Microbes as a challenge to concepts of marine ecosystem analysis

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ABSTRACT: As theory of science is subject to conflicting ideas, the role of microbiology in marine ecosystem analysis is viewed from extremely different positions. Combined descriptive and experimental approaches have elucidated key functions of microorganisms that challenge the traditional, macro-organism-dominated concepts in ecosystem ecology. This point is illustrated, in particular, by examples of microbe-mediated pathways in the benthic-pelagic coupling of energy flow and carbon cycling. In this context, the role of bacterial biofilms and benthic macrofauna as well as their interaction in marine sediment biogeochemistry is emphasized.

"Bacteria and bacteriologists are the lowest forms of life" (E. McCoy)

THE DILEMMA IN PHILOSOPHY OF SCIENCE

Ecology is considered as a holistic science (Odum, 1977). Hence, terms like "microbial ecology" may sound like a contradictio in adjectu. On the other hand, recent progress in microbe-oriented ecological research indicates a growing impact of microbiology on ecosystem analysis. Because of the most obvious biogeochemical interactions between microorganisms and their environment, microbes appear as particularly suitable objects for studying ecosystems which, according to Tansley's (1935) definition, represent functional units of both an organism complex and its physicochemical environment.

Concepts and methodological approaches to ecosystems suffer from grave uncertainties: Ecosystem concepts are not only dimensionless (Reiners, 1986); even the existence of ecosystems is sometimes questioned (Jordan, 1981). Scientific methodologies based on experimental falsification (Popper, 1971) are at best successfully applied in certain, less qualified subdivisions (Rowe, 1961) such as population or community ecology. However, philosophers in science have yet to suggest a scientific method for ecosystem studies (Pomeroy et al., 1988). Considering this confusion about ecological principles and strategies (Schlegel, 1986), it is not surprising that small, viz. "reductionist", solutions are embraced. In the attempt to understand the ecology of ecosystems, culture experiments can be considered as necessary, yet insufficient, pieces of evidence. Yet, reductionist

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claims that microbiological studies of pure cultures alone represented microbial e c o l - o g y (rather than ecological m i c r o b i o l o g y !) are at odds with the intention and history of ecological research (Rigler, 1975).

Rapid development of phylogenetic, molecular taxonomy of microorganisms (Amann et al., 1991; Stackebrandt et al., 1993) and growing interest in community diversity (Margulis, 1993) promise to enable future microbial ecologists to copy the far more successful approaches of their colleagues in zoology and botany. Yet, there may be insurmountable obstacles in analysing the population dynamics and bioactivity of microorganisms in their natural habitats in a similar way as it is achieved in the ecology of macro-organisms (Brock, 1987). In the absence of binding concepts in ecology, it should even be questioned whether microbial ecologists should unreflectingly follow in the footsteps of their more advanced counterparts in macro-organism-oriented ecology.

Experimental microbial ecology

In dealing with microbial aspects of marine ecosystem research, it has long been customary to rely on some kind of reductionist backbone in order to corroborate conclusions from outdoor observations (e.g. Colwell & Morita, 1974). More recently, microbial physiologists testify their growing interest in ecology and have even begun emphasizing the need of extending collateral research in order to be better prepared for the complex questions raised in microbial ecology (Schlegel, 1986). In fact, current progress related to ecosystem analysis on the less complex experimental level of bacterial physiology is documented by impressive examples (e.g. Stetter, 1986; Widdel, 1988). Finally, there are numerous precedents for the use of bacterial isolates from aquatic ecosystems (e.g. Reichardt, 1974, 1989b; Reichardt & Morita, 1982) to investigate "subsystem feedbacks that control large ecosystems" (Odum [1975], cited by Wiebe [1984]).

Typical properties, such as their small size, their extremely short generation times and high population densities always make cultured microorganisms superior candidates for most economic experiments using highly miniaturized culture systems. As a kind of rapidly responding reference base for ecological modelling, or as handy test systems designed to prove hypotheses being derived from field data, experimental microbial ecology could assume a promotive driving function in marine ecology, being comparable, for example to bacterial genetics in another field of science.

Yet conclusions drawn from any experiment are limited by their methodological scope and cannot easily be extrapolated to different ranges of complexity. Occasionally, undue over-extrapolations of reductionist approaches have gained widespread public attention, such as hypotheses related to inorganic carbon limitation (Goldman et al., 1972), or to the efficiency of bacterial decomposition in the deep-sea, as reviewed by Sieburth & Dietz, 1974. Obviously the best safeguard against such erroneous conclusions is greatly increased communication between all lines of ecosystem research, even if no agreement on strategy and methodology can be reached.

It seems that progress in ecosystem analysis will depend on a strategy that can integrate both holistic and reductionist approaches. Although standing in opposition to each other, these two approaches are also complimentary (Rigler, 1975; Brock, 1987). Neither descriptive ecology operating with normative or probabilistic statements nor inductive research alone will lead to universal laws (Pomeroy et al., 1988).

Microbe-specific functions

It is not exaggerated to say that microbiology has altered our understanding of ecosystem functioning (Wiebe, 1984; Pomeroy & Alberts, 1988). Firstly, because of the unique physiological diversity of prokaryotes, this group of microbes serves various functions on different trophic levels. Some of these functions are not encountered in higher forms of life, since physiological classification of prokaryotes, according to their sources of energy (light or chemical), of carbon (inorganic or organic) and their reduction equivalents (inorganic or organic) leads to (2^3 =) eight combinations. It needs no further explanation that this fact renders the traditional macro-organism-based autotrophy/ heterotrophy concepts obsolete (Reichardt, 1978; Schlegel, 1986). Further problems result from the existence of both facultative and obligate metabolic pathways, in addition to the fact that some physiologically extremely versatile bacteria evade any straightforward (eco)physiological classification (e.g. Shively & Barton, 1991). Among the main factors being responsible for current stirrings of the foundation of Lindeman's (1942) traditional trophic level concept, growing recognition of bacterial eco-physiology plays a dominant role (Pomeroy & Alberts, 1988), although not the only one (Mann, 1988).

Secondly, prokaryotes are the main determinants of biogeochemical pathways, and therefore indispensable for our knowledge of cybernetic control functions (Wiebe, 1984). Hence, if there is too little interaction between biogeochemists and ecosystem ecologists (Pomeroy & Alberts, 1988), microbial ecology will provide an optimal platform in order to change this.

Microbe-mediated benthic-pelagic coupling

With growing public interest in global element cycling, particular attention is drawn to marine ecosystems (Degens, 1989). The example of carbon flux indicates dramatic changes at the main boundary layers of the water column with atmosphere and sediment (Fig. 1). Transitions of microbe-mediated pathways of carbon cycling and energy flow between water and sediment provide a good illustration of how microbiological key functions are integrated in marine ecosystem analysis.

"Top-down" supply on organic carbon to aphotic benthic communities is mostly patchy and, particularly in the deep-sea, subject to extended periods of shortage. Most marine bacteria do not form spores, but dispose of a more efficient strategy to maintain their omnipresence, also during starvation: starving cells of heterotrophic bacteria undergo a number of cytological changes that enable them to survive extended periods of nutrient limitation. They do not lose their capacity to respond without delay, once organic nutrients become available again. Thus, heterotrophic bacteria can act as primary, most reactive coupling agents in pelagic-benthic energy flow.

As shown for species of *Vibrio* and *Cytophaga*, two of the most frequently isolated bacterial genera in marine habitats, starvation enables heterotrophic bacteria not only to utilize extremely low quantities of nutrients; it also increases their competence for adhesion to particles (Kjelleberg et al., 1987). This aspect of a "starvation-survival-strategy" can also be viewed as a potential nucleus for the formation of microbial biofilms on solid surfaces.
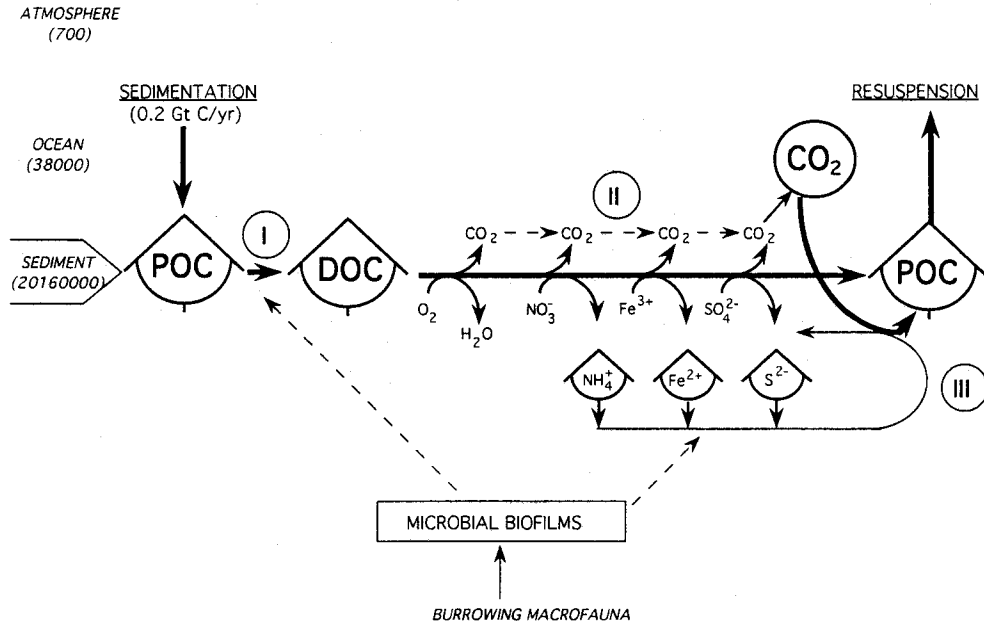
Fig. 1. Schematic and grossly simplified presentation of bacteria-mediated key processes in benthic-pelagic coupling of carbon cycling and energy flow. Global carbon pools (brackets) in Gt, according to Degens (1989)

I. Extracelluar enzymatic conversion of particulate organic carbon (POC) into assimilable dissolved organic carbon (DOC)

II. Heterotrophic assimilation and dissimilation of DOC in gradually O_2-depleted sediment, generating potential energy carriers for chemosynthesis (not completely listed).

III. Chemoautotrophic de novo synthesis of POC as bacterial biomass

Biofilms

Whereas most investigations in marine microbiology seem to deal with freely suspended (planktonic) cells – let alone the legions of culture experiments –, the most striking and abundant manifestation of microbes in the aquatic ecosystems are microbial biofilms (Costerton et al., 1987). Often like oases in nutrient-deficient environments, biofilms constitute centres of maximum bioactivity. Typically they consist of metabolically interdependent microorganisms in a matrix of exopolymeric substances (EPS).

These bacterial aggregates fill a gap in our understanding of an obviously rate-limiting process, the transformation of non-assimilable organic detritus particles to assimilable dissolved organic matter, a step that is catalyzed by extracellular enzymes (Reichardt, 1986). The bacterial enzymes involved in this extracellular decomposition acquire a high efficiency and are largely protected from dilution when they remain trapped within a biofilm matrix that ensures a close contact with the degradable particle (Cooksey, 1992; Lamed et al., 1987; Reichardt et al., in prep.). Preferably on aging algal detritus (Reichardt, 1981), potent degraders of polysaccharides belonging to the genus of *Cytophaga* are able to form highly developed gliding biofilms. These constitute a most cooperative formation of gliding bacterial cells that excrete their polysaccharide-degrad-

ing enzymes together with copious amounts of matrix-forming mucus (Reichardt, unpubl.).

Associations with macroorganisms

Microbial biofilms are often associated with living or dead marine plants (Reichardt & Diekmann, 1985; 1987) as well as with animals (e.g. Grossmann & Reichardt, 1991; v. Juterzenka & Reichardt, 1991), suggesting some kind of mutualism, an emergent property that controls population structures besides competition and predation (Wiebe, 1984).

Since the discovery of chemoautotrophic symbionts at hydrothermal vent sites (Cavanaugh et al., 1981), the general importance of macrofauna for the enrichment of marine bacteria has gradually been recognized (Reichardt et al., 1991). In common bioturbated sediments, perizoic biofilms at burrow linings of benthic infauna become the sites of maximum microbial activities (Reichardt, 1988; 1989a). This can be interpreted as an indication of a positive feed-back control.

Redox gradients and storage of potential energy carriers

Microbial decomposition of organic carbon leads to oxygen depletion followed by the sequential reduction of alternative terminal electron acceptors such as nitrate, nitrite, ferric iron, manganese, sulfate, or carbon dioxide. In the extreme case of eutrophied, sulfidic sediments, this sequence of events will finally cause the elimination of most of the benthic macrofauna. In any case, however, it marks a turning point of the energy flow: instead of "top-down" transport of organic energy carriers for the benthic heterotrophic communities, potential energy carriers for chemoautotrophic biosynthesis (linked eventually to some kind of "bottom up" energy flow via resuspension) will accumulate at low redox potentials (Fig. 1).

This store of energy carriers may or or may not be tapped without delay. Most rapid tapping ensues, wherever a close contact is established between the anaerobically respiring producers and the chemoautotrophic consumers of the reduced compounds. In marine sediments, metabolic coupling between sulfate-reducing heterotrophs and sulfide-oxidizing chemoautotrophs, for example, may take place in consortia (Jørgensen, 1977) as well as in perizoic biofilms (Reichardt, 1989a).

On the other hand, sequestration of those potential energy sources by diagenetic processes may stretch the time span between their production and consumption enough to extend the time scale of ecosystem analysis into geological dimensions. This could bring back to the minds of marine ecologists the too often neglected dimension of time that is accessible, however, by descriptive, rather than experimental, approaches.

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