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Long- and short-term photoacclimation in epipsammon from non-tidal coastal shallows compared to epipelon from intertidal mudflat



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ABSTRACT

Long- and short-term photoacclimation and their interaction were determined in two types of microphytobenthos assemblages, i.e. epipelon from an intertidal mudflat and epipsammon from non-tidal sandy coastal shallows collected during summer and autumn months. Microphytobenthos photophysiology was assessed from steady-state light curve (SSLC) and rapid light-response curves (RLC) of variable chlorophyll fluorescence. The epipelon was low light acclimated, whereas in the epipsammon high light acclimation was observed. The epipelon turned out to be more susceptible to high light and in autumn a clear down turn in the relative electron transport rates was recorded. Long-term photoacclimation strongly affected both microphytobenthos types' short-term light responses. The epipelon acclimated to high ambient light intensities through the decreased light absorption and energy dissipation. The epipsammon, on the other hand, developed physiological flexibility allowing efficient use of the absorbed light and thus providing protection against higher irradiance.

1. Introduction

Microphytobenthos is an ecological formation comprising photosynthetic organisms, including mainly: diatoms, cyanobacteria, euglenophytes, green algae etc., growing on various substrata in shallow aquatic ecosystems (Round, 1971). Microphytobenthos plays a key role as a significant primary producer (MacIntyre et al., 1996). It is an important source of food for benthic and pelagic organisms as well (Lucas et al., 2001). It stabilizes sediment surface through the mucilage production (Sutherland et al., 1998) and mediates numerous geochemical processes by regulating nutrients turnover in the sediment and their fluxes at the water-sediment interface (e.g. Sundbäck et al., 2006).

The biomass and functioning of microalgae in marine coastal ecosystems is controlled by various environmental factors, including: light, temperature, nutrients, tides and sediment type which appear to affect the presence of cyanobacteria and certain microalgal groups and thus the structure of the assemblage (MacIntyre et al., 1996). Consequently, microphytobenthos inhabiting soft sediments is traditionally separated into two groups, i.e. epipelon typical of muddy sediments, usually dominated by free-living, large, biraphid diatoms, and epipsammon present in sandy sediments, consisting of small-sized diatoms with a substantial contribution of other algal groups such as coccoid chlorophytes, euglenophytes etc., and cyanobacteria (Round, 1971). Sediment also determines light regime within, which depends on its granulometry (Kühl et al., 1994). This further affects microphytobenthos species composition, photosynthetic pigments, biomass distribution and primary productivity (e.g. Barranguet et al., 1998; Jesus et al., 2009).

Being exposed to highly dynamic environments, microphytobenthos optimizes its photosynthetic rates through photoacclimation, i.e. mechanisms allowing microalgae to efficiently use available light and protect themselves from excessive irradiance. Photoacclimation results from biophysical changes in photosynthetic systems and operates within constraints set by evolutionary adaptations (Falkowski and Raven, 1997; Talmy et al., 2013). At the community level, photosynthetic responses are dependent on the microphytobenthos type and its inherent features. Epipelon photo-regulates using physiological as well as behavioral mechanisms. Its migratory behavior is considered to be a key feature guaranteeing epipelon's maximum productivity. Epipsammon, on the other hand, exclusively uses physiological mechanisms to optimize its photosynthesis and photoprotection, expressing no vertical migration rhythms (Jesus et al., 2009; Cartaxana et al., 2011; Pniewski et al., 2015). The photophysiology of diatom-dominated epipelon has been well recognized, whereas a gap exists in the understanding of photoacclimation in taxonomically diverse epipsammon. Therefore, further in-depth studies on its photophysiology are

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necessary (Jesus et al., 2009).

Pulse Amplitude Modulated (PAM) fluorometry has been widely applied to study microphytobenthos (e.g. Serôdio et al., 1997; Jesus et al., 2006; Lefebvre et al., 2011). It proved to be a fast, sensitive and non-invasive tool lending an insight into the microalgal biochemical processes (Mouget and Tremblin, 2002) by providing information on the photochemical efficiency of photosystem II (PSII) (Δ F/Fm', the effective quantum yield of PSII; Genty et al., 1989). $\Delta F/Fm'$ reflects the proportion of absorbed light used for photochemistry therefore, it can give a measure of the relative linear electron transport rate (rETR; Maxwell and Johnson, 2000) which plotted against irradiance allows for construction of fluorescence light-response curves (LCs). The fluorescence LCs are often used as a proxy for traditional photosynthesis-irradiance (P-E) curves, in which algal material is allowed to acclimate to a series of relevant irradiances when the measurements of steady-state photosynthetic rates are taken (SSLCs). SSLCs reflect algal potential photosynthetic activity and are used to characterize long-term photoacclimation status by means of the light saturation index E_k (Henley, 1993; Ralph and Gademann, 2005). Contrary to SSLCs, rapid light curves (RLCs) use very short light steps (10-30 s) and they can be completed in < 2 min preserving photophysiological characteristics of microphytobenthos (Serôdio et al., 2006). RLCs depend on immediate light history showing light acclimation state developed over past few minutes, which is confounded by microphytobenthos' long-term prehistory (Ralph and Gademann, 2005). A relationship between SSLCs and RLCs was previously studied in epipelon (Serôdio et al., 2006). No such attempt, however, was made to characterize the variability of long and short-term photosynthetic activity in epipsammon.

Therefore, the main goal of this study was to compare and contrast photosynthetic activity in two types of microphytobenthos assemblages, i.e. epipelon from an intertidal mudflat (Aiguillon Bay, the Atlantic, France) and epipsammon from non-tidal sandy coastal shallows (Puck Bay, the Baltic, Poland), emphasizing differences between them. In the study, measurements were conducted on microphytobenthos communities collected in summer and autumn. The long-term photoacclimation status of microphytobenthos was assessed by means of steady-state light response curves of chlorophyll variable fluorescence, i.e. rETR vs. *E* (SSLCs) and NPQ (non-photochemical quenching) vs. *E* curves, variations of the RLC patterns with changing ambient light conditions were described and the influence of long-term photoacclimation status on the short-term photosynthetic activity of microphytobenthos communities was evaluated.

2. Materials and methods

2.1. Research areas and sampling

Samples were collected in two different areas. The first station was Esnandes in Aiguillon Bay located along the French Atlantic coast (47° 00' N, 1° 05' W). The bay is dominated by intertidal mudflats composed of fine mud with a mean size grain ranging from 7 to $13\,\mu m$ (Guarini et al., 2004). The maximum tidal range reaches ca. 6 m. Low water spring tides tide occurs at midday resulting in a long diurnal emersion period. During neap tides, high tide occurs in the middle of the day causing two short diurnal low tides in the morning and in the late afternoon (Herlory et al., 2005). The second station was Władysławowo in Puck Bay (54° 43' N, 18° 34' E) which is a subregion of the western part of the Gulf of Gdańsk (The Baltic Sea, Poland). Bottom sediments are dominated by fine sands with 69% of particles between 250 and 500 µm (Jankowska and Łęczyński, 1993). Sampling was carried out during two seasons, in summer and autumn 2007. At the intertidal site, samples were taken during two summer and two autumn months, i.e. June/July and November/December, respectively. At the non-tidal site, the sampling was carried out in August (summer) and October (autumn). At both sites, samples were collected 5 times each season (ones every 5 to 7 days). Sampling usually took place before noon and during

each sampling day, light intensity and temperature values were measured at the sediment surface using LI-189 and LI-1400 Datalogger (Li-Cor, Lincoln, Nebraska, USA) with a cosine collector LI-192 and Multiparameter WTW meter (WTW GmbH, Weilheim, Germany), respectively. On the intertidal mudflat the observed maximum light intensity reached ca. 2700 and ca. 560 μ mol m⁻² s⁻¹ in summer and autumn, respectively. Whereas at the non-tidal site light intensity at the sediment surface was lower, up to ca. $1220 \,\mu mol \, m^{-2} \, s^{-1}$ in summer and ca. $260 \,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$ in autumn. Despite different sampling months, average seasonal temperatures for both sites matched; average temperature reached ca. 20 °C in summer (in Aiguillon Bay it was 20.2 ± 0.8 °C whereas in Puck Bav 18.7 \pm 1.6 °C) and ca. 10 °C in autumn (7.6 \pm 2.7 °C and 10.6 \pm 0.8 °C in Aiguillon Bay and Puck Bay, respectively). The measured temperatures and light values reflected their seasonal variation patterns (the Baltic site, e.g. Kaczmarek and Dera, 1998, Rak and Wieczorek, 2012; the Atlantic site, unpubl data).

2.2. Algal material preparation

In Aiguillon Bay samples were collected as described in Herlory et al. (2007). During low tide the upper ca. 2 mm of the sediment were scrapped from the randomly chosen area. To collect microphytobenthos samples, the method of Eaton and Moss (1966) based on the natural ability of microalgae to move was used. The method allows collecting motile cells actively forming biofilms at the mud surface (Haubois et al., 2005). Sediment samples were placed in trays and covered with 2 nylon nets with mesh of $100 \,\mu\text{m}$, and left till the beginning of the low tide the next day. When algae appeared on the net surface they were washed with filtered sea water of salinity 35. In Puck Bay sediment cores (10 cm in diameter) were taken as presented in Dahl and Blanck (1996). The top centimeter of the collected sediment cores was cut off and placed in filtered sea water of salinity 6.7. Subsequently, an epipsammic assemblage was separated from the sediment as described by Pniewski et al. (2015). First, sediment samples were mixed and sonicated for 5 min to detach and resuspend algal cells adhering to sediment particles. The cell suspension was separated from the sediment and filtered through planktonic net (100 µm) in order to remove as many small invertebrates as possible.

Microphytobenthos species composition from both studied sampling sites, described in detailed elsewhere (Pniewski et al., 2015, 2017), differed significantly. Epipelon samples were exclusively composed of diatoms. In summer the assemblages were dominated by Navicula sp. (> 85% of the total cell count), while in autumn four species prevailed, i.e. Plagiotropis tayrecta T. B. B. Paddock, Plagiotropis sp., Pleurosigma aestuarii (Brébisson ex Kützing) W. Smith and Gyrosigma sp., constituting ca. 91% of all cells. The epipsammic assemblages were dominated by diatoms which constituted 51 and 59% of the community biomass in summer and autumn, respectively. The same five diatom species dominated throughout the year (> 57% of the total cell count), i.e.: Halamphora coffeiformis (C. Agardh) Levkov, Fragilaria sopotensis Witkowski and Lange-Bertalot, Nitzschia aurariae Cholnoky, Opephora mutabilis (Grunow) Sabbe and Wyverman and Planothidium delicatulum (Kützing) Round and L. Bukhtiyarova. Other taxonomic groups which significantly contributed to the assemblage biomass were green algae, euglenophytes and cyanobacteria.

Prepared suspensions (ca. 300 ml) were kept overnight and during the next day in a growth chamber at constant light and temperature conditions; low light intensity of ca. $50 \,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$ with 14:10 L:D photoperiod and temperatures corresponding to the seasonal means observed in the environment, i.e. $10\,^{\circ}\text{C}$ in autumn and $20\,^{\circ}\text{C}$ in summer.

2.3. Fluorescence measurements

Measurements of chlorophyll *a* fluorescence were carried out three times a day using a computer-operated Diving-PAM (Walz, Effeltrich,

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