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Fish Growth

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Introduction

The more than 3 m long ocean sunfish *Mola mola* develops from an egg that is about a millimeter in diameter. The anadromous brown trout *Salmo trutta* often hatches in a small stream in the midst of a forest, migrates after one or more years into the sea for foraging, and eventually returns as an adult to the natal stream for spawning. As fish grow through their life, they often occupy different habitats, are threatened by different predators, and rely on different food resources. Understanding how these complexities shape life-time patterns of animal growth is a large and active field of research. In this article, we examine one component of this research by reviewing the most common mathematical models that have been used to describe and interpret the growth of fish. These models have been developed for several purposes, including identifying and comprehending the causes of individual variability, to predict consequences for fisheries yield, and to improve production in fish farming.

Experimental studies and descriptive field-based research have provided valuable insight that has increased our knowledge of fish growth in both the laboratory and the wild. Modeling fish growth is a worthy endeavor because it allows us to better understand the mechanisms underlying how and why a fish grows; it provides a means of calculating parameters that can be readily compared across populations, and we can use these growth models as parts of larger, more comprehensive models to study trophic interactions or ecosystem dynamics. However, modeling has the most to offer when used in conjunction with experiments and field work. In a cyclic manner, models can generate hypotheses for experiments, and experiments can test model assumptions and predictions.

This article only considers models for individual fish growth. Models are also used for describing the growth of an entire fish stock in biomass or abundance, for example, logistic models with exponential population growth limited by a carrying capacity such as in Lotka–Volterra models (see Fishery Models and Growth Models). Such population models underlie general concepts in fisheries science (e.g., the maximum sustainable yield) and are still used in the assessment and management of fish stocks. They do not, however, contain information about individual size, which is a drawback since survival probability and reproductive rates often change as an individual grows. As a consequence, the distribution of individual body sizes in the population will influence population dynamics and the population's overall growth rate. These effects become particularly strong in long-lived species. More recent approaches therefore combine individual growth models of the type described in this article with size-specific rates for survival and reproduction to

model population dynamics. With information about size distribution or abundance, one can thereafter scale predictions for individual growth trajectories up to the whole population. This process can result in more accurate estimates of population abundance and biomass, and also offer advantages for research, for example, in population dynamics, ecological interactions, and life-history theory (see Life-History Patterns). Scaling up can be done using cohorts that consist of identical fish with average parameter values. In reality, however, a parameter value such as mean growth rate emerges from individuals that have different physiological growth capacities and experience different environmental conditions. Both these types of variances can be included by modeling the population as a collection of individuals. The individual-based approach is more computer intensive, and offers advantages where individual differences and environmental variation are important components of population dynamics.

Processes of Fish Growth

Metabolism and Scaling

Two important processes for growth are anabolism (building molecules and new tissue) and catabolism (breaking down of molecules and old tissue). Together with the biochemical processes required for maintenance of the body, locomotion, and other activities, these processes are collectively termed metabolism. Across different taxa, metabolic processes often scale as power laws of body size. For example, standard metabolic rate B (energy consumption; measured in watts) is proportional to a power function of body mass W (kg) as

$$B = B_0 W^{0.71} \qquad [1]$$

Such scaling relationships, also called allometric relationships, are convenient mathematical properties that underlie most models of fish growth. The proportionality coefficient B_0 varies, most importantly in relation to temperature such that organisms with higher body temperatures have higher metabolic rates. There is usually variation in the exponent depending on species or taxonomical group; the value of 0.71 in eqn [1] applies when one includes all animals, plants, and unicellular organisms for which temperature-corrected measurements of metabolic rate exist.

Fish Are Often Indeterminate Growers

Unlike most mammals, birds, and insects, fish often continue to grow after they reach sexual maturity. Although growth typically slows down just before sexual maturation as resources are channeled to gonads and reproduction, it can still continue for quite some time after maturation. This is called indeterminate growth, in contrast to determinate growth where any increase in body size ceases after maturation. In order for a model to describe growth in fish, it should therefore permit growth to be indeterminate, and it should model growth during the entire life span of the fish, not only during the juvenile and immature phases.

Basic Growth Models

Fish growth models can be divided into two categories. The first category includes statistically based models for fish growth. The models of this type often assume that growth is a function of the current body size of the individual, and they ignore or have only a loose connection to the biology behind the actual growth processes. A handful of different statistical models are available that fit empirical data quite well: for example, the Logistic, Gompertz, Monomolecular, and Richards growth models (Table 1). As discussed later, most uses of the von Bertalanffy growth model should also be classified as statistically based. In some applications, correlations with quantifiable physical or biological variables, such as temperature or food availability, may be built into parameters of the statistically based models.

The second category is mechanistically based growth models, derived from the biological processes that govern growth. Most often they include considerations about bioenergetics (the acquisition of energy and its use for all the processes that are underway in an organism) and how these scale with body size. These models may refer explicitly to processes that rely on temperature, body size, or food availability, and can thus be predictive and more nuanced than the statistical growth models. Mechanistically based models also have the advantage that as we learn more about the physiological and ecological processes, in general or for a particular species, this

Table 1 Statistically based models for fish growth

Growth model	Growth function $f(W)$	How is growth rate related to weight?
Logistic	$K(1 - W/W_\infty)$	Growth rate linear function of W
Gompertz	$K(\ln W_\infty - \ln W)$	Growth rate linear function of $\ln W$
Monomolecular	$K[(W_\infty/W) - 1]$	Growth rate rectangular hyperbolic function of W
Richards	$[1 - (W/W_\infty)^n]k/n$	Growth rate linear function of W^n

Growth is a function of body weight (W); k, n, and W_∞ are constants.
From Wootton RJ (ed.) (1998) *Ecology of Teleost Fishes*, 2nd edn., table 6.2, p. 132. Dordrecht: Kluwer Academic Publishers.

knowledge can be built into the model to improve it. Although mechanistically based models are better for understanding and predicting growth, their use has been limited because they require more biological understanding and parameters that can be difficult to quantify. When the processes or parameters are uncertain, there may be good reasons to prefer a statistically based model.

The von Bertalanffy Growth Model

The classic among growth models for fish was derived by Ludwig von Bertalanffy and adapted to use in fisheries by Ray Beverton and Sidney Holt. The von Bertalanffy growth model incorporates indeterminate growth and fits well with observed data, both for individual growth trajectories and for population averages (**Figure 1**). Its mechanistic derivation assumes that the processes of anabolism and catabolism have different exponents in their scaling relationships. Anabolism, or the acquisition of resources, is assumed to be proportional to body surface and thus scales with $W^{2/3}$, whereas the catabolic costs of activity and maintenance are assumed proportional to body mass and scale as W^1. Denoting the proportionality coefficient for anabolism and catabolism a and c, respectively, the growth rate in mass can be expressed as

$$\frac{dW}{dt} = aW^{m_1} - cW^{m_2} \quad [2]$$

where the exponent for anabolism, $m_1, = 2/3$, and the exponent for catabolism, $m_2 = 1$, are as indicated above. The result is that as the individual grows larger, more and more of the available energy will be used for maintenance and growth will slow down and eventually stop. This

asymptotic body size is denoted W_∞ and L_∞ for weight and length, respectively.

For calculating the length L at a given time t, the above equation can be rearranged to obtain

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right) \quad [3]$$

or, for calculating the weight W at time t,

$$W_t = aW_\infty \left(1 - e^{-k(t-t_0)}\right)^b \quad [4]$$

where k is the growth coefficient and t_0 is the hypothetical age at which L (and thus W) equals zero, and b is the exponent of the age-length relationship $W = aL^b$. In **Figure 1**, the effects of different asymptotic lengths and growth coefficients on the resulting lifetime growth trajectories are illustrated. From these graphs it is easy to see the asymptotic nature of the von Bertalanffy growth curve: it approaches the asymptotic length L_∞ with a declining growth rate defined by k.

Critique of the von Bertalanffy model

Even though widely used and despite its simplicity and elegance, the von Bertalanffy growth model has drawbacks. First, the exponents that were used in the original derivation have later been shown to be wrong: both catabolism and anabolism scale with exponents in the range 0.7–0.8 in most fish species studied. Second, the mechanism that was used to explain the asymptotic body size in the von Bertalanffy derivation was that all the available energy was used for maintenance, leaving the fish with only enough energy to feed and digest but not to grow (or any other activity for that matter). By adopting the perspective of life-history theory, which dictates that
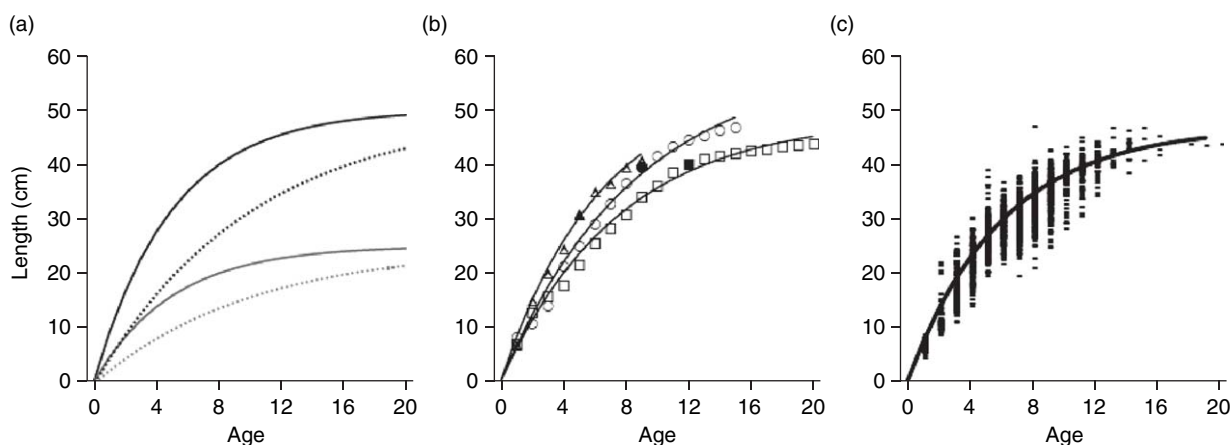
Figure 1   The von Bertalanffy growth model. (a) Examples of von Bertalanffy growth curves for different values of asymptotic length L_∞ (black lines: $L_\infty = 50$ cm; gray lines: $L_\infty = 25$ cm) and growth parameter k (solid lines: $k = 0.2$, dotted lines: $k = 0.1$). (b) Length-at-age for three different smallmouth bass *Micropterus dolomieu* individuals from Lake Opeongo, Canada. Filled symbols represent the observed age at first spawning and fits represent individual von Bertalanffy growth curves. (c) Observations of individual length-at-age across a population of smallmouth bass *M. dolomieu* from Lake Opeongo, Canada. The line is the fitted population-level von Bertalanffy growth curve.

the body is a tool for efficient reproduction, we can see that the fish should stop growing when it is most efficient at acquiring energy that can be used to produce offspring, that is, not when the difference between anabolism and catabolism is zero but when the difference is at its maximum. Third, the von Bertalanffy curve fits well for adult growth but represents juvenile growth less accurately. In the juvenile phase, individuals devote all available energy into growing somatic tissues – muscles, bones, and the like – and do not expend energy for producing reproductive material. Empirically, many studies suggest that length growth is linear prior to sexual maturation, and that growth decelerates when energy is used for gonad development and reproduction. This expected change in growth rate at maturation is not included in the von Bertalanffy growth curve.

In summary, although the von Bertalanffy growth model fits well with observations for fish after maturation, it does less well in describing immature fish growth, and the mechanisms that are underlying it have turned out to be false. Two newer models address these drawbacks and they will be explained in the following two sections: first, Derek Roff included the costs of maturation and derived a mechanistic growth model that is more consistent with fish physiology and empirical observations of gonad maturation; later, Nigel Lester and colleagues developed a mechanistic model similar to Roff's, resulting in a model that, during the postmaturation phase, is mathematically very similar to the von Bertalanffy model but with parameters that are biologically more meaningful.

Roff's Model

The Roff model is derived from a simple bioenergetics relationship. First, the total body mass W is divided into somatic mass M and gonads G, that is, $W = M + G$. Next, the available energy E (in mass equivalents) is assumed divided between the somatic mass and the gonads:

$$W_{t+1} = W_t + E_t - G_{t+1} \quad [5]$$

Here the time step t is the duration of one reproductive cycle, commonly 1 year for temperate species. By assuming $W \propto L^3$ and support from empirical data showing that length growth for immature fish is linear with an annual length increment of h_0 per time, length can be modeled for immature fish as

$$L_{t+1} = L_t + h_0 \quad [6]$$

and from maturation onwards,

$$L_{t+1} = \frac{L_t + h_0}{(1 + R_{t+1})^{\frac{1}{3}}} \quad [7]$$

Here R is the gonado-somatic index (GSI), equal to gonad mass divided by the somatic mass. Therefore, there is a
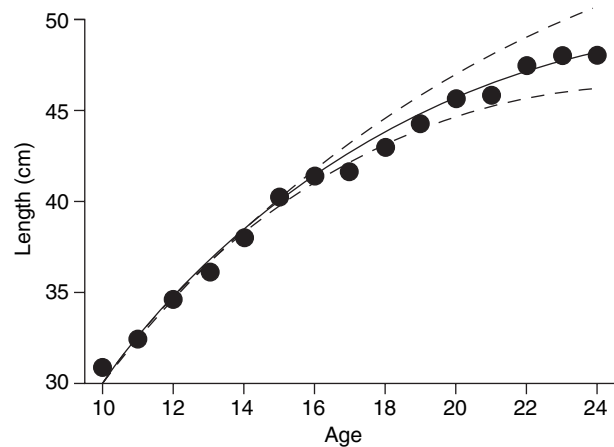
Figure 2 Observed length at age (●) of American plaice averaged over immature and mature individuals, and predicted growth curves according to the Roff model. The fitted curves all have growth rate (h in equations 6 and 7) of 2.28 cm yr^{-1}, and the GSI (R in eqn [7]) is 0.103 for the solid line fitting the observed pattern best, and 0.08 and 0.12 for the lower and upper dashed lines, respectively. The observed mean length at age t is calculated as: $\sum_{a=11}^{20} p_a L_{a,t}$, where p_a is the proportion maturing at age a (maturation is occurring over age classes 11–20) and L_a is the length at age t of fish that mature at age a. Adapted from Roff DA (1983) An allocation model of growth and reproduction in fish. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 1395–1404, figure 3.

direct tradeoff between investment into gonad tissue and body growth.

Although GSI could change with age or length, a constant GSI is often assumed in order to parametrize the growth model. Roff found relatively good agreement between predicted and actual size at age when assuming a constant GSI for American plaice *Hippoglossoides platessoides* (**Figure 2**).

The Roff model is based on more physiologically sound mechanisms than the von Bertalanffy model: namely, that after maturation, available energy should be allocated to reproduction as well as to growth. The parameters of the Roff model (i.e., growth rate, GSI, age at maturation) are also easier to measure and are easier to give a biological interpretation than the von Bertalanffy parameters. Related to this last point is that the GSI, growth rate, and age at maturation are fitness determining, genetically controlled life-history traits which makes the Roff model a good candidate also for addressing questions in life-history evolution.

Critique of the Roff model

Although the Roff growth model is based on more physiologically relevant mechanisms than the von Bertalanffy growth model, it has several simplifications that under some circumstances could be violated. First, Roff assumes that immature growth is linear rather than having this feature emerge from underlying mechanisms. Second,

although it is not necessary to always do so, the GSI is commonly assumed constant throughout life; this assumption allows a smooth growth curve to be drawn and facilitates parametrization. Third, the simple allometric relationships that are assumed (e.g., $W \propto L^3$) might not always hold.

Merging the von Bertalanffy and Roff Models

Nigel Lester, Brian Shuter, and Peter Abrams showed how the mechanisms of the Roff model can lead to the von Bertalanffy growth equation by making a few specific assumptions. Based on empirical evidence from fish, Lester *et al.* assume that the scaling exponents for anabolism and catabolism are the same, that is, $m_1 = m_2 = 2/3$. This leads to linear length growth prior to maturation. As mature fish grows, however, surplus energy, which is proportional to $W^{2/3}$, will increase, but not as much as the gonads, which are proportional to W^1. The model therefore predicts asymptotic growth after maturation because the proportion of available resources devoted to gonads and reproduction increases. The resultant postmaturation asymptotic growth curve now becomes

$$L_{t+1} = \frac{3}{3+R}(L_t + b_0) \qquad [8]$$

This postmaturation growth curve has the same shape as the von Bertalanffy growth curve, and the parameters of the von Bertalanffy model can therefore be expressed using the biological parameters of the Roff model:

$$L_\infty = \frac{3b_0}{R} \qquad [9]$$

$$k = \ln(1 + R/3) \qquad [10]$$

The re-parametrization allows fishery biologists to use familiar parameters to describe growth while at the same time giving those parameters more biological meaning than was available previously. This relationship only holds, however, when $m_1 = m_2 = 2/3$ and under isometric growth, that is, $W = bL^3$.

More Detailed Growth Models

Several models have delved more into the details of feeding or bioenergetics to predict growth in fish, and five additional modeling frameworks should be highlighted.

First, a group of researchers at the University of Wisconsin–Madison has produced a software package for modeling the bioenergetics and growth of fish (Fish Bioenergetics, now in its version 3.0). Their basic equation states that an individual's energy budget has to balance:

$$\text{Consumption} = \text{Metabolism} + \text{Wastes} + \text{Growth}$$

They then identify the following subcategories:

$$\text{Metabolism} = \text{Standard metabolism} + \text{Cost of activity} \\ + \text{Digestion}$$

$$\text{Wastes} = \text{Egestion} + \text{Excretion}$$

$$\text{Growth} = \text{Somatic growth} + \text{Gonad production}$$

Each process is thereafter explained in detail and equations are given for size and temperature dependence where necessary. They have also collected necessary parameters for ~30 species of marine and freshwater fishes.

Second, the research groups of Andre deRoos (University of Amsterdam, The Netherlands) and Lennart Persson (Umeå University, Sweden) have highlighted the ecological implications of size and growth in theory, modeling, experiments, and field work. Their models are called physiologically structured population models, and are based on a set of differential equations for feeding, including competition, mortality including cannibalism and starvation, and other relevant physiological processes. These models are more technical to implement because they involve frequency and density dependence, but in return, they predict a population's size structure and a rich array of ecological consequences.

Third, Bas Kooijman and colleagues (Vrije Universiteit Amsterdam, The Netherlands) have been developing the theory of dynamic energy budgets (DEB). DEB models are based on the division of an individual's energy into two compartments: structural body mass and reserves. As the individual forages, energy goes to the reserve from where it is distributed to other functions. The energy can be used, following simple mechanistic rules, for somatic maintenance, reproductive maintenance, and reproduction, or it can be used to increase the structural body mass. What makes DEB models dynamic is the fact that the energy allocation rules can change as an individual grows through life, reflecting the different phases of the life cycle. The theory covers all living organisms and provides explanations of how certain physiological traits are scaled with body size.

Fourth, William Neill and his research group at Texas A&M University have developed very detailed simulation software called Ecophys. Fish that predicts the growth of individual fish in a time-varying physical environment. Including factors such as temperature, salinity, oxygenation, and pH, their model quantifies bioenergetics, growth, and stress of individual fish. The model was applied operationally for estimating stocking densities of red drum, and is also in use for monitoring growth and welfare in aquaculture.

Fifth, the traits that govern the division of resources between growth on the one hand and maturation and reproduction on the other can be parametrized using life-history evolution. Several modeling tools are available, such as individual-based genetic-algorithm models or state-dependent optimization models, and they can be

combined with several of the growth models above to find adaptive life-history strategies. This approach has the advantage that it can predict how growth might change when the biotic or abiotic environment changes, for example, due to changes in predation, temperature, harvest, or other aspects of environment. The drawback with evolutionary models is that they often become vulnerable to the underlying assumptions, since they not only predict growth given empirical observations, but should in principle also predict the observed growth given the environmental and ecological forcing on the system.

Further Complexity

A central property of any model is its limitations and the parts of reality it has left out. Some of the more detailed models described above already incorporate some of this complexity, at the cost of being less general. This reflects an important challenge in modeling: that of choosing a model with the right balance between realism and complexity on the one hand, and tractability, transparency, and computing requirements on the other. The level of complexity also has to reflect the purpose of the modeling exercise. It is often difficult to see which elements a simple model has omitted, what the potential consequences are, and how this limits the assertions one can make based on a model. The following list, by no means intended to be complete, provides a brief discussion of some factors that further influence fish growth.

Physiological Tradeoffs

Deciding whether to invest energy into reproduction or growth is not the only tradeoff that fish face in their energy allocation. Under some circumstances, for example, under heavy size-selective predation, fish might increase their survival more by growing out of the size window of predation than by maintaining investments in the immune system. Fish can thus be thought of as taking a calculated risk by lowering their immune responses in order to grow faster, and although this increases the risk of infections, it may increase overall survival on a longer timescale. Similar physiologically driven tradeoffs exist for example between escapement capability and growth rate.

Behavioral Tradeoffs

There are also a number of behavioral tradeoffs that make fish compromise their growth rate. Under strong predation pressure, fish might spend more time hiding than foraging and consequently, growth rate will decrease. Similarly, fish may voluntarily abstain from foraging if food-mediated parasites compromised health, survival, or growth.

Density Dependence

Individuals do not live in isolation but are part of populations and communities. The resources in a given habitat have to be divided not only between individuals of the same species but also with species that have similar food preferences. Obviously, the amount of food available for an individual affects its growth rate. One can quantify density-dependent effects in a modification of the von Bertalanffy growth equation. The density-dependent asymptotic length $L_{\infty B}$ (note the index B to distinguish it from asymptotic length without the density effect) may be expressed as

$$L_{\infty B} = L_\infty - gB \qquad [11]$$

where g is a competition coefficient defining how strongly the asymptotic length decreases with increasing biomass B (**Figure 3**). In an analysis of fisheries data across different species, 9 out of 16 fish stocks examined showed density-dependent growth. Also, the effect of density dependence was stronger in unproductive areas that originally harbored low fish biomass compared to richer areas with denser fish populations.

Compensatory Growth

Food distribution in the wild is not only spatially but is also temporally patchy. As a consequence, fish might experience periods of low food availability and even starvation. When food availability reverts to normal levels, fish can exhibit faster growth rates than they would during steady resource conditions. In this way, individual fish are capable of restoring their original growth trajectories. This phenomenon is termed compensatory growth (note that density-dependent growth introduced in the previous paragraph has also been called compensatory growth by some authors). The advantages for such compensatory growth are speculated to be related to size-dependent mortality and fecundity, size-specific feeding competition, and food availability.

Environmental Variability

Many of the growth models above are designed for fisheries purposes and therefore, updated on a yearly basis to fit annual sampling programs. This ignores the effects of seasonality on growth and reproduction, which are pronounced in boreal and temporal ecosystems (e.g., because of temperature and light variation) and common even in tropical lakes and oceans (e.g., because of rainy seasons or lunar cycles).

Seasonality in growth arises through direct effects such as temperature limitation on physiological growth rates or

(a)

(b)
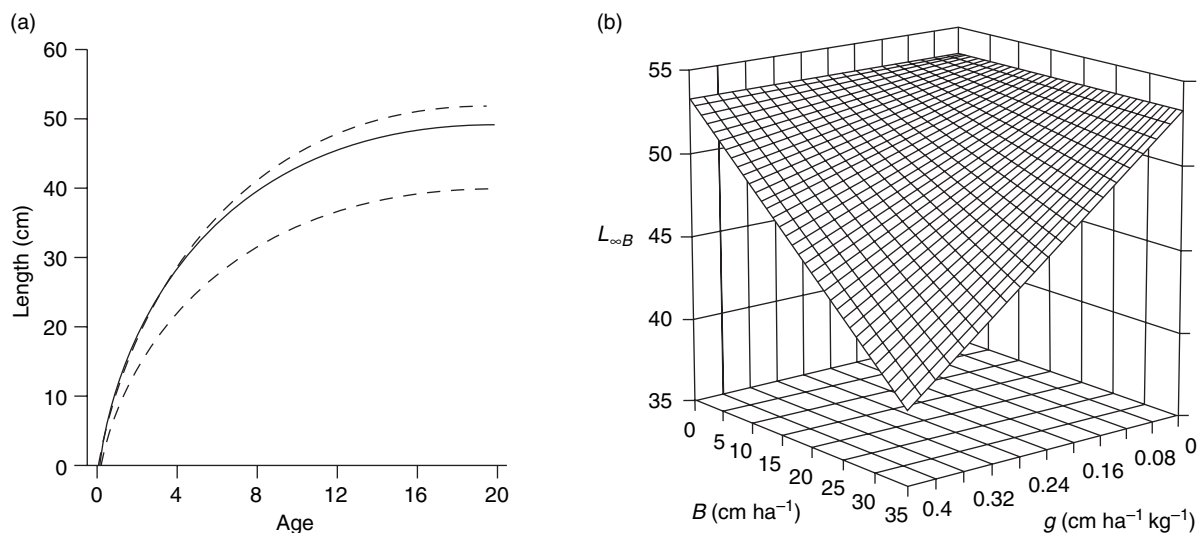
Figure 3 Density-dependent growth. (a) The effect of population density on growth of a freshwater salmonid *Coregonus hoyi* from Lake Michigan. This population was estimated to have $L_\infty = 53.3$ cm, $k = 0.21$, $g = 0.378$ cm kg^{-1} ha^{-1}, average biomass $B = 8.8$ kg ha^{-1} (solid line), lowest observed $B = 1$ kg ha^{-1} and highest observed $B = 33$ kg ha^{-1} (upper and lower dashed lines, respectively). (b) Increasing population density B and competition coefficient g decrease the asymptotic length $L_{\infty B}$.

productivity cycles in food resources, but also indirectly through establishing fixed points that the annual timing of events has to conform to. For instance, the match–mismatch hypothesis predicts particularly favorable temporal windows for the development of eggs and larvae, which in turn sets constraints for the phenology of migrations, spawning, and thereby also for growth. Such seasonality can be taken into account when modeling fish growth, but it requires shorter time intervals for updating the individual size and explicit modeling of the ecological factors that underlie seasonality.

Typically, physiological rates, such as growth rate, have an optimum for any given environmental variable, and if the level of the environmental variable is above or below this, the physiological rate slows down (**Figure 4**). This effect can be taken into account when modeling growth. For example, the von Bertalanffy growth equation (eqn [3]) can be modified to include the effect of environmental variability on growth. An environmental variable such as temperature, salinity, or oxygen saturation can be transformed to a coefficient X_E:

$$X_E = \frac{(E - E_{\min})(E - E_{\max})}{(E - E_{\min})(E - E_{\max}) - (E - E_{\text{opt}})^2} \quad [12]$$

where $E_{\min}$, $E_{\max}$, and E_{opt} are the minimum, maximum, and optimum environmental variables, respectively. The growth coefficient k from the von Bertalanffy growth equation can then be calculated by multiplying the growth coefficient in the optimal temperature k_{opt} with the environment coefficient:

$$k = k_{\text{opt}} X_E \quad [13]$$
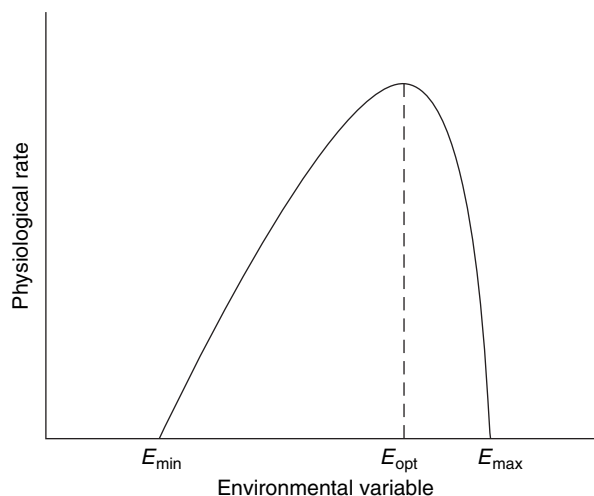
Figure 4 Relationship between an environmental variable E (e.g., temperature) and a physiological rate such as growth rate. Different physiological processes may have different optima, feeding, and digestion might, for example, have higher temperature optimum than metabolic rate or aerobic scope. Adapted from Mallet JP, Charles S, Persat H, and Auger P (1999) Growth modelling in accordance with daily water temperature in European grayling (*Thymallus thymallus* L.) *Canadian Journal of Fisheries and Aquatic Sciences* 56: 994–1000, figure 3.

The Role of Sex and Sexual Selection

Most mechanistically based growth models, including the Roff and Lester *et al.* models, describe the lifetime growth patterns of female fish. Models of male fish growth are more infrequent. For example, in the Roff and Lester *et al.*

models, reproductive investment is defined by the gonado-somatic index which measures investment in gonad tissue. This is thought to accurately depict the reproductive investment of females because most of their reproductive energy is allocated to development of ovaries, in contrast to males that often invest less energy in testes but more energy in reproductive behavior. Such reproductive activities include display, defending territories, competing for females, and guarding offspring. Most models have focused on female growth because it is easy to measure the mass of ovaries, whereas it can be difficult to quantify the energy expended on aggression or courtship behavior. The downside of focusing only on females is that many fish display sexual dimorphism in growth, and we are missing important information when not explicitly considering the growth and investment of males. It is likely that future models incorporating male reproductive investment and growth will reveal important insights into sexual selection in fish and its consequences for behavior, population dynamics, and fisheries yield.

A common assumption when using growth models in life-history theory is that larger size equates to higher fitness (see Fitness); this is true for females where fecundity is often limited by body size. When males are considered, however, this picture may change due to sexual selection and female choice. During the reproductive season, investments in secondary sexual characters, display behavior, territory defense, or aggression toward competitors may compromise growth but lead to increases in fitness through components that are not directly related to size.

Life-History Evolution

Studying life histories means paying attention to the great variety of reproductive strategies present in nature. Key life-history traits are the state-specific rates of survival, growth, and fecundity. The importance of growth in life-history evolution comes through the fact that bigger body size is associated with several fitness-related advantages, for example, higher fecundity, reduced predation, and higher success in parental care. At the same time, the models discussed above have shown us that growth requires resources that could have been spent on gonad production and reproduction. How can we then define what kind of life history an individual should follow? In principle, it is extremely simple: the life history that is most effective at spreading the genes for that life history will, with time, become dominant in the population.

If mortality is high there might not be any advantage for an individual to delay maturation – if it does delay it might suffer mortality before having a chance to reproduce. On the other hand, if an individual can increase its survival probability by growing larger and out of the preferred size range of its predators, then intensive growth and delayed maturation might be desirable. To test such hypotheses one often starts with a growth model of a type described above, and then changes individual life-history traits to investigate evolutionarily stable strategies under a given ecological setting.

Summary

Growth of fish is based on metabolic processes, most importantly anabolism (building molecules and new tissue) and catabolism (breaking down of molecules and old tissue). Modeling growth can be carried out on many different levels of detail. The simplest level is provided by statistical models such as Logistic, Gompertz, Monomolecular, and Richards growth models. Also, the widely used von Bertalanffy model can be classified as a statistically based growth model. More realism is achieved with mechanistically based growth models, where the actual processes underlying growth are modeled, often including bioenergetics. Mechanistically based models often allow growth to differ between the juvenile phase (in which length growth often approaches linearity) and the postmaturation phase (where growth slows down as energy is diverted into reproduction). Mechanistically based growth models thus link closely with the field of life-history evolution, as the dilemma of whether an individual should invest into growth or reproduction lies at the heart of life-history theory. A suite of environmental (e.g., temperature, seasonality, oxygenation) and ecological (e.g., density dependence, anti-predator behavior, sexual selection) factors affect growth and can in principle be modeled. Including more detail in a growth model can improve realism but comes at a cost, for example, in tractability, transparency, or computing time. Consequently, the merits and faults of each modeling approach need to be weighed carefully and the choice of model should depend on the research question at hand.

See also: Body Size, Energetics, and Evolution; Fisheries Management.

Further Reading

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Fish Health Index *See* Coastal and Estuarine Environments

Fisheries Management

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Introduction

The role of ecological models in fisheries science is primarily for stock assessment, and stock assessment is about making quantitative predictions about population change in response to alternative management choices. A stock assessment model is actually a collection of several submodels that deal with specific components of the entire system, and the level of complexity of each of these submodels can range from simple with very few unknown parameters to very complex with thousands of unknown parameters. Regardless of the level of complexity among competing models, there are three basic objectives that we hope to obtain in fisheries stock assessment:

1. Stock status: to specifically assess the current level of exploitation (the fraction of the total population that is being removed each year) and the current abundance relative to some management target.
2. Stock productivity: to specifically assess the shape of the underlying production function and the level of exploitation deemed sustainable. Also, to determine which harvest policies should be used to ensure sustainability.
3. Stock reconstruction: to specifically assess how the components of population change (recruitment, mortality, net migration) have varied over time, and whether or not these variations are related to fishing and/or environmental changes.

A typical modern-day stock assessment usually begins with the third objective in order to examine the first two objectives.

The basic structure for any assessment model requires at least five key components (**Figure 1**), and each of these components are linked such that a simple change in the data or assumption about the model structure could ultimately redefine the management objective. Overall, there are two key parameters of interest in fisheries stock assessment models: (1) a parameter that defines the overall population scale (i.e., how large is the population), and (2) a parameter that defines the underlying production function (i.e., the intrinsic rate of growth or how resilient the population is to disturbance). The interplay between these two parameters ultimately defines the suitable range of alternative harvest policies.

The essential components of a fisheries stock assessment model outlined in **Figure 1** will form the basic outline for this article. We will begin with a description of the types of data that are frequently encountered and used in fisheries stock assessment. Then we provide a few examples of the types of population dynamics models and error structures that are used to make inference about components of population change over time. Following this, we will discuss how the population models are used to generate predicted observations in order to proceed with the next step of the assessment − comparing