Reproductive Cycles of the Bivalve Molluscs Atactodea striata (Gmelin), Gafrarium tumidum Röding and Anadara scapha (L.) in New Caledonia

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Abstract

Monthly samples of the bivalves Atactodea striata, Gafrarium tumidum and Anadara scapha were collected over 1 year from the littoral zone on the south-western coast of New Caledonia. A. striata and G. tumidum were studied by macroscopic examination of gonads and microscopic examination of gamete smears. For A. scapha, only microscopic examination was used. A. striata and G. tumidum are dioecious, whereas A. scapha is a protandric hermaphrodite. Sexual differentiation begins at a shell length of 20 mm for A. striata and G. tumidum and 22 mm for A. scapha. The three species have an extended or continuous breeding period, although, in all three, sexual activity peaks in the hot season.

Introduction

The littoral clams Atactodea striata (Gmelin, 1791: Mesodesmatidae), Gafrarium tumidum Röding, 1798 (Veneridae) and Anadara scapha (L., 1758: Arcidae) are gathered for food in many countries of the Indian Ocean (Nayar and Rao 1985) and South-East Asia (Nielsen 1976; Purchon and Purchon 1981; Davy and Graham 1983; Toral-Barza and Gomez 1985). In New Caledonia, these species could possibly be of commercial value, and a number of studies are being undertaken to assess their economic potential. An understanding of their reproductive biology is an important prerequisite for assessing the regeneration capacities of natural stocks and interpreting growth patterns. The reproduction of A. striata and G. tumidum has never yet been the subject of any specific studies, unlike the reproduction of A. scapha (or A. antiquata: Lamy 1904; Rost and Soot-Ryen 1955), whose reproductive cycle was investigated in the Philippines (Toral-Barza and Gomez 1985). For each of the species considered in the present paper, the shell length at first maturation, the sex ratio and the process of gametogenesis in the course of an annual cycle is determined. The different stages of the reproductive cycle are characterized by histological examination.

Materials and Methods

The reproductive cycles of A. striata, G. tumidum and A. scapha were studied over one annual cycle by monthly sampling of about thirty large-sized specimens of each species. A. striata was collected from the sandy beach at Karikate from December 1989 to November 1990. G. tumidum and A. scapha were collected from littoral seagrass beds at Tomo and Teremba, respectively, from July 1989 to July 1990. The three sites are located along the south-western coast of New Caledonia $(20-22^{\circ}30'S, 164-167^{\circ}E)$. In order to determine the shell length at first maturation, a large number of specimens of all sizes was taken from each site on several occasions. In the laboratory, each bivalve was measured along its maximum anterior-posterior axis to the nearest 0.5 mm. The gonad, which envelops the visceral mass, was observed macroscopically and its external appearance carefully noted. Each gonad

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Fig. 1. Different gametogenic stages (see text for explanation) observed in bivalves: (A) Stage 0 A. striata; (B) Stage 1 male A. striata; (C) stage 2 male G. tumidum.



Fig. 1 (continued). (D) Stage 2 female G. tumidum; (E) Stage 3 male A. striata; (F) Stage 3 female A. scapha. SG, spermatogonium; SZ, spermatozoa; DOC, degenerating oocyte; OC, oocyte; OG, oogonium.

was then dissected and the specimen sexed; any gametes present were recovered and examined microscopically. For histological examinations, gonads of a few specimens of each species were fixed in Bouin's fixative for 24 h. Tissues were embedded in paraffin after dehydration in alcohol. Sections $5-7 \mu m$ thick were stained with Masson's trichrome solutions (Fig. 1).

The results obtained with the two types of gonad observations enabled four development stages, common to all three species, to be identified: Stage 0, immature—no gonad visible, nor any gametes (Fig. 1A); Stage 1, maturing—body incompletely covered by gonad, some sperm, moderately active (Fig. 1B), or broad-based oocytes with an intermediate diameter and the nucleus staining more darkly than the cytoplasm; Stage 2, mature—swollen gonad completely covering the body, sperm very active (Fig. 1C), or large round oocytes with a small stalk attachment and the cytoplasm staining more darkly than the nucleus (Fig. 1D); and Stage 3, regression—flaccid gonad with a small amount of gametes, very active sperm (Fig. 1E), or degenerating oocytes (Fig. 1F).

For A. scapha, only microscopic observation based on the amount and structure of gametes could be used to describe the sexual maturation cycle because of the thick tegument covering the body.



Results

Length at First Maturation and at First Spawning

Fig. 2 shows the length-frequency distributions both of the entire population samples of A. striata, G. tumidum and A. scapha examined and of the sexually differentiated individuals. For each species, immature individuals, represented by the differences between the values of the overlaid histograms, are present in every size group. The immature stage therefore constitutes a well defined phase in the sexual cycle. First maturation occurs at about 20 mm shell length for A. striata and G. tumidum and 22 mm shell length for A. scapha. Fig. 3 shows the length-frequency distributions of the specimens collected at the regression stage. First spawning occurs at 22, 24 and 30 mm shell length for A. striata, G. tumidum and A. scapha, respectively, showing that the first gamete maturation cycle is very rapid.



Fig. 3. Length-frequency distributions of bivalves collected at the stage of sexual regression: (a) A. striata, (b) G. tumidum, (c) A. scapha.

Overall Sex Ratio and Relation between Sex and Shell Length

The overall sex ratio for each species was estimated from the total number of samples. No case of simultaneous hermaphroditism was found in this study. The male/female (M/F) ratio was 0.92 for A. striata, and the null hypothesis of an equal number of males and females can not be ruled out for this species ($\chi^2 = 0.43$, P > 0.05). On the other hand, for G. tumidum (M/F = 1.13, $\chi^2 = 6.28$, P < 0.05) and A. scapha (M/F = 1.47, $\chi^2 = 8.62$, P < 0.05), the sex ratio was significantly different from 1.



The length-frequency distributions of males and females of each species are shown in Fig. 4. The null hypothesis of independence between sex and length can be accepted for A. striata ($\chi^2 = 9.39$, P > 0.05, d.f. = 5) but definitely not for G. tumidum ($\chi^2 = 15.70$, P < 0.05, d.f. = 8) or A. scapha ($\chi^2 = 38.01$, P < 0.01, d.f. = 5). At the Karikate beach locality, A, striata is therefore a gonochoristic bivalve. For G. tumidum, calculation of the partial χ^2 suggests merely that females significantly outnumber males at shell lengths of 30-32 mm ($\chi^2 = 4.17$, P < 0.05) and that males outnumber females at shell lengths of 38-40 mm; ($\chi^2 = 6.98$, P < 0.01). For other length intervals, the numbers of males and females are not significantly different (χ^2 tests). G. tumidum is therefore gonochoristic at

the Tomo seagrass-bed locality. For A. scapha, calculation of the partial χ^2 shows that males significantly outnumber females at shell lengths of 34-42 mm, that the hypothesis of a sex ratio equal to 1 can not be rules out at shell lengths of 42-46 mm, and that females significantly outnumber males at shell lengths of 46-54 mm. At the Teremba locality, A. scapha thus shows a sex inversion that reflects a protandric hermaphroditism.



Fig. 5. *A. striata*: stages in the reproductive cycle (1, maturing; 2, fully mature; 3, regressing; 0, immature).

Reproductive Cycles

The reproductive cycle of A. striata (Fig. 5) was divided into three major phases: (1) a maturation phase from August to October, (2) a phase of sexual maturity and/or regeneration of gametes from November to April, and (3) a resting place from May to July. The distinction between the maturation phase and the phase of sexual maturity is not very clear-cut because, with very few exceptions, a variable percentage of individuals at each of the four sexual stages was in fact found in the A. striata population from August through April. During this period, spawning thus occurs successively in a certain number of individuals. Two instances of more massive spawning were recorded at the beginning of March and the beginning of May.

Annual variations in the percentage of G. tumidum at the various sexual stages are shown in Fig. 6. Three phases were identified: (1) a maturation phase in July and August, (2) a sexual maturity phase from September to March, and (3) a sexual-regression phase from April to June. Here again the distinction between the three phases is not very clear-cut because a number of fully mature individuals and, with three exceptions, of sexually regressing individuals was in fact found throughout the year. From September onwards, the G. tumidum population is thus characterized by nearly continuous partial spawning, though only in March does spawning occur simultaneously in a large number of individuals.

Annual variations in the percentage of A. scapha at the various sexual stages, as shown in Fig. 7, enable three phases to be distinguished: (1) a maturation and/or sexual-maturity phase from September to December, (2) a regression and/or resting phase from January to May, and (3) a resting phase from June to August. Massive spawning thus appears to occur in the A. scapha population between December and January. The presence of sexually regressing individuals from September onwards shows that partial spawning is taking place in the population during the period preceding massive spawning. ::





Fig. 7. A. scapha: stages in the reproductive cycle (1, maturing; 2, fully mature; 3, regressing; 0, immature).

Discussion and Conclusions

Coe (1943) first noted the occurrence, in bivalves, of various types of sex changes. Protandric hermaphroditism has been reported in several species, including *Pinctada fucata* (Tranter 1959), *Chlamys varia* (Lucas 1965) and *Argopecten irradians* (Sastry 1968). Coe (1943), Tranter (1958) and Sastry (1968) pointed out that genetic sex determination in bivalves was very unstable and could be modified by changes in nutritional conditions. These authors concluded that there was a relationship between protandry and limited food availability. Yankson (1982) found a similar relationship for *Anadara senilis*, the proportion of young males being greater in an enclosed lagoon with a low nutrient content than in an adjacent lagoon that communicated with the sea. However, at the Teremba locality, the protandry observed in *A. scapha* does not appear to be linked to nutritional factors because the microphytobenthic chlorophyll a content of the sediment, which represents an important part of the available food for the bivalve, is very high throughout the year (Baron, unpublished data).

The sequence of events forming the reproductive cycles of invertebrates is known to be strongly affected by physical and biological environmental factors. In low latitudes, bivalves tend to have a long breeding season (Giese 1959). Evidence of this prolonged breeding is the simultaneous presence within a population of all sexual-development stages. The growth rate of the gametes thus varies with individuals, suggesting a specific response to the environmental factors. The occurrence of successive individual spawnings has been linked by previous authors to the presence, in the gonads, of gametes at all stages of maturity (Tranter 1958; Shafee and Lucas 1980). In the present study, a similar overlapping of different generations of gametes was noted for A. striata, G. tumidum and A. scapha, as shown for a female of G. tumidum in Fig. 1D.

In temperate areas, temperature plays a very important part in triggering bivalve gametogenesis and spawning (Mann 1979; Shafee and Lucas 1980; Griffiths 1981; Mackie 1984; Hadfield and Anderson 1988; Harvey and Vincent 1989). In tropical areas, temperature variations over the year are less marked; on the other hand, wide and periodic salinity variations may occur, particularly in areas affected by the monsoon, and many authors (Rao 1967; Nagabhushanam and Talikhedkar 1977; Broom 1983; Natarajan and John 1983; Jayabal and Kalyani 1987) have demonstrated the impact of the combined action of temperature and salinity on the reproductive cycles of molluscs. In the coastal waters of New Caledonia, salinity variations are relatively small (Dandonneau *et al.* 1981)—between 34 and 36—and the effect of this parameter on the onset and speed of gametogenesis in *A. striata, G. tumidum* and *A. scapha* was therefore negligible, although short-lived salinity fluctuations after heavy rains act as a cue for spawning.

The protracted breeding season of tropical bivalves often features one or two peak reproductive periods during the course of a year (Alagarswami 1966; Squires et al. 1973; Mane and Nagabhushanam 1979; Broom 1983; Toral-Barza and Gomez 1985; Borrero 1986). When such peaks occur in a population, the parameters governing the reproductive cycle are easier to determine. The observed seasonality in fact results from a similar response by a large number of individuals who previously responded more or less independently to the existing environmental factors. This seasonality was established for the three bivalve species investigated here: reproduction peaks were seen in G. tumidum and A. scapha, and to a lesser extent in A. striata, from November to March during the Southern Hemisphere summer, whereas sexual regression was found to occur in these species when the temperature dropped at the beginning of the cool season. In the Philippines, reproduction of A. scapha also peaks when temperatures are highest (Toral-Barza and Gomez 1985). Temperature therefore definitely appears to affect reproductive patterns in the bivalves investigated, at least during part of the year. The daily temperature fluctuations to which intertidal organisms are exposed are much sharper in the warm season, when the effect of the sun is strongest, and these fluctuations of variable magnitude may well trigger spawning in bivalves. However, the fact that spawning also occurs at other times of the year shows that temperature is not the only factor affecting gametogenesis.

A relationship between the reproductive cycles of bivalves and food availability has been demonstrated, in temperate areas, by several authors, including, just recently, Hadfield and Anderson (1988) and Shafee (1989). However, functional chlorophyll a assessments carried out on the sites considered in the present study (Baron, unpublished data) showed high concentrations of pigments on the one hand and no seasonal variation in these concen-

trations on the other. The existence of a chlorophyll a content that is always adequate for gamete maturation seems to be an important factor for protracted continuous reproductive activity. However, the differences observed between the reproductive cycles of three species exposed to similar temperature and salinity conditions tend to confirm that bivalve reproduction is partly controlled by endogenous factors, as was recently noted by Hadfield and Anderson (1988).

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