
Ecophysiological model of growth and reproduction of the black pearl oyster, *Pinctada margaritifera*: potential applications for pearl farming in French Polynesia

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Abstract:

A model of bioenergetics of the black pearl oyster (*Pinctada margaritifera*) was built to simulate growth, reproduction and spawning in suspended culture at field sites in Takapoto lagoon (French Polynesia). This model was based on allometric scaling of physiological functions and scope for growth (SFG) calculations. The input functions were clearance rate (CR, l day⁻¹), retention efficiency (RE, %) for each kind of particle encountered in suspended matter, pseudofaeces and faeces productions (PF and F, mg C day⁻¹), excretion and respiration rate (U and R, mg C day⁻¹). The assimilated carbon (i.e., SFG, mg C day⁻¹) was partitioned to the three internal state variables (somatic tissue, shell and gonad) according to the asymptotic increase of the reproductive effort (ER, %) with the age. Given organic and mineral particulate matter in suspension in lagoon water (POM and PIM, mg L⁻¹) and assuming that the taxonomic composition of POM was fairly constant throughout the year, the model predicted annual evolution of total tissue weight (W_{Tissue} , g dry weight), shell weight (W_{Shell} , g DW) and gonad weight (W_{Gonad} , g DW) of pearl oysters at various ages. Data on tissue and shell growth, but also on gonad development of cultivated pearl oysters, acquired in 1997–1998 in Takapoto lagoon, were used to validate the model outputs. Results of the simulations indicated that the *P. margaritifera* growth model provided realistic growth trajectories for shell, somatic tissue and gonad, for pearl oysters aged from 1 to 4 years.

For scientists, this validated model is very useful to understand more extensively feeding processes and reproduction features of *P. margaritifera* in Polynesian lagoons. It provides also valuable information for pearl farmers and for management of cultured populations, especially concerning the time to produce a pearl, spat collection, density in system culture, choice of farming site and carrying capacity of the whole lagoon. In this respect, the model demonstrates that local overdensity must be avoided especially when water current is low (<1 cm s⁻¹) and that global consumption of the cultivated pearl oyster stocks plays a insignificant role in comparison with the consumption of all the natural bivalves occurring in the lagoon.

Nevertheless, this first growth model developed for *P. margaritifera* was only validated for a Takapoto atoll and presents several limitations concerning especially the temperature effect and the range of food concentration. Consequently, some improvements will be necessary to apply this work to other pearl farming sites in French Polynesia.

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Nevertheless, this first growth model developed for *P. margaritifera* was only validated on Takapoto atoll and presents several limitations concerning especially the temperature effect and the range of food concentration. Consequently, some improvements would be necessary to generalise this work on other pearl farming sites of French Polynesia.

Key words : Tropical lagoon - Suspension feeding - Carrying capacity - Scope for growth - Food depletion - Pearl farming.

1. INTRODUCTION

In French Polynesia, black pearl aquaculture has played an increasing role since 1980. Today, production is approaching six metric tons of pearls (i.e. 160 millions of US dollars). After the large scale mortality which decimated cultivated pearl oysters, *Pinctada margaritifera*, in several atolls in 1985, French Polynesian authorities decided to set up a general research programme on the pearl oyster (PGRN). The main objective of PGRN was to assess the carrying capacity of a lagoon for pearl oyster farming, by taking Takapoto lagoon (Tuamotu archipelago, French Polynesia) as a study site.

Although the black pearl oyster was naturally one of the most abundant bivalves in the benthic fauna of Polynesian atoll lagoons, the development of pearl culture moved these benthic bivalves progressively into the pelagic environment, since farmers suspend pearl oysters on long-lines in mid-water. Thus, understanding the relationships between cultivated pearl oyster and pelagic food web is essential to study the carrying capacity of a given lagoon. To reach this aim, a first step is to build a deterministic ecophysiological model for cultivated pearl oysters in lagoon environment, explaining individual growth over several years, as a function of food availability and composition. Such a model is very useful since it provides validated bivalve requirements which are necessary in carrying capacity calculations.

Physiological models explaining the growth of cultivated molluscs in their environment in relation to food supplies have already been achieved on numerous bivalves species (e.g. Bacher et al., 1991; Powell et al., 1992; Schneider, 1992; Raillard et al., 1993; Van Haren and Kooijman, 1993; Barillé et al., 1997; Grant and Bacher, 1998; Scholten and Smaal, 1998). Generally, these models are based on the Scope for Growth concept and use a complete sequence of steps in nutrition and resources allocation.

This approach is applied here for the first time on *P. margaritifera*. In this respect, all the feeding processes previously studied in Polynesia (Robert et al., 1998; Pouvreau, 1999; Pouvreau et al., 1999a,b) were integrated in the present model. Furthermore, since adult pearl oysters are able to spawn several times a year (Thielley, 1993; Buestel et al., 1995; Pouvreau, 1999), reproductive effort was also incorporated in this growth model.

First, this study presents a global dynamic carbon model explaining individual growth and reproduction of *P. margaritifera* in a lagoon environment (Takapoto lagoon) over several years, as a function of food availability and composition. In order to validate the model, simulations of growth and reproduction were systematically tested against measurements.

Second, applications of the validated model for pearl farming in Polynesia are also presented. Information of potential interest for pearl farmers is given, especially concerning spat collection and rate of nacreous deposition. Carrying capacity of Polynesian pearl farming sites is also approached : (1) at local scale (i.e. the system culture), we tested potential effect of density (POM-depletion) on the growth of pearl oyster ; (2) at a global scale (i.e. the whole lagoon), we computed, on the basis of model calculations, the clearance time of the cultivated and natural bivalve populations (Dame and Prins, 1998).

2. MATERIALS AND METHODS

2.1. Model design and states variables

Several simplifications were made to streamline the model for which a conceptual design is described on Fig. 1. The model uses a balanced carbon budget approach to simulate separately growth in shell and growth in total soft tissue including gonad. This model is based on (1) the widely applied (reviewed in Bayne, 1998; Hawkins et al., 1998a) Scope for Growth (SFG) concept (Bayne, 1976); (2) allometric relations between physiological functions and dry tissue weight (W_{Tissue}). The SFG concept, already used in many models (e.g. Bacher et al., 1991; Schneider, 1992; Raillard et al. 1993; Barillé et al., 1997), assumes that energy or matter gained by food acquisition is equal to the energy or matter lost for maintenance, growth and reproduction. In this work, SFG is calculated as the difference between carbon acquired by feeding processes and lost by respiration (supposedly a measure of maintenance) and excretion for one individual, as follows :

$$\text{SFG} = \text{FR} - (\text{PF} + \text{F} + \text{R} + \text{U}), \text{ where}$$

SFG = scope for growth ($\text{mg C d}^{-1} \text{ ind}^{-1}$)
 FR = consumption (retained organic matter, $\text{mg C d}^{-1} \text{ ind}^{-1}$)
 PF, F = pseudofaeces and faeces production ($\text{mg C d}^{-1} \text{ ind}^{-1}$)
 R = respiration ($\text{mg O}_2 \text{ d}^{-1}$, converted in $\text{mg C d}^{-1} \text{ ind}^{-1}$)
 U = urea and amino acid excretion (converted in $\text{mg C d}^{-1} \text{ ind}^{-1}$)

If $\text{SFG} > 0$, carbon is partitioned into shell, soma and gonad (Resources allocation). If more carbon is required for maintenance (Respiration) than available from food (Assimilation), SFG becomes negative and carbon is mobilised firstly from gonad (utilisation of energy reserves). Therefore, states variables of the model were : (1) shell, (2) somatic tissue and (3) gonadal tissue. Shell represents the organic matrix. Somatic tissue includes gill, mantle, muscles and digestive gland (+viscera). Gonadal tissue includes developing and mature gametes.

2.2. Environmental factors

Temperature in this tropical environment, and especially in Takapoto lagoon, does not present great seasonal variations (from 26 to 30°C during "normal year", i.e. without El Niño event), so that temperature effect on pearl

oyster physiology has not yet been demonstrated (Robert et al., 1998; Pouvreau et al., 1999b) and, consequently, was not included in the present model (this first limitation is analysed in discussion part). Alternatively, forcing functions in the model were pelagic food concentration and composition in Takapoto lagoon water. Potential food for pearl oysters was expressed as total particulate matter (TPM, mg l^{-1}), and consisted of particulate inorganic matter (PIM, mg l^{-1}) and particulate organic matter (POM, mg l^{-1}). PIM and POM were monitored once a week from March 1997 to March 1998, always at the same hour (14:00, Fig. 2). This sampling hour generally corresponds to the daily maximum of seston concentration whereas minimum values were generally reached around 6:00 (Charpy, 1996; Buestel and Pouvreau, 2000). In order to take into account these night and day variations and avoid over-estimation of the daily mean, PIM and POM measured at 14:00 were corrected by 0.7. This value was obtained previously on the basis of several night and day measurements. Afterwards, POM was converted into carbon (POC, mgC l^{-1}) by using a conversion factor (POM/POC=2, Mann, 1979 for bivalve flesh; Parsons et al., 1961 for algae composition; Quemeneur and Marty, 1992 and Galois et al., 1996 for total suspended matter).

In *P. margaritifera*, retention efficiency is nearly null for 1 μm particles and becomes maximal for $> 5 \mu\text{m}$ particles (Pouvreau et al., 1999a; Yukihiro et al., 1999). Therefore, a part of POM cannot be directly retained on *P. margaritifera* gill. In this respect, POM in Polynesian lagoon need to be reviewed (Table 1) so that our model uses POM according to its size as input for consumption. Suspended matter is generally composed of a living (bacteria, phytoplankton, protozoan and zooplankton) and detritus material. In lagoonal waters, free bacteria were the smallest living particles (0.4 μm). A part of them are fixed on larger particles but scarce data (Torreton and Dufour, 1996) are not sufficient to establish an order of magnitude. Phytoplankton is divided into two groups: (1) picophytoplankton ($< 2 \mu\text{m}$) which includes prokaryotic cyanobacteria (*Synechococcus* sp. and *Prochlorococcus* sp.) and eukaryotic algae (picoeukaryotes, Charpy and Blanchot, 1998), and (2) phytoplankton, which includes nano and micro-algae. Detritus is also divided into two groups : (1) pico-detritus ($< 2 \mu\text{m}$), and (2) larger detritus called micro-detritus. Protozoa are mainly heterotrophic nano- and micro-plankton and include ciliates, heterotrophic flagellates and dinoflagellates, foraminifers and radiolarians. Zooplankton consists mainly of micro-plankton and includes especially appendiculates and larvae of various species (naupliar copepods and bivalves, crustaceans and polychaetes larvae). Particulate matter $> 200 \mu\text{m}$ (mesoplankton) are not taken into consideration in this work because of their probable low representation in the diet of the bivalves. The contribution of each of these previous components to the total particulate organic matter was assumed to be

fairly constant (trophic web in equilibrium, suggested by the low standard deviation in Table 1) and was estimated on the basis of the review described in Table 1.

2.3. Physiological mechanisms formulations

Each term presented in the SFG equation (see previous paragraph) was computed as a function of the forcing variables (exogenous factors) or/and the dry tissue weight, W_{Tissue} (endogenous factor). The physiological functions were studied extensively in previous works (Robert et al., 1998; Pouvreau, 1999; Pouvreau et al., 1999a,b) and the useful equations are summarised in Table 2. In the following paragraphs, we remind only what it is necessary to understand the model conceptualisation.

2.3.1. Food acquisition

Pearl oysters obtain their food by processing large amount of waters thanks to a high clearance capacity (Pouvreau et al., 1998 and 1999a for Polynesian water, Yukihiro et al., 1998a for Australian water; and Hawkins et al., 1998b for Malaysian water). Using biodeposition method (Iglesias et al., 1998), the clearance rate CR (l d^{-1}) was estimated *in situ* on 196 oysters of various sizes under several natural seston load conditions, and varied according to the PIM and POM concentration as an allometric function of dry tissue weight W_{Tissue} (g), as follows (Pouvreau et al., 1999b):

$$\text{CR} = 647.04 (\pm 60.48 \text{ SE}) \bullet \text{PIM}^{-0.42 (\pm 0.05 \text{ SE})} \bullet \text{POM}^{0.96 (\pm 0.11 \text{ SE})} \bullet W_{\text{Tissue}}^{0.61 (\pm 0.04 \text{ SE})}; (n=196, R^2=0.75, P<0.05)$$

The well-developed gill of pearl oysters can efficiently retain particles $> 2 \mu\text{m}$ (Pouvreau et al., 1999a ; Yukihiro et al., 1999). So each of the previous compartments in seston is retained differently according to its approximate mean size S_z (μm , equivalent spherical diameter) and according to the retention spectrum RE (%) given by Pouvreau et al. (1999a), which exhibits the following logistic pattern :

$$\text{RE} = 100/(1+52.16 \bullet 0.137^{S_z}); (n=16, R^2 = 0.86, P<0.05)$$

Mean size of bacteria, cyanobacteria, pico-detritus, picoeukaryotes was assumed to be approximately equal in mean to 0.4, 0.8, 1 and 1.2 μm , respectively, giving a retention efficiency equal to 2, 6, 12 and 15 %, respectively, for these pico-particles ($< 2 \mu\text{m}$). Micro-particles ($> 2 \mu\text{m}$) were supposed to be retained in mean at 60 %. Then, the amount of retained organic matter, FR_{POM} ($\text{mg C d}^{-1} \text{ ind}^{-1}$) was computed as follows :

$$\text{FR}_{\text{POM}} = \text{CR} \bullet [0.02 \text{ POC}_{\text{bacteria}} + 0.06 \text{ POC}_{\text{cyanobacteria}} + 0.12 \text{ POC}_{\text{picodetritus}} + 0.15 \text{ POC}_{\text{picoeukaryotes}} + 0.6 \text{ POC}_{\text{microparticules}}]$$

2.3.2. Biodeposition

Prior to ingestion, particles with low organic content are generally rejected in pseudofaeces. In *P. margaritifera*, the quantity of organic matter lost in pseudofaeces (PF_{POM} , mg C d⁻¹ ind⁻¹) was measured *in situ* (Takapoto lagoon) and varied according to POM, PIM and W_{Tissue} , as follows (Pouvreau et al., 1999b):

$$PF_{POM} = 32.16 (\pm 2.16 \text{ SE}) \bullet POM \bullet [PIM - 0.18 (\pm 0.02 \text{ SE})] \bullet W_{Tissue}; (n=196, R^2=0.69, P<0.05)$$

For $PIM < 0.18 \text{ mg l}^{-1}$, there is no pseudofaeces production. This minimum PIM-concentration is called the pseudofaeces production threshold.

The remaining organic material ($FR_{POM} - PF_{POM}$) is ingested. A great part of the ingested organic matter is absorbed during intestinal transit. The non-absorbed organic material is ejected in faeces. Mineral matter is assumed to be not at all absorbed. In *P. margaritifera*, the organic faeces production (F_{POM} , mg C d⁻¹ ind⁻¹) was measured *in situ* for various seston load and composition and followed the equation (Pouvreau et al., 1999b):

$$F_{POM} = 480.00 \bullet W^{0.49 (\pm 0.72 \text{ SE})} \bullet (1 - e^{-0.66 (\pm 0.06 \text{ SE}) \cdot TPM}); (n=196, R^2=0.66, P<0.05)$$

2.3.3. Oxygen consumption and excretion

Routine oxygen consumption (Bayne, 1976) was monitored *in situ* (Takapoto lagoon) on various sizes of animal and at different seasons (Robert et al., 1998). This routine respiration rate represented in fact the metabolic requirements, i.e. routine metabolism and overheads for growth (soma and shell matrix) and also for reproduction, since a pearl oyster is more or less always in gametogenesis. These authors showed that respiration R (converted in mg C d⁻¹) varied mainly according to W_{Tissue} , as follows (Robert et al., 1998) :

$$R = 7.38 (\pm 1.20 \text{ SE}) \bullet RQ \bullet W_{Tissue}^{0.73 (\pm 0.004 \text{ SE})}; (n=113, R^2=0.76, P<0.05)$$

Knowing the proximal composition of the diet of pearl oysters in Takapoto lagoon (proteins=0.5, carbohydrates=0.25 and lipids=0.25, Buestel and Pouvreau, 2000), it was possible to estimate the respiratory coefficient, RQ, i.e. moles of CO₂ liberated per mole of O₂ consumed (%), according to Gnaiger (1983). RQ was equal to 0.92, falling in the range given by Hawkins and Bayne (1985). Anaerobic metabolism is supposed to be insignificant since oysters are never emersed in the lagoon environment and oxygen is always in over-saturation in Takapoto lagoon (Haumani Gaby, Pers. comm.).

Excretion rate, U (converted in mg C d⁻¹), was measured under laboratory conditions (Méro, 1996; Pouvreau et al., 1998) which simulated those of the lagoon environment. Carbon losses appeared when urea and amino acids

were excreted. Urea and amino acids represented less than 10% of the total ammonia excreted, and increased with dry tissue weight, as follows :

$$U_{\text{amino acids, urea}} = 0.02 (\pm 0.001 \text{ SE}) \bullet W_{\text{Tissue}}^{0.78 (\pm 0.06 \text{ SE})}; (n=36, R^2=0.84, P<0.05)$$

2.3.4. Resources allocation to growth and reproduction

Rules specifying the animal priorities for resources partitioning are not well-known. Different prior assumptions have been made concerning energy allocation between shell growth, tissue growth and reproductive outputs (Ross and Nisbet, 1990; Van Haren and Kooijman, 1993). For this model, we assume the two following rules :

(1) If absorbed carbon exceeds uptake for maintenance (Respiration) and losses in excreted urea and amino acids, the scope for growth (SFG, mgC h^{-1}) is positive and this surplus is partitioned into shell matrix, somatic and gonadal compartments. Dry shell, tissue and gonad weight (W_{shell} , W_{tissue} , and W_{gonad}) are, then, calculated from their respective carbon input and ash ratio (Ash_{Shell} , Ash_{Tissue} and Ash_{Gonad}). Allocation to gonad, i.e. reproductive effort (ER), increases with age (e.g. Bayne and Worrall, 1980; Thompson, 1984; Rodhouse et al., 1984). Considering that ER was approximately equal to 0, 9, 22 and 35 % for pearl oysters of year class 0, 1, 2 and 3, respectively, (experimental data, Pouvreau, 1999), a classical logistic pattern according to the age was proposed here (see Table 2) to model ER. For the present, we make no difference between ER for males and ER for females, since during the 4 first years of life, cultivated pearl oyster are mainly males. The sex inversion causes probably physiological transformation, but we have not enough data to model this aspect. Part of carbon, which is not driven to gonad, i.e. (1-ER), is allocated to soma and shell matrix. Shell growth is proportional to somatic growth with a constant allocation to shell ($Alloc_{\text{Shell}}=0.6$, Pouvreau, 1999) and to soma ($1-Alloc_{\text{shell}}$).

(2) When respiratory requirements and excretory losses exceed available absorbed carbon, SFG becomes negative and carbon is mobilised from gonad tissue, playing a kind of storage role. In fact, storage is virtually non-existent in this tropical bivalve (Buestel et al., 1995). So that, as soon as the food supply is sufficient, gonad development commences. Such an opportunistic strategy reproduction differs from the conservative strategy in many temperate bivalves, for which reserves are accumulated before gametogenesis. Validity of the model (accordance between simulation and observation) will imply that assumptions (1) and (2) are reasonably reliable.

2.3.5. Gametes release

Those (Thielley, 1993; Buestel et al., 1995; Pouvreau, 1999) who have worked on reproduction of this species in Polynesian lagoons have come to the same conclusion : pearl oysters are able to spawn several times and

throughout the year. When food is sufficient for several weeks (i.e. POM x Days), the gonad expands due to gametogenesis. Various stressful exogenous factors (e.g. change in temperature, in salinity, in atmospheric pressure) are supposed to constitute spawning cues. Nevertheless, endogenous factors can also be involved : in this first model, gamete release, which is supposed to be complete and instantaneous, occurs when gonadosomatic ratio exceed a maximal value ($RGS_{max} > 0.29$, Pouvreau, 1999).

2.3.6. Shell and pearl formation

Dry shell weight (W_{Shell}) is used to compute the shell height (H_{Shell} , Dorso-ventral axis, mm) and the shell thickness (T_{Shell} , Hinge line, mm) according to the specific allometric relationships (Table 2 and Pouvreau, 1999). Assuming that nacreous deposition on shell by mantle activity exhibits the same rate as nacreous deposition on the nucleus implanted in gonad diverticula, time of pearl formation, t_{end} , can be calculated from the integral function :

$$T_{Pearl} = \int_{t_0}^{t_{end}} \frac{dT_{Shell}}{dt} dt, \text{ where}$$

T_{pearl} = Thickness of the nacreous layer for a marketable pearl ($T_{pearl} = 1.2$ mm)

t_{end} = Time to obtain a marketable pearl.

2.3.7. Depletion calculation

The filtration activity of dense aggregations of bivalves could locally deplete seston in water (Fréchette et al., 1989) especially if the currents that supply seston are too low to replenish completely the ingested particles. Since (1) *P. margaritifera* exhibits high clearance activity, (2) lagoon currents are generally low and (3) food supply is limited, depletion conditions can occur in culture system according to density and flow velocity (Fig. 3).

The seston concentration POM(x) within a culture of suspended bivalves is determined as a balance between the transport of particles from remote sources (flow velocity, U), the local production of new particles (primary production, PP), and the removal of particles due to feeding of bivalves populations (density.consumption, d.FR_{POM}) or sinking (sinking rate, SR) :

$$\frac{\partial POM}{\partial t} = -U \cdot \frac{\partial POM}{\partial x} + PP - d.CR.POM - SR$$

Two assumptions were made to simplify calculations : (1) the local production and the sinking rate are negligible in comparison with transport ($PP \ll U \cdot \frac{\partial \text{POM}}{\partial x}$ and $SR \ll U \cdot \frac{\partial \text{POM}}{\partial x}$); (2) the system is in steady state ($\frac{\partial \text{POM}}{\partial t} = 0$). With such assumptions, depletion ratio after i long line systems, D_i , i.e. (POM after i long

lines)/(POM entered the system), is equal to :

$$D_i = e^{-\frac{d \cdot CR \cdot i}{U}}, \text{ where}$$

D_i = depletion ratio after i long lines

d = linear density on long lines (ind. m^{-1})

CR = clearance rate of pearl oysters (converted in $m^3 s^{-1}$)

i = number of juxtaposed long lines

U = flow velocity ($m s^{-1}$)

2.4. Simulations and validation

The model was implemented in STELLA software (High Performance Systems, Hannover, NH, USA). List of equations, parameters and variables are presented in Table 2 and Table 3. Model results (predicted values) were compared to data on shell, soma and gonad growth of various age-groups of pearl oysters measured in 1997-1998 (observed values, Pouvreau et al., 2000). This allowed assessment of both the shape of the trajectory of total tissue and shell weight as well as the numerous peak weights observed for gonads.

3. RESULTS

3.1. Model evaluation and validation

The growth of the pearl oysters is presented in Fig. 4 (a, b, c), expressed as total dry tissue weight (W_{Tissue} , g), dry shell weight (W_{Shell} , g) and dry gonad weight (W_{Gonad} , g), and compared with measured data of 1, 2 and 3 year-old pearl oysters cultivated during the 1997-98 sampling period. The agreement between observed and predicted values was fairly good for shell, tissue and gonad ($R^2=0.99$, $R^2=0.98$ and $R^2=0.92$ respectively, Fig. 4 d, e, f). Shell growth was completely explained as well as gonad development. Modelled total tissue growth appeared to closely follow observed tissue growth except during the warmer month (December-March) when the model had a tendency to overestimate somatic growth and during the fresher month (June-September) during which the model showed a slight underestimation. Except for this last feature, the *P. margaritifera* growth model showed in general a fairly good reliability and predicted both growth and reproduction for cultivated pearl oysters from 1 to 4 year-old in Takapoto lagoon.

3.2. Physiological processes

Once the model is validated, assessment of the main physiological processes and their temporal variations were derived from the model (Fig. 5). *In situ* CR mean value varied roughly from 200 to more than 1500 l d⁻¹ for a pearl oyster aged from 1 to 4 years (Fig. 5a). This high clearance activity brought to pearl oyster large amounts of food (Consumption, FR) averaging 20 and 80 mg C d⁻¹ according to the age of pearl oyster (Fig. 5b). High values of FR were encountered in December when POM load and seston composition were favourable, low values in July. A part of consumed matter was lost as pseudofaeces, which occurred all year (Fig. 5c) and varied from roughly 2 to 7 mg C d⁻¹. The highest values of organic PF were encountered when PIM was the highest (e.g. March–April). The other part was lost through faeces production (F) which varied in mean from 10 to more than 30 mg C d⁻¹ according to the age of pearl oyster (Fig. 5d). The amount of ingested matter which was really absorbed (absorption, A_{bR} , Fig. 5e) varied in mean from 15 to 35 mg C d⁻¹. Model calculated also scope for growth (SFG, Fig. 5f) : for most of the time, SFG was positive (from 10 to 30 mg C d⁻¹ with the age), allowing regular growth and gametogenesis.

3.3. Productions

Two productions were analysed further because of their potential interest for pearl oyster farming : (1) gonad development for spat collection, and (2) rate of nacreous deposition on shell and nuclei.

Simulated annual evolution of the gonad was presented on Fig. 4C. In age-group 1, dry gonad weight increased during the year (acquisition of maturity) and a hypothetically spawning occurred in January 1998. In age-group 2, a large increase was observed during the first 6 months. Then, a spawning occurred in October, and again in January. In age-group 3, spawning was simulated in May, and again in October, December and in January. The model predicted no release during winter season. Furthermore during this last season, a decrease in gonad weight is simulated by the model. It appeared from model simulation that spat collection would be better in summer. The intensity (production of gametes, Pr) of each release was calculated by the model (Table 4). Pr was proportional to W_{Tissue} (g), according to linear equation :

$$\text{Pr (g)}=0.086 W_{\text{Tissue}} \text{ (R}^2=0.99, n=7, P<0.001)$$

Gametes released by a 1 year-old pearl oyster seemed to be insignificant, however, a pearl oyster spawns in mean 100-200 mg in its second year, and more than 700 mg in its fourth year.

Shell formation (nacreous deposition and shell height increasing) was also simulated by the model. Fig. 6 shows that nacreous deposition and shell height increment varied according to food annual variations, but also according to the age of pearl oyster. The mean daily nacreous deposition was equal in mean to $7.1 \mu\text{m d}^{-1} \text{ ind}^{-1}$ for a 1 year-old pearl oyster. This value decreased to only $2.5 \mu\text{m d}^{-1} \text{ ind}^{-1}$ for 3 year-old pearl oysters. Since a black pearl must have a nacreous layer of at least 1 mm to be marketable, time to produce a pearl estimated by the model was roughly equal to 16 months in a 3 year-old pearl oyster. This simulated time is in total concordance with observed value (approx. 16-18 months). Since the mean daily nacreous deposition decreased with the age of pearl oyster, time to produce a pearl would be reduced in younger animals : 10 months for a 2 year-old pearl oyster and 6 months for a 1 year-old pearl oyster.

3.4. Food supply and POM depletion

Since concentration of POM is generally low (i.e. never in excess for *P. margaritifera*), a slight decrease would have a great impact on the growth and the reproduction of pearl oysters. With the help of the model, we tested the effect of POM decrease on growth. Fig. 7A shows that the decrease in tissue, gonad and shell weight becomes significant (>20%) if level in POM is 20% lower during one year. For > 30% POM reduction around the bivalve, the decrease in tissue and gonad weight is very important (>50%). Decrease in shell weight is less important since shell is assumed to be not resorbed, when SFG is negative.

Such a POM reduction was also tested, on a 3 year-old pearl oyster, on the time to produce a marketable pearl (t_{end} , in month) and on the number of gametes releases (n_{gametes}) by year (Fig. 7B). Both variables showed a high

dependence to POM decrease. When POM is reduced by 10%, the number of releases becomes equal to 3 y^{-1} and time for pearl formation increases to 22 month (initial values were respectively equal to 4 y^{-1} and 16 months). For $> 20\%$ POM decrease, t_{end} reaches roughly 30 months and increases dramatically afterwards, while n_{gametes} becomes equal to 1 y^{-1} for 20% POM reduction and null thereafter. Thus, a reduction of 20% of POM around the bivalve for protracted periods constitutes a limit which should not be exceeded.

There are several factors which may cause such a POM-reduction. Among these factors, filtration activity of dense aggregations of bivalves is well-known to locally deplete POM, especially when (1) water currents are low, (2) clearance rates of bivalves are high and (3) food supply is limited. Since culture of pearl oyster in lagoon environment generally meet these three conditions, we tested the cross-effect of both density in culture system and flow velocity on food depletion (Fig. 8). The culture system was assumed to be long-lines, and flow direction was set perpendicular to the long lines. In this case, POM depletion is largely insignificant ($< 20\%$) if flow velocity is above 1 cm s^{-1} . Alternatively, for flow velocities $< 0.1 \text{ cm s}^{-1}$, POM depletion becomes high ($> 60\%$). For flow velocity comprised between 0.1 cm s^{-1} and 1 cm s^{-1} , various cases are encountered according to the number of long-lines and the linear density (see Fig. 8). In a lagoon environment, current is often around 1 cm s^{-1} . Consequently, to avoid POM-depletion, linear density must be kept below 20 ind. m^{-1} .

4. DISCUSSION

4.1. Model validation

This growth model has the advantages of integrating all the existing knowledge acquired on *P. margaritifera* physiology in Takapoto atoll or in laboratory experiments close to Polynesian lagoonal conditions. Agreement between simulations and observations tends to demonstrate that (1) the input data concerning food were appropriate ; (2) the main physiological functions governing the bivalve were well-understood, and (3) model parameters estimation errors were presumably low.

Food sources : Firstly, this model demonstrated effectively that POM > 2 μm (micro-algae, protozoan, micro-zooplankton and detritus) in suspension in Takapoto lagoon water was sufficient to explain observed growth rate. In that respect, the role played by picoplankton (< 2 μm , e.g. picoeukaryotes, cyanobacteria, bacteria and picodetritus) in the pearl oyster diet is directly insignificant, but may become indirectly significant if ingested by higher trophic levels (i.e. protozoan and micro-zooplankton, e.g. Le Gall et al., 1997; Dupuy et al., 1999) or incorporated with colloids in large structures (marine snow or aggregates). These assumptions firstly enounced in Pouvreau et al. (1999a) are clearly confirmed in a quantitative way by this model.

Physiological processes : The model supports our knowledge and assumptions on the physiology of *P. margaritifera* in its Polynesian lagoon environment. Clearance activity of *P. margaritifera* appeared effectively to be very high : simulated daily mean calculated over a period of one year was roughly equal to 1500 l d^{-1} for adult oysters. This value is in total agreement with previous laboratory or field observations (Pouvreau et al., 1998; Yukihiro et al., 1998a; Pouvreau et al., 1999a,b) and supports Jørgensen's (1990) assumption that the capacity for water processing in bivalves is an adaptation to the concentration of suspended food. Clearance activity was negatively related to PIM and positively related to POM concentration in the seston range commonly observed in Polynesian lagoon water i.e. TPM comprised between 0.6 and 1.3 mg l^{-1} . It is reasonable to assume that under higher TPM (so higher PIM), the clearance capacity of *P. margaritifera* would decrease. Yukihiro et al. (1998b) have shown that *P. margaritifera* reduces its clearance activity as seston load increases, but these authors fed pearl oysters with an algal diet under laboratory conditions and feeding behaviour in natural habitats may differ. Since various atolls (>80) exist in the Polynesian archipelago, various TPM concentrations may be encountered, and it would be useful to study *in situ* variations of *P. margaritifera* pumping or clearance rate for larger TPM range, in order to apply the growth model in other atoll lagoons.

Losses of organic matter as PF was low in *P. margaritifera* since it represented less than 10% of the particulate carbon retained on gill. Nevertheless, TPM concentrations showed direct effects on pseudofaeces production, so that PF production would be further analysed under a wider range of natural seston load in order to test the ability of pearl oyster to live in more turbid waters as those encountered in lagoon of high island of Polynesia.

4.2. Model uncertainty

Despite the apparent reliability of the growth model, some differences remain between the model and the observed data and may reasonably be explained by several factors which were disregarded.

Food sources : First, the model attempts to incorporate, with different efficiencies, all kind of particles (living cells and detrital matter) which occur in the atoll lagoon mid-waters. Partitioning organic particles in various compartments according to their size and their trophic position was twofold : (1) pearl oysters differentially retain particles according to their size, so that POM cannot be totally incorporated as food for this bivalve; and (2) linking pearl oyster growth sub-model with trophic web model would be easier in further work.

Although a wide review has been made to ensure an accurate estimation of the mean POM taxonomic composition, in reality, suspended particles are much more complex since : (1) aggregates building was not taken into account and (2) food web was supposed to be always in equilibrium.

Less is known about aggregates especially in lagoon environment, but these particles are generally embedded in mucus to constitute large and fragile structure called "marine snow" (e.g. Marshall, 1968; Coles and Strathmann, 1973). Since the size of marine snow is $> 1 \mu\text{m}$, it would be efficiently retained on pearl oyster gills. However, these structures are fragile, so it is difficult to make assumptions. Further field experiments should focus on aggregates, their role in the pearl oyster diet and in the trophic web.

The second hypothesis, underlying the model inputs, was that the food web was in equilibrium, so that contribution of each compartment to the total POM-biomass was roughly constant all year round. Although this assumption was also the basis of the food web model proposed also for Takapoto lagoon by Niquil et al. (1998) and although seasonal variations are weak in this environment, further field experiments with an appropriately large sampling scheme should be conducted.

Physiological processes : Utilisation of food sources and translation to bivalve tissue involves several steps which were successively simplified to be modelled. These simplifications may violate some biological features, but simplifications are necessary to assist building and application of a model.

A major source of uncertainty was related to the fact that the temperature is not incorporated in the present model. During "normal" annual cycle (without El Niño event), water temperature varied from 26 to 30°C (Pouvreau et al., 2000) and, in such a narrow range of variation, we did not succeed to demonstrate any effect of temperature on the physiology of *P. margaritifera* (Robert et al., 1998; Pouvreau 1999; Pouvreau et al., 1999b). Nevertheless, during El Niño year, water temperature may reach 31.5°C in Takapoto atoll. During such an event, temperature would have presumably significant physiological effects, especially on clearance activity and O₂ consumption (e.g. Bougrier et al., 1995 ; Haure et al., 1998 for temperate species) but also on gametogenesis. Growth data, which were used to validate the model, were obtained during an El Niño year (1997-98). This feature probably explains the fact that the model slightly overestimated observed growth in warmer months. Incorporation of temperature will also be necessary to generalise the model to other pearl farming sites of French Polynesia for which temperature may vary from 22 to 32°C according to the latitude.

4.3. Model predictions

This growth model proposed for cultivated pearl oysters gave preliminary information relevant to pearl farming management and carrying capacity.

4.3.1. Spat collection

Temperature is commonly assumed as a determinant factor in maturation and gamete release. Our model suggests that, in a tropical environment with narrow range of temperature variation such as Takapoto atoll, POM be considered the main determinant factor. If temperature variations may act as a trigger for release, POM determines gametogenesis. In winter (June-September), spat settlement is generally not observed (Prou et al., 1999). Our model suggests that POM supplies are sufficient during winter months to ensure somatic growth, but insufficient to permit rapid gametogenesis. Alternatively, recruitment is generally observed several times between November and May (Prou et al., 1999), implying that several release events may occur in the warm season (Thielley, 1993; Buestel et al., 1995). This was predicted by our model (4 simulated releases in adult oysters between October and May) by considering only POM supplies. With further validation, it may be possible to predict peak recruitment periods and thus allow farmers to more effectively deploy collectors.

4.3.2. Pearl formation

The model assumes that the rate of nacreous deposition is the same on shell as it is on implanted nuclei. Such an assumption appears valid as the time to produce a marketable pearl simulated by the model was roughly the

same as the time commonly observed in field (i.e. 16-18 months). Further, daily increments of nacreous deposition are in agreement of those found experimentally by Caseiro (1993). In this respect, the model showed that the rate of nacreous deposition is faster in young oysters. In fact, in young oysters (< 2 year-old), reproductive effort is low, so that nearly all the scope for growth is devoted to somatic and shell tissue. If these young oysters were able to be nuclei-implanted, the time to produce a marketable pearl would be reduced. However, young pearl oysters are generally too small to be easily implanted without damage. So, a compromise would be found between an oyster large enough to be implanted, but not too old to have a low increment rate : a 2 year-old pearl oyster (80 mm in height) would be the best compromise.

4.3.3. Carrying capacity

Carrying capacity can be approached at a local scale, i.e. density on long-lines and problem of food depletion, or/and at a global scale, i.e. total biomass in the whole lagoon and problem of overstocking.

On a local scale, model simulations showed that under low current conditions (< 1 cm s⁻¹), POM depletion might occur. If such conditions should remain for several weeks, a decrease of the growth would occur, especially in area where long-lines are dense. Rougerie (1979) measured effectively currents from 10 to less than 1 cm s⁻¹ according to depth and wind conditions, so that POM-depletion may presumably occur. We have no other field data to support such results, but they will be checked in further field studies.

At a global scale, calculation of the total clearance time associated with primary production time (B/P, in days) would be a good indicator of occasional excess in stocks of bivalves. The clearance time (CT, in days) of a bivalve population is defined as “the time that is theoretically needed for the total bivalve filter feeder biomass within an ecosystem to filter particles from a volume of water equivalent to the total system volume” (Dame and Prins, 1998). Using stock assessments and model results on annual mean consumption of *P. margaritifera*, CT was calculated for cultivated pearl oysters but also for natural pearl oysters (Table 5) and extrapolated for other suspension feeding bivalves known in Takapoto lagoon assuming that cultivated pearl oyster and sessile bivalves feed with the same rate and on the same pool and size of material. If only cultivated pearl oysters were taken into account, the CT was very high, i.e. more than 1000 days, in comparison with primary production time (approx. 1 day). In that respect, cultivated pearl oysters would play an insignificant role in the global lagoon ecosystem. Alternatively, if all the potential trophic competitors (Addessi, 1997b), are taken into consideration, CT decreased to roughly 6 days, whereas production time is approx. equal to 1 day.

This lagoon environment falls within the fast systems (short turnover times) according to Dame and Prins (1998), and fits well with their assumptions that fast systems are generally smaller with denser populations of bivalves. This system differs strongly from Marennes-Oléron Bay (Héral, 1991), South San Francisco bay or North Inlet where suspension feeders population are dominated by harvested bivalves, which act strongly on the system. In Takapoto lagoon, and presumably other Polynesian lagoons, suspension feeders are dominated by natural bivalves which play the major role in the system. From now, a global (and strongly simplified) vision of the trophic food web in a cultivated ecosystem as Takapoto lagoon can be proposed (Fig. 9). This preliminary scheme describes the previous conclusion, i.e. the insignificant role of the cultivated population in the whole system. Thus, for pearl farming management, it is evident that the exploited stock could be increased without damage provided long-lines systems are well spaced and the abundance of trophic competitors is taken into consideration.

CONCLUSION

Simulation of growth and reproduction for an individual pearl oyster under natural food gave realistic results over a period covering a complete rearing cycle. Thus, the model can be used as a useful tool in predicting growth, gametogenesis and pearl formation. Nevertheless, validation of this model in other lagoons devoted to pearl culture will be necessary. This model gives first indications of the carrying capacity on a local and global scale. Further works will focus on the interaction (i.e. feedback) between pearl oysters, pelagic food web and potential competitors in a more complex trophic web model. Validation of the density effect on food depletion around long-lines would also be necessary.

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Table 1 : POC concentration ($\mu\text{gC l}^{-1}$) for the main groups of the particulate organic matter in Polynesian atoll lagoons. Mean values were re-calculated from several works conducted, between 1975 and 1998, in mid-waters of Takapoto or Tikehau lagoon. Calculations were obtained by using the following conversion factor : C/Chl $a = 50$ for phytoplankton (Charpy and Charpy-Roubaud, 1990); C/Chl $a = 82$ for cyanobacteria (Charpy et al., 1992); POM to POC conversion factor = 0.5. As authors have not used the same size-fractioning, some approximations have been made in the table. Global mean (+/- SE) and contribution of each group were computed on the basis of all these published values. Note that the total mean of POC is rather constant and independent of the study around $0.180 \text{ mg C l}^{-1}$, i.e. $\sim \text{POM}=0.40 \text{ mg l}^{-1}$, showing the strong stability of this parameter between years.

* References : 1. Sournia and Ricard (1975); 2. Sournia and Ricard (1976); 3. Renon (1977); 4. Blanchot et al. (1989); 5. Leborgne et al. (1989); 6. Charpy and Charpy-Roubaud (1990); 7. Charpy and Charpy-Roubaud (1991); 8. Charpy et al. (1992); 9. Charpy et al. (1994); 10. Vacelet et al. (1996); 11. Charpy (1996); 12. Torr ton and Dufour (1996); 13. Torr ton et al. (1997); 14. Charpy et al. (1997); 15. Charpy and Blanchot (1998); 16. Loret (1998); 17. Niquil (1998); 18. Pouvreau (1999); 19. This study.

Size and taxonomic composition		References*																		Global mean (+/- SE)	% of the total POC	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18			19
< 2 μm	Bacteria				17		17			16	3		23	13				15			15 +/- 2	8%
	Cyanobacteria				10				16	7		13				13		16			12 +/- 1	7%
	Picoeukaryotes				2		3			6		4				13		63			15 +/- 10	8%
	PicoDetritus				118		82			60								50			78 +/- 15	41%
	POC < 2 μm				147		102			89								143			120 +/- 15	64%
> 2 μm	Phytoplankton				1		6			5	4	3				8	50			11 +/- 7	6%	
	Protozoa				3		2			0						10	31			9 +/- 6	5%	
	Zooplankton			4	3	7	2			4							2			4 +/- 1	2%	
	Micro-Detritus				34		84			38							23			45 +/- 14	24%	
	250 μm > POC > 2 μm				41		94			47					35		106			68 +/- 15	36%	
All sizes	Detritic POC				152		166			98						73	137			122 +/- 17	65%	
	Living POC				36		29			37						176				66 +/- 36	35%	
	Autotrophic POC	6	28		13		9			18		20		16		129	20			38 +/- 13	20%	
	Heterotrophic POC				23		20			20						48				27 +/- 7	15%	
	Total POC		160		188		196	192		135	180				115		249	175	195		188 +/- 12	

Table 2: Model variables and values of the coefficients used in the growth model. * References : 1. Pouvreau et al. (1999b); 2. Dufour and Torr ton (1996); 3. Pouvreau et al. (1999a); 4. Loret (1998); 5. Pouvreau et al. (1998); 6. Robert et al. (1998); 7. This study; 8: Pouvreau (1999).

Acronym	Value	Unit	Comment	References*
STATES VARIABLES				
SHELL	f(TIME)	g	Biomass of shell	
SOMA	f(TIME)	g	Biomass of soma	
GONAD	f(TIME)	g	Biomass of gonad	
FORCING VARIABLES				
POM	f(TIME)	mg l ⁻¹	Particulate organic matter in suspension	
PIM	f(TIME)	mg l ⁻¹	Particulate inorganic matter in suspension	
POC _i	f(TIME)	mgC l ⁻¹	Carbon concentration in each POM-group i	
FUNCTIONS AND COEFFICIENTS				
Clearance Rate : CR = a_{CR} x PIM^{b_{CR}} x POM^{c_{CR}} x W^{d_{CR}}				
a _{CR}	647.04	l d ⁻¹ g ⁻¹	Proportionality coefficient	1
b _{CR}	-0.42	-	PIM-exponent coefficient	
c _{CR}	0.96	-	POM-exponent coefficient	
d _{CR}	0.61	-	W-exponent coefficient	
Consumption Rate : FR_{POM} = CR x Sum (aRE_i/100 x POC_i)				
Gill retention efficiency :				
aRE _{bacteria}	2	%	for bacteria	2
aRE _{cyanobacteria}	6	%	for cyanobacteria	
aRE _{picodetritus}	12	%	for picodetritus	3
aRE _{picoeukaryotes}	15	%	for picoeukaryotes	
aRE _{phytoplankton}	60	%	for phytoplankton	4
aRE _{zooplankton}	60	%	for zooplankton	
aRE _{microdetritus}	60	%	for microdetritus	
aRE _{protozoa}	60	%	for protozoa	
PF Production : PF_{POM} = a_{PF_{POM}} x (PIM-MIN_{PF}) x POM x W^{b_{PF_{POM}}}				
a _{PF_{POM}}	32.16	mg C d ⁻¹ g ⁻¹	Proportionality coefficient	1
MIN _{PF}	0.18	mg l ⁻¹	PIM-threshold	
b _{PF_{POM}}	1	-	W-exponent coefficient	
Faeces Production : F_{POM} = a_{F_{POM}} x (1-e^{-b_{F_{POM}}TPM}) x W^{c_{F_{POM}}}				
a _{F_{POM}}	480.00	mg C h ⁻¹ g ⁻¹	Asymptotical value	1
b _{F_{POM}}	0.06	-	TPM-parameter	
c _{F_{POM}}	0.59	-	W-exponent coefficient	

Acronym	Value	Unit	Comment	References*	
FUNCTIONS AND COEFFICIENTS					
Amino-acids and urea excretion Rate: U = a_U x W^{b_U}					
a _U	0.02	mg C d ⁻¹ g ⁻¹	Proportionality coefficient	5	
b _U	0.78	-	W-exponent coefficient		
Respiration Rate : R = RQ x a_R x W^{b_R}					
a _R	7.38	mg C d ⁻¹ g ⁻¹	Proportionality coefficient	6*	
b _R	0.73	-	W-exponent coefficient		
RQ	0.92	%	Respiratory quotient	7	
Reproductive effort : ER = a_{ER}/(1+b_{ER} x e^{-c_{ER} x age})					
a _{ER}	0.60	-	Asymptotic value	8	
b _{ER}	74	-	Rate of maturation acquisition		
c _{ER}	1.4	year ⁻¹	Rate for reach asymptotic ER		
Shell and pearl formation : H_{shell} = a_H W^{b_H} ; T_{shell} = a_T W^{b_T}					
H _{shell}	Output	mm	Shell Height	8	
a _H	23.56	-	Coef. of proportionality		
b _H	0.31	-	Exponent coefficient		
T _{shell}	Output	mm	Shell Thickness		
a _T	1.30	-	Coef. of proportionality		
b _T	0.34	-	Exponent coefficient		
t _{end}	Output	month	Time to obtained a marketable pearl		
T _{pearl}	1.2	mm	Thickness of the nacreous layer for a marketable pearl		
Other coefficients					
Alloc _{Shell}	0.6	%	allocation to shell matrix		
Eff	0.8	%	Efficiency storage utilisation		
RGS _{max}	0.29	%	Maximal gonado-somatic ratio		
Ash _{Shell}	0.95	%	Ash percentage in shell		
Ash _{Gonad}	0.12	%	Ash percentage in gonad		
Ash _{Soma}	0.11	%	Ash percentage in soma		

* Converted using 1 mg O₂ = 0.696 ml O₂ and 1 ml CO₂ = 0.53 mg C

Table 3 : Model equations

SCOPE FOR GROWTH (mgC d⁻¹) :	
SFG= FR _{POM} - (PF _{POM} + F _{POM} + U+R)	
CARBON ALLOCATION (mgC d⁻¹) :	
<i>If SFG > 0 :</i>	ToGONAD = ER•SFG ToSOMA = (1-ER) •(1-Alloc _{shell}) •SFG ToSHELL = (1-ER) •(Alloc _{shell}) •SFG
<i>If SFG < 0 :</i>	ToGONAD = SFG+ (1-Eff)•SFG <i>If GONAD=0 then ToSOMA = SFG+ (1-Eff)•SFG</i> ToSHELL = 0
SPAWNING (mgC) :	
<i>If RGS > RGS_{max}</i>	SPAWNING= GONAD
DIFFERENTIAL EQUATIONS :	
	dGONAD/dt = ToGONAD dSHELL/dt = ToSHELL dSOMA/dt = ToSOMA
WEIGHT (g) :	
	W _{Tissue} = SOMA/(1-Ash _{Tissue})+GONAD/(1-Ash _{Gonad}) W _{Gonad} = GONAD/(1-Ash _{Gonad}) + DG•SOMA/(1-Ash _{Tissue}) W _{Shell} = SHELL/(1-Ash _{Gonad}) DG=Fraction in weight of the digestive gland in the total tissue weight

Table 4 : Date and intensity (Pr, mg) of the gametes release given by the model according to the age and to the dry tissue weight (W_{Tissue}) of pearl oyster in the 1997-98 period in Takapoto lagoon.

Age-group	Date of spawning	Pr (mg)	W (g)
1	07/01/98	172	2.2
2	20/10/97	453	5.1
	30/12/97	545	6.2
3	10/05/97	545	6.5
	02/10/97	629	7.4
	29/11/97	671	7.8
	27/12/97	705	8.2

Table 5 : Clearance time (days) for each population of suspension-feeding bivalves encountered in the Takapoto lagoon. Specific comments : (1) Gaby Haumani (pers. comm.); (2) Assuming a ratio 1/10 between pearl oysters on spat collectors and *P. maculata*; (3) Zanini (1995); (4) Addressi (1997a); (5) Calculated using retention efficiency spectrum of bivalves and taxonomic composition of POC.

Population of bivalves		Stocks	Individual Consumption	Total Consumption	POC available for bivalves ⁽⁵⁾	Clearance Time
		(10 ⁶ ind.)	(mg C d ⁻¹ ind ⁻¹)	(mT C d ⁻¹)	(mT C)	(days)
Stocks on system culture	Cultivated pearl oyster	2 ⁽¹⁾		0.07	135	1880
	Class I	0.9	20	0.02		
	Class II	0.4	60	0.02		
	Class III	0.4	75	0.03		
	Associated trophic competitors	10 ⁽²⁾	13	0.13	135	1041
Natural stocks on bottom	Natural pearl oyster	4 ⁽³⁾	42	0.17	135	810
	Trophic competitors					
	<i>Arca ventricosa</i>	635 ⁽⁴⁾	32	20.2	135	7
	<i>Pinctada maculata</i>	31 ⁽⁴⁾	13	0.4	135	347
	<i>Chama iostoma</i>	53 ⁽⁴⁾	26	1.4	135	97
Total				22.4	135	6

FIGURES

Fig. 1 : Schematic of the conceptual pearl oyster growth model.

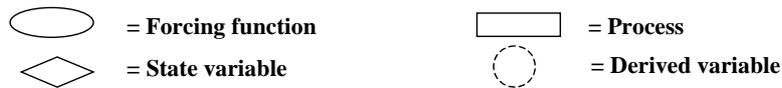


Fig. 2 : Annual evolution of forcing function (daily mean value for PIM and POM, mg l^{-1} , +/- SE) during 1997-98 in station 1 of Takapoto lagoon.

Fig. 3 : Long lines systems and principle of food depletion.

Fig. 4 : Results of simulated (thick line) and measured (\square) individual growth of *Pinctada margaritifera* during 1997-98 in the three age-groups in station 1 in Takapoto lagoon. a : Growth in shell (dry weight, W_{Shell} , g) ; b : Growth in total tissue (dry weight, W_{Tissue} , g) ; c : Growth in gonadic tissue (dry weight, W_{Gonad} , g). Arrows indicate spawning events. Plots d, e and f describes predicted value (Y-axis) vs observed data (X-axis) for each of the state variables of the growth model.

Fig. 5 : Annual variations of the main feeding processes and the scope for growth of *Pinctada margaritifera* for each of the three age-groups of pearl oysters (age-group 1 : thick line ; age-group 2 : normal line ; age-group 3 : fine line). CR = clearance rate, FR_{POM} = Organic consumption rate, PF_{POM} and F_{POM} = Biodeposition rates, A_bR = Absorption rate ($\text{A}_b\text{R} = \text{FR}_{\text{POM}} - \text{PF}_{\text{POM}} - \text{F}_{\text{POM}}$) and SFG = Scope for growth.

Fig. 6 : Simulated annual evolution of the rate of nacreous deposition and the daily increment in shell height ($\mu\text{m d}^{-1} \text{ ind}^{-1}$) in the three age-groups of pearl oysters.

Fig. 7 : a : Effect of 1-year-POM depletion on final weight of shell, tissue and gonad for an age-group 3 pearl oyster; b : Effect of 1-year-POM depletion on the time necessary to achieve a pearl (t_{End} , \square) and on the number of gametes releases (n_{gametes}) in one year (\blacktriangle) for an age-group 3 pearl oyster.

Fig. 8 : POM depletion (value in %) according to the number of successive long-lines, the flow velocity and the linear density in each line. Areas in grey and black represent conditions for which POM depletion is assumed to have negative effects on growth, reproduction and pearl formation.

Fig. 9 : Conceptual design of the trophic relationship in the pelagic web around cultivated pearl oysters. Biomass are expressed in metric ton of carbon for the whole lagoon (TC), Fluxes (gross primary production, gPP, and bivalve filtration rate, FR) are expressed in TC d^{-1} .

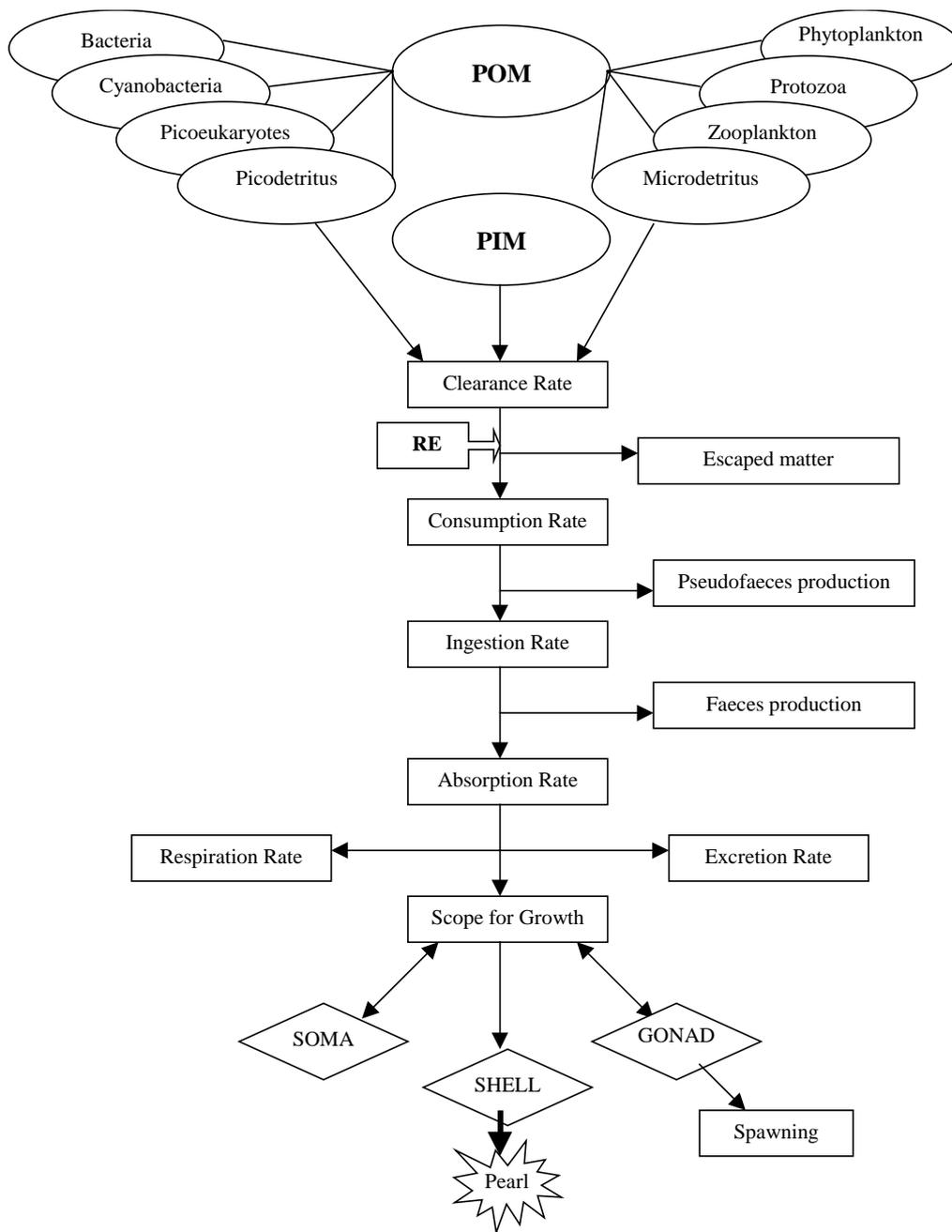


Figure 1

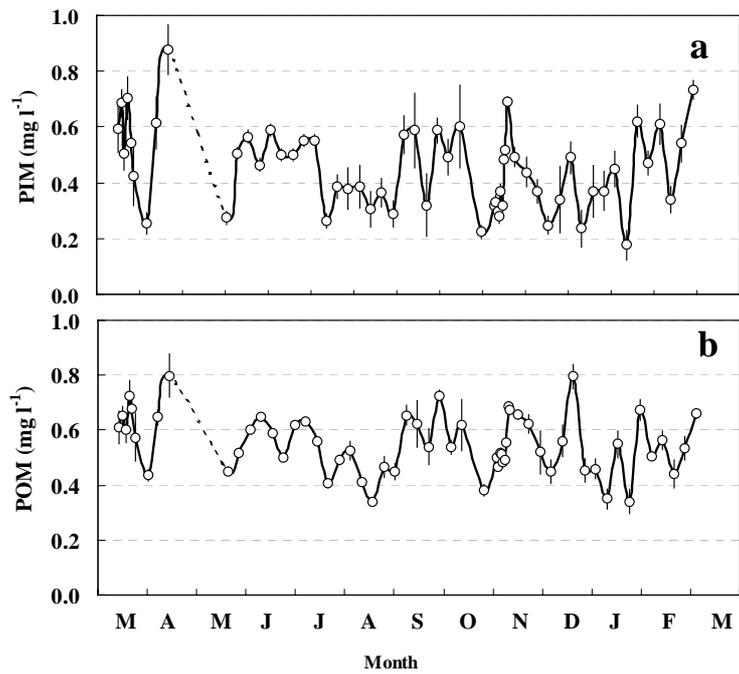


Figure 2

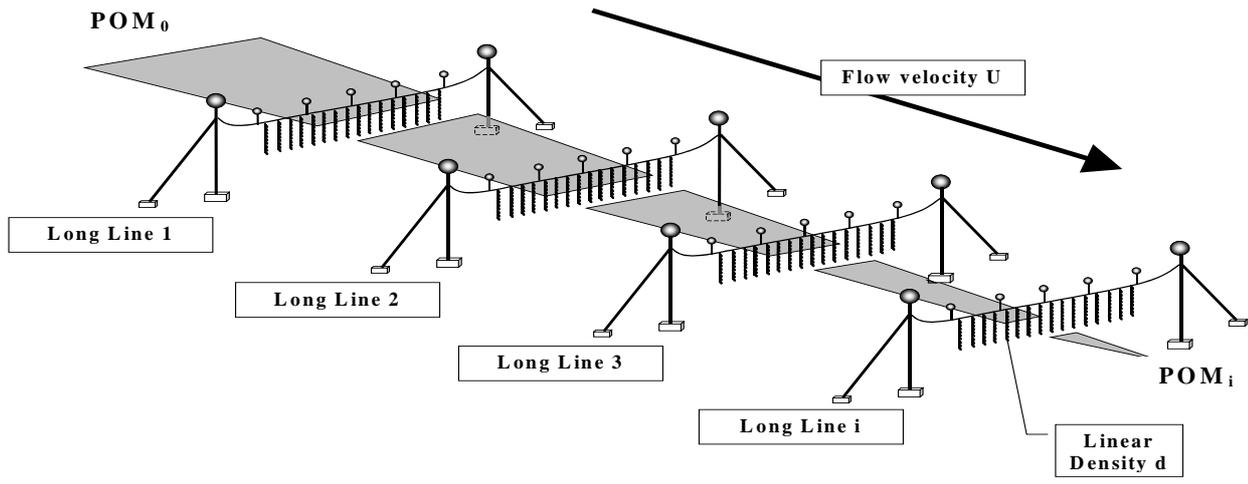


Figure 3

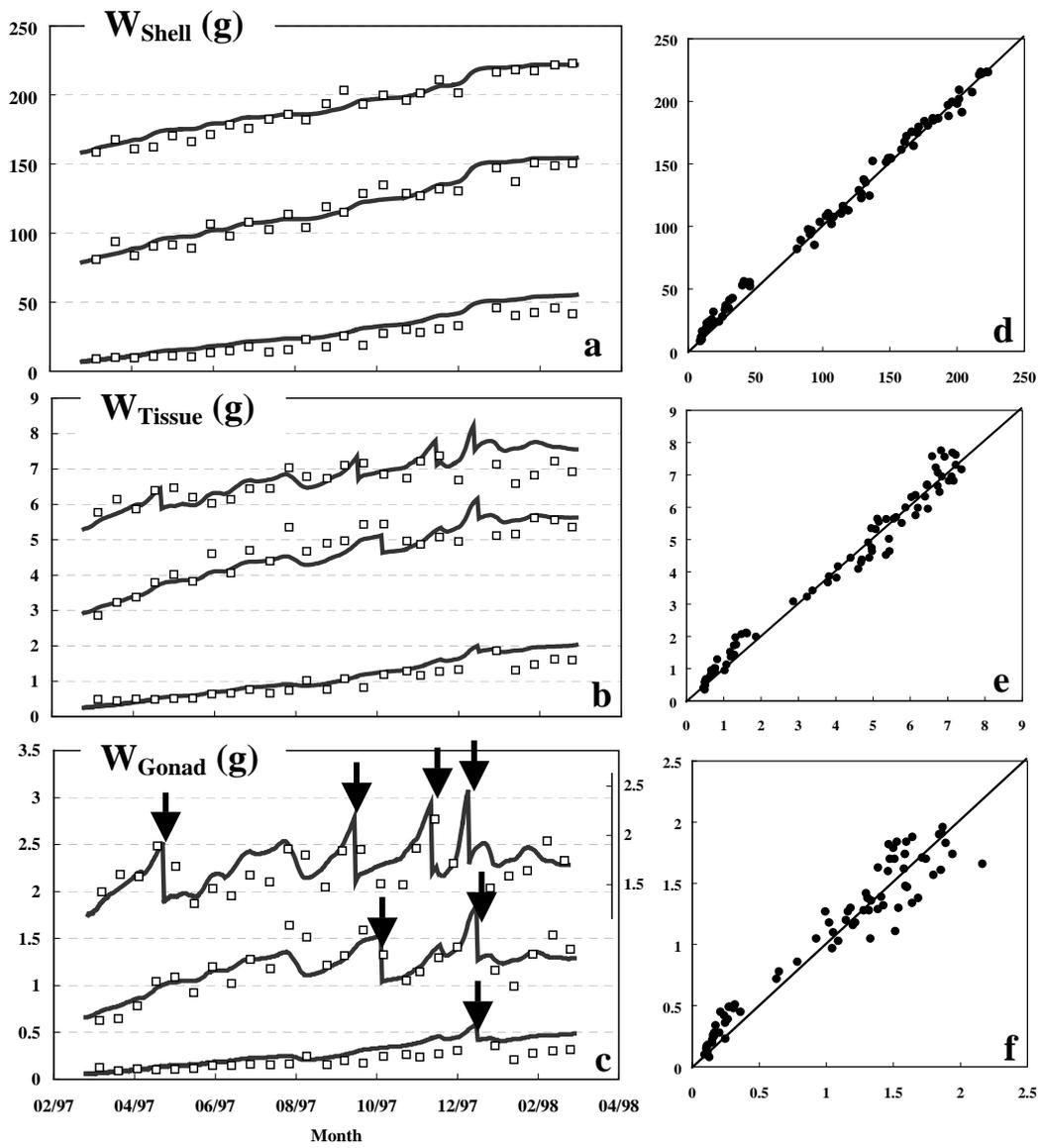


Figure 4

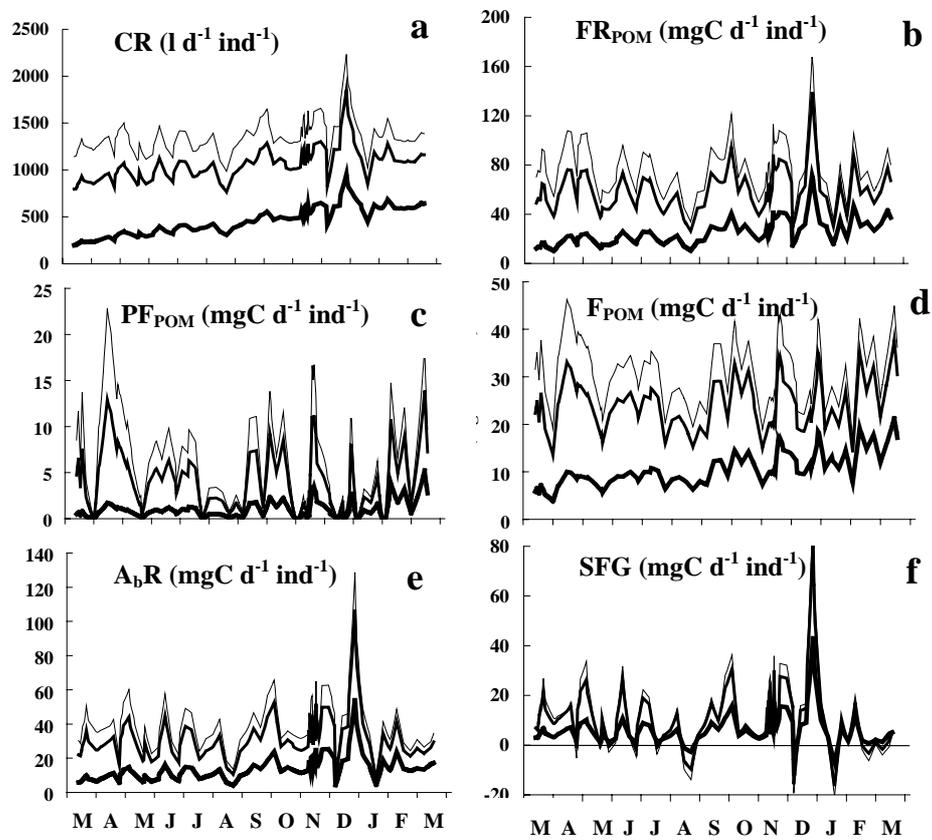


Figure 5

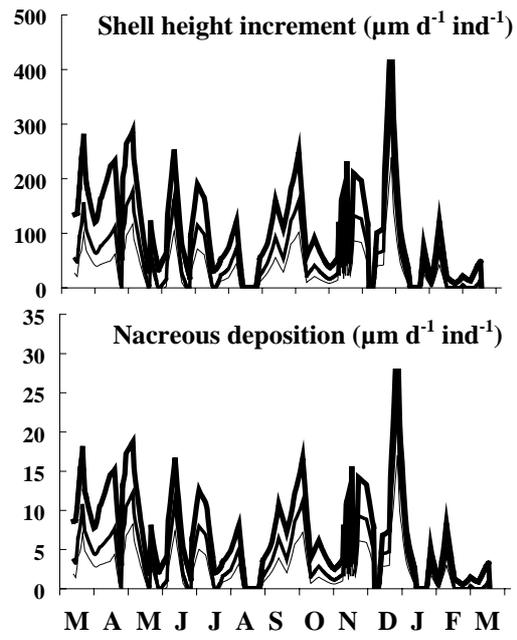


Figure 6

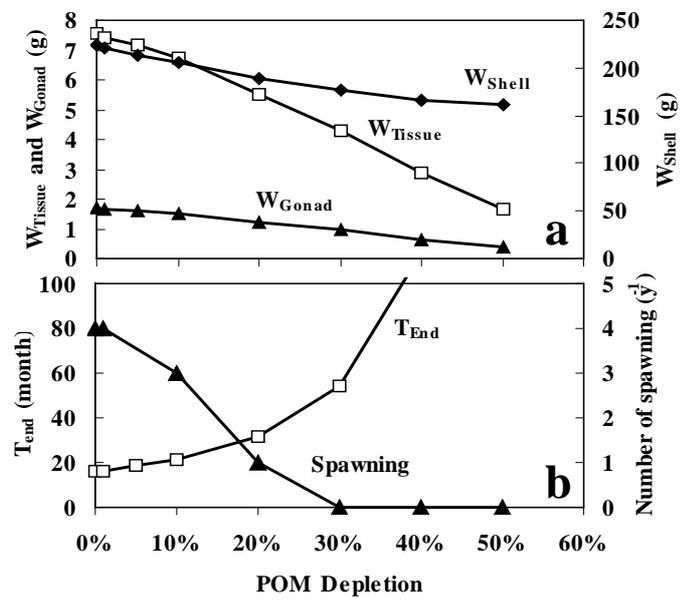


Figure 7

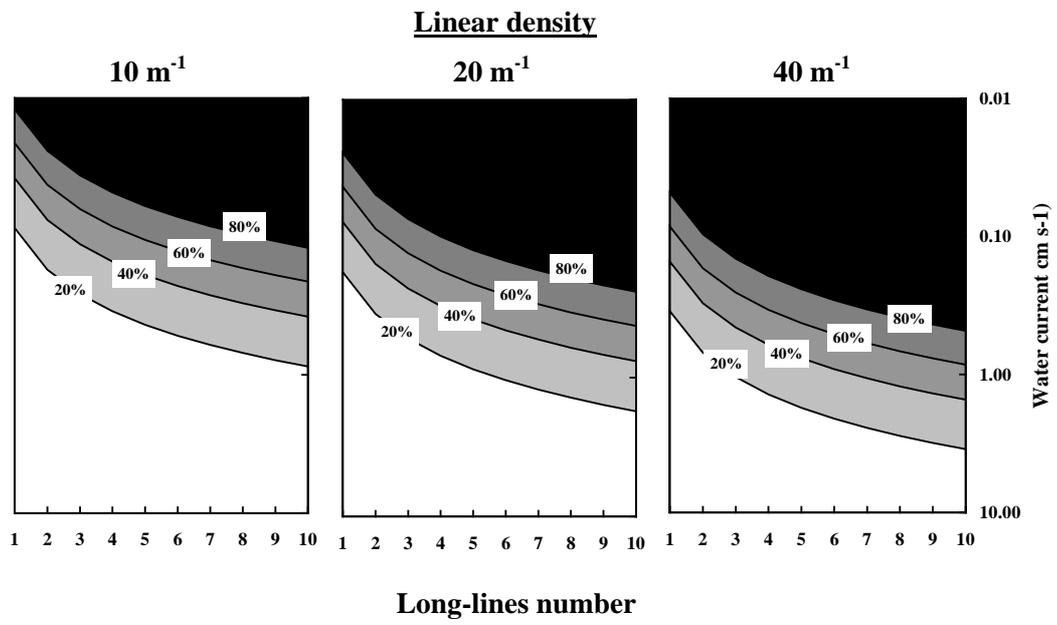


Figure 8

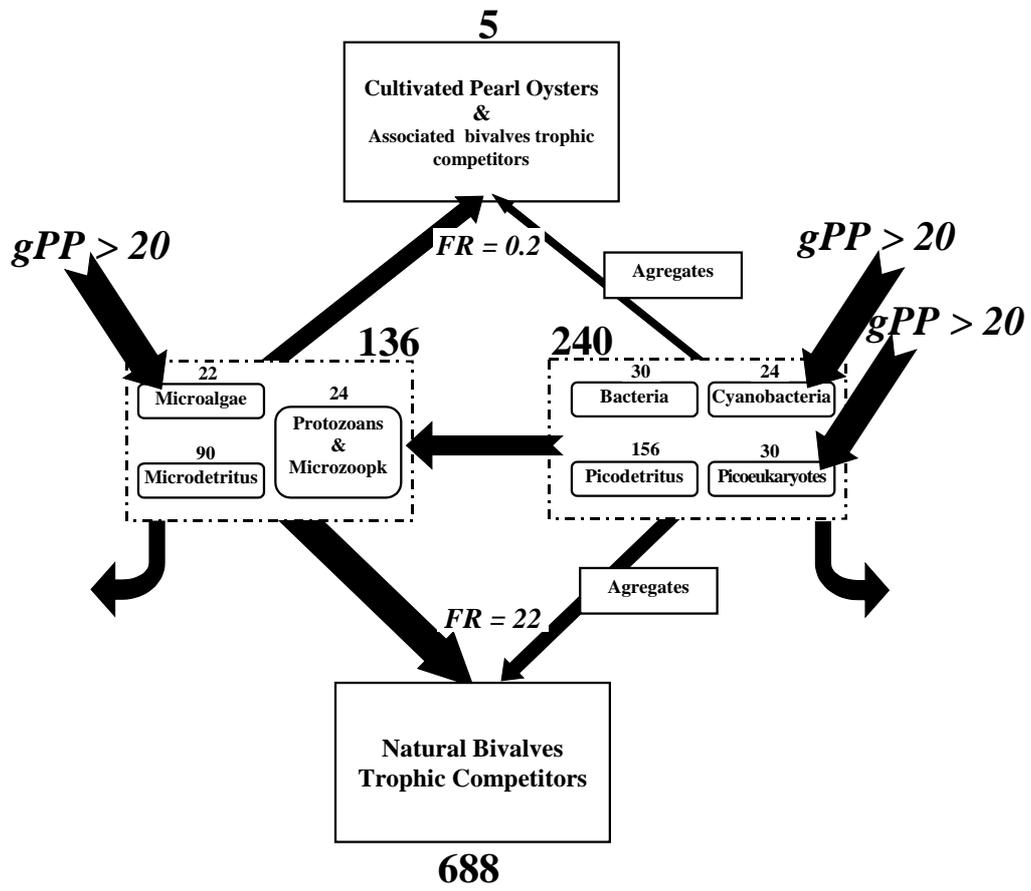


Figure 9