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REPRODUCTION OF THE SPIDER CRAB *Maja squinado* (BRACHYURA: MAJIDAE) IN THE SOUTHERN GALICIAN COAST (NW SPAIN)

E. González-Gurriarán, L. Fernández, J. Freire, R. Muiño and J. Parapar

Departamento de Bioloxía Animal, Universidade da Coruña.
Campus da Zapateira s/n. E-15071 A Coruña. Spain

ABSTRACT

The spider crab *Maja squinado* is a species of great commercial interest on the coast of Galicia (NW Spain). A study is being carried out on the biology and fishery of this species to improve the management of the fishery. This paper deals with different aspects of the reproductive biology of *Maja squinado*, based on field and laboratory studies.

Monthly samples (December 1991 to May 1993) were taken from the commercial fishery of the southern Galician coast (outer Ría de Arousa and neighbouring open coastal area). In the summer and winter of 1992, additional samples were taken in juvenile crabs areas. Population structure, breeding cycle, reproductive cycle based on gonad development stages are analyzed in order to define the seasonal reproductive pattern of gonad maturation and breeding. Laboratory studies were carried out to analyze the number of broods per reproductive period, incubation time, and whether or not consecutive spawnings were dependent on remating.

Gonad development begins after the pubertal moult has occurred (in late summer or early autumn). In December specimens with gonads in late stages of development begin to appear, and the females will spawn for the first time in late winter or early spring. From April until September the percentage of ovigerous females is over 75 %. As the incubation period progresses, the ovaries of ovigerous females reach more advanced stages of maturity in order to carry out the next spawning.

The average incubation period under experimental conditions lasted 40 days in summer (mean temperature 18.4 °C), and 58 days in spring and autumn (mean temperature 15.8 °C). Time between hatching and the following spawning was an average of 3.4 days. In the laboratory up to four consecutive broods were obtained without mating. Considering the length of the breeding cycle and the high percentage of ovigerous females, most individuals are estimated to have three consecutive broods during the yearly cycle.

INTRODUCTION

The spider crab, *Maja squinado*, fishery is highly important in Galicia (NW Spain). Catches in Spain range between 40 and 229 mt a year with a mean value of 122 mt from 1986 to 1990 (according to the FAO Yearbooks of Fisheries Statistics). Galicia accounts for approximately 73 % of the total catch, and represents over 80 % of the value in pesetas (Anuarios de Pesca Marítima of the Ministerio de Agricultura, Pesca y Alimentación). Even though the total catches in Spain are very low compared to other European countries (corresponding to 3 % of the Northeast Atlantic, according to FAO data), *M. squinado* is a species of great socio-economic value. In Galicia there are 300 boats that carry out this fishery in the rías and coastal zones for more than 6 months a year. This species is caught using gears such as tangle net and glass box, and on occasion, traps.

Until the present time, this species has been fished in Galicia without any information on its biology. The management of the fishery requires biology and fishery studies, in order to optimize its exploitation. As part of these studies, information on reproductive biology is of paramount importance. Research carried out on the reproduction of several species of the family Majidae draws special attention to two characteristic aspects, namely: the existence of a terminal moult and its significance in terms of sexual maturity (Carlisle, 1957; Conan & Comeau, 1986; Cormier *et al.*, 1992; Paul & Adams, 1984; Teissier, 1935), and the role of the structures related to sperm storage and egg fertilization (Adams & Paul, 1983; Beninger *et al.*, 1988; Diesel, 1989).

The data available on the reproductive cycle of *Maja squinado* are from the west coast of Ireland (Brosnan, 1981; Rodhouse, 1984), the south of England (Edwards, 1979), French Brittany (Kergariou, 1971, 1975) and the Adriatic Sea (Stevcic, 1967, 1977). The information provided by these studies covers only partial aspects of reproduction and in some cases is not at all precise, and shows major geographical differences.

In contrast to the lack of data available on the reproduction of the spider crab, there is a wealth of information on another species of Majidae, which is an important fishery in the Northwest Atlantic, the snow crab *Chionoecetes opilio* (see reviews by Conan *et al.*, 1990 and Elner & Beninger, 1992). This has enabled the establishment of a model pertaining to the cold water species, which is not, however, widely applicable to the species that live in our latitudes.

This paper, which is the first part of a study on the reproductive biology of *Maja squinado* in Galician waters, analyzes the population structure, reproductive cycle, based on the analysis of gonads, breeding cycle and number of broods, mating behaviour and mating season.

MATERIAL AND METHODS

Commercial catches were sampled at the port of O Grove (Pontevedra) in the Ría de Arousa, which is the most important port dealing in the sale of the spider crab from the fishery in Galician waters. These catches come mostly from boats that fish with tangle net gears in the outer ría area and adjacent coast at depths ranging approximately from 15 to 40 m (Fig. 1). Glass box fishermen, who work in the shallow areas of the Peninsula of O Grove, at depths ranging from 1 to 8 m also contribute to these catches, but to a lesser extent. Sampling took place monthly from December 1991 to May 1993, 3-5 days a month depending on the volume of the catches. Sample size varied according to the time of year, especially during the closed season (June 1st - November 30th 1992), when catches decreased in some months (Table 1).

The following data were recorded for each individual: sex, carapace length in mm (measured between the posterior margin of the cephalothorax and the joint point of the frontal spines). In females, the presence of eggs in the abdomen (differentiating those having eggs in late development stages - dark grey in colour), the presence of egg cases from the last hatching, and broods with a small number of eggs were recorded. From December 1992 on, immature females with flat abdomens were noted.

Spider crab catches are basically made up of animals that reached maturity during the summer prior to the beginning of the fishing season. From September to December, specimens appeared in the catches that reached maturity the year before or earlier (showing a large amount of epibionts and a worn, scraped carapace). Therefore, in this study two separate groups of animals are considered. Those undergoing the pubertal moult and reaching maturity in summer 1991, are referred to as PM 91. (They appear in the samples from December 1991 to December 1992 and are recorded at less than 1% during the following months.) Those reaching maturity during summer 1992, making up part of the commercial catches from September 1992 until the end of the fishery season in May 1993 are referred to as PM 92.

Complementary experimental samples were taken using glass box gear in the northern area of the Península de O Grove during the months of July, August and December 1992 (Table 2). These samplings which yielded mainly juveniles and pre-pubertal specimens were aimed at gathering data on both reproduction and maturity as well as on diet and growth.

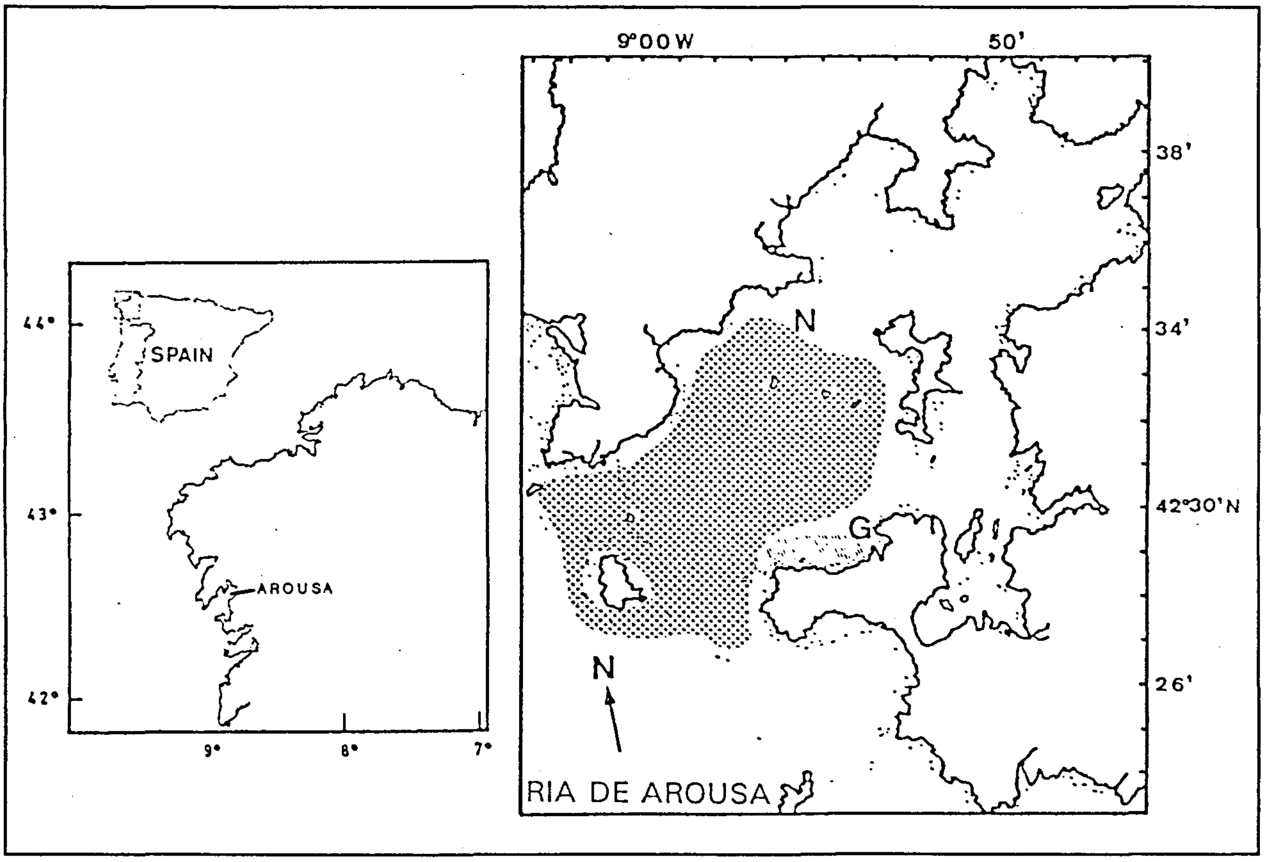

Figure 1. *Maja squinado*. Sampling areas for the reproduction study in the Ría de Arousa and adjacent coast (Galicia, NW Spain). G: Sampling area where the glass box was used. N: Fishery area for the commercial fleet using tangle nets.

On a monthly basis 25-35 females from commercial catches were analyzed, and the following data were recorded: carapace length, wet weight in g, the presence of eggs in the abdomen and their stage of development, intermoult stage (all of the specimens used were in the intermoult stage, as they had already undergone the terminal moult) and morphometric data (for maturity studies) and epibionts. Each animal was dissected, with the subsequent extraction of the gonads and seminal receptacles (in this paper the term spermatheca will be used). Gonad wet weight (±0.1 g), color, and diameter of the oocytes (greatest diameter in μm of a subsample of 20 oocytes, measured using a microscope with a reticular eyepiece and a magnification between 40x and 100x) were recorded. Gonad subsamples fixed in Bouin and transferred 24-48 h later to 70° alcohol for subsequent histological analyses. Four stages of maturity in gonads were determined based on macroscopic criteria and histological examinations using Masson's trichrome stain.

After extraction the spermatheca were frozen at -25 °C and stored for future analysis. After being thawed, they were dissected and examined. Repletion was determined by the material transferred by males and stored, and divided into five categories : 0 = empty spermatheca; 1 = remains of spermatozoa and/or spermatophores; 2 = abundant presence of materials; 3 = material filling approximately between

1/2 and 3/4 of spermatheca capacity; 4=full or nearly full spermatheca. In cases where materials pertaining to different matings were clearly defined, the number was counted, and the state of disintegration and color were recorded. A sample of the contents was examined under the microscope with a magnification of 65x-250x in order to observe spermatophores and/or spermatozoa. The examination of subsamples of spermatheca was carried out using histological techniques with light microscopy, scanning electron microscopy, (SEM) and transmission electron microscopy (TEM). The spermatheca of the females caught with the glass box in July, August and December 1992 were also analyzed.

Egg mass was separated from each ovigerous female by cutting the base of the pleopods. A subsample of 20 fresh eggs was measured (greatest and smallest diameter in μm, measured under a microscope with a magnification of 40x, using a reticular eyepiece), and they were classified into three developmental stages: A= Orange eggs spawned recently with no pigmentation; B= eggs with slight pigmentation; C= dark grey eggs with complete pigmentation,almost ready to hatch. The egg mass was fixed in formaline 4% and transferred to 70° alcohol after 48 h. A subsample of between 150 and 250 eggs was fixed in Bouin and transferred after 24-48 h to 70° alcohol for later microscopic analysis in order to determine the substage of development.

Incubation experiments were carried out in the laboratory for the purpose of obtaining larvae to be used in larval biology research. They also provided supplementary information on consecutive broods for the same female (number of broods, time between broods, and duration of the incubation). In the first experiment 6 females were held in tanks between March and July 1992 until February 1993. Only 4 females provided data; the other two specimens died due to problems with the water flow. One or two females were placed in separate 50 l tanks, with open circuit flow (approximately 2 l/min), aireation and fluctuations in daylight (low intensity). The specimens were fed mussels, supplemented with sea urchins and seaweeds. Water temperature was checked on a daily basis. A second experiment began on March (5 females) and on April (3 females) in 1993. This experiment was interrupted on May 26th due to problems with the water quality as a result of the "Aegean Sea" oil spill. All the females were held in tanks with eggs, checked daily, with a subsample being taken every 3-4 days in order to determine the stage of development and to measure the greatest and smallest diameters of 10 eggs using a microscope. The day hatching took place as well as the next spawning and any other incidence were recorded.

Specimens of both sexes were held in captivity, which allowed mating to be observed under experimental conditions. From August 1992 to May 1993 eight males and nineteen females, that had already undergone the terminal molt in the laboratory, were held in a 1.70 x 0.52 x 0.30 m tank with an open circuit flow of 10 l/min, aireation and fluctuations in daylight. They were fed with mussels, seaweeds and sea urchins. Matings were also observed in large volume tanks (between 10 and 50 m^3) in commercial holding facilities. Additional observations were carried out in the field during glass box fishery operations.

RESULTS

Population Structure

The two areas studied differ greatly (Tables 1 and 2). The shallow water population, sampled using the glass box, is basically made up of immature animals (mean size : 109.4 mm in July; 111.4 mm in August; 95.1 mm in December, 1992, for females). In the month of August there is a remarkably high population of morphometrically mature females (45.7%), while in July and December they comprise only 13.0 and 9.1% of the female population. The mean size of mature females is 146.6 mm. Since most individuals undergo the prepubertal moult in the summer or early autumn (unpublished data), in August there is an increase in the percentage of mature individuals in the early stages of the intermoult cycle. Mature animals then migrate to deeper waters and are recruited to the tangle net fishery. There are no significant differences between the number of males and females caught in either of the two months sampled (test X^2, $P > 0.1$).

Table 1. *Maja squinado*. Number of specimens sampled monthly from commercial catches. The number of females sampled additionally during the closed season that were fished and kept in commercial holding facilities during the corresponding month is indicated in parenthesis. Morphometrically immature and mature females, and those reaching sexual maturity in 1991 (PM91) and 1992 (PM92) are indicated. In November the sampling size is smaller due to the fact that the fleet did not fish for most of the month. nd= Data not available.

	Dec91	Ja92	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Ja93	Feb	Mar	Apr	May
Males	195	194	219	232	202	164	nd	nd	nd	nd	224	52	397	230	266	159	203	106
Females	161	110	150	127	182	171	95	42	26	120	187	77	330	184	132	132	157	139
							(166)	(32)	(43)	(11)	(48)	(16)						
Inmature	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	10	7	9	19	41	18
Mature	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	320	177	123	113	116	121
PM91	nd	nd	nd	nd	nd	nd	nd	nd	nd	38	48	6	11	1	1	1	4	0
									(11)	(48)	(16)							
PM92	--	--	--	--	--	--	--	--	--	82	139	71	309	176	122	112	112	121
% ♀ PM91	--	--	--	--	--	--	--	--	--	31.7	25.7	7.8	3.4	0.6	0.8	0.9	3.4	0.0

Samples from areas where commercial fishery takes place, using gears consisting mainly of tangle nets, are, for the most part, made up of mature animals. Between March and May, which coincides with the end of the fishery season, catches are greatly reduced, and the percentage of immature females increases (between 12.9 and 26.1%). Over 85% of immature females are under 135 mm CL, and at 130 mm 50% of the specimens are mature. The number of males is always greater than the number of females from December to April, making up between 52.6 and 66.8% of the catches. In May, the sex-ratio is reversed, with females being slightly more dominant in the catches (51.0 and 56.7% for each year). The difference in sex-ratio could be attributed to the dynamics of the fishery itself (greater catchability of males due to differences in the moult cycle determined by sex, where males attain the terminal intermoult stage early).

Table 2. *Maja squinado*. Number of specimens caught in experimental samplings using the glass box gear in shallow water areas. Females are separated according to whether they are morphometrically immature or mature, and development stages of the gonads in mature females are indicated.

	July 92	August 92	December 92
Males	63	77	42
Females	69	81	55
Inmature females	60	44	50
Mature females			
Gonad stage I	9	37	0
Gonad stage II	0	0	5
% mature ♀	13.0	45.7	9.1

Specimens recruit to the fishery the same year they undergo the pubertal moult. Between December and May, over 96% of the mature females caught had undergone their pubertal moult the previous summer (fishing season 1992 - 1993, PM92). In September, animals recently recruited begin to be marketed and represent 68.3% of the females. The remaining specimens come from recruitments from previous years (Table 1).

Analysis of Gonads and Reproductive Cycle

Four stages of gonad maturity were established:

Stage I. Undeveloped gonads, white or light cream colored. Small, immature oocytes (mean greatest diameter 264 μm), with perfectly visible nucleus and nucleolus that are of large size compared to the size of the oocyte.

Stage II. Developing gonads, cream colored to pale orange. Oocytes with a mean greatest diameter of 453 μm, and a nucleus almost always clearly defined. Oocytes show some yolk formation, mainly in the outer area.

Stage III. Gonads spreading widely through the cephalothoracic cavity, orange colored. Nucleus generally not visible. Large oocytes (mean greatest diameter 673 μm), with abundant immature yolk and granulations of mature yolk that occupy most of the cytoplasm.

Stage IV. Completely mature gonads filling up the cephalothoracic cavity, bright orange in color. Large, well developed oocytes (mean greatest diameter 845 μm), with clearly differentiated yolk granulations that occupy all of the cytoplasm.

In females having stage II, III and IV gonads, there are always some immature oocytes, but in very small proportions.

Gonad development begins after the pubertal moult, when the animals reach sexual maturity. This moult takes place in the summer or early autumn in most individuals. All of the morphometrically immature females (with flat abdomens) analyzed, that were caught exclusively in experimental samplings (N = 154) had undeveloped gonads (Table 2). The mature specimens, in the early post-ecdysial period after the pubertal moult or in the early intermoult stage C_1, caught in July and August, always had stage I gonads (N = 46).

The analysis of the evolution of the reproductive cycle is based on the stages described above (Fig. 2) in addition to oocyte size and gonosomatic indices. The analysis of the reproductive cycle of individuals reaching the pubertal moult in the summer of 1991 (PM91) was begun in December of that year. Females were found to have gonads in late stages of development, several months after the pubertal moult had occurred (stages III and IV represent 67.9%). However, the analysis of PM92 individuals began in September, shortly after the pubertal moult took place, at a time when animals in the intermoult stage begin to be caught. During this month only animals having gonads in Stages I and II (55.6 and 44.4% respectively) are found (Fig. 2). In October and November, animals with stage III gonads appear in a low percentage (<15%), and the population is mainly composed of animals in stage II. In December stage IV animals begin to appear (PM92, 13.3% and PM91 25.0%), ready to spawn.

Between December and May, when individuals belonging to the two cohorts (PM91 and PM92) were analyzed, there is a similar pattern in the reproductive cycle of both cohorts. The proportion of animals in stage IV increases progressively up to May, when they represent 100 % of non-egg-bearing females. During the summer non-ovigerous females, whose pubertal moult took place the year before and whose first brood had already been spawned in spring (data from PM91), had stage III and IV gonads. The percentage in stage III increased in autumn, reaching 100% in November, which marks the end of the breeding period. In December animals in stage IV begin to make their appearance, and they will start a second breeding cycle later. There was only a small number of individuals caught in the fishery that had undergone the pubertal moult the year before (<1%, Table 1), due to the great fishing pressure the population was subject to during the fishing season that began just after the pubertal moult. This makes it difficult to do a follow-up study, after the first breeing season.

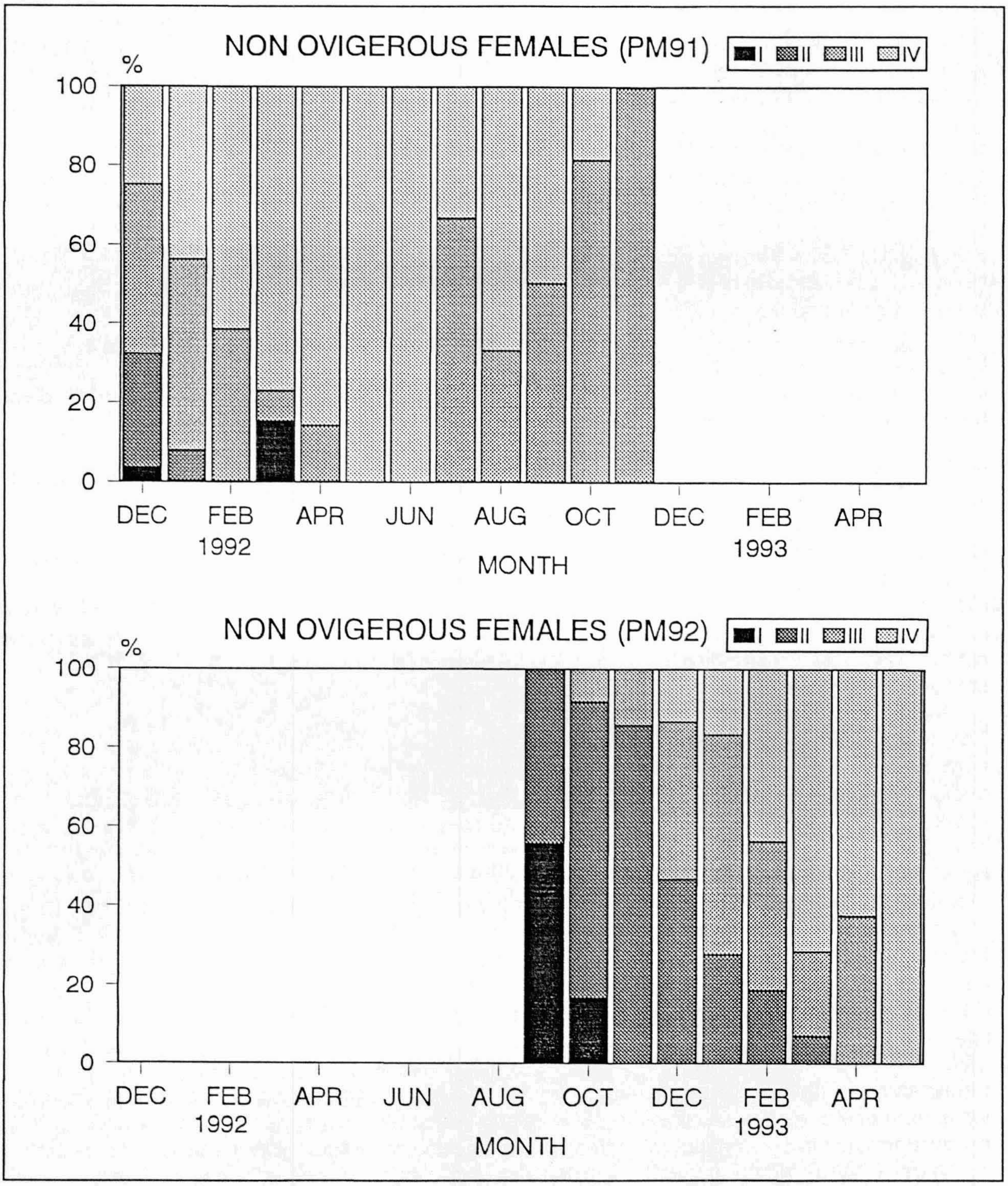

Figure 2. *Maja squinado*. Reproductive cycle of non-ovigerous females. The percentage of females in different stages of gonad development for each month is shown. PM91 = females that reached sexual maturity in 1991. PM92 = females that reached sexual maturity in 1992.

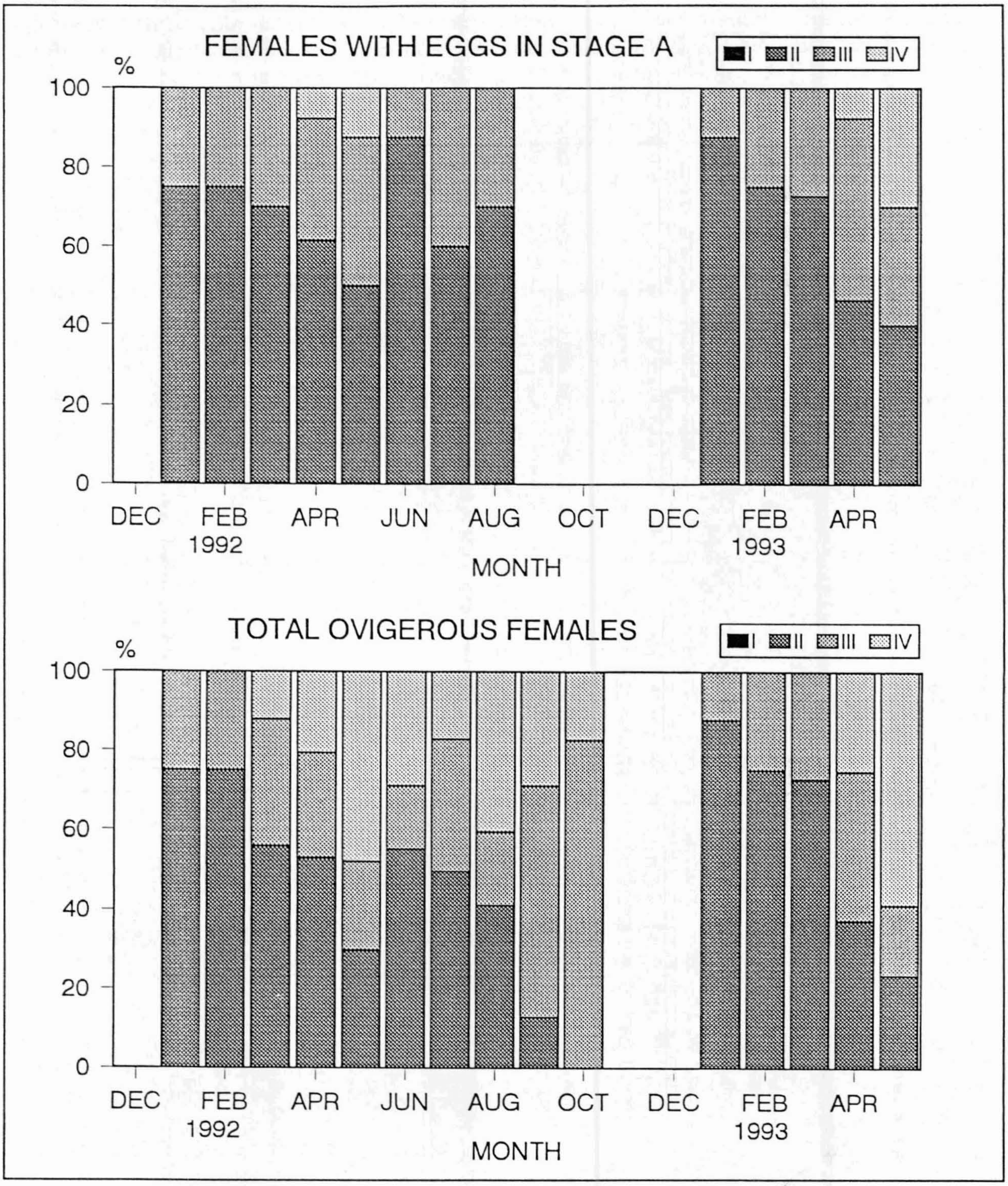

Figure 3. *Maja squinado*. Reproductive cycle of ovigerous females. The percentage of females in different stages of gonad development for each month is shown, for females having stage A eggs and for the total number of ovigerous females (weighting the data from gonad analyses for females in stages A, B and C for the percentage of females in the different stages of egg development in the catches).

The stage of maturity of the ovaries in ovigerous females advances as the incubation period progresses, in order to carry out the next brood. Females that have recently spawned, with eggs in stage A (N= 146), have ovaries mostly in stages II and III (64.4 and 31.5% respectively), and only 4.1% of the females analyzed were in stage IV. On the other hand, females having eggs ready to hatch, in stage C (N= 44) have ovaries only in stages III and IV (17.4 and 82.6% respectively). Practically all females in stage III were caught in September and October, in the last months of the breeding period. Although the size of the sample is small for females in stage B (N= 15), ovary development is in between that of females in A and C (20.0% in stage II, 26.7% in III and 53.3% in stage IV).

The analysis of the monthly evolution of the developmental stage of the gonads in females carrying eggs in stage A does not point to a clear seasonal pattern (Fig. 3), except during the period when the first brood of the year is spawned (between January and May). During this time stage II is dominant in January and February (over 75%), with stages III and IV reaching between 40 and 60% in April and May. Data for all ovigerous females examined were also analyzed, weighting the data from gonad analyses for females in stages A, B and C by the proportion of females with eggs in different development stages in the catches During the first part of the breeding cycle, the pattern is similar to that of females with eggs in stage A, as they represent almost all the ovigerous females. In the following months the percentage of females in stage III increases, reaching 82.5 % in October.

Breeding Cycle and Number of Broods

Once females have carried out the pubertal moult in late summer or early autumn, their ovaries begin to develop, and it is in late winter or early spring when they spawn for the first time. No ovigerous females were found between September and November in the cohort that had just reached maturity. Since the catches included immature females (with flat abdomens and undeveloped gonads) as well as specimens that had undergone the pubertal moult, the breeding cycle was analyzed using animals with a minimum carapace length of 130 mm (Fig. 4). At this size 50% of the females are mature and only one specimen measuring over 140 mm was found to be immature (153 mm CL).

There is a small percentage of ovigerous females in December and January (from 1.2 to 8.3%), which increases rapidly, reaching 59.8 and 69.0% in March (for PM91 and PM92 respectively). From April to September the mean percentage of ovigerous females is 77.4% in PM91 (the values for PM92 in April and May are 81.1 and 85.2% respectively). In October and November there is a sharp drop in females with eggs (33.3 and 9.1% respectively), which marks the end of the breeding season. On occasion we found ovigerous females with broods that were smaller than normal, representing 3.8 % of the ovigerous females. This could be related to the existence of non-fertilized clutches.

The appearance of ovigerous females with eggs in a late stage of development almost ready to hatch (stage C) follows a similar cycle, with an initial delay of about two months (Figs. 4 and 5). Females with stage C eggs first appear in March (< 4%) and in May - June, the first peak occurs. During these months between 23.8 and 25.0% of the population has stage C eggs (making up between 29.1 and 33.3% of the ovigerous females). This peak which corresponds to the hatching of the first brood could be caused by a synchronism in the period when the first spawning takes place. Until October the percentage of females having late stage eggs makes up between 16.7 and 37.8% of the population. During this time, as the breeding period progresses, these females comprise an increasing proportion of the ovigerous animals, reaching 50% in September and 87.5% in October (Fig. 5), which marks the end of the breeding period.

During the months that most of the ovigerous females show stage C eggs, at the end of the breeding season, there is a sharp increase in non-breeding females with egg cases attached to the abdominal pleopods (Fig. 5). In October and November 71% of the non-ovigerous females have egg cases attached to the abdominal pleopods, belonging to the last brood of the cycle.

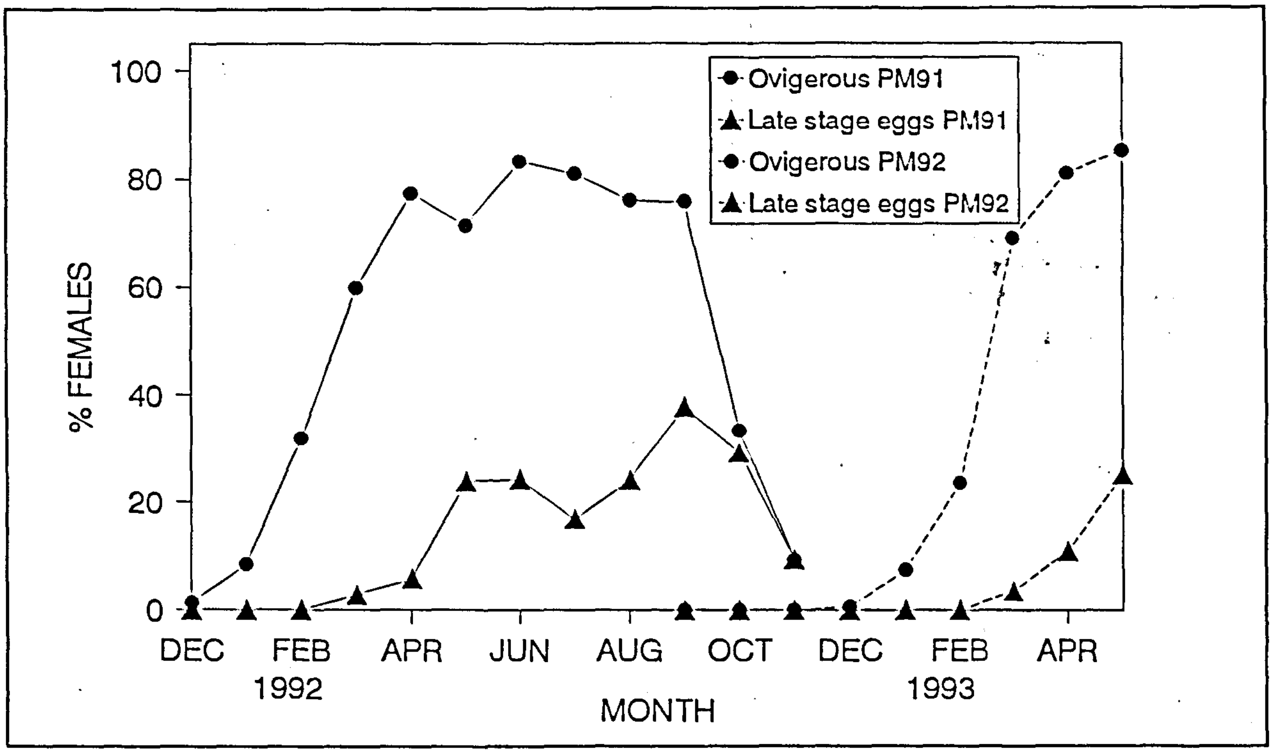

Figure 4. *Maja squinado*. Breeding cycle corresponding to females ≥ 130 mm carapace length. The percentage of ovigerous females and females with eggs in late development stages (C) with regard to the total number of females sampled is shown. PM91 = Females that reached sexual maturity in 1991. PM92 = Females that reached sexual maturity in 1992.

The length of the incubation period under experimental conditions (Fig. 6), using data from specimens that completed their entire incubation in the laboratory with the production of viable larvae, fluctuated between 34 and 62 days. The mean duration in July and September was 40 days (N = 5) at a temperature ranging from 16.7 to 19.5 °C (mean temperature 18.4 °C). The mean duration in May, June, October and November was 58 days (N = 4) at temperatures between 14.2 and 17.8 °C (mean temperature 15.8 °C). The time elapsed between hatching and the next spawning fluctuated between 1 and 6 days, with a mean value of 3.4 days (N = 15) between consecutive broods. The number of fertile broods for the three individuals that spawned more than once in the laboratory was 1, 3 and 4 (a fifth brood took place in an animal with partial hatching), notwithstanding the fact that at least one more brood would have taken place in the natural environment. The experimental data correspond to isolated females, that carried out consecutive spawnings using material stored in the spermatheca. One or more non-fertilized clutches often occurred at the end of the breeding period. In these cases the females would gradually lose their eggs, and after an average of 21 days the whole brood would have disappeared completely (N = 10).

Mating. Fecundation Season and Frequency

In laboratory experiments, using specimens that had previously undergone the pubertal moult, two matings were observed. The male places itself with the ventral part of its body facing upward and the female positions itself on top with the ventral part of its body facing the male's. This behaviour has been described earlier (Brosnan, 1981; Hartnoll, 1969). The same type of behaviour was observed in a number of matings carried out both in large volume tanks as well as in the field. In all cases the female had a hard carapace and no matings took place immediately following ecdysis. Couples were made up of morphometrically mature animals. No courtship was observed either before or after mating. Most matings carried out in captivity were observed between October and December, and occasionally in July and August. Matings observed in the field were recorded mostly between January and March. Under experimental conditions there were cases where females mated successively with several males in a short period of time.

The spermathecae from 46 females caught in experimental samplings with the glass box in July and August, having undergone the pubertal moult that same summer, were found to be empty. However, the analysis of the spermathecae of mature animals with hard carapace throughout the yearly cycle, allows us to define the existence of previous matings and to identify between 1 and 3 defined masses pertaining to several matings and/or different males. The existence of spermathecae in ovigerous females with stored sperm corroborates the possibility that consecutive broods occur without the need for previous mating. The analysis of spermathecae currently underway will contribute more specific information on the season and frequency of mating.

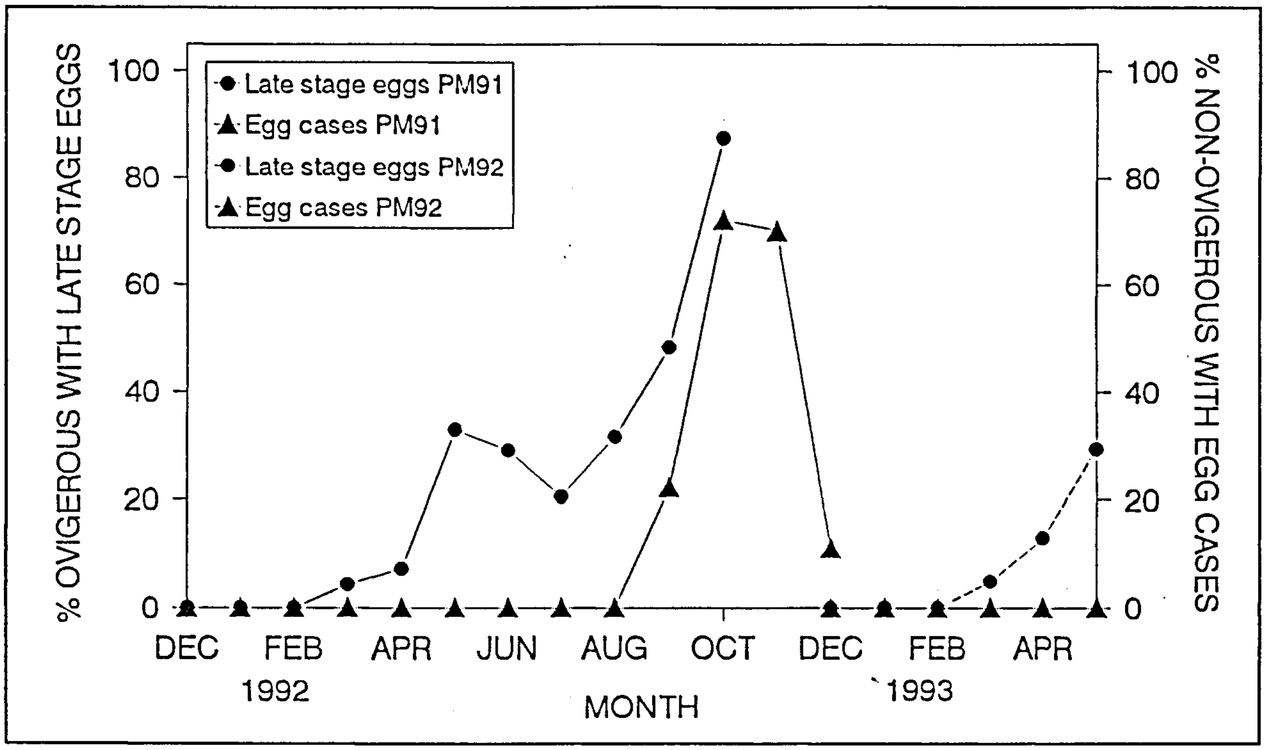

Figure 5. *Maja squinado*. Evolution of the percentage of females having eggs in late development stages (C) with regard to the total number of ovigerous females and females with egg cases with regard to the total number of non-ovigerous females.

DISCUSSION

The terminal moult is a crucial event in the life history of *Maja squinado* as in other majids, marking the end of growth and the point at which sexual maturity is reached (Carlisle, 1957; Teissier, 1935). In female spider crabs this pubertal moult brings about important morphological changes which affect, among other parts of the body, the abdomen. It bulges and becomes wider and the pleopods develop fully, which will allow attachment and incubation of the eggs after spawning (Hartnoll, 1969; Teissier, 1935). There is a coordination between morphometrical and physiological maturity, determined by the pubertal moult, after which gonad maturation begins. All of the morphometrically immature specimens analyzed had undeveloped gonads (stage I).

The pubertal moult on the southern coast of Galicia takes place in most animals in summer and occasionally at the beginning of autumn. In September females with gonads in the early stages of development begin to appear (stages I and II, 56 and 44% respectively). In December, the first specimens with fully developed gonads (stage IV) appear. The percentage of females ready to spawn increases until May, when they make up 100% of the non-ovigerous females. Gonad maturation marks the inmediate beginning of the breeding cycle.

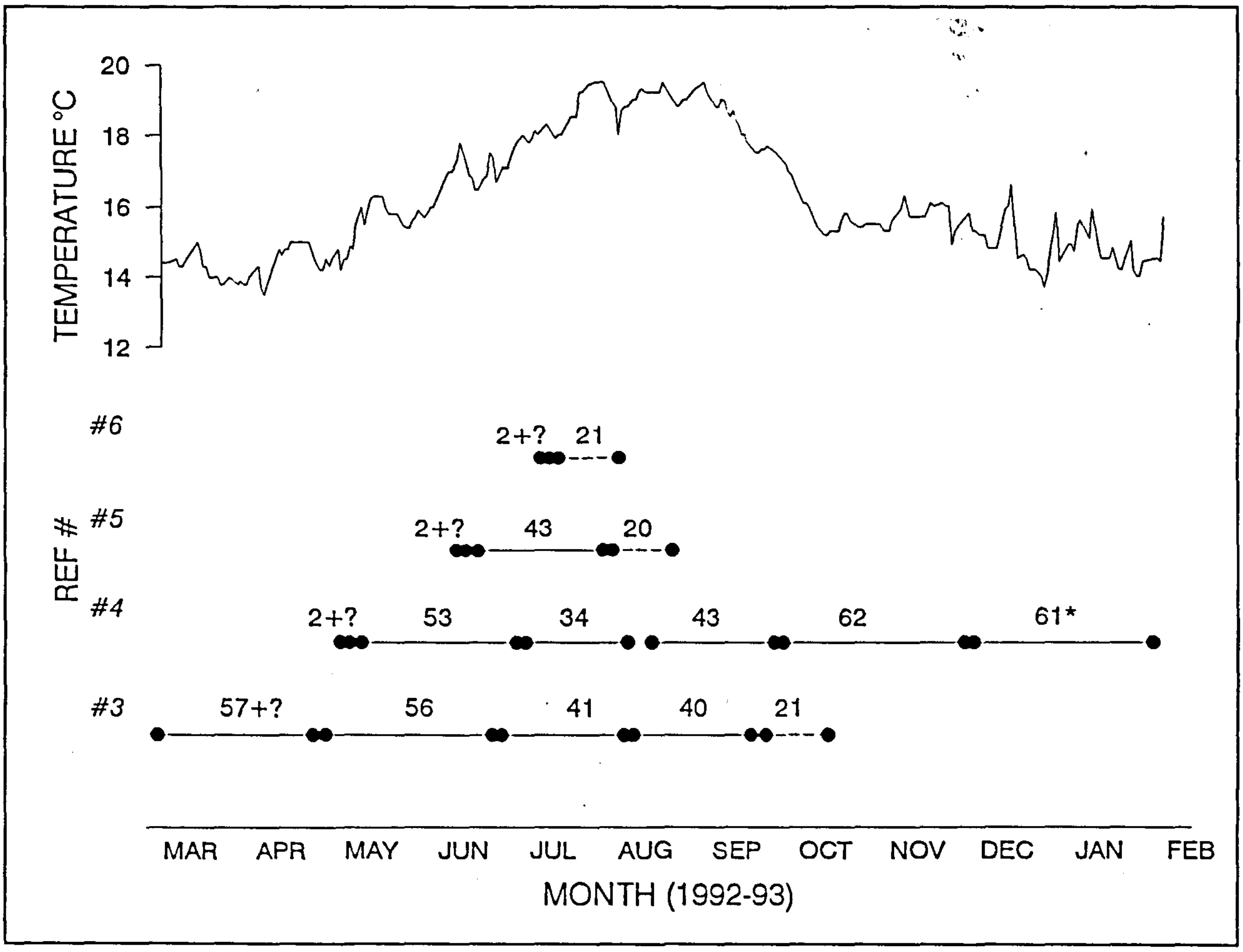

Figure 6. *Maja squinado*. Duration (days) of consecutive broods of four females kept in experimental conditions without males. For the first brood of each female, the number of days from the time they were held in the laboratory to the day hatching took place is shown. The broken line indicates broods that did not develop because they were not fertilized. * = Brood with partial hatching, mostly non-fertilized eggs. The evolution of the temperature in the tanks used is shown.

In December ovigerous females can be found occasionally. Their percentage in the population increases in January, and in March they represent 59-69%. Between April and September, the percentage of ovigerous females is greater than 75%, reaching values of 85%. In October and November there is a sharp drop in the proportion of ovigerous females, which signals the end of the breeding season. This period during which ovigerous females are dominant, coincides, to a large extent, with other geographical areas. On the west coast of Ireland, the presence of ovigerous females is recorded between March and September (Brosnan, 1981; Rodhouse, 1984), and hatching occurs in September in the area of the Isle of Man (Hartnoll, 1965).

Edwards (1979) reports that most females carry eggs between May and September in the south of England, and ovigerous females do not appear there later than October. In Brittany the breeding cycle begins in May and ends in August (English Channel) or September (Morlaix) (Kergariou, 1971). The first spawning is reported to occur between February and May (Kergariou, 1975). In the Adriatic Sea ovigerous females appear between March and September (Stevcic, 1967). There is an observation for the coast of the Sahara (García Cabrera, 1972) in which it is reported that almost all the females are ovigerous in January. The references pertaining to different geographical areas show only the season when ovigerous females appear, but they do not generally contribute data that deal with their relative importance in the population, or these data may be based on small samples, which would make it difficult to carry out a more detailed analysis.

Although in general no great geographical differences were found in the breeding period, there were, however, major differences in the number of broods, ranging between one and three. In areas close to the northern boundary of the distribution of *Maja squinado*, this species has one brood per year on the west coast of Ireland (Brosnan, 1981; Rodhouse, 1984) and on the Isle of Man (Hartnoll, 1965). On the south coast of England, there is also only one yearly brood (Carlisle, 1957; Edwards, 1979). On the coast of Brittany, however, two broods were reported during the breeding period; the first between February and May, especially in the latter, and the second from late June to August (Kergariou, 1971, 1975). In the Adriatic Sea there are three broods; the first between March and May, the second from late May to early July, and the last brood from July to August (Stevcic, 1967).

For seven months (from March to September) an average of 76% of the females are ovigerous in the south coast of Galicia. The mean duration of incubation under experimental conditions is 40 days in summer (mean temperature 18.4 °C) and 58 days in spring and autumn (mean temperature 15.8 °C). Average temperatures on the bottom in the research area are 12.5 to 14.5 °C in spring and 13.5 to 15.5 °C in summer, reaching 17.5 °C in areas less than 10 m deep (data from the Centro Galego para o Control da Calidade do Medio Mariño of the Xunta de Galicia, and our own data). Considering the above and the fact that the time between hatching and the following brood is an average of 3.4 days (in other geographical areas it varies between 2 and 4 days, Kergariou, 1971, 1975, 1984, or a few unspecified number of days Stevcic, 1967), the number of broods per year for one female in southern Galicia is estimated to be three.

The incubation period in other geographical areas is variable, and clearly dependant on temperature. In Britanny it fluctuates between 45 days at 13-15 °C and 60 days at 11.5-12.9 °C (Kergariou, 1971), although the same author later quotes a duration of 47 days at 16.8 °C and 74 days at 14 °C (Kergariou, 1975, 1984). Stevcic (1967) does not give specific data on the incubation duration in the Adriatic; based on data given for consecutive broods, it appears to fluctuate between 45 and 75 days. Brosnan (1981) reports an incubation period of 43 to 47 days (referring to the Irish coast under experimental conditions at 15 °C). The longest time reported for incubation in England and Ireland (9 months, Carlisle, 1957; 5-6 months, Edwards, 1979) may be attributed to the existence of a period of diapause. Wear (1974) describes a period of diapause at 11-15 °C, lasting up to six weeks, which means that the total incubation period lasts 100 days in addition to the length of diapause.

The existence of three consecutive broods in *Maja squinado* during the breeding period, with only a few days elapsing between spawning and hatching, brings about the maturation process of the ovaries simultaneous to the development of the eggs during incubation. Ovigerous females with eggs in the early stages of development have gonads mainly in stages II and III, either beginning to develop or already in a late stage of development (64 and 32% respectively). Females with late stage eggs generally have fully developed ovaries, stage IV (83%), ready for the next brood. In October, which coincides with the end of the breeding cycle, females that are incubating their last brood still have gonads in stage III, in order to begin a new breeding cycle. This has also been cited by other authors (Brosnan, 1981; Edwards, 1979; Rodhouse, 1984).

The increasing appearance of females with fully developed eggs in southern Galicia in May-June corresponds to the hatching of the first brood. The greater variability in temperature values during the summer in nearby zones within the research area (range of 2-4 °C), produces less synchronism in incubation and can be the reason that there is no appearance of a clear peak indicating hatching of the second brood during a specific season. Considering the experimental data, hatching of the second brood would take place, mostly in July-August. The third and last hatching would occur mainly in September-October. After this hatching, 71% of the non-ovigerous females present remains of egg cases on the pleopods. In Britanny and the English Channel, research has been done on the appearance of larvae in plankton, enabling the hatching season to be determined. In southern Britanny zoeas appear from June to October with a peak in July and another in August-September (Martin, 1983), which coincides with data from Kergariou (1971, 1975) on the evolution of the breeding cycle. In areas near the English Channel, zoeae appear from July to October, with a sole peak corresponding to the only brood of the year (Martin, 1980, 1985).

A controversial point about mating in *Maja squinado* is the moult stage of the female and whether or not a previous mating is necessary for the fertilization of eggs from consecutive broods. Early observations of pods of animals of both sexes (Carlisle, 1957) pointed to the existence of mating between males having a hard carapace and females that had moulted and still had a soft carapace. This author mentions that it is not possible for females with a hard carapace to mate (implying that females mated only once after the pubertal moult). He states that females store sperm in the seminal receptacle to be used months later when they spawn.

All the authors later agree that multiparous females with hard carapaces do mate, as is mentioned in this paper (Brosnan, 1981; Hartnoll, 1969; Kergariou, 1971, 1975, 1984; Stevcic, 1977). Primiparous females studied in the waters of Galicia do not mate until they have a hard carapace, which appears to coincide with the behaviour of most females in other geographical areas (Brosnan, 1981; Hartnoll, 1969; Kergariou, 1971; Stevcic, 1977). The possibility that primiparous females mate immediately after the female moult (Hartnoll, 1969; Stevcic, 1977) has not been ruled out. However there is a tendency to restrict this behaviour to animals that make up large pods of both sexes (Carlisle, 1957; Hartnoll, 1969).

Kergariou (1975, 1984) does not accept the possibility that sperm may be stored. Both this author and Stevcic (1967) claim that prior mating is necessary for each consecutive brood that takes place during the breeding cycle. The role of the spermatheca as a receptacle that stores materials transferred by the male during mating was described by Carlisle (1957) and Hartnoll (1965, 1969). Our data show the role of the spermatheca as a receptacle for sperm storage, and contribute new information on the existence of multiple broods without the necessity of previous matings for each one. The sperm which is stored and transferred by one or more males allows up to 4 or 5 broods to be fertilized during the breeding cycle under experimental conditions. The spermathecae analyzed throughout the yearly cycle, both in non-ovigerous and ovigerous females, have frequently stored sperm forming 1 to 3 masses, that can be available for use in several broods.

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BIBLIOGRAPHY

ADAMS, A.E. & A.J. PAUL, 1983.- Male parent size, sperm storage and egg production in the crab *Chionoecetes bairdi* (Decapoda, Majidae). *Int. J. Invert. Reprod.* 6:181-187.

BENINGER, P.G., R.W. ELNER, T.P. FOYLE & P.H. ODENSE, 1988.- Functional anatomy of the male reproductive system and the female spermatheca in the snow crab *Chionoecetes opilio* O. Fabricius (Decapoda: Majidae) and a hypothesis for fertilization. *J. Crust. Biol.* 8:322-332.

BROSNAN, D.M., 1981.- Studies on the biology, ecology and fishery of the spider crab *Maia squinado* Herbst (1768) off the west coast of Ireland. M. Sc. Thesis, Department of Zoology, University College Galway, Ireland, 133pp.

CARLISLE, D.B., 1957.- On the hormonal inhibition of moulting in decapod Crustacea. II. The terminal anecdysis in crabs. *J. mar. biol. Ass. U.K.* 36:291-307.

CONAN, G.Y. & M. COMEAU, 1986.- Functional maturity and terminal molt of male snow crab, *Chionoecetes opilio*. *Can. J. Fish. Aquat. Sci.* 43:1710-1719.

CONAN, G.Y., R.W. ELNER & M. MORIYASU, 1990.- Review of literature on life histories in the genus *Chionoecetes* in light of the recent findings on growth and maturity of *C. opilio* in eastern Canada. *In, The Proceedings of the international symposium on king and Tanner crabs.* B. Melteff (ed.), pp. 163-179. Lowell Wakefield Fisheries Symposia Series. University of Alaska, Alaska Sea Grant Report 90-04.

CORMIER, R.J., A.R. FRASER, R.F.J. BAILEY & N. RAYMOND, 1992.- Hemolymph ecdysone concentration as a function of sexual maturity in the male snow crab (*Chionoecetes opilio*). *Can. J. Fish. Aquat. Sci.* 49:1619-1623.

DIESEL, R., 1989.- Structure and function of the reproductive system of the symbiotic spider crab *Inachus phalangium* (Decapoda: Majidae): Observations on sperm transfer, sperm storage and spawning. *J. Crust. Biol.* 9:266-277.

EDWARDS, E., 1979.- Preliminary results of an investigation on a new fishery for spider crabs (*Maia squinado*) along the south coast of England. *ICES, Shell. Comm.*, C.M. 1979/K:14, 9pp.

ELNER, R.W. & P.G. BENINGER, 1992.- The reproductive biology of snow crab, *Chionoecetes opilio*: A synthesis of recent contributions. *Amer. Zool.* 32.524-533.

GARCÍA CABRERA, C., 1972.- Estudio biológico pesquero del Centollo en aguas del litoral sahariano. *Bol. Inst. Esp. Oceanog.* 156:1-36.

HARTNOLL, R.G., 1965.- The biology of spider crabs: A comparison of British and Jamaican species. *Crustaceana* 9:1-16.

HARTNOLL, R.G., 1969.- Mating in Brachyura. *Crustaceana* 16:161-181.

KERGARIOU, G., 1971.- L'araignée de mer, *Maia squinado* L., sur le littoral de Bretagne. *Science et Pêche, Bull. Inst. Pêches marit.* 205:11-19.

KERGARIOU, G., 1975.- Contribution à l'étude de la reproduction de l'araignée de mer (*Maia squinado* H.). *ICES, Shell. Benth. Comm.*, C.M. 1975/K:34, 8pp.

KERGARIOU, G., 1984.- L'araignée de mer, *Maia squinado* H. Biologie et exploitation. *La Pêche maritime* 1279:575-583.

MARTIN, J., 1980.- Abondance de larves d'étrille (*Macropipus puber*, L.), d'araignée (*Maia squinado*, Herbst) et de torteau (*Cancer pagurus*, L.) sur la côte ouest du Cotentin (manche) de 1977 a 1979. *ICES, Shell. Comm.*, C.M. 1980/K:21, 15pp.

MARTIN, J., 1983.- Période d'éclosion des larves d'araignée (*Maia squinado*, Herbst) en baie d'Audierne (Bretagne sud) en 1979 et 1980. *ICES, Shell. Comm.*, C.M. 1983/K:30, 10pp.

MARTIN, J., 1985.- Abondance et distribution des larves d'araignée (*Maia squinado* Herbst) en Manche en 1983. *ICES, Shell. Comm.*, C.M. 1985/K:24, 11pp.

PAUL, A.J. & A.E. ADAMS, 1984.- Breeding and fertile period for female *Chionoecetes bairdi* (Decapoda, Majidae). *J. Crust. Biol.* 4:589-594.

RODHOUSE, D.M., 1984.- Experimental fishing for the spider crab, *Maia squinado*: sea and laboratory trials. *J. mar. biol. Ass. U.K.* 64:251-259.

STEVCIC, Z., 1967.- A short outline of the biology of the spinous spider crab. *Bull. Sci. Conseil Acad. RSF Yugoslavie*, Section A 12:313-314.

STEVCIC, Z., 1977.- Contribution a la connaissance de la reproduction de l'araignée de mer (*Maja squinado*). *Rapp. Comm. int. Mer Médit.* 24:177-178.

TEISSIER, G., 1935.- Croissance des variants sexuels chez *Maia squinado* L.. *Trav. Sta. Biol. Roscoff* 13:99-130.

WEAR, R.G., 1974.- Incubation in British decapod Crustacea, and the effects of temperature on the rate and sucess of embryonic development. *J. mar. biol. Ass. U.K.* 54:745-762.