Benthic carbon budget for the Bay of Saint-Brieuc (Western Channel). Application of inverse method

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ABSTRACT

A steady-state energy flow model is proposed for the benthic fine sand community of the Bay of Saint-Brieuc. The main objective is to assess the relative importance of benthic processes associated with the carbon cycle in an eutrophicated bay. Available data include biomass estimates of the major trophic groups and measurements of the most critical fluxes : particulate organic carbon sedimentation, community respiration, microbial production. A balanced annual carbon budget is estimated using an inverse method, particularly appropriate in food web research where the number of unknowns is far higher than the number of independent observations. The method offers the possibility of taking dynamical constraints into account, by introducing global flow measurements, for example, and of reducing the initial uncertainty in the fluxes. The annual carbon budget provided by the model outlines the major features of the flows of the carbon cycle. The potential supply of energy (328 g C m^{-2} y^{-1}) is significantly higher than the total demand of the benthic consumers. So a large fraction (46 %) of the total carbon input is not used by the benthic food web. Then the role of this eutrophicated bay as potential source of carbon for the adjacent sea is discussed.

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RÉSUMÉ

Bilan des flux de carbone au sein du système benthique de la baie de Saint-Brieuc (Manche Ouest). Application de la méthode inverse

Un modèle de flux d'énergie à l'état stable est proposé pour la communauté des sables fins de la baie de Saint-Brieuc. L'objectif est d'évaluer l'importance relative des principaux processus benthiques associés au cycle du carbone dans une baie eutrophisée. Les données disponibles correspondent aux mesures de biomasses des organismes répartis en unités trophiques et à l'estimation de certains flux globaux, tels que la sédimentation du carbone organique particulaire, la consommation en oxygène du sédiment, et la production microbienne benthique. La méthode utilisée est une technique inverse (Mercier, 1986) qui permet d'obtenir un bilan équilibré en carbone, compatible avec les mesures de terrain et respectant les hypothèses de fonctionnement. Cette application illustre l'intérêt de la méthode inverse dans le domaine de l'étude des réseaux trophiques, où le nombre d'inconnues est toujours très supérieur au nombre d'observations indépendantes. Elle offre la possibilité d'introduire des contraintes de fonctionnement, définies par la mesure des flux globaux, et permet de réduire notablement l'incertitude sur les principaux flux. Le bilan annuel établi par le modèle résume les principales caractéristiques du cycle du carbone. L'apport en énergie (328 g C m^{-2} y^{-1}) est significativement plus élevé que la demande totale des organismes benthiques.

Aussi, une fraction importante (46 %) de cet apport n'est pas utilisée par le réseau trophique benthique. Le rôle de cette baie eutrophisée comme source potentielle de carbone pour les zones marines voisines est discuté.

INTRODUCTION

Over the past two decades, increasing interest has been expressed in the energy flow through coastal ecosystems. Some insight into the problem has been gained by studying the annual budget of carbon cycling. In coastal areas, some budget estimations are derived from detailed prognostic models (Warwick *et al.*, 1979; Baretta and Ruardij, 1988; 1989; Chardy and Dauvin, 1992), but most of them are based on diagnostic steady-state models which either lead to balanced budgets (Baird and Milne, 1981; Dame and Patten, 1981; Kuipers *et al.*, 1981; Joiris *et al.*, 1982; Klepper and Van de Kamer, 1988) or unbalanced budgets (De Wilde and Beukema, 1984; Pearson and Rosenberg, 1992). All these approaches require a large number of estimations and approximations. Although the idea that most of the pelagic primary production in shallow waters is channeled to the benthos is well recognized (Joiris *et al.*, 1982; Billen and Lancelot, 1988; Wollast, 1991), there is no general agreement concerning the fate of organic matter reaching the bottom communities. Depending on the ecosystem features, the total energy demand by the benthic communities may be either significantly lower (De Wilde and Beukema, 1984) or higher (Baretta and Ruardij, 1989; Pearson and Rosenberg, 1992) than the potential food supply. Such a question is linked to the role of source or sink of organic carbon in the shallow waters.

In this note, we study the case of the Bay of Saint-Brieuc (western Channel). The role of the benthic system in the global carbon cycle of the area is assessed by combining, within an inverse model, direct estimates of external fluxes (sedimentation, respiration) and a steady-state model of the benthic food web. From an "input-output" viewpoint, closing the benthic carbon budget requires estimation of three components: 1) carbon sedimentation and local microphytobenthic production; 2) losses through respiration; 3) exported and burial fluxes.

Large uncertainties are associated with the direct measurement of carbon fluxes and their use with a steady-state model has not always been successful. The inverse procedure proposed here makes it possible to ascertain whether the external flux estimates are consistent with the hypothesis on the trophic relationships within the benthic food web summarized by the steady-state model that was developed. Inferences on both internal and external fluxes are attempted simultaneously using an inverse method procedure.

MATERIAL AND METHODS

The studied area

The Bay of Saint-Brieuc is a shallow sea area on the northern coast of Brittany (France), with a large opening to the Western Channel (Fig. 1). The subtidal area investigated covers 174 km², with an average depth of about 10 m. Hydrodynamic patterns exhibit limited water exchanges with the open sea, despite a high tidal amplitude, with a mean of *ca.* 8 m, reaching a maximum of 13 m during spring tides. Tidal and wind mixing promote longitudinal and vertical homogeneity of the water column.

Figure 1

Benthic assemblages in the Bay of Saint-Brieuc (from Gros et Hamon, 1988).

Les peuplements benthiques de la baie de Saint-Brieuc (extrait de Gros et Hamon, 1988).
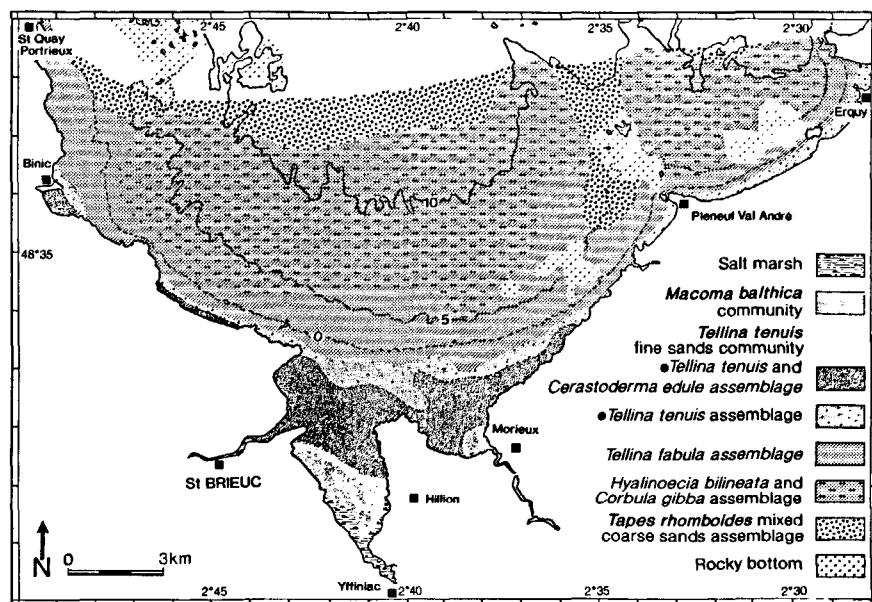
Salinities vary in the range of 30-34.5, except during the very high river flow.

A fine sand community is present in more than 80 % of the subtidal area (Fig. 1). Two main assemblages can be distinguished: the *Tellina fabula* and the *Hyalinoecia bilineata* sub-communities. The seaward border of the studied area is covered by heterogeneous sediments with a *Tapes rhomboides* assemblage.

In recent years, the bay has been influenced by an increase of urban sewage and the use of fertilizers. Correlatively, eutrophic conditions are enforced, and manifested by blooms of sea lettuce, the green macroalgae *Ulva*.

Methods

The compartmental flow diagram, shown in Figure 2 summarizes our model of the general structure of the fine sand community of the Bay of Saint-Brieuc.

The state variables of the model (Fig. 2) are classical benthic compartments defined according to feeding type and individual size. The structure of the food web is closely related to previous modelling attempts where the benthic system was fully represented, such as the Askö-Landsort area, Baltic Sea (Jansson, 1978), the Ems estuary, Netherland coast (Baretta and Ruardij, 1988), the Chesapeake Bay (Wulff and Wlanowicz, 1989), the Bay of Morlaix, Western Channel (Chardy and Dauvin, 1992). Sources of food for each compartment are defined by a diet matrix (Tab. 1 *B*) using results and discussions provided by the above models. The meiofauna compartment includes a carnivorous feeding mode represented by a cannibalistic self-loop. Interactions between compartments are described following the basic equation:

$$\frac{d X_j}{dt} = \Sigma F_{ij} - \Sigma F_{jk}$$

X_j are the state variables. ΣF_{ij} designates the sum of inputs to "j" (consumption) and ΣF_{jk} the sum of outputs from "j" (predation, respiration, egestion, non predatory mortality). The system is driven by the input of energy expressed by the sedimentation of organic carbon from the water column and the microphytobenthic production.

The system of coupled ordinary differential equations describing the exchanges of carbon between the seven state variables is solved for the fluxes by an inverse procedure assuming a steady-state. Our data parameters are derived from observations of biomasses and estimates of physiological rates. The constraints are mass conservation equations and observations of global fluxes (e.g. community respiration). This information will be used to estimate the fluxes and improve our knowledge of the parameters.

Inverse problems in food web research have been recently investigated by Vezina and Platt (1988). The inversion procedure is a powerful tool for addressing the common situation where the number of independent observations available is far less than the number of unknown parameters.

Similar problems are encountered in other fields, such as physical oceanography (Mercier, 1986). The purpose is to
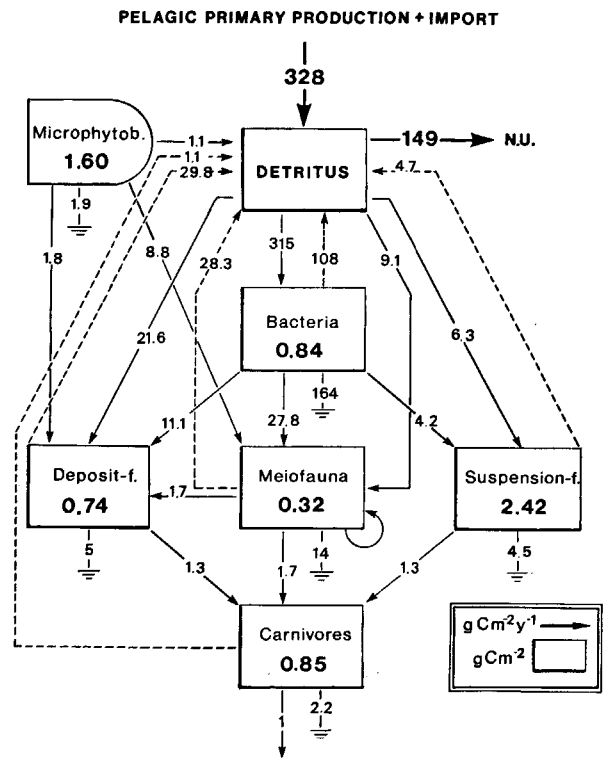

Figure 2

Annual carbon budget of the benthic system in the Bay of Saint-Brieuc : inverse solution. Biomasses in g C m⁻². Fluxes in g C m⁻² y⁻¹. $\rightarrow$ *: trophic fluxes.* $\rightarrow$ *; faeces + non predatory mortality;* $\mp$ *: respiration; N.U.: non utilized energy (exported or buried).*

Bilan annuel en carbone du système benthique de la baie de Saint-Brieuc : résultats de la méthode inverse. Biomasses en g C m⁻². Flux en g C m⁻² y⁻¹. $\rightarrow$: flux trophique ; $\rightarrow$: fèces + mortalité autre que prédation ;$\mp$: respiration ; N.U. : énergie non utilisée (exportée ou enfouie).

estimate the flow network that conserves mass, satisfies biological constraints based upon the knowledge of ecological processes, and fits field measurements. The non-linear inverse procedure proposed in this paper is presented in details in Mercier (1986).

The inverse analysis requires initial values for the state variables (biomass of the compartments) and for the physiological rates to be estimated (Tab. 1 *A*) as well as estimates of the associated uncertainties. For field observations, as biomasses, the calculated standard deviation would be the most appropriate measurement of uncertainty. For physiological rates, an *a priori* variance is assumed according to an expected coefficient of variation of 50 % related to an empirical uncertainty. Obviously, determination of the probability distribution of the parameters is impossible. Expressing uncertainty as a variance is a procedure which assigns weight to the prior parameter estimates in accordance with the actual knowledge.

Available data

Available information on the system comes from two sources : direct measurements derived from the literature for both biomasses and global fluxes, and *a priori* information for the physiological rates.

Table 1

Initial and adjusted values used in the inverse procedure.

Valeurs initiales et valeurs ajustées utilisées dans la méthode inverse.

A: Yearly mean biomasses, in $g\ C\ m^{-2}$, and physiological rates in $g\ C\ (g\ C)^{-1}\ y^{-1}$ for biotic compartments. Initial values and adjusted values in parentheses.

A : Biomasses moyennes annuelles en g C m^{-2}, et taux physiologiques en g C (g C)$^{-1}$ a^{-1} pour les compartiments biologiques. Valeurs initiales et valeurs ajustées entre parenthèses.

Ecological group	B		P/B ratio	R		M		E	
Bacteria	1	(0.84)	200 (180)	200	(196)	120	(128.7)		
Meiofauna	0.30	(0.32)	15 (14.6)	44.7	(44.1)	3.75	(3.74)	0.60	(0.56)
Suspension feeders	2.42	(2.42)	0.8 (0.75)	1.8	(1.8)	0.20	(0.20)	0.40	(0.40)
Deposit-feeders	0.74	(0.74)	3.0 (2.53)	6.8	(6.8)	0.75	(0.75)	0.80	(0.81)
Carnivores	0.85	(0.85)	1.2 (1.49)	2.7	(2.6)	0.30	(0.30)	0.20	(0.20)

B: biomass; R: respiration rate; M: non predatory mortality rate; E: egestion rate (dimensionless).
* Respiration of microphytobenthos is a fraction of the primary production. For detritus, the refractory fraction is assumed to be 50 %. The adjusted value is 54.5 %.

B : biomasses ; R : taux de respiration ; M : taux de mortalité non lié à la prédation ; E : taux d'égestion (sans dimension).
* Pour les détritus, la fraction réfractaire est fixée à 50 %. La valeur ajustée est 54,5 %.

B. Diet composition matrix for trophic groups. Trophic sources are expressed as percentage of total diet. Initial values and adjusted values in parenthesis.

B. Tableau du régime alimentaire des groupes trophiques. Les sources trophiques sont exprimées en pourcentage du régime total. Valeurs initiales et valeurs ajustées entre parenthèses.

Sources Consumers	Micro-phytobenthos	Detritus	Bacteria	Meiofauna	Suspension feeders	Deposit -feeders
Bacteria		100				
Meiofauna	19 (18.3)	19 (18.9)	57 (57.7)	5 (5.1)		
Suspension feeders		60 (60)	40 (40)			
Deposit-feeders	5 (4.9)	60 (59.6)	30 (30.8)	5 (4.7)		
Carnivores				40 (40)	30 (30.1)	30 (29.9)

C. Measurement of global flows in $g\ C\ m^{-2}\ y^{-1}$. Initial values and adjusted values in parentheses.

C. Mesures effectuées sur les flux globaux en g C m^{-2} a^{-1}. Valeurs initiales et valeurs ajustées entre parenthèses.

SEDIMENTATION FLOW	325	(328)
TOTAL RESPIRATION	202	(192)
BACTERIAL PRODUCTION	180	(151)

Measurements

The present investigation is based upon observations made seasonally in the Bay of Saint-Brieuc from 1987 to 1991. Patterns of benthic communities, species composition and standing stocks have been defined by Gros et Hamon (1988). Allocation of macrofauna species to trophic groups has been performed from a review of the published literature concerning coastal macrozoobenthos feeding. The characteristic species belonging to each group are :

• Filter feeders

Tapes rhomboides, Corbula gibba, Ensis ensis, Crepidula fornicata, Chaetopterus variopedatus, Upogebia deltaura.

• Deposit feeders

Tellina fabula, Pectinaria koreni, Ampharete grubei, Clymene oerstedii, Sipunculus nudus, Ampelisca brevicornis.

• Carnivores

Nassarius reticulatus, Buccinum undatum, Acrocnida brachiata, Hyalinoecia bilineata.

Meiofauna biomass in the upper five centimetres of sediment is available from the studies by Bodin et al. (1985; 1989) and Le Guellec et Bodin (1992; Tab. 1 A). Microphytobenthos standing stock, measured as chlorophyll a concentration in the first upper centimetre of sediment, has been investigated by Bodin et al. (1989; Tab. 1 A).

690

In order to quantify the bacterial production in the upper layer of the sediment, tritiated thymidine incorporation (Moriarty, 1986) has been performed by Cahet (1989) on the upper first centimetre, where most of the microbial activity occurs, according to the results of Moriarty et al. (1991) and Craven and Jahnke (1992).

The downward flux of particulate organic matter from the water column is investigated by deployments of sediment trap experiments (Chardy et al., 1992). Resuspension is estimated by a simple two-source mixing model, taking into account organic content of water column and sediment particles (Tagushi, 1982). Beside the processes of sinking, the reactivity of the organic matter in the water column has been performed by incubation method (Arzul et al., 1990).

Total benthic community metabolism was determined monthly by in situ oxygen consumption in a benthic chamber (Monbet et al., 1991), at three stations (Tab. 1 C). The benthic respiration can be expressed by oxygen uptake only if a correction is made for chemical oxidation. Support from inorganic chemical uptake measurement in the sediment is not available in the present study. Results of chemical oxygen uptake recorded from formalin-poisoned core experiments range between 0 % (Smith et al., 1972) and 70 % (Dale, 1978) of the total O_2 consumption. Studies related to coastal fine sand sediment, comparable to the Bay of Saint-Brieuc case study, provide values for chemical uptake from 20 to 42 % of the total sediment uptake (Smith et al., 1972; Van Raalte, 1978; Grant, 1986; Anderson and Helder, 1987; Cammen, 1991). A mean value of 30 % for chemical oxygen consumption is assumed in this study to deduce the biological respiration from the total demand.

A priori information

No field information is available from the studied area for microphytobenthic primary production. However, similar conditions of chlorophyll and light exist in the Bay of Douarnenez, France. The value of 10 g C m^{-2} y^{-1} found there will be taken as an a priori estimate for the microphytobenthic production in the Bay of Saint-Brieuc.

Formulation of the model requires knowledge of consumption within the various heterotrophic compartments, which is estimated according to the general equation C = P + R + E, where C = consumption, P = production, R = respiration and E = egestion. Production/biomass ratios are derived from population studies of the dominant species or calculated from the relationships "P/B-lifespan" established by Robertson (1979). Initial value of annual bacterial "P/B" ratio is approximated using the work of Schwinghamer et al. (1986). The respiration rates for macrofauna and meiofauna are derived from the production/respiration relationship established by Schwinghamer et al. (1986). Egestion is deduced from specific values for assimilation efficiencies published in the literature. For benthic bacteria, the production/respiration ratio is assumed to be 0.5 (Bratbak, 1987). Except for benthic bacteria which consume only detritus, the other compartments feed on more than one food source. The proportion of each source to any consumer is defined according to the knowledge of the feeding

type of the main compartments previously discussed in similar models [Tab. 1 B (Pace et al., 1984; Baretta and Ruardij, 1989; Wulff and Ulanowicz, 1989)].

An a priori standard deviation(s) assigned to most of the parameters is calculated from a coefficient of variation (s/x) equal to 50 %, x being the mean.

RESULTS AND DISCUSSION

The annual carbon budget for the Bay of Saint-Brieuc is proposed in Figure 2. Fluxes are calculated with the adjusted values of the state variables and parameters provided by the inverse solution (Tab. 1 A). The solution proposed is dependent on a priori information on biomass, physiological rates, field observation, and weight imposed on data (variances). The parameter resolutions given between brackets in Table 1 best fit the mass conservation assumption and the biological constrains. Each of these values would require a detailed discussion. Within the context of the global carbon cycle, we shall limit our comments to the major flows of the system and the consistency of some critical fluxes.

General features of the carbon budget exhibit a high input of energy (340 g C m^{-2}. y^{-1}), mainly due to the sedimentation process (328 g C m^{-2} y^{-1}). Microphytobenthic primary production is negligible (11.7 g C m^{-2} y^{-1}) according to the low penetration of the photosynthetically available radiation, which decreases by an average of 96 % from the surface to 5 m depth, mainly due to high concentrations of suspended material (annual mean = 7.2 mg l^{-1}; Chardy et al., 1992). The direct measurement of vertical particle flux is a matter of considerable controversy (see Wassmann et al., 1991 for review), especially in coastal waters where particle resuspension from the seafloor is an important process. The simple two-source mixing model (Tagushi, 1982), based on organic content of the water column particles and the sediment, has been applied on our sediment trap data. This method yields an approximate correction for resuspension, but does not consider the "rebound particles" sensu Walsh et al. (1988), and the initial value for the sedimentation rate is questionable. Surprisingly, the deviation between prior estimate and adjusted value provided by the model is low. Comparisons with published data suggest that the input of particulate organic carbon into the benthic system of the Bay of Saint-Brieuc is among the highest reported values in coastal waters, but is still three times lower than in the Chesapeake Bay (Wulff and Vlanowicz, 1989).

The total input of organic carbon is divided into two parts : an easily metabolized fraction which is consumed by the benthos and a "not used" fraction (Odum, 1971) which is either incorporated in the sediment or exported. The latter fraction accounts for 46 % (149 g C m^{-2} y^{-1}) of the organic carbon supply and supports the idea that the area is a potential source or (and) sink for carbon.

Burial flux measurement is not available in this study, but Blackburn (1991) admits, as an order of magnitude, that most of sediments have a burial efficiency (burial rate/sedimentation rate) between 1 and 30 % for organic carbon. This would lead to a burial flux between 3.28 and 98.4 g C

m^{-2} y^{-1} in the Bay of Saint-Brieuc. The low organic carbon content (< 1 %: Gros and Hamon, 1988) of the sediment does not support the hypothesis of a significant accumulation of organic carbon in this subtidal area, where tidal current velocities are important. According to Canfield (1989) and following Wollast's assumptions (1991), the amount of organic carbon preserved in the region of high sedimentation would be about 10 % of sedimented organic carbon. This would lead to the conclusion that in the Bay of Saint-Brieuc roughly 33 g C m^{-2} y^{-1} is preserved in the sediment and 116 g C m^{-2} y^{-1} is exported.

The sum of annual respiratory flows, corresponding to the total benthic consumption, is 192 g C m^{-2} y^{-1} which fits relatively well the results of Monbet et al., 1991 (202 g C m^{-2} y^{-1}). The benthic microflora production being low, the contribution of autotrophic respiration is negligible. The previous value is equivalent to a mean daily oxygen uptake of 1.40 g O_2 m^{-2}, which is close to the upper bounds of the sediment oxygen demand rates summarized from the literature by Seiki et al. (1989). Estimates of annual respiration of the subtidal fine sand community off Sapelo Island (Georgia) by Smith (1971), provide higher results, equivalent to 362 g C m^{-2} y^{-1}.

Bacterial respiration represents the largest contribution to the total uptake of oxygen (85 %), the macrofaunal component being insignificant (6 %), when compared to the total community energy demand. These crude estimates enforce the role of the microbiota as key organisms in the cycling of organic matter in the sediments.

The sum of all flows to detritus is 501 g C m^{-2} y^{-1}. This confirms the status of "detritus-dominated system" of the Bay of Saint-Brieuc. An important fraction (34 %) of the energy flowing through the detritic compartment is cycling within the benthic system and is due to egestion and non-predatory mortality processes. The contribution of the bacteria to this recycled carbon is significant, considering that most of the microbial production in the sediment is not consumed by grazers (Kemp, 1987). A global approach to the trophic network confirms that the rate of bacterial productivity is several times greater than the maximum ingestion rate of consumers (Alongi, 1988). The flux of material through bacteria in a detritus-dominated system is still a matter of considerable speculation, but the tentative balanced budget presented here supports the notion that non-predatory mortality for this compartment may be high.

With respect to the flow diagram exhibited in Figure 2, the macrofauna production contributes to a very small part (5 g C m^{-2} y^{-1}) of the total heterotrophic production (160 g C m^{-2} y^{-1}). The total mean annual biomass of macrofauna amounts to 4 g C m^{-2}, thus the P/B ratio for the macrobenthic community is 1.25, which is in conformity with the values reported in the literature for fine sand communities (for review, see Dauvin, 1984). The calculated meiofauna production (4.7 g C m^{-2} y^{-1}) is very closed to the macrofaunal one, although the biomass of meiofauna is only 9 % of that of macrofauna.

Slight variations are observed (< 10 %) between the initial and a posteriori parameter values (Tab. 2), except for bacterial biomass and respiration rate, labile fraction of the

Table 2

Consistency ranges derived from the balanced solution for two input values corresponding to the upper (244 g C m^{-2} y^{-1}) and lower (406 g C m^{-2} y^{-1}) boundaries of the confidence interval (t = 0.05) of the sedimentation rate.

Intervalles de cohérence déduits de la solution équilibrée pour deux valeurs d'entrée d'énergie correspondant à la limite inférieure (244 g C m^{-2} a^{-1}) et supérieure (406 g C m^{-2} a^{-1}) de l'intervalle de confiance (t = 0,05) du taux de sédimentation.

	Initial range	Consistency range
Total respiration (g C m^{-2} y^{-1})	[101-303]	[191-214]
Bacterial production (g C m^{-2} y^{-1})	[68-292]	[130-162]
Labile fraction of the sedimented material	[25-75 %]	[49-59 %]

organic carbon and total bacterial production. Fluxes through the bacteria compartment rely the most on a priori guesses, the associated error is large, and the inverse estimates of these fluxes are, as expected, significantly different from the measured ones. Several problems are encountered in the assessment of bacterial production. Thymidine uptake is a pulse-label method with short incubation time (10 mn). Many different conversion factors such as cells produced per mole of thymidine incorporated have been published (Moriarty, 1988). The rationale, the advantage and sources of error in the use of thymidine for ecological studies have been reviewed by Moriarty (1986; 1988). Calculation of annual flow rates from such circumscribed information is obviously subjected to considerable uncertainty. Moreover, we cannot be certain whether the growth rate measured during incubation experiments is continuous or discontinuous in the field. The same fundamental limitation exists with in situ respiration measurements over short periods (two-three hours). The mean annual flows are deduced from ad hoc observations and this discrepancy between the time scales of analytical experiments and global budget leads to an indeterminacy in the data which is not considered in the model.

As a general remark, we may note that considering the high level of energy input and the resulting secondary production of the upper part of the benthic food chain, the whole system has a low energy transfer efficiency and the "not used" energy is high. Comparison with other eutrophicated areas where summaries of energy flows have been published suggests a strong similarity with the Chesapeake Bay ecosystem (Wulff and Ulanowicz, 1989) and underlines structural and functional differences with the Kattegat ecosystem (Pearson and Rosenberg, 1992). It becomes evident that eutrophicated conditions do not lead to a unique energy flow pattern.

The description of the general trophic network of the Bay of Saint-Brieuc is based on various kinds of data containing a large measure of arbitrariness. What is derived from the model is itself subjected to uncertainty. Seeking extreme solutions for a given constraint is a possible way to deduce the pertinent limits of some critical fluxes. One relevant

question is, "what are the upper and lower values for total respiration when the system is forced with the limit values of the confidence interval of the carbon input ?". A new uncertainty interval may be deduced, so called "consistency range" by Klepper and Van de Kamer (1988). The results obtained by the following procedure provide a comparison between the initial uncertainty range (deduced from calculated or assumed variance) and the consistency uncertainty range. Some major carbon flows or parameters are presented in Table 2. The consistency range is much narrower than the initial range, especially when the uncertainty around the first estimate is large. By considering every process simultaneously, the model leads to a significant decrease of the uncertainty on some critical fluxes. As mentioned by Klepper and Van de Kamer (1988), the more uncertain flows are constrained by the better-known flows and not *vice versa*.

CONCLUSION

The benthic system of the Bay of Saint-Brieuc is a typical detritus-dominated system where the total demand of the benthic consumers is significantly lower than the supply of energy. Most of the carbon input is channeled to the microbial compartment which contributes to 85 % of the carbon mineralization, while the macrofauna contribution to the community metabolism is low. Most of the available organic carbon is fully recycled to CO_2 through the bacterial biomass. The "not used" energy represents about 46 % of the annual carbon reaching the bottom. A low organic matter content measured in the sediment (< 1 %) suggests that this area is not an accumulation centre for organic carbon and that only a small fraction of the non utilized material is buried. The general picture outlined by the benthic carbon budget is that the fine sand community of the Bay of Saint-Brieuc is a low energy transformer and a potential source of carbon for deeper waters. These results underline the particular importance of the coastal eutrophicated areas in the carbon cycle of the shelf ecosystems.

These general features are derived from a data set containing more assumptions and arbitrariness than measurements. As any carbon budget approaches are based on hypothetic trophic relationships within the food web, the results should be regarded with extreme caution. A food web is an undetermined system. The knowledge required to solve the system outspaces our capacity to make all the necessary measurements and experiments at any one site. Furthermore, direct estimate of most of the flows is impracticable. Thus, determining the carbon flow pathways of an ecosystem is an inverse problem. The analysis presented here illustrates two specific applications of the method : 1) constraining the solution with field observations on global fluxes such as community respiration and microbial production; 2) decreasing the uncertainty on the critical fluxes. Even if a requirement for conservation of mass alone (the balanced solution) does not guarantee a realistic flow network (Vezina and Platt, 1988), the inverse procedure appears as a powerful tool to generate a solution compatible with field observations and physiological assumptions.

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