Bacterioplankton population dynamics in a changing ocean

Linnaeus University Dissertations
No 204/2014

BACTERIOPLANKTON POPULATION DYNAMICS IN A CHANGING OCEAN

MARKUS LINDH

LINNAEUS UNIVERSITY PRESS

Bacterioplankton population dynamics in a changing ocean
Doctoral dissertation, Department of Biology and Environmental Science,
Linnaeus University, Kalmar, Sweden, 2014

Cover art: Jennie IJL Sjöström, by the courtesy of Mouth and Foot Painting
Artists Worldwide
ISBN: 978-91-87925-38-2
Published by: Linnaeus University Press, 351 95 Växjö
Printed by: Elanders Sverige AB, 2014

Abstract

Lindh, Markus (2014). *Bacterioplankton population dynamics in a changing ocean.* Linnaeus University Dissertations No 204/2014. ISBN: 978-91-87925-38-2. Written in English with a summary in Swedish.

Bacterioplankton is characterized by high diversity, short generation times and rapid turnover. Despite their small size, these numerous microorganisms are a fundamental piece of aquatic ecosystems by channeling carbon to higher trophic levels through dissolved organic matter utilization. Yet, several gaps remain in our knowledge and understanding of bacterioplankton populations regarding detailed temporal dynamics, and mechanisms determining biogeographical patterns and potential responses to climate change. The aim of this thesis was to examine responses in bacterioplankton community composition and function when challenged by natural and anthropogenically-induced change in environmental conditions.

High temporal resolution analysis of bacterioplankton population dynamics in the Baltic Sea indicated detailed seasonal responses. It also showed a similar but wide spectrum of niche differentiation patterns within several major bacterial groups. Analysis of geographic distributions of marine bacterial populations revealed bimodal occupancy-frequency patterns in bacterial communities, indicating that the presence of many locally rare taxa along with a few locally abundant taxa were explained by stochastic variation in colonization and extinction rates. Experimental manipulations with natural marine bacterioplankton assemblages revealed both specialist and generalist strategies in utilizing specific dissolved organic carbon compounds. When subjected to experimentally increased sea surface temperatures, lowered pH and additions of terrigenous carbon, some populations decreased in relative abundance while others were stable; concomitantly, many populations increased in relative abundance. Shifts in bacterial community composition were shown to correlate with changes in community functioning, but detection of such correlations depended largely on the detail of phylogenetic analysis and successional stage of the communities.

The results in this thesis suggest that both natural and anthropogenically-induced changes in environmental conditions promote simultaneous adjustment and replacement of bacterial populations tightly linked with metabolic plasticity. These trade-offs play a significant role for understanding the relationship between bacterioplankton population dynamics and potential shifts in carbon cycling properties. We also show the importance of regional effects in shaping bacterial community composition, crucial for interpreting bacterioplankton distribution patterns. In conclusion, this thesis emphasizes the critical importance of connecting analysis of bacterioplankton population dynamics with examination of ecological mechanisms to improve our understanding of factors that regulate the distribution and activity of distinct bacterioplankton populations.

Key words: marine microbiology, ecology, bacterioplankton, community composition, diversity, seasonality, biogeography, bimodal, metapopulation, community functioning, climate change, environmental disturbance

Sammanfattning

Hälften av all fotosyntes på vår planet utförs av växtplankton. De producerar organiskt material som utgör grunden för näringskedjan i havet. Ungefär hälften av det organiska material som produceras av växtplankton utnyttjas inte direkt, utan omsätts istället av bakterieplankton som lever och växer fritt i vattenmassan eller på olika partiklar. Bakterieplankton spelar därmed en nyckelroll i ekosystemet genom sin konsumtion av organiskt kol som för energi högre upp i näringskedjan. Trots deras nyckelroll i akvatiska miljöer vet vi fortfarande mycket lite om bakteriernas detaljerade säsongsmönster, mekanismer bakom rumsliga mönster och hur olika populationer kan komma att svara på klimatförändringar. Målet med denna avhandling var att undersöka hur specifika populationers dynamik och ekosystemfunktion påverkas av naturliga eller klimatorsakade förändringar i havsmiljön.

Våra resultat av högupplöst säsongsbunden dynamik i Östersjöns bakteriesamhälle avslöjar en liknande bred uppdelning av ekologiska strategier inom varje större grupp av bakterier, både i relativ abundans och temporal fördelning. Utbredning i rum och tid av många lokalt ovanliga populationer jämfört med få lokalt vanliga populationer förklarades genom stokastisk variation i kolonisations- och utdöendehastigheter. Vidare tyder experimentella studier med tillsatser av olika kolkällor på att marina bakterier har olika ekologiska strategier, där populationer är specialister eller generalister i utnyttjandet av enskilda kolkällor. Med hjälp av experiment med naturliga bakteriesamhällen bekräftade vi tydliga temperatureffekter på bakteriesamhällets sammansättning, och en mindre effekt av lägre pH - som dock tillsammans med förhöjd temperatur bidrog till en tydlig synergistisk effekt på artsammansättningen. Ökad temperatur tillsammans med tillsats av terrestert kol gav också en stor effekt på bakteriesamhällets struktur och ekosystemfunktion och pekar på en potentiellt viktig påverkan av ökad framtida nederbörd och avrinning från vattendrag till havet. Samtliga tre experiment med fokus på klimatpåverkan bekräftade förekomsten av populationer som försvann eller minskade i relativ abundans vid klimatpåverkan (känslighet), medan andra var stabila (resistens). Samtidigt svarade många populationer positivt på klimatorsakade förändringar i havsmiljön och ökade i relativ abundans (respons) samtidigt som bakteriernas ekosystemfunktion påverkades positivt.

Sammanfattningsvis visar denna avhandling att vissa nya bakteriepopulationer kan etablera sig och ersätta andra samtidigt som vissa befintliga populationer anpassar sin livsstrategi och ekologi till förändringar i havsmiljön. Vi visar också vikten av regionala effekter, d.v.s. kolonisation och utdöende, för bakteriesamhällets struktur, viktigt för tolkningen av biogeografiska mönster och den genomiska potentialen hos specifika populationer. Denna avhandling poängterar därmed betydelsen av att koppla studier av ekologiska mekanismer till både rumsliga och temporala spridningsmönster hos bakterier och till populationers kapacitet att svara på och anpassa sig till förändringar i havsmiljön.

“

To see the world, things dangerous to come to, to see behind walls, draw closer, to find each other, and to feel. That is the purpose of life.

”

Life Magazine motto in Secret life of Walter Mitty

Till Emma
för allt du gjort för mig

List of papers

This thesis is based on the following papers, which will be referred to in the text by their roman numbers. Reprints of published papers were made with the permission from Environmental Microbiology.

I. **Lindh, M.V.**, Sjöstedt, J., Andersson, A.F., Baltar, F., Hugerth L. W., Lundin, D., Muthusamy, S., Legrand, C., Pinhassi, J. (2014) Disentangling seasonal bacterioplankton population dynamics by high frequency sampling.
Environmental Microbiology (in press), doi: 10.1111/1462-2920.12720.

II. **Lindh, M.V.**, Sjöstedt, J., Ekstam, B., Casini, M., Hugerth, L, Lundin, D, A.F. Andersson, Andersson, A., Legrand, C., Pinhassi, J. (2014) Bimodal occupancy frequency distributions in marine bacterial communities – the importance of regional dynamics. (*Manuscript*).

III. Gomez-Consarnau, L., **Lindh, M.V.**, Gasol, J.M., Pinhassi, J. (2012) Structuring of bacterioplankton communities by specific dissolved organic carbon compounds. *Environmental Microbiology* **14**: 2361-2378.

IV. **Lindh, M.V.**, Riemann, L., Baltar, F., Romero-Oliva, C., Salomon, P.S., Graneli, E., Pinhassi, J. (2013) Consequences of increased temperature and acidification on bacterioplankton community composition during a mesocosm spring bloom in the Baltic Sea. *Environmental Microbiology Reports* **5**: 252-262.

V. **Lindh, M.V.**, Lefébure, R, Degerman R, Lundin, D, Andersson, A., Pinhassi, J. (2014) Consequences of increased terrestrial dissolved organic matter and temperatures on bacterioplankton community composition during a mesocosm experiment in the Baltic Sea.
(*In review*)

VI. **Lindh, M.V.**, Figueroa, D., Sjöstedt, J., Lundin, D., Andersson, A., Legrand, C., Pinhassi, J. (2014) Transplant experiments uncover Baltic Sea basin-specific responses in bacterioplankton community composition and metabolic activities.
(*Submitted to Frontiers in Microbiology*)

Additional published work executed during the Ph.D study but not included in this thesis:

Sarmento, H., Romera-Castillo, C., **Lindh, M.**, Pinhassi, J, Sala Montserrat M., Gasol J. M., Marrase C., Taylor G. T. (2013) Phytoplankton species-specific release of dissolved free amino acids and their selective consumption by bacteria. *Limnol Oceanogr* **58**: 1123–1135.

Akram, N., Palovaara, J., Forsberg, J., **Lindh, M.V.**, Milton, D.L., Luo, H. et al. (2013) Regulation of proteorhodopsin gene expression by nutrient limitation in the marine bacterium Vibrio sp. AND4. *Environ Microbiol* **15**: 1400-1415.

Forss, J., Pinhassi, J., **Lindh, M.**, and Welander, U. (2013) Microbial diversity in a continuous system based on rice husks for biodegradation of the azo dyes Reactive Red 2 and Reactive Black 5. *Bioresour Technol* **130**: 681-688.

Baltar, F., **Lindh, M.V.**, Parparov, A., Berman, T., and Pinhassi, J. (2012) Prokaryotic community structure and respiration during long-term incubations. *Microbiol Open* **1**: 214-224.

TABLE OF CONTENTS

INTRODUCTION

"We know more about space than we know about the oceans."
D. Attenborough

Marine bacteria and Archaea, collectively known as bacterioplankton, are a fundamental piece of the planktonic food-web puzzle and the whole aquatic ecosystem. It has been estimated that there are 10^{29} prokaryotic cells inhabiting the oceans, vastly outweighing any larger organisms, both in sheer numbers and, despite their microscopic size, in total biomass (Whitman et al., 1998). In fact, a typical bacterial cell is approximately 1 µm in diameter and if one would place each cell of the oceans on a straight line, it would extend about 2.5 million light years (reaching the Andromeda galaxy; oral presentation by Jed Fuhrman). However, bacterioplankton is not only numerically abundant but is also characterized by large diversity, short generation times and rapid turnover (Pedros-Alio, 2006, Noble and Fuhrman 2000). Microbial ecologists have asked three fundamental questions during the last couple of decades concerning bacterioplankton: Who are they? What do they do? What is their ecological role in the marine environment? In order to interpret bacterioplankton processes in the marine environment, there is a need to identify bacterial community composition and functional patterns. In addition, microbial ecologists need to differentiate between superficially minor details that may be critical for the big picture and those that are simply local outliers of no broad significance. There is now ample evidence that bacterioplankton activity and community composition play a central role in regulating biogeochemical cycles of elements, primarily carbon (Azam et al., 1983, Azam et al., 1994, Pinhassi et al., 1999, Carlson et al., 2004, Moran et al., 2004, Bidle and Azam 2001, Robinson and Williams 2005, Arnosti et al., 2005). However, several gaps remain in our knowledge and understanding of bacterioplankton regarding detailed temporal dynamics, and mechanisms determining biogeographical distribution and potential responses to climate change.

The Microbial Loop

It was not until the 1970's and early 1980's that the status of bacterioplankton was recognized to be a significant part of organic matter flux and recycling to higher trophic levels via the so-called microbial loop (Pomeroy 1974; Azam et al., 1983) (Fig. 1). About 50% of the atmospheric CO_2 is fixed by photosynthesizing phytoplankton in surface waters (Field et al., 1998) resulting in 45 gigatons of organic matter per year (Falkowski et al., 1998). Although a matter of debate and depending on ecosystem, around 50% of the organic matter produced by phytoplankton, are utilized by bacterioplankton (Cole et al., 1988), and re-enters the "traditional food-web" by predation and grazing (Azam et al., 1983). Recent data suggest that this portion of organic matter, around 25 gigatons per year, is also corresponding to a spectrum of labile to recalcitrant dissolved organic carbon (DOC), collectively forming the largest flux of carbon in the sea (Hansell 2013). Thus, a major part of the carbon in the sea is channeled to higher trophic levels by bacterioplankton through dissolved organic matter utilization.

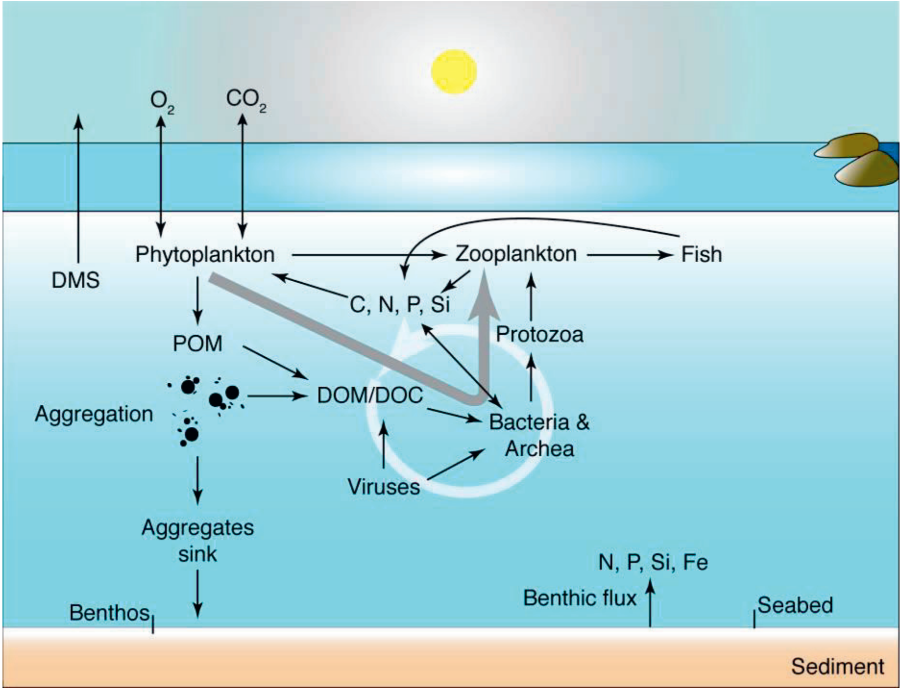

Figure 1. The Microbial loop (Azam et al., 1983). The grey arrow denotes the direction of organic matter utilization and transfer to higher trophic levels by bacterioplankton and the white arrow denotes the recycling of organic matter by predation and grazing. Modified from (Azam and Malfatti 2007).

Community Composition

As for macroorganisms, microbial community composition or community structure refers to the identity of organisms (taxa) and their frequency distribution in an environment/ecosystem. A multitude of experimental and *in situ* approaches have revealed the importance of different factors, in regulating bacterioplankton community composition, including for example a series of physicochemical and biological factors (Teeling et al., 2012, Kritzberg et al., 2006, von Scheibner et al., 2014, Allgaier et al., 2008, Sjöstedt et al., 2012b). In addition, years of research have shown a close link between bacterial community composition and ocean biogeochemistry (Carlson et al., 2004, Moran et al., 2004, Bidle and Azam 2001, Robinson and Williams 2005, Arnosti et al., 2005). Since only a small fraction of all bacteria are cultivable, phenotypic identification of bacteria is problematic and does not mirror the complete bacterioplankton diversity. Microbiologists therefore use culture-independent genetic identification techniques to differentiate between bacterial taxa. Identification of individual populations is often done by division of bacterioplankton into specific phylotypes or operational taxonomic units (OTUs) following sequencing of the 16S rRNA gene fragments and taxon delineation at a specific sequence identity threshold (typically 97%). The relatively highly conserved 16S rRNA genes are parts of prokaryotic ribosomes (18S rRNA genes in eukaryotes) but also contain hypervariable regions (Head et al., 1998). Technical advances in the form of high-throughput sequencing have increased the sequencing resolution and thereby the detection levels of individual OTUs by several orders of magnitude. As a result the field of marine microbial ecology have advanced from describing mostly major bacterial groups or a few dominant populations to resolving up to thousands populations over different temporal and spatial scales (Poisot et al., 2013).

Seasonal succession

Stratification and physical mixing of the water column lead to changes in environmental conditions for many ecosystems. Concurrent utilization of nutrients by phytoplankton in spring, summer and autumn, cause a seasonal succession of phytoplankton and bacterioplankton populations (Martin 2012) (Fig. 2). Seasonal studies of dynamics in bacterioplankton composition have mostly sampled natural populations monthly over single or several years (Cotner et al., 1997, Pinhassi and Hagström, 2000, Church et al., 2003, Schauer et al., 2003, Fuhrman et al., 2006, Alonso-Saez et al., 2008, Nelson et al., 2008, Andersson et al., 2010, Gilbert et al., 2012, Hatosy et al., 2013). These studies have established that there are broad scale seasonal changes in community composition of bacterioplankton over the year, with a pronounced regularity in the reappearance of major populations between years. However, to fully recognize bacterial community responses to seasonal events, it is critical to measure the presence/absence and relative abundance of specific bacterial populations on relevant temporal scales *in situ*. Bacterioplankton communities have turnover times of around 3-5 days (Noble and Fuhrman 2000) and specific populations are therefore expected to change on shorter time-scales than the typically monthly samplings carried out in seasonal studies (Fuhrman et al., 2006, Andersson et al., 2010, Pinhassi and Hagström 2000). Moreover, high temporal resolution sampling was recently shown to catch responses from days to weeks in the relative abundance of specific bacterial populations in two independent studies (Needham et al., 2013, Teeling et al., 2012). In addition, Vergin and colleagues (2013) noted that there are few established links between standard environmental variables and particular bacterial populations. Thus, high temporal resolution analyses of bacterioplankton population dynamics over longer time scales within a year could be a way for achieving an improved understanding of bacterioplankton responses and ecological mechanisms to changes in environmental conditions.

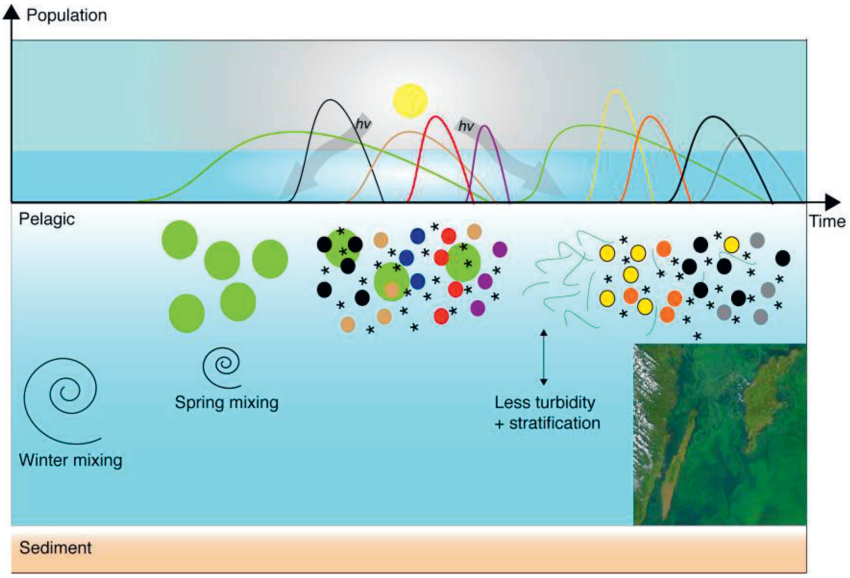

Figure 2. Seasonal succession of phytoplankton and bacterioplankton. Curves indicate population abundance. Arrows denote light (hv). Green points are spring phytoplankton (diatoms and dinoflagellates) and green filaments are summer Cyanobacteria. Modified from (Martin 2012). Insert is a satellite picture from a Baltic Sea summer cyanobacterial bloom on the 5th of July 2005, Credit: Jeff Schmaltz NASA.

Biogeographic distribution

Biogeography is the study of species distributions over space and time. Biogeographical patterns on both small scales (1-100 km) and larger scales (>100 km) show that specific bacterioplankton populations can be widespread, but also that most populations are biogeographically distinct and often separated by currently unknown physical or biological barriers (Barberan and Casamayor 2010, Pommier et al., 2007, Pinhassi et al., 2003, Brown et al., 2012, Sul et al., 2013, Ghiglione et al., 2012). An alternative hypothesis suggests that if the sequencing resolution would increase further, everything would in fact be everywhere, i.e. all populations are cosmopolitan and not endemic (Gibbons et al., 2013). Nevertheless, the underlying cause of specific biogeographical patterns among marine bacterioplankton is poorly understood. In addition, high-throughput sequencing is remarkably underused in the context of investigating biogeography of bacterioplankton (Poisot et al., 2013). Several mechanisms ranging from neutral mechanisms to dispersal limitation and species sorting have been suggested to explain bacterioplankton distribution patterns (Hellweger et al., 2014, Hanson et al., 2012, Lindström and Langenheder 2012). However, efforts to investigate species abundance patterns over both spatial and temporal scales incorporating positive feedback mechanisms between local abundance and regional distribution are essentially lacking in aquatic systems (Fig. 3) (McGeoch and Gaston, 2002). Species-abundance patterns may be simply yet intrinsically linked to processes involved in structuring ecological communities and could reveal underlying patterns and generalities of how organisms appear in nature.

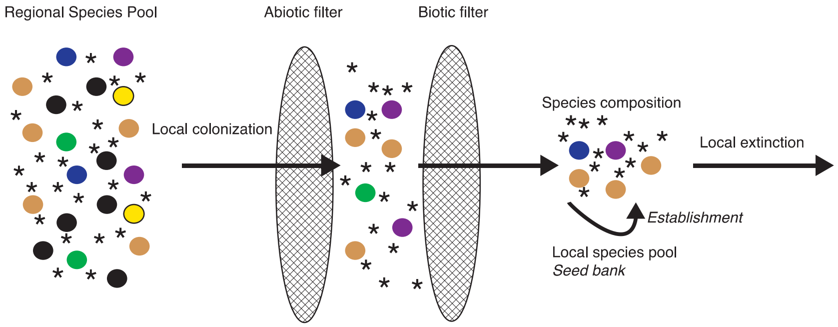

Figure 3. Regional and local dynamics involved in shaping species composition. Species from a regional pool are filtered by abiotic and biotic factors and successful populations colonize a local site thus establishing the local species composition. But species are also subjected to local extinction. If species are regionally rare the chances of successful dispersal diminishes rapidly, as exemplified by green and yellow populations. Modified from (Gibson et al., 2012).

A metapopulation is a regional group of connected species where each metapopulation is influenced by population increases (i.e. replication and immigration) and population decreases (i.e. mortality and emigration). Metapopulation models are frequently used to describe species-abundance patterns for terrestrial animals, plants and insects (McGeoch and Gaston, 2002 and references within), and in a few cases for aquatic organisms (Soininen and Heino, 2005; Hercos et al., 2013). In general, metapopulation theory has provided insight in conservation biology and whether colonization takes place despite extinctions resulting from natural causes e.g. forest wildfires and anthropogenic causes e.g. agriculture, other land-use goals and overfishing. But more importantly, metapopulation models have the potential of connecting bacterial species-abundance patterns and regional vs. local effects in terms of colonization and extinction of species (gain and loss of OTUs). For example, Hanski (1982) suggested a framework based on observations of bimodal occupancy frequency distribution of different species ranging from insects to plants, to understand the correlations between local abundance and regional occupancy. Hanski's core-satellite hypothesis predicts a bimodal occupancy frequency distribution (i.e. the number of species occupying different number of sites) where regionally common organisms (core populations) have a higher colonization probability and a lower mortality risk as opposed to regionally rare organisms (satellite populations) (Hanski 1982; Box 1). An alternative model predicts instead a unimodal distribution and a linear relationship between colonization/extinction rates and occupancy (Levin, 1974).

Box 1. Hanski's metapopulation model

Hanski's core-satellite hypothesis (1982) is based on Levin's original model (Levin, 1974) calculated as follows:

$$dP/dt = CP(1 - P) - EP$$

where **P is the fraction of occupied sites**, **C is colonization rate** and **E is extinction rate**. When $P = 1$, occupancy is 100% and all sites are occupied and when $P = 0$, occupancy is 0%, meaning regional extinction. Colonization rate is the change in number of colonized empty sites over time. Extinction rate is the change in number of lost sites over time. If C is greater than E plus the variance in E ($C > E + \sigma^2_E$), then Levin's model predicts a unimodal distribution (i.e. a occupancy-frequency pattern characterized by one peak). Hanski modified the model to:

$$\mathbf{dP/dt = CP(1 - P) - EP(1 - P)}$$

Hanski's model predicts a quadratic function of both C and E and takes into account regional effects, i.e. immigration of species from a regional pool, also known as the rescue effect. Thus, if the variance in S ($C - E$) is greater than S (i.e. $\sigma^2_S > S$) the model predicts a bimodal species distribution (i.e. a occupancy-frequency pattern characterized by two peaks).

Bimodal occupancy frequency distributions are characterized by a pattern where most species are found at a single site and an initial, monotonical decrease of species with number of sites occupied, followed by an increase in species that occur at all sites. Hanski's prediction of bimodality is different from other occupancy frequency distributions like unimodality described in Levin (1974), by incorporating the rescue effect - the idea that immigration of populations from surrounding sites reduces the probability of local extinction (Hanski and Gyllenberg 1993) (Box 1). The value of the core-satellite hypothesis is significant since it explains the long known bimodal distribution pattern of species described by the "Law of frequency" (Raunkiaer 1913, 1918, 1934). Hanski's model further contributed to put focus on metapopulation dynamics and distribution patterns in local patches influenced by regional dynamics instead of considering the local environments as the essential ecological units. Efforts to connect diversity with ecosystem function and the disproportionate role of dominant species in controlling this relationship have been linked to Hanski's core-satellite hypothesis (Gibson et al., 1999). For example, Hanski's model provides a theoretical basis for the division between "subordinate" (satellite), "transient" and "dominant" (core) species and how successful traits are determined by colonization and extinction probabilities. Although, the core-satellite hypothesis have been tested and confirmed frequently in terrestrial environments (Gotelli and Simberloff 1987; Ely and

Gibson 1996; Unterseher et al., 2011; Simons et al., 2014) few have investigated this model in aquatic environments (Soininen and Heino, 2005; Hercos et al., 2013). The often negative effects of dominance on ecosystem function was highlighted by Hillebrand et al., (2008), and core-satellite dynamics may be key in understanding and monitoring anthropogenic effects on ecosystems strongly influenced by bacterioplankton diversity and functioning. Taken together, empirical testing of metapopulation models is generally lacking and may provide knowledge and mechanisms to explain biogeographic patterns of bacterioplankton in the sea and the distribution of many rare vs. a few abundant populations in the local environment.

Rare vs. Abundant

Studies focusing on bacterioplankton community composition have typically shown a general rank-abundance distribution of few abundant taxa followed by a long tail of many rare taxa among populations in the sea (Rappe and Giovannoni, 2003, Pedros-Alio, 2006, Sogin et al., 2006, Pedros-Alio, 2012, Galand et al., 2009) (Box 2). The rare bacterioplankton contribute to most of the diversity in the ecosystem but populations in this “seedbank” may be growing slowly or not at all (Pedros-Alio, 2006). However, it is becoming increasingly clear that although currently abundant taxa likely carry out most of the activity in the ecosystem, rare taxa can rapidly become abundant in response to changes in environmental conditions (Lennon and Jones, 2011, Sjöstedt et al., 2012b). Still, only few studies have carried out sampling at temporal resolution necessary to observe such transitions *in situ* (but see Campbell et al., 2011, Teeling et al., 2012, Needham et al., 2013, Alonso-Saez et al., 2014). At present, the factors that govern this general pattern of rare and abundant bacterial populations are unknown, but may for example result from unidentified biological or physical niche constraints in the aquatic environment (Pedros-Alio, 2012, Lennon and Jones, 2011). Alternatively, positive feedback mechanisms between local abundance and the regional distribution of populations, as described above, could shape the division of rare vs. abundant populations. Altogether, for bacterioplankton, it is very common to be rare and very rare to be common in the sea. However, ecological mechanisms and temporal transitions between being rare and abundant remain largely unknown.

Box 2. Rare vs. Abundant

For clarification purposes it is common to define at which relative abundance an OTU is abundant or rare in a community (Pedros-Alio, 2006). Common abundance ranges are:

”Rare” – Relative abundance < 0.1%

“**Abundant**” – Relative abundance >1%

Other definitions typically shift the range of rare to lower relative abundances e.g. <0.01% (Galand et al., 2009).

Marine dissolved organic matter (DOM) composition

The quality and composition of DOM is partly dependent on its origin, which can be: allochtonous (i.e. transported into the sea by e.g. river outflows) or autochtonous (i.e. produced *in situ* by e.g. phytoplankton) (Kirchman, 2008; Kritzberg et al., 2004). It is known that the composition of autochtonous DOM influences the community composition of bacterioplankton and thereby potentially biogeochemical cycling of carbon (Riemann et al., 2000, Pinhassi et al., 2004, Teeling et al., 2012, Dinasquet et al., 2013, Sarmento et al., 2013). For example, Sarmento and colleagues (2013) recently showed that phytoplankton produce species specific DOM, varying in composition and resulting in a differential response in bacterial community composition. In comparison, the effect of allochtonous DOM and subsequent microbial responses in community composition in the marine environment is less studied (Herlemann et al., 2014, Kisand et al., 2002, Rochelle-Newall et al., 2004, Kisand et al., 2008, Teira et al., 2009, Grubisic et al., 2012, Rocker et al., 2012). However, shifts in bacterioplankton community composition in response to allochtonous DOM additions are well documented in freshwater systems (e.g. Lindström, 2000, Eiler et al., 2003, Haukka et al., 2005, Kritzberg et al., 2006, Hutalle-Schmelzer et al., 2010). Since bacterioplankton are the main contributors to the transformation of marine DOM, much attention have been put on the role of bacterioplankton community composition in this biogeochemical process. However, the relationship between DOM composition and bacterioplankton community composition is still not completely understood.

A potential reason for changes in community composition in response to exposure to DOM of different origin/quality could be niche differentiation at the population level. For example, particular bacterial populations may be able to utilize several DOC compounds while others are only capable of utilizing a few specific compounds, i.e. generalist and specialist dynamics (Langenheder et al., 2005). Different degrees of generalist versus specialist behavior in bacterial communities may also explain why community composition does not necessarily need to change when subjected to an environmental disturbance (Langenheder et al., 2005, Allison and Martiny, 2008, Mou et al., 2008). Thus, to establish the level of adaptation or sensitivity of bacterioplankton communities to natural changes in environmental conditions it is essential to investigate specific bacterial populations and their responses to different DOM sources and specific DOC compounds.

Community composition and ecosystem function

A fundamental question in ecology focuses on whether shifts in diversity and community composition due to changes in environmental conditions also result in changes in bacterial community ecosystem functioning. Traditionally, two important ecological frameworks can be recognized, targeted alone or simultaneously: (i) population and community ecology, typically aiming to understand population interactions and differences in community composition between and within communities, and (ii) ecosystem ecology typically aiming to understand bacterial community functioning and energy flows in different systems (Loreau, 2000). Since bacterioplankton communities are characterized by high productivity, rapid turnover and relatively short generation times, they have a remarkable capability in responding both in metabolic activity and in community composition to environmental disturbances, such as changes in temperature, pH and nutrient additions (Allison and Martiny, 2008). Considering the above sections on community composition, it is clear that bacterioplankton regulate the biogeochemical cycling of nutrients (e.g. carbon) where changes in bacterial community composition affects metabolic activity relevant for this processing (Bidle and Azam, 2001, Moran et al., 2004, Arnosti et al., 2005, Robinson and Williams, 2005). Alternatively, rearrangement of bacterial assemblages affects only the pathway of responses but not the resulting metabolic activity (Comte and Del Giorgio, 2011). Still, little is known about how bulk bacterial community composition affect community functioning and how sensitive or resistant bacterial communities and individual bacterial taxa are to environmental disturbances (Allison and Martiny, 2008, Comte and Del Giorgio, 2011, Langenheder et al., 2005). Bacterial communities could in theory respond to environmental disturbances in 4 distinct ways (Box 3).

Box 3. Community responses to environmental disturbance

Sensitivity – when community composition is altered by environmental disturbance.

Resistance – when community composition is not altered by environmental disturbance.

Resilience – when community composition is initially altered by environmental disturbance but returns to the original composition.

Functional redundancy – when composition remains altered but contains functionally redundant taxa that performs like the original community.

In addition, the insurance hypothesis or portfolio effect stipulates that sensitive communities may perform like the original community, or better, by the ability to recruit new taxa, from the large number of species held by the community (Allison and Martiny, 2008, Loreau, 2000). This hypothesis is particularly important for interpreting changes in bacterioplankton diversity when communities are challenged by alterations in environmental conditions. Potential links between changes in environmental conditions and bacterial community composition, diversity and functioning are not completely understood. More specifically, there are few studies focusing on this relationship between bacterial community composition and functioning for bacterioplankton responding to anthropogenically-induced environmental change.

Climate change

The issue of adaptation or sensitivity, i.e. adjustment or replacement of OTUs *sensu* (Allison and Martiny, 2008, Comte and Del Giorgio, 2011) is critically important for understanding bacterial communities responding to changes under other environmental conditions, e.g. anthropogenically-induced changes. Projections of climate change in the aquatic environment implicate ecosystem changes of unparalleled extent. In the “business as usual” scenario, the Intergovernmental Panel on Climate Change (IPCC) projects a global temperature increase of 1.4 to 5.8°C and a global atmospheric CO_2 increase of 400 atm, resulting in lower pH by approximately 0.4 units until 2100 (Stocker et al., 2013). Moreover, in the Baltic Sea region the Swedish meteorological and hydrological institute (SMHI) projects increased precipitation by up to 48% until 2100, leading to lower salinities and increased output of allochtonous matter from river discharge (Meier, 2006).

Temperature regulates bacterial growth and can be a major driver of compositional shifts among bacterioplankton (Müren et al., 2005, Sommer et al., 2007, Hoppe et al., 2008, von Scheibner et al., 2014). Therefore, increased sea surface temperatures due to climate change will likely affect the seasonal dynamics of particular bacterial populations. Similarly, increased CO_2 concentrations resulting in lowered seawater pH may affect bacterioplankton growth and composition directly or indirectly by affecting DOM release and composition of higher trophic levels (Allgaier et al., 2008, Vega Thurber et al., 2009, Arnosti C et al., 2011, Joint et al., 2011, Witt et al., 2011). Further, like increased temperature and lowered pH, an increase in loading of allochtonous carbon and lower salinity will likely influence growth and community composition of marine bacterioplankton. In fact, bacterioplankton respond to allochtonous carbon (Kisand et al., 2002, Rochelle-Newall et al., 2004, Kisand et al., 2008, Teira et al., 2009, Kritzberg et al., 2004, Kritzberg et al., 2006, Grubisic et al., 2012, Rocker et al., 2012), and salinity (Langenheder et al., 2003, Sjöstedt et al., 2012b), affecting the composition of bacterial communities. Although bacterioplankton responses to climate change-related variables have been tested individually, they have not been considered in combination, and documented responses at high taxonomic resolution are essentially lacking.

The Baltic Sea and Linnaeus Microbial Observatory

The primary study area of the papers included in this thesis is the Baltic Sea, but also material from the Mediterranean Sea and global data from the International Census of Marine Microbes (ICoMM) have been used. In addition to Linnaeus Microbial Observatory (LMO), (N 56°55.851, E 17°03.640), other Baltic Sea stations are located in the Western Gotland Sea, west to Northwest of Öland (see insert Fig. 4) and the NB1 station (N 63°31.0000, E 19°48.1166) in the Bothnian Sea approximately 7 km off the coast of Norrbyn, close to the Öre river outflow (Ågren et al., 2008) are also studied in the present thesis (Fig. 4). The following paragraphs is an attempt to summarize key hydrological and physicochemical features of the Baltic Sea and the main field station LMO, but also known literature regarding pelagic bacterioplankton community composition in this semi-enclosed sea.

The 377,000 km^2 large Baltic Sea is the second largest brackish sea on Earth, next after the Black Sea. The water volume is around 21,700 km^3 and the drainage area spans ~90 million people in 14 different countries. This brackish system varies in both hydrology and physicochemical features and consists of a 2000 km long salinity gradient ranging from marine to truly freshwater conditions through several basins of which three are major; the Baltic Proper (BP), the Bothnian Sea (BS) and the Bothnian Bay (BB) (Omstedt et al., 2014) (Fig. 4). In addition to strong shifts in salinity, the Baltic Sea is also characterized by different magnitudes of river outflows, transferring freshwater and terrestrial DOM to coastal waters, with seasonal variation (Omstedt et al., 2014; Zweifel et al., 1993, Hansson et al., 2011). Areas in the Baltic Sea are also periodically affected by wind-driven upwellings, relatively common due to the geography of this semi-enclosed system (Omstedt et al., 2014; Lehmann A., 2008). Our main field station LMO is located in the Western Gotland Sea, approximately 12 km off the coast of Öland (Fig. 4). Water samples are taken from the surface around 2 m and the depth on the site is around 40 m. LMO is situated between SMHI/HELCOM monitoring stations BY38 and BY39. Station BY38 illustrates the general hydrology, nutrient and oxygen dynamics in the Western Gotland Basin (Fig. 5). Isopleths in Figure 5 show a permanent halocline at approximately 60-70 m depth that has slightly shallowed during the 1990s. Below the halocline water renewal follows the major Baltic inflow pattern with a salinity peak following e.g. the 2003 inflow. Below the halocline the water has been anoxic since the end of the 1990s, as shown by oxygen concentrations, absence of nitrate and accumulation of ammonia. However, the entire water column of LMO is located above the permanent halocline. A seasonal thermocline is established at approximately 20 m depth in summer that deepens during autumn. Between the seasonal thermocline and the permanent halocline a cold winter water layer is established. Nutrient depletion by phytoplankton during the productive season, however, reaches down to the permanent halocline. In essence, the distribution of individual bacterioplankton populations at LMO is likely not limited by any hydrological barriers and only occasionally affected by strong vertical mixing of the water column.

Several experiments focusing on surface bacterioplankton community composition have been carried out in the Baltic Sea, as summarized in Table 1. Most of these investigations have focused on spatial distributions and effect of nutrient additions (Table 1). A majority of the studies show that bacterial community composition is sensitive to changes in environmental conditions such as nutrient inputs and changes in salinity (Dinasquet et al., 2013, Sjöstedt et al., 2012b). In fact, salinity changes have been reported to be the major driver of the spatial OTU distribution in the Baltic Sea (Herlemann et al., 2011, Dupont et al., 2014). Although these effects influence bulk bacterioplankton community composition, adjustment and replacement of taxa likely occur at different taxonomic levels. Thus, studies of the potential sensitivity or adaptability of particular populations in Baltic Sea bacterial communities responding to e.g. increased temperature and precipitation may provide understanding as to what ecological consequences climate change will have on the Baltic Sea ecosystem.

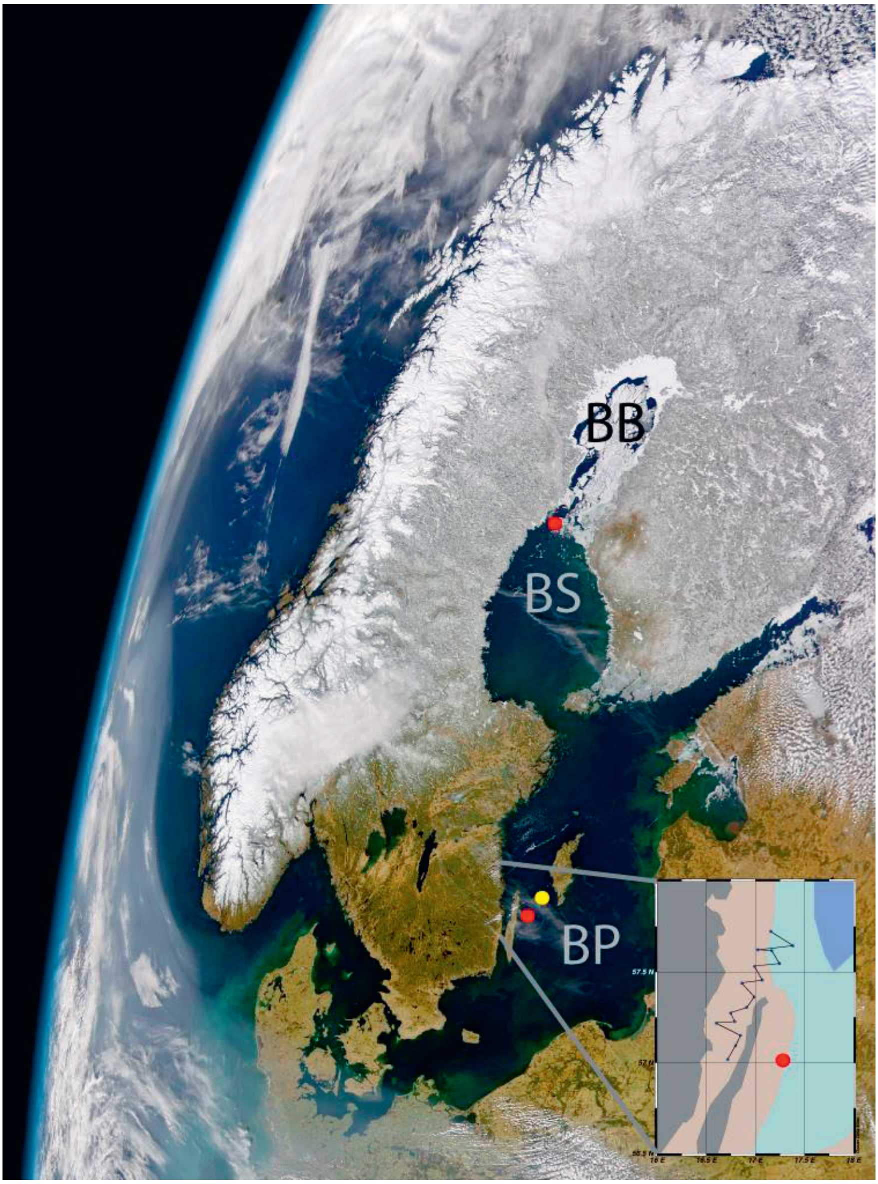

Figure 4. Satellite picture of the Baltic Sea on April 1st 2004. Red circles denote LMO and NB1 field stations. Yellow circle denote SMHI/HELCOM station BY38. BP = Baltic Proper, BS = Bothnian Sea, BB = Bothnian Bay. Insert show stations sampled in the western Gotland Sea. Image courtesy: the SeaWiFS Project, NASA/Goddard Space Flight Center, and ORBIMAGE. More information, collection of data and live monitoring are now available from an automated buoy at LMO "Öland Öst": http://www.smhi.se/hfa_coord/BOOS/Kustmat/Kustmat.html showing temperature, salinity, chlorophyll a and water oxygen measurements.

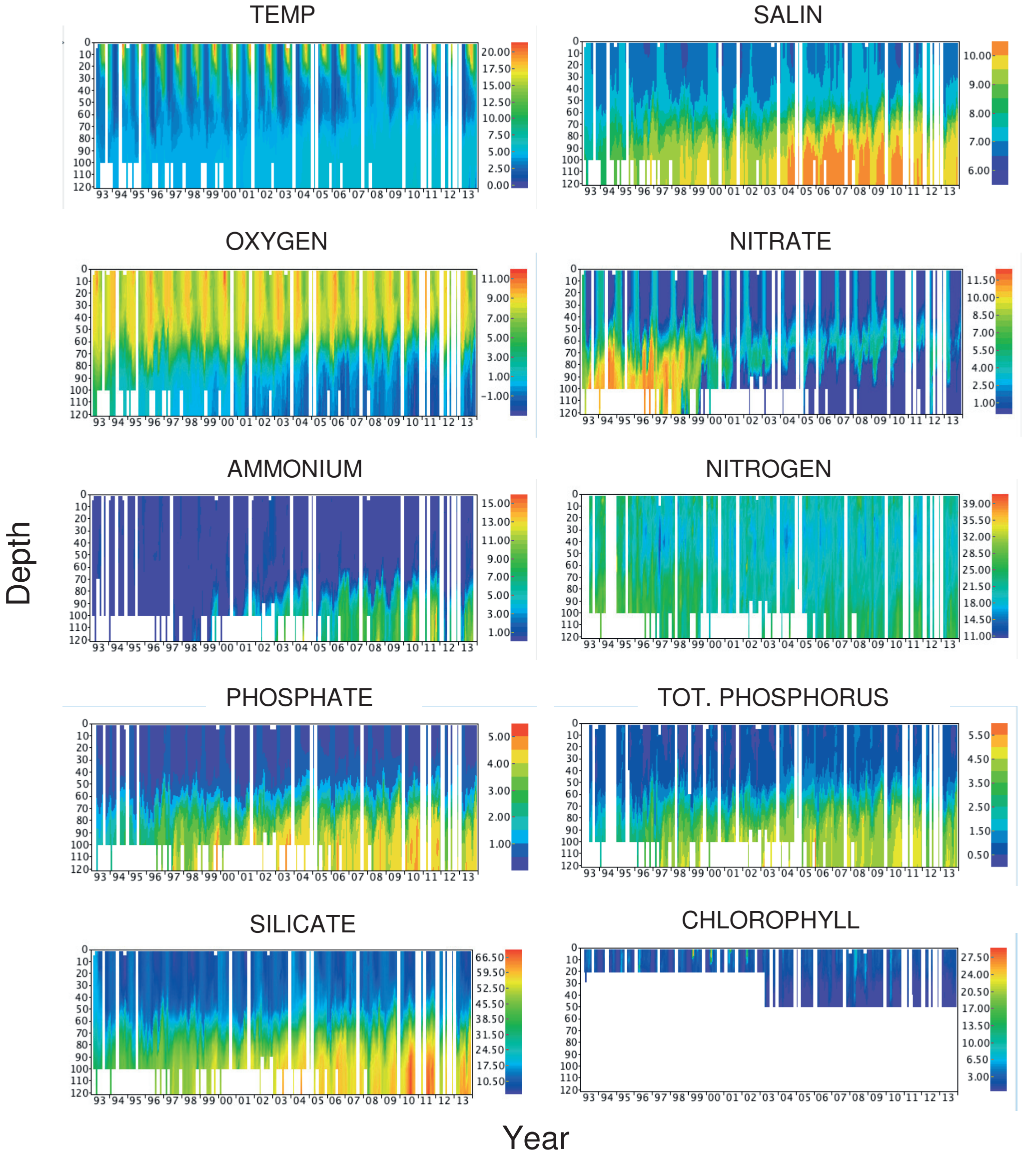

Figure 5: Isopleths of hydrological parameters, inorganic nutrient concentrations and chlorophyll a concentrations at station BY38. Units are mmol m^{-3} for nutrients, ml l^{-1} for oxygen and mg m^{-3} for Chl a.

Table 1. Summary of Baltic Sea pelagic microbial studies in which data on bacterioplankton community composition is available. Asterisk (*) denote papers included in this thesis.

Study/ Disturbance	No. of studies Total: 46	Location/Source	Key findings	References
Seasonal	5	Baltic Proper, Gulf of Gdansk, Gulf of Finland	Bacterial taxa display seasonal niche differentiation.	(Pinhassi and Hagström, 2000, Riemann et al., 2008, Andersson et al., 2010, Piwosz et al., 2013, Kaartokallio et al., 2008)
Spatial	11	Entire Baltic Sea, Bothnian Sea, Bothnian Bay, Gulf of Finland	Abundance and distribution of bacterial taxa change with environmental conditions and differ between the Basins.	(Hagström et al., 2000, Kisand et al., 2005, Salka et al., 2008, Holmfeldt et al., 2009, Herlemann et al., 2011, Koskinen et al., 2011, Brettar et al., 2012, Bergen et al., 2014, Dupont et al., 2014, Laas et al., 2014, Salka et al., 2014)
Temperature	6	Bothnian Sea, Bothnian Bay, Kiel Bight, Gulf of Finland, Western Baltic Sea	Bacterial communities and specific taxa respond to changes in temperature.	(Sommer et al., 2007, Kuparinen et al., 2011, Lindh et al., 2013*, Eiler et al., 2007, Sjöstedt et al., 2012a, von Scheibner et al., 2014,)
Nutrient additions	9	Baltic Proper, Bothnian Sea, Gulf of Finland, Bothnian Bay	Bacterial communities and specific taxa can respond to changes in DOM and can often utilize allochtonous DOM.	(Gomez-Consarnau et al., 2012*, Kisand et al., 2002, Kisand and Wikner, 2003, Sipura et al., 2005, Grubisic et al., 2012, Tammert et al., 2012, Degerman et al., 2013, Dinasquet et al., 2013, Herlemann et al., 2014)
Salinity	3	Bothnian Sea, Gulf of Finland, Baltic Proper	Salinity regulates bacterioplankton community composition.	(Langenheder et al., 2003, Kaartokallio et al., 2005, Sjöstedt et al., 2012b)
Other studies	12	Gulf of Finland, Bothnian Sea, Baltic Proper, Western Baltic Sea	Specific bacterial taxa degrade hydrocarbon. Antibiotic resistance genes are correlated with community composition. Vibrio bacteria depend on environmental conditions. The underlying water community and specific environmental conditions shape Bacterioneuston communities.	(Hofle and Brettar, 1995, Pinhassi et al., 1997, Simu and Hagström, 2004, Eiler and Bertilsson, 2006, Eiler et al., 2006, Tuomainen et al., 2006, Stolle et al., 2010, Lindroos et al., 2011, Stolle et al., 2011, Reunamo et al., 2013, Viggor et al., 2013, Tiirik et al., 2014)

AIMS

"As for me, I am tormented with an everlasting itch for things remote.
I love to sail forbidden seas, and land on barbarous coasts."
H. Melville – Moby Dick

The overall objective of this PhD study was, firstly, to determine how natural environmental changes occurring on different temporal scales affect bacterioplankton populations, and to determine mechanisms that contribute to determining biogeographical patterns. Secondly, to investigate how climate change-induced shifts in key environmental factors, i.e. lowered pH, increased temperature, lowered salinity and increases in allochtonous carbon, affect the dynamics of specific bacterial groups or populations. A schematic summary of the aims is presented in Figure 6, and the specific aims were as follows:

- The aim of **Paper I** and **II** was to investigate niche differentiation and the relative importance of regional dynamics among bacterioplankton on relevant spatio-temporal scales in the sea.
- The aim of **Paper III** was to investigate the relevance of different carbon substrates in promoting the success of specific bacterial taxa.
- The aim of **Paper IV**, **V and VI** was to resolve combined climate change effects on bacterioplankton dynamics. This included effects of increased temperature and lowered pH (**Paper IV**), and increased temperature and allochtonous carbon (**Paper V**). To simulate effects of increased riverine discharge, transplant and re-transplant experiments with bacterial assemblages between Baltic Proper seawater (salinity 7) and Bothnian Sea water (salinity 3) were carried out (**Paper VI**).

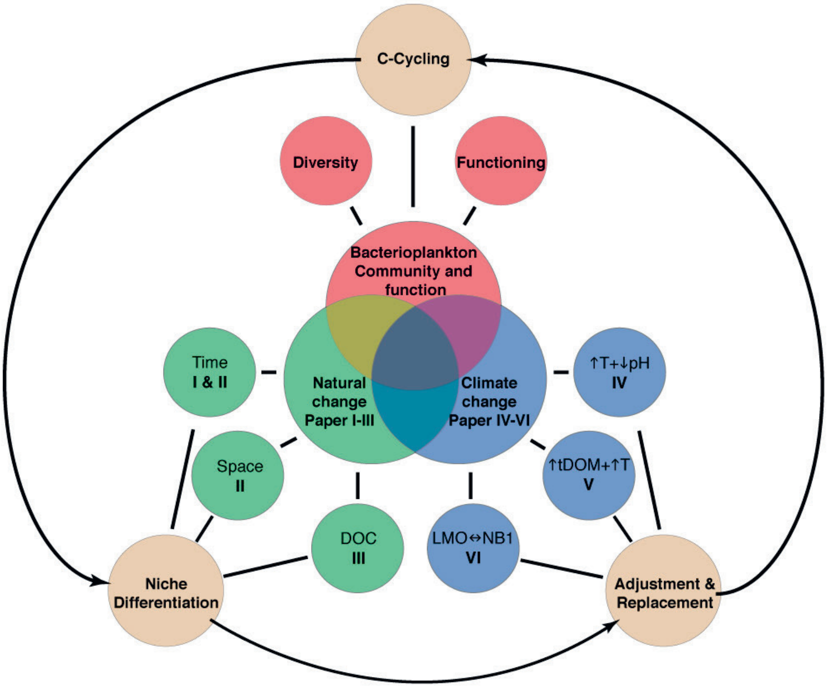

Figure 6. Schematic representation of the contents and aims of papers included in this thesis. ***Paper I-III*** *cover bacterial responses to natural changes (green bubbles), while* ***Paper IV-VI*** *cover responses to anthropogenically induced changes in the marine environment (purple bubbles), which both potentially contribute to shifts in bacterioplankton community and ecosystem function (light-red bubbles). The light-brown bubbles and outer arrows indicate themes to which the studies in the thesis may contribute deepened understanding.*

RESULTS AND DISCUSSION

> *"I seldom end up where I wanted to go, but almost always end up where I need to be."*
>
> D. Adams

Natural environmental change

Paper I & II – Spatiotemporal population dynamics

Seasonal studies define broad shifts in bacterioplankton composition (Fuhrman et al., 2006, Andersson et al., 2010, Pinhassi and Hagström 2000). The findings in **Paper I** confirm a distinct seasonal succession among marine bacterial populations, and contribute to establishing links between community compositional shifts and change in environmental parameters on a more detailed timescale. **Paper I** further highlights that high temporal resolution sampling has the potential to uncover a very wide spectrum of bacterioplankton population dynamics, resulting both from differences in abundances and in temporal patterns of individual populations. Specifically, similar variations in niche differentiation of being mostly abundant, transient and rare were found within each major bacterial group. This variety of population dynamics is intriguing, but may to some extent complicate ambitions of finding causal relationships between environmental variables and changes in bacterial community composition.

Analyses based on sampling at any particular geographic location may raise questions about whether the temporal dynamics observed at that location reflect arbitrary shifts in water masses or represent actual biological succession in bacterioplankton communities driven by changes in environmental conditions. However, beyond the correlation analyses with environmental variables observed in **Paper I**, the high frequency of sampling indicates potential links between seasonal "events" and dynamics in bacterioplankton community composition, suggesting that a major part of observed population dynamics reflects successional transitions. Thus, bacterial population dynamics in the offshore Baltic Sea appear to reflect primarily the impact of biological transitions, allowing interpretations of ecological processes coupled with bacterioplankton communities.

In **Paper II** we observed a positive interspecific relationship between local abundance and regional occupancy. This is in accordance with several studies, both in terrestrial and aquatic ecosystems and for micro- and macro-organisms (e.g. Östman et al., 2010). However, this relationship is highly dependent on community similarity and may change on different spatial scales. Nevertheless, the finding of locally abundant species also being regionally widespread is linked to a second pattern; the species-abundance distribution. The data presented in **Paper II** is the first to describe bimodal occupancy frequency patterns in bacterioplankton communities (Fig. 7A). These findings suggest that stochastic variation in the rates of local extinction and/or colonization (Fig. 7B; C) are sufficiently large to result in a bimodal species distribution pattern, following the previously mentioned core-satellite hypothesis (Hanski, 1982). The key factor in the core-satellite hypothesis is the significance of rescue effects for common species and that the effect of stochastic variation in colonization- and extinction rates is highest on species with intermediate occupancy (Gyllenberg and Hanski, 1997). In other words, due to strong regional effects few locally rare populations succeed to colonize new habitats (satellite populations). In contrast, it is common that populations with high abundance and high occupancy (core populations) become more established, and that rare populations become even rarer. Nevertheless, **Paper II** also showed that some populations were occasionally easily dispersed despite low regional occupancy, what we refer to as “microbial rain”. This expands the concept of "propagule rain" (Gotelli, 1991) in general ecology for use also in microbial oceanography. Overall, this study moves beyond describing patterns among specific bacterioplankton populations to infer evidence from theoretical ecology and ecological mechanisms by using metapopulation models to explain dynamics of bacterioplankton communities.

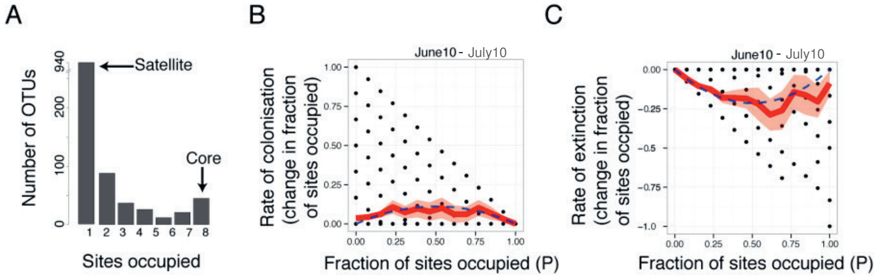

*Figure 7. Example of a bimodal occupancy frequency distribution of OTUs (A), colonization rate (B), and extinction rates (C) from the spatiotemporal study in June 2010, **Paper II**. Colonization and extinction rates are plotted against occupancy. Each dot represents the change in fraction of sites occupied from June to July for individual OTUs. The red line indicates mean and the red shaded area around the mean is standard error. Blue dashed line indicates the quadratic curve of observed data fitted by non-linear least squares to the metapopulation model by Hanski (1982).*

Overall, the bimodality and observed colonization and extinction rates in **Paper II** is in agreement with Hanski’s core-satellite hypothesis (1982) and not with alternative models like unimodality suggested by Levin (1974). However, the lack of bimodality observed in several global datasets may suggest important scale effects of time and space. Alternatively, strong shifts in environmental conditions within different oceanic regions could affect the shape of the occupancy frequency distribution. Observations of frequently occurring species also being locally abundant may also be explained by neutral mechanisms in combination with dispersal (Sloan et al., 2006, Woodcock et al., 2006; Economo and Keitt, 2008). Nevertheless, the observed bimodality, coupled with strong regional effects, suggests that most bacterial populations exhibit biogeographical endemism as opposed to everything being everywhere (Pommier et al., 2007, Sul et al., 2013, Ghiglione et al., 2012, Gibbons et al., 2013). Collectively, the core-satellite hypothesis provides a framework for the biogeographic distribution of bacterial populations and the classification of abundant and rare taxa. Thus, origin, dispersal and extinction of species in addition to interactions among organisms as well as with their physical and biotic environments collectively play important roles for determining bacterioplankton population dynamics.

Paper III – Dissolved organic compound utilization

The concentration and quality of specific dissolved organic carbon compounds, resulting largely from the decay of phytoplankton blooms, vary on both temporal and spatial scales (Suttle et al., 1991, Rich et al., 1996, Obernosterer et al., 1999, Covert and Moran, 2001, Ho et al., 2002). These variations cause a succession of bacterial community composition (Martin, 2012, Teeling et al., 2012, Sarmento et al., 2013, Riemann et al., 2000, Pinhassi et al., 2004). It is therefore not surprising that particular bacterial populations differ in their preference for different dissolved organic compounds due to niche differentiation (Teeling et al., 2012, Sarmento et al., 2013). However, Mou and colleagues (2008) showed that most bacterial phylotypes responded to additions of specific carbon compounds, i.e. a dominant generalist behavior. Results from **Paper III** showed distinct but variable degrees of substrate utilization among bacterioplankton populations. The spectrum of organic compound utilization could be divided into “strict specialists”, i.e. bacteria responding to only one carbon compound, “moderate specialists”, i.e. populations responding to a few carbon compound and “generalists”, i.e. populations responding to many different carbon compounds. Still, it is likely that even “strict specialists” can utilize more than one organic compound. Similarly, “generalists” may not be able to consume all available carbon compounds in the sea. These data highlight mechanisms and ecological adaptations of specific bacterial populations, relevant for understanding carbon compound utilization but also for interpreting the effect of environmental disturbances.

Anthropogenic environmental change

The results in **Paper I-III** highlighted different ecological strategies (niche differentiation) and degrees of generalist and specialist behavior among specific bacterial populations. **In Paper IV-VI** potential adaptations among bacterioplankton populations in responding to climate change were examined, as summarized in Table 2.

Paper IV – Temperature and pH effects

In the mesocosm experiment with increased temperature and lowered pH presented in **Paper IV**, temperature had a higher impact on Baltic Proper bacterioplankton communities than lowered pH. The results in **Paper IV** further show that while some bacterioplankton populations were predominately abundant at ambient temperature, they were sensitive to increased temperature. On the other hand, other populations replaced these sensitive populations at increased temperatures (Table 2). Temperature regulates the composition of bacterial communities in various aquatic environments (Simon et al., 1999, Hoppe et al., 2008, Adams et al., 2010, Dziallas and Grossart, 2011, von Scheibner et al., 2014). For example, von Scheibner and colleagues (2014) showed that specific populations replaced others at higher temperatures, emphasizing a shift towards a more heterotrophic system in the Baltic Sea due to increased temperatures. In addition, temperature shifts may change the capability of bacterioplankton to degrade and utilize dissolved organic matter (Kirchman et al., 2005). Thus, climate warming poses a substantial threat for the structure and function of the entire aquatic food-web by changing the flow of energy, with specific bacterioplankton populations playing key roles.

Climate warming will not be the only driver to potentially influence bacterioplankton dynamics, but will most likely be accompanied by lowered pH resulting from increased atmospheric concentrations of CO_2 (Stocker et al., 2013). The direct effects of lowered pH in shaping bacterioplankton community composition can be different due both to seasonal changes and to biological shifts in pH by e.g. phytoplankton blooms (Joint et al., 2011). Nevertheless, indirect effects mediated through phytoplankton are highly relevant for understanding potential pH responses of bacterioplankton (Allgaier et al., 2008). However, such trophic cascades may complicate the interpretations of lowered pH and is difficult to reproduce in mesocosm experiments. In **Paper IV** a limited impact of acidification on bacterioplankton community composition was found, but when combined with increased temperature specific phylotypes proliferated (Table 2). In other words, by combining two relevant climate change factors we observed a synergistic effect on bacterioplankton community composition. These results emphasize the importance of combining several anthropogenically-induced environmental conditions to fully understand consequences of future climate change scenarios for bacterioplankton.

Paper V & VI – Increased precipitation

In **Paper V** the effect of increased temperature combined with additions of allochtonous matter for Bothnian Sea bacteria was investigated. The results in **Paper V** indicate differential responses among different bacterial populations to combined alterations in temperature and allochtonous matter (Table 2). Lefébure et al., (2013) reported an increase of bacterial heterotrophic production in the same mesocosm experiment as analyzed in **Paper V**. Thus, the two studies collectively indicate the potential of these climate effects to induce shifts in both bacterial community composition and community functioning. Ultimately this could affect carbon cycling in the future Baltic Sea. Substantial effects of temperature and terrestrial DOM on bacterioplankton growth and composition was also shown in the northern Baltic Sea (Degerman et al., 2013). In that study, temperature increases were shown to regulate bacterial composition to a small extent while enhanced terrestrial DOM inputs affected community structure substantially. Overall, the results in **Paper V** are in accordance with previous studies reporting both adaptation and replacement of populations in other aquatic systems (Langenheder et al., 2005, Comte and Del Giorgio, 2011). Thus, how individual bacterial populations differ in their response to environmental disturbance has implications for metabolic activity that heavily influence community functioning and the flow of carbon, potentially pushing toward a more heterotrophic system in brackish seawater.

In addition, current models on climate change project that the Baltic Proper will develop an environment similar to the Bothnian Sea, i.e. lower salinity and increased allochtonous matter inputs (Meier 2006). Salinity is an important factor in structuring bacterioplankton communities and salinity dependent distribution of bacterial populations has been reported in the Baltic Sea (Herlemann et al., 2011, Dupont et al., 2014). In the Baltic Sea, these salinity dependent patterns may also be enhanced due to the long residence time (i.e. >5 yrs) (Riemann et al., 2008).

Also allochtonous matter is known to influence bacterioplankton community composition (Lindström, 2000, Kisand et al., 2002, Eiler et al., 2003, Rochelle-Newall et al., 2004, Haukka et al., 2005, Kritzberg et al., 2006, Kisand et al., 2008, Teira et al., 2009, Hutalle-Schmelzer et al., 2010, Grubisic et al., 2012, Rocker et al., 2012). In **Paper VI** the relationships between metabolic activity and phylogenetic placement of different taxa responding to changes in environmental conditions were investigated. Transplant and re-transplant microcosms with Baltic proper bacteria growing in Bothnian Sea water and vice versa and with re-transfer to water from their original environment was used as a proxy to the effect of increased riverine discharge. The results in **Paper VI** emphasize distinct basin-specific responses of the investigated bacterial communities. Specific bacterial populations replaced others when challenged by new environmental conditions, but also adjustable populations were successful when challenged by new environmental conditions. Some populations were primed and responded slightly in the first transplant to a specific seawater medium, but thanks to this priming continued to increase considerably during the re-transplant in both seawater media (Table 2).

Table 2. Examples of bacterioplankton population dynamics in response to anthropogenically induced changes in environmental conditions in ***Paper IV-VI****. Group names are abbreviated: Actino – Actinobacteria, Alpha – Alphaproteobacteria, Bact. – Bacteroidetes, Beta – Betaproteobacteria, Cyano – Cyanobacteria, Gamma – Gammaproteobacteria, Verr. – Verrucomicrobia. tDOM*$_H$*+T indicate increased terrestrial DOM and temperature. Resistant, sensitive and responsive indicate stability, decrease and increase in relative abundance to changes in environmental conditions, respectively. In Paper VI transplants are indicated with bacterial source (b) → seawater media (sw).*

OTU	Species (closest relative)	Group	Response	Legend
KM-13	Unc. Betaprot. clone 4887-27F	Beta	■	**Paper IV** ■ No resp. (resistant) ▼ 3°C 🔺 6°C 🟡 Low pH
KM-12	Unc. Bact. DGGE band B4-A2	Bact.	▼	
KM-25	*Flavobacterium terrigena* DS-20	Bact.	▼	
KM-6	Arctic sea ice bacterium	Beta	▼	
KM-15	Unc. bacterium clone GOP_J	Cyano	🔺	
KM-11	Unc. bacterium DGGE gel band	Bact.	🔺	
KM-14	Unc. Alphaprot. clone 4473-27F	Alpha	🔺	
KM-30	Unc. Betaprot clone	Beta	🔺+🟡	
UMU_000004	uncl. *Roseobacter* clade	Alpha	■	**Paper V** ■ Resistant to tDOM$_H$+T 🔵 Sensitive to tDOM$_H$+T 🟣 Responsive to tDOM$_H$+T
UMU_000001	hgcI clade	Actino	🔵	
UMU_000002	CL500-29	Actino	🔵	
UMU_000026	LD-29	Verr.	🔵	
UMU_000003	SAR11 clade	Alpha	🟣	
UMU_000000	*Burkholderia*	Beta	🟣	
UMU_000011	*Comamonadaceae*	Beta	🟣	
UMU_000009	*Owenweeksia*	Bact.	🟣	
TR_000037	SAR11 clade	Alpha	*In situ* only	**Paper VI** □LMO$_b$ → LMO$_{sw}$ ❍NB1$_b$ → NB1$_{sw}$ ●NB1$_b$→LMO$_{sw}$ ■LMO$_b$→NB1$_{sw}$ ■* LMO$_b$ →NB1$_{sw}$ → NB1$_{sw}$ ●* NB1$_b$ →LMO$_{sw}$ → LMO$_{sw}$ △LMO$_b$ →NB1$_{sw}$ → LMO$_{sw}$ ▲NB1$_b$ →LMO$_{sw}$ → NB1$_{sw}$
TR_000014	uncl. *Roseobacter* clade	Alpha	*In situ* +□+■	
TR_000006	*Rheinheimera sp.*	Gamma	□+■ +■*	
TR_000010	*Pseudomonas sp.*	Gamma	■ +■*+△	
TR_000005	*Limnobacter sp.*	Beta	■ +■*+△	
TR_000033	*Brevundimonas sp.*	Alpha	■*+△	
TR_000007	*Rheinheimera sp.*	Gamma	●+●*+▲	
TR_000001	*Pseudomonas sp.*	Gamma	❍+●+●*+▲	

Populations from the Baltic Proper were particularly successful in the Bothnian Sea environment, and were coupled to increased metabolic activity (Table 2). Moreover, a significant relationship between changes in bacterial community composition and shifts in community functioning was found in **Paper VI**. This relationship was not found at low phylogenetic resolution and not in the re-transplant experiment. The latter could be argued to be an effect of investigated bacterial populations being functionally redundant. However, our analysis suggests that successional progression following the additional disturbance (re-transplant) could temporarily affect relationships between community composition and community functioning - thus cautioning against rapid conclusions on functional redundancy of bacterial populations/species. Taken together, increased riverine discharge could have a significant effect on bacterial community structure tightly linked with metabolic activity. Further, our findings suggest that priming effects resulting from sizeable environmental events could translate into long-term changes in bacterial carbon cycling properties.

CONCLUSIONS AND PERSPECTIVES

In this thesis, I have mainly covered the Baltic Proper, but conclusions can in theory be applied to all three major basins of the Baltic Sea as well as coastal and semi-enclosed seas around the world. The results showed distinct niche differentiation and substantial population-level responses occurring within each major bacterial group to both natural and anthropogenically-induced changes. Moreover, regional effects influence the dynamics and distribution of bacterioplankton in the sea. This understanding is essential for interpreting biogeographical patterns of bacterioplankton in the sea. In addition, shifts in community composition were linked to responses in metabolic activity on several occasions. Changes in environmental conditions are important for the structure and function of bacterial communities, and may ultimately lead to shifts in biogeochemical cycling of elements such as carbon (Fig. 8). In conclusion, this thesis emphasizes the critical importance of connecting analysis of bacterioplankton population dynamics with examination of ecological mechanisms in order to improve our understanding of factors that regulate the distribution and activity of distinct bacterioplankton populations. In addition, the studies included in this thesis show that (with future perspectives in italics):

- Seasonality and variation in environmental conditions and subsequent microbial responses play significant roles in shaping marine bacterioplankton communities. This thesis shows that analysis of shifts in bacterial community composition and rates of change in relative abundance at a high phylogenetic and temporal resolution may provide clues to how often environmental disturbances of different impact occur. *In this sense, individual populations may act as bioindicators providing a feasible way of constraining the periods during which currently unknown specific variables, be it physical, chemical or biological, affect the planktonic community. Measurements of specific populations over time may provide a framework to monitor the health status of the sea.*
- Future selective forces in the marine environment will include among others increased sea surface temperatures, lower pH, increased allochtonous carbon inputs and decreased salinity. I show that bacterioplankton populations are adjustable and in part replaceable in the event of such environmental

disturbances, coupled with metabolic plasticity. A change in environmental conditions will therefore likely be advantageous to many bacterial populations, while disadvantageous to others, potentially shifting the metabolic outcome and energy flows in the Baltic Sea ecosystem. *In order to fully understand and predict future climate change effects, bacterioplankton should be integrated in food-web and biogeochemical models. Such efforts can be aided by measurements of primary production, respiration and bacterial heterotrophic production coupled with environmental data and bacterial community composition over spatio-temporal scales.*

- The distribution of microbes in the sea is supposed to be little limited by physical barriers. While dispersal may be widespread, the present work shows that regional effects are important for structuring bacterioplankton composition. Thus, as generally recognized in terrestrial ecology, the colonization of local sites by populations from a regional pool could be an important mechanism for regulating the genomic potential among bacterioplankton for biogeochemical processes. *However, whether there is a scale effect for regional dynamics needs further attention. Such efforts could in part be resolved by comparing beta-diversity patterns and bimodality in samples covering different spatial scales and different ecosystems. Experiments with entrapment of bacteria (i.e. allowing only flow of nutrients without immigration of bacteria) vs. natural in situ conditions (i.e. both nutrients and bacterial immigration) at a single station would also be needed to examine regional effects on both community structure and ecosystem functioning.*

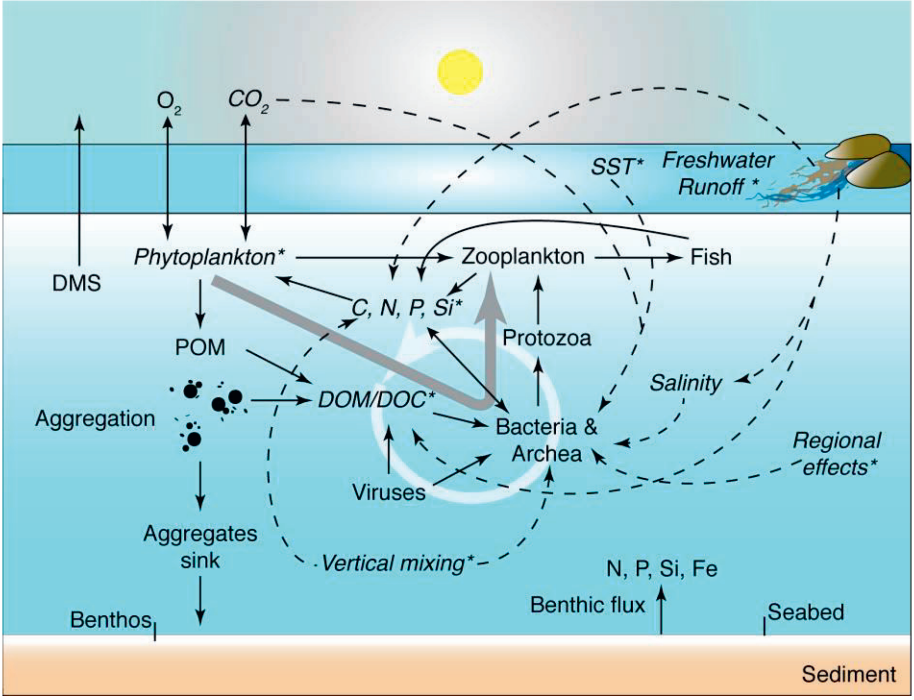

Figure 8. Causal-loop diagram indicating ecosystem-wide effects in carbon cycling due to responses among bacterioplankton populations to natural and anthropogenic disturbances. Italics and dashed lines denote changes in environmental variables covered in this thesis and asterisks indicate significant effects on bacterioplankton community composition. SST = sea surface temperature. Modified from (Azam and Malfatti, 2007).

ACKNOWLEDGEMENTS

“Big ocean, exploding sky, those are things I understand,
I'm fairly good at getting people inspired, but I'm awfully bad at
saying goodbye.”
F. Hyvönen – Saying Goodbye

The past years have been a lot of “ups” and “downs” but together they form an important life experience and many lessons learnt. I want to thank Jarone three times for these years. First, because you convinced me to continue doing research and start my PhD. Second, for making things work the last year from distance since I was on the west coast and you on the east coast either in Sweden or the US. Third, because you are a great inspirer and an extremely nice person. Thank you!

Although we did not meet and talk as much as I would have wished Catherine, the “corridor” meetings have often been inspiring and enough to move forward in science. And the occasional gossip can save an otherwise gloomy day. Your commitment to both science and public outreach is encouraging and you are one of the reasons I want to continue with teaching.

Thank you Börje for opening up a new world. Although we have often wandered off the subject and into an ecological parenthesis you have showed that ecology is limitless and guided me to ask the “interesting” questions.

To the past and present members of the Marine Microbial Ecology group, Laura, Camilla, Julie, Hanna F, Hanna A, Hanna B, Lovisa, Fede, Neelam, Devi, Sandra, Karin, Joakim, Christofer, Johanna, Jeremy, Åke, Lasse, Sabina, Daniel, Stina and Carina. Without you the everyday life would be nothing, and by asking and being asked question we do not only progress in the lab but also in our understanding of science. Thank you Johanna for collaborations and help with writing our papers and nice company to courses in Lund. Thank you Stina, for keeping in touch via skype and making me feel part of the group although I was on the right side of Sweden. Federico showed me a different way of looking at life, maybe spiritual is the wrong word but it helped both in life and science, I would have wished to spend more time together and that we should have met a long time ago.

Thank you to the the members of the “neighbor” groups for interesting and fun conversations. Special thank you for the never-tiring help with sampling and sample processing from Kalle, Kris Emil and Emmelie.

Nice collaborations have been done with the scilifers DubbelAnders and Luisa. But also with Agneta, Daniela and Owen in Umeå. Many thanks!

Although sometimes excruciatingly difficult to retrieve any DNA from your samples Jörgen, our collaboration have been very interesting and so far resulted in one published paper and one in prep.

Thank you to the administration at BOM, you have always been very helpful and I hope you understand that I don’t just smile in the corridors to be polite but because I really appreciate you and your work.

Meetings and courses organized by the graduate research school Geneco have been much appreciated and have provided a nice atmosphere and network of colleagues. The courses with Björn Canbäck have been especially rewarding!

The EcoChange Research programme gave me an opportunity to study climate change effects in the Baltic Sea and I want to applaud the efforts of making such an extensive collaboration between colleagues from different parts of Sweden. Congratulation’s for a nice endeavor and hope you get more funding!

Thanks to Bärbel Muller-Karulis for help with the oceanographic description of the Western Baltic Sea. Data were downloaded from the Baltic Environmental Database at Baltic Nest Institute, Stockholm University and were contributed by Federal Maritime and Hydrographic Agency in Germany (sent by German Oceanographic Data Center in Hamburg), IOW, SMHI, SYKE and Finnish Marine Institute.

Special thanks to Anders and Sabina, with your help the seemingly impossible is possible, ranging from saving molten plastic in the autoclave to sampling with pumps at LMO and extracting and PCRing thousands of samples. And you are probably the nicest people I have met.

It is perhaps good that we don’t see each other so often because I sometimes talk too much about science and teaching, but my friends provide the backbone for reality outside of academia, and I love to hear that you are simply happy, which makes me proud in a strange way.

Slutligen till min familj vill jag säga tack till mamma och pappa för allt stöd genom skolan och för att du tog med mig ut en stjärnklar kväll 1997 för att titta på kometen Hale-Bopp mamma. Du kanske inte vet det men ”Genetiken i bild och bubblor” startade hela min karriär inom molekylär-/mikrobiologin, tack Marie! Till sist, tack till Emma för att du finns i mitt liv och jag får dela livet med dig och med Rufus. Jag älskar er!

REFERENCES

Adams, H.E., Crump, B.C., and Kling, G.W. (2010) Temperature controls on aquatic bacterial production and community dynamics in arctic lakes and streams. *Environ Microbiol* **12**: 1319-1333.

Allgaier, M., Riebesell, U., Vogt, M., Thyrhaug, R., and Grossart, H.P. (2008) Coupling of heterotrophic bacteria to phytoplankton bloom development at different pCO(2) levels: a mesocosm study. *Biogeosci* **5**: 1007-1022.

Allison, S.D., and Martiny, J.B. (2008) Resistance, resilience, and redundancy in microbial communities. *Proc Natl Acad Sci U S A* **105**: 11512-11519.

Alonso-Saez, L., Sanchez, O., Gasol, J.M., Balague, V., and Pedros-Alio, C. (2008) Winter-to-summer changes in the composition and single-cell activity of near-surface Arctic prokaryotes. *Environ Microbiol* **10**: 2444-2454.

Alonso-Saez, L., Zeder, M., Harding, T., Pernthaler, J., Lovejoy, C., Bertilsson, S., and Pedrós-Alió, C. (2014) Winter bloom of a rare betaproteobacterium in the Arctic Ocean. *Front in Microbiol* **5**.

Andersson, A.F., Riemann, L., and Bertilsson, S. (2010) Pyrosequencing reveals contrasting seasonal dynamics of taxa within Baltic Sea bacterioplankton communities. *ISME J* **4**: 171-181.

Arnosti, C., Durkin, S., and Jeffrey, W.H. (2005) Patterns of extracellular enzyme activities among pelagic marine microbial communities: implications for cycling of dissolved organic carbon. *Aquat microb ecol* **38**: 135-145.

Arnosti C, Grossart HP, Mühling M, Joint I, and Passow U (2011) Dynamics of extracellular enzyme activities in seawater under changed atmospheric pCO2: a mesocosm investigation. *Aquat Microb Ecol* **64**: 285-298.

Azam, F., and Malfatti, F. (2007) Microbial structuring of marine ecosystems. *Nat Rev Microbiol* **5**: 782-791.

Azam, F., Smith, D.C., Steward, G.F., and Hagström, Å. (1994) Bacteria-organic matter coupling and its significance for oceanic carbon cycling. *Microb Ecol* **28**: 167-179.

Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyerreil, L.A., and Thingstad, F. (1983) The Ecological Role of Water-Column Microbes in the Sea. *Mar Ecol-Prog Ser* **10**: 257-263.

Barberan, A., and Casamayor, E.O. (2010) Global phylogenetic community structure and beta-diversity patterns in surface bacterioplankton metacommunities. *Aquat Microb Ecol* **59**: 1-10.

Bell, T., Newman, J.A., Silverman, B.W., Turner, S.L., and Lilley, A.K. (2005) The contribution of species richness and composition to bacterial services. *Nature* **436**: 1157-1160.

Bergen, B., Herlemann, D.P.R., Labrenz, M., and Jürgens, K. (2014) Distribution of the verrucomicrobial clade Spartobacteria along a salinity gradient in the Baltic Sea. *Environ Microbiol Rep*.

Bidle, K.D., and Azam, F. (2001) Bacterial control of silicon regeneration from diatom detritus: Significance of bacterial ectohydrolases and species identity. *Limnol and Oceanogr* **46**: 1606-1623.

Brettar, I., Christen, R., and Hofle, M.G. (2012) Analysis of bacterial core communities in the central Baltic by comparative RNA-DNA-based fingerprinting provides links to structure-function relationships. *ISME J* **6**: 195-212.

Brown, J.H. (1984) On the relationship between abundance and distribution of species. *Am Natural* **124**: 255-279.

Brown, M.V., Lauro, F.M., DeMaere, M.Z., Muir, L., Wilkins, D., Thomas, T. et al., (2012) Global biogeography of SAR11 marine bacteria. *Mol Syst Biol* **8**: 595.

Campbell, B.J., Yu, L., Heidelberg, J.F., and Kirchman, D.L. (2011) Activity of abundant and rare bacteria in a coastal ocean. *Proc Natl Acad Sci U S A* **108**: 12776-12781.

Carlson, C.A., Giovannoni, S.J., Hansell, D.A., Goldberg, S.J., Parsons, R., and Vergin, K. (2004) Interactions among dissolved organic carbon, microbial processes, and community structure in the mesopelagic zone of the northwestern Sargasso Sea. *Limnol and Oceanogr* **49**: 1073-1083.

Church, M.J., DeLong, E.F., Ducklow, H.W., Karner, M.B., Preston, C.M., and Karl, D.M. (2003) Abundance and distribution of planktonic Archaea and Bacteria in the waters west of the Antarctic Peninsula. *Limnol and Oceanogr* **48**: 1893-1902.

Cole, J.J., Findlay, S., and Pace, M.L. (1988) Bacterial production in fresh and saltwater ecosystems: a cross-system overview. *Mar ecol prog ser* **43**: 1-10.

Comte, J., and Del Giorgio, P.A. (2011) Composition influences the pathway but not the outcome of the metabolic response of bacterioplankton to resource shifts. *PLoS One* **6**: e25266.

Comte, J., Fauteux, L., and del Giorgio, P.A. (2013) Links between metabolic plasticity and functional redundancy in freshwater bacterioplankton communities. *Front in Microbiol* **4**.

Cotner, J.B., Ammerman, J.W., Peele, E.R., and Bentzen, E. (1997) Phosphorus-limited bacterioplankton growth in the Sargasso Sea. *Aquat Microb Ecol* **13**: 141-149.

Covert, J.S., and Moran, M.A. (2001) Molecular characterization of estuarine bacterial communities that use high- and low-molecular weight fractions of dissolved organic carbon. *Aquat Microb Ecol* **25**: 127-139.

Degerman, R., Dinasquet, J., Riemann, L., de Luna, S.S., and Andersson, A. (2013) Effect of resource availability on bacterial community responses to increased temperature. *Aquat Microb Ecol* **68**: 131-142.

Dinasquet, J., Kragh, T., Schroter, M.L., Sondergaard, M., and Riemann, L. (2013) Functional and compositional succession of bacterioplankton in response to a gradient in bioavailable dissolved organic carbon. *Environ Microbiol* **15**: 2616-2628.

Dupont, C.L., Larsson, J., Yooseph, S., Ininbergs, K., Goll, J., Asplund-Samuelsson, J. et al., (2014) Functional Tradeoffs Underpin Salinity-Driven Divergence in Microbial Community Composition. *PLoS ONE* 9: e89549.

Dziallas, C., and Grossart, H.P. (2011) Temperature and biotic factors influence bacterial communities associated with the cyanobacterium Microcystis sp. *Environ Microbiol* **13**: 1632-1641.

Economo, E.P., and Keitt, T.H. (2008) Species diversity in neutral metacommunities: a network approach. *Ecol Lett* 11: 52-62.

Eiler, A., and Bertilsson, S. (2006) Detection and quantification of Vibrio populations using denaturant gradient gel electrophoresis. *J Microbiol Methods* **67**: 339-348.

Eiler, A., Johansson, M., and Bertilsson, S. (2006) Environmental influences on Vibrio populations in northern temperate and boreal coastal waters (Baltic and Skagerrak Seas). *Appl Environ Microbiol* **72**: 6004-6011.

Eiler, A., Gonzalez-Rey, C., Allen, S., and Bertilsson, S. (2007) Growth response of Vibrio cholerae and other Vibrio spp. to cyanobacterial dissolved organic matter and temperature in brackish water. *FEMS Microbiol Ecol* **60**: 411-418.

Eiler, A., Farnleitner, A.H., Zechmeister, T.C., Herzig, A., Hurban, C., Wesner, W. et al., (2003) Factors controlling extremely productive heterotrophic bacterial communities in shallow soda pools. *Microb Ecol* **46**: 43-54.

Ely, J.S. & Gibson, D.J. (1996) The core-satellite species hypothesis: it's significance in southern Illinois. Bull Ecol Soc of Am, **77** (Suppl.), 129.

Falkowski, P.G., Barber, R.T., and Smetacek, V. (1998) Biogeochemical Controls and Feedbacks on Ocean Primary Production. *Science* **281**: 200-206.

Field, C.B., Behrenfeld, M.J., Randerson, J.T., and Falkowski, P. (1998) Primary Production of the Biosphere: Integrating Terrestrial and Oceanic Components. *Science* **281**: 237-240.

Fuhrman, J.A., Hewson, I., Schwalbach, M.S., Steele, J.A., Brown, M.V., and Naeem, S. (2006) Annually reoccurring bacterial communities are predictable from ocean conditions. *Proc Natl Acad Sci U S A* **103**: 13104-13109.

Galand, P.E., Casamayor, E.O., Kirchman, D.L., and Lovejoy, C. (2009) Ecology of the rare microbial biosphere of the Arctic Ocean. *Proc Natl Acad Sci U S A* **106**: 22427-22432.

Ghiglione, J.F., Galand, P.E., Pommier, T., Pedros-Alio, C., Maas, E.W., Bakker, K. et al., (2012) Pole-to-pole biogeography of surface and deep marine bacterial communities. *Proc Natl Acad Sci U S A* **109**: 17633-17638.

Gibbons, S.M., Caporaso, J.G., Pirrung, M., Field, D., Knight, R., and Gilbert, J.A. (2013) Evidence for a persistent microbial seed bank throughout the global ocean. *Proc Natl Acad Sci U S A* **110**: 4651-4655.

Gibson, D.J., Allstadt, A.J., Baer, S.G., and Geisler, M. (2012) Effects of foundation species genotypic diversity on subordinate species richness in an assembling community. *Oikos* **121**: 496-507.

Gibson, D.J., Ely, J.S., and Collins, S.L. (1999) The core-satellite species hypothesis provides a theoretical basis for Grime's classification of dominant, subordinate, and transient species. *Journal of Ecology* **87**: 1064-1067.

Gilbert, J.A., Steele, J.A., Caporaso, J.G., Steinbrueck, L., Reeder, J., Temperton, B. et al., (2012) Defining seasonal marine microbial community dynamics. *ISME J* **6**: 298-308.

Gomez-Consarnau, L., Lindh, M.V., Gasol, J.M., and Pinhassi, J. (2012) Structuring of bacterioplankton communities by specific dissolved organic carbon compounds. *Environ Microbiol* **14**: 2361-2378.

Gotelli, N.J. & Simberlo., D. (1987) The distribution and abundance of tallgrass prairie plants: a test of the core-satellite hypothesis. *Am Nat* **130**, 18-35.

Gotelli, N.J. (1991) Metapopulation models: the rescue effect, the propagule rain, and the core-satellite hypothesis. *Am Nat* **138**: 768-776.

Grubisic, L.M., Brutemark, A., Weyhenmeyer, G.A., Wikner, J., Båmstedt, U., and Bertilsson, S. (2012) Effects of stratification depth and dissolved organic matter on brackish bacterioplankton communities. *Mar Ecol Prog Ser* **453**: 37-48.

Gyllenberg, M., and Hanski, I. (1997) Habitat Deterioration, Habitat Destruction, and Metapopulation Persistence in a Heterogenous Landscape. *Theor Pop Biol* **52**: 198-215.

Hagström, A., Pinhassi, J., and Zweifel, U.L. (2000) Biogeographical diversity among marine bacterioplankton. *Aquat Microb Ecol* **21**: 231-244.

Hansell, D.A. (2013) Recalcitrant dissolved organic carbon fractions. Ann Rev *Mar Sci* **5**: 421-445.

Hanski, I. (1982) Dynamics of regional distribution – the core and satellite species hypothesis. *Oikos* **38**: 210-221.

Hanski, I., and Gyllenberg, M. (1993) Two General Metapopulation Models and the Core-Satellite Species Hypothesis. *Am Nat* **142**: 17-41.

Hanson, C.A., Fuhrman, J.A., Horner-Devine, M.C., and Martiny, J.B. (2012) Beyond biogeographic patterns: processes shaping the microbial landscape. *Nat Rev Microbiol* **10**: 497-506.

Hansson, D., Eriksson, C., Omstedt, A., and Chen, D. (2011) Reconstruction of river runoff to the Baltic Sea, AD 1500–1995. *Int J Climat* **31**: 696-703.

Hatosy, S.M., Martiny, J.B.H., Sachdeva, R., Steele, J., Fuhrman, J.A., and Martiny, A.C. (2013) Beta diversity of marine bacteria depends on temporal scale. *Ecology* **94**: 1898-1904.

Haukka, K., Heikkinen, E., Kairesalo, T., Karjalainen, H., and Sivonen, K. (2005) Effect of humic material on the bacterioplankton community composition in boreal lakes and mesocosms. *Environ Microbiol* **7**: 620-630.

Head, I.M., Saunders, J.R., and Pickup, R.W. (1998) Microbial evolution, diversity, and ecology: A decade of ribosomal RNA analysis of uncultivated microorganisms. *Microb Ecol* **35**: 1-21.

Hellweger, F.L., van Sebille, E., and Fredrick, N.D. (2014) Biogeographic patterns in ocean microbes emerge in a neutral agent-based model. *Science* **345**: 1346-1349.

Herlemann, D.P., Labrenz, M., Jurgens, K., Bertilsson, S., Waniek, J.J., and Andersson, A.F. (2011) Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. *ISME J* **5(10)**: 1571–1579.

Herlemann, D.P., Manecki, M., Meeske, C., Pollehne, F., Labrenz, M., Schulz-Bull, D. et al., (2014) Uncoupling of bacterial and allochtonous dissolved organic matter dynamics in decomposition experiments. *PLoS One* **9**: e93945.

Hillebrand, H., Bennett, D.M., and Cadotte, M.W. (2008) Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* **89**: 1510-1520.

Ho, T.-Y., Scranton, M.I., Taylor, G.T., Varela, R., Thunell, R.C., and Muller-Karger, F. (2002) Acetate cycling in the water column of the Cariaco Basin: seasonal and vertical variability and implication for carbon cycling. Limnol *Oceanogr* **47**: 1119-1128.

Hofle, M.G., and Brettar, I. (1995) Taxonomic diversity and metabolic-activity of microbial communities in the water column of the central Baltic Sea. *Limnol and Oceanogr* **40**: 868-874.

Holmfeldt, K., Dziallas, C., Titelman, J., Pohlmann, K., Grossart, H.P., and Riemann, L. (2009) Diversity and abundance of freshwater Actinobacteria along environmental gradients in the brackish northern Baltic Sea. *Environ Microbiol* **11**: 2042-2054.

Hoppe, H.G., Breithaupt, P., Walther, K., Koppe, R., Bleck, S., Sommer, U., and Jurgens, K. (2008) Climate warming in winter affects the coupling between phytoplankton and bacteria during the spring bloom: a mesocosm study. *Aquat Microb Ecol* **51**: 105-115.

Hutalle-Schmelzer, K.M., Zwirnmann, E., Kruger, A., and Grossart, H.P. (2010) Changes in pelagic bacteria communities due to leaf litter addition. *Microb Ecol* **60**: 462-475.

Joint, I., Doney, S.C., and Karl, D.M. (2011) Will ocean acidification affect marine microbes? *ISME J* **5**: 1-7.

Kaartokallio, H., Laamanen, M., and Sivonen, K. (2005) Responses of Baltic Sea ice and open-water natural bacterial communities to salinity change. Appl *Environ Microbiol* **71**: 4364-4371.

Kaartokallio, H., Tuomainen, J., Kuosa, H., Kuparinen, J., Martikainen, P., and Servomaa, K. (2008) Succession of sea-ice bacterial communities in the Baltic Sea fast ice. *Polar Biol* **31**: 783-793.

Kirchman, D.L., Malmstrom, R.R., and Cottrell, M.T. (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.

Kirchman, D.L. (2008) Introduction and overview. *In*: Kirchman D.L (ed.), Microbial ecology of the oceans. 2nd edition. Wiley-Liss, pp. 1-23. USA.

Kisand, V., and Wikner, J. (2003) Combining culture-dependent and -independent methodologies for estimation of richness of estuarine bacterioplankton consuming riverine dissolved organic matter. *Appl Environ Microbiol* **69**: 3607-3616.

Kisand, V., Cuadros, R., and Wikner, J. (2002) Phylogeny of culturable estuarine bacteria catabolizing riverine organic matter in the northern Baltic Sea. Appl *Environ Microbiol* **68**: 379-388.

Kisand, V., Andersson, N., and Wikner, J. (2005) Bacterial freshwater species successfully immigrate to the brackish water environment in the northern Baltic. *Limnol and Oceanogr* **50**: 945-956.

Kisand, V., Rocker, D., and Simon, M. (2008) Significant decomposition of riverine humic-rich DOC by marine but not estuarine bacteria assessed in sequential chemostat experiments. *Aquat Microb Ecol* **53**: 151-160.

Koskinen, K., Hultman, J., Paulin, L., Auvinen, P., and Kankaanpää, H. (2011) Spatially differing bacterial communities in water columns of the northern Baltic Sea. *FEMS Microbiol Ecol* **75**: 99-110.

Kritzberg, E., Cole, J.J., Pace, M.L., Granéli, W., and Bade, D.L. (2004) Autochthonous versus allochthonous carbon sources of bacteria: Results from whole-lake C-13 addition experiments. *Limnol and Oceanogr* **49**: 588-596.

Kritzberg, E.S., Langenheder, S., and Lindström, E.S. (2006) Influence of dissolved organic matter source on lake bacterioplankton structure and function--implications for seasonal dynamics of community composition. *FEMS Microbiol Ecol* **56**: 406-417.

Kuparinen, J., Autio, R., and Kaartokallio, H. (2011) Sea ice bacterial growth rate, growth efficiency and preference for inorganic nitrogen sources in the Baltic Sea. *Polar Biol* **34**: 1361-1373.

Laas, P., Simm, J., Lips, I., and Metsis, M. (2014) Spatial variability of winter bacterioplankton community composition in the Gulf of Finland (the Baltic Sea). *J Mar Syst* **129**: 127-134.

Langenheder, S., Lindström, E.S., and Tranvik, L.J. (2005) Weak coupling between community composition and functioning of aquatic bacteria. *Limnol and Oceanogr* **50**: 957-967.

Langenheder, S., Kisand, V., Wikner, J., and Tranvik, L.J. (2003) Salinity as a structuring factor for the composition and performance of bacterioplankton degrading riverine DOC. *FEMS Microbiol Ecol* **45**: 189-202.

Lefébure, R., Degerman, R., Andersson, A., Larsson, S., Eriksson, L.O., Bamstedt, U., and Bystrom, P. (2013) Impacts of elevated terrestrial nutrient loads and temperature on pelagic food-web efficiency and fish production. *Glob Chang Biol* **19**: 1358-1372.

Lehmann A., M.K. (2008) Upwelling in the Baltic Sea - A review. *J Mar Syst* **74**.

Lennon, J.T., and Jones, S.E. (2011) Microbial seed banks: the ecological and evolutionary implications of dormancy. *Nat Rev Microbiol* **9**: 119-130.

Levin, S.A. (1974) Dispersion and population interactions. *Am Nat* **108**: 207-228.

Lindh, M.V., Riemann, L., Baltar, F., Romero-Oliva, C., Salomon, P.S., Graneli, E., and Pinhassi, J. (2013) Consequences of increased temperature and acidification on bacterioplankton community composition during a mesocosm spring bloom in the Baltic Sea. *Environ Microbiol Rep* **5**: 252-262.

Lindroos, A., Marta Szabo, H., Nikinmaa, M., and Leskinen, P. (2011) Comparison of sea surface microlayer and subsurface water bacterial communities in the Baltic Sea. *Aquat Microb Ecol* **65**: 29-42.

Lindström, E.S. (2000) Bacterioplankton Community Composition in Five Lakes Differing in Trophic Status and Humic Content. *Microb Ecol* **40**: 104-113.

Lindström, E.S., and Langenheder, S. (2012) Local and regional factors influencing bacterial community assembly. *Environ Microbiol Rep* **4**: 1-9.

Loreau, M. (2000) Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91**: 3-17.

Martin, A. (2012) The Seasonal Smorgasbord of the Seas. *Science* **337**: 46-47.

Martiny, J.B.H., Bohannan, B.J.M., Brown, J.H., Colwell, R.K., Fuhrman, J.A., Green, J.L. et al., (2006) Microbial biogeography: putting microorganisms on the map. *Nat Rev Microbiol* **4**: 102-112.

McGeoch, M.A., and Gaston, K.J. (2002) Occupancy frequency distributions: patterns, artefacts and mechanisms. *Biol Rev* **77**: 311-331.

Meier, H.E.M. (2006) Baltic Sea climate in the late twenty-first century: a dynamical downscaling approach using two global models and two emission scenarios. *Clim Dyn* **27**: 39-68.

Moran, M.A., Buchan, A., Gonzalez, J.M., Heidelberg, J.F., Whitman, W.B., Kiene, R.P. et al., (2004) Genome sequence of Silicibacter pomeroyi reveals adaptations to the marine environment. *Nature* **432**: 910-913.

Mou, X., Sun, S., Edwards, R.A., Hodson, R.E., and Moran, M.A. (2008) Bacterial carbon processing by generalist species in the coastal ocean. *Nature* **451**: 708-711.

Müren, U., Berglund, J., Samuelsson, K., and Andersson, A. (2005) Potential effects of elevated sea-water temperature on pelagic food webs. *Hydrobiol* **545**: 153-166.

Needham, D.M., Chow, C.E.T., Cram, J.A., Sachdeva, R., Parada, A., and Fuhrman, J.A. (2013) Short-term observations of marine bacterial and viral communities: patterns, connections and resilience. *ISME J* **7**: 1274-1285.

Nelson, J.D., Boehme, S.E., Reimers, C.E., Sherrell, R.M., and Kerkhof, L.J. (2008) Temporal patterns of microbial community structure in the Mid-Atlantic Bight. *FEMS Microbiol Ecol* **65**: 484-493.

Noble, R.T., and Fuhrman, J.A. (2000) Rapid virus production and removal as measured with fluorescently labeled viruses as tracers. *Appl Environ Microbiol* **66**: 3790-3797.

Obernosterer, I., Kraay, G., de Ranitz, E., and Herndl, G.J. (1999) Concentrations of low molecular weight carboxylic acids and carbonyl compounds in the Aegean Sea (Eastern Mediterranean) and the turnover of pyruvate. *Aquat Microb Ecol* **20**: 147-156.

Omstedt, A., Elken, J., Lehmann, A., Leppäranta, M., Meier, H.E.M., Myrberg, K., and Rutgersson, A. (2014). Progress in physical oceanography of the Baltic Sea during the 2003–2014 period. *Prog Oceanogr*: **128**, 139-171.

Pedros-Alio, C. (2006) Marine microbial diversity: can it be determined? *Trends in Microbiol* **14**: 257-263.

Pedros-Alio, C. (2012) The rare bacterial biosphere. *Ann Rev Mar Sci* **4**: 449-466.

Pinhassi, J., and Hagström, A. (2000) Seasonal succession in marine bacterioplankton. *Aquat Microb Ecol* **21**: 245-256.

Pinhassi, J., Zweifel, U.L., and Hagstroëm, A. (1997) Dominant marine bacterioplankton species found among colony-forming bacteria. Appl and *Environ Microbiol* **63**: 3359-3366.

Pinhassi, J., Winding, A., Binnerup, S.J., Zweifel, U.L., Riemann, B., and Hagström, A. (2003) Spatial variability in bacterioplankton community composition at the Skagerrak-Kattegat Front. *Mar Ecol Prog Ser* **255**: 1-13.

Pinhassi, J., Azam, F., Hemphala, J., Long, R.A., Martinez, J., Zweifel, U.L., and Hagström, A. (1999) Coupling between bacterioplankton species composition, population dynamics, and organic matter degradation. *Aquat Microb Ecol* **17**: 13-26.

Pinhassi, J., Sala, M.M., Havskum, H., Peters, F., Guadayol, O., Malits, A., and Marrase, C. (2004) Changes in bacterioplankton composition under different phytoplankton regimens. *Appl and Environ Microbiol* **70**: 6753-6766.

Piwosz, K., Salcher, M.M., Zeder, M., Ameryk, A., and Pernthaler, J. (2013) Seasonal dynamics and activity of typical freshwater bacteria in brackish waters of the Gulf of Gdańsk. *Limnol and Oceanogr* **58**: 817-826.

Poisot, T., Pequin, B., and Gravel, D. (2013) High-throughput sequencing: a roadmap toward community ecology. *Ecol Evol* **3**: 1125-1139.

Pomeroy, L.R. (1974) The Ocean's Food Web, A Changing Paradigm. *BioScience* **24**: 499-504.

Pommier, T., Canback, B., Riemann, L., Bostrom, K.H., Simu, K., Lundberg, P. et al., (2007) Global patterns of diversity and community structure in marine bacterioplankton. *Mol Ecol* **16**: 867-880.

Rappe, M.S., and Giovannoni, S.J. (2003) The uncultured microbial majority. *Annu Rev Microbiol* **57**: 369-394.

Raunkiaer, C. (1913) Formationsstätistiske Undersøgelser paa Skagens Odde. *Bot Tidskr Kobenhavn* **33**: 197-228.

Raunkiaer, C. (1918) Recherches statistiques sur les formations vegetales. *Biol Medd* **1**: 1-80.

Raunkiaer, C. (1934). The life forms of plants and statistical plant geography. Clarendon Press, Oxford.

Reunamo, A., Riemann, L., Leskinen, P., and Jorgensen, K.S. (2013) Dominant petroleum hydrocarbon-degrading bacteria in the Archipelago Sea in South-West Finland (Baltic Sea) belong to different taxonomic groups than hydrocarbon degraders in the oceans. *Mar Pollut Bull* **72**: 174-180.

Rich, J.H., Ducklow, H.W., and Kirchman, D.L. (1996) Concentrations and uptake of neutral monosaccharides along 140'W in the equatorial Pacific: Contribution of glucose to heterotrophic bacterial activity and the DOM flux. *Limnol Oceanogr* **41**: 595-604.

Riemann, L., Steward, G.F., and Azam, F. (2000) Dynamics of bacterial community composition and activity during a mesocosm diatom bloom. *Appl and Environ Microbiol* **66**: 578-587.

Riemann, L., Leitet, C., Pommier, T., Simu, K., Holmfeldt, K., Larsson, U., and Hagström, A. (2008) The native bacterioplankton community in the central Baltic sea is influenced by freshwater bacterial species. *Appl and Environ Microbiol* **74**: 503-515.

Robinson, C., and Williams, P.J.l. (2005) Respiration and its measurements in surface marine waters. *In* Respiration in Aquatic Ecosystems. Williams, P.J.l. (ed). New York: Oxford University Press.

Rochelle-Newall, E.J., Pizay, M.D., Middelburg, J.J., Boschker, H.T.S., and Gattuso, J.P. (2004) Degradation of riverine dissolved organic matter by seawater bacteria. *Aquat Microb Ecol* **37**: 9-22.

Rocker, D., Brinkhoff, T., Grüner, N., Dogs, M., and Simon, M. (2012) Composition of humic acid-degrading estuarine and marine bacterial communities. *FEMS Microbiol Ecol* **80**: 45-63.

Salka, I., Moulisova, V., Koblizek, M., Jost, G., Jürgens, K., and Labrenz, M. (2008) Abundance, depth distribution, and composition of aerobic bacteriochlorophyll a-producing bacteria in four basins of the central Baltic Sea. *Appl Environ Microbiol* **74**: 4398-4404.

Salka, I., Wurzbacher, C., Garcia, S.L., Labrenz, M., Jürgens, K., and Grossart, H.P. (2014) Distribution of acI-Actinorhodopsin genes in Baltic Sea salinity gradients indicates adaptation of facultative freshwater photoheterotrophs to brackish waters. *Environ Microbiol* **16**: 586-597.

Sarmento, H., Romera-Castillo, C., Lindh, M., Pinhassi, J., Sala, M.M., Gasol, J.M. et al., (2013) Phytoplankton species-specific release of dissolved free amino acids and their selective consumption by bacteria. *Limnol Oceanogr* **58**: 1123-1135.

Schauer, M., Balague, V., Pedros-Alio, C., and Massana, R. (2003) Seasonal changes in the taxonomic composition of bacterioplankton in a coastal oligotrophic system. *Aquat Microb Ecol* **31**: 163-174.

Simon, M., Glockner, F.O., and Amann, R. (1999) Different community structure and temperature optima of heterotrophic picoplankton in various regions of the Southern Ocean. *Aquat Microb Ecol* **18**: 275-284.

Simons, N.K., Gossner, M.M., Lewinsohn, T.M., Lange, M., Türke, M., and Weisser, W.W. (2014) Effects of land-use intensity on arthropod species abundance distributions in grasslands. *J Anim Ecol* DOI: 10.1111/1365-2656.12278.

Simu, K., and Hagström, A. (2004) Oligotrophic bacterioplankton with a novel single-cell life strategy. *Appl Environ Microbiol* **70**: 2445-2451.

Sipura, J., Haukka, K., Helminen, H., Lagus, A., Suomela, J., and Sivonen, K. (2005) Effect of nutrient enrichment on bacterioplankton biomass and community composition in mesocosms in the Archipelago Sea, northern Baltic. *J Plankt Res* **27**: 1261-1272.

Sjöstedt, J., Hagström, A., and Zweifel, U.L. (2012a) Variation in cell volume and community composition of bacteria in response to temperature. *Aquat Microb Ecol* **66**: 237-246.

Sjöstedt, J., Koch-Schmidt, P., Pontarp, M., Canback, B., Tunlid, A., Lundberg, P. et al., (2012b) Recruitment of members from the rare biosphere of marine bacterioplankton communities after an environmental disturbance. *Appl Environ Microbiol* **78**: 1361-1369.

Sloan, W., Lunn, M., Woodcock, S., Head, I.M., Nee, S., and Curtis, T.P. (2006) Quantifying the roles of immigration and chance in shaping prokaryote community structure. Environ Microbiol **8**: 732-740.

Sogin, M.L., Morrison, H.G., Huber, J.A., Mark Welch, D., Huse, S.M., Neal, P.R. et al., (2006) Microbial diversity in the deep sea and the underexplored "rare biosphere". *Proc Natl Acad Sci U S A* **103**: 12115-12120.

Soininen, J., and Heino, J. (2005) Relationships between local population persistence, local abundance and regional occupancy of species: distribution patterns of diatoms in boreal streams. *J Biogeogr* **32**: 1971-1978.

Sommer, U., Aberle, N., Engel, A., Hansen, T., Lengfellner, K., Sandow, M. et al., (2007) An indoor mesocosm system to study the effect of climate change on the late winter and spring succession of Baltic Sea phyto- and zooplankton. *Oecologia* **150**: 655-667.

Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J. et al., (2013) Climate change 2013: The physical science basis. Intergovernmental Panel on Climate Change, Working Group I Contribution to the IPCC Fifth Assessment Report (AR5) (Cambridge Univ Press, New York).

Stolle, C., Nagel, K., Labrenz, M., and Jurgens, K. (2010) Succession of the sea-surface microlayer in the coastal Baltic Sea under natural and experimentally induced low-wind conditions. *Biogeosci* **7**: 2975-2988.

Stolle, C., Labrenz, M., Meeske, C., and Jurgens, K. (2011) Bacterioneuston community structure in the southern Baltic sea and its dependence on meteorological conditions. *Appl Environ Microbiol* **77**: 3726-3733.

Sul, W.J., Oliver, T.A., Ducklow, H.W., Amaral-Zettler, L.A., and Sogin, M.L. (2013) Marine bacteria exhibit a bipolar distribution. *Proc Natl Acad Sci* U S A **110**: 2342-2347.

Suttle, C.A., Chan, A.M., and Fuhrman, J.A. (1991) Dissolved free amino acids in the Sargasso Sea: uptake and respiration rates, turnover times, and concentrations. *Mar Ecol Prog Ser* **70**: 189-199.

Tammert, H., Lignell, R., Kisand, V., and Olli, K. (2012) Labile carbon supplement induces growth of filamentous bacteria in the Baltic Sea. *Aquat Biol* **15**: 121-134.

Teeling, H., Fuchs, B.M., Becher, D., Klockow, C., Gardebrecht, A., Bennke, C.M. et al., (2012) Substrate-Controlled Succession of Marine Bacterioplankton Populations Induced by a Phytoplankton Bloom. *Science* **336**: 608-611.

Teira, E., Nieto-Cid, M., xc, and lvarez-Salgado, X.A. (2009) Bacterial community composition and colored dissolved organic matter in a coastal upwelling ecosystem. *Aquat Microb Ecol* **55**: 131-142.

Tiirik, K., Nõlvak, H., Oopkaup, K., Truu, M., Preem, J.-K., Heinaru, A., and Truu, J. (2014) Characterization of the bacterioplankton community and its antibiotic resistance genes in the Baltic Sea. *Biotech and Appl Biochem* **61**: 23-32.

Tuomainen, J., Hietanen, S., Kuparinen, J., Martikainen, P., and Servomaa, K. (2006) Community Structure of the Bacteria Associated with Nodularia sp. (Cyanobacteria) Aggregates in the Baltic Sea. *Microb Ecol* **52**: 513-522.

Vega Thurber, R., Willner-Hall, D., Rodriguez-Mueller, B., Desnues, C., Edwards, R.A., Angly, F. et al., (2009) Metagenomic analysis of stressed coral holobionts. *Environmental Microbiology* **11**: 2148-2163.

Vergin, K.L., Beszteri, B., Monier, A., Thrash, J.C., Temperton, B., Treusch, A.H. et al., (2013) High-resolution SAR11 ecotype dynamics at the Bermuda Atlantic Time-series Study site by phylogenetic placement of pyrosequences. *ISME J* **7**: 1322-1332.

Viggor, S., Juhanson, J., Jõesaar, M., Mitt, M., Truu, J., Vedler, E., and Heinaru, A. (2013) Dynamic changes in the structure of microbial communities in Baltic Sea coastal seawater microcosms modified by crude oil, shale oil or diesel fuel. *Microbiol Res* **168**: 415-427.

von Scheibner, M., Dörge, P., Biermann, A., Sommer, U., Hoppe, H.-G., and Jürgens, K. (2014) Impact of warming on phyto-bacterioplankton coupling and bacterial community composition in experimental mesocosms. *Environ Microbiol* **16**: 718-733.

Whitman, W.B., Coleman, D.C., and Wiebe, W.J. (1998) Prokaryotes: The unseen majority. *Proc Natl Acad Sci U S A* **95**: 6578-6583.

Witt, V., Wild, C., Anthony, K.R., Diaz-Pulido, G., and Uthicke, S. (2011) Effects of ocean acidification on microbial community composition of, and oxygen fluxes through, biofilms from the Great Barrier Reef. *Environ Microbiol*.

Woodcock, S., Curtis, T.P., Head, I.M., Lunn, M., and Sloan, W. (2006) Taxa-area relationships for microbes: the unsampled and the unseen. *Ecol Letters* **9**: 805-812.

Zweifel, U.L., Norrman, B., and Hagström, A. (1993) Consumption of Dissolved Organic-Carbon by Marine-Bacteria and Demand for Inorganic Nutrients. *Mar Ecol Prog Ser* **101**: 23-32.

Ågren, A., Jansson, M., Ivarsson, H., Bishop, K., and Seibert, J. (2008) Seasonal and runoff-related changes in total organic carbon concentrations in the River Öre, Northern Sweden. *Aquat Sci* **70**: 21-29.

Östman, O., Drakare, S., Kritzberg, E.S., Langenheder, S., Logue, J.B., and Lindstrom, E.S. (2010) Regional invariance among microbial communities. *Ecol Lett* 13: 118-127.