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**LA THÈSE A ÉTÉ
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Population Biology and aspects of energy use
of the northern population of
Atlantic mackerel, Scomber scombrus L.

by

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Submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

at

Dalhousie University

August, 1976

Approved:

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ABSTRACT

The Atlantic mackerel, Scomber scombrus L. occur from May to November in Canadian waters. Spawning of the northern population occurs in the Gulf of St. Lawrence during June. Both northern and southern population overwinter along the continental slope. A winter fishery which expanded rapidly to 386,000 MT in 1972 has been exploiting these fish. The proportion of each population in the fishery cannot be determined because of the difficulty of separating the populations.

Minimum swimming speeds of the continuous swimming mackerel are 1/L/sec, consistent with hydrodynamic theory. Mackerel swim slower than most other scombroids. Fat is the most important variable influencing minimum seasonal variation in swimming speed. Cost of swimming varies with velocity squared.

Mackerel are oblique schoolers and school size varies with area and season. A theoretical model of feeding suggests a large advantage to a school predator when searching for aggregated prey. Filter feeding behaviour and continuous swimming also increases the efficiency of exploiting a patchy environment.

The estimated spawning stock in 1968 and 1969 of 5×10^9 fish formed the basis for a modified virtual population estimate for 1960-1974. The estimates are sensitive to the mortality level, however, for $M=0.30$, the population pattern is similar to that indicated by other published data although my estimates are double those used by ICNAF. Ricker type stock recruit curve is evident. The seasonal migration of mackerel transfer energy and materials between the Gulf of St. Lawrence and the Shelf regions.

ACKNOWLEDGEMENTS -

This work was carried out at the Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, while I was a recipient of a Fisheries Research Board of Canada Scholarship at Dalhousie University, Halifax, Nova Scotia. I am grateful to the various personnel at the Marine Ecology Laboratory who supplied technical assistance for this study. I wish to extend a special thanks to Mr. Tim Lambert for his support and Dr. B. S. Muir, under whose direct supervision this study was carried out. Mr. Norman Jeffrey, Defence Research Establishment, Atlantic, was particularly helpful in advising me on the hydrodynamic aspects of this study. Dr. D. Irwin, Physics Department, College of Cape Breton, offered useful criticisms on the hydrodynamic manuscript. Drs. E. T. Garside, I. A. McLaren, E. L. Mills of Dalhousie University read and offered useful comments on the manuscript. I especially wish to thank Dr. L. M. Dickie for his continued support, encouragement and helpful suggestions on this manuscript. Any mistakes, of course, are my own. A special thanks: to P. Ervin, B. Timmons and J. MacKay for assistance in typing; to J. Shaw for assistance with the figures; and to L. Clemens for editorial assistance.

SECTION A

CHAPTER 1

SYNOPSIS OF BIOLOGICAL DATA
OF THE NORTHERN POPULATION ATLANTIC MACKEREL
SCOMBER SCOMBRUS

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ABSTRACT

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 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.

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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, MS 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. MS 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 cold water 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 explores some of the paradoxes of their energetics.

The first chapter represents a synopsis of biological data collected from 1962-1974 on the Atlantic mackerel and serves as an introduction for the subsequent chapters. The next two chapters explore some of the theoretical aspects of the biology of mackerel. Chapter two examines the hydrodynamics of swimming mackerel and the implications for energy budgets and food search; while chapter three presents a feeding model which explores the implication of continuous swimming and schooling for food search in a heterogeneous environment. The final chapter discusses population dynamics, productivity, and recruitment.

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 to 1973. Additional samples were obtained during research cruises using baited hooks, gangs of graded gill nets, and otter trawls. The fish were measured for fork length (FL). Measurements of total length (TL) were available for 1960-61 (Bergeron, 1961, 1962) and for 1962-1964 (MacKay, MS 1967). These were converted to FL using a conversion factor of:

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

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 immersed in 95% ethanol.

Otoliths are reliable indicators of age for Atlantic mackerel (Steven, 1950; MacKay, MS 1967). However, otoliths from fish older than 6 years produce a greater percentage of unreadable and questionable ages. Ages of fish older than 10 years 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 (y/c). As a result I have combined the 1960 y/c with the 1959 y/c. This should not produce any serious errors in age estimation as the 1960 y/c was very weak (MacKay, MS 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 year 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, MS 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 50g or less in a drying oven at 50°C until a constant weight was obtained.

Ovaries from 3 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 formaldehyde, 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 to 1972 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 (1976 a). 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 (Figure 1 in Muir and Newcombe, MS 1973). The open mouth area (A_m) can be determined by

$$A_m = AB\pi \frac{1}{4} \quad (4)$$

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 0.01g on a pan balance.

Observations of mackerel swimming, feeding, and schooling behaviour have been made in a circular raceway 76cm wide and 56.4cm deep. The behaviour was observed directly, photographed and video taped for later analysis. MacKay (1976 a) and Muir and Newcombe (MS 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 traphets. Further information on schooling behaviour has been obtained from observations of fish schooling at the surface and from comments of fishermen.

BIOLOGICAL SYNOPSIS

A. Systematic Position and Description

The Atlantic mackerel, Scomber scombrus (Linnaeus, 1758), is placed in the Order Perciformes (Berg, 1947) or Percomorphi (Reagan, 1929), Sub-order 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 Scombroidae 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 (1976 a). 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 are borne on each premaxillary, maxillary, vomer, and palatine bone. A large transparent adipose eyelid

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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 streamline contour of the head. The first of two dorsal fins originated at the level of the pectoral fins and is supported by 10 to 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 swim bladder 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 to 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.

B. Range

The 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 the Chesapeake Bay in the south and the east coast of Newfoundland and the Gulf of St. Lawrence in the north.

C. 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 1925-1928 (Sette, 1950; MacKay, MS 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, MS 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, MS 1970).

Moore et al. (1975) have 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 (Section K) 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 of 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 by which

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particular year classes occur in Canadian waters during June strongly suggests that the northern spawning group is indeed a separate population. Sette's (1950) term "contingent" has not found widespread 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, MS 1975a; Beckett et al., MS 1974; Moores et al., 1975; Stobo and Hunt, MS 1974) have recently reviewed Sette's (1950) hypothesis of two populations and have accepted his conclusions.

D. Commercial Fishery

The annual commercial catch of mackerel off the North American coast has undergone wide fluctuations (Sette and Needler, 1934; MacKay, MS 1967). The fluctuation in Canadian waters is illustrated in Figure 1. In 1884, the North American total catch was 105,700 metric tons (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 has continued to increase until 1973 when it reached 419,300 MT. The difference between highest and lowest catch is almost 2 orders of magnitude.

Until 1962, the North American mackerel fishery was carried out exclusively¹ by Canada (including Newfoundland)

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

and the United States. Beginning in 1962, Bulgaria, Democratic Republic of Germany (GDR), Federal Republic of Germany (FRG), Poland, Romania, and the Union of Soviet Socialist Republics (USSR) have developed a winter fishery along the edge of the continental slope from Georges Bank to Hudson Channel. This fishery grew very rapidly from 1400 MT in 1961 to 386,000 MT in 1972 (Table I) but has decreased in 1973, 1974 and 1975. Because of fear of overfishing of the mackerel stocks, the International Commission for the North-west Atlantic Fisheries (ICNAF) has established a system of total allowable catch (TAC) allocated by country for the various ICNAF subareas (SA) and statistical areas (SA) (Figure 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. The 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 (Figure 1), the seasonal pattern of the Canadian fishery has been quite constant. The seasonal catch

distribution for different areas in SA 4 during 1924 - 1929 is similar to that for 1957 - 1966 (MacKay, MS 1967) and the same pattern is evident during 1969 - 1973 (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 (Section F).

The mackerel catch off the south and east coasts of Newfoundland (SA 3) is related to water temperatures (Templeman, 1966). Catches have 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.

E. Fishing Gear

The mackerel fishery is carried out by a variety of types of gear. Gills nets, trap nets, 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 1970 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 1800 tons (Anderson, MS 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-year 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. Gill nets take 28% of the catch, mainly in June and July when they supply bait for the lobster fishery. In division 4Vn trap nets account for 30% of the fishery, and purse seines take 40%. The trap net 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 gill net fishery. In division 4X the fishery is primarily a trap net 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 gill net and then traps and weirs. The majority of the purse seines in SA 4 are operating from small modified lobster boats usually less than 45 feet 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 sets. 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 sink 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.

F. 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, MS 1967; MS 1973) 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 migrate offshore; although fish occasionally strike inshore. The inshore catch in SA, 4X and 4W is largely dependent on surface temperatures and food availability.

Changes in length frequency with time are illustrated in Figure 3 which presents sampling from St. Margarets Bay,

typical of division 4X. The largest fish arrive first about mid-May, but the main groups are not present until June. As indicated later (Section I), 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 which are 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 Figure 4 which shows that in most years the size of adult fish that are 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, MS 1971; 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 mid-summer.

The large scale movement of both immature and mature fish has ceased by early July. This is substantiated by tagging studies in St. Margarets Bay (4X) during July of 1966, 1967 and 1968 (MacKay, MS 1973a). Of 1,299 fish tagged and released, 140 were recaptured within 78 days. 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 influences 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, MS 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 Island were the lowest on record, over 1 C below the long term average (Lauzier and Hull, MS 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 can not 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 underrepresented in these areas during summer. Comments from fishermen suggest they 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, the Atlantic coast of Nova Scotia (4X) normally has a different size composition from that of the Gulf of St. Lawrence (4T). From 1965 to 1970, only 1967 and

1969 had similar frequencies for the two areas (Figure 5).
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 y/c's are present in the two areas, their sizes are often different. For example, in 1970, the 1969 y/c fish sampled in 4X during July, August and September were all significantly larger than the same y/c fish sampled in 4T (Appendix III).

The difference in size of mackerel during the summer between 4X and 4T 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. Margarets 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 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, MS 1967). It is noted that other southern species including Scomber japonicus are occasionally found in this Eastern Canadian area during summer (MacKay and Gilhen, MS 1973).

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 y/c composition as those in SA4; 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 7C. 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 pass through the southern Gulf of Maine and mix with the southern population. In general, the southern population overwinter 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, two from the Newfoundland tagging and two from the tagging on the outer coast of Nova Scotia, were recovered a few months later, from January 12-25, 1974, by Polish trawlers fishing in Hudson Canyon.

Further information on the overwintering area was recently presented by Stobo (MS 1976) and Anderson and Almeida (MS 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.

G. Age Composition

Information on age and length was available for ICNAF statistical districts 4X, 4Vn, and 4T from 1962 to 1973. I have used detailed length frequencies (Appendix 1¹ in this study; Appendix IV, MacKay, MS 1967) and age-length keys

¹Appendices I, II, and III are stored on file at the Marine Ecology Laboratory, Dartmouth, Nova Scotia.

(Appendix II) to obtain age composition 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 the year. The resulting age composition for the spawning and summer population is presented in Figure 6 for 1965-1974. A detailed table of y/c compositions for 1962-1973 is presented in another paper in this series (MacKay, 1976b).

It is crucial for a subsequent population estimate (op. cit.) 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, MS 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 gill net catches, a wide range of mesh sizes ($\frac{1}{2}$ " to 3") was used.

The best indicator of the reliability of the y/c composition data particularly for the spawning period is the consistency of the estimates from year to year (Figure 6; Table 2, MacKay, 1976b). Additional estimates of y/c composition in 1973 are available for SA3 and from two other sources (Stobo and Hunt, MS 1974; Moore's 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 1963-1959 y/c's for all periods are consistently higher. The explanation for the difference is in time of sampling. As indicated previously (Section F), 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 overrepresent the older fish. By contrast, Stobo and Hunt's sampling was done later in the period and apparently underrepresents the older fish. On the other hand, their samples yielded nearly 25% 5-year olds (1968 y/c) and only 6% 2-year olds (1971 y/c). The high

representation of 5-year olds does not appear in their samples in later periods of the year, and the proportion of 2-year olds increases significantly. My early sampling contained few small fish, and I did not encounter significant numbers of 2- and 5-year 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 y/c was dominant while during summer the 1971 y/c was next in abundance.

Two mackerel year classes, that of 1959 and 1967, have dominated the northern population during the last 15 years. The 1959 y/c first appeared in strength in 1960 (MacKay op. cit.) and was still evident in the spawning population in 1973.

The 1967 y/c has been dominant in the summer population since 1968 (Figure 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 (Section I). In 1972, this y/c was 2.5 times more abundant than the 1959 y/c. No other year classes have shown the persistence of 1959 and 1967, and indications from the ICNAF fishery in 1975 are that 1970-1974 y/c's have all been weak.

H. Sex and Maturity

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% females prior to 1970 to 53% females from 1970 - 1973. Moores et al. (1975) found an even higher preponderance of females (60%) in Newfoundland waters during 1970 - 1973. 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 y/c's is delayed due to density dependent growth. First maturity for the 1959 y/c's did not occur until age 3; while 100% maturity for the 1959 and 1967 y/c's 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, MS 1976; Moores et al., 1975) does not apply to the 1959 and 1967 y/c's which appear to have a lower percentage maturity for a given size than the nondominant y/c's. The maturity size relationship may be also related to cohort abundance.

My earlier studies (MacKay, MS 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 y/c fish in 1969 and 1970 allowed a test to 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. 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.

J. Weight Relationships

(i) 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 - 1973 (Moore et al., 1975) and SA 4 in 1974 (Hunt, MS 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 Figure 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.

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

Equations derived by Moore et al. (1975) for mackerel in Newfoundland waters also show the 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.

(ii) Gonad weights

The parameters of the power curve for gonad weights on length for 1969 - 1973 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 Figure 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 decreases 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.

The seasonal changes in dry weights of ovaries and testis are indicated in Figure 8. In early June the ovaries

contain 36% dry material, 14% more than the testis. As the spawning season progresses, relative dry weight decreases to 23% for ovaries and 19% for testis. Then the relative dry weight increases abruptly in early July when spawning is completed and the gonads are reabsorbed. Figure 9 illustrates the 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.

(iii) Total Body Weights

The change in total body weight (somatic and gonadal) is presented in Figure 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 (Section F) but also are 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.

J. 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 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 hydromechanics of a swimming mackerel (MacKay, 1976a); while the mouth area is used in a theoretical feeding model (MacKay, 1976c).

K. Growth

(i) 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, MS 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 (Figure 10). The fish hatched in late June-early July at a size of about .3 cm, reached a size of 16.5 cm two and a half months later, and grew to about 20.0 cm by late November 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 Figure 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.

(ii) 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 growth of second year fish of the 1965 y/c at three different locations is compared to growth of the 1959 y/c in its second year in Figure II. 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.

(iii) 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 represents the younger fish.

The length 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 y/c's are smaller than the non-dominant y/c's at each age up to at least 6 years of age. This difference is the result of a smaller size of the 1959 and 1967 y/c's 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 size at age for the non-dominant y/c's 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 (Students t: test $p < 0.05$) than the lengths of these ages after 1967.

L. Spawning

(i) 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, MS 1970; Dannevig, 1919; Sette, op. cit.). Some eggs and larvae are also found in the Bay of Fundy and in the inshore and off-shore coastal waters of Nova Scotia (see Arnold, MS 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 (MS 1970) in his extensive plankton sampling during the 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 mackerel eggs are restricted to waters above 10 C (Arnold; Sette, 1943).

(ii) 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)³⁷.

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 seasons in the Gulf of St. Lawrence, extensive sampling indicated a four-week spawning period peaking during the last week of June (T. Lambert, MEL, Pers. Comm.).

(iii) 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 14, a, 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.

Bigelow and Welsh (1972) 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 seven days (175 hours) at 11 C (Worley, 1933).

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

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.) suggest 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 (above 10°C) there during the spawning period probably release the majority of their eggs in one batch.

(iv) 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 97g 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..

$$F = 4450.5GW \quad (5)$$

Using this relationship with the average gonad weights for 1969-1973 (Table 10), the fecundity of a 35cm female mackerel would be 211,400 eggs and for a 40cm female 397,200 eggs.

M. 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 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 reaches 22% for fall fish. A maximum fat value of 25.5% occurred in a 39cm fish captured in November, 1965.

Fat content of fall mackerel were determined in this present study (Table 19). The fat content varied with fish size, being lowest in the smallest fish. Fish above 30cm had fat values between 13 and 18%. The inverse relationship between fat level and feeding is mentioned in section N and is consistent with the crucial role of fat in overwintering success (MacKay, 1975a).

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 the 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 males have more fat than in females except for the testis 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 testis 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 previous reported values for Atlantic mackerel and other Scombroids (Bailey, 1952; Magnuson, 1970).

N. 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) reports 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 (0.2mm 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 content. At this time pteropods often predominate, and this contributes an odour to the flesh of mackerel (Ackman et al., 1973). 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 of St. Margarets 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 seconds to a minute 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 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 the 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-elective filtering of plankton occurred. Muir and Newcombe

(MS 1973) indicated that mackerel while filtering can select larger particles such as euphausiids by deviating the 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.

O. Feeding Behavior

Mackerel feed by two methods, (Sette, 1950; Bigelow and Schroeder, 1953). Large plankton and small fish are actively pursued and engulfed individually (particulate feeding). By 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. (Moore et al., 1965).

A detailed laboratory study of filter feeding has been carried out by Muir and Newcombe (MS 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 0.4×0.2 mm. Clogging of the pore did not appear to be a problem even at high plankton concentrations as feeding bouts of up to one minute 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 increases 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, unpublished data).

Increasing evidence is accumulating that plankton generally occurs as patches (Cassie, 1963; Platt, et al., 1970; Wiebe, 1970). These patches would supply suitable densities to allow filter feeding to occur. In fact, other behavioral responses such as non-random search pattern in the vicinity of potential food (Muir and Newcombe, op. cit.), 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 gm) stopped filter

feeding. At higher plankton concentrations (140 gm/l), particulate food reduced filter feeding by about 25%. When particles such as euphausiids were present in the plankton, the mackerel veered 10 to 20° to engulf the euphausiid while still maintaining their filter feeding behavior.

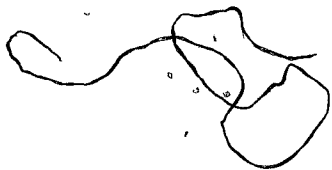
Sette (1950) describes schooling behavior of mackerel while filter feeding in a confining outdoor pool. The school swam in an elliptical path about 3 m in diameter lying in an inclined plan. The upper limb was at the surface; while the lower limb was about a meter deep. Filter feeding occurred on the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

The schools observed by Sette were more compact when feeding than when not feeding. In our experiments (Muir and Newcombe, MS 1973) carried out in a circular raceway, not only was behavior 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.

P. Schooling


(i) Schooling Behavior

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 show organized action (Radakov,



1972). An obligate school is a group of fish which could not exist without schooling (Breder, 1967). Mackerel certainly fit this category. When maintained singly in a respirometer apparatus, for example, they show abnormal behavior 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 (see 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° turn.



In accord with work on most other schooling fish (see 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 behavior; while normal behavior 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 suggest 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 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 four hours while it maintained itself within a 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 approaches 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 to 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 behavior 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 which created a small whirlpool in the centre of the

school. Purse seine fishermen report seeing whirlpools in which the water in the centre 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.

(ii) School Size

Mackerel schools may vary in size with season. Radakov (1973), 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 (MS 1975) has examined size of S. scombrus schools on Georges Bank during winter. Using hydroacoustic

techniques corroborated with data from trawl catches, he determined the shape of the schools was ellipsoidal, being about 10 times longer than deep. Average length was 148 m (range .5 to 962 m); while height was 13.5 m (range .1 to 71.6 m).

Volume of schools varied from 10m^3 to $27 \times 10^6\text{m}^3$. Density of fish within a school varied from .1 to 6.5 fish/ m^3 ; 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, with the smaller schools being more dense. A school of $2,500\text{m}^2$ had a density of 6.5 fish/ m^3 ; while a school of $6,000\text{m}^3$ had a density of 0.1 fish/ m^3 . 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 trap-net log books¹ from St. Margarets 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 pursed 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 lbs were most frequent; while in

¹Fishermen reported all catches including cases where fish were known to have escaped or were released due to the lack of a market.

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 for St. Margarets Bay (Figure 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. Margarets 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, MS 1973b).

REFERENCES

- Ackman, R. G., and C. A. Eaton. 1971. Mackerel, lipids and fatty acids. Can. Inst. Food Technol. J. 4: 469-474.
- Ackman, R. G., J. Hingley, and K. T. MacKay. 1972. Dimethyl sulfide as an odour component in Nova Scotia fall mackerel. J. Fish. Res. Bd. Canada 29: 1085-1088.
- Anderson, E. D. MS 1975a. The effect of a combined assessment for mackerel in ICNAF subareas 3, 4 and 5 and statistical area 6. Int. Comm. Northw. Atlant. Fish., Res. Doc. 75/14, Ser. No. 3458: 1-14.
- Anderson, E. D. MS 1975b. Relative abundance of Atlantic mackerel off the northeastern coast of the United States. Int. Comm. Northw. Atlant. Fish., Res. Doc. 75/15, Ser. No. 3465: 1-20.
- Anderson, E. D., and F. Almeida. MS 1976. Distribution of Atlantic mackerel in ICNAF Subarea 5 and Statistics Area 6 based on research vessel spring trawl surveys, 1968-1975. Int. Comm. Northw. Atlant. Fish. Res. Doc. 76/VI/13, Serial No. 3782: 1-13.
- Arnold, P. W. MS 1970. Spawning and aspects of the early life history of the Atlantic mackerel (Scomber scombrus L.) in the Gulf of St. Lawrence. B.Sc. Thesis. Acadia University, Wolfville, Nova Scotia. 73 pp.

Bailey, B. E. 1952. Marine oils with particular reference to those of Canada. Fish. Res. Board Can. Bull. 89: 413 pp.

Beckett, J. S., W. T. Stobp, and C. A. Dickson. MS 1974. Southwesterly migration of Atlantic mackerel Scomber scombrus, tagged off Nova Scotia. Int. Comm. Northw. Atlant. Fish., Res. Doc. 74/94, Ser. No. 3330: 2pp.

Berg, L. S. 1940. Classification of fishes both recent and fossil. Trav. Inst. Zool. Acad. Sci. U.R.S.S., 5: 87-517. Reprint, 1947, Edwards brothers; Ann Arbor, Mich.

Bergeron, J. 1961. Rapport preliminaire des travaux sur la biologie du Maquereau (Scomber scombrus L.) du Golfe Saint-Laurent. Rapp. Ann. 1960. Sta. Biol. Mar. Grande-Rivière: 77-85.

Bergeron, J. 1962. Deuxieme echantillonnage de Maquereau (Scomber scombrus L.) aux Iles-de-la-Madeleine. Rapp. Ann. 1961. Sta. Biol. Mar. Grande-Rivière: 81-84.

Bigelow, H. B., and W. C. Schroeder. 1953. Fishes of the Gulf of Maine. U. S. Fish and Wildlife Serv., Fish. Bull. 74, Vol. 53: 577 pp.

Bigelow, H. B., and W. W. Welsh. 1925. Fishes of the Gulf of Maine, Bull. U. S. Bur. Fish. Vol. 40. Part 1, Doc. 965: 567 pp.

Bligh, E. G., and W. J. Dyer. 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37: 911-917.

Breder, C. M., Jr. 1959. Studies on social groupings in fishes. Bull. Amer. Mus. Nat. Hist., 117: 393-482.

Breder, C. M., Jr. 1965. Vortices and fish schools. Zoologica. 50: 97-114.

Breder, C. M., Jr. 1967. On the survival value of fish schools. Zoologica. 52: 25-40.

Bulleid, E. R., and D. M. Steven. 1972. Measurements of primary and secondary productivity in the Gulf of St. Lawrence. Marine Sci. Center (McGill Univ.) MS. Report No. 21: 111 pp.

Cassie, R. M. 1963. Micro-distribution of plankton. Oceanog. Marine Biol. (H. Barnes (ed.)) 1: 223-252.

Cullen, J. M., E. Shaw, and H. A. Baldwin. 1965. Methods for measuring the three-dimensional structure of fish schools. Anim. Behav. 13: 534-543.

Dannevig, A. 1919. Canadian fish eggs and larvae: pp 1-80. In J. Hjort. Can. Fish. Expedition 1914-1915. Dept. Naval Service Canada, Ottawa, King's Printer.

Deuel, D. G. 1973. Salt-water angling survey. U. S. Dept. Com., Cur. Fish. Stat. No. 6200: 54 pp.

Environment Canada. 1975. Monthly Meteorological Summary, Sydney, N. S., June, July.

Elminowicz, A. MS 1975. Size and density of mackerel schools measured by echo sounders and catches. Int. Comm. Northw. Atlant. Fish., Res. Doc. 75/41. Ser. No. 3520: 9 pp.

Flo, A., N. Hagen, and V. Mohr. 1972. Fat tissues in fish: Report on preliminary studies during the period 1.9-31.12. 1972. (Transl. from Norwegian). Fish. and Mar. Serv. Environ. Can. Transl. Ser. 2981: 23 pp.

Fraser-Brunner, A. 1950. The fishes of the family Scombridae. Ann. Mag. Nat. Hist. Ser. 12: 131-163.

Galtsoff, R. S. 1924. Seasonal migration of mackerel in the Black Sea. Ecology 5: 1-5.

Garstang, W. 1898. On the variation, races and migrations of the mackerel, Scomber scombrus. J. Mar. Biol. Assoc. 5: 235-295.

Hunt, J. J. MS 1975. Canadian mackerel catches (m.t.) and numbers at age in Subarea 4 for 1974. Int. Comm. Northw. Atlant. Fish., Res. Doc. 75/92. Ser. No. 3571: 6 pp.

Hunter, J. R. 1968. Effect of light on schooling and feeding of jack mackerel, Trachurus symmetricus. J. Fish. Res. Bd. Canada 25: 393-407.

ICNAF. MS 1975. Provisional nominal catches in the North-west Atlantic, 1974. Int. Comm. Northw. Atlant. Fish., Summ. Doc. 75/32. Ser. No. 3590: 29 pp.

ICNAF. MS 1976. Provisional nominal catches in the North-west Atlantic, 1975. Int. Comm. Northw. Atlant. Fish. Summ. Doc. 76/VI/35, Serial No. 3923.

- Isakov, V. T. MS 1976. On some results of biological studies on mackerel from the Northwest Atlantic. Int. Comm. Northw. Atlant. Fish., Res. Doc. 76/VI/52, Ser. No. 3838: 1-14.
- Lacroix, G., and G. Filteau. 1969. Les fluctuations quantitative du zooplankton de la Baie-des-Chaleurs (Golfe Saint Laurent) I. Conditional hydroclimatiques et analyse volumetrique. Naturaliste Can. 96: 359-397.
- Lauzier, L. M., and J. H. Hull. MS 1969. Coastal station data: Temperatures along the Canadian Atlantic Coast, 1921-1969. Fish. Res. Bd. Canada Tech. Rept. 150: 25 pp.
- Leim, A. H., and W. B. Scott. 1966. Fishes of the Atlantic coast of Canada. Bull. Fish. Res. Bd. Canada, No. 1-5: 485pp.
- Lett, P. F., A. C. Kohler, and D. N. Fitzgerald. MS 1975. The influence of temperature on the interaction of the recruitment mechanisms of Atlantic herring and mackerel in the Gulf of St. Lawrence. Int. Comm. Northw. Atlant. Fish., Res. Doc. 75/33. Ser. No. 3512: 16pp.
- MacKay, K. T. MS 1967. An ecological study of mackerel Scomber scombrus (Linnaeus) in the coastal waters of Canada. Fish. Res. Bd. Canada Tech. Rept. 31: 127pp.
- MacKay, K. T. MS 1973a. Aspect of the biology of Atlantic mackerel in ICNAF Subarea 4. Int. Comm. Northw. Atlant. Fish., Res. Doc. 73/70, Ser. No. 3019: 11pp.

MacKay, K. T. MS 1973b. Mackerel population dynamics -
1973. Report prepared for Marine Ecology Laboratory.
Bedford Inst. Ocean. Dartmouth, N. S.

MacKay, K. T. 1976a. Hydrodynamics of the negatively
buoyant Atlantic mackerel Scomber scombrus.
Chapter 2, this study.

MacKay, K. T. 1976b. Population dynamics and productivity
of the northern population Atlantic mackerel Scomber
scombrus. Chapter 4, this study.

MacKay, K. T. 1976c. Feeding strategy in a patchy
environment. A theoretical analysis of feeding in the
Atlantic mackerel Scomber scombrus. Chapter 3, this
study.

MacKay, K. T., and E. T. Garfield. 1969. Meristic analysis
of Atlantic mackerel Scomber scombrus, from the North
American coastal population. J. Fish. Res. Bd. Canada
26: 2537-2540.

MacKay, K. T., and J. Gilhen. MS 1973. The occurrence of
unusual fishes in the vicinity of Prospect and St.
Margaret's Bay, Nova Scotia. Unpublished manuscript.

MacKinnon, J. C. 1972. Summer storage of energy and its
use for winter metabolism and gonad maturation in
American plaice (Hippoglossoides platessoides). J.
Fish. Res. Bd. Canada 29: 1749-1759.

Magnuson, J. J. 1970. Hydrostatic equilibrium of
Euthynnus affinis, a pelagic teleost without a gas
bladder, Copeia, 1970: 56-85.

Martell, A. M. MS 1967. Report of mackerel survey 1967.

MS Rept., Fish. Res. Bd. Canada. Biological Station,
St. Andrews, New Brunswick: 14 pp.

Matsui, T. 1967. Review of the mackerel genera Scomber
and Rastrellinger. Copeia, 1967: 71-83.

Moore, J. A., G. H. Winters, and L. S. Parsons. 1975.

Migration and biological characteristics of Atlantic
mackerel (Scomber scombrus) occurring in Newfoundland
waters. J. Fish. Res. Bd. Can. 32: 1347-1357.

Muir, B. S., and C. A. Newcombe. MS 1973. Laboratory
observations in filter feeding in Atlantic mackerel,
Scomber scombrus.

Nilsson, D. 1914. A contribution to the biology of the
mackerel. Cons. Inter. Explor. Mer., Pub. Circon.,
No. 69: 1-61.

Parr, A. E. 1927. A contribution to the theoretical
analysis of the schooling behaviour of fishes.
Occasional papers, Bingham Oceanogr. Coll. No. 1:
1-32.

Parsons, L. S. 1970. Northern range extension of the
Atlantic mackerel, Scomber scombrus, to Black Island,
Labrador. J. Fish. Res. Bd. Canada 27: 610-613.

Parsons, L. S., and V. M. Hodder. 1970. Occurrence of
juvenile and spawning Atlantic mackerel in south-
eastern Newfoundland coastal waters. J. Fish. Res.
Bd. Canada 27: 2097-2100.

- Parsons, L. S., and J. A. Moores. 1974. Long distance migration of Atlantic mackerel (Scomber scombrus), J. Fish. Res. Bd. Canada 31: 1521-1522.
- Platt, T., L. M. Dickie, and R. W. Trites. 1970. Spatial heterogeneity of phytoplankton in a near-shore environment. J. Fish. Res. Bd. Canada 27: 1453-1473.
- Radakov, D. V. 1972. Schooling in the ecology of fish. Izdatel'stvo "Nauka", Moscow (English translation) Halsted Press, John Wiley & Sons, New York, 1973: 173 pp.
- Reagan, C. T. 1929. Fishes, pp. 305-328. In Encyclopedia Brittanica, 14th Ed., 9.
- Sette, O. E. 1943. Biology of the Atlantic mackerel (Scomber scombrus) of North America. Part 1. Early history. U. S. Fish. Wildlife Service. Fish. Bull. 38 (50): 149-237.
- Sette, O. E. 1950. Biology of the Atlantic mackerel (Scomber scombrus) of North America. Part 2. Migration and habits. Ibid. 49 (51): 251-358.
- Sette, O. E. and A. W. H. Needler. 1934. Statistics of the mackerel fishery off the east coast of North America. 1804 to 1930. U. S. Bur. Fish. Invest. Rept. No. 19: 41-48.
- Shaw, E. 1962. The schooling of fishes. Sci. Am. 206: 128-138.

- Shaw, E. 1970. Schooling in Fishes. Critique and review pp. 452-480. Chapter in Development and Evolution of Behaviour: essays in memory of T. C. Schneirla, L. R. Aronson, E. Toback, D. S. Lehrman and J. S. Rosenblatt (eds) W. H. Freeman, San Francisco.
- Smith, R. L. 1974. The population pp. 21-25. In Ecology and Field Biology. Second Ed., Harper and Row, New York.
- Sokal, R., and F. J. Rohlf. 1969. Biometry: W. H. Freeman and Co., San Francisco: 776 pp.
- Stansby, M. E., and J. M. Lemon. 1941. Studies in the handling of fresh mackerel (Scomber scombrus). U. S. Dept. of Int. Fish and Wildlife Service. Res. Doc. 1: 46 pp.
- Steven, G. A. 1950. Contribution to the biology of the mackerel Scomber scombrus L. 111. Age and growth. J. Mar. Biol. Assoc. 30: 549-568.
- Stobo, W. T. MS 1976. Movements of mackerel tagged in subarea 4. Int. Comm. Northw. Atlant. Fish. Res. Doc. 76/VI/49, Serial No. 3835: 1-5.
- Stobo, W. T., and J. J. Hunt. MS 1974. Mackerel biology and history of the fishery in Subarea 4. Int. Comm. Northw. Atlant. Res. Doc. 74/9, Ser. No. 3155.
- Templeman, W. 1966. Marine resources of Newfoundland. Bull. Fish. Res. Bd. Canada. 154: 170 pp.

Van Olst, J. C., and J. R. Hunter. 1970. Some aspects of the organization of fish schools. J. Fish. Res. Bd. Canada 27: 1225-1238.

Wiebe, P. H. 1970. Small-scale spatial distribution in oceanic zooplankton. Limnol. and Oceanog. 15: 205-217.

Winter, G. H. MS 1975. Population dynamics of the Southern Gulf of St. Lawrence herring stock complex and implications concerning its future management. Ph.D. Thesis. Dalhousie University, Halifax, Nova Scotia. 142 pp.

Worley, L. G. 1933. Development of the egg of the mackerel at different constant temperatures. Journ. Gen Physiology 16: 841-857.

TABLE 1

Catch of Atlantic Mackerel from the ICNAF Area 1961-1964
(after Anderson, MS, 1975a, ICNAF MS, 1975, and ICNAF, MS,
1976).

Catch in Metric Tons

YEAR	TOTAL ICNAF AREA	ICNAF ^a 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

TABLE 2

Average monthly catch in % of total of Atlantic mackerel in ICNAF subarea 4 by months and ICNAF divisions based on an average for 1969-1973, (after Stobo and Hunt, MS, 1974).

	MONTH								
<u>DIVISION</u>	5	6	7	8	9	10	11	12	TOTAL
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

Proportion of Canadian mackerel catch obtained from ICNAF
SA 2, 3 and 4, 1961-1975.

% of Total Canadian Catch					
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	16	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 % based on 1969-1973 data after Stobo and Hunt (MS, 1974).

<u>ICNAF Division</u>	<u>Trawl</u>	<u>Gill Net</u>	<u>Handline</u>	<u>Trap Weir</u>	<u>Purse Seine</u>	<u>Misc.</u>
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

TABLE 5

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

S P A W N I N G

YEAR	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
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

S U M M E R

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 (MS, 1974) (2) Present study and (3) Moores et al (1974).

		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+		
DATE	ICNAF DIV.	SOURCE												
to July 15	4T				0.6	5.4	23.7	37.3	16.7	4.8	1.8	3.8		
June	4Vn, 4T				2.0	4.0	6.3	39.5	17.5	5.6	4.9	20.2		
July 16- Sept. 15	4T	0.3	25.4	14.7	9.2	13.7	25.5	7.9	1.9	0.4	0.8	4.2		
July-Aug.	4T	2.1	25.0	5.9	5.3	11.3	31.4	8.6	4.6	1.9				
June-Nov.	4X, 4Vn 4T	0.5	10.8	21.0	9.1	9.0	14.7	21.4	8.2	2.5	0.9	1.8		
June-Nov.	4T		0.4	23.5	12.8	8.6	15.3	26.6	9.1	2.2	0.5	1.2		
June-Oct.	4T, 4Vn		1.1	15.3	5.6	5.9	11.7	34.7	11.7	4.4	2.2	7.6		
June-Sept.	4T			16.0	12.0	10.5	8.0	32.0	11.0	8.0		3.5		

TABLE 7

Sex ratio of the northern population Atlantic macrarel sampled in ICAI SA 4 during 1963, 1965-1973. χ^2 values calculated after Sokol and Rohlf (1969) $\chi^2_{.05(1)} = 3.84$

	YEAR									
	1963	1965 ¹	1966 ¹	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				

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

TABLE 8

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

Date	ICNAF Division	MALE No. Length	FEMALE No. Length	Immature No. 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 - Aug., 1970	4X, 4T	45 30.1 (± 0.42)	33 30.0 (± 0.44)	

TABLE 9

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

DATE	COEFFICIENTS		DEGREES OF FREEDOM	F	CALCULATED SOMATIC WEIGHT (CM)		
	a	b			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	2,335	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
						(442-454)	(618-678)
Oct. 20,25	.0045	3.269	46	261		501	775
			Males			(490-512)	(736-815)
June	.0042	3.250	58	714		439	677
			Females			(432-449)	(662-698)
June	.0036	3.297	93	1,542		442	687
						(433-452)	(676-698)
(C)							
NEWFOUNDLAND (1) (SA3 and 4R)							
June-July 1970-1973	.00396	3.21			289	475	729
September 1970-1973	.00527	3.15			312	507	773
(D)							
CANADIAN WATERS (SA4)							
1974 May-Oct.	.00366	3.301			275	457	710

1 The regression equation for Newfoundland waters was converted to fork length using $TL = FL/.916$ (MacKay, MS, 1967).

TABLE 10

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

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

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

(A)

YEAR	a	b	DEGREES OF FREEDOM	F	CALCULATED GONAD WEIGHTS	
					35	40
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
------	-------	-------	----	----	------	-------

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

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		1m #20 plankton net
August 4	Grindstone Magdalen Islands Quebec	5	7.7	dip net (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

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 parenthesis)

	<u>Length (cm)</u>													
Age:	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	25.7	30.1	32.2	34.0	35.0	36.2	37.4	38.3	38.2	37.9	39.6			
NON-DOMINANT	(+36)	(+89)	(+69)	(+97)	(+38)	(+65)	(+1.04)	(+20)						
NON-DOMINANT	26.6	31.5	32.7	33.8										
PRE 1967	(+10)	(+50)	(+90)	(+48)										
NON-DOMINANT	25.3	28.5	31.6	34.5										
POST 1967	(+34)	(+24)	(+1.10)	(+40)										

TABLE 14

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

(a)

Stage	A	B	C
Depth	%		
Surface	83	28	1
5 M	15	53	51
10 M	2	19	48

(b)

Stage	1	11	111	1V
Depth		%		
Surface	75	13	8	4
15 M	72	14	11	4

TABLE 16

Development stages of mackerel eggs
and duration of each stage (after
Arnold MS, 1970).

Stage I - fertilization to formation of
embryonic shield (30 hrs.)

Stage II - embryonic shield to closure of
blastopore; embryo covers half
the egg circumference (75 hrs.)

Stage III - lifting of tail from yolk (50 hrs.)

Stage IV - tail curves back and touches
head (20 hrs.)

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

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)

FAT CONTENT (%)						
ORGAN						
MONTH	SEX	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

TABLE 19

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

STOMACH CONTENT

<u>LENGTH</u> <u>(CM)</u>	<u>WEIGHT</u> <u>(G)</u>	<u>FAT</u> <u>(%)</u>	<u>WEIGHT</u> <u>(G)</u>	<u>% OF</u> <u>BODY WEIGHT</u>
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

TABLE 20

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Rates of turning for S. scombrus in relation to presence and distribution of plankton and plankton odor.

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
Odor	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

TABLE 21

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

	CATCH (LBS.) / TRAP NET HAUL			
	< 100	101-1000	1001-10,000	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	
Sept. 1969		10	11	4
" 1970		-	6	8
Oct. 1969	2	2	4	
" 1970			2	
Nov. 1969		1	2	
" 1970				
Dec. 1969			1	
" 1970				
Total	16	52	104	35

TABLE 22

Distribution of catch of Atlantic mackerel captured in a trap-net, French Village, Nova Scotia during 1969.

CATCH(LBS.)/TRAP NET HAUL

		101 500	501 1000	1001 2000	2001 3000	3001 4000	4001 5000	5000+	Average Numbers/ Catch
	< 100								
June	2	2	4	6		2		2	1796
July		4	3	10	5	2	1	3	4181
August		9	5	7				1	2974
Sept.	4	11	2	5					1108
Oct.	2	2	2						337
TOTAL	8	28	16	28	5	4	1	6	

CAPTIONS FOR FIGURES

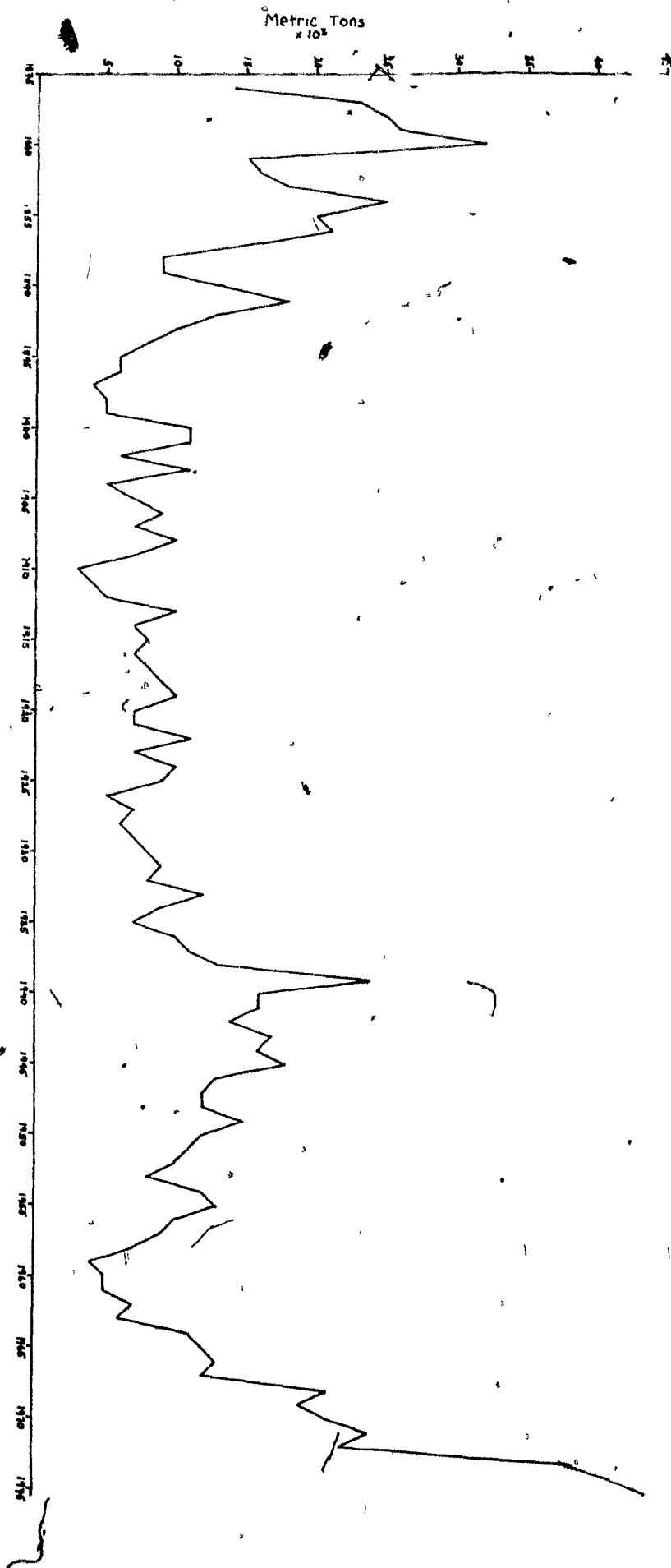
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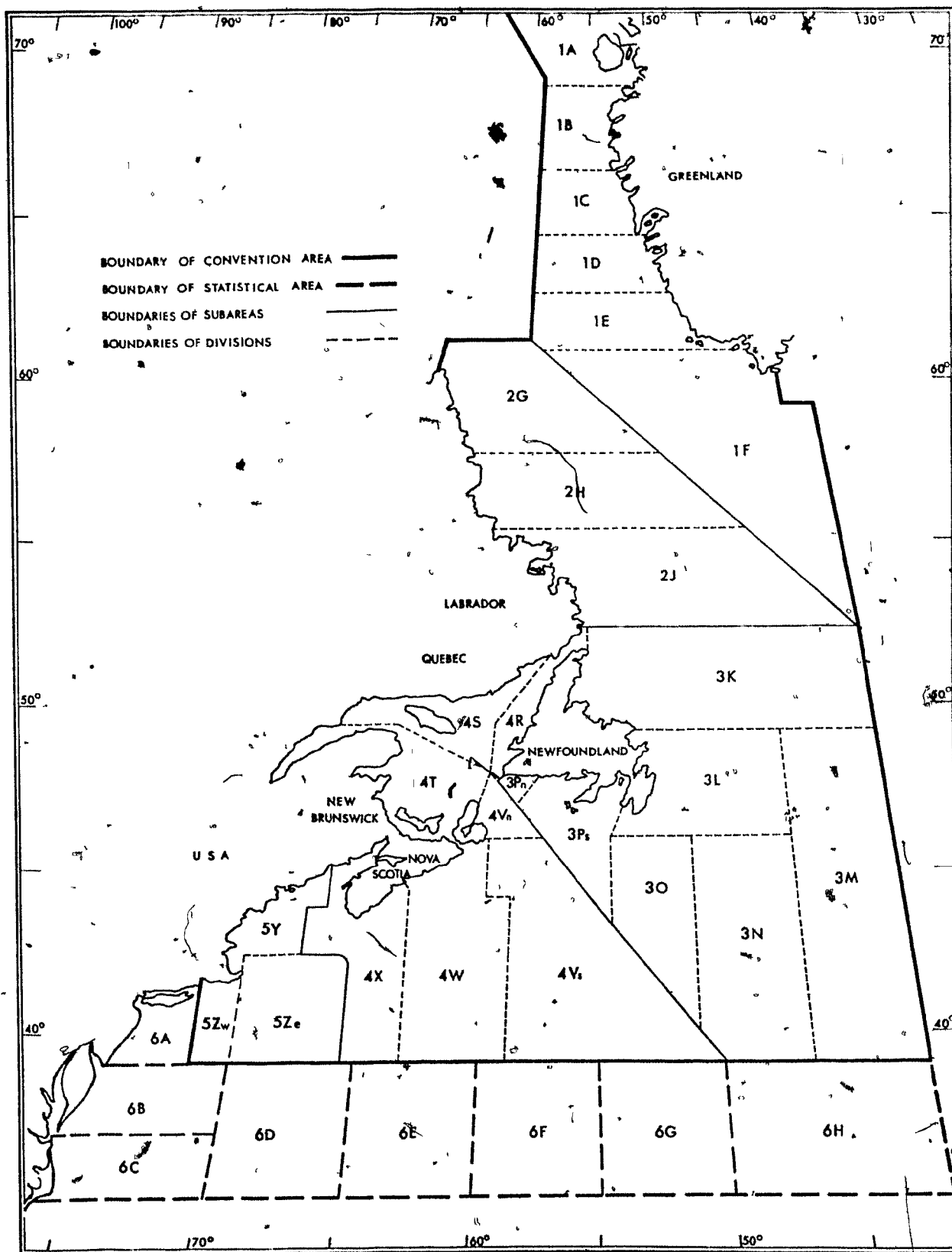
Figure 8. Percentage dry weight of gonadal tissue for male and female mackerel at different times during the spawning period.

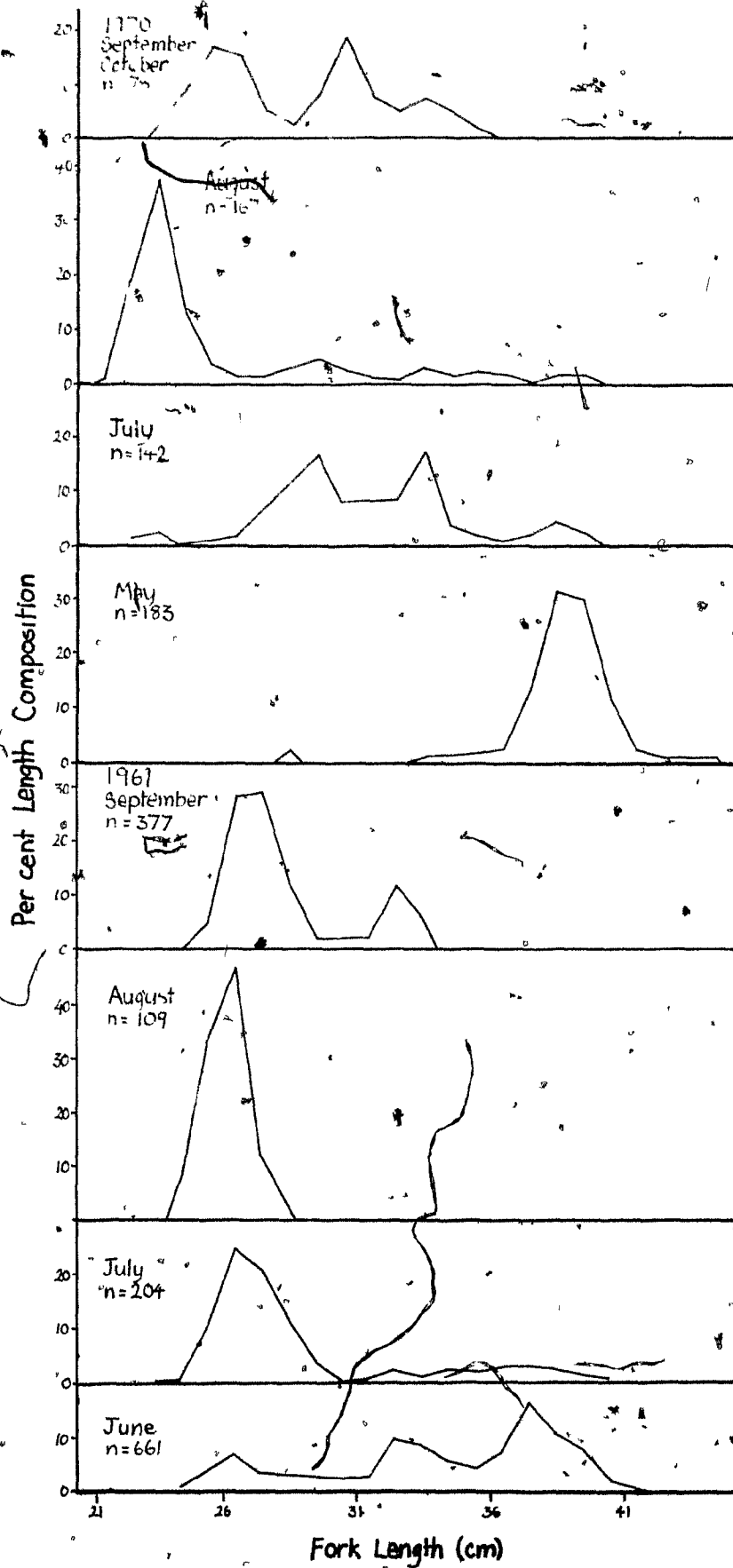
Figure 9. Dry weight of gonadal tissue for 35 and 40 cm male and female mackerel during the spawning period.

Figure 10. Growth rates of Age 0 Atlantic mackerel from the southern (after Sette, 1943) and northern populations.

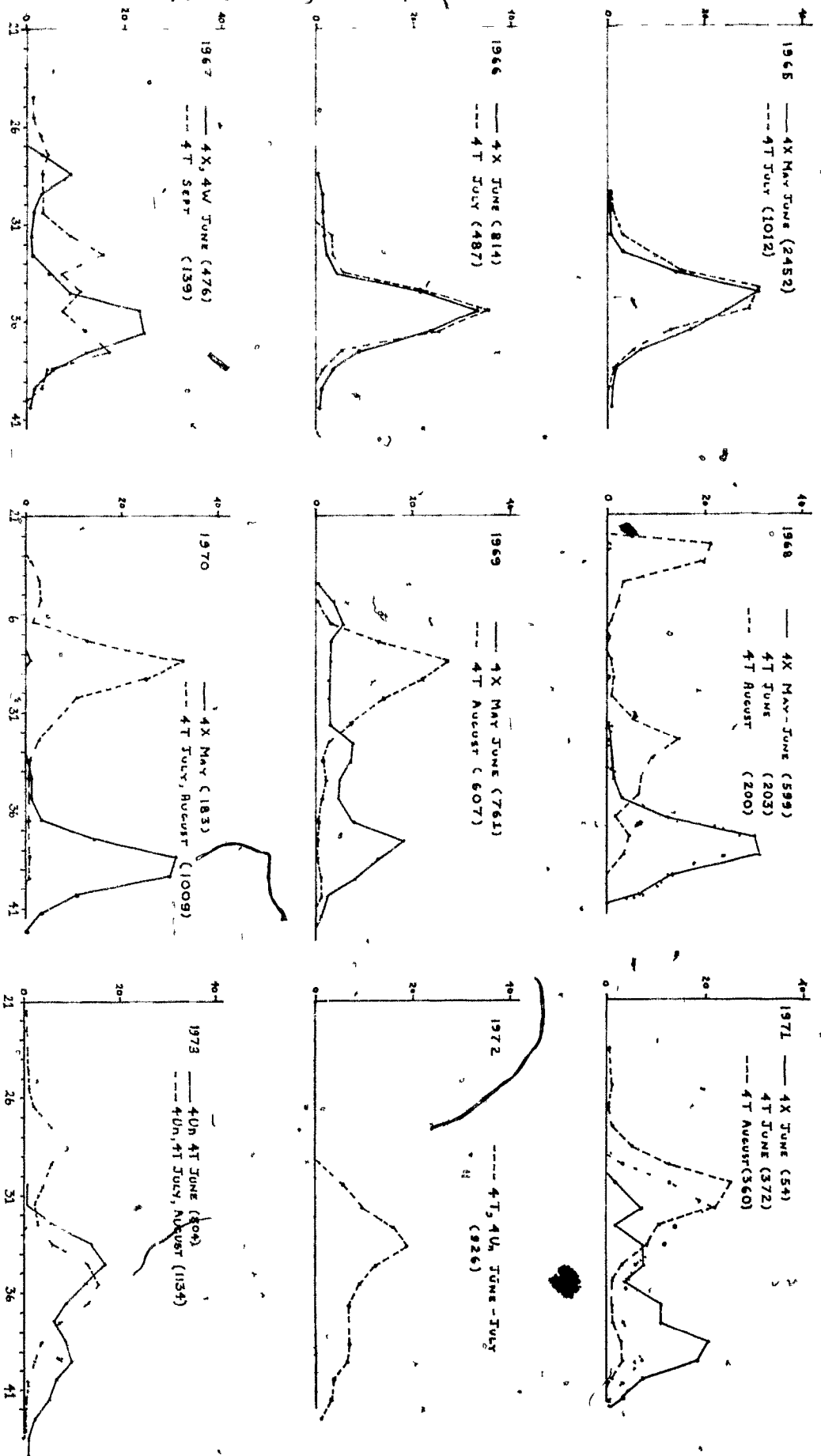
Figure 11. Growth rates of Age I Atlantic mackerel for the 1965 year class from three locations compared to the 1959 year class.

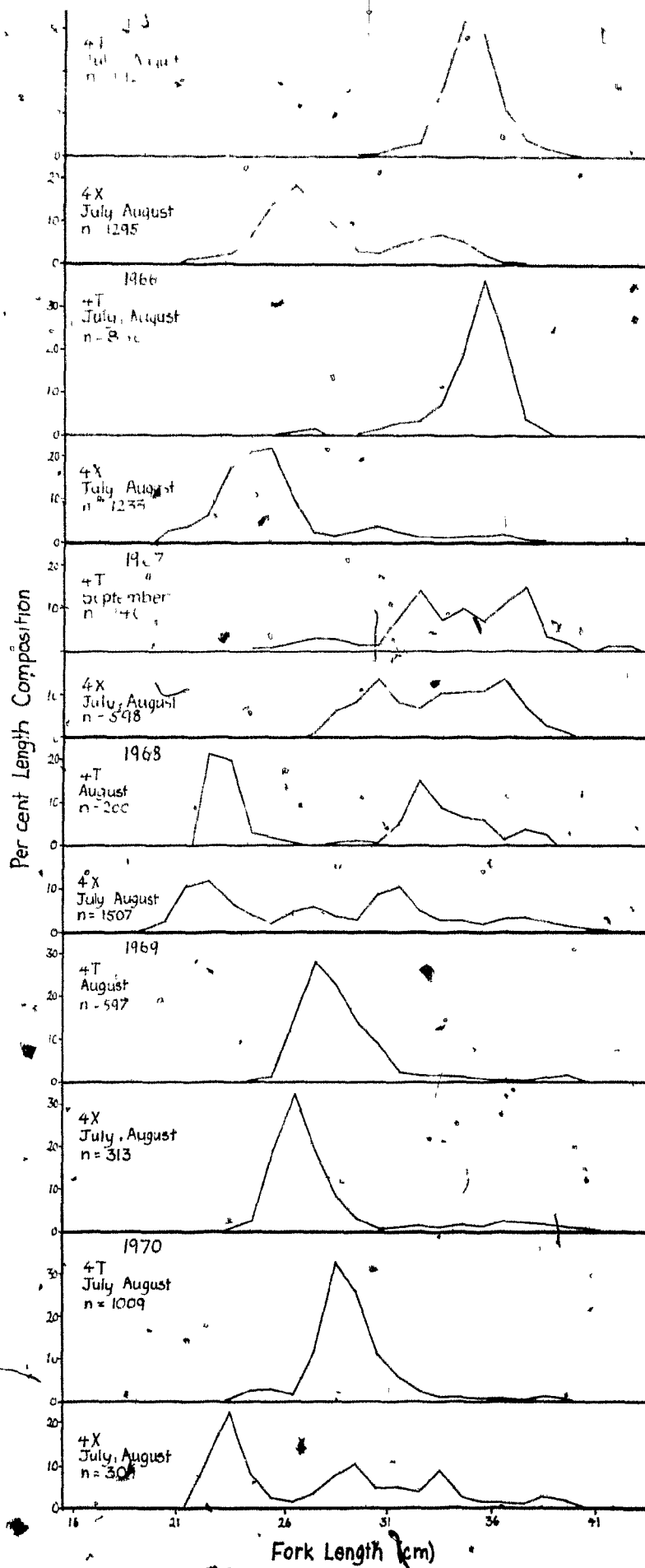


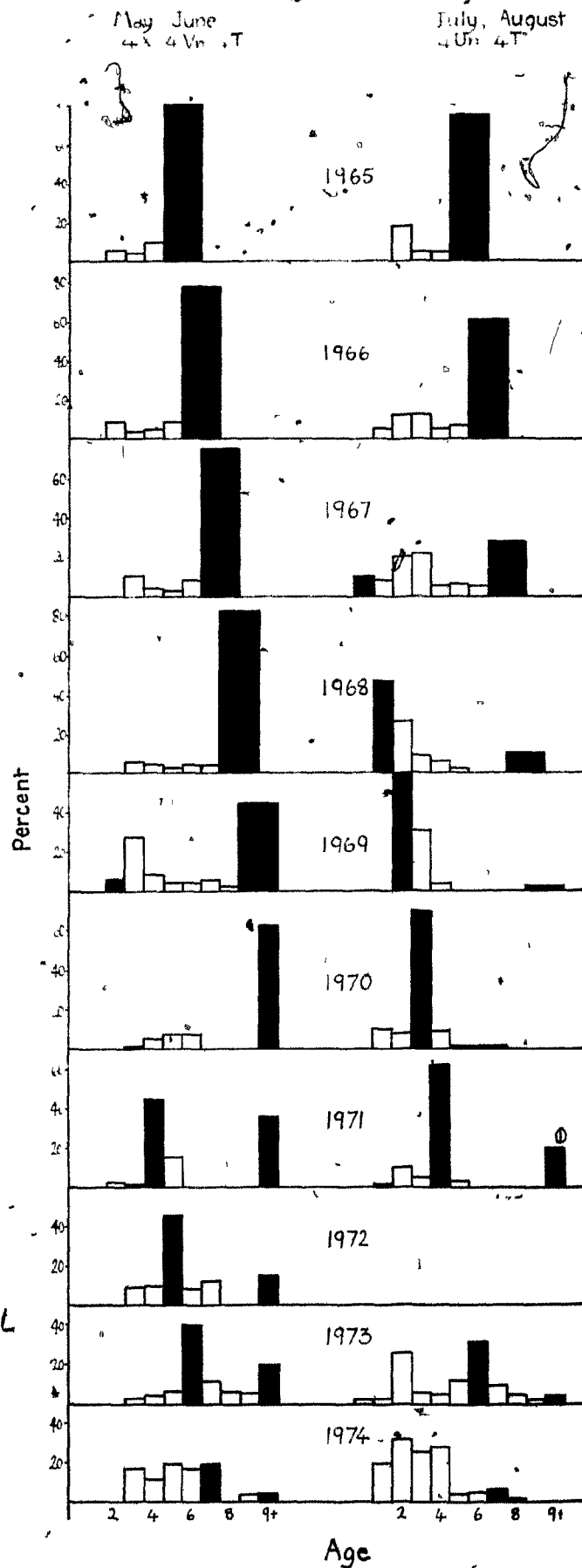


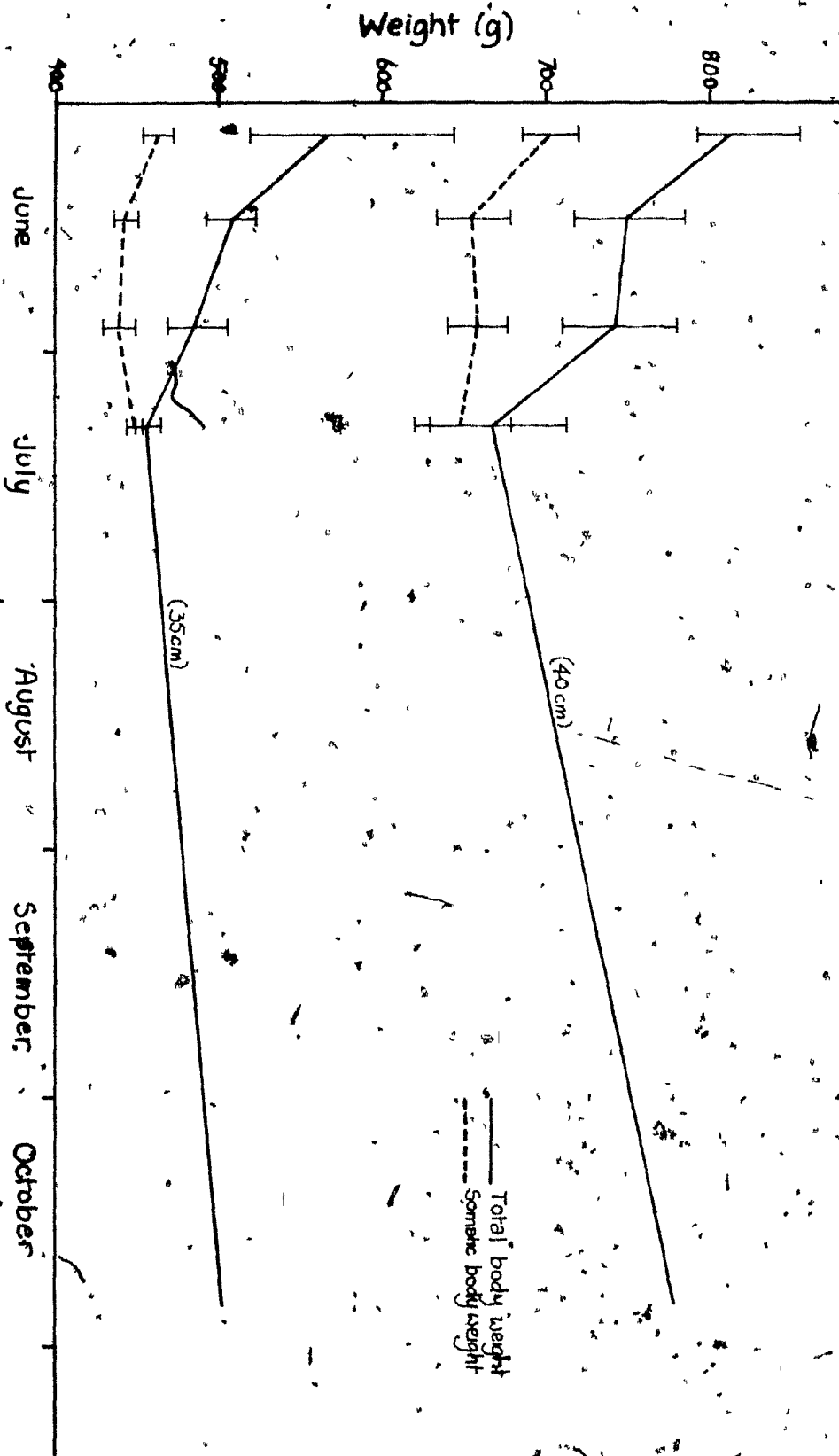


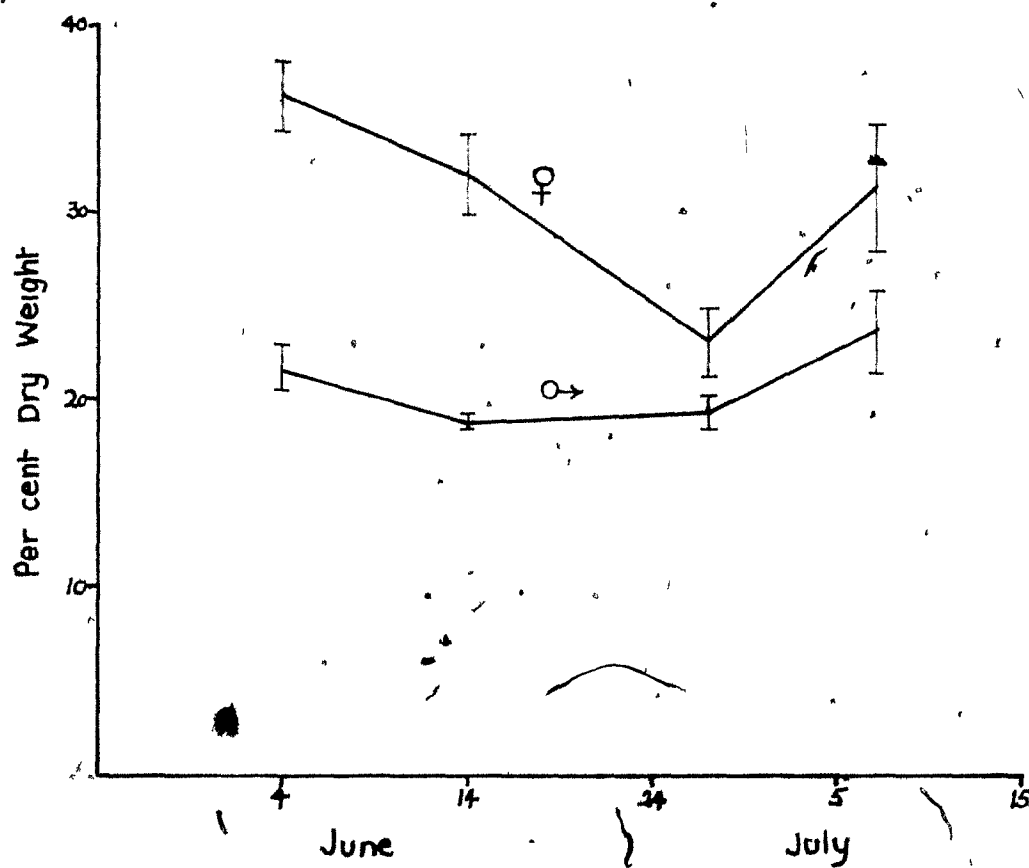
Per cent Length Composition

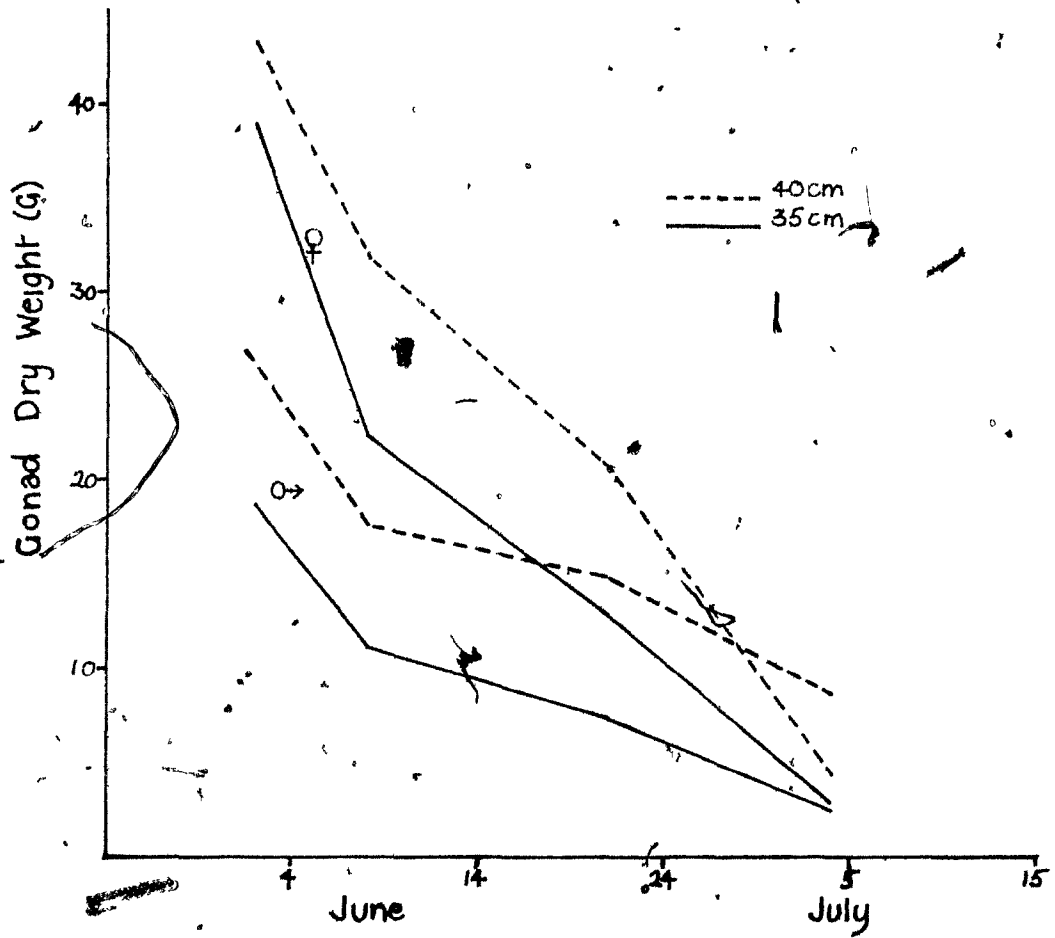


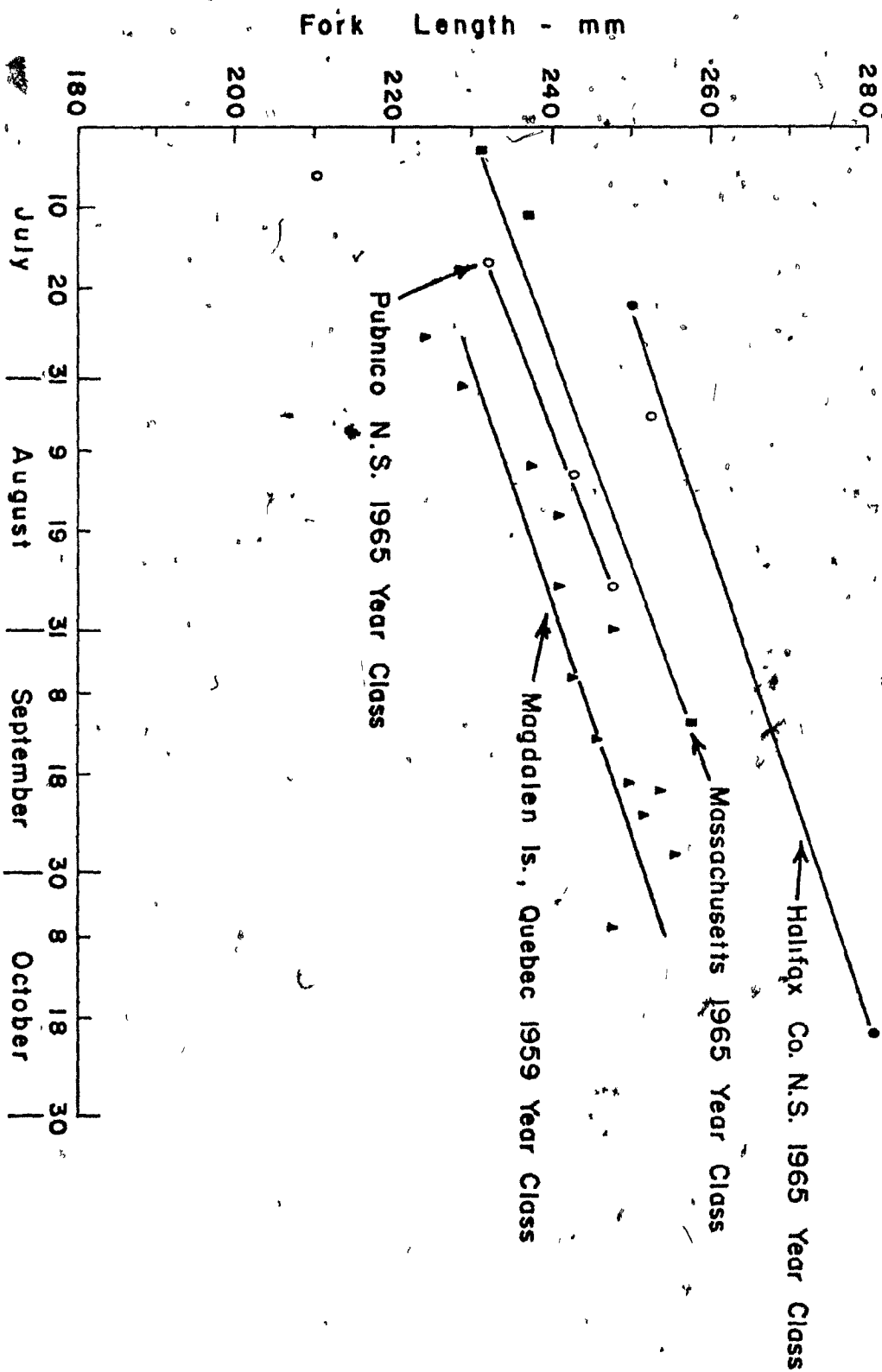


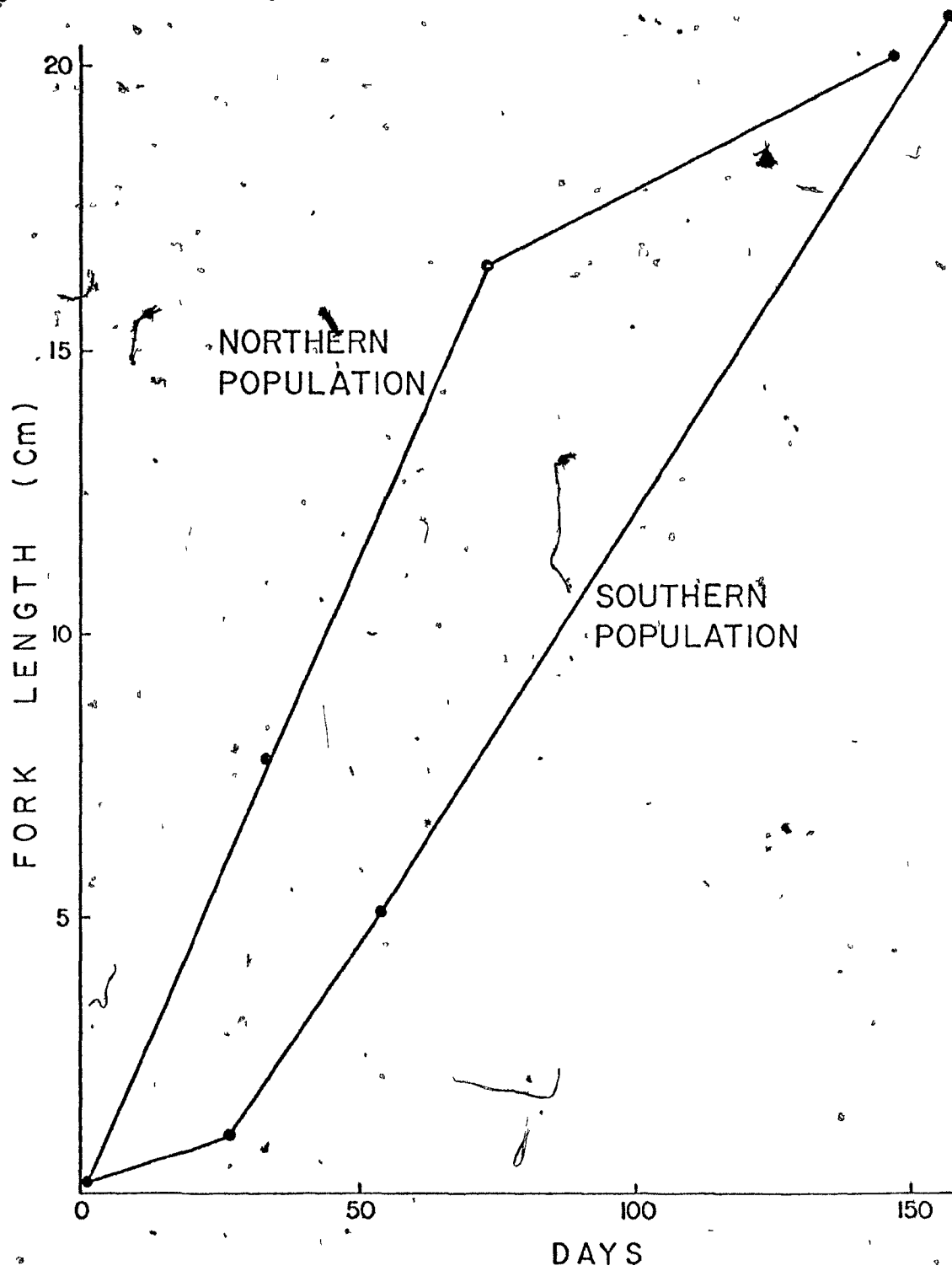












SECTION B

1 COLOUR

CHAPTER 2

Hydrodynamics
of the Atlantic Mackerel
Scomber scombrus L.

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ABSTRACT

Minimum swimming speeds for the negatively buoyant Atlantic mackerel, were determined by analysis of fish swimming in a circular raceway. Minimum speeds ranging from 1.2 to 0.8 lengths per second for 19 and 32 cm fish, respectively. Light flashes, addition of food odour, or food increased swimming speed. Speed was greater in the mornings than in the afternoons and evenings.

Minimum swimming speeds were consistent with hydrodynamic theory. Mackerel have various adaptations such as efficient large pectoral fins, use of the caudal fin as a lifting hydrofoil, position of the center of buoyancy, and low fat density which allow them to swim slower than other scombroids of the same size. Calculated minimum speeds are lowest from October to March when needs for energy conservation are maximal, faster speeds occur during spring when feeding is intensive and migration commences. Fat content is the most important of the six variables influencing seasonal changes in swimming speed.

The cost of swimming varies with velocity squared. Constant swimming is therefore costly. However, it must confer an advantage on mackerel as they are more abundant and have a more rapid growth rate than their neutral buoyant competitors such as Atlantic herring. This advantage could be an increase in the area searched, thus increasing the encounter rate with aggregated prey.

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INTRODUCTION

In consideration of energy intake, energy conservation, and production in fish populations, the Atlantic mackerel, *Scomber scombrus* L., provides several enigmas, if not paradoxes, of energy use (MacKay, 1967a). Mackerel have lost their swim bladder and are unable to pump water over their gills (Hall, 1930). They must, therefore, swim continuously to maintain hydrostatic equilibrium and respire using ram ventilation. Mackerel also make long migrations of 600 to 2,300 km to the Scotian and New England Shelf region, returning in spring to feed and spawn. However, despite the high level of activity and resulting high metabolic expenditure, mackerel have more rapid individual growth rates and are more abundant than the Atlantic herring, *Clupea harengus*, with which they share the pelagic environment. It is of considerable interest to understand the energetics of the mackerel population and to appreciate how they attain these high efficiencies. For example, mackerel represent significant transfer agents for materials and energy between the Gulf of St. Lawrence and the Scotian and New England Shelf. Furthermore, mackerel are currently experiencing high fishing pressure.

In this paper I have analyzed the swimming behaviour of the Atlantic mackerel. I then used hydrodynamic considerations applied by Magnuson (1970, 1973) to several



related species along with life history, morphological, and behavioural information on *Scomber scombrus*. The results lead to an appreciation of the factors underlying continuous swimming and indicate a paradox of energy usage which is explored in a separate paper (MacKay, 1976a).

Two size groups of mackerel were obtained, either from commercial mackerel trapnets or by angling with barbless hooks. These fish were transferred to the Marine Ecology Laboratory in 1.2 m circular tanks containing sea water into which oxygen was bubbled. The fish were then moved to the experimental tanks with temperature-controlled circulating sea water and held for two to eight months prior to experimentation.

The experimental tank consisted of a 2.4 m diameter tank with a smaller 0.9 m diameter tank in the centre. The fish moved continuously in the 0.8 m wide and 0.6 m-deep circular raceway between the two tanks. A plexiglass cover floating on the surface prevented surface rippling and aided photography.

The mackerel were exposed to a constant artificial illumination, with some diurnal variation caused by natural light entering via a skylight. Additional illumination was used during measurements of swimming speed, and initially caused an ~~increase~~ in swimming speed. The fish adapted to the new light level and resumed their normal swimming speed within one to two hours. A 2 hour period was allowed before measurements of swimming speed were made.

Initial observations showed that the fish were sensitive to movement and noise in the vicinity of the tank. The

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tank was surrounded by black PVC film to minimize disturbance. In addition, noise and movement in the vicinity of the tank were avoided during measurements of swimming speed.

The fish were monitored by two TV cameras. One camera fitted with a wide angle lens mounted above permitted a view of one quarter of the tank; while a second camera was placed beside a plexiglass side-viewing port. Switching from one camera to the other was accomplished manually by the observer who was located in a room adjacent to the experimental set up. During the experiment, the signals from the cameras were recorded on 0.13 cm video tape.

Observation of the fish in the raceway indicated that they normally schooled and followed a circular path. Therefore, swimming speeds could be determined if the time for completion of one circuit and the distance travelled in that circuit were known. Occasionally, fish turned during a circuit or did not school, but these cages were not used for measurements of swimming speed.

The time for the school to complete a circuit was determined during replay of the video tape, using a stop watch. The diameter of the path was more difficult to obtain. In the initial trial, a vertical line was drawn through the centre of the screen of the television monitor. As each individual fish passed this line, the video tape recorder was stopped and the location of the fish from the edge of the tank was measured. The relative position as determined from the TV monitor was converted to an actual

diameter measurement by proportion. In later trials, a meter rule was placed across the plexiglass lid, so that it was located in the centre of the field of the monitor during playback. This allowed direct reading of the distance from the edge of the tank. These measurements were subject to errors due to parallax and refraction.

Corrections for parallax were made assuming the fish were swimming at a depth of 0.1 m. Even if the fish were swimming 0.3 m below the surface, the error due to parallax, taking the extreme deviation from the centre would result in an error of only 1 cm/sec. In fact, this error would be much less, as the fish seldom swam in the outer edges of the field, and the errors due to refraction tend to cancel out those of parallax.

Swimming speed was obtained as the average for all fish in a school during five circuits. Measurements were repeated every 2-5 minutes, depending on fish size. Swimming speeds were determined for each size of fish on two occasions about a week apart. Differences between swimming speeds were tested using the student T-test.

Swimming speeds were initially determined on non-feeding fish. Subsequently, speeds were determined for fish exposed to plankton essence or euphausiids (12 gms). Plankton essence was prepared by passing thawed plankton (50 mg/l) collected from the Gulf of St. Lawrence through a 7 μ filter. The filtrate was then added to the tank through a perforated plastic pipe connected to an overhead reservoir (Muir and Newcombe, MS 1973).

During the measurement of swimming speed, 35 mm photographs were taken from above and through the side-viewing port with the aid of a strobe flash unit. These photographs were enlarged and used to determine attributes of the pectoral and caudal fins during swimming.

Calculations of drag and lift require measurements of various body dimensions, areas, centre of gravity, fish weight, and fish density. These measurements were determined for the experimental fish and a series of freshly caught fish sampled from commercial and experimental catches during 1970, 1971, and 1972.

The length, width, and depth of the body and fins were determined using a measuring board and calipers. Additional measurements were taken of the thickness of the pectoral and caudal fins using calipers.

The relative position of the pectoral and caudal fins was also determined.

The surface area of the body was estimated from body widths and depths at seven predetermined locations between the snout and the tip of the caudal peduncle. The surface area for each section was calculated assuming the first and last sections were cones and the rest were cylinders; then the surface area for each section were summed.

The areas of the pectoral and caudal fins were determined by planimetry from outline tracings of the fins. These tracings were also used to calculate a mean chord for the fins.

Fish density was determined from the weight of a fish in air and in water (with care being taken to dislodge any air entrapped in the mouth) plus the density of the water.

Centre of gravity was determined using the method suggested by Magnuson (1970). Temperature and salinity were determined during the swimming speed experiments and were used to calculate sea water density.

THEORETICAL CONSIDERATIONS

Lift and drag are basic concepts of hydrodynamics and aerodynamics. The following section outlines these principles.

Further detail is given by Hoerner (1965), Perkins and Hage (1949), Prandtl and Tietjens (1934 a,b). In addition, Webb (1975) gives an excellent review of their applicability to fish propulsion. Discussion of the application of lift concepts to negatively buoyant fishes is presented by Magnuson (1970, 1973).

A) Drag

Hydrodynamic drag is the result of movement of a fluid over a body and is the resultant force vector in the direction of movement. While the theory usually considers that the fluid is moving relative to a solid body, it is also valid when a solid body is moving relative to the fluid. Here I consider the fish moving relative to the water.

Hydrodynamic drag is composed primarily of two components: frictional drag and pressure drag. However, a third source of drag, induced drag, will also be considered.

Frictional drag, often called surface resistance or skin-friction drag, is a force tangential to the surface. It is caused by sheer stresses due to viscosity and velocity gradients at the boundary surface. This drag is affected primarily by the surface of the body and can be predicted from hydrodynamic considerations. The equation as given by Prandtl and Tietjens (1934a) is:

$$D = 1/2 \rho A U^2 C_f \quad (1)$$

where D = drag (dynes), ρ = fluid density (g/cc), U = speed (cm/sec), A = total area of wetted surface (cm²), and C_f = coefficient of frictional drag.

C_f is a non-dimensional number which is dependent on the Reynolds number, (R), a dimensional number which relates friction to viscous forces and can be calculated from equation 2.

$$R = \frac{\rho L U}{\mu} \quad (2)$$

L is the average length of the surface in the direction of movement, and μ is the kinematic viscosity. $\mu = 0.01$ at the temperatures and densities encountered during these experiments.

Reynolds numbers range from 10^3 for small fish larvae to 10^8 for the blue whale (Webb, 1975). At Reynolds numbers below 5×10^5 , laminar flow prevails. R for most small fish at normal cruise speeds is $< 5 \times 10^5$, and laminar flow should occur. However, the flow over an undulating body, such as a swimming fish, is more complicated. Rosen (1959) has suggested that the flow over swimming fish and cetaceans is a modified laminar flow consisting of a series of vortices. The hydrodynamic characteristics of this type of flow are unknown, but the drag coefficient should not be much higher than that for laminar flow. In this analysis, I have used the equation for laminar flow, although this may result in

a low estimate for drag.

$$C_{F_{LAM}} = 1.33 R^{-1/2} \quad (3)$$

Pressure drag or form drag is a force normal to the boundary. It is caused primarily by boundary layer separation and is dependent on the shape of the moving body. This type of drag is more difficult to predict from hydrodynamic theory, and coefficients usually are based on test data.

The third source of drag, induced drag or drag due to lift, is similar to pressure drag, but is directly associated with the production of lift and is due to the creation of vortices at the tips and trailing edges of the lifting surfaces. Hoerner (1965) gives an equation for determining the induced drag coefficient, C_I , of flat plates:

$$C_I = C_L^2 / \pi AR \quad (4)$$

where C_L is the coefficient of lift, and AR is the aspect ratio of the lifting surface. The aspect ratio is the ratio of the fin span to the average chord (Alexander, 1967).

B) Lift.

A lift force is required to maintain hydrostatic equilibrium in a negatively buoyant fish. The required lift is equal to the weight of the fish minus the buoyancy, and can be estimated from an equation given by Magnuson (1970).

$$L = 1 - \frac{p}{D_F} M_F g \quad (5)$$

L = required lift in dynes

M_F = mass of the fish

g = acceleration due to gravity, 980 cm/sec²

p = density of seawater, g/cc

D_F = density of fish, g/cc

The amount of lift (L) produced by a lifting hydrofoil is dependent on the lift coefficient (C_L) the density of the medium (p) the area of the foil section (A) and the square of the velocity (U) and is given by a standard hydrodynamic equation (Prandtl and Tietjens, 1934a).

$$L = 1/2 p A U^2 C_L \quad (6)$$

Rearranging to solve for C_L we have:

$$C_L = \frac{2L}{pAU^2} \quad (7)$$

In the case of a swimming fish, the area of the foil section is not only the exposed area of the pectoral fins but also includes the area through the body (fuselage) between the two exposed pectoral fins.

Using reasoning similar to that of Alexander (1967), Magnuson (1970) and following principles outlined by Prandtl and Tietjens (1934a), Perkins and Hage (1949) and Daily and Harlemen (1966), the importance of the various lifting surfaces were evaluated. Lift for a swimming fish

comes from three sources: the pectoral fin, the body, and the caudal region. Thus the total lift is equal to the sum of the components and is given by equation 8.

$$L_t = L_f + L_b + L_c \quad (8)$$

L_t = total lift

L_f = lift of the pectoral fins

L_b = lift of the body

L_c = lift of the caudal region

For the fish to be in rotational equilibrium, the lifting moments posterior to the centre of gravity must balance those anterior to it. Therefore, we have the following:

$$l_f L_f + l_b L_b = l_c L_c \quad (9)$$

l_f, l_b, l_c are the distance from the centre of gravity where the lift force is applied.

In order to evaluate equations (8) and (9), it was necessary to determine one of the lift components. The lift coefficient for the body could be evaluated using an equation suggested by Hopkins (1951). The equation and the parameters used in its solution are given in Appendix I.

A further source of lift is the vertical component of the thrust vector when the tail has a positive angle of attack. The expected lift from this source is given by the equation:

$$L_{th} = T \sin \alpha \quad (10)$$

L_{th} = lift due to thrust in dynes

T = total thrust in dynes

α = angle of attack of the caudal fin

RESULTS

A) Swimming Speeds

The results of the swimming speed experiments are presented in Table 1. Average swimming speeds of undisturbed 32 cm mackerel were 27.0 and 29.5 cm/sec for the two trials and minimum speeds for one circuit were 26 and 27 cm/sec. The difference between swimming speeds of the same fish taken 12 days apart was significant ($P < .001$). The action of the strobe unit used for photography increased the swimming speed to 28.9 and 34.6 cm/sec for the two trials. Differences between disturbed and undisturbed swimming speeds are significant ($P < .001$) for both trials.

Small mackerel (19 cm) had average swimming speeds ranging from 20.9 to 24.6 cm/sec and minimum swimming speeds between 18.4 and 21.4 cm/sec. There was a significant difference ($P < .001$) in the swimming speeds of these small fish at different times on the same day, but no significant difference in speeds measured a week apart when both were measured in the afternoon.

The data are rearranged in Table 2 to allow comparison of swimming speeds during morning and afternoon. It is apparent that the fish swam slower during afternoons than in the morning. It was not clear whether this represents an inherent rhythm within the fish or reflected the activity pattern of the laboratory.

Absolute swimming speeds of 32 cm fish were faster than those of 19 cm fish but the smaller fish swam faster relative to body length. The small fish swam faster than 1.1 lengths per second (L/sec); while the larger 32 cm fish swam about 0.9 L/sec.

Swimming speeds normally increased when the fish were disturbed or fed. Speeds for the 32 cm fish were just over 1 L/sec when stimulated with plankton essence, and increased to 1.5 L/sec while filter feeding. The 19 cm fish averaged 1.7 L/sec while feeding on dead euphausiids. The speed gradually declined after feeding, reaching the minimum speed of 1.1 L/sec seven hours later. A maximum speed of 13 L/sec (247.5 cm/sec) for one small fish was recorded during feeding on dead euphausiids. The magnitude and duration of these increased swimming speeds associated with feeding are discussed in more detail by Muir and Newcombe (MS 1973). Table 3 gives an example of the effect of plankton odour and plankton on swimming speed taken from their results.

Minimum or basal speed for 32 cm mackerel was 27 cm/sec, and 21 cm/sec for the 19 cm mackerel. Newly caught 32 cm mackerel swam slightly faster during their first month in captivity (MacKay, unpublished data). This may represent an adaptation to the experimental tanks. Nevertheless, normal cruising speeds of wild mackerel should be slightly above basal as even while non-feeding, normal disturbances in the environment should increase the speeds. Furthermore,

Lambert (unpublished data) found that speed increases after a meal and gradually decreases as the food is digested. Magnuson (1967) found that injection of food extracts into the water increased the swimming speed of skipjack tuna above the basal level. Nevertheless, basal speeds are probably realized in nature during periods of energy conservation, such as over-wintering, and during darkness."

B) Attitude of the Fins During Swimming

Our photographs show that during normal swimming the first dorsal fin is withdrawn into a slit and the pelvic fins are pressed flat against the body. During slow continuous swimming the pectorals are completely extended, acting as wings or hydrofoils. In addition, fish were observed occasionally to be gliding with the caudal fin almost horizontal, acting as a lifting hydrofoil. The extension of the pectorals and the horizontal caudal fin are shown in Figure 1.

The pectoral fins became less extended as speed increased. Figure 2a illustrates the sweepback of the pectoral fins at a swimming speed of about 35 cm/sec, and the angle of the trailing edge is 56° . The performance of the fin changes greatly with sweepback. The fully extended fin is compared to a sweptback fin (Figure 2) in Table 4. As sweepback increases aspect ratio, total area, and exposed area of the lifting surface decrease while the ratio of total area to exposed area increases. All of these affect the performance of the fin as a lifting hydrofoil.

Examination of 16 mm movies (courtesy of C. Newcombe)

of mackerel swimming in a turbulent flow channel showed that the pectoral fins may be used in a complex manner. They have a positive angle of attack and are cambered. Fish are able to vary the angle of attack, camber, and sweepback. All are features affecting the efficiency of wings or hydrofoils.

C) Body Dimensions

Regression equations of body weight, pectoral fin area, fuselage area, and caudal fin area on fork length are presented in Table 5. Weight-length relationships are discussed in more detail in an earlier paper in this series (MacKay 1976b). Although there are seasonal and yearly variations in the length-weight relationships, for convenience, I have used only one equation (Table 5) for the weight calculations. All these regression equations are used in the subsequent calculations of drag and lift of wild fish.

The exponent of all these equations relating area measurements to fish length is close to 2, a result which is expected on the basis of allometric growth. Magnuson (1973) obtained regression equations for the pectoral fins of eight scombroids and found in all of these that the exponents of these allometric equations were close to 2. My exponent for pectoral area of *Scomber scombrus* of 2.27 is closest to Magnuson's value for the Kawakawa, *Euthynnus affinis*.

Various terms are used in subsequent discussion, and these are similar to those used by Magnuson (1970, 1973). These terms are presented in Table 6.

The average weight, body and fin dimensions and various ratios, taken from fish at the end of the swimming speed experiments, are presented in Table 7. Relative positions of the centre of gravity, of the pectoral and caudal fin, and fish density also are required for lift calculations. These measurements are presented in Table 8.

D) Drag

i) Frictional drag. The body, pectoral fins, caudal fins, ventral fins (second dorsal and anal), and the finlets are all subject to frictional drag during constant swimming. The five dorsal and five anal finlets are not considered in the following drag analysis because their area is only 8% of that of the pectorals. Furthermore, they appear to function primarily for drag reduction by controlling cross flow and preventing boundary layer separation (Walters 1962). Magnuson (1970) suggests that the finlets of *Euthynnus affinis* allow some cross flow over the keel. Nevertheless, their drag should be less than their drag reduction and their exclusion from the subsequent analysis would not significantly change the drag estimate.

The drag coefficient, C_F , at Reynolds numbers where laminar flow prevails would be increased by surface roughness. However, mackerel have small ctenoid scales embedded in a mucous covering, creating a smooth surface; thus the drag coefficient should be close to the theoretical minimum given by equation 3.

The frictional drag was calculated for each of the four components, the body, the caudal fin, the pectoral fins, and the ventral fins for the 32 cm fish used in the swimming speed experiments swimming at the minimum speed of 27 cm/sec. The length, Reynolds number, drag coefficient, surface area, and drag for each component are presented in Table 9.

ii) Pressure drag. Pressure drag on a streamlined body with a thickness ratio comparable to that of a mackerel body (.12) would be about 25% of the frictional drag (Hoerner, 1965; Daily and Harleman, 1966). While the fins are similar to flat plates and data from the above sources suggest the pressure drag on them should be almost zero, Brown and Muller (1970) suggest that the drag on the fins of *Euthynnus pelamis* might be as high as 50% of the total frictional form drag. However, this value is probably too high in light of the numerous anatomical adaptations of scombroids, which appear to prevent boundary layer separation (Walters 1962), the cause of pressure drag. Some of the adaptations which maintain the boundary layer are present in *Scomber scombrus*, notably the ventral finlets allowing cross flow over the keel, the high aspect ratio caudal fin and the fleshy keel at the caudal root. The scales at the base of the second dorsal fin also appear to be arranged in flow channels, which should further lower the form drag of this fin. In addition, the camber of the pectoral fins can be varied and could be maintained at an optimum angle of attack, thus minimizing the most significant component of pressure drag, that due to non-ideal angle of

attack (N.J. Jeffrey, Pers. Comm.). I have used a compromise value of 25% of the frictional drag for all the fins in the subsequent analysis of pressure drag but this value may still be too high.

iii) Induced Drag. Induced drag or drag due to lift is present for each lifting surface which includes the body, pectoral, and caudal fins. The induced drag coefficient (C_I) for the pectoral and caudal fins can be calculated from equation 4 using the lift coefficients calculated in the next section on lift. The calculated C_I is substituted into equation 1 to determine the induced drag. All these values are presented in Table 10. The C_I for the pectoral fins of 0.08 agrees with test data (Hoerner, 1965), although one might expect a cambered surface to have a lower drag coefficient. The C_I for the caudal fin is somewhat less than the C_I for the pectoral fins.

The induced drag of a mackerel body can be obtained using coefficients given by Hoerner. This induced drag of a streamlined body is only 25% of the pressure drag.

iv) Total Drag. The three types of drag for each body component and their percentage composition of the total are presented in Table 11. The total drag on a 32 cm fish swimming at 27 cm/sec in sea water with a density of 1.0215 g/cc is 2430 dynes. Induced drag comprises about 50% while frictional drag accounts for a further 40%. Form drag comprises only 10% and as discussed earlier, but even this may be an overestimation. Of the individual components subject to

drag, the pectorals have the highest drag as a result of their important function in creating lift. The body and caudal fin contribute 28% and 24%, respectively, to the total drag, while the ventral fins contribute only 3% to the drag.

E) Lift

The lift required to maintain hydrostatic equilibrium for a 32 cm fish swimming at 27 cm/sec in seawater of a density of 1.0215 g/cc can be calculated from equation 5 using the relevant parameters from Table 2. The required lift is 18,317 dynes.

○ This lift is supplied by the pectoral fins, the body, and the caudal fin. Magnuson (1970) showed that the caudal peduncle of *Euthynnus affinis* supplied about 20% of the total lift at slow speeds. However, the caudal peduncle of *Scomber scombrus* lacks the keel present in *Euthynnus affinis*, and the cylindrical peduncle of mackerel would not produce significant lift. I have omitted the peduncle as a source of lift in the subsequent analysis.

While the pectoral fins of mackerel are clearly lifting surfaces (Figure 1), the body may also produce lift. Strongly cambered bodies of sturgeon and shark produce lift at zero angle of attack. The body of *Scomber scombrus* is not cambered but is similar to a body of an airship hull, which produces practically no lift at zero angle of attack (Hoerner, 1965). However, mackerel swim with a positive angle of attack (Muir and Newcombe, MS 1973), which can produce lift. The average

angle of attack for 32 cm mackerel determined at basal swimming speed by Muir and Newcombe was 9° . I have used an angle of attack of 10° for the subsequent analysis of lift.

Magnuson did not consider the caudal fin of *Euthynnus affinis* as a lifting surface because the fin did not tilt from the vertical. Aleev (1963), on the basis of Figure 1 from Gray (1933), suggested that the caudal fin of *Scomber scombrus* did tilt toward the horizontal. The caudal fin of fish in the experimental tanks clearly showed this phenomena (Figure 2). The caudal fin of *Scomber scombrus* does act as a hydrofoil and produces lift, and I have considered it in this analysis.

A fourth source of lift may be present. That is, if the caudal fin has a positive angle of attack, the horizontal directed thrust or propulsion has a vertical component. As this source of lift is applied in the caudal region, I have not analyzed it separately but have considered it a part of the lift from the caudal fin.

In order to evaluate each of the three sources of lift, it was necessary to evaluate one of the components in detail. The lift coefficient for the body (C_{LB}) at a 10° angle of attack was evaluated first, using the equations and parameters given in Appendix I.

The body lift coefficient of .137 was then substituted into equation 6. The lift supplied by the body was calculated as 2673.5 dynes. Knowing body lift, simultaneous equations 8 and 9 can be solved for one of the other lift components

and the other obtained by substitution. Parameters used in the solution of these equations are given in Table 12. The distance of each center of lift from the center of gravity (l_b , l_p , and l_c) was determined from Table 8 assuming that the center of lift for each component is similar to that for airfoils, that is, 25% from the leading edge (Perkins and Hage, 1949).

Once each lift component was determined, the lift coefficient for the pectorals (C_{Lfe}) and for the caudal fin (C_{Lc}) could be obtained from equation 7.

The lift (L) the lift coefficient (C_L) the surface loading, and the percentage of total lift for each component are summarized in Table 12.

As might be expected, the pectoral fins are the most effective and important lifting surfaces. They supplied 62% of the total lift and had the highest lift coefficient of 1.1. The caudal fin supplied 24% of the required lift with a surface loading of about half of the pectorals and C_{Lc} of 0.7. The body at a 10° angle of attack produced only 14% of the total lift, even with a potential lifting area twice that of the pectorals.

Similar calculations for lift were made for the small fish (19 cm). The lift required to maintain hydrostatic equilibrium for these fish is 1649.0 dynes. If the pectoral fins of the small fish supply the same percentage of lift (62%) as they do for the larger fish, the lift generated by the pectorals is 1022 dynes. Using parameters from Table 7,

C_{Lfe} can be calculated from equation 7 and is 0.49. This lift coefficient is less than half of that for the larger fish. The parameters used in the calculations of lift and C_{Lfe} for the small fish are presented in Table 13.

DISCUSSION

A) Drag

Hydrodynamic drag has been determined for numerous fishes ranging from sharks to scombroids and for marine mammals (see Webb, 1975). These earlier studies of maximum swimming speeds combined with an analysis of power output versus speed suggested "Gray's paradox", that hydrodynamic theory holds for small fish and large cetaceans but not for barracuda or intermediate sized cetaceans (Gray, 1936; Gero, 1952; Bainbridge, 1960). One had to either hypothesize that these animals had a much higher (7X) energy output per muscle mass than other animals or they were able to maintain laminar flow over their bodies at speeds where rigid bodies showed turbulent flow.

Subsequent work has suggested various possible modifications in the earlier calculations. An increased efficiency of the propulsion system would reduce the apparent energy requirement, and it has become increasingly clear that there are various anatomical, behavioral and physiological drag reduction mechanisms which are important among both fishes and cetaceans (Webb, 1975). For example, elaborate mechanisms for reducing friction are present. The barracuda has friction reducing slimes (Rosen and Cornford, 1971); while the castor oil fish (*Ruvettus pretiosus*) has elaborate subdermal spaces which operate with ctenoid scales as vortex generators, thus maintaining the boundary layer and reducing friction (Bone, 1972).

The control of boundary layer separation and subsequent drag reduction has been crucial in the evolution of fast moving fishes. The large scombroids have numerous anatomical adaptations for boundary layer control (Aleev, 1963; Walters, 1962). These adaptations include body shape, which encourages laminar flow over most of the body at Reynolds numbers of 2×10^6 , roughened body surface, and caudal peduncle finlets. These adaptations do not function at the high R of the fishes' maximum speeds, but Magnuson (1973) suggests that the critical factor in scombroid evolution has been adaptations to the minimum swimming speeds where flow would be laminar. *Scomber scombrus*, which operates at lower R than the large scombroids, also has many of the above drag reduction mechanisms. In addition, Ovcharov (1970) has shown that the gill filaments and gill rakers of *Scomber scombrus* are arranged as baffleplates, which ensure that exit water from the operculum is laminar, thus preserving the boundary layer. In fact, one gets the impression that scombroids and other fast swimming fishes possess adaptations which make them more efficient than comparable rigid bodies. The phenomenon of dynamic overshoot, discussed later, is an example of this in mackerel.

Previous measurements of drag values for *Scomber scombrus* have been determined by freefall measurements (Richardson, 1936) and by towing measurements (Webb after Bone 1975). Richardson's values are much higher (2.5 orders of magnitude) than the theoretical predictions. However, Webb suggests his measure-

ments were in error as the fish may not have reached the terminal velocity. The drag measurements by Bone for mackerel are close to the theoretical, predictions and are very close to my calculations. For a 35 cm mackerel swimming at 30 cm, Bone found a drag of 900 dynes and a C_D of .0043, compared to a drag of 970 dynes for the frictional and pressure drag on the body, caudal, and ventral fins and a C_D for the body of .0046 for my results. However, if from my more detailed analysis of results, the pectoral fins and the induced drag are included, the estimate of total drag (Table 11) is more than double that derived by Bone.

Bainbridge (1960, 1962), after an analysis of maximum swimming speeds of neutrally buoyant fishes, developed a general relationship for total drag. The total drag was 1.2 times that of the frictional drag on the body, i.e. $1.2 C_f$ (Bainbridge, 1962). This agreed with a coefficient derived by Gero (1952) of $1.22 C_f$. Drag on the negatively buoyant scombroids is much higher. In addition to the present study, Brown and Muir (1970) calculated the drag components for a 44 cm skipjack tuna, *Euthynnus (Katsuwonus) pelamis*. They included drag due to lift and also gill drag, since skipjack use ram ventilation to obtain respiration gases. Gill drag accounted for only 7% of the total swimming drag for skipjack tuna, and I have not included it in the subsequent discussion. A comparison of the results is presented in Table 14 along with the inclusive drag coefficient, and establishes that the inclusive drag coefficient for these scombroids is much

higher than for the fish Bainbridge studied. The drag associated with lift (that is, the induced drag plus the frictional and pressure drag for the pectoral fins which generate lift) may be removed from the total (Table 14). The total drag not associated with lift is still greater than the $1.2 C_f$ (body) suggested by Bainbridge due to the frictional and induced drag from the caudal and ventral fins.

A high proportion of drag is associated with lift, 35% for *Euthynnus pelamis* and 60% for *Scomber scombrus*. There is thus a double penalty for negatively buoyant fishes; the drag due to the generation of lift and, secondly, the associated increase in drag while swimming fast enough to generate the lift necessary to maintain hydrostatic equilibrium. The important evolutionary and energetic implications of this double cost are considered briefly in a later section.

B) Cost of Swimming

Of prime interest in this analysis is the behaviour of the drag components as speed increases. Provided the angle of attack remains constant and laminar flow prevails, the frictional drag on the body and ventral fins is proportional to $U^{1.5}$; while the pressure and induced drag is proportional to U^2 (Alexander, 1967). The drag on the caudal fin should follow roughly the same rule. However, as discussed later in the section on lift, the lift due to the thrust component will increase with speed, thus lowering the need for lift from the tail itself, which consequently lowers the induced drag for the caudal fin. Drag on the pectorals is less predictable. As speed increases, sweepback increases resulting in a decrease in

exposed area, span, and aspect ratio, and the center of lift moves posteriorly (Table 4 and Figure 3). All these features affect the lift and drag performance of these fins, most noticeably by lowering the lift coefficient.

In an attempt to evaluate the changes in drag with increase in speed, I will consider three cases. The first one was considered previously, i.e., where the pectorals were fully extended and swimming was at a basal speed of 27 cm/sec. The second is that in which the "wings" are swept back 56° , as shown in Figure 3, at a speed of 35 cm/sec. Information from Table 4 was used to calculate a lift coefficient for that speed. A third case is that in which all lift is supplied by the body and the pectorals are completely retracted and pressed to the body. The speed calculated by equations 9 and 12, assuming a 10° angle of attack, was 88 cm/sec for this case. The total lift for each speed is presented in Table 15.

The power, P , required to overcome the drag resistance, D_t , can be calculated by

$$P = \frac{D_t U}{nt np} \quad (11)$$

nt is the efficiency of conversion of chemical energy to mechanical work in muscle which equals 0.20 (Lehniger, 1965), and np is the efficiency of converting mechanical work in the muscles to propelling power. The constant np is assumed to be 0.85, which is higher than that of a well designed propeller (Bainbridge, 1961), but probably realistic for the efficient propulsion of a scombroid. The resulting costs are presented in Table 15, converted from ergs/sec to gcal/hr.

These three costs were fitted to an exponential equation and the equation for metabolism due to swimming (M_S), as a function of swimming speed is $M_S = 0.06U^{1.94}$. Alexander (1967) suggests the cost of swimming should be proportional to $U^{2.5}$ or U^3 , as the individual drag components are proportional to either $U^{1.5}$ or U^2 and the required power is proportional to U . Ware (Pers. Comm.) also finds cost of swimming in sockeye salmon to be proportional to $U^{2.5}$. Unfortunately it is not possible to induce mackerel to swim at different speeds under conditions where metabolism due to swimming can be determined in order to resolve this difference. However, in a negatively buoyant fish pectoral area decreases as velocity increases, thus reducing a significant component of the drag at low speeds and lowering the exponent for the cost of swimming to two.

The metabolism of an unfed mackerel of about 32 cm swimming at 35 cm/sec is 220 g cal/hr (44 mg O_2 /hr) (T. Lambert, Pers. Comm.). The hydrodynamic cost of swimming is 67.0 g cal/hr (Table 15), 30% of the total metabolism. Brown and Muir (1970) estimated that swimming accounted for 17% of the total metabolism for skipjack tuna.

C) Lift

The pectoral fins of the mackerel are its most efficient lifting surface, a conclusion in keeping with Magnuson's (1970)

conclusions for *Euthynnus affinis*. The lift coefficient (C_{Lp}) for *Scomber scombrus* was 1.1, higher than the 0.8 for *Euthynnus affinis*. The pectorals of mackerel are very efficient lifting surfaces, having a C_{Lp} comparable to that of the most efficient non-slotted airfoils (Perkins and Hage, 1949). In fact, C_{Lp} should be even higher because the area of the pectorals is an overestimate which I have taken from flattened fins, whereas the pectorals normally are cambered. While C_{Lp} is near the maximum for unslotted rigid airfoils, there are various dynamic features of the pectorals which support an estimate of the high lift coefficient. N. Jeffry (Pers. Comm.) suggests that mackerel by varying camber, sweepback, and angle of attack simultaneously could take advantage of the phenomenon of dynamic overshoot, or Katzmayer effect, thus acquiring a higher lift coefficient than that of a comparable rigid body. This Katzmayer effect has been suggested for various other fishes (see Nursall, 1962). Interference with lift can increase or decrease the lift supplied by the fins of the body. Studies on airfoils and torpedoes (Lawrence and Flax, 1954; Chen, 1963) suggest that the interference would be favourable if the lifting surface has a moderate to high aspect ratio, is located near the midpoints of the dorsal and ventral margins, and has a body diameter to span ratio between 0.2 - 0.4. All of these features are present in mackerel; thus, the body interference may contribute to the high lift coefficient of the pectoral fins.

The potential lifting area of the body is twice that of the pectorals, but the low aspect ratio and camber contributes to its inefficiency in producing lift. The scombroid body is designed more to reduce drag (Aleev, 1963; Walters, 1962) than produce lift.

The caudal fin is an efficient lifting surface supplying over 20% of the required lift at basal swimming speeds. As the caudal fin also supplies the forward thrust, it is acting as a lifting surface during only part of the tail beat cycle. Even assuming that for half of each cycle the tail is acting as a lifting hydrofoil, the lift coefficient (C_{Lc}) would be 1.4, which is higher than that produced by a cambered plate ($C_L=1.1$) at Reynolds numbers similar to those at which the fin was operating (Magnuson, 1970 after Schmitz, 1960). This high lift efficiency is unexpected in a structure which is designed primarily for propulsion (Alexander, 1967; Lighthill, 1969). However, as mentioned earlier, a fourth source of lift has been included with the caudal fin, that of the vertical component of the thrust vector when the tail region has a positive angle of attack. The expected lift from this source, L_{th} , at a swimming speed of 27 cm/sec can be calculated from equation 10, and is only 10% of the total caudal lift at an angle of attack of 10° . As speed increases, L_{th} increases and may contribute most of the lift posterior to the center of gravity at higher speeds, thus relieving the caudal fin of having to tilt to produce lift. However, at low swimming speeds the caudal fin would appear to be an extremely

efficient lifting surface.

This discussion of lift assumes that the center of buoyancy and center of gravity coincide. This may not be the case for *Scomber scombrus* as measurements of the center of buoyancy suggests it is .005 to .007 FL, posterior to the center of gravity, and may change seasonally (Magnan, 1929; Bone, after Magnuson, 1970). If the center of buoyancy is posterior to the center of gravity, the buoyancy force, which is much larger than the other forces, would lower the lift required from the caudal region considerably. This would explain the apparently high lifting efficiency of the caudal fin.

The pectoral lift coefficient, C_{Lfe} , of .49 for the 19 cm fish was less than half of the C_{Lfe} for the 32 cm fish. If the pectoral fins of the smaller fish are less efficient than those of the larger fish, they would supply less lift than the 62% I have assumed and C_{Lfe} would be higher. An alternative hypothesis is that the smaller fish are required to swim faster than the basal swimming speed to obtain sufficient food to support their rapid growth. Thus, the limit on lower swimming speed would not be based on the efficiency of the lifting surfaces but on considerations of food search. D. Ware (Pers. Comm.) offers some support for this hypothesis as he suggests that optimal cruising speed is a function of body length and decreases with increased length.

D) Seasonal Changes in Basal Swimming Speed

The preceding discussion has supported the conclusion of Magnuson (1970, 1973) that minimum swimming speeds of

constantly swimming scombroids are consistent with hydrodynamic considerations. Magnuson obtained an equation to predict minimum swimming speed (U_m)

$$U_m = \left(\frac{2L_t P}{p C_{lfe} \bar{A}_{ft}} \right)^{1/2} \quad (12)$$

When P is the percentage of total lift (L_t) supplied by the pectoral fins, and \bar{A}_{ft} is the total area of the pectoral lifting surface including the area of the body at the level of the pectorals.

The minimum swimming speed can be expected to change seasonally as growth and changes in fish density, and sea water density occur. A possible seasonal cycle of temperature, salinity, length, and fat content with the appropriate fish weight, fish and seawater density and pectoral lifting area was assembled for each month for three ages (Table 16).

In setting up the appropriate temperature and salinity regime, I have used a yearly migration pattern for the northern population as outlined by Sette (1950) and MacKay (1976b). Data on temperature and salinity are from Lauzier and Hull (MS 1969) and Hachey (1961). Seawater densities were calculated from Knudsen's hydrographic tables.

Fish lengths were based on growth data from MacKay (1976b), assuming a six month growth season. Fish weights were calculated from the body length-somatic weight regression (Table 2) with the addition of gonad weights also calculated from a

body length-gonad weight regression after MacKay. The gonads were assumed to start developing in March, with first maturity occurring at a length of 30 cm.

Fish density varies seasonally with fat content. A detailed fat cycle for the northern population is not available, but MacKay summarizes the available data which was used to assemble the fat cycle presented in Table 16. The maximum fat content appears to be lower for smaller fish than larger fish (*op.cit.*). I have, however, assumed the same fat cycle for the three sizes of fish used in the minimum swimming speed calculations. Fat density for mackerel appears to be lower than for other Scombroids (*op.cit.*). I use a value of 0.91 g/cc for mackerel fat in the subsequent calculation.

Fish density can be approximated by modifications of an equation proposed by Horak (1966). Magnuson (1970) gives an equation that approximates fish density, D_f .

$$D_f = 1.100 + \left(\frac{1.100 - D_{ff}}{(0 + 100)} \right) (P) \quad (13)$$

D_{ff} is fat density and P is the percentage of fat

Using $D_{ff} = .91$, the equation simplifies to:

$$D_f = 1.100 - 0.0019P \quad (14)$$

I have used this equation in the following calculations of fish density and swimming speed. However, D. Irwin (Pers. Comm.) points out that the exact equation can be derived from:

$$D_f = \frac{M_f}{\frac{M_f}{.91} \frac{P}{100} + \frac{M_f (1-P)}{1.10 \cdot 100}} \quad (15)$$

where M_f is the total mass of the fish. This expression can be simplified to:

$$D_f = 1.10 \left(\frac{.1}{1 + \frac{0.19}{0.19} \frac{P}{100}} \right) \quad (16)$$

and a linear approximation can be obtained using the binomial theorem.

$$D_f = 1.1000 - 0.0023 P \quad (17)$$

However, the use of equation 14 in the calculation of fish density produces an error of less than 1%.

The pectoral lifting area was calculated from the regression equation for pectoral area and fuselage area (Table 5). Preliminary calculations had suggested that the pectorals supplied 70% of the required lift (P_{LT}) and C_{Lfe} was 1.2, and these were used in the subsequent calculations. The use of the more precise final values, $P_{LT} = 62\%$ and $C_{Lfe} = 1.1$, would result in a difference of only 2% in the predicted minimum swimming speeds.

The predicted minimum swimming speeds in cm/sec and L/sec are shown in Figure 3. It is apparent that there is seasonal variation in both absolute and relative

swimming speeds for the three age groups. The lowest speeds occur from October to March, at a time when feeding appears to be minimal (Sette, 1950) and when energy conservation would be most important. The highest minimum speeds occur in the spring when feeding is very intensive to supply the material for the production of gonadal tissue. This maximum also coincides with the spring migration during which the fish move from the continental shelf region into the Gulf of St. Lawrence. Predicted minimum swimming speeds decline through the summer, remaining fairly constant from September to December, and gradually increase from January to May.

The predicted speeds for the Age I fish are probably underestimated. As mentioned previously, the fat content for these small fish is lower than that used in the calculations. Furthermore, the lower C_{Life} for these small fish would also result in a higher actual speed.

These variations in minimum swimming speed are the result of simultaneous changes in at least six variables: length, weight, percent fat, fat density, temperature, and salinity. The effect of these variables was tested by assuming an initial state (Table 17) and allowing each variable to vary within the ranges indicated. The effect of changing only one variable at a time on minimum speed is given in Figure 4. Temperature and salinity and fat density have little effect on swimming speed; while a change in the percentage of fat has the greatest effect.

Fat is the most important variable in determining seasonal variation in the minimum swimming speed. During the overwintering period when food is scarce, energy conservation is important and a lower minimum swimming speed would mean a saving of energy. Assuming the energetic cost of swimming varies as U^2 (discussed earlier), then the difference between 15 and 20% fat would result in a difference in energy consumption of about 20%. This results in a positive feedback system, where a fish with lower fat draws on its fat reserves faster than that of a fatter fish. Therefore, the acquisition of high fall fat content would be crucial for overwintering success, and the fat cycle would be expected to be subject to high selection pressure. An example of adaptation which would be useful for mackerel is the seasonal variation in fat density shown by herring (Ackman and Eaton, 1970) in which the lowest fat density occurs during late winter when fat levels are the lowest.

The predicted minimum swimming speed also was calculated for a range of fork lengths, assuming the initial state of the other variables as given in Table 16. I have assumed also that the lift coefficient for the pectorals and the percentage of lift supplied by the pectorals was constant over the size range. The range of fork lengths tested except for the largest (45 cm) were within the range of the values used to calculate the regressions.

The minimum swimming speed (cm/sec) increased with

increase in length while the speed relative to body lengths decreased (Figure 5a and b). This increase in absolute speed but decrease in relative speed has been observed and predicted for minimum speeds of other scombroids (Magnuson, 1970, 1973) and for maximum endurance speeds of goldfish, *Crassius auratus*, and trout, *Salmo gairdneri*, (Bainbridge, 1960, 1962) and also for sustained swimming speed of sockeye salmon, *Oncorhynchus nerka* (Brett, 1965).

Using equation 18 to relate speed to length,

$$U_m = aL^b \quad (18)$$

constants a and b were calculated from the appropriate regression. The equation for minimum swimming speed for mackerel was $U_m = 5.44 L^{0.47}$. The exponent was similar to the 0.5 for minimum speed for *Euthynnus affinis* (Magnuson, 1970) and for sustained swimming in sockeye salmon, *Oncorhynchus nerka* (Brett, 1965).

E) Evolution and Adaptive Implications

The minimum swimming speeds of mackerel were about 1 L/sec, agreeing with the predicted optimum cruising speed for fishes determined by Weihs, (1973a). This speed appears to be adequate for food search and migration in many fishes (Anon. 1973, *op. cit.*).

This minimum speed for *Scomber scombrus* is lower than for seven of the eight scombroids examined by Magnuson (Table 18).

In fact, *Acanthocybium solanderi*, the only scombroid swimming slower than *Scomber scombrus*, has a large gas bladder.

Walters (1962) and Zharov (1967) have pointed out the striking anatomical and physiological adaptations of scombroids to locomotion and hydrodynamic efficiency. Magnuson (1970, 1973) further suggests that these adaptations have been designed for continuous slow swimming, rather than burst speeds. The results of this study indicate that *Scomber scombrus* has adaptations which allow it to swim slower than other scombroids of a comparable size.

Table 19 compares the mass, density, pectoral area, and pectoral area to mass ratios of *Scomber scombrus* to the eight scombroids studied by Magnuson (1973), all for 30 cm fish. *Scomber scombrus* had the lowest mass, the second lowest density, and the third highest pectoral area. The pectoral area to mass ratio was the highest, the same as for *Thunnus obesus*. Other features such as low fat density, flexing of the caudal fin to act as a hydrofoil, position of the center of buoyancy, and a very efficient pectoral lifting surface contribute to this low swimming speed. Furthermore, the seasonal fat cycle is an important component of adaptation for low swimming speeds. *Scomber scombrus* occurs further north than other scombroids and is the only scombroid to face the problem of overwintering in a non-feeding state. These adaptations for a low minimum speed are essential for survival during this period.

Negative buoyancy imposes an extra cost on a continuously swimming fish. This extra cost is the cost of swimming fast enough to remain in hydrostatic equilibrium. This is greater than the cost to a neutrally buoyant fish swimming at the same speed because of the extra drag associated with the generation of lift. This is, in effect, a double penalty for negative buoyancy. This cost must be matched by an increased ability to obtain energy. This raises a paradox of how negatively buoyant fish can compete with neutrally buoyant fishes.

Weih's (1973b) has suggested that negatively buoyant fishes are able to exploit a larger sea space for feeding and predator avoidance than neutrally buoyant fishes. The negative buoyancy allows fish to undergo rapid changes in depth; while constant swimming allows for an increased range. However, this explanation does not hold for all cases. Yuen (1970) determined the swimming behavior of two small (40 - 50 cm) skipjack tuna, using ultrasonic transmitters. During daylight, the fish remained in the vicinity of a bank, apparently searching for food and feeding. Within a couple of hours of sunset, they left the bank swimming at the surface and travelling from 25 to 106 km away from the bank, normally returning to the bank by sunrise. One fish was followed for six days, and returned to the bank on five of those mornings.

This navigational and time sensing ability indicates a non-random search pattern. The nightly forays away from the

bank imposed by the need for constant swimming could be interpreted as an energy wastage. However, the initial discovery of these feeding banks may have been the result of a wide ranging search pattern imposed by the negative buoyancy.

There must be a large energetic advantage for the Atlantic mackerel due to constant swimming. In comparison to mackerel, the Atlantic herring migrate much less and spend long periods during winter virtually motionless. (Winters, 1975). A recent comment in Nature (Anon., 1973) suggests that on the basis of hydromechanics a migratory fish should grow less than a non-migratory fish. Mackerel are not only more migratory than herring, they are also continuous swimmers. Yet, mackerel are more abundant in the Gulf of St. Lawrence than herring and they grow twice as fast (MacKay, 1975b).

Constant swimming in mackerel would appear to be an aid in food search as it forces the fish to cover a wide grazing area. In fact, their minimum swimming speed of 1 L/sec is the same as optimal speeds required for food search and migration in other fishes (Ware, 1975; Weihs, 1973a). I explore optimal swimming speeds in mackerel further in a theoretical model of feeding, where I show that search speed is an important component in feeding on prey aggregated into patches (MacKay, 1976c). Furthermore,

filter feeding behaviour (Muir and Newcombe, MS 1973; MacKay, 1976c) is an adaptation for exploiting patches rather than individual particles. Thus, mackerel are searching for and feeding on patches in the same way that herring or trout are searching for and feeding on individual particles. The high productivity of mackerel depends on their ability to efficiently exploit this higher level of spatial organization (patches) better than their neutrally buoyant competitors like herring.

The schooling behaviour of mackerel poses a further energy paradox. The preceding discussion of drag considered inertial and viscous forces as the only forces acting on moving bodies such as swimming mackerel. A third force, that of gravity, comes into play when an object is moving close to the air-water interface (Webb, 1975). The increased drag can be quite large, for example Hertel (after Webb) calculated increased drag of 5 times the frictional drag for a dolphin-shaped body when swimming 0.5 body diameters from the surface. Observations in the Gulf of St. Lawrence indicate that schooling at the surface by mackerel is a normal phenomenon during summer. The energetic gain from this behaviour may be from the increased concentration of zooplankton that are often concentrated near the surface.




TABLE 1

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Swimming speeds of captive Atlantic mackerel, *Scomber scombrus*, during non-feeding and feeding periods. (Standard errors of the measurements in parenthesis).

Date	Time	Number		Average cm/sec	SWIMMING SPEEDS		
		Fish	Circuits		Minimum L/sec	Minimum for one circuit cm/sec	Minimum L/sec
32cm fish, undisturbed							
26/10/71	18:45	6	7	27.0 ($\pm .33$)	.84	26.0	.81
8/11/71	10:45	4	6	29.5 ($\pm .75$)	.92	27.0	.84
32cm fish, disturbed - (flash photos)							
26/10/71	19:00	6	3	28.9 ($\pm .38$)	.90	28.3	.88
8/11/71	11:00	4	5	34.6 ($\pm .56$)	1.08	32.9	1.03
32cm fish, disturbed (plankton essence)							
26/10/71	19:10	6	7	32.6 (± 1.87)	1.02	28.4	.89
8/11/71	12:45	4	6	36.7 (± 1.44)	1.15	32.1	1.00
32cm fish, disturbed (plankton)							
26/10/71	19:30	6	14	47.2 (± 1.69)	1.48	41.1	1.28
8/11/71	13:00	4	10	48.8 (± 1.17)	1.53	43.0	1.34
19cm fish undisturbed							
17/1/72	14:15	4	3	21.8 (± 2.33)	1.15	18.4	.97
24/1/72	10:00	3	9	24.6 ($\pm .60$)	1.29	21.4	1.13
24/1/72	19:45	3	3	20.9 ($\pm .92$)	1.10	19.1	1.01
19cm fish disturbed (euphausiids)							
24/11/72	11:40	3	3	31.6 ($\pm .58$)	1.66	30.5	1.61

TABLE 2

Swimming speeds of captive Atlantic mackerel, *Scomber scombrus*, during morning and afternoon. (**difference highly significant, number of trials in parenthesis). Data from table 1.

SWIMMING SPEEDS (CM/sec)

	32 cm fish		19 cm
	Undisturbed	Disturbed Flash	Undisturbed
Morning	29.5(1)	34.6** (1)	24.6** (1)
Afternoon	27.0(1)	28.9** (1)	21.8** (2)

TABLE 3

Effect of plankton concentration and plankton odour on swimming speed of 32 cm Atlantic mackerel, *Scomber scombrus*. (After Muir and Newcombe, MS 1973).

Plankton conc. (mg/l)	Swimming speed	
	cm/sec	BL/sec
odour only	47	1.47
.4	35	1.09
.8	40	1.25
1.5	48	1.50
3	41	1.28
6	48	1.50
12	50	1.56
98	66	2.06

TABLE 4

Comparison of the effect of sweepback on the pectoral fins of continuously swimming mackerel. Measurements determined from Figure 1 and 2.

Speed	27 cm/sec	35 sc/sec
Sweepback	0°	56°
Aspect ratio	4.85	2.76
Total Utility Surface (relative to head area)	1.11	1.0
Exposed area (relative to head area)	.64	.51
Total area: exposed area	1.74	1.95
Chord at fuselage	2.6	3.1
Area fuselage	10.05	12.2

TABLE 5

Regression equations relating various parameters of fish size on fork length (cm) for the northern population of the Atlantic mackerel, *Scomber scombrus*. Sample taken from commercial and experimental catches during 1970 - 1972.

Component	Equation	Correlation Coefficient
Weight (g)	$\log W = \log .0059 + 3.154 \log FL$.993
Pectoral fin area (2)	$\log A_{pe} = 2(\log .0023 + 2.270 \log FL)$.977
Fuselage area at the level of the pectoral fins	$\log A_{fu} = \log .0049 + 2.207 \log FL$.970
Caudal fin area	$\log A_c = \log .0073 + 2.196 \log FL$.991

TABLE 6

Definition of some terms used in calculations of drag and lift.

M_F	= fish mass (g)
D_F	= density of fish
ρ	= density of water (g/cc)
FL	= forklength (cm)
SL	= standard length (cm)
A	= area (cm ²)
AR	= aspect ratio
S	= span (cm)
MC	= mean chord (cm)
TR	= thickness ratio
Λ	= sweepback angle (degrees)

The following subscripts are used with some of the above terms:

b	= body
fe	= pectoral fins (2)
fu	= fuselage at the level of the pectorals
ft	= total lifting surface of the hydrofoils
c	= caudal fin
t	= total

TABLE 7

Various measurements, dimensions and ratios used in calculations of drag and lift for fish used in the swimming speed experiment. Methods of measurement or calculations and description of terms are described in the text. (Standard errors in parenthesis).

Date	8/11/71	24/1/72
p	1.0217	1.0215
Temp. (C)	17	17
Number of fish	3	3
Mf (g)	316.8 (± 9.4)	53.0 (± 5.8)
Df (g/cc)	1.0508 ($\pm .002$)	1.0552 ($\pm .002$)
FL (cm)	31.8 (± 1.2)	18.6 (± 2.9)
SL (cm)	31.0 (± 1.7)	18.2 (± 2.9)
A_b (cm ²)	296.6	-
A_{fe} (cm ²)	17.8 ($\pm .80$)	6.5 ($\pm .34$)
A_{fu} (cm ²)	10.1 ($\pm .59$)	2.80 ($\pm .23$)
A_{ft} (cm ²)	27.9 (± 1.21)	9.3 ($\pm .56$)
A_c (cm ²)	17.0 ($\pm .70$)	-
S_{ft} (cm)	10.8 ($\pm .21$)	-
S_c (cm)	7.1 ($\pm .10$)	-
MC _p (cm)	2.1 ($\pm .05$)	-
MC _c (cm)	2.4 ($\pm .03$)	-
AR _p	5.1 ⁰	-
AR _c	3.0 ⁰	-
TR _b	.11	-
TR _{fe}	.03	-
TR _c	.04	-
Λ_c	57.3 ⁰ (± 1.2)	-

TABLE 8

Relative positions of origin of caudal and pectoral fins, center of gravity and the densities of two size groups of Atlantic mackerel, *Scomber scombrus*, captured in August, 1972. (Standard error in parenthesis).

Fork length (cm)	24.3 (± 5.55)	31.1 (± 8.28)
Number	4	6
Snout to pectoral fin	.2425	.2417
Origin (%FL)	($\pm .003$)	($\pm .002$)
Snout to center of gravity (% FL)	.399 ($\pm .01$)	.420 ($\pm .01$)
Snout to caudal fin	.922	.916
Origin (%FL)	($\pm .003$)	($\pm .003$)
Fish density, D_F	1.0615 ($\pm .001$)	1.0558 ($\pm .002$)

TABLE 9

Lengths, Reynold's number (R), frictional drag coefficient (C_f), area of wetted surface (A), and estimated frictional drags for body and fins of a 32 cm Atlantic mackerel swimming at 27cm/sec.

Component	Length (cm)	R	C_f	A (cm ²)	Drag (dynes)
Body	29.4	81,540	.0046	296.6	508
Pectoral fins	2.1 ⁽²⁾	5,793	.017	35.6 ⁽¹⁾	225
Caudal fins	2.4	6,619	.016	34.0 ⁽¹⁾	203
Ventral fins	1.5	4,138	.02	8.3 ⁽¹⁾	64

¹ these areas are based on twice the planform area to allow for both surfaces of the fins.

² this length based on the mean chord, i.e. the length in the direction of movement.

TABLE 10

Estimates of induced drag and the parameters used in the calculations for two lifting surfaces of a 32 cm Atlantic mackerel swimming at 27 cm/sec.

Component	C_L	Aspect ratio	C_D	A (cm ²)	Drag (dynes)
Pectoral	1.1	5	.08	27.9	831
Caudal	.69	3	.05	17.0	317

TABLE 11

Estimates of drag components on the body and fins of a
32 cm Atlantic mackerel, *Scomber scombrus*, swimming at
27cm/sec.

	<u>Frictional drag</u>	<u>Pressure drag</u>	<u>Induced drag</u>	<u>Total</u>	<u>% of Total</u>
Body	508	127	32	667	27.5
Pectoral fins	225	56	831	1112	45.8
Caudal fins	203	51	317	571	23.5
Ventral fins	64	16	--	80	3.4
Total	1000	250	1180	2430	
% of total	41.2	10.3	48.6		

TABLE 12

Lift, lift coefficient, surface loading, and percentage of total lift produced by the three lifting surfaces: pectoral fins, caudal fins, and body for a 32 cm captive Atlantic mackerel.

U	27
FL (cm)	31.8
ρ (g/cc)	1.02172
L_t (dynes)	18,317.4
<u>Body at 10°</u>	
l_b (cm)	5.4 (.17 FL)
L_b (dynes)	2673.5
A_b (cm ²)	52.4
CL_b	.137
% of total lift	14.6
Surface loading (dynes/cm ²)	51.0
<u>Pectorals</u>	
l_{fe} (cm)	5.1 (.16 FL)
L_{fe} (dynes)	11,281.9
A_{fe} (cm ²)	27.85
C_{Lfe}	1.09
% of total lift	61.6
Surface loading (dynes /cm ²)	405.1
<u>Caudal</u>	
l_c (cm)	16.5 (.52 FL)
L_c (dynes)	4362.1
A_c (cm ²)	17.02
C_{Lc}	.688
% of total lift	23.8
Surface loading (dynes/cm ²)	256.3

TABLE 13

Estimates of lift and the coefficient of lift for the pectoral fins and the parameters used in the calculations for 19 cm Atlantic mackerel swimming at 21 cm/sec.

Parameters		Estimates	
ρ (g/cc)	1.0217		
D_F (g/cc)	1.0552		
M_F (g)	53.0	L_t (dynes)	= 1649.0
g (cm)	980	L_{fe} (dynes)	= 1022.4
A_p (cm)	9.3	C_{Lfe}	= .49

TABLE 14 .

Comparison of total drag and drag not associated with lift for *Euthynnus pelamis* and *Scomber scombrus* to allow for comparison with an inclusive drag coefficient (given in parenthesis) proposed by Bainbridge (1962).

Species	Speed (cm/sec)	A_b (cm ²)	C_f	D (dynes)	Total Drag not associ- ated with lift (dynes)	Drag associ- ated with lift (%)
<i>Euthynnus pelamis</i>	66	890	.0025	13,730 (2.5 C_f)	8950 (1.6 C_f)	35
<i>Scomber scombrus</i>	27	297	.0046	2,430 (4.8 C_f)	969 (1.9 C_f)	60

TABLE 15

Cost of swimming at three speeds for the Atlantic
mackerel, *scomber scombrus*.

Speed (cm/sec)	27	35	88
Total drag (dynes)	2405	3747	7756
Cost (g/cal/hr)	33.0	66.7	346.8

TABLE 16

Parameters for the Atlantic Wackerel, Used To Calculate Lift and Minimum Swimming Speed In Cm/Sec and In BL/second Over a Seasonal Cycle for A) Age I, B) Age IV, and C) Age XII.

Month	A	6	7	8	9	10	11	12	1	2	3	4	5
FL (cm)		22.40	23.56	24.72	25.88	27.04	28.20	28.20	28.20	28.20	28.20	28.20	28.20
FAT %		5	8	12	18	18	18	16	14	12	8	5	5
M _F (g)		107.1	125.6	146.2	168.9	193.9	221.4	221.4	221.4	221.4	221.4	221.4	221.4
D _F (g/cc)		1.0905	1.0848	1.0772	1.0658	1.0658	1.0658	1.0696	1.0734	1.0772	1.0848	1.0905	1.0905
Temp (°C)		10	15	17	15	10	9	7	7	7	7	7	8
Sal. (o/oo)		31	28	27	28	29	31	34	34	34	34	34	31
p (g/cc)		1.0238	1.0205	1.0193	1.0205	1.0223	1.0240	1.0266	1.0266	1.0266	1.0266	1.0266	1.0241
A _{fe} (cm ²)		12.02	13.45	14.97	16.57	18.27	20.05	20.05	20.05	20.05	20.05	20.05	20.05
L (dynes)		6418.0	7292.1	7700.0	7030.5	7762.9	8512.5	8715.6	9452.9	10185.1	11664.0	12707.4	13204.9
U (cm/sec)		24.66	24.89	24.27	22.02	22.02	21.99	22.22	23.15	24.02	25.68	26.84	27.39
U (BL/Sec)		1.1	1.1	1.0	0.9	0.8	0.8	0.8	0.8	0.9	0.9	1.0	1.0
Month	B	6	7	8	9	10	11	12	1	2	3	4	5
FL (cm)		30.80	31.34	31.88	32.42	32.96	33.50	33.50	33.50	33.50	33.50	33.50	33.50
FAT %		5	8	12	18	18	18	16	14	12	8	5	5
M _F (g)		307.8	308.9	326.0	343.8	362.2	381.2	381.2	381.2	381.2	381.2	396.0	410.9
D _F (g/cc)		1.0905	1.0848	1.0772	1.0658	1.0658	1.0658	1.0696	1.0734	1.0772	1.0848	1.0905	1.0905
Temp (°C)		10	15	17	15	10	9	7	7	7	7	7	8
Sal. (o/oo)		31	28	27	28	29	31	34	34	34	34	34	31
p (g/cc)		1.0238	1.0205	1.0193	1.0205	1.0223	1.0240	1.0266	1.0266	1.0266	1.0266	1.0266	1.0241
A _{fu} (cm ²)		24.39	25.35	26.33	27.33	28.35	29.40	29.40	29.40	29.40	29.40	29.40	29.40
L (dynes)		18445.2	17936.3	17176.4	14309.3	14495.3	14654.8	15004.4	16273.7	17534.2	20028.5	22727.0	24501.9
U (cm/sec)		29.36	28.44	27.32	24.46	24.15	23.83	24.08	25.08	26.04	27.83	29.64	30.81
U (BL/Sec)		1.0	0.9	0.9	0.8	0.7	0.7	0.7	0.7	0.8	0.8	0.9	0.9
Month	C	6	7	8	9	10	11	12	1	2	3	4	5
FL (cm)		38.10	38.20	38.30	38.40	38.50	38.60	38.60	38.60	38.60	38.60	38.60	38.60
FAT %		5	8	12	18	18	18	16	14	12	8	5	5
M _F (g)		646.1	576.8	581.5	586.3	591.2	596.0	596.0	596.0	596.0	596.0	627.3	658.4
D _F (g/cc)		1.0905	1.0848	1.0772	1.0658	1.0658	1.0658	1.0609	1.0734	1.0772	1.0848	1.0905	1.0905
Temp (°C)		10	15	17	15	10	9	7	7	7	7	7	8
Sal. (o/oo)		31	28	27	28	29	31	34	34	34	34	34	31
p (g/cc)		1.0238	1.0205	1.0193	1.0205	1.0223	1.0240	1.0266	1.0266	1.0266	1.0266	1.0266	1.0241
A _{fe} (cm ²)		39.12	39.35	39.58	39.81	40.04	40.27	40.27	40.27	40.27	40.27	40.27	40.27
L (dynes)		38714.8	33487.4	30638.0	24406.8	23662.0	22913.8	23460.4	25445.1	27415.9	31316.0	35997.8	69269.6
U (cm/sec)		33.58	31.19	29.77	26.47	25.97	25.46	25.73	26.80	27.81	29.73	31.87	33.33
U (BL/Sec)		0.9	0.8	0.8	0.7	0.7	0.7	0.7	0.7	0.7	0.8	0.8	0.9

TABLE 17

Initial state of variables important in determining the basal swimming speed of *Scomber scombrus* and the range over which each is varied.

	Initial state	Range
Temperature ($^{\circ}\text{C}$)	7	7 - 20
Salinity (o/oo)	34	26 - 34
Fat (%)	8	5 - 20
Density, fat (g/cc)	.91	.89 - .96
Fork length (cm)	30	15 - 45

TABLE 18

Swimming speeds of various sizes of nine scombroids, either with a gas bladder present (P) or absent (A).^a Speeds for *S. scombrus* are from this study. All other speeds after Magnuson (1973).

Species	Size cm	Speed L/sec		Gas Bladder
		mean not fed	minimum observed	
<i>Acanthocybium solanderi</i>	Adult	.33	.12	P
<i>Auxis rochei</i>	31	2.19	1.80	A
<i>Euthynnus affinis</i>	36	2.11	1.97	A
<i>Euthynnus pelamis</i>	38	1.55	1.14	A
	39	2.17	1.66	
	48	1.49	1.35	
<i>Sarda chilensis</i>	57	1.54	.89	A
<i>Scomber scombrus</i>	19	1.15	.97	A
	32	.84	.81	
<i>Scomber japonicus</i>	25	1.20		P
<i>Thunnus albacares</i>	35	1.31	1.17	P
<i>Thunnus obesus</i>	36	1.31	1.20	P
	55	1.08	.98	

TABLE 19

Comparison of mass, density, pectoral area, and ratio of pectoral area to mass for nine Scombroids based on 30cm fish. Data on *Scomber scombrus* from this paper, all others from Magnusson, (1973).

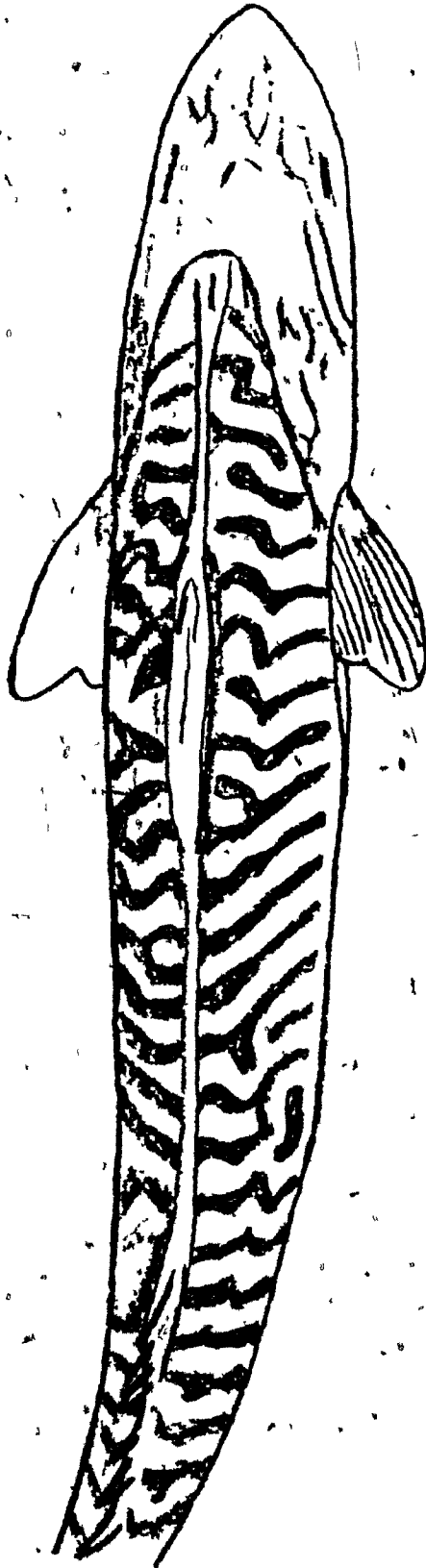
Species	Mass (g)	Density (g/cc)	Pectoral Area (Cm ²)	Pectoral area: mass
<i>Scomber scombrus</i>	269.2	1.056	23.0	.085
<i>Scomber japonicus</i>	348.89	1.054	16.2	.046
<i>Acantho- cybium solandieri</i>	-	-	12.5	.036
<i>Sarda chiliensis</i>	405.3	1.075	14.6	.038
<i>Auxis rochei</i>	445.5	1.086	16.8	.044
<i>Euthynnus affinis</i>	469.4	1.087	20.9	.034
<i>Euthynnus pelamis</i>	450.1	1.090	15.2	.064
<i>Thunnus albacares</i>	551.8	1.086	35.2	.077
<i>Thunnus obesus</i>	478.6	1.066	37.0	.085

CAPTIONS FOR FIGURES

- Figure 1: Photograph of swimming Atlantic mackerel, *Scomber scombrus*, showing pectoral fins fully extended and the caudal fin tilted to the horizontal.
- Figure 2: Tracing of photographs of a swimming Atlantic mackerel, *Scomber scombrus*, (A) with the pectoral fins swept back 56° and (B) with the fins fully extended.
- Figure 3: Seasonal variation in minimum swimming speed, cm/sec and length (L)/sec for three ages of the northern population of the Atlantic mackerel, *Scomber scombrus*. Variables used in the calculations are given in Table 16.
- Figure 4: Changes in minimum swimming speed of the Atlantic mackerel, *Scomber scombrus*, with changes in (A) % fat, (B) temperature, (C) fat density, and (D) salinity.
- Figure 5: Changes in minimum swimming speed with increases in length in L/sec (A) and cm/sec (B) for Atlantic mackerel, *Scomber scombrus*.

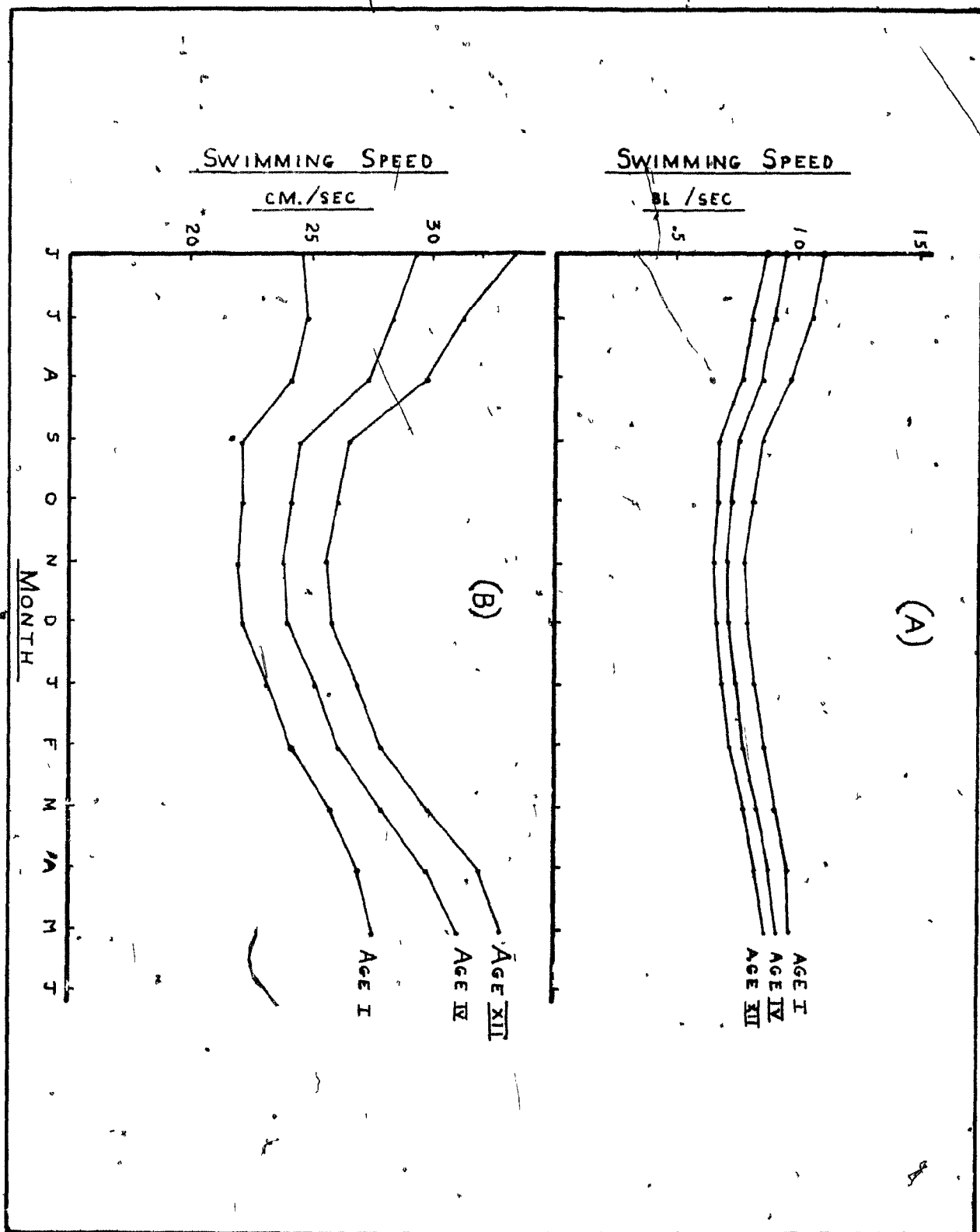


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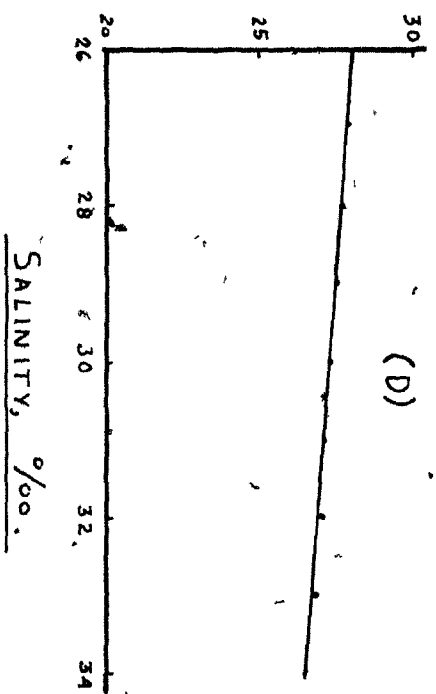
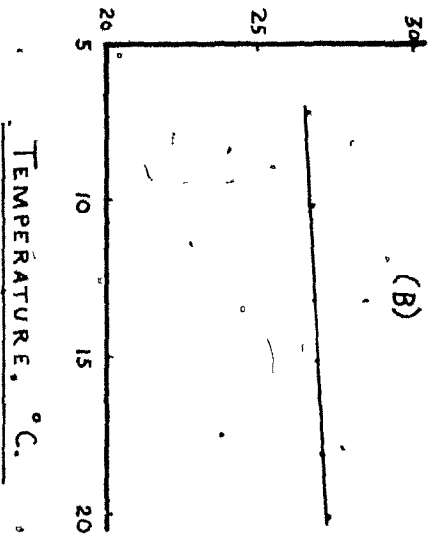
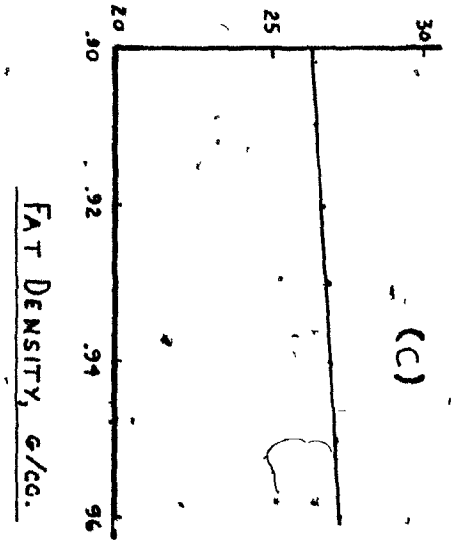
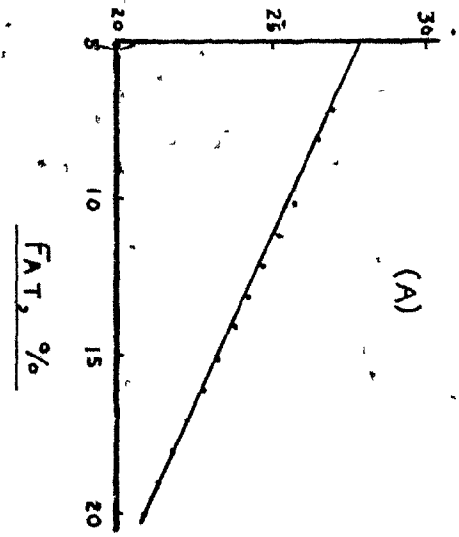


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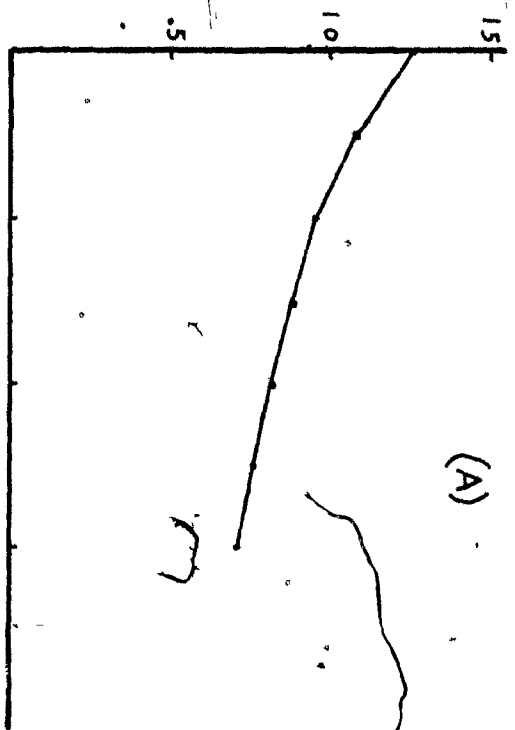




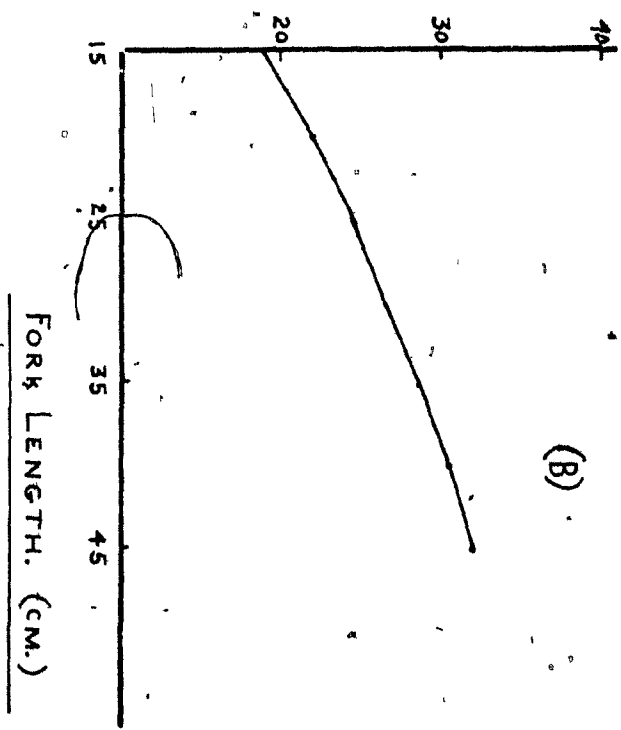
SWIMMING SPEED CM./SEC



SWIMMING SPEED BL / SEC



SWIMMING SPEED CM / SEC.



FORK LENGTH. (CM.)

REFERENCES

- Ackman, R.G. and C.A. Eaton, 1970. Biochemical implications of seasonal trends in the iodine values and free fatty acid levels of commercially produced Atlantic Coast herring oils. J. Fish. Res. Board Can. 27: 1669-1683.
- Alcev, Yu.G., 1963. Function and gross morphology in fish. Izd. Abad. Nauk. SSSR. Moscow. 245 (English translation. Israel Program for Scientific Translations. 1773, 1969).
- Alexander, R.McN., 1967. Functional design in Fishes, Hutchinson and Co., London. 160 pp.
- Anon., 1973. Hydromechanics of fish migration. Nature, 245: 7.
- Bainbridge, R., 1960. Speed and stamina in three fish. J. Exp. Biol. 37: 129-153.
- Bainbridge, R., 1962. Training, speed and stamina in trout. J. Exp. Biol. 39: 537-555.
- Bone, Q., 1972. Buoyancy and hydrodynamic functions of integument in the castor oil fish, *Ruvettus pretiosus*, (Pisces: Gempylidae) Copeia, 1972: 78-87.
- Brett, J.R., 1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 22: 1491-1501.
- Brown, G.E. and B.S. Muir, 1970. Analysis of ram ventilation of fish gills with application to skipjack tuna (*Katsuwonus pelamis*). J. Fish. Res. Board Can. 27: 1637-1652.

- Chen, C.F., 1963. An analytical study of the hydrodynamic performance of winged, high density torpedoes. Hydronautics Inc., Tech. Rept. 349-1, pp.
- Daily, J.W. and D.R.F. Harleman, 1966. Fluid Dynamics, Addison Wesley Publ. Co., Reading Mass., 454 pp.
- Gero, D.R., 1952. The hydrodynamic aspects of fish propulsion. Am. Museum Novitates, 1601: 1-32.
- Gray, J., 1933. The movement of fish with special reference to the eel. J. Exp. Biol. 10: 88-102.
- Gray, J., 1936. Studies in animal locomotion VI. The propulsive powers of the dolphin, J. Exp. Biol. 13: 192-199.
- Hachey, H.B., 1961. Oceanography and Canadian Atlantic waters. Bull. Fish. Res. Board Can., No. 134. 120 pp.
- Hall, F.G., 1930. The ability of the common mackerel and certain other marine fishes to remove dissolved oxygen from sea water. Am. J. Physiol. 93: 417-421.
- Harris, J.F., 1936. The role of the fins in the equilibrium of the swimming fish. I. wind tunnel tests on a model of *Mussetelus canis*. J. Exp. Biol. 13: 476-493.
- Hoerner, S.F., 1965. Fluid dynamic drag. S.F. Hoerner (Publisher), Medlund Park, N.J. 82 pp.

- Hopkins, D.J., 1956. A semi-empirical method for calculating the pitching movement of bodies of revolution at low Mach numbers. ~~NACA~~ - Res. Memo, R.M. - A51C14.
- Horak, D.L., 1966. A densitometric method for determining body fat concentration in fish. Trans. Am. Fish. Soc. 95: 318-320.
- Kerr, S.R., 1971. Prediction of fish growth efficiency in nature. J. Fish. Res. Board Can. 28: 809-814.
- Lauzier, L.M. and J.H. Hull, MS 1969. Coastal station data temperatures along the Canadian Atlantic coast, 1921 - 1969. Fish. Res. Board Can. MS Rept. No. 150, 25 pp.
- Lehninger, A.L., 1965. Bioenergetics. W.A. Benjamin Inc., New York, N.Y. 258 pp.
- Lighthill, M.J., 1969. Hydromechanics of aquatic animal propulsion. Ann. Rev. Fluid Mech. I: 413-446.
- MacKay, K.T., 1976a. Feeding strategy in a patchy environment - a theoretical analysis of feeding in the Atlantic mackerel, *Scomber scombrus*. Chapter 3, this study.
- MacKay, K.T., 1976b. Synopsis of biological data on the northern population of the Atlantic mackerel, *scomber scombrus*. Chapter 1, this study.
- MacKay, K.T., 1976c. Population dynamics and bioenergetics of the northern population of the Atlantic mackerel. Chapter 4, this study.
- Magnan, A., 1929. Les caractéristiques géométriques et physiques des poissons. Ann. Sci. Nat. Zool. 10^e, Sér. 13: 1971-1981.

- Magnuson, J.J., 1969. Swimming activity of the scombioid fish *Euthynnus affinis* as related to search for food. FAO (Food Agric. Organ. U.N.) Fish. Rep. 62: 439-451.
- Magnuson, J.J., 1970. Hydrostatic equilibrium of *Euthynnus affinis*, a pelagic teleost with a gas bladder. Copeia 1970: 56-85.
- Magnuson, J.J., 1973. Comparative study of adaptations for continuous swimming and hydrostatic equilibrium of scombroid and xiphooid fishes. Fishery Bulletin 71: 337-356.
- Muir, B.S. and C.P. Newcombe, MS 1973. Laboratory observations in filter feeding in Atlantic mackerel, *Scomber scombrus*. Unpublished Manuscript MEL.
- Nuissall, J.R., 1962. Swimming and the origin of paired appendages. Am. Zoologist 2: 127-141.
- Ovcharov, O.P., 1970. Hydrodynamic role of the branchial system in fishes under the passive way of respiration. Zool. Zh. 44: 1583-1585 (Transl. by Fish. Res. Board Can. Transl. Ser. No. 1823).
- Perkins, C.D. and R.E. Hage, 1949. Airplane performance, stability and control. John Wiley and Sons, New York.
- Prandtl, L. and O.G. Tietjens, 1934a. Fundamentals of hydro and aeromechanics. New ed. 1957. Dover Books, New York, N.Y. 270 pp.
- Prandtl, L. and O.G. Tietjens, 1934b. Applied hydro and aeromechanics. New ed. 1957. Dover Books, New York, N.Y. 311 pp.

Richardson, E.G., 1936. The physical aspects of fish locomotion. J. Exp. Biol. 13: 63-74.

Rosén, M.W., 1959. Water flow about a swimming fish. U.S. Nav. Ord. Test Stat. China Lake, Calif., Tech. Publ. (NOTS TP) 2298: 1-96.

Rosen, M.W. and N.F. Cornford, 1971. Fluid friction of fish slimes.. Nature 234: 49-51.

Sette, O.E., 1950. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part 2. Migration and Habits. U.S. Fish. Wildlife Service. Fish. Bull. 38(50): 149-237.

Walters, V., 1962. Body form and swimming performance in the scombroid fishes. Am. Zool. 2: 143-149.

Ware, D.M., 1975. Growth, metabolism and optimal swimming speed of a pelagic fish. J. Fish. Res. Board Can. 32: 33-41.

Webb, P.W., 1975. Hydrodynamics and energetics of fish propulsion. Bull. Fish. Res. Board Can., No. 190. 158 pp.

Weihs, D., 1973a. Optimal fish cruising speed. Nature 245: 48-50.

Weihs, D., 1973b. Mechanically efficient swimming techniques for fish with negative buoyancy. J. Mar. Res. 31: 194-209.

Winters, G.H., 1975. Population dynamics of the southern Gulf of St. Lawrence herring stock complex and implications concerning its future management. Ph.D. thesis, Dalhousie University: 142 pp.

Yuen, Henry S.H., 1970. Behavior of skipjack tuna
(*Katsuwonus pelamis*) as determined by tracking
with ultrasonic devices. J. Fish. Res. Board
Can: 27: 2071-2079.

Zharov, V.L., 1967. Classification of the scombroid
fishes (suborder Scombroidei, order Perciformes)
Vop. Ikhtiol. 7: 209-224 (Trans. U.S. Bur. Comm.
Fish. Biol. Lab. Honolulu, Hawaii).

APPENDIX I

The coefficient of lift, C_{Lb} , can be calculated from equation 1, proposed by Hopkins (1951). This equation uses potential flow theory to calculate the lift on the forward portion of the body; while lift over the posterior part of the body is estimated by relating the local transverse force for the inclined body to the drag force for a circular cylinder.

$$C_{Lb} = \frac{(k_2 - k_1) 2\alpha}{A} \int_0^{x_0} \frac{dS}{dx} dx + \frac{2\alpha^2}{A} \int_{x_0}^L \eta r C_{dc} dx \quad (1)$$

The portion of the body to which potential flow theory applies, x_0 is given by equation 2, which is a regression calculated from test data (op.cit.).

$$\frac{x_0}{L} = 0.378 + 0.527 \frac{x_1}{L} \quad (2)$$

The apparent mass factor $(k_2 - k_1)$ and the drag proportionality factor η are both functions of fineness ratio N (equation 3). Whereas, the cross-drag coefficient (C_{dc}) is a function of the cross Reynold's number R_{ec} given in equation 4. The three preceding factors are determined from graphs based on test data.

$$\eta = \frac{L}{2r_0} \quad (3)$$

$$R_{eC} = \frac{2rU \sin \alpha}{\mu}$$

The symbols used in the calculation are listed in Table A1 while the relevant parameters are presented in Table A2. C_{LB} was calculated as 0.137 and this value is used in the calculations of the various lift components.

TABLE A1

Symbols used in calculation of body lift.

A	-	body surface area, cm^2 (excluding keel)
α	-	angle of attack, radians
C_{d_c}	-	cross drag coefficient
C_{Lb}	-	lift coefficient for the body
g	-	free stream dynamic pressure, g/cm^2
$k_2 - k_1$	-	apparent mass factor
L	-	body length, cm (excluding keel)
η	-	drag proportionality factor
r	-	body thickness, cm
r_o	-	maximum body radius, cm
S	-	body cross sectional area normal to the longitudinal axis at any station, cm^2
U	-	free stream velocity, cm/sec
μ	-	kinematic viscosity = $.01 \text{ cm}^2/\text{sec}$
x_o	-	the longitudinal distance from body nose over which potential flow theory applies, cm
x_1	-	the longitudinal distance from body nose to the point at which $\frac{ds}{dx}$ has a maximum negative value, cm

TABLE A2

Parameters used in the calculation of the coefficient of lift, C_{L_b} , using a method proposed by Hopkins (1951).

L	=	28.5
r_o	=	2.0
r	=	7.13
$k_2 - k_1$	=	0.895
A	=	52.4
α	=	.174
x_o	=	22.1
$S_o \frac{dS}{dx} dx$	=	21.48
N	=	0.65
$\int_{x_o}^L \eta r C_{d_c} dx$	=	12.47
C_{L_b}	=	0.137

APPENDIX REFERENCES

Hopkins, E.J., 1951. A semi-empirical method for calculating the pitching movement of bodies of revolution at low Mach numbers. NACA RM A51C14: 27 pp.

SECTION C

COLOUR

CHAPTER 3

Feeding strategy for a patchy environment:

a theoretical analysis of feeding in the Atlantic mackerel

Scomber scombrus.

ABSTRACT

A theoretical model is developed to test the hypothesis that fish schooling is advantageous for planktivorous fish when searching for aggregated prey. The model uses parameters for the continuously swimming Atlantic mackerel. A two-dimensional linear search for randomly distributed patch centres is assumed. Once patches have been located, the school switches to a filter feeding mode removing plankton until a lower threshold of plankton density is reached. Schooled predators have a decided advantage over individual predators. Increased reactive distance effects only single fish and small schools while increased inter-fish distance has a greater effect on larger schools. The model is insensitive to prey size and prey density but is sensitive to the parameter of patch distribution and density.

A comparison of output from the model with data on stomach contents suggests the model is useful in predicting the range of patch sizes preyed upon by mackerel. In addition to schooling, mackerel have other adaptations such as continuous swimming, non-random search pattern in the vicinity of the patch and filter feeding, which allow for efficient utilization of a patchy environment.

LIST OF FIGURES

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INTRODUCTION

Atlantic mackerel, Scomber scombrus, feed by two methods. They can particulate feed by engulfing prey individually or filter feed by straining water and feeding on zooplankton en masse. Muir and Newcombe (MS 1973) have carried out a laboratory analysis of filter feeding. Their results indicate that swimming speed and relative importance of filtering are related to plankton concentration. Filter feeding is initiated only at plankton concentrations above 3 mg/l; 50% filtering occurred at 20 mg/l and 100% filtering at 140 mg/l. However, plankton densities in the Gulf of St. Lawrence range from .1 to 1.5 mg/l and average .4 to .5 (LaCroix and Filteau, 1969; MacKay, unpublished results) below the threshold for filter feeding. An examination of stomach contents of mackerel from the Gulf of St. Lawrence indicates that filter feeding does occur in nature as zooplankton predominates.

The resolution of this apparent paradox lies in the hypothesis that plankton occurs as patches. Increasing evidence suggest that both phytoplankton and zooplankton patches are a common occurrence in the marine environment (Cassie, 1963; Platt et al., 1970; Wiebe, 1970). The patches appear to occur on various size scales, but they are concentrated from 2.5 to 1000 times the average ocean

background (Platt and Denman, 1975; Wiebe, 1970).

Mackerel not only require patches in order to filter feed, but they have other behavioural adaptations that enable them to identify patches and remain within a patch while filtering (Muir and Newcombe, MS 1973; MacKay, 1976a). Thus the feeding behaviour of mackerel appears to be adapted for exploiting a patchy environment.

I have suggested previously that continuous swimming imposed on mackerel because of their lack of a swim bladder and the resulting negative buoyancy is also an aid in obtaining food in a patchy environment (MacKay, 1976b). Thus, continuous swimming would increase the search area and increase the probability of encounter with patches.

A dominant feature of mackerel life history is their schooling behaviour. They are obligate schoolers with schools breaking up only on dark nights (Breder, 1959; MacKay, 1976a). Various explanations have been offered for the adaptive values of schooling. The accuracy of navigation is increased by schooling (Saila and Shappy, 1963; Patten, 1964). Schooling in fish and other forms of aggregation such as flocking in birds appears to offer a partial protection from predation particularly when the predator is solitary (Brock and Riffenburgh, 1960; Williams, 1964; Vine, 1970). In addition, a schooling species may be hydrodynamically more efficient than non-schoolers (Breder, 1965; Wiebe, 1973a).

Schooling behaviour in mackerel appears to have several functions. Assistance in migration, protection from predation, and hydrodynamic efficiency are all important for the survival of mackerel. However, I do not feel that these functions adequately explain the importance of schooling behaviour to mackerel. Schooling can assist in feeding under some conditions. Sette (1950) has suggested that schooling behaviour increases the efficiency of filter feeding by mackerel such that zooplankton avoidance is minimized. The advantage of schooling in searching for an aggregated prey has been suggested previously (Olson, 1964; Radokov, 1972) although it does not appear to have been explored formally. In fact Eggers (1976) suggests that schooling is disadvantageous when prey are randomly distributed.

It would appear intuitively obvious that as school size increases the searching time for aggregated prey should decrease. However, what is not so obvious is the effect of competition on the average ration per fish. Eggers (1976) points out the change in prey density which would occur as a school removes food from the water columns. The fish in the anterior part of the school would obtain more food than those in the posterior. However, if patches are sufficiently dense to allow more than one pass, the dynamic nature of the

fish within the school would minimize this within school competition. In this paper I use a theoretical model to explore the effects of schooling of planktivorous fish while feeding in a patchy environment.

THE MODEL

In order to examine the effect of a heterogeneous environment on feeding in a pelagic fish such as the Atlantic mackerel, I have constructed a computer simulation using FORTRAN. The simulation consists of a number of interlocking submodels illustrated in Figure 1.

The predator or school submodel, determines size and shape of the school, reactive distance, speed of movement and weight of the fish all in relation to fish length. In the prey submodel information is produced on size and distribution of the prey patches in relationship to average prey density and prey particle size.

The act of feeding is divided into two processes, searching and feeding. The search submodel assumes a random search for patches using a search speed parameter compatible with a constantly swimming fish such as mackerel. Once a food patch has been encountered the feeding mode is assumed. The feeding submodel uses parameters for a filter feeding mackerel (Muir and Newcombe, MS 1973).

The simulation outputs are time spent searching and ration/fish/day. The model can be tested against empirical data on mackerel stomach contents (MacKay, unpublished data).

The various symbols and variables used in the simulation are presented in Table 1 and 2. Details of the equations used in the simulation are presented in the following

description of each submodel, while the computer program and a sample of the output are presented in Appendix I.

A) School

The predator or school submodel is restricted to two dimensions. For further simplicity the school is considered to be a right angled diamond shape with the individuals in it forming a square matrix (Figure 2) similar to the diagonal arrangement suggested by Cullen et al. (1965), Van Olst and Hunter (1970), and Radakov (1972). This school shape allows easy calculation of school dimensions. In the present calculations the sides of the diamond are equal, i.e. using the matrix terminology, column length (L_c) equals row length (L_r). Row length would be the sum of the interfish distances plus the fish snout width, W_{sn} .

$$L_r = N_r W_{sn} + (N_r - 1) D_{IF} \quad (1)$$

However, as W_{sn} is small, equation 1 can be simplified by assuming that D_{IF} also accounts for W_{sn} . Thus, the row length is given by -

$$L_r = D_{IF} N_r \quad (2)$$

School area (A_s) is then simply

$$A_s = L_r^2 \quad (3)$$

The width of the search path (SP) of the school is equal to the length of a diagonal which can be determined by Pythagoras theorem:

$$SP = (L_r^2 + L_c^2)^{1/2} \quad (4)$$

In the simulation the numbers of fish per school, N_s was increased approximately an order of magnitude for successive runs. However, in order to maintain the number of fish per row as a whole number the nearest lower perfect square was determined and this used as the new school number. For example, the initial N_s was 1. This was increased to 10 and then readjusted to 9, the nearest perfect square. (Table 3).

B) Prey

The initial runs of the simulation assumed a spherical particle approximating the size of a mackerel egg (diameter = 1 mm). Prey volume, V_{Pr} is then:

$$V_{Pr} = 4/3\pi r^3 \quad (5)$$

The volume of most prey species can be better approximated by the volume of an oblate spheroid -

$$V_{Pr} = 4/3\pi ab^2 \quad (6)$$

where a and b are the major and minor axis respectively.

Equation 6 was therefore used to calculate the volume for various sizes of prey from copepods to small fish. An empirical relationship between a and b was established by measuring length and weights of three common types of prey. The relationship found for copepods, is $a = 0.19b$, for euphausiids, $a = 0.11b$ and for fish (5-10cm), $a = 0.15b$. However, the model proved insensitive to changes in prey size and shape so I have used a spherical particle of 1mm diameter for all the runs.

The weight of an individual prey, Wt_{Pr} assumes a particle density of 1.03 g/cc slightly denser than surface water in the Gulf of St. Lawrence during summer (MacKay, 1976b). Where volume is expressed in m^3 -

$$Wt_{Pr} = V_{Pr} 1.03 \times 10^6 \quad (7)$$

"If prey are distributed at random then their pattern approximates a Poisson distribution and the mean equals the variance. However, randomness of individuals in nature is a rather rare phenomenon (Cassie, 1963) and a more realistic assumption is that prey have a contagious or patchy distribution. For the purposes of the model I assume that the patch centers are randomly distributed. This may indeed occur in nature (Cassie, 1963; Wiebe, 1970).

The basic relationship for the prey generating sub-model is that over a large area, the average prey density (D_{Pr}) below a m^2 of sea surface in grams is a function of

the number of patches/m² (N_{Pa}), the volume of each patch/m³ (V_{Pa}), and the density of the patch in g/m (D_{Pa}). This relationship is summarized in equation 8.

$$D_{Pr} = N_{Pa} V_{Pa} D_{Pa} \quad (8)$$

Normally D_{Pr} and N_{Pa} are held constant while for successive runs V_{Pa} takes different values within set limits, D_{Pa} is then calculated by rearrangement of equation 8 as:

$$D_{Pa} = D_{Pr} / N_{Pa} V_{Pa} \quad (9)$$

Similarly the number of prey in any patch ($N_{Pr_{Pa}}$) can be obtained from equation 10.

$$N_{Pr_{Pa}} = D_{Pa} / Wt_{Pr} \quad (10)$$

The range of values for D_{Pr} used in the model is set within realistic limits by assuming that 50% of the plankton above 15m, the average depth of the thermocline over the Magdalen Shallows during August (Hachey, 1961), is available for concentration into patches. In subsequent runs of the simulation this assumption is relaxed to study cases where all, or 10% of the plankton above 15m, is present in patches.

A minimum patch volume, $V_{Pa} (min)$ can be calculated from the volume of individual prey V_{Pr} and the number of prey/patch, $N_{Pr_{Pa}}$ assuming that even the densest swarms of plankton have spaces between organisms equal to the volume of the prey.

$$V_{Pa(min)} = N_{Pr} 2V_{Pr} \quad (11)$$

Once $V_{Pa(min)}$ was determined, it was increased by increments of 10 for subsequent runs until patch overlap became a problem; that is the distribution approached randomness.

The diameter of the patches is a critical parameter in the search submodel. This diameter is dependent on the shape of the patches. Patches are normally considered to be two dimensional (Platt and Denman, 1975) however; realistically they must have a verticle dimension no matter how small. I have allowed patch shape to vary from a sphere to cylinders ranging in depth (h) from 0.1 to 10m.

Patch radius (r_{Pa}) for a spherical patch is:

$$r_{Pa} = (3 V_{Pa}/4\pi)^{1/3} \quad \text{and} \quad (12)$$

$$r_{Pa} = (V_{Pa}/\pi h)^{1/2} \quad (13)$$

for a cylindrical patch.

The horizontal area of a patch (A_{Pa}) would of course be:

$$A_{Pa} = \pi r_{Pa}^2 \quad (14)$$

The overlapping of patches is a situation which is difficult to handle mathematically and probably does not occur in nature. This problem was resolved by Paloheimo (1970) who added a function to his patch generating function

which excluded overlapping patches and produced an anti-contagious distribution. To accomplish a similar end I have derived an index of aggregation (IA):

$$IA = N_{Pa} \cdot A_{Pa} \quad (15)$$

The lower the index, the higher the aggregation while a random distribution occurs as IA approaches 1. For the present simulation the index of aggregation was restricted to 0.5 so that the probability of overlap is small. An upper limit on patch area can now be determined by rearranging equation 15.

$$A_{Pa}(\text{Max}) = .5/N_{Pa} \quad (16)$$

C) Search

Assuming a two dimensional linear search model for a prey distribution approximating a random or Poisson series, the number of prey encountered in any unit of time is:

$$N_{t_{Pr}} = U_{Se} \cdot 2r_{Se} \cdot N_{Pr} \quad (17)$$

where U_{Se} is the distance searched per unit of time, $2r_{Se}$ is the search diameter and N_{Pr} is the numerical density of prey. Using reasoning similar to that employed by Paloheimo and Dickie (1964) and Kerr (1971), the average area which contains only one particle is $1/D_{Pr}$ and the time required to find one particle by random search, t_{Se} is:

$$t'_{Se} = 1/U_{Se} \cdot 2r_{Se} \cdot D_{Pr} \quad (18)$$

However, in the present model search is not for an individual particle, but for aggregations of particles, whose centers are randomly distributed. Thus the time to locate one patch (t_{Se}) is given by:

$$t_{Se} = 1/U_{Se} \cdot 2r_{Se} \cdot N_{Pa} \quad (19)$$

The search diameter, for a visual predator searching as a school for patches of prey will be:

$$2r_{Se} = RD_F + SP + 2r_{Pa} \quad (20)$$

which is the sum of the reactive distance (or sight distance) of the fish (RD_F) and the search path (SP) which is obtained from equation 4 plus a term to account for the patch diameter ($2r_{Pa}$) (equation 12 or 13).

D) Feeding

The feeding model considers only a filter feeding predator with the following additional restrictions, that the predator school shape is maintained while feeding so that the school is capable of making successive sweeps through the patch until the patch density is lowered below a certain threshold.

The initial algorithm for feeding allowed for calculation of ration, RW , and time spent filtering, t_{F1} ,

however, the calculations are time consuming. Even with a large, high speed computer a large number of iterations are necessary which created problems of storage and resulted in excessively long runs. In order to allow for faster computing time to enable the testing of more variables, I have simplified the calculation of ration and have not calculated t_{F1} . The initial equations are presented in Appendix II.

The simplified calculation of ration removes the constraint of satiation and assumes that whenever a predator school encounters a patch, all the available food (i.e. that above the feeding threshold, Th_{F1}) will be consumed. Th_{F1} is taken to be $3g/m^3$ but probably is a function of prey density. Thus $R/\text{fish/day}$ is

$$R_F = (D_{Pa} - Th_{F1}) N_{Me}/D_F \quad (21)$$

where N_{Me} is the number of meals/day for a 15 hour day as given by:

$$N_{Me} = 15/t_{Se} \quad (22)$$

where t_{Se} is in hours and D_F is the numerical density of predators (fish)/ km^2 .

These calculations give the same results as would the detailed calculations but they do not allow for calculation of t_{F1} .

The total ration for each fish is expressed as a % of body weight by the following relationship:

$$RW_F = 100 \frac{R_F}{Wt_F} \quad (23)$$

where the weight of fish (Wt_F) in g is determined by the general weight-length relationship (MacKay, 1976a)

$$Wt_F = 0.0059 L^{3.154} \quad (24)$$

where L is fork length in cm.

The general model then considers that the predator can be aggregated into schools and is searching for aggregations or patches of prey. A random search pattern is employed while searching for patch centers. When the patches are encountered the predator switches to the feeding mode passing back and forth through the patch until the prey density is lowered to a certain threshold when feeding stops and random search resumes. For the initial runs no allowances are made for satiation of the predator but feeding is assumed to occur only during the 15 hours of daylight. For these initial runs the density of predators equals 77284 fish/km², a density similar to that estimated by MacKay (1976c) for the 1968 and 1969 spawning period. The average prey density is assumed to be 0.4g/m³ the average density determined by plankton net tows (op. cit.).

RESULTS

An example of the general output of the model is presented in Figure 3. In this run school size was allowed to vary from 1 to 77284 fish while fish length, interfish distance, reactive distance, swimming speed, filtering speed, prey size and prey shape were all held constant as per Table 2. Patch number and area were allowed to vary but I have presented results for only a couple of representative patch areas and patch numbers.

It is obvious from Figure 3 that school size has a major effect on searching time (t_{se}) and ration (RW). As school size increases t_{se} decreases, this decrease is more apparent when patch area is small. Ration increases as school size increases and also increases with increasing patch area. However, ration at any one patch area is constant and independent of abundance of patches. It is apparent that schooling confers a large advantage on a predator when searching and feeding on an aggregated prey.

The advantage of schooling is that the search diameter increases as more fish are added to the school. This results in a decrease in the time to find a patch and results in a greater number of meals. This more than makes up for the greater number of fish feeding on each patch.

Searching diameter can also be changed by increasing the spacing within schools. The results of varying the interfish distance (D_{IF}) are presented in Figure 4A. The effect of changing D_{IF} is greater in the larger schools while as would be expected there is no effect on a single fish.

Reactive distance, RD like D_{IF} is a parameter related to vision. However, it is more important to single fish and small schools than to larger schools, Figure 4B. As this variable only has an effect at the edge of the school it is clear that the magnitude of its effect will depend on the school size.

The effect of varying search speed (U_{Se}) from 10-40 cm/sec is examined in Figure 5. An increase in search speed has a large effect on t_{Se} . For example, t_{Se} is lowered from 534 hours at 10 cm/sec to 133 hours at 40 cm/sec for a single fish and from 34 hours to 8 hours for the school of 77284 fish. Ration increases as speed increases. The ration for a single fish increased from 0.3 to 2.0 as speed changed from 10 to 40 cm/sec.

The previous results have assumed that the predator has an unlimited capacity and that satiation does not occur. The maximum ration for a mackerel based on my observations of stomach contents (MacKay, unpublished data) is about 10% of body weight. For a 32 cm fish the maximum ration would be 33 grams. The results presented in Table 3 compare ration

when satiation is or is not assumed for a dense patch (1 patch/km² and patch area = 13.9 m², Figure 3). There is a lowering of the ration for all school sizes but the difference is small as in most cases the predator is not satiated. Under most conditions of patch density used in this simulation satiation does not occur.

In Figure 6 the effect of varying fish size is examined. Search speed was 1 L/sec for all cases. The changes in t_{Se} are similar to those illustrated in Figure 5 where search speed is varied while fish length is held constant. However, relative ration (% BW) decreases as fish length increases (Figure 6B) but the absolute ration (Figure 6C) increases as fish length increases. Smaller fish have a smaller mouth area and a slower filtering speed therefore they spend a longer time filtering than larger fish. While it is of considerable interest to determine the relative efficiencies of various sizes of fish at filter feeding on patchily distributed prey it is beyond the scope of this model. However, examination of stomach contents suggest smaller fish contain a higher proportion of larger food items than do larger fish. This suggests that they cannot meet their higher metabolic demands by filter feeding alone.

I have so far considered only attributes of the predator which affect feeding on an aggregated prey. The

model also allows various parameters related to patch size and distribution vary. Two different patch numbers are compared in Figure 3. There is a direct relationship between t_{se} and patch numbers as an increase from 1 to 100 patches km^2 results in a 100 fold decrease in t_{se} . However, ration size is independent of patch number. When patch number increases and patch area is held constant the calculated patch density has to decrease, so that, while t_{se} decreases and more patches are encountered per day the food obtained from each patch is also much less. The net result of these changes is that ration does not change with patch number. This is undoubtedly an oversimplification as feeding efficiency would be higher in the more dense patches thus a higher ration would be obtained when patches were less numerous and therefore more dense.

Changes in patch area have a more pronounced effect on small schools than on large schools (Table 4). For example, an increase in patch area of 100 fold from 13.9 to 1390 m^2 results in an 8 fold reduction in t_{se} from 167 to 20 hours for a single fish but t_{se} changes only 2 fold from 10.8 to 5.2 hours for the largest school. Ration increases as prey area increases with the smaller schools experiencing the greatest effect. The highest rations for all schools occurred at the largest patch area.

Variations in prey density affect the outcome of the simulation by changing the minimum prey area and thus their effects (Table 4B) on t_{se} are similar to that when area is changed. An increase in prey density increases the ration for all school sizes but the smaller schools benefit more than the large ones. It is clear from Table 4A that patch area is much more important to the predator than is patch density.

Patch shape also affects patch area and therefore, t_{se} and RW. Figure 7 examines searching time when the patch is assumed to be a sphere, and a cylinder with depths varying from 1 cm to 10 m. As would be expected the behaviour of the simulation to variation in patch depth is similar to that for patch area. The effect is greatest on a single fish and there is virtually no effect for the largest schools. This influence of patch depth will be less when patch area is large. In order to minimize the effect of changes in patch depth, I have assumed a cylindrical patch whose depth is 0.1 times the diameter, for all standard runs of the simulation.

The proportion of the plankton which is actually in patches in nature is not known. In Table 5 I test three possible cases. While the middle case produce a different area, thus making comparisons difficult it is apparent that for similar patch areas ration increases with patch density. For the standard runs of the simulation I assume that the patches contain half of the available plankton.

The model clearly indicates that schooling is of considerable advantage to a predator searching for an aggregated prey. In the examples given here under all conditions of patch size, shape, and density the 77,286 fish/ km^2 would obtain a greater ration by searching as a single school. Furthermore in almost all conditions the single large school encountered a patch within a day whereas single fish and smaller schools often search for more than 5 days before encountering food.

Under some conditions of patch distribution smaller schools would have an advantage. The model has not considered these. Schools are more compact when feeding (Radakov, 1972; Sette, 1950) and are probably able to conform to the shape of the patch. However, it would be difficult to proportion the food in a patch equally amongst the school when patch area is smaller than the school area. As schools are held together by a balance of attractive and repulsive forces (Breder, 1954) the schools would tend to break up when some fish were feeding and others were not. Furthermore, as patch number increases there is a high probability that a large school would be encountering two patches simultaneously. When this happens the dynamic nature of the school would result in a splitting of the school. Thus it is reasonable to assume that when the patch area is less than the school area the school cannot be

maintained and breaks up into smaller units.

As the model indicates, ration is independent of patch number, thus I have been able to plot a ration for each patch area for the various school sizes (Figure 8). Adding minimum school area for each school allows a test of the model against observable facts.

Minimum school area can be calculated from equation 2 and 3 assuming that the densest school has a D_{IF} of $0.2L$ (Van Olst and Hunter, 1970).

During late May and early June, mackerel caught along the Atlantic Coast of Nova Scotia often have stomachs full of euphausiids with stomach weights occasionally exceeding 10% of body weight, with an average value of 1-3%.

If 50% of the plankton is in patches, then a school of 784 to 7744 fish, feeding on patches ranging in area from 3 to 300 m^2 would account for the observed ration. If only 10% of the plankton is in patches, then a school of 77,000 fish would obtain a ration of 3 to 44% when feeding on patches ranging in area from 300 to $3,000 \text{ m}^2$.

During summer in the Gulf of St. Lawrence small zooplankton species predominate in the stomach contents and rations seldom exceed 1%, averaging less than 0.5%.

School size off the north shore of Prince Edward Island in the Gulf of St. Lawrence is about 10,000 fish (MacKay). The observable ration can only be obtained if less than 10% of plankton is contained in patches and the fish are feeding

on patches of 3 to 300 m².

Further information is required on the parameters of patch distribution in nature before any further refinements on the predictability of this model are attempted. However, this model appears to be useful in predicting the scales of patch size that are being exploited by schooling filter feeding fish.

DISCUSSION

The model suggests that there is a considerable advantage to a schooling predator searching for patches of prey. The literature on schooling (Breder, 1959, 1965, 1967; Radakov, 1972; Shaw, 1970; see MacKay, 1976a for a review of schooling in mackerel) indicates that fish schools offer an extremely adaptable unit capable of exploiting patches. Schools are very dynamic, they behave as a unit and change size and shape constantly (Radakov, 1972).

The size of schools is an important component in decreasing search time and thereby increasing ration. School size can be increased in two ways: by adding more fish, or increasing the spacing between fish. In fact, these two mechanisms are ideal ways for increasing search efficiency as they do not increase energetic costs but, on the contrary, they increase hydrodynamic efficiency (Breder, 1960; Wiehs, 1973a), thereby lowering costs.

Interfish distances for many fish species vary from 0.2 to $1L_F$ (Van Olst and Hunter, 1970) and may be determined by hydrodynamic considerations (Wiehs). If this distance can be increased during searching, it would further increase the efficiency of search. Radakov (1972) suggests that this may occur as schools of many species are more widely spaced when not

feeding, i.e. searching. The most efficient searching shape would be a wide spaced wing formation, a shape that has been observed (op. cit.).

I have assumed that schools are two dimensional. If patches are concentrated at any predictable depth such as the surface or thermocline, a flattened school would be most efficient as search could be restricted to two dimensions. However if patches are distributed throughout the water column, then an ellipsoidal school shape should prove optimal.

Reactive distance is important for a solitary searching predator such as a trout (Kerr, 1971). In fact, this appears to be partially responsible for size selectivity by such fish with RD being proportional to prey size. However, the present simulation indicates that increases in RD are only effective for single fish or small schools.

Many fish rely on sight to locate prey. However, the restricted visibility afforded by the aquatic medium does not allow for efficient solitary predators, with the exception of those that use other long range stimuli such as high frequency sounds or pressure waves. Whereas in terrestrial environments reactive distance can be many miles for predatory birds. Thus limited visibility in the aquatic medium would appear to place greater emphasis on other means of increase search area such as schooling or increased swimming speed.

While prey size and density are important in determining growth efficiency for a solitary searching trout (Kerr, 1971), a schooling predator searching for aggregation of prey appears to be much less responsive to prey size and prey average density. Mackerel do select larger particles during feeding, however, the search component is independent of prey size. What is of the most importance to a schooling predator is the density, area and abundance of patches. Thus, an increase in prey aggregation has the same effect as increasing prey size or density (Ivlev, 1955; Kerr, 1971).

The negative buoyancy of mackerel imposes on them a constant searching speed of about 1 L/sec. This speed appears to be optimal for food search and navigation in many fish species (Anon., 1973; Ware, 1975; Wiehs, 1973b). Certainly, the simulation indicates the importance of swimming speed on increasing ration. The successful exploitation of a patchy environment requires a wide ranging search pattern such as would be expected from a continuously swimming fish.

The behaviour of mackerel in the vicinity of patches appears to be ideally suited for efficiently exploiting these patches. Mackerel show a non-random search pattern in the vicinity of patches and are able to use nonvisual cues such as odour to assist in this search. Once a patch has been found, they are capable of remaining within the patch and adjusting their filtering rate to the plankton concentration (MacKay, 1976; Muir and Newcombe, MS 1973).

As search appears independent of prey size, it would be advantageous to be able to handle a wide range of particle sizes. Filter feeding can be adjusted to varying prey size, as the gill rakers can adjust their mesh size and filter feeding fish can vary to include larger particles such as euphausiids in their filtering path without changing filter feeding. Larger particles, if present alone, are pursued and handled individually by particulate feeding. The transition from filtering to particulate feeding occurs readily at low plankton densities but not at higher densities (Muir and Newcombe, MS 1973).

Mackerel feeding behaviour appears to be a highly efficient process capable of handling and processing a wide range of prey sizes. In fact, filter feeding appears to be the most efficient mechanism for handling small zooplanktons as it lowers the cost and time of handling individual particles. Thus, it appears that schooling, continuous swimming and filter feeding are important adaptations which allow mackerel to successfully exploit a patchy environment.

REFERENCES

- Anon. 1973. Hydromechanics of fish migration.
Nature 245:7
- Breder, G.M., Jr. 1954. Equations descriptive of fish
schools and other animal aggregations.
Ecology 35:361-370
- Breder, G.M., Jr. 1959. Studies on social groupings in
fishes. Bull. Am. Mus. Nat. Hist. 117: 397-481
- Breder, G.M., Jr. 1965. Vortices and fish schools.
Zoologica 50: 97-114
- Breder, G.M., Jr. 1967. On the survival value of fish
schools. Zoologica 52: 25-40
- Brock, V.E. and R.H. Riffenburgh, 1960. Fish schooling: a
possible factor in reducing predation.
J. Conseil Int. Explor. Mer. 25: 307-317
- Cassie, R.M., 1963. Microdistribution of plankton. Oceanogr.
Mar. Biol. Ann. Rev. 1: 223-252
- Cullen, J.M., E. Shaw and H.A. Baldwin, 1965. Methods for
measuring the three-dimensional structure
of fish schools. Anim. Behav. 13: 534-543
- Eggers, D.M., 1976. Theoretical effect of schooling by
planktivorous fish predators on rate of prey
consumption. J. Fish. Res. Board Can.
33: 1964-1971

- Hachey, H.B. 1961.. Oceanography and Canadian Atlantic waters.. Bull. Fish. Res. Bd. Canada, No. 134:120pp.
- Ivlev, V.S. 1955. Experimental ecology of the feeding of fishes. Pischepromizdat, Moscow. (Trans. D. Scott, Yale University Press, New Haven, 1961). 302pp.
- Kerr, S.R. 1971. Prediction of fish growth efficiency in nature. J. Fish. Res. Bd. Canada 28:809-814.
- Lacroix, G. and G. Filteau. 1969. Les fluctuations quantitative du zooplankton de la Baie-des-Chaleurs (Golfe Saint Laurent) I. Conditional hydro-climatiques et analyse volumetrique. Naturaliste Can. 96:359-397.
- MacKay, K.T. 1976a. Synopsis of biological data on the northern population of the Atlantic mackerel, Scomber scombrus. Chapt. 1, this study.
- MacKay, K.T. 1976b. Hydrodynamics of the negatively buoyant Atlantic mackerel, Scomber scombrus. Chapt. 2, this study.
- MacKay, K.T. 1976c. Population dynamics and productivity of the northern population of Atlantic mackerel, Scomber scombrus. Chapt. 4, this study.
- Muir, B.S. and C.P. Newcombe. MS 1973. Laboratory observations in filter feeding in Atlantic mackerel, Scomber scombrus. MEL, unpublished manuscript.

Olson, F.C.W., 1964. The survival value of fish schooling.

J. Cons. Int. Explor. Mer. 25: 307-317

Paloheimo, J.E., 1971. On a theory of search. Biometrika

58: 61-75

Paloheimo, J.E. and L.M. Dickie, 1964. Abundance and

fishing success. Rapp. Process - Verbaux

Reunions Cons. Perm. Int. Explor. Mer.

155: 152-163

Patten, B.C., 1964. The rational decision process in

salmon migration. J. Cons. Int. Explor.

Mer. 28: 410-417

Platt, T. and K.L. Denman, 1975. A general equation for

the mesoscale distribution of phytoplankton

in the sea. Mem. Soc. Royale des Sciences

de Liege, 6 Ser., VII 31-42

Platt, T., L.M. Dickie and R.W. Trites, 1970. Spatial

heterogeneity of phytoplankton in a near

shore environment. J. Fish. Res. Board Can.

27: 1453-1473

Radakov, D.V., 1972. Schooling in the ecology of fish.

Izdatel stuo "Nauka", Moscow. (English

Trans. Holstead Press, John Wiley & Sons,

New York, 1973: 173 pp.

Saila, S.B. and R.A. Shappy. 1963. Random movement and

orientation in salmon migration. J. Cons.

Int. Explor. Mer. 28:153-166.

Sette, O. 1950. Biology of the Atlantic mackerel, Scomber scombrus of North America. Part II. Migration and habits. Fish. Bull., Fish and Wildlife Serv. 51(49):251-358.

Shaw, E. 1970. Schooling in Fishes: critique and review (pp. 452-480). In: Development and evolution of behaviour: Essays in memory of T.C. Schneirla. L.R. Aronson, E. Tobach, D.S. Lehrman and J.S. Rosenblatt (eds.). W.H. Freeman, San Francisco.

Vine, J. 1971. Risk of visual detection and pursuit by a predator and the selective advantage of flock behaviour. J. Theor. Biol. 30:405-422.

Van Olst, J.C. and J.R. Hunter. 1970. Some aspects of the organization of fish schools. J. Fish. Res. Bd. Canada 27:1225-1238.

Ware, D.M. 1975. Growth, metabolism and optimal swimming speed of a pelagic fish. J. Fish. Res. Bd. Canada 32:33-41.

Wiebe, P.H. 1970. Small scale spatial distribution in oceanic zooplankton. Limnol. Oceanog. 15:205-217.

Wiehs, D. 1973a. Optimal fish cruising speed. Nature 245:48-50.

Wiehs, D. 1973b. Mechanically efficient swimming techniques for fish with negative buoyancy. J. Mar. Res. 31:194-209.

Williams, G. 1964. Measurements of consociation among
fishes and comments on the evolution of
schooling. Publ. Mus. Michigan State
21:351-383.

Appendix I. Fortran program of a simulation of feeding of the Atlantic mackerel.

PROGRAM MCKEREL 73/73 OPT=1		FTN 4.4+R4Q1	76/11/01. 18.08.09.
1	PROGRAM MCKEREL (INPUT, OUTPUT, TAPE3=INPUT, TAPE6=OUTPUT, TAPE25)	MACK	2
	COMMON FL, FISH1, FISH4, FISH5, F1, HVS, FISHW,	COMDEX	2
	1EFF, PATCHN, PATCHY, PATCHO, PREYD, PREYV, PREYJ, PREYTW, PRGOPA,	COMDEX	3
	2 DIAMB, PATCH1000, SERCHD, SHJLN, SHJLA, SHJLO, RA(3600),	COMDEX	4
	3 IR, KE, INVS, IMNS, SECS, ROW, RT, CAL, KI, R(1000)	COMDEX	5
	4 IA, J, L, I3, KEN, KAN	COMDEX	6
	5, IMP, IMIN, REC, PATN, RATT, RD, TIMESE, PATCHA	COMDEX	7
	6, RATT, TIME1, TIMEI, RATTI, LEN, AK	COMDEX	8
	9, PREYD, PREYJ, RAKESP, K	COMDEX	9
10	IK=0	DEBUG2	10
	IA=1	MACK	11
	IB=0	MACK	12
	KI=0	MACK	13
15	K=0	MACK	14
	KEN=0	COR21	15
	IF=1	MACK	16
	C THESE STATEMENTS ALLOW FOR THE USE OF THE BETWEEN PATCHES OPTION	DEBUG2	17
20	READ(5,22)K	DEBUG2	18
	WRITE(6,23)K	DEBUG2	19
	22 FORMAT(2X, I2)	DEBUG2	20
	23 FORMAT(14, *K=*, I2)	DEBUG2	21
	C THIS ALL FOR MULTIPLE READS SO THAT THE VARIABLES CAN BE CHANGED	COR28	22
25	READ(5,21)KE	COR28	23
	21 FORMAT (I2)	COR28	24
	DO 100 IK=1, KE	D5	25
	LEN=0	COR28	26
	IA=0	COR28	27
	IB=0	COR28	28
30	KI=0	COR28	29
	READ (5,10) SHJLN, FL	MACK	30
10	FORMAT (5X, F4.2, 2X, F5.3)	MACK	31
	READ(5,20)PREYD, PATCHN, PRAD	DEBUG2	32
	20 FORMAT(5X, F2.2, F10.3, I2X, F10.8)	DEBUG2	33
35	PREYV=4.1879*PRAD**3	DEBUG2	34
	PREYJ=PREYV*1000000*1.03	DEBUG2	35
	C PREYD IS CONVERTED TO AN INTEGRATED VALUE/M2, ASSUMING THE	D5	36
	C THEPNOCLIE IS AT 15 M	D5	37
40	PREYD=15*PREYD	D5	38
	PREYN=PREYD/PREYV	DEBUG2	39
	WRITE(6,24) PREYV, PREYJ, PREYN	DEBUG2	40
24	FORMAT(2X, *PREY VOLUME=*, F10.3, *M3, *, *PREY WEIGHT=*, G10.3, *G*,	DEBUG2	41
	1 *NUMBER OF PREY/M3=*, F10.3)	DEBUG2	42
32	FORMAT(11, 5X, F4.2, 2X, F5.3)	COR1	43
45	READ(5,40)FISH, RED	DEBUG1	44
40	FORMAT(1X, F5.3, 2X, F6.2)	DEBUG1	45
	FISH=FISH*FL	D1	46
	RD=RED	DEBUG2	47
	FISHV=FL	COR33	48
50	FORMAT(F7.4)	MACK	49
	PREYD=PREYV*PREYN	MACK	50
	SHJLN=SHJLN	MACK	51
	PATCHX=PATCHN	MACK	52
55	PREYX=PREYD	MACK	53
	CALL SCHOOL	MACK	54
	GO TO 3	MACK	55
	11 CONTINUE	MACK	56
PROGRAM MCKEREL 73/73 OPT=1		FTN 4.4+R4Q1	76/11/01. 18.08.09.
	CALL SCHOOL2	MACK	27
	CONTINUE	MACK	28
60	IF (IB.LT.0) CALL PREY1	COR26	29
	IF (IB.LT.0) GO TO 2	COR26	30
	CALL PREY	MACK	31
	GO TO 2	MACK	32
65	9 CONTINUE	MACK	33
	CALL PREY2	MACK	34
	2 CONTINUE	MACK	35
	IF (SHJLN.GE.100000.160) GO TO 13	F1	36
	CALL SEARCH	MACK	37
70	IF (TIMESE.LE.20.0) GO TO 4	DEBUG1	38
	CALL FILTER	MACK	39
	CALL OUTPUT4	COR25	40
	GO TO 5	DEBUG1	41
	4 CONTINUE	DEBUG1	42
	CALL OUTPUT5	DEBUG1	43
75	5 CONTINUE	DEBUG1	44
	IF (LEN.EQ.100) GO TO 100	COR25	45
	GO TO 11	COR25	46
13	CONTINUE	COR1	47
	SCHOOLN=1	COR25	48
80	CALL SCHOOL	COR25	49
	IF (IA.LT.0.AND.IB.LT.0) GO TO 8	COR1	50
	PREYD=PREYX	MACK	51
	IB=0	MACK	52
	IA=0	MACK	53
85	IF (IB.LT.0.AND.FISH1.EQ.0.2*FL) GO TO 12	COR1	54
	GO TO 9	COR25	55
12	CONTINUE	MACK	56
	IF (SHJLN.EQ.1) GO TO 11	COR1	57
	GO TO 11	COR1	58
90	8 CONTINUE	MACK	59
100	CONTINUE	COR28	60
	STOP	MACK	61
	END	MACK	62


```

1 SUBROUTINE SCHOOL
  COMMON FL,FISH,FISHAN,FISHVF,FISHVS,FISHW,
  1 EFF,PATCHN,PATCHV,PATCHD,PREYD,PREYV,PREYW,PREYVW,ORGOPA,
  2 DIAMP,PAT,4(1000),SERCH,SHOJLN,SHOJLA,SHOJLD,RA(3600),
  3 IR,KE,IRAS,IRINS,SECS,RJWRT,KAL,KI,R(1000)
  4 IA,J,L,IR,KAN
  5 IHR,TIN,SEC,RAT,RATT,RD,TIMES,PATCHA
  6 RATE,TIMES1,TIM2,RATI,LEN,AK
  7 PREYD,PREYV,PREYW,K
  10 C THIS SUBROUTINE CALCULATES THE REQUIRED DIMENSIONS OF A FISH SCHOOL AND
  C A SQUARE SCHOOL SHAPE WITH DIRECTION OF MOVEMENT ALONG ONE OF THE DIAG
  C FISH WEIGHT IS CALCULATED FROM A REGRESSION BASED ON 1967-1970
  FISHW=.0055*((FL*100.)*.3.154)
  15 CONTINUE
  ROWN=SQRT(SCHOOLN)
  IRDN=IFIX(ROWN)
  SHOJLN=FLD(RODN**2)
  IF (IRDN,EO.1) GO TO 20
  IRDN=RODN
  GO TO 23
  20 IRDN=2
  23 CONTINUE
  C THIS CALCULATES SCHOOL DIAMETER ASSUMING THAT .6FL INTER FISH DIST.
  C ACCOUNTS FOR SNOUT WIDTH ALSO
  FISHX=FISH*1
  DSHOJLA=IFISHX*FLD(RODN)
  SHOJLA=DSHOJL*DSHOOOL
  SHOJLD=SQRT(2*(DSHOJL*DSHOOOL))
  ROWN=FLD(RODN)
  RJW=FLD(RODN)
  RETURN
  ENTRY SHOJLZ
  SHOJLN=SHOJLN*10.
  IF(SHOJLN,GE,100000.)GO TO 16
  GO TO 15
  35 16 CONTINUE
  RETURN
  END

```

```

MACK 34
COMDEK 3
COMDEK 4
COMDEK 5
COMDEK 6
COMDEK 7
O4 2
O4UG2 1
MACK 61
MACK 62
MACK 64
COR29 2
MACK 66
MACK 67
MACK 68
MACK 69
MACK 70
MACK 71
MACK 72
MACK 73
MACK 74
DEBUG1 11
DEBUG1 12
DEBUG1 13
DEBUG1 14
DEBUG1 15
DEBUG1 16
MACK 77
MACK 78
MACK 79
MACK 80
MACK 81
F1 2
COR24 2
MACK 83
MACK 90
MACK 91

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```

1 SUBROUTINE PREY
  COMMON FL,FISH,FISHAN,FISHVF,FISHVS,FISHW,
  1 EFF,PATCHN,PATCHV,PATCHD,PREYD,PREYV,PREYW,PREYVW,ORGOPA,
  2 DIAMP,PAT,4(1000),SERCH,SHOJLN,SHOJLA,SHOJLD,RA(3600),
  3 IR,KE,IRAS,IRINS,SECS,RJWRT,KAL,KI,R(1000)
  4 IA,J,L,IR,KAN
  5 IHR,TIN,SEC,RAT,RATT,RD,TIMES,PATCHA
  6 RATE,TIMES1,TIM2,RATI,LEN,AK
  7 PREYD,PREYV,PREYW,K
  10 C THIS SUBROUTINE OUTPUTS PATCH NUMBER, PATCH AREA, AND PATCH DENSITY, AND
  C ALLOWS FOR THE VARIATION OF THE THREE FACTORS
  C PREY DENSITY IS HELD CONSTANT FOR THIS RUN
  LA=0
  25 CONTINUE
  C THESE STATEMENTS ALLOW FOR FEEDING BETWEEN PATCHES
  IF(KNEAL)GO TO 10
  PREYD=.5*PREYD
  PREYV=.5*PREYV
  ORGOPA=PREYD/PATCHN
  GO TO 11
  10 CONTINUE
  C ORGOPA=THE NUMBER OF ORGANISMS PER PATCH
  ORX=PREYD/PATCHN
  ORGOPA=ORX
  25 11 CONTINUE
  ORN=ORGOPA/PREYW
  PATCHV=ORN*2*PREYV
  ENTRY PREY1
  30 24 CONTINUE
  RD=((PATCHV/(.2*3.1416))**.5*(1./3.))
  DIAMP=2*RD
  PATCHA=RD*RJ*3.1417
  ORGOPA=ORX
  PATCHD=ORGOPA/PATCHV
  IF (PATCHD,LE,PREYD) GO TO 23
  C THIS CALCULATES A PATCH WITH DEPTH 1/10 THAT OF THE DIAMETRE
  RETURN
  40 23 CONTINUE
  ENTRY PREY2
  LA=0
  C INCREASE PATCH VOLUME
  PATCHV=10*PATCHV
  IB=-1
  45 C TEST FOR PATCHINESS APPROACHING A RANDOM DISTRIBUTION
  PATCHD=(PREYD/PATCHN)/PATCHV
  IF (PATCHD,GT,PREYD) GO TO 24
  C CHANGE PATCH NUMBER
  22 PATCHN=10*PATCHN
  IB=-2
  50 C TEST FOR PATCH NUMBER=0.1
  IF(PATCHN,LE,0.01)GO TO 25
  LA=2
  RETURN
  55 END

```

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MACK 92
COMDEK 2
COMDEK 3
COMDEK 4
COMDEK 5
COMDEK 6
COMDEK 7
O4 2
O4UG2 1
MACK 99
MACK 100
MACK 101
MACK 102
MACK 103
DEBUG2 16
DEBUG2 17
D12 2
D12 2
DEBUG2 20
DEBUG2 21
DEBUG2 22
DEBUG2 23
MACK 104
D9 1
DEBUG2 24
DEBUG2 25
D5 3
D5 6
MACK 107
MACK 108
D12 3
D12 4
F1 2
DEBUG2 27
D5 7
MACK 111
D5 12
COR1 12
COR1 13
MACK 116
COR25 7
MACK 117
MACK 118
COR26 3
MACK 119
D5 11
MACK 121
MACK 122
MACK 123
COR27 2
D5 12
B3 1
COR25 8
MACK 127
MACK 128

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MACK	129
CMONDEK	2
CMONDEK	3
CMONDEK	4
CMONDEK	5
CMONDEK	6
CMONDEK	7
D4	2
DEAUG2	1
MACK	136
MACK	137
MACK	143
MACK	144
MACK	145
MACK	146
MACK	148
MACK	149
CDR21	3
MACK	150
COR27	3
COR4	1
COR21	5
COR4	5
COR21	6
MACK	152
MACK	153

PAGE _____

COR21	14
COR21	15
COR21	16
COR21	17
COR21	18
MACK	159
MACK	160

PAGE

MACK	161
COMDEX	2
COMDEX	3
COMDEX	4
COMDEX	5
COMDEX	6
COMDEX	7
04	2
DEBUG2	1
MACK	168
MACK	169
MACK	170
D11	1
MACK	171
COR31	1
MACK	171
MACK	174
MACK	175
MACK	176
D5	14
DAY	1
D5	15
D5	16
MACK	179
MACK	180
D8	1
D8	2
MACK	3
MACK	182
MACK	183
F1	4
F1	5
F1	6
F1	7
F1	8
MACK	184
DEBUG2	30
MACK	186
MACK	187
DEBUG2	31
DEBUG2	32
MACK	190
MACK	191
COR1	14
F1	9
F1	10
F1	11
F1	12
F1	13
COR22	2
COR22	3
F1	13
F1	13
F1	16
F1	17
F1	18
COR22	5

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COR22	8
A1	7
A1	8
COR1	23
F1	19
DEBUG2	49
F1	20
F1	22
F1	23
F1	8
DAY	9
DAY	

76711/01. 18.08.09.

FTN 4.4+R401

SUBROUTINE OUTPUT 73/73 OPT=1

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115 WRITE(6,511) SCHOOLN,PATCHN,PATCHA,IHRS,IMNS,SECS,SECRT,RAFT,
      1 RATION,RATI
      IF(SCHOOLN.EQ.1) WRITE(6,525) PA,PATCHD
      525 FORMAT(1B,*,AVAILABLE RATION=*,G10.3,*,PATCH DENSITY=*,G10.3)
      511 FORMAT(1H,4X,F9.1,20,F10.8,132,G10.3,T46,15,153,13,158,F6.2,
      1 173,310.4,183,4(2X,G10.3))
      RETURN
      120 ENTRY OUTPUTS
      WRITE(6,500)
      600 FORMAT(1H,4X,*,SEARCHING TIME IS LESS THAN 20*SECONDS*)
      RETURN
      125 END
  
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Appendix II

Alternative algorithm for feeding subprogram.

In the main model, search was assumed to be a two-dimensional process; however, feeding is three-dimensional. In order to allow for this, I have considered the prey patches to be made up of a series of thin cylinders, each 5 cm deep. The predator feeds in a given cylinder until the density of prey in that cylinder has been lowered below the feeding threshold. The predator then starts feeding on the next cylinder and so on.

The ration, R_F , obtained by an individual fish is:

$$R_F = D_{Pr} V_{F1} E \quad (1)$$

where V_{F1} is the volume of water filtered during feeding and E is the efficiency of filtering taken as 0.8 in this model. V_{F1} can be determined from equation 2:

$$V_{F1} = U_{F1} A_{Fm} t_{F1} \quad (2)$$

where U_{F1} is the speed while filtering, A_{Fm} is the mouth area while filtering, and t_{F1} , the time spent searching.

A_{Fm} (cm^2) can be determined from an empirical equation given by MacKay (1976c):

$$A_{Fm} = 0.0132L^{1.895} \quad (3)$$

where L is fork length in cm.

Appendix II

• If U_{Fi} is known, then t_{Fi} is:

$$t_{Fi} = 2r_{Pa}/U_{Fi} \quad (4)$$

U_{Fi} is taken to be 1.5L/sec after MacKay (1976b), although it may also be a function of prey density (Muir and Newcombe, MS 1973).

Equation (1) gives only the ration for an individual fish. The ration for a school, R_s would be:

$$R_s = R N_s \quad (5)$$

However, this assumes that the same volume of water is not filtered more than once. This premise is valid only for wing formations or widely spaced schools. In more compact schools, the plankton density is constantly being lowered by the preceding fish. In order to consider this type of feeding, it is necessary to reconsider the matrix model of school shape (Figure 2).

The first wave of fish (row 1 and column 1) encounter the original plankton density within the patch D_{Pa} , but the second wave of fish encounters a density $D_{Pa} - R_1$; the third group, $D_{Pa} - R_1 - R_2$ and so on. The number of fish in each wave within the school, N_F is given by:

$$N_F = 2L_r - (2n - 1) \quad (6)$$

Appendix II

The ration for one pass through the patch is given by equation 7.

$$R_S(1) = \sum (D_{Pa} - R_L)^{N_F W_F^E} \quad (7)$$

while the ration for all passes through the patch is:

$$R_S = \sum_n R_S(n) \quad (8)$$

Feeding continues until either one of two conditions is met: (1) the stomachs are full (i.e., 10% of body weight [MacKay, unpublished data]), or (2) when D_{Pa} is reduced to a threshold below which filtering does not occur. For the initial runs, this threshold is 3 g/m^3 .

The total ration for each school is converted to a ration per fish and expressed as a % of body weight by the following relationship:

$$RW_F = 100 \frac{R_S}{N_S W_F} \quad (9)$$

where the weight of fish in g is determined by the general weight-length relationship (MacKay, 1976a).

$$W_F = 0.0059 L^{3.154} \quad (10)$$

where L is fork length in cm.

TABLE 1

List of symbols and subscripts used in a simulation for the Atlantic mackerel feeding on aggregated prey.

SYMBOL

A - area	R - ration
D - density	RW - ration as % of body weight
D ₁₁ - distance to nearest neighbour	RD - reactive distance
E - efficiency of filter feeding	SP - search path
h - height	t - time
L - length	Th - threshold
N - number	U - swimming speed
r - radius	V - volume
	W - width
	Wt - weight

SUBSCRIPTS

c - column	r - row
F - individual fish	S - school
F ₁ - filter feeding	Se - search
M - mouth	Sn - snout
Pa - patch	
Pr - prey	

TABLE 2

Initial state and range of variables used in simulation of feeding of the Atlantic mackerel in a patchy environment.

VARIABLE	INITIAL STATE	RANGE
A_{Pa} - Patch area		varies with D_{Pr} , N_{Pa} and assumptions of patch shape
D_{lIF} - interfish distance (m)	$0.6 L_F$	$.2L_F - 1L_F$
D_{Pr} - Prey density g/m^2	6.0	1.5-15
L_F - Fish fork length (m)	0.32	.15-.50
N_{Pa} - Number of patches (km^2)		1-1000
N_S - Number of fish/school		1-77284
RD - Reactive distance (m)	0.5	.25-10
U_{Se} - Swimming speed while searching (m/sec)	0.32	0.10-0.40
U_{F1} - Swimming speed while filter feeding (m/sec)	$1.5L_F$	
Patch shape	cylinder with depth 0.1 diameter	sphere to cylinder of depth 0.1 to 10
Proportion of prey in patch	.5	0.1 - 1.0
Prey diameter	1mm	
Prey shape	cylinder	

TABLE 3

Comparison of ration (% BW/fish/day)

when the predator is assumed to have (A) an unlimited capacity or (B) when the predator stops feeding at 10% body weight. (1 patch/km², Patch area = 13.9 m², Fish length = 32 cm, all other variables as in Table 2).

Number fish/ school	Ration A	Ration B
1	1.06	0.90
9	1.22	1.04
81	1.56	1.32
784	2.61	2.21
7744	5.91	5.02
77284	16.40	12.00

Table 4 Changes in search time (t_{se}) in hours and ration as % of body weight (RW), with variations in patch area for a simulation based on a constantly swimming filter feeding fish such as the Atlantic mackerel, A) area changes as volume is increased 10X, B) area changes as prey density increases Half the plankton is present as patches

(A)										
Patch area (m^2)	13.9		64.4		298.7		1,386.4		5,434.1	
Patch density (g/m^3)	5×10^5		5×10^4		5×10^3		515		51.5	
School No	t_{se}	RW	t_{se}	RW	t_{se}	RW	t_{se}	RW	t_{se}	RW
1	166.9	1.1	86.4	2.1	42.3	4.2	20.2	8.7	9.5	17.5
9	144.3	1.2	79.9	2.2	40.7	4.3	19.8	8.9	9.4	17.7
81	113.5	1.6	69.5	2.5	37.8	4.7	19.1	9.2	9.2	18.0
784	67.8	2.1	49.2	3.6	30.9	5.7	17.1	10.2	8.8	19.0
7744	29.8	5.9	25.6	6.9	19.6	9.0	13.0	13.5	7.5	22.1
77284	10.8	16.4	10.1	17.4	9.0	19.5	7.3	24.0	5.2	32.0

(B)										
Patch area (m^2)	5.5		11.4		13.9		20.1		25.5	
Prey density (g/m^2)	3		9		12		21		30	
School No	t_{se}	RW	t_{se}	RW	t_{se}	RW	t_{se}	RW	t_{se}	RW
1	238.0	0.2	180.2	0.7	116.9	1.1	143.2	2.2	129.5	3.4
9	194.6	0.2	154.1	0.9	144.3	1.2	126.2	2.5	115.5	3.8
81	142.5	0.3	119.5	1.1	113.5	1.6	102.0	3.0	94.9	4.9
784	77.2	0.6	69.9	1.9	67.8	2.6	63.5	4.9	60.7	7.3
7744	31.5	1.4	30.2	4.4	29.8	5.9	29.0	10.7	28.4	15.6
77284	11.0	4.0	10.5	12.3	10.8	16.4	10.6	29.0	10.6	41.8

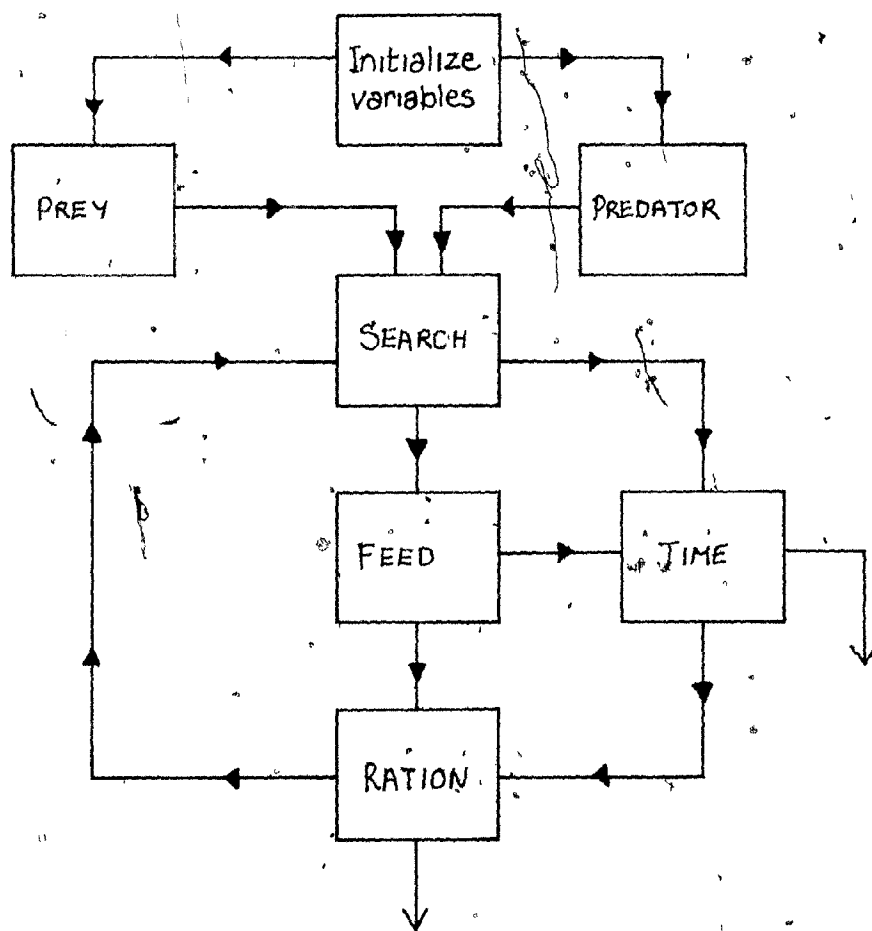
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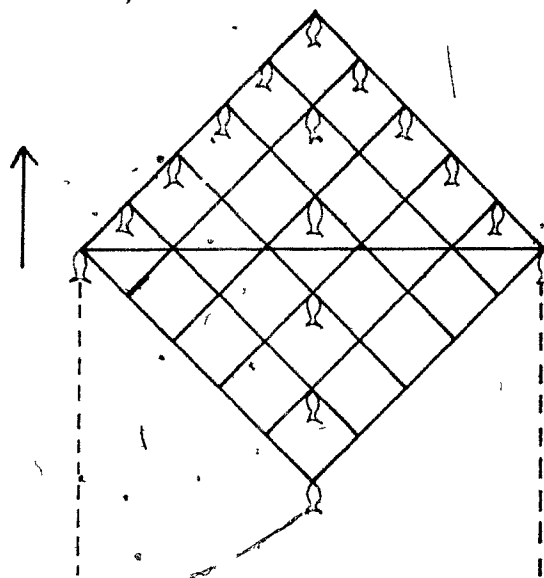
Changes in searching time (t_{Se}) and ration as % of body weight (RW) for a constantly swimming fish such as the Atlantic mackerel for different proportions of plankton in a patch.

Proportion of plankton in patch (%)	100	/	50		10	
Patch area (m ²)	22.0		13.9		22.0	
Patch density (g/m ³)	5.2 x 10 ⁵		9.0 x 10 ⁵		5.2 x 10 ⁴	
Fish/School						
	t _{Se}	RW	t _{Se}	RW	t _{Se}	RW
1	137.9	2.6	166.9	1.1	137.9	0.3
9	122.1	2.9	144.3	1.2	122.1	0.3
81	99.3	3.6	113.5	1.6	99.3	0.4
784	62.5	5.7	67.8	2.6	62.5	0.6
7744	28.7	12.3	29.8	5.9	28.7	1.2
77284	10.6	33.3	10.8	16.4	10.6	3.3

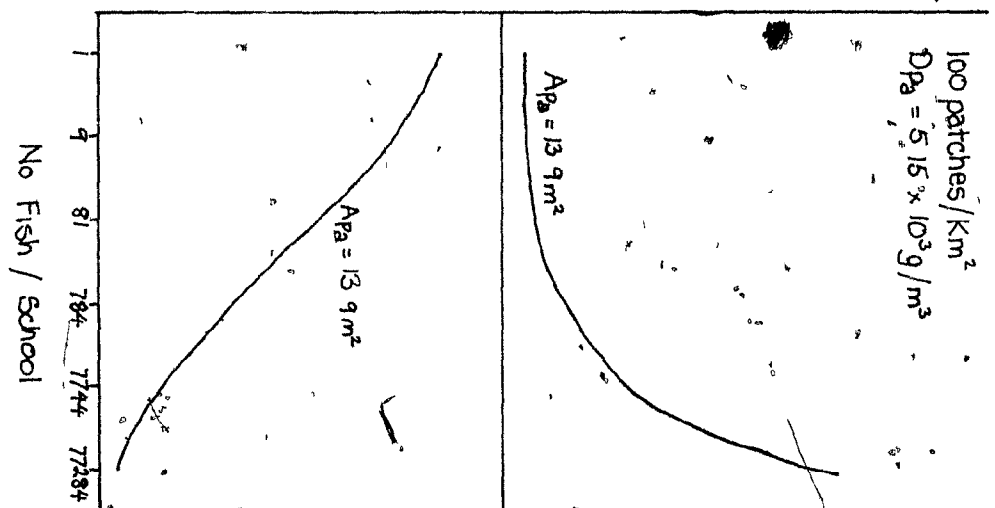
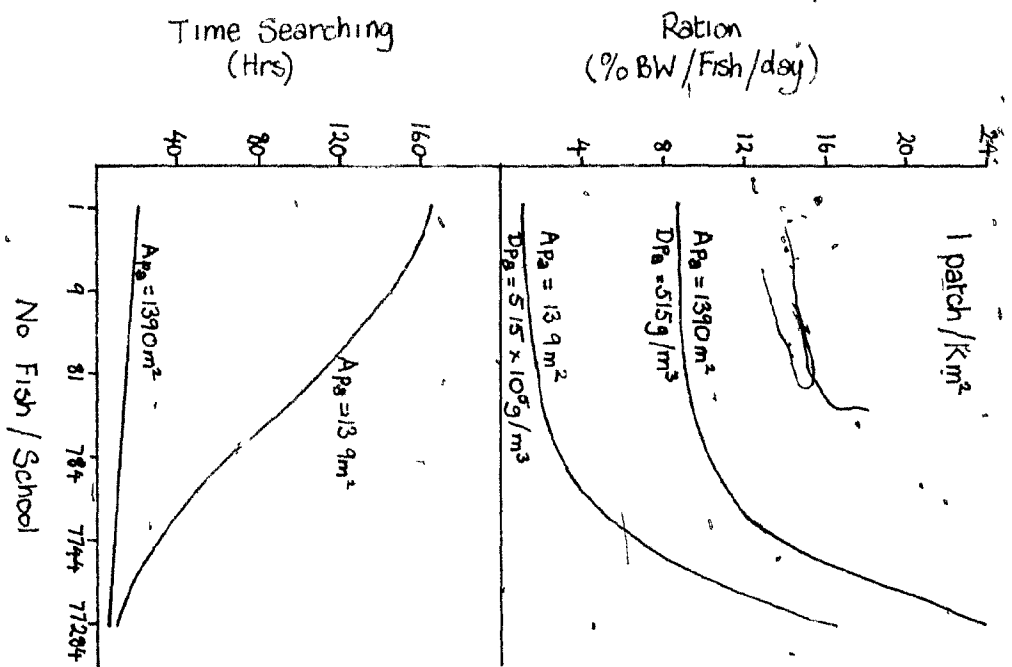
CAPTIONS FOR FIGURES

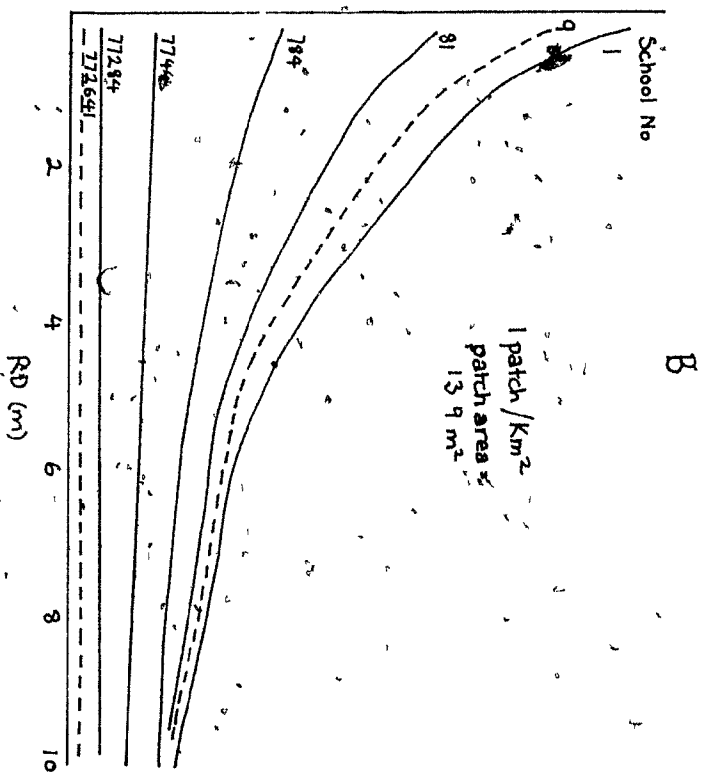
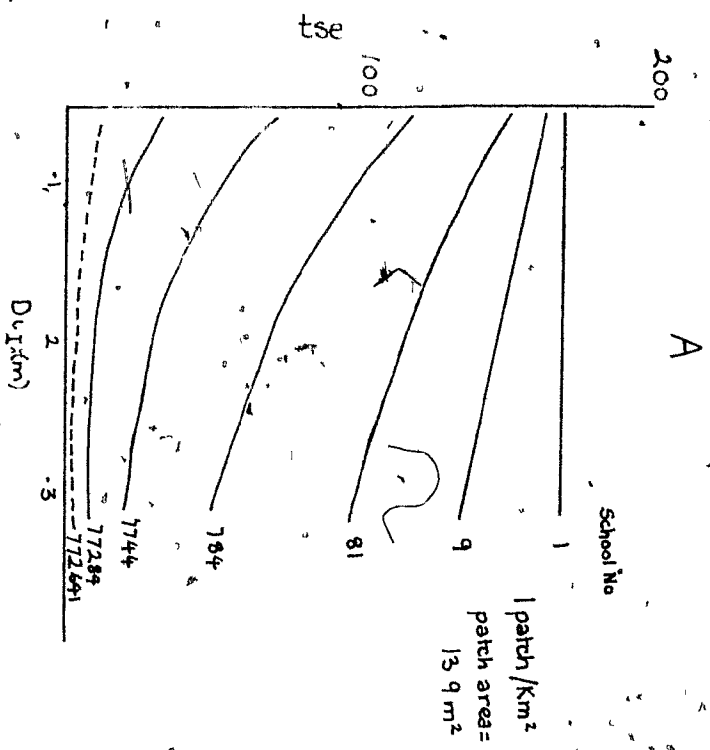
- Figure 1: Schematic diagram for a simulation of the Atlantic mackerel, feeding on aggregated prey.
- Figure 2: Diamond-shaped school of Atlantic mackerel used in the feeding simulation.
- Figure 3: Output of the simulation indicating time searching (t_{se}) and ration (RW) for various school sizes for different patch areas and numbers.
- Figure 4: Effect of varying interfish distance (D_{IF}) and reactive distance (RD) on time searching (t_{se}).
- Figure 5: Changes in time searching (t_{se}) and ration (RW) with changes in searching speed (U_{se}) for various school sizes.
- Figure 6: Changes: (A) in time searching (t_{se})
(B) in relative ration and
(C) in absolute ration, with changes in fish length.
- Figure 7: Change in time searching (t_{se}) with different shapes of patches, from a sphere to a cylinder of varying depths.
- Figure 8: Change in ration with changes in patch area. Vertical lines mark the minimum school area for each school.

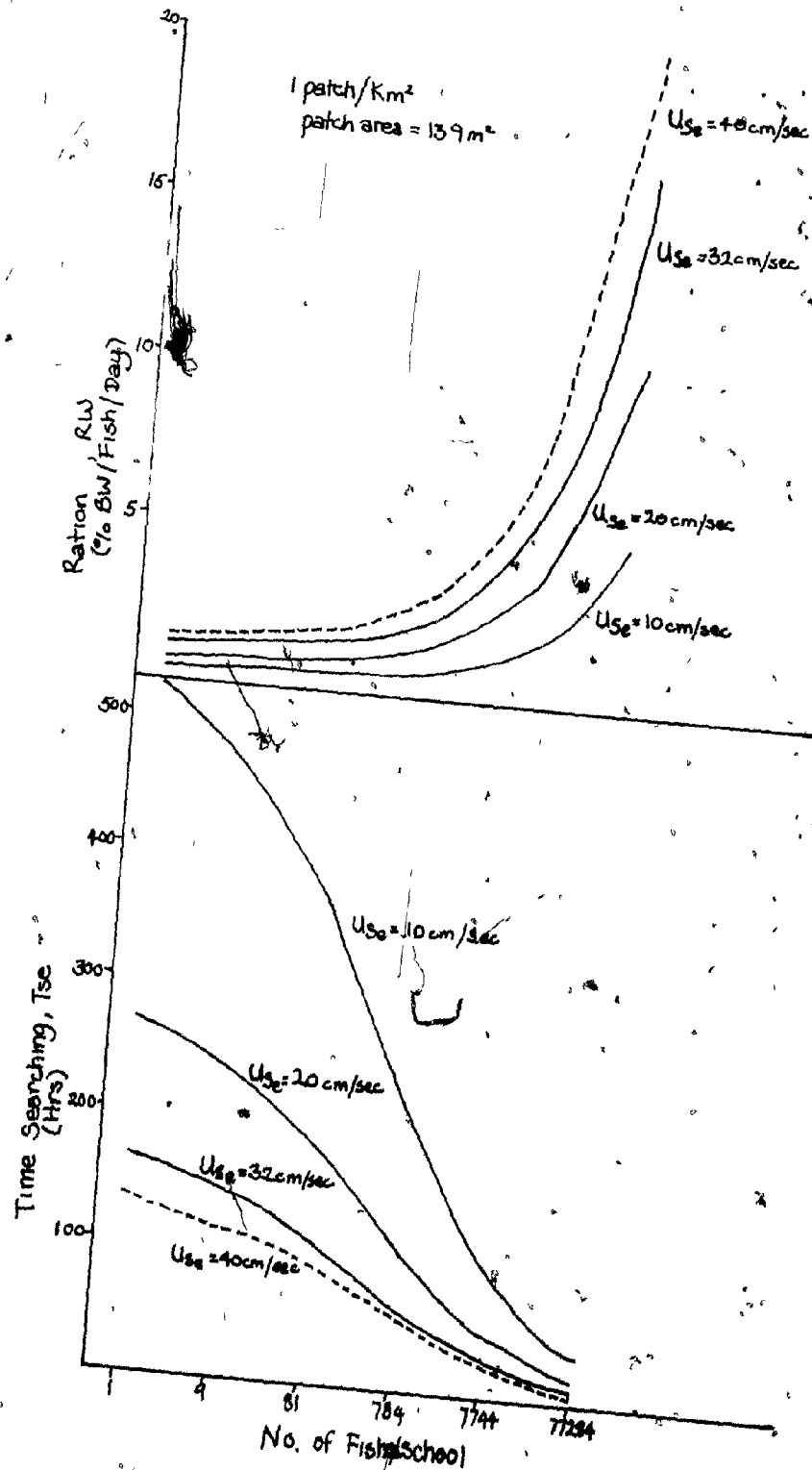


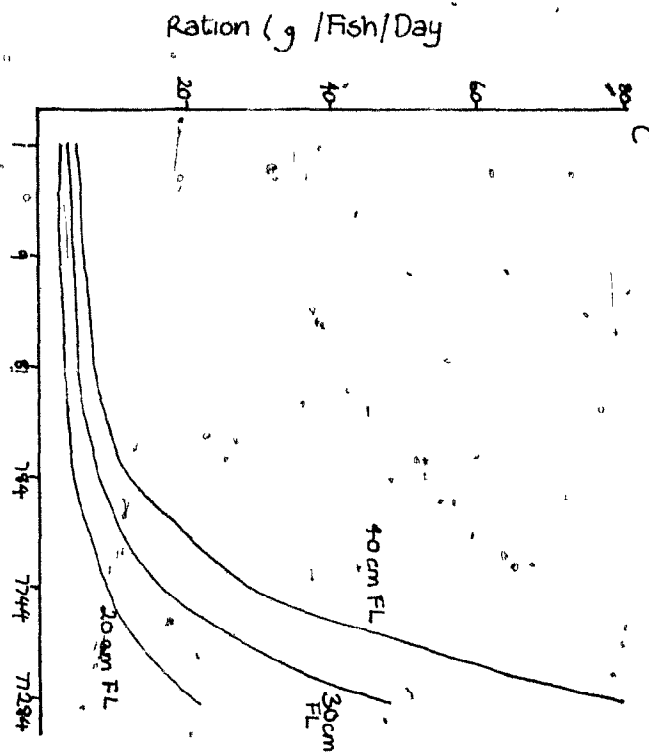
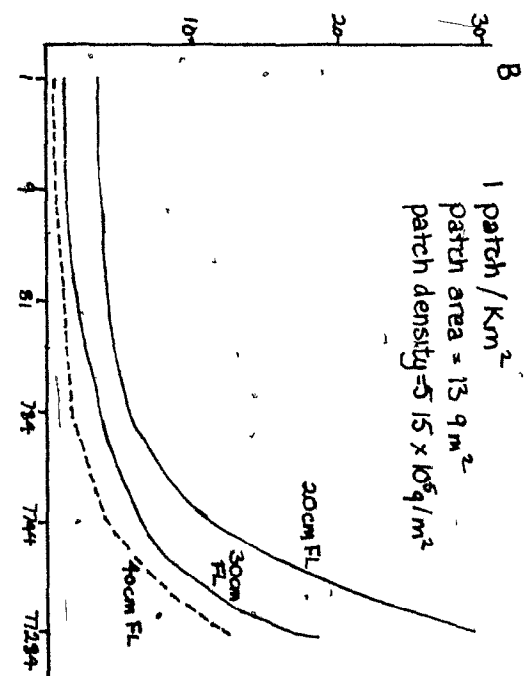
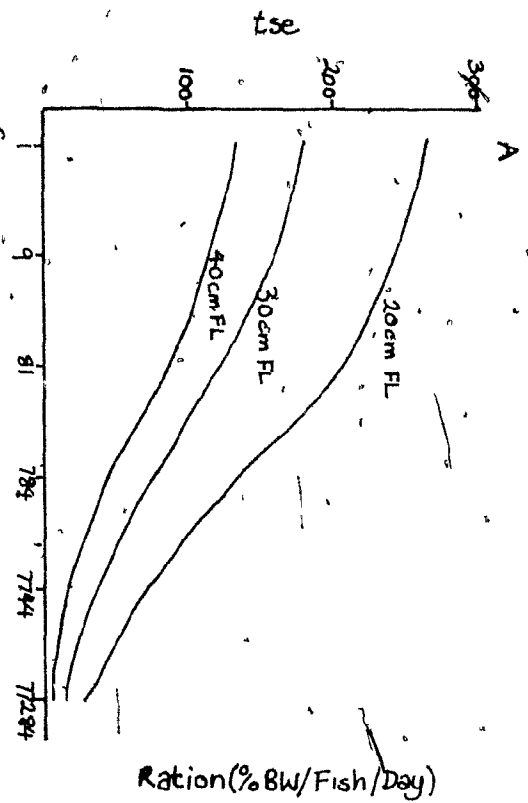


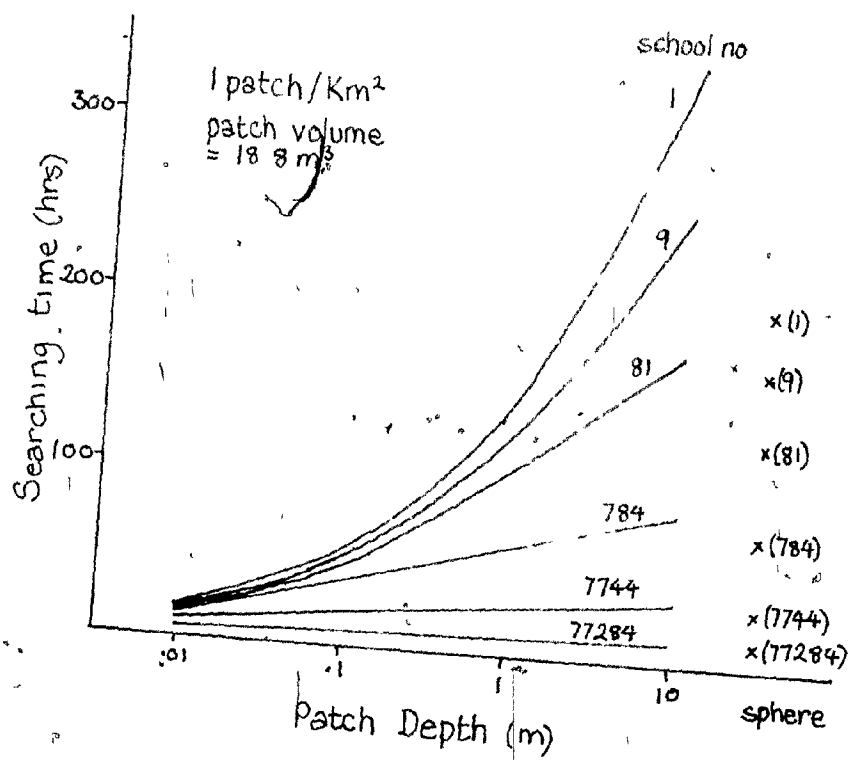
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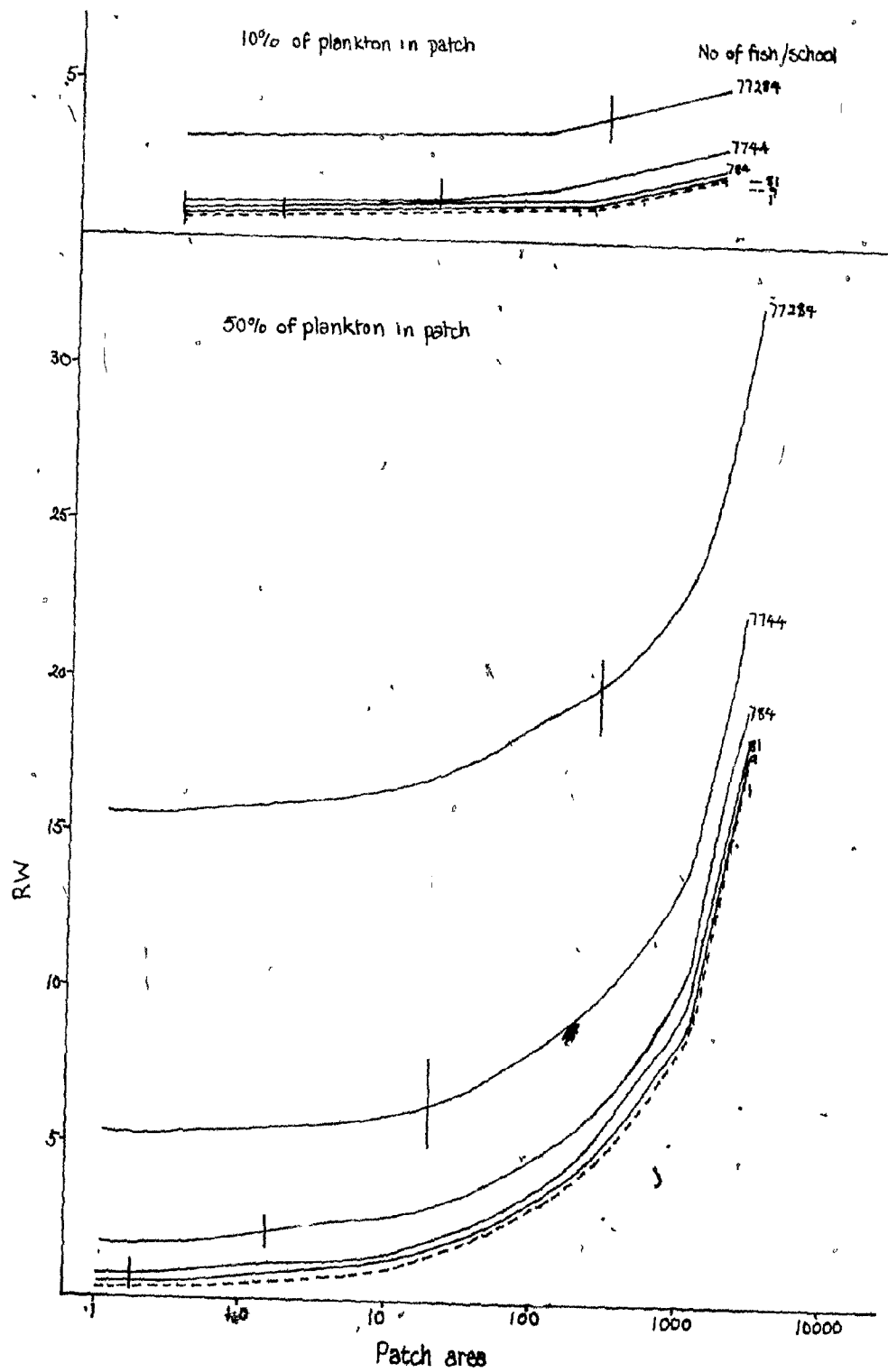












SECTION D

COLOUR

CHAPTER 4

Population dynamics and productivity of the
northern population of Atlantic mackerel

Scomber scombrus L.

ABSTRACT

Data on egg abundance are used to estimate the size of the northern population of Atlantic mackerel during 1967-1969. The spawning stock was 5.1×10^9 fish during 1968 and 1969. The abundance in 1967 was only 0.3×10^9 fish due to unusual oceanographic conditions which prevented most of the spawning stock from entering the Gulf of St. Lawrence. Stock abundance was calculated from the estimates for 1968 and 1969 for both spawning population and total population from 1960-1974, assuming two levels of mortality. At $M = 0.15$, total population ranged from 1 to 18×10^9 , while biomass varied from 1 to 7×10^6 MT. Both numbers and biomass are more variable for $M = 0.30$, with numbers ranging from 5 to 52×10^9 while biomass ranged from 0.4 to 8×10^6 MT. Population estimates for both mortality levels were higher than are estimates based on virtual population analysis.

Annual mackerel productivity has varied widely depending on the influence of dominant year classes. Gonad production is important and occasionally exceeds somatic production. The seasonal migration of mackerel transfers materials and energy between the Gulf of St. Lawrence and the Atlantic Shelf region. In 1968-1969, mackerel accounted for a net export of 5×10^9 Kcal of energy and 60×10^3 MT of protein from the Gulf.

The stock recruit relationship is of the Ricker type indicating a strong negative feedback from population size to recruitment. Recruitment appears to be controlled by density dependent intra- and inter-cohort competition and predation.

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I. INTRODUCTION

The northern population of the northwest Atlantic mackerel, Scomber scombrus L., is extremely important in the productivity of the Gulf of St. Lawrence. Mackerel may control herring recruitment (Winters, 1975) and appear to control zooplankton size composition (MacKay, unpublished data). In fact, Lett et al. (MS, 1975) have suggested that mackerel are the driving force within the pelagic fish community of the Gulf of St. Lawrence.

Mackerel spawn over the Magdalen Shallows in June, during which time mackerel eggs comprise a sizable portion of the zooplankton biomass. The growth rate of young is rapid, and the juveniles appear to use the large food items present in inshore and estuarine areas to maintain this growth rate. Adults are found throughout the Gulf of St. Lawrence where they filter feed on zooplankton and particulate feed on larger organisms such as euphausiids, fish larvae, and small fish such as capelin. During the summer, they accumulate enough fat to sustain them during an overwintering non-feeding period outside the Gulf. Furthermore, the seasonal migration in spring and fall couples the Gulf of St. Lawrence with the Atlantic coast shelf system.

Surprisingly, little is known about mackerel population dynamics and bioenergetics. In this paper, I synthesize twelve years of mackerel research to shed some light on the role that mackerel play in the dynamics of the productivity system of

the Gulf of St. Lawrence. Other papers in this series have summarized the available biological data on the northern population, examined the hydrodynamics of the constantly swimming mackerel, and explored the role of constant swimming, schooling, and filter-feeding on feeding on patchily distributed prey (MacKay, 1976 a,b,c).

II. METHODS OF CALCULATION

A) Population abundance.

Conventional methods of estimating populations, such as catch and effort or tag-recapture, are not useful for under-exploited fish stocks. The northern population of mackerel has only recently experienced high fishing pressure and that fishing pressure occurs during the overwintering period when they are mixed with the southern population and the proportion of the northern population in the fishery is unknown. However, a population estimate can be obtained from the analysis of egg abundance over the spawning grounds. Beverton and Holt (1956) considered this method suited to pelagic spawning fish, and Sette (1943) used egg surveys to estimate the abundance of the spawning stock of the southern population of mackerel.

Data suitable for estimating the northern population are available from two sources. Extensive plankton sampling for mackerel eggs during the spawning season (June 16-20, 1967; June 18-24, 1968; and June 11-20, 1969) was carried out by Arnold (MS 1970). The available data included surface distribution of eggs as sampled by a #0, 1m ring net for 1967-1969 and distribution at 15m for 1967-1968. The data are summarized by Arnold in a series of figures (see Figure 1 for example) in which the egg numbers are plotted for each station. In addition, during the 1969 cruise, highspeed Miller samplers were towed at five different depths yielding information on depth distribution. Additional information on egg abundance

is available for 1968 (June 17-22) from two vessels from the Bedford Institute of Oceanography (BIO), the M.V. BRANDAL and C.S.S. DAWSON working over the Magdalen Shallows. From these cruises total number of eggs is available for vertical hauls with either a 3/4 or 1/2 m Hensen net. (Anon, MS 1970). While the fish eggs were not identified as to species, my inspection of the samples indicates that mackerel eggs were overwhelmingly predominant, to the point where an assumption that all eggs in the sample were mackerel eggs would not be seriously in error.

Arnold's review of the literature on distribution of mackerel eggs and his own data support Sette's (1943) conclusion that the Gulf of St. Lawrence is the major spawning area of the northern mackerel population. Within the Gulf of St. Lawrence, spawning is concentrated in the southwestern portion of the Magdalen Shallows between the Magdalen Islands and Gaspé. I have confined my analysis to the Magdalen Shallows excluding Georges Bay, Northumberland Strait, and the interior of the Baie du Chaleur, where the abundance of mackerel eggs is relatively low.

While the egg sampling was unequal from year to year and at no time was the density of sampling very high (Figure 1), the results of all three years indicate a rather large scale, apparently non-random pattern of concentration. To better define the nature of this pattern, the area of the Magdalen Shallows may be subdivided into smaller areas following the lines of latitude and longitude. The resulting grid in Figure 1 overlays the result of Arnold's surface sampling for 1968.

The area of each grid was calculated by a planimeter, and the available egg density data were converted to numbers of eggs per m^2 of sea surface within each grid. The BIO sampling was made by vertical hauls so it was necessary only to adjust them for net area. However, Arnold's sampling was by horizontal tows, and the data are given as egg numbers per m^3 ; so that it was necessary to calculate an integrated value for the vertical distribution from the observed values.

As data were available for surface and 15m, and mackerel eggs were concentrated at the surface and not found below 25 m (Arnold, MS 1970; Sette, 1943), it was logical to assume a regular rate of decrease in egg numbers from surface to 15m and another rate to 25m. The vertical egg distribution is, thus, approximated by a trapezium, whose area can be calculated by the following equation:

$$\sum E = \frac{15(E_0 + E_{15}) + 10E_{15}}{2} \quad (1)$$

where E_0 and E_{15} are egg abundances at surface and 15m.

The number of eggs for each block can be obtained from the area of the block times the number of eggs/ m^2 ; while the number of eggs for all blocks is obtained by summing the block totals.

However, this represents standing stock rather than production. To calculate total egg production for the 4 week spawning period of this northern population, I have used a normal curve to represent the change in egg abundance

with time, following the example of Saville (1956) who found this approximation useful for Faroe haddock. Total egg production for the southern mackerel population was determined by Sette (1943), assuming seven different egg renewals. However, the use of a normal curve for the northern population is more reasonable considering their short spawning period.

Density data for eggs were, of course, not obtained simultaneously, but over the period of as much as 2 weeks for each cruise. To facilitate calculation of egg production, I have assumed that each sample was taken on the midpoint of each cruise. I have then taken this midpoint to represent the peak of spawning, and the sum of all eggs is proportional to the productivity on that day. However, this sum represents all stages of eggs. Arnold found that 73.5% of eggs sampled during 1967-1969 were Stage 1 (first 30 hours). I have, therefore, used this value to convert total egg count to the equivalent daily production of eggs. This estimate of daily production can then be converted to total production by reference to a table of normal deviates. For a four-week spawning period, the daily production represents 5.6% of the total production. Due to the assumption of a normal curve, this estimate represents only 95% of the total spawning, and a conversion to 100% was necessary.

Further data are necessary to convert this value of egg production to population and biomass. The relevant year-class composition, fish length and weights, and gonad weights for 1967-1969 are summarized in Table 1.

Fecundity was determined from the gonad weights using an equation from MacKay (1976a) and is presented in Table 1. The resulting estimate of population was multiplied by two to account for males (sex ratio = 1:1).

B) Population abundance 1960-1975

A population estimate for each year 1960-1974 could be determined using the egg abundance estimates for 1968 and 1969¹ as a baseline.

The population size on January 1, 1969 was first obtained from the average of the 1968 and 1969 estimates of spawning stock. The abundance of each cohort could be obtained from the year class composition for the spawning period in 1969.

Year class compositions based on age-length keys were available for 1962-1973 for two periods representing the spawning and summer populations (Table 2). The year class composition for the summer population was based on sampling from 4T during July and August and occasionally September and October. This year class composition was more variable than that for the spawning population, reflecting the higher sampling error and the disproportionate number of younger fish present in the Southern Gulf.

The spawning population is best sampled in 4Vn and 4T during June, but only in 1971-1973 was sampling concentrated in this area. However, the same length and age composition is found in 4W and 4X during May and June as is found in 4Vn and 4T during July. Therefore, these data for 4W and 4X were used

¹Egg abundance in 1967 was much lower than in 1968 and 1969, apparently because of a change in migration pattern due to unusual oceanographic conditions (MacKay, 1976a) and I have, therefore, not used the 1967 estimate.

to obtain year class composition for the spawning population in years other than 1971-1973. The resulting age estimates are consistent from year to year and agree quite well with other age estimates (MacKay, 1976a).

The 1966, 1967, and 1968 cohorts were not adequately represented in the spawning population in 1968 and 1969 as they were not fully recruited. The 1966 y/c became fully recruited at age 3 in 1969. The proportion of this y/c in the spawning population in 1969 was used to obtain an estimate of its abundance for January 1, 1969. The 1967 and 1968 y/c were fully recruited in 1972. Their abundance in that year was determined from their percentage composition in relationship to the persistent 1959 y/c. Their abundance in 1969 was then determined by backcalculation using the method described below.

The size of each cohort in other years can be determined if the natural and fishing mortalities are known. The abundance of each cohort on January 1 for each year from 1968-1960 could be backcalculated using the basic equation of the cohort analysis, a modification of the virtual population analysis (Pope, 1972).

$$N_i = N_{(i+1)} e^M + C_i e^{M/2} \quad (2)$$

where N_i is the cohort abundance in year 1,

$N_{(i+1)}$ is the cohort abundance in year 2,

M is the natural mortality rate and

C_i is catch of the cohort in year 1.

Likewise the population from 1969 onward could be calculated from a rearrangement of equation 2

$$N_{(i + 1)} = N_1 e^{(-M)} - C_1 e^{(-M/2)} \quad (3)$$

Abundances estimates for the 1970-1972 y/c's could not be obtained by the present analysis but estimates were available from Anderson (MS 1975a). The abundance of the 1969 year class which was fully recruited in 1973 was obtained in a similar manner to that for the 1967 and 1968 y/c's.

Two estimates of natural mortality were used: $M = 0.15$ and $M = 0.30$. While M may vary with age and stock abundance (Beverton and Holt, 1957), I assume that M is constant.

Catch data for each year class from 1968-1974 for the entire ICNAF fishery is available from Anderson (MS 1975a). I have adjusted these data for the proportion of the catch that could belong to the northern population by assuming that all the catch except that made in SA 5 and 6 during June-October belongs to the northern population. This was done using detailed catch information from Anderson (MS 1975b). For years prior to 1968 I have assigned the entire ICNAF catch to the northern population.

C) Spawning population

The abundance estimates of the spawning portion of the stock were necessary to establish a stock recruit relationship. The estimates for 1967 to 1969 were taken directly from the population estimate based on the egg abundance information. The estimates for fully recruited year classes in other years

are based on the results of the cohort analysis. For year classes which are partially recruited, the age composition data (Table 2) used to determine a proportion of that year class relative to another dominant year class. This proportion is used to obtain the numbers of spawners for that cohort.

The estimates for egg abundance and cohort analysis for 1968 and 1969 are in close agreement; however, the 1967 estimate based on egg abundance is much lower than that for the cohort analysis. As I argue later (See Results) unusual oceanographic conditions appeared to have prevented a sizable portion of the spawning stock from entering the Gulf of St. Lawrence. Instead they remained and spawned on the outer coast of Nova Scotia. I, therefore, use the much lower estimates based on the egg abundance data to represent the abundance over the normal spawning grounds, the Magdalen Shallows.

D) Production

Biomass calculations required both number and weight at age for each year class. Numbers at age were obtained from the preceding estimation of population size (Table 7). Lengths at age for each year class were obtained from the age-length data, converted to weights using the appropriate length-weight regression (MacKay, 1976a) for 1969-1973. Prior to 1969, weight was determined from an average weight-length regression of

$$SW = .0059 (FL)^{3.154} \quad (4)$$

where SW is somatic weight in grams and FL is fork length in cm.

In order to calculate mean biomass, it was necessary to obtain weights for January. I have used a regression equation determined for fall 1973 (MacKay). The lengths used for calculation of these weights were the lengths for the following June, as they approximate the lengths in fall and winter.

Somatic productivity could be estimated according to Chapman (1971) as:

$$P_s = G\bar{B} \quad (5)$$

where mean annual biomass, \bar{B} was determined from:

$$\bar{B} = \frac{B_{J_1} + B_{Ja_2} + B_{J_2}}{3} \quad (6)$$

B_{J_1} , B_{Ja_2} , and B_{J_2} are biomass on July 1 of year one, biomass in January 1 of year two, biomass on July 1 of the second year, respectively.

The instantaneous growth coefficient, G , can be calculated as:

$$G = \ln W_2 - \ln W_1 \quad (7)$$

where W_1 and W_2 are weights in July of year one and weights on July 1 of year two, respectively.

Gonadal productivity (P_g) is simply the number of spawning fish on July 1 (N_J) times the gonad weight.

$$P_g = N_J \quad GW \quad (8)$$

Gonad weights were determined from the regression appropriate to each year (op.cit.). Prior to 1969, I have used the 1972 gonad weight-length regression, which appears to yield

and mortality. Estimates of production were made separately for each year-class and then summed for each year.

The amount of material and energy transferred to and from the Gulf of St. Lawrence by the northern hake population could be calculated for 1968-1969 using the estimates of biomass and production. As there is only a 3% difference between the biomass estimates for the two mortality estimates, I have used only the values for $M = 0.29$. Information on fat content and water content of the fish was obtained from MacKay (1976a). The caloric equivalents used were 9.45 Kcal/g for fat and 5.65 Kcal/g for protein (Brett and Warren, 1971).

III. RESULTS

A) Population abundance

(1) 1967-1969

The average rectangular egg abundance (M^3) for surface and 15m from Arnold's data for each block is presented in Table 3. These data were used to calculate the integrated values presented in Table 4 where they are compared with the values obtained from the BIO data. In 1969, no information was available on egg abundance at 15m. In order to obtain an approximation of the integrated value from the surface value, I have used a conversion factor of 10. This conversion factor was obtained from a comparison of the surface values (Table 3) with the integrated values (Table 4) for 1967 and 1968.

Sampling was restricted in 1967, but the area sampled contained 5% of the eggs in 1968 and 1969 when the surveys were more extensive and representative. The 1967 values were multiplied by 1.9 to account for the larger spawning area.

Inspection of the raw data on egg distribution indicates a large variability. This is documented in Table 5a which indicates the means and variances from three different blocks in 1968 for the three types of sampling. The variances for all blocks and samples are larger than the mean. Variance larger than the mean indicate an aggregation or patchy distribution (Pielou, 1969). It is also apparent that catches in the horizontal tows made by Arnold had much lower variances than catches in the vertical hauls. This is to be expected

if distribution is patchy. The horizontal tows would tend to integrate the small scale patchiness.

The estimated abundances of the northern spawning population of mackerel are presented in Table 4 which details the steps used in these estimates. The spawning population was 0.30 billion (i.e., 0.3×10^9) fish in 1967, 5.11 billion in 1968, and 5.09 billion in 1969.

It is difficult to ascribe significance to these population estimates as the most serious weakness of the use of egg surveys for estimating population abundance is that given extensive samples, the combination of spatial and temporal variability of the sampling data do not allow for calculation of confidence limits (English, 1964; Saville, 1964).

In spite of these difficulties the number of eggs in 1967 is over an order of magnitude lower than in 1968 or 1969, a difference which is significant at $p < 0.02$ using the Student t test (Table 5b). The large increase in population between 1967 and 1968 cannot be accounted for by the recruitment of the 1965 year-class, which was relatively small (Table 1). It could be argued that the sampling in 1967 missed substantial portions of the Gulf where spawning could have been intense. This appears very unlikely as the area covered in 1967 contained 67% of the eggs in Arnold's 1968 sampling and 52% of the eggs in the 1969 sampling. There is some evidence that the spawning population behaved abnormally in 1967 and that unusual oceanographic conditions prevented the majority of the spawning stock from entering the Gulf

of St. Lawrence. For example the commercial catch in the Gulf of St. Lawrence was only 28% of the total compared to a long term average of 45%. Furthermore the commercial catch during summer on the outer Nova Scotian coast was well above average, and there was the abnormal occurrence of large fish eggs and larvae on that coast during 1967 (MacKay, 1976a; Martell, MS 1967).

There are various sources of errors in the estimate of population. One of these possible sources of error is the approximation of the total number of eggs obtained from Arnold's data by Equation 1. Using the results of Arnold's Miller samplers from 1969, I compare my approximation to the values derived from the 12 typical profiles he presents. The difference between the two values ranged from +28 to -24%; however, there was an average difference of only 4%.

Clearly the duration of spawning and the shape of the egg production curve will affect the estimates of population size. I have used a two-week spawning period in an earlier preliminary estimate (MacKay, MS 1973) and that yields an estimate half that of the present estimate. However, the best information is that spawning occurs over a four-week period (MacKay, 1976a; Lambert Pers. Comm.). Detailed sampling for the four-week period is not available, thus we can do little but to assume that spawning activity follows a normal curve. Furthermore, the assumption that the day of sampling represents the peak of spawning is undoubtedly false;

errors of this assumption can only lead to an under-estimate of the true total egg production. I have not attempted to analyze for temporal variation, since it is so confounded with spatial patchiness as to make any such refinements inappropriate, at best.

The fecundity estimate is a most critical parameter affecting the estimate of numbers directly. I present a relationship for fecundity (MacKay, 1976a):

$$F = 4450.5 \text{ GW} \quad (9)$$

where GW is gonad weight which can be determined from gonad weight-length regressions given by MacKay. The resulting fecundity of a 40cm fish would be 400,000 eggs, the estimate used by Sette (1943).

A more detailed analysis of fecundity carried out in 1972 (Lambert, Pers. Comm.) was frustrated by the presence of different sizes of presumptive ova, leading to difficulties in interpreting which become eggs and were spawned and which were retained in the ovaries. Furthermore, there does appear to be a density dependent relationship (See Recruitment) which causes year to year variability in gonad weights. In the absence of more precise information, I have used my data on fecundity combined with gonad weights to obtain the relative fecundity (Table 1). However, it is most important, for any future use of egg production to estimate mackerel abundance, that more precise estimates of fecundity be obtained.

ii) Population abundance 1960-1975

An estimate of the abundance of each year class in the northern population for 1960-1975 for two levels of M are presented in Table 7A and B.

The two estimates of mortality indicate different population patterns (Figure 2). For $M = 0.15$, the population decreased slightly from 13 to 7×10^9 fish between 1962 and 1966; then increased to 18×10^9 with recruitment of the 1967 year class, and has gradually decreased to 7×10^9 fish in 1975. For $M = 0.3$, the population decreased rapidly from 52 to 11×10^9 fish from 1962 to 1966, increased to 22×10^9 with the recruitment of the 1967 year class, and rapidly declined to 3×10^9 fish in 1975. Prior to 1970, the estimated population for $M = 0.3$ is higher than for $M = 0.15$, but the situation is reversed after 1970 (Figure 2) due to the lower estimate of the 1967 y/c produced by the higher M estimate.

Abundance of the 1959 year class has ranged from 13 to 1×10^9 fish for $M = 0.15$ and 51 to 0.5×10^9 fish for $M = 0.3$. The 1967 year class has ranged from 11 to 3×10^9 fish for $M = 0.15$ and from 13 to 1×10^9 fish for $M = 0.3$.

In spite of the large variation in estimated numbers of mackerel, biomass for both mortality estimates has been remarkably constant. This is particularly so for $M=0.15$, biomass has ranged from a low of 2×10^6 metric tons (MT) in 1960 to a high of 5×10^6 MT in 1969 (Figure 2). Biomass for $M = 0.30$ has varied somewhat more and shows a different pattern, declining from a high of 8×10^6 in 1961 to a low of 2×10^6 MT in 1973.

B) Stock - recruit relationship

Estimates of the spawning stock for the two mortality values are presented in Table 8. The 1959 y/c has clearly dominated the spawning stock while the 1967 y/c has been important only since 1971. Total spawning stock has varied 2 orders of magnitude for both the mortality estimates.

Knowledge of the stock-recruit relationship is of considerable interest to management of the northern population of mackerel. In Table 9 I compare numbers of spawners, biomass of spawners and biomass of total stock to numbers of recruits at age 1, for both mortality estimates. The data suggests a general inverse stock-recruit relationship such that large year classes are produced only when spawning stock is low. A better relationship appears to exist when comparing total stock biomass to recruitment. This is indicated in Figure 3, where I have fitted Ricker type recruitment curves (Ricker 1975) to the data for both $M = 0.15$ and $M = 0.30$. The maximum level of recruitment is obtained when the stock is 1.3×10^6 MT for $M = 0.15$ and 1.2×10^6 MT for $M = 0.30$.

C) Productivity

In most considerations of productivity in unexploited populations, it is assumed that biomass, productivity, and the P/B ratio are fairly constant from year to year as a consequence of equilibrium populations with a stable age distribution. In the northern population of mackerel, age composition has fluctuated widely as the result of dominant year classes.

These impose fluctuations in biomass, productivity, and P/B. Estimates of these population attributes based on the two mortality levels are presented in Figure 3 and Table 10.

Unfortunately, my data do not permit realistic inclusion of fish in their first half year of life because estimates of growth and mortality are not available for them. The contribution of these youngest fish to biomass would be insignificant; however, their growth rate is clearly high; so that their inclusion would increase productivity significantly, particularly in 1967 when it would easily have equalled that of the rest of the stock.

Somatic production has fluctuated about an order of magnitude for both mortality estimates being influenced by the age structure of the population. Somatic productivity is highest when young fast growing fish dominate as in 1960, 1961 and 1968 and 1969. These estimates of productivity are underestimates particularly for 1967 because of the exclusion of fish in their first half year of life. Production may be even more variable than I have indicated because of the annual variations in the weight-length relationship (MacKay 1976a) which are not included prior to 1969.

Gonadal productivity has also varied almost an order of magnitude, but has remained quite constant over the 1964-1973 period. Gonad production is an important component of total production and often equals or is greater than somatic production, as in 1965, 1966, and 1971. It is apparent from examining the production of individual year classes (MacKay,

unpublished data) that gonadal production far exceeds the somatic production for older fish.

Turnover rate or P/B is usually applied to a single cohort or an equilibrium population. In this study, I examine a population P/B ratio. This ratio (Table 10) shows variations influenced primarily by the variable productivity. Of considerable interest is the close agreement of this ratio for the two mortality estimates, as inclusion of all the cohorts and gonadal production does not change the independence of the P/B ratio with mortality.

Somatic and gonadal production represents two different production systems. Somatic production is obtained from the Gulf of St. Lawrence system during July-October, when mackerel are feeding on zooplankton. This productivity is stored mainly as fat. It is exported from the Gulf when the fish leave and is used to provide energy for the overwintering period. Gonadal production is derived during a short period of intense feeding on large food items such as euphausiids and fish larvae in the New England and Scotian shelf regions. Thus, gonadal production represents an export from the shelf regions; and as this production is released as sex products, it represents a direct import into the Gulf of St. Lawrence system.

Using the estimates for 1968 and 1969, it is possible to indicate the magnitude of these transfers between the Gulf of St. Lawrence and the New England and Scotian shelf regions. These transfers are indicated in Table 11. There is a net

loss of both materials and energy from the Gulf of St. Lawrence. The loss of protein is 60,000 MT which is equivalent to the commercial catch of herring in 1969 in the Gulf of St. Lawrence. The input due to the sex products is 60,000 MT. As these sex products are released on spawning, they represent a sizable input of protein directly into the Gulf system.

The seasonal migration of mackerel results in a net export of 5.25×10^9 Kcal of energy from the Gulf of St. Lawrence. This large export of energy is mainly in the form of fat and is used by mackerel during the overwintering period. The winter fishery recaptured only 3% of this energy.

IV. DISCUSSION

A) Comparison with other estimates

Estimates of the total mackerel stock including both northern and southern populations exploited by the ICNAF fishery are available (Anderson, MS, 1975a; MS, 1975b; ICNAF, MS, 1976). These estimates are based on a virtual population analysis (VPA) by cohort analysis (Pope, 1972), using a natural mortality estimate of $M = 0.3$.

The results of Anderson's (MS, 1976a) estimates and my estimates for 1969 and 1973 are compared in Table 12. In 1969 my estimates based on egg abundance information indicates a population of 17.4×10^9 mackerel, 36% higher than Anderson's estimate. In 1973 my population estimates are also higher than Anderson's. For $M = 0.15$ I estimate 12.6×10^9 fish double the 6.0×10^9 fish estimated by the VPA analysis, while for $M = 0.30$ I estimate 8.4×10^9 fish. My estimates of biomass show an even greater difference from Anderson's. In 1969 I indicate a biomass of 4.7×10^6 MT, almost three times greater than his estimate, while in 1973 my estimates of biomass are 7.23 and 2.5×10^6 MT for $M = 0.15$ and $M = 0.30$ compared to 1.3×10^6 MT for Anderson's estimates.

As I have discussed previously the estimate of population for 1969 based on egg abundance information has numerous potential sources of error which make it impossible to place confidence limits on the estimates. Nevertheless, this estimate does suggest that the northern population could have accounted for the entire ICNAF fishery.

While VPA is used widely in assessing fish stocks it too is very sensitive to assumptions of natural mortality and availability and vulnerability of a cohort to the fishery. Unfortunately, while our techniques for assessing stock abundance are at best rather crude the management decisions require rather precise information on stock size. For example, the ICNAF mackerel assessment meeting (ICNAF, MS, 1976) recommends a drastic reduction in fishing effort to allow the spawning stock to build up from the estimated $.35 - .43 \times 10^6$ MT. However, my estimates of spawning stock extrapolated to 1976 suggest 1 to 2×10^6 MT more fish than the ICNAF estimates. If this larger stock is present it could support a considerable exploitation. It is therefore important to examine the discrepancies between the two estimates.

The main difference between our estimates is my higher estimates for the 1959 and 1967 y/c's. In 1969 I indicate

3.30×10^9 mackerel of the 1959 y/c, 55 times greater than Anderson's estimate. It is obvious from the age composition data (Table 2) that this year class has been dominant in the northern population and it was still evident in the spawning population during 1973. Clearly this year class has been underrepresented in the ICNAF fishery as only in 1968 has this year class been a major component of the ICNAF fishery (Isakov, 1973). It is possible that these larger older fish may have a greater net avoidance or they may overwinter in areas which are not being heavily fished.

My estimate for the 1967 y/c in 1969 is double that of Anderson's. However, my estimate of this year class is sensitive to errors in the estimation of the 1959 y/c as the baseline abundance of the 1967 y/c was not determined until it was fully recruited in 1972. It is certainly clear from both our estimates that this year class has been important in both the northern population and the total ICNAF fishery, with over 2×10^9 fish of this year class captured since 1968.

Both the YPA and my estimates for years other than 1968 and 1969 are sensitive to the level of natural mortality. As natural mortality for most fish populations is difficult to measure, I have used two estimates. The lowest estimates I consider is the lowest reasonable estimate for a long lived pelagic fish. $M = 0.20$ appears reasonable for the Atlantic herring in the Gulf of St. Lawrence (Winters, 1975) while

M for North Sea mackerel appears to range from 0.15 to 0.25. I have used $M = 0.30$ as an upper limit; this is the estimate accepted by ICNAF for stock assessment purposes and the value used by Anderson (MS 1976a).

Of interest is the different pattern of abundance which results from the two mortality estimates (Figure 2). For $M = 0.15$, biomass remained constant from 1960 to 1967 then moved to a new plateau with the recruitment of the 1967 y/c and biomass has remained high. On the other hand, for $M = 0.30$, biomass was very high in the early 1960's, decreased to 1967, increased slightly to 1968 and has continued to decline. It is also apparent that the major decline in biomass occurred prior to the large increase in the fishery.

Anderson (MS 1976) has recently examined indices of mackerel abundance based on research vessel surveys and commercial fishery catch. It appears on the basis of these that mackerel abundance increased to 1968 and has declined steadily since 1968. This decline in mackerel biomass gives some support to a higher estimate of M . Certainly, the higher estimate gives population estimates closer to those of Anderson than does the low estimate.

B) Recruitment

Various environmental variables such as temperature, lowered surface salinities, fresh water runoff, zooplankton abundance, the fungus, *Ichthyophonus hoferi* and abnormal winds can all influence successful recruitment in mackerel (MacKay, MS 1967; Sutcliffe, 1972; Sette, 1943).

However, the stock recruit curves (Figure 4) indicate a strong inverse relationship between stock size and recruitment. In the following I present some of the density dependent mechanisms which may influence recruitment in mackerel.

Density dependent fecundity has been suggested by Bigelow and Schroeder (1953) to explain density dependent recruitment in mackerel. Detailed information on gonad weights for 1969-1973 (MacKay, 1976a) allows a test of the density dependent hypothesis. The results for 37.7 cm fish are presented in Table 13. Gonad weights and fecundity have increased while total stock density has decreased.

The linear regression equations calculated from these data (Table 13, B) have a high correlation coefficient. Thus density dependent fecundity has occurred during this period. However, this has not resulted in any significant increase in recruitment during this period (Table 9).

The most important regulatory mechanisms on fish population abundance are density dependent larval growth and mortality (Cushing, 1974) and in fact, these two variables are probably linked (Ware, 1975). Density dependent growth does occur during the early life history of mackerel. I have shown (MacKay, 1976a) that size at age 1 for the abundant 1959 and 1967 y/c's is smaller than that for all other less abundant y/c's. However, density dependent mortality is not well documented for fish populations but is usually invoked to explain population stability (Ware, 1975).

A hint at the density dependent mechanism underlining larval survival can be obtained using some limited larval abundance data collected during July 1967, 1968 and 1969 in an Issacs-Kidd midwater trawl (Arnold, MS 1970). Sampling, cruise dates, and cruise tracks were similar for each year, but the sampling in 1969 was more intensive. Table 14 compares egg abundance, larval abundance, and estimated recruits at age 1 for each year. Larvae were more abundant in 1967 than 1968 or 1969; however, due to the patchiness of the larval distribution, the variance are larger than the

mean it is not possible to show significance. However, it is clear that mortalities were over a magnitude and perhaps 40 times greater in 1968 and 1969 than in 1967 which suggests a strong density-dependent mortality in the first few weeks of larval life. The interesting feature of Table 14 is that mortality after mid-July appears related to density of the older fish in the summer population, rather than to the size of the cohort. Thus, two different types of density-dependent mechanisms may be acting on young mackerel: 1) an early intense intracohort competition or predation; and 2) subsequent predation by other cohorts on the young larvae and juveniles.

Ricker (1975) considers the type of recruit curve in Figure 4 a modification of the basic recruitment (Ricker) curve and the presence of the "steep right limb" indicates intense competition for limited food. Intense intracohort competition does occur in the closely related Pacific mackerel, Scomber japonicus (Bardach et al., 1972).

The rapid early growth rate of Atlantic mackerel larvae suggests a strong dependence on an abundant food supply. It would appear from Table 14 that the initial larval density determines the "all or nothing" effect. A large concentration of larvae would compete for a limited supply of food so that survival would be low. Whereas, a lower number of larvae would be able to obtain more food and experience greater survival. In addition to intracohort competition, larval predation

also occurs as mackerel larvae make up 20% of the food in the stomachs of larvae larger than 10 mm (Arnold, MS 1970).

Intracohort competition and predation do not appear to have been important after July 20. In fact, the 1968 and 1969 y/c's decreased in abundance relative to the 1967 y/c in spite of the fact that in 1967 the larvae were more abundant than in 1968 and 1969 (Table 14). A density-dependent relationship between the total stock and the larvae (i.e., intercohort competition and predation) may account for the change in relative abundance after July 20.

Egg cannibalism by adults does occur during the spawning season, but it accounts for a mortality rate of no more than 1% per day (MacKay, unpublished data) and is insignificant when compared to the natural mortality of mackerel eggs (D. Ware, pers. comm.). However, larval and juvenile predation by age 1 and older fish may be important. Only a few mackerel larvae have been found in mackerel stomachs, but inferences from laboratory feeding studies and analysis of stomach contents suggest that if larvae or juveniles are encountered, they will be eaten. There is selection for food particles the size of larvae (MacKay, 1976a; Muir and Newcombe, MS 1973). Furthermore, immature fish which arrive in the Gulf of St. Lawrence about July 1 show greater size selection than the adults for food particles the size of larvae. The schooling behaviour and movement of juveniles to very near-shore areas may be a

mechanism to minimize this predation. Predation by larger fish on juveniles does occur during the fall migration (MacKay, 1976a).

In summary, recruitment in mackerel is governed by an inverse relationship between population numbers or biomass and survival of new recruits. This relationship appears to be maintained by density-dependent fecundity, intense early intracohort competition for food, followed by predation of larvae and juveniles by older fish (age 1 and older). The combined result of these mechanisms is a very strong negative feedback with large year-classes produced only when the total population is small.

REFERENCES

Anderson, E.D. MS 1975a. Reassessment of mackerel in ICNAF subareas 3, 4, and 5 and statistical area 6. Int. Comm. Northw. Atlant. Fish., Res. Doc. 75/103, Ser. No. 3595:22pp.

Anderson, E.D. MS 1975b. The effect of a combined assessment for mackerel in ICNAF subareas 3, 4, and 5 and statistical area 6. Int. Comm. Northw. Atlant. Fish., Res. Doc. 75/14, Ser. No. 3458:14pp.

Anderson, E.D. MS 1976. Measures of abundance of Atlantic mackerel off the northeastern coast of the United States. Int. Comm. Northw. Atlant. Fish., Res. Doc. 76/VI/12, Ser. No. 3721:18pp.

Atch., Ms 1970. Zooplankton, summary report no. 10, Canadian Oceanographic Identification Centre, National Museum of Natural Sciences, Ottawa:40pp.

Arnold, P.W. MS 1970. Spawning and aspects of the early life history of the Atlantic mackerel (Scomber scombrus L.) in the Gulf of St. Lawrence. B.Sc. Thesis. Acadia University, Wolfville, N. S.:73pp.

Bardach, J.E., J.H. Ryther and W.O. McLarney. 1972. Aquaculture; the farming and husbandry of freshwater and marine organisms. John Wiley and Sons, New York:868pp.

Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. Fishing Invest., London (2), 19:533pp.

Bigelow, H.B. and W.C. Schroeder. 1953. Fishes of the Gulf of Maine. U.S. Fish and Wildlife Serv., Fish. Bull. 74, vol. 53:577pp.

Chapman, D.W. 1971. Production. (pp. 199-214). In: W.H. Ricker (ed.), Methods for assessment of fish production in fresh waters. IBP Handbook 3 (2nd Ed.), Blackwell Scientific Pub. Oxford, England.

Cushing, D.H. 1974. The possible density-dependence of larval mortality and adult mortality in fishes. (pp. 103-111). In: J.H.S. Blaxter (ed.), The early life history of fish. Springer-Verlag, New York, N. Y.

Davis, G.E. and E.E. Warren. 1971. Estimation of food consumption rates. (pp. 227-248). In: W.H. Ricker (ed.), Methods for assessment of fish production in fresh waters. IBP Handbook 3 (2nd Ed.), Blackwell Scientific Pub., Oxford, England.

English, T.S. 1964. A theoretical model for estimating the abundance of planktonic fish eggs. Rapp. P. V. Reun. Cons. Perm. Int. Explor. Mer. 155:161-170.

Hunt, J.J. MS 1975. Canadian mackerel catches (m.t.) and numbers at age in subarea 4 for 1974. Int. Comm. Northw. Atlant. Fish., Res. Doc. 75/92. Ser. No. 3571:6pp.

ICNAF. MS 1976. Report of standing committee on research and statistics. May - June 1976. App. VII Report of the ad hoc mackerel working group. Int. Comm. Northw. Atlant. Fish.: 1-9.

Isakov, V.J. MS 1973.

Lett, P.F., W.T. Stobo and W.G. Doubleday. MS 1975. A system stimulation of the Atlantic mackerel fishery in INCAF subareas 3, 4, and 5 and statistical area 6: with special reference to stock management. Int. Comm. Northw. Atlant. Fish., Res. Doc. 75/32. Ser. No. 3511:1-10.

MacKay, K.T. MS 1967. An ecological study of mackerel, Scomber scombrus (Linnaeus) in the coastal waters of Canada. Fish. Res. Bd. Canada: Tech. Rept. 13: 127pp.

MacKay, K.T. MS 1973. Aspect of the biology of Atlantic mackerel in ICNAF subarea 4. Int. Comm. Northw. Atlant. Fish., Res. Doc. 73/70, Ser. No. 3019:11pp.

MacKay, K.T. 1976a. Biological synopsis of the northern population of Atlantic mackerel. Chapter 1, this study.

MacKay, K.T. 1976b. Hydrodynamics of the Atlantic mackerel, Scomber scombrus. Chapter 2, this study.

MacKay, K.T. 1976c. Feeding strategy in a patchy environment, a theoretical analysis of feeding in the Atlantic mackerel, Scomber scombrus. Chapter 3, this study.

Martell, A. MS 1967. Biological survey of the Atlantic mackerel in eastern Canadian waters - Summer 1967.

MS Rept. Biological Station St. Andrews, N.B. 14pp.

Muir, B.S. and C.P. Newcombe. MS 1973. Laboratory observations in filter feeding in Atlantic mackerel,

Scomber scombrus. MS Rept. Marine Ecology Laboratory, Bedford Institute of Oceanography.

Moore, J.A., G.H. Winters and L.S. Parsons. 1975. Migration and biological characteristics of Atlantic mackerel, (Scomber scombrus) occurring in Newfoundland waters. J. Fish. Res. Bd. Canada 32:1347-1357.

Pielou, E.C. 1969. An introduction to mathematical ecology.

John Wiley and Sons, New York, N.Y. 286pp.

Pope, J.G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis.

Int. Comm. Northw. Atlant. Fish. Res. Bull. 9:65-74.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Bd. Canada Bull. 191:382pp.

Saville, A. 1956. Eggs and larvae of haddock (Gadus aeglefinus) at Faroe. Mar. Res. Scot. 1956, (4).

Saville, A. 1964. Estimation of the abundance of fish stock from egg and larval studies. Rapp. P.V. Reun. Cons. Perm. Int. Explor. Mer. 155:164-170.

Sette, O.E. 1943. Biology of the Atlantic mackerel, (Scomber scombrus) of North America. Part 1.

Early life history. U.S. Fish and Wildlife Serv., Fish. Bull. 38:149-237.

Sutcliffe, W.H., Jr. 1972. Some relations of land drainage, nutrients, particulate material and fish catch in two Eastern Canadian bays.

29:357-362.

Ware, D.M. 1975. Relation between egg size, growth and natural mortality of larval fish. J. Fish. Res. Bd. Canada 32:2503-2512.

Winters, G.H. 1975. Population dynamics of the Southern Gulf of St. Lawrence herring stock complex and implications concerning its future management. Ph.D. Thesis. Dalhousie University, Halifax, N. S. 142pp.

Table 1: Age composition, lengths, weights, average gonad weights and relative fecundity for the spawning population of the northern population Atlantic mackerel for three years.

Year	1967			1968			1969		
Year Class	%	FL (cm)	W (g)	%	FL (cm)	W (g)	%	FL (cm)	W (g)
1959--									
1960	69	36.5	499	79	37.7	553	50	38.8	634
1961	7	35.6	461	4	38.5	591	2	38.5	615
1962	3	35.2	445	4	38.0	567	3	37.5	563
1963	4	34.4	414	3	36.4	495	3	37.5	563
1964	16	33.2	370	5	35.6	461	3	36.0	492
1965				4	35.5	457	7	33.9	403
1966				2	31.8	323	28	32.3	343
1967							4	27.5	201
Weighted Average		35.8	473		37.8	556		36.1	496
Average Gonad Weight		47.0			62.3			47.8	
Estimated Fecundity	209,200			277,300			212,700		

Table 2. Percent year class composition of the northern population during spawning (sp) and summer (su) in the Gulf of St. Lawrence, 1962-1973

Year	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974 ²
Year/Class	Sp Su	Sp Su	Sp Su	Sp Su	Sp Su	Sp Su	Sp Su	Sp Su	Sp Su	Sp Su	Sp Su	Sp Su	Sp Su
pre 1959	31	14	1	1	1								
1959-1960	68 99	86	78	82 85	81 61	69 28 ¹	79 10	50 2	85 21	33 9	19	20 42	2 0
1961	1 1		13	10 5	7 7	7 5	4 -	2 -					
1962			7	4 5	3 5	3 6	4 -	3 -					
1963				3 5	2 12	4 4	3 2	3 -					
1964					6 11	16 21	5 7	3 -	48 0			5 2	1 0
1965					2	1 20	4 9	7 2	8 1		6	6 4	4 0
1966						7	2 26	28 31	5 5	16 14	6	18 9	6 1
1967						9	45	84	1 63	46 62	47	40 31	22
1968									7	2 4	7	6 11	18 4
1969									23	3 10	14	4 5	19 5
1970										1 1	1	2 6	11 17
1971												5 5	17 15
1972												2	32
1973													20

1. Based on only one sample in 4T for September.

2. After Hunt MS, 1975.

3. Based on samples from October.

Table 3: Average number of mackerel eggs per m³ at surface (0-2m) and 15m based on horizontal tows with a #0-1 metre plankton net towed during June over the Magdalen Shallows of the Gulf of St. Lawrence (data after Arnold, MS, 1970). Number of samples in parentheses.

Depth	1967		1968		1969
	0-2m	15m	0-2m	15m	0-2m
Block Number					
1a			126.1 (2)	47.9 (2)	6.3 (5)
1b	0.02 (6)	0.0 (6)	43.5 (7)	21.4 (6)	40.0 (8)
1c					0.5 (2)
1d			0.1 (7)	0.1 (7)	4.0 (8)
1e					0.5 (7)
2a			124.0 (5)	38.5 (5)	156.0 (5)
2b	0.12 (1)	0.07 (1)	214.0 (2)	54.9 (2)	86.0 (9)
2c	1.78 (8)	0.38 (8)	97.4 (10)	9.9 (10)	80.8 (9)
2d			7.5 (6)	5.0 (6)	9.7 (5)
2e			2.6 (5)	2.5 (5)	6.4 (11)
3a			331.9 (3)	13.8 (3)	125 (3)
3b			63.2 (4)	4.5 (4)	29 (3)
3c	11.94 (5)	2.47 (5)	19.6 (6)	4.8 (5)	51.5 (9)
3d	8.70 (3)	0.67 (3)	8.4 (1)	4.6 (1)	30 (1)
3e					

Table 4: Area and numbers of mackerel eggs per m² of sea surface for various blocks within the Magdalen Shallows during mid-June 1967, 1968, 1969. Description of calculations in text.

Area Km ²		1967		1968		1969	
Source		Arnold	Arnold	BIO ¹	BIO ²	Average	Arnold
Block #							
1 a	4224	0.14	1544.5			1544.5	60.6
1 b	6000		593.8	334.7	517.4	482.0	384.6
1 c	3224			86.6	0.0 ³	43.3	5.0
1 d	1319		1.5			1.5	38.5
1 e							5.0
							52.9
2 a	6896	1.83	1411.3			1411.3	1500.1
2 b	8396		2291.3	631.6	1006.7	1309.9	827.0
2 c	8620		854.3	629.6	691.1	725.5	777.0
2 d	8103		118.8			118.8	93.0
2 e	4310		45.8			45.8	615.0
							5.0
3 a		120.40					
3 b	3655						
3 c	4413		2661.8			2661.8	1202.0
3 d	6758		530.3			530.3	279.0
3 e	517		207.0			207.0	495.0
			120.5			120.5	288.5
Total							
Area	66,435						

1. Vertical tows with 1/2m Hensen net from CSS PAWSON.
2. Vertical tows with 3/4m Hensen net from MV BRANDAL
3. One single very large value was excluded from this average.

Table 5: Variability of mackerel eggs sampled in the Gulf of St. Lawrence (A), in 1968 by three different types of gear and (B) in 1967, 1968, 1969

(\bar{x} = mean
v = variance
n = sample number, and
cf = confidence limits at $P < 0.05$)

(A)				
SOURCE	ARNOLD (1M NET)		DAWSON	BJO BRANDAL
	SURFACE	15M (1/2 M NET)	(3/4 M NET)	
BLOCK #	NUMBER EGGS/M ³		NUMBER EGGS/NET HAUL	
1b \bar{x}	43.5	21.43	65.8	229
v	2770	850	13,005	128,214
n	7	6		7
2b \bar{x}	214.0	54.9	124.1	445.5
v	9934	560	26,959	226,881
n	3	3	11	22
3c \bar{x}	97.4	9.9	123.7	305.8
	17,203	183	53,315	135,829
	10	10	11	14

(B)			
YEAR	1967	1968	1969
BLOCK #			
1b			
2b			
2c \bar{x}	4.36	76.33	57.40
3c			
3d			
cf	± 6.30	± 46.56	± 21.04
n	23	30	43

Table 6: Calculations of the spawning stock of the northern population of Atlantic mackerel using egg abundance data from Arnold (MS, 1970). Assumptions and calculations in text.

YEAR	1967	1968	1969
Number of eggs at peak of spawning 10^9	2239.6 (1)	51,227.6	39,139.5
Number of stage I eggs 10^9	1646.1	37,652.3	28,767.5
Total egg production 4 wk spawning 10^9 (2)	30,946.7	707,863.2	539,390.6
Total number of spawning stock 10^9	0.30	5.11	5.09
Biomass of spawning stock 10^6 MT	0.15	2.85	2.52

1. Corrected for total spawning area.
2. Corrected for 100 percent of eggs.

Table 7: Estimates of year class abundance of the northern population, Atlantic mackerel for two estimates of mortality,
(A) $M = 0.15$, (B) $M = 0.30$

(A) $M = 0.15$

Year	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975
Year Class																
Pre 1959	0.16	0.14	0.12	0.10	0.09	0.08										
1959-1960	13.15	11.32	9.73	8.37	7.20	6.18	5.31	4.55	3.90	3.30	2.84	2.44	2.10	1.81	1.56	1.34
1961			0.43	0.37	0.32	0.27	0.24	0.20	0.17	0.15	0.13	0.11	0.10	0.08	0.07	0.06
1962				0.44	0.38	0.33	0.28	0.24	0.21	0.18	0.15	0.13	0.11	0.10	0.09	0.07
1963					0.32	0.27	0.24	0.20	0.17	0.15	0.13	0.11	0.10	0.08	0.07	0.06
1964						0.38	0.33	0.28	0.24	0.21	0.18	0.16	0.13	0.12	0.10	0.09
1965							0.61	0.53	0.45	0.39	0.30	0.24	0.17	0.11	0.09	0.07
1966								2.18	1.85	1.56	1.28	0.96	0.63	0.45	0.35	0.29
1967									11.06	9.45	8.02	6.58	5.19	4.12	3.37	2.80
1968										1.49	1.19	1.00	0.77	0.49	0.27	0.13
1969											2.51	2.05	1.54	1.13	0.75	0.54
1970												1.31	0.95	0.64	0.27	0.11
1971													2.1	1.5	0.8	0.37
1972														2.0	1.4	0.80
TOTAL	13.31	11.46	10.28	9.28	8.31	7.51	7.01	8.18	18.05	16.88	16.75	15.09	13.89	12.63	9.19	6.73

(B) M = 0.30

Year	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975
Year Class																
Pre 1959	0.63	0.46	0.34	0.26	0.19	0.14										
1959-1960	50.93	37.69	27.88	20.63	15.26	11.29	8.34	6.15	4.53	3.30	2.43	1.79	1.33	0.99	0.73	0.54
1961		1.65	1.27	0.94	0.70	0.52	0.39	0.28	0.21	0.15	0.11	0.08	0.06	0.05	0.03	0.02
1962				1.09	0.81	0.60	0.44	0.33	0.24	0.18	0.13	0.10	0.07	0.05	0.04	0.03
1963					0.70	0.52	0.38	0.28	0.24	0.16	0.11	0.07	0.04	0.03	0.02	0.01
1964						0.73	0.54	0.40	0.29	0.21	0.15	0.10	0.06	0.04	0.03	0.02
1965							0.98	0.73	0.54	0.39	0.27	0.17	0.09	0.04	0.02	0.00
1966								2.91	2.14	1.56	1.10	0.68	0.40	0.22	0.13	0.07
1967									13.41	9.88	7.21	5.03	3.29	2.12	1.41	0.95
1968										1.57	1.08	0.78	0.49	0.20	0.01	-0.08
1969											2.32	1.62	0.98	0.52	0.18	0.04
1970												1.31	0.95	0.64	0.27	0.11
1971													2.10	1.50	0.8	0.37
1972														2.00	1.4	0.80
TOTAL	51.56	38.15	29.49	22.92	17.66	13.80	11.06	11.08	21.57	17.40	14.91	11.73	9.86	8.39	5.07	2.96

Table 8. Estimates of spawning stock for various year classes for the northern population, Atlantic mackerel for two estimates of mortality, (A) $M = 0.15$, (B) $M = 0.30$

(A) $M = 0.15$

Year	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
Year Class																
Pre 1959	0.18	0.15	0.13	0.11	0.10	0.09	0.07									
1959-1960				0.26	0.61	6.69	5.75	4.93	0.21	4.04	2.55	2.64	2.27	1.96	1.62	1.43
1961						0.30	0.26	0.22	0.02	0.20	0.10	0.12	0.11	0.09	0.08	0.07
1962						0.36	0.31	0.26	0.01	0.20	0.15	0.14	0.12	0.11	0.10	0.08
1963							0.26	0.22	0.01	0.15	0.15	0.12	0.11	0.09	0.08	0.07
1964								0.31	0.05	0.26	0.15	0.17	0.15	0.13	0.11	0.10
1965									0.00	0.20	0.36	0.28	0.21	0.14	0.10	0.08
1966										0.10	1.43	1.12	0.80	0.59	0.49	0.32
1967											0.20	0.03	4.43	4.66	3.75	3.09
1968													0.15	0.63	0.38	0.20
1969													0.22	-1.34	0.94	0.65
1970														0.11	0.18	0.19
1971																0.59
1972																
1973																
TOTAL	0.18	0.15	0.13	0.37	0.71	7.44	6.65	5.94	0.30	5.15	5.09	4.62	8.57	9.85	7.83	6.87

(B) M = 0.30

Year	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
Year Class																
Pre 1959	0.74	0.55	0.40	0.30	0.23	0.17	0.13									
1959-1960				0.66	1.44	13.28	9.82	7.25	0.21	4.04	2.55	2.11	1.56	1.16	0.86	0.64
1961						0.61	0.45	0.33	0.02	0.20	0.10	0.10	0.07	0.06	0.04	0.03
1962						0.71	0.52	0.39	0.01	0.20	0.15	0.12	0.09	0.06	0.05	0.04
1963							0.45	0.33	0.01	0.15	0.15	0.09	0.06	0.04	0.03	0.02
1964								0.59	0.05	0.26	0.15	0.13	0.08	0.05	0.04	0.03
1965										0.20	0.36	0.22	0.14	0.04	0.03	0.01
1966										0.10	1.43	0.89	0.54	0.31	0.18	0.10
1967											0.20	0.03	3.26	2.71	1.77	1.18
1968													0.09	0.35	0.11	0.01
1969													0.14	0.75	0.35	0.11
1970														0.05	0.11	0.19
1971																0.59
1972																
1973																
TOTAL	0.74	0.5	0.40	0.96	1.67	14.77	11.37	8.89	0.30	5.15	5.09	3.69	6.03	5.58	3.57	2.95

Table 9. Comparison of numbers and biomass of spawners, and total biomass to number of recruits at Age 1 for the northern population Atlantic mackerel.

YEAR	M = 0.15				M = 0.30			
	Spawning Stock Numbers $\times 10^9$	Biomass $\times 10^6 \text{ MT}$	Total Stock Biomass $\times 10^6 \text{ MT}$	Recruits (n+1) Numbers $\times 10^9$	Spawning Stock Number $\times 10^9$	Biomass $\times 10^6 \text{ MT}$	Total Stock Biomass $\times 10^6 \text{ MT}$	Recruits (n+1) Numbers $\times 10^9$
1959	0.18	0.10	0.10	13.15	0.74	0.41	0.41	50.93
1960	0.15	0.09	1.40	-	0.53	0.33	5.07	-
1961	0.13	0.08	2.39	0.43	0.40	0.25	7.42	1.27
1962	0.37	0.15	2.98	0.44	0.96	0.40	8.00	1.09
1963	0.71	0.26	2.77	0.32	1.67	0.63	6.42	0.70
1964	7.44	2.70	2.77	0.38	14.77	5.36	5.47	0.73
1965	6.65	2.62	2.98	0.61	11.37	5.04	5.16	0.98
1966	5.94	3.28	3.85	2.18	8.89	4.09	4.26	2.91
1967	0.30	0.15	0.50	11.06	0.14	0.06	0.42	13.41
1968	5.15	2.58	4.21	1.49	5.15	2.82	4.65	1.57
1969	5.09	2.90	4.86	2.51	5.09	2.44	4.70	2.32
1970	4.62	2.65	5.05	1.31	3.69	2.10	4.11	1.31
1971	8.57	3.59	7.04	2.10	6.03	2.42	3.47	2.10
1972	9.85	4.02	6.59	2.00	5.58	2.28	2.8	2.00

Table 10: Productivity biomass ratios for the northern population Atlantic mackerel for two estimates of mortality.

YEAR	P/B	
	$M = 0.15$	$M = 0.30$
1960	0.69	0.70
1961	0.37	0.36
1962	0.06	0.06
1963	0.13	0.14
1964	0.30	0.30
1965	0.18	0.20
1966	0.17	0.17
1967	0.38	0.38
1968	0.36	0.37
1969	0.18	0.18
1970	0.19	0.21
1971	0.17	0.17
1972	0.27	0.25

Table 11: Exchange of protein and energy between the Gulf of St. Lawrence and the New England-Scotian Shelf.

	Protein 10 ⁶ MT	Fat	Energy 10 ⁹ K cal
<u>Export</u>			
October 1968	1.00	.76	12.83
<u>Import</u>			
June somatic tissue 1969	0.88	0.23	7.15
gonad tissue	0.06	0.01	0.43
<u>Total</u>			
<u>Difference</u>	0.06	.52	5.25
<u>Fishery</u>	0.01	.01	0.15
SA 4, 5, 6 November, 1968 May, 1969			

Table 12: Comparison of population estimate from
(1) the present study, and
(2) Anderson (MS, 1975a), for 1969 and 1973.

Source	1969			1973	
	1	2		1	2
Year/class	M=0.30	M=0.30	M=0.15	M=0.30	M=0.30
1959-60	3.30	0.06	1.81	0.99	0
1961	0.15	0.05	0.08	0.05	0
1962	0.18	0.10	0.10	0.05	0
1963	0.16	0.12	0.08	0.03	0.01
1964	0.21	0.14	0.12	0.04	0.02
1965	0.39	0.46	0.11	0.01	0.05
1966	1.56	1.70	0.45	0.22	0.14
1967	9.88	5.40	4.12	2.12	0.66
1968	1.57	3.10	0.49	0.20	0.62
1969			1.13	0.52	0.31
1970			0.64	0.64	0.64
1971			1.50	1.50	1.50
1972			2.00	2.00	2.00
TOTAL Numbers x 10 ⁹	17.40	11.20	12.60	8.40	5.95
Biomass x 10 ⁶ MT	4.70	1.73	7.23	2.5	1.32

Table 13 - A) Comparison of estimates of mackerel population abundance with gonad weights and fecundity. Gonad weights and fecundity after MacKay (1976a).
 B) Least squares regression of fecundity (F) on total stock abundance (P) for two mortality estimates for 37.7 cm mackerel.

Year		Population Abundance $\times 10^9$		Gonad Weight for 37.7 cm fish (g)	Fecundity for 37.7 cm fish ($\times 10^4$)
		M = 0.15	M = 0.30		
1969	SS	5.1	5.1	62.4	27.8
	TS	16.9	17.4		
1970	SS	4.6	3.7	66.8	29.7
	TS	16.8	14.9		
1971	SS	8.6	6.0	68.5	30.5
	TS	15.1	11.7		
1972	SS	9.6	5.6	68.6	30.5
	TS	13.9	9.9		
1973	SS	7.8	3.6	80.6	35.9
	TS	12.6	8.4		

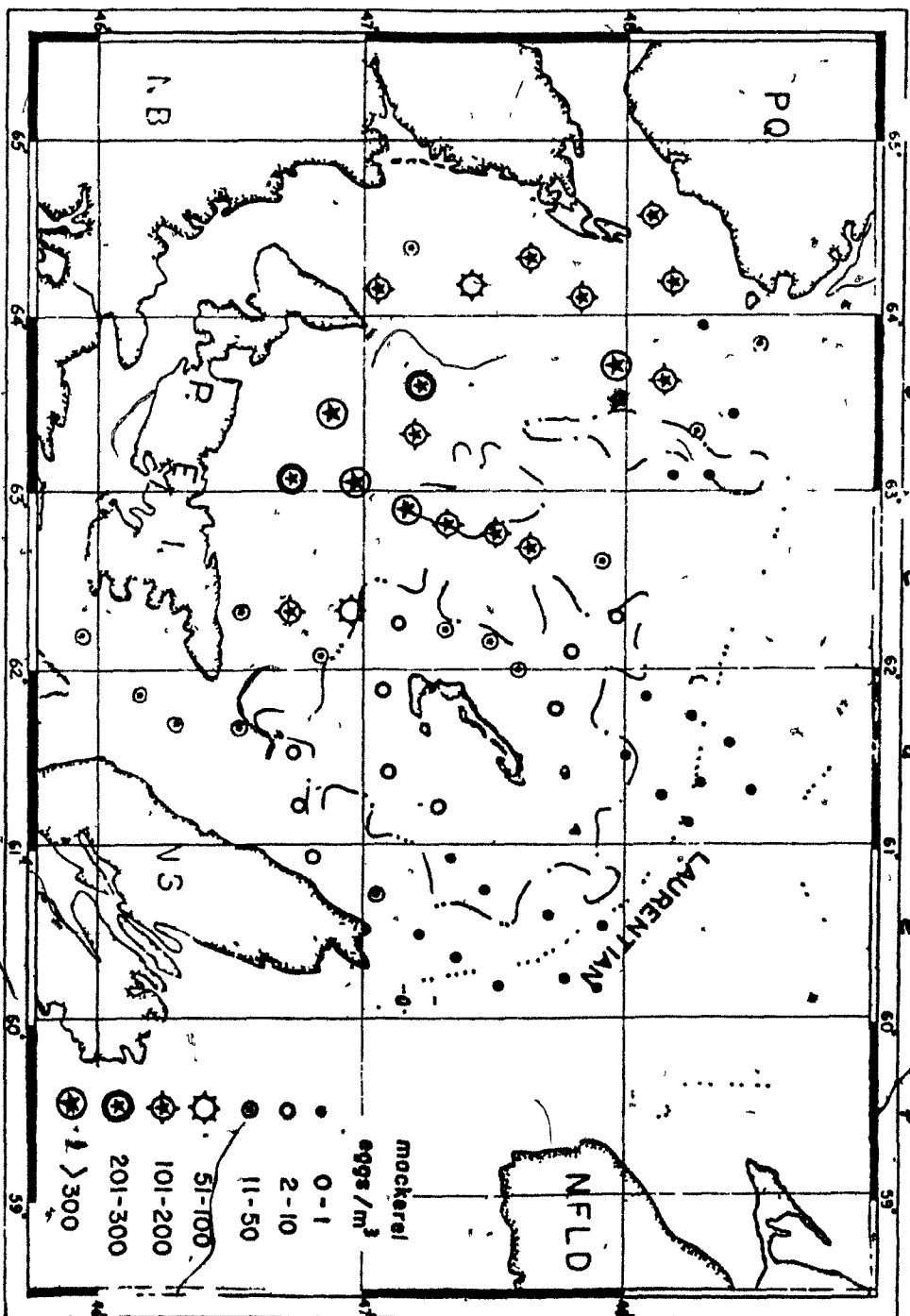
Mortality Estimate	Regression Equation	Correlation Coefficient (r^2)
0.15	$F = 1.42 + 52.30 P$	-.876
0.30	$F = 0.69 + 39.47 P$	-.840

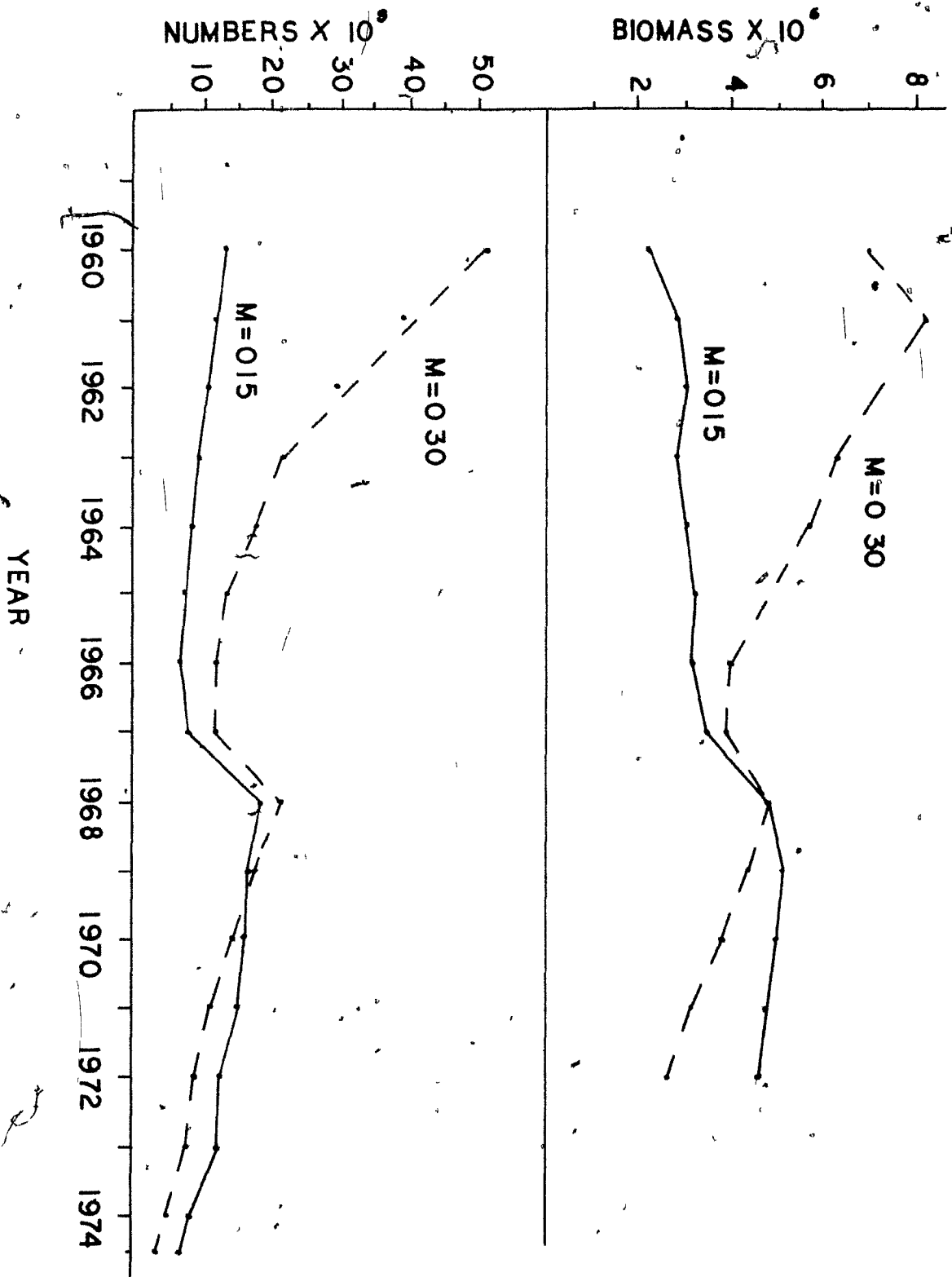
Table 14: Index of abundance of total stock, eggs, larvae and number of recruits at Age 1 for the northern population of Atlantic mackerel 1967-1969. All numbers expressed as proportion of 1967 abundance which equals 1.

YEAR	Total Stock July 1	Eggs June 20	Larvae July 20	Recruits Age 1 - July 1
1967	1	1	1	1
1968	6.8	22.9	0.4	0.1
1969	5.9	17.4	0.6	0.2

CAPTIONS FOR FIGURES

- Figure 1: Surface distribution of mackerel eggs June 18 to June 26, 1968 (taken from Arnold, MS 1970). Letters and numbers indicate a grid following the lines of latitude and longitude.
- Figure 2: Estimates of numbers and biomass for the northern population of Atlantic mackerel using two estimates of mortality.
- Figure 3: Somatic production (P_S) and gonadal production (P_G) for the northern population of Atlantic mackerel, 1960-1973, for $M = 0.15$ and $M = 0.30$.
- Figure 4: Stock recruitment relationship of the northern population of Atlantic mackerel based on the Ricker type recruitment curve for two estimates of natural mortality. Solid points - $M = 0.15$, X's - $M = 0.30$.





PRODUCTION
MT X 10⁶

