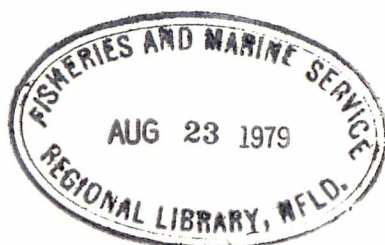


Synopsis of Biological Data of the Northern Population Atlantic Mackerel (*Scomber scombrus*)

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SYNOPSIS OF BIOLOGICAL DATA OF THE NORTHERN POPULATION
ATLANTIC MACKEREL (*Scomber scombrus*)

by

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ABSTRACT

MacKay, K. T. 1979. Synopsis of biological data of the northern population Atlantic mackerel *Scomber scombrus*. Fish. Mar. Serv. Tech. Rep. 885, vi + 26 p.

The northern population of Atlantic mackerel, *Scomber scombrus* L., spawns in the Magdalen Shallows during June. The adults remain in the Gulf of St. Lawrence where they build up fat while feeding on zooplankton. Juvenile fish are found in inshore areas of the Canadian Atlantic from July to October. They feed on larger food particles than the adults. Mackerel leave Canadian waters in October. The southern population spawns south of Long Island during April-May and moves northward to the Gulf of Maine during summer. Stragglers may occasionally reach Canadian waters. Both populations overwinter in deep water along the Continental Slope where they have been heavily exploited by a winter fishery which peaked at 386,000 metric tons (MT) in 1972.

Two year-classes have dominated the northern population; both have grown slower and matured later than the other year-classes.

Somatic weights and gonad weights vary from year to year but seasonal variations are greater than yearly variations. While ovaries and testes do not differ in weight, the dry weight content of ovaries is higher.

Mackerel are obligate schoolers during the day. School size varies from 1000 fish in St. Margaret's Bay to 10,000 fish on the north shore of Prince Edward Island and to 80,000 fish during winter in the Georges Bank area.

Key words:

RÉSUMÉ

MacKay, K. T. 1979. Synopsis of biological data of the northern population Atlantic mackerel *Scomber scombrus*. Fish. Mar. Serv. Tech. Rep. 885, vi + 26 p.

La population septentrionale de maquereaux de l'Atlantique, *Scomber scombrus* L., fraie dans les bas-fonds des Îles de la Madeleine au mois de juin. Les adultes restent dans le golfe Saint-Laurent où ils accumulent leurs réserves de graisse en se nourrissant de zooplancton. De juillet à octobre, on trouve les jeunes poissons dans les régions côtières des eaux canadiennes de l'Atlantique. Ils se nourrissent de particules plus grosses que les adultes. Les maquereaux quittent les eaux canadiennes en octobre. La population méridionale fraie au sud de Long Island en avril et mai, puis, pendant l'été, remonte vers le nord dans le golfe du Maine. Quelques vagabonds pourront, de temps à autre, atteindre les eaux canadiennes. Les deux populations passent l'hiver dans les eaux profondes qui bordent le talus continental où la pêche d'hiver les exploite abondamment, avec un maximum de 386 000 tonnes métriques en 1972.

Deux classes de l'année ont dominé la population septentrionale; elles se sont toutes deux développées plus lentement et ont atteint leur maturité plus tard que les autres classes de l'année.

Le poids somatique et le poids des gonades varient d'une année à l'autre, mais les variations entre saisons sont plus importantes que les variations entre années. Alors que le poids des ovaires et celui des testicules sont identiques, en poids desséché, le contenu des ovaires est plus élevé.

Pendant la journée, les maquereaux ne peuvent s'éloigner du banc. La taille des bancs varie, de 1 000 poissons dans la baie St. Margaret à 10 000 poissons sur la côte nord de l'Île du Prince-Edouard et à 80 000 poissons pendant l'hiver dans la région du banc George.

INTRODUCTION

The Atlantic mackerel, *Scomber scombrus* L., is abundant in surface coastal waters of the Canadian Atlantic from June to October. During the fall mackerel disappear from these waters and move to overwintering areas along the edge of the continental shelf from Sable Island to south of Long Island. Mackerel reappear in surface waters along the coast during May and early June, moving into the warmer waters of the Gulf of St. Lawrence to spawn during late June. Another group, the southern population, spawns in the vicinity of Long Island during April-May and moves as far north as the Gulf of Maine during summer. However, it has not been possible to separate the northern and southern groups into distinct populations using meristic, biochemical, or growth characters (MacKay 1967; MacKay and Garside 1969).

In recent years an offshore winter fishery for mackerel has developed off the New England coast. This fishery, which has grown almost exponentially, exploits both southern and northern stocks.

Mackerel are important in the productivity system of the Gulf of St. Lawrence from June to October. They are the main fish consumers of zooplankton and may be the driving force in the pelagic system controlling herring and other fish populations (Winters 1975; Lett et al. 1975). In addition, because of their migratory nature and the heavy fishing during overwintering, they represent important agents of transfer of material and energy between the Gulf of St. Lawrence system and the continental shelf regions of Nova Scotia and New England.

The importance of mackerel in the productivity system poses a paradox. Their constant swimming and tropical origin require a higher metabolic rate than their coldwater competitors, such as herring. Yet mackerel show rapid growth and high abundance. An understanding of both biology and fisheries management hinges on knowledge of how mackerel obtain these high efficiencies at such apparently high basic costs, compared to the successful but more conservative herring.

This study examines the biology of the Atlantic mackerel found in the coastal waters of Atlantic Canada and summarizes data collected from 1962-74. This synopsis serves as an introduction to subsequent papers which explore some of the theoretical aspects of the biology of mackerel. They examine: the hydrodynamics of swimming mackerel and the implications for energy budgets and food search; a feeding model which explores the implication of continuous swimming and schooling for food search in a heterogeneous environment; and a final paper discusses population dynamics, productivity, and recruitment (MacKay 1976a, b, c).

MATERIALS AND METHODS

Mackerel were sampled from the inshore commercial fishery along the Atlantic coast of Nova Scotia and the Gulf of St. Lawrence during May-October, 1965-73. Additional samples were obtained during research cruises by use of baited hooks, gangs of graded gillnets, and other trawls. The fish were measured for fork length (FL). Measurements of total length (TL) were available for

1960-61 (Bergeron 1961, 1962) and for 1962-64 (MacKay 1967). These were converted to fork length, using a conversion factor of:

$$FL = 0.916 TL \quad (1)$$

after MacKay (op. cit.).

Otoliths were obtained about once a week from 50 to 100 of the fish used for length determination. These fish were selected at random except, in 1973, when otoliths were obtained from size-selected fish, so that, where possible, 5-10 otoliths were obtained for each 10-mm size group.

Otoliths were obtained by making a transverse incision through the head at the level of the first colour bar. Both sagittae were extracted from the sacculus, using forceps, and cleaned on the back of the hand. Each pair of otoliths was stored dry in a numbered slot in a tray holding 100 otoliths. Subsequently the otoliths were permanently mounted, using ethylene chloride, in depressions in black plexiglass blocks. Age determinations were made by stereoscopic observation of the otoliths which were immersed in 95% ethanol.

Otoliths are reliable indicators of age for Atlantic mackerel (Steven 1950; MacKay 1967). However, otoliths from fish older than 6 yr produced a greater percentage of unreadable and questionable ages. Ages of fish older than 10 yr were difficult to determine. These ages were reported as 10+. In 1962 there was an unusually narrow summer otolith zone which resulted in errors in age determination of the 1959 year-class. As a result I have combined the 1960 year-class with the 1959 year-class. This should not produce any serious errors in age estimation as the 1960 year-class was very weak (MacKay 1967). While the actual birth date is about July 1, a birth date of January 1 was assumed for convenience of description, and fish were classed as 1 yr old on their first January 1.

Sex and maturity were determined by examinations of the gonads during autopsy. Four maturity stages were adopted: immature, maturing, ripe and running, and spent (see MacKay 1967). The gonads were carefully removed from either fresh or thawed fish and weighed on a pan balance. Dry weights of gonads were obtained by drying 50 g or less in a drying oven at 50°C until a constant weight was obtained.

Ovaries from three fish captured June 12, 1969, were used to estimate fecundity. The thawed ovaries were agitated by a magnetic stirrer. The gonadal tissue was removed and the resulting suspension of eggs was fixed with 10% formalin, vacuum filtered and weighed. Subsamples of 0.5 g of eggs were counted during microscopic observation. Small presumptive ova were not counted.

Total body weights were obtained from fresh or fresh-frozen fish weighed on a pan balance to the nearest 0.01 g. Somatic weights were obtained by subtracting gonad weights from total body weight. Corrections were made for stomach contents when necessary.

Regression equations were calculated for somatic body weight (SW) on fork length (FL) assuming a power curve relationship of the form

$$SW = aFL^b \quad (2)$$

where a and b are fitted parameters derived from a

least squares regression on double log transformed data. The regression equations of gonad weight (GW) on fork length also assume a power curve relationship, but gonads of fish below 25 cm have a negligible weight. Therefore, an equation of the form

$$GW = a(FL - 25)^b \quad (3)$$

was used. Tests of significance for the regressions were performed using an F test in which the test ratio is the mean square due to the linear regression over the unexplained mean square which measures the error mean square. This method and other statistics for the regressions are after Sokal and Rohlf (1969).

The length-weight data for 1969-72 were analyzed separately for each year. A more detailed analysis was made of the 1973 data when separate regression equations were calculated for each sampling date, month, and sex.

During the course of this study numerous measurements of body dimensions were made. Methods for measurement of pectoral and caudal fin areas and body area at the level of the pectoral fins are presented in MacKay (1976a). When mackerel filter feed, the mouth is open wide, and the opening forms an ellipse with the semi-major axis (A) oriented vertically and the semi-minor axis (B) oriented horizontally (Fig. 1 in Muir and Newcombe 1973). The open mouth area (A_m) can be determined by:

$$A_m = AB \frac{\pi}{4} \quad (4)$$

Dimensions of the two axes were determined while the mouth of freshly caught fish was forced open maximally, and the area was calculated from equation 4. Regression equations for pectoral and caudal fin areas, body area at the level of the pectoral fin, and mouth area, all related to fork length, were calculated assuming a power curve relationship.

Determinations of total lipid content of mackerel tissue were made using the rapid extraction technique developed by Bligh and Dyer (1959). Stomachs were removed from freshly caught or frozen mackerel and preserved with 10% formalin in plastic "whirl pak" bags. Stomach contents for any one sample were grouped according to fish size and the contents analyzed for particle size. The contents were suspended in water, then rinsed through a series of different sized sieves. Blot-dried weights of each fraction were obtained to the nearest 0.01 g on a pan balance.

Observations of mackerel swimming, feeding, and schooling behaviour have been made in a circular raceway 76 cm wide and 56.4 cm deep. The behaviour was observed directly, photographed and videotaped for later analysis. MacKay (1976a) and Muir and Newcombe (1973) give further details on the experimental tank and the analytical procedure. Schooling behaviour has also been observed under field conditions by underwater observations using SCUBA and underwater photography of mackerel in capture gear, such as purse seines or mackerel trapnets. Further information on schooling behaviour was obtained from observations of fish schooling at the surface and from comments of fishermen.

SYSTEMATIC POSITION AND DESCRIPTION

The Atlantic mackerel, *Scomber scombrus* (Linnaeus, 1758), is placed in the order Perciformes (Berg 1940) or Percomorphi (Reagan 1929), suborder Scombroidei and the family Scombridae. The family is closely allied to the family Thunnidae which includes the large, fast-swimming tunas. In the genus *Scomber*, Matsui (1967) includes three species, *Scomber australasicus* (Cuvier), *Scomber scombrus*, and *Scomber japonicus* (Houttuyn). The Atlantic chub mackerel, *Scomber colias* (Gmelin), is considered to be synonymous with *Scomber japonicus* (Fraser-Brunner 1950; Matsui 1967). Both *S. scombrus* and *S. japonicus* occur in the northwest Atlantic. However, *S. japonicus* has a more southern distribution and a well-developed air bladder that is absent in *S. scombrus*. All of the Scombridae are of tropical origin while *S. scombrus* has the most northerly distribution.

Atlantic mackerel appear to be designed for efficient hydrodynamic performance. The following description is compiled from Bigelow and Schroeder (1953), Leim and Scott (1966), and MacKay (1976a): The body is elongate and fusiform, tapering to a narrow caudal peduncle bearing two short lateral keels. The head is long and the large mouth extends under the middle of the eye. A single row of small slender teeth is borne on each premaxillary, maxillary, vomer, and palatine bone. A large transparent adipose eyelid partially covers the eye. This structure is more prominent during late fall and appears not only to offer a site for fat storage but also contributes to the streamlined contour of the head. The first of two dorsal fins originated at the level of the pectoral fins and is supported by 10-14 rather weak spines which can be completely adducted into a mid-dorsal groove. The second dorsal fin is approximately the same length as the first dorsal but only half as high and is supported by 12 (9-15) soft rays. The space between the two dorsal fins is twice the base length of the fins. This large space between the two dorsal fins is an anatomical feature that may be used to separate the Atlantic mackerel from the other scombroids. The anal fin has one spiny ray and 12 (9-14) soft rays. The caudal peduncle has five (4-6) small dorsal and anal finlets similar in form. The caudal fin is broad and deeply forked. The pectoral fins are located high on the side, a short distance behind the opercular opening. During slow swimming they are extended and act as cambered hydrofoils; but during more rapid swimming, they can be swept back until they are completely pressed to the body. The pelvic fins are small and thoracic in position. They are normally pressed to the body but are extended during turning. The ctenoid scales are small, and the skin has a velvet texture. The fish are negatively buoyant as the result of the absence of a swimbladder and are required to swim continuously to maintain hydrostatic equilibrium.

The body is countershaded as in many pelagic fish. The upper surface is a dark steel-blue colour with 23-24 dark wavy bars stopping about the midline. The lower sides are silvery, sometimes bearing black

spots, and the belly is silvery white. The pectoral, dorsal, and caudal fins are black or dusky, while the jaws and opercula are silvery.

RANGE

Atlantic mackerel are found over the continental shelf on both sides of the Atlantic Ocean between 30° and 52° north latitude. In the northeastern Atlantic, mackerel are found in coastal waters from Spain to Norway and also occur in the Mediterranean and Black Sea. Mackerel from European waters are considered to be a separate race from the mackerel in North American waters (Garstang 1898).

Mackerel in the northwest Atlantic range from northern North Carolina to Black Island, Labrador (Bigelow and Schroeder 1953; Parsons 1970). During the summer, mackerel are most abundant in coastal waters and support a commercial fishery between Chesapeake Bay in the south and the east coast of Newfoundland and the Gulf of St. Lawrence in the north.

POPULATION

On the basis of the analysis of size composition of many samples of commercially caught mackerel collected from 1926 to 1935, Sette (1950) separated mackerel from the northwest Atlantic into northern and southern "contingents." This separation into two contingents was substantiated by tagging carried out during 1925-28 (Sette 1950; MacKay 1967). An analysis of these two groups for differences in growth rates, isoenzyme pattern of lactate dehydrogenase (LDH) and malic dehydrogenase (MDH), and meristic characters yielded no obvious differences (MacKay 1967; MacKay and Garside 1969). There are, however, two discrete spawning areas on the North American coast (Sette 1943). The southern spawning grounds encompass an area from Cape Hatteras to Cape Cod, with spawning commencing in mid-April in the southern part and progressing northward until June (Cape Cod region). The northern spawning area is much more restricted in time and place. It is concentrated over the Magdalen Shallows (Gulf of St. Lawrence) during early June to early July and peaks in the latter half of June (Arnold 1970).

Moore et al. (1975) suggested that, due to the earlier spawning of the southern contingent, the growth rates of the two groups should differ and serve as a tool to allow separation. However, there is no *a priori* reason to suspect a difference in growth rate. In fact, evidence will be presented later (p. 15) that the warm temperatures and better feeding conditions existing in the north compensate for the shorter growing season, so that the size at any age is similar for both groups.

In spite of the difficulty in establishing differences between the two groups of mackerel, the absence of post-spawning fish which might appear from migration of the earlier spawning southern contingent and the regularity with which particular year-classes occur in Canadian waters during June strongly suggest that the northern spawning group is indeed a separate population. Sette's (1950) term "contingent" has not found wide usage in the ecological literature. I suggest the more widely used term "population" be used to distinguish these groups. The current definition of population as a group of animals of the same kind occupying a particular space and capable of interchanging genetic material (Smith 1974) certainly fits the southern and northern mackerel groups.

Various authors (Anderson 1975a; Beckett et al. 1974; Moore et al. 1975; Stobo and Hunt 1974) have recently reviewed Sette's (1950) hypothesis of two populations and have accepted his conclusions.

COMMERCIAL FISHERY

The annual commercial catch of mackerel off the North American coast has undergone wide fluctuations (Sette and Needler 1934; MacKay 1967). The fluctuation in Canadian waters is illustrated in Fig. 1. In 1884, the North American total catch was 105,700 MT which fell to a low of 5,700 MT in 1910. The large catch of 1884 was not surpassed until 1969, but subsequently annual catch continued to increase until 1973 when it reached 419,300 MT. The difference between highest and lowest catch is almost two orders of magnitude.

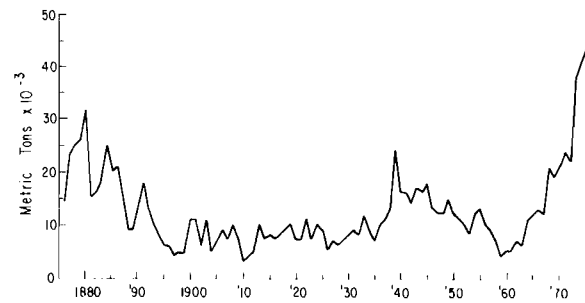


Fig. 1. Variation in the annual commercial catch of mackerel in Canadian waters (ICNAF SA 3 and 4) from 1876 to 1975.

Until 1962, the North American mackerel fishery was carried out exclusively¹ by Canada (including Newfoundland) and the United States. Beginning in 1962, Bulgaria, the Democratic Republic of Germany (GDR), the Federal Republic of Germany (FRG), Poland, Romania, and the Union of Soviet Socialist Republics (USSR) developed a winter fishery along the edge of the continental slope from Georges Bank to Hudson Channel. This fishery grew very rapidly from 1,400 MT in 1961 to 386,000 MT in 1972 (Table 1) but decreased in 1973, 1974 and 1975. Because of fear of overfishing of the mackerel stocks, the International Commission for the Northwest Atlantic Fisheries (ICNAF) established a system of total allowable catch (TAC) allocated by country for the various ICNAF subareas (SA) and statistical areas (SA) (Fig. 2).

The total mackerel catch in waters adjacent to Canada (SA 2, 3, 4) did not increase as rapidly as the fishery in SA 5 and 6. The catch of 4,300 MT in 1959 increased to 21,000 MT in 1968 and was maintained around 20,000 MT until 1973 when a substantial increase occurred. The higher catches of 38,000 MT in 1973, 44,000 MT in 1974, and 36,000 MT in 1975 were largely the result of increased USSR fishing in SA 4. The fishery had been primarily a Canadian fishery, but the USSR proportion of the catch increased from 30% in 1967 to 67% in 1975.

¹A minor French fishery was carried out in the vicinity of St. Pierre and Miquelon.

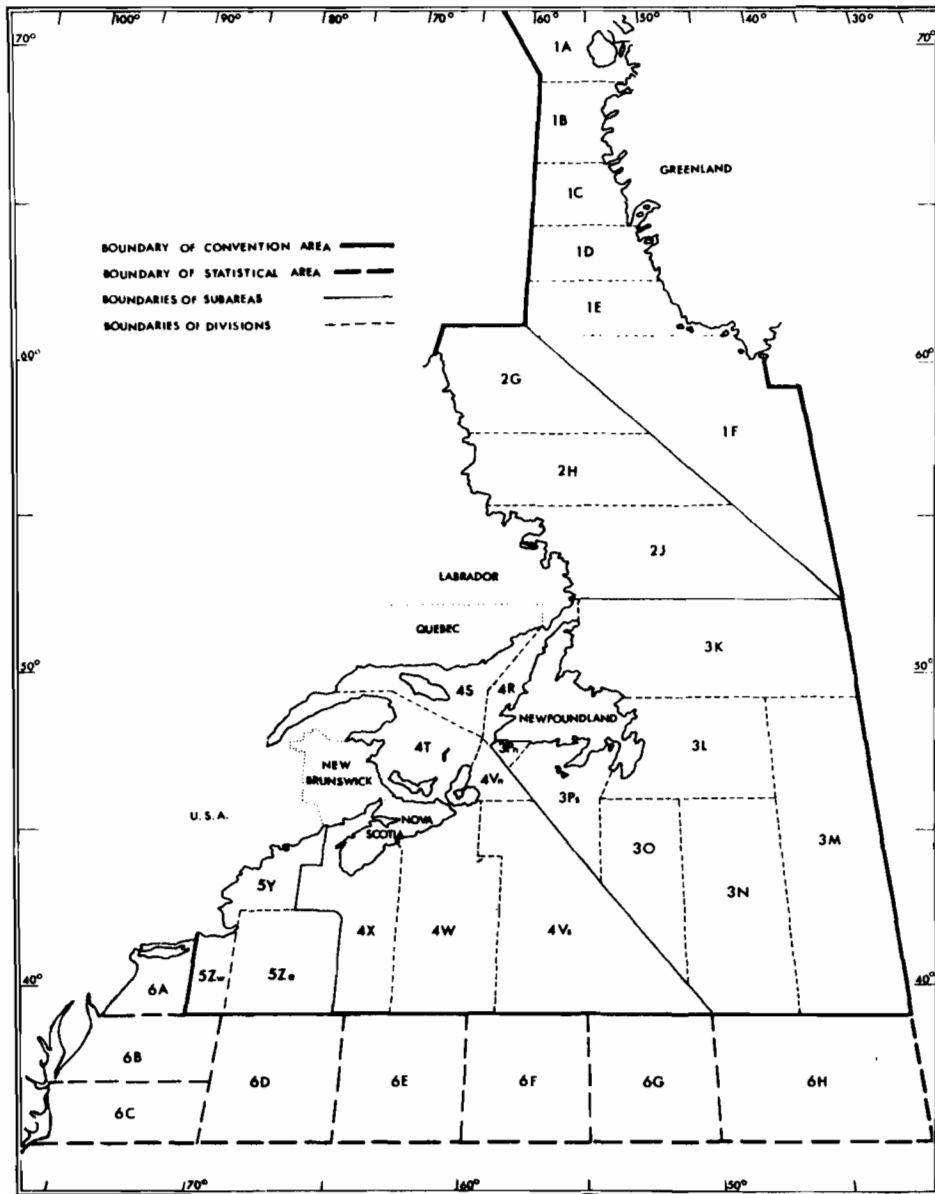


Fig. 2. Subareas and divisions of the ICNAF statistical area.

Table 1. Catch in metric tons of Atlantic mackerel from the ICNAF area 1961-75 (after Anderson 1975a; ICNAF 1975, 1976).

Year	Total ICNAF Area	ICNAF SA 3+4	Canada	United States
1961	6,831	5,470	5,459	1,361
1962	7,914	6,865	6,801	938
1963	8,982	6,473	6,363	1,320
1964	12,231	10,960	10,786	1,644
1965	16,128	11,590	11,185	1,988
1966	22,252	12,821	11,577	2,724
1967	34,120	11,559	11,181	3,891
1968	80,811	20,787	11,134	3,929
1969	131,830	18,635	13,257	4,364
1970	230,608	20,986	15,690	4,049
1971	373,033	24,289	14,735	2,406
1972	409,724	22,360	16,254	2,006
1973	419,306	38,142	21,247	1,336
1974	338,642	44,482	16,702	536
1975	287,069	36,160	13,447	1,978

GDR, FRG, Poland, and Romania also captured small quantities of mackerel in SA 4.

In spite of large changes in mackerel catches from year to year (Fig. 1), the seasonal pattern of the Canadian fishery has been quite constant. The seasonal catch distribution for different areas in SA 4 during 1924-29 is similar to that for 1957-66 (MacKay 1967) and the same pattern is evident during 1969-73 (Table 2).

This seasonal catch distribution is related to migration patterns. The earliest catches are made on the Atlantic coast in 4X and 4W during late May; the peak catches in these areas occur in June as the northern population migrates to the Gulf of St. Lawrence. At the entrance to the Gulf (4Vn) the peak catches occur in June and October as fish enter and leave the Gulf of St. Lawrence. Peak catches in the Gulf of St. Lawrence occur in July after spawning has occurred.

Normally about 45% of the commercial catch in Canadian waters occurs in the Gulf of St. Lawrence (4R, 4S, 4T) and 50% occurs off the Atlantic coast of Nova Scotia (4Vn, 4W, 4X) (Table 3). Occasionally major departures from this pattern occur as in 1962, 1967, 1969 and 1975. These changes may be related to sea surface temperatures (see pg. 7).

The mackerel catch off the south and east coasts of Newfoundland (SA 3) is related to water temperatures (Templeman 1966). Catches varied from none in 1959 to a high of 3,900 MT in 1975 which was 28% of the total Canadian catch (Table 3). Occasionally catches are taken off Labrador (SA 2); for example, during 1970 and 1971 catches were 20 and 207 MT respectively.

FISHING GEAR

The mackerel fishery is carried out by a variety of types of gear. Gillnets, trapnets, and handlines have been used since at least the 19th century. The oldest method of catching mackerel is by handline, using minced fish as bait to attract schools. In the mid 19th century this was the main method of fishing for mackerel, particularly by New

England fishermen as they followed the migrating mackerel up the coast to the Gulf of St. Lawrence.

Purse seines were introduced in 1870 and by 1880 had become the main method of capture used by New England fishermen (Sette and Needler 1934). This transition to purse seines was accompanied by a decline of fishing in the Gulf of St. Lawrence by New Englanders. Canadian fishermen did not adopt purse seines until the turn of the century.

The present mackerel fishery is centered in SA 5 and 6 during December-April. This fishery, which accounts for over 80% of the total catch, exploits fish from both the southern and northern populations. Bottom or mid-water trawls towed by large vessels account for most of the fishery. In 1973, 90% of this catch was taken by vessels greater than 900 tons while 75% was taken by vessels over 1,800 tons (Anderson 1975b).

The summer fishery for mackerel in United States waters is less than 0.5% of the total catch and is concentrated near shore. The United States catch may be much higher than the ICNAF statistics suggest since sports fishing catches are not recorded. Estimates based on angler surveys are available at 5-yr intervals. In 1970 the estimated angler take was 32,078 MT, which was 13% of the total commercial landings reported by ICNAF (Deuel 1973).

The Canadian fishery is carried out with a variety of gear (Table 4). In 4S and 4T purse seines account for over 50% of the catch. Purse seining is carried out from June to October with the most fish being taken in July. Gillnets take 28% of the catch, mainly in June and July when they supply bait for the lobster fishery. In 4Vn trapnets account for 30% of the fishery, and purse seines take 40%. The trapnet fishery is most important in June as mackerel move into the Gulf of St. Lawrence to spawn, while purse seines operate from July to November with the largest catches being made in October as mackerel leave the Gulf of St. Lawrence. The fishery in 4W is primarily a spring and fall gillnet fishery. In 4X the fishery is primarily a trapnet or weir operation lasting from May to December with the largest catches occurring in August.

Purse seining is the most important method of catching mackerel in SA 4, followed by gillnet and then traps and weirs. The majority of the purse seines in SA 4 are operated from small modified lobster boats usually less than 14 m (45 ft) in length. In fact, the large purse-seine boats which were successful at herring fishing have not been successful at exploiting mackerel. There are various reasons for this failure. The size of mackerel schools in the southern Gulf of St. Lawrence appears to yield an uneconomic return for large seine nets. Many of these schools are found in inshore shoal areas which require a shallow seine net and detailed knowledge of bottom conditions and, when large concentrations of mackerel are found, the gilling of the heavier-than-water fish sinks the net allowing schools to escape or causing difficulty in pursing the net. Thus, the Canadian mackerel fishery is primarily a small-boat fishery carried out by "inshore fishermen" using relatively simple technologies as opposed to the highly technical, capital intensive, offshore, winter trawl fishery carried out in SA 5 and 6.

Table 2. Average monthly catch in percent of total of Atlantic mackerel in ICNAF Subarea 4 by months and ICNAF division based on an average for 1969-73, (after Stobo and Hunt 1974).

Division	Month								Total
	5	6	7	8	9	10	11	12	
4S + 4T	0.1	11.7	43.7	21.5	15.2	6.8	1.1	0.0	43.8
4Vn	0.6	30.3	14.0	4.2	12.5	31.7	6.5	0.0	17.2
4W	6.9	40.8	16.5	6.1	6.6	9.3	13.8	0.1	9.2
4X	9.6	23.0	17.2	20.0	15.6	7.7	6.3	0.8	29.9
Average	4.3	26.5	22.9	13.0	12.5	13.9	6.9	0.2	

Table 3. Percentage of total Canadian catch obtained from ICNAF SA 2, 3 and 4, 1961-75.

Year	SA 2 and 3	4R,S,T	4Vn	4W	4X
1961	19	36	11	13	22
1962	9	26	11	12	42
1963	4	43	14	12	26
1964	8	50	10	13	20
1965	2	41	10	12	36
1966	1	46	11	17	25
1967	0	29	18	19	33
1968	2	46	16	10	26
1969	2	28	16	16	37
1970	5	38	18	6	34
1971	10	41	13	9	28
1972	10	48	13	6	24
1973	8	47	18	6	18
1974	11	42	15	8	24
1975	28	16	16	8	32

Table 4. Average commercial catch of Atlantic mackerel for each type of gear as percent based on 1969-73 data after Stobo and Hunt (1974).

ICNAF Division	Trawl	Gillnet	Handline	Trap weir	Purse seine	Misc.
4S & 4T	0.05	28.1	3.0	2.0	55.0	11.9
4Vn	0.01	7.8	14.6	30.5	39.4	7.8
4W	0.01	64.1	7.1	14.7	0.3	13.8
4X	0.07	26.3	0.5	46.7	0.3	26.2
Total	0.04	27.5	4.6	21.6	30.6	15.7

MIGRATION

The basic pattern of migration of both the southern and northern populations has been outlined by Sette (1950). My analysis of length frequencies, results of tagging, observations of the seasonal distribution of catch, and comments made by fishermen (MacKay 1967, 1973a) supports the pattern of migration of the northern population suggested by Sette (1950).

The spring migration of the northern population involves movement in a series of waves along the Scotian Shelf from the overwintering area to the spawning ground in the Gulf of St. Lawrence. During this movement mackerel feed extensively on euphausiids and fish larvae while they build up gonadal tissue. The main body of fish migrates offshore, although fish occasionally strike inshore. The inshore catch in 4X and 4W is largely dependent on surface temperatures and food availability.

Changes in length frequency with time are illustrated in Fig. 3 which presents sampling from

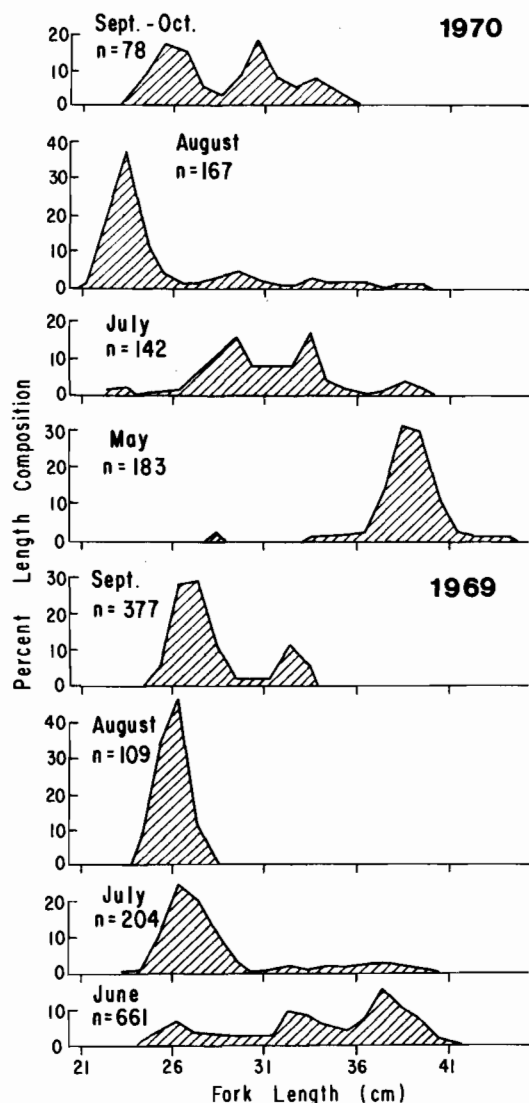


Fig. 3. Monthly length frequencies for Atlantic mackerel sampled in the vicinity of St. Margaret's Bay, Nova Scotia (4X) during 1969 and 1970.

St. Margaret's Bay, typical of Div. 4X. The largest fish arrive first about mid-May, but the main groups are not present until June. As indicated later (see p. 12), the first arrivals are not only longer but are heavier and have larger gonads for a given length than the main body of fish. The fish found in 4X during May and June move on to the Gulf of St. Lawrence and spawn over the Magdalen Shallows. This is verified by the data of Fig. 4, showing that in most years the sizes of adult fish present in 4X and 4Vn in June are subsequently found in 4T during July and August. Data obtained by tagging of spring migrating fish (MacKay 1973a; Sette 1950) also support this interpretation.

By the end of June and early July the adults have completed spawning in the Gulf of St. Lawrence. Some stragglers remain and spawn in the northern part of the Gulf of Maine and along the coast of Nova Scotia (4Vn, 4W, 4X).

Immature fish migrate later and more slowly, reaching the Atlantic coast of Nova Scotia (4X, 4W) about July 1. They remain in many of the bays and coves throughout the summer. In most years the immature fish are also found in the southern Gulf of St. Lawrence (4T) in midsummer.

The large-scale movement of both immature and mature fish has ceased by early July. This is substantiated by tagging studies in St. Margaret's Bay (4X) during July of 1966, 1967 and 1968 (MacKay 1973a). Of 1,299 fish tagged and released, 140 were recaptured within 78 d. All except one was within 25 km of the release site, and the one exception had moved only 60 km.

The spring and fall migratory movements of mackerel, like those of many fishes, are probably controlled by changes in photoperiod. However, these movements may also be influenced by temperature. The occurrence of mackerel off the coasts of Newfoundland and Labrador appears to be related to above average temperatures (Templeman 1966; Parsons 1970). Temperatures also influence the autumn migration of *S. scombrus* in the Black Sea, which is initiated by a drop in surface temperature but is independent of the temperature at which the drop occurs (Galtsoff 1924). A similar situation may account for the sudden departure of mackerel from the Gulf of St. Lawrence following October storms (MacKay 1967).

The temperature regime at the entrance to the Gulf of St. Lawrence may also influence migration. As noted previously (Table 3), the commercial fishery in the Gulf of St. Lawrence in 1962, 1967, 1969 and 1975 was less than 30% of the total Canadian catch compared to the normal 45%. In each of these years temperatures appeared to have been below normal.

In 1962 and 1969 the July surface temperatures for Entry Island, Magdalen Islands, were the lowest on record, over 1°C below the long-term average (Lauzier and Hull 1969). In both these years a large portion of the population was immature. These fish normally reach Canadian waters in early July. The below average temperatures of the Gulf may have prevented a portion of these fish from entering the Gulf of St. Lawrence. In both these years July surface temperatures for the Atlantic coast were near average (op. cit.).

In 1967 the effect on the migration pattern was on the mature fish moving into the Gulf to spawn. The May temperature for Entry Island was the lowest on record, 2.5°C below average. While the June

temperature was near average, sea ice was still present in Cabot Strait in early June. These cool temperatures may have prevented a sizable portion of the spawning stock from entering the Gulf of St. Lawrence. Evidence on egg abundance supports this hypothesis. Mackerel eggs were 23 times more abundant in 1968 than in 1967, a fact that cannot be accounted for by newly recruited spawners (Mackay 1976b). In 1967, while spring warming was retarded, once warming began it occurred very rapidly as July and August temperatures for the Gulf of St. Lawrence were above average and the August temperature was 1°C above any previously reported.

Surface temperatures are not available for 1975; however, air temperature data for Sydney, N.S. (Environment Canada 1975) indicate a similar pattern to 1967. May and early June temperatures were below average, including a record 10-mm snowfall on June 9. However, late June and July temperatures were above average and the total hours of sunshine surpassed the previous record set in 1967.

In most years the majority of adults of the northern population remain within the Gulf of St. Lawrence during summer, where increases in fat and somatic tissues occur while the fish are feeding on zooplankton. Movement of mackerel within the Gulf of St. Lawrence cannot be determined from the tagging returns, but the monthly catch statistics suggest the following movements: local concentrations are present along the southern shore and Gaspé in July, along the north shore in August, and around the Magdalen Islands and Prince Edward Island in August and September. In October, as the fish leave the Gulf of St. Lawrence through the Cabot Strait, catches are concentrated along Cape Breton Island.

Different sizes of mackerel appear to be concentrated in different areas of the Gulf of St.

Lawrence. A detailed examination of length-frequency data suggests that fish smaller than 30 cm are plentiful in the Northumberland Strait, St. Georges Bay, and off the east coast of Prince Edward Island. Fish from 30 to 37 cm are plentiful around the Magdalen Islands and the north shore of Prince Edward Island, while fish larger than 37 cm are under-represented in these areas during summer. Comments from fishermen suggest that larger fish may be found in the northern areas of the Gulf of St. Lawrence and off Gaspé. These larger fish reappear in the commercial fishery in October.

During summer, mackerel off the Atlantic coast of Nova Scotia (4X) normally have a different size composition from those in the Gulf of St. Lawrence (4T). Only 1967 and 1969 showed similar frequencies for the two areas (Fig. 5) but, as previously indicated, 1967 and 1969 may have had unusual oceanographic conditions which resulted in a portion of the northern population remaining in 4X. Even when the same year-classes are present in the two areas, their sizes are often different. For example, in 1970, the 1969 year-class fish sampled in 4X during July, August, and September were all significantly larger than the same year-class fish sampled in 4T (Appendix III).

The difference in size of mackerel between 4X and 4T during the summer may simply reflect the absence of older fish in 4X and the use of the bays and coves as a nursery area for the younger immature fish. However, there is also the possibility that some fish of the southern population may reach the Atlantic coast of Nova Scotia during summer. One tagging carried out in June 1927 at St. Margaret's Bay, Halifax County, Nova Scotia, added support to this hypothesis (Sette 1950). Five (33%) of the tagging returns occurred during the summer of 1928 from New Jersey to Cape Cod after the northern population should have left this area. While Sette

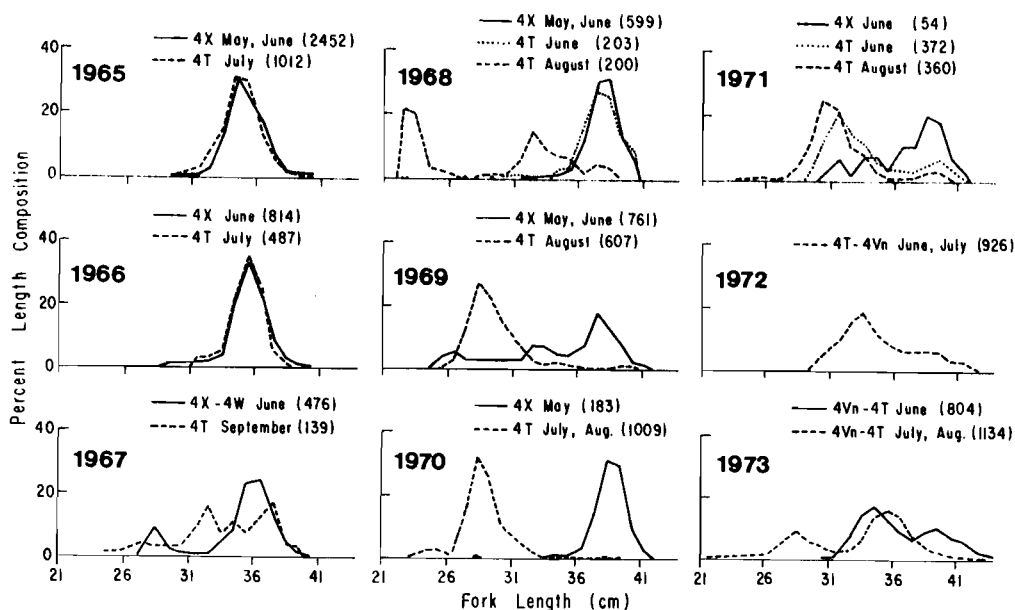


Fig. 4. Length frequencies of Atlantic mackerel sampled in 4X during May-June and in 4T, 4Vn during June and July-September, 1965-73.

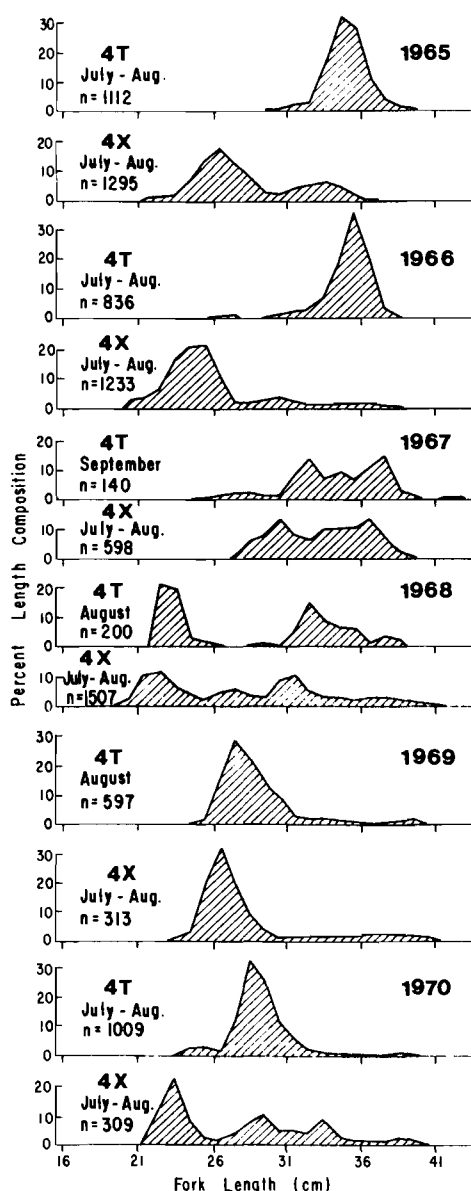


Fig. 5. Length frequencies of Atlantic mackerel in ICNAF Div. 4X and 4T sampled during summer (July, August) 1965-70.

suggested that these may have been stragglers injured by the tag and unable to return to the northern area, I prefer the alternate explanation that there is limited mixing of the two spawning groups and that members of the southern population occasionally appear along the Nova Scotia coast (4X) during summer (MacKay 1967). It is noted that other southern species, including *Scomber japonicus*, are occasionally found in this eastern Canadian area during summer (MacKay, unpubl. data).

In recent years the abundance of mackerel in Newfoundland waters has increased. The main commercial catches are on the east coast (3K and 3L) (Moore et al. 1975). However, mackerel occur as far north as Black Island, Labrador (Parsons 1970) and are also present on the west coast of Newfoundland. Recent tagging results suggest that mackerel in

Newfoundland waters undergo extensive movements during the summer. Tagging during July in the Strait of Belle Isle yielded returns in September from the west coast of Newfoundland, Northumberland Strait, Gulf of St. Lawrence, and Trinity Bay on the east coast of Newfoundland. As indicated later, mackerel sampled in Newfoundland waters had the same year-class composition as those in SA 4, although the fish tended to be larger and heavier at each age, and they exhibited a slightly different sex and maturity pattern.

Mackerel leave Canadian waters from September to November and proceed to the overwintering area. Sette (1950) found that mackerel overwintered in water above 7°C. This overwintering area appears to be a narrow band of water on the edge of the continental shelf from Cape Hatteras to Georges Bank and possibly as far northeast as Sable Island. As mackerel leave Canadian waters, a portion of them passes through the southern Gulf of Maine and mixes with the southern population. In general, the southern population overwinters farther south than the northern population (Sette).

The intense offshore winter mackerel fishery has undoubtedly discovered the main overwintering concentration. However, the proportion of each population in the fishery is still unknown. Recent returns of tagged fish confirm that northern population fish are present in this fishery. Parsons and Moores (1974) report a single recapture south of Long Island from the release of tagged fish in northeastern Newfoundland in 1972. Tagging conducted in 1973 in Newfoundland waters, in the Gulf of St. Lawrence, and on the outer coast of Nova Scotia yielded 28 recaptures in SA 5 and 6. In fact, 4 recaptures, 2 from the Newfoundland tagging and 2 from the tagging on the outer coast of Nova Scotia, were recovered a few months later, January 12-25, 1974, by Polish trawlers fishing in Hudson Canyon.

Further information on the overwintering area was recently presented by Stobo (1976) and Anderson and Almeida (1976). Mackerel appear to overwinter along the edge of the continental shelf primarily from Georges Bank to Cape Hatteras. From 1968 to 1975, there has been a pronounced northeasterly shift in the position of the overwintering concentrations, from the middle Atlantic area to the southern New England-Georges Bank area. This shift appears to have been the result of a general warming trend during winter.

AGE COMPOSITION

Information on age and length was available for ICNAF statistical divisions 4X, 4Vn, and 4T from 1962 to 1973. I have used detailed length frequencies (Appendix I in this study; Appendix IV, MacKay 1967) and age-length keys (Appendix II)² to obtain age compositions for the spawning and summer populations in the Gulf of St. Lawrence. Parameters of the spawning population were based on sampling in 4X, 4Vn, and 4T during May and June, while the summer population is represented by sampling in 4T during July, August and occasionally September. For periods in which a specific age-length key is not available, I have used data from an adjacent time period. For example, in 1968 and 1969, there was no age-length information for the summer population; therefore, I have used the May-June age-length keys throughout

²Appendix II is stored on file at the Marine Ecology Laboratory, Dartmouth, Nova Scotia.

the year. The resulting age composition for the spawning and summer population is presented in Fig. 6 for 1965-74. A detailed table of year-class compositions for 1962-73 is presented in MacKay (1976b).

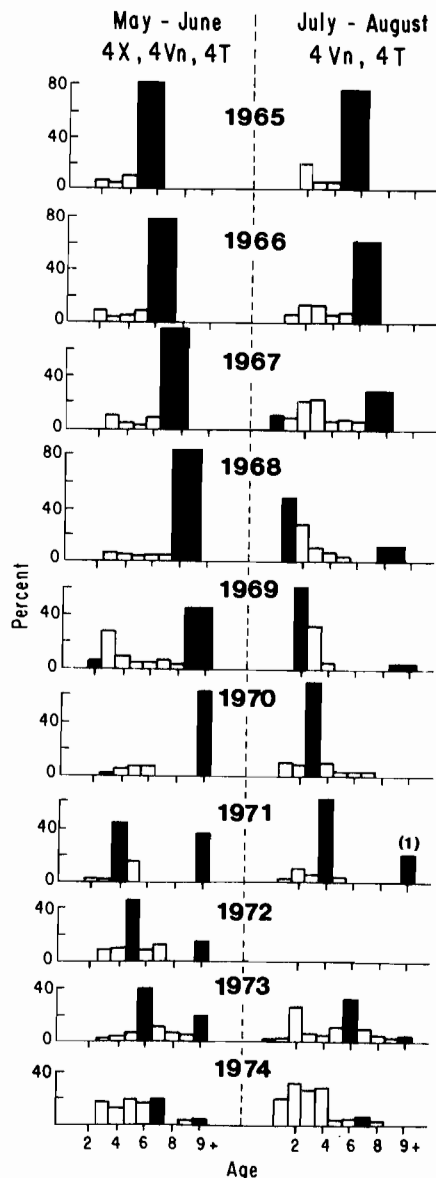


Fig. 6. Age composition of the spawning population and the summer population based on age-length keys; 1974 data from Hunt (1975); all other data from this study (1959 and 1960 year-classes are combined).

It is crucial for a subsequent population estimate (MacKay 1976b) that the information on year-class composition be representative and free from systematic errors. A comparison of the numbers of length measurements and of age determinations for the spawning and summer periods for each year is presented in Table 5. The most complete sampling has been of the spawning population for which 1965, 1966, 1968, 1972, and 1973 offer the best coverage. Furthermore, during the spawning period there is a high degree of homogeneity between samples (MacKay 1967). Sample bias due to gear selectivity should be

minimal as the majority of samples (90%) were obtained from purse seines, trapnets, and hook and line which appear to be non-size selective. In years such as 1971, when many of the samples for spawning population data were from gillnet catches, a wide range of mesh sizes (13-76 mm) was used.

The best indicator of the reliability of the year-class composition data, particularly for the spawning period, is the consistency of the estimates from year to year (Fig. 6; Table 2, MacKay 1976b). Additional estimates of year-class composition in 1973 are available for SA 3 and 4 from two other sources (Stobo and Hunt 1974; Moores et al. 1975). The results are compared in Table 6. There is substantial agreement between these independent estimates of age composition, but my estimates for the combined 1963-59 year-classes for all periods are consistently higher. The explanation for the difference is in the time of sampling. As indicated previously (see p. 7), the larger and older fish appear in the inshore areas of SA 4 in late May to early June, followed by the main body of fish in June, and then the younger immature fish appear in early July. My sampling in June 1973 was concentrated in 4Vn and 4T. However, no samples were obtained in the second half of June due to a violent storm on June 17 which destroyed most fishing gear in 4Vn and in a part of 4T. Fishing in these areas was not resumed until early July. My sampling would, therefore, tend to over-represent the older fish. By contrast, Stobo and Hunt's sampling was done later in the period and apparently under-represents the older fish. On the other hand, their samples yielded nearly 25% 5-yr-olds (1968 year-class) and only 6% 2-yr-olds (1971 year-class). The high representation of 5-yr-olds does not appear in their samples in later periods of the year and the proportion of 2-yr-olds increases significantly. My early sampling contained few small fish, and I did not encounter significant numbers of 2- and 5-yr-olds until the July-August samples when all sets including the Newfoundland samples (SA 3 and 4R) showed agreement. Apparently the variation in representation of the small fish included some components of seasonal migration patterns along with influences of local sampling errors. In all 1973 samples, the 1967 year-class was dominant while during summer the 1971 year-class was next in abundance.

Two mackerel year-classes, that of 1959 and 1967, have dominated the northern population during the last 15 yr. The 1959 year-class first appeared in strength in 1960 (MacKay op. cit.) and was still evident in the spawning population in 1973. The 1967 year-class has been dominant in the summer population since 1968 (Fig. 5), although it made up less than 5% of the spawning population in 1969 and 1970. In 1971, it comprised 46% of the spawners and may not have been fully recruited to the spawning population until 1972 (see p. 12). In 1972, this year-class was 2.5 times more abundant than the 1959 year-class. No other year-classes have shown the persistence of 1959 and 1967, and indications from the ICNAF statistics for 1975 are that 1970-74 year-classes have all been weak.

SEX AND MATURITY

The sex ratio of the northern population is 1:1. There is some variation from year to year (Table 7); however, it was only in 1968 and 1969 that there was a significant departure from a 1:1 sex ratio. The proportion of females has increased (Table 7) from 48% prior to 1970 to 53% from 1970-73. Moores et al. (1975) found an even higher preponderance of females

Table 5. Numbers of length measurements and age determinations for the spawning and summer populations 1962-1973.

	Y e a r											
	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
<u>Spawning</u>												
Length measurements	860	522	618	2652	816	355	803	660	208	426	916	799
Age determinations	-	36	28	517	288	342	112	75	47	-	111	176
<u>Summer</u>												
Length measurements	-	197	-	1112	1202	201	200	600	1266	360	-	1234
Age determinations	-	-	-	261	254	-	-	-	363	68	-	253

Table 6. Year-class composition of the northern population of Atlantic mackerel sampled in 1973 by (1) Stobo and Hunt (1974), (2) present study, and (3) Moores et al. (1975).

	Year class	1973	1972	1971	1970	1969	1968	1967	1966	1965	1964	1963- 1959
	Age	0	1	2	3	4	5	6	7	8	9	9+
<u>Date</u>	<u>ICNAF Div.</u>	<u>Source</u>										
to July 15	4T	1		6.0	0.6	5.4	23.7	37.3	16.7	4.8	1.8	3.8
June	4Vn, 4T	2			2.0	4.0	6.3	39.5	17.5	5.6	4.9	20.2
July 16-												
Sept. 15	4T	1	0.3	25.4	14.7	9.2	13.7	25.5	7.9	1.9	0.4	0.8
July-Aug.	4T	2	2.1	25.0	5.9	5.3	11.3	31.4	8.6	4.6	1.9	4.2
June-Nov.	4X, 4Vn											
	4T	1	0.5	10.8	21.0	9.1	9.0	14.7	21.4	8.2	2.5	1.8
June-Nov.	4T	1		0.4	23.5	12.8	8.6	15.3	26.6	9.1	2.2	1.2
June-Oct.	4T, 4Vn	2	1.1	15.3	5.6	5.9	11.7	34.7	11.7	4.4	2.2	7.6
June-Sept.	4T	3		16.0	12.0	10.5	8.0	32.0	11.0	8.0		3.5

Table 7. Sex ratio of the northern population of Atlantic mackerel sampled in ICNAF SA 4 during 1963, 1965-73; χ^2 values calculated after Sokol and Rohlf (1969) $\chi^2_{.05(1)} = 3.84$.

	Y e a r									
	1963	1965 ^a	1966 ^a	1967	1968	1969	1970	1971	1972	1973
♀ %	46.0	47.6	51.1	50.8	40.9	42.0	53.5	48.2	50.6	62.0
	48.0			53.3						
TOTAL	211	1131	499	1000	364	177	215	224	71	151
	3382			661						
χ^2	1.37	2.61	0.24	0.26	12.06	4.53	1.05	0.29	0.01	2.48
	5.70			2.94						

^aAn earlier report of 1 male to 1.06 females for 1965 and 1966 (MacKay 1967) is in error.

(60%) in Newfoundland waters during 1970-73. The sex ratio of mackerel in European waters also approaches a 1:1 ratio (Garstang 1898; Nilsson 1914; Steven 1950).

First maturity in mackerel normally occurs when the fish attain a length greater than 30 cm, about age 2. The maturity of dominant year-classes is delayed due to density dependent growth. First maturity for the 1959 year-class did not occur until age 3, while 100% maturity for the 1959 and 1967 year-classes did not occur until at least age 5 (MacKay 1976b; Moores et al. 1975).

Maturity is apparently a function of fish size and is independent of age. Certainly the earlier maturing or precocious fish are larger than immature fish of the same age (Table 8). However, data on maturity as a function of size (Isakov 1976; Moores et al. 1975) do not apply to the 1959 and 1967 year-classes which appear to have a lower percentage maturity for a given size than the non-dominant year-classes. The maturity size relationship may be also related to cohort abundance.

My earlier studies (MacKay 1967) indicated that females were slightly, but significantly, larger than the males. I attributed this difference in length to the tendency of some males to be precocious; thus the slower growth associated with maturity occurred, on the average, earlier in males than in females. An examination of a limited number of 1967 year-class fish in 1969 and 1970 allowed a test of this hypothesis (Table 8). While the sample size was small, there was a significant ($p < 0.005$) departure from a 1:1 sex ratio among the mature fraction, indicating that the males may mature earlier than females. However, in these samples there was no difference in length of males and females in 1969 or 1970. Moores et al. (1975) found that in Newfoundland waters females matured earlier than males. It appears that there are differences in sex ratio, maturity rate, and differential male-female growth rate related to year-class, stock density and perhaps locality. These differences are relatively small and can probably be neglected in most population and production descriptions and calculations.

WEIGHT RELATIONSHIPS

Somatic weights

The parameters of the power curve for calculations of somatic body weight from body length for each year from 1969 to 1973 are presented in Table 9a. All the equations supplied a highly significant fit to the data. The exponents of the power curve vary from year to year ranging from 2.9 to 3.3. Only the lowest exponent, that for 1972, is not significantly different from 3. All the other exponents are significantly greater than 3.

Length-weight equations for mackerel sampled in Newfoundland waters in 1970-73 (Moores et al. 1975) and SA 4 in 1974 (Hunt 1975) are presented in Table 9c. The exponents for all these are also slightly greater than 3.

An indication of the variation in somatic body weight from year to year can be obtained by comparing the calculated weights for 30-, 35-, and 40-cm fish (Table 9a). While there is very close agreement from year to year, the weights of 35- and 40-cm mackerel in 1972 are lower than in any other years.

There are seasonal changes in condition factor. The fish become fatter in the autumn prior to their migration. Data on length-weight for various dates in 1973 are presented in Table 9b. The exponents vary throughout the season, tending to be higher in the fall; however, these exponents do not differ significantly from 3. The seasonal trend is further illustrated in Fig. 7, and it is apparent that the somatic weights in fall are higher than in spring. These seasonal trends in somatic weights are greater than the year-to-year variations.

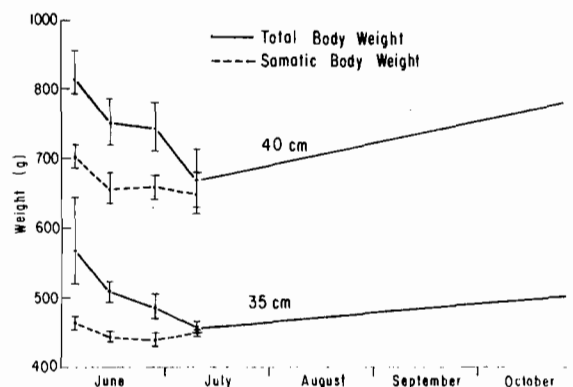


Fig. 7. Change in somatic and total body weight of 35- and 40-cm mackerel from June to October.

While females are slightly larger than males of the same age (MacKay 1967), there is no difference in somatic weights for the same length (Table 9a).

Equations derived by Moores et al. (1975) for mackerel in Newfoundland waters also show the same seasonal trend with fish being heavier in October. Weights calculated from their equations are significantly heavier than weights of fish in 4X, 4Vn, and 4T for June-July. However, during the fall there is no significant difference in weights between mackerel off Newfoundland and those off Cape Breton.

Gonad weights

The parameters of the power curve for gonad weights on length for 1969-73 are presented in Table 10a. The gonad weights are more variable than the somatic weights. For any one year, the variance of the gonad weights is higher than for somatic weights, while between years, there are large and significant differences in the exponents. The exponents range from 1.2 in 1971 to 1.9 in 1970.

Part of the variability in the gonad weights may result from differences in time of spawning relative to the dominant seasonal cycle but, unfortunately, the data do not permit me to analyze for this separately. However, the seasonal change is illustrated in Fig. 7 which shows data for change in weight during a single spawning season from June 4 to July 9. The difference between total and somatic body weight reflects gonad weight. The wet weights of gonads decrease from 103.5 and 120.8 g to 10.2 and 21.5 g for 35- and 40-cm fish respectively. While the regression equations are different for males and females (Table 10b), there is no significant difference between the calculated gonad weights for males and females.

Table 8. Numbers and mean fork length (cm) (95% confidence limits in parentheses) of male, female and immature fish of the 1967 year-class of Atlantic mackerel sampled in 1969 and 1970.

Date	ICNAF Division	Male No.	Male Length	Female No.	Female Length	Immature No.	Immature Length
June 16, 1969	4X	10	28.5 (±0.46)	2	28.5 (±2.94)	2	26.0 -
August 5-8, 1969	4T	18	28.4 (±0.52)	7	28.4 (±0.58)	74	27.6 (±0.27)
June-August, 1970	4X, 4T	45	30.1 (±0.42)	33	30.0 (±0.44)		

Table 9. Parameters for regression equations of somatic weight (SW) in grams on fork length (FL) in cm for the northern population of Atlantic mackerel and calculated weights for three sizes of fish (SW = aFL^b); (A) sampled during 1969-73, (B) detailed sampling in 1973, (C) in Newfoundland waters (Moore et al. 1975), and (D) in Canadian waters for 1974 (Hunt 1975). Confidence limits at P = .05 are given in parentheses.

Date	Coefficients		Degrees of freedom	Calculated somatic weight (cm)			
	a	b		l	30	35	40
(A)							
1969	.0033	3.324	347	20,853	268	448	698
1970	.0060	3.158	266	12,424	277	451	688
1971	.0054	3.181	50	17,574	270	441	674
1972	.0120	2.945	143	803	269	423	627
1973-June	.0036	3.294	152	2,336	264	441	684
1973-July	.0240	2.766	49	248	292	448	642
1973-Oct.	.0045	3.269	46	261	303	501	775
(B)							
June 4	.0073	3.109	48	107		463	701
June 14	.0138	2.919	49	462		443	654
June 27	.0086	3.049	53	591		437	657
July 9	.0240	2.766	49	248		448	648
Oct. 20, 25	.0045	3.269	46	261		(442-454)	(618-678)
						501	775
June	.0042	3.250	58	714		(490-512)	(736-815)
						439	677
June	.0036	3.297	93	1,542		(432-449)	(662-698)
						442	687
						(433-452)	(676-698)
(C)							
Newfoundland ^a (SA 3 and 4R)							
June-July 1970-73	.00396	3.21			289	475	729
September 1970-73	.00527	3.15			312	507	773
(D)							
Canadian waters (SA 4)							
1974 May-Oct.	.00366	3.301			275	457	710

^aThe regression equation for Newfoundland waters was converted to fork length using TL = FL/.916 (MacKay 1967).

Table 10. Parameters for regression equations of gonad weight (GW) in grams on fork length (FL) in cm for the northern population of Atlantic mackerel and calculated weights for two sizes of fish ($GW = a(FL - 25)^b$).

A) Sampled during June 1969-73, B) Detailed sampling in 1973

All regressions supply a significant fit to the data unless noted (NS).

Year	a	b	Degrees of freedom	F	Calculated gonad weights	
					35 cm	40 cm
(A)						
1969	.549	1.856	144	229	39.4	83.6
1970	.497	1.921	71	113	41.4	90.3
1971	3.475	1.173	39	17	51.8	83.3
1972	1.795	1.432	142	70	48.5	86.7
1973	1.936	1.465	151	110	56.5	102.3
(B)						
June 4	43.05	.381	48	.6(NS)	103.5	120.8
June 14	6.843	.975	49	10	64.6	95.8
June 27	1.923	1.400	53	26	48.3	85.2
July 9			39	6	10.2	21.5
Males						
June	.488	1.995	58	55	48.2	108.2
Females						
June	3.730	1.220	93	60	61.9	101.6

The seasonal changes in dry weights of ovaries and testes are indicated in Fig. 8. In early June the ovaries contain 36% dry material, 14% more than the testes. As the spawning season progresses, relative weight decreases to 23% for ovaries and 19% for testes. Then the relative dry weight increases

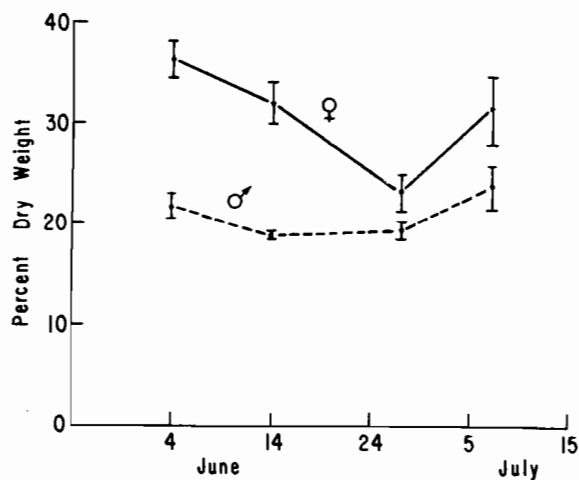


Fig. 8. Percentage dry weight of gonadal tissue for male and female mackerel at different times during the spawning period.

abruptly in early July when spawning is completed and the gonads are reabsorbed. Figure 9 illustrates the

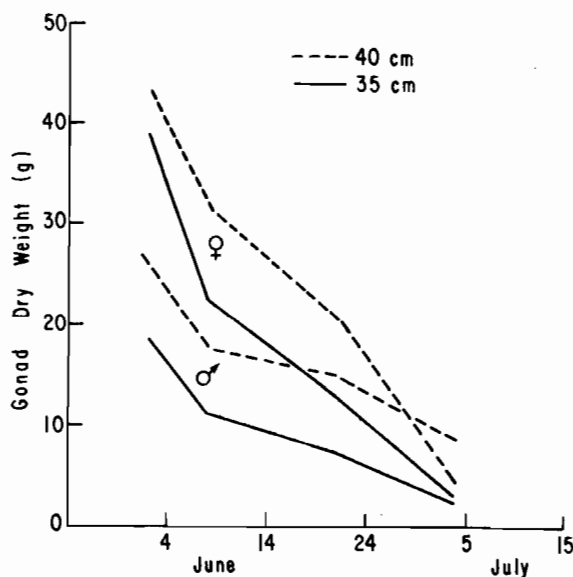


Fig. 9. Dry weight of gonadal tissue for 35- and 40-cm male and female mackerel during the spawning period.

changes in the percentage dry weight during the spawning season for 35- and 40-cm females and males. The decrease in relative dry weight of the ovaries just prior to spawning (June 14) due to an increase in water content is a phenomenon well known for other fish, such as the American plaice (MacKinnon 1972). Males show relatively smaller changes during this period; and while testes are not significantly lighter in terms of wet weight than ovaries, they contain significantly less dry matter. This indicates a different growth pattern during gonad deposition for males and females. Evidently females divert more energy than the males into production of gonadal tissue.

Total body weights

The change in total body weight (somatic and gonadal) is presented in Fig. 7 for 35- and 40-cm fish. There is a decrease in body weight associated with spawning; however, not all the weight change is a result of spawning. The fish which arrive first appear to be not only longer (see p. 7) but also heavier and have larger gonads than the later arrivals. Total body weight increases during the summer as the condition of the fish improves and fat is accumulated; however, for a given length, the weight of fish in the fall is still less than the total weight in the spring because of the presence of the gonads at that time.

BODY PROPORTIONS

The regression equations for the various body parts related to body length are given in Table 11. All of the exponents related to area are close to

Table 11. Coefficients of regression equations for various body components (cm^2) of the Atlantic mackerel based on fork length (cm).

Body component	Coefficients		Correlation coefficient
	a	b	
Pectoral fin area	.0023	2.270	.977
Fuselage area at the level of the pectoral fin	.0049	2.207	.970
Caudal fin area	.0073	2.196	.991
Mouth area	.0132	1.895	.980

2.0, which is expected on the basis of allometric growth. The pectoral fin, fuselage, and caudal fin areas are discussed further in connection with the hydrodynamics of a swimming mackerel (MacKay 1976a), while the mouth area is used in a theoretical feeding model (MacKay 1976c).

GROWTH

Early growth

Growth of mackerel in the first year is very rapid. Age 0 fish appear to reach a size of 20 cm by the autumn (MacKay 1967). Difficulties in capturing

post larvae and juveniles have made it hard to follow the growth of the young of the year. However, in 1971, a few samples were obtained (Table 12) which allowed the plotting of a growth curve (Fig. 10). The fish hatched in late June-early July at a size of about 0.3 cm, reached a size of 16.5 cm 2 1/2 mo later, and grew to about 20.0 cm by late November

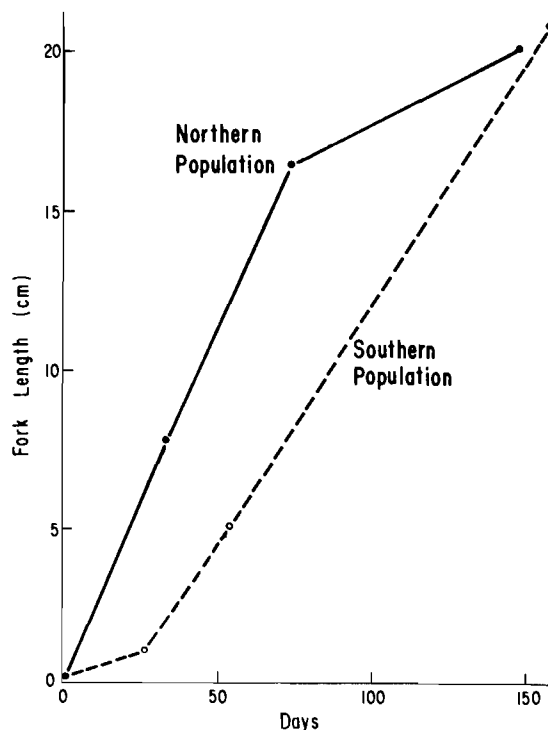


Fig. 10. Growth rates of age 0 Atlantic mackerel from the southern (after Sette 1943) and northern populations.

when they had completed their year's growth. Fish from the southern population show a similar growth. Sette's (1943) data are also plotted on Fig. 10. While the size of the young-of-the-year at the end of the growing season from both populations is similar, fish of the northern population are spawned later, have a shorter growing season, and show a more rapid early growth. This more rapid growth of the northern population occurs even though it is at the northern limit of its range. The warm temperatures during summer and the high productivity of the Gulf of St. Lawrence appear to compensate for the shorter growing season, and results in growth rates during the first year that are similar to those of the southern population.

Growth in second year

Growth of mackerel in the second year appears to commence in May and June prior to their arrival in Canadian waters. Fish sampled in late June and July already have a discernible summer growth on the otoliths. Growth in the second year is much slower than the first year's growth, but is still more rapid than in subsequent years.

Size in the second year varies from location to location and from year-class to year-class. The

Table 12. Location, average length and method of capture of young-of-the-year mackerel captured during 1971.

Date	Location	Number captured	Average length (cm)	Method of capture
June 21-25	Southern Gulf of St. Lawrence	Many eggs (1 mm) no larvae		1-m #20 plankton net
August 4	Grindstone Magdalen Islands Quebec	5	7.7	dipnet (at night)
September 9-15	Ellerslie, P.E.I.	17	16.5	hook and line
November 24	Emerald Bank Scotian Shelf	2	20.3	otter trawl

growth of second-year fish of the 1965 year-class at three different locations is compared to growth of the 1959 year-class in its second year in Fig. 11.

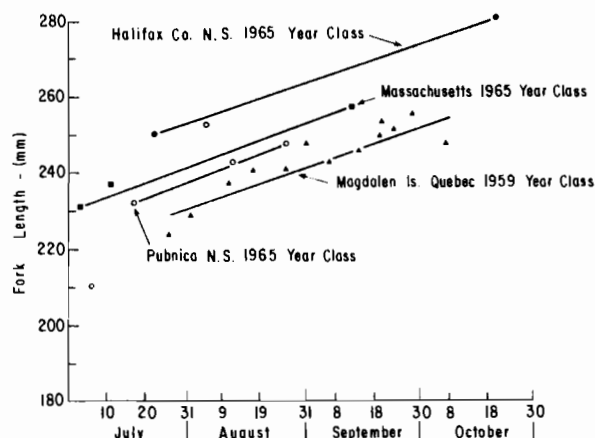


Fig. 11. Growth rates of age I Atlantic mackerel for the 1965 year-class from three locations compared to the 1959 year-class.

While the four groups have different intercepts, there is no significant difference in slopes of the growth rates. The differences in sizes, therefore, appear to have been established in the first year. It is also apparent that for the 1965 year-class the Massachusetts sample is midway between the other two, so that it is not possible to separate these northern and southern groups on the basis of either size-at-age or growth rate.

Growth of dominant and non-dominant year-classes

Lengths-at-age have been calculated for each year-class from age-length keys (Appendix II). The length frequencies for fully recruited fish have been based on the June sampling. For immature fish I have used data for July which better represent the younger fish.

The lengths-at-age for the dominant 1959 and 1967 year-classes are compared to the combined

lengths for all the non-dominant year-classes in Table 13. The dominant year-classes are smaller than the non-dominant year-classes at each age up to at least 6 yr of age. This difference is the result of a smaller size of the 1959 and 1967 year-classes at age 1. This appears to reflect intra-cohort competition during the first year and to offer an example of density dependent growth such that, the smaller the year-class, the faster the growth rate in the first year, and vice versa (MacKay 1976b).

A density dependent growth pattern is also evident for the non-dominant fish. The sizes-at-age for the non-dominant year-classes prior to and after 1967 are compared in Table 13. The lengths of fish at age 1 and 2 prior to 1967 when cohort size was lower are significantly larger (Student's *t* test, $p < 0.05$) than the lengths of these ages after 1967.

SPAWNING

Area

The northwest Atlantic mackerel spawn in two separate areas (Sette 1943). The southern population spawns between Chesapeake Cape and Cape Cod along the inner portions of the Continental Shelf. Spawning begins in mid-April in the south and continues through May and early June as spawning progresses northeastward along the coast as far as the Gulf of Maine.

The most important spawning area for the northern population is the Gulf of St. Lawrence (Arnold 1970; Dannevig 1919; Sette 1943). Some eggs and larvae are also found in the Bay of Fundy and in the inshore and offshore coastal waters of Nova Scotia (Arnold 1970), while spawning fish and juvenile mackerel are occasionally captured in eastern Newfoundland waters (Parsons and Hodder 1970). However, mackerel eggs and larvae are most abundant in the Gulf of St. Lawrence, concentrated in the southwestern portion of the Magdalen Shallows between the Magdalen Islands and Gaspé. Arnold (1970), in his extensive plankton sampling during 1967, 1968 and 1969 spawning seasons, found 90% of all mackerel eggs over the Magdalen Shallows. Smaller concentrations of eggs were found in Northumberland Strait. A few eggs were found on the west coast of Newfoundland, but very few eggs occurred over the Laurentian Channel. This is related to the cooler temperatures in this region, as

Table 13. Comparison of length-at-age for dominant and non-dominant year-classes. (All lengths determined from means based on age-length keys for June-July; standard errors in parentheses.)

Age:	Length (cm)													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<u>Year-class</u>														
1959	22.4	28.1	31.6	32.0	33.0	35.3	35.8	36.5	37.7	38.8	39.2	39.2	39.4	40.4
1967	22.5	27.5	28.9	30.5	32.7	35.3								
Average non-dominant	25.7 (±.36)	30.1 (±.89)	32.2 (±.69)	34.0 (±.97)	35.0 (±.38)	36.2 (±.65)	37.4 (±1.04)	38.3 (±.20)	38.2	37.9	39.6			
Non-dominant pre-1967	26.6 (±.10)	31.5 (±.50)	32.7 (±.90)	33.8 (±.48)										
Non-dominant post-1967	25.3 (±.34)	28.5 (±.24)	31.6 (±1.10)	34.5 (±.40)										

mackerel eggs are restricted to waters above 10°C (Arnold 1970; Sette 1943).

Season

Intensive spawning of the northern population is restricted to a relatively short period between mid-June and mid-July, although mackerel eggs have been collected in the Gulf of St. Lawrence from late May to early August (Arnold 1970). Arnold assumed peak spawning occurred in late June to early July; however, he did not have samples from early July. During the 1972 mackerel spawning season in the Gulf of St. Lawrence, extensive sampling indicated a 4-wk spawning period peaking during the last week of June (T. Lambert, MEL, pers. comm.).

Behaviour

While the spawning act has not been observed, it is clear that the sex products are released into surface waters. The pelagic eggs are normally concentrated in the upper 10 m with half occurring in the first metre (Table 14a, b). Lambert (pers. comm.) observed a large concentration of newly

spawned eggs in the upper 10 cm. The surface-skimming Neuston net accounted for 30% of the mackerel eggs in some of his samples. As the season progressed, the depth distribution deepened, associated with a deepening of the thermocline. Sette (Table 15a) indicates that later stages of eggs were found deeper in the water column. Arnold's results (Table 14b) do not show this; however, his samples were dominated by newly spawned eggs.

Bigeiow and Welsh (1925) state that mackerel spawning occurs chiefly at night. However, Sette (1943) concludes that there was no preference for any particular time of day or night.

Development of mackerel eggs is temperature dependent and takes 7 d (175 h) at 11°C (Worley

Table 14. Vertical distribution of mackerel eggs (a) for the southern population (after Table 2, Sette 1943), and (b) for the northern population collected by a series of Miller samplers (after Fig. 16, Arnold 1970).

(a)		(b)	
Depth	%	Depth	%
Surface	50	Surface	48
1 m	30	9.1 m	29
10 m	18	18.3 m	9
20 m	2	27.4 m	7
35 m	0	36.6 m	6
		45.5 m	1

Table 15. Vertical distribution of mackerel eggs by stages (a) for the southern population (after Table 3, Sette 1943), and (b) for the northern population (after Table 5, Arnold 1970).

Stage	A	(a) B	C
Depth	%		
Surface	83	28	1
5 m	15	53	51
10 m	2	19	48

Stage	I	(b) II	III	IV
Surface	75	13	8	4
15 m	72	14	11	4

1933). A description of each of the four stages used by Arnold (1970) and the duration of each stage are given in Table 16.

Table 16. Development stages of mackerel eggs and duration of each stage (after Arnold 1970).

Stage I - fertilization to formation of embryonic shield (30 h)
Stage II - embryonic shield to closure of blastopore; embryo covers half the egg circumference (75 h)
Stage III - lifting of tail from yolk (50 h)
Stage IV - tail curves back and touches head (20 h)

Sette (1943, after Moore 1899) states that spawning of the southern population occurs in batches with only 50,000 eggs per female released at one time. However, an examination of mackerel ovaries from the Gulf of St. Lawrence for stage of maturity (this study; Lambert, pers. comm.) suggests that females of the northern population must release many more eggs than 50,000 at a time. In fact, the ripe fish which enter the Gulf of St. Lawrence and encounter the warmer waters there (above 10°C) during the spawning period probably release the majority of their eggs in one batch.

Fecundity

Sette (1943) reviewed the early literature on fecundity and concluded that 400,000 eggs per average-size female was a realistic estimate for the fecundity of the southern population. A detailed estimate of the fecundity of the northern population has been hampered by difficulties in interpreting which of the different sizes of presumptive ova become eggs and are spawned and which are retained in the ovaries (Lambert, pers. comm.). Preliminary estimates of fecundity are available from three large female mackerel captured during June 12, 1969. The fish averaged 38.2 cm (SD = ±10.1) FL, and the gonads weighed 97 g and contained an estimated 431,700 eggs. While the confidence limits are 50% of the mean, these estimates are in agreement with Sette's.

Fecundity (F) can be calculated from the appropriate gonad weights (GW) by the following relationship:

$$F = 4450.5 \text{ GW} \quad (5)$$

Using this relationship with the average gonad weights for 1960-73 (Table 10), the fecundity of a 35-cm female mackerel would be 211,400 eggs and for a 40-cm female 397,200 eggs.

FAT CONTENT

A seasonal fat cycle for mackerel sampled in New England waters can be determined from the values given by Stansby and Lemon (1941). The fat content is low in the spring and increases to a peak of 18% in August (Table 17). Fall fat content is lower, but there is more variability than at other seasons, with

Table 17. Fat cycle for Atlantic mackerel sampled in New England waters. Values after Stansby and Lemon (1941) with additional values from Table 2, Sette (1950).

Month	Fat content %
April	4.4
May	8.5
June	8.3
July	10.6
August	18.4
September	6.5
October	12.9
November	13.9

individual values ranging from 6.5 to 19.5%. A detailed fat cycle for the northern population is not available, but Ackman and Eaton (1971) quote some unpublished observations of the Fish Inspection Laboratory, Halifax. The 8% fat of spring fish increases rapidly and reached 22% for fall fish. A maximum fat value of 25.5% occurred in a 39-cm fish captured in November 1965.

Fat content of fall mackerel was determined in this present study (Table 19). The fat content varied with fish size, being lowest in the smallest fish. Fish above 30 cm had fat values between 13 and 18%. The inverse relationship between fat level and feeding is mentioned on p.19 and is consistent with the crucial role of fat in overwintering success (MacKay 1976a).

Table 18. Percent lipid in various tissues of the Atlantic mackerel sampled in 1965 and 1966 during spring and fall (after Ackman and Eaton 1971).

Month	Sex	Fat content (%)				
		Light muscle	Dark muscle	Belly flap	Liver	Gonad
May, June	M,F	2.5	10.7	21.5	7.9	3.0
August, October	F	8.9	16.3	29.3	11.4	
May, June	M	2.8	12.5	24.1	10.2	2.1
May, June	M	2.2	8.8	18.9	5.5	3.9

Fat content also varies from tissue to tissue. Table 18 compares percentage of fat between males and females for spring and fall mackerel for five tissues. Dark muscle contained a higher percentage of fat than light muscles, while the belly flap contained the highest percentage of fat. However, because of the greater weight of the light muscle, it is the most important fat depot in mackerel (Flo et al. 1972). The gonads contain only 3% fat in the spring and are not present in fall fish. All other tissues contain more fat in the fall. All tissues in

Table 19. Quantity of food compared to fat levels for different sizes of Atlantic mackerel, *Scomber scombrus*, captured on Emerald Bank, Scotian Shelf, November 24, 1971. All weights determined from the length-weight regression for 1971. Number of fish in parentheses.

Length (cm)	Weight (g)	Fat (%)	Stomach content	
			Weight (g)	% of body weight
19.5 (4)	69		1.83 (4)	2.7
25.1 (5)	153	6.7 (1)	3.06 (5)	2.0
26.0 (4)	171		4.31 (4)	2.5
28.0 (4)	217	11.4 (3)	2.56 (4)	1.2
31.3 (10)	309	14.0 (2)	1.10 (10)	0.4
34.7 (3)	429	17.6 (1)	.81 (3)	0.2

males have more fat than in females except for the testes which contain half the fat of ovaries.

The iodine values (IV) of mackerel fat varied from tissue to tissue. The gonads had the highest IV values, being over 200 for testes and around 190 for ovaries. The IV of other tissues varied from 114 to 170.

The density of mackerel fat can be calculated using data from Ackman and Eaton (1971) and a table relating IV to fat density (Ackman and Eaton 1970). The average density of mackerel fat was between .90 and .91. This is lower than the previously reported values for Atlantic mackerel and other Scombroids (Bailey 1952; Magnuson 1970).

FEEDING

Atlantic mackerel feed on a variety of foods: copepods (particularly *Calanus finmarchicus*), larval crustaceans, larval molluscs, fish eggs, larvae, juvenile and adult small fish, and large Crustacea such as euphausiids and shrimp (Bigelow and Schroeder 1953; Sette 1950). Moores et al. (1975) report that mackerel in Newfoundland waters feed on capelin and other fish, euphausiids, hyperiid amphipods, decapod larvae, copepods, and gastropod larvae. An analysis of mackerel feeding associated with this present study confirms the wide variety of organisms in stomach contents. Larger food items such as capelin, juvenile herring, various fish larvae, euphausiids, shrimp, hyperiid amphipods, and chaetognaths dominated the stomach contents of fish from the outer coast of Nova Scotia during the spring. During summer in the Gulf of St. Lawrence, a large variety of zooplankton organisms were consumed. While copepods predominated, Cladocera, larval euphausiids and decapods, polychaetes, the pelagic tunicate *Oikopleura*, bivalve larvae, mackerel eggs, fish larvae, and even large diatoms (0.2-mm diameter) were

all present in stomach contents.

In the autumn off of the outer coast of Nova Scotia, juvenile mackerel, euphausiids, and copepods were all present in adult stomach contents. At this time pteropods often predominate, and this contributes an odour to the flesh of mackerel (Ackman et al. 1972). Little feeding occurs during winter, and the majority of the winter-caught mackerel have empty stomachs (Sette 1950).

Occasionally rather odd items are found in the stomachs. During spring, mackerel off St. Margaret's Bay often contain a few Compositae seeds. Mackerel captured along with herring in weirs in the Bay of Fundy often have stomachs full of herring scales, while trawl-caught mackerel also have fish scales in their stomachs. Other items are engulfed but are subsequently expelled. I observed a small school of mackerel in Bedford Basin attempting to consume a floating cigarette filter. Fish would come to the surface to capture the floating filter only to have the filter bob to the surface 30 s to 1 min later after they had expelled it. This occurred at least 15 times.

Fish length, fat content, and food consumption in the autumn may be related (Table 19). While the sample size is too small on which to perform a multiple regression analysis, the relationship appears clear. The smallest fish have the lowest fat content and the most food (compared to body weight) in their stomachs, while the larger fish have a higher fat content and less food in their stomachs. As the acquisition of a high fall fat content is important for overwintering survival (MacKay 1976a), a feedback from fat content to feeding level would have an important adaptive function.

The size of particles eaten by mackerel varies with area and season but, in general, reflects the size composition of zooplankton. A preliminary analysis of food sizes in stomach contents indicates that, in the Gulf of St. Lawrence where feeding on zooplankton occurs throughout the summer, there is a generally higher proportion of large particles in the stomach than would be expected if non-effective filtering of plankton occurred. Muir and Newcombe (1973) indicated that mackerel (while filter feeding) can select larger particles such as euphausiids by slightly deviating from their swimming path. In addition, the data indicate that the smaller fish were more highly selective than the larger fish since they contained a higher proportion of larger particles than did the larger fish.

FEEDING BEHAVIOUR

Mackerel feed by two methods (Sette 1950; Bigelow and Schroeder 1953). Large plankton and small fish are actively pursued and engulfed individually (particulate feeding). In contrast, smaller organisms are filtered *en masse* using the primary and secondary gill rakers (filter feeding). Particulate feeding predominates in the spring and the fall, while filter feeding predominates during the summer in the Gulf of St. Lawrence. Small fish may spend a higher proportion of their time particulate feeding than do larger fish. The diet of mackerel from Newfoundland waters suggests that particulate feeding occurs there throughout the season (Moores et al. 1975).

A detailed laboratory study of filter feeding has been carried out by Muir and Newcombe (1973). During filter feeding the mouth and opercula are

opened maximally. The gill rakers and their secondary teeth form a filter. The pore size of the filter of a 32-cm mackerel was 0.4 x 0.2 mm. Clogging of the pore did not appear to be a problem even at high plankton concentrations as feeding bouts of up to 1 min were observed. Occasional closures of the mouth and adduction of the opercula resulted in back flushing of the gill rakers, such that the plankton was dislodged and entrapped by the pharyngeal pads which passed food to the esophagus.

Plankton odour and plankton increase swimming speed and turning rate. Filter feeding was not elicited at plankton concentrations below 3 mg/L. The incidence of filter feeding increased with increasing plankton concentration. At 3 mg/L the incidence of filtering was 15% and at 24 mg/L it was 57%, while 100% filtering did not occur until there was a concentration of 140 mg/L. Plankton concentrations in nature are much lower than these. Values ranged from 0.2 to 1.3 mg/L for the Gulf of St. Lawrence with means around 0.4 to 0.5 mg/L (Bulleid and Steven 1972; Lacroix and Filteau 1969; MacKay, unpubl. data).

Increasing evidence is accumulating that plankton generally occurs as patches (Cassie 1963; Platt et al. 1970; Weibe 1970). These patches would supply suitable densities to allow filter feeding to occur. In fact, other behavioural responses such as a non-random search pattern in the vicinity of potential food (Muir and Newcombe 1973), schooling, and continuous swimming (MacKay 1976a, 1976c) appear to be adaptations for food search in a patchy environment.

Muir and Newcombe also investigated the transition from filter feeding to particle feeding. At 9 mg/L the addition of only one large particle (fish flesh 1 g) stopped filter feeding. At higher plankton concentrations (140 g/L), particulate food reduced filter feeding by about 25%. When particles such as euphausiids were present in the plankton, the mackerel veered 10-20 degrees to engulf the euphausiid while still maintaining their filter-feeding behaviour.

Sette (1950) describes schooling behaviour of mackerel filter feeding in a confining outdoor pool. The school moved in an elliptical path about 3 m in diameter lying in an inclined plane. The upper limb was at the surface, while the lower limb was about 1 m deep. Filter feeding occurred on the ascending segment of the ellipse.

The schools observed by Sette were more compact when feeding than when not feeding. In experiments (Muir and Newcombe 1973) carried out in a circular raceway, not only was behaviour influenced by plankton density and plankton odour but also by the distribution of the plankton. When plankton was distributed throughout the tank, mackerel circled in the raceway while filter feeding. If plankton was introduced as a discrete patch, the turning rate increased (Table 20) and smaller fish (19 cm) were able to maintain themselves within the patch by swimming in a tight circle.

SCHOOLING

Schooling behaviour

The Atlantic mackerel is an obligate schooling fish. The term "school" is used here to describe a temporary group of individuals of the same species which actively maintain contact with each other and

Table 20. Rates of turning for *S. scombrus* in relation to presence and distribution of plankton and plankton odour.

Length (FL) cm		32.0	32.0	19.0
No. of fish		4	6	4
Distribution		homogenous	patchy	patchy
Stimulus	Time (min)	Number of 180° turns/fish/min		
None	-	0	0	0
Odour	1	0	1.6	-
	2	0	0.3	-
	3	0	0	-
	4	0	0.2	-
	5	0	0.2	-
	6	0	0	-
Plankton	1	1.4	2.3	2.0
	2	0	1.0	1.5
	3	0	0.8	3.3
	4	0	0	2
	5	0	0	1.5
	6	0	0	2
	7	0	0	1
	8	0	0	1
	9	0	0	0

show organized action (Radakov 1972). An obligate school is a group of fish that could not exist without schooling (Breder 1967). Mackerel certainly fit this category. When maintained singly in a respirometer apparatus, for example, they show abnormal behaviour by being in a constant state of agitation. This effect is known in many other schooling fish. Metabolic rate is often higher and feeding rate lower for such fish when they are held alone rather than maintained as a group and allowed to school (Radakov 1972).

Mackerel schools do not show dominance or hierarchy. In our experimental tanks the position within the school was constantly changing. Observations of mackerel captured in a trapnet again indicated a constant flux within the school. In addition, any change in direction resulted in a change in leaders when the outside fish become leaders in a 90-degree turn.

In accord with work on most other schooling fish (Shaw 1970; Radakov 1972), vision in mackerel is the most important factor in attraction and communication within the school. Parr (1927), working with the closely related *Scomber japonicus* (*colias*), showed that temporary blinding prevented schooling behaviour, while normal behaviour returned with the return of vision. In our experimental tanks a blind individual was unable to join the other schooling fish yet was still able to circle in the raceway.

Schools of many fishes appear to disperse in darkness, but jack mackerel, *Trachurus symmetricus*, may maintain school formation near the surface on moonless but starlit nights (Hunter 1968). Radakov (1972) reports that schools of many plankton-feeding fish disperse at night at light levels above which feeding can occur and reform in the morning after

they have started feeding. While I have not directly observed mackerel under conditions of low light, information from gillnet catches suggests that schooling may occur at night during spring and fall. These schools may be maintained by bioluminescence prevalent at that time (Sette 1950). Schools may disperse on some dark nights in the Gulf of St. Lawrence, as individual mackerel can be attracted to a light after dark and subsequently captured, but schools are not observed.

Radakov (1972) suggests that schools of many plankton feeders undergo repeated reorganization during daylight hours, either merging with other schools or breaking into smaller schools. In the Gulf of St. Lawrence, mackerel frequently school at the surface and can be observed from some distance by the rippling on the surface. Under these situations mackerel schools appear as discrete and fairly stable structures. In August 1972, in Pleasant Bay, Magdalen Islands, a large mackerel school (50 x 10 m) was observed for about 4 h while it maintained itself within 100 m of an anchored ship.

While there is fluidity among individuals within a school, at any one time a mackerel school shows parallel orientation, and this is polarized (Breder 1959). While no formal analysis of the three-dimensional structure of these schools has been attempted, the arrangements of fish within a mackerel school approach the diagonal arrangement suggested by Cullen et al. (1965) and Van Olst and Hunter (1970).

Interfish distances have been reported for *Scomber japonicus* by Van Olst and Hunter. Interfish distances are much greater for small fish, but for fish of 7-35 cm (SL) the distance was .6 to .4 lengths. Observations in our tanks suggest that *S. scombrus* has similar interfish distances.

Breder (1959) and Radakov (1972) describe transmission of waves of excitation passing through a school. While examining the large mackerel school mentioned previously, both gannets, *Morus bassanus*, and black-backed gulls, *Larus marinus*, were observed flying over and occasionally diving into the school. Immediately a wave of small splashes moved over the water as the fish raised their first dorsal fins. This wave of splashes if initiated at one end of the school moved the whole length of the school and often flowed back again. If the impulse originated in the center of the school, it spread in both directions. This behaviour appeared to have an adaptive function as it presumably lowered the predation rate of the birds by obscuring vision.

Another example of coordinated activity by schools was evident off the north shore of Prince Edward Island. Occasionally schools were observed swimming in a circular motion that created a small whirlpool. Purse-seine fishermen report seeing whirlpools in which the water was depressed over 1 m.

Mackerel school according to size. Sette (1950) suggested that the young-of-the-year school together, as do yearlings, but they may sometimes join schools of adults. While the adults do not appear to separate themselves into sizes, larger fish may school deeper during summer than schools of smaller mackerel. Differences in swimming speed between different sizes appear to be the mechanism by which the schools are kept distinct. My observations show that schooling according to size is most prevalent during spring and fall, but may break down during summer. Underwater observations of a school encircled by a purse seine indicated that various

sizes of mackerel were integrated into a single school. In addition, three other pelagic species were present in the same schools: herring, *Clupea harengus*; alewife, *Alosa pseudoharengus*; and shad, *Alosa sapidissima*.

School size

Mackerel schools may vary in size with season. Radakov (1972), summarizing much of the Russian work on schooling, suggests that mackerel schools in the Black Sea in June are small, only 10-50 fish while, at the end of summer, schools comprise several thousand fish. Schools of *S. japonicus* are variable in size and include schools up to 50,000 to 100,000 fish.

Elminowicz (1975) examined size of *S. scombrus* schools on Georges Bank during winter. By using hydroacoustic techniques corroborated by data from trawl catches, he determined the shape of the schools as ellipsoidal. The schools were about 10 times longer than deep with an average length of 148 m (range .5 to 962 m) and a depth of 13.5 m (range .1 to 71.6 m).

Volume of schools varied from 10 m³ to 27 x 10⁶ m³. Density of fish within a school varied from 0.1 to 6.5 fish/m³, although the densities may have been underestimated due to the assumption of no net avoidance (op. cit.). The density of fish varied with school size, the smaller schools were denser. A school of 2,500 m² had a density of 6.5 fish/m³, while a school of 6,000 m³ had a density of 0.1 fish/m³. I have calculated the average size of mackerel schools from Elminowicz's data as being 77,400 fish.

During spring and summer in Canadian waters, mackerel schools are smaller. Estimates of school size can be obtained from trapnet log books³ from St. Margaret's Bay, Nova Scotia (4X). If catches in these traps are of only single schools, then school size varies from less than 100 to 80,000 fish (Table 21). However, many traps are not pursued every day due to rough seas, and undoubtedly capture numerous schools over a couple of days. One trap in the interior of the Bay was checked every day and presents a complete record for 1969 (Table 22). In June and July catches of 1,000-2,000 lb were most frequent, while in August and September the catches were most frequent in the 100-500 lb range. I have converted these weights to numbers using the length frequencies of St. Margaret's Bay (Fig. 3) and the appropriate length-weight regressions (Table 9 and 10). The average number of fish per catch varies from 4,000 in July to 300 in October. Assuming these catch figures represent only one school, the school size in the interior of St. Margaret's Bay ranges from 300 to 4,000 with the majority of schools being of 1,000-2,000 fish.

Mackerel schools off the north shore of Prince Edward Island may be somewhat larger. Based on a questionnaire completed by purse-seine fishermen, the average school size is about 10,000 fish (MacKay 1973b).

³Fishermen reported all catches including cases where fish were known to have escaped or were released due to the lack of a market.

Table 21. Distribution of catch of Atlantic mackerel taken in trapnets, St. Margaret's Bay, Nova Scotia, based on log books.

	≤100	Catch(lb)/trapnet haul		
		101-1,000	1,001-10,000	10,000 +
May 1969	6	1		
" 1970		1		
June 1969	3	3	14	7
" 1970	4	8	7	-
July 1969		6	14	10
" 1970	1	7	16	3
August 1969		9	12	3
" 1970		4	15	
September 1969		10	11	4
" 1970		-	6	8
October 1969	2	2	4	
" 1970			2	
November 1969		1	2	
" 1970				
December 1969			1	
" 1970				
Total	16	52	104	35

Table 22. Distribution of catch of Atlantic mackerel captured in a trapnet, French Village, Nova Scotia, during 1969.

	Catch (lb)/trapnet haul								Average numbers/ catch
	≤100	101-500	501-1,000	1,001-2,000	2,001-3,000	3,001-4,000	4,001-5,000	5,000+	
June	2	2	4	6		2		2	1,796
July		4	3	10	5	2	1	3	4,181
August		9	5	7				1	2,974
September	4	11	2	5					1,108
October	2	2	2						337
Total	8	28	16	28	5	4	1	6	

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APPENDIX I

Length frequencies by month and ICNAF Division for Atlantic mackerel sampled in Canadian waters 1967-73.

YEAR	1967									1968									1969									1970										1971									1972									1973																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																								
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1. Excludes one sample from June 30
2. Includes one sample from June 30