



Adaptation of marine plankton to environmental stress by glycolipid accumulation



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ABSTRACT

A systematic investigation of non-phosphorus containing glycolipids (GL) was conducted in the northern Adriatic Sea during two years at two stations with different nutrient loads. GL concentration varied both spatially and temporally, with values of 1.1–21.5 µg/L and 0.4–44.7 µg/L in the particulate and the dissolved fraction, respectively. The highest concentrations were measured during summer in surface waters and at the more oligotrophic station, where GL yields (% of total lipids) were often higher than 20% and 50% in the particulate and dissolved fractions, respectively. To obtain more insight into factors governing GL accumulation autotrophic plankton community structure (pico-, nano- and microplankton fractions), chlorophyll *a*, heterotrophic bacteria and nutrient concentrations were measured together with hydrographic parameters and sunlight intensity. During the investigated period smaller autotrophic plankton cells (pico- and followed by nanoplankton) prevailed in abundance over larger cells (microplankton), which were found in large numbers in freshened surface samples. Several major findings resulted from the study. Firstly, during PO₄ limitation, particularly at the oligotrophic station, enhanced glycolipid instead of phospholipid accumulation takes place, representing an effective phosphate-conserving mechanism. Secondly, results suggest that at seawater temperatures >19 °C autotrophic plankton considerably accumulate GL, probably to achieve thermal stability. Thirdly, high sunlight intensities seem to influence increased GL accumulation; GL possibly plays a role in cell mechanisms that prevent/mitigate photooxidation. And finally, substantial accumulation of GL detected in the dissolved fraction could be related to the fact that GL do not contain biologically relevant elements, like phosphorus, which makes them an unattractive substrate for enzyme activity. Therefore, substantial portion of CO₂ could be removed from the atmosphere in P-limited regions during summer via its capture by plankton and conversion to GL.

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1. Introduction

Lipids are essential for every living organism as they play vital roles in membrane composition and the regulation of metabolic processes. They represent carbon rich organic matter with a very high energetic value, thus being an important metabolic fuel. Lipids differ in their chemical structure to a substantial degree and contain different functional groups which consequently influences their reactivity. However, molecular structure is not the only factor

relevant for organic matter reactivity, as the fate of which also depends on environmental conditions (Wakeham and Canuel, 2006). In the marine environment the main origin of lipids is in phytoplankton as well as autotrophic bacteria (cyanobacteria) (Guschina and Harwood, 2009) and, to a much lesser extent, heterotrophic bacteria (Shaw, 1970). Plankton are constantly challenged with various abiotic stresses, with light intensity and temperature probably the most important and best-studied environmental factors affecting the lipid composition of photosynthetic tissues or organisms (Guschina and Harwood, 2009). Furthermore, nutrient availability has a significant impact and broad effects on the lipid composition of algae (Guschina and Harwood, 2009). Characterization of marine lipids on a molecular level enables their

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use as good geochemical markers for the identification of different sources and processes of organic matter in the sea (Parrish et al., 1988; Christodoulou et al., 2009).

Glycolipids (GL) are the most common non-phosphorous lipids in the biosphere and account for 80% of the membrane lipids found in green plant tissues (Härtel et al., 2000). The most common glycolipids in plankton are mono- and di-galactosyldiacylglycerols (MGDG and DGDG) and sulfoquinovosyldiacylglycerol (SQDG) although mannose, glucose and glucuronic acid are also found as constituent sugars in GL (Guschina and Harwood, 2009; Shaw, 1970). Phytoplankton has a glycolipid composition similar to that of higher plants. In algae and cyanobacteria, as in higher plants, GL are located predominantly in photosynthetic membranes (thylakoids) where they are the most abundant type of lipids (Guschina and Harwood, 2009). Reported composition of lipid classes for numerous phytoplankton species have revealed a contribution of GL to total lipids in the range of 31–55% (Parrish et al., 1996; Guschina and Harwood, 2009). The contribution of GL to total lipids during summer in the northern Adriatic exceeds 20% (Frka et al., 2011). The amount of glycolipids present in heterotrophic bacterial lipids is usually quite small (Shaw, 1970). Goutx et al. (1989) reported an average value of GL in total lipids of several marine heterotrophic bacteria to be 3.1%.

Coastal seas, as is the northern Adriatic Sea (NA), are strongly influenced by biological, chemical, and physical processes on short time scales and are therefore more susceptible to environmental perturbations, especially in recent times in the face of significant ecosystem changes. The NA is a shallow sea (depth < 50 m) and shows a seasonal thermal cycle typical of temperate latitude seas. It is a highly variable and dynamic environment with a close coupling between river-borne nutrients, net productivity and vertical carbon fluxes. The most important source of nutrients is the Po River, located on the western side of the NA, together with regenerated nutrients from the bottom layer (Degobbis et al., 2000). The productivity of the NA is among the highest in the Mediterranean (Giordani et al., 2002). Phytoplankton abundances exhibit large interannual variability although the peaks of production are primarily driven by the flooding or drought of the Po River (Bernardi Aubry et al., 2012). Recently, a decreasing trend of chlorophyll *a* (Chl *a*) concentration in the NA (Mozetič et al., 2010) was noted and followed by increased nutrient limitation (Djakovac et al., 2012), reduced organic matter production (Gašparović, 2012) as well as a decrease in abundance of microplankton (Marić et al., 2012) and increase in nanoplankton abundance (Mozetič et al., 2012). At the same time a drastic reduction in heterotrophic bacteria abundance occurred in the area, while cyanobacteria, characteristic for nutrient poor waters, did not show any corresponding reduction in abundance (Ivancić et al., 2010a).

In the light of recent findings on enhanced sulfo-glycolipid synthesis by phytoplankton under PO_4 scarcity (e.g. Van Mooy et al., 2009; Van Mooy and Fredricks, 2010; Pependorf et al., 2011), and recent reports on reduction in the concentrations of orthophosphate in the NA (Djakovac et al., 2012) we would expect increased concentrations of GL in the NA. For this purpose we aimed to examine the spatio-temporal dynamics of GL and to understand: (1) their biological origin, as well as influence of (2) nutrients and of (3) physical factors (sunlight and temperature) on GL production. Therefore, we quantified GL, both in particles and the dissolved phase over a two year period, and compared these data to heterotrophic bacteria and pico-, nano- and micro-phytoplankton abundance. To help understand the influence of nutrient concentrations on GL production, we have performed sampling at two stations having opposing trophic levels. Significant annual temperature and sunlight variations enabled determination of the influence of these physical factors on GL annual distribution.

Thus, we consider the NA as a good platform for studying GL dynamics in the marine environment.

2. Methods

2.1. Sampling and sample treatment

Sampling was performed in the NA (Fig. 1) throughout the time period from January 2008 to January 2010 at the eastern oligotrophic station 107 (32 Nm off the Po River delta, depth 37 m) and at the western mesotrophic station 101 (12 Nm off the Po River delta, depth 32 m). Station 107 is, at least in autumn and in winter, under a prevailing influence of oligotrophic, high salinity waters from the central Adriatic (Gilmartin et al., 1990), while station 101 is often under direct influence of the freshwater outflows. Water samples were taken approximately monthly at 0, 5, 10, 20 (30 m) depths and 2 m above the bottom with 5-L Niskin bottles from the RV “Vila Velebita”.

For lipid class determination, 3 L of seawater were passed through a 200 μ m stainless steel screen to remove zooplankton and larger particles. Immediately after sampling, seawater was filtered at ~ 12 kPa vacuum pressure through 0.7 μ m Whatman GF/F filters pre-burned at 450 °C/5 h. Filters were stored in liquid nitrogen until the particulate lipid extraction. Filtrates, containing dissolved lipids, were stored in dark bottles until extraction by liquid–liquid extraction with dichloromethane (twice at pH 8 and twice at pH 2) that was performed within 24 h. Particulate lipids were extracted by a modified one-phase solvent mixture of dichloromethane–methanol–water procedure (Blight and Dyer, 1959). Ten micrograms of internal standard n-hexadecanone were added to each sample before the extraction for the estimation of lipid recovery.

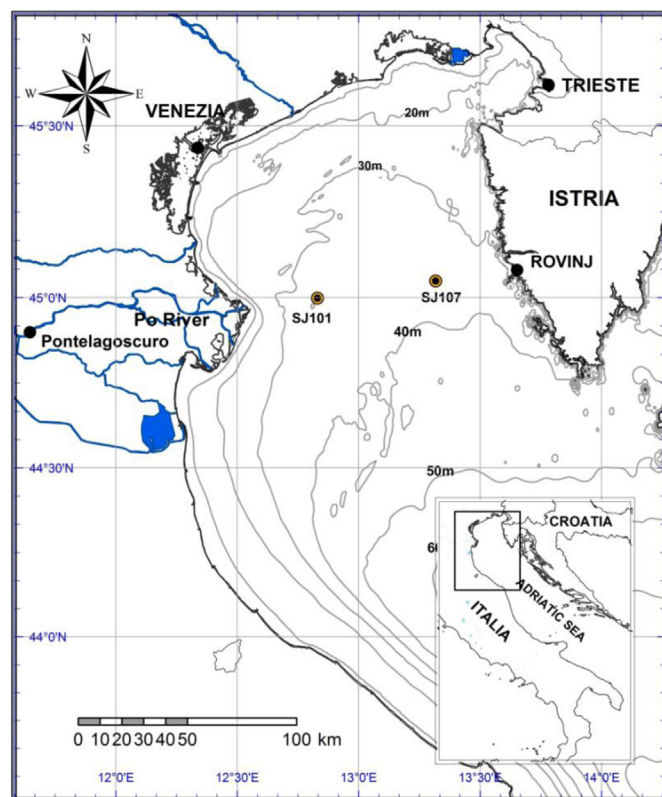


Fig. 1. Study area in the northern Adriatic Sea showing position of the stations 107 and 101.

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