

Potential Variability in the Paternal Contribution to Stock Reproductive Potential of Northeast Arctic Cod (*Gadus morhua*)

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Abstract

There has been a growing interest in determining the stock reproductive potential (SRP) as a means to better understand the recruitment dynamics of a fish population. The focus in SRP studies has, with a few notable exceptions, been on numbers, maturation and fecundity of females and thereby total egg production (TEP). In the past the SRP of northeast Arctic cod (*Gadus morhua*) was estimated from TEP over the years 1946 to 2005. In this paper we present estimates of the corresponding total viable sperm production (VSP) based on sperm characteristics from published literature on other cod stocks. There have been large changes in VSP, which to a certain extent reflect changes in the mature biomass of the stock. There was a relatively large variability in the relationship between VSP and TEP in this stock. Since 1946 there have also been changes in mean length of mature males and females with a tendency toward smaller fish in the most recent time period. With the relatively large decline in mean size of mature females and the tendency to mature at a smaller size in the latter years the mature fish of both sexes are now of a similar mean size. The relationship between mean size of mature males and females is substantially different than when the stock was large in the early part of the time series. This could have implications for fertilization success, a factor that is dependent on the dynamics of both sexes in relation to each other. Utilisation of fertilization rates based on the sex ratio and sperm fertilization potential based on the condition of the fish allowed the TEP to be adjusted to an 'estimate' of total fertilized eggs, thus including both male and female characteristics in an estimate of SRP. The resulting fertilized egg to recruit plot showed a similar degree of variability as the SSB to recruit plot, however, the pattern was slightly different.

Key words: Barents Sea, maturity, northeast Arctic cod, paternal effects, sex ratio, spermatozoa, stock reproductive potential.

Introduction

Stock reproductive potential (SRP) (Trippel, 1999) is largely measured by the 'egg production' of a fish

population (e.g. Tomkiewicz *et al.*, 2003), however, whether SRP is adequately represented by egg production alone requires further testing (Marshall *et al.*, 1998). Variations in the numbers of males and sperm production

in male fish could have a significant effect on the SRP (Trippel, 1999, 2003; Tomkiewicz *et al.*, 2003). In fact Trippel (2003) found that marginally more of the variance in age-3 recruitment in cod (*Gadus morhua*) off Newfoundland and Labrador could be explained by estimating viable sperm production rather than Spawning Stock Biomass (SSB).

It is assumed that there is always an excess of sperm compared to the availability of eggs and this is one of the many reasons why male state-variables have not been included in estimating Stock Reproductive Potential. However, reversing the trend is not easy, because it is not always evident which characteristics are most important to include and what the best measurements of male, or sperm, quality may be.

Male characteristics may affect SRP directly, for example by influencing the number of successful fertilizations. This is especially an issue where size selective harvesting has altered the sex ratio in species with sexually dimorphic growth (*e.g.* Rijnsdorp and Ibelings, 1989; Jakobsen and Ajiad, 1999; Bromley, 2000; Kell and Bromley, 2004). In Atlantic cod, females tend to be larger than males (Hunt, 1996) and they choose larger males during spawning (Warner *et al.*, 1995; Forsgren *et al.*, 1996). However even if a large male often dominates, it is usual for multiple males to contribute sperm to most spawnings (Bekkevold *et al.*, 2002). Thus sperm competition is high and certain sperm characteristics would be expected to be good indicators of reproductive potential. Sperm quality is a variable trait, as is sperm quantity. Vladic and Järvi (2001) found that differences in sperm quality between sexually mature resident Atlantic salmon (*Salmo salar*) parr and anadromous males allowed the smaller parr males a fair chance when it comes to sperm competition with dominant males. Warner *et al.* (1995) found that male coral reef fish with the highest daily mating success produced the fewest sperm per mating. Thus the specific variable that can represent male quality and its contribution to the fertilization success of a population is still unknown (Rakitin *et al.*, 1999a; Trippel, 2003; Trippel and Neil, 2004).

Trippel (2003) presents an equation for estimating viable sperm production (Total Viable Sperm Production, VSP) and thus provides an alternative to Total Egg Production (TEP) as a proxy for SSB. The present contribution uses the VSP to explore variations in the viable sperm production of the northeast Arctic cod stock off northern Scandinavia over the historical time series (1946–2005). Many of the relationships such as the proportion of testes weight to total body weight, spermat-

ocrit and sperm fertilization potential have been taken from published literature and are often not specific to this stock. Where data exists for the northeast Arctic cod stock they are presented. Here we also examine the dynamics of the mature male population and raise questions as to whether there is any necessity to consider the male part of the population as important for calculation of stock reproductive potential.

Methods

Basic population data

Population numbers at age (1946–2005) were obtained from the ICES Virtual Population Analyses (VPA) (ICES, 2006). These data were then applied to the annually varying Age-length-keys (ALK) (1946–2005, data provided by C.T. Marshall (University of Aberdeen, Scotland, UK), see Marshall *et al.* (2006) for methods of application) to give the numbers of individuals in each 5 cm length class. The sex ratio (1946–2005 data provided by C.T. Marshall) was applied to these numbers to give the numbers of males and females in each length class. The protocols given in Marshall *et al.* (2006) were followed for modelling the sex ratio using the female to male sex ratio in 5 cm length classes. A logistic equation using the logit function and an assumed binomial error function was fitted to the data for fish >80 cm for each year. The sex ratio was assumed to be 1:1 for fish 80 cm or less (Marshall *et al.*, 2006). The age-based maturity ogive (annually varying between 1946 and 2005) given in ICES (2006) with the correction for females (Marshall *et al.*, 2006) was then applied to the numbers of females at age and length to give the mature portion of the female population. In the case of males the combined male:female annually varying ogive (ICES, 2006) was applied to the ALKs and the whole mature population size and age distribution estimated. The mature male portion of the population was taken as the difference between the total and the female portion of the mature population.

The weight at length was estimated from the annually varying length-weight relationships (estimated for the period 1946–2001) presented in Marshall *et al.* (2004). New relationships for 2002–2005 were provided by C.T. Marshall. Marshall *et al.* (2006) noted that there were discrepancies in the length and weight data for the period 1981 to 1984. The estimated weights at lengths resulted in two abnormally high condition factor years and two very low condition years. As condition may be a major factor contributing to annual variations in fecundity and sperm production, these four abnormal years were not used in any subsequent calculations.

Estimation of annual sperm production

The general method for estimating sperm production is laid out in Trippel (2003) but is reproduced here with minor variations:

$$VSP = \sum_{i=1, l=2.5}^{I, L} n_{i,l} p_{i,l} t_{i,l} v_{i,l} s_{i,l} f_{i,l}$$

where VSP = Viable Sperm Production (this is given as VSPP or Viable Sperm Produced by Population in Trippel (2003)), i = age in years with I being the oldest age class, l = 5 cm length classes with L being the largest length class, and for each age and length class, $n_{i,l}$ = number of males, $p_{i,l}$ = proportion of mature males, $t_{i,l}$ = mean testes weight (kg) of males, $v_{i,l}$ = mean volume (ml) of semen produced per kg of testes weight, $s_{i,l}$ = mean number of spermatozoa per ml of semen, and $f_{i,l}$ = sperm fertilization potential as a function of Fulton's condition factor (K) (Nash *et al.*, 2006).

Estimation of condition. Trippel (2003) used Fulton's condition factor ($K = 100W/L^3$), where W = fish whole weight (g) and L = total length (cm), in the estimations of fertilization success therefore Fulton's condition factor is used here. Using the annually varying length/weight relationship the weight (W_{estim}) was estimated for each length class and then divided by the cube of the median length. A weighted mean male population condition was estimated:

$$\bar{K} = \frac{\sum K}{N}$$

where N = the number of individuals used to estimate the mean condition.

Estimation of GSI and testes weight. Trippel and Morgan (1994) give GonadoSomatic Indices (GSI) of 6% for 4 year olds rising to 13% for 12 year olds. GSI is given as:

$$GSI = \frac{W_T}{W} 100\%$$

where W_T = testes weight and W = fish whole weight (taken from the annually varying estimate of weight). In the case of northeast Arctic cod 0% was applied to 3 year olds and 6% to 4 year olds. The percentage was increased by 1 to 13% for 12 year olds and 13% also applied to the plus age group (13+) (Nash and Kjesbu, unpublished data for northeast Arctic cod sampled off northern Norway (Andenes) in 2004 and 2005; $n = 111$).

Estimation of total sperm per male. The percentage of testes weight that was assumed to be connective tissue, primary spermatogonia and residual unspawned

sperm was set to be 3% (Trippel and Morgan, 1994). The removal of this percentage gave the weight of semen, which was converted to a volume using a value of 1.04 (Trippel, 2003).

$$S_w = 0.97W_T, \text{ and}$$

$$S_v = 1.04S_w$$

where S_v = volume of semen, S_w = weight of semen and W_T = testes weight.

The number of sperm per ml was estimated using the formula of Rakitin *et al.* (1999b) and a spermatocrit of 0.6 (see Trippel, 2003). This gives a value of 1.16×10^{10} sperm ml^{-1} .

Sperm fertilization potential. The sperm fertilization potential (f) in each length class was estimated using the method in Trippel (2003) as:

$$f_l = 1.544K_l - 1.028$$

where K_l is Fulton's condition factor for a specific length class. Trippel and Neilson (1992) suggest that the fertilization potential of cod sperm is generally between 0.3 and 0.7 and this formula should allow this sort of variation. Here the weight at length and hence condition was estimated for the midpoint of a length class in the population, therefore the potential range in condition factor was somewhat restricted. This could have the effect of reducing the potential dynamic range of total sperm production.

Egg fertilization rates based on numbers of males per female. One stage further than that presented by Trippel (2003) is to consider the fertilization rates based on male : female proximity and behavior. Rowe *et al.* (2004) present two equations for fertilization rates based on the numbers of males per female. The study suggests a very rapid increase in fertilization rate (Fr) with numbers of males per female (N_m). The non-constrained relationship (not forced through the origin) was used here:

$$Fr = 1.00 - 0.42 \exp(-1.00N_m)$$

This function could be used to estimate the numbers of fertilized eggs (N_E) from the Total Egg Production (TEP):

$$N_E = TEP Fr$$

Estimation of annual total egg production

The annual egg production was estimated from the numbers of mature females at length using the generalized fecundity equation given in Marshall *et al.* (2006: equation 9):

$$e_L = \exp(-15.090 + 3.595 \ln L + 1.578 \ln K_n)$$

where e_L = fecundity for a length class L cm; Kn = relative condition factor (Ricker, 1975).

The relative condition factor (Kn) was estimated as the ratio between the estimated weight (W_{estim}) at length from the annually varying length-weight relationships (see above) and the expected weight at length (W_{expect}). The following equation given by Marshall *et al.* (2006) was used:

$$W_{expect} = \exp(-5.472 + 3.171 \ln L).$$

Statistical tests

Logistic equations were fitted to the sex ratio at length data using the logit function and an assumed binomial error function using S-PLUS 7.0 (Insightful Corp, USA). Correlations between parameters were undertaken either using Spearman Rank tests where data were not normally distributed or linear regression (GLM) (using STATISICA ver. 8, StatSoft Inc, USA).

Results

Population level variations in sperm production

Mean length and Condition factors of males. Over the period 1946–2005 the mean length of mature males has varied, with a trend toward shorter mean lengths (Spearman Rank: $R = -0.731$; $P < 0.05$; $N = 60$) (Fig. 1A).

In general, Fulton's condition factor (K) tends to increase with increasing length of the fish. Despite the general trend of decreasing mean weight, overall, there was a significant trend toward increasing weighted mean condition factor over time (Spearman Rank: $R = 0.693$; $P < 0.05$; $N = 56$) (Fig. 1B). The overall range for the weighted mean condition factor was 0.67–1.15, however, the majority of the values were between 0.73–0.93. Data were not used for 1981–1984 as the weight data are suspect and this has a very large effect on the condition factor and hence calculated sperm production. These years were not used for the estimation of egg production either.

Trends in sperm fertilization potential and viable sperm per male. The mean sperm fertilization potential is related to the mean condition of the fish (Fig. 1B) and viable sperm per mature male is also related to both of these (Fig. 2). Over the period 1946–2005 mean sperm fertilization potential tended to increase (Spearman Rank: $R = 0.699$; $P < 0.05$; $N = 56$), however, there was no such obvious trend in viable sperm per male (Spearman Rank: $R = 0.230$; $P > 0.05$; $N = 56$). Mean sperm

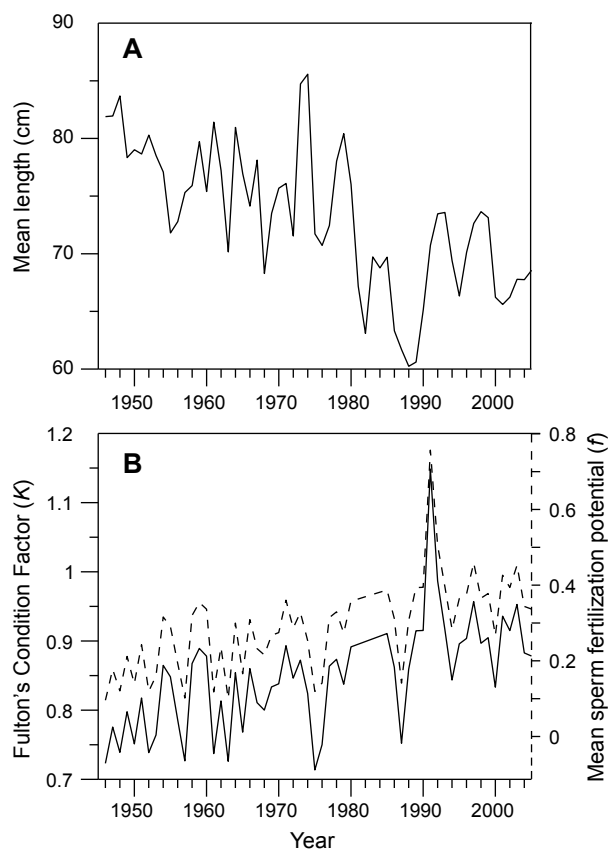


Fig. 1. Annual variation in: **A**) mean length, and **B**) weighted mean Fulton's condition factor (K) (solid line) and mean sperm fertilization potential (f) (dashed line) for mature male northeast Arctic cod.

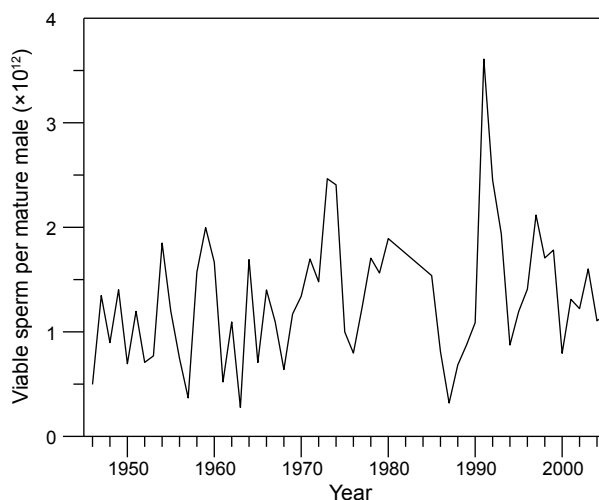


Fig. 2. Annual variation in viable sperm per mature male northeast Arctic cod.

fertilization potential of the mature male population ranged from 0.07–0.75. Mean viable sperm per mature male ranged from 0.3 – 3.9×10^{12} . The periodic variation

in amount of viable sperm per male essentially reflects the periodic changes in mean length of the males in the population, however, the longer term change does not reflect the general decline in mean length of the mature male population.

The distribution of viable sperm production across length classes. To illustrate the variability in sperm production, at the population level, across size classes, three years (1947, 1949 and 1992) when there was a relatively high spawning stock biomass and two years (1970 and 2000) when spawning stock biomass was low are shown in Fig. 3. In later years the larger sized fish did not occur in the population. In 1992 the peak in viable sperm production was at a similar level to the earlier period, however, there was still a truncation of sperm production for larger males.

The modeled impact of poor condition, allied with a relatively low estimate of spawning stock (SSB) (see Fig. 8A) on viable sperm production is further illustrated in the year 2000. Here the sperm production is particularly low across all length classes and there is no clearly identifiable peak in viable sperm production at length. There is also a relatively higher contribution from the smaller length classes.

Relative sizes of males and females. During the period 1946–1981 the mean length of mature females was

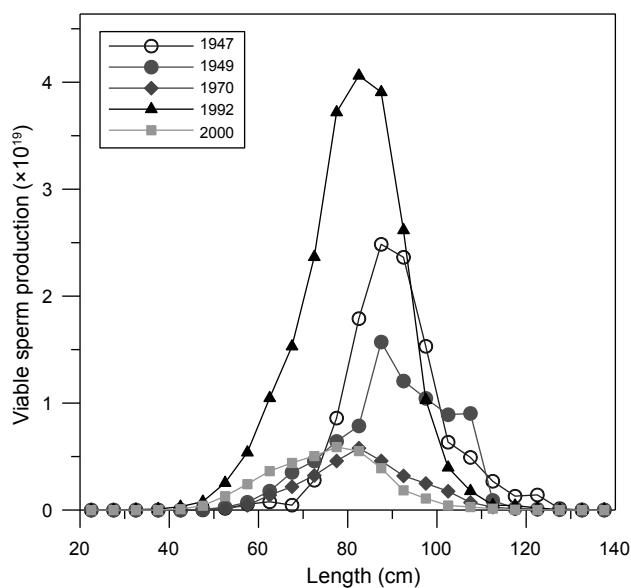


Fig. 3. Variation in viable sperm production by length class for three years (1947, 1949 and 1992) of high Spawning Stock Biomass (SSB) and two (1970 and 2000) of low SSB of northeast Arctic cod.

generally greater than the mean length of males by 10% or more and often greater than 13% (Fig. 4). After 1982 there was a greater parity in mean length of males and females and very rarely were the female mean lengths 13% greater than the male mean lengths. An illustration of the changes in length frequency for males and females is given in Fig. 5 for selected years. Between the late 1940s and the present there have been substantial changes in the length frequencies of both males and females. Similarly there have also been changes in abundance.

Changes in the male to female proportions in the mature stock and potential effect on spawning. Over the time period 1946–2005 there have been fairly large changes in the proportions of males and females in the mature part of the stock (Fig. 6). The male portion of mature fish has ranged between 0.38–0.75. Again there appears to be some periodicity in the fluctuations with an overall upward trend (toward a ratio slightly more in favour of males).

The variation can also be viewed as the number of mature males per mature female. The range has been

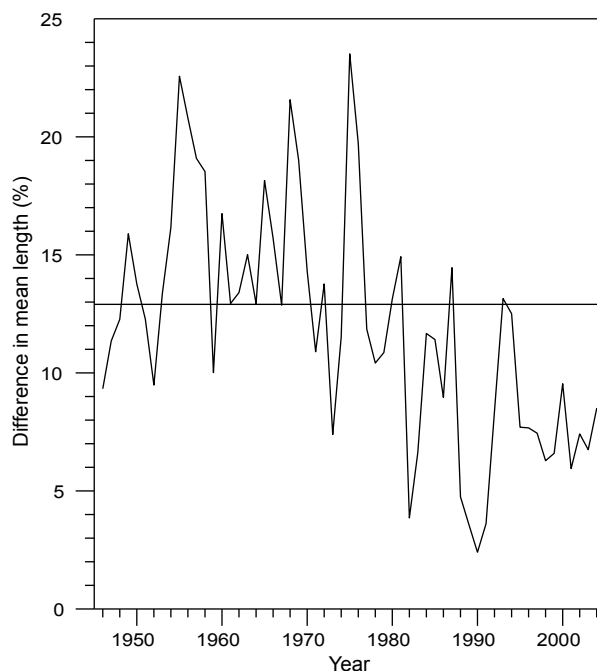


Fig. 4. Percent difference in mean length of mature females versus mature males in northeast Arctic cod. Positive values indicate females generally longer than males. Horizontal line at 13% is the level where the difference in lengths between males and females begins to become large enough that more than one male will be necessary to fertilize a single batch of eggs from one female (Rakitin *et al.*, 2001).

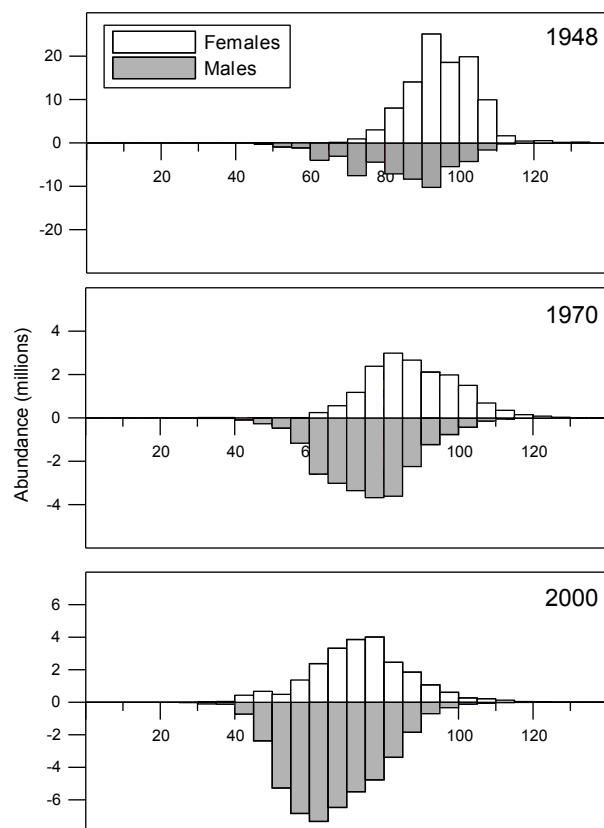


Fig. 5. Length frequencies of mature male and female northeast Arctic cod in three years of the time series, 1948 when the stock was large, 1970 when the stock was depleted and changing in abundance and structure and 2000 in a recent period after a recovery of the stock size.

approximately 0.6 to 3. Since the early 1980s there has been more than 1 male per female.

If the egg fertilization rate is related to the number of males per female, then Fig. 6B suggests that there has been a change over time. It appears that the fertilization rates may, in general, be higher in the last 20 years than in the first part of the time series.

Population level variations in sperm production

Total sperm production. The estimated total sperm production, without accounting for the sperm fertilization potential (f) generally followed the trend in SSB (Fig. 7B). There was a significant linear relationship between the two variables ($R^2 = 0.92$, $N = 54$, $P < 0.001$). Considerable variability was introduced with the inclusion of f to estimate the VSP (Fig. 7B), however, there was still a significant linear relationship between the two ($R^2 = 0.58$, $P < 0.001$), which was also evident in the re-

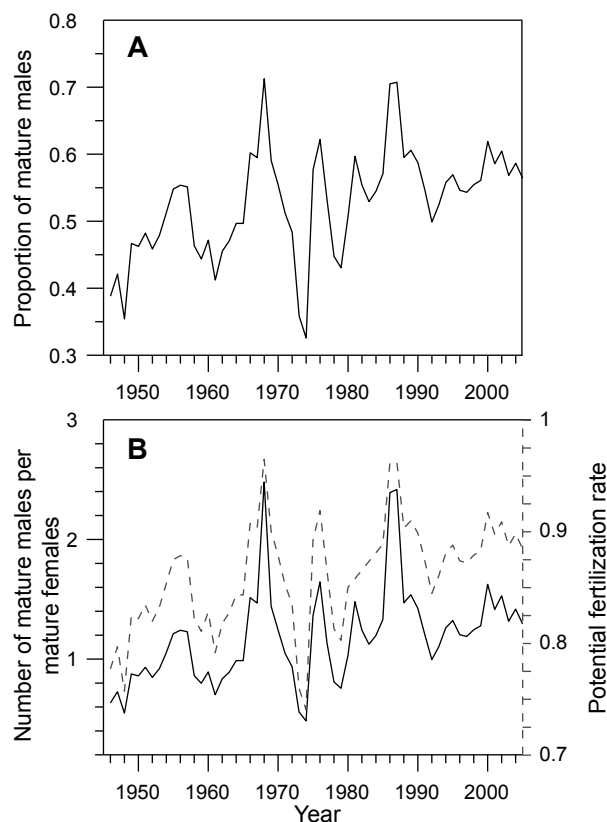


Fig. 6. Annual changes in: **A**) the proportion of males in the mature stock, and **B**) the number of mature males per mature female (solid line) and potential fertilization rate based on the male : female sex ratio (dashed line) of northeast Arctic cod. Fertilization rate relationship taken from Rowe *et al.* (2004).

lationship between SSB and VSP (Fig. 7C: $R^2 = 0.34$, $P < 0.001$).

Trends in population level sperm production and its relationship to recruitment. Interannual variability in the total sperm production was high (Fig. 8B) as reflected in the plot of SSB versus viable sperm production (Fig. 7C). The general decline from 1946–1990 with a general increase and decline over the 1990s mimicked the change in spawning stock biomass (Fig. 8A). In contrast, the sperm production at very high spawning stock biomasses in the early part of the time series was remarkably low. The major difference between the SSB and sperm production was that the increase in sperm production in the 1990s took sperm production to levels higher than seen at higher SSBs. Over this time series the mean size of mature males declined (Fig. 1A) and, as shown earlier, there was a general increase in the sperm fertilization potential.

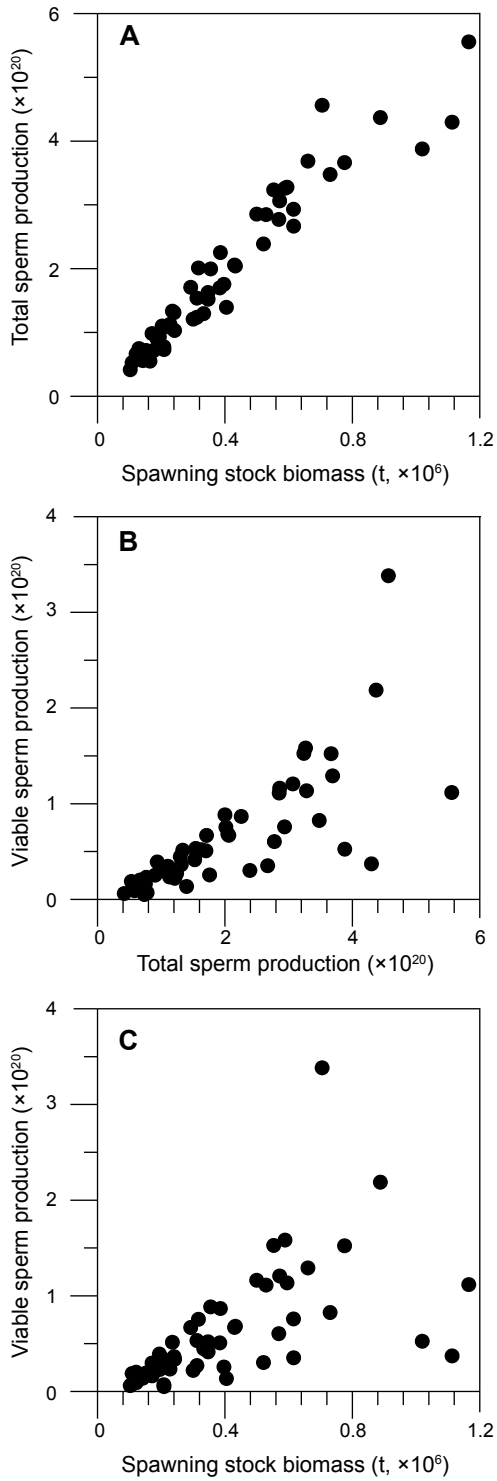


Fig. 7. Spawning stock and sperm production relationships for northeast Arctic cod over the period 1946–2005. **A)** SSB versus sperm production, **B)** Total sperm production versus viable sperm production (the effect of male condition), and **C)** SSB to viable sperm production.

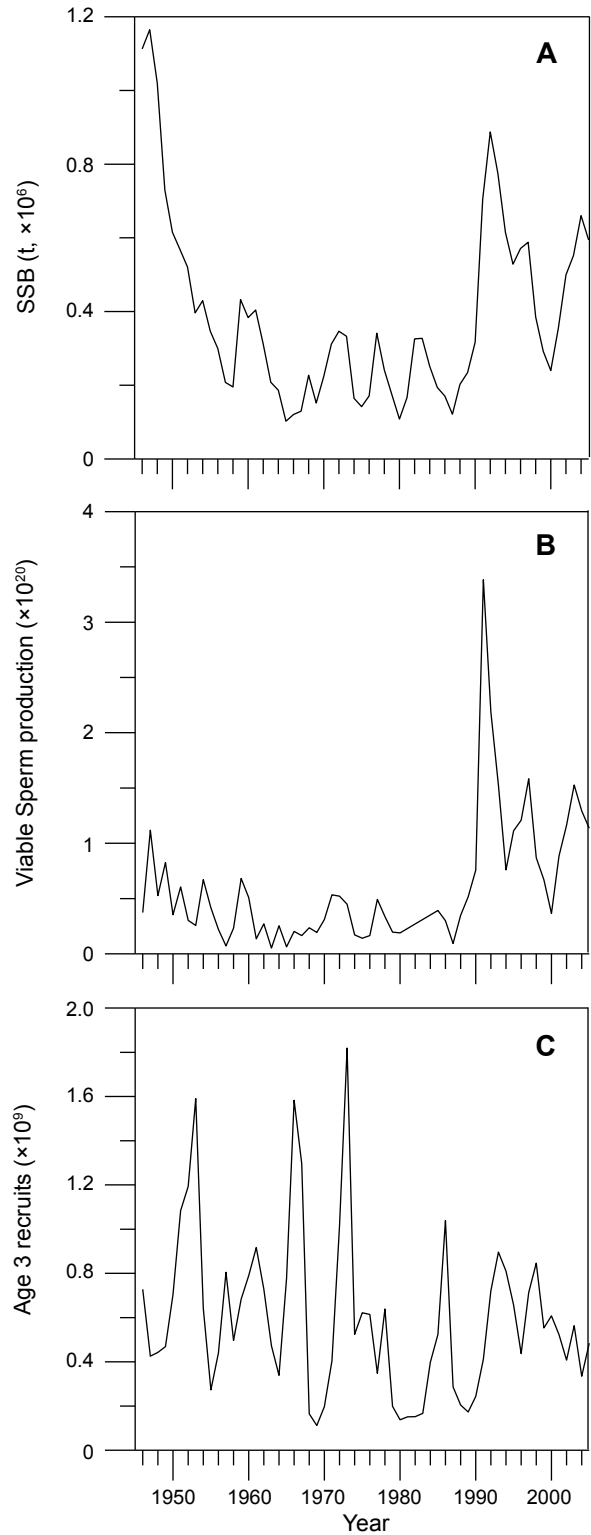


Fig. 8. Annual trends in northeast Arctic cod stock parameters. **A)** Spawning Stock Biomass (SSB) from VPA (ICES, 2006), **B)** viable sperm production (VSP), and **C)** age 3 recruits.

The plot of sperm production versus age 3 recruits (Fig. 9B) does not indicate a clearer relationship than seen with a plot of SSB versus age 3 recruits (Fig. 9A). Over the time-series the numbers of viable sperm that could be released for each age 3 recruit varied between 3.8–440 billion.

The interplay between the population level egg and sperm production. In general there is a positive trend between the total egg production (TEP) and viable sperm production (VSP) (Fig. 10). However, there is considerable variation in the quantities of sperm available at given levels of egg production and vice versa. Also,

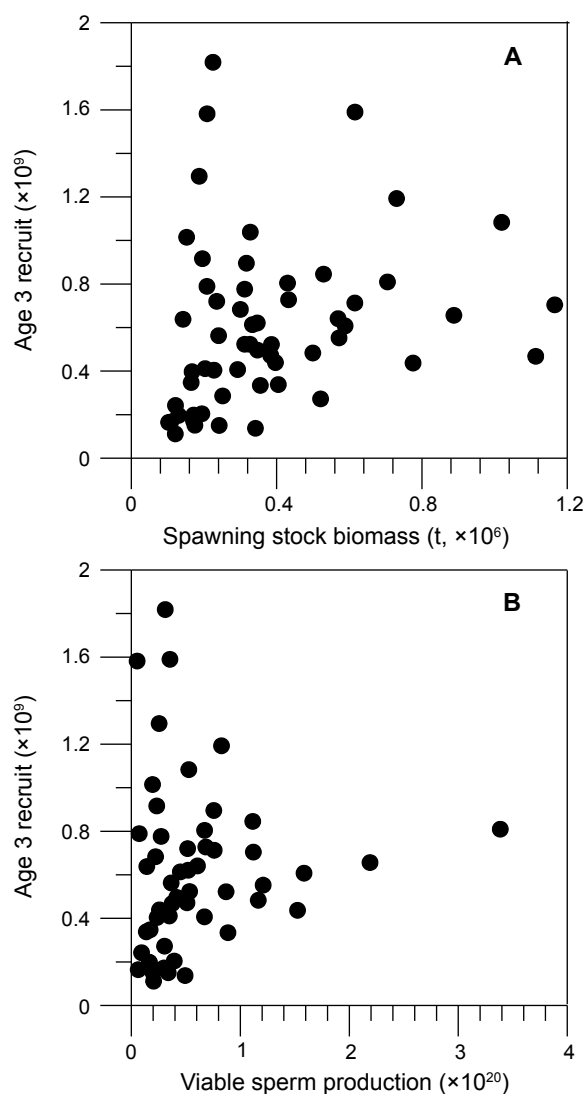


Fig. 9. Northeast Arctic cod Recruitment relationships. **A)** Spawning Stock Biomass (SSB) and age 3 recruits, and **B)** viable sperm production (VSP) and age 3 recruits.

because of the relatively lower condition at the higher stock sizes and also because sperm fertilization potential is postulated to be quite severely impacted by levels of condition, there is a tendency for relatively less available sperm at higher egg availabilities. Over the time series, the ratio of available viable sperm for each egg ranged between 0.2–1.9 million.

There are a number of ways that the inclusion of male biological data could contribute to estimates of SRP. Here we examine the impact of converting egg production to viable egg production by adjustment of the fertilization rate (basically the influence of the male:female ratio) with further modification based on the fertilization potential (f). The modification of the egg production to potentially fertilized eggs through the fertilization rate does not change the perception of viable egg production (Fig. 11a). There is still a significant linear relationship between the two variables ($R^2 = 0.99$, $P < 0.001$), however, the slope is significantly less than one (0.799, standard error = 0.0097). The introduction of the fertilization potential increases the perceived viable egg production considerably, however, there is still a significant relationship between the egg production estimated from the females alone and the fertilized eggs (Fig. 11B; $R^2 = 0.41$, $P < 0.01$). This results in a fertilized egg to recruitment plot as shown in Fig. 11C which appears slightly different from the standard SSB to recruitment plot shown in Fig 9A.

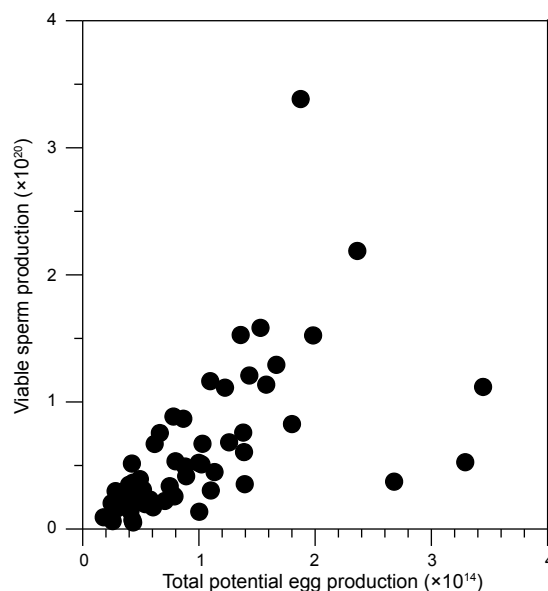


Fig. 10. Relationship between annual total egg production (TEP) and annual viable sperm production (VSP) for northeast Arctic cod (1946–2005).

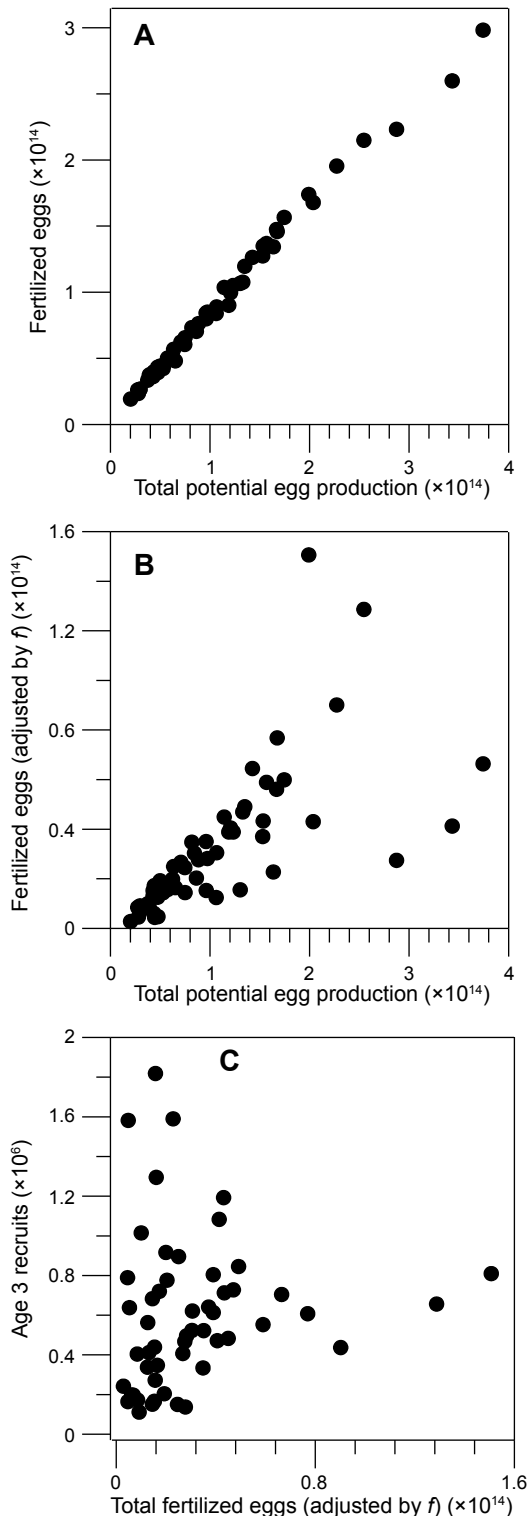


Fig. 11. Stock Reproductive Potential for northeast Arctic cod (1946–2005). **A**) TEP versus fertilized eggs (based on fertilization rate), **B**) TEP versus fertilized eggs (based on fertilized eggs adjusted by sperm fertilization potential (f), and **C**) fertilized eggs (adjusted by f) versus age 3 recruitment.

Discussion

In general, there has been considerable effort applied to defining the reproductive status of a stock (SRP) through fecundity and annual egg production. However, the definition of SRP also includes male characteristics (Trippel, 1999). Despite this recognition of the ‘whole’ reproductive population, biological data about males have been largely ignored. There are a number of reasons why the males have been overlooked in this type of research. Firstly the sperm production is generally assumed to be in excess for fertilization of eggs. There are very few examples of ‘unfertilized’ eggs being sampled in the wild (see Howell *et al.* 1991 for common sole *Solea solea*) so there is an assumption that fertilization rates are generally high. Given these points the perceived principal driving forces for a stock’s reproductive potential is assumed to be related to female factors such as condition, fecundity at the individual level and population size structure at the population level. Whilst female condition can be an indication of annual fecundity or egg production of a fish (Marshall *et al.*, 2006; Thorsen *et al.*, 2006), in paired matings of captive haddock (*Melanogrammus aeglefinus*) (over the observed range of condition factors) Trippel and Neil (2004) indicated that male condition rather than female condition explained most of the variability in fertilization success.

The present study utilizes testes and sperm characteristics relationships determined for other stocks since the relevant information either has not been collected or collated for northeast Arctic cod. Where data for northeast Arctic cod do exist *e.g.* GSI and condition data, the ranges are similar to those reported in the literature for other cod stocks. In some instances the relationships *e.g.* fertilization rate (Rowe *et al.*, 2004) have been determined for captive fish and this may not be representative of field situations. In this case it could be argued that wild and laboratory fish (contained in relatively small tanks) do not behave in the same way. This essentially highlights the point that further studies on male reproduction (and probably more importantly for both sexes) in the wild are needed.

One major problem is how exactly to implement information concerning males in to the estimation of SRP. We have presented information on viable sperm production (VSP) but have not developed this further. As to how this information could be combined with the TEP to give an estimate of SRP, we only consider fertilization rates and success and have presented TEPs for northeast Arctic cod that take some male characteristics into account. This is by no means ideal and further research is

needed to determine the measures that need to be incorporated into the estimation of a meaningful SRP. There is a strong possibility that the behaviour of the species will also need to be incorporated, including such information as potential miss-match in mean size of males and females.

Rakitin *et al.* (2001) found that in experimental competitive mating situations, males of a similar length (*i.e.* within 13%) of the female were able to sire entire batches of offspring. Bekkevold *et al.* (2002) also showed a decline in offspring sired with an increasing difference in size between males and females. This was also true for males being larger than females. In addition, the close alignment of the genital openings during the ventral mount is presumably necessary to achieve a high fertilization rate (Brawn, 1961). However, there is the possibility of eggs not being fertilized by the 'mounting' male and these eggs being wafted away 'down stream' to be fertilized by other males (see Fig. 9 in Trippel 2003). This is possible because unfertilized eggs and sperm can remain viable for more than one hour in seawater (Kjørsvik and Lønning, 1983; Trippel and Morgan, 1994) and the sperm cells swim slowly (Trippel and Neilson, 1992; Litvak and Trippel, 1998). This also allows for multiple paternity; a factor seen by Bekkevold *et al.* (2002) and Bekkevold (2006). There have been a number of studies examining the spawning of northeast Arctic cod in the wild such as mixing of stocks, sex ratios on the spawning grounds, spawning behaviour (including lekking mating systems) and sound production (*e.g.* Nordeide, 1998; Nordeide and Kjellsby, 1999; Nordeide and Folstad, 2000). Still, there are many unanswered questions related to all aspects of spawning of cod in the wild.

In the northern Grand Bank and southern Scotian Shelf, spawning shoals of Atlantic cod often had skewed sex ratios with a high proportion of males ready for spawning in some shoals and a high proportion of females finished with spawning in others (Morgan and Trippel, 1996). Females went towards deeper waters after completing spawning (Morgan and Trippel, 1996) which might be a problem during size selective harvesting. Differences in size between male and female cod and shifts in the ratios could occur during severe exploitation. The consequences could be changes in the fertilization rates of eggs and possibly in the genetic structuring of the population through changes in multiple paternities. In northeast Arctic cod, females dominated the large length classes and older age classes but with increased exploitation this changed with a major reduction in the mean size of spawning females. In addition, there was a reduction in mean size of spawning males. The conse-

quences of this for the fertilization success are unknown, especially considering that the present size structure of the population is different from the late 1940s. If there is a simultaneous size-mediated shift in the fertilization success then this could constitute a shift in the potential stock reproductive potential.

In experimental work with single males and females, fertilization success was >90% (Kjesbu *et al.*, 1996), however, the experimental work given in Rowe *et al.* (2004) suggests that the proportion of eggs fertilized declines with the reduction in number of spawning males per female. The data suggests that there may also be an increased variance in individual reproductive success with declining abundance *i.e.* an Allee effect (Frank and Brickman, 2000). If there is the 'population thinning' hypothesis then one can see that density declines as population size declines. If the population retains a similar density but simply contracts its distribution then it is difficult to argue that a decline in male availability.

The sperm fertilization potential varies according to the condition of the fish (Trippel, 2003) with Fulton's condition factor (K) being used in the calculations. One of the problems with K is size dependence; longer fish tend to have a higher condition factor *per se* than shorter fish. This may cause bias in the effective fertilization potential depending on the mean length of the male population. One solution may be to use the relative condition Kn (as used for the females (Scott *et al.*, 2006)), however, a new relationship between Kn and fertilization potential will need to be estimated.

The relationship between SSB and total viable sperm production (Fig. 7C) indicates that there is considerable variation in sperm production at any given SSB. In addition there is relatively less sperm production per unit SSB at the higher SSBs. This suggests a compensatory, density-dependent effect or may be indicative of more complex dynamics in the structural changes occurring in the stock.

The relationship between Total Egg Production and Total Sperm Production has a similar form to the SSB to Total Sperm Production relationship. One major unknown is whether there is always sufficient sperm available. The estimation of viable sperm per egg is hugely in favour of the sperm and suggests that available sperm is not a problem, but, this is estimated as a ratio of sperm to egg and does not include a measure of sperm quality. In the mating process males tend to aggregate and in general it is one male that is fertilizing a female's eggs.

In this case the ratio of available sperm to each egg is not a simple ratio of the two fishes' gametes. How this could influence fertilization rates is totally unknown. Replacing SSB with total sperm production does not clarify the underlying relationships between reproductive potential (SRP) and eventual recruitment at age 3 in this stock (Fig. 9A and B).

One factor that can affect the SRP is skipped spawning (Rideout *et al.*, 2000, 2005), primarily due to annual energy allocations between growth and reproduction (see Jørgensen *et al.*, 2006). This has not been considered here and is probably a phenomenon of both males and females, even though the research to date has primarily only considered females. In relation to males, there is also the perception that the greatest fertilization success lies with the largest males (Bekkevold *et al.*, 2002; Bekkevold, 2006). This will have implications for the effective population size and possibly the genetic composition of the stock. The SRP needs to be studied in more detail and further investigations undertaken into whether the male portion of the stock needs to be considered or can simply be ignored, provided shifts in *e.g.* sex ratios are not extreme.

There is clearly a need to investigate the contribution that males make to a Stock's Reproductive Potential. The present data indicate that there is potential for a paternal influence, however, a full evaluation and testing of the contribution of males needs species, population and stock specific data on male characteristics. This will need to include the influence of compatibility between males and females on *e.g.* spawning success and egg viability (Trippel and Morgan, 1994; Hutchings *et al.*, 1999; Trippel *et al.*, 2000, 2005; Sailant *et al.*, 2001; Wedekind *et al.*, 2001; Trippel and Neil, 2004) as well as estimates of the subsequent offspring success.

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