VARIABILITY IN MEDIAN SIZE AND AGE AT SEXUAL MATURITY OF ATLANTIC COD, *GADUS MORHUA*, ON THE SCOTIAN SHELF IN THE NORTHWEST ATLANTIC OCEAN

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ABSTRACT

Median length and age at sexual maturity of Atlantic cod on the Scotian Shelf declined about 50% in most stocks between 1959 and 1979. Atlantic cod in more northerly stocks matured at older ages than did those in more southerly stocks. Males generally matured at younger ages and smaller sizes than did females. Large, immature Atlantic cod disappeared from the stocks between 1959 and 1979. During 1975-79, virtually all Atlantic cod age 5 and older were mature. The decline in median length and age at sexual maturity may be due to the commercial fishery removing larger, older immature fish, a general decline in stock biomasses between 1960 and 1975 due to heavy exploitation, or both.

Vertebrate population dynamics are determined by the composite effects of reproduction, growth, dispersal, and mortality. The median age at which individuals attain sexual maturity profoundly impacts potential population growth (Cole 1954; Stearns 1976). Size and age at sexual maturity are the direct linkage between individual growth and reproductive potential of a population, and therefore they are parameters of prime concern in population dynamics.

Atlantic cod, *Gadus morhua*, is economically the most important finfish species landed in the Atlantic region of Canada. Heavy exploitation in the 1960's and early 1970's resulted in declines in stock biomass of many Atlantic cod stocks in the Maritimes (Halliday 1976; Beacham 1980). Canadian landings of Atlantic cod on the Scotian Shelf [Northwest Atlantic Fisheries Organization (NAFO) Divisions 4VWX] (Fig. 1) increased in the late 1970's while landings by other countries, chiefly Spain and the Soviet Union (Halliday 1976), declined. The southern Gulf of St. Lawrence cod stock (Division 4T) also supports an extensive fishery (Beacham 1980).

Spawning biomass of a stock is of direct concern in the management of a fishery and can be evaluated, when the abundance and proportion mature at each age are known. The presence of Atlantic cod in several areas of NAFO Subarea 4 (McKenzie 1956; McCracken 1959; Templeman 1962; Martin and Jean 1964) presented an opportunity to investigate variation in median size and age at sexual maturity of Atlantic cod among areas. The major purpose of this paper is to present historical changes in median size and age at maturity for Atlantic cod in NAFO Subdivisions 4Vn and 4Vs and Divisions 4W and 4X and to attempt to account for some of this variability among cod in these areas.

MATERIALS AND METHODS

Data analyzed in this paper were collected during 1959-79 from groundfish surveys of the Canadian research vessels MV *Harengus*, *E. E. Prince*, and *A. T. Cameron*. In 1970, annual stratified random design groundfish surveys were initiated on the Scotian Shelf with the July surveys of the *A. T. Cameron*. Previous to 1970, surveys were not always conducted annually in the areas examined for the present analysis. Annual values for median (50% mature point) length and age at sexual maturity of Atlantic cod on the Scotian Shelf before 1970 were calculated from any survey during the summer, not only July. Maturity ogives based on length and age were calculated for four periods in the study, each corresponding to about a 5-yr interval. All surveys conducted in each interval were included in the calculation of the maturity ogives. All Atlantic cod in the surveys for which maturity stage was recorded and either length or age were known were included in the determination of median size and age at maturity. Details of the surveys, including vessels and gear used and areas surveyed, were outlined by Halliday and Koeller (1981). Fork length (centimeters) and maturity stage

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Manuscript accepted September 1982.
FISHERY BULLETIN: VOL. 81, NO. 2, 1983.

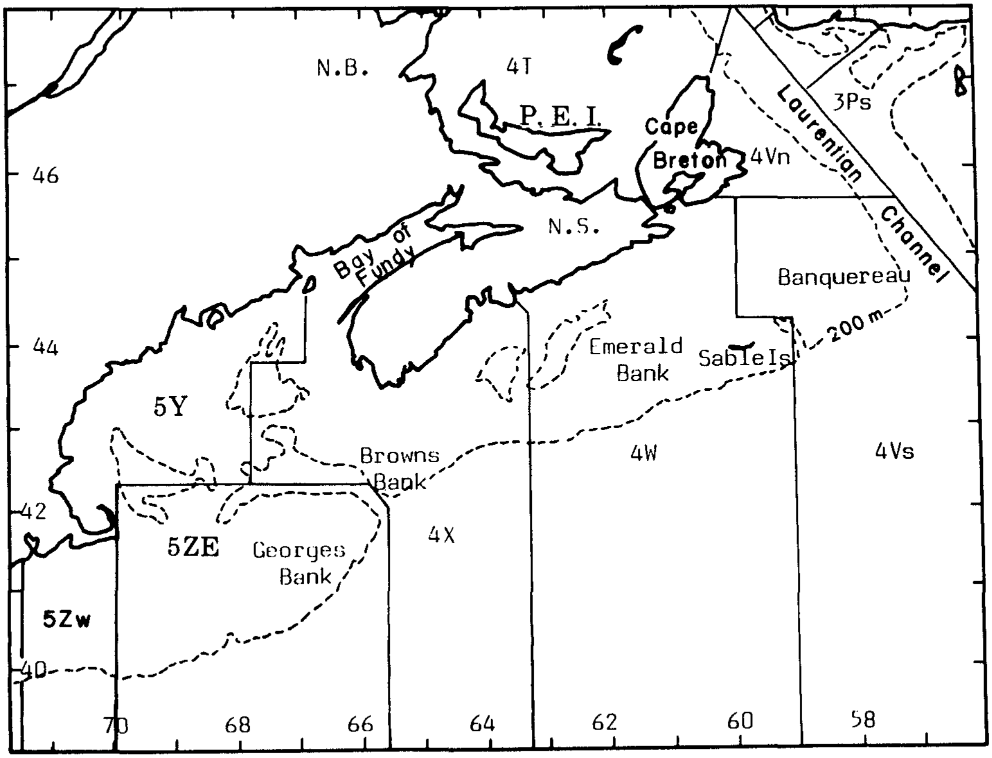

FIGURE 1.—Northwest Atlantic Fisheries Organization areas on the Scotian Shelf (Divisions 4VWX).

of Atlantic cod were recorded at sea, and otoliths were saved for later age determination according to the method of Kohler (1964). The validity of using otoliths in determining age of Atlantic cod was demonstrated by Kohler (1964) and May (1967). Powles (1958) outlined the classification of the gonads used in assessing maturity stage for this study.

The transition from immature to the mature condition in fish usually occurs over a range of length and age in the form of a sigmoid curve. From the percentages of mature Atlantic cod (gonads in ripening, ripe, spawning, spent, or recovering condition) in 2 cm length intervals in the survey or period under consideration, the median length at sexual maturity (L_{50}) was calculated by probit analysis following the technique of Leslie et al. (1945). Median age at sexual maturity (A_{50}) was calculated in a similar way by grouping the data in 1-yr intervals. Maturity ogives were plotted by eye. In some cases on the Scotian Shelf, annual values for median size and age at sexual maturity could not be calculated because Atlantic cod were not sampled in that year or because so few Atlantic cod were sampled that insufficient data were available for probit analysis.

RESULTS

Subdivision 4Vn

Atlantic cod caught in Subdivision 4Vn may be derived from three stocks. Atlantic cod from Division 4T overwinter in Subdivision 4Vn (McCracken 1959; Martin and Jean 1964), so that Atlantic cod caught between January and April may be from the Division 4T stock. Atlantic cod from Subdivision 4Vs migrate into Subdivision 4Vn during the summer, and Halliday (1974) assumed that Atlantic cod caught by commercial otter trawlers in Subdivision 4Vn during May-December were migratory cod from Subdivision 4Vs or Division 4W. There is also a local stock in Subdivision 4Vn that is exploited by the inshore fishery. Research vessel trawl surveys have been used previously to assess stock status of the inshore cod stock (Beacham et al. 1980), so it was assumed in the present analysis that the inshore stock was sampled by the surveys.

The L_{50} values of Atlantic cod sampled in Subdivision 4Vn declined from a high of 61 cm for males and 65 cm for females in 1959 to a low of 34 cm for males and 32 cm for females in 1978, but increased in 1979

(Fig. 2). Females generally matured at greater median lengths than did males, and with the difference between the sexes greater in the 1960's than in the 1970's.

The A_{50} values indicate trends similar to those of length, being about 5.7 yr for males and 6.7 yr for females in 1960, reaching a minimum in 1978 of 2.6 yr for both males and females, and increasing in 1979 (Fig. 3). During 1959-63, males tended to mature at younger ages than did females, but since 1969, median age at maturity between sexes has been similar. No values were calculated for 1975 and 1976 because of small sample sizes.

Maturity ogives based on length and age were calculated for four periods in this study, each corresponding to a 5-yr interval. L_{50} values during 1959-64 were 52 cm for males and 55 cm for females, but declined significantly ($P<0.01$) to 36 and 34 cm, respectively, during 1975-79. The trend towards the removal of larger, immature fish with time was apparent (Fig. 4). The transition from the all immature to 100% mature condition occurred over progressively shorter length ranges.

Changes in percent mature by age indicate an increase in percent mature at age through time (Table 1). There was a particularly striking increase in rates of maturity for males and females ages 3 and 4. About 90% of age-4 females were mature during 1975-79,

TABLE 1.—Percentage of sexually mature Atlantic cod by age and sex caught during Canadian groundfish surveys in Subdivision 4Vn, 1959-79. Sample sizes are in parentheses for individual ages and 95% confidence limits for A_{50} (years).

Age (yr)	1959-64	1965-69	1970-74	1975-79
		Male		
2	0.0 (102)	0.0 (5)	0.0 (94)	21.1 (19)
3	1.6 (126)	0.0 (15)	5.4 (92)	57.1 (67)
4	23.2 (168)	48.0 (25)	50.6 (85)	81.4 (94)
5	44.3 (131)	66.7 (18)	86.1 (129)	93.6 (60)
6	67.5 (197)	77.8 (9)	97.4 (76)	100.0 (37)
7	73.3 (206)	100.0 (16)	100.0 (57)	100.0 (10)
8	81.2 (117)	94.1 (17)	100.0 (27)	100.0 (12)
9	90.6 (96)	100.0 (14)	100.0 (13)	100.0 (11)
10	94.4 (71)	100.0 (1)	80.0 (5)	100.0 (9)
11	100.0 (38)	100.0 (6)	100.0 (3)	100.0 (2)
A_{50}	5.40(5.23-5.58)	4.39(4.01-4.79)	4.04(3.91-4.17)	2.80(2.54-3.08)
		Female		
2	0.0 (85)	0.0 (8)	0.0 (77)	9.5 (22)
3	0.0 (124)	5.3 (19)	6.1 (99)	63.1 (71)
4	4.0 (152)	50.0 (24)	34.3 (102)	90.0 (117)
5	17.3 (127)	66.7 (15)	83.6 (140)	100.0 (65)
6	49.1 (218)	91.7 (12)	97.7 (88)	100.0 (48)
7	64.2 (243)	100.0 (21)	98.4 (62)	100.0 (26)
8	76.6 (154)	100.0 (19)	100.0 (41)	100.0 (21)
9	91.6 (107)	93.3 (15)	100.0 (16)	100.0 (6)
10	91.2 (91)	100.0 (5)	100.0 (9)	100.0 (4)
11	94.7 (38)	100.0 (10)	100.0 (6)	100.0 (1)
12	89.5 (19)	100.0 (5)	100.0 (2)	100.0 (2)
13	100.0 (12)	100.0 (7)	100.0 (2)	100.0 (3)
A_{50}	6.34(6.19-6.51)	4.20(3.88-4.55)	4.20(4.07-4.33)	2.78(2.59-2.99)

whereas only 4% were classified as mature during 1959-64. During 1959-64, A_{50} for males was 5.4 yr and that of females 6.3 yr, whereas during 1975-79, these values were 2.8 yr for both males and females, the decline being significant ($P<0.01$). A_{50} declined faster in males than in females. These data also indicate that older, immature Atlantic cod disappeared from the area through time, probably through commercial exploitation.

Subdivision 4Vs

L_{50} for Atlantic cod in Subdivision 4Vs had the same general decreasing trend with time as in other areas, declining from 51 cm for males and 54 cm for females in 1959 to about 35 cm for males and 33 cm for females in 1977 (Fig. 5). There appeared to be a rapid drop in the median length at maturity in the early 1970's, and an increase since 1977. However, given the variability in the measurements, it is uncertain if these were actual trends or due to sampling variability.

A_{50} displayed trends similar to those of length, being about 5.6 yr for males and 5.7 yr for females in 1959, and declining to about 2.4 yr for males and 2.3 yr for females in 1977 (Fig. 6). Atlantic cod matured, on average, at older ages in the early 1960's than did those in the 1970's. Males again tended to mature at smaller sizes and younger ages than did the females.

The maturity ogives for length indicate trends similar to Atlantic cod in Subdivision 4Vn for the periods under consideration. Larger, immature fish have been eliminated from the stock over time, and the transition from the immature to the mature state occurred over a smaller length interval with time (Fig. 7). During 1959-64, the transition from 0% mature to 100% mature occurred over a 40 cm interval of length for both males and females, but from 1975 to 1979, this transition occurred over a 20 cm length interval. L_{50} values in 1959-64 were 47 cm for males and 44 cm for females, but these values declined to 38 cm for both males and females in 1975-79 ($P<0.01$).

Changes in percent mature by age indicate marked increases over time for age-3 and -4 Atlantic cod (Table 2). However, the data for the 1965-69 interval were sparse and may not be indicative of the stock in this period. These data also indicate that between 10 and 15% of age-2 Atlantic cod became mature in 1975-79, whereas virtually no age-2 Atlantic cod were mature in the 1960's. This trend was also apparent in Atlantic cod caught in Subdivision 4Vn. During 1959-64, median age at maturity for males was 5.4 yr and that of females 5.2 yr, whereas in 1975-

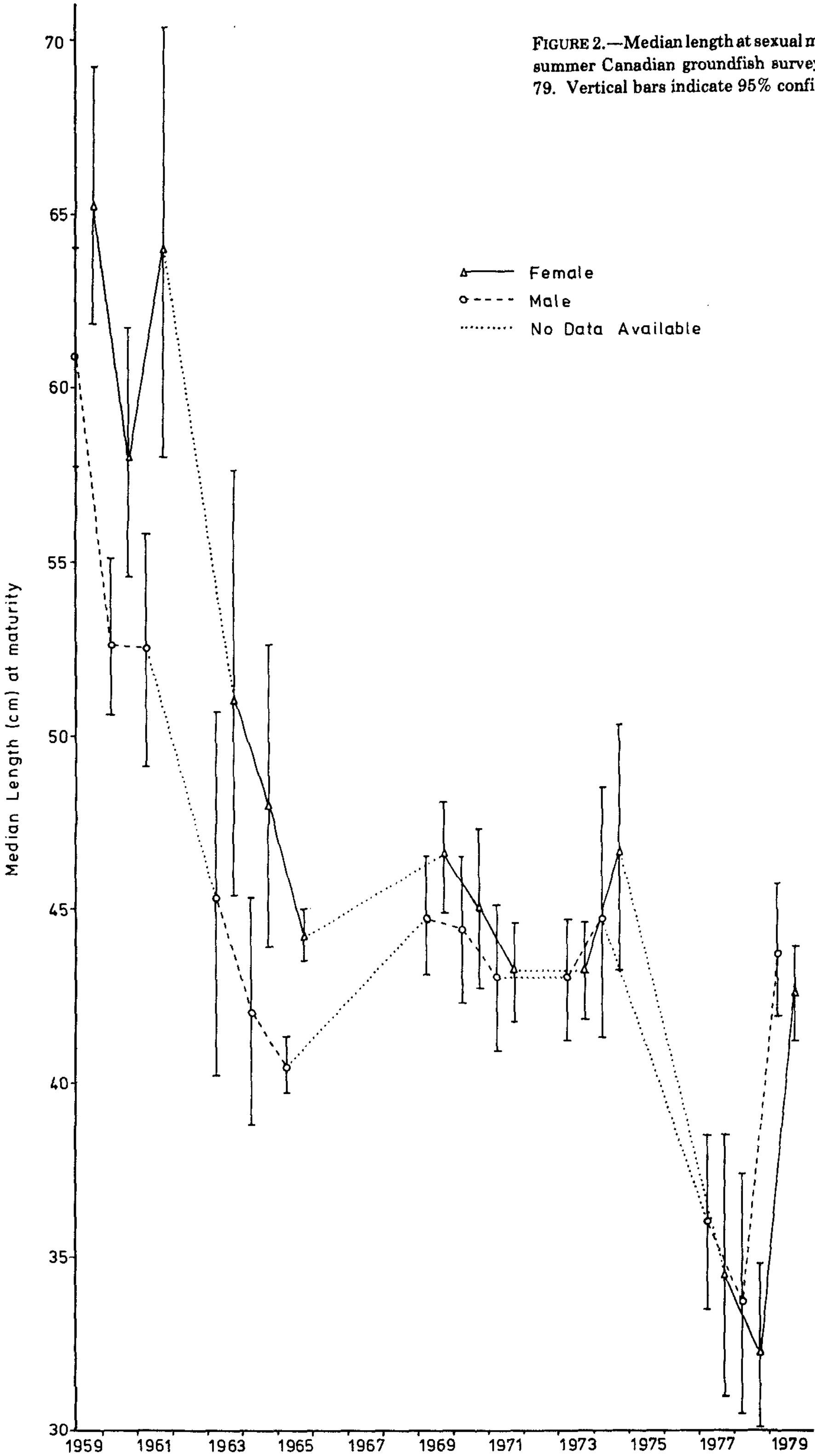

FIGURE 2.—Median length at sexual maturity for Atlantic cod during summer Canadian groundfish surveys in Subdivision 4Vn, 1959-79. Vertical bars indicate 95% confidence limits.

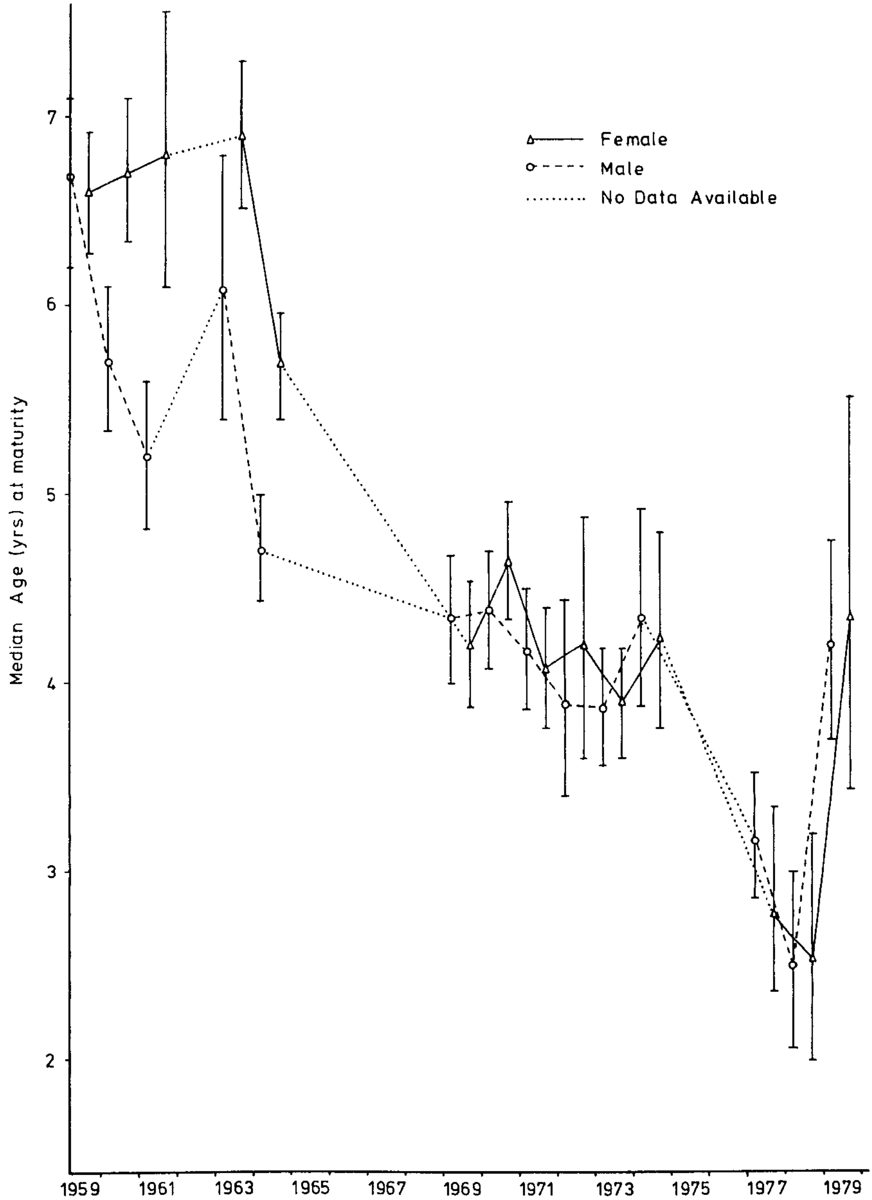

FIGURE 3.—Median age at sexual maturity for Atlantic cod during summer Canadian groundfish surveys in Subdivision 4Vn, 1959-79. Vertical bars indicate 95% confidence limits.

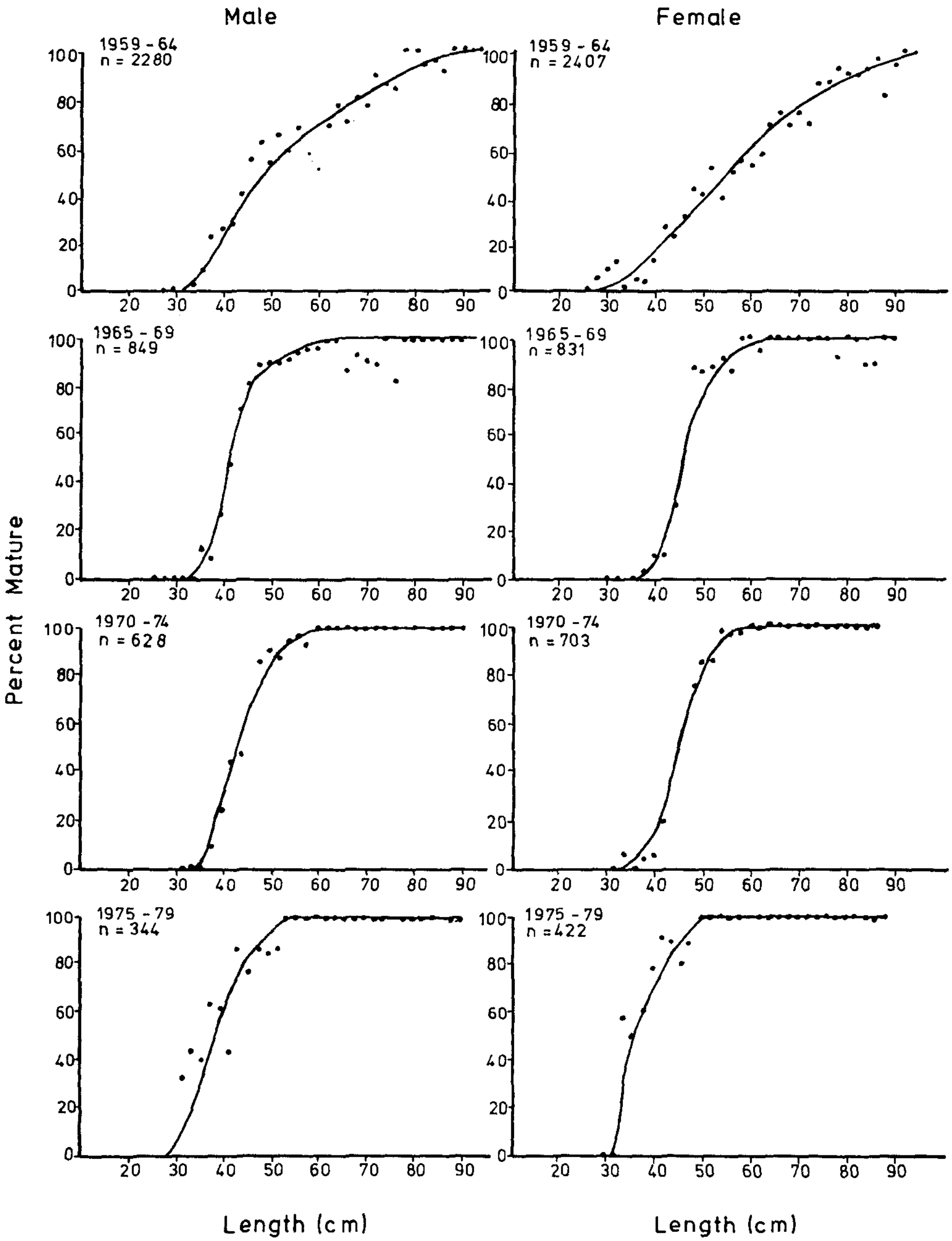

FIGURE 4.—Maturity ogives for Atlantic cod caught during Canadian groundfish surveys in Subdivision 4Vn, 1959-79.

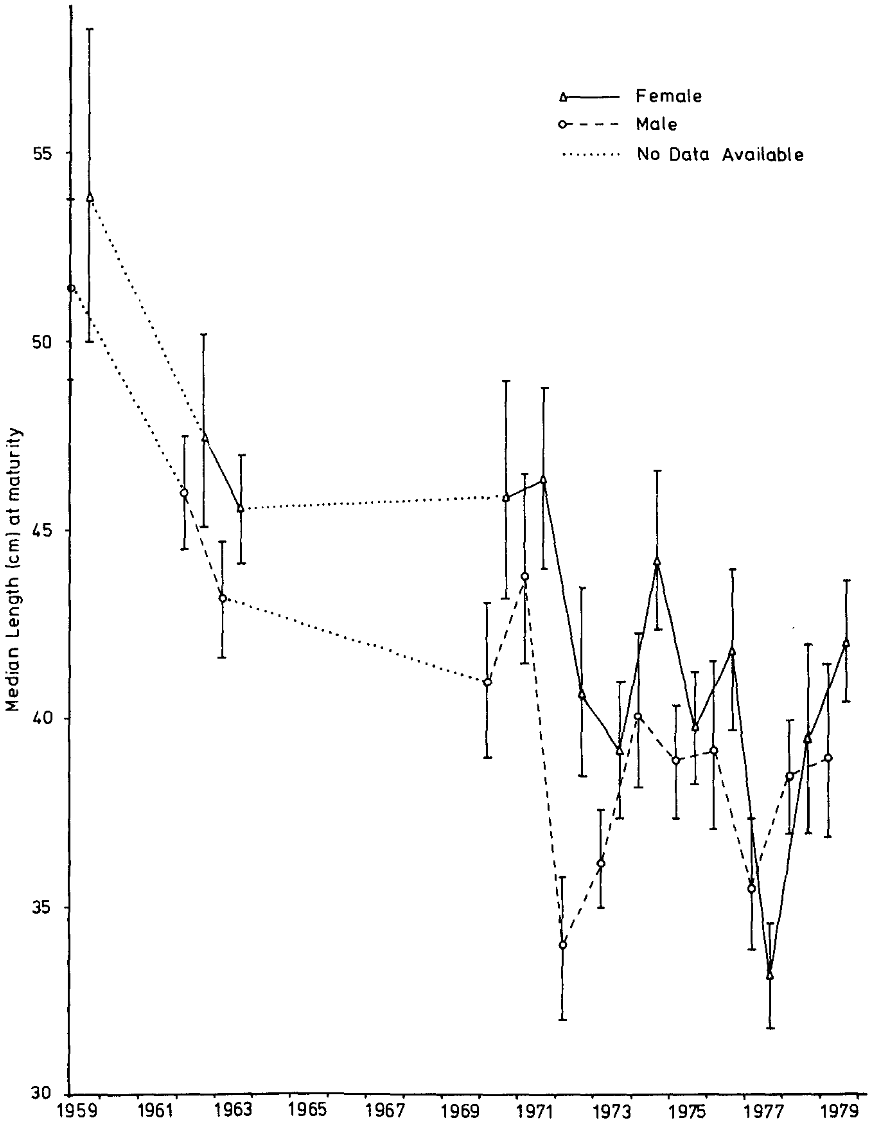

FIGURE 5.—Median length at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Subdivision 4Vs, 1959-79. Vertical bars indicate 95% confidence limits.

79, median age was 2.7 yr for males and 2.9 yr for females, a significant decline ($P<0.01$).

Division 4W

Atlantic cod populations in Subdivision 4Vs and Division 4W are considered to be a unit stock for management purposes (Gray 1979). There were similar trends in L_{50} between Atlantic cod in Subdivision 4Vs and those of Division 4W (Fig. 8). In particular, there was a rapid decline in L_{50} between 1969 and 1972, with L_{50} for males declining from 48 to 37 cm in 4 yr, and with values for females declining from 50 to 36 cm. Subsequently, L_{50} values for both sexes have generally remained below 40 cm. Atlantic cod in Division 4W were similar to those of the other areas in regards to a decrease in L_{50} with time. The difference in lengths in which males and females attained maturity was greater in the 1960's than in the 1970's, indicating that the rate of decline in L_{50} was faster in females than in males.

A_{50} values declined over time until the early 1970's (Fig. 9). A low value of 2.2 yr for males and 2.3 yr for females was reached in 1978, a decrease of about

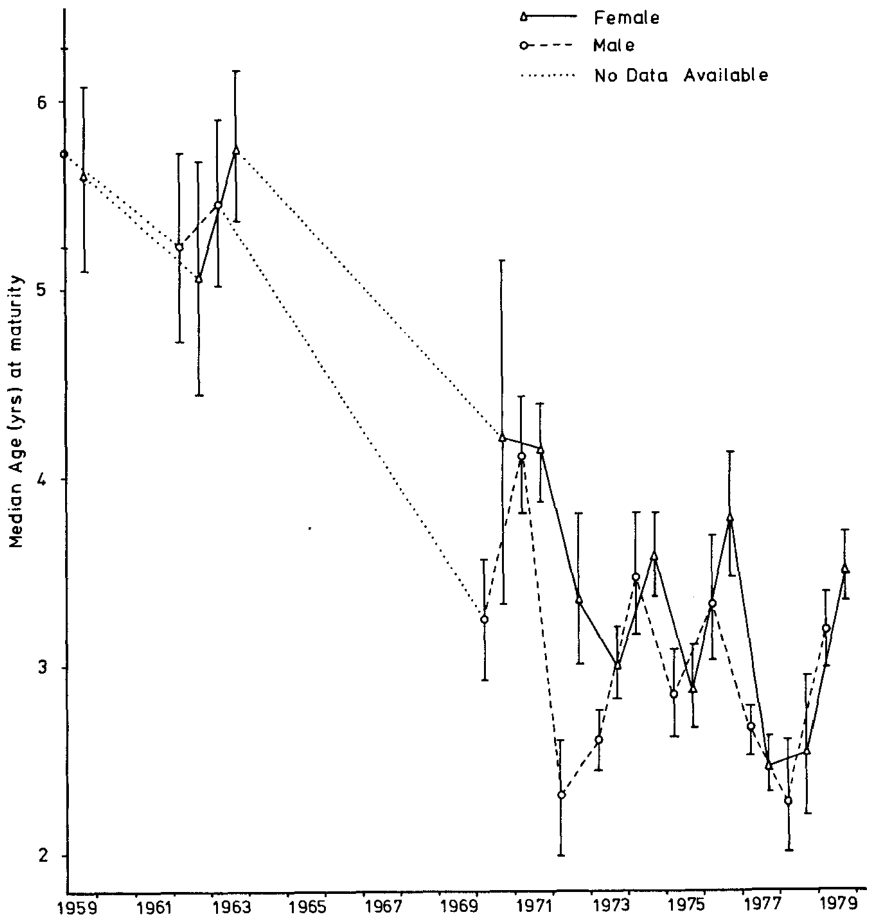

FIGURE 6.—Median age at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Subdivision 4Vs, 1959-79. Vertical bars indicate 95% confidence limits.

TABLE 2.—Percentage of sexually mature Atlantic cod by age and sex caught during Canadian groundfish surveys in Subdivision 4Vs, 1959-79. Sample sizes are in parentheses for individual ages and 95% confidence limits for A_{50} (years).

Age (yr)	1959-64	1965-69	1970-74	1975-79	Age (yr)	1959-64	1965-69	1970-74	1975-79
		Male					Female		
1	0.0 (19)	— (0)	0.0 (44)	0.0 (23)	1	25.0 (4)	— (0)	0.0 (46)	0.0 (9)
2	0.0 (60)	25.0 (4)	13.2 (250)	15.2 (126)	2	0.0 (79)	0.0 (1)	5.7 (299)	10.0 (142)
3	2.5 (121)	75.0 (8)	40.0 (205)	62.9 (251)	3	2.0 (102)	75.0 (12)	25.0 (228)	55.7 (266)
4	10.4 (106)	78.3 (23)	80.1 (141)	91.7 (140)	4	23.0 (100)	85.7 (14)	59.9 (157)	91.0 (163)
5	37.4 (83)	100.0 (11)	95.6 (90)	95.9 (119)	5	38.8 (80)	100.0 (9)	95.9 (98)	97.4 (107)
6	74.2 (93)	90.9 (11)	97.9 (48)	100.0 (36)	6	76.0 (121)	94.1 (17)	97.2 (72)	100.0 (50)
7	88.1 (109)	100.0 (9)	100.0 (37)	100.0 (24)	7	89.4 (113)	100.0 (8)	100.0 (23)	100.0 (28)
8	87.9 (66)	100.0 (1)	100.0 (11)	100.0 (17)	8	81.8 (77)	100.0 (2)	100.0 (15)	100.0 (6)
9	87.2 (39)	100.0 (1)	100.0 (2)	100.0 (12)	9	88.5 (52)	100.0 (3)	100.0 (6)	100.0 (5)
10	94.4 (36)	100.0 (2)	100.0 (1)	100.0 (5)	10	100.0 (49)	— (0)	100.0 (5)	100.0 (3)
11	90.9 (11)	100.0 (1)	100.0 (3)	— (0)	A_{50}	5.19(6.19-6.51)	2.45(1.61-3.77)	3.53(3.41-3.65)	2.86(2.76-2.97)
12	80.0 (10)	100.0 (1)	— (0)	— (0)					
13	100.0 (1)	100.0 (1)	— (0)	100.0 (1)					
A_{50}	5.43(5.23-5.64)	2.40(1.37-5.44)	3.07(2.96-3.18)	2.72(2.60-2.83)					

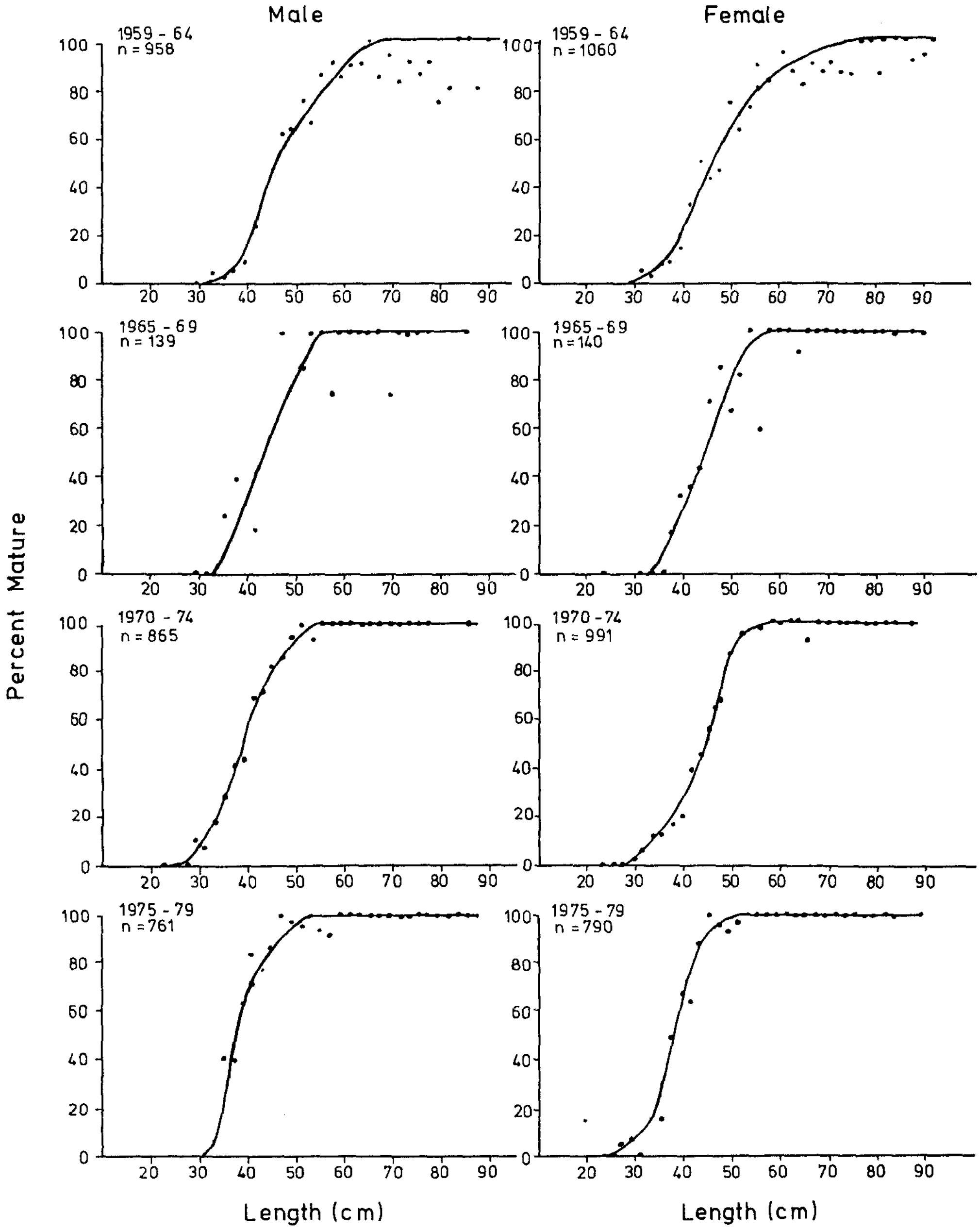

FIGURE 7.—Maturity ogives for Atlantic cod caught during Canadian groundfish surveys in Subdivision 4Vs, 1959-79.

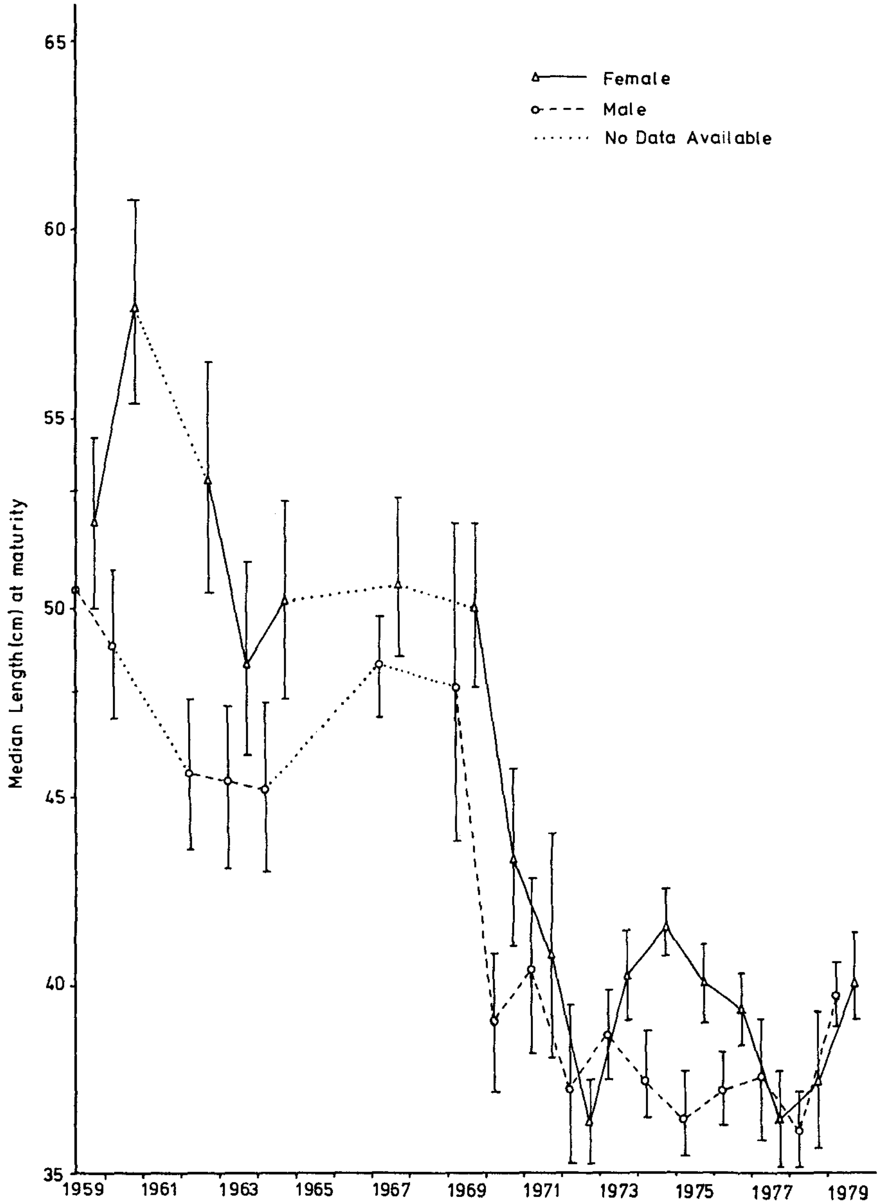

FIGURE 8.—Median length at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Division 4W, 1959-79. Vertical bars indicate 95% confidence limits.

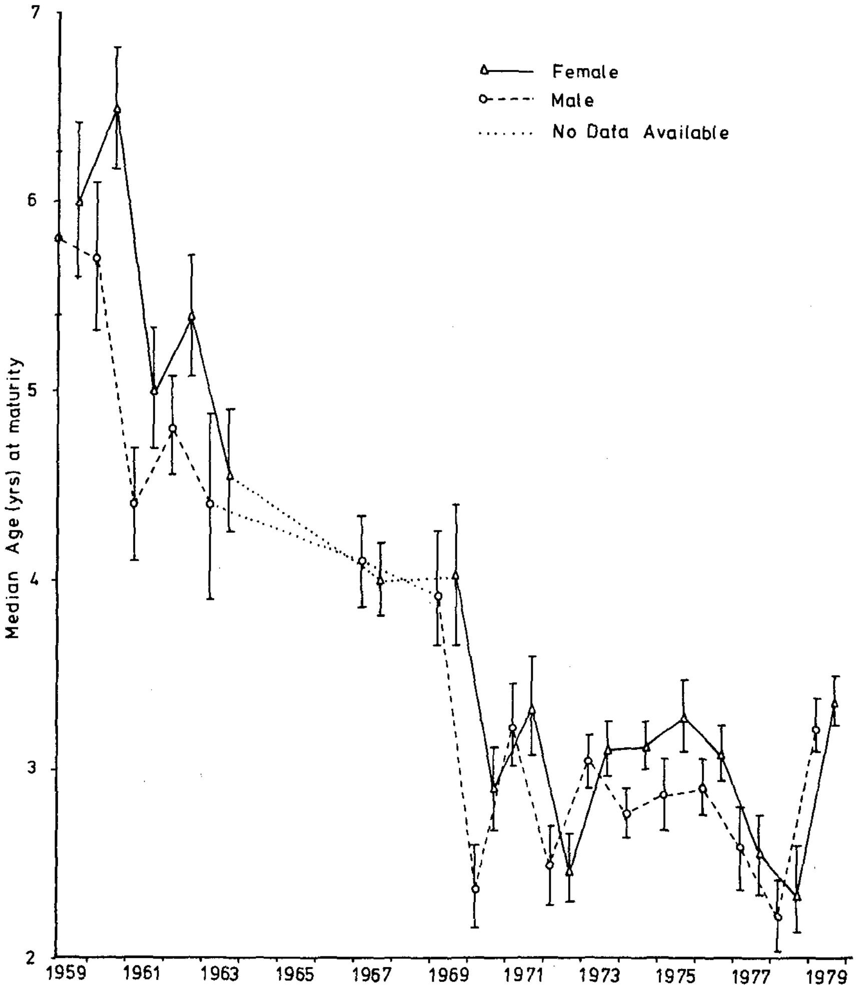

FIGURE 9.—Median age at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Division 4W, 1959-79. Vertical bars indicate 95% confidence limits.

60% from the 1959 values. The A_{50} value increased in 1979, though further data are necessary to determine if this is a general trend.

The maturity ogives, based on length, indicated that the trend for elimination of larger, immature Atlantic cod seen in other cod in other areas was also present in this area (Fig. 10). L_{50} values for Atlantic cod in 1959-64 were 46 cm for males and 52 cm for females, but in 1975-79, these values were 37 and 39 cm, respectively. The values in 1975-79 were lower than those in any of the previous three periods ($P<0.05$). The trend for a transition from an immature to a mature state over a smaller length interval through time was also apparent. The transition occurred over a 45 cm length interval in 1959-64, but over a 25 cm interval in 1975-79.

Changes in percent mature by age indicate an increase through time (Table 3), and males and females ages 3-5 showed marked increases in percent mature over time. Age-2 Atlantic cod also showed marked increases, with about 18% of the males and 11% of the females classified as mature in 1975-79, whereas <1% were mature during 1959-64. A_{50} values in 1959-64 were 4.7 yr for males and 5.0 yr for females, and these values declined in 1975-79 to 2.7 yr for males and 2.9 yr for females ($P<0.01$). These trends are indicative of a shifting of the A_{50} to younger ages.

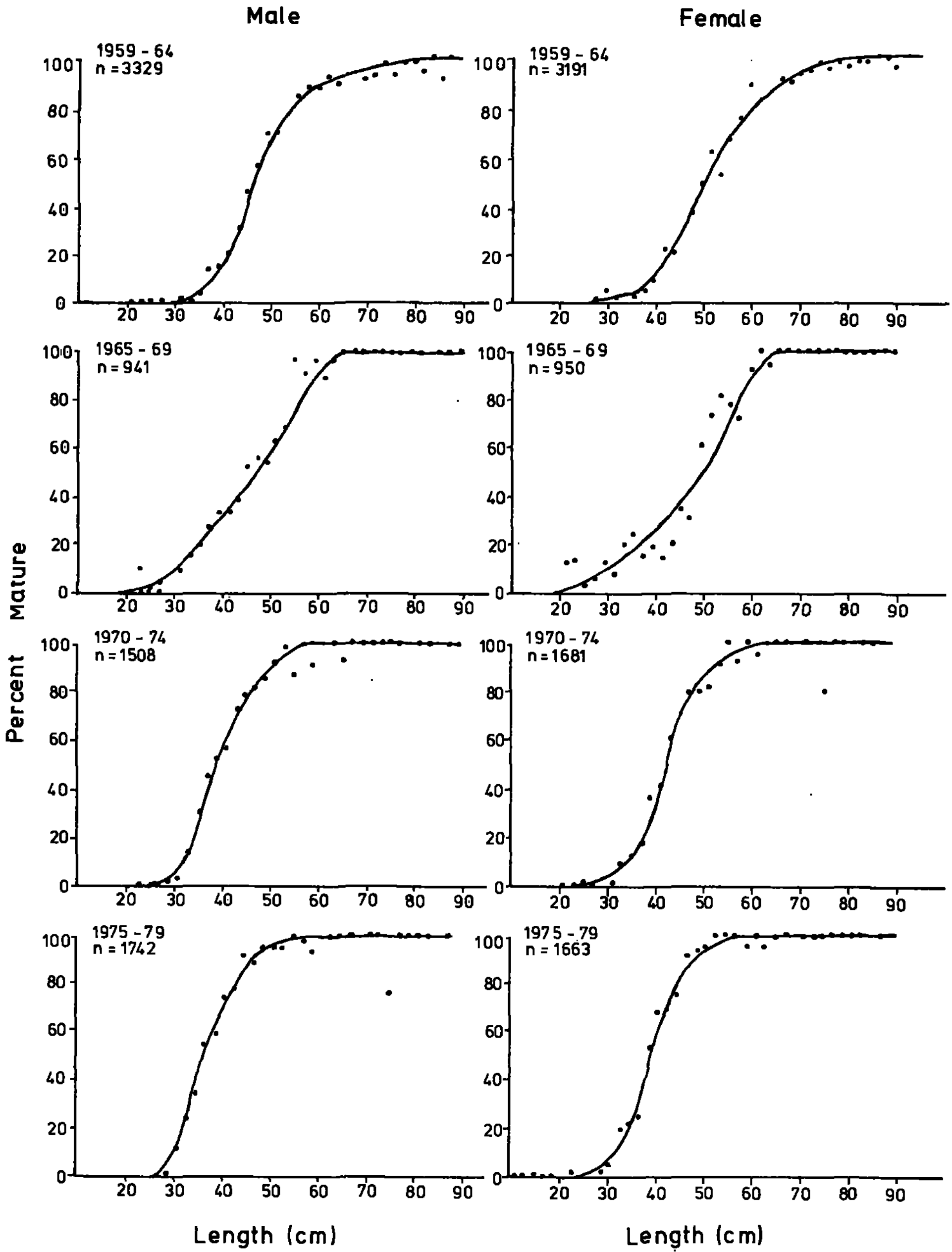

FIGURE 10.—Maturity ogives for Atlantic cod caught during Canadian groundfish surveys in Division 4W, 1959-79.

TABLE 3.—Percentage of sexually mature Atlantic cod by age and sex caught during Canadian groundfish surveys in Division 4W, 1959-79. Sample sizes are in parentheses for individual ages and 95% confidence limits for A_{50} (years).

Age (yr)	1959-64	1965-69	1970-74	1975-79
		Male		
1	0.0 (59)	0.0 (7)	0.0 (146)	0.0 (120)
2	0.7 (143)	7.4 (81)	16.1 (416)	17.5 (307)
3	5.0 (282)	25.3 (178)	51.7 (395)	65.6 (466)
4	26.3 (205)	48.6 (177)	82.8 (250)	89.3 (421)
5	57.7 (208)	91.2 (91)	87.7 (114)	94.3 (261)
6	83.6 (280)	95.8 (71)	91.3 (46)	97.9 (95)
7	90.0 (250)	98.4 (63)	100.0 (36)	100.0 (26)
8	99.3 (141)	100.0 (14)	100.0 (17)	100.0 (6)
9	97.2 (71)	100.0 (12)	100.0 (4)	100.0 (2)
10	93.1 (58)	100.0 (14)	100.0 (3)	— (0)
11	100.0 (21)	100.0 (1)	100.0 (1)	100.0 (1)
A_{50}	4.69(4.58-4.80)	3.72(3.58-3.86)	2.94(2.85-3.03)	2.67(2.59-2.76)
		Female		
1	0.0 (60)	0.0 (4)	0.0 (144)	0.0 (106)
2	0.6 (177)	10.1 (79)	8.2 (486)	11.0 (287)
3	7.0 (259)	17.2 (221)	43.6 (404)	54.3 (421)
4	14.6 (212)	36.3 (171)	73.9 (284)	88.4 (445)
5	45.7 (184)	81.9 (72)	91.8 (134)	99.3 (228)
6	75.4 (236)	89.8 (49)	95.0 (40)	98.2 (110)
7	90.2 (245)	90.6 (64)	97.1 (34)	100.0 (31)
8	95.9 (170)	100.0 (14)	100.0 (15)	100.0 (4)
9	95.2 (105)	100.0 (17)	100.0 (14)	100.0 (4)
10	100.0 (77)	100.0 (14)	100.0 (12)	— (0)
A_{50}	4.95(4.83-5.07)	4.16(3.99-4.35)	3.19(3.11-3.28)	2.87(2.80-2.95)

Division 4X

Atlantic cod in Division 4X are managed as a separate unit, though inshore and offshore stocks may mix. Trends in L_{50} were not as clear as in other stocks, although there was a decrease with time until 1978 (Fig. 11). The L_{50} values were 51 cm for males and 52 cm for females in 1963, but these values had declined to 38 cm for males and 35 cm for females in 1978. Females generally attained maturity at greater lengths than did males, but there has been little difference between sexes over time. The data suggest that there was a decrease in L_{50} in 1970-71, as happened in 4VsW Atlantic cod.

A_{50} values have declined with time, but age samples in the early 1960's had small sample sizes. There was a rapid decline in A_{50} between 1969 and 1972 with values for males declining from 3.9 to 2.2 yr and for females from 5.0 to 2.4 yr (Fig. 12). In 1978, A_{50} values were calculated to be <2 yr for both males and females. Males generally matured at younger ages than did females.

The maturity ogives, based on length, indicate that there has been some elimination of larger, immature fish from Division 4X Atlantic cod with time, but that the transition from the immature to the mature state during 1975-79 still occurred over the largest length interval of the areas analyzed, being about 35 cm for males and 40 cm for females (Fig. 13). In 1959, L_{50} was 57 cm for males and 46 cm for females, but these values declined to 45 cm for both males ($P<0.05$) and females during 1975-79. The 100% mature value during 1975-79 was not attained until lengths were >65 cm.

Changes in percent maturity with age indicate an increasing trend with time, but the increase in percent maturity with time has not been as marked as in other Atlantic cod stocks (Table 4). A_{50} values in 1959-64 were 4.8 yr for males and 3.7 yr for females, but during 1975-79 these values declined to 2.8 yr for males ($P<0.01$) and 2.9 yr for females ($P<0.05$). Increases in percent mature were most apparent in males ages 2-5 and females ages 2-4. Median age at maturity has been generally <3 yr in the 1970's.

TABLE 4.—Percentage of sexually mature Atlantic cod by age and sex caught during Canadian groundfish surveys in Division 4X, 1959-79. Sample sizes are in parentheses for individual ages and 95% confidence limits for A_{50} (years).

Age (yr)	1959-64	1965-69	1970-74	1975-79
		Male		
1	0.0 (2)	— (0)	0.0 (47)	0.0 (35)
2	0.0 (12)	0.0 (30)	15.3 (183)	21.1 (204)
3	16.2 (37)	8.6 (58)	59.5 (227)	56.3 (288)
4	29.3 (75)	72.7 (55)	83.4 (169)	81.7 (355)
5	47.1 (68)	98.2 (55)	92.7 (123)	93.4 (182)
6	72.9 (59)	98.0 (50)	97.4 (78)	97.1 (136)
7	88.2 (51)	100.0 (19)	97.6 (42)	100.0 (63)
8	100.0 (60)	100.0 (11)	100.0 (22)	100.0 (35)
A_{50}	4.76(4.52-5.01)	3.69(3.54-3.84)	2.83(2.72-2.94)	2.78(2.67-2.89)
		Female		
1	0.0 (0)	— (0)	0.0 (50)	0.0 (56)
2	10.0 (20)	0.0 (31)	13.7 (182)	15.6 (238)
3	24.3 (37)	8.9 (56)	55.6 (216)	57.0 (335)
4	57.8 (90)	64.4 (45)	73.1 (197)	83.5 (351)
5	81.5 (81)	87.7 (57)	83.5 (121)	85.2 (250)
6	77.8 (54)	100.0 (57)	94.5 (91)	93.6 (125)
7	94.9 (59)	100.0 (21)	97.4 (39)	96.3 (80)
8	96.2 (26)	100.0 (10)	100.0 (25)	100.0 (34)
9	100.0 (8)	100.0 (5)	100.0 (16)	100.0 (18)
A_{50}	3.72(3.44-4.01)	3.84(3.66-4.02)	3.03(2.90-3.17)	2.88(2.77-2.99)

Comparisons Among Areas

Several trends were apparent when all areas were considered in the multiyear grouping of groundfish surveys. Median lengths at maturity tended to decline through time in all areas in which Atlantic cod were surveyed (Table 5). The differences in L_{50} values among Atlantic cod decreased with time, so that values for Atlantic cod in all areas except those in Division 4X were similar in the period 1975-79.

In an analysis of trends in A_{50}, there was a trend for younger ages at maturity over time. Differences among areas generally decreased with time, so that in the period 1975-79, A_{50} values were about 2.7 yr for

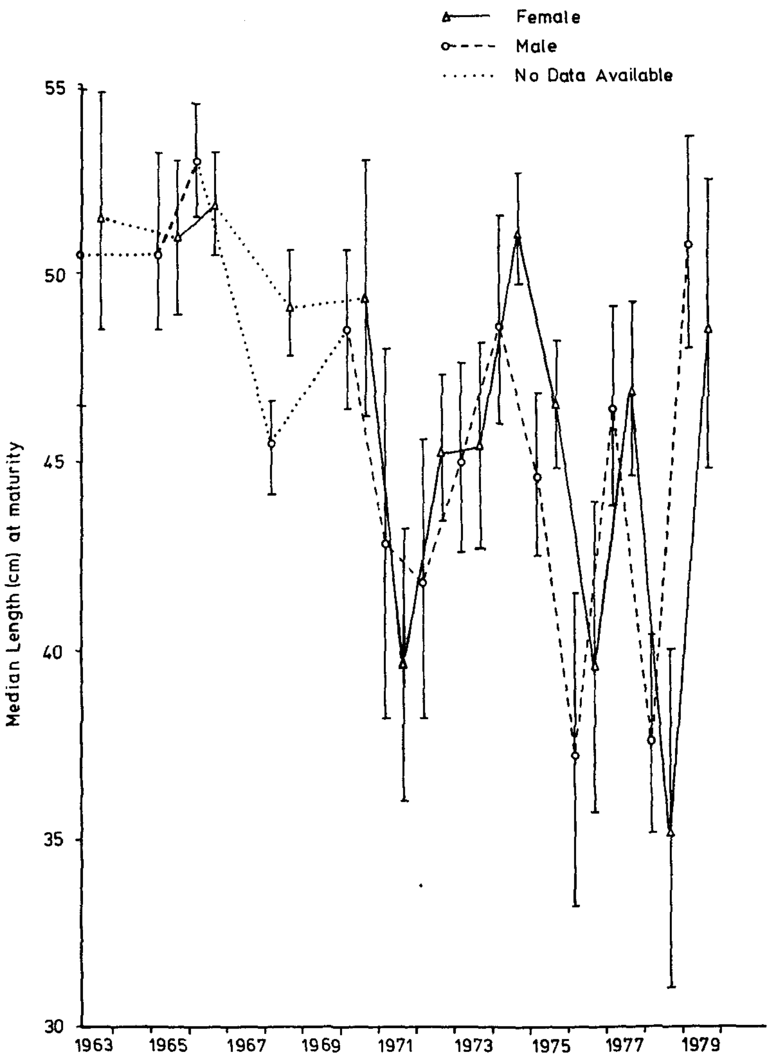

FIGURE 11.—Median length at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Division 4X, 1959-79. Vertical bars indicate 95% confidence limits.

males and about 2.9 yr for females on the Scotian Shelf. Bottom water temperatures derived from the groundfish surveys indicated that Subdivision 4Vn had the coldest water temperatures during 1970-74 (3.6°C) and Division 4X the warmest (6.9°C), with the rest of Scotian Shelf temperatures between these extremes. There was a general trend for greater A_{50} values to be found in stocks in colder waters, and Atlantic cod growth rates on the Scotian Shelf were correlated with water temperature (Beacham 1982), so there was a trend for stocks that have a lower growth rate to have a higher median age at sexual maturity.

DISCUSSION

The Atlantic cod stocks on the Scotian Shelf were subject to high rates of exploitation in the 1960's and early 1970's and consequently declined in biomass (Gray 1979). The declines in median size and age at sexual maturity were thus concurrent with declines in stock biomass. However, with the introduction of quota management and improved recruitment, stock biomasses have generally increased since 1975.

The mean size and age of Atlantic cod in the landings of the commercial fishery in Subarea 4 have declined with time (Beacham 1982), but this cannot

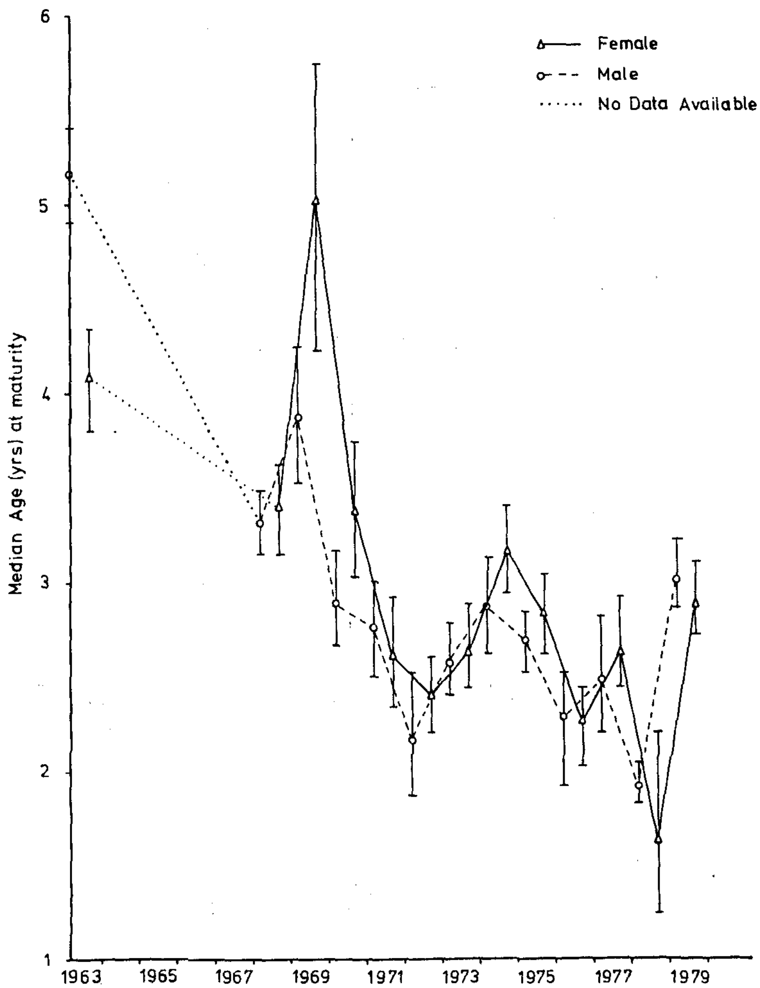

FIGURE 12.—Median age at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Division 4X, 1959-79. Vertical bars indicate 95% confidence limits.

account for the decline in median size and age at sexual maturity. Larger Atlantic cod are less abundant than they once were, but during 1975-79, virtually all Atlantic cod 60 cm long were mature in the stocks examined, while in the 1960's, 50% of 60 cm Atlantic cod could be immature. For the decline in median size and age at sexual maturity to be accounted for by a decline in mean size and age of the stock, sampling gears in the 1960's would have to have selected larger, immature fish while avoiding smaller, mature ones, an unlikely situation.

Median length and age at maturity of the 4VsW Atlantic cod stock declined rapidly between 1969 and 1972. Nominal catches from this stock peaked in 1968, with over 80,000 t reported by all countries, and with the Spanish catch reported at over 50,000 t (Halliday 1976). Halliday noted that there were sharp declines in the catch rates of Spanish pair trawlers subsequent to 1968. The rapid decline in median size and age at sexual maturity subsequent to 1968 may suggest that these parameters were responding rapidly to a decrease in stock biomass, although this interpretation is open to question. Stock biomasses have increased in the late 1970's (Beacham et al. 1980; Gray 1979), but there has been no corresponding increase in median size or age at maturity.

Median length and age at sexual maturity for Atlantic cod in the northwest Atlantic have been an area of some research. Variability in median length at sexual

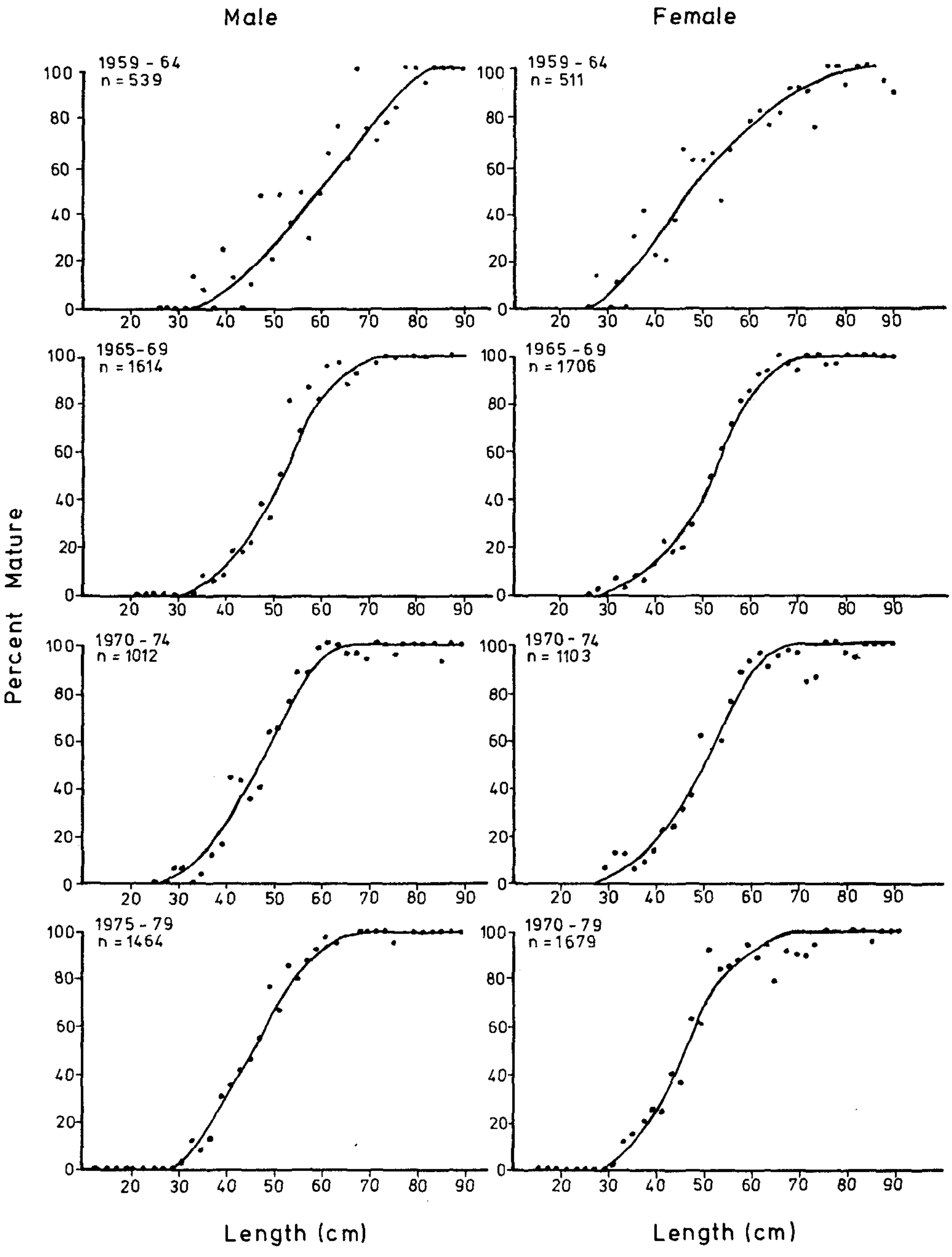

FIGURE 13.—Maturity ogives for Atlantic cod caught during Canadian groundfish surveys in Division 4X, 1959-79.

TABLE 5.—Median length (cm) at sexual maturity of Atlantic cod in areas 4Vn, 4Vs, 4W, and 4X, as calculated from Canadian groundfish surveys from 1959-64, 1965-69, 1970-74, and 1975-79. 95% confidence limits are in parentheses. Sample sizes are indicated in Figures 4, 7, 10, and 13.

Division	1959-64	1965-69	1970-74	1975-79
		Males		
4Vn	51.82	41.08	42.62	36.31
	(49.96-53.75)	(40.22-41.95)	(41.66-43.61)	(33.73-39.10)
4Vs	47.31	42.26	38.46	37.59
	(45.84-48.83)	(40.21-44.42)	(37.68-39.25)	(36.83-38.37)
4W	46.01	43.54	39.27	37.23
	(45.19-46.85)	(42.38-44.73)	(38.63-39.92)	(36.64-37.84)
4X	57.09	49.16	45.67	44.74
	(54.99-59.27)	(48.30-50.04)	(44.64-46.71)	(43.83-45.67)
		Females		
4Vn	54.55	44.85	44.09	34.11
	(53.37-55.77)	(44.21-45.50)	(43.29-44.89)	(31.73-36.67)
4Vs	43.70	43.31	42.26	37.61
	(37.12-51.88)	(40.47-46.36)	(41.44-43.10)	(36.83-38.42)
4W	52.00	45.66	41.68	38.88
	(51.55-52.45)	(44.25-47.12)	(41.03-42.34)	(38.27-39.49)
4X	46.08	48.68	47.91	44.77
	(42.86-49.55)	(47.80-49.57)	(46.75-49.10)	(43.94-45.62)

maturity for Division 4T Atlantic cod was investigated by Powles (1958), who found that during the summers of 1955 and 1956, median lengths at maturity for females were between 52 and 57 cm, and those for males between 50 and 53 cm. Wiles and May (1968) found that, by grouping data between 1947 and 1966, the median lengths at sexual maturity in the northern Gulf of St. Lawrence cod stock (Divisions 3Pn-4RS) were 46 cm for males and 50 cm for females, corresponding to median ages at maturity of 5.1 and 6.1 yr, respectively. Minet (1978), investigating the same stock in 1973, found results very similar to those of Wiles and May (1968). Pinhorn (1969) found similar results for Atlantic cod in Subdivision 3Pn in 1952, but median ages apparently increased to 6.3 yr for males and 6.7 yr for females in 1957. Fleming (1960) found that Atlantic cod in the same area matured between 6.6 and 6.8 yr from 1947 to 1950. Thus it appears for the northern Gulf of St. Lawrence cod stock, there has not been a marked decline in median age at sexual maturity with time. Hansen (1949) reported that size and age at maturity of Atlantic cod in the West Greenland stock declined from 1917 to 1936, an analogous trend to that indicated for Atlantic cod on the Scotian Shelf by the present study.

Gunter (1950) found that fish inhabiting regions of higher water temperature grew faster initially, attained sexual maturity earlier, and were of smaller final size than the same species in regions of lower water temperature. However, Fleming (1960) found that Atlantic cod in the Labrador area of Newfoundland attained sexual maturity at younger ages, but grew more slowly than did Atlantic cod in stocks further south. Fleming attributed this result to Atlantic cod in poorer environments maturing earlier than those in more favorable environments. The present study, in agreement with Gunter's (1950) conclusions, indicated that Atlantic cod stocks inhabiting regions with warmer water temperature matured earlier than did those in colder regions.

Median size and age at maturity are heavily dependent upon growth rate. Molander (1925) found that in Baltic witch flounder, *Glyptocephalus cynoglossus*, stocks with faster growth rates matured at younger ages but at larger lengths than did fish in slower growing stocks. During 1975-79 in the present study, Atlantic cod tended to mature at the same length (Table 5), but northern stocks matured at older ages than did Atlantic cod in more southerly stocks. Alm (1959) noted that faster growing fish attained sexual maturity earlier than did slower growing fish, and the results of the present study support that conclusion.

Growth rates in Atlantic cod have been shown to be inversely related with stock biomass (Lett and Doubleday 1976; Beacham 1980), with growth rates increasing as stock biomass declines. Templeman and Bishop (1979) attributed a decline in median age at maturity in haddock, *Melanogrammus aeglefinus*, to an increase in growth rate coincident with declining stock density, an idea that implicitly assumes a minimum threshold or minimum range for size at maturity. They also suggested that a decline in median length at maturity occurred, owing to a decrease in growth rates, implicitly assuming a minimum threshold for age at maturity. If Templeman and Bishop's (1979) assertions are general, then declines in median length and age at maturity should not occur concurrently.

All the Atlantic cod stocks examined in the present study showed a downward trend both in median size and median age at sexual maturity with time. Several hypotheses would explain these events. However, to the extent that size and age at maturity are genetically determined (Alm 1959), fish which mature at smaller sizes or younger ages had a selective advantage during the intensive fishery that has occurred on many of the Atlantic cod stocks since 1960 in Subarea 4. These genotypes reproduce before being fully recruited to the fishery, whereas genotypes that mature at larger lengths or older ages tend to be removed before reproduction. This process could contribute to the decreasing abundance of larger, immature fish with time and account for the shifting of the maturity ogives towards smaller sizes and younger ages. Size-selective fishing has been postulated to account for declines in size of individuals through the disproportionate removal of fast-growing individuals (Ricker et al. 1978; Favro et al. 1979). It may be, therefore, that late-maturing genotypes were removed from the Atlantic cod stocks in a period of heavy exploitation.

Environmental and genetic effects are difficult to separate. There may be a lag effect if size and age at sexual maturity have not increased at the same rate as stock biomass. Because fish attaining maturity at low stock biomass remain mature with increasing biomass, then the lag in increase in size and age at maturity results from year classes spawned under high stock biomass conditions requiring a longer period to attain maturity. There was an increase in median size and age at maturity in 1979 for Atlantic cod stocks on the Scotian Shelf, but further data are necessary to determine if this will be continuing. If median size and age at sexual maturity increase in the next 5-10 yr to levels similar to those between 1959 and 1964, this would suggest that these parameters were responding to stock biomass with a lag effect, although this interpretation is confounded by a decline in fishing intensity and thus selection. However, if median size and age at sexual maturity remain at the 1975-79 levels or decrease for the next 5-10 yr, this would suggest that there has been a genetic change within the stocks, with Atlantic cod maturing at larger sizes and older ages being selected against.

The rapid recoveries of many groundfish stocks during periods of restricted exploitation after heavy fishing, with no apparent genetic change, suggest that biomass has greater influence on variability in population parameters than do genetic changes. Heavily exploited stocks of North Sea cod and haddock recovered rapidly during World War II, when fishing mortality was reduced (Gulland 1971). Pacific halibut, *Hippoglossoides stenolepis*, stocks recovered from low population levels with no apparent genetic change (Miller 1957).

In summary, the present study has indicated that there has been a decline in median length and age at sexual maturity for Atlantic cod in several areas in NAFO Subarea 4 in the 1960's and 1970's. However, whether this decline can be ascribed to genetic or to environmental changes cannot be determined because application of the selective force (fishing intensity) concurrently changes the environment (stock biomass). Controlled selection experiments may provide some indication of potential for genetic change in Atlantic cod.

ACKNOWLEDGMENTS

I am indebted to those people who have crewed the research vessels and aged the Atlantic cod. Charles J. Krebs of the University of British Columbia wrote the computer program for probit analysis. Albert Vromans ably assisted in much of the analysis. M. C. Healey (Pacific Biological Station), R. G. Halliday (Marine Fish Division), and two referees made many helpful comments on a draft of this manuscript. The manuscript was prepared with the assistance of the staff at the Pacific Biological Station.

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