
Growth and gonad development of the tropical black-lip pearl oyster, *Pinctada margaritifera* (L.), in the Gambier archipelago (French Polynesia)

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Abstract:

The growth and reproductive cycle of cultured black-lipped pearl oysters, *Pinctada margaritifera* (L.), were studied in the Gambier Islands (134°52' W, 23°07' S) from September 2002 to August 2003. Temperatures were recorded throughout the year, revealing seasonal temperature variations between 22.3 and 27.8°C. The mean annual chlorophyll *a* value, as computed from satellite data, was $0.188 \pm 0.075 \mu\text{g L}^{-1}$. To study growth and reproduction, 720 two-year-old individuals were ear hung on long-lines suspended at a depth of 7 m. Samples were taken twice a month to obtain the following measurements: shell height; wet weight of flesh and total oyster; dry weight of adductor muscle, mantle and visceral mass; and glycogen content. Gonad development was also studied by histology on parallel samples. Growth was relatively fast during the first 6 months of the study: average shell height increased from 89.1 ± 9.1 to 119.7 ± 10.8 mm and total weight from 93.4 ± 24.5 to 155.1 ± 33.6 g, between September and the end of March. Subsequently, from April to August, no significant growth was observed for shell and flesh, while the muscle weight decreased significantly. Condition index (CI), defined as the ratio of wet weight of the visceral mass to shell weight, and histological changes in the gonad revealed 3 significant reproductive events of different intensities. The analysis of correlations revealed a specific effect of the chlorophyll *a* concentration on the growth of shell and soma, and one of the temperature on tissue glycogen content. This study also showed also that CI could be an efficient indicator of reproductive events in pearl oyster. It thus appears that the development of gonads goes on throughout the year in the Gambier Islands, without any detectable phase of sexual rest.

Keywords: Pearl oyster – *Pinctada margaritifera* – Growth – Reproduction – Temperature – Chlorophyll – Seasonality – Gambier archipelago

45 **Introduction**

46 Pearl oyster farming in French Polynesia is spread over a large geographical area.
47 Environmental conditions vary between islands in this part of the South Pacific, particularly
48 due to differences in their latitudinal position. Seasonal cycles are more marked in southern
49 Polynesia than further north. The annual reproductive cycle of *Pinctada margaritifera* was
50 studied in the Takapoto atoll of the northern Tuamotu Islands, showing that reproduction
51 occurs throughout the year due to a high average temperature with low seasonal variation
52 (Thielley 1993, Pouvreau *et al.* 2000a). Adequate data on the marine environment and the
53 reproduction of pearl oysters are, however, not yet available for other islands with pearl oyster
54 farming. The largest thermal amplitude in French Polynesia (Salvat *et al.* 2008) is observed in
55 the Gambier Islands (134°52' W, 23°07' S). Although reproduction of *P. margaritifera* still
56 occurs in these islands, its reproductive cycle has not yet been described.

57 In the southern part of its distribution (Australia), the reproductive cycle of *Pinctada albina*
58 has been observed to be modulated by seasonal temperature variations (O'Connor 2002). The
59 reproductive cycle of the pearl oyster *Pinctada mazatlanica* is also affected by seasonal
60 variations in temperature in Baja California (Saucedo *et al.* 2002), where a period of intense
61 sexual activity is observed in September when water temperature is high. Temperature
62 changes due to El Nino and La Nina events have also been reported to affect the reproductive
63 cycle of *P. mazatlanica* (Garcia-Cuellar *et al.* 2004).

64 The trophic environment is also known to act on the reproductive status of *P. margaritifera*
65 (Pouvreau, *et al.* 2000b). In French Polynesia, due to low chlorophyll *a* concentrations, the
66 trophic environment is considered oligotrophic. Data on phytoplanktonic pigments have been
67 obtained in the Takapoto atoll in northern Tuamotu (southern hemisphere), where
68 concentration in chlorophyll *a* ranged between 0.05 and 0.46 $\mu\text{g} \cdot \text{L}^{-1}$ (Delesalle *et al.* 2001).

69 Very little information on these parameters has been collected for the southern islands
70 (Gambier Islands).

71 The objective of the present study was to examine the effect of the annual cycle of
72 temperature and chlorophyll *a* concentration on the reproductive cycle of *P. margaritifera*, to
73 determine whether local environmental conditions in the Gambier Islands induce any marked
74 seasonality in the reproductive cycle of this tropical pearl oyster species.

75 **Material and methods.**

76 ***Gambier Islands***

77 Pearl culture has developed in several sites in the Gambier Islands (134°52' W & 23°07' S), an
78 Archipelago located in southeast French Polynesia (South Pacific).

79 ***Environmental data***

80 Temperature was recorded hourly *in situ* using an automatic sensor (TidbiT temp Logger-
81 Onset®). Chlorophyll *a* concentration (*Chl a*) data were derived from radiometric ocean
82 colour provided by the Sea viewing Wide Field of view Sensor (SeaWiFS) onboard the
83 [SeaStar spacecraft](#) (McClain et al., 2004). *Chl a* data were provided weekly from September
84 2002 to August 2003.

85 ***Sampling***

86 Growth and reproduction of *P. margaritifera* were studied in pearl oysters reared in the
87 Gambier lagoon (134°52' W, 23°07' S). The cultivation technique was similar to that
88 commonly used in commercial farms. Suspended long-lines were immersed at a depth of 7 m
89 and pearl oysters were 'ear hung' on downlines in groups of ten. The reproductive cycle was
90 studied over a year (from September 2002 to August 2003) by systematic sampling of 30
91 randomly selected individuals every 15 days. These pearl oysters were collected, cleaned of
92 fouling organisms and sent by air to the Ifremer laboratory on Tahiti Island.

93 ***Biometry***

94 For all specimens (n = 720), total weight and height of the shell were measured prior to
95 dissection, weighing, sexing and histology. Sex was determined by rapid microscopic
96 observation of fresh gonad smears. Glycogen content was then measured on 5 dried oysters
97 for each sampling and the visceral mass of 15 other oysters was placed in Davidson's fixative
98 for gonad histology.

99 Total wet flesh weights were obtained after 15 min of draining. After flesh dissection, the
100 same operation was conducted separately on adductor muscle, gills + mantle and the visceral
101 mass (gonad + digestive gland). Condition index (CI) was computed as the ratio of visceral
102 mass weight to shell weight.

103 ***Glycogen measurement***

104 Dry tissues of oyster were powdered and a 10-mg sample was then homogenized in 1 ml of
105 de-ionized water. Changes in the glycogen composition of tissue over the year were
106 quantified using the phenol-sulphuric acid method of Dubois *et al.* (1956).

107 ***Histology***

108 After dissection, gonadal tissue samples were placed in Davidson's fixative for five days,
109 after which they were preserved in 70 % ethanol. Samples were then dehydrated through a
110 graded ethanol series, embedded in paraffin, sectioned at 3–4 μm on a rotary microtome,
111 stained with Giemsa dye and, finally, mounted on microscope slides. Sections were made in
112 the gonad area, between the proximal end of the gut loop and the base of the foot. Slide
113 preparations were examined with a light microscope to scan the entire gonadal area and assess
114 follicle stages. Reproductive stages of gonad development are based on the description by
115 Pouvreau *et al.* (2000a) shown in table 1.

116

117 ***Statistics***

118 The growth parameters shell height, total weight, flesh and tissue weights and glycogen
119 content in dried tissue are presented on the figures, with vertical bars representing the 95 %
120 confidence intervals. Correlations between environmental and physiological variables were
121 tested using the critical value table for Pearson's correlation coefficient at the 5 % alpha level
122 and 108 df. The null hypothesis was rejected when $r < 0.195$.

123 **Results**

124 ***Environmental data***

125 Water temperature gradually increased from the end of September up to a peak in March and
126 then declined to its lowest value in August. Mean annual water temperature was 25.42 ± 1.75
127 °C, with a minimum of 22.3 °C and a maximum of 27.8 °C (Fig. 1a). The annual mean value
128 of *Chl a* was $0.188 \pm 0.075 \mu\text{g L}^{-1}$, while the maximum value of $0.436 \mu\text{g L}^{-1}$ was reached in
129 August 2003 (Fig. 1b). The gaps in the data are due to cloud cover.

130 ***Pearl oyster growth***

131 Shell height and total weight increased regularly over the sampling period (Fig. 2a, 2b). The
132 growth rates in terms of shell height and total weight were $87.40 \mu\text{m.d}^{-1}$ and 176.1g.d^{-1} ,
133 respectively. From September 2002 to February 2003, flesh dry weight remained stable (Fig.
134 2c). A rapid increase then occurred from February 2003 to mid March 2003, followed by a
135 period during which mean flesh dry weight stabilised once more. Muscle dry weight showed
136 large variations over the year, with the highest value in mid-March (Fig. 3). Changes in
137 weight of the visceral mass were recorded twice, in mid-April and mid-August. (Fig. 3).

138 ***Gametogenic cycle***

139 The condition index (CI) showed three significant decreases, the first in December, the second
140 in March and the third in June, while two non-significant changes of CI occurred in May and

141 August (Fig. 4). Three significant increases of CI were recorded during this study; the first
142 time was in October, one month before the first significant decrease, the second time was in
143 April, just after the second significant decrease, and the third in July, just after the third
144 significant decrease (Fig. 4).

145 The temporal distribution of maturity stages over the year is shown in Figure 5. The three
146 significant CI decreases coincided with increases in the frequency of inactive (0) and early
147 gametogenic (1) stages, and the decrease in frequency of stages 2 to 5, thus meaning that three
148 significant spawning events had occurred. The first spawning event in December was
149 smallest, since the frequency of the stage 0 and 1 was low. The spawning event in March
150 affected > 70 % of oysters, since these were found to be at stage 1 of the maturity index,
151 while in May and June, spawning only affected > 30 %. In August, the non-significant
152 decrease of CI coincided with a 7 % frequency of stage 1.

153 ***Sex ratio***

154 The sex of all individuals was determined during this study. Figure 6a illustrates the change in
155 of this protandrous alternate hermaphrodite sex ratio over the year, while figure 6b represents
156 the change in sex ratio according to the size of individuals. On average, 7 % of individuals
157 were female, the highest value being 14 %. Only animals larger than 80 mm were female. The
158 proportion of females increased up to 22 % for individuals larger than 140 mm.

159 ***Glycogen content***

160 Glycogen content in muscles significantly increased to 200 mg. g⁻¹ between February and
161 May. In February, glycogen content increased significantly in the mantle, while it remained
162 unchanged in the visceral mass (Fig. 7).

163 ***Regression analysis***

164 Growth parameters (shell, flesh and tissue) were positively ($p < 0.05$) correlated with Chl *a*
165 (Table 2). Glycogen content in VM and gill-mantle were negatively with Chl *a*, but glycogen
166 content in all tissues was positively correlated with water temperature (Table 2). Data related
167 to reproductive processes (CI) were not correlated with either chlorophyll or water
168 temperature (Table 2).

169 **Discussion**

170 ***Environmental data***

171 Temperature recordings during this study (2002-2003) revealed an annual thermal amplitude
172 (6 °C) that was smaller than the one observed in 1998-1999 (8 °C) during the strong El Niño-
173 La Niña events. In comparison, the thermal amplitudes observed in the atolls of northern
174 French Polynesia were 2 °C in 1990-1991 (Buestel and Pouvreau, 2000) and 4 °C in 1998-
175 1999 (Pouvreau, 1999). Radiometric ocean colour derived from satellite observations was
176 extracted for the eastern part of the Gambier archipelago in 2002 and 2003. Two difficulties
177 arose. One was due to cloud cover, which interrupted the continuity of the time series. The
178 second was related to the fact that ocean color is derived from radiance leaving the water,
179 which may be influenced by water depth and bottom albedo (Maritorena et al., 1994).
180 Interpretation of Chl *a* variability must therefore to be considered with caution. However, the
181 annual mean (0.19 $\mu\text{g. L}^{-1}$) and amplitude range of Chl *a* reported here are in agreement with
182 values and seasonal patterns reported in several atolls in French Polynesia from *in situ*
183 measurements (Charpy 1996; Intes et al. 1990). When considering the Chl *a* time series
184 extended to the beginning of 2002 (data not shown), the maximum value of Chl *a* that we
185 report here in August appears to be related to the Chl *a* seasonal cycle. This Chl *a* maximum
186 in austral winter is also a typical seasonal pattern of Chl *a* in Polynesian lagoons (Charpy
187 1996; Charpy et al, 2009). The large variations of Chl *a* recorded during this study are also

188 consistent with those measured in water samples from another Polynesian lagoon, Takapoto
189 (Buestel and Pouvreau, 2000). These previous authors attributed this high variability to local
190 meteorology (wind and precipitation), which had short-term, and night/day rhythms affecting
191 some parameters (temperature and chlorophyll *a*).

192 ***Growth***

193 Growth rate of pearl oysters seemed to be faster during the first six months of this study since
194 the shell height and the total weight increased by 25 mm and 63 g, respectively, in this period.
195 No further significant changes in growth were then observed from April to August. In the size
196 class considered (2-year-old oysters), shell growth was equivalent to that of oysters studied by
197 Buestel and Pouvreau (1994) in Takapoto, where shell growth was found to be 30 mm over a
198 whole year. Shell growth dynamics of pearl oysters observed in the present work were similar
199 to those found in a study conducted in 1998-1999 in the Gambier Islands (Pouvreau and Prasil
200 2001).

201 Our results showed that pearl oyster growth in the Gambier Islands was correlated with Chl *a*
202 resources, which correspond to food supply, but not with temperature. The comparison of *P.*
203 *margaritifera* growth between oysters reared in Gambier (this study; Pouvreau and Prasil
204 2001) and those reared in Pioneer Bay, north Queensland (18°37' S, 146°30' E), Australia
205 (Yukihira *et al.* 2006), reveals a similar annual growth pattern. The two sites have similar
206 temperatures, and a similar conclusion was drawn: that temperature had no significant effect
207 on growth rates of *P. margaritifera* over the annual cycle.

208 Somatic growth pattern showed two phases. From September 2002 to February 2003, the
209 flesh dry weight did not change significantly, but in March 2003 it doubled. Flesh dry weight
210 then remained stable until August 2003. This change was mainly due to muscle increase, with
211 visceral mass and mantle accounting for less. This growth event coincided with the maximum

212 temperature observed during the study, but the examination of correlations only indicated a
213 significant relationship with chlorophyll *a*.

214 ***Reproductive activity***

215 Pearl oyster reproduction was studied by Thielley (1993), and the reproductive cycle was
216 described by Pouvreau *et al.* (2000a) in the Takapoto atoll, northern Tuamotu. These authors
217 showed that, in a fairly stable tropical environment, *P. margaritifera* is a multiple spawner
218 with an opportunistic reproductive strategy that allows investment of any surplus energy into
219 gamete production throughout the year. CI variations in the present study were related to
220 quantitative losses of weight caused by gamete releases, while the histological analysis
221 revealed a degree of synchronicity within the population. Three spawning periods were
222 characterized by significant decreases of CI; these occurred in December 2002, March 2003
223 and June 2003. The decreases of CI corresponded precisely to periods of gamete release, as
224 confirmed by histological examination of gonadic stages. The first gamete emissions can be
225 regarded as resulting from the accumulation of gametes during winter. The second spawning,
226 which occurred when temperature was maximal, involved most of the oysters since
227 histological analysis showed that 80 % of them were at stage 1 or 2. This spawning was
228 followed by rematuration. A third spawning occurred in June, when the temperature
229 descended below 24 °C, as shown by a significant decrease in CI and the stages shown in the
230 histological analysis. After this event, however, 30-40 % of individuals remained at
231 histological stage 1 of maturity and a similar proportion remained at stage 2 until the
232 beginning of August. At the end of August, a non-significant decrease in CI occurred when 7
233 % of the pearl oysters were at histological stage 1; these observations could indicate a
234 spawning event, despite the fact the temperature reached 22 °C.

235 Histology validated the interest of CI as spawning indicator for the pearl oyster. Spawning
236 were triggered when CI was around 0.08 %. Before each significant spawning event, the CI

237 values were 0.084, 0.070 and 0.076 respectively in December, March and June. This study
238 has shown that CI was not correlated with temperature and did not offer any new evidence to
239 support the hypothesis that spawnings were influenced by temperature. The greatest variations
240 in CI corresponded to the spawning in December, when temperature increased up to 25 °C;
241 the one in March, when the temperature was maximal (28 °C); and the one in June, when the
242 temperature decreased below 24 °C.

243 *Sex ratio*

244 The proportion of females (7 %) did not differ from the observations made by Pouvreau *et al.*
245 (2000a) in Takapoto. Indeed, for the age/size class considered here (2-year-old oysters, 100-
246 110 mm height), the sex-ratio in Takapoto was 0.1 female/1 male. The evolution noted over
247 the year of our study was typical of this age group, in which the first inversions of sex are
248 normally known to occur (Thielley 1993). The population raised in the Gambier Islands,
249 therefore, did not differ from populations grown elsewhere in this respect.

250 *Glycogen storage*

251 Marine bivalves show cycles of energy storage and utilization that are closely related to
252 gametogenic cycles. Most species are able to store nutrient reserves during periods of food
253 abundance. These reserves are mobilized during periods of food depletion and high energy
254 demand (Bayne 1976; Barber and Blake 1981; Heude-Berthelin *et al.* 2000). During
255 gametogenesis, high-energy demands are made due to maintenance costs and gamete
256 synthesis; these have to be met by the food supply and/or stored reserves. In *P. mazatlanica*,
257 growing on the west coast of the Gulf of California, glycogen stored in the muscle and
258 digestive gland were actively used for gametogenesis (Saucedo *et al.* 2002). In *P.*
259 *margaritifera*, our results show that glycogen obtained from ingested food was mainly stored
260 in the adductor muscle and secondarily in the digestive gland, to be later used for ATP needs
261 and to produce gametes. We studied the relationship between the glycogen storage cycle and

262 gametogenesis of the pearl oyster *P. margaritifera* over the annual cycle (September 2002 to
263 August 2003). Glycogen content increased drastically, showing a 20-fold increase in muscle
264 from February 2003 to May 2003. The energy stored in the muscle could also be used at the
265 time of spawning to achieve vigorous valve movement and to increase the pressure on the
266 gonad to expel the gametes. Our result shows that the maximum glycogen content in the
267 muscle corresponded to the spawning period from March to June. Changes in glycogen
268 content were correlated with temperature in the muscle, mantle and visceral mass (digestive
269 gland and gonad), and with chlorophyll in the visceral mass. Our study confirms that mantle
270 tissue has a negligible role in storage of nutrients during reproduction in *P. margaritifera*.
271 Few changes were observed in the visceral mass over the study period. The digestive gland
272 considered as a short term storage organ (Saucedo *et al.* 2002; Vite-Garcia *et al.* 2008) did not
273 accumulate glycogen over a long period.

274 ***Conclusion***

275 The main goal of this work was to examine the hypothesis that the highest thermal amplitude
276 recorded in southern French Polynesia could generate seasonal variation of reproduction in *P.*
277 *margaritifera*. This study was conducted in the Gambier Islands, where pearl farming is an
278 important industry, and has shown that a seasonal cycle in the reproduction of the pearl
279 oysters does not exist in this area. This study showed that CI (wet weight of gonad/shell
280 weight) could be a good indicator of reproductive events in the pearl oyster. It thus appears
281 that the development of gonads goes on throughout the year in the Gambier Islands, without
282 any detectable phase of sexual rest.

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Figures

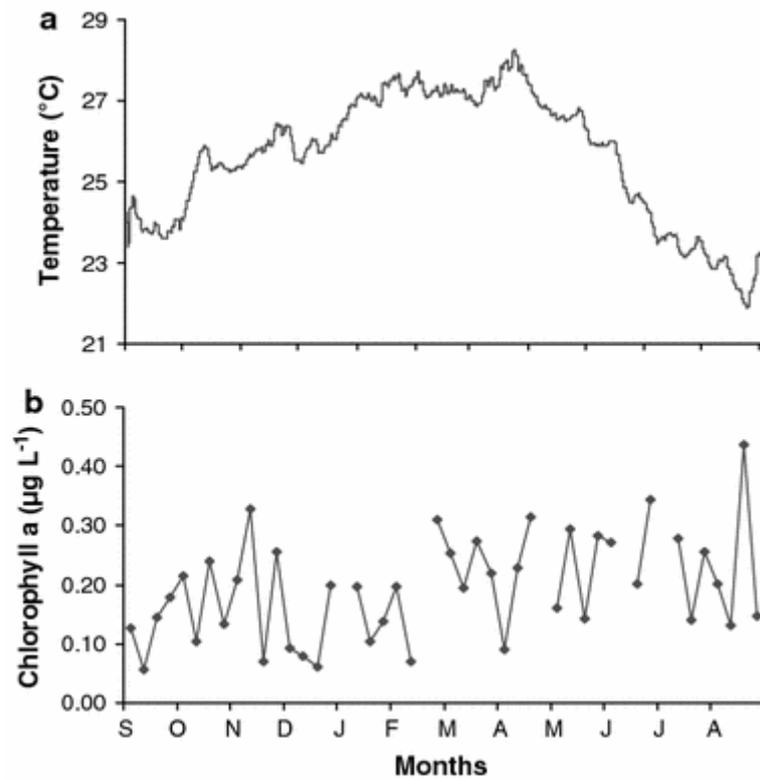


Fig. 1 Variations in temperature (a) and chlorophyll a (b) in 2002–2003 in Gambier Island. Chl a concentrations of Gambier Island (134°52' W & 23°07' S) were derived from available ocean colour data (SeaWiFS project)

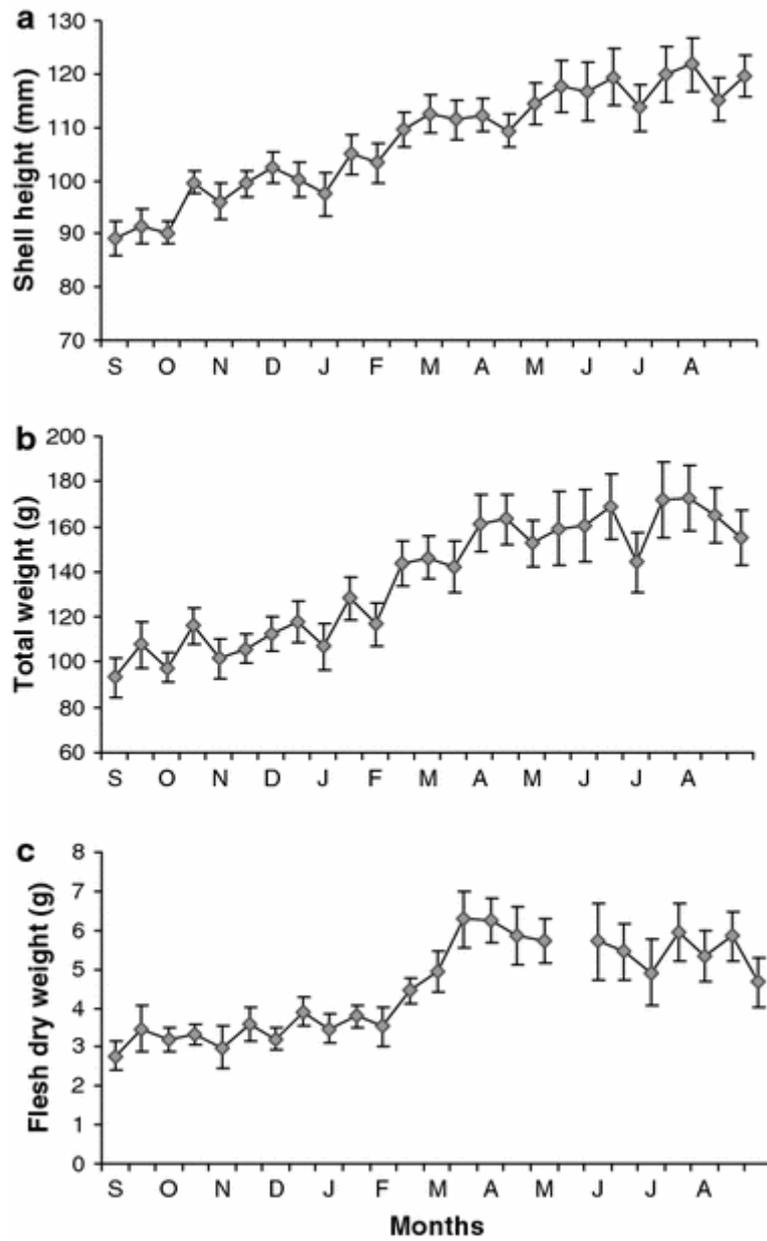


Fig. 2 Shell height (a), total weight (b) and flesh dry weight (c) (mean and confidence interval, $\alpha = 5\%$, $n = 30$) in 2002–2003 in Gambier Island

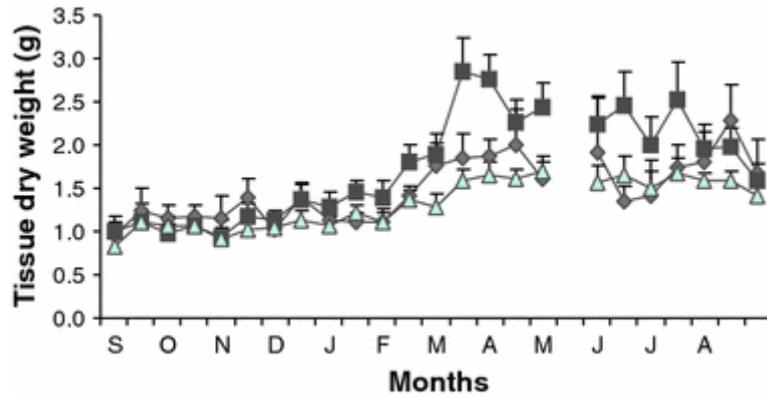


Fig. 3 Tissue dry weight (mean and confidence interval, $\alpha = 5\%$, $n = 15$) in 2002–2003 in Gambier Island: muscle (grey circles), visceral mass (black rhombuses) and gill-mantle (grey squares)

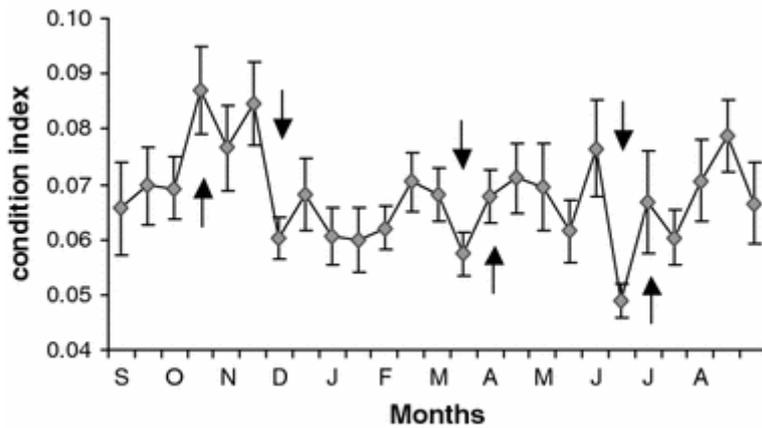


Fig. 4 Condition index (CI) (mean and confidence interval, $\alpha = 5\%$, $n = 30$) in 2002–2003 in Gambier Island (CI = visceral mass/shell weight). *Arrows indicate significant increase and reduction in conditioning indexes*

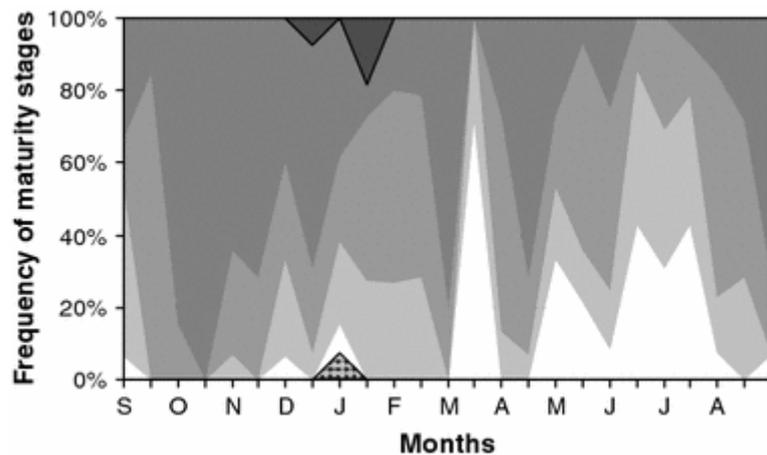


Fig. 5 Histological analysis of the evolution in the frequency of gonadal development stages in 2002–2003 in Gambier Island. *Dotted white on black = stage 0 (undetermined or inactive), white = stage 1 (spawning ripe, distended and confluent follicles, entirely filled), clear*

grey = stage 2 (actively developing without mature gametes), mid-grey = stage 3 (near ripe follicles with mature gametes), dark grey = stage 4 (spawning ripe, distended and confluent follicles, entirely filled), black = stage 5 (partially spawned, partially empty lumen), ($n = 15$)

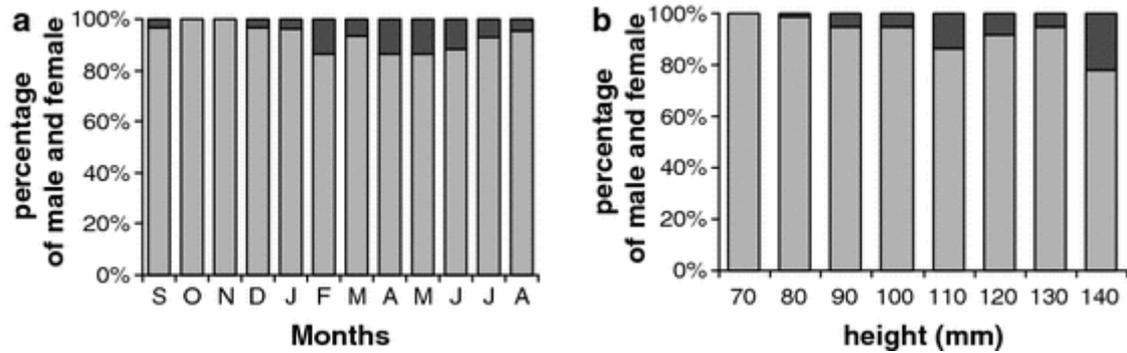


Fig. 6 Sex ratio of *P. margaritifera* in 2002–2003 in Gambier Island (a) and according to shell height (b). Female = black, male = grey ($n = 15$)

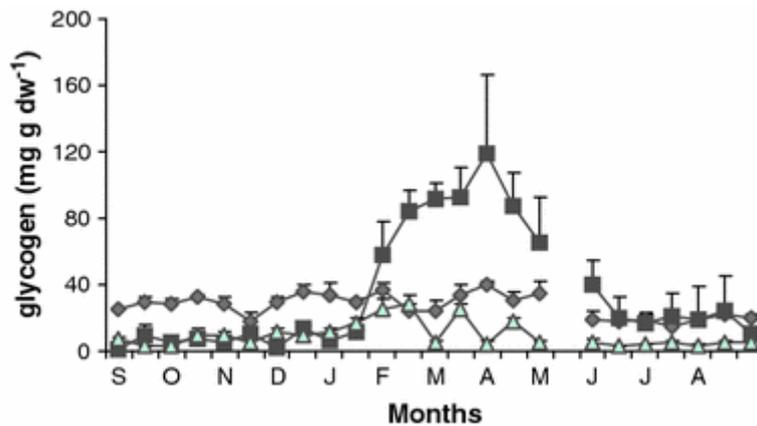


Fig. 7 Glycogen content (mean and confidence interval, $\alpha = 5\%$, $n = 5$) in 2002–2003 in Gambier Island: muscle (grey circles), visceral mass (black rhombuses), gill-mantle (dark rhombuses)

Tables

Table 1 Criteria for histological scoring of gametogenic stages according to Pouvreau et al. (2000a)

Histological criteria	Score
Undetermined or inactive	0
Early gametogenesis, numerous gonidia, small follicles	1
Actively developing without mature gametes	2
Near ripe follicles with mature gametes	3
Spawning ripe, distended and confluent follicles, entirely filled	4
Partially spawned, partially empty lumen	5

Table 2 Correlations of chlorophyll *a* or water temperature (WT) with growth parameters, glycogen content and condition index of *Pinctada margaritifera* off Gambier Island with Pearson correlation analysis ($N = 110$, $\alpha = 0.05$)

	Chlorophyll	Temperature
Shell height	0.433	-0.159
Total weight	0.351	-0.107
Flesh weight	0.239	-0.138
Tissue weight		
Visceral mass	0.215	-0.098
Add. muscle	0.306	0.023
Gill-mantle	0.334	-0.363
Glycogen		
Visceral mass	-0.310	0.602
Add. muscle	0.113	0.588
Gill-mantle	-0.267	0.623
Condition index	-0.134	-0.043

The significant correlation values are in bold