# Small-scale temporal and spatial variation in Atlantic cod (*Gadus morhua*) life history

**Tara M. McIntyre and Jeffrey A. Hutchings**

**Abstract:** Life histories of Atlantic cod (*Gadus morhua*) from the Gulf of St. Lawrence south to Georges Bank differ significantly through time and space. Within the Southern Gulf, fecundity per unit body mass differed by more than 40% over short (2 years) and long (42–45 years) periods of time. Significant variation in size-specific fecundity is also evident among populations: Southern Gulf cod produce almost 30% more eggs per unit body mass than those on Georges Bank, whereas fecundity of Scotian Shelf cod is almost half that of cod in Sydney Bight. Compared with those on Georges Bank, Southern Gulf cod life histories are characterized by high fecundity, late maturity, high gonadosomatic index, and large eggs. Relative to the influence of body size, neither temporal nor spatial differences in fecundity can be attributed to physiological condition, as reflected by liver weight, hepatosomatic index, and Fulton's *K*. Delayed maturity and higher reproductive allotment among Southern Gulf cod can be explained as selection responses to slower growth, higher prereproductive mortality, and fewer lifetime reproductive events. Patterns of covariation in heritable, fitness-related traits suggest the existence of adaptive variation and evolutionarily significant units at spatial scales considerably smaller than the species range in the Northwest Atlantic.

**Résumé :** Les cycles biologiques des morues franches (*Gadus morhua*) de l'Atlantique, depuis le golfe du Saint-Laurent jusqu'au banc Georges, diffèrent significativement dans le temps et dans l'espace. Dans la partie sud du golfe, la fécondité par unité de masse corporelle varie de plus de 40 % sur des périodes courtes (2 ans) et longues (42–45 ans). Des variations significatives de la fécondité reliée à la taille s'observent aussi entre les populations: les morues du sud du golfe produisent presque 30 % de plus d'oeufs par unité de masse corporelle que celles du banc Georges, alors que la fécondité des morues de la plate-forme néo-écossaise est presque la moitié de celle des morues de la baie de Sydney. Par comparaison aux cycles biologiques des morues du banc Georges, les cycles des morues du sud du golfe se caractérisent par une forte fécondité, une maturation tardive, un indice gonadosomatique élevé et de gros oeufs. Par comparaison à l'influence de la taille, la condition physiologique, telle que reflétée par la masse du foie, l'indice hépatosomatique et le *K* de Fulton, n'explique ni les différences spatiales, ni les différences temporelles de la fécondité. La maturation tardive et une allocation plus importante dans la reproduction chez les morues du sud du golfe peuvent s'expliquer comme des réactions sélectives à une croissance plus lente, une mortalité pré-reproductive plus importante et un nombre plus limité d'occasions de reproduction durant la vie. Les patterns de covariation des caractéristiques héritables reliées au fitness font croire à une variation adaptative et à l'existence d'unités évolutives significatives à des échelles spatiales considérablement plus petites que l'aire de répartition de l'espèce dans le nord-ouest de l'Atlantique.

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## Introduction

Fundamental to life history theory is the assumption that natural selection favours those patterns of covariation in life history traits that maximise individual fitness. As such, fitness can be represented by *r*, the intrinsic rate of natural increase, and defined as either the rate of spread of an allele or the fitness of a genotype (Roff 2002). In population biology, *r* refers to the rate of growth over time of the number of individuals within the same population. From a conservation perspective, when a population has been considerably reduced in size, the time required for recovery to former levels of abundance depends on that population's maximum rate of increase, $r_{max}$ (Hutchings 1999). Similarly, from a resource management perspective, $r_{max}$ is positively correlated with sustainable rates of exploitation (Myers et al. 1997). Thus, the question of how fitness, as reflected by an individual's life history, affects population growth rate is of considerable interest.

To explain why population growth rates might differ, one requires an understanding of the adaptive and nonadaptive basis for life history trait variation within and among populations. One also requires information on the degree to which life histories differ through time and across space. In this regard, an issue of increasing importance to marine conservation biology concerns the degree to which widely distributed, broadcast-spawning marine fish exist as single populations

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throughout a given contiguous range or as smaller evolutionarily significant units (ESUs), reflecting adaptation to environmental conditions at smaller geographical scales (Waples 1998). Importantly, if individual life histories, and the population growth rates that they determine, differ at spatial scales smaller than those identified by resource management plans and species recovery programmes, it is unlikely that the objectives of these programmes will be realised.

Within this context, our work centres on describing and assessing the adaptive significance of temporal and spatial variation in the life history of Atlantic cod (*Gadus morhua*) from several stocks in the Northwest Atlantic: Southern Gulf of St. Lawrence (Northwest Atlantic Fisheries Organization (NAFO) division 4T); Sydney Bight (NAFO division 4Vn); Eastern Scotian Shelf (NAFO divisions 4Vs and 4W); and Georges Bank (NAFO division 5Ze) (Fig. 1). The spatial scale of our analysis corresponds to a level at which statistically significant genetic variability among cod has been reported. Differences in allelic variability at several microsatellite DNA loci have been documented between cod from Southern Gulf and Eastern Scotian Shelf (Ruzzante et al. 2000) and between cod from Eastern Scotian Shelf and Georges Bank (Ruzzante et al. 1998), lending credence to the premise that our life history comparisons have been made at a scale at which the genetic exchange of individuals appears to be relatively low. Also, the spatial scale of our analysis of Northwest Atlantic cod expands that encompassed by Pinhorn's (1984) study of temporal differences in size-specific fecundity of Newfoundland cod.

Among life history traits, we focus on size-specific fecundity and other metrics of reproductive investment, such as allocation of body tissue to gonads, age and size at maturity, and egg size. In addition to providing insights into cod life history variability across biologically meaningful scales, the potential utility of this work is reflected by arguments that direct metrics of fecundity may provide more accurate predictions of recruitment than spawner biomass (Marshall et al. 1998). Quantifying spatial differences in fecundity – body size regressions, for example, allows one to evaluate the degree to which geographical differences in recruitment might be attributable to differences in the number of eggs produced per individual during spawning, while controlling for potential effects of condition and body mass.

We also quantify population differences in Fulton's *K* and hepatosomatic index (HSI), metrics of physiological condition thought to be reliable proxies for the effect of environmental change on individual energy content and reproductive potential (Kjesbu et al. 1998; Marshall et al. 1999; Lambert and Dutil 2000). To test the veracity of this hypothesis, we examined whether Fulton's *K*, HSI, and liver weight are important determinants of size-specific fecundity within populations of cod in the Northwest Atlantic. We conclude by describing spatial patterns of life history trait covariation and assessing their adaptive significance.

## Materials and methods

### Collection of samples

Ovaries containing ripening eggs were examined from prespawning cod obtained from random samples of mature and immature fish captured from Northwest Atlantic waters encompassing the Canadian Maritime provinces (Fig. 1). Compared with preceding stages of maturity, ripening ovaries are larger, taking up more than one-half of the body cavity, and the oocytes are opaque and creamy yellow-orange in colour, because of the accumulation of yolk. Before release from the ovary, these oocytes are hydrated, giving them a transparent appearance. We excluded ovaries containing oocytes at this final stage of development, given the possibility that some may have already been spawned.

Ovaries containing ripening eggs were sampled from cod obtained by bottom trawl from randomly chosen locations throughout each management unit. Those from Eastern Scotian Shelf ($n$ = 17 tows) and Georges Bank ($n$ = 27 tows) were collected in February and March 1999 and 2000, during the annual groundfish research surveys conducted by the Canadian Department of Fisheries and Oceans (DFO). In the Southern Gulf of St. Lawrence, ovaries containing ripening eggs were collected in July 1998 and 1999 from random samples of cod ($n$ = 23 tows) captured by fishermen engaged in a DFO-monitored Sentinel Fishery survey. Random samples from Sydney Bight were collected by one of us (T.M.M.) and by employees of the 4Vn Sentinel Fisheries Association from bottom-trawl surveys conducted under the auspices of the DFO, mainly in September of 1998 and 1999, with some samples obtained in July and August of both years ($n$ = 34 tows).

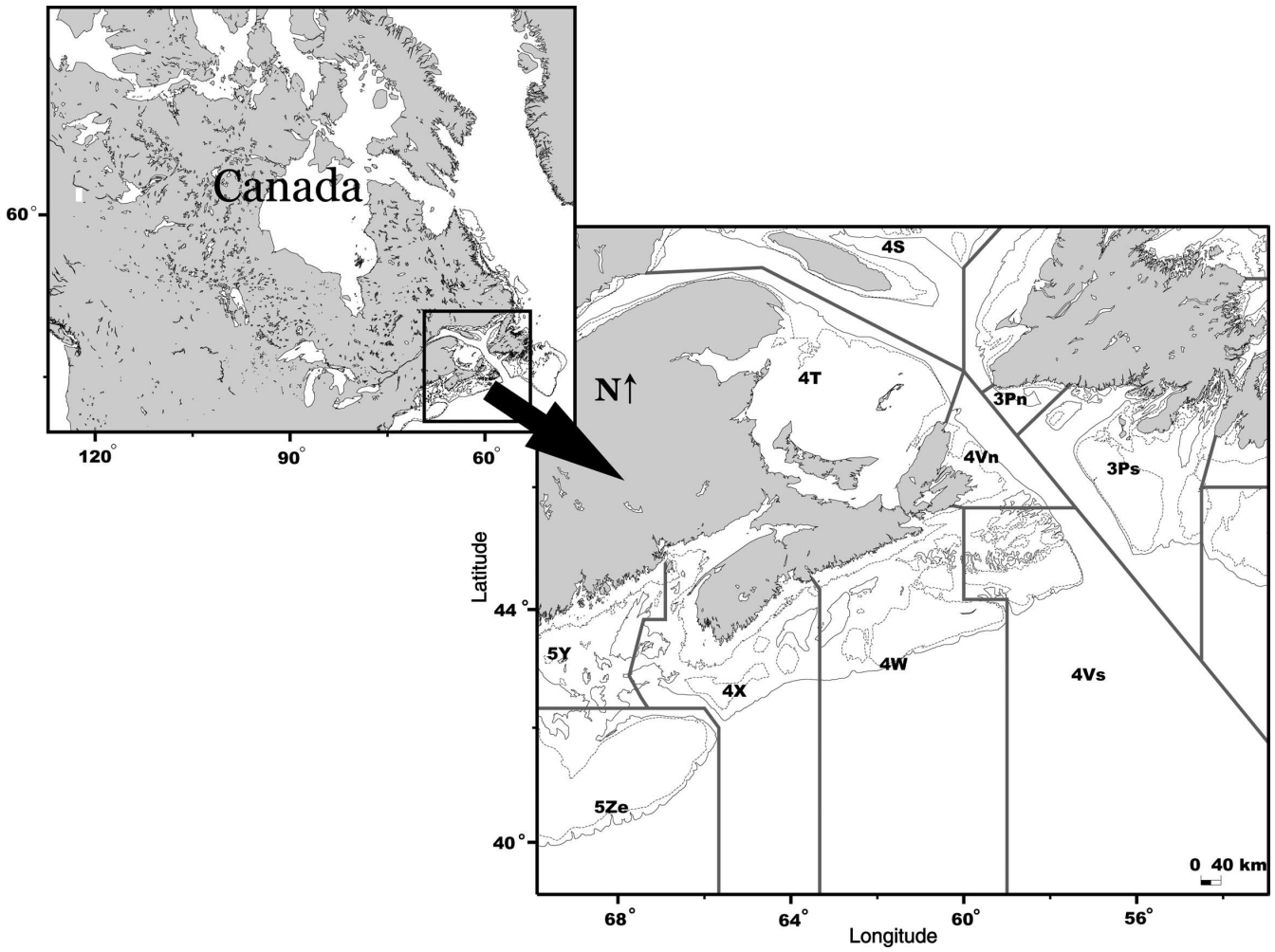
All samples were labelled and frozen until processed in the lab, whereafter detailed measurements and otoliths were obtained. The former included total length (nearest centimetre) and total weight (nearest gram) for fish sampled from all areas and liver and ovary weights (nearest 0.1 gram) for fish collected in the Southern Gulf of St. Lawrence and Sydney Bight. Ages were determined from otoliths by experienced DFO staff in Moncton and St. Andrews, N.B., and in Dartmouth, N.S.

### Estimation of fecundity and physiological condition

Following Buzeta and Waiwood (1982), ovaries were placed in glass jars containing Gilson's fluid (Snyder 1983), a chemical solution that degrades ovarian tissue without damaging oocytes. Jars were shaken periodically over a period of at least 12 weeks before ovarian tissue had been sufficiently degraded to allow for separation of the eggs. Ovaries too large to be fully contained in the glass jars were sectioned and weighed to the nearest 0.01 gram. For these samples, either one lobe of the ovary or the anterior portion of a lobe was excised from the entire ovary. Given that oocytes are homogeneously distributed throughout an ovary (Kjesbu 1988), the number of oocytes in one portion of an ovary should be comparable to the number of oocytes in another portion of an ovary of the same weight.

After the ovarian membrane and connective tissue had degraded to the extent that most oocytes were loose in the jars, the samples were washed through sieves of mesh sizes 1400 and 182 μm. The 1400-μm sieve retained most of the ovarian tissue, whereas the 182-μm sieve separated vitellogenic (mature) oocytes from previtellogenic (immature) oocytes. Our choice of mesh size was based on the Kjesbu et al.'s (1990) report that the onset of vitellogenesis occurs at an oocyte diameter of approximately 180 μm, an observation consistent with Morrison's (1990) description of cod gametogenesis.

**Fig. 1.** Life history data were obtained from Atlantic cod (*Gadus morhua*) sampled from four Northwest Atlantic Fishery Organization (NAFO) management divisions: Southern Gulf of St. Lawrence (NAFO Division 4T), Sydney Bight (4Vn), Eastern Scotian Shelf (4Vs and 4W), and Georges Bank (5Ze). The solid lines delineate the 200-m depth contour.




This mesh size is considerably smaller than those used by Buzeta and Waiwood (1982; 250 μm) and by Powles (1957, 1958; 212 μm) in their studies of the fecundity of Southern Gulf cod sampled in 1980 and 1955–1956, respectively. To estimate the degree to which the larger mesh sizes would have underestimated fecundity, we compared the weight of eggs that passed through mesh sizes of 182 and 253 μm for 24 randomly chosen ovaries of Southern Gulf cod sampled in 1998 and 1999. On average, 3.6% of the eggs (by weight) in an ovary retained by the smaller mesh passed through the larger mesh. Given that these eggs would have been the smallest in each ovary, the numerical reduction in fecundity would have been greater than 3.6%. As a consequence, we will have underestimated any differences in size-specific fecundity between cod sampled in the late 1990s with those sampled decades earlier.

It is possible that our means of preserving the gonads (they were frozen before preservation in Gilson's fluid) could affect our estimates of size-specific fecundity. If freezing is more likely to damage the chorion of small eggs than large eggs and if Gilson's fluid is more likely to destroy small eggs than large eggs, then our absolute estimates of fecundity per unit body mass will have been underestimated. To our knowledge, such effects of freezing and Gilson's fluid on small eggs have not been documented in the primary literature. On the other hand, given that Gilson's fluid is known to slightly increase average egg size (Tanfermin 1991), any potential losses of small eggs may have been countered by an increase in estimated fecundity resulting from retention of eggs that, in a fresh state, would have passed through our 180-μm mesh. In any event, even if our preservation method did introduce a bias, it will not qualitatively affect our results given that any bias would have been consistent among all samples.

After each sample had been cleaned, vitellogenic oocytes were transferred to a known volume of water in a 4000-mL beaker and placed on a stirring plate above which a hand drill, with a stirring stick attached, was positioned. The magnetic stirrer was operated in one direction while the drill was operated in the reverse direction. The combination of the two devices increased the agitation of the mixture and minimized the effect of centrifugal force. When the oocytes appeared to be homogeneously distributed throughout the beaker, a 1- or 2-mL subsample was removed with a Stempel pi-

pette. Oocytes in each of 3–5 subsamples per ovary were counted manually, using a binocular microscope.

Following Buzeta and Waiwood (1982) and Lambert and Dutil (2000), only those counts with a coefficient of variation (CV) of 10% or less were used in the data analysis. Fecundity (i.e., the number of vitellogenic oocytes) was estimated as

$$(1) \qquad F = F_{sub} \times V_{samp}/V_{sub} \times W_t/W_s$$

where $F_{sub}$ is the mean number of eggs in subsample, $V_{samp}$ is the volume (mL) of sample in the beaker, $V_{sub}$ is the volume (mL) of subsample, $W_t$ is the total weight (g) of ovaries, and $W_s$ is the weight (g) of ovary section processed. A total of 233 ovaries, all of which were at the same stage of gonadal development, met our CV criterion. Adding the 47 samples from Powles' (1957, 1958) work and the 30 samples from Buzeta and Waiwood's (1982) study, data from a total of 310 ovaries were available for analysis.

Two condition indices and one metric of reproductive allotment were calculated for each fish. Fulton's *K* was calculated by dividing the somatic body weight (total body weight minus the gonad weight) by body length cubed and then multiplying by 100. The hepatosomatic index, HSI, was calculated by dividing liver weight by total body weight (to allow for comparison with other studies, acknowledging that some authors use somatic weight alone) and multiplying by 100. The gonadosomatic index, GSI, which reflects the proportional allocation of body tissue to the gonads, is equal to the ovary weight divided by total body weight and multiplying by 100 (Wootton 1998).

### Statistical analysis

To model associations between fecundity and potential predictors of fecundity, we used a generalized linear model (GLM), incorporating a gamma response distribution coupled with a log-link function to connect the mean to the linear predictor(s) (Venables and Ripley 1998). In GLMs, the mean is modelled as a function of the covariates. As recommended by Venables and Ripley (1998), we used the gamma distribution to account for the increased variance in fecundity that we observed with increasing body size. The regression equation corresponding to this method, $Y = e^{ax+b}$, has a linear exponent. For some of the predictor variables examined here, for which no curvature in the fecundity data was observed across the range of explanatory variables, an identity link provided the best fit to the data. The regression equation corresponding to these GLMs was a simple linear expression, $Y = ax + b$. An analysis of covariance (ANCOVA) was used to test for annual differences in the slopes and intercepts of the fecundity – body size regressions within each population.

To assess the goodness-of-fit of each model, an analysis of deviance was used to identify the GLM that maximized the proportion of explained variation (PEV) in fecundity. To calculate the PEV, one compares the explained variation in the dependent variable before the addition of a predictor variable (null deviance) with the explained variation remaining in the model after the predictor variable has been added (residual deviance). The PEV for each fitted model is equal to (null deviance – residual deviance)/null deviance. Potential predictors of fecundity analysed here included body length, body weight, age, Fulton's *K*, liver weight, HSI, gonad weight, and GSI. Analyses of variance were used to test for differences in reproductive age, *K*, HSI, and GSI among populations. When appropriate, *p* values were corrected for multiple comparisons.

## Results

### Size at reproduction

The average size of Atlantic cod from which fecundity data were collected differed significantly among populations, being largest for cod on Georges Bank (79.4 ± 2.0 cm standard error, SE) and smallest for those on the Eastern Scotian Shelf (54.7 ± 1.8 cm) (Table 1).

Body size was the primary determinant of fecundity within the populations examined here, although the relative importance of size differed among years (Table 2). Of the two metrics of body size considered here, weight was generally a better predictor of fecundity than length. For Southern Gulf cod, weight explained 39% (1998 data) to 81% (1980 data) of the variation in fecundity. Weight also explained less variation in fecundity in 1998 for Sydney Bight cod (34%) than it did in 1999 (65%). Combining the 1998–2000 data for the relatively few ($n = 29$) mature cod sampled on Eastern Scotian Shelf, weight accounted for only 25% of the variation in fecundity. By comparison, weight accounted for large yet similar amounts of variation in fecundity for Georges Bank cod sampled in 1999 (77%) and 2000 (86%).

### Temporal variation in fecundity–size relationships

To examine short- and long-term changes to size-specific fecundity within a single population, our fecundity data for Southern Gulf cod sampled in 1998 and 1999 were compared with those reported by Powles (1957, 1958) and by Buzeta and Waiwood (1982) for Southern Gulf cod sampled in 1955 and 1956 and in 1980, respectively. Both weight and length data were available for the 1980 cod, whereas only length data were reported for cod sampled in the 1950s. To ensure that cod of the same body sizes were compared in the ANCOVA, the weight range was limited to between 1800 and 8100 g, and the length range was limited to between 56 and 95 cm.

Size-specific fecundity of Southern Gulf cod differed over both short (2 years) and long (42–45 years) periods of time (Fig. 2). Although there was no significant difference in the slopes of either the fecundity–length and fecundity–weight regressions ($p > 0.6$ for all regressions), the ANCOVA indicated significant differences in the intercepts ($p < 0.0001$). Upon closer examination, the intercepts of the 1998 fecundity–size regressions were significantly less than those fitted to data for the other years (fecundity–length regression, $p < 0.01$; fecundity–weight regression, $p < 0.002$). Comparing the estimated fecundity for 70-cm cod (using the regressions presented in Table 2), Southern Gulf cod sampled in 1998 produced 775 000 eggs on average compared with 1.1 million eggs produced by the average 70-cm cod during the other time periods (1955–1956, 1980, 1999).

For cod inhabiting Georges Bank and Sidney Bight (there were insufficient data to undertake a temporal comparison for Eastern Scotian Shelf cod), neither the slopes nor the

**Table 1.** Metrics of life history and physiological condition within four populations of Northwest Atlantic cod.

| Population | Year | Length (cm) | Age (years) | GSI (%) | Fulton's *K* | HSI (%) | Relative egg size (mg) |
|---|---|---|---|---|---|---|---|
| Southern Gulf | 1955–1956 | 81.7±3.1 | 8.8±0.4 | | — | — | — |
| | | (*n* = 47) | (*n* = 44) | | | | |
| | 1980 | 73.4±3.1 | — | 11.7±0.7 | 0.90±0.02 | — | 0.34±0.03 |
| | | (*n* = 30) | | (*n* = 30) | (*n* = 30) | | (*n* = 30) |
| | 1998 | 72.7±1.5 | 9.6±0.2 | 15.1±0.6 | 0.90±0.02 | 5.1±0.2 | 0.57±0.04 |
| | | (*n* = 35) | (*n* = 33) | (*n* = 35) | (*n* = 35) | (*n* = 35) | (*n* = 23) |
| | 1999 | 60.7±2.6 | 7.4±0.3 | 13.0±0.9 | 0.86±0.01 | 3.3±0.4 | 0.50±0.04 |
| | | (*n* = 30) | (*n* = 30) | (*n* = 30) | (*n* = 30) | (*n* = 30) | (*n* = 27) |
| | All years | 73.3±1.5 | 8.6±0.2 | 13.6±0.4 | 0.89±0.01 | 4.3±0.2 | 0.46±0.02 |
| | | (*n* = 142) | (*n* = 107) | (*n* = 95) | (*n* = 95) | (*n* = 65) | (*n* = 80) |
| Sydney Bight | 1998 | 59.8±1.8 | 7.3±0.6 | 7.5±0.9 | 0.97±0.02 | 5.6±0.6 | 0.23±0.04 |
| | | (*n* = 27) | (*n* = 10) | (*n* = 26) | (*n* = 27) | (*n* = 27) | (*n* = 26) |
| | 1999 | 58.1±1.9 | 7.5±0.6 | 6.7±0.5 | 0.89±0.03 | 4.3±0.4 | 0.17±0.02 |
| | | (*n* = 16) | (*n* = 15) | (*n* = 16) | (*n* = 16) | (*n* = 16) | (*n* = 16) |
| | All years | 59.2±1.3 | 7.4±0.4 | 7.2±0.6 | 0.94±0.02 | 5.1±0.4 | 0.21±0.02 |
| | | (*n* = 43) | (*n* = 25) | (*n* = 42) | (*n* = 43) | (*n* = 43) | (*n* = 42) |
| Eastern Scotian Shelf | 1998, 1999 | 55.3±4.2 | 8 | 8.1±1.1 | 0.76±0.02 | 2.9±1.0 | 0.30±0.06 |
| | | (*n* = 10) | (*n* = 1) | (*n* = 10) | (*n* = 10) | (*n* = 2) | (*n* = 9) |
| | 2000 | 54.4±1.8 | 5.1±0.2 | 6.5±0.9 | 0.81±0.02 | 3.6±0.3 | 0.24±0.06 |
| | | (*n* = 19) | (*n* = 19) | (*n* = 19) | (*n* = 19) | (*n* = 7) | (*n* = 19) |
| | All years | 54.7±1.8 | 5.2±0.2 | 7.1±0.7 | 0.79±0.02 | 3.4±0.3 | 0.26±0.04 |
| | | (*n* = 29) | (*n* = 20) | (*n* = 29) | (*n* = 29) | (*n* = 9) | (*n* = 28) |
| Georges Bank | 1999 | 74.0±2.7 | 5.0±0.3 | 11.9±1.2 | 0.94±0.01 | — | 0.40±0.03 |
| | | (*n* = 56) | (*n* = 50) | (*n* = 55) | (*n* = 55) | | (*n* = 49) |
| | 2000 | 86.7±2.6 | 6.3±0.3 | 11.5±0.4 | 0.99±0.01 | — | 0.37±0.02 |
| | | (*n* = 41) | (*n* = 40) | (*n* = 41) | (*n* = 41) | | (*n* = 41) |
| | All years | 79.4±2.0 | 5.6±0.2 | 11.7±0.7 | 0.96±0.01 | — | 0.39±0.02 |
| | | (*n* = 97) | (*n* = 90) | (*n* = 96) | (*n* = 96) | | (*n* = 90) |

**Note:** GSI, gonadosomatic index (gonad weight/total body weight); *K*, somatic weight/length$^3$; HSI, hepatosomatic index (liver weight/total body weight). Data are means ± standard error.

intercepts of the fecundity–size regressions differed over the 2-year time periods for which data were available (Fig. 3).

### Spatial variation in fecundity–size relationships

Size-specific fecundity differed significantly among Atlantic cod populations, as reflected by differences in the slopes and intercepts of the fecundity–size regressions. To examine spatial differences in fecundity by ANCOVA (using population as the factor variable), the yearly data were pooled for each population (the 1998 data were excluded for Southern Gulf cod given the aforementioned differences in the regression for this year). Given the significant effects of length on fecundity (Table 2) and to allow for inclusion of Powles' (1957, 1958) data, our spatial analysis was restricted to the fecundity–length relationships alone. The ANCOVA could not be used to compare all of the populations in a single analysis because the models that provided the best fit to the size and fecundity data did not have the same form for each population, being exponential for Southern Gulf and Georges Bank cod but linear for the Eastern Scotian Shelf and Sydney Bight populations.

Although there were no differences in regression slopes, significant differences in the intercepts of the fecundity–length regressions ($p < 0.01$) revealed differences in size-specific fecundity between the northern- and southern-most populations considered in our study. Comparing the estimated fecundity of 70-cm cod, size-specific fecundity of Southern Gulf cod (1.1 million eggs) was 27% higher than that estimated for Georges Bank cod (866 000 eggs). By contrast, the slopes of the fecundity–size regressions for Eastern Scotian Shelf and Sydney Bight cod differed from one another, the rate at which fecundity increased with length being greater for Sydney Bight cod than for cod on Eastern Scotian Shelf.

### Age at reproduction

The average age of fish from which ripe ovaries were sampled tended to decline with latitude (Table 1). For cod sampled between 1998 and 2000, the youngest age at reproduction declined from 5 and 4 years for Southern Gulf and Sydney Bight cod, respectively, to 3 and 2 years for cod on Eastern Scotian Shelf and Georges Bank, respectively. Comparing the mean age of reproductive cod from the northern- and southern-most populations examined here, Georges Bank females were significantly younger (5.6 ± 0.2 years) than those in the Southern Gulf (8.6 ± 0.2 years) ($p < 0.001$). Similarly, the incidence of reproduction among cod younger than 5 years was 36.7% among Georges Bank females compared with <1% for Southern Gulf cod.

Although age had lower explanatory power than either body length or weight, it did account for a significant amount of variation in fecundity in three of four populations, ex-

**Table 2.** Regression model parameter estimates for fecundity–size relationships within four populations of Atlantic cod.

| Population | Year(s) | *n* | Size variable | Model | Slope | Intercept | PEV | *p* |
|---|---|---|---|---|---|---|---|---|
| Southern Gulf | 1955, 1956 | 47 | Length | E | 0.036 | 11.52 | 0.70 | <0.0001 |
| | 1980 | 30 | Weight | E | 0.0002 | 13.02 | 0.81 | <0.0001 |
| | | | Length | E | 0.046 | 10.86 | 0.78 | <0.0001 |
| | 1998 | 35 | Weight | E | 0.0003 | 12.59 | 0.39 | 0.0001 |
| | | | Length | E | 0.043 | 10.55 | 0.37 | <0.0001 |
| | 1999 | 30 | Weight | E | 0.0004 | 12.23 | 0.66 | <0.0001 |
| | | | Length | E | 0.060 | 9.66 | 0.71 | <0.0001 |
| | 1980, 1999 | 60 | Weight | E | 0.0003 | 12.62 | 0.72 | <0.0001 |
| | 1955, 1956, 1980, 1999 | 107 | Length | E | 0.044 | 10.83 | 0.73 | <0.0001 |
| Sydney Bight | 1998 | 27 | Weight | L | 346.64 | 11 099 | 0.34 | 0.0018 |
| | | | Length | L | 36 530 | –1 362 418 | 0.38 | 0.0005 |
| | 1999 | 16 | Weight | L | 393.04 | 28 035 | 0.65 | <0.0001 |
| | | | Length | L | 37 625 | –1 400 390 | 0.63 | 0.0002 |
| | 1998, 1999 | 43 | Weight | L | 352.93 | 38 127 | 0.39 | <0.0001 |
| | | | Length | L | 36 983 | –1 379 115 | 0.43 | <0.0001 |
| Eastern Scotian Shelf | 1998–2000 | 29 | Weight | L | 240.86 | 83 046 | 0.25 | 0.0038 |
| | | | Length | L | 16 517 | –466 525 | 0.28 | 0.0025 |
| Georges Bank | 1999 | 55 | Weight | L | 321.24 | –143 687 | 0.77 | <0.0001 |
| | | | Length | E | 0.056 | 9.70 | 0.73 | <0.0001 |
| | 2000 | 41 | Weight | L | 340.44 | –94 437 | 0.86 | <0.0001 |
| | | | Length | E | 0.042 | 11.00 | 0.82 | <0.0001 |
| | 1999, 2000 | 96 | Weight | L | 336.03 | –153 199 | 0.80 | <0.0001 |
| | | | Length | E | 0.052 | 10.03 | 0.75 | <0.0001 |

**Note:** E, exponential model ($Y = e^{ax+b}$); L, linear model ($Y = ax + b$); PEV, percentage explained variation.

plaining 23% ($p < 0.0001$), 26% ($p = 0.006$), and 53% ($p < 0.0001$) of the variation in fecundity for Southern Gulf, Sydney Bight, and Georges Bank cod, respectively.

### Effects of condition on fecundity

Physiological condition, as reflected by Fulton's *K* and the hepatosomatic index (HSI), differed by varying degrees within and among populations. For the Southern Gulf, the only population for which a long-term temporal comparison was possible, Fulton's *K* did not differ significantly among cod sampled in 1980, 1998, and 1999 (Table 1). However, significant differences were evident among populations ($p < 0.001$), being lowest for Eastern Scotian Shelf cod (0.79 ± 0.02) and highest for cod on Georges Bank (0.96 ± 0.01). Comparing the relative size of the livers, the HSI of Southern Gulf cod was significantly lower in 1999 (the year of higher size-specific fecundity) than it was in 1998 ($p < 0.0001$), although there were no differences in HSI for Sidney Bight cod between the same years.

To examine the effects of condition on egg number per female, Fulton's *K* and HSI were added separately to the fecundity – body size GLM regressions to determine whether they explained a significant amount of variation in fecundity additional to that attributed to body length or weight alone. Georges Bank was the only population for which Fulton's *K* explained a significant amount of variation in fecundity in addition to that explained by body size (length). However, although the statistical significance was high ($p < 0.0001$), biologically the increase in explained variation was only 3% above the 75% explained by length alone. Notably, the amount of variation in fecundity explained by weight alone (80%) in Georges Bank cod exceeded the combined variation explained by length and Fulton's *K*.

In general, neither the proportional nor absolute weights of the liver were correlated with fecundity. The HSI, measured at the time of spawning, was not significantly associated with fecundity within either of the two years during which cod were sampled from the Southern Gulf and Sidney Bight. To assess the potential influence of HSI several months before spawning, we examined data on liver weights obtained for 18 Southern Gulf cod of sizes similar to those sampled during the summer of 1999, caught in the autumn of 1998 by the Department of Fisheries and Oceans (G. Chouinard, Department of Fisheries and Oceans, P.O. Box 5030, Moncton, NB E1C 9B6, Canada, personal communication). Although HSI from cod sampled in September 1998 was significantly related to the fecundity of cod sampled the following July, the PEV (0.21) for this fecundity–HSI relationship was much less than the variation explained by weight and length alone in 1999 (0.66 and 0.71, respectively). When the HSI for cod sampled in September 1998 was added to the fecundity–weight and fecundity–length models for cod sampled in 1999, the increase in PEV was not statistically significant.

When either body weight or length was combined with liver weight as predictors of fecundity for Sydney Bight and Southern Gulf (1999) cod, the explained variation did not increase significantly beyond the PEV of fish weight or length alone ($p > 0.39$). Liver weights of Southern Gulf cod sampled in 1998 explained marginally more variation in fecundity (identity link model: PEV = 0.44) than either fish length (PEV = 0.37) or fish weight (PEV = 0.39) alone; addition of fish length or weight to the fecundity – liver weight model

**Fig. 2.** Associations between log(fecundity) and (*a*) body length and (*b*) total body weight for female Atlantic cod (*Gadus morhua*) in the Southern Gulf of St. Lawrence. In Fig. 2*a*, the solid line represents data pooled from 1955, 1956, 1980, and 1999 and the broken line represents data from 1998 only. In Fig. 2*b*, the solid line represents data pooled from 1980 and 1999 and the broken line represents data from 1999 only. Symbols: squares, 1955 and 1956; circles, 1980; triangles, 1998; crosses, 1999.

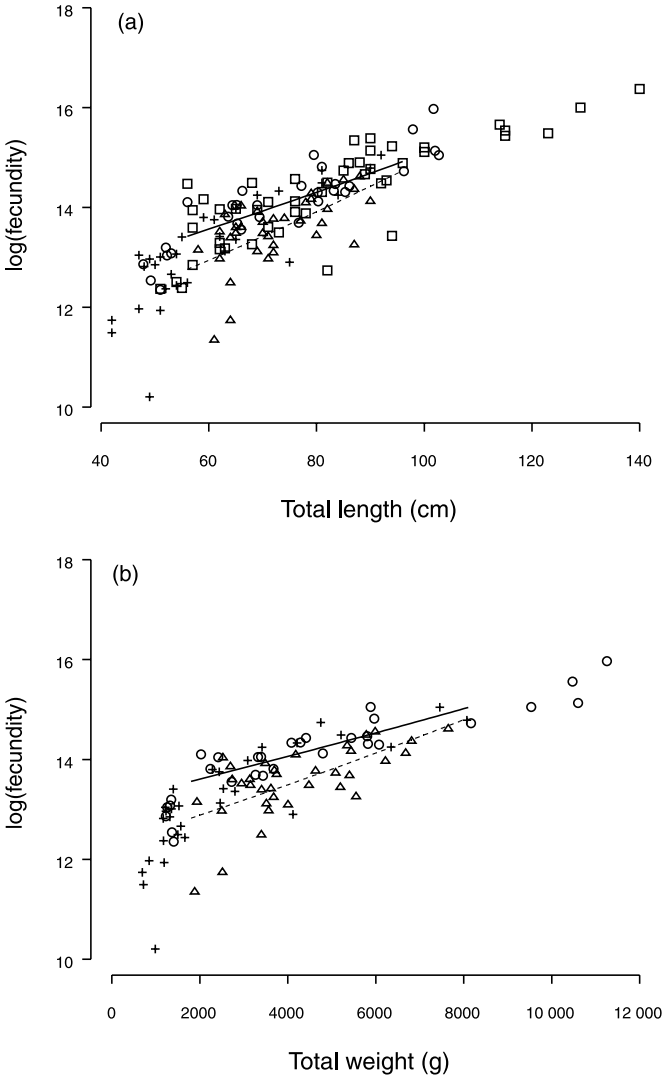
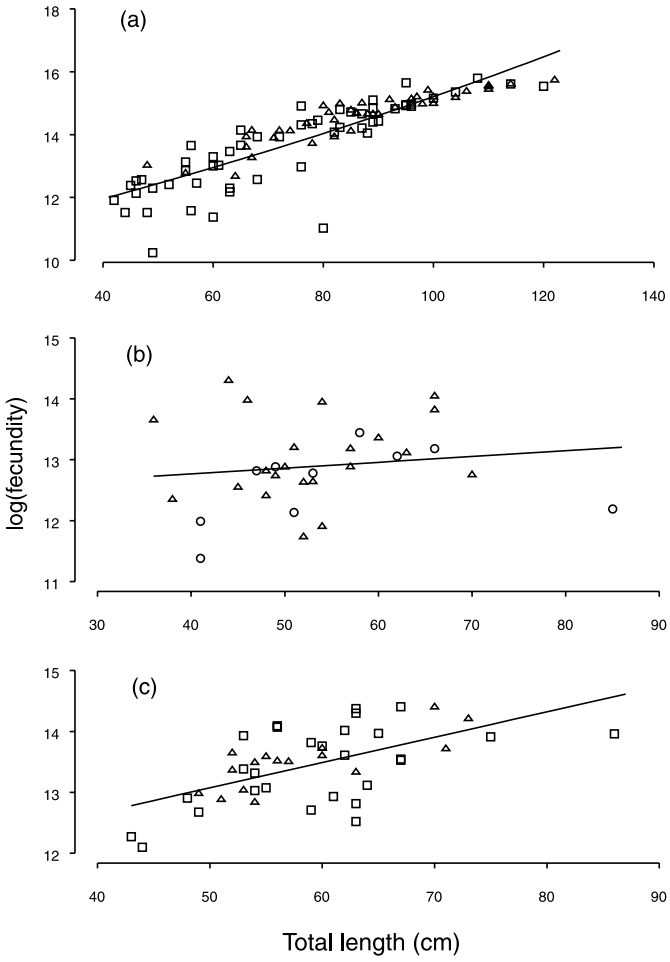



**Fig. 3.** Associations between log(fecundity) and total body length within three populations of female Atlantic cod (*Gadus morhua*): (*a*) George Bank (squares, 1999; triangles, 2000); (*b*) Eastern Scotian Shelf (circles, 1998 and 1999; triangles, 2000); (*c*) Sydney Bight (squares, 1998; triangles, 1999).



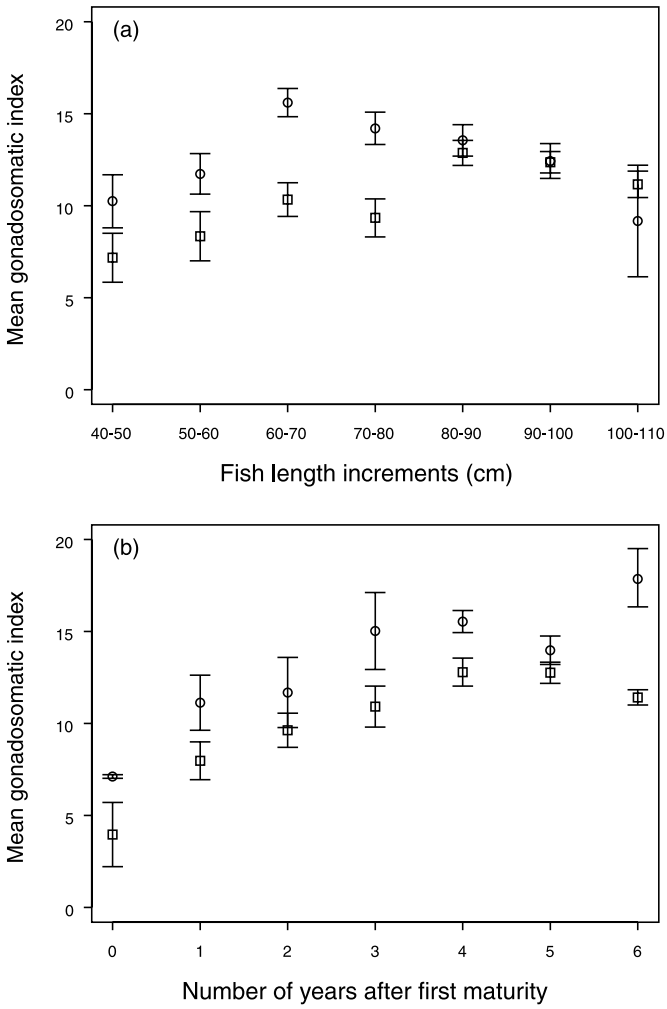

did not significantly increase the amount of explained variation ($p > 0.05$).

## Gonadosomatic index

The proportional allocation of body tissue to the gonads, for individuals whose ovaries were at the same developmental stage, differed significantly among years in the Southern Gulf of St. Lawrence and among populations in the Northwest Atlantic (Table 1). Within the Southern Gulf, the average GSI of cod sampled in 1998 (15.1 ± 0.6%) was significantly ($p = 0.0007$) greater, despite having a lower size-specific fecundity, than that of cod sampled in 1980 (11.7 ± 0.7%). Among populations, the GSI was lowest for Eastern Scotian Shelf (7.1 ± 0.7%) and Sydney Bight cod (7.2 ± 0.6%), which corresponded with their lower size-specific fecundity at the population level. Comparing cod from the northern- and southern-most populations, the GSI of Georges Bank cod (11.7 ± 0.7%) was significantly ($p < 0.001$) lower than that of cod sampled from the Southern Gulf (13.6 ± 0.4%) (Table 1). Controlling for body size and parity (approximated by the potential number of annual reproductive events), GSI was higher for Southern Gulf cod than it was for cod on Georges Bank (Fig. 4)

When used as a predictor of fecundity in the generalized linear model, GSI was significantly related to fecundity only for cod on Georges Bank (PEV = 0.205; $p < 0.0001$). However, fish weight alone explained much more variation in the model than GSI, and the addition of GSI to the fecundity – fish weight model did not significantly increase the PEV of the model ($p > 0.2$). Although ovary weight was significantly associated with fecundity in all areas (PEV ranging between 0.21 and 0.68; $p < 0.004$) except Eastern Scotian Shelf ($p = 0.50$), the amount of variation in fecundity ex-

**Fig. 4.** Gonadosomatic index ((gonad weight/total body weight) × 100%; ±1 standard error) of female Atlantic cod (*Gadus morhua*) on Georges Bank (squares) and Southern Gulf of St. Lawrence (circles) as functions of (*a*) total body length and (*b*) number of years after the earliest observed age at reproduction within each population.




plained by ovary weight was always less than that explained by body weight or body length alone.

### Egg size

Average relative egg size per female was measured by dividing total ovary weight by egg number within females with ovaries at the same stage of development (see Materials and methods), a calculation that will underestimate actual egg weight because of the inclusion of unknown amounts of gonadal tissue in the numerator. Relative egg size differed significantly among populations ($p < 0.001$), being smallest for Scotian Shelf and Sydney Bight cod (Table 1). Comparing the northern- and southern-most populations, Southern Gulf cod produce significantly larger eggs than cod from Georges Bank cod ($p = 0.014$).

## Discussion

Life histories of Northwest Atlantic cod differ at relatively small scales through time and space. Within the Southern Gulf population, average fecundity per unit body mass varied significantly over short (2 years) and long (42–45 years) periods of time, differing by more than 40% among years. Indeed, given that the mesh size used to separate the relatively large vitellogenic oocytes from the smaller previtellogenic oocytes was smaller than those used in previous work (Powles 1957, 1958; Buzeta and Waiwood 1982), the reduction in size-specific fecundity that we document here for Southern Gulf cod in the late 1990s, relative to that recorded decades earlier, has almost certainly been underestimated. Spatially, significant variation in size-specific fecundity was also evident among populations. Southern Gulf cod produce almost 30% more eggs per unit body mass than those on Georges Bank, whereas the fecundity of Eastern Scotian Shelf cod is about half that of cod in Sydney Bight. In general, relative to the influence of body size, neither temporal nor spatial differences in fecundity can be attributed to individual differences in physiological condition, as reflected by the hepatosomatic index and Fulton's *K*. However, patterns of covariation in several life history traits (including age and size at maturity, reproductive allotment, egg size, and growth rate) are consistent with those predicted by life history theory. We suggest that spatial differences in heritable fitness-related traits among cod populations, previously demonstrated to be genetically distinguishable, is consistent with the hypothesis of adaptation to local environments.

### Temporal variation in size-specific fecundity

The substantive temporal differences in fecundity documented here for Southern Gulf of St. Lawrence cod appear to be similar to those documented elsewhere. For females 70 cm in length, size-specific fecundity differed 42% between the two time periods for which significant differences in length–fecundity regressions existed (period 1, 1998; period 2, 1955/1956, 1980, 1999). Based on fecundity estimates presented by Marteinsdottir and Begg (2002) for 70-cm cod, the temporal difference reported here for Southern Gulf cod might in fact be deemed low, given the 106% and 76% annual differences reported for Icelandic and Northeast Arcto-Norwegian cod, respectively. However, these latter two percentages may unduly overestimate temporal variability in size-specific fecundity within these populations, given that the years in which fecundity–length regressions did not differ from one another was not reported for either of these stocks. For example, even though there was no statistical difference between the Southern Gulf cod fecundity–length regressions for the years 1955–1956, 1980, and 1999, the estimated fecundity of a 70-cm cod ranged between 1.045 million and 1.303 million eggs. Using the high annual estimate of 1.303 million and comparing it with the estimate for 70-cm cod in 1998 (775 000), one would have concluded that size-specific fecundity differed 68%, rather than the more statistically defensible 42%, among years.

We are unable to identify the specific environmental factors responsible for temporal differences in size-specific fecundity of Southern Gulf cod. Although water temperature has been implicated as contributing to temporal and spatial variability in fecundity among cod off Newfoundland (Pinhorn 1984) and in the Baltic (Kraus et al. 2000), temperatures in the Southern Gulf did not differ appreciably between 1998 and 1999 (Drinkwater et al. 2001). Nonetheless,

it is important to recognise that such short-term variability in size–fecundity can exist (Marteinsdottir and Begg 2002; present study) and that population demography is likely to be affected as a result. The potential consequences of such interannual variability in reproductive allotment to recruitment underscores the importance of quantifying the effects of fecundity on year-class strength (Marshall et al. 1999; Köster et al. 2000) and draws attention to a potential source of nonstationarity in stock–recruitment relationships (Walters and Korman 2001).

### Causes of temporal variation in size-specific fecundity: a critique

With one exception (liver weight explained 5% more variation in fecundity than body weight among Southern Gulf cod in 1998), body size was the best predictor of fecundity within all populations, explaining significantly more variation than age, Fulton's *K*, HSI, liver weight, and ovary weight, none of which significantly increased the explained variation in fecundity when included in either fecundity–length or fecundity–weight regression models.

Although it is not unreasonable to expect metrics of condition to be associated with fecundity, it is important that one be able to distinguish the statistical, and biological, influence of these metrics on female egg number from the effect of body size alone. Kjesbu et al. (1998), for example, reported that liver weight, when added as an explanatory variable to a fecundity–length regression for Northeast Arctic cod, contributed significantly to fecundity. Yet the variation in fecundity explained by both of these variables ($r^2$ = 0.93) was not significantly greater than that explained by fish length alone ($r^2$ = 0.92) and was less than that explained by fish weight alone ($r^2$ = 0.94). In a laboratory study of Northern Gulf of St. Lawrence cod, Lambert and Dutil (2000) reported that Fulton's *K*, measured at the time of spawning, accounted for 14–23% of the variation in fecundity and egg dry weight in addition to the 49–51% explained by length alone. Unfortunately, these authors did not report the variation in fecundity accounted for by body weight alone, which often explains more of the variation in fecundity than length (Wootton 1998), nor did they account in their regression models for the fact that *K* and length are not independent of one another, thus inflating the variation in fecundity explained by *K* (a statistical deficiency common to much of the work in this area). Recently, Marteinsdottir and Begg (2002) reported a statistically significant influence of HSI on fecundity in Icelandic cod. Although they did not report the explained variance in fecundity attributable to HSI, based on their sums of squares table (table 6 in Marteinsdottir and Begg 2002), it appears that liver condition explained 3%, or less, of the variation in fecundity in addition to that explained by body size alone.

We do not wish to suggest that condition does not influence fecundity. As decades of life history research have revealed, the existence of physiological precursors to, and costs associated with, reproduction is one of the fundamental premises of life history theory (Wootton 1998; Roff 2002). However, the present study does raise questions concerning the ubiquity of condition effects on fecundity, the degree to which field data can be used to quantify accurately such effects, the biological and environmental conditions under which such effects might be most evident, and the influence of condition on fecundity per se relative to its effect on other facets of reproduction, such as behaviour.

As noted above, the lack of influence noted here may reflect the difficulty in determining the time of year, or indeed the age, at which the effect of body condition on fecundity is greatest. For example, based on field data collected by Eliassen and Vahl (1982), condition may have its greatest effect on fecundity 4–6 months before spawning, the period when cod are accumulating energy before reproduction. Also, just before spawning, cod ovaries contain oocytes that will be spawned in both the current and subsequent spawning seasons (Kjesbu et al. 1990), suggesting that the number of oocytes produced each year is determined at least 1 year, and possibly 2 years, before reproduction. In addition, failure to detect a strong influence of condition on fecundity would not be surprising if the proportional allocation of a female's gonads to present and future spawning events differed within and among populations (which it almost certainly does). Thus, any effect of condition on fecundity may be greatest not during the current spawning season but on subsequent spawning seasons (Kjesbu et al. 1996; Schwalme and Chouinard 1999).

In addition to the interpretive and inferential limitations raised above, lack of association between condition and fecundity may reflect a diminishing effect of condition above some threshold level, indicative of an asymptotic association between fecundity and condition. If so, a biologically relevant influence of condition on fecundity would not be realised unless condition fell below that threshold. Based on recruitment data for Northeast Arctic cod reported by Marshall et al. (1999), such a threshold for HSI may be approximately 6%. However, we note that the HSI values for Southern Gulf and Sydney Bight cod in 1998 and 1999 (ranging from 3.3% to 5.6%) were all below this threshold estimate. Although Marshall et al.'s (1999) data were averages of monthly values for a particular length class of cod, their findings lead us to conclude that the range in HSI documented here should have been within the range at which HSI might be predicted to have its strongest influence on fecundity.

Notwithstanding the apparent lack of influence of condition on fecundity reported here and elsewhere (Ma et al. 1998; Kraus et al. 2000), condition may still be an important determinant of recruitment (Marshall et al. 1999). But rather than affecting the number of eggs that a female produces, the primary effect of condition on offspring production may well be realised through spawning behaviour. This is supported by the observation that more than half of the lipid losses resulting from reproduction can be attributed to nongonadal tissues in the few fishes for which such an effect has been examined, e.g., Atlantic salmon, *Salmo salar* (Jonsson et al. 1991), and brook trout, *Salvelinus fontinalis* (Hutchings et al. 1999).

### Adaptive significance of spatial differences in life history trait covariation

Northwest Atlantic cod life histories differ significantly across relatively small geographic scales. Based on the data presented here for cod inhabiting the waters of the Southern Gulf, Sidney Bight, Eastern Scotian Shelf, and Georges Bank, population differences in life history are reflected by among-

population variation in age and size at maturity, reproductive allotment, fecundity, egg size, and individual growth rate, fitness-related traits known to be heritable in fishes (Wootton 1998; Roff 2002).

A comparison of cod from the southern and northern geographical limits of the present study reveals consistent patterns of covariation in several life history traits. Relative to females in the Southern Gulf, Georges Bank cod mature earlier in life, produce fewer and smaller eggs per unit of body mass, and allocate proportionately less of their body tissue to gonads. But despite maturing at considerably different ages, there are few differences in size at maturity between populations. Based on data collected in the present study, minimum size at maturity was equal (42 cm), as were the 25% quartile lengths at reproduction (62–63 cm), suggesting that Georges Bank cod experience significantly faster rates of growth than Southern Gulf cod.

These patterns of trait covariation are consistent with expectations based on life history theory; as such, they can be explained as adaptive responses by cod to their local environments. Compared with Georges Bank females, Southern Gulf cod take longer (about 3 years longer) to reach a size at which reproduction is possible, because of their slower growth rate, meaning that Southern Gulf cod almost certainly experience higher cumulative mortality than Georges Bank cod during the prereproductive phase of life. All else being equal, once Southern Gulf cod reach maturity, their probability of survival to death will be less than that for Georges Bank cod. In response to this higher mortality before reproduction and to an expected fewer number of lifetime reproductive events, theory would predict that Southern Gulf cod would expend greater reproductive effort during spawning (Roff 2002), a prediction borne out by higher size-specific fecundity and GSI.

Based on a series of recent geographical comparisons of fitness-related traits in north temperate marine fish, it is becoming evident that adaptive variation can exist at spatial scales considerably smaller than previously thought. For Northwest Atlantic cod, genetic differences have been documented in growth rate and food conversion efficiency (Purchase and Brown 2001), in antifreeze proteins (Goddard et al. 1999), and in the influence of light intensity on growth and survival in early life (Puvanendran and Brown 1998). Among Northeast Atlantic marine fishes, such as Atlantic halibut (*Hippoglossus hippoglossus*) and turbot (*Scophthalmus maximus*), there is similar evidence for genetic differences in growth rate and feeding efficiency among geographically disparate populations (Imsland et al. 2000; Jonassen et al. 2000).

Differences in Atlantic cod life history can be expected to manifest themselves at the population level as differences in $r_{max}$, the parameter of primary importance when assigning sustainable rates of harvest and when evaluating the conservation status and extinction probability of depleted populations (Hutchings 2003). The finding that life histories can vary across relatively small geographical scales is germane to the issue of whether evolutionarily significant substructuring exists among Atlantic cod populations in the Northwest Atlantic. Given that significant genetic differences have been detected among Atlantic cod populations at spatial scales similar to, or smaller than, those of the present study (Ruzzante et al. 1998; Pogson et al. 2001), the patterns of covariation among heritable traits documented here are consistent with the hypothesis that this species exists in the Northwest Atlantic as multiple, locally adapted populations at spatial scales considerably smaller than the range of the species. The challenge to marine population ecologists and geneticists will be in delineating these population boundaries.

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## References

Buzeta, M.I., and Waiwood, K.G. 1982. Fecundity of Atlantic cod (*Gadus morhua*) in the Southwestern Gulf of St. Lawrence. Can. Tech. Rep. Fish. Aquat. Sci. No. 1110.

Drinkwater, K.F., Pettipas, R.G., and Petrie, D.M. 2001. Physical environmental conditions in the southern Gulf of St. Lawrence in 2000. Can. Sci. Advis. Secret. Res. Doc. 2001/053.

Eliassen, J.-E., and Vahl, O. 1982. Seasonal variations in biochemical composition and energy content of liver, gonad and muscle of mature and immature cod, *Gadus morhua* (L.), from Balsfjorden, northern Norway. J. Fish Biol. **20**: 707–716.

Goddard, S.V., Kao, M.H., and Fletcher, G.L. 1999. Population differences in antifreeze production cycles of juvenile Atlantic cod (*Gadus morhua*) reflect adaptations to overwintering environment. Can. J. Fish. Aquat. Sci. **56**: 1991–1999.

Hutchings, J.A. 1999. The influence of growth and survival costs of reproduction on Atlantic cod, *Gadus morhua*, population growth rate. Can. J. Fish. Aquat. Sci. **56**: 1612–1623.

Hutchings, J.A. 2003. Update COSEWIC status report on Atlantic cod *Gadus morhua* in Canada. *In* COSEWIC assessment and status report on the Atlantic cod *Gadus morhua* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.

Hutchings, J.A., Pickle, A., McGregor-Shaw, C.R., and Poirier, L. 1999. Influence of sex, body size, and reproduction on overwinter lipid depletion in brook trout. J. Fish Biol. **55**: 1020–1028.

Imsland, A.K., Foss, A., Nævdal, G., Cross, T., Bonga, S.W., van Ham, E.H., and Stefansson, S.O. 2000. Countergradient variation in growth and food conversion efficiency of juvenile turbot. J. Fish Biol. **57**: 1216–1226.

Jonassen, T.M., Imsland, A.K., FitzGerald, R., Stefánsson, M.Ö., Bonga, S.W., van Ham, E., Nævdal, G., and Stefansson, S.O. 2000. Geographic variation in growth and food conversion effi-

ciency of juvenile Atlantic halibut related to latitude. J. Fish Biol. **56**: 279–294.

Jonsson, N., Jonsson, B., and Hansen, L.P. 1991. Energetic cost of spawning in male and female Atlantic salmon (*Salmo salar* L.). J. Fish Biol. **39**: 739–744.

Kjesbu, O.S. 1988. Fecundity and maturity of cod (*Gadus morhua* L.) from Northern Norway. ICES CM 1988/G:28.

Kjesbu, O.S., Witthames, P.R., Solemdal, P., and Greer Walker, M. 1990. Ovulatory rhythm and a method to determine the stage of spawning in Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **47**: 1185–1193.

Kjesbu, O.S., Solemdal, P., Bratland, P., and Fonn, M. 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **53**: 610–620.

Kjesbu, O.S., Witthames, P.R., Solemdal, P., and Greer Walker, M. 1998. Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. J. Sea Res. **40**: 303–321.

Köster, F.W., Hinrichsen, H.-H., St. John, M.A., Schnack, D., MacKenzie, B.D., Tomkiewicz, J., and Plikshs, M. 2000. Developing Baltic cod recruitment models. II. Incorporation of environmental variability and species interaction. Can. J. Fish. Aquat. Sci. **58**: 1534–1556.

Kraus, G., Müller, A., Trella, K., and Köster, F.W. 2000. Fecundity of Baltic cod: temporal and spatial variation. J. Fish Biol. **56**: 1327–1341.

Lambert, Y., and Dutil, J.D. 2000. Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy. Can. J. Fish. Aquat. Sci. **57**: 815–825.

Ma, Y., Kjesbu, O.S., and Jørgensen, T. 1998. Effects of ration on the maturation and fecundity in captive Atlantic herring (*Clupea harengus*). Can. J. Fish. Aquat. Sci. **55**: 900–908.

Marshall, C.T., Kjesbu, O.S., Yaragina, N.A., Solemdal, P., and Ulltang, O. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? Can. J. Fish. Aquat. Sci. **55**: 1766–1783.

Marshall, C.T., Yaragina, N.A., Lambert, Y., and Kjesbu, O.S. 1999. Total lipid energy as a proxy for total egg production by fish stocks. Nature (Lond.), **402**: 288–290.

Marteinsdottir, G., and Begg, G.A. 2002. Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod, *Gadus morhua*. Mar. Ecol. Prog. Ser. **235**: 235–256.

Morrison, C.M. 1990. Histology of the Atlantic Cod, *Gadus morhua*: an atlas. Part Three. Reproductive tract. Can. Spec. Publ. Fish. Aquat. Sci. No. 110.

Myers, R.A., Mertz, G., and Fowlow, S. 1997. The maximum population growth rates and recovery times of Atlantic cod (*Gadus morhua*). Fish. Bull. U.S. **95**: 762–772.

Pinhorn, A.T. 1984. Temporal and spatial variation in fecundity of Atlantic cod (*Gadus morhua*) in Newfoundland waters. J. Northw. Atl. Fish. Sci. **5**: 161–170.

Pogson, G.H., Taggart, C.T., Mesa, K.A., and Boutilier, R.G. 2001. Isolation by distance in the Atlantic cod, *Gadus morhua*, at large and small geographical scales. Evolution, **55**: 131–146.

Powles, P.M. 1957. Studies of feeding and reproduction of cod (*Gadus callarias* L.) in the Southwestern Gulf of St. Lawrence. M.Sc. thesis, University of Western Ontario, London, Ont.

Powles, P.M. 1958. Studies of reproduction and feeding of Atlantic cod (*Gadus callarias* L.) in the Southwestern Gulf of St. Lawrence. J. Fish. Res. Board Can. **15**: 1383–1402.

Purchase, C.F., and Brown, J.A. 2001. Stock-specific changes in growth rates, food conversion efficiencies, and energy allocation in response to temperature change in juvenile Atlantic cod. J. Fish Biol. **58**: 36–52.

Puvanendran, V., and Brown, J.A. 1998. Effect of light intensity on the foraging and growth of Atlantic cod larvae: interpopulation difference? Mar. Ecol. Prog. Ser. **167**: 207–214.

Roff, D.A. 2002. Life history evolution. Sinauer, Sunderland, Mass.

Ruzzante, D.E., Taggart, C.E., and Cook, D. 1998. A nuclear DNA basis for shelf- and bank-scale population structure in northwest Atlantic cod (*Gadus morhua*): Labrador to Georges Bank. Mol. Ecol. **7**: 1663–1680.

Ruzzante, D.E., Taggart, C.T., Lang, S., and Cook, D. 2000. Mixed-stock analysis of Atlantic cod near the Gulf of St. Lawrence based on microsatellite DNA. Ecol. Appl. **10**: 1090–1109.

Schwalme, K., and Chouinard, G.A. 1999. Seasonal dynamics in feeding, organ weights, and reproductive maturation of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. ICES J. Mar. Sci. **56**: 303–319.

Snyder, D.E. 1983. Fish eggs and larvae. *In* Fisheries techniques. *Edited by* L.A. Nielsen and D.L. Johnson. American Fisheries Society, Bethesda, Md. pp. 165–197.

Tanfermin, J.D. 1991. Suitability of different formalin-containing fixatives for the eggs of freshwater Asian catfish, *Clarias macrocephalus* (Gunther). Isr. J. Aquacult. Bamidgeh, **43**: 57–61.

Venables, W.N., and Ripley, B.D. 1998. Modern applied statistics with S-PLUS. 2nd ed. Springer-Verlag, NewYork.

Walters C., and Korman, J. 2001. Analysis of stock–recruitment data for deriving escapement reference points. *In* Stock, recruitment and reference points: assessment and management of Atlantic salmon. *Edited by* E. Prévost and G. Chaput. Hydrobiologie et aquaculture, INRA, Paris. pp. 67–94.

Waples, R.S. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. J. Hered. **89**: 438–450.

Wootton, R.J. 1998. Ecology of teleost fishes. 2nd ed. Kluwer Academic, Dordrecht.