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Growth model of the Pacific oyster, *Crassostrea gigas*, cultured in Thau Lagoon (Méditerranée, France)

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Abstract

We developed a growth model for the oyster *Crassostrea gigas* cultured in Thau Lagoon. The oyster standing stock in the lagoon ranged between 10,000 and 15,000 tons a year. Two culture methods are presently in use in Thau Lagoon which are used in about the same proportions. At seeding, initial size of oysters is different among methods. The model was calibrated on (1) growth data accounted for both culture methods and (2) hydrobiological data (temperature, salinity, suspended particulate matter and chlorophyll *a*), both recorded in several sites in the lagoon between March 2000 and October 2001. The lagoon is slightly eutrophic: total chlorophyll *a* and total particulate matter averaged 1.2 μg l^{-1} and 2.2 mg l^{-1}, respectively. Organic content accounted for ca. 40–50% of particulate matter. There was no seasonal trend in seston, whereas temperature and salinity were minimal in winter. Oyster growth varied among sites in response to spatial variations in seston. Growth was maximal in summer and minimal in winter because of temperature seasonality. For each location, we modelled growth as a function of particulate organic matter and temperature. Chlorophyll *a* was left out of the model because of a weaker fit with growth. Growth was modelled as $G = a\mathrm{POM}^b T^c Y^d$, where G is the growth rate in shell length (mm day^{-1}) or in mass (g day^{-1}), POM is particulate organic matter (mg l^{-1}), T is temperature (°C) and Y is either shell length (mm) or mass (total individual mass or dry flesh mass in g). Allometry (Y^d) allowed us to use the same

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model for both culture methods. The model yielded a good fit with actual size, either as measured by shell length ($R^2 = 0.96$) or total individual mass ($R^2 = 0.93$).

Keywords: Trophic resource; Oyster farming; Length–mass relationships; Growth model

1. Introduction

Thau Lagoon (France) is an important shellfish culture area of Pacific oysters (*Crassostrea gigas*) and Mediterranean mussels (*Mytilus galloprovincialis*) (Fig. 1). Total standing stock varies between 14,000 and 20,000 tons a year (Gangnery, 1999). Oysters account for about three quarters of the total cultured biomass. In Thau Lagoon, shellfish are fixed on ropes, which are suspended in the water column from culture tables (see Legend to Fig. 2). Rope length varies between 2 and 6 m depending on water depth.

In order to assess annual shellfish production of the lagoon and predict changes in standing stock, Gangnery et al. (2001) recently developed a population dynamics model, based on a continuous equation of oyster density as a function of mortality rate, individual growth rate and inter-individual variability. In this first study, a sub-model simulated growth of oysters known as "collées", whereas a second method, known as "pignes" (see Legend to Fig. 2), is also in use. Both methods are used in about the same proportions. Oyster growth in the lagoon and especially "collées" oysters has been documented in a

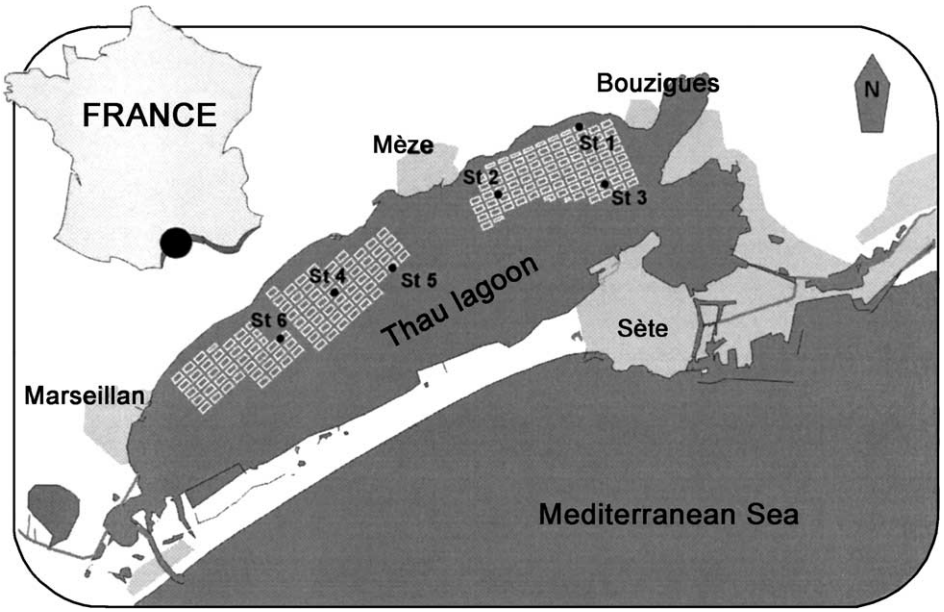

Fig. 1. Map of Thau Lagoon showing the sampling sites.

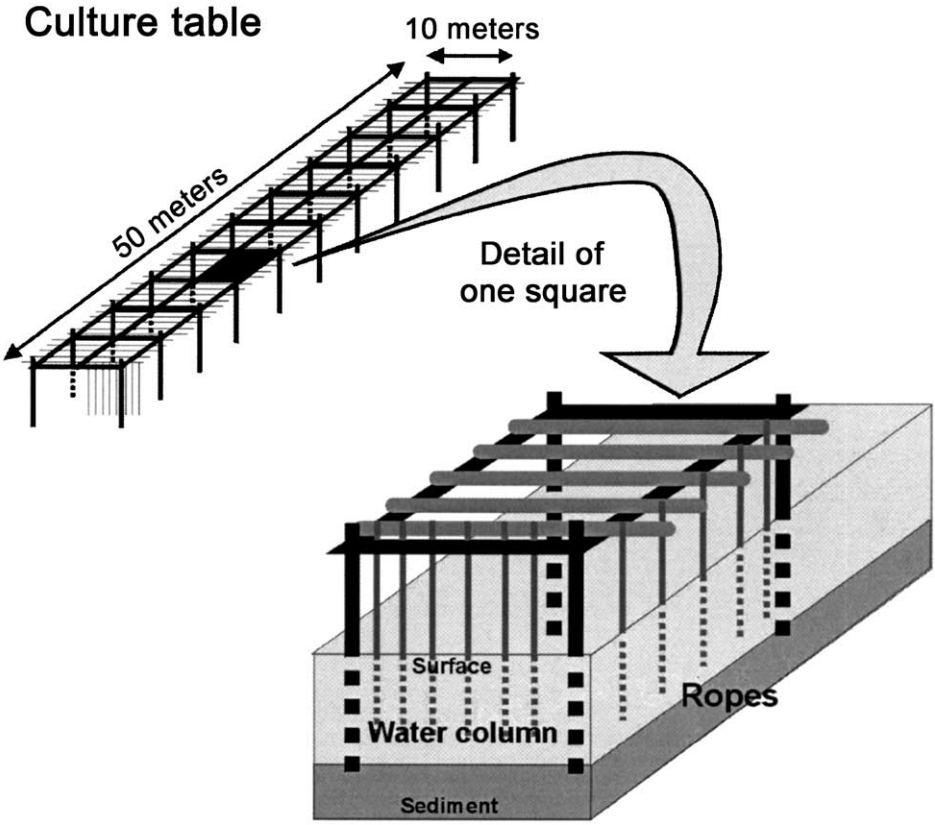

Fig. 2. Sketch of typical oyster table used in Thau Lagoon. Tables are made of railway bars pushed in the sediment (in black on the figure). These bars support horizontal iron bars (in grey) from which the ropes are suspended in the water column. Each table typically supports a total of 1000 ropes. "Collées" oysters are glued on ropes in groups of three individuals using cement. "Pignes" oysters are obtained from individual oysters settling naturally on empty oyster shells used as collectors. These collectors are inserted in the strands of ropes (ca. one collector every 20 cm). Oyster farmers may use the word "pignes" to designate either the set made of a collector and its associated oysters or individual oysters obtained by this method. As growth proceeds, "pignes" end up making large, intricate oysters hummocks. "Collées" oysters reach market size in 12 months while "pignes" oysters need ca. 18 months.

number of studies in terms of spatial variability or density effects on growth (Medelgi, 1988; Pichot et al., 1991; Fleury et al., 2001a; Alunno-Bruscia et al., 2001). The effect of culture method on growth, however, was never studied.

Growth is also dependent on environmental parameters (e.g. food supply, temperature) whose effects have been documented in a large body of literature (see Bayne and Newell, 1983 for a review on mussels; Wilson, 1987; Brown and Hartwick, 1988a for *C. gigas*). In Thau Lagoon, there are spatial variations in food availability (Tournier and Pichot, 1987; Jarry et al., 1990, 1991). These variations are reflected in oyster growth (Pichot et al., 1991; Fleury et al., 2001a) but the relationship was not fully established.

In the present study, we collected growth data so as to account for a maximum of growth variability including culture method and spatial variability. In addition, to investigate the effect of the seeding date on growth, two surveys were initiated at two different phases of the annual cycle. Environmental parameters were recorded to explain oyster growth and a growth model was calibrated. The objectives of this study were threefold:

(1) to assess food availability for oysters in Thau Lagoon,
(2) to assess the effect of site, culture method and seeding date on oyster growth,
(3) to develop a more realistic growth sub-model for *C. gigas* cultured in Thau Lagoon than that used in Gangnery et al. (2001).

In a further step, which is not included in the present study, this sub-model will be used in the population model to account for the dynamics of the whole oyster stock as explained by Gangnery et al. (2001).

2. Materials and methods

2.1. Study area

The study was carried out between March 2000 and October 2001. Thau Lagoon is 19 km long, 4.5 km wide (Latitude 43°20′ N and Longitude 3°40′ E, Fig. 1) and mean depth is 5 m. Shellfish are cultured in three areas of the lagoon (Bouzigues, Mèze and Marseillan), which cover about 20% of the total surface. The lagoon connects with the Mediterranean Sea through the narrow channel of Sète. Other connections are negligible.

2.2. Environmental parameters

Environmental parameters were measured every second week in six sites located in the three shellfish farming areas (Fig. 1). Sampling sites 1, 2 and 3 were located in the Bouzigues area, where standing stock is the highest. Sampling sites 4 and 5 were located in the Mèze area and site 6 was in the Marseillan area. Sites 1, 4 and 6 were ca. 4-m deep, sites 2 and 5 were 5-m deep and site 3 was the deepest with 6 m.

Temperature and salinity were routinely recorded using a WTW-LF-197S conductimeter 1 m below the surface and 0.5 m above the bottom. Salinity data near the bottom are not available from October 2000 to January 2001 because of instrument failure.

In order to estimate trophic resources potentially available for oysters, suspended particulate matter (total, organic and inorganic fractions) and phytoplankton biomass, as estimated by total and size-fractionated chlorophyll *a* were sampled. Picoplanktonic cells are very abundant in Thau Lagoon (Vaquer et al., 1996) but are not consumed efficiently by oysters (Dupuy et al., 2000). Therefore, water samples were size-fractionated to remove picoplankton from the chlorophyll *a* estimates. Triplicate samples (2 l for suspended matter and 60 ml for chlorophyll *a*) were taken using a Niskin bottle at 1 m below the

surface, based on the assumption that the water column was homogeneous (Gasc, 1997). Samples were kept in dark bottles and taken back to the laboratory as soon as sampling (occurring between 0900 and 1300 h) was finished.

Particulate matter samples were filtered through pre-combusted (500 °C for 3 h) and pre-weighed Whatman GF/F filters, rinsed with isotonic ammonium formate to remove salts and stored at − 20 °C until analysis. Filters were dried for 24 h at 60 °C and weighed for total particulate matter (TPM, mg dry mass l^{-1}). Inorganic matter (PIM, mg ash dry mass l^{-1}) was given by mass of ash remaining after burning at 500 °C for 5 h. Organic matter (POM, mg ash free dry mass l^{-1}) was given by losses at ignition. Organic content (OC) was estimated as the ratio of POM to TPM.

Total chlorophyll *a* samples (total chl *a*, μg l^{-1}) were directly filtered through Whatman GF/F filters, whereas size-fractionated chlorophyll *a* samples were filtered through 2 μm Nuclepore membrane filters to collect the phytoplankton fraction larger than 2 μm (chl *a*>2, μg l^{-1}). Filtrates were re-filtered through Whatman GF/F filters to obtain the small size fraction (chl *a*<2, μg l^{-1}). Filters were frozen at − 20 °C until analysis. Chlorophyll *a* and pheopigments were extracted in 90% acetone for 12 h and analysed with a Turner Designs TD 700 fluorometer (Neveux, 1983). Size-fractionated chlorophyll *a* was estimated only in sites 2, 3, 4 and 6. PC<2 was defined as the ratio of chlorophyll *a* particles smaller than 2 μm.

2.3. Growth measurement

2.3.1. Biological material

Oysters were installed on ropes on two occasions (i.e. two seeding dates) for the two culture methods: in late March 2000 and late September 2000 for "collées" oysters (groups C1 and C2, respectively) and in late March 2000 and mid-October 2000 for "pignes" oysters (groups P1 and P2, respectively). In further developments, seeding dates 1 and 2 refer to groups C1–P1 and C2–P2, respectively. The oysters were installed in four sites (sites 2, 3, 4 and 6, Fig. 1). Growth was measured over 1 year. Therefore, we obtained 16 growth curves (2 culture methods × 2 seeding dates × 4 sites). All procedures and materials were similar to those used by oyster farmers. Because natural spat fall in Thau Lagoon is insufficient, oyster farmers import spat from hatcheries or other French areas where natural spat fall is abundant (mainly in Bay of Arcachon and Marennes-Oléron Basin). In our experiment, "collées" oysters were from hatcheries (GRAINOCEAN, for C1 and SATMAR, for C2). C1 oysters were pre-grown in Ireland for 12 months. They were 49.5 ± 2.5 (SD) mm long and weighed 7.9 ± 0.7 (CI) g at seeding. C2 oysters were pre-grown in Brittany for 13 months. They were 46.5 ± 3.1 (CI) mm and weighed 11.9 ± 1.4 (CI) g at seeding. P1 and P2 oysters were collected (and shortly pre-grown) in Marennes-Oléron Basin during the summers of 1999 and 2000, respectively. P1 oysters were a few millimetres long while P2 oysters were barely visible to the naked eye at the time of seeding. Rope length varied according to water depth. They were 4.5 and 5 m long at sites 2 and 3, respectively, and 3 m long at sites 4 and 6. Shellfish density on the ropes was adjusted to 34 individuals per meter of rope for "collées" oysters and 5 "pignes" hummocks per meter of rope for "pignes" oysters. These values are commonly used by oyster farmers.

2.3.2. Sampling design

Growth was monitored monthly during spring and summer and every second month during fall and winter. On each occasion, one rope for each culture method was randomly sampled. All individuals of a "collées" rope were declumped, cleaned of fouling organisms and taken back to the laboratory. For "pignes" oysters, five "pignes" hummocks were randomly sampled from the rope and oysters were handled in the same way as for "collées". A sub-sample of 30 individuals was randomly chosen for growth measurements.

2.3.3. Biometry

Shell length (L in mm) and total wet mass (MTOT in g) were measured on each individual (digital calliper MITUTOYO, accuracy: 0.01 mm and OHAUS balance, accuracy: 0.1 g). Flesh was separated from the shell and total wet flesh mass (after draining for 5 min, WFM in g) and total dry flesh mass (after a complete freeze-drying cycle, DFM in g) were recorded (METTLER balance, accuracy: 0.001 g). Dry shell mass (DSM in g) was measured after 4 drying days at ambient temperature.

At the beginning of the study, "pignes" oysters were too small to allow for routine measurements. Such measurements were made from April 2000 (P1) and March 2001 (P2) onwards.

2.4. Statistical analyses

2.4.1. Environmental parameters

Temporal and spatial variations of environmental parameters were tested by analysis of variance (ANOVA, Sokal and Rohlf, 1981). In the statistical designs, three fixed factors were crossed (i.e. date, depth and site) for physical parameters (i.e. T, S) and two factors (i.e. date and site) were crossed for trophic parameters (i.e. POM, PIM, chl $a<2$, chl $a>2$ and total chl a). For temperature and salinity, the interaction of date, depth and site was not tested because the readings were not replicated. All data were tested for normality and homoscedasticity (F-test). Heteroscedastic data were log-transformed ($\log(x+1)$, Sokal and Rohlf, 1981). All percentage data (i.e. PC < 2 and OC) were arcsine-transformed (Sokal and Rohlf, 1981). Modalities of each factor were classified by multiple comparison analyses (Tukey test) to test for differences among groups.

2.4.2. Growth

Length–mass relationships were fitted according to the equation $M = a_1 \times L^{b_1}$, where M are mass variables (MTOT, DFM and DSM) and a_1 and b_1 are adjusted parameters. L–M relationships were calculated for each site, culture method and seeding date (16 equations for each mass variable). Effects of site, culture method and seeding date were assessed by comparing the allometric exponent b_1 using ANCOVA (Sokal and Rohlf, 1981).

2.4.3. Growth model

A numerical model of growth was developed to predict growth as a function of environmental variables. Growth rate (G, mm day^{-1} or g day^{-1}) was modelled as a

function of temperature, food source and individual size according to the following equation:

$$G = aF^bT^cY^d = \mathrm{d}Y/\mathrm{d}t \quad (1)$$

where F is food concentration (μg l^{-1} or mg l^{-1}), T temperature (°C) and Y is individual length (mm) or mass (g).

Growth estimates at the beginning of the experiment were used as initial conditions in the model. The model was run for 1 year with a 1-day time step. The parameters of Eq. (1) were identified by minimisation using an optimisation algorithm based on the simplex method (Press et al., 1992).

3. Results

3.1. Environmental parameters

Salinity and temperature showed a clear seasonal pattern with maximal values observed during summer (40 psu in October 2000 and 27 °C in August 2001; Fig. 3) and minimal

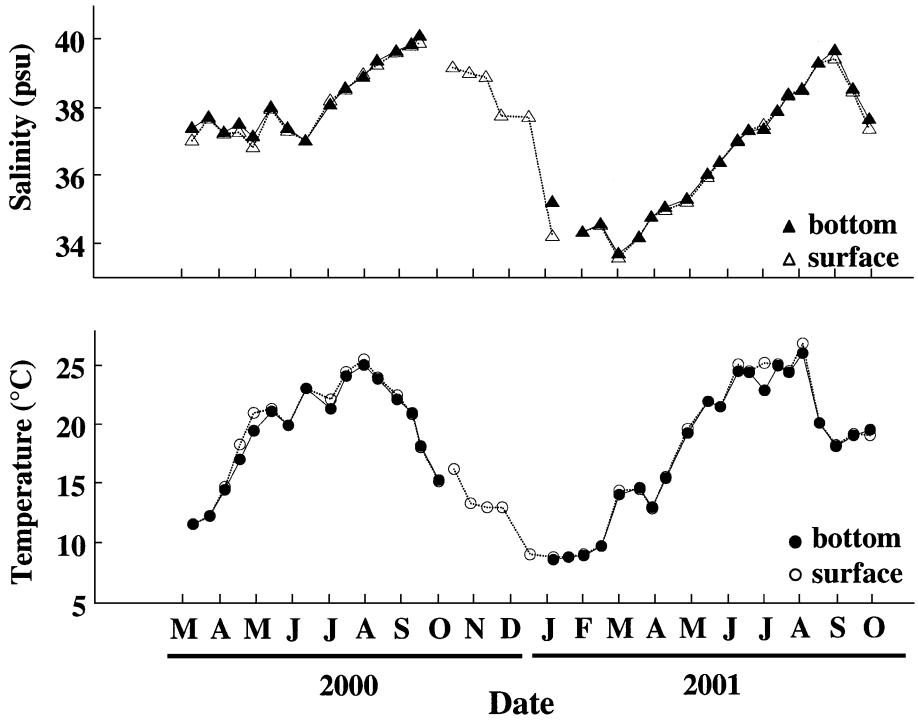

Fig. 3. Mean salinity and temperature over the six sites between March 2000 and October 2001.

values recorded during winter (34 psu and 8.5 °C in February 2001). Temperature always reached maximal values before salinity, which suggested an annual basis for correlation between these two parameters. Spatial variations between the sites were significant only for temperature ($P<0.01$). Site 1 exhibited slightly higher mean temperature ($\Delta T=+0.2$ °C) than the other sites. This difference, however, may be due only to the fact that the shallow site 1 was always sampled at the end of our lap (at midday) when temperature was often higher. Salinity did not vary between sites ($P>0.1$). Depth effects were significant for both salinity and temperature ($P<0.001$). Thermal stratification of the water column was stronger in spring and summer. In such instances, the difference between surface and bottom could reach 3 °C, as seen in July 2001, especially in sites 1, 2 and 3. Salinity was not stratified with depth, except on a single episode in January 2001, for sites 1, 2 and 3 only ($\Delta S=2$ psu).

Concentration in TPM averaged 2 mg l^{-1} over the study period. TPM typically ranged between 0.5 and 5 mg l^{-1} (with a maximum of 10 mg l^{-1}, data not shown). TPM, PIM and POM reached higher values the first year of the study, which showed an inter-annual variability ($P<0.001$; Fig. 4). However, no seasonal trend was recognisable. PIM and POM were correlated ($r=0.68$, $P<0.001$) and differed significantly among sites

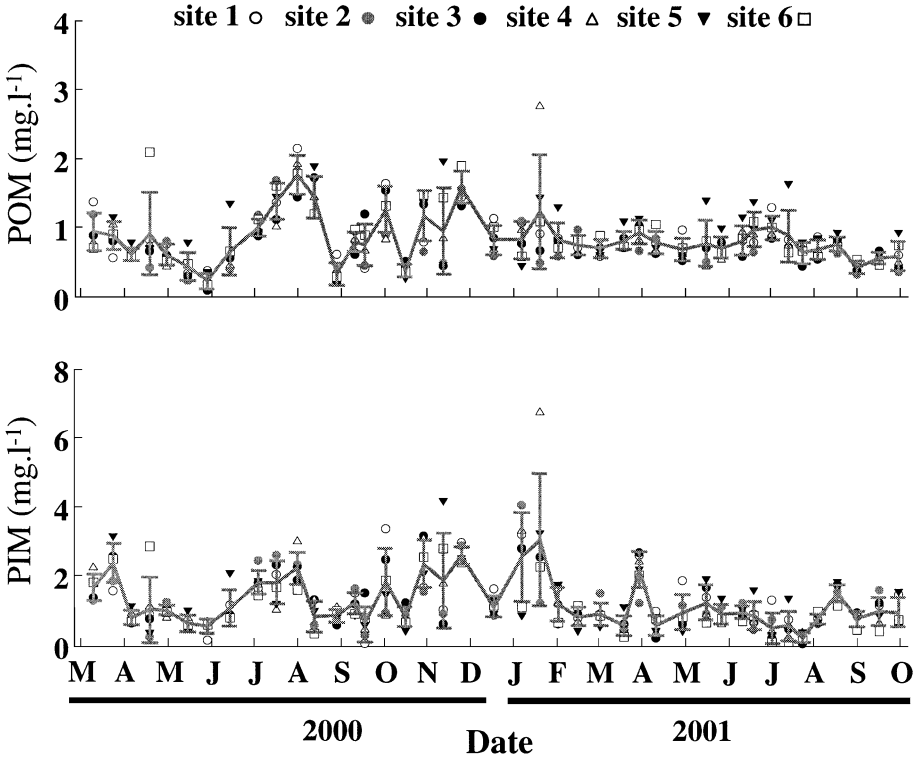

Fig. 4. Variations in POM and PIM between March 2000 and October 2001. The solid grey line is mean concentration with standard deviation over the six sites.

($P<0.01$). The significant interaction between temporal and spatial variations for PIM, POM and OC ($P<0.001$) indicated that ranking of sites was not constant date by date. But generally speaking, according to Tukey's tests, sites 1 and 5 had the highest average PIM values ca. 1.3 mg l^{-1}, site 6 had the lowest average value (1.1 mg l^{-1}) and sites 2, 3 and 4 were intermediate. Four different groups with decreasing mean POM concentrations were identified: site 5 (1 mg l^{-1}), site 6 (0.91 mg l^{-1}), sites 1 and 4 (ca. 0.83 mg l^{-1}) and sites 2 and 3 (ca. 0.75 mg l^{-1}). Consequently, sites 5 and 6 had a high OC value (ca. 48%), as compared to the other sites (ca. 42%).

All chl *a* fractions exhibited both significant temporal and spatial differences with a significant interaction effect ($P<0.001$; Fig. 5). Chl *a*>2 and total chl *a* were strongly correlated ($r=0.94$, $P<0.001$), whereas chl $a<2$ was less correlated to both these variables ($r=0.4$ for correlation with total chl *a* and $r=0.2$ for correlation with chl *a*>2, $P<0.01$ in both cases). Total chl *a* and chl *a*>2 concentrations were maximum in summer at all sites, especially in August 2001 with a peak around 6.5 μg l^{-1}. Total chl *a* and chl *a*>2 concentrations were lowest in November 2000 (ca. 0.4 μg l^{-1}). Mean total chl *a* averaged 1.2 μg l^{-1} over the study period and showed a greater spatial variability during

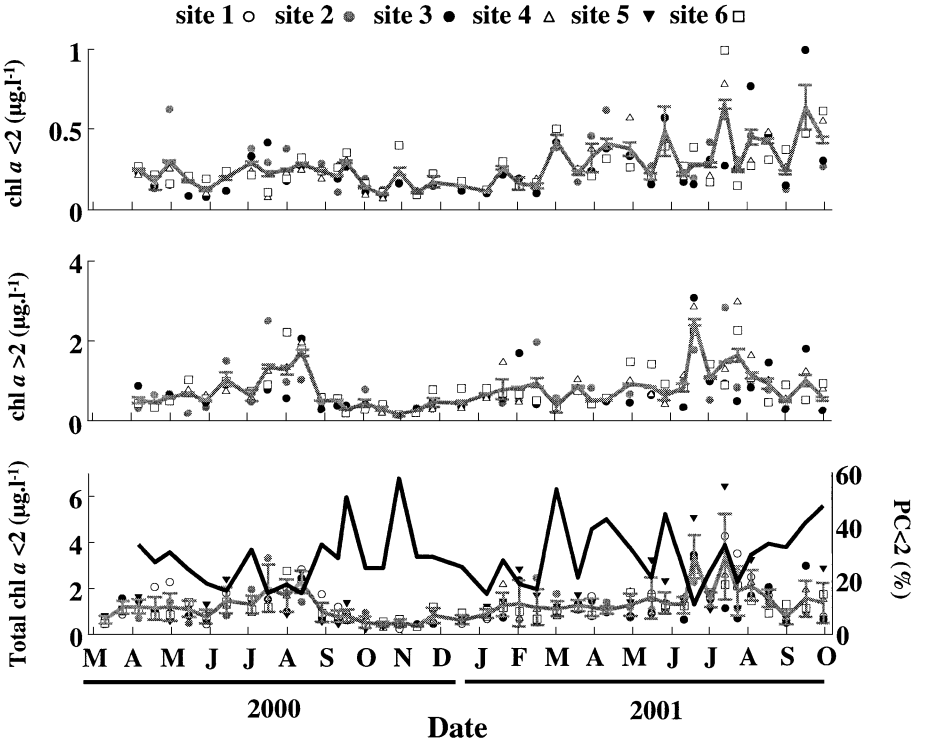

Fig. 5. Variations in total and size-fractionated chlorophyll *a* between March 2000 and October 2001. The solid grey line is mean concentration with standard deviation over sites. The solid black line is the percentage of chlorophyll *a* lower than 2 μm in total chlorophyll *a*.

periods with highest concentrations. On average, chl a>2 accounted for 70% of total chl a. Chl a<2 concentration was quite variable from date to date. High values of PC<2 were generally associated with low total chl a concentrations. Unlike POM, chlorophyll a and especially chl a<2 reached higher values the second year of the study. POM and total chl a were slightly correlated ($r=0.27$, $P<0.01$).

Mean total chl a was highest in site 5 (1.5 μg l^{-1}), lowest in site 3 (1 μg l^{-1}) and decreased regularly from site 1, 4, 6 to 2. Site 2 showed the highest mean chl a<2 concentration (0.28 μg l^{-1}) and the highest mean PC<2 value. Sites 4 and 6 had significant higher mean chl a>2 (ca. 0.85 μg l^{-1}) than sites 2 and 3 (ca. 0.74 μg l^{-1}).

Combining results obtained for suspended matter and chlorophyll a allowed us to rank the sites and to define a spatial trophic gradient. Site 5 appeared as the richest site. Site 6 and then sites 1 and 4 were intermediate. Site 6 also showed the highest OC value. Finally, sites 3 and 2 were the poorest sites with a special situation in site 2, which presented the highest content of chl a<2.

3.2. Oyster growth

3.2.1. Growth rates

3.2.1.1. Seeding date 1. Growth (length or mass) of C1 oysters was seasonal (Fig. 6). The annual growth cycle could be divided into three parts: (1) a lag phase (from late March to late May 2000) (2) an exponential phase during summer (from June to late September 2000) and (3) a stationary phase during fall and winter (from October 2000 to mid-March 2001). After 1 year, mean final shell length ranged between 88.1 mm (site 2) and 101.8 mm (site 6). Mean MTOT ranged between 69.3 g (site 2) and 96 g (site 6). Individual mass at harvest ranged between 60 and more than 100 g. DSM followed the same pattern as MTOT (data not shown). Spatial variability was stronger for dry tissue mass growth than for other growth variables. Mean final DFM ranged between 1.2 g (site 2) and 2.69 g (site 6). DFM seemed to vary according to short-term patterns. As judged from the rather high within-site variation coefficients calculated for DFM (ca. 35%), these variations were non-significant in many cases. In other cases, growth of shell and flesh were both negative, which suggests that variability in mass was attributable to inter-individual variability among oysters sampled on successive dates rather than to temporal variability.

Growth of P1 oysters was seasonal for both flesh mass and shell length (Fig. 6). There was, however, a lag phase in flesh growth but not in shell growth. Shell length increase was exponential during spring and summer (from late March to late September 2000), but negligible during fall and winter (from November 2000 to mid-March 2001). For mass variables, the annual cycle was identical but a lag phase preceded the exponential one. At the end of the experiment, mean final shell length ranged between 79.3 mm (site 3) and 87.2 mm (sites 2 and 6). By March 2001, oysters had not yet reached a marketable MTOT with a maximum at 51.8 g (site 6). DSM showed similar temporal patterns. Like C1 oysters, the effect of site on P1 oyster growth was more pronounced for dry tissue mass than for other variables. Mean final DFM varied between 0.82 and 1.32 g (sites 3 and 6, respectively).

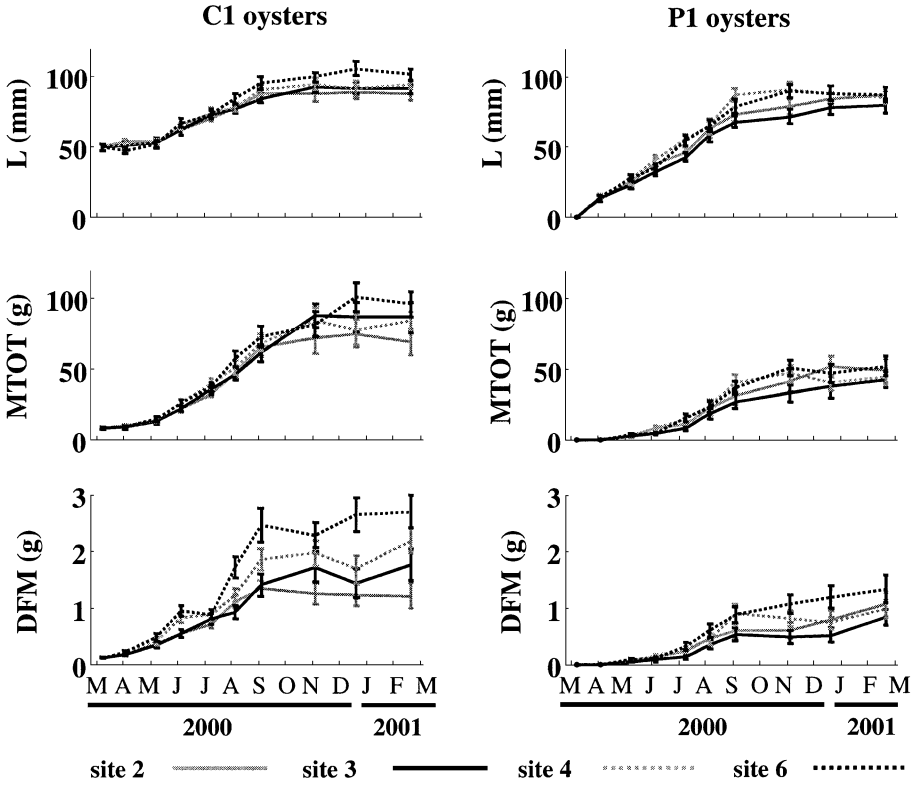

Fig. 6. Variations (means and 95% confidence limits) in *L*, MTOT and DFM of oyster groups C1 and P1 for each site and culture method.

3.2.1.2. Seeding date 2. Irrespective of the culture method, differences were apparent in the shape of growth curves when compared to seeding date 1 (Fig. 7). For C2 oysters, growth in shell length was regular during the study period, whereas two periods could be identified in mass growth: (1) a first long stationary phase during fall and winter (from late September 2000 to April 2001) and (2) an exponential phase during spring and summer (from April to mid-September 2001). Mean final shell length was ca. 80 mm in all sites. Plateau values of MTOT were lower than those obtained for C1 oysters but close to a marketable mass (ca. 70 g). Weak spatial variations of DFM were observed compared to C1 oysters and mean final DFM ranged between 1.7 g (sites 2, 3 and 4) and 2.01 g (site 6). A significant decrease in DFM ($\Delta DFM = -0.17$ g) was observed in site 3 between June 12 and July 16. This might be due to a gamete emission since no associated decrease was observed in other variables nor at other sites.

For P2 oysters, growth curves could also be divided in two parts: (1) a long stationary phase from fall to mid-winter for shell length and from fall to mid-spring for mass and (2) an exponential phase from mid-winter (shell length) or mid-spring (mass) to mid-fall. After 1 year, mean shell length ranged between 72.3 mm (site 2) and 80.4 mm (site 6).

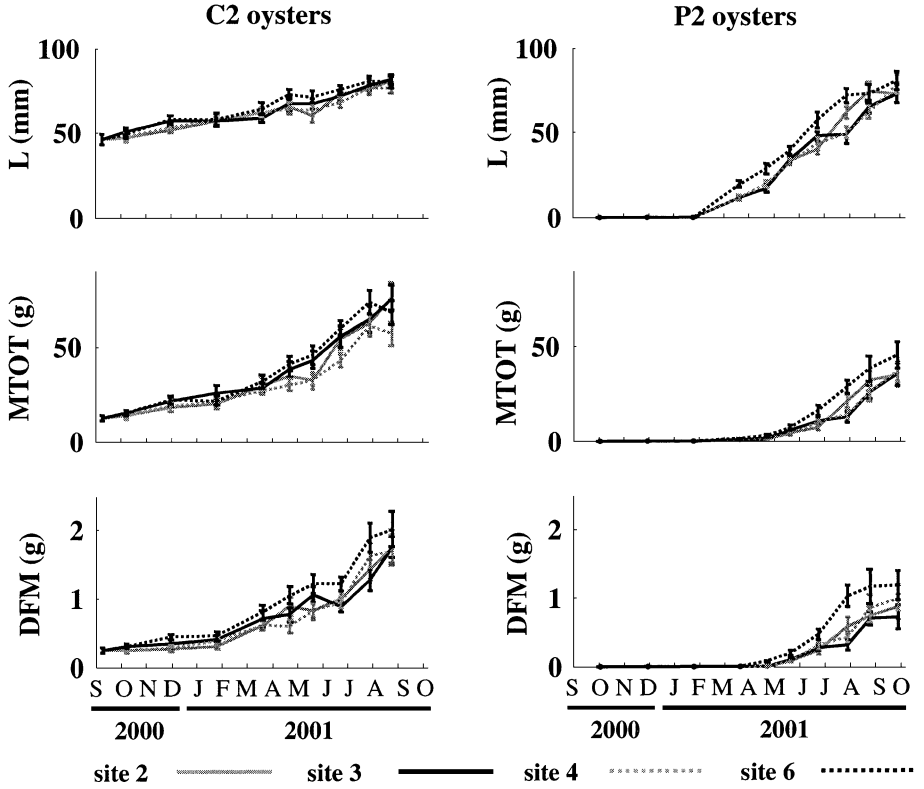

Fig. 7. Variations (means and 95% confidence limits) in *L*, MTOT and DFM of oyster groups C2 and P2 for each site and culture method.

Mean final MTOT was much lower than marketable mass (maximum ca. 45.2 g in site 6). Mean final DFM ranged between 0.7 g (site 3) and 1.17 g (site 6).

Generally, seeding date induced a shift in growth curves: groups C1 and P1 were characterised by an exponential phase when temperature was high, followed by a stationary phase during cool conditions, whereas groups C2 and P2 began with a long stationary phase (fresh season) followed by an exponential one (warm season). Undoubtedly, site 6 exhibited the best growth performances. Ranking the three other sites was more difficult due to interactions between culture method and seeding date.

3.2.2. Length–mass relationships

Allometric exponent b_1 calculated for all sites, culture methods and seeding dates is shown in Fig. 8 and statistical results are summarised in Table 1. In all cases, regression models were significant and R^2 ranged between 0.7 and 0.9 ($P<0.001$).

3.2.2.1. Effect of site. For MTOT and DSM, we found a significant site effect on b1 value except for P2 oysters (ANCOVA, $P>0.1$). Site effects were essentially due to sites 6

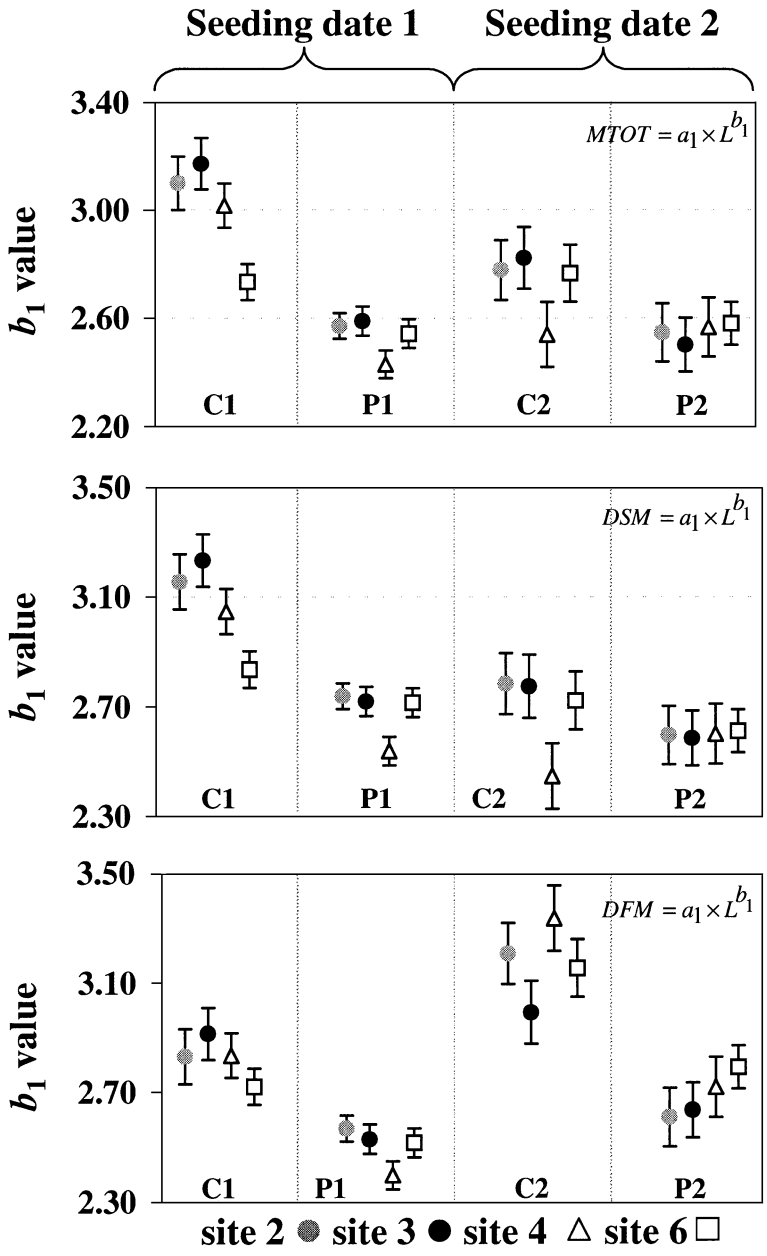

Fig. 8. Values and standard errors of the exponent b_1 of allometric relationships between length and mass variables for each combination of site, culture method and survey.

Table 1
Effect of site, seeding date and culture method on the allometric exponent b_1

Type effect on b_1 value	L–MTOT	L–DSM	L–DFM
Site			
C1	***	***	NS[a]
P1	*	***	NS[a]
C2	*	**	NS[a]
P2	NS[a]	NS[a]	NS[a]
Seeding date			
"collées"—St 2	**	***	**
"collées"—St 3	**	***	**
"collées"—St 4	***	***	**
"collées"—St 6	NS[a]	NS[a]	**
"pignes"—St 2	NS[a]	NS[a]	***
"pignes"—St 3	NS[a]	NS[a]	***
"pignes"—St 4	NS[a]	NS[a]	***
"pignes"—St 6	NS[a]	NS[a]	***
Culture method			
Seeding date 1—St 2	***	***	***
Seeding date 1—St 3	***	***	***
Seeding date 1—St 4	***	***	***
Seeding date 1—St 6	**	NS[a]	***
Seeding date 2—St 2	*	NS[a]	***
Seeding date 2—St 3	**	NS[a]	***
Seeding date 2—St 4	NS[a]	NS[a]	***
Seeding date 2—St 6	NS[a]	NS[a]	***

L: shell length, MTOT: total individual mass, DSM: dry shell and DFM: dry flesh mass.
[a] NS = $P > 0.05$.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

(C1 oysters) and 4 (P1 and C2 oysters) for which b_1 was smaller (ANCOVA, $P < 0.05$). On the opposite, there was no significant site effect on b_1 for DFM (ANCOVA, $P > 0.1$). Consequently, we used a single equation (i.e. a common b_1 parameter value for the four sites) for each oyster group C1, P1, C2 and P2 in further tests.

3.2.2.2. Effect of seeding date. For MTOT and DSM, b_1 was not significantly affected (ANCOVA, $P > 0.05$) by seeding date except for "collées" oysters in sites 2, 3 and 4 (ANCOVA, $P < 0.01$). In these latter cases, b_1 was higher for C1 than for C2. For DFM, there was a significant effect of seeding date (ANCOVA, $P < 0.01$) and b_1 value was systematically smaller for oyster groups 1 (2.97 and 2.52 for C1 and P1, respectively) than for oyster groups 2 (3.18 and 2.72 for C2 and P2, respectively).

3.2.2.3. Effect of culture method. For MTOT, culture method generally had a significant effect (ANCOVA, $P < 0.05$) on b_1, except for oyster groups C2 and P2 in sites 4 and 6

Table 2
Optimised coefficients and significance tests of growth models $G = a\mathrm{POM}^b T^c Y^d$

	L	MTOT	DFM
Coefficients			
a	9.42×10^{-4}	3.77×10^{-5}	5.95×10^{-6}
b	0.86	0.40	0.38
c	3.36	2.50	2.36
d	− 1.12	0.41	0.33
Statistical results			
n	144	140	133
R^2	0.96	0.93	0.77
P	< 0.001	< 0.001	< 0.001

(ANCOVA, $P > 0.05$). b_1 was higher for "collées" than for "pignes" oysters. For DSM, culture method had not significant effect (ANCOVA, $P > 0.05$) except for oyster groups C1 and P1 in sites 2, 3 and 4 (ANCOVA, $P < 0.001$). For DFM, the effect of culture method

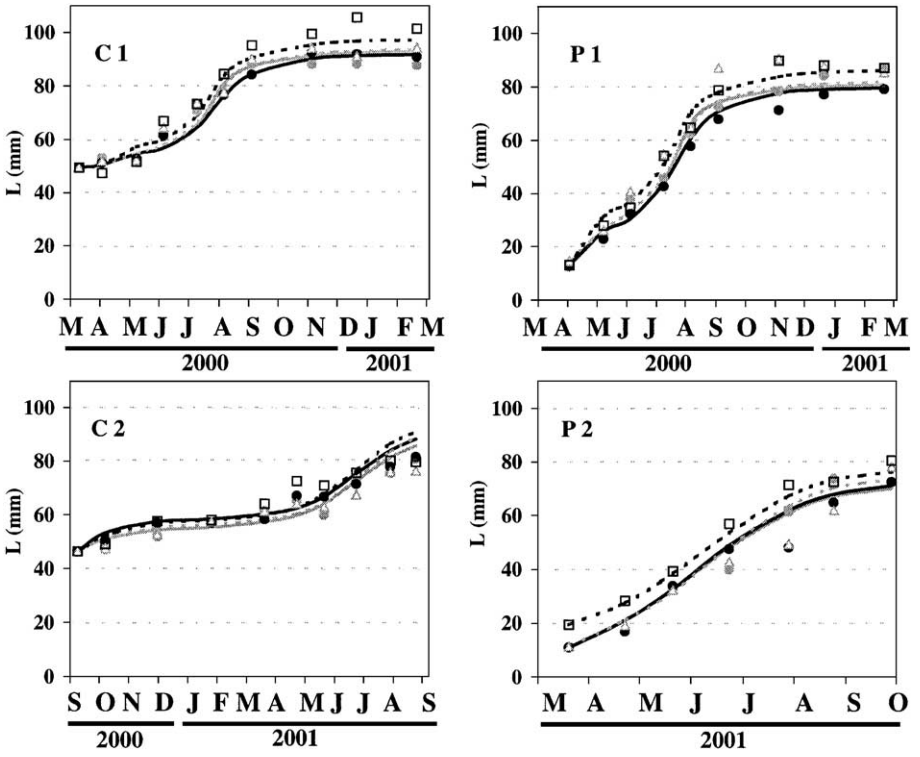

Fig. 9. Mean individual growth in L simulated by the individual growth model (lines), compared to observed values (symbols) for each site, culture method and seeding date combination (site 2, site 3, site 4, site 6).

was clearly significant (ANCOVA, $P<0.001$) and b_1 values were systematically higher for "collées" than for "pignes" oysters.

3.3. Growth model

Growth and environmental data were used to calibrate a growth model according to Eq. (1). We used POM as a measure of food availability, since POM gave a better fit than other available food sources (total chl *a*, chl *a*>2 and chl *a*<2, simulations not shown) and Eq. (1) became $G=a\mathrm{POM}^{b}T^{c}Y^{d}$. Optimised coefficients and significance tests of the model were summarised in Table 2. We found $a=3.77\times10^{-4}$ and $a=5.95\times10^{-6}$, $b=0.4$ and $b=0.38$, $c=2.50$ and $c=2.36$, and $d=0.41$ and $d=0.33$ using MTOT and DFM, respectively, as measures of oyster size. When using L as the measure of oyster size, we found $a=9.42\times10^{-4}$, $b=0.86$, $c=3.36$ and $d=-1.12$.

Observed and simulated growth are shown in Figs. 9–11 for L, MTOT and DFM, respectively. Simple linear regression comparing observed and simulated data confirmed

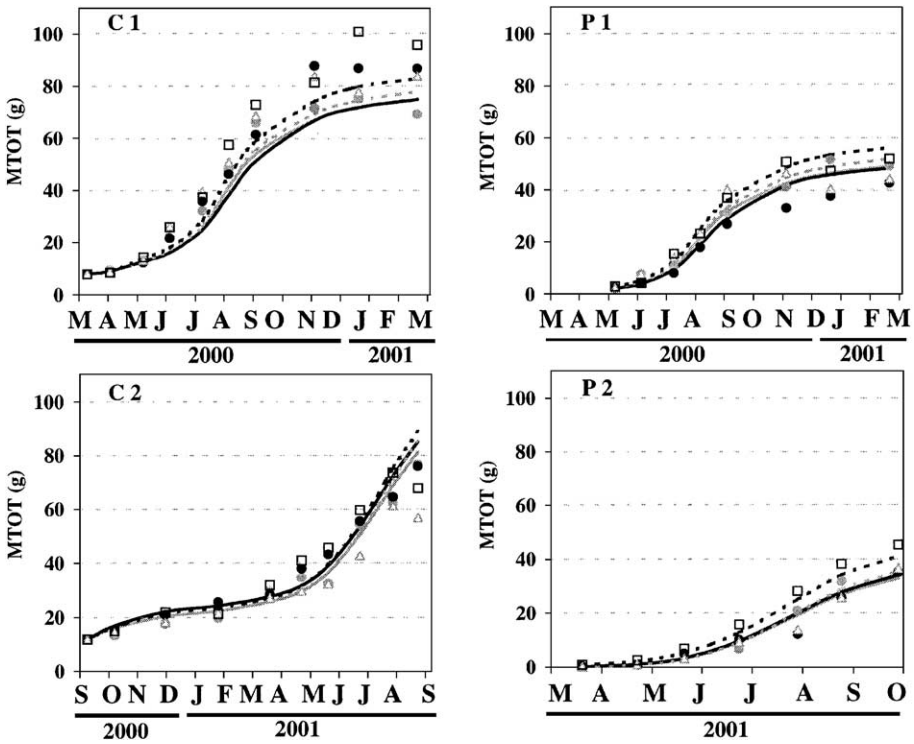

Fig. 10. Mean individual growth in MTOT simulated by the individual growth model (lines) compared to observed values (symbols) for each site, culture method and seeding date combination (—●— site 2, —●— site 3, ···△··· site 4, ···□··· site 6).

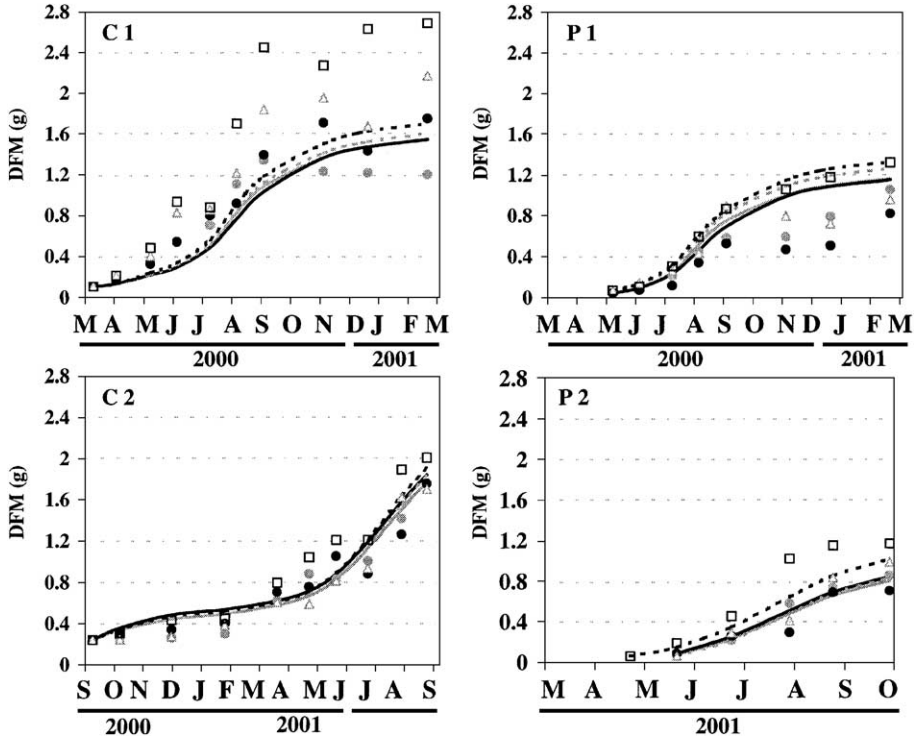

Fig. 11. Mean individual growth in DFM simulated by the individual growth model (lines) compared to observed values (symbols) for each site, culture method and seeding date combination (—●— site 2, —●— site 3, ···△··· site 4, ···□··· site 6).

that this form of model (Eq. (1)) is adequate with a significant correlation whatever the variable ($P<0.001$). Regression slopes between observed and predicted data were significantly different from 1 for MTOT and DFM ($P<0.001$) but not for L ($P>0.05$).

For MTOT, discrepancies were essentially observed for the highest values that the model could either overestimate (P1 and C2 oysters) or underestimate (C1 oysters). Discrepancies in simulated DFM also showed underestimation problems, especially for C1 oysters. Overestimation was clear for P1 oysters, especially in site 3.

4. Discussion

4.1. Environmental parameters

In the present study, temperature and salinity were close to values usually reported in literature for Thau Lagoon (Pichot et al., 1991; Gasc, 1997; Alunno-Bruscia et al., 2001). Temperature stratification sometimes occurs and is related to season (surface waters are

colder during winter and warmer during summer than bottom waters). Stratification features in salinity are due to rainfall and input from the watershed (Gasc, 1997).

Few suspended particulate matter data are available for Thau Lagoon. Pichot et al. (1991) reported that mean TPM was 3.2 mg l^{-1} in 1989 and 9.4 mg l^{-1} in 1990–1991, while POM averaged 1 mg l^{-1} in 1990–1991 with an organic content ca. 37%. These values are close to our results except for TPM measured in 1990–1991. POM values recorded by Alunno-Bruscia et al. (2001) in site 4 averaged 1.5 mg l^{-1} in 1999–2000, with OC averaging 65%. This is higher than our findings for the same location (0.83 mg l^{-1} for POM and 42% for OC). Inter-annual variability could be the main cause, as suggested by the high growth rates of bivalves recorded in 1999. Another difference is that Alunno-Bruscia et al. (2001) found a seasonal pattern (maximal values in summer 1999), which was not observed during our experiments. Assuming a POM/POC ratio of 2.5, particulate organic carbon (POC) levels reported by Gasc (1997) are similar to POM levels found in our study. Mean POC recorded in 2000–2001 varied from 31.2 to 41.6 μM, depending on sites, which was similar to POC measured in 1993–1994 (ca. 25 μM, Gasc, 1997).

In Thau Lagoon, chlorophyll *a* concentration is generally low, typically less than 3 μg l^{-1} (Tournier and Pichot, 1987; Jarry et al., 1990, 1991; Vaquer et al., 1996; Gasc, 1997; Chrétiennot-Dinet and Courties, 1997; Alunno-Bruscia et al., 2001; Souchu et al., 2001). Peak concentrations may reach 35 μg l^{-1} during blooms, as recorded in November 1993 inside the shellfish area of Bouzigues (Gasc, 1997). Early studies concluded to the existence of a decreasing chlorophyll *a* gradient along the NE–SW axis of the lagoon (Tournier and Pichot, 1987; Jarry et al., 1990, 1991). This gradient could be mainly due to marine water exchanges through the channel of Sète. The input of marine water presumably created a front, leading to phytoplanktonic production. This gradient was not reflected in our experiment. For instance, site 5, which was located near the middle part of the lagoon, exhibited higher mean concentration than site 3, which was located near Sète. On the other hand, Souchu et al. (2001) reported a decreasing chlorophyll *a* gradient within shellfish zones. We found no evidence for this in our study (Fig. 5). Vaquer et al. (1996) and Chrétiennot-Dinet and Courties (1997) reported that picophytoplanktonic cells (size <2 μm) were very abundant and comprised procaryotic picoplankton (cyanobacteria) and mainly eucaryotic picoplankton with the endemic species *Ostreococcus tauri*. Vaquer et al. (1996) found a seasonal trend in the annual dynamics of eucaryotic picoplankton, but not for procaryotic picoplankton. In our study, we observed no seasonal pattern for chlorophyll *a* particles smaller than 2 μm (Fig. 5). Picophytoplankton was abundant in terms of cell density, but accounted for a minor part of phytoplankton biomass when measured in terms of chlorophyll *a*. In our study, picophytoplanktonic chlorophyll *a* (mean concentration 0.25 μg l^{-1}) amounted to 30% of total chlorophyll *a*. These results are in agreement with those reported by Vaquer et al. (1996) (0.35 μg l^{-1} and 29.8%, respectively).

Among ecosystems supporting an intensive shellfish production, Thau Lagoon presents a particular situation, mainly characterised by low concentration in chlorophyll *a* and suspended particulate matter (Table 3). Seto Inland Sea (Japan) is probably the site presenting the closest characteristics with Thau Lagoon in terms of available food (Kobayashi et al., 1997). Seston in Thau Lagoon shows a high organic content, which is among the highest reported in literature (Table 3).

Table 3
Growth rates of *C. gigas* and trophic resources recorded in different geographic areas

Area	Culture method	Chl *a* (μg l^{-1})	TPM (mg l^{-1})	OC (%)	Time of seeding	Initial MTOT (g)	*G*	Reference
Normandy (France)	Rack culture	0.15–17[a]	–	–	March 2000	28.1	0.28	Fleury et al., 2001a,b; Daniel and Le Goff, 2002
South Brittany (France)	Rack culture	0.2–6	5–31[b]	60–70[b]	March 2000	28.1	0.38	Fleury et al., 2001a; Camus, pers. comm.
Marennes-Oléron bay (France)	Rack culture	0.01–55[c]	0.1–564[c]	5–35[c]	March 2000	28.1	0.22	Fleury et al., 2001a; Razet, pers. comm.
Arcachon (France)	Rack culture	0.02–30[d]	1.7–108[d]	–	March 2000	28.1	0.30	Fleury et al., 2001a; Auby et al., 1999
Thau Lagoon (France)	Suspended culture—"collées"	0.4–3.3	0.5–5	mean: 40–50	March 2000	28.1	0.46	Fleury et al., 2001a; this study
Thau Lagoon (France)	Suspended culture—"collées"	0.4–3.3	0.5–5	mean: 40–50	March 2000	7.9	0.67	this study
Thau Lagoon (France)	Suspended culture—"pignes"	0.4–3.3	0.5–5	mean: 40–50	March 2000	0.34	1.52	this study
Ria De Aveiro (Portugal)	Suspended culture in baskets	–	5–80	mean: 18	May 1990	~5	0.58	Almeida et al., 1999
Lima estuary (Portugal)	Suspended culture in baskets	–	3–11	mean: 20	May 1990	~5	0.59	Almeida et al., 1999
Lemmens inlet (Canada)	Suspended culture in lantern nets	0.5–50	–	25–90	June 1984	~15	0.41	Brown and Hartwick, 1988a; Brown, 1988
West Vancouver (Canada)	Suspended culture in lantern nets	0.5–47	–	25–55	June 1984	~15	0.24	Brown and Hartwick, 1988a; Brown, 1988
Seto inland Sea (Japan)	Suspended culture	0.1–7	–	–	May 1996	5.8	1	Kobayashi et al., 1997
Eo estuary (Spain)	Rack culture in bags	–	–	–	March 1994	~ 30 (high growth)	0.24	Cigarria, 1999
						7 (slow growth)	0.31	

G is expressed as $(\log(\mathrm{MTOT}_f/(\mathrm{MTOT}_i)/(t_f - t_i)) \times 100$, where *f* is final size and *i* is initial size.

[a] Recorded in the Baie des Veys in 2000–2001.

[b] Recorded only in spring and summer 2001.

[c] Recorded in 1977–1998.

[d] Recorded in 1988–1997.

4.2. Oyster growth

4.2.1. Temporal and spatial variations

In our study, seasonality of oyster growth could not be attributed to variations in food supply, which showed no seasonal trend. However, annual variations in temperature coincided with variations in growth. Including a temperature term in the growth model allowed us to reproduce the exponential and stationary phases of growth trajectories (Figs. 6 and 7). Oysters seeded in spring were larger than those seeded in fall, despite both groups being grown for an equal amount of time. The same was found for *M. galloprovincialis* cultivated in the Ria de Arousa in Spain (Pérez Camacho et al., 1991). As far as grow out only is considered, clearly seeding in spring is advantageous. On the other hand, the condition index, which could be computed for instance as the ratio DFM:MTOT was higher for oysters seeded in fall, as shown by length–mass relationships (Table 1). In Thau Lagoon, oyster farmers seeded a large part of the oysters in spring. Based on the present results, it appears that spring is the most appropriate seeding time for obtaining appropriate-sized individuals (a large part of landings are made in December, on a rather short lapse of time).

Spatial variations in growth could be explained partly by spatial variations in food supply. Site 6 exhibited the best growth performances and had the highest mean POM as well as organic content. Relationships between trophic variables and growth in other sites were unclear. However, POM was the trophic variable giving the best adjustment to our data in the growth model. Furthermore, the exponent b_1 in the allometric equations relating DFM and MTOT to L suggested that condition index was highest in site 6. Brown and Hartwick (1988a) also noticed higher DFM:DSM ratios at fast growth sites. More generally, b_1 values were reported to vary greatly depending on site-related factors. In the relation between DFM and L, b_1 was found to be equal to 3.43 for *C. gigas* reared in Seto Inland sea (Japan) (suspended culture, Kobayashi et al., 1997) and 6.21 in the Korean Kamakman Bay (suspended culture, Hyun et al., 2001).

4.2.2. Effect of farming conditions

Length–mass relationships varied among culture methods. In many occasions, the exponent b_1 was significantly higher for "collées" oysters than for "pignes" oysters, suggesting a higher length-specific mass (MTOT or DFM) for "collées" oysters. This result is consistent with field observations on "pignes" oysters, which tended to exhibit a better growth in length than in mass. This might be due to high densities and clumping of "pignes" oysters. In contrast, "collées" oysters are distributed regularly along the ropes and are seeded at a lower density. At each sampling, "pignes" oysters that could be easily separated from the collectors were counted in order to assess the population density on hummocks. Maximal mean density varied between 30 ($\pm$ 8 CI) oysters/collector for P1 and 20 ($\pm$ 9 CI) oysters/collector for P2. Differences between the two oyster groups were due to differences in spat fall abundance. At the end of our experiment, the mean density was minimal ca. 13 ($\pm$ 7 CI) oysters/collector. The reduction of oyster density through time presumably reflected losses through self-thinning or losses of large individuals at sampling. Compared to "collées" oysters, which were seeded at a density of 34 individuals/rope-meter, the initial seeding density for "pignes" oysters varied between

100 and 150 oysters/rope-meter (5 collectors/rope-meter) and dropped to ca. 65 oysters/rope-meter after 1 year.

In terms of growth rate, the single effect of culture method could not be assessed because differences in initial size (MTOT 7–12 g for "collées" vs. ca. <0.1 g for "pignes") and history of spat (birth in hatchery vs. natural spat) also influence growth performances.

4.2.3. Comparison with other areas

Table 3 reports the growth rates of *C. gigas* recorded in France and elsewhere in the world. In France, the monitoring network REMORA, which has been already described in Gangnery et al. (2001) and Fleury et al. (2001b), allows us to compare *C. gigas* growth among French areas which support intensive shellfish farming. Growth rates in Thau Lagoon are well-known to be typically the highest recorded in France (Fleury et al., 2001a). In our experiments, growth rates of "collées" oysters were in the range of those observed in REMORA in 2000, although slightly higher (0.67 vs. 0.47% MTOT day^{-1}) due to smaller initial mass. For the same reason, growth rates of "pignes" oysters were higher still (1.52% MTOT day^{-1}). Compared to growth rates recorded elsewhere in the world, growth of "pignes" oysters in Thau Lagoon is the highest recorded, despite smaller initial mass (0.34 g). Growth rates reported by Kobayashi et al. (1997) in Seto Inland Sea in Japan, where the concentration in total chlorophyll *a* is similar to Thau Lagoon, are among the best reported (1% MTOT day^{-1}). At approximately the same initial mass, growth rates reported by Almeida et al. (1999) in Portugal (0.59% MTOT day^{-1}) are quite similar to values recorded in the present study for "collées" oysters, despite seston quality, as measured by OC, being lower than in Thau Lagoon. The smallest growth rates reported were recorded in Canada and in Spain (0.24% MTOT day^{-1}) (Brown and Hartwick, 1988a and Cigarria, 1999, respectively) and are in the range of values measured in France on the Atlantic coast, particularly in Normandy and in Marennes-Oléron Basin (0.28 and 0.22% MTOT day^{-1}, respectively).

4.3. Modelling strategy

Several strategies could be used to model oyster growth. A first approach is to use statistical models developed to identify key predictors of growth. These models usually use linear multiple regression where instantaneous growth rate is expressed as a function of environmental variables (e.g. temperature, salinity, available food) and initial size (Hall, 1984; Brown, 1988). Such studies have led to developing habitat suitability indices (Brown and Hartwick, 1988b; Roland, 1990). However, these models are of limited applicability for predicting growth because (1) they are based on a linear growth and (2) they are not dynamic (size incrementation at each time step). A second approach is to develop ecophysiological models based on an energy budget of the animals. Currently, such models are widely used in bivalves studies, e.g. Ross and Nisbet (1990), Van Haren and Kooijman (1993), and Dowd (1997) for *Mytilus edulis*, Powell et al. (1992) for *C. virginica*, Pouvreau et al. (2000) for *Pinctada margaritifera*, Solidoro et al. (2000) for *Tapes philippinarum* and Bacher et al. (1991), Raillard et al.

(1993), Barillé et al. (1997), and Ren and Ross (2001) for *C. gigas*. Knowledge of key physiological functions is a prerequisite for such models. These models compute the balance between energy acquisition, as governed by clearance rate, consumption rate, food ingestion and absorption, and energy losses through respiration, excretion and biodeposit production. Energy acquisition and losses depend on both physiological processes and environmental parameters (e.g. temperature, food quantity and quality). Currently, available information was not sufficient for using an ecophysiological approach and we developed a third approach based on an empirical model. This dynamic model simulated growth by computing instantaneous growth rate as a function of environmental variables. This approach was used in a previous study (Gangnery et al., 2001) where growth rate was expressed as a function of chlorophyll *a* and mass and parameters estimates were obtained from the REMORA network in 1998. The Gangnery et al. (2001) model failed to reproduce the stationary phase observed in winter 2000/2001. One reason for this may be that the REMORA data were recorded between March and December, i.e. before growth became asymptotic. This led us to include temperature in the model, as it has the same seasonality as growth. Furthermore, temperature is well-known to be a determining factor in bivalve growth. Generally, the model provided good estimates of variations in growth of shell length and total individual mass, but not of dry flesh mass. This discrepancy might result from dry flesh mass being easily affected by short-term events (mass loss related to periods of low trophic resources or spawning). This kind of variability cannot be simulated by our equation in its present form since positive values of POM, temperature and size always imply positive growth. An ecophysiological approach could be an alternative way to better predict changes in dry flesh mass.

5. Conclusion

Growth rates measured in Thau Lagoon are among the highest recorded in the world, whereas concentrations in available food (POM and total chl *a*) are very low. The growth model developed in this study uses a single equation to simulate growth in several sites, for several seeding dates and culture methods. The general growth pattern (seasonality) was driven by temperature, whereas differences among sites were driven by variability in particulate organic matter. POM was the best index of trophic resources. This model may prove useful in an updated version of the population dynamics model of Gangnery et al. (2001).

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