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Microphytobenthic primary production as ^{14}C uptake in sublittoral sediments of the Gulf of Trieste (northern Adriatic Sea): Methodological aspects and data analyses

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Abstract

From January 2003 to December 2004 microphytobenthic primary production was estimated both from in situ (MPPs) and in the laboratory (MPPp) ^{14}C-incubation of slurries collected in a coastal site of the Gulf of Trieste (northern Adriatic Sea). MPPs values varied from -7.54 ± 3.12 to 34.59 ± 7.66 mg C m^{-2} h^{-1} over the whole period. The lowest MPPs were observed in November 2003 and August 2004, while the highest MPPs in July 2003 and May 2004, in correspondence with high PAR at the bottom. Significant correlations between MPPs and the microphytobenthic biomass (BIOM) ($r = 0.75$, $p < 0.001$), between MPPs and PAR at the bottom ($r = 0.54$, $p < 0.01$) and between MPPs and OXY ($r = 0.50$, $p < 0.05$) were revealed. MPPp values were higher than MPPs ones in 15 out of 23 observations, with the highest MPPp recorded in July 2003. At 17 m depth a seasonal pattern of sampling months was revealed by the cluster analysis. The role of abiotic parameters in determining this seasonal pattern was highlighted by the PCA, with the first axis correlated with MPPs and PAR, and the second one with temperature. Applying the fuzzy sets it resulted that spring months showed a higher degree of membership with MPPs, summer months with temperature and autumn–winter months with OXY. The microphytobenthic community did not seem to be photosynthetically active throughout the study period. From August–September to December low or negative MPPs values were recorded. We infer that during these months a shift from the autotrophic to heterotrophic metabolism of the benthic microalgae occurred in correspondence with low PAR and/or high temperature at the bottom. Despite the progressive lowering of the trophy of the study area occurred during the last 20 years, we found higher primary production values than those estimated two decades earlier.

Keywords: ^{14}C uptake; benthic diatoms; microphytobenthos; primary production; northern Adriatic Sea; slurry technique

1. Introduction

The importance of benthic microalgae for ecosystem primary production on a global scale was underlined by a compilation based on 85 worldwide studies (Cahoon, 1999). Before that several reviewers have attempted to estimate the contribution of benthic microalgal production to the total oceanic production. Martin et al. (1987) and Longhurst et al. (1995) estimated that 0.7% of the total oceanic production and 2.4–3.7% of the continental shelf production is due to benthic microalgae. There is the need to evaluate the magnitude and distribution of benthic microalgal production and biomass in continental shelf and other subtidal, neritic ecosystems and to consider the broader implications of this evaluation (Cahoon, 1999 and references therein).

There is not yet a standard method for measuring microphytobenthic primary production. Most studies quantifying

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benthic microalgal production have used some variant of the light–dark chamber method and measurements of either dissolved oxygen flux or uptake of ^{14}C-labelled substratum (Cahoon, 1999). Non-destructive methods as different oxygen sensing techniques (Glud et al., 2000) and variable fluorescence techniques as Pulse Amplitude Modulated fluorescence (Schreiber et al., 1986) are now widely used to determine high-resolution distribution of microphytobenthic photosynthesis in time and space. However, microelectrodes are fragile and require delicate instrumentation that complicates in situ studies while fluorescence techniques still offer only relative photosynthetic rate measurements. Extensive replications are needed to quantify the spatial variability when estimates are scaled up to larger areas (Migné et al., 2004).

The use of ^{14}C tracer to estimate primary production in sediments was applied for the first time by Grøntved (1960) who processed the upper 2 cm of sediment. Grøntved's method was modified by Gargas (1970) who considered only the surface 2 mm of the sediment inoculating $H^{14}CO_3^-$ in the light and in the darkness. It is generally known that a dark exchange of CO_2 takes place which has nothing to do with photosynthesis. In situ, where many organisms are present together with the autotrophic algae, dark fixation may become relatively high when very low production is measured. For this reason, dark bottles are employed in addition to the ordinary clear bottles and the dark fixation rates are subtracted from the ordinary measurements (Steemann-Nielsen, 1963). Unlike the oxygen method where oxygen uptake in the dark bottle does represent respiration, the ^{14}C uptake in the dark bottle does not. It measures two components: active (non photosynthetic incorporation of ^{14}C, inhibited in the light) and inactive fixation (adsorption of ^{14}C onto the cell walls). Dark incubations always indicate a positive carbon uptake (Legendre et al., 1983). Especially when dark fixation constitutes a sizable fraction of the total carbon fixed, e.g. in an oligotrophic pelagic system such as the Gulf of Trieste (Fonda Umani et al., 2004; Paoli et al., 2006), it is common to find dark fixation equal to light fixation (Morris et al., 1971). Moreover, since the process of dark carbon fixation is at least partially under the influence of enzymes, the dark fixation can be expected to be influenced by temperature. Legendre et al. (1983) found that ^{14}C incorporation in darkness is a function of temperature: higher the temperature to which algae are exposed during dark incubation, higher the dark fixation.

Considerable published information exists describing intertidal and shallow subtidal microphytobenthic productivity. However, corresponding description of sites >15 m in depth are limited (Gillespie et al., 2000 and references therein). The applied methods and problems involved in estimating the benthic primary production in subtidal ecosystems are different than those encountered in mudflats. We found a paucity of exhaustive primary production ^{14}C methodology descriptions in the sediment matrix. Measuring productivity in sediment samples collected in the field and returned to the laboratory has been a frequent practise. It is highly likely that this approach introduces artefacts of light quality, porewater quality and temperature (Cahoon, 1999). The light and dark HCO_3^- fixation of intact cores with $H^{14}CO_3^-$ added to the water overlying the sediment could solve the problems of changed light conditions and interrupted fluxes. However, large changes in pH at the sediment surface during illumination indicate that the assumption of similar HCO_3^- specific activities in the porewater and in the overlying water may not hold (Revsbech and Jørgensen, 1981 and references therein). All these shortcomings can be avoided by processing the collected cores immediately on board and incubating the resuspended sediment in situ. The main advantage of the slurry technique is that primary production can be measured with high spatial resolution. Moreover, it can be used on any type of sediment, it is easy to apply, and no special incubation equipment is needed (Jönsson, 1991). The major drawback of the slurry technique is that microalgae which are suspended in the overlying water can lead to an overestimate of the in situ production of the layered community by exposing cells, buried in dark layers of the sediment, to light (Gould and Gallagher, 1990). For this reason Sundbäck et al. (1990) suggested that a correction factor to intact core should be applied. Furthermore, although ^{14}C-uptake experiments with sediment slurries can be useful to measure photosynthetic parameters, it is difficult to calculate the effective in situ production from these estimates as the chemical microgradients existing in the sediments are destroyed. ^{14}C-slurry techniques therefore give a potential estimate of the primary production rates (Barranguet et al., 1998).

Benthic community metabolism has been previously investigated in the Bay of Piran, located in the Gulf of Trieste, by Herndl et al. (1989). They measured in situ benthic O_2-fluxes using continuous recording by polarographic O_2-sensors, reporting microphytobenthic gross primary production and community respiration. The latter study was performed from 1985 to 1987, when the Gulf of Trieste was considered a eutrophic environment (Degobbis et al., 2000). In the last two decades, the trophic state of the system has progressively lowered (Paoli et al., 2006). This tendency was recently observed also in the sediment, where the microphytobenthic community was found to be P and Si limited (Cibic et al., 2007). Consequently, in the present study we supposed to obtain primary production estimates lower than those found by Herndl et al. (1989) 20 years ago.

The purposes of this study were to underline the methodological issues arising from the use of the ^{14}C tracer in sediment slurries and to test a number of hypotheses: (1) a seasonal pattern in the primary production in a sublittoral site; (2) to what extent primary production is controlled by irradiance and/or temperature at 17 m depth; (3) whether the microphytobenthic community remains photosynthetically active throughout the year or not.

2. Study site and sampling

The study site, located in the Gulf of Trieste, has been described and graphically presented in Cibic et al. (2007). The investigated station (st. C1) was situated 200 m offshore (45° 42.05′ N, 13° 42.60′ E) at a depth of about 17 m, within