Evaluation of a new method for estimating the maximum annual reproductive rate of bony fish at low population densities

by

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Acknowledgements

Abstract

Serious concern has been raised about the number of overfished populations and it is well established that industrial fishing harvests more than can be replaced by reproduction. Knowledge about the maximum annual reproductive rate (α) of fish populations at low densities is important to enhance fisheries management towards sustainability. This important life history trait can be expressed as the number of replacement spawners that are produced per spawner per year in the absence of fishing. In the current study a new method was thoroughly tested, which allows deriving the annual reproductive rate from length frequency samples. 244 length frequency samples were analysed and additional parameters were obtained from published data or empirical equations. Estimates for thirteen investigated commercial stocks of the North Atlantic ranged from $\alpha = 1.08$ to 3.61. Annual estimates of the maximum annual reproductive rate from 244 length frequency samples were log-normal distributed and the 95% confidence limits ranged from 2 to 2.4 with a geometric mean of 2.2. No significant difference was found when results were compared with published estimates of α derived with an independent method ($t_{0.4;\ 0.05}$, Prob. = 0.67, n = 10). The results of this study support the suggested generalisation that the maximum annual reproductive rate is relatively constant and typically between 1 and 7 with a median that is more likely located at the lower end of this range. This means that recruitment of the majority of fish species is sufficient to replace the number of spawners in a single spawning period if recruits are allowed to attain maturity.

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1. Introduction

Global marine fishery is approaching its upper limit and serious concern has been raised about the ecological impacts of industrialized fishing on exploited fish stocks. It is well established that most commercial fisheries harvest more fish than can be replaced by reproduction and growth (Pauly et al. 1998; Myers & Worm 2004), which is usually referred to as overfishing. Froese and Kesner-Reyes (2002) found that in 1999 about 50% of world fisheries were overfished, had collapsed or were closed. The number of overfished populations strongly suggests that management has failed to achieve a principal goal, namely sustainability (Botsford et al. 1997). This is supported by the paradoxical situation in the North Atlantic, the region with the longest tradition of fisheries management, that has higher rates of overfishing of exploited species (60%) than the worldwide mean (Froese and Kesner-Reyes 2002). As a consequence, fishery scientists have to cope with low population densities for most exploited fish stocks. Besides ecological considerations, further collapses and closings of fisheries are a severe threat to the 200 million people directly employed by the fisheries industry (FAO 1993). Consequently, it is a necessity to improve fishery management to sustain fish stocks as natural resources in the long run. Understanding population dynamics of fish is essential for the development of enhanced fisheries management strategies (Walter 1998). Myers et al. (1999) suggest the maximum annual reproductive rate at low population densities to be an important life history trait, which can be used as a relatively simple tool for fishery management.

1.1 Background

The reproductive rate of animals is defined as the average number of offspring that survive to a certain age (Charlesworth 1994). If this age is set as age at first maturity, then the reproductive rate can be expressed as the number of replacement spawners per spawner. Population theory suggests that this rate will be near its maximum at low population size far from the carrying capacity of the ecosystem (e.g. Myers 2001). Thus, the maximum annual reproductive rate α can be defined as the average number of replacement spawners that are produced per spawner per year at low population densities in the theoretical absence of anthropogenic mortalities. Myers et al. (1999) presented values for 57

commercial species based on analysis of spawner-recruitment samples for 700 stocks and found α to be surprisingly constant generally ranging between 1 and 7. The maximum annual reproductive rate is central to the following applications: (1) sustainable exploitation rates (Myers 2001, Myers and Worms 2004), (2) defining the fishing mortality that would drive a population to extinction (Mace 1994, Myers 2001, Myers and Worms 2004, Dulvy et al. 2004) and (3) understanding the mechanisms of reproduction success to enhance fisheries management toward sustainability (Froese 2004a). Additionally, it was shown that the maximum annual reproductive rate is closely related to one of the most fundamental parameters in population ecology, the intrinsic rate of population increase (Myers et al. 1997, Smith et al. 1998). When applied to fish biology, the intrinsic rate of population increase provides a measure of the maximum population growth rate of depleted fish populations (Myers et al. 2001) and is the key to various fishery management decisions such as setting the maximum sustainable yield (Pauly 1984) or estimating resilience to anthropogenic mortality rates and the recovery potential of populations (Myers 1997;, Musick 1999, Myers et al. 2001, Myers and Worm 2004).

1.2 The purpose of this study

The method provided by Myers et al. (1999) is very data intensive and thus not widely applicable. Froese (2004b) presented a new method which allows estimating the maximum annual reproductive rate from length frequency samples.

The main objective of this study is to test Froese´s (2004b) method for estimating the maximum annual reproductive rate, its assumptions and the sensitivity to input parameters and compare estimates of α with those published by Myers et al. (1999). Additionally, an attempt will be made to develop criteria for the selection of suitable length frequency data. Length frequency data are a standard output of every fishery survey and are more widely available. Froese (2004b) suggests that the annual reproductive rate can be estimated from two length frequency samples that are the same number of years apart as it takes fish to attain maturity, so that the first sample contains the number of spawners and the second sample contains the number of first-time spawners that resulted from the previous spawning event. However, for many stocks subsequent length frequency data over several years are not accessible or do not exist. This can be attributed to deficiencies in data storage and management, lack of stock assessments and perceived ownership of data (Zeller et al. 2005). For these cases, Froese (2004b) suggest to estimate the maximum

annual reproductive rate from one sample assuming that in the absence of major demographic events the shape of a given length frequency curve is relatively similar over a period of time. This is the first time that this suggestion is submitted to a thorough test. The simplification will be tested by applying it to several data sets over successive years. If it can be justified, it will be used to derive α for larger number of samples. Finally, the potential usefulness of the new method will be explored and an approach will be provided to incorporate a precautionary principle for management purposes.

2. Materials and Methods

2.1 Formulation

The Advanced Length Frequency Wizard (Froese 2004b) is available as an online-tool in FishBase 2005 (Froese and Pauly 2005, www.fishbase.org) and was used here for the estimation of the maximum annual reproductive rate α. Parameters, definitions and abbreviations used in this study are explained in Table 2.1.

Table 2.1: Summarisation of the parameters and abbreviations used in this study

Parameters	Description
Spawners	Number of mature fish observed in a length frequency sample, calculated as the sum of all fish greater than and equal to the length at first maturity
Replacement Spawners	Number of first-time spawner in a length frequency sample corrected for the effect of fishing mortality
L_m	Mean length at first maturity, in cm.
t_m	Mean age at first maturity, in years.
L_{max}	Mean length of largest length classes in a length frequency time series, in cm
VBGF	Von Berterlanffy Growth Function: $L_t = L_{inf}(1 - e^{(-K(t - t_0))})$, where L_t is the length of the fish at age t.
L_{inf}	Parameter of the VBGF; infinitive or asymptotic length, expresses the mean length that fish would reach if they have indeterminate growth, in cm
K	Parameter of the VBGF; the growth coefficient K expresses the rate at which fish approach the asymptotic length L_{inf}, in year $^{-1}$.
t_0	Parameter of the VBGF; defined as the hypothetical age that fish would have at length zero, if they grow accordingly to the curve of the VBGF
M	Natural mortality, in year^{-1}.

According to Myers et al. (1999), the maximum annual reproductive rate α can be defined as the average number of replacement spawners that are produced per spawner per year at low population size in the absence of fishing mortality after a time delay for the age at first

maturity. Considering length frequency samples, α can also be expressed as the relationship between the numbers of observed spawners S_t in year t, and the number of potential replacement spawners R_{t+tm} in the year t plus the age at maturity t_m (Froese 2004b).

$$\alpha_{tm} = R_{t+tm} / S_t \tag{1}$$

Assuming that subsequent annual length frequencies are not significantly different in the absence of demographic trends, Froese (2004) suggests a simplification by estimating α from one length frequency sample:

$$\alpha_t = R_t / S_t, \tag{2}$$

If the length at which 50% of the specimens reach L_m is known and assumed to be knife-edge, then all fish larger than L_m in the length frequency sample can be considered to be spawners. The number of fish within the length class of L_m was interpolated to extract the number of spawners from this length class. For example, if the class width was 34.0 - 34.9 cm and L_m was 34.2 cm, then 80% of the specimens in this length class were assumed to be mature. Then the sum of fish observed in all larger length classes was added (Figure 2.1).
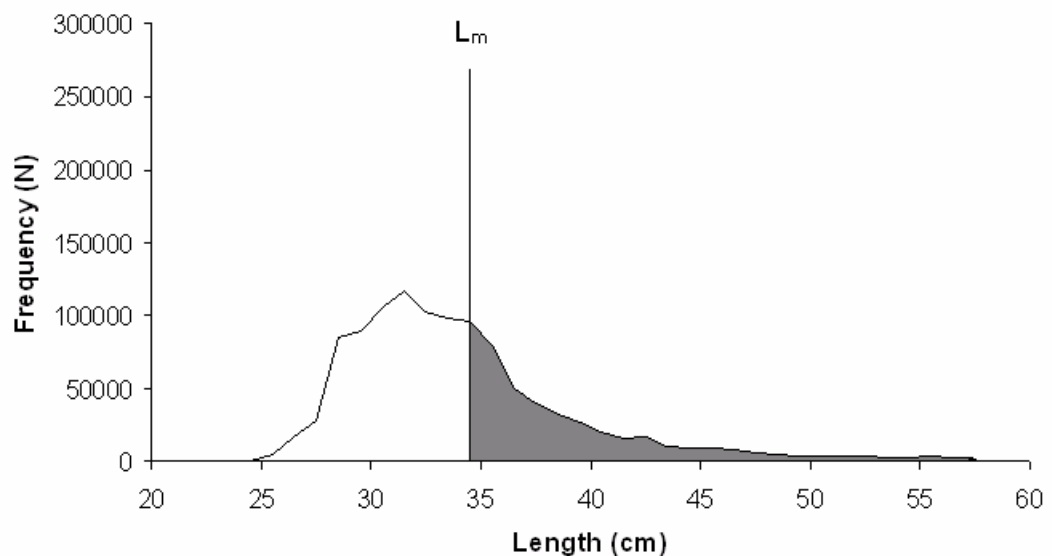
Figure 2.1 Length frequency sample (solid line), with length referring to mid-class length and range of spawners represented by the shaded area. Celtic sea plaice 1999; Source: Fishbase 2005 (Froese & Pauly 2005)

Two adjustments were necessary for the estimation of number of potential replacement spawners:

(1) The length frequency sample was corrected for the selection effect of the sampling gear, which causes the decline on the left descending side of the length frequency curve, although the length structure of population not affected by demographic trends should always have more smaller than larger fish. This was done by using a back-calculating approach suggested by Pauly (1984) (Figure 2.2, dotted line). This results in the number of fish in the first length class accessible to the gear, if the gear had caught them with the same probability as the length classes in the right side of the length frequency sample.

(2) The length frequency sample was corrected for the effect of fishing mortality (Figure 2.2, dashed line), where the number of fish in the first length class as established in (1) is then only reduced by natural mortality.
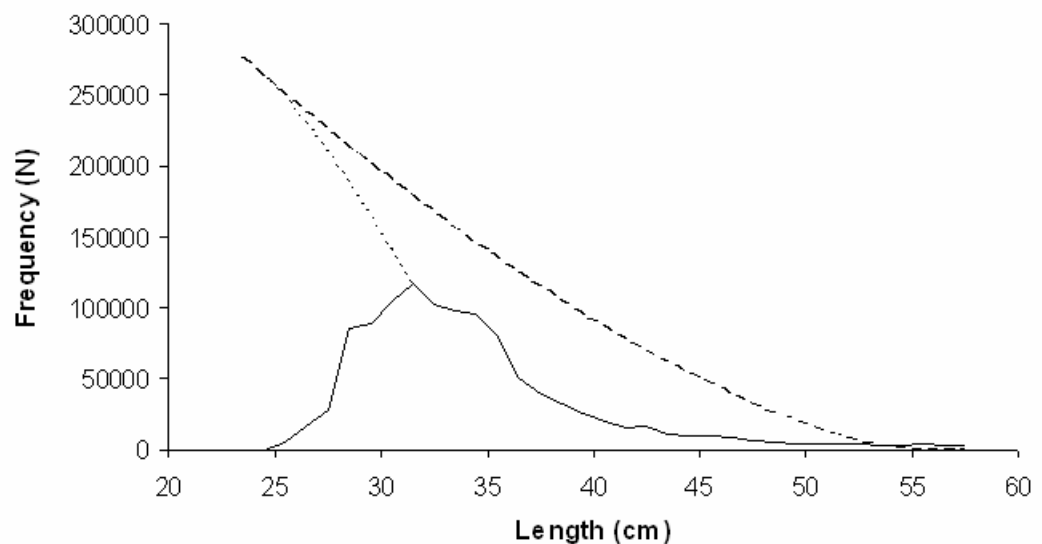
Figure 2.2 Length frequency sample (solid line) adjusted for no effect of gear selection (dotted line) and no effect of fishing mortality F (dashed line). For Celtic Sea plaice 1999; Source: Fishbase

The number of potential replacement spawners was defined as the number of fish in the corrected sample (Fig.2.3) within the length range of $L_{tm-0.5}$ to $L_{tm+0.5}$, i.e. the number of fish with lengths corresponding to the age at first maturity plus-minus half a year. The two adjustments are explained below in more detail.
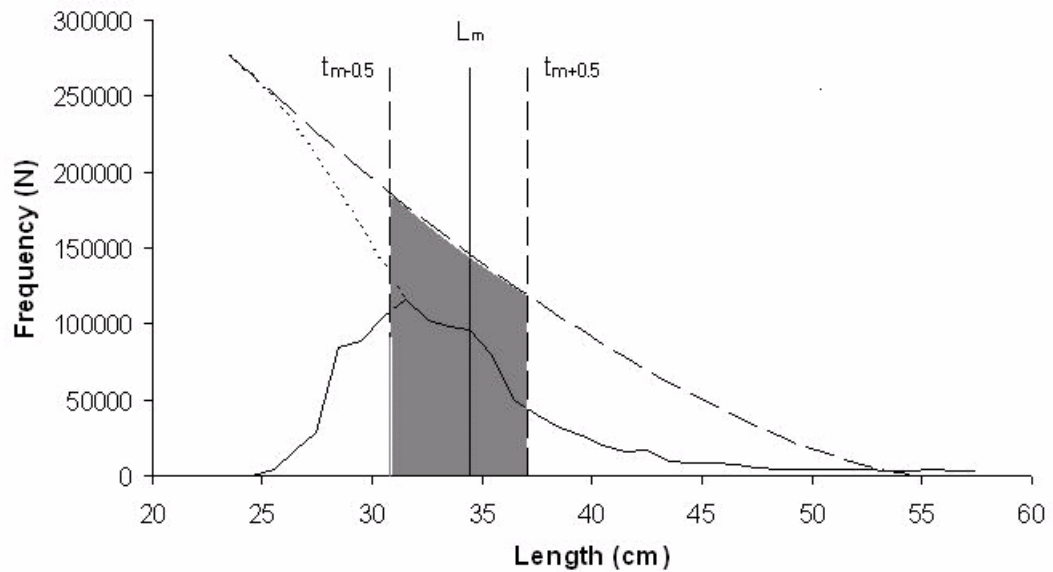
Figure 2.3 Same as Figure 2.2, but with length range of replacement spawners superimposed. Celtic sea plaice 1999; Source: FishBase

Adjustment (1): Pauly (1984) suggested that a length-converted catch curve can be used to derive the number of fish which would have been caught had they been fully recruited. The expression "fully recruited" used in this context refers to the effect of gear selection as well as to the effect originating from different distribution patterns in space and time of age groups not being fully recruited to the adult stock (Daniel Pauly UBC, Vancouver, pers. comm.). Length-converted catch curves were constructed by multiplying the number of fish in each length class by the growth rate dl/dt of the fish in that class. The log-transformed product results in the linear equation (3):

$$\ln(N_i * dl/dt) = a + bt,\tag{3}$$

where a is the intercept with the ordinate, b is the slope and t is the age corresponding to the length class, respectively (Figure 2.4).
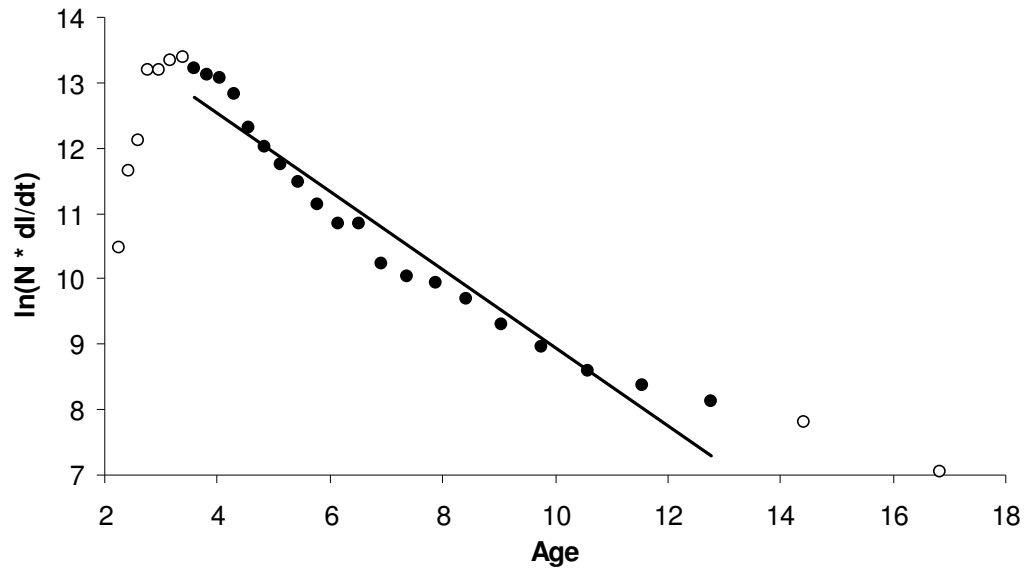
Figure 2.4: Example of a length-converted catch curve for Celtic sea plaice 1993; **Solid dots**: Fully selected length classes; **Open dots**: Not fully selected and thus excluded length classes; A linear regression was applied to fully selected length classes: slope = -0.60; intercept = 14.92, $r^2 = 0.94$

The growth rate dl/dt was estimated from the VBGF:

$$\textbf{dl/dt} = \textbf{L}_{\textbf{inf}} * \textbf{K} * \textbf{exp}(\textbf{-K}(\textbf{t}_0 - \textbf{ln}(\textbf{1} - \textbf{Lt/Linf / K}))), \tag{4}$$

while the age t corresponding to L_t, was computed from the conversion of the VBGF:

$$\textbf{t} = \textbf{t}_0 - \textbf{ln}(\textbf{1} - \textbf{L}_t\textbf{/L}_{\textbf{inf}}) \textbf{ / K.} \tag{5}$$

The first fully selected length class was determined by choosing the highest point of the right descending arm of the length-converted catch curve. Points to the left and outliers of larger length classes at the very right end were excluded (open dots, Figure 2.4). A linear regression was performed with identified length classes (solid dots, Figure 2.4).

The inversion of the slope derived from the linear regression can be directly used to estimate the total mortality Z (Pauly 1984). Based on a step-wise interpolation between M and Z, where Z approaches M when moving left from the first fully selected length class to the first selected length class, the number of fish which should have been caught if they were fully recruited, were extrapolated as shown in Figure 2 (dotted line), following the steps provided by Pauly (1984). Natural mortality was assumed to be the same for all

selected lengths. This method thus provided estimates for numbers of fish of length classes not fully represented in the length frequency sample.

Adjustment (2): Froese (2004b) provides a new approach to adjust the length frequency sample again by correcting it for the effect of fishing mortality, i.e. to obtain numbers of fish in length classes if the population was only reduced by natural mortality. Froese (2004b) suggests that the number of fish in length class which should have been caught without the effect of fishing mortality N(F) can be estimated by performing an additional extrapolation:

$$N(F)_t = N(F)_{t-1} * \exp(-M * t), \tag{6}$$

where the previously derived number of fish of the smallest length class fully represented in the sample is used as the starting point (Figure 2.2 dashed line) and t is the mean age corresponding to a length class. The length range of potential replacement spawners $L_{tm+/-0.5}$ can then be estimated from the VBGF:

$$L_{tm+/-0.5} = L_{inf}(1 - \exp(-K+/-0.5 - t_0))). \tag{7}$$

The number of potential replacement spawners was finally derived by using an interpolation to extract the number of replacement spawners from length classes $L_{tm+0.5}$ and L_{tm-05} and adding the sum of fish in length classes within this length range.

2.2 Data selection and treatment

It was tried to obtain length frequency data of all species investigated by Myers et al. (1999) from two main data sources:

(1) The length frequency sample collection of FishBase 2005 (Froese and Pauly 2005)

(2) Length frequency data which stem from scientific bottom trawl surveys conducted in the North Atlantic.

Latter data were officially requested from the International Council for Exploration of the Sea (ICES), the Department of Fisheries and Oceans, Canada (DFO) and the Federal Research Centre of Fisheries, Germany (BFA).

The new method outlined here can be described as a meta-analytical approach to obtain estimates for maximum annual reproductive, using a combination of established methods and some new approaches. The new method critically depends on various assumptions and criteria. The following criteria were used to select representative and suitable length frequency data for subsequent analysis.

List of criteria:

(1) The number of spawners is fully represented in the sample; i.e. the estimated L_m should be right of or close to the first fully recruited length class in the length frequency distribution.

(2) Length frequency samples for the same population in subsequent years are not significantly different and do not show trends over time, i.e. unique events such as a collapse of fish stocks and extremely strong or weak year classes that would strongly effect subsequent years are not known or visible.

(3) The gear in question is a trawl or has a selection curve like a trawl[*].

(4) The smallest selected length class is fully recruited to the sampling design[*].

(5) The sample in question is large enough to provide an accurate reflection of the population structure over the period of time considered[*].

[*]Adopted from Pauly (1984)

To meet the first criterion, data sets were only used where the mid-length of the fully selected class did not exceed length at maturity by more than 15%. For example, length frequency samples obtained for the George Bank cod exhibited an average first fully selected length class at 50 cm (1987-1996) and 54 cm (1997-2005), while the length at first maturity was 45 cm and 40 cm, respectively. This resulted in exceeding the length at maturity by 21% and 47% and resulted in an exclusion of this data set.

The second criterion was only applied to samples affected by significant events such as the collapse of the northern cod in 1993 (Myers et al., 1997; DFO, 2002; DFO, 2003) or the enormous number of recruits resulting from the strong 1999 year class of the North Sea haddock (Anon. 2005a). The third criterion was fulfilled by considering only length frequency data that stemmed from trawl surveys.

With regard to the fourth criterion, the highest peak of the length frequency curve was assumed to be the first fully recruited length class in the sample. Difficulties occurred in time series of North Sea cod, haddock and whiting, where samples exhibited two peaks of the length frequency curves that could be attributed to two successive cohorts (year

classes) with a time difference of one year. A simple test was performed to determine if the length class of the first peak was fully represented in the sample. Note that the cohort represented in the first peak in the year t_a corresponds to the cohort represented in the second peak in the year t_{a+1}. Hence, the number of fish in the length class of the second peak at the time t_{a+1} has to be smaller than the number of fish in the length class of the first peak at the time t_a, because of the effect of mortality over time (Figure 2.5).
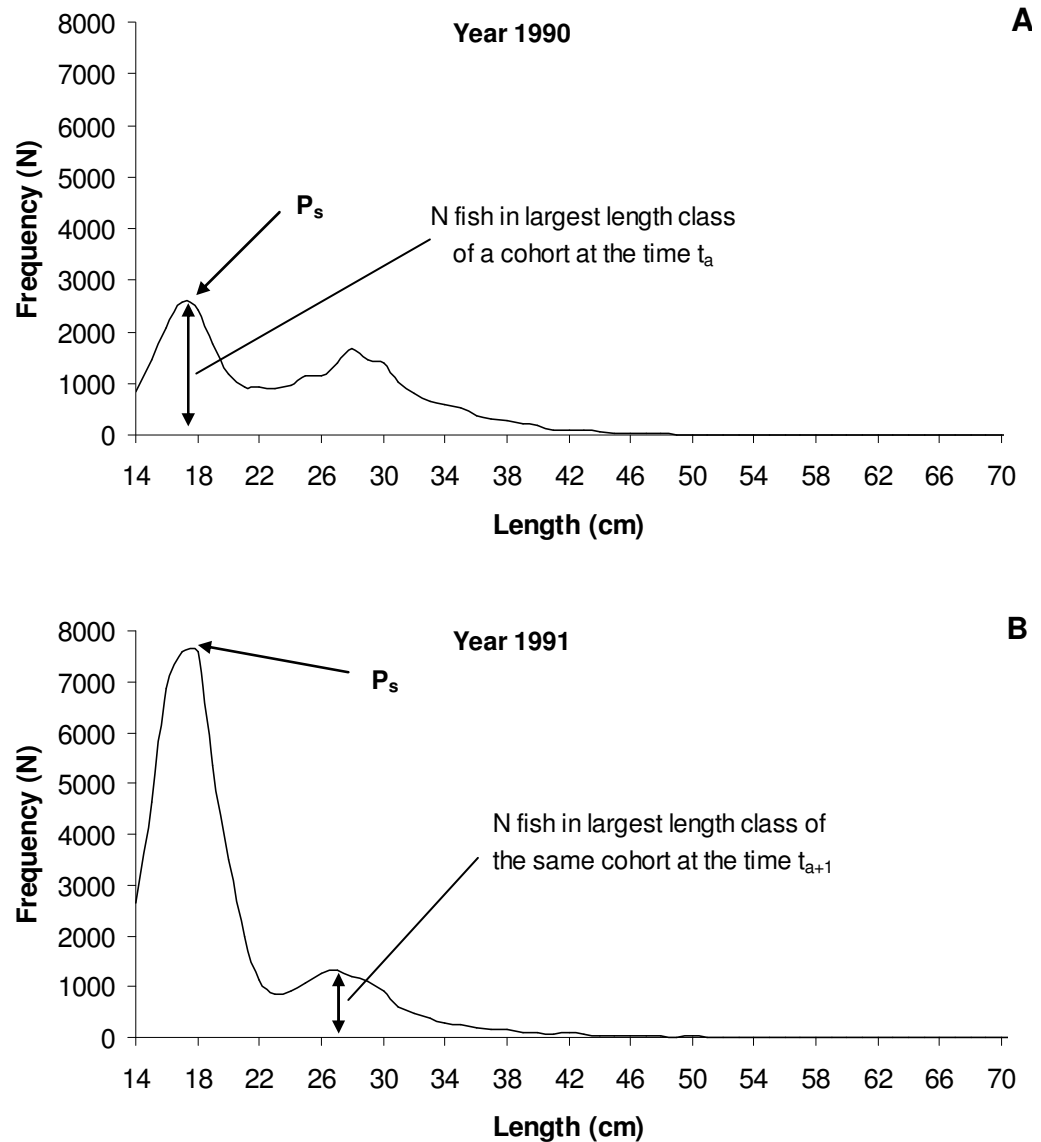
Figure 2.5 A comparison between the numbers of fish in largest length classes of the peak in year t_a and the second peak in year t_{a+1} belonging to the same cohort. For North Sea haddock samples of the years 1990 and 1991. P_s indicates the point of the smalles selected length class.

If this is found to be true for more than 80% of the samples of a time series, then the length class of the first peak was accepted as fully recruited for the stock in question. According to suggestions made by Daniel Pauly (UBC, Vancouver, pers. comm.), peaks of small

length classes that were found to be not fully recruited were subsequently removed from the sample.

Strong year classes are usually easily visible over successive years of the length frequency samples. To avoid an overestimation of α, highest peaks in large length classes were ignored. The selection point was then set at peaks of length classes which were previously assumed to be fully represented in the sample.

Criterion 5 was assumed to be met when the survey design covered a wider area over several years. For the purpose of this study, only time series over a period of at least ten years were considered.

Many frequency data compiled in FishBase 2005 (Froese and Pauly 2005) failed the outlined criteria. Thirteen different stocks of ten species were finally selected for this study, all from the North Atlantic and identified by ICES subdivions, see Figure 2.6 and Table 2.2.
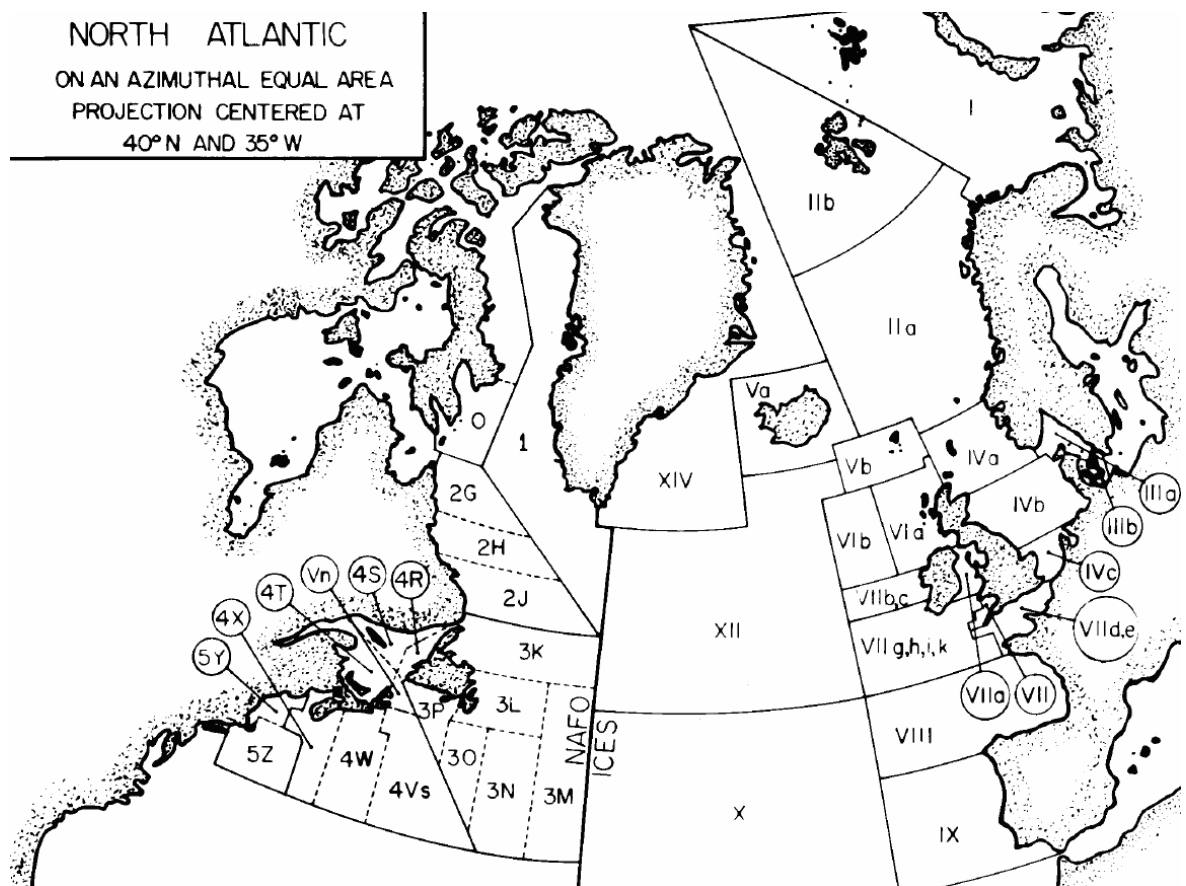
Figure 2.6 Map of the North Atlantic showing ICES and NAFO fisheries management areas. Length-frequency data from following regions were used in this work: North Sea (ICES Sub-area IV) including Skagerrak (ICES Division IIIa) and Eastern Channel (ICES VIId), Scotian Shelf (ICES 4VWX), Western Channel (ICES Division VIIe) and Celtic Sea (ICES Divisions g,h), Scotian Shelf (NAFO 4VWX,), Georges Banks NAFO 5z), and Western Greenland (NAFO 1). (ICES: International Council for Exploitation of the Sea; NAFO: Northwest Atlantic Fisheries Organisation)

Table 2.2 List of stocks used for the estimation of the maximum annual reproductive rate α. To locate Sub-areas and Divisions, see Figure 2.6.

Common name	Scientific name	Stock area	Sub-area/ Division	Source	Period
Cod	*Gadus morhua*	North Sea	ICES IV, IIIA, VIId	1	1983-2005
Haddock	*Melanogrammus aeglefinus*	North Sea	ICES IV, IIIA, VIId	1	1983-2005
Silver Hake	*Merluccius bilinearis*	Scotian Shelf	NAFO 4VWX	2	1970-2004
Whiting	*Merlangius merlangus*	North Sea	ICES IV, IIIA, VIId	1	1983-2005
Herring	*Clupea harengus*	North Sea	ICES IV, IIIA, VIId	1	1983-2005
Sprat	*Sprattus sprattus*	North Sea	ICES IV, IIIA, VIId	1	1983-2005
Plaice	*Pleuronectes platessa*	Western Channel	ICES VIIe	4	1991-2001
		Celtic Sea	ICES VIIg,h	4	1991-2001
Sole	*Solea solea*	Biscay	Celtic Sea	4	1991-2001
		Western Channel	ICES VIIg,h	4	1991-2001
		Celtic Sea	ICES IX	4	1991-2001
Yellowtail flounder	*Limanda ferruginea*	Scotian Shelf	NAFO 4VW	2	1970-2004
Redfish	*Sebastes mentella*	Western Greenland	NAFO 1	3	1994-2004

Sources: **1.** International Council for Exploitation of the Sea (ICES), **2.** Department for Fisheries and Ocean, Canada (DFO), **3**. Federal Research Centre of Fisheries, Germany (BFA), **4.** FishBase 2005 (Froese & Pauly 2005)

Six requested data sets were excluded from this study, because spawners were not fully represented in the sample (Criterion 1). These were Southern and Scotian Shelf stocks of cod and haddock (NAFO, 4X), Scotian Shelf Pollack (4VWX), Southern Scotian Shelf yellowtail flounder and Georges Bank cod (5z). The reasons for failing this criterion can be most likely attributed to rough sampling conditions in 4X and relatively large mesh sizes used in 4x and 5z (Donald Clark, DFO, pers. comm.). The Eastern Scotian Shelf Cod and Haddock data sets were excluded, because of failing criterion two.

ICES provided standardized length frequency data of North Sea stocks as catch per unit effort (CPUE) fragmented in rectangles. For the purpose of this study, it was assumed that life history traits do not vary significantly between different stocks throughout the North Sea. Consequently, the rectangles were pooled to obtain yearly length frequencies for the whole North Sea (ICES areas IV, IIIa, VIId). These length frequencies were re-standardized by dividing each CPUE per length class by the number of rectangles sampled each year.

2.3 Estimation of parameters

The new method developed by Froese (2004b) relies on various life history parameters. For the purpose of reproducibility, life history parameters were estimated using a standardised procedure.

L_{max} was estimated by computing, for a given stock, the mean of all largest length classes across annual samples. Then the asymptotic length, L_{inf}, was estimated using the empirical equation by Froese & Binohlan (2000):

$$\text{Log}_{10}L_{inf} = 0.044 + 0.9841 * \log_{10}L_{max}. \qquad (8)$$

Age and length at first maturity data were primarily collated from ICES Working Group Reports and DFO Stock Status Reports. If such data were not or only partly available, maturity data for specific stocks were collated from the MATURITY table available in FishBase 2005 (Froese & Pauly 2005). Primarily, maturity data were chosen to be the length and age where 50% of the females of the respective stocks attained maturity. The median was chosen, if several estimates were available for a stock (e.g. North Sea cod).

If there were no estimates for L_m or t_m available for the studied area or for an adjacent area (e.g. Western Greenland redfish), L_m was estimated using the empirical relationship suggested by Froese and Binohlan (2000):

$$\text{Log}_{10}L_m = 0.898 * \text{Log}_{10}L_{inf} - 0.0781. \qquad (9)$$

Maturity ogives of L_m data were accessible for various stocks managed by the DFO. Time series of 50% female maturity often showed a significant decline of L_m. In this case a L_m corresponding in time to the respective L-F samples was chosen. The relationship L_m/L_{max} known as reproductive load (Beverton and Hold 1957; Charnov, 1993) was applied to estimate L_m from L_{max} when estimates of L_m were not covering all periods of the length frequency time series. For example, values estimated and obtained from ogives for silver hake *Merluccius bilinearis* were $L_{max} = 62$ cm and $L_m = 27$ cm for the period of 1970-1978 and $L_{max} = 59.1$ cm and $L_m = 25.5$ cm for 1979 – 1985 and $L_{max} = 56.3$ cm for the period of 1986 – 2004. The relationship L_m/L_{max} gives the quotient of 0.44 and 0.43 for the two periods, respectively. The mean of computed quotients multiplied by L_{max} gives $L_m = 24.3$ cm for the period of 1986 - 2004 where L_m is unknown.

Neither K nor L_{inf} alone have the dimension of growth in length per time (Pauly, 1996). Therefore, growth as described by the VBGF is not comparable using only one parameter at the time. This led to the development of a comparable growth index Ø´ (Munro and Pauly, 1983), which is assumed to be relatively constant within a population (Pauly et al. 1996).

$$Ø´ = Log_{10}K + 2Log_{10}L_{inf} \qquad (10)$$

This interdependence between K and L_{inf} (Munro and Pauly 1983) allows estimating K from a stock specific L_{inf} which was felt to be better than choosing independent unpaired K and L_{inf} estimates from literature.

The parameters K and t_0 were estimated following an approach suggested by Froese and Binohlan (2003). Two interdependent equations were applied for this purpose. Equation 3 is the re-arranged von Bertalanffy growth function (VBGF) and equation 4 is an empirical formula by (Pauly 1979) to estimate the t_0 of the VBGF.

$$K = \ln(1 – L_m/L_{inf}) / (t_m – t_0) \qquad (11)$$

$$log_{10} – t_0 = -0.3922 – 02752 * log_{10}L_{inf} – 1.038log_{10}K \qquad (12)$$

Ø´ (equation 3) was applied when L_{inf} and L_m varied over time and t_m was only known for one period. In this case, K was calculated from equation (3) and (4) for this period. Ø´ was computed using K and Linf given by equation (5). K was then estimated from the specific L_{inf} of the period in question and the previously obtained Ø´. Finally, unknown t_m was computed using the VBGF.

Natural mortality rates were collated from the POPGROWTH table in FishBase 2005 (Froese and Pauly 2005) or obtained from the empirical equation of Pauly (1980):

$$\text{Log}_{10}M = -0.066 - 0.279\text{Log}_{10}L_{inf} + 0.6543\log_{10}K + 0.4534\log_{10}T, \tag{13}$$

where T is the annual mean water temperature of the studied area. All estimated parameters were used in subsequent analysis.

2.4 Sensitivity analysis

A sensitivity analysis (Pauly 1984) was performed to test the sensitivity of the new method. The estimated input parameters L_{inf}, L_m, K and M were varied between -20% and +20%. The parameters L_{max} and t_0 were ignored here due to their correlation with L_{inf} and K, respectively (see equations 2, 4 and 5). For the purpose of this analysis, three different samples were tested. The sensitivity is expressed in the "D-measure", which describes the percent of change between unperturbed output and perturbed output, i.e. after changing one parameter at the time by a fixed percentage. Estimates for α were set as unperturbed output. The investigated parameters were subsequently varied which resulted in the perturbed output of α´. The "D-measure" was then computed from equation 6:

$$\text{D-measure } (\%) = (\alpha´ - \alpha) / \alpha * 100. \tag{14}$$

2.5 Statistic analysis

The maximum annual reproductive rate was estimated across all available and accepted length frequency samples of a given stock. Following Myers et al. (1999), values of α were log-transformed and assumed to be log-normal distributed. Natural logarithms were used to allow direct comparison with the estimates of α by Myers et al. (1999). Mean ln(α) was then calculated

The new method as used here is based on the simplification suggested by Froese (2004b) that α can be estimated from one length frequency sample. To test this simplification, values of α derived from single length frequency samples were compared with those derived from subsequent samples with a time delay of t_m. In this context, the time at first maturity t_m was used as integer, due to the well-defined yearly spawning seasons of investigated stocks.

Myers et al (1999) provided estimates of ln(α) at species level. If α in this study was available for more than one stock of a given species, mean α was computed and compared pair-wise with the estimates by Myers et al. (1999).

According to the comments provided for the intrinsic rate of population increase by Hutchings (2001), α as estimated in this study is a deterministic value and environmental perturbations are not incorporated. The stochastic estimate of α, $α_s$ is expressed here as:

$$α_s = \exp(\ln(α) - 1/2(σ^2)), \tag{15}$$

where $α_s$ is the stochastic α and $σ^2$ is the variance in ln(α) through time (Lande 1993).

3. Results

3.1 Input parameters

Table 3.1 shows values of the various input parameters used to estimate α for the thirteen stocks analysed in this study, together with reproductive load (L_m/L_{max}) and the growth index Ø´. The column `References´ indicates the literature sources used. Decimals in the t_m column are results of estimating the theoretical age at which 50% of the female reach maturity. In reality, however, spawning is an annual event. Thus, t_m was rounded when selecting length frequency samples containing replacement spawner of a given spawning event.

Median length at first maturity (L_m = 33cm) for the North Sea haddock and was found to be too high when considering recent ICES data of L_m = 25cm for this stock (Anon. 2004); instead the mean of the largest and smallest estimate (L_m = 29.8 cm) was used.

Table 3.1: Input parameters for ten species and thirteen stocks. The calculation of parameters is described in the Material and Methods section

Species	Stock	L_{max} (cm)	L_{inf} (cm)	L_m (cm)	t_m (years)	K (1/year)	M (1/year)	t_0 (years)	Ø´	L_m/L_{max}	Period (years)	References
Cod	North Sea	126.0	129.1	60.0	3.8	0.14	0.18	-0.82	3.37	0.48	1983-2005	4, 6, 10
Haddock	North Sea	71.1	73.5	29.8	2.5	0.15	0.24	-0.83	2.91	0.42	1983-2005	1, 4, 6, 8
Whiting	North Sea	53.3	55.4	25.1	2.0	0.23	0.30	-0.62	2.85	0.47	1983-2005	4, 6, 10
Sprat	North Sea	16.6	17.6	10.5	2.0	0.38	0.66	-0.50	2.07	0.63	1983-2005	4, 6, 10
Herring	North Sea	34.4	35.9	24.0	3.0	0.29	0.43	-0.55	2.57	0.70	1983-2005	4, 6, 10
Plaice	Western Channel	63.2	65.5	34.5	3.0	0.20	0.30	-0.86	2.93	0.55	1991-2001	2, 3, 6, 10
	Celtic Sea	62.2	64.6	34.5	3.0	0.20	0.30	-0.86	2.92	0.55	1991-2001	2, 3, 6, 10
Sole	Western Channel	53.0	55.1	29.0	3.2	0.19	0.25	-0.69	2.76	0.55	1991-2001	2, 3, 6, 10
	Celtic Sea	49.2	51.2	27.8	2.8	0.23	0.25	-0.63	2.79	0.57	1992-2001	2, 3, 6, 10
	Bay of Biscay	49.5	51.5	28.8	3.2	0.21	0.25	-0.69	2.75	0.58	1991-2001	2, 3, 6, 10
Silver hake	Scotian shelf	62.0	64.3	27.0	2.0	0.20	0.30	-0.69	2.92	0.44	1970-1978	7, 10
		59.1	61.3	25.5	1.8	0.22	0.33	-0.63	2.92	0.43	1979-1985	7, 10
		56.3	58.4	24.3	1.7	0.24	0.35	-0.58	2.92	0.43	1986-2004	7, 10
Yellowtail flounder	Scotian shelf	51.0	53.0	28.0	3.2	0.19	0.30	-0.81	2.68	0.55	1970-1978	8, 10, 11
		48.7	50.7	27.0	3.1	0.20	0.31	-0.73	2.68	0.55	1979-1985	8, 10, 11
		43.7	45.5	24.0	2.6	0.23	0.36	-0.65	2.68	0.55	1986-2004	8, 10, 11
Deepwater redfish	Western Greenland	41.7	43.5	24.7	13.6	0.05	0.11	-3.22	1.98	0.59	1994-2004	6, 7, 10

References: 1. Anon. (2002), 2. Anon. (2004). Anon. (2005a), 4. Anon. (2005b), 5. Binohlan (1998), 6. Binohlan and Pauly (1998), 7. DFO (1999), 8. DFO (2000), 9. Fowler and Stobo (2000), 10. Froese (2004b), 11. O´Brien (1993)

3.2 Sensitivity of the new method

Figure 3.1 shows changes in α resulting from variations of input parameters by fixed percentages +/- 1%, +/- 5%, +/- 10% and +/- 20%, respectively. For example, a 20% reduction of L_{inf} for the North Sea cod resulted in a change of α by -53%, while a 20% reduction of M resulted in a change of 11.7%. The North Sea cod represented the largest investigated species with highest estimates of L_{inf} and L_m, where L_m had the greatest distance to the right of the first fully selected length class (Figure 3.1A). The North Sea haddock (Figure 3.1B) and the Scotian shelf yellowtail flounder (Figure 3.1C) represented median-sized species, with estimates of L_m close to first fully selected length classes, but with different shapes of the length frequency curves. The sprat was the smallest species in this study with highest estimates for K and M (Figure 3.1D)
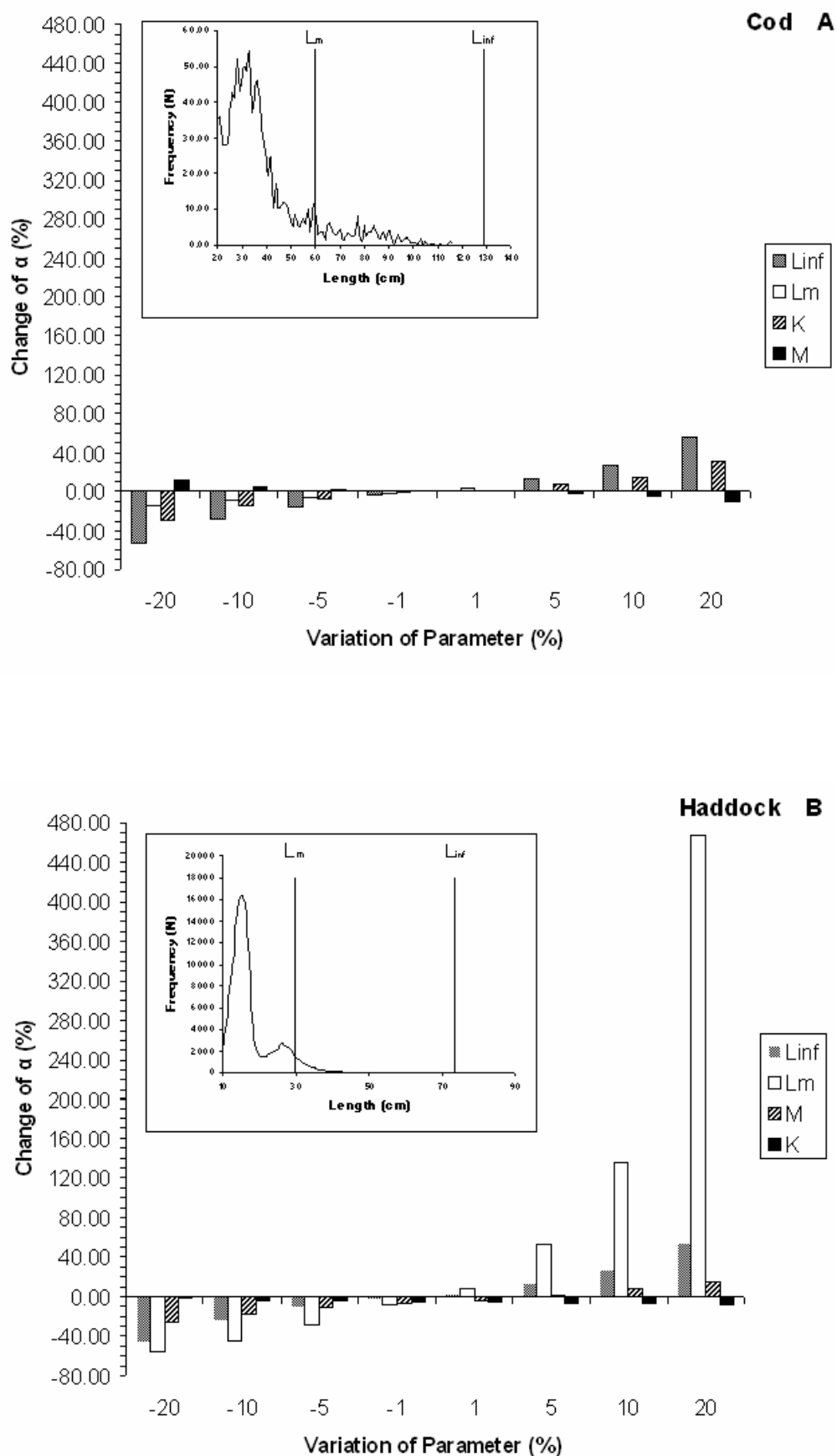
Figure 3.1 A-B Results of the sensitivity analysis L-F-samples used are inserted in the graphs. The columns indicate the change in α resulting from parameters modulation by a fixed percentage. **A**: North Sea cod 2005, **B**: North Sea haddock 1995

Figure 3.1 continued, C-D. C: Scotian shelf yellowtail flounder 1973 **D**: North Sea sprat 1999
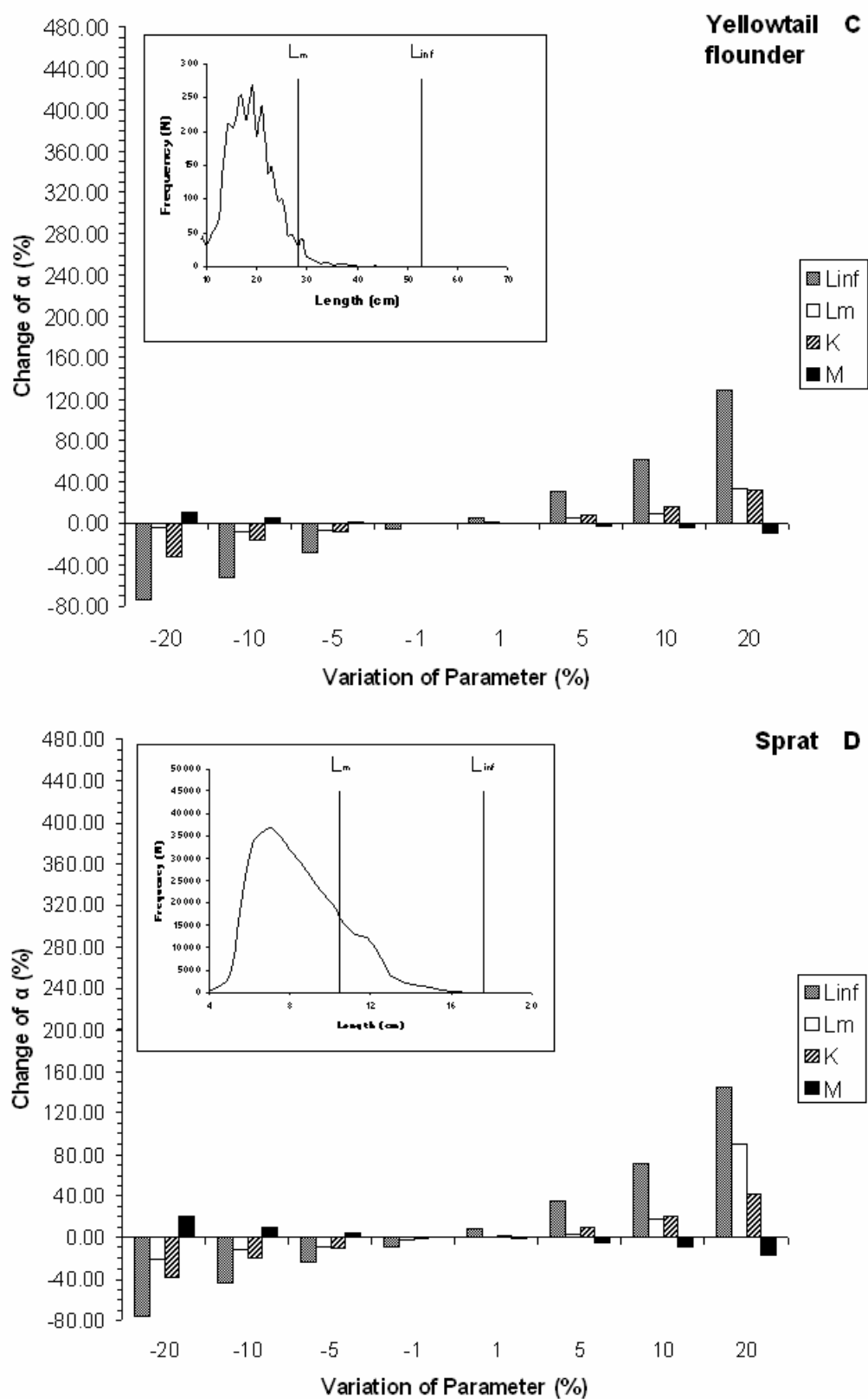
3.3 Test of assumptions

The assumption that there was no significant difference between α estimated from one length frequency sample at a time and α_{tm} estimated from two length frequency samples with the time difference t_m, was tested using two-sampled t-tests. The deepsea redfish was excluded from the analysis because estimated age at first maturity (t_m) was more than 13 years but data were available for only 11 years, i.e. the two length frequency sample method could not be applied. The log-transformed α passed normality tests (Skewness, Kurtosis and Omnibus test). Normality of the North Sea sprat estimates was rejected by the Omnibus test; however, it was accepted by Skewness and Kurtosis tests. The null hypothesis was accepted for all investigated data sets ($p > 0.05$), i.e. no significant difference was found between log-transformed means of α derived from single length frequency samples and log-transformed means of α_{tm} derived from two length frequency samples that were t_m apart (Table 3.2)

Table 3.2 Results of the two sampled t-tests as described in the text.

Species	Stock	$\ln(\alpha)-\ln(\alpha_{tm})$	T-Value	Prob.	Decision(5%)	Power ($\alpha=0.05$)
Cod	North Sea	0.18	0.81	0.41	Accept H_0	0.125
Haddock	North Sea	-0.13	-0.43	0.67	Accept H_0	0.016
Whiting	North Sea	-0.01	-0.51	0.61	Accept H_0	0.077
Herring	North Sea	-0.19	-0.58	0.57	Accept H_0	0.086
Sprat	North Sea	-0.01	-0.04	0.97	Accept H_0	0.050
Silver hake	Scotian shelf	-0.09	-0.48	0.63	Accept H_0	0.076
Yellowtail flounder	Scotian shelf	0.03	-0.12	0.91	Accept H_0	0.051
Plaice	Western Channel	0.23	0.83	0.41	Accept H_0	0.124
	Celtic Sea	0.11	1.24	0.23	Accept H_0	0.214
Sole	Western Channel	0.13	1.13	0.27	Accept H_0	0.060
	Celtic Sea	0.12	0.83	0.41	Accept H_0	0.123
	Gulf of Biscay	0.01	0.14	0.88	Accept H_0	0.052

Graphical comparisons of time series of α and α_{tm} also showed similar trends, when α and α_{tm} compared so, that number of replacement spawners of α and α_{tm} was estimated from the same sample of year t_a and the number of replacement spawners of α_{tm} was derived from the year t_a minus the number of years it takes to attain the age at first maturity, t_{a-tm} (Figure 3.2). For example, the rounded estimate of t_m was four years for the North Sea Cod, thus α derived from the year 1994 was compared with α_{tm} derived from the length frequency samples of the year 1990 (spawners) and 1994 (replacement spawners) (Figure 3.2 A). Note also that geometric means of α and α_{tm} were not significantly different (inserted in Figure 3.2).
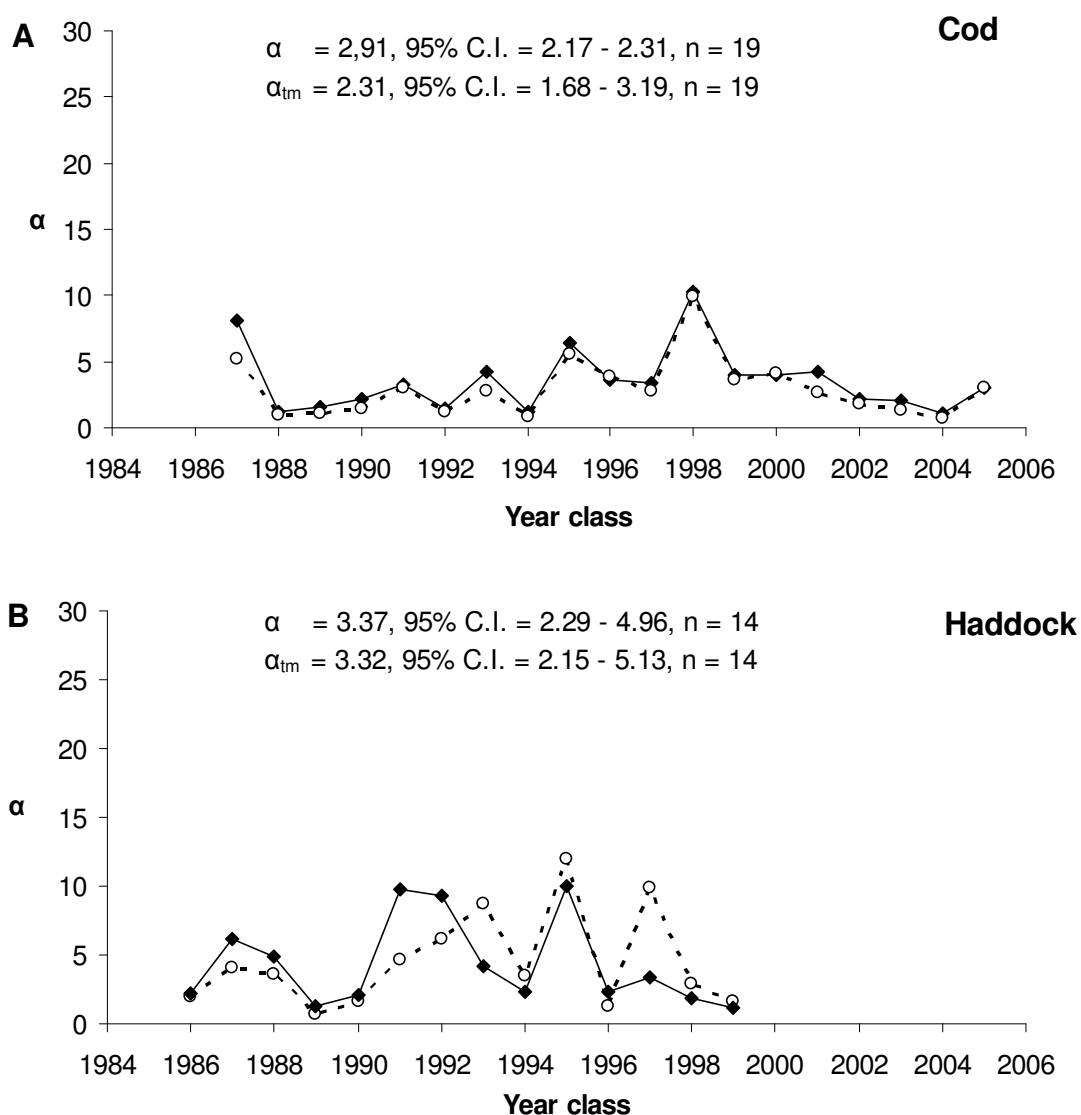
Figure 3.2A-B Comparison of α estimated from one length frequency sample at a time vs. α_{tm} estimated from two length frequency samples with a time difference t_m. Replacement spawners were estimated from the same samples in both approaches. Geometric means and its 95% C.I. are inserted into the graphic. **A**: North Sea cod **B**: North Sea haddock

C Whiting

α = 2.94, 95% C.I. = 2.56 - 2.39, n = 21
$α_{tm}$ = 2.99, 95% C.I. = 2.28 - 3.94, n = 21

D Herring

α = 3.51, 95% C.I. = 2.19 - 5.63, n = 20
$α_{tm}$ = 4.39, 95% C.I. = 2.64 - 7.29, n = 20

E Sprat

α = 2.01, 95% C.I. = 1.21 - 3.32, n = 21
$α_{tm}$ = 2.04, 95% C.I. = 1.26 - 3.32, n = 21
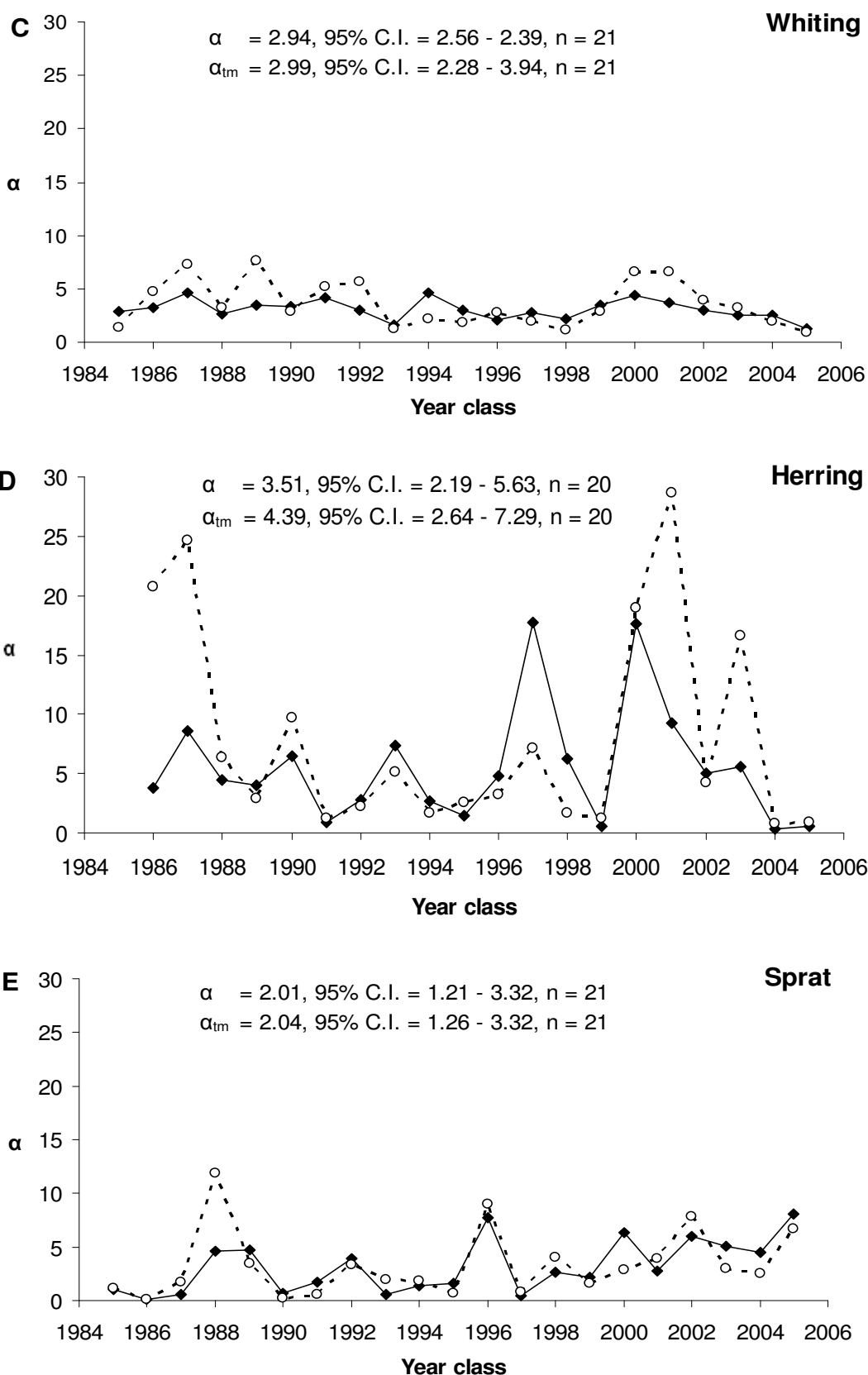
Figure 3.2 continued, C-E. **C**: North Sea whiting. **D**: North Sea herring. **E:** North Sea sprat

3.4 Estimates of the maximum annual reproductive rate α

The advanced length frequency wizard (Froese 2004b) in FishBase was used to compute the maximum annual reproductive rate α for 244 length frequency samples. After exclusion of outliers (distance from the mean larger than three standard deviations) annual estimates of α were log-normal distributed, see Figure 3.3 (see also Meyers et al. (1999)). Mean α and related statistics are listed in Table 3.3. The stochastic value of α is diminished as the function of variance of α and was calculated as $\alpha_s = \exp(\ln(\alpha) - 0.5 * \sigma^2)$ (Lande 1003). The years 2000-2005 were excluded from the analysis of the North Sea haddock, because they violated the criterion of no strong inter-annual trends (see Materials and Methods section).
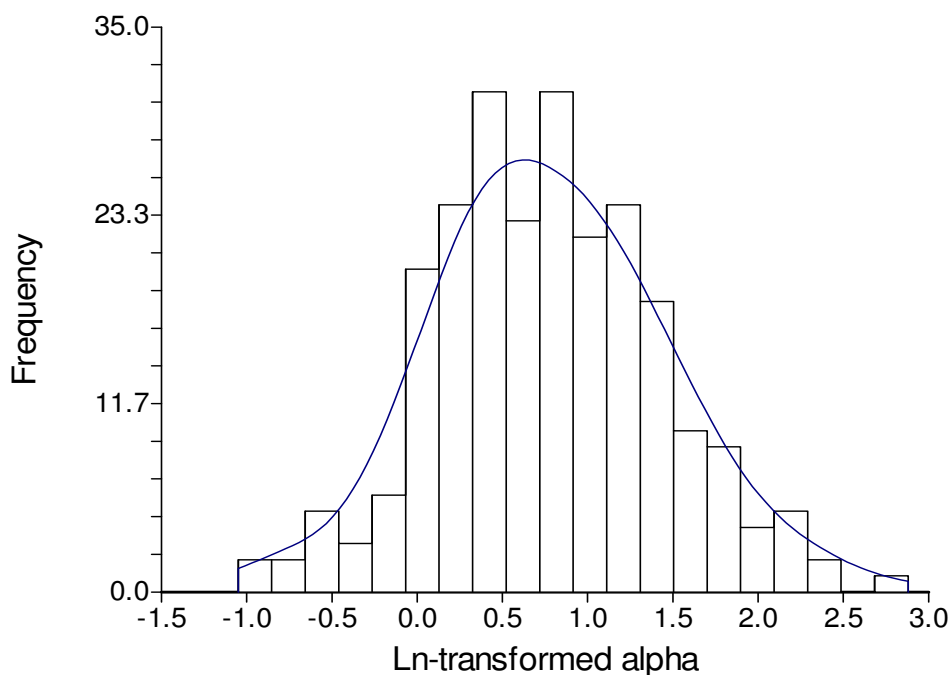
Figure 3.3 Histogram showing frequency distribution of annual ln-transformed values of α, with normal distribution line superimposed (mean $\ln(\alpha) = 0.78$, SD = 0.68, n = 234). Formal normality tests (Hinze, 2001) accepted normal distribution.

Table 3.3 Estimates of the maximum annual reproductive rate α for ten species and 13 stocks. α: the median α, α = exp(μ). C.I. 95%: 95% confidence interval of α. ln(α): the mean μ of the log-transformed annual estimates of α.. σ: standard deviation of ln(α). σ²: variance of ln(α). $α_s$= stochastic estimate of α, $α_s$ = exp(ln(α) – 0.5 * σ²).

Species	Stock	α	C.I. 95%	ln(α)	σ	$α_s$	Years
Clupeidae							
Herring	North Sea	3.61	2.34 - 5.57	1.28	1.03	2.11	23
Sprat	North Sea	2.34	1.27 - 3.21	0.71	1.14	1.07	23
Gadidae							
Cod	North Sea	2.76	1.58 - 3.46	1.01	0.68	2.19	23
Haddock	North Sea	2.92	2.12 - 4.05	1.07	0.74	2.14	17
Whiting	North Sea	2.57	2.37 - 3.24	0.94	0.55	2.21	23
Silver hake	Scotion shelf	2.18	1.92 - 2.48	0.78	0.36	2.04	35
Pleuronectidae							
Yellowtail flounder	Scotian shelf	1.89	1.63 - 2.63	0.64	0.46	1.7	35
Plaice	WesternChannel	2.05	1.79 - 2.36	0.72	0.23	1.99	11
	Celtic Sea	2.12	1.46 - 3.06	0.75	0.13	1.98	11
Soleidae							
Sole	Western Channel	1.13	1.03 - 1.15	0.11	0.15	1.11	11
	Celtic Sea	1.49	1.15 - 1.93	0.4	0.41	1.37	10
	Gulf of Biscay	1.39	1.32 - 1.79	0.39	0.19	1.37	11
Scorpaenidae							
Red fish	Western Greenland	1.08	0.66 - 1.79	0.08	0.84	0.76	11

3.5 Comparison of data

Estimates of the maximum annual reproductive rates α obtained from this study were compared with those published by Myers et al. (1999). A paired t-test was performed to compare mean α for each species. The difference between $α_{(this\ study)}$ minus $α_{(Myers\ et\ al.\ 1999)}$ was not significantly different from zero ($t_{0.4;\ 0.05}$, Prob. = 0.67, n = 10). Figure 3.4 shows a comparison at species level.
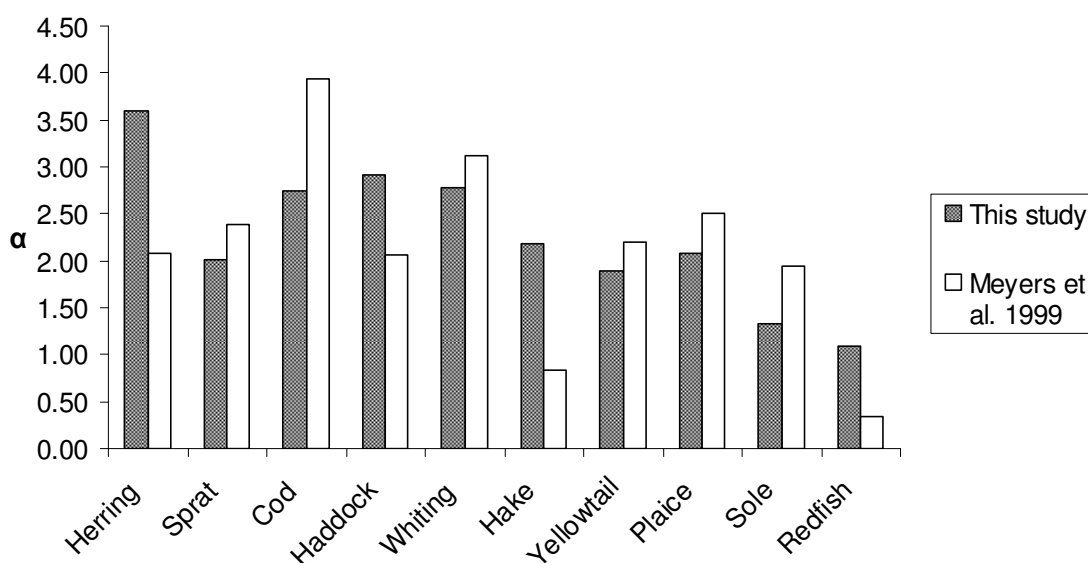
Figure 3.4 Comparison between values of α derived in this and those published by Myers et al. (1999).

In Figure 3.5, values of α for the five investigated families were compared with values provided by Myers et al. (1999). For this purpose, family means for the maximum annual reproductive rate α were calculated from the species means.
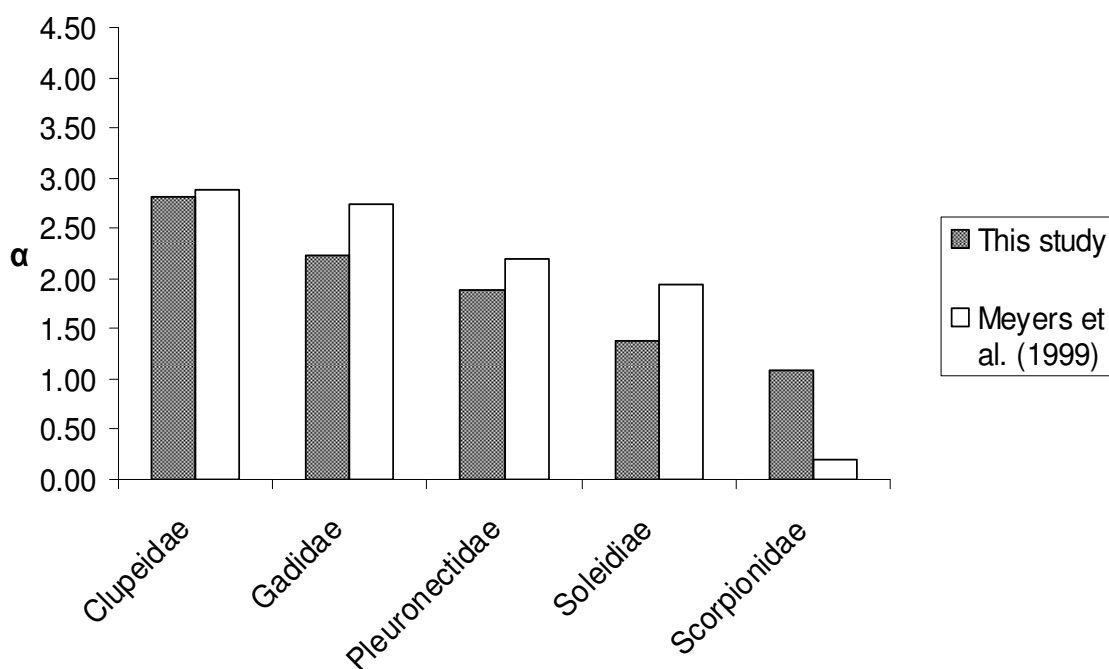
Figure 3.5 Comparison between family means of α derived in this study and those published by Myers et al. (1999).

4. Discussion

Currently, all published estimates for the maximum annual reproductive rate as defined in this study are derived from the method provided by Myers et al. (1999). This is the first time that the alternative method developed by Froese (2004b) has been thoroughly tested based on analyses of 244 length frequency samples covering thirteen stocks and ten species. The results reveal that the new method can be used to derive reasonable estimates of the maximum annual reproductive rate, as they are consistent with the findings by Myers et al. (1999). Moreover, the two methods can be considered as independent from each other. This is very important as it reduces uncertainties about the maximum annual reproductive rates of bony fish. The independence of the two methods is founded in the use of different data sources and estimation techniques. The method presented by Myers et al. (1999) relies on spawner-recruitment relationships, which are reconstructed from catch at age data. The estimation of the spawner-recruit relationship requires various intensive analysis techniques and was thus described as perhaps the most difficult work in fisheries stock assessment (Hilborn and Walters 1992), while the method suggested by Froese (2004b) is based on analysis of length frequency data, which can be applied to the estimation method without any major modifications.

Gullan and Rosenberg (1992) suggested that the biggest advantage of length-based methods is that the basic data are quick and easy to obtain, whereas catch at age data are relatively unavailable because of difficulties with aging. However, a crucial assumption for Froese´s (2004b) method, which can be generalised for most length-based analyses, is that the length frequency data to the right of the smallest selected length class accurately reflects the length structure of the real population. In some cases, this assumption might be violated, which led to the development of a list of criteria for the selection of length frequency samples (see Materials and Methods), which has proved to be useful throughout this study.

Daniel Pauly (UBC, Vancouver, pers. comm.) suggested excluding length classes not fully represented in the sample. This suggestion was applied to samples of the North Sea cod and North Sea haddock, where tests show that length classes of the first peak observed in the length frequency sample were not fully recruited. The exclusion of these length classes has certain advantages. The back-calculation of the fish which would have been caught if they were fully vulnerable to the gear (Pauly 1984) and the subsequent correction for the

effect of fishing mortality (Froese 2004b) are based on the assumption that natural mortality is the same for all selected length classes. However, it is quite likely that natural mortality is higher among fish of smaller length classes (Gullan and Rosenberg 1992). In initial runs of the method, smaller length classes were not excluded, generally resulting in higher estimates for the numbers of potential replacement spawners and thus higher estimates of the maximum annual reproductive rate. Unfortunately, subjectivity remains concerning the extent of length class exclusion, which could not be expressed in quantitative terms. However, this should not considerably affect the overall validity of the results, as potential biases would only slightly change the estimates of α.

4.1 Sensitivity of the method

The input parameters in Table 3.1 describe average life history traits across many individuals of one stock and if certain input parameters are inaccurate, they have different effect on the estimated α. Figure 3.1 shows the sensitivity of α to variations of the input parameters asymptotic length (L_{inf}), length at first maturity (L_m), growth coefficient (K) and natural mortality (M). The parameter with the highest uncertainty is probably the natural mortality, which is generally assumed to be poorly known (Gullan and Rosenberg 1992, Denney et al. 2002). An unexpected result of the performed sensitivity analysis is that α is considerably insensitive to changes in M (Figure 3.1). This is surprising because M is the key parameter for the two adjustments applied to correct the length frequency samples for the effects of gear selectivity and fishing mortality (see Materials and Methods). Generally, M is negatively correlated with estimates of α, while changes of L_{inf} and K are positively correlated (Figure 3.1). Gullan and Rosenberg (1992) suggested that it is a reasonable expectation to estimate L_{inf} to within 10%, which can be considered as relatively well know in contrast to various other input parameters used for stock assessments. Fortunately, α appears to be most sensitive to changes in L_{inf} for all investigated samples, the value which is the easiest to be determined. For example, variations of L_{inf} and K by 10% resulted in changes of α ranging from 23 to 70% and 14 to 23%, respectively (Figure 3.1). However, we have to consider that the high sensitivity of L_{inf} and K is the result of changing only one parameter at the time. In the current study, K was calculated, among others, from a stock specific L_{inf} (equation 11). This estimation method has the advantage that L_{inf} and K counterbalance each other and overestimations of L_{inf} would result in smaller K values, approximately reduced by the same magnitude,

which is explained by equation (11). For example, a change of L_{inf} estimated for the North Sea cod by +10%, results in reduction of K by 12% when calculated from equation (11). This means that α is less sensitive to variations of L_{inf} and K when both parameters are considered simultaneously.

The sensitivity of the length at first maturity (L_m) was found to be highly variable among investigated samples. This variability is caused by the different steepness of the slopes at the point of the intersection between L_m and the length frequency curve. A steeper slope generally resulted in higher sensitivity of α in relation to variations of L_m. (Figure 3.1). For example, the slope at the point of the intersection between L_m and the length frequency curve was found to be steepest in the length frequency sample of the North Sea Haddock and the frequencies number of fish in length range +/-10% of L_m declined from 2721 to 950 (slope = -295.23) (inserted L-F sample, Figure 3.1 B). In contrast, the gentlest slope was observed in the North Sea cod length frequency sample (inserted L-F sample, Figure 3.1 A), where the number of fish in the length range +/-10% of L_m declined from 7 to 6 (slope = -0.11). Consequently, the sensitivity of α to variations of L_m was highest for the length frequency sample of the North Sea haddock (Figure 3.1 B) and lowest for the length frequency sample of the North Sea Cod (Figure 3.1 A).

Generally, the results obtained from the sensitivity analysis suggest that most attention must be devoted to increasing the accuracy of L_{inf} and L_m, rather than concentrate on better estimates of K and M. However, L_{inf} and L_m can usually be assumed to be well known as L_{inf} can be estimated from the largest fish in the sample (Pauly 1984, Gullan and Rosenberg 1992, Froese and Binohlan 2000). L_m can be directly measured as a standard routine of research surveys.

4.2 Simplification test

Findings of the performed simplification tests justified deriving α from one length frequency sample at the time as suggested by Froese (2004b). This has the advantage of obtaining more annual estimates of α from a given length frequency time series and more importantly, obtaining estimates of α for species to which the two sample method cannot be applied.

Estimating α from one sample assumes that length frequencies are relatively similar over a period of time in the absence of major demographic events (Froese 2004b). This simplification was tested by comparing α derived from one length frequency sample with α_{tm} derived from two length frequency samples that were the same number of years apart that it takes fish to attain the age of maturity. The two sampled t-test routine of NCSS 2000 (Hinze 2001) was used to test the null hypothesis that there is no significant difference between log-transformed annual estimates of α and α_{tm}. The null hypothesis ($p > 0.05$) was accepted for all tested stocks (Table 3.2), i.e no significant difference was found between the two approaches. However, it is important to consider that all tested length frequency samples ranged over ten years and significant differences might occur when log-transformed values of α are compared over a shorter period of time.

After the acceptance of the null hypothesis for all tested data sets, it was decided to submit the suggestion by Froese (2004b) to closer examination. Interestingly, Figure 3.2 shows similar trends of α and α_{tm} when α estimated from the length frequency sample at the year t_a was compared with α_{tm} derived from the number of replacement spawners at the same year t_a and the number of spawners at the year t_{a-tm}, i.e. the year t_a minus the number of years it takes fish to attain the age of first maturity. The example of the length frequency samples for the North Sea cod in Figure 4.1 illustrates the effect that was generally observed when α (solid line, solid dots) derived from the year t_a was compared with α_{tm} (dotted line, open dots) derived from the number of spawners at the same year and the number of replacement spawners derived from the year t_{a+tm} Figure 4.1 B), in contrast to the trends observed when using the previously discussed comparison (Figure 4.1 B).
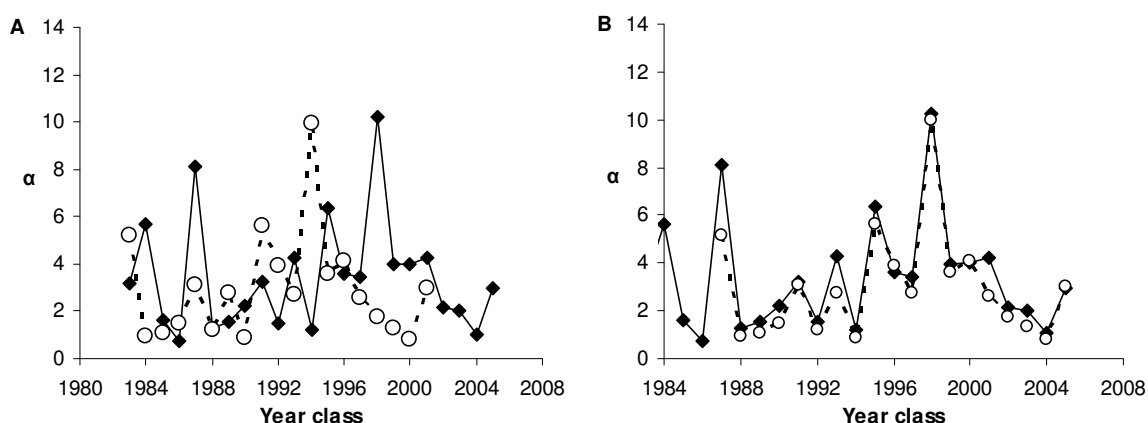

Figure 4.1 A and B show the contrast of two approaches for the comparison of α (solid line, solid dots) and α_{tm} (dotted line, open dots); see text for detailed description

The obvious mismatch of α and α_{tm} in Figure 4.1 A is explained by the high variability in the numbers of replacement spawners observed in the length frequency samples. Consequently, the good fit of α and α_{tm} in Figure 4.1 B has to be interpreted as a result of the relative constancy in the numbers of spawners. The higher variability among numbers of replacement spawners was found in all data sets. This is not surprising considering environmental processes whose impact on pre-adult survival varies between years (e.g. MacKenzie et al. 2003). The findings obtained from the graphical comparison suggest that the numbers of spawners are relatively constant and if this is given, replacement spawner variability has limited impact on the applicability of the simplification suggested by Froese (2004b). In practice, this means that it is only necessary to consider major demographic events that affect the abundance of spawners as a criterion to estimate α from one length frequency sample at the time.

4.3 Maximum annual reproductive rates

Myers et al. (1999) suggested that the maximum annual reproductive rate is relatively constant and typically between 1 and 7. Probably the most important outcome of this study is that results are consistent with this generalisation. The consistency of estimated maximum annual reproductive rates is strongly supported by mainly three findings:

(1) Mean α of the ten species was found to be 2.3 (95% C.L. 1.8 -2.7), with confidence limits clearly within the range of 1 to 7.

(2) The obtained mean across all 244 annual estimates of α is 2.2 (95% C.L. 2.0 -2.4), also with confidence limits within the suggested range (see also Figure 3.3).

(3) The pair wise comparison between estimates of α obtained from this study and values published by Myers et al. (1999) indicate no significant difference (paired t-test, $t_{0.4;\ 0.05,}$ Prob. = 0.67, n = 10).

These results indicate that maximum annual reproductive can be expected around 2 for the majority of bony fish. Reproductive rates can be highly variable among stocks within a species (MacKenzie et al. 2003) and species estimates of α published by Myers et al. (1999) were generally estimated from a larger numbers of widely distributed stocks. For example, Table 3.3 shows that estimates of α were highest for the North Sea herring (α = 3.61, 95% C.L. 2.34 – 5.57), which was the only obtained stock for this species. In contrast, Myers et al. (1999) estimated the species mean α to be around 2, which is surprisingly low in comparison with other species, such as cod. They suggested that the

reason for the low α was probably the incorporation of several depleted stocks, including the Iceland stock and the Norwegian stocks. In comparison to these stocks, the North Sea herring is in a relatively good state, which might explain the observed difference and illustrates the uncertainty of the pair wise comparison. However, it should neglect the similar trends, as Figure 3.5 show that family means of α are surprisingly consistent when compared with those published by Myers et al. (1999).

The confidence limits of single stock estimates ranged between 1 and 5.57, except for the deepsea redfish (α = 1.1 95% C.L. 0.66 – 1.77). (Table.3.3). It is quite likely that the average α for this species is below 1, which would be consistent with the findings for the *Sebastes* species in general (Myers et al. 1999). Even though, α might be higher or lower for some species, this should not interfere with the generalisation that most future estimates for bony fish can be expected to be above one. This means that under optimum conditions the majority of bony fish have the potential to replace the number of spawners in a single spawning season, as long as they are allowed to attain maturity. The latter is unfortunately not considered in most management regimes, because most fish are caught before they can reach the length at maturity (Froese and Kesner-Reyes 2002), which is generally known as recruitment overfishing (Froese 2004a).

The maximum annual reproductive rate was shown to be important for the understanding of the factors and mechanisms that control the reproduction success of bony fish (Denny et al. 2002, Froese and Luna 2004, Myers and Barrowman 1996). The practical usefulness of α was explored by Myers and Worm (2004) who used the estimates published by Myers et al. (1999) to predict the collapse and extinctions of sensitive species under current levels of fishing mortalities and demonstrated that the survival of sensitive species of the Northwest Atlantic can only be ensured by reducing fishing mortalities by 40-80%. Additionally, α can be used to construct a simple framework for the evaluation of management regimes. The biological limit of fishing mortality F_{lim} is used as a reference point in fisheries management and can be defined as the fishing mortality that would drive a population to extinction (Mace 1994).

Myers and Mertz (1998) provided a formula which allows the calculation of F_{lim} from the estimated values of α. It is implicitly given by:

$$\alpha = \exp(F_{lim}(t_m - t_{rec} + 1) * (1 - \exp(-(M + F_{lim})), \qquad\qquad ....(16)$$

where t_{rec} is the age at which fish enter the fishery (Myers and Mertz 1998). For example ICES suggested a biological limit of fishing mortality for the North Sea cod of 0.86, while the minimum landing size is suggested to be 35cm (Anon. 2005a). The corresponding age (t_{rec}) of approximately 1.4 years can be easily calculated from the von Bertalanffy growth function when using the parameters for the North Sea Cod in Table 3.1.

Estimated parameters for the North Sea cod then suggest $\alpha = 2.76$, $t_m = 3.8$, $t_{rec} = 1.4$ and $M = 0.18$. When applying these parameters to equation (16), the resulting F_{lim} is 0.51. This reveals that F_{lim} is overestimated for the given fishing regime or in other words that the suggested minimum landing size is to small to sustain high fishing pressures. This is obviously the case when considering the critical status of the North Sea cod. Note that the estimated F_{lim} is conservative as fishery mortality is assumed to be knife-edge and bycatch is not considered (Myers and Mertz 1998).

4.4 Precautionary approach

It is widely accepted that environmental conditions have a significant impact on the abundance of fish stocks (Hilborn 1995). The incorporation of environmental influences on life histories traits has been suggested by Lande (1993). Myers et al. (1999) adopted this suggestion for the annual reproductive rate by adding such variance to α. Here, it was decided to adopt the originally suggestion of Lande (1993) and subtract the variance from α (equation 7), as a precautionary measure. This is because a lower value of α reduces the probability of overestimating the ability of a population at low density to withstand fishing pressure, especially in the face of unknown future environmental conditions. In general, populations at low densities are expected to have less resilience to threats of genetic, demographic and environmental variability (Lande 1993) and Hunchings (2001) emphasised that among these threats, the environmental stochasticity and therefore unpredictable changes in age-specific survival is probably the most important. Figure 4.2 shows a graphical comparison between α and its stochastic estimate α_s obtained for the thirteen investigated stocks in Table 3.2. The greater the distance from the one-one line, the greater the variance in interannual variability of α and the smaller the stochastic

estimate α_s. For example, the highest variance in annual estimates of α was found for the North Sea herring. Although, the North Sea herring also indicate the highest average reproductive rate, the expectations expressed in α_s are relatively low in comparison with other species such as cod or whiting (Figure 4.2).
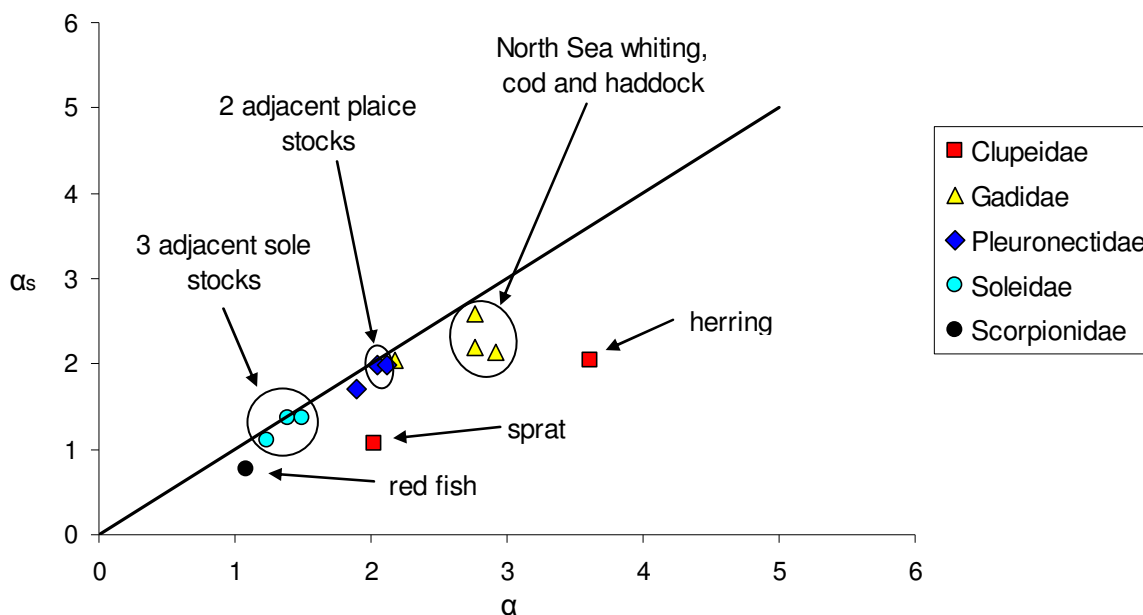
Figure 4.2 Graphical comparison between estimates of α and their stochastic estimate α_s. The stocks are grouped by families.

The low expectations for the clupeids are not unreasonable, because their pelagic environment is distinct by highly variable environmental conditions. If several years of poor environmental conditions occur, especially when combined with high fishing pressure, stocks can quickly decline in abundance (Watanabe et al. 1995). In the current study, subsequent years of low reproductive rates were particularly estimated for the North Sea sprat, which indicates such negative environmental effects. Similarly, MacKenzie et al. (2003) found several years of low recruitment for the Norwegian Spring herring. In contrast, flatfish (here: Solidae and Pleuronectidae) exhibit less variance, however in combination with lower average reproductive rates. Although, the interannual variance of α observed for the deepsea redfish might be due to the small sample size and difficulties of sampling this great depth, the low value of α_s suggests that this species is probably not very resistant to commercial exploitation which is consistent with the considerations of various authers (Robert 2002, Drevetnjak 2003). Figure 4.2 indicates highest expectations for the North Sea gadoids which might explain why cod stocks were resistant to collapse for so many years despite high exploitation rates (Myers et al. 1997). The example Northern cod in the Northwest Atlantic, however, probably best demonstrates that the reproductive

potential should never be overestimated, because, even though the replacement potential of the spawning stock was apparently sufficient, the stock collapsed in the late 1980´s which can be mainly attributed to the high fishing mortality (Myers et al. 1996). Therefore, the stochastic estimate of α should be incorporated into a precautionary approach, particularly when α is used for management purposes.

Additionally, Figure 4.2 indicates that interannual variability is increasing with higher reproductive rates. Although, this trend is not statistical significant, it gets more apparent when combined with the trend revealed from comparison between family means of α (Figure 3.5). A reasonable explanation for these trends would be that species of different families adapted their reproductive rates to specific ecological niches with different variability's in environmental conditions, which is generally supported by the findings of MacKenzie et al. (2003). The high α observed for the clupeids would then be an adaptation to highly variable conditions in the pelagic environment, while the lowest estimates for deep sea representatives of the family Scorpionidae (*Sebaste spp.*) would be explained by the stable conditions in the deep sea (Figure 3.5). Similarly, but in a smaller scale differences between gadoids and flatfish species (Pleuronectidae and Soleidae) could be explained by different stabilities in the micro environments. Although, the three families are bottom dwellers (demersal), they are adapted to different ecological niches, which might differently affect their survival probability in certain stages of their development. This could be also explaining the differences between species of the same family. Annual reproductive rates for the North Sea cod, Haddock and Whiting were found to be higher than for the Scotian shelf silver hake and the environmental conditions can be assumed to be more stable in deeper waters at continental slope, the habit of the silver hake, than the environmental conditions in the shallow North Sea. However, an accurate answer for these differences needs further investigations.

4.5 Limitations and further research suggestions

A clear limitation is that the new method cannot be applied to semelparous species such as Pacific salmons (*Oncorhyncus spp.*). This is due to the specific life history of this species as the majority of spawners die after spawning. This means that the length structure of the population can not be represented by one length frequency sample, because the distinct cohorts are differently distributed in space and time. It is interestingly to note that Myers et

al. (1999) derived their method from the spawner-recruit relationships of the Pacific Salmons. Similar difficulties might occur with highly migrating stocks, especially when they form size-segregated and change distribution with abundance (Jennings et al. 2001). It should be emphasised that the here tested method do not circumvent difficulties of representative sampling, however further research should be carried out to develop further quantitative criteria for the selection of accurate length frequency samples.

An unexpected limitation was the difficulties to obtain length frequency data and it appears that the importance of long time series of such data has been widely ignored. Certainly, further research is necessary to test the new method and reduce remaining uncertainties by applying it to wider range of species and larger data sets. For this purpose, data storage should be improved and length frequency data should be easier accessible, which would also enhance the transparency of fishery management as recommended by Froese (2004a).

5. Conclusion

The strength of the new method for estimating the maximum annual reproductive rate is that it relies on data which should be quick and easy to obtain. Additionally, the findings of this study justify estimating the annual reproductive rate from one length frequency at the time, which allows obtaining proxies of α when long time series are unavailable. The lack of very long time-series can be overcome by examining many data sets using meta-analysis techniques to study multivariate length frequency samples. In this case, stock specific average annual reproductive rates can be expected to be more variable. However, the overall findings should be similar and estimates of α can be expected to be typically between 1 and 7 with a median located at the lower end of this range. This means that most bony fish have the potential to produce sufficient replacement spawners within a single spawning period, if management regimes allow them to reach the age at first maturity. On the other hand, the annual reproductive rate appears to be bound on an upper limit and the results of this study reveal that the expected annual reproductive rate for many species is between 1 and 4 and even lower when incorporating potential environment perturbations.

Knowledge about the maximum annual reproductive rate can greatly reduce the uncertainties of the biological processes underlying the population dynamics of exploited species. This study demonstrates the usefulness of Froese´s (2004b) method for estimating this important life history trait. Therefore, I conclude that it has the potential to become an established and powerful tool in fishery science.

6. References

Anon. (2002). Report of the Working Group on the Assessment of Southern Shelf Demersal Stocks. *ICES Doc. C.M.,* 2002/ACFM:05

Anon. (2004a). Answer to Special Request from the European community and Russia for the Rockall Haddock. *ICES Doc.*, W:\acfm\acfmwg\Anwer to Request on Rockall Haddock.doc

Anon. (2005a). Report on the Assessment of Demersal Stocks in the North Sea and Skagerrak. *ICES. Doc. C.M.*, 2005/ACFM:07

Anon. (2005b). Report of the Working Group on the Assessment of Southern Shelf Demersal Stocks. *ICES Doc. C.M.,* 2005/ACFM:03

Beverton, R.J.H. and Holt, S.J. (1959). A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In: The lifespan of animals. (Wohstenholme, G. E. and O'Conner, M. Eds.). Churcill, London, pp. 142-180.

Binohlan, C. (1998). The MATURITY table. In *FishBase 98: concepts, design and data sources* (Froese, R. & Pauly, D., eds.), ICLARM, Manila,. pp.176-179.

Binohlan, C. & Pauly, D. (1998a). The POPGROWTH table. In *FishBase 98: concepts, design and data sources* (Froese, R. & Pauly, D., eds.), ICLARM, Manila, , pp. 124-129.

Botsford, L.W., Castilla, J.C. and Peterso, C.H. (1997). The management of fisheries and marine ecosystems. *Science*, **222**: 509-515

Charlesworth (1994). *Evolution in age-structured populations,* Cambridge University Press, Cambridge

Denny, N.H., Jennngs, S. and Reynolds, J.D. (2002). Life-history correlates of maximum annual reproductive rates in fisheries. *Proceedings of the Royal Society B*, **269**, 2229-2237

DFO 1999. Silver Hake on Scotian Shelf (Div.4VWX). DFO *Science Stock Status Report,* A3-09(1999)

DFO 2001. Haddock Eastern Scotian Shelf (Div.4TVW). *DFO Science Stock Status Report,* 2003/020

DFO 2002. Haddock on the Eastern Scotian Shelf (Div.4TVW). *DFO Science Stock Status Report,* A3-06(2002)

DFO 2003. Eastern Scotian Shelf Cod. *DFO Science Stock Status Report.* 2003/020 Canadian Stock Assessment Secretariat Research Document 2000/144

Drevetnjak, Konsatantin (2003). How about harvesting of red fish in the Barrents and Norwigian Sea in the XXI century. *ICES Annual Science Conference,* CM2003/U03

Dulvy, N.K., Ellis, J.R., Goodwin, N.B., Alastair, G., Reynolds, J.D. and Jenning, S. (2004). Methods assessing extinction risks in marine fishes. *Fish and Fisheries*, **5**: 255-276

FAO (1993) *Fisheries statistics series* No.111, p.72

Fowler, G.M. and Stobo, W.T. (2000). Status of 4VW American Plaice and Yellowtail Flounder. *Canadian Stock Assessment Research Document*, 2000/144

Froese, R. and Binohlan, C. (2000). Empirical relationships to estimate the asymptotic length, length at first maturity, and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *Journal of Fish Biology*, **56**:758-733

Froese, R, and Binohlan, C. (2003). Simple methods to obtain preliminary growth estimates for fishes. *Journal of Applied Ichthyology*, **19**: 376-379

Froese, R. and Kesner-Reyes, K. (2002). Impact of fishing on the abundance of marine species. *ICES CM,* **12**: 1-12

Froese, R. and Luna, S. (2004). No Relationship between fecundity and annual reproductive rate in bony fish. *Acta Ichthyologia et Piscatoria*, **34**: 11-20

Froese, R. (2004a). Keep it simple: three indicators to deal with overfishing. *Fish and Fisheries,* **5**: 86-91

Froese, R. (2004b). Length-frequency analysis wizard. *World Wide Web electronic publication*, www.fishbase.org (available from the Tools section of the respective species pages).

Froese, R. and D. Pauly. Editors. (2005). FishBase. *World Wide Web electronic publication,* www.fishbase.org, version (02/2005).

Gullan, J.A. and Rosenber, A.A. (1992). A review of length-based approaches to assessing fish stocks. *FAO Technical Paper*. No. 323, FAO, Rome, p. 100

Hilborn, R. and Walters, C.J. (1992). *Quantitative fisheries stock assessment: choice dynamics, and uncertainty*, Chapman and Hall, New York

Hilborn, R.M. and Peterman, R.M. (1995). The development of scientific advice with incomplete information in the context of the precautionary approach. In : Precautionary approach to fisheries. Part 1: Guidelines on the precautionary approach to capture fisheries and species introductions. *FAO Fisheries Technical Paper,* No. 350, Part 1. Rome

Hinze, J. (2001) *NCSS and PASS Number Cruncher Statistical Systems*, Kaysville, Utah

Hutchings J.A. (2001) Conservation biology of marine fishes: perception and caveats regarding assignment of extinction risk. *Canadian Journal of Fisheries and Aquatic Science,* **58**: 108-121

Jennings, S., J.D. Reynolds and S.C. Mills (1998). Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society B,* **265**: 333-339.

Jennings, S., Kaiser, M.J. and. Reynolds, J.D. (2001) *Marine Fisheries Ecology*, Blackwell Science Ltd, Oxford, pp. 178-204

Lande, R. (1993). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist*, **142**: 911-927

Mace, G.M. (1994) Classifying threatened species: means and ends. *Philosophical transactions of the Royal Society B*, **344**: 91-97

MacKenzie, B.R., Myers, R.A. and Bowen, K.G. (2003). Spawner-recruit relationships and fish stock carrying capacity in aquatic ecosystems. *Marine Ecology Progress Series,* **248**: 209-220

Munro, J. L. and Pauly, D. 1983. A simple method for comparing the growth of fishes and invertebrates. *Fishbyte* **1**: 5-6.

Musick, J., (1999). Criteria to define extinction risk in marine fishes. *Fisheries,* **24**: 6

Myers and Barrowman (1996). Is fish recruitment related to spawner abundance? *Fishery Bulletin*, **94**: 707-724

Myers R.A., Hutchings J.A. and Barrowman, N.J. (1996). Hypotheses for the decline of cod in the North Atlantic. *Marine Ecology Progress Series*, **130**: 293-308

Myers, R., Mertz, G., and Fowlow, P.S. (1997). Maximum population growth rates and recovery times for Atlantic cod, *Gadus morhua. Fishery Bulletin*, **95**: 762-772

Myers, R. and Mertz, G (1998). The limits of exploitation: A precautionary approach. *Ecological Applications***, 8**: 165-169

Myers, R.A., Bowen, K.G. and Barrowman, N.J. (1999). Maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Science,* **56**: 2404-2419

Myers, R.A., and Worm, B. (2004). Extinction, survival, or recovery of large predatory fishes. *Philosophical transactions of the Royal Society B,* **360**:175-192

Myers, R.A. (2001). Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytical approaches. *Journal of marine science*, **58**: 937-951

O´Brien, Loretta (1999). Factors influencing the rate of sexual maturity and the effect on spawning stock for Georges Bank and Gulf of Maine Atlantic Cod *(Gadus morhua)* Stocks. *Journal of Northwest Atlantic Fishery Science*, **25**: 179-203

Pauly, D. (1979). Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy´s growth formula. *Berichte des Instituts für Meereskunde der Univ. Kiel*, No. 63

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour l'Exploration du Mer,* **39**:175-192.

Pauly, D. (1984). *Fish population dynamics in tropical waters: a manual for use with programmable calculators*. ICLARM Studies and Reviews 8, Manila, Philippines, 325 p.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. (1998). Fishing down marine food webs. *Science*, **279**: 860-863

Smith, S.E., Au, D.W. and Show, C. (1998). Intrinsic rebound of 26 species of Pacific sharks. *Marine and Freshwater Research* **41**: 663-678

Robert, C.M. (2002). Deep impact: the rising tool of fishing in the deep sea. *Trends in Ecology and Evolution,* **17**: 242-245

Walter, C.J. (1998). Evaluation of quota management policies for developing fisheries. *Canadian Journal of Fisheries and Aquatic Science,* **55**: 2691-2705

Watanabe, Y., Zenitani, H., Kimura, R. (1995). Population decline of the Japanese sardine *(Sardinops melanosticus)* owing to recruitment failures. *Canadian Journal of Fisheries and Aquatic Science,* **52**: 1609-1616

Zeller, D., Froese, R. and Pauly, D. (2005). On losing and recovering fisheries and marine science data. *Marine Policy* **29**: 69-73