Microphytobenthic primary production and sedimentary carbohydrates along salinity gradients in the lagoons of Grado and Marano (Northern Adriatic Sea)

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Abstract

Primary production of the microphytobenthic community and carbohydrates concentrations were studied in the lagoonal system of Grado and Marano, located in the Northern Adriatic coast. Sediment samples were collected along a salinity gradient. Abundance and species composition of the microphytobenthic communities were analysed and the benthic microalgal biomass was estimated as Chlorophyll a (Chl a). Primary production of benthic diatoms was estimated using ¹⁴C-tracer. Extracellular carbohydrates were extracted from the sediment and separated in two operationally defined fractions (colloidal and EDTAextractable). Salinity was higher in the Grado lagoon, where the benthic microalgal community was mainly composed of marine diatoms. In the Marano lagoon, which has a lower salinity, freshwater species were also found. In both lagoons, photosynthetic efficiency showed an inverse relationship with salinity and a direct relationship with the main biological variables. Photosynthetic activity was directly related to Chl a and abundance of benthic microalgae, suggesting that in the benthic system microalgal community is responsible for primary production. Overall, salinity was also influent on the microphytobenthic primary production, which was greater in the more saline Grado lagoon.

Introduction

The domain of benthic primary production is confined in shallow coastal waters and less than 30% of continental shelf waters may support benthic microalgal photosynthesis (Meyercordt & Meyer-Reil, 1999; Goto et al., 1999). The importance of benthic microalgae as primary producers in shallow estuarine and coastal lagoon ecosystems is well documented (Barranguet et al., 1998). In coastal lagoons, primary production of microphytobenthos may equal or exceed that of phytoplankton, contributing significantly to the total ecosystem production (Cahoon & Cooke, 1992). Diatoms (Bacillariophyceae) dominate this microalgal benthic communities in temperate areas. Diatoms are known to produce copious amounts of extracellular carbohydrates. Recent investigations have demonstrated that photosynthetically fixed carbon, released by diatoms and collectively termed ''colloidal carbohydrate'', includes both low molecular weight (colloidal carbohydrates, coll) and increasingly larger polymeric molecules (extracellular polymeric substances, EPS) (de Brouwer & Stal, 2001; Goto et al., 2001). The relative composition and production rates of low and high molecular weight components of colloidal carbohydrates vary with the tidal cycle, light intensity, nutrient availability and the taxonomic composition of the microphytobenthic biofilm (Smith & Underwood, 2000). EPS constitute the attached fraction, tightly linked to the diatom

cell and directly associated with their movement (de Brouwer & Stal, 2001; Goto et al., 2001; Smith & Underwood, 2000).

In shallow water ecosystems the most important limiting factor for benthic photosynthesis is light availability at the sediment surface, which, besides water depth, strongly depends on the optical properties of the water (Kirk, 2000). Suspended matter and phytoplankton diminish water transparency. Concentrations of both commonly increase towards the coast, causing an increase of water turbidity. Therefore, even shallow, coastal waters may sustain rather poor benthic primary production, since the higher light availability with decreasing water depth may be counteracted by higher particle concentrations in the water (Meyercordt & Meyer-Reil, 1999). In intertidal sediments microphytobenthos communities have to adapt to a series of stress factors such as sediment transport, gradients in light, variations in temperature, nutrient concentrations and salinity gradient (Sdrigotti & Welker, 2002). Salinity, has been generally considered as one of the main ecological constrains of communities' distribution in paralic environments (Guelorget & Perthuisot, 1992).

The aim of this work was to investigate how benthic microalgal communities and photosynthetic activity can be influenced by different salinity regimes in the Northern Adriatic lagoonal system of Grado and Marano. The microphytobentic primary production was also estimated with 14° C-tracer method.

Study site

The Grado and Marano system composes of two lagoons which are located along the Northern Adriatic coast, within the Isonzo and Tagliamento rivers $^{\circ}$ 40'–45 $^{\circ}$ 45' N, 13 $^{\circ}$ \degree 05′–13 \degree 35′ E, Fig. 1). The lagoons are separated from the sea by a longshore bar composed of islets and more or less persistent sand barries. To the North, they are delimited by the rather irregular coastline, extending for about 35 km with an average width of 5 km. A long and deep navigable canal separates the Marano lagoon (western part of the system) from the Grado lagoon (eastern part of the system). The identification of this paralic system as two lagoons is based on geomorphologic and hydraulic differences. The Marano lagoon is a semi enclosed tidal basin, limited by the Tagliamento River delta westward. It is shallow, with a few areas above the sea level and several channels, receiving freshwaters from the adjacent rivers. Conversely, the Grado lagoon is shallower, has a series of morphological relieves (islands) and marshes, and receives freshwater from a single tributary, the Natissa river (Marocco, 1995).

The sampling stations are located along two transects in a virtually undisturbed zone of two navigable canals, without seagrass and macroalgal communities (Fig. 2). Along the Grado transect, stations are: St. 1-internal $(45^{\circ} 44.14' N,$ 13° 20.61' E) 1.4 m depth, St. 2-intermediate (45° 42.75′ N, 13° 20.6′ E) 1.9 m depth and St. 3-external $(45^{\circ} 41.30' N, 13^{\circ} 22.12' E)$ 1.9 m

Figure 2. Satellite image of the Grado and Marano lagoon with the sampling stations indicated.

depth. Along the Marano transect, stations are: St. 4-internal $(45^{\circ} 44.89' N, 13^{\circ} 14.30' E)$ 1.7 m depth, St. 5-intermediate $(45^{\circ} 44.10' N, 13^{\circ}$ 14.47 \textdegree E) 1.3 m depth and St. 6-external (45 \textdegree) 43.10 $^{\prime}$ N, 13 $^{\circ}$ 43.10 $^{\prime}$ E) 0.7 m depth. The average distance between the two transects is 8300 m, while the distance between St. 1 and St. 2 is 2500 m, between St. 2 and St. 3 is 3200 m, between St. 4 and St. 5 is 1500 m and between St. 5 and St. 6 is 2000 m.

Along the Grado transect, the sediment texture varies from mud to sandy-mud and sand from St. 1 to St. 3, whilst in the Marano lagoon sediment is sandy at St. 4 and St. 5 and muddy at St. 6 (Marocco, 1995).

Recent studies evidenced high nutrient concentrations (Claus Falconi, pers. comm.). However, it is assumed that the microphytobenthic community has access to an inexhaustible nutrient supply from the sediment porewater (Granéli $\&$ Sundbäck, 1985 and references therein).

Materials and methods

Samplings were carried out on May, 27th 2002 in the Grado lagoon from 9 to 11 a.m. during the ebb-tide, and in the Marano lagoon during the flood-tide from 1 to 4 p.m. (Fig. 3).

Photosynthetically active radiance (PAR) was recorded with a multiparametric probe PNF-300A (Biospherical Instrument Inc.) and light attenuation at the bottom was calculated.

Salinity was recorded with a Microprocessor Conductivity Meter LF 196. Undisturbed sediment samples were collected with a light gravity core sampler (intenal diameter of 3.5 cm) (Meischner & Rumohr, 1974). The cores were transported to the laboratory in the afternoon of the same day. Sediment subsamples for measurements of primary production, benthic microalgal abundance and species composition, Chl a concentration and carbohydrate fractions were sampled with cut-off plastic syringes (i.d. 10 mm). Microphytobenthic gross primary production (PP, mgC $m^{-2} h^{-1}$) was estimated in the laboratory as 14C uptake. Subsamples were taken from the surface of undisturbed sediment cores with cut-off 5 ml plastic syringes. The top 2 mm of sediment was removed from three replicates and it was homogenised and resuspended in 21 ml glass vials with filtered seawater $(0.2 \mu m)$ filter). A volume of 10.5 μ l ¹⁴C (1 μ Ci ml⁻¹ $NaH¹⁴CO₃$ was inoculated (Steeman-Nielsen, 1952). Samples were placed in polycarbonate bottles, screened by photographic filters to simulate the natural light attenuation of 41% and incubated in a thermostatic bath for 2 h, at the in

Figure 3. Tidal amplitude forecast for the Gulf of Trieste on May, 27th 2002. The equivalent water depth is reported for each sampling time in each lagoon. Data were kindly provided by the CNR, Istituto Talassografico di Trieste.

situ temperature. Subsequently, unincorporated inorganic 14 C was removed by adding 1 ml of HCl 5 N and samples were left under hood for 24 h. Ten ml of the Scintillation cocktail Ultima Gold XR (Packard) were added and the activity of labeled carbon was determined using a QuantaSmart TriCarb liquid scintillation analyzer (Packard). Benthic microalgal abundance (ABU, cell g^{-1}) was determined in the surficial sediment layer (0–1 cm) according to Welker & Nichetto (1996). Qualitative analyses of microphytobenthic communities were performed by floras of Van Heurck (1899), Germain (1981), Dexing et al. (1985), Ricard (1987) and Tomas (1997).

Chlorophyll a (Chl a, μ g g⁻¹) was analysed in the 0–1 cm sediment horizon. Pigments were extracted in 90% acetone and analysed following the spectrofluorometric method of Lorenzen & Jeffrey (1980).

Different carbohydrate fractions were analysed on lyophilized sediment samples. The lyophilized sediment (100–200 mg) was extracted with 1.5 ml of distilled water for 1 h at 30 $^{\circ}$ C. The extract was centrifugated for 5 min at 7500 rpm, and the colloidal carbohydrate fraction of the supernatant was determined. Subsequently, the pellet was incubated with 1.5 ml of 0.1 M Na_2 EDTA for 18 h at 4 °C. The extract was centrifugated for 5 min at 6000 \times g, and the EDTA-extractable carbohydrate fraction of the supernatant was assayed. The carbohydrate fraction was measured spectrophotometrically using the phenol-sulphuric acid assay in 1 ml of supernatant (Dubois et al., 1956), modified by Gerchacov & Hatcher (1972) for sediment samples. Carbohydrate concentrations, obtained as equivalent-glucose, were transformed into carbon using a conversion factor 0.45 g C g^{-1} (Fichez, 1991).

All determinations were carried out in triplicates, with standard deviation lower than 20% for ABU, 5% for Chl a, 30% for PP, 10% for colloidal carbohydrates and 5% for EPS.

Results

PAR attenuation at the bottom ranged from about 39% (Grado lagoon) to 42% (Marano lagoon) of the incident light.

The main physical and chemical variables are reported in Table 1. Temperature at the bottom was $18.7 \degree$ C in the Grado lagoon and $19.8 \degree$ C in Marano. The mean salinity was 32.1 psu in the Grado lagoon and 24.4 psu in the Marano lagoon. Along the Grado transect mean ABU and PP were $3.39 \pm 3.9 \times 10^4$ cell g⁻¹ and 5.1 \pm 3.3 mgC m⁻² h⁻¹, respectively, while in Marano mean ABU and PP were $7.22 \pm$ 1.8×10^4 cell g⁻¹ and 2.5 ± 1.3 mgC m⁻² h⁻¹, respectively (Fig. 4a, b).

Overall, the microphytobenthic community was mainly composed by diatoms (Bacillariophyceae), with a few indeterminate flagellates. Among diatoms, 45 taxa were identified with a dominance of benthic species (82%) and a smaller percentage of planktonic species (18%). The number of species was greater in the Marano sites than in the Grado lagoon. In the Grado lagoon the number of species decreased from St. 1 to St. 3; in Marano the St. 4 and St. 5 had approximately an equivalent number of species, whilst species number was lower at St. 6. In the Grado lagoon only marine species were found, while in the Marano sites fresh water species were present, namely Odontella spp., Cymbella

amphicephala, Eunotia alpina and Amphora acutiuscula (Germain, 1981). In both external stations epipsammic diatoms (about 65%) prevailed, with the dominance of Amphora veneta, Cocconeis spp., Cymbella spp. and Tabellaria fenestrata. At the internal stations, an epipelic community was established, with Navicula directa, Navicula spp., Nitzschia tryblionella, Nitzschia sigma and Nitzschia spp.). Average benthic Chl a was $3.8 \pm 1.7 \mu$ g g⁻¹ in the Grado lagoon and 6.5 \pm 5.0 μ g g⁻¹ in the Marano lagoon (Figure 4a, b). Photosynthetic efficiency (EFF), was estimated as the ratio between PP and Chl a. EFF ranged from 1.06 at St. 3 to 1.56 at St.1 in the Grado lagoon, and varied from 0.32 at St.5 to 1.46 at St.6, in the Marano lagoon (Fig. 5). Average EPS extracted in EDTA from the first sediment layer amounted to 521.5 \pm 356.7 μ g g⁻¹ along the Grado transect and to 576.2 \pm 293.5 μ g g^{-1} in Marano. The mean value of colloidal carbohydrates was 53.0 \pm 7.1 μ g g⁻¹ in Grado and $48.6 \pm 16.5 \mu g g^{-1}$ in Marano. The ratio between EPS and colloidal carbohydrates in Grado was almost equal in both the internal and intermediate stations but it decreased from the intermediate to the external station. In Marano the highest value of the ratio was recorded in the intermediate station, and the lowest one in the external station (Fig. 6a, b).

Discussion

Along the two transects we found different salinity regimes: the Marano lagoon receives freshwaters from 6 rivers (Aussa-Corno system, Zellina, Cormor, Turgnano and Stella rivers), whilst the Grado lagoon has a single tributary (Natissa river). For this reason, the Grado lagoon, lacking fresh water supplies, is more saline than Marano. Along the Grado transect, salinity values were more homogeneous and on average higher than those recorded in Marano. In Grado, the samples were collected during the flood tide while in Marano during the ebb-tide. Consequently, the lower value of salinity recorded in the inner station of Marano is probably due to both the ebb-tide and the larger supply of freshwater (Fonda Umani & Specchi,

The microphytobenthic ABU found in this study appeared comparable with those reported by Sdrigotti & Welker (2002) for the Marano lagoon and by Blasutto et al. (2003) for subtidal sediments of shallow coastal waters in the Gulf of Trieste. Our ABU was lower than that found by Facca & Sfriso (2002) in the central part of the Venice Lagoon. Along both transects from the inner to the outer station both ABU and Chl a decreased while salinity increased. Particularly, in Grado, the decrease of ABU and Chl a occurred abruptly from the inner station to the intermediate one (Chl a decreased by 48% , ABU by 78%), while in Marano we observed the same trend from the intermediate station to the external one, where Chl a decreased by 92% and ABU by 38%. At St. 6 a high ABU with a low amount of Chl *a* was recorded. At this station, the microphytobenthic community was characterised by the prevalence of small size species (*Navicula* spp.) with a low content of Chl a . Chl a is widely used as good biomass indicator for phytoplankton (Jeffrey et al., 1997 and references therein). Chl a is commonly used as a biomass indicator also in sediments (de Jonge, 1980; Miles & Sundbäck, 2000; Blasutto et al., 2003), although the living fraction of the micro-

Table 1. Abiotic and biotic variables in the Grado and Marano lagoons

Location		Salinity (psu)	ABU $(10^4$ cell g^{-1})	Chl a $(\mu g g^{-1})$	Net PP $(mgC \ m^{-2} h^{-1})$	EPS $(\mu g g^{-1})$	coll $(\mu g g^{-1})$
Grado	St.1	29.3	7.81	5.8	9.0	650.1	44.8
	St.2	33.0	1.67	3.0	3.6	796.1	57.1
	St.3	33.9	0.69	2.7	2.8	118.3	57.0
Marano	St.4	15.6	8.12	9.6	3.5	711.2	65.2
	St.5	27.1	8.37	9.0	2.9	778.0	48.6
	St.6	30.4	5.16	0.7	1.1	239.5	32.1

1982).

Figure 4. Variations of chlorophyll a (Chl a), microphytobenthic abundance (ABU), salinity and benthic microalgal primary production (PP) in Grado (a) and Marano (b).

algal biomass can be overestimated (up to 50%), due to the interference of photosynthetic degradation products (de Jonge & Colijn, 1994). Moreover, sedimentary photosynthetic pigments are often of different origins, since they can be due to the sedimentation of phytoplankton species and particulate matter of riverine origin.

Gross primary production rates reported in this study are the first determined with the 14 C-tracer method in an intertidal lagoon ecosystem in the Northern Adriatic Sea. These PP values are significantly lower than those estimated with oxygen measurements in the Marano lagoon (Sdrigotti & Welker, 2002). Nevertheless, the rates we obtained are comparable with those estimated with oxygen method in a non-tidal sandy beach of the Gulf of Gdansk (southern Baltic) (Urban-Malinga & Wiktor, 2003). Our PP rates are also comparable with those determined as 14 C-uptake in subtidal sites (Barranguet et al., 1998; Miles & Sundbäck, 2000), in the estuarine littoral of Southern Baltic

(Yap, 1991), Wakamura Estuary, Japan (Goto et al., 1998), and two shallow coastal lagoons with low salinity levels (Kirr-Bucht and Rassower Storm) in the Southern Baltic Sea (Meyercordt & Meyer-Reil, 1999). By contrast, the gross benthic primary production of this study is lower than that obtained in an eutrophic coral reef lagoon (Clavier & Garrigue, 1999).

Since in our samples macroalgae were totally absent, we can infer that the microphytobenthos was the main community responsible for primary production. PP, ABU and Chl a showed the same pattern despite different sediment subsampling methods being used to determine these variables. A decrease of PP by 60% along the Grado transect from the internal to the intermediate station and by 20% from the intermediate to the external station (total decrease of 80%) was observed. Along the Marano transect, PP abruptly decreased (65%) from the intermediate to the external station, while from the internal to the

SALINITY VS EFF

Figure 5. Salinity and photosynthetic efficiency (EFF) in the Grado and Marano lagoons.

Figure 6. Variations of the ratio of extracellular polymeric substances (EPS) to colloidal carbohydrates (coll) in relation with sediment texture in the Grado (a) and Marano (b) lagoons.

intermediate station PP decreased by 17% (a total drop of 82%). Tolomio (1976a, b) found in the Grado lagoon an evident relationship between marine waters and species diversity of phytoplankton during different tidal phases. This finding was assumed as an artifact, and salinity was not considered as a limiting or stressing factor for the development of euryhaline phytoplankton species. Neverthless, along the two transects we observed an inverse relationship between salinity and all the biological or biochemical variables (PP, Chl a, ABU and carbohydrates). This finding is in agreement with Alberighi et al. (1997), who obtained an inverse relationship between phytoplanktonic PP and salinity in a study carried out in the Northern Adriatic Sea. The highest PP found in the inner stations considered in this study, could be ascribed to the influence of larger amounts of nutrient-rich freshwaters.

In the current study, the PP recorded in the Grado lagoon was more than 8 times greater than in the Marano lagoon, although the average salinity was lower in the latter site. Along the Grado transect the salinity range was narrow and probably allowed the establishment of a more stable and less stressed microphytobenthic community. This community was characterised by a minor biodiversity and seemed to be more productive.

EFF, as the ratio between PP and Chl a , revealed a different trend along the two transects. Along the Grado transect, the PP to Chl a ratio showed a slight decrease from the inner to the outer station with a low variability degree. Along the Marano transect, EFF was characterised by an increase of almost five fold from the intermediate to the external station. This was probably due to the shallower depth of this station (ca. 70 cm), and to the higher light penetration.

The community structure was also related to the sediment texture, the epipsammic species being dominant in the sandy stations and the epipelic species prevailing in the muddy sites. Sediment texture is a very important factor to select species composition of microphytobenthic communities. Cohesive sediments enable the development of epipelic species capable of moving through the sediment and of producing large amounts of EPS. Sand supports the development of epipsammic species, which adhere to the grains by means of apical pads, stalks and tubes (Miles $&$ Sundbäck, 2000). For this reason, in the external stations where the sediment is prevalently sandy the amounts of EPS decreased, while in the internal stations the epipelic community was responsible for a larger EPS production.

The EPS and colloidal carbohydrate patterns were related with Chl a and ABU, according to de Brouwer & Stal (2001). A direct relationship between colloidal carbohydrates and photosynthetic activity was also reported by Miles $&$ Sundbäck (2000), Smith & Underwood (2000) and Blasutto et al. (2003). In the Marano lagoon, the two carbohydrate fractions showed a similar distributions with a decrease from the inner to the outer stations, whilst in the Grado lagoon the water soluble fraction increased from St. 1 to St. 3. Moreover, in the internal station of Grado, the concentration of the colloidal carbohydrates was lower than should be expected from the high PP. Colloidal carbohydrates of recent production can rapidly disappear from the system, they being either washed away or utilised by heterotrophic consumers (de Brouwer & Stal, 2001).

In conclusion, the primary production in the Grado and Marano lagoons depends upon the benthic microalgal community. The highest production rates were found in the more saline Grado lagoon, where the low salinity fluctuation rather than freshwater inputs favoured the establishment of a more stable and less stressed microphytobenthic community. Likely, under these conditions a lower biodiversity was accompanied by a greater primary productivity. However, along with salinity, turbidity, sediment resuspension, nutrients, competition with other primary producers have to be considered for a more detailed description of the transitional ecosystems.

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