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Spatial and temporal dynamics of size-structured photosynthetic parameters (PAM) and primary production (^{13}C) of pico- and nano-phytoplankton in an atoll lagoon

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ABSTRACT

Atoll lagoons display a high diversity of trophic states due mainly to their specific geomorphology, and probably to their level and mode of human exploitation. We investigated the functioning of the Ahe atoll lagoon, utilized for pearl oyster farming, through estimations of photosynthetic parameters (pulse amplitude modulation fluorometry) and primary production (^{13}C incorporation) measurements of the size structured phytoplankton biomass (<2 μm and >2 μm). Spatial and temporal scales of variability were surveyed during four seasons, over 16 months, at four sites within the lagoon. While primary production (P) was dominated by the picophytoplankton, its biomass specific primary productivity (P^B) was lower than in other atoll lagoons. The variables size fraction of the phytoplankton, water temperature, season, the interaction term station * fraction and site, explained significantly the variance of the data set using redundancy analysis. No significant trends over depth were observed in the range of 0–20 m. A clear spatial pattern was found which was persistent over the seasons: south and north sites were different from the two central stations for most of the measured variables. This pattern could possibly be explained by the existence of water cells showing different water residence time within the lagoon. Photoacclimation strategies of the two size fractions differed through their light saturation coefficient (higher for picophytoplankton), but not through their maximum photosynthetic capacity (ETR_{max}). Positive linear relationships between photosynthetic parameters indicated that their dynamic was independent of light availability in this ecosystem, but most probably dependent on nutrient availability and/or rapid changes in the community structure. Spatial and temporal patterns of the measured processes are then further discussed in the context of nutrient availability and the possible role of cultured oysters in nutrient recycling.

1. Introduction

Atolls are ring-shaped coral reefs, each enclosing a lagoon, and are characterized by a very small land area compared to the total area. Most of these coral reef ecosystems are situated in the Pacific or Indian ocean under tropical or sub-tropical climates (Kinsey and Hopley, 1991). Atoll lagoons are highly productive ecosystems compared to the oligotrophic surrounding waters and often support significant aquaculture production (e.g. pearl oyster farming) and fisheries (Sournia and Ricard, 1976). The atoll geomorphology and its correlated water residence time greatly influence its trophic status and food web organization (Pagès et al., 2001). As their geomorphology differs from one another, this leads to a wide range of lagoon ecological functioning; each lagoon being a stable state of a given trophic state (Dufour and Harmelin-Vivien, 1997).

Atoll lagoons can be viewed as continuous reactors in the oligotrophic ocean, efficiently processing the low nutrient tropical waters (Furnas et al., 1990; Hatcher, 1997). In atoll lagoons with greater depth than classical coral reef ecosystems, biomass of phytoplankton is usually low (between 0.2 and 0.6 μg Chl a L^{-1}), but provides most of the total primary production with high rates of biomass specific primary production (from 2.6 to 21 mg C mg Chl a^{-1} h^{-1}, Charpy et al., 1997). Autotrophic picoplankton (<2 μm) such as cyanobacteria (*Synechococcus* and *Prochlorococcus* species) and picoeukaryotes accounts for most of the biomass (usually >80%) and most of the primary production (>60%) of the phytoplankton; the remaining part being carried out by cells of larger sizes belonging to nanophytoplankton such as Dinophyta, Haptophyta and diatoms (Delesalle et al., 2001).

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In order to define an atoll lagoon typology, Delesalle and Sournia (1992), and later Charpy et al. (1997) and Pagès et al. (2001), compared the trophic state of numerous atoll lagoons (30 atolls for the most complete study). At this macroscopic scale, they found that water residence time (i.e. the opposite of water renewal rate) and biomass of phytoplankton were positively correlated between atolls. Torréton et al. (2002) observed the same pattern for primary production on a more restricted number of atolls (12). Besides these, studies of spatio-temporal variability within single atolls are scarce. Torréton et al. (2002) stated that there were no spatial or seasonal variations in primary production within 12 atoll lagoons. On the contrary, Delesalle et al. (2001) recorded spatial heterogeneity in phytoplankton biomass during some seasons in Takapoto atoll. Actually, only one large data set incorporating spatio-temporal variability (on a monthly scale) of phytoplankton biomass and primary production has so far been published (Takapoto and Tikehau atolls; Charpy, 1996). The spatio-temporal patterns were neither presented nor discussed in this study because all sites were pooled horizontally. Water residence time varies daily due to differences in swell, wind or tide conditions (Andréfouët et al., 2001), and varies spatially within atoll lagoons depending on water circulation (Dumas et al., 2012). This may generate significant variations in the trophic state of a single atoll in its temporal and spatial components, as observed in New Caledonia lagoon (Torréton et al., 2007, 2010).

Tuamotu atoll lagoons host highly productive pearl oyster (*Pinctada margaritifera*) farming. Oysters are cultivated on suspended ropes so that these suspension feeders can access the pelagic environment food sources. Pearl oysters are able to process seston from 5 to 7 μm (Pouvreau et al., 2000). Consequently, they are not sustained directly by the main compartment of phytoplankton i.e. picoplankton. Mixotrophic and heterotrophic cells serve as a trophic link between picoplankton and the oysters (Loret et al., 2000). In the size range of cells that can be processed by oysters, carbon concentration of hetero-mixotrophs and autotrophs are in the same order of magnitude (Loret et al., 2000). Estimating primary production of the larger cell (>2 μm nanophytoplankton) is crucial in evaluating the carrying capacity of these lagoon atolls for filter feeders and also for aquaculture. In addition, the introduction of cultured bivalves into an ecosystem can lead to complex spatio-temporal patterns with local depletion of seston (Officer et al., 1982; Prins et al., 1995) and localized increases in nutrient regeneration (Grangeré et al., 2010). Hence, the primary productivity can be increased at the costs of the filtered and regenerated biomass.

The aim of our study was to determine the photosynthetic parameters and the primary production of the size structured phytoplankton biomass (<2 μm and >2 μm) of an atoll lagoon exploited for pearl oyster farming (Ahe atoll). Our study was the first to pay attention to the spatial (lagoon surface and depth) together with temporal (seasonal and day to day) variations. We hypothesized that geomorphology (and subsequent water residence time and water circulation) and aquaculture activities of the Ahe atoll, may lead to differences in primary production compared to previous studied atolls. In addition to traditional incubation of carbon isotopes, we used the pulse amplitude modulation (PAM) fluorometry method, based on variable chlorophyll fluorescence of photosystems II (PSII), which allows fast measurements of the electron transport rate (ETR) and subsequent photosynthetic parameters, to unravel the physiological and photoacclimation status of the phytoplankton.

2. Materials and methods

2.1. Study site

The Ahe atoll (14.5° S, 146.3° W) is located in the northwestern part of the French Polynesia Tuamotu Archipelago 500 km northeast of the main island, Tahiti. The lagoon has a surface area of about 142 km^2, and a mean depth of 41.7 m, with several deeper areas around 70 m. Ahe is defined as a semi-enclosed atoll (Fig. 1). One active pass is located in the western part of the lagoon (209 m width and 10 m deep) and several reef-flat spillways (30 cm deep on average) are distributed along the reef's rim (ca 5% of the total perimeter), mostly in the southern part of the lagoon (Dumas et al., 2012). The average water residence time is estimated at 252 days (Dumas et al., 2012). Ahe lagoon supports an important pearl oyster aquaculture industry. In 2008, there were 86 farms, but after the dramatic fall in the price of pearls, there remained only 65 farms at the end of 2010 (Lo-Yat A., pers. com.).

2.2. Sampling design

Four different surveys were conducted in May (14, 16, 20 and 23) and October (16 and 20) 2008, and February (17, 21 and 24), and August (20, 21 and 24) 2009. Samples were collected from three different depths (0.5 m, 10 m and 20 m), at four different sites (L01, L03, L09 and L11), along a northeastern/southwestern transect (Fig. 1), giving a total of 12 water samples per sampling day. Two to four daily samplings were carried during each season, between 8 am and 10 am and on the same date. On one occasion in August 2009, sites were not sampled on the same date: L01 and L03 on the 20th; L09 and L11 on the 21th. Samples were taken using a Niskin bottle (5 L), and kept in plastic bags in the dark until further processing.

2.3. Irradiance and water temperature

Vertical profiles of water temperature were measured using a YSI 600 probe coupled to an ultra miniature light intensity recorder (MDS-MkV/L, Alec electronics). Irradiance was also measured continuously using the same equipment cis above close to the site L11 at a depth of 5 m.

2.4. Size-structured primary production

The stable isotope ^{13}C was used to measure primary production. Polycarbonate Nalgene flasks (600 mL) were filled from the plastic bags kept in the dark within 2 h of sampling with 0.6 mL of ^{13}C-labeled sodium bicarbonate solution added (6 g of $NaH^{13}CO_3$, 99% ^{13}C, in 250 mL of de-ionized water, Eurisotop). The final concentration of ^{13}C in each bottle was 285.7 μmol $^{13}C\ L^{-1}$ on average. Bottles from the different sites were all incubated at the same site (L11) at their respective sampling depth. Incubation started between 10 am and 11 am and lasted between 4 and 6 h. After incubation, 300 mL of the flasks contents were filtered onto a precombusted 25 mm Whatman GF/F glass filter (total) and 300 mL were fractionated by serial filtration onto a 2 μm Millipore polycarbonate filter and GF/F for the <2 μm size class. At the end of filtration, 100 μL of 0.5 N HCl were added to the filters to remove any carbonates. After 3 h, the filters were rinsed with distilled water to remove the acid and dried for 24 h at 60 °C. Isotopic enrichment ($\delta^{13}C$) and carbon content were measured 1 month later using an elemental analyzer (Eurovector) for particulate C (% C) coupled to an isotope ratio mass spectrometer (IRMS GV Isoprime instrument) for C isotopes. Analytical precision was estimated at 0.05 for $\delta^{13}C$, and 0.005 for % C based on repeated internal standards. Carbon fixation rates (primary production: P) were calculated according to Slawyk et al. (1977) using the natural $\delta^{13}C$ for phytoplankton of 1.089. Biomass specific primary production rates (P^B) were calculated using the chlorophyll *a* concentration data carried out on the same data set by Charpy et al. (2012).