JOURNAL OF CRUSTACEAN BIOLOGY, 28(2): 262–269, 2008

SCHEDULE OF REPRODUCTIVE EVENTS AND MATURITY AT SIZE OF THE PATAGONIAN STONE CRAB *PLATYXANTHUS PATAGONICUS* (BRACHYURA, PLATYXANTHIDAE)

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A B S T R A C T

The most significant events of the reproductive cycle of the Patagonian stone crab, *Platyxanthus patagonicus*, were studied in specimens sampled in northern Patagonian gulfs from August 2004 to May 2006. Male and female crabs were assigned to stages of a scale of gonad maturity. Females were also classified according to the presence/absence of embryos on the pleopods and of spermatic content in the spermathecae. Ogives were fitted to maturity at size data. The highest frequency of pre-ovigerous females and spermathecae with hardened seminal contents occurred during the fall and winter. Fifty percent of the females reached ovarian maturity at 66.4 mm CW. Ovigerous females were frequent from mid-fall to mid-spring, peaking during early winter and mid-spring, and were unusual or absent during the summer months. Post-ovigerous females were present in samples in all months but May and June 2005, being frequent from late-spring to early-fall. Specimens with spent ovaries were common in all seasons but summer, while those with mature or recovering ovaries were present in samples taken in all months but August 2004 and May-June 2005. Fifty percent of the males reached testes maturity at 54.7 mm CW. Males larger than this size showed mature gonads year round, but a pulse of individuals with recovering testes was observed during the winter of 2005 and early-fall of 2006. Our results show that mating occurs during the fall months, spawning and embryonic incubation extends from fall to early spring, and hatching takes place during late-spring and early-summer.

KEY WORDS: Brachyura, stone crab, *Platyxanthus patagonicus*

INTRODUCTION

The Patagonian stone crab, *Platyxanthus patagonicus* A. Milne-Edwards, 1879, is a brachyuran distributed in the Southwest Atlantic from southern Brazil (Coelho and Ramos, 1972; Melo, 1990) to San Jorge Gulf, Argentina (Inada et al., 1986; Boschi et al., 1992), at depths ranging from 20 to 155 m (Inada et al., 1986). The species is a member of the Platyxanthidae, which includes a few other South American species such as *P. orbignyi* H. Milne Edwards and Lucas, 1843, from Peru and Chile, *P. crenulatus* A. Milne-Edwards, 1879, from Uruguay and central Argentina, and *Homalaspis plana* H. Milne Edwards, 1834, from Chile (Guinot, 1977). Studies on the reproduction of the family have been few and include work on the reproductive cycle and size at first maturity of *P. orbignyi* (Gonzales et al., 1991; Quipán and Delgado, 1991; Ishiyama et al., 1995) and *H. plana* (Gamonal and Cerisola, 1986; Carvacho et al., 1995).

In northern Patagonia, *P. patagonicus* reaches up to 146 mm in CW and almost 1 kg in total fresh weight. As in other members of Platyxanthidae and Xanthidae, the so-called "stone crabs", males display a conspicuous enlargement of the chelae in comparison to females, which becomes evident after the onset of sexual maturation. This makes them a valuable target for fishing (Restrepo, 1992; Carsen et al., 1996). During the last 30 years, the world annual catch of marine brachyurans rose from 334,000 to 1,361,000 t (FAO, 2005). Even though true crabs have an important economic potential, they currently are very lightly exploited in coastal waters of Argentina (Wyngaard et al., 2001). The development of a new fishery presents managers with the challenge to design a strategy that can ensure sustainability in the absence of historical information on the abundance and productivity of the resource (Perry et al., 1999). Some species of crabs have several reproductive features, e.g., marked sexual dimorphism, polygyny, and assortative mating, that have allowed sustainable management based on size limits, targeting of males only, and seasonal closures related to the reproductive cycle (Hankin et al., 1997; Sideek et al., 2004). However, several examples exist in which additional control measures, such as the monitoring of the per-capita female reproductive contribution and the sex ratio, need to be implemented to avoid recruitment overfishing (Orensanz et al., 1998, 2004; Lipcius and Stockhausen, 2002).

Regardless of the potential of its fishery, *P. patagonicus* has not been studied in detail so far (Wyngaard et al., 2001). Only one work was published on the biology of the species, dealing with the estimation of fecundity at size and size at morphological maturity (Carsen et al., 1996). Many aspects of its reproduction remain to be investigated, including the relationship between molting and mating, sperm storage and the potential for sperm competition, mechanisms of sexual attraction (chemicals release, visual or sonorous displays, etc.), mating behavior (agonistic fights, mate selection strategies), sexual dimorphism, and assortative mating, among others. Since crabs have become a classic model for the study of mating strategies (Urbani et al., 1998), these aspects of their reproductive biology are not only

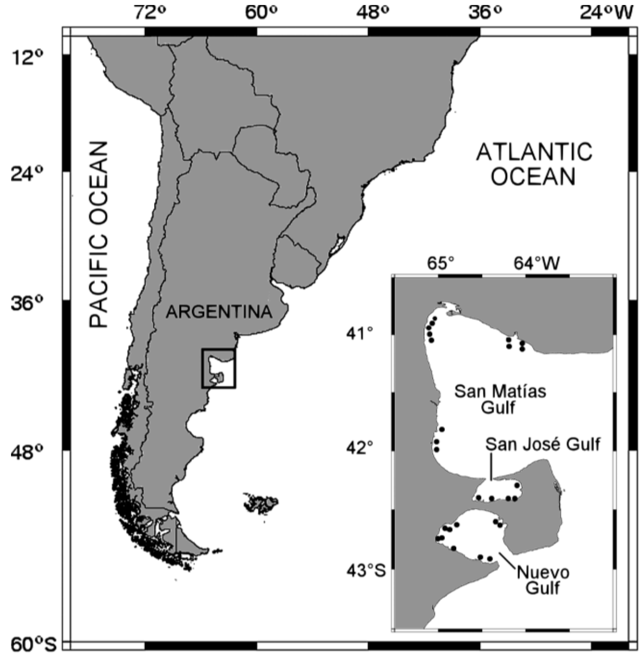

Fig. 1. Study area. Dots indicate sampling sites in the three northern Patagonian gulfs.

scientifically interesting, but also have growing management implications.

The objective of this work is to provide an analysis of the reproductive cycle and the size at maturity of *P. patagonicus* in coastal waters of northern Patagonia (41°-43°S) in anticipation of the beginning of its exploitation.

Materials and Methods

Sampling and Study Area

Sampling was conducted in several coastal locations of the northern Patagonian gulfs (San Matías, San José and Nuevo gulfs, 40°-43°S) (Fig. 1) within a depth-range of 10-96 m, employing semi-rigid inflatable boats, the research vessel CENPAT I from the National Patagonian Center, and commercial artisanal fishing boats. Crabs were captured with cylindrical baited traps (diameter: 260 mm; length: 500 mm; mesh size: 10 mm) and hand-collected by SCUBA diving on the sea bottom. From February 2003 to January 2004, eight preliminary fishing trials were conducted, and from August 2004 to May 2006 regular sampling was completed on a monthly basis.

General Characterization

Carapace width (CW), measured between the distal ends of the postero-lateral spines, was measured with a digital caliper to the lowest 0.01-mm, and fresh weight to the lowest 1-g was registered using a Mettler P3N scale. Individuals were sorted by sex based on visual inspection of the abdomen width. Also, crabs were classified into stages of the molting cycle using the following subjective scale: 1) very recent post-molt: weak, almost immobile with jelly consistency; 2) recent post-molt: white ventrally, intense orange dorsally, paper shelled consistency; 3) late post-molt: mobile, semi-hardened consistency; 4) early intermolt: hard exoskeleton, bright-orange dorsally, with no to few epibionts; 5) late intermolt: hard exoskeleton, pale orange with numerous epibionts on the carapace. Individuals infested with sacculinid rizhocephalan castrating parasites were separated for further study.

Mating

To establish the time of the year in which mating occurs, the spermathecae of all females were dissected and observed under a light microscope (10×6 magnifications). Females showing hardened contents within the spermathecae were considered to have mated recently.

Gonad Maturity

Sexual maturity of *P. patagonicus* of both sexes was determined by classifying individuals on stages of a scale of gonad development based on macroscopic observation of the consistency, volume and color of ovaries and testicles (Table 1). Male classification also took into account the volume of the vasa deferentia and the presence of spermatophores within their lumina (Table 1). The relative frequencies of each stage of sexual maturity in the samples obtained from August 2004 to May 2006 were analyzed to describe the reproductive cycle of males and females. Also, to describe the chronology of changes in the ovary, a gonadosomatic index was estimated as: GSI = ovary wet weight/crab wet weight $\times$ 100, from monthly subsamples of 10 females taken randomly from November 2004 to November 2005. Logistic curves of physiological maturity were fitted to data on the percentage of individuals with mature gonads at different size-classes by means of non-linear regressions. CW_{phys} 50% (for females: CW at which 50% of the crabs show mature, spent, or recovering ovaries; for males: CW at which 50% of the individuals were at mature, spent, or recovering stages of physiological maturity) were obtained from the curves fitted to maturity-at-size-class parameters.

Reproductive Schedule: Spawning, Embryonic Development, and Hatching

All females carrying ova or developing embryos attached to the pleopod setae were classified as ovigerous. From May 2005 to May 2006, the color of the egg (embryo) mass of ovigerous females was registered as an indicator of embryonic maturity. Recently spawned egg masses were purple to terracotta in color; the mass of embryos with forming eyes progressively acquired a brown color, and ready-to-hatch egg masses became dark-brown. Females showing clean pleopod setae or broken chorion fragments adhered to the pleopods were respectively classified as pre-ovigerous or post-ovigerous after careful observation under the dissecting microscope. The relative frequency of females in each category was analyzed in samples obtained from August 2004 to May 2006. Females that were ovigerous or post-ovigerous and those that had already spawned and molted being at a recent post-molt stage and displaying both clean pleopod setae and recovering ovaries, were all considered functionally mature. A logistic curve of functional maturity was fitted to the percentage of functionally mature females relative to the total number of females at different size classes. CW_{func} 50% (CW at which 50% of the females are functionally mature) was obtained from the parameters of the curve of functional maturity.

Table 1. Scale of physiological sexual maturity of male and female *Platyxanthus patagonicus*.

Stage	Males	Females
Immature	Testes not visible to the naked eye; vasa deferentia resemble translucent filaments only visible under dissecting microscope	Ovary undetectable to the naked eye, only visible under the dissecting microscope as a translucent filament
Maturing	Small testes and thin vasa deferentia detectable to the naked eye	Ovary detectable to the naked eye, as a creamy to pink filament
Mature	Testes swollen, opaque and white; vasa deferentia swollen and pink, containing abundant spermatophores	Ovary swollen, voluminous, dark pink to purple in color, containing easily detectable vitellogenic oöcytes
Spent	Testes whitish and lax; vasa deferentia contain no to few spermatophores	Ovary lax, creamy in color, flattened and containing few or no vitellogenic oöcytes
Recovering	Testes white and swollen; vasa deferentia lax and containing no spermatophores	Ovary swollen and partly vacuous, light cream to pink in color, containing abundant vitellogenic and scattered atretic oöcytes

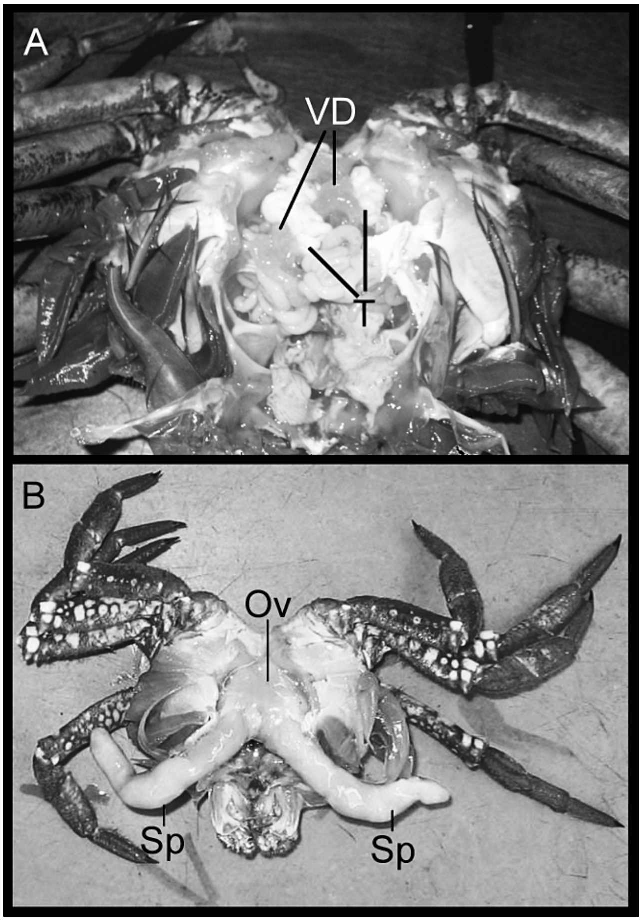

Fig. 2. Dorsal view of the reproductive system of *Platyxanthus patagonicus*. A, 124.4-mm CW male showing swollen testes and vasa deferentia; B, 75.2-mm CW female displaying spermathecae with hardened seminal contents. T = testes, VD = vasa deferentia, Sp = spermathecae, Ov = ovary.

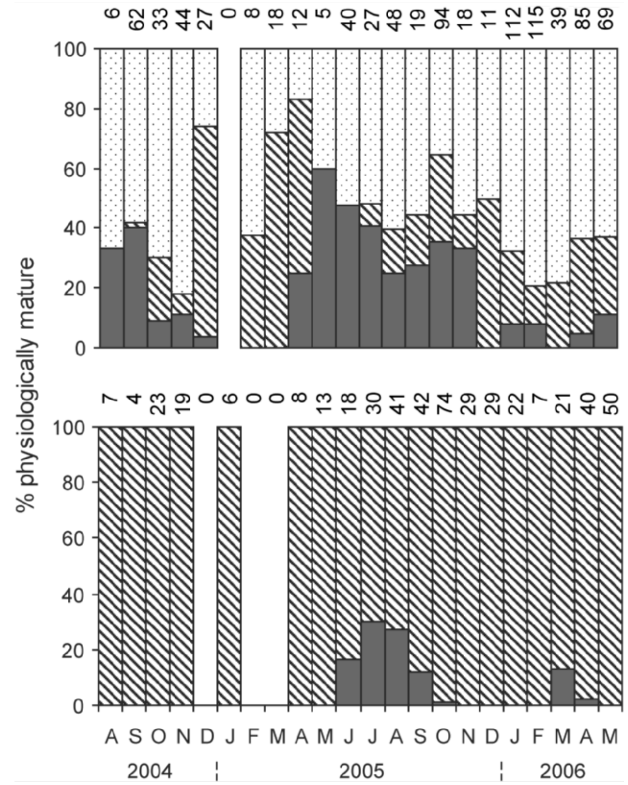

Fig. 3. Monthly variation of the percentage of *Platyxanthus patagonicus* female (top) and male (bottom) at different stages of physiological maturity. Obliquely-dashed bars: mature; dotted bars: recovering, and dark bars: spent. Males and females in immature and maturing stages were excluded from the analysis. Figures on top of the bars represent number of individuals in each sample.

Results

Sampling

During the period of this study, a total of 1771 individuals of *P. patagonicus* (1061 females and 710 males) were collected. Of this total number, 1254 were captured in baited traps and 517 were collected by SCUBA diving. Out of three months (October and November of 2005 and January of 2006) in which rough weather conditions prevented sampling by SCUBA diving, relative proportion of specimens captured with the last method varied within 17-48%. CW ranged from 18.9 to 126.6 mm and from 14.5 to 145.3 mm for females and males respectively. Mean CW in monthly samples showed little variation, ranging within 90.1-119.2 mm for males and 87.3-106.4 mm for females. More than 95% of the individuals sampled had CW greater than 60 mm.

Mating

Spermathecae with hardened seminal contents (Fig. 2) were found in winter to spring (July-October) of 2005 and in fall (March-May) of 2006, exclusively in late postmolt and early intermolt females. No mating pair was observed during the study.

Gonad Maturity

Females with mature ovaries were well represented from spring (October) of 2004 to fall (April) of 2005 and from late winter (August) of 2005 to fall (May) of 2006 (Fig. 3). Females with recovering ovaries were abundant in all of the months sampled (Fig. 3). Highest relative frequencies of females with spent ovaries were observed from winter to spring (August-September) of 2004 and fall to spring (April-November) of 2005 (Fig. 3). GSI showed increasing values from late spring to summer, a sharp decline in mid fall, low values during late fall months, and a gradual increase during the next winter and spring (Fig. 4). CW_{phys} 50% estimated for female *P. patagonicus* was 66.4 mm (Fig. 5).

Most males were in mature stage year round; males with recovering gonads were found in late fall-early spring (June-September) of 2005 and early fall (March-April) of 2006 (Fig. 3). No spent males were registered through the study period. CW_{phys} 50% estimated for males was 54.7 mm (Fig. 5).

Reproductive Schedule: Spawning, Embryonic Development and Hatching

Ovigerous females were well represented in the samples year round, except for the summer months (December of

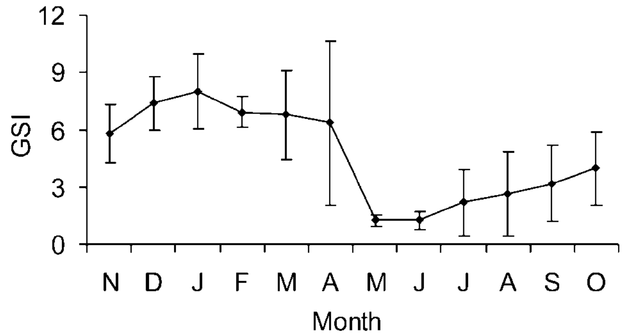

Fig. 4. Monthly variation of the gonadosomatic index (GSI) of female *Platyxanthus patagonicus* from November 2004 to October 2005. Dots = mean values, bars = mean +/– standard deviation.

2004-January of 2005 and December 2005-April 2006), with peaks of abundance in spring (August-October) of 2004, late fall-winter (May-July) of 2005, spring (October-November) of 2005, and fall (May) of 2006 (Fig. 6). Color of the egg mass varied through the reproductive season. Purple to terracotta egg masses were more frequent in May-August of 2005 and in May of 2006, while brown and dark-brown egg masses prevailed from September of 2005 to March of 2006 (Fig. 6). The size frequency distribution of all ovigerous females collected showed a bimodal pattern (Fig. 7). Post-ovigerous females were present in all monthly samples, being more frequent in December-April (Fig. 6). Most pre-ovigerous females were found in July-November of 2005 and March-May of 2006 (Fig. 6). CW_{func} 50% estimated for female *P. patagonicus* was 66.8 mm (Fig. 8).

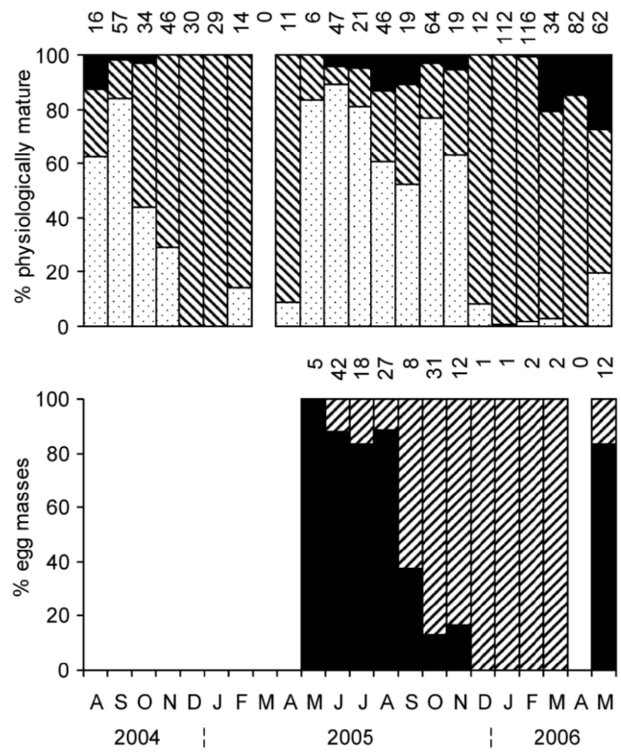

Fig. 6. Top: Monthly variation in the percentage of pre-ovigerous (dark bars), post-ovigerous (obliquely dashed bars), and ovigerous (dotted bars) female *Platyxanthus patagonicus*. Bottom: Percentage of purple (dark bars) and brown to terracotta (obliquely-dashed bars) ovigerous masses. Figures on top of the bars represent number of individuals in each sample.

Discussion

In this study, most of the specimens captured with baited traps were larger than 60 mm CW; smaller individuals being almost exclusively found by SCUBA diving, under macro-algae holdfasts and mollusk shells, or in small holes dug in the mud. Also, individuals in early post-molt stage were almost absent from trap samples, making necessary the use of the two supplementary sampling techniques to understand the population structure of the species. Bias towards large specimens due to trap selectivity has been reported for crabs (Taggart et al., 2004; Bellchambers and de Lestang, 2005). Other possible sources of bias include gear selectivity by sex, reproductive stage, and phase of the molting cycle (Taggart et al., 2004). Factors that have been pointed out as the source of sampling selectivity include ontogenetic change in feeding habits, size-related hierarchical access to traps, cannibalism avoidance by smaller individuals, and habitat segregation by size (Williams and Hill, 1982; Brêthes et al., 1987; Miller, 1990; Oliva et al., 1997; Bellchambers and de Lestang, 2005).

In this work, spermathecae displaying hardened seminal contents were considered to be indicative of recent mating. Hardened seminal contents were found in late-postmolt or early-intermolt females and were always voluminous. In advanced-intermolt stage females, seminal contents showed a liquefied aspect, making it more subjective to determine fullness/emptiness by direct observation. This change in seminal content consistency is similar to that reported by

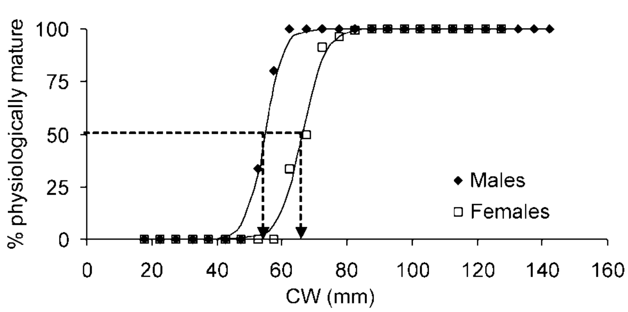

Fig. 5. Physiological maturity curves and CW_{phys} 50% estimated for male and female *Platyxanthus patagonicus*.

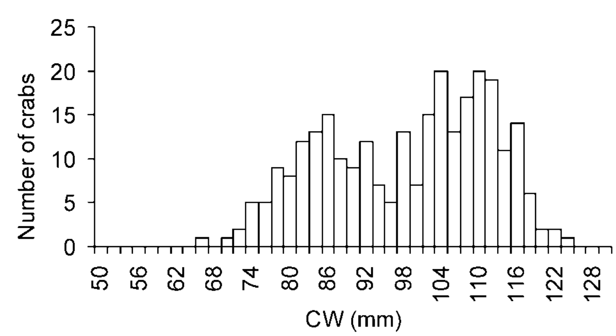

Fig. 7. Carapace width (CW) frequency distribution of *Platyxanthus patagonicus* ovigerous females.

Diesel (1989, 1991), who described the process of seminal plasma hardening during seminal content transfer in *Inachus phalangium*, and observed a posterior loosening within the spermathecae. In many crab species (portunids, cancrids and some xanthids and majids) mating occurs immediately after the female's ecdysis, before the exoskeleton is calcified (soft-shell mating), while in others (most majids and many xanthids) it occurs during the intermolt period (hard-shell mating) (Hartnoll, 1969; Diesel, 1991, Donaldson and Adams, 1989). Spermathecae displaying hardened seminal contents were found only in females captured between late winter and early spring of 2005 and in the fall of 2006. As previously mentioned, these females were either in late-postmolt or early-intermolt stages and they displayed clean gonopodal setae, showing that *P. patagonicus* is a soft-shell mating species. In constrast, in *H. plana* it has been reported that mating occurs soon after the female's exoskeleton hardens (Carvacho et al., 1995).

Throughout the maturation process crab gonads undergo a gradual change in color and morphology related to histological changes, which are easily detected by visual inspection (Du Preez and Mc Lachlan, 1984; Ishiyama et al., 1995; Alunno-Bruscia and Sainte-Marie, 1998). The gonads of *P. patagonicus* showed a sequence of color change with progressive maturity (Table 1) similar to that reported for *P. orbignyi* in Peruvian coastal waters (Ishiyama et al., 1995). However, the seasonal pattern of ovarian maturation found in *P. patagonicus*, i.e., females with mature ovaries well represented from spring to fall and those with spent ovaries more frequent from fall to the next spring, showed a schedule opposite to that reported by Ishiyama et al. (1995) for *P. orbignyi*, i.e., females with mature ovaries frequent from fall to spring and those with spent ovaries well represented in spring and summer. On the other hand, maturation of male *P. patagonicus* showed little seasonality: most specimens were in mature stage in all months sampled and only a small percentage was in the recovery stage in late fall-early spring of 2005 and fall 2006. A similar pattern has been reported for other crab species (Melville-Smith, 1987; Mantelatto and Fransozo, 1999). Nonetheless, since morphological changes in crab testes and vas deferens are not as marked as those in the ovaries (Nagao and Munehara, 2003), further analysis based on histology may provide a more detailed pattern on the chronology of testis maturation.

The color of the egg-mass carried by ovigerous females has been extensively used to determine the maturity of crab embryos (Moriyasu and Lantelgne, 1998; Yosho, 2000; Pinheiro and Hattori, 2003; García-Guerrero and Hendrickx, 2004). In *P. patagonicus*, as in other crab species (Moriyasu and Lanteigne, 1998; Yosho, 2000), recently extruded eggs display the same color as the mature ovary (purple), while pigmentation of the forming eyes in developing embryos turns the egg mass darker (brown to black). In this study, ovigerous females were present in the samples from fall to spring, with peaks of abundance during late fall-winter and spring, which reflects a wide spawning and incubating season. However, taking into consideration that ovigerous females carrying purple egg masses were mostly present from late fall to winter (Fig. 6), and that the female's GSI

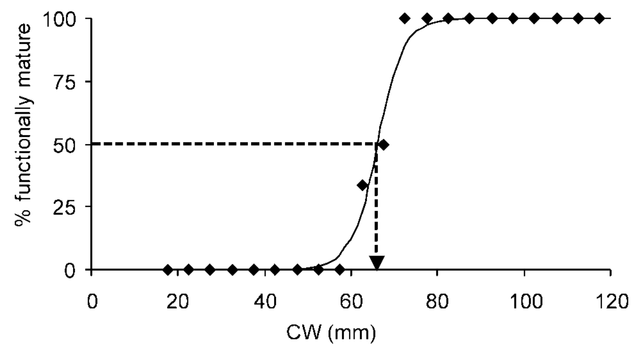

Fig. 8. Functional maturity curve and CW_{func} 50% estimated for female *Platyxanthus patagonicus*.

showed a marked decline in fall with low values through late fall and winter (Fig. 4), it becomes clear that the main spawning events occurred during that period, in contrast to several other stone crabs which spawn during spring and summer (Cheung, 1969; Ishiyama et al., 1995; Oshiro, 1999). Accordingly, the highest proportion of post-ovigerous females of *P. patagonicus* was observed during spring and summer, showing that spring marks the start of the hatching season. Since SST in the region during spring and summer ranges within 10°-16°C (Fig. 9) and the only known registers of the presence of *P. patagonicus* larvae are from SST within 11°-16°C (Iorio and Boschi, 1986), this conclusion seems reasonable. Larval life of *P. patagonicus* comprises four zoeal stages before molting to megalopa, taking approximately one month to its completion at temperatures typical from the spring-summer season (Iorio and Boschi, 1986). Ten-year averaged mean monthly surface seawater temperatures (SST) are similar at both latitudinal extremes of the study area (41°S and 43°S), showing at most a 1°C difference during the summer and winter months (Fig. 9). Therefore, in this study the whole area was considered homogeneous in terms of SST (one of the environmental variables likely to have greater effects on the schedule of reproduction).

The achievement of sexual maturity in crustaceans has three components: 1) physiological (marked by gonadal maturity); 2) morphometric (defined by allometric changes associated with the development of sexual secondary characters), and 3) functional (acquired by the attainment of all the necessary functionalities, including behavioral, needed for effective reproduction) (Somerton, 1980; Paul, 1992; Sainte-Marie et al., 1995). In many decapods, the sizes at which the three components are met do not match each other (Sainte-Marie and Hazel, 1992; Stevens et al., 1993; Jivoff, 1997). In female *P. patagonicus*, estimated CW_{phys} 50% and CW_{func} 50% were 66.4 and 66.8 mm respectively, closely matching the 64.7 mm CW_{morph} estimated by Carsen et al. (1996). The bimodality observed in the size frequency distribution of ovigerous females suggests that *P. patagonicus* females are sexually mature during the last two instars. Male CW_{morph} as reported by Carsen et al. (1996) (63.2 mm) is larger than the 54.7 mm CW_{phys} 50% estimated by us. Similar differences in size at the different components of maturity of males have been reported for other brachyurans and anomurans (Conan and

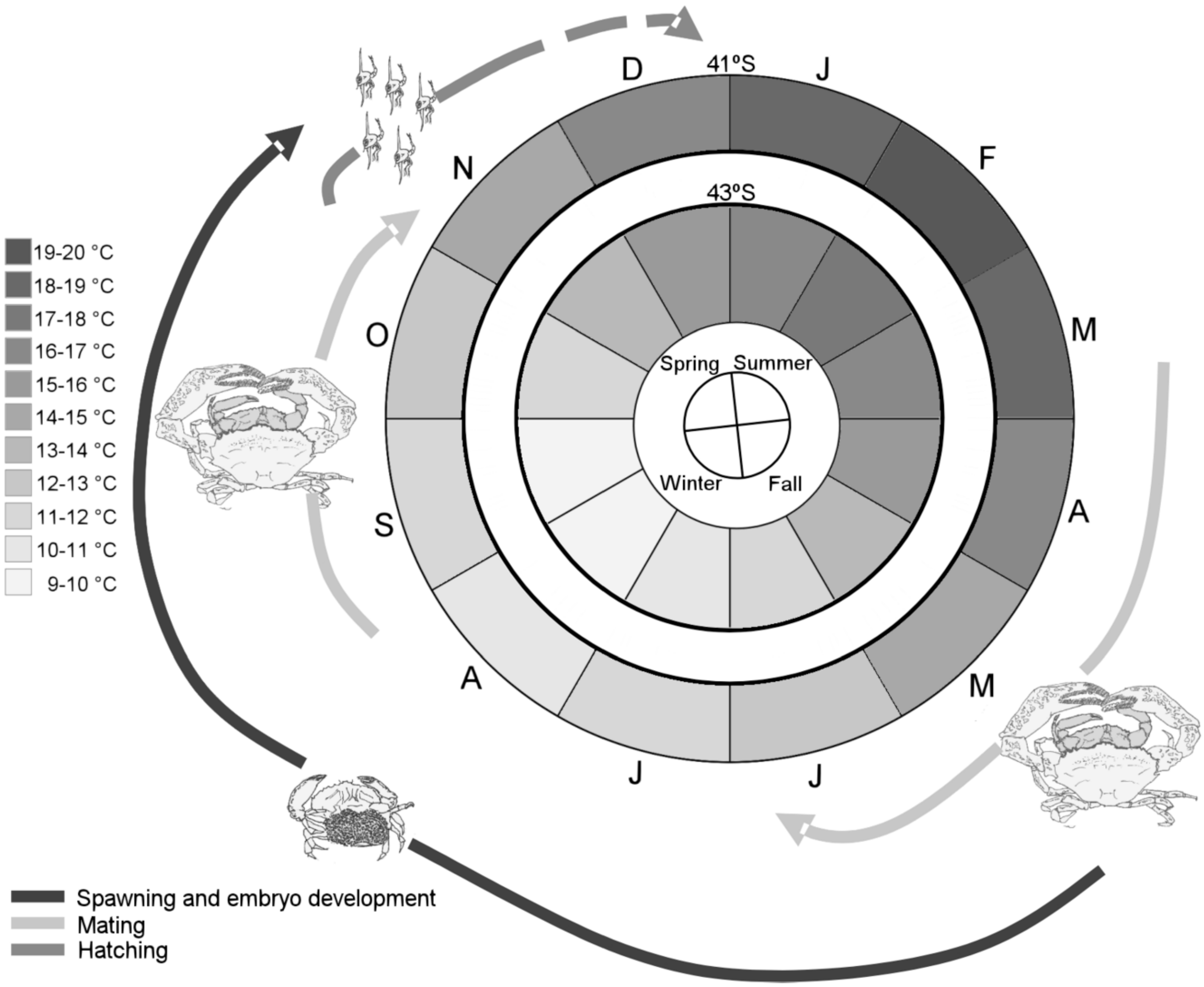

Fig. 9. Schematic representation of the annual schedule of reproductive events of *Platyxanthus patagonicus* in northern Patagonia (Argentina) relative to months, seasons and temperatures. Temperatures at the latitudinal extremes (41° and 43°S) of the study area represent the 1°C-ranges including 10-year-averaged mean monthly SST.

Comeau, 1986; Paul, 1992; Orensanz et al., 1995; Sainte-Marie et al., 1995). Also, differences in CW_{phys} 50% between males and females like those reported here are available in the literature (Lovrich and Vinuesa, 1993).

In conclusion, our data shows that in the northern Patagonian populations of *P. patagonicus*: 1) mating occurs in fall and late-winter to spring; 2) ovaries are spent during late-fall and gradually mature from winter to spring, reaching maximum maturity in summer; 3) testicles are mature year round, with a small proportion in recovery stage in fall-spring; 4) spawning takes place mainly from late-fall to winter, extending to some extent to spring; 5) females incubate their embryos from late-fall to spring; and 6) the hatching period begins in spring and could extend to summer (Fig. 9).

Acknowledgements

We want to express our gratitude to Dr. José M. Orensanz for his advice, which resulted essential for the completion of this study, and to Ricardo Vera, Néstor Ortiz and Miguel Angel (Hormiga) Díaz, from the Nautical Department of National Patagonian Center for the full support provided during sampling activities in the three northern Patagonian gulfs. Also, we are thankful to Dr. Enrique Morsán and the Nautical Department of the Almirante Storni Marine Biology and Fisheries Institute, for his collaboration in sampling logistics in northern San Matías Gulf and to two anonymous reviewers for their constructive comments on this work. The study was fully founded by project BID OC-AR 1728 PICT 14700 from the Argentinean National Agency of Scientific and Technologic Promotion (ANPCYT) and the National Patagonian Center (CENPAT-CONICET).

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RECEIVED: 12 March 2007.
ACCEPTED: 16 August 2007.