GROWTH AT MOULT, INTERMOULT PERIOD AND MOULTING SEASONALITY OF THE SPIDER CRAB *Maja brachydactyla:* COMBINING INFORMATION FROM MARK-RECAPTURE AND EXPERIMENTAL STUDIES

A. Corgos, M. P. Sampedro, E. González-Gurriarán and J. Freire

(AC, EG-G and JF) Departamento de Bioloxía Animal, Bioloxía Vexetal e Ecoloxía, Universidade da Coruña, Campus da Zapateira s/n, E-15071 A Coruña, Spain; (M-PS) Instituto Español de Oceanografía. Centro Oceanográfico de A Coruña, Muelle de Ánimas s/n, Apdo. 130, E-15080 A Coruña, Spain. (JF,Correspondence: jfreire@udc.es)

ABSTRACT

An analysis of growth at moult (for both the prepubertal and terminal moults), moulting seasonality and the intermoult period in the spider crab *Maja squinado* in the Ría de A Coruña (NW Spain) was carried out based on a mark-recapture experiment. Crabs between 70 and 130 mm carapace length (CL) undergo a mean increase at moult of 32.4% from their pre-moult size. Generalised Linear Models (GLMs) were used to construct growth models, employing a combination of information from the mark-recapture study and other previous studies performed in both laboratory and extensive culture, to estimate the effects of the biological variables and the study method. No differences were found in the growth rate between males and females. However, the effects of the study method, the pre-moult CL and the interaction between them were significant. The smallest-sized crabs undergo a greater increase in size in the laboratory and culture studies, while the largest individuals undergo greater growth in the field. The mean intermoult period estimated for prepubertal moults in the field ranged from 50 to 86 days, which

is similar to the 84.7 days observed in the laboratory study. The prepubertal moults occurred primarily in spring and autumn in the field, while under culture conditions, the crabs moulted mainly in the spring. The intermoult period for terminal moults was estimated to be around 90 days, slightly lower than the value of 104 days obtained in the laboratory. The terminal moult took place generally in summer (June-September) both at sea as well as in culture experiments. The intermoult period of juveniles at sea was highly variable, and some of the specimens did not moult for more than 5 months.

Maja brachydactyla Balss, 1922 (see Neumann, 1998 for taxonomic status, corresponding to the North Atlantic species previously known as *M. squinado*) 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).

The analysis of growth in crustaceans is problematic due, on the one hand to the fact that it is a discontinuous process carried out by moulting, and on the other, that these animals lack anatomical structures that could allow to estimate the age of each individual directly (Hartnoll, 2001). Growth models in crustaceans consist of two components (size increase at moult, MI, and the duration of the intermoult period, IP), which are dependent upon the body size, which depends, in turn, on the animal. Therefore any growth model for crustaceans must include the relationships between the size increase at moult, the duration of the intermoult period and body size (Botsford, 1985).

The methodology of growth studies entails another major problem, since in the experimental approaches used both in the laboratory and in culture on a larger scale, there may be factors involved such as handling, temperature, food or available space which could affect growth, thereby leading to great differences with respect to growth at sea (Drach, 1939; González-Gurriarán, 1981, 1985; González-Gurriarán *et al*., 1998a; Le Foll, 1993; Wilber and Wilber, 1989). Moreover, growth studies in the field using direct methods (mark-recapture) are difficult as well as costly to carry out, since they involve large sampling periods and the need to mark a large number of individuals, given the generally low recapture and high tag loss at moult rates (Le Foll, 1993). Up to now, previous studies on growth at moult of *Maja brachydactyla* have been based on experiments done in the laboratory (Teissier, 1935; Drach, 1939; Le Foll, 1993; González-Gurriarán *et al.*,1995; Iglesias *et al.,* 2002), and in extensive culture (González-Gurriarán *et al.*,1995; Iglesias *et al.,* 2002), because previous mark-recapture studies (Edwards, 1979; Le Foll, 1993) did not generate sufficient data to be able to derive any reliable conclusions. In the present study, with the the use of tags that are retained during the moulting process, we were able to obtain growth at moult data for *M. brachydactyla* at sea.

An indirect study method commonly employed is the use of the population size structure to obtain statistical relationships between age and size. This method adapts easily to cold-waters decapods, such as the species of *Chionoecetes*, *Paralithodes* and *Nephrops*, since they show a slow growth and a population structure composed of only one annual cohort, which is conducive to the analysis of size frequency distributions (Castro, 1995; Donaldson *et al*., 1992; Sainte-Marie *et*

al., 1995). In species like the spider crab *Maja* brachydactyla, however, which has several annual recruitment pulses (González-Gurriarán *et al.,* 1993, 1998b), and a high degree of individual variability in growth rates, the size frequency distributions are multimodal and are difficult to analyse (Kergariou, 1984; Le Foll, 1993). For all of these reasons, and as mentioned above, in this species growth has been studied mainly by using direct methods in the laboratory or culture to estimate the increase in size at moult. However, recent studies (Corgos, 2004; Sampedro *et al.*, 2003) have reported preliminary approaches to estimate growth in this species through the analysis of size frequency distributions.

Data analysis and the interpretation of the results on growth in decapods have generally been carried out separately for each methodology applied to the same species or for the same study method in different geographic areas (for example Wainwright and Armstrong, 1993 studying *Cancer magister*, or González-Gurriarán *et al.,* 1998a for *Nephrops norvegicus*). An alternative approach would consist of modelling growth including all the sources of information available within the same statistical framework. Cruywagen (1997), for instance, applied a Generalised Linear Model (GLM) to the growth of the lobster *Jasus lalandii* to determine interannual and geographical variation by using data from different studies.

The purpose of the present study is to analyse growth at moult of *Maja brachydactyla* in the Ría de A Coruña (NW Spain) using data from a mark-recapture experiment and to compare it with two other previous studies performed in the laboratory and extensive culture. On the basis of data taken from the three studies discussed above, a growth model combining the different sources of information will

be constructed. Also included will be supplementary information on the intermoult period and the seasonality of the moult at sea based on data obtained from the mark-recapture experiment.

MATERIALS AND METHODS

Monthly samplings were carried out between December 1997 and November 1999 using experimental traps in the Ría de A Coruña, a small oceanic embayment located in the NW of Galicia (NW Spain) (Corgos, 2004). Three shallow water (5-15 m) sampling stations were selected along the ría and one other station was located in deeper waters (25-30 m) in the central channel of the ría, which constitutes the migration corridor for postpubertal adults.

The following data were recorded for every crab captured: sex, morphometric maturity (Corgos and Freire, submitted; Sampedro *et al.*, 1999), and stage of the intermoult cycle (estimated by the hardness of the exoskeleton and the presence of a new internal carapace in crabs approaching moult), relative age (based on the degree of epibiosis and carapace erosion, see Fernández *et al*., 1998) to distinguish recent postpubertal adults from crabs that had reached maturity in previous years.

After the biological data were recorded, each specimen was tagged and released back into the area where it had been caught. T-bar anchor tags model FD 89-SL, manufactured by Floy Tag® (Seattle, Washington, USA) with a single code and a telephone number to submit recapture information, were used. The tag was inserted at the base of the 5th pereiopod on the epimeral line separating the cephalothorax

from the abdomen. These tags are inserted into the musculature with the filament and vinyl tube remaining on the outside so that they will stay in place during ecdysis.

During the sampling period, a total of 15085 specimens were caught, 10304 of which were tagged. A total of 715 were recaptured in experimental samplings, which is equivalent to a recapture rate of 6.9%. Of the recaptured crabs, 36 specimens moulted at least once after being tagged. One of these specimens was found to have moulted more than once, since its size increase (141%) was much greater than any increment corresponding to just one moult (González-Gurriarán *et al.*, 1995; Le Foll, 1993). Individual growth was examined by using the data from individuals that had undergone only one moult. The specimens that did not moult between tagging and recapture showed a mean difference (in absolute value) in the carapace length (CL) obtained at the time of tagging and recapture of 0.94 mm (range: 0.0-9.6 mm). This value may be considered as an error estimator in the measurement of body size.

The recaptures reported by the commercial fishery provided almost no information on growth, since it was only possible to record the size of the recaptured individual on very few occasions. Only one of the crabs that moulted retaining the tag and was recaptured by the commercial fishery, could be measured, but it was not used to estimate growth at moult since its growth rate (71.9%) indicated that it had moulted more than once.

The comparison of growth at sea with other studies was carried out using data from experiments performed by González-Gurriarán *et al.* (1995) in the laboratory and extensive culture. In the laboratory experiment 37 specimens (17 males and 20

females) were held in a 2 x 1 m tank with a water level of 0.20 m, a water flow of roughly 10 l/min and a photoperiod cycle (12 hours of light and 12 hours of darkness) under dimly light conditions. Specimens were placed in individual plastic mesh cages measuring 0.46 x 0.36 m. The cages were initially divided into 4 sections and the space occupied by the crabs was enlarged gradually as they moulted and increased in size. The crabs were fed mainly a diet of mussel (*Mytilus galloprovincialis*) with the occasional addition of sea urchins (*Paracentrotus lividus*) and brown and red seaweeds.

The extensive culture experiment was performed in two 2.75 x 1.85 x 0.75 m iron cages covered with a plastic netting with a mesh size of 2 x 2 cm (with 95 specimens in cage I and 60 in cage II) and a volume of 13.8 m^3. The cages were closed completely and suspended at a depth of 1-2 m. These cages were set out on the north coast of the outermost part of the Ría de Arousa, in a tank with a capacity of 103.7 m^3. The bottom was made up of rocks and sand with a water depth ranging from 3 to 6 m depending on the pumping volume, tide height and location of the tank. The tank was located only a few metres off the coast and subject to the natural changes in the photoperiod. Water was pumped in for 3-4 hours a day with a flow of 3000 l/min (see González-Gurriarán *et al.* (1995) for more details).

Data Analysis

In addition to the data obtained in the mark-recapture experiment, to construct models for growth at moult, we used data from 67 moults in the laboratory and 120 carried out in extensive culture and reported by González-Gurriarán *et al.* (1995).

Growth at moult was estimated by the percentage of size increment at moult (PIM) = ((post-moult CL – pre-moult CL)/ pre-moult CL) · 100, since previous studies point to a better fit with models based on the PIM repect to the absolute moult increment (Corgos 2004; Somerton, 1980; Wainwright and Armstrong, 1993; González-Gurriarán *et al.*,1995).

Generalised Linear Models (Mc Cullagh and Nelder, 1989; Chambers and Hastie, 1992) were used to combine the information on growth reported by different studies and to estimate the effects of the biological variables and study method. The study method, moult type (prepubertal vs. terminal), sex and pre-moult CL (CLpre) were used as independent variables. Generalised Linear Models are commonly applied to analyse any ANCOVA type design with continuous and discrete variables, as well as any multiple regression design with continuous variables. These models allow for the inclusion of different sources of information and are therefore an excellent tool to use in the analysis of growth variability in relation to biotic and environmental factors.

The GLMs were fit by using the PIM as the dependent variable, a normal error distribution and a log-link function. A normal distribution was used since the PIM is distributed normally (Kolmogorov-Smirnov test, $p>0.05$).

In the extensive culture, there was no information available on moult type, therefore it was not possible to include simultaneously the moult type and the three studies in the model. For this reason two models were estimated:

- Model 1: data from the three studies are included but moult type is omitted,

$\log PIM = b_0 + b_1 \cdot CLpre + b_2 \cdot sex + b_3 \cdot study + interactions$

- Model 2: the extensive culture study is omitted so that moult type can be included,

$\log PIM = b_0 + b_1 \cdot CLpre + b_2 \cdot sex + b_3 \cdot moult + b_4 \cdot study + interactions$

Each model was tested for the significance of each effect and all the interactions. The final model selected included only significant effects and interactions. The significance of each effect was assessed by means of the Wald (W) statistic, which tests the significance of the regression coefficient. It is based on the property of the asymptotic normality of the maximum likelihood coefficients and is calculated as:

$W = \beta \cdot 1/Var(\beta) \cdot \beta$

where β represents the estimated coefficients, and *Var(*β*)* represents the asymptotic variance of the estimated coefficients. The Wald statistic follows a Chi-square distribution (Mc Cullagh and Nelder, 1989).

The estimation of the approximate duration of the intermoult period at sea can only be obtained in cases where an individual that has recently moulted is tagged and recaptured in the early post-moult stage (B, Sampedro *et al.*, 2003). In all the other cases the time elapsed between tagging and recapture will always be greater than the real intermoult period. Moreover, the time elapsed between the tagging and recapture of specimens that did not grow will always be less than the intermoult period. So, in prepubertal moults, the mean intermoult period in the natural environment will be greater than the mean time elapsed between the tagging and recapture of crabs that did not grow during this interval and shorter than the mean time elapsed between the tagging and recapture of crabs that did undergo growth in

the period ranging between tagging and recapture. In the calculation of these mean times, we did not take into account crabs that were recaptured the same month of tagging or those that moulted more than once in the interval between tagging and recapture.

In the case of the intermoult period previous to the terminal moult, it is only possible to take into account the mean time elapsed between the tagging and recapture of the crabs that carried out the terminal moult between tagging and recapture, since there is a broad range of sizes at which juveniles may undergo the terminal moult. It is therefore impossible to identify the juveniles that are going to carry out the terminal moult and did not grow in the interval between tagging and recapture to calculate the mean intermoult period. In this case we will make use of data regarding moulting seasonality and the mean intermoult period for crabs that had carried out the terminal moult and more than one moult between tagging and recapture to estimate an approximate intermoult period for the crabs that had undergone the terminal moult.

RESULTS

Growth at sea. A comparison with growth in the laboratory and extensive culture

The mean increase in size at moult in the field observations was 32.4% with regard to the pre-moult size and ranged between 22.9 and 45.7%. These values were similar in males and females in both the prepubertal and terminal moults (Table 1). The mean growth in the laboratory was 31.9%, with males and females showing similar values, but in the terminal moults, the growth rate was nearly 10% less. The

extensive culture exhibited a mean growth rate of 31.4%, and, again there was very little difference between sexes. Both the laboratory and culture experiments presented wider ranges of percentage increments than in the field, with growth rates ranging from 18.2 to 45.2% in the laboratory and from 15.6 to 41.5 % in the culture.

In GLM model 1, the significant effects were the study method, pre-moult CL and the interaction between the two ($P<0.05$, Table 2). Neither the effect of sex or any of the other interactions were found to be significant. The significance of the interaction between the pre-moult CL and study method indicate the existence of differences in the effect of the premoult CL on growth depending on the study method. Therefore, the premoult CL has a considerable influence on the laboratory study (Figure 1), exhibiting the growth curve a very pronounced negative slope. In the culture study the CL also had a strong negative effect, while in the mark-recapture study, the CL had a lesser impact and the slope was not as pronounced. This would indicate that the smaller-sized individuals undergo greater growth in the laboratory and culture studies, whereas the larger-sized crabs grow more at sea.

In model 2, which includes the moult type (based only on the mark-recapture and laboratory studies), the significant effects were pre-moult CL, moult type and the interaction between the two ($p<0.05$, Table 3). The effects of the study method, sex and other interactions were not significant. Similar to what occurred in model 1, the effect of CL is important, and the interaction between the CL and moult type reveals a higher growth rate in the terminal moult in smaller-sized crabs and a higher growth in the prepubertal moults in large specimens, although this is only applicable to the size ranges where the prepubertal and terminal moults overlap (Figure 2).

Intermoult period and growth seasonality based on mark-recapture data

Prepubertal moults --- It was only possible to estimate the approximate intermoult period in one case, since the crab was tagged and recaptured in the postmoult stage, which lasted 97 days. A mean time of 86.7 d elapsed between the tagging and recapture of the juveniles that had carried out prepubertal moults (Table 4), while the mean time interval between the tagging and recapture of the juveniles that did not moult during this period was 50.3 d (Table 4). Therefore, the average intermoult period for prepubertal moults in the field ranged between approximately 50 and 86 d.

In most of the cases where the crabs did not moult between tagging and recapture, they had been recaptured one or two months after tagging. There were, however, some instances where specimens were recaptured after 3, 4 and even more than 6 months (206 days) without having moulted (Table 4). In the great majority of these cases the intermoult period lasted from autumn until the following spring, and in some crabs from summer until the following spring (Figure 3).

These ecdyses took place primarily in spring and autumn (from March to May and in September 1998, and in April and September1999), coinciding with the moulting peaks observed at the population level (unpublished data), although specimens that moulted in summer were also observed (Figure 4).

Terminal moult --- In crabs that carried out the terminal moult, the mean time interval between tagging and recapture was 133.7 d (Table 4), although this time interval is longer than the mean duration of the real intermoult period. If we take into account only the specimens recaptured during the postmoult period (although we only have 3 observations), the mean time interval between tagging and recapture was 98 days.

In all the cases, moulting occurred during the summer, since the crabs that had undergone the terminal moult were recaptured mainly between June and September (Figure 4).

The recapture of two individuals which underwent more than one moult between tagging and recapture provided supplementary information on intermoult period. In the first case a juvenile female was tagged in December 1997 measuring 60.2 mm CL and was recaptured as adult in October with a size of 145.1 mm, which led us to estimate that it had carried out three moults during this period. Bearing in mind that the terminal moult was probably carried out in summer, the mean intermoult period would be around 88 days. In the second case, a male spider crab was caught and tagged in January 1998 with a CL of 75.9 mm, and recaptured as adult by the commercial fishery in December of the same year, with a CL of 130.5 mm. This crab had probably undergone two moults (the terminal moult in summer), which means that the intermoult period would be roughly 90 days.

DISCUSSION

The growth rate at moult in the Ría de A Coruña was high, with a mean value of 32.3% of pre-moult CL, and some observations with values over 45%, which was similar to the results obtained in laboratory and extensive cultures. The use of GLMs allowed us to combine different sources of information (from studies based on different methodologies) and incorporate them into a growth model, discriminating the effect of the different factors involved in a statistically robust approach. These growth models made it possible to corroborate the importance of the effect of pre-moult body size and study method, while other variables have far less influence on growth. In the model 1 the pre-moult size and study method had an important effect, whereas sex did not have any impact on growth. In another laboratory study, Le Foll (1993) analysed his data in combination with those reported by Drach (1939) and Teissier (1935), obtaining growth rates in prepubertal moults (33% for females and 32.8% for males) similar to our results. He did not find any significant differences between males and females, either. The slopes of the growth curves in model 1 (laboratory > extensive culture > mark-recapture) highlight the negative effect of the culture conditions on growth. These results agree with previous studies performed on *M. brachydactyla* (Drach, 1939) and other decapods (González-Gurriarán, 1981, 1985; González-Gurriarán *et al.,* 1998a; Wilber and Wilber, 1989) which demonstrate that in the laboratory the growth rate increases with tank volume and decreases with the holding time. Capture and handling may also cause changes in growth or alter the physiological factors that govern the periodicity of moults. Iglesias *et al.* (2002) report that *M. brachydactyla* is highly sensitive to handling in the early life-history stages and these authors obtained much higher growth rates in extensive culture than in the laboratory.

In model GLM 2, the influence of the pre-moult size and moult type (not included in model 1), is again clear, while the sex factor and study method have no significant effect on growth. The larger negative slope obtained for the terminal moults in the laboratory confirms the importance of the space available and its negative influence on growth under culture conditions. Similarly, Le Foll (1993) did not observe any significant differences in growth rates between males and females as regards terminal moults (28.9% for males and 28.8% for females), although they were significantly lower than the prepubertal moults in males, but not in females.

Our results reflect the wide variability in the growth rate of *M. brachydactyla*, in both the prepubertal and terminal moult, regardless of the methodology used, which would point to the existence of other factors, besides available space and pre-ecdysial size, that could affect the growth rate. This variability renders an analysis of growth based on size frequency distributions especially complex.

The mean intermoult period estimated in the field for prepubertal moults (between 50 and 86 days) is similar to the 84.7 days reported by González-Gurriarán *et al.* (1995) in their laboratory study. In our field study, however, we observed high variability in the intermoult period, and in fact several specimens were recaptured after more than 5 months without having moulted. For this reason, it is highly likely that environmental and/or density dependent factors, in addition to the physiological stage, are of utmost importance in determining the duration of the intermoult period and the number of annual moults. The prepubertal moults occurred mainly in spring and autumn at sea, whereas under culture conditions they took place generally in spring, although the absence of the autumn peak may be due to the fact that most of

the specimens held in the laboratory reached maturity in summer. Even though we have little data available to make an accurate estimation of the intermoult period prior to the terminal moult, the recapture of specimens in post-moult that had moulted more than once in the interval between tagging and recapture, would indicate that this period lasts roughly 90 days, slightly under the 104 days obtained in the laboratory (González-Gurriarán *et al.*, 1995) and the 135-150 days estimated by using data from exuviae aged with radioisotopes (Le Foll *et al*., 1989), and similar to the estimations for prepubertal moults. The terminal moult took place mainly in summer (June-September) in both the field observations and under culture conditions.

ACKNOWLEDGEMENTS

The authors would like to thank Juan Otero, *Patrón* (Skipper) of the vessel “Bolvina”, to Cristina Bernárdez and Patricia Verísimo for their help in fieldwork and to Mauricio Urcera for his help in the extensive culture studies. This study was made possible by research grants XUGA10301B97 funded by the Dirección Xeral de Universidades e Investigación, Consellería de Educación e Ordenación Universitaria, Xunta de Galicia, and REN2000-0446MAR funded by the Spanish Ministerio de Ciencia y Tecnología (MCYT).

LITERATURE CITED

Balss, H. (1922). Crustacea VII: Decapoda Brachyura (Oxyrhyncha und Brachyrhyncha) und geographische Übersicht über Crustacea Decapoda.---In Michaelsen W. (Ed.), Beiträge zur Kenntnis der Meeresfauna Westafricas. Hamburg:Friedrichsen and Co., 3, 69 -- 110.

Botsford, L. W. (1985). Models of growth. Pp. 171--188. *in* Crustacean Issues, vol 3: Factors in adult growth. A. A. B. A. Wenner, ed. Rotterdam, Netherlands

Castro, M. (1995). Use of length-frequency analysis for estimating the age structure of the catch of *Nephrops norvegicus* (Crustacea: Nephropidae).---ICES Marine Science Symposium 199: 301--309.

Chambers, J. M. and T. J. Hastie (1992). Statistical models. Chapman and Hall. New York. 608 pp.

Corgos, A. (2004). Estrategia vital, estructura espacial y dinámica poblacional de la centolla, *Maja squinado* (Decapoda: Majidae). Departamento de Bioloxía Animal, Bioloxía Vexetal e Ecoloxía. Universidade da Coruña: Tesis Doctoral. 312 pp.

--- and J. Freire (submitted). 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.---ICES Journal of Marine Science.

Cruywagen, G. C. (1997). The use of generalized linear modelling to determine inter-annual and inter-area variation of growth rates: The cape rock lobster as example.---Fisheries Research 29: 119--131.

Donaldson, W. E., S. Byersdorfer, D. Pengilly and S. F. Blau (1992). Growth of red king crab, *Paralithodes camtschaticus* (Tilesius, 1815), in artificial habitat collectors at Kodiak, Alaska.---Journal of Shellfish Research 11: 85--89.

Drach, P. (1939). Mue et cycle d'intermue chez les crustacés décapodes.---Annales del Institut Océanographique, Paris 19: 103--391.

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

González-Gurriarán, E. (1981). Preliminary data on the population dynamics of the velvet swimming crab (*Macropipus pube*r L.) in the RÍa de Arousa (Galicia, NW Spain). ICES, Shellfish Committee. C.M. 1981/K:16**:** 21.

González-Gurriarán, E. (1985). Crecimiento de la nécora *Macropipus puber* (L.) (Decapoda, Brachyura) en la Ría de Arousa (Galicia, NW España), y primeros datos sobre la dinámica de la población.---Boletín del Instituto Español de Oceanografía 2: 33--51.

González-Gurriarán, E., L. Fernández, J. Freire and R. Muiño (1998b). 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.

---, ---, ---, --- and J. Parapar (1993). Reproduction of the spider crab *Maja squinado* (Brachyura: Majidae) in the southern Galician coast (NW Spain). ICES, Shellfish Committee. C.M. 1993/K:19**:** 15.

---, J. Freire, A. C. Fariña and A. Fernández (1998a). Growth at moult and intermoult period in the Norway lobster *Nephrops norvegicus* from Galician waters.---ICES Journal of Marine Science 55: 924--940.

---, ---, J. Parapar, M. P. Sampedro and M. Urcera (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. (2001). Growth in Crustacea - twenty years on.---Hydrobiologia 449: 111--122.

Iglesias, J., F. Sánchez, C. Moxica, L. Fuentes, J. J. Otero and J. L. Pérez (2002). Datos preliminares sobre el cultivo de larvas y juveniles de centolla *Maja squinado* Herbst, 1788 en el Centro Oceanográfico de Vigo del Instituto Español de Oceanografía.---Boletín. Instituto Español de Oceanografía 18(1-4): 25--30.

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

Le Foll, D., E. Brichet, J. L. Reyss, C. Lalou & D. Latrouite (1989). Age determination of the spider crab *Maja squinado* and the European lobster *Homarus gammarus* by $^{228}Th/^{228}Ra$ chronology: possible extension to other crustaceans. Canadian Journal of Fisheries and Aquatic Sciences 46: 720-724.

Le Foll, D. (1993). Biologie et exploitation de l'araignée de mer *Maja squinado* Herbst en Manche Ouest. Université de Bretagne Occidentale. IFREMER, RI DRV 93--030: 524 pp.

McCullag, P. and J. A. Nelder (1989). Generalized Linear Models. Chapman and Hall. London. 509 pp.

Neumann, V. (1998). A review of the *Maja squinado* (Crustacea: Decapoda: Brachyura) species-complex with a key to the eastern Atlantic and Mediterranean species of the genus.---Journal of Natural History 32: 1667--1684.

Sainte-Marie, B., S. Raymond and J.-C. Brêthes (1995). Growth and maturation of the benthic stages of male snow crab, *Chionoecetes opilio* (Brachyura: Majidae).---Canadian Journal of Fisheries and Aquatic Sciences 52: 903--924.

Sampedro, M. P. (2001). Crecimiento de la centolla, *Maja squinado* (Herbst, 1788) (Decapoda: Majidae). Departamento de Bioloxía Animal, Bioloxia Vexetal e Ecoloxía. Universidade da Coruña: Tesis Doctoral. 163 pp.

---, E. González-Gurriarán and J. Freire (2003). Moult cycle and growth of Maja squinado (Decapoda: Majidae) in coastal habitats of Galicia, north-west Spain.---Journal of The marine Biological Association of the United Kingdom 83: 995--1005.

---, ---, --- and R. Muiño (1999). Morphometry and sexual maturity in the spider crab Maja squinado (Decapoda: Majidae) in Galicia, Spain.---Journal of Crustacean Biology 19 (3): 578--592.

Somerton, D. A. (1980). Fitting straight lines to Hiatt growth diagrams: a re-evaluation.---Journal du Conseil international de l'Exploration de la Mer 39: 15-19.

Teissier, G. (1935). Croissance des variants sexuels chez L.---Travaux de l'Station Biologique de Roscoff 13: 99--130.

Wainwright, T. C. and D. A. Armstrong (1993). Growth patterns in the Dungeness crab (*Cancer magister* Dana): synthesis of data and comparison of models.---Journal of Crustacean Biology 13: 36--50.

Wilber, D. H. and T. P. Wilber. Jr (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.

Table 1. Comparison of the growth at moult of *Maja brachydactila* obtained using different methodologies: mark-recapture in the Ría de A Coruña and experimental conditions (laboratory and extensive culture). The following data are shown: mean growth (as the percentage of moult increment and moult increment in mm), standard deviation, minimum and maximum, minimum and maximum CL and number of specimens used in each study, distinguishing between sexes (M: males; F: females) and moult type (prepubertal vs. terminal).

Methodology		Mark-recapture							Laboratory							Extensive culture		
Moult		Prepubertal			Terminal				Prepubertal			Terminal						
Sex		M	F	Total	M	F	Total	Total	M	F	Total	M	F	Total	Total	M	F	Total
PMI	Mean	32.7	32.0	32.3	32.9	32.3	32.4	32.4	36.3	35.8	36.0	25.5	27.1	26.5	31.9	30.8	31.9	31.4
	SD	2.7	6.0	4.4	6.9	3.9	4.7	4.5	3.3	4.5	3.9	4.2	4.2	4.2	6.2	5.2	4.3	4.8
	Min	29.9	23.5	23.5	26.0	22.9	22.9	22.9	31.0	28.1	28.1	20.1	18.2	18.2	18.2	15.6	20.5	15.6
	Max	37.5	39.4	39.4	45.7	39.0	45.7	45.7	42.2	45.2	45.2	34.2	34.2	34.5	45.2	41.3	41.3	41.5
MI	Mean	31.5	26.8	29.1	34.9	36.2	35.8	33.5	27.9	28.0	28.0	27.5	29.6	28.8	28.3	27.3	29.9	28.6
	SD	5.1	5.4	5.5	6.8	3.6	4.5	5.8	3.5	3.1	3.3	3.1	4.5	4.1	3.6	5.9	3.7	5.1
	Min	22.4	19.1	19.1	29.9	26.5	26.5	19.1	22.0	20.6	20.6	23.0	18.7	18.7	18.7	15.0	21.0	15.0
	Max	36.9	32.4	36.9	47.5	42.1	47.5	47.5	34.6	32.9	34.6	34.6	37.6	37.6	37.6	44.0	42.0	44.0
Premoult CL																		
	Mean	96.2	83.8	90.0	106.9	112.7	111.2	103.9	77.2	78.9	78.1	108.9	109.4	109.3	91.6	89.8	94.7	92.2
	Min	73.1	76.1	73.1	93.7	97.2	93.7	73.1	61.3	65.5	61.3	94.4	89.4	89.4	61.3	62.0	73.0	62.0
	Max	112.8	94.3	112.8	119.5	130.0	130.0	130.0	96.7	93.6	96.7	118.5	122.8	122.8	122.8	160.0	128.0	160.0
	N	6	6	12	6	17	23	35	18	20	38	18	11	29	67	60	60	120

Table 2. Results of the Generalized Linear Model 1 fitting the PIM data which include the three growth studies (mark-recapture, laboratory and extensive culture). The models were fitted using a log-link with normal distribution of error. Degrees of freedom, Wald statistic (W), significance level and the coefficients of each effect are given. The main effects are premoult CL, sex and study method. The coefficients express the difference between each factor level and the first level (the one does not included in parentheses).

Effect	Coefficient	S. E.	D.F.	W	p
Sex (F)	0.054	0.069	1	0.608	0.435
Methodology 1 (Mark-recapture)	-0.274	0.120	2	14.862	0.001
Methodology 2 (Laboratory)	0.315	0.083			
Premoult CL	-0.005	0.001	1	55.133	0.000
Interactions					
Sex (F) x Methodology (MR)	-0.066	0.120	2	4.104	0.128
Sex (F) x Methodology (LAB)	-0.079	0.083			
Sexo (F) x premoult CL	0.000	0.001	1	0.432	0.511
Methodology (MR) x premoult CL	0.003	0.001	2	17.141	0.000
Methodology (LAB) x premoult CL	-0.004	0.001			
Sex (F) x Methodology (MR) x premoult CL	0.001	0.001	2	3.306	0.191
Sex (F) x Methodology (LAB) x premoult CL	0.001	0.001			

Table 3. Results of the Generalized Linear Model 2 fitting the PIM data which include the mark-recapture and laboratory studies. The models were fitted using a log-link with normal distribution of error. Degrees of freedom, Wald statistic (W), significance level and the coefficients of each effect are given. The main effects are pre-moult CL, sex, moult type and study method (only mark-recapture and laboratory). The coefficients express the difference between each factor level and the first level (the one does not included in parentheses).

Effect	Coefficient	S. E.	D.F.	W	p
Sex (F)	-0.099	0.148	1	0.445	0.505
Moult (prepubertal)	-0.324	0.148	1	4.788	0.029
Methodology 2 (MR)	-0.205	0.148	1	1.919	0.166
Premoult CL	-0.005	0.002	1	12.720	0.000
Interactions					
Sex (H) x Moult (pre)	0.162	0.148	1	1.202	0.273
Sex (F) x Methodology (MR)	0.106	0.148	1	0.511	0.475
Moult (pre) x Methodology (MR)	-0.114	0.148	1	0.595	0.440
Sex (F) x premoult CL	0.001	0.002	1	0.313	0.576
Moult (Pre) x premoult CL	0.003	0.002	1	4.708	0.030
Methodology (MR) x premoult CL	0.003	0.002	1	2.799	0.094
Sex (F) x Moult (pre) x Methodology (MR)	-0.203	0.148	1	1.890	0.169
Sex (F) x Moult (pre) x premoult CL	-0.002	0.002	1	1.292	0.256
Sex (F) x Methodology (MR) x premoult CL	-0.001	0.002	1	0.313	0.576
Moult (Pre) x Methodology (MR) x premoult CL	0.001	0.002	1	0.223	0.637
Sex (F) x Moult (Pre) x Methodology (MR) x premoult CL	0.002	0.002	1	1.838	0.175

Table 4. Mean time elapsed between the tagging and recapture of crabs that moulted once in the interval between tagging and recapture (omitting crabs that were recaptured the same month and one specimen that did not grow after 324 days) differentiating among moult type (prepubertal vs. terminal) and juveniles that did not grow between tagging and recapture.

Moult	Mean	N	SD	Min	Max
Prepubertal	86.7	10	40.22	28.0	128.0
Terminal	133.7	21	42.04	70.0	238.0
No moult (juveniles)	50.4	384	32.99	20.0	206.0

FIGURE CAPTIONS

Figure 1. Relation between PIM and pre-moult CL obtained by fitting GLM model 1. Only variables having a significant effect in model ($logPIM = b_0 + b_1 \cdot CLpre + b_2 \cdot study + b_3 \cdot CLpre \cdot study$) are included.

Figure 2. Relation between PIM and pre-moult CL obtained by fitting GLM model 2. Only variables having a significant effect in model ($logPIM = b_0 + b_1 \cdot CLpre + b_2 \cdot muda + b_3 \cdot muda \cdot CLpre$) are included.

Figure 3. Seasonality of the intermoult period in juvenile males and females captured in shallow waters. Minimum intermoult time was estimated on the basis of recaptured crabs that did not moult between tagging and recapture. Each segment represents a specimen and the start and finish dates indicate the time of tagging and recapture. Specimens recaptured during the same month that they were tagged or specimens that did not grow between tagging and recapture are not represented. In cases where specimens had a similar size and date, only one is shown.

Figure 4. Seasonality of the intermoult period on the basis of mark-recapture data. Each segment shows the mark-recapture record of an individual crab. The CL at the time of tagging is given. Points represent the time of tagging and recapture. Horizontal lines indicate that the time of moulting is not known and vertical lines show the early post-moult stage at the time of tagging and/or recapture (i.e., the proximity of moulting). For crabs in post-moult stage at the time of tagging, the pre-moult CL was estimated by assuming a percentage of moult increment of 32%.

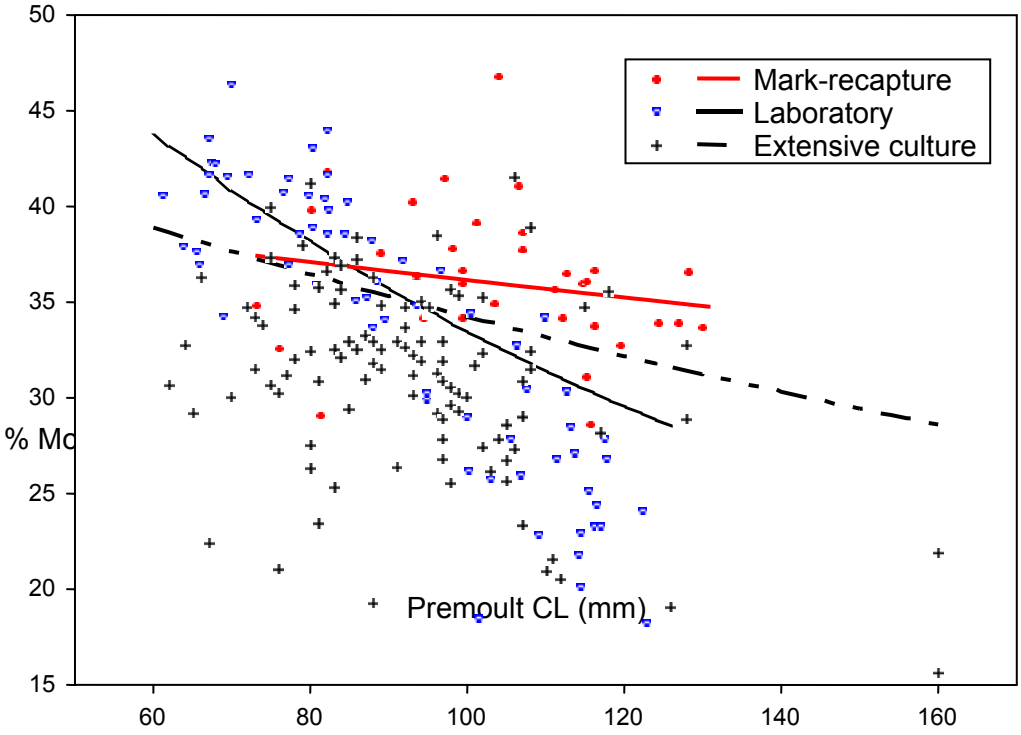

Figure 1. Corgos *et al*., Growth at moult of *Maja Brachydactyla*.

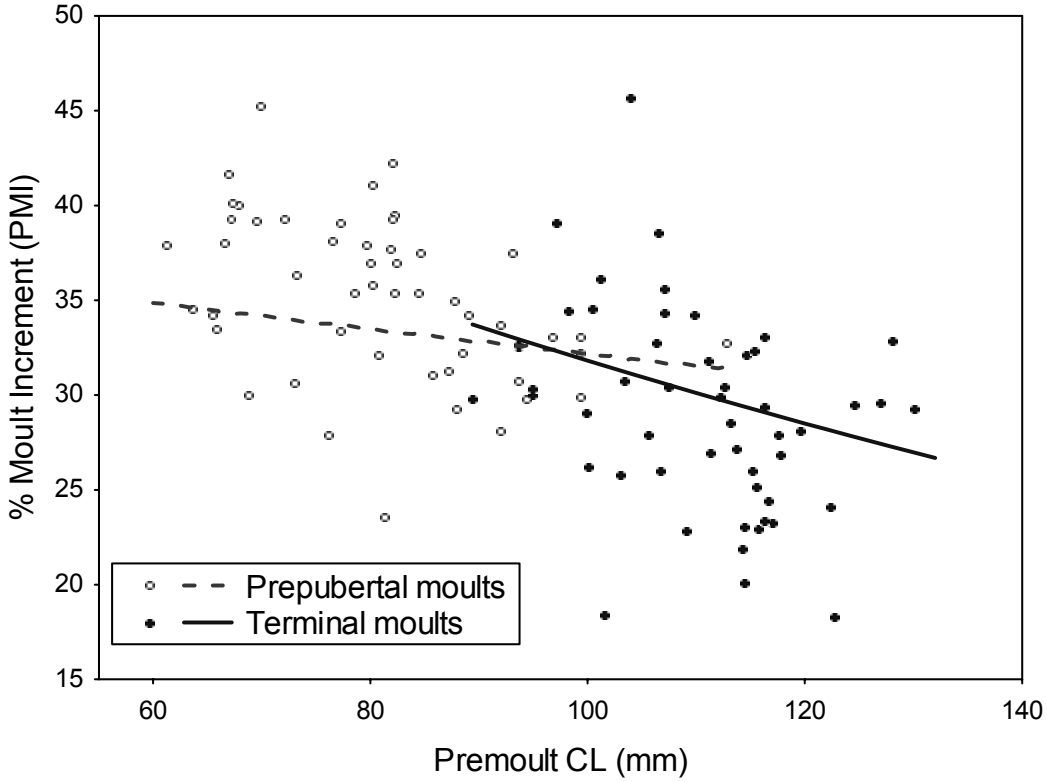

Figure 2. Corgos *et al*., Growth at moult of *Maja Brachydactyla*.

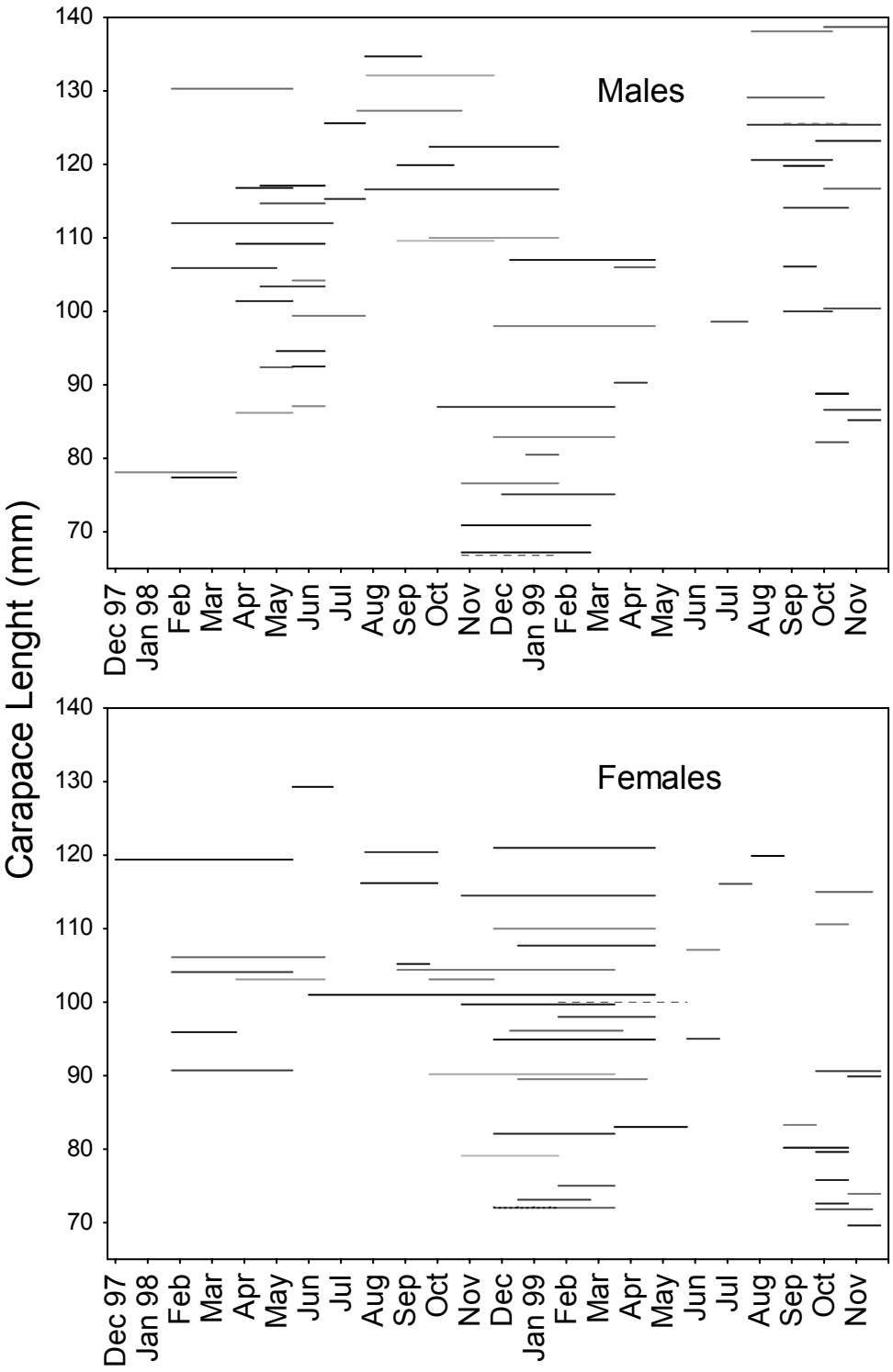

Figure 3. Corgos *et al*., Growth at moult of *Maja Brachydactyla*.

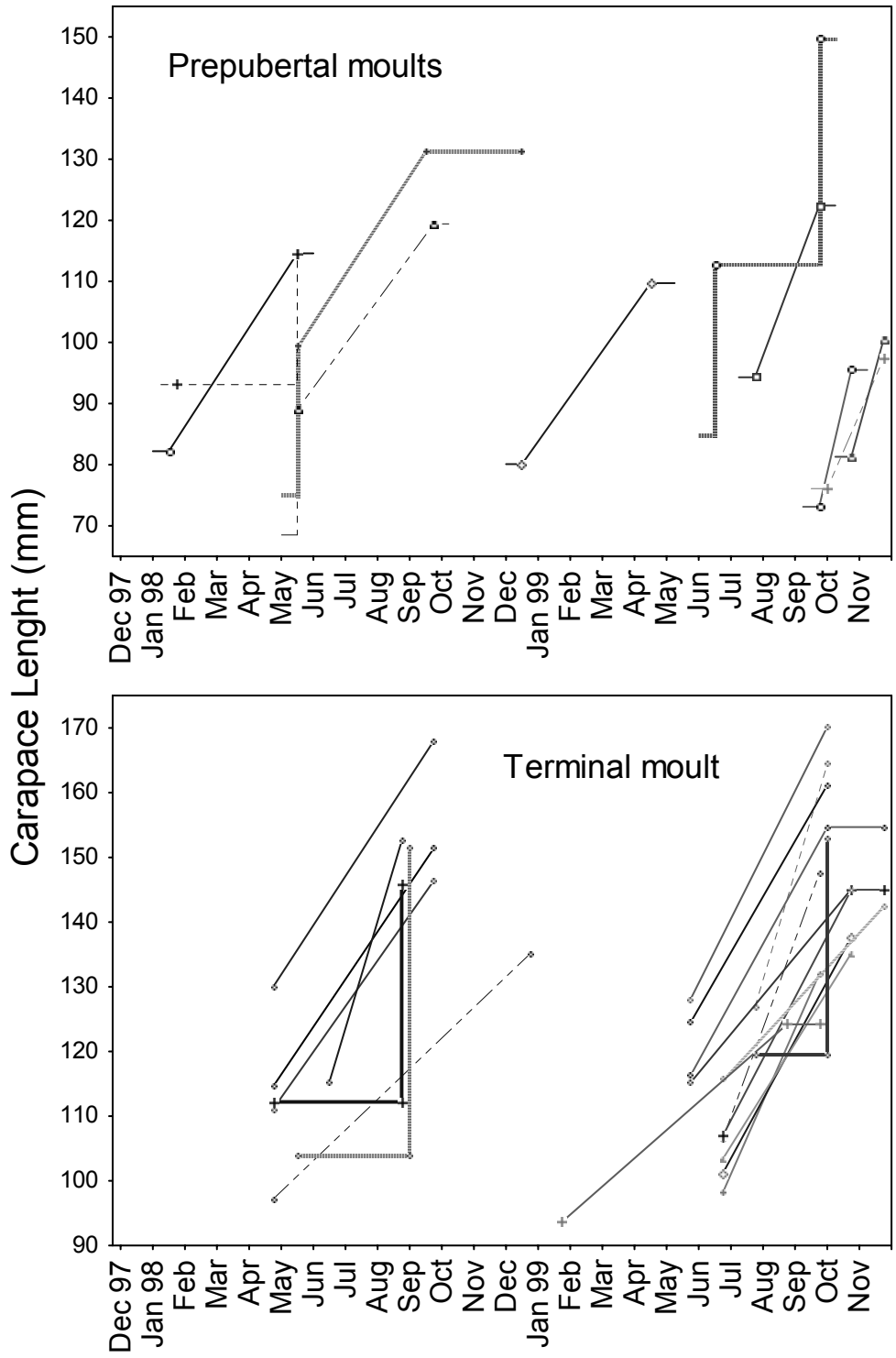

Figure 4. Corgos *et al*., Growth at moult of *Maja Brachydactyla*.