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A first step towards modelling confinement of paralic ecosystems

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Abstract : This paper deals with the concept of *confinement* of paralic ecosystems. It presents a modelling procedure in order to compute the *confinement* field of a lagoon without tide. Then it realizes an improvement in this concept allowing it to be used for tide-influenced lagoons. This improvement consists essentially in including the tide wave into the *confinement* computation. Finally, using a simplified model of benthic population dynamics, this improved version shows that *confinement* may explain benthic population distribution even in paralic ecosystems with strong tide.

Keywords: Confinement, paralic ecosystems, tide, benthic species, lagoon ecological factors.

1 Introduction

The concept of *confinement* was introduced by Guélorget and Perthuisot (1983) as the pertinent parameter controlling the features of living macrobenthic populations in paralic ecosystems which are ecosystems encountered in estuaries, lagoons or closed bays.

A wide comparative study (Perthuisot, 1975; Guélorget and Perthuisot, 1982; Perthuisot and Guélorget, 1983; Guélorget and Perthuisot, 1983; Guélorget et al., 1983; Guélorget and Perthuisot, 1984; Perthuisot and Guélorget, 1987; Perthuisot and Guélorget, 1992) on zonal qualitative and quantitative biological organisation in habitats along the Mediterranean coasts showed that species distribution is not mainly related to salinity. Instead, the presence of a given species in a given place of a paralic ecosystem is related to the time for the sea water to reach this place. Indeed, this amount of time is relevant to decreasing availability of nutrients coming from the sea and it is therefore considered as a measure of *confinement*.

Confinement cannot be measured *in situ*. Guélorget and Perthuisot (1983) proposed biological indicators of *confinement*. More precisely, they proposed a division of paralic ecosystems into a

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series of six zones, each one corresponding to a level in a *confinement* scale, and dominated by specific species.

Confinement has been widely tested throughout numerous regions: The Red Sea (Ibrahim et al., 1985), The Persian Gulf (Perthuisot and Jauzein, 1978), Guadeloupe (Guélorget et al., 1990), The Baltic and Belt seas (Muus, 1967), and tested for the microfauna of foraminifers in Mediterranean regions (Guélorget et al., 1983), in African coasts (Debenay et al., 1993) and in South Brittany, France (Redois and Debenay, 1996).

Indisputably, *Confinement* is regarded as the right parameter explaining the distribution of species in paralic ecosystems which are not influenced by tide or if the characteristic size of the considered ecosystem is large compared with tide-influenced zones.

On the other hand, *Confinement* seems to be regarded as incompatible with paralic ecosystems in regions where tide is strong. The key argument leading to such a conclusion is that the zonal organisation of species in a strong-tide context is very different from the zonal organisation in a low-tide context. For instance, when it came to macrobenthic species, (Barnes, 1994) showed that this difference was very clear. This author appraises the “application of Guélorget and Perthuisot’s concept to the paralic ecosystem and confinement to macrotidal Europe”: “it is concluded that confinement is only marginally applicable to brackish-water systems in macrotidal region”. Concerning foraminifers, the comparison of the distribution in Mediterranean paralic ecosystems (see the review in Murray, 1991; Favry et al., 1997, 1998; Guelorget et al., 1999) and in paralic ecosystems located on Eastern Atlantic coasts, (see the review in Murray, 1991; Debenay, 1995; Redois and Debenay, 1996; Debenay, 2000; Debenay et al., 2000 ; Debenay and Guillou, 2002; Debenay et al., 2006) shows that two species can be separated in a strong-tide context and co-exist in the absence of tide.

From our point of view, those sensible remarks on zonal organisation do not call into question the pertinence of *confinement* for describing living organisation even in strong-tide regions. They rather brought to light that the *confinement* measurement tool, based on biological indicators built by Guélorget and Perthuisot (1983) for Mediterranean paralic ecosystems, is not an ad-hoc tool to measure *confinement* in tide-influenced paralic ecosystems.

Modelling is certainly a good way to go further in this debate and more generally to understand the precise role of *confinement* in the living organisation of paralic ecosystems. Indeed, as *confinement* cannot be measured *in situ*, having software on disposal would be nice in order to have access to the *confinement* value in any place of a given paralic ecosystem. In the future, such software could contribute to the explanation of the different biological zonations occurring in paralic ecosystems or to predict new biological zonation after the construction of harbour, sea wall, dredging, Modelling *confinement*, as a first step in that direction, is then clever.

Modelling also allows one to enter the tide wave into the *confinement* computation. Hence, it is a good way to improve the *confinement* framework to be used to explain species repartition in paralic ecosystems influenced by tide.

The influence of tide on living organisation has already been modelled in other contexts. For instance Focardi et al. (1989), Dejak et al. (1987), Carreras and Menéndez (1990) and more recently Perriáñez (1998) used tidal hydrodynamic simulations in order to deduce pollutant diffusion in marine and paralic ecosystems. The effort in modelling the response of paralic ecosystem to physical forcings like tide was first led by Melaku Canu et al. (2004) and continued by Bendoricchio and De Boni (2005), Ferrarin and Umgiesser (2005), Cucco and Umgiesser (2006) and Marinov et al. (2006). In those references, heavy finite element simulations are led to deduce hydrodynamic fields. From those, parameters having ecological meaning are deduced. The most common parameters computed are residence time, temperature or salinity. But none of those references led any investigation concerning *confinement*.

The aim of this work is to introduce the modelling and computation of *confinement*. More

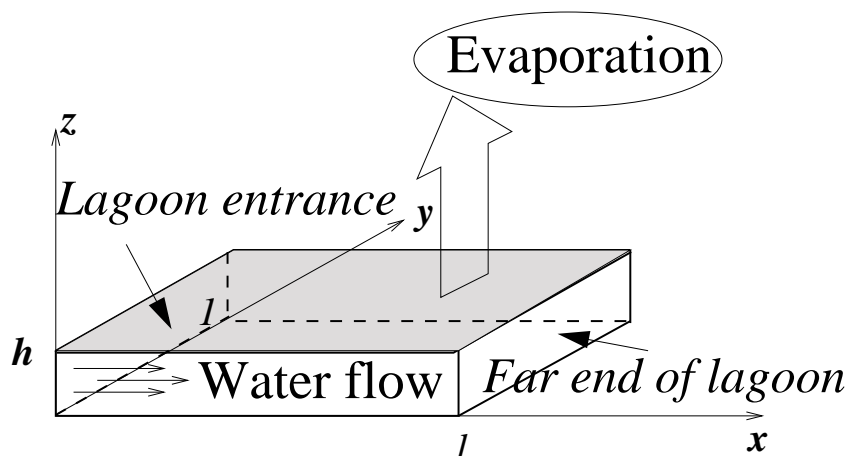


Figure 1: Geometry of the considered lagoon.

precisely, we produce a modelling procedure to compute *confinement* in a parallelepipedal lagoon without tide. Then, we improve this *confinement* computation procedure in order to use it in the same parallelepipedal lagoon but influenced by tide. More precisely, we present a way to compute what we call *instantaneous confinement* which, in a given place and at a given time, gives the amount of time the water which is presently there has spent in the lagoon water mass. We also compute *effective confinement* that we define as the mean time for the sea water to reach a given point of the lagoon. Finally, we explore a way to explain, using *confinement*, benthic population organisation in tide-influenced paralic ecosystems. For this, we build a very simplified ecological model. It consists in considering that, in a lagoon, the growth rate of benthic species depends on *instantaneous confinement*. Then by entering the tide wave in this model, we compute what we call *specific confinement effective sensitivity* indicator. Then using a simplified criterion involving this indicator, we locate places of the lagoon where a given species may grow. Using this model, in a lagoon with tide and in a lagoon without tide, we get different zonal organisation. This backs up our point of view that *confinement* is pertinent even in a tide-influenced paralic ecosystem.

2 Computation of the *confinement* in a lagoon without tide

We establish the formulas allowing the computation of the *confinement* field in a lagoon which is not tide-influenced. By definition, the *confinement* value in any point of the lagoon is the time for the sea water to reach this point. We consider a lagoon which is a parallelepiped with length l , from the lagoon entrance to the lagoon far end and with depth h . We assume that it is of unit width and we consider x , $0 \leq x \leq l$ as the distance of a given point of the lagoon from the lagoon entrance (see figure 1).

We suppose that the water displacements inside the lagoon are solely governed by evaporation. To describe this process we let the constant η be the hydric deficit which is defined as the water volume that evaporates through a surface unit during a time unit. We consider that evaporated water is immediately replaced by surrounded water.

We assume that water velocity is constant along vertical lines and that it decreases proportionally to the distance x , from a maximum in $x = 0$ to 0 in $x = l$.

The water volume that evaporates from the lagoon during a time unit is given, under above assumptions, by the product of the lagoon surface area by η that is $l\eta$. From this, we obtain that

the volume of the lagoon entering water is $l\eta$ per time unit and as a consequence of this, the velocity of the water in $x = 0$ is $l\eta/h$. Using that the velocity decreases proportionally to x , we get that the water velocity in a point whose distance from the lagoon entrance is x is

$$v(x) = \frac{(l-x)\eta}{h}. \quad (2.1)$$

From this expression of the velocity field, we may compute $X(t)$ which is the distance a water particle covers from the lagoon entrance in a time t . $X(t)$ is the solution to the following ordinary differential equation

$$\frac{dX}{dt} = v(X), \quad X(0) = 0, \quad (2.2)$$

and then is given by

$$X(t) = l(1 - e^{-\eta t/h}). \quad (2.3)$$

Now the inverse problem of computing the *confinement* value $T(x)$, *i.e.* the time for a water particle to reach a point at distance x from the lagoon entrance consists in inverting equality (2.3). Then we obtain the *confinement field*, defined for $x \in [0, l]$ by

$$T(x) = -\frac{h}{\eta} \ln\left(\frac{l-x}{l}\right). \quad (2.4)$$

3 Computation in a lagoon with tide

In this section we adapt the previously presented *confinement* computation procedure to tide-influenced lagoons. For this we give a way to compute what we call *instantaneous confinement* which is, in a given point of the lagoon and at a given time, the amount of time the water which is at the considered time in the considered point has spent inside the lagoon water mass. This way consists in introducing a reference configuration which is the volume occupied by the lagoon water mass when the sea level reaches its maximum and a real configuration which, at any time, contains the lagoon water mass. The velocity field is then computed in the real configuration and transported in the reference configuration. From this transported field, we can compute a *confinement* field in the reference configuration from which we deduce the *instantaneous confinement* field. Then we explain the way to obtain the *effective confinement* which is time average of the *instantaneous confinement*. We then apply this computation procedure to an example.

3.1 Reference and real configuration

We consider, as in section 2, that the lagoon is again a parallelepiped but depth $h(t)$ depending on time and ranging from a maximum depth H to a minimum $H - M$, *i.e.*

$$\begin{aligned} H - M \leq h(t) \leq H \text{ with } 0 < M < H, \\ \exists s_1 \in \mathbb{R}, s_2 \in \mathbb{R} \text{ such that } h(s_1) = H, \quad h(s_2) = H - M. \end{aligned} \quad (3.1)$$

In order to manage comings and goings of the lagoon water mass induced by tide, we introduce a reference configuration which is defined as the parallelepiped Π occupied by the lagoon water mass when h reaches its maximum. We set $\Pi = \Omega \times [0, H]$ with $\Omega = [0, l] \times [0, 1]$ and inside Ω points are located by (ξ, ζ) .

Since the water is incompressible, at any time the lagoon water mass remains inside a parallelepiped whose volume is the same as Π . This parallelepiped is called “the real configuration” $\mathcal{P}(t)$ (see figure 2) and we have

$$\mathcal{P}(t) = \mathcal{O}(t) \times [0, h(t)], \text{ with } \mathcal{O}(t) = [0, \lambda(t)] \times [0, 1], \quad (3.2)$$

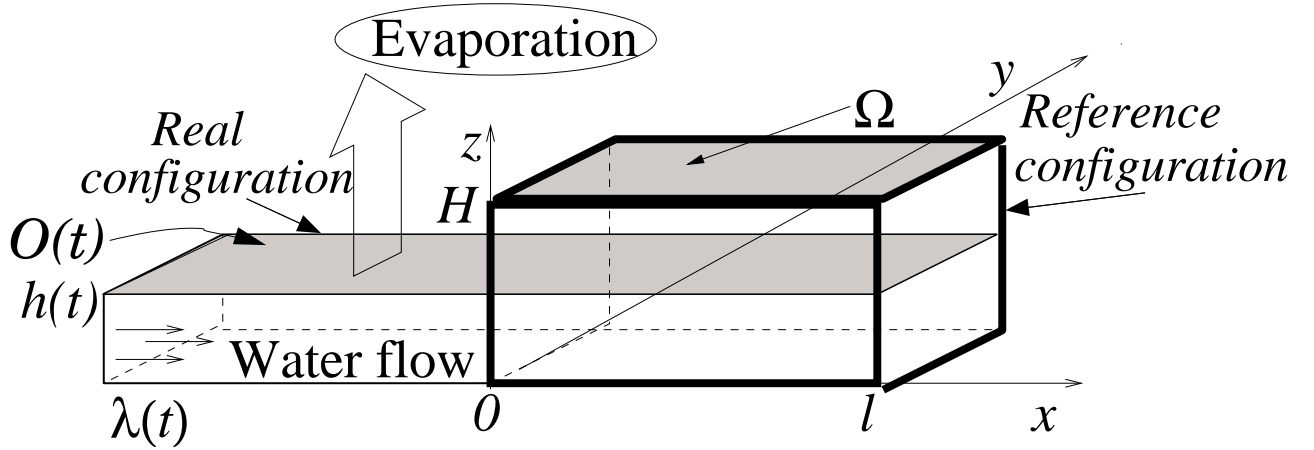


Figure 2: Reference and real configurations for a tide-influenced lagoon

where

$$\lambda(t) = l - \frac{lH}{h(t)}. \quad (3.3)$$

We define the mapping $(\tilde{x}, \tilde{y}) \equiv (\tilde{x}(t, \xi, \zeta), \tilde{y}(t, \xi, \zeta))$ from Ω onto $\mathcal{O}(t)$ which gives at any time t the position in the real configuration of any point (ξ, ζ) of the reference configuration. We have

$$\tilde{x}(t, \xi, \zeta) = l + \frac{H}{h(t)}(\xi - l), \quad \tilde{y}(t, \xi, \zeta) = \zeta. \quad (3.4)$$

The inverse mapping from $\mathcal{O}(t)$ onto Ω , which gives the point of the reference configuration which is in position (x, y) of the real configuration at time t , is given by

$$\tilde{\xi}(t, x, y) = l + \frac{h(t)}{H}(x - l), \quad \tilde{\zeta}(t, x, y) = y. \quad (3.5)$$

3.2 Assumptions

As previously, we assume that the lagoon water mass is submitted to a constant hydric deficit η and that evaporated water is immediately replaced by surrounded water. We also assume invariance of the velocity along vertical lines, along y -axis and linear decrease along x -axis from a maximum in $\lambda(t)$ to 0 in l .

Finally, we assume that the sea water may enter the lagoon water mass only through the surface located in $x = \lambda(t)$: $\{\lambda(t)\} \times [0, 1] \times [0, h(t)]$.

3.3 Water velocity in the real configuration

Since the lagoon water mass is always above $\mathcal{O}(t)$ and since the area of $\mathcal{O}(t)$ is $l - \lambda(t) = lH/h(t)$, the water volume that evaporates from the lagoon water mass per time unit is $\eta lH/h(t)$. We then deduce that this same volume of sea water enters the lagoon water mass through the moving lateral surface $\{\lambda(t)\} \times [0, 1] \times [0, h(t)]$. Hence, since the area of this surface is $h(t)$, we get that the entering water velocity relatively to the moving surface $\{\lambda(t)\} \times [0, 1] \times [0, h(t)]$ is $\eta lH/(h(t))^2$. Hence, since

$\frac{d\lambda}{dt}(t)$ is the velocity of this moving surface, the velocity of the entering water is

$$v(t, \lambda(t), y) = \eta \frac{lH}{(h(t))^2} + \frac{d\lambda}{dt}(t) = \frac{\eta + h'(t)}{(h(t))^2} lH, \quad (3.6)$$

Now, using the linear decrease of the velocity, we get the velocity field of the water in the real configuration:

$$v(t, x, y) = \frac{\eta + h'(t)}{(h(t))^2} lH \frac{l-x}{l-\lambda(t)} = \frac{\eta + h'(t)}{h(t)} (l-x) \quad (3.7)$$

3.4 Water velocity in the reference configuration

The velocity given by (3.7) contains time oscillations from positive to negative values. Hence, we cannot directly carry out the same treatment as in the end of section 2. We first need to bring the field v back in the reference configuration. This yields a new velocity field ν which is such that the trajectories computed using it and transported by (\tilde{x}, \tilde{y}) , which maps the reference configuration onto the real configuration, are the trajectories computed using v . In other words, considering $(\Xi, Z) \equiv (\Xi(t, \xi_0, \zeta_0), Z(t, \xi_0, \zeta_0))$ solution to

$$\frac{d\Xi}{dt} = \nu(t, \Xi, Z), \quad \frac{dZ}{dt} = 0, \quad \Xi(0) = \xi_0, \quad Z(0) = \zeta_0, \quad (3.8)$$

and $(X, Y) \equiv (X(t, x_0, y_0), Y(t, x_0, y_0))$ solution to

$$\frac{dX}{dt} = v(t, X, Y), \quad \frac{dY}{dt} = 0, \quad X(0) = x_0, \quad Y(0) = y_0, \quad (3.9)$$

we define ν to be such that

$$(\tilde{x}(t, \Xi, Z), \tilde{y}(t, \Xi, Z)) = (X(t, \tilde{x}(0, \xi_0, \zeta_0), \tilde{y}(0, \xi_0, \zeta_0)), Y(t, \tilde{x}(0, \xi_0, \zeta_0), \tilde{y}(0, \xi_0, \zeta_0))). \quad (3.10)$$

Taking the time derivative of (3.10) and comparing with (3.8) yields

$$\frac{\partial \tilde{x}}{\partial t} + \frac{\partial \tilde{x}}{\partial \xi} \nu = v, \quad \frac{\partial \tilde{y}}{\partial t} = 0, \quad (3.11)$$

giving

$$\nu(t, \xi, \zeta) = \nu(t, \xi) = \frac{v(t, \tilde{x}(t, \xi, \zeta), \tilde{y}(t, \xi, \zeta)) - \frac{\partial \tilde{x}}{\partial t}(t, \xi, \zeta)}{\frac{\partial \tilde{x}}{\partial \xi}(t, \xi, \zeta)} = -\frac{\eta}{h(t)} (\xi - l). \quad (3.12)$$

We see that $\nu(t, \xi, \zeta)$ remains a constant sign, hence we can use a treatment close to what is done in the end of section 2.

3.5 Confinement in the reference configuration

The trajectory (Ξ, Z) in the reference configuration of a water particle entering the lagoon water mass at $t = 0$ is solution to

$$\frac{d\Xi}{dt} = \nu(t, \Xi) = -\frac{\eta}{h(t)} (\Xi - l), \quad \frac{dZ}{dt} = 0, \quad \Xi(0) = 0, \quad Z(0) = y_0, \quad (3.13)$$

and then is given by

$$\Xi(t) = \left(1 - \exp\left(-\eta \int_0^t \frac{ds}{h(s)}\right)\right) l, \quad Z(t) = y_0. \quad (3.14)$$

Now, the *confinement* field $\tau(\xi, \zeta)$ in the reference configuration gives for any $(\xi, \zeta) \in \Omega$ the time for the trajectory (Ξ, Z) to reach it. As $h > 0$, the function $I(t)$ defined by

$$I(t) = \eta \int_0^t \frac{ds}{h(s)}, \quad (3.15)$$

is increasing, then it is a bijection from $[0, +\infty)$ onto $[0, +\infty)$. We may then consider the inverse function I^{-1} and from (3.14), which also reads $\Xi(t) = (1 - e^{-I(t)})l$, we may deduce

$$\tau(\xi, \zeta) = \tau(\xi) = I^{-1}\left(-\ln\left(\frac{l-\xi}{l}\right)\right). \quad (3.16)$$

3.6 Instantaneous and effective confinement in the real configuration

For any point (x, y) inside the lagoon, *i.e.*

$$(x, y) \in \mathcal{O}(t), x > 0. \quad (3.17)$$

We define the *instantaneous confinement* value $\bar{T}(t, x, y)$ as the amount of time the water which is in (x, y) at t spent inside the lagoon water mass. In other words, it is the reference configuration *confinement* τ transported by (\tilde{x}, \tilde{y}) . We then get that $\bar{T}(t, x, y)$ is the following time oscillating function:

$$\bar{T}(t, x, y) = \tau(\tilde{\xi}(t, x, y), \tilde{\zeta}(t, x, y)) = I^{-1}\left(-\ln\left(\frac{h(t)}{H}(x-l)\right)\right). \quad (3.18)$$

Now the *effective confinement* value in any point (x, y) of the lagoon is the averaged value of the *instantaneous confinement*:

$$T(x, y) = \int I^{-1}\left(-\ln\left(\frac{h(t)}{H}(x-l)\right)\right) dt, \quad (3.19)$$

where $\int dt$ has the following definition: for ω -periodic functions, $\int dt = \frac{1}{\omega} \int_0^\omega dt$ and for almost periodic functions, $\int dt = \lim_{A \rightarrow +\infty} \frac{1}{2A} \int_{-A}^A dt$.

3.7 Numerical application

In order to illustrate that the previous computation procedure is operable, we apply it on a parallelepipedal lagoon with length $l = 1000m$ and with the water depth $h(t)$ which is the periodic function with modulated amplitude, oscillating between $H = 8m$ and $H - M$ with $M = 5m$ and represented in figure 3. The main period is $T_{tide} = 1day$ and the amplitude is periodically modulated with period $T_{coef} = 10days$. The precise definition of $h(t)$ is

$$h(t) = H - g(t)M, \quad (3.20)$$

with

$$g(t) = \frac{H\alpha(t)}{H - M(1 - \alpha(t))}, \quad \alpha(t) = \frac{1}{2}\left(1 - \gamma(t) \cos\left(\frac{t}{T_{tide}}\right)\right), \quad (3.21)$$

and where the function $\gamma(t)$ gives the tide coefficient variation:

$$\gamma(t) = \frac{1}{1+c}\left(1 + c \cos\left(\frac{t}{T_{coef}}\right)\right), \quad 0 < c < 1. \quad (3.22)$$

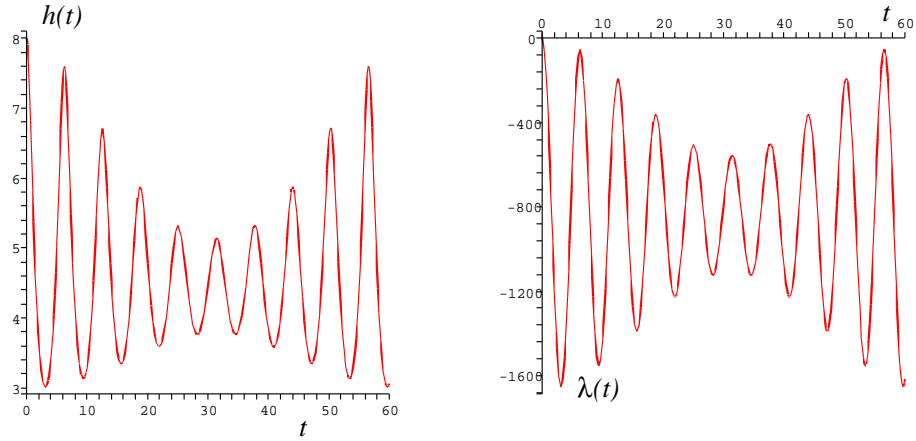


Figure 3: Time variations of the water depth $h(t)$ and of the lagoon water mass limit $\lambda(t)$.

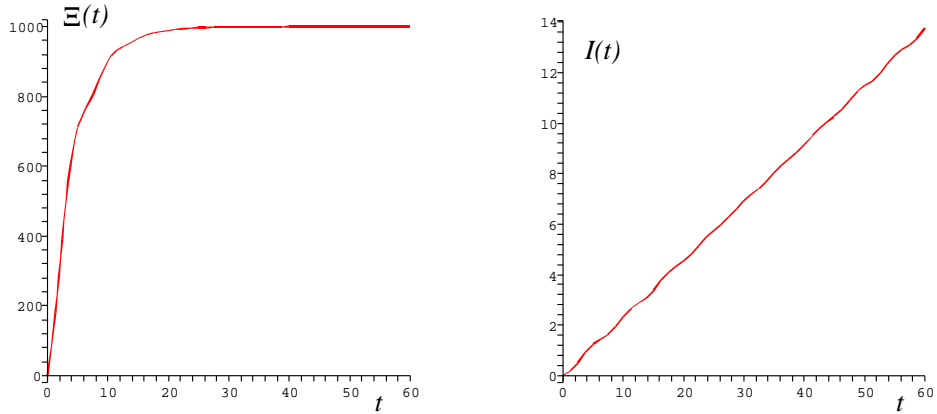


Figure 4: Time variations of $\Xi(t)$ and $I(t)$.

In practice, we take $c = \frac{1}{2}$ and $\eta = 1$. We chose this function $h(t)$ since it allows explicit computations, using maple 9, for a large part of them. The limit $\lambda(t)$ of the lagoon water mass is also a periodic function with modulated amplitude. It is given in figure 3. On the way to compute the *confinement* field in the lagoon, we first compute the trajectory $\Xi(t)$ of a water particle in the reference configuration and the function $I(t)$ given by (3.15). They are given in figure 4. We can see that $\Xi(t)$ is a positive function, close to $l(1 - e^{-ct})$ for a constant c , and perturbed by small oscillations. We can also observe that $I(t)$, which is close to ct for a constant c , is indeed an increasing function that can be inverted. Computing the function I^{-1} using the numerical methods of maple 9 and applying formula (3.16) we get the reference configuration *confinement* field $\tau(\xi)$ which is given in figure 5. This figure shows that $\tau(\xi)$ is close to $c \ln((l - \xi)/l)$ for a constant c . Interpretation of this curve allows us to conclude, for instance, that in a given point the lagoon water mass whose distance from the lagoon water mass entrance is 90% of the total lagoon water mass length, the value of the *confinement* is about 10 *days*. From $\tau(\xi)$ we can obtain the *instantaneous confinement* and then the *effective confinement* inside the lagoon. Figure 6 gives the *effective confinement* value in any point of the lagoon. In this same figure, we also have drawn the *confinement* that would exist in the same parallelepipedal lagoon if the depth remained constant with value H . We see that tide makes

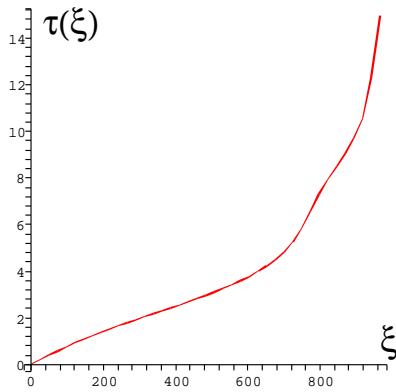


Figure 5: *Confinement* $\tau(\xi)$ in the reference configuration.

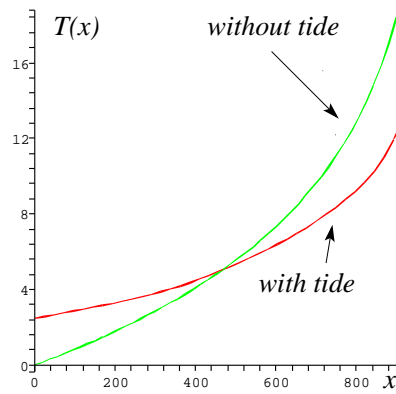


Figure 6: *Effective confinement* $T(x)$ in the lagoon with tide (*i.e.* with water depth $h(t)$) and *confinement* in the same lagoon if the water depth remains constant and is worth H .

the value of *effective confinement* increase at the lagoon entrance and decrease at the far end of the lagoon.

4 Specific *confinement* sensitivity

In this section we illustrate that *confinement* is an explanatory parameter of biological zonation in a paralic ecosystem, even when influenced by tide. For this, we begin by building a very simplified model of population dynamics, involving *instantaneous confinement*, in a lagoon.

We consider that the global increase rate μ , taking into account life expectancy, reproduction ability, and death rate of a given species depends only on the *instantaneous confinement* value. Then in a given point of the lagoon where the *instantaneous confinement* is $\bar{T}(t)$, the ordinary differential equation modelling the evolution of the considered species density $f(t)$ is

$$\frac{df}{dt}(t) = \mu(\bar{T}(t))f(t), \quad (4.1)$$

and then if $f(s)$ is the value of this density in a previous time, we have the following formula giving $f(t)$:

$$f(t) = f(s) \exp\left(\int_s^t \mu(\bar{T}(\sigma)) d\sigma\right), \quad (4.2)$$

In view of (4.2) we can infer that a population of the considered species may grow only in places where $\int_s^t \mu(\bar{T}(\sigma)) d\sigma$ is positive and large enough on periods of time which are long enough, or in other words where $\int \mu(\bar{T}(\sigma)) d\sigma > 0$. This leads us to call $\int \mu(\bar{T}(\sigma)) d\sigma$ the *specific confinement effective sensitivity* indicator and it seems to be reasonable to consider that a population of the considered species may be met only in lagoon points where

$$\int \mu(\bar{T}(\sigma)) d\sigma > 0. \quad (4.3)$$

Having this criterion at hand, we now show that it allows us to predict that some species may share an ecological niche in a lagoon without tide but live separately in a lagoon with tide, and vice versa. For this, we consider examples of species for which we make assumptions on how sensitive to *instantaneous confinement* they are. Then, we compute the *specific confinement effective sensitivity* indicator for those examples of species in a lagoon without tide and in a lagoon with tide and we deduce the predicted zonation in both cases.

We first consider two examples of species we call S_a and S_b . We assume that their global increase rates are the following functions of *instantaneous confinement*:

$$\mu_a(\bar{T}) = -\log\left(\exp\left(\left(\sin\left(\frac{6}{C_M}(\bar{T} + \frac{C_M}{10})\right) + 1\right)^3 - 1 + \log(e-1)\right) + 1\right) + 1, \quad \text{for } S_a, \quad (4.4)$$

$$\mu_b(\bar{T}) = -\log\left(\exp\left(\left(-\sin\left(\frac{6}{C_M}\bar{T}\right) + 1\right)^3 - 1 + \log(e-1)\right) + 1\right) + 1, \quad \text{for } S_b, \quad (4.5)$$

drawn in figure 7; where $C_M \approx 16.8$ is a characteristic value of the *confinement* near the far end of the lagoon if the water depth is constant with value H .

With those assumptions, species S_a does not tolerate weak *confinement* while strong *confinement* is quite good for its growth. The situation is in complete opposition to what happens with species S_b . Moreover, the value of *instantaneous confinement* beyond which μ_a is negative is smaller than the one underneath which μ_b is positive. Then, if we look at the parallelepipedal lagoon of section

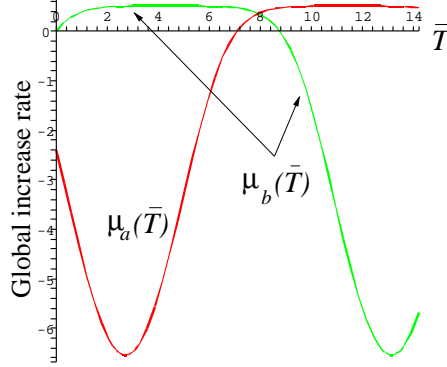


Figure 7: *Instantaneous confinement* dependence of increase rates $\mu_a(\bar{T})$ and $\mu_b(\bar{T})$

3, with constant depth H and with no tide, we can represent functions $\mu_a(T(x))$ and $\mu_b(T(x))$ and determine the place in the lagoon where $\mu_a(T(x)) > 0$ and where $\mu_b(T(x)) > 0$, or in other words, where species S_a and S_b may be met. We can see in figure 8 that the ecological niches of S_a and S_b are partially superposed.

If we consider now a tide-influenced lagoon, in any point of it the *instantaneous confinement* value is time oscillating. On the other hand, even if our assumption is that strong *confinement* is quite favourable to the development of species S_a , weak *confinement* quickly causes major damage amongst their eventually existing representatives. Hence, confronted with the time oscillating *instantaneous confinement* induced by tide, species S_a may not grow in regions where the *instantaneous confinement* reaches, even in a ephemeral way, values which are too weak. In the same way, species S_b may not develop in regions where the *instantaneous confinement* reaches values which are too strong .

In the case when the tide wave to which the lagoon is submitted is given by function $h(t)$ of formula (3.20), the *specific confinement effective sensitivity* indicators $\int \mu_a(\bar{T}(\sigma, x)) d\sigma$ and $\int \mu_b(\bar{T}(\sigma, x)) d\sigma$ are given in figure 9 for any point x of the lagoon. Using criterion (4.3), we consider that S_a may be met in points where $\int \mu_a(\bar{T}(\sigma, x)) d\sigma > 0$ and that S_b may be met in points where $\int \mu_b(\bar{T}(\sigma, x)) d\sigma > 0$. We can see that here there is no shared living area.

In the same way, we consider two other species S_c and S_d with global rates

$$\mu_c(\bar{T}) = \log \left(\exp \left(\left(\sin \left(\frac{6}{C_M} \bar{T} \right) + 1 \right)^3 - 1 + \log(e - 1) \right) + 1 \right) - 1, \quad \text{for } S_c, \quad (4.6)$$

$$\mu_d(\bar{T}) = \log \left(\exp \left(\left(-\sin \left(\frac{6}{C_M} \bar{T} \right) + 1 \right)^3 - 1 + \log(e - 1) \right) + 1 \right) - 1, \quad \text{for } S_d, \quad (4.7)$$

drawn in figure 10.

With those rates, species S_c develops well when the *confinement* is weak but badly when the *confinement* is strong. This situation is in complete opposition to what happens with species S_d . For those species, figure 11 represents functions $\mu_c(T(x))$ and $\mu_d(T(x))$ and determines the place where species S_c and S_d live. This shows that they live on non-intersecting areas in a lagoon with no tide.

Yet, although strong *confinement* is not favourable to the the development of species S_c , it does not rapidly cause a lot of damage to their existing representatives. Hence, with a tide induced time

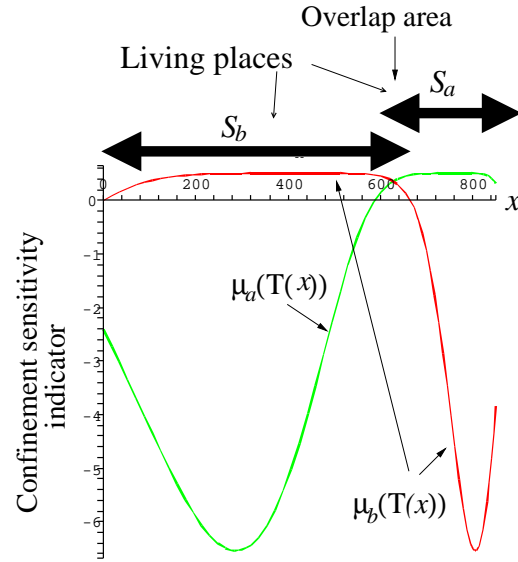


Figure 8: Functions $\mu_a(T(x))$ and $\mu_b(T(x))$ and living places of species S_a and S_b in the lagoon if the water depth remains constant and is worth H .

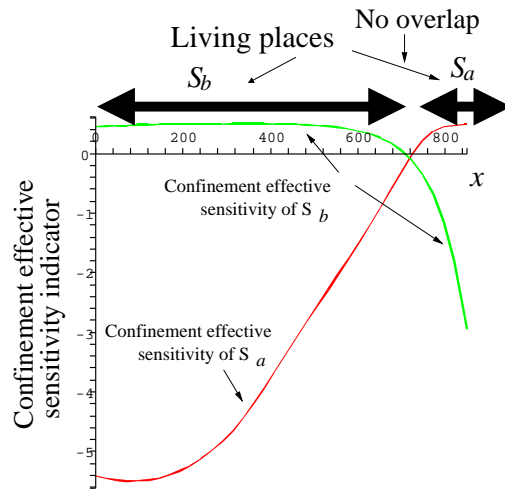


Figure 9: *Specific effective confinement sensitivity* and living places of species S_a and S_b in the lagoon with tide.

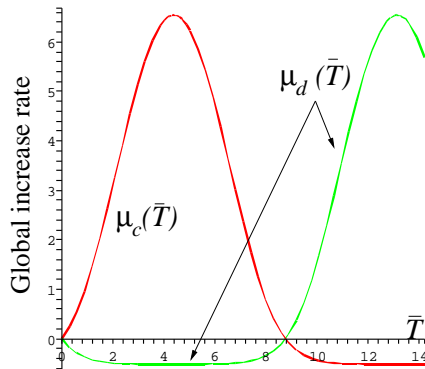


Figure 10: *Instantaneous confinement* dependence of increase rates $\mu_c(\bar{T})$ and $\mu_d(\bar{T})$

oscillating *instantaneous confinement*, species S_d may develop under a stronger *effective confinement* than the maximal *confinement* encountered if there is no tide. However, species S_d may develop under a weaker *effective confinement* and figure 12 shows that their respective living areas intersect when confronted to the tide phenomenon.

5 Conclusion and perspectives

In this paper, we take the definition of the *confinement* value in a point of a lagoon as the time for the sea water to reach this point. With this definition, in section 2, we give a way to compute the *confinement* field in a lagoon not influenced by the tide phenomenon. If the lagoon is a parallelepiped of length l , unite width and depth h , if the hydric deficit, which is the water volume that evaporates through a surface unit during a time unit, is constant with value η , we establish the following formula giving the value of the *confinement* in a point of the lagoon whose distance from the lagoon entrance is x :

$$T(x) = -\frac{h}{\eta} \ln \left(\frac{l-x}{l} \right). \quad (5.1)$$

In section 3, we improve the computation procedure to apply it to tide-influenced lagoons. If the lagoon is the same parallelepiped as previously, with the difference that the depth is a function of time $h(t)$ varying between two values $H - M$ and H , defining

$$I(t) = \eta \int_0^t \frac{ds}{h(s)}, \quad (5.2)$$

and denoting I^{-1} its inverse function, then in a given point whose distance from the bay entrance is x , the value of the *effective confinement* is

$$T(x) = \int I^{-1} \left(-\ln \left(\frac{h(t)l-x}{Hl} \right) \right) dt. \quad (5.3)$$

In section 4, considering species with an increase rate which depends on *confinement*, we define a *specific confinement effective sensitivity* indicator. Using this indicator, we show that it seems to be possible to predict the living features of benthic species lagoons influenced by tide. In particular, we use it to explain why two species may live together in a lagoon without tide but live separately in a lagoon with tide, and vice versa.

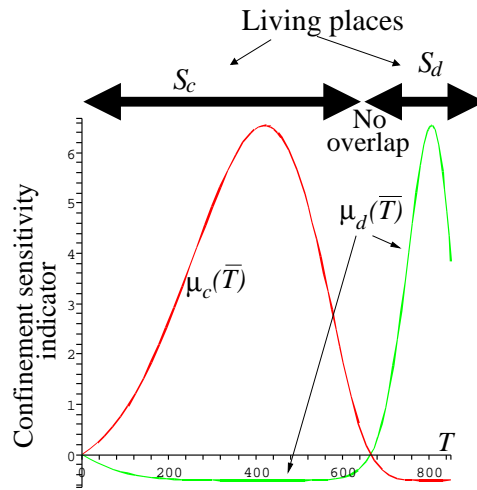


Figure 11: Functions $\mu_c(T(x))$ and $\mu_d(T(x))$ and living places of species S_c and S_d in the lagoon if the water depth remains constant and is worth H .

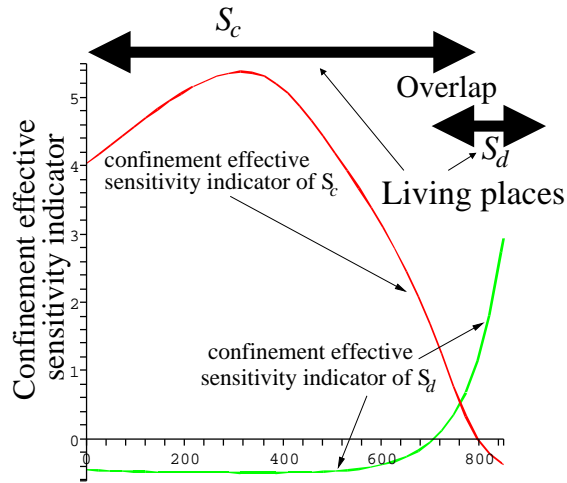


Figure 12: *Specific effective confinement sensitivity* and living places of species S_c and S_d in the lagoon with tide.

This is convincing enough to contemplate carrying out supplementary studies in forthcoming papers.

From the environmental point of view, it is important to enrich our modelling procedure in order to be able to compute, using the numerical analysis routine, the *confinement* for a lagoon with any shape, with any bathymetry, with hydric deficit depending on time and position and taking into account fresh water supplied by rivers. This has to be done in both cases with and without tide.

We also need to include in the model other pertinent parameters such as salinity, ion concentration, and possibly others in order to get a realistic ecological description of paralic ecosystems.

Such a suitable model could then be incorporated in a Decision Support System for Coastal Planning.

From the mathematical point of view it would be of great interest to establish a partial differential equation giving the *confinement* field as a result for any lagoon without tide. Then, using an homogenisation procedure we would be able to deduce an averaged partial differential equation giving, as a result, the *effective confinement* field for any lagoon with tide.

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References

- Barnes R. S. K. (1994). A critical appraisal of the application of Guélorget and Pertuisot's concept of the paralic ecosystem and confinement to macrotidal Europe. *Estuarine, Coastal and Shelf Sciences*, 38, 41–48.
- Bendoricchio, G. and De Boni, G. (2005). A water-quality model for the Lagoon of Venice, Italy. *Ecological Modelling* 184 (1), 69–81.
- Carreras, P. E. and Menéndez, A. N. (1990). Mathematical simulation of pollutant dispersion. *Ecological Modelling* 52, 29–40.
- Cucco, A. and Umgiesser, G. (2006). Modeling the Venice Lagoon residence time. *Ecological Modelling* 193 (1-2), 34–51.
- Debenay, J.P., (1995). Can the confinement index (calculated on the basis of Foraminiferal populations) be used in the study of coastal evolution during the Quaternary. *Quaternary International* 30, 89–93.
- Debenay, J.P. (2000). Foraminifers of paralic tropical environments. *Micropaleontology* 46 (1), 153–160.
- Debenay, J.P., Bicchi, E., Goubert, E. and Armynot du Châtelet, E. (2006). Spatio-temporal distribution of benthic foraminifera in relation to estuarine dynamics (Vie estuary, Vendée, W France) *Estuarine, Coastal and Shelf Science* 67 (1-2), 181–197.
- Debenay, J.P., Guillou, J.J. (2002). Ecological transitions indicated by foraminiferal assemblages in paralic environments. *Estuaries* 25 (6A), 1107–1120.

- Debenay, J.P., Guillou, J.J., Redois, F. and Geslin, E. (2000). Distribution trends of foraminiferal assemblages in paralic environments. A base for using foraminifera as bioindicators *Environmental Micropaleontology*. Martin R.E. ed. Kluwer Academic, New York 15, 39–67.
- Debenay, J. P., Perthuisot, J. P. and Colleuil, B. (1993). Expression numérique du confinement par les peuplements de foraminifères. app. aux domaines paral. actuels afri. w. C. R. Acad. Sci., Paris, série II 316 (2), 1823–1830.
- Dejak, C., Mazzei Lalatta, I., Messina, E. and Pecelik, G. (1987). Steady-state achievement by introduction of true tidal velocities in a pollution model of the Venice Lagoon. *Ecological Modelling* 37 (1-2), 59–79.
- Favry, A., Guelorget, O., Debenay, J.P., Lefebvre, A. and Perthuisot, J.P. (1997). Distribution and organisation of present foraminifera in Kalloni Bay (Greece) *Oceanologica Acta* 20 (2), 387–397.
- Favry, A., Guelorget, O., Debenay, J.P. and Perthuisot, J.P. (1998). Distribution des peuplements de foraminifères actuels dans une lagune méditerranéenne: Étang du Prévost. *Vie et milieu* 48 (1), 41–53.
- Ferrarin, G. and Umgiesser, G. (2005). Hydrodynamic modeling of a coastal lagoon: The Cabras lagoon in Sardinia, Italy. *Ecological Modelling* 188 (2-4), 340–357.
- Focardi, S., Deneubourg, J. L. and Chelazzi, G. (1989). Theoretical analysis of rhythmical clustering in an intertidal gastropod. *Ecological Modelling* 44 (3-4), 177–194.
- Guelorget, O., Favry, A., Debenay, J.P. and Perthuisot, J.P., (1999). Paralic ecosystems: distribution of present foraminifera in ponds of Diana and Urbino (Corsica). *Vie et Milieu* 49 (1), 51–68.
- Guélorget, O., Frisoni, G. F. and Perthuisot, J. P. (1983). La zonation biologique des milieux lagunaires : définition d'une échelle de confinement dans le domaine paralyque méditerranéen. *Journal de Recherche Océanographique* 8, 15–36.
- Guélorget, O., Gaujous, D., Louis, M. and Perthuisot, J. P. (1990). Macrobenthofauna of lagoons in Guadeloupean mangroves (Lesser Antilles) : role and expression of confinement. *Journal of Coastal Research* 6, 611–626.
- Guélorget, O. and Perthuisot, J.P. (1982). Structure et évolution des peuplements benthiques en milieu paralyques. Comparaison entre un modèle déssalé (l'Étang du Prévost, France) et un modèle sursalé (La Bahiert el Biban, Tunisie). Conséquences biologiques et géologiques. *Journal de Recherche Océanographique*, Paris 7, 2–11.
- Guélorget, O. and Perthuisot, J. P. (1983). Le domaine paralyque. Expressions géologiques biologique, et économique du confinement. *Presse de l'école normale supérieure 16-1983*, 45 rue d'Ulm, Paris, 136 p.
- Guélorget, O. and Perthuisot, J. P. (1984). Indicateurs biologiques et diagnostique écologique dans le domaine paralyque. *Bulletin d'écologie*, Brunoy 15, 67–76.

- Ibrahim , A., Guélorget, O., Frisoni, G. G., Rouchy, J. M., Martin, A. and Perthuisot, J. P. (1985). Expressions hydrochimiques, biologiques et sédimentologiques des gradients de confinement dans la lagune de Guemsah (Golfe de Suez, Egypte). *Oceanologica Acta* 8, 303–320.
- Marinov, D., Norro, A., and Zaldívar, J. M. (2006). Application of COHERENS model for hydrodynamic investigation of Sacca di Goro coastal lagoon (Italian Adriatic Sea shore) *Ecological Modelling* 193 (1-2), 52–68.
- Melaku Canu, D., Solidoro, C. and Umgiesser, G. (2004). Erratum to "Modelling the responses of the Lagoon of Venice ecosystem to variations in physical forcings": [*Ecol. Model.* 170 (2003) 265–289]. *Ecological Modelling* 175 (2), 197–216.
- Murray, J.W. (1991). *Ecology and Palaeoecology of benthic foraminifera*. Longman Scientific Technical, New-York, 397 p.
- Muus, B. H. (1967). The fauna of Danish estuaries and lagoons. *Meddeleser fra Danmarks Frikeri-og Havunderogelser (Ny Serie)* 5, 1–316.
- Periáñez, R. (1998). A three dimensional σ -coordinate model to simulate the dispersion of radionuclides in the marine environment: application to the Irish Sea. *Ecological Modelling* 114 (1), 59–70.
- Perthuisot, J. P. (1975). La Sebka el Melah de Zarzis. Génèse d'un bassin salin paraliq. *Travaux du Laboratoire de Géologie de l'École Normale supérieure, Paris* 9, 1–252.
- Perthuisot, J. P. and Guélorget, O. (1983). Le confinement, paramètre essentiel de la dynamique biologique du domaine paraliq. *Sciences Géologiques, Bulletin. Institut de Géologie, Strasbourg* 14, 25–34.
- Perthuisot, J. P. and Guélorget, O. (1987). Les milieux paraliqes : diversité et unité. *Bulletin d'Écologie, Brunoy* 18, 159–167.
- Perthuisot, J. P. and Guélorget, O. (1992). Morphologie, organisation hydrologique, hydrochimie et sédimentologie de bassins paraliqes. *Vie et Milieu* 42, 93–109.
- Perthuisot, J. P. and Jauzein, A. (1978). Le Khour el Aadid, lagune sursalée de l'Émirat du Qatar. *Revue de Géographie Physique et de géologie dynamique, Paris* 22, 347–358.
- Redois, F. and Debenay, J. (1996). Influence du confinement sur la répartition des foraminifères benthiques : exemples de l'estran d'une ria mésotidale de Bretagne méridionale. *Revue de Paléobiologie* 15 (1), 243–260.