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LINKING THE THERMOHALINE CIRCULATION TO THE COMPOSITION AND ACTIVITY OF PROKARYOTIC COMMUNITIES

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The horizontal transport of deep-water masses plays a major role in controlling the Earth's climate and is a central topic in physical oceanography. However, the deep ocean is a cold, dark environment where biological activity depends on a scant "rain" of organic materials from the surface where sunlight enables the growth of algae. Therefore, biological and biogeochemical oceanographers have traditionally focused their studies on the vertical flux from the surface layers to the deep ocean. We now have challenged this approach by following the horizontal movement of the two major branches of the North Atlantic Deep Water (NADW), covering a stretch comprising roughly 50 years of circulation from its source in the Greenland-Iceland-Norwegian Sea as part of the global thermohaline circulation. Although deep-sea prokaryotes (Bacteria and Archaea) were present in lower numbers than in surface waters, they are well adapted to their dark environment and exhibit higher activity than previously assumed. We found that the distinct major deep-water masses harbor distinct prokaryotic communities with successional changes as the water mass progresses in the oceanic conveyor belt.

Introduction

The cooling of the surface waters in the Greenland-Iceland-Norwegian (GIN) Sea and the subsequent large scale deep water formation is known as the North Atlantic Deep Water (NADW) formation. It is the major driving force of the oceanic conveyor belt system, connecting the waters of all our oceans (Fig.1) Recently, it has been found that the deep water formation in the GIN Sea is more variable than hitherto assumed. This variability in the deep water formation influences the circulation pattern of the oceanic conveyor belt system which, in turn, influences both, the global climate and the oceanic carbon cycling (see Intermezzo).

The multidisciplinary project TRANSAT, funded by ALW-NWO focuses on the link between the thermohaline ocean circulation and the transformation processes of dissolved organic matter (DOM) by the microbial community. We followed the two major branches of the NADW from their formation in

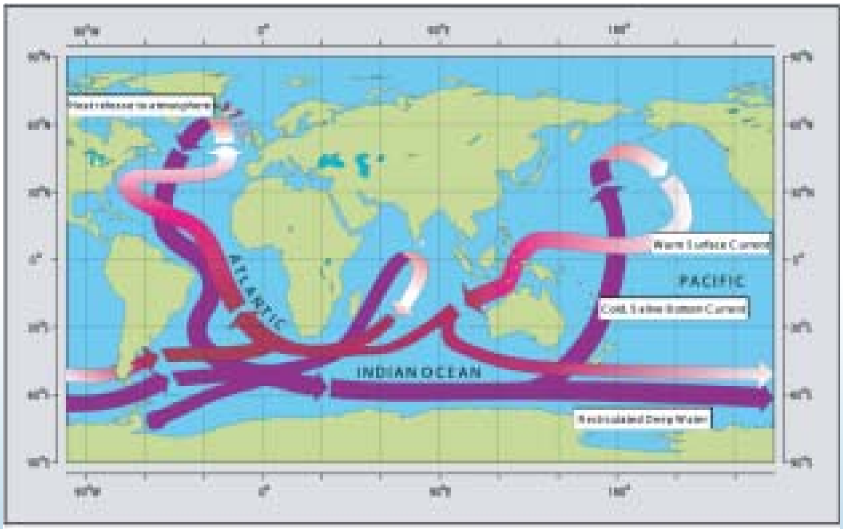

Fig. 1. Simplified conveyor belt scheme of the oceanic thermohaline circulation.

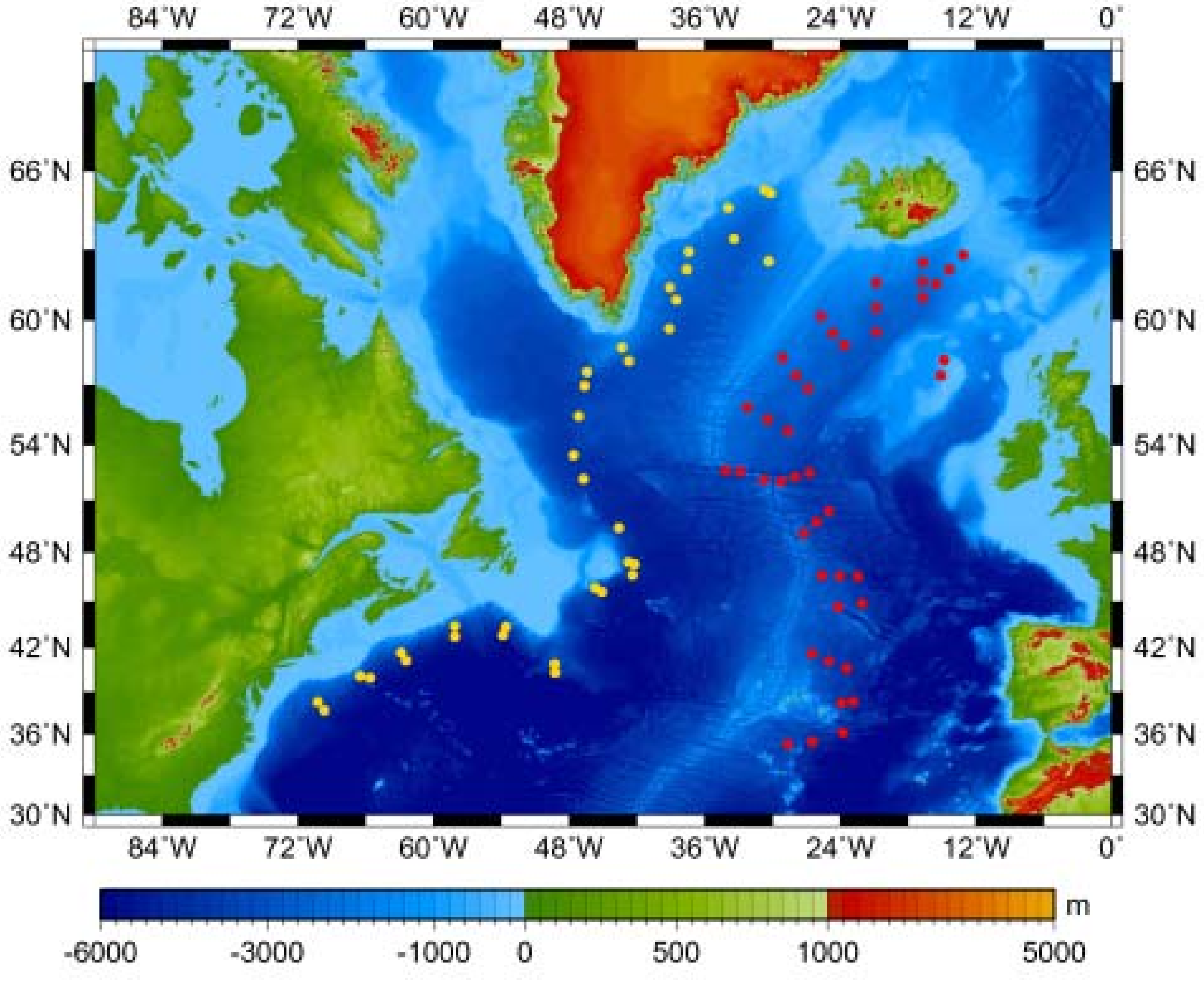

Fig. 2. The TRANSAT cruise tracks following the two branches of the North Atlantic Deep Water (NADW) from near its region of formation in the Greenland-Iceland-Norwegian Sea over more than 4000 km corresponding to about the first 50 years of NADW in the oceanic conveyor belt. Stations occupied are indicated by red dots for TRANSAT-1 and yellow dots for the TRANAT-2 cruise.

the GIN-Sea over more than 4000 km (Fig. 2), and determined the community composition and the major activity parameters of the prokaryotic (Archaea and Bacteria) community such as cell production, respiration and enzymatic activity. These biological parameters were related to the physical and chemical characteristics of the major water masses.

As the NADW gets older, along the TRANSAT-transects from north to south, the apparent oxygen utilization increased, coinciding with a decrease in dissolved organic carbon, nitrogen and phosphorus. At the same time, the levels of inorganic nitrogen and phosphorus increased in concentrations by 20% and 30%. The spatial development of all these parameters indicate remineralization activity of the deep water prokaryotic community, making nutrients available for new life. These signs of high activity of the deep water community were confirmed by single cell analyses using micro-autoradiography combined with a highly sensitive fluorescence in situ hybridization technique (more details of this technique are given in the contribution of Eva Teira et al. under the Department of Biological Oceanography).

Degradation of dissolved organic matter (DOM) in the deep ocean

The DOM in the deep ocean is considered to be refractory in nature and prokaryotes are the principal transformers of this material. Most of the DOM molecules used by prokaryotes have a molecular weight above 600 molecular weight (MW). The uptake sites at the cell wall, however, allow only molecules smaller than 600 MW to pass; thus prokaryotes produce enzymes that are active outside the cell (ecto-enzymes). They cleave large molecules in seawater, and thereby enable the cells that synthesize these enzymes to take up the small cleavage products – a process coined 'hydrolysis-uptake coupling'. Surprisingly, a higher ecto-enzymatic activity per prokaryotic cell was found in the deeper layers than in surface waters, indicating active transformation of deep water DOM by the prokaryotes. This is illustrated in Fig. 3 for two of such enzymes, β–glucosidase and phosphatase. The β–glucosidase actvity in the NADW was particularly high above the Charlie-Gibbs Fracture zone. As indicated by remote sensing, an intensive phytoplankton bloom was present there while we sampled and the high β–glucosidase activity in the deep waters of this area might reflect the sedimentation of dead material from the bloom. We also detected high phosphatase activity in the deep ocean, which was quite unexpected since the endproduct of phophatase activity, inorganic phosphate, is present at high concentrations in these deep waters, thus there is no reason to express phosphatase to obtain phosphate to maintain prokaryotic activity. There is evidence that this phosphatase expression might be related to the cleavage of organo-phosphorus compounds, such as phospho-esters and phosphonates. Thus, the deep water prokaryotic community might express phosphatase activity not to acquire phosphorus but rather carbon to sustain its energy source for metabolic activity.

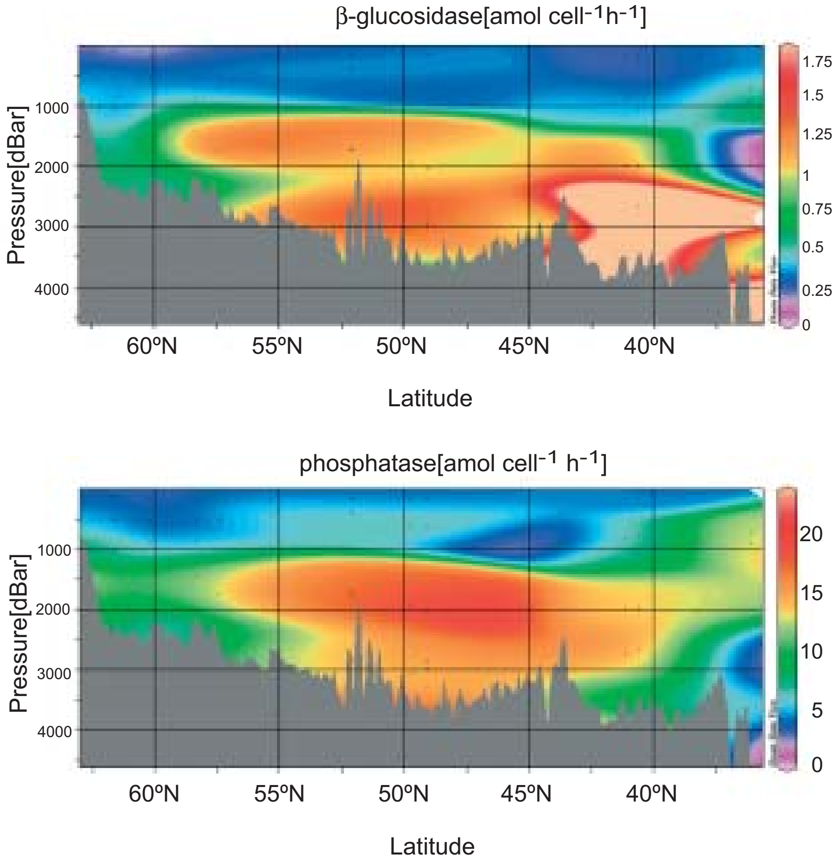

Fig. 3. Dynamics in prokaryotic ectoenzyme activity per cell in the water masses sampled during TRANSAT-1. Upper panel: β–glucosidase, lower panel: phosphatase.

Most of the DOM pool still cannot be characterized on a molecular level. Moreover, the characteriz-

able portion of the DOM declines with depth in the water column. While about 20-40% of the DOM can be characterized in oceanic surface waters, only about 5-10% of the deep water DOM is characterizable on a molecular level. It is therefore impossible to determine the subtle alterations in the composition of the DOM pool in the oceanic conveyor belt as the water gets older. As prokaryotic species have evolved over 3 million years in earth history, one might expect that a substantial part of the heterotrophic component of the marine prokaryotes have attained a high level of speciation in utilizing different components of the DOM pool as a carbon and energy source. Consequently, changes in the composition of the prokaryotic community likely reflect the subtle changes in the quantity and quality of the DOM and might therefore be a more sensitive indicator of changes in the DOM pool than chemical analyses allow us to resolve currently. Since the composition and the quality of the DOM probably changes during the lateral transport of the major water masses driving the thermohaline ocean circulation mainly due to prokaryotic activity, we hypothesized that these major water masses carry not only their own distinct DOM pool but related to that, also their specific prokaryotic community.

The shipboard party.

Bacterioplankton community composition

Fingerprinting techniques of the 16S rRNA gene enabled us to obtain an overview of the composition of the prokaryotic community in a specific sample. By comparing all the different samples collected in the different water masses, similarity analyses can be performed. For the bacterioplankton, we demonstrated that each of the six specific clusters identified were affiliated to specific major water masses (Fig. 4). Thus, each of the major water masses of the North Atlantic carries its own specific 'bacterioplankton community fingerprint', most likely reflecting the subtle differences in the chemical composition of the DOM in these water masses.

More detailed analyses are currently performed to refine this emerging view on the link between the major water masses driving the thermohaline ocean circulation, the deep-water microbiota and its activity, the composition of the DOM pool and its transformation rate. These complex interactions will be resolved in the frame of a multidisciplinary theme as formulated in the new Science Plan of the NIOZ where physical and microbiological oceanographers are working in concert with biogeochemists to shed light on the largely unexplored 'Dark Ocean Processes'.

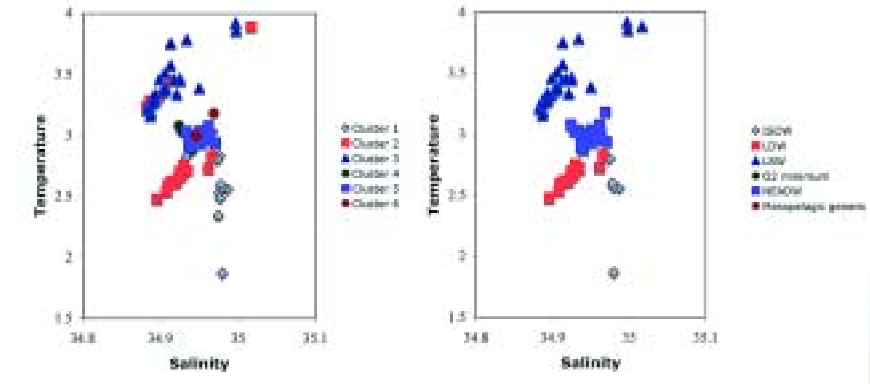

Fig. 4. Specific bacterioplankton communities (clusters 1-6, left panel) match with specific water masses (right panel) as defined by the salinity-temperature characteristics. ISOW-Iceland-Scotland Overflow Water, LSW-Labrador Sea Water, NEADW-North East Atlantic Deep Water, LDW-Lower Deep Water, O2 minimum-oxygen minimum layer. Bacterial community analysis was done by terminal restriction fragment length polymorphism (T-RFLP) of the 16S rRNA gene.

The oceanic conveyor belt and the remineralization of DOM

While the turnover of the water masses in the oceanic conveyor belt system is around 1500 years, the turnover of dissolved organic matter (DOM) in the deep waters is much longer, around 6000 years. Thus, on average, the deep water DOM is cycled 4 times within the conveyor belt system before it is completely remineralized. As a consequence of conveyor belt circulation of deep water masses, the deep water DOC concentration decreases from around 45 µM in the NADW to 37 µM in the deep waters of the Pacific, i.e., a decline of 8 µM C = 20% of the original concentration. Recently, it has been hypothesized that the degradation of the deep water DOC must take place in a non-continuous way involving interactions between abiotic transformation of DOC (chemical, photochemical) and microbial degradation and remineralization.

Due to this critical lack of a mechanistic understanding of the DOM transformation in the deep sea (which comprises the largest single system of the world's oceans with about 80% in volume) it has been impossible to make any predictions on the future development of the deep sea as a potential buffer reservoir in the biogeochemical flux of elements like carbon, nitrogen and phosphorus in a changing climate.