



Inorganic carbon fluxes at the water–sediment interface in five littoral systems in Spain (southern Europe)

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Abstract

The benthic fluxes of dissolved inorganic carbon have been measured in five different littoral ecosystems in Spain (Southern Europe). The values measured by means of benthic chambers ranged between 30 and 378 mmol m⁻² d⁻¹ and may be considered relatively high. They were linearly correlated with the organic carbon content in surface sediments. The concentration of dissolved inorganic carbon in interstitial water presents a strong vertical gradient (30 mM at 25 cm), with diffusive fluxes between 0.1 and 14.1 mmol m⁻² d⁻¹. The comparison between diffusive fluxes and benthic chamber (*in situ*) fluxes shows the important role of the benthic macrofauna irrigation processes in relation to species exchange across the sediment–water interface.

Abbreviations: DIC – Dissolved Inorganic Carbon; LOICZ – Land–Ocean Interaction in the Coastal Zone; OMEX – Ocean Margin Exchange; OC – Organic Carbon; DO – Dissolved oxygen

Introduction

Littoral zones only comprise approximately 7% of the total area of the oceans but they are very important since they are, geochemically and biologically, the most active areas of the biosphere and exchange considerable quantities of material and energy with the open ocean (Gattuso et al., 1998). These zones are characterized for their high productivity and for receiving substantial quantities of organic material and nutrients, mainly from the rivers; some 90% of total supplies of these reach the oceans this way (Gibbs, 1981). More than 20% of primary oceanic productivity takes place in littoral systems (Wollast, 1998), which represents a large supply of autochthonous organic material. On the sediment in particular, between 25% and 50% of the primary productivity is deposited (Wollast, 1991). This organic material sediments rapidly and its mineralization by different routes, both aerobic and anaerobic, gives rise to considerable fluxes of inorganic carbon across the water–sediment interface. These benthic fluxes present a high variability

ranging between 2 and 700 m⁻² d⁻¹ in littoral ecosystems (e.g. Andersen & Hargrave, 1984; Mackin & Swider, 1989; Forja et al., 1994; López et al., 1995; Glud et al., 1998; Rysgaard, 1998; Jahnke & Jahnke, 2000).

The release of inorganic carbon from sediments could make that some littoral systems act as a source of CO₂ to the atmosphere, in contrast to the global behaviour of the ocean (Kempe & Pegler, 1991; Boehme et al., 1998; Frankignoulle et al., 1998). However, it is difficult to model the complex behaviour of coastal zones, and the wide diversity of systems together with the intrinsic heterogeneity that they present, in many cases requires individualized study of particular systems. In fact, various international projects (e.g. LOIS, OMEX) have been set up with the objective of obtaining more knowledge of the carbon cycle and nutrient cycle in coastal zones.

This paper presents some of the factors that affect the variability of the inorganic carbon benthic fluxes in 5 different littoral ecosystems selected in Spain. To this end, the fluxes of dissolved inorganic



Figure 1. Localization of the coastal system in the spanish coast.

carbon (DIC) and oxygen (DO) have been studied using benthic chambers; in addition, the diffusive fluxes obtained from the vertical concentration gradients in the interstitial water of sediment samples have been characterized.

Materials and methods

Description of sampling station

Figure 1 is a map showing the location of the zones studied on the coasts of Spain. The Bay of Cádiz (CB) is a temperate, shallow-water coastal ecosystem that covers an area of 38 km². This zone receives urban effluents from a population of 600 000 inhabitants. Two different sampling stations were selected. Previous studies provide data of the spatial and seasonal variations in benthic fluxes of inorganic carbon and nutrients at this site (Gómez-Parra & Forja, 1993; Forja et al., 1994; Forja & Gómez-Parra, 1998). The second estuary area selected is that of the Palmones river and the adjacent salt-marshes covering approximately 2 km² (PE). This ecosystem is a representative example of the final riverbed of a small river basin and receives organic matter from urban and industrial sources. Sampling was performed at four selected stations. The third zone studied is the estuary of the Odiel river (OdE) with an area of 71 km², which is severely affected by industrial wastes. The four stations were located at the outer part of the estuary. The Ason estuary (AE) is the fourth zone elected; it consists of a broad area of saltmarshes formed by the confluence of several rias that supply organic material and sediments

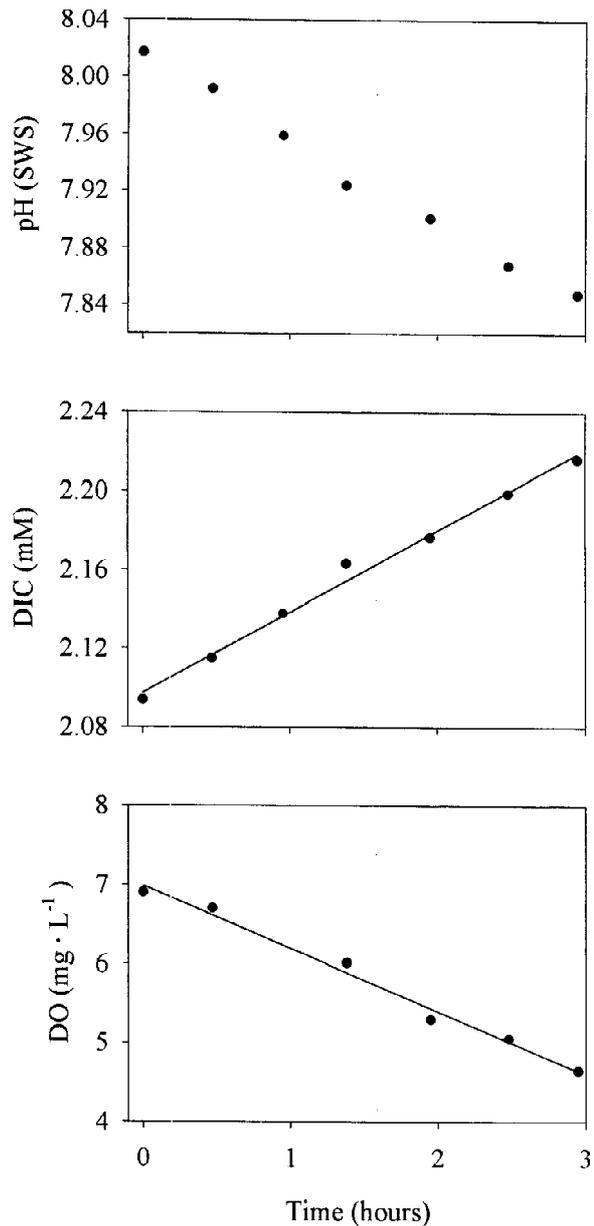


Figure 2. Dissolved inorganic carbon (DIC), pH (SWS) and dissolved oxygen (DO) evolution into a benthic chamber.

from the basins drained; this complex of marshes and rivers covers an area of 35 km². Samples were taken at 5 stations located along the length of the estuary. The fifth study area selected is the Oka estuary (OE), which covers an area of approximately 230 km². It forms part of the Biosphere Reserve of Urdaibai. The final stretch of 12 km of the river takes the form of a ria extending to its mouth, where it forms a wide estuary, at which point our sampling station was located.

Table 1. Intervals of variation of depth, temperature and salinity at the zones studied. The granulometric distribution of the surface sediments is also included

Site	Date	Water depth (m)	Temp (°C)	Salinity	Granulometry (mm)
Bay of Cádiz	July 98	1.7–5.7	13.6–18.6	36.3–37.3	0.20–0.33 (sand)
Estuary of Palmones (Cádiz)	November 98	2.0–5.0	13.0–26.9	30.2–36.9	0.07–0.28 (sand)
Odiel Estuary (Huelva)	September 98	2–4.7	19.1–24.0	36.3–38.4	0.03–0.18 (sand–slime)
Ason Estuary	June 98	0.9–2.0	17.0–20.9	23.7–33.4	0.04–0.34 (sand–slime)
Oka Estuary	June 98	1.5	17.7	33.7	0.10 (sand)

These five littoral systems are listed in Table 1, which gives the dates of sampling, the intervals of variation of depths, salinities and temperatures for each.

Benthic fluxes: measurements and analytical methods

Fluxes *in situ* were measured using two Plexiglass opaque benthic chambers and were constructed with a semi-ellipsoid shape of circular section measuring 0.385 m². Their volume ranged from 59.1 to 89.8 l. The chamber design included a recirculation pump to avoid stratification inside (Gomez-Parra & Forja, 1992) providing a simulation of water current at a range of velocities between 5 and 30 cm s⁻¹ near to the bottom. The chambers remained on the sea bottom for 4–5 h, and samples were collected every 30 min. Samples were kept at 4 °C and analyzed within 6 h of collection. Initial pH (SWS) was measured with combined glass electrodes (Metrohm, ref. 6.0210.100) and alkalinity by potentiometric measurement (Metrohm 716 DMS). Measurements performed on the samples taken from the benthic chambers were based on sample quantities of very close to 100 g weight (± 0.001 g) and in the case of samples of interstitial water, volumes of 2.000 ml were used. In samples of sea water, the valuations were performed with HCl 0.1 M in NaCl 0.7 M, while in estuarine water samples, they were performed with HCl 0.1 M. In the latter case, the effect of the dilution on the ionic strength was taken into account during the course of the valuation. The concentration of dissolved inorganic carbon (DIC) was obtained from the initial pH and from the total alkalinity. The accuracy of the DIC quantification method is ± 5 μ M. Dissolved oxygen (DO) was measured using the Winkler method (Grasshoff et al., 1983) and the salinity by means of an induction salinometer (Beckman, Mod. RS-10).

For the study of the diffusive fluxes, sediment gravity cores (60 mm inner diameter) were taken by scuba and were transported refrigerated to the laboratory within 3 h. For the extraction of interstitial water, the gravity cores were sliced at 1 cm intervals and the sections thus obtained were centrifuged at 15 000 g for 30 min. Sediment cores and subsequent analysis were carried out under an inert (N₂) atmosphere. Sulfate was determined gravimetrically and chloride by potentiometric evaluation (Metrohm 670). Porosity was calculated from water loss after drying at 80 °C until constant weight. The organic carbon (OC) content was determined according to the method of El Rayis (1985) from sediment previously dried, milled and sieved to 63 μ m.

Results

The benthic fluxes have been calculated from the dimensions of the chambers and from the fits of the variations in concentration with time, to linear or exponential equations (Forja et al., 1994; Forja & Gómez-Parra, 1998). In Figure 2 is shown an example of the evolution of the pH and the concentrations of inorganic carbon and oxygen inside of a benthic chamber. In most of the samples studied, the evolution over time is of the linear type. It can be appreciated from Figure 2 that, in line with increasing time of incubation, there is an increase of DIC accompanied by a decrease in oxygen and pH. These variations are related to the intensity of the diagenetic processes of the organic matter in the sediments.

Figure 3 shows the evolution with depth in the sediment of variable related to the behaviour of inorganic carbon, for the more marine stations of the 5 systems studied. In spite of the large differences between them,

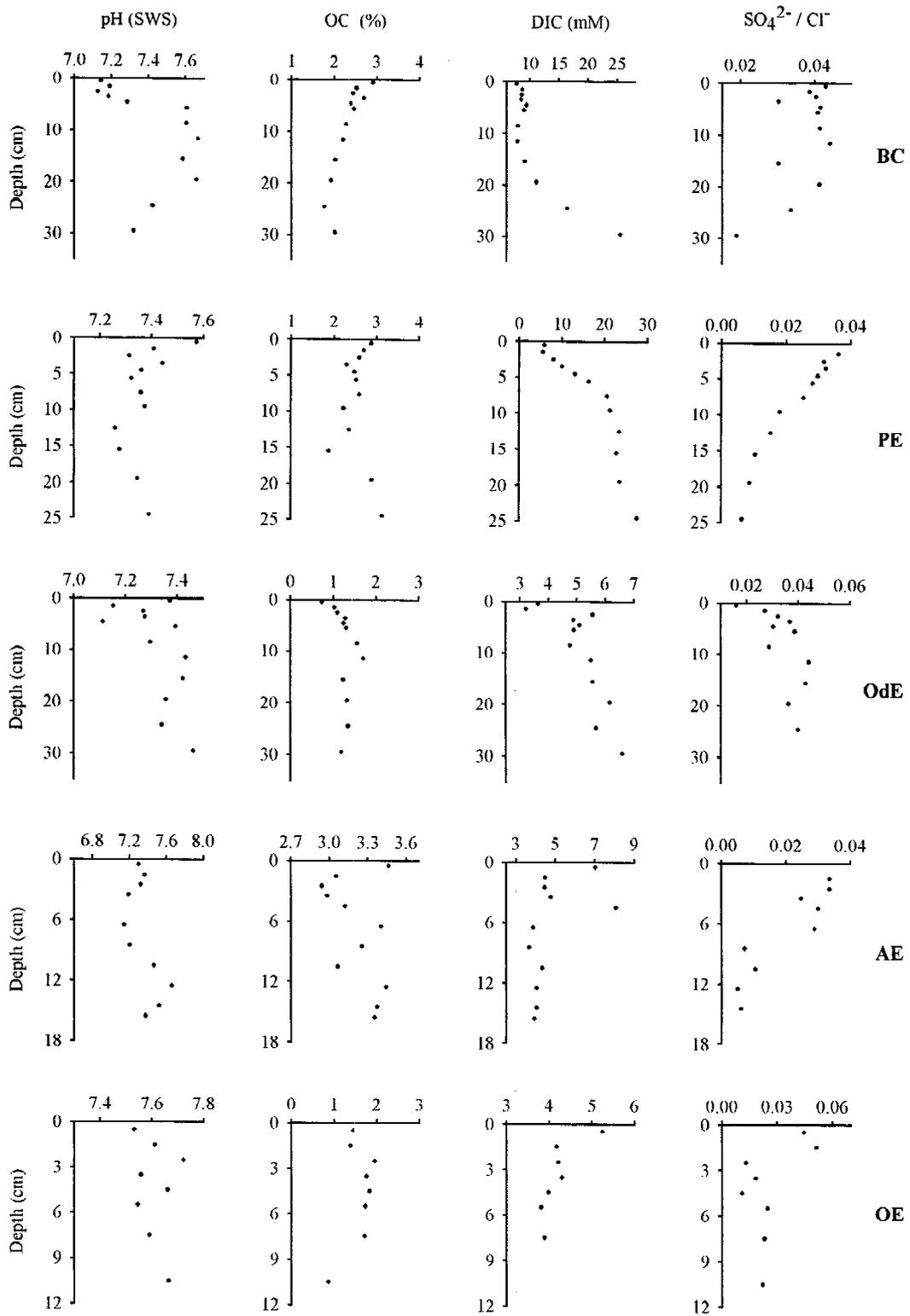


Figure 3. Vertical variations in sediments of pH (SWS), organic carbon concentration (OC), the dissolved inorganic carbon concentration (DIC), and the ratio sulfate/chloride in the more marine stations.

some general trends can be observed. The content of organic carbon in the sediment remains relatively constant and a slight decrease with depth can be appreciated, related to the high efficiency of the aerobic and anaerobic routes of oxidation of the organic material (Balzer, 1984, Thamdrup & Canfield, 1996). In parallel, there is a progressive increase of the concentration of inorganic carbon with depth, reaching a value of 30 mm at a depth of 25 cm, in the estuary of the river Palmones (PE). The evolution of the $\text{SO}_4^{2-} / \text{Cl}^-$ ratio with the depth of sediment, in all the systems with the exception of the Odiel estuary where it hardly varies at all, is indicative that the sulfate participates actively in the degradation of the organic material. The value of pH in the interstitial water do not experiment any well-defined trend with depth.

The diffusive flux was calculated by means of Fick's law (Berner, 1976):

$$F = \phi D_s \left(\frac{\partial C}{\partial z} \right)_{z=0}$$

where ϕ is the porosity, C is the porewater concentration, z is the depth, and D_s is the molecular diffusion; $(\partial C / \partial z)_{z=0}$ is the concentration gradient across the water-sediment interface and was calculated by means of the linear fitting of C against z for the surface layer of the sediment. D_s was obtained from the empirical expression proposed by Sweert et al. (1991). An average coefficient of diffusion at infinite dilution (D_0) has been used, taking into account the concentrations of carbonate and bicarbonate and the values of D_0 for these species at 25 °C proposed by Li & Gregory (1974).

Table 2 shows the intervals of variation of diffusive and in situ fluxes of DIC in the zones studied. Diffusive fluxes values ranged from 0.1 (Ason Estuary) to 14.1 $\text{mmol m}^{-2} \text{d}^{-1}$ (Palmones estuary) and the in situ fluxes between 34.2 (Cadiz Bay) to 378.4 $\text{mmol m}^{-2} \text{d}^{-1}$ (Oka estuary), respectively.

In the Ason estuary, the content of OC (%) is higher than in the rest of the systems (Table 2), which is due to this estuary being at the confluence of several rivers each of which supply relatively large quantities of organic material and sediments from the land area drained by them. These high values are reflected in the benthic fluxes of oxygen and DIC, which reach values of -117.9 and $260.1 \text{ mmol m}^{-2} \text{d}^{-1}$, respectively.

Discussion

The interstitial water of marine sediments is characterized by normally having high concentrations of inorganic carbon and nutrients. In spite of the great variability between the zones studied, a progressive increase of the inorganic carbon dissolved in the interstitial water, with increasing depth, has generally been detected, as in most littoral zones. This behaviour has been widely described in the bibliography (Emerson et al., 1980; Devol, 1987; Hansen & Blackburn, 1991; Barbanti et al., 1995; Komada et al., 1998). However, these profiles are usually irregular, due mainly to the great vertical heterogeneity presented by the sediments of the zone, as well as to the intense processes of irrigation of the benthic macrofauna.

In all of the systems studied, diffusive exchanges estimated from the observed porewater gradients are significantly less than those estimated with the benthic flux chambers. The main reasons for these differences in estimates are undoubtedly irrigation by benthic organisms and the heterogeneity of the sediment. The spatial resolution that has been used in the study of the sediment cores (1 cm), may also contribute to these differences between the *in situ* and diffusive fluxes. The under-estimation of the benthic fluxes of inorganic carbon calculated in sediment cores has been described by Glud et al. (1988) and Forja & Gómez-Parra (1998). This phenomenon has also been found in the exchange of other substances, mainly nutrients (e.g. Aller et al., 1985; Hopkinson, 1987; Jahnke & Jahnke, 2000). All this demonstrates that the chamber incubations are required to provide accurate estimates of benthic fluxes.

Figure 4 shows the evolution of the average fluxes of DIC and DO with the temperature in each of the littoral zones studied. In spite of the high values of these fluxes in the Oka estuary, in comparison with the rest of the zones, it can be observed from these graphs how an increase of the DO and DIC fluxes is produced with increased temperature. The relationship between the fluxes and temperature exists because the processes of degradation of the organic material mediated by the microorganisms show a high dependence on temperature (Aller, 1980; Aller & Benninger, 1981). Observations made in marine coastal areas with large variations in the temperature of the bottom water have revealed that low temperatures tend to reduce microbial activity (Shiah, 1994; Thamdrup et al., 1998) and, therefore, gives rise to less benthic fluxes.

Table 2. Porosity (ϕ) and organic carbon (OC) content of the surface sediments (depth < 5 cm), together the benthic fluxes (in $\text{mmol m}^{-2} \text{d}^{-1}$) of dissolved oxygen (DO) and dissolved inorganic carbon (DIC) (*in situ* and diffusive) in the coastal systems studied

Site	ϕ	OC (%)	DO <i>in situ</i> flux	DIC <i>in situ</i> flux	DIC diffusive flux
Bay of Cádiz	0.52–0.84	1.5–2.6	–65.6–(– 31.84)	34.2– 97.5	0.3–3.3
Estuary of Palmones (Cádiz)	0.68–0.73	1.4–2.8	–147.5–(–111.3)	86.8–256.2	1.5–14.1
Odiel Estuary (Huelva)	0.42–0.55	1.1–2.4	–120.31–(– 41.2)	139.7–287.5	0.9–8.7
Ason Estuary	0.33–0.53	2.2–3.7	–117.9–(– 41.6)	66.2–260.1	0.1–2.6
Oka Estuary	0.35	1.2	–181.3	378.4	1.8–3.4

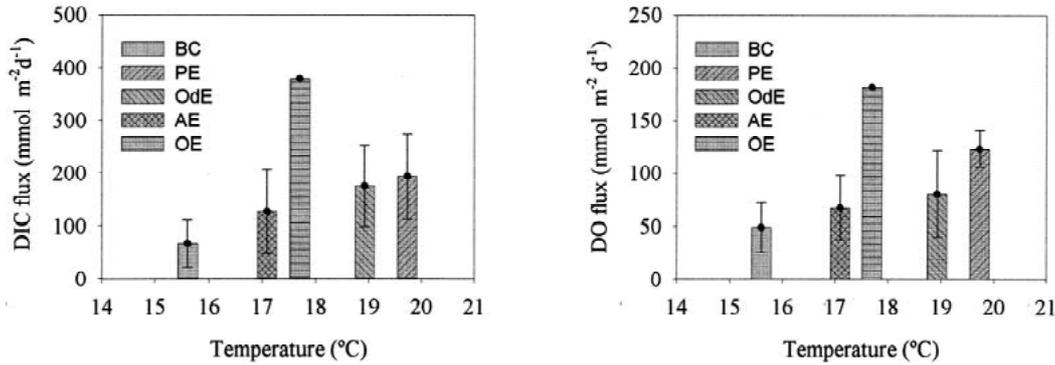


Figure 4. Mean values of dissolved inorganic carbon (DIC) and dissolved oxygen (DO) benthic fluxes versus temperature of the studied coastal zones.

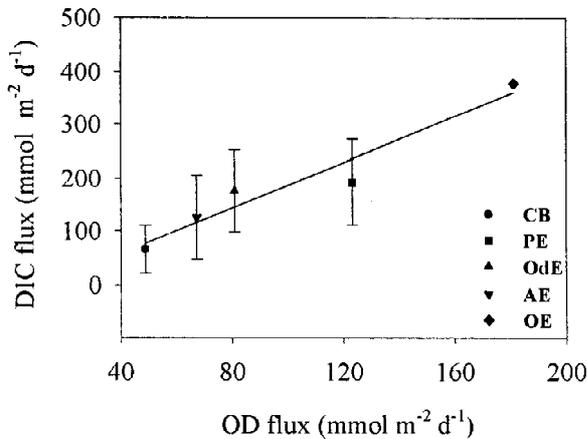


Figure 5. Relationship between of dissolved inorganic carbon and dissolved oxygen benthic fluxes.

The relationship between the average benthic fluxes of DIC and DO in each of the zones studied is shown in Figure 5. Both fluxed are very well correlated ($r^2 = 0.94$), which shows us that when more oxygen is consumed in the sediment, for the re-mineralization of the organic matter, a great flux of DIC is produced in

the overlying water. The slope of the line has a value of 2.14 (this being the Community Respiration Quotient, or CRQ), which indicates to us that the organic material in these Spanish coastal zones studied is degraded by both aerobic and anaerobic processes.

From Table 3 high variability can be observed in the inorganic carbon fluxes measured using chambers, with the lowest value of $8.8 \text{ mmol m}^{-2} \text{d}^{-1}$ being presented in the Fjords of Arctic Norway (Glud et al., 1998) and the highest value of $732 \text{ mmol m}^{-2} \text{d}^{-1}$ in shallow littoral ecosystems located in the Balearic Islands (López et al., 1995). The values of the inorganic carbon fluxes obtained in this study range between 35 and $378 \text{ mmol m}^{-2} \text{d}^{-1}$ (Table 2), and can be considered relatively high.

Conclusions

The benthic fluxes of inorganic carbon and oxygen measured in these Spanish littoral zones are relatively high in comparison with other littoral systems described in the literature.

Table 3. Benthic fluxes of dissolved inorganic carbon measured with benthic chamber in other marine ecosystems. The fluxes are expressed in $\text{mmol m}^{-2} \text{d}^{-1}$

Site	Depth. (m)	Temp (°C)	CO ₂ (%)	DIC Flux	Reference
S. Francisco Bay (S California)	1.5–14	14.3–14.5	1.4	17.0– 29.0	Hammond et al. (1985)
Cape Lookout Bight (N Carolina)	–	12.0–27.5	3.3–5.0	31.0–162.7	Martens & Klump. (1987)
Tomales Bay (California)	4–6	–	–	14.4– 26.0	Dollar et al. (1991)
Albufera of Majorca (Mediterráneo)	–	28.5–31.9	–	63.4–732.0	López et al. (1995)
Cádiz Bay (Spain)	2–14	18.4± 6.8	2.2–3.1	154.6–224.5	Forja & Gómez-Parra (1998)
Fjords of Arctic Norway	115–329	–1.7–7.0	1.5–2.5	8.8– 19.8	Glud et al. (1998)

These fluxes show a direct relationship with water temperature, such that at increasing temperatures, the microbial activity in the sediment is greater and, therefore, higher fluxes are produced across the water-sediment interface.

The correlation between benthic chamber fluxes of dissolved inorganic carbon and dissolved oxygen confirms that CO₂ and O₂ fluxes are coupled processes in Spanish coastal sediments. The ratio between the two types of flux has a value of 2.1 (CRQ), which is indicative of the importance of the anaerobic routes for the degradation of the organic matter in the zones studied.

The comparison between diffusive fluxes and benthic chamber (*in situ*) fluxes shows the important role of the benthic macrofauna irrigation processes in relation to species exchange across the sediment-water interface.

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References

- Aller, R. C., 1980. Diagenetic processes near the sediment-water interface of Long Island Sound. I. Decomposition and nutrient element geochemistry (S, N, P). *Adv. Geophys.* 22: 237–350.
- Aller, R. C. & L. K. Benninger, 1981. Spatial and temporal patterns of dissolved ammonium, manganese, and silica fluxes from bottom sediments of Long Island Sound, U.S.A. *J. mar. Res.* 39: 295–314.
- Aller, R. C., J. E. Mackin, W. J. Ullman, W. Chen-Hou T. Shing-Min, J. Jian-Cai, S. Yong-Nian & H. Jia-Zhen, 1985. Early chemical diagenesis, sediment-water solute exchange, and storage of reactive organic matter near the mouth of the Changjiang, East China Sea. *Cont. Shelf Res.* 4: 227–251.
- Andersen, F. O. & B. T. Hargrave, 1984. Effects of *Spartina* detritus enrichment on aerobic/anaerobic benthic metabolism in an intertidal sediment. *Mar. Ecol. Prog. Ser.* 16: 161–171.
- Balzer, W., 1984. Organic water degradation and biogenic cycling in a nearshore sediment (Kiel Bight). *Limnol. Oceanogr.* 29: 1231–1246.
- Barbanti, A., M. C. Bergamini, F. Frascari, S. Miserocchi, M. Ratta & G. Rosso, 1995. Diagenetic Processes and Nutrient Fluxes at the Sediment-Water Interface, Northern Adriatic Sea, Italy. *Mar. Freshwat. Res.* 46: 55–67.
- Berner, R. A., 1976. Inclusion of adsorption in the modeling of early diagenesis. *Earth Planet. Sci. Lett.* 29: 333–340.
- Boehme, S. E., C. L. Sabine & C. E. Reimers, 1998. CO₂ fluxes from a coastal transect: a time-series approach. *Mar. Chem.* 63: 49–67.
- Devol, A. H., 1987. Verification of flux measurements made with *in situ* benthic chambers. *Deep Sea Res.* 34: 1007–1026.
- Dollar, S. J., S. V. Smith, S. M. Vink, S. Obrebski. & J. T. Hollibaugh, 1991. Annual cycle of benthic nutrient fluxes in Tomales Bay, California and contribution of the benthos to total ecosystem metabolism. *Mar. Ecol. Prog. Ser.* 79: 115–125.
- El Rayis, O. A., 1985. Re-assessment of the tritration methods for determination of organic carbon in recent sediments. *Rapp. Comm. int. Mer Médit.* 29: 45–47.
- Emerson, S., R. Jahnke, M. Bender, P. Froelich, G. Klinkhammer, C. Bowser & G. Setlock, 1980. Early diagenesis in sediments from the eastern equatorial Pacific, 1. Pore water nutrient and carbonate results. *Earth Planet Sci. Lett.* 49: 57–80.
- Forja, J. M., J. Blasco & A. Gómez-Parra, 1994. Spatial and seasonal variation of 'in situ' benthic fluxes in the Bay of Cádiz (SW Spain). *Estuar coastal shelf Sci.* 39: 127–141.
- Forja, J. M. & A. Gómez-Parra, 1998. Measuring nutrient fluxes across the sediment-water interface using benthic chambers. *Mar. Ecol. Prog. Ser.* 164: 95–105.
- Frankignoulle M., G. Abril, A. Borges, I. Bourge, C. Canon, B. Delille, E. Libert & J.-M. Théate, 1998. Carbon Dioxide Emissions from European Estuaries. *Science* 282: 434–436.
- Gattuso, J. P., M. Frankignoulle & R. Wollast, 1998. Carbon and carbonate metabolism in coastal aquatic ecosystems. *Annu. Rev. Ecol. Syst.* 29: 405–434.
- Gibbs, R. J., 1981. Sites of the rivers derived sedimentation in the ocean. *Geology* 9: 77–80.

- Glud, R. N., O. Holby, F. Hoffmann & D. E. Canfield, 1998. Benthic mineralization and exchange in Arctic sediments (Svalbard, Norway). *Mar. Ecol. Prog. Ser.* 173: 237–251.
- Gómez-Parra, A. & J. M. Forja, 1992. Significance of benthic regeneration in nutrient balance in the Bay of Cadiz, SW Spain (a shallow semi-closed coastal ecosystem). *Sci. Tot. Envir. Suppl.* 1992: 1079–1086.
- Gómez-Parra, A. & J. M. Forja, 1993. Benthic nutrient fluxes in Cadiz Bay (SW Spain.). *Hydrobiologia* 252: 23–34.
- Grasshoff, K., M. Ehrhardt & K. Kremling, 1983. *Methods of Seawater Analysis*. Verlag Chemie, R.F.A. 259–260.
- Hammond, D. E., C. Fuller, D. Harmon, B. Hartman, M. Korosec, L. G. Miller, R. Rea, S. Warren, W. Berelson & S. W. Hager, 1985. Benthic fluxes in San Francisco Bay. *Hydrobiologia* 129: 69–90.
- Hansen, L. S. & T. H. Blackburn, 1991. Aerobic and anaerobic mineralization of organic material in marine sediment microcosms. *Mar. Ecol. Prog. Ser.* 75: 283–291.
- Holligan, P. M. & W. A. Reiners, 1992. Predicting the Responses of the Coastal Zone to Global Change. In Woodward, F. I. (ed.), *Global Climate Change*. Academic Press, London: 212–255.
- Hopkinson, C. S., 1987. Nutrient regeneration in shallow-water sediments of the estuarine plume region of the nearshore Georgia Bight, U.S.A. *Mar. Biol.* 94: 127–142.
- Jahnke, R. A. & D. B. Jahnke, 2000. Rates of C, N, P and Si recycling and denitrification at the U.S. Mid-Atlantic continental slope depocenter. *Deep-Sea Res. I* 47: 1405–1428.
- Kempe, S. & K. Pegler, 1991. Sinks and sources of CO₂ in coastal seas: in North Sea. *Tellus* 43B: 224–235.
- Komada, T., C. E. Reimers & S. E. Boehme, 1998. Dissolved inorganic carbon profiles and fluxes determined using pH and P_{CO₂} microelectrodes. *Limnol. Oceanogr.* 43(5): 769–781.
- Li, Y. H. & S. Gregory, 1974. Diffusion of ions in seawater and in deep sea sediments. *Geochim. Cosmochim. Acta* 40: 257–266.
- López, P., M. Vidal, X. Lluch & J. A. Morguí, 1995. Sediment metabolism in a Transitional Continental/ Marine Area: The Albufera of Majorca (Balearic Islands, Spain). *Mar. Freshwat. Res.* 46: 45–53.
- Mackin, J. E. & K. T. Swider, 1989. Organic matter decomposition pathway and oxygen consumption in coastal marine sediments. *J. mar. Res.* 47: 681–716.
- Martens, C. S. & V. Klump, 1987. Biogeochemical cycling in an organic-rich coastal marine basin 4. An organic carbon budget for sediments dominated by sulfate reduction and methanogenesis. *Geochim. Cosmochim. Acta* 48: 1987–2004.
- Rysgaard, S., B. Thamdrup, N. Risgaard-Petersen, H. Fossing, P. Berg, P. B. Christensen & T. Dalsgaard, 1998. Seasonal carbon and nutrient mineralization in a high-Arctic coastal marine sediment, Young Sound, Northeast Greenland. *Mar. Ecol. Prog. Ser.* 175: 261–276.
- Shiah, F. K., 1994. Temperature and substrate regulation of bacterial abundance, production and specific growth rate in Chesapeake Bay, U.S.A. *Mar. Ecol. Prog. Ser.* 103: 297–308.
- Sweerts, J. R., C. A. Kelly, J. W. M. Rudd & T. E. Cappenberg, 1991. Similarity of whole-sediment molecular diffusion coefficients in freshwater sediments of low and high porosity. *Limnol. Oceanogr.* 36: 335–342.
- Thamdrup, B. & D. E. Canfield, 1996. Pathways of carbon oxidation in continental margin sediments off central Chile. *Limnol. Oceanogr.* 41(8): 629–1650.
- Thamdrup, B., J. Hansen & B. B. Jørgensen, 1998. Temperature dependence of aerobic respiration in a coastal sediment. *FEMS Microbiol. Ecol.* 25: 189–200.
- Wollast, R., 1991. The coastal organic carbon cycle: fluxes, sources and sinks. In Mantoura R. F. C., J.-M. Martin & R. Wollast (eds), *Ocean Margin Processes in Global Change*. Wiley & Sons, Chichester, U.K.: 365–381.
- Wollast, R., 1998. Evaluation and comparison of the global carbon cycle in the coastal zone and in the open ocean. In: Brink, K. H. & A. R. Robinson (eds), *The Sea*. Wiley & Sons, New York: 213–252.