Interactions of the fishery of the spider crab *Maja squinado* with mating, reproductive biology and migrations

Juan Freire, Luis Fernández and Eduardo González-Gurriarán

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In this paper different aspects of the fishery and life history of the spider crab *Maja squinado* in southern Galicia (NW Spain) are analyzed to evaluate the potential effects of the fishery on the sperm limitation of the reproductive effort (egg production) of the population. Juveniles of the spider crab inhabit shallow waters (<15 m), where they carry out a terminal moult in August-September, attaining sexual maturity when they are 2+ years old. A short time after the terminal moult (October-November), adults migrate to deeper waters (up to 100 m), where mating occurs (January-February). Field and laboratory data show that multiple matings and sperm storage in female seminal receptacles occur, indicating that females are able to fertilize multiple broods during the annual breeding cycle using stored sperm.

The spider crab is the target of a tangle-net fishery, characterized by a very high fishing effort similar for both sexes. The fishing season is from November-December until May-June and is mostly dependent on migrating animals. Data from catch composition (percentage of recent recruits at the beginning of the season), recaptures from the fishery of females tagged with ultrasonic transmitters and electronic archival tags, and CPUE trends over the course of the fishing season (Leslie analyses of stock depletion) indicate that more than 90% of postpubertal (primiparous) adults are caught during the fishing season. The fishery is almost exclusively dependent on the autumn recruitment of the annual cohort of primiparous adults. Most of the catches are made in autumn and early winter, before or during the mating season (for 4 fishing seasons an average of 45 and 66% of the catches are made before January and February respectively).

The volume of sperm stored in the seminal receptacles and the percentage of females with sperm is lower for females caught in the field during or immediately after the mating season than for females kept in laboratory with a high density of males, and decreases throughout the annual breeding cycle. These two facts may be brought about the low density of both sexes in the mating grounds due to fishery exploitation. We hypothesized that, although sperm limitation probably does occur, the main factor in the severe fishery induced limitation of the reproductive effort of the Galician spider crab populations, as opposed to other crab fisheries targeting only males, is the mortality imposed on females before or during breeding. More information about mating habitat, seasonality and behaviour would be needed for an accurate evaluation of the potential effects of the fishery (and of different management strategies) on sperm limitation.

Key words: life history, *Maja squinado*, mating, migrations, mortality, reproductive effort, seasonality, spider crab, tangle-net fishery

J. Freire, L. Fernández and E. González-Gurriarán: Departamento de Bioloxía Animal, Bioloxía Vexetal e Ecoloxía, Universidade da Coruña, Campus da Zapateira s/n, E-15071 A Coruña, Spain. E-mail: jfreire@udc.es

Introduction

The reproductive behaviour of decapod crustaceans is complex, owing to their need to mate and copulate and to the ability of females to store the sperm from one or more copulations (Hartnoll, 1969; Christy, 1987; Diesel, 1991; Subramonian, 1993). This storage takes place in special structures, the seminal receptacles, which keep the sperm viable for extended periods of time and which may be used in the fertilization of consecutive broods throughout the annual breeding cycle or broods corresponding to consecutive annual cycles (Diesel, 1989, 1991; Sainte-Marie and Lovrich, 1994; Sainte-Marie and Carriére, 1995; González-Gurriarán *et al.*, 1997).

The decapod fisheries generally show a high rate of exploitation and in a number of species the exploitation rate differs depending on the sex, to the point where in some cases there are only male fisheries (Caddy, 1989). These characteristics of the fisheries in addition to reproductive behavior may determine the existence of a process of sperm limitation of the reproductive potential of the populations subject to exploitation: a dwindling production of eggs in the female population due to a lack of sperm for fertilization (Smith and Jamieson, 1991; Sainte-Marie *et al.*, 1997). This effect may be particularly important in fisheries targeting males, which were thought to be protected against overfishing due to the fact that females were not exploited.

The spider crab *Maja squinado* (Decapoda, Majidae) is the target of an intensive fishery in several areas of the NE Atlantic and some stocks show signs of overfishing (Anonymous, 1996; this paper). This species is an example of a crab of considerable commercial interest where fishing targets both males and females. This paper reviews different aspects of the life history of *Maja* (particularly its reproductive biology, mating and migrations) on the coast of southern Galicia (NW Spain), especially in the Ría de Arousa and the adjacent coastal area, and it presents an analysis of information pertaining to seasonality and the effort of the tangle-net fishery which targets this species. A temporal correlation is established between the fishery and life-history events (particularly mating) in order to raise the question as to what part of the population takes part in mating. Lastly, there is a discussion of the evidence supporting possible sperm limitation of the exploited populations of this species and the possible limitation mechanisms of the reproductive potential due to the effect of the fishery.

Life history of *Maja squinado*: reproduction, mating and migrations

Postlarval settlement of *Maja* probably occurs from late spring to autumn, and juveniles inhabit shallow (<15 m) rocky kelp forests and sandy areas presenting restricted movements (González-Gurriarán and Freire, 1994; Hines *et al.*, 1995) (Fig. 1). Juveniles attain sexual maturity after a terminal moult that takes place in summer (González-Gurriarán *et al.,* 1995), when crabs are 2+ years old (unpublished data).

Postpubertal adults carry out an autumn migration to deep soft bottoms (approx. 40 to 100 m) (González-Gurriarán and Freire, 1994; Hines *et al.,* 1995; unpublished data) associated with the beginning of the development of the seminal receptacles and of gonad maturation in females (González-Gurriarán *et al.*, 1993, 1997). Data from samplings in shallow habitats show a peak in the appearance of postpubertal adults from August to October, while they are practically non-existent in November (Fig. 2a). Moreover, ultrasonic telemetry and mark-recapture experiments using electronic archival tags (which record the temperature and depth at which the animal was located) carried out with adult females indicate that migration to deeper waters takes place primarily in November (ranging from September to January) and lasts around 10 days (Fig. 2b). The return migration to shallow waters usually occurs in January and February, immediately following mating, to carry out the incubation of the first annual brood. Although there are no data available on males, according to observations by fishermen, they do not participate in the return migration to shallow waters, but rather remain in their wintering habitats.

The annual breeding period of *Maja* on the southern coast of Galicia ranges from March until November, and the number of broods a year per primiparous female is estimated to be three, with spawnings probably occurring from May to November (González-Gurriarán *et al.,* 1993; 1997).

Data from the analysis of seminal receptacles of field caught females (González-Gurriarán *et al.*, 1997; Fig. 3) and of females tagged with archival tags (Fig. 2; unpublished data) indicated that mating occurs in the wintering habitats, mainly in January and February, when females have gonads in an advanced maturation stage (González-Gurriarán *et al.*, 1997). In both primiparous and multiparous females, mating in *Maja* is carried out only by animals having hard shells, with no courtship prior to copulation or post-copulatory mate guarding. The presence of multiple sperm masses (generally 1-3) in the seminal receptacles and the differences in coloration and relative size between them indicate that females of *Maja* carry out consecutive matings with different males. Sperm transferred by one or more males will remain in the seminal receptacles to be used in the fertilization of consecutive broods without the need for the animals to have copulated prior to spawning (González-Gurriarán *et al.*, 1997). In fact there was a decrease in the amount of sperm stored during the mating season throughout the annual breeding cycle. (Fig. 3).

Seasonality and effort of the tangle-net fishery for *Maja squinado*

The fishery of *Maja* on the coast of Galicia is carried out using multiple gears, although it mainly involves the artisanal fleets in specific geographical areas that use the glass-box (fishing in shallow habitats, approx. <7 m, at low tide) and traps, as well as a tangle-net fleet that operates throughout the distribution area of the spider crab. Most of the catch is the result of the tangle-net fishery, which depends directly on the activity of the crabs, and particularly on their directional movements or migrations.

The open season for the *Maja* fishery in Galicia is between November-December and May-June, depending on the year (Fig. 4). The seasonality of the catches is similar all over the Galician coast. This paper includes information on the landings carried out in the port of

O Grove (Ría de Arousa, southern Galicia), the most important port in the area, which in the last years has accounted for approx. 20% of the total catch in Galicia. Most of the catches are carried out during the initial stage of the fishing season, which coincides with the migration period (Fig. 4). Thus, during the open fishing seasons from 1989/90 to 1992/93 an average of 45% of the landings from the tangle-net fishery (obtained from the daily monitoring of the landings of 12 vessels that were representative of the fleet) were carried out prior to January and 66%, prior to February (unpublished data). It should be noted that before the fishing season officially opens (from September to November), a presumably large amount of catches are taken, which would mean that the fishing rate of the stock during the initial stage is probably even higher.

Different methods have been used to estimate the fishing mortality throughout a fishing season (Table 1). Although the methods of estimation used are potentially biased, they all result in high mortality values which are similar to each other (a mean mortality rate per fishing season of 91%). The exploitation of *Maja* in Galicia depends, for the most part, on the annual recruitment of the crabs that reach sexual maturity in the summer and start their migration in autumn. Each cohort is cut by over 50% in the first two months of fishing and by over 90% by the end of the season.

Effects of the fishery on the reproductive effort: Sperm limitation?

As a result of fishing mortality, over 90% of the adult population of *Maja* on the coast of southern Galicia is made up of crabs that reached sexual maturity during the preceding summer; therefore the reproductive success of the population depends on the annual recruitment. A comparison of the seasonality of the life-history events and of the fishery shows that less than half of each cohort will have the opportunity to mate in the wintering habitats, due to the depletion of the stock caused by the fishery. Females that survive the fishing season will be able to spawn an average of 3 times, although, only a small percentage of the population (less than 10%) will achieve this reproductive success.

The possible existence of sperm limitation in this species depends primarily on two factors. Firstly, the low population density that reaches the mating season (as compared to a non-exploited potential population) could cause a decrease in the availability of males able to mate and therefore sperm limitation. In contrast, the mating system of this species whereby females copulate in hard-shelled condition and may mate during incubation, lengthens the period of availability for mating, as compared to other crabs where the females can only mate immediately after ecdysis (Christy, 1987), which would act as a mechanism inhibiting sperm limitation.

The fullness of the receptacles and the percentage of females with stored sperm held in the laboratory (with a high density of males) was greater than that of females in the field (González-Gurriarán *et al.*, 1997; Fig. 3), which indicates that the availability of males in the field may determine mating opportunities and the volume of sperm stored by females during the mating season. In the field, the fullness of the receptacles decreases after the first annual spawning and throughout the reproductive cycle, and a high percentage of females (>60%) do not have sperm stored during the breeding cycle, which would mean that they must depend on new copulations for the fertilization of subsequent broods. These facts, which are indicative of a certain sperm limitation, could be due to the low density of both sexes in the mating grounds as a result of the fishery exploitation.

Based on the above, we hypothesyzed that although sperm limitation probably does occur, it would not be the main factor in the severe fishery induced limitation of the reproductive effort of the Galician spider crab populations. Unlike other crab fisheries targeting only males (Smith and Jamieson, 1991; Sainte-Marie *et al.*, 1997), the spider crab fishery seems to limit the egg production of this species mainly due to the mortality imposed on females before and during breeding. More information about mating habitat, seasonality and behaviour would be needed to obtain an accurate evaluation of the potential effects of the fishery (and of different management strategies) on sperm limitation of reproductive effort.

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Figure legends

Figure 1. Diagram of the life history of the females of *Maja squinado* on the coast of southern Galicia (NW Spain). Data from González-Gurriarán and Freire (1994), González-Gurriarán *et al*. (1993, 1995, 1997, unpublished data) and Hines *et al.* (1995). In the case of males (not shown), the main differences are due the fact that the gonads begin to mature before the pubertal moult and these animals do not appear to carry out the return migration to shallow waters.

Figure 2. Seasonality of the migrations of females of *Maja squinado* on the coast of southern Galicia (NW Spain). (a) Monthly evolution of the percentage of postpubertal adult females as compared to the total number of females caught in shallow waters (<7-8 m) using the glass-box in the Ría de Arousa in 1992 (☐) (González-Gurriarán *et al.*, 1995) and in 1994/95 (-☐-) (unpublished data). (b) Seasonality of the migration of adult females tagged with ultrasonic transmitters and electronic archival tags which record the temperature and depth of the microhabitat of the individual. The date when females began to migrate to deeper waters is shown, as recorded by telemetry in 1993/94 (☐) (González-Gurriarán and Freire, 1994), as well as the migration periods of females tagged with archival tags in 1996 and recaptured by the commercial fishery (unpublished data) (heavy line: migration to deeper waters, fine line: return migration to shallow waters. Also shown are the recapture date and the reproductive stage of the female : ☐, empty seminal receptacles, non-ovigerous; ☐, receptacles with sperm from recent copulation, ovigerous). The upper section shows the average migration and recapture dates and the lower section includes information pertaining to each of the tagged females.

Figure 3. Evolution of sperm storage in the seminal receptacles of females of *Maja squinado* a throughout the reproductive cycle along the coast of southern Galicia. Sperm storage was measured by the fullness of the receptacles (mean and confidence interval of 95%) on a scale of 0 (no sperm) to 4 (full receptacles) and by the percentage of females with empty receptacles (with no sperm or remains of fluid, stages 0 and 1). In the gonad maturation phase, different stages are distinguished, ranging from 1 (undeveloped gonads) to IV (mature gonads close to spawning). Data are also shown for females held in captivity in conditions with a high density of males and in which gonads were analyzed during the mating season (January). Data from González-Gurriarán *et al.* (1997).

Figure 4. (a) Monthly trend of the landings of *Maja squinado* carried out in the port of O Grove (Ría de Arousa, southern Galicia) from 1959 to 1991. Fishing seasons from November to June (until 1968) and from December to June (starting in 1969) are separated, and for each series the mean monthly percentage of landings (±SE) for each month compared to the total catches during the fishing season is shown. (b) Weekly landings of the spider crab in the port of O Grove pertaining to 12 vessels that use tangle-net gears and which are representative of the fleet operating in the area (an earlier analysis points to similar landing trends in the different vessels, for which aggregated data are provided). The time series shown correspond to seasons 1989/90 to 1992/93.

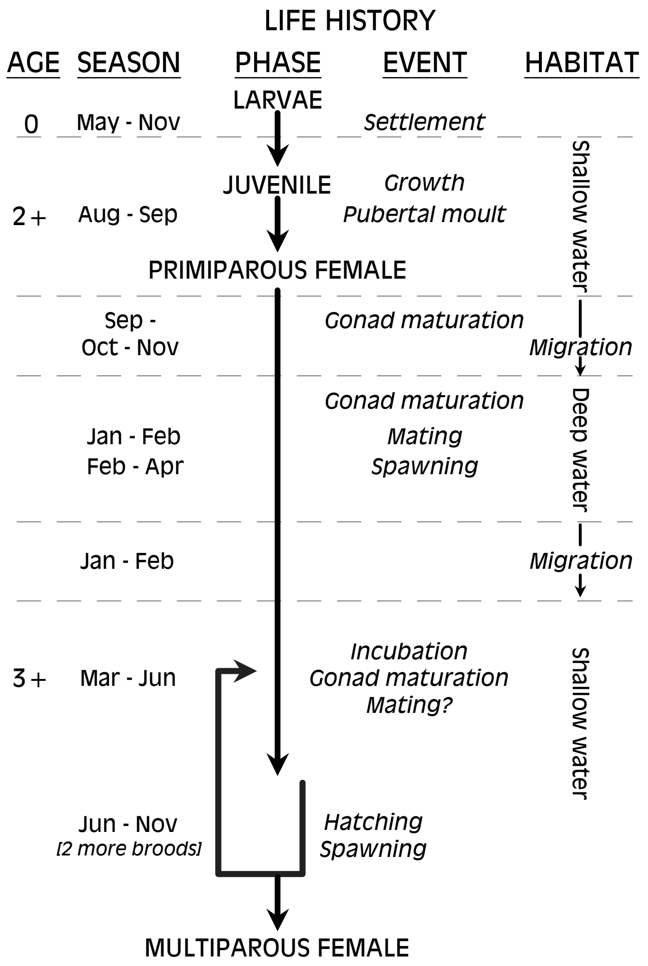
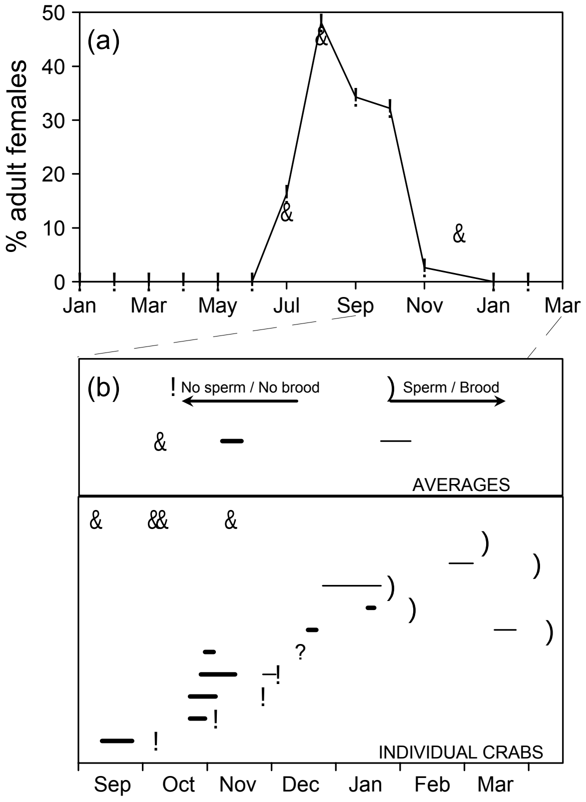


Figure 1. Freire *et al.*



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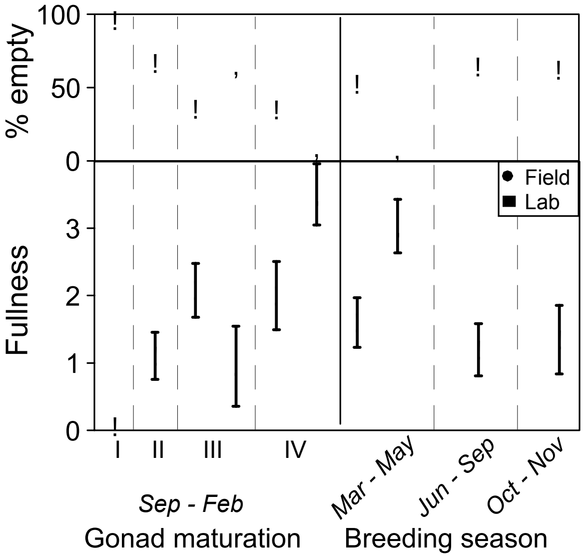

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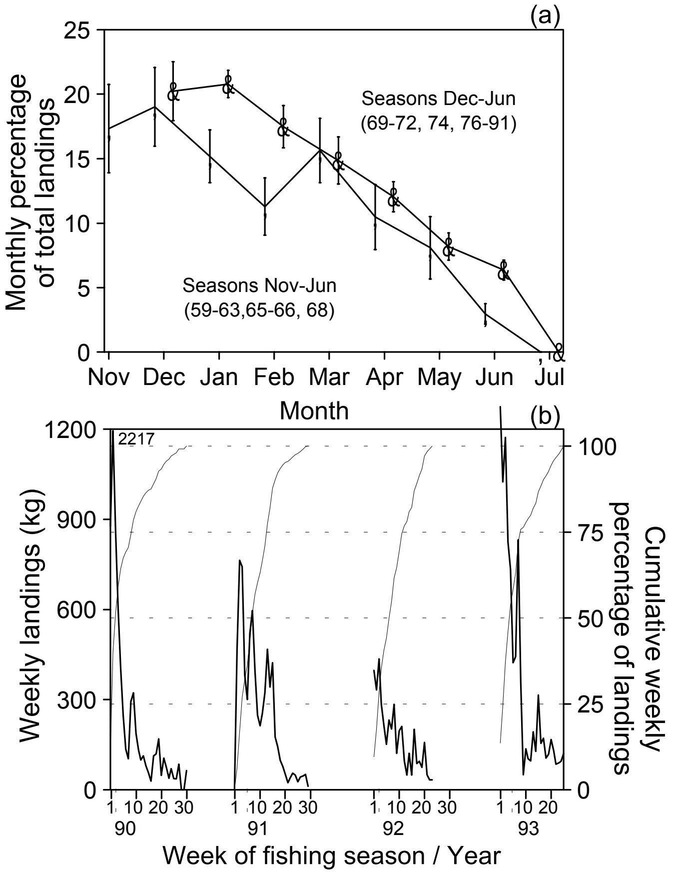

Figure 4. Freire *et al.*

Table 1. Mortality estimates of the population of *Maja squinado* in southern Galicia (Ría de Arousa and adjacent coast):

(a) *Structure of the exploited population*: ratio of multiparous females to the total number of females landed at the port of O Grove in November and December 1992, after recruitment to the fishing of the new cohort (see Fig. 2). A constant recruitment is assumed in the consecutive fishing seasons. Total number of females sampled = 397. Data from González-Gurriarán et al. (1993).

(b) *Mark-recapture experiments using electronic tags*: Recaptures of females tagged with ultrasonic transmitters and electronic tags by means of the tangle-net and glass-box fisheries. Females were released in July and August 1996 (unpublished data; see Fig. 2b). Estimates are based on the fitting of a life table for the period ranging from September to May, which corresponds to the actual duration of the fishing season. Estimates would be considered minimum values due to the possibility of unreported recaptures and the assumption of no natural mortality. N = 15 females and 18 releases (11 recaptures).

(c) *Leslie analysis of stock depletion*, based on weekly landings of 12 vessels in the port of O Grove (unpublished data; see Fig. 3 and text). The method assumes that neither natural mortality nor recruitment exists (the fishing seasons opened in December when most of the population has begun to migrate and therefore have been recruited to the fishery). The spatial distribution of the fishing effort of the fleet follows the autumn migration, therefore the stock may be considered as remaining "stationary" in relation to the fishery.

Method	Type of mortality	Fishing season	Period	Rate of mortality
(a) Structure of exploited population	Total	1991/92	Sep 91 - Dec 92	0.96
(b) Mark-recapture with electronic archival tags	Fishing	1996/97	Sep 96 - May 97	0.81
(c) Leslie analyses of stock depletion	Fishing	1989/90	Dec 89 - Jun 90	0.93
	Fishing	1990/91	Dec 90 - May 91	0.88
	Fishing	1991/92	Dec 91 - May 92	0.88
	Fishing	1992/93	Dec 92 - May 93	1.00