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IN SITU METABOLISM OF A BENTHIC COMMUNITY IN A SHALLOW BRACKISH LAGOON

(Fish-impoundments of Arcachon Bay – Atlantic coast – France)

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MÉTABOLISME AÉROBIE
CONSOMMATION D'OXYGÈNE
PRODUCTION D'OXYGÈNE
COMMUNAUTÉ BENTHIQUE
LAGUNE SAUMÂTRE PEU PROFONDE

RÉSUMÉ – Le métabolisme d'une communauté benthique en milieu lagunaire saumâtre peu profond a été étudié *in situ*. Durant une année, la production et la consommation d'oxygène ont été mesurées chaque mois, à l'aide d'enceintes cylindriques en plexiglas. Simultanément le méio- et le macrobenthos ont été échantillonnés. L'évolution saisonnière de la demande en oxygène apparaît fortement corrélée à la température (r=0,88). Au cours de l'année, la consommation d'oxygène et la biomasse benthique varient en sens inverse. La quantité d'oxygène captée annuellement a été estimée en tenant compte des diminutions de consommation qui interviennent quand la concentration en oxygène dissous est inférieure à 2 mg/l. La valeur obtenue (1660 g $O_2.m^{-2}.an^{-1}$) est très élevée et concorde avec les résultats obtenus dans des milieux analogues par d'autres auteurs. La consommation d'oxygène durant le printemps et l'été représente 80 % de la demande annuelle; bien qu'élevée, la production (1360 g $O_2.m^{-2}.an^{-1}$) est inférieure à la consommation au cours de ces saisons.

METABOLISM
O_2 UPTAKE
O_2 PRODUCTION
BENTHIC COMMUNITY
SHALLOW BRACKISH LAGOONS

ABSTRACT – The metabolism of a benthic community in shallow brackish impoundments of Arcachon Bay was studied *in situ* by monthly measurements of O_2-uptake and O_2-production during one year using Plexiglas cylinders. Benthic meio– and macrofauna were sampled simultaneously. Seasonal variations of O_2-uptake appeared to be closely correlated with temperature (r = 0.88). O_2-uptake and benthic biomass varied inversely over the year. The annual O_2-uptake was estimated, taking into account a decrease of the rate of O_2-uptake which occurs when the O_2 concentration falls below 2 $mg.l^{-1}$. The value we obtained (1660 g $O_2.m^{-2}.yr^{-1}$) is very high and is consistent with other results for similar environments. The O_2-demand throughout spring and summer represents 80 % of the annual consumption and, in spite of a high production (1360 g $O_2.m^{-2}.yr^{-1}$), O_2-uptake is more important than O_2-production during these seasons.

INTRODUCTION

The fish-impoundments of Arcachon bay (Atlantic coast, France) (Fig. 1) constitute a shallow brackish ecosystem, used for extensive fish-breeding. The study of metabolic activities, especially O_2-consumption, is of particular interest because of the ecological and economic consequences of frequent O_2-deficiencies due to eutrophication. The purpose of this study was to characterize and to quantify the metabolism of the benthic community through O_2-production and O_2-uptake *in situ* measurements. The choice of an *in situ* method was based on several factors. Firstly, it was impossible to reproduce fluctuations of environmental parameters in the laboratory. Secondly, field measurements can be conducted over greater surfaces than is possible with laboratory measurements. Using this method, it is not possible to estimate intensities of the different O_2-consuming processes individually (aerobic respiration of the fauna, bacterial activity, and chemical oxidation of reduced compounds). We have not attempted to separate biological and chemical O_2 demand. There is no satisfactory method for doing this. The use of formaldehyde is criticized by several authors (Dale, 1978; Hargrave & Phillips, 1981). The role of each component in total O_2-demand was also studied. The results will be the subject of another publication (in preparation).

DESCRIPTION OF SITE STUDIED

The fish-impoundments are shallow, brackish lagoonal systems which cover a large surface (1,000 ha) and are isolated from Arcachon Bay by an embankment. Waters are renewed periodically through the action of several sluice gates. Numerous studies have been carried out in these fishponds including those of Labourg (1979) on macrofauna, Castel & Lasserre (1977) on meiofauna, and Baleux *et al.* (1979a-b) on bacteria.

Our station is indicated on Fig. 1. In this area, the water depth fluctuates around 20 cm. The sediment is partially covered with sea grass (*Ruppia cirrhosa*). The surface sediment is oxidized all year to a depth of a few millimeters.

MATERIAL AND METHODS

Field measurements were conducted monthly over a period of one year. They included meio– and macrobenthos sampling, and measurements of salinity, temperature, O_2-content, O_2-production and O_2-uptake.

Temperature and O_2-concentration were measured hourly in the water, using an Orbisphere oxymeter. To sample meiofauna, four handle-cores ($S = 10$ cm^2) were collected. Macrobenthos was sampled using an Ekman grab (four replicates of 225 cm^2). O_2-production and O_2-uptake were measured using Plexiglas cylinders : two transparent (750 and 1.250 cm^2) and two dark (1.000 and 1.500 cm^2) (Jorgensen, 1980; Hargrave & Phillips, 1981; Van Es, 1982; Asmus, 1982). Changes of O_2 concentration were recorded on a chart-recorder. The duration of the incubations was 8 to 10 hours. Inside the enclosures the water was gently stirred in order to prevent O_2 stratification. The water depth in the cylinders ranged between 13 and 20 cm. Transparent cylinders were installed at the beginning of the day but dark cylinders were installed later (11 a.m.) because O_2-content was very low at the beginning of the day. From April, when *Ruppia* plants start to grow, one dark and one transparent cylinder were installed above sediment with *Ruppia* plants and others above sediment without plants.

Fig. 1. – Map of Arcachon Bay and localisation of fish-impoundments of Certes; position of our study site (marked with a star).

Meiofauna and macrofauna were sorted after sieving on 63 µm and 0.5 mm sieves respectively. Meiofaunal biomass was estimated from the data of J. Castel (pers. comm.). Macrofauna were weighed with a Mettler balance after drying at 60°C over 48h (Dry Weight : D W).

RESULTS

Physical and chemical parameters

Over one year, salinity ranged from 8 to 35 ‰. In accordance with Venice classification (1958), this station is located in a poly-mesohaline area. The extent of temperature fluctuations between autumn-winter and spring-summer (Fig. 2A) and the magnitude of diel variations of O_2-content (Fig. 2B) illustrate the environmental conditions in this area.

Meio- and macrobenthic biomass

In order to assess the roles of different components in the community's metabolism, macrofauna have been divided into small macrofauna and large macrofauna. Such a distinction was already proposed by Gerlach *et al.* (1985), based on the study of a muddy-sand subtidal community. In this work, distinction was made by taking into account percentages of individuals retained by a 0.5 mm sieve or by a 1 mm sieve respectively. Small macrofauna included *Tubificoides pseudogaster, Polydora ligni, Streblospio shrubsolii,* and *Chironomus salinarius* larvae. Large macrofauna included *Nereis diversicolor* and *Hydrobia ven-*

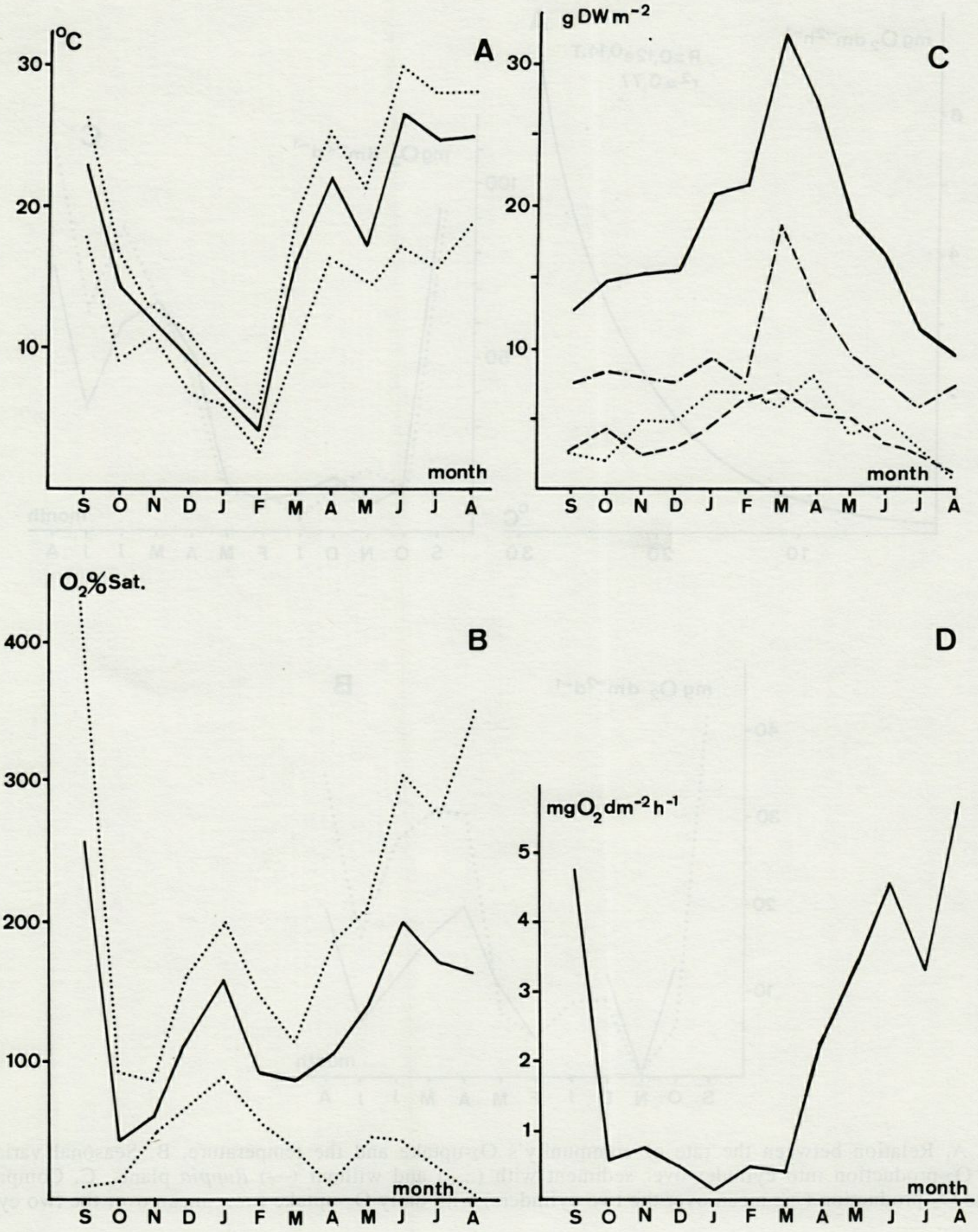

Fig. 2. – A, Daily and seasonal variations in temperature (— : daily average,..... : minimal and maximal values registered during each period of field measurements). B, Daily and seasonal variations in dissolved O_2-content, expressed by percentage of saturation (— : daily average,..... : minimal and maximal values registered during each period of field measurements). C, Seasonal variations in biomass of meiofauna (– – –), small macrofauna (.....), large macrofauna (· · – · –) and in total biomass (—). D, Seasonal variations in the rate of the community's O_2-uptake (mean over the two cylinders).

trosa. Nematodes, Copepods, Ostracods and Turbellarians constituted the meiobenthos.

All faunal groups showed similar seasonal variations (Fig. 2C). Biomass increased during winter to reach a maximal value at the end of winter or beginning of spring. It then decreased. Minimal values were registered in August. A similar seasonal variation of meio– and macrobenthos was also observed by Rudnick *et al.* (1985) for an estuarine community. Total biomass (Fig. 2C) varied between 32 g D W m^{-2} in March and 9.8 g D W m^{-2} in August. Over a year, meiofauna,

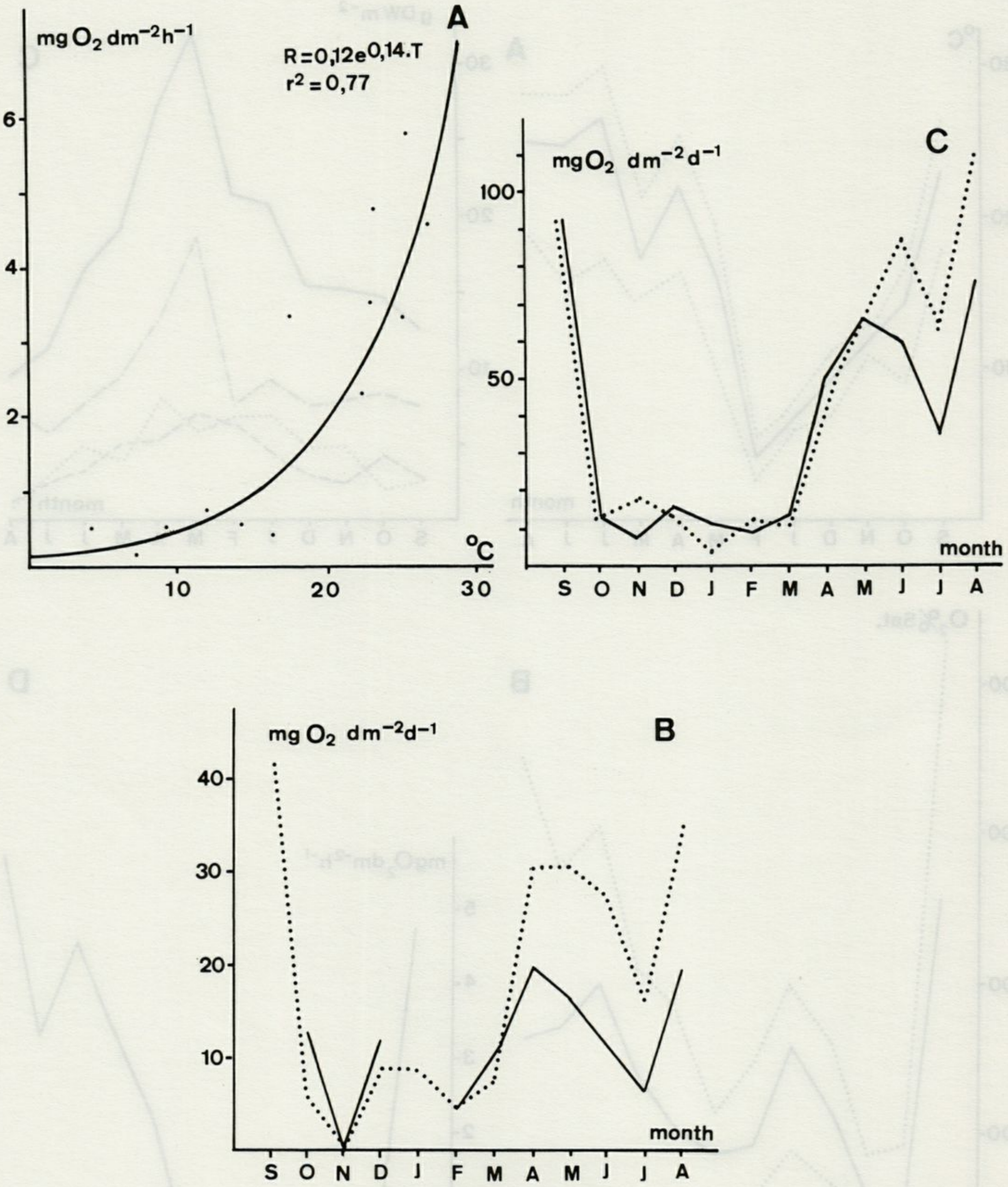

Fig. 3. – A, Relation between the rate of community's O_2-uptake and the temperature. B, Seasonal variations in daily net O_2-production into cylinder over sediment with (.....) and without (—) *Ruppia* plants. C, Comparison of daily gross O_2-production (—: mean over the two cylinders) with daily O_2-uptake (..... : mean over the two cylinders).

small macrofauna, and large macrofauna contributed 22, 25 and 53 %, respectively, to the total biomass. Compared with intertidal or estuarine communities, the macrobenthic/meiobenthic biomass ratio we obtained (3.5) was very low. This result is in accordance with Gerlach's hypothesis (Gerlach 1971) about the relative importance of meiofauna in brackish waters. Along with meiobenthic biomass increase, a decrease of macrobenthic biomass can occur in areas renewed weekly. Such decreases are linked to seasonal O_2-deficiencies (Rosenberg *et al.* 1977, Jorgensen 1980, Rosenberg 1980).

Oxygen-uptake measurements

Significant decreases of O_2-uptake rates were observed toward the end of the incubation during spring and summer measurements. The decrease represented 40 % of initial rates and generally occurred when O_2-concentration in the cylinders fell below 2 mg l^{-1}. Usually, such phenomena are not taken into account (Hargrave 1969, Kemp & Boynton 1981) but in these fish-ponds, such a value is often registered. This leads us to the assumption that the O_2-uptake rate decreases occurring in the cylinders could be representative of *in* *situ* regulations. Study of seasonal variations was made with initial rates but calculation of annual O_2 consumption was made by integrating these regulations of respiratory activity (Thimel, 1988).

Spatial fluctuations between the two cylinders were not important. Averages did not differ significantly (Student's test) so the mean value of the two cylinders was used (Fig. 2D).

During autumn-winter, the O_2-uptake rate is less than 1 mg O_2 dm^{-2} h^{-1} and the average over the cold season equals 0.47 mg O_2 dm^{-2} h^{-1}. O_2 consumption quickly increased between March and April (6 fold). During spring and summer values ranged from 2.30 to 5.75 mg O_2 dm^{-2} h^{-1}. The average oxygen consumption over the warm season was 4.01 mg O_2 dm^{-2} h^{-1} and represents 8.5 times the mean rate of the cold season O_2-uptake. Several regression analyses were tested. O_2 consumption appears to be highly significantly correlated only with temperature (Fig. 3A). This factor explains 77 % of the variance. There are no significant relations between O_2-uptake and O_2-content or salinity. Moreover, it must be noted that O_2-uptake and benthic biomass vary inversely over the year.

Annual oxygen-uptake

Annual O_2-uptake was calculated by taking into account the effects of low oxygen concentration previously mentioned. Diel measurements of dissolved O_2-content were conducted in these fish-ponds (Labourg, unpublished; Escaravage pers. com.). They showed that during summer O_2 was less than 2 mg l^{-1} from 0 to 7 a.m. From this, we have posed the following hypothesis : between April and September, the hourly O_2-uptake rate from 0 to 7 a.m. represents 40 % of diurnal hourly rate. Consequently, daily O_2-uptake equals 83 % of the value obtained by multiplying the diurnal hourly rate by 24. The sum of daily O_2-uptake provides following results. Over the cold season, O_2-uptake amounted to 205 g O_2 m^{-2}. Taking regulations into account, O_2-uptake over the warm season amounted to 1,460 g $O_2 m^{-2}$ whereas it amounted to 1,750 g $O_2 m^{-2}$ if regulations are ignored. Thus annual consumption amounted to 1,660 g O_2 m^{-2} yr^{-1}.

Oxygen-production measurements

From April net production was much higher in transparent cylinders containing *Ruppia* than those including sediment without *Ruppia* (Fig. 3B). O_2-production by microphytobenthos was not negligible however and during autumn-winter negative values of net production often occurred.

To assess gross production, O_2-uptake was subtracted from the net O_2-production mean value (mean over the two cylinders). Daily O_2-uptake and daily O_2-gross production can be compared (Fig. 3C). During summer, consumption greatly exceeds production. Annual gross production was estimated to 1,360 g O_2 m^{-2} yr^{-1}, so the O_2 budget is lower than 1 (O_2-production/O_2-consumption = 0.82).

DISCUSSION AND CONCLUSION

Benthic communities in fish-impoundments are characterized by intense metabolic activity during spring and summer (Castel & Lasserre 1977). This study clearly shows the importance of the O_2-demand fluctuation between cold and warm season as it increases 8.5 fold. Van Es (1982) found a similar result in an estuarine benthic community. The correlation between seasonal O_2-uptake variations and temperature has been shown in several studies (Nixon & Oviatt 1973; Jorgensen 1977; Hargrave & Phillips 1981). In marine sediments exposed to small temperature fluctuations, Dale (1978) did not identify clear seasonal variations. The Q_{10} value we obtained from the linear relationship between log R/log T equals 4.06. This is higher than most published values from coastal environments. Although O_2-concentration appears to have a strong effect on the community's O_2-demand, we did not find any correlations between seasonal variations and O_2-concentration. Some authors found such a relationship (Hargrave & Phillips 1981; Kanneworff & Christensen 1986). In fish-impoundments, O_2-concentration varies greatly but quickly so that the O_2-dependent regulations occur periodically but in a short period of time. Moreover, temperature fluctuations are very important and can conceal the O_2 influence. However, for an O_2-deficient benthic community, Kanneworff & Christensen (1986) found that O_2-uptake over the year represents 80 % of theoretical O_2-demand under steady O_2-concentration conditions and our results are in agreement with theirs.

The main difference between fish-impoundments and other environments is the intensity of the metabolic activity. Compilation of published values (Table 1) shows that our result is among the highest and agrees with those concerning similar environments. In coastal areas, we have noted that O_2-uptake increases when marine influence decreases (Van Es 1982; Nowicki & Nixon 1985). Water depth also seems to be a determining factor. Shallow and brackish waters present the highest range of O_2-demand.

Like O_2-uptake, O_2-production is very much higher in fish-impoundments than in other areas. For a sandy tidal community, Asmus (1982b) ob-

Table I. – Comparison of daily or annual community O_2 consumption in marine and coastal communities. * : results for different stations.

Locality	Daily O2 cons. g O2.m-2.d-1	Annual O2 cons. g O_2.m-2.y-1	References
Abyssal zone			
North eastern Atlantic	0.11 (summer)	-	Patching *et al.* (1986)
Continental shelf			
Eastern Passage - Canada	-	257 (mean over two replicates)	Hargrave & Phillips (1981)
Oyster Ground - North Sea	-	150	De Wilde *et al.* (1984)
Oresund - Denmark	-	143	Kanneworff & Christensen (1986)
Tidal areas			
Northern Wadden Sea	0.17 (winter) 1.70 (summer)	-	Asmus (1982a)
Northern Wadden Sea	-	256	Asmus (1982b)
Northern Wadden Sea	-	186 to 770*	Asmus & Asmus (1985)
Estuaries, fjords			
Limfjorden - Denmark	-	397	Jorgensen (1977)
Lindaspollene - Norway	-	132	Dale (1978)
Ems Dollard - Wadden Sea	-	189 to 683*	Van Es (1982)
Fanafjorden - Norway	-	104 to 119*	Wassman (1984)
Coastal bays, lagoons, salt marshes with tidal influence			
Coastal lagoon - Georgia Bight USA	2.90 (summer)	-	Hopkinson & Wetzel (1982)
Coastal lagoon - Rhode Island USA	-	589 to 803*	Nowicki & Nixon (1985)
Kiel Bight - Swedish coast	2.30 to 5.90 (summer)	-	Asmus *et al.* (1980)
Tidal salt marsh - Louisiana USA	-	823	Hopkinson *et al.* (1978)
Shallow brackish waters			
Salt marsh - Cape Cod USA	-	2,080	Howes *et al* (1984)
Fish impoundments - Atlantic coast - France	1.14 (winter) 6.70 (summer)	1,660	This study
Shallow sound - Northern Baltic	-	-	Jansson & Wulff (1977)
(*Ruppia* community)	2.15 (summer)	-	
(*Cladophora* community)	5.94 (summer)	-	

tained 458 g O_2 m^{-2} yr^{-1}. Along an estuary, Van Es (1982) found O_2-production ranging from 82 to 628 g O_2 m^{-2} yr^{-1}. However, this high production cannot offset the high consumption. Existence of an O_2 budget lower than 1 has been observed by Van Es (1982) in the inner part of an estuary and by Nowicki & Nixon (1895) in a coastal lagoon.

We observed that O_2-demand increases when benthic biomass decreases. The biomass decrease is mainly due to decreases in population densities. From March to July, the population density of meiofauna was reduced 2.9-fold, that of small macrofauna 2.6-fold, while that of large macrofauna was quite steady. Considering a Q_{10} value of 2,05 (Warwick *et al.* 1979; Banse, 1982; Schwinghammer *et al.*, 1986), combination of individual rates of O_2-consumption increase and population density decrease shows that meio– and macrofauna cannot be responsible for the sharp increase of total O_2-demand.

Knowing the O_2-gross production, plant respiration can be assessed. In accordance with Jansson & Wulff (1977) concerning *Ruppia* sp., we have considered that plant respiration equals 30 % of gross production. Using this percentage, plant annual respiration amounts to 408 g O_2 m^{-2} yr^{-1}. Concerning microphytobenthos, percentage respiration/gross production is higher (Jansson & Wulff 1977). Because it is impossible to separate clearly *Ruppia* O_2-production and microphytobenthic O_2-production, we preferred to use a single value. Therefore, the plant respiration value must be considered as a minimal value. It represents 25 % of

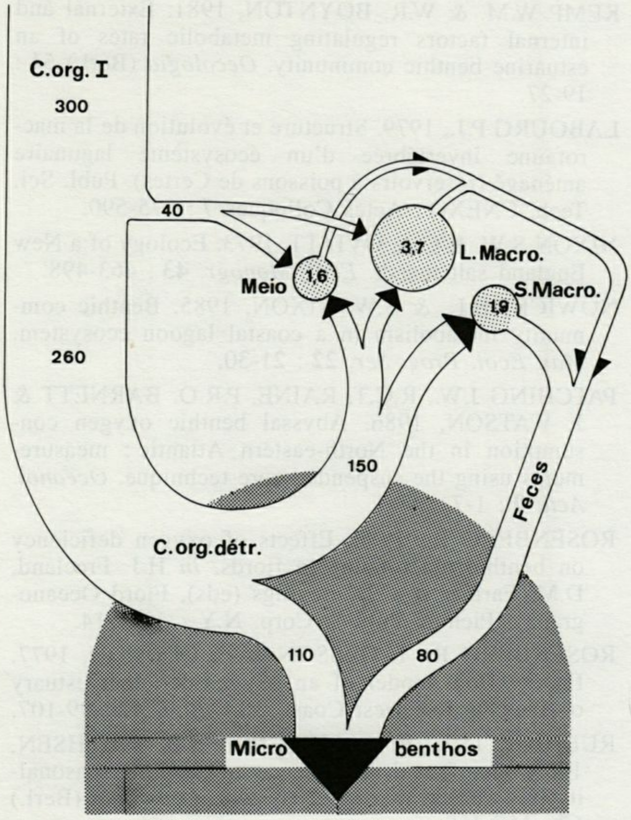

Fig. 4. – Schematic diagram of primary organic carbon utilisation. Fluxes are in g C.m^2.yr^{-1}. Numbers in circles are the values, in g C.m^{-2}, of annual mean biomass of meiofauna (Meio), small macrofauna (S Macro) and large macrofauna (L Macro).

annual O_2-demand. Although these values represent rough estimate, it is clear that the important phytal biomass which characterizes lagoonal environments also appears as a significant factor for the high community's O_2-uptake.

Assessments of the roles of meio-and macrofaunal components based on data from the literature have given the following results. Over the year, meio– and macrofauna contribute 8 and 12 %, respectively, to total O_2-demand. Microbenthos including microfauna and bacteria, contributes 55 % to total O_2-demand and constitutes the major component, especially during spring and summer. According to Caumette (1987), sulfate-reduction is the main process for organic matter mineralization in marine and lagoonal areas. In salt marshes, Howarth & Teal (1979) found the highest sulfate-reduction rate among published values. Thus concerning our study site, we can suppose that the O_2-demand ensuing from the bacterial activity is a dominant pathway. This conclusion is strenghtened by two observations. The Q_{10} value for the community's O_2-demand (Q_{10}=4) is close to sulfate-reduction Q_{10} observed by Jorgensen (1977) (Q_{10}=3 on temperature range from 0 to 30°C). The rapid increase of O_2-demand between March and April appears to be characteristic of a bacterial activity.

Finally a schematic diagram of primary organic carbon utilisation was made (Fig. 4). It showed that only 40 % of the primary production is assimilated by the secondary trophic level. Owing to the weakness of sea water fluxes, the excess of primary production cannot be exported. A high supply of detritic organic matter is thus provided to bacteria. The thermic consequences of the shallowness probably induce the low rate of sulfate-reduction during winter. The spring rise of temperature brings about the start of sulfate-reduction which increases all the more because the amount of detritic organic matter is high. Thus the stock of reduced compounds also increases as does consequently O_2-uptake required to oxidize them.

REFERENCES

ASMUS H., 1982a. Field measurements on respiration and secondary production of a benthic community in the Northern Wadden Sea. *Neth. J. Sea Res.* **16** : 403-413.

ASMUS R., 1982b. Field measurements on seasonal variation of the activity of primary producers on a sandy tidal flat in the Northern Wadden Sea. *Neth. J. Sea Res.* **16** : 389-402.

ASMUS H. & R. ASMUS, 1985. The importance of grazing food chain for energy flow and production in three intertidal sand-bottom communities of the Northern Wadden Sea. *Helgoländer wiss. Meeresunters* **39** : 273-301.

ASMUS H., H. THEEDE, H.G. NEUHOFF & W. SCHRAMM, 1980. The role of epibenthic macrofauna in the oxygen budget of *Zostera* communities from the Baltic Sea. *Ophelia* supp. **1** : 99-111.

BALEUX B., P. CAUMETTE & M. TROUSSELLIER, 1979a. Numération et approche qualitative des populations bactériennes des lagunes aménagées de Certes (Arcachon). I. Bactéries hétérotrophes aérobies. Publ. Sci. Tech. CNEXO : Actes Colloques 7 : 503-528.

BALEUX B., P. CAUMETTE & M. TROUSSELLIER, 1979b. Numération et approche qualitative des populations bactériennes des lagunes aménagées de Certes (Arcachon). II. Bactéries sulfo-oxydantes photosynthétiques. Publ. Sci. Tech. CNEXO : Actes Colloques 7 : 529-542.

BANSE K., 1982. Mass-sealed rates of respiration and intrinsic growth in very small invertebrates. *Mar. Ecol. Prog. Ser.* **9** : 281-297.

CASTEL J. & P. LASSERRE, 1977. Colonisation et distribution spatiale des Copépodes dans des lagunes semi-artificielles. *In* B.F. Keegan, P.O. Ceidigh & P.J.S. Boaden (eds), Biology of benthic organisms. Pergamon Press : 129-146.

CAUMETTE P., 1987. Rôle des bactéries phototrophes et des bactéries sulfo-oxydantes dans les milieux lagunaires. O.R.S.T.O.M. (ed), Coll. Etudes et Thèses, Paris, 305 p.

DALE T., 1978. Total, chemical and biological oxygen consumption of the sediments in Lindaspollene, Western Norway. *Mar. Biol.* **49** : 333-341.

DE WILDE P.A.W.J., E.M. BERGHUIS & A. KOK, 1984. Structure and energy demand of the benthic community of the oyster ground, central North Sea. *Neth. J. Sea Res.* **18** : 143-159.

GERLACH S.A., 1971. On the importance of marine meiofauna for benthos communities. *Oecologia* (Berl.) **6** : 176-190.

GERLACH S.A., A.E. HAHN & M. SCHRAGE, 1985. Size spectra of benthic biomass and metabolism. *Mar. Ecol. Prog. Ser.* **26** : 161-173.

HARGRAVE B.T., 1969. Similarity of oxygen uptake by benthic communities. *Limnol. Oceanogr.* **14** : 801-805.

HARGRAVE B.T. & G.A. PHILLIPS, 1981. Annual *in situ* carbon dioxide and oxygen flux across a subtidal marine sediment. *Estuar. coast. shelf Sci.* **12** : 725-737.

HOPKINSON C.S. & R.L. WETZEL, 1982. *In situ* measurements of nutrients and oxygen fluxes in a coastal marine benthic community. *Mar. Ecol. Prog. Ser.* **10** : 29-35.

HOPKINSON C.S., J.W. DAY & B.T. GAEL, 1978. Respiration studies in a Louisiana salt marsh. Ann. Centr. Cienc. del Mar y Limnol. Univ. Nal. Auton. México **5** : 225-238.

HOWARTH R.W. & J.M. TEAL, 1979. Sulfate reduction in a New England salt marsh. *Limnol. Oceanogr.* **24** : 299-1013.

HOWES B.L., J.W.H. DACEY & G.M. KING, 1984. Carbon flow through oxygen and sulfate reduction pathways in salt marsh sediments. *Limnol. Oceanogr.* **29** : 1037-1051.

JANSSON B.O. & F. WULFF, 1977. Ecosystem analysis of a shallow sound in the Northern Baltic. A joint study by the Askö group. Contrib. Askö Lab. Univ. Stockholm **18** : 1-160.

JORGENSEN B.B., 1977. The sulfur cycle of a coastal marine sediments (Limfjorden, Denmark). *Limnol. Oceanogr.* **22** : 814-832.

JORGENSEN B.B., 1980. Seasonal oxygen depletion in the bottom waters of a Danish fjord and its effect on the benthic community. *Oikos* **34** : 68-76.

KANNEWORFF E. & H. CHRISTENSEN, 1986. Benthic community respiration in relation to sedimentation of phytoplankton in the Oresund. *Ophelia* **26** : 269-284.

KEMP W.M. & W.R. BOYNTON, 1981. External and internal factors regulating metabolic rates of an estuarine benthic community. *Oecologia* (Berl.) **51** : 19-27.

LABOURG P.J., 1979. Structure et évolution de la macrofaune invertébrée d'un écosystème lagunaire aménagé (réservoirs à poissons de Certes). Publ. Sci. Tech. CNEXO : Actes Colloques **7** : 575-590.

NIXON S.W. & C.A. OVIATT, 1973. Ecology of a New England salt marsh. *Ecol. Monogr.* **43** : 463-498.

NOWICKI B.L. & S.W. NIXON, 1985. Benthic community metabolism in a coastal lagoon ecosystem. *Mar. Ecol. Prog. Ser.* **22** : 21-30.

PATCHING J.W., R.C.T. RAINE, P.R.O. BARNETT & J. WATSON, 1986. Abyssal benthic oxygen consumption in the North-eastern Atlantic : measurements using the suspended core technique. *Oceanol. Acta* **9** : 1-7.

ROSENBERG R., 1980. Effects of oxygen deficiency on benthic macrofauna in fjords. *In* H.J. Freeland, D.M. Farmer & C.D. Levings (eds), Fjord Oceanography. Plenum Publish Corp, N.Y. : 499-514.

ROSENBERG R., I. OLSSON & E. OLUNDH, 1977. Energy flow model of an oxygen-deficient estuary on the Swedish west Coast. *Mar. Biol.* **42** : 99-107.

RUDNICK D.T., R. ELMGREN & J.B. FRITHSEN, 1985. Meiofaunal prominence and benthic seasonality in a coastal marine ecosystem. *Oecologia* (Berl.) **67** : 157-168.

SCHWINGHAMER P., B. HARGRAVE, D. PEER & C.M. HAWKINS, 1986. Partitioning of production and respiration among size groups of organisms in an intertidal benthic community. *Mar. Ecol. Prog. Ser.* **31** : 131-142.

THIMEL A., 1988. Etude *in situ* du métabolisme aérobie d'une communauté benthique dans une lagune mixohaline peu profonde. Thèse Doctorat, Université Bordeaux I, 161 pp.

VAN ES F.B., 1982. Community metabolism of intertidal flats in the Ems-Dollard Estuary. *Mar. Biol.* **66** : 95-108.

WARWICK R.M., I.R. JOINT & P.J. RADFORD, 1979. Secondary production of the benthos in an estuarine environment. *In* R.L. Jefferies & A.J. Davy (eds), Ecological processes in coastal environments. Blackwell, Oxford : 429-450.

WASSMAN P., 1984. Sedimentation and benthic mineralization of organic detritus in a Norwegian Fjord. *Mar. Biol.* **83** : 83-94.

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