**How variable is the fecundity within and between cod stocks?**

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Stock reproductive potential is determined by the number of fish at age, sex ratio, proportion of mature female at age and fecundity. Fecundity data, which are fundamental in estimating egg production are not collected routinely for most fish stocks. Thus, variability in fecundity is largely ignored in the estimations of reproductive potential. The objective of this study was to identify patterns of spatial and temporal variation in the fecundity within and between different stocks of Atlantic cod (*Gadus morhua*) in the North Atlantic and Baltic Sea. A review of fecundity data for cod of different stocks and years was made. The examination of fecundity at size indicated a very large variability in the fecundity of cod between stocks and years. The fecundity of a 60 cm cod varied from 210 000 eggs to 2 250 000 eggs. Baltic and North Sea cod stocks were very distinct from the others, highest fecundity-at-size notwithstanding years being observed for these stocks. A different pattern of variation was observed for the other stocks. Temporal variation in fecundity appeared as important as or even more important than differences associated with stocks. Without excluding genetic differences, variations in the environmental conditions and fishing pressure could possibly explain much of the variation in the fecundity of these stocks. At a smaller scale, it also appears that the increase in the reproductive investment with age/size can differ between stocks and years. Thus, routine measurement of fecundity should be essential in estimating reproductive potential of cod.

Keywords: fecundity, *Gadus morhua*, spatial and temporal variation, environmental influences

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**Introduction**

The number of fish at age, length at age, sex ratio, proportion of mature female at age and fecundity are the essential reproductive characteristics needed to determine stock reproductive potential. Data for most of these characteristics have been extensively collected but the possibility of estimating potential egg production/ reproductive potential is constrained by the scarcity of fecundity data (Tomkiewicz et al. 2003). Thus, estimations of egg production of stocks are often obtained from fecundity-length relationships measured at a different time period or obtained from other populations. This approach may however, lead to biased estimates of egg production. Fish fecundity varies extensively in natural populations. Important variations are observed both within and between populations of the same species (Kjesbu et al. 1998, Kraus et al. 2002, Marteinsdottir and Begg 2002, Lambert et al. 2003).

Several factors have been shown to influence fecundity. These include fish size, nutritional status (determined by different indices of condition), food abundance/ availability/ consumption, growth, temperature, fish density, biomass index and parental genes (studies reviewed in Lambert et al. 2003). Studies within cod stocks indicated that predictive models to estimate potential fecundity could be developed as potential fecundity was strongly related to different biological/environmental variables. However, the relative importance of these factors in producing individual, annual and geographical variation in fecundity has not been widely investigated.

The objective of this study was to review available data on cod and characterize the patterns of variation in fecundity within and between stocks. Cluster analysis was used to detect patterns of spatial and temporal variation in the fecundity-length relationships of cod in the North Atlantic and Baltic Sea.

**Material and Methods**

Potential fecundity data published in scientific journals and reports as well as unpublished data made available to the authors were used to develop a database on the fecundity of cod. Data were first assigned a stock membership using NAFO and ICES management units. Information on sampling areas, sampling dates and spawning dates were compiled. Each observation was represented by a stock membership, a sub-division if available, and a year. As individual data were not available in all studies, most of the analyses were conducted on the relationships between fecundity and some independent variable. For each observation, the type of relationship describing the variation in fecundity, the coefficient of determination and the size range of cod were noted. In the different studies, different formulations were used to express the variation in fecundity. Potential fecundity was related to length or weight using linear regressions, power or exponential functions on untransformed or transformed data. Original relationships were used to generate the values of potential fecundity and size (i.e. length or weight) for the observed size range of cod. Parameters of the relationships for Southern Newfoundland cod (Pinhorn 1984) were solved graphically. Length-weight relationships obtained for the same stocks and years were used to transform weight data into length. Length data were expressed as fork length. Total length ($L_{tot}$) was converted into fork length ($L_{fork}$) using the formula:

$$L_{fork} = 0.0498 + 0.981 \, L_{tot} \qquad r^2 = 0.99 \quad \text{(Lambert, Y. pers. comm.)}$$

Data on potential fecundity and fork length were then used to generate a standardized relationship for each stock and year. A power relationship ($PF = a \, L_{fork}^{b}$) between potential fecundity (PF) and fork length ($L_{fork}$) was selected as the standard relationship.

Length was preferred to weight as an independent variable as weight can be a biased predictor of fecundity in species or populations showing large seasonal variations in length-weight relationships. At least in cod, it has been demonstrated that somatic weight can vary significantly between the onset of maturation, overwintering and pre-spawning period (Eliassen and Vahl 1982, Lambert and Dutil 1997, Schwalme and Chouinard 1999). Changes in environmental conditions influencing the seasonal variation in weight, differences in the time of sampling between years within populations or between populations may result in different fecundity-weight relationships while in reality the number of eggs in relation to length could have remained unchanged.

As in many fish species, significant differences in the values of the parameters (intercept and slope) describing the relationships between fecundity and size have been detected between populations, geographic areas, and years (Marteinsdottir and Begg 2002, Lambert et al. 2003). However, the absence of individual data for all relationships and the violation of the assumption of homogeneity of slopes between relationships following logarithmic transformations do not allow the use of analysis of covariance to compare the relationships. Instead, we applied cluster analysis using parameters derived from relationships between fecundity and size for comparisons between the different stocks and years. To take into account the differences in both intercept and slope of the different relationships, fecundity data were examined using two variates: the fecundity at a fixed size and the value of the slope of the regression. A fixed size of 60 cm was selected as spawning fish of that size can be observed in almost all stocks.

Cluster analysis represents a multivariate statistical method that can be used to classify observations into subgroups without a priori classification. This statistical procedure was used to classify the fecundity data in a way that maximize within-group similarity while minimizing among-group similarity. Hierarchical clustering (agglomerative clustering) was performed using Ward's minimum variance method with standardized variates. Similarity values for linkage between observations were used to determine the number of clusters. Cluster analysis was conducted with SAS/STAT Version 8.2, CLUSTER procedure (SAS Institute Inc.)

**Results**

Fecundity data from 13 cod stocks located on both sides of the North Atlantic and the Baltic Sea were included (Table 1). For each stock, data covering a period of 2 to 10 different years were obtained. The longest series were available for the Eastern Baltic, Iceland, and Northeast Arctic stocks. Overall, a database containing 77 observations describing relationships between fecundity and length for different stocks, sub-divisions and years was constructed (Table 2).

Important differences in the size range of reproductive cod were observed between stocks and years assuming that observed size ranges reflect the size composition of reproductive fish. The size of mature cod can vary from 27 cm to 140 cm (Table 2, Fig. 1). However, size range between 55 cm and 85 cm appear to be common for most stock and years. The potential fecundity over the total size range of cod for all stocks and years varied between 150,000 eggs and 25 million eggs. A 10.7 fold difference in the potential fecundity of a 60 cm cod was observed between stocks and years; potential fecundity varying between 209,000 eggs and 2.22 million eggs (Fig. 1). The slopes of the relationships also varied greatly with minimum and maximum values of 1.145 and 5.455, respectively. A mean value of 3.37 (± 0.7) was observed for the different relationships.

Cluster analysis resulted in the formation of 12 groups reflecting variations in the fecundity at 60 cm and in the slope of the relationships (Fig. 2). The proportion of the variance accounted for by the 12 clusters (R-squared) was around 93% (Fig. 2). The pseudo $t^2$ statistic indicated possible clustering levels at 12 or 7 clusters. It was decided to keep 12 clusters as the use of 7 clusters was generating a large range in the fecundity at 60 cm within some of the clusters. Each cluster included 2 to 16 fecundity-length relationships (Table 3). The only exception was for cluster 7 which only included the fecundity-length relationship of cod from Southern Labrador and Eastern Newfoundland in 1968.

The fecundity of a 60 cm cod on Flemish Cap in 1984 (cluster 12) was 209,000 eggs compared to 2.22 millions eggs for a cod of the same size in Eastern Baltic in 1996 (cluster 1) (Fig. 3). Highest fecundities at 60 cm were observed in clusters 1 to 4 while steepest slopes of fecundity-length relationships were observed in clusters 4, 5, 11, and 12. Clusters 1 to 4 were made of Eastern Baltic and North Sea cod stocks. Cluster 1 represented by Eastern Baltic cod only was separated from the other clusters by the high fecundities at 60 cm (1.8 to 2.25 million eggs). Lower fecundities at 60 cm (1.35 to 1.9 million eggs) were observed in clusters 2 to 4. The separation between these clusters was largely associated with differences in the slopes of the fecundity-length relationships. Iceland cod stock was represented in 3 clusters (8, 11, and 12) but most of the years were included in cluster 11, which was characterized by a mean fecundity at 60 cm of 732,000 eggs (±125,000) and high slopes (3.96 to 4.62). The other clusters (5 to 10 and 12) were not made of particular cod stocks.

Cluster analysis revealed important differences in the fecundity at size within stocks. For many stocks, differences in the fecundity between years within the stock resulted in the membership of that stock in different clusters. The fecundity at 60 cm varied between 361,000 and 988,000 eggs in Iceland cod (clusters 8 and 12), and between 1.37 and 2.22 million eggs in Eastern Baltic (clusters 1 and 3). Moreover, important short term changes (i.e. successive years) were also observed in many stocks. In Iceland cod, the fecundity at 60 cm increased from 361,000 to 917,000 eggs (154%) between 1998 and 1999. Increases of 62% and 35% in the fecundity at 60 cm were observed in Eastern Baltic cod between 1995 and 1996 and in Northeast Arctic cod between 1988 and 1989, respectively. On the other hand, similar fecundities at 60 cm were observed for stocks that were very distant geographically. For example, similar fecundities were observed for Northern Gulf of St. Lawrence cod in 2002 (932,000 eggs) and Northeast Arctic cod in 2003 (976,000 eggs) (cluster 8). These similarities

in the fecundity at size were not always corresponding to similar fecundity-length relationships. Very different patterns of variation in fecundity were observed in Iceland (cluster 11) and Georges Bank (cluster 8) cod in 2000. Although both stocks were showing identical fecundity at 60 cm (730,000 and 723,000 eggs), the difference in the slope of the regressions resulted in an 81% difference between the fecundities at 100 cm.

A significant (P<0.0002) decrease in the slope of the fecundity-length relationships was observed with increasing fecundities at 60 cm (Fig. 3). However, patterns of variations in the fecundity-length relationships were different within stocks (Fig. 4). A significant negative relationship was observed between fecundity at 60 cm and the slope of the regression for Iceland and Northeast Arctic cod stocks (P<0.004). However, a steeper slope was observed for Iceland cod indicating a higher increase in potential fecundity with increasing size in that stock. In Eastern Baltic cod where fecundities at 60 cm were higher than 1.25 million eggs, no significant relationship was observed (P>0.13) between the fecundity at 60 cm and the slope of the regression. Possible relationships were not examined for the other stocks as the number of years for which data were available was not large enough.

Potential fecundity-length relationships for each cluster were generated using mean values of fecundity at 60 cm and the slopes of the regressions in each cluster (Fig. 5). The different forms of the regressions closely reflect the differences in the fecundity at size, the rate of change in fecundity with increasing size or both between the groups resulting from the cluster analysis.

**Discussion**

A wide variation in the fecundity of cod was observed in the different stocks and the largest variability was associated with the size of the fish. Moreover, the importance of size was even greater in situations where the slopes of the regressions between fecundity and length were increasing. For similar length-weight relationships, relative fecundity (number of eggs/g of fish) for different sizes of fish would be comparable for fecundity-length relationships with slopes close to 3. However, relative fecundity between a size of 60 cm and a size of 100 cm would increase by a factor of 1.7 and 2.8 for slopes of 4 and 5, respectively. For example, the relative fecundity of Iceland cod in 1998 where a high slope was observed (b=5.4550) increased from 381 eggs/g for a 70 cm cod to 796 egg/g for a 120 cm cod (Marteinsdottir and Begg 2002).

The cluster analysis using the fecundity at 60 cm and the slopes of the fecundity-length relationships revealed these important patterns of variation in fecundity between stocks and years. Notwithstanding differences in fecundity associated with size, significant variations in the fecundity at a fixed size were observed between stocks and years. Although less extreme, these variations were nevertheless significant. The grouping of fecundity-length relationships of different years for the same stock in different clusters also demonstrates the importance of environmental conditions in producing significant changes in the fecundity of cod. In many cases, successive years within stocks were not even classified in the same clusters.

Many environmental and or biological factors can generate the differences in the fecundity of cod and explain the differences between the clusters. Differences can be

the result of short term responses associated with the nutritional status of the fish, food availability, growth, and/or environmental temperature (Lambert et al. 2003). Variations in fecundity might also reflect different life history responses of populations resulting in different age/size at maturity, reproductive investment, egg size, and survival (Roff 2002).

Nutritional condition, which can be estimated from different indicators (Fulton's K, liver index) is different between stocks and years. Higher fecundities at 60 cm are observed for stock and years where the condition factor was at its highest level. Mean condition factor values for Eastern Baltic cod were between 1.10 and 1.20 (Kraus et al. 2000) while available data for other stocks and years with fecundity at 60 cm below 1.25 million eggs indicated mean condition factors below 1.0 (Marshall et al. 1998, Lambert and Dutil 2000, Lambert et al. 2000, Marteinsdottir and Begg 2002, McIntyre and Hutchings 2003). The large seasonal variation in the nutritional condition of cod in the Northeast Arctic (Kjesbu et al. 1998, Marshall et al. 1998) and Northern Gulf of St. Lawrence (Lambert and Dutil 2000, Lambert et al. 2000) and the poor condition observed near the spawning period in some years could indicate that these fish are in food-limited environments or subjected to very large fluctuations in food supply in comparison to Eastern Baltic cod which show higher and less variable condition (Lambert et al. 2003). As a result, potential fecundity was influenced by different indices of fish condition in Northeast Arctic cod (i.e. liver index) and in Northern Gulf of St. Lawrence cod (i.e. condition factor) but not in Baltic cod (Kraus et al. 2000). This would indicate the presence of a threshold value in the condition factor above which energy reserves are not limiting size-specific reproductive investment. Fecundity above this level would be high and more importantly influenced by current food intake as indicated by the significant relationship observed between fecundity and prey availability index for Eastern Baltic cod (Kraus et al. 2002). Atresia levels could also be largely reduced above this level. The threshold level in the condition factor for cod based on the results of the cluster analysis could possibly be around 1.0-1.1.

Although showing a high level of condition, growth and productivity, Eastern Baltic cod is not amongst the highest productive stocks  based on growth and surplus production per capita (Dutil and Brander 2003). West Scotland, Iceland, and Georges Bank cod which are well represented in clusters 5, 8, 9, and 11 were classified as more productive stocks. Clusters including most data for these stocks are characterised by lower fecundity at 60 cm but faster increases in fecundity with increasing size (i.e. higher slopes). These results could indicate very different strategies of energy allocation between growth and reproduction. High reproductive effort at all sizes in Eastern Baltic cod could result in lower growth rates and lower increases in fecundity with increases in size (slopes between 2.0 and 3.7). In Iceland and Georges Bank cod, lower reproductive effort could result in higher growth rates and higher increases in fecundity with increasing sizes (slopes between 3.4 to 5.5).

The same reasoning could be used to explain similarities in the fecundity-length relationships for stocks with very different levels of productivity. For example, Georges Bank and Southern Gulf of St. Lawrence cod in 1999 are both included in cluster 9 even though Southern Gulf of St. Lawrence cod stock has been classified as one of the less productive cod stock (Dutil and Brander 2003). McIntyre and Hutchings (2003) observed higher GSI in Southern Gulf of St. Lawrence than in

Georges Bank. This difference was interpreted as an indication of higher reproductive investment in Southern Gulf of St. Lawrence cod in response to slower growth, longer time to reach maturity, and higher prereproductive mortality. Similar fecundity at 60 cm between the 2 stocks despite higher GSI in the Southern Gulf might result from the larger egg size observed for cod in that stock (McIntyre and Hutchings 2003).

Differences in the relative energy investment per egg between stocks and years can influence the fecundity-length relationships. Many studies indicated that egg diameter or dry weight increased significantly with female length, weight and/or age (studies reviewed in Lambert et al. 2003). There are also several indications that egg size is declining with increasing temperature (Chambers 1997). Temperature also has an important influence on growth, food intake, and condition. Many studies showed the relations between temperature and these parameters (Brander 1995, Dutil and Brander 2003, Ratz and Lloret 2003). Direct effect of temperature may be hard to detect as it very often covary with food availability and metabolic rate (Kraus et al. 2002). Based on mean temperatures encountered by the different stocks (Brander 1995, Kraus et al. 2000) there is, however, some indications that the temperature is increasing between clusters separated by different fecundity at 60 cm (clusters 6-8, and 10 (~ 2-4°C) vs clusters 1-3 (~4.5-7°C) and clusters separated by the slopes of the fecundity-length relationships (clusters 1-3 (~4.5-7°C) vs cluster 4 (~6.5-8.6°C); clusters 6-8, 10 (~2-4°C) vs clusters 9, 11 (~4-5.8°C)). However, a closer examination of the temperatures for each year and stock is necessary to validate these trends.

Increased reproductive effort (i.e. fecundity) is often hypothesized to result from increased exploitation of stocks to compensate higher adult mortality and shorter life span. Variation in the fecundity of cod between the 1960s, early 1970s and 2000s for North Sea and Southern Newfoundland cod appear consistent with this hypothesis. The fecundity of North Sea cod between 1969 and 1972 (clusters 2 and 8) was lower than in 2002 and 2003 (cluster 4). In Southern Newfoundland, the fecundity between 1966 and 1970 (cluster 6 and 10) was lower then in 2001 (cluster 8).

Clusters, which are each represented by a characteristic fecundity-length relationship (Fig. 5) appear to be separated from each other by a combination of biological/environmental factors. Parameters describing nutritional status, growth, reproductive effort, temperature and stock characteristics (biomass level, growth per capita, surplus production etc.) for the different stocks and years could be used to disentangle the relative importance of these variables and be used to predict fecundity in specific environmental conditions and/or determine fecundity for data poor stocks living in specific environmental conditions.

This study further shows the important variability observed in the fecundity of cod. It also demonstrates that the patterns of variation in fecundity, which are influenced by many factors with varying relative importance depending on stock characteristics and environmental conditions. However, variability in the fecundity may also reflect some genetic component to the determination of fecundity that may be resolved by statistical analysis controlling biological/environmental effects (Hewison 1997).

Finally, this study emphasises the need to estimate on a routine basis, the fecundity and the reproductive potential of cod stocks. More precise measurements of

reproductive potential might eventually lead to stronger stock-recruitment relationships.

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Table 1. List of stocks and years used for the comparisons of the fecundity of cod in the North Atlantic and Baltic Sea.

| Stock | Division | Symbol | Time period | Reference |
|---|---|---|---|---|
| Eastern Baltic | ICES SD 25-32 | BA | 1987-1992, 1995-1996, 1998-1999 | (Kraus et al. 2000) (Kraus et al. 2002) |
| Iceland | ICES Va | IC | 1960, 1967, 1995-2000 | (Joakimsson 1969) (Schopka 1971) (Marteinsdottir and Begg 2002) |
| Northeast Arctic | ICES I-II | NA | 1986-1989, 1999-2000, 2003-2004 | (Kjesbu et al. 1998) Kjesbu unpublished |
| North Sea | ICES IVa-c VIId | NS | 1969-1972, 1999, 2002-2003 | West 1970 in (Yoneda and Wright 2004) (Oosthuizen and Daan 1974) (Yoneda and Wright 2004) |
| West of Scotland | ICES VIa | WS | 1969-1970, 2002-2003 | West 1970 in (Yoneda and Wright 2004) (Yoneda and Wright 2004) |
| Georges Bank | NAFO 5-6 | GB | 1999-2000 | (McIntyre and Hutchings 2003) |
| Southern Labrador and Eastern Newfoundland | NAFO 2J3KL | NC | 1964, 1966-1968 | (May 1967) (Postolakii 1967) (Pinhorn 1984) |
| Northern Gulf of St. Lawrence | NAFO 3Pn4RS | NG | 1995, 1998, 2001-2002 | (Lambert et al. 2000) Lambert unpublished |
| Sidney Bight | NAFO 4Vn | SB | 1998-1999 | (McIntyre and Hutchings 2003) |
| Southern Grand Bank | NAFO 3NO | SC | 1964-1965 | (May 1967) |
| Southern Gulf of St. Lawrence | NAFO 4T-Vn (Nov.-April) | SG | 1955-1956, 1980, 1998-1999 | (Powles 1958) (Buzeta and Waiwood 1982) (McIntyre and Hutchings 2003) |
| Southern Newfoundland | NAFO 3Ps | SN | 1966-1967, 1969-1970, 2001 | (Pinhorn 1984) Lambert unpublished |
| Flemish Cap | NAFO 3M | FC | 1979, 1984 | (Wells 1986) |

Table 2. Regression parameters for the standardized relationships between potential fecundity (PF) and fork length ($L_{fork}$) of cod for the different stocks and years. For each stock and year, spawning time, sampling dates, formulation of the original relationship, coefficient of determination ($r^2$), size range, number of observations and the slope (b) and intercept (a) of the standardized relationship are presented.

| Stock | Year | Symbol | Spawning time | Sampling dates | Original relationship (formulation) | $r^2$ | Size range (cm) | n | Standardized relationship ($PF = a\,L_{fork}^{\,b}$) | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | b | a |
| BA | 1987 | BA87 | March | March - Sept. | $PF = a\,L_{tot}^{\,b}$ | 0.76 | 32-104 | 64 | 2.512 | 51.753 |
| BA | 1988 | BA88 | March-May | March - Sept. | $PF = a\,L_{tot}^{\,b}$ | 0.68 | 27-76 | 115 | 2.922 | 9.7662 |
| BA | 1989 | BA89 | April | March - Sept. | $PF = a\,L_{tot}^{\,b}$ | 0.76 | 37-62 | 65 | 3.662 | 0.5718 |
| BA | 1990 | BA90 | March-April | March - Sept. | $PF = a\,L_{tot}^{\,b}$ | 0.74 | 35-68 | 104 | 2.762 | 24.506 |
| BA | 1991 | BA91 | March | March - Sept. | $PF = a\,L_{tot}^{\,b}$ | 0.77 | 38-87 | 77 | 2.772 | 18.85 |
| BA | 1992 | BA92 | March | March - Sept. | $PF = a\,L_{tot}^{\,b}$ | 0.93 | 41-98 | 43 | 3.262 | 2.7466 |
| BA | 1995 | BA95a | April-May | March - Sept. | $PF = a\,L_{tot}^{\,b}$ | 0.46 | 37-77 | 114 | 2.232 | 155.67 |
| BA | 1995 | BA95b | May | March - Sept. | $PF = a\,L_{tot}^{\,b}$ | 0.8 | 33-90 | 66 | 2.322 | 102.12 |
| BA | 1996 | BA96a | April-May-July | March - Sept. | $PF = a\,L_{tot}^{\,b}$ | 0.77 | 36-84 | 91 | 2.922 | 14.163 |
| BA | 1996 | BA96b | April | March - Sept. | $PF = a\,L_{tot}^{\,b}$ | 0.67 | 45-68 | 28 | 2.732 | 26.154 |
| BA | 1996 | BA96c | April | March - Sept. | $PF = a\,L_{tot}^{\,b}$ | 0.67 | 42-75 | 40 | 2.041 | 406.51 |
| BA | 1998 | BA98 | March - Apr. | March - Sept. | $PF = b\,W + a$ | | 35-91 | 40 | 3.154 | 4.1738 |
| BA | 1999 | BA99 | Apr. - July | March - Sept. | $PF = b\,W + a$ | | 26-126 | 65 | 2.982 | 9.636 |
| BA | 2000 | BA00 | March - May | March - Sept. | $PF = b\,W + a$ | | 28-108 | 94 | 2.837 | 16.623 |
| FC | 1979 | FC79 | Feb. - March | Jan. -Feb. | $PF = a\,L_{fork}^{\,b}$ | 0.78 | 44-70 | 15 | 3.855 | 0.0869 |
| FC | 1984 | FC84 | Feb. - March | Jan. -Feb. | $PF = a\,L_{fork}^{\,b}$ | 0.41 | 63-91 | 11 | 4.804 | 0.0006 |
| GB | 1999 | GB99 | Feb-March | Nov.-May | $PF = e^{a\,L_{fork} + b}$ | 0.73 | 40-120 | 55 | 4.152 | 0.0219 |
| GB | 2000 | GB00 | Feb-March | Nov.-May | $PF = e^{a\,L_{fork} + b}$ | 0.82 | 50-120 | 41 | 3.396 | 0.6612 |
| IC | 1960 | IC60 | March-May | Jan. - Feb. | $PF = a\,L_{fork}^{\,b}$ | 0.53 | 58-94 | 42 | 3.073 | 3.59 |
| IC | 1967 | IC67 | March-May | Jan. - Feb. | $PF = a\,L_{fork}^{\,b}$ | 0.84 | 54-125 | 49 | 3.459 | 0.5997 |
| IC | 1995 | IC95 | March-May | Jan. - Feb. | $PF = a\,L_{fork}^{\,b}$ | 0.81 | 67-125 | 264 | 4.460 | 0.0082 |
| IC | 1996 | IC96 | March-May | Jan. - Feb. | $PF = a\,L_{fork}^{\,b}$ | 0.9 | 57-133 | 160 | 4.226 | 0.0269 |
| IC | 1997 | IC97 | March-May | Jan. - Feb. | $PF = a\,L_{fork}^{\,b}$ | 0.62 | 67-128 | 160 | 4.625 | 0.00366 |
| IC | 1998 | IC98 | March-May | Jan. - Feb. | $PF = a\,L_{fork}^{\,b}$ | 0.83 | 59-129 | 88 | 5.458 | 0.000078 |
| IC | 1999 | IC99 | March-May | Jan. - Feb. | $PF = a\,L_{fork}^{\,b}$ | 0.88 | 59-133 | 102 | 4.102 | 0.05036 |
| IC | 2000 | IC00 | March-May | Jan. - Feb. | $PF = a\,L_{fork}^{\,b}$ | 0.86 | 63-131 | 96 | 4.538 | 0.00677 |
| NA | 1986 | NA86 | March - Apr. | Feb.-March | $PF = a\,L_{tot}^{\,b}$ | 0.89 | 55-135 | 50 | 3.778 | 0.12504 |
| NA | 1987 | NA87 | March - Apr. | Feb.-March | $PF = a\,L_{tot}^{\,b}$ | 0.81 | 52-86 | 25 | 3.841 | 0.08294 |
| NA | 1988 | NA88 | March - Apr. | Feb.-March | $PF = a\,L_{tot}^{\,b}$ | 0.91 | 50-122 | 49 | 3.907 | 0.06697 |
| NA | 1989 | NA89 | March - Apr. | Feb.-March | $PF = a\,L_{tot}^{\,b}$ | 0.92 | 50-126 | 111 | 3.358 | 0.85635 |
| NA | 1999 | NA99 | March - Apr. | Feb.-March | $PF = a\,L_{tot}^{\,b}$ | 0.75 | 67-121 | 94 | 3.629 | 0.2462 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| NA | 2000 | NA00 | March - Apr. | Feb.-March | $PF = a\,L_{tot}^{b}$ | 0.75 | 57-101 | 80 | 3.730 | 0.16214 |
| NA | 2003 | NA03 | March - Apr. | Feb.-March | $PF = a\,L_{tot}^{b}$ | 0.83 | 58-117 | 48 | 3.392 | 0.9078 |
| NA | 2004 | NA04 | March - Apr. | Feb.-March | $PF = a\,L_{tot}^{b}$ | 0.87 | 63-121 | 48 | 3.643 | 0.2425 |
| NC | 1964 | NC64a | March-July | Apr.-May | $\log PF = b\,\log L_{fork} + a$ | 0.87 | 50-105 | 28 | 3.630 | 0.2291 |
| NC | 1964 | NC64b | March-July | Apr.-May | $\log PF = b\,\log L_{fork} + a$ | 0.53 | 66-108 | 21 | 2.510 | 33.113 |
| NC | 1964 | NC64c | March - July | Feb.-March | $PF = a\,L_{fork} + b$ | 0.59 | 45-77 | 65 | 2.538 | 15.007 |
| NC | 1966 | NC66 | March-July | Feb.-March | $\log PF = b\,\log L_{fork} + a$ | | 61-118 | 12 | 2.963 | 3.9985 |
| NC | 1967 | NC67a | March-July | May | $\log PF = b\,\log L_{fork} + a$ | | 65-109 | 19 | 2.553 | 35.522 |
| NC | 1967 | NC67b | March-July | March May | $\log PF = b\,\log L_{fork} + a$ | | 60-108 | 28 | 3.684 | 0.1952 |
| NC | 1968 | NC68a | March-July | May | $\log PF = b\,\log L_{fork} + a$ | | 65-109 | 39 | 2.448 | 33.581 |
| NC | 1968 | NC68b | March-July | April | $\log PF = b\,\log L_{fork} + a$ | | 60-108 | 50 | 2.290 | 63.081 |
| NC | 1968 | NC68c | March-July | March-Apr. | $\log PF = b\,\log L_{fork} + a$ | | 61-118 | 50 | 1.145 | 8105.9 |
| NG | 1995 | NG95 | Apr-June | April-May | $PF = a\,L_{fork}^{b}$ | 0.70 | 37-65 | 53 | 3.964 | 0.065 |
| NG | 1998 | NG98 | Apr-June | April-May | $PF = a\,L_{fork}^{b}$ | 0.72 | 35-60 | 120 | 3.860 | 0.151 |
| NG | 2001 | NG01 | Apr-June | April-May | $PF = a\,L_{fork}^{b}$ | 0.79 | 37-90 | 220 | 3.265 | 1.4587 |
| NG | 2002 | NG02 | Apr-June | April-May | $PF = a\,L_{fork}^{b}$ | 0.73 | 38-65 | 72 | 3.527 | 0.499 |
| NS | 1969 | NS69 | Dec. - May | Dec. - May | $PF = a\,L_{tot}b$ | 0.65 | 41-86 | 52 | 2.973 | 7.0392 |
| NS | 1970 | NS70a | Jan. - Feb. | Jan. - March | $PF = a\,W + b$ | 0.81 | 60-130 | 45 | 4.186 | 0.0206 |
| NS | 1970 | NS70b | Dec. - May | Dec. - May | $PF = a\,L_{tot}b$ | 0.65 | 41-86 | 52 | 2.973 | 7.0392 |
| NS | 1971 | NS71 | Jan. - Feb. | Jan. - March | $PF = a\,W + b$ | 0.69 | 60-130 | 39 | 3.106 | 2.9094 |
| NS | 1972 | NS72 | Jan. - Feb. | Jan. - March | $PF = a\,W + b$ | 0.96 | 60-130 | 8 | 3.215 | 2.0326 |
| NS | 1999 | NS99 | Dec. - May | Jan. - March | $PF = a\,L_{tot}b$ | 0.97 | 27-97 | 47 | 3.743 | 0.2852 |
| NS | 2002 | NS02a | Dec. - May | Jan. - March | $PF = a\,L_{tot}b$ | 0.86 | 38-107 | 109 | 3.733 | 0.381 |
| NS | 2002 | NS02b | Dec. - May | Jan. - March | $PF = a\,L_{tot}b$ | 0.97 | 27-97 | 47 | 3.743 | 0.2852 |
| NS | 2003 | NS03a | Dec. - May | Jan. - March | $PF = a\,L_{tot}b$ | 0.86 | 38-107 | 109 | 3.733 | 0.381 |
| NS | 2003 | NS03b | Dec. - May | Jan. - March | $PF = a\,L_{tot}b$ | 0.97 | 27-97 | 47 | 3.743 | 0.2852 |
| SB | 1998 | SB98 | July-Sept | Apr.-mid-Jul | $PF = a\,L_{fork} + b$ | 0.38 | 45-75 | 27 | 2.942 | 4.5868 |
| SB | 1999 | SB99 | July-Sept | Apr.-mid-Jul | $PF = a\,L_{fork} + b$ | 0.63 | 50-75 | 16 | 2.610 | 19.026 |
| SC | 1964 | SC64 | Apr.-June | Apr.-May | $\log PF = b\,\log L_{fork} + a$ | 0.76 | 62-120 | 41 | 3.810 | 0.0891 |
| SC | 1965 | SC65a | Apr.-June | Apr.-May | $\log PF = b\,\log L_{fork} + a$ | 0.755 | 62-120 | 41 | 3.810 | 0.0891 |
| SC | 1965 | SC65b | Apr.-June | Apr.-May | $\log PF = b\,\log L_{fork} + a$ | 0.70 | 60-120 | 40 | 3.880 | 0.0537 |
| SG | 1980 | SG80 | Apr-mid July | May-June | $PF = a\,L_{fork}^{b}$ | 0.81 | 48-103 | 30 | 3.280 | 1.1 |
| SG | 1998 | SG98 | Apr-mid July | July | $PF = e^{a\,Lfork + b}$ | 0.37 | 58-90 | 35 | 3.139 | 1.2792 |
| SG | 1999 | SG99 | Apr-mid July | July | $PF = e^{a\,Lfork + b}$ | 0.71 | 40-90 | 30 | 3.734 | 0.1459 |
| SG | 1955-1956 | SG56 | Apr-mid July | May-Sept | $PF = a\,L_{fork}^{b}$ | 0.83 | 51-140 | 43 | 3.500 | 0.38 |
| SN | 1966 | SN66 | Feb.-July | Apr.-May | $\log PF = b\,\log L_{fork} + a$ | 0.52 | 64-113 | 96 | 2.420 | 53.703 |
| SN | 1967 | SN67 | Feb.-July | Apr.-May | $\log PF = b\,\log L_{fork} + a$ | | 51-128 | 13 | 2.710 | 12.549 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| SN | 1969 | SN69 | Feb.-July | March | $\log PF = b \log L_{fork} + a$ | | 51-128 | 43 | 3.485 | 0.1889 |
| SN | 1970 | SN70 | Feb.-July | Feb.-March | $\log PF = b \log L_{fork} + a$ | | 51-128 | 45 | 3.283 | 0.6488 |
| SN | 2001 | SN01 | Apr-June | April-May | $PF = a L_{fork}^{b}$ | 0.86 | 41-110 | 85 | 3.476 | 0.6646 |
| WS | 1969 | WS69 | Dec. - May | Dec. - May | $PF = a L_{tot}^{b}$ | 0.74 | 48-101 | 69 | 3.123 | 4.0716 |
| WS | 1970 | WS70 | Dec. - May | Dec. - May | $PF = a L_{tot}^{b}$ | 0.74 | 48-101 | 69 | 3.123 | 4.0716 |
| WS | 2002 | WS02 | Dec. - May | Jan. - March | $PF = a L_{tot}^{b}$ | 0.87 | 41-97 | 50 | 4.044 | 0.0838 |
| WS | 2003 | WS03 | Dec. - May | Jan. - March | $PF = a L_{tot}^{b}$ | 0.87 | 41-97 | 50 | 4.044 | 0.0838 |

Table 3.  Cod stocks and years included in each cluster.

| Cluster | Stock | Time period |
|---|---|---|
| 1 | Eastern Baltic | 1990; 1996a,b; 1999; 2000 |
| 2 | Eastern Baltic | 1991-1992; 1998 |
|  | North Sea | 1969; 1970b |
|  | West Scotland | 1969-1970 |
| 3 | Eastern Baltic | 1987; 1995a, b; 1996c |
| 4 | Eastern Baltic | 1989 |
|  | North Sea | 2002a; 2003a |
| 5 | Northern Gulf St. Lawrence | 1998 |
|  | North Sea | 1999; 2002b; 2003b |
|  | West Scotland | 2002-2003 |
| 6 | Southern Labrador & Eastern Newfoundland | 1964b, c; 1966; 1967a; 1968a, b; |
|  | Sidney Bight | 1998-1999 |
|  | Southern Newfoundland | 1966-1967 |
| 7 | Southern Labrador & Eastern Newfoundland | 1968c |
| 8 | Iceland | 1960; 1967 |
|  | Georges Bank | 2000 |
|  | Northeast Arctic | 1989; 2003 |
|  | Northern Gulf St. Lawrence | 2001-2002 |
|  | North Sea | 1971-1972 |
|  | Southern Gulf St. Lawrence | 1980 |
|  | Southern Newfoundland | 2001 |
| 9 | Flemish Cap | 1979 |
|  | Georges Bank | 1999 |
|  | Northeast Arctic | 1986-1988; 1999; 2000; 2004 |
|  | Southern Labrador & Eastern Newfoundland | 1964a; 1967b |
|  | North Sea | 1970a |
|  | SC | 1956; 1964; 1965a, b |
|  | Southern Gulf St. Lawrence | 1999 |
| 10 | Southern Gulf St. Lawrence | 1998 |
|  | Southern Newfoundland | 1969-1970 |
| 11 | Iceland | 1995-1997; 1999-2000 |
|  | Northern Gulf St. Lawrence | 1995 |
| 12 | Flemish Cap | 1984 |
|  | Iceland | 1998 |
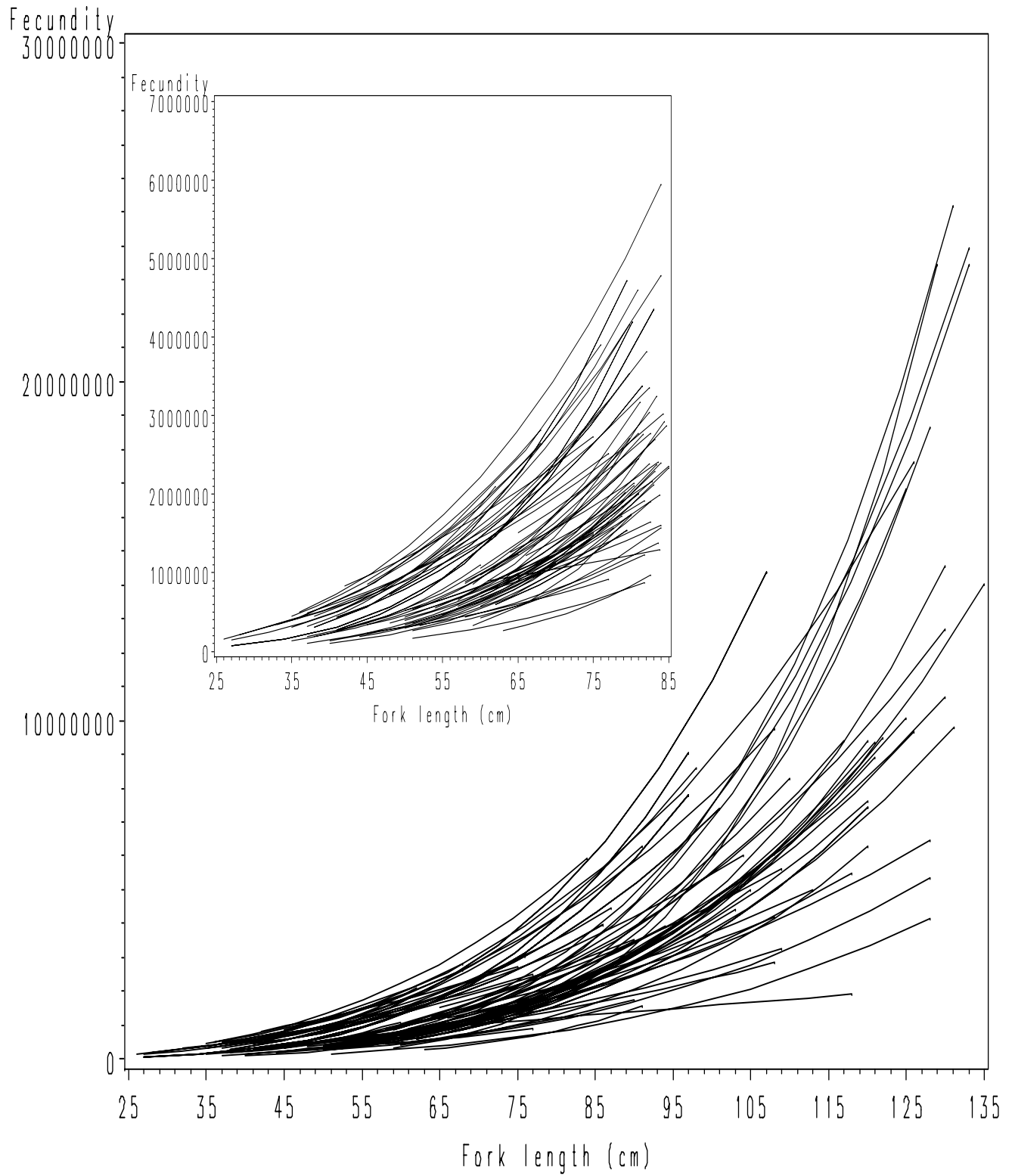
Fig. 1. Power regressions describing the relationships between potential fecundity and length of cod for the different stocks and years.
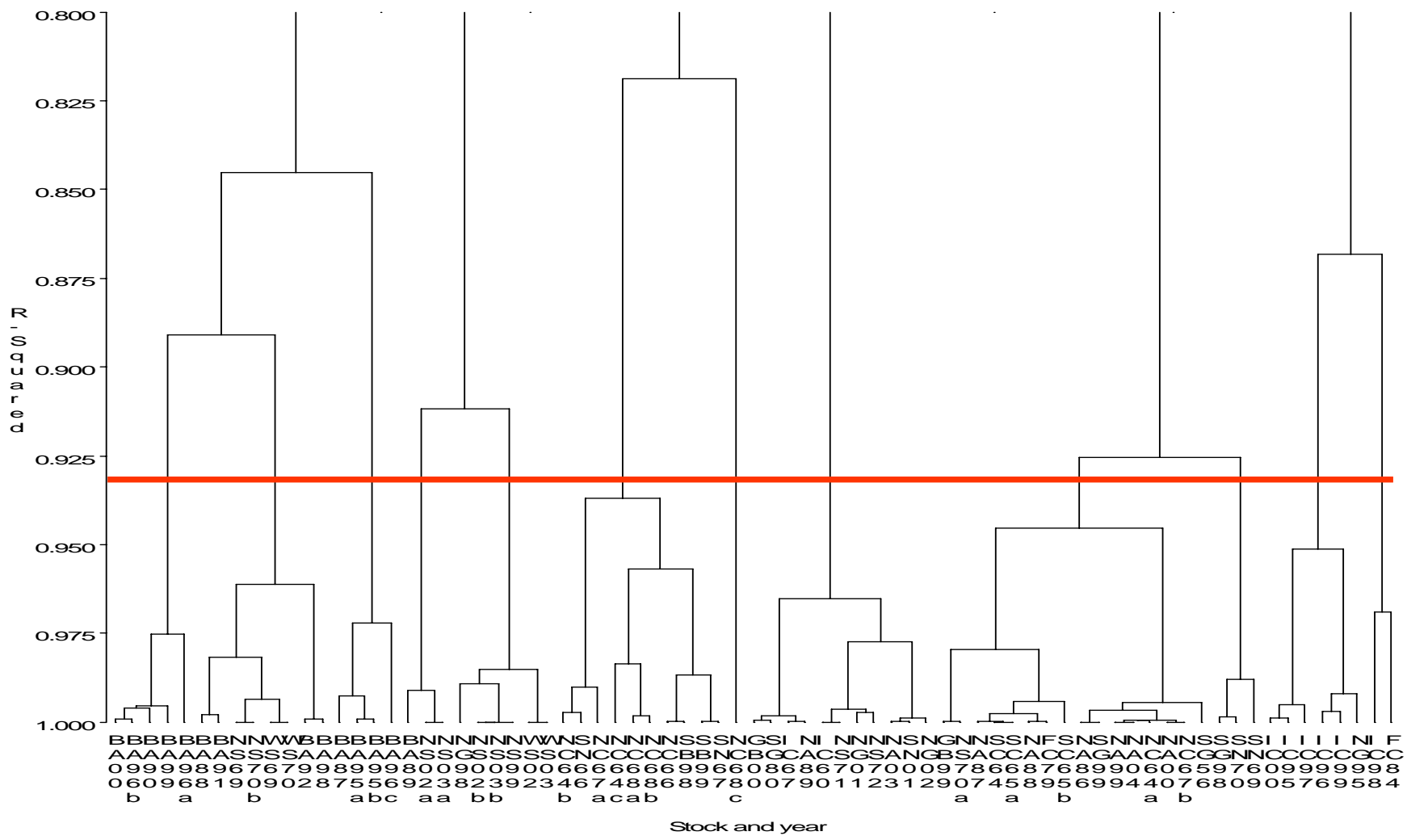
Fig. 2. Hierarchical cluster tree of the potential fecundity of the 13 stocks for different years using potential fecundity at 60 cm and the slope of the relationship between potential fecundity and length as variates. The reference line indicates the level used to delineate clusters.
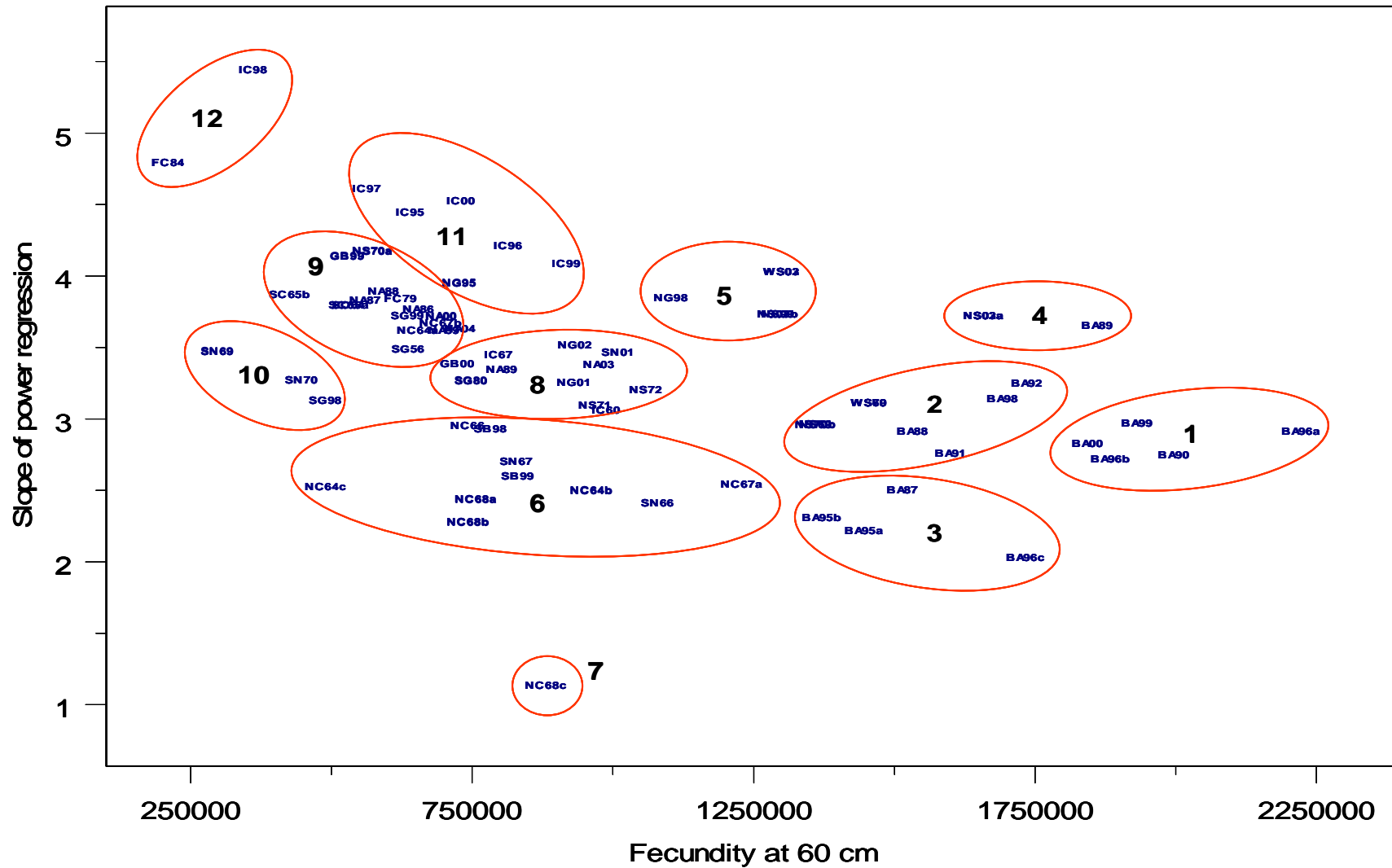
Fig. 3. Groups of cod stocks and years resulting from cluster analysis realised with potential fecundity at 60 cm and the slope of the regressions between potential fecundity and fork length. Data points represent stock membership and year of sampling (Table 2).
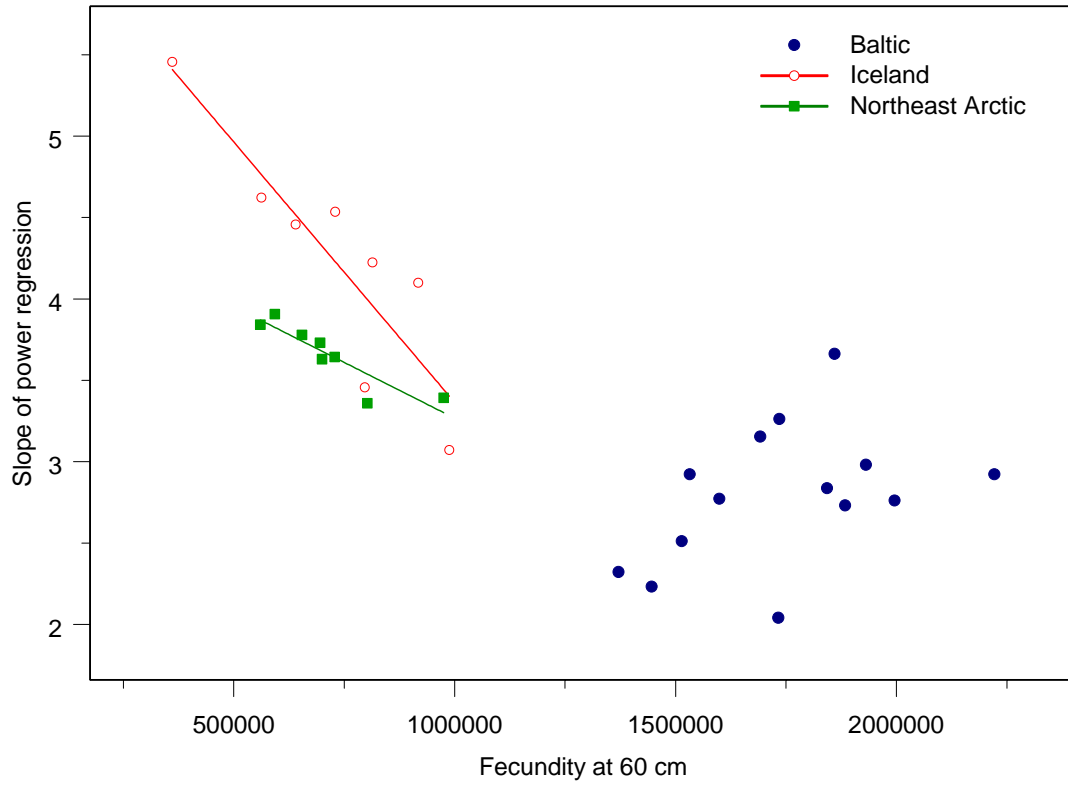
Fig. 4. Relationships between fecundity at 60 cm and the slope of the fecundity-length relationship for Eastern Baltic, Iceland and Northeast Arctic cod.
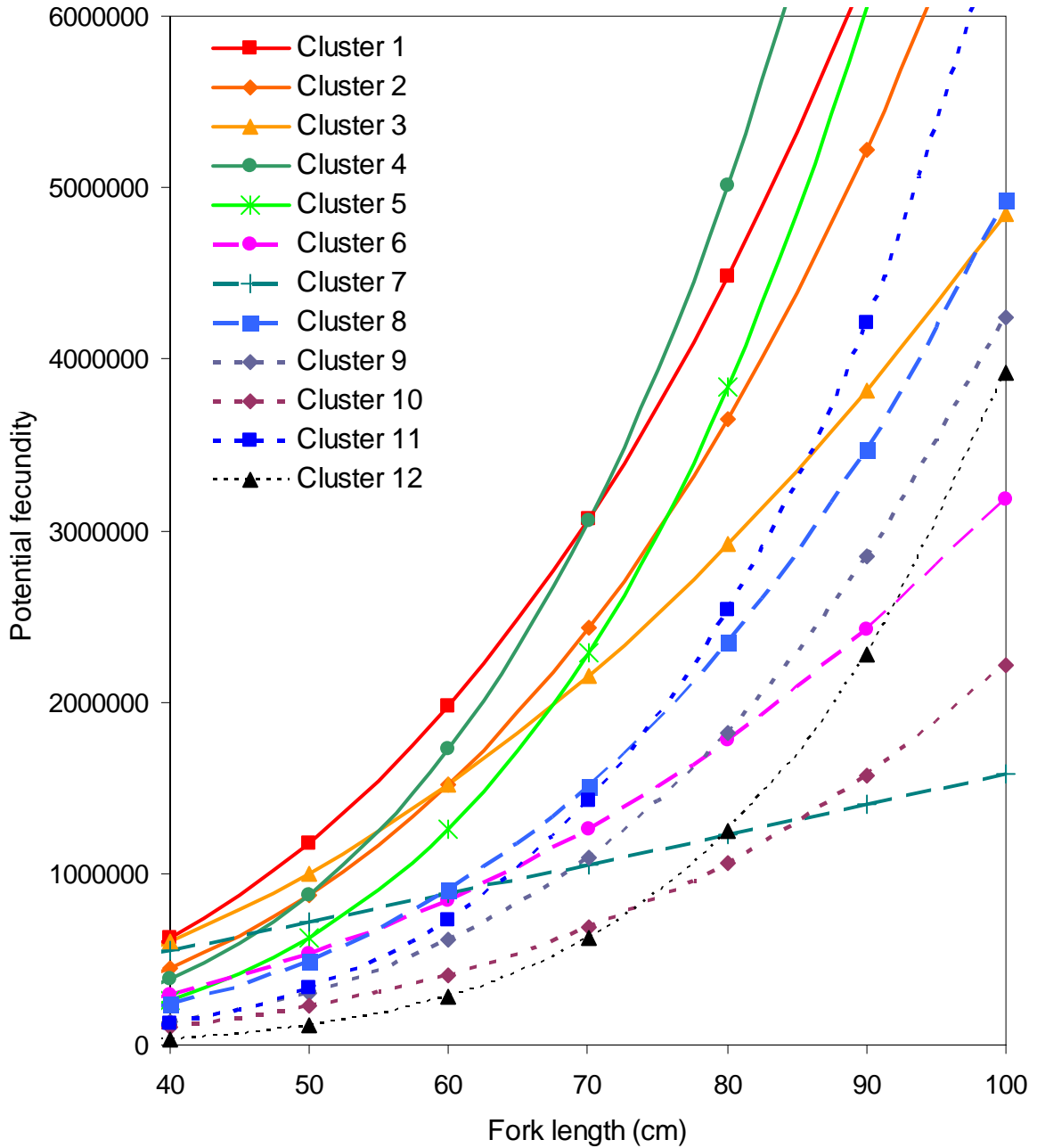
Fig. 5. Relationship between potential fecundity and length for each cluster estimated from mean slope and fecundity at 60 cm within each cluster.