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Reproductive biology and relative growth in the spider crab *Maja crispata* (Crustacea: Brachyura: Majidae)*

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SUMMARY: A series of life-history traits in the spider crab *Maja crispata* were studied on the island of Ischia (Italy) during four sampling periods in 1982: sex ratio, relative growth, sexual maturity, reproductive season, number of eggs per female, copulation and brood sequence. A total of 104 males and 86 females were captured. Mature animals were present year around. The greatest relative abundance of mature animals in both sexes was found in the warmer season. Three postlarval growth stages were distinguishable in males: crabs with juvenile morphological characteristics and immature gonads (between 1.69 and 5.03 cm carapace length), crabs with juvenile morphological characteristics and mature gonads (between 3.59 and 6.11) and crabs with adult morphological characteristics and mature gonads (between 4.98 and 7.16). In females, only two postlarval stages were detected: juveniles (between 1.87 and 4.62) and adults (between 3.56 and 6.11). Mature females with full seminal receptacles were always present. Breeding period extends from May to September. Mean number of eggs was 11473 per female. Breeding sequences in two females kept in the laboratory varied between 5 and 7 broods per year, at intervals of between 21 and 32 days.

Key words: Crustacea, Brachyura, spider crabs, *Maja crispata*, reproduction, relative growth, Mediterranean Sea.

RESUMEN: BIOLOGÍA REPRODUCTIVA Y CRECIMIENTO RELATIVO EN EL CANGREJO ARAÑA *MAJA CRISPATA* (CRUSTACEA: BRACHYURA: MAJIDAE). – Varios rasgos de la historia de vida del cangrejo araña *Maja crispata* fueron estudiados en la isla de Ischia (Italia) durante cuatro períodos de muestreo en 1982: proporción de sexos, crecimiento relativo, madurez sexual, período reproductivo, número de huevos por hembra, cópula y sucesión de camadas. Se capturó un total de 104 machos y 86 hembras. Animales maduros estuvieron presentes durante todo el año. La mayor abundancia relativa de animales maduros en ambos sexos se encontró durante el período más caluroso. Tres fases del crecimiento postlarval fueron determinadas en machos: cangrejos con características morfológicas juveniles y gónadas inmaduras (entre 1.69 y 5.03 cm de longitud de caparazón), cangrejos con características morfológicas juveniles y gónadas maduras (entre 3.59 y 6.11), y cangrejos con características morfológicas adultas y gónadas maduras (entre 4.98 y 7.16). En hembras se encontraron sólo dos fases postlarvales: juveniles (entre 1.87 y 4.62) y adultas (entre 3.56 y 6.11). Hembras maduras con receptáculos seminales llenos estuvieron siempre presentes. El período de cría se extiende de mayo a septiembre. El promedio del número de huevos fue de 11473 por hembra. La sucesión de camadas en dos hembras mantenidas en el laboratorio varió entre 5 y 7 puestas por año, a intervalos de entre 21 y 32 días.

Palabras clave: Crustacea, Brachyura, Majidae, *Maja crispata*, reproducción, crecimiento relativo, Mar Mediterráneo.

INTRODUCTION

A wealth of literature deals with a variety of reproductive aspects of spider crabs, covering topics on reproductive behaviour, reproductive effort, seasonality, growth and sexual maturity (Paul and Paul, 1996; Jones and Hartnoll, 1997, among others). Knowledge of reproductive potential, seasonality, growth and sexual maturity in spider crabs has been of significant importance for some species being

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commercially exploited, such as *Maja squinado* (González-Gurriarán *et al.*, 1998) and *Chionoecetes opilio* (Saint-Marie *et al.,* 1995). Importance of morphological changes in maturity has been well documented in majids by several authors (Hartnoll, 1978; Sampedro *et al.,* 1999).

The decorator crab *Maja crispata* is known to live in the Mediterranean Sea (Zariquiey-Álvarez, 1968), and several studies have dealt with its ecology and its taxonomic, behavioural, anatomical, and dietary features (among others) (Schäfer, 1954; Schöne, 1976; Stevcic, 1985; Carmona-Suárez, 1990, 2002). In spite of this, few publications have examined its reproductive traits (Lo Bianco, 1908; Schöne, 1967).

The present study was performed to provide baseline data on population parameters that have not yet been investigated in the spider crab *Maja crispata*, such as sex ratio, achievement of sexual maturity, copulation, reproductive season, reproductive effort and brood sequence as well as relative growth. Such baseline information is crucial for future studies of this species' dynamics in the Mediterranean Sea, in environments that are threatened by invasive algae (Ceccherelli *et al.*, 2000).

MATERIALS AND METHODS

Sampling sites were located in the area of Castello Aragonese on the island of Ischia-Italy, in the Tyrrhenean Sea (40º42'N and 13º55'W) (Fig. 1). Four sampling periods (February, May/June, August/September and November/December 1982) were used in a mosaic habitat complex consisting of rocky sublittoral, *Posidonia* meadows, and dead *Posidonia*-rhizomes at a depth of between 0 and 5 m, well protected from the open sea (Fig. 1).

Crabs were captured using SCUBA equipment from sampling sites chosen randomly by tossing a 1-m^2 quadrate haphazardly. Capture methodology is described in detail in Carmona-Suárez (2002). For relative growth analysis, additional specimens were obtained from local fishermen. Captured crabs were taken to the laboratory of the Marine Biological Station in Ischia. Some of them were transported alive to the Marine Biological Department (University of Vienna- Austria) for further observations. The rest were stored at -10ºC. After thawing, they were sexed, measured and their gonadal stage was determined. In females, seminal receptacles were visually examined, in order to establish the grade of "fullness".

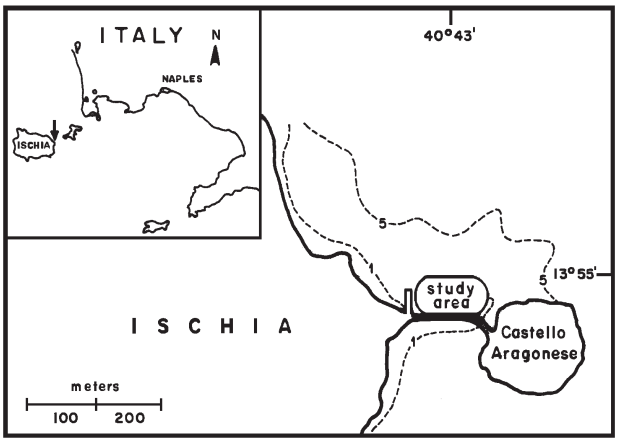

FIG. 1. – Location of island and sampling site. Numbers refer to depth in metres.

They were classified either "full" or "empty". In ovigerous females, numbers of eggs were quantified.

The different maturity stages were determined by a power regression analysis, using the methodology described by Hartnoll (1978). Morphological (chelae in males and pleon in females) and physiological (gonadal development) changes were taken into account, transforming data to logarithm base 10. Carapace length (CL) in both sexes was measured from the basal region between the frontal teeth to the posterior-median edge. In males, chelae width (CW) was measured at the articulation between the propodus and the dactylus. In females, width of the abdomen (AW) was measured at the 5th abdominal segment. Measurements were taken with a 0.1-mm precision caliper. Gonadal development was determined by changes in colour and consistency of the gonads.

Eggs from ovigerous females were carefully detached from the pleopods. A sample from each clutch was observed under the microscope for measurements using a graduated reticule. The number of eggs per female was estimated using both a gravimetric (Fielding and Haley, 1976) and a volumetric method (Díaz *et al.*, 1983).

Brood sequence was observed in crabs maintained in closed-water-circulating aquaria with filtering systems and sufficient aeration in a temperature-controlled room in the Marine Biological Department in Vienna (Austria). A day/night light period was used. Copulation observations were carried out *in situ*, in aquaria using recently captured animals (Ischia), and in aquaria with animals kept for longer periods (Vienna). In both cases, each crab pair was held in a separate aquarium.

TABLE 1. – Comparison of sex ratios of *Maja crispata*.

Period	Males	Females	df	Gadj	p
February	17	12	1	0.424	> 0.05
May/June	34	26	1	0.529	> 0.05
August/September	21	20	1	0.012	> 0.05
November/December	32	28	1	0.132	> 0.05
All samples	104	86	1	0.852	> 0.05

Sex ratios were compared with a G-test; carapace length in females and egg counting methods were compared with a t-student test. Regression analyses were conducted using standard least squares (Sokal and Rohlf, 1995), and differences between regression coefficients were analysed with an F test. All calculations were done with the computer program Statistica (Statsoft, 1992).

RESULTS

One hundred and twenty-six square metres were searched in February, 256 m^2 in May/June, 453 m^2 in August/September and 195 m^2 in November/December. A total of 104 males and 86 females were captured. There were no significant differences in the sex ratio from the Mendelian proportion (1:1) in each of the sampling periods and considering all the periods together (Table 1). More significant than the plain sex ratios is the relationship between individuals with mature and immature gonads, due to its direct connection with reproduction. A comparative table was generated for the determination of the gonadal stages, taking into account colour and consistence of the gonads (Table 2). Animals with mature gonads were present in all the sampling periods. Their abundance was higher, than that of individuals with immature gonads. The highest abundance of animals from both sexes with mature gonads was found in the warmer season (August/September), when females reached a proportion of 20:1 (mature: immature), and males reached a proportion of 4:1 (Fig. 2).

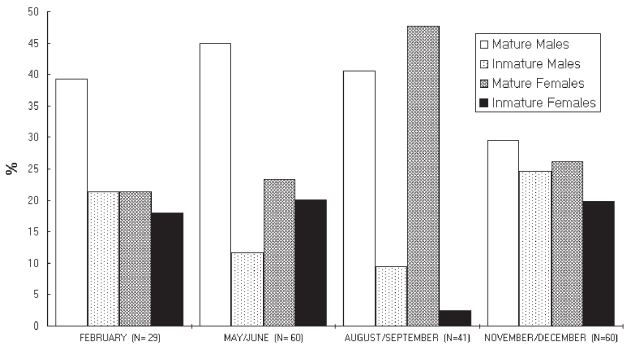

FIG. 2. – Relative abundance of crabs with mature and immature gonads during the four sampling periods.

Relative growth analyses in males were conducted in three separate groups: crabs with morphological juvenile characteristics and immature gonads (JI); crabs with juvenile morphological characteristics and mature gonads (JM); and crabs with morphological adult characteristics and mature gonads (AM) (Fig. 3A). JI crab size ranged between 1.69 and 5.03 cm carapace length; JM crabs ranged between 3.59 and 6.11 cm, and AM crabs between 4.98 and 7.16 cm. Transition from JI to JM males takes place in a size range between 3.63 and 5.01 cm carapace length, with a significant change in the slope from 1.3 to 2 ($F= 974.15$; $p < 0.001$; $df= 78$) (Fig. 3A). On the other hand, the moult of puberty (transition from JM to AM) happens between 5 and 6.5 cm carapace length, with a significant change in the slope from 2 to 1.6 ($F= 1289.53$; $p < 0.001$; $df= 79$) (Fig. 3A). Regression equations are shown in Table 3. Morphological changes were evident in adult males. In these, the chela grows in length as well in width, developing an additional tooth on the internal side of the dactylus.

Two separate groups were analysed in females: juveniles (JF) or prepuberty females (elongated pleon), and adults (AF) or postpuberty females (circular pleon). JF ranged between 1.87 and 4.62 cm

TABLE 2. – Characteristics of gonads during development stages for *Maja crispata*. Stages 1 and 2 correspond to immature gonads. Stages 3 and 4 correspond to mature gonads.

Sex	Stage 1	Stage 2	Stage 3	Stage 4
Males	Almost absent, very small, transparent	Less transparent, thin, soft	White colour, semicompact	Compact form, white colour, large volume
Females	Almost absent, very small, transparent	Milky white, thin, soft	Light orange, covers a great . part of the internal organs	Orange-red, covers whole carapace region

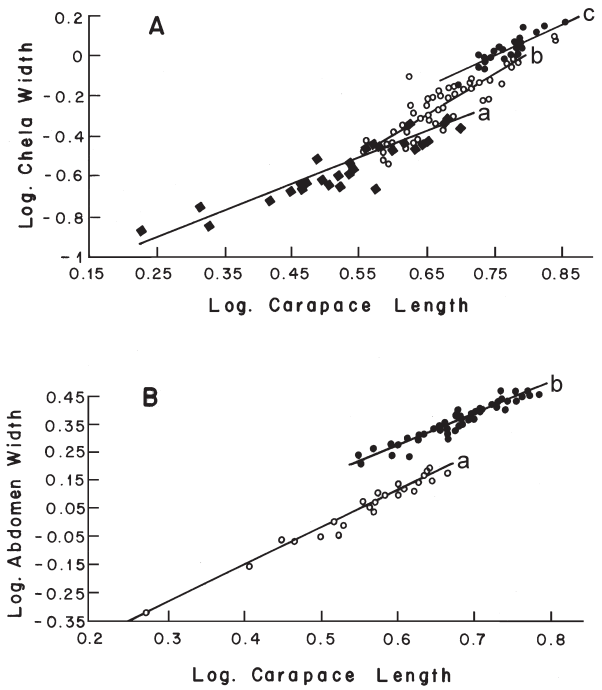

FIG. 3. – Relative growth in *Maja crispata*. A: (a) males with juvenile morphological characteristics and immature gonads, (b) males with juvenile morphological characteristics and mature gonads, (c) males with adult morphological characteristics and mature gonads. B: juvenile (a) and adult (b) females.

carapace length, and AF between 3.56 and 6.11. The moult of puberty takes place between 3.7 and 4.7 cm carapace length (Fig. 3B), changing the slope from 1.3 to 1.1. Although slopes are not significantly different ($F= 0.1094$; $df= 83$; $p > 0.05$), mean carapace length between the two stages (juvenile vs. adult) differ significantly ($t= 7.778$; $df= 83$; $p < 0.001$). Regression equations are shown in Table 3. Females displayed mature gonads only after the puberty molt and throughout most of the year; only in November/December were some postpuberty females found with immature gonads. Also, almost all ovigerous females had mature gonads.

TABLE 4. – Observed copulations in *Maja crispata.* Mj= Male with juvenile morphological characteristics; Ma= Male with adult morphological characterisitics; Fa= Adult female.

Month	Crab Pairs	Time of day	Temperature (°C)	Remarks
Ischia				
November	Mj/Fa	Night	16	Aquarium
November	Mj/Fa	Night	16	Aquarium
May	Mj/Fa	Night	17-18	Aquarium
May	Mj/Fa	Afternoon	22.5	Aquarium Ovigerous
June	Mj/Fa	Night	24-25	*In situ*
August	Ma/Fa	Night	26-27	*In situ* Ovigerous
September	Ma/Fa	Night	24.5	Aquarium Ovigerous
Vienna				
March	Mj/Fa	Afternoon	17-18	Aquarium
April	Mj/Fa	Noon	19-20	Aquarium
May	Ma/Fa	Noon	23	Aquarium Ovigerous
May	Ma/Fa	Afternoon	21	Aquarium Ovigerous
June	Mj/Fa	Afternoon	22	Aquarium Ovigerous
July	Mj/Fa	Noon	22.5	Aquarium
August	Ma/Fa	Afternoon	24	Aquarium

The breeding season appears to extend from May to September. From the whole adult female population in each sampling period, 36% of ovigerous females were found in May/June (n= 13), and 81% in August/September (n= 20). No ovigerous females were captured in February and in November/December. Sixteen ovigerous females were used to determine their number of eggs. Both methods showed that number of eggs per female varied between 5600 and 19000 (volumetric method), and between 4800 and 19800 eggs (gravimetric method); however, as the differences were not significant ($t= 0.04$; $df= 30$; $p > 0.05$), the results were pooled giving a mean estimate of 11473 eggs per female ($SD= 4787.8$; $n= 32$). Egg size ranged between 290 and 400 μm in diameter ($n= 244$; $Mean= 318$; $SD= 24.2$).

TABLE 3. – Relative growth in *Maja crispata*. Regression lines of carapace length (CL) against chela width (CW) of males with juvenile morphological characteristics and immature gonads (JI), males with juvenile morphological characteristics and mature gonads (JM), and males with adult morphological characteristics and mature gonads (AM). Regressions lines of carapace length (CL) against abdomen width (AW) of juvenile (JF) and adult (AF) females. Measurements in cm were log-transformed.

	Regression line	n	r	p
Males				
JI	Log CW= -1.24+ 1.30* Log CL	33	0.914	< 0.005
JM	Log CW= -1.60+ 2.01* Log CL	50	0.845	< 0.005
AM	Log CW= -1.17+ 1.56* Log CL	32	0.868	< 0.005
Females				
JF	Log AW= -0.67+ 1.30* Log CL	25	0.985	< 0.005
AF	Log AW= -0.39+1.12* Log CL	60	0.957	< 0.005

TABLE 5. – Brood sequence in two ovigerous females of *Maja crispata* maintained in aquaria in Vienna (Austria). Bs= Brood sequence; a= Intervals in days between each brood; b= Incubation time in days; °c= Mean temperature and standard deviation (n in parenthesis). * = Eggs eaten by the female; ** = Female died.

	Bs	a	b	°C		Bs	a	b	°C
Female 2	1		3*	22±0.4 (3)	Female 1	1		32	19±1.1 (32)
	2	28	26	24±1.5 (26)		2	40	22	22±1.1 (22)
	3	5	14*	23±0.5 (14)		3	3	21	22±0.8 (21)
	4	12	21	21±1.1 (21)		4	14	25	24±1.2 (25)
	5	21	22	20±0.5 (22)		5	27	14*	23±0.8 (14)
						6	19	22	20±0.4 (22)
						7	26	**	

A total of 14 isolated copulatory crab-pairs were observed in Ischia and Vienna. Five adult males and 9 males with juvenile morphological characteristics were observed copulating with hard-shelled adult females. Six of these females were ovigerous. In Ischia, where natural light conditions were present, copulation took place mostly at night in May, June, August, September and November, in a temperature range between 16 and 27°C (Table 4).

Adult females with full seminal receptacles were captured during all the sampling periods, but the lowest percentages from the total adult females in each period occurred in November/December (February 71.4%, n= 7; May/June 69.2%, n= 13; August/September 95.0%, n= 20; November/December 25.0%, n= 20).

Breeding sequences were observed in two mature females, each held in an aquarium together with an adult male. For these crabs the breeding sequence was 5 and 7. Intervals between broods varied from 21 to 32 days (Mean= 23.6 SD= 3.16; n= 18), with temperatures ranging from 19 to 24ºC (Mean= 22; SD= 1.66; n= 11) (Table 5).

DISCUSSION

From the reproductive point of view, the puberty moult in males (transition from JM to AM) may not be as important as the ability to reach gonadal maturity. This would explain the high incidence of males with mature gonads still exhibiting juvenile characters (57%), and the fact that these were observed copulating with mature females. Although females with mature gonads were present throughout the year, ovigerous females appeared only during the warmer period (May to September), coinciding with those indicated by Lo Bianco (1908) in the Gulf of Naples, and by Pesta (1918) in the Adriatic Sea. The absence of ovigerous females in February and November/December may be due to the low temperatures that dominate in the winter months.

The three differentiated male groups discovered in this study can be defined using the terminology given by Sampedro *et al.* (1999): males with juvenile morphological characteristics and immature gonads= immature juveniles; males with juvenile morphological characteristics and mature gonads= adolescent juveniles; and males with adult morphological characteristics and mature gonads= adults.

As determined in this study, reproduction begins in May, but it peaks between August and September when females have the highest percentage of mature gonads, the highest percentage of ovigerous individuals, and full seminal receptacles. As stated before, *M. crispata* can produce at least 5 to 7 broods in the laboratory, and may be even more productive in its natural environment. In a study conducted by Hines (1982), spider crabs bred 3 to 10 times a year, which is many times more than members of other families that generally breed only once or twice per year.

In spite of the low numbers of individuals captured, the reproductive cycle of *M. crispata* reflects a high degree of adaptation to the strong seasonal variations in the environments that it inhabits. Furthermore, females have the capability to copulate several times with different males, even if they are ovigerous. This assures egg fertilisation (where several clutches of eggs are produced during the year), high larval production, an increase in genetic flow, and thus an increase in the survival chances of the population.

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