To diversity and beyond

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Citation for published version (APA):
Rozema, P. D. (2017). To diversity and beyond: Shifting Antarctic microbial communities along environmental gradients. [Groningen]: University of Groningen.

Summary

The changing climate of our planet holds extensive consequences for many regions. Antarctica is a continent mostly covered by snow and ice, and is surrounded by the Southern Ocean, and therefore highly vulnerable. It is easy to imagine that changes in air and water temperature strongly affect this continent. After all, a temperature slightly above or below 0°C is a world of difference on an ice covered continent. As a consequence of this warming marine-terminating glaciers and ice sheets floating on the ocean are retreating of collapsing.

One of the most strongly affected regions is the coastal region of the Antarctic Peninsula, the northernmost area of Antarctica. The Antarctic Peninsula is of volcanic origin and is separated from South America by the 5000m deep Drake Passage. Winter sea ice cover is declining along the west Antarctic Peninsula as the onset of ice formation is delayed while ice melt in spring occurs earlier. Consequently, the increase in open water area results in deeper vertical mixing as the ocean surface is exposed to the strong winter winds. In addition to the changes in sea ice, the majority of the glaciers on the west side of the Antarctica Peninsula are in retreat. This is mostly due to warmer waters originating from deep water layers which melt the glaciers from underneath, therefore thinning and shorting them. This fresh melt water promotes stratification (formation of different water layers) of the water column during summer because the fresh water is lighter than the underlying sea water.

As the different water layers hardly mix, the populations of micro-organisms can be different between the water layers. Moreover, this effect is enhanced by for example differences in nutrient and/or sun light availability. Yet, the stratification of the water column can be undone: strong winds could mix of the surface layers and therefore homogenize the surface ocean. Thus, the warming of the Antarctic Peninsula causes complex changes, beyond only increasing the temperature. These changes affect the marine food web as the physical and chemical environment controls marine productive and structuring of the ecosystem.

Marine micro-organisms are globally extremely divers in shape, size and function. As in the terrestrial system, organisms that fix use solar energy to fix CO_2 in a process

called photosynthesis form the bottom of the food chain. In the ocean, these are microscopically small algae called phytoplankton which are eaten by small and large grazers (herbivores). The best known of these grazers in the Southern Ocean are krill, shrimp-like creatures only a few centimeters long. These grazers are pivotal in the classical Antarctic food web as these are readily edible by for example penguins and whales. When phytoplankton are not consumed, it sinks to the deep ocean where the fixed CO_2 can be stored for a long time, offsetting some of the CO_2 input into the atmosphere. Yet, small and light algae species sink too slow and therefore their algal biomass is mostly broken-down by bacteria. Thus, the previously fixed CO_2 remains in the upper water layers. Therefore, species composition, and average size, of the phytoplankton community determine how algal biomass is processed in the food web.

Phytoplankton are responsible for 50% of the global oxygen production and a large part of the storage of CO_2 in the deep ocean. Some phytoplankton species (flagellates) are small, light and mobile, they have tail (flagellate) used for swimming. Other species are large and have a heavy silica cell wall. These species are often referred to as “algae in a glass house” and are called diatoms. We know that both groups of phytoplankton are common in the coastal waters of the Antarctic Peninsula. Not only do these micro-algal groups differ size and mobility, but also in their uptake capacity of dissolved nutrients, such as nitrate and phosphate, and their preferences for variability in light intensity. Moreover, krill prefer diatoms over flagellates as their main food source.

The open Southern Ocean is known as a region where the most important nutrients (nitrate, phosphate and silicate) are not limiting to phytoplankton growth. Yet, trace elements such as iron and zinc are limiting. In contrast, it is assumed that coastal regions are not limited by trace elements due to the proximity to sources such as rocks and sediment. The overall contrasting conditions between the open and coastal ocean force the phytoplankton species to adept to these different, yet specific and highly variable conditions. Not only can nutrient concentrations vary greatly, but also the variability sea-ice cover, salinity, stratification, light intensity and seasonal dynamics in grazing contribute to a highly variable environment of the coastal ocean and therefore drive the adaption of the different phytoplankton species. These species employ a range of strategies to cope with these conditions, for example certain phytoplankton species combine photosynthesis with the eating of bacteria. Therefore, it is easy to imagine the evolution of a large number of phytoplankton species, each with a different shape, flexibility and function optimized for a specific set of preferred conditions. The combination of these properties and conditions determines the place, also known as niche, a certain species fulfills within the ecosystem.

While "species" is the lowest taxonomic level that we know, not all individuals within a species are identical. We often use the definition of 97% similarity in DNA before attributing micro-organisms to the same species. As such, there can be variants within species which prefer slightly different environmental conditions. For example, we know of some phytoplankton species with a high-light and a low-light variant. These variants are genetically nearly identical, therefore they belong to the same species, but occupy different niches in the ecosystem. Such variants of a species are also known as ecotypes. Because these ecotypes occur under different environmental conditions, they can also fulfill different ecosystem functions.

In this thesis I discuss a number of questions related to these micro-organisms. The over-arching question is: "How does the microbial community in the coastal region of the west Antarctic Peninsula vary in abundance and composition, and how is this driven by changes in the physical and chemical environment?" This question was subdivided into multiple smaller, and more specific questions which are discussed in the different chapters. For this research we made use of both previously collected samples (Chapters 2 and 4),, and measurements and samples collected specifically for this research funded by NWO (Chapters 3, 5, and 6). These latter samples were collected during two Antarctic summers (Jan 2013-Mar 2013 and Nov 2013-Mar 2014) at Rothera, a British research station. This station is situated on the west Antarctic Peninsula at Ryder Bay, where a study site occupied since 1997 is situated, the RaTS-site. At and round this site is where all of the samples discussed in this thesis are collected.

In **Chapter 2** we studied to what extent sea-ice cover during winter, and water column stabilization during spring and summer governed phytoplankton species composition. Previous research has established that total phytoplankton biomass depended on water column stability. I hypothesized that phytoplankton species composition also varied between years with high or low total summer phytoplankton biomass. We confirmed this hypothesis through the analysis of a time series collecting data since 1997. Winters with low sea ice cover, and therefore a deeply mixed water column, resulted in less phytoplankton biomass and a lower contribution of large diatoms in favor of small flagellates. The results of this study were summarized in a conceptual model where summers resulting from winters differing in sea ice cover are clearly separated. Moreover, we have added summers of intermediate levels of biomass: for example a winter with low sea ice cover but relative warm and stable spring conditions can still result in average phytoplankton biomass levels without a reduction in relative diatom abundances.

In **Chapter 3** the productivity of phytoplankton at the RaTS-site during the summer of 2013-2014 was analyzed as a function of the environmental conditions. Different (climate)models calculate how much CO_2 is absorbed by phytoplankton, yet it is important to calibrated and improve those models using field measurements. In the polar regions, the production process (photosynthesis) is primarily regulated by light availability as this limits growth due to low angles of irradiance, it is nearly dark during winter, or sea ice cover. Moreover, it is likely that the availability of nutrients, such as nitrate or iron, is relevant. To unravel these abiotic factors , but also the importance of phytoplankton species composition, CO_2 uptake experiments were conducted using natural phytoplankton communities. These results were analyzed using a self-learning model to understand which parameters influenced CO_2 uptake most strongly. Surprisingly, we learned that nitrogen (nitrate and nitrite) availability was a governing factor. Probably because iron-availability was high enough to allow biomass accumulation to a level where nitrogen became the limiting element. Also, the results show that phytoplankton community composition does not directly affect uptake. This is unexpected as we know from laboratory studies that different species have different uptake rates. Thus, environmental conditions are many times more important than biological variability with regards to CO_2 uptake. Therefore, we could accurately estimate phytoplankton productivity by only three parameters, light, total biomass and nitrogen availability.

In **Chapter 4** was investigated which environmental parameters influenced the species composition of the bacterial and phytoplankton communities. Previous investigations of the phytoplankton community used microscope or pigments analyses, yet these techniques are costly or lack taxonomic resolution. Here, we investigated a small piece of the genetic material of these species to identify them and get an idea of their abundance. Moreover, using this approach we could study the bacteria and phytoplankton simultaneously. This allowed us to compare both components of the microbial system and study how these are controlled by their environment. Our results suggest that, in contrast to what is generally assumed, limitation of nutrients does occur during summer. Which nutrient varied between the different phases of the summer season. Both nitrogen and phosphorus concentrations were occasionally near or below the detection levels. Also, the variations in these different nutrients strongly influenced phytoplankton diversity while water column stability (stratification) was another strong influence. Storms can cause abrupt changes in the water column stability by mixing the water. These moments of strong wind mixing influenced nutrient and light availability and drastically changed the phytoplankton community within days. Changes in the bacterial community were mostly depended on total phytoplankton biomass. Also, the data suggests that bacterial diversity was depended on phytoplankton community composition albeit delayed by two weeks. This dependency is understandable as the composition of the organic material on which bacteria grow varies between different phytoplankton species.

In **Chapter 5** was the availability of various trace elements and major nutrients during the summer over 2012-2014 investigated. Samples were collected at multiple depths at the RaTS-location for the measurement of nitrate, nitrite, phosphate, silicate, iron, manganese, zinc, cadmium, cobalt and copper. First of all, we showed that several trace elements were present in such low concentrations that they most likely hampering phytoplankton growth. Moreover, we confirmed our earlier findings (from **Chapter 3**) and showed that all major nutrients (thus nitrate, phosphate and silicate) can be reduced by phytoplankton to very low concentrations. Also, nutrient dynamics differed greatly between the two different summers. Finally, we showed that flagellates and diatoms take up major nutrients and trace elements in different ratios. Thus, these results underline that the majority of the measured nutrients and trace elements are relevant for determining species composition but more importantly: they control phytoplankton abundance to a great extent.

In **Chapter 6** we investigated the existence of different ecotypes for the flagellated species. Previous studies, including **Chapters 2, 3** and **5** of this thesis, have mainly used pigments to assess crude phytoplankton species composition. Yet, in **Chapter 6** we employed new DNA techniques to detect and describe species during two austral summers (2012-2014). It is generally assumed that the haptophyte *Phaeocystis antarctica* and the cryptophyte *Geminigera cryophila* are the two dominant flagellated species. Yet, we showed the presences of a second haptophyte species, probably *P. jahnii*. Additionally, we observed a second haptophyte genus, namely *Chrysochromulina* that was equally abundant as *Phaeocystis* during the first summer. We also confirm the presence of different ecotypes within all the investigated species. For example, for *G. cryophila* we observed three different ecotypes of which two had contrasting preferences for salinity, thus suggesting an open ocean ecotype and one associated with fresher water. The existence of these different ecotypes means that they occupy different niches, and potentially fulfill different roles in the ecosystem. Finally, we strongly suspect to have identified a cryptophyte specific grazer, the dinoflagellate *Prorocentrum*. This could mean that *G. cryophila* is thightly regulated by top-down grazing pressure, a mechanism we did not identify for the other flagellated species.

The research conducted in this thesis has increased our understanding of the strong dynamics in microbial species composition, abundance, and production along the rapidly changing Antarctic Peninsula. Most of these factors, such as: sea-ice cover, melting glaciers, wind mixing and nutrient availability, are all governing the microbial community and are undergoing rapid change. This thesis already shows years where the phytoplankton community composition has shifted away from the classical coastal Antarctic system. Such deviations are likely to occur more frequently in the near future given the current trends in the local and global climate. Therefore, the impact on the food web and CO_2 storage capabilities of the Southern Ocean will only become more evident.