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Variation in the frequency of skipped spawning in Atlantic cod (*Gadus morhua*) off Newfoundland and Labrador

R. M. Rideout, M. J. Morgan, and G. R. Lilly

Macroscopic maturity data collected between January and March of 1978−2004 during groundfish surveys were analysed to determine the frequency of skipped spawning for Atlantic cod (*Gadus morhua*) populations in the Northwest Atlantic. Nearly 18% of the 6583 potential female spawners sampled during this period would not have spawned in the subsequent spawning season. The frequency of skipped spawning was much higher on the Flemish Cap (NAFO Division 3M, ∼33%) and off the south coast of Newfoundland (Subdivision 3Ps, ∼21%) than that in three areas off eastern Newfoundland and southern Labrador (Divisions 3L, ∼8%; 3K, ∼3%; and 2J, <1%). Annual variation in the frequency of skipped spawning was apparent in all areas. Skipped spawning was most common in fish of medium size (60−79 cm). Non-reproductive cod were characterized by lower liver condition than reproductive cod, but not a lower gutted condition. Generalized linear models suggested that relative liver weight was the best predictor of spawning probability, and that age, length, and relative body condition were not good predictors. Models of spawning probability based on relative liver condition suggest that female fish in poor condition in 3KL are more likely to spawn than fish of equal condition in areas 3M and 3Ps.

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Introduction

A growing body of evidence suggests that adverse environmental conditions can result in fish suppressing gamete development and subsequently failing to spawn. This interruption of the normal ripening cycle can occur in both recruit- and repeat-spawners. In the latter case, failure to spawn results in non-annual or skipped spawning (reviewed by Rideout *et al.*, 2005). Skipped spawning can take place through failure to start vitellogenesis or by starting vitellogenesis and subsequently undergoing mass atresia of all vitellogenic oocytes. It is usually linked to poor nutritional condition attributable to reduced prey availability (Rideout *et al.*, 2005). For example, skipped spawning in northern Canadian lakes has been attributed to the short growing season, which may not allow fish to accumulate sufficient energy to support egg production in consecutive years (Kennedy, 1953; Dutil, 1986). Likewise, for orange roughy (*Hoplostethus atlanticus*) off Australia, skipped spawning may result from the scarce or patchy prey

available in this species' deepwater habitat (Bell *et al.*, 1992). Experimental work on captive fish has demonstrated that skipped spawning can be induced through nutritional deprivation (Hislop *et al.*, 1978; Burton and Idler, 1987; Rijnsdorp, 1990; Maddock and Burton, 1994). Skipped spawning may also be related to low availability of specific types of prey. For example, Rideout and Rose (in press) demonstrated that cod (*Gadus morhua*) of medium size that failed to ripen successfully had significantly higher $\delta^{13}C$ values than fish that would have spawned, suggesting that they fed more extensively on benthic organisms (presumably pandalid shrimp) than pelagic organisms (presumably capelin, *Mallotus villosus*). For Flemish Cap cod, skipping a spawning season was linked to low liver condition (Morgan and Lilly, in press), perhaps as a result of fluctuations in the availability of juvenile redfish as prey (Lilly, 1985; Walsh *et al.*, 1986).

From a life-history standpoint, skipped spawning may be an adaptive trait. Jørgensen *et al.* (2006), based on an energy-allocation life-history model, suggested that spawning

should be skipped if the expected future gain in reproductive output, discounted by survival, is greater than the expected reproductive success in the current year. Small, short-lived fish are likely to have fewer opportunities to reproduce than longer-living species, and are therefore more likely to invest maximum energy in each reproductive episode even at the risk of increasing post-spawning mortality (i.e. less likely to skip an opportunity to reproduce; Rideout *et al.*, 2005). In longer-living species, however, suppressing gamete development in a year of poor condition can increase the probability of surviving to spawn in subsequent years. In Atlantic cod, skipping spawning when the probability of post-spawning survival is low, such as when fish are in poor condition (Lambert and Dutil, 2000), may increase an individual's lifetime reproductive output by >40% (Rideout *et al.*, 2005).

For cod, skipped spawning appears to be widespread, with reports of non-reproductive fish from the Northwest Atlantic (Walsh *et al.*, 1986; Burton *et al.*, 1997; Schwalme and Chouinard, 1999; Rideout *et al.*, 2000; Morgan and Lilly, in press; Rideout and Rose, in press), the Baltic Sea (Shirokova, 1969), and the Barents Sea (Woodhead and Woodhead, 1965; Oganesyan, 1993; Marshall *et al.*, 1998). Although such reports suggest that reproductive development may be interrupted over the entire geographic range of cod, data are usually insufficient to determine

the frequency of skipped spawning in any given area or year. The frequency of skipped spawning has been reported to be very high (sometimes in excess of 40%) for both Flemish Cap (Walsh *et al.*, 1986) and Smith Sound cod (Rideout and Rose, in press). However, cod aggregations in both these areas are somewhat different from those in other parts of the Northwest Atlantic. Cod on the Flemish Cap, an isolated bank to the east of Grand Bank (Figure 1), do not migrate off the Cap and are genetically distinct from other cod stocks (Beacham *et al.*, 2000). Cod in Smith Sound, a small fjord-like inlet on the east coast of Newfoundland (NAFO Division 3L), may not be genetically distinct from fish in nearby areas (Beacham *et al.*, 2000), but they behave differently from most cod in the 2J + 3KL area in that they reside inshore throughout winter instead of undertaking the offshore migration to warmer water historically characteristic of offshore populations (Goddard and Fletcher, 1994; Rose, 2003). The high frequency of skipped spawning observed in these areas may not be typical of cod throughout the Newfoundland and Labrador area.

Determining the frequency of skipped spawning is important in understanding the true reproductive potential of a fish population. For example, Rideout and Rose (in press) reported that failure to account for non-reproductive
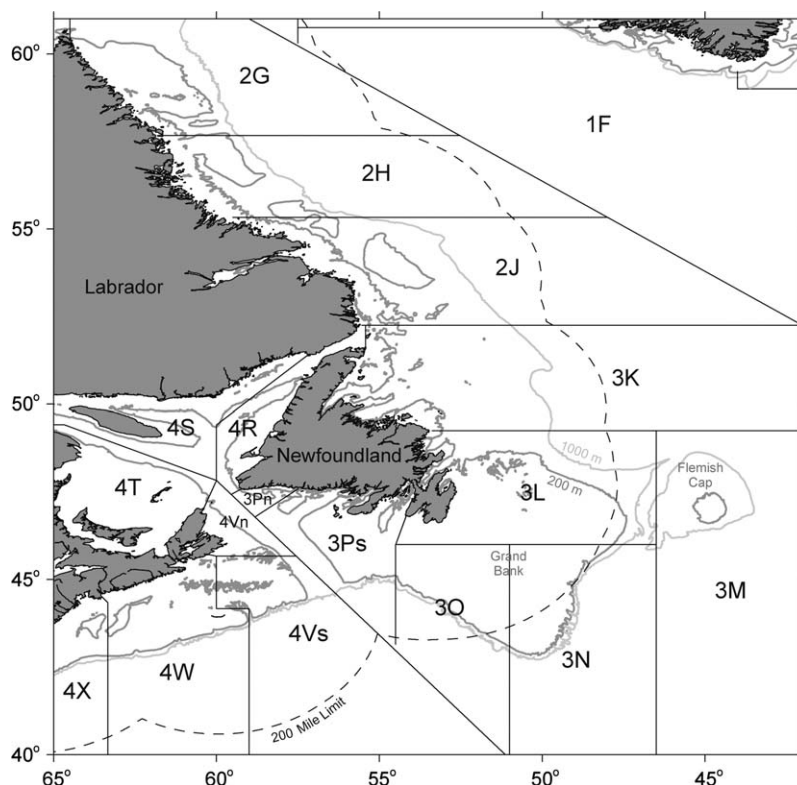
Figure 1. Map of the Northwest Atlantic showing NAFO Divisions and the Canadian 200-nautical-mile boundary.

individuals could result in overestimation of population egg production by 8–41% annually in the Smith Sound cod aggregation. Limit reference points under the precautionary approach are often chosen as the spawning-stock biomass below which recruitment is seriously impaired (Mace and Sissenwine, 1993; Shelton and Rivard, 2003). Additionally, predictions about the potential for depleted stocks to rebuild will depend on the underlying assumptions about the stock-recruit relationship. Therefore, reliable estimates of reproductive potential, including the frequency of spawning omission, will play an important role in effective management.

In the current study, we use research vessel survey data to assess the frequency of skipped spawning in NAFO Divisions 2J, 3K, 3L, and 3M, and in Subdivision 3Ps, in an attempt to gauge the significance of skipped spawning to the overall productivity of cod stocks.

Methods

Data collected during bottom trawl and acoustic surveys, as well as tagging studies (Table 1), were used to determine the frequency of skipped spawning in NAFO Divisions 2J, 3K, 3L, and 3M, and in Subdivision 3Ps. All fish were collected offshore. Only data for females were considered. Maturity stages were assigned according to the classification of Templeman *et al.* (1978) following macroscopic inspection of the ovaries. Females with small, pink ovaries were classified as immature, and those with opaque oocytes as ripening. Only data from January to March were included in the analyses. Females with small, firm, red ovaries with no opaque oocytes at that time of year were considered non-reproductive (i.e. skipped spawners; corresponding to the "spent L" maturity stage of Templeman *et al.*, 1978). Previous studies on Northwest Atlantic cod

Table 1. Summary of cod sampling (SR = stratified random; fish sampled = all females collected).

NAFO Division	Year	Month	Survey type	Fish sampled (*n*)	NAFO Division	Year	Month	Survey type	Fish sampled (*n*)
2J	1978	2	SR	118	3L	1989	2	Acoustic	218
2J	1981	3	Tagging	39	3L	1991	2	Acoustic	81
2J	1982	3	Tagging	57	3L	1992	3	Acoustic	36
2J	1986	2	SR	172	3M	1978	1	SR	315
2J	1987	2	Acoustic	75	3M	1978	2	SR	688
2J	1988	2	Acoustic	103	3M	1979	1	SR	95
2J	1990	2	Acoustic	91	3M	1979	2	SR	426
2J	1991	2	Acoustic	86	3M	1979	3	Special	100
2J	2003	1	SR	94	3M	1980	1	SR	374
3K	1978	3	SR	121	3M	1981	1	SR	372
3K	1979	3	Tagging	151	3M	1982	1	SR	63
3K	1980	3	Tagging	136	3M	1982	2	SR	168
3K	1981	3	Tagging	39	3M	1983	2	SR	1 889
3K	1982	3	Tagging	44	3M	1983	3	Special	64
3K	1983	3	Tagging	206	3M	1984	2	SR	1 705
3K	1986	2	SR	244	3M	1985	2	SR	2 068
3K	1987	2	Acoustic	348	3P	1978	2	SR	58
3K	1988	2	Acoustic	413	3P	1979	2	SR	271
3K	1989	2	Acoustic	214	3P	1979	3	SR	41
3K	1990	2	Acoustic	322	3P	1980	3	SR	332
3K	1991	2	Acoustic	228	3P	1981	3	SR	328
3K	1992	2	Acoustic	68	3P	1985	3	SR	376
3K	2003	1	SR	203	3P	1986	3	SR	472
3K	2004	1	SR	271	3P	1987	2	SR	295
3L	1980	3	Tagging	230	3P	1987	3	SR	29
3L	1982	3	Tagging	78	3P	1987	3	SR	224
3L	1983	3	Tagging	97	3P	1988	1	SR	129
3L	1984	1	SR	69	3P	1988	2	SR	363
3L	1984	2	SR	98	3P	1989	2	SR	432
3L	1985	1	SR	421	3P	1990	2	SR	319
3L	1985	2	SR	63	3P	1991	2	SR	417
3L	1986	1	SR	115	3P	1992	2	SR	289
3L	1986	2	SR	181	3P	1993	2	SR	205
Total									18 437

have demonstrated the majority of such ovaries to be undergoing mass atresia of all vitellogenic oocytes (Walsh *et al.*, 1986; Rideout *et al.*, 2000), which would have rendered the fish incapable of spawning in the upcoming spawning season. In this case, the phrase non-reproductive is used to indicate a potential spawner that fails to complete vitellogenesis and is therefore not capable of spawning. The phrase post-mature non-reproductive has been used previously to include only non-spawning fish that have spawned successfully in the past (Burton and Idler, 1984). Without the use of histology, it was not possible to distinguish between fish that had spawned in the past and those that had not (Rideout *et al.*, 2005). The frequency of skipped spawning per area or year was calculated as the number of non-reproductive females divided by the total number of mature females sampled. Fish were grouped into 10-cm size classes in order to compare the frequency of skipped spawning among cod of different size.

Condition indices were compared between reproductive and non-reproductive females to test the hypothesis that skipped spawning was caused by insufficient energy reserves to fuel gamete development. For this purpose, only fish that were ripening but showed no signs of having started to spawn were included as reproductive, whereas those that had started or finished spawning were not included in the analyses. None of the non-reproductive females collected from 2J had been sampled for body weight data, so 2J was excluded from the analyses of condition. Only a limited number of non-reproductive cod from 3K and 3L had been sampled for weight, so the areas were pooled as 3KL. Fulton's K was calculated as $K = W(100/L^3)$, where W is gutted weight in g and L is fork length in cm. Hepatosomatic index was calculated as $HSI = (\text{liver weight}/W)100\%$. To alleviate possible correlations between condition indices and fish length, comparisons between reproductive and non-reproductive individuals were made by grouping fish into 10-cm size classes. Condition indices were then compared for each size class using single-factor analysis of variance. In addition, alternative length-independent indices of condition were calculated. Relative K (K_r) and relative liver condition (LK_r) were calculated from:

$$K_r = W/\widehat{W}$$

$$LK_r = LW/\widehat{LW},$$

where W is the gutted body weight, LW is the liver weight, and $\widehat{W}$ and $\widehat{LW}$ are the predicted body weight and liver weight, respectively, from the following length/weight relationships:

$$\log W = \text{intercept} + \log(L) + (\log(L))^2$$

$$\log LW = \text{intercept} + \log(L) + (\log(L))^2.$$

Using quadratic rather than linear relationships resulted in relative condition indices that were not correlated with length ($p = 0.9526$ for K_r; $p = 0.3536$ for LK_r) whereas those produced using linear relationships were correlated with length ($p = 0.0005$ for K_r; $p = 0.0003$ for LK_r). For comparisons among areas, K_r and LK_r were based relative to predicted values from the relationships between length and gutted weight and length and liver weight, for all data combined. However, when examining these condition indices within a single area, they were looked at relative to predicted values based on fish only from that area.

Generalized linear models were used to determine if age, length, K_r, or LK_r significantly influenced the probability of spawning. Ripening females were considered spawners (1), and non-reproductive females were considered non-spawners (0). Age and length were modelled as class variables, and K_r and LK_r were modelled as continuous variables. Because of limited sample size in some size classes, each factor was tested separately instead of trying to build an overall model containing several factors. All models had a logit link function and a binomial error structure. Analyses were restricted to fish between 40 and 90 cm because few fish smaller or larger than this range were available.

Pseudo r^2 values (Swartzman *et al.*, 1992) were calculated in order to compare the proportion of the deviation accounted for by age, length, K_r, and LK_r. This pseudo coefficient of determination was calculated as the deviance in the model containing only the intercept minus the deviance after adding the main factor (e.g. LK_r), divided by the null deviance of the model containing only the intercept.

Results

A total of 18 437 female fish were sampled between 1978 and 2004 (Table 1). Of these, 6583 were considered potential spawners, and nearly 18% of the potential spawners were non-reproductive. There was a high degree of spatial and temporal variability in the frequency of non-reproductive fish (Table 2), with a very low frequency in NAFO Divisions 2J and 3K (<4%), slightly higher in 3L (~8%), and very high in 3M (~33%) and 3Ps (21%). Within 3M the proportion ranged from >15% in 1982 to nearly 51% in 1978, and in 3Ps it ranged from 11% in 1987 to nearly 46% in 1978. In 2J, non-reproductive fish were observed in only 1 of the 9 years sampled, although sample sizes were generally small. In 3K, 5 of the 15 years that fish were sampled revealed no evidence of skipped spawning, and in the remaining years the proportion of non-reproductive fish ranged from <1% to nearly 19%. In 3L, there were 4 years with no non-reproductive fish, whereas the remaining 5 years had between 5% and 21% non-reproductive females. Although the data were temporally variable, there were no temporal trends in the proportion of non-reproductive individuals (Table 2).

Overall, the proportion of non-reproductive fish was greatest between 60 and 79 cm (Table 3). In 3L and 3Ps, the greatest proportion of non-reproductive fish was in the

Table 2. Proportion of non-reproductive female cod per year and NAFO Division off Newfoundland and Labrador. Sample sizes are given in parenthesis.

Year	2J	3K	3L	3M	3Ps
1978	2.94 (34)	0 (8)	—	50.97 (414)	45.83 (24)
1979	—	18.92 (37)	—	38.17 (262)	21.93 (114)
1980	—	1.61 (62)	0 (106)	21.95 (205)	28.85 (104)
1981	0 (30)	0 (15)	—	23.61 (233)	15.56 (135)
1982	0 (57)	0 (41)	0 (69)	15.15 (99)	—
1983	—	0 (172)	0 (73)	26.47 (306)	—
1984	—	—	12.5 (32)	30.00 (150)	—
1985	—	—	10.87 (230)	40.13 (157)	23.35 (197)
1986	0 (59)	0 (120)	7.21 (97)	—	30.26 (228)
1987	0 (59)	1.98 (252)	—	—	11.21 (232)
1988	0 (11)	6.38 (251)	—	—	18.85 (244)
1989	—	6.29 (143)	20.83 (120)	—	22.07 (222)
1990	0 (10)	3.33 (210)	—	—	21.28 (141)
1991	0 (16)	0.87 (115)	5.41 (37)	—	19.43 (211)
1992	—	3.57 (28)	0 (13)	—	15.24 (164)
1993	—	—	—	—	26.23 (122)
2003	0 (29)	7.50 (40)	—	—	—
2004	—	6.98 (43)	—	—	—
All years	0.33 (305)	3.45 (1 537)	8.11 (777)	33.68 (1 826)	21.09 (2 138)

60−89 cm range, whereas in 3M the greatest proportion was in the 50−79 cm size range.

Differences in Fulton's condition factor between reproductive and non-reproductive females were generally small, whereas the hepatosomatic index was significantly ($p < 0.05$) smaller in non-reproductive individuals than in individuals that were ripening, in nearly all size classes (Figure 2). Differences in liver size between reproductive and non-reproductive females were also evident when measured as relative liver condition (Figure 3).

Results of the generalized linear models confirmed that relative liver condition had the largest influence on the probability of spawning in Newfoundland and Labrador cod (Table 4). Overall, the model containing LK_r explained >17% of the variability in the probability of spawning; all

other factors explained <2.2% of the variability. When analysed by area, the model containing liver condition explained 14%, 18%, and 12% of the variability in the probability of spawning in areas 3KL, 3M, and 3Ps, respectively. Although some other factors had statistically significant influences on the probability of spawning, the amount of variation explained by those factors was very low. For example, in 3Ps, the effect of K_r was significant ($p = 0.0015$), but the model explained just 1.2% of the observed variation.

The effect of LK_r on the probability of spawning is apparent both when calculated relative to all fish sampled and when calculated relative to only the fish sampled in that given area (Figure 4). There was a significant area effect on the relationship between LK_r and the predicted probability of spawning ($p < 0.0001$), all three NAFO

Table 3. Proportion of non-reproductive female Atlantic cod per size class and NAFO Division. Data are pooled for the years 1978−2004. Sample sizes are given in parenthesis.

| Size class (cm)	2J	3K	3L	3M	3Ps	All areas
30−39	—	0 (2)	—	33.33 (3)	0 (2)	14.28 (7)
40−49	0 (79)	1.52 (132)	0 (9)	2.97 (101)	1.15 (87)	1.47 (408)
50−59	0 (82)	2.89 (485)	2.46 (122)	40.27 (293)	10.84 (286)	13.09 (1 268)
60−69	0 (81)	4.55 (549)	10.41 (221)	55.42 (554)	31.47 (429)	26.72 (1 834)
70−79	0 (48)	2.91 (241)	13.37 (172)	34.96 (389)	33.55 (456)	24.43 (1 306)
80−89	7.69 (13)	4.21 (95)	9.23 (130)	16.03 (262)	26.40 (322)	17.52 (822)
90−99	0 (2)	0 (20)	2.78 (72)	5.31 (113)	14.00 (250)	9.41 (457)
100+	—	7.69 (13)	0 (51)	1.80 (111)	3.60 (306)	2.91 (481)
All sizes	0.33 (305)	3.45 (1 537)	8.11 (777)	33.68 (1 826)	21.09 (2 138)	17.97 (6 583)
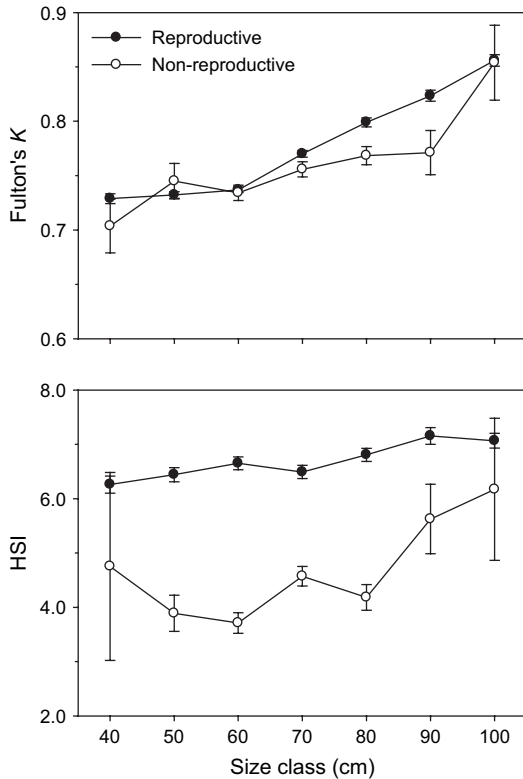
Figure 2. Comparison of condition indices for reproductive and non-reproductive Atlantic cod. Data are pooled for all years and areas. Error bars represent ±1 s.e.

Divisions differing from each other (Figure 4a). These differences are particularly evident at very low values of LK_r. Fish in 3KL were more likely to spawn at low LK_r than fish from other areas.

Comparison of LK_r values between areas using single-factor analysis of variance suggested a difference in condition ($p < 0.0001$) between the study areas, and *a posteriori* analyses revealed cod to be in significantly better condition in 3KL than in 3Ps, but not than in 3M, and no significant difference was found in condition between 3M and 3Ps.

Discussion

The data support the hypothesis that skipped spawning is relatively common for Newfoundland and Labrador cod, and not just confined to somewhat isolated and perhaps nutritionally deprived populations such as those of Smith Sound (Rideout *et al.*, 2000; Rideout and Rose, in press) and the Flemish Cap (Walsh *et al.*, 1986; Morgan and Lilly, in press). The widespread skipping of spawning by cod is not entirely a surprise, because many such claims have been made previously for the species (Woodhead and Woodhead, 1965; Oganesyan, 1993; Burton *et al.*, 1997;
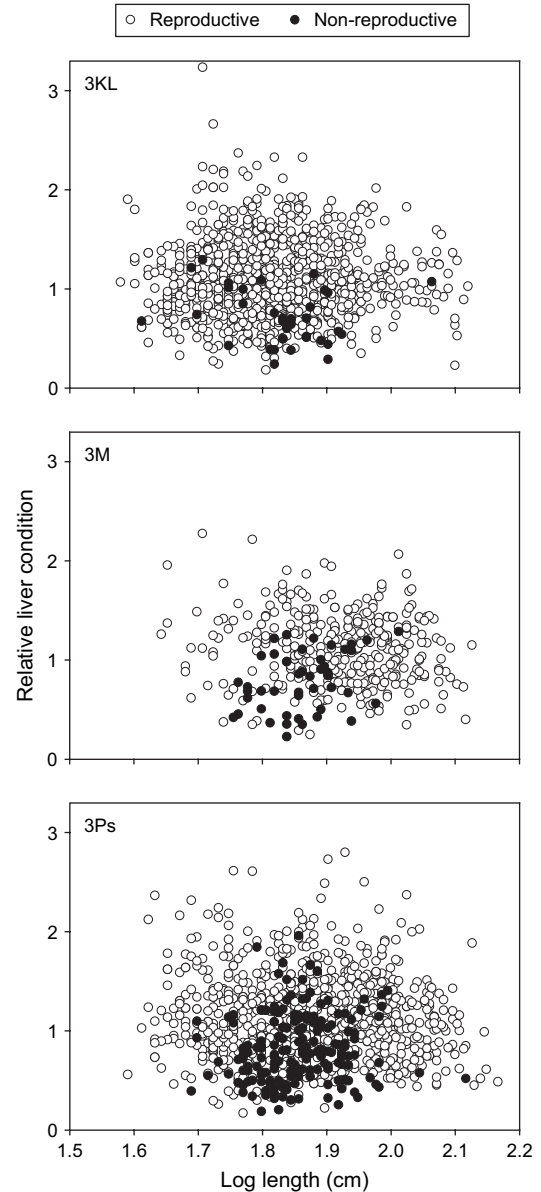

Figure 3. Comparison of relative liver condition for reproductive and non-reproductive Atlantic cod from NAFO Divisions 3KL, 3M, and 3Ps. Data are combined for the years 1978−2004.

Marshall *et al.*, 1998; Schwalme and Chouinard, 1999). Reports of skipped spawning are not limited to cod, but have been made for a number of freshwater, anadromous, and marine fish (reviewed by Rideout *et al.*, 2005). In the Northwest Atlantic, skipped spawning has been reported for other important commercial groundfish such as winter flounder (*Pseudopleuronectes americanus*; Burton and Idler, 1984), American plaice (*Hippoglossoides platessoides*; Pitt, 1966), and Greenland halibut (*Reinhardtius hippoglossoides*; Walsh and Bowering, 1981).

Table 4. Results of generalized linear models demonstrating the effect of fish age, length, relative body weight (K_r), and relative liver weight (LK_r) on the probability of spawning by Atlantic cod. Age and length were modelled as class variables.

NAFO	Effect	Deviance	χ^2	p	r^2
Overall	Age	1 531.3	17.49	<0.0001	0.011
	Length	1 515.3	33.40	<0.0001	0.022
	K_r	1 524.1	7.48	0.0062	0.005
	LK_r	1 204.7	252.94	<0.0001	0.174
3KL	Age	265.7	2.04	0.1534	0.008
	Length	302.6	5.74	0.3320	0.019
	K_r	304.7	1.60	0.2061	0.005
	LK_r	250.4	40.79	<0.0001	0.140
3M	Age	223.3	3.35	0.0671	0.015
	Length	226.7	12.12	0.0332	0.051
	K_r	233.4	0.00	0.9563	0.000
	LK_r	187.8	41.34	<0.0001	0.180
3Ps	Age	755.6	6.90	0.0086	0.009
	Length	806.7	45.68	<0.0001	0.054
	K_r	838.7	10.07	0.0015	0.012
	LK_r	700.8	99.16	<0.0001	0.124

What may be somewhat surprising is the extent of skipped spawning observed for cod. Energy-allocation life-history models for cod have predicted large proportions of skipped spawning (Jørgensen *et al.*, 2006), but the data presented here are among the first to support this prediction. In all, 18% of the potential female spawners sampled since 1978 (in the winter) would not have spawned. In areas 3M and 3Ps, the extent of skipped spawning in some years was >40%. Such findings can greatly influence perceived stock productivity and management strategies. With so many potential spawners failing to spawn in a given year, erroneous inclusion of these fish as part of the spawner biomass can result in overestimating population reproductive potential. For example, Rideout and Rose (in press) reported that failure to recognize the non-spawning portion of the adult cod biomass in Smith Sound, Newfoundland, resulted in overestimation of total egg production by 8−41% annually between the years 1999 and 2004.

The notable extent of skipped spawning was not characteristic of all areas analysed. Northern areas (2J + 3KL) appeared to contain very few non-reproductive females, in comparison with 3M and 3Ps. It is uncertain why such differences exist, but in cod and other species, skipped spawning has been related to fish nutritional condition and diet (Kennedy, 1953; Hislop *et al.*, 1978; Dutil, 1986; Burton and Idler, 1987; Rijnsdorp, 1990; Maddock and Burton, 1994; Rideout *et al.*, 2000; Rideout and Rose, in press). The prey spectrum of cod on the Flemish Cap (3M) is particularly narrow, consisting largely of shrimp, hyperiids, and redfish (Lilly, 1985; Albikovskaya and Gerasimova, 1993; Casas and Paz, 1996). It has been speculated that high levels of skipped spawning in this area in some years

may be related to low abundance of juvenile redfish (Walsh *et al.*, 1986). Capelin has historically been the most important prey item for cod in other areas, and low abundance of capelin has had negative impacts on cod reproductive success. For example, both reduced fecundity and skipped spawning in Barents Sea cod have been attributed to low abundance of capelin (Oganesyan, 1993; Kjesbu *et al.*, 1998; Marshall *et al.*, 1998). The low $\delta^{13}C$ signatures of non-reproductive cod from inshore Newfoundland suggested that they had been feeding less on capelin and more on shrimp than reproductive cod (Rideout and Rose, in press). Changes in capelin distribution during the time-frame of this study make it difficult, however, to explain differences in the prevalence of skipped spawning between 2J + 3KL and 3Ps on the basis of capelin availability. Distribution and abundance of capelin began shifting south in the late 1980s, and capelin became less available to fish in the north, while remaining prominent in the diet of cod more to the south (Lilly, 1994; Carscadden and Nakashima, 1997; Rose and O'Driscoll, 2002). Capelin have been prominent in the diet of 3Ps cod in recent years (Rose and O'Driscoll, 2002; Rideout and Rose, in press). Soviet research suggested that sandlance (*Ammodytes* spp.) was a major prey item for cod in this area in 1959 and 1960 (Popova, 1962). No feeding data, however, are available for cod in 3Ps for the years examined in the current study. The high levels of skipped spawning observed for cod in this area might indicate low levels of capelin or sandlance feeding during these years. Alternatively, cod may have skipped spawning despite feeding on capelin or sandlance. The energy-allocation life-history model presented by Jørgensen *et al.* (2006) predicted the prevalence of skipped spawning to increase not only at low but also at high prey availability. This latter scenario is based on the fact that improved growth through increased food intake should increase future fecundity, making skipping spawning in favour of continued feeding an attractive option for increasing lifetime reproductive output.

If diet is responsible for the differences in the propensity to skip spawning in the different areas, it is only partially reflected in the differences in fish condition between the three areas. For example, fish in 3KL were in better condition than those from 3Ps (data for all years combined), which may partially explain the lesser probability of skipping spawning in 3KL. However, the condition of fish in 3KL did not differ significantly from that of fish in 3M, and 3M actually had the highest proportion of non-reproductive fish. It is important here to remember that fish condition in this region follows a seasonal cycle, increasing over the summer feeding period and decreasing during the reproductive period, when feeding is highly reduced. Therefore, the condition of fish when they are sampled may not reflect their condition when the decision to skip spawning was made. Burton (1994) suggested that a critical period exists for winter flounder, whereby individuals not attaining sufficient food immediately following the
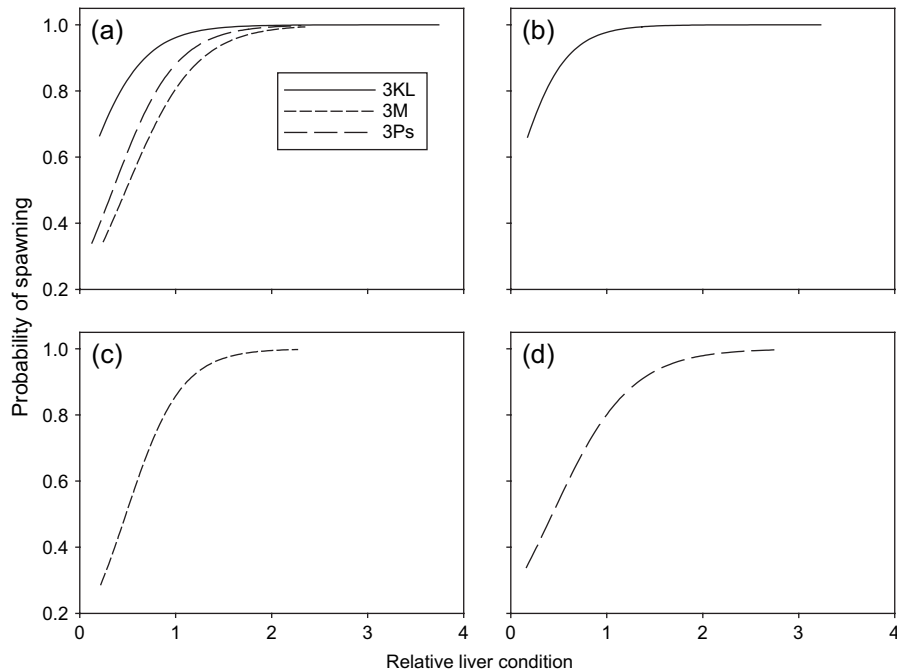
Figure 4. The probability of spawning based on relative liver condition for female cod. (a) Liver condition is expressed relative to the predicted value from a relationship between liver weight and length based on fish from all areas combined and including an area effect in the model. For (b) 3KL, (c) 3M, and (d) 3Ps, liver condition is expressed relative to fish from the respective areas, and the probability of spawning is modelled separately for each area.

completion of spawning would not spawn in the subsequent year. If a similar pattern exists for cod, then the condition indices that most explain the decision to skip spawning may occur before it is even possible to distinguish spawners from those that will skip spawning.

It is important here to distinguish between the probability of being an adult and the probability of an adult fish spawning (or skipping spawning). The probability of a fish being an adult tends to increase with age and size (Korsbrekke, 1999; Morgan and Colbourne, 1999), but it can also be influenced by fish condition (Bromley *et al.*, 2000; Marteinsdottir and Begg, 2002; Morgan, 2004) and growth rate, fish with fast growth rates maturing earlier (Rijnsdorp, 1993; Morgan and Colbourne, 1999). In addition, temperature can influence the timing of maturation through influences on growth rate (Sandstrom *et al.*, 1995). In the case of skipped spawning, a fish has already achieved sexual maturity so the probability of spawning in the upcoming season is less dependent on size and more dependent on the amount of energy stored in the liver and available to be allocated to gonad and gamete development.

Relatively low levels of skipped spawning were observed in 3L between 1980 and 1992. In contrast, high levels of skipped spawning were noted in inshore portions of 3L between 1999 and 2004 (Rideout *et al.*, 2000; Rideout and Rose, in press). It is uncertain if these differences reflect temporal changes in environmental conditions or spatial differences between inshore and offshore areas. It is of note that

Rideout and Rose (in press) reported the greatest proportion of non-reproductive fish in the smallest size class of potential spawners (40–49 cm), whereas here we observed most non-reproductive fish in the 60–79 cm size range. Data reported here are from 1978 to 2004, but come mainly from the period before 1992, whereas the findings of Rideout and Rose (in press) are based only on data from 1999 to 2004. There have been large decreases in size at maturity of cod over recent decades (Olsen *et al.*, 2005). The large number of skipped spawners found here at 60–79 cm would encompass the size range where fish were maturing for the first time. In other species, such as *Solea solea* (Ramsay and Witthames, 1996) and *Reinhardtius hippoglossoides* (Walsh and Bowering, 1981), interruptions in gamete development are more common in smaller, potentially first-time spawners. Engelhard and Heino (2005), on the other hand, suggested that skipped spawning in Atlantic herring (*Clupea harengus*) was most common among potential second-time spawners.

In this study, we utilize a long-term cod data set that includes macroscopically determined maturity data, which admittedly could produce less accurate results than analyses based on histology (Tomkiewicz *et al.*, 2003; Vitale *et al.*, 2006). While this could reduce the accuracy of our findings, we believe that the impact is relatively small, because previous histological work confirmed the existence of a large proportion of skipped spawners in the area (Walsh *et al.*, 1986; Rideout *et al.*, 2000). In addition, because the data set encompasses a 27-year period and was compiled by

numerous individuals, there is the potential for temporal variability as well as variability between observers in the accuracy of assigning maturity stages macroscopically. The use of macroscopically determined maturity stages is therefore considered a limitation of this study, and we encourage the use of histologically determined maturity for such work whenever possible.

Data presented here clearly suggest that skipped spawning in Newfoundland and Labrador cod is more common and widespread than perhaps previously believed. Although liver condition appears to influence the probability of spawning, there are spatial differences among areas with respect to the effects of liver condition. These results indicate that a global model to predict the probability of spawning by cod is likely not appropriate, and that there is a need to examine potential spatial differences in the bioenergetics of this species.

Acknowledgements

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