Age-specific paternal influences on reproductive success of Atlantic cod (Gadus morhua L.) of the Grand Banks, Newfoundland

Edward A. Trippel and M. Joanne Morgan

Declining numbers of old fish and some possible effects that this may have on a stock's spawning period and on the production of viable progeny were examined for Atlantic cod (Gadus morhua L.) of the Grand Banks, Newfoundland. Investigations utilized 18 years of spring research-vessel survey data spanning April to June and sampling of offshore spawning assemblages in the years 1991-1993. Analyses concentrated on paternal attributes and demonstrated that young mature males (ages 5-6 years) usually completed their spawning season before older males. Spermatocrit was highly variable (0.13-0.96) within and across twelve age groups and was not correlated with age or gonadosomatic index. The paternal influence on hatching success varied by up to 2.25-fold. However, with respect to all paternal parameters examined, i.e., age, body length, gonadosomatic index, and spermatocrit, there occurred no significant correlate with hatching success. In light of the abrupt decline of age 7+ fish in 1991 on the Grand Banks, and the faster depletion of the testes in young, relative to old fish, this stock may experience a shortening of the spawning season in future years relative to the historical average. Findings also indicate that spermatogenesis proceeded under the cold-water conditions of 1990-1992.

Introduction

Assessment of spawning-stock biomass in relation to recruitment potential and stock rebuilding is currently an important issue for fisheries managers of Canadian Northwest Atlantic groundfish stocks. Elsewhere, the identification and recommendation of spawning-stock biomass levels to safeguard against stock collapse have made the assumption that gamete quality is not a function of the reproductive experience of the individual, be they virgin, repeat spawner, or potentially senescent (Goodyear and Christensen, 1984; Gabriel et al., 1989; Serebryakov, 1990; Mace and Sissenwine, 1993, and others). If gamete quality and related fertilization and hatching success change with reproductive experience, then the stock component of a stock-recruitment relationship should also be adjusted for gamete quality in relation to the relative abundance of different mature age groups in the population. The abrupt decline in 1991 of age 7+ Atlantic cod (Gadus morhua L.) of the Grand Banks, Newfoundland, to a level of about 10% of the long-term average (Baird et al., 1992) and the concurrent decline in age and size at sexual maturity (Morgan et al., 1993) suggest that evaluation of gamete quality in relation to parent reproductive history may be an important prerequisite to the development of a sound management strategy designed to enhance stock recovery. Improving our understanding of the male's role in progeny production in this commercially exploited species is critical to this process.

The reproductive biology of cod in relation to age and body size has been studied much more for females (Sorokin, 1957; Shapiro, 1988. Kjesbu, 1989; Kjesbu et al., 1991) than for males. Those aspects of male cod reproduction that have been reported on, e.g., testes weight, gonadosomatic index, and sperm motility (Sor-
Reproductive success of Atlantic cod on the Grand Banks, Newfoundland

Okin, 1960; Krivobok and Tokareva, 1972; Westin and Nissling, 1991), were measured for cod occurring in the Northeast Atlantic, the Baltic, and the Barents Sea. Only recently have some of these characteristics been evaluated for Northwest Atlantic cod, and these analyses have been restricted to captive cod of Scotian Shelf origin (Trippel and Neilson, 1992). Furthermore, compared to other fishes (Trippel and Harvey, 1990; Ridgway et al., 1991), very little is known about the relative importance of different age groups of male cod with respect to overall female spawning success.

The purpose of this study was to document the influence of age on several reproductive attributes of male cod collected from Grand Banks, Newfoundland, and to discuss the implications of these results with respect to future recruitment in this currently depressed stock. Specifically, we examined (i) temporal synchrony in testes depletion as a function of age, (ii) spermatocrit in relation to age and gonadosomatic index, and (iii) sperm potency and associated hatching success in relation to age and body size.

Methods

Cod were collected from spawning aggregations on 28–30 May 1991, 27–30 May 1992, and 5–6 June 1993 from NAFO Subdivision 3L of the Grand Banks. In 1991, collections focused on the Virgin rocks area (46°00’N 50°00’W), whereas in 1992 and 1993 cod were collected closer to the edge of the continental shelf (48°50’N 50°00’W) (Fig. 1). Cod were captured by otter trawl in 15–30 min tows at bottom depths ranging from 75 to 85 m in 1991 and from 340 to 380 m in 1992 and 1993. Bottom temperatures ranged from −0.6 to 0.9°C in 1991, from 2.2 to 2.7°C in 1992, and from 3.0 to 3.4°C in 1993.

Fork length, body weight (W), gonadal stage of development (Templeman et al., 1978; Morrison, 1990), testes weight (T), and gonadosomatic index (GSI = (T/W) × 100)) were determined for 168 males in 1991 and 157 males in 1992. Otoliths were extracted from these fish and ages assessed. Spermatocrit is a measure of the proportion of semen occupied by sperm cells and has implications for fertilization success in the wild (Bouck and Jacobson, 1976). Spermatocrit was estimated by spinning two samples of semen from each male in non-heparinized tubes in a centrifuge for 10 min at 7500 rpm and measuring the proportion of semen occupied by packed sperm cells in each sample. Mean values were used to represent spermatocrit of a male; the two samples from the same individual were commonly within 2–3% of each other. We evaluated the temporal synchrony of gonadal depletion across age classes using two methods. First, the gonadosomatic indices of different age classes were compared. Presumably, those fish closer to the completion of spawning would have lower values than fish just starting spawning. Employment of GSI for this purpose seemed justified as the GSI of spent males has been reported to be unrelated to body size (i.e., <2%) in the Pacific cod (Gadus macrocephalus).

Figure 1. Study area showing the collection sites and location of Station 27.
(Templeman, 1985). Second, the percentage occurrence of unspent mature males of each age class from spring groundfish research vessel survey data spanning April to June, 1973–1992, was calculated. The main spawning period of cod in Division 3L generally ranges from 1 May to 1 July (Myers et al., 1993). From the April to June samples, the description of the maturity stages comprising unspent males are those pertaining to be maturing to spawn in the year of capture (ripening or ripe) as well as those having some milt extruded, though with residual milt remaining in the testes and vas deferentia (partially spent). Spent males were characterized as having completed spawning in the year of capture, with recovery not sufficiently advanced for the outer edges of testes to be pinkish or greyish in colour (Templeman et al., 1978).

On 26 May 1992 and on 5–6 June 1993, sperm and eggs were stripped from several cod to examine fertilization and hatching success of eggs sired by different sizes and ages of males in a manner similar to that reported in Trippel and Neilson (1992). In 1992, ten males 40–67 cm in length were used in crosses with eggs of a six-year-old, 51 cm and 1185 g female. In 1993, six males 45–66 cm were crossed with a seven-year-old, 48 cm, 1030 g female and four males 51–65 cm were crossed with a six-year-old, 48 cm and 845 g female (crosses in 1993 were conducted in triplicate, whereas in 1992 no replicates were performed). For each cross, 100–200 eggs were placed in a beaker containing a 1:100 semen:seawater suspension of 250 ml; each sperm mixture was prepared immediately before the addition of eggs. Eggs and sperm were left in the beaker for 1 min, during which time they were stirred six times and then poured onto a 300 μm mesh screen to remove excess sperm. Eggs were returned to the beaker and 250 ml of sea water was added. Crosses were conducted in beakers kept on crushed ice. They were incubated at 2°C for 8–12 h, which ensured that any zygotes formed could be identified by the presence of 2–4 blastomeres. A light microscope (magnification ×40) was used to estimate percentage fertilization of each cross. Because of conditions at sea, accurate estimates of fertilization success were not obtained in 1993, though a qualitative examination revealed high fertilization rates and good egg quality (Kjørsvik et al., 1990). After assessment of fertilization, eggs were returned, maintained at 2°C and water was exchanged daily. Three days after initiation of the crosses, eggs were transferred from the research vessel “Alfred Needler” to the Northwest Atlantic Fisheries Centre, where they were maintained at 4°C. Hatching occurred from 13 to 14 June 1992 and from 21 to 25 June 1993 (17–18 and 15–20 d post-fertilization, respectively). Hatching success was evaluated by recording the number of larvae in each incubator two days after the completion of hatching. Pearson product-moment correlation coefficients were computed among the various reproductive attributes. Student’s t-test and Duncan’s multiple range test were used to examine for statistically significant differences in fertilization rate and hatching rate among males (SPSS, 1990).

Results
Although high variability was evident within age classes, young males more frequently exhibited gonadal conditions indicative of ending their spawning season sooner than old males. This was noticeable from the gonadosomatic index values in 1991 and 1992 (Fig. 2A) and from the spring research vessel survey data (Table 1; Fig. 3). Specifically, the mean GSIs of mature cod increased with age from 6% for age 4 to 13% for age 12 fish in 1991. Mean GSIs through ages 5–10 increased from 5 to 11% in 1992 (calculated from individual values in Fig. 2A). GSI was positively correlated with both age \( r = 0.48, p < 0.01 \) in 1991; \( r = 0.58, p < 0.01 \) in 1992 and fork length \( r = 0.40, p < 0.01 \) in 1991; \( r = 0.52, p < 0.01 \) in 1992). Analysis of spring research survey data spanning 1973–1992 indicated that the incidence of mature males still retaining sperm (i.e., unspent) was highest among age 9+ fish, whereas there were higher occurrences of spent gonads among young cod (ages 5–8) (Fig. 3). Interestingly, in 9 of the 14 years of sampling since 1976 the very young males (age 4) exhibited a higher incidence of the unspent condition as opposed to those that were slightly older (ages 5–8). Moreover, in 9 years all age 4 males captured had not initiated spawning (i.e., gonad ripe).

Table 1. Spring groundfish research vessel surveys for Division 3L indicating the number of captured mature male cod that were aged.

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of mature males in age sample</th>
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<tbody>
<tr>
<td>1973</td>
<td>138</td>
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<tr>
<td>1974</td>
<td>38</td>
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<tr>
<td>1989</td>
<td>371</td>
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<tr>
<td>1990</td>
<td>230</td>
</tr>
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Spermatocrits were highly variable within and across age groups in both 1991 and 1992, ranging from 0.13 to 0.96 (Fig. 2B). Age and spermatocrit were not significantly correlated \( r = 0.02, p > 0.05 \) in 1991; \( r = 0.06, p > 0.05 \) in 1992. In both years, mean spermatocrits ranged from 0.35 to 0.50 for ages 4–16 (Fig. 2B). Spermatocrit and GSI were not correlated \( r = 0.04, p > 0.05 \) in 1991; \( r = 0.06, p > 0.05 \) in 1992; Fig. 2C), although spermatocrit was high (>0.85) for several males having nearly depleted testes (GSI < 3%).

Fertilization rates in 1992 for small cod (40–50 cm, 520–940 g, age 5–6) and medium-size cod (61–67 cm, 1910–2435 g, age 7–10) were on average 80% (range 70–86%) and 87% (range 85–93%), respectively (differ-
Figure 3. Percentage occurrence of ripe and partly spent mature male Atlantic cod (i.e., unspent males) of the Grand Banks in relation to age from data collected during research vessel spring groundfish surveys of April to June, 1973–1992. Refer to Table 1 for dates and sample size of each survey.
Reproductive success of Atlantic cod on the Grank Banks, Newfoundland

Mean hatching rates spanned 2 to 18% for the other males used in 1993 and were not significantly different from one another (Duncan's multiple range test, p > 0.05, represented by open triangles in Fig. 4). The paternal parameters examined in 1993, as in 1992, did not correlate with hatching success (r < 0.10, p > 0.05; Fig. 4).

Discussion
The influence of parent age on spawning times may have important implications for recruitment. Cod spawning activity in Division 3L of the Grand Bank occurs predominantly from 1 May to 1 July with peak activity occurring from mid-May to early June (Myers et al.,...
In light of these spawning times, results from the present study indicate that a greater degree of spawning by young males occurs in early May, whereas older fish continue to spawn into June. The differential success of gametes spawned at different times of the spawning period is of significance to understanding annual variations in recruitment (e.g. the match–mismatch hypothesis; Sinclair and Tremblay, 1984; Lambert and Ware, 1984), especially in consideration of the recent reduction in numbers of old fish from this stock. That is, in the near future, a higher concentration of spawning and the stock's overall zygote production may occur by young fish during the early part of this stock's historical spawning period (all other factors such as environmental influences being equal). The change of a parent stock from one consisting of many to one consisting of few age classes may negatively affect recruitment. Presumably, an extensive multi-age spawning stock would spread its egg production over a longer time period than a spawning stock comprised of few young age classes, hence improving the chances that at least some portion of the stock's egg production is matched with environmental and feeding conditions favourable to larval survival. This situation may be widespread over the Grand Banks, as our evaluation of asynchronous spawning with respect to age has been confirmed for cod in other regions of the Northwest Atlantic (Hutchings and Myers, 1993).

A large proportion of the age 4 mature males had failed to commence spawning by the time of the spring surveys of April–early June. These findings have implications for the estimation of spawning-stock biomass in that the inclusion of these young fish may lead to overestimated values of spawning potential. In white sucker (Catostomus commersoni), 60% of young, small precocious males failed to spawn and underwent gonadal atresia in a small Ontario lake (Trippel, 1984), whereas in another lake, gonadal atresia was widespread among all ages of females and was associated with a low abundance of males (Trippel and Harvey, 1990). Sampling Grand Banks cod during July and August would be required to substantiate whether these age 4 males failed to spawn (and underwent gonadal atresia) or whether they started their spawning season much later than older cod. These younger males may comprise a greater portion of the spawning stock than in earlier years, as the age at 50% maturity of males in Division 3L from 1981 to 1992 has declined significantly from 5.2 to 4.3 years over this period (Morgan et al., 1993).

Grand Banks cod declined abruptly in abundance during 1991 (Baird et al., 1992; Parsons, 1993) and their principal prey, capelin (Mallotus villosus), declined from 7 million tonnes in 1990 to 0.1 million tonnes in 1991 and was 0.2 million tonnes in 1992 (Miller, 1992). In our trawl samples, the relative abundance of age 7 and older male cod declined from 53 to 16% between 1991 and 1992. At Station 27 (Fig. 1), water temperatures have been below normal throughout the water column since 1983 (Drinkwater, 1993) and were especially cold during the period of gametogenesis prior to the 1991

![Station 27](image)

Figure 5. Water temperature of the lower and upper layers at Station 27 from April 1990 to May 1992.
spawning season (Fig. 5). The findings of this study indicate that spermatogenesis did proceed and was not seriously impeded under these cold water conditions.

High variability in spermatocrit across all ages was observed. We found no connection between the relative amount of sperm remaining in the testes and spermatocrit; except in some instances when the testes comprised <3% of total body weight and the semen was thick (spermatocrit >0.85). The range of spermatocrit in Atlantic cod is similar to that of the related freshwater burbot (Lota lota) (mean = 0.67, range 0.36-0.91) and was higher than values reported for salmonids and coregonids (means 0.18-0.34) (Piironen and Hyvarinen, 1983).

Spermatocrit as a measure of sperm density has implications for fertilization success, as a higher density of sperm would theoretically result in higher sperm:egg micropyle encounter rates. A review of the literature on spermatocrit in teleost fishes has shown spermatocrit, or its close correlate, sperm density, not to be correlated with fertilization success in concentrated sperm mixtures in two of three studies; however, in diluted suspensions, sperm density correlated positively with fertilization success in all instances (Trippel and Neilson, 1992). In captive cod of Scotian Shelf origin, spermatocrit (range = 0.18-0.99) failed to correlate significantly with egg fertilization success (r < 0.30) (Trippel and Neilson, 1992). In the present study, the spermatocrit of individual cod, ranging from 0.26 to 0.51, also failed to correlate with fertilization rates ranging from 70 to 93% in a semen dilution of 1:100. Experiments involving more diluted suspensions of semen would be useful to further evaluate sperm potency of wild fish.

In summary, empirical evidence agrees with previous work done on captive cod and does not support the hypothesis that spermatocrit and sperm potency vary as a function of male age and that weighting of different age groups on these aspects is unnecessary to fine-tune estimates of spawning-stock biomass. Apparently, a pertinent finding from the study is the faster depletion of testes in young, relative to old fish, which may have serious implications for spawning times and future recruitment success in this age-truncated stock. We have also shown that the paternal influence on hatching success can be quite high, which to our knowledge has not been previously documented in wild Atlantic cod.

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References


