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Reproduction of *Annachlamys flabellata, Comptopallium radula* and *Mimachlamys gloriosa* (Mollusca: Pectinidae) in the south-west lagoon of New Caledonia

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Abstract

In the south-west lagoon of New Caledonia, the first sexual maturity size is 45 mm for *Annachlamys flabellata* (Bernadi), 60 mm for *Comptopallium radula* (L.) and 50 mm for *Mimachlamys gloriosa* (Reeve). The global sex-ratio was not significantly different from 1:1 for *C. radula* unlike *A. flabellata* and *M. gloriosa* (1.3:1 for two species). The significantly greater mean size of females suggests a protandric sex reversal. The reproductive cycle was studied monthly for two years for *M. gloriosa* and one year for *C. radula* and *A. flabellata*, then weekly over periods of 12 months for *M. gloriosa* and 6 months for *C. radula*. Reproduction of the three species occurs throughout the year with a maximal activity during the warm season. *M. gloriosa* and *C. radula* are capable of spawning several times a month. Fluctuations of reproductive intensity are related to temperature and salinity fluctuations.

Keywords: Bivalve, Pectinid, Pacific, New Caledonia, lagoon, reproduction.

*Reproduction d'*Annachlamys flabellata, *de* Comptopallium radula *et de* Mimachlamys gloriosa *(Mollusques: Pectinidés) dans la lagon sud-ouest de Nouvelle-Calédonie.*

Résumé

Dans le lagon sud-ouest de Nouvelle-Calédonie, la maturité sexuelle est atteinte à une taille de 45 mm pour *Annachlamys flabellata* (Bernardi) de 60 mm pour *Comptopallium radula* (L.) et de 50 mm pour *Mimachlamys gloriosa* (Reeve). Le sex-ratio global ne diffère pas significativement de 1:1 pour *C. radula*, contrairement aux deux autres espèces (1.3:1). La taille moyenne des femelles est significativement plus grande que celle des mâles, ce qui suggère une possibilité d'inversion du sexe au cours de la croissance. Le cycle reproducteur de *M. gloriosa* a été étudié mensuellement pendant deux ans pour *M. gloriosa* et pendant une année pour *C. radula* et *A. flabellata*. Les données ainsi obtenues ont été précisées par des prélèvements hebdomadaires pendant 12 mois pour *M. gloriosa* et 6 mois pour *C. radula*. Les trois espèces peuvent se reproduire toute l'année mais elles présentent une activité reproductrice maximale pendant la saison chaude (décembre à février). *M. gloriosa* et *C. radula* sont susceptibles de pondre plusieurs fois dans un même mois. Les quantités de gamètes émises sont liées aux variations de la température et de la salinité.

Mots-clés : Bivalve, Pectinidé, Pacifique, Nouvelle-Calédonie, lagon, reproduction.

INTRODUCTION

On the soft bottoms of New Caledonia lagoons, molluscs form a large and very diverse group (Bouchet, 1979) and 30 pectinid species have been recognized so far (Dijkstra *et al.*, 1989). In the south-west lagoon, scallops constitute a significant part of benthic populations as regards both number and weight (Chardy *et al.*, 1987; Chardy and Clavier, 1988). The more common species are *Mimachlamys gloriosa* (Reeve, 1853), *Bractechlamys vexillum* (Reeve, 1853), *Comptopallium radula* (L., 1758) and *Juxtamusium coudeini* (Bavay, 1803). Only the first three species are

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large enough for human consumption. *Annachlamys flabellata* (Bernardi, 1860) and *Amusium balloti* (Bernardi, 1861) are also relatively large but not frequently found in the south-west lagoon. Most of these filter feeders live resting on the substrate, covered by a thin sediment layer. Only *M. gloriosa* is fixed to various substrates by a byssus.

As pointed out by Barber and Blake (1991), information on reproduction is important to the understanding of the life history for management of commercial fisheries. This paper is a first contribution to the knowledge of New Caledonian pectinid reproduction and deals with *A. flabellata*, *C. radula* and *M. gloriosa* populations of the south-west lagoon. *A. flabellata* and *M. gloriosa* live in shallow water on sand bottoms with macrophytes (Dijkstra *et al.*, 1990 *a*) and they are largely distributed in the lagoons, whereas *C. radula* is restricted to muddy or muddy sand bottoms and lives under dead corals, masses of seaweed or wrecks in coastal bays (Dijkstra *et al.*, 1990 *b*).

MATERIAL AND METHODS

Samples of scallops were collected by SCUBA in the vicinity of Noumea (22° 15′ S-166° 25′ E). *A. flabellata* and *C. radula* were sampled from November 1988 to February and March 1990 respectively. Reproduction of *C. radula* was also studied weekly from 29/01/1990 to 26/07/1990 to assess short-term variations. The low density of *A. flabellata* does not permit weekly collection. The reproductive cycle of *M. gloriosa* was studied monthly for two years (August 1987-July 1989) and then weekly from 27/07/1989 to 26/07/1990. For each species, fifty specimens per sample were examined.

In the laboratory, samples were studied within three hours of collection. The height of shells (H) was measured with a vernier calliper to the nearest 0.1 mm, from the apex to the superior edge after removal of epibionts (abundant on *M. gloriosa*). The sexual maturity of each gonad was characterized according to a macroscopic scale defined for the three species (*tabl.* 1) and validated by histological examinations. The gonad was then assigned to gender, dissected out and weighed after over-drying at 60 °C for 48 hours to obtain the dry gonad weight (dGW). The dry gonad index :

$$[dGI = dGW.10^6/H^3]$$

was calculated from each set of samples. The cube function in the denominator is linearly related to total tissue weight but is more precise than the latter which may vary seasonally; it is often used for Pectinid reproduction species (Perodou and Latrouite, 1981; Bricelj *et al.*, 1987; Wilson, 1987). Only Pectinidae that had reached sexual maturity size (stage 3, 4 and 5) were taken into account for computation of gonad index. The temperature of sea water as well as the salinity rates near Noumea were recorded during the *M. gloriosa* weekly sample period. Relationships between weekly variations in gonad index and these environmental parameters are assessed using linear regressions. Lunar influence is assessed by comparison of mean gonad indexes calculated between full and new moon, and between new and full moon.

RESULTS

Initial sexual maturity sizes, corresponding to the smallest individuals with mature gonads (stage 4), are about 45 mm for *A. flabellata*, 60 mm for *C. radula* and 50 mm for *M. gloriosa* (*fig.* 1). The male/female (M/F) ratios are not significantly different from 1 for *C. radula* (M/F = 1.1, $\chi^2 = 1.93$, $p > 0.05$), unlike *A. flabellata* (M/F = 1.3, $\chi^2 = 7.55$, $p < 0.05$), and *M. gloriosa* (M/F = 1.3, $\chi^2 = 12.47$, $p < 0.05$). Sex-ratios vary according to the size of individuals (*fig.* 2)

Table 1. – Macroscopic aspect of gonads at various stages of sexual development.

Stages of sexual development	Description
IMMATURE (stage 1)	Gonad very small, not pigmented, flaccid
DIFFERENTIATED GONAD (stage 2)	Little gonadal development; onset of pigmentation
ADVANCED DEVELOPMENT (stage 3)	Gonad increases in volume; digestive loop still detectable. Gonad white in males and orange (*C. radula* and *M. gloriosa*) or pink (*A. flabellata*) in females
MATURITY (stage 4)	Gonad firm, full and bulging, cream-coloured in males, dark orange (*C. radula* and *M. gloriosa*) or bright red (*A. flabellata*) in females, digestive loop not visible, mature follicles externally visible as a mosaic-like network
SPENT (stage 5)	Gonad flaccid and wrinkled; greyish in males and dull orange in females, digestive loop visible

and the null hypothesis of independence between sex and shell height is not accepted for any species ($\chi^2=56.67$, $\chi^2=50.80$ and $\chi^2=32.03$, for *A. flabellata*, *C. radula* and *M. gloriosa* respectively, $p<0.05$). Males dominate in small sizes whereas females are in greater proportion among older individuals. Equal numbers of males and females are only observed for shell heights corresponding approximately to the average size of mature specimens (*fig.* 1).

Examination of monthly samples reveals a great irregularity in *M. gloriosa* gonad index evolution (*fig.* 3), without a clear trend. Macroscopic records of gonad development during the years 1987, 1988 and 1989 (*fig.* 4) confirm this lack of periodicity in the reproductive cycle. In fact, weekly sampling is necessary to demonstrate most spawning. The evolution of dGI values (*fig.* 5) is a result both of gamete shedding and gametogenesis process. Consequently, obvious decreases in gonad index indicates principal spawning (*fig.* 5). Over 53 weeks, 11 major spawning events were observed. In February two spawnings were recorded but none in June. Some irregularities in the curve are minor spawning or indicates oocytes resorption in gonads. Regeneration of the gonad is sometimes very quick, especially in February when the gonad index increases from 2.2 to 5.4 in one week. In spite of gonad index

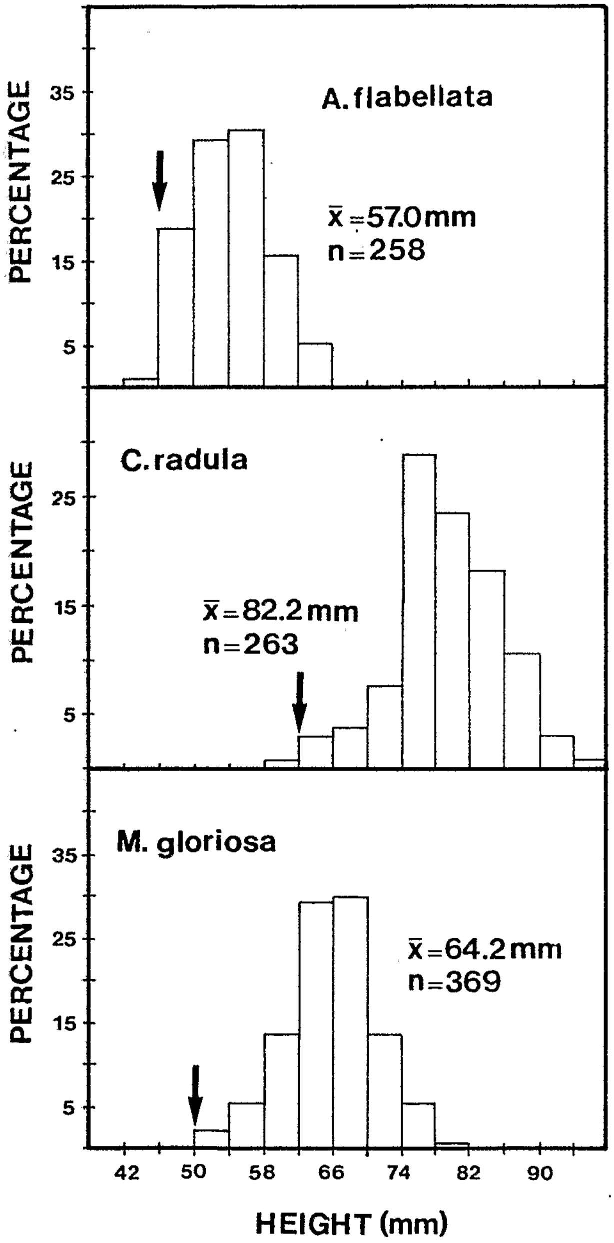


Figure 1. – Size frequency distributions of mature individuals. Arrow indicate initial sexual maturity sizes. x̄ is the mean distribution size.

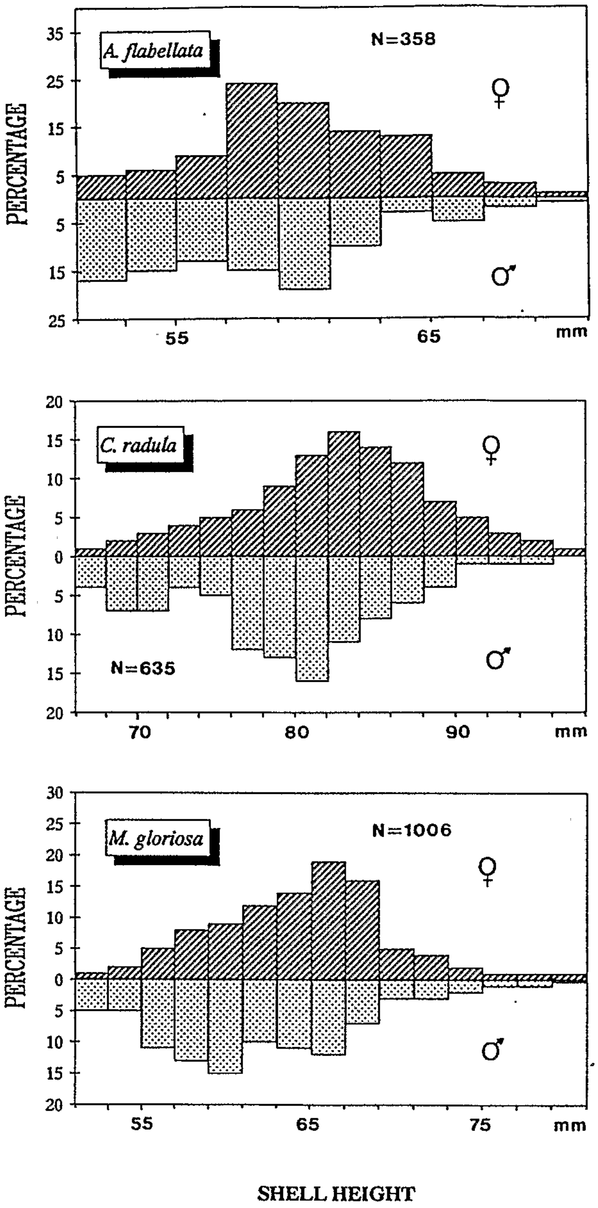


Figure 2. – Size frequency distributions for mature females and males.

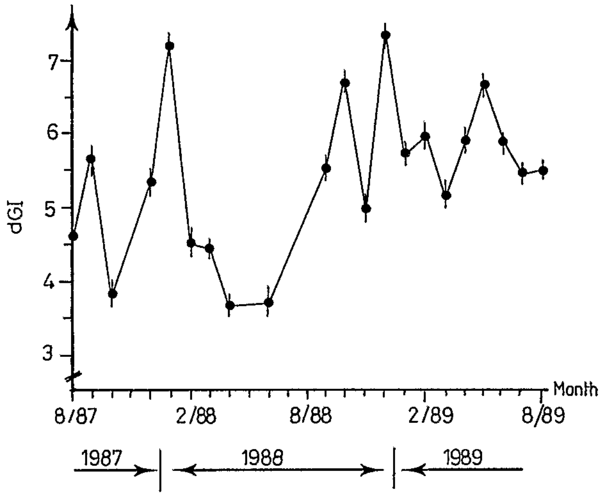


Figure 3. – *M. gloriosa.* Monthly dry gonad index average evolution. Vertical bars indicate standard errors.

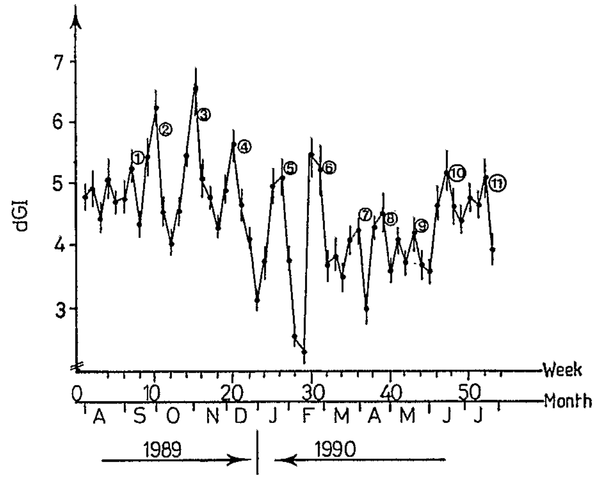


Figure 5. – *M. gloriosa.* Weekly dry gonad index evolution. Vertical bars represent standard errors. Major spawning are numbered.

curve irregularities, a minimum can be detected in the general trend during the warm season (January-February), indicating a more intense sexual activity. Moreover, this period corresponds to the maximal variations in gonad index. Therefore, in the south-west lagoon of New Caledonia, *M. gloriosa* spawns throughout the whole year with a maximal activity during the warm season.

The monthly evolution of *C. radula* gonad index is also irregular but better defined, with a minimum between October and December and low values from February to September (*fig.* 6). Values of dGI are significantly different from one year to the next, for a same month (t tests, $p<0.05$). Stage 5 (post spawning) gonads are observed every month but clearly dominates in April and May, suggesting a preferential reproduction during these months (*fig.* 7). To clarify the timing of *C. radula* reproduction, the dGI evolution was also described at shorter interval during a six month period (February-June) (*fig.* 8). Six major spawning are detected in 26 weeks: two in February, one in March, one in April and two in July. No evidence of gamete release between the thirteenth and twenty-third weeks is found. Consequently, *C. radula*, like *M. gloriosa* has no restricted reproductive period

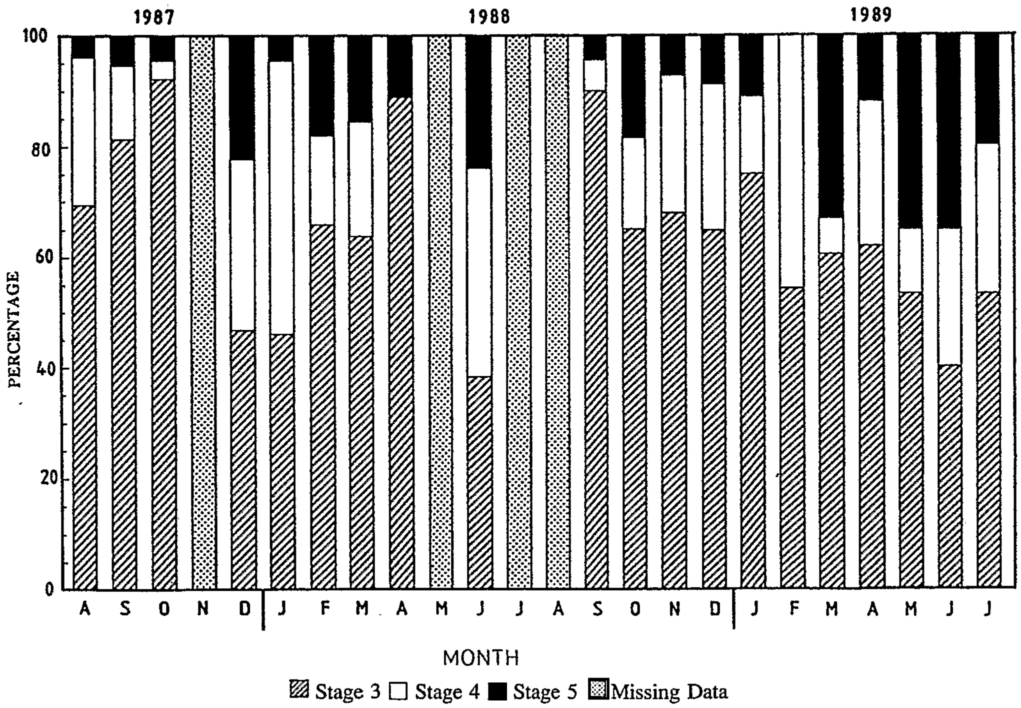


Figure 4. – *M. gloriosa.* monthly evolution of gondal development stage frequency. *See table 1* for explanation of terms.

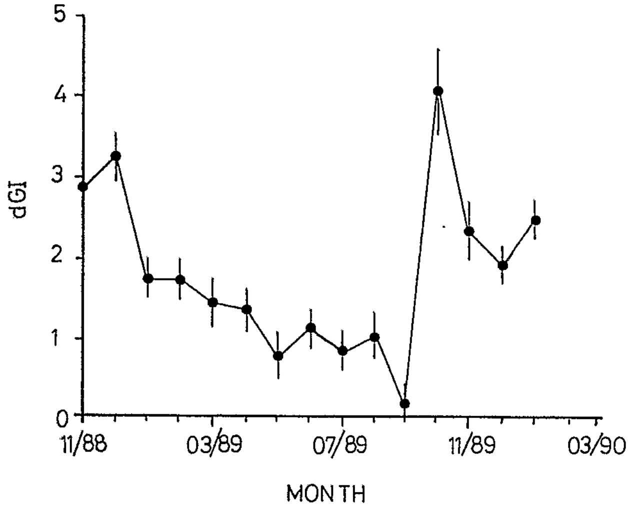


Figure 6. – *C. radula*. Monthly dry gonad index average evolution. Vertical bars indicate standard errors.

and the species is able to spawn several times a month. Fluctuations of reproductive intensity are however relatively apparent with a maximum in April-May.

Unlike the other species under study, *A. flabellata* dGI monthly evolution shows a relatively clear annual cycle with a minimum in February and high values from May to November (*fig.* 9). November to March dGI values are not significantly different from one year to the next (*t* tests, $p>0.05$). However, other decreases of dGI corresponding to secondary spawning are observed during the year. The percentage of spent gonads is minimal from August to November or December and maximal in January and February (*fig.* 10). Thus, *A. flabellata* is able to spawn most of the year but its main reproductive period clearly

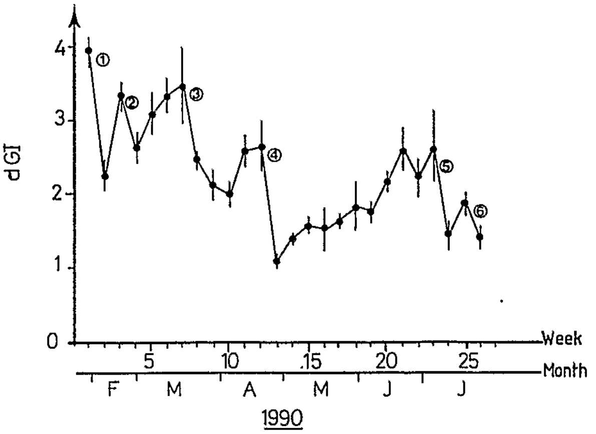


Figure 8. – *C. radula*. Weekly dry gonad index evolution. Vertical bars represent standard errors. Major spawning are numbered.

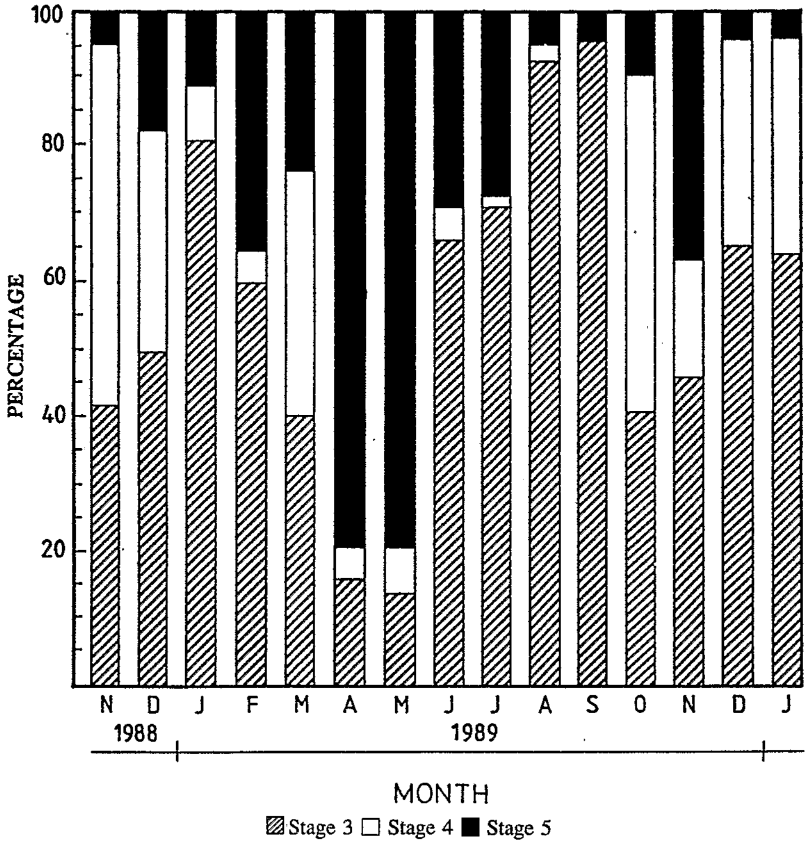


Figure 7. – *C. radula.* monthly evolution of gonadal development stage frequency. *See table 1* for explanation of terms.

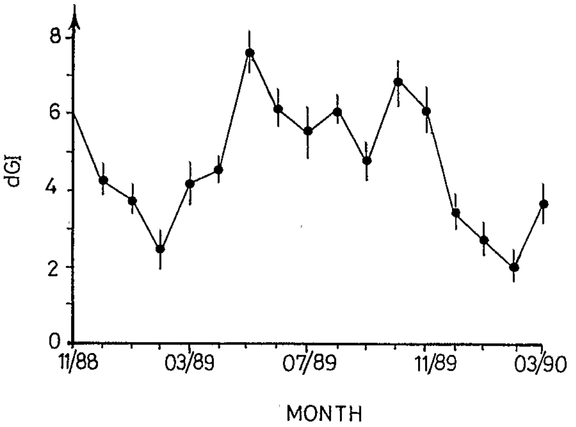


Figure 9. – *A. flabellata*. Monthly dry gonad index average evolution. Vertical bars indicate standard errors.

extends over the warm season, from November to February.

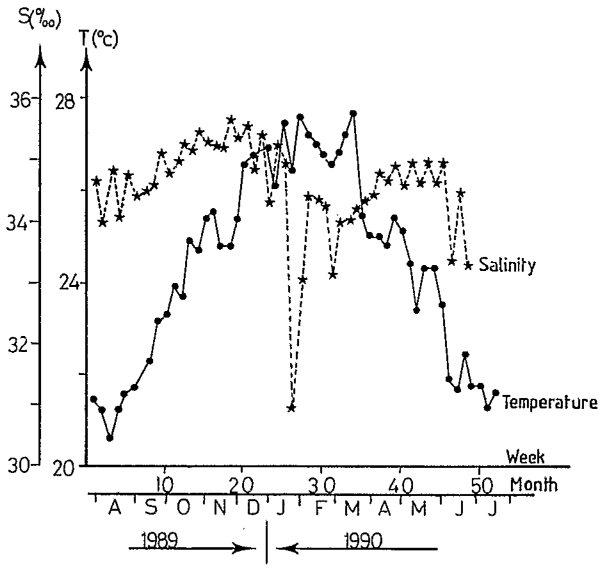
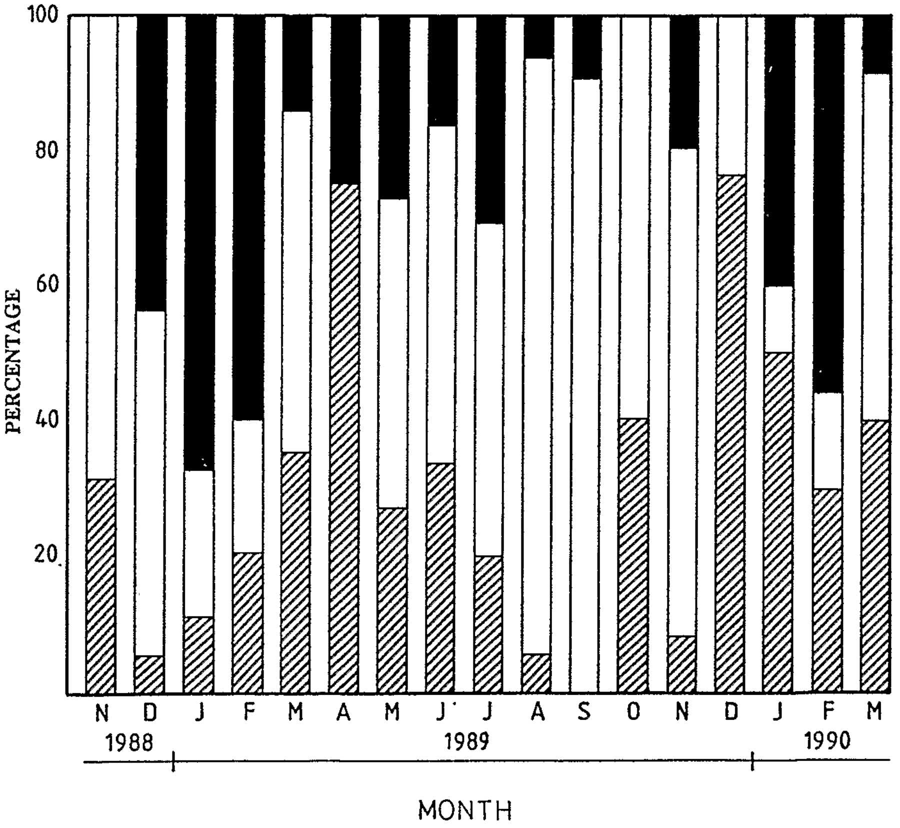


Figure 11. – Weekly salinity and temperature evolution during *M. gloriosa* reproduction study.

Salinity and temperature evolution in the course of the *M. gloriosa* reproduction study are indicated in *figure* 11. Negative variations in *M. gloriosa* dGI, considered as spawning, are significantly correlated with variation in temperature (r=0.61, p=0.01), but only the greatest decreases in dGI (>1.2 week^{-1}) were correlated with salinity (r=0.85, p=0.03). Spawning n° 1 and n° 2 (*fig.* 5) are related to a rise in the temperature of the seawater which went from 21.5 to 23.6 °C. In the same way, water temperature rises from 24.6 to 27.4 °C just before spawning n° 4. A



▨ Stage 3 ☐ Stage 4 ■ Stage 5

Figure 10. – *A. flabellata*. Monthly evolution of gonadal development stage frequency. *See table 1* for explanation of terms.

temperature drop can also set off spawning, such was the case for spawning n° 3, 8 and 9 when temperature changed from 25.5 to 24.6 °C, from 25.4 to 23.3 °C and from 24.3 to 21.6 °C respectively. However, the strongest weekly variation in dGI (n° 6) was due to a change in salinity (from 34.95 to 31.00 %). Spawning n° 5, 7, 10 and 11 were also associated with a drop in salinity.

DISCUSSION

Relationships between sex-ratios and shell heights suggest a protandric sex reversal for the three species under study. This characteristic is nevertheless progressive and limited to a relatively small proportion of the populations, males being found in great size classes, too. According to Mackie (1984), bivalves with only a single sexual change during their life have consecutive hermaphroditism. Protandric sex reversal has been described for other pectinids (Lucas, 1963; Maru, 1978) and for New Caledonia bivalves (Baron, 1992).

The three species under study are likely to release their gametes throughout the year, even if some short-term variations in gonad index may be partly related to oocytes resorption. The successive spawning periods are followed by short gonadal restoration phases. However, a reproductive cycle always exists but concerns the intensity of spawning. In spite of similar environmental conditions, the amplitude of the reproductive cycle differs for the three species. This cycle is faintly marked for *M. gloriosa*, better defined for *C. radula* and relatively clear for *A. flabellata*. Major reproductive events occur during the warm season or when water temperature begins to decrease for *C. radula*. Generally, pectinid reproduction periods are restricted to a few months (*see* Barber and Blake, 1991, for a review), but New Caledonian species are able to reproduce all year round. This could be related to the weak seasonal effect occurring in New Caledonia with only a 6-7 °C annual thermal amplitude. Sause *et al.* (1987) suggested that Pectinid species in the southern hemisphere like *Pecten alba*, spawn during the same range of calendar months as species in the northern hemisphere. In New Caledonia, this is the case for the three species studied in this paper. New Caledonia Pectinidae are located in relatively calm lagoon water and they are not food limited. Rougerie (1986) showed that concentrations in chlorophyll which exceeded 1 mg.m^{-3} were currently measured close to Noumea. Under optimum food conditions spawnings were triggered by climatic conditions such as temperature and salinity but it appears difficult to determine their relative influence in nature to set off spawning of Pectinids in New Caledonia. However, saline shock was more effective than temperature fluctuations to induce *M. gloriosa* spawning in the laboratory (Lefort, 1992). In numerous species lunar phase is considered an important factor in provoking spawning. Among some scallops, especially *Pecten opercularis* (Thorson, 1950) and *Pecten maximus* (Mason, 1958) "epidemic" lunar phase-released spawning was observed. Each species released more eggs between the full and new moon than between the new and full moon. Such a relationship between lunar phase and reproduction does not hold for *M. gloriosa* and the mean gonad index variations are not significantly different between the full and the new moon and between the new and the full moon (*t* test, $p > 0.05$).

Spawning of the three Pectinid species studied in this paper is correlated with thermal seawater variations, and with salinity for *M. gloriosa*. These environmental parameters may trigger spawning by their variations but they are not inhibitory to reproduction, owing to the low seasonal changes in New Caledonia lagoons. In fact, observed variations in reproductive activities are probably related to a joint operation of parameters including temperature and food supply (Barber and Blake, 1991). The favourable values of these parameters allow pectinids to spawn all year round in spite of the energy demand of the reproduction process.

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