Intensive rearing of juvenile oysters *Crassostrea gigas* in an upwelling system: optimization of biological production

Cédric Bacher [(1)] and Jean-Pierre Baud [(2)]

[(1)] *IFREMER, BP 133, 17390 La Tremblade, France.*
[(2)] *IFREMER Polder des Champs, 85230 Bouin, France.*

Received April 8, 1991; accepted April 13, 1992.

Bacher C., J.-P. Baud. *Aquat. Living Resour.*, 1992, **5**, 89-98.

Abstract

Seasonal growth of juvenile oysters (*Crassostrea gigas*) kept in an intensive upwelling system was studied from 1984 to 1986 in 60 to 90-day growth experiments. Saline ground water was used to produce *Skeletonema costatum* which was injected as food into the water supplying the upwelling system. Oyster density, water flow, phytoplankton concentration, temperature and frequency of food addition were controlled. Oyster growth was analysed with multidimensional contingency tables and correspondence analysis. The factors, in order of decreasing influence on growth, were temperature, food concentration and oyster density. A rearing strategy was deduced from the growth analysis for summer and winter. In summer, the density of 120,000 oysters/m^2, the flow rate of 1 liter/d/oyster and the food concentration of 0.5 10^9 phytoplankton cells/litre gave the most interesting results. The oysters grew from 0.014 g to 2.2 g after 60 days. In winter, the heat exchanger was necessary to increase the temperature from the 5°C naturally observed to the 11°C required for valuable growth. Oyster density and food concentration were the same as in summer. For a flow rate equal to 3 liter/day/oyster, oysters grew from 0.01 g to 0.5 g within 100 days. The cost and profit computations were derived from these strategies. It was concluded that this type of nursery would be profitable in spring, summer, and autumn but not in winter due to the high cost of heating the water.

Keywords : *Crassostrea gigas, Skeletonema costatum*, economic efficiency, multidimensional contingency table analysis, correspondence analysis, growth, nursery.

Élevage intensif d'huîtres juvéniles Crassostrea gigas *dans un système d'upwelling: optimisation de la production biologique.*

Résumé

La croissance d'huîtres juvéniles *Crassostrea gigas* a été étudiée dans un système d'upwelling. Des expériences d'une durée de 60 à 90 jours ont été menées durant les hivers 1984 et 1985, et les étés 1984 à 1986. L'eau salée souterraine a été utilisée pour produire la diatomée *Skeletonema costatum*, source de nourriture injectée ensuite dans le circuit d'eau de mer alimentant les juvéniles. La densité d'huîtres, le débit d'eau de mer, la concentration de nourriture, la température et la fréquence des apports de nourriture sont les paramètres contrôlés. La croissance des huîtres a été étudiée à l'aide de l'analyse de contingence multidimensionnelle et de l'analyse des correspondances; les paramètres ont été hiérarchisés par ordre d'influence décroissante: température, concentration de nourriture et densité d'huîtres. Cette optimisation a conduit à définir deux stratégies d'élevage. En été, une densité de 120 000 individus/m^2, un débit de 1 l/jour/huître et une concentration de 0,5 10^9 cellules phytoplanctoniques/l ont conduit à des croissances de 0,014 g à 2,2 g en 60 jours. En hiver, un échangeur thermique a été nécessaire pour faire passer l'eau de mer d'une température de 5°C à 11°C. Les mêmes densités et concentrations, jointes à un débit de 3 l/jour/huître, ont permis à des huîtres de 0,01 g d'atteindre 0,5 g en 100 jours. Les coûts de production et les profits ont èté évalués pour chaque stratégie d'élevage. Le bilan est optimum quand le système est utilisé en continu durant les saisons de printemps, d'été et d'automne. En hiver, le surcoût lié à l'utilisation de l'échangeur thermique rend le système non rentable.

Mots-clés : *Crassostrea gigas*, *Skeletonema costatum*, rentabilité économique, table de contingence multidimensionnelle, analyse des correspondances, croissance, nourricerie.

INTRODUCTION

The rearing of young bivalves in upwelling systems is considered an important technological step by many authors (Bayes, 1981; Rodhouse and O'Kelly, 1981; Lucas and Gérard, 1981; Saint-Félix *et al.*, 1984; Manzi *et al.*, 1984). This stage, which takes place between hatchery production and the start of subsequent growth of shellfish to market size, allows a more efficient year-round production of juveniles. Juveniles are fed with phytoplankton produced either within the same units (Spencer *et al.*, 1986; Spencer, 1988) or in units devoted to primary production (Claus *et al.*, 1983; Rodhouse *et al.*, 1983; Baud and Bacher, 1990). Intensive upwelling culture results in low mortality and better growth at high densities. Moreover, the sizes of individuals are kept fairly homogeneous. The final condition index of the individuals reared in an upwelling system is good enough to keep on rearing them in a natural system.

The main constraints to growth of bivalves in an upwelling system are temperature, quantity of food, density of bivalves, and the flow rate of sea water. The purpose of this study is to estimate the best combination of these parameters, indicated by growth performance of juvenile *Crassostrea gigas*, and to assess the sensitivity of growth to each variable. The diatom *Skeletonema costatum* was used to feed the juvenile oysters in winter or in summer (Baud, 1991). Feeding levels, oyster densities and flow rates are defined for winter and summer to enable the best set of parameters to be selected. Juvenile growth performances are incorporated into the computation of an economic budget (costs due to production of phytoplankton, purchase of oyster spat, water heating, investments; profits due to the sale of oysters). The system efficiency is then evaluated for several rearing strategies based on production during the whole year or for selected parts of the year. Similar experimental design and data analysis previously employed for *Ruditapes philippinarum* (Baud and Bacher, 1990), enable feeding behaviour of these two species to be compared.

EXPERIMENTAL SYSTEM AND METHOD

The design of the experimental system, described in Baud and Bacher (1990), is briefly summarized below.

Rearing technique

The saline ground water, continuously supplying the nursery, passed through a heat exchanger to warm it during winter or to cool it during summer. The use of heat exchanged water is referred to as EXC, or water at ambient temperature as NAT. Saline ground water, although suitable for culturing *Skeletonema costatum*, was not suitable for rearing the juvenile oyster, because of its high pH and ammonia content.

Skeletonema costatum, grown in 50 m^3 tanks filled with ground water, was used as a food in all experiments. Food was injected into the sea water supplying the nursery, either discontinuously (3 h with food alternating with 2 h without) or continuously. Four

Table 1. – Rearing parameters for *Crassostrea gigas* for each tube (50 cm diameter). Flow rate: FR1 = 1 m^3/h, FR3 = 3 m^3/h. Density: D25 = 25,000 oysters per tube, D50 = 50,000 oysters per tube. Chlorophyll *a* concentration (*Skeletonema costatum*): C0 = 0 µg/l, C1 = 20 µg/l, C2 = 40 µg/l, C4 = 80 µg/l (continuous or discontinuous injection). Food injection frequency: DISC = discontinuous feeding, CONT = continuous feeding (see text). Quality of water: NAT – natural water (ambient temperature), EXC = heat exchanged water.

	Parameter levels				
Season	Winter 1984 (3/Jan.-26/March)	Winter 1985 (3/Dec.-4/March)	Summer 1984 (24/July-2/Oct.)	Summer 1985 (28/June-10/Sept.)	Summer 1986 (19/June-18/Aug.)
Flow rate of sea water	FR1, FR3	FR1, FR3	FR1, FR3	FR3	FR3
Density	D25, D50	D25, D50	D25	D25, D50	D25
Skeletonema Feeding concentration	C0, C2	C1, C2, C4	C0, C1, C2, C4	C0, C1, C2, C4	C2
Feeding frequency	DISC	DISC	DISC	DISC	CONT, DISC
Quality of water	NAT	EXC	NAT, EXC	NAT	NAT

food concentrations (0, 20, 40, 80 µg chlorophyll *a*/l) were used (*table* 1).

The oysters were delivered by the SATMAR hatchery (France) at an initial total weight of 0.014 g. The oysters were contained in vertical, 50 cm diameter tubes at two densities (25,000 or 50,000 individuals per tube). The tubes were supplied with an upwelling water flow at two levels (1 m^3/h, 3 m^3/h) (*table* 1).

Oyster density per tube, sea-water flow rate, quantity and frequency of injected food, and temperature were controlled during winter or summer. These parameters were combined to assess their influence on oyster growth, totalling 36 growth survey experiments. Each experiment lasted 90 days in winter or 70 days in summer 1984 to 1986.

Methods of growth analysis

Contingency tables

At the end of each experiment, the individuals in each tube were sorted according to size (*table* 2).

Table 2. – Mean length, mean weight, and dry weight of various size classes of *Crassostrea gigas* obtained by sieving from the same nursery. The size class notation refers to the mesh size of the sieve. The standard deviation is shown in parentheses.

Mesh size of sieve (mm)	Length (mm)	Weight (g)	Dry weight (mg)
S2	4.4 (0.2)	0.014 (0.001)	
S6	10.5 (0.6)	0.19 (0.01)	
S8	13.8 (0.5)	0.41 (0.02)	15.2 (1.98)
S10	20.5 (0.5)	0.96 (0.06)	41.1 (2.05)
S14	24.7 (0.8)	1.93 (0.13)	81.1 (9.45)
S18	29.9 (1.0)	3.90 (0.48)	187.2 (23.24)

Contingency tables were constructed to compare the influence of the controlled parameters on the oysters, size distribution. Multidimensional contingency table analysis yields a generalization of the more classical two-dimensional analysis, since it permits the growth effects of combinations of different factors to be studied (Freeman and Dickie, 1979). Each row corresponds to a size class, considered as a level of the growth factor. The columns and the other dimensions of the table represent levels of the factors (e.g. food concentration, temperature, etc). The number of individuals corresponding to the combinations of factor levels are entered in each cell of the table. *Figure* 1 summarizes the concept.

Analyses were carried with linear, hierarchical models (Sokal and Rohl, 1981). A log-likelihood function was computed in each case to test the interaction between the factors. For instance, interaction between the growth factor and one or two other factors could be assessed by testing the value of the corresponding log-likelihood function. The procedure is described in more detail by Baud and Bacher (1990). To summarize, all the interactions were introduced in the model. The removal of each level of interaction was then tested through the building of sub-models which were compared with the previous one by calculating the loss of information from one model to the other. The objective was to obtain a model as simple as possible which only took significant interactions into account. Both the goodness-of-fit of the final model and the loss of information were tested with a χ^2, asymptotical law of the log-likelihood function (Sokal and Rohlf, 1981).

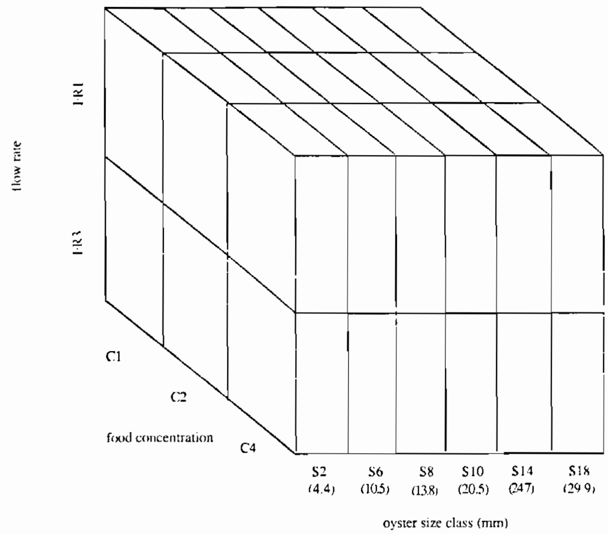

Figure 1. – Three-dimensional representation of a contingency table combining the three factors, flow rate (levels FR1, FR3), food concentration (levels C1, C2, C4) and size class. Results were obtained from several experiments at the end of which the juveniles were sorted by size. The number of individuals related to the combination of the three factors is entered in the corresponding cell of the table.

Because of the reduced number of experiments, not all the factor combinations were possible. The following factors were combined with the growth factor (levels are within brackets):

– concentration (C1, C2, C4) × density (D25, D50) in summer 1985 with natural water,

– concentration (C1, C2, C4) × flow rate (FR1, FR3) in summer 1984 with natural water,

– temperature (NAT, EXC) × flow rate (FR1, FR3) × concentration (C0, C2) in summer 1984,

– concentration (C1, C2, C4) × flow rate (FR1, FR3) × density (D25, D50) in winter 1985 with heat exchanged water.

For simplicity, only some results are shown.

Table 3. – Example of a contingency table used for correspondence analysis of the growth of oysters. In this case, 6 experiments were concerned (rows 1 to 6). The individuals were sorted at the end of the experiments from size S0 to size S18. The number of individuals corresponding to each size class and each experiment are recorded in the cells of the table. Since the experiments combined the food concentration factor (levels C1, C2, C4) and the density of individuals factor (levels D25, D50), these factors were used as dummy variables. Therefore, when a particular level was used in an experiment, a 1 was entered into the corresponding cell of the table, and a 0 otherwise.

Experiment	Mesh size of the sieve (S)					Food concentration (C)			Density (D)	
	S0	S8	S10	S14	S18	C1	C2	C4	D25	D50
1	4	18	28	18	5	1	0	0	0	1
2	0	10	28	26	16	1	0	0	1	0
3	18	15	25	15	7	0	1	0	0	1
4	4	9	20	30	25	0	1	0	1	0
5	10	13	25	15	15	0	0	1	0	1
6	4	5	15	27	38	0	0	1	1	0

Correspondence analysis

The same combinations of factors were examined by correspondence analysis. In each case, two-dimensional tables were constructed. The rows corresponded to the size classes, and the columns represented the experiments (*table* 3). The controlled factors of the growth survey experiments used for the analysis were introduced as dummy variables to display their relationship with growth. For example, a value of 0 or 1 was entered in the corresponding column each time the density level was D25 or D50. Baud and Bacher (1990) described this as a practical way of visualizing interactions between factors.

RESULTS

Growth of *Crassostrea gigas*

The initial size of individuals ranged from 4.0 to 4.8 mm. At the end of an experiment, the oysters in each upwelling tube were sorted into size groups (*table* 2). The results of the contingency table analyses are given only for a few cases (*table* 4), namely when the interactions were such that the study of sub-tables was unnecessary.

Summer

• ***Concentration, density, size class contingency table*** (*table* 4 *a*). – Three levels of food concentration and two levels of oyster density from six experiments were combined. Computations of the log-likelihood function showed that the interactions between concentration and size class and between density and size class were significant. The model comprising these two terms showed a significant goodness of fit and thus could be considered as an acceptable representation of the information contained in the table. Oyster size distribution showed that increasing density or decreasing food concentration resulted in a lower growth performance. Judging from the large differences in likelihood ratios obtained when the density factor or the concentration factor was removed, it was apparent that the effect of density was greater than that of food concentration, although there were small differences in the number of degrees of freedom.

Correspondence analysis illustrates the results graphically (*fig.* 2). Since the first two axes represented 98% of the global variability of the data, information brought by the other axes was omitted. The projections of the size classes on the first axis were related to a growth gradient. The same axis separated the two density levels, which confirmed the negative correlation between the growth performance and the density of oysters. Similarly, separation between the low (C1, C2) and the high food concentrations (C4) was consistent with the previously observed significant interaction between the growth and food concentration factors. The separation between C1 and C2 food concentrations on the second axis was mainly due to the proximity of the first size class (S0) and the C2 level. Because of the minor information given by the second axis and the strong correlation between the first axis and the growth performance, no significant difference between C1 and C2 could be derived from the correspondence analysis. Further, a more important effect on growth of density compared with the food concentration was seen from the stronger separation between these factors on the first axis.

• ***Concentration, flow rate, size class contingency table*** (*table* 4 *b*) – Six experiments were used to assess the effects of food concentration and flow rate in size frequency. The final model consisted of the interaction between food concentration and size class. The flow rate effect could not be considered as significant, although the removal of the interaction between the flow rate and the size class yielded a consistent loss of information.

As before, correspondence analysis was used to establish correspondence between size classes and the different levels of the factors, and to hierarchize the effects of these factors (*fig.* 3). The first two axes explained 98% of the variance and, with the exception of the smallest size class (S0), the first axis was correlated with the size distribution. The lower impact of

Table 4. – Each table (*a*, *b*, *c*) shows hierarchized models derived from the model containing all the effects of 2nd order interactions. *G* represents the logarithm of the maximum likelihood and provides a test of the model goodness of fit, d*G* is a measure of the loss of information between the first model and its sub-model, df is the degree of freedom used in testing the significance of *G* and d*G*. In all tables, valid models (*) are underlined. We look for the lowest order valid model.

4 a) C = food concentration, D = oyster density, S = size class. Both concentration and density had an effect on the growth (model CS + DS). d*G* was significant for the sub-models CS, DS derived from the model CS + DS. The interactions CS and DS had then to be taken into account. The *G* test of the model CS + DS was significant, therefore the model was considered as valid.

	CD + CS + DS (*)	
	G = 4.6, 8 df	
d*G* = 56, 4 df	d*G* = 35, 8 df	d*G* = 0.4, 2 df
CD + CS	CD + DS	CS + DS (*)
G = 61, 12df	*G* = 40, 16 df	*G* = 5, 10 df
	d*G* = 55, 4 df	d*G* = 34, 8 df
	CS	DS
	G = 60, 14 df	*G* = 39, 18 df

4 b) C = food concentration, F = flow rate, S = size class. The only remaining interaction is the CS, meaning that the influence of the food concentration on the oyster growth was significant. Besides, it is worth seeing that the effect of the flow rate was not significant only at a 7% level (see d*G* = 10, 5 df).

	CF + CS + FS (*)	
	G = 5.1, 10 df	
d*G* = 11, 5 df	d*G* = 137, 10 df	d*G* = 1, 2 df
CF + CS	CF + FS	CS + FS (*)
G = 16, 15 df	*G* = 142, 20 df	*G* = 6, 12 df
	d*G* = 136, 10 df	d*G* = 10, 5 df
	FS	CS
	G = 142, 22 df	*G* = 16, 17 df

4 c) T = temperature, C = food concentration, F = flow rate, S = size class. The final model contained a third order interaction between temperature, concentration and size class. The table had to be divided in to sub-tables in order to study the interactions existing between some factors for each level of the last one, e.g. concentration, or temperature (results not shown).

3rd ORDER (*)	*G* = 9.1, 5 df
TCS (*)	*G* = 23, 6 df
2nd ORDER	*G* = 56, 21 df

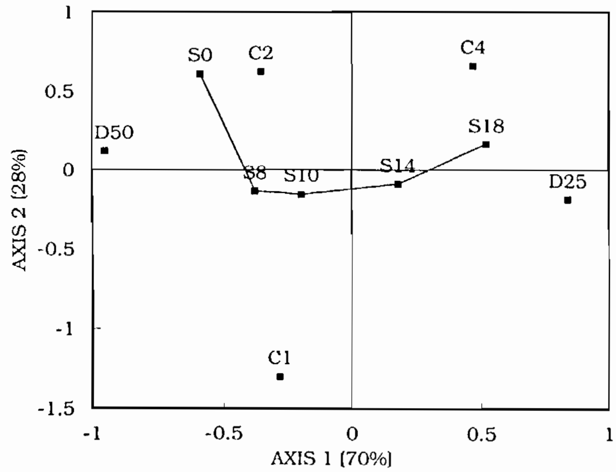

Figure 2. – Correspondence analysis of the growth of oyster in summer: food concentration × oyster density, with a flow rate FR3 ($3 \ m^3/h$). The controlled parameters were projected as illustrative variables.

Notations for *figs.* 2-5: S *i*: number of oysters in size class *i*. FR1, FR3: levels of the flow rate ($1 \ m^3/h$, $3 \ m^3/h$). D25, D50: levels of the density (25,000; 50,000 oysters per tube). NAT, EXC: natural water, heat-exchanged water. C0, C1, C2, C4: levels of phytoplanktonic food concentration.

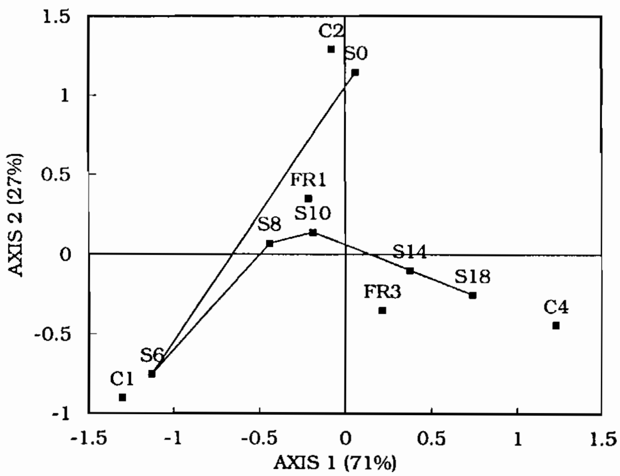

Figure 3. – Correspondence analysis of the growth of oysters in summer: food concentration × flow rate, with a density D25 (see *fig.* 2 for notations).

the flow rate is clearly demonstrated from the projection of the two levels (FR1, FR3) near the centre of the graph. Since the FR3 level was projected near the upper size classes (S14, S18), growth was slightly improved by the use of that flow rate. High concentration of food (C2, C4) was obviously favourable to growth, as was observed previously.

● ***Temperature, concentration, flow rate, size class contingency table*** (*table* 4 *c*). – The influence of temperature was assessed in combination with food concentration and flow rate. These factors, each at two levels (eight combinations) provided the data for the construction of a four-dimensional contingency table. The complete model explaining the whole information contained all the possible 3rd order interactions between the factors. Since the final model contained

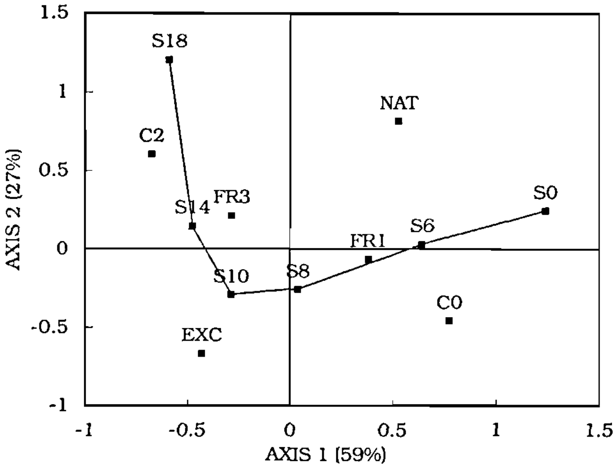

Figure 4. — Coorrespondence analysis of the growth of oysters in summer: food concentration × flow rate × temperature (see *fig.* 2 for notations).

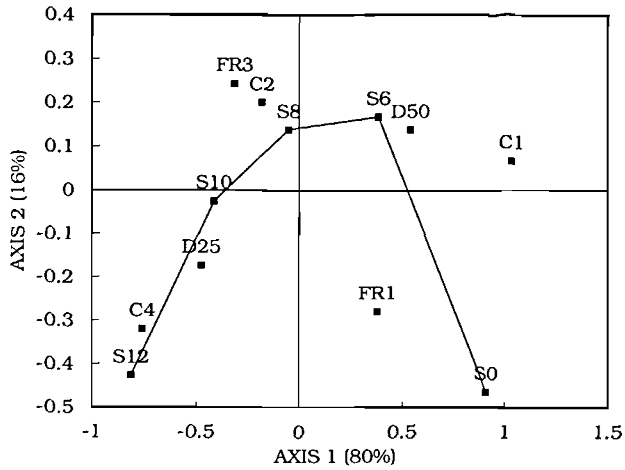

Figure 5. Correspondence analysis of the growth of oysters in winter: flow rate × oyster density × food concentration (see *fig.* 2 for notations).

one significant 3rd order interaction (between temperature, concentration and size class), this third order interaction obscured simpler 2nd order effects. Therefore, the table was divided into sub-matrices according to the levels of temperature or concentration. In cooled water, the only significant effect was that of concentration. In natural sea water (highest temperature), there was a significant interaction between flow rate and concentration. The effect of the temperature could be observed at each food concentration level while the flow rate had an effect only at zero concentration (C0).

Figure 4 illustrates the main effects of the factors on the growth gradient projected onto the first plane (axes 1 and 2, representing 86% of the variance). Not all the interactions suggested by the previous analysis were seen, but a non-linearity of the growth gradient was evident. This non-linearity could possibly be related to complex influences of the factors and to the correlation between growth gradient and food concentration. The segment linking the two levels of temperature was more or less perpendicular to the growth gradient and to the segments formed by the levels of the other factors, suggesting that no obvious relation existed between this factor and the growth gradient.

In addition to the previous analyses, the influence of the food injection frequency was tested for two experiments in which other parameters were kept constant (summer 1986, *table* 1). A sheer χ^2 test was used in order to compare the size distributions at the end of each experiment. It showed that injection frequency had a clearly significant effect ($\chi^2 = 9.3$, 3 d.f.) with discontinuous feeding enhancing oyster growth in these experiments.

Winter

The effects of flow rate, concentration and density in heated water in winter, analysed from the results of 12 experiments, yielded a four-dimensional contingency table. Hierarchization of the models resulted in loss of all but the concentration/flow rate/size class interaction. The effect of oyster density was independent of other parameters, but the flow-rate effect could not be ignored because of the previously found interaction. Data were then analysed by constructing sub-tables for each flow-rate value. At constant flow rate, effect of concentration was then shown to be significant.

By separating the low and high food concentration, it was found that the flow rate had a different effect when the concentration was low (C1) or high (C4). For instance high flow rate enhanced growth at low food concentrations.

The correspondence analysis (*fig.* 5) yielded less information. Even though the complex interactions previously found could not be assessed with the projections of the factor levels on the first plane (explaining 96% of the variance), the effects could be hierarchized in the following order: food concentration, density, flow rate.

Economic analysis

In this paper oyster growth has been used to define the most useful set of parameter values, associated with food injection frequency, temperature, food concentration, oyster density and flow rate, according to the season (*table* 5). In winter, food concentration, C2, flow rate, FR1, and heater water were the most useful combination and resulted in a mean growth from 0.01 to 0.51 g for 100 days. In summer, food

Table 5. — Strategies of rearing defined after the growth analyses.

Season	Quality of water	Density	Flow rate	Injected flow rate and concentration	Frequency
Winter	Exchanged heat water (10°C)	25,000/tube 12.7 ind/cm^2	1 m^3/h/tube 0.67 ml/min/ind.	150 l/h/tube 0.5 10^6 cell/ml	discontinuous 14 h/24 h
Summer	Natural water (20°C)	25,000/tube 12.7 ind/cm^2	3 m^3/h/tube 2 ml/min/ind.	150 l/h/tube 0.5 10^6 cell/ml	discontinuous 14 h/24 h

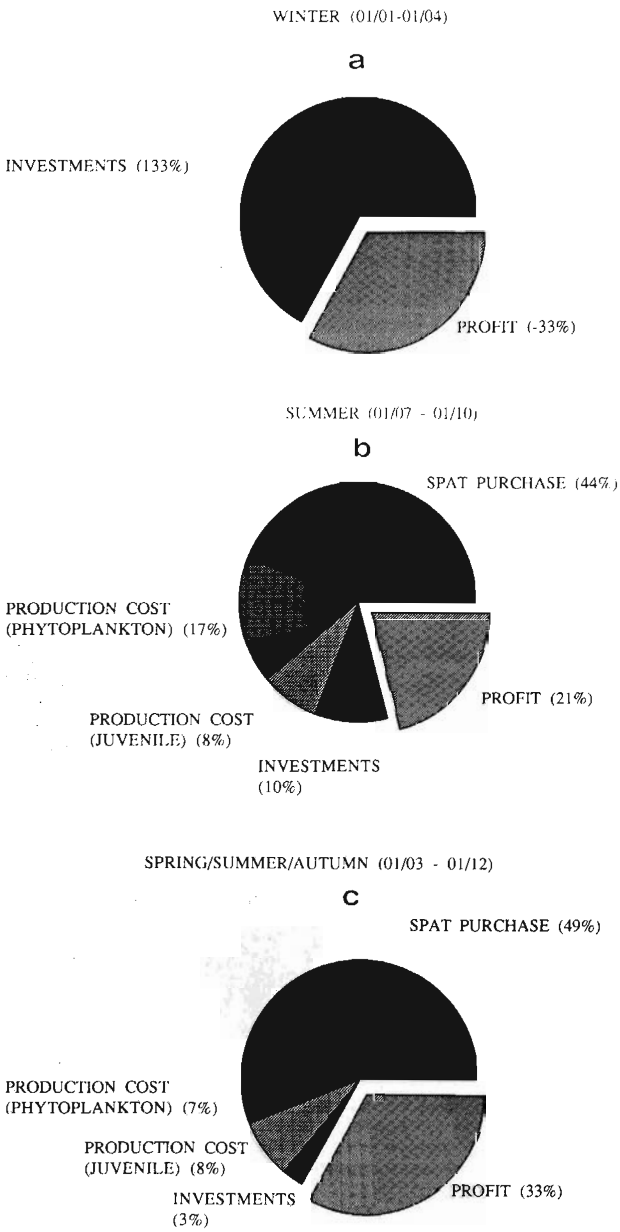

Figure 6. — Computations of the profits and different costs due to the purchase of oysters, expense for the phytoplanktonic food, reimbursement of the investment, wages for personnel and other direct costs, for 10^6 juvenile oysters per season for different seasons. The economic efficiency was negative during winter (*a*) and satisfying in summer (*b*). The most efficient strategy was used in spring, summer and autumn (*c*).

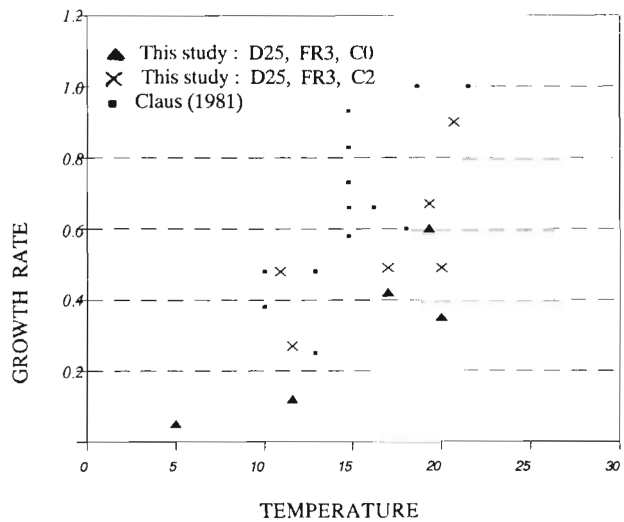

Figure 7. — Instantaneous growth rate for 30 days (G30) for shell length of juvenile oysters as a function of temperature. $G30 = 30/t \ln(Lf/L0)$, where t is the time of the experiment (day), L0 and Lf, the initial and final weights (g).

concentration, C2, flow rate, FR3, and natural sea water were the most useful. The mean weight reached after 60 days was 2.2 g. A preliminary economic assessment according to different rearing strategies was based on the previous information. The cost of producing 10^6 juvenile oysters per season (3 months) was computed for the different seasons. The profits from the sale of oysters at the end of the rearing period and the various costs (e.g. purchase of oysters, producing phytoplankton, reimbursement of investment, wages and other direct costs) were calculated and compared. *Figure* 6 shows the components of the whole budget. The economic efficiency was negative in winter, mainly because of the use of heated water and the low growth of the oysters. During summer, the system was not very efficient because of the low amount of oysters yielded during that season compared with the production over one year. Interestingly, the use of the system in spring, summer and autumn was the most efficient strategy, with 33% of the budget related to the profit. Owing to the fact that the system was used continuously, the reimbursement and the food cost contribution tended to decrease from 27% in the summer strategy to 10%. In this case, the cost of juveniles represented almost 50% of the budget.

Table 6. – Calculation of the daily available phytoplanktonic food according to different levels of food concentration and flow rate compared with other studies. Results are expressed in number of phytoplanktonic cells per ml (cell/ml), per day (cell/d), or mass of cells per day and per mass unit of oyster live weight (mg/d/g live weight) computed for size S2.

Units	Levels C2, FR1	Levels C4, FR1	Levels C4, FR3	Matthiessen and Toner (1966)	Tenore and Dunstan (1973)	Spencer (1988)	Urban *et al.* (1983)	Wang *et al.* (1990)
10^5 cell/ml	1.5	3	1		2			
10^8 cell/day	2.5	5	1.7	11				
mg/d/g	0.6	1.2	3.6			8	4-15	35

DISCUSSION

The results of multidimensional analysis (contingency table and correspondence analysis) may be compared to those obtained in a previous study on the growth of *Ruditapes philippinarum* (Baud and Bacher, 1990). One difference between the two species is related to the influence of the food injection frequency which was not as important for the clams. This influence was already mentioned by Langton and Gabbott (1974), and Langton and McKay (1976) who have shown that discontinuous feeding (alternatively 6 h feeding, 6 h at rest) is favourable to the growth of the juvenile oysters. In our studies, the flow rate had a lesser effect on oysters than on clams.

The analysis yielded a classification of the controlled parameters according to their influence on the growth of oysters. Temperature was responsible for the greatest differences in growth of the juvenile oysters. This result is supported by the data obtained by Claus (1981) from a bibliographic review. Instantaneous growth factor G30 (Ricker, 1968) was computed for 30 individuals held at concentrations C0, C2, density D25 and flow rate FR3. These values were compared with those in Claus (1981) (*figure* 7). The results showed the strong influence of temperature on juvenile oysters, growth. Therefore, obtaining satisfactory growth performance required the use of heated water in winter.

Besides temperature, food concentration and oyster density were important. Depending on the season, the most important factor appeared to be either the food concentration (winter) or the oyster density (summer). There was no detectable relationship between growth and food ration expressed as the ratio between the food concentration and the flow rate. This result does not correspond with that of Spencer *et al.* (1986), who found a large effect of flow rate on *Crassostrea gigas* growth in upwelling systems supplied with either natural waters or fertilized waters. In that case, however, the flow rate, instead of being kept constant, was adjusted weekly to the oyster biomass during the six-week duration of the experiments. Spencer (1988) also found an optimal food ration (expressed in mg/h/g live weight) depending on the oyster initial weight. This author added that the influence of the ration or the flow rate may be masked because of the interaction between food concentration and flow rate, as was also observed in our experiments. Other authors emphasize that food adjustment to the biomass may result in a greater efficiency of the upwelling system (Manzi *et al.*, 1984) since the flow rate (Rodhouse and O'Kelly, 1981) and the ration (Tenore and Dunstan, 1973; Urban *et al.*, 1983) depend on the biomass. The mean values derived from these previous studies are in good agreement with optimal values resulting from our analysis (*table* 6). For *Crassostrea virginica*, Wang *et al.* (1990) measured a mean removal of particles of 35 mg/d/g of oyster, which is higher than the available food in our study (lying between 0.6 and 3.6 mg/d/g). This was explained by considering that the oysters rapidly yield pseudofaeces as the food concentration increases.

The flow rate acted on the growth with natural sea water (no phytoplankton injected). Injection of phytoplankton produced a positive effect of low flow rate in winter and a slight effect of high flow rate in

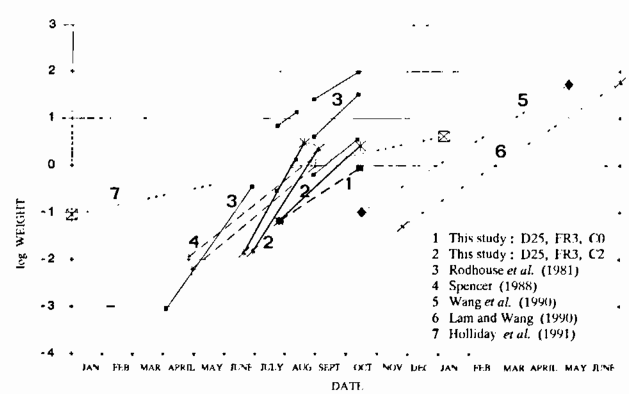

Figure 8. – Comparison of the growth performance with previous results from upwelling systems used for intensive rearing. The graph gives the initial and the final live weight (in a logarithmic scale), the season and the duration of the experimental survey. The slopes of the curves illustrate the efficiency of each system. It may be seen that our results are satisfactory when phytoplanktonic food is injected (concentration C2).

summer. Because of interactions between the parameters, also found by Spencer *et al.* (1986), the meaning of such influences is difficult to assess. Lam and Wang (1990) showed that there was an influence of the flow rate on *Crassostrea virginica* growth when a shrimp pond effluent was used as a food source. Initial size of their oysters (3.6 g) was far higher than in our study. The temperature also lay above 22°C, which is the upper range of ours in summer. These differences apart, the author emphasized the influence of dissolved oxygen concentration on the growth. Their measurements showed that this concentration was related with the flow rate. Besides, the relationship between the flow rate and the temperature given by Rodhouse and O'Kelly (1981) is in good agreement with our results concerning the optimal flow rate in summer and winter when it is applied to the parameters of our study.

It is thus very important to define carefully the parameter level since too large a food ration may not be optimal for the growth and may increase mortality (Spencer, 1988). Urban *et al.* (1983) also found that growth efficiency is almost constant when the food ration reaches a threshold value. In contrast, growth efficiency is dramatically lower when the ration lies below this level. Our results have shown that neither the highest concentration (C4) nor the highest flow rate yielded significantly better growth performance than the intermediate levels of these parameters. The lowest concentration (C0) resulted in only minor increases of weight. The proposed values for the parameters are intermediate ones (0.5 10^9 phytoplankton cells/litre, flow rate 1 litre/d/oyster in winter; same food concentration and flow rate 3 litre/d/oyster in summer), and should produce satisfactory growth performance and cost of phytoplankton production. The density D25 (25,000 individuals per tube) was proposed for each season in accordance with information on mortality rate during the experiments (unpublished data), which was mainly influenced by the density. At a density of 25,000 individuals, the mortality rate ranged from 11.8 to 13% depending on the temperature. This was similar to the mean rates given by Spencer *et al.* (1986) which were shown to be independent of the flow rate and slightly dependent on the use of fertilizer to enrich the water. Converted to number of individuals per unit area, this figure (120,000 per m^2) may be compared to the density used in a natural-waters system (e.g. Holliday *et al.*, 1991) where growth performance is the same order of magnitude with a density lower by a factor 10.

The economic system viability was studied to take into account the different costs of the purchase of phytoplankton and oysters, the use of a heat exchanger and investments (Baud, 1991). Profits were computed under different hypotheses: production only in winter or in summer, or production in spring, summer and autumn. It was clearly shown that the cost of the heat exchanger could not be compensated by production if the system were to be used only in winter. Profit was almost optimal when the system was used throughout the year, except in winter. This strategy should be selected since it shortens the rearing cycle of the oysters. This preliminary result, which extrapolated information from technical and biological results, should precede a complete economic study. Although our system was experimental, the development of commercial production units based on the same features would seem to be viable since our intensive rearing system was shown to yield oysters within 60 days at the size suitable for ongrowing in the field upto the market weight (35 g). Another argument for developing the transfer of our results is connected to the low cost of production of phytoplankton that can reach up to 85% of the whole cost in a hatchery or a nursery (Bolton, 1982). In our study, the cost of producing phytoplankton was generally lower than other figures given in the literature (Loring, in De Pauw (1981); Walne, 1976; De Pauw, 1981; Spencer *et al.*, 1986). The growth performances were also comparable to those given by Rodhouse *et al.* (1981) and Spencer (1988) who used upwelling systems for intensive rearing in spring or summer (*fig.* 8). They were also equivalent to the figures given by Wang *et al.* (1990) and Lam and Wang (1990) when using the effluent of a shrimp pond as an intensive source of food. The growth performances computed from our data were greater than the ones derived from the literature, strengthening the previous conclusion on the rearing system efficiency.

Acknowledgements

The authors thank G. Cowie for his help and suggestions about the manuscript.

REFERENCES

Baud J. P., C. Bacher, 1990. Use of saline ground water for intensive rearing of *Ruditapes phillippinarum* juveniles in a nursery system. *Aquaculture*, **88**, 157-178.

Baud J. P., 1991. Utilisation d'eaux salées souterraines en baie de Bourgneuf pour le prégrossissement intensif de mollusques filtreurs en nourricerie. Diplôme de Recherche Universitaire, Univ. Nantes, 80 p.

Bayes J. C., 1981. Forces upwelling systems for oysters and clams using impounded water systems. *In:* Nursery

Culturing of Bivalve Molluscs, C. Claus, N. de Pauw, E. Jaspers ed., Spec. Publ. Eur. Maricult. Soc., Bredene, 7, 73-83.

Bolton E. T., 1982. Intensive marine bivalve cultivation in a controlled recirculating seawater prototype system. Univ. Delaware Sea Grant Publication, DEL-SG-07-82, 165 p.

Claus C., 1981. Trends in nursery rearing of bivalve molluscs. *In:* Nursery Culturing of Bivalve Molluscs, C. Claus, N. de Pauw, E. Jaspers ed., Spec. Publ. Eur. Maricult. Soc., Bredene, 7, 1-33.

Claus C., H. Maeckelberghe, N. de Pauw, 1983. Onshore nursery rearing of bivalve molluscs in Belgium. *Aquacult. Eng.*, **2**, 13-16.

De Pauw N., 1981. Use and production of microalgae as food for nursery bivalves. *In:* Nursery Culturing of Bivalve Molluscs, C. Claus, N. de Pauw, E. Jaspers ed., Spec. Publ. Eur. Maricult. Soc., Bredene, 7, 35-69.

Freeman K. R., L. M. Dickie, 1979. Growth and mortality of the blue mussel in relation to environmental indexing. *J. Fish. Res. Board Can.*, **36**, 1238-1249.

Holliday J. E., G. B. Maguite, J. A. Nell, 1991. Optimum stocking density for nursery culture of Sydney rock oysters (*Saccostrea commercialis*). *Aquaculture*, **96**, 7-16.

Lam C. Y., Wang J. K., 1990. The effects of feed water flow rate on the growth of aquacultured *Crassostrea virginica* in Hawaï. *Aquacult. Eng.*, **9**, 411-427.

Langton R. W., P. A. Gabbott, 1974. The tidal rhythm of extracellular digestion and the response to feeding in *Ostrea edulis*. *Mar. Biol.*, **24**, 181-187.

Langton R. W., G. U. McKay, 1976. Growth of *Crassostrea gigas* (Thunberg) spat under different feeding regimes in a hatchery. *Aquaculture*, **7**, 225-233.

Lucas A., A. Gérard, 1981. Space requirement and energy cost in some types of bivalve nurseries. *In:* Nursery Culturing of Bivalve Molluscs, C. Claus, N. de Pauw, E. Jaspers ed., Spec. Publ. Eur. Maricult. Soc., Bredene, 7, 151-170.

Manzi J. J., N. H. Hadley, C. Battey, R. Haggerty, R. Hamilton, M. Carter, 1984. Culture of the northern hard clam, *Mercenaria mercenaria* (Linné) in a commercial-scale upflow, nursery system. *J. Shellfish Res.*, **4**, 119-124.

Matthiessen G. C., R. C. Toner, 1966. Possible methods of improving the shellfish industry of Martha's Vineyard Duke's county, Massachusetts. The Marine Foundation Inc., 1-138.

Ricker W. E., 1968. Methods for assessment of fish production in fresh waters. IBP Handbook n° 3, Blackwell Scientific Publications, Oxford, 348 p.

Rodhouse P. G., M. O'Kelly, 1981. Flow requirements of the oysters *Ostrea edulis* L. and *Crassostrea gigas* Thunberg in an upwelling column system of culture. *Aquaculture*, **22**, 1-10.

Rodhouse P. G., B. Ottway, G. M. Burnell, 1981. Bivalve production and food chain efficiency in an experimental nursery system. *J. mar. biol. Ass. U.K.*, **61**, 243-256.

Rodhouse P. G., C. Roden, M. E. Somerville-Jacklin, 1983. Nutritional value of micro-algal mass cultures to the oyster, *Ostrea edulis* L. *Aquaculture*, **32**, 11-18.

Saint-Félix C., J. P. Baud, P. Hommebon, 1984. Diversification de la production conchylicole. Élevage de la palourde japonaise en baie de Bourgneuf. *Science et Pêche*, **344-345-346**, 2-22.

Sokal R. R., F. J. Rohlf, 1981. Biometry. The principles and Practice of Statistics in Biological Research. Freeman, San Francisco, 859 p.

Spencer B. E., M. J. Akester, I. Mayer, 1986. Growth and survival of seed oysters in outdoor pumped upwelling systems supplied with fertilized sea water. *Aquaculture*, **55**, 173-189.

Spencer B. E., 1988. Growth and filtration of juvenile oysters in experimental outdoor pumped upwelling systems, *Aquaculture*, **75**, 139-158.

Tenore K. R., W. M. Dunstan, 1973. Comparison of feeding and biodeposition of three bivalves at different food levels. *Mar. Biol.*, **21**, 190-195.

Urban E. R., G. D. Pruder Jr., C. J. Langdon, 1983. Effect of ration on growth and growth efficiency of juveniles of *Crassostrea virginica* (Gmelin) *J. Shellfish Res.*, **3**, 51-57.

Walne P. R., 1976. Factors affecting the relation between feeding and growth in bivalves. *In:* Harvesting polluting waters, O. Devik Ed., Plenum Press, New York, 169-176.

Wang J. K., C. Y. Lam, G. S. Jakob, 1990. Preliminary investigation of an oyster-shrimp joint production system. Transactions of the ASAE, Am. Soc. Agric. Eng., **33**, 975-980.