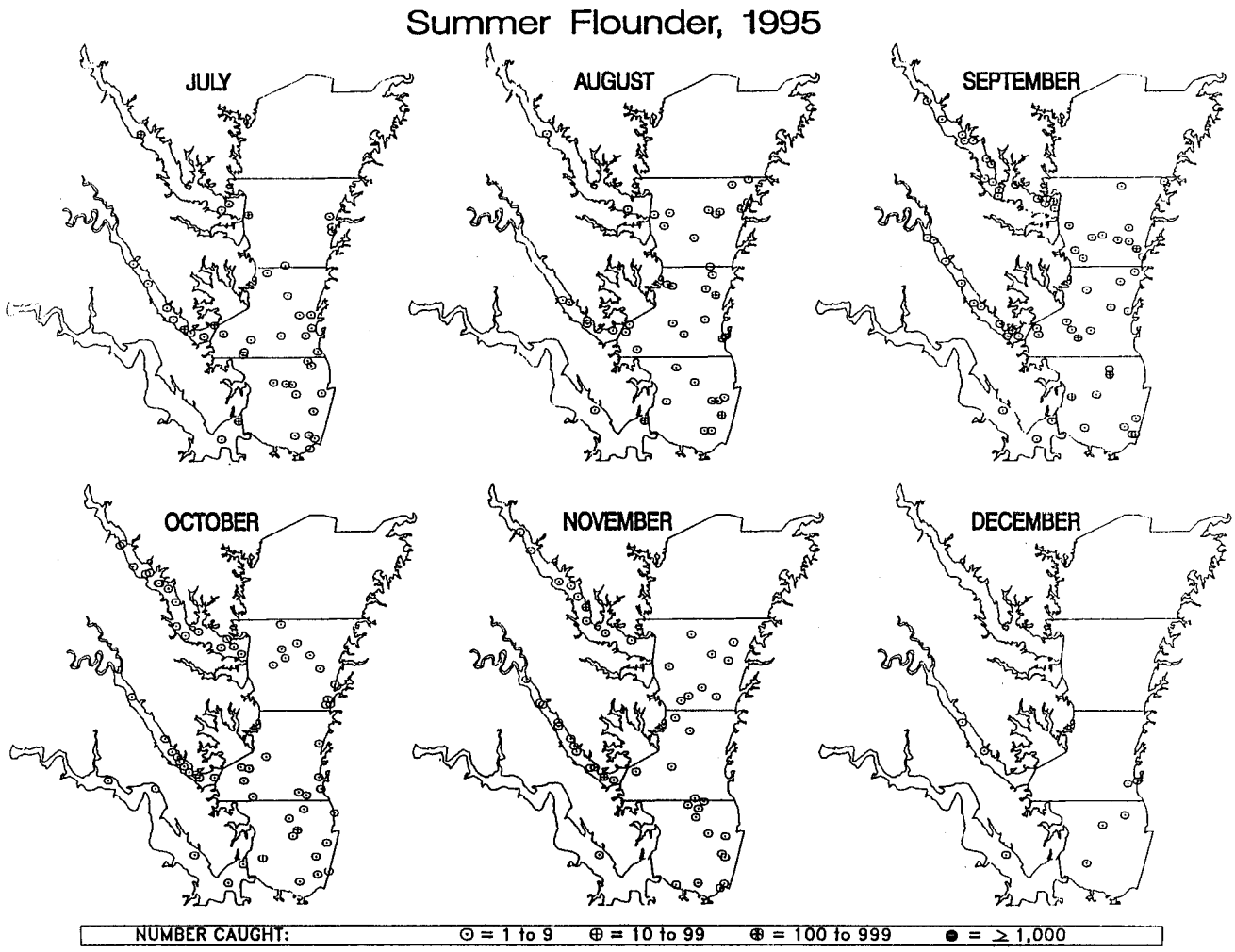
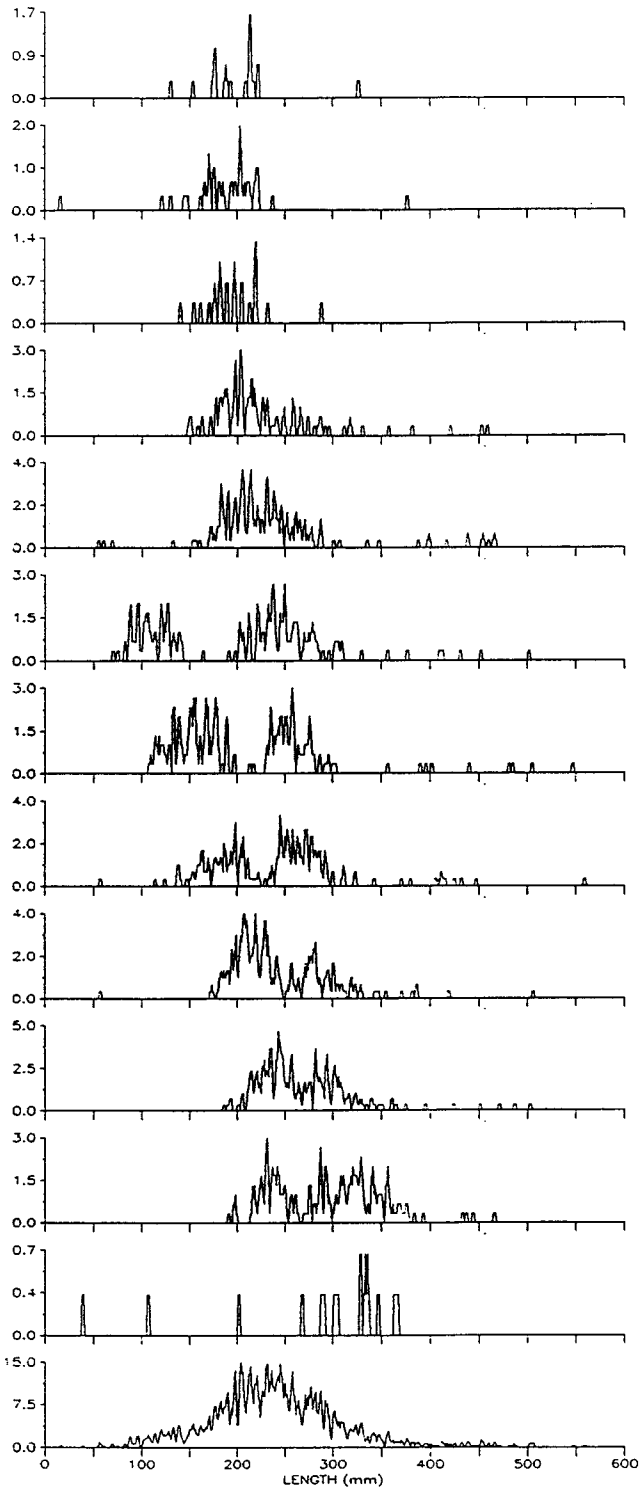


Figure 25. cont'd.



JANUARY	950109 – 950113				
NO. CGHT.	–	19	MEAN SIZE	–	199.1
NO. MEAS.	–	19	S.E. SIZE	–	9.1
NO. HAULS	–	40	MIN. SIZE	–	128
CAT./HAUL	–	0.5	MAX. SIZE	–	325
FEBRUARY	950201 – 950216				
NO. CGHT.	–	42	MEAN SIZE	–	187.4
NO. MEAS.	–	42	S.E. SIZE	–	7.3
NO. HAULS	–	73	MIN. SIZE	–	14
CAT./HAUL	–	0.6	MAX. SIZE	–	375
MARCH	950301 – 950313				
NO. CGHT.	–	23	MEAN SIZE	–	194.2
NO. MEAS.	–	23	S.E. SIZE	–	6.4
NO. HAULS	–	40	MIN. SIZE	–	138
CAT./HAUL	–	0.6	MAX. SIZE	–	286
APRIL	950406 – 950418				
NO. CGHT.	–	105	MEAN SIZE	–	225
NO. MEAS.	–	105	S.E. SIZE	–	5.6
NO. HAULS	–	73	MIN. SIZE	–	146
CAT./HAUL	–	1.4	MAX. SIZE	–	457
MAY	950503 – 950511				
NO. CGHT.	–	176	MEAN SIZE	–	231.1
NO. MEAS.	–	176	S.E. SIZE	–	5
NO. HAULS	–	79	MIN. SIZE	–	53
CAT./HAUL	–	2.2	MAX. SIZE	–	465
JUNE	950601 – 950614				
NO. CGHT.	–	165	MEAN SIZE	–	200.8
NO. MEAS.	–	165	S.E. SIZE	–	6.6
NO. HAULS	–	88	MIN. SIZE	–	68
CAT./HAUL	–	1.9	MAX. SIZE	–	500
JULY	950705 – 950724				
NO. CGHT.	–	181	MEAN SIZE	–	208
NO. MEAS.	–	181	S.E. SIZE	–	5.8
NO. HAULS	–	88	MIN. SIZE	–	106
CAT./HAUL	–	2.1	MAX. SIZE	–	545
AUGUST	950801 – 950810				
NO. CGHT.	–	195	MEAN SIZE	–	237.7
NO. MEAS.	–	195	S.E. SIZE	–	4.7
NO. HAULS	–	88	MIN. SIZE	–	55
CAT./HAUL	–	2.2	MAX. SIZE	–	557
SEPTEMBER	950905 – 950920				
NO. CGHT.	–	210	MEAN SIZE	–	241.4
NO. MEAS.	–	210	S.E. SIZE	–	3.5
NO. HAULS	–	105	MIN. SIZE	–	55
CAT./HAUL	–	2	MAX. SIZE	–	504
OCTOBER	951002 – 951018				
NO. CGHT.	–	224	MEAN SIZE	–	266.2
NO. MEAS.	–	224	S.E. SIZE	–	3.3
NO. HAULS	–	105	MIN. SIZE	–	184
CAT./HAUL	–	2.1	MAX. SIZE	–	501
NOVEMBER	951110 – 951133				
NO. CGHT.	–	170	MEAN SIZE	–	292.2
NO. MEAS.	–	170	S.E. SIZE	–	4.1
NO. HAULS	–	99	MIN. SIZE	–	189
CAT./HAUL	–	1.7	MAX. SIZE	–	464
DECEMBER	951201 – 951213				
NO. CGHT.	–	16	MEAN SIZE	–	281.9
NO. MEAS.	–	16	S.E. SIZE	–	23.1
NO. HAULS	–	102	MIN. SIZE	–	37
CAT./HAUL	–	0.2	MAX. SIZE	–	365
JAN – DEC	950109 – 951213				
NO. CGHT.	–	1526	MEAN SIZE	–	237.3
NO. MEAS.	–	1526	S.E. SIZE	–	1.8
NO. HAULS	–	980	MIN. SIZE	–	14
CAT./HAUL	–	1.6	MAX. SIZE	–	557

Figure 26. Monthly length frequency summary for summer flounder in the main stem of Chesapeake Bay and the major Virginia tributaries (Rappahannock, York, James Rivers) from January-December 1995. The y-axis represents the total number caught for each size class, in mm. The bottom plot is a summary of all fish for the entire year. Adapted from Geer and Austin (1996).

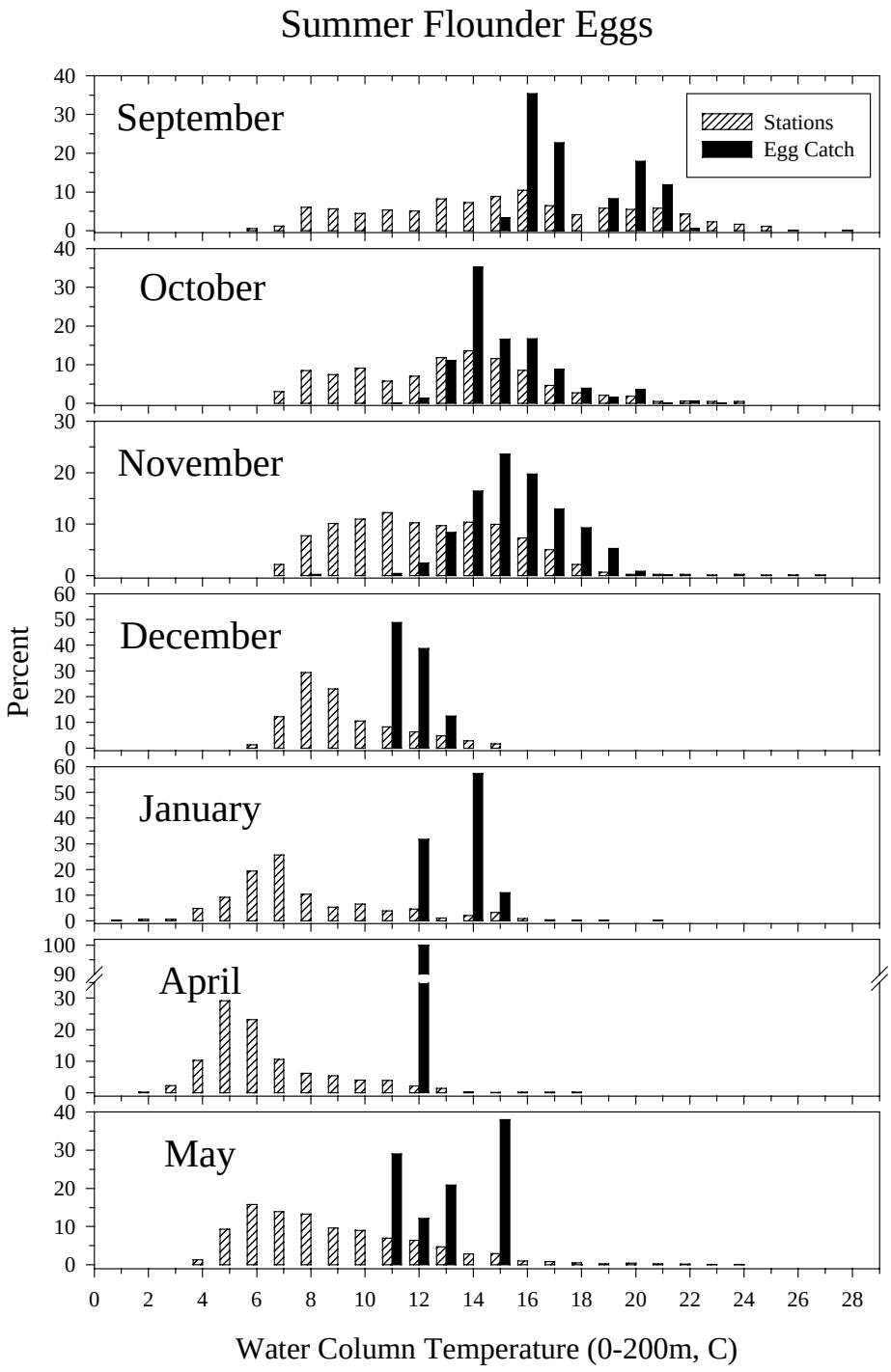


Figure 27. Abundance of summer flounder eggs relative to water column temperature (to a maximum of 200 m) based on NEFSC MARMAP offshore ichthyoplankton surveys [1978-1987, all years combined; see Reid *et al*. (1999) for details]. Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).

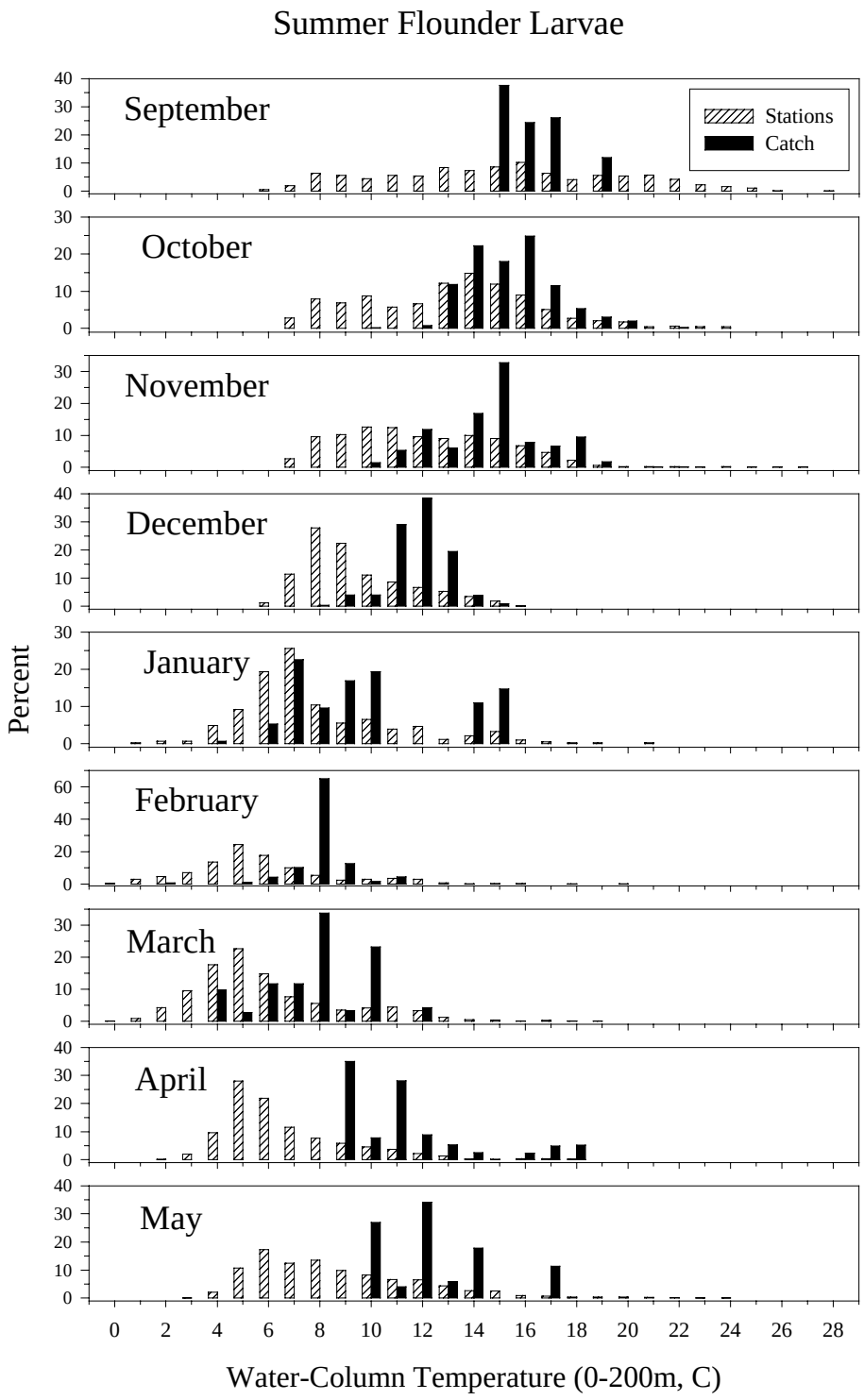


Figure 28. Abundance of summer flounder larvae relative to water column temperature (to a maximum of 200 m) based on NEFSC MARMAP offshore ichthyoplankton surveys [1977-1987, all years combined; see Reid *et al.* (1999) for details]. Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).

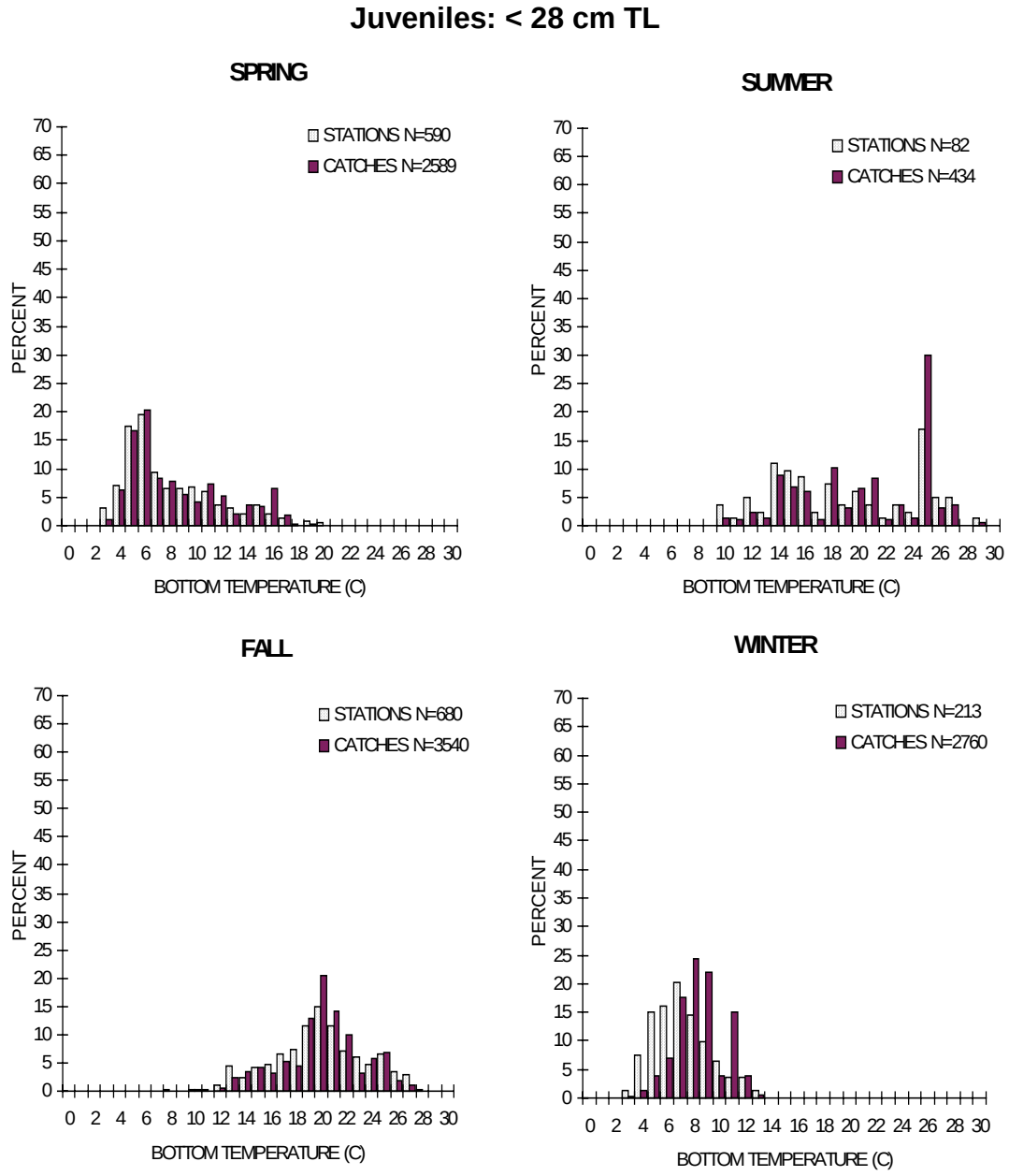


Figure 29. Seasonal abundance of juvenile summer flounder relative to bottom water temperature based on NEFSC bottom trawl surveys [1963-1997, all years combined; see Reid *et al.* (1999) for details]. Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).

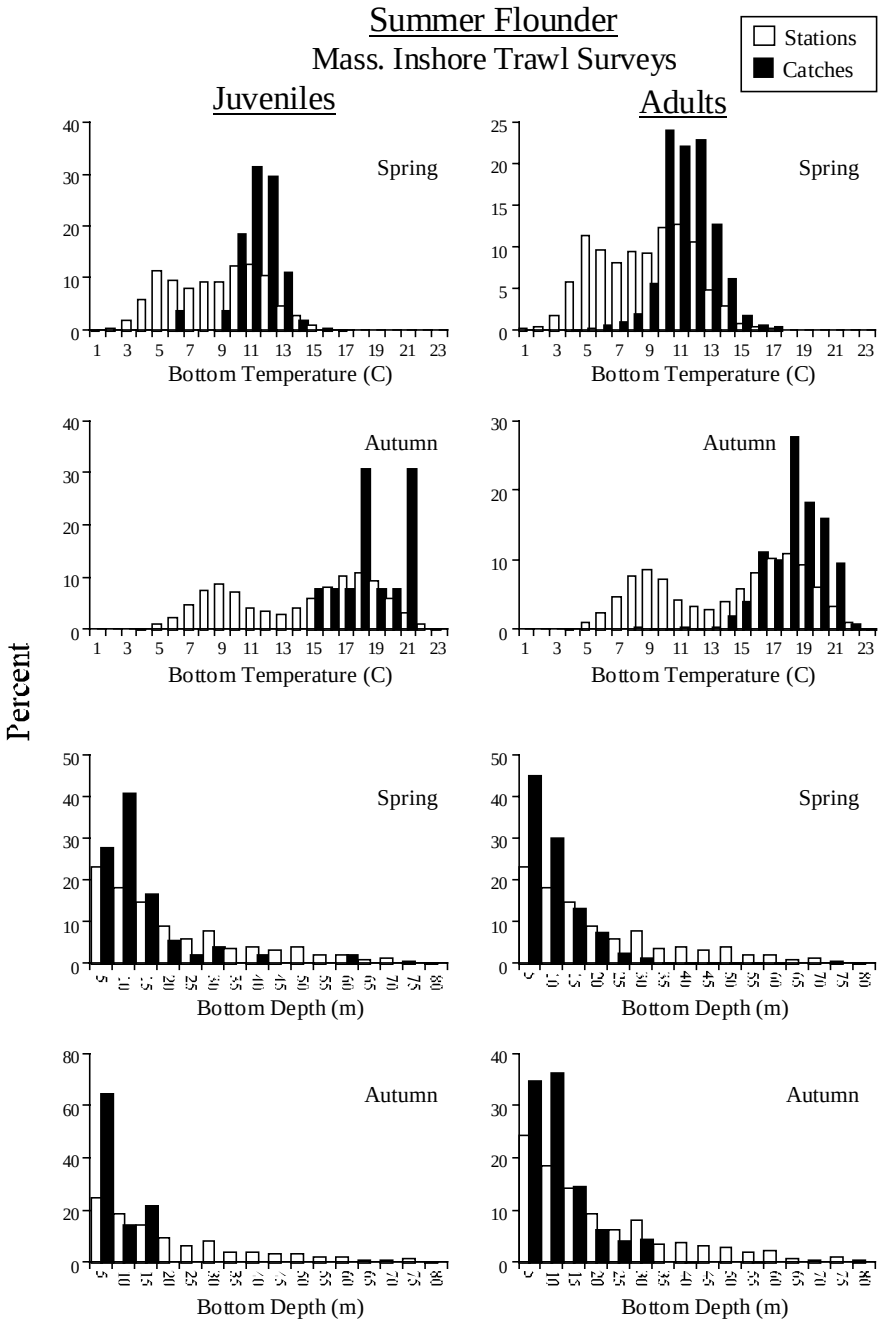


Figure 30. Abundance of juvenile and adult summer flounder relative to bottom water temperature and depth based on Massachusetts inshore trawl surveys (spring and autumn 1978-1996, all years combined). Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).

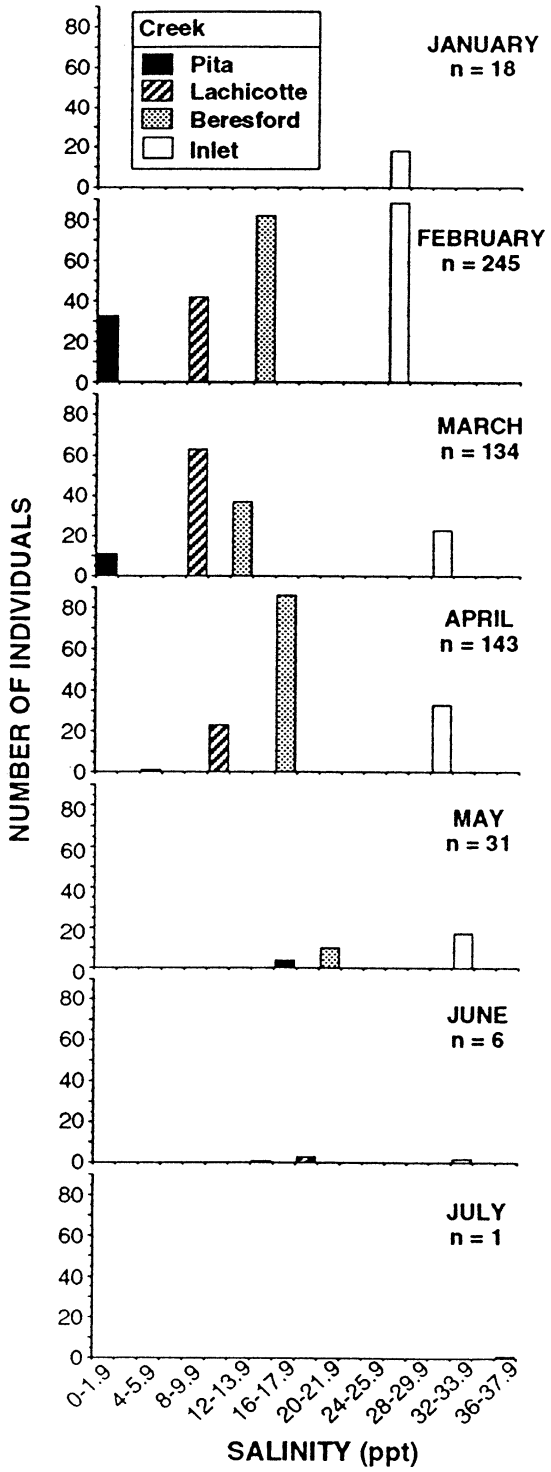


Figure 31. Abundance of juvenile summer flounder relative to salinity in four Charleston Harbor, South Carolina marsh creeks during 1987. Fish were collected using a rotenone/block net method [data based on Wenner *et al.* (1990a)]. Adapted from Able and Kaiser (1994).

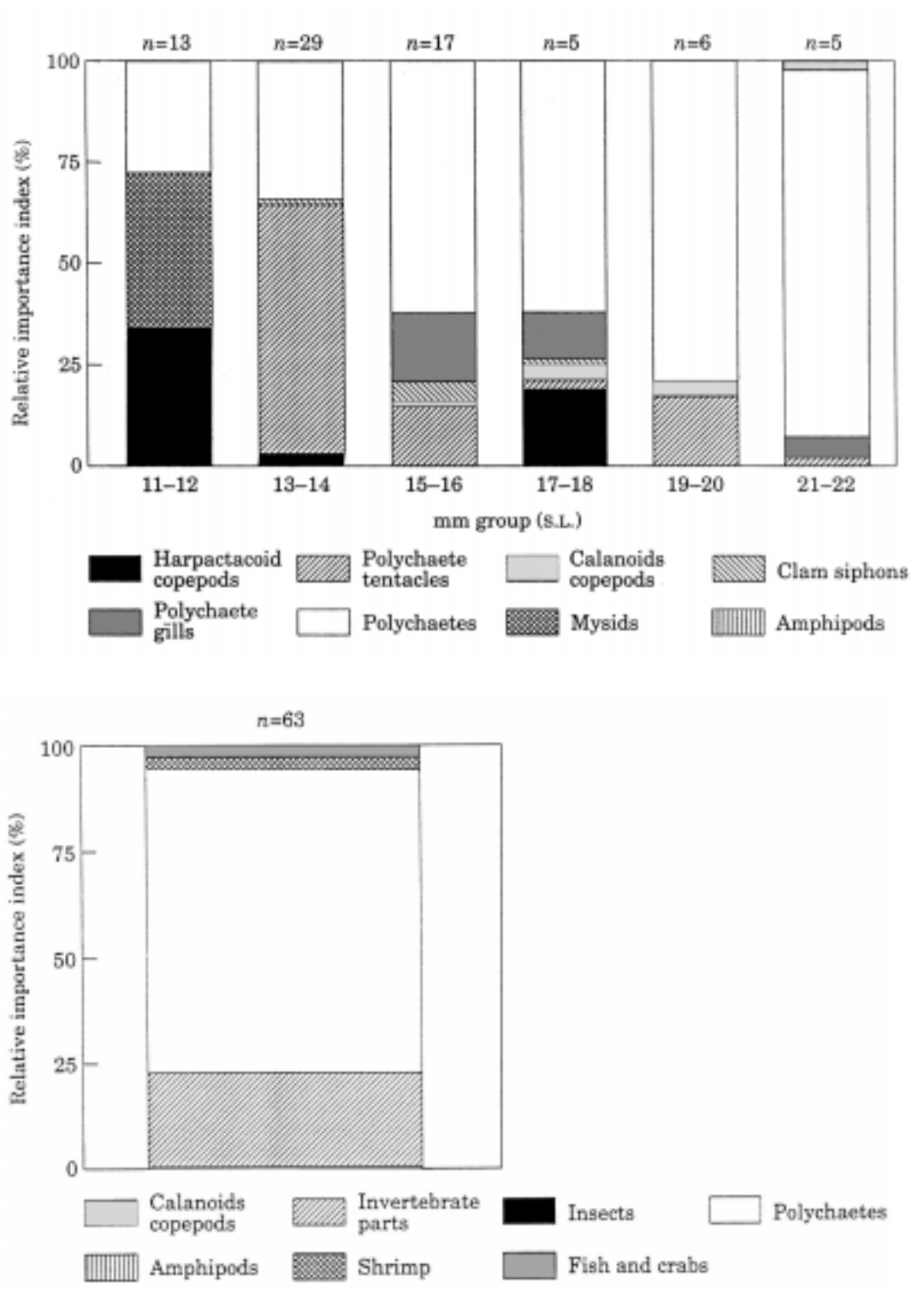


Figure 32. Relative importance of each diet item (percentage of total number multiplied by the frequency of occurrence) to: (top) different length groups of summer flounder during the immigration period, January-March 1988, in the Newport and North Rivers, North Carolina; and (bottom) to 20-60 mm SL summer flounder following segregation from southern flounder in April-June 1988 in the Newport and North Rivers, North Carolina. Relative importance values are presented as the percentage of the sum of all values for (top) each 2 mm length group and for (bottom) each species. Adapted from Burke (1995).

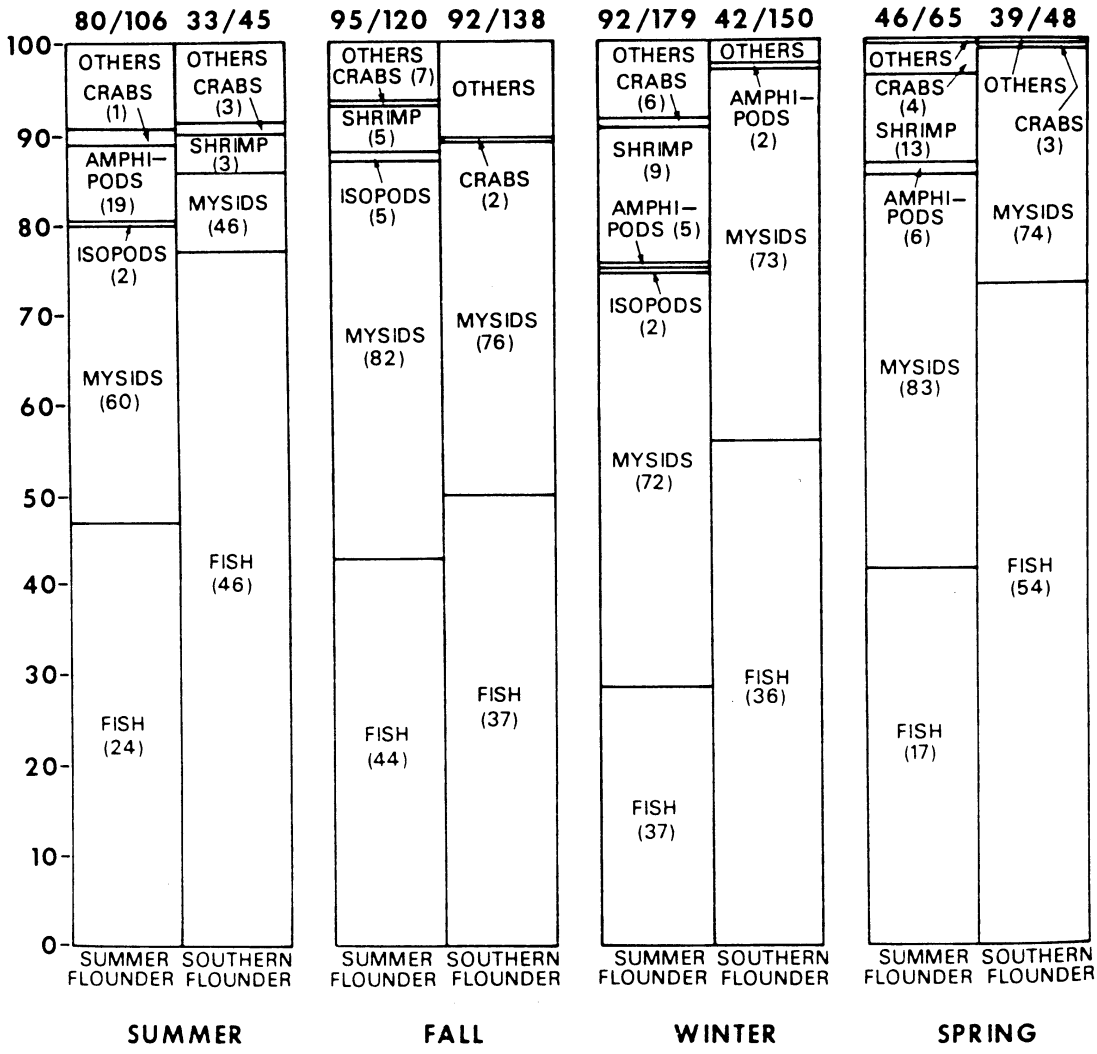


Figure 33. Percentage of volume and (in parentheses) percentage of occurrence of food items occurring in the seasonal diet of young (100-200 mm TL) summer and southern flounder from the Neuse River and Pamlico Sound, North Carolina. Numbers above each bar graph indicate the number of stomachs with food/the total number of stomachs examined. Adapted from Powell and Schwartz (1979).

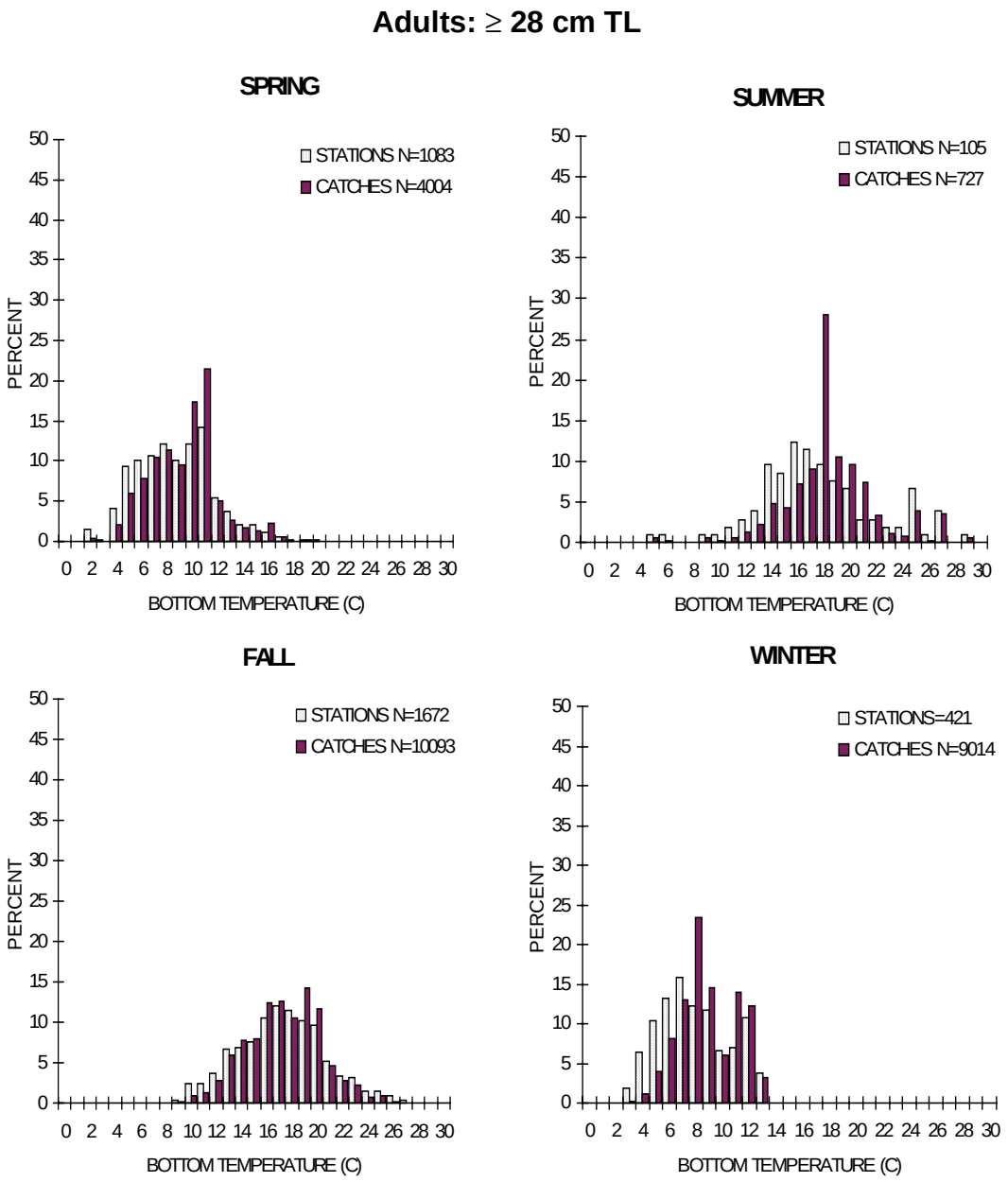


Figure 34. Seasonal abundance of adult summer flounder relative to bottom water temperature based on NEFSC bottom trawl surveys [1963-1997, all years combined; see Reid *et al.* (1999) for details]. Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m^2).

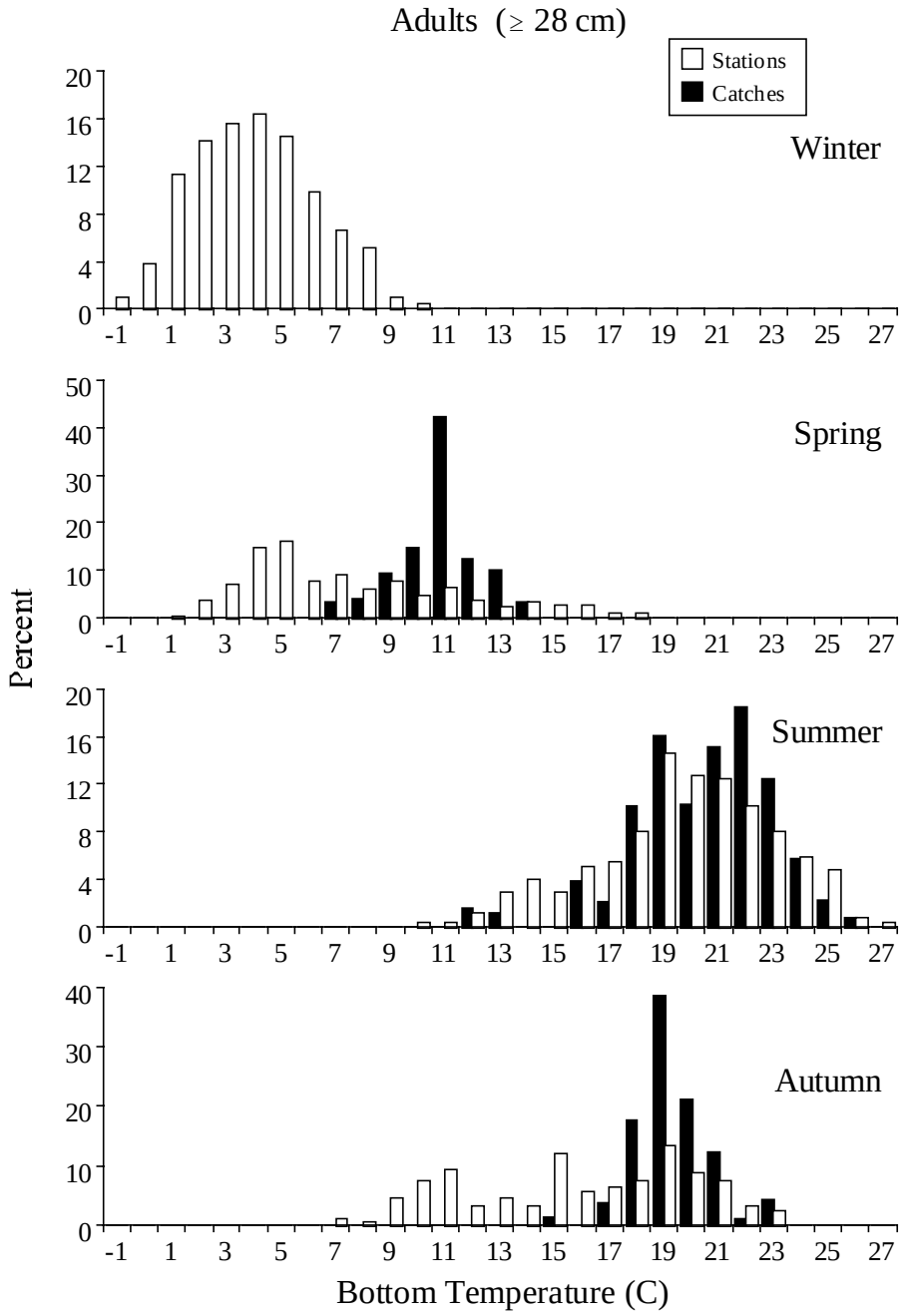


Figure 35. Seasonal abundance of adult summer flounder relative to mean bottom water temperature based on Rhode Island Division of Fish and Wildlife bottom trawl surveys of Narragansett Bay, 1990-1996 [see Reid *et al.* (1999) for details]. Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all catches.

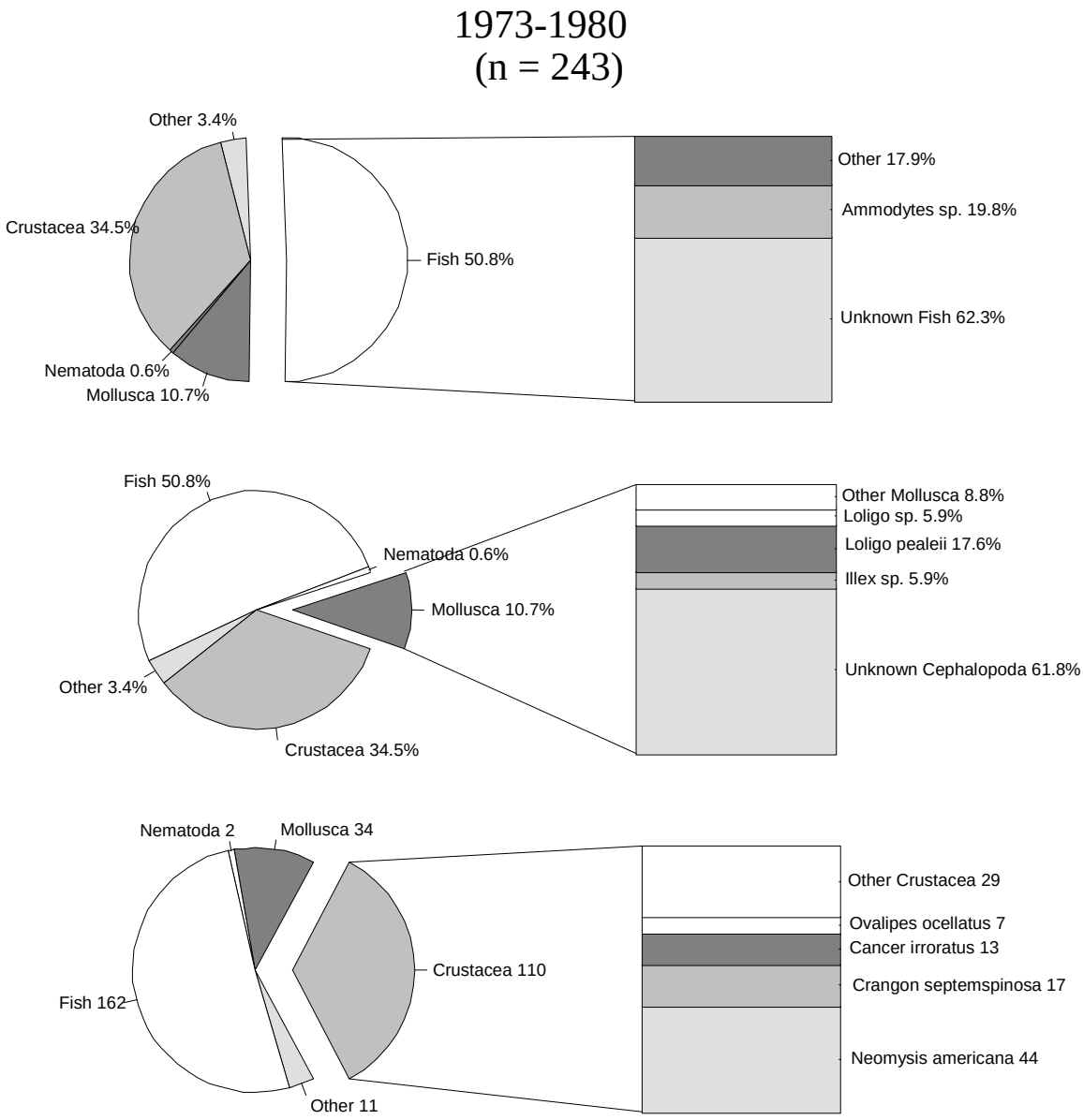


Figure 36. Abundance (percent occurrence) of the major prey items in the diet of summer flounder collected during NEFSC bottom trawl surveys from 1973-1980 and 1981-1990, focusing on fish, crustaceans, and mollusks. The category “animal remains” refers to unidentifiable animal matter. Methods for sampling, processing, and analysis of samples differed between the time periods [see Reid *et al.* (1999) for details].

1981-1990
(n = 469)

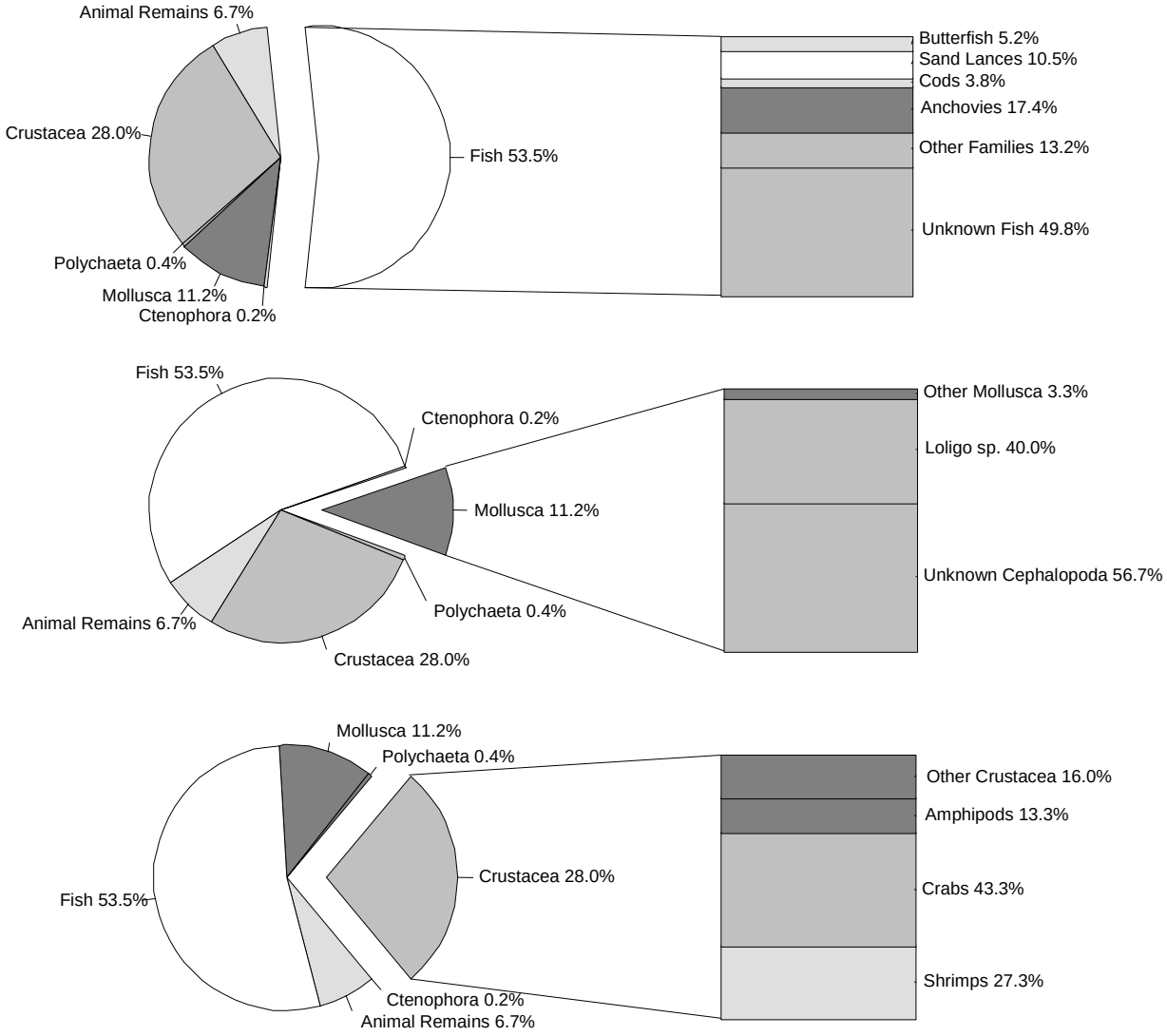


Figure 36. cont'd.

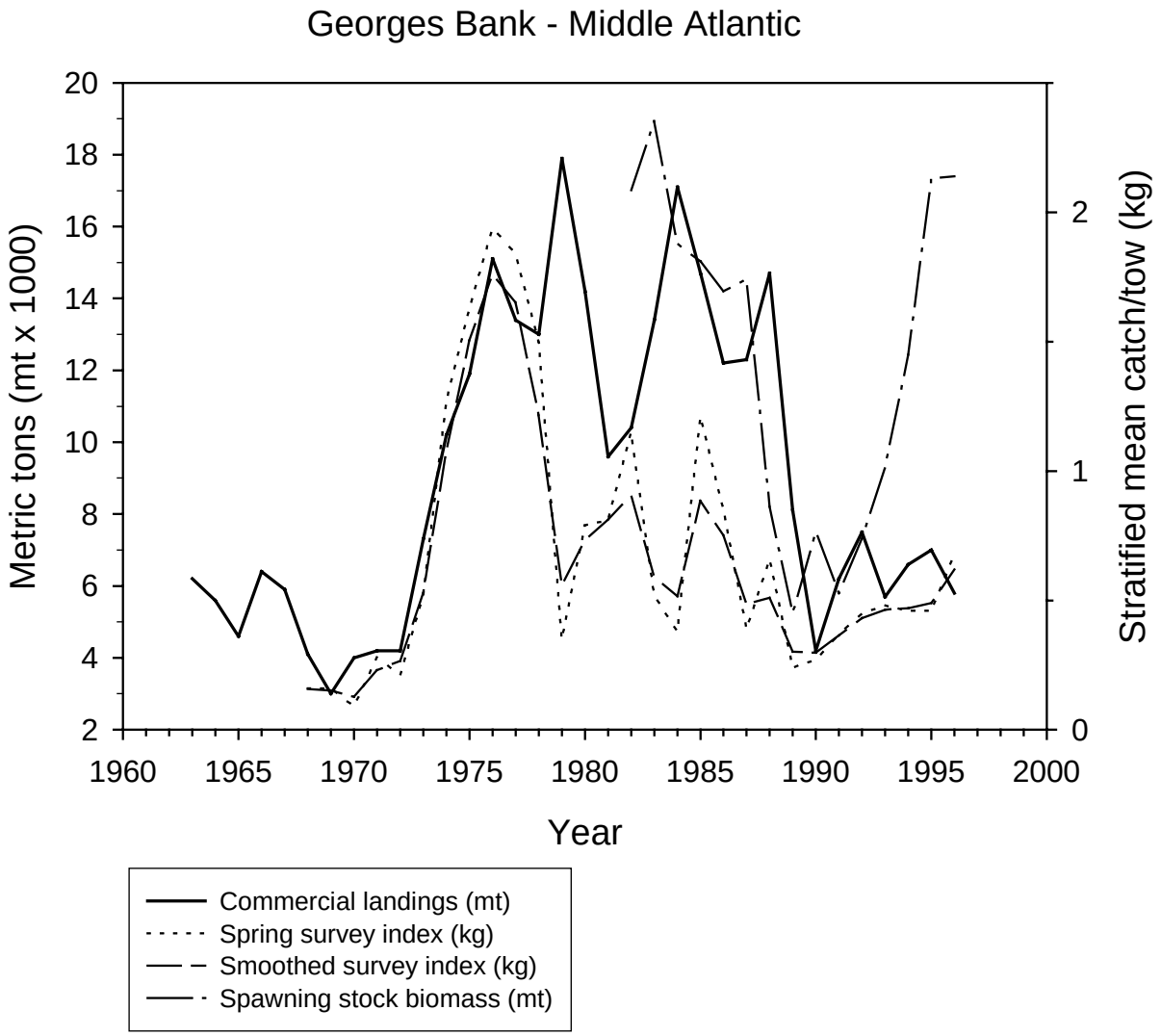


Figure 37. Commercial landings, NEFSC survey indices, and stock biomass for summer flounder on Georges Bank and in the Mid-Atlantic region.

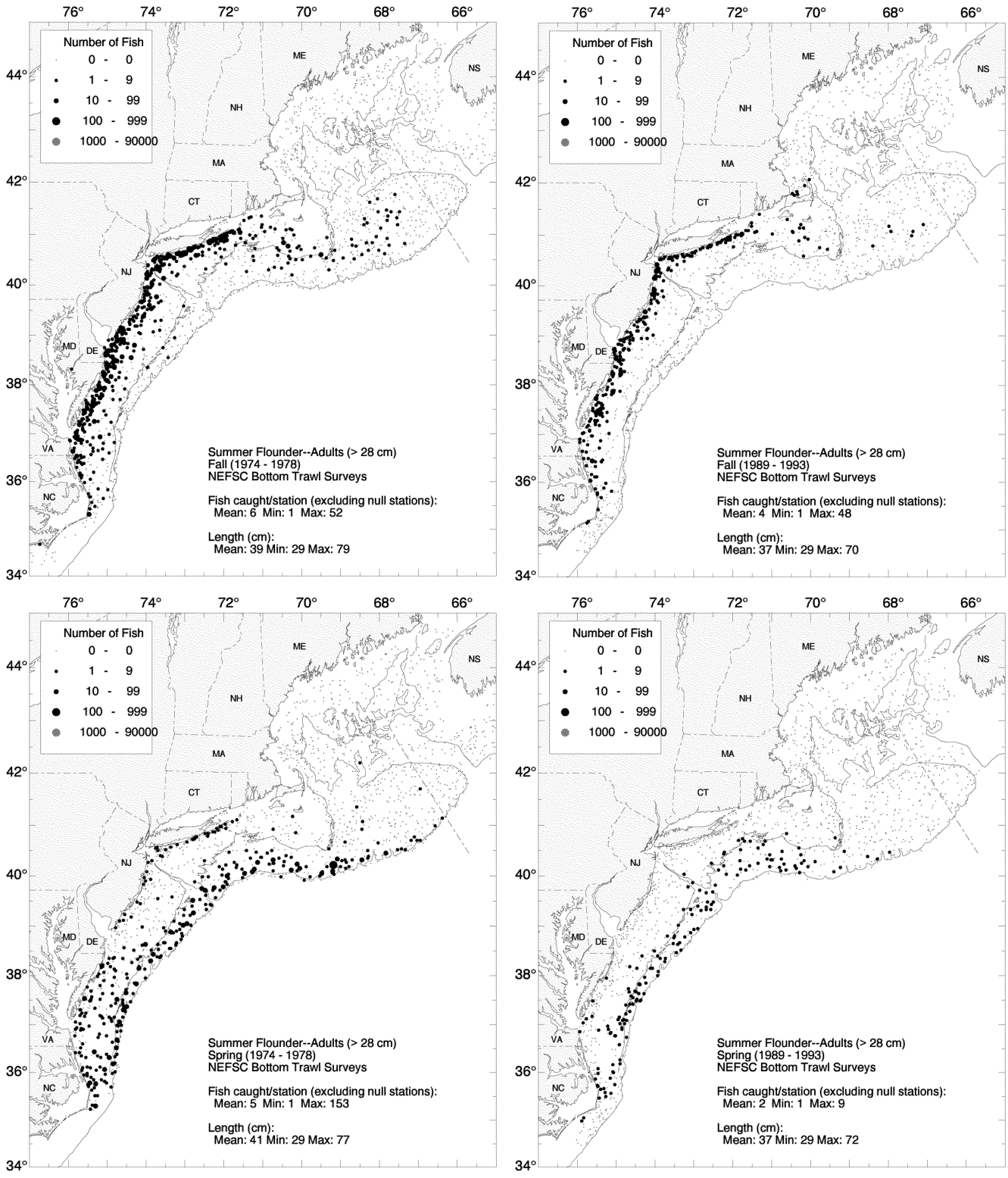


Figure 38. Distribution and abundance of adult and juvenile summer flounder during a period of high abundance (1974-1978) and a period of low abundance (1989-1993) based on spring and fall NEFSC bottom trawl surveys [see Reid *et al.* (1999) for details].

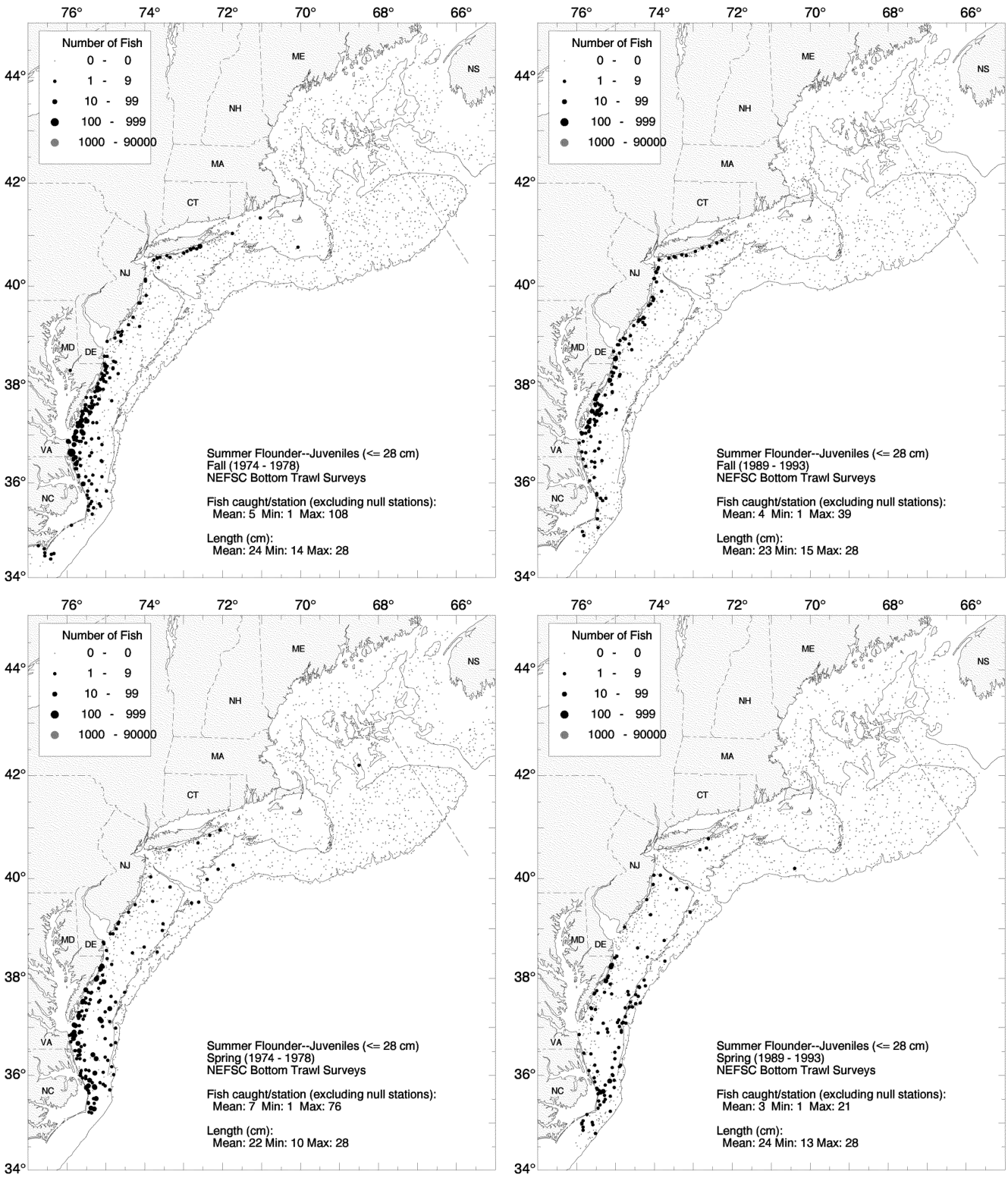


Figure 38. cont'd.

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