

Did population collapse influence individual fecundity of Northwest Atlantic cod?

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Stares, J. C., Rideout, R. M., Morgan, M. J., and Brattey, J. 2007. Did population collapse influence individual fecundity of Northwest Atlantic cod? – *ICES Journal of Marine Science*, 64: 1338–1347.

We examined the influence of population collapse on individual potential fecundity and total population egg production (TEP) of three northwest Atlantic cod (*Gadus morhua*) populations: northern cod (Divisions 2J3KL), southern Grand Bank cod (NAFO Divisions 3NO), and southern Newfoundland cod (Subdivision 3Ps). Fecundity at length increased in conjunction with population collapse for two (3NO, 3Ps) of the three populations. Subsequent moderate population recovery between the 1990s and 2000s in 3Ps was accompanied by a decrease in fecundity at length. A large decrease in fecundity at length for 3NO during the same time period, despite little or no population recovery, coupled with the fact that there was no obvious difference in fish condition between the two time periods, suggested that density-independent factors could be contributing to the changes in fecundity. Use of pre-collapse fecundity–length relationships to estimate TEP in the post-collapse period resulted in underestimation of TEP by as much as 30% in 3NO and 46% in 3Ps, whereas in 2J3KL, TEP was overestimated by as much as 18%. Although the results do not fully support the hypothesis of an inverse relationship between population size and fecundity, they do demonstrate the variable nature of cod fecundity which, if not accounted for, can lead to erroneous perceptions of stock reproductive potential.

Keywords: egg production, fecundity, *Gadus morhua*, reproduction, reproductive potential, spawning.

Received 20 February 2007; accepted 13 July 2007.

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Introduction

Traditional estimates of the reproductive potential of a fish stock are based primarily on spawning-stock biomass (SSB). This practice has been challenged in recent years, because variation in many factors that are not reflected in SSB can influence the overall egg production of the stock (Marshall *et al.*, 1998; Scott *et al.*, 1999). Including additional information such as sex ratio, age structure, size or age at maturity, and fecundity can result in different trends in estimates of stock reproductive potential and perceived health of the stock (Marshall *et al.*, 1998; Marteinsdottir and Thorarinsson, 1998; Kraus *et al.*, 2002; Morgan and Brattey, 2005; Rideout and Morgan, 2007). It is therefore vital to understand whether changes in population size might influence these reproductive parameters.

Size and age at maturity are perhaps the best studied reproductive traits and, for many fish populations, have declined in response to reductions in population size (Rijnsdorp, 1989; Jørgensen, 1990; Morgan and Colbourne, 1999). Such changes are sometimes attributed to size-selective harvesting, which creates selective pressure to mature earlier and results in heritable changes in size and age at maturity (Reznick *et al.*, 1990; Olsen *et al.*, 2004; Barot *et al.*, 2005). In some cases, however, size at maturity has increased quickly in response to population recovery

(Muth and Ickes, 1986), suggesting that initial collapses in size at maturity might be at least partially phenotypically based.

Data on the fecundity of fish are not as readily available as maturity data (Tomkiewicz *et al.*, 2003), so less is known about the influence that changes in population size have on fecundity. Studies with multiple consecutive years of fecundity data encompassing a period of major population change are rare. A notable exception is the orange roughy (*Hoplostethus atlanticus*) stock off the east coast of Tasmania. Overfishing of that stock resulted in a 50% decline in population size between 1987 and 1992, whereas annual data suggested that fecundity increased by 20% over the same period (Koslow *et al.*, 1995). Likewise, fecundity of pike (*Esox lucius*) increased during the period 1964–1967 as pre-spawning adult biomass decreased (Kipling and Frost, 1969). Such studies suggest an inverse relationship between stock size and fecundity. This is supported by studies on fresh-water fish populations that are exploited experimentally (Healey, 1978; Baccante and Reid, 1988) or through natural predation (Reznick *et al.*, 1990). Explanations for the increase in fecundity during population decline include (i) a resulting decrease in fish density and thus a competitive release of resources, which in turn allows each remaining fish to attain higher condition and produce greater numbers of eggs, and (ii) selective pressure to maximize

reproductive output at an earlier age, resulting in heritable increases in egg production.

A more common approach to exploring the relationship between population size and fecundity has been to compare fecundity prior and subsequent to a major change in population size. If fecundity is influenced by population size, then there should be a marked difference in fecundity between the two extremes in population size (i.e. pre- and post-collapse). For example, Yoneda and Wright (2004) reported that inshore North Sea cod (*Gadus morhua*) were more fecund during a period of low spawning stock size (2002, 2003) than they were during a period of high spawning stock size (1969, 1970). The findings for North Sea haddock (*Melanogrammus aeglefinus*) were similar, with a marked increase in fecundity at low population size (Wright, 2005). Bowen *et al.* (1991) reported that fecundity of lake herring (*Coregonus artedii*) was higher when population size was low. Rijnsdorp (1991) compared fecundity of North Sea plaice (*Pleuronectes platessa*) among three time periods and found fecundity to be generally higher from 1977 to 1985 than it was in the periods 1947–1949 and 1900–1910. Bagenal (1966) examined all plaice fecundity data published for the entire range of the species as well as population size at the time of sample collection, and concluded that fecundity in that species was density-dependent. The density-dependent nature of fish fecundity is also reflected in populations that have recovered from overexploitation, such as North Sea plaice (Rijnsdorp, 1994) and walleye (*Sander vitreus*; Muth and Ickes, 1986), fecundity decreasing again following population growth. Relationships between fecundity and population size could not be demonstrated for some fish populations (Schueller *et al.*, 2005). In such cases, it is possible that any density-dependent relationship may be masked by density-independent factors and by the inherently highly variable nature of fish fecundity (e.g. Bagenal, 1957; Rideout and Morgan, 2007).

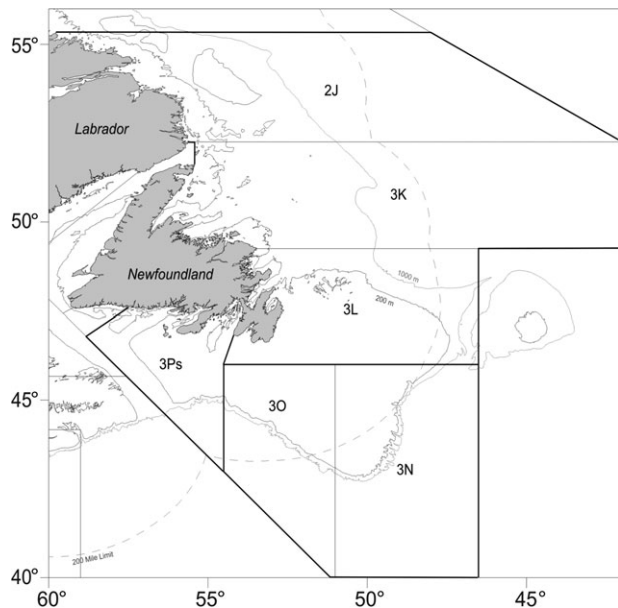


Figure 1. Map of the northwest Atlantic, showing the areas inhabited by the study populations: northern cod (NAFO Divisions 2J3KL), southern Grand Banks cod (NAFO Div. 3NO), and southern Newfoundland cod (NAFO Subdivision 3Ps).

Three Northwest Atlantic cod stocks (Figure 1), northern cod (NAFO Divisions 2J3KL), southern Grand Bank cod (Divisions 3NO), and southern Newfoundland cod (Subdivision 3Ps), have undergone major declines in population size during the past several decades (Brattey *et al.*, 2005; Power *et al.*, 2005; Lilly *et al.*, 2006). Southern Newfoundland cod is the only population to show any significant sign of recovery (Figure 2). For each population, the major drop in population size was accompanied by a decrease in size and age at maturity (Morgan and Brattey, 2005). However, the impact that the dramatic decline in population size has had on fecundity of Northwest Atlantic cod has not been explored. The only fecundity data reported for these populations was collected before the major decline. May (1967) collected fecundity data for northern cod (2J3KL) in 1964 and for southern Grand Bank cod in the years 1964–1965. Pinhorn (1984) presented fecundity data for southern Newfoundland cod collected during the period 1967–1970. Fecundity data for cod

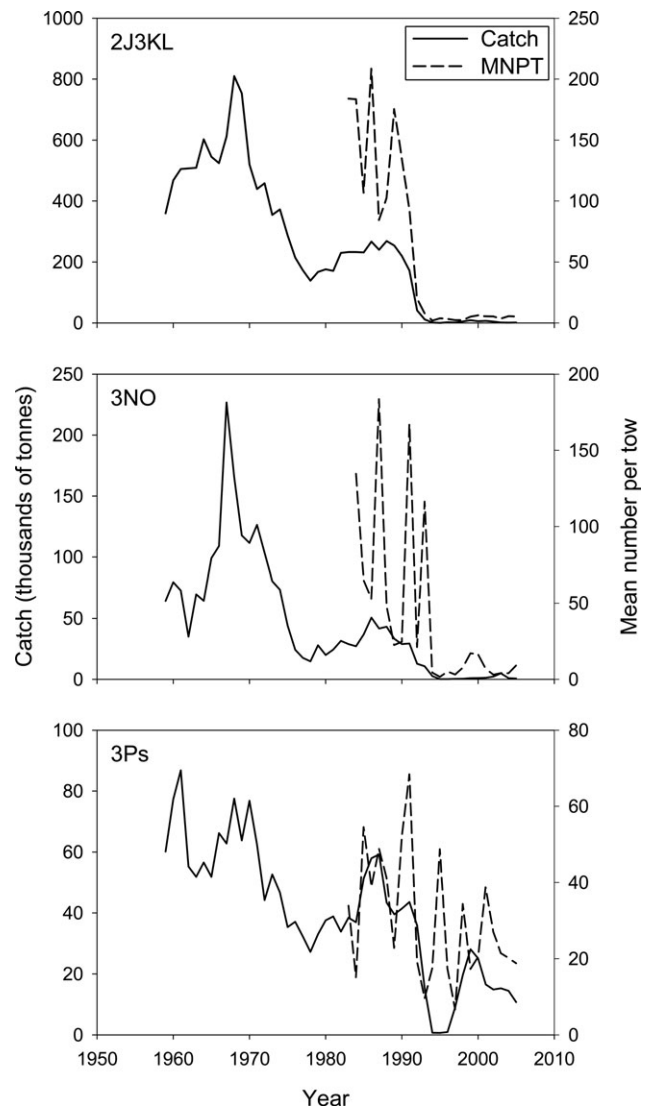


Figure 2. Trends in northwest Atlantic cod total commercial catch and mean number of individuals per tow (MNPT) from AUTUMN Canadian research vessel surveys. Data from: 2J3KL (Lilly *et al.*, 2006), 3NO (Power *et al.*, 2005), and 3Ps (Brattey *et al.*, 2005).

collected off Labrador in 1964 are also available in the Russian literature (Postolakii, 1967), but sampling locations are not well defined. Here, we present fecundity data collected subsequent to the population decline (late 1980s to the early 1990s) and compare them with the already published pre-decline data to test the hypothesis that fecundity responds inversely to changes in population size (i.e. whether there is an increase in fecundity after population collapse). In addition, we use data collected during the years 2002–2004 to investigate whether or not the recent moderate recovery of the southern Newfoundland cod population has resulted in a subsequent decline in fecundity.

Material and methods

Ovaries were collected from 559 Northwest Atlantic cod (Table 1) during spring bottom trawl surveys conducted by Fisheries and Oceans Canada research vessels. Northern cod (NAFO Divisions 2J3KL; Figure 1) were collected during the years 1988–1990. Southern Grand Bank cod (Divisions 3NO; Figure 1) and southern Newfoundland cod (Subdivision 3Ps; Figure 1) were collected over two time periods: 1993–1995 and 2002–2004. Females were designated as ripening for the upcoming spawning season, based on macroscopic inspection of the ovaries. Only ovaries containing opaque oocytes but no clear oocytes were included, because the presence of clear oocytes would indicate that spawning had already started (and therefore that egg counts may not be accurate). Fork length was recorded for all fish. Whole weight was

also recorded for all fish from 3NO and 3Ps, but for fewer than 20% of fish from 2J3KL.

Ovaries were sliced longitudinally and placed in Gilson's fluid for 4–6 weeks (slightly longer for large ovaries) to facilitate the breakdown of ovarian connective tissue. Before the late 1970s, the Gilson's fluid was based on the formulation of Simpson (1951), which contained mercuric chloride. However, mercuric chloride has since been replaced by zinc chloride to reduce the toxicity of this fixative (Barszcz, 1976). First generation oocytes (i.e. >200 µm, those that would have been spawned in the current year) were separated from second-generation (i.e. immature) oocytes and connective tissue by rinsing through a series of sieves. The cleaned oocytes were stored in ethanol until counted.

Oocytes were fractionated down to a countable number using a modified whirling vessel (Wiborg, 1951). Each spinning of the whirling vessel resulted in one-tenth of the number of oocytes being extracted from the vessel. The one-tenth sample could then be placed back into the vessel to obtain a one-hundredth sample of oocytes. The process was continued until the subsample was considered large enough to give an accurate count, but small enough to make manual counting practical, typically 800–2000 oocytes. Counting was done manually under a stereomicroscope. Four subsamples were collected from each pair of ovaries, but the last two were only counted if the difference between the first two counts was >5%. The mean oocyte count was scaled up, based on the fraction number (i.e. the proportion of the whole sample that was counted), to obtain the overall individual

Table 1. Relationships between potential fecundity and fork length (cm) ($F = aL^b$) for Northwest Atlantic cod sampled during various time periods.

Area	Year(s)	Month(s)	<i>n</i>	Length	<i>a</i>	<i>b</i>	<i>r</i> ²	<i>p</i> -value	50 cm	70 cm	90 cm
2J3KL	1964	March–May	55	50–126	0.636	3.397	0.84	<0.0001	0.38	1.18	2.77
	1988–1990	February–June	186	41–111	0.213	3.627	0.87	<0.0001	0.31	1.05	2.61
	1988	February–May	89	41–109	0.183	3.659	0.87	<0.0001	0.30	1.03	2.59
	1989	February–May	64	44–111	0.349	3.502	0.86	<0.0001	0.31	1.01	2.44
	1990	May–June	33	45–105	0.144	3.752	0.87	<0.0001	0.34	1.21	3.10
3NO	1964–1965	March–May	75	61–127	0.057	3.885	0.70	<0.0001	(0.23)	0.84	2.23
	1993–1995	April–May	87	40–124	0.416	3.499	0.84	<0.0001	0.37	1.19	2.86
	1993	April–May	63	40–120	0.387	3.529	0.90	<0.0001	0.38	1.26	3.05
	1994	May	15	47–124	0.103	3.805	0.79	<0.0001	0.30	1.08	2.81
	1995	May	9	52–89	–	–	–	0.3122	–	–	–
	2002–2004	April–June	50	45–109	7.656	2.713	0.52	<0.0001	0.31	0.78	1.53
	2002	April–May	22	45–109	15.541	2.500	0.43	0.0008	0.27	0.64	1.19
	2003	May–June	20	50–108	15.825	2.587	0.80	<0.0001	0.39	0.94	1.80
	2004	May	8	57–89	–	–	–	0.2608	–	–	–
3Ps	1967–1970 ^a	February–May	103	51–128	0.417	3.370	0.82	<0.01	(0.22)	0.69	1.61
	1993–1995	February–April	143	39–109	0.800	3.352	0.69	<0.0001	0.40	1.22	2.84
	1993	February–April	67	43–89	0.274	3.618	0.73	<0.0001	0.38	1.30	(3.22)
	1994	April	43	39–98	0.124	3.824	0.65	<0.0001	0.39	1.41	3.69
	1995	April	33	45–109	18.289	2.598	0.54	<0.0001	0.47	1.14	2.18
	2002–2004	April–May	93	42–113	10.160	2.757	0.72	<0.0001	0.49	1.24	2.48
	2002	April	40	47–103	12.095	2.706	0.60	<0.0001	0.48	1.19	2.35
	2003	April	35	42–106	9.952	2.782	0.80	<0.0001	0.53	1.35	2.72
	2004	April–May	18	43–113	2.071	3.121	0.86	<0.0001	0.42	1.19	2.60

Estimated fecundities (10⁶) at 50, 70, and 90 cm are shown. Fecundity estimates in parentheses are outside the observed length range.

^aAs published by Pinhorn (1984).

potential fecundity estimate (from here on referred to simply as fecundity).

The relationship between fecundity and fish length was explored using linear regression based on log–log transformed data. Because sampling procedures followed those used in previous studies for the same populations (May, 1967; Pinhorn, 1984), comparisons of fecundity prior and subsequent to the major population decline could be made. In May's (1967) analyses, fish from the northernmost part of Division 3N were included as part of the 3L population, and 3L was analysed separately from Divisions 2J3K. Here, we reanalyse these data without the spatial adjustments and present data for 2J3KL as a whole, because fish in these divisions are managed as a single population. For 2J3KL and 3NO cod, fecundity was compared between time periods using analysis of covariance (ANCOVA), with log length as covariate. For 3NO, this analysis included two post-collapse periods. The original data from Pinhorn's (1984) fecundity analyses were not available, so comparisons between pre- and post-collapse periods for 3Ps were made using an *F*-test (SAS Institute Inc., 1999) to examine the probability that the newer data produced regression coefficients that did not differ from the published values. Comparisons between the two post-collapse periods for 3Ps were again made using ANCOVA. All comparisons between time periods were carried out over the entire size range of fish sampled, as well as only the size range common to the time periods being compared. This was to ensure that any difference in fecundity–length relationships was not simply attributable to differences in the size of sampled fish. Comparison of intercepts was disregarded when there was a significant difference in slope.

For those fish that had weight data, relative fecundity (F_r) was calculated as the number of eggs produced per gramme of total body weight. Relative condition (K_r) and relative liver condition (LK_r) were also calculated for these fish according to the following equations:

$$K_r = \frac{W}{\hat{W}}$$

$$LK_r = \frac{LW}{\hat{LW}},$$

where W is whole body weight, LW liver weight, and \hat{W} and \hat{LW} the predicted body weight and liver weight, respectively, from the linear log length–log weight or log length–log liver weight relationships. Weight data were not available for 3Ps samples collected before population decline, which left comparisons of K_r limited to 1964 vs. 1988–1990 for 2J3KL, 1964–1965 vs. 1993–1995 vs. 2002–2004 for 3NO, and 1993–1995 vs. 2002–2004 for 3Ps. Liver weight data were not available for samples from 2J3KL or those collected before population decline from the other two areas, so comparisons of relative liver condition were limited to the 1990s vs. the 2000s for 3NO and 3Ps. Generalized linear models with a gamma error structure and identity link function were used to compare relative fecundity and relative condition indices between time periods.

To illustrate the impact of any potential changes in fecundity on the perceived productivity of the stocks, total population egg production (TEP) was calculated for the post-collapse time period(s) using both relationships derived during the pre-collapse period as well as the period-specific fecundity estimates. TEP was calculated

as the estimated number of eggs produced at age multiplied by the estimated number of mature females at age. Numbers-at-age were derived from age-structured population analyses (Shelton and Lilly, 2001; Bratley *et al.*, 2005; Power *et al.*, 2005). Estimates of proportion mature and proportion female at age were derived from survey data (Morgan and Bratley, 2005), and multiplied by the number-at-age to produce estimates of the number of mature females at age. Fecundity-at-age was derived from fecundity at length by using the mean length-at-age in each year and either the historical fecundity–length relationship or the period-specific relationships derived here.

The number of eggs produced per recruit was calculated as a measure of individual egg production rate:

$$\sum_{a=1}^j N_a P M_a F_a,$$

where N_a is numbers-at-age ($N_a = N_{a-1}e^{-0.2}$) starting with 1 recruit at age 0, j the maximum age in the age-structured population analyses used in the TEP estimates above ($j = 20$ for 2J3KL, 12 for 3NO, 14 for 3Ps), $P M_a$ the proportion mature-at-age, and F_a the fecundity-at-age ($F_a = cL^b$, where L is the mean length-at-age, and c and b the coefficients from the fecundity–length relationship).

The fecundity–length relationship, $P M_a$, and mean length were those from the years in which the eggs per recruit were being calculated, so all three varied, not just the fecundity-at-length.

Results

The relationship between fecundity and fish length was highly significant in all areas for all time periods as well as in individual years, except for Southern Grand Bank cod in 1995 and 2004, for which sample sizes were very small (Table 1).

Comparisons between pre- and post-population decline (Table 2; Figure 3) for each area suggested no change in fecundity in 2J3KL between 1964 and 1988–1990. For 3NO, differences in the slope of the fecundity–length curves between pre- and post-decline were significant when based on all data collected, but were not significant when restricted to a common size range, suggesting that the presence of smaller reproductive fish and the lack of large fish in the post-decline periods was influencing the slope of the curves. Comparison of intercepts revealed that fecundity was significantly higher in the 1990s than in the 1960s. In 3Ps, fecundity changed significantly between the pre- and post-decline periods. Comparison of the 1990s with the 1960s revealed a difference in intercept, fecundity being higher in the 1990s than in the 1960s when analysed over a common size range.

Comparisons of fecundity were also made between the 1990s and 2000s for 3NO and 3Ps (Table 2; Figure 3). In 3NO, fecundity dropped significantly by the 2000s, to the point where it was even lower than it was in the 1960s. In 3Ps, the slope of the fecundity–length curve decreased significantly between 1993–1995 and 2002–2004, but was still higher than in the 1960s.

There was significant interannual variability in fecundity in 2J3KL with higher fecundity in 1990 than in 1988 and 1989 (Table 3). For 3NO, there was no difference in fecundity–length relationships for 1993 and 1994 and any difference between 2002 and 2003 disappeared when analysed over a common size range. There was no significant interannual variability in either the 1990s or 2000s for 3Ps.

Table 2. Comparison of fecundity–length relationships between time periods for Northwest Atlantic cod.

Area	Time periods	Size range (cm)	p-values	
			Slope	Intercept
2J3KL	1964 vs. 1988–1990	All sizes	0.3214	0.0664
		50–111	0.6404	0.0538
3NO	1964–1965 vs. 1993–1995 vs. 2002–2004	All sizes	0.0230	–
		61–109	0.4012	0.0001 ¹
3Ps	1967–1970 vs. 1993–1995	All sizes	0.9229	0.3977
		51–128	0.0750	0.0179
	1967–1970 vs. 2002–2004	All sizes	0.0009	–
		51–128	0.0010	–
	1993–1995 vs. 2002–2004	All sizes	0.0249	–
		42–109	0.0452	–

Analyses were performed using ANCOVA except for comparisons with the historical data for 3Ps, where *F*-tests were used to compare slope and intercept with previously published parameter estimates. Analyses were performed for all fish sampled as well as for only those in the size range common to the time periods being compared. Comparisons of intercepts were not performed when slopes were significantly different.

¹Multiple comparisons grouping: 1964–1965^b, 1993–1995^a, 2002–2004^c. Time periods with different superscripts are significantly different.

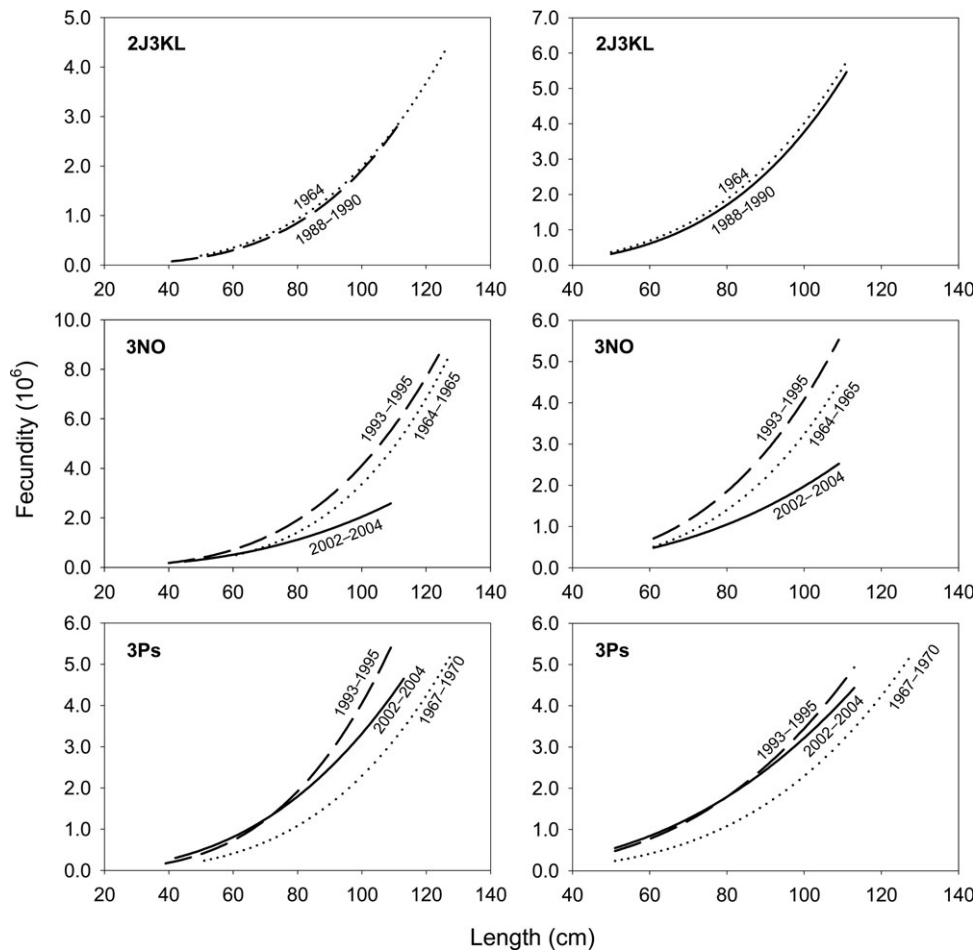


Figure 3. Relationships between fecundity and length ($F = aL^b$) for Northwest Atlantic cod prior and subsequent to population collapse. Panels on the left represent regression equations calculated using all available data. Panels on the right represent regression equations calculated using only size ranges common to the time periods being compared, except for 1967–1970 in 3Ps, where data were not available to restrict the size range. Years with different superscripts are significantly different.

Table 3. Analysis of covariance results for the comparison of fecundity–length relationships among years within time periods for Northwest Atlantic cod.

Area	Years	Size range (cm)	p-values	
			Slope	Intercept
2J3KL	1988–1990	All sizes	0.6963	0.0278 ¹
		46–105	0.1035	0.0120 ¹
3NO	1993, 1994	All sizes	0.4991	0.4380
		47–120	0.2492	0.4614
	2002, 2003	All sizes	0.9060	0.0414
		50–108	0.7330	0.2189
3Ps	1993–1995	All sizes	0.0508	0.9867
		45–89	0.7085	0.9239
	2002–2004	All sizes	0.6607	0.3307
		47–103	0.7423	0.5679

Analyses are performed for all fish sampled as well as for only those in the size range common to the years being compared.

¹Multiple comparisons grouping: 1988^a, 1989^a, 1990^b. Years with different superscripts are significantly different.

Table 4. Summary of relative fecundity data for northwest Atlantic cod.

Population	Period	Relative fecundity				
		n	Minimum	Maximum	Mean	s.d.
2J3KL	1964	22	194.7	591.8	380.6	100.0
	1988–1990 ^a	33	141.2	606.6	381.4	104.1
3NO	1964–1965	28	74.1	519.2	310.2	125.5
	1993–1995 ^b	87	63.8	757.6	423.4	143.2
	2002–2004	50	32.4	702.7	310.4	146.8
		93	60.0	1 220.2	461.2	174.7
3Ps	1993–1995	142	60.3	1 058.5	437.0	168.8
	2002–2004	93	60.0	1 220.2	461.2	174.7

Significant relative fecundity–length relationships

^arelf = 162.6 + 3.2 length ($r^2 = 0.20$; $p = 0.01$)

^brelf = 290.4 + 1.7 length ($r^2 = 0.07$; $p = 0.01$).

Relative fecundity of Northwest Atlantic cod ranged from 32 to 1220 eggs g⁻¹ (Table 4). Relationships between relative fecundity and fish length were not significant except for 1988–1990 cod from 2J3KL and 1993–1995 cod from 3NO. Relative fecundity did not differ significantly between 1964 and 1988–1990 in

2J3KL (Table 5). Relative fecundity in 3NO was significantly higher in the 1990s than in either the 1960s or 2000s, but there was no difference between the 1960s and 2000s. The lack of weight data for 3Ps in the years 1967–1970 prevented a comparison of relative fecundity between pre- and post-collapse periods, but there was no difference between 1993–1995 data and those for 2002–2004.

Relative condition (K_r) did not change subsequent to population collapse in 2J3KL or 3NO (Table 5). Weight data were not available for 3Ps in the period 1967–1970, so comparisons could not be made for that area. Liver weight data were not available for the pre-collapse period in any of the areas examined, so comparisons of relative liver condition were limited to post-decline periods. Relative liver condition was significantly lower in the period 2002–2004 than in 1993–1995 in 3NO, but there was no difference between these two periods for 3Ps.

The influence of changes in individual fecundity at length on TEP was explored by calculating TEP for the post-collapse period(s) using not only the period-specific fecundity data, but also the fecundity–length relationships from the pre-collapse period (Figure 4). Results indicate that TEP in 2J3KL was 6–18% lower in the post-decline period than would have been suggested by the old fecundity data. In 3NO, TEP was 27–30% higher in the 1990s and 2–16% lower in the 2000s than would have been predicted with the old fecundity data. In 3Ps, TEP was 43% higher in the 1990s and 43–46% higher in the 2000s than was suggested by the use of the old fecundity data.

The number of eggs produced per recruit increased following population collapse in all three areas (Figure 4). In 3NO, eggs per recruit declined between the 1990s and 2000s, but in 3Ps, there was no apparent change between the two periods.

Discussion

Data presented here for Northwest Atlantic cod lend some support to the notion of an inverse relationship between population size and fecundity, but the results are not unequivocal. Two of the cod populations in question (Southern Grand Bank and southern Newfoundland) did exhibit an increase in fecundity following collapse of the stocks in the late 1980s and early 1990s, whereas the third (northern cod) showed no significant change in fecundity during the marked decline in population size. The apparent difference among stocks in the response of fecundity to population collapse could be partially attributable to the different time periods examined. The post-collapse data for 3NO and 3Ps were collected after the populations had already declined to their lowest level, whereas the data for northern cod were collected while the

Table 5. Comparison of relative condition indices between pre- and post-population decline for Northwest Atlantic cod.

Population	Condition index	Time periods compared	p-value
2J3KL	F_r	1964 vs. 1988–1990	0.9755
	K_r	1964 vs. 1988–1990	0.0697
3NO	F_r	1964–1965 vs. 1993–1995 vs. 2002–2004	<0.0001 ¹
	K_r	1964–1965 vs. 1993–1995 vs. 2002–2004	0.2378
	LK_r	1993–1995 vs. 2002–2004	<0.0001
	F_r	1993–1995 vs. 2002–2004	0.2904
3Ps	K_r	1993–1995 vs. 2002–2004	0.0579
	LK_r	1993–1995 vs. 2002–2004	0.5749
	F_r	1993–1995 vs. 2002–2004	0.5749

¹Multiple comparisons grouping: 1964–1965^a, 1993–1995^b, 2002–2004^a. Time periods with different superscripts are significantly different.

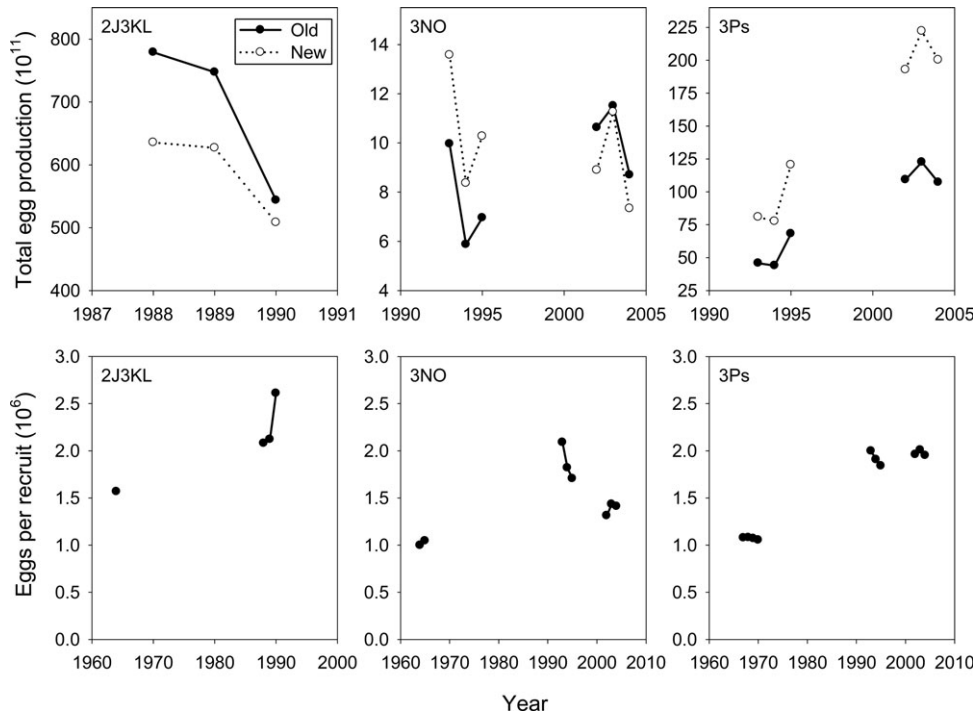


Figure 4. Upper panels: comparison of TEP for the post-population decline period(s) calculated using both the pre-population decline fecundity–length relationship as well as the period-specific relationships. Lower panels: comparison of the number of eggs produced per recruit prior and subsequent to population collapse.

population was declining and before the lowest population size had been reached. The 3Ps cod population has shown moderate population growth since its collapse in the late 1980s and early 1990s and, as per the density-dependent hypothesis, demonstrated a decrease in fecundity between the 1990s and 2000s. The 3NO population, however, has shown little or no recovery over that time but experienced a dramatic decline in fecundity (greater than the change from pre- to post-collapse) which is inconsistent with the hypothesis of an inverse relationship between population size and fecundity.

Although most of the work to date supports the density-dependent nature of fish fecundity (Bowen *et al.*, 1991; Winters *et al.*, 1993; Koslow *et al.*, 1995; Yoneda and Wright, 2004; Wright, 2005), this is not the first study that failed to find complete support for such a relationship. For example, Schueller *et al.* (2005) found that walleye fecundity in Big Crooked Lake, Wisconsin, between 1997 and 2003 was not significantly related to population density. Those authors suggested that fecundity may be related to population density over a broader range of population density than was observed in their study. This argument is unlikely to be applicable in the current study, because the time periods covered extremes in population size. Other factors, however, may have made it difficult to identify a density-dependent relationship. First, changes in population size are considered here to be accompanied by changes in fish density. However, contraction of a population's distribution towards a preferred habitat during periods of low population size has been demonstrated previously for fish (MacCall, 1990; Simpson and Walsh, 2004), including northern cod (Atkinson *et al.*, 1997), and could reduce or prevent corresponding changes in density. The notion that fecundity changes in response to change in population size is based on the assumption that changes in the number

of individual fish alters the amount of resources available per individual, but this is unlikely to be the case if density does not change. In addition, the predicted increase in resource availability during population decline is based on the assumption that prey abundance remains constant. This is clearly not the case. In fact, the abundance and distribution of capelin (*Mallotus villosus*), one of the preferred prey of cod (Lilly, 1994; Carscadden *et al.*, 2001), may have changed just before the decline of Northwest Atlantic cod stocks (Carscadden and Nakashima, 1997; Rose and O'Driscoll, 2002).

Other reproductive traits have also changed for Northwest Atlantic cod over the period of major population decline, including size- and age-at-maturity, which has decreased significantly for all three populations (Morgan and Bratney, 2005). The changes in maturity have been attributed, at least partially, to fishery-induced evolution (Olsen *et al.*, 2004), whereby size-selective harvesting (i.e. increased mortality in the older age classes) results in selection for increased reproductive effort at younger age classes (Law, 1979; Michod, 1979). Such selective pressure could conceivably also lead to changes in fish fecundity. However, the fact that fecundity-at-length in both 3NO and 3Ps quickly dropped again between 1993–1995 and 2002–2004 suggests that changes in fecundity during stock collapse were not genetically based, but were more likely a phenotypically plastic response to changing environmental conditions. The potential link between resource availability (measured as fish condition) and fecundity could not be demonstrated here, but has been demonstrated at both an individual and a population level for other cod stocks (Kjesbu *et al.*, 1998; Marshall *et al.*, 1998; Lambert and Dutil, 2000; Marteinsdottir and Begg, 2002; Rätz and Lloret, 2003). Perhaps a comparison of liver condition prior and subsequent to population collapse would have been more informative, because the lipids used in

egg production are stored primarily in this organ (Lambert and Dutil, 1997). Unfortunately, we were unable to examine the effect of population collapse on liver condition because of a lack of pre-collapse data on liver weight.

Because of the seasonal pattern of gamete growth and concurrent changes in condition for temperate fish, the timing of sampling can impact the potential relationship between fecundity and condition. For example, the condition of fish at the time of capture may not reflect the condition at the time that fecundity was set. Skjæraasen *et al.* (2006) reported that lipid reserves of cod best predicted fecundity when measured ~3–4 months before spawning, around the start of vitellogenesis. However, sampling fish several months in advance of spawning might result in biased fecundity estimates. Thorsen *et al.* (2006) reported that potential fecundity of cod was significantly reduced by atresia during vitellogenesis. Sampling for fecundity earlier in the ripening process could therefore lead to large differences between potential and realized fecundity (i.e. the number of eggs actually spawned). Variability in the timing of sampling relative to spawning time could also contribute to the perception of temporal changes in fecundity. However, this does not appear to have contributed to the changes in fecundity observed here. For example, fecundity increased between the pre- and post-collapse period for 3NO and also between the 1990s and 2000s for 3Ps. In both cases, however, the timing of sampling was actually slightly later for the period with the greatest fecundity (Table 1). Therefore, based on the findings of Thorsen *et al.* (2006), timing of sampling in this case may have served to minimize the potential for observed differences in fecundity rather than creating the perception of temporal changes in fecundity.

Density-independent factors can also influence fecundity. Low water temperature has been linked to reduced egg production in other fish (Hodder, 1965; Pawson *et al.*, 2000), and implicated in skipped spawning for cod (Rideout *et al.*, 2000). However, vertically averaged oceanic temperature for the northern cod stock actually declined from the late 1960s to the mid-1990s, and was particularly cold during the period of collapse between the early 1980s and the early 1990s (Rose *et al.*, 2000). Also, temperature does not explain the fact that fecundity decreased between the 1990s and 2000s not only in 3Ps, where some population recovery was observed, but also in 3NO, which showed little or no sign of recovery. In fact, bottom temperatures in the Northwest Atlantic were generally higher in the early 2000s than in the 1990s (Colbourne *et al.*, 2006).

Although fecundity data were not entirely supportive of increased egg production at low population size, the combination of these data with reduced size-at-maturity data (Morgan and Brattey, 2005) suggested an overall increase in reproductive investment, measured as eggs per recruit, in the post-collapse period. However, reproductive investment cannot be measured definitively without some measurement of egg size. For example, Rijnsdorp (1991) reported that the low fecundity observed for North Sea plaice between 1947 and 1949 was not accompanied by similar reductions in gonad weight, and he therefore interpreted the reduced fecundity not as reduced reproductive investment, but rather as a switch from production of large numbers of small eggs to production of fewer large eggs. Egg sizes were not monitored during the current study.

Fecundity data are generally the least readily available of all data used to estimate stock reproductive potential (Tomkiewicz *et al.*, 2003). Although there have been a number of recent fecundity

studies for other cod populations (Kjesbu *et al.*, 1998; Kraus *et al.*, 2000; Marteinsdottir and Begg, 2002; Koops *et al.*, 2004), the most recent fecundity data for the populations surrounding Newfoundland were collected between 1964 and 1970 (May, 1967; Pinhorn, 1984). Recent attempts to model TEP for these populations have had to rely on these historical data and treat fecundity as temporally invariant (Morgan and Brattey, 2005; Rideout and Rose, 2006). Results presented here confirm that fecundity in northwest Atlantic cod in fact exhibits a high degree of variability, and whatever the cause of this variability, treating fecundity as invariant can result in highly erroneous perceptions of stock reproductive potential. These findings are supported by recent work on other northwest Atlantic groundfish (Rideout and Morgan, 2007). Until such time as variability in fecundity can be understood and predicted, the regular and frequent collection of fecundity data is strongly encouraged in order to estimate with greater accuracy the reproductive potential of fish populations.

Acknowledgements

Financial support was provided by Fishery Products International Ltd, the Canadian Centre for Fisheries Innovation, Memorial University of Newfoundland, Fisheries and Oceans Canada, and the Fisheries Science Collaborative Program. Thanks are extended to J. Wroblewski and the late J. Brown for their advice on the project, and to the many technical staff and ships' crews that were involved in sample collection. D. Maddock Parsons, C. Purchase, and two anonymous reviewers made helpful comments on an earlier version of the manuscript.

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doi:10.1093/icesjms/fsm127