

A simple approach for the estimation of food consumption from growth rates at different environmental conditions and its application to juvenile cod (*Gadus morhua* L.) of a fjordic sea loch on the west coast of Scotland

Ein einfacher Ansatz für die Schätzung der Nahrungsaufnahme aus Wachstumsraten bei unterschiedlichen Umweltbedingungen und seine Anwendung auf juvenilen Kabeljau (*Gadus morhua* L.) aus einem Fjord an der Westküste Schottlands.

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Abstract

Growth and condition of fish are functions of available food and environmental conditions. This led to the idea of using fish as a “consumption sensor” for the measurement of food intake over a defined period of time. A bio-physical model for the estimation of food consumption was developed based on the von Bertalanffy model. Whereas some of the input variables of the model, the initial and final lengths and masses of a fish and the temperature within the time period considered can easily be measured, internal characteristics of the species have to be determined indirectly. Three internal parameters are used in the model: the maintenance consumption at 0°C, the temperature dependence of this consumption and the food efficiency, the percentage of the ingested food utilized. Estimates of the parameters for a given species can be determined by feeding experiments. Here, data from published feeding experiments on juvenile cod, *Gadus morhua* L., were used to validate the model. The average of the relative error for the food intake predicted by the model for individual fish was about 24 %, indicating that fish used the food with different efficiencies. However, grouping the fish according to size classes and temperature lowered the relative error of the predicted food intake for the group to typically 5 %. For a group containing all fish of the feeding experiment the relative prediction error was about 2 %.

Zusammenfassung

Wachstum und Kondition der Fische sind von der verfügbaren Nahrung und von Umweltbedingungen abhängig. Dies führte zur Idee, Fisch als „Konsum-Sensor“ für die Messung der Nahrungsaufnahme über einen definierten Zeitraum zu verwenden. Auf Grundlage des von Bertalanffy-Modells wurde ein bio-physikalisches Modell zur Schätzung der Futtermittelaufnahme entwickelt. Während einige der Eingangsgrößen des Modells leicht gemessen werden können (Anfangs- und Endlänge und -körpermasse der Fische und die Temperatur innerhalb des betrachteten Zeitraum), können interne Parameter der betrachteten Art nur indirekt bestimmt werden. Drei interne Parameter werden in dem Modell verwendet: Die Erhaltungskonsumtion bei 0°C, die Temperaturabhängigkeit dieser Rate und der Wirkungsgrad der Nahrung (der Anteil der Nahrung, der aufgenommen und verwendet und nicht ungenutzt wieder ausgeschieden wird). Die Modellparameter für eine bestimmte Art können durch Fütterungsversuche bestimmt werden. Um das Modell zu validieren wurden Daten aus veröffentlichten Fütterungsversuchen mit juvenilen Kabeljau (*Gadus morhua* L.) verwendet. Modell und Wirklichkeit weichen in der Regel voneinander ab. Der durchschnittliche relative Fehler der durch das Modell vorhergesagten Nahrungsaufnahme betrug für Einzelfische etwa 24%, was darauf hinweist, dass einzelne Fische die Nahrung mit unterschiedlichen Wirkungsgraden verwerten. Allerdings senkte die Gruppierung der Fische nach Größenklassen und Temperatur den relativen Vorhersagefehler für die Nahrungsaufnahme der Gruppe auf etwa 5%. Für alle Fische im Fütterungsversuch ist der relative Vorhersagefehler etwa 2%.

1. Introduction

The estimation of food consumption by fish stocks in combination with information about the composition of the diet is needed to understand the trophic

interactions in ecosystems. Additionally, this information can be used in stock assessment in Multi Species Virtual Population Analysis (MSVPA) to assess natural

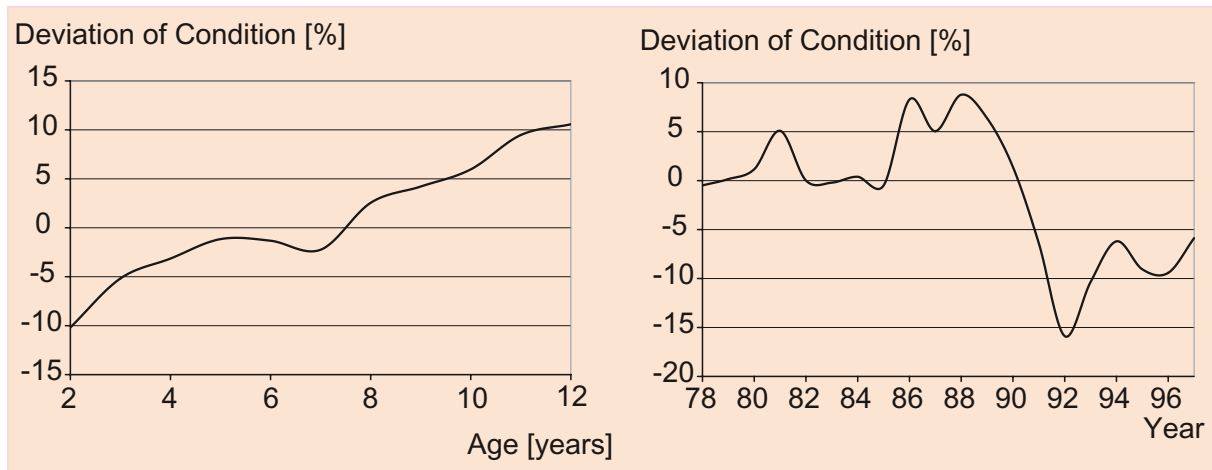


Figure 1. Deviation of condition from mean value of the period 1978 – 1998 of all age groups for cod in NAFO Division 2J+3KL (Lilly 1998) as a function of age (left) and time (right)

Abbildung 1. Abweichung der Kondition vom Mittelwert für den Zeitraum 1978 - 1998 berechnet für alle Altersgruppen von Kabeljau in NAFO-Gebiet 2J+3KL (Lilly 1998) als Funktion des Alters (links) und als Funktion der Zeit (rechts).

mortality, M , of certain prey species. Three approaches have been widely used to estimate food consumption rates of fishes. The first approach combines mean stomach contents in the field and knowledge of the rate of gastric evacuation (Bajkov 1935, Elliott and Persson 1978, Garcia and Adelman 1985). The second is a bioenergetics approach which determines the total energy requirements of the fish. This usually involves field estimates of growth rate and laboratory measurements of the energy utilized by metabolism and lost through faeces and excretion (e.g. Kitchell et al. 1977, Stewart et al. 1983, Stewart and Binkowski 1986, Rudstam 1988, Schaeffer et al. 1999). In the third approach, consumption is estimated by a combination of field growth data and experimentally derived food conversion data (Pauly 1986, Andersen and Riis-Vestergaard 2004, Temming and Herrmann 2009), an approach on which the present paper is based.

Food consumption in excess of the maintenance ration results in fish growth. Therefore using the differential approach $m' = m'_{as} - m'_{out}$ (e.g. Pütter 1920, von Bertalanffy 1934, 1938) as the difference between anabolism, m'_{as} and catabolism, m'_{out} for the estimation of food consumption appears self-evident. Given the assumption that the condition (equation 1) of the fish remains constant, the von Bertalanffy-equation (von Bertalanffy 1938) for length- and mass growth is the solution of the differential equation. However, the condition in fishes is often variable (e.g. Lilly 1998, Dutil et al. 2003, Casini et al. 2006, Óskarsson 2008) leading to incorrect estimates of food consumption.

The condition of fish is a function of age, but varies also with season (figure 1) (Lilly 1998). The relation between mass, m , condition, q , and length, l , in fish can be described by equation (1):

$$m(t) = q(t) l(t)^3 \quad (1)$$

Mass, length and also the condition are functions of time, t . The variable q is defined as the ratio of body mass and the cube of length of fish (this is different from Fulton's condition factor (Ricker 1975)). Isometric growth is always assumed within the short duration of the feeding experiments even if the allometry may change with age or size in longer intervals. The influence on changes in body mass of changes in condition and changes in length can be compared by the following differential (equation 2):

$$dm = 3 l^2 q dl + l^3 dq \quad (2)$$

Data from an experimental study on Atlantic cod, *Gadus morhua* L. (Soofiani 1983), allow estimates of the effects of changes in condition and length on changes in mass. For a cod of 300 mm length and a condition of 0.01046 g cm⁻³, a 1 % change in length results in a change in mass of about 3 %, whereas a change in condition of 1 % changes mass by only about 1 %. Although the fact that changes in condition result in lesser changes in mass, these changes should not be neglected. To improve the accuracy of the consumption estimate from growth measurements, the condition should be included in the estimation as a variable. However, a solution of the differential equation which describes length and condition of the fish as a function of time does not yet exist.

In the present paper, we distinguish between length growth and growth (or change) in condition, $q(t) = m(t)/l(t)^3$. Both types of growth require a supply of mass and energy respectively (through feeding) in

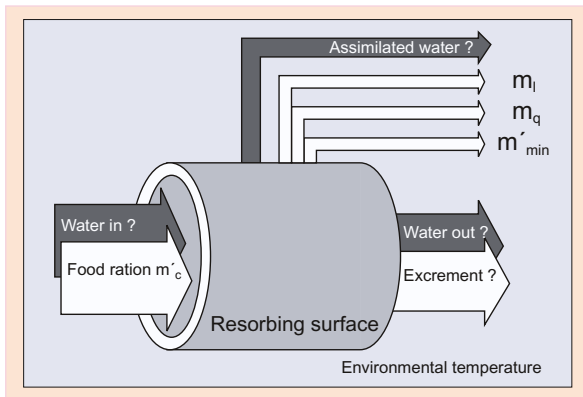


Figure 2. Growth of length and condition by food consumption in excess of the maintenance metabolism (m'_c = food ration in $g \times d^{-1}$, m'_{min} = maintenance ration in $g \times d^{-1}$, Δm_l and Δm_q = change of mass in length l and condition q).
Abbildung 2. Wachstum in Länge und Kondition in Abhängigkeit von der Nahrungsaufnahme über den Erhaltungsstoffwechsel hinaus (m'_c = Fütterungsration [$g \times d^{-1}$], m'_{min} = Erhaltungsration [$g \times d^{-1}$], Δm_l und Δm_q = Änderung der Masse durch Längen- und Konditionsänderung).

excess of the maintenance needs (figure 2). Different feeding regimes result in changes in water content of fish (Holdway and Beamish 1984, Jobling 1994, Ali et al. 2003). However, since the effect of changes in water content on body mass are low compared to changes in overall body mass, absorption and dispersion of water were not considered in the model. The determination of dry masses would increase the costs of the procedure considerably, while not increasing the precision of the measurements substantially (wet masses of food were used in the feeding-growth experiments for testing this model).

The aim of this paper was the development of a simple approach for the estimation of food consumption of Atlantic cod from growth rates measured under different environmental conditions. The "sensor" fish was calibrated within feeding experiments (Soofiani 1983, Hawkins et al., 1985) by estimating values of the internal parameters applying the developed equation. The calibration enables us to use this "sensor" later for estimates of food consumption of fish in the wild.

2. Material and Methods

The individual mass is a function of the length, l and the condition, q of fish (equation(1)). The differential change of the individual mass, dm can be described by the total derivative (equation 3) as:

$$dm = dm_l + dm_q = \left. \frac{\partial m}{\partial l} dl \right|_{q=const.} + \left. \frac{\partial m}{\partial q} dq \right|_{l=const.} \quad (3)$$

$$\Delta m \approx \Delta m_l + \Delta m_q = \frac{\partial m}{\partial l} \Delta l + \frac{\partial m}{\partial q} \Delta q$$

The total differential change of the individual mass, dm is the sum of differential mass changes caused by length growth, dm_l and change in condition, dm_q . Both parts of the sum can be computed independently for constant q and l respectively. However, the measurement of infinitesimal changes within a differential small time interval is not applicable in practice. The practical sampling intervals of mass growth, $\Delta m = m_l - m_0$ are usually larger. Using differential equations, however, results in proper estimation only in the vicinity of the observed time interval. To achieve precise estimates for larger sample intervals, the differential equation (equation 3) must be solved. The length growth and change in condition takes place at the same time. Therefore an approximation has to be introduced. The condition was assumed to be constant for length growth and the length was assumed to be constant for change in condition even if the allometry and length may change with age or size; the changing variables were replaced by their mean values within the considered interval – the so-called "operation points" (equation 3). This is a term used in electrical engineering for small signal analysis – every non-linear element can be linearized around its operation point. For the computation of Δm_l , the constant condition was assumed to be the linear mean of the condition, $q_m = (q_0 + q_1)/2$ within the sample interval. In a similar way, the operation point relative to length was assumed to be $l_m = (l_0 + l_1)/2$ for the computation of Δm_q , where l_0 , q_0 and m_0 are the values of the appropriate variables at the starting point of the interval and l_1 , q_1 and m_1 are the values at the end of the interval. This approximation restricts the independent computation of m_l and m_q marginally. However, it can be assumed that the errors close to the starting point may be compensated by errors in the opposite direction close to the end of the interval for each variable and the introduced overall error may be negligible for sufficient small intervals. For the description of differential changes (equation 3) the von Bertalanffy approach (1934, 1938, 1949) was used in a form presented in Beverton and Holt (1957):

$$m' = m'_{as} - m'_{out} = H s - k m \quad (4)$$

Following the concept of Pütter (1920) the growth ration, m' is the difference between two processes, anabolism, m'_{as} and catabolism, m'_{out} (please note that in this paper we distinguish between ration and rate in measurements concerning feeding and growth. A ration is a measuring unit per time interval [$g \times d^{-1}$] while a rate is ration that is standardized by the current variable value, often stated in percent per day [e.g. the catabolism rate, k is measured $\% \times d^{-1}$]). It can be assumed that the assimilated ration, m'_{as} for anabolism is proportional to the resorption rate of nutritive material and therefore proportional to the magnitude of

the resorbing surface. Therefore, the variable, H can be interpreted as a mass flow rate (according to explanation above it should be called mass flow ration [$\text{g} \times \text{m}^{-2} \times \text{d}^{-1}$]) through the digestive organs, a ration of synthesis of mass per unit "physiological resorbing surface". The resorbing surface, s is assumed to be proportional to the square of the fish length:

$$s = p l(t)^2 \quad (5)$$

where p is a constant. However, k can be interpreted as a rate of catabolism measured in percentage of body mass per day [$\% \times \text{d}^{-1}$]. The body mass of fish is assumed to be proportional to the cube of the fish length. However, here we assume that, in contrast to the von Bertalanffy approach, the condition q is variable and a function of time (equation 1).

2.1. Mass flow rate for length growth, Δm_l and maintenance at constant condition

To compute the mass flow rate, H as a function of length growth for a constant mean condition, $q = q_m$ it is necessary to express equation (4) in terms of lengths. Differentiating equation (1) with respect to l we get after rearrangement:

$$dm = 3 l^2 q_m dl \quad (6)$$

Inserting equation (1), equation (5) and equation (6) into equation (4) and rearranging again we get:

$$dl = \frac{H p - k l q_m}{3 q_m} dt \quad (7)$$

The solution of the differential equation is:

$$l = \frac{H p}{k q_m} + e^{\frac{k t}{3}} K \quad (8)$$

For the determination of the constant, K the initial condition $l_{(t=0)} = l_0$ was chosen, resulting in:

$$K = l_0 - \frac{H p}{k q_m} \quad (9)$$

Inserting this result into equation (8) and rearranging according to the mass flow rate, H we get:

$$H = H_l + H_{min} = \frac{k q_m \left(l_0 - l_1 e^{\frac{k t}{3}} \right)}{p \left(1 - e^{\frac{k t}{3}} \right)} \quad (10)$$

This result for H as a function of length growth within the time interval t contains both the mass flow rate necessary for length growth, H_l and the maintenance mass-flow rate, H_{min} necessary to keep the fish alive at the present length and condition.

2.2. Mass flow rate for growth of condition, Δm_q and maintenance at constant length

In a second step the equation for the mass flow rate, H as a function of change in condition for a constant mean length, $l = l_m$ was derived. Here, we have to express equation (4) in terms of condition. Differentiating equation (1) with respect to q and rearranging we get:

$$dm = l_m^3 dq \quad (11)$$

Inserting equation (1), equation (5) and equation (11) into equation (4) we get after rearrangement:

$$dq = \frac{H p - k l_m q}{l_m} dt \quad (12)$$

The solution of the differential equation is:

$$dq = \frac{H p - k l_m q}{l_m} dt \quad (13)$$

For the determination of the constant, K , the initial condition $q_{(t=0)} = q_0$ was chosen, resulting in:

$$K = q_0 - \frac{H p}{k l_m} \quad (14)$$

Inserting the constant K into equation (13) and rearranging according to the mass flow rate, H we get:

$$H = H_q + H_{min} = \frac{k l_m (q_0 - q_1 e^{k t})}{p (1 - e^{k t})} \quad (15)$$

The result for H as a function of change in condition contains similar to length growth both again, the mass flow rate necessary for change in condition, H_q and the maintenance mass flow rate, H_{min} necessary to keep the fish alive.

2.3. Mass flow rate for the combined growth of length and condition

To compute the mass flow rate necessary for combined growth of length and change in condition the sum of equation (10) and equation (15) can be used. However, the sum of the equations contains the maintenance mass flow rate, H_{min} twice. Therefore, we have to subtract the maintenance mass flow rate from this sum. Introducing the condition for zero growth $l_m = l_0 = l_1$ and $q_m = q_0 = q_1$ into equation (10) and equation (15), respectively, these equations can be used for the derivation of maintenance mass flow rate at the operation point. We get in each case for the mean maintenance mass flow rate within the interval, t :

$$H_{min} = \frac{k l_m q_m}{p} \quad (16)$$

If at a constant condition, q_m the fish doesn't grow in length ($l_0 = l_1$ equation (10)) or if at a constant length, l_m the fish doesn't grow in condition ($q_0 = q_1$ equation (15)) is the same. Therefore, it is no surprise that we obtain for both considered growth equations the same result (equation (16)). Adding equation (10) and equation (15) and subtracting equation (16) we obtain equation (17):

$$H = H_l + H_q + H_{min} = \frac{k q_m \left(l_0 - l_1 e^{\frac{k t}{3}} \right)}{p \left(1 - e^{\frac{k t}{3}} \right)} + \frac{k l_m (q_0 - q_1 e^{k t})}{p (1 - e^{k t})} - \frac{k l_m q_m}{p} \quad (17)$$

The mass flow rate, H (equation 17) could be used to compute the food consumed within a time interval. The catabolic rate, k , and therefore the maintenance rate is a function of the temperature. This dependency has to be introduced. For an easier handling in practice, the mass flow rate, H has to be expressed in terms of variables which can be measured more easily than H itself.

2.4. Maintenance rate, catabolism and temperature

For the derivation of the maintenance rate, equation (4) is used normalized to the instantaneous body mass of fish:

$$G = \frac{m'}{m} = \frac{H s}{m} - k = C_{as} - k = \eta C - k \quad (18)$$

where G [% $\times d^{-1}$] is the growth rate of fish and C_{as} is the assimilation rate, the mass flow rate through the digestive organs normalized to the present body mass [% $\times d^{-1}$]. Here, we have to take into account that within the transfer from one trophic level to the next not all consumed food can be assimilated by the resorbing surface, some percentage of consumed food is lost in faeces and excreted unutilized by the fish. Therefore, the food efficiency, η was introduced expressed as a percentage of consumed food rate, C (equation 18). The food consumed and used for "external work" and "internal work" (Ivlev 1939, Temming and Herrmann 2009) is not available for growth. That part of the food can be computed at zero mass growth, $m' = 0 g \times d^{-1}$ – in this case the catabolism of body mass is just prevented by the maintenance rate. Rearranging equation (18) we get for zero mass growth, $G = 0 \% \times d^{-1}$:

$$k = C_{as min} = \eta C_{min} \quad (19)$$

The catabolism rate, k is equal to maintenance assimilation rate or is proportional to the maintenance food rate, C_{min} [% $\times d^{-1}$], the quantity of food consumed per time interval divided by instantaneous body mass of fish. Catabolism, and therefore also the maintenance rate, is a function of temperature, T , on thermodynamic grounds (Kelso 1972, Hawkins et al. 1985, Jobling 1988, Davies and Massey 1997):

$$C_{min} = C_0 e^{k_T T} \quad (20)$$

where C_0 is the maintenance rate at $T = 0^\circ C$ and k_T is a temperature constant.

Inserting equation (19) and (20) into equation (18) results after rearrangement in:

$$\eta = \frac{C_{as}}{C} = \frac{G + k}{C} = \frac{G}{C - C_0 e^{k_T T}} \quad (21)$$

The food efficiency, η (equation (21)), is similar but not identical to the so called net conversion efficiency, $NCE = G/(C - C_{min})$; both parameters are not directly comparable. Like other authors (NCE or $K3$ as defined by Wootton 1990, Temming and Herrmann 2009), it is assumed that the food $C = C_{as} + DF$ consists of a

digestible, C_{as} , and an indigestible portion, DF (dietary fibres – see also figure 2). The digestible portion $C_{as} = G + C_{min}$, but not the dietary fibres can be used for maintenance and growth. The efficiency η is therefore a property of food.

2.5. Food consumption within a certain time interval

The left component of the right side of equation (4) expresses anabolism. Inserting equation (5) into equation (4) we get:

$$\eta m'_c = m'_{as} = H l^2 p \quad (22)$$

Condrey (1982) reviewed published data on growth-relationships for fish and concluded that there is more often a linear relationship between growth and ingestion in particular for short time intervals. Introducing this into equation (22) the mass, m_c consumed within the time interval, t , can be achieved by integrating over this function:

$$m_c = \int_0^t \frac{H (K t + l_0)^2 p}{\eta} dt \quad (23)$$

with $K = \frac{l_1 - l_0}{t}$

Here, we reflect on the initial condition that for fish-length growth the resorbing surface is growing proportional to the square of the fish length (equation 5), however, the mass-flow rate (or rate of anabolism), H remains constant (equation 4). Solving the integral and rearranging to mass flow rate, H we get:

$$H = \frac{3 \eta m_c}{(l_0^2 + l_0 l_1 + l_1^2) p t} \quad (24)$$

Equating the right sides of equation (17) and equation (24), introducing equation (20) and the operation-point concept described above, the consumed mass of food, m_c can be computed:

$$m_c = \frac{(l_0^2 + l_0 l_1 + l_1^2) t C_0 e^{k_T T}}{6} \times \left(\frac{\left(\frac{m_0}{l_0^3} + \frac{m_1}{l_1^3} \right) \left(l_0 - l_1 e^{\frac{\eta t C_0 e^{k_T T}}{3}} \right)}{1 - e^{\frac{\eta t C_0 e^{k_T T}}{3}}} + \frac{(l_0 + l_1) \left(\frac{m_0}{l_0^3} - \frac{m_1}{l_1^3} e^{\eta t C_0 e^{k_T T}} \right)}{1 - e^{\eta t C_0 e^{k_T T}}} - \frac{(l_0 + l_1) \left(\frac{m_0}{l_0^3} + \frac{m_1}{l_1^3} \right)}{2} \right) \quad (25)$$

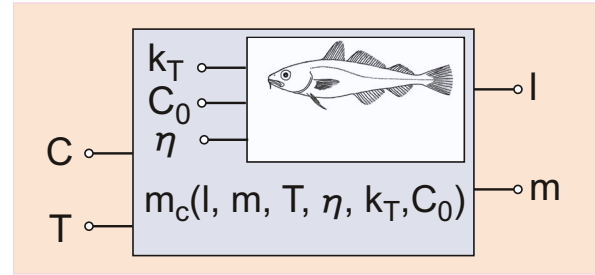


Figure 3. Fish as a “black box” experiencing the input signals food rate, C and temperature, T and responding with increments in length, l and mass, m per time interval, t for the estimation of the internal parameters temperature constant, k_T and maintenance rate C_0 at 0°C and the food efficiency η during feeding experiments.

Abbildung 3. Fisch als „Black Box“, auf den für die Schätzung der internen Parameter (Temperaturkonstante, k_T , Erhaltungsrate C_0 bei 0°C und Nahrungswirkungsgrad η) während der Fütterungsversuche die Eingangssignale Fütterungsrate, C und Temperatur T einwirkt und welcher dann mit der Änderung der Länge l und Masse m pro Zeitintervall, t reagiert.

Even though equation (25) looks intricate, it contains, apart from three internal parameters, only the time interval, t , the lengths, l_0 and l_1 , the masses, m_0 and m_1 and the temperature, T , which all can be measured easily. It is not possible to measure the values of the internal parameter – the temperature constant k_T , the maintenance rate C_0 , and the food efficiency – of fish directly. This, however, can be done indirectly by the measurement of the “system response” observed during feeding experiments (see figure 3).

2.6. Calibration of the “measuring sensor” fish by feeding experiments

For the estimation of the internal parameters, temperature constant k_T , maintenance rate C_0 at 0°C and food efficiency η , the data were used had been published by Soofiani (1983) and Hawkins et al. (1985) for juvenile cod at different environmental conditions characteristic of a fjordic sea loch on the west coast of Scotland. Fish caught with hand lines in shallow water were kept in large rectangular tanks and acclimated to experimental temperatures for at least four weeks before experiments began. The experiments were carried out for three size classes and four different temperatures. The fish were fed pre-weighed rations of pellets, often taken avidly, every second day, made

up from a mixture of the four major components of the natural diet in Loch Torridon, viz. polychaetes, molluscs, crustaceans, and fish briefly described in Hawkins et al. (1985). However, the appropriate items were not always available and on occasion other natural prey was substituted. It was assumed, however, that the diet had approximately the same composition, energy and water content as the natural food of cod. The pellets were kept in a deep freeze before being presented to the fish. For the indirect measurements

of the internal parameters the analyzed "black box" fish (figure 3) was charged over a period of time, t by the "test signals" food ration, m'_c and temperature, T within that period. By observing the system response (values and increments in length, l and mass, m) the internal parameters can be computed if the variables are connected in some way by an underlying equation (equation 25).

Fish were fed at a constant rate, C . Therefore, the daily ration, m'_c , as adapted (increased) to the mass growth

Table 1. Experimental data for food consumption and growth rates of juvenile cod (*Gadus morhua* L.) at different environmental conditions in a fjordic sea loch on the west coast of Scotland (Soofiani 1983).

Table 1. Fütterungs- und Wachstumsraten der Versuche für juvenilen Kabeljau (*Gadus morhua* L.) bei unterschiedlichen Umgebungsbedingungen in einem Fjord an der Westküste von Schottland (Soofiani 1983).

Duration [days]	Initial length [cm]	Initial mass [g]	Final length [cm]	Final mass [g]	Period ration experiments [g]	Period ration model [g]
Temperature: 7 °C, Size class 2 (23.5 -30.0 cm)						
56	28.0	227.4	30.0	264.9	137.8	251.0
56	28.0	217.1	31.0	301.1	560.1	476.8
56	28.5	189.7	30.0	256.3	370.9	383.1
56	28.5	212.0	29.0	215.4	99.3	77.8
56	26.0	182.1	29.0	244.3	315.2	359.8
56	27.0	192.5	30.0	280.4	403.9	488.6
56	28.0	197.5	30.0	257.4	389.8	352.3
56	25.5	160.1	28.0	224.3	252.9	362.6
56	28.0	200.9	29.0	232.3	397.9	212.9
56	28.0	182.3	30.0	271.9	485.8	493.9
50	28.0	198.2	28.0	189.2	45.5	6.6
56	27.0	218.0	28.0	232.6	148.9	135.0
56	28.5	203.1	30.0	258.0	276.3	329.3
50	30.0	248.8	32.0	314.3	299.9	386.2
56	30.0	255.3	31.0	272.7	208.5	159.5
Rel. Error = 1.9%		Sum: 4392.5 4475.3				
Temperature: 10 °C, Size class 1 (16.0 -23.0 cm)						
75	22.0	103.7	24.0	134.1	169.4	208.9
75	20.0	85.7	26.5	183.5	542.1	541.2
75	23.0	102.4	23.0	109.5	101.7	90.5
75	21.5	91.4	24.0	117.5	199.0	181.1
75	19.5	67.2	23.0	106.6	250.3	235.0
75	16.0	44.2	21.0	91.2	371.7	261.9
75	22.0	113.1	23.0	110.5	48.6	47.3
45	23.0	112.5	24.5	146.0	149.5	201.7
45	23.0	92.0	25.0	155.0	325.7	340.3
Rel. Error = -2.3%		Sum: 2157.9 2107.9				
Temperature: 10 °C, Size class 2 (23.5 -30.0 cm)						
75	27.5	180.3	29.0	237.5	285.1	384.9
75	28.0	194.3	30.0	250.4	391.9	386.9
75	25.0	169.4	29.0	254.1	493.9	518.6
75	29.0	231.7	30.0	235.8	149.0	144.3
75	26.0	151.0	29.5	229.0	373.4	473.8
61	28.0	280.7	30.0	298.2	164.2	210.4
62	30.0	315.4	34.0	405.8	467.3	594.8
75	27.0	177.7	29.0	227.2	280.9	344.7
75	25.0	150.6	28.5	238.5	509.2	523.0
75	29.0	213.9	29.5	186.0	138.0	-27.3
75	26.0	171.1	27.5	189.5	104.1	184.4
Rel. Error = 11.4%		Sum: 3357.0 3738.5				
Temperature: 10 °C, Size class 3 (30.5 -40.0 cm)						
75	32.0	318.8	38.0	565.6	1230.4	1411.4
75	31.0	282.9	33.0	371.2	684.4	596.5
75	39.0	589.1	42.5	699.2	744.0	872.7
75	40.0	619.9	40.0	565.4	284.5	53.8
62	34.0	416.7	35.5	427.3	311.4	237.2
61	30.5	279.4	35.5	373.7	438.2	598.2
45	34.0	432.5	37.5	640.4	970.4	1165.2
45	32.5	326.5	34.0	402.3	496.9	479.6
45	33.0	360.9	33.0	356.3	204.9	92.5
45	32.0	321.8	33.0	354.6	386.6	265.4
45	33.5	389.5	35.5	464.2	328.5	494.5
Rel. Error = 3.1%		Sum: 6080.1 6267.0				
Temperature: 15 °C, Size class 1 (16.0 -23.0 cm)						
75	19.0	65.6	21.5	98.6	211.8	232.2
67	17.0	44.8	21.5	111.6	465.3	377.5
75	18.5	54.0	21.0	84.8	173.8	209.9
75	21.0	80.2	21.0	65.3	51.8	-5.3
66	20.0	68.4	24.5	157.3	614.5	509.2
75	20.5	67.7	22.5	97.4	193.2	216.9
56	22.0	95.5	25.5	174.9	563.3	468.9
56	19.0	53.6	22.0	108.2	307.6	313.6
56	21.5	74.0	21.5	70.9	77.5	34.5
56	22.0	92.7	23.5	125.0	213.3	228.5
56	21.0	79.4	23.0	126.3	270.1	293.5
56	19.5	73.0	20.5	83.4	89.8	103.1
56	20.5	77.6	21.5	99.1	137.5	163.1
Rel. Error = -6.6%		Sum: 3369.6 3145.6				
Temperature: 15 °C, Size class 2 (23.5 -30.0 cm)						
75	24.0	117.0	28.5	210.5	692.7	593.1
75	23.5	117.5	27.0	182.8	343.5	448.1
75	26.0	172.8	26.0	159.0	77.1	84.9
75	25.0	133.8	28.5	243.2	753.5	690.3
Rel. Error = -2.7%		Sum: 1866.8 1816.4				
Temperature: 18 °C, Size class 2 (23.5 -30.0 cm)						
50	24.5	133.2	27.0	184.7	367.2	379.4
50	27.0	167.8	28.0	187.8	208.9	245.2
50	27.0	186.4	27.5	170.9	75.9	75.7
50	24.0	136.6	24.5	133.1	126.1	96.5
46	24.5	133.2	26.5	196.7	464.4	430.3
50	28.5	231.9	30.5	247.9	237.5	279.2
50	24.0	134.1	27.0	180.1	298.5	352.5
50	26.5	165.3	27.0	175.3	192.4	191.0
50	28.5	215.0	28.5	195.0	96.4	76.0
50	27.0	178.5	28.0	193.0	170.9	225.6
50	25.0	153.2	27.5	183.2	291.8	285.8
50	26.0	150.6	26.5	177.6	215.0	267.4
Rel. Error = 5.8%		Sum: 2744.9 2904.7				

of the cod (equation 26). C was expressed in terms of the equivalent wet mass of natural food composing the diet, as a percentage of the initial body mass [$\% \times d^{-1}$].

$$C = \frac{m'_c(t)}{m(t)} \approx \frac{2 m_c}{(m_0 + m_1) t} \quad (26)$$

The fish were weighed at regular intervals. To improve the accuracy of measurements, the fish were not fed for two days prior to each weighing to minimize the mass of food in the stomach in each of the experiments (Soofiani 1983). At the end of the experiment, the total intake of pellets was calculated, and divided by the duration of the experiment and mean mass of fish at the beginning, m_0 and at the end, m_1 to give the daily rate, C . That part of data used in this paper for the computation of the internal parameters, k_T and C_0 and the food efficiency, η , provided by Soofiani (1983) is summarized in Table 1. The estimation (MLS) was conducted by varying C_0 , k_T and η (using equation 25 and carried out by Solver within Excel) to achieve least squares relative to C . Estimations of the standard deviations in the three internal parameters were determined by jackknifing (Gray and Schucany 1972).

As can be seen later, the experimental and computed growth data fit better with larger feeding data during the calibration of the model. This is the case for large feeding ratios, $m'_c = \Delta m_c / \Delta t$, but also for large feeding rates, C (equation 26). The daily rate, C , was chosen to give each fish independent of individual mass and duration of the experiment the same weight in the estimation. The choice of feeding ratios instead of feeding rates would grant larger fish a greater weight in the estimation.

3. Results

The least squares estimation yielded a temperature constant of $k_T = 0.108 \pm 0.002 \text{ } ^\circ\text{C}^{-1}$, the maintenance rate at $0 \text{ } ^\circ\text{C}$, in $C_0 = 0.242 \pm 0.011 \text{ } \% \times d^{-1}$ and for the food efficiency, in $\eta = 20.8 \pm 0.2 \text{ } \%$. It was assumed that the parameters k_T , C_0 and η were constant for all individual fishes. The relative errors of the food rate estimated by the model decrease with increasing food rates (figure 4). Close to the maintenance rate, the differences between food rates measured during the experiment and food rates predicted by the model were large due to large differences in the individual maintenance rates of fish. The mean value of relative prediction errors for an individual fish is $24 \text{ } \%$. It can be expected that measurement errors for the estimation of food consumption of wild cod, are

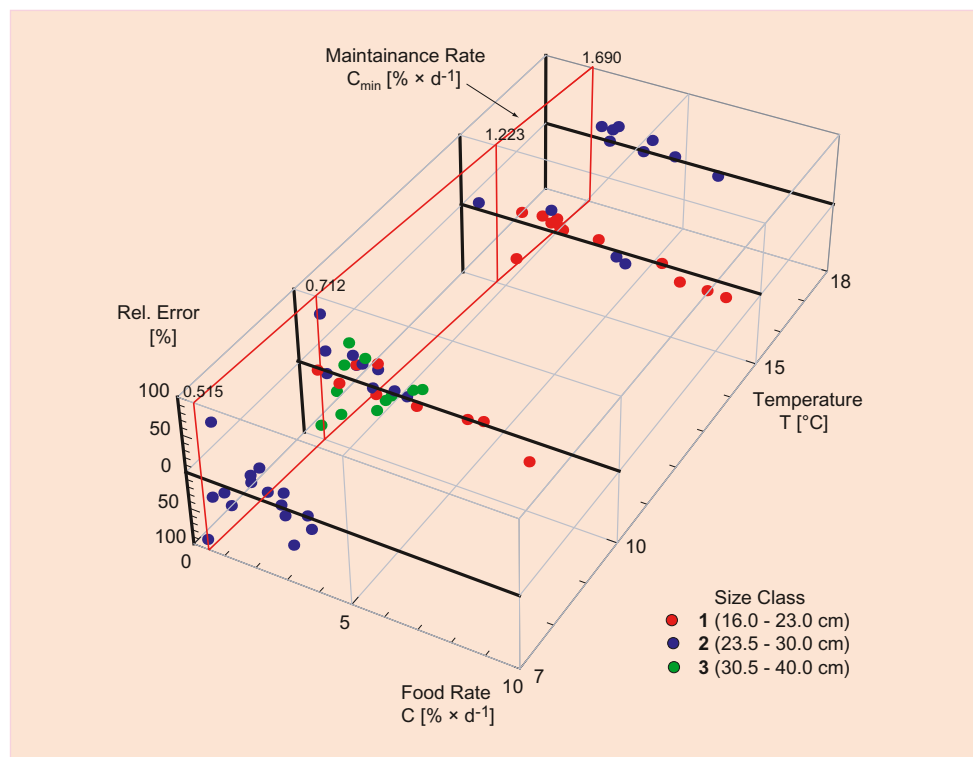


Figure 4. Relative prediction error of modeled food consumption for the feeding experiments as a function of food rate (C – ingested amount of food as a percentage of body mass of per day, [$\% \times d^{-1}$]) and environmental temperature.

Abbildung 4. Relativer Vorhersagefehler der modellierten Nahrungsaufnahme für die Fütterungsversuche in Abhängigkeit von der Fütterungsrate (C – aufgenommene Nahrungsmenge als Prozentsatz der Körpermasse pro Tag [$\% \times d^{-1}$]) und der Umgebungstemperatur.

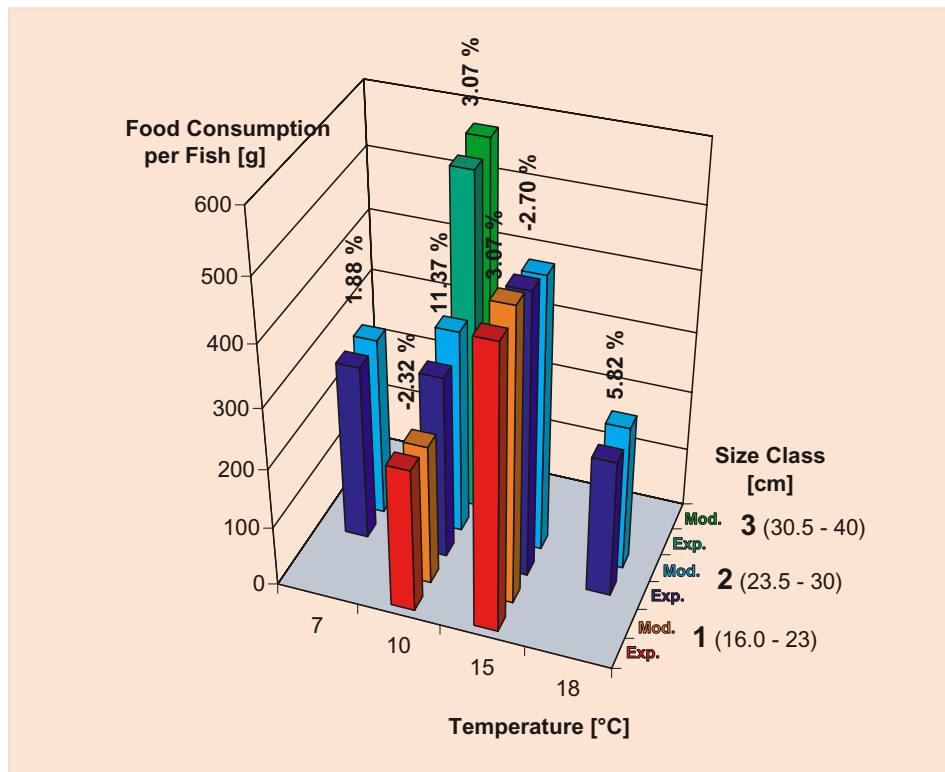


Figure 5. Comparison of mean food consumption per cod of feeding experiments (Soofiani 1983) and corresponding predicted values of the model for different temperature- and size classes.

Abbildung 5. Vergleich der mittleren Futteraufnahme pro Kabeljau aus Experimenten (Fütterungsversuche – Soofiani 1983) und entsprechend vorhergesagten Schätzergebnissen des Modells für unterschiedliche Temperatur- und Größenklassen.

comparable with the errors observed during the feeding experiments. However, for modeling ecosystems the interaction of groups of fish has to be computed and not the interaction of individual fishes. Grouping the fish into temperature and length groups reduces the prediction errors of the group (figure 5). Table 1 shows the experimental data used for the estimates of food consumption and also the sum of consumed food as well as the values predicted by the model. The deviations between experimental data and predicted values are small (table 1). Therefore, for a group of fish, the mean value of the relative prediction error is typically lower than for an individual fish. Relative errors observed for individual fish are canceling out each other due to their random statistical properties. The prediction error for small groups here was about 5 %. For the total group (all fish within the feeding experiment) the relative error was about 2 %.

4. Discussion

The model predicted the food consumption of juvenile cod in the feeding experiments by Soofiani (1983) and Hawkins et al. (1985) accurately. The average of the relative error of the predicted food intake of approx. 5 %, with fish grouped according to size classes and temperatures, demonstrates the precision of our model. Such a good match is not common in

similar investigations comparing consumption model predictions with observed consumption (Hansson et al. 1996, Worischka and Mehner 1998, Maes et al. 2005).

An understanding of predator-prey relationships is highly relevant for ecosystem modelling. The predictive power of our model is therefore encouraging. We can assume that this model may not only answer the question of “what eats what?”, but it may additionally answer the question “what eats what and to what extent?”. Prior to discussing this question, we will have to discuss questions and possible drawbacks concerning the experiments that form the basis of the validation of our model and the food consumption model.

The juvenile cod in the experiments were fed with pellet food. This may be a drawback in the use of the data from the experiments of Soofiani (1983) and Hawkins et al. (1985), since the physical characters of food per se may have an influence on food efficiency. Dos Santos et al. (1993) observed lower gross conversion efficiencies ($GCE = G/C$, with G = increase in weight or total energy content and C = weight or energy content of food consumed during a certain time interval) of up to 25 % in cod (*Gadus morhua* L.) feeding on minced herring (*Clupea harengus* L.) paste compared to cod feeding on natural herring. Additionally, Jobling

(1986) showed that the food conversion efficiency with a diet of pellets was generally lower than that of natural food. This may have been the case here, too, a fact that Hawkins et al. (1985) discuss. We estimated a food efficiency of approx. 21 %. Pellets may rapidly disintegrate in the experimental tanks leading to an overestimation of the amount of food consumed, artificially altering the estimated conversion efficiency of the fish. We were not able to determine whether this might have occurred in the experiments of Soofiani (1983), but from the description of the experimental procedure we concluded that a disintegration of the pellets before the consumption by the fish could be possible. An advantage of the experiments was that the fish were fed pellets that were made from a mixture of the four major components of the natural diet in Loch Torridon, the area in which the fish were caught. We are aware that laboratory estimates of the food efficiency η form an essential basis of the applicability of our model to field consumption and that these experiments need to be conducted as closely resembling field conditions as possible. Independent of the above mentioned concerns, we are confident that the experiments that form the basis for the validation of our model were suitable for this purpose.

The obvious advantage of our model is that the input variables, i.e. initial and final lengths and masses and the ambient temperatures over the relevant time period measured, can easily be determined directly on field surveys. The three internal parameters, the maintenance consumption at 0°C, the temperature dependence of consumption and the η can only be determined indirectly in laboratory experiments. This feature is common to most consumption models, linking field observations with laboratory measurements. The advantage here is that the feeding-growth experiments that generate the internal parameters used in our model can be relatively simply conducted in the laboratory. In comparison with bioenergetics models, where numerous different parameters have to be estimated in laboratory experiments (Karjalainen et al. 1997) that all have to be integrated into the model, the number of parameters in our model remains straightforward. This feature lowers the number of sources of error in comparison with the bioenergetics model, where for many fish species parameters have to be borrowed from related species to fill the knowledge gaps concerning the parameters needed in those consumption models (Rudstam 1988, Ney 1993, Arrhenius 1998). The other class of commonly used consumption models, combining field stomach estimates with laboratory derived estimates of the temperature and mass-dependency of the gastric evacuation rate requires fewer parameters estimated in the laboratory (Pennington 1985, Köster and Möllmann 2000). Gastric evacuation in fishes appears to be highly variable between species and even within a species depending on e.g. food type

and energy density of the prey and lively discussions are still ongoing about the correct evacuation model, i.e. if the gastric evacuation progresses rather linearly or exponentially, or something in between (Persson 1986, Bromley 1994, Bochdansky and Deibel 2001, Andersen and Beyer 2005). These disadvantages may introduce a bias in the consumption estimates from the two model types mentioned, often leading to ample discrepancies between the estimates of both models (Hansson et al. 1996, Worischka and Mehner 1998, Maes et al. 2005).

A general drawback in the use of all models is the need for the estimation of food efficiencies for numerous food compositions, fish sizes and temperatures, since these factors are known to influence the food conversion efficiency (e.g. Jones and Hislop 1978, Chen 1989, Björnsson et al. 2001). Since in cod the diet generally reflects prey availability (Link and Garrison 2002) and this species experiences different food supplies during different seasons, the variable food composition results in different values for food conversion efficiency, as observed in laboratory experiments with cod feeding on Crangon (*Crangon crangon*) and cod flesh (Jones and Hislop 1978) and Saffron Cod *Eleginus gracilis* (Tilesius) feeding on squid *Todarodes pacificus* and Japanese sandlance *Ammodytes personatus* (Chen 1989).

During the feeding experiments, the energy content of the food was relatively constant due to the constant food composition. However, fish often consume food of different compositions depending on the season and spatial overlap with prey species. The fraction of fish prey in the food of carnivorous fish like cod generally increases with increasing size (Link and Garrison 2002). The food efficiency, η , is therefore a function of time and most likely of the spatial distribution of predator and prey. This emphasizes the need for 1) an adequate sampling scheme of the food/prey in the field and 2) for laboratory feeding experiments that use a range of food compositions. A possible outcome of laboratory experiments could be that the average η for one species may well be suited for the consumption estimation by our model for other species (inhabiting similar niches). Irrespective of that, producing laboratory data on η under different conditions remains a future task.

Prior to the application of this model to field data, some additional problems have to be solved. The feeding-growth experiments were conducted under controlled laboratory conditions. However, life in the ocean is far more complex than an environmentally controlled laboratory tank. This factor may induce errors in the estimation of consumption, because more energy is expended in a complex environment and so is not available for growth. Equation (20) describes the tem-

perature dependency of the maintenance rate of the fish. Within the temperature range characteristic of the distribution of cod, the maintenance rate can increase three or fourfold. Hence, it is important to incorporate the behaviour and the habitat of the fish in the consumption estimation, and in the case of changes in the ambient temperature and other relevant abiotic variables to measure the variables sufficiently often.

An interesting question is why the relative error is higher at lower food rates compared to the error at higher food rates (figure 4). There are several possible explanations. First, problems in determining the food ration consumed, as discussed above, could explain the differences. This is unlikely, since these problems tend to occur when high rations are being fed. A second explanation could be differences in the activity of the fish, leading to less energy available for growth for the most active fish. In the field, an enhanced activity while searching for food may lead to a net energy gain. This was not possible under laboratory conditions with fixed feeding intervals. In general, researchers have measured activity differences in cod. Large intra-specific differences in magnitude of oxygen consumption were observed in Atlantic cod during swimming in a tunnel respirometer (Tang et al. 1994), an observation that was supported by measurements of the swimming metabolism of Atlantic cod by Björnsson (1993), who observed that the difference in swimming metabolism between the most active and the least active fish became almost fivefold. The third explanation relates to physiological reactions to reduced food rations. Several authors have observed in feeding-growth trials with cod and turbot *Scophthalmus maximus* (L.) a correlation between ration size and body water content (e.g. Holdway and Beamish 1984, Van Ham et al. 2003) over the course of an experiment, with higher water contents in the treatments with lower rations. This indicates that the relatively higher deviation observed between the model and the experiments of Hawkins et al. (1985) at lower food rations may be due to differences in the water content of the fish. While cod held at high rations mainly grow by synthesizing new tissue do cod held at low rations grow by synthesizing new tissue (at a lower percentage of body mass than cod at higher rations) and additionally by storing water in tissues such as muscle. For practical reasons, our model works with wet masses. A bias due to differences in the almost constant body-mass-water content is unlikely because changes in body weight by food intake are much larger than by the storage of water within the body. However, changes in body-mass-water content may lead to higher relative errors at lower food rations. This estimation procedure most likely has to be applied to field stomach samples with varying water content (due to the sampling procedure). Presumably, dry masses of prey items have to be estimated, which will have to be extrapolated

to water contents of prey in natural populations. The water content of fish, which is dependent on the prey spectrum and, therefore, variable, does not appear to be a problem, since it is sufficiently constant.

In the present form can our model be applied without restriction to juvenile fish only, since the spawning cycle is not included in the equations. In adult fish the accumulated energy is partitioned into somatic and gonadal growths, which directly compete with each other. The somatic growth is often reduced during the reproductive phase, as the reproductive growth is often prioritized (Koch and Wieser 1983). The investment of energy into reproduction is generally increasing with the age of fish. For example in female northern pike (*Esox lucius* L.) the annual investment of energy in reproduction increased from 0 % in the first year of life to 11-16 % over the second, third and fourth, while the somatic investment declined from 42 % to 5-8 % (Diana 1983). In an energy budget model of North Sea saithe (*Pollachius virens*; Andersen and Riis-Vestergaard 2004) the gonadal energy content was assumed to increase linearly with time. The reproductive losses were also addressed in the bioenergetics model for northern cod by Krohn et al. (1997), where the annual reproductive loss for female cod was estimated to be 16 – 23 % of the energy content of the whole body. These numbers were based on energy density measurements of cod eggs by Daan (1975) and Hislop and Bell (1987). It will be a future task to extend our model by accounting for the energy expenditure due to spawning as compared to energy used for somatic growth.

In the present study, we present a relatively simple but effective approach for the estimation of food consumption from growth rates in the field as potentially basic data for the estimation of the natural mortality of prey species. The application of our model to data of juvenile cod of a fjordic sea loch results in a typical relative error of 5 % for the predicted food intake for a group of similar sized fish (2 % for all fish of the feeding experiment). This encouraging result indicates the applicability of our model to the field situation. An advantage compared to the above mentioned consumption models based on bioenergetics and gastric evacuation is the small number of parameters that have to be estimated in laboratory trials. Combined with field data on ambient temperatures, lengths and masses of predator species (in this case juvenile cod), we are able to estimate relatively precise consumption estimates. A future task will be to incorporate the proportion of total ingested energy allocated to gonadal growth into the model and to encourage laboratory work on the estimation of the internal parameters, maintenance consumption at 0°C, the temperature dependence of this consumption and the food efficiency, needed for consumption estimations.

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