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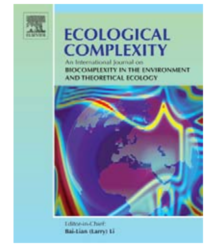

Review

Ecological pyramid of dissipation function and entropy production in aquatic ecosystems

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ABSTRACT

Food chain and food web have been, thus far, depicted by number of individuals, matter (biomass) and energy, but not by the concept concerning to the second law of thermodynamics. The present paper takes up three U.S. mid-Atlantic estuaries and delineates marine trophic structure in the term of the concept of this missing link: the second law of thermodynamics.

Homeostatic structure and function of living systems is maintained by chemical, physical and organic activities in biotic systems. These activities are supported by chemical energy released by decomposition of macromolecules in organisms by oxygen incorporated from the outside (respiration). This chemical energy finally becomes heat energy and is discarded to the outside. This heat energy is dissipation function in thermodynamics, and dissipation function divided by absolute temperature of organism–water is entropy production.

As example, mid-Atlantic estuaries on the eastern U.S. coast are analyzed, based on the study of (Monaco, M.E., Ulanowicz, R.E., 1997. Comparative ecosystem trophic structure of three U.S. mid-Atlantic estuaries. Mar. Ecol. Prog. Ser. 161, 239–254). They give 13–14 trophic compartments in each estuaries, and respiration and other characteristic quantities for each trophic compartments. Trophic position of compartment in each estuary is adopted and arranged in accord to the food web diagrams of (Monaco, M.E., Ulanowicz, R.E., 1997. Comparative ecosystem trophic structure of three U.S. mid-Atlantic estuaries. Mar. Ecol. Prog. Ser. 161, 239–254). Plots of trophic number versus respiration become of half-pyramid shape, which is also applied to dissipation function because respiration is equal to dissipation function in thermodynamics.

Annual average temperature at average depth in Narragansett estuary is, for example, 10.0 °C (=283.2 K). The difference between maximum and minimum temperature at averaged depth is 14.2 °C (=287.4 K). This difference is small compared with the absolute temperature scale. Hence let us make an approximation that the temperature of the water body of this estuary is about constant and uniform over a year and 10.0 °C = 283.2 K. Entropy production is obtained by dividing dissipation function by this value. Pattern of trophic position versus entropy production multiplied by the temperature is of similar shape to dissipation function: half-pyramid. Other two estuaries show similar results.

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Contents

1. Introduction

In old-days ecology, trophic structure of an ecosystem is represented by linear food chain and/or ecological pyramid (Odum, 1971). As the development of ecological studies, it turns out to be appropriate to describe ecological trophic structure by two-dimensional food webs. Food webs have been depicted by number of individuals, biomass and energy of trophic compartments, but have not been described by quantities concerning the concept of the second law of thermodynamics (cf. energy is the key concept of only the first law). In the present study, marine trophic structure is delineated in the term of the concept of the second law of thermodynamics for the first time.

The key concept of the second law of thermodynamics is entropy, but entropy itself cannot be measured or cannot be calculated in biotic systems; in contrast, entropy production can be estimated (Aoki, 2001). Entropy production and its related concept dissipation function in thermodynamics are concerned with respiration of biotic systems as shown below.

2. Respiration – dissipation function – entropy production

Homeostatic structure and function of living systems is supported by chemical, physical and organic activity in biotic systems. These activities are irreversible and produce entropy (entropy production) by the second law of thermodynamics.

Biotic activity within organisms is maintained by oxygen uptake and carbon dioxide discharge (respiration). Incorporated oxygen decomposes macromolecules (carbohydrate, protein, lipid) in organic matter in the body and liberates chemical energy. This chemical energy is used to activate chemical reactions and motions of matter to hold organic matter in ‘‘living state’’. Chemical energy thus used finally becomes heat energy and is discarded from the organisms with carbon dioxide. This heat energy is dissipation function in thermodynamics (Zotin, 1990). Associated with dissipation function, entropy production produced by irreversible processes in the organism is discarded to the outside. The entropy production is given by dissipation function divided by absolute temperature of the organism-surrounding water (Haase, 1969; Zotin, 1990).

Thus, respiration–dissipation function–entropy production are closely related, though they are measured by different physical units. Respiration is measured by oxygen uptake per unit time (e.g., litter per hour) and dissipation function is measured by energy outflow per unit time (e.g., kcal per hour). For example, in well-known human body, 1 L oxygen absorbed (respiration) corresponds to 4.83 kcal heat outflow (dissipation). Also, respiration is measured by excretion of carbon dioxide, or by corresponding biomass from organisms which is determined as the difference between digested food and production (Browder, 1993). The reader is referred to Lampert (1984) for the method of measurement of respiration in aquatic systems.

3. Respiration of the estuaries

Let us take up, as examples, three mid-Atlantic estuaries, Narragansett, Delaware, Chesapeake Bays on the eastern U.S. coast (Monaco and Ulanowicz, 1997). In diagrams in their paper, each estuary is shown to be composed of 13–14 trophic compartments. Biomass of each trophic compartment, biomass flow among trophic compartments, flow to detritus, export/import to/from outside and respiration of each trophic compartment are given. Units of biomass are $mg\,C\,m^{-2}$ and units of flow are $mg\,C\,m^{-2}\,yr^{-1}$. From these diagrams, biomass, respiration and its ratio to biomass (specific respiration) for each trophic compartment are obtained. Trophic position is adopted as:1 – phytoplankton, 2 – benthic algae, ..., 13 – carnivorous fish (see the figure captions). Note that order of trophic position is in accord with Monaco and Ulanowicz (1997) but numbering is inverted in Narragansett Bay and Delaware Bay, in the present paper.

Let us take up Narragansett estuary as an example. The trophic position versus respiration of the each trophic compartment in unit of $g\,C\,m^{-2}\,yr^{-1}$ is shown in Fig. 1. Generally, larger the trophic position, respiration becomes smaller. It approximately consists of half pyramid. Fig. 2 shows trophic position versus respiration per biomass in unit of yr^{-1} (specific respiration) in semi $\log_{10}$ scale. The general trend of trophic position versus $\log_{10}$ (respiration/biomass) is the same: as the trophic position becomes larger, specific respiration becomes smaller. Longer tail for small trophic levels in Fig. 2 shows that respiration (strength of activity) per biomass is larger for smaller organisms.

4. Dissipation function and entropy production

As shown in Section 2, respiration equals dissipation function for each trophic position. Figs. 1 and 2 show dissipation