Northwest Atlantic Fisheries Organization

The Effect of Age on the Seasonality of Maturation and
Spawning of Atlantic Cod, *Gadus morhua*, in the Northwest Atlantic

by

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Abstract

We analyzed 45 years of research trawl survey data from 7 regions in the Northwest Atlantic (Newfoundland and Labrador) to assess the influence of age on the timing of maturation and spawning in male and female Atlantic cod, Gadus morhua. Older individuals of both sexes initiated and completed spawning later, and spawned for a greater length of time, than younger individuals. Within regions, males were in spawning condition for longer periods of time than females. Among regions, spawning duration of males (age=11 yr) averaged 43.5 ± 13.6 days and was significantly longer than that of females (age=11 yr; 25.2 ± 8.4 days). The strong association between age and time of spawning provides empirical evidence of size-specific, assortative mating in cod.

The decline in recruitment of cod in NAFO Division 2J3KL since 1963 is associated with a dramatic reduction in the fecundity contribution of older (15-20 yr) individuals relative to younger (7-9 yr) individuals. Our results indicate that this increase in proportional abundance of younger individuals should be concomitant with a decline in the duration of spawning time, reducing the probability that larval emergence will match peak abundances of zooplankton. Thus, age-dependence of maturation and spawning times provides a mechanism by which size-selective mortality against larger, older individuals can increase variability in recruitment in Atlantic cod.

Introduction

Temporal variation in the timing of reproduction represents a potentially important source of variability in the recruitment of juveniles to the adult portion of any fish population. The physical environment, for example, might delay or unduly extend the spawning period through temperature-induced constraints on the migration of adults to spawning habitat or on the physiological processes associated with maturation. Individual factors such as age and body size can also influence the timing of reproduction. If it is advantageous to spawn as early as possible in the spawning season, older females may spawn earlier than younger females because of sexual selection, by males, for large body size (e.g. kokanee salmon, Oncorhynchus nerka, Foote 1988). Similarly, smaller female salmonids may delay reproduction until larger females have spawned to reduce egg mortality by egg nest superimposition (van den Berghe and Gross 1984; Myers 1986). Alternatively, larger individuals may reproduce later than smaller individuals because of longer maturation periods effected by generally slower metabolic rates or by greater, size-independent energy costs (Peters 1983).

Age-specific differences in the rate of gonadal development or in the duration of spawning should increase recruitment variability when the age-specific survival of adults varies from one generation to the next. Variability in survival is common in commercially exploited populations. Recruitment of Atlantic cod, Gadus morhua, (as determined by virtual population analysis; Baird et al. 1992) in North Atlantic Fisheries Organization (NAFO) Division 2J3KL off Labrador and northern Newfoundland varied by almost an order of magnitude from 1963 to 1988 (Fig. 1A). The temporal decline in cod abundance was accompanied by an overall 85% reduction in the total fecundity of old individuals (15-20 yr) relative to the total fecundity of young individuals (7-9 yr) (Fig. 1B) (age ranges were chosen simply to be representative of old and young mature fish). This reduction may be indicative

of a progressive decrease in the proportion of older females in the spawning population and a concomitant narrowing of the variation in age among reproductive individuals. If age significantly influences the timing of reproduction, then a decline in the number of age classes during spawning may shorten the duration of the spawning season and reduce the likelihood that larvae begin feeding during the period of peak zooplankton abundance. Our objective is to use research trawl data, collected over 45 years, to determine the influence of age on the timing of maturation and spawning in male and female Atlantic cod.

Materials and Methods

Spawning times were calculated from research trawl surveys conducted between 1947 and 1991 by the Canadian Department of Fisheries and Oceans and its predecessors. Prior to the early 1970's, cod were sampled systematically by line transect surveys. Surveys undertaken since that time were randomly stratified by depth. We combined all research surveys for our analyses. Data were analyzed for each of 7 geographical areas in the Newfoundland/Labrador Region (Fig. 2). These areas included NAFO Divisions 3L, 3N, 3O, and 3Ps in entirety. Divisions 4R and 4S in the northern Gulf of St. Lawrence were combined (4RS). Data from Divisions 2J and 3K were represented by Belle Isle Bank in the north and by Funk Island Bank in the south. Flemish Cap (NAFO Division 3M), Hamilton Bank (2J), and the northern coast of Labrador (2GH) were excluded from the analyses because of insufficient data. Ice cover restricted extensive sampling during spawning in Belle Isle and Funk Island banks. Myers et al. (1993) provide a summary of the monthly samples available from these regions.

Individuals were analyzed by sex and by maturation stage (following Templeman et al. 1978) (Table 1). Females were divided into three stages: maturing (eggs opaque and visible to naked eye), spawning (ovary containing clear eggs, clarity being indicative of hydration and readiness for release; cf. Kjesbu 1989; Rijnsdorp 1989), and spent (ovaries whitish-grey or bluish-grey, slack and often wrinkled, residual eggs often present). The three maturation stages for males were: maturing (colour of testes ranging from gray or pink to white, little or no sperm in the vas deferentia), spawning (testes and vas deferentia white and full of milt), and spent (testes grey or pink, milt not evident in outer edges at the time that all females are spent).

To examine the influence of age on the timing of a given maturation stage, all individuals whose gonads were in a developmental state preceding the stage of interest were classified 0 and all remaining individuals were classified 1. Age determinations were calculated from otoliths. We used a maximum likelihood probit analysis to analyze the effects of age on the timing of 2 maturity stages (spawning, spent). The probability, p, of an individual maturing at age a yr on day of year t was assumed to be

(1) $$p = \Phi(\beta_0 + \beta_1 t + \beta_2 a)$$

where Φ is the cumulative distribution function for the standard normal distribution and β_0, β_1, and β_2 are the probit regression parameters. For a given t, the standard deviation of the timing of each stage at a given age a is $1/\beta_2$. Following the PROC PROBIT procedure in SAS (SAS Institute 1989), the standard errors of the parameters were inflated by a heterogenity factor if there was a lack of fit caused by extra-binomial variation. This extra-binomial variation is expected because of cluster sampling from trawls and perhaps microgeographic or interannual variability in maturity.

We defined the times of initiation and cessation of spawning of individuals aged a years as the day of year, t, on which 50% of the fish were expected to be in a spawning or spent condition, respectively. Thus, given that $0.5 = \Phi(0)$, times of spawning initiation and cessation can be calculated as

(2) $$t = (-\beta_0 - \beta_2 a) / \beta_1 \quad .$$

Spawning duration was defined as the difference in times of spawning initiation and spawning cessation.

Results

Age had a significantly positive effect on the initiation and cessation of spawning for males and females in all regions (Table 2). Older individuals of both sexes completed

spawning later than younger individuals (Figs. 3 and 4). Younger individuals began spawning before older individuals in all regions although the age effect was not significant for either males or females in 3L and 4RS.

The slopes of the probit regressions relating age to the cessation of spawning were greater than the slopes of the regressions between age and the initiation of spawning in all but two cases (Figs. 3 and 4). The probability of obtaining 12 such deviations among the 14 cases observed is significantly greater than expected by chance alone (sign test; t_s=3.77 > $t_{0.01[13]}$=3.01). This slope divergence, which was more evident among males, indicates that older individuals have a longer reproductive period than younger individuals. The two regions in which the slopes did not diverge for females (Belle Isle and Funk Island banks) were characterized by disproportionately low sample sizes of spawning individuals (Table 1).

Spawning duration for males aged 11 (the mid-range of 6 to 16 yrs) (range: 22 days in 3N to 57 days in 4RS) was longer than that for similarly aged females (range: 6 days in Belle Isle Bank to 32 days in 3O) within each region. Among regions, the spawning duration of males aged 11 yr (38.6 $\pm$ 13.8 days) was significantly greater than that for females (19.8 $\pm$ 11.5 days; $F_{[1,12]}$ = 7.58; p=0.017, p was assessed from 1000 data randomizations; cf. Manly 1991). If the two regions for which sample sizes of spawning individuals were disproportionately small (Belle Isle and Funk Island banks) are excluded, spawning duration of 11-year-old males and females increases to 43.5 $\pm$ 13.6 and 25.2 $\pm$ 8.4 days, respectively, and remains significantly different between sexes ($F_{[1,8]}$ = 6.52; p=0.034).

Discussion

The classical explanation of the timing of reproduction in marine pelagic fish is given by Cushing's (1969) match-mismatch hypothesis. This model assumes that spawning time is constrained by the necessity of maximizing the overlap between larval abundance and the seasonal supply of zooplankton. If this hypothesis is true, our results suggest that the timing of the peak of larval abundance is not precise because of age-specific effects on the timing of reproduction. We found that age has a positive effect on the timing of maturation and spawning in male and female Atlantic cod. Although at variance with long-accepted notions in the literature (e.g., Jónsson 1961; Harden Jones 1968), our results are consistent with studies for which empirical data on maturation are available (e.g. Jónsson 1982) .

Ellertsen et al. (1989:216), citing Sorokin's (1957) discussion of the Barents Sea cod stock, stated that "it is well known that larger and older fish spawn earlier than first time spawners." With respect to the Icelandic cod stocks, Jónsson (1961:131) also remarked that "it is a well known fact, that the first-time spawners start spawning later in the season than the older ones" although he provided no data to support this assertion. The conclusion that older cod spawn earlier than younger cod is based primarily on commercial fish catch data from Lofoten, Norway, the main spawning area for the Barents Sea population (Pedersen 1984). These data (Sund 1938; Rollefsen 1940) indicated that the size of cod in commercial catches declined from mid-February through March. While these data suggest that older fish arrive on the spawning grounds before younger fish, it seems unwarranted to then conclude that older cod spawn before younger cod. According to Bergstad et al. (1987), spawning in Lofoten occurs primarily from mid-March through mid-April. Given that fish of all sizes and ages are present in the Kabelvåg, Sørvågen, Balstad and Værøy regions of Lofoten by mid to late March (Sund 1938; Rollefsen 1940), the data do not imply that time of spawning is inversely related to age.

Our conclusion that age is positively associated with spawning time is supported by Jónsson's (1982) maturity data on Icelandic cod. He combined data from 1953 to 1974 and documented a progressive increase in the proportional representation of older spawning fish (sexes combined) throughout the spawning period. The relative importance of his suggestion that young spawners also spawn near the end of the spawning period is difficult to assess because he did not report age- and size-specific sample sizes. Recent spermatological data on spawning cod from NAFO region 3L collected by E.A. Trippel and M.J. Morgan (Fisheries and Oceans, Biological Station, St. Andrews, NB, Canada E0G 2X0 and Fisheries and Oceans, P.O. Box 5661, St. John's, NF, Canada A1C 5X1, personal communications) indicated that younger males had depleted or spent their sperm volume before older males had begun to spawn. These data provide firm empirical evidence of the positive association between age and time of spawning that we documented for Newfoundland/Labrador region cod. The negative correlation between age and spawning time that has been documented in herring, Clupea harengus, (Iles 1964; Lambert 1987) and in brown trout, Salmo trutta, (Elliott 1984) may reflect size-dependent, competitive interactions associated with spawning on a substrate. Although laboratory work indicates that some hydrated eggs are always present in females once they have begun to spawn (Kjesbu 1988), it is possible that some of the females

we classified as maturing females (because of an absence of hyaline eggs) may have been spawning. However, the similarity of the age-related effects on spawning between females and males (whose maturation states are more easily identifiable) suggests that any misclassifications were unlikely to bias our results.

The data suggest that the duration of spawning increases with increasing age for both male and female cod. Such an association may or may not be adaptive. There can be considerable selective advantages to spreading reproduction over time to reduce temporal variance in offspring production (Gillespie 1977). By spawning over a wider seasonal window, an individual reduces the probability of having its offspring experience sub-optimal conditions for growth and survival, e.g. entrainment off the continental shelf by Gulf Stream warm core rings (Myers and Drinkwater 1988). Alternatively, physical factors may effect lengthened spawning by older individuals. Given that females release their eggs in multiple batches and that the interval between batches is approximately constant (Kjesbu 1989), larger females would be expected to spawn over a longer period of time than smaller females simply because of the former's greater fecundity (May 1967) (unless larger females extrude more eggs per batch). A second, non-adaptive explanation is that space limitations within a female's body prevent the hydration of her entire complement of eggs at one time. Thus, larger females would be forced to hydrate their eggs over a longer period of time than smaller females.

The reliability of our data can be assessed by comparing our indirect estimates of spawning duration with estimates measured in the laboratory. Excluding Belle Isle and Funk Island banks, spawning duration for female cod averaged 25 days. Kjesbu (1989) documented spawning intervals of 47, 51 and 60 days for 3 female Norwegian cod reproducing in tanks at 5-8°C. However, given that the cod in this study were approximately 2.5 times as fecund as those reared in the wild (Kjesbu 1989), the expected spawning intervals of cod in the wild, calculated by reducing Kjesbu's (1989) estimates by 2.5, would be 19, 20, and 24 days - estimates similar to ours. K. Waiwood and C. Chambers (Fisheries & Oceans, Biological Station, St. Andrews, NB, Canada E0G 2X0 and Huntsman Marine Science Centre, St. Andrews, NB, Canada E0G 2X0, personal communications) documented a median spawning duration of 30-34 days for 10 northwest Atlantic female cod at 4°C in the laboratory. Egg surveys from 1976-1982 in Lofoten, Norway, (Pedersen 1984; see also Ellertsen et al. 1989) provide additional evidence that 25-35 days is a reasonable estimate of individual spawning duration. The presence of newly-hatched eggs (less than 2 days old) in Lofoten is restricted to a relatively short period of time. Using the data provided by Pedersen (1984), we calculated the standard deviation of the duration of newly-hatched eggs to be only 10.4 days. As this parameter incorporates variability among all spawning individuals, it is unlikely that the spawning duration of any single individual in Lofoten will, on average, be much greater than 30 days. In summary, the similarity of our estimates of spawning duration with those measured in the laboratory and estimated from egg surveys suggest that our data represent reasonable approximations of reproduction in the wild.

Our finding that both younger males and younger females initiate and complete spawning prior to their older counterparts provides indirect empirical evidence of assortative mating in cod. A strong argument for assortative mating can be made from the behavioural data provided by Brawn (1961) in her description of cod spawning in the laboratory. She noted that, after mounting the female dorsally, the male slips down on one side of the female, clasping her with his pelvic fins, and lies "in an inverted position below the female with the ventral surfaces of both fish and their genital apertures closely pressed together" (Brawn 1961:187). Clearly, the probability of egg fertilization will be maximized when the vents of the spawning pair coincide, as would be the case for individuals of the same size.

The delay in spawning of older individuals, relative to younger individuals, may simply be the consequence of a delay in maturation. If the rate of production of gonadal tissue is largely independent of body size, as would be expected (Calder 1984) at the low temperatures (-1° to 3° C) at which Newfoundland/Labrador cod mature, then larger, older fish should take longer to produce their entire volume of ova or sperm than smaller, younger individuals because larger fish produce more eggs and sperm than smaller fish.

Our results provide strong evidence that the duration of spawning increases with age. The relative abundance of older cod in NAFO subareas 2J3KL has decreased dramatically since 1963, suggesting that the duration of spawning has also declined in this population (cf. Fig. 1). Given that increased fishing mortality will generally reduce the proportion of older fish in a population, this may increase variability in recruitment by decreasing the average age of spawning. Such an increase in recruitment variability has been hypothesized to exist at low stock sizes (Daan 1978; Shephard and Cushing 1990). Increased proportional representation of younger individuals in the spawning population should reduce variability both in spawning times and in the temporal presence of larvae in early life. The latter will reduce the probability that larval emergence will coincide with peak abundances of zooplankton. The age-dependence of maturation and spawning demonstrated here provides a mechanism by which size-selective mortality against larger, older individuals can increase variability in recruitment in Atlantic cod.

Acknowledgements

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Table 1. Sample sizes of Atlantic cod in various reproductive stages (see text for
explanation) in research trawls conducted off Newfoundland from 1947 to 1991.

| Region | Females | | | Males | | |
	Maturing	Spawning	Spent	Maturing	Spawning	Spent
Belle Isle	1360	118	14263	1279	335	14133
Funk Island	1328	99	3973	1385	191	2475
3L	2928	1167	5480	3438	1832	6289
3N	1073	209	1574	1149	416	4760
3O	1447	299	1070	1492	557	1237
3Ps	2376	249	764	2926	396	817
4RS	1164	119	2099	4855	338	6877

Table 2. Probit regression coefficients (β_1 in Eqn. 1) of the effects of age on the timing of
reproduction in female and male Atlantic cod (standard errors in parentheses).

| Region | Females | | Males | |
	Spawning	Spent	Spawning	Spent
Belle Isle	-0.135*** (0.013)	-0.129*** (0.013)	-0.144*** (0.015)	-0.201*** (0.040)
Funk Island	-0.120*** (0.019)	-0.113*** (0.017)	-0.133*** (0.017)	-0.203*** (0.022)
3L	0.001 (0.007)	-0.064*** (0.008)	-0.008 (0.010)	-0.070*** (0.012)
3N	-0.108*** (0.009)	-0.155*** (0.017)	-0.054*** (0.009)	-0.149*** (0.011)
3O	-0.101*** (0.011)	-0.223*** (0.028)	-0.065*** (0.009)	-0.200*** (0.017)
3Ps	-0.050*** (0.012)	-0.077*** (0.014)	-0.060*** (0.013)	-0.108*** (0.023)
4RS	-0.033 (0.020)	-0.053* (0.021)	-0.054 (0.039)	-0.075** (0.027)

* $.01 < p \leq .05$
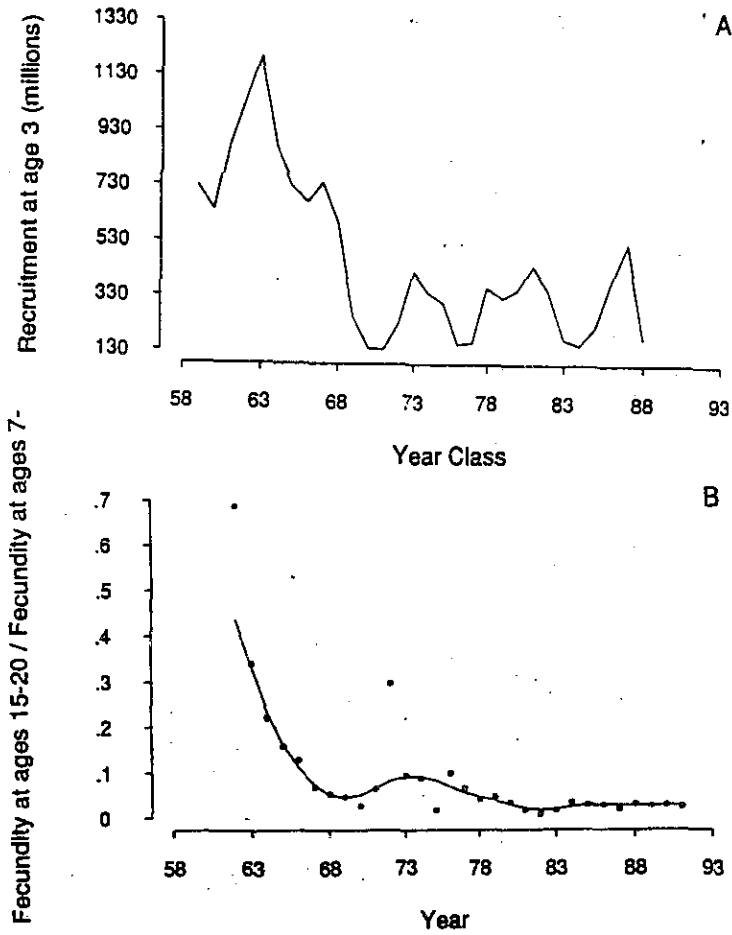
** $.001 < p \leq .01$

*** $p \leq .001$

Figure 1. A. Recruitment at age 3 for cod in NAFO subareas 2J3KL, as calculated by virtual population analysis. B. The ratio of eggs produced by older cod (ages 15-20) to that produced by younger cod (ages 7-9). The fecundity at age data were calculated from May (1967) and the numbers at age were estimated from catch at age data (Baird et al. 1992). The observations were smoothed by an algorithm that uses running medians (cf. Tukey 1977).
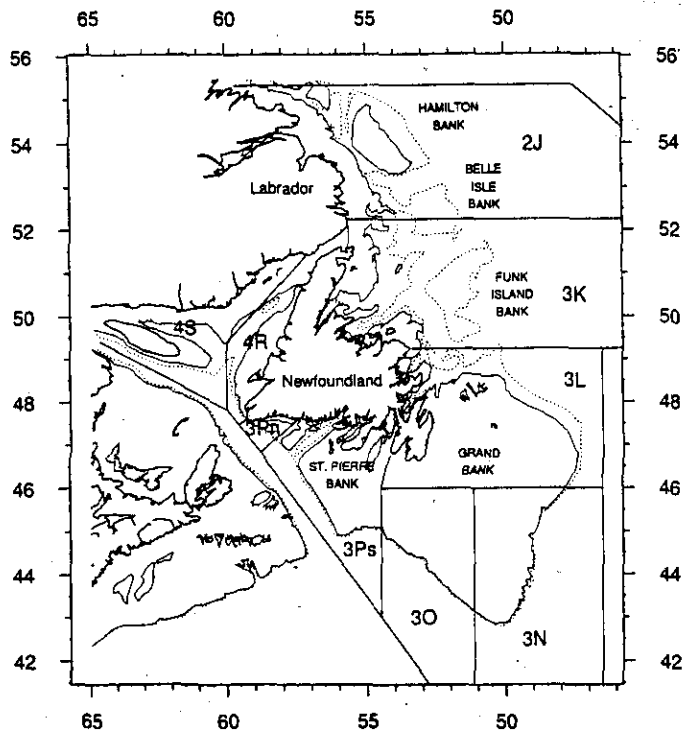

Figure 2. Map of the study region, including NAFO divisions. Depth contours are 200 m (solid lines) and 300 m (dashed lines).
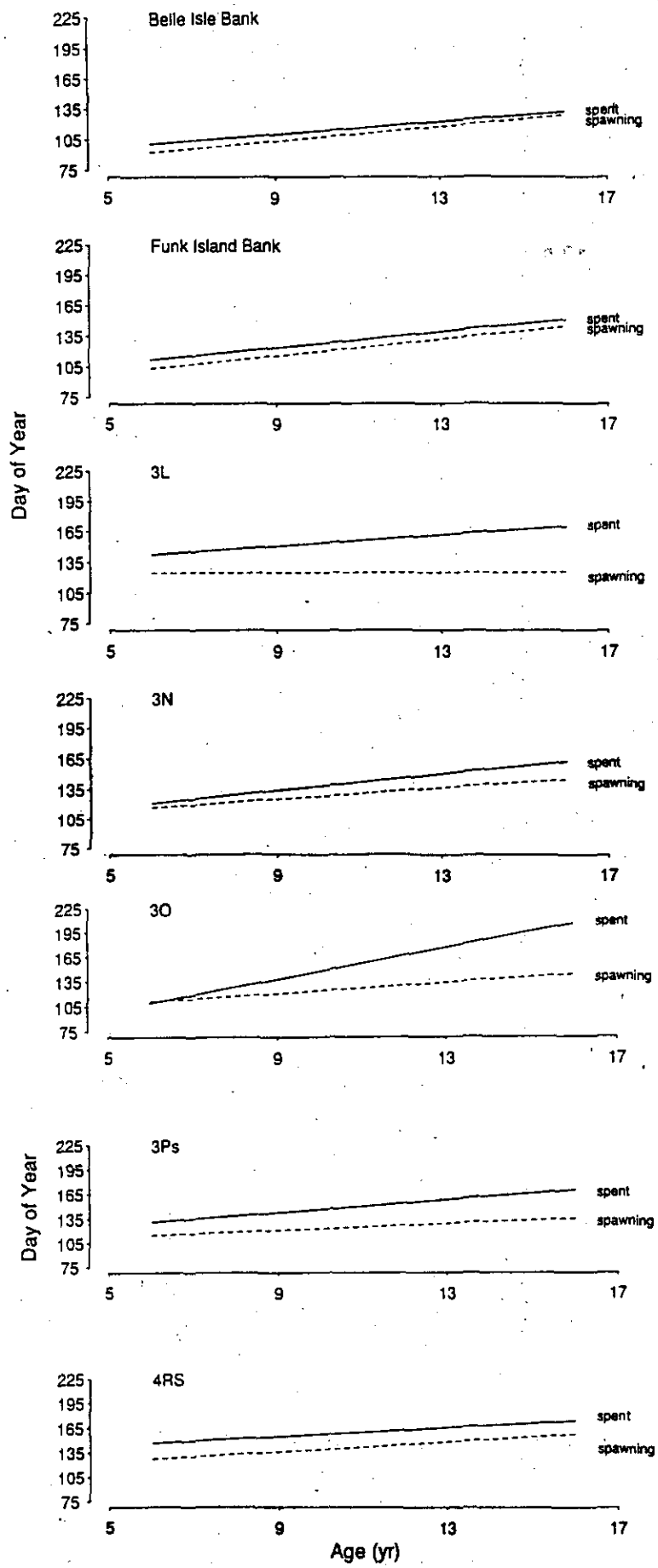
FEMALES

Figure 3. The estimated relationship between age and the day of year at which 50% of female cod enter into spawning and spent maturation states. See text for details.
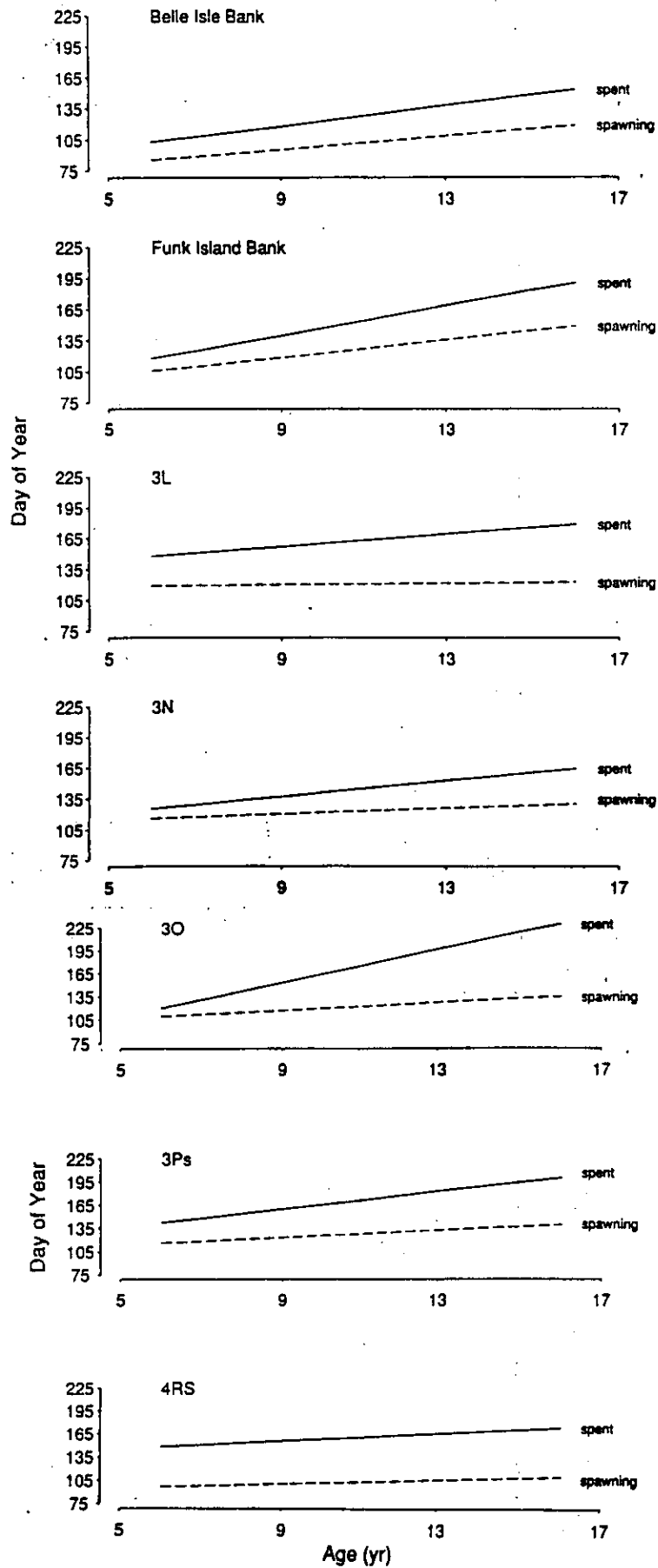
MALES

Figure 4. The estimated relationship between age and the mean day of year at which 50% of male cod enter into spawning and spent maturation states. See text for details.