Patterns in microphytobenthic primary productivity: Species-specific variation in migratory rhythms and photosynthesis in mixed-species biofilms

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ABSTRACT: The importance of temporal changes in the vertical distribution of microphytobenthic algae on the overall functioning of intertidal biofilms were investigated with low-temperature scanning electron microscopy and high-resolution single-cell fluorescence imaging of photosystem II efficiency (estimated by the fluorescence parameter F_q'/F_m') in intact cores maintained in tidal mesocosms. Early morning biofilms consisted of smaller naviculoid and nitzschioid taxa or euglenoid species. By midday, *Gyrosigma balticum* and *Pleurosigma angulatum* were dominant. Some taxa (e.g., *Plagiotropis vitrea*) disappeared from surface layers after midday. Species composition continued to change toward the end of the photoperiod, with G. balticum dominating in diatom-rich biofilms. In *Euglena*-rich biofilms, initial dense surface films of euglenids became progressively dominated by smaller diatoms. F_q'/F_m' (measured at a photosynthetically active photon flux density (PPFD) of 220 µmol m^{-2} s^{-1}) of individual cells of all taxa declined significantly after midday, but increased toward dusk. There were significant differences in F_q'/F_m' between species, particularly after midday. F_q'/F_m' versus irradiance curves and relative electron transport rate ($rETR_{max}$) showed higher efficiencies and $rETR_{max}$ for euglenids, whereas *G. balticum*, *Nitzschia dubia*, and small *Nitzschia* sp. were shade-adapted with low values of F_q'/F_m', $rETR_{max}$, and E_{sat}. *G. balticum*, *P. vitrea*, and *N. dubia* showed rapid vertical migration away from the surface with increasing irradiance. Euglenids, *P. angulatum*, and *N. dubia* exhibited their highest $rETR_{max}$ values at midday. E_{sat} for algal cells was between 500 and 600 µmol m^{-2} s^{-1}, except for *N. dubia* and small *Nitzschia* sp., which had an E_{sat} of 300 µmol m^{-2} s^{-1}. Differences in behavioral and photophysiological traits between microphytobenthic taxa could be a form of niche separation and need to be incorporated into conceptual models of daily patterns of production in intertidal biofilms.