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Factors influencing particulate lipid production in the East Atlantic Ocean

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ABSTRACT

Extensive analyses of particulate lipids and lipid classes were conducted to gain insight into lipid production and related factors along the biogeochemical provinces of the Eastern Atlantic Ocean. Data are supported by particulate organic carbon (POC), chlorophyll *a* (Chl *a*), phaeopigments, Chl *a* concentrations and carbon content of eukaryotic micro-, nano- and picophytoplankton, including cell abundances for the latter two and for cyanobacteria and prokaryotic heterotrophs. We focused on the productive ocean surface (2 m depth and deep Chl *a* maximum (DCM)). Samples from the deep ocean provided information about the relative reactivity and preservation potential of particular lipid classes. Surface and DCM particulate lipid concentrations (3.5–29.4 $\mu g\ L^{-1}$) were higher than in samples from deep waters (3.2–9.3 $\mu g\ L^{-1}$) where an increased contribution to the POC pool was observed. The highest lipid concentrations were measured in high latitude temperate waters and in the North Atlantic Tropical Gyral Province (13–25°N). Factors responsible for the enhanced lipid synthesis in the eastern Atlantic appeared to be phytoplankton size (micro, nano, pico) and the low nutrient status with microphytoplankton having the most expressed influence in the surface and eukaryotic nano- and picophytoplankton in the DCM layer. Higher lipid to Chl *a* ratios suggest enhanced lipid biosynthesis in the nutrient poorer regions. The various lipid classes pointed to possible mechanisms of phytoplankton adaptation to the nutritional conditions. Thus, it is likely that adaptation comprises the replacement of membrane phospholipids by non-phosphorus containing glycolipids under low phosphorus conditions. The qualitative and quantitative lipid compositions revealed that phospholipids were the most degradable lipids, and their occurrence decreased with increasing depth. In contrast, wax esters, possibly originating from zooplankton, survived downward transport probably due to the fast sinking rate of particles (fecal pellets). The important contribution of glycolipids in deep waters reflected their relatively stable nature and degradation resistance. A lipid-based proxy for the lipid degradative state (Lipolysis Index) suggests that many lipid classes were quite resistant to degradation even in the deep ocean.

1. Introduction

Investigations of quantity, characterization, and distribution of marine organic matter are important to understand the role of marine sources and sinks of organic carbon. Marine organic matter is predominantly of autochthonous origin, produced by the phytoplankton community and heterotrophic organisms. Phytoplankton accounts for about 95% of the primary production in the ocean and about half of all primary production on Earth (Field et al., 1998). In general, open ocean primary production is mainly driven by picophytoplankton and nanophytoplankton. Microphytoplankton biomass shows a larger variability than smaller phytoplankton on seasonal and interannual time scales (Uitz et al., 2010).

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Phytoplankton blooms cover a wide range of scales from small, sporadic blooms stimulated by event scale processes to the basin scale spring blooms covering the North Atlantic (Ducklow and Harris, 1993).

Lipids are important components of photosynthetically produced particulate organic carbon (POC) (Yoshimura et al., 2009). Polar lipids, in particular phosphatidylglycerols, diphosphatidylglycerols, phosphatidylethanolamines and phosphatidylcholines, are biomembrane structure components and reflect the organic matter associated with living organisms (Derieux et al., 1998). The neutral lipids, triacylglycerols and wax esters, represent metabolic reserves. Triacylglycerols are the main phytoplankton storage lipids whereas marine zooplankton also store energy as dense wax esters (Lee et al., 2006) that are usually also found in their fecal pellets (Wakeham et al., 1984). Glycolipids (GL) are the most common non-phosphorous polar lipids in the biosphere (Härtel et al., 2000). In algae, as in higher plants and cyanobacteria, GL are predominantly located in the photosynthetic membranes (thylakoids) (Guschina and Harwood, 2009) where they are the most abundant type of lipids. Diacylglycerols, monoacylglycerols and free fatty acids are breakdown products and characterize lipid degradation (Parrish, 1988; Goutx et al., 2003). Fatty alcohols originate mainly from degradation of zooplankton wax esters. The "Lipolysis Index" (LI) has been defined by Goutx et al. (2003) and indicates the degree of lipid degradation. The quantity and quality of lipids depend on the life cycle stage of the primary producers and environmental factors (Zhukova and Aizdaicher, 2001). The characterization of marine lipids on a molecular level enables their use as efficient geochemical markers for the identification of sources, carbon cycling and reactivity of organic matter in the ocean.

Oceans are systems of physically-driven, biologically controlled chemical cycles which regulate the planetary climate over large spatial and temporal scales (Ducklow, 2003). Longhurst (2007) produced an ecological scheme dividing the oceans into a system of regions, named biogeographic provinces, which are regions or water masses with similar physical (e.g. sea surface temperature, mixed-layer depth, and bathymetry) and biological (e.g. chlorophyll *a* concentration, photosynthetic parameters, and biomass vertical profile) characteristics. The most fundamental distinction among provinces in the Atlantic Ocean is between the coastal and open ocean domains (Sathyendranath et al., 1995). However, there is little information about the quality and quantity of lipids in different oceanic provinces.

In this work, we aimed to examine lipids under the range of various biological and chemical conditions that exist over a long north–south transect through the East Atlantic to gain insight into: (i) their biological origin, (ii) influence of inorganic nutrient availability on lipid production and composition and (iii) distribution of the lipids within the water column. We quantified lipid classes in the particulate matter from the surface productive layers and the deep ocean waters and compared these data with the plankton community structure. To understand the influence of environmental conditions we performed sampling at stations encompassing a wide range of trophic states.

2. Material and methods

2.1. Study area and sample collection

Water sampling was conducted from 31 October to 3 December, 2008, during the R/V Polarstern cruise ANT-XXV/1. The sampling locations, extending from 49°N to 26°S, are shown in Fig. 1a. Samples were collected continuously at the surface (ca. 2 m), at various depths of the deep Chl *a* maximum (DCM; 25–105 m), and in the deep ocean (805–5563 m; Fig. 1b). The different symbols in the figures refer to the different biogeochemical provinces introduced by Longhurst (2007): the Northeast Atlantic Shelves Province (1st: NECS; 4–50°N; Sta. 4 and 5; down triangles); the North Atlantic Drift (2nd: NADR; 44–48°N; Sta. 9–22; squares); the North Atlantic Subtropical Gyre-East (3rd: NASE; 26–44°N; Sta. 24–63; up triangles); the North Atlantic Tropical Gyral Province, touching the Canary Current Coastal Province (4th: NATR; 13–25°N; Sta. 65–105; stars); the Western Tropical Atlantic Province (5th: WTRA; 11–12°N; Sta. 107–109; hexagons); the Eastern Tropical Atlantic Province (6th: ETRA; 11°N–8°S; Sta. 119–162; rhombs); the South Atlantic Gyral Province (7th: SATL; 11–22°S; Sta. 167–195; circles); the Benguela Current Coastal Province (8th: BENG; 23–31°S; Sta. 200–214; right triangles).

Surface water samples were collected with the so-called 'Fish' sampler (Sarthou et al., 2003), which had a fish-like floating body with Teflon tubing and pumping. It was fixed alongside the ship, providing a continuous flow of water from ~2 m water depth. Samples from various depths of DCM and deep waters were taken using 12 L Niskin bottles mounted on a CTD-rosette.

2.2. Eukaryotic plankton cell abundance and pigment analysis

Cell abundances of eukaryotic nano- and picophytoplankton and cyanobacteria (including *Synechococcus* and *Prochlorococcus*) were assessed using flow cytometry. Full descriptions of the method for the flow-cytometric enumeration of autotrophic cells are provided in Taylor et al. (2013). The data have been published in PANGAEA (http://dx.doi.org/10.1594/PANGAEA.823283).

The composition of phytoplankton pigments which are soluble in organic solvents was analyzed by high performance liquid chromatography (HPLC) following the method by Barlow et al. (1997), slightly modified by Hoffmann et al. (2006), and adapted to our instruments as described in Taylor et al. (2011). The data have been published in PANGAEA (http://dx.doi.org/10.1594/PANGAEA.819070).

The relative proportions of eukaryotic micro- (20–200 μm), nano- (2–20 μm) and picophytoplankton (< 2 μm) were estimated from the concentrations of 7 diagnostic pigments after Uitz et al. (2006). Briefly

$$\%\ \text{Pico} = 100 \times (0.86\ \text{Zea})/\text{DPw}$$

$$\%\ \text{Nano} = 100 \times (1.27\ 19\text{HF} + 1.01\ \text{TChl}b + 0.35\ 19\text{BF} + 0.6\ \text{Allo})/\text{DPw}$$

$$\%\ \text{Micro} = 100 \times (1.41\ \text{Fuco} + 1.41\ \text{Peri})/\text{DPw},$$

where DPw = 0.86 Zea + 1.01 TChl*b* + 1.27 19HF + 0.35 19BF + 0.6 Allo + 1.41 Fuco + 1.41 Peri; Zeaxanthin (Zea), total Chlorophyll-*b* (TChl*b*), 190-hexanoyloxyfucoxanthin (19HF), 190-butanoyloxyfucoxanthin (19BF), Alloxanthin (Allo), Fucoxanthin (Fuco), Peridinin (Peri). An additional correction for Fuco, accounting for the contribution by haptophytes (identified by the marker pigment 19HF) was applied as detailed in Hirata et al. (2011). The percentage of Chl *a* in individual classes is calculated from their calculated percentage and the total Chl *a*.

The carbon content of phytoplankton was calculated from the Chl *a* after Pérez et al. (2006) using the carbon to Chl *a* (C/Chl *a*) ratios of 77 for eukaryotic picophytoplankton and of 186 for eukaryotic nano- and microphytoplankton for surface samples, and for the DCM samples the C/Chl *a* ratios were 17 for eukaryotic pico- and 58 for nano- and microphytoplankton.

2.3. Prokaryotic heterotroph abundance

The number of total prokaryotic heterotrophs including bacteria and archaea were estimated by a culture independent microscopic