Systmod II: Approaching a real dynamic computer model for fish stock assessment and development of fishery strategies

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Abstract

Simulating development of fish stocks may be as complex as calculation of the development of the atmosphere, which is treated in meteorology as an initial value problem in physics. This approach was first proposed by Abbe and Bjerknes in the beginning of the 20^{th} century and today huge systems of differential equations are used to predict the weather. A similar approach to fisheries biology and ecology requires a real dynamic population model, which calculates the development of fish stocks from an initial state with equations that are independent of time. Here we present Systmod II, which uses a length-based growth function with a parameter for environmental variation and length-based data structure. The model uses monthly time steps to integrate population growth by moving fish to higher length groups as they grow. Since fish growth and maturity correlate more with length than with age, this gives comprehensive and clear results. The model was validated for Norwegian Spring-Spawning herring, using observed data from ICES working groups, and correlations (R[sup]2[sup]) between simulated and observed stock (total stock, spawning stock and catchable stock, numbers and biomass) were above 0.93. At present, the model makes reliable predictions on the short term (3 year for herring). For long term forecasts, better predictions of recruitment are needed. Since length is the main variable of the growth function, the state of the fish stock, including variability in length per yearclass, can be measured [b]in situ[b]using hydro-acoustic trawl surveys. Data for modelling of many of the relations are still lacking, but can be filled in from future field studies.

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Introduction

Research in fisheries management aims at calculating the impact of fisheries on the fish stocks and determining how to obtain the maximum sustainable yield (MSY) (Pitcher & Hart 1982). An operative real dynamic population model, which calculates changes in population size and biomass independent of time is needed for this purpose. In mathematical terms, such a model is often formulated with differential equations where the change is initially measured as a function of time. The time factor is then removed by integration.

The factors governing the development of fish stocks may be as complex as the atmospheric processes that determine the weather. At the turn of the twentieth century, Abbe (1901) and Bjerknes (1904) proposed that predicting the weather could be treated as an initial value problem of mathematical physics. Today this translates into huge systems of differential equations used to predict the weather weeks and months ahead (Bauer et al. 2015). In fisheries biology the initial value problem can be expressed as: 1) The state of the stocks based on observations at a moment in time. 2) The future state of the stocks calculated using a sufficiently accurate population dynamical model. The complexity of fishery biology and ecology is huge, however, over time an increased understanding of the driving forces involved will enable more precise forecasts.

Calculations used for fish stock assessment are most often based on the model of Beverton and Holt (1957), but this model is not real since it uses the von Bertalanffy (1938) growth function, which has age, e.g. accumulated time, as the independent variable. Beverton and Holt (1957) assume constant growth in year classes, although in real life, fish growth depends on environmental factors, such as water temperature and access to food. The tools used to simulate the impact of fishing strategies and to develop sustainable fisheries, are therefore not optimal.

A real dynamic growth function, where length increment is expressed as a function of length, independent of time, was postulated by Hamre *et al*. (2014):

$$dL = k \cdot (Lmax - Ls) \qquad (1)$$

The equation states that individual length increment in fish has only one parameter, Lmax, and maximal length increment per unit energy consumption occurs when the individual is small and decreases to zero as the fish approaches Lmax. The equation has two factors, one growth dynamic factor (Lmax-Ls) and the environmental factor, k. When the environmental conditions are constant over the lifetime of one yearclass, the function is linear for that yearclass. The equation is actually similar to equations published by Gulland and Holt (1959) and Chapman (1961), but uses Lmax instead of L_∞ and defines k as a factor determined by the environment instead of only referring to it as a growth rate.

The equation of Hamre et *al.* (2014) was validated using empirical data and described more than 90 % of the variation in the growth of zebrafish and cod held under controlled and semi-controlled conditions and also showed good correlation with registered growth in several commercially harvested fish stocks (Hamre et al. 2014). Systmod (Hamre & Hatlebakk 1998), makes a computer based integration by summing weight increments in timesteps of one month which can be considered small enough to approach the real dynamic model.

The objective of this study is to present Systmod II, a yearclass-length-structured real dynamic population model to improve the prediction of fish stock biomass, where we use the large pelagic Norwegian spring spawning (NSS) herring stock as a case study. The growth function proposed by Hamre *et al*. (2014) has been implemented in the modified Systmod II computer model where all input and output data are structured in year-class (cohort) and length groups. The model can be expanded to treat interactions between multiple marine species and effects of environmental variation such as climate change.

Materials and methods

An overview of the model is given in Figure 1a. The status of the initial stock has the format given in Table 1 (the stock matrice) and is fed into the model from an external file (see figure 1, overview of the model). The simulation develops in monthly time steps for growth and mortality and in yearly time steps for recruitment. For every time step, the status of the stock changes accordingly.

For each yearclass, the fish are distributed into length groups (Table 1). In each time step, the mortality is subtracted from the number of fish in each cell. Then the length increment for the time step and length group is calculated and the groups of individuals which reach the next length groups are moved accordingly (Figure 1 c). The proportion (P_i) to be moved is calculated by the following equation

$$P_i = (dL * G_m) / LGs \qquad (2)$$

G_m is monthly growth as a proportion of the assumed annual growth, dL (Table 2). LGs is the size of the length groups. In this model, the LGs is 1 cm. If P_i becomes more than one, the excess will go to the next length group, and so on. The amount of individuals from one length group will always end up in two other groups (one group if P_i is an integer value). When P_i is less than one, the first of these groups will be the same as the origin (not being moved). NSS herring has limited or no feeding activity during the winter. Modelled growth is therefore variable through the year with a peak in the summer (Table 2).

The validity of this approximation to integration is inversely proportional to the length of the time step. Systmod II uses monthly time steps and can be considered a reasonable approximation to a real dynamic population model. The accuracy of the growth calculation is higher if the difference between monthly dL and LGs is not very much higher than one.

Growth

The simulation of growth (Figure 1b) is based on the equation of Hamre *et al.* (2014):

$$dL = k \cdot (Lmax - Ls) \qquad (1)$$

where dL is length increment, k quantifies the sum of environmental factors that affect growth, Lmax and Ls are the maximum and measured length of the fish. Lmax may be genetically determined and varies between individuals, fish stocks or fish populations. The average Lmax for a yearclass or a group of yearclasses can be entered into the model with or without a standard deviation.

Observed growth in herring in the yearclasses 1985 to 1995, allowed k to be quantified (Figure 2; (Hamre et al. 2014)). Fish ranging from 3 to 9 years old in each year class generally had similar k, while one and two year old fish had a k which was lower than in 3-9 years old fish in the periods from 1984-85 and in 1992-94. In these periods the 3-9 year old fish also tended to have lower k than at the peak in 1988. Based on this information we plotted the environmental factor, k, in 1, 2 and 3-9 year old fish against a measure of fish density (Figure 3) and obtained three second order polynomials which explained 43-51 % of the variation, showing that k is high at low fish abundance and decreases as the abundance increases. These equations are used during the simulations in the present study, but the model can also be run with individually entered k values for the three age-ranges. In the model, the equations are facilitated for three variables for environmental influences; food availability, temperature and fish density, to the first and second order and their interactions, but since we do not know how food availability and temperature affect growth in herring, these factors are set to zero in the present study.

Mortality

A proportion of the fish is removed from every cell at each time step due to natural mortality (M) and fishing mortality (F) by the following equation (Beverton & Holt 1957):

$$N_{t+1} = N_0 * e^{-(M+F)} \quad (3)$$

where N is the number of individuals and *t* is the timestep. In the model it is also possible to enter a measure of predation (P) which would be necessary in a multispecies model, but this is disabled at the moment due to the fact that herring is the only species in this model (Figure 1d).

For simulation of historical data in this study, M was assumed to be 0.9 for age 0-2 years and 0.15 for older herring, in all year-classes (ICES 2009). Observed F was calculated per year based on observed total stock biomass and catch statistics and was only applied for the part of the stock above the harvest limit of 24 cm length.

Recruitment

The modelling of recruitment is shown in Figure 1e. For simulation of historical data, the measured recruitment per year-class is read into the model. The model also has an opportunity to apply the recruitment equation of Beverton and Holt (1957).

Maturation

It is assumed that herring become mature above 28 cm total length

Structuring the indata

The initial stock (Figure 1a) and the simulated stock per timestep, is structured in yearclass and length groups as shown in Table 1. This is also the case for data on the observed stock, which are used for comparison to the simulations. The observed number of fish per cohort and year and their average weights were extracted from the ICES (2009) working group report where the data are calculated from the catch statistics by the VPA method (virtual population analyses). The average lengths of each cohort in each year was derived from back-calculated length data from samples of mature fish caught at the spawning grounds (Holst 1996). Average condition factors were calculated from the above mentioned weight and length data (Fulton 1904). The average standard deviations in length in the years 1989 to 2002 was used to distribute the fish from each cohort in length-groups (Table 1 and Supl. File 2). However, in the future, the number of fish per cohort and length group can be obtained by hydroacoustic trawl surveys, as has been applied in the capelin stock assessment in the Barents Sea (Hamre & Tjelmeland 1982; Nakken & Dommasnes 1975). A representation of the distribution of capelin by age and length was made by measuring length and by reading otoliths to obtain age from trawl samples. Based on these data, the model Systmod, which simulated the results of different harvesting strategies, was established to give scientific advices on the capelin fishery in the Barents Sea (Hamre & Tjelmeland 1982).

Transition to biomass

The transition to biomass is obtained by the use of a standard Fulton's condition factor (Fulton 1904). In the future, condition factors in the length and age groups will be measured in trawl samples. At this point, there is no option for simulating condition factors which are dependent on the environment, but this can be included in the future.

Statistics

Regression analyses and correlations were performed using the software GraphPad Prism (ver 6.05, GraphPad Software Inc., La Jolla, CA, USA).

Results

Validation of the model

Values of the environmental factor (k) observed by Hamre et al. (2014) in the year-classes 1982-1994 were plotted against fish abundance (the number of three-year-old fish in the analyzed year-class and the two previous year-classes). This gave the equations $k = 0.3798 - 0.00686\ x + 6.86*10^{-5}\ x^2$ R^2=0.52 for 1 year old fish, $k = 0.4092 - 0.0066\ x + 6.92 * 10^{-5}\ x^2$, R^2=0.50 for 2 year old fish and $k = 0.4045 - 0.0023\ x + 2.37 * 10^{-5}\ x^2$, R^2=0.43 for 3-9 year old fish (Figure 3), which were used to calculate k in the simulations.

Observed and simulated increase in length by age in the year classes 1982-1990, using an average Lmax of 35.5 cm and the above equations for abundance dependent k, gave correlations of R^2=0.99-1.00, except for the year 1987, where R^2 was 0.97 (Figure S1). In the yearclasses 1990-2000, an Lmax of 34.5 cm gave the best correlation between simulated and observed growth (data not shown).

The development in the number of fish in each yearclass by age for the yearclasses 1982-1990 is shown in Figure S2. To obtain these graphs, the model was run using observed fishing

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intensity (F) per year and natural mortalities of 0.9 for 1-2 year old fish and 0.15 for 3-9 year old fish. The correlation between observed and simulated number of fish by age in each yearclass was R^2= 0.99-1.00, except the yearclass 1986 where R^2=0.93. When the number of fish per year was distributed into length groups, the correlations between observed and simulated data in the years 1982 to 1990 varied between R^2=0.51 and R^2=0.96 (Figure 4).

Simulating the biomass per lengthgroup each year between 1982 and 1990, gave the graphs in Figure 5, showing how the fish grow, die and mature. The development of the 1983 yearclass, which comprises the major part of the biomass during the whole period, can serve as a good illustration of the process. Fig S3 shows how the yield in biomass distributes in lengthgroups. When the fish in the 1983 yearclass grow out of one lengthgroup and into the next, the yield becomes negative in the first and positive in the second lengthgroup. Again it is the 1983 yearclass that is most important for the yield in the period 1982-1990.

The simulated and observed total number of fish and their biomass calculated using the Fultons condition factor in each lengthgroup is given per year for the period 1982 to 2004 in Figure 6. The simulation was started with the state of the stock in 1982; e.g. all simulated results are based on the initial input data from 1982 given in Table 1 and the calculations run by the simulation model for each month and year thereafter. The environmental input (k) was calculated by the equations given in Figure 1c, Lmax was set at 35.5 cm, historical recruitment values and observed F were used. There was a 100% correlation between simulated and observed total number of fish over the whole period, showing the large yearclasses in 1983, 1991, 1992, 1998, 1999 and 2002 (Figure 6a). When simulating the number of fish above minimum catch length and the number of mature fish, the correlation declined to R^2=0.94-0.95 (Figure 6b). The correlations between observed and simulated biomass, obtained using Fulton's condition factor in each lengthgroup, was R^2=0.97 for the total stock biomass (TSB) and R^2=0.96 for the spawning stock biomass (SSB; Figure 6c). The fishing intensity (F) was low at about 0.05 during the years 1982 to 1993, except in 1986 where F=0.2 (Figure 6d), which correlated to a huge decline in TSB from 1985 to 1986 of 3.7 mill tons, or approximately 2/3 of the stock (Figure 6c). Figure 5 shows that the 1983 yearclass contributed most to the catches this year. From 1994, F gradually increased to 0.2 in 1997-2000 and then declined again to 0.09 in 2003 (Figure 6d). F had a large effect on development of the stock biomass, which increased from 1993 until 1997, then stagnated and declined slightly until 2003 when it increased again after F was decreased from the year 2000 (Figure 6c).

The historical recruitment in the stock is shown in Figure 7. The 1983 yearclass was the first large yearclass after the collapse of the stock in the 1960ies. Recruitment is very variable and depends only partly on the spawning stock biomass (Figure 6c).

Sensitivity analyses

The effect of varying k from 0.2 to 0.5 and Lmax from 33 to 37 cm, was simulated for the 1990 yearclass and the results are given in Figure S5. The individual size of medium aged fish was most affected by variation in k and the size of the larger and older fish was most affected by varying Lmax. Both modifications had an impact on biomass development from 1990 until 2000. The simulations with varying k were run with an Lmax of 34.5 cm and those with varying Lmax were run with k calculated by the equations in Figure 3. Historical recruitment and observed F were used for both simulations.

Discussion

Length-structured models of the development of fish populations have the advantage over age based models, that real growth and maturation of fish are better correlated to size than to age (Amara & Lagardere 1995; Aritaki & Seikai 2004; Bertalanffy 1938; Hamre & Tjelmeland 1982; Sæle & Pittman 2010), and this makes the modelling and the results thereof more comprehensive. The differential equation which describes growth in the present study (Hamre et al. 2014) uses length, not time, as the independent variable and is therefore real and dynamic, provided that the time-steps used for calculating length increment (dL) are small. Recent development of acoustic methods, may create opportunities for measurement of length of individual fish *in situ*, and this makes length based growth and simulation methods even more relevant.

The growth function of this study cannot be integrated, but integration is obtained through Systmod II: the program calculates the length increment in each cell of the length- and age-structured population, and moves the fish upwards in the lengthgroups as they grow. Before moving the fish out of each cell, the mortality is calculated from natural- and fishing-mortality and dead fish are removed. SystmodII is modified from the model of Hamre and Hatlebakk (1998) and Hamre and Moen (2008). The original version simulates stock development and interactions of herring, capelin and cod in the Barents Sea, and uses the conventional von Bertallanffy growth equation, while the present model contains the growth function of Hamre et al. (2014) and is developed only for one species, in order to show how the simulations commence. The intention is that SystmodII can be used for one species simulations, and as a module in ecosystem/multispecies simulations in the future.

Similar growth functions as that of Hamre et al. (2014) have been published before (Chapman 1961; Gulland & Holt 1959; Sparre & Venema 1998), but these functions are rarely used in fisheries and ecosystem modelling and fisheries management, where the preferred model is the conventional von Bertallanffy growth function (Angelini & Moloney 2007; Christensen et al. 2005; Hilborn 2012). Furthermore, the former publications of linear growth models, assume k to be constant over the lifespan of the fish and the same in different yearclasses, in line with Beverton and Holt (1957). This assumption is not met by nature, where food availability, temperature and other environmental factors have large impacts on growth. This is illustrated for herring by Husebø et al. (2009). In line with their study, our data indicate that k is dependent on the yearclass strength; in the strong yearclasses, k is lower than in the yearclasses with low numbers of fish, and the 1-3 year old fish, which are the most abundant, have markedly lower k than 3-9 year old fish. In the yearclasses with low numbers of fish, k is most often high and stable over the lifespan of the fish. The relation explains approximately 50% of the variability in k and may have to do with lower food availability per individual when fish abundance is high. Another possible explanation is that the large yearclasses more often spend their first years in the Barents sea where the temperature is lower than in the Norwegian sea (Holst 1996). The model includes scenarios of varying temperatures and critical low food abundance, for example when food drops below a critical level due to competition with other species or to other environmental factors. However, these scenarios are not covered here, due to lack of data to model the relation between food availability, temperature and k.

Another difference between our growth function (Hamre et al. 2014) and the previous ones (Chapman 1961; Gulland & Holt 1959; Sparre & Venema 1998), is the use of Lmax instead of L_∞, which on first sight may seem of minor importance. However, L_∞ involves time and is therefore not compatible with a real dynamic growth equation. Lmax can be understood as a real quantity, characteristic for the individual, the population or the fish stock. For example, different subpopulations can have different Lmax, Lmax may be genetically determined, modulated by the environment or a result of the interaction between the two. In practical terms, however, there is no difference between Lmax and L_∞ in the way they are used in the different equations.

Validation of the model is provided using data from the VPA of herring (ICES 2009), the equations obtained for k and historical recruitment. The validation is mainly a test that the model calculations are correct. The growth was calculated as an increase in mean length by age over different yearclasses and development of the number of fish in each yearclass was calculated using observed F and natural mortalities given by ICES (2009). Both these exercises gave excellent correlations between simulated and observed values. When the data were integrated to show the distribution of the number of fish over lengthgroups for each year between 1982 and 1990, the correlations were weaker. The reason may be that the initial stock in the simulation and the observed data used an assumed variance over an observed mean, since the real variation in the data is not known. When the data were summed to produce the total number of fish in each year, the correlation between observed and simulated data was again excellent, while dividing the stock into catchable fish and spawning stock lead to slightly weaker correlations. The correlations were further weakened, but only slightly, when the number of fish was converted to biomass, probably due to poor precision of the condition factors calculated from measurements of length and weight in trawl samples. At present, the condition factors are static values fed into the model from an external file, however, they will be dependent on food availability and other environmental factors, a feature that can be added when data are available. In summary, the model has a perfect fit between simulated and observed data on the number of fish per year, and provides excellent calculations of catchable stock biomass, TSB and SSB.

The large and unpredictable variation in recruitment in the stock complicates long term modelling of the stock development and catch estimations, which requires knowledge of the yearclass strength of the catchable fish. Research is needed, and is under way, to better understand the mechanisms that determine recruitment (see for example Fiksen & Slotte 2002; Skagseth et al. ; Sætre et al. 2002). With the present knowledge, Systmod II can be used to make reasonably accurate predictions of development of the stock and stipulated catches three years ahead for herring. The observation that strong yearclasses of herring coincide with periods of high temperature in the Norwegian- and Barents Sea region (Marty & Fedorov 1963; Sætersdal & Loeng 1984) was used successfully in simulations with the original version of Systmod (Hamre 2003; Hamre & Hatlebakk 1998; Hamre & Moen 2008).

Conclusion

We have presented a real dynamic computer model for stock assessment and prediction of stock development, which can be used when treating fisheries management as an initial value problem of physics, similar to modelling of the athmosphere (Abbe 1901; Bauer et al. 2015; Bjerknes 1904). At present, the forecast will be reliable when the yearclass strength of catchable fish is known, e.g. 3 years ahead for Norwegian spring spawning herring. For long term forecast, better predictions of recruitment are needed. Growth and maturation of fish are better correlated to length than age and catch limits are given at a certain fish size. The length-based model is therefore more comprehensive than the currently most used age-based models. Since length is the main variable of the growth function in Systmod II, the state of the fish stock, including variability in length per yearclass, can be measured *in situ* using hydro-acoustic trawl surveys.

Data for modelling of many of the relations are still lacking, but can be filled in from future field studies. We hope that Systmod II will be part of the tool box used by fish stock managers in the future for sustainable management of fisheries.

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Figures and Tables

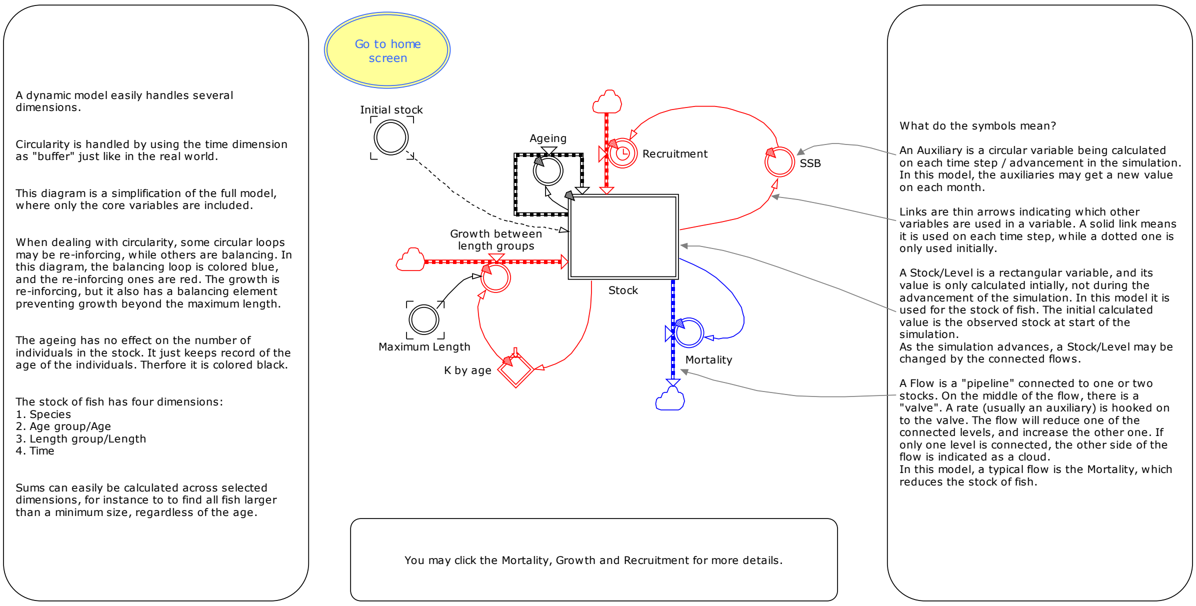


Figure 1a. Overview of the model. The initial stock is fed into the system in the format given in Table 1. In every time step in the simulation, the stock matrice, e.g. the number of fish per length-group and age, is modified by the three connected flows; growth, mortality and recruitment. The first operation is to remove the fish that have died due to fishing or by natural mortality. This number is calculated for every length group and subtracted. The second operation is to manage the growth. When the fish in one length group grows with one cm, all the fish are moved to the next length group, If they grow 1.5 cm, 67% of the fish is moved to the next length group and 33% are moved up two length groups. Equation 2 is used for this calculation. Every year, a new yearclass is recruited into the simulation as one year olds, based on the considerations in figure 3.

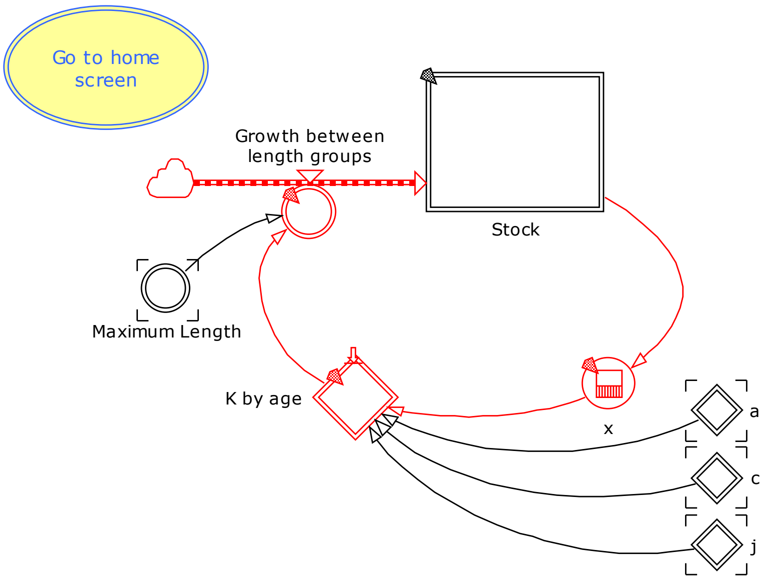


Figure 1b. Simulation of lengthwise growth. Growth is simulated for every time step as dL= k . (Lmax-Ls) (Hamre et al. 2014). L max is fed into the model from an external file. K can be set for the different age groups or calculated based on stock size (see text and Figure 1c).

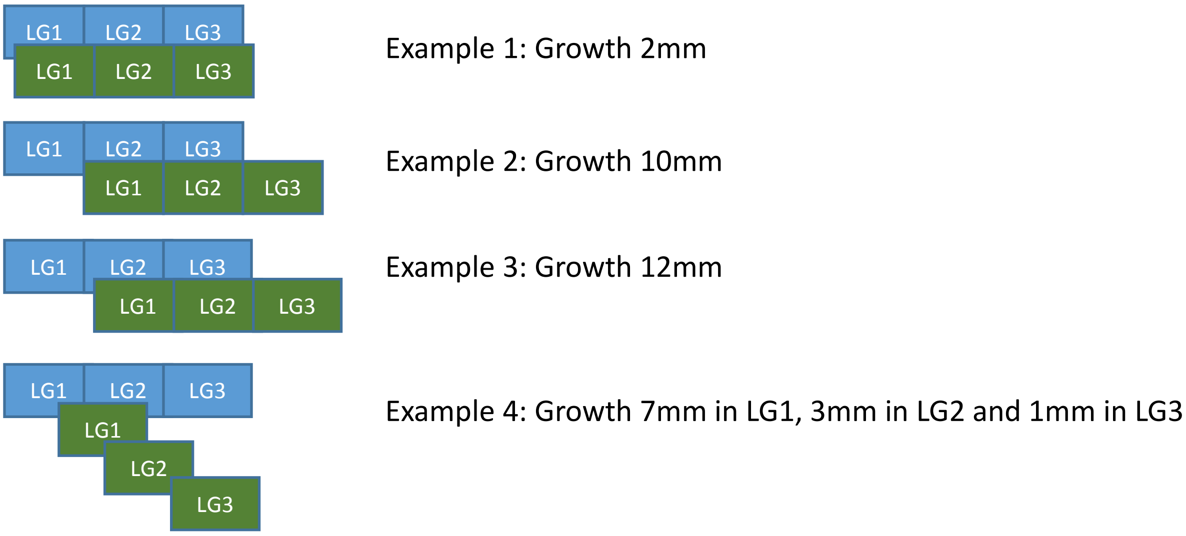


Figure 1c. Handelling of growth in Systmod II. The blue boxes represent 100% of the fish in each lengthgroup at time t, the green boxes represent the same fish at after one timestep (one month, t+1), when they have been moved to larger lengthgroups according to the formula Pi = dL * Gm / LGs. Gm is monthly growth as a proportion of the assumed annual growth, dL (Table 2). LGs is the size of the length groups, here 1 cm. In example 2, with 12 mm growth, 80% of the fish from LG1 will end up in LG2, and 20% will end up in LG3.

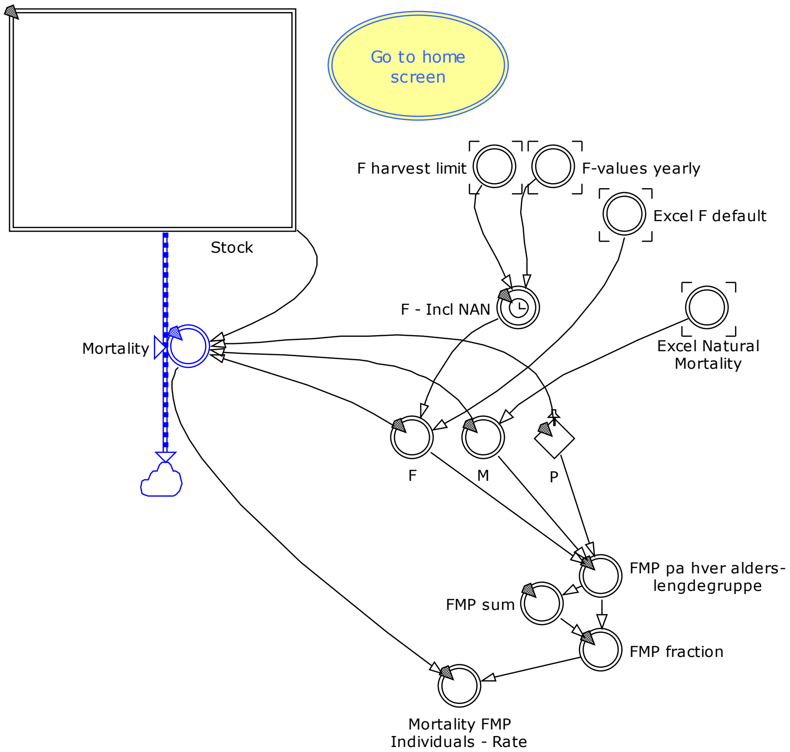
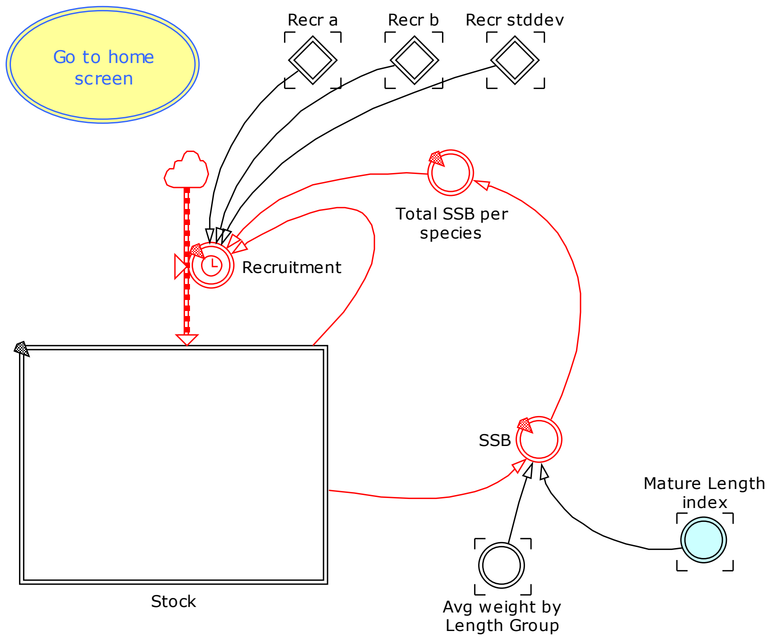


Figure 1d. Simulation of mortality. Total mortality can be simulated as a function of Fishing mortality (F) and Natural mortality (M), where M can be further separated into natural mortality and predation (P), if the model is to be linked to similar models of predator stocks (M= e^{F+M+P}). F and M can be retrieved from an external file. F is characterized both by size limitations for fishing and by the amount of fish to harvest. The mortality is calculated for each cell in the length and age matrice representation of the fish stock.



506
507
508 Figure 1e. Simulation of recruitment. For simulations to compare the simulated and historical
509 data, recruitment is read from data on historical recruitment. For simulations forward in time,
510 recruitment is calculated from spawning stock biomass (Beverton & Holt 1957).
511
512

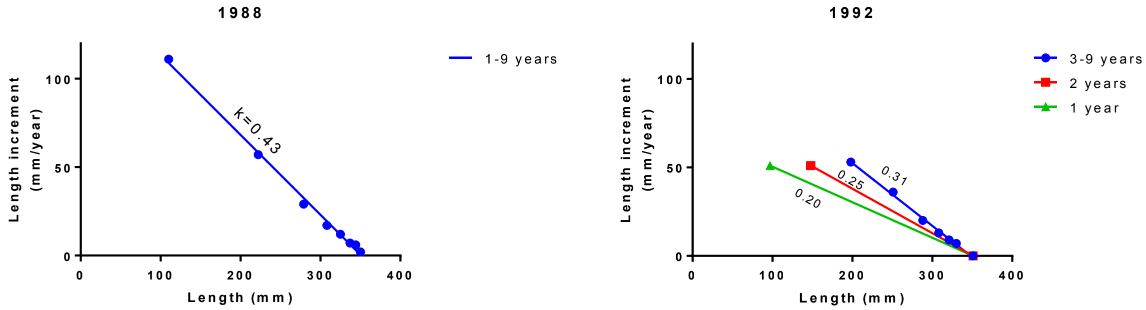


Figure 2. Graphs represent the equation for length increment vs body length: dL = k · (Lmax – Ls); dL = -k*Ls + k*Lmax (Hamre et al. 2014), for herring of the 1988 and 1992 yearclasses. The slope k (given in the graph) is a parameter dependent on the environment, Ls is measured length and Lmax is the average maximal length of herring. The 1988 yearclass is relatively small, not subject to density dependent growth and has a high and stable k throughout life. In the large 1992 yearclass, k is lowered, particularly in one and two year old fish.

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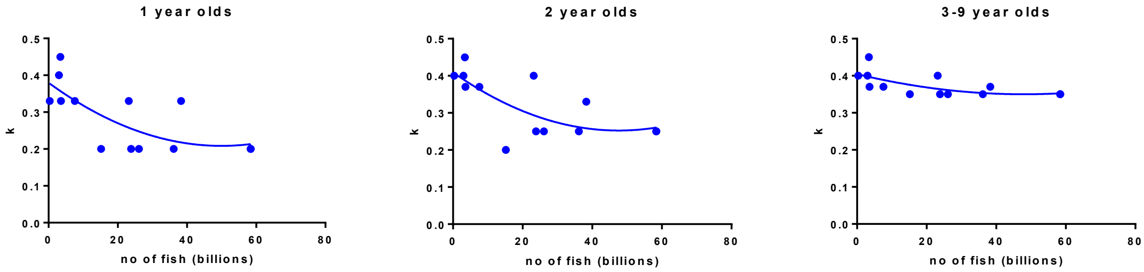


Figure 3. Observed k in the year-classes 1982-1994 plotted against the number of three-year-old fish (billion individuals) in the analyzed year-class and the two previous year-classes as a measure of fish density. The equations are; 1 year olds, $k = 0.3798 – 0.00686\ x + 6.86*10^{-5}\ x^2$ $R^2=0.52$; 2 year olds, $k = 0.4092 - 0.0066\ x + 6.92 * 10^{-5}\ x^2$, $R^2=0.50$; 3-9 year olds, $k = 0.4045 – 0.0023\ x + 2.37 * 10^{-5}\ x^2$, $R^2=0.43$. These equations were used to calculate k in the simulations of historical data.

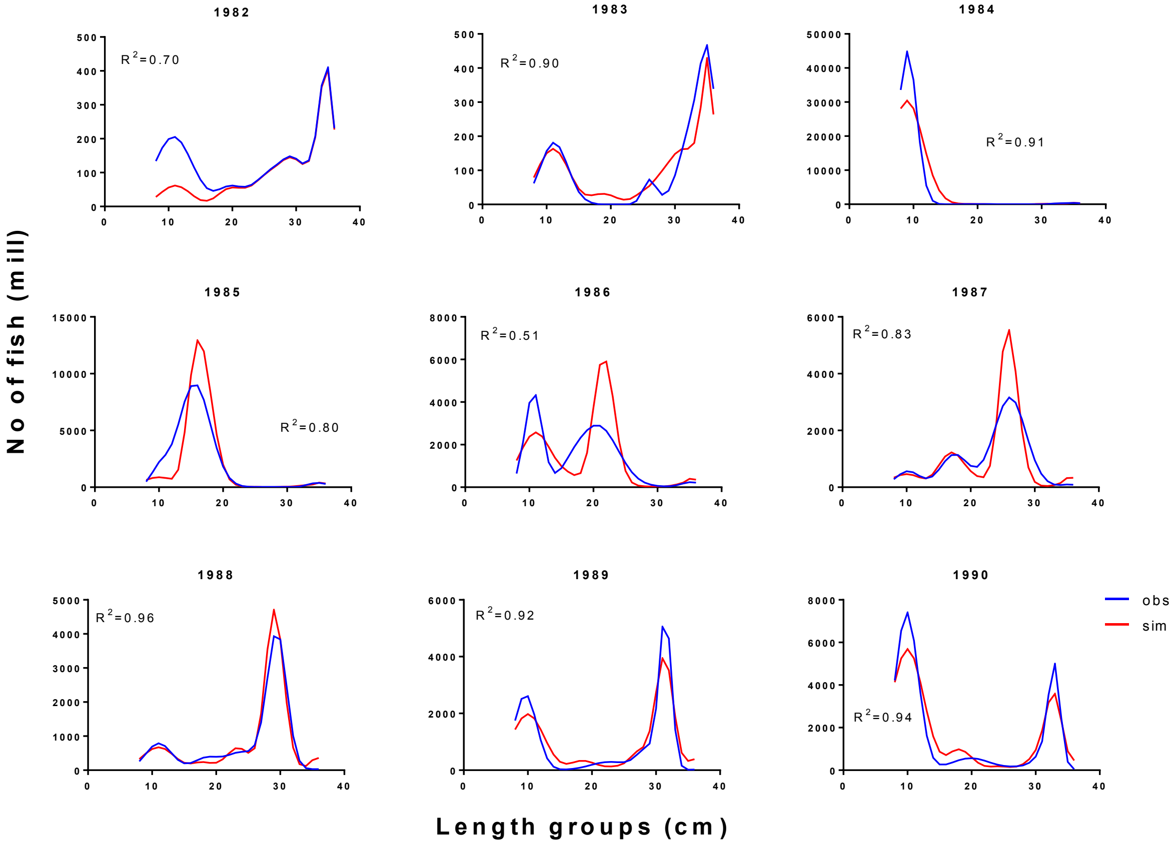


Figure 4. Observed and simulated number of fish per year, distributed by length, in the stock of Norwegian Spring-spawning herring from 1982 until 1990.

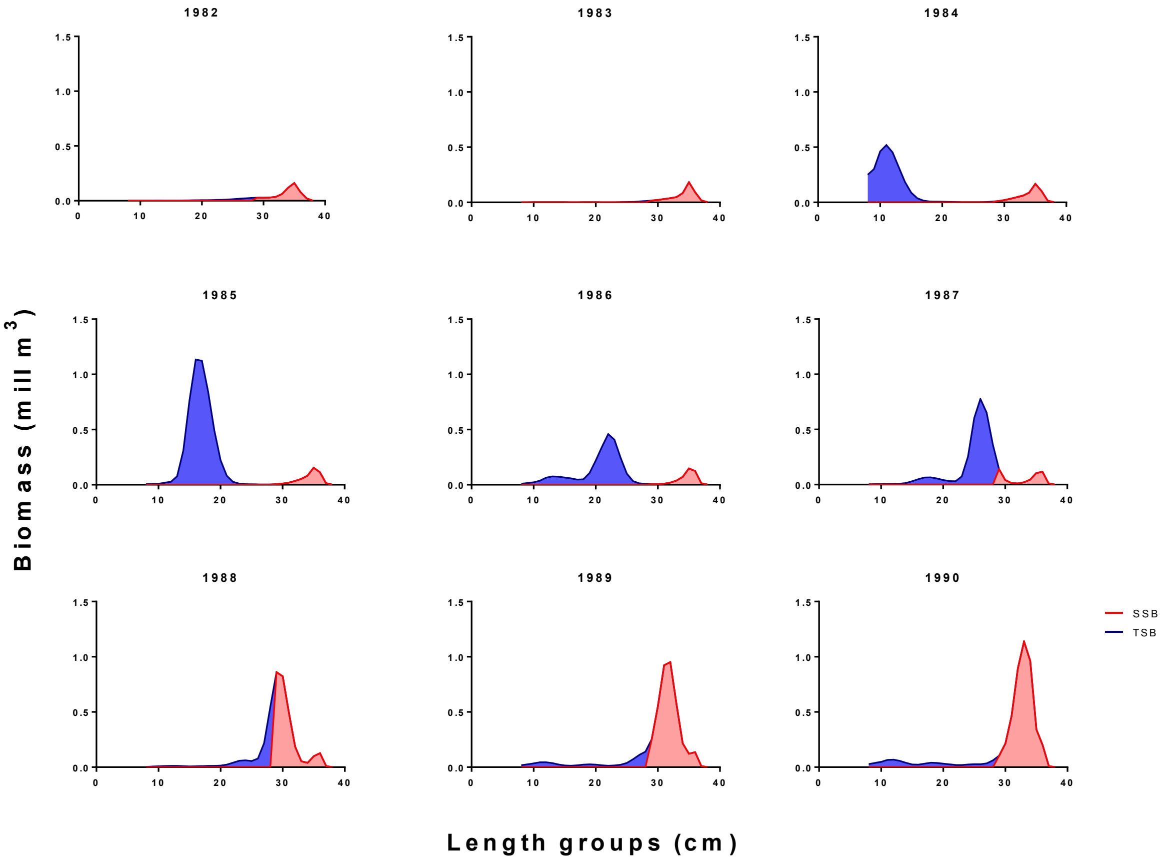
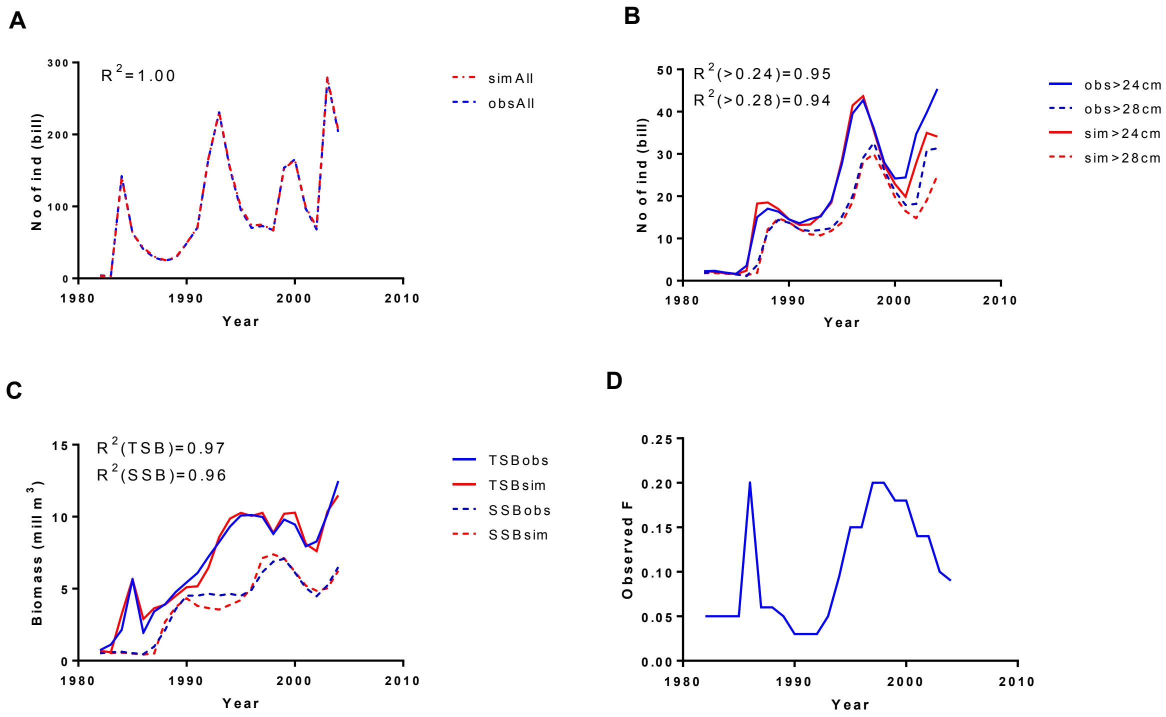


Figure 5. Simulated biomass (obtained by multiplying the data in Figure 4 by the Fulton condition factor) distributed by length in the years 1982 until 1990, in the stock of Norwegian Spring-spawning herring. Blue, immature fish, red, mature fish (>28 cm total length).



Figur 6. Development of the whole stock of Norwegian Spring-spawning herring from 1982 until 2004 in number of individuals A) in the whole population and B) in fish larger than 24 and 28 cm, taken to represent fish above the minimum catch length and mature fish, respectively. C) the total and spawning stock biomass (TSB and SSB) and D) calculated F based on stock assessment and catch statistics, assuming natural mortality (M) of 0.15 in fish above the minimum length (ICES 2009).

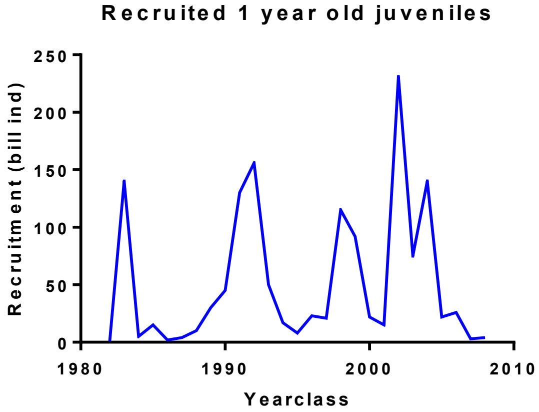


Figure 7. Recruitment as one year old juveniles per yearclass in the stock of Norwegian Spring-Spawning herring from 1982 until 2008. Data were taken from ICES working group reports.

Table 1. The format of the dataset represented in the stock matrice, the example is the herring stock in the year 1982, which is the input dataset used for validation of the model in this study. The 1981 year-class is 1 year old and is represented in the first column, thereafter come the -80, -79, -78 year-classes and so on. In this dataset, fish distribute in the length groups around the mean according to the average standard deviations in length in the years 1989 to 2002. In the future, the number of fish per age and length group can be measured by acoustics and entered in the file. One dataset for each year between 1982 and 2006 can be established and all of them can be used to initiate the model. The input data for the model are given in supplementary file 2.

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15+	Sum
No of fish (10^{-3})	441926	241117	828689	351935	239585	411576	99443	236034	287235	3309	96	226	36752	45	346	
Mean length (cm)	10.8	19.5	26.6	29.9	33.0	34.4	34.7	34.8	35.4	35.7	35.9	35.9	36.0	36.0	36.0	
Mean weight (kg)	0.007	0.048	0.132	0.203	0.276	0.301	0.299	0.294	0.314	0.330	0.335	0.335	0.338	0.338	0.338	
SD length	1.3	1.5	1.5	1.5	1.1	1.0	1.0	0.9	0.9	0.9	0.9	0.9	0.9	0.8	0.8	
C at mean length	0.58848	0.64997	0.69747	0.75904	0.76808	0.74066	0.71551	0.69855	0.70851	0.72475	0.72475	0.72475	0.72475	0.72475	0.72475	
Length groups (cm)																
6.5	440	0	0	0	0	0	0	0	0	0	0	0	0	0	0	440
7.5	4792	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4792
8.5	27682	0	0	0	0	0	0	0	0	0	0	0	0	0	0	27682
9.5	84744	0	0	0	0	0	0	0	0	0	0	0	0	0	0	84744
10.5	137472	0	0	0	0	0	0	0	0	0	0	0	0	0	0	137472
11.5	118173	0	0	0	0	0	0	0	0	0	0	0	0	0	0	118173
12.5	53829	2	0	0	0	0	0	0	0	0	0	0	0	0	0	53831
13.5	12993	31	0	0	0	0	0	0	0	0	0	0	0	0	0	13025
14.5	1662	322	0	0	0	0	0	0	0	0	0	0	0	0	0	1984
15.5	113	2157	0	0	0	0	0	0	0	0	0	0	0	0	0	2269
16.5	4	9453	0	0	0	0	0	0	0	0	0	0	0	0	0	9457
17.5	0	27121	0	0	0	0	0	0	0	0	0	0	0	0	0	27121
18.5	0	50934	0	0	0	0	0	0	0	0	0	0	0	0	0	50934
19.5	0	62615	5	0	0	0	0	0	0	0	0	0	0	0	0	62620
20.5	0	50387	77	0	0	0	0	0	0	0	0	0	0	0	0	50464
21.5	0	26542	829	0	0	0	0	0	0	0	0	0	0	0	0	27371
22.5	0	9152	5878	1	0	0	0	0	0	0	0	0	0	0	0	15030
23.5	0	2066	27278	15	0	0	0	0	0	0	0	0	0	0	0	29358
24.5	0	305	82871	179	0	0	0	0	0	0	0	0	0	0	0	83355
25.5	0	30	164801	1441	0	0	0	0	0	0	0	0	0	0	0	166271
26.5	0	2	214527	7604	0	0	0	0	0	0	0	0	0	0	0	222133
27.5	0	0	182798	26272	1	0	0	0	0	0	0	0	0	0	0	209070
28.5	0	0	101959	59414	37	0	0	0	0	0	0	0	0	0	0	161410
29.5	0	0	37226	87953	775	1	0	0	0	0	0	0	0	0	0	125954
30.5	0	0	8897	85228	7656	57	3	2	0	0	0	0	0	0	0	101843
31.5	0	0	1392	54060	35284	2068	158	172	13	0	0	0	0	0	0	93147
32.5	0	0	143	22446	75821	25913	2974	4589	786	3	0	0	4	0	0	132679
33.5	0	0	10	6101	75968	112226	18906	37861	14246	73	1	2	241	0	2	265635
34.5	0	0	0	1085	35490	167955	40490	96716	77215	601	12	28	3692	4	32	423286
35.5	0	0	0	126	7731	86857	29214	76502	125147	1436	39	93	14438	18	139	341583
36.5	0	0	0	10	785	15521	7101	18737	60652	989	34	82	14438	18	139	118350
37.5	0	0	0	0	37	958	582	1421	8790	196	8	19	3692	4	32	15705
Sum:	441904	241117	828689	351935	239584	411555	99427	236000	286849	3297	95	225	36506	45	344	

Table 2. Assumed monthly growth (Gm) in percentage of yearly growth

Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
0 %	0 %	0 %	0 %	6 %	24 %	29 %	24 %	9 %	5 %	0 %	0 %

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