Aquat. Living Resour. 14 (2001) 155−163

S0990744001011202/FLA

Growth of the black-lip pearl oyster, *Pinctada margaritifera*, at nine culture sites of French Polynesia: synthesis of several sampling designs conducted between 1994 and 1999

Stéphane Pouvreau[a,b,d]*, Vincent Prasil[c]

[a] *CREMA (CNRS–IFREMER), BP 5, 17137 L'Houmeau, France*

[b] *IFREMER-COP, BP 7004, Taravao, Tahiti, French Polynesia*

[c] *Service des ressources marines, BP 20, 98713 Papeete, Tahiti, French Polynesia*

[d] *Present address: Laboratoire de physiologie des invertébrés marins, Station expérimentale d'Argenton, Ifremer, Presqu'île du Vivier, 29840 Argenton-en-Landunvez, France*

Received 31 January 2000; accepted 22 March 2001

Abstract − Between 1994 and 1999, several sampling designs were used to measure the growth of the black-lip pearl oyster, *Pinctada margaritifera* var. *cumingi* at different sites in French Polynesia. Using a common statistical method, growth data were analysed for nine sites and showed significant geographic variability. Parameters of the Von Bertalanffy model, fitted on the nine data sets, ranged from 147 to 186.5 mm for the H_∞ parameter and from 0.42 to 0.58 year^{-1} for the k parameter. The ϕ parameter (combination of H_∞ and k) provided a ranking classification of growth in these nine sites: growth was low in closed atoll lagoons, such as Takapoto, whereas the island lagoons and ocean habitat supported a very promising shell growth. Calculated on the basis of these models, two parameters of interest for pearl farming were computed: 1) the time for pearl oysters to reach a size of 100 mm (size at which they are suitable for nucleus implantation), which ranged from 21 to 26 months, and 2) the annual shell growth increment at this size (correlated to the rate of nacreous deposition on the pearl), which varied from 19.7 to 31.8 mm·year^{-1}. The combination of these two sets of results demonstrated that the time necessary to produce a comparable pearl varied significantly according to the site. Several hypotheses to explain the differences observed in the growth of *P. margaritifera* in these nine sites are proposed. The most reasonable would appear to be: 1) the negative effect of high temperature (> 30°C), and 2) the degree of water renewal and food supply around the bivalve. Although this paper demonstrated significant variability in growth performance in the nine investigated sites, further investigations are needed, especially concerning the flesh growth rate. Indeed, this highly relevant parameter, which reflects both bivalve health and the suitability of farming sites, has received very little attention to date.

growth / pearl oyster / *Pinctada margaritifera* / tropical lagoon / Von Bertalanffy model

Résumé − Croissance de l'huître perlière, *Pinctada margaritifera*, dans neuf sites différents de Polynésie française : bilan de plusieurs plans d'échantillonnage menés entre 1994 et 1999. Plusieurs plans d'échantillonnage, conduits de 1994 à 1999, ont permis de mesurer la croissance de l'huître perlière, *Pinctada margaritifera* var. *cumingi*, en différents sites de la Polynésie française. En utilisant une méthode statistique commune, les données de croissance ont montré une variabilité géographique significative entre les neuf sites. Les paramètres du modèle de Von Bertalanffy, ajustés sur chacun des neuf jeux de données, varient de 147 à 186,5 mm pour la hauteur asymptotique H_∞ et de 0.42 à 0.58 an^{-1} pour le taux de croissance k. L'utilisation du paramètre ϕ (une fonction des paramètres H_∞ et k) donne un indice pertinent de classement de la croissance dans ces neuf sites: dans les lagons d'atolls fermés, comme Takapoto, la croissance des huîtres est plus faible que dans les lagons d'îles hautes ou en milieu océanique. Pour chacun des sites, un modèle est ensuite proposé. Calculé sur la base de ces modèles, le temps nécessaire à une huître perlière pour atteindre la taille de greffe (H = 100 mm) est compris entre 21 et 26 mois et le taux de croissance annuel en coquille à cette taille varie de 19.7 à 31.8 mm·an^{-1}. La combinaison de ces deux résultats démontre que le temps nécessaire pour produire une perle comparable est significativement différent entre les sites. Plusieurs hypothèses sont proposées pour expliquer ces différences de croissance, les plus probables sont : 1) l'effet négatif des hautes températures (> 30°C), et 2) le taux de renouvellement de l'eau et de la nourriture autour des bivalves. En complément de cette étude, de nouveaux travaux concernant la variabilité géographique de la croissance en chair et la reproduction de *P. margaritifera* en Polynésie française serait à envisager.

**Correspondence and reprints.*
E-mail address: spouvrea@ifremer.fr (S. Pouvreau).

croissance / huître perlière / *Pinctada margaritifera* / lagon tropical / modèle de Von Bertalanffy

1. INTRODUCTION

The black-lip pearl oyster, *Pinctada margaritifera* (Linnaeus, 1758) var. *cumingi* (Reeve), is found throughout the Indo–Pacific region and is abundant in the atoll lagoons of French Polynesia where it is cultivated for its lucrative black pearls. The problem of culture technique, which has varied considerably over the last 20 years, has now been settled (subsurface long line systems). Spat settles onto artificial material placed in the lagoon (spat collectors) and is left growing on the collectors for up to six months. They are then transferred to various on growing systems (lantern nets or down lines). Pearl seeding operations begin at about 2 years of age, and a pearl is produced approximately 18 months after implantation (grafting). After pearl collecting, healthy oysters are generally reimplanted to produce additional pearls.

Recently, the density of cultivated pearl oysters has increased dramatically in several atoll lagoons. In light of this, an important research program (PGRN project) was undertaken to determine the carrying capacity (see review on this topic, in several shellfish ecosystems, by Héral et al., 1989; Grant et al., 1993, and Kashiwai, 1995) of atoll lagoons, by selecting Takapoto Lagoon (Tuamotu Archipelago, French Polynesia) as a study site.

Another aim of PGRN project was to improve knowledge on the growth performance of *P. margaritifera* in several Polynesian lagoons. Studying growth is of interest for pearl farming, since 1) growth constitutes a useful indicator of both pearl oyster health and the suitability of the environment, as it represents the integrated response of the entire physiological activity of the organisms, and 2) shell growth rates can provide precious information on pearl growth since shell increment and deposition of nacreous matter on the implanted nucleus are strongly correlated (Coeroli and Mizuno, 1985). However, growth rates of tropical bivalves, especially Pteriidae, are poorly documented. Some measurements have been made for *P. margaritifera* var. *erythraensis* in the Red Sea (Nasr, 1984) and in India (Chellam, 1978, 1988) and some data are available for *P. margaritifera* var. *cumingi* from the Cook Islands (Sims, 1993; 1994) and from two lagoons in French Polynesia (Coeroli et al., 1984; Pouvreau et al., 2000b).

To enhance our knowledge, this paper gives a wide overview of the growth variability of *P. margaritifera* in nine different Polynesian sites, by using all the growth data available to date concerning *P. margaritifera* in French Polynesia. These data were obtained thanks to 4 complementary sampling campaigns conducted during the PGRN project.

2. MATERIALS AND METHODS

2.1. Study sites

Growth of cultivated pearl oysters was studied at nine sites in French Polynesia. Experimental populations were set up in six atolls (Takapoto, Takaroa, Fakarava, Manihi, Rangiroa, Mangareva), in two high islands (Raiatea-Tahaa, Vairao on Tahiti) and in the open ocean (near Takapoto Lagoon) *figure 1* and *table I*. All theses islands or atolls were chosen based on their accessibility by aircraft. Most of them are pearl farming sites. The lagoons differ widely in the surface areas that they cover (from 81 to 1592 km^2). Some of them are completely closed (i.e. very few active channels between the lagoon and the ocean, as is the case for Takapoto), whereas others are largely opened (i.e. large active channels, such as at Rangiroa and Mangareva). To give an idea of the residence time of water for each of theses sites, an opening index (*table I*) was calculated, which is the percentage of channel against the total coral rim (in linear metres) on the basis of the geomorphologic data provided by Andrefouët (1998).

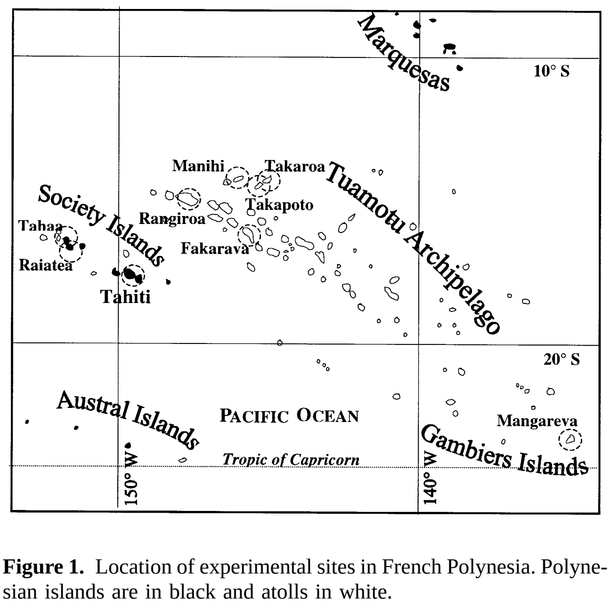

Figure 1. Location of experimental sites in French Polynesia. Polynesian islands are in black and atolls in white.

Table I. Characteristics of the eight lagoons where growth of pearl oyster was investigated.

Sites	Latitude S	Longitude W	Lagoon area (km^2)	Opening index (%)	Water temperature (min–max; °C)
Atolls or pseudo-atolls					
Takapoto	14°63’	145°21’	81	3	25.7–30.4
Takaroa	14°45’	144°96’	89	5	26.0–30.5
Manihi	14°40’	145°96’	165	8	26.5–30.6
Rangiroa	15°14’	147°60’	1592	27	26.0–30.0
Fakarava	16°29’	145°59’	1112	39	25.4–30.0
Mangareva*	23°10’	134°95’	395	high	21.3–28.8
High islands					
Vairao (Tahiti)	17°45’	149°30’	Reef system	high	25.3–29.5
Tahaa-Raiatea	16°42’	151°27’	Reef system	high	25.5–29.7

An additional experimental station (site 9) was set up directly in the ocean, near Takapoto Lagoon. The opening index is defined as the percentage of channel against the total coral rim (in linear metres) on the basis of the geomorphologic data provided by Andrefouët (1998).

Table II. Main characteristics of the four sampling campaigns conducted during PGRN project.

Sampling designs	Studied years	Age group (year)	Sampling method	Sampling step (month–1)	Samples size	Sites
I	1994–1996	1	Sacrifice	0.17	60	Rangiroa
II	1997–1998	2–3	Sacrifice	2	120	Takapoto
III	1997–1998	1.5	Sacrifice	0.33	30	Ocean
IV	1998–1999	1.5	Semi-conservative	0.33	Variable, > 30	Raiatea-Tahaa, Vairao, Mangareva, Takapoto, Takaroa, Manihi, Fakarava

The two sampling methods used were: 1) the ‘sacrifice’ method, which involved periodically sampling and dissection of the oysters, and 2) the ‘semi-conservative’ method, which involved consecutive measurements of tagged oysters.

2.2. Sampling schemes and growth measurement

Pearl oyster growth was assessed in these nine sites with the help of four complementary sampling designs. The first three campaigns (designs I, II, III) were conducted at a single site, respectively in Rangiroa, in Takapoto and in the Ocean near Takapoto. The fourth campaign (IV) was conducted at five other atolls and two high islands. The main characteristics of these sampling designs are briefly summarised in *table II*.

Farming of these experimental pearl oysters was conducted by the SRM field laboratories, using the same cultivation technique. This technique closely approximated that used by professional oyster farms. Pearl oysters were ‘ear hung’ on down line and suspended at low densities (< 20 oysters·m^{-3}) on long lines at a depth of approximately 7–10 m. For each of these experimental populations, the age of the pearl oysters was estimated based on the summer spat fall. Error in estimation was ± 3 months.

All these sampling designs included periodical measurement of growth of experimental pearl oysters, over a minimum of one year. Design II (Takapoto) is described in detail by Pouvreau et al. (2000b). Growth was followed every fortnightly for one year (from March 1997 to April 1998) on two age groups (2 and 3 year old at the beginning of the study) using a sacrifice method (height measurement, weighing and dissection). Additional data concerning growth of young oysters (< 1 year old) were also provided. For the other designs, growth was followed on a single age group (> 1 year old) for more than 1 year (15 months for design IV and 24 months for design I) using a sacrifice method (sampling designs I and III) or a semi-conservative method, i.e. consecutive measurements of tagged oysters (sampling design IV). These last designs were respectively conducted from 1994 to 1996 for design I, from 1997 to 1998 for design III and from 1998–1999 for design IV. The sampling frequencies were generally lower than for sampling design II: every 3 months for sampling III and IV, every 6 months for sampling I.

Each time, measurement were taken of a large number of oysters ($n > 30$) using a common method: after removing the fouling organisms, shell increment (dorso–ventral height, H in millimetres) was measured externally according to Hynd (1955), from the heel to the furthermost edge of the non-nacreous border, excluding digitate processes. Data concerning other biometric measurements (shell and flesh weights), which were acquired only during sampling II and III, are not presented here. These data are the object of another study (Pouvreau et al., 2000b).

2.3. Data analysis

Due to differences between sampling designs, the most appropriate method was to fit an empirical growth model expressing shell size (height, H, in millimetres) as a function of age (t, in years) on each data set. The second step was to compare the growth models obtained. The Von Bertalanffy model (Von Bertalanffy, 1938) was used in our work in order to allow a comparison with previous works (Sims, 1994). Extended models (Moreau, 1987; Schnute and Richards, 1990) are, as a general rule, more appropriate although less commonly used (Roff, 1980). The Von Bertalanffy equation is as follows:

$$H = H_\infty [1 - e_0^{-k(t-t)}]$$

where H is the height in millimetres at time t, H_∞ is the asymptotic (or theoretical maximum) height in millimetres, t the age in years and k the rate at which the asymptotic value is approached in year–1. The non-linear model was fitted by minimising the residual sum of squares using the Marquardt algorithm (a simplex derivative method) and the Statgraphics plus Software. Significance of each parameter estimate and comparisons between models were tested by computing F ratios based on residual mean square obtained after non-linear adjustment procedures.

Once models were validated and compared, parameter estimates were used to calculate several variables of interest for pearl farming. H_∞ and k were used to calculate a growth performance index Φ ($\Phi = \log k + 2 \log H_\infty$, e.g. Moreau, 1987; Munro and Pauly, 1983). A higher value for Φ indicates a higher growth performance. Two other parameters, T_{100} and P_S, useful to evaluate growth performance, were also deducted from each of these models. The T_{100} parameter corresponds to the time to reach the size of the first nucleus implantation ($H \approx 100$ mm) and P_S is the mean annual shell growth increment after this time. P_S is of interest since it gives an indirect but reliable index of nacreous deposition rate on the pearl nucleus (Coeroli and Mizuno, 1985). It was calculated, by using each Von Bertalanffy model, as being the difference between shell size at T_{100} and shell size at (T_{100} + 1 year). Lastly, these two parameter were plotted together to generate an XY-chart which provides a visual quick-classification of pearl farming performances and/or potentialities of the nine investigated sites.

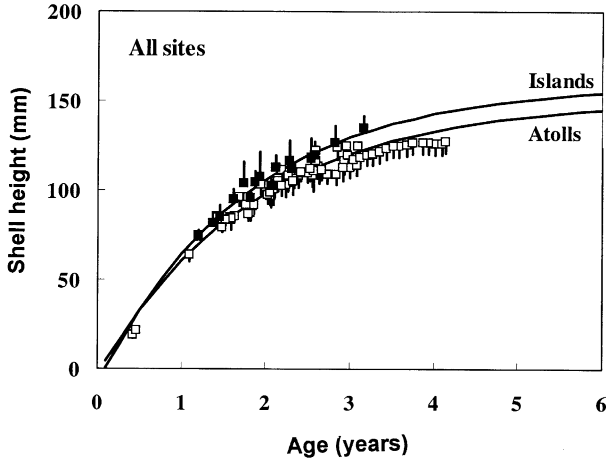

Figure 2. Comparisons between growth of *P. margaritifera* in culture in atolls (□), islands and in open ocean (■). Means ± SE.

3. RESULTS

3.1. Von Bertalanffy models

Results of the four sampling designs are described in *figure 2*. Differences between sites were small: the mean size for a 3 year old pearl oyster was within the narrow range from 119 mm (± 6.9 SD) to 135 mm (± 6.9 SD) depending on culture site. Nevertheless, *figure 2* indicates that the highest values were generally obtained on islands or in the open ocean, whereas smaller sizes were reached in atoll lagoons. The Von Bertalanffy model, fitted on these two groups, generated the following results (H in millimetres; t in years):

– Islands and ocean group:
$H = 160.0 \quad [1 - e^{-0.57 \times (t - 0.10)}]$, ($df$ = 1 246; F_{ratio} = 53 604; $R^2 = 0.80$, $P < 0.05$),

– Atoll lagoon group: $H = 151.2\ [1 - e^{-0.54 \times (t - 0.05)}]$, ($df$ = 4 295; F_{ratio} = 289 917; $R^2 = 0.81$, $P < 0.05$).

Fittings of these models were highly significant ($R^2 > 0.80$). The hypothesis of common parameters between models was rejected (F_{ratio} = 330.4;

Table III. Results of Von Bertalanffy parameter estimates for each of the nine sites.

Sites	H_∞ (mm)	k (year^{-1})	t_0 (year)	F ratio	R^2
Takapoto	147.0±2.0	0.54±0.01	0.06±0.03	98 321	0.87
Fakarava	153.1±3.3	0.49±0.02	0.06±0.03	62 336	0.83
Takaroa	155.2±2.7	0.58±0.02	0.06±0.03	60 119	0.88
Manihi	159.6±3.2	0.49±0.02	0.06±0.03	73 890	0.86
Rangiroa*	164.8±4.5	0.46±0.02	0.06±0.03	9 770	0.98
Mangareva*	165.3±3.4	0.48±0.02	0.06±0.03	74 664	0.81
Vairao (Tahiti)	186.5±5.4	0.42±0.02	0.12±0.03	44 204	0.87
Tahaa-Raiatea*	178.0±6.3	0.50±0.03	0.12±0.03	22 719	0.76
Ocean*	184.0±12.8	0.47±0.05	0.12±0.03	12 033	0.92

H_∞: asymptotic value; k: growth parameter; t_0: adjustment parameter; F_{ratio}: value of the Fisher's test performed on the analysis of variance of the model adjustment; R^2: coefficient of determination. * paired sites for which model parameters were not significantly different.

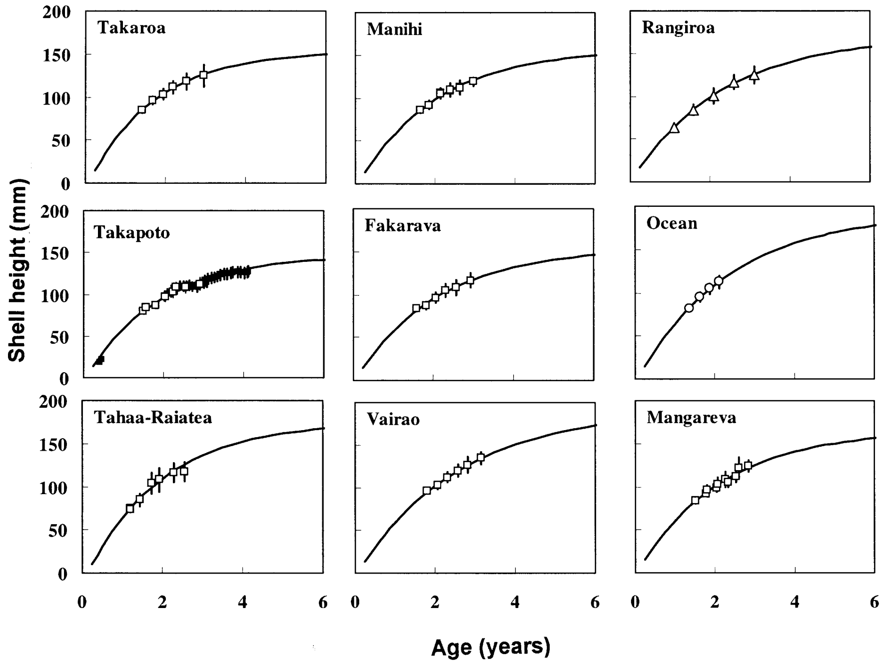

Figure 3. Von Bertalanffy models for the growth of *P. margaritifera* at nine sites in French Polynesia. Means ± SE.

$P < 0.05$). Both H_∞ and k were higher in island and ocean sites (160.0 mm and 0.57 year^{-1}, respectively) than in atoll sites (151.2 mm and 0.54 year^{-1}, respectively).

The Von Bertalanffy model was subsequently applied, separately, to each of the nine data sets (*table III*). Previous tests for common parameters showed that the adjustment parameter, t_0, was not significantly different within either the atoll group ($F_{ratio} = 0.30$, $P > 0.05$) or the islands group ($F_{ratio} = 0.74$, $P > 0.05$). Consequently, this parameter was set as being common between the equations of both groups. Concordance between models and observations are shown on *figure 3*. Adjustment of each model was satisfactory (R^2 was always above 0.75). The asymptotic size, H_∞, ranged from 147.0 mm (± 2.0 SE) to 186.5 mm (± 5.4 SE) according to the study sites. In accordance with previous results, the lowest H_∞ values were obtained in atolls. The k parameter varied from 0.42 year^{-1} (± 0.02 SE) to 0.58 year^{-1} (± 0.02 SE) according to the site, although no significant differences were demonstrated between the atoll group and the island group for this parameter (ANOVA, $F_{ratio} = 2.55$, $P = 0.15$).

Figure 4 provides a synthesis of all of these models and reveals that growth differences between atolls and islands became highly significant for > 2 year old pearl oysters, whereas below this size growth was generally similar. This graph also demonstrates that some models exhibit exactly the same shape. Paired comparisons were performed to test the hypothesis of a common value of H_∞, k and t_0 between these close models. Concerning the atoll group, tests revealed that models for Rangiroa and Mangareva were not significantly different ($F_{ratio} = 3.79$, $P > 0.05$). The same hypothesis was also accepted between Tahaa-Raiatea and Ocean ($F_{ratio} = 0.13$, $P > 0.05$).

3.2. Site classification

Several calculations of interest were deduced from these models (*table IV*). Firstly, the growth performance index Φ, was computed and ranged from 4.07 to 4.21. In accordance with previous results, Φ values were significantly lower (ANOVA, $F_{ratio} = 7.81$, $P = 0.03$) in atolls ($\Phi = 4.09 \pm 0.02$ SE) than on islands or in open ocean ($\Phi = 4.16 \pm 0.02$ SE). The lowest growth performances occurred in Takapoto and Fakarava ($\Phi = 4.07$ in both atolls), whereas the highest performances were observed in Tahaa-Raiatea and in open ocean ($\Phi = 4.20$ and 4.21, respectively). Two other parameters were computed: the time for pearl oysters to reach a size of 100 mm, T_{100}, and the annual growth increment after this time, P_S. T_{100} ranged from 21 to 26 months, and this time was longer in atolls (around 25 months) than in islands or open ocean (around 22 months). Conversely, P_S was lower in atolls ($P_S = 21.3 \pm 0.9$ mm·year^{-1}) than on islands or in open ocean ($P_S = 26.1 \pm 0.6$ mm·year^{-1}). The lowest values were reached in Takapoto and Fakarava (19.7 and 20.8 mm·year^{-1}, respectively), whereas the highest values were obtained in Tahaa-Raiatea and open ocean (30.8 and 31.8 mm·year^{-1}, respectively).

Table IV. Growth potentialities of the nine sites based on three parameters.

Sites	ϕ	T_{100} (months)	P_S (mm·year^{-1})
Atolls	4.09	25	21.3
Takapoto	4.07	26	19.7
Fakarava	4.07	26	20.8
Takaroa	4.15	22	24.4
Manihi	4.10	25	23.1
Rangiroa*	4.11	25	24.4
Mangareva*	4.12	24	24.8
Islands and ocean	4.16	22	26.1
Vairao (Tahiti)	4.16	23	29.6
Tahaa-Raiatea*	4.20	21	30.8
Ocean*	4.21	21	31.8

Φ: growth performance index; T_{100}: time to obtain a 100 mm height pearl oyster; P_S: annual growth increment at this size. * paired sites for which model parameters were not significantly different.

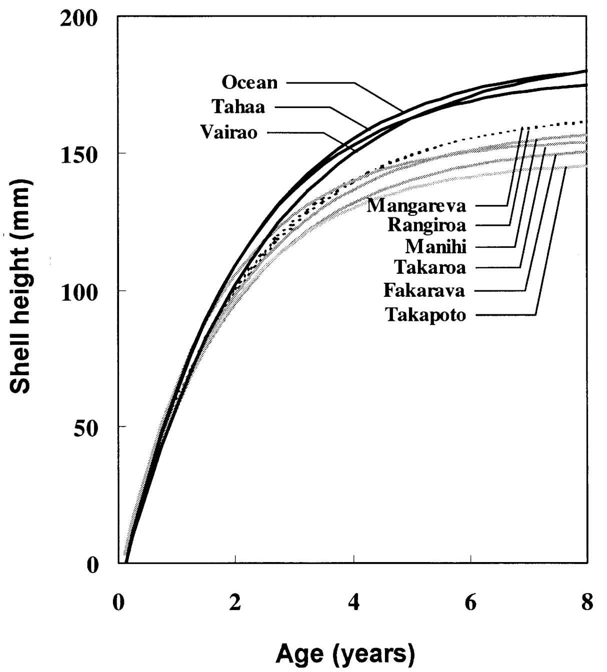

Figure 4. Comparison between the nine growth models obtained for *P. margaritifera*. Models obtained in ocean or island sites were significantly higher than models obtained in atolls sites.

Using these last results, the potential pearl farming performances for each of the nine sites were described by plotting P_S versus T_{100} (*figure 5*). Three distinct groups were observed: 1) high performance sites (i.e., low T_{100}, high P_S) are located in the upper left corner (Ocean, Tahaa-Raiatea, Vairao), 2) medium

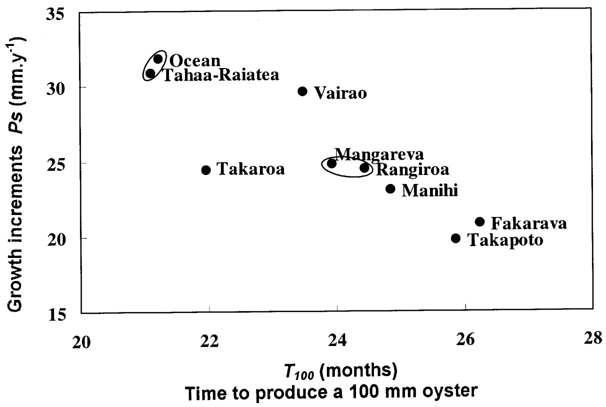

Figure 5. Annual growth increment P_S versus T_{100}. Sites for which differences were not significant are circled.

performance sites are located in the middle of the figure (Mangareva, Takaroa, Rangiroa, Manihi), and 3) lower performance sites are represented in the lower right corner (Takapoto and Fakarava).

4. DISCUSSION

4.1. Von Bertalanffy growth model

As a general rule, growth rates are directly related to bivalve age. Shell growth in *P. margaritifera* was rapid up to the third year and became reduced thereafter, regardless of study site (this work but also Nalluchinnappan et al., 1982; Gervis and Sims, 1992; Numaguchi, 1994). This decrease with age is strongly linked to the progressive investment in reproduction, since the part of the scope for growth which is allocated to reproduction, called the reproductive effort (*ER*; Thompson, 1984), is lost for shell or tissue growth. This decrease can also be explained on the basis of physiological concepts (anabolism/catabolism budget, Von Bertalanffy, 1957). Whatever the explanation, bivalves progressively reach a maximum size. The shape of the growth curve obtained is often assessed using the Von Bertalanffy model, a model widely applied in the fisheries literature (see review in Moreau, 1987). This equation is very convenient to describe and summarise growth data. Nevertheless, this kind of equation has also been widely criticised (e.g. Roff, 1980) and other more generic models have been proposed as a replacement (Schnute and Richards, 1990). In this work, the Von Bertalanffy equation was used in order to allow a comparison with growth curves previously obtained for Pteriidae. For information, we have also proposed other growth models for *P. margaritifera* cultivated in Takapoto (Pouvreau et al., 2000b).

Requirements to fit a Von Bertalanffy equation are generally as follows: 1) age is assumed to be well known, and 2) growth data should cover a wide range of ages. In the available data sets, these conditions were partly met. The age was estimated based on the summer spat fall, such that error in estimation was ± 3 months. Such uncertainties with respect to age may have consequences on the t_0 parameter estimates. Moreover, for some sites the range of age variation was too restricted (for example for the Ocean site) also leading to a less accurate fitting. Future work on *P. margaritifera* growth in Polynesia should take into account these remarks on methodology.

4.2. Growth variability

Conspecific bivalves generally display a considerable inter-specific range of growth rates. For Pteriidae, particularly the *Pinctada* genus, the lowest H_∞ values have been obtained for *P. fucata* (Chellam, 1988), *P. mazatlanica* (Saucedo and Monteforte, 1997) and *P. margaritifera* var. *erythraensis* (Elnaeim, 1984), which average 79.3, 84.9 and 125.5 mm, respectively. Conversely, these three small sized species exhibit higher *k* values and their life expectancies are shorter, being in the order of 3–4 years (Gervis and Sims, 1992). The highest H_∞ values within the *Pinctada* genus would appear to have been obtained for *P. maxima* (Yukihira et al., 1999, reported maximum mean shell height above 200 mm). In this respect, a classification of pearl oyster growth performance is proposed on the basis of the Φ parameter (a combination of *k* and H_∞), since Φ depends strongly on the species (*figure 6*). This graph clearly demonstrates that *P. margaritifera* holds an intermediary position among the pearl oyster growth potentialities.

Concerning intra-specific growth variability, our study demonstrated that *P. margaritifera* var. *cumingi* exhibited significant differences between the sites

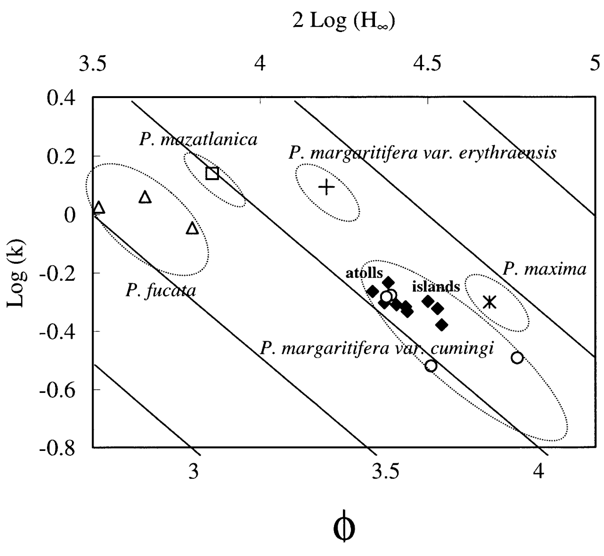

Figure 6. 3-D plot linking the growth parameters (*k*, H_∞ and Φ) for several species of pearl oysters.

investigated in French Polynesia. The growth performance index Φ ranged, respectively, from 4.09 to 4.21 in our study. The Φ value, recalculated from data previously obtained in Takapoto by Coeroli et al. (1984), was equal to 4.22 (H_∞ = 148.9 mm and k = 0.76 year^{-1}), which was in total concordance with our results. Working in the Cook Islands, Sims (1994) also compared growth of *P. margaritifera* var. *cumingi* at different sites and under different culture conditions. The reported Φ values for these cultivated pearl oyster ranged widely, from 3.99 to 4.29, according to the investigated site and/or culture technique. Although the range of variation was higher than in our study, the global mean was similar, being in the order of 4.1, thus implying that similar medium growth occurs at both the Cook Islands and French Polynesia. In both regions, however, significant inter-site variations were recorded.

Within a given genus, intra-specific growth variations of a cultivated bivalve can be due to many interacting endogenous and exogenous factors. Among the endogenous factors, genetic potentialities and neurohormonal expression are presumably the most important. Among exogenous factors, the environment (food supply, temperature, etc.) and farming conditions (density, depth, trophic competitors) are certainly predominant.

Concerning this last point, previous studies have demonstrated that depth, stocking density and biofouling are responsible for growth differences in pearl oysters cultures (Chellam, 1978; Nasr, 1984). In the present study, farming conditions were very similar between sampling designs (long line system, 7–10 m deep), the density was low (< 20 oysters·m^{-3}) and pearl oysters were cleaned periodically to prevent bio-fouling. Farming conditions can therefore not explain the significant differences observed between the atolls and islands.

Genetic differences between experimental populations can also be involved, that is to say populations that do not have exactly the same origin. This hypothesis was easy to reject, however, since the growth curves of the same population placed in Vairao lagoon and Takapoto Lagoon exhibited completely different growth curves at these two sites.

Consequently, the environment was certainly the most important factor causing the variability in growth observed in this study. Bivalve growth increments are, in fact, known to be strongly influenced by environmental conditions such as food supply and water temperature (e.g. Pandya, 1976; Gokhale et al., 1954; Del Rio-Portilla et al., 1992 for Pteriidae). In our study, water temperature values were available for the nine sites (*table I*). It is apparent that sites with low growth performances were those for which temperature reached or exceeded 30°C. Such high temperatures may have negative effects on pearl oyster growth by increasing basal metabolism. However, although this hypothesis seems reasonable, further investigations are required to test the effect of high temperature

(> 30°C) on the growth of *P. margaritifera*. Moreover, testing this hypothesis is all the more interesting since such high temperatures are generally more frequently encountered during El Niño events.

Polynesian atoll lagoon waters are characterised by very low particulate organic matter (POM) concentra tions (e.g. Charpy et al., 1997; Buestel and Pouvreau, 2000), whereas POM is generally more abundant in island lagoons as a result of terrigeneous inputs (Ricard and Delesalle, 1984;Ricard and Rougerie, 1984). Such a difference in POM concentrations between atolls and islands, which results in a difference in the amount of potential food for pearl oysters, should at least partly explain the variability in growth observed between these two habitats. However, this hypothesis does not hold true in the present study, as growth of pearl oysters in open ocean was demonstrated to be maximal, an environment that is well known to contain lower POM values than do lagoons (Charpy et al., 1997). In fact, this paradoxical observation is explained by the fact that *P. margaritifera* has been shown to be 1) adapted to fast growth in low turbid environments thanks to a high pumping activity ensured by large developed gills (Pouvreau et al., 1999), and 2) less efficient than *P. maxima* when turbidity increases significantly (Yukihira et al., 1999).

Another environmental parameter may also be determinant in the growth of *P. margaritifera*: the very high pumping capacity of *P. margaritifera* implies that there is a high renewal of food supply around the bivalve, which is ensured by a sufficient water current around the long lines (Pouvreau et al., 2000a). Consequently, instead of POM concentration, the factor responsible for such growth variability is perhaps flow velocity and consequent food renewal at the study site. This hypothesis is in total accordance with the negative effect of water confinement on pearl oyster growth (Pagès et al., 2001). Unfortunately, current speed values were not available for the investigated sites. Personal diving observations, however, suggest that, in closed lagoons such as Takapoto, currents are presumably lower than those in either open ocean or open lagoons, such as Rangiroa or Vairao. Consequently, it would appear that water flow and food renewal are the determinant factors in the growth of *P. margaritifera* and further investigations will need to explore this area of research.

5. CONCLUSIONS AND PERSPECTIVES

We can conclude that the black-lip pearl oyster *Pinctada margaritifera* var. *cumingi* exhibits relatively fast growth in Polynesian waters. This growth performance is intermediate in comparison to that of *P. fucata* and *P. maxima*. Moreover, a geographic growth variability was demonstrated with higher performances in island lagoons and in open ocean than in atoll lagoons. It should be noted that our work, as is true for other growth studies conducted on pearl oysters, was restricted to the measurement of shell increments (e.g. Coeroli et al., 1984; Gervis and Sims, 1992; Sims, 1994; Saucedo and Monteforte, 1997), since nacre is the main product of this particular activity. Growth rate in terms of tissue weight, however, may also be of interest, especially to test pearl oyster health (index condition). Few studies have focussed on this aspect of pearl oyster research (Pouvreau et al., 2000b). Consequently, although the present study has demonstrated significant differences in growth performance between several sites of French Polynesia, further investigations involving condition index and mortality parameters are required to adequately test and classify the suitability of potential pearl farming sites in French Polynesia.

Acknowledgements. This work is a synthetic study of several sampling designs engaged during the *Programme général de recherche sur la nacre*, which was coordinated in French Polynesia by the SRM (*Service des ressources marines*). Sampling designs were conducted thanks to the valuable field assistance of numerous voluntary pearl farmers, the SRM field laboratories (G. Haumani, I. and J. Moeroa, J. Flores, L. Orbeck, P. Choune, E. Millaud, H. Leduc, A. Pellan, M. Pakai) and the Dive Services Company (P. Jilcot, S. Diallo). This work had also benefited from the very useful help, comments and advice of the SMA (H. Leduc) and SRM centres (C. Monier, L. Henmann, J.M. Laughlin), IFREMER–COP (J. Prou, A. Bodoy, J. Tiapari, A. Bennett, H. Teissier, F. Lagarde, M. Garnier, S. Robert, G. Jonquières and X. Caisey), IRD (J. Pagès), CAIRAP (B. Costa) and UPF (C. Payri, L. Addessi), implanted on Tahiti Island. Special thanks to Dr. M. Johnson for her very beneficial English corrections.

References

Andrefouët, S., 1998. Apport de la télédétection à une approche descriptive et fonctionnelle des systèmes coralliens de Polynésie Française. Thesis. Université du Pacifique, Tahiti.

Buestel, D., Pouvreau, S., 2000. La matière particulaire des eaux du lagon de Takapoto: nourriture potentielle pour les élevages d'huîtres perlières. Oceanol. Acta 23, 193–210.

Charpy, L., Dufour, P., Garcia, N., 1997. Particulate organic matter in sixteen Tuamotu Atoll lagoons (French Polynesia). Mar. Ecol. Prog. Ser. 151, 55–65.

Chellam, A., 1978. Growth of pearl oyster *Pinctada fucata* in the pearl culture farm at Veppalodai. Indian J. Fish. 25, 77–83.

Chellam, A., 1988. Growth and biometric relationship of pearl oyster *Pinctada fucata* (Gould). Indian J. Fish. 35, 1–6.

Coeroli, M., De Gaillande, D., Landret, J.P., 1984. Recent innovations in cultivation of molluscs in French Polynesia. Aquaculture 39, 45–67.

Coeroli, M., Mizuno, K., 1985. Study of different factors having an influence upon the pearl production of the black-lip pearl oyster, Proceedings of the 5th International Coral Reef Symposium, Tahiti, pp. 551–556.

Del Rio-Portilla, M.A., Re-Araujo, A.D., Voltolina, D., 1992. Growth of the pearl oyster *Pteria sterna* under different thermic and feeding conditions. Mar. Ecol. Prog. Ser. 89, 221–227.

Elnaeim, A.G., 1984. Variability in growth of the mother of pearl oyster (*Pinctada margaritifera*) in the Red Sea (Sudan). Ph. D. Thesis. Dalhousie University, Halifax, NS.

Gervis, M.H., Sims, N.A., 1992. The biology and culture of pearl oysters (Bivalvia: Pteriidae). ICLARM Stud. Rev., 21.

Gokhale, S.V., Eswaran, C.R., Narasimhan, R., 1954. Growth rate of the pearl oyster *Pinctada pinctada* in the Gulf of Kutch with a note on the pearl fishery of 1953. J. Bombay Nat. Hist. Soc. 52, 124–136.

Grant, J., Dowd, M., Thompson, K., Emerson, C., Hatcher, A., 1993. Perspectives on field studies and related biological models of bivalve growth and carrying capacity. In: Dame, R.F. (Ed.), Bivalves Filter Feeders in Estuarine and Coastal Ecosystem Processes. NATO ASI Series G33. Springer-Verlag, Berlin, pp. 371–421.

Héral, M., Bacher, C., Deslous-Paoli, J.M., 1989. La capacité biotique des bassins ostréicoles. In: Troadec, J.P. (Ed.), L'homme et les ressources halieutiques. Ifremer, Paris, pp. 225–259.

Hynd, J.S., 1955. A revision of Australian pearl shells, genus *Pinctada*. Aust. J. Mar. Freshwater Res. 6, 98–137.

Kashiwai, M., 1995. History of carrying capacity concept as an index of ecosystem productivity (review). Bull. Hokkaido Natl. Fish. Res. Inst. 59, 81–100.

Moreau, J., 1987. Mathematical and biological expression of growth in fishes: recent trends and further developments. In: Summerfelt, R.C., Hall, G.E. (Eds.), Age, growth of fish. Iowa State University Press, Ang, IA, pp. 81–113.

Munro, J.L., Pauly, D., 1983. A simple method for comparing the growth of fishes and invertebrates. Fishbyte 1, 5–6.

Nalluchinnappan, I., Sudhandra dev, D., Irulandi, M., Jeyabaskaran, Y., 1982. Growth of pearl oyster *Pinctada fucata* (Gould) in cage culture at Kundugal channel, Gulf of Mannar. Indian J. Mar. Sci. 11, 193–194.

Nasr, D.H., 1984. Feeding and growth of the pearl oyster *Pinctada margaritifera* (L.) in Dongonab Bay, Red Sea. Hydrobiologia 110, 241–245.

Numaguchi, K., 1994. Growth and physiological condition of the japanese pearl oyster, *Pinctada fucata martensii* (Dunker, 1850) in Ohmura bay, Japan. J. Shellfish Res. 13, 93–94.

Pagès, J., Andrefouët, S., Delesalle, B., Prasil, V., 2001. Hydrology and trophic state in Takapoto atoll lagoon: comparison with other Tuamotu lagoons. Aquat. Living Resour. 14.

Pandya, J.A., 1976. Influence of temperature on growth ring formation in the pearl oyster, *Pinctada fucata* (Gould) of the Gulf of Kutch. Indian J. Mar. Sci. 5, 249–251.

Pouvreau, S., Bacher, C., Héral, M., 2000a. Ecophysiological model of growth and reproduction of the black pearl oyster, *Pinctada margaritifera*, in the planktonic food web of Takapoto Lagoon (French Polynesia). Aquaculture 186, 117–144.

Pouvreau, S., Jonquières, G., Buestel, D., 1999. Filtration by the pearl oyster, *Pinctada margaritifera*, under conditions of low seston load and small particles size in a tropical lagoon habitat. Aquaculture 176, 295–314.

Pouvreau, S., Tiapari, J., Gangnery, A., Lagarde, F., Garnier, M., Teissier, H., Haumani, G., Buestel, D., Bodoy, A., 2000b. Growth of the black-lip pearl oyster, *Pinctada margaritifera*, in suspended culture under hydrobiological conditions of Takapoto Lagoon (French Polynesia). Aquaculture 184, 133–154.

Ricard, M., Delesalle, B., 1984. Le lagon de Scilly. In: Les écosystèmes lagonaires de Polynésie française, état des connaissances (Ed.), Orstom Éditions, Papeete, pp. 107–109.

Ricard, M., Rougerie, F., 1984. Baie de Port-Phaeton. In: Les écosystèmes lagonaires de Polynésie française, état des connaissances (Ed.), Orstom Éditions, Papeete, pp. 92–94.

Roff, D.A., 1980. A motion for the retirement of the Von Bertalanffy function. Can. J. Fish. Aquat. Sci. 37, 127–129.

Saucedo, P., Monteforte, M., 1997. In situ growth of pearl oysters *Pinctada mazatlanica* (Hanley, 1856) and *Pteria sterna* (Gould, 1851) under repopulation conditions at Bahia de La Paz, Baja California Sur, Mexico. Aquac. Res. 28, 367–378.

Schnute, J.T., Richards, L.J., 1990. A unified approach to the analysis of fish growth, maturity, and survivorship data. Can. J. Fish. Aquat. Sci. 47, 25–40.

Sims, N.A., 1993. Size, age and growth of the black-lip pearl oyster, *Pinctada margaritifera* (L.) (Bivalvia, Pteriidae). J. Shellfish Res. 12, 223–228.

Sims, N.A., 1994. Growth of wild and cultured black-lip pearl oysters, *Pinctada margaritifera* (L.) (Bivalvia, Pteriidae). Aquaculture 122, 181–191.

Thompson, R.J., 1984. Production, reproductive effort, reproductive value and reproductive cost in a population of the blue mussel *Mytilus edulis* from a subartic environment. Mar. Ecol. Prog. Ser. 16, 249–257.

Von Bertalanffy, L., 1938. A quantitative theory of organic growth. Hum. Biol. 81, 181–213.

Von Bertalanffy, L., 1957. Quantitative laws on metabolism and growth. Q. Rev. Biol. 32, 217–231.

Yukihira, H., Klumpp, D.W., Lucas, J.S., 1999. Feeding adaptations of the pearl oysters *Pinctada margaritifera* and *P. maxima* to variations in natural particulates. Mar. Ecol. Prog. Ser. 182, 161–173.