

Timing and seasonality of the terminal moult and mating migration in the spider crab, *Maja brachydactyla*: evidence of alternative mating strategies

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Abstract

Timing and synchronisation at individual and population levels of the processes related to the terminal moult, gonad maturation, accumulation of energy reserves and migration in the spider crab *Maja brachydactyla* are analyzed. Also, the intra- and intersexual variability is established. Two hypotheses are tested to explain the temporal and population variability: 1) physiological hypothesis: males and females begin migration when they reach the appropriate physiological stage (the optimum level of energy reserves); and 2) mating opportunities hypothesis: the timing of the migration maximise mating opportunities and mate quality. Our results show that males carry out the terminal moult before females, the former having a peak in July and the latter in August. The onset of gonad maturity in females occurs between two and three months after they have reached morphometric maturity (starting in October), coinciding with the period prior to and during the mating migration to deep waters. In an analysis of the spermathecae of primiparous females, it was found that practically no mating activity occurred in shallow waters, while the first copulations took place in the migration corridor. However probably most of the mating activity occurs in deep mating grounds. Males reached gonad maturity prior to morphometric maturity. On average, males started migrating on 8 October, while females began migration on 16 October, which would corroborate previous evidence pointing to an earlier starting date for males. No differences were observed in the physiological status

(muscle, gonad and hepatopancreas relative mass) between migrating and non-migrating crabs, which is a clear indication that the physiological hypothesis does not hold true for this species. A higher percentage of postmoult crabs were caught in the migration corridor than in shallow waters. The physiological condition improved over time in both males and females in the specimens caught in the shallow area as well as in the migration corridor. Therefore, the crabs that start migrating first did so in poorer physiological condition. Moreover, the early migrators had a significantly lower mean size than the late migrators. Our results would suggest that variability within populations and between sexes is related to the different reproductive strategies and not to a physiological limitation. Thus, the poor-quality males (with a reduced competitive ability) would migrate at the beginning of the season (prior to or in synchronisation with the first females), whereas the high-quality males might delay migration until they have accumulated a high level of reserves, because they would be able to displace low-quality males at mating habitats.

Keywords: reproductive strategies, physiological condition, mating opportunities, migration, decapod crustaceans

INTRODUCTION

Juveniles of *Maja brachydactyla* (see Neumann, 1998 for taxonomic status, corresponding to the North Atlantic species previously known as *M. squinado*) live primarily in shallow waters (González Gurriarán & Freire, 1994; Hines *et al.*, 1995; Le Foll, 1993; Meyer, 1993; Sampedro, 2001; Freire *et al.*, 2002). During the summer of their second or third year of life (depending on the recruitment season) these crabs carry out the terminal moult, associated to the onset of sexual maturity (Corgos, 2004; Corgos and Freire, submitted; Corgos *et al.*, submitted; Freire *et al.*, 2002; González Gurriarán *et al.*, 1995; Le Foll, 1993; Meyer, 1993; Sampedro *et al.*, 1999). Between late summer and early autumn adult specimens carry out a reproductive migration to deep waters, as has been observed in different areas on the European coast (Camus, 1983; Edwards, 1980; Freire & González Gurriarán, 1998; Freire *et al.*, 1999; González Gurriarán & Freire, 1994; Kergariou, 1976, 1984; Latrouite & Le Foll, 1989; Le Foll, 1993; Meyer, 1993; Stevcic, 1973). Although information is scarce on the mating behavior of the spider crab in the field, on the basis of available evidence mating is known to take place mainly in deep waters, where aggregations could be formed (González Gurriarán *et al.*, 2002). The terminal moult,

gonad maturity, migration and mating are factors that are closely interrelated and play an important role in the life history of the spider crab, since they will determine drastic changes in the spatial structure and demography of the populations and are fundamental in terms of reproductive success.

It has been widely documented that migrating animals store energy reserves before they begin to migrate in order to ensure the success of the migration (Dingle, 1996). In the spider crab, migration entails a drastic change in activity (rapid movements of over 1-10 km·day⁻¹, after a juvenile phase with only small-scale movements (10s or 100s m·day⁻¹, Freire & González Gurriarán, 1998; González Gurriarán & Freire, 1994; González Gurriarán *et al.*, 2002; Hines *et al.*, 1995). This migration, however, takes place after the terminal moult –a critical process physiologically and energetically. Therefore, during a short period directly after the moult and prior to migration, the processes related to the recover after ecdysis and the storage of the energy needed for migration must be carried out. Differences between males and females in the timing of migrations in other geographic areas have been reported; particularly the fact that males start to migrate before females (Stevcic, 1973). This differential behaviour may be related to the reproductive strategies of the two sexes, as has been observed in other vertebrate species and other arthropods (Morbey & Ydenberg, 2001) .

Spider crab males compete for females, which gives rise to agonistic interactions (information based on direct observations by fishermen of occasional matings in shallow waters), and females may mate with several males (González Gurriarán *et al.*, 1998). Information based on observations of the mating activity of crabs held in captivity and at sea would indicate that both males and females mate in hard carapace condition (no mating has ever been observed immediately after the moult). It is possible for ovigerous females to mate, and courtship prior to copulation does not take place, nor does pre- or post-copulatory mate guarding (González Gurriarán *et al.*, 1998). This mating behaviour differs from the characteristics defined for other majids (Claxton *et al.*, 1994; Jones & Hartnoll, 1997; Sainte-Marie *et al.*, 1999). The fact that females have a hard carapace during mating determines the characteristics of the mating system. On the one hand, it means that it is not necessary for these crabs the existence of mate guarding aimed at protecting females with a soft carapace from predators (e.g. Hartnoll, 1969; Jivoff, 1997a; Wilber, 1989) and/or ensuring the paternity of the brood (Diesel, 1991; Jivoff, 1997a), although postcopulatory

mate guarding have been observed in hard-shell females of *Chionoecetes opilio* (Claxton *et al.*, 1994). On the other hand, in the case of the spider crab, all the adult females are receptive, which means that the operative sex-ratio, defined as the number of sexually active males versus the number of fertilisable females (Emlen & Oring, 1977), is equal to the effective sex-ratio.

The timing and synchronisation of the biological processes associated with reproductive migrations, at the individual and population levels, and the sexual differences observed in the spider crab may be explained by two sets of alternative hypotheses:

- Physiological hypothesis: males and females start migrating when they have reached the appropriate physiological status (an optimum level of energy reserves). Therefore the variability within populations and sexes would be related to the physiological stage, depending on the timing of the terminal moult and the energy recovery rate. Both processes may be variable between sexes, with the energy needed for reproduction, and among body sizes.

- Mating opportunity hypothesis: the timing of the migration should maximise mating opportunities and mate quality. Once a minimum physiological condition is reached, males would migrate at the appropriate time to intercept and mate with the greatest possible number of females in the mating habitats (in the spider crab these would include zones where females may be intercepted during migration and/or in deep waters). For females the optimum strategy would be to mate with the best-quality available males. The variability within populations and sexes would be related to different reproductive strategies and not to a physiological restriction (possibly once a minimum level of energy reserves has been reached). According to this hypothesis, the intrasexual variability would be determined by the inter-individual differences in quality.

The present study is a detailed analysis of the timing and synchronisation at the individual and population levels of processes related to the terminal moult, gonadal maturation, accumulation of energy reserves and migration in the spider crab. Intra- and intersexual and intra-population variability in the above processes are analyzed. Our results will allow to compare, at least in part, the hypotheses proposed above related to the causes of the

timing and synchronization of the processes linked to migrations. Specifically, the following predictions will be tested:

- Physiological hypothesis: 1) The physiological condition of the postpubertal adults caught in the migration corridor would be better than that of crabs still remaining in shallow waters. This pattern should be observed throughout the entire migration period. The physiological condition during the migration season would improve gradually in crabs from shallow waters, while it would remain relatively constant in time in individuals captured in the migration corridor (Figure 1). 2) Sexual differences in timing would depend on the differential physiological condition of each sex, related to differences in the timing of the terminal moult.

- Mating opportunity hypothesis: 1) At any given moment, crabs in migration and in shallow waters would not necessarily exhibit any differences in their physiological condition. 2) Poorer quality males would migrate earlier and possibly before females to maximise their encounter probability. In both males and females poorer quality individuals (in the case of crustaceans this refers to animals having a smaller body size and/or lower robust physiological condition) would carry out migration earlier to maximise the possibility of mating encounters. Therefore, the physiological condition would improve throughout the migration period in both shallow waters and the migration corridor.

From the standpoint of males, mating probability depends on the abundance of females and on the competition among males, which means that the temporal distribution of mating opportunities throughout the season is probably unimodal. At the beginning, mating probability would be low owing to the absence of females in the mating zones. As females start arriving, these odds would likely increase until they reached a maximum value. Then the probability would diminish, since the density of males would attain a maximum and the competition among them would cause mating probability to decrease (Figure 2).

According to the mating opportunity hypothesis, early migrating males would be smaller and have a poorer physiological condition, but they would be the first to arrive at the mating zones. Besides being able to mate with females during migration, they would have a higher probability of mating with the first females to arrive at the mating zones (Figure 2, A). The density of females would increase over time, but so would the density of males, so

the percentage of intercepted females would gradually decline due to the competition (Figure 2, B), until it reached a minimum level that would coincide with the maximum density of males (Figure 2, C).

Late migrating males would arrive at the mating zones later, but they would be larger in size and in stronger physiological condition, which means that they would be better competitors than the early migrators. As density of females increases, the mating probabilities of these males would increase (Figure 2, B) until a maximum value is reached, coinciding with the maximum density of females in the zone (Figure 2, C).

MATERIAL AND METHODS

Monthly samplings were carried out between December 1997 and November 1999. From late summer until autumn, sampling effort was increased to obtain more detailed information on the migration of adults. Sampling was carried out using experimental traps (50 cm height, with upper and lower diameters of 110 cm and 100 cm respectively, and an entry of 22 cm and a 50 mm mesh, Corgos & Freire, submitted). The sampling area was the Ría de A Coruña, a small oceanic bay located off the NW coast of Galicia (NW Spain). One shallow water (5-15 m) sampling station was selected in the inner area of the ría (Bastiagueiro) and another one in deeper waters (25-30 m) in the central channel of the ría, which constitutes the migration corridor for postpubertal adults. In the inner area of the ría, where there is high abundance of *Maja brachydactyla*, sampling was carried out along a transect on the longitudinal axis of the ría where seven tows were carried out deploying the traps parallel to the coast. Tows were separated approximately 180 m from each other (Figure 3).

The following data were recorded for each specimen captured: sex, morphometric maturity (Corgos, 2004; Corgos & Freire, submitted; Sampedro *et al.*, 1999), stage of the intermoult cycle (estimated by the hardness of the exoskeleton and the presence of a new internal carapace in crabs approaching moult, Sampedro *et al.*, 2003), and the relative age on the basis of the degree of epibiosis and carapace wear (see Fernández *et al.*, 1998), to distinguish the recent postpubertal adults from specimens that had reached maturity in previous years.

To analyze the reproductive stage and physiological condition of males and females, adult females and juvenile and adult males were sampled monthly from July to December 1998 (morphology of the abdomen makes possible to determine the maturity stage directly in females; Sampedro *et al.*, 1999). The maturity stage of males was determined later on the basis of their morphometry. Samples were obtained from both shallow areas and the central channel, although for several reasons in the channel data were obtained only for females in September and November, and for males in November. Males with CL > 60 mm were selected and divided into size classes of 20 mm with a final class of specimens of over 160 mm. A sample made up of a maximum of 10 males belonging to each size class captured in the shallow area was transported to the lab. A sample of 5 males from the three larger size classes was obtained from the captures in the channel, since smaller-sized crabs were not caught in this area. Adult females with a CL greater than 100 mm were selected and grouped into size classes of 40 mm and a sample of 5 specimens from each size class of crabs caught both in the shallow area and the channel was taken to the lab.

The crabs were dissected to determine the gonadal maturity stage in females (following the classification proposed by González Gurriarán *et al.*, 1993, 1998), gonad dry weight, fullness and the number of sperm masses in the spermathecae in the case of females (following the classification proposed by González Gurriarán *et al.*, 1993, 1998), and the presence of spermatophores and gonadal dry weight in males. The gonad, hepatopancreas and the muscle of the second right-hand pereiopod of each specimen were extracted and held for 48 h at 60 °C to obtain the dry weight (Corgos and Freire, submitted). Morphometrically juvenile males were omitted from the analysis of the physiological condition.

Data analysis

The energetic status of each individual was estimated by means of condition indices (CI) based on the dry weight of the gonad, muscle and hepatopancreas. The condition indices were estimated as the residuals of an allometric regression ($\text{Log } Y = \log a + b \cdot \log \text{CL}$) of the dry weight of each type of tissue respect to the carapace length (Figure 4). The regressions were fitted to the data from the adult specimens caught between June and December 1998. Multiparous adults and juveniles were not included in the analyses.

To test differences in the condition indices between migrators and non-migrators over time, according to the predictions from the hypotheses, the time series corresponding to the condition indices of the crabs captured in shallow waters was fit to a second order polynomial regression: $CI = a + b \cdot \text{date} + c \cdot \text{date}^2$. Next, the condition index from specimens captured in the channel (these data were only obtained in some of the months) were compared the trend of with data from Bastiagueiro. Significant differences between the two areas were accepted when the mean CI of the channel fell outside the 95% confidence band of the regression for the shallow area.

The moult stage was used as an additional body condition indicator, since the crabs in postmoult are in poorer condition than those in the intermoult or premoult stage. The differences in the moult stage between migrators (early and late) and non-migrators were determined by means of a log-linear analysis on the frequency of males and females in postmoult in Bastiagueiro and in the channel in September and October 1998.

Based on data on catch-per-unit-effort (CPUE; crabs-trap⁻¹) collected while sampling the channel between July and December 1998, the mean starting date of migration was estimated, considering that the adults captured in the channel had recently begun to migrate. The mean date was obtained as the average of the sampling dates weighted by the CPUE.

An analysis of variance (ANOVA) was performed to test differences on the mean body sizes of the migrators and non-migrators, using data from males and females caught in Bastiagueiro and the channel in September and October 1998.

RESULTS

Seasonality and sexual differences in the terminal moult

Adult males in postmoult began to appear in the catches from Bastiagueiro in April, with their abundance undergoing a rapid increase, reaching high levels in June and a maximum in July. In September, the abundance of postmoult adults dropped sharply and continued to decrease more gradually until the complete disappearance of these crabs in December (Figure 5). Postmoult females began to be caught in shallow waters in July, attaining

maximum abundance in August. They dropped sharply in September and had practically disappeared by October (Figure 5). The pattern was repeated in both 1998 and 1999 and males were found to carry out the terminal moult one month earlier than females. The maximum numbers of postmoult adult males and females were found in July and August respectively. The terminal moult period in males lasted longer than in females (postmoult males were found from April until November in 1998) In 1999, there would seem to be greater synchronisation, since adult males did not were caught until June.

Gonadal development and mating

Adult females 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 were in stage I) and until November females did not attain more advanced developmental stages (II and III). No females were found with gonads in an advanced stage of development (IV) in either the shallow area or in the channel. In the channel 64% of the females had gonads in stage II and 27% in stage III between November and December. Therefore in females the gonads began to mature between two and three months after the terminal moult, during the period immediately preceding or during their migration to deep waters.

The analysis of the spermathecae of primiparous females revealed that the number of matings in the shallow zone was very low, since 97% of females (N=124) showed empty spermathecae. An increase in mating frequency was observed in the channel, given that over 21% of the females studied (N=23) had mated. These results would indicate that mating may be carried out in the migration corridors, but most likely it is in the deep waters where most of the mating activity takes place (Table 1). All the females analysed exhibited a single sperm mass. In the shallow area, in contrast, two multiparous females that were captured had 7 sperm masses in each spermatheca, presenting differences in colour and volume, which would point to the existence of long intervals between matings (González-Gurriarán *et al.*, 1998).

After examining the gonads of the male crabs, it was evident that, unlike the females, gonadal maturation takes place prior to morphometric maturity. Over 60% of the juveniles examined (N=382) had spermatophores, and more than 76% of the juveniles with a CL >

96 mm as well as all of the morphometrically mature crabs had spermatophores. Therefore, males are functionally mature and ready to mate immediately after the terminal moult (see Corgos and Freire, submitted).

Sexual differences in the timing of the start of migration

On the basis of the sampling carried out in the inner ría, it was possible to carefully monitor the small-scale movements of the adults and the start of their migration (Figure 6). In July 1998 the mean CPUE of males was much greater than that of females (4.2 and 0.5 crabs-trap⁻¹ respectively). Males were also found to be scattered around the innermost part of the ría and near the shoreline. In August the average CPUE of females found in the inner ría increased (3.8 crabs-trap⁻¹), and males had moved to the outermost zone near the channel. By September, the large concentration of males in the outer part of the inner area had disappeared, which would imply that they had started migration, whereas the females had moved to the outer zone. In October, the few males left in the area started moving to the outer zone and leaving the area, while the females were concentrated in the outer part of the shallow area. In November, the catches yielded few adults, although some females were still found in the outermost area, which means that the females migrated between October and November. By December practically all the adults had left the area.

The catches taken in the channel confirm this seasonal migratory pattern (Figure 7). They were concentrated in the months of September and October; however maximum catches of males were obtained in September and those of females in October. Males exhibited a broader migratory period than females (Figure 7), with stable catches between 25 September and 23 October. The first females, on the other hand, were caught on 25 September, from which time catches increased gradually until they reached a clear peak on 23 October. On average males started migrating on 8 October, while females did so on 16 October.

Body condition at the start of migration

From July to December, adult males in Bastiagueiro underwent a progressive increase in the relative weight of the muscle, gonad and hepatopancreas (Figure 8). It was only possible to compare the physiological condition in the channel zone (migrators) and

shallow area (non-migrators) in November. During this month migrators presented condition indices similar to those of non-migrators in all the tissues analysed.

The condition index in females found in the shallow areas showed a gradual increase in the case of the gonad, but this was not so in the case of the muscle or hepatopancreas (except for very low values in the latter tissue in September). The adult females captured in the channel had slightly higher gonad condition values in November as compared to the shallow zone, while no differences were observed in September (Figure 9). The physiological condition of the muscle was similar in November, which was the only month in which information was available for the channel. The physiological condition of the hepatopancreas, however, was similar in the two areas in both September and November.

The percentage of postmoult males and females in each zone was higher in September than October (Figure 10), and in both months the percentage was higher in the channel than in Bastiagueiro (log-linear analysis of the effects of sampling station, date and sex on the percentage of specimens in the postmoult stage, showed the significant variables to be sampling station and date, $X^2=5.53$, $p = 0.35$). This would imply that the condition of the early migrators is poorer than crabs that migrate later.

Body size at the start of migration

The mean size (CL) of males and females was compared between Bastiagueiro and the channel in September and October. Females were significantly larger than males, and in Bastiagueiro as well as in the channel for both males and females, the largest sizes were found in October (ANOVA, $N=1198$; effect of date and sex $p<0.001$; effects of sampling station and all interactions, $p>0.2$). None of the interactions proved to be significant, which was an indication that the smaller-sized specimens of both males and females started migrating earlier (Figure 11).

DISCUSSION

The present study provides evidence as to the existence of synchronisation in the timing of the terminal moult, gonadal development and migration in the spider crab. The inter- and

intrasexual differences related to these phenomena may reflect different types of behaviour and reproductive strategies that would be compatible with the mating opportunity hypothesis discussed above. However, our results contradict some of the predictions made in the physiological hypothesis.

In order to mate, an organism must be in the appropriate physiological condition, as well as having a suitable location in space and time (Correa & Thiel, 2003). In *M. brachydactyla*, males probably reach maturity and develop gonads before females in order to be physiologically prepared to mate at the time and place where the encounter with the adult female occurs. Considering the date when migration starts and the fact that in December and January, ovigerous females begin to appear in the catches in the shallow areas (unpublished data), aggregation and mating in deep waters must occur over the course of a short period. As females have spermathecae, they are able to mate when their gonads are in early stages of development, fertilising the broods later.

In the Ría de A Coruña, the terminal moult takes place in shallow waters between April and August. Males undergo the terminal moult one month earlier than females. González Gurriarán *et al.* (1995) obtained similar results with this species under culture conditions, while in more northern latitudes, the cycle is delayed, owing possibly to the differences in the thermal regime. In the English Channel the crabs undergo the terminal moult in late summer and early autumn and adults that have recently reached the postpubertal stage start to be captured in August-September, presenting maximum catches in early autumn (Le Foll, 1993; Meyer, 1993).

Considering that the mean duration of the migration to deep waters was estimated to be 5.7 days (ranging between 2 and 14 days) in the Ría de Arousa (González Gurriarán *et al.*, 2002), the fact that adults were caught in the channel during a period of roughly 30 days would clearly point to the existence of individual differences at the time migration begins. In our study area males began to migrate on average eight days before females (8 and 16 October respectively). Using telemetry, González Gurriarán *et al.* (2002) estimated the mean date of the start of migration for females in the Ría de Arousa to be 1 November 1996, although according to more recent studies, the average starting date of migration varied slightly (10 October in 1998, 26 September in 1999, and 30 September in 2000 in

the Ría de Arousa, and 29 September in 2000 in the Ría de A Coruña) (Bernárdez and González Gurriarán, personal communication).

If we consider the mean starting date of migration in both areas sampled (Figure 12), there would seem to be a high level of spatial synchronisation within the same year (see 1998 and 2000 in Coruña and Arousa), and the interannual variability was around 36 days. Therefore the start of migration would appear to be triggered by or produced in response to oceanographic or environmental phenomena (González Gurriarán *et al.*, 2002; González Gurriarán & Freire, 1994; Freire *et al.*, 1999).

Stevcic (1973) reported that males left the shallow areas of the Adriatic Sea before the females, although migration took place much earlier than in our study area (April and May). In the English Channel, migration occurred between September and January (Le Foll, 1993). Thus, considering the average duration of migration in this geographic area, individual differences may also take place at the start of migration, although the autor does not examine this aspect in detail.

The earlier arrival of males to the mating zones is a phenomenon known as protandry (Morbey & Ydenberg, 2001). In our study, males started migrating, on average, before females, and it is therefore quite likely that at first there is a higher proportion of males in the mating zones. An analysis of the captures in the channel during the migration shows that over the entire period both males and females migrated, as would be expected in a species where the females are polyandric (Zonneveld, 1992). In view of the captures obtained in the migration corridor, males were found to have a broad migration period without a specific peak, whereas females, which started migration at the same time as males, exhibited a clear peak on 23 October 1998, after which catches were virtually non-existent. These results indicate that the migration of males is not as synchronised as that of females, rather males carried out migration gradually over a 30 day period, while most females migrated between 15 and 28 October 1998.

Mating takes place generally after migration in the deep-water wintering habitats, although copulation could occur also during migration (21% of the females caught in the channel had sperm in the spermathecae). These data largely coincide with those reported by González Gurriarán *et al.* (1998) in the Ría de Arousa, where the spermathecae of 100% of

the primiparous females caught in the shallow zone were found to be empty. On the other hand, catches of multiparous females having several sperm masses, along with direct observations by fishermen, support the hypothesis that mating does occur in shallow waters, but probably restricted to multiparous females. In latitudes located farther to the north, matings were observed in shallow waters from May to July on the Irish coast (Brosnan, 1981), and starting in June on the French coast (Kergariou, 1984). On the basis of these observations, these authors report that mating generally occurs in summer, although to support this hypothesis, it would be necessary to carry out an analysis of the spermatheca content of females in wintering habitats.

The analysis of catches in the shallow area and the migration corridor and condition indices may be used as indicators of the reproductive strategies of *M. brachydactyla*. The condition indices of the tissues analysed were similar in the shallow area and the migration corridor, i.e., no differences were observed in the body condition between migrators and non-migrators, which would clearly imply that the physiological hypothesis is not supported in this case. The physiological condition increased over time in males and females both in crabs caught in Bastiagueiro and in the migration corridor. Consequently, crabs that migrate first, do so in poorer physiological condition. Moreover, the early migrators were smaller in size than the late migrators. These evidences support the mating opportunity hypothesis. Poorer quality males (smaller sized and in poorer physiological condition) migrated earlier, which gives them mating opportunities that would not be feasible if they had to compete with the late migrators, which are larger in size and in better physiological condition.

In both majids (Conan & Comeau, 1986; Elner & Beninger, 1995; Ennis *et al.*, 1990; Sainte-Marie *et al.*, 1997; 1999; Rondeau & Sainte-Marie, 2001; Stevens *et al.*, 1993) as well as other decapods (Correa *et al.*, 2003; Jivoff, 1997b; Van Der Meeren, 1994; Wada *et al.*, 1997) agonistic interactions have been observed between males prior to mating, in which the large-sized individuals exclude the smaller ones. At other times the small males are rejected by the females (Goshima *et al.*, 2000). For this reason the larger-sized males are more likely to mate than the smaller-sized animals. This hypothesis is corroborated by observations in the field, where mating majid males were seen to be generally larger than the females (Brosnan, 1981; Conan & Comeau, 1986; Ennis *et al.*, 1988; Paul, 1992; Powell *et al.*, 1972).

Encounters of a male with females and other males may provide sociosexual (the potential number of mating opportunities and the level of competition from other males) and determine, at least in part, the mating strategies used by males (Wada *et al.*, 1999). In the spider crab, it might be that, in addition to the number, males also use information related to the size of other males to decide the timing of the start of the migration. Furthermore, it may even be hypothesised that juveniles use this information to decide when to carry out the terminal moult, since a great deal of evidence, such as the broad overlapping size range between juveniles and adults or the large interindividual differences in the duration of the intermoult period (Corgos, 2004; Corgos *et al.*, submitted) support this hypothesis.

The less competitive (smaller-sized) male decapod crustaceans tend to avoid direct agonistic encounters with larger males (Clark, 1997; Ra'anan & Sagi, 1985) and they adopt alternative mating strategies such as intercepting females moving to the mating areas (Van Der Meeren, 1994), or copulating quickly while two dominant males are competing for a receptive female (Clark, 1997; Correa *et al.*, 2003). In the present study the less competitive males migrated earlier to the mating zones probably to be able to copulate before the more competitive males arrived.

In other majids such as *Chionoecetes opilio* (Sainte-Marie *et al.*, 2000) and *Inachus phalangium* (Diesel, 1990), the sperm masses are stored dorsoventrally in the spermathecae when they are not too full, i.e., the last sperm mass is stored closer to the oviduct. This stratification favours that the sperm of the last male fertilize the brood, and therefore the paternity is attributed to only one male. In both species males used several strategies to promote their own paternity. Males of *C. opilio* invest more sperm in females that had mated previously than in virgin females in order to displace and isolate the sperm deposited earlier (Rondeau & Sainte-Marie, 2001), while males of *I. phalangium* displace previously deposited masses by transferring large amounts of seminal plasma which hardens forming a gel that completely seals off the previously deposited masses (Diesel, 1990). All of these strategies favour the paternity of the last male to mate with a female. In our study, the high-quality males (larger and in better physiological condition) would be the last to mate. In *M. brachydactyla*, however, the arrangement of the sperm masses is different than what was observed in the above species. When several masses are present, they are arranged parallel to the main axis of the spermathecae, and if the spermathecae are

full, the arrangement is not stratified (González Gurriarán *et al.*, 1998; Freire, unpublished data). Although all of these authors reported some differences in the size of the masses, they were attributed to different storage time or the possibility of having been used in part to fertilise a brood, and not to the existence of sperm competition. On the basis of these findings, there is no evidence that the last males to mate (those of better quality) have a greater probability of ensuring their paternity.

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Table 1. Temporal evolution of spermatheca repletion (percentage of specimens with sperm) of primiparous females in shallow water and in the central channel of the Ría de A Coruña.

	Shallow water		Migration corridor	
	N	%	N	%
Jul 98	20	10.0		
Aug	19	0.0		
Sep	32	0.0	9	0.0
Oct	24	0.0	1	0.0
Nov	15	0.0	11	45.5
Dec	14	7.1	2	0.0
Total	124	2.4	23	21.7

FIGURE LEGENDS

Figure 1. Physiological hypothesis. Temporal evolution of the physiological condition in a cohort of adults after the terminal moult (see Introduction for details).

Figure 2. Mating opportunity hypothesis. A, B and C represent three periods corresponding to the initial, intermediate and final stages of migration (see Introduction for details).

Figure 3. Location and sampling areas in the Ría de A Coruña. The transect comprising 7 trap tows in the inner shallow area is shown. Latitude is given for each tow on the transect (see Figure 6).

Figure 4. Relation between body size and dry weight of the tissue analysed (gonad, muscle and hepatopancreas) to estimate the physiological condition of each sex. The allometric regression fitted in each case is shown.

Figure 5. A comparison of the monthly evolution of the proportion of adult males and females in postmoult stage (related to total catches including adults and juveniles) captured in shallow waters.

Figure 6. Spatial structure of the adult population in Bastiagueiro in the period prior to and at the start of migration. The catch per unit of effort is given (crabs·trap⁻¹ and a 95% confidence interval of the mean) along the transect sampled (each 10th of a degree is equivalent to 182 m) (see Figure 3).

Figure 7. Abundance of adults in the channel (mean crabs·trap⁻¹ with a 95% confidence interval of the mean) during each month of the sampling (upper), and on each day of sampling during migration (lower) in 1998. The arrows indicate the mean date of the start of migration for each sex.

Figure 8. Temporal evolution of the condition index (CI) of each tissue in adult males in Bastiagueiro (individual observations, sample size for each month and polynomial regression with 95% confidence interval are shown) and in the central channel (mean and 95% confidence interval, only in November, N=14).

Figure 9. Temporal evolution of the condition index (CI) of each tissue in adult females in Bastiagueiro (individual observations, sample size for each month and polynomial regression with 95% confidence interval are shown) and in the central channel (mean and 95% confidence interval, only in September and November, N=14).

Figure 10. Monthly percentage of adult males and females in postmoult (stage B) captured in Bastiagueiro and in the channel in the period prior to and at the start of migration. Sample size is indicated in each case (ND= no data).

Figure 11. Mean size (with 95% confidence interval) of the adult males and females captured in Bastiagueiro and in the channel at the start of migration.

Figure 12. Mean dates of the start of migration estimated in the present study and in others carried out in the rías of A Coruña and Arousa using ultrasonic telemetry and electronic

data-loggers (data from 1996 in González-Gurriarán *et al.*, 2002; Bernárdez and González-Gurriarán, unpublished data).

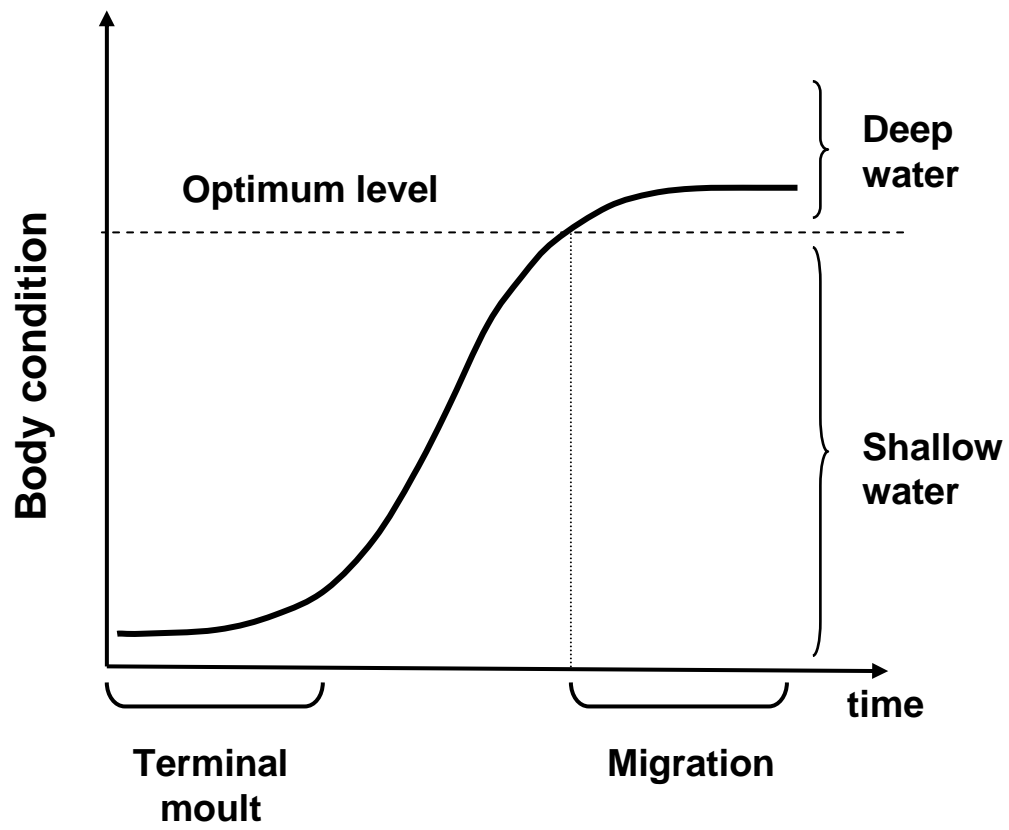


Figura 1. Corgos *et al.* Reproductive strategies in *Maja brachydactyla*

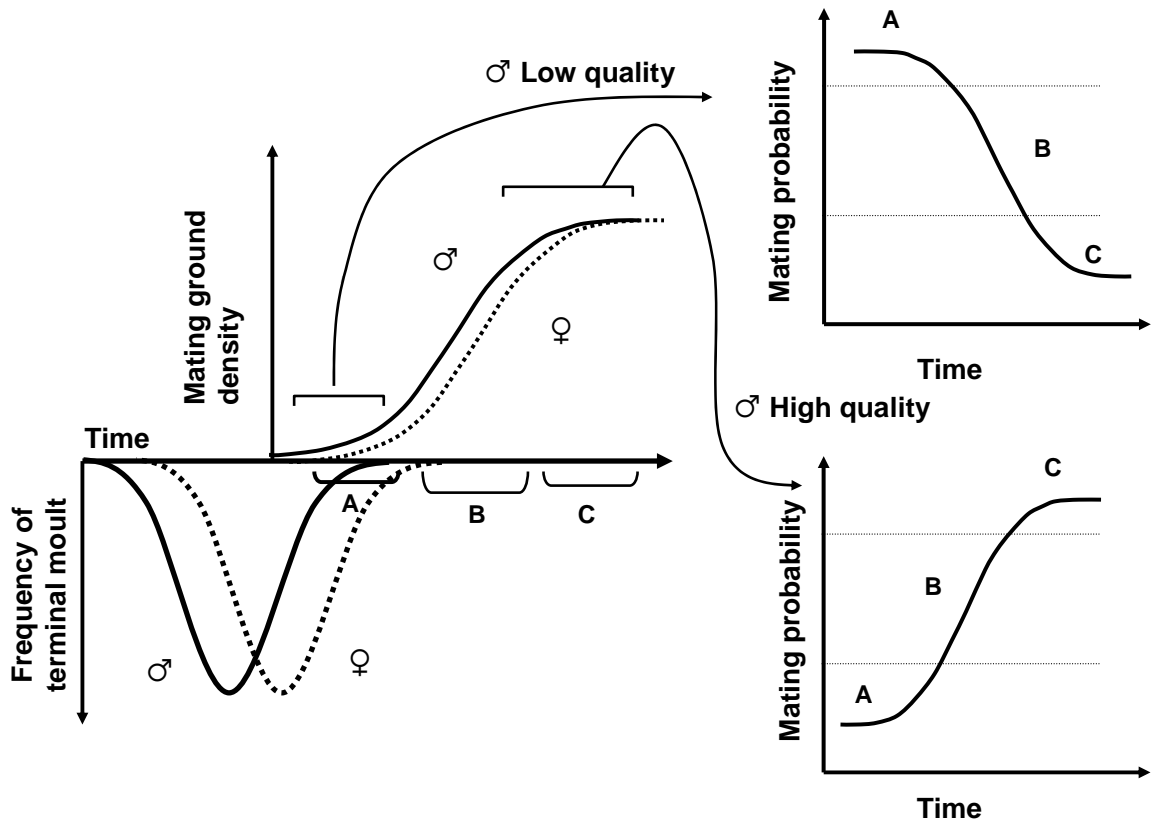


Figura 2. Corgos *et al.* Reproductive strategies in *Maja brachydactyla*

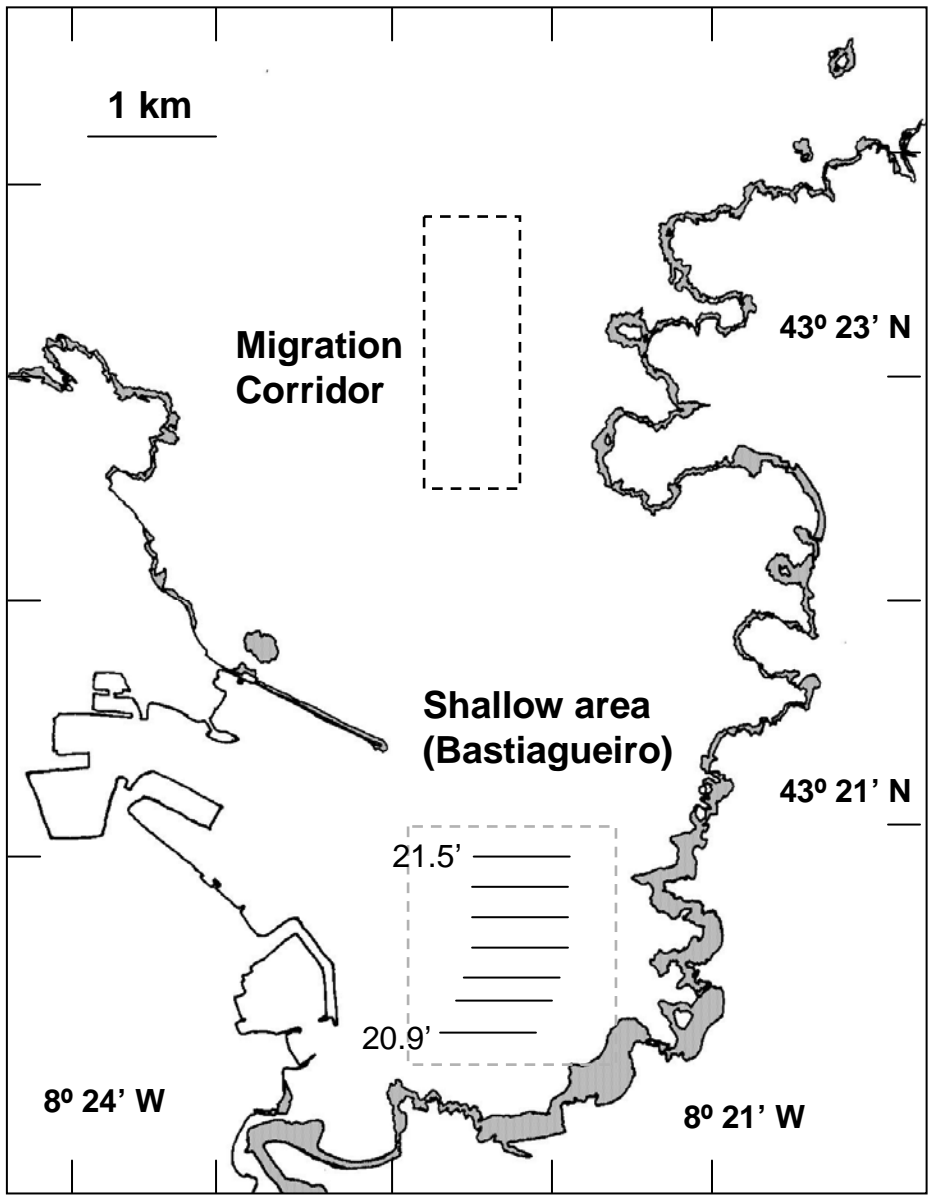


Figure 3. Corgos *et al.* Reproductive strategies in *Maja brachydactyla*

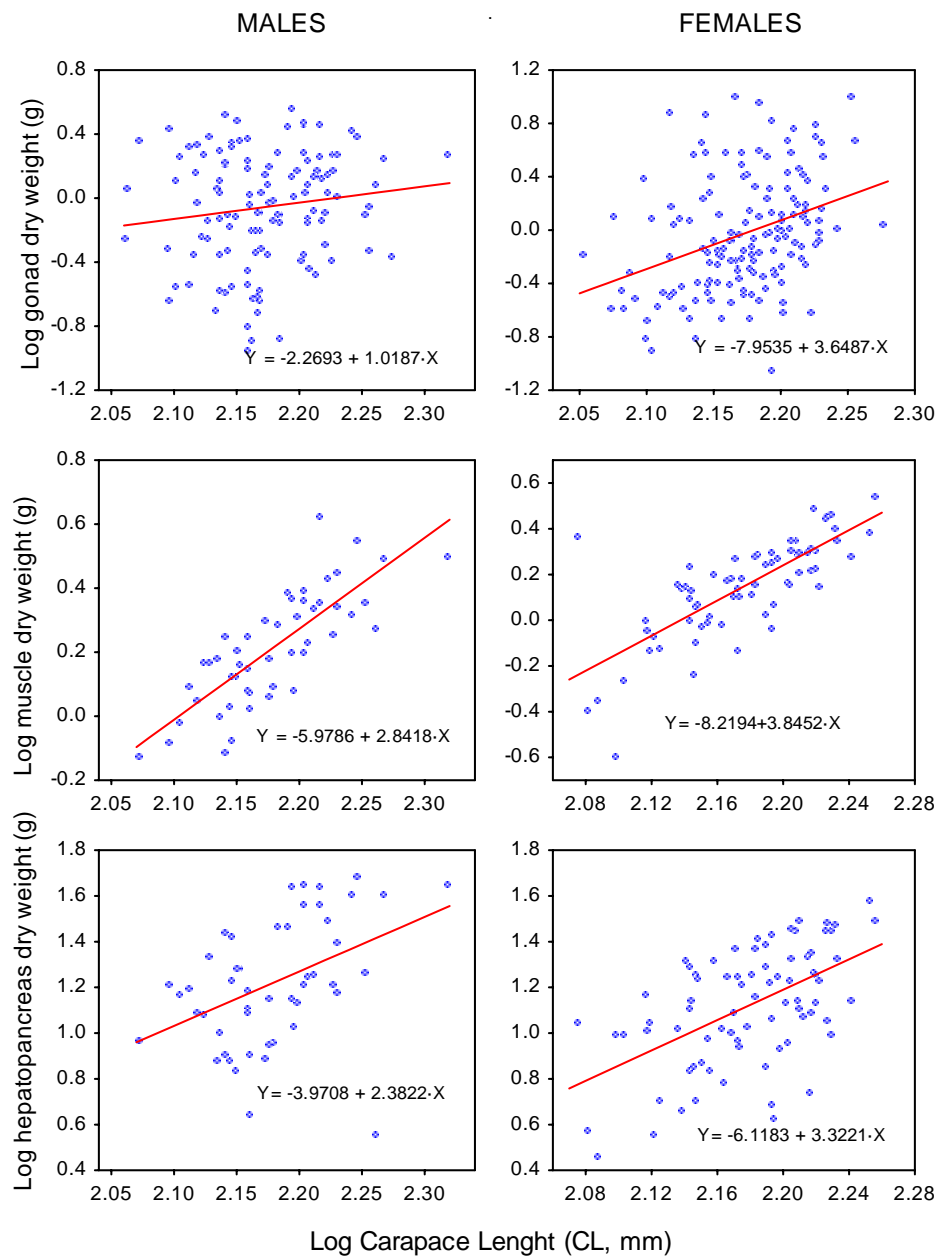


Figura 4. Corgos *et al.* Reproductive strategies in *Maja brachydactyla*.

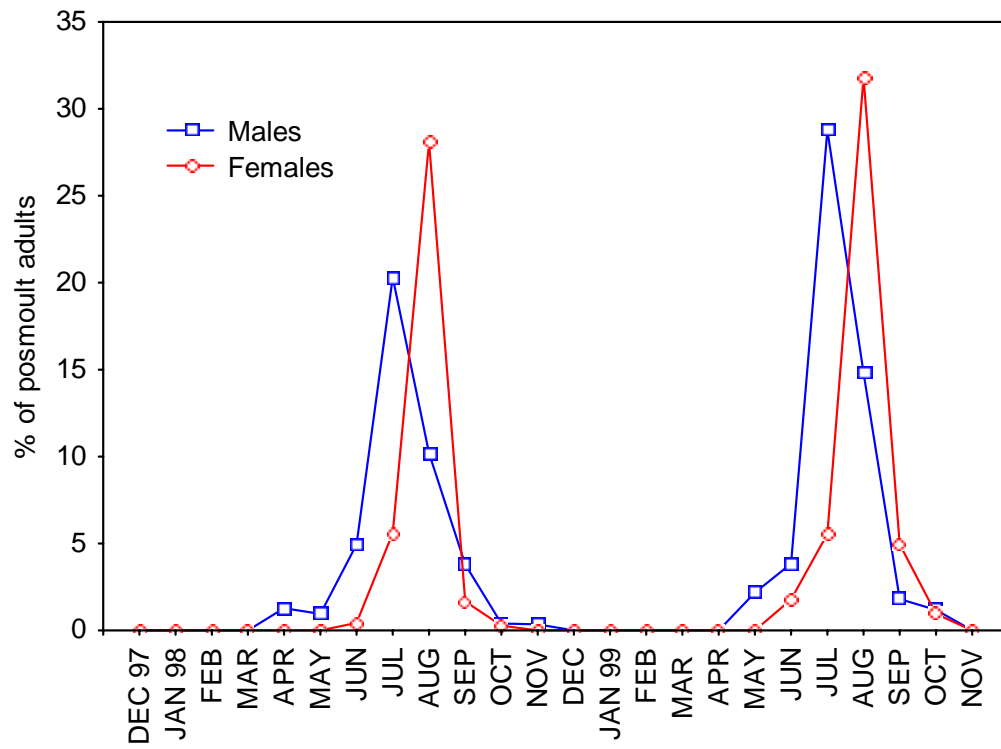


Figura 5. Corgos *et al.* Reproductive strategies in *Maja brachydactyla*

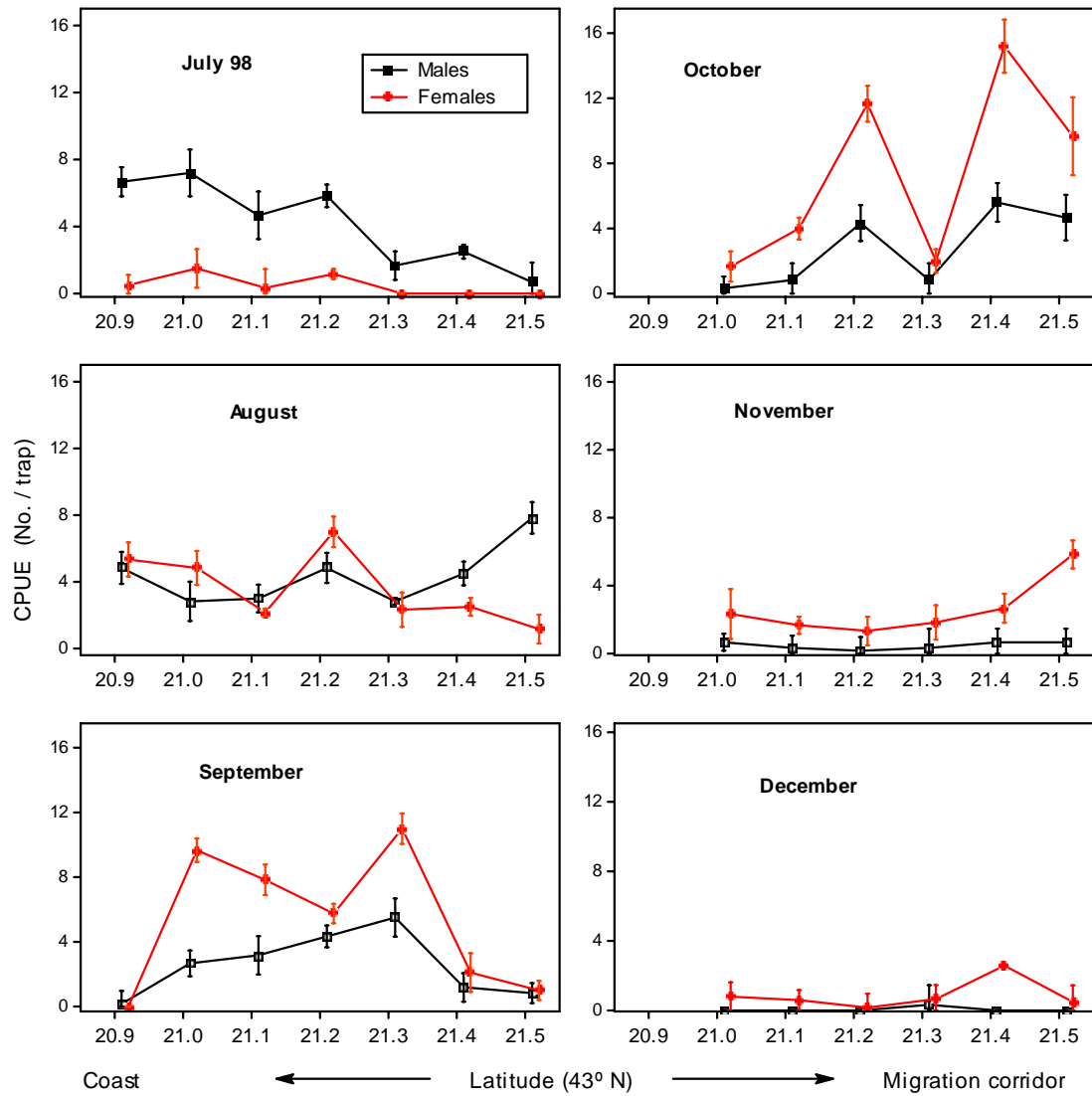


Figura 6. Corgos *et al.* Reproductive strategies in *Maja brachydactyla*

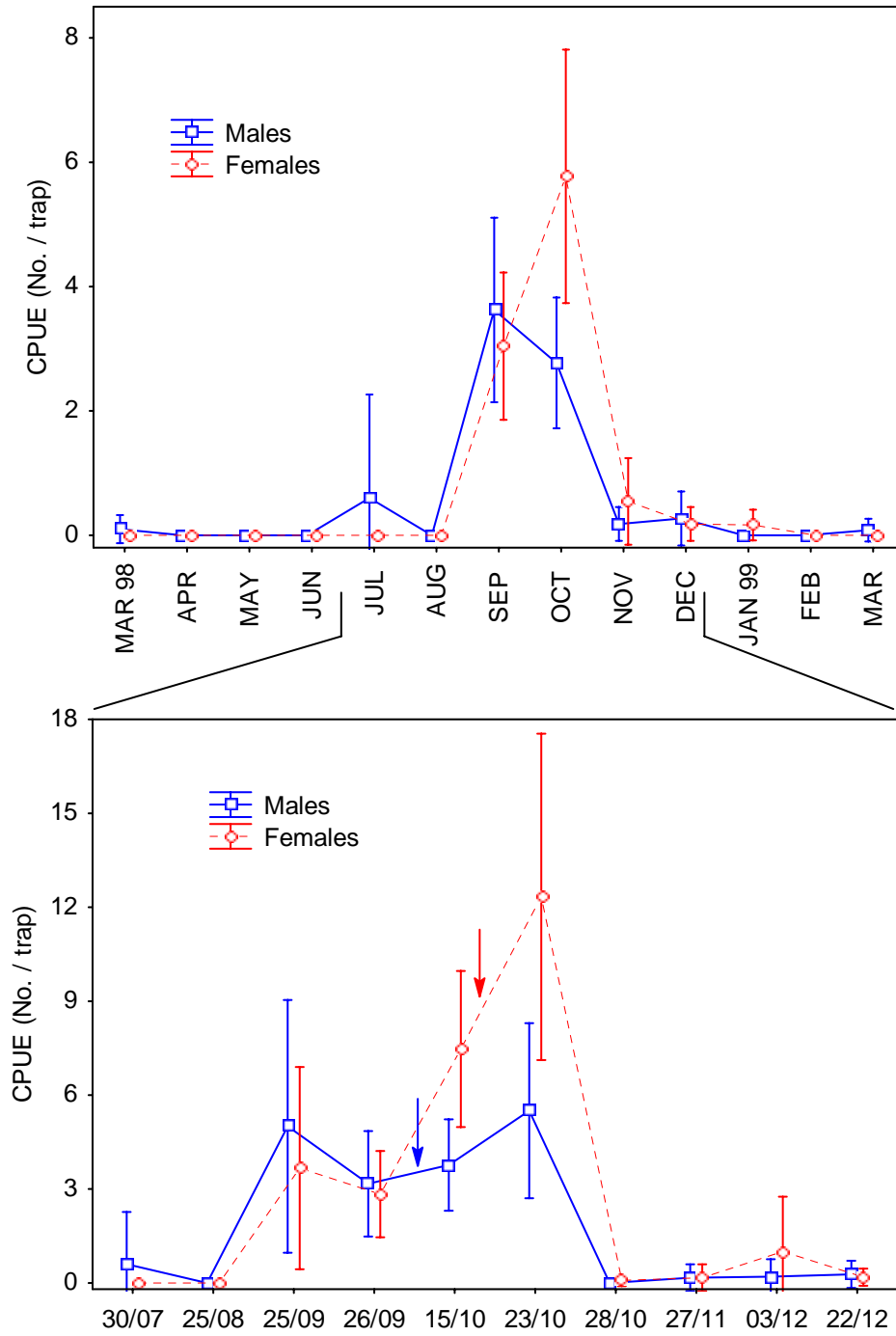


Figura 7. Corgos *et al.* Reproductive strategies in *Maja brachydactyla*

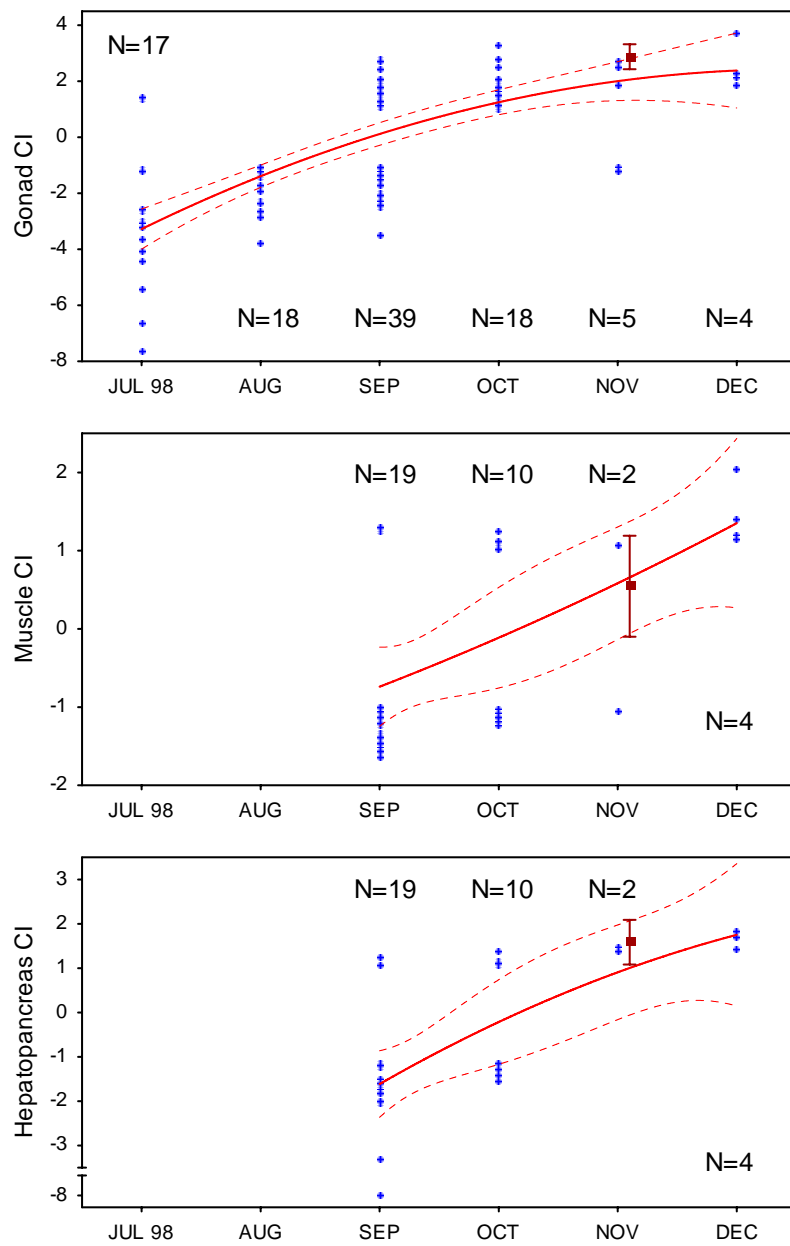


Figura 8. Corgos *et al.* Reproductive strategies in *Maja brachydactyla*

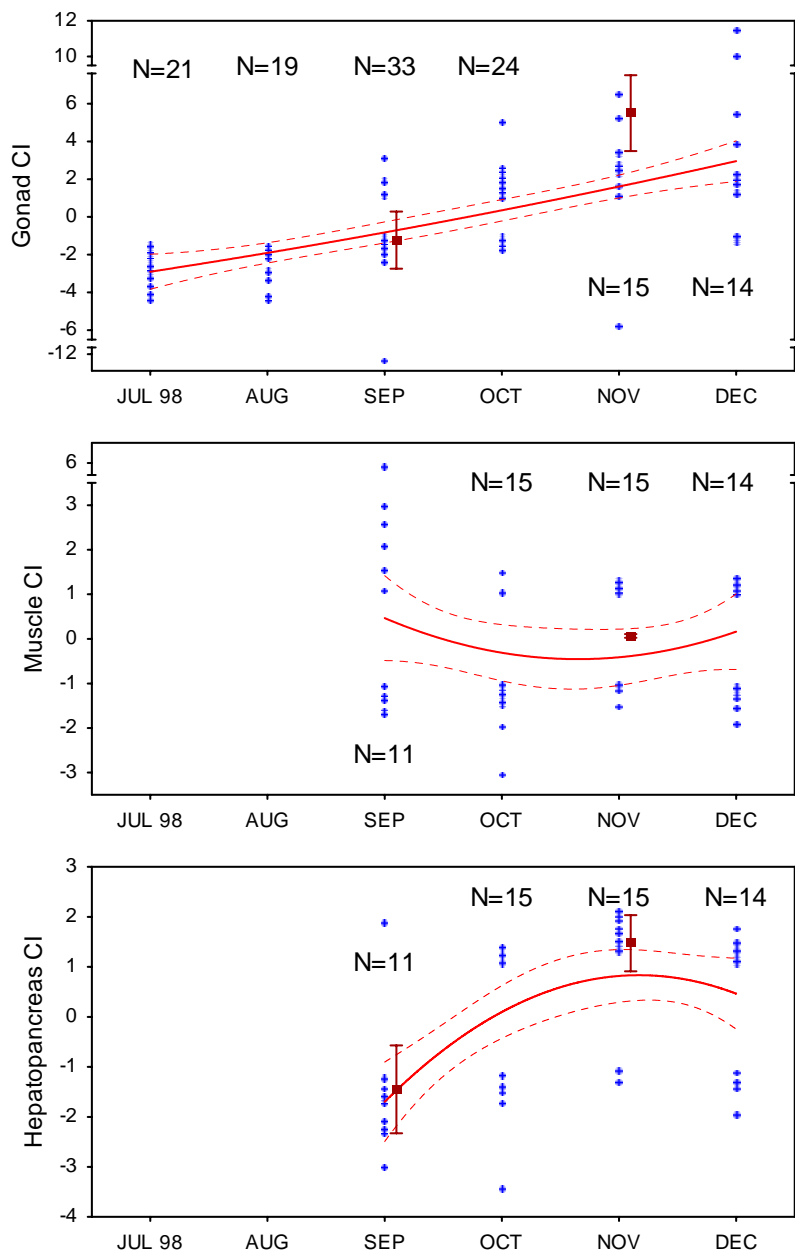


Figura 9. Corgos *et al.* Reproductive strategies in *Maja brachydactyla*

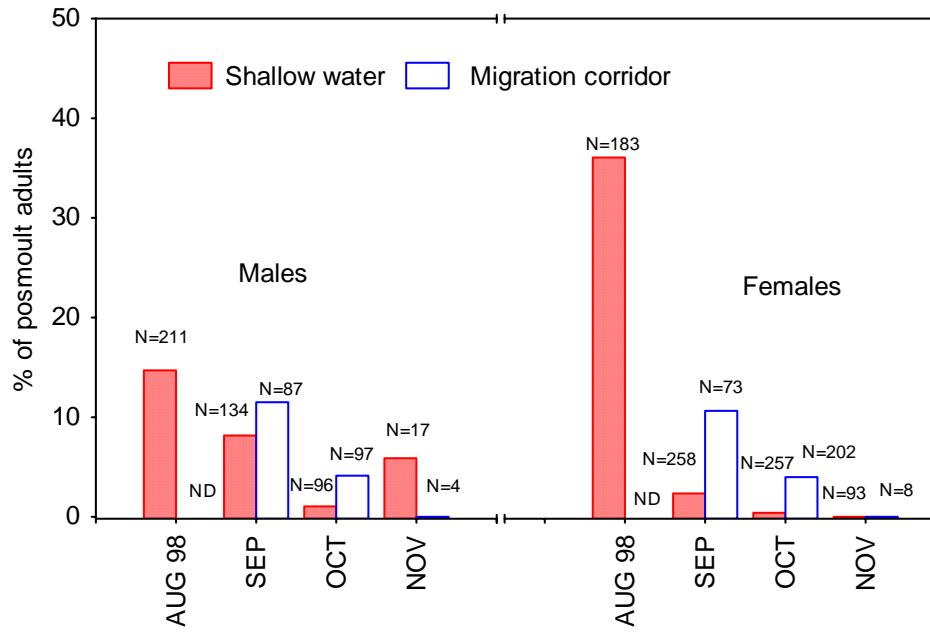


Figura 10. Corgos *et al.* Reproductive strategies in *Maja brachydactyla*

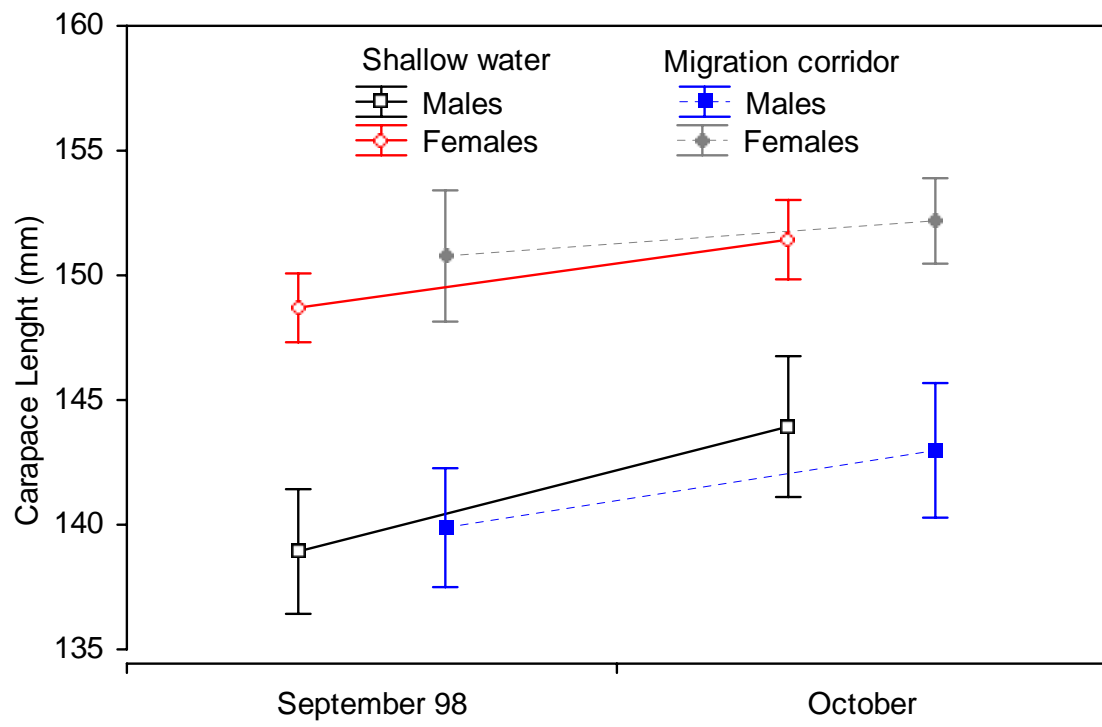


Figura 11. Corgos *et al.* Reproductive strategies in *Maja brachydactyla*.

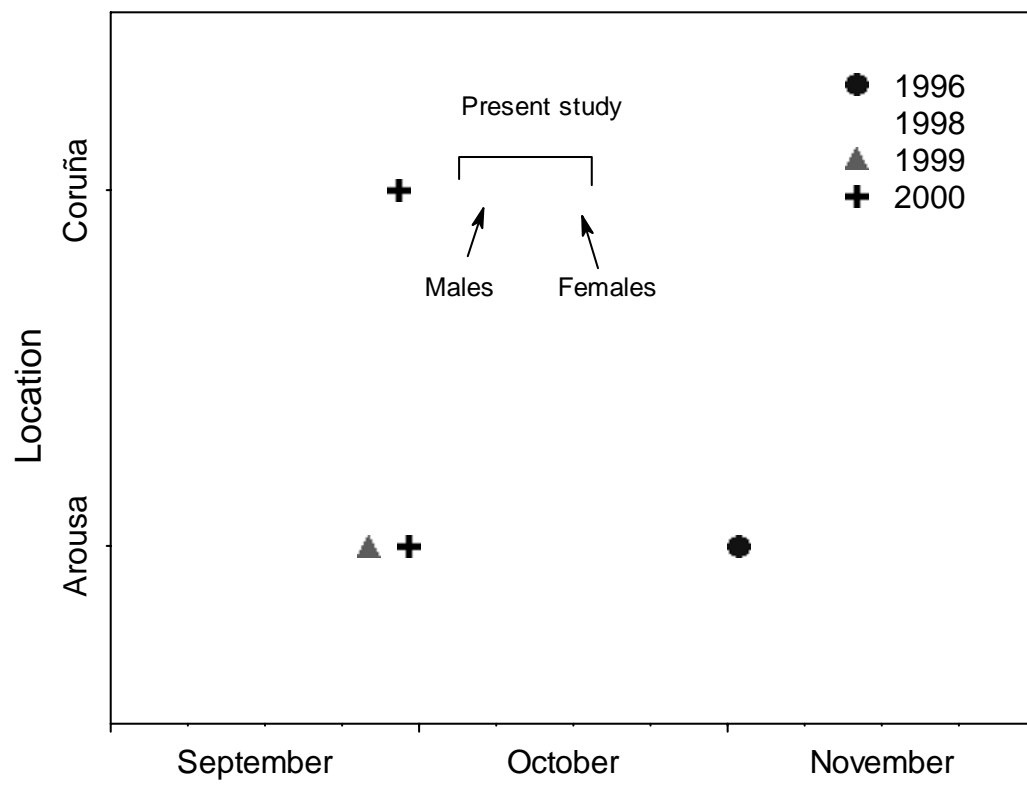


Figure 12. Corgos *et al.* Reproductive strategies in *Maja brachydactyla*