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INTRODUCTION

In areas where oyster or mussel culture is very intensive, declines of growth rate and decreases of survival rate have occurred. For these reasons, plans have been proposed to regulate the cultivated biomasses in order to fit the carrying capacity of the different ecosystems (Heral et al 1990; Heral, 1991). In areas where new aquaculture of molluscs is beginning, oyster or mussel farmers need to know how large the extension of the culture could be and what the maximal densities should be in order to obtain the maximum economic benefit. Furthermore, as mollusc cultures are developed in coastal areas, they are very susceptible to changes in environmental conditions that can modify trophic relationships, or directly reduce growth rate, physiological functions, recruitment and mortality processes. To give responses to these three types of questions concerning regulation, development, and environmental impact, it is necessary to build models. These models should predict responses in terms of bivalve growth rate in relation to the different management strategies, taking into account biomasses, new species and environmental modifications that can be planned. Two types of models have been developed to achieve these goals, (i) general models based on long term series of population dynamics of the cultivated species, and (ii) trophic models that describe the main relationships that govern the major fluxes of energy, carbon or nutrients in ecosystems.

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Locality	Total weight after 12 months (g)	Total weight after 24 months (g)
Emsworth Harbour (U.K.)	34	100
	(5) 60	
Newton Bay (U.K.)	52	
Linne Mhiurich (U.K.)	14	58
Emsworth Harbour (U.K.)	20	70
		(16 months)
Menai Straits (U.K.)	50	130
Rossmore (Ireland)	46	—
Carlinglard	16	—
Bullinakill	6	—
Carna	3	—
Flensburg		60
Baltic North Sea	8	
(Germany)	(12)60	
Flensburg Fjord (Germany)	24	—
Oualidia (Maroc)	(6) 43	120
Etel (France)	12—29	—
Marénnes-Oléron (France)	48	60
Marennes-Oléron (France)	35	60
Thau (France)	35—50	68
		116 (20 months)
Corse (France)	—	100 (17 months)
Arcachon (France)	15	58 (30 months)
	(18 months)	
Marénnes-Oléron (France)	8	27 (30 months)
	(18 months)	
Bretagne Sud (France)	28	99 (30 months)
	(18 months)	
Marénnes-Oléron (France)	1970 50	100
	1972 33	75
	1974 20	50
	1975—1981	40
	20	
	1984 15	30
Fish pond (Israel)	(4) 79	—
	92	
Lim Canal (Yugoslavia)	26	103

Note: Number in parenthesis represents weight at the beginning of the culture.

Table 1. Growth performance of the cupped oyster *Crassostrea gigas* on the European and Mediterranean coast. (from Heral and Deslous-Paoli (1991).

Substantial differences in growth rates were recorded for the same species in different areas for different countries, but also in the same bay at different levels of exploitation of the area (Table 1).

The main factor which can explain this variability is the available food which depends on two factors: first, the nutritional value of the bay for the mollusc which is a function of (i) the phytoplanktonic productivity, (ii) the estuarine organic matter inputs and (iii) the hydrodynamic characteristics of the bay in terms of current velocities, residence time of water masses and the time of immersion of the mollusc beds. Different bays, lochs, estuaries were tested for *C. gigas* growth and some sites showed ten times more growth than others. In these experiments the tested animals were in small quantities without any other large cultivation, e.g., mussels, scallops, clams, or abundant wild populations of molluscs in the area. The growth results indicate the level of the molluscan trophic capacity for each sector. The second factor affecting growth is the impact of density on the available food on two scales, (i) the local density, which is the density of the unit of culture. It is known that oyster or mussel growth is related to available settlement surfaces (Shafee and Sabatie, 1986; Berthome et al 1984; Boromthanarat and Deslous-Paoli, 1988). These observations for juveniles were also valid for adults. Several authors have shown that growth was a function of the density on the ground, in baskets, in racks or in ponds. This local interdependence is a function of food and space limitation (Frechette and Lefaivre, 1990; Frechette et al 1992). (ii) On a broad scale there is the impact of the total biomass of cultivated or wild populations. Heral et al (1986) found that for the bay of Marennes-Oleron there is a relationship (Fig. 1) between the decrease of the annual growth and the development of the total cultivated biomass of Pacific oyster for the last 15 years.

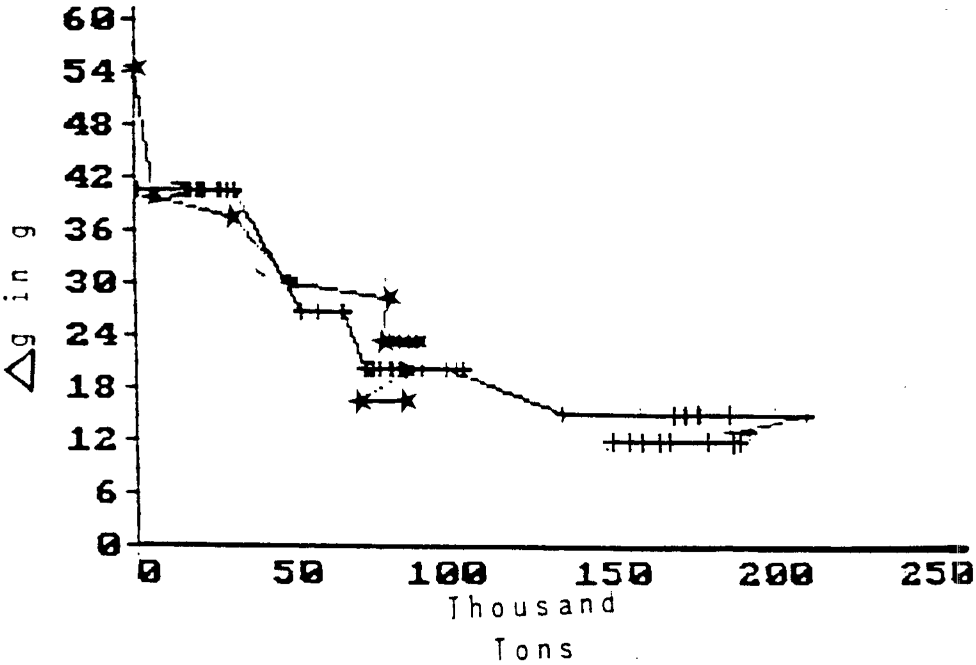


Fig. 1. Evolution of the annual growth rate of Portuguese oyster (+) and Japanese oyster (*) in relation to the total biomass of oysters in the bay of Marennes-Oleron (from Heral, 1991) .

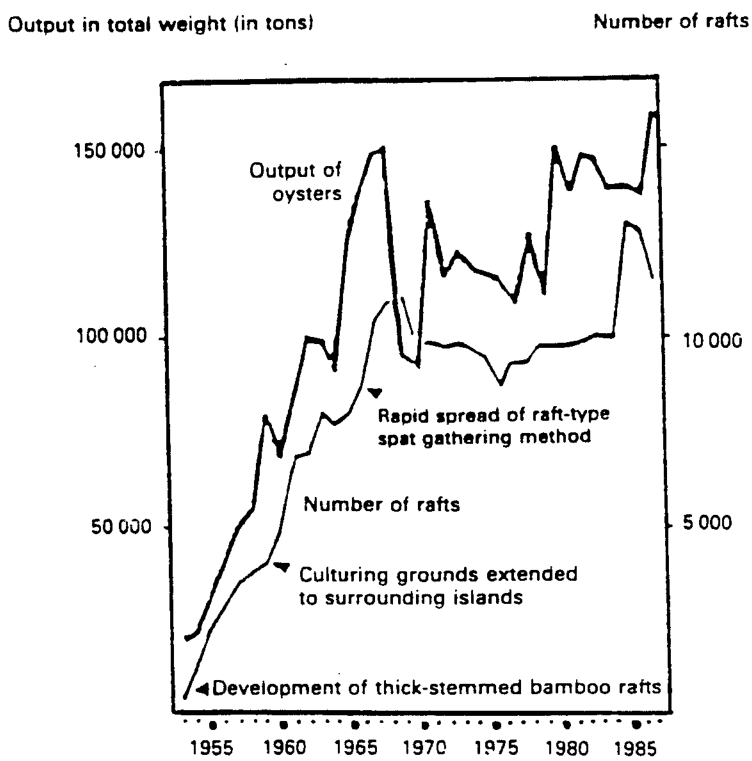


Fig. 2. Evolution of the annual production of oyster and the number of rafts in Hiroshima Bay (from Heral, 1991).

As to the collection of data on growth rate and mortality rate, they can be directly measured in *in situ* experiments or obtained from farmers. These methods gave different results because the farmers carried out all sorts of activities during the culture process (technical aspect, culture rotations). Annual production data also had to be collected. This data could be obtained by inquiries to the local administrations or from the professionals at the different fisheries or aquaculture operations. The data can also come from aerial observations of the intertidal areas as described by Bacher et al. (1986) and Heral (1991). Recording long term time series of oyster production produced clear trends of production which could be related to the management strategies that have been developed and to changes in environmental conditions.

HISTORICAL DATA SET

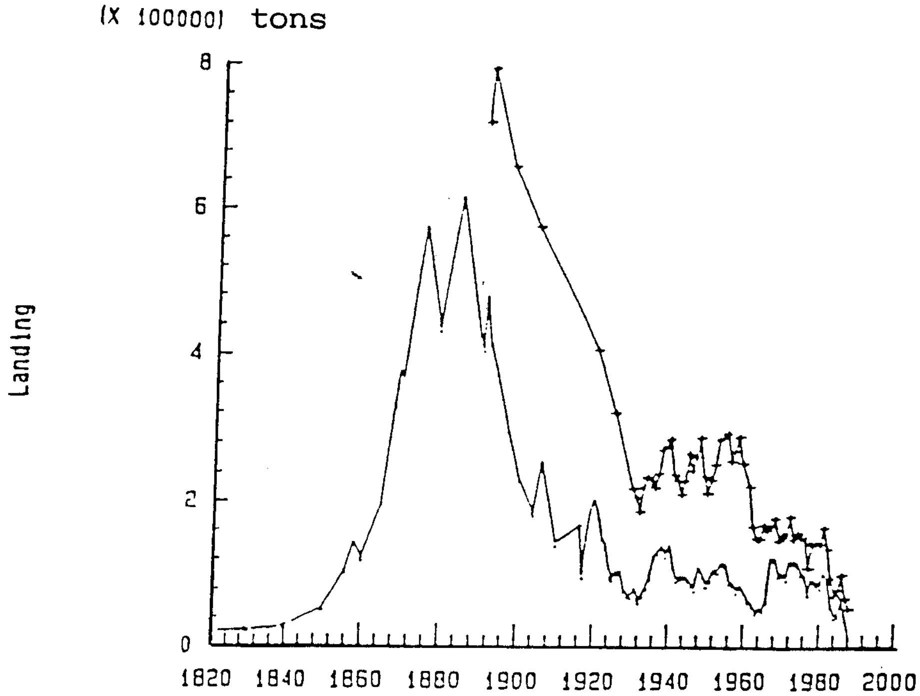
A number of examples of the major world oyster bays will be successively analysed:Hiroshima Bay, Chesapeake Bay, Marennes-Oleron Basin and Arcachon Basin.

Hiroshima Bay:The evolution of the number of rafts and the oyster production was monitored since 1950, before the boost of the production (Anonymous in Heral, 1991; Fig. 2). Until 1980, oyster growth reached market size in one year. After that date, a continuous increase of number of rafts and production (54,000 tons to 110,000 tons) induced a decrease in growth rate to 2 years that modified oyster turnover and profitability. For these reasons the oyster men associate in cooperative societies decided to reduce the number of rafts to re-obtain their initial growth rate. To maintain the biomass at the same level each year, they decided to fix the necessary number of spat collectors function of the exportation and the hardening processes. It is emphasized that this type of management has been possible only because Japanese oyster farmers are highly organized.

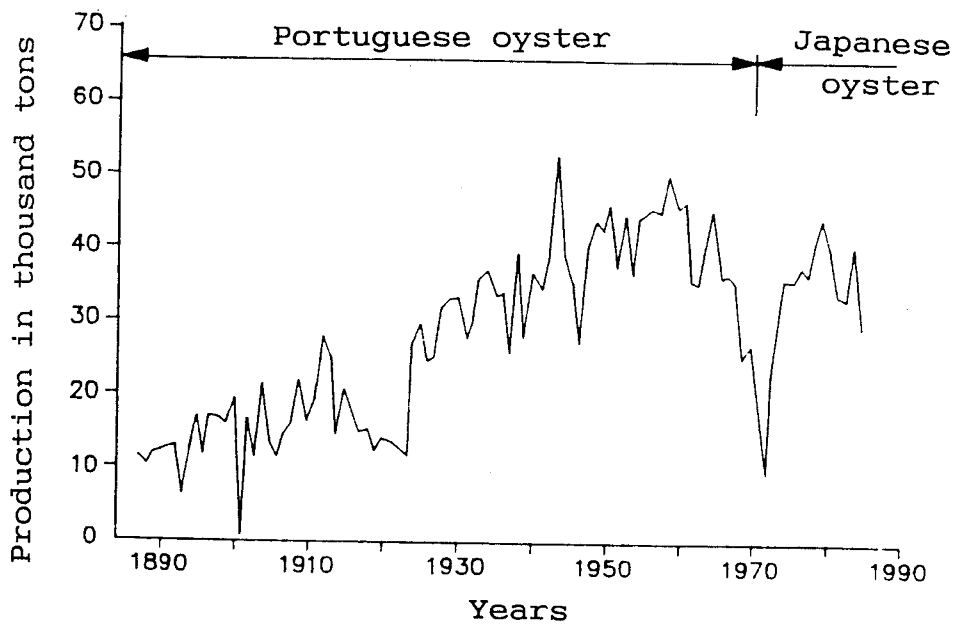
Chesapeake Bay: The landings from 1820 to the present show different trends of oyster production (Fig. 3; Heral et al 1990; Rothschild et al 1993). Three main periods were identified:(1) an increase in oyster fishery from 1840 to 1890 with a large overfishing and the destruction of oyster habitat caused by fishing gear, mainly dredging; (2) the decrease of landings from 1900 to 1980 due to the failure of the reseeding plan connected to the deterioration of environmental conditions, in particular, heavy sedimentation in relation with deforestation and anoxic conditions in summer; (3) the last decrease in production (1981-1988) was caused by high morality related to disease (MSX and *Perkinsus marinus*), predation and poor management practices which contributed to the spread of the diseases.

Marennes-Oleron Basin: The bay is the main European area of oyster production. Change in the production of the cupped oyster has been estimated since the beginning of the century with three difference sources of data (Heral et al 1986; Fig. 4). It is apparent that (1) there was low production from 1890 to 1927 related to the development of Portuguese oyster culture and to the fisheries practices which exploited natural oyster beds; (2) after 1927, there was an increase in production due to the beginning of oyster culture obtained by the control of recruitment using spat collectors and by the development of breeding techniques. Production increased until 1960, (3) from 1960 to 1969 severe declines of the growth rate were observed in relation to over exploitation. Oyster physiological condition was poor and densities were very high. All factors were converging to enhance the spread of disease. It is now known that an iridovirus caused the disappearing of *C. angulata*. It has been replaced by the Japanese oyster *C. gigas* (see Grizel and Heral, 1991). Oyster production reached previous levels quickly with the same overstocking consequences.

Arcachon Basin: The long term time series for this bay (Deltreil, personal communication; Fig. 5) showed the same pattern as Marennes-Oleron bay but with two severe environmental crises:(1) during 1950-1970, oyster production and recruitment deteriorated. This was caused by effluent of a pulp mill that discharged into the bay. The production of the oyster factory increased ten-fold between 1950 and 1960 from 1970 onwards the wastes have been collected in a sewage that discharges outside of the bay (Heral et al; 1990), (2) from 1977 to 1981: the decrease in production was related to contamination of the bay by Tributiltin (TBT) which reduced recruitment (His and Robert, 1980) and caused malfunction of the calcification processes of



'ig. 3. Trends in the oyster production, in total weight
[aryland part (-), Chesapeake Bay (+) (from Heral et al 1990)



'ig. 4. Evolution of annual oyster production in Marennes-
leron Basin (from Heral et al 1986).

the oyster shell (Alzieu and Heral 1983). After the ban of the TBT antifouling paint, recruitment and oyster growth returned to earlier levels (Alzieu et al 1985).

These different case studies clearly illustrated the three main factors that can largely alter mollusc production: diseases, environmental damages and overstocking.

GENERAL DYNAMIC POPULATION MODELS

Dynamic population models were designed to give management authorities an indication of the carrying capacity of a bay. They are based on the assumption that, for the given period, environmental factors have a constant mean, although a certain variation can occur around this mean. Thus, environmental parameters are not included in the regulations. Historical data from long time series allow the building of dynamic population models. For the bay of Marennes-Oleron, data sets have been collected for production, growth and mortality rates for the same years. These data showed that growth rates had decreased for both Portuguese and Pacific oyster while the mortality rate had increased (Fig. 6). The stocks in culture (biomass) have been calculated from the annual production, taking into account growth and mortality (Fig. 7). These calculations gave results comparable with the estimates of stock size obtained by sampling for the recent years.

The establishment of a relationship between the stock and production showed clearly an asymptotic value of 40,000 tons. This level corresponded to the maximum production capacity of the ecosystem (Fig. 8). This definition describes the carrying capacity of the bay for oyster cultivation during the period. Maximum production of the ecosystem can be determined by an equation of the same type as the one used for the growth of the populations. So the Von Bertalanffy equations $P = P_{max}\ (1-e^{-KB})$ fits the data well (P_{max} is the maximum production of the bay, B is the cultivated stock). For Marennes-Oleron for *C. angulata* $K = 0.026 \times 10^{-3}$ and P_{max} = 41,800 tons and for *C. gigas* $K = 0.028 \times 10^{-3}$ and P_{max} = 52,450 tons. The yield P/B in relation to the stock followed a negative exponential curve as the evolution of the annual growth rate in relation to the stock.

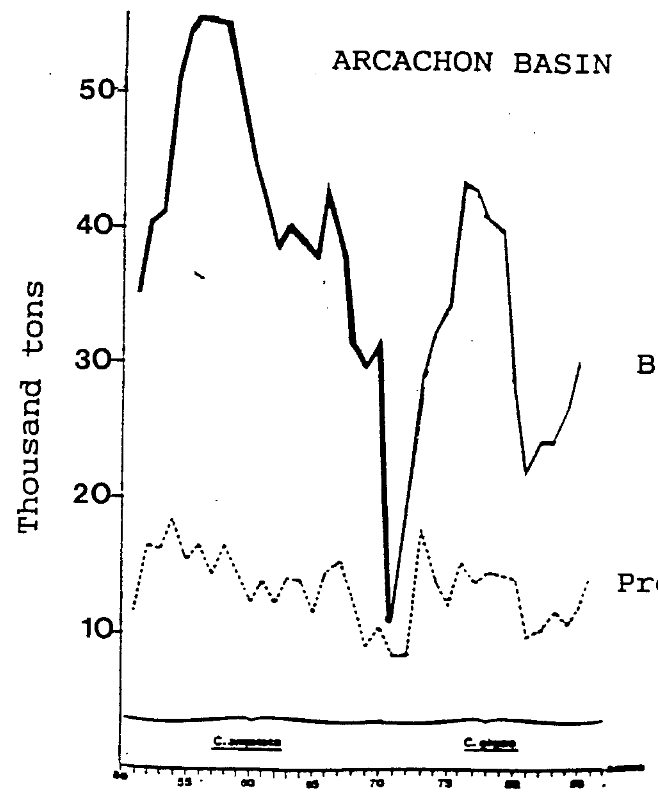
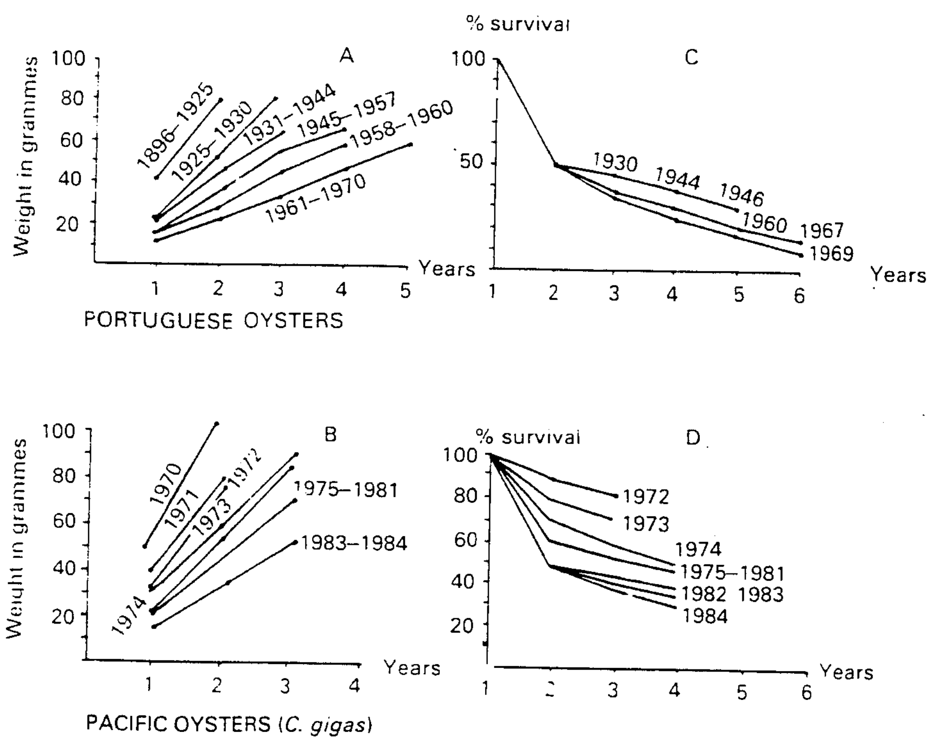


Fig. 5. Development of the oyster stock in Arcachon Bay (from Deltreil, personal communication).



ig. 6. Change in growth rate needed for an oyster to reach arket size (A: Portuguese oysters; B: Pacific oysters) and urvival rates after the first year of culture (C: Portuguese ysters; D: Pacific oysters) (from Heral et al 1986).

a stock of Portuguese oysters of 130,000 tons but also with a stock of Japanese oyster of 80,000 tons. This difference between the two species can be explained by the energetic demand of each oyster: the assimilation of food by the Japanese oyster is 1.7 times greater than by the Portuguese oyster (Heral et al 1986). For management and to estimate the impact of these two oysters, this transformation coefficient must be used.

These models showed that without management of cultivated oysters, the stocks tended to exceed the minimal biomass necessary to reach the maximum potential production. If stock regulation is applied, it gives oyster farmers the advantages of shorter breeding cycle and decreased mortality, which results in better profits.

ANALYTICAL MODEL

The quality of a model is dependent on its hypothesis, but its accuracy depends on the quality of the data sets that have been collected in the ecosystem. For these reasons, it is important to focus attention on the minimal data necessary to build a carrying capacity model.

(1) For hydrodynamic data, simultaneous records of tidal levels are necessary as well as precise and recent bathymetry. Some long time series of current velocity and direction could be of interest knowledge of wind action is necessary.

(2) Meteorological records, such as temperature, wind (strength and direction) and day light, have to be taken frequently over long time periods (10 years) to obtain mean values of different typical conditions with their probability of occurrence intensity.

(3) For sediment suspension and resuspension data, the area has to be mapped with physical characteristics of the sediment. This should be done several times a year because of seasonality of the meteorological conditions. Turbulence is one of the key factors controlling erosion in coastal areas. To study it, it is useful to have a data set on waves with their refraction-diffraction processes as well as measurements on wavelets created by local wind.

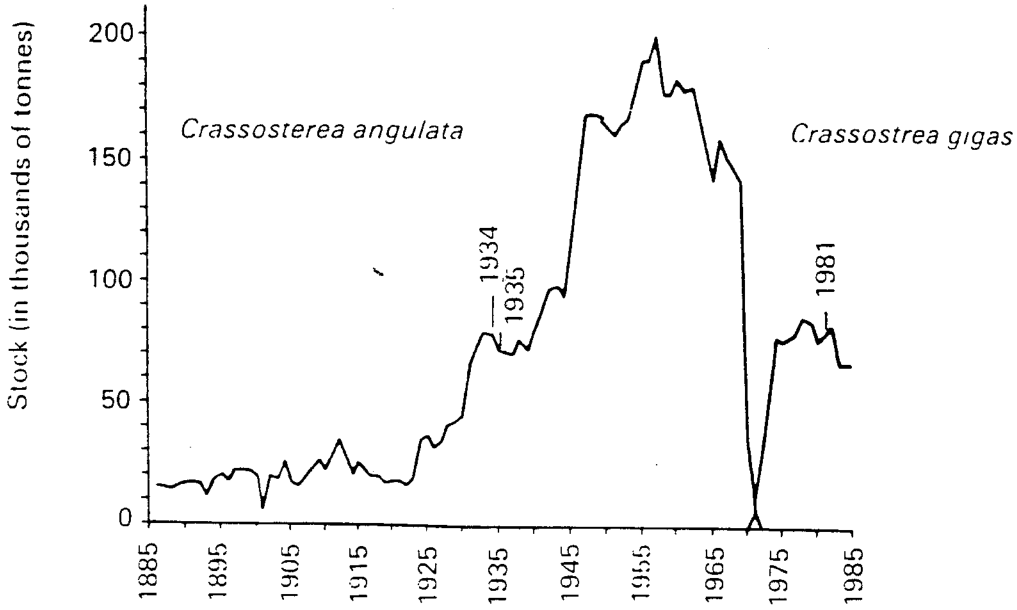


Fig. 7. Calculated evolution of the total biomass of cultivated oysters in the bay of Marennes-Oleron. (from Heral et al 1986)

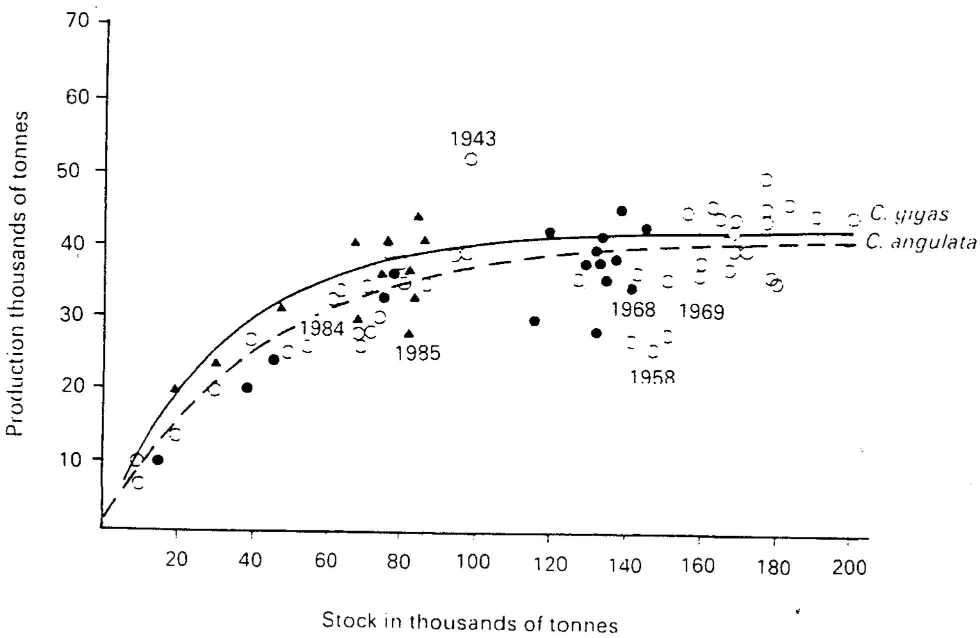


Fig. 8. Evolution of the annual production of the stock in culture for *Crassostrea angulata* (o), *Crassostrea gigas* (•) and for *Crassostrea gigas* converted in equivalent Crassostrea

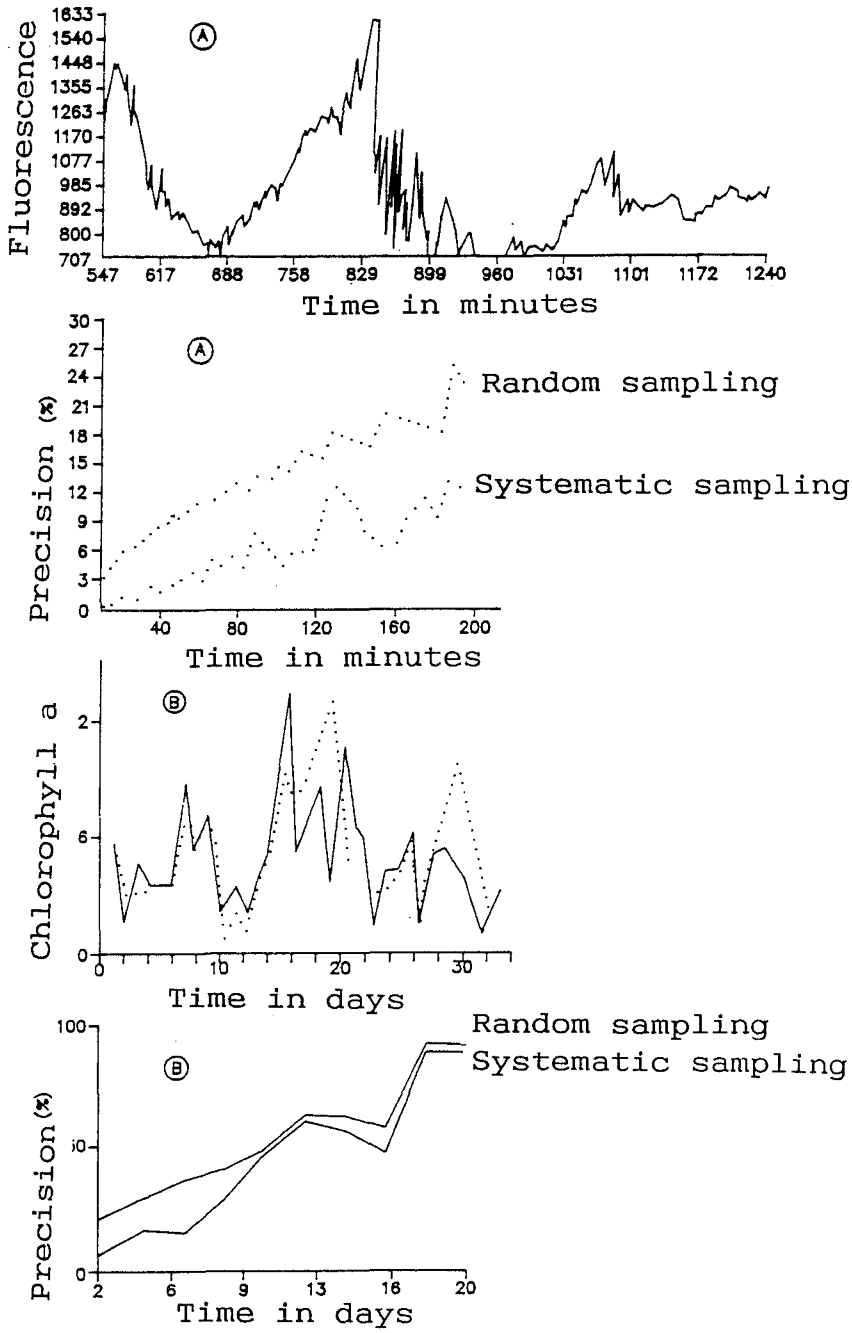


Fig. 9. Precision at the level of 95 % of the intradiurnal mean of the signal (A) as a function of the sampling time and the nature of the sampling (systematic or random sampling). Precision at the 95 % level for the interdiurnal monthly mean of the signal (B) as a function of the sampling time and the nature of the sampling (from Heral et al 1990).

For the water column, sampling strategy must be defined depending on the precision that will be introduced in the model and the time scale of the model. Figure 9 shows, for example, how intense the sampling must be to have good precision on phytoplankton biomasses on a daily or monthly basis. Furthermore, to validate advection dispersion models, continuous records of salinity are required in the different limit conditions. In parallel, continuous record of turbidity are very useful to validate a particular model of transport and sedimentation or erosion processes.

For primary production, for phytoplankton and phytobenthos, the use of photosynthetron techniques allows the determination of the different Michaelis-Menten parameters. A knowledge of nutrient loads from the river and fluxes from the sediment is important to estimate their respective contribution. Determination of limiting factors of phytoplankton production by test in bioassays will define the primary production model as either nitrogen or phosphorus based.

Trophic competitors, such as zooplankton and benthic populations, are estimated by adequate sampling strategies. For molluscs, stratified sampling based on granulometry and bathymetry with optimal allocation as a function of the variance could be a good compromise (Sauriau, 1992). Special techniques with the help of aerial observations or remote sensing are useful to contribute to the estimation of the cultivated biomasses. Population dynamics of the targeted cultivated species have to be followed in different areas to compare results given by the molluscs growth rate model and the observations.

After these intensive phases of acquiring a data set, which can take several years of multidisciplinary research, the main biomasses, production, and fluxes must be compared to identify which are the main processes that control the turnover of the ecosystem (Fig. 10).

It is only these main processes that will be retained for the ecological carrying capacity model. This preliminary work is crucial. Further validity of the model will depend on whether, at this stage, the crucial choices have been well made.

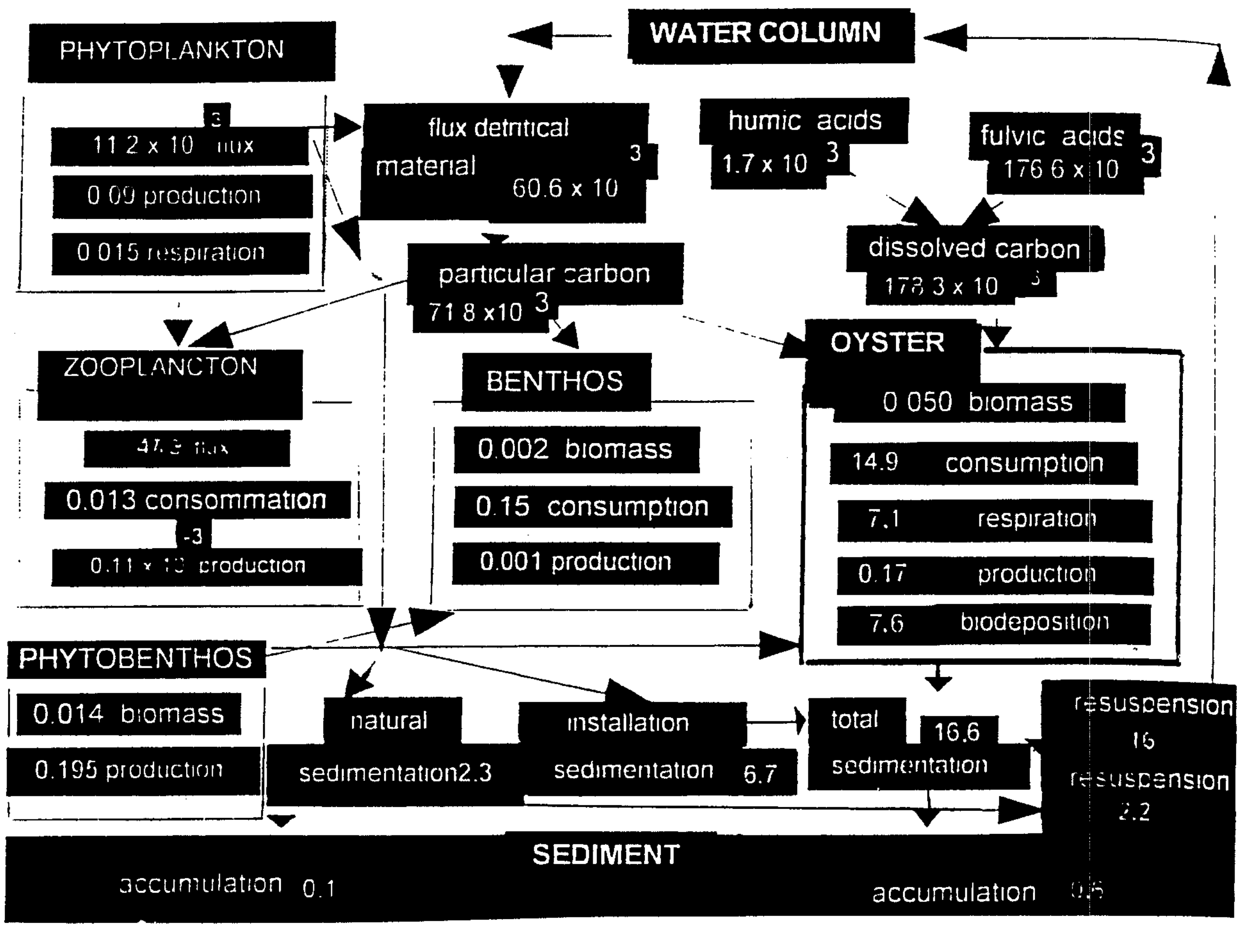


Fig 10. Fluxes of carbon in kg m^{-2} year^{-1} in Marennes-Oleron (from Heral unpublished data).

Figure 10, for Marennes-Oleron bay, shows obviously that suspension and resuspension processes must be retained as well as the phytobenthos production. Detrital organic material is also a significant compartment. Trophic competitors, both benthic wild molluscs populations and zooplankton, play a secondary role in this ecosystem.

The following design could be retained for Marennes-Oleron bay (Figure 11.):

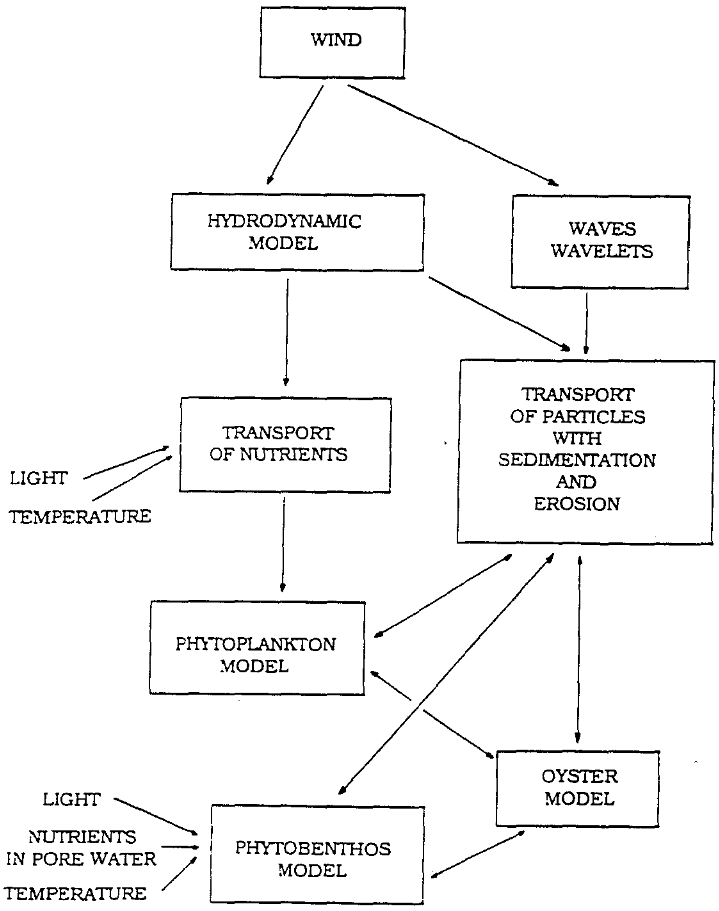


Fig. 11. Scheme of the main trophic interaction in Marennes-Oleron bay.

Food consumption

$Q_{[d,p,m]} = SES_{[d,p,m]} \cdot F$

$Qt = F / (Ws^{bf}) \cdot SES$

$F = F0 \cdot e^{(kf \cdot \min(0,\, Ts - SES))} \cdot Ws^{bf}$; $SES = SES_d + SES_p + SES_m$

Ingestion

$I_{[d,p]} = (1 - PF_o) \cdot Q_{[d,p]}$; $I_m = (1 - PF_m) \cdot Q_m$

$$PF_{[o,m]} = PFX_{[o,m]} \cdot {}^{(1 - e(kp[o,m] \cdot \min(0,\, C1 - Qt)))} + (1 - PFX_{[o,m]}) \cdot {}^{(1 - e(kp2 \cdot \min(0,\, C2 - Qt)))}$$

Absorption

$A_{[d,p]} = ae \cdot I_{[d,p]}$; $EA_{[d,p]} = A_{[d,p]} \cdot X_{[d,p]}$

$ae = aet \cdot TMP + ae0$; $X_d = (ES - SES_p \cdot X_p) / SES_d$

$ES = SES_L \cdot X_L + SES_G \cdot X_G + SES_P \cdot X_P$

Metabolic cost

$R = (art \cdot TMP + ar0) \cdot Ws^{br}$; $ER = R \cdot X_{O2}$

Spawning effort

$P = ap \cdot Wj^{bp}$; $p = P^{(1/dp)}$

Scope for growth

$dWj/dt = ((EA_d + EA_p) - ER) \cdot 10^{-3} \cdot pc \cdot TIM - p \cdot Wj$; $Ws = Wj \cdot Y_b$

PARAMETER	DEFINITION	UNITY
ae	Absorption efficiency	
ae0	Absorption efficiency at t=0°C	
aet	Slope of the absorption function of temperature	
ap	Constant for spawning effort	
ar0	Respiration at t=0°C	$mlO2\ h^{-1}\ gPs^{-1}$
art	Slope of the respiration function of temperature	$mlO2\ h^{-1}\ gPs^{-1}\ °C^{-1}$
$A_{[d,p]}$	Particular absorption	$d \to mgPs\ h^{-1}\ ind^{-1}$
bf	Allometric exponent for filtration	
bp	Allometric exponent for spawning	
br	Allometric exponent for respiration	
C1,C2	Level of pseudofeces production	$mgPs\ h^{-1}\ gPs^{-1}$
dp	Duration of the spawning period	j
$EA_{[d,p]}$	Energy absorbed	$J\ h^{-1}\ ind^{-1}$
ER	Metabolic cost	$J\ h^{-1}\ ind^{-1}$
ES	Total energy of the seston	$J\ l^{-1}$
F	Filtration rate	$l\ h^{-1}\ ind^{-1}$
F0	Standart filtration rate	$l\ h^{-1}\ gPs^{-1}$
$I_{[d,p,m]}$	Particular ingestion	$mgPs\ h^{-1}\ ind^{-1}$, $p \to \mu gChla\ l^{-1}\ ind^{-1}$
kf	Filtration exponent	
kp_{1o}, kp_{1m}, kp_2	Pseudofeces production exponents	
p	Daily ratio of the weight for the spawning effort	
P	Total ratio of the weight for the spawning effort	
pc	Percentage of absorption in energy for the flesh growth	
$PFX_{[o,m]}$	Thresold of pseudofeces production	
$PF_{[o,m]}$	Rate of pseudofeces production	
Qt	Total consumption	$mgPs\ h^{-1}\ gPs^{-1}$
$Q_{[p,d,m]}$	Particular consumption	$mgPs\ h^{-1}\ ind^{-1}$
R	Respiration	$mlO2\ h^{-1}\ ind^{-1}$
$SES_{[p,d,m,P,L,G]}$	Sestonic concentration of the water column	$mgPs\ l^{-1}$, $p \to \mu gChla\ l^{-1}$
TIM	Immersion ratio	
TMP	Water temperature	°C
Ts	Level of cloging	$mgPs\ l^{-1}$
W_j	Calorific content of the oyster flesh	$kJ\ ind^{-1}$
W_s	Dry weight of the oyster flesh	$gPs\ ind^{-1}$
X_{O2}	Energetic conversion for oxygen	$J\ mlO2^{-1}$
X_p	Energetic conversion for chlorophyl	$J\ \mu gChla^{-1}$
$X_{[d,P,L,G]}$	Energetic conversion of the weight of seston	$J\ mgPs^{-1}$
Y_b	Conversion in weight of the energetic value of the oyster flesh	$gPs\ kJ^{-1}$
Y_p	Conversion in dry weight of the chlorophyl	$mgPs\ mgChla^{-1}$

Table 2 : Processes presented in the model, variables and parameters used. The suffixes d, p, m, o, P, L, G, refer respectively to detrital organic matter, phytoplankton, particulate inorganic matter, particulate organic matter and particulate proteins, lipids, carbohydrates. The suffixes 1 and 2 refer to the two stages of the law of pseudofaeces production (from Raillard et al., 1993).

Oyster model

The objective of this model is to predict the growth rate in relation to environmental conditions (T, quantity and quality of food, mineral seston loads). These models cannot include all the physiological results, for example, ingestion rate in relation to the size of the particles. The general equation of the energy budget of oyster populations is established following the equation

$$\mathbf{P = A - R = C - (F + U) - R}$$

where **A** = assimilation, **R** = respiration, **F** = particulate excretion (feces and pseudofeces), **U** = dissolved excretion, C = consumption, **P** = production (**P = Pg + Pr + Ps** with **Pg** = production of the flesh, **Pr** = production used for the reproduction, **Ps** = production of the shell + mucus). Table 2 shows the different laws we have retained until this date for the *Crassostrea gigas* species (Raillard et al 1993) and the results of the model are shown in Fig. 12. Further physiological measurements are required to improve ingestion and assimilation function.

Connection of the different submodels

As time and spatial scales have to be consistent between physical models and biological ones, a box structure is applied to the oyster production area. The Lagrangian residuals of a tide are calculated and are the base for spatial box design. The time scale is the tidal cycle (Bacher, 1989). It has been demonstrated that this design does not alter physical characteristics, such as, residence time. Until now, resuspension and sedimentation terms have been calculated with the original hydrodynamic mesh and the mean values are calculated for each box within the grid (Raillard, 1992).

The ecosystem model is built with a stock of oysters of two age classes in each box, and the growth model is a function of the food that is transported by the physical model. The trophic molluscan shellfish competitors and their assimilation of food are introduced in each box as driving variables. This

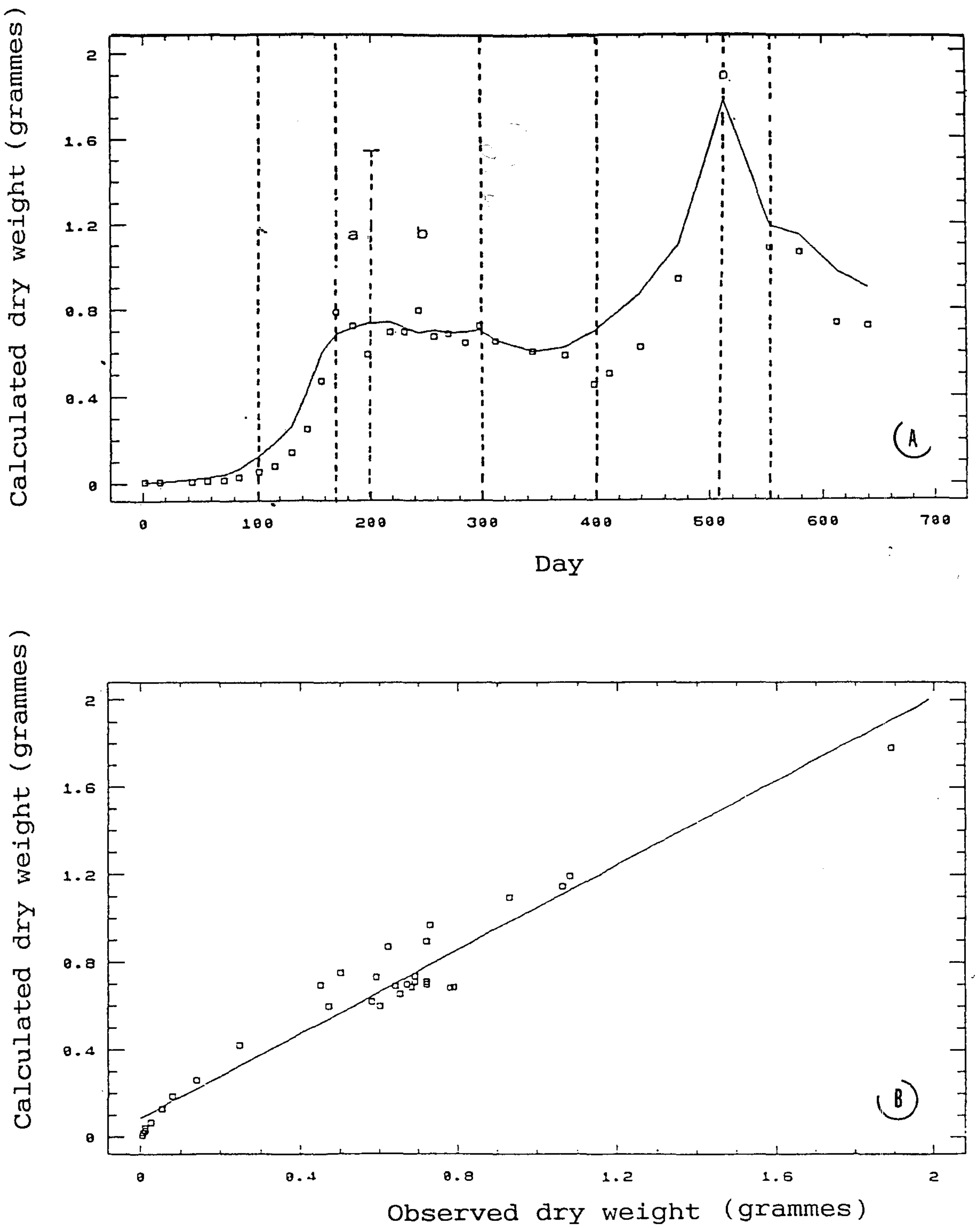


Fig. 12. Results of simulated and measured individual growth (O) of the flesh of *Crassostrea gigas* (KJ) during two years : (a) temporal distribution of S and M; (b) linear regression between simulation and observations (a = 0.96, b = 1.74).

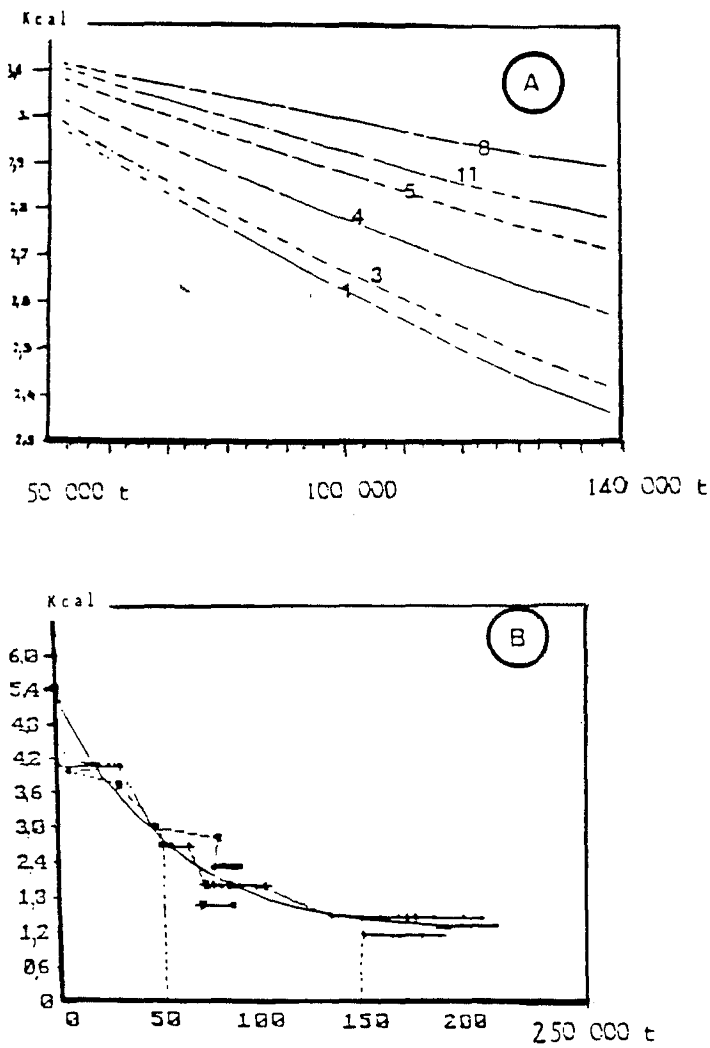


Fig. 13. (A) Simulation of annual production according to the analytical model (from Bacher 1991), (B) annual production of one oyster, results of the global model (from Heral 1986).

approach permits fluctuations in the cultivated stocks of oysters and allows predictions of growth rates in the different areas. The comparison between the results of the general model (Fig. 13B) and the simulation of the analytical model (Fig. 13A) demonstrates the same effects of the total cultivated biomass on the annual growth rate, but with more precision for the different areas with the analytical model. Sensitivity analysis was applied to the level of biomass, to seston load or to the nitrogen quantity (Bacher et al 1991; Bacher, 1991; Raillard and Menesguen 1991; Raillard 1992).

CONCLUSION

To date, these models use many simple hypotheses, but they indicate the future research needs to provide a useful management tool. They demonstrate that a multidisciplinary approach of biologists, physical and chemical scientist and sedimentologists could predict changes in the growth rate of the cultivated species as a function of the food and of all other factors, particularly pollution, that can modify the quality and quantity of the trophic requirements. It is evident that to be predictive and to be a management tool it is necessary to go further in the study of energy demands of the oysters for particulate and dissolved substances. Alternatively, a phytoplanktonic model, that simulates the variations of the input of nutrients from the estuary, would be helpful for the study of the consequences of the use of freshwater on oyster production.

With the results of the EEC TROPHEE programme, we hope we will be able to develop more deterministic laws for the physiology, recycling of nutrients and phytobenthos production and to increase the predictivity of the models.

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