**REVIEW ARTICLE**

**Modelling growth and body composition in fish nutrition: where have we been and where are we going?**

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**Abstract**
Mathematical models in fish nutrition have proven indispensable in estimating growth and feed requirements. Nowadays, reducing the environmental footprint and improving product quality of fish culture operations are of increasing interest. This review starts by examining simple models applied to describe/predict fish growth profiles and progresses towards more comprehensive concepts based on bioenergetics and nutrient metabolism. Simple growth models often lack biological interpretation and overlook fundamental properties of fish (e.g. ectothermy, indeterminate growth). In addition, these models disregard possible variations in growth trajectory across life stages. Bioenergetic models have served to predict not only fish growth but also feed requirements and waste outputs from fish culture operations. However, bioenergetics is a concept based on energy-yielding equivalence of chemicals and has significant limitations. Nutrient-based models have been introduced into the fish nutrition literature over the last two decades and stand as a more biologically sound alternative to bioenergetic models. More mechanistic models are required to expand current understanding about growth targets and nutrient utilization for biomass gain. Finally, existing models need to be adapted further to address effectively concerns regarding sustainability, product quality and body traits.

**Keywords:** modelling, fish, growth, body composition, nutrition.

**Introduction**
Aquaculture has become a multinational industry over the last 30 years and is expected to maintain an average annual growth rate of > 4% over the period 2010–2030 (Brugère & Ridler 2004). Greater demand for fish, combined with the reduction in capture fisheries and more affordable retail prices for several species, has contributed to foster and sustain the aquaculture industry (NRC 1999; FAO 2006). However, intensification and potential for development of the aquaculture sector have created challenges regarding profitability, environmental sustainability and product quality, most of which are related ultimately to nutrition (e.g. Naylor, Goldburg, Primavera, Kautsky, Beveridge, Clay, Folke, Lubchenco, Mooney & Troell 2000; Watanabe 2002). These concerns along with uncertainties surrounding production costs stress, among other things, the need to develop accurate tools to manage production and predict scenarios soundly.

Here, mathematical modelling – defined as the use of equations to describe or simulate processes in a system – represents an effective approach to taking up the challenges that aquaculture is facing. Mathematical models in animal nutrition have proven indispensable in estimating growth and feed requirements that have always represented major fields of interest in livestock production (Kellner 1911; Murray 1914; Brody 1945; Blaxter 1989; Baldwin 1995; Dumas, Dijkstra & France 2008). In aquaculture, the quality, safety and health benefits of fish products are now of increasing interest (Hocquette,
Richardson, Prache, Médale, Duffy & Scollan 2005; Caswell 2006; Mozaffarian & Rimm 2006). Composition of fish with reference to carcass yield, fatty acid composition and levels of lipid and contaminants has recently received further attention in studies on nutrition, genetics and health (Rasmussen 2001; Blanchet, Lucas, Julien, Morin, Gingras & Dewailly 2005; Hamilton, Hites, Schwager, Foran, Knuth & Carpenter 2005; Tobin, Kause, McEntyssai, Martin, Houlihan, Dobly, Kiessling, Rungruangpak-Torrissen, Ritola & Ruohonen 2006).

This article begins by summarizing briefly the biological properties of fish growth. Thereafter, major current models applied in fish nutrition are reviewed and challenged. Finally, a global perspective is offered and future directions in modelling are suggested to address better the concerns in fish production.

**Biological properties of fish growth**

Despite its complexity, growth takes place in a highly organized scheme in animals. Diverse regulatory strategies exist in organisms to adjust influx of chemicals (amino acids, fatty acids, minerals, etc.) and excretion of waste products even in a disruptive environment in order to maintain homeostasis (Nelson & Cox 2000). As growth processes do not occur in a chaotic manner, they can be generally described and predicted using conventional mathematics.

Growth, body composition and metabolic utilization of nutrients or allocation of resources are related to each other and change considerably during the lifespan of animals. Growth trajectories of animals – defined here as the pattern of weight gain achieved through time – display an almost universally sigmoidal shape with an asymptotic body size at adult stage (Fig. 1a). It is well documented that growth rate increases during the juvenile stage, i.e. the so-called self-accelerating phase of growth, and levels off when the animal approaches the adult stage or induces reproductive growth. This last portion of the growth curve is also referred to as the self-inhibiting phase of growth (Brody 1927; Charnov, Turner & Winemiller 2001; Lester, Shuter & Abrams 2004). In contrast with birds and mammals, several species of fish, molluscs, crustaceans and amphibians are capable of growing well beyond their size at sexual maturity. These organisms display a much less evident self-inhibiting phase (Fig. 1b). This phenomenon, also referred to as indeterminate growth, results in a debatable position of asymptotic weight at the adult stage. Indeterminate growth is regulated by environment and genetics (Sebens 1987), which affect the physiological capacity of an organism to synthesize muscle fibres throughout its life cycle (Biga & Goetz 2006). Another peculiarity of fish is their ectothermic nature. Growth rate of fish is thus highly dependent on water temperature. To date, few attempts have been made to describe fish growth with an algebraic expression that accommodates their ectothermic nature and indeterminate growth.

**Current models in fish nutrition**

The complexity of interactions in nutrition, the vast amount of information available nowadays and the substantial cost of experiments make the use of mathematical models appealing. Models are helpful tools in that they have the ability to represent complex phenomenon (e.g. growth) in a relatively simple way [e.g. weight gain as a function of protein deposition (PD)]. The following sections review briefly extant models currently applied in fish nutrition.

**Simple growth functions**

Growth functions are any models where weight or length (dependent variable, y) is calculated using time, t, as the predictor (independent variable) taking the form y = f(t), where f represents some functional relationship. Growth functions are usually analytical solutions to differential equations that can be fitted to

![Figure 1](https://example.com/figure1.png)

*Figure 1* Typical growth trajectory of (a) terrestrial animals and (b) fish
the growth data generally by means of non-linear regression analysis (Thornley & France 2007). The sigmoidal or curvilinear shape of the growth trajectory indicates that linear regression is not suitable to describe growth, unless only small portions of the curve are considered. For this reason, growth functions stand presumably as the best means of estimating animal growth. Because a large number of growth functions had been proposed in the last century, only those that have been widely applied in fish studies or that have considered the effect of temperature on growth of ectotherms are discussed here. For a broader description of extant growth functions in animal science and theories associated with them, the reader is referred to Ricker (1979), Parks (1982), Ratkowsky (1990), Seber and Wild (2003) and Thornley and France (2007).

**von Bertalanffy equation**

The equation of von Bertalanffy (1957) stands as the most studied and applied growth function to predict growth of fish and other ectotherms (Ricker 1979; Hernandez-Llamas & Ratkowsky 2004; De Graaf & Prein 2005; Katsanevakis 2006). The equation was first proposed by Püttner (1920), a German fish biologist, who conceptualized growth as anabolism prevailing over catabolism. The differential and integral forms of this equation, currently referred to as the von Bertalanffy equation, are

\[
\frac{dW}{dt} = \eta W^b - kW
\]

\[
W = \left[ W_f - \left(W_f - W_0 \right)e^{-kt}\right]^{1/\theta}
\]

where \( \eta \) and \( \kappa \) are rate parameters for anabolism and catabolism, respectively, \( k \) is a rate constant equal to \( \kappa(1 - b) \), and \( \nu \) equals \( 1 - b \). The allometric exponent \( b \) is allowed to vary between 0 and 1. The equation has an asymptote, a flexible point of inflection, and adheres to the law of allometry (0 < \( b < 1 \)). Various rearrangements of the von Bertalanffy equation exist in the literature (Ricker 1979; Katsanevakis 2006).

The assumption regarding an asymptotic final size led to unrealistic values for indeterminate growers and, for this reason, was regarded as a mathematical artefact rather than a fact of nature (Knight 1968; Roff 1980). Parker and Larkin (1959) removed the catabolic part of Eq. (1) in order to relax the constraint on the final asymptote and suggested estimating \( \mu \) and \( b \) by fitting to particular life history groups and growth stanzas:

\[
\frac{dW}{dt} = \mu W^b
\]

The assumption that growth is determined by the difference between anabolism and catabolism has been proven inaccurate because it overlooks the role of timing of maturation on the shape of the growth curve (Day & Taylor 1997; Lester et al. 2004). Evidence suggests that the change in growth rate of indeterminate growers results from the decision to allocate more resources towards gonad development rather than movement towards equilibrium between anabolism and catabolism (Day & Taylor 1997; Czarnoleski & Kozlowski 1998; Charnov et al. 2001). However, the effect of reproduction is not always perceptible in ectotherms with indeterminate growth, especially in an environment with fluctuating water temperatures (Dumas & France 2008).

(Correction added on 9 September 2009, after first online publication: In the sentence containing Equation (1), ‘\( \nu \) equals 1\( b \)’ was corrected to ‘\( \nu \) equals 1 − \( b \)’)

**Thermal-unit growth coefficient (TGC)**

The French botanist Réaumur laid the basis of the thermal-unit concept in 1735 in an attempt to explain the time required from sowing to harvesting of crops by summing the degré-chaleur over that period (Allen 1976; Bonhomme 2000). The concept was introduced in ichthyology at the turn of the 20th century (Belehádek 1930). Although Norris (1868) noted that the development rate of trout eggs varies with temperature, Wallich (1901) apparently first applied the concept of the thermal unit to record the development of fish eggs. Wallich (1901) defined one thermal unit as 1°F above 32°F during 1 day, meaning that the mean daily water temperature of 36°F is equivalent to four thermal units. Krogh (1914) showed that the relationship between developmental rate (usually in % day⁻¹) and temperature (°C) exhibited a straight line (slope has degree-day as denominator) over a certain range of temperature. The time and thermal summation (degree-day) needed for hatching fish eggs can thus be estimated using a simple regression equation (Krogh 1914; Embody 1934; Hayes 1949).

The thermal-unit concept was also applied to estimate growth of hatched fish. Iwama and Tautz (1981),
who did not use the concept explicitly, started from
Eq. (2) and related the rate parameter for anabolism
to mean daily water temperature averaged over the
rearing period (T):
\[
\frac{dW}{dt} = \mu TW^b
\] (3)
where \(\mu (> 0)\) has units of \(\text{g}^{1-b}/(\text{C day})^{-1}\), \(T\) (a constant)
is water temperature (°C) and the allometric
exponent \(b (> 0)\) is dimensionless. Integrating Eq. (3)
yields
\[
\int_{W_0}^{W} \frac{dW}{W^b} = \mu T \int_{0}^{t} dt
\]
\[
W^{1-b} = W_0^{1-b} + \mu T(1-b)t
\] (4)

where \(W_0\) is the initial (time 0) value of \(W\). Starting
from Iwama and Tautz (1981), Cho (1992) explicitly
introduced the degree-day concept into their model
and proposed, without formal mathematical derivations,
a modification to Eq. (4):
\[
W_n^{1/3} = W_0^{1/3} + \frac{\epsilon}{1000} \sum_{i=1}^{n} T_i
\]
where \(\epsilon [\text{g}^{1/3}/(\text{C day})^{-1}]\) is TGC and \(T_i\) (°C)
is mean daily temperature.

From an inspection of Eq. (1) and Eq. (3), it is evident
that the TGC model is a special case of von Bertalanffy’s equation with
\[
\mu = \frac{3 \times \text{TGC} \times T}{1000}, b = 2/3, \lambda = 0
\]
The TGC model has since been widely used in the aquaculture literature (e.g. Einen, Holmefjord, Åsgård & Talbot 1995; Kaushik 1998; Willoughby 1999; Stead & Laird 2002; Hardy & Barrows 2002). This simple model has been adapted recently to the different growth stanzas of rainbow trout (Oncorhynchus mykiss, Walbaum) across life stages (Dumas, France & Bureau 2007). Despite its convenience, the thermal-unit approach can entail systematic errors in situations where the temperature moves too far away from the optimum for growth (Krogh 1914; Hayes 1949; Ricker 1979; Jobling 2003).

**Exponential equation or specific growth rate (SGR)**
The origin of SGR goes back in 1798 and was developed to address demographic concerns. Reverend Thomas Malthus, a mathematician, published an essay in 1798 in which he stated that the human popula-
lation increased according to a geometric progression (Gilbert 1993). His model, known as Malthus’ Law or the Malthusian Model, corresponds to the exponential growth equation:
\[
W = W_0e^{\mu t}
\]
where \(W\) is body weight, \(W_0\) is body weight at time
\(t = 0\), \(\mu\) is a growth coefficient (in units of per unit of

time) and time \(t\) is measured as age.

The growth coefficient \(\mu\) is better known as SGR,
which is used ubiquitously in fish studies. The equation
for SGR (\(\mu\)) is
\[
\mu = \frac{\ln W_f - \ln W_0}{t_f}
\]
where \(W_f\) is the final body weight (g) and \(t_f\) is the time
(days) between \(W_0\) and \(W_f\).

The SGR has often been proposed as a growth model in aquaculture (Willoughby 1999; Alan/C204, Kabri & Paspatis 2001) even though it gives no consideration to the effect of body weight and temperature on the growth of fish. Keeping in mind these drivers of fish growth, Brett (1974) determined different SGR for various water temperatures and body weights and entered the values (observed and extrapolated by eye) into tables that served afterwards to predict fish growth according to prevailing conditions (Brett 1974; Willoughby 1999). However, the relationship between SGR and temperature can be affected by the amplitude of temperature fluctuations (Brett 1979; Xu 1996). In other words, growth rates observed at constant temperature (e.g. 15 ± 0 °C) might differ from those at an average temperature (e.g. 15 ± 4 °C), especially when fluctuations occur over a short period of time.

The SGR model is based on the incorrect assumption that fish growth is continually exponential. This has proven not to be the case and, therefore, growth predictions have to be re-calculated every time the predicted growth curve moves too far away from the observed trajectory (Brett 1979). Unlike Brett (1974), Elliott (1975) plotted the relationships between SGR, body weight and temperature and derived the following equation to predict the growth of brown trout Salmo trutta (Linné):
\[
\frac{dW}{dt} = (a + bT)W^{1-b_1}
\] (5)
with the integral form (provided \(T\) is assumed constant):
\[
W = \left[b_1(a + bT)t + W_0^{b_1}\right]^{1/b_1}
\]
where $b_1$, $b_2$, and $a$ are weight exponent (dimensionless), slope [% (day °C)$^{-1}$] and intercept [% (day $^{-1}$)] of the relationship between SGR (% day$^{-1}$) and $T$ (°C) respectively.

The Elliott model is often used to investigate fish growth, especially in the ecology literature (Craig 1982; Allen 1985; Jensen 1990). From an inspection of Eqns (1) and (5), it is evident that the Elliott model is also a special case of von Bertalanffy’s equation with $\lambda = 0$

Moreover, Eq. (3) of Iwama and Tautz (1981) has many similarities to Eq. (5). Therefore, Elliott (1975) introduced the effect of temperature into Eq. (2) of Parker and Larkin (1959) before Iwama and Tautz (1981).

Equation (5) needs to be solved repeatedly over the growing period because slope and intercept change with water temperature and body weight (Fig. 2). This drawback limits application of the Elliott (1975) model because predictions can be applicable only to very short intervals and preclude comparison between studies, especially under fluctuating water temperatures.

Elliott, Hurley and Fryer (1995) revised the Elliott model and included considerations for optimum ($T_{\text{opt}}$) and limiting ($T_{\text{lim}}$) temperatures for growth (Fig. 2). The resulting equation takes the form

$$W = \frac{W_0^b + bc(T - T_{\text{lim}})T_{\text{opt}}}{100(T_{\text{opt}} - T_{\text{lim}})}$$

where $c$ is the SGR of a 1 g fish at $T_{\text{opt}}$. $T_{\text{lim}}$, the SGR at a given temperature at which SGR is 0, is the optimum temperature, $T_{\text{lim}} = T_L$, if $T_{\text{opt}}$ or $T_{\text{lim}} = T_U$ if $T > T_{\text{opt}}$.

Equation (6) is valid as long as the water temperature does not change. Under fluctuating temperature conditions, the equation needs to be extended and body weight at the end of a growing period ($W_1, W_2, \ldots, W_k$) needs to be predicted using the following:

$$W_k^b = W_0^b + \frac{bc}{100} \left( \frac{(T_1 - T_{\text{lim}})T_{\text{opt}}}{T_{\text{opt}} - T_{\text{lim}}} + \frac{(T_2 - T_{\text{lim}})T_{\text{opt}}}{T_{\text{opt}} - T_{\text{lim}}} \right. + \left. \ldots + \frac{(T_k - T_{\text{lim}})T_{\text{opt}}}{T_{\text{opt}} - T_{\text{lim}}} \right)$$

where $T_1, T_2, \ldots, T_k$ correspond to average temperature (°C) for intervals 1, 2, $\ldots$, $k$, and $t_1, t_2, \ldots, t_k$ are in days.

The authors reported that Eq. (7) yields significant discrepancies when the growing period exceeded 3 months (Elliott et al. 1995). Furthermore, the assumption of a fixed growth rate $c$ in Eqns (6) and (7) is contrary to the biology and growth trajectory of fish.

Another exponential fish growth model was proposed more recently by Lupatsch and Kissil (1998): $Y = aX^e^{\kappa T}$ where $Y$ and $X$ are weight gain (g fish $^{-1}$ day$^{-1}$) and body weight (g fish $^{-1}$), respectively; $a$ and $\kappa$ are constants, $b$ is weight exponent (dimensionless) and $T$ is water temperature (°C). This equation is also a special case of the von Bertalanffy with $\eta = ae^{\kappa T}$ and $\kappa = 0$ in Eq. (1):

$$\frac{dW}{dt} = a \kappa e^{\kappa T}W^b$$

Let

$$\frac{dW}{dt} = Y; W = X$$

Therefore,

$$Y = aX^b e^{\kappa T}$$

This model has been used successfully to describe the growth trajectory of warmwater fish species such as gilthead seabream (Lupatsch & Kissil 1998), European sea bass (Lupatsch, Kissil & Sklan 2001), white grouper (Lupatsch & Kissil 2005) and barramundi (Glencross 2006) within a relatively narrow range of temperature ($\sim 20\text{–}27$ °C). It assumes an exponential relationship between water temperature and growth rate, which can be true only for a certain range of optimal temperature, and appears in disagreement with the thermal-unit concept and reaction kinetic models for ectotherms. The latter showed that growth rate is inhibited at high temperature, and relationship between growth rate and temperature displays an asymmetric bell-shaped curve (Sharpe & DeMichele 1977; Schofield, Sharpe & Magnuson 1981).

(Correction added on 9 September 2009, after first online publication: In the sentence ‘This equation is also a special case of the von Bertalanffy with $\eta = \Theta e^{\kappa T} \ldots$; the symbol $\Theta$ was corrected to $a$.)

**Figure 2** Effects of body weight (BW) and temperature on specific growth rate (SGR). Lower ($T_L$) and upper ($T_U$) temperatures indicate where SGR is zero (adapted from Elliott 1975).
Based on visual appraisal of typical growth curves (e.g. Fig. 1), animals do not grow geometrically, i.e. exponentially, across life stages. The exponential growth function is therefore not suitable for accurately predicting or describing the growth trajectory of fish and other animals. Furthermore, this function yields unavoidably systematic deviations (Fig. 3). Growth data on Arctic charr *Salvelinus alpinus* (Linneä) obtained from Simmons (1997) are used here to compare the TGC and SGR models (constant water temperature: 12 °C; duration: 112 days). Using the latter equation, growth is underestimated from 1.5 g (\(W_0\)) to 174.2 g (\(W_f\)) whereas body weight increases steeply from 174.2 to 678 g over a 56-day period, which is unrealistic. This is in agreement with Brett (1974, 1979) and Cho (1992) who pointed out that SGR leads to underestimation of growth between values of \(W_0\) and \(W_k\) used to compute SGR and to serious overestimations of weight gain beyond \(W_k\).

In spite of its limitations, SGR remains widely accepted by editors and recommended ubiquitously in the fish literature likely because of its ease of use (Barton 1996; Willoughby 1999; Alan/C204r/C204 et al. 2001; Stead & Laird 2002). At best, SGR can serve in comparing different performances, although comparisons using SGR are valid only if fish have similar \(W_0\) and \(W_k\) and are reared at the same water temperature because, as stated earlier, growth rate of fish varies with size and temperature. For all the reasons mentioned above, SGR finds very little biological support and is therefore largely unsuitable as a fish growth model and tool to compare short-term growth performance.

### Simple models of feed conversion to biomass

Goals in animal nutrition are arguably to maximize the conversion of inputs (e.g. feed, investments) into high-quality outputs over a short period of time. Improving the conversion of dietary inputs to lean rather than adipose tissue growth is of benefit to producers and consumers. It can also contribute to reduced waste outputs and provide room for manoeuvre given the volatility of profit margins. As a consequence, several studies have turned their attention towards feed efficiency, protein utilization and lipid distribution as a function of fish size, feeding level and alternative ingredients for example (Aursand, Bleivik, Rainuzzo, Jørgensen & Mohr 1994; Azevedo, Cho, Leeson & Bureau 1998; Lupatsch, Kissil, Sklan & Pfeffer 2001; Cheng, Hardy & Usry 2003). These studies have generated a large amount of information (e.g. on body composition) that still needs to be explored and synthesized.

Most of these studies were designed to describe animal responses (e.g. weight gain) within specific experimental conditions. Unfortunately, their ability to describe a wide array of animal responses in varying situations is limited because their experimental designs prevent representation of the mechanisms in the internal structure of the organism that are responsible for the observed responses. For this reason, several mathematical modellers have insisted on the need to move from a requirement-based (input^output) to a rate:state approach where the major variables in play can be described and related dynamically, similar to a metabolic pathway (AFRC 1991; Thornley & France 2007; López 2008). The rate:state formalism consists of representing the rate of change of pools, referred to as state variables, using differential equations (Dijkstra, Mills & France 2002). Such formalism considers the state of a pool as the result of dynamic exchanges, i.e. influx (e.g. protein synthesis) and efflux (e.g. protein degradation) of substances. Differential equations are a valuable tool and have been proven essential in dynamic modelling in describing the behaviour of a system concisely and efficiently (Kleiber 1961; France & Kebreab 2006). The rate:state formalism is discussed further in Nutrient-based models.

### Bioenergetic models

Animal energetics refers to the quantitative study of energy exchanges induced by metabolic processes in
living organisms to stay alive, grow and reproduce (Nelson & Cox 2000). Energy exists in materials of dietary and body origin and is released in the form of heat to support work (Blaxter 1989).

Models constructed on the basis of bioenergetic principles utilize mathematical equations describing the heat transactions and adhere generally to a factorial scheme, also referred to as an energy budget. The factorial approach follows from the metabolizable energy concept (Armsby 1903; HMSO 1975), where energy expenditures or heat production are allocated to different metabolic processes according to an order of priority (NRC 1993; Bureau, Kaushik & Cho 2002). Inspired by Ivlev (1939) and Winberg (1956), Warren and Davis (1967, 1968) adhered to the factorial approach and proposed a simple additive equation to describe the energy budget of fish:

\[ C = F + U + \Delta B + R \]  

(8)

where \( C \) is intake of energy and \( F \) and \( U \) are energy losses in faeces, and urine and gills respectively (all variables in units of MJ day\(^{-1}\)). Variable \( \Delta B \) represents growth (energy gain) of the fish and \( R \) is energy loss through metabolic processes associated with maintenance and heat increment of feeding. Each component of the equation is described using mathematical relationships derived mostly using statistical analyses.

Equation (8) gained acceptance in fisheries and was adopted by Ricker (1968), Elliott (1976a, b) and Kitchell, Stewart and Weininger (1977). A systematic terminology for the description of energy budget and metabolic processes in animal nutrition was developed later by NRC (1981), and heat losses were categorized as shown in Fig. 4.

Fish growth has usually been predicted using two different approaches in bioenergetic models. One way of forecasting fish growth assumes that energy intake drives weight gain. This assumption is encountered mostly in fisheries and ecology studies because availability of food in natural ecosystems often limits fish growth (Elliott 1976a, b; Kitchell et al. 1977; From & Rasmussen 1989). An alternative approach considers genetic or desired growth rate rather than nutrition as the factor limiting animal growth (Hubbell 1971; Calow 1973; Oldham, Emmans & Kyriazakis 1997). Here, intake of energy is a function of the requirements of the individual to achieve a given growth capability or growth target. This approach was suggested by Winberg (1956, p. 174) and is mostly used in aquaculture where fish are generally fed to satiation with nutritionally complete diets (Cho 1990; Lupatsch, Kissil & Sklan 2001; Zhou, Xie, Lei, Zhu & Yang 2005). Genetically determined growth capability of fish is assessed using simple growth functions, especially the TGC model and the

![Diagram](https://example.com/diagram.png)

**Figure 4** Factorial framework of energy partitioning in typical bioenergetic models intended to evaluate feed requirements. Each metabolic process results in heat loss that is determined mostly using regression equations. For further information on definitions of terms and mathematical description of metabolic processes, the reader is referred to NRC (1981) and Bureau et al. (2002).
Bioenergetic models predict energy gain, but they provide little information on the chemical composition (moisture, protein, lipid and ash) of biomass gain. This characteristic has two significant drawbacks. Firstly, the bioenergetic models can entail systematic errors because the relationship between recovered energy and weight gain changes across life stages (Bureau et al. 2002). More energy is contained per unit of biomass gain for a large fish (e.g. 10 kJ g⁻¹ BW) than for a small fish (e.g. 5 kJ g⁻¹ BW) under typical rearing conditions. Studies have shown that the composition of biomass gain includes more lipid and less water in a large fish than in a small fish (Shul'man 1974; Dumas, de Lange, France & Bureau 2007). Protein and lipid deposition (LD) are two distinct biological processes driven by different factors or determinants that are overlooked in bioenergetic models. Secondly, the recovered energy can serve to determine the energy retention efficiency, but it is of no utility in assessing the efficiency of nutrient utilization or rates of deposition unless reliable equations are developed to describe body composition across life stages.

It has been shown that feed evaluation systems and animal growth models based on bioenergetics have major limitations (Birkett & de Lange 2001a; Bajer, Whitlette & Hayward 2004; Dijkstra, Kebreab, Mills, Pellikaan, López, Bannink & France 2007). Feed evaluation systems cannot rely on bioenergetics exclusively and have to consider dietary proteins and other nutrients, especially with fish that rely heavily on proteins to meet their metabolic needs. Moreover, digestible proteins, along with dietary amino acids, affect feed efficiency and nitrogen retention efficiency significantly (Azevedo, Leeson, Cho & Bureau 2004a; Encarnação, de Lange, Rodehutscord, Hoehler, Bureau & Bureau 2004; Booth, Allan & Anderson 2007). The effect of protein intake, and not only energy, on fish growth performance was soon acknowledged and included in models to estimate feed requirements, weight gain, and efficiency of energy and protein retention of African catfish (Machiels & Henken 1986), tilapia (van Dam & De Vries 1995), carp (Schwarz & Kirchgesner 1995), European sea bass (Lupatsch, Kissil & Sklan 2001, Lupatsch et al. 2003), gilt-head sea bream and white grouper (Lupatsch et al. 2003; Lupatsch & Kissil 2005).

Although the factorial approach assumes that energetic costs of metabolic processes are additive, evidence suggests that energy is allocated in a compensatory fashion, i.e. according to the metabolic scope of the animal at a particular life stage (Wieser 1989; Rombough 1994). This particularity may explain why the concept of energy requirement for maintenance remains debatable and is affected by body composition and other factors such as ambient temperature and breed (e.g. Close, Mount & Brown 1978; ARC 1981; Thompson, Meiske, Goodrich, Rust & Byers 1983; Campbell, Crim, Young & Evans 1994; Knap 2000). For instance, models based on bioenergetic principles assume that growth and feed efficiency will be nil when animals are fed a maintenance ration (recovered energy = 0). This assumption has been proven inaccurate in fish, as well as in other animals, where positive weight gain was still observed even though animals were fed at or below a maintenance ration and the whole-body energy balance was negative (Huisman 1976; Le Dividich, Vermorel, Noblet, Bouvier & Aumaitre 1980; Meyer-Burgdorff, Osman & Günther 1989; Lupatsch, Kissil & Sklan 2001; Bureau, Hua & Cho 2006).

Bioenergetic models have also been used to estimate feed requirements of fish and waste outputs from fish culture operations (Winberg 1956; NRC 1993; Cho & Bureau 1998; Lupatsch & Kissil 1998, 2005). Assessing waste outputs requires good estimates of body composition in order to compute, for example, nitrogen and phosphorus discharge into the environment.

**Nutrient-based models**

Historically, animal nutritionists first considered nutrients (i.e. chemicals and macromolecules that provide essential nourishment for maintenance, growth and reproduction) rather than energy to study the conversion of feed to biomass (for a review, see Dumas et al. 2008). Chemical (water, nitrogen, fat, minerals and carbon) and physical (bone, muscle, adipose tissue, blood, skin, hair and offal) composi-
tions of carcass and chemical composition of feed-stuffs were estimated for farm animals before the 20th century (Wolff 1895). Wolff (1895) appears to be the first to adopt a factorial approach to describe relatively and in detail the fate of dietary nitrogen, carbon and fat with consideration of intake, losses through faeces and urine, and recovery as body fat and body flesh in the carcass.

In view of the limitations of bioenergetics, animal nutritionists and growth modellers have returned to more nutrient- or biochemical-oriented approaches (e.g. Machiels & Henken 1986; Gerrits, Dijkstra & France 1997; Birkett & de Lange 2001b). These nutrient-based models may be defined as mechanistic systems designed to simulate the fate of dietary nutrients, with consideration of utilization of amino acids, fatty acids and their precursors. Similar to bioenergetics, nutrient-based models serve to predict growth, nutrient requirements and waste outputs.

Figure 5 Example of a factorial framework of nutrient partitioning (adapted from Blaxter & Mitchell 1948; Birkett & de Lange 2001a). Flow of nutrients through each metabolic process (intake, faecal and urinary excretion, anabolism and catabolism, basal metabolism and production) is determined mostly using regression and mass balance equations.

Figure 6 Example of a simple compartmental framework of nutrient partitioning (adapted from Gill et al. 1989). Flow of nutrients between each pool (amino acids, fatty acids, protein and lipid in the viscera and dressed carcass) is determined using differential and stoichiometric equations.

However, these models further explain the processing of nutrients by considering intermediary metabolism and are therefore more mechanistic. Bioenergetic models are mostly descriptive, rely on a rather simple framework of energy transaction, represent energy using units of joules or calories and overlook the stoichiometry of energy-yielding nutrients. Nutrient-based models are more explanatory, rely on metabolic pathways of nutrients, represent energy in terms of ATP (e.g. mol ATP per molecule substrate), and consider the stoichiometry of chemical reactions. These nutrient-based models have been shown to be effective for mammals and fish (e.g. Gill, Thornley, Black, Oldham & Beever 1984; van Dam & De Vries 1995).

Partitioning of nutrients can follow either a factorial or a compartmental scheme. Figures 5 and 6 illustrate and contrast the factorial and compartmental approaches respectively. The former approach is consistent with conventional bioenergetic models and adheres to the same assumptions (e.g. energy is allocated according to a hierarchy, metabolic processes are additive). The latter was introduced in the 1950s into animal nutrition by Blaxter, Graham and Wainman (1956)—these authors did not nominate it as compartmental or mechanistic modelling, though—and consists of subdividing a given level of organization (e.g. whole animal, tissue, cell) into different pools (e.g. amino acids in the blood, intracellular glucose) (Thornley & France 2007).

Pools are referred to as state variables (i.e. a quantity that defines the size of the pool at a given point in time) and can be in steady state (e.g. blood glucose in a fasting animal) or non-steady state (e.g. muscle protein content in a growing animal). Flows of substrates (e.g. lysine and other metabolites) between pools and into and out of the system are represented as terms within differential equations, which are usually...
based on rules of stoichiometry and saturation kinetics. Unlike equations based on regression analysis, differential equations suit the mathematical description of dynamic systems better because they can exhibit a wide array of behaviour (May 1976; Dijkstra & France 1995).

The compartmental approach overcomes, to a certain extent, the lack of flexibility and theoretical basis associated with the underlying assumptions of the factorial approach (AFRC 1991; Beever, France & Alderman 2000), but may require comprehensive datasets. Compartmental models for animals have been designed for a wide range of purposes (e.g. to predict feed intake, digestion rate, growth) since 1980 (Maës & Henken 1986; Imamidoost & Cant 2005; Bar, Sigholt, Shearer & Krogdahl 2007).

In nutrient-based models, growth results from accretion of chemicals (mostly water, protein, lipid and ash), not energy as assumed fundamentally in bioenergetic models. Therefore, the accuracy of these models depends on consistent mathematical description of the relationships between nutrient deposition and weight gain.

Modelling body composition and rates of nutrient deposition in farm animals

The reliability of bioenergetic and nutrient-based models depends to a considerable extent on valid estimates of nutrient deposition rates. Moreover, the search for optimal nutrient conversion into biomass and maximum profits, as well as concerns regarding product quality (e.g. fatness, fatty acid composition and bio-accumulation of various constituents) and environmental sustainability are strong motives for modelling body composition and nutrient deposition in farm animals.

Numerous data exist on body composition of various fish species, especially rainbow trout, European sea bass and white grouper (e.g. Reinitz 1983; Lupatsch, Kissil & Sklan 2001; Lupatsch & Kissil 2005). From these studies, it can be concluded that whole-body protein contents are comparable between species and constant across the grow-out phase, and the contents of moisture, lipid, ash and energy vary in a similar pattern among species as fish size increases (cf. Lupatsch, Kissil & Sklan 2001; Bureau et al. 2002).

In the past, boundaries or limits to contents of body water (BH2O), body protein (BP), body lipid (BL) and body ash (BA) in fish have not been determined from large datasets (cf. Shearer 1994; Jobling 2001; Lupatsch, Kissil & Sklan 2001; Bureau et al. 2002). Recently, Dumas, de Lange et al. (2007) developed equations to predict body composition in rainbow trout using data from 66 studies. These equations account for the variation in body composition, represent possible benchmarks for future comparison and provide reliable foundations for assessment of the effects of different factors on the composition of growth in fish.

Estimating body composition and rates of nutrient deposition using regression analysis

Mathematical description of body composition in animal nutrition started > 60 years ago. McMeekan (1941) stressed the importance of assessing meat quality in animal production and addressing requirements of specific markets. The author recognized the technical difficulty, high cost and time requirement associated with chemical analysis and insisted on the need to develop indices of composition, i.e. mathematical equations. McMeekan (1941) proposed linear regression equations to predict contents of not only body fat but also muscle and bones in bacon pigs. Equations were of the form

\[ y_i = \beta_0 + \beta_1 x_i \]

where \( y_i \) is the \( i \)th fitted value of the outcome (i.e. skeleton, muscle or fat) in units of g, \( \beta_0 \) is the intercept, \( \beta_1 \) is the slope and \( x_i \) is the \( i \)th value of a given predictor (e.g. length of carcass). McMeekan (1941) overlooked the effect of body weight on carcass composition. Moreover, he did not describe body composition with equations of allometric form \( (y_i = 10^{b_0} \times x_i^{b_1}) \) even though, in his days, the concept of allometry was commonly applied in biology to designate rate of change between different anatomical characteristics of an organism (for a review, see Gayon 2000). Furthermore, the allometric equation had already been used in animal production to examine the rate of fat deposition in different body parts of poultry (Lerner 1939). Almost 30 years later, Kotarbiński (1969) related body protein to fat-free lean mass and body water to body protein using linear regressions of allometric form. She also related body ash to body protein assuming an isometric rather than an allometric relationship. These isometric and allometric relationships based on regression analysis still prevail in estimating body composition of farmed animals, including fish (Parker & Vanstone 1966; Groves 1970; ARC 1981; Weatherley & Gill 1983; de Lange, Morel & Birkett 2003; Dumas, de Lange et al. 2007).
Rates of nutrient deposition have been a topic of interest and have found several applications in animal nutrition for the last 40 years (Osilage & Fliegel 1965; Thorbek 1969). Assessing rates of nutrient deposition, mostly protein deposition (PD) and lipid deposition (LD) represents a comprehensive way of examining efficiency of utilization of feed components for growth, and effects of genetics, nutrition and environment on composition of the growth response and dietary requirements (Black, Davies, Bray, Giles & Chapple 1995; Schinckel & de Lange 1996). Because growth and PD are associated, the amino acid profile in PD can serve in approximating amino acid requirements of growing animals (e.g. Möhn & de Lange 1998).

In fish, description of the nutrient deposition rate has received little attention to date, despite its simplicity, relevance and acceptance in modelling growth of livestock species over the past three decades (ARC 1981; Black et al. 1995; NRC 1996, 1998). To our knowledge, the concept of nutrient deposition rate was introduced recently into the fish literature and consisted of describing rates of PD, LD and ash deposition on a degree-day basis in rainbow trout across life stages (Dumas, de Lange et al. 2007). Such quantitative description still needs to be extended to other strains and fish species.

Estimating nutrient deposition using explicit partitioning rules

Partitioning rules attempt to represent the utilization of dietary nutrients or energy for protein relative to LD and have often served as a means to adjust for body composition, especially in pig nutrition. Partitioning rules and their associated partitioning factors figure among the debatable parameters in nutrition modelling, and the reader is referred to reviews by de Lange, Morel and Birkett (2008), Sandberg, Emmans and Kyriazakis (2005a, b) and Emmans and Kyriazakis (1997) for more details. The present section describes the partitioning rules encountered in fish nutrition models.

Rule 1: Body composition regulates dietary nutrient partitioning

The first rule assumes that growing animals regulate the breakdown of protein and lipid according to their current and/or target body lipid to body protein ratio (BL:BP). Machiels and Henken (1986) introduced this rule into fish nutrition. Preferential body lipid to body protein ratio (prefBL:BP), minimum value for this ratio (minBL:BP) and mature lipid weight to mature protein weight (mBL:mBP) are variations of the BL:BP ratio that have been proposed over the last 15 years (Whittemore 1995; Emmans & Kyriazakis 1999).

Whittemore (1995) estimated the minBL:BP for pigs to be 0.5:1. In a study conducted by Reinitz (1983), the BL:BP ratio for juvenile rainbow trout stabilized at 0.1:1 during 84 to 140 days of starvation (fish were still alive). This value may be considered as the minBL:BP ratio for that species at that size (< 10 g).

The BL:BP ratio has been arbitrarily set as a parameter in order to avoid unrealistic prediction of body composition (Machiels & Henken 1986). Although these authors did not further justify their concept, the BL:BP ratio finds biological support. Indeed, the correction in body composition that occurs during compensatory growth lends credence to the concept. For instance, Kyriazakis and Emmans (1992) showed that farm animals following a period of nutritional limitation seek to correct their body composition in order to return to the normal or preferential body composition needed to achieve their growth target.

The fraction of energy requirements that is supplied by oxidation of body fat increases non-linearly as the BL:BP ratio becomes higher (Machiels & Henken 1986). Neither Machiels and Henken (1986) nor Kyriazakis and Emmans (1992) proposed an equation to describe this non-linear relationship explicitly.

Despite some biological support, the concept remains highly empirical and its purpose appears more to accommodate the prediction of body composition than to describe the real metabolic processes (Sandberg et al. 2005a). Intake of dietary energy and digestible amino acids, and not only target BL:BP ratio at a given body weight, affects the partitioning of energy between PD and LD in growing animals (Emmans & Kyriazakis 1997; Encarnação et al. 2004; Weis, Birkett, Morel & de Lange 2004). Finally, variations in photoperiod and temperature are other factors likely to affect the BL:BP ratio in fish (e.g. Brown 1957; Jobling 2001; Hemre & Sandnes 2008).

Rule 2: Protein intake regulates dietary nutrient partitioning

Starting with Machiels and Henken (1986), van Dam and De Vries (1995) moved away from the constraint on BL:BP ratio. They related the proportion of energy
obtained from oxidation of body fat (or body protein) to protein-feeding level rather than the BL:BP ratio. They did not measure oxidation of body constituents per se, but rather estimated it using a calibration procedure. Their results indicated a positive relationship between body protein oxidation and both dietary protein intake and the protein to gross energy (P:GE) ratio of the diet. These observations are in agreement with other studies on fish (Halver & Hardy 2002; Azevedo et al. 2004a). Their concept, namely AALIRAT (i.e. auxiliary variable determining the proportion of ATP requirement provided by oxidation of body fat), has the advantage of representing the efficiency of protein use and the protein-sparing effect of extra energy.

The models proposed by Machiels and Henken (1986) and van Dam and De Vries (1995) estimated fat deposition poorly, indicating that nutrient partitioning is not just a matter of BL:BP ratio or level of dietary protein intake. These discrepancies result to some extent from inaccurate assumptions regarding the energetic costs of metabolic transactions. Both models set a fixed value for ATP requirement for protein synthesis [0.06 and 0.075 mol ATP g^{-1} protein synthesized in Machiels and Henken (1986) and van Dam and De Vries (1995) respectively], but this energetic cost seems to be rather variable across studies (Jobling 1985; Rombough 1994).

Machiels and Henken (1986), along with van Dam and De Vries (1995), assumed that no dietary nutrients were oxidized to support energy requirements for maintenance and growth, an assumption that has been proven inaccurate in mammals and fish (Lyndsay 1976; Kim, Grimshaw, Kayes & Amundson 1992; Stoll, Burrin, Jahoor, Henry, Yu & Reeds 1998; Halver & Hardy 2002). The models of Machiels and Henken (1986) and van Dam and De Vries (1995) recognized the existence of amino acid and glucose blood pools (cf. their flow diagrams). However, no attempt was made to describe these pools mathematically because they were not considered a source of ATP.

Rule 3: Biochemical saturation kinetics regulates dietary nutrient partitioning

The saturation kinetic approach is used in compartmental modelling and utilizes enzyme-kinetic equations such as the Michaelis–Menton and the Hill (e.g. Gill et al. 1984; Pettigrew, Gill, France & Close 1992; Bar et al. 2007). Flows of biochemical entities (e.g. amino acids, fatty acids, glucose, volatile fatty acids and acetyl-CoA) are regulated by their respective concentration in pools and by various constants (e.g. maximum velocity and substrate affinity). The constraints on nutrient partitioning no longer refer directly to explicit fixed ratios (e.g. minBL:BP). Certain biochemical transactions can exert control over others and kinetic constants such as maximum velocity (V_{max}) can serve to achieve a realistic body composition (Halas, Dijkstra, Babinszky, Versteegen & Gerrits 2004). Nevertheless, this approach can fail to represent accurately observed empirical relationships. For instance, the predicted relationships between energy intake and PD displayed a curvilinear shape, whereas observed data followed a linear pattern in evaluating a model designed to partition dietary nutrients in growing pigs (Halas et al. 2004). Assumptions are sometimes made in models based on saturation kinetics that basically mask a lack of precise knowledge and may lead to discrepancies.

A global and fresh perspective on describing composition of fish growth

Describing body composition and effects of nutrient deposition on weight gain is crucial in animal nutrition modelling (NRC 1998; Kyriazakis 1999; de Lange et al. 2003). Partitioning of nutrients in models based on energy and nutrient metabolism needs to rely on equations that reflect accurately the limits or boundaries to body nutrient contents in fish (From & Rasmussen 1984; Lupatsch, Kissil & Sklan 2001; Bureau et al. 2002). Assuming the allocation of dietary nutrients responds to an organized biological scheme, various deterministic equations can therefore be developed to describe body composition and deposition of body constituents (e.g. protein, lipid, water, ash and, eventually, amino acids and fatty acids).

The dependence of bioenergetic growth models on accurate estimation of body composition has been stressed in several fish studies (Cui & Wootton 1988; From & Rasmussen 1989; Jobling 1994; Cui & Xie 2000). To date, several bioenergetic models have assumed a constant energy content per unit of fish biomass or energy retention per unit of time (Winberg 1956; Solomon & Brafield 1972; Elliott 1976a; Kitchell et al. 1977; Brett 1995). However, body lipid has been shown to vary with plane of nutrition and age or life stage in fish and unavoidably affects the energy content of the body (Weatherley & Gill 1987; Azevedo et al. 2004a; Azevedo, Leeson, Cho & Bureau 2004b).
Cui and Wootton (1989) observed that energy content of fish biomass was a major parameter affecting the accuracy of bioenergetic models, especially at low and high feeding levels. Quantitative description of body composition in growing fish and of feed utilization thus becomes essential if systematic errors in bioenergetic models are to be avoided.

The equations developed in Dumas, de Lange et al. (2007) addressed, to a certain extent, the need to consider the effect of body composition in bioenergetic models by indicating that body energy content as protein can be easily predicted whereas prediction of body energy as lipid requires further modelling studies. Moreover, it is easier and probably more accurate to predict BW from BP than from recovered energy. The results of Dumas, de Lange et al. (2007) provide realistic bounds for different body constituents that can help setting correct assumptions and accurate relationships in nutrient-based models.

In models based on nutrient partitioning, seemingly arbitrary rules founded on untested assumptions (Cui & Xie 2000) were set to avoid unrealistic estimates of body composition (see,”Estimating nutrient deposition using explicit partitioning rules”). Most nutrient-based models fail to define quantitatively what the realistic bounds are for different body constituents (e.g. BP). This has led to assumptions that can be misleading. For instance, van der Meer and van Dam (1998) applied a minimum BL content of 1% relative to BW, a value that is unlikely to occur in fed fish (restricted or not) weighing > 3 g (Phillips Jr, Livingston & Dumas 1960; Reinitz 1983).

Body protein in fish remains at a stringent constant fraction of BW across life stages (Groves 1970; Lupatsch et al. 2003; Dumas, de Lange et al. 2007). Regression analysis is therefore an appropriate tool to describe the relationship between BW and BP. Although BL and BA are highly correlated with BW, large variability across life stages suggests the need for more comprehensive models. Rates of PD and LD varied across life stages and higher values of PD and LD were observed in fish with faster growth rates (Dumas, de Lange et al. 2007). Dietary lipid intake promoted LD, but not PD, in certain studies on rainbow trout (Rasmussen, Ostenfeld & McLean 2000; Gélineau, Bollet, Corraze & Boujard 2002; Chaiyapechara, Casten, Hardy & Dong 2003). Therefore, genotype, life stage and life history and feeding regime (diet composition and ration) stand out as explanatory variables to be included in future mechanistic models to predict better the composition of biomass gain.

Relationships between body constituents and BW across life stages of fish differ from that of other farm animals. In contrast to beef cattle and pigs, BP is highly and linearly associated with BW even beyond market size (cf. Dumas, de Lange et al. 2007 with Black, Cambel, Williams, James & Davies 1986 and NRC 1996). Similarly, BL and BH₂O contents appear more linearly related to BW in fish than in other livestock species (Black et al. 1986; NRC 1996). Percentage of dressed carcass of fish is, similar to ducks and small game birds, relatively constant, whereas it increases with BW up to market size in other animals such as pigs, broiler chickens and turkeys (Black et al. 1986; Swatland 1994; Landgraf, Susanbeth, Knap, Looft, Plastow, Kalm & Roehe 2006; Dumas, de Lange et al. 2007). Unlike other livestock species (e.g. NRC 1998), the relationship between daily PD and BW in fish displays a pattern with no negative slope in older animals (Dumas, de Lange et al. 2007).

In contrast to contemporary perceptions (Elliott 1976b; Shearer 1994), evidence suggests that BP varies isometrically with BW (i.e. assumes the same rate of change between absolute BP content and BW) in fish (Dumas, de Lange et al. 2007).

Concluding remarks: towards mechanistic modelling of fish growth

Variations in growth trajectory, body composition and rates of nutrient deposition are, to date, better described than explained, although certain hypotheses have been suggested. Explanatory studies are therefore required to further improve our understanding of the underlying mechanisms responsible for these variations.

Sexual maturation stands out as a mechanism likely governing growth trajectory and thus rates of nutrient deposition. Triggering the maturation process in salmonids involves a reduction or cessation of feed intake, deterioration of flesh quality, development of large gonads and secondary sexual characters, and greater catabolism of body protein and body lipid stores to supply nutrients for new tissue synthesis (Love 1980; Sargent, Tocher & Bell 2002; Roth, Dorenfeld Jenssen, Magne Jonassen, Foss & Imsland 2007). Ageing entails a decrease in the efficiency of nutrient utilization in mammals and fish (Brody 1945; Weatherley & Gill 1987).

It is not yet clear as to what the determinants of sexual maturation in fish are. It appears that environmental conditions at embryonic and larval stages,
along with genetics, interact to program the growth trajectory and the age at sexual maturity throughout the ontogeny of rainbow trout. The effect of incubation temperature on growth rate could affect the timing of sexual maturity ultimately. Evidence suggests that temperature during egg incubation could be responsible for muscle growth dynamics before the first spawning in fish (Johnston, Manthri, Alderson, Smart, Campbell, Nickell, Robertson, Paxton & Burt 2003; Albokhadaim, Hammond, Ashton, Simbi, Bayol, Farrington & Stickland 2007; Martell & Kiefer 2003; Albokhadaim, Hammond, Ashton, Simbi, Bayol, Farrington & Stickland 2007; Martell & Kiefer 2003). Intermediate temperature during incubation promotes hyperplasia and thus growth rate at the juvenile stage (Fauconneau & Paboeuf 2001; Rowlerson & Veggetti 2001; Steinbacher, Haslett, Obermayer, Marschallinger, Bauer, Sänger & Stoiber 2007).

Body lipid stores are possibly another determinant of the onset of sexual maturation. Feeding level and energy intake, which are known to govern the energy stores (i.e. body lipid content) in fish (Azevedo et al. 1998; Rasmussen & Ostenfeld 2000; Yamamoto, Shima, Furuita & Suzuki 2002), may induce or delay the timing of sexual maturation because lipid reserves have been shown to influence maturation in fish (Rowe, Thorpe & Shanks 1991; Silverstein, Shearer, Dickhoff & Plisetskaya 1998). In contrast, other studies concluded that growth rate has a greater role in triggering the maturation process than body lipid stores (Shearer, Parkins, Gadberry, Beckman & Swanson 2006; Beckman, Gadberry, Parkins, Cooper & Arkush 2007). Here, the effect of growth rate and nutrition may have been confounded and new studies are thus required to elucidate the answer to this question.

To sum up, current understanding of causality and relationships between environmental conditions during egg incubation, muscle growth dynamics, plane of nutrition, growth rate and timing of sexual maturation is fragmentary and has not yet been well described quantitatively. These factors affect growth trajectory, body composition and nutrient deposition in fish and will have to be described better in order to develop meaningful mathematical models.

To conclude, there is a need to synthesize available information and develop flexible explanatory models. Mechanistic models designed to simulate different scenarios are crucial to progress towards optimization of feed efficiency and growth, reduction of waste outputs, prevention of sexual maturation and, therefore, deterioration of growth rate and flesh quality before fish reach market size in order to avoid a decline in profitability of fish culture operations. Moreover, future models should be developed to accommodate changes in outcomes of interest to the private sector. More than 60 years ago, animal growth stood as the main concern (Robertson 1923; Wright 1926; Brody 1945). Models were thus developed or adapted to predict weight gain with respect to time. Nowadays, the composition of weight gain, yield of particular anatomical parts and food safety represent new topics of interest to the animal production industry because of the continually evolving eating habits of consumers and increasing public awareness of healthiness and environmental sustainability (Young, Northcutt, Buhr, Lyon & Ware 2001; Hocquette et al. 2005; Torstensen, Bell, Roselund, Hendersen, Graff, Tocher, Lie & Sargent 2005; Caswell 2006). Here, mathematical modelling serves as a useful tool to meet current and prospective challenges, extract further information and help orient future research programmes in fish nutrition.

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