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Production of bacterioplankton with special reference to dynamics of dissolved organic matter in a hypereutrophic lake

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Abstract

In lake water of Lake Kasumigaura, Japan, an increase in dissolved organic matter by phytoplankters as well as by waterchestnut (*Trapa bispinosa*) leads to an increase in the population density of bacterioplankton. Although the production sources of these dissolved organic materials vary throughout the year, the nature of bacterioplankton fluctuation can be approximated by a simple formula using the regression coefficient $F = 23.11$ ($F_{0.01} = 7.68$); $\log Y = 12.94 + 0.5 \sin \frac{\pi}{190.4} (t + 23.3)$ where Y is the density of bacterioplankton, and t is days throughout the year.

Introduction

The aquatic ecosystem is a dynamic system of biochemical changes at the expense of solar energy. The solar energy is the primary energy source for photosynthetic organisms which subsequently also is used by many heterotrophic organisms through different food webs. There are two kinds of food chains: the grazing food chain based on autotrophic production and the detritus food chain based on heterotrophic production; together they comprise the food web of an ecosystem. The detritus food chain is defined as utilizing dead organic matter which is connected to microorganisms and then to detritivores and their predators (ODUM 1971). The primary nembers of this food chain are bacteria in most aquatic ecosystems. PARSONS and STRICKLAND (1962) may have been the first to speculate on the quantitative significance of heterotrophic microorganisms in the world oceans. They estimated the mean standing crop of these organisms to be approximately 0.1 mg C per m^3 in the oceans of the world between 50 °N and 50 °S, while the amounts would be less in the arctic regions. This heterotrophic production of organic materials per unit volume of seawater (i.e., approximately 0.1 mg $C \cdot m^{-3}$) was estimated to be as much as 0.5 to 1 per cent of photosynthetic production by phytoplankton in the euphotic zone. When it is taken into account that the depth of the total water column in the ocean is fifty times or more that of the euphotic zone, the heterotrophic production beneath a unit area of the coastal ocean environment could be of the same order as photosynthetic production of the phytoplankton.

The heterotrophic bacteria utilize a wide variety of organic compounds in natural waters. The constituents of these compounds may be divided into three broad

Table 1
Turnover time of organic compounds in different watermasses

Type of watermass	Turnover time Amino acids Mono-saccharides Organic acids etc.	Cellulose Chitin etc.	Aquatic humus etc.
Oligotrophic			
Surface layer	several tens of days	a few years	between several tens of years and several hundreds of years (?*)
Deep layer	between a few months and a few years (?*)	a few tens of years (?*)	several thousands of years
Mesotrophic	between a few days and several tens of days	several months	several tens of years
Eutrophic	a few days	between several tens of days and several months	several years (?**)
Hypereutrophic	less than a few days	between several days and several tens of days	between half a year and one year

* calculated using our data and JANNASCH et al. (1971)
** speculated and not yet determined

categories with special reference to the biodegradation: (1) constituents easily metabolizable by most microorganisms such as amino acids, mono-saccharides and organic acids; (2) constituents moderately resistant to biochemical breakdown such as cellulose and chitin; and (3) refractory constituents highly resistant to biochemical breakdown such as aquatic humus. Each of these constituents has been found to have various turnover times in different watermasses of aquatic environments (Table 1). The turnover time of easily metabolizable constituents has been estimated by WRIGHT and HOBBIE uptake kinetics (1966) to be less than a few days in hypereutrophic waters, a few days in eutrophic waters, between a few days and several tens of days in mesotrophic waters, several tens of days in the surface layer of oligotrophic waters, or between a few months and a few hundred years in the deep oceans (BURNISON and MORITA 1974; HAMILTON and PRESLAN 1970; HOPPE 1978; PARSONS et al. 1977; SEKI 1979; SEKI et al. 1972a, 1974a, 1975, 1980a, 1980b, 1980c). The turnover time of moderately resistant constituents has been estimated by mathematical models approximated by in situ data and simulated in situ data to be between several days and several tens of days in hypereutrophic waters, between several tens of days and several months in eutrophic waters, several months in mesotrophic waters, a few years in the surface of oligotrophic waters, or a few tens of years in the deep layer of oligotrophic waters (GOCKE 1977, HOOD and MEYERS 1973; MATSUO et al. 1979; SEKI 1965a, 1965b; YAMAMOTO and SEKI 1979). The turnover time of refractory constituents has been estimated by mathematical models approximated by in situ data or steady-state kinetics according to OLSON (1963) to be between half a year and one year in hypereutrophic waters, several years in eutrophic waters, several tens of years in mesotrophic waters, between several tens of years and hundreds of years in the surface layer of oligotrophic waters, or several thousands of years in the deep layer of oligotrophic waters (NAKANO and SEKI in press; SEKI et al 1968; SKOPINTSEV 1966). It is thus apparent from these estimations that the bacterial activities are dependent qualitatively and quantitatively on the organic materials in natural waters. This in turn shows that the biomass production of heterotrophic bacteria should be greatly affected by the eutrophication of natural waters.

Three categories are evident in the production process for heterotrophic bacteria of aquatic environments: (1) free-living bacterioplankton with active transport systems for highly efficient assimilation of organic substrates such as *Achromobacter aquamarinus* (strain 208) (JANNASCH 1967); (2) stalked bacteria adherent to the interface between liquid phase and solid or gaseous phase such as *Caulobacter* (JANNASCH 1960; STOVE and STANIER 1962); and (3) bacteria tending to clump or form an aggregate so that each bacterium builds a construction with other bacteria to include organic materials (BARBER 1966; PARSONS and SEKI 1970). In any of these categories, the standing stock of bacteria as the primary producers of biomass in the detritus food chain has primarily reached a steady-state equilibrium with continual biomass supply from organic debris and continual removal by grazing of detritivores.

The major fraction of organic debris is present in a dissolved form in most aquatic environments. Heterotrophic bacterioplankton prefer this dilute nutrient solution but they cannot be enumerated or cultured with conventional enrichment media primarily because of a quantitatively low nutrient requirement (e.g. SEKI et al 1972b). Accordingly, special attention has been paid to the productivity of bacterioplankton. Although natural populations cannot be simulated in a chemostat, the chemostat system has been successfully applied to approximate a process of production and grazing of a certain population from the autecological point of view (e.g., JANNASCH 1970). From the synecological point of view, however, approximation of the process may be only possible by using mathematical models. The most highly dynamic case of the process can be expected for natural populations in a hypereutrophic environment. Lake Kasumigaura in Japan is such an environment since the population density of blue-green algae during the summer bloom is the highest (682 μg ATP/l) that can be expected in any aquatic system, reflecting the extreme end of eutrophication. Total organic matter in this environment was shown to approximate the following distribution in relative units (NAKANO and SEKI in press): organic solute 100, detritus particle 200, phytoplankton 400, and bacteria and allied microorganisms 60 during the period without an algal bloom. This distribution can be compared with that in oligotrophic oceanic waters (SEKI 1970); organic solute 100, detritus particle 10, phytoplankton 2, and bacteria and allied microorganisms 0.2. Therefore, the population density of bacterioplankton was approximately three orders of magnitude greater than that in the oligotrophic marine environment (Fig. 1), and in turn the bacterial assimilation rates of organic solute could be expected to be extraordinarily high.

Materials and methods

Bacterioplankton was enumerated in a bacterial counting chamber under a Nikon phase contrast microscope. Dissolved organic carbon (DOC) was determined by TOC Analyzer Model 915 B (Beckmann, Fullerton) followed by the filtration of water sample using Gelman glass filter type A (pore size; 0.3 μm). Other procedures for this study were identical to those described by SEKI et al. (1979).

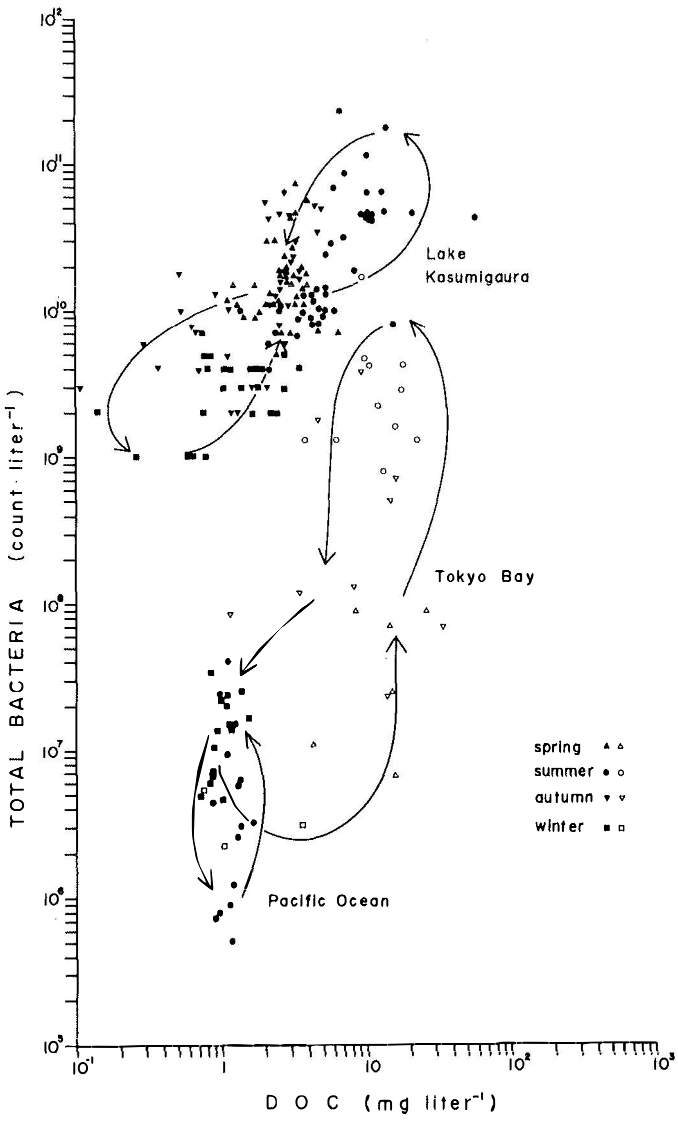

Figure 1

Relationship between standing stock of bacterioplankton and dissolved organic carbon in various natural waters.

Results and discussion

In the case of Lake Kasumigaura, the standing stock of dissolved organic matter and bacterioplankton depending on it for nutrition oscillated in a complicated manner, but the fundamental wave in the oscillation must have been caused by the formation of dissolved organic matter by phytoplankton and waterchestnut. Actually, the seasonal fluctuation of bacterioplankton was highly significant and could be approximated by a simple curve over the year ($F = 23.11$, $F_{0.01} = 7.68$),

$$\log TB = 12.94 + 0.5 \sin \frac{\pi}{190.4} (t + 23.3)$$

where TB is standing stock of bacterioplankton (counts/m^2), and t is the number of days elapsed since May 1, 1978. The oscillation in concentration of dissolved organic matter and abundance of bacterioplankton may be approximated more precisely by a sine or cosine curve as there should be an equilibrium between input, chiefly supplied from phytoplankton, and output, chiefly assimilated by bacterioplankton: Even though the organic supply from a phytoplankton bloom might accumulate in the early stages of a bloom, the bacterioplankton then increases its population density by utilizing the nutrient. Thereafter, an increase of the bacteria density leads to an active consumption of the organic matter by heterotrophs with the release of inorganic nutrients available for the formation of the next phytoplankton bloom. Amplitudes in the oscillation of this steady-state equilibrium of bacterial production and consumption (mg $C \cdot m^{-3}$ per day) were 6.6 during the blue-green algal bloom in summer, 3.0 durning the eukaryotic algal bloom in spring, 0.37 between these blooms, and 2.3 after the spring bloom (Fig. 2).

Due to such excitation of heterotrophic processes according to the degree of eutrophication, the fraction of organic matter increases firstly in heterotrophic microorganisms, secondly in phytoplankton, and finally in detritus (Fig. 3). The precedence of heterotrophic processes over autotrophic processes must be

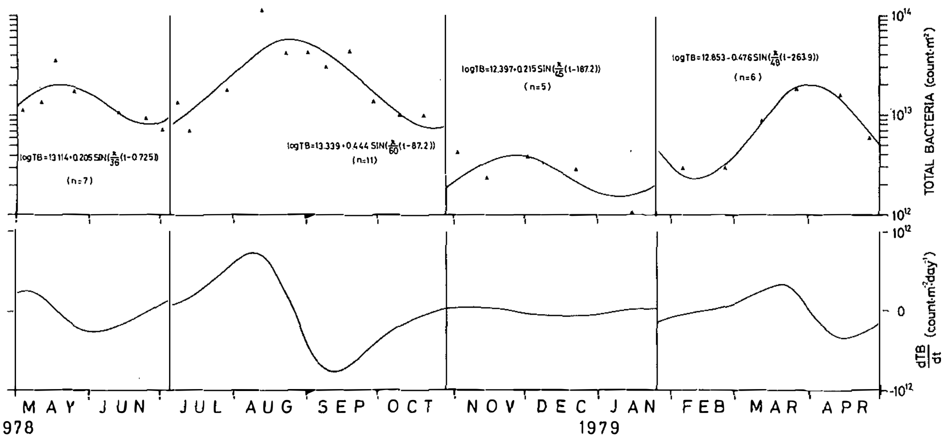

Figure 2

Seasonal fluctuation of the standing stock and productivity of bacterioplankton in the watercolumn of Lake Kasumigaura. Modified from NAKANO and SEKI (in press) favourable not only for encouraging the detritus food chain but also for the stability of an ecosystem in maintaining a steady-state type such as oligotrophic or eutrophic, otherwise the excess production of organic matter leads the system into disequilibrium resulting in a change in water type.

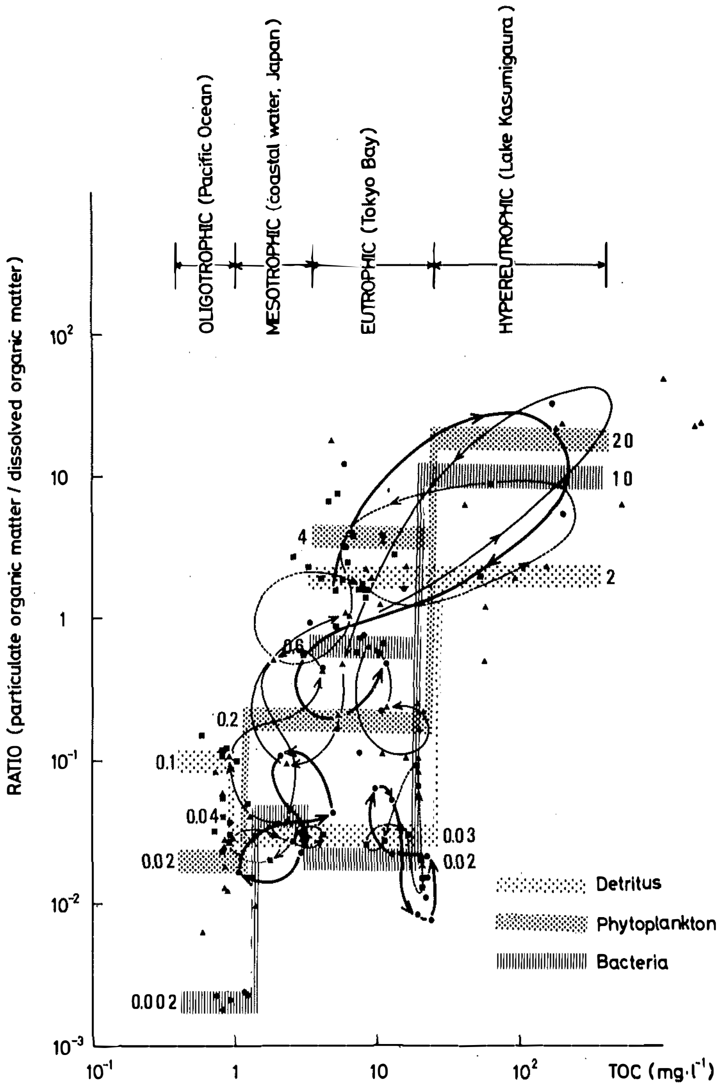

Figure 3

Constituent distribution of organic matter in various aquatic environments with special reference to eutrophication. (data from SEKI 1979; SEKI et al. 1972a, 1972b, 1974a, 1974b, 1975, 1980a, 1980b, 1980c)

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