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Photosynthetic parameters and primary production, with focus on large phytoplankton, in a temperate mid-shelf ecosystem

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ABSTRACT

Annual variability of photosynthetic parameters and primary production (PP), with a special focus on large (i.e. >2 μm) phytoplankton was assessed by monthly photosynthesis-irradiance experiments at two depths of the southern Bay of Biscay continental shelf in 2003. Integrated chl *a* (22–198 mg m^{-2}) was moderately dominated by large cells on an annual basis. The March through May dominance of diatoms was replaced by similar shares of dinoflagellates and other flagellates during the rest of the year. Variability of photosynthetic parameters was similar for total and large phytoplankton, but stratification affected the initial slope α^B [0.004–0.049 mg C mg chl a^{-1} h^{-1} (μmol photons m^{-2} $s^{-1})^{-1}$] and maximum photosynthetic rates P_m^B (0.1–10.7 mg C mg chl a^{-1} h^{-1}) differently. P_m^B, correlated positively with α^B only for the large fraction. P_m^B tended to respond faster to ambient irradiance than α^B, which was negatively correlated with diatom abundance in the >2 μm fraction. Integrated PP rates were relatively low, averaging 387 (132–892) for the total and 207 (86–629) mg C m^{-2} d^{-1} for the large fraction, probably the result of inorganic nutrient limitation. Although similar mean annual contributions of large phytoplankton to total values were found for biomass and PP (~58%), water-column production to biomass ratios (2–26 mg C mg chl^{-1} d^{-1}) and light utilization efficiency of the >2 μm fraction (0.09–0.84 g C g chl^{-1} mol $photons^{-1}$ m^2) were minimum during the spring bloom. Our results indicate that PP peaks in the area are not necessarily associated to maximum standing stocks.

1. Introduction

Phytoplankton is the foundation of marine food webs in pelagic waters and consequently its biomass, usually expressed as chlorophyll *a* concentration, is widely used as an indicator of ecosystem productivity and trophic status. However, photosynthetic carbon fixation is also dependent on light, nutrient availability and community composition among other factors, indirectly related to standing stocks. In temperate waters the predictable nature of the first two factors associated with seasonal variations in water column stability also influence largely the composition of phytoplankton dominant assemblages (e.g. Cullen et al., 2002). However, due to the transient nature of phytoplankton blooms, changes in community composition are much more difficult to predict than most physico-chemical properties. A marked dominance of chain forming diatoms in the algal blooms occurring in late winter-early spring and autumn in temperate coastal waters is well documented (Ianson et al., 2001; Winder and Cloern, 2010). For the rest of the year, non-diatomaeous pico- and nanophytoplankton and occasionally big dinoflagellates (Cullen et al., 2002) dominate. Reports on seasonal changes in bulk and size-fractionated biomass and community composition have increased largely over the last decades. Fewer descriptions of complete annual cycles of pelagic photosynthesis and primary production are available. In European waters, the studies we are aware of are mostly restricted to inshore waters (Tillmann et al., 2000; Marty and Chiavérini, 2002; Cermeño et al., 2006; Gameiro et al., 2011).

Photosynthesis-irradiance relationships or *P-E* curves are a convenient and widespread way of describing the physiological and acclimation response of phytoplankton assemblages to environmental changes (Sakshaug et al., 1997). Previous research has shown that photosynthetic parameters differ in the time-scales of response to new conditions established within the water column (Lewis et al., 1984). For instance, Geider (1993) noticed that

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stratification triggers changes in maximum chlorophyll normalized photosynthetic rate (P^B_m) but is usually less visible in the slope of the light-limited region (α^B), claimed to be more constant than the former parameter (Behrenfeld et al., 2004; but see Cullen and Lewis, 1988). The frequent covariation of both photosynthetic parameters, extensively reviewed by Behrenfeld et al. (2004), has intrigued aquatic phycologists, but we still lack a complete mechanistic explanation for the so-called E_k-independent (i.e. strong positive correlation between P^B_m and α^B) or E_k-dependent (no P^B_m-α^B covariation) variability. Saturation irradiance (E_k) in turn frequently reflects current or recent light regimes (Tilstone et al., 2003).

Butrón et al. (2009) have reviewed available studies on size-fractionated phytoplankton biomass and primary production in nearshore and estuarine ecosystems of the Bay of Biscay, but we lack information about offshore waters. They concluded that bays and the outer areas of large estuaries usually exhibit marked phytoplankton peaks in spring, when the most favourable conditions for the development of phytoplankton are attained, since irradiances are high enough by that time and nutrients can become limiting in summer. However, on an annual basis riverine nutrient inputs are sufficient to sustain dominance by large (i.e. >2 μm) cells. In the southern Bay of Biscay open continental shelf, an annual cycle of photosynthetic carbon fixation by picophytoplankton and its relationship with community structure and growth rates were already described in Morán (2007), who concluded that approximately half of total primary production was accounted for by the smallest size-class. Here, we focus on the photosynthetic performance of large cells and the whole phytoplankton assemblage. The objectives of this study are 1) to describe and analyze seasonal variations in photosynthetic performance and primary production rates of total phytoplankton and the fraction >2 μm in relation to water-column properties, and 2) to explore the potential of intra-annual variability for predicting the total amount of organic carbon entering the food web using chlorophyll and environmental variables.

2. Methods

2.1. Environmental variables

Physico-chemical variables were measured and biological samples were collected at a continental shelf station (43.7°N, 5.6°W, 110 m depth) from January to December 2003 as detailed in Morán (2007). This is the central station of the monthly RADIALES transect off Xixón in the central Cantabrian Sea (southern Bay of Biscay) on board the RV 'José de Rioja. Vertical profiles of temperature and salinity were obtained with a SeaBird 25 CTD probe and photosynthetically active radiation (PAR, 400–700 nm) was measured with a Biospherical QSP-2200 spherical quantum sensor. After calculation of the vertical light extinction coefficients (K_d), optical depths (ζ) for the water samples taken for the photosynthetic parameters experiments were determined as K_d z, with z as the original depth. Actual daily surface irradiance (PAR) on the date of the monthly experiments (E_0) was measured with a LI-192SA (LI-COR) quantum sensor, ranging from 10.0 to 38.4 mol photons m^{-2} d^{-1}. Additionally, climatological monthly values of PAR based on horizontal insolation averaged for 22 years (NASA) were used as the expected irradiance at the surface without cloud cover ($E_{0\ exp}$). These values were higher than the measured E_0 with heavily overcast skies on three occasions, but otherwise there was a very good correspondence between both surface daily PAR estimates ($r = 0.99$, $p << 0.001$, $n = 9$).

For chlorophyll *a* concentration (chl *a*), 100 ml samples taken at 8 discrete depths (0, 10, 20, 30, 40, 50, 75 and 100 m) were sequentially filtered through 20, 2 and 0.2 μm Millipore polycarbonate filters (47 mm diameter). The filters were kept frozen at −20 °C until analysis. Usually within 1 wk they were then placed in 90% acetone at 4 °C for 24 h and the fluorescence of the extract was measured without acidification using a Perkin Elmer LB-50s spectrofluorometer (excitation at 440 nm, emission at 685 nm), periodically calibrated with pure chl *a* solution. Chl *a* in the picoplanktonic, nanoplanktonic, and microplanktonic size fractions was estimated as the amounts retained on the 0.2, 2 and 20 μm filters, respectively. Additionally, 100 ml chl *a* samples from the two depths of the *P-E* relationships determinations were taken and processed as detailed in Morán (2007). Samples for analyzing nitrite, nitrate, phosphate and silicate were immediately frozen and their concentrations determined in the laboratory with a Technicon autoanalyzer following standard procedures (Grasshoff et al., 1999).

2.2. Large phytoplankton community composition

Samples for large (large nano-plus microplankton) phytoplankton community composition were taken monthly at 0, 30 and 75 m. 100 ml were collected in brown glass bottles, preserved with acid Lugol's solution and kept in the dark until analysis under an inverted microscope using the Utermöhl (1958) technique. Diatoms, dinoflagellates, flagellates and ciliates were quantified and differentiated into size classes. Interpolation was used for deriving the abundance of the 4 broad taxonomical groups at the depth of the subsurface chlorophyll maximum when sampling depths were not coincident with those of the *P-E* experiments. Integrated abundances from 0 to 75 m were also calculated (cells m^{-2}). Total phytoplankton includes the picoplanktonic groups analyzed by flow cytometry and described in detail in Morán (2007). Some small cells within the nanoplankton size-class (i.e. 4–8 μm in diameter) may have been missed by combining both counting methods but we believe that total cell number estimates were close to actual values.

2.3. Photosynthetic parameters

Samples for the *P-E* experiments were collected at approx. 2 m and the depth of the subsurface chl *a* maximum (Morán, 2007), hereinafter referred to as 'surface' and 'deep'. Full details of the experimental setup, irradiance measurements within the incubator and sample processing are given in Morán (2007). The method used for separating large (nano-plus microphytoplankton) from picophytoplankton carbon fixation involved specific *P-E* curve fitting for three fractions, total, >2 and <2 μm. Two different models were used to fit chl *a*-normalized hourly primary production rates, depending on the presence [Platt et al., 1980, Eq. (1)] or absence of photoinhibition [Webb et al., 1974, Eq. (2)]:

$$P^B = P^B_s\left[1 - \exp\left(-\alpha^B E / P^B_s\right)\right]\left[\exp\left(-\beta^B E / P^B_s\right)\right] \quad (1)$$

$$P^B = P^B_m\left[1 - \exp\left(-\alpha^B E / P^B_m\right)\right] \quad (2)$$

in which P^B is the chl.*a*-normalized photosynthetic rate (mg C mg chl a^{-1} h^{-1}), P^B_m is the maximum chl.*a*-normalized photosynthetic rate (same units as P^B; P^B_m is calculated as $[P^B_m \times (\alpha^B/(\alpha^B + \beta^B)) \times (\beta^B/(\alpha^B + \beta^B)]^{\beta B/\alpha B}$ in Platt's et al. model, with P^B_s as the maximum chl.*a*-normalized photosynthetic rate without photoinhibition), α^B is the initial, light-limited slope [mg C mg chl a^{-1} h^{-1} (μmol photons m^{-2} $s^{-1})^{-1}$], β^B is the photoinhibition parameter (same units as α^B), *E* is the experimental irradiance (μmol photons m^{-2} s^{-1}) and E_k is the saturation irradiance (same units as *E* and calculated as P^B_m/α^B).