Vol. 53: 169–178, 1989 | MARINE ECOLOGY PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published April 27

Benthic community metabolism and microbial dynamics in the Gulf of Trieste (Northern Adriatic Sea)

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ABSTRACT: Benthic O_2-fluxes of sublittoral sediments were measured in situ using continuous recording by polarographic O_2-sensors. Three stations (7, 15, and 22 m deep) were investigated at ca 2 mo intervals in the Northern Adriatic Sea over a 19 mo period. High chl *a* contents of the sediments were found in spring (March, April) and fall (September, October) while sediment bacterial numbers fluctuated in an inconsistent pattern. Porewater dissolved organic carbon (DOC) exhibited strong seasonal variation with highest concentrations in September (20 mg C l^{-1}); subsequently porewater DOC declined to ca 5 mg C l^{-1} (March-April). In general, porewater DOC increased slightly with depth down to the 10–15 cm horizon. Benthic respiration was found to be temperature dependent; below 10 °C about 6 mg C m^{-2} h^{-1} were respired while at 20 °C the rate was 17 mg C m^{-2} h^{-1}. Microphytobenthos gross primary production (GPP) was detected even at the deepest station and remained fairly constant from March to September (ca 100 mg C m^{-2} d^{-1}). Total community metabolism calculated over 24 h revealed net community production in spring for the shallowest station only. Highest net system consumption rates were obtained in September for all 3 stations ranging from 220 to 520 mg C m^{-2} $(24\ h)^{-1}$ caused by increased heterotrophic activity as indicated by high night-time respiration rates. Calculated O_2-consumption of the sediment and the water column below the thermocline indicates that subthermocline water column respiration was the principal cause for near-bottom hypoxia rather than sediment oxygen demand if the thermocline was at least 2 m above bottom. At a thermocline depth of 1.5 m above bottom, sediment O_2-uptake and subthermocline water column respiration were equally important.

INTRODUCTION

It is generally thought that most pelagic primary production in shallow coastal waters enters the benthic food web (Smetacek 1984). Therefore, benthic mineralization is essential for providing nutrients for phytoplankton growth, thus creating a tight coupling between the pelagic and benthic processes in nearshore marine ecosystems (Hargrave 1980, Nixon et al. 1980, Zeitzschel 1980). This benthic nutrient regeneration is mainly governed by the activity of bacteria (Meyer-Reil 1986). It is, therefore, of considerable importance to follow seasonal development of benthic bacterial biomass and its activity. However, information on fluctuations in bacterial abundance over an annual cycle is limited. While Cammen (1982) and Montagna (1982) were unable to detect any significant variations among seasons, Rublee (1982) and DeFlaun & Mayer (1983) report on positive correlations between bacterial numbers and temperature of sediments. A detailed study on the seasonal development of bacteria in sublittoral sediments by Meyer-Reil (1983, 1984) revealed a close coupling in the development of bacterial populations and sedimentation events. The sediment-water interface has been demonstrated to harbor twice the bacterial biomass of deeper sediment layers (Novitsky 1983). Since the primary input to the benthos is detritus, superficial sediment layers receive more nutrient input than deeper sediment communities (Novitsky 1987).

As mentioned above the magnitude of benthic mineralization influences the availability of regener-

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0171-8630/89/0053/0169/$ 03.00

ated nutrients for phytoplankton production. Various techniques have been developed to measure benthic metabolism; each of them has its shortcoming (Pamatmat 1984). Measurements of heat production are theoretically correct; however, only very small samples can be used and disturbance of the sediment structure cannot be avoided which makes interpretation of the data difficult. Disturbance of the sediment enhances microbial activity and heterogeneity of the sediment makes the results non-representative for total community respiration. Although Pamatmat (1984) cautioned that oxygen uptake measurements may underestimate actual total benthic community metabolism, we used this approach to facilitate comparison between the autotrophic and the heterotrophic component of the aerobic benthic system under investigation (van Es 1982).

In recent years, the Northern Adriatic Sea was repeatedly subjected to oxygen deficiencies of near-bottom layers (Fedra et al. 1976, Stachowitsch 1984, Faganeli et al. 1985). Officer et al. (1984) demonstrated that the principal cause of anoxia phenomena in Chesapeake Bay (USA) was water column stratification and benthic respiration of accumulated organic detritus. In the Northern Adriatic Sea, however, the situation may be different due to the shallowness of the area. As shown in a previous study, sufficient light penetrates to the bottom to support microphytobenthos primary production (Herndl et al. 1987).

The aim of the study was: (1) to follow the rate of benthic mineralization over an annual cycle to estimate the potential role of benthic metabolism in causing suboxic conditions in near-bottom waters; (2) to evaluate the importance of microphytobenthos primary production in supplying organic matter for benthic respiration and for creating oxygen deficiencies in subthermocline waters; (3) to investigate the influence and adaptive capacity of microphytobenthos to different light- and temperature-regimes; and (4) to determine seasonal fluctuations in sediment bacterial biomass in relation to ecological events.

MATERIAL AND METHODS

Samples were taken at 1 to 2 mo intervals at 3 locations (Stn E, 7 m; Stn MA, 15 m; and Stn F 22 m deep) in the Gulf of Trieste (Northern Adriatic Sea) from September 1985 to April 1987. For a more detailed description of the sampling locations consult Herndl et al. (1987). Briefly, Stn E is considered to be representative for the shallow sublittoral at the lower margin of the boulder field which is characteristic for large parts of the coastline, while Stn MA – in the center of the Bay of Piran – reflects typical embayment conditions. Stn F represents conditions in the central part of the Gulf of Trieste. Sediments at Stn E consist of medium to fine sand while at Stn MA silt and clay prevail (Ranke 1976). At Stn F fine sand and silt dominate the sediment structure.

In situ work described below was carried out by SCUBA-diving. Production and consumption of O_2 by the sediment community (including autotrophic and heterotrophic organisms) were measured. Transparent acrylic chambers were used in duplicates, each covering a sediment surface area of 0.07 m^2 and containing 6.1 l of ambient water. This volume of incubated water prevented the O_2-concentration from deviating more than 25 % of the initial concentration over a 24 h incubation period. Continuous recording of the O_2 content of the enclosed water was achieved by means of a battery-driven underwater-respiration set equipped with polarographic oxygen sensors of the Clark type (YSI) as described in detail by Svoboda & Ott (1983). Care was taken to maintain current speeds within the chambers typical for near-bottom waters of the study area, since Boynton et al. (1981) clearly demonstrated the dependence of sediment respiration on current speed. Current speeds within the chambers were adjusted to ambient water current velocity by means of magnetic stirrers mounted in small glass chambers and connected with the acrylic jars by Tygon tubes (30 cm long, 0.6 cm inner diameter). Near-bottom current velocity was determined by a fluorescent dye released from a syringe. Sediment O_2 production and consumption estimates were corrected for the planktonic contribution to O_2 changes within the incubation chambers by enclosing near-bottom water in small (900 ml) jars. O_2-evolution within this small chamber was measured using the same technique as for sediments. Readings obtained from these water incubations were also used for metabolism estimates of the near-bottom water column. For comparison with values reported elsewhere, the oxygen data were converted to carbon equivalents by assuming a photosynthetic and respiratory quotient of 1.0 (Oviatt et al. 1986b). Gross primary production (GPP) was calculated assuming that the benthos respires equal quantities during day- and night-time; therefore, mean nocturnal respiration h^{-1} was added to the measured diurnal (defined as period from sunrise to sunset) net flux h^{-1} to obtain GPP rates h^{-1}. The sum of diurnal net flux and nocturnal respiration gives the daily net flux.

Light as photosynthetically active radiation (PAR; 400 to 700 nm) was monitored continuously using an instrument designed for underwater-investigations by Machan (1973). Quantum sensors were deployed in duplicate 20 cm above bottom in the vicinity (within 1 m) of the incubation chambers. Temperature was recorded continuously during each incubation.

Sediment cores (5 cm inner diameter) were taken in quadruplicate in the vicinity of the incubation chamber at the end of each sediment metabolism measurement. Within 1 h of collection the uppermost 1 cm of the sediment was removed from 2 cores with a spatula and extracted in acetone for 2 h according to the method of Colijn & Buurt (1975). Absorbance of the centrifuged extract was measured spectrophotometrically. After thoroughly rinsing the remaining sediment with distilled water to remove salts the sediment was dried at 70 °C to constant dry wt to allow expression of the chl *a* content per g sediment dry wt.

Dissolved organic carbon (DOC) of the sediment porewater was determined by cutting sediment cores into slices and centrifuging them at 23 000 × *g* for 15 min. The supernatant water was subsequently filtered through precombusted (450 °C for 6 h) Whatman GF/F filters and stored frozen until analysis. Samples for DOC were measured using a Beckman Tocamaster 915-B. This instrument measures the CO_2 evolution after high temperature combustion of the sample. Quite recently, Sugimura & Suzuki (1988) demonstrated that high temperature combustion yields higher concentrations than the commonly used persulfate technique.

In order to determine sediment bacterial numbers, cores were taken in duplicate from the sediment enclosed by the incubation jar after removing the chamber. Disturbance of the sediment surface was minimized when the chambers were lifted. The cores were brought to the laboratory and cut into slices (generally within 2 h after sampling). Between 0.2 and 0.5 cm^3 of the sediment was transferred into a vial filled with a 2% (v/v) formaldehyde/0.2 µm Nuclepore-filtered seawater solution. Prior to ultrasonication this slurry was made up to 20 ml with double-filtered (0.2 µm Nuclepore) seawater. Subsequently, the mixture was ultrasonicated to liberate sediment attached bacteria from their substrates as described by Ellery & Schleyer (1984). Thereafter 0.1 ml of the suspension was withdrawn and made up to 5 ml with double-filtered seawater which represented a 1000-fold dilution of the original sample. Bacteria were stained with acridine orange following Hobbie et al. (1977). At least 300 bacterial cells were counted per sample. Bacterial cell dimensions were determined from visual estimates during acridine orange direct counting, in which 100 to 150 rods and 50 to 70 cocci were measured and the mean volume calculated. For conversion of bacterial biovolume to carbon biomass the value given in Lee & Fuhrman (1987) of 3.8×10^{-13} g C μm^{-3} bacterial cell was used. The sediment was treated in the same way as described for chl *a* analysis to express cell numbers and carbon biomass per g sediment dry wt.

RESULTS

Temperature and light

At the sediment-water interface highest temperature was recorded in September (ca 20 °C); temperatures below 10 °C were measured between January and April (Fig. 1). Lowest temperature measured was 7 °C at Stns F and MA in February 1987. All light measurements were performed under near optimum conditions (i.e. bright sunshine). Differences in light conditions

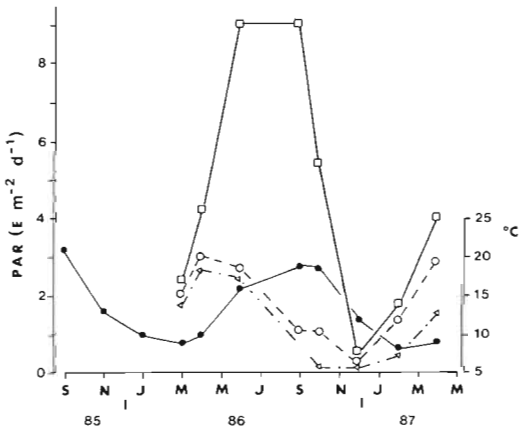

Fig. 1. Seasonal variations in temperature of the sediment surface at Stn MA (●), and PAR-levels (integrated diurnal records) of Stns E (□), F (△), and MA (○); PAR measured 20 cm above bottom

among the stations were obvious as shown by integrated photon fluxes in Fig. 1 Maximum PAR levels were measured during midday in June 1986; at the shallowest station (E; 7 m) we obtained 412 µE m^{-2} s^{-1}, at Stn MA (15 m) 123 µE m^{-2} s^{-1} and at Stn F (22 m) 93 µE m^{-2} s^{-1}. Minimum noontime photon fluxes were recorded in December 1986 ranging from 10.2 (Stn F) to 35.3 µE m^{-2} s^{-1} (Stn E).

Microphytobenthos, sediment bacteria and porewater-DOC

Microphytobenthic biomass measured as chl *a* content of the uppermost 1 cm sediment layer ranged from 5 to 11.8 µg chl *a* g^{-1} (sediment dry wt) at Stn F and from 3.2 to 13.1 µg chl *a* g^{-1} (sediment dry wt) at Stn MA (Fig. 2). Unfortunately, no data are available for Stn E. High chl *a* contents of the sediments were found in spring (March, April) and fall (September, October); especially Stn MA exhibited pronounced seasonal variations in benthic chl *a* with a decrease to about one-third of bloom values, however the contribution of sedimented phytoplankton to the measured benthic chl *a* concentration remains unknown.

Sediment bacterial numbers were inversely correlated with the grain size distribution of the stations (data not shown); Stn MA sediment with its high content of silt and clay (data given in Ranke 1976) exhibited the highest numbers. Bacterial numbers generally decreased about 2 orders of magnitude from the uppermost 1 cm layer to 20–25 cm (the deepest layer investigated). Fig. 3 shows the seasonal variation of sediment bacterial numbers of the 0–1 cm layer and the 5–7 cm layer (approximately the redox-potential discontinuity layer) of the 3 stations (Fig. 3a) and the corresponding porewater-DOC concentrations until June 1986 (for Stns F and MA only) (Fig. 3b). While bacterial numbers followed similar trends at Stns MA and E over most of the time, Stn F exhibited a more inconsistent fluctuation. The observed decrease in bacterial numbers of the superficial layer at Stn MA from September 1985 to March 1986 was not detectable in the following year. During fall 1986 we observed an increase until December. Similar fluctuations were observed in the 5–7 cm layer although to a lesser extent. Bacterial biovolume varied more with depth than seasonally. Mean volume of rod-shaped bacteria increased significantly from 0.193 μm^3 (SD = 0.07, n = 106) of the surface layer bacteria to 0.445 μm^3 (SD = 0.11, n = 125, ANOVA, $p < 0.001$) at the 5–7 cm layer due to the predominance of filamentous bacteria. Biovolume of cocci varied from 0.04 to 0.06 μm^3 regardless of depth and season.

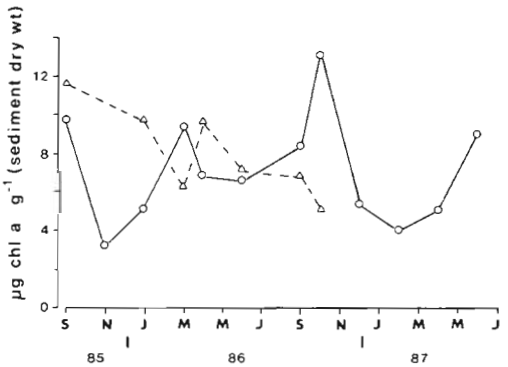

Fig. 2. Seasonal variations in chl *a* contents of the uppermost 1 cm sediment layer of Stn F (△) and MA (○). Each point represents mean of 3 replicate estimates

Porewater-DOC showed a strong seasonal variation with highest concentrations detectable in September. At both stations porewater-DOC declined from about 20 mg C l^{-1} (September) to ca 5 mg C l^{-1} (March-April) and began to increase again thereafter (Fig. 3b). Generally, DOC contents in porewaters increased slightly with depth down to 10–15 cm and declined again in deeper sediment layers (down to 25 cm – the maximum depth investigated). At Stn F, DOC concentrations in

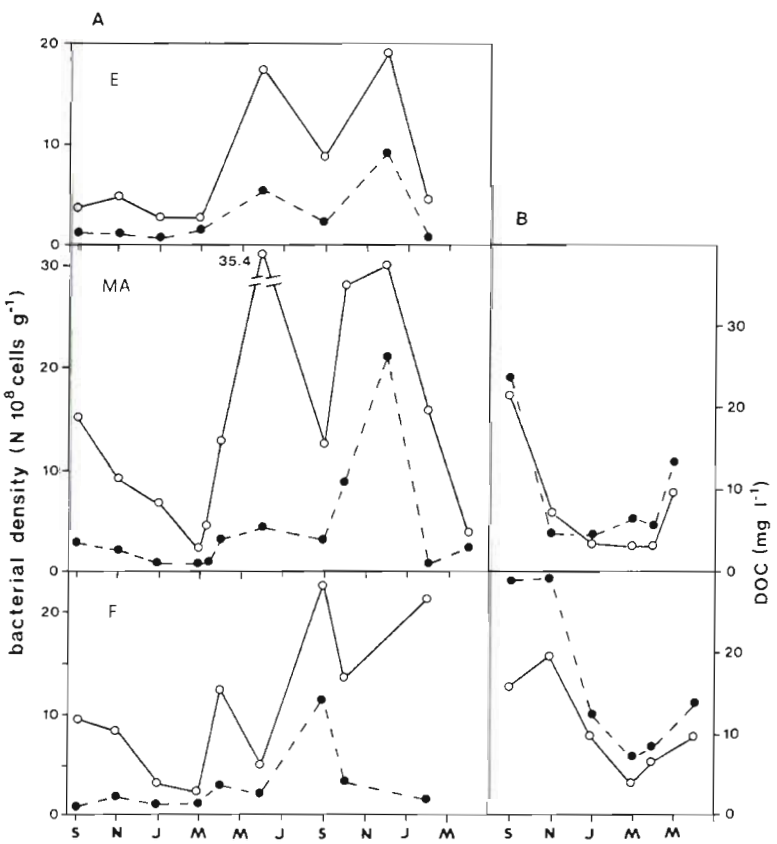

Fig. 3. Seasonal variations in (A) benthic bacterial densities and (B) DOC-concentrations of the porewaters of the 3 stations investigated. For DOC, data are given only from September 1985 to June 1986; no DOC data are available for Stn E. (○) 0–1 cm, (●) 5–7 cm sediment horizons

the 5–7 cm layer were up to twice the concentrations of the surface layer in fall. During winter, however, DOC contents of deeper sediment layers approached concentrations of the top cm layer

Sediment O_2-production and consumption

Examples of 2 characteristic daily cycles of O_2-fluxes are shown together with the corresponding PAR-values in Fig. 4 for opposite ecological situations. In March 1986, when temperature at the sediment surface was below 10 °C, O_2-net production was obtained for all 3 stations while in September only Stn E exhibited O_2-net production. In March, night-time respiration varied between 10 (Stn F) and 32 mg O_2 m^{-2} h^{-1} (Stn E); however, in September respiration rates of more than 40 mg O_2 m^{-2} h^{-1} were recorded for Stn E and F. At Stn E, O_2 production started at PAR-levels of about 25 µE m^{-2} s^{-1} in both March and September, at Stn MA at PAR-levels of ca 10 µE m^{-2} s^{-1} and at Stn F at levels below 5 µE m^{-2} s^{-1}. PAR at Stn E was found to be higher in September than in March while at the deeper stations (MA and F) higher PAR-levels were recorded in March. Possible reasons and implications are discussed below. In 48 out of sixty 24 h in situ measurements we observed higher benthic respiration rates h^{-1} during dusk as compared to the subsequent night-time hours. While this difference was significant (ANOVA, $p < 0.01$), respiration rate during dawn was not signifi-

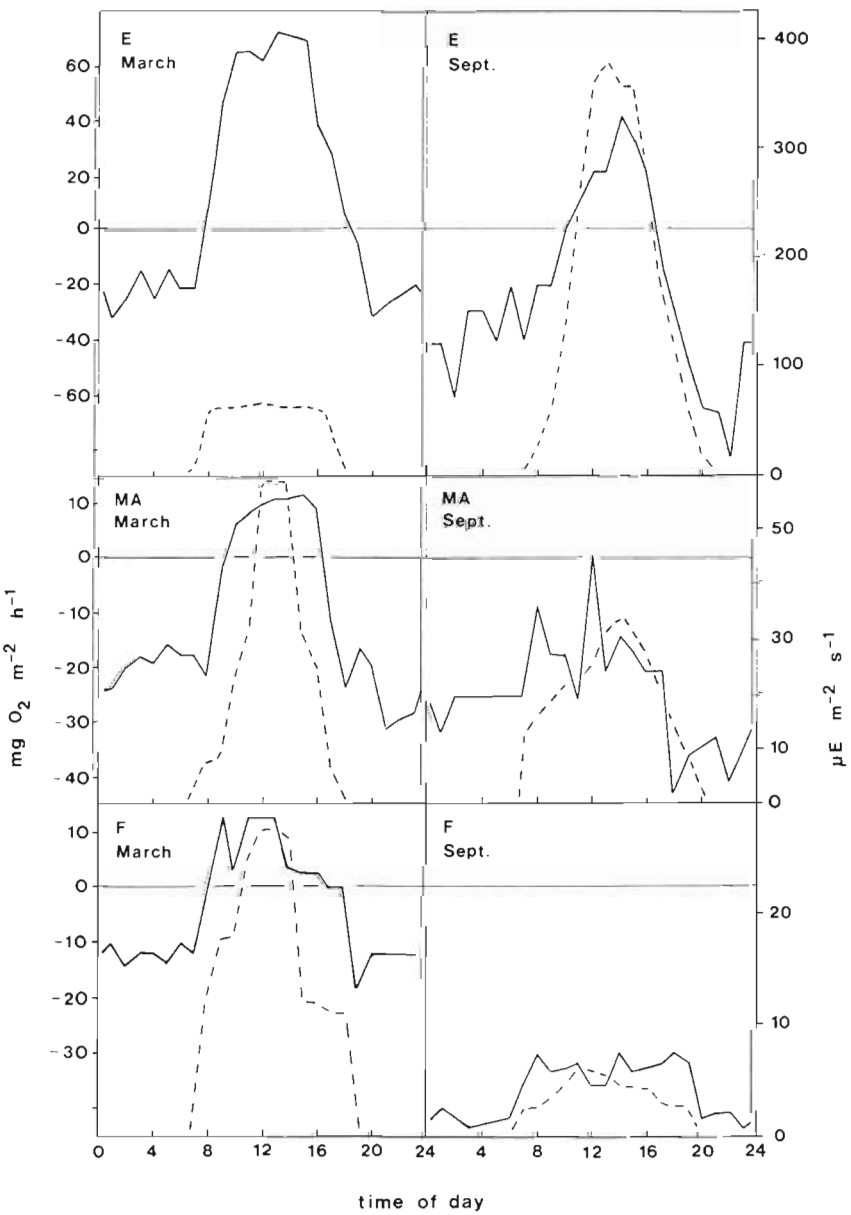

Fig. 4. Hourly net sediment O_2-flux of 2 representative days of March and September. Broken lines indicate PAR; note scale changes among different panels

cantly higher (ANOVA, $p > 0.1$) than previous night-time respiration rates.

System budgets over the entire investigation period are shown in Fig. 5. Gross primary production in terms of carbon was calculated assuming that the benthos respires equal quantities during day- and night-time. Highest gross production was obtained in March and April. Despite the depth difference between Stns MA

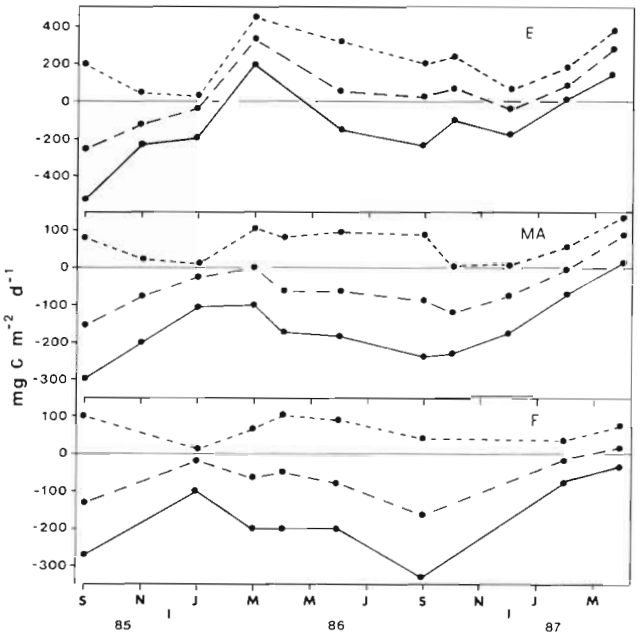

Fig. 5. Seasonal variations in benthic metabolism: gross primary production (GPP) (-----), net diurnal flux (– – –) and daily net O_2-flux (——) of the 3 stations

and F gross production rates (ca 100 mg C m^{-2} d^{-1}) remained fairly constant from March to September and decreased to about 10 mg C m^{-2} d^{-1} during winter. Net diurnal fluxes indicate that Stn E was autotrophic during daytime over almost the entire year. However, from September 1985 to January 1986 respiration prevailed over production. During daytime both deeper stations respired more than the microphytobenthos produced (except in April 1987 when high gross primary productivity coincided with unusually low temperatures). Total system metabolism (i.e. net diurnal + nocturnal flux) calculated over 24 h revealed net system production in spring (February to May) at Stn E while Stns MA and F remained heterotrophic throughout the investigation period; only in April 1987 diel production prevailed over consumption at Stn MA (Fig. 5). Highest system consumption rates were obtained in September for all 3 stations, ranging from 220 to 520 mg C m^{-2} d^{-1} due to increased heterotrophic activity (i.e. night-time respiration) and slightly decreasing gross primary production (Fig. 5). While benthic respiration increased exponentially with temperature (Fig. 6) the increase in gross primary production appeared to be slightly diminished at higher PAR levels (> 6 E m^{-2} d^{-1}) (Fig. 7). Only at the shallowest station (E), however, PAR reached levels where the yield in gross production was reduced (Fig. 7).

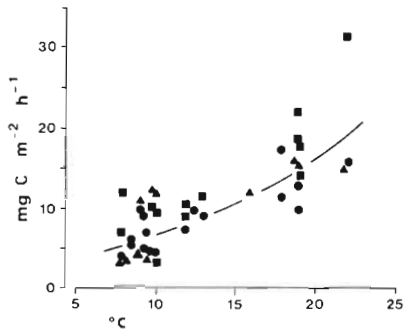

Fig. 6. Dependence of benthic respiration on sediment temperature. Values for Stn E (■), MA (●), and F (▲)

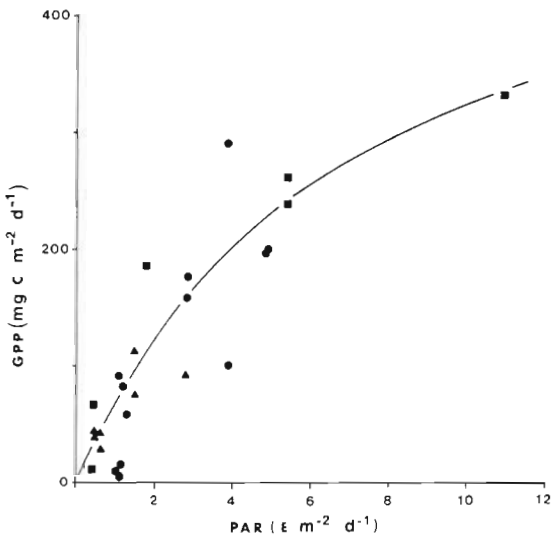

Fig. 7. Benthic gross primary production (GPP) as a function of daily PAR; for symbols see Fig. 6

DISCUSSION

Impact of benthic O_2-flux on summer hypoxia

The shallow Northern Adriatic Sea is severely subjected to near-bottom hypoxia during prolonged water column stratification (Stachowitsch 1984, Faganeli et al. 1985). At Stn F, sediment oxygen demand during late summer (September) amounted to 1024 mg O_2 m^{-2} d^{-1} while benthic gross primary production accounted for 120 mg O_2 m^{-2} d^{-1} which means that only about 12% of the O_2 demand was covered by

autochthonous production (data derived from Fig. 5). In September 1986 a pronounced thermocline was detected 4 m above bottom. Below this thermocline, water column O_2-flux measurements revealed a net daily O_2 demand of 840 mg O_2 m^{-3} d^{-1}; O_2 consumption of the water column below the thermocline (4 m) amounted therefore to 3360 mg O_2 m^{-2} d^{-1} which is 3.3 times the O_2 demand of the underlying sediment. The O_2 demand of the sediment plus the 4 m water column below the thermocline amounted to 4384 mg O_2 $(4\ m)^{-3}$ d^{-1}. Assuming no additional O_2 input and an O_2 content of saturated seawater of 7.4 mg O_2 l^{-1} at 19 °C, the available O_2-pool would be depleted within 7 d. During this period (September 1986) Stachowitsch (unpubl.) measured O_2 concentrations in the water layers 1 to 2 m above bottom. Within 13 d the O_2 content dropped from 6.4 to 3.2 mg O_2 l^{-1}, which corresponds to a decrease of 985 mg O_2 $(4\ m)^{-3}$ d^{-1}, or 22.5 % of the actually measured O_2 demand below the thermocline. The difference between actually measured oxygen demand of the sediment and water and the daily decline in the O_2 content in the near bottom water layer may serve as a rough estimate on the magnitude of the daily O_2 import due to diffusive flux across the thermocline and probably more importantly due to horizontal advection; O_2 supply by advection and diffusion processes may therefore only account for 77.5 % of the actual O_2 demand of both the subthermocline water and the underlying sediment.

We consider the principal cause of near bottom hypoxia in the Northern Adriatic during summer to be enhanced water column respiration below the thermocline rather than the sediment; Oviatt et al. (1986a) studying nutrient-enriched mesocosms arrived at a similar conclusion. This figure would change, however, if the subthermocline-water column is shorter than in our example. Applying our results to the anoxia event in the Northern Adriatic Sea in 1983, sediment O_2-uptake and water column respiration were equally important in creating O_2 deficiency since the pronounced thermocline was established about 1.5 m above bottom (Stachowitsch 1984). Considering the relatively thin sediment layer where O_2 is available as terminal electron acceptor compared to the water column, sediment oxygen demand on a volume basis amounts to 20 µg O_2 cm^{-3} d^{-1} which is ca 100 times the O_2 demand of the water column (0.25 µg O_2 cm^{-3} d^{-1}).

Comparison of the continuous O_2-recording method with extrapolation techniques

In the present study we measured the O_2-flux of sediments in situ by continuously recording O_2-concentrations of water enclosed with sediments. Most studies dealing with productivity and respiration measurements are performed around noontime and converted to a daily estimate by introducing a factor. Table 1 gives a comparison of daily gross primary production estimates derived from formulas commonly used with continuous recordings. It is obvious that those formulas which take solar radiation into account (Formulas A, B) give more reliable estimates than formulas simply assuming a constant ratio between mid-day production and daily productivity (Formulas C, D). The recently developed formula of Shaffer & Onuf (1985) possibly provides an even better estimate than those presented in Table 1, however, no data are available on the mean daily solar radiation for the average day of the month which is necessary for calculation.

A conspicuous feature detected in 48 out of sixty 24 h in situ measurements was an up to twice as high benthic respiration rate h^{-1} during dusk as compared to the subsequent night-time hours. An increased respiration rate during dawn was observed in about half of the experiments although this was not as pronounced as during dusk. This respiratory pattern – also reported by Pamatmat (1968) – may be partly explained by enhanced respiration of reserve products accumulated during the light phase which may enable the microphytobenthos to sustain protein synthesis during the dark period (Cook 1966, Foy & Smith 1980). It is

Table 1. Comparison of benthic gross primary production (GPP) estimates derived from noontime measurements using Formula A (Leach 1970), B (Zedler 1980), C (Joint 1978), and D (Wetzel 1983) with continuous recordings over 24 h. GPP is given in mg O_2 m^{-2} d^{-1} together with the % deviation. Formula A: GPP of the incubation period × (PAR of the entire day:PAR of the incubation period); B: GPP = noontime production × 0.64 × daylength × (mean daily PAR for the period:daily PAR for the day); C: GPP = noontime GPP (h^{-1}) × hours of daylight; D: GPP = noontime production represents 80 % of GPP

Formula	Stn E (June 86)		Stn MA (June 86)		Stn MA (April 87)	
	GPP	% dev.	GPP	% dev.	GPP	% dev.
A	954.6	+ 7.9	1035.7	+33	380.5	− 8.6
B	1094.4	+23.8	752.6	− 3.3	382.3	− 8.2
C	1710	+93.4	1176	+51	597.3	+43.4
D	1368	+54.7	940.8	+20.9	477.9	+14.7
This study	884.3	–	778.3	–	416.5	–

unlikely, however, that the microphytobenthos alone accounts for the observed high dusk and dawn respiration rates. Since a great deal of attention was paid to excluding larger infauna organisms (by avoiding placement of the incubation chambers over openings of burrows) the respiration peak probably does not simply reflect macrofauna activity patterns. Dusk and dawn peaks in activity were shown to occur in pelagic bacteria at Stn F (Herndl & Malacic 1987); similar diel activity patterns are also exhibited by benthic bacteria (Moriarty & Pollard 1981, Meyer-Reil 1986).

These high respiration rates during changes from light to dark phase have implications for interpretation of O_2-uptake measurements using conventional techniques since most of these studies are performed around noontime by placing translucent and opaque chambers over the sediment for about 2 to 4 h. This abrupt change from light to dark may cause severe overestimations of respiration rates (Table 1).

Factors controlling the benthic O_2-flux

As shown in Fig. 7 microphytobenthos production is detectable at mean daily PAR-levels of about 5 μE m^{-2} s^{-1} (0.4 E m^{-2} d^{-1}). Similar compensation levels have been reported by Colijn & DeJonge (1984). Our in situ measurements revealed no adaptation of the microphytobenthos to different light regimes. Seasonal differences in daily O_2-fluxes of the sediment are governed by a combination of photon flux penetrating to the bottom and temperature as demonstrated for the 2 extreme situations in Fig. 4. In September, photon flux is only about one-third of the PAR-level of March at the deeper stations (Stns F and MA) due to the condensation of flocculent material in the near-bottom layer. Additionally, high densities of large amorphous aggregates (marine snow) in the water column may significantly reduce photon flux to the bottom (Herndl 1988).

Sediment temperature in March is about 10 °C lower than in September, resulting in a respiration rate approximately half the September level as shown in Fig. 6. The combination of high PAR-levels and low temperatures leads to moderate microphytobenthos production during early spring. Contrarily, in September high temperature and low PAR-levels increase sediment respiration and decrease gross primary production, respectively. A similar seasonality has been reported for the intertidal of the Bay of Fundy, Canada (Hargrave et al. 1983).

At present, the response of benthic bacteria to sedimentation events is under discussion. Cammen (1982) and Montagna (1982) detected no significant variation in microbial density while DeFlaun & Mayer (1983) report on positive correlations between bacterial density and temperature. Meyer-Reil (1983, 1986, 1987) found a pronounced microbial response to sedimentation events not only in biomass but also in microbial enzymatic activities. In the present study we obtained fluctuations in bacterial densities over 2 orders of magnitude. Bacterial density decreased continuously from September 1985 to March 1986. Subsequently, bacterial numbers increased coinciding with the decay of the spring phytoplankton blooms (Herndl et al. 1987). Generally, sediment bacteria of the 0–1 cm layer respond more rapidly to ecological events than bacteria of the 5–7 cm sediment layer (Fig. 3a); however, in the uppermost sediment layer we did not further discriminate between the layer of the sediment-water interphase and the horizons below. Novitsky (1983, 1987) detected a highly active microbial community in the superficial sediment layer with an up to 2 orders of magnitude higher biomass as compared to the horizons immediately below.

Highest DOC concentrations in the porewater of the sediments were found in September and decreased rapidly until March; thereafter DOC contents increased again suggesting that phytoplankton may supplement the porewater-DOC pool. Calm weather conditions during summer are characterized by a pronounced stratification of the water column and the formation of large amorphous aggregations which tend to accumulate at the pycnocline (Herndl & Peduzzi 1988, Herndl 1989). These aggregations – highly enriched in microbial biomass – create a 'false benthos' (sensu Sieburth 1987) at this boundary layer. The increase in specific density of these aggregations due to attachment of inorganic solids leads to an episodic sinking of this aggregate-layer to the sediment surface where it appears as a distinct brownish cover of the sediment surface and of sedentary organisms (Herndl & Peduzzi unpubl.). The episodic sedimentation of the aggregate-layer may contribute significantly not only to the observed high porewater-DOC concentrations but also to subthermocline hypoxia during late summer.

In summary, high temperature and reduced PAR-levels due to flocculent material in the near-bottom layers increase respiration and decrease microphytobenthos productivity during summer leading to hypoxia phenomena during periods of prolonged stratification. Benthic bacteria exhibit seasonal fluctuations suggesting rapid response to ecological events as demonstrated in this study by corresponding fluctuations of bacteria and porewater-DOC.

Acknowledgements. We gratefully acknowledge the assistance of F. Kravos, J. Forte and V Bernetic during work at sea. We thank C. Schiller and G. O. Schinner for their indispensable help in diving and L.-A. Meyer-Reil, J. A. Ott and 3 anonymous

referees for valuable comments on a former draft of the manuscript. M. Stachowitsch provided some of his unpublished data and B. Lorenz improved the English. The hospitality of the staff of the Marine Biology Station Piran is also gratefully acknowledged. Funds were provided by the Austrian Science Foundation (FWF projects 6138 and 6695), the Emil-Boral Foundation, and the Slovenian Research Community.

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Manuscript first received: September 13, 1988
Revised version accepted: February 7, 1989