



Microbial ecology: from local to global scales

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ABSTRACT: Over the past 30 yr, microbial ecology has taken major leaps in bringing microscopic organisms into the context of aquatic ecosystems and shown that they regulate carbon and nutrient processes on a global scale. More recently, molecular biology has enabled prokaryotic organisms to be identified at the species level and contributed information on functional groups of specific significance to the ecosystem. Although microbial ecology has covered all common aquatic systems it has spatially been focused on a narrow range of habitats, leaving, for example, polar ice with modest activity and the deep, dark oceans practically untouched. In addition, temporal scales have been skewed towards daylight studies and only recent studies have focused on day/night process controls, recognizing that the diel rhythm is connected to fast-growing prokaryotic organisms. The key to going forward with predictions on the fate of microbial food webs in the ecosystem is to recognize physical structures and their persistence in the water body and identify the biological hotspots in terms of spatial and temporal significance. The present ecological models do not handle short-term, spatially restricted hotspot events adequately. Evidently, we need to combine our research efforts into targeted approaches, coupling modeling activity with physical and chemical oceanography as well as fisheries biology and 'sell our goods', even though our primary interest is microbial processes. Understanding the micro-environment of a single cell and its interaction with the environment should, by extrapolation, enable us to predict global processes. In the nitrogen cycle, this understanding has evolved rapidly, but in the carbon cycle, the role of microbes is still far from fully understood, especially in terms of loss processes. This should rapidly be addressed, instead of undertaking further major questionable experiments such as fertilizing the seas at very large scales.

KEY WORDS: Aquatic microorganism · Process rate · Molecular biology · Functional groups · Polar ice · Dark oceans · Biological hotspots · Societal needs

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INTRODUCTION

The Symposium on Aquatic Microbial Ecology (SAME) series was established by merging 2 symposia, the International Workshop on the Measurement of Microbial Activities in the Carbon Cycle of Aquatic Environments and the European Marine Microbiology Symposium (EMMS), during the 7th occasion of the meetings (EMMS 7). The former series started in 1977, initiated by J. Overbeck from the Max-Planck-Institut in Plön, Germany, as Society of International Limnology (SIL) workshops. Overbeck's personal interest in microbial ecology was key to facilitating meetings with a focus on microbes and thus introducing new tools to the community of microbial ecologists. The latter series

started in 1982 in Marseille as a European contribution to marine microbial ecology. Both symposium series developed from their early focus, to cover microbial ecology in a variety of habitats throughout aquatic environments without geographic or national restrictions, and thus an international perspective was obvious. It was also obvious that EMMS 7 was organized with a global perspective by inviting a large number of aquatic microbial ecologists who had participated in both meetings on various occasions and were internationally recognized scientists. At EMMS 7, a decision was taken by the International Scientific Committee to fuse both meetings under the name SAME.

Over the past 30 yr, microbial ecology has taken major leaps with improved tools, which brought micro-

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scopic organisms into the context of aquatic ecosystems. In the 1970s, radiotracer techniques for the measurement of turnover rates of pools of dissolved carbohydrates, sugars, etc. (Wright & Hobbie 1966, Azam & Holm-Hansen 1973, Gocke 1977) revealed high process rates of heterotrophic bacteria, suggesting cell doubling times from hours to tens of hours.

With the advancement of microscopic observation techniques (Hobbie et al. 1977) and quantification of bacterial growth (Hagström et al. 1979, Fuhrman & Azam 1980, 1982), the concept of a microbial loop (Azam et al. 1983) could be included in aquatic food web representations (Williams 1981). From the very beginning, the primary methodological question was how to obtain information on microbial growth rates without enclosing the sample in incubation vials, but using true *in situ* measurements instead. The elegant technique by Hagström et al. (1979)—determining the frequency of dividing cells in a sample—offered this possibility. However, due to the laborious sample processing requirement, the technique did not achieve popularity among microbial ecologists. In spite of methodological limitations, the field of aquatic microbial ecology was quickly globalized in terms of spatial and temporal studies on rates and biomass in various habitats.

SAME MEETINGS SINCE EMMS 7

For about a decade, microbial ecology research proceeded with the quantification of rates and biomass in various habitats (e.g. Kirchman et al. 1982, Kirchman & Rich 1997, Ducklow 2000) and the characterization of regulatory mechanisms of bacterial growth (e.g. Pomeroy et al. 1991, Heinänen & Kuparinen 1992, Rivkin & Anderson 1997, Touratier et al. 1999), until molecular biology brought new tools to the field, enabling the identification of prokaryotic organisms at the species level and contributing information on functional groups of specific significance to the ecosystem. Today, the uptake of small molecules can be related to bacterial and archaeal species and to specific linkages between organisms in the microbial food web, as shown for example by Al-Sarawi et al. (2007). The results from the Arabian Gulf showed that sodium pyruvate was, in most cases, the carbon and energy source most commonly utilized by surface water bacteria, although the other test carbon sources were also utilized, but by fewer numbers of bacteria. The most common bacteria isolated on these other carbon sources were *Pseudoalteromonas*, *Vibrio*, *Cobetia* and *Roseobacter*.

Dissolved carbohydrates have been the major focus in the study of dissolved organic matter (DOM) dynam-

ics (Williams 2000). However, the role of dissolved proteins in shaping bacterial community structures has now also been demonstrated. During a spring phytoplankton bloom in North Sea waters (Sintes et al. 2007), a high exponential relationship between the abundance of *Phaeocystis* and the concentration of dissolved protein ($r = 0.96$) was found, indicating significant release of dissolved proteins and the possibility that dissolved protein dynamics might play a major role in shaping the bacterioplankton community composition in these waters.

An interesting new discovery is related to the global CO₂ cycle. A significant contribution of dark CO₂ incorporation was detected in the autotrophic processes at the whole lake level, and changes in prokaryotic community composition were clearly observed along vertical profiles (Casamayor et al. 2007). According to the vertical carbon fixation profiles, the chemolithoautotrophic guild comprises a metabolically complex, taxonomically diverse, active group of aerobic, microaerophilic, and anaerobic microorganisms that are finely adapted to vertical physico-chemical gradients and can coexist in the water column.

The SAME meetings have moved the focus from European microbial habitats to global microbial ecology and covered all common aquatic habitats, both fresh and seawater. The presented studies, however, underscore the logistic constraints in obtaining biological information on aquatic systems and have thus mostly focused on habitats close to research institutions and shallower waters, rather than more distant and volumetrically abundant open ocean waters, about which a minor amount of information is available. For instance, oceans contain 97% of the Earth's water, while lakes and rivers contain only 0.6% and the rest is trapped in polar ice and glaciers (2.4%). However, roughly half of the presentations still concern freshwater ecosystems (Table 1). Moreover, since 75% of ocean water is below the photic layer, we can truly say that microbial ecology has been focused on the illuminated compartment of aquatic systems, and only briefly touched the volumetrically more important part, the deep oceans (Herndl et al. 2005, 2008, this Special).

New and promising perspectives from SAME 10

While molecular biology provided new tools for all fields of biological sciences in the 1990s, the following decade was charged with hopes that new applications and discoveries in aquatic microbial ecology would further the understanding of species interactions and critical functions of the ecosystem. The EMMS 7 included promising openings for microbial diversity

Table 1. Distribution of lectures (%) given at select meetings from 2000 to 2007 across major aquatic systems. <<: small portion of 0.6% of global water. Baltic Sea ice is combined with polar ice and glaciers as it is comparable to first-year polar ice in terms of structure and brine channels

	Global distribution of water (%)	EMMS 7	SAME 8	SAME 9	SAME 10
Oceans (including Baltic Sea)	97	64	56	44	59
Polar ice and glaciers (including Baltic Sea ice)	2.4	0	3	9	1
Lakes	0.6	21	22	30	20
Rivers and streams	<<0.6	15	18	16	16
Groundwater	<<0.6	0	1	1	3

and evolution, and opened up perspectives on functions and organisms responsible for some of the key fluxes in the microbial food web. With the hopes of including new concepts in aquatic microbial ecology, the SAME 8 meeting became loaded with molecular biology lectures. However, many had little ecological relevance or connection to important fluxes of the ecosystem. New and exciting insights concerning the nitrogen cycle have been provided by studies on functional diversity and new discoveries of species and functions (e.g. anammox process), providing us with a new perspective on nitrogen regulation of aquatic systems (Kuenen 2008). Based on the outcome of the SAME 8 meeting, SAME 9 tried to stimulate more ecologically oriented lectures, and succeeded partially in reducing the number of molecular biology presentations. This attempt to focus more on ecology was continued during the SAME 10 meeting, extending the ecological scope even further to more societally relevant studies.

Light vs. dark domain, photostimulation and photochemistry

The influence of photochemistry on microbial processes has been presented at recent meetings (e.g. Tranvik & Bertilsson 2001). The observations demonstrated significant differences between light vs. dark incubations, thus addressing the relevance of the incubation conditions and the temporal scale of measurements. Tranvik & Bertilsson (2001) observed photostimulation of leucine incorporation rates (LIR) over the course of 1 yr when comparing dark vs. light incubations (paired *t*-test, $p < 0.001$, $n = 61$), thus questioning the widespread use of the dark incubation method. Consequently, incubations under *in situ* conditions should also include ambient light conditions.

Studies of bacterial particle attachments point out the importance of darkness for rate values. Ghiglione et al. (2007) showed pronounced diel variations in the activity of attached bacteria in the upper mixed water

column, with higher activities at night. Under mesotrophic conditions, the contribution of attached bacteria to total bacterial activity increased from less than 10% during daytime to 83% at night. Under summer oligotrophic conditions, free-living bacteria dominated and contributed the most important part of the bacterial activity during both day and night, whereas attached bacteria were much less abundant but presented the highest cell-specific activities. These diel and seasonal variations in activities were concomitant with changes in bacterial community structure. Based on capillary electrophoresis single-strand conformation polymorphism (CE-SSCP) analysis (Delbes et al. 2000, Hong et al. 2007), the number of attached CE-SSCP peaks suggested that particles are colonized by a relatively limited number of ubiquitous ribotypes. In addition, most of these ribotypes were free-living, suggesting that attached bacteria probably originate from the colonization of newly formed particles by free-living bacteria. The observations also point out the importance of *in situ* conditions in terms of light for accurate rate measurements (Ghiglione et al. 2007).

Steps have been taken recently to study waters of the dark ocean, as 75% of ocean water is in persistent darkness. Diving down into the darkness means that changes in pressure have to be taken into account. The conversion factors established for leucine and thymidine incorporation in surface waters may lead to strongly biased production estimates for the dark ocean without an adjustment for changes in pressure. The A-PROACH (adaptive pressurized ocean analysis chamber) (Steffen et al. 2003) can be a valuable instrument for the study of deep-sea microbial communities under realistic conditions, generating appropriate thermodynamic and hydrodynamic conditions. Tamburini et al. (2007) suggested that deep water carbon flux measurements do not account for enough carbon when compared to particle sedimentation studies. This discrepancy may derive from unnatural incubation conditions and wrong conversion factors; thus, studies in those directions have to be initiated. Realistic estimates of the levels of bacterial processes in deep

Oceans are vital for current models related to global change and carbon fluxes in the deep ocean. For example, in a study of chemoautotrophy in the North Atlantic, Reinthaler & Herndl (2007) suggested that in the top 500 m, chemoautotrophy was on average twice as high as heterotrophic prokaryotic production. In the deeper water layers, however, heterotrophic prokaryotic production was 4 times higher than chemoautotrophic production. Depending on the extent of primary productivity in the surface ocean, depth-integrated chemoautotrophy in the meso- and bathypelagic realm was in the range of 1 to 10%. Thus, on a basin-scale, chemoautotrophy might be an important and hitherto unrecognized sink of CO₂ in the dark ocean and a substantial source of primary production for the dark ocean's microbial food web.

A major advance in process studies at smaller spatial scales was made using microfluidic channels to study microbial behaviour and ecology in a patchy seascape (Seymour & Stocker 2007). The experiments revealed that some species of phytoplankton, heterotrophic bacteria and phagotrophic protists are adept at locating and exploiting microscale resource patches within time frames of <1 min. Microfluidics are a novel and flexible approach for studying aquatic microbial ecology, and due to its ability to accurately create realistic flow fields and substrate gradients at the microscale, it is ideally applicable to examinations of microbial behavior at the smallest scales of interaction.

An interesting 1-D model study of the role of semi-labile DOM was presented from the Hawaii Ocean Time-Series (HOTS) site (Luo & Ducklow 2007). The model represented bacteria-DOM processes differently from previous models in 4 ways, including (1) continuous lability of semi-labile DOM determined by nutrient content, (2) selective semi-labile DOM uptake by bacteria, (3) continuous inorganic nutrient limitation on bacterial growth even if DOM is enriched in nutrients, and (4) variable bacterial growth efficiency dependent on bacterial production. The model tentatively indicated that semi-labile DOM is a steady food source and on average can support up to half the bacterial carbon requirement. This study reveals the importance of semi-labile DOM to maintain the bacterial biomass, and may explain the largely uncoupled dynamics between primary and bacterial production.

Benthic realm

A major advance in sediment process studies has been made by combining microsensor measurements with sediment surface topography scanning in the Wuemme river bed (Janssen et al. 2007). The new approach allows improved understanding of biogeo-

chemical processes in advection-controlled systems. High flow velocities and the presence of ripples on the surface of the Wuemme river bed led to significant differences in oxygen distribution. Lower oxygen penetration depths were observed at the downstream slope of the ripple compared to the upstream slope. Together with additional measurements (current velocities, bed-form mobility, sediment permeability and oxygen consumption rates), the resulting topographies and oxygen distributions can also serve as a basis for numerical modeling in order to generalize the obtained findings.

Sea ice habitats

Despite the significance of this habitat, only a few studies have dealt with sea ice microbial communities (Sullivan & Palmisano 1984, Sullivan 1985, Kottmeier et al. 1987, Kottmeier & Sullivan 1988, Lizotte 2003). When seawater freezes, salt becomes concentrated in fine channel structures (the brine channels), which allow a microbial food web to develop and interact with the environment. Some basic knowledge exists on carbon and nitrogen processes within brine channels (Kottmeier et al. 1987, Priscu et al. 1990, Priscu & Sullivan 1998, Lizotte 2003, Kaartokallio et al. 2005, 2006), but the research is still in an early phase compared to other aquatic habitats. Moreover, the ongoing global change is most dramatically affecting sea ice in polar regions, and thus more solid knowledge on biological processes related to the meltdown is crucially needed. Near-zero temperature environments have been of interest for biotechnology concerning discoveries of enzyme adaptation and species evolution and distribution, but knowledge on functional diversity and the effect of melting and light regime on the biogeochemistry of sea ice habitats is scarce (Petri & Imhoff 2001, Brinkmeyer et al. 2003). However, the literature suggests that periodic high growth rates may be found within sea ice, but a comprehensive understanding of the effects on global ecology is still lacking (e.g. Dieckmann & Hellmer 2003).

SERVICES TO SOCIETY

Recognizing appropriate spatial and temporal scales and coupling with physical parameters

A large amount of biological activity is concentrated in restricted habitats, so called 'hot spots'. Hot spots cover different spatial scales from μm (Long & Azam 2001, Kaartokallio et al. 2006) to tens of km, as seen in harmful algal blooms in the Baltic (see Fig. 1), and

extending over hundreds of km as seen in global chlorophyll distribution from satellite images (global productive areas). Hot spots also cover temporal scales from minutes, as shown by the microfluidic technique (Seymour & Stocker 2007), to years as shown in the deep ocean volcanoes. Deep-ocean hot spots with persistence in space and time can be handled in terms of predicting the influence on the surrounding water bodies. The water column hot spots are more difficult to handle, as thorough knowledge of the ecology of the persisting species, their growth characteristics and the physical realm must be considered simultaneously. Further complication arises from the fact that patchiness appears differently with respect to biomass, particles and processes. All particle patches need not be hot

spots in terms of the process rates under study; thus, contradictory results may be obtained, with decreasing variability of measured rates at increasing scales as noted by Fuhrman & Steele (2008, this Special) and shown in the Baltic sediments by Tuominen et al. (1998).

The key to going forward with predictions on the role of the microbial food web in the fate of the ecosystem is to recognize the physical structures and their persistence in the water body, and identifying the hot spots in terms of spatial and temporal persistence. Current ecological models do not handle short-term, spatially restricted hot spot events adequately, although they may be crucial to the overall status of the aquatic systems. Harmful algal events have

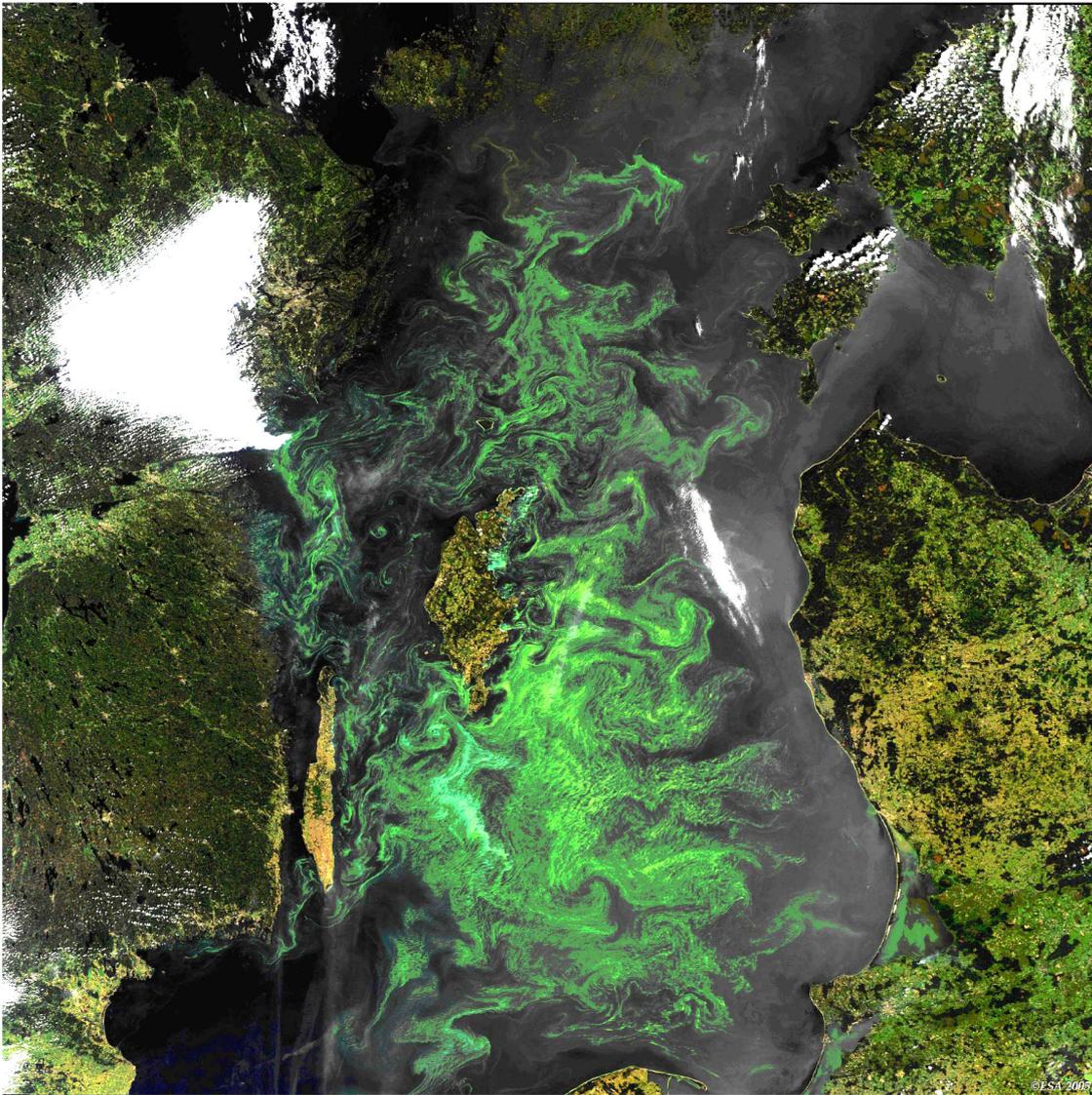


Fig. 1. Satellite image of algal blooms over the central Baltic Sea on 13 July 2005. This medium resolution imaging spectrometer (MERIS, orbit 17611) image shows a large population of algal blooms (green colour in the centre of the image). Available at: http://earth.esa.int/ew/special_events/Baltic_Sea_Algal/

helped in this direction. This was demonstrated with cyanobacteria in the Baltic Sea by Laanemets et al. (2006), who showed that several preconditions have to match to make the event harmful compared to ordinary summer growth (Fig. 2). At the smallest spatial and temporal scales, we are still lacking good techniques to study single cells and their influence on the physical environment. A recent discovery of *Synechococcus* fixing nitrogen at night time (Wasmund et al. 2001, Zehr et al. 2001) is a good example of a process that was overlooked because of an inappropriate measurement scale. Finding nitrogen-fixing genes together with a series of sensorial genes in cyanobacteria has opened up new questions as to how these genes respond to a changing environment, and the future may hold some answers concerning the interaction between the environment and toxin-producing genes.

And what about selecting a correct scale for experiments? The global carbon dioxide surplus in the atmosphere has raised a serious question of pumping CO₂ into the ocean via Fe enrichment of the high nutrient-low chlorophyll (HNLC) seas. Experiments at different scales (bottles and large-scale experiments) have shown that, theoretically, sequestration is possible, but other experiments have shown potential risks in large-scale enrichment experiments due to unpredictable physics and species development (Boyd et al. 2007). Although most of the scientific community is against the enrichment exercises, those in favor claim that the failures have been due to their small temporal and spatial scales. How far can we go with such messages from the part of the scientific community that risks Fe

enrichment of the seas? How should we present the scientific data and conclusions to society so they can be used as a basis for policy that is not detrimental to the ocean and global environment? A challenge for marine microbial ecologists and marine biogeochemists is to generate syntheses that are scientifically sound and at the same time accessible to policy makers.

Spatial and temporal scales of variability in bacterial assemblage composition

Fuhrman & Steele (2008) have recorded patterns in bacterial assemblages that are significant to ecological modeling and important knowledge for the general public. They found that, at the largest spatial scale, diversity is generally highest at low latitudes and lowest in polar environments, which is comparable to the basic pattern in animal and plant ecology reported in classical textbooks. The observations of microscale patchiness were comparable to other findings (e.g. Long & Azam 2001), resulting in approximations of regular patch sizes in oceans at km scales. The temporal scale observations have also been vital for improved ecological modeling, showing that communities change little within days, but markedly over months, yet reassemble to a similar composition after about a year, suggesting variability in species composition and functionality over seasonal scales (Fuhrman & Steele 2008). These observations from various aquatic systems imply that plankton patches are scaled according to the hydrographic properties of the system (pond, lake, sea) and to the seasons, so that physical structures more than nutri-

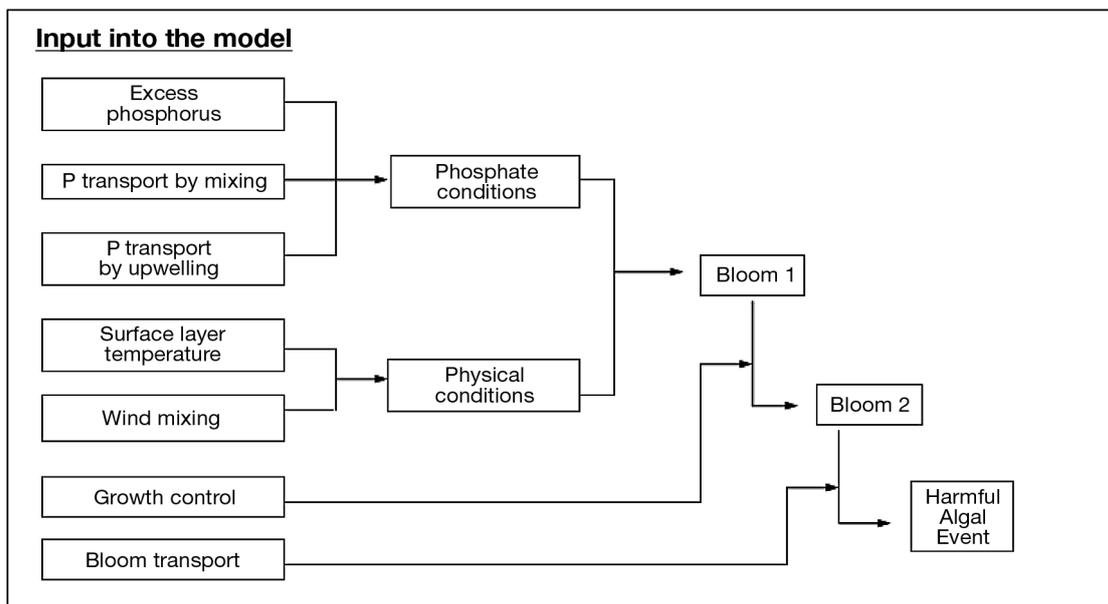


Fig. 2. Fuzzy logic model compartments for cyanobacterial blooms in the Baltic Sea. From Laanemets et al. (2006); used by permission

tional conditions regulate the patch size and the lifetime of a patch in terms of community structure and functionality.

Delivery of the message to society

SAME meetings have had a tendency to depart from their original ecological purpose towards the direction of specialized, detailed, and often genomic studies of specific microbes, which as such have been scientifically much appreciated, but remain isolated from the larger ecological context. Thus, we are faced with a situation where microbial ecology is becoming a confusing and uncertain topic for the wider public and the answers to societal environmental problems are not forthcoming in an accessible manner.

What is the role of the microbial food web in the process of global change, and what can we say from microbial ecology studies to enable societies to make a better world in terms of environmental quality? What other services can aquatic microbial ecologists provide to governments and environment regulating agencies? Are we able to tell managers how to improve water quality of aquatic habitats, and to provide them with advanced biotechnology and useful innovative techniques to facilitate water management? Is the information from our experiments significant for ecological modeling or do we need to increase/decrease our scales of experiments to produce more coherent views? Are models adequately handling microbial processes, microbial diversity and drivers of microbial ecology? These are some of the questions which remain to be answered for aquatic microbial ecology to be of service to society.

Accomplishment or failure in connection with society

Since most of the microbial ecology research falls in the good, excellent or superior category in scientific evaluations, then why are microbes hidden under the other 'main' levels of food webs in global modeling and regulation of the ecosystems? If the science has been good, where does this minute attention in global models come from and how do we solve this problem? Evidently we need to couple our research efforts into targeted environments with modeling activity together with physical and chemical oceanography as well as with fisheries biology, even though our primary interest would be to focus on microbial processes. The European Union has tried to force scientists to establish networking and in some cases with good success. However, top-down controlled science is not the best approach and thus microbial ecologists should 'sell

their wares' and convince global-scale modelers of the importance of microorganisms. As the saying goes 'small streams make a big river' and in many global processes prokaryotes are the organisms which turn the big wheel and keep it rolling. Understanding the environment of a single cell and its interaction with the environment should enable us by extrapolation to predict global processes. In the nitrogen cycle, this understanding has evolved rapidly and bacterial contribution in the global inventories has been generally accepted; however, in the carbon mass balance the microbial role is still far from fully understood, especially in terms of loss processes (del Giorgio & Williams 2005) and this should rapidly be corrected before further major questionable experiments, such as fertilizing the seas on a larger scale, are undertaken.

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