

**PAME-Nor: DOC turnover in polar microbial food webs.****Summary**

Microbial communities, including phytoplankton, protozoa, bacteria, archaea, fungi and virus, are by far the most abundant and the most taxonomic and genetically diverse group of organisms in marine pelagic ecosystems. Biological activity, biomass, production and remineralization in these systems are essentially microbial while higher trophic levels play a minor role in quantitative terms. Microorganisms are the main drivers of biogeochemical cycles and the major producers and consumers of green-house gases, and they are therefore significant players in regulating the ecosphere.

The main hypothesis of PAME-Nor is that heterotrophic bacteria in the photic zone of polar pelagic ecosystems may be in two different states, carbon- or mineral nutrient limited, and that the state realized directs the composition of the microbial community and the flux of carbon and other elements through the food web.

Our field experiments and campaigns will investigate the POC-DOC flux and the ability of the polar microbial ecosystems to consume organic material. By focussing on the role of the microbial food web in the ocean's C-cycle, our study will have direct implications for atmospheric uptake of CO<sub>2</sub> and thus the role of Polar oceans in climate change. Another highly relevant aspect of our research is that bioremediation and bacterial consumption of oil spills in Arctic waters may be anticipated to depend strongly on which of the two states the pelagic ecosystem reside in.

**Research objectives**

Our primary objective is to understand how trophic mechanisms in the microbial food web influence the balance between production and consumption of dissolved organic carbon (DOC) and to explore how such mechanisms in arctic waters can be understood using conceptual and numerical models developed for temperate waters.

In our present models, the nature of bacterial growth rate limitation is a key element in the coupling between production and consumption of DOC. Our secondary objectives are hence:

- To test the specific working hypothesis that heterotrophic bacteria in the photic zone of polar pelagic ecosystems may be in two different states with carbon- or mineral nutrient limited growth, respectively.
- To explore the consequences of these two different states for microbial biodiversity, for microbial food web structure and for element transfer pathways.

To achieve this we will

- Conduct field experiments in arctic ecosystems designed to test the hypothesis that DOC variations is linked to trophic control mechanisms and diversity in polar microbial food webs (WP 1).
- Conduct a field campaign to investigate how the physiological and nutritional state of the heterotrophic bacterial community varies over time and in space in selected arctic ecosystems and how these variations are coupled to microbial community structure and diversity (WP 2). The fulfilment of this WP is subject to ship-time availability, should ship-time not be available, the economic resources will be transferred to WP1.
- Conduct laboratory experiments where novel techniques, hypothesis and field observations are subjected to critical examination under controlled conditions (WP 3).

## **PAME and PAME-Nor**

The PAME consortium is a cluster of IPY proposals (EoIs) and a number of individual scientists/research groups (<http://www.uib.no/pame>). Each of these will as PAME subprojects seek national funding and logistic support for cruises, field work and research according to their own and national priorities. The overall objectives are nevertheless the same as outlined in the PAME proposal and the research will be carried out in close international collaboration. All subprojects funded will as far as possible contribute to other subprojects by providing access to field campaigns and by participation in field campaigns organized by others. The PAME Coordinating Committee will work to ensure that infrastructure and logistics are used efficiently, that samples can be obtained as required and that scientific expertise and analytical programs can be complemented to obtain complete datasets during all activities.

PAME-Nor will as subproject in PAME be responsible for two mesocosm experiments at Ny-Ålesund, Svalbard, and for a Barents Sea – Ice edge cruise. Other PAME sub-projects have implemented participation in these field activities in their plans and proposals and this participation is important although not indispensable for PAME-Nor. Due to budget restrictions PAME-Nor will only participate in other field campaigns to the extent that extra funding can be obtained. PAME-Nor will have the main responsibility for coordination of PAME.

The PAME-Nor added value to PAME is thus that we organize and provide logistics and infrastructure for two major field activities in the arctic region that are important also to other subprojects; and that we have taken responsibility for coordinating PAME as an IPY activity.

## **Polar microbiology**

### ***State of the art and challenges***

Many aspects of marine pelagic ecology can be understood from a simple nutrient-phytoplankton-zooplankton (NPZ) concept of a linear pelagic food web. An intensive research effort in marine microbiology over the last 2-3 decades has, however, made it very clear that the intermediate “phytoplankton” compartment in reality consists of a complex microbial food web containing both autotrophs and heterotrophs, osmotrophs (feeding on dissolved substrates) and phagotrophs (ingesting particles). There are mixotrophic forms of eukaryotic organisms combining these life strategies, as there are bacteria mixing heterotrophy with different light-based energy acquisition mechanisms, both cases blurring the traditional autotroph-heterotroph distinction in food web concepts. There are also viruses, probably infecting all microbial groups, influencing diversity as well the biogeochemical pathways, and there members belonging to the *Archea* kingdom, with a role in this microbial food web not yet understood.

Even more than describing the members of this microbial food web, the present challenge is to understand how they act together as a system, and whether there are fundamental differences in this system’s behaviour in Polar when compared to temperate waters. There are data to suggest that system behaviour can be understood in much the same manner in polar as in temperate waters (Kirchman et al. 2005; Thingstad and Martinussen 1991) indicating that availability of nutrients, light, and hydrographical properties of the water column are the essential driving forces explaining differences in food web behaviour. There has, however, also been claims that differences in temperature adaptation in different groups of micro-organisms (Pomeroy and Deibel 1986; Pomeroy and Wiebe 2001) leads to more fundamental differences in this part of the pelagic ecosystem when comparing polar with temperate waters.

For PAME-NOR, our working hypothesis is the conservative one that polar microbial food webs are driven by essentially the same mechanisms as temperate ones. This does not mean that the necessary result is similarly structured microbial food webs in polar and temperate waters. One essential driving force is believed to be the predation pressure creating cascading top-down effects in this tightly coupled food-web, another is nutrient availability. Since polar copepods have seasonal vertical migration patterns and since water column stability has particular characteristics in e.g. areas with melt-water from ice, the result may very well be special properties in polar microbial food webs.

### ***Climate change***

Microbial food web behaviour is a pivoting point where issues such as biogeochemistry and food production for higher trophic levels link with biodiversity, organism physiology and life strategies at the microbial level. By focussing on the role of the microbial food web in the ocean's C-cycle, our study will have direct implications for the role of Polar oceans in climate change. Due to the interconnectedness, however, our study will by necessity also involve the other issues. Our experiments and investigations will focus on the ability of the polar microbial ecosystems to consume organic material. Accumulation of un-degraded organic material, and thus an increasing potential for uptake of atmospheric CO<sub>2</sub> obviously implies a decoupling between production and consumption. Our proposal is designed to improve our understanding of the mechanisms in the system leading to such decoupling.

### ***Scientific rationale and hypothesis***

Present theory (e.g. Thingstad et al. 2002) and observation indicate that the microbial part of the pelagic ecosystem may have two states, one where the growth rate of heterotrophic bacteria is limited by the supply of bioavailable organic carbon, and the other where the growth rate is limited by another element (typically N, P or Fe) (e.g. Havskum et al. 2003; Pomeroy et al. 1995; e.g. Rivkin and Anderson 1997; Thingstad et al. 2005; Van Wambeke et al. 2002; Zohary et al. 2005). The potential implications for the ocean's carbon cycle are large since, in the mineral nutrient limited state, bacterial carbon demand may not match the autochthonous production of organic carbon in the system, and DOC may theoretically accumulate in the photic zone, even in forms otherwise easily accessible to biodegradation. Understanding the mechanisms leading to the two states is also fundamental to understanding how the microbial part of the food web works in polar regions; if bacteria are C-limited, one would expect the temperature dependence of bacterial activity to follow the temperature dependence of the autochthonous processes releasing bioavailable organic carbon from the food web, while in the mineral nutrient limited state, it would be the temperature dependence of the mechanisms controlling remineralization and algal-bacterial competition for mineral nutrients that determines bacterial activity.

Since the competitive challenges forcing the bacterial community would be very different in the two cases, presumably selecting for "C-specialists" and "mineral nutrient specialists", respectively, we hypothesize that the composition of the bacterial community, and then also the community of bacteriophages (Thingstad 2000) is related to the two states of limitation.

Present evidence of the status of bacterial limitation in polar waters seems to indicate that both states occur. Graneli et al. (2004) concluded on C-limitation from a cruise covering different zones in the Southern ocean, as did Oliver et al. (2004) from studies during the SOFeX iron-fertilization experiment. Arrieta et al. (2004), however, concluded on bacterial Fe-limitation during the EisenEx experiment. High arctic lakes and ponds have been concluded to have P-limited bacteria (Graneli et al. 2004), while some information from the Arctic Ocean seem to indicate C-limited bacteria (Kirchman et al. 2005).

***The main hypothesis of PAME-Nor is that heterotrophic bacteria in the photic zone of polar pelagic ecosystems may be in two different states, carbon- or mineral nutrient limited, and that the state realized directs the composition of the microbial community and the flux of carbon and other elements through the food web.***

We will look at the mechanisms leading to these two states, their consequences for the marine C-cycle, for microbial biodiversity, and for element fluxes through the pelagic food web in polar regions.

The implications of such a hypothesis are more profound than perhaps visible at first sight. In terms of the oceanic C-cycle, the dissolved organic (DOC) pool is the second largest (next to DIC) reservoir of carbon in the marine pelagic, containing about an order of magnitude more carbon than the particulate (POC) pool. Only a decade ago, this large DOC pool was considered inert, and

of little importance for our understanding of the dynamic role of the ocean in the global C-cycle. Following the introduction of more precise methodologies, however, it has been shown that the photic zone ecosystem can have a DOC pool that is highly dynamic over seasonal time scales; concentrations typically doubling during the stratified season; making the POC-DOC fluxes a quantitatively important part of the oceanic C-cycle. Seasonal accumulation has been found in environments with highly different environmental characteristics such as the Mediterranean (Copin-Montegut and Avril 1993) and the North Atlantic (Børshheim and Mykkestad 1997; Børshheim 2000), differing not only in temperature, but also in seasonal light cycle and stratification patterns. Since this accumulation is not locked to nitrogen and phosphorous in a Redfield stoichiometry, at least not to the same degree as POC, transport of this material to deep waters by mixing is controlled in manners fundamentally different from those controlling the particulate C-pump.

Another highly relevant aspect in Norway is that of bioremediation. With increased Russian and Norwegian oil transport and exploration expected in the Barents Sea, an understanding of the mechanisms controlling the fate of an oil spill would seem an urgent priority. It is well established that bacterial degradation of crude oil in the marine environment is limited, not primarily by the presence of a bacterial sub-population with the special enzymatic machinery required for hydrocarbon oxidation, but by the lack of mineral nutrients required for growth of this sub-population (Al-Darbi et al. 2005; Atlas 1981; Atlas 1985). The possibilities for bacterial consumption of oil spills in Arctic waters would thus be expected to depend strongly on which of the two states the pelagic ecosystem reside in.

The build-up of DOC in the top layer implies a decoupling between production and bacterial consumption of the material. Two, not mutually exclusive, mechanisms have been suggested for this decoupling: The material may 1) be in a chemical form making it inaccessible to the bacteria over the appropriate time scale (weeks-months) and at the ambient temperature of the ecosystem in question, or 2) bacterial growth is limited by other elements (e.g. N, P or Fe), preventing sufficient activity to consume the otherwise bioavailable pool of DOC (BDOC) at a rate matching that at which it is produced.

The principles behind present theories linking food web structure to bacterial growth rate limitation can be heuristically understood without the help of mathematical models: In a food web dominated by osmotrophs (organisms feeding on dissolved substrates, i.e. phytoplankton and bacteria), there will be little recycling, high competition for mineral nutrients, and high probability for mineral nutrient limitation of heterotrophic bacteria. In this situation, one would expect a succession with biomass moving “upwards” in the food web towards predators, thereby decreasing the competitive pressure among remaining osmotrophs at the same time as recycling increases; the expected effect being an increased probability for a shift to C-limitation of the heterotrophic bacteria (Thingstad et al. submitted). Interfering with this is of course the release of organic substrates from differently structured food webs. From the above argument, one would also expect the rate at which the osmotroph-phagotroph successions proceed, to influence the timing of the system transition from mineral-nutrient limited to C-limited bacteria. Since the diatom-copepod transfer is slower than the trophic transfer from small flagellates to micro-zooplankton, the consequence is that diatom-dominated communities would be expected to have a higher probability for staying in the state with mineral nutrient limited bacteria. This prediction of the theory has been confirmed experimentally in mesocosm experiments (Havskum et al. 2003) following the consumption of added glucose by planktonic systems perturbed with mineral nutrients (nitrate and phosphate) in the presence and absence of silicate.

Attempting to model mathematically the observed responses (Thingstad et al. in press), we found it impossible to reproduce the observed differences in primary production between diatom and non-diatom dominated communities, without assuming a strong tendency towards C-overflow production in diatoms, i.e. a mechanism whereby diatoms continue to fix carbon, even when the production of new cells is restricted due to mineral nutrient limitation. The consequence would seem to be that C-fixation may be under strict nutrient control in flagellate-dominated systems, while in diatom-dominated systems, light would be expected to be the more immediate controlling

factor. A higher than Redfield organic-C:mineral nutrient ratio in diatom dominated mesocosms seems to be a repeated observation in mesocosms (Egge and Jacobsen 1997) and diatom dominance thus also seems to influence the production as well as the consumption side of the organic material production-consumption balance, both mechanisms shifting the system towards the state with mineral nutrient limited bacteria. Since the diatom dominance is very variable both along longitudinal transects in the Greenland Sea (Erga et al. 2005), in the Barents Sea spring blooms (Luchetta et al. 2000; Pautova and Vinogradov 2001; Rat'kova and Wassmann 2002; Wassmann et al. 1999), and in the Southern Ocean (Garibotti et al. 2005a; Garibotti et al. 2005b; Korb et al. 2005; Leblanc et al. 2005), the diatom influence on the state of the pelagic food web, and therefore Si availability and other factors controlling diatom abundance in polar waters links closely into our focus in PAME-Nor.

Our theoretical considerations suggested that food webs with biomass shifted “upwards” towards zooplankton would be likely to have C-limited bacteria. One particular aspect of polar ecosystems is the seasonal copepod hibernation in deep waters with subsequent spring migration to the photic zone. Polar systems may thus have a kind of “inverted succession”, starting with high zooplankton biomass in the spring before the phytoplankton bloom, and ending with low biomass in the autumn as the down-migration depletes the surface layer of its copepod stock. Applying the above arguments to the Disco Bay ecosystem, data seem to support the expectation of C-limited bacteria in the period with copepod presence, possibly shifting to mineral nutrient limitation in conjunction with the autumn depletion of the surface layer copepod stock (Thingstad et al. 2002). More investigations would be needed from other regions before this could be generalized, but it illustrates the need for a system approach in order to understand the behaviour of polar ecosystems.

### **Work Packages**

The core experimental work (WP 1) consists of two mesocosm experiments (2007 and 2008) at Ny-Ålesund (Spitsbergen), using water collected in the photic zone in Kongsfjorden outside of the silt-containing region influenced by land run-off. In order to make as direct comparisons as possible with a more temperate system (Isefjorden, Denmark), we will in 2007, with minor modifications, follow the experimental design of Havskum et al. (2003). The experiment in 2008 will primarily serve as a safety back-up option in case the 2007 experiment fails. Should the 2007 experiment work successfully and not leave us with the need for a replication, we will use the 2008 opportunity to run a different design. One possibility would be to study the effects of light on algal-bacterial competition; thus simulating one of the effects of changing ice-cover.

The field campaign (WP 2) will be designed to help us extrapolate from the mesocosm experiments. We will select a core set of measurements thought to provide us with key information on the C-limited versus mineral nutrient limited state of the heterotrophic bacteria, and collect a sufficient set of other measurements to be able to test our hypotheses on how these states are related to the structure of the photic zone pelagic food web. We also want to use the campaigns to collect samples to test the hypothesis that the bacterial and viral community compositions are related, and forced by the C-limited versus mineral nutrient limited status. Since availability of ship-time is not secured, execution of WP2 is conditioned by granting of ship time. Should it turn out impossible to arrange for suitable cruise work, the economic resources allocated to WP2 will be transferred to WP1 to allow a more complete measurement programme in the mesocosm experiments.

The research carried out as mesocosm experiments and during the field campaign will be corroborated by experimental studies under controlled conditions in the laboratory (WP 3). Some of the core measurements are based on novel techniques and hypothesis and need further testing in the laboratory to verify their use on arctic microbial communities growing at low temperature. We will also include experiments to study the role of nutrient availability and temperature on the elemental composition and physiological condition of different microbial populations, and the effect of these environmental variables on microbial and viral activity, trophic control mechanisms and population interactions.

Outreach activities and coordination of PAME are described WP4 and WP5 respectively.

### WP 1: Field Experiments at Ny Ålesund, Svalbard 2007 experiment

**Tentative design:** Modified after Havskum et al. (2003) we plan to use 10 experimental units (Fig. 1), 8 of these will receive a daily dose of nitrate and phosphate (50 nM) in Redfield ratio, but split into two gradients (denoted -Si and +Si in Fig.1) of increasing daily additions of an easily degradable source of organic-C (probably as glucose) receiving 0x, 0.5x, 1x, and 3x the Redfield ratio in organic-C, relative to the mineral nutrient addition. The two remaining units will be used as controls, one with no addition to check the effect of water enclosure alone, and one with 3x organic-C to check the effect of adding organic material but no mineral nutrients. The two gradients will run in parallel until the naturally occurring Si starts to become depleted, thereafter Si will be added to keep the +Si gradient replete in free Si.

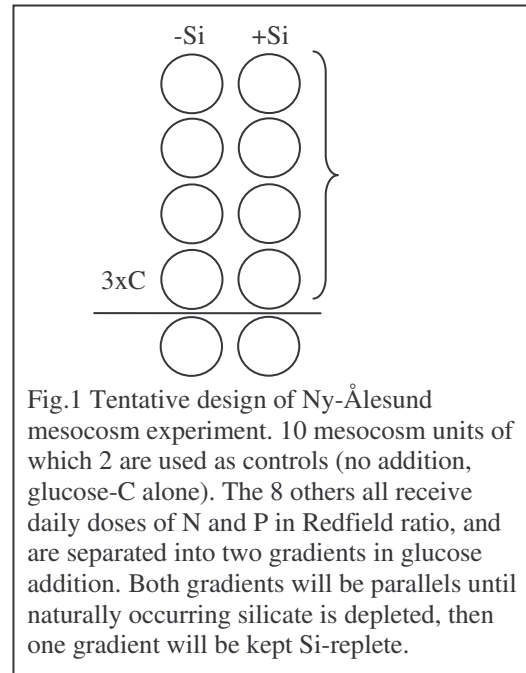


Fig.1 Tentative design of Ny-Ålesund mesocosm experiment. 10 mesocosm units of which 2 are used as controls (no addition, glucose-C alone). The 8 others all receive daily doses of N and P in Redfield ratio, and are separated into two gradients in glucose addition. Both gradients will be parallel until naturally occurring silicate is depleted, then one gradient will be kept Si-replete.

### 2008 experiment

Should we conclude that there is no need to replicate the 2007 experiment we foresee a design in 2008 using shaded microcosms to study the effect of reduced light conditions on degradation of organic-C. Such a design could allow us to include treatments with crude oil as an extra C-source. We expect, however light to have more complicated effects in this case since illumination of crude oil both produces strongly toxic photo-oxidation products (Pengerud et al. 1984), affects the emulsion-forming properties of the oil (Thingstad and Pengerud 1983), and probably also release water soluble, degradable products to the water.

### **Tentative list of variables to be measured:**

Due to the restricted budget, we will design a minimum set of measurement parameters to be financed over the IPY grant, probably including:

- dissolved nutrients (DIN, DIP, DOC, Si)
- size spectra of chl-a and biomass (based on XRF-determination of the elements C,N,P and Si)
- affinity and physiological measurements to determine type of limitation for bacterial growth.

While this should give us data that allows us to address our main hypothesis of a connection between food web structure, mineral nutrient limited bacterial growth, it will not provide us with any detailed information, neither on rates, population dynamics, nor on biodiversity. The potential return on the heavy investment in setting up and running the mesocosms will thus be poorly exploited. Additional measurements wanted in order to characterise the microbial responses include :

**Standing stocks:** Microbial pico- and nano-plankton by flow cytometry and micro-plankton by FlowCam. Microscopic counts for heterotrophic flagellates. Meso-zooplankton counts, species composition and biomass, initial and end. Degradable part of the DOC-pool.

**Rates:** Bacterial production by <sup>3</sup>H-leucine, primary production by <sup>14</sup>C, oxygen consumption / production by light/dark bottles and optode. Grazing rates by micro-zooplankton, gut content in copepods by molecular methods.

Diversity: Denaturant Gradient Gel Electrophoresis for bacterial diversity (DGGE) and Pulse-Field Gel Electrophoresis (PFGE) for viral diversity.

To the extent possible such measurements will be included, either as contributions from other PAME-partners, or by financing sought from other sources.

**Practical issues:** The project is registered at The Marine Laboratory / Kings Bay and preliminary booking has been made. The new 31' workboat purchased by Kings Bay in 2006 may be used for collecting water if near-shore water should be too silt-containing. Ny Ålesund was visited in summer 2006 for planning and discussions of practical issues.

### **WP 2: Field Campaign. Barents Sea-Ice edge - Cruise**

Due to economic constraints, WP2 has in this revised proposal been reduced from five to a single field campaign. This will be a dedicated biological – biogeochemical cruise in the Barents Sea - Ice edge region. The aim will be to help us extrapolate mesocosm results to natural arctic waters.

Measurement programme will be designed based on the same philosophy as in WP1. To be able to compare results, the same set of core parameters will be included in WP1 and WP2. Additional measurements will be added to WP2, subject to economic and also logistic constraints (e.g. berths available). The sampling and measurement programmes will be co-ordinated with other research teams that participate in the field campaign.

We anticipate the cruise to be a coordinated national IPY activity and remain flexible with respect to transects and timing. Several of our collaborators have expressed their interest in participating in the cruise. Should it turn out impossible to obtain suitable ship-time, the economic resources for WP2 will be transferred to WP1 to allow a more complete measurement programme for the 2008 mesocosm experiment.

### **WP 3: Laboratory studies**

The objective of this work package is to establish an experimental basis for confident interpretation of field data. Based on experiments in cold waters (Raunefjorden, western Norway) we have strong reasons to believe that the elemental composition (e.g.  $[Mg^{2+}]/[Na^+]$  ratio) of single cells and communities is a signature of nutritional status and physiological condition and hence that it may be used as an indicator of carbon vs. inorganic nutrient limitation, and that it relates to regulation of viral activity. The hypothesis is based on compelling experimental studies and field observations (Heldal et al. 2005; Tuomi et al. 1995; Vrede et al. 2002) but further studies are required to confirm that the approach is applicable to arctic microbial communities growing in cold waters.

We know that the Mg content of marine bacteria is very variable, with shifts for the whole population apparently linked to growth conditions (Heldal et al. 2005). The hypothesis is that the production of organic osmolytes is too expensive during periods when the heterotrophic bacteria are C-limited and that the lack of organic osmolytes somehow is being compensated by an increased Mg-content which is detectable as an increased cellular  $[Mg^{2+}]/[Na^+]$  ratio. Laboratory experiments with arctic microbial assemblages and pure cultures of psychrophilic bacteria will be designed to test the hypothesis and to underpin interpretation of field data. With a confirmative conclusion we will have an elegant and incubation-free method to determine the limitation status of bacteria in marine ecosystems which will be an invaluable tool for understanding the dynamics of DOC variations and their relation to trophic control mechanisms.

Viruses depend on their host for proliferation and viral activity in natural ecosystems is thus expected to be closely linked to the nutritional status and physiological condition of the bacterial community. Experiments will be conducted to test if viral production and frequency of visibly infected cells can be related to detectable changes in cellular elemental composition. If such a

relation can be established we may be able to interpret and understand the rapid changes in viral abundance and in frequency of infected cells observed in natural ecosystems (Bratbak et al. 1990; Bratbak et al. 1992; Heldal and Bratbak 1991; Hennes and Simon 1995; Jiang and Paul 1994; Rodriguez et al. 2000; Weinbauer et al. 1995). Microbial activity, physiological processes, the frequency of dead, dormant and active cell, and microbial interactions (e.g. competition and predation) may in addition to nutrient availability also regulated by temperature.

#### **WP 4: Outreach**

We will as a general activity use every opportunity to communicate to the general public via web pages, TV, radio and newspapers the importance of our research and the historical significance IPY. The overall objective for this activity will be to increase public understanding of the important role bacteria and other microorganisms play in natural marine ecosystems.

For public outreach of the PAME and the PAME-Nor activities we will collaborate with the Communication and Media department at UiB and their television production unit Univisjon (<http://www.univisjon.no>). Teams from Univisjon will record broadcast quality videomaterial from field and other research activities. This material may be used to illustrate and impart knowledge about the ecological significance and importance of marine microbes in polar regions. Univisjon will identify topics, cases and activities suitable for TV and web-TV presentation. They will edit short stories suitable for magazine programs and web-tv. In addition to this they will develop an idea for a documentary about the subject.

The Univisjon producers and directors have extensive experience in producing and developing science TV-documentaries and series that reach out to a wide audience and increase popular knowledge and understanding of science.

#### **WP 5: Coordination of PAME**

The Marine Microbiology Research Group has played an active and leading role in organizing and developing PAME as a research activity in IPY and it is our ambition to maintain a leading role in PAME also during the IPY. Our role in this position will be to ensure that all members of PAME work together to reach our common research objectives as outlined in the PAME project description and to meet our obligations to IPY as articulated in current policy documents.

Most of the work will be carried out through open e-mail communication and discussions but meetings and workshops will be instrumental to efficient planning and organization. We will also maintain a webpage for internal information, exchange of data and public outreach. The details of this work package have to await decisions regarding national funding of PAME partners and sub-projects but we foresee that we need a “kick-off” meeting in early 2007, a workshop for discussion of results and further planning in late 2007 - early 2008, and a closing workshop in the first half of 2009. Travel costs will be on the participants but we funding to cover a minimum of organisational costs have been included in the budget.

The coordination activity will be important to make PAME a successful research activity in IPY, but the costs will be kept at a minimum. Three person months per year to coordinate the various research activities and ensure efficient communication between the participating scientists, to organize outreach and to maintain web pages should be sufficient. Travel money for the activity leader to attend meetings and to meet with other subprojects in PAME has also been included in the budget.

#### **Quality and capability of the research group**

The Marine Microbiology Research Group includes three professors/senior scientists, five associate professors, research scientists and post docs, four PhD students, three laboratory engineers and 4-8 master students. The overall objective of the group's research is to establish a better experimental and theoretical fundament for understanding how biodiversity, population dynamics, and biogeochemical cycling are controlled in the marine pelagic ecosystem. The group has over the last

20 years played an active role in establishing the presence of the microbial part of the food web, its structure and its function. During the last 10 years 120 articles in internationally refereed journals with an accumulated citation score of more than 5000 times (ISI statistics March 2006), has been published with co-authors from this group. We have developed methods for determining the biomass and elemental composition of microorganisms in natural samples and pioneered research on the ecological significance of viruses. The work is closely linked to development of conceptual and mathematical models that integrate biogeochemical cycling, microbial diversity, population dynamics and trophic interactions into one common theoretical framework. The research group has a considerable joint experience in management of large research projects, in designing and conducting mesocosm experiments, and in carrying out field campaigns.

The group has excellent research facilities with state of the art instrumentation covering most aspects of modern microbiological and molecular techniques. Of special relevance to the present project is our flowcytometer lab with a FACSCalibur and a FACS Aria for routine analysis and high speed sorting of cells and viruses, and a FlowCam for counting and imaging of microplankton (20-200 $\mu$ m). The chemical lab has a Shimadzu TOC-5000 total organic carbon analyzer and a dedicated capillary spectrophotometer for high sensitivity measurements of phosphate (detection limit ~10nM P). A Bruker S4 Pioneer XRF analyzer for bulk measurements of elemental composition (C - U) of marine particles will be installed is installed autumn 2006, and is expected to provide an exceptional facility for precise, and rapid determination of POM multi-elemental composition. Excellent electron microscope facilities with TEM and SEM equipped for X-ray microanalysis are available at the University of Bergen, Science Faculty.

We enjoy a worldwide research network and collaborate with outstanding scientists in PAME that that will complement our in-house qualifications and resources on specific work packages.

## LITERATURE CITED

- Al-Darbi, M. M., N. O. Saeed, M. R. Islam, and K. Lee. 2005. Biodegradation of natural oils in seawater. *Energy Sources* **27**: 19-34.
- Arrieta, J. M., M. G. Weinbauer, C. Lute, and G. J. Herndl. 2004. Response of bacterioplankton to iron fertilization in the Southern Ocean. *Limnology and Oceanography* **49**: 799-808.
- Atlas, R. M. 1981. Microbial degradation of petroleum hydrocarbons: An environmental perspective. *Microbiol.Reviews* **45**: 180-209.
- . 1985. Effects of hydrocarbons on microorganisms and petroleum biodegradation in Arctic ecosystems., p. 63-99. *In* Engelhardt [ed.], *Petroleum effects in the arctic environment*. Elsevier App.Sci.Publ. N.Y.
- Bratbak, G., M. Heldal, S. Norland, and T. F. Thingstad. 1990. Viruses as partners in spring bloom microbial trophodynamics. *Applied and Environmental Microbiology* **56**: 1400-1405.
- Bratbak, G., M. Heldal, T. F. Thingstad, B. Riemann, and O. H. Haslund. 1992. Incorporation of Viruses into the Budget of Microbial C-Transfer - a 1st Approach. *Marine Ecology-Progress Series* **83**: 273-280.
- Børsheim, K., and S. Myklestad. 1997. Dynamics of DOC in the Norwegian Sea inferred from monthly profiles collected during 3 years at 66 degrees N, 2 degrees E. *Deep Sea Res. Part I* **44**: 593-601.
- Børsheim, K. Y. 2000. Bacterial production rates and concentrations of organic carbon at the end of the growing season in the Greenland Sea. *Aquat. Microb. Ecol.* **21**: 115-123.
- Copin-Montegut, G., and B. Avril. 1993. Vertical distribution and temporal variation of dissolved organic carbon in the North-Western Mediterranean Sea. *Deep Sea Res.* **40**: 1963-1972.
- EGGE, J. K., and A. Jacobsen. 1997. Influence of silicate on particulate carbon production in phytoplankton. *Mar.Ecol.Prog.Ser.* **147**: 219-230.
- Erga, S. R., K. Aursland, Ø. Frette, B. Hamre, J. K. Lotsberg, J. J. Starnes, J. Aure, F. Rey, and K. Starnes. 2005. UV transmission in Norwegian marine waters: controlling factors and possible effects on primary production and vertical distribution of phytoplankton. *Mar.Ecol.Prog.Ser.* **305**: 79-100.
- Garibotti, I. A., M. Vernet, and M. E. Ferrario. 2005a. Annually recurrent phytoplanktonic assemblages during summer in the seasonal ice zone west of the Antarctic Peninsula (Southern Ocean). *Deep-Sea Research Part I-Oceanographic Research Papers* **52**: 1823-1841.
- Garibotti, I. A., M. Vernet, R. C. Smith, and M. E. Ferrario. 2005b. Interannual variability in the distribution of the phytoplankton standing stock across the seasonal sea-ice zone west of the Antarctic Peninsula. *Journal of Plankton Research* **27**: 825-843.
- Graneli, W., S. Bertilsson, and A. Philibert. 2004. Phosphorus limitation of bacterial growth in high Arctic lakes and ponds. *Aquatic Sciences* **66**: 430-439.
- Havskum, H., T. F. Thingstad, R. Scharek, F. Peters, E. Berdalet, M. M. Sala, M. Alcaraz, J. C. Bangsholt, U. L. Zweifel, A. Hagstrom, M. Perez, and J. R. Dolan. 2003. Silicate and labile DOC interfere in structuring the microbial food web via algal-bacterial competition for mineral nutrients: Results of a mesocosm experiment. *Limnol.Oceanogr.* **48**: 129-140.
- Heldal, M., and G. Bratbak. 1991. Production and Decay of Viruses in Aquatic Environments. *Marine Ecology-Progress Series* **72**: 205-212.
- Heldal, M., S. Norland, E. S. Erichsen, G. Bratbak, R.-A. Sandaa, A. Larsen, and F. Thingstad. 2005. Mg<sup>2+</sup> plays an important role in marine bacteria. Abstract. American Society for Limnology and Oceanography (ASLO) Summer Meeting, Santiago de Compostela, Spain, June 19-24, 2005.
- Hennes, K. P., and M. Simon. 1995. Significance of bacteriophages for controlling bacterioplankton growth in a mesotrophic lake. *Appl. Environ. Microbiol.* **61**: 333-340.

- Jiang, S. C., and J. H. Paul. 1994. Seasonal and Diel Abundance of Viruses and Occurrence of Lysogeny/Bacteriocinogeny in the Marine-Environment. *Marine Ecology-Progress Series* **104**: 163-172.
- Kirchman, D. L., R. R. Malmstrom, and M. T. Cottrell. 2005. Control of bacterial growth by temperature and organic matter in the Western Arctic. *Deep-Sea Research Part II-Topical Studies in Oceanography* **52**: 3386-3395.
- Korb, R. E., M. J. Whitehouse, S. E. Thorpe, and M. Gordon. 2005. Primary production across the Scotia Sea in relation to the physico-chemical environment. *Journal of Marine Systems* **57**: 231-249.
- Leblanc, K., C. E. Hare, P. W. Boyd, K. W. Bruland, B. Sohst, S. Pickmere, M. C. Lohan, K. Buck, M. Ellwood, and D. A. Hutchins. 2005. Fe and Zn effects on the Si cycle and diatom community structure in two contrasting high and low-silicate HNLC areas. *Deep-Sea Research Part I-Oceanographic Research Papers* **52**: 1842-1864.
- Luchetta, A., M. Lipizer, and G. Socal. 2000. Temporal evolution of primary production in the central Barents Sea. *Journal of Marine Systems* **27**: 177-193.
- Muller, F. L. L., and A. Larsen. 2004. Interactions between algal/bacterial populations and trace metals in fjordic surface waters during a nutrient-stimulated diatom bloom. *Abstracts of Papers of the American Chemical Society* **227**: U1106-U1107.
- Oliver, J. L., R. T. Barber, W. O. Smith, and H. W. Ducklow. 2004. The heterotrophic bacterial response during the Southern Ocean Iron Experiment (SOFeX). *Limnology and Oceanography* **49**: 2129-2140.
- Pautova, L. A., and G. M. Vinogradov. 2001. Southeastern Barents Sea plankton in April 2000. *Oceanology* **41**: 211-217.
- Pengerud, B., F. Thingstad, K. Tjessem, and A. Aaberg. 1984. Photo-induced toxicity of North Sea crude oils toward bacterial activity. *Mar.Pollut.Bull.* **15**: 142-146.
- Pomeroy, L. R., and D. Deibel. 1986. Temperature regulation of bacterial activity during the spring bloom in Newfoundland coastal waters. *Science* **233**: 359-361.
- Pomeroy, L. R., J. E. Sheldon, W. M. J. Sheldon, and F. Peters. 1995. Limits to growth and respiration of bacterioplankton in the Gulf of Mexico. *Mar.Ecol.Prog.Ser.* **117**: 259-268.
- Pomeroy, L. R., and W. J. Wiebe. 2001. Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria. *AQUATIC MICROBIAL ECOLOGY* **23**: 187-204.
- Rat'kova, T. N., and P. Wassmann. 2002. Seasonal variation and spatial distribution of phyto- and protozooplankton in the central Barents Sea. *Journal of Marine Systems* **38**: 47-75.
- Rivkin, R., and M. Anderson. 1997. Inorganic nutrient limitation of oceanic bacterioplankton. *Limnol.Oceanogr.* **42**: 730-740.
- Rodriguez, F., E. Fernandez, R. N. Head, D. S. Harbour, G. Bratbak, M. Heldal, and R. P. Harris. 2000. Temporal variability of viruses, bacteria, phytoplankton and zooplankton in the western English Channel off Plymouth. *Journal of the Marine Biological Association of the United Kingdom* **80**: 575-586.
- Thingstad, T., and B. Pengerud. 1983. The Formation of Chocolate Mousse from Statfjord Crude-Oil and Seawater. *Mar Pollut Bull* **14**: 214-216.
- Thingstad, T. F. 2000. Elements of a theory for the mechanisms controlling abundance, diversity, and biogeochemical role of lytic bacterial viruses in aquatic systems. *Limnol.Oceanogr.* **45**: 1320-1328.
- Thingstad, T. F. and others in press. Ability of a "minimum" microbial food web model to reproduce response patterns observed in mesocosms manipulated with N and P, glucose, and Si. *J Mar. Systems*.
- Thingstad, T. F., T. Kragh, and M. Søndergaard. submitted. Trophic control mechanisms for the consumption of bioavailable allochthonous DOC: Interpretation of mesocosm results using a conceptual model. *Limnol.Oceanogr.*
- Thingstad, T. F. and others 2005. Nature of phosphorus limitation in the ultraoligotrophic eastern Mediterranean. *Science* **309**: 1068-1071.

- Thingstad, T. F., and I. Martinussen. 1991. Are bacteria active in the cold pelagic ecosystem of the Barents Sea? *Polar Research* **10**: 255-267.
- Thingstad, T. F., T. G. Nielsen, A. S. Hansen, and H. Levinsen. 2002. Control of bacterial production in cold waters. A theoretical analysis of mechanisms relating bacterial production and zooplankton biomass in Disko Bay, Western Greenland. *Mar Ecol-Prog Ser* **228**: 15-24.
- Tuomi, P., K. M. Fagerbakke, G. Bratbak, and M. Heldal. 1995. Nutritional Enrichment of a Microbial Community - the Effects on Activity, Elemental Composition, Community Structure and Virus Production. *Fems Microbiology Ecology* **16**: 123-134.
- Van Wambeke, F., U. Christaki, A. Giannokourou, T. Moutin, and K. Souvemerzoglou. 2002. Longitudinal and vertical trends of bacterial limitation by phosphorus and carbon in the Mediterranean Sea. *Microb.Ecol.* **43**: 119-133.
- Vrede, K., M. Heldal, S. Norland, and G. Bratbak. 2002. Elemental composition (C, N, P) and cell volume of exponentially growing and nutrient-limited bacterioplankton. *Applied and Environmental Microbiology* **68**: 2965-2971.
- Wassmann, P., T. Ratkova, I. Andreassen, M. Vernet, C. Pedersen, and F. Rey. 1999. Spring bloom development in the marginal ice zone and the central Barents Sea. *Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I* **20**: 321-346.
- Weinbauer, M. G., D. Fuks, S. Puskaric, and P. Peduzzi. 1995. Diel, Seasonal, and Depth-Related Variability of Viruses and Dissolved DNA in the Northern Adriatic Sea. *Microbial Ecology* **30**: 25-41.
- Zohary, T., B. Herut, M. D. Krom, R. F. C. Mantoura, P. Pitta, S. Psarra, F. Rassoulzadegan, N. Stambler, T. Tanaka, T. F. Thingstad, and E. M. S. Woodward. 2005. P-limited bacteria but N and P co-limited phytoplankton in the Eastern Mediterranean - a microcosm experiment. *Deep-Sea Res. Part II-Top. Stud. Oceanogr.* **52**: 3011-3023.