

# Modelling oyster population dynamics in a Mediterranean coastal lagoon (Thau, France): sensitivity of marketable production to environmental conditions

Aline Gangnery<sup>a,b,\*</sup>, Cédric Bacher<sup>b</sup>, Dominique Buestel<sup>c</sup>

<sup>a</sup>*Ifremer, Laboratoire Conchylicole de Méditerranée, Avenue Jean Monnet, BP 171, 34 203 Sète Cedex, France*

<sup>b</sup>*CREMA, Centre de Recherche sur les Ecosystèmes Marins et Aquacoles, Place du Séminaire, BP 5, 17 137 L'Houmeau, France*

<sup>c</sup>*Ifremer-COP, Centre Océanologique du Pacifique, Taravao, Tahiti, French Polynesia*

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## Abstract

A population dynamics model was used to simulate variations in the standing stock of the Pacific oyster, *Crassostrea gigas*, to assess the marketable production in Thau Lagoon (France) and to evaluate the sensitivity of this production to environmental conditions. The model is based on a continuous equation of the oyster abundance as a function of individual growth rate, inter-individual growth variability and mortality rate. The growth model depends on water temperature, particulate organic matter concentration and total individual mass. Inter-individual growth variability was introduced into the general population dynamics equation by a diffusion coefficient  $K$  that was set to 0.05. The population dynamics model took into account the two culture methods (i.e. “collées” and “pignes” oysters) and rearing strategies of oyster farmers by using timetables of seeding and harvesting obtained through interviews of oyster farmers. Distributions of standing stocks were obtained through assessments conducted in the lagoon in March 2000, October 2000 and March 2001 and were used to calibrate the model. The model estimated the total marketable production at ca. 17,900 t between March 2000 and March 2001. The major part of the production (ca. 70%) was in spring. Seventy percent of the annual production came from “collées” oysters. Sensitivity analyses showed that the key parameters are those related to harvesting. The model was used to evaluate the effects of different environmental conditions (e.g. a decrease in the oyster growth rate, a harvesting closure due a toxic algae bloom, a massive summer mortality due to an anoxic crisis) on

\* Corresponding author. CREMA, Place du Séminaire, BP 5, 17 137 L'Houmeau, France. Tel: +33-5-46-50-94-40; fax: +33-5-46-50-06-00.

E-mail address: [agangner@ifremer.fr](mailto:agangner@ifremer.fr) (A. Gangnery).

short- and long-term variations in the standing stock and the production for both culture methods. A decrease in the growth rate of ca. 20% resulted in losses of 18% in the first year of production for both culture methods. Long-term simulations showed that the production of “pignes” oysters was more affected than that of the “collées” oysters (reductions of 26% and 4%, respectively). Simulated scenarios included a 2-month long harvesting closure (i.e. November and December) or a massive summer mortality (i.e. 45% and 20% for “collées” and “pignes” oysters, respectively). No long-term effect was predicted for either event, although losses of ca. 10% were estimated in the first year of production for both culture techniques. The model can be a useful tool for predicting marketable production of oysters as a function of rearing strategy and environmental conditions.

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**Keywords:** Oyster farming; Inter-individual growth variability; Distributions; Standing stock; Marketable production

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## 1. Introduction

The modelling of exploited bivalve population dynamics has been investigated in an increasing number of studies during the past 10 years. Some authors have coupled population dynamics with ecophysiological or ecosystems models and concentrated on ecological aspects related to the impact of molluscs on an ecosystem through food consumption and biodeposition (Guarini, 1994 for mussels *Mytilus edulis* and *Mytilus galloprovincialis*), or the response of molluscs, in terms of growth and reproduction, to environmental conditions (Powell et al., 1995; Hofmann et al., 1992, 1994 and Dekshenieks et al., 2000 for *Crassostrea virginica*; Kobayashi et al., 1997 and Hyun et al., 2001 for *Crassostrea gigas*). Other authors have applied population dynamics models to resource management (Powell et al., 1997; Klinck et al., 2001; de Waal and Cook, 2001; Pastres et al., 2001). For example, Borja and Bald (2002) developed a population dynamics model for a Spanish clam fishery (*Ruditapes decussatus*) to determine how the timing of fishing seasons and the number of fishermen act on captures and on the minimum sustainable biomass. These models vary in the accuracy with which population dynamics are described: accuracy of biological (e.g. growth, mortality) and human (e.g. seeding and harvest rates) processes involved in exploited population dynamics and accuracy of populations size structure.

A population dynamics model was specifically developed for assessing the marketable production of *Crassostrea gigas* reared in the Thau Lagoon (France) (Gangnery et al., 2001). This model simulates oyster abundance, as a function of the growth rate and the mortality rate and is similar to the one discussed in Gros and Hamon (1989) in which an assessment of the standing stock variations of a cockle (*Cerastoderma edule*) in the Bay of Saint Brieuc (Brittany, France) was made with an explicit description of the size distribution of the cockle stock. Furthermore, we added to this general equation the inter-individual growth variability and the seeding and harvesting rates. The objective of this new study is to update the model that was previously published to make more realistic simulations and predictions. In Thau Lagoon, oyster farmers use two different rearing techniques, called “collées” and “pignes”. “Collées” oysters are glued on ropes with

cement, whereas “pignes” oysters are obtained from individual oysters settling naturally on empty oyster shells used as collectors and inserted in the strands of ropes (see Gangnery et al. (2003) for a detailed description of culture methods and rearing structures used in the lagoon). In the previous model, Gangnery et al. (2001) focused on dynamics of “collées” oysters. “Pignes” oysters were not included in the earlier model due to incomplete information about growth and seeding and harvesting rates that were needed to estimate parameters for processes. New studies were recently conducted to improve and extend the population dynamics model to “pignes” oysters at the site; the results of these studies were used to update the previously published model. Firstly, an empirical growth model was developed for the two culture methods (Gangnery et al., 2003). Secondly, seeding of new individuals and the harvest rate were improved for “collées” oysters and determined for “pignes” oysters through interviews of oyster farmers (Gangnery, 2003).

The updated model was calibrated on observed data sets recorded in 2000–2001 and used to evaluate variations in the whole oyster standing stock and marketable production between March 2000 and March 2001. Sensitivity analyses were carried out to identify key parameters of the model. Furthermore, the model was used to evaluate the consequences of different scenarios on the marketable oyster production in Thau Lagoon: (i) a decrease in the oyster growth rate, (ii) a temporary harvesting closure due to a toxic algae bloom and (iii) a massive mortality due to an anoxic crisis. For each case study, the sustainability of the marketable production was examined over different time-scales.

## 2. Material and methods

The population dynamics model and parameters used has been extensively described in a previous work (Gangnery et al., 2001). The following paragraphs (see also Table 1), summarise the main components of the model, its new parameter set and the simulations.

### 2.1. Population dynamics model

The population dynamics were described with the standard equation based on growth and mortality (Gurney and Nisbet, 1998), which was augmented with a harvest rate and individual growth variation expressed as a random dispersion of mass. Eq. (1) expresses the variation in the number of individuals whose total individual mass is  $w$ , at time,  $t$ :

$$\frac{\partial}{\partial t} n(w, t) + \frac{\partial}{\partial w} G(w, t) n(w, t) = K \frac{\partial^2}{\partial w^2} n(w, t) - mn(w, t) - r(w, t) n(w, t) \quad (1)$$

where,  $n(w, t)dw$  is the number of individuals whose mass is in the range,  $w$  to  $w+dw$ , at time,  $t$ ;  $G(w, t)$  is the growth rate ( $\text{g day}^{-1}$ );  $K$  is the diffusion coefficient ( $\text{g}^2 \text{day}^{-1}$ ) and is related to the individual growth variance;  $m$  is the mortality rate ( $\text{day}^{-1}$ ) and is independent of both individual mass and time; and  $r(w, t)$  is the harvest rate ( $\text{g day}^{-1}$ )

Table 1

Model variables and parameters values used in the population dynamics model

Abbreviation	Value	Unit	Comment	Reference <sup>a</sup>
<i>State variable</i>				
$N$	$f(\text{time}, w)$		Oyster abundance	
<i>Forcing variables</i>				
POM	$f(\text{time})$	$\text{mg l}^{-1}$	Particulate organic matter	1
$T$	$f(\text{time})$	$^{\circ}\text{C}$	Water temperature	1
<i>Functions and parameters</i>				
Growth rate $G = a \times \text{POM}^b \times T^c \times w^d$				
$a$	$3.77 \times 10^{-5}$	$\text{l mg}^{-1} \text{ } ^{\circ}\text{C}^{-1} \text{ day}^{-1}$	Proportionality coefficient	1
$b$	0.40	–	POM exponent	1
$c$	2.50	–	$T$ exponent	1
$d$	0.41	–	Mass exponent (allometry)	1
<i>Inter-individual variability</i>				
$K$	0.05	$\text{g}^2 \text{ day}^{-1}$	Diffusion coefficient	This study
<i>Seeding</i>				
$N$		Nb	Abundance of seeded oysters during the simulation	
	$4.75 \times 10^7$		“collées” oysters-simulation $Sa$	This study
	$2 \times 10^8$		“pignes” oysters-simulation $Sa$ (at 8 g)	This study
	$1.71 \times 10^7$		“collées” oysters-simulation $Sb$	This study
	$4.5 \times 10^7$		“pignes” oysters-simulation $Sb$ (at 8 g)	This study
$w_0$	8	g	mass at seeding for “collées” and “pignes” oysters	2
$S_T$	2700	$\text{day } ^{\circ}\text{C}$	Threshold for growth delay used for “pignes” oysters	This study
$F_{SC}$	Range: 0–15	%	Monthly seeding frequency for “collées” oysters	2
$F_{SP}$	Range: 0–17	%	Monthly seeding frequency for “pignes” oysters	2
<i>Harvest</i>				
$r = \left( \frac{w - w_{\min}}{w_{\max} - w_{\min}} \right)^{\alpha}$		$\text{day}^{-1}$	Probability of harvest as a function of mass	
$w_{\min}$	75	g	Minimum mass at harvest	2
$w_{\max}$	180	g	Maximum mass in the system	2
$\alpha$	2	–	Curvature parameter of the sigmoid	This study
$h = r \times F_h$		$\text{day}^{-1}$	Probability of harvest as a function of mass and time	
$F_h$	Range: 34–78	%	Monthly harvest frequency for the two culture methods	2
<i>Mortality</i>				
$m$	10	$\% \text{ year}^{-1}$	Percentage of mortality	3

<sup>a</sup> References: <sup>1</sup>Gangnery et al., 2003; <sup>2</sup>Gangnery, 2003; <sup>3</sup>Gangnery et al., 2001.

which is a function of individual mass and time. The population level is maintained through the seeding,  $e(t)$  ( $\text{day}^{-1}$ ), of young oysters of mass  $w_0$ , which also therefore represents the minimum mass class. The total oyster standing stock in the lagoon and the instantaneous marketable production can be derived from Eq. (1) as explained in Gangnery et al. (2001).

## 2.2. Growth model and inter-individual growth variability

Based on surveys conducted in 2000–2001 in the lagoon, the growth rate ( $G$  in  $\text{g day}^{-1}$ ) was modelled as a function of water temperature ( $T$  in  $^{\circ}\text{C}$ ), particulate organic matter concentration (POM in  $\text{mg l}^{-1}$ ) and the total individual mass ( $w$  in  $\text{g}$ ) according to the following equation [see Gangnery et al. (2003) for a detailed description]:

$$G = 3.77 \times 10^{-5} \text{POM}^{0.4} T^{2.5} w^{0.41} = dw/dt \quad (2)$$

with  $n = 140$ ,  $R^2 = 0.93$  and  $P < 0.001$ . The same equation was used for the two culture methods. Water temperature governed the seasonal pattern of oyster growth observed in Thau Lagoon and POM concentration influenced spatial patterns.

The  $K$  coefficient was also calibrated using growth measurements made during 2000 and 2001 (Gangnery et al., 2003), according to the method explained in Gangnery et al. (2001).

## 2.3. Seeding, harvest and mortality

Information about seeding and harvesting were obtained directly from oyster farmers. A sample of 60 oyster farmers was randomly chosen from the 600 operating in the lagoon, and interviews were conducted during spring 2001 (Gangnery, 2003). The goal of the interviews was to analyse the production systems used in the lagoon and to create a typology of oyster farmers based upon their rearing strategies.

### 2.3.1. Seeding

Three parameters are needed to define oyster seeding: (i) the number of oysters added to the lagoon per year, (ii) the annual timetable used by the oyster farmers and (iii) the oyster's mass ( $w_0$ ).

The total number of oysters seeded in the lagoon was estimated through optimisation. The optimisation criterion used was to minimise the deviation between the simulated and observed distributions at the end of the simulation.

The annual seeding timetable showed that seeding mainly took place at the beginning of the year (January to April) and to a lesser extent in fall (October and November, Fig. 1). Seeding was avoided in summer (July and August) when higher temperatures implied stressful conditions. Low seeding rates were also observed in December when the farmers prepared for the Christmas sale season.

The  $w_0$  of “collées” oysters averaged 8 g. For “pignes” oysters,  $w_0$  was not well known because the individuals weighed a few milligrams and are difficult to measure. In the population dynamics model, we chose to make the  $w_0$  for “pignes” oysters and “collées” oysters equal (8 g), and we introduced a delay in the seeding. This delay

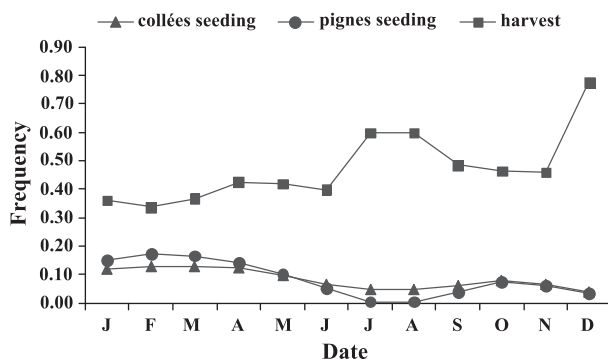


Fig. 1. Seeding and harvesting timetables used by oyster farmers in Thau Lagoon.

corresponded to the time required for the “pignes” oysters to reach a mass of 8 g and was based on the calculated daily cumulative temperature, in units of day-degrees (Theisen, 1973; Bayne and Worrall, 1980). For each “pignes” oyster cohort seeded daily in the lagoon, the daily cumulative temperature (i.e. number of day-degrees) was computed. When the cumulative temperature reached a required threshold value, the cohort was seeded with a mass of 8 g. The threshold value was obtained from growth data recorded in 2000–2001 (Gangnery et al., 2003). For oysters seeded in March 2000, a mean mass of 8 g was reached after ca. 100 days, which corresponds to ca. 1800 day-degrees. Oysters seeded in October 2000 reached the same mass after ca. 250 days of growth, which corresponds to ca. 3600 day-degrees. The difference between the two values came from the seeding period and different size at seeding. As oysters farmers do, “pignes” oysters seeded in March 2000 were settled on collectors in the summer 1999 whereas oysters seeded in October 2000 were settled on collectors in the summer 2000. In the model, a constant mean value of 2700 day-degrees was used to estimate a new annual seeding timetable representative of the seeding of 8 g individuals.

### 2.3.2. Harvest

The harvest depends on both the individual mass and the season. Like in Gangnery et al. (2001), dependency upon mass has been taken into account with a sigmoid function (see Table 1). The harvest criteria were identical for both “collées” and “pignes” oysters:  $w_{\min}$  (minimum mass set for harvest in g) and  $w_{\max}$  (maximum mass) were 75 and 180 g, respectively, according to the oyster farmers’ interviews. The curvature parameter for the sigmoid,  $\alpha$ , was set to 2.

Time dependency (i.e. monthly frequencies of harvest) was obtained through the annual timetable given by the oyster farmers (Fig. 1); harvest timetables were identical for “collées” and “pignes” oysters. December was a peak period of harvest followed by summer, especially the months of July and August. Other periods of the year were slack periods, in particular the beginning of the year.

At each time step and for each mass class, the harvest rate was computed by multiplying the probability,  $r$ , obtained from the sigmoid by the corresponding monthly frequency of harvest from the interviews.

### 2.3.3. Mortality

The percentage of mortality was assessed to be 10% per year and was assumed to be constant (Gangnery et al., 2001).

### 2.4. Observed standing stock distributions

On three occasions (March and October 2000 and March 2001), in situ surveys were conducted to assess the distribution of “collées” and “pignes” oyster standing stocks in the lagoon. The surveys relied on a stratified sampling combined with cluster sampling. The primary sampling unit was a 5-m square and the secondary units were 50-cm rope segments. All oysters fixed to a rope segment were collected and taken back to the laboratory. The oysters were then separated and cleaned of fouling organisms. Next, the total individual mass of each oyster was recorded, along with the number of oysters per sample, the number of ropes per square and the rope length. Between 334 and 1301 individual oysters were measured to obtain each distribution.

### 2.5. Model calibration and production assessment in years 2000 and 2001

Starting with the different variables parameterised previously (growth rate, inter-individual variability, seeding, harvest and mortality), the model was calibrated on distributions recorded in October 2000 and March 2001, and used to assess the marketable production obtained between March 2000 and March 2001. Two simulations were run for each culture method: from March to October 2000 (i.e. simulation *Sa*) and from October 2000 to March 2001 (i.e. simulation *Sb*). The initial conditions were given by the observed distribution recorded in March and October 2000 for simulations *Sa* and *Sb*, respectively. Simulations were run with a 1-day time step and mass classes of 2 g.

### 2.6. Sensitivity analyses

Sensitivity analyses were conducted on several parameters to assess their impact on the model results. For single parameters (i.e. minimum and maximum mass at harvest, curvature parameter of the sigmoid, threshold of cumulative temperature, diffusion coefficient and mortality rate), each parameter was varied by  $\pm 10\%$  and the results of each run were analysed using a sensitivity index (SI, Eq. (3)) to calculate the resulting percentage change in the stock and the production:

$$SI = \frac{1}{n} \sum_{t=1}^n \frac{|X_t^1 - X_t^0|}{X_t^0} 100 \quad (3)$$

where  $n$  is the number of simulated days,  $X_t^0$  is the stock or the marketable production value predicted with the standard simulation at time,  $t$ , and  $X_t^1$  is the stock or the production value predicted with a new parameter value at time,  $t$ . The mean of  $-10\%$  and  $+10\%$  SI was calculated. SI values were calculated for each simulation period and each culture method.

For multiple parameters (i.e. seeding and harvest timetables), the sensitivity was assessed by running 100 simulations for each parameter in which each monthly frequency was chosen randomly within  $\pm 20\%$  of the standard value. The analysis was conducted on the 1-year simulations (March 2000 to March 2001) of each culture method. The total numbers of oysters seeded were based on optimised values corresponding to each period of the year (see Table 1). Simulations were run with a 1-day time step and mass classes of 2 g.

### 2.7. Scenarios

Four scenarios were studied to examine the sensitivity of the marketable production of oysters. Both short-term (years 2000–2001) and long-term (several years) variations were examined. All the simulations had identical initial conditions: those observed in March 2000. The numbers of seeded oysters were based on optimised values corresponding to different periods of the year, and were the same each year (see Table 1).

#### 2.7.1. Scenario 1

The first scenario was devoted to studying the effect of seasonal variations of the growth rate. Twelve simulations (one per month) were run to assess the effect of the seeding date on the marketable production. Initial conditions were set to zero and for each simulation, 1000 oysters were seeded in a given month. The estimated marketable production was characterised in terms of quantity and temporal distribution.

#### 2.7.2. Scenario 2

We were interested in inter-annual variation of growth rate caused by changes in environmental conditions. Growth data obtained from the REMORA network (REseau Mollusques des Rendements Aquacoles, in French) between 1994 and 2001 (Fleury, personal communication) were used to estimate inter-annual variations of the growth rate of *Crassostrea gigas* in Thau Lagoon (Fleury et al., 2001; Gangnery et al., 2001). The maximum growth rates were recorded in 1999 and the minimum ones in 2001; the variation between the maximum and minimum rates reached 20%. For each of these years, Eq. (2) was fitted to the corresponding growth data. Only the first parameter (i.e. parameter  $a$ , see Table 1) was re-estimated for each growth data set. Other parameter values were unchanged. As both POM and water temperature data were not available for 1999, we used data recorded in 2000 and 2001 (Gangnery et al., 2003). Parameter  $a$  was estimated at  $3.64 \times 10^{-5}$  and  $2.81 \times 10^{-5}$  for years 1999 and 2001, respectively. As the value obtained for year 1999 was smaller than the value originally estimated (i.e.  $3.77 \times 10^{-5}$ ), we only tested the value obtained for year 2001. Simulations were run with parameter values of  $2.81 \times 10^{-5}$  (i.e. minimum growth rate) and  $3.77 \times 10^{-5}$  (i.e. maximum growth rate) for both culture methods.

#### 2.7.3. Scenario 3

The third case concerns the effects of a toxic algae bloom on the marketable production. In 1998, *Alexandrium tamarense* was recorded in concentrations high enough to require a harvesting closure of shellfish between 05 November and 29 December (Abadie et al., 1999). In 2001, another bloom occurred and harvesting was halted between 06 November



and 28 November. Hence, simulations were run with no harvest between 05 November and 28 December of the first year and then compared to simulations without harvest closures.

#### 2.7.4. Scenario 4

In August 1997, an anoxic event in the lagoon led to shellfish mortality in ca. 18% of the total cultured area (Souchu et al., 1998). We used this estimate to model a similar event in August 2000. In March 2000, “collées” and “pignes” oysters occupied ca. 34% and 13% of the cultured area, respectively. Therefore, simulations were run with mortality rates of ca. 45% and 20% for “collées” and “pignes” oysters, respectively. The mortality event was placed on 29 August of the first year of the simulation.

### 3. Results

#### 3.1. Inter-individual growth variability

A  $K$  value set to 0.05 made the best fit between observed and simulated standard deviations (Fig. 2) and the regression slope between observed and predicted data was not statistically different from 1 ( $n = 140$ ,  $P < 0.001$ ). Discrepancies mainly occurred at the end of experiments where simulated standard deviations were underestimated.

#### 3.2. Observed distributions in 2000 and 2001

In March 2000, three cohorts were identified in the standing stock of “collées” oysters (Fig. 3). The first cohort consisted of young individuals with a mass between ca. 8 and

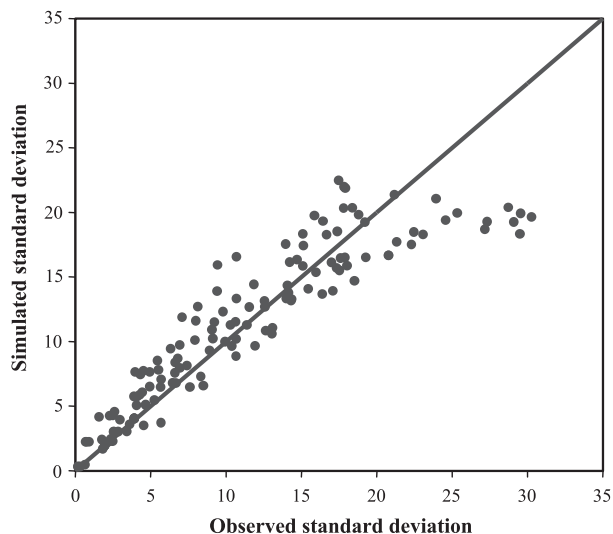


Fig. 2. Observed vs. simulated standard deviation of mass for a  $K$  value equal to 0.05.

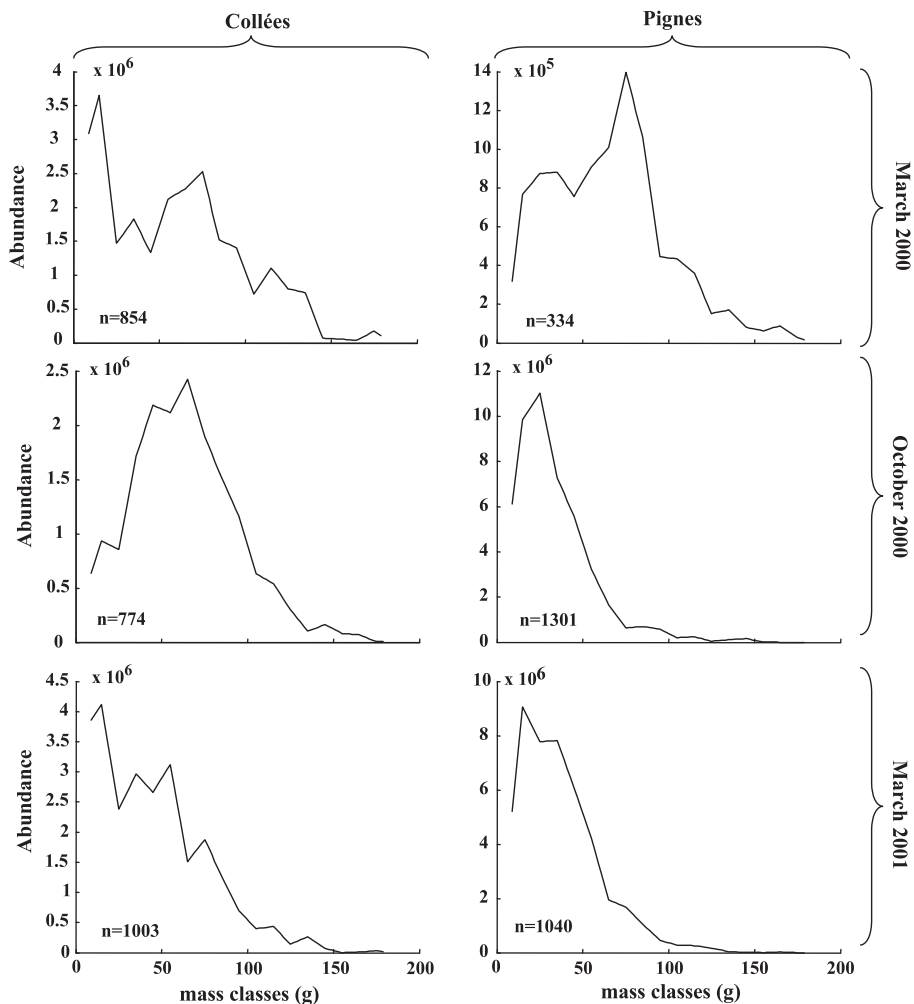


Fig. 3. Distributions of in situ “collées” and “pignes” oyster standing stocks in March 2000, October 2000 and March 2001. The number of oysters measured to obtain each distribution is indicated.

20 g. Two other cohorts were identified: one which reached marketable mass at around 75 g, and a second whose mass ranged between 110 and 150 g. For “pignes” oysters, only two cohorts were identified in March 2000. The first cohort contained relatively young individuals (10–40 g) and individuals with a mean mass of ca. 75 g constituted the second cohort. Standing stocks were assessed at 6700 and 3300 t for “collées” and “pignes” oysters, respectively.

In October 2000, both “collées” and “pignes” oysters were centered on one cohort with mean masses of ca. 60 and 25 g, respectively. The “collées” oyster stock largely consisted of individuals near the marketable mass. Standing stocks were assessed at 5400 and 7300 t for “collées” and “pignes” oysters, respectively.

While in March 2000, “collées” oysters dominated the standing stocks, the situation was reversed in both October 2000 and March 2001. In March 2001, the distribution of “pignes” oysters remained unchanged with only one cohort and mainly young individuals. For “collées” oysters, a high peak of young individuals was present but an important fraction of heavy individuals (mass > 50 g) was also found. Standing stocks reached 4900 and 8300 t for “collées” and “pignes” oysters, respectively.

### 3.3. Simulations in 2000 and 2001

#### 3.3.1. Seeding

The estimated numbers of seeded oysters (Table 1) used the timetables given in Fig. 1. In simulation *Sa*, “collées” oysters seeding took place mainly in April and May (ca.  $12 \times 10^6$  individuals per month; Fig. 4). From June through October, ca.  $6 \times 10^6$  individuals per month were seeded. In simulation *Sb*, maximum seeding occurred during January through March (ca.  $4 \times 10^6$  individuals per month). Seedings were lower from October to December (ca.  $2 \times 10^6$  individuals per month).

For “pignes” oysters, the timetable of 8 g individuals and the corresponding timetable of individuals with a mass at a few milligrams were also shown in Fig. 4. In simulation *Sa*, seeding at a mass of 8 g was maximum between mid-July and mid-August (ca.  $90 \times 10^6$ ). Seedings between March and mid-July and after mid-August were lower (ca.  $10\text{--}20 \times 10^6$  individuals per month). The corresponding timetable of “pignes” oysters seeded with a mass at a few milligrams showed a seeding between September 1999 and June 2000. The main seeding occurred between January and April (ca.  $30\text{--}40 \times 10^6$  individuals per month). In simulation *Sb*, seeding at 8 g took place mainly in fall 2000 and to a lesser extent in March 2001. No seeding was observed between mid-November 2000 and mid-March 2001. This corresponded to a seeding at a few milligrams in June and September 2000, with no seeding during summer 2000.

#### 3.3.2. Final distributions

The observed and simulated distributions for simulation *Sa* were in reasonable agreement (Fig. 5). For “collées” oysters, the model simulated correctly the main peak (mass ca. 60 g), although the number of young individuals (mass ca. 8 g) was overestimated. For “pignes” oysters, the main peak (ca. 25 g) was correctly simulated but the height was lower.

The results of the simulation *Sb* contained more discrepancies between observed and simulated distributions, especially for “collées” oysters. The model did not reproduce the amount of individuals with masses between 10 and 65 g and overestimated the peak of very young individuals (ca. 8 g). However, the model simulated correctly the oyster cohort of more than 65 g. For “pignes” oysters, the model accurately reproduced the single peak. Slight discrepancies were observed for smaller and higher masses. The number of individuals between 40 and 90 g was overestimated.

#### 3.3.3. Variations in standing stock and marketable production

In simulation *Sa*, the standing stock of “collées” oysters initially decreased at a high rate; several days into the simulation, the rate of decrease slowed and appeared more

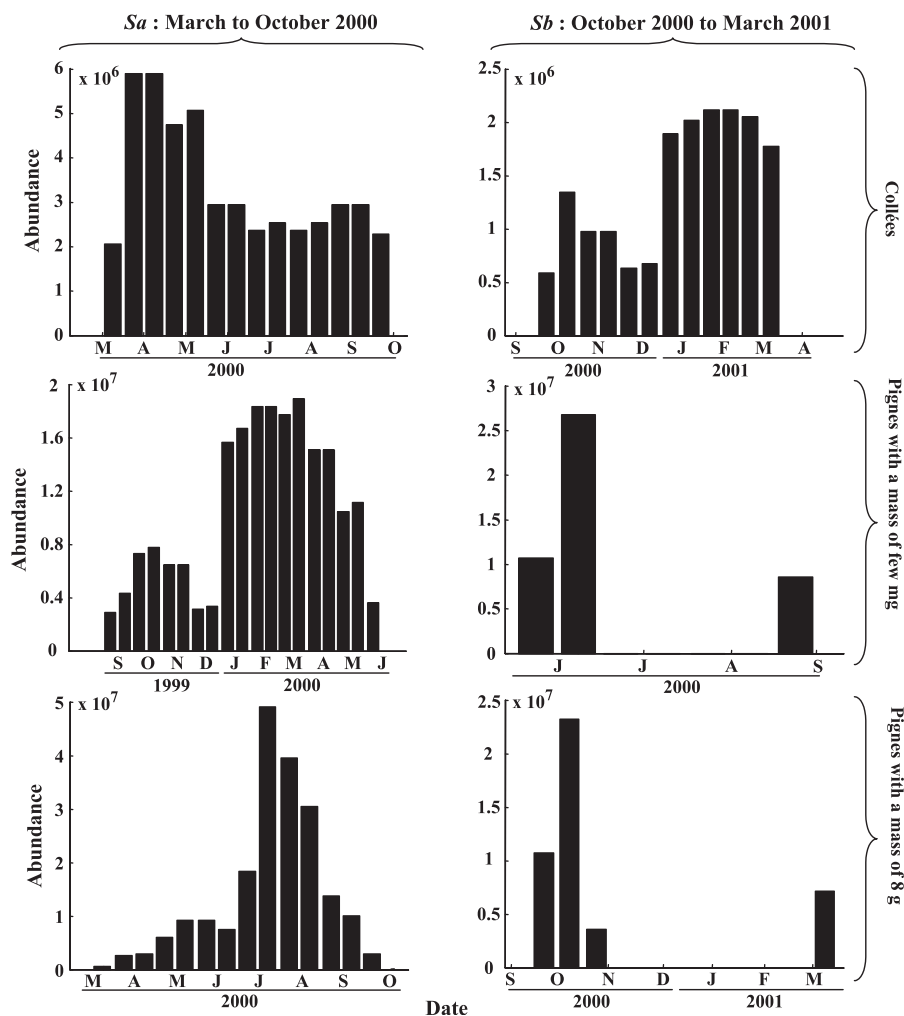


Fig. 4. Abundance of oysters seeded in the lagoon per 15-day interval for each simulation period (Sa: from March to October 2000; Sb: from October 2000 to March 2001) and both culture methods. For “pignes” oysters, two timetables are shown: oysters seeded at a few milligrams and oysters seeded at a mean mass of 8 g.

regular (Fig. 6). For “pignes” oysters, the standing stock decreased from March (ca. 3300 t) to the end of April (ca. 2300 t) and then increased from May to October. Simulated standing stocks were assessed at 4100 and 7100 t at the end of the simulation period for “collées” and “pignes” oysters, respectively. In comparison with the observed values, the simulated standing stocks were underestimated by about 1300 and 200 t for “collées” and “pignes” oysters, respectively. The cumulative production increased to about 8900 and 4100 t in October for “collées” and “pignes” oysters, respectively. The turnover of the populations that is defined as the ratio between the

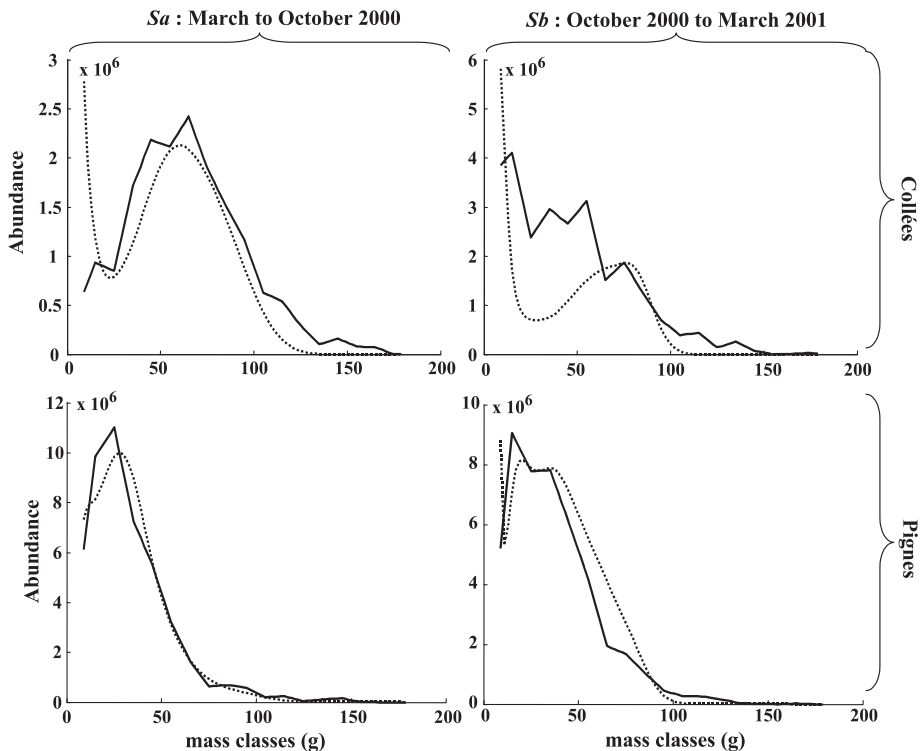


Fig. 5. Observed (solid line) and simulated (dotted line) distributions of “collées” and “pignes” oyster standing stocks in October 2000 (simulation *Sa*) and March 2001 (simulation *Sb*).

number of individuals seeded per year and the mean number of individuals in the lagoon was estimated at 0.51 and 1.96 per year for “collées” and “pignes” oysters, respectively.

In simulation *Sb*, the standing stock of “collées” oysters decreased regularly whereas the cumulative production increased to 3340 t. For “pignes” oysters, the standing stock and the cumulative production increased slightly; at the end of the simulation, the cumulative production reached 1520 t. In March 2001, simulated standing stocks were assessed at 3300 and 9200 t for “collées” and “pignes” oysters, respectively. The final standing stock of “collées” oysters was underestimated compared to the observed one (4900 t), whereas the simulated value was overestimated for “pignes” oysters (8300 t). The turnover of the populations was estimated at 0.26 and 0.2 per year for “collées” and “pignes” oysters, respectively.

Irrespective of the culture method, the model assessed the total annual production at about 17,900 t between March 2000 and 2001. Approximately 70% of the annual production was in spring and summer, whereas fall and winter were less productive seasons. The major part of the annual production came from the “collées” oysters (ca. 70%). According to standing stocks assessments, the oyster density in cultivated areas was

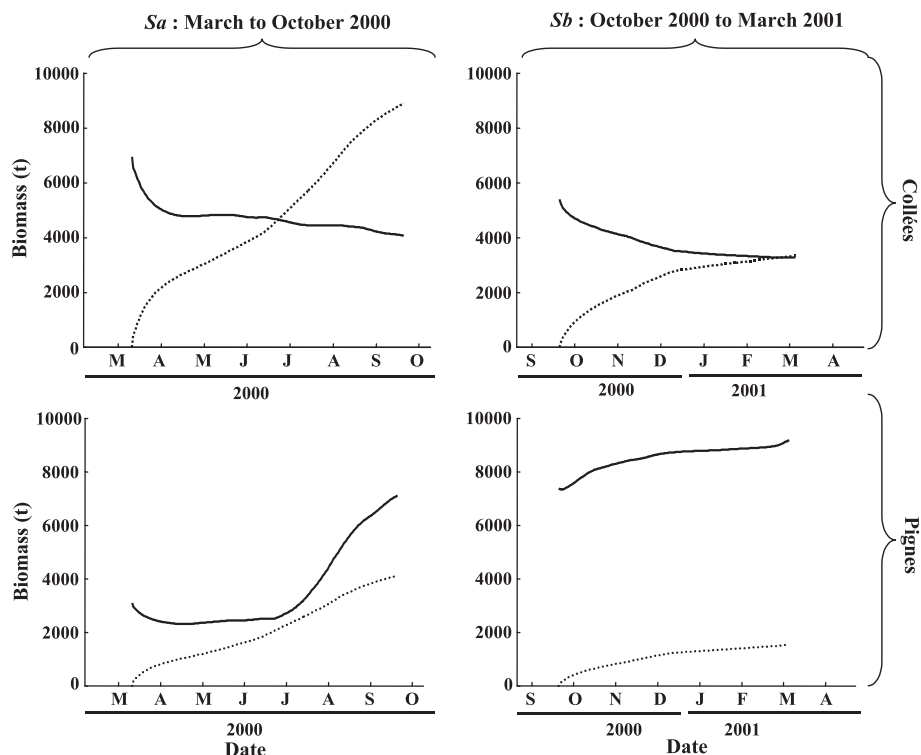


Fig. 6. Variations in the standing stock (solid line) and the cumulative production (dotted line) simulated by the model from March to October 2000 (*Sa*) and October 2000 to March 2001 (*Sb*) for both culture methods.

estimated at ca. 260 and 520 oysters  $\text{m}^{-2}$  for “collées” and “pignes” oysters, respectively. Consequently, the mean yields were calculated to be ca. 25 and 21  $\text{kg m}^{-2}$  in spring and summer for “collées” and “pignes” oysters, respectively (equivalent to around 12.5 and 10.4 t per culture table). These values decreased to ca. 13 and 3.5  $\text{kg m}^{-2}$  in fall and winter for “collées” and “pignes” oysters, respectively (equivalent to around 6.5 and 1.7 t per culture table).

### 3.3.4. Sensitivity analyses

Sensitivity analyses showed that the parameters governing the harvest (i.e.  $\alpha$ ,  $w_{\min}$  and  $w_{\max}$ ) had the most effect on stock and production (Fig. 7). A variation of  $\pm 10\%$  in  $\alpha$  and  $w_{\max}$  induced a mean variation of ca. 5% in both the stock and the production, and when the  $w_{\min}$  was varied this value reached more than 10%. The effect of  $w_{\min}$  on production was highest for “pignes” oysters in simulation *Sb* with a variation of ca. 23%. The magnitude of the change was dependent on the culture technique and the simulation period.

A  $\pm 10\%$  variation of the diffusion coefficient ( $K$ ) and the mortality rate ( $m$ ) had almost no effect on stock and production. Varying the water temperature threshold ( $S_T$ )

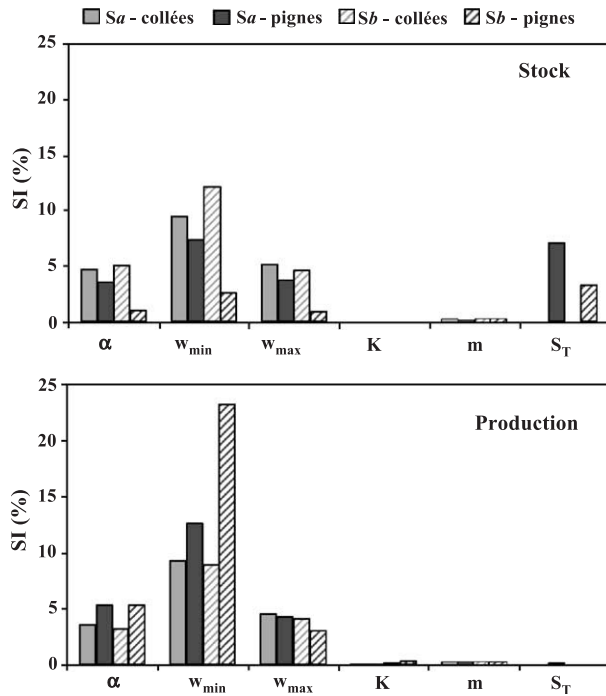


Fig. 7. Sensitivity index computed for individual parameters for each simulation period (*Sa* and *Sb*) and both culture methods.

used for “pignes” oysters in the simulation *Sa* caused a 5% mean variation in the stock but no variation was observed in the production.

A  $\pm 20\%$  variation in seeding and harvest monthly frequencies had minimal effects on stock and production, except for the seeding of “pignes” oysters (Fig. 8). After 1 year, the standing stock of “pignes” oysters reached  $9200 \pm 370$  t (SD over the 100 simulations) when variations in the seeding timetable were made, and  $9200 \pm 14$  t (SD) for variations in the harvesting timetable. In comparison, the effect on the production of “pignes” oysters was small (cumulative production of  $5200 \pm 34$  t and  $\pm 23$  t (SD) for seeding and harvest variations, respectively). The “collées” oysters had standard deviations for stock and production values that varied between  $\pm 21$  and  $\pm 103$  t (Fig. 8).

### 3.4. Scenarios

#### 3.4.1. Scenario 1: seasonal variations in oyster growth rate

Because of oyster growth seasonality and the time needed to reach a marketable mass, the production and the shape of the production curve were dependent on the seeding date (Fig. 9). For oysters seeded from January to June, production began between 5 and 7 months after seeding. The harvest timetable yielded two peaks of production having different heights according to the month of seeding. The first peak occurred between 7 and

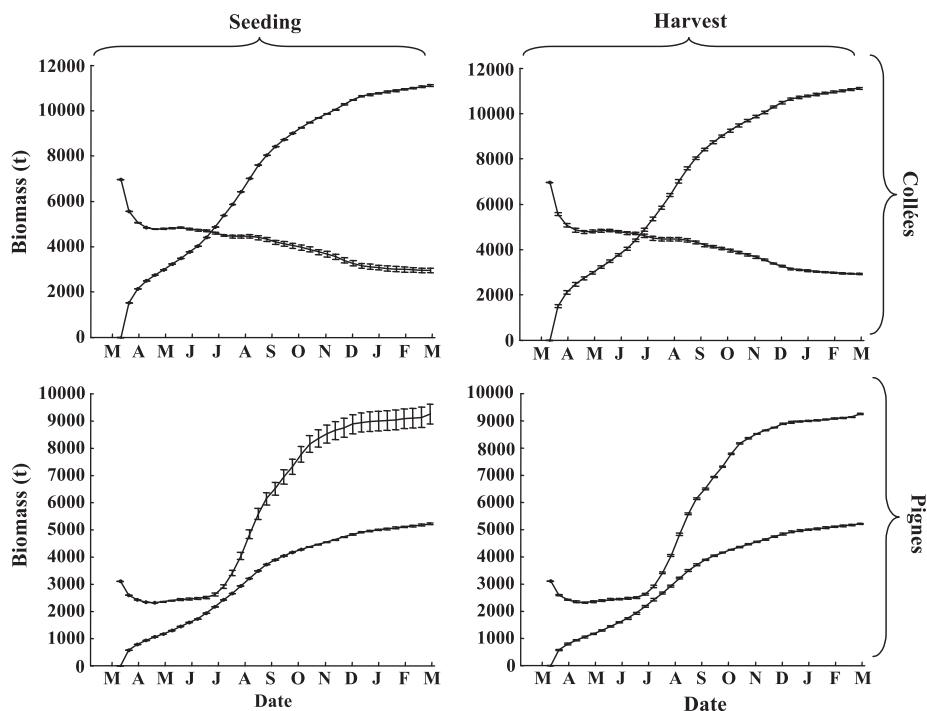


Fig. 8. Model sensitivity to seeding and harvesting timetables. For each parameter and each culture method, mean standing stock and cumulative production are presented with their standard deviation over the 100 simulations.

11 months after seeding and corresponds to the end of the first year of growth (September to December). The second peak corresponds to the summer of the second year and occurred 14 to 19 months after seeding. All oysters were harvested after, at most, about 21 months of rearing.

For oysters seeded from July to December, production began between 9 and 11 months after seeding. A seeding in July and August led to one major peak of production in the summer subsequent, and harvest was less spread out (ca. 7 months). When a seeding occurred between September and December, two peaks were recorded. All oysters were harvested after, at most, about 24 months of rearing. Cumulative productions were similar whatever the seeding month, although oysters seeded from April to August (ca. 94 kg) were somewhat higher than those seeded during October through December (ca. 87 kg) (Fig. 9).

### 3.4.2. Scenario 2: inter-annual variations in oyster growth rate

Long-term simulations using minimum and maximum growth rate values showed that “collées” oysters had a large decrease in standing stock during the first year of the simulations (Fig. 10). The decrease was more pronounced when the growth rate was maximised. At the end of first year, the standing stock reached ca. 3200 and 3600 t for the maximum and minimum growth rates, respectively. During the second year, the



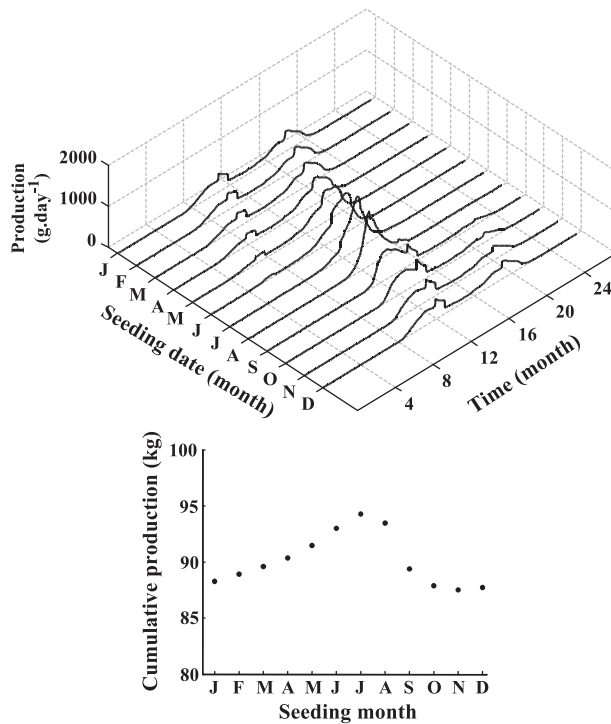


Fig. 9. Effect of the seeding month on the daily marketable production and the cumulative production obtained from 1000 oysters.

increase in the standing stock progressed regularly and the standing stock remained at higher levels when the growth rate was minimised. The model reached equilibrium in the third year. The standing stock then varied between 3000 and 3600 t when the growth rate was maximised and 3600 and 4600 t when it was minimised. Stock values fell to a minimum level the first half of the year and rose to maximum levels during the second half. A large decrease was noticeable at the end of the year. The maximum annual production was obtained during the first year of the simulation (ca. 10,600 and 8700 t for the maximum and minimum growth rates, respectively). At equilibrium, the annual production values for the maximum and minimum growth rates were somewhat similar (ca. 5800 and 5600 t, respectively).

With respect to the “pignes” oysters, the model needed about 6 years to reach equilibrium (Fig. 10). The standing stock increased steadily during the first year of the simulation and reached a value of ca. 8400 and 6800 t for the maximum and minimum growth rates, respectively. After the sixth simulation year, the oscillations stabilised between 7,500 and 10,000 t in both cases. The cumulative production was very low in the first year (ca. 4900 and 4000 t for the maximum and minimum growth rates, respectively); at equilibrium the cumulative production reached a value of ca. 16,000 and 11,700 t for the maximum and minimum growth rates, respectively. In contrast to the results for the

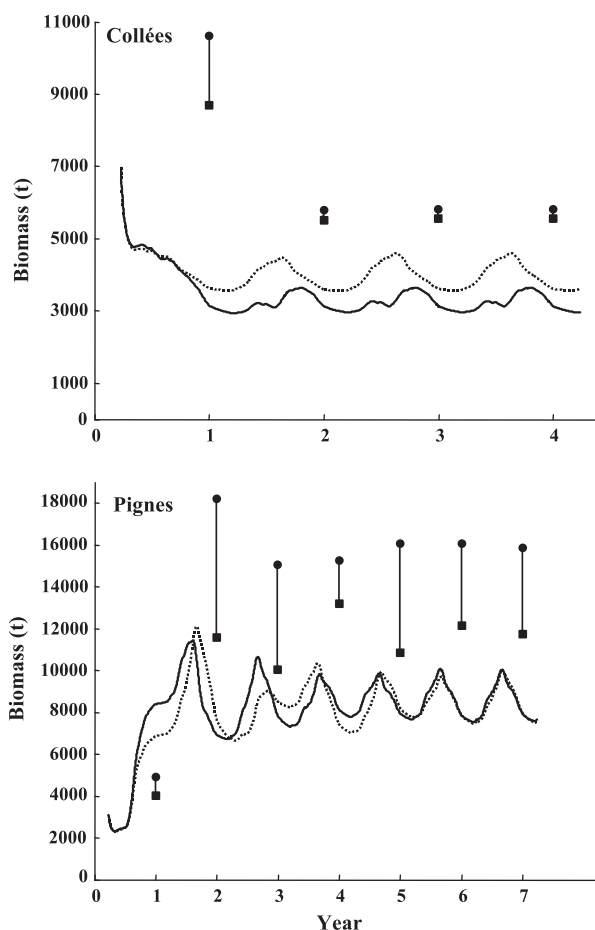


Fig. 10. Effect of a growth rate variation on short and long term variations of the standing stock and annual production for both culture methods. Standing stock is represented by a solid line for maximum growth rate and a dotted line for minimum growth rate. Annual production is represented by a circle for maximum growth rate and a square for minimum growth rate.

“collées” oysters, the minimum growth rate drastically reduced the annual production when equilibrium conditions were reached in the model.

### 3.4.3. Scenario 3: effect of a harvesting closure

For “collées” oysters, a harvesting closure implied a decrease of ca. 1000 t in the cumulative production of the first year of a simulation compared to a simulation without a closure (Fig. 11); this decrease was offset in the second year by an increase of 1000 t. As a consequence of the closure, the standing stock increased by 1000 t during the first year. Simulation values with and without harvesting closure became similar during the third year for both the standing stock and the cumulative production.

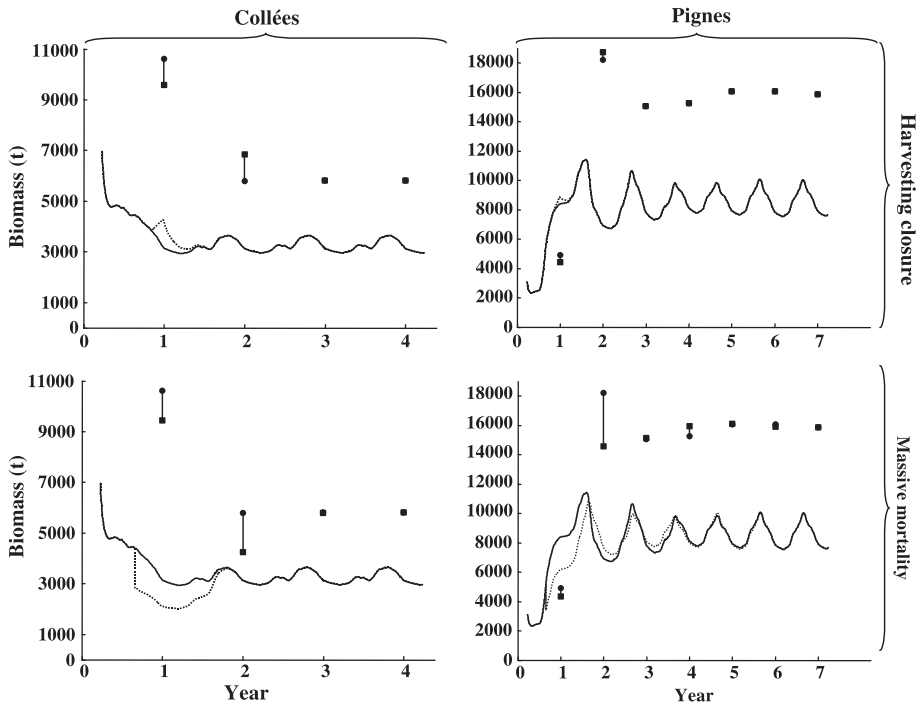


Fig. 11. Effect of a harvesting closure and a massive summer mortality on short and long term variations of the standing stock and annual production for both culture methods. Standing stock is represented by a solid line for simulations without closure and mortality and a dotted line for simulations with closure or mortality. Annual production is represented by a circle for simulations without closure and mortality and a square for simulations with closure or mortality.

Parallel effects of harvest closure were observed on “pignes” oysters, but they were less pronounced. The cumulative production loss due to harvesting closure was estimated at ca. 500 t for the first year and offset by an increase in the standing stock of + 500 t. The loss of cumulative production in the first year was compensated for by the estimated increase in production during the second year. Simulation values with and without closure became similar during the third year.

#### 3.4.4. Scenario 4: effect of a massive mortality

A massive summer mortality of “collées” oysters, implied a decrease of ca. 1200 and 1600 t in the estimated cumulative production during the first and the second years, respectively (Fig. 11). The decrease in the standing stock was ca. 1100 t during the first year. Simulation values with and without mortality became similar during the third year of simulation.

For “pignes” oysters, the decrease in the estimated cumulative production was ca. 600 t the first year and reached ca. 3700 t the second year. The decrease in the standing stock reached ca. 2200 t for the first year of the simulation. Estimates with and without mortality became similar during the fifth year.

## 4. Discussion

### 4.1. Parameterisation of the model: comparison with the previous study

#### 4.1.1. Growth variability

In this study, a value of 0.05 for the diffusion coefficient was sufficient to reproduce the inter-individual growth variability observed in our growth experiments. In Gangnery et al. (2001), we set  $K$  to the value of 0.8. The difference between the two  $K$  values could be explained in part by the variance in the observed data. In the previous study, the calibration of  $K$  relied on growth data recorded from “collées” oysters during a period of ca. 9 months (March to December 1998); at the end of the experiment, the maximum mean standard deviation of mass was ca. 25 g.

In the experiments conducted during 2000–2001, the maximum mean standard deviation was lower for a longer duration (i.e. 12 months): 24 and 19 g for “collées” and “pignes” oysters, respectively. The higher inter-individual variability observed in 1998 could be due to the higher mass reached by these oysters at the end of experiments (masses higher than 100 g were observed) and could yield a higher value of the diffusion coefficient. However, sensitivity analyses showed that  $K$  was not a key parameter in the model predictions.

#### 4.1.2. Seeding

In comparison with the parameterisation used in the previous work, information available on seeding was more detailed, especially concerning the timetable used by oyster farmers. Monthly seeding frequencies were applied in the current model, whereas previously seeding was assumed to be constant, except during summer (July 01 to September 30) when seeding was zero.

#### 4.1.3. Harvest

Parameters used to simulate the harvest have been substantially modified in the present model. Monthly harvest frequencies gave a more precise harvest timetable in the updated model. In the previous version of the model, the dependence upon time was introduced by three coefficients, allowing only three periods with different harvest rates in the simulations. According to the results obtained from the interviews with oyster farmers, the minimum mean mass at harvest ( $w_{\min}$ ) was higher than the value used in the earlier model (75 vs. 60 g), and the maximum mean mass at harvest was ca. 125 g (Gangnery, 2003). However, individuals with a mass higher than 125 g were observed in distributions of standing stock assessments (Fig. 3); therefore, the  $w_{\max}$  value was set to 180 g, which represents the maximum mass observed (Fig. 3). Previously, the  $w_{\max}$  was set to 120 g according to preliminary interviews (Gangnery et al., 2001).

The new parameterisation suggested that the curvature parameter of the harvest sigmoid function ( $\alpha$ ) should be re-estimated. In the previous work,  $\alpha$  was set to 3 to obtain a mean mass at harvest of ca. 90 g. Using the same value of  $\alpha$  in the updated model, resulted in a mean mass at harvest of ca. 120 g. In order to obtain a mean mass of 90 g at harvest,  $\alpha$  would have to be set to 1. A  $\alpha$  value of 1 led to the poorest fit of the model with the observed distributions. We found a reasonable agreement between observed and simulated

data using a  $\alpha$  value of 2 and obtained a mean mass at harvest of about 106 g. This compromise was also justified by the fact that the mean mass at harvest observed in the lagoon was affected by inter-annual variability. For example, Buestel et al. (1998, 2001) showed that the mean mass at harvest was 95 and 102 g in December 1996 and 1999, respectively. This variability was due mainly to the inter-annual variability of the growth rate related to environmental conditions.

#### 4.2. Model calibration

Irrespective of the culture method used, the population dynamics model reproduced well the distributions recorded in October 2000. The adjustment was less accurate in March 2001, in particular for the “collées” oysters. For this oyster type, the model underestimated the standing stock of individuals weighing between 15 and 65 g. A transfer of oysters from “pignes” standing stock to “collées” standing stock, which was not taken into account in the model, could explain this underestimation. This transfer is used frequently by oyster farmers at two points in the rearing cycle (Gangnery, 2003). “Pignes” oysters could be transferred after 1 year of growth in the lagoon when their mean mass reaches ca. 30 g. Or the fraction of “pignes” oysters that did not reach a marketable mass at harvest (i.e. after a “normal” rearing cycle of  $\pm 18$  months) could be kept cemented on ropes and then transferred to the “collées” standing stock; this process may occur with oysters having a maximum mean mass of ca. 50 g. The model’s overestimate of “pignes” oysters with a mass between 40 and 60 g in March 2001, suggests such a transfer.

#### 4.3. Oyster production in the lagoon

In Gangnery et al. (2001), we obtained a production of ca. 10,000 t of “collées” oysters between March and December 1999. To compare production assessments, we have run a new simulation for the year 1999 with the parameterisation developed in this study; only the growth model and the diffusion coefficient previously parameterised were conserved. The number of individuals seeded was optimised on the basis of the distribution of the standing stock as recorded in November 1999. Under these conditions, the model assessed the production at ca. 11,800 t in December 1999 (simulation not shown) which is slightly higher than both the value estimated previously (10,000 t) and the value estimated for “collées” oysters in simulation *Sa* (March–October 2000, the production was ca. 8900 t). The numbers of individuals seeded during the simulation period were  $9.2 \times 10^7$  and  $4.7 \times 10^7$  in 1999 and 2000, respectively. Seeding was higher in 1999 along with the amount of standing stock at the end of the year (i.e. 8850 t in November 1999 and 5400 t in October 2000). The model assessed similar marketable productions in both 1999 and 2000.

During 2000–2001, the population dynamics model assessed the annual oyster production of the lagoon at ca. 17,900 t. This predicted production is higher than the generally quoted production value for the lagoon of ca. 13,000 t (Anonymous, 1998). Using long-term simulations without modifying rearing strategies, the model predicted a theoretical annual production of ca. 21,800 t (5800 t from “collées” and 16,000 t from “pignes” oysters). These simulations showed that the production system was not at equilibrium in 2000–2001.

An annual production of 17,900 t yields an average P/B ratio of 1.7 (with a mean standing stock of 10,300 t), but the simulations showed that the P/B ratio varied during the year and some periods were more favourable to higher production. During spring and summer, the P/B ratio was 1.58, whereas this value dropped to 0.39 in fall and winter.

The model also showed that the two culture methods made different contributions to the total production and had different levels of productivity. In 2000–2001, it was the “collées” oysters that made the major contribution to the total production. This culture method also had a higher P/B ratio (ca. 2.88) than for “pignes” oysters (ca. 0.93). Thus, in our model, “collées” oysters clearly appeared to be advantageous for oyster farmers in terms of productivity and mean yields, which especially in fall and winter also appeared higher for “collées” oysters. However, oyster farmers’ strategies also depend on spat supply from shellfish basins of the Atlantic coast and the proportion of “collées” and “pignes” oysters seeded in the lagoon could vary. For instance, as shown by simulated numbers of oysters seeded in the lagoon, the seeding of “pignes” oysters was higher than the seeding of “collées” oysters ( $24.7 \times 10^7$  vs.  $6.4 \times 10^7$  for “pignes” and “collées” oysters seeded between March 2000 and March 2001, respectively). One hypothesis to explain this modification in farmers’ strategies is the exceptional storm that occurred on the Atlantic coast at the end of 1999. This storm resulted in large losses of oysters. Consequently, “collées” oysters would have been less available than “pignes” oysters for farmers of Thau because they were used in priority by farmers from Atlantic basins.

In comparison with other French basins, which support an important volume of shellfish culture, Thau Lagoon had the highest P/B ratio. In Normandy, P/B values ranged between 0.5 and 0.7 depending on the site (Goulletquer et al., 1994). For Marennes-Oléron Bay and the Bay of Bourgneuf, the P/B ratio reached 0.4 and 0.3, respectively (Héral, 1993; Barillé-Boyer et al., 1997). The data available in the literature on P/B ratios recorded from ecosystems supporting oyster culture are sparse. Nevertheless, the high P/B ratio and the high productivity of Thau Lagoon were also confirmed by the high growth rates as was seen previously (Gangnery et al., 2003).

#### 4.4. Resource management

To maximise production, a seeding in July would have a slight advantage for oyster farmers in the Thau Lagoon. However, simulations did not take into account stressful conditions induced by a seeding in summer and leading to a possible higher mortality rate. Furthermore, the timing of market demand and the type of market also have to be considered, because they determine when the preferential harvest periods occur and the marketable mass of oysters. For instance, the production was less spread out for a seeding in July and August compared to a seeding in December. In addition, the rearing time was shorter for a seeding during the first half of the year. The mean mass at harvest differed according to the seeding date, with a maximum mean mass for seeding dates in July (ca. 105 g), and a minimum mean mass obtained for seeding dates in November–December (ca. 99 g).

The model also showed how the standing stock and production are affected by events like inter-annual variations in growth rate, a bloom of toxic algae implying a temporary

harvesting closure or massive mortality of oyster stocks. For a decrease in growth rate, the model predicts losses in short-term production (i.e. during the first year) that would be high for both culture methods (ca. 18% loss). Long-term annual production would remain relatively unaffected for “collées” oysters but were rather different for “pignes” oysters with a loss of ca. 26% when the growth rate decreases.

For the two other scenarios (a harvesting closure in the event of a toxic algae bloom, or mass mortality due to anoxic conditions in the water column), predictions for long-term production by both culture methods remained similar to the null condition. However, the model predicted smaller production in the short-term (i.e. in the two first years) especially in the case of a massive mortality. However, the same strategies of seeding and harvest were used in each year following the event, something that the oyster farmers would probably not do. The farmers would possibly apply different rearing strategies such as an intensive seeding the year following an anoxic crisis. Thus, our model would predict well the short-term changes due to the event, but additional information about the oyster farmers’ strategies would be required to make accurate long-term predictions.

#### 4.5. Generalisation of the model

In this study, the population dynamics model and especially the associated parameterisation were specific of the Thau Lagoon and of the local strategies used by oyster farmers. The use of a continuous equation in time was required because the seeding of new oysters was continuous in the lagoon. Nevertheless, the general equation of the model is generic and could be applied to other shellfish sites or other species. For instance, the same model was recently applied to the Mediterranean mussel, *Mytilus galloprovincialis*, reared in the same site and for which the rearing cycle was slightly different (Gangnery et al., in press). In this study, harvest depends simultaneously on time and individual mass but other criteria could be integrated. As already mentioned for mussels reared in several sites (Pérez Camacho et al., 1991; Gangnery et al., in press), harvest could also depend on condition index of individuals, represented for instance by the ratio between total individual mass and dry flesh mass. Such a relation could be taken into account in the model by the introduction of a correlation between total mass and dry flesh mass or by simulating dry flesh mass as a state variable as well as total mass.

### 5. Conclusion

In this study, the parameter estimates of a previously published population dynamics model were improved by adding new information on oyster growth rates in a Mediterranean coastal lagoon and the resource management techniques (i.e. seeding and harvest) applied by oyster farmers. The model was then used to assess oyster production. Several data sets on standing stock distributions provided the initial conditions for the simulations and calibration. Between March 2000 and March 2001, the annual oyster production was estimated to be 17,900 t. The major part of this production was obtained in spring and summer from one culture method: “collées” oysters. Long-term simulations reached equilibrium at a theoretical annual production of ca. 21,800 t.



The model was also used to estimate short- and long-term losses in marketable production that were related to different scenarios. Minimising the oyster growth rate implied long-term losses of production would be higher for “pignes” oysters (26% loss at equilibrium compared to the maximum growth rate) than for “collées” oysters (4% loss at equilibrium). A temporary harvesting closure or a massive mortality had short-term effects on production, but no lasting long-term effects for either type of culture method. In the case of the harvesting closure, losses predicted during the first year of the simulation were compensated for in the second year, when rearing practices were unchanged. Nevertheless, using this model for accurate resource management requires following changes in the oyster farmers rearing practices after environmental events. The model was shown to be particularly sensitive to parameters governing the harvest and the applicability of this type of model depends on these parameters being well known.

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### References

- Abadie, E., Amzil, Z., Belin, C., Comps, M.A., Elzière-Papayanni, P., Lassus, P., Le Bec, C., Marcaillou-Le Baut, C., Nézan, E., Poggi, R., 1999. Contamination de l’étang de Thau par *Alexandrium tamarense*. Episode de novembre à décembre 1998. In: Ifremer (Ed.), Bilans & Perspectives, Observation et surveillance de la mer côtière. 44 pp.
- Anonymous, 1998. CEPRALMAR - Bilan d’activités 1992–1997. CEPRALMAR, Montpellier (95 pp.).
- Barillé-Boyer, A.L., Haure, J., Baud, J.P., 1997. L’ostréiculture en baie de Bourgneuf. Relation entre la croissance des huîtres *Crassostrea gigas* et le milieu naturel. Rapport interne IFREMER DRV/RA/Bouin 97-16. 173 pp.
- Bayne, B.L., Worrall, C.M., 1980. Growth and production of mussels *Mytilus edulis* from two populations. Mar. Ecol. Prog. Ser. 3, 317–328.
- Borja, A., Bald, J., 2002. Proposal for a management model for clam (*Ruditapes decussatus*) exploitation in the Basque country (Northern Spain). In: Duarte, P. (Ed.), Proceedings of the International Conference on Sustainable Management of Coastal Ecosystems, Lisbon, Spain, 3rd–5th November 1999, pp. 129–140.
- Buestel, D., Chabirand, J.M., Oheix, J., Pichot, Y., Vercelli, C., 1998. Programme qualité des mollusques 1996. Grille nationale de qualité des huîtres, *Crassostrea gigas*. Analyse des huîtres commercialisées en Méditerranée. Rapport de contrat FIOM/IFOP/Régions Basse-Normandie, Pays de Loire/Ifremer, Palavas-Les-Flots. 44 pp.
- Buestel, D., Alunno-Bruscia, M., Chabirand, J.M., Vercelli, C., Oheix, J., Pichot, Y., Gangnery, A., 2001. Qualité des huîtres creuses *Crassostrea gigas* élevées dans le bassin de Thau et influence de la densité d’élevage sur la qualité. Recommandations pour l’élaboration d’un schéma des structures des élevages de mollusques du bassin de Thau. Rapport de contrat UE/PESCA. IFREMER/Région Languedoc-Roussillon/SRC Méditerranée. 101 pp.
- Dekshenicks, M.M., Hofmann, E.E., Klinck, J.M., Powell, E.N., 2000. Quantifying the effects of environmental changes on an oyster population: a modeling study. Estuaries 23, 593–610.
- de Waal, S., Cook, P.A., 2001. Use of a spreadsheet model to investigate the dynamics and the economics of a seeded Abalone population. J. Shellfish Res. 20, 863–866.



- Fleury, P.G., Goyard, E., Mazurié, J., Claude, S., Bouget, J.F., Langlade, A., Le Coguic, Y., 2001. The assessing of Pacific oyster (*Crassostrea gigas*) rearing performances by the IFREMER/REMORA network: method and first results (1993–98) in Brittany (France). *Hydrobiologia* 465, 195–208.
- Gangnery, A., 2003. Etude et modélisation de la dynamique des populations de bivalves en élevage (*Crassostrea gigas* et *Mytilus galloprovincialis*) dans le bassin de Thau (Méditerranée, France) et des ascidies solitaires associées. Thèse de Doctorat, Université de Montpellier II. 175 pp.
- Gangnery, A., Bacher, C., Buestel, D., 2001. Assessing the production and the impact of cultivated oysters in the Thau lagoon (Mediterranean, France) with a population dynamics model. *Can. J. Fish. Aquat. Sci.* 58, 1012–1020.
- Gangnery, A., Chabirand, J.M., Lagarde, F., Le Gall, P., Oheix, J., Bacher, C., Buestel, D., 2003. Growth model of the Pacific oyster, *Crassostrea gigas*, cultured in Thau Lagoon (Méditerranée, France). *Aquaculture* 215, 267–290.
- Gangnery, A., Bacher, C., Buestel, D., in press. Application of a population dynamics model to the Mediterranean mussel, *Mytilus galloprovincialis*, reared in Thau Lagoon (France). *Aquaculture*.
- Gouletquer, P., Joly, J.P., Kopp, J., Legagneur, E., Moriceau, J., Ruelle, F., 1994. L'ostréiculture sur la côte Ouest du Cotentin. Rapport interne IFREMER DRV/RA/PB 94-02. 85 pp.
- Gros, P., Hamon, D., 1989. Estimation de la biomasse des bivalves intertidaux (moule, coque) exploités en baie de Saint-Brieuc (Manche Ouest). Rapport interne IFREMER DERO/EL/89-25. 137 pp.
- Guarini, J.M., 1994. Modélisation de la dynamique de la production des moules cultivées en baie de Saint-Brieuc (Manche ouest): quantification de la demande énergétique du cheptel et des flux de matière échangés dans l'écosystème. Rapport de DEA, Université de Liège/Ifremer. 73 pp.
- Gurney, W.S.C., Nisbet, R.M., 1998. *Ecological Dynamics*. Oxford Univ. Press, New York. 335 pp.
- Héral, M., 1993. Why carrying capacity models are useful tools for management of bivalve molluscs culture. In: Dame, R.F. (Ed.), *Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes*. Springer-Verlag, Berlin, pp. 455–477.
- Hofmann, E.E., Powell, E.N., Klinck, J.M., Wilson, E.A., 1992. Modeling oyster populations: III. Critical feeding periods, growth and reproduction. *J. Shellfish Res.* 11, 399–416.
- Hofmann, E.E., Klinck, J.M., Powell, E.N., Boyles, S., Ellis, M., 1994. Modeling oyster populations: II. Adult size and reproductive effort. *J. Shellfish Res.* 13, 165–182.
- Hyun, K.H., Pang, I.C., Klinck, J.M., Choi, K.S., Lee, J.B., Powell, E.N., Hofmann, E.E., Bochenek, E.A., 2001. The effect of food composition on Pacific oyster *Crassostrea gigas* (Thunberg) growth in Korea: a modeling study. *Aquaculture* 199, 41–62.
- Klinck, J.M., Powell, E.N., Kraeuter, J.N., Ford, S.E., Ashton-Alcox, K.A., 2001. A fisheries model for managing the oyster fishery during times of disease. *J. Shellfish Res.* 20, 977–989.
- Kobayashi, M., Hofmann, E.E., Powell, E.N., Klinck, J.M., Kusaka, K., 1997. A population dynamics model for the Japanese oyster, *Crassostrea gigas*. *Aquaculture* 149, 285–321.
- Pastres, R., Solidoro, C., Cossarini, G., Melaku Canu, D., Dejak, C., 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system. *Ecol. Model.* 138, 213–245.
- Pérez Camacho, A., Gonzales, R., Fuentes, J., 1991. Mussel culture in Galicia (N.W. Spain). *Aquaculture* 94, 263–278.
- Powell, E.N., Klinck, J.M., Hofmann, E.E., Wilson-Ormond, E.A., Ellis, M.S., 1995. Modeling oyster populations: V. Declining phytoplankton stocks and the population dynamics of American oyster (*Crassostrea virginica*) populations. *Fish. Res.* 24, 199–222.
- Powell, E.N., Klinck, J.M., Hofmann, E.E., Ford, S., 1997. Varying the timing of oyster transplant: implications for management studies. *Fish. Oceanogr.* 6, 213–237.
- Souchu, P., Abadie, E., Vercelli, C., Buestel, D., Sauvagnargues, J.C., 1998. La crise anoxique du bassin de Thau de l'été 1997. Bilan du phénomène et perspectives. Rapport Interne IFREMER DEL/ST/98.04. 33 pp.
- Theisen, B.F., 1973. The growth of *Mytilus edulis* L. (Bivalvia) from Disko and Thule district, Greenland. *Ophelia* 12, 59–77.