NOAA Technical Memorandum NMFS-NE-141

## Essential Fish Habitat Source Document:

# Atlantic Mackerel, Scomber scombrus, Life History and Habitat Characteristics 

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

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# Essential Fish Habitat Source Document: 

# Atlantic Mackerel, Scomber scombrus, Life History and Habitat Characteristics 

Anne L. Studholme, David B. Packer, Peter L. Berrien, Donna L. Johnson, Christine A. Zetlin, and Wallace W. Morse

U. S. DEPARTMENT OF COMMERCE William Daley, Secretary<br>National Oceanic and Atmospheric Administration<br>D. James Baker, Administrator<br>National Marine Fisheries Service<br>Penelope D. Dalton, Assistant Administrator for Fisheries<br>Northeast Region<br>Northeast Fisheries Science Center<br>Woods Hole, Massachusetts

# Editorial Notes on Issues 122-152 in the <br> 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 122152.

## 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.

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## 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., Robinset al. 1991²), mollusks (i.e., Turgeon et al. $1998^{\text {b }}$ ), and decapod crustaceans (i.e., Williams et al. $1989^{\text {c }}$ ), and to follow the Society for Marine Mammalogy's guidance on scientific and common names for marine mammals (i.e., Rice 1998d). 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 1998e).

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## 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.

Jeffrey N. Cross, Chief<br>Ecosystems Processes Division Northeast Fisheries Science Center

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## INTRODUCTION

Atlantic mackerel, Scomber scombrus L. (Figure 1), is a fast swimming, pelagic schooling species distributed in the northwest Atlantic from the Gulf of St. Lawrence to Cape Lookout, North Carolina (Sette 1943, 1950; Anderson 1976; MAFMC 1994). While there are two separate spawning contingents in the northwest Atlantic (Sette 1950), since 1975 all mackerel in this area have been assessed as a unit stock (Anderson 1982) and are considered one stock for management purposes (MAFMC 1994). Atlantic mackerel are managed under the Mid-Atlantic Fishery Management Plan for Atlantic mackerel, squid and butterfish (MAFMC 1994). This EFH source document provides information on the distribution, life history and habitat characteristics of Atlantic mackerel in the northwest Atlantic extending from Cape Hatteras to Georges Bank and the Gulf of Maine.

## LIFE HISTORY

A brief synopsis of the life history of Atlantic mackerel is provided in Amendment \#5 to the Fishery Management Plan for Atlantic Mackerel, Squid and Butterfish Fisheries (MAFMC 1994). More specific information is provided here and in other reviews (see Sette 1943, 1950; Bigelow and Schroeder 1953; Collette, in prep.). Since there is an important winter fishery on Atlantic mackerel on the eastern continental shelf where they occur (Maguire et al. 1987), the two major spawning contingents (see below) are managed as a single transboundary stock. Thus, where appropriate, information will be provided on both northern and southern groups.

## EGGS

The eggs of Atlantic mackerel are pelagic and spherical, ranging in size from $1.01-1.28 \mathrm{~mm}$ (avg. $=1.3 \mathrm{~mm}$ ) in diameter, and have one oil globule ranging from 0.22-0.38 mm (avg. $=0.29 \mathrm{~mm}$ ) in diameter (Berrien 1975). Sampling in the Gulf of St. Lawrence indicates that egg size decreased over time and in relation to ambient temperatures (Ware 1977).

## LARVAE

Larvae average about 3.1-3.3 mm standard length (SL) at hatching and have a large yolk sac; the eyes are large and unpigmented (Sette 1943; Bigelow and Schroeder 1953; Colton and Marak 1969; Berrien 1975; Ware and Lambert 1985; Scott and Scott 1988). Hatching occurs at 90-120 h post-fertilization at an average temperature of $13.8^{\circ} \mathrm{C}$ (Berrien 1975). The 50\% threshold for the onset of feeding is 3.8 mm (Ware and Lambert 1985). At about $4-6 \mathrm{~mm}$ the yolk sac is absorbed by which time there is a considerable
change in body pigmentation and by 192 h , teeth are present (Berrien 1975). Larvae undergo major changes in body form and Sette (1943) describes a transition stage between the larval and post-larval stages ( $\sim 9-10 \mathrm{~mm}$ ) where fins are in various stages of development. This probably enhances successful prey capture as well as predator avoidance (Ware and Lambert 1985). To maintain rapid growth rates, with average digestive times of 1-2 h, Peterson and Ausubel (1984) concluded that the larvae must feed constantly.

## JUVENILES

Post-larvae gradually transform from planktonic to swimming and schooling behavior at about 30-50 mm (Sette 1943). Fish reach a length of about 50 mm in approximately two months at which time they closely resemble adults and reach 20 cm in December after about one year of growth (Sette 1943; Bigelow and Schroeder 1953; Anderson and Paciorkowski 1980; Berrien 1982; Collette, in prep.). Kendall and Gordon (1981) show somewhat faster larval and juvenile growth rates based on daily growth increments from otoliths taken from fish collected in the Middle Atlantic Bight; i.e., approximately $70-80 \mathrm{~mm}$ in two months; however, these were not verified by comparison with fish of known age. Ware and Lambert (1985) found that in St. Georges Bay, Nova Scotia, at $15-17^{\circ} \mathrm{C}$, growth rates of juveniles (> 15 mm ) averaged $0.73 \mathrm{~mm} / \mathrm{d}$ from birth to metamorphosis, similar to the estimates by Kendall and Gordon (1981). Using daily growth rings, D'Amours et al. (1990) estimated that young mackerel from the northern contingent would grow faster earlier in their first growing season which would be consistent with Sette's (1950) conclusions. However, Simard et al. (1992) calculated that growth curves of juvenile Atlantic mackerel, based on otolith samples from the northern and southern spawning groups were not significantly different at least up to 90 days in age.

## ADULTS

By the end of their second year, Atlantic mackerel attain a size of about 26 cm and after five years about 33 cm (Anderson 1973; Isakov 1973; Stobo and Hunt 1974). Fish that are 6 years old can reach a length of $39-40 \mathrm{~cm}$. Based on studies of Canadian mackerel, MacKay (1967) theorized that growth is population density dependent; i.e., that abundant year classes grow more slowly than less abundant year classes, although Moores et al. (1975) did not find this to be true for Newfoundland fish. Overholtz (1989) found the 1982 cohort to be one of the slowest growing on record; it is one of the largest recruiting year-classes recorded. Large differences in mackerel growth suggest that year-class size partially influences the initial pattern of growth during a cohort's first years (Overholtz et al. 1991b). Thus, early growth may be related to year-class size, while stock size
may be more influential after the juveniles join the offshore adults (Overholtz et al. 1991b; Collette, in prep.).

The adults are highly mobile and school. They are obligate swimmers due to the absence of a swimbladder and the necessity for ram gill ventilation to meet blood oxygenation demands (Roberts 1975). Nevertheless this species exhibits diurnal changes in activity, swimming faster during the day than at night (Olla et al. 1975, 1976). Under laboratory conditions, at temperatures ranging from 7.3$15.8^{\circ} \mathrm{C}$ (within their preferred range), swimming speed of adults averaged $36 \mathrm{~cm} / \mathrm{s}$ during the day and $29 \mathrm{~cm} / \mathrm{s}$ at night (Olla et al. 1975, 1976). The fish continued to school both day and night although there were diurnal changes in cohesiveness of the group.

## REPRODUCTION

There is some variation in estimates of size and age at maturity. Based on samples of Atlantic mackerel collected from 1987-1989 by the Northeast Fisheries Science Center (NEFSC) groundfish surveys, median length at maturity $\left(\mathrm{L}_{50}\right)$ was 25.7 cm for females and 26.0 cm for males; median age ( $\mathrm{A}_{50}$ ) was 1.9 years for both ( O 'Brien et al. 1993). By age 3, $99 \%$ of the females and $97 \%$ of the males were mature (O'Brien et al. 1993). Fish collected in Newfoundland waters from June-September 1970-1973 had higher values for $\mathrm{L}_{50}$ of 34 cm and 35 cm for females and males respectively (Moores et al. 1975). MacKay (1967) reported first spawning for mackerel occurred at age 2 and at lengths > 30 cm for fish collected in May-July 1965-1966 from the Gulf of St Lawrence and coastal Nova Scotia and Massachusetts. These differences in median maturity may be due to the slower growth of larger year classes that may delay spawning from one to three years (MacKay 1973; Overholtz 1989). Consequently, both year-class size and adult stock size may be important factors regulating growth in Atlantic mackerel (Overholtz 1989; Overholtz et al. 1991b).

Spawning occurs during spring and summer and progresses from south to north as the surface waters warm and fish migrate (Sette 1943). There are two spawning contingents; a southern group that spawns primarily in the Mid-Atlantic Bight and Gulf of Maine from mid-April to June and a northern contingent that spawns in the southern Gulf of St. Lawrence from the end of May to mid-August (Berrien 1982). The southern contingent begins the spring spawning migration by moving inshore between Delaware Bay and Cape Hatteras, usually between mid-March and mid-April depending to some extent on water temperature (Berrien 1982). The northern contingent begins to move inshore off southern New England usually in late May, mixing temporarily with part of the southern contingent before migrating eastward along the coast of Nova Scotia. Here other mackerel schools from offshore join the fish before moving into the Gulf of St. Lawrence to spawn
(Berrien 1982). Small fish (< 30 cm ) lag behind larger fish and spawn later (Berrien 1982).

Most of the spawning occurs in the shoreward half of continental shelf waters, although there is some spawning on the shelf edge and beyond (Berrien 1982; Collette, in prep.). Sette (1943) described the area bordered by southern New England and the Middle Atlantic states as the most important spawning grounds for mackerel. Current information indicates that the oceanic bight between Chesapeake Bay and southern New England is the most productive area. The Gulf of St. Lawrence is somewhat less so although the southern side is considered extremely productive for the northern contingent (MacKay 1973) while the Gulf of Maine and coast of outer Nova Scotia are the least (Sette 1950; Collette, in prep.). Some open bays; i.e., Cape Cod Bay and Massachusetts Bay, are sites of some importance with spawning fish abundant or common from May to July and August (Table 1). While according to Wheatland (1956), spawning occurs rarely in Gardiner's Bay and Long Island Sound, recent assessments of relative abundance of eggs and larvae in these areas show that both life stages are highly abundant and abundant in April and May (Table 2). Well-enclosed bays, especially those receiving considerable river inflow such as Chesapeake Bay and Delaware Bay show little evidence of spawning (Table 2).

Atlantic mackerel are serial, or batch spawners, with estimates of total fecundity ranging from 285,000 to 1.98 million eggs for southern contingent mackerel between 31 and 44 cm fork length (FL) (Morse 1980). Based on a very limited sample of northern contingent mackerel, fecundity estimates ranged from 211,000 to 397,000 eggs for 35 and 40 cm females respectively (MacKay 1973). Analysis of egg diameter frequencies indicate that five to seven egg batches are spawned by each female (Morse 1980).

## FOOD HABITS

Atlantic mackerel are opportunistic feeders that can ingest prey either by individual selection of organisms or by passive filter feeding (Pepin et al. 1988). Filter feeding occurs when small plankton are abundant and mackerel swim through patches with mouth slightly agape, filtering food through their gill rakers (MacKay 1979). According to MacKay (1979), particulate feeding is the principal feeding mode in the spring and fall, while filter feeding predominates in the summer in the Gulf of St. Lawrence. Moores et al. (1975) maintain that the diet of fish from Newfoundland suggests that particulate feeding occurs there throughout the season.

Larvae feed primarily on zooplankton (Collette, in prep.). First-feeding larvae ( 3.5 mm ) collected from Long Island Sound were found to be phytophagous while slightly larger individuals (> 4.4 mm ) fed on copepod nauplii (Peterson and Ausubel 1984; Ware and Lambert 1985). Fish $>5 \mathrm{~mm}$ fed on copepodites of Acartia and Temora
while diets of fish > 6 mm contained adult copepods (Peterson and Ausubel 1984). Larvae > 6.4 mm were also cannibalistic, feeding on $3.5-4.5 \mathrm{~mm}$ conspecifics (Peterson and Ausubel 1984; Fortier and Villeneuve 1996). Consumption rates of larvae average between 25 and $75 \%$ body weight per day and they probably feed continuously. Larvae feed selectively, primarily on the basis of prey visibility (Peterson and Ausubel 1984). Fortier and Villeneuve (1996), studying larval mackerel from the Scotian Shelf, found that with increasing larval length, the diet shifted from copepod nauplii to copepod and fish larvae; the fish larvae included yellowtail flounder, silver hake, redfish and a large proportion of conspecifics. Predation was stage-specific; only the newly hatched larvae of a given species were ingested. However, piscivory was limited at densities of fish larvae $<0.1 / \mathrm{m}^{3}$ and declined with increasing density of nauplii and with increasing number of alternative copepod prey ingested.

Juveniles eat mostly small crustaceans such as copepods, amphipods, mysid shrimp and decapod larvae (Collette, in prep.). They also feed on small pelagic mollusks (Spiratella and Clione) when available (Collette, in prep.). Adults feed on the same food as juveniles but diets also include a wider assortment of organisms and larger prey items. For example, euphausiid, pandalid and crangonid shrimp are common prey; chaetognaths, larvaceans, pelagic polychaetes and larvae of many marine species have been identified in mackerel stomachs (Collette, in prep.). Bigelow and Schroeder (1953) found many Gulf of Maine mackerel feeding on Calanus as well as other copepods. Larger prey such as squids (Loligo) and fishes (silver and other hakes, sand lance, herring, and sculpins) are not uncommon, especially for large mackerel (Bowman et al. 1984). Under laboratory conditions, mackerel also fed on Aglantha digitale, a small transparent medusa common in temperate and boreal waters (Runge et al. 1987). The 1973 -1990 NEFSC bottom trawl survey data on food habits for two size classes of mackerel ( $11-30 \mathrm{~cm} ; 30-50 \mathrm{~cm}$ ) for 1973-1980 and 1981-1990 reflects this diversity (Figure 2). While there is variability between the two size classes and between the two survey periods, copepods, euphausiids and various crustaceans could be considered relative staples in the diet.

Immature mackerel begin feeding in the spring; older fish feed until gonadal development begins, stop feeding until spent and then resume prey consumption (Berrien 1982; Collette, in prep.). Under experimental conditions in which larval fish (3-10 mm in length) were presented as part of natural zooplankton assemblages, prey preference by mackerel was positively size selective and predation rates were not influenced by larval fish density (Pepin et al. 1987). Subsequent studies indicated that mackerel may achieve a higher rate of energy intake by switching to larger prey and increasing search rate as prey size and total abundance increase (Pepin et al. 1988). Filter feeding activity also increased with increasing prey density and Pepin et al. (1988) suggest that feeding rates under natural
conditions of prey abundance ( 0.1 g wet weight $/ \mathrm{m}^{3}$ ) indicate that mackerel would not be satiated if foraging were restricted only to daylight.

## PREDATION

Predation has a major influence on the dynamics of northwest Atlantic mackerel (Overholtz et al. 1991b). In fact, predation mortality is probably the largest component of natural mortality on this stock, and based on model predictions, may be higher than previously thought (Overholtz et al. 1991b). Atlantic mackerel serve as prey for a wide variety of predators including other mackerel, dogfish, tunas, bonito, and striped bass (Collette, in prep.). Small mackerel are prey for Atlantic cod and squid, which feed on fish < 10 to 13 cm in length (Collette, in prep.). Pilot whales, common dolphins, harbor seals, porpoises and seabirds are also significant predators (Smith and Gaskin 1974; Payne and Selzer 1983; Overholtz and Waring 1991; Montevecchi and Myers 1995). Other predators include swordfish, bigeye thresher, thresher, shortfin mako, tiger shark, blue shark, spiny dogfish, dusky shark, king mackerel, thorny skate, silver hake, red hake, bluefish, pollock, white hake, goosefish and weakfish (Scott and Tibbo 1968; Maurer and Bowman 1975; Stillwell and Kohler 1982, 1985; Bowman and Michaels 1984; Collette, in prep.).

## MIGRATION/STOCK STRUCTURE

As stated previously, the two major spawning contingents are managed as a single transboundary stock. Sette (1950) described northern and southern population contingents of Atlantic mackerel in the northwest Atlantic with different spring and autumn migration patterns and summer distributions. Various methods have attempted to discriminate the two contingents in the northwest Atlantic, including meristic analyses (MacKay and Garside 1969), comparison of parasitic fauna (Isakov 1976), genetic variability (Maguire et al. 1987) and differences in otoliths (Gregoire and Castonguay 1989; Castonguay et al. 1991). While there were some significant differences, overlaps in character distributions have prevented the development of a useful discrimination method.

During the winter, Atlantic mackerel apparently overwinter in deep water of the continental shelf from Sable Island Bank, off Nova Scotia to the Chesapeake Bay region and in spring move inshore and northeast; this pattern is reversed in the fall (Sette 1950; Leim and Scott 1966; MacKay 1967; Berrien 1982). In April and early May the fish form the two spawning aggregations; i.e., a southern contingent that spawns off New Jersey and New York, and a northern contingent that spawns in the Gulf of St. Lawrence.

As fish from the southern contingent move northeast along the coast, they are joined by the schools from the
northern contingent which are also moving inshore. The overwintering area and timing of migration varies annually, probably influenced by meteorological events or regional conditions with low spring temperatures significantly delaying the timing, extent and duration (Murray et al. 1983; Murray 1984). In fact, the seasonal cycle in temperature in the waters of the Mid-Atlantic and southern New England [well-mixed water column in winter with temperatures $<4^{\circ} \mathrm{C}$ near the coast to $>8^{\circ} \mathrm{C}$ near the shelf edge; warming surface layers in spring and gradual warming from south (to $25^{\circ} \mathrm{C}$ ) to north (to about $18^{\circ} \mathrm{C}$ ) and subsequent fall cooling] is certainly an important environmental factor influencing migration and distribution (Overholtz et al. 1991a). This is supported by field studies that have shown that mackerel are intolerant of temperatures $\left\langle 5-6^{\circ} \mathrm{C}\right.$ or $>15-16^{\circ} \mathrm{C}$ (Overholtz and Anderson 1976) and laboratory studies that have confirmed that as temperatures departed from preferred ranges $\left(7.3-15.8^{\circ} \mathrm{C}\right)$ swimming speeds of adult mackerel increased, reflecting thermal avoidance (Olla et al. 1975, 1976). By late April and May, the southern contingent is distributed off New Jersey and Long Island moving into the western side of the Gulf of Maine by June and July, and returning to the shelf edge probably between Long Island and Chesapeake Bay by October (Sette 1950; Berrien 1982).

The northern contingent, by late spring, has moved inshore off southern New England, mixing temporarily with the southern contingent before migrating eastward along the coast of Nova Scotia, and moving into the Gulf of St. Lawrence where they spawn in June and July. Some fish however, remain along the coasts of Maine and Nova Scotia throughout the summer. These fish again mix with fish from the southern group in late fall in the Gulf of Maine before moving to the outer shelf between Sable Island Bank and Long Island to overwinter (Sette 1950; Parsons and Moores 1974; Moores et al. 1975). Temperature may not be as limiting for this contingent since D'Amours and Castonguay (1992) found that mackerel occurred in June in the Cabot Strait off of eastern Cape Breton Island at $2.8^{\circ} \mathrm{C}, 4^{\circ} \mathrm{C}$ colder than the $7^{\circ} \mathrm{C}$ isotherm proposed by Sette (1950) as the thermal barrier to northern migration.

## HABITAT CHARACTERISTICS

An extensive literature review and synthesis has provided detailed information on the life history and habitat requirements of Atlantic mackerel (Table 3). The review is primarily limited to U.S. waters; however, due to the intermixing of the two contingents, some information also relates to fish in Canadian waters.

## EGGS

The eggs are pelagic in water over 34 ppt (Fritzsche 1978), floating in surface waters above the thermocline or in the upper 10-15 m (Sette 1943; Berrien 1982). Incubation
time depends primarily on temperature: at $11^{\circ} \mathrm{C}, 7.5$ days; at $13^{\circ} \mathrm{C}, 5.5$ days and at $16^{\circ} \mathrm{C}, 3.6$ days (Worley 1933). Lanctot (1980) had similar results: at $11^{\circ} \mathrm{C}, 8$ days; at $13^{\circ} \mathrm{C}$, 5.8 days and at $16^{\circ} \mathrm{C}, 3.9$ days.

Based on the NEFSC Marine Resources Monitoring, Assessment, and Prediction (MARMAP) offshore ichthyoplankton surveys, eggs were collected at near surface temperatures ranging from $5-23^{\circ} \mathrm{C}$ with the largest proportion between $\sim 7^{\circ} \mathrm{C}$ and $16^{\circ} \mathrm{C}$ (Figure 3). In April, the highest abundances were collected from $7-9^{\circ} \mathrm{C}$; in May, from $9-12^{\circ} \mathrm{C}$; in June, from $10-12^{\circ} \mathrm{C}$; while the few collected in July and August were at a wide range of temperatures (11$23^{\circ} \mathrm{C}$ ) (Figure 3). This is consistent with findings by Berrien (1978) who reported that for May 1966, the weighted mean surface temperature for all eggs collected from Martha's Vineyard to Chesapeake Bay was $11.0^{\circ} \mathrm{C}$ (range $6.3-16.9^{\circ} \mathrm{C}$ ) with $97 \%$ collected at $8.7-13.8^{\circ} \mathrm{C}$. Sette (1943), for eggs collected in 1932, reported a weighted mean of $10.9^{\circ} \mathrm{C}$ surface temperature with $98 \%$ occurring from $9.0-13.5^{\circ} \mathrm{C}$.

Mortality may be influenced by acclimation temperatures of adult fish (Lanctot 1980). Worley (1933) found minimal mortality at $16^{\circ} \mathrm{C}$ which corresponded to capture temperature of the adults. Lockwood et al. (1977) found mortalities $<20 \%$ between 9.4 and $15.1^{\circ} \mathrm{C}$. Ware and Lambert (1985) also found that egg mortality rates of mackerel from St. Georges Bay, Nova Scotia were highly correlated with the rate of warming during the spawning season.

Salinities may also affect survival. Peterson and Ausubel (1984) attributed high egg mortality to unusually low salinities ( 23 ppt ) in Long Island Sound as compared with usual values of 25-27 ppt.

Eggs were collected at depths in the water column ranging from $10-325 \mathrm{~m}$; the majority were collected from 30-70 m (Figure 3). In April, the highest numbers of eggs were collected at depths of $10-30 \mathrm{~m}$; in May from 30-50 m; in June, July and August, at depths of 30-70 m (Figure 3). Ware and Lambert (1985) found that mackerel eggs in St. Georges Bay tended to concentrate near the surface, particularly under light winds and declined exponentially with depth with the rate of decline a function of egg diameter and temperature gradient in the top 5 m .

## LARVAE

Based on the NEFSC MARMAP ichthyoplankton surveys, larvae are found at water column temperatures ranging from $6-22^{\circ} \mathrm{C}$ with the largest proportion between about $8^{\circ} \mathrm{C}$ and $13^{\circ} \mathrm{C}$ (Figure 4). In May, the majority of larvae were found at $8-10^{\circ} \mathrm{C}$; in June at $8-11^{\circ} \mathrm{C}$; in July at $8^{\circ} \mathrm{C}$ and $10-11^{\circ} \mathrm{C}$; and in August at $9^{\circ} \mathrm{C}$ and $12-13^{\circ} \mathrm{C}$ (Figure 4). For larvae collected during May, June and August 1966, Berrien (1978) indicated that surface water temperatures ranged from $12.3-20.7^{\circ} \mathrm{C}$ with $96 \%$ occurring from 13.7$16.8^{\circ} \mathrm{C}$. Ware and Lambert (1985) found that larval mortality rates ( $\sim 42 \% / d$ ) were positively correlated with
temperature.
Larvae were collected at depths ranging from 10-130 m (Figure 4). With the exception of July when $50 \%$ were collected at a depth of 70 m , larvae were primarily distributed at depths $\leq 50 \mathrm{~m}$ (Figure 4). Sette (1943) reports that larvae vertically migrate diurnally from the surface at night to the thermocline during the day. Ware and Lambert (1985) found that in St. Georges Bay, recently-hatched larvae were collected at depths of 5-10 m and as they grew, moved progressively closer to the surface during the day; at sizes ranging from 3-8 mm, median depth increased at a rate of $0.7 \mathrm{~m} / \mathrm{d}$.

## JUVENILES

Based on the 1963-1997 NEFSC bottom trawl surveys, juveniles in the fall were caught at temperatures ranging from $4-22^{\circ} \mathrm{C}$, with the majority (>55\%) occurring at $10^{\circ} \mathrm{C}$. In the winter $90 \%$ were collected at $5-6^{\circ} \mathrm{C}$ (range: $3-12^{\circ} \mathrm{C}$ ) (Figure 5). The temperatures at which juveniles were found were a little broader in spring $\left(4-17^{\circ} \mathrm{C}\right)$ and summer (4$19^{\circ} \mathrm{C}$ ). Although the majority of juveniles (> $60 \%$ ) were still found at $5-6^{\circ} \mathrm{C}$ in the spring, by summer they wee found at higher temperatures with $>40 \%$ collected at $8^{\circ} \mathrm{C}$ and $40 \%$ at $13^{\circ} \mathrm{C}$ (Figure 5).

In the fall, the majority of juveniles (>77\%) were at depths of 20-40 m (range: surface to 320 m ); in the winter > $60 \%$ were at slightly deeper depths ( $50-70 \mathrm{~m}$ ) while by spring they were widely dispersed through the water column (surface to 340 m ) but concentrated (> $75 \%$ ) at depths ranging from $30-90 \mathrm{~m}$ (Figure 5). By summer, fish were higher in the water column (surface to 210 m ) with $\sim 94 \%$ distributed from 20-50 m in two peaks (Figure 5).

Based on collections from the 1978-1996 Massachusetts inshore bottom trawl surveys, juveniles were most abundant at $11^{\circ} \mathrm{C}$ in spring and 9 and $13^{\circ} \mathrm{C}$ in autumn, and at depths of 10 and 50 m in the spring and 25 and 60 m in the autumn (Figure 6).

Based on collections from the 1990-1996 Rhode Island Narragansett Bay bottom trawl surveys, juveniles were captured in summer at bottom depths between 6.1-15.2 m (20-50 ft) and were most abundant at 12.2-15.2 m (40-50 ft) (Figure 7). They were caught at bottom temperatures of $19^{\circ} \mathrm{C}$ in summer and at 11 and $15^{\circ} \mathrm{C}$ in autumn (Figure 7).

Juveniles collected in otter trawl surveys in the HudsonRaritan estuary (New York and New Jersey) during July 1997 were found at depths ranging from 4.9-9.8 m. Salinities ranged from 26.1-28.9 ppt, dissolved oxygen from $7.3-8.0 \mathrm{mg} / \mathrm{l}$ and temperatures from $17.6-21.7^{\circ} \mathrm{C}$ (S. Wilk, NMFS, NEFSC, James J. Howard Marine Sciences Laboratory, Highlands, NJ, personal communication).

## ADULTS

Based on the NEFSC bottom trawl surveys, adults in
the fall were found at a slightly narrower range of temperatures $\left(4-16^{\circ} \mathrm{C}\right)$ with $>80 \%$ caught from $9-12^{\circ} \mathrm{C}$ (Figure 8). Winter distribution was similar to that of the juveniles with nearly $70 \%$ at $5-6^{\circ} \mathrm{C}$ (range: $3-13^{\circ} \mathrm{C}$ ) (Figure 8). In the spring, temperature ranges were similar $\left(2-14^{\circ} \mathrm{C}\right)$, but adults were distributed more evenly through a temperature band of $5-13^{\circ} \mathrm{C}$ with $>25 \%$ at $13^{\circ} \mathrm{C}$ (Figure 8). By summer, fish were found at temperatures ranging from $4-14^{\circ} \mathrm{C}$ with $>30 \%$ at $10-11^{\circ} \mathrm{C}$ and $>35 \%$ at $14^{\circ} \mathrm{C}$ (Figure 8). These temperatures are within the ranges previously reported for mackerel. In addition, Bigelow and Schroeder (1953) indicate that the highest temperature at which mackerel are commonly found is $20^{\circ} \mathrm{C}$ while commercial catches are sometimes taken at $7^{\circ} \mathrm{C}$. In the northern Gulf of St. Lawrence, concentrations of mackerel were found at $4^{\circ} \mathrm{C}$; however, the overall probability of occurrence inshore was higher when near-bottom temperatures were $\geq 7^{\circ} \mathrm{C}$ (Castonguay et al. 1992).

As stated previously in the migration section, field studies have shown that mackerel are intolerant of temperatures $<5-6^{\circ} \mathrm{C}$ or $>15-16^{\circ} \mathrm{C}$ (Overholtz and Anderson 1976) and laboratory studies have confirmed that as temperatures departed from preferred ranges (7.3$15.8^{\circ} \mathrm{C}$ ), swimming speeds of adult mackerel increased, reflecting thermal avoidance (Olla et al.1975, 1976). Again, temperature may not be as limiting for the northern contingent since D'Amours and Castonguay (1992) found that mackerel occurred in June off of eastern Cape Breton Island at $2.8^{\circ} \mathrm{C}, 4^{\circ} \mathrm{C}$ colder than the $7^{\circ} \mathrm{C}$ isotherm proposed by Sette (1950) as the thermal barrier to northern migration.

Based on the NEFSC bottom trawl surveys, adults in the fall were spread from $10-340 \mathrm{~m}$; however $>50 \%$ were caught at $60-80 \mathrm{~m}$ (Figure 8). By winter, while fish were still found at depths of $10-270 \mathrm{~m}, \sim 50 \%$ were found at depths of $20-30 \mathrm{~m}$ (Figure 8). By spring fish were broadly dispersed from the surface to as deep as 380 m ; however, around $25 \%$ were at depths of 160-170 m (Figure 8). By summer, schools had again moved upward in the water column, swimming at depths of $10-180 \mathrm{~m}$ with $>60 \%$ at depths of $50-70 \mathrm{~m}$ (Figure 8). This depth range is broader than reported by Bigelow and Schroeder (1953) who stated that while mackerel can swim as deep as 183 m , in spring, summer and into fall they swim at depths of $46-55 \mathrm{~m}$ or less. According to Sette (1950) larger fish tend to swim deeper than smaller ones.

In the northern Gulf of St. Lawrence, vertical distribution was greatest at 15 and 35 m with mackerel occurrences positively correlated with downwelling events and the onshore advection of warm surface waters (Castonguay et al. 1992).

Based on Massachusetts inshore bottom trawl surveys, adults were most abundant at $14^{\circ} \mathrm{C}$ in spring with the few found in autumn at 10 and $15^{\circ} \mathrm{C}$. They were also found at depths of 10 m in the spring while the few found in the autumn were at 50 m (Figure 6).

Based on Rhode Island Narragansett Bay bottom trawl surveys, a single adult was caught in winter at a depth of
30.5 m and at a bottom temperature of $5^{\circ} \mathrm{C}$.

Factors controlling spawning time are unclear. Morse (1980) indicated that the regularity in spawning shown by Ware (1977) points to an internal control or constant external stimulus; e.g., photoperiod changes, which ensures that peak hatching occurs at the time of maximum zooplankton abundance. Based on field investigations (Nichols and Warnes 1993) and laboratory observations (Walsh and Johnstone 1992), there appears to be no diel periodicity in spawning and no significant peaks either during the day or night. Sette (1943) noted that temperature $<7^{\circ} \mathrm{C}$ is a limiting factor in migration which subsequently affects timing of spawning in specific locations. Based on the NEFSC MARMAP ichthyoplankton surveys, spawning does not begin until temperatures reach $\sim 7-8^{\circ} \mathrm{C}$, with most occurring between 9 and $14^{\circ} \mathrm{C}$ (Berrien 1982; Collette, in prep.). Sette (1943) stated that peak spawning occurs within that range at around $10-12^{\circ} \mathrm{C}$ at salinities $>30 \mathrm{ppt}$. These temperatures were in the preferred range $\left(7-16^{\circ} \mathrm{C}\right)$ determined for adult mackerel in the laboratory (Olla et al. 1975, 1976). Thus the spawning season is progressively later as water temperatures warm and fish migrate from south to north.

## GEOGRAPHICAL DISTRIBUTION

Northwest Atlantic mackerel are primarily found in the open sea (although rarely beyond the continental shelf) from Black Island, Labrador (Parsons 1970) to Cape Lookout, North Carolina (Collette and Nauen 1983). Eggs, larvae and juveniles also found at varying levels of abundance in bays and estuarine areas from New Jersey north through New England and into Canadian waters (see also Sette 1950; Tables 1, 2).

## EGGS

The NEFSC MARMAP ichthyoplankton surveys found eggs from offshore waters off Chesapeake Bay to Georges Bank and the Gulf of Maine (Figure 9). Egg production progressed northward from April through May, June and July as would be expected based on the spawning/migratory patterns of adults. For example, egg production in April extended from Chesapeake Bay to coastal New Jersey and along the south shore of Long Island. In May, egg production extended from the shelf waters off New Jersey to Nantucket, the southern edge of Georges Bank and the western Gulf of Maine; in June production extended off southern Rhode Island, in the region of Massachusetts Bay and the western Gulf of Maine (Figure 9). By July, some eggs were collected along Georges Bank, while by August, few, if any, eggs were found. Highest densities (eggs/10 m${ }^{2}$ ) were in May (> 39,000) and June (>53,000). This pattern of production and distribution is consistent with previous reports (Sette 1943; Bigelow and Schroeder 1953; Collette,
in prep.). Eggs have been collected from early June to midAugust on the southern side of the Gulf of St. Lawrence (Sette 1943) and this area is considered an extremely productive spawning ground (Collette, in prep.).

## LARVAE

The NEFSC MARMAP ichthyoplankton surveys also found larvae ( $<13 \mathrm{~mm}$ ) from waters off Chesapeake Bay to the Gulf of Maine, although more were concentrated offshore of Delaware Bay to Massachusetts Bay from inshore waters to the seaward limits of the survey (Figure 10). Larvae were collected from May through August with the highest average mean density ( $>10,000 / 10 \mathrm{~m}^{2}$ ) occurring in June and ranging from inshore to offshore from southern New England to the Hudson Canyon with considerable numbers collected north of Cape Cod. This was north of where larvae were most abundant (> 2000/10 $\mathrm{m}^{2}$ ) in May. Mean densities were low in July ( $\leq 102 / 10 \mathrm{~m}^{2}$ ) with few, if any, $\left(\leq 32 / 10 \mathrm{~m}^{2}\right.$ ) collected in August (Figure 10). Berrien (1978) reported that in May 1966, larvae were caught between Chesapeake Bay and Oregon Inlet, North Carolina across the continental shelf, while by June larvae had spread from Martha's Vineyard to Currituck Beach, North Carolina. The highest abundance was off Montauk Point, New York. By June, most larvae occurred to the north, while in August few were caught. This pattern also corresponds with previous reports by Sette (1943).

## JUVENILES AND ADULTS

Collections of Atlantic mackerel from the NEFSC bottom trawl surveys show that the distributions of juveniles ( $\leq 25 \mathrm{~cm}$ ) and adults ( $\geq 26 \mathrm{~cm}$ ) ranged from Cape Hatteras to Georges Bank, and southwestern Nova Scotia and the Gulf of Maine (Figure 11). The distribution of both life stages was generally similar although in spring adults tended to be distributed further offshore than the juveniles, along the outer edge of the Continental Shelf. In the fall, a few juveniles were collected in the near coastal waters of the Mid-Atlantic Bight and southern New England, particularly eastern Long Island, while adults were absent. The mean number of fish caught was highest in winter for adults (106/station) and in summer for juveniles (351/station), with more collected in the spring than in the fall reflecting the movements of the southern spawning contingent inshore. The highest abundance in spring occurs in the oceanic waters between Chesapeake Bay and southern New England, as the fish move north. Winter and summer distributions are presented as presence/absence data, precluding a discussion of abundances.

Based on the Massachusetts inshore bottom trawl surveys, occurrences of Atlantic mackerel were higher for juveniles in the autumn and for adults in the spring (Figure 12). In the autumn, most juveniles ( 10 to < 1391 fish/tow)
were caught in and around the waters off Cape Ann although small numbers ( 1 to < 500 fish/tow) were collected in Cape Cod Bay, primarily off Race Point. In the spring, the catch was highest ( 100 to < 101 fish/tow) along Vineyard Sound. In the fall, only two adults were collected (one in Cape Cod Bay, one off Cape Ann). In spring, the greatest numbers of fish ( 25 to < 37 fish/tow) were found in Nantucket Sound with lesser numbers ( 5 to $<25$ fish /tow) also collected there and south of Cape Ann in the northern end of Massachusetts Bay. From 1 to < 5 fish/tow were also caught at several stations in and around Cape Cod in the spring. This would correspond with the spawning and migration patterns described above.

From 1960-1970, 112 species of fishes were collected in coastal Massachusetts waters as part of the Massachusetts coastal zone survey (Clayton et al. 1978). Indices were prepared on percent frequency of occurrence of various life stages with the term "random" used to designate marine species which may randomly occur in the estuary and percentages based on the total number of fish (all species) collected in the whole survey. The following list indicates areas where Atlantic mackerel were recorded, the life stage, and relative frequency.

| Location | Life stage | Frequency of <br> Occurrence |
| :--- | :--- | :--- |
| Annisquam/ <br> Gloucester | Adults | Random; < 1\% of <br> collection |
| Salem Harbor | Eggs | Random; < 1\% of <br> collection |
| Lynn/Saugus | Adults | Random; < 1\% of <br> collection |
| Rocky Point/ <br> Plymouth | Eggs/larvae | Common; 1-4.99\% <br> of collection |
| Cape Cod <br> Canal | Eggs/larvae | No information |
| Taunton River/ <br> Mount Hope <br> Bay | Adults | Random; < 1\% of <br> collection |

A total of 92 Atlantic mackerel were caught during the Rhode Island Narragansett Bay bottom trawl surveys. They were captured in low numbers at all but four stations and in all years except 1990 and 1995. Juveniles were present in summer and autumn and a single adult was caught in winter. The length frequencies by season show juveniles from 7-17 cm total length (TL) occurred in summer and from 18-23 cm TL occurred in winter. Juveniles were caught throughout much of the Bay but the highest catch was made at the ocean station in autumn ( 2.3 fish/tow; Figure 13). The single adult was caught farther up the Bay near Newport.

Survey data from the Connecticut bottom trawl surveys in Long Island Sound indicated that although few Atlantic mackerel were collected, analysis of length-frequency data indicated that both juveniles and adults were present at different times and distributed differently (Gottschall et al.,
in review). This is confirmed by recent analysis of the 19921997 survey results (Figure 14). Adults (> 28 cm ; range 3649 cm ) were present in the spring and according to Gottschall et al. (in review) into midsummer and distributed throughout the sound. In contrast, juveniles ranging from $12-24 \mathrm{~cm}$ were collected in the autumn (primarily September and October) at depths $<18 \mathrm{~m}$ from Norwalk to the Housatonic River along the Connecticut shore (Gottschall et al., in review).

Few ( $\mathrm{n}=12$ ) Atlantic mackerel were collected in otter trawl surveys in the Hudson-Raritan estuary from 1992 to 1997. All were juveniles ranging from $7-8 \mathrm{~cm}$ and were collected during one survey in July 1997; most were collected on the eastern edge of Staten Island (S. Wilk, personal communication).

## Estuarine Distribution (ELMR)

The NOAA/National Ocean Service (NOS) Estuarine Living Marine Resources (ELMR) program reviewed the distribution and relative abundances of mackerel in estuaries from Waquoit Bay, Massachusetts to the Cape Fear River, North Carolina. The data were based on three salinity zones, i.e., tidal ( $0.0-0.5 \mathrm{ppt}$ ), mixed ( $0.5-25 \mathrm{ppt}$ ) and seawater (> 25 ppt ). Summaries of these distributions are presented in Table 1 for northwestern Atlantic estuaries (Jury et al. 1994) and in Table 2 for southern New England and Mid-Atlantic estuaries (Stone et al. 1994).

## STATUS OF THE STOCKS

Total domestic landings, including commercial and recreational, of Atlantic mackerel in the northwest Atlantic were 32,100 metric tons (mt) in 1993, 16\% less than 1992 landings (Anderson 1995; Figure 15). Canadian landings totaled 26,900 mt in 1993, a record since 1986, whereas United States commercial and recreational landings in 1993 were only 4,500 and 500 mt , respectively (Anderson 1995). Recent improvements in recruitment and reduced average annual landings enabled the Atlantic mackerel stock to recover from low biomass levels in the late 1970's (Anderson 1995; Figure 15).

From 1973-1977, Total Allowable Catches (TAC) were set for the southern spawning contingent in Northwest Atlantic Fisheries Organization (NAFO) Subareas 5 and 6 and for the northern contingent. However, there is no evidence for genetic differences between the contingents (MacKay 1967) and distinctions have not been made to determine individual contingent contributions to the total population (Garrod 1975). As a result, Atlantic mackerel have been managed as a unit stock since 1975 (Anderson 1982).

Atlantic mackerel landings reached a peak in the early 1970s of approximately $400,000 \mathrm{mt}$ but were drastically reduced to $30,000 \mathrm{mt}$ in the late 1970s (Anderson 1995;

Figure 15). Throughout 1980-1988, landings increased to an average $82,700 \mathrm{mt}$ until Total Allowable Level of Foreign Fishing (TALFF) regulations for distant water fleet fishing activities in the northwest Atlantic were eliminated in 1992 and landings subsequently decreased to $32,000 \mathrm{mt}$ in 1993 (Anderson 1995).

Northeast Fisheries Science Center fall and spring trawl survey data and assessment analyses indicate Atlantic mackerel stock biomass levels increased from 300,000 mt to 1.6 million mt in the years 1962-1969; however, levels decreased to an average 776,000 mt during 1977-1981 (Anderson 1995; Figure 15). Stock biomass increased steadily throughout the 1980s and in 1990 to approximately 3 million mt, which is the current estimated biomass level (Anderson 1995; Figure 15). Spawning stock biomass (50\% of age 2 and $100 \%$ of age 3 and older mackerel) increased from 600,000 mt in 1982 to more than 2 million mt in 1990, and has remained at or above that level since that time.

Regulations on landings of Atlantic mackerel were enforced in 1976 in hopes of reducing fishing effort so as to ensure reproductive success in the population by keeping spawning stock levels above devastating levels. Recruitment has increased since 1976-1980 and strong year classes were evident in 1982, 1987, 1988, and 1990-1993 (Northeast Fisheries Science Center 1996). The northwest Atlantic mackerel stock is currently at a high level of biomass and is underexploited (Northeast Fisheries Science Center 1996).

## RESEARCH NEEDS

As stated by Overholtz et al. (1991b) and based on the results of model projections, unless the impacts of compensatory mechanisms are accounted for, evaluations of current stock status using the current standard assessment methodology may in fact be optimistic and risky if catches are increased to high levels. These authors indicate that two advances would help to improve assessments: (1) an MSVPA to provide correctly scaled estimates of recruitment, and (2) a general prediction mortality model that would provide useful estimates of M2's for forecasting purposes. Other data that will be important include monitoring weights of individual fish to assess future changes, annual tracking of sexual maturity of age 2 and age 3 fish, additional food habits sampling at critical times and places and information on predation mortality of age-0 mackerel. Improved predation models that account for predator preference and prey abundance would allow for more accurate predictions of the impacts of these factors.

In addition, even though Atlantic mackerel is managed and assessed as one stock throughout the U.S. EEZ, the question of multiple stocks still needs to be settled from a scientific standpoint. This could be addressed via new technologies such as microconstituent analysis of otoliths using inductively coupled plasma mass-spectrometry (ICPMS).

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Table 1. Summary of the distribution and abundance of Atlantic mackerel in northwestern Atlantic estuaries based on Jury et al. (1994). Data reliability: ${ }^{* * *}=$ Highly Certain, ${ }^{* *}=$ Moderately Certain, $*=$ Reasonable Inference. Relative abundance: $\mathrm{H}=$ highly abundant, $\mathrm{A}=$ abundant, $\mathrm{C}=$ common, $\mathrm{R}=$ rare, $0=$ not present, $\mathrm{N}=$ no data presented, $\mathrm{NI}=$ no data available, $\mathrm{NZ}=$ zone not present.

| Estuaries and Rivers | Life Stage | Relative Abundance and Distribution (months) months shown as (1)-(12); i.e., January = (1) |  |  | Data Reliability |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $\begin{gathered} \hline \text { Tidal Fresh } \\ 0.0-0.5 \mathrm{ppt} \\ \hline \end{gathered}$ | $\begin{gathered} \hline \text { Mixing Zone } \\ 0.5-25 \mathrm{ppt} \\ \hline \end{gathered}$ | Seawater Zone $>25 \mathrm{ppt}$ |  |
| Passamaquoddy Bay | Adults (A) | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6-9), \mathrm{R}(10)$ | ** |
|  | Spawning adults (S) | 0 | 0 | 0 | ** |
|  | Eggs (E) | 0 | 0 | NI | * |
|  | Larvae (L) | 0 | 0 | NI | * |
|  | Juveniles (J) | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6-9), \mathrm{R}(10)$ | ** |
| Englishman/Machias Bay | A | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6-9), \mathrm{R}(10)$ | * |
|  | S | 0 | 0 | 0 | * |
|  | E | 0 | 0 | NI | * |
|  | L | 0 | 0 | NI | * |
|  | J | 0 | $\mathrm{R}(6-10)$ | $\mathrm{R}(6-10)$ | * |
| Narraguagus Bay | A | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6-9), \mathrm{R}(10)$ | * |
|  | S | 0 | 0 | 0 | * |
|  | E | 0 | 0 | NI | * |
|  | L | 0 | 0 | NI | * |
|  | J | 0 | R (6-10) | R (6-10) | * |
| Blue Hill Bay | A | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6-9), \mathrm{R}(10)$ | * |
|  | S | 0 | 0 | 0 | * |
|  | E | 0 | 0 | NI | * |
|  | L | 0 | 0 | NI | * |
|  | J | 0 | R (6-10) | R(6-10) | * |
| Penobscot Bay | A | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6-9), \mathrm{R}(10)$ | ** |
|  | S | 0 | 0 | 0 | ** |
|  | E | 0 | 0 | $\mathrm{R}(6-7)$ | ** |
|  | L | 0 | 0 | R(6-7) | ** |
|  | J | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6-9), \mathrm{R}(10)$ | ** |
| Muscongus Bay | A | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6,8-9), \mathrm{A}(7), \mathrm{R}(10)$ | * |
|  | S | 0 | 0 | 0 | ** |
|  | E | 0 | 0 | 0 | ** |
|  | L | 0 | 0 | 0 | ** |
|  | J | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6,8-9), \mathrm{A}(7), \mathrm{R}(10)$ | * |
| Damariscotta River | A | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6,8-9), \mathrm{A}(7), \mathrm{R}(10)$ | ** |
|  | S | 0 | 0 | 0 | ** |
|  | E | 0 | 0 | 0 | ** |
|  | L | 0 | 0 | 0 | ** |
|  | J | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6,8-9), \mathrm{A}(7), \mathrm{R}(10)$ | ** |
| Sheepscot River | A | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6,8-9), \mathrm{A}(7), \mathrm{R}(10)$ | *** |
|  | S | 0 | 0 | 0 | ** |
|  | E | 0 | 0 | 0 | ** |
|  | L | 0 | 0 | 0 | ** |
|  | J | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6,8-9), \mathrm{A}(7), \mathrm{R}(10)$ | *** |
| Kennebec/Androscoggin Rivers | A | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6,8-9), \mathrm{A}(7), \mathrm{R}(10)$ | ** |
|  | S | 0 | 0 | 0 | ** |
|  | E | 0 | 0 | 0 | ** |
|  | L | 0 | 0 | 0 | ** |
|  | J | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6,8-9), \mathrm{A}(7), \mathrm{R}(10)$ | ** |

Table 1. cont'd.

| Estuaries and Rivers | Life Stage | Relative Abundance and Distribution (months) months shown as (1)-(12); i.e., January = (1) |  |  | Data Reliability |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Tidal Fresh $0.0-0.5 \mathrm{ppt}$ | $\begin{gathered} \text { Mixing Zone } \\ 0.5-25 \mathrm{ppt} \\ \hline \end{gathered}$ | Seawater Zone $>25$ ppt |  |
| Casco Bay | A | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6-9), \mathrm{R}(10)$ | * |
|  | S | 0 | 0 | 0 | ** |
|  | E | 0 | 0 | NI | * |
|  | L | 0 | 0 | NI | * |
|  | J | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6-9), \mathrm{R}(10)$ | * |
| Saco Bay | A | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6-9), \mathrm{R}(10)$ | * |
|  | S | 0 | 0 | 0 | ** |
|  | E | 0 | 0 | 0 | * |
|  | L | 0 | 0 | 0 | * |
|  | J | 0 | $\mathrm{C}(6-9), \mathrm{R}(10)$ | $\mathrm{C}(6-9), \mathrm{R}(10)$ | * |
| Wells Harbor | A | NZ | R (6-10) | R (6-10) | * |
|  | S | NZ | 0 | 0 | ** |
|  | E | NZ | 0 | 0 |  |
|  | L | NZ | 0 | 0 | * |
|  | J | NZ | $\mathrm{R}(6-10)$ | $\mathrm{R}(6-10)$ | * |
| Great Bay | A | 0 | 0 | R (5-11) | * |
|  | S | 0 | 0 | 0 | *** |
|  | E | 0 | C(5-7) | $\mathrm{C}(5), \mathrm{A}(6-7)$ | * |
|  | L | 0 | $\mathrm{C}(5-7), \mathrm{R}(8)$ | $\mathrm{C}(5-7), \mathrm{R}(8)$ | * |
|  | J | 0 | 0 | C(5-11) | * |
| Merrimack River | A | 0 | $\mathrm{R}(5-10)$ | NZ | ** |
|  | S | 0 | 0 | NZ | ** |
|  | E | 0 | H(5-6), C(7) | NZ | ** |
|  | L | 0 | C(5-8) | NZ | ** |
|  | J | 0 | R (5-10) | NZ | ** |
| Massachusetts Bay | A | NZ | NZ | $\mathrm{C}(5-10), \mathrm{R}(11)$ | *** |
|  | S | NZ | NZ | $\mathrm{C}(5-8)$ | * |
|  | E | NZ | NZ | $\mathrm{C}(5), \mathrm{A}(6,7), \mathrm{R}(8)$ | * |
|  | L | NZ | NZ | $\mathrm{C}(5), \mathrm{A}(6,7), \mathrm{R}(8)$ | * |
|  | J | NZ | NZ | $\mathrm{C}(5-10)$ | *** |
| Boston Harbor | A | NZ | R(5), C(6-9) | R(5), C(6-9) | ** |
|  | S | NZ | 0 | 0 | * |
|  | E | NZ | $\mathrm{R}(5,8), \mathrm{C}(6,7)$ | $\mathrm{C}(5,8), \mathrm{A}(6,7)$ | * |
|  | L | NZ | $\mathrm{R}(5), \mathrm{C}(6-8)$ | $\mathrm{C}(5), \mathrm{A}(6,7) \mathrm{R}(8)$ | * |
|  | J | NZ | R(5), C(6-10) | $\mathrm{R}(5), \mathrm{C}(6-10)$ | ** |
| Cape Cod Bay | A | NZ | $\mathrm{C}(5-8), \mathrm{R}(9)$ | $\mathrm{A}(5-7), \mathrm{C}(8-11)$ | ** |
|  | S | NZ | 0 | A(5-7) | * |
|  | E | NZ | C(5-8) | $\mathrm{H}(5,6), \mathrm{A}(7), \mathrm{C}(8)$ | ** |
|  | L | NZ | C(5-8) | $\mathrm{H}(5,6), \mathrm{A}(7), \mathrm{C}(8)$ | ** |
|  | J | NZ | C(5-10) | $\mathrm{A}(5-8), \mathrm{C}(9-11)$ | ** |

Table 2. Summary of the distribution and abundance of Atlantic mackerel in southern New England and Mid-Atlantic estuaries based on Stone et al. (1994). Data reliability: ${ }^{* * *}=$ Highly Certain, ${ }^{* *}=$ Moderately Certain, $*=$ Reasonable Inference. Relative abundance: $\mathrm{H}=$ highly abundant, $\mathrm{A}=$ abundant, $\mathrm{C}=$ common, $\mathrm{R}=$ rare, $0=$ not present, $\mathrm{N}=$ no data presented, $\mathrm{NI}=$ no data available, $\mathrm{NZ}=$ zone not present.

| Estuaries and Rivers | Life Stage | Relative Abundance and Distribution (months) months shown as (1)-(12); i.e., January = (1) |  |  | Data <br> Reliability |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $\begin{aligned} & \hline \text { Tidal Fresh } \\ & 0.0-0.5 \mathrm{ppt} \end{aligned}$ | $\begin{gathered} \hline \text { Mixing Zone } \\ 0.5-25 \mathrm{ppt} \\ \hline \end{gathered}$ | $\begin{gathered} \text { Seawater Zone } \\ >25 \mathrm{ppt} \\ \hline \end{gathered}$ |  |
| Waquoit Bav | Adults (A) | NZ | 0 | R (5.6). C(7-9) | * |
|  | Spawning adults (S) | NZ | 0 | 0 | ** |
|  | Eggs (E) | NZ | 0 | R(5-8) | * |
|  | Larvae (L) | NZ | 0 | R (5-8) | * |
|  | Juveniles (J) | NZ | 0 | R(5-9) | * |
| Buzzards Bay | A | NZ | 0 | $\mathrm{C}(3,4,11,12), \mathrm{R}(5-9)$ | ** |
|  | S | NZ | 0 | 0 | ** |
|  | E | NZ | R(5-8) | $\mathrm{A}(5,6), \mathrm{C}(7), \mathrm{R}(8)$ | * |
|  | L | NZ | $\mathrm{R}(6-8)$ | $\mathrm{R}(5-8)$ | * |
|  | J | NZ | $\mathrm{R}(5-9)$ | $\mathrm{R}(5-9)$ | * |
| Narragansett Bay | A | 0 | 0 | C(5-9) |  |
|  | S | 0 | 0 | 0 | ** |
|  | E | 0 | R(5-7) | $\mathrm{A}(5,6), \mathrm{C}(7)$ | ** |
|  | L | 0 | R(5-7) | C(5,6), R(7) | * |
|  | J | 0 | R(5-9) | C(5-9) | * |
| Long Island Sound | A | 0 | 0 | $\mathrm{C}(4-11)$ | * |
|  | S | 0 | 0 | R(4-6) | *** |
|  | E | 0 | 0 | $\mathrm{C}(4,6), \mathrm{A}(5)$ | *** |
|  | L | 0 | 0 | $\mathrm{C}(5), \mathrm{R}(6)$ | *** |
|  | J | 0 | $\mathrm{R}(4,5)$ | $\mathrm{C}(4-11)$ | * |
| Connecticut River | A | 0 | 0 | NZ | ** |
|  | S | 0 | 0 | NZ | *** |
|  | E | 0 | 0 | NZ | ** |
|  | L | 0 | 0 | NZ | ** |
|  | J | 0 | 0 | NZ | ** |
| Gardiners Bay | A | NZ | 0 | $\mathrm{C}(4,5), \mathrm{R}(6-11)$ | * |
|  | S | NZ | 0 | R (4-6) | * |
|  | E | NZ | 0 | $\mathrm{H}(4), \mathrm{A}(5), \mathrm{C}(6)$ | ** |
|  | L | NZ | 0 | $\mathrm{H}(4), \mathrm{A}(5), \mathrm{C}(6)$ | ** |
|  | J | NZ | 0 | $\mathrm{C}(4-11)$ | ** |
| Great South Bay | A | NZ | 0 | $\mathrm{C}(4,5), \mathrm{R}(6-11)$ | * |
|  | S | NZ | 0 | 0 | ** |
|  | E | NZ | 0 | C(4) | ** |
|  | L | NZ | 0 | C(5) | ** |
|  | J | NZ | 0 | $\mathrm{C}(4-11)$ | * |
| Hudson/Raritan River | A | 0 | 0 | $\mathrm{C}(4,5,10,11), \mathrm{R}(6,9,12)$ | * |
|  | S | 0 | 0 | 0 | * |
|  | E | 0 | 0 | 0 | * |
|  | L | 0 | 0 | 0 | * |
|  | J | 0 | $\mathrm{R}(4-6,10-12)$ | $\mathrm{C}(4-6,10,11), \mathrm{R}(7-9,12)$ | * |
| Barnegat Bay | A | 0 | 0 | 0 | *** |
|  | S | 0 | 0 | 0 | *** |
|  | E | 0 | 0 | R (4-6) | ** |
|  | L | 0 | 0 | R (4-6) | ** |
|  | J | 0 | 0 | R (5-9) | ** |
| NJ Inland Bays | A | 0 | 0 | 0 | *** |
|  | S | 0 | 0 | 0 | *** |
|  | E | 0 | 0 | R(4-6) | ** |
|  | L | 0 | 0 | R (4-6) | ** |
|  | J | 0 | 0 | R(5-9) | ** |
| Delaware Bay | A | 0 | 0 | R(3-5) | ** |
|  | S | 0 | 0 | 0 | *** |
|  | E | 0 | 0 | 0 | *** |
|  | L | 0 | 0 | 0 | *** |
|  | J | 0 | 0 | 0 | *** |

Table 2. cont'd.

| Estuaries and Rivers | Life Stage | Relative Abundance and Distribution (months) months shown as (1)-(12); i.e., January = (1) |  |  | Data Reliability |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $\begin{aligned} & \hline \text { Tidal Fresh } \\ & 0.0-0.5 \mathrm{ppt} \\ & \hline \end{aligned}$ | $\begin{gathered} \hline \text { Mixing Zone } \\ 0.5-25 \mathrm{ppt} \\ \hline \end{gathered}$ | $\begin{gathered} \text { Seawater Zone } \\ >25 \mathrm{ppt} \end{gathered}$ |  |
| Delaware Inland Bavs | A | NZ | 0 | R (3-5) | ** |
|  | S | NZ | 0 | 0 | *** |
|  | E | NZ | 0 | 0 | *** |
|  | L | NZ | 0 | 0 | ** |
|  | J | NZ | 0 | 0 | ** |
| Chincoteague | A | NZ | NZ | 0 | *** |
|  | S | NZ | NZ | 0 | *** |
|  | E | NZ | NZ | 0 | *** |
|  | L | NZ | NZ | 0 | *** |
|  | J | NZ | NZ | 0 | *** |
| Chesapeake Bay | A | 0 | R(1-3) | R(1-3) | ** |
|  | S | 0 | 0 | 0 | *** |
|  | E | 0 | 0 | 0/NI(4-5) | ** |
|  | L | 0 | 0 | R(5) | ** |
|  | J | 0 | $\mathrm{R}(1-4,11,12)$ | $\mathrm{R}(1-4,11,12)$ | ** |
| Chester River | A | 0 | 0 | NZ | *** |
|  | S | 0 | 0 | NZ | *** |
|  | E | 0 | 0 | NZ | *** |
|  | L | 0 | 0 | NZ | *** |
|  | J | 0 | 0 | NZ | *** |
| Choptank River | A | 0 | 0 | NZ | *** |
|  | S | 0 | 0 | NZ | *** |
|  | E | 0 | 0 | NZ | *** |
|  | L | 0 | 0 | NZ | *** |
|  | J | 0 | 0 | NZ | *** |
| Patuxent River | A | 0 | 0 | NZ | *** |
|  | S | 0 | 0 | NZ | *** |
|  | E | 0 | 0 | NZ | *** |
|  | L | 0 | 0 | NZ | *** |
|  | J | 0 | 0 | NZ | *** |
| Potomac River | A | 0 | 0 | NZ | *** |
|  | S | 0 | 0 | NZ | *** |
|  | E | 0 | 0 | NZ | *** |
|  | L | 0 | 0 | NZ | *** |
|  | J | 0 | 0 | NZ | *** |
| Tangier/Pocomoke | A | NZ | 0 | NZ | *** |
|  | S | NZ | 0 | NZ | *** |
|  | E | NZ | 0 | NZ | *** |
|  | L | NZ | 0 | NZ | *** |
|  | J | NZ | 0 | NZ | *** |
| Rappahannock River | A | 0 | R (1-3) | NZ | ** |
|  | S | 0 | 0 | NZ | *** |
|  | E | 0 | 0 | NZ | *** |
|  | L | 0 | 0 | NZ | *** |
|  | J | 0 | $\mathrm{R}(1-4,11,12)$ | NZ | ** |
| York River | A | 0 | R (1-3) | NZ | ** |
|  | S | 0 | 0 | NZ | *** |
|  | E | 0 | 0 | NZ | *** |
|  | L | 0 | 0 | NZ | *** |
|  | J | 0 | $\mathrm{R}(1-4,11,12)$ | NZ | ** |
| James River | A | 0 | $\mathrm{R}(1-3)$ | NZ | ** |
|  | S | 0 | 0 | NZ | *** |
|  | E | 0 | 0 | NZ | *** |
|  | L | 0 | 0 | NZ | *** |
|  | J | 0 | $\mathrm{R}(1-4,11,12)$ | NZ | ** |

Table 3. Summary of life history and habitat parameters for Atlantic mackerel, Scomber scombrus.

| Life Stage | Size and Growth | Geographic Location | Habitat | Temperature |
| :---: | :---: | :---: | :---: | :---: |
| Eggs ${ }^{1}$ | Diameter: 1-1.3 mm, avg. $=1.1$ mm .1 oil globule, avg. 0.3 mm diameter. In Gulf of St. <br> Lawrence egg size decreased over time and in relation to ambient temperature (avg. diam. $=1.3 \mathrm{~mm}$ in June, 1.1 mm in August). | Offshore waters of Chesapeake Bay to southern side of Gulf of St. Lawrence with majority on shoreward side of continental shelf. Varying abundances in bays and estuaries from New Jersey to Canada. Highest abundances in May, June in southern New England - MidAtlantic region. | Eggs pelagic, distributed at depths ranging from 10 325 m , majority from 3070 m ; depth varies with season, egg diameter, thermocline. | Eggs collected at $5-23^{\circ} \mathrm{C}$, highest abundance from $\sim 7-16^{\circ} \mathrm{C}$ with range related to season. In May, weighted mean surface temperature $=$ $11^{\circ} \mathrm{C}$ for eggs from Martha's Vineyard. Egg mortality rates ( $\sim 41 \% / \mathrm{d}$ ) correlated with rate of warming during spawning season since acclimation temperature of adults related to egg mortality. Mortality $<20 \%$ from $9.4-15.1^{\circ} \mathrm{C}$. Incubation temperature dependent: 7.5 d at $11^{\circ} \mathrm{C}$ to $\sim 3 \mathrm{~d}$ at $20^{\circ} \mathrm{C}$. Temperatures must be $>\sim 7^{\circ} \mathrm{C}$ for development. |
| Larvae ${ }^{2}$ | Larvae average 3.1-3.3 mm SL with large yolk sac. Postlarvae are $11-50 \mathrm{~mm}$. Teeth present at 192 h after hatching. | Larvae (< 13 mm ) occur primarily in offshore waters from Chesapeake Bay to southern Gulf of St. Lawrence. Similar to distribution of eggs, some larvae also collected in open bays and estuaries. Highest abundances in May offshore from Delaware Bay to Hudson Canyon; by June, highest abundance ranges from Hudson Canyon north to southern New England and north of Cape Cod. | Most distributed at depths from $10-130 \mathrm{~m}$, usually at < 50 m . Depth varies diurnally, also with age and with thermocline; i.e., newly hatched larvae found between 5-10 m during the day, however, as they grow theyre at depths closer to the surface. | Hatching occurs $\sim 90-120 \mathrm{~h}$ at average temperature of $13.8^{\circ} \mathrm{C}$. Yolk sac stage complete by 137 h at this temperature. Larvae collected at $6-22^{\circ} \mathrm{C}$; highest abundance at $8-13^{\circ} \mathrm{C}$. Changes in abundance at different temperature ranges related to season; i.e., increasing from May through August. Larval mortality rates (~ 35$42 \% / \mathrm{d}$ ) may be partially correlated with temperature. |
| Juveniles ${ }^{3}$ | Postlarvae transform from planktonic to swimming and schooling behavior at $\sim 30-50$ mm ; reach 50 mm in $\sim 2$ months; 20 cm after 1 y (rates may be faster in mid-Atlantic: ~ $70-80 \mathrm{~mm}$ in 2 months). Northern contingent fish may grow faster in 1st year than southern contingent, but may not be significantly different for first 90 days. | Southwestern Nova Scotia, Gulf of Maine, Georges Bank to Cape Hatteras - distribution changes seasonally. Late summer/fall primarily along western shores of Gulf of Maine, around Cape Ann, inshore areas of New England (includes estuaries in Rhode Island, Connecticut), eastern Long Island. In spring, although common offshore, some are further inshore than adults and found in some Mid-Atlantic estuaries until fall. | Depth varies seasonally. Offshore in fall, most abundant at $\sim 20-40 \mathrm{~m}$, range from 0-320 m. In winter, $50-70 \mathrm{~m}$. Spring, although dispersed through water column, concentrated $30-90 \mathrm{~m}$. Move higher in summer to 20-50 m, range from 0-210 m. | At $15-17^{\circ} \mathrm{C}$ growth rates of fish $>15 \mathrm{~mm}$ averaged $0.73 \mathrm{~mm} / \mathrm{d}$. Juveniles found from 4 $22^{\circ} \mathrm{C}$, most at $10^{\circ} \mathrm{C}$. Temperature distribution offshore changes seasonally as average temperature ranges increase: in winter/spring, most found $5-6^{\circ}$, in summer at $8-13^{\circ} \mathrm{C}$. Similar associations inshore: Massachusetts, $11^{\circ}$ in spring, 9 and $13^{\circ}$ in fall; Rhode Island, $19^{\circ}$ in summer, 11 and $15^{\circ} \mathrm{C}$ in fall. |
| Adults ${ }^{4}$ | Males/females grow at same rate, reaching maximum age of ~ 20 y , with maximum fork length of $\sim 47 \mathrm{~cm}$. Reach 26 cm by second year, 33 cm by fifth year. By age 6, may be 39-40 cm . Spring weight for 35 cm fish is $\sim 0.5 \mathrm{~kg}$; fall is 0.6 kg . Growth may be population density dependent; year class size partially influences initial growth during cohort's first years. | Two major contingents in NW Atlantic. Fish overwinter in deep water of shelf from Nova Scotia to Cape Hatteras. In spring, two groups formed: fish from southern group move inshore and northward along coast, joined by northern group moving inshore. By late Apr./May southern group found off New Jersey, Long Island, moving to western Gulf of Maine by summer, returns to shelf edge between Long Island - Chesapeake Bay in Oct. Northern group mixes briefly with southern group late spring off New England, migrates east along Nova Scotia into Gulf of St. Lawrence; some fish remain along Maine/Nova Scotia coast. By late fall, this contingent mixes with southern group in Gulf of Maine before returning to outer shelf. | Depth changes seasonally, perhaps influenced by prey availability. Fall: 10-340 $\mathrm{m},>50 \%$ at $60-80 \mathrm{~m}$. Winter: $\sim 50 \%$ at $20-30 \mathrm{~m}$. Spring: down to 380 m , ~ $25 \%$ at $60-170 \mathrm{~m}$. <br> Summer: > $60 \%$ at 50-70 m . Larger fish deeper than smaller ones. Distribution may also be correlated with downwelling events and onshore advection of warm surface water. | Seasonal temperature cycles influence migration/distribution. Field studies: intolerant of temperatures $<5-6^{\circ} \mathrm{C}$ or $>15-16^{\circ} \mathrm{C}$. Lab: prefer $7-16^{\circ}$, lethal at $<2^{\circ}$ or $>28.5^{\circ}$. Offshore distribution varies with seasonal temperature changes. Fall: $>80 \%$ at $9-12^{\circ}$. Winter: $\sim 70 \%$ at $5-6^{\circ}$. Spring $>25 \%$ at $13^{\circ}$. Summer: $>30 \%$ at $10-11^{\circ},>35 \%$ at $14^{\circ}$. Massachusetts: spring most at $14^{\circ}$, fall at $10^{\circ}$ and $15^{\circ}$. In northern Gulf of St. Lawrence, adults in colder temperatures $\left(4^{\circ}\right)$; however, probability of occurrence higher when temperatures $\geq 7^{\circ} \mathrm{C}$. |
| Spawning Adults ${ }^{5}$ | $\mathrm{L}_{50}$ for females $=25.7 \mathrm{~cm}$, males =26.0; $\mathrm{A}_{50}$ for both $=1.9$ y. By age $3,99 \%$ of females, $97 \%$ of males mature. <br> Newfoundland fish have higher $\mathrm{L}_{50}$ values: females $=34 \mathrm{~cm}$, males $=35 \mathrm{~cm}$. Gulf of St. Lawrence, coastal Nova Scotia, Massachusetts fish spawn first at age 2 , lengths $>30 \mathrm{~cm}$. Differences in median maturity may be due to slower growth of larger year classes that may delay spawning from one to three years. | Spawning progresses from south to north. Southern contingent spawns in Mid-Atlantic Bight and Gulf of Maine mid-Apr.-June, northern in southern Gulf of St. Lawrence May-Aug. Most spawning in shoreward half of continental shelf, some on shelf edge and beyond. Most productive between Chesapeake Bay/southern New England, less in Gulf of St. Lawrence, Gulf of Maine, Nova Scotia coast. Some spawning in open bays; e.g., Cape Cod, Massachusetts Bays. Less in enclosed bays; e.g., Chesapeake, Delaware Bays. |  | Spawning begins when temperatures are $\geq 7^{\circ} \mathrm{C}$ (peak $9-14^{\circ} \mathrm{C}$ ) and progresses from southern to northern waters during adult migration. |

Table 3. cont'd.

| Life Stage | Salinity | Prey | Predators | Notes |
| :---: | :---: | :---: | :---: | :---: |
| Eggs ${ }^{1}$ | Although eggs are collected in waters ranging from estuaries ( $18-25 \mathrm{ppt}$ ) to full seawater (> 30 ppt ), mortality is higher at lower salinities (< 25 ppt ). |  |  |  |
| Larvae ${ }^{2}$ | Although larvae are occasionally collected in open bays and estuaries at salinities < 25 ppt , the largest abundances are found in higher salinities of > 30 ppt in offshore waters. Mortality may be related to salinities of $\leq 23 \mathrm{ppt}$. | $50 \%$ threshold for first feeding is 3.8 mm , all larvae feeding by 4.5 mm . Diet related to larval size: first feeding larvae may be phytophagous; individuals $>4.4 \mathrm{~mm}$ feed on copepod nauplii; > 5 mm , copepodites; > 6 mm adult copepods. Diets of larger larvae shift to include fish larvae: yellowtail flounder, silver hake, redfish; > 6 mm are cannibalistic on smaller conspecifics which may make up as much as $20 \%$ of larval fish consumed. <br> However, piscivory is density dependent; i.e., limited at densities of fish larvae $<0.1 \mathrm{~m}^{3}$ and declines with increasing density of nauplii, switching to copepods. | Mackerel > 6 mm are cannibalistic on smaller conspecifics of 3.5-4.5 mm. | Calculated mean digestive times ~ 1-2 h ; to maintain rapid growth rates larvae must feed continually for about $15 \mathrm{~h} / \mathrm{d}$. Diet may reflect most abundant food items capable of being ingested due to width of mouth gape. Factors influencing mortality include zooplankton abundance, wind driven surface currents, epizootics in addition to temperature and appropriate food supply. |
| Juveniles ${ }^{3}$ | Juveniles found in some inshore bays and estuaries as well as offshore at salinities > 25 ppt . | Principal prey include small crustaceans, such as copepods, euphausiids, amphipods, mysid shrimp, decapod larvae. Also small pelagic mollusks, chaetognaths, nematodes, ammodytes, other larval fish. | Same as for adults, but for juveniles specifically: Atlantic cod, squid, seabirds. | Atlantic mackerel are opportunistic feeders that can ingest prey either by individual selection of organisms or by filter feeding (see adults, below). |
| Adults ${ }^{4}$ | Found in open sea although occasionally in open bays with lower salinity limits of $\sim 25 \mathrm{ppt}$. | Opportunist feeders. Filter feeding or individual selection. Diet similar to juveniles, but wider range and larger prey items. Includes euphausid, pandalid, and crangonid shrimps; chaetognaths, larvaceans, pelagic polychaetes, squids. Calanus and other copepods, amphipods, other planktonic organisms. Fishes: sand lances, herring, silver and other hakes, sculpins. Lab studies: small medusae common to temperate waters; also, where prey abundance is only 0.1 g wet weight $/ \mathrm{m}^{3}$, mackerel may not be satiated if feeding was restricted to daylight. | Mortality from predation may be the most important source of natural mortality. Predators include conspecifics, tunas, bonito, striped bass, pilot whales, common dolphins, harbor seals, porpoises, seabirds, swordfish. Sharks: shortfin mako, tiger, blue, bigeye thresher, spiny dogfish. Other predators: king mackerel, thorny skate, silver hake, red hake, bluefish, pollock, white hake, goosefish, weakfish. | Although there are two major contingents of the population they are managed as a single transboundary stock. Shifts in feeding mode may be related to season for fish in the Gulf of St. Lawrence while diet of fish in Newfoundland indicates that particulate feeding may occur throughout the season. |
| Spawning <br> Adults ${ }^{5}$ | Peak spawning occurs at salinities > 30 ppt . | Fish feed until gonadal development begins, then stop feeding until spent, feeding then resumes. | Same as for adults in general. | Mackerel are serial, or batch, spawners. Fecundity of southern contingent: 285,000-1.98 million eggs for 31-44 cm fish. Northern contingent: 211,000 to 397,000 eggs for 35 and 40 cm females, respectively, with 5-7 batches. Control of spawning time is unclear although there may be both endogenous and exogenous factors which ensures peak hatching at the time of maximum zooplankton abundance. No evidence of diel periodicity in spawning. |

${ }^{1}$ Worley (1933), Jury et al. (1994), Sette (1943), Berrien (1975, 1978), Ware (1977), Fritzsche (1978), Lanctot (1980), Peterson and Ausubel (1984), Ware and Lambert (1985), Stone et al. (1994), Collette (in prep.)
${ }^{2}$ Sette (1943), Bigelow and Schroeder (1953), Colton and Marak (1969), Berrien (1975, 1978, 1982), Peterson and Ausubel (1984), Ware and Lambert (1985), Scott and Scott (1988), Jury et al. (1994), Stone et al. (1994), Fortier and Villeneuve (1996), Collette (in prep.)
${ }^{3}$ Sette (1943, 1950), Bigelow and Schroeder (1953), Anderson and Paciorkwski (1980), Kendall and Gordon (1981), Berrien (1982), Ware and Lambert (1985),
Pepin et al. (1988), D’Amours et al. (1990), Simard et al. (1992), Jury et al. (1994), Stone et al. (1994), Collette (in prep.)
${ }^{4}$ Sette (1950), Leim and Scott (1966), MacKay (1967), Scott and Tibbo (1968), Anderson (1973), Isakov (1973), Parsons and Moores (1974), Stobo and Hunt (1974), Maurer and Bowman (1975), Moores et al. (1975), Olla et al. (1975), Overholtz and Anderson (1976), MacKay (1979), Berrien (1982), Stillwell and Kohler (1982, 1985), Murray et al. (1983), Bowman and Michaels (1984), Bowman et al. (1984), Murray (1984), Runge et al. (1987), Dery (1988), Pepin et al. (1988), Overholtz et al. (1991b), Castonguay et al. (1992), Collette (in prep.)
${ }^{5}$ Sette (1943), MacKay (1967, 1973), Ware (1977), Morse (1980), Berrien (1982), Overholtz (1989), Overholtz et al. (1991b), Walsh and Johnstone (1992), Nichols and Warne (1993), O'Brien et al. (1993), Jury et al. (1994), Stone et al. (1994), Collette (in prep.)


Figure 1. The Atlantic mackerel, Scomber scombrus (from Goode 1884).
a) 1973-1980
$\underset{(\mathrm{n}=49)}{11-30 \mathrm{~cm}}$

b) $\mathbf{1 9 8 1 - 1 9 9 0}$

$$
\underset{\substack{11-30 \mathrm{~cm} \\(\mathrm{n}=105)}}{ }
$$

$31-50 \mathrm{~cm}$
$(\mathrm{n}=128)$


Figure 2. Abundance (percent occurrence) of the major prey items in the diet of Atlantic mackerel collected during NEFSC bottom trawl surveys from 1973-1980 and 1981-1990. The 11-30 cm size range corresponds, at least roughly, to juveniles, and the $30-50 \mathrm{~cm}$ size class corresponds to adults. The category "animal remains" refers to unidentifiable animal matter. Methods for sampling, processing, and analysis of samples differed between the time periods [see Reid et al. (1999) for details].


Figure 3. Abundance of Atlantic mackerel eggs relative to surface water temperature ( $0-15 \mathrm{~m}$ ) and bottom depth based on NEFSC MARMAP ichthyoplankton surveys (April to August 1978-1987; all years combined). Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 m${ }^{2}$ ).


Figure 4. Abundance of Atlantic mackerel larvae ( $<13 \mathrm{~mm}$ ) relative to water column temperature (to a maximum of 200 m ) and bottom depth based on NEFSC MARMAP ichthyoplankton surveys (May to August 1977-1987; all years combined). Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all standardized catches (number/10 $\mathrm{m}^{2}$ ).


Figure 5. Seasonal abundance of juvenile Atlantic mackerel relative to bottom water temperature and depth based on NEFSC bottom trawl surveys (1963-1997; 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 $\mathrm{m}^{2}$ ).


Figure 6. Abundance of juvenile ( $\leq 25 \mathrm{~cm}$ ) and adult ( $\geq 26 \mathrm{~cm}$ ) Atlantic mackerel relative to bottom water temperature and depth based on spring and autumn Massachusetts inshore bottom trawl surveys (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 $\mathrm{m}^{2}$ ).


Figure 7. Seasonal abundance of juvenile Atlantic mackerel ( $<26 \mathrm{~cm}$ ) relative to bottom depth and bottom water temperature based on Rhode Island Narragansett Bay trawl surveys (1990-1996; all years combined). Open bars represent the proportion of all stations surveyed, while solid bars represent the proportion of the sum of all catches.

Adults: $\geq 26 \mathrm{~cm}$ TL




SPRING
SUMMER



Figure 8. Seasonal abundance of adult Atlantic mackerel relative to bottom water temperature and depth based on NEFSC bottom trawl surveys (1963-1997; 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 $/ 10 \mathrm{~m}^{2}$ ).


Figure 9. Distribution and abundance of Atlantic mackerel eggs collected during NEFSC MARMAP ichthyoplankton surveys from April to August, 1977-1987 [all years combined; see Reid et al. (1999) for details]. Egg densities are represented by dot size.



Figure 9. cont'd.


Figure 10. Distribution and abundance of Atlantic mackerel larvae collected during NEFSC MARMAP ichthyoplankton surveys from May to August, 1977-1987 [all years combined; see Reid et al. (1999) for details]. Larval densities are represented by dot size.


Figure 10. cont'd.


Figure 11. Seasonal distribution and abundance of juvenile ( $\leq 25 \mathrm{~cm}$ ) and adult ( $\geq 26 \mathrm{~cm}$ ) Atlantic mackerel collected during NEFSC bottom trawl surveys, 1963-1997 (all years combined). Densities are represented by dot size in spring and fall plots, while only presence and absence are represented in summer and winter plots [see Reid et al. (1999) for details].


Figure 11. cont'd.


Figure 12. Distribution and abundance of juvenile ( $<26 \mathrm{~cm}$ ) and adult ( $\geq 26 \mathrm{~cm}$ ) Atlantic mackerel in Massachusetts coastal waters collected during the spring and autumn Massachusetts inshore trawl surveys [1978-1996, all years combined; see Reid et al. (1999) for details].

Juveniles (<26 cm)


Figure 13. Seasonal distribution and relative abundance of juvenile ( $<26 \mathrm{~cm}$ ) Atlantic mackerel collected in Narragansett Bay during Rhode Island bottom trawl surveys (1990-1996; all years combined). 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 14. Distribution, abundance, and length frequency distribution of juvenile and adult Atlantic mackerel collected in Long Island Sound during spring and autumn Connecticut bottom trawl surveys [1992-1997, all years combined; see Reid et al. (1999) for details].

## Labrador - North Carolina



Figure 15. Commercial landings and stock biomass for Atlantic mackerel from Labrador to North Carolina.

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## Publications and Reports of the Northeast Fisheries Science Center

The mission of NOAA's National Marine Fisheries Service (NMFS) is "stewardship of living marine resources for the benefit of the nation through their science-based conservation and management and promotion of the health of their environment." As the research arm of the NMFS's Northeast Region, the Northeast Fisheries Science Center (NEFSC) supports the NMFS mission by "planning, developing, and managing multidisciplinary programs of basic and applied research to: 1) better understand the living marine resources (including marine mammals) of the Northwest Atlantic, and the environmental quality essential for their existence and continued productivity; and 2) describe and provide to management, industry, and the public, options for the utilization and conservation of living marine resources and maintenance of environmental quality which are consistent with national and regional goals and needs, and with international commitments." Results of NEFSC research are largely reported in primary scientific media (e.g., anonymously-peer-reviewed scientific journals). However, to assist itself in providing data, information, and advice to its constituents, the NEFSC occasionally releases its results in its own media. Those media are in three categories:

NOAA Technical Memorandum NMFS-NE -- This series is issued irregularly. The series includes: data reports of longterm or large area studies; synthesis reports for major resources or habitats; annual reports of assessment or monitoring programs; documentary reports of oceanographic conditions or phenomena; manuals describing field and lab techniques; literature surveys of major resource or habitat topics; findings of task forces or working groups; summary reports of scientific or technical workshops; and indexed and/or annotated bibliographies. All issues receive internal scientific review and most issues receive technical and copy editing. Limited free copies are available from authors or the NEFSC. Issues are also available from the National Technical Information Service, 5285 Port Royal Rd., Springfield, VA 22161.

Northeast Fisheries Science Center Reference Document -- This series is issued irregularly. The series includes: data reports on field and lab observations or experiments; progress reports on continuing experiments, monitoring, and assessments; background papers for scientific or technical workshops; and simple bibliographies. Issues receive internal scientific review but no technical or copy editing. No subscriptions. Free distribution of single copies.

Fishermen's Report and The Shark Tagger -- The Fishermen's Report (FR) is a quick-turnaround report on the distribution and relative abundance of commercial fisheries resources as derived from each of the NEFSC's periodic research vessel surveys of the Northeast's continental shelf. There is no scientific review, nor any technical or copy editing, of the FR; copies are available through free subscription. The Shark Tagger(TST) is an annual summary of tagging and recapture data on large pelagic sharks as derived from the NMFS's Cooperative Shark Tagging Program; it also presents information on the biology (movement, growth, reproduction, etc.) of these sharks as subsequently derived from the tagging and recapture data. There is internal scientific review, but no technical or copy editing, of the TST; copies are available only to participants in the tagging program.

To obtain a copy of a technical memorandum or a reference document, or to subscribe to the fishermen's report, write: Research Communications Unit, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543-1026. An annual list of NEFSC publications and reports is available upon request at the above address. Any use of trade names in any NEFSC publication or report does not imply endorsement.


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