

Reference-growth rate – a simple and handy parameter summarizing the influence of environmental conditions

Referenzwachstumsrate - ein einfacher und handlicher Parameter zur Zusammenfassung des Einflusses von Umweltbedingungen

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Abstract

Environmental changes may have an impact on life conditions of the fish, e.g. food supply for the fish. The prevailing environmental conditions apply evenly to all age groups of one stock. Small fish have high growth rates, whereas large fish grow with low rates. But, it can be shown on the basis of the von Bertalanffy-growth model that it is sufficient to know only the growth rate of one single age group to compute the growth rates of all other age groups. The growth rate of a reference fish G_{RF} (e.g. a fish with a body mass of 1 kg) was introduced as a reference growth describing the current food condition of all age groups of the stock. As an example a time series of the reference-growth rate of the northern cod stock (NAFO, 3K) was computed for the time span 1979 to 1999. For the northern cod stock it can be observed that environmental conditions caused growth rates below the long-term mean for seven years in a row. After a prolonged hunger period the fish stock collapsed in 1992 also by the impact of fisheries - and this was probably not a coincidence. Now, with the reference-growth rate G_{RF} a simple and handy parameter was found to summarize the influence of the environmental conditions on growth and other derived models and therefore makes it easier to compute the influence of environmental changes within stock assessment.

Zusammenfassung

Veränderungen der Umwelt können Auswirkungen auf die Lebensbedingungen der Fische haben, z. B. auf das Nahrungsangebot der Fische. Die vorherrschenden Umgebungsbedingungen wirken gleichmäßig auf alle Altersgruppen eines Bestandes, wobei typischer Weise kleine Fische hohe Wachstumsraten haben, während die großen Fische mit niedrigen Raten wachsen. Auf der Grundlage des von Bertalanffy-Wachstumsmodells kann gezeigt werden, dass es ausreicht, nur die Wachstumsrate von einer einzigen Altersgruppe zu kennen, um die Wachstumsraten von allen anderen Altersgruppen berechnen zu können. Die Wachstumsrate eines Referenz-Fisches (z.B. eines Fisches mit einer Körpermasse von 1 kg) wurde als Referenz-Wachstum G_{RF} eingeführt, die den aktuellen Zustand des Nahrungsangebots für alle Altersgruppen des Bestandes beschreibt. Als Beispiel wurde einer Zeitreihe der Referenz-Wachstumsraten des nördlichen Kabeljaubestandes (NAFO, 3K) für die Zeitraum 1979 bis 1999 berechnet. Für diesen Kabeljaubestand war zu beobachten, dass Umgebungsbedingungen für sieben Jahre in Folge Wachstumsraten unter dem langjährigen Mittelwert verursachten. Nach einer längeren Hungerperiode kollabierte dieser Fischbestand im Jahr 1992 auch durch den Einfluß der Fischerei - und dies war sicher kein Zufall. Jetzt, mit der Referenz-Wachstumsrate G_{RF} , ist ein einfacher und handlicher Parameter gefunden, der es gestattet den Einfluss der Umweltbedingungen auf die Wachstumsbedingungen und andere davon abgeleitete Modelle zusammenzufassen. Dies macht es einfach, den Einfluss von Umweltveränderungen innerhalb der Bestandsabschätzungen zu berechnen.

1. Introduction

For the description of differential changes in fish growth the von Bertalanffy approach (1934, 1938 and 1949) has been used (see equation (1)); here presented in a shape as given in Beverton and Holt (1957):

$$\begin{aligned} m' &= m'_{as} - m'_{out} \\ m' &= H s - K m \end{aligned} \quad (1)$$

According to the concept of Pütter (1920) the differential growth, m' is the difference between two processes, anabolism, m'_{as} and catabolism, m'_{out} . The variable, H in the concept of Pütter (1920) can be interpreted as the mass flow rate through the digestion organs; the material flow per unit “physiological resorbing surface” and time span [$\text{kg} \times \text{cm}^{-2} \times \text{year}^{-1}$]. The variable K [year^{-1}] is the catabolism rate, proportional to the individual body mass. According to the underlying concept the mass flow rate is assumed to be constant for all fish living under the same environmental conditions, but varies with food availability. The resorbing surface, s [cm^2] is assumed to be proportional to the square of the fish length, l [cm] (equation (2)):

$$s = p l^2 \quad (2)$$

We use the square of the fish length substitutional for the surface of the digestive organs; at which p is a unit-free constant. For the individual body mass we need a proxy, expressed in terms of fish length, as well. The relation between mass, m [kg] and length of fish, l [cm] is described by the condition, q [$\text{kg} \times \text{cm}^{-3}$] (equation (3)):

$$m = q l^3 \quad (3)$$

Notice that this is different from the Fulton's condition factor (Ricker 1975). Solving the differential equation (1) we get:

$$l = \frac{H p}{K q} \left(1 - e^{-\frac{K t}{3}} \right) \quad (4)$$

with $l_{\infty} = \frac{H p}{K q}$

The solution of the differential equation (4) is well known and described in many text books (e.g. Beverton and Holt 1957). Summarising $(H p)/(K q)$ in equation (4) for length at an infinite age, l_{∞} results in the well-known von Bertalanffy function for length (von Bertalanffy 1934). However, instead of introducing l_{∞} and m_{∞} (the length and mass of a fish at an infinite age), we introduce here the assimilation rate A_{RF} of a “reference fish” having the “reference length”, l_{RF} and “reference mass” (with $m_{RF} = q l_{RF}^3$). To explain this equation (1) is standardized to the current body mass. Inserting now equation (2) and (3) into equation (1), we get after rearrangement: (5)

$$\frac{m'}{m} = \frac{H s}{m} - K = \frac{H p}{l q} - K \quad (5)$$

$$G = A - K$$

$$\text{with } G = \frac{m'}{m} \text{ and } A = \frac{m'_{as}}{m} = \frac{H s}{m} = \frac{H p}{l q}$$

The growth rate G is the difference between assimilation rate, A and catabolism rate, K . Please note that the rates described in this paper are values standardized by the current mass and have therefore, the unit [% $\times \text{year}^{-1}$]. The product of A and l is always constant,

$$A l = A_{RF} l_{RF} = \frac{H p}{q} \quad (6)$$

since the right hand side of equation (6) consists of constants only (according to the basic assumption of the derivation of the von Bertalanffy-growth equation (4)). Equation (6) shows clearly that the assimilation rate, A is a function of fish length. By the simple appliance of the rule of proportion we can compute the assimilation rate for all fish lengths, if the length of the “reference fish”, l_{RF} is given and the assimilation rate, A_{RF} of the same fish is known. Therefore, A_{RF} can be considered as a key parameter of length growth for the whole length range – this is one of the main basics of this paper. The same applies for mass growth. From equation (4) and equation (6) the following equation can be derived directly:

$$l = l_{RF} \frac{A_{RF}}{K} \left(1 - e^{-\frac{K t}{3}} \right) \quad (7)$$

The length of the “reference fish”, l_{RF} can be chosen arbitrarily, therefore, equation (7) is also a two-parameter function like the traditional von Bertalanffy equation (4). Using equation (3) and the length-growth equation (7) the mass-growth equation (8) can be derived:

$$m = m_{RF} \left(\frac{A_{RF}}{K} \left(1 - e^{-\frac{K t}{3}} \right) \right)^3 \quad (8)$$

For the length and mass of fish at an infinite age, l_∞ and m_∞ there is:

$$l_\infty = l_{RF} \frac{A_{RF}}{K} \quad (9)$$

$$m_\infty = m_{RF} \left(\frac{A_{RF}}{K} \right)^3$$

$$\text{with } m_{RF} = q l_{RF}^3$$

Notice, equation (8) is only a different shape of the usual von Bertalanffy-growth equation; however, not concealing the fact that growth of fish depends mainly on the availability of food. Especially from fresh-water lakes it is well known that fish living in poor environmental conditions (with low food availability) reach only a low l_∞ and m_∞ and vice versa. One can find lots of publications that describe the relationship between long-term constant feeding conditions and growth. However, food supply may change during fish life. Over time each variation of environment conditions would require a new solution for the differential equation. Mathematically, this is often a difficult or even impossible matter. Some publications can be found describing the relationship between food intake and growth. The state of the art is summarized in Bethke and Bernreuther (2010). A general method to solve this problem is to divide the entire time range into subsections and to assume constant conditions for the individual sections. However, also for these simplified assumptions solution finding may sometimes be difficult, but still possible, however, much easier for differential equations. If we assume constant conditions, which are not constant in reality, then the solution is flawed. But using a difference equation instead of a solution of a differential equation, there are errors, too. But we can reduce these errors by a recursive application of the difference equation for a shorter period of time. A major objective of this study is to analyze the influence of the time span on the accuracy of the estimate.

Equation (8) is an example function in this paper with given parameters for a mean food supply over the whole lifespan. But it is assumed that only a limited time span is observable. This is a common situation in fishery biology, because most times old fish are rare due to overfishing. By fitting difference equations to the supporting points provided by equation (8), it should be clarified whether it is possible to estimate the parameters of a growth function in the same way. In the second part the difference equations were used to estimate a time series of reference-growth rates of the northern cod stock (NAFO, 3K) for the time span 1979 to 1999. The reference-growth rate

$G_{RF} = A_{RF} - K$ (growth rate of a reference fish – e.g. a fish with a body mass of 1 kg) describes the current food condition of all age groups of the stock and summarizes the environmental impacts for a certain time interval into one parameter.

2. Material and methods

2.1. Difference-growth equation – growth within a time interval

For the derivation of the difference-growth equation it is assumed that the environmental conditions are constant within an interval but vary in successive time intervals. This applies more precisely for shorter intervals than for longer intervals. Therefore, the accuracy of the results mainly depends on the time span in which the conditions are assumed to be constant. One task of this paper is the analysis of the influence of this time span on the accuracy of the estimation. Changing the differential equation (5) into a difference equation results in:

$$\frac{m'}{m} \sim \frac{\frac{\Delta m}{\Delta t}}{m} = A - K \quad (10)$$

$$\text{with } m' \sim \frac{\Delta m}{\Delta t} = \frac{m_1 - m_0}{\Delta t} \text{ and } m = \frac{m_0 + m_1}{2}$$

Since it can be assumed that the slope of body mass values within an interval is linear we approximate the instantaneous fish mass, m by the linear mean of the mass at the start, m_0 and end, m_1 of the interval, Δt (Figure 1). Solving equation (10) for m_1 results in:

$$m_1 = m_0 \left(\frac{4}{2 - (A - K) \Delta t} - 1 \right) \quad (11)$$

The individual body mass of fish m_0 and m_1 can be measured easily. Equation (11), however, still contains two unknown parameters. Therefore, we need at least another independent equation (or more) to determine the parameters A and K . For zero growth in equation (10) we can directly see that K can be interpreted also as a maintenance assimilation rate. The catabolism rate (and also the maintenance-assimilation rate) is assumed to be species dependent. Therefore, the parameter estimation has to be conducted for different assimilation rates; however, the catabolism rate can be the same.

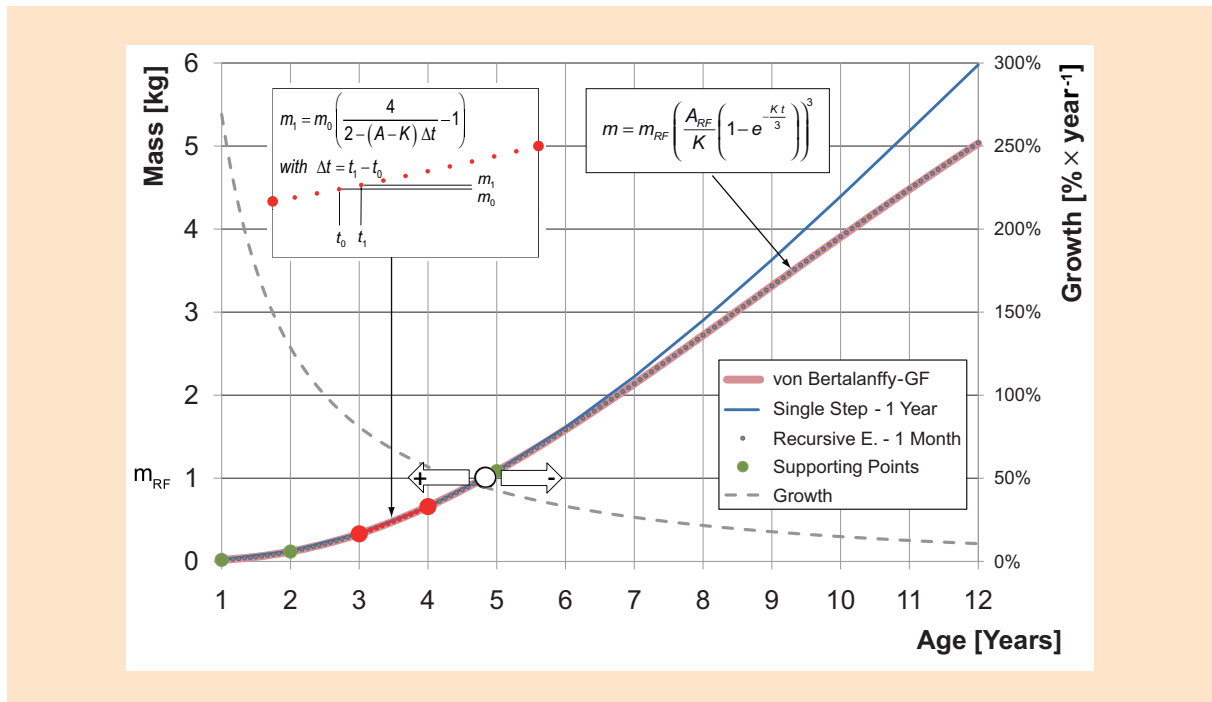


Figure 1: Estimation of the von Bertalanffy-growth parameter, $G = A - K$ of the northern cod of area NAFO, 2J3KL using five supporting points within an age range of 1 – 5 years and different approaches for describing growth

Abbildung 1: Schätzung der von Bertalanffy-Wachstumsparameter, $G = A - K$ des nördlichen Kabeljaus des Gebietes NAFO, 2J3KL anhand von fünf Stützstellen in dem Altersbereich von 1 bis 5 Jahren

2.2. Assimilation and growth

As in the introduction already mentioned small fish grow very fast, whereas large fish grow slower. The reason for the different growth rates are the different assimilation rates of small and large fish. Using the relation $AI = A_{RF} / I_{RF}$ (equation (6)) and inserting equation (3) into this relation yields:

$$\frac{m}{m_{RF}} = \frac{m_0 + m_1}{2 m_{RF}} = \frac{A_{RF}^3}{A^3} \quad (12)$$

The ratio is valid for the mean body mass, m of all fish living under the same condition. Since m_{RF} is a constant this ratio varies with changing mean in individual body mass e.g. for fish belonging to different age groups. In equation (12) we have three unknown variables. At the beginning of the interval, Δt only m_0 is known (Figure 1). The individual body mass at the end of the

interval m_1 depends on the assimilation rates A and A_{RF} . Therefore, an additional equation is needed. This problem is solved by approximating the instantaneous fish mass, m in equation (12) by the linear mean of the mass at the start, m_0 and the mass at the end, m_1 of the interval, Δt (equation (10) and equation (12)). This results in the following rearrangement:

$$m_1 = 2 m_{RF} \left(\frac{A_{RF}}{A} \right)^3 - m_0 \quad (13)$$

From equation (13) can be seen that the end mass m_1 depends apart from the constant factor $2 m_{RF}$ only on the initial mass and the cube of the ratio A_{RF} / A . Equating the right hand sides of equation (11) and equation (13) and rearranging for calculating the assimilation rate, A results in:

$$A = \frac{\left(A_{RF}^3 m_{RF} \left(9 (2 + K \Delta t) m_0^2 + \sqrt{3 m_0^3 (2 A_{RF}^3 m_{RF} \Delta t^3 + 27 (2 + K \Delta t)^2 m_0)} \right) \right)^{1/3}}{6^{2/3} m_0} - \frac{A_{RF}^3 m_{RF} \Delta t}{\left(A_{RF}^3 m_{RF} \left(54 (2 + K \Delta t) m_0^2 + \sqrt{108 m_0^3 (2 A_{RF}^3 m_{RF} \Delta t^3 + 27 (2 + K \Delta t)^2 m_0)} \right) \right)^{1/3}} \quad (14)$$

Table 1: Specified values of the growth parameters for the analysis of the accuracy of parameter estimation:
Tabelle 1: Vorgabewerte der Wachstumsparameter bei der Genauigkeitsanalyse der Parameterschätzung:

$m_{RF} = 1 \text{ kg}$	$A_{RF} = 83.1 \% \times \text{year}^{-1}$	$m_{\infty} = 10.61 \text{ kg}$
$l_{RF} = 46.52 \text{ cm}$	$K = 37.8 \% \times \text{year}^{-1}$	$l_{\infty} = 102.2 \text{ cm}$
$q = 9.93 \times 10^{-6} \text{ kg/cm}^{-3}$		

The equation (14) looks complicated and was obtained using Mathematica (Wolfram Research Inc. 2008), but the equation consists only of constants and the following variables: A_{RF} , K , m_0 , m_{RF} , Δt . Whereas the reference-body mass, m_{RF} can be chosen arbitrarily, the variables m_0 and Δt can easily be measured. The catabolism rate, K depends more or less exclusively on the species and only to a much smaller extent on the living conditions. It is assumed to have the same value K under the given environmental conditions in our example for all age groups. The equation (14) allows us to compute the individual assimilation rate for the initial mass at the beginning of the time interval. Applying equation (14) in equation (11) the assimilation rate of the reference fish, A_{RF} and the value of K can be estimated by a least square fit if the initial mass, m_0 and the end masses, m_1 , m_2 ... of two or more successive intervals and Δt are known.

2.3. Reference Assimilation, reference-growth rate and stock data

The chosen reference values for the example are leaned towards mean growth of the northern cod of NAFO area 2J3KL (Table 1). For computing the sample points, using the modified von Bertalanffy-mass growth equation (8), only the values for, m_{RF} , A_{RF} and K are used. The other parameters provide a more complete overview. The shape of the growth function is illustrated in Figure 1. This figure shows the following consecutive body-mass-at-age samples (index = age [years]): $m_1 = 0.018 \text{ kg}$, $m_2 = 0.117 \text{ kg}$, $m_3 = 0.331 \text{ kg}$, $m_4 = 0.659 \text{ kg}$ and $m_5 = 1.085 \text{ kg}$. Only these five samples (supporting points) and the equations (11) and (14) were used for the accuracy analysis of the growth-parameters estimation of A_{RF} and K . This was done by least square fitting. Remembering that the es-

Table 2: Individual body mass of northern cod of NAFO area 3K of the age groups 2 – 12 from time span 1978 – 2000 (Lilly 1998). Framed cells were excluded from computations, because the number of fish ($n \leq 5$) for the mean body-mass computation was too low

Tabelle 2: Körpermasse des nördlichen Kabeljau NAFO Gebiet 3K der Altersgruppen 2 – 12 des Zeitraums 1978 bis 2000 (Lilly 1998). Eingehakt Zellen wurden aus Berechnungen ausgeschlossen, da die Zahl der Fische für die Berechnung der mittleren Körpermasse zu niedrig war ($n \leq 5$)

Year/Age	2	3	4	5	6	7	8	9	10	11	12
1978	0.171	0.410	0.876	1.478	2.393	2.938	5.830	4.671	6.499	5.243	9.492
1979	0.207	0.577	1.190	1.644	2.259	3.161	4.281	4.861	4.608	8.365	10.190
1980	0.238	0.578	0.950	1.410	2.011	3.462	3.179	6.003	7.532	13.000	7.097
1981	0.275	0.720	1.222	1.730	2.051	2.620	5.051	7.332	6.321	9.326	8.103
1982	0.234	0.738	1.218	1.555	1.966	2.445	3.151	4.375	6.192	6.515	9.555
1983	0.227	0.540	1.120	1.670	2.114	2.804	3.440	3.736	4.862	7.512	6.047
1984	0.146	0.404	0.867	1.412	2.041	2.343		3.693	4.667	6.300	6.089
1985	0.209	0.466	0.891	1.219	1.818	2.590	3.396	4.149	4.890	6.520	6.329
1986	0.192	0.454	0.817	1.154	1.993	2.421	3.739	3.247	4.920	5.847	6.465
1987	0.204	0.493	0.904	1.350	1.409	2.580	2.784	3.398	5.354	10.631	7.017
1988	0.177	0.476	0.838	1.411	1.734	2.264	3.012	4.257	4.888	5.408	7.628
1989	0.193	0.491	0.874	1.325	1.821	2.190	2.566	3.229	4.204	4.604	5.593
1990	0.190	0.414	0.761	1.100	1.630	1.908	2.203	2.441	2.711	3.251	3.665
1991	0.213	0.423	0.705	1.006	1.517	1.923	2.274	2.626	3.107	4.933	3.222
1992	0.205	0.398	0.665	0.947	1.301	1.828	2.561	2.190			
1993	0.205	0.473	0.735	1.119	1.296	1.461	2.290				
1994	0.217	0.434	0.688	1.188	1.442	1.978	2.326				
1995	0.153	0.362	0.649	0.907	1.527			3.280			
1996	0.206	0.380	0.721	1.161	1.898	3.240					
1997	0.230	0.543	0.979	1.619			2.610				
1998	0.150	0.547	0.868	1.299	1.874	2.550	6.320	5.310			
1999	0.238	0.468	0.888	1.346	1.560	3.743		6.130	7.270		
2000	0.194	0.443	0.818	1.189	2.060	3.330					

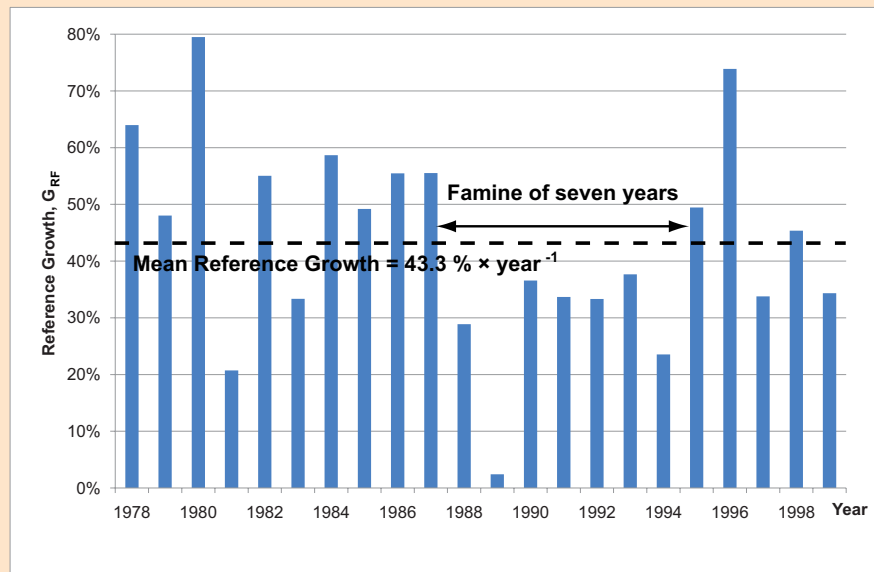


Figure 2: Reference growth, $G_{RF} = A_{RF} - K$ of the northern cod stock of the NAFO-area 3K (catabolism rate, $K = 37.81 \% \times \text{year}^{-1}$ for the whole NAFO-area 2J3KL), based on the data provided by Lilly (1998)

Abbildung 2: Referenz Wachstum, $G_{RF} = A_{RF} - K$ des nördlichen Kabeljaubestandes des NAFO-Gebietes 3K (Abbaurate, ermittelt aus dem Gesamtgebiet 2J3KL), basierend auf Daten, bereitgestellt durch Lilly (1998)

timisation result originates from difference equations and not from the solution of a differential equation. Accurate results can be expected only for short time intervals. Comparing the iteration results of the difference equation with the specified values obtained

from von Bertalanffy-growth equation for different time intervals points out the influence of the duration of time interval (see Figure 1). To benefit from short intervals, apart from one computation on a yearly basis in a single step, recursive computations were car-

Table 3: Results of the growth-parameter estimation for different time intervals. The time span between the supporting points is always one year; however, recursive computations were carried out on a quarterly or on a monthly time basis (see details in Figure 1)

Tabelle 3: Ergebnisse der Wachstumsparameterschätzung für verschiedene Zeitintervalle. Die Zeitspanne zwischen den Stützstellen ist immer ein Jahr, aber die rekursiven Berechnungen wurden auf einer vierteljährlichen oder auf einer monatlichen Zeitbasis durchgeführt (Einzelheiten siehe Abbildung 1)

Variable	Specified V.	Unit	Estimation V. for Interval Δt		
Δt	1	[year]	1	0.25	0.083
K	37.81	$[\% \times \text{year}^{-1}]$	26.73	36.89	37.70
ΔK	0	$[\%]$	-29.32	-2.44	-0.28
A_{RF}	83.10	$[\% \times \text{year}^{-1}]$	72.74	82.27	83.01
ΔA_{RF}	0	$[\%]$	-12.47	-1.01	-0.12
m_{∞}	10.62	[kg]	20.16	11.09	10.67
Δm_{∞}	0	$[\%]$	89.89	4.49	0.51
G	45.29	$[\% \times \text{year}^{-1}]$	46.01	45.38	45.30
ΔG	0	$[\%]$	1.59	0.20	0.02

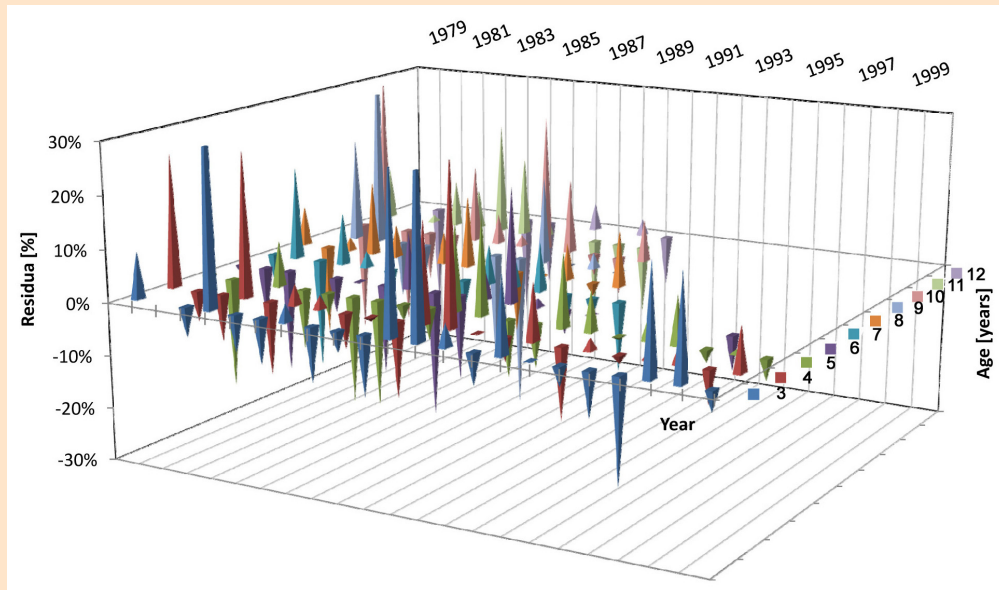


Figure 3: Normalized residuals of the measured and estimated end-body mass (equation (11) and equation (14)) observed during the reference-growth estimation, $G_{RF} = A_{RF} - K$ of the northern cod stock of the NAFO-area 3K ($K = 37.81 \% \times \text{year}^{-1}$), based on the data provided by Lilly (1998)

Abbildung 3: Normierte Residuen zwischen gemessenen und geschätzten Endmassen (Gleichung (11) und Gleichung (14)) zu verzeichnen während der Wachstumsschätzung, $G_{RF} = A_{RF} - K$ für den nördlichen Kabeljaubestand des NAFO-Gebietes 3K ($K = 37.81 \% \times \text{year}^{-1}$) basierend auf Daten von Lilly (1998)

ried out on a monthly ($\Delta t = 1/12 = 0.083$ years, see details in Figure 1) and on a quarterly time basis ($\Delta t = 1/4 = 0.25$ years). The least square fitting was always carried out for only the five supporting points and not for the intermediate values between the supporting points.

More important for the stock management than reference assimilation is the reference growth, $G_{RF} = A_{RF} - K$. This is the growth rate of a reference fish, here assumed with an individual body mass of 1 kg, used for computing the expected individual growth of fish for constant environmental conditions throughout the whole life span. Environmental conditions may change during lifespan of a fish, but it can be assumed that the conditions are constant for a shorter span. Here we assume that the environmental conditions for all age groups of a species are constant for the time span of one year. Computations are exemplified by data of individual body-mass growth of northern cod of NAFO area 3K (Lilly 1998) of the age groups 2 – 12 from the time span 1978 – 2000 (Table 2). The data were used to compute the reference-growth rates of all age groups of northern cod of the NAFO area 3K on a yearly basis where varying environmental conditions were assumed. The individual body-mass data of successive years were used for growth computation, e.g. the age group 2 in 1978 becomes age group 3 in 1979. Therefore, the following values were used: $m_{2,1978} = 0.171 \text{ kg} \rightarrow m_{3,1979} = 0.577 \text{ kg}$; $m_{3,1978} \rightarrow m_{4,1979}$; $m_{4,1978} \rightarrow m_{5,1979}$; ...for the computation of reference growth in

1978. Again the equations (11) and (14) were used for the growth-parameter estimation. The values were computed recursively on a monthly basis. The least squares estimation was carried out by Solver within Excel and are explained in detail in the Appendix.

3. Results

The equation (8) reveals the relationship between growth and food intake – this is the main result. The results of the analysis of the influence of sample frequency on growth-parameter estimation are summarized in Table 3.

As expected the estimation accuracy has increased with shorter intervals. Whereas the estimation of the prior specified values of the given example for a one-year-estimation interval resulted in large errors (see Table 3 for $\Delta t = 1$ year : specified: $K = 37.81 \% \times \text{year}^{-1}$, estimated: $K = 26.73 \% \times \text{year}^{-1}$, $\Delta K = - 29.32 \%$), the errors for the same number of supporting points for recursive estimation for intervals of one month were below 1 % (see Table 3 for $\Delta t = 0.083$ years : specified: $K = 37.81 \% \times \text{year}^{-1}$, estimated: $K = 37.70 \% \times \text{year}^{-1}$, $\Delta K = - 0.28 \%$).

The catabolism rate K is a constant assumed to depend on the considered species of a certain stock e.g. the NAFO-area K 2J3KL. Therefore, a joint catabolism rate was computed for the three sub-areas (2J, 3K and 3L). The assimilations rate A , as well as

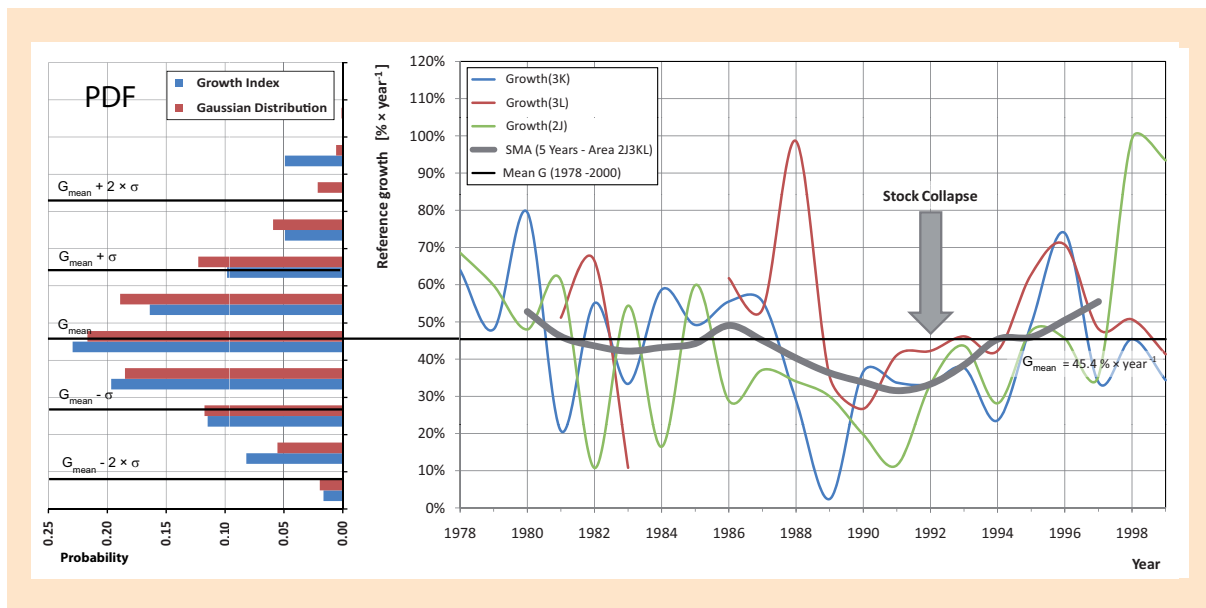


Figure 4: Reference growth, $G_{RF} = A_{RF} - K$ of the northern cod stock of the NAFO-area 2J3KL (catabolism rate, $K = 37.81 \% \times \text{year}^{-1}$), simple moving average (SMA) of the reference-growth rate of the total area and probability density function (PDF) of the reference-growth rate, based on the data provided by Lilly (1998)

Abbildung 4: Referenz Wachstum, $G_{RF} = A_{RF} - K$ des nördlichen Kabeljaubestandes des NAFO-Gebietes 2J3KL (Katabolismusrate, $K = 37.81 \% \times \text{year}^{-1}$), einfacher gleitender Mittelwert (SMA), der Referenz-Wachstumsrate der gesamten Fläche und Wahrscheinlichkeitsdichtefunktion (PDF) der Referenz-Wachstumsrate basierend auf Daten von Lilly (1998)

the growth rate G , depends on the food availability – A and G , and can be different in each area. Here it is assumed that the estimated catabolism rate, $K = 37.81 \% \times \text{year}^{-1}$ is valid for the whole NAFO-area 2J3KL, whereas the given example (Figure 2) presents only the reference growth, $G_{RF} = A_{RF} - K$ of the northern cod stock of the NAFO-area 3K. As already mentioned, equation (11) (and equation (14)) was applied for the parameter estimation within a least-square-fitting procedure. Figure 3 shows the residuals observed during the estimation procedure normalized to the mean value of the individual body mass.

4. Discussion

Providing applicable equations to describe the growth in dependence on food is the main result of this publication. The new formula of the von Bertalanffy equation (8) is of theoretical significance and reveals the relationship between growth and food intake, in contrast to the traditional one. The use of this new formula is beneficial because fish is always able to reach the reference mass during its life span since the reference-body mass can be chosen arbitrarily also and in a way that the accordant age group is not completely wiped out by fishery or natural causes before the reference-body mass is reached. The variables needed for modeling can always be measured or estimated

from experimental data. The assimilation rate, A_{RF} (or growth rate, G_{RF}) of a reference fish of a stock of a certain area can be used instead of m_{∞} for describing the environmental condition of fish during its lifespan – in this case only for the mean food conditions of the whole life span. Therefore, Figure 1 illustrates in the given example the mean growth of the northern cod of NAFO area 2J3KL. A mean 1 kg-northern cod is 4.8 years old. If, for example, a cod with this body mass is six years old, the fish grows slower than at mean conditions ($G_{RF} < G_{RF\text{mean}}$). But if the same fish is four years old then that fish grows somewhat faster ($G_{RF} > G_{RF\text{mean}}$). This is indicated by white arrows in Figure 1.

The difference equation (11) is more handy to use than the differential equation. Modeling varying environmental conditions is easy to do with the difference equation. Reasons for the sometimes large amount of residuals could be caused by changes in mean conditions during the observed time span. An introduction of measurement errors could have been caused by misreading during the age determination of cod. Also the basic assumptions may not always fit equally well to the observed conditions in that area, especially if the fish changes its feeding behavior. It is known for older northern cod that cannibalism plays an increasingly important role

(Anderson and Gregory 2000). Nevertheless, the possibility to summarize the growth of all age groups of a stock into one reference parameter to describe food supply within a certain time interval and area, is a big improvement (see equation (13) and (14)). Seasonal growth equations can be modeled easily, trends of food supply, caused e.g. by environmental changes, can be detected and described – the derived difference equations create a large number of new possibilities for modeling. One potential application of the reference-growth rate could be the risk assessment within the exploitation management of stocks. At the beginning of the fishing year, at the time when the fishing quotas are set the future growth is still unknown. As shown

in Figure 4, the probability that a stock in one year did not grow at all is not zero and it can therefore be very doubtful whether the stock biomass can compensate the impact of fishing by growing in some years. The differences between a “good” and a “bad” year can be large (see Figure 5). A strong fishing on a poorly growing stock for a long period can definitely lead to a stock collapse. In a good year of growth, however, a strong harvest can be easily more than compensated – the stock biomass grows faster than the fisherman can harvest. The advantage (and disadvantage) of estimating growth parameters with difference equation instead of differential equation is obvious. Solutions found with differential equations are very useful for

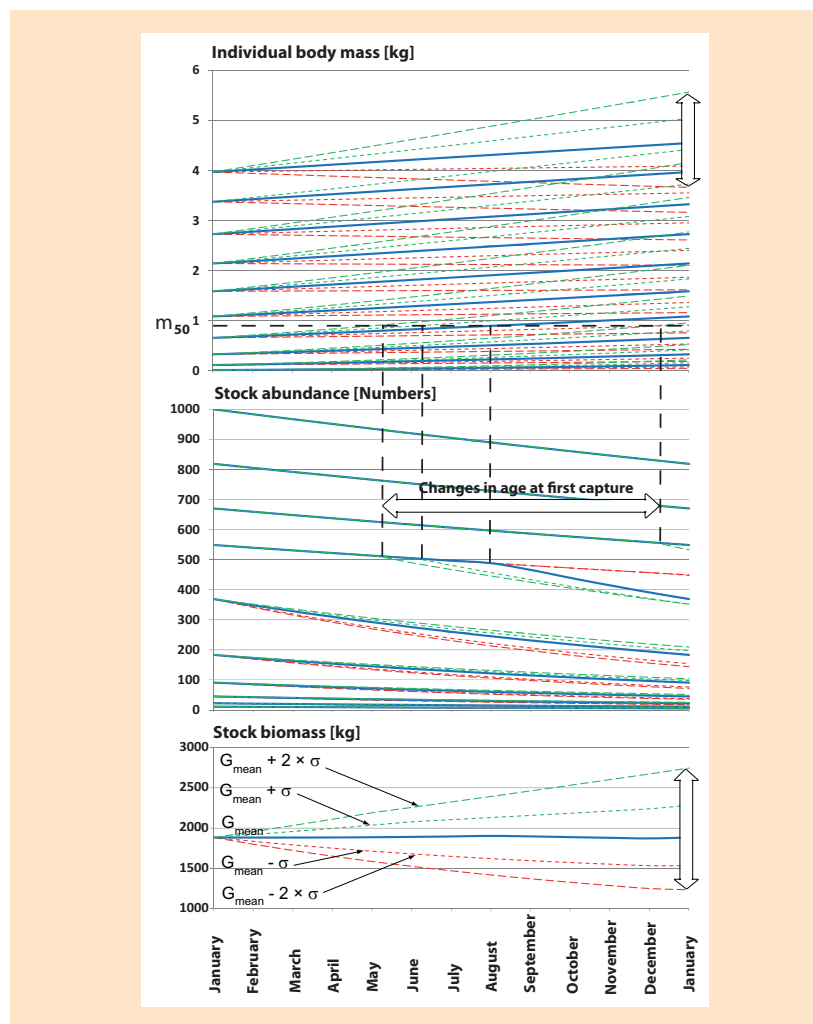


Figure 5: Changes in individual body mass, abundance, age at first capture and stock biomass as for a model-cod stock exploited with a knife edge selection function a function of growth rate (compare with Figure 4). Initial conditions: Cod stock in an equilibrium, constant catches per year, mean growth $G_{\text{mean}} = 45.4\%$, $K = 37.7\%$, number of recruits $N_R = 1000$, natural mortality $M = 0.2 \text{ year}^{-1}$, fishing mortality for mean growth $F = 0.5 \text{ year}^{-1}$, individual body mass at first capture $m_{50} = 0.914 \text{ kg}$

Abbildung 5: Änderungen in der Körpermasse, Bestandsgröße, dem Alter beim ersten Fang und der Bestandsbiomasse als Funktion der Wachstumsrate (vgl. Abb. 4) für einen Modell-Kabeljaubestand befischt mit einer “knife edge”-Selektionsfunktion. Ausgangsbedingungen: Kabeljaubestand im Gleichgewicht, konstante Fänge pro Jahr, mittleres Wachstum $G_{\text{mean}} = 45.4\%$, $K = 37.7\%$, Zahl der Rekruten $N_R = 1000$, natürliche Sterblichkeit $M = 0.2 \text{ year}^{-1}$, fischereiliche Sterblichkeit für mittleres Wachstum $F = 0.5 \text{ year}^{-1}$, Körpermasse beim ersten Fang $m_{50} = 0.914 \text{ kg}$

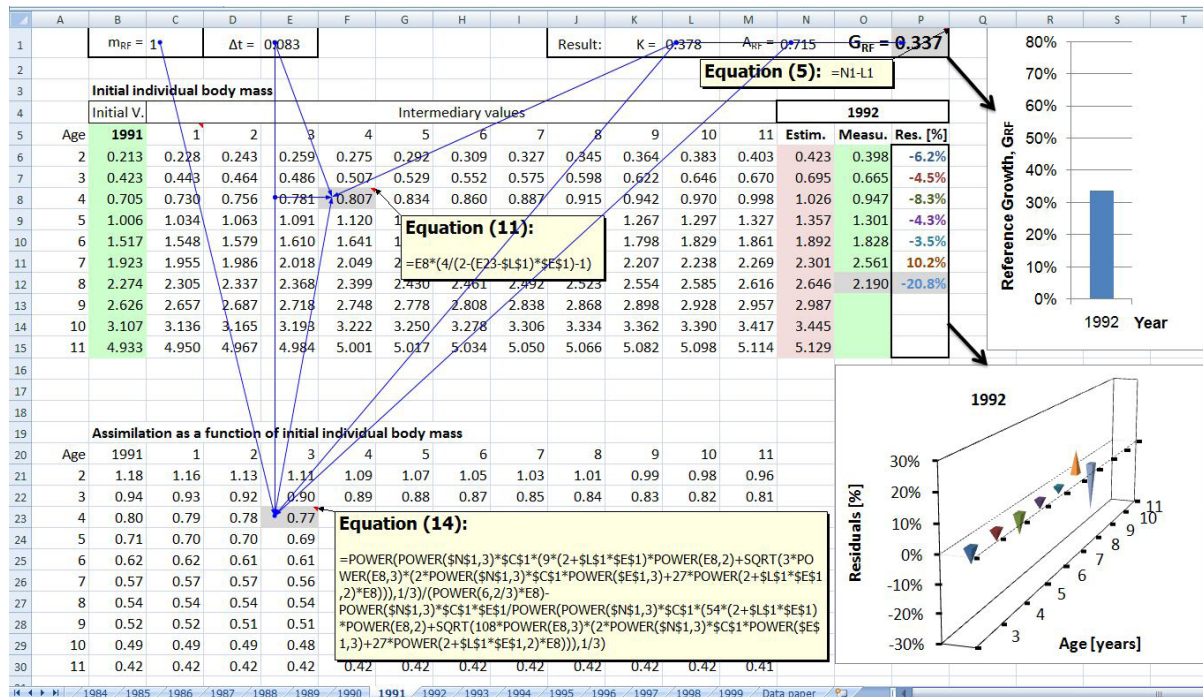


Figure 6: Screenshot of the MS Excel-spreadsheet for the calculation of the estimates with the least square method (compare the upper diagram with Figure 2 and the lower diagram with Figure 3)

Abbildung 6: Screenshot der Excel-Tabelle benutzt für die Schätzung mit Methode der kleinsten Fehlerquadrate (vgl. das obere Diagramm mit Abbildung 2 und das unteren Diagramm mit Abbildung 3)

theoretical derivations. For practical use, e.g. for stock assessment, the difference equations, however, have significant advantages. Difference equations will be established probably more and more as in other areas of science. The former disadvantage, the need of more computing power to provide accurate results, does no longer exist.

5. Appendix

The derivation of the von Bertalanffy-growth equation (8) was based on the assumption that environmental conditions are constant over the entire fish life. In this case the von Bertalanffy-growth equation (8) delivers accurate parameter estimates for fish growth. However, the need to assume constant conditions is a considerable disadvantage. Within a certain interval this assumption may be correct but in larger time intervals the environmental conditions may change and must be modeled differently in successive intervals. While the solutions of differential equations for time-dependent conditions get very complex the same changing conditions can be introduced easily into difference equations (e.g. Equation (11)). While the differential equations are mathematically often unsolvable, with difference equations almost always

a solution can be found. Difference equations, however, have the disadvantage that the parameter estimates are less accurate. This disadvantage decreases with estimations carried out for shorter time intervals. The accuracy of the results mainly depends on the time span in which we assume the conditions to be constant. However, surveys are often performed on annual basis. Since no intermediate values are measured constant conditions throughout the year are assumed, but intermediate values can be computed for constant conditions e.g. on a monthly basis (Figure 6). However, only the values at the supporting points – the dates when surveys were carried out – will be used for the least square estimation of growth parameters. The condition of all age groups of the stock can be summarized by the reference growth $G_{RF} = A_{RF} - K$ (growth rate of a reference fish – e.g. a fish with a body mass of 1 kg). The reference growth mainly depends on the reference-assimilation rate A_{RF} . Whereas the catabolism rate K is independent of the individual body mass, the reference values G_{RF} and A_{RF} must always be specified together with the appropriate reference mass. Equation (11), contains two parameters – A and K . The catabolism rate K is assumed to be a species dependent parameter constant for all samples. The individual body mass at the end of the interval m_t (Equation (11)) depends on the assim-

lation rate A . However, A changes with the individual body mass even if A_{RF} may be constant. Therefore, before Equation (11) can be solved, A has to be computed. This can be done by Equation (14) using the following variables: A_{RF} , K , m_0 , m_{RF} , Δt (see Figure 6). Applying equation (14) and equation (11) the assimilation rate of the reference fish, A_{RF} and the value of K can be estimated by a least square fit, if the initial mass, m_0 and the end masses, m_1 , m_2 ... of successive intervals, Δt are known. In the given example the supporting points have an annual and the intermediate values a monthly basis. The estimated value for A_{RF} is only valid for the year 1991, whereas K is valid for all age groups and sample intervals (see Figure 6). Please note that samples were excluded from the estimate, when the mean body mass was calculated from masses of only five or less fish (this is indicated by the light gray color of age group 9 in the 1992 data).

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