Morphometric and gonad maturity in the spider crab *Maja brahcydactyla*. A Comparison of methods for the estimation of the size at maturity in species with determinate growth

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ABSTRACT

Ontogenetic changes in the relative growth of males and females of the spider crab *Maja brachydactyla*, a species with terminal moult and determinate growth, were analyzed and related to their reproductive (maturity) status. Sampling was carried out in the Ría de A Coruña (NW Spain) from December 1997 to November 1999. A combination of principal component analysis of morphometric variables, non-hierarchical K-means cluster and discriminant analysis allowed to differentiate two morphometric groups of males defined as juvenile and adult phases and develop statistical methods to assign maturity status to individual crabs. A significant change in allometry of cheliped size was detected in juvenile males with a breakpoint at 96.2 mm carapace length (CL), separating the inmature and adolescent phases. Histological analysis of males showed that more than 60% of morphometrically juveniles and 100% of morphometrically adults presented spermatophores in the gonad. Size at gonad maturity in males (estimated as CL_{50}) was 96.2 mm CL. Size at morphometric maturity was estimated comparing two methodologies: the size at 50% maturity (CL_{50}) and the median size of adult cohorts. For the whole sampling period, two adult-year classes, CL_{50} was estimated to be 136.5 mm for males and 130.3 mm for females, while median size of adult cohorts for the same period was estimated to be 139.9 mm for males and 148.7 mm for females. In all cases the size at maturity obtained from the median of the cohort was greater than the one resulting from the CL_{50} method with differences of over 20 mm, showing the bias that methods based in CL_{50} could cause in animals with determinate growth. Due the spatial segregation of adults and juveniles and the

availability of morphological and morphometrical methods to estimate the maturity status of any crab, we propose a combination of spatial closures and direct protection of juvenile habitat as management strategies alternative to minimum landing sizes.

INTRODUCTION

The spider crab *Maja brachydactyla* (Crustacea, Brachyura) (the NE Atlantic species previously known as *M. squinado*, see Newman, 1998 for taxonomic status) is characterised by a determinate growth consisting of two main postlarval phases –the juvenile or growth phase and the adult or reproductive phase. These two phases are separated by a terminal moult after which the individual reaches sexual maturity and stops growing (González- Gurriarán et al., 1995; Sampedro et al., 1999). At this moult crabs undergo morphological changes as well as alterations in the relative size of the chelipeds in males and the abdomen in females (Teissier, 1933, 1935; Hartnoll, 1963; Sampedro et al., 1999), which make it possible to distinguish between adults and juveniles. These changes in the external morphology of the individuals have been used by many authors to estimate maturity in this species (Le Foll, 1993; Le Foll et al., 1993; Sampedro et al., 1999) as well as other majids (eg., Somerton, 1980; Comeau & Conan, 1992; Conan & Comeau, 1986).

The estimate of the size at sexual maturity plays a key role in the assessment and management of commercially exploited populations and is often used as a benchmark to establish minimum catch and/or landing sizes. There are two problems involved in the determination of this parameter: a) the selection of a biological criterion to identify mature animals, and b) the definition of a criterion and statistical methodology to estimate the size at the onset of maturity in a specific population.

In decapods, different criteria have been used to identify sexual maturity in individuals. A number of authors have taken gonad maturity as a criterion using the presence of spermatophores as indicators in males and gonadal development, the presence of sperm in the spermatheca or the presence of a clutch in females (see Paul, 1992 for a summary and references). In many brachyuran species, gonad maturity does not necessarily coincide with functional maturity (defined as the capacity to mate effectively).

Therefore gonad maturity (defined as the physiological capacity to produce gametes) may not be sufficient to define functional maturity, which is a broader concept that should also include mating ability depending on physiological, behavioural and morphological aspects. Since the external morphological changes are the ones that mark the end of all the processes that determine maturity in majids as well as in other decapods, this is the criterion that is commonly used to classify individuals as mature or immature (Somerton, 1980, 1981; Conan & Comeau, 1986; Paul, 1992; Paul & Paul, 1990; Sainte-Marie et al., 1995).

In terms of the statistical criterion required to estimate the size at maturity at the population level, the most frequent method used in decapods is the 50% maturity size (CL_{50}), based on the classification of the specimens from a sample into mature and immature and the estimation of body size in which 50% of the specimens are found to be mature. This methodology assumes that maturity is attained in a narrow range of sizes and that there is a sigmoidal type relation between size and the percentage of mature animals (Roa et al., 1999). The CL_{50} may be interpreted as the size at which a randomly chosen specimen has a 50% chance of being mature (Somerton, 1980). However in animals with determinate growth which exhibit a halt in growth after maturity is reached, as is the case of *M. brachydactyila*, the variability in the abundance of the different cohorts (or year classes) may bias the estimation of the CL_{50} obtained using point samples of juveniles and adults from different cohorts. Somerton (1981) has described this problem and proposes an alternative method for animals that undergo the terminal moult based on the median size of the adult year class.

The spider crab has been the object of partial studies regarding the criteria to be used in determining maturity, without considering gonadal development in males. There is only one study, however, that deals with the estimation of the size at maturity of a population using the CL_{50} criterion (Sampedro, 2001). Nonetheless, as this species of majid has a terminal moult, this method may be considerably biased. In this chapter these questions will be discussed on the basis of data obtained from samplings carried out in the Ría de A Coruña over the course of two consecutive years, which produced detailed information on the structure and dynamics of the population of *Maja brachydactyla* and the processes of gonadal development and morphometric maturity. The specific objectives are as follows:

1) Analyse the association between the process of gonad and morphometric maturity in males of *M. brachydactyla* and the onset of the reproductive cycle.
2) Estimate the size at sexual maturity of males and females of this population, comparing the two methodologies described above. The sample design allowed us to use transversal methods to estimate CL_{50} and longitudinal methods (monitoring cohorts of adults in time) to estimate median size of adult cohorts. Spatial variability of size at maturity will be discussed by comparing our results with those from other geographic areas, analysing the possible artefacts caused by the different methodologies used.
3) Analyze interannual variability (between year classes) in the size at maturity.

MATERIAL AND METHODS

The study area was the Ría de A Coruña (8º22'W, 43º21'N), a small oceanic bay located in the NW of Galicia Freire et al. (2002) and Corgos (2004) have synthesised the structure and population dynamics of *Maja brachydactyla* in this geographic zone. Monthly samplings were carried out from December 1997 until November 1999 using experimental traps with a 50mm mesh. Sampling was done in shallow areas (5-20 m) located in the inner and middle areas of the ría inhabited by juveniles and postpubertal adults, and in an area of greater depth (25-31 m) in the central channel, which is used as a migratory corridor by adults that have recently attained maturity and are heading towards deep mating habitats (Corgos, 2004; Freire et al., 2002).

Each individual caught was examined and the following data recorded: sex, carapace length (CL measured with a calliper to the nearest 0.1 mm) between the point where the rostral spines join and the posterior end of the cephalothorax, right cheliped height in males (RCH, **¡Error! Vínculo no válido.**in the posterior area of the dactyl insertion, shape of the abdomen in females (the morphological change that takes place at the terminal moult permits the direct identification of juvenile females which exhibit a flat abdomen with undeveloped pleopods and adults with a domed abdomen, see Sampedro et al., 1999), macroscopic stage of the intermoult cycle (intermoult, premoult and early postmoult, according to the classification of Drach & Tchernigovtzeff, 1967 with some minor modifications, see Sampedro et al., 2003) and relative age (on the basis of the degree of epibiosis and carapace erosion, see Fernández et al., 1998), to differentiate the recent postpubertal adults from the individuals that had reached sexual maturity in previous years.

In order to analyse the reproductive stage in males and females between July 1998 and June 1999, a monthly sample was obtained to examine the gonads of adult females (N=170) and of juvenile and adult males (N=382 and 128 respectively) from the shallow and deep sampling areas. Juvenile females were not analyzed because gonad development starts after the terminal moult (Sampedro et al., 1999). Males measuring between 60 and 160 mm CL were selected and divided into 20 mm size classes (with a final size class including individuals > 160 mm). A maximum of 10 males specimens of each size class caught in the shallow area was taken to the laboratory every month. A maximum of 5 males from the three largest size classes was obtained in the channel (the smaller-sized crabs were not caught in this zone). Females measuring over 100 mm CL were selected and grouped into 3 size classes of 40 mm. A maximum sample of 5 females from each size class caught in the shallow area as well as in the channel was taken to the laboratory.

The specimens were dissected to determine the gonad maturity stage. For females the classification proposed by González-Gurriarán et al. (1993, 1998) was applied. In the present study, only primiparous females, which had recently attained sexual maturity and had not yet spawned, were included. The presence of spermatophores was determined by examining a squash of the gonad sample under the microscope. The gonad from each specimen was extracted and kept for 48h at 60º C to obtain the dry weight.

Statistical Analyses:

(a) *Morphometric maturity*

Females. The morphological change that occurs in the abdomen during the terminal moult makes it possible to identify juvenile and adult females (Sampedro et al., 1999). Due to the fact that the onset of gonad maturity in females begins one or two months after the terminal moult, we may consider morphological maturity as a good indicator of sexual maturity (González-Gurriarán et al., 1993 1998; Sampedro et al., 1999).

Males. In males the onset of gonad and morphometric maturity do not coincide and there are no obvious morphological traits to distinguish between juveniles and adults. Therefore morphometric methods must be used (Sampedro et al., 1999). In the spider crab the terminal moult marks the complete development of the secondary sexual traits. After this moult, the chelipeds exhibit a high positive allometry in their relative growth and an increase in relative size, and males are considered to be morphometrically mature. The relative growth of the chelipeds is used to discriminate between life-history stages (Sampedro et al., 1999). This study followed the statistical methodology used by Sampedro et al. (1999) with some minor modifications.

The allometry of the chelipeds was estimated by a simple linear regression using $\log_{10}$-transformed data. [RCH was used as cheliped size, given that according to Sampedro et al., (1999) out of all the different cheliped measurements, height is the one with the greatest discriminating potential between the life history stages]

$$\log_{10} \mathrm{RCH} = \log_{10} a + b \cdot \log_{10} \mathrm{CL}$$

A principal component analysis (PCA) was carried out with the above variables ($\log_{10}$ RCH and $\log_{10}$ CL). This analysis allowed to distinguish two groups of males which would represent juveniles and adults. Individuals were assigned to each group using a non-hierarchal classification procedure (K-means cluster). This method is based on establishing a predetermined number of groups –in this case, two- and assigning individuals to one of the groups according to their loads on the two axes of the PCA by means of an iterative process to minimise intra-group variance and to maximise between-group variance. Using the results of the classification method, a discriminant analysis to obtain a discriminating function that permitted any individual to be classified as a juvenile or an adult on the basis of cheliped height and carapace length.

Juveniles measuring less than 80 mm CL had a lower allometric level than the larger-sized individuals, which created a curvilinear logarithmic relation. The linear discriminating function did not provide a good discrimination between the two stages. Moreover, these crabs were clearly immature as they have not developed gonads and their size was substantially lower than the size at maturity put forth by other authors. For these reasons, we decided to make an a priori classification determining as juveniles those individuals with a CL < 80 mm and excluding them from the discriminant analysis.

(b) *Allometry in juvenile males*

To determine whether there are allometric changes in juveniles, as have been proposed for this and other majid species (Conan & Comeau, 1986; Sainte-Marie et al., 1995; Sampedro et al., 1999), we compared one- and two-stage relative growth models. Using piecewise linear regression with a breakpoint, two allometric equations were fitted and a breakpoint was estimated. The fitting of the two-stage model was compared with a model based on only one phase using the F-statistic with 2 and NP degrees of freedom:

$$F= [(SSR1-SSR2)/2] / [SSR2/(N-P)]$$

Where P is the number of parameters (in this case, 4); N is the number of observations and SSR1 and SSR2 are the sum of the residual squares from the one- and two-stage models respectively.

(c) *Size at maturity*

Two methods were used to determine size at maturity in both males and females:

1) The size of 50% maturity (CL_{50}) for which a logistic regression was performed relating body size (CL) and maturity stage (classifying specimens into juveniles or adults depending on their morphometry).

2) The median size of adult cohorts estimated using the complete sample for a given cohort.

Both methods were applied independently to data from 1998 and 1999 and pooling the two years. As regards CL_{50}, data used included cohorts of adults that reaching maturity that year and different cohorts of juveniles that will reach maturity in the next two years.

RESULTS

A total of 14983 specimens were caught: 7430 males (5888 juveniles and 1542 adults, classified using the discriminant function presented below) and 7553 females (5393 juveniles and 2160 adults, classified on the basis on abdominal morphology). Catch per unit of effort (CPUE) during the sampling period (CORGOS, 2004) indicated an important peak in juvenile recruitment in the shallow areas in autumn (October-November) and in winter (January) and smaller peak were seen in summer (July). Postpubertal adult males were detected in shallow areas from April to October and in the migratory corridor between September and November. Adult females were found in the shallow area from July to December and in the deep zone between September and December. These results would indicate that the juveniles caught between September and August and the adults caught from March to December belong to the same year class.

Morphometric maturity in males:

The percentages of variance explained by the PCA performed using morphometric variables were 97.8% and 2.2% for axes I and II (Figure 1). According to the loads on axes I and II, each specimen was classified into one of the two groups (adults or juveniles) using the K-means classification analysis. The discriminant function obtained to distinguish the maturity stage was (Fig. 2):

$$\log_{10}RCH = 1.899 + 1.467 \cdot \log_{10} CL \ (P<0.001)$$

which divides the cluster efficiently into the two previously classified groups and allows for the correct classification of 98.9% of the specimens (100% in juveniles and 96.1% in adults). According to this classification the size range of juvenile males was between 25 and 174 mm CL and in adults from 91 to 208 mm CL. For comparative purposes, the juvenile females measured between 25 and 169 mm CL, while adults ranged from 99 to 188 mm.

Allometry in juvenile males:

A two-stage growth model was found to have a better fit than a single relative growth model (piecewise linear regression with a breakpoint, $P<0.001$, $R^2=0.975$, Fig.3).

The second-phase males (identified as adolescents) had chelipeds with a higher allometric level than the first-pase crabs (immature), with slope values of 1.6 and 1.2 respectively. The CL at the breakpoint was 96.2 mm. Therefore, juveniles that are equal to or greater than this size may be considered adolescents and those that are smaller, immature animals.

Gonad maturity in males:

Crabs used in the analysis of the gonads and classified as juveniles in terms of their morphometry had sizes of between 62 and 173 mm CL, while adult sizes ranged from 115 and 208 mm CL (Table 1). All the morphometrically mature individuals had spermatophores, whereas they appeared in only 60.2% of the juveniles. Juveniles with spermatophores presented a mean CL of 118.4 mm, while juveniles without spermatophores measured 92.4 mm on average. Within the juveniles, 71.5% of the morphometrically immature animals did not exhibit spermatophores, while 76.7% of the morphometrically adolescent specimens were found to have them.

The gonad maturity size, defined as the CL at which 50% of the males exhibited spermatophores, was estimated by means of the following logistic regression:

$P=e^{(-6..215+0.065 \cdot CL)}/1+e^{(-6.215+0.065 \cdot CL)}$ ($p<0.001$).

Males reach gonad maturity at 96.2 mm CL, a size that coincides with the breakpoint separating immature individuals from adolescents. These results would indicate that males reach physiological or gonad maturity one or two moults before the terminal moult occurs, after which they attain the morphometric or functional maturity.

The gonad dry weight of adults was over 10 times higher than that of the juveniles (mean gonad dry weights of 1.1 g and 0.1 respectively). The gonad mass remained constant in juveniles over time, whereas in adults, a rapid increase was seen between August and December (Figure 4). Adolescents had a mean gonad weight that was almost 8 times higher than the immature specimens (mean gonad dry weights of 0.14 g and 0.02 respectively), although a seasonal pattern of gonadal development was not detected (Figure 5). Consequently, even though they did have spermatophores, there was no evidence of gonadal development in juveniles.

Gonad maturity in females:

A total of 163 morphometrically mature females were examined, 138 of which were caught in the inner area of the ría and 25 in the central channel. They showed a clear seasonal pattern of gonadal maturation. After the terminal moult, females had gonads in the early stages of development (between July and October 93% of the females are in stage I) (Figure 6) and until November females did not attain more advanced developmental stages (II and III). It is interesting to note that no females were found with gonads in an advanced stage of development (IV) in either the shallow area or in the channel.

In the shallow area between November and December, 58% of the females had gonads in stage II, and 19% in stage III. In the channel the maturity stage was slightly more advanced than in the shallow area since during this period 64% of the females had gonads in stage II and 27% in stage III (Figure 6). Therefore in females the gonads began to mature between two and three weeks after the terminal moult, during the period immediately before or during their migration to deep waters. The gonad dry weight was found to increase as the developmental stage advanced, so gonadal development is reflected in the gradual increase in gonad weight over time (Figure 7).

Size at morphometric maturity:

Once the specimens have been classified into juveniles or adults using the morphometric methods described earlier, the size at morphometric maturity of the population was estimated. The sizes at maturity estimated through logistic regression (CL_{50}) for the entire sampling period (Table 2) were 136.5 mm CL for males and 130.3 mm for females. We detected slight differences between the two years in males, with the 1999 data giving a CL_{50} almost 6 mm larger than the 1998 data, while in females the difference was less than 2 mm.

When the median size of the adult cohort was used, the differences between the 1998 and 1999 year classes were 1.9 mm in males and 3.3 mm in females (Table 3). For the overall sampling period, the median CL was 139.9 mm and 148.8 mm in males and females respectively. In all cases the size at maturity obtained from the median of the cohort was greater than the one resulting from the CL_{50} method with differences of over 20 mm. In contrast to the results of CL_{50}, the median size at maturity of the female cohorts was considerably greater than that of males (up to 11.2 mm in 1998), while the differences for each sex between year classes were minor.

DISCUSSION

The size at the onset of sexual maturity is one of the most important parameters of the life cycle of crustaceans and its estimation has been attempted by many different methodologies. Traditionally studies have been conducted on two processes related to maturity: reproductive capacity (gonadal development, presence of spermatophores, etc.) (Conan & Comeau, 1986; Paul, 1992; Sainte-Marie et al., 1995) and morphometric changes that occur when maturity is reached (Somerton, 1980; 1981; Conan & Comeau, 1986; Paul, 1992; Paul & Paul, 1990; Sainte-Marie et al., 1995). Methods based on reproductive capacity make it possible to determine the size at which an individual is physiologically mature. Morphometric changes, on the other hand, point to allometric changes in the growth of different parts of the body related to functional maturity, whereby the animal is able to mate.

In many brachyuran species gonad maturity does not coincide with morphometric maturity (Conan & Comeau, 1986). In both this study on *Maja brachydactyla* as well as in others reporting on different majids such as *Chionoecetes opilio* (Conan & Comeau, 1986; Sainte-Marie et al., 1995) *Chionoecetes bairdi* and *Paralithodes camtschatica* (Paul, 1992) spermatophores were detected in the gonads of morphometrically immature specimens, which would imply that physiological maturity occurs prior to morphometric maturity in males. Physiological maturity in decapods usually takes place when the animals reach morphometric adolescence, one or two moults before morphometric maturity. Hartnoll (1965) highlights the fact that the presence of spermatophores is only circumstantial evidence of maturity and an adequate demonstration of this would require mating experiments. Several laboratory studies have shown that morphometrically immature males of *Chionoecetes* and *Paralithodes* were capable of mating (Paul & Paul, 1990; Paul, 1992). Yet Conan & Comeau (1986) did not observe pre-copulatory behaviour in morphometrically immature animals as big or bigger than morphometrically mature active specimens with spermatophores.

Majid males observed to mate in the field are usually morphometrically mature (Powell et al., 1972) and larger in size than females (Brosnan, 1981; Conan & Comeau, 1986; Ennis et al., 1988; Paul, 1992; Powell et al., 1972). Prior to mating, agonistic interactions take place between males (Conan & Comeau, 1986; Elner & Beninger, 1995; Ennis et al., 1990; Sainte-Marie et al., 1997; 1999; Rondeau & Sainte-Marie, 2001; Stevens et al., 1993; Correa et al., 2003; Jivoff, 1997; Van Der Meeren, 1994; Wada et al., 1997; direct observations of fishers for *Maja brachydactila*) during which large individuals may exclude smaller crabs. Sometimes smaller males are rejected by females (Goshima et al., 2000), and it is possible that small sized-males may not be able to mate with large females, since the allometric increase in the size of the chelipeds is also related to the role they play in supporting the female during courtship and mating (Brosnan, 1981; Jivoff, 1997; Rodhouse, 1984). Rodhouse (1984) performed laboratory experiments on *Maja brachydactyla* where the large males prevented the smaller ones from entering into the traps with bait. This same behaviour might occur when the animals are competing for females.

The above results on majids would suggest that, although a morphometricaly immature male might be physiologically mature, it is very unlikely that this animal will be able to mate in the field. Furthermore, of the morphometrically mature specimens, the larger-sized crabs will have a competitive advantage and be able to mate with a greater number of females. Therefore a male crab that has attained gonad maturity may not be functionally mature. In *M. brachydactyla* as in many other species, the production of spermatophores, and consequently gonad or physiological maturity, takes place prior to the terminal moult and/or morphometric maturity. So, a morphometrically immature individual is potentially able to mate with a female (as has been demonstrated in laboratory studies), but, is unlikely to mate in the field, and even more unlikely in the case at hand, as mating occurs during migration and in deep waters, and juveniles do not migrate. In view of the above, it should be more appropriate to estimate size at maturity on the basis of morphometric criteria, and according to the suggestions of Hartnoll (1965), experimental studies may present a biased image of sexual maturity in natural populations.

In the Ría de A Coruña, *Maja brachydactyla* females carry out the terminal moult in shallow waters between June and September, with a peak in August (CORGOS, 2004). However, we did not observe an important number of specimens with gonads in an advanced stage of development (II and III) until November. Therefore it is possible to estimate that gonads begin to develop 2-3 months after the terminal moult. This pattern of gonad maturation is similar to the one presented by González-Gurriarán et al. (1993) in th Ría de Arousa (150 km from the study area in the south of Galicia) and García-Flórez & Fernández-Rueda (2000) on the coast of Asturias (200 km north of the study area). In the present study, however, no females were observed to have gonads in development stage IV. In the Ría de Arousa primiparous females were reported in Stage IV gonads from December onwards and on the Asturian coast (where primiparous females were not differentiated from multiparous females), they were detected from October. This difference may be due to the fact that in the above mentioned papers samples were taken from the commercial fishery which operates mainly in deep waters, while in this study the females were caught in shallow waters during the period before migration.

As *M. brachydactyla* stops growing once it reaches sexual maturity and it is possible to stablish the relative age of the adult specimens, the median size of adult cohorts should be the best estimate of the size at maturity of the population (Somerton, 1981). This parameter presented much less interannual variability than the CL_{50} what was calculated using logistic regression with cross-sectional data. These results would indicate that median size may be far more robust and less influenced by the strength of the year class of the juveniles, by the relative abundance of adults and juveniles and by the differential mortality rates, as reported by Somerton (1981). In our case the onset of sexual maturity starts in summer, the most favourable season from an oceanographic standpoint and when the fishing season is closed, so there would not be a high mortality rate or variability related to size. Despite all of the above, considerable differences, as 20 mm in females, were detected between the sizes at maturity resulting from the two methods.

The size at maturity obtained using the CL_{50} criteria for females in the entire sampling period is similar to the size reported by Sampedro et al. (1999) in the Ría de Arousa (130.4 mm) and slightly higher in males (136.5 and 132.7 mm respectively). On the other hand, in the Asturian coast García-Flórez & Fernández-Rueda (2000), who used the mean size of adult females as the size at maturity, reported substantially smaller sizes (133.5 mm in 1997 and 124.4 mm in 1998) as compared to the results in the Ría de A Coruña (median sizes of 150.1 mm in 1998 and 147.1 mm in 1999). These differences between nearby geographic areas may be attributed the potential to bias caused by the sampling method, as on the Asturian coast, samples from the commercial fishery were used and fishers generally discard recently molted crabs having a soft carapace or less muscle mass. Both carapace hardness and muscle development are processes that require long periods in large specimens, so discards tend to increase with body size, which would bias the size at maturity obtained by García-Flórez & Fernández-Rueda (2000).

Currently, a minimum landing size of 120 mm CL is stablished in the Spanish fisheries for *Maja brachydactyla*. Our results indicate that an important proportion of juveniles are larger than the minimum size. However, there is a large variability in size at maturity (the terminal size) within a cohort and any realistic minimum size will cause a part of the adult cohort to be unfished. In the long term, the protection of small adults could generate a strong selective pressure on size at maturity in exploited populations. According to these aspects, the regulation based in cut-off sizes seems not to be an adequate management strategy. Two aspects of the biology of *M. brachydactyla* could allow alternativee strategies: the spatial segregation of adults and juveniles and the availability of morphological and morphometrical methods to estimate the maturity status of any crab. In this sense a combination of spatial closures and direct protection of juvenile habitat could be more effective protecting the juvenile cohorts without the undesirable selective effects of minimum sizes.

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Table 1. Gonad analysis for males of *Maja brachydactyla*. Body size statistics (carapace length, CL) of individuals with presence or absence of spermatophores for the different morphometric categories (adults, adolescents and inmatures) are shown (SD = standard deviation).

Presence of spermatophores	N	%	CL (mm)				
			Mean	Median	Min.	Max.	SD
Juveniles							
Inmature	130	34.0	81.0	80.7	59.7	96.0	9.88
Yes	37	28.5	84.9	87.6	61.5	95.9	8.69
No	93	71.5	79.5	78.0	59.7	96.0	9.94
Adolescents	252	66.0	122.0	119.9	96.2	173.4	18.56
Yes	193	76.6	124.8	123.9	96.3	173.4	18.73
No	59	23.4	112.6	109.0	96.2	161.3	14.63
Adults							
Yes	128	100.0	149.5	146.9	115.1	208.0	16.71

Table 2. Morphometric size at 50% maturity (CL_{50}) and parameters of the logistic regression Prob (maturity)= $e^{-(B0+B1\cdot LC)}/(1+e^{-(B0+B1\cdot LC)}$ obtained for each year class and the whole sampling period for males and females. $P<0.001$ in all cases. $CL_{50}=-B_0/B_1$. N = sample size.

	N				
	Juveniles	Adults	B_0	B_1	CL_{50}
1998					
Males	2092	924	-14.236	0.109	130.8
Females	1972	1204	-35.375	0.272	130.3
1999					
Males	2235	615	-15.730	0.115	136.3
Females	2049	937	-31.649	0.246	128.7
Total					
Males	5888	1542	-14.082	0.103	136.5
Females	5392	2158	-32.834	0.252	130.3

Table 3. Morphometric size at maturity estimated as the median size of the adult year classes for 1998, 1999 and the whole sampling period. Number of analyzed individuals (N), and maximum and minimum size of adults are shown.

		CL (mm)		
	N	Median	Min	Max
1998				
Males	924	139.2	93.6	198.8
Females	1204	150.4	100.0	187.7
1999				
Males	615	141.1	90.5	200.7
Females	937	147.1	98.5	186.3
Total				
Males	1539	139.9	90.5	200.7
Females	2141	148.7	98.5	187.7

FIGURE LEGENDS

Figure 1. Distribution of individuals in the first two axes extracted from the principal component analysis (PCA) carried out for the variables carapace lenght (CL) and right cheliped height (RCH) for males of *Maja brachydactyla*. Based on the grouping obtained by the K-means cluster, individuals considered juveniles (○) and adults (+) are shown separately. Males smaller than 80 mm (CL) were excluded from the analysis.

Figure 2. Discriminant analysis between juveniles (○) and adult (+) males of *Maja brachydactyla* for the relationship of carapace length to right cheliped height.

Figure 3. Relative growth phases for juvenile males of *Maja brachydactyla*. Equations fitted for inmatures and adolescents and CL at breakpoint (CL_b), obtained with the piecewise linear regression, are shown.

Figure 4. Monthly evolution of mean gonad dry weight (g) for juvenile and adult males of *Maja brachydactyla* captured in shallow waters. 95% confidence interval of the mean is shown.

Figure 5. Monthly evolution of gonad dry weight (g) for juvenile males of *Maja brachydactyla* (distinguishing inmatures and adolescents) captured in shallow waters. 95% confidence interval of the mean is shown.

Figure 6. Monthly evolution of gonad development for adult females captured in shallow waters (upper graph) and migration corridor (lower graph). Number of individuals analyzed each month are shown (N).

Figure 7. Monthly evolution of mean gonad dry weight (g) for adult females captured in shallow waters. 95% confidence interval of mean is shown.

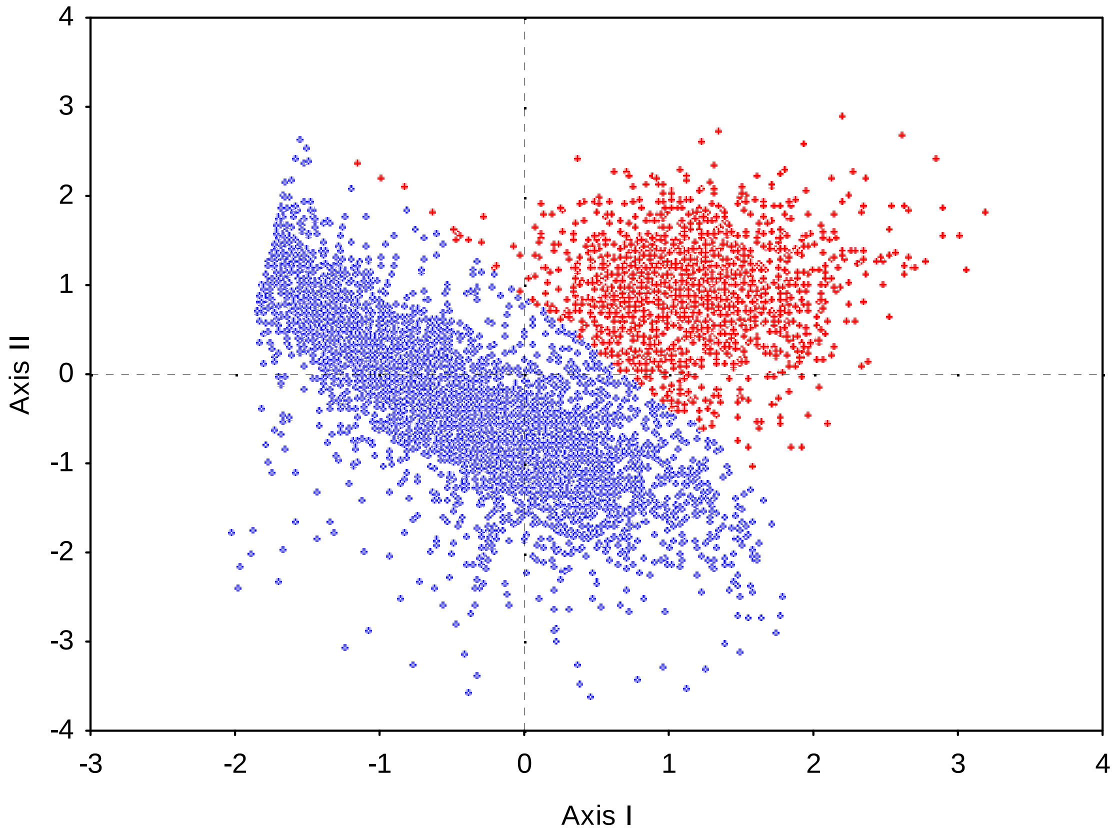

Figure 1. Corgos & Freire. Morphometric and gonad maturity in *Maja*

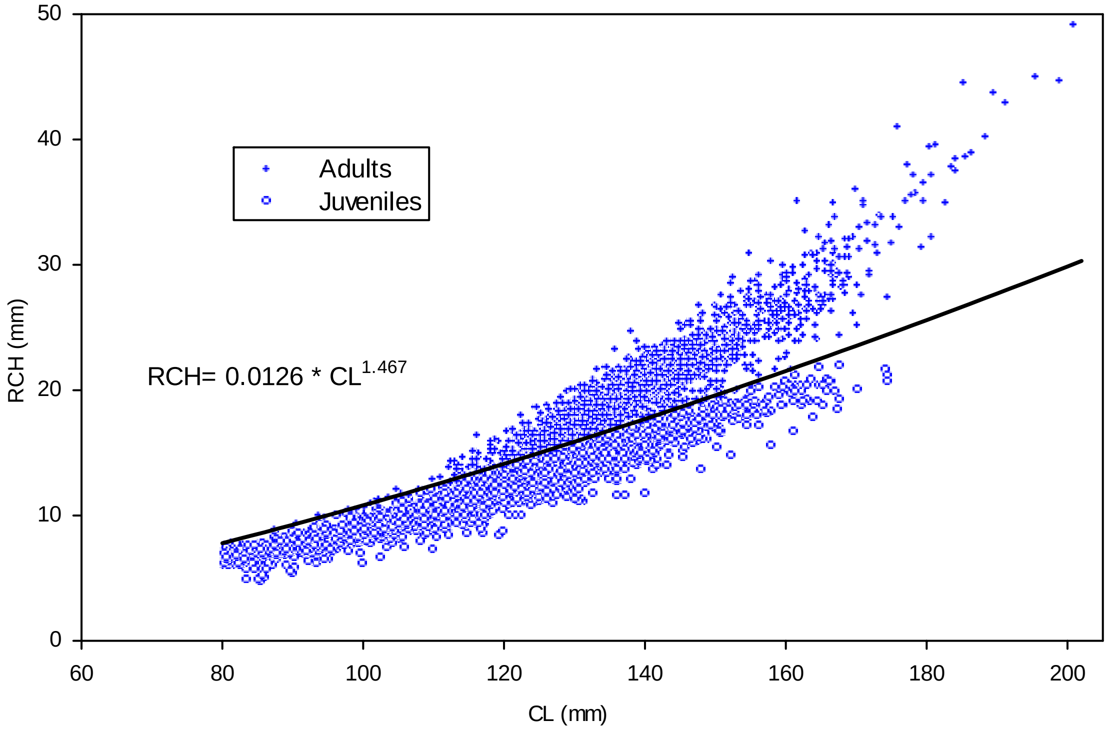

Figure 2. Corgos & Freire. Morphometric and gonad maturity in *Maja*

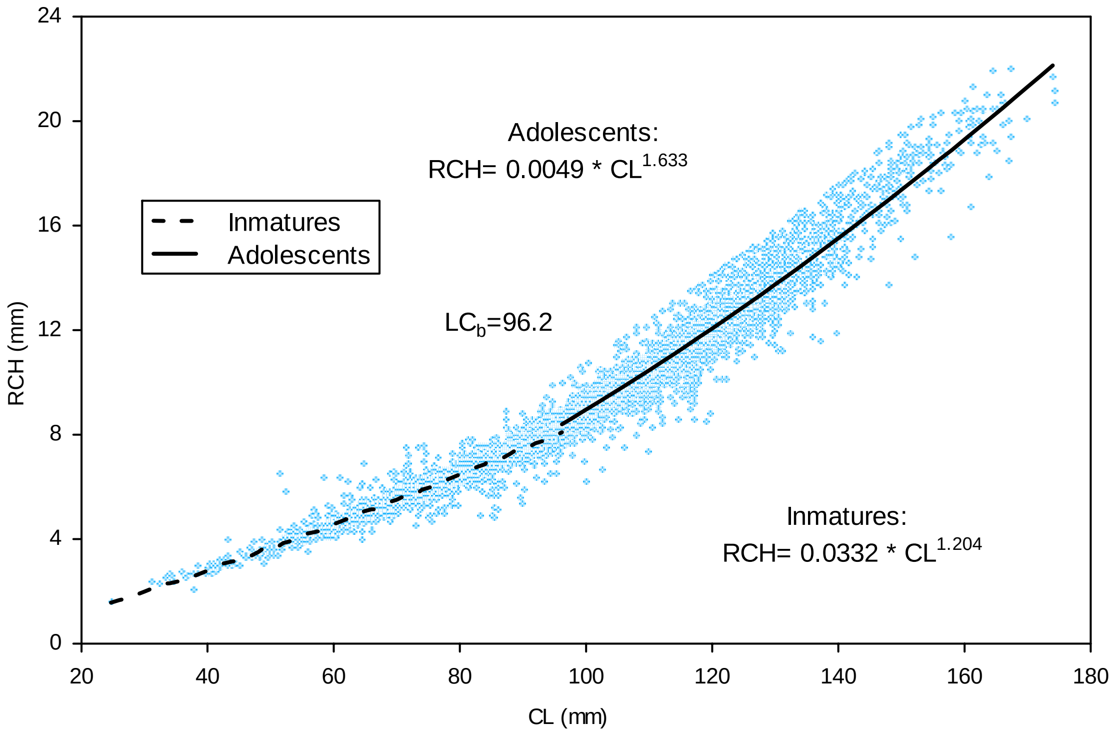

Figure 3. Corgos & Freire. Morphometric and gonad maturity in *Maja*

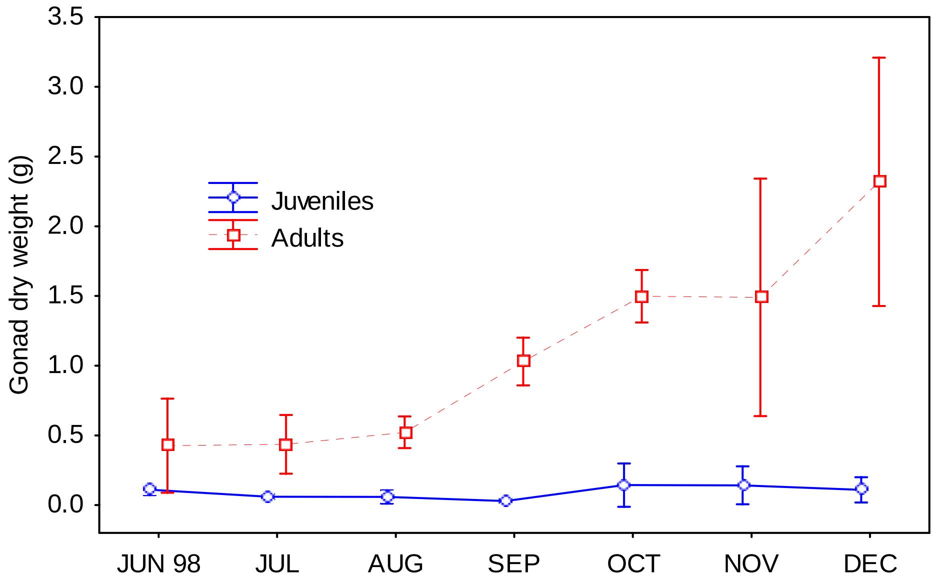

Figure 4. Corgos & Freire. Morphometric and gonad maturity in *Maja*

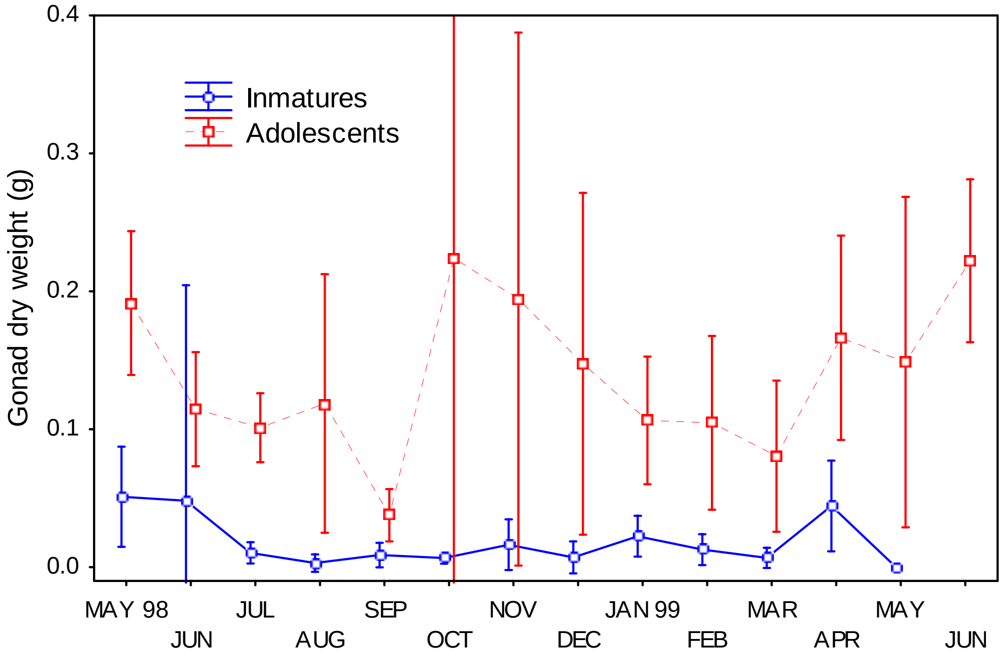

Figure 5. Corgos & Freire. Morphometric and gonad maturity in *Maja*

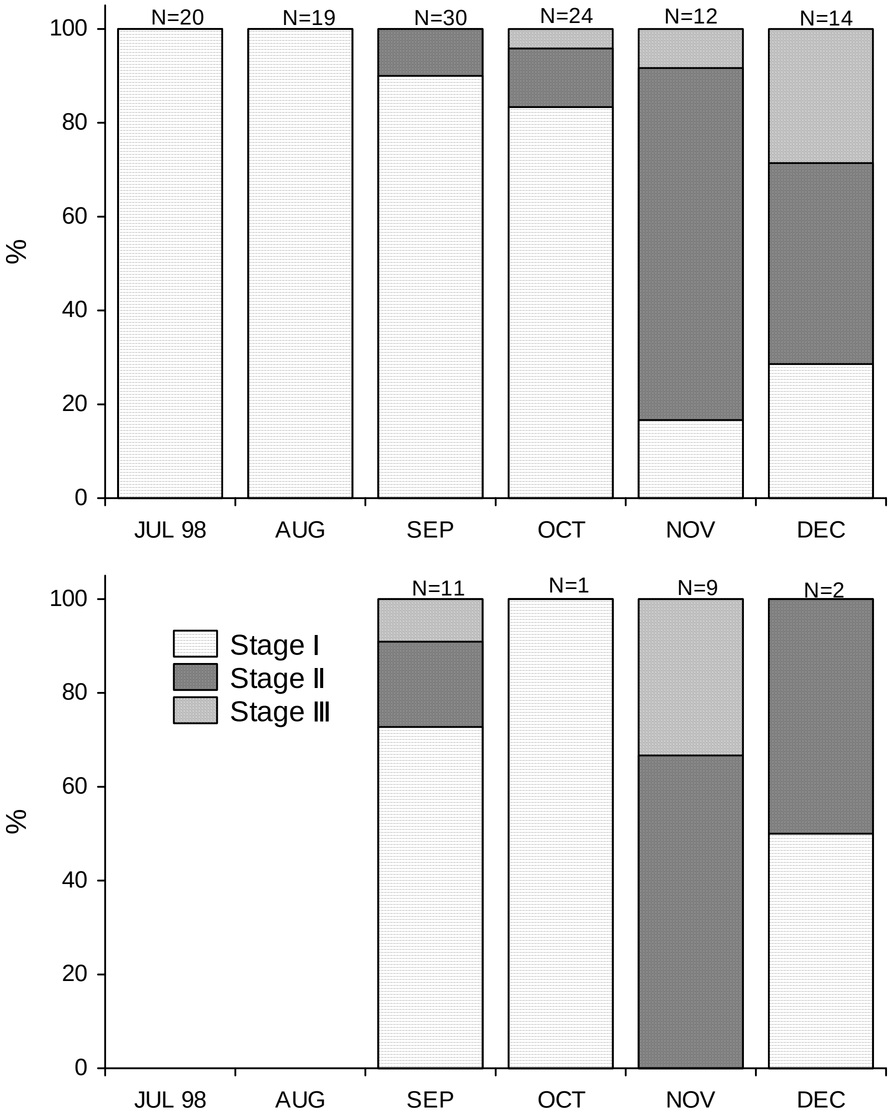

Figure 6. Corgos & Freire. Morphometric and gonad maturity in *Maja*

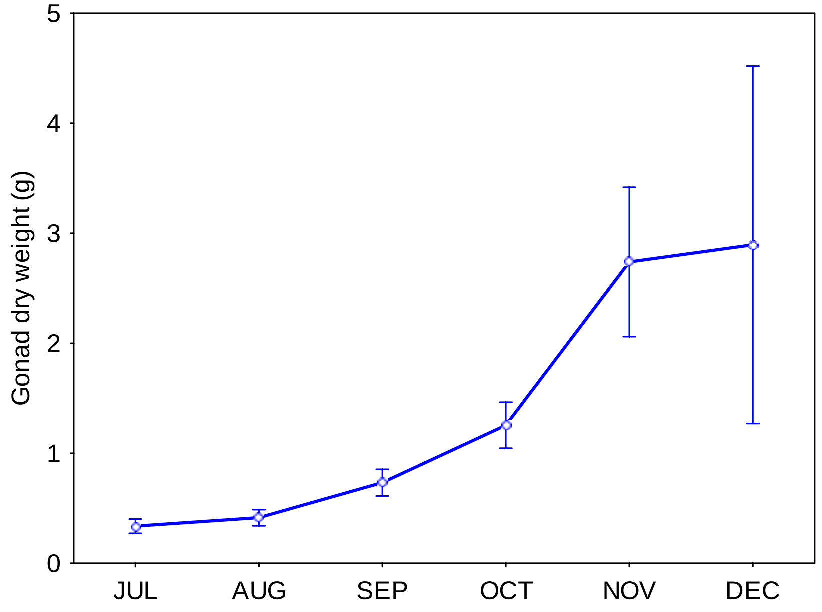

Figure 7. Corgos & Freire. Morphometric and gonad maturity in *Maja*