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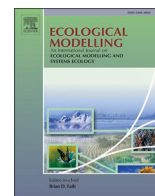
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# Light niche construction: Motility of sediment-inhabiting diatoms determines the experienced light environment

João Serôdio<sup>\*</sup>, Alexandra Bastos, Jérôme Morelle, Silja Frankenbach

Department of Biology and CESAM – Centre for Environmental and Marine Studies, University of Aveiro, Campus de Santiago, Aveiro, 3810-193, Portugal

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## ABSTRACT

Diatoms are an extraordinarily diverse, evolutionarily successful, and ecologically important group of single-cell algae. Diatoms of the group of the pennates are particularly important in estuarine sedimentary habitats, where they form highly productive microphytobenthos communities that cover extensive areas of intertidal flats. The pennates are capable of directed motility, an evolutionary and unique trait amongst diatoms, which has long been hypothesized to confer a critical adaptive advantage, by enabling these cells to vertically migrate within the photic zone of the sediment and behaviorally regulate light exposure. This study investigated the role of diatom motility on the active regulation of light exposure by developing a model to quantitatively characterize and compare the experienced light environment of individual cells of two life forms of pennate diatoms that inhabit intertidal estuarine sediments: epipelagic species, motile cells dominant in fine sediments, and epipsammic species, non-motile or slowly motile cells, that colonize coarser sediments. The conceptual framework of the model was based on the identification and parameterization of the main controlling factors of the light regime perceived by cells inhabiting the two types of sedimentary environments: (i) solar irradiance incident at the sediment surface, determined by the superimposition of the tidal cycle on the day-night cycle; (ii) light attenuation within the sediment; (iii) sediment mixing by tidal currents or bioturbation, repositioning the cells in the sediment column; (iv) cell velocity, as a function of light intensity and of the photoacclimation state of the cells that determines their photosynthetic light preferences. The model was run for realistic scenarios based on published ecological, photophysiological and cellular motility data (light attenuation, mixing depth, photosynthesis light-response curves, cell velocity), simulating (i) the variation in the vertical position of a diatom cell due to vertical migration and (ii) the irradiance level to which it is exposed at each moment. The results confirm the hypothesis that epipelagic and epipsammic diatoms experience a significantly different light environment. Vertical migration enables motile species to experience a much less variable light regime, with increased mean daily light doses received. In contrast, non-motile species experience a much more unstable light environment, including the frequent exposure to supersaturating light levels and to periods of prolonged darkness. These results have important ecological significance, as they support the adaptive value of light-driven motility as a form of optimizing photosynthesis and growth, and they identify vertical migration as a niche-construction activity, allowing motile diatoms to regulate the light environment they experience through habitat selection.

## 1. Introduction

Diatoms are single-cell photoautotrophic eukaryotic microalgae renowned for their unique silica-based cell walls, ubiquitous in virtually all marine and freshwater habitats, living in suspension in the water column or attached to substrata (Armbrust, 2009). Diatoms form an extremely diverse, evolutionarily successful, and ecologically important group of algae. Their photosynthesis captures 40% of the total carbon fixed by marine ecosystems, the equivalent to 20–25% of the Earth's

global carbon fixation, an amount comparable to that fixed by all the terrestrial rainforests combined (Field et al., 1998). Particularly in coastal and estuarine ecosystems, the primary production carried out by diatoms represents a key source of carbon for trophic webs, supporting a range of animal populations, from small crustacean to commercially valuable fishes, seabirds, and marine mammals (Benoiston et al., 2017). In estuaries and shallow coastal zones, diatoms are the dominant group of primary producers, both in the water column (phytoplankton) and in the sediment and other benthic habitats (microphytobenthos).

<sup>\*</sup> Corresponding author.

E-mail address: [jserodio@ua.pt](mailto:jserodio@ua.pt) (J. Serôdio).

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Diatoms are particularly important in sedimentary habitats, where they largely dominate the microphytobenthic communities, forming highly productive biofilms that cover extensive areas of intertidal flats or shallow subtidal sediments (Underwood and Kromkamp, 1999). The microphytobenthos plays key roles in the functioning of estuarine and coastal ecosystems (Hope et al., 2019). Its productivity ranks among the highest in marine ecosystems and, in tidal estuaries it acts as a major carbon sink, in some cases surpassing the ecosystem-level primary production of the phytoplankton (Frankenbach et al., 2020). It further mediates nutrient cycling (Hochard et al., 2010) and the fluxes across the water/air-sediment interface (Eyre et al., 2011), promotes sediment biostabilization (Paterson et al., 2018), and through resuspension to the water column, contributes to the planktonic primary productivity (Brito et al., 2012).

The diatom species that form sedimentary microphytobenthic communities belong predominantly to the group of the raphid pennate diatoms, simultaneously the most evolutionarily recent, having appeared only ca. 30 million years ago, and presently the largest group of diatoms (Armbrust, 2009; Kooistra et al., 2007). In contrast with their planktonic ancestors, raphid pennates are capable of directed motility, a unique trait amongst diatoms, made possible by the appearance of the raphe, a longitudinal thin and long slit through the surface of the cell wall (Nakov et al., 2018). Most commonly, diatoms move through gliding, a form of locomotion consisting in movements parallel to the longitudinal axis of the cell, when in close contact with hard surfaces, and involving the adhesive extrusion of mucilaginous extracellular polymeric substances through the raphe (Edgar and Pickett-Heaps, 1984).

Directed motility has been hypothesized to have conferred a critical adaptive advantage to pennate diatoms, explaining their evolutionary success and their fast evolution (Cohn et al., 2015; Nakov et al., 2018). It is seen as a key adaptation to the sedimentary environment, allowing cells to colonize new niches and to rapidly respond to environmental physical and chemical microgradients (UV and visible light, gravity, temperature, salinity, desiccation, pH, nutrients, carbon and pheromones) and to actively exploit resource heterogeneity while avoiding unfavorable regions of the microhabitat (Seródio, 2021).

In sedimentary microphytobenthos, diatom motility is mostly manifested by the synchronized vertical movement of massive numbers of cells to and from the surface of the sediment (Coelho et al., 2011; Palmer and Round, 1967). Vertical migration follows well defined patterns, including the upward movement towards the surface at the beginning of daytime periods of low tide, followed by the downward migration in anticipation of tidal flood or night (Consalvey et al., 2004; Seródio, 2021). This vertical migratory behavior is considered as a critical trait and a key adaptation to the sedimentary environment, as it affects several aspects of the biology and ecology of sediment-inhabiting pennate diatoms (Seródio et al., 2001). It regulates and enhances photosynthetic activity and carbon assimilation, determines nutrient uptake and sexual reproduction (Saburova and Polikarpov, 2003), and is controlled by an endogenous biological clock (Palmer and Round, 1967).

A longstanding idea is that raphid pennates use vertical migration to adjust their vertical position in the sediment to regulate light exposure (Admiraal, 1984; Seródio et al., 2001). In the nutrient-rich conditions of estuarine sediments, light is argued to be the most important limiting factor for photosynthesis and growth, and the ability to regulate light exposure is key to cope with the conditions of the intertidal sedimentary environment. Due to the strong light attenuation in sediments and to the frequent remixing of the sediment by tidal currents and bioturbation, diatom cells may be displaced to deep layers where light levels are too low to support growth or be directly exposed to sunlight at the surface (Frankenbach et al., 2019; Morelle et al., 2021). On the other hand, diatoms can be deposited at the surface, where exposure to high light levels can cause photoinhibition, a major factor limiting of photosynthesis (Raven, 2011), especially if exacerbated by the stressful conditions common in the intertidal environment (Laviale et al., 2015). In this

context, vertical migration has been hypothesized to confer the two-fold possibility of avoiding dark or low light regions of the sediment and of escaping photoinhibitory light levels near the surface, overall optimizing photosynthesis and growth (Admiraal, 1984; Consalvey et al., 2004).

This ‘behavioral photoprotection hypothesis’ is supported by diverse experimental evidence (Frankenbach et al., 2018). Strong support comes from the observation that vertical migration is regulated by light intensity, following a well-defined biphasic light-response pattern comprising upward migration under low light (positive phototaxis) and downward migration under high light (negative phototaxis), with the rate of descend depending on light intensity (Du et al., 2010; Laviale et al., 2016; Seródio et al., 2006). Further evidence supporting that vertical migration may be effective in regulating light exposure comes from the comparable scales of the photic zone of the sediment (<500  $\mu\text{m}$ ; (Cartaxana et al., 2011; Kromkamp et al., 1998; Seródio et al., 2001)) and of the size of most pennate diatom cells (10–70  $\mu\text{m}$ ; (Jesus et al., 2009)). Considering the velocities attainable by pennate diatom cells, it appears plausible that vertical migration can be fast enough to allow cells to traverse the whole photic zone (corresponding a few cell lengths) in a short period (Cohn et al., 2015; Consalvey et al., 2004; Seródio et al., 2001).

The role of motility on the physiology and productivity of microphytobenthos communities has been often addressed by the comparative study of two life forms of pennate diatom species, taxonomically closely related and occurring virtually sympatrically (e.g. same tidal flat of the same estuary), but with distinct motility capacity (Ribeiro, 2000; Sabbe, 1997): epipellic forms, motile species, dominant in fine sediments, where they glide freely between the sediment particles; and epipsammic, non-motile or slowly motile species, inhabiting coarser sediments, where they live attached to sediment particles (Barnett et al., 2015; Cartaxana et al., 2011; Frankenbach et al., 2018; Jesus et al., 2009; Juneau et al., 2015; Ribeiro et al., 2013).

The rationale underlying the comparative study of epipellic and epipsammic forms is the assumption that motility determines not only the light levels to which the cells are exposed, but also, and critically, the variability of the light regime experienced by the two types of life forms in their corresponding sedimentary habitats. Having the capacity to adjust their position along the vertical light gradient as incident light changes across the day, epipellic cells are expected to experience a less variable light environment than epipsammic ones; not able to move, these cells will be exposed to whatever light levels reach the depths where they happen to be located, experiencing a much more variable and possibly extreme light environment (Barnett et al., 2015).

This assumption, although seeming plausible, has not been verified and, to our knowledge, no attempts have been made to quantify the consequences of motility on the light regime perceived by sediment-inhabiting diatoms. The migratory behavior of diatoms has been the subject of modeling studies, but not explicitly considering the control by light (Cao et al., 2013; Marques da Silva et al., 2020). The present study addresses this question by developing a model to quantify the effects of diatom motility on the experienced light exposure of individual cells inhabiting intertidal estuarine sediments. The general conceptual framework of the model is based on the main controlling factors of the light regime to which cells inhabiting a intertidal sedimentary environment are exposed to: (i) solar irradiance incident at the sediment surface, considering the interference of the tidal cycle on the day-night cycle; (ii) light attenuation within the sediment, dependent on its granulometry; (iii) sediment mixing due to tidal currents or bioturbation; (iv) diatom cell velocity, as a function of light intensity and time of day. Numerical simulations were run for realistic scenarios based on published ecological, photophysiological and cellular motility data, in order to characterize and compare the light environment perceived by epipellic (motile) and epipsammic (immotile and slowly motile) life forms, both in terms of mean hourly and daily light dose received and of its variability across hourly and daily time scales.

## 2. Materials and methods

### 2.1. Conceptualization

The model developed in this study aimed to quantify the effects of diatom motility on the experienced light exposure of individual cells inhabiting intertidal estuarine sediments. Effects of cellular directed motility were addressed by modeling two main contrasting scenarios: diatom communities dominated by motile epipellic species, colonizing fine sediments (thereafter referred to as EPL; Table 1), and diatom communities dominated by slowly motile or immotile epipsammic species (thereafter referred to as EPM). Conceptually, the model considered four main factors forcing the exposure of cells to light (Fig. 1):

- (i) variation of solar irradiance incident at surface of the sediment, parameterized as  $E(0, t)$ , which was considered identical for the EPL and the EPM scenarios (Fig. 1A, B);
- (ii) light attenuation within the sediment, determining the vertical distribution of light and the depth of the sedimentary photic zone, parameterized by the attenuation coefficient  $k_E$ ; in sediments composed by finer particles, epipellic cells are exposed to a steeper vertical light gradient and a shallower photic zone due to a higher light attenuation, than the epipsammic ones inhabiting coarser sediments (Fig. 1C, D);
- (iii) mixing depth,  $z_{mix}$ , determining the vertical position of cells,  $z_{cell}$ , at the beginning of each light period; the coarser sediment particles in the EPM scenario allow for a deeper mixing than in the EPL scenario (Fig. 1C, D);
- (iv) cell velocity, determining the capacity to behaviorally regulate the experienced light exposure, by escaping the aphotic layers of the sediment and reaching the photic zone, and by migrating downwards under excess light intensities; parameterized as  $v(E(z_{cell}, t), t)$ , reflecting the dependency of light intensity and time of day  $t$ ; in the case of epipsammic communities, two scenarios were considered: epipsammic motile species (EPM-M), slowly moving cells (Fig. 1D) and epipsammic non-motile species (EPM-NM), for which  $v = 0$ .

Two other processes were also considered. First, the semi-lunar (fortnight) variability in light exposure conditions determined by the delay of the low tide exposure from day to day (four scenarios, Fig. 2). Second, the photoacclimation state of epipellic and epipsammic cells, parameterized by photosynthetic light response curves, including the photoacclimation parameter  $E_k$ , used to define the ranges of light intensities corresponding to light limiting ( $E < E_k$ ) and excessive, super-saturating light conditions ( $E > E_k$ ) (Fig. 1A, B).

### 2.2. Validation of model parameters

Most of the values and range of variation of the parameters of the model were based on laboratory and field observations and ecological data collected over almost two decades on epipellic and epipsammic communities and their sedimentary habitats on two intertidal sites of the

Ria de Aveiro, a tidal estuarine ecosystem in the west coast of Portugal (Bueno-Pardo et al., 2018). These data include (Table 2): hourly variation of solar irradiance and semi-lunar variation of tidal exposure (Frankenbach et al., 2020; Seródio et al., 2008), sediment granulometry and associated light attenuation (Frankenbach et al., 2020; Seródio et al., 2007), diatom photophysiology, including detailed data on photoacclimation and photosynthetic light response (Frankenbach et al., 2018; Seródio et al., 2007), epipellic and epipsammic species composition (Frankenbach et al., 2018; Seródio et al., 2007), and diatom photobehavior, namely light-induced and endogenously controlled vertical migration (Coelho et al., 2011; Laviale et al., 2016; Seródio et al., 2006). The exceptions refer to data on diatom velocity light response, that were based on published data concerning diatoms grown in culture (Cohn et al., 2003; Consalvey et al., 2004; McLachlan et al., 2009; Seródio, 2021). As most observations refer to the same epipellic and epipsammic communities and habitats within the same ecosystem, the model parameters were validated by a consistent and coherent data set.

### 2.3. Model outline

In summary, the model simulates (i) the changes in the vertical position (depth below the sediment surface) of a diatom cell due to vertical migration during the course of the diurnal low tide periods occurring for one day, and (ii) the irradiance level to which it is exposed at each moment. At the beginning of each light period, the cell depth is reset, being determined by a random value within the mixing zone, simulating the effects of tidal currents and bioturbation. The velocity (magnitude and vertical direction) of the cell at each depth is determined by the light available at that depth and on the cell's photosynthetic light preferences. By running the model for multiple days (see below), the light regime perceived by the cells can be characterized, both in terms of location and of variability in the daily light dose received. The modeling workflow is summarized in Fig. 3.

To assess the impact of cellular motility on the perceived light regime, the model was run for various scenarios. Firstly, using realistic parameter values for epipellic, epipsammic-motile (EPM-M scenario) and epipsammic non-motile (EPM-NM scenario) communities and their sedimentary habitat (Table 2). Secondly, by systematically varying the parameters characterizing cell velocity and mixing depth, to evaluate the relative impact of these main factors.

#### 2.3.1. Solar irradiance at surface

The hourly variation of irradiance incident at the surface of the sediment,  $E(0, t)$ , was simulated by a gaussian curve (Guo, 2017):

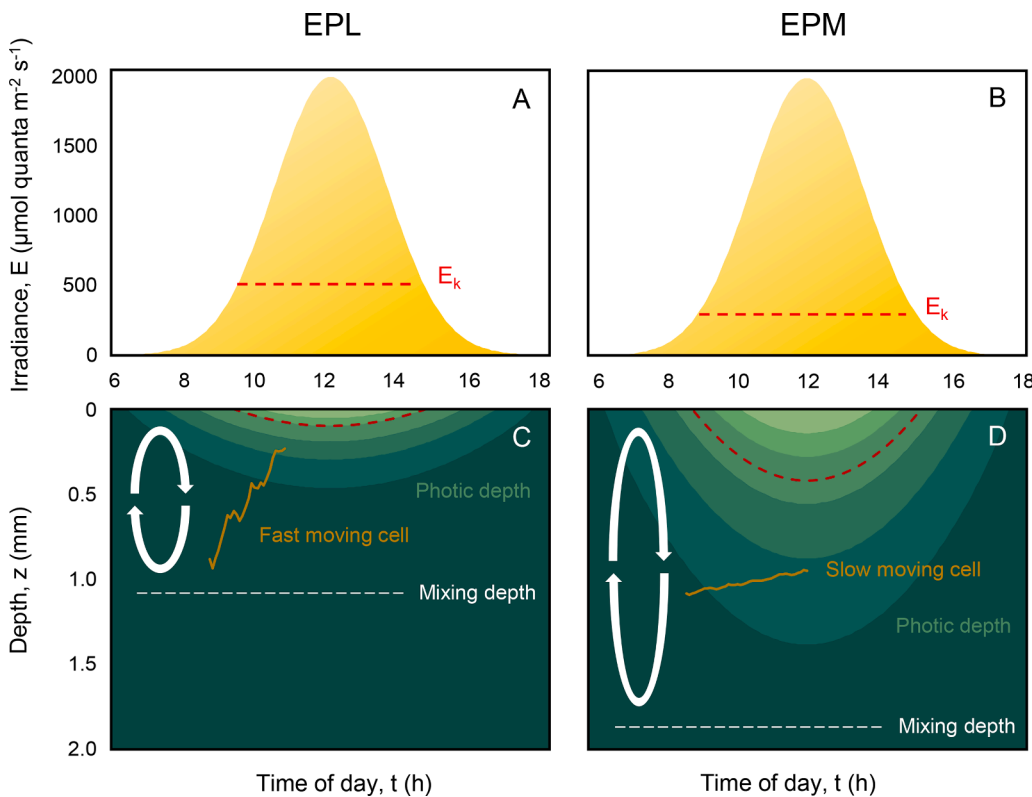
$$E(0, t) = E_m e^{-\frac{(t-t_n)^2}{c}} \tag{1}$$

where  $t_n$  is the time of solar noon,  $E_m$  is the maximum irradiance, occurring when  $t = t_n$ , and  $c$  is the steepness of the curve, measuring the rate of change of instantaneous solar irradiance over time. For simplicity, the values of  $E_m$  and  $t_n$ , corresponding to the solar zenith, were set to  $2000 \mu\text{mol quanta } m^{-2} s^{-1}$  and 12:00, respectively (Fig. 2), and  $c$  was estimated from fitted Eqn. (1) to in situ data measured in the Ria de Aveiro during a clear sky summer day (Seródio et al., 2008).

The semi-lunar variation of available light associated to the progression of the tide from one day to the next was considered by simulating four different scenarios, approximately as observed in the Ria de Aveiro (Seródio et al., 2008, 2007): low tide in the middle of the day, occurring during spring tides (ST); high tide in the middle of the day, and low tide during the morning and afternoon, occurring during neap tides (NT); intermediate situations (ST-NT and NT-ST) (Fig. 2). For each of these scenarios, it was assumed that no light is available for the cells during high tide periods, either due to submersion in turbid water or due to downward vertical migration during submersion.

**Table 1**  
Abbreviations.

Name	Description
EPL	Epipellic
EPM	Epipsammic
EPM-M	Epipsammic motile
EPM-NM	Epipsammic non-motile
NT	Neap tides
PAR	Photosynthetically Active Radiation
PSII	Photosystem II
ST	Spring tides
rETR	Relative electron transport rate of PSII



**Fig. 1.** Conceptual representation of the main components of the model, highlighting the main differences between the two main scenarios under study: fine sediment inhabited by motile, fast-moving epipellic species (EPL) (A, C) and coarser sediment inhabited by non-motile or slowly moving species (EPM) (B, D). A, B. Hourly variation in solar irradiance incident of the sediment surface, and photoacclimation parameter  $E_k$ , higher for the EPL scenario and lower for the EPM scenarios (dashed red lines). C, D. Corresponding hourly variation of light penetration in the sediment (green bands correspond to 1000, 500, 125, 20 and 2  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ ), mixing depth (white arrows) and cell vertical migration (simulated trajectories in yellow). In the EPL scenario, fast-moving cells in a finer sediment are exposed to a sharper vertical light gradient and a resulting shallower photic zone, and to a shallower mixing zone. In the EPM scenario, coarser sediments inhabited by slow moving or immotile diatoms, the photic zone and the mixing zone are deeper. For simplicity, the effects of tidal submersion on light availability are shown in Fig. 2.

### 2.3.2. Light attenuation in the sediment

The vertical variation of light available within the photic zone of the sediment at each moment of the day,  $E(z, t)$ , was described by an negative exponential function, based on irradiance data measured with detailed (sub-millimeter) vertical resolution on two types of sediment of the Ria de Aveiro colonized by epipellic and epipsammic diatom communities (Frankenbach et al., 2020). Light penetration was quantified by the light attenuation coefficient,  $k_E$ , which was higher for the EPL scenario (finer sediment,  $k_E = 9.0 \text{ mm}^{-1}$ ; Table 2) and lower for the EPM scenario (coarser sediment,  $k_E = 6.1 \text{ mm}^{-1}$ ), to calculate the light available at the cell depth,  $E(z_{\text{cell}}, t)$ :

$$E(z_{\text{cell}}, t) = E(0, t)e^{-k_E z_{\text{cell}}} \quad (2)$$

It was assumed that light attenuation was constant over time and not affected by cell self-shading.

### 2.2.3. Sediment mixing

To simulate the effects of the mixing of the upper layers of the sediment by tidal currents, especially during ebb and flood, or due to bioturbation during high tide cover, the vertical position of the cell was newly defined at set at the start of each new low tide light period. Due to the lack of data on the impact of sediment mixing on the redistribution of cells with depth, this process was modelled by attributing to  $z_{\text{cell}}$  a random value between  $z = 0$  and  $z = z_{\text{mix}}$ . For each mixing event, it was assumed a complete homogenization of the sediment across the whole mixing zone, meaning that all depths between 0 and  $z_{\text{mix}}$  were equally probable for defining  $z_{\text{cell}}$  (uniform distribution). Because fine sediments colonized by epipellic diatoms tend to be much more cohesive than the coarser sediments colonized by epipsammic diatoms (Ubertini et al., 2015),  $z_{\text{mix}}$  was considered to be smaller for the former ( $z_{\text{mix}} = 2 \text{ mm}$ ) than for the later ( $z_{\text{mix}} = 10 \text{ mm}$ ) (Fig. 1C, D; Table 2).

### 2.2.4. Cell light preferences and photoacclimation state

A key feature of this model is the explicit dependency of cell behavior (velocity and vertical direction) on light intensity. However, the motility

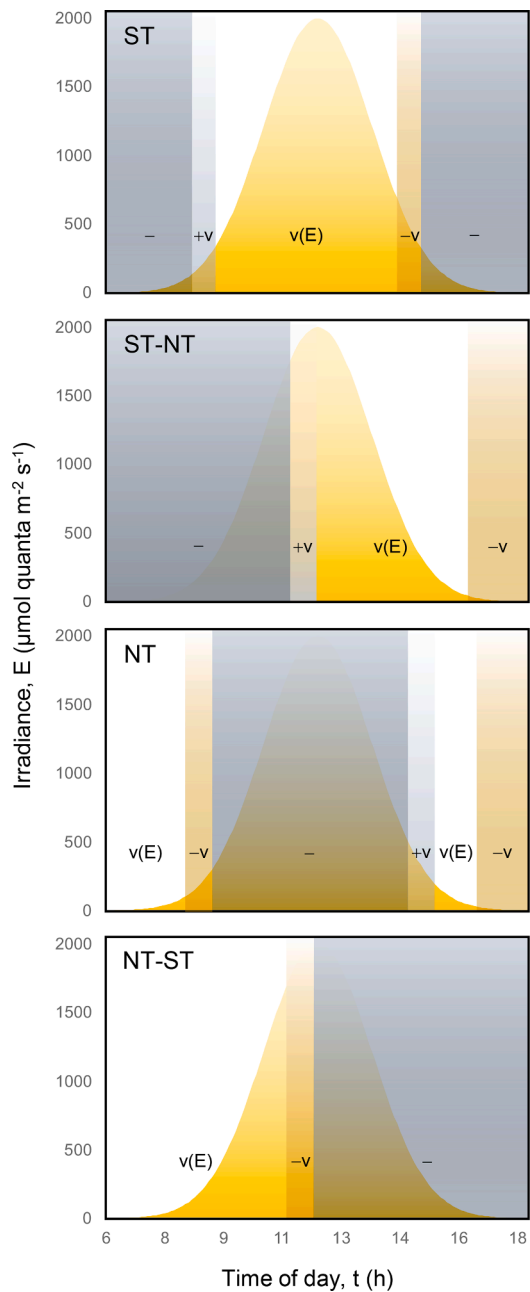
response of the cells is not considered to depend on light levels *per se*, but on the light levels when compared to the cell 'light preferences', determined by its photosynthetic light response (see below). The rationale is that cells will migrate vertically trying to optimize photosynthesis, avoiding dark or limiting light levels as well as super-saturating intensities. The range of intensities that are considered too low and too high is determined by the photoacclimation state of the cells, typically characterized by light-response curves of photosynthesis and in particular by the light-acclimation parameter  $E_k$  (Ezequiel et al., 2015). Here, the model used data referring to light-response curves of rETR, the relative electron transport rate of photosystem II (PSII), an established proxy of diatom photosynthetic rates (Barranguet and Kromkamp, 2000; Morelle and Claquin, 2018; Seródio et al., 2007), measured on epipellic and epipsammic communities of the Ria de Aveiro (Frankenbach et al., 2018) (Table 2; Fig. 4A). The light-response curves of rETR were characterized by the initial slope of the curve ( $\alpha$ ), the maximum rETR level ( $rETR_m$ ) and  $E_k$ .

### 2.2.5. Cell velocity

The variation of cell velocity with depth and light intensity was modelled to ensure (i) a light dependency functionally identical to the relationship experimentally documented by McLachlan et al. (2009) and (ii) positive velocity (upward migration) for light limiting levels ( $E < E_k$ ) and negative velocity (downward migration) for super-saturating levels ( $E > E_k$ ). The variation of cell velocity as a function of light,  $v(E)$ , was based on the normalized rate of variation of rETR with  $E$ ,  $\Delta rETR/\Delta E$ :

$$v(E) = v_m \frac{\Delta rETR/\Delta E(E) - \Delta rETR/\Delta E(E_k)}{\max(|\Delta rETR/\Delta E(E)|)} \quad (3)$$

where  $v_m$  is the maximum cell velocity. To ensure that  $v(E) = 0$  for  $E = E_k$ , normalization was done separately for  $E < E_k$  and  $E > E_k$ . The relationship between cell velocity with light intensity and the photosynthetic light response (rETR vs  $E$  curves) is shown in Fig 4. Eq. (3) displays the main features of the observations of McLachlan et al. (2009): (i) cell velocity decreases with light intensity, with maximum velocity being



**Fig. 2.** Time series of solar irradiance used to simulate the hourly variation of incident light periods along the semi-lunar (fortnightly) spring-neap tidal cycle, from spring tide (ST; one light period, centered in the middle of the day) to neap tide (NT; two light periods, one in the morning and another in the afternoon) and two intermediate stages (ST-NT and NT-ST). Unshaded and dark-yellow vertical bars represent periods of low tide exposure. For the periods represented by unshaded bars, cell velocity was considered as light-driven ( $v(E)$ ) and was calculated by Eqn. (3). Shaded (dark and light gray) vertical bars represent periods of submersion during high tide, during which no light is considered available for the cells (-). Thinner bars (dark-yellow and light gray) indicate periods when cell movement was considered as endogenously controlled: during pre-light exposure periods, during high tide, cells moved upward at speed  $v_m$  for 30 min (+v); during pre-sunset or pre-high tide, during low tide exposure, cells moved downward at speed  $v_m$  for 30 min (high tide) or 120 min (sunset) (-v).

observed for very low light or dark; (ii) under low light, cells move towards the light source, and under high light they move away from light. Eq. (3) was applied to the EPL and EPM-M scenarios, while for the EPM-NM scenario, cell velocity was considered as zero. For epipelagic

cells, the value of  $v_m$  was considered as the mean value of published vertical diatom gliding speeds, compiled in Seródio (2021) (Table 2). Considering the inexistence of data for cell velocity of epipsammic motile diatoms,  $v_m$  was defined as 10 times smaller than the values for used for the epipelagic. The cell position at each new time  $t_{i+1}$  ( $\Delta t = t_{i+1} - t_i$ ) was calculated from cell velocity and the depth at the previous time  $t_i$ :

$$z_{cell}(t_{i+1}) = z_{cell}(t_i) + v(E_{z_{cell}})\Delta t \quad (4)$$

The model also considers another well-known and critical aspect of the motility behavior of sediment-inhabiting pennate diatoms: the endogenously controlled, gravity-driven and light-independent vertical migration before the start (upward migration before sunrise or before end of high tide cover) and the end (downward migration before sunset or incoming high tide) of light exposure periods. Based on detailed data for the epipelagic communities of the Ria de Aveiro (Coelho et al., 2011; Frankenbach et al., 2014), the model considers that cells start migrating upwards 30 min before start of diurnal low tide periods, and start migrating downwards 30 min before high tide and 2 h before sunset (if during low tide) (Fig. 2).

The model also considers another important feature of diatom gliding, the ‘reversal autonomous rhythm’ (Wenderoth and Rhiel, 2004), which consists in the continuous back and forth movement of the cells, causing directed progression to depend on the relative time between reversal of the direction of the movement (Seródio, 2021). This aspect was included in the model by considering cell velocity to be given by a random number from a Normal distribution with mean  $v(E, t)$  and standard deviation  $\sigma_v(E, t)$ . Based on the observations of Cohn et al. (2003)  $\sigma_v$  was set to 10% of the value of  $v$  (Table 2).

### 2.2.6. Model implementation and outputs

For each day, the model was run with a time step  $\Delta t = 5$  min, computing the total daily light dose to which the cell is exposed (LD), given by the cumulative product of incident light at depth  $z_{cell}$  and the time step:

$$LD = \sum_{t_i} E(z_{cell}, t_i)\Delta t \quad (5)$$

and the exposure to excess light ( $E_{Ek}$ ), given by the number of hours that the cells were exposed to  $E > E_k$ . For each scenario, the model was run for 1000 days to obtain a frequency distribution of LD, which was characterized in terms of central tendency (mean LD,  $\overline{LD}$ ) and dispersion (coefficient of variability of LD,  $CV_{LD}$ ), as well as the proportion of days the cells did not receive any light ( $LD_0$ ) (Table 3).

## 3. Results

### 3.1. General comparison between EPL and EPM scenarios

Fig. 5 illustrates individual runs of the model, showing the trajectories of cells starting from two depths (0.5 and 2.0 mm) for the three scenarios EPL, EPM-M and EPM-NM, considering a full photoperiod, not interrupted by submersion by high tide. Epipelagic cells are fast enough to be able to reach the photic zone during the early parts of the day (Fig. 5D). Cells starting at the deeper layer  $z_{cell} = 2.0$  mm reach the upper layers of the sediment only 2–3 h later, although not compromising the exposure to high light levels for most of the day (Fig. 5A). It is noticeable a slight downward migration during the middle of the day, when solar irradiance incident the surface and upper layers attains supersaturating levels. In the EPM-M scenario, the slower cell velocity implies that only cells starting at shallower depths are able to reach the photic zone during the course of the day (Fig. 5B, E). Cells starting at deeper layers, as in the example of  $z_{cell} = 2.0$  mm, may only reach the lower regions of the photic zone and be exposed for very low light levels (Fig. 5B). In contrast, the light exposure of immotile cells (EPM-NM scenario) is completely dependent on the depth where cells are

**Table 2**

Model parameters. Values in parentheses indicate the range used in the simulations run for testing effects of cell velocity and mixing depth.

Name	Description	Units	Values			References
			EPL	EPM-M	EPM-NM	
$\alpha$	Initial slope of a rETR vs. $E$ curve	$\mu\text{mol quanta}^{-1} \text{m}^2 \text{s}$	0.74	0.54	0.54	(Frankenbach et al., 2018)
$c$	Steepness of the hourly change of $E$	$\text{h}^{-1}$	0.21	0.21	0.21	(Seródio et al., 2008)
$\Delta\text{rETR}/\Delta E$	Rate of change of rETR with $E$	$\mu\text{mol quanta}^{-1} \text{m}^2 \text{s}$	–	–	–	(Frankenbach et al., 2018)
$\Delta t$	Time step	Min	5	5	5	–
$E(z)$	PAR irradiance at depth $z$	$\mu\text{mol quanta } m^{-2} \text{s}^{-1}$	0–2000	0–2000	0–2000	–
$E_k$	Light-saturation parameter of a rETR vs. $E$ curve	$\mu\text{mol quanta } m^{-2} \text{s}^{-1}$	416.3	284.4	284.4	(Frankenbach et al., 2018)
$E_m$	Maximum PAR irradiance during the day	$\mu\text{mol quanta } m^{-2} \text{s}^{-1}$	2000	2000	2000	–
$k_E$	Light attenuation coefficient	$\text{mm}^{-1}$	9.0	6.1	6.1	(Frankenbach et al., 2020)
$\text{rETR}_m$	Maximum rETR in a rETR vs. $E$ curve	–	308.4	153.7	153.7	(Frankenbach et al., 2018)
$\sigma_v$	Standard deviation of the Normal distribution of $v$	$\mu\text{m } \text{s}^{-1}$	$0.2v$	$0.2v$	–	(Cohn et al., 2003)
$t$	Time of day	h	6–18	6–18	6–18	–
$t_n$	Time of solar noon	h	12	12	12	–
$v$	Vertical cell velocity	$\mu\text{m } \text{s}^{-1}$	–0.45–0.45	–0.045–0.045	0	–
$v_m$	Maximum cell velocity	$\mu\text{m } \text{s}^{-1}$	0.225 (0.11–0.45)	0.023 (0.01–0.05)	0	(Seródio, 2021)
$z$	Depth	mm	–	–	–	–
$z_{\text{cell}}$	Depth of the cell	mm	–	–	–	–
$z_{\text{mix}}$	Mixing depth	mm	2 (0.25–10.0)	10	10	–

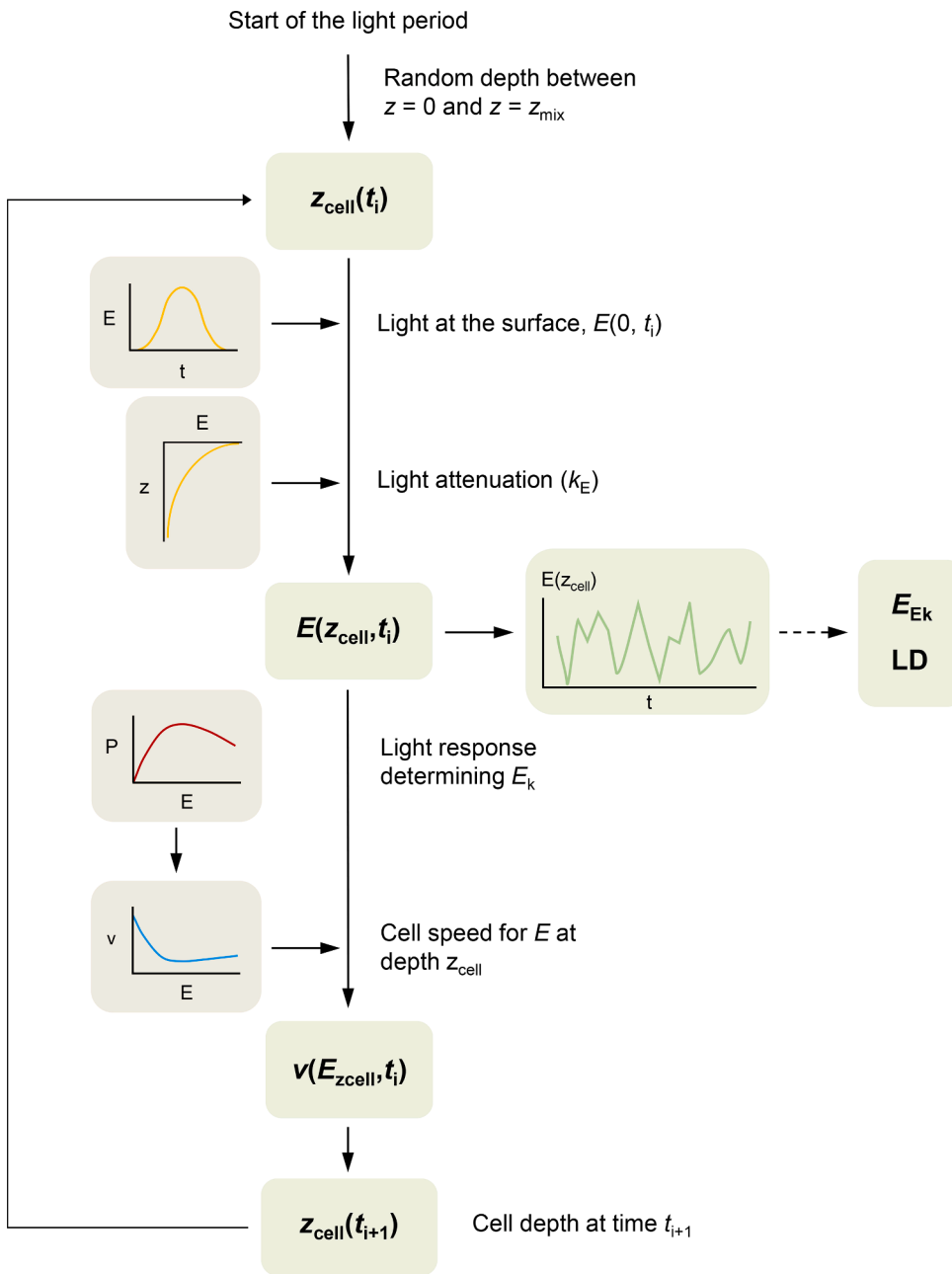
deposited (Fig. 5C, F). Non-motile epipsammic cells that happen to be close enough to the surface (e.g.  $z_{\text{cell}} = 0.5$  mm) may be exposed to relevant light levels, although not being able to explore the light gradient and regulate light exposure. Non-motile cells may stay all day under low, light-limiting levels or on the contrary experience super-saturating light levels (cases not shown). Fig. 5 also illustrates the endogenously controlled behavior of epipelagic cells (and to a lesser extent, also motile epipsammic cells) reflected in upward migration before sunrise and downward migration before the end of the light period.

Running the model for a large number of days (1000) allowed to compare the three scenarios regarding the light regime perceived by the cells, characterized in terms of mean values and variability of received daily light dose (Fig. 6). The most evident result is the clear difference between EPL and both EPM scenarios, with the former showing a much higher mean and a lower variability in LD values, indicating how cell motility effectively contributes to lower the inter-day variability in experienced daily light dose. For the EPL scenario,  $\overline{\text{LD}}$  reached around  $335 \text{ mmol quanta } m^{-2}$  and a  $\text{CV}_{\text{LD}}$  was below 3% (Fig. 6B), while for the EPM scenarios,  $\overline{\text{LD}}$  remained below  $52 \text{ mmol quanta } m^{-2}$  and  $\text{CV}_{\text{LD}}$  reached much higher values, above 217% and 364% for EPM-M and EPM-NM, respectively (Fig. 6D, F). Also significant is the difference in the shape of the frequency distribution of LD, very symmetrical in the EPL scenario while highly (positively) skewed in EPM, with a large proportion of days with very low or no light received by the cells (Fig. 6D, F). In contrast with the EPL scenario, for which cells are exposed to light in all simulated days, in the EPM scenarios, cells are expected to experience continuous darkness for the majority of the days ( $\text{LD}_0$  around 60% and 70% for EPM-M and EPM-NM, respectively).

### 3.2. Variation along the spring-neap tidal cycle

Figs. 5 and 6 served to illustrate the main features of the model and to exemplify a situation with no changes in light availability associated to the interference of submersion in high tide, as would occur for example in shallow subtidal habitats. The inclusion in the model of tidal submersion periods and their progression along the day during the spring-neap cycle confirmed the main overall differences between the EPL and EPM scenarios described above, but also revealed a larger complexity and diversity in the perceived light regime. Fig. 7 shows examples of epipelagic cell trajectories for the four scenarios of tidal submersion described above. A common aspect of all cases, contrasting with the previous simulations (Fig. 5, 6) is the shorter periods of light exposure, the most extreme situation being the case of neap tides (NT), when diurnal low tide is restricted to early morning and late afternoon (Fig. 7C, G). The effective period of light exposure is even shorter, as cells take some time to reach the photic zone during the beginning of the light periods and migrate downwards before high tide or night. As a consequence, when light period starts at middle of the day (ST, ST-NT), cells may reach the photic zone later than in days when exposure periods start before sunrise (NT-ST).

These aspects become more apparent when running the model for multiple days (Fig. 8). As seen for the case of no tidal interference, the consideration of tides also led to much higher  $\overline{\text{LD}}$  values, and much lower  $\text{CV}_{\text{LD}}$ , for the EPL than for the EPMs scenarios, for all tidal conditions. For the EPL scenarios, the frequency distributions of LD are overall symmetrical, although now showing a tendency to be negatively skewed, especially for the cases of ST and NT, caused by a higher frequency of days with low LD, when cells start from deep layers when light at the surface is already high (middle of the day). In contrast, in the case of NT-ST the distribution is more symmetrical, as cell upward migration starts with sunrise and cells reach the surface when light still relatively



**Fig. 3.** Workflow of the running of the model. Each day starts by determining the cell depth  $z_{cell}$ , given by a random value the mixing zone (between 0 and  $z_{mix}$ ). For each time of the day  $t_i$ , light available at depth  $z_{cell}$ ,  $E(z_{cell}, t_i)$ , is calculated by considering solar irradiance at the surface,  $E(0, t_i)$  Eqn. (1), and the light attenuation within the photic zone, determined by  $k_E$  (Eqn. (2)). Based on  $E(z_{cell}, t_i)$  and on the time of day, and on the photosynthetic light response of the cells (characterized by  $E_k$ ), the cell velocity,  $v(z_{cell}, t_i)$  is calculated to determine the new cell position at the next time step  $t_{i+1}$  (Eqn. (3) and (4)). Successive values of  $E(z_{cell}, t_i)$  obtained for each day are used to calculate the number of excess light exposure,  $E_{Ek}$ , and the daily light dose received, LD (dashed arrow; Eqn. (5)). The model is run for 1000 days to obtain a frequency distribution of LD and calculation of measures of location ( $\bar{LD}$ ) and dispersion ( $CV_{LD}$ ), as well as percentage of days in the dark ( $LD_0$ ).

low. As before, the frequency distributions for the EPM scenarios are in all tidal cases very positively skewed due to a large fraction of days of no light exposure ( $LD_0$  varying between 25.1 and 79.2%). A novel type of distribution appears for the EPM-NT scenarios, characterized by two large peaks, one corresponding to days with very low or null light exposure (as seen before) and a second corresponding to the days when cells experience relevant light exposure in one of the two diurnal low tide periods.

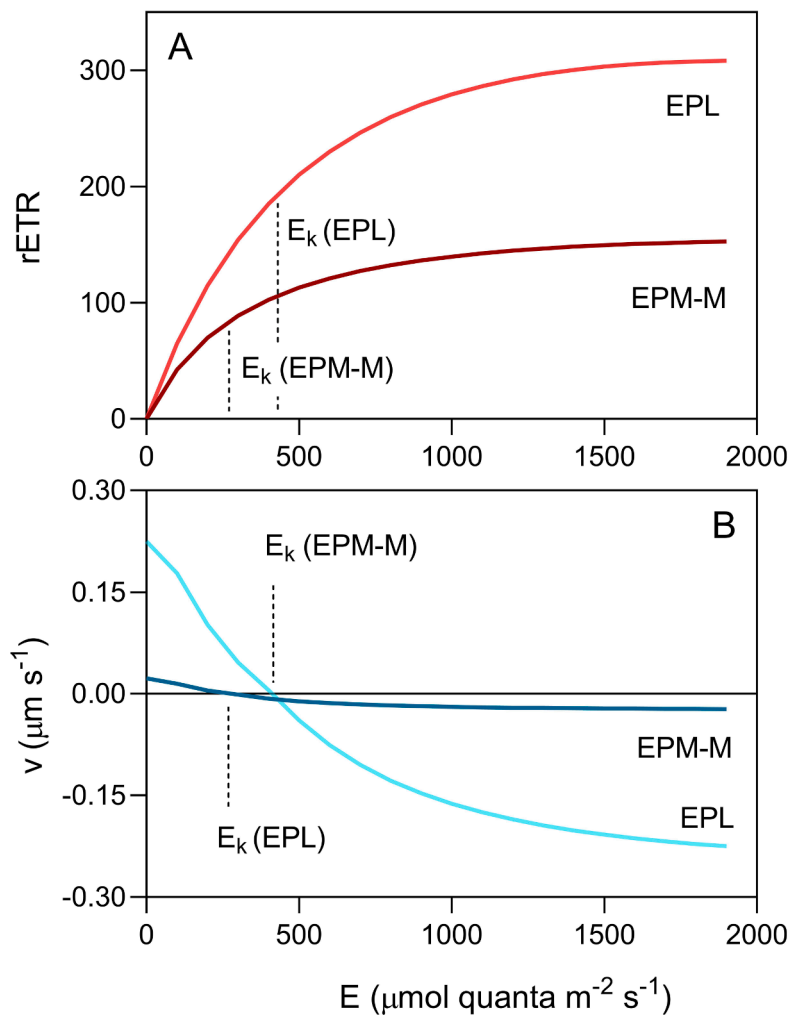
### 3.3. Generalized effects of mixing depth and cell velocity

While the previous results refer to particular values of  $z_{mix}$  (0.5 and 2 mm) and cell velocities (0.225 and 0.023  $\mu m s^{-1}$  respectively for the EPL and EPM-M scenarios), the results presented in Fig. 9 expand the results of the simulations carried out for particular values of mixing depth and cell velocity shown above.  $\bar{LD}$ ,  $CV_{LD}$ ,  $LD_0$  and  $E_{Ek}$  were calculated for a large range of mixing depths (0–12 mm) and cell

velocities (0.113–0.459  $\mu m s^{-1}$ ). In general terms, the increase in  $z_{mix}$  causes, for the same cell velocity, a decrease in  $\bar{LD}$  and  $E_{Ek}$  (Fig. 9A, C), and an increase in  $CV_{LD}$  and  $LD_0$  (Fig. 9B, D). The decrease in  $\bar{LD}$  and  $E_{Ek}$ , and the increase in  $CV_{LD}$  and  $LD_0$ , become less important as cell velocities increase.

In the case of  $\bar{LD}$  (Fig. 9A), the effect of  $z_{mix}$  is due to the fact that cells deposited in deeper layers tend to take more time to reach the photic zone, thus decreasing the amount of time of exposure to high light levels. However, this effect tends to become less significant for faster cells, as higher cell velocities may compensate for deeper  $z_{cell}(t_0)$  and make the cell depth at the start of the day less critical.

A similar situation occurs with  $E_{Ek}$  (Fig. 9C): the chances of exposure to supersaturating light decrease with the increase in mixing depth and cell velocity, both contributing to lower the time spent in layers of sediment close to the surface when incident light is very high. This overall pattern is however inverted for very low mixing depths, in which case the cells are positioned close to the surface, and the slower ones will



**Fig. 4.** A. Light response curves of  $rETR$ , as measured for epipelagic and epipsammic communities (data from Frankенbach et al. (2018)), with indication of the different value of the light acclimation parameter,  $E_k$ . B. Light dependence of cell velocity for the scenarios EPL and EPM-M ( $v = 0$  for EPM-NM), positive (upward migration) when  $E < E_k$ , negative (downward migration) when  $E > E_k$ , and null ( $v = 0$ ) when  $E = E_k$ .

**Table 3**  
Model outputs.

Name	Description	Units
$CV_{LD}$	Coefficient of variation of LD (%)	-
$E_{Ek}$	Time the cell is exposed to $E > E_k$	h
LD	Daily light dose	$\text{mmol quanta m}^{-2}$
$\overline{LD}$	Mean LD	$\text{mmol quanta m}^{-2}$
$LD_0$	Proportion of days in the dark (%)	-

be exposed to supersaturating light for longer periods.

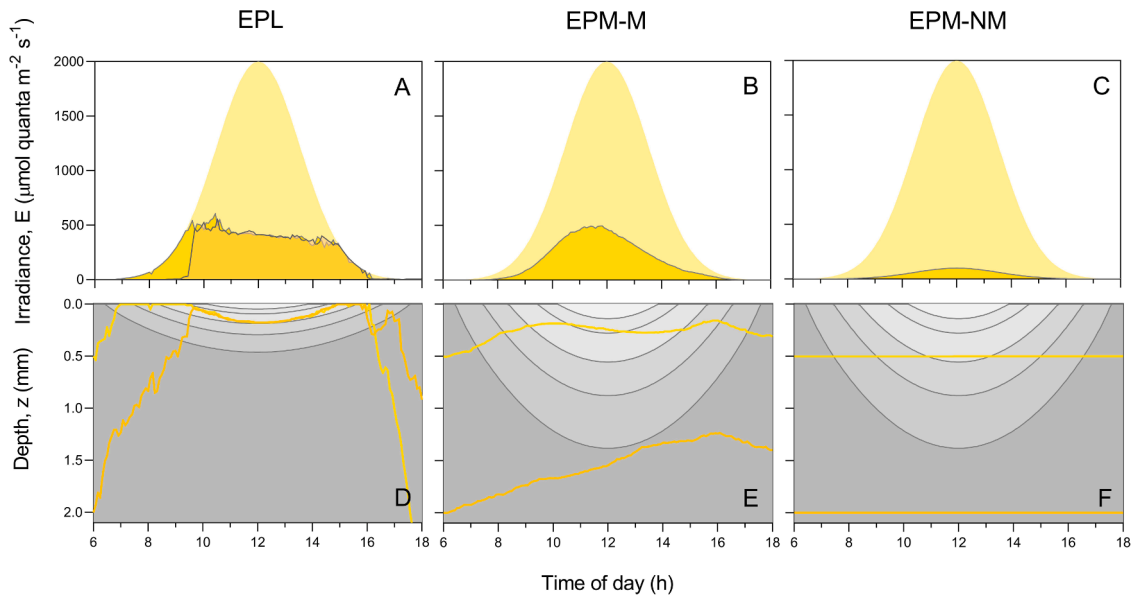
The effects of mixing depth on the variability of the perceived light regime ( $CV_{LD}$ ; Fig. 9B) are directly due to the fact that higher  $z_{mix}$  cause a larger distribution of  $z_{cell}(t_0)$  values and thus of the variation in light received along the day. As for  $\overline{LD}$ , this effect may be largely attenuated by an increase in cell velocity, as faster cells will reach more quickly the (same) optimal light levels. The increased variability in LD that follows the increase in  $z_{mix}$  is also responsible for the dependence of  $LD_0$  (Fig. 9D): higher  $z_{mix}$  increase the probability that cells are moved to deeper layers of the sediment, taking more time to reach the photic zone during the course of the day. Again, faster cells will tend to overcome

this effect and experience a lower number of days without any light exposure.

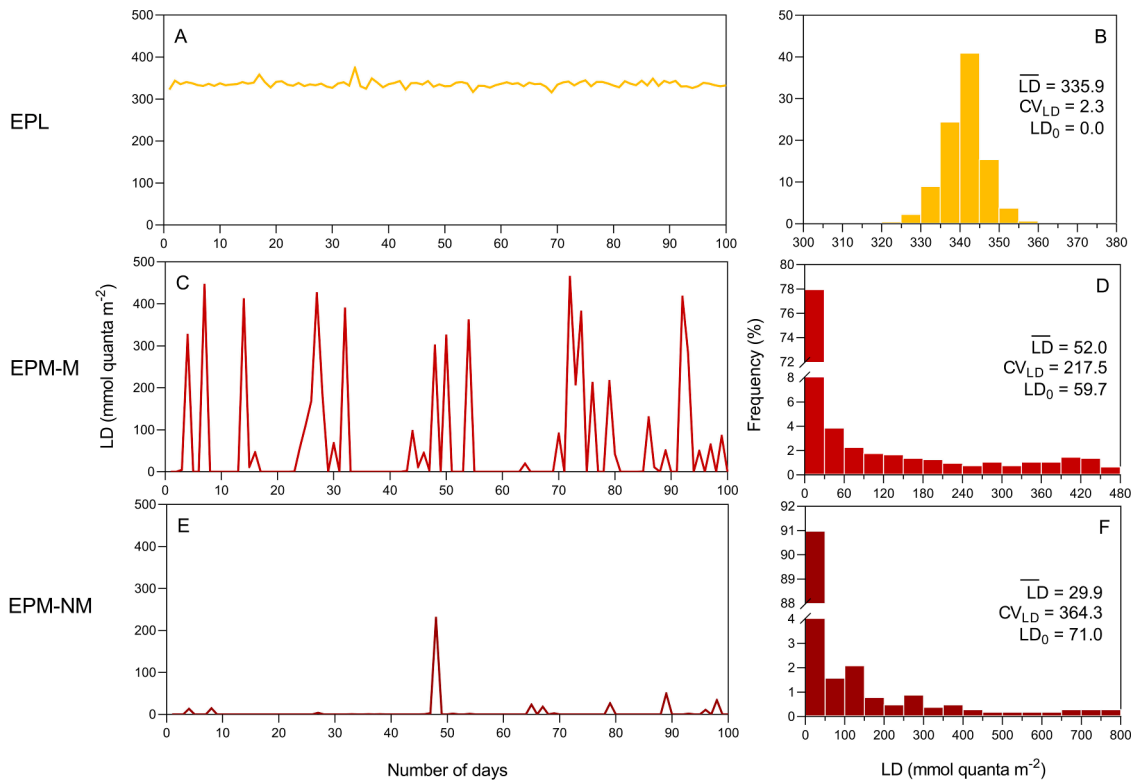
#### 4. Discussion

##### 4.1. Epipelagic and epipsammic diatoms differ in their experienced light environment

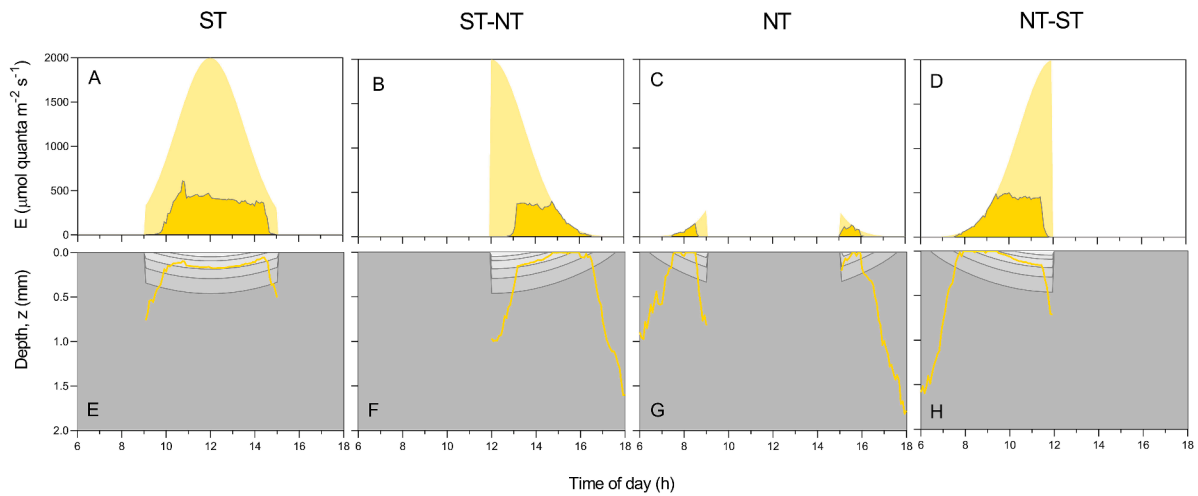
Vertical migration has long been recognized to be an important aspect of microphytobenthos ecology (Admiraal, 1984; MacIntyre et al., 1996; Underwood and Kromkamp, 1999). By enabling diatom cells to exploit the heterogeneities of the sedimentary microenvironment at the sub-millimeter scale, it contributes to enhance photosynthesis of the biofilm and the primary productivity of the intertidal flats at the ecosystem level (Pinckney and Zingmark, 1993; Seródio and Catarino, 2000). This study further shows that vertical migration can be expected to substantially affect the effective light environment experienced by motile diatoms, both in terms of mean values and of variability of daily light dose received, including the frequency of the exposure to supersaturating light levels and of prolonged darkness periods. Overall, the results of the study confirm the common assumption that epipelagic and epipsammic diatoms likely experience a significantly different light regime, with motile epipelagic diatoms effectively experiencing to a much less variable light environment, with increased mean daily light doses, when compared to immotile and slowly motile life forms. Due to their



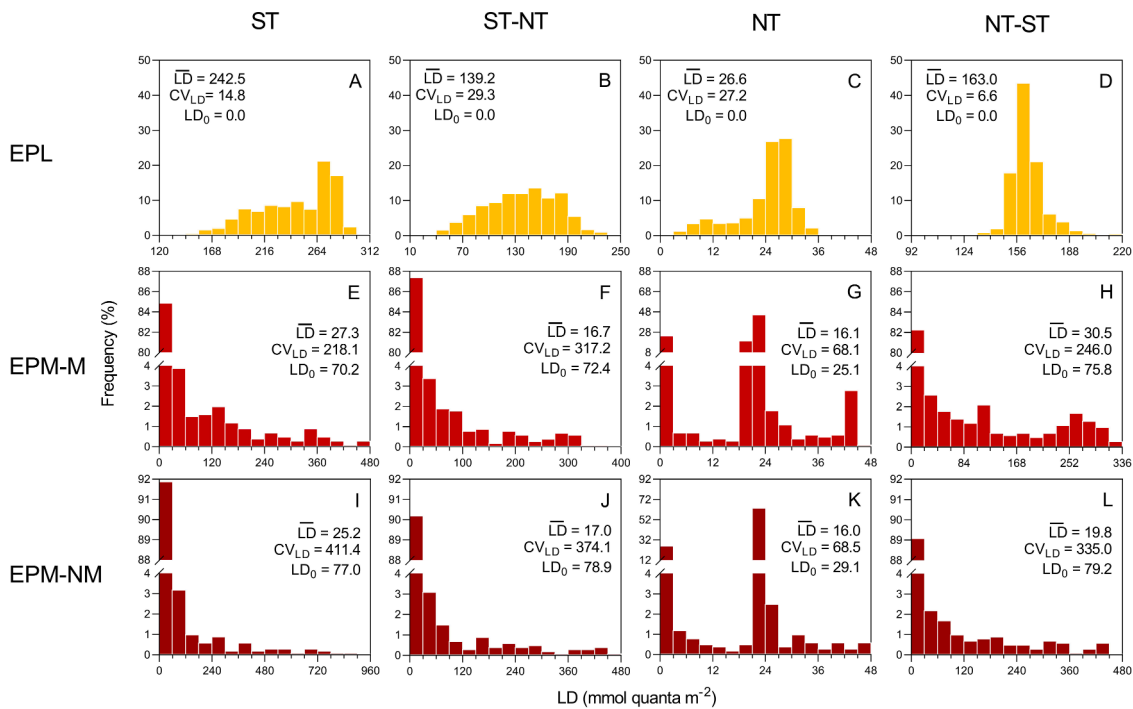
**Fig. 5.** Examples of individual runs of the model, illustrating the trajectories of cells starting at different depths (0.5 and 2.0 mm), in relation to the photic zone of the sediment, for the scenarios EPL (A, D), EPM-M (B, D) and EPM-NM (C, F). Bottom panels (D-F) depict the hourly variation of cell depth along the day,  $z_{cell}(t)$  (yellow and orange lines), and top panels (A-C) show the corresponding experienced light by the cells,  $E(z_{cell}, t)$  (dark yellow and orange areas), in relation to solar irradiance incident at the sediment surface (background light yellow areas). In the case of cells starting at  $z_{cell} = 2.0$  mm in the EPM-M and EPM-NM scenarios (panels E, F; orange lines), the upward migration speed was so low (or null) that the cells did not reach the photic zone and the corresponding top panels (B, C) do not show the values of  $E(z_{cell}, t)$ . Gray bands in panels D-F represent (top to bottom) 1000, 500, 125, 20 and 2  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ , calculated using  $E(0,t)$ , calculated by Eqn. (1) and Eqn. (2), using the values of  $k_E$  in Table 2. Simulations without considering the interference of submersion during high tide on available light.



**Fig. 6.** Outputs of the model after running for multiple days, for the scenarios and conditions exemplified in Fig. 5: EPL (A, B), EPM-M (C, D) and EPM-NM (E, F). Panels on the left (A, C, E) show the daily variation of experienced daily light dose, LD (for simplicity, only 100 days are shown). Histograms on the right (panels B, D, F) show the resulting relative frequency distribution of LD (based on 1000 days), with indication of mean values ( $\bar{LD}$ ), coefficient of variation ( $CV_{LD}$ ) and percentage of days in the dark ( $LD_0$ ).



**Fig. 7.** Example of individual runs of the model for the four different tidal stages along the semi-lunar spring-neap tidal cycle. During high tide periods, solar irradiance incident at the sediment surface (background light yellow areas) was considered null. For simplicity, only the EPL scenario is shown. As in Fig. 5, bottom panels (E-H) show cell trajectories (yellow lines) in relation to the sedimentary photic zone (gray bands: 1000, 500, 125, 20 and 2  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ ), and the upper panels (A-D) show the hourly variation of experienced light by the moving cells (dark yellow areas) in relation to light levels incident at the surface.



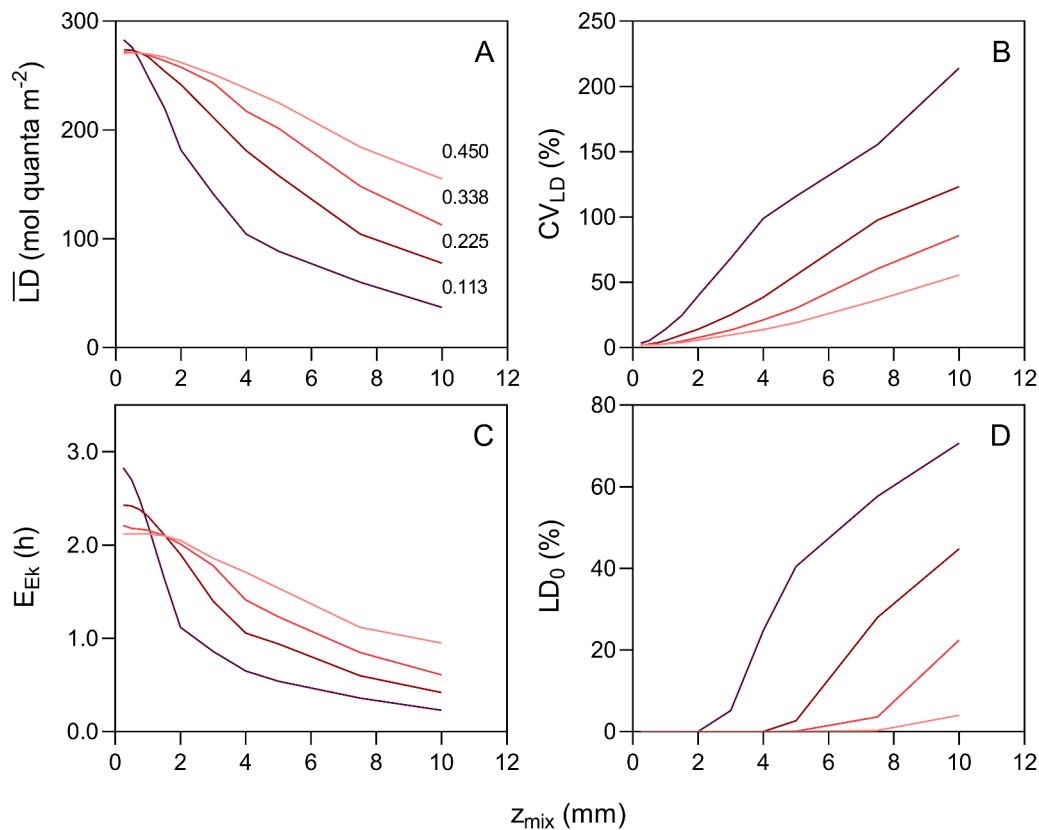
**Fig. 8.** Outputs of the model after running for 1000 days, for the four different tidal stages along the semi-lunar spring-neap tidal cycle. Histograms show the resulting relative frequency distribution of LD for the scenarios EPL (A-D), EPM-M (E-H) and EPM-NM (I-L), with indication of mean values ( $\bar{LD}$ ), coefficient of variation ( $CV_{LD}$ ) and percentage of days in the dark ( $LD_0$ ).

lack of motility to counteract their repositioning in the sediment column by external factors (tide, bioturbation), epipsammic cells can be expected to undergo continuous periods of several consecutive days in the dark, a situation unlikely to occur for epipelagic species.

A key factor justifying the difference in results produced for the EPL and EPM scenarios is naturally cell velocity. However, cell velocity is only meaningful when considered in relation to the distances needed to be covered by cells to significantly change their light exposure within the photic zone or, when starting from deeper layers, to reach the photic zone. By identifying and evaluating the relative importance of the various endogenous (cell motility, photoacclimation state) and exogenous (light incident and attenuation) factors, this study highlights that

what is critical for the effectiveness of motility in determining the light environment experienced by the cells is the relationship between cell velocity and the depths of the photic zone and of the mixing zone.

In the case of cells within the photic zone, it is the relationship between  $v$  and  $k_E$  that mostly determines the capacity to regulate light exposure. A steeper light gradient (higher light attenuation,  $k_E$ ) corresponds to a shallower photic zone and to shorter distances need to be covered by the cells to experience a significant change in received light. Inversely, for the same light attenuation, higher cell velocities enable cells to cover a larger range of light intensities in a short time. High cell velocities also favor coping with high frequency variability in incident light, such as due to passing clouds or sun flecks (for submerged sites).



**Fig. 9.** Generalized effects of mixing depth and cell velocity (numbers in panel A) and on the main outputs of the model regarding excessive light exposure ( $E_{Ek}$ , C) and LD: mean values ( $\overline{LD}$ , A), coefficient of variation ( $CV_{LD}$ , B) and percentage of days in the dark ( $LD_0$ , D). Simulations run only for the ST tidal scenario.

Considering realistic combinations of values for  $v$  and  $k_E$ , this study shows that vertical migration by epipelagic diatoms may be effective in helping cells regulate absorbed light, supporting the hypothesis that diatom motility is a key functional trait with high adaptive value. The effectiveness of vertical migration to regulate light exposure is benefited in the sedimentary environment, since a linear vertical displacement is expected to correspond to an exponential variation in received light intensity (Laviale et al., 2016), which may favor the detection and sensing of light gradients.

Also the relationship between  $v$  and  $z_{mix}$  appears crucial in conditioning the role of vertical migration in regulating experienced light. When the mixing depth is deeper than the photic zone, cells can be displaced to dark layers of the sediment, in which case gravity-driven motility is especially important to regain access to illuminated layers. In this context, cell velocity becomes critical to enable cells to escape the aphotic layers and reach the photic zone ('escape velocity'), as it determines the distance possible to cover before the next mixing event. Deeper mixing (higher  $z_{mix}$ ), especially if combined with a thin photic zone (high  $k_E$ ), requires higher cell velocities to compensate for the longer distance to cover. As cell velocity is biologically limited to a certain maximum value, deep mixing and high light attenuation conditions are expected to increase the inter-day variability in light dose received and the frequency of days in permanent darkness.

#### 4.2. Vertical migration constructs a light niche

A major result of this study is that vertical migration does not only cause epipelagic diatoms to experience higher mean light levels but also a substantially lower variability in the received light. This result has an important ecological significance, as it identifies cell motility as a form of counteracting the environmental stochasticity introduced by sediment mixing, supporting its adaptive value in the sedimentary intertidal

environment. The reduction of experienced variability in light exposure appears especially relevant in the intertidal environment, because it does not only contribute to avoid extreme light levels, but also minimize the synergistic effects of high light in conjunction with other extreme conditions occurring during low tide, such as desiccation (Coelho et al., 2009) or extreme salinities or temperatures (high or low; Frankenbach et al., 2020; Laviale et al., 2015)).

The ecological significance of diatom motility can be further considered in the light of the niche construction theory. Being defined in generic terms as the effects of the activity of organisms on their environment, the idea of niche construction is commonly associated to the modification of habitats by the behavior of animal species (Laland et al., 1999; Post and Palkovacs, 2009). The enhanced stability in light exposure conditions promoted by diatom vertical migration is defining of one of the expected consequences of niche construction, which is the buffering of perceived environmental variability (Laland et al., 2017). The behavioral regulation of light exposure can be thus seen as a niche-construction activity as it results in the modification of the environment perceived by the cells, making it more consistent and predictable, and within a narrower range of favorable conditions.

In the case of motile diatoms, however, niche construction takes place not as in the more common sense of organisms modifying their environment, but through the process of habitat selection, also recognized as a mean by which organisms regulate the environment they experience (Clark et al., 2020). It functions by the selection of a particular sub-set of microhabitats from the range of available environments and is expected to increase the fitness of the organisms by promoting a match between their traits and the experienced environmental conditions (Edelaar and Bolnick, 2019). Epipelagic diatoms use light-directed motility to select a limited range of light conditions, characterized by high light and low variability, that can thus be defined as a 'constructed light niche'. It may happen, however, that the selection

of light conditions through vertical migration may result in the concurrent limitation of the range of exposure to other environmental factors, that vary vertically in the sediment. This is the case of oxygen and pH (Brotas et al., 2003; Cook and Røy, 2006; Seródio et al., 2007) but also likely carbon and nutrients (Hochard et al., 2010; Vieira et al., 2016), all directly affected by diatom photosynthetic activity, and varying along the microscale of the photic zone of the sediment. This may result in the construction of an ecological niche characterized not just by a limited set of light conditions but of other ecological factors.

#### 4.3. Implications for productivity and photoacclimation

The predictions of the model in relation to experienced average daily light dose and its variability also have implications regarding photosynthetic rates and productivity. For the case of the EPL scenario, the consistent exposure of the cells to high light levels, but not exceeding  $E_k$  substantially or for prolonged periods, is expected to result in higher hourly and daily photosynthetic rates of individual cells. By predicting that motile cells spend most of their time under optimal light conditions, around  $E_k$ , biofilm-level primary productivity can thus be expected to be maximized. In contrast, non-motile or slowly motile cells under the EPM scenario, the inability to optimize light exposure through vertical migration may be expected (other things being equal) to result in lower productivity rates.

These characteristics of the light environment are critical for determining the photosynthesis carried out at the pre-defined photophysiological state of the cells. However, they may in turn be expected to have consequences back to the niche construction activity that cause them.

One major prediction of the niche construction theory is the possibility of a feedback loop between the modified environment and the organisms, resulting in a self-reinforced process (Laland et al., 2017). One way through which this may occur is by a reduction in adaptive phenotypic plasticity of organisms involved in niche construction. Because of the reduction in perceived environmental variability, functional traits associated to the modified environmental conditions are expected to show a reduced phenotypic variation (Edelaar and Bolnick, 2019; Laland et al., 2017). In the case of epipellic diatoms, such a process can be expected to take place regarding photoacclimation, involving the functional traits associated to the photophysiological use and response to changes in light intensity. Under the relatively invariable perceived light environment created because of vertical migration, epipellic cells may have less need to change their photoacclimation state. And because the selected light conditions are defined by their photoacclimation state in the first place, this particular state will tend to be maintained, through a self-reinforcing feedback loop. Being able to select light levels of the sediment column that match the light levels to which they are acclimated, their photoacclimation state will only be reinforced as no advantages come from changing it. In contrast, epipsammic diatoms are subjected to a much variable light environment, in which case they may frequently undergo short-term changes in photoacclimation state. It is thus expectable that, in comparison with the epipellic species, epipsammic diatoms may be selected for a larger photoacclimation capacity.

Another prediction of niche construction theory is that the feedback from niche construction activities and the environment may result in the reduction of the variability of the selective environmental gradients, making natural selection more stable, directed and consistent (Laland et al., 2017). Environment-buffering niche construction may thus gain an adaptive nature, modifying the selection for ecophysiological or behavioral traits and their associated gene frequencies (Clark et al., 2020).

In the case of epipellic diatoms, niche construction through vertical migration could have adaptive consequences for example by reinforcing, through the type of positive feedback described above, the selection for traits that favor the match between photophysiological traits and the

selected light microenvironment. If vertical migration enables exposure to high light levels, with the potential to promote higher photosynthetic rates and growth, then the selection for traits that enable to cope with high light, such as higher light-saturated photosynthetic rates (e.g. enhanced functioning of the Calvin cycle) or more efficient photo-protection (e.g. more efficient xanthophyll cycle and photosystem II repair) may be expected to increase. Furthermore, this may occur not just by the selection of traits that match the experienced environmental conditions, but also by reinforcing systematic and directed natural selection for the functional traits that enable cells to reach those conditions. Considering that the constructed light regime promotes more stable and optimal conditions for photosynthesis and growth, faster and more responsive species have an advantage over slower or immotile ones, which can increase the evolutionary pressure for motility-enhancing traits (e.g. frustule and raphe morphology, EPS production and composition). On the other hand, living under more stable light conditions may decrease the capacity to deal with variable light, further increasing the advantages in the ability to search for less variable light conditions, again favoring the selection for higher cellular motility.

Motility may be advantageous and likely selected for in fine sediments, where the movement of cells between sediment particles is possible. However, in coarser sedimentary environments, characterized by large interstitial spaces and low organic matter content, favoring the attachment of cells to the sediment particles to avoid being washed away, the selection for motility no longer exists and diatom communities are dominated by epipsammic, non-motile forms.

#### 4.4. Model assumptions

This study represents the first attempt to quantify how diatom motility affects their experienced light environment. Numerous studies have addressed the motility of diatoms but only a few provided estimates of distances covered by moving cells, based on cell velocity (Seródio, 2021). To our knowledge, none considered diatom motility in the context of the light gradients of the sediment photic zone in a quantitative manner, likely due to the difficulty in studying experimentally cell light exposure in micrometer-scale light gradients. This study addressed this question by developing and running a model based on available ecological data, allowing to construct realistic scenarios representative of the contrasting characteristics of epipellic and epipsammic diatom communities and their habitat. Nevertheless, a number of assumptions had to be considered:

- (i) The model was run only for a clear-sky scenario, not considering the common situation of passing clouds, that would introduce a larger variability in the outputs of the model. This option was made as the study was intended to focus on characteristics inherent to the sedimentary system, to better investigate the differences between the EPL and EPM scenarios. The use of natural time series of incident sunlight would obscure the underlying patterns resulting from the main factors under study.
- (ii) The model assumed that during submersion by high tide, no light is available to the diatoms, even if at the surface of the sediment. This is a common assumption (Daggers et al., 2018; Frankenbach et al., 2020; Seródio and Catarino, 2000) justified by the high turbidity of shallow estuarine water and the downward migration away from surface of diatoms before tidal flood.
- (iii) Although the exponential vertical attenuation of light is supported by extensive experimental data, the model did not consider two other factors that are expected to affect the light microenvironment available to the cells: self-shading due to light attenuation by other cells ( $k_E$  was assumed constant over depth and time) and changes in light spectrum, due to spectrally biased absorption by photosynthetic pigments. This option was chosen for simplicity and because of the lack of detailed data. However, although there is evidence that coarser sediments may be more homogeneous and with

less microalgal biomass than finer ones (Morelle et al., 2020), the main conclusions of the study would likely not be substantially affected, considering the very large differences observed between the EPL and EPM scenarios.

(iv) Sediment mixing was modelled by considering a complete homogenization from surface to  $z_{\text{mix}}$ . The resulting uniform distribution between  $z = 0$  and  $z = z_{\text{mix}}$  and the discrete separation between the mixed and the unmixed regions below is certainly a major simplification but was justified for simplicity and by the lack of data. Nevertheless, the assumption that the mixture depth is larger than the photic zone seems very plausible, especially for fine sediments (EPL scenario) considering the very thin photic zone. Also, a deeper mixing depth for coarser sediments (EPM scenario) is reasonable to expect considering that these sediments are less cohesive (Ubertini et al., 2015). The existing uncertainty on the values for  $z_{\text{mix}}$  was overcome by quantitatively comparing a wide range of mixing depths in combination with various cell velocities. Another assumption of this study was to consider mixing events for every day, while it is conceivable that significant mixing events may not occur for several days, and cells may stay at the same depth from one day to the next.

(v) Cell velocity was modeled as a function of light intensity based on the assumption that cells behave independently of each other, when it is conceivable that for dense biofilms cells closer to the surface will affect the light intensity and quality of the light reaching the cells positioned below (self-shading; see above). The model also did not consider the well-studied differential light (and spectral) sensitivity of the regions of the same diatom cell (Cohn et al., 2016), a factor that might help guide the cells in the heterogeneous light microenvironment formed within the sediment particles.

(vi) The responses of pennate diatoms to environmental factors are known to vary markedly between species. Species-specific responses have been documented for factors relevant for the modeling of diatom photobehavior such as cell velocity (Bertrand, 1990; Cohn and Weitzell, 1996; Du et al., 2012) and the response to light intensity (Cohn et al., 2004, 2015; Cohn and Weitzell, 1996; Du et al., 2012) and spectrum (Cohn and Weitzell, 1996; McLachlan et al., 2009). While this study considered the effects of cell velocity by running the model for a wide range of values, it did not address the effects of different light preferences (both in terms of motility and photosynthesis) nor consider how this diversity of responses might coexist in the same biofilm. Considering the large variation in the light response between species it is conceivable that each species constructs its own light niche, resulting in a species-specific use of the light gradients. The complexity introduced by species-specific responses might even be augmented due to the fact that diatom motility responses can be modulated by the presence of cells of a second species (Cohn et al., 2015, 2003).

## 5. Conclusions

The results of this study support the often-assumed hypothesis that motility enables epipelagic diatom forms to experience a significantly different light environment than their epipsammic counterparts. Considering realistic values for cell velocity, light penetration and mixing depth, the study shows that vertical migration may be expected to effectively enable epipelagic diatoms to experience a much more stable light regime, with higher daily light doses, than non-motile or slowly motile epipsammic forms. These, in turn, can be expected to experience a light regime characterized by the exposure to supersaturating light levels and to prolonged periods of darkness. The modeling approach here used allowed to identify the relationship between cell velocity and sediment light attenuation as the main factor determining the capacity of the diatom cells to behaviorally regulate light exposure. These results have important ecological significance, as they highlight the adaptive value of light-driven motility as a form of counteracting the high

variability of the estuarine intertidal environmental, and as a niche-construction activity, allowing epipelagic diatoms to regulate the environment they experience through a process of habitat selection.

## CRedit authorship contribution statement

**João Seródio:** Conceptualization, Methodology, Writing – original draft. **Alexandra Bastos:** Validation, Writing – review & editing. **Jérôme Morelle:** Validation, Writing – review & editing. **Silja Frank-ebach:** Validation, Writing – review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. João Seródio reports financial support was provided by FCT - Foundation for Science and Technology.

## Data availability

Data will be made available on request.

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