



SCIENTIFIC COUNCIL MEETING - 2008

Report of the NAFO Scientific Council Working Group on Reproductive Potential

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Progress of the NAFO Working Group on Reproductive Potential was provided by E.A. Trippel (Chair). The establishment of the Working Group on Reproductive Potential followed a recommendation of the Symposium on "Variations in Maturation, Growth, Condition and Spawning Stock Biomass Production in Groundfish" hosted by NAFO Scientific Council from 9-11 September 1998, Lisbon, Portugal. The Working Group is comprised of 21 members representing 8 countries (Canada, Denmark, Iceland, Norway, Russia, Spain, United Kingdom, and USA).

The 7th Meeting of the NAFO WG on Reproductive Potential was held at IPIMAR in Lisbon, Portugal, October 4-6, 2007. There were 17 WG participants spanning 8 countries: Tara Marshall (UK), Richard Nash (Norway), Olav Kjesbu (Norway), Gerd Kraus (Denmark), Joanne Morgan (Canada), Rosario Dominguez (Spain), Loretta O'Brien, (USA), Nathalia Yaragina (Russia), Yvan Lambert (Canada), Rick Rideout (Canada), Peter Witthames (UK), Hilario Murua (Spain), Peter Wright (UK), Holger Haslob (Germany), Rich McBride (USA), Fran Saborido-Rey (Spain) and Ed Trippel (Canada). A meeting of the EU COST Research Network Action Fish Reproduction and Fisheries (FRESH) (Coordinator: Fran Saborido-Rey) was also held during this period. Mutual benefits of having the two groups meet together were achieved as both have complimentary science and management advice objectives. Local arrangements for the meeting were provided by Joao Periera (IPIMAR, Lisbon, Portugal) which were greatly appreciated.

The objectives of the WG meeting were to review and discuss (i) material from 2nd set of ToRs (Co-Leaders providing brief overviews), (ii) findings of the NAFO/PICES/ICES Symposium on Reproductive and Recruitment Processes of Exploited Marine Fish Stocks held in Lisbon Oct 1-3, (iii) break-out groups for discussion of final items of 2nd set of ToRs (data analyses, MS prep/edits, publications), (iv) new lines of research, for development of a 3rd set of ToRs to be presented to NAFO Scientific Council in June 2008, (v) selection of candidate new ToR Co-Leaders. The joint meetings with FRESH allowed the WG to be aware of the planned work of that group. The WG will follow the work of FRESH closely and incorporate the results of that group into its own work where appropriate. This will avoid duplication of effort between the groups and allow the WG to bring more results to the attention of Scientific Council.

Significant progress on the majority of the second set of ToRs was achieved over the previous year, both during the meeting and intersessionally, however ToRs 1 and 6 were relatively inactive. A brief summary of progress and future plans of each ToR are given below. In addition, significant progress was made towards drafting a 3rd Set of Terms of References. The update on the 2nd Set of ToRs and the newly drafted 3rd Set of ToRs were presented to NAFO Scientific Council in June 2008.

2nd Set of Terms of References

ToR 1: Co-Leaders: Jonna Tomkiewicz (Denmark) and Jay Burnett (USA)

Complete inventory of available data in standardized format on reproductive potential for fish stocks of the North Atlantic and Baltic Sea.

Members: everyone

Shifts in emphasis of the work activities of the two ToR Co-Leaders in their respective institutes have led to an inability to make progress for this ToR. NAFO Scientific Council Studies Number 37 produced by the NAFO WG on Reproductive Potential remains as the sole source for summarizing availability of data for estimating reproductive potential for selected stocks in the North Atlantic (n= 53 stocks).

ToR 2: Co-Leaders: Yvan Lambert (Canada) and Gerd Kraus (Germany)

Explore the use of correlation analysis to estimate the reproductive potential of fish stocks having limited data availability.

Members: Hilario Murua (Spain), Nathalia Yaragina (Russia), Gudrun Marteinsdottir (Iceland), Peter Wright (UK), Peter Witthames (UK)

ToR 3: Co-Leaders: Hilario Murua (Spain) and Gerd Kraus (Germany)

Model the inter-annual and inter-stock variability in size-dependent fecundity for stocks having multi-year estimates.

Members: Olav Kjesbu (Norway), Peter Witthames (UK), Rick Rideout (Canada), Tara Marshall (UK), Yvan Lambert (Canada), Gudrun Marteinsdottir (Iceland)

The above two terms of reference are related and have been joined.

The objectives of these two ToRs are to (i) identify patterns of variation in fecundity between different stocks of the same species, (ii) find environmental and biological factors that explain these patterns of variation and (iii) assign data poor stocks to environmental data groups and apply fecundity models of rich stocks of the same environmental data group to predict fecundity.

The results on the variability in the fecundity of cod between several stocks and years presented in the previous year constituted the basis of a manuscript presented at the Symposium on Reproductive and Recruitment Processes of Exploited Marine Fish Stocks in Lisbon in October 2007. In this paper, the pertinence for closely monitoring fecundity of marine fish species was examined. The importance and scale of variation in potential fecundity was first examined using as specific examples Atlantic cod (*Gadus morhua*) and herring (*Clupea harengus*) (Fig. 1). It was apparent that fecundity could vary widely between individuals of the same population (e.g., by female size), and between years, populations, and species. Furthermore, these variations were likely to be adaptive and such variation had obvious importance for stock assessment and management of fisheries.

It was hypothesized that the absence of time series on fecundity was associated with the large use of SSB as a proxy of reproductive potential and stock-recruitment relationships in age-structured population models. The lack of fecundity data is often the result of the fact that the measurement of fecundity was time consuming and costly. However, many studies demonstrate that SSB may not be a good proxy of reproductive potential. New methodological developments are allowing more time efficient measurement of fecundity. Using an “auto-diametric method” with cod, it is shown that the calibration curve necessary for the determination of fecundity does not vary between years within a stock and between stocks of the same species (Fig.2) indicating that this method can be of general application and can be used as a tool to easily monitor yearly variations in potential fecundity.

The variability in potential fecundity between years observed for different species and stocks has been analysed in relation to influential factors known to modulate potential fecundity. These relations were used to develop generalized linear models explaining interannual variations in potential fecundity for different cod and haddock stocks. For example, differences in the potential fecundity-length relationships observed between the years for cod in the northern Gulf of St. Lawrence were associated with differences in the mean condition factor of maturing fish sampled at the same periods and years (Fig. 3). This dependence of potential fecundity on length and condition factor was evaluated using a multiple regression model. Both fork length and condition factor had significant effects on potential fecundity and the regression model explained 79% of the total variability in potential fecundity (Table 1).

Generalized linear models using co-variate or multiple regression factors to incorporate significant influential factors explaining inter-annual variations in potential fecundity can thus advantageously be used to hindcast and predict variations in potential fecundity. The combination of time series of potential fecundity data obtained from monitoring and/or the development of generalized linear potential fecundity models to demographic parameters largely available for exploited marine fish stocks allows the monitoring of total egg production of stocks (TEP). Numerous studies indicate that estimates of reproductive potential produced by including this

improved biological information on reproductive characteristics (including potential fecundity) changed the perception of the size of some spawning stock and levels of stock productivity.

The monitoring of TEP from yearly determinations of fecundity and other demographic parameters commonly measured (population numbers-at-age, lengths-at-age, sex ratio-at-age, proportion of females that are mature-at-age) provides the empirical values for key life history traits necessary for the calculation of the intrinsic rate of population increase (r), an essential parameter in population dynamics and evolutionary ecology. This approach applied to cod in the northern Gulf of St. Lawrence indicated that the values of the intrinsic rate of population increase estimated from a close monitoring of the reproductive potential were lower than previous estimates based the general characteristics of the stocks (Table 2). These low empirical values of the intrinsic rate of population increase for the NGSL cod stock are not unexpected and could be realistic since this stock that collapsed in the early 90's has not shown signs of recovery. Development of this analytical approach, beginning with collection of the required fecundity data, may lead to considerable advancement of our understanding of the productivity and resiliency of exploited fish stocks. Such information has practical application to determine stock rebuilding strategies, to examine the impact of fishing on rebuilding time, and to disentangle the relative role of different demographic parameters (growth, age at maturity, fecundity, juvenile and adult survival etc.) on r and recovery.

ToR 4: Co-Leaders: Tara Marshall (UK) and Joanne Morgan (Canada)

Explore how the current use of biological reference points and medium-term projections can be adapted to include new information on reproductive potential.

Members: Loretta O'Brien (USA), Hilario Murua (Spain), Gudrun Marteinsdóttir (Iceland), Gerd Kraus (Germany), Yvan Lambert (Canada), Jonna Tomkiewicz (Denmark).

A manuscript has been completed (and a poster presented at the Symposium on Reproductive and Recruitment Processes of Exploited Marine Fish Stocks) exploring the impact of alternative indices of reproductive potential (RP) on perceptions of population productivity. Data from 8 populations from across the north Atlantic were available. These were Georges Bank cod (*Gadus morhua*, NAFO Div. 5Z), northern Gulf of St. Lawrence cod (NAFO Div. 3Pn4RS), southern Grand Bank cod (NAFO Div. 3NO), Grand Bank American plaice (*Hippoglossoides platessoides*, NAFO Div. 3LNO), Icelandic cod (ICES Div. Va), Northeast Arctic cod (ICES Subareas I and II), Baltic cod (ICES III d SD 25-32), and northern hake (*Merluccius merluccius*, ICES Div. IIIa, SA II, IV, VI, VII and Div. VIIIa, b, d). For each population, four indices of reproductive potential were calculated. The four indices of RP started with an assumption of constant reproductive characteristics (RP_{CONSTANT}) and then included increasing biological complexity, adding variation in maturation (RP_{SSB}), sex ratio (RP_{FSB}) and fecundity (RP_{TEP}). Perceptions of stock productivity were greatly affected by the choice of index of RP. Population status relative to reference points (Fig. 4), RP per recruit and projections of population size all varied when alternative indices of RP were used (Fig. 5). There was no consistency in which index of RP gave the highest or lowest estimate of population productivity, but rather this varied depending on how much variation there was in the reproductive biology of the population and the age composition (Fig. 6). Estimates of sustainable harvest levels and recovery time for depleted populations can vary greatly depending on the index of RP.

ToR 5: Co-Leaders: Peter Wright (UK) and Ed Trippel (Canada)

Explore the consequences of fishery-induced changes in the timing and location of spawning to reproductive success.

Members: Jonna Tomkiewicz (Denmark), Saborido-Rey (Spain), Rick Rideout (Canada), Chris Chambers (USA), Joanne Morgan (Canada), and Gudrun Marteinsdottir (Iceland)

This topic is being explored by a review of the theory and evidence that spawning time varies and early survivorship of progeny is related to birth date. A manuscript entitled "Fishery-induced demographic changes in the timing of spawning: consequences to reproductive success" was submitted to Fish and Fisheries in March 2008. This review considers the consequence of reproductive timing to progeny survival and the effect that reductions in the size and age composition of the spawning stock have on this relationship. In many multiple batch spawners, individuals spawn progressively earlier within a season and produce more egg batches over a

longer period as they get older, thus extending their lifetime spawning duration. As a consequence stock demography can have a significant effect on reproductive timing and the magnitude of such an effect can be comparable to environmentally induced variability. Empirical estimates of selection on birth date, from experiments and using otolith microstructure, demonstrate that there is considerable variation in selection on birth date within a spawning season. The few multi-year studies that have linked egg production with the survival of progeny to the juvenile stage further highlight the uncertainty that adults face in timing their spawning to optimise offspring survival (see Figure 7). The production of many small batches of eggs over a long period of time within a season is likely to decrease the variance and increase the mean progeny survival. Hence, by reducing the average lifetime spawning duration within a fish stock, fishing pressure could be increasing the variability in reproductive success and reducing the long term reproductive potential of a stock. Modelling approaches are suggested to better quantify the likely impact of changing spawning times on year-class strength and life-time fitness. Nevertheless, the evidence presented strengthens the need to avoid severely age truncated fish stocks.

A second study on the effect of age on spawning time in gadoids based on maturity data from regular research survey sources is also being conducted. Progress has been slow although the content of the manuscript was decided at the Lisbon meeting and most analyses have now been conducted. The ToR members intend to have the manuscript complete by the next NAFO WG meeting with the lead author being either Peter Wright or Rick Rideout. Regular research survey sources do not provide the ideal source of data for this analysis because the temporal resolution is too short to examine the response of the two key transitions between developing and spawning and spawning and spent. Therefore, all analyses were standardised to considering proportion spent. Generalized linear models with logit link function and binomial error were used to estimate the proportion of spent fish on each day and the day of the year on which 50% of the fish were spent. Unlike some past studies the effect of age was modelled as a discrete (or class) variable since there was no a priori reason to expect that the effect of age would be continuous. To examine the data for a possible year:age interaction the results of the above model were compared to a model that did not contain a year effect. Overdispersion was a common problem in the data and so standard errors were inflated by a dispersion parameter. Examples of the modelled age effect in females for the stocks considered is given in Figure 8. Note that the spent condition is reached earlier in the year for younger vs. old individuals of each species.

ToR 6: Co-Leaders: Fran Saborido-Rey (Spain) and Joanne Morgan (Canada)

Provide recommendations for the collection of required data in existing research surveys, sentinel fisheries and captive fish experiments that are required to improve annual estimates of reproductive potential for stocks varying in data availability.

Members: Anders Thorsen (Norway), Rick Rideout (Canada), Ed Trippel (Canada), Jonna Tomkiewicz (Denmark), Pauline King (Ireland), and Jay Burnett (USA).

Recently a COST Research Network Action has been approved (COST Action FA0601 “Fish Reproduction and Fisheries”). The NAFO WG recommended including workshops 1-3 detailed below as part of the events to be organized within the COST Action. These 3 workshops will be organized in 2008-2010. The fourth workshop was discussed at the June 2008 Scientific Council meeting and is recommended to form part of the 3rd Set of ToRs for the NAFO WG on Reproductive Potential.

Four (4) workshops are being considered:

1. *Methodology and quantification using stereology (relatively limited number of species)*

- Gametogenesis patterns in our commercial species males and females, comparison of macroscopic vs. histology assessment and linking macroscopic images and histological descriptions.
- Criteria to interpret follicle stages in whole mounts. Rates of follicle growth and regression and identification of females that skip spawning using POFS and ovary Tunica diameter.
- Quantification using auto diametric and Dissector methods.

2. *Identification and classification of reproductive strategies (including range of species with families having different reproductive strategies)*

- Comparison of female and male gametogenesis across species and reproductive strategies.
- Consideration of different aspects for classifying the reproductive strategy of teleosts.

- Discussion of methodology needed to assess reproductive strategies.
- Useful protocols for staining various cells components and structures.
- Agree on guidelines and produce an illustrated atlas on reproductive strategies and comparative gametogenesis.

3. *Fecundity of determinate and indeterminate teleosts (examples of different types)*

- Different methodologies to assess fecundity of determinate and indeterminate female spawners.
- Methods to identify and quantify atresia.
- Estimation of potential and realized egg production of determinate and indeterminate spawners.
- Methods to determine male spermatozoa production and fertilization capacity?

4. *Incorporating estimates of reproductive potential into stock assessment*

- Data necessary for estimating reproductive potential.
- Considerations for the collection and analyses of data on reproductive potential.
- Hands on work on incorporating existing data.

ToR 7: Co-Leaders: Loretta O'Brien (USA) and Nathalia Yaragina (Russia)

Explore the effects of the environment on Stock Reproductive Potential and how these relate to ToRs 2, 3 and 4.

Members: Chris Chambers (USA), Gerd Kraus (Germany), Rick Rideout (Canada), Yvan Lambert (Canada), Olav Kjesbu (Norway), Anders Thorsen (Norway), Tara Marshall (UK), Coby Needle (UK).

Environmental influences on stock reproductive potential (SRP) were investigated using the intrinsic rate of population increase r , derived from life table analysis, that incorporates characteristics (e.g. growth rate, fecundity, etc.) which are also associated with SRP.

Trends in r were compared among nine Atlantic cod *Gadus morhua* stocks (Northern Gulf of St. Lawrence, Northeast Arctic, Georges Bank, Gulf of Maine, Baltic, Icelandic, Irish Sea, Flemish Cap, and West of Scotland) with time series varying in length between 22 and 56 years for the time period 1946-2005 (Fig. 9). Cod west of Scotland had the highest r over the observed period while Northern Gulf of St. Lawrence cod had the lowest r . Tests for significant differences of mean r between stocks indicated **six** distinct groups, for example, cod from Northern Gulf of St. Lawrence and West of Scotland were significantly different from each other and the other four stock-groups (Table 3).

Further work includes:

- Incorporate annual survivorship
- Derive model based annual estimates of fecundity
- Explore what factors differentiate these stocks into 6 groups
- Estimate variance of input data to Euler-Lotka equation
- Conduct simulations to test sensitivity of r to input values

FUTURE ACTIVITIES

The 8th Meeting of the NAFO Working Group on Reproductive Potential is proposed to be held in Palermo, Italy during November 17-21, 2008. This will be the kick-off meeting for the 3rd Set of ToRs. It is proposed that this be a joint meeting with COST/FRESH to help facilitate mutual progress and collaboration where relevant on these important fishery science and management initiatives. The NAFO/PICES/ICES Symposium clearly confirmed the benefits that can be achieved by the integration of reproductive biology into the study and management of global marine stocks. The continued poor record of recruitment and stock recovery signals the

importance of investing further energy into this area of fishery science and its application to NAFO scientific advice.

Discussion was made of the possible entry into a formal relationship between NAFO and COST/FRESH. It was recommended that the two groups maintain an informal working relationship as this type of relationship is adequate to develop the collaborations among scientists that would be beneficial towards addressing the ToRs.

3rd Set of Terms of Reference

ToR 1: Explore and conduct evaluation of underlying assumptions of protocols used to estimate total realized egg production of selected marine species and stocks

Co-Leaders: Rick Rideout (DFO, Canada) and Rosario Dominguez (CSIC, Spain)

Several marine laboratories in the North Atlantic have initiated routine fecundity estimation for key fish stocks. This information is being used to (i) help improve the estimation of stock reproductive potential (ii) understand population productivity and (iii) predict stock recovery rates. However, there is a lack of standardization and calibration of various methods to estimate fecundity among laboratories. For example, some laboratories have only recently initiated the autodiometric method and are developing appropriate calibration curves. On the other hand, observations have been made that indicate atresia and timing of sampling can influence estimates of total egg production. Techniques to quantify atresia (vitellogenic oocyte resorption) will be developed and evaluated in this ToR. This will involve histological analyses accompanied by computerized image analysis.

Establish Standard Operating Procedures:

- Provide uniform and standardized procedures for routine fecundity analyses in laboratories using a variety of methods, i.e. autodiometric method, image analysis
- Evaluate histological techniques for assessment of atresia

Validation of Assumptions:

- Test assumptions of different fecundity methods (i.e. the autodiometric method) and parameters associated with fecundity estimation
- Estimate down regulation of fecundity and quantification of atresia and non-annual spawning

ToR 2: Explore and investigate the potential effects of changes in water temperature and food supply on reproductive success in selected marine species and stocks

Co-Leaders: Richard McBride (NMFS, USA) and Stylianos Somarakis (HCMR, Greece)

Environmental factors can modify the reproductive potential of fish stocks and thereby influence recruitment. Annual variations in water temperature and potential increases due to climatic warming will presumably act strongly to influence gonadal development and reproductive success. Prey resources also vary and influence fish condition which in turn affects reproductive output. In this ToR, using data on specific stocks and laboratory experiments, the influence of specific abiotic and biotic factors on gonadal development and spawning will be evaluated pending available data.

Abiotic: Examine changes in water temperature (short and long-term) and their effects on timing and duration of spawning, fecundity, egg size and fertilization success

Biotic: Assess variation in prey resource type and abundance and their effects on egg production and gamete quality

ToR 3: Undertake appraisal of methods to improve fish stock assessments and fishery management advice that incorporate new biological data for highly exploited and closed fisheries

Co-Leaders: Joanne Morgan (DFO, Canada) and Loretta O'Brien (NMFS, USA)

The depressed and age-altered state of many marine fish stocks has led to reduced landings and in some instances fishery closures. New biological data associated with these altered states will be used to forecast recruitment and improve the accuracy of stock assessment advice. Building on information from previous WG ToRs, the intrinsic rate of population increase will be utilized to assess the timeframe for selected stocks to recover under various fishing and environmental conditions.

Recruitment prediction: Improve prediction of incoming year class size and develop new stock-recruitment models and biological reference points based on better estimates of stock reproductive potential. This includes testing whether more complex indices of reproductive potential result in better estimates of recruitment and limit reference points. Develop scenarios which model population reproductive responses to extrinsic factor data developed in ToR 2.

Stock recovery: Evaluate the intrinsic rate of increase of selected stocks under differing conditions of reproductive potential and levels of fishing mortality to aid in the development of reopening criteria. Estimate recovery time for specific stocks to achieve target biomass levels.

Egg production methods can estimate spawner biomass and/or stock numbers independently of commercial fisheries data. Improved information on stock reproductive potential is improving the accuracy of these methods. The daily egg production method is being explored to evaluate adult stock size for determinate spawning species in the Baltic and North Seas. For this ToR a meta analysis/review of this topic will be conducted to inform Scientific Council of advances in this area.

ToRs will be explored for stocks in the NAFO area where possible (e.g. 3NO cod, 3LNO American plaice, 3M cod, 3LNO yellowtail flounder, 2+3KLMNO Greenland halibut; Georges Bank cod) but stocks from the northeast Atlantic will be included as additional sources of information.

NAFO Scientific Council approved the new set of ToRs and recommended the development of a Workshop on ToR 3. This Workshop should be held in ~3 years to help facilitate the transfer of techniques developed by WG members to stock assessment personnel that routinely conduct NAFO stock assessments. It is anticipated that one of the outputs of this workshop will be a manual on the integration of data on reproductive potential into stock assessments.

Table 1. Summary statistics of the multiple regression model relating potential fecundity to fork length and somatic condition factor (Ks) for cod in the northern Gulf of St. Lawrence. Fish sampled in the years 1995, 1998, 2001, and 2002 were used for the analysis.

	d.f.	Sum of Sq	Mean sq	F	Pr(F)
ln (Length)	1	133.5529	133.5529	1637.585	< 0.0001
ln (Ks)	1	8.6658	8.6658	106.257	< 0.0001
Residuals	459	37.4337	0.0816		

Model: $fec = \exp(-14.525 + 3.630 \ln(L) + 1.515 \ln(Ks))$ $r^2 = 0.79$

Table 2.. Intrinsic rate of population growth (r), annual rate of increase in percent per year (% / year) and doubling time in years (DT) for different cod stocks in the Northwest Atlantic.

	Stock	R	% / year	DT
Present study	N. Gulf of St. Lawrence (3Pn4RS)	0.023 – 0.12	2.3 – 12.9	5.7 – 30.1
Myers et al. (1997)	Labrador/N.E.	0.17	18.5	4.1
	Newfoundland (2J3KL)	(corrected to 0.26)	(29.7)	(2.7)
	S. Grand Bank (3NO)	0.27	31.0	2.6
	N. Gulf of St. Lawrence (3Pn4RS)	0.20	22.1	3.5
	St. Pierre Bank (3Ps)	0.31	36.3	2.2
	S. Gulf of St. Lawrence (4TVn)	0.15	16.2	4.6
Hutchings (1999)	Labrador/N.E. Newfoundland (2J3KL)	0.14 - 0.16	15.0 – 17.4	4.3 – 5.0

Table 3. SNK multiple range test indicating 6 significant groups of intrinsic rate of increase ' r ' for 12 Atlantic cod stocks.

SNK Multiple Range Test on Means			
Group	Mean	Years	Stock
A	0.5411	16	West of Scotland
B	0.4873	16	Irish Sea
C	0.3408	16	Baltic 26
C	0.3345	16	Baltic 25
C	0.3257	16	NE Arctic
C	0.3166	16	Flemish Cap
D	0.2892	16	Baltic 28
D	0.2817	16	Gulf of Maine
D	0.2813	16	Icelandic
E	0.2649	16	Georges Bank
E	0.2431	16	Baltic 25-32
F	0.0304	16	No.Gulf of St. Lawrence

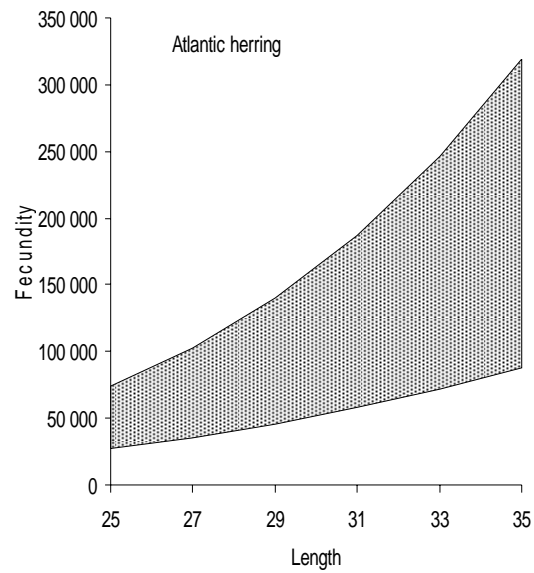
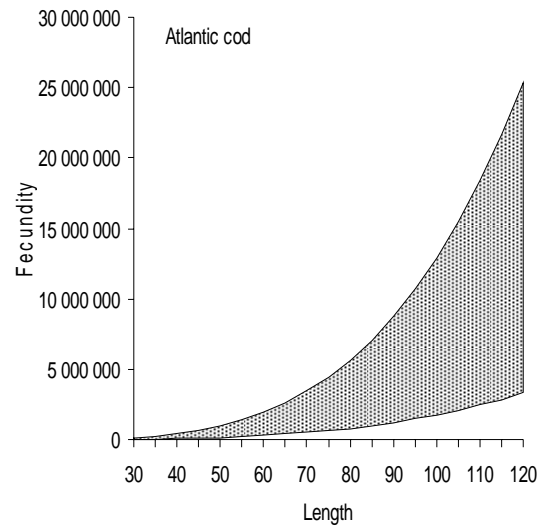


Figure 1. Range of variation in the potential fecundity of Atlantic cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus*). Minimum and maximum values of potential fecundity for each species were obtained from fecundity-length relationships observed for different populations, geographic areas and years.

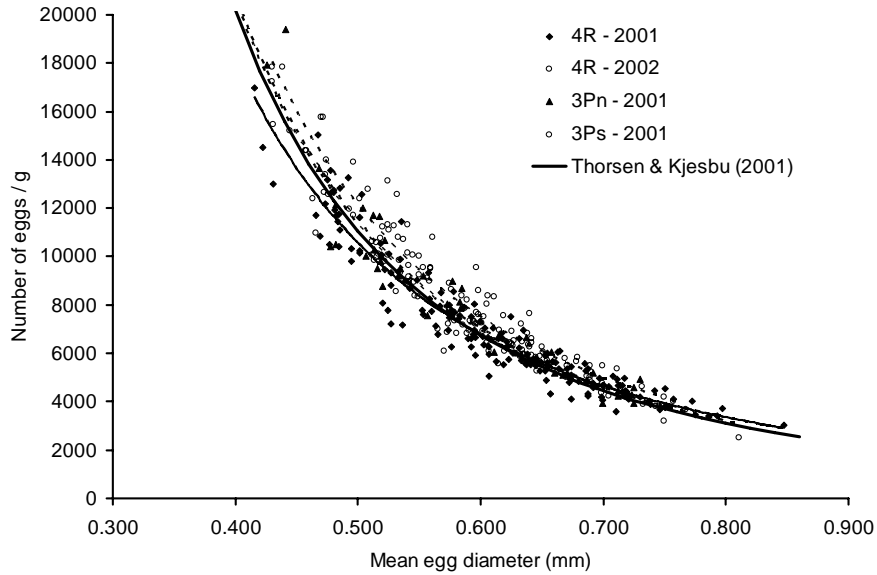


Figure 2. Relationship between mean egg diameter and number of eggs/g for Atlantic cod sampled in different areas and years. Data for cod from the northern Gulf of St. Lawrence (4R and 3Pn) and southern Newfoundland (3Ps) are presented along with the relationship obtained by Thorsen and Kjesbu (2001) for Northeast Arctic cod.

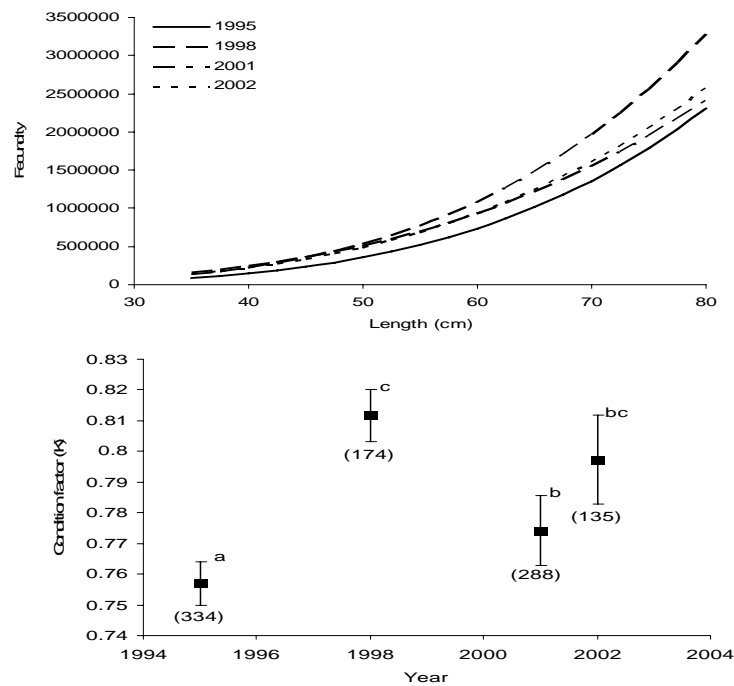


Figure 3. Fecundity-length relationships (upper panel) and mean condition factor of maturing cod (lower panel) in the northern Gulf of St. Lawrence in 1995, 1998, 2001, and 2002. Significant differences in the condition factor between years are identified by different letters. Number of female fish for each year are presented in parenthesis.

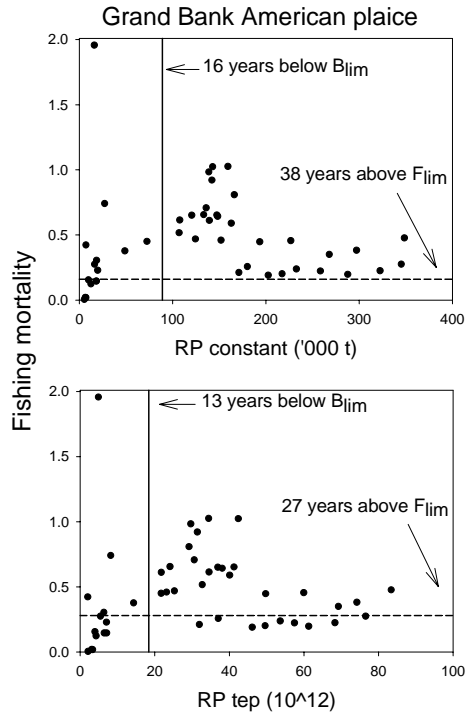


Figure 4. Index of RP and Fishing mortality for Div. 3LNO American plaice for two different indices of RP (constant and total egg production). The vertical lines indicate B_{lijm} and the dashed horizontal lines F_{lijm} . Reference points were calculated separately for each index of RP.

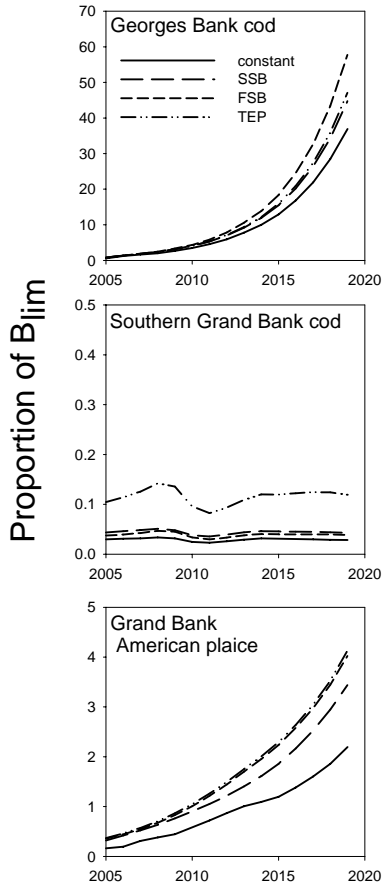


Figure 5. Proportion of B_{lim} for each index of reproductive potential to $RP_{constant}$ for 3 populations for every year of 15 year projections (at $F=0$) of population size.

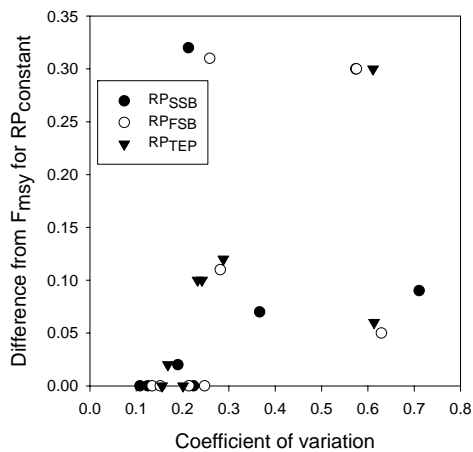


Figure 6 Absolute value of F_{MSY} estimated for the particular index of RP minus the F_{MSY} estimated for that population for $RP_{constant}$ plotted against the coefficient of variation of the ratio of each index of RP to $RP_{constant}$. Different symbols represent the different indices of reproductive potential.

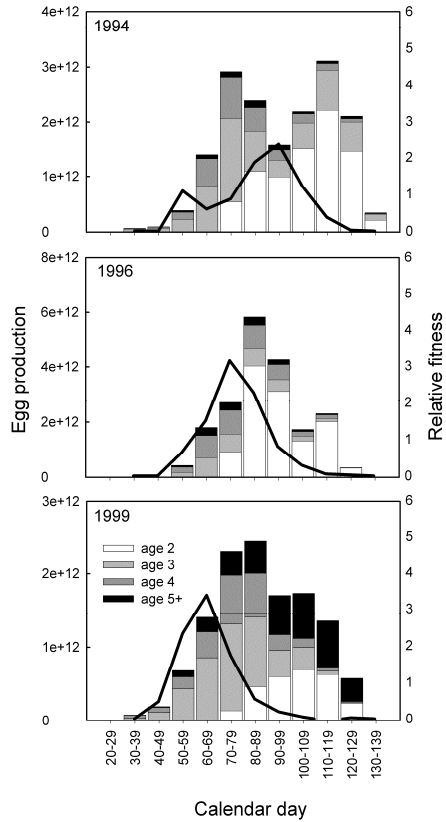


Figure 7. Temporal changes in age-stratified egg production of North Sea haddock and relative fitness (bold curve) based on the difference in proportions of eggs produced and demersal juveniles for a given date from the 1994, 1996 and 1999 year-classes. Re-drawn from Wright and Gibb (2005).

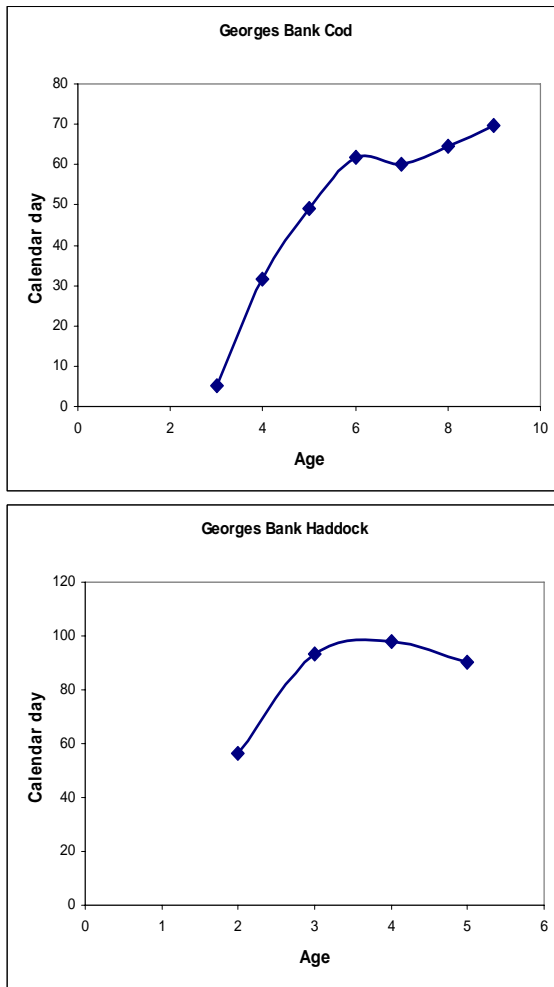


Figure 8. Age related differences in the proportion of 50% spent female Atlantic cod and haddock of Georges Bank in relation to calendar day.

Estimates of r for each stock

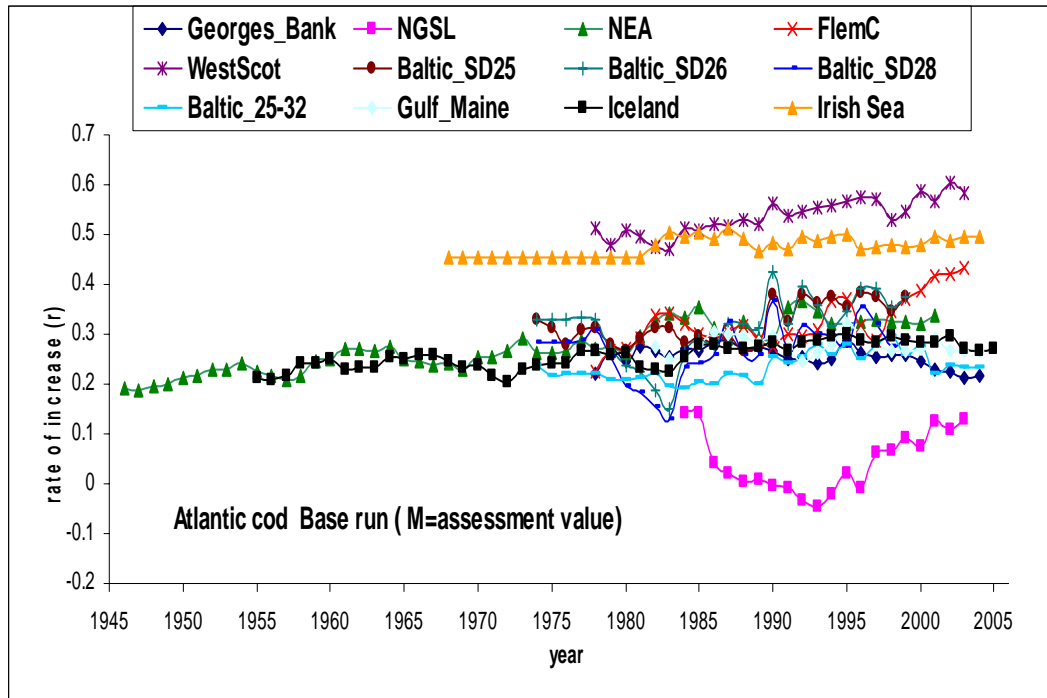


Figure 9. Estimates of the intrinsic rate of population increase, ' r ', for 12 Atlantic cod stocks.