



## Effects of mixing-induced irradiance fluctuations on nitrogen uptake in size-fractionated coastal phytoplankton communities



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### ABSTRACT

In coastal waters subjected to strong tidal forcing, phytoplankton populations are exposed to highly variable light regimes. To grow under such fluctuating light environments, phytoplankton adjust their physiological properties. Here, we investigated nitrogen (N) uptake patterns in the western English Channel to determine whether phytoplankton modify their physiological processes involved in N uptake in response to changing irradiance conditions induced by spring-neap tidal cycles. Nitrate ( $\text{NO}_3^-$ ) and ammonium ( $\text{NH}_4^+$ ) uptake kinetics as a function of irradiance ( $V_N$ - $E$  curves) were assessed using  $^{15}\text{N}$  tracer techniques on two size fractions ( $<10$  and  $>10 \mu\text{m}$ ) of phytoplankton collected at 50% and 1% of surface irradiance during two spring-neap tidal cycles. Overall, the results showed that both small and large phytoplankton, whatever their vertical position in the water column, increased their maximum uptake capacity and their light utilization efficiency for the two N substrates following the decrease in vertical mixing intensity. Moreover, the improvement of irradiance conditions at neap tides was of greater benefit for the larger cells than for the smaller ones and was more favorable for  $\text{NO}_3^-$  uptake than for  $\text{NH}_4^+$  uptake. These findings show that the light regime fluctuation resulting from the relaxation of tidal mixing during spring-neap tidal cycle leads to profound physiological adjustments of N uptake processes in phytoplankton communities. They suggest that the changes in  $\text{NO}_3^-$  uptake by large phytoplankton associated with the fortnightly spring-neap tidal cycle can account for most of the deviation in background productivity in the western English Channel which is based on  $\text{NH}_4^+$  and is dominated by small cells. The dynamic light regime inherent to macrotidal coastal ecosystems could therefore determine, to a large extent, the importance of new vs. regenerated production as well as the size structure of the phytoplankton community.

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### 1. Introduction

In coastal waters, the intensity of vertical mixing exerts strong control on the growth of plankton primary producers and it has a profound impact on the structure of phytoplankton communities by mediating not only nutrient availability but also, and to a large extent, access to light (Huisman et al., 1999, 2004). Light availability varies strongly depending on both the vertical extent and the intensity of mixing processes as well as on the timescales of stabilization–destabilization patterns in the water column. To survive in such widely fluctuating light environment, phytoplankton populations can evolve, according to light-acclimation theory, by

adjusting their optical and physiological properties (Falkowski and LaRoche, 1991). Field and experimental data have provided detailed knowledge on acclimation strategies in response to irradiance changes, including regulation of intracellular pigment content (Dubinsky and Stambler, 2009; Shibata et al., 2010), changes in the stoichiometry of elements required for light harvesting and photosynthesis such as Fe or Mn (Raven, 1990; Sunda and Huntsman, 2004) or elements associated with a variation in growth rate such as C, N and P (Sterner and Elser, 2002; Dickman et al., 2006; Finkel et al., 2006). The physiological adjustments of phytoplankton cells in response to changes in irradiance are often characterized with kinetic parameters derived from relationships between the rates of C fixation and irradiance (the so-called  $P$ - $E$  curve) (MacIntyre et al., 2002; Behrenfeld et al., 2004; Dubinsky and Stambler, 2009). These photo-physiological indices have been widely used to examine the underlying biophysical, biochemical

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and metabolic processes controlling the photosynthetic activity of phytoplankton in their natural environment (Sakshaug et al., 1997). Interestingly, it has been highlighted that both the light-saturated rate of photosynthesis ( $P_{max}$ ) and photosynthetic efficiency ( $\alpha$ ) are strongly affected by photoacclimation processes during the various timescales of the tidal cycle, i.e., the high–low tide cycle (Lizon et al., 1995; Jouenne et al., 2005) and the spring–neap tidal cycle (Lizon et al., 1998). The use of N compounds by phytoplankton, like C fixation, is dependent on light as an energy source, either directly or indirectly through photosynthesis (MacIsaac and Dugdale, 1972; Syrett, 1981). One can, therefore, also expect a physiological regulation of the processes involved in N uptake in response to rapid irradiance changes. The N uptake response to irradiance can be described by a modification of the model used for the  $P$ – $E$  curve (Platt et al., 1980). This relationship is affected by the form of N taken up (Muggli and Smith, 1993; Kudela et al., 1997; Kudela and Cochlan, 2000; Fan and Glibert, 2005), by the physiological status of the population (Cochlan et al., 1991b; Clark et al., 2002; Flynn et al., 2002), and appear to vary with cell size (Frenette et al., 1998; Maguer et al., 2011) and to differ among specific groups (Clark et al., 2002; Lim et al., 2006). To our knowledge, no study has examined whether physiological adjustments modify these relationships in fluctuating light conditions, such as those induced by the tidal cycle.

In the coastal waters of the western English Channel, physical forcing induced by tidal currents and wind action is strong enough to prevent seasonal stratification, so that phytoplankton cells are continuously entrained below the euphotic zone, reducing the light available to them. As a result, phytoplankton production, as measured by C and N uptake, appears to steadily increase concomitantly with incident light and the euphotic layer depth (Boalch et al., 1978; L'Helguen et al., 1996). These observations lead to the conclusion that N uptake is strongly limited by light throughout the year (L'Helguen et al., 1996). It was also postulated that the high contribution of ammonium ( $\text{NH}_4^+$ ) to total N uptake, as well as the dominance of small sizes in phytoplankton communities is controlled by physical forcing, and thus indirectly by the light regime inherent in such a system (Wafar et al., 2004). Recently, size-dependent uptake kinetics of nitrate ( $\text{NO}_3^-$ ) and  $\text{NH}_4^+$  as function of irradiance have provided support for these hypotheses (Maguer et al., 2011). Although the western English Channel is defined as a well-mixed system, the decrease of tidal currents from spring to neap tides can lead to weak and transient stratification (L'Helguen et al., 1996), providing different light conditions for phytoplankton in the water column. Under such conditions, a drop in  $\text{NO}_3^-$  concentration in the upper layer is observed in phase with a rapid increase in large-size phytoplankton biomass (L'Helguen et al., 1996), suggesting that this new light regime is more favorable for  $\text{NO}_3^-$  use by the largest phytoplankton.

The present study sought to examine N uptake patterns in the western English Channel to determine whether natural phytoplankton population adjusts the physiological processes involved in N uptake in response to the fluctuating irradiance conditions induced by the tidal cycle. Our aim was to assess the importance of light regime fluctuations in controlling the nature of the primary production (new vs. regenerated production, *sensu* Dugdale and Goering, 1967) and the size structure of phytoplankton communities in macrotidal coastal ecosystems. We addressed these questions by examining the kinetics of N uptake according to irradiance ( $V_N$ – $E$  curves) at high frequency over the May–June period following the periodicity of the spring–neap tidal cycle. Since physiological adjustments may vary with cell size and N substrate, we tested for differences between small and large size fractions (<10  $\mu\text{m}$  and >10  $\mu\text{m}$  of size) and between  $\text{NO}_3^-$  and  $\text{NH}_4^+$ .

## 2. Materials and methods

### 2.1. Field site and sampling strategy

Experiments were conducted at a study site investigated previously (48°45'N, 3°57'40"N; mean depth: 45 m; L'Helguen et al., 1996; Wafar et al., 2004; Maguer et al., 2011). Data were obtained between 12 May and 20 June 2005 covering two spring–neap tidal cycles. Sampling was performed between 7:00 a.m. and 8:00 a.m. local time and around mid-tide to minimize effects potentially due to daily high–low tidal cycle variability. Water samples were collected with a sampling interval of 2–6 days for typical hydrographic (temperature), chemical ( $\text{NO}_3^-$  and  $\text{NH}_4^+$ ) and biological [particulate organic nitrogen (PON) and carbon (POC)] parameters and with a 6–8 day sampling interval for N uptake experiments (Table 1). Before each sampling, a seabird SBE 19 system equipped with a quantum sensor (Biospherical Instruments) was used to describe the vertical structure of the water column and acquire the vertical profile of photosynthetically active radiation (PAR, 400–700 nm). Water samples were obtained at depths of 50% and 1% of surface PAR ( $E_0$ ) using 5 or 30 L PVC Niskin bottles.  $^{15}\text{N}$  experiments were started within 1 h after taking water samples.

### 2.2. Chemical and biological analysis

$\text{NO}_3^-$  concentrations were measured with a Technicon Auto-Analyzer II, following the procedures outlined in Wood et al. (1967).  $\text{NH}_4^+$  concentrations were determined manually in triplicate using the indophenol blue method (Koroleff, 1970). Analytical precisions were  $\pm 0.05$  and  $\pm 0.02 \mu\text{mol L}^{-1}$  for  $\text{NO}_3^-$  and  $\text{NH}_4^+$ , respectively. PON and POC concentrations were measured on total and size-fractionated (<10  $\mu\text{m}$ ) samples. They were estimated directly after filtration (<100 mm Hg) of 1 L of seawater on pre-combusted (4 h at 450 °C) Whatman 25 mm GF/F glass fiber filters for the total phytoplankton sample and after filtration through a 10  $\mu\text{m}$  pore size polycarbonate filter (gentle suction) for the <10  $\mu\text{m}$  size fraction. The GF/F filters were kept frozen. Prior to the in-lab analysis (see below), the filters were placed in a drying oven (60 °C) for 24 h. PON and POC concentrations for >10  $\mu\text{m}$  size fraction were obtained by subtracting the <10  $\mu\text{m}$  size fraction values from the total PON and POC, respectively.

### 2.3. Nitrogen uptake versus irradiance experiments

N uptake rates were estimated from the accumulation of  $^{15}\text{N}$  isotopically labeled dissolved N substrates in the particulate material. Each water sample was dispensed into a series of eight acid-clean polycarbonate Nalgene bottles (2 L) to which  $^{15}\text{N}$  substrates in

**Table 1**

Physical characteristics of the water column during the study.  $K_z$  is the light attenuation coefficient ( $\text{m}^{-1}$ ),  $Z_e$  the euphotic zone depth (in m),  $E_p$  the potential energy (in  $\text{J m}^{-3}$ ). \* indicates the days on which the  $^{15}\text{N}$  experiments were conducted.

	Tidal range (m)	$K_z$ ( $\text{m}^{-1}$ )	$Z_e$ (m)	$E_p$ ( $\text{J m}^{-3}$ )
12 May*	5.5	0.17	22	0.2
18 May*	3.0	0.20	24	6.1
25 May*	7.4	0.15	24	0.1
27 May	6.7	0.17	38	0.2
1 June*	4.6	0.10	43	4.0
3 June	5.2	0.10	41	0.2
8 June*	6.0	0.16	38	0.1
10 June	5.3	0.17	35	0.2
16 June*	3.4	0.13	35	9.5
20 June	5.6	0.13	36	0.2

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