

# Moult cycle and growth of *Maja squinado* (Decapoda: Majidae) in coastal habitats of Galicia, north-west Spain

María-Paz Sampedro\*, Eduardo González-Gurriarán<sup>††</sup> and Juan Freire<sup>†</sup>

\*Instituto Español de Oceanografía, Centro Oceanográfico de A Coruña, Muelle de Ánimas s/n, Apartado 130, 15080 A Coruña, Spain. <sup>†</sup>Departamento de Biología Animal, Biología Vegetal e Ecoloxía, Universidade da Coruña, Campus da Zapateira s/n, 15071 A Coruña, Spain. <sup>††</sup>Corresponding author, e-mail: egg@udc.es

Over the course of the moult cycle of *Maja squinado*, the spider crab changes in the hardness and colour of the carapace were assessed and used as methods to identify the intermoult stage in each individual. This intermoult staging was later verified by means of the microscopic observation of the maxilla. These staging techniques made it possible for the prompt identification of the principal intermoult stages—postmoult, intermoult and premoult. In 90% of the cases analysed, there was a correlation between the presence of an underlying carapace and a pink colour of the abdominal vein in crabs in advanced premoult stages.

The seasonality of the moult was studied based on the number of specimens in the postmoult stage. There were two main moulting periods—the first occurring in April, and the second, longer period was between July and November. A hypothetical growth model was established and growth rates were determined by length–frequency distribution analyses. Three groups of juveniles and one group of adults were identified. The adults were only found among the population between July and October. In both males and females, the moult increment rate was lower in terminal moults (mean=22%) than in juvenile or prepubertal moults (mean=27%).

## INTRODUCTION

Growth in crustaceans is characterized by the periodic replacement of the exoskeleton which takes place during the ecdysis process. For most of its life history, the animal is preparing for or recovering from ecdysis through physiological, metabolic, biochemical and behavioural changes (Chang, 1995). Since crustaceans lose all of their hard parts during the moulting process, there is no method that can directly determine the age of these crabs. Studies of growth under experimental conditions provide data on the duration of the intermoult period and the growth rate during ecdysis, however the results cannot be extrapolated to the natural environment (Drach, 1939; Wilber & Wilber, 1989; González-Gurriarán et al., 1995). Another study technique involves tag–recatch experiments carried out in the field. Among the disadvantages to this method is that a large number of individuals must be tagged and the loss of tag at moult. Other methods that have been introduced recently estimate the age of individuals by measuring the natural radioisotopes in the exoskeleton (Le Foll et al., 1989) or by quantifying the concentration of lipofuscin in the brain (Tully, 1993; Sheehy et al., 1998; Ju et al., 1999). Analyses of growth by monitoring size modes that correspond to age-classes through length–frequency distributions can provide important information on population structure and on aspects related to growth, mortality and recruitment of the species (Botsford, 1984; Caddy, 1986; Castro, 1995; González-Gurriarán et al., 1998).

The spider crab, *Maja squinado* (Herbst, 1788) (*Maja brachydactyla* Balss, 1922, according to the proposal of

Neumann (1998)), is a species of great commercial value, geographically distributed along the East Atlantic Ocean, from the North Sea to North Africa as well as in the Mediterranean Sea (Ingle, 1980). *Maja squinado* has a complex biological cycle, with varying habitat requirements and changes in behaviour depending on the growth phase and the specific time period in the life history (González-Gurriarán & Freire, 1994; González-Gurriarán et al., 2002). Moreover, the spider crab undergoes a terminal moult (Sampedro et al., 1999) which divides the life history of the species into two stages: an early growth period with a short larval life stage (Lebour, 1927) and a juvenile stage (Teissier, 1935; Carlisle, 1957; Hartnoll, 1963) and a second reproductive period, during which time the animal does not grow in size. Therefore, the study of the growth of this species includes the early postlarval stage and the juvenile stage.

The aim of this paper is to analyse different aspects of the moult cycle and growth of a spider crab population inhabiting coastal areas of the Ría de Arousa. The moult cycle of this population was examined over a yearly cycle and the individual moult stage was identified using macroscopic and microscopic criteria. Macroscopic methods, commonly employed by fishermen, are calibrated in terms of the microscopic classification proposed by Drach (1939) and later applied to most scientific research (Stevenson, 1972; Aiken, 1973; Lyle & MacDonald, 1983; Moriyasu & Mallet, 1986; O'Halloran & O'Dor, 1988). Lastly, based on the size–frequency distribution analysis, a possible growth model for males and females is proposed and growth rates during terminal and non-terminal moults in the field are

determined. The obtained results will be compared with previous information about growth in the laboratory of crabs sampling in the same study area (González-Gurriarán et al., 1995).

## MATERIALS AND METHODS

### *Sampling*

The area chosen for the study was the north coast of the O Grove Peninsula, located on the left-hand shore of the outer Ría de Arousa (north-west Spain) (Figure 1). During the juvenile stage, spider crabs inhabit coastal zones with depths of less than 10–15 m and mixed bottoms of sand and rock (González-Gurriarán & Freire, 1994; González-Gurriarán et al., 2002). After the terminal moult, the adult individuals migrate to deeper waters (González-Gurriarán et al., 2002), where mating probably occurs. Only the adult females return to the shallower waters to spawn.

Monthly samplings were carried out between February 1994 and February 1995, and a total of 2463 individuals were analysed, consisting of 1237 males and 1226 females. The specimens were caught by professional fishermen using the method known as the glass box 'espello'. This gear is made of a wooden box in the shape of a truncated pyramid. In the larger, square base a piece of glass is installed. From small vessels (<4 m length), the fishermen lower the 'espello' so that it floats on the water surface, allowing them to see the bottom. The depth to which they can see depends on the transparency of the water. When they locate a specimen, it is caught and hauled on board with a long pole that has a curved hook on the end.

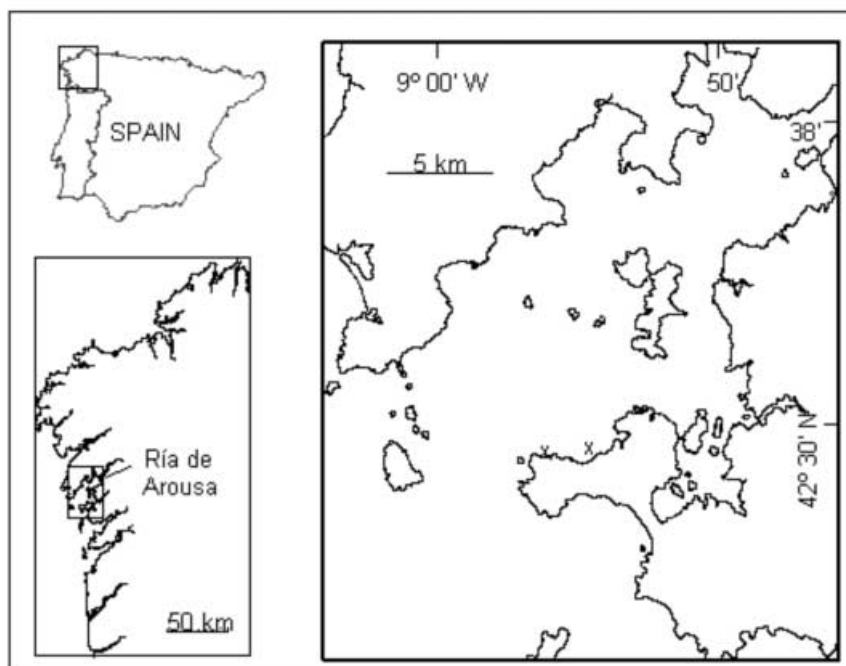
The crabs were sexed according to the morphology of the abdomen, which is narrow and triangular-shaped in males and wider and rounder in females. Females were divided into juveniles and adults, distinguished by the shape of the abdomen, which is flat in juveniles and

convex in adults. Males were found to have two growth periods: a juvenile and an adult phase, which were identified by the relative size of the chelipeds (Sampedro et al., 1999). The carapace length was measured in all specimens from the posterior end of the cephalothorax to the point where the rostral spines join, using a digital calliper and adjusting the measurement to the nearest 0.1 mm. The right cheliped height from the posterior area of the dactylus insertion, and the length from the base of the carpus insertion to the inferior part of the dactylus articulation were also measured in males.

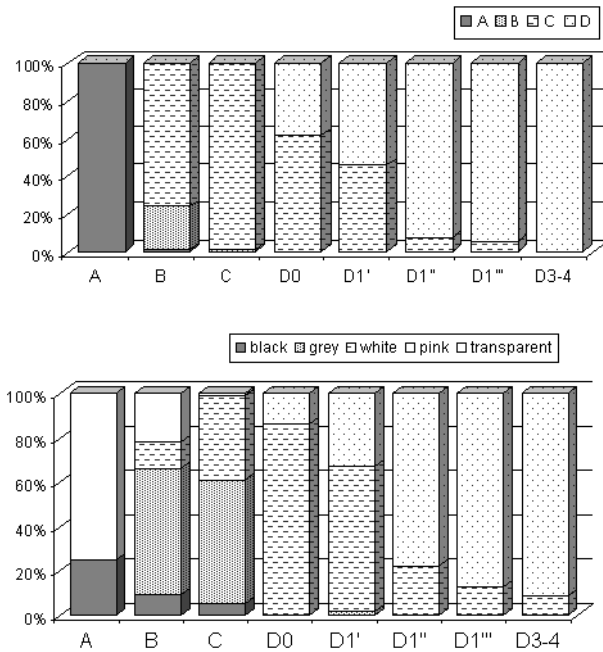
### *Intermoult stages*

The intermoult stage was determined by means of three techniques based on the observation of morphological changes. Two methods—carapace hardness and the colour of the abdominal vein—use macroscopic criteria; and the third method is based on the observation of the maxilla endite under the microscope. With the latter method it is possible to observe internal morphological changes in the tegument directly related to the moult, leading to the precise identification of the intermoult stages and sub-stages. Carapace hardness and abdominal vein colour are techniques used by fishermen and professionals in the marketing industry to determine the meat content of the crabs. This paper assesses the accuracy of the identification of the intermoult stage with the results of the microscopic observation of the basal endite on the second maxilla.

The method that uses carapace hardness is based on the consistency of the tegumentary skeleton. By applying pressure with the fingers on the posterior dorsal part of the carapace and the dactylus of the last pair of legs, it is possible to determine carapace hardness. This has been divided into four stages as follows: Stage A, characterized by a soft body, full of water, which becomes completely deformed by finger pressure; Stage B, a soft, flexible



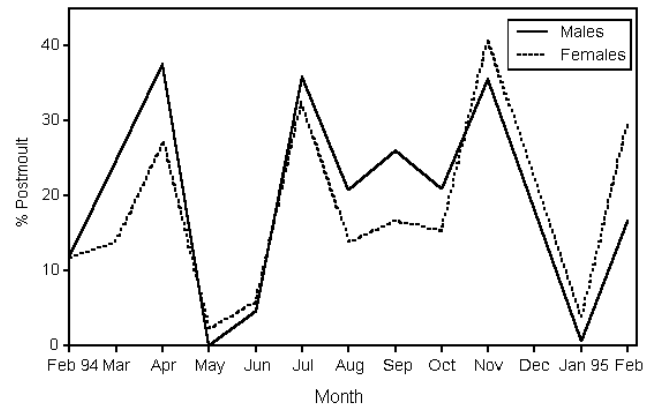
**Figure 1.** Map of the Ría de Arousa (north-west Spain), showing the location of the study area.



**Figure 2.** Association between intermoult stage identified by the setae morphology of second maxilla and the carapace condition (top) and the colour of abdominal vein (bottom) in *Maja squinado*.

carapace that does not become deformed (in the early stage it has a parchment-like consistency and the different body parts gradually begin to harden); Stage C, all the body parts are rigid and no depression is observed; Stage D, normal carapace hardness (by breaking the apical end of the dactylus of the last pereiopod, it is possible to see that a new carapace is being formed under the existing one).

The method involving the abdominal vein identifies colour changes in the ventral part of the sternal region.



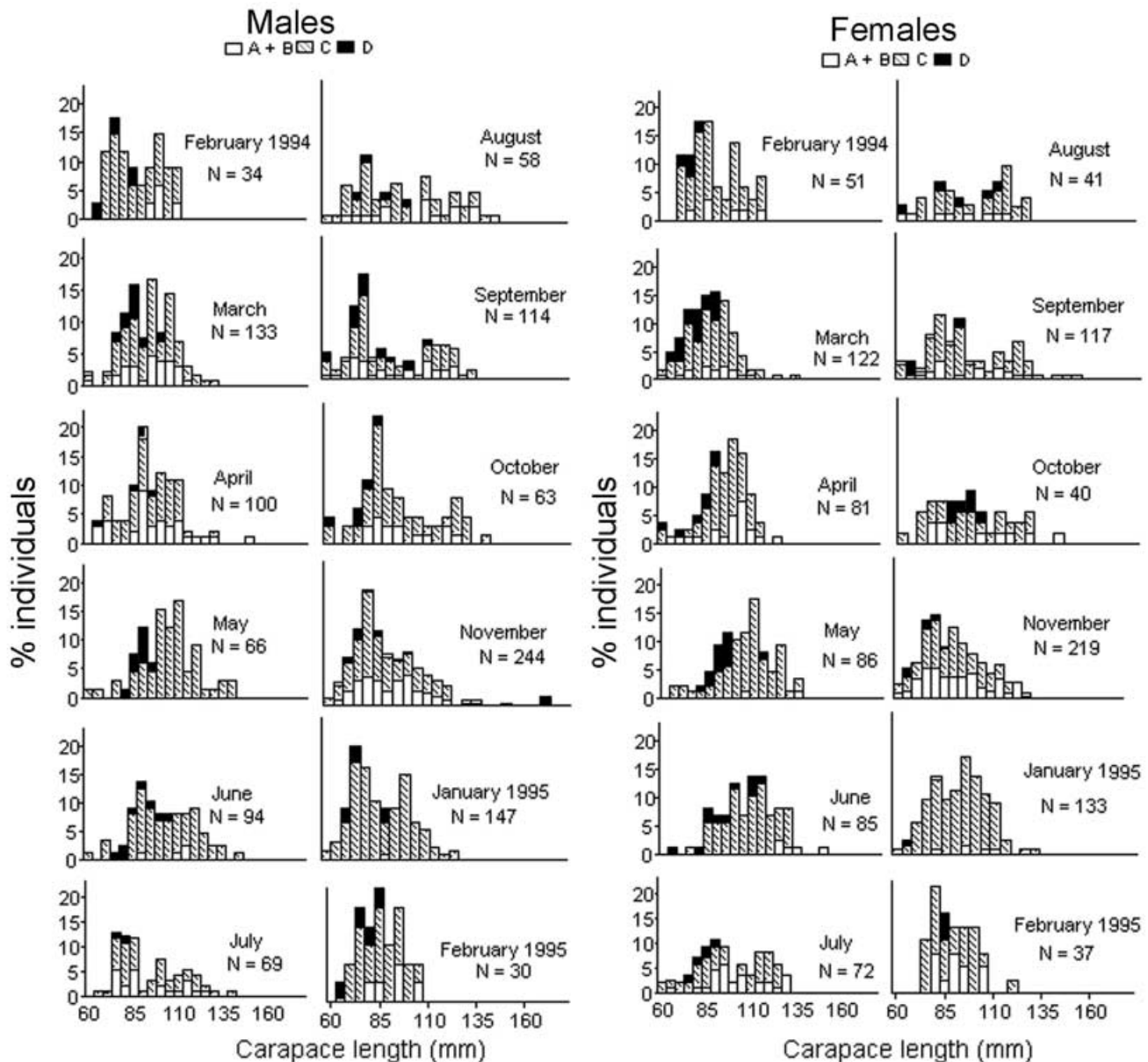
**Figure 3.** Monthly evolution of percentage of postmoult individuals (Stage A + Stage B) from February 1994 to February 1995, in a coastal population of spider crab. Males and females are shown separately.

This area is where the last section of the hindgut, covered with muscle and tissue, is found. In crabs that have recently moulted, exhibiting little muscle and high water content, the hindgut is visible through the transparent shell, which gives this area a blackish or grey coloration. In specimens in the intermoult stage, the musculature covers the intestine, obstructing the view of the hindgut and the colour is predominantly white. In the premoult stage, the formation of a new carapace underneath the existing one gives the area a pink colour. These two methods based on macroscopic criteria were applied in the field immediately after the animal was caught.

The microscopic method follows the classification criteria put forth by Drach (1939) and Drach & Tchernigovtzeff (1967). These authors observed changes in the growth of the setae in the mouthparts related to the moult cycle. This widely used model has been adapted to different crustaceans such as shrimps (Scheer, 1960), *Thalassinidea*

**Table 1.** Monthly percentage of each intermoult stage identified by the microscopic observation for males and females, from a coastal population of *Maja squinado*.

		Feb '94	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Jan '95	Feb '95
Males	A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0
	B	11.8	24.8	37.6	0.0	4.7	35.8	20.8	26.1	19.4	35.6	0.7	16.7
	C	79.4	60.8	57.4	87.9	86.2	61.0	74.4	61.3	71.6	59.2	92.4	69.9
	D <sub>0</sub>	0.0	3.0	1.0	6.1	3.4	3.2	2.4	2.1	1.5	0.4	1.4	0.0
	D <sub>1</sub> '	5.9	2.3	4.0	3.0	2.3	0.0	1.2	3.5	4.5	0.4	2.0	6.7
	D <sub>1</sub> ''	2.9	2.3	0.0	1.5	2.3	0.0	1.2	2.1	0.0	0.8	0.7	6.7
	D <sub>1</sub> '''	0.0	4.5	0.0	1.5	1.1	0.0	0.0	2.8	1.5	2.0	1.4	0.0
	D <sub>3-4</sub>	0.0	1.5	0.0	0.0	0.0	0.0	0.0	2.1	0.0	1.6	1.4	0.0
E	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
Females	A	2.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0
	B	9.8	13.9	27.4	1.2	5.9	32.6	13.9	16.6	13.6	41.0	3.8	29.7
	C	80.3	64.9	63.7	82.5	81.1	61.5	79.7	76.8	74.5	53.9	94.6	64.9
	D <sub>0</sub>	2.0	8.2	0.0	3.5	4.7	3.5	3.8	1.2	1.7	0.5	0.0	2.7
	D <sub>1</sub> '	3.9	5.7	6.3	3.5	3.5	1.2	0.0	2.4	0.0	1.8	0.0	0.0
	D <sub>1</sub> ''	0.0	4.1	0.0	2.3	2.4	1.2	1.3	1.2	3.4	2.3	0.0	2.7
	D <sub>1</sub> '''	2.0	1.6	1.3	2.3	1.2	0.0	1.3	0.0	3.4	0.5	0.8	0.0
	D <sub>3-4</sub>	0.0	1.6	1.3	3.5	1.2	0.0	0.0	1.8	1.7	0.0	0.8	0.0
E	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	



**Figure 4.** Size–frequency distributions of juvenile male and female *Maja squinado*, from February 1994 to February 1995. Crabs are grouped by size-classes of 5 mm CL, and the main intermolt stages are identified (postmolt, Stages A + B, intermolt, Stage C, and premolt, Stage D).

(Daguerre de Hureaux, 1970) and lobsters (Kamiguchi, 1968). In order to observe setae under the microscope, part of the body must be transparent. In the spider crab the basal endite of the second maxilla was chosen. The maxilla was extracted from the live animal with tweezers and preserved in vials filled with seawater at a temperature ranging between 2 and 3°C. The intermolt stage was always determined during 24 h after the sample was collected, with the assistance of an optical microscope at a magnification of 40× and 100×. By observing the morphology of the setae and the condition of the epidermis, eight stages were able to be identified: two postmolt stages (A and B), an intermolt stage (C) and five premolt stages or substages ( $D_0$ ,  $D_1'$ ,  $D_1''$ ,  $D_1'''$  and  $D_{3-4}$ ).

In order to study the moult cycle, the intermolt stage was determined by using microscopic criteria. The specimens were monitored monthly in each of the intermolt stages, according to sex and state of maturity.

#### *Analysis of length–frequency distributions*

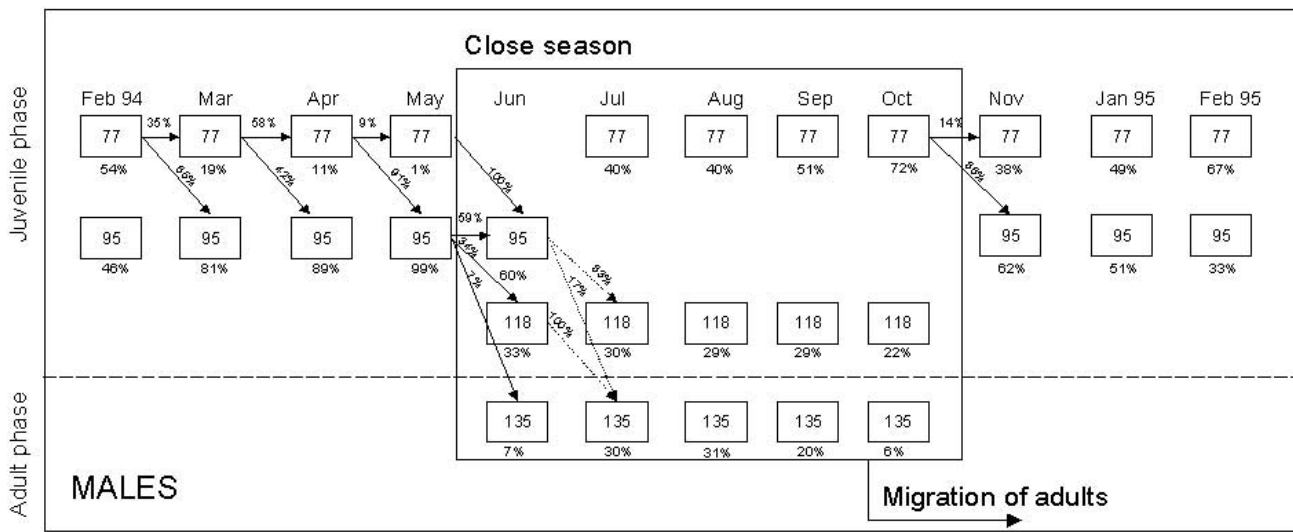
The analysis of the length–frequency data was performed using the computer program MIX (version 3.1) (MacDonald & Pitcher, 1979; MacDonald & Green, 1985). This program adjusts the distributions to groups of data using the method of the greatest likelihood and estimates the ratio of each component, the mean and standard deviation. Each monthly sampling grouped the individuals into 25 size-classes with a 5 mm amplitude, indicated by the mean point of the interval. The analyses were performed separately for males and females and for the juvenile and adult growth stages. Previous tests had been done using size-classes having the smallest amplitude (3 and 4 mm) which did not allow us to identify a coherent pattern of evolution for the population.

There is a drawback that must be taken into account in the analysis procedure of the evolution of the length–

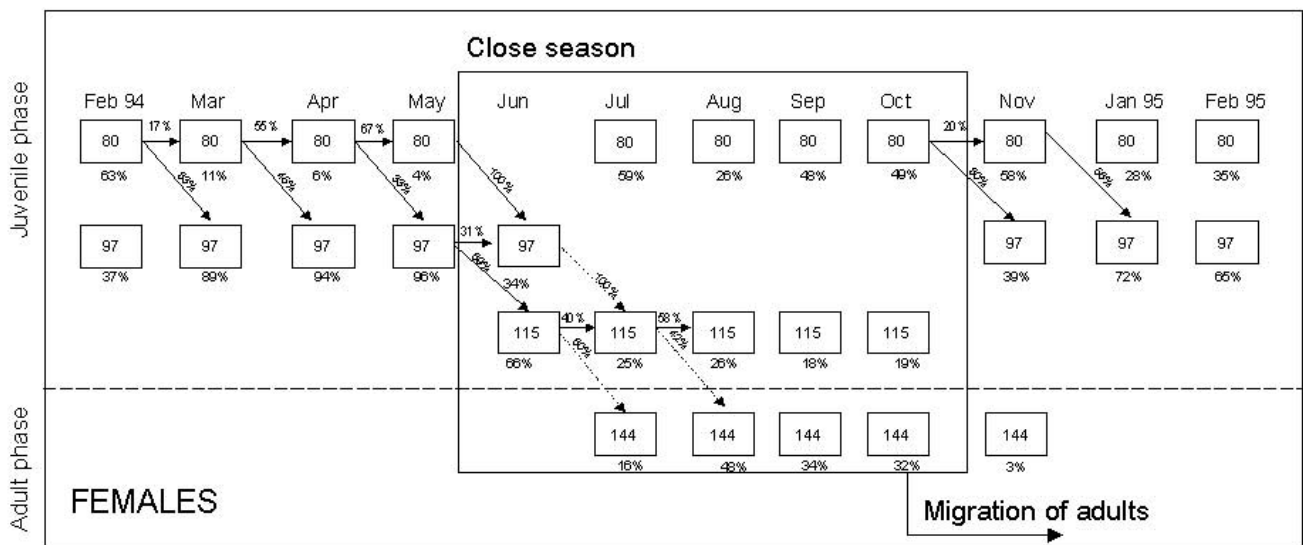
**Table 2.** Results from modal analysis of size–frequency distributions of males and females captured in shallow waters. Mean size (mm CL), standard deviation (SD) and the proportion of each component to the others, are indicated. Goodness-of-fit (P) is also indicated. Juvenile and adult phase are analysed separately.

	Juvenile												Adult					
	Component 1				Component 2				Component 3				Adult					
	proportion	mean	sd	proportion	mean	sd	proportion	mean	sd	df	$\chi^2$	P	mean	sd	df	$\chi^2$	P	
<b>Males</b>																		
Feb 1994	0.544	74.08	5.28	0.456	98.35	7.54	–	–	–	8	2.82	0.945	–	–	–	–	–	–
Mar	0.189	77.51	4.49	0.811	93.71	12.35	–	–	–	13	13.55	0.594	–	–	–	–	–	–
Apr	0.106	65.34	2.57	0.890	93.12	11.90	–	–	–	13	14.84	0.318	–	–	–	–	–	–
May	0.015	58.83	5.11	0.985	101.36	12.00	–	–	–	16	15.92	0.458	–	–	–	–	–	–
Jun	–	–	–	0.643	91.21	12.87	0.357	118.62	9.35	15	18.97	0.215	–	–	–	–	–	–
Jul	0.574	81.64	8.59	–	–	–	0.426	113.57	12.31	17	27.46	0.052	128.85	10.05	16	10.51	0.839	
Aug	0.578	79.16	10.48	–	–	–	0.422	118.18	13.21	18	18.53	0.421	132.90	8.59	13	5.84	0.938	
Sep	0.637	76.80	10.17	–	–	–	0.363	119.09	11.19	17	26.32	0.069	143.21	11.45	16	10.13	0.860	
Oct	0.775	83.50	12.12	–	–	–	0.225	121.57	7.02	14	14.93	0.383	–	–	–	–	–	
Nov	0.380	75.93	6.13	0.620	94.37	17.30	–	–	–	17	18.07	0.384	–	–	–	–	–	
Jan 1995	0.492	73.62	6.16	0.508	95.75	10.41	–	–	–	11	8.36	0.691	–	–	–	–	–	
Feb 1995	0.672	77.49	7.39	0.328	94.25	9.80	–	–	–	7	3.09	0.877	–	–	–	–	–	
<b>Females</b>																		
Feb 1994	0.634	79.96	7.27	0.366	101.46	8.45	–	–	–	10	11.47	0.323	–	–	–	–	–	–
Mar	0.114	75.14	5.85	0.886	90.80	12.58	–	–	–	13	13.52	0.409	–	–	–	–	–	–
Apr	0.055	60.48	3.77	0.945	95.62	10.76	–	–	–	12	10.22	0.597	–	–	–	–	–	–
May	0.042	65.03	4.38	0.958	103.02	13.85	–	–	–	19	12.26	0.874	–	–	–	–	–	–
Jun	–	–	–	0.343	90.92	11.04	0.657	112.48	11.89	16	17.65	0.345	–	–	–	–	–	–
Jul	0.698	85.82	13.50	–	–	–	0.302	117.73	5.79	12	6.54	0.886	136.43	13.31	19	12.82	0.848	
Aug	0.499	78.26	12.42	–	–	–	0.501	112.09	6.49	11	15.98	0.142	140.79	12.44	17	12.99	0.370	
Sep	0.731	80.57	12.11	–	–	–	0.269	117.73	7.05	13	18.56	0.138	148.19	11.10	15	14.73	0.471	
Oct	0.721	82.97	11.87	–	–	–	0.279	115.57	10.40	15	10.38	0.795	145.92	9.49	14	12.07	0.601	
Nov	0.597	81.88	11.34	0.403	104.28	21.69	–	–	–	20	35.24	0.019	–	–	–	–	–	
Jan 1995	0.279	73.80	6.67	0.721	94.73	10.55	–	–	–	12	8.45	0.749	–	–	–	–	–	
Feb 1995	0.346	77.38	5.09	0.654	92.03	9.42	–	–	–	10	7.04	0.722	–	–	–	–	–	

A



B



**Figure 5.** Hypothetic growth model for (A) male and (B) female *Maja squinado*, based on results from modal analysis of size–frequency distributions. Weighted means for each component and the transfer percentage among components are shown (dashed lines are used in cases with no clear evolution). Close season, for the area and period of sampling, is framed. Start of adult migration is also indicated (González-Gurriarán & Freire, 1994).

frequency distributions, the size selection owing to the fishing gear. Among other factors, this selective process affects the smallest sizes in the catch. The gear used is the ‘espello’ that requires the fisherman to actually see the specimens. The specimen with the shortest carapace length (CL) caught was a female measuring 47.5 mm. The length range used in the analysis was 58–178 mm, including crabs having a CL of < 58 mm (N=18) in the first size interval.

Growth rates in the field were estimated based on the results obtained from the identification of the normal

population groups. In order to do this, the size increment was calculated by assuming the pre-ecdysis size to be the mean size of the previous group the month before. Earlier papers on the growth of *Maja squinado* in the laboratory (González-Gurriarán et al., 1995), revealed that the growth rate during the terminal moult was different from the growth achieved in previous moults. Therefore, the growth analysis was performed separately for juveniles and adults. In adults, the adjustment was made in the samples from July to October, which were the only months when adults

**Table 3.** Growth rates (percentage increment) estimated for non-terminal moults (1st juvenile component to 2nd juvenile component and 2nd juvenile component to 3rd juvenile component) and terminal moults (3rd juvenile component to adult component) in male and female *Maja squinado*.

	Males			Females		
	1st–2nd	2nd–3rd	3rd–adult	1st–2nd	2nd–3rd	3rd–adult
February 1994	–	–	–	–	–	–
March	26.5	–	–	(13.6)	–	–
April	20.2	–	–	27.3	–	–
May	(55.2)	–	–	(70.6)	–	–
June	(55.1)	(17.0)	(8.6)	39.8	(9.0)	–
July	–	24.5	17.0	–	29.5	21.3
August	–	–	21.2	–	–	19.6
September	–	–	–	–	–	32.2
October	–	–	–	–	–	23.9
November	(13.0)	–	–	25.7	–	–
January 1995	26.1	–	–	(15.7)	–	–
February	28.0	–	–	24.7	–	–

were recorded in the population because of the autumn migration (González-Gurriarán & Freire, 1994). Although adults were observed in the June and October male samplings and the November sampling of females, their number was so few that we were unable to calculate the parameters.

## RESULTS

### *Calibration of intermoult-staging techniques*

By observing the state of the carapace it was possible to begin to determine the main divisions of the intermoult cycle. Stage A specimens exhibited a total correlation between the carapace stage and the intermoult stage, determined by examining the mouthparts under the microscope (Figure 2). However, 77% of the crabs in the advanced postmoult stage (B), should have been in Stage C on the basis of microscopic observation of the maxilla. One of the macroscopic traits that was indicative of premoult was the presence of a new carapace underneath the existing one. In keeping with this, over 90% of the specimens in the advanced premoult stage (substages  $D_1''$ ,  $D_1'''$  and  $D_{3-4}$ ) exhibited an underlying carapace.

Four main colours of the abdominal vein were considered: black, grey, white and pink. Black is the typical colour of crabs in the postmoult stage, and together with grey, these colours were found in approximately 60% of the individuals in Stage B. The abdominal vein was transparent in the rest of the crabs (Figure 2). Stage C individuals had a grey or white vein, although, in a small number of individuals, it was black. The initial premoult stages showed a predominance of specimens with a white coloured abdominal vein (86% of the specimens in  $D_0$ ), which gradually increased to a pink colour with the approach of ecdysis (from 33% to 91% between Stage  $D_1'$  and Stage  $D_{3-4}$ ). An abdominal vein with a pink colour was clearly associated with the presence of a second carapace under the existing one and with pre-ecdysial changes in the mouthparts. The colour of the abdominal vein is a quick way to identify the moult stage the animal is in,

although there may be some interference, due to the subjective nature of this method and to the possible effect of external elements, or factors related to the animal itself, such as its habitat and feeding habits.

### *Moult seasonality*

In the spider crab population under study, there were two main moulting periods. The first took place in early spring and the second lasted from July until November (Table 1). The first month of sampling produced a small percentage of specimens in the postmoult stage (12% of the males and 10% of the females). These values increased in spring, particularly in April, which had the highest percentages of individuals that had recently moulted from the first moult period (38% of the males and 27% of the females). In May and June there was a decline in the number of crabs in the postmoult stage, accounting for 6% of the population at most. During the summer and autumn, the monthly percentages of postmoult stage crabs fluctuated between 14% and 41%. In winter both sexes remained largely in the intermoult stage (>92% of the specimens in January). In the monthly evolution of the percentages of specimens in the postmoult stage, males and females were found to have similar moult cycles, although the higher values for males at the beginning of the two moult periods would seem to indicate that males were slightly more advanced (Figure 3).

### *Analysis of length–frequency distributions: growth model*

Figure 4 presents the length-class–frequency distributions pertaining to each intermoult stage. Prior to the first moult period, the population is made up of juveniles less than 110 mm in length. During the months of March and April it was the smallest sized members of the population that underwent moulting. In summer and autumn the length range increased with the incorporation of small sized specimens from recruitment as well as the new adults into the population. During these months it was possible to

observe individuals on the verge of moulting and others that had recently moulted across the entire size range. At the end of autumn, the adults vanished from the study area, with the population consisting only of specimens with a CL of < 110 mm, mostly in the intermoult stage.

The results obtained based on the identification of components of the population were similar in both males and females (Table 2). Over the course of the year, three juvenile components and one adult component were identified. The three juvenile groups were not present in all of the months and the adult component only appeared between July and October. In order to monitor each group and consolidate the mean values, the average annual weighted length was calculated based on the sampling size and the percentage it accounted for in each monthly sampling as compared to the total population consisting of juveniles and adults (Figure 5). The mean weighted lengths in males were 77, 95 and 118 mm, for the three juvenile components and 135 mm for the adult group. In females the values were 80, 97 and 115 mm for the three juvenile components and 144 mm for the adult component.

Based on the monthly evolution of the percentages of each group, a possible specimen transfer model between components was derived. This model provides an overall, simplified view of the evolution of the population over a yearly cycle. The model was created by assuming that the mortality rate was equal in all the size groups and that there were no immigration processes from other populations. According to this model, there was a moult period between February and March, during which time 65% of the males and 83% of the females from the first group became part of the second size group. The crabs continued to move into the second group between March and May, although a smaller number did so. In late spring males belonging to the 2nd group with a mean length of 95 mm moulted to the 3rd juvenile component (83%) or to the adult group (18% of the cases). Females belonging to the 2nd size group moulted and moved into the 3rd group between May and June. The first group reappeared in July, accounting for 40% of the males and 59% of the females. The number of males gradually increased until October when they accounted for 72%, at which time there was another moult period in this size group. Females also entered into the 2nd group, but in a smaller percentage.

The first adult males were seen in June, although, due to their small number, it was not possible to identify an adult component in this sampling. The first adult females appeared in July, corresponding to the terminal moults of specimens belonging to the 3rd size group. The ratio of adults increased until August with values of 30% and 48% for males and females respectively. Between the end of summer and the beginning of autumn there was a decline in the percentage of adults and the 3rd juvenile group, and these components did not reappear during the rest of the sampling. Adult males vanished from the population before females did, and in October males accounted for only 6% while females made up 32%.

The growth rates in the field varied considerably (Table 3). The estimates that presented extreme values, compared with previous information on the moulting behaviour of this species (González-Gurriarán et al., 1995), were not taken into account (Table 3: values in parentheses). In the non-terminal moults (between the 1st and

2nd group and between the 2nd and 3rd group) the growth rate fluctuated between 20% and 40%. The mean growth rate in a non-terminal moult was 25.1% in males and 29.4% in females. During the moult where the animal moved from the 3rd group into the adult group—the terminal moult—the growth rate ranged 17% to 32%, with a mean value of 19.1% in males and 24.2% in females.

## DISCUSSION

The inspection of the mouthparts has been used in Majids as a general technique to determine the intermoult stage (Moriyasu & Mallet, 1986; O'Halloran & O'Dor, 1988; Dawe et al., 1992; Hoenig et al., 1994). Of the three techniques used in intermoult staging, observation under the microscope is the least subjective method and the one that allows the identification of the greatest number of stages and substages, but it is slow and impractical in fieldwork. However, the identification of the first post-moult stage (Stage A) using this technique is complex, due to the flexibility of the animal's carapace. A more reliable method in this case is the observation of carapace hardness. The inspection of the abdominal vein is a quick and highly accurate way to identify the advanced premoult stages (D<sub>1</sub>' and subsequent stages). Classification based on microscopic criteria had a higher correlation with carapace hardness and the colour of the vein. Moreover, there was a large proportion of individuals that were unable to be assigned to one of the stages by using the colour of the vein as a criteria, primarily affecting postmoult stage specimens.

The population of *Maja squinado* under study presented a moulting pattern with two peaks—one in the spring and the other in summer–autumn, which coincided with the common model for large-sized decapods in temperate waters (Conan, 1985). While moulting is a response to the regulation of the endocrine system (Skinner, 1985; Chang, 1989, 1995), there are external factors that may have an effect on its seasonality. In keeping with this, the highest percentages of postmoult stage specimens coincided with an increase in water temperature, shortly before the time when food became more readily available in spring, as well as during the phytoplankton peak in autumn.

The monthly evolution in the moult cycle was similar in both males and females, although males were slightly ahead of females. In the first few months of the moulting period, there was a higher percentage of male crabs in the postmoult stage. In many brachyurans the earlier moulting of the males is linked to the fact that mating requires the males to be in the intermoult stage and females in the postmoult stage. In the spider crab mating may take place when both sexes are in the intermoult stage, so the slightly earlier moulting of the male specimens could be related to the difference in the energy balance linked to the start of the reproduction period and/or the migration of adult males to deeper waters ahead of time (González-Gurriarán & Freire, 1994). This movement requires the crabs to have recovered from moulting, which is why they tend to undergo ecdysis slightly earlier.

Previous works have reported that some spider crab populations (Carlisle, 1957), and other majids such as *Libinia emarginata* (DeGoursey & Stewart, 1985; DeGoursey & Auster, 1989), migrate to shallower waters to moult. The



populations studied here, however, remained in the shallow areas of the Ría de Arousa, on bottoms of both rock and sand, all year round. The crabs moult in these zones, where food is plentiful and there is sufficient protection from predators. They only leave these habitats once the terminal moult has taken place, when they have grown to a size that will serve as protection, which is related to oceanographic changes or the start of the reproduction cycle (González-Gurriarán & Freire, 1994; González-Gurriarán et al., 1998; González-Gurriarán et al., 2002).

Although the make-up of the catches differed depending on the gear used in the sampling, an overall pattern in seasonal variations was able to be extracted. The specimens caught in winter and spring were immature, measuring less than 110 mm in length. This size increased until June, with the appearance of the first adult animals that remained in the population until November. As immigration had not been previously detected in the population and there are no data available on these processes, we would assume that these specimens reached maturity chiefly in the summer of that year. Therefore the terminal moult of this population would have occurred between June and August in shallow areas. In the populations of the English Channel, the terminal moult occurs in late summer and early autumn (De Kergariou, 1984; Meyer, 1993), although these authors also reported that the appearance of the first adults varied from year to year.

From August until November, the percentage of adults and the 3rd group of juveniles gradually decreased until they completely disappeared from the population. There are two phenomena involved in this event: on the one hand, the movement of adults towards nearby areas within the Ría and, secondly, the effect of fishing activities. Although the fishing season had not officially begun, illegal fishing might have considerable repercussions on the specimens, especially on those over 120 mm.

In late autumn, adults began to migrate to deeper zones. This is a phenomenon common to the species that has also been reported in populations of the English Channel (Edwards, 1980; Latrouite & Le Foll, 1989; Le Foll, 1993), in the south of Great Britain (Camus, 1983) and in the Adriatic Sea (Stevcic, 1973). The migration studies carried out on populations inhabiting the Ría de Arousa (González-Gurriarán & Freire, 1994; González-Gurriarán et al., 2002) have related these migrations and activity changes in general to both ontogenetic factors as well as the need for the crabs to adapt to changes in environmental conditions, such as wind shifts, the start of the rainy season and temperature drops. This would indicate that the deeper zones, where the crabs migrate to, have slightly higher temperatures in winter than the bottoms where the crabs originate from.

As there are no data that would indicate that juveniles migrate to deeper zones like the adults do, and in many cases they reach marketable sizes, it would be possible to infer that the disappearance of the 3rd juvenile group was due, at least in part, to the fact that they were caught by fishermen. The long-term biological impact of catching these specimens might lead to the disappearance of the size-class, which, in the next moult would reach maturity with maximum sizes among the adults. Owing, in all probability, to a new recruitment and the adult migration

discussed above, in November the population was again comprised mostly of small-sized juveniles.

The February samplings (1994 and 1995) exhibited the lowest catch density, which may reflect changes in the activity of the population. The catchability of a species depends on the intermoult stage. An animal is less susceptible to being caught during the premoult and early postmoult stages, while this disposition increases during the late postmoult and intermoult stages (Newman & Pollock, 1974; Chittleborough, 1975). In a study of the populations in the English Channel, De Kergariou (1984), suggested that juveniles of 30 mm stop growing in the winter and moult to reach 70 mm in the summer. This agrees with our findings in this study, where specimens measuring from 60 to 85 mm start to join the population in July. Drach (1939) reported that an average-sized specimen (80–120 mm) moults twice a year, at the beginning of summer and in autumn. Under experimental conditions, it was found that in the juvenile stage *Maja squinado* underwent 2–3 moults with two peaks; one in spring and the other in summer–autumn (González-Gurriarán et al., 1995). Le Foll (1993) believes that it is possible for large-sized individuals to undergo as many as three moults during the year of their terminal moult. Le Foll (1993) and De Kergariou (1976) consider that while, in some cases it takes three years for crabs to reach the adult stage, in general an individual attains this stage in two years, which is deemed to be a rapid growth rate. The spider crab is assumed to have a wide-ranging individual variability in terms of growth, which would explain the presence of adults in a broad spectrum of sizes (Sampedro et al., 1999). This variability may be attributed to lower growth rates in the moulting period and/or differences in the total number of moults, considering the broad range of the breeding cycle and the number of clutches (González-Gurriarán et al., 1996; González-Gurriarán et al., 1998) which inhibits the modal integration of the size structure.

Highly variable growth rates have been found in the growth study performed in the field. The mean moult increment rates were lower in the field than the values obtained in lab experiments with populations from the same area (González-Gurriarán et al., 1995), in both non-terminal moults (27.2% in the field vs 36.1% in laboratory experiments) and terminal moults (22.5% vs 26.5%). Higher moult rates shown by animals held in captivity should have been due to more favourable conditions such as adequate temperature and greater availability of food, and less expenditure of energy as the animals were in protected conditions. Although, it must be taken into account that the overlap between modes may obstruct the exact identification of the population groups, which would cause underestimated percentages of moult increment in the field. The values were also lower than those estimated by Le Foll (1993) in a English Channel population, who reports that the growth rate is 29%, in the terminal moult and 33% in the non-terminal moults. In this case, differences on size of animals between populations can explain this variability.

Information on the periodicity of moulting and the characterization of the habitats where it occurs, in addition to data on the composition and growth of the spider crab populations living in coastal waters will make it easier to interpret other aspects of the biology, population

dynamics and the behaviour of this species. This knowledge may also be applied to catch management, in order to prevent the fishery of crabs in the postmoult stage, which are of little commercial value, and of crabs that have not yet reached maturity.

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## REFERENCES

- Aiken, D.E., 1973. Proecdysis, setal development, and molt prediction in the american lobster (*Homarus americanus*). *Journal of the Fisheries Research Board of Canada*, **30**, 1337–1344.
- Botsford, L.W., 1984. Effect of individual growth rates on expected behavior of the northern California Dungeness crab (*Cancer magister*) fishery. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 99–107.
- Caddy, J.F., 1986. Size frequency analysis in stock assessment—some perspectives, approaches and problems. *Proceedings of the Gulf and Caribbean Fishery Institute*, **37**, 212–238.
- Camus, P., 1983. Résultats d'une opération de marquage d'araignée de mer (Herbst) adult en baie d'Audierne (Bretagne Sud). *International Council for the Exploration of the Sea, Shellfish Committee*, CM 1983/K:29, 11 pp.
- Carlisle, D.B., 1957. On the hormonal inhibition of moulting in decapod Crustacea. II. The terminal anecydysis in crabs. *Journal of the Marine Biological Association of the United Kingdom*, **36**, 291–307.
- Castro, M., 1995. Use of length–frequency analysis for estimating the age structure of the catch of *Nephrops norvegicus* (Crustacea: Decapoda). *International Council for the Exploration of the Sea, Marine Science Symposia*, **199**, 301–309.
- Chang, E.S., 1989. Endocrine regulation of moulting in Crustacea. *Reviews in Aquatic Sciences*, **1**, 131–157.
- Chang, E.S., 1995. Physiological and biochemical changes during the molt cycle in decapod crustaceans: an overview. *Journal of Experimental Marine Biology and Ecology*, **193**, 1–14.
- Chittleborough, R.G., 1975. Environmental factors affecting the growth and survival of juvenile western rock lobsters *Panulirus longipes* (Milne-Edwards). *Australian Journal of Marine and Freshwater Research*, **26**, 177–196.
- Conan, G.Y., 1985. Periodicity and phasing of molting. In *Crustacean Issues*. Vol. 3. *Factors in adult growth* (ed. A. Wenner), pp. 73–99. Rotterdam: A.A. Balkema.
- Daguerre de Hureaux, N., 1970. Recherches sur *Upogebia littoralis* Risso (Décapode, Anomoure). I. Étude du cycle d'intermue. *Bulletin de la Société des Sciences Naturelles et Physiques du Maroc*, **50**, 67–81.
- Dawe, E.G., Hoenig, J.M., O'Keefe, P.G. & Moriyasu, M., 1992. Molt indicators and growth per molt for male snow crabs (*Chionoecetes opilio*). *International Council for the Exploration of the Sea, Shellfish Committee*, CM 1992/K:35, 15 pp.
- DeGoursey, R.E. & Auster, P.J., 1989. Aspects of a mating aggregation of the spider crab *Libinia emarginata*. In *Proceedings of the American Academy of Underwater Science, 9th Annual Symposium, Woods Hole*, pp. 83–90.
- DeGoursey, R.E. & Stewart, L., 1985. Spider crab podding behavior and mass molting. *Underwater Naturalist (Bulletin of the American Littoral Society)*, **15**, 13–16.
- De Kergariou, G., 1976. Premiers résultats obtenus par marquage de l'araignée de mer, *Maia squinado*, déplacements, mortalité par pêche. *International Council for the Exploration of the Sea, Shellfish and Benthos Committee*, CM 1976/K:14, 6 pp.
- De Kergariou, G., 1984. L'araignée de mer, H. Biologie et exploitation. *La Pêche Maritime*, **1279**, 575–583.
- Drach, P., 1939. Mue et cycle d'intermue chez les crustacés décapodes. *Annales del Institut Océanographique, Paris*, **19**, 103–391.
- Drach, P. & Tchernigovtzeff, C., 1967. Sur le méthode de détermination des estades d'intermue et son application générale aux crustacés. *Vie et Milieu*, **18**, 595–609.
- Edwards, E., 1980. Preliminary results of a tagging experiment on the spider crab (*Maja squinado*) in the English Channel. *International Council for the Exploration of the Sea, Shellfish Committee*, CM 1980/K:12, 7 pp.
- González-Gurriarán, E., Fernández, L., Freire, J. & Muiño, R., 1996. Reproductive biology of the spider crab *Maja squinado* (Decapoda, Majidae) based on the analysis of seminal receptacles. *International Council for the Exploration of the Sea, Shellfish Committee*, CM 1996/K:29, 17 pp.
- González-Gurriarán, E., Fernández, L., Freire, J. & Muiño, R., 1998. Mating and role of seminal receptacles in the reproductive biology of the spider crab *Maja squinado* (Decapoda, Majidae). *Journal of Experimental Marine Biology and Ecology*, **220**, 269–285.
- González-Gurriarán, E. & Freire, J., 1994. Movement patterns and habitat utilization in the spider crab *Maja squinado* (Herbst) (Decapoda, Majidae) measured by ultrasonic telemetry. *Journal of Experimental Marine Biology and Ecology*, **184**, 269–291.
- González-Gurriarán, E., Freire, J. & Bernárdez, C., 2002. Migratory patterns of female spider crabs *Maja squinado* detected using electronic tags and telemetry. *Journal of Crustacean Biology*, **22**, 91–97.
- González-Gurriarán, E., Freire, J., Fariña, A.C. & Fernández, A., 1998. Growth at moult and intermoult period in the Norway lobster *Nephrops norvegicus* from Galician waters. *ICES Journal of Marine Science*, **55**, 924–940.
- González-Gurriarán, E., Freire, J., Parapar, J., Sampedro, M.P. & Urcera, M., 1995. Growth at moult and moulting seasonality of the spider crab, *Maja squinado* (Herbst) (Decapoda: Majidae) in experimental conditions: implications for juvenile life history. *Journal of Experimental Marine Biology and Ecology*, **189**, 183–203.
- Hartnoll, R.G., 1963. The biology of Manx spider crabs. *Proceedings of the Zoological Society of London*, **141**, 423–496.
- Hoenig, J.M., Dawe, E.G. & O'Keefe, P.G., 1994. Molt indicators and growth per molt for male snow crabs (*Chionoecetes opilio*). *Journal of Crustacean Biology*, **14**, 273–279.
- Ingle, R.W., 1980. *British crabs*. London: Oxford University Press.
- Ju, S.J., Secor, D.H. & Rodger-Harvey, H., 1999. Use of extractable lipofuscin for age determination of blue crab *Callinectes sapidus*. *Marine Ecology Progress Series*, **185**, 171–179.
- Kamiguchi, Y., 1968. A new method for the determination of intermolt stages in the freshwater prawn, *Palaemon paucidens*. *Zoological Magazine (Tokyo)*, **77**, 326–329.
- Latrouite, D. & Foll, D.L., 1989. Données sur les migrations des crabes tourteau *Cancer pagurus* et les araignées de mer *Maja squinado*. *Océanis*, **15**, 133–142.
- Le Foll, D., 1993. *Biologie et exploitation de l'araignée de mer Maja squinado Herbst en Manche Ouest*. PhD thesis, Université de Bretagne Occidentale, France.
- Le Foll, D., Bricchet, E., Reyss, J.L., Lalou, C. & Latrouite, D., 1989. Age determination of the spider crab *Maja squinado* and the European lobster *Homarus gammarus* by  $^{228}\text{Th}/^{228}\text{Ra}$  chronology: possible extension to other crustaceans. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 720–724.
- Lebour, M.V., 1927. The larval stages of the Plymouth Brachyura. *Proceedings of the Zoological Society of London*, **1**, 473–560.
- Lyle, W.G. & MacDonald, C.D., 1983. Molt stage determination in the Hawaiian spiny lobster *Panulirus marginatus*. *Journal of Crustacean Biology*, **3**, 208–216.
- MacDonald, P.D.M. & Green, P.E.J., 1985. *User's guide to program MIX: an interactive program for fitting mixture distributions*. Ontario, Canada: Ichthus Data Systems.

- MacDonald, P.D.M. & Pitcher, T.J., 1979. Age-groups from size frequency data: a versatile and efficient method of analyzing distribution mixtures. *Journal of the Fisheries Research Board of Canada*, **36**, 987–1001.
- Meyer, C.G., 1993. *The biology and fishery of the spider crab (Maja squinado) around Jersey (Channel Islands)*. MSc thesis, University of Plymouth, Plymouth, UK.
- Moriyasu, M. & Mallet, P., 1986. Molt stages of the snow crab *Chionoecetes opilio* by observation of morphogenesis of setae on the maxilla. *Journal of Crustacean Biology*, **6**, 709–718.
- Neumann, V., 1998. A review of the *Maja squinado* (Crustacea: Decapoda: Brachyura) species-complex with a key to eastern Atlantic and Mediterranean species of the genus. *Journal of Natural History*, **32**, 1667–1684.
- Newman, G.G. & Pollock, D.E., 1974. Biological cycles, maturity and availability of rock lobster *Jasus lalandii* on two South African fishing grounds. *Investigational Report, Sea Fisheries Branch, Union of South Africa*, **107**, 1–16.
- O'Halloran, M.J. & O'Dor, R.K., 1988. Molt cycle of male snow crabs, *Chionoecetes opilio*, from observations of external features, setal changes, and feeding behavior. *Journal of Crustacean Biology*, **8**, 164–176.
- Sampedro, M.P., González-Gurriarán, E., Freire, J. & Muiño, R., 1999. Morphometry and sexual maturity in the spider crab *Maja squinado* (Decapoda: Majidae) in Galicia, Spain. *Journal of Crustacean Biology*, **19**, 578–592.
- Scheer, B.T., 1960. Aspects of the intermolt cycle in natantians. *Comparative Biochemistry and Physiology*, **1**, 3–18.
- Sheehy, M., Caputi, N., Chubb, C. & Belchier, M., 1998. Use of lipofuscin for resolving cohorts of western rock lobster (*Panulirus cygnus*). *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 925–936.
- Skinner, D.M., 1985. Moulting and regulation. In *The biology of Crustacea*, vol. 9 (ed. D.E. Bliss and L.H. Mantle), pp. 43–146. New York: Academic Press.
- Stevcic, Z., 1973. Les migrations de l'Araignée de mer. *Rapports de la Commission Internationale de la Mer Méditerranée*, **21**, 597–598.
- Stevenson, J.R., 1972. Changing activities of the crustacean epidermis during the molting cycle. *American Zoologist*, **12**, 373–380.
- Teissier, G., 1935. Croissance des variants sexuels chez *L.* *Travaux de l'Station Biologique de Roscoff*, **13**, 99–130.
- Tully, O., 1993. Morphological lipofuscin (age pigment) as an indicator of age in *Nephrops norvegicus* and *Homarus gammarus*. *International Council for the Exploration of the Sea (CM Papers and Reports)*, CM 1993/K:18, 10 pp.
- Wilber, D.H. & Wilber, T.P., 1989. The effects of holding space and diet on the growth of the West Indian spider crab *Mithrax spinosissimus* (Lamarck). *Journal of Experimental Marine Biology and Ecology*, **131**, 215–222.

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