Assessing the production and the impact of cultivated oysters in the Thau lagoon (Mediterranee, France) with a population dynamics model

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Abstract: The Thau lagoon (France) has been studied for many years because of its ecological interest related to economic activities: shellfish cultivation, tourism, and industry. The standing stock of cultivated filter feeders is around 20 000 t and consists of two main species, the Japanese oyster *Crassostrea gigas* and the Mediterranean mussel *Mytilus galloprovincialis*. To predict changes in the standing stock and the annual production, a mathematical model of the population dynamics was defined. It was based on the continuous equation of the density as a function of the mortality rate, the individual growth rate, and the interindividual variability. The daily growth rate was derived from field surveys and depended on the phytoplankton concentration and individual weight. The model also took into account the rearing strategy of the producers defined by the timetable of seeding and harvesting, obtained by an inquiry among the producers and used to simulate real cases of standing stock changes. The model was also used to assess the potential impact on the environment through the computation of the food consumption, which was compared with the residence time and the primary production.

Résumé : Ses nombreuses activités économiques (élevage conchylicole, tourisme et industrie) font de l'étang de Thau (France), un site intéressant d'un point de vue écologique. C'est pourquoi, des études y sont menées depuis plusieurs années. La biomasse de mollusques en élevage dans l'étang est de l'ordre de 20 000 tonnes. Deux espèces y sont élevées : l'huître creuse, *Crassostrea gigas*, et la moule de Méditerranée, *Mytilus galloprovincialis*. Un modèle mathématique de dynamique de population a été élaboré permettant de prédire les variations temporelles de la biomasse ainsi que la production annuelle du bassin. Ce modèle est basé sur une équation continue de la densité, fonction de la mortalité, de la croissance individuelle et de la variabilité inter individuelle. Le taux de croissance dépend de la concentration en phytoplancton et du poids total individuel. Le modèle intègre également les stratégies d'élevage, i.e., l'ensemencement et la récolte, définies à partir d'enquêtes réalisées auprès des producteurs. Il permet ainsi de simuler des cas réels de variations de biomasse. Dans un second temps, le calcul de la consommation phytoplanctonique par les bivalves permet d'estimer leur impact sur l'écosystème. La consommation est comparée au temps de résidence et à la production primaire dans l'étang.

Introduction

The Thau lagoon is an important shellfish centre for both Japanese oysters (*Crassostrea gigas*) and Mediterranean mussels (*Mytilus galloprovincialis*) (Fig. 1). The annual production is not known accurately but is estimated to be around 12 000 t for oysters only, representing most of the regional production and roughly 10% of the national production (Anonymous 1998). This situation has led to a large number of scientific studies. Among others, the National Coastal Oceanographic Programme, launched in 1991, has a dual objective: a general analysis of the behaviour of this lagunar ecosystem and the creation of tools both to monitor and to simulate the changes in such systems. The present work is carried out within the scope of this programme.

Shellfish farming is part of the ecosystem and interacts with the other components of the environment. The impact of shellfish farming on the ecosystem depends on the quantities reared (Mazouni et al. 1998), and its assessment requires an accurate knowledge of the standing stock of cultivated bivalves and of the weight distribution. Evaluations of the standing stock of cultivated shellfish were undertaken in the Thau lagoon from 1980 to 1987 (Hamon and Tournier 1980, 1984, 1990). A new sampling strategy was developed in 1998 (Gangnery 1998) and tested in July 1998 and April 1999. The estimates of standing stock yield discrete values, whereas there are, all year-round, important variations in both the total biomass and its distribution, depending on season, environment, and rearing practices.

From this perspective, a modelling effort has been undertaken, and this work is devoted to deriving a preliminary model of the population dynamics. The population is struc-

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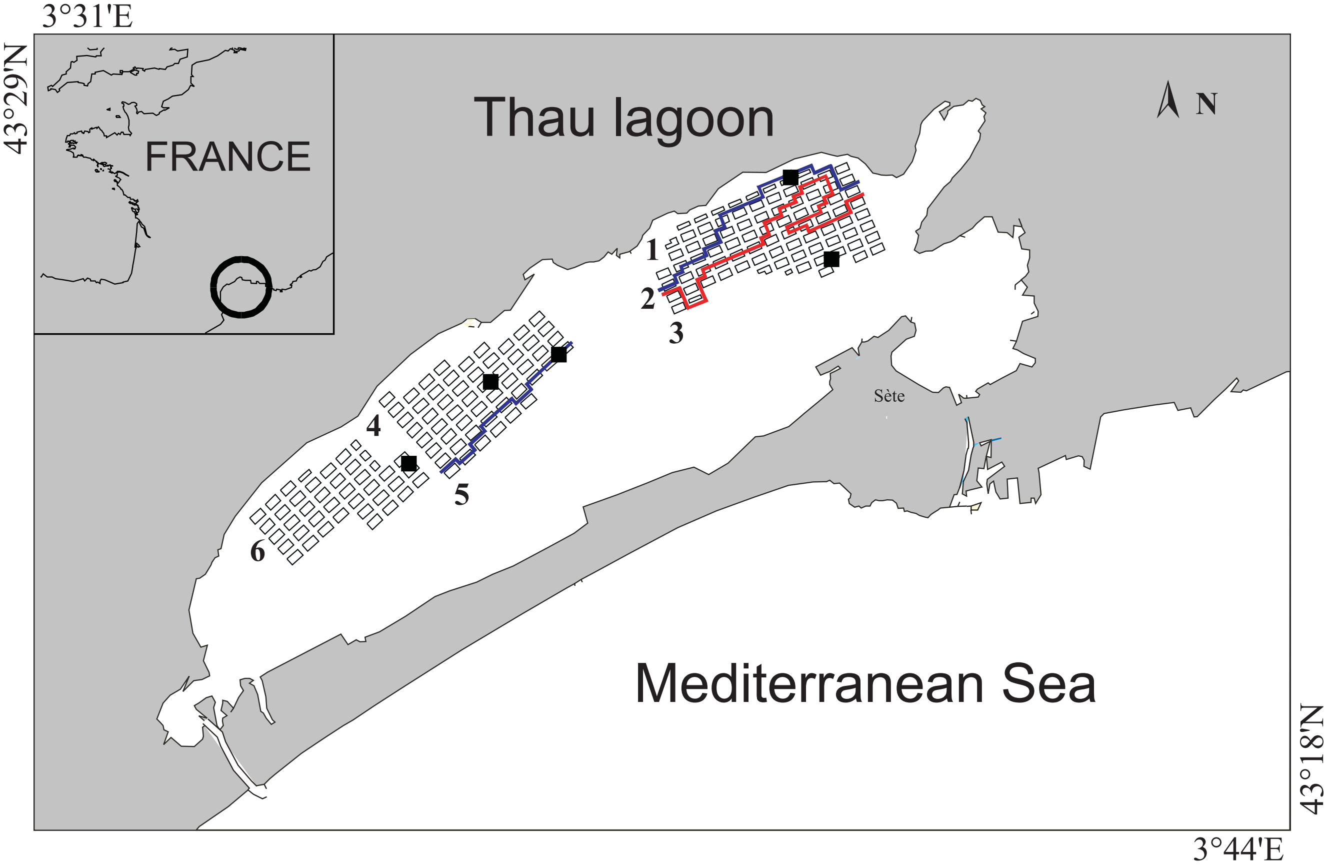
Fig. 1. Map of the Thau lagoon showing the six geographic strata and the five sampling sites (solid squares) of the oyster growth monitoring network (REMORA).



tured in weight classes and the model simulates the variation in time of the abundances in each weight class, the total standing stock, and the production of the system. The mathematical background can be found in Gurney and Nisbet (1998), and applications of such models have been carried out on cultivated mussels in Saint Brieuc Bay (Guarini 1994) to quantify the energy needs of the standing stock and the flux of particulate matter with the other parts of ecosystem (water column and sediment). The same type of population model has been coupled with an ecosystem model to estimate the carrying capacity of Carlingford Lough (Ireland) (Ferreira et al. 1998). In our study, we focused on the detailed description of the short-term variability and the weight distribution of the population and how the production is related to the population dynamics. The driving processes are the individual growth, the variation between individuals, the seeding (which is the input into the model), and the harvest and mortality (which are the outputs). The model accounts for geographical location but is not yet able to account for the mussels and the different rearing methods of oysters due to insufficient data on growth. As a first step, this study concerns only a fraction of the oyster standing stock, corresponding to one culture method that represents about 60% of the total oyster biomass in the lagoon. Then, the model is used to simulate the variations in the biomass in 1999, the initial conditions being those given by the estimate of the standing stock in April 1999. The model is applied to assess the impact of the population in terms of consumption of the available food.

Material and methods

Population dynamics model

The model chosen for this study is a continuous temporal model of the demographic structure of the *C. gigas* standing stock. The character chosen as representative of the demographic structure was the total individual fresh weight (including shell). The standing stock dynamics were described with the standard equation based on growth and mortality (Gurney and Nisbet 1998). The equation was augmented with a harvesting rate and individual growth variation expressed as a random dispersion of the weight; this formulation is commonly used in physics to quantify the random diffusion of particles. Equation 1 expresses the variation in the number of individuals whose weight is *w* at time *t*:

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

where $n(w,t)\mathrm{d}w$ is the number of individuals whose weight is in the range w to $w + \mathrm{d}w$ at time t, $G(w,t)$ is the growth rate (grams per day) and is a function of the weight of the individuals and of the chlorophyll *a* concentration in the environment, K is the diffusion coefficient (grams squared per day) and is related to the individual growth variance, m is the mortality rate (per day) and is independent of both individual weight and time, and $r(w,t)$ is the harvest rate (grams per day) and is a function of individual weight and time. The population level is maintained through the seeding $e(t)$ (per day) of new individuals of weight w_0, which is the minimum weight class (Fig. 2). Equation 1 has no analytical solution. In the following, the semiimplicit Crank–Nicholson method, which is unconditionally stable, has been used (Churchhouse 1981; Koutitas 1988).

The total standing stock S (tonnes) in the lagoon can be obtained for time t with

$$S(t) = \int_{w_0}^{w_{\max}} n(w,t)w\,\mathrm{d}w \tag{2}$$

where w_0 is the weight of the new animals and $w_{\max}$ is the maximum individual weight.

Similarly, the instantaneous production P (tonnes), which represents the fraction of the standing stock that can be harvested at time t, can be derived with

$$P(t) = \int_{w_{\min}}^{w_{\max}} r(w,t)n(w,t)w\,\mathrm{d}w \tag{3}$$

where $w_{\min}$ is the minimum weight for the beginning of the harvest.

Seeding, harvest, and mortality

Seeding

Seeding parameters have been gathered from the oyster farmers through inquiries concerning the timing of farming activities. The main aim of these inquiries was to clarify the farming strategy of the Thau lagoon oyster farmers during the different rearing stages: seeding of young oysters, growth duration with the different rearing techniques, harvesting periods, and marketing characteristics of oysters (weight).

Based on this inquiry, a preliminary timetable of oyster farming has been established. These inquiries have also given some data on the quantities and characteristics of young individuals being bred, have helped to formulate the harvest model, and have given insights into mortality. For the sake of simplicity, seeding has been considered to be constant year-round, except during the summer (July, August, and September) when it is zero.

Harvest

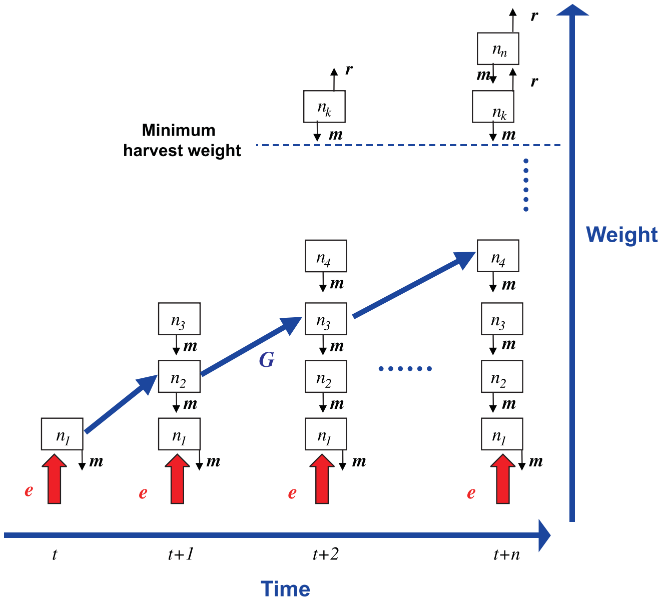
The harvest depends on the weight of the individuals and the period of the year. The dependency with weight has been taken into account with the sigmoid function given by

$$r = \left(\frac{w - w_{\min}}{w_{\max} - w_{\min}}\right)^{\alpha} \tag{4}$$

where w is the total individual fresh weight (grams) of the animals, $w_{\min}$ is the minimum weight set for harvest (60 g), $w_{\max}$ is the maximum weight set for an individual in the lagoon (120 g), and α is the curvature parameter for the sigmoid.

The animals can be harvested from 60 g up, and all the animals above 120 g are harvested. The curvature of the sigmoid has been set at 3, implying an average weight at harvesting of about 90 g. The probability of harvest during different periods of the year as given by the sigmoid function is corrected by a coefficient. According to the inquiries, it was considered that 50% of the harvest takes place at the end of the year (October 1 to December 31), 30% in summer (July 1 to September 30), and the remaining 20% spread out during the rest of the year. The following coefficients have been chosen for each of these periods: $r_1 = r$ for the end of the year (October 1 to December 31), $r_2 = 0.5r$ for the summer (July 1 to September 30), and $r_3 = 0.1r$ for the rest of the year.

Fig. 2. Conceptual scheme of the population dynamics model, where n is the number of individuals whose weight is in the range w to $w + \mathrm{d}w$ at time t, G is the growth rate (g·day^{-1}), K is the diffusion coefficient (g^2·day^{-1}) and is related to the individual growth variance, m is the mortality rate (day^{-1}), r is the harvest rate (g·day^{-1}), and e is the seeding.



Mortality

Save for exceptional events, such as accidental anoxic crises occurring in summer, storms, or predation by oyster drills, natural mortality is generally low in the Thau lagoon. Based on a growth-monitoring network named REMORA (Fleury et al. 1999) and on the inquiries, the annual mortality rate was set at about 10% and was taken as constant.

Formulation of the growth rate

Formulation of the growth rate rests mainly on the REMORA network data and on chlorophyll *a* measurements carried out in the Thau lagoon in 1998. The French REMORA network, established in 1993, consists of the simultaneous introduction of homogeneous sets of individuals (same origin and approximately the same weight) in all the shellfish cultivated areas in order to monitor their growth rate. In 1998, the introduction took place in the beginning of March at five sites in the lagoon (Fig. 1), the average weight of the individuals being 29.6 g. Three growth measurements were made on the oysters: June, September, and December. For each, 30 individuals randomly chosen on a rope were weighed and measured.

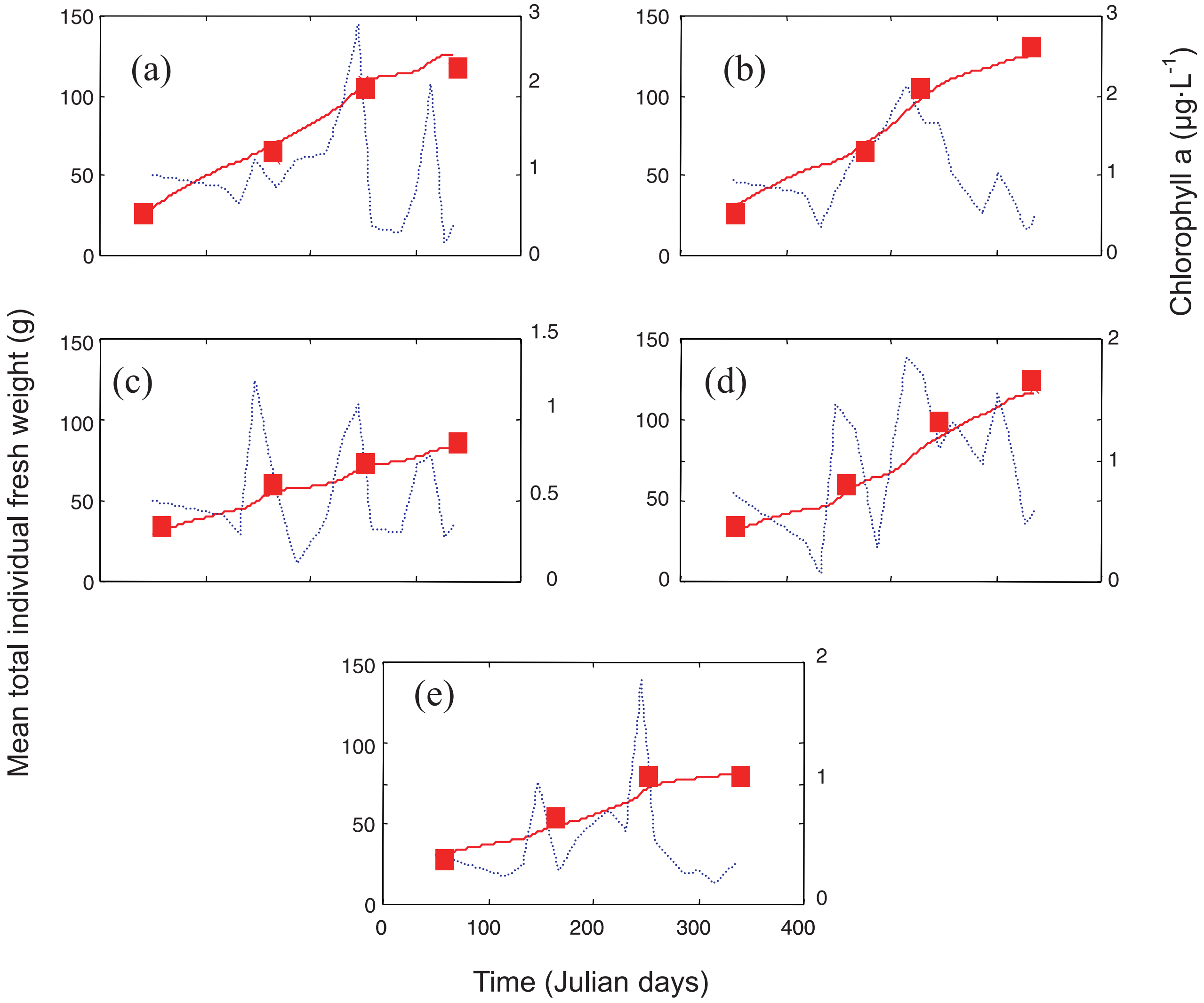
The growth of the oysters is a direct function of the available food in the environment. Bimonthly measurements of chlorophyll *a* were carried out in the lagoon from April 28 to November 24. Water samples were taken at the five REMORA sites (Fig. 1). The growth rate is assumed to depend on the individual weight, and we used an allometric growth rate as a function of chlorophyll *a* concentration and individual weight:

$$G(w,t) = aC(t)w^b \tag{5}$$

where $C(t)$ is the chlorophyll *a* concentration (micrograms per litre) and w is the individual weight (grams).

The growth model is represented by

Fig. 3. Mean individual growth simulated by the growth model (solid line) and compared with the observed values (squares). The chlorophyll *a* measured in 1998 is also shown for the different geographic strata (dotted line). (*a*) Stratum 1; (*b*) stratum 3; (*c*) stratum 4; (*d*) stratum 5; (*e*) stratum 6.



$$\frac{dw}{dt} = G. \tag{6}$$

The initial conditions were those observed for REMORA: a group of individuals with a known average weight. The numerical integration was achieved with a time step of 1 day over a 1-year simulation period. The parameters *a* and *b* were adjusted with the REMORA measurements: three observations in each of five out of six strata, spread out during the year, of the average population growth. An optimisation algorithm based on the simplex method (Press et al. 1992) yielded the *a* and *b* coefficients that gave the closest simulated weight to that observed in REMORA.

Assessment of the interindividual growth variability

The *K* coefficient was also adjusted to the measurements made during REMORA in 1998. The population model, without seeding or harvest (the REMORA conditions), simulated the average growth and gave the standard deviation of the average weight. The observed points, together with their standard deviation, were placed on the same diagram. The coefficient *K* can then be adjusted in such a manner that the individual simulated variance will fit as well as possible with the experimentally observed variance. The simulation period was 1 year, with a time step of 1 day and weight classes of 4 g.

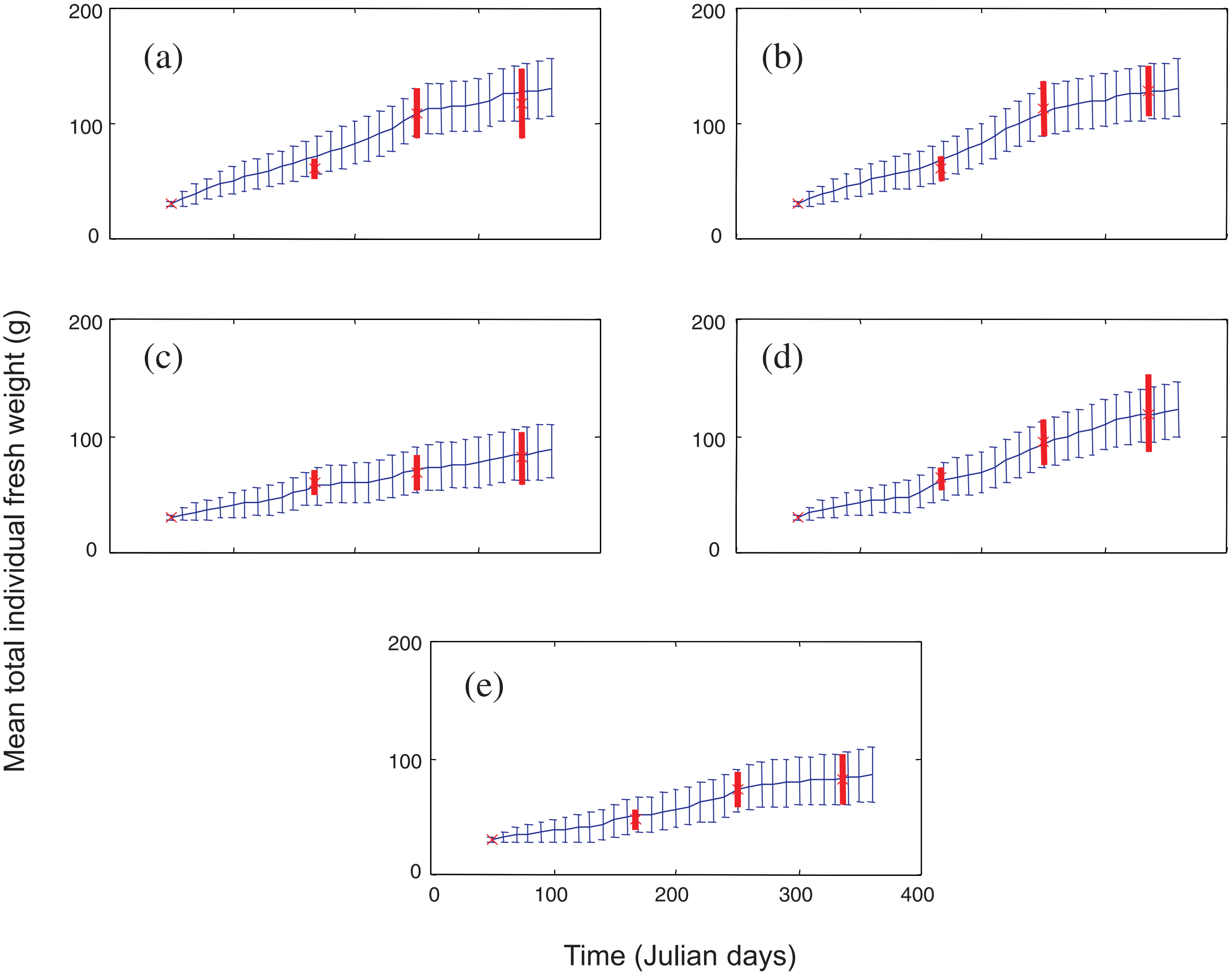
Simulation of the stock and production

Starting from the different variables parameterised previously (seeding, growth rate, variability between individuals, harvesting and mortality rates), the population model was used to simulate the changes in the standing stock and in the production of Japanese oysters. The initial conditions were the distribution of the standing stock in April 1999 and the total number of oysters for each geographic stratum. The same initial distribution of the sample was adopted for the whole lagoon, so that all of the geographic strata presented the same initial distribution. The simulation period was 9 months (April to December 1999) and the model was integrated with a time step of 1 day and weight classes of 4 g. The weight distributions, standing stocks, and productions of the five strata were computed.

Impact assessment

Consumption of phytoplankton, excretion of dissolved organics and inorganics, and biodeposition may result in environmental im-

Fig. 4. Mean individual growth and standard deviation (thick bar) measured during the oyster growth monitoring period (REMORA network) and simulated (thin bar) by the population dynamics model applied to the REMORA initial weight distribution. (*a*) Stratum 1; (*b*) stratum 3; (*c*) stratum 4; (*d*) stratum 5; (*e*) stratum 6.



pact due to modifications to ecosystem dynamics (Dame 1993; Bacher et al. 1997). We focused here on food consumption, which was derived from the population dynamics model by adding an equation for the individual clearance rate as a function of temperature and individual weight (Bougrier et al. 1995):

$$(7)\qquad c(w,t) = [(4.83 - 0.013)(T - 18.95)^2]w^{0.44}$$

where T is the water temperature (measured series of values), w is the individual dry weight of the soma, and c is the clearance rate (cubic metres per day per individual). The REMORA data yielded a conversion factor from total fresh weight to dry meat weight equal to 0.0234. This coefficient was used to rewrite eq. 7 as a function of the total weight. The total clearance rate (cubic metres per day) was calculated as

$$(8)\qquad C(t) = \int_{w_0}^{w_{\max}} n(w,t)c(w,t)\mathrm{d}w.$$

The clearance time CT (days) is a key parameter used in the carrying capacity assessments (Dame and Prins 1998) and was written as

$$(9)\qquad \mathrm{CT}(t) = \frac{V}{C(t)}$$

where V is the volume of the lagoon. CT quantified the time needed by the population to clear the surrounding water and can be compared with the water residence time and the food production time (Dame and Prins 1998).

Results

The unknown parameters, e.g., the growth rate and the dispersion coefficients, were first determined. Their values were used in the population model to simulate the weight distribution and to derive the standing stock and production variations. Combining individual clearance rates and variation in the weight distribution allowed the computation of the clearance time by the population.

Growth parameters

The optimised coefficients were a = 0.65 and b = –0.38, and comparison between the adjusted simulation values and

Fig. 5. Weight distribution of the oyster population derived from the standing stock assessment carried out in April 1999 used as the initial condition in the population dynamics model.

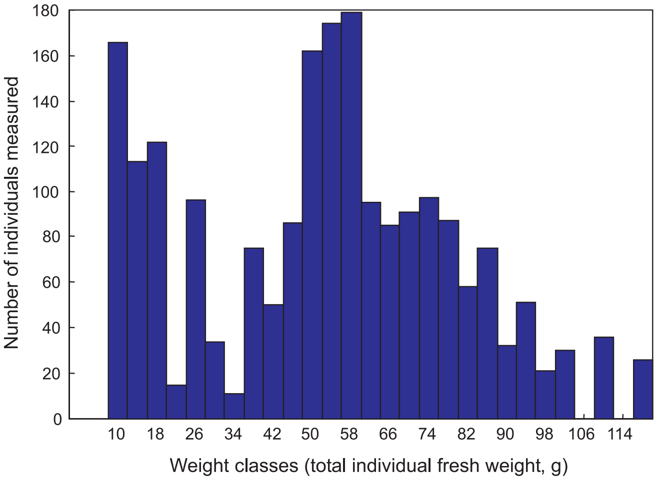
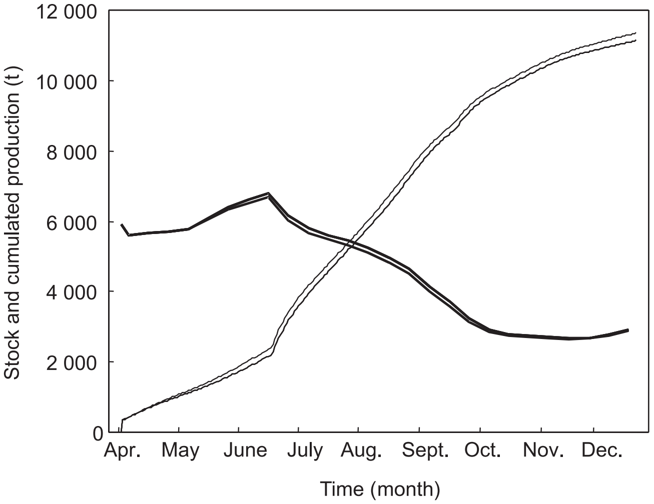


Fig. 6. Simulated stock (thick lines) and cumulative production (thin lines) between April and December 1999 for two different values of the dispersion coefficient used to represent the individual growth variability.



those observed with the REMORA network showed an acceptable goodness-of-fit (Fig. 3). A simple linear regression comparing the observed average weights with those simulated confirmed that the model was adequate, with a slope equal to 1 and a significant correlation ($P < 0.001$). After simulating the dynamics of the REMORA data and comparison of the simulated and observed standard deviations, the diffusion coefficient was set to 0.8. The observed and simulated standard deviations showed a reasonable agreement (Fig. 4), and the correlation between the two series was still highly significant ($P < 0.001$). However, the slope was equal to 0.57 instead of 1 and the model overestimated the lowest values and underestimated the highest values.

Variations in stock and production

The model of the population dynamics was run with the initial weight distribution in April 1999 (Fig. 5) using the above growth parameters. In April 1999, two major cohorts were identified in the sample of oysters. The first cohort contained young individuals with an average weight ranging from 10 to 20 g, whereas the second contained adults with an average weight ranging from 50 to 60 g total individual fresh weight. The population also contained many individuals having reached a commercial weight, with an individual weight ranging from 60 to 90 g. There was a deficit in the classes of 20–40 g.

The model predicted a slight decrease in the standing stock beginning in April and then an increase until mid-June, close to 1000 t, to reach a maximum of about 7000 t (Fig. 6). Starting in mid-June, the standing stock again decreased until November, reached a minimum of less than 3000 t, and then increased slightly to about 3000 t by year's end. The cumulative production showed an important harvest in the first week of the simulation period. It then grew steadily and reached a total of 11 000 t for the whole period of April to December 1999. A sensitivity analysis to the dispersion coefficient representing the individual growth variability was carried out. A second simulation with no variability ($K = 0$) was run and the comparison of the productions and standing stocks showed that the differences between the two simulations were less than 3% (Fig. 6).

Regarding the weight distribution, there was again an important cohort around an average weight of 60 g at the beginning of April, soon harvested because the individuals had reached a commercial weight (Fig. 7). The young oysters present at the start of the simulation reached a peak of 60 g in September. During the summer, the lack of seeding led to a depletion of individuals in the lower weight classes. Frequencies of the weight distribution were determined for each stratum on the last day of the simulation (Fig. 8). Since the seeding and the harvesting rates are the same for all strata, as well as the initial conditions of the simulation, the chlorophyll *a* concentration was responsible for the differences in the variations in the standing stock in the different strata. These different growth rates also yielded different harvests.

Clearance time

The individual clearance rate was computed for each weight class as a function of time using the temperature data (Fig. 9). The values lay between 40 and 160 $\mathrm{L \cdot day^{-1} \cdot individual^{-1}}$, the highest values being obtained when the temperature reached the value corresponding to the maximum of the clearance rate in the function given by Bougrier et al. (1995). The temporal fluctuations were minor compared with the influence of the individual weight, and the clearance rate was lower during low-temperature events, e.g., at the end of the year. Combining this function with the simulation of the population dynamics yielded clearance time estimates between 3 and 8 days with low values in April when the stock was maximal (Fig. 10).

Discussion

In this study, population dynamics are represented with a continuous time- and weight-dependent equation, which includes the seeding and harvesting strategies. Ferreira et al. (1998) used a similar equation (however, without the individual variability term) coupled with an ecosystem model in

Fig. 7. Simulated standing stock as a function of weight and time.

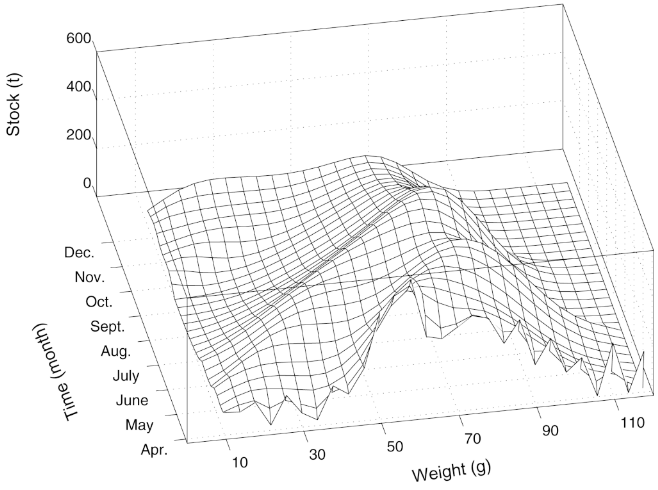
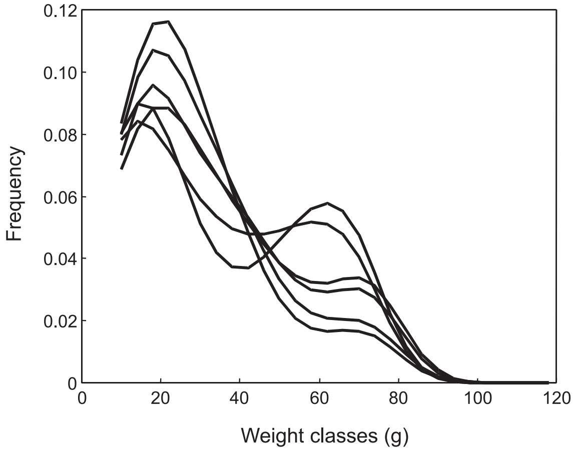


Fig. 8. Simulated final weight distribution in the different strata of the lagoon.



their study of the trophic capacity of Carlingford Lough (Ireland). This approach was well adapted to our first objective, which was to assess the standing stock changes and composition and the production for given trophic conditions and farming practices. As noted in the present simulation, the presence of a high weight mode observed in the initial distribution (April 1999), coupled with a rapid growth rate, explained a large production as early as the middle of the year and a steady decrease in the standing stock as the production was marketed. We found that the annual production was almost three times as high as the average standing stock, which demonstrates the high productivity of the lagoon. One must look at the events of 1998 (the sales embargo for sanitary reasons at the end of the year; Gangnery 1999) to explain the origin of this initial distribution. Other simulations (not shown in this paper) showed the sensitivity of the standing stock and production to the seeding timetable. Modifying the duration and the intensity of the seeding yields considerable change to the production and the standing stock and the weight distribution. In order to make the model operational, i.e., to predict with enough accuracy the expected production, a more complete inquiry will be carried out among the farmers.

Fig. 9. Individual clearance rate for each weight class as a function of time.

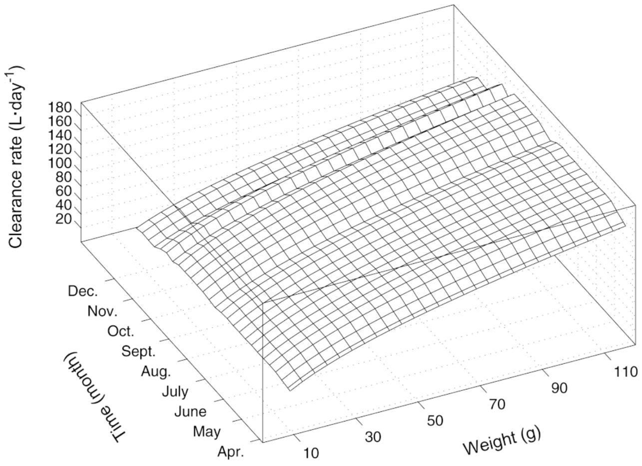
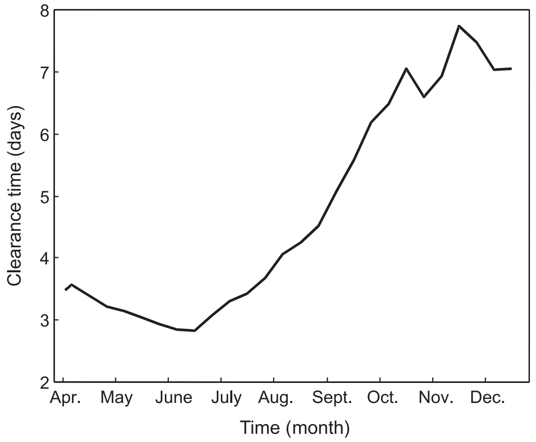


Fig. 10. Total clearance time of the simulated cultivated population by month.



By comparing geographic strata between and within cultivated areas, we have demonstrated the influence of different trophic conditions such as food concentrations (e.g., chlorophyll *a*) on weight distributions. Monitoring of food concentration at different sites only provides an idea of the spatial variability and remains a source of uncertainty affecting model outputs (e.g., production and weight distribution). These uncertainties could be addressed by running several simulations with different food concentrations using Monte Carlo techniques.

Differences in experimental growth between individuals could have provided another source of variability. These variations were addressed with the use of a random diffusion coefficient (Brownian motion). Although individual growth rates are, in part, related to nonrandom genetic factors, we did not consider individual trajectories in our analysis and application of this coefficient was acceptable. However, results showed that the use of such a coefficient could underestimate or overestimate the variability between individuals, even if the increase in variability with time was correctly predicted. We then used a sensitivity analysis that showed that although unexpected, growth variability did not actually change the mean growth of the population, although incorporation provided a more accurate picture of weight distribution.

As far as the oyster growth rate could be predicted by a simple function of chlorophyll *a*, which characterised the available phytoplanktonic food, a detailed description of the ecophysiology of the *C. gigas* was not required here to simulate the population dynamics as in Powell et al. (1992), Hofmann et al. (1992, 1994) for the American oyster *Crassostrea virginica*, Raillard and Ménesguen (1994), and Kobayashi et al. (1997) for *C. gigas*. In those studies, the ecophysiological responses to environmental factors such as temperature and particulate inorganic and organic matter must be quantified in order to predict the individual growth. As for environmental impact assessment, ecophysiological models may be coupled with ecosystem models to account for the effect of food consumption by the cultivated species on the nitrogen dynamics (Raillard and Ménesguen 1994; Bacher et al. 1998; Ferreira et al. 1998). In the Thau lagoon, the effect of the oyster stock on the ecosystem dynamics has been simulated by Bacher et al. (1997) and Chapelle et al. (2000). It was shown that the food consumption and biodeposition due to the oysters would modify the food concentration and the primary production. These impacts are varying in time due to several environmental factors, e.g., temperature, nutrient inputs from the watershed, and wind. In these studies, however, the standing stock was kept constant because of the lack of information on its temporal variation, and it is one of our goals to fill in this gap and provide some complementary clues on the impact. We focused here on the assessment of the clearance time variability due to the temporal variability of the standing stock. For this estimation, we assessed the volume of water within the cultivated area considered in the population dynamics model, e.g., 10% of the total area of the lagoon. The simulated standing stock represented only a fraction of the total standing stock, since we considered only one cultivation technique due to the lack of information on the individual growth rates in the other cases. The oyster density is not uniform, since the oysters are attached to ropes hanging from tables that are separated by large alleys (Mazouni et al. 1998). As a consequence, the local density is higher than the uniform density that we put in our calculation. The average figure of 5 days that we obtained should therefore be considered as a reasonable approximation of the clearance time at the scale of the cultivated area. The effect of the cultivated filter feeders on the ecosystem and the feedback on growth depend on several factors; among these, the water renewal time, the rate of primary production, the degree of nutrient recycling, the clearance time, and the biodeposition rate due to the cultivated filter feeders are the most important (Bacher et al. 1997; Dame and Prins 1998; Prins et al. 1998). In the Thau lagoon, the renewal time of the water in the cultivated areas depends on the wind, which drives the whole hydrodynamics (Millet 1989). Whatever the meteorological conditions, however, the current velocity in the lagoon is generally lower than 10 $\mathrm{cm \cdot s^{-1}}$ and an average value of 5 $\mathrm{cm \cdot s^{-1}}$ is realistic. We considered a typical length of 2000 m, which yielded a residence time of 0.5 day. Actually, the water residence time depends on the spatial scale and the calculation does not consider that the lagoon is almost a closed system having small exchanges with the sea. An estimation of the average primary production was given by Chapelle et al. (2000) as 60 $\mathrm{mg\ N \cdot m^{-2} \cdot day^{-1}}$. Considering an average phytoplankton concentration of 1 $\mathrm{mmol\ N \cdot m^{-3}}$, an average depth of 4 m yielded a turnover rate of 1 day. Again, this computation does not account for the temporal and spatial variability, which may change this value by an order of magnitude. Comparing the residence time, the turnover time, and the clearance rate shows that the standing stock would probably influence the food concentration. It is therefore likely that this impact would in turn modify the individual growth rate and the population dynamics of the cultivated mussels and oysters. To make our model operational, we have to address more thoroughly the links between the ecosystem dynamics and the feedback on the cultivated population dynamics. Our next effort will be to develop the same type of population model for the mussels and the whole oyster standing stock and to include the ecosystem dynamics described by Chapelle et al. (2000).

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