博士論文（要約）

A comprehensive life history model of aquatic organisms based on the allometric scaling law

（アロメトリースケーリング則にもとづく水圏生物の包括的な生活史モデルに関する研究）

Akihiro Manabe

真鍋　明弘

Introduction

Life history modeling is a fundamental approach to understand the life history of an organism through combinations of biological models. Life history models estimate, analyze, and predict the biological and ecological phenomena and thus, playing a vital role for stock assessment, fishery management, and conservation. Therefore, the validity of the models is fundamental to sustainable approaches toward ecosystem. However, the traditional approach to aquatic organisms treats each life history traits separately, not considering the mechanisms and trade-offs between each trait. On the other hand, owing to the wide variation in body size of aquatic organisms, body size plays a pivotal role on various biological and ecological phenomena in aquatic ecosystems. Allometric scaling law can be utilized to describe the life history of organisms continuously throughout the stages with different body size. With body size as an axiom, in the present study, a comprehensive life history model is derived and presented which satisfies the following requirements: (1) it is based on the biologically rational allometric size-scaling law, and (2) consists of explicit and straightforward functions with minimal parameters (3) to describe growth, reproduction, and survival process appropriately, (4) which are extendable to various forms in the presence of additional factors.

Growth-reproductive investment model

A pair of new growth and reproductive investment models for fish and aquatic organisms are derived considering an allocation of allometrically produced surplus energy between somatic growth and reproduction.

$$\text{Growth model} \quad w = \hat{w}\tau^{r}\left[1-\left[\max\left(0,1-(1-q)\frac{t-t_0}{\tau}\right)\right]^{\frac{1}{1-q}}\right]^{r}$$

Reproductive investment model $\frac{1}{w}\frac{dF}{dt} = r\left(\frac{w}{\hat{w}}\right)^{-\frac{1}{r}}\left[1-\left[1-\frac{1}{\tau}\left(\frac{w}{\hat{w}}\right)^{\frac{1}{r}}\right]^{q}\right]$

The novel growth function can describe growth trajectories from determinate to indeterminate growth by adjusting the value of the ‘growth indeterminacy exponent’ q. The timing of maturation and attainable body size can be adjusted by the ‘maturation timing parameter’ τ while maintaining a common growth trajectory before maturation. The present growth function is a comprehensive growth function in which exponentials in the traditional monomolecular, von Bertalanffy growth function (VBGF), Gompertz, logistic, and Richards functions are replaced with q-exponentials defined in the non-extensive Tsallis statistics; therefore the present growth function is named as “generalized-q VBGF."

The generalized q-VBGF is fitted to the length-at-age data of two species of fish (willowy flounder *Tanakius kitaharae*, Alaska pollock *Gadus chalcogrammus*), one invertebrate species (snow crab *Chionoecetes opilio*), and one marine mammal species (Antarctic minke whale *Balaenoptera bonaerensis*) to validate the performance using three fitting methods; standard, shared-parameter, and simultaneous fitting. In the standard fit, the performance of the generalized q-VBGF is fitted to male and female data of willowy flounder and Alaska pollock. The performance is compared using AIC and BIC against four traditional models (VBGF, Gompertz, logistic, Richards) and one model considering energy allocation (extended-VBGF). The performance of the generalized q-VBGF is found to be appropriate for two cases while in two other cases, extended-VBGF and Richards model are considered as the most appropriate for each case; however, with the small difference in BIC to Richards model for male Alaska pollock, the generalized q-VBGF is also found to be equivalently appropriate. In the shared parameter fit, the generalized q-VBGF appropriately describes the size difference between sexes of willowy flounder and Alaska pollock while sharing the growth in the immature stages between both sexes. For Antarctic minke whale and snow crab, the generalized q-VBGF appropriately describes the determinate growth of different year-classes of Antarctic minke whale and of groups with different terminal instars of snow crab while sharing the growth in the immature stages. In the simultaneous fit, the generalized q-VBGF estimates the somatic growth and the gonad weight of Alaska pollock simultaneously with a narrower confidence interval of each parameter. The estimated parameters suggest that the relationship between τ and rq can interpret various life history strategies and also suggest that $\tau * rq$ may act as a life history invariant.

Survival model

A new survival model is derived based on the biological mechanisms of natural mortality (predation) based on the allometric scaling law as:

$$N_t = N_0 \exp\left[-\nu \widehat{w}^{-\mu} \tau^{-\mu r} \int_0^t \left[1 - \left[\max\left(0, 1 - (1-q)\frac{s-t_0}{\tau}\right)\right]^{\frac{1}{1-q}}\right]^{-r} ds\right].$$

The allometric function of natural mortality coefficient $\left(\frac{1}{N}\frac{dN}{dt} = -\nu w^{-\mu}\right)$, which is the fundamental assumption of the survival model, is fitted to the actual natural mortality coefficient at weight data for justification. Fitting to the collected data from the published literature shows the relationship as $M = 6.213 w^{-0.376}$. Based on the present survival model, a new theoretical approach to estimate natural mortality coefficient based on the balance of biomass between the spawned eggs and adults, by taking gonado-somatic index into account.

Life history strategy analysis

The present growth, reproductive investment, and survival models are combined as a comprehensive life history model to analyze a life history strategy study by Katsukawa et al. (2002). The total expected fecundity of a population to evaluate the reproductive fitness is calculated as:

$$\text{Total expected fecundity} = \sum_{j=1}^{100} \log_{10} \int_0^{t_{max}} \left(\frac{dF}{dt}\right) S_j dt,$$

and the optimal strategy to maximize it is estimated for predictable and unpredictable environments. In predictable environments, determinate growth strategy is the optimal life history strategy owing to the bang-bang control of the surplus energy allocation which maximizes the fecundity per reproduction. In unpredictable environments, indeterminate growth is prominently selected as the optimal life history strategy when the stochasticity of environment $\sigma \geq 2.5$. The determinate growth with substantial energy allocation to reproductive investment before maturation $(q = 0.620 \sim 0.776)$ is selected as the optimal life history strategy when $1.7 \leq \sigma < 2.5$. The values of q and τ increase concurrently and the lifetime fecundity of a population decreases as σ increases. The increase in q allowed organisms to exhibit a risk-aversive strategy called ‘bet-hedging strategy’ by exhibiting continuous growth and multiple reproductions, which can abide the “bad” year and wait for the “good” year despite considerably less fecundity compared to organisms with a determinate growth strategy.

General Discussion

In the present study, a comprehensive life history model of aquatic organisms based on allometric size-scaling is derived and presented. The generalized q-VBGF describes the trajectories of both determinate and indeterminate growth species appropriately, and the simultaneous fitting with the reproductive investment provides an example of a more appropriate estimation of somatic growth and gonadal growth. The survival model is derived from the size-dependent natural mortality coefficient and the generalized q-VBGF to express the changing mortality with somatic growth. With common parameters on the growth-reproductive investment model and the survival model, the present life history model can estimate and analyze the life history of organisms in consideration of various trade-offs and applied to various traditional life history strategy hypotheses. Simple life history strategy models (r/K selection and fast-slow life history continuum) are expressed by the difference of τ and the three-end-point life history model by Winemiller and Rose (1992) is expressed by the combination of q, τ, and t_0.

The present life history model provides a comprehensive perspective regarding fishery management in consideration with various trade-offs and life history strategies. The increased accuracy on the estimation of growth, reproduction, and survival can improve the forecast of population dynamics of fishery stock and the effectiveness of fishery management. Also, the present life history model can qualify and quantify the parameters of different populations of the same species to compare and contrast the effect of the environment including fishing pressure on life history traits and evaluate the "healthiness" of populations.

Considering the current status of climate change and environmental variability, it is most likely to affect the life history of many aquatic organisms. With the present life history model, scientists can understand, analyze, and estimate the change in life history traits and strategy comprehensively to adjust the fishery management adaptively. Humankind, being responsible for preventing further extinction of species and devastation of aquatic ecosystems, needs to apply and enforce proper management and conserve fishery stocks and aquatic ecosystem. In order to enforce appropriate management considering the life history of fishery stocks, further application of the present comprehensive life history model incorporating allometric scaling law will be necessary by many scientists and researchers.