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Role of instantaneous and long-term water movements on the recruitment and life of benthic fauna in the English Channel*

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Abstract : In some cases, the state of the art in hydrodynamical coastal studies now makes possible a good estimation of water movements at time scales ranging from a few minutes to a few months or years. The Channel which is tidally dominated, is in this favourable situation.

Taking the example of the benthic fauna, a discussion is presented on the possible responsibility of hydraulic factors on the life conditions of marine animals :

–eggs and larvae dispersion by instantaneous currents.

–passive transport of those elements during a few weeks by residual currents.

–stress exerted on the bottom and on adult animals by maximum velocities.

Some theoretical hypothesis are proposed and a numerical simulation is done to explain how animals may manage in their energetic environment to maintain and increase their populations.

1. Introduction

The life of marine organisms, their abundance, morphology and their reproductive conditions are probably dependent on a number of external factors, some of which may have an hydrodynamic origin. Marine currents may carry animals, eggs, larvae and nutrients. They may also model bed morphology and determine superficial sediment composition. They are thus, directly or indirectly, a fundamental component of the many factors responsible for the existence of benthic communities.

Investigations in that direction requires, at least, a detailed knowledge of currentologic characteristics at time scales ranging from a few seconds to several weeks, which is very difficult to obtain. However in some circumstances, mathematical models now give this information and make possible to progress. This is attempted here for the case of the English Channel, which is quite shallow (depths generally lower than one hundred meters) and where marine currents are essentially induced by the tide, which is an easy situation from the modelling point of vue.

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2. Some hydrodynamic peculiarities of the channel

The main characteristic of the Channel is the intense tidal currents. Two knots is an average value for a medium tide (Fig.1 and 2). As the waters are generally shallow and bathymetry often irregular, tidal currents create long term velocities which are called tidal residuals (CHENG *et al.*, 1986; ORBL and SALOMON, 1988; SALOMON *et al.*, 1988). Their average amplitude is about 5cm/s but can be much higher (Fig. 3).

The wind is another driving mechanism for water movements. It cannot be compared, in strength, to the instantaneous tidal movements, but may be greater than tidal residuals. The main difference is that wind being always changing in speed and direction, part of its effect vanishes on long time scales. In contrast although modulated on different periods (14 days, 28 days...) tide is permanent and continuously reinforces its action.

Density gradients are due to temperature and salinity differences. Both are weak in the Channel due to the intense mixing action of the tide, a moderate insolation and the absence of high fresh water discharge, except locally near the Seine estuary (average flux of 400 m^3/s).

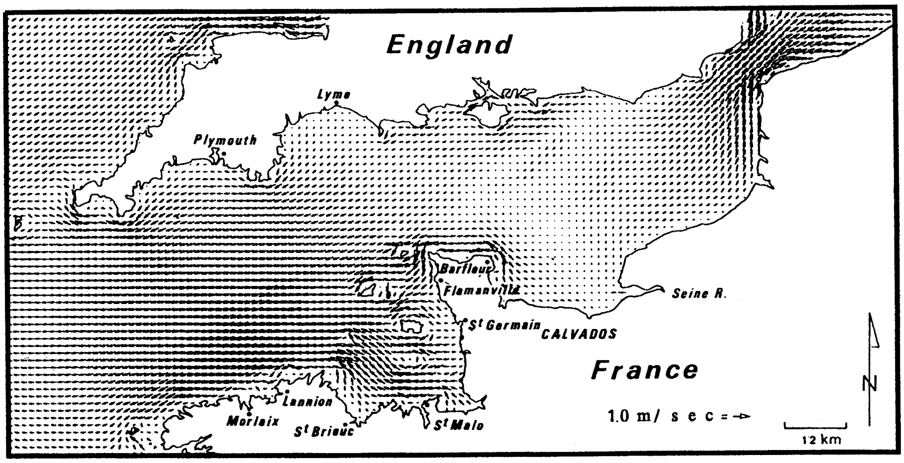

Fig. 1: Example of instantaneous velocity field.

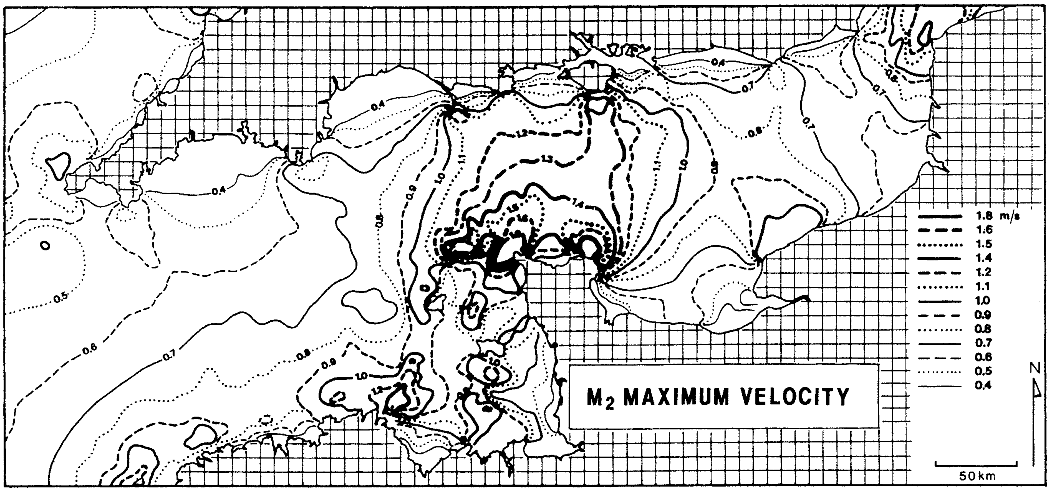

Fig. 2. Isolines of maximum instantaneous velocity during a tidal cycle.

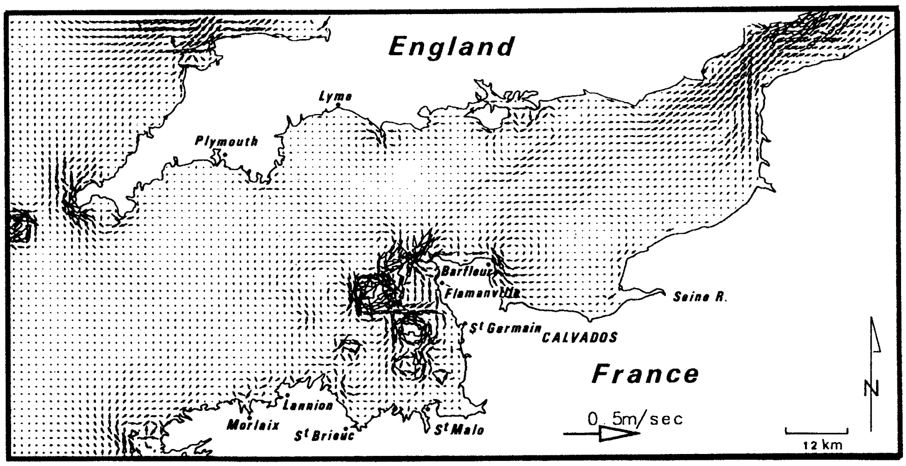

Fig. 3 · Residual velocities.

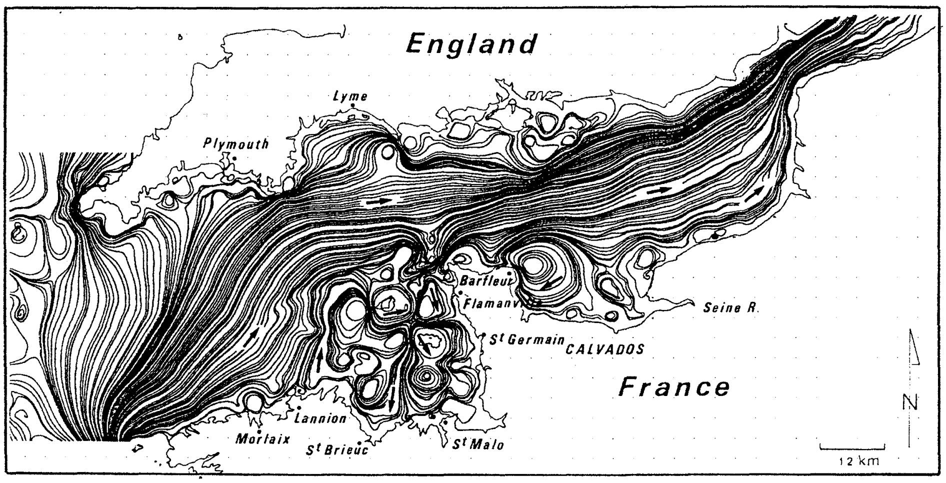

Fig. 4 : Long-term trajectories.

3 . Materials and methods: The two-dimensional numerical model

All information presented herafter is derived from a two dimensional vertically averaged currentologic model of the Channel (Salomon et Breton, 1990a). It is a submodel inserted inside a more global one of the whole North European shelf (Salomon et Breton, 1990b).

The numerical technique involves finite differences and allows for an automatic treatment of the coast and shoaling banks. The mesh size is one square nautical mile. The model computes instantaneous and residual velocities and trajectories through the "barycentric technique" detailed in Salomon *et al*. (1988). Fig. 1 shows an example of an instantaneous velocity field and Fig. 4 presents long term trajectories for a yearly averaged tide and wind situation.

To compute also the relative effect of mixing and transport the model is completed by a sequence of advectiondispersion calcula tion. This second part of the model uses the same grid to solve the advectiondiffusion equation in its usual form :

$$\frac{\partial C}{\partial t} + u\frac{\partial C}{\partial x} + v\frac{\partial c}{\partial y} - k\frac{\partial^2 C}{\partial x^2} - k\frac{\partial^2 C}{\partial y^2} = 0$$

c : concentration, or number of elements per unit volume.
u, v : velocity components.
k : dispersion coefficient.
x, y : horizontal coordinates.
t : time.

More computational details can be found in Salomon *et al*. (1991).

4 . Results and discussion

a) Theoretical arguments

Bottom stress

Marine currents exert a force which is roughly proportional to the square of speed, on the sea bed and the marine organisms to be found there. Thus it is not surprising that a very close similarity exists between superficial sediment composition and maximum tidal currents. It can also be imagined that this parameter plays a direct role by the force exerted on the animals which, unable to withstand it, are carried away, and indirectly by erosion/deposition of fine sedimentary particles. On the contrary, other species may appreciate such zones where fluxes of dissolved nutrients may be higher than elsewhere. As a consequence we may hypothesize Fig. 2 to be a rough indicator of the possibility for an adult population, having specific requirements about instantaneous velocities, to exist in any place.

-Residual movement and dispersion

Eggs and larvae, when released, are advected and dispersed by currents. The pelagic life time being usually longer than the tidal period, the resulting movement may be computed by the residual velocity, whereas dispersion may be evaluated by the following general considerations:

From a point source corresponding to an adult, a patch is created. Its width (B) increases with time, according to the OKUBO formula (1968):

$$B = at^m$$

where $a = 0.00208$

$m = 1.17$ m.k.s.

To compare this expansion with advection, a velocity (Ve) will be defined as the rate of increase of the patch dimension:

$$Ve = mat^{m-1}$$

This shows that the fringe spreads out with a velocity increasing with time. Ve is about 1 cm/s after an hour and 3 cm/s after a month. From which it is clear that the possibility for a patch to remain nearly at the same position as the adult colony depends on the relative magnitude of this expansion velocity and the residual velocity:

Where the residual velocity is weak (about 1 cm/s), it can hardly exceed the dispersion effects. A preferential direction of movement exists but dispersion makes it possible for larvae to proceed in all directions from the location of the adult colony and even back wards, against the current. This gives the larvae the possibility to remain at the same place in significant quantities (Fig. 5a) but inversely restrains the possible dissemination of the colony.

If the velocity is strong enough (order of 3 cm/s) larvae have no more possibility to resist and will be carried away from the original colony. For it to maintain at the same place it is then necessary that the trajectory be either closed (gyre) and travelled through in a time duration similar to the eggs and larvae lifetime, or connected to other colonies, each feeding the other (Fig. 5b).

Those criteria are supposed to apply more constraints to short lifetime species, for which every spawning has to be successful. In the opposite case one can imagine that occa-

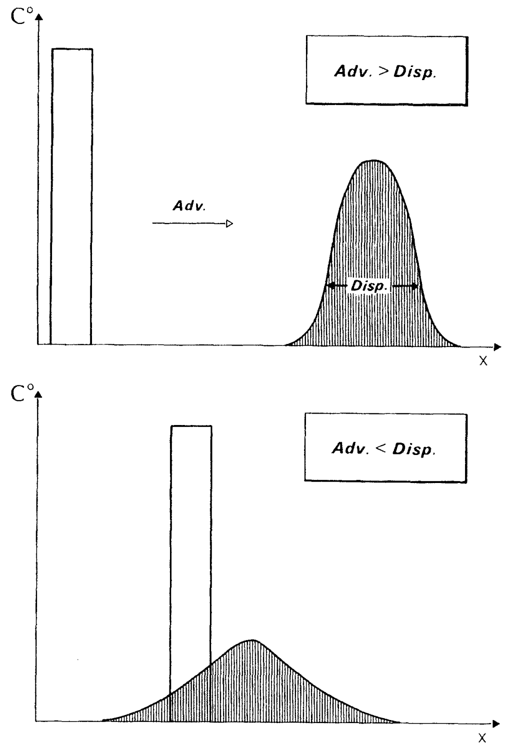

Fig. 5. Relative predominance of dispersion and advection.

sional and favorable meteorological events may be enough to allow the colony to survive.

In the case of medium residual velocity (here about 1-2 cm/s) which is the most frequent, the rate of maintenance of young animals around the spawning place will be rather low unless the settlement is of great geographical extent. Their trajectory will eventually remain highly dependant on meteorological and other fotuitous events. Those areas seem *a priori* favourable to uniformly distributed species, which means not very sensitive to other environmental parameters such as instantaneous velocities, sediment composition or depth.

b) Application to the Channel

Based on the preceeding arguments, one can try to exploit the knowledge of instantaneous and residual velocities to get a better understanding of how some species may use their physical environment to succeed in their recruitment task.

The first apparent feature of long term trajectories (Fig. 4) is the WestEast circulation in the axis of the Channel. It makes North-South connections difficult and may cause a separate development of colonies on both sides. This seems to be particularly true for the English coast from which no path exists for passive particles or animals to go southward. HOLME (1966) mentions more than twenty different species "present along the south coast of England but rare or absent from the French side", among which *Nucula turgida, Ensis ensis, Acrocnida brachiata, Nassarius reticulatus, Ophilura albida* and *ophiura texturat a*... The same author gives fifteen examples of species present throughout the length of the Channel, but mainly on the French side in the eastern Channel: *Lithothamnion calcare um, Astarte triangularis*... Such observations give support to the present statement.

Some areas where residuals are weak and/or rotational seem suitable for the existence of important colonies. Such is the case, on the French coast, for the Bays of SaintBrieuc and the eastern part of the Bay of Seine, although this last one appears very sensitive to the wind and occasionally to fluvial dis charge. On the English coast Lyme and Plymouth bays seem also favorable to permanent settlements.

The Channel islands region is of greatest interest. Intense gyres can be observed (the same for the Scilly surroundings), which are permanent and insensitive to meteorological conditions. Those vortices are places of high shear and probably of intense mixing. They may consequently produce a high dissemination of any passive material. An interesting point will be to investigate if the spatial distribution of other physical parameters to which the adult phase is linked (instan taneous velocities, depths...) is not too heterogeneous for a particular species to be widly distributed.

Generally speaking, a permanent point of convergence along the coastline may favour a discontinuity in coastal populations. Such is the case of the Barfleur headland and the vicinity of PerrosGuirec which seems to be the origin of a streamline which isolates the Channel island region. It is tempting here to make the hypothesis that the natural advective border is one of the reasons for the individualisation of "Sarnian" species (HOLME, 1966) such as *Venus verrucosa, Calyptraea chinensis*, etc.

On the contrary and divergence of coastal currents may favour an homogeneity of populations already existing off the coast (Bay of Seine, region of St Malo).

c) Quantitative results

In 9 arbitary and different locations, a source function has been assumed on the bottom, which introduces instantaneously in the water column a certain number of passive elements (eggs) which are then transported and dispersed according to the equation above for a duration of three weeks. Living particles are then supposed to fall down on the bottom. Fig. 6 is the result of this numerical simulation. It shows the ratio between the number of particles emitted per square meter at the source and the number which are collected on a similar bottom area after the hydrodynamic step. This indicator of the hydraulic efficiency during the pelagic phase is contoured for values of 1/100 and above.

Previous statements are then confirmed and detailed:

Colony n° 1 will recieve his own production in proportions of about 0.01, whereas the center of the patch is moved 25 kilometers to the east. Ratios there are about 0.1 of the initial value. The population appears to have more facility to be slowly translated eastward than to remain at the same place.

Colony n° 2 has both of these possibilities. It can either emigrate towards the northwest or stay at the same place in great proportions (>0.1). In reality the wealth of benthic populations which is observed in the Bay of Saint Brieuc, even for such heavily exploited populations as scallops, is probably related to these physical mechanisms.

Colony n° 3 suffers from a very high dispersion to the south and to the north-east. Compared to the previous example, Hydrodynamic parameters reduce the ability

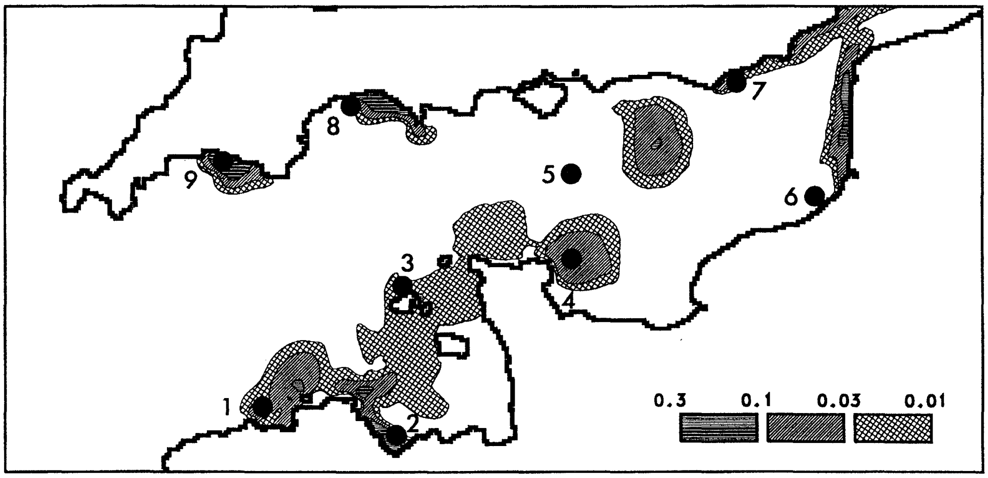

Fig. 6. Ratio collected/emitted larvae per unit bottom area after 3 weeks of movement and mixing. Discs indicate initial position of colonies.

of this colony to stay at the same place by a factor of 10. Inversely, if other interfering mechanisms were so favourable in this region that this ratio did not constitute a severe handicap, the population would have the ability to spread over hundreds of square kilometers in a single larval phase, which is not the usual case.

Juveniles from colony n° 4 are uniformly distributed and confined inside the gyre where they appeared. It seems to give a reasonable efficiency to its spawning without any spatial progression.

Colony n° 5 loses all its production. It cannot exist, except if other similar populations were existing upstream, i.e. west of it.

Colonies n° 6 and n° 7 are in similar situations. Most of their larvae remain along the coast with few perpendicular dispersion, but are translated some 40 km to the north or to the east. It reveals the continuous movement of the populations in direction of the North Sea, especially along the French coast. Such observations have already been done and reported by LAGADEUC and BRYLINSKY (1987) for *Polydora* ciliata larvae. These authors indicate a longshore drift of the animals at a speed ranging between 1.6 and 3.3 kilometers per day, perfectly coherent with what is found here. Nevertheless Colony 7 partially remains at the same place and keeps some chance to perpetuate even if being alone.

Colony n° 8 is essentially in a similar situation as the previous one. Its spawning is slowly carried to the east but part of it remains at the same place and may allow a settlement permanency.

Colony n° 9 is in the most favourable situation. No marked residual velocity and little dispersion make easy for the larvae to stay where they were spawned in amounts of the same order of magnitude as three weeks earlier.

The discussion above was restricted to advection and dispersion of eggs and larvae. It is clear that innumerable other factors exist which might be included and combined with the previous ones to go more deeply into the dynamic of the arbitrary species considered here. Even restraining our investigations to physical parameters it would be easy to combine factors related to the pelagic phase with those related to the benthic one: water depth, maximum and minimum velocity, bottom composition, temperature, etc. All parameters which are already known and will be incorporated to this work in the near future, for continu ation.

5. Conclusion

In some circumstances, mathematical models now make possible to get a reasonable knowledge of water movements at time scales comparable with those concerning biology. In such cases it appeared fascinating to try, by theoretical computations, to imagine how animals manage to use their environment.

Instantaneous velocity fields give indications on the possibility for benthic animals to find adequate hydraulic and sedimentologic conditions to live ; residual circulation and dispersion reveal the possibility for the populations to spread, to be translated, or to remain confined during their pelagic lifetime. The numerical simulation quantifies the role of physical parameters and makes the basis for a discussion on the relative potentialities of different zones for recruitment of benthic populations, all other factors remaining unchanged.

The purpose of this paper was to make an attempt in that direction, based on the knowledge of long term movements. Although theoretical, the discussion seems to have raised some points confirmed by observations. It is thus considered promising and will be pursued by combining other physical param eters.

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Résumé: Dans certains cas, l'état de nos connaissances en hydrodynamique des zones côtières permet aujourd'hui de connaitre le mouvement des eaux à des échelles de temps allant de quelques minutes à quelques mois ou à quelques années. La Manche, dont la courantologie est dominée par la marée, se trouve dans cette situation favorable.

En prenant l'exemple de la faune benthique, on presente ici une discussion du rôle possible des facteurs hydrauliques sur les conditions de vie des animaux marins:

–la dispersion des oeufs et larves par les courants instantanés
–le transport passif de ces éléments durant plusierus semaines par les courants résiduels
–la force exercée sur le fond et les animaux adultes lors des instants de fort courant.

Quelques hypothèses théoriques et une simulation numérique sont présentées pour expliquer comment les animaux peuvent utiliser un environnement hydraulique fortement énergétique pour maintenir ou développer leurs populations.