## 論文の内容の要旨

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論文題目 A size-structured matrix model to simulate dynamics of community size spectra in marine ecosystems

(海洋生態系における生物群集のサイズスペクトルの動態をシミュレートするサイズ 構成行列モデル)

A remarkable regularity of marine ecosystems is that a log–log plot of abundance against body mass over the range from bacteria to whales without accommodating species identity results in a linear size spectrum with a slope of approximately –1. Several types of size-based models have been developed to model the dynamics of size spectra of marine communities, in which larger individuals prey on smaller ones, and to investigate impacts of environmental changes or anthropogenic perturbation. However, these previous models are governed by continuous differential equations and therefore may not always be easy or convenient in practical applications. Nonlinear patterns of size spectra with cutoffs and/or waves are often observed in nature and predicted from the size-based models. Nevertheless, the determinants of these properties of size spectra are still poorly studied.

This study begins by developing a simple and easy-to-use size-structured matrix model to simulate dynamics of marine communities and reproduce their size spectra. Then, sensitivity test of the model was performed by manipulating its parameter values. Finally, determinant factors of slopes and nonlinear patterns of size spectra were elucidated based on biomass flows within the size spectrum.

## 1. Construction of the size-structured matrix model

To represent a community structure, a column vector whose entries give the abundance of individuals in each size class was defined. Individuals with different body masses were discretized into logarithmically equally spaced size classes and divided into two groups: the primary producers' group to produce the only input to the community, and the consumers' group to prey on other organisms smaller than themselves. The dynamics among individuals in the community were governed by processes of predator–prey interactions, reproduction, metabolism, and natural mortality. All these processes were structured by simple body size power functions and the model was designed based on the mass conservation principle in the community (*i.e.*, no biomass is wasted).

As a result, a unified size-structured matrix model to reproduce size spectra was obtained by representing each of these processes in a matrix form. By running the model within 40 years, a steady state of the community could be reached. It was shown that a linear size spectrum with a slope of approximately –1 can be reproduced successfully by using the reference values of the model parameters, which is consistent with the values reported in empirical studies.

## 2. Sensitivity of marine size-spectra to model parameters

To show the sensitivity of size spectra to the values of model parameters, numerical simulations were conducted by manipulating the parameter values separately in a range around their reference values. Results showed that wave-like size spectra appear when some parameter values such as the factor of reproduction rate and the exponent of natural mortality rate are decreased. Besides, size spectra with cut-offs at size classes with large body size are often observed if some parameter values such as the factor or the exponent of reproduction rate is increased.

A likely explanation for the occurrence of waves is that an increase or decrease in parameter values can cause an accumulation of the largest individuals, and then, owing to the top-down

cascade, the abundance of their most preferred prey individuals is suppressed, thereby releasing individuals in the next-lower trophic level from predation, producing a pattern of alternating high and low abundance in the size spectrum. As a consequence, the wavelength depends heavily on the predator–prey mass ratio. On the other hand, the occurrence of cut-offs is caused by a more rapid decrease in number of individuals around the size classes with the largest body size, as a consequence of a higher energy cost in reproduction or in metabolism, a lower prey consumption rate, a higher natural mortality rate, *etc*.

To demonstrate the usefulness of the model, effects of fishing on the size spectra under a balanced fishing pattern and an unbalanced fishing pattern were also investigated. Results indicated that catching individuals under a balanced fishing pattern over a wide range of body size classes has less impact on marine communities and can achieve higher yields as compared to an unbalanced fishing pattern in which only individuals of large body size are exclusively targeted.

## 3. Determinant factors of marine size-spectra patterns

To explore the determinants of the slopes and the patterns of size spectra, a detailed analysis based on a consideration of biomass flow within the community was carried out. For each distinct size class in an equilibrium state, there must be a mass balance established between the gains due to prey consumption and the losses due to being eaten, natural mortality, metabolic and reproductive costs, as well as biomass transitions between adjacent size classes due to individual growth and mass decrease. The biomass flows for each size class *i* can be divided into: (i) biomass flows between size class *i* and its adjacent size classes and (ii) biomass flows between size classes. If the biomass entering size class *i* from distant size classes due to predation is less than the biomass leaving that size class to distant size classes, either as eggs, metabolites, preys, or carrion, then the net biomass entering size class *i* from size class *i*-1 should be more than the biomass leaving size class *i* and entering size class *i*+1 to make up for the losses.

Numerical calculations showed that the difference between the biomass entering size class i

from distant size classes and the biomass leaving size class *i* to distant size classes varies with body size, causing corresponding variation in the biomass flows between adjacent size classes, and thus, the expected size spectra show wave-like patterns. Results demonstrated that both kinds of biomass flows (i) and (ii) contribute to the properties of size spectra. The biomass flows between adjacent size classes correspond to the growth of individuals, and moreover, a previous study derived a proportional relationship between average growth efficiency and trophic transfer efficiency (TTE; measured as the predator net production to prey net production ratio), indicating that TTE plays an important role in determining the slopes and variations of size spectra. Results showed that the slopes of size spectra are independent of the average values of TTE; however, variation in TTE with body mass contributes to the variation in slopes for different size ranges. The ratio of TTE at size class *i*-1 to TTE at size class *i* and slope index show similar behavior and have approximately equal average value of 1, suggesting that TTE ratio can be considered as the determinant factor of slopes and variation patterns of size spectra. A size spectrum with a slope exactly equal to -1 can be expected when TTE ratio between two adjacent size classes is independent of body mass.

The slopes and intercepts of size spectra have been recognized as important indicators to evaluate the states of marine communities. However, the existence of cut-offs and/or waves may result in inadequate slope estimates if reliance is placed solely on a simple linear regression analysis. Unlike previous complicated models, the matrix model developed in this study is systematically constructed based on simple body size power functions. The matrix algorithms developed in this study can reduce the computational time needed to calculate size spectra. As a result of its flexibility, the model can be easily extended or modified to explore community- or population-level dynamics.