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Species-specific sensitivity of dinoflagellate cysts to aerobic degradation: A five-year natural exposure experiment

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ABSTRACT

Post-depositional sedimentary dinoflagellate cyst associations undergo species-selective degradation under oxic conditions. However, there is little known about the temporal relationship between oxygen concentration and bulk dinocyst degradation rate over the time scale of several years, and if this degradation is mainly microbial or chemical. Whilst the overall sensitivity of heterotrophic dinoflagellate cysts is well documented, sensitivity differences within this group have not been studied. Here we examine the rates of cyst degradation of heterotrophic species over short temporal scales across an anoxic–oxic gradient. Sediment with a known dinoflagellate cyst association largely dominated by heterotrophic dinoflagellates, were connected to trap arrays at two different locations, Cap Blanc (NW Africa) and Gotland Basin (central Baltic Sea) and exposed to four different ambient oxygen concentrations representing a complete oxic gradient from 5.1 mL/L to sulphate bearing anoxic waters. Two treatments of either gauze or dialyse membrane in triplicate were established to investigate the effects of chemical or bacterial degradation. Cyst loss was significant at oxic settings, rapidly occurring within the first year of exposure (32%) whereas no significant degradation was observed for suboxic and anoxic exposures. Compiling the degradation rates of individual species under the different exposure settings reveals an overall species sensitivity ranking amongst cysts of heterotrophic species. Species of average resistance: *Bitectatodinium spongium*, *Brigantedinium* spp., *Echinidinium* spp., *Echinidinium aculeatum*, and *Gymnodinium trapeziforme*. Species more resistant than average: *Stelladinium robustum* and *Trinovantedinium applanatum*. We observe that oxic degradation of cysts of heterotrophic dinoflagellates is fast and selective with maximal cyst association changes during the first year of oxic exposure. These aspects have to be taken into account in palaeoenvironmental and palaeoceanographic reconstructions where bottom/pore water conditions of the upper sediments are oxygenated.

1. Introduction

Sedimentary organic-walled dinoflagellate cyst associations are widely used to reconstruct past marine environments (Rochon et al., 1999; de Vernal et al., 2001; Pospelova et al., 2008). Especially in high productivity areas and regions where other microfossils are absent, for instance when dissolution-affected carbonate and silicate based microfossils, dinoflagellate cysts are extremely useful to reconstruct upper water environmental and oceanographic conditions (Bijl et al., 2013; Jaramillo et al., 2017). They are especially suitable to reconstruct the trophic state of the photic zone, productivity, temperature, salinity and sea ice cover (Marret, 1994; Radi and de Vernal, 2004; Mertens et al., 2012; Zonneveld et al., 2012; de Vernal et al., 2013; Bringué et al., 2016). Furthermore, dinoflagellate cysts are biostratigraphically important and as such are widely used in the petroleum exploration industry (Crux et al., 2010; De Schepper, 2013).

In order to establish a reliable palaeoenvironmental or palaeoceanographic reconstruction based on sedimentary dinoflagellate cyst associations it is essential to know if, and to what extent the primary signal that reflects upper water conditions, has been altered during the settling and preservation processes. Oxygen concentration is a major factor influencing organic matter degradation. This aerobic degradation is highly selective (see review in e.g. Zonneveld et al., 2010). During the last decades, it became clear also that organic-walled dinoflagellate cysts are prone to species specific aerobic degradation (e.g. Versteegh and Zonneveld, 2002; Reichart and Brinkhuis, 2003; McCarthy et al., 2004; Zonneveld et al., 1997, 2007, 2008, 2010; Bockelmann et al., 2007; Prebble et al., 2013). Meanwhile indications for selective preservation have become available from a wide range of marine settings ranging from the high latitudes towards the tropics and from high productivity regions such as upwelling and river plume systems towards the open ocean (e.g. Brinkhuis, 2003; McCarthy et al.,

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2004; Zonneveld et al., 2008; Kupinska et al., 2012; Heikkilä et al., 2014, 2016). The most sensitive dinoflagellate cyst species are produced by heterotrophic peridinioid dinoflagellates, whereas the most resistant dinoflagellate cysts are produced by phototrophic gonyaulacoids (Table 1, Zonneveld et al., 2008). Recently it has been discovered that this might be related to the molecular composition of the cyst-walls that appear to differ between heterotrophic and phototrophic dinoflagellates (Versteegh et al., 2007, 2012; Bogus et al., 2012, 2014; Mertens et al., 2015a, b). Cysts from phototrophic dinoflagellates consist of a cellulose-like glucan, whereas those of heterotrophic dinoflagellates consist of a nitrogen-rich glycan.

So far, cyst degradation studies in natural settings provided no indication of species specific degradation during the settling process but only at and in the sea floor. Furthermore, they showed that selective cyst degradation was restricted to oxic environments only. As a result, it became clear that in anoxic environments the complete sediment cyst association can reflect in detail changes in upper water cyst production. In oxic settings, however, only the most resistant cyst species reflect their primary signal whereas concentrations of the more sensitive species are usually reduced by degradation processes.

Beside selective degradation that has to be taken into account when interpreting fossil cyst associations in terms of environmental reconstruction, one can directly study the processes, rates and environmental conditions that underlie cyst degradation. For instance, a method has been suggested to use the species-selective degradation of dinoflagellate cysts to reconstruct past bottom/pore water oxygen concentrations (Versteegh and Zonneveld, 2002; Zonneveld et al., 2007). These authors assumed that the character of the degradation process follows a first order process:

$$\ln(C_0/C_t) = kt \quad (1)$$

where ln = natural log, C_0 = initial concentration (cysts/g), C_t = concentration (cysts/g) at time t; k = degradation constant and t = exposure time.

Versteegh and Zonneveld (2002) and Zonneveld et al. (2007) noted that often a linear relationship can be observed between the cyst accumulation rates (AR) of different cyst species groups in sediments that have not been prone to aerobic OM degradation and in sediment trap samples.

$$AR \text{ Species group A} = \alpha \times AR \text{ Species group B} \quad (2)$$

where AR = accumulation rate, and α is a constant, regionally determined which relates the production of Species group A to Species group B.

If "α" in a certain region is known, the initial accumulation rate (AR) of Species group B can be calculated based on the AR of Species group A. In an empirical survey of surface sediments, Zonneveld et al. (2007) determined a region-specific value for "α" for a Species group A that included resistant species and a Species group B that included degradation sensitive species (species correspond to those listed in Table 1). Successively they reconstructed the initial accumulation rate (AR_0) of the degradation sensitive species group B. By replacing in Eq. (1) "C" with "AR" a new AR-based "kt" could be calculated. It appeared that this AR-based "kt" strongly relates to the bottom water oxygen concentrations. However, the above-mentioned method can only be applied if cyst degradation indeed follows a first order process and if "kt" is related to ambient oxygen concentrations. So far studies that test if these assumptions hold are lacking.

In general, very little is known about the degradation rates of sensitive dinoflagellate cysts in natural settings. The only experiment carried out so far, is an in-situ 15-month incubation experiment (Urania and Bannock Basins, eastern Mediterranean) that compared cyst degradation in highly oxic water to that in anoxic water (Kodrans-Nsiah et al., 2008). This experiment showed that the cyst concentrations (measured in cysts/g) of groups of species belonging to the genera *Brigantedinium* and *Echinidinium* dropped 24% to 57% in sediments exposed to oxic waters whereas other species did not show signs of degradation. However, this experiment covered only a few cyst species, compared extremes in ambient oxygen concentrations and studied a limited time interval with only two sampling points that are 15 months apart. No information is present yet on the shape of the cyst degradation curves through time and in relation to intermediate oxygen concentrations. Here, we report on the results from an extended in-situ incubation sampling at one year intervals for five years, taking into account more species and oxygen levels. We addressed the following questions:

1. How do total dinocyst degradation rates differ across different oxygen concentrations over a time period of 5 years?
2. Is dinocyst degradation in natural settings mainly microbially or chemically controlled?
3. Are cyst degradation rates similar amongst species of the heterotrophic group?

2. Experimental setup

To assess the effects of aerobic and anaerobic degradation on the abundance and assemblage composition of dinocysts in sediments, we applied the method of Kodrans-Nsiah et al. (2008). A reference sediment sample with a known concentration and assemblage composition of dinoflagellate cysts was exposed to different ambient oxygen concentrations, over a period of up to 5 years. To assess whether degradation of dinocysts is chemical or microbial, autoclaved sediment was either transferred into bags composed of dialyse membrane ("condition A"), or 5 μm polycarbonate gauze ("condition B", Plate I). The dialyse membrane allows the penetration of oxygen, but not that of microbes; in contrast to the 5 μm gauze, which allows both oxygen and microbe penetration. All exposures were carried out in triplicate.

The reference sediment was collected from the oxygen minimum zone (OMZ) of the eastern Arabian Sea/Pakistan margin where oxygen concentrations of <0.05 mL/L O_2 prevail throughout the year, between about 100 and 1000 m water depth (Fischer et al., 2012). We assume that surface sediments within this zone have undergone minimal diagenetic alteration. These sediments were retrieved by multicore during METEOR cruise 74/3 in November 2007, at the site of core GeoB 12312-3 (24 53.07′N, 63 01.64′E, depth − 654 m, bottom water oxygen concentrations were below detection limit). Sediment material was stored at −20 °C immediately after recovery to prevent diagenetic processes altering the cyst association.

Bulk sediment was autoclaved, homogenised and divided into aliquots of 10 mL of wet sediment. Half of the aliquot was stored in dialyse membrane bags, the other half in 5 μm polycarbonate gauze. Successively the dialyse and gauze bags were covered with a nylon protection sheet that allowed free penetration of sea water. The material was placed in cylinders open at the bottom and top to allow free penetration of sea water. Six cylinders containing three dialyse bag aliquots and three gauze bag aliquots were connected. Five of these connected cylinder sets were arranged on top of each other in a PVC container, drilled with 20 mm pores to allow free flow of seawater through the device (Plate I). Aliquots of the reference sediment were stored at −20 °C — this sediment serves as the baseline (Year 0) from which the degradation effects are measured.

The in-situ exposure experiments were carried out in the Gotland Basin (central Baltic Sea, Fig. 1), and the eastern Atlantic Ocean off Cape Blanc (NW Africa, Fig. 1). For the Cap Blanc experiment, the PVC containers were mounted to wires of sediment traps at two depths within the water-column of the Cape Blanc Sediment Trap Array (21°16.85′N, 20°47.80′W). The ambient waters at the upper position (1228 m, intermediate oxygen (I), "CB Upper") consist of South Atlantic Intermediate Waters (SAIW) that have an intermediate oxygen concentration of 3.8 mL/L, temperature of 5.7 °C, salinity of 35.1, silicate concentration of 23 μM/L (Boyer et al., 2013), and pH of 7.9 (Key et al., 2004). Waters