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Dynamics of bacterioplankton in oligotrophic and eutrophic aquatic environments: bottom-up or top-down control?

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Abstract

Measurements of bacterial biomass, production and mortality have been carried out in a large range of aquatic environments, including eutrophic and oligotrophic ones. The general trends of variations of bacterial biomass, size, specific growth rate and mortality rate in all these environments are examined. The overall flux of bacterial production is taken as an index of the flux of organic matter available to bacteria, thus characterizing the richness of the environment. Bacterial biomass is roughly proportional to richness, while mean cell size increases with it. The turnover rate of biomass, as revealed either by growth or by mortality rates, appears to be fairly independent of richness.

These observations are compatible with a simple resource-limited (bottom-up controlled) model of the dynamics of bacterioplankton. On the other hand, they are in contradiction with the predictions of a predator-controlled (top-down controlled) model.

Introduction

For about ten years, methods have been available for measuring both biomass and production of bacteria in aquatic environment (Daley & Hobbie, 1975; Fuhrman & Azam, 1980, 1982). More recently, methods have been described for evaluating grazing and mortality rates of bacterioplankton (Servais *et al.*, 1985, 1989; McManus & Furhman, 1988). Altogether, these methods provide a good description of the dynamics of heterotrophic bacterioplankton in aquatic environments (see Billen *et al.*, 1988a). Using these methods, the Groupe de Microbiologie des Milieux Aquatiques at the University of Brussels has carried out studies on the microbial ecology of a large number of marine and freshwater aquatic systems, ranging from highly eutrophic (the Scheldt estuary and its tributaries (Billen *et al.*, 1988b); the Meuse river (Servais, 1989)) to mesotrophic (the Belgian coastal zone of the North Sea (Billen & Fontigny, 1987)) and oligotrophic (the Southern Ocean (Billen *et al.*, 1987) or the drinking water from the distribution network in Parisian suburbs (Servais *et al.*, in press)). Because the same methods were used with only minor modifications in all these environments, these studies offer the possibility of comparing bacterial dynamics in systems of very different trophic status.

This paper presents a synthesis of these data. The basic question addressed is that of the control of bacterioplankton and its dependence on the richness of the environment. More specifically: is heterotrophic bacterioplankton biomass con-

trolled by 'bottom-up' effects *i.e.* by the resources in available organic matter, or by 'top-down' effects, *i.e.* by the grazing pressure exerted by predators?

For the needs of the discussion, a suitable index of richness of the environment has to be defined. Richness is a dynamic concept. It is related to the flux of available resources much more than to the standing stock of these resources. For the case of the heterotrophic bacterial community, richness consists in the flux of input of biodegradable organic matter, whatever the origin of this flux (phytoplankton activity or allochtonous inputs) might be. A direct measurement of this flux, including pelagic carbon fixation and additional allochtonous inputs, is not easy to obtain routinely. However, provided the system is not too far away from steady state, organic matter is taken up by bacteria at a rate close to its production rate, maintaining the stock at a low, quasi constant level. Under these conditions, the flux of bacterial utilization of organic matter, or the flux of bacterial production, which, as a first approximation, is proportional to the former, can be considered as a good index of richness of the environment. This is the approach used in this study for comparing spot determination of bacterial biomass and production in a large range of aquatic environments.

Methods

Bacterial numbers were counted by epifluorescence microscopy after acridine orange staining (Daley & Hobbie, 1975). Photographs of about three fields were taken and the bacterial size distribution was measured on enlargements of these photographs. Biomass was calculated from abundance and biovolume distribution using the biovolume dependent conversion factors recently proposed by Simon & Azam (1989).

Bacterial production was estimated by ^{3}H-thymidine incorporation according to the methods described by Fuhrman & Azam (1980, 1982). A conversion factor into cell production was experimentally determined for each environment by the method proposed by Riemann *et al.* (1987). The conversion factors found in the different environments are given in Table 1.

Table 1. Experimentally determined conversion factors relating bacterial cell production to ^{3}H-thymidine incorporation into cold TCA insoluble fraction.

Environment	Cell produced per nmol Thy incorporated into cold TCA insoluble material
Scheldt River and estuary	$1.25\,10^9$
Meuse River	$0.5\,10^9$
North Sea (coastal zone)	$1.7\,10^9$
Prydz Bay (Antarctica)	$5\,10^9$
Drinking water (Parisian suburbs)	$0.5\,10^9$

Bacterial growth rate is calculated as the ratio between cell production and bacterial abundance.

Mortality and grazing rate were determined as described by Servais *et al.* (1985, 1989).

Results

Figure 1 shows the data of bacterial biomass plotted against bacterial production in the different sites considered. As can be judged from the bacterial production values, variations in richness between the environments making up our data base cover 5 orders of magnitude. Biomass values also cover this range of variation. Biomass indeed appears roughly proportional to the richness of the medium (slope close to 1 in log-log plot). Such proportionality would not have been observed with bacterial abundance. Indeed, bacterial numbers and bacterial biomass are not proportional in the whole range of environments considered here, as very different size classes of bacteria dominate in each of them (Fig. 2). Small forms (0.3 to 0.7 μm cocci) dominate in oligotrophic systems, while larger rods are present in eutrophic waters.

The proportionality observed between bacterial biomass and bacterial production (Fig. 1) implies a fairly constant growth rate. As a matter of fact, Fig. 3 shows that the growth rate varies by only 2 orders of magnitude for the 5 orders of magni-

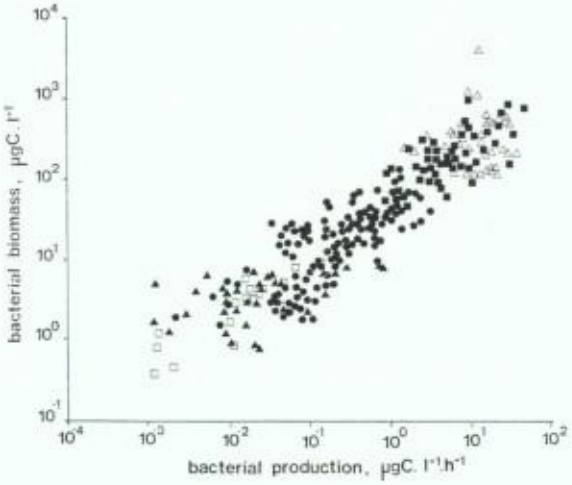

Fig. 1. Bacterial biomass plotted against bacterial production in individual samples from Scheldt River and estuary (△), Meuse River (■), coastal zones of the North Sea (●), Prydz Bay (Antarctica) (▲) and drinking-water distribution network of the Parisian suburbs (□). The flux of bacterial production can be considered here as a general index of the richness of the environment.

log-log linear correlation: log(biomass) = 1.67 + 0.7 log(production) $r = 0.91$ ($n = 288$)

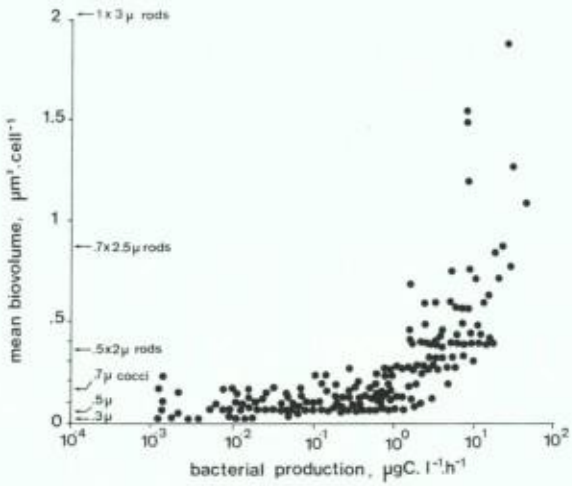

Fig. 2. Mean cellular volume of the bacterial community in the different environments considered, plotted against the flux of bacterial production as a measure of richness.

tude range of richness. Moreover, the lowest values recorded in oligotrophic situations might be underestimated, because of the possible presence of a larger fraction of inactive dormant or resting cells in the biomass there. In meso- and

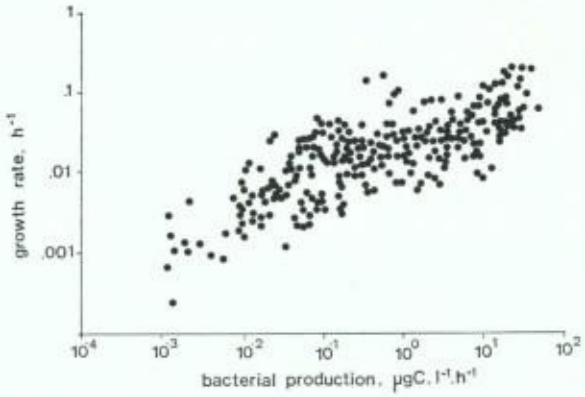

Fig. 3. Mean bacterial growth rate plotted against bacterial production as a measure of richness in the different environments considered.

log-log linear correlation: log(growth rate) = −1.7 + 0.33 log(production) $r = 0.73$ ($n = 288$)

eutrophic waters, the growth rates fluctuate around a mean value of 0.02 h^{-1}, corresponding to a generation time of about 35 h.

Still more clearly apparent is the lack of important variations in mortality rates between the different environments considered (Fig. 4). Mortality rates are situated at the mid-range of growth rates.

The method used for determining bacterial mortality (Servais *et al.*, 1985) allowed us to distinguish between grazing by protozoans and mor-

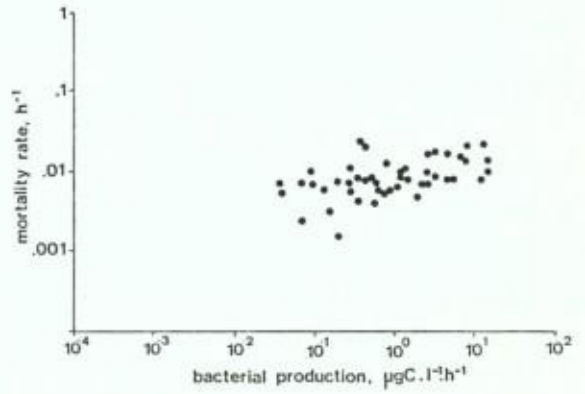

Fig. 4. Rate of total bacterial mortality plotted against bacterial production as a measure of richness in the different environments considered.

log-log linear correlation: log(mortality rate) = −2.1 + 0.26 log(production) $r = 0.6$ ($n = 49$)

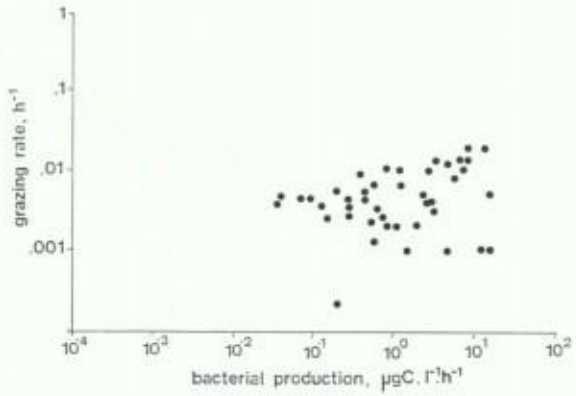

Fig. 5. Rate of bacterial grazing plotted against bacterial production as a measure of richness in the different environments considered.

log-log linear correlation: log(grazing rate) = −2.4 + 0.21 log(production) $r = 0.35$ ($n = 49$)

tality due to another cause (spontaneous or virus-induced lysis, bacterial predation...). No distinct trend appears for grazing rate. Grazing appears as a variable and not always dominant fraction of total mortality (Fig. 5).

Discussion

The major trends apparent from the data discussed above can be summarized as follows:

1. Bacterial biomass is proportional to the richness of the environment. It reflects directly the trophic status of the system.
2. The turnover of bacterial biomass, as revealed by growth rate or by mortality, appears largely independent of the richness of the environment.

The latter observation might seem paradoxical: it implies that eutrophic systems do not distinguish themselves from oligotrophic ones by a higher growth rate of the bacterial community.

We will show however that this conforms with the predictions of a simplified model of bacterioplankton dynamics discussed elsewhere in another context (Billen *et al.*, 1988a) (Fig. 6). The model assumes that organic substrates (S) are produced at a rate p, which thus represents the richness of the system. The substrates are utilized by bacteria (B) according to Michaelis-Menten kinetics. Growth of bacteria is proportional to the uptake of substrates and their mortality is first-order with respect to their biomass.

The rate of change of S and B can thus be written:

$$\frac{dS}{dt} = p - b_{max}\frac{S}{S + K_s}B \qquad (1)$$

$$\frac{dB}{dt} = Yb_{max}\frac{S}{S + K_s}B - k_dB \qquad (2)$$

where

p is the input of organic substrates characterizing the richness of the system;

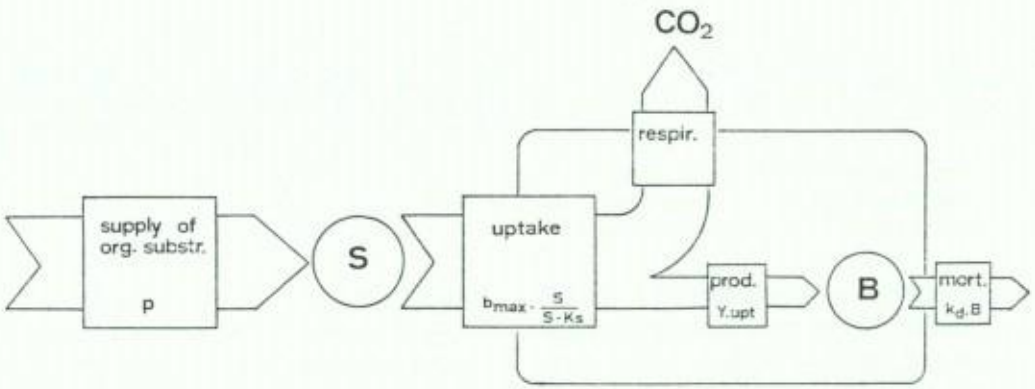

Fig. 6. Approximate representation of the model of bacterioplankton dynamics discussed in the text.

b_{max} is the maximum rate of uptake of organic matter;
K_s is the half-saturation constant of substrate uptake;
Y is the growth yield;
k_d is the first-order mortality rate constant.

At steady state, the model predicts that substrate concentration is maintained at a value independent of p, and dependent only on the physiological characteristics of bacterial uptake:

$$S = \frac{K_s}{\frac{Yb_{max}}{k_d} - 1}$$

Consequently, the growth rate, which depends only on substrate concentration, is constant:

$$\mu = Yb_{max}\frac{S}{S + K_s} = k_d$$

Only the biomass is a direct function of substrate production p:

$$B = \frac{Y}{k_d}p$$

The model thus predicts the major trends observed in our data.

These conclusions, however, are highly dependent on the way the model represents the process of bacterial mortality.

Let us consider another model, including predator (Z)-controlled grazing mortality instead of first-order bacterial mortality. This model represents a top-down control of the bacterial compartment, while the preceding model, ignoring the dynamics of predators, corresponded to simple bottom-up control. The equations can be written:

$$\frac{dS}{dt} = p - b_{max}\frac{S}{S + K_s}B \qquad (1')$$

$$\frac{dB}{dt} = Yb_{max}\frac{S}{S + K_s}B - z_{max}\frac{B}{B + K_B}Z \qquad (2')$$

$$\frac{dZ}{dt} = Y' z_{max}\frac{B}{B + K_b}Z - k_z Z \qquad (3)$$

where

z_{max} is the maximum rate of bacterial grazing per unit predator biomass;
K_b is the half-saturation constant of bacterial grazing;
Y' is the growth yield of the predators;
k_z is the first-order mortality rate of predators.

At steady state this model now predicts that bacterial biomass is independent of the richness of the medium, being determined by the parameters characterizing grazing:

$$B = \frac{K_b}{\frac{Y' z_{max}}{k_z} - 1}$$

Conversely, the growth rate and the mortality rate are predicted to be proportional to p:

$$k_d = \mu = \frac{Y}{K_b}\left(\frac{Y' z_m ax}{k_z} - 1\right)p$$

The predictions of this latter predator-controlled model are thus contractory with the trends apparent from our experimental observations, where bacterial biomass was found to be proportional to richness, while growth and mortality rates were independent of it. The former resource-controlled model, correctly predicts these trends. This suggests that in the environments studied here, even if grazing undoubtedly contributes to bacterial mortality, the bacterial compartment is not primarily controlled by the dynamics of bacterial grazers, but is controlled more strongly by the amount of resources available.

Basically, the prediction of these trends results from the structure of equation (2), in which neither the term representing bacterial growth, nor that representing bacterial mortality explicitly involves phagotrophic protozoa. However, more subtle interactions than those taken into account in the above models might be operative in con-

trolling bacterial dynamics. For example, Sherr *et al.* (1988) recently reviewed a number of possible mechanisms by which phagotrophic protozoa, beside their direct grazing on bacteria, could also indirectly regulate bacterial growth. These mechanisms all involve mineral nutrient limitation of bacterial growth. Such limitation is highly unlikely, however, in the environments constituting our data base (excepted for some of our North Sea samples). Possibly therefore, our conclusion that in the environments studied here, the bacterial compartment is not primarily controlled by the dynamics of phagotrophic zooplankton, could not apply to situations where, in addition to organic carbon control, mineral nutrient limitation of bacterial growth occurs. It would be interesting to extend the reasoning presented here to broader data bases.

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