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Research Article

Studies on the reproductive dynamics of *Pleoticus muelleri* (Bate, 1888) (Crustacea, Decapoda, Solenoceridae) of Patagonia, Argentina

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ABSTRACT. Certain aspects of the reproductive dynamics of Argentine red shrimp *Pleoticus muelleri* (Bate, 1888), distributed between 42°-47°S and 62ºW, were investigated. Data and samples were collected during 36 INIDEP research cruises and 87 commercial fishing fleet trips between 1994-2010. Mature and inseminated females size structure as well as the frequency distribution of macroscopic maturity stages of adult females were analyzed on space-time bases. The seasonal development of ovarian maturity stages microscopically determinated was also assessed. Statistical treatment of data included multivariate scaling and cluster analysis. The reproductive activity of the shrimps showed latitudinal differences concerning its onset and duration that could be associated with the variability of environmental conditions. We discuss a shoreward movement of spawning females related to the presence of coastal hydrographic processes that would ensure retention and food for survival of early life stages.

Keywords: Penaeoidea, Patagonian shrimp, reproduction, southwestern Atlantic, Argentina.

Estudios sobre la dinámica reproductiva del langostino *Pleoticus muelleri* (Bate, 1888) (Crustacea, Decapoda, Solenoceridae) de Patagonia, Argentina

RESUMEN. Se estudian ciertos aspectos de la dinámica reproductiva del langostino *Pleoticus muelleri* (Bate, 1988) en el área comprendida entre 42º-47ºS y 62ºW. Los datos y las muestras analizadas provienen de 36 campañas de investigación del INIDEP y de 87 viajes de la flota comercial langostinera realizados entre 1994 y 2010. Se analiza la estructura de tallas de las hembras maduras e impregnadas, al igual que la distribución de frecuencias de los distintos estadios de madurez sexual de las hembras adultas diferenciados macroscópicamente, desde un enfoque espacio-temporal. La evolución estacional de los estadios de desarrollo ovárico determinados histológicamente también fue contemplada. El tratamiento estadístico de los datos comprendió un escalamiento multivariado y un análisis de agrupamiento jerárquico. La actividad reproductiva del langostino presenta diferenciaciones latitudinales con respecto a su inicio y duración que podría relacionarse con la variabilidad de las condiciones ambientales. Se discute la relación entre el movimiento hacia la costa de las hembras impregnadas y la presencia de procesos hidrográficos costeros que asegurarían la retención y disponibilidad de alimento para la supervivencia de las primeras etapas de vida.

Palabras clave: Penaeoidea, langostino patagónico, reproducción, Atlántico sudoccidental, Argentina.

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INTRODUCTION

The *Pleoticus muelleri* (Bate, 1888) red shrimp fishery is one of the most important in Argentina as it represents a significant percentage of the total fishery exports (Bertuche *et al*., 2000, 2005). It occurs mainly in the Patagonian region between 43º and 47ºS in waters under the jurisdiction of the Chubut and Santa

Cruz provinces, specifically in the San Jorge Gulf, and in national waters. This fishery began in 1980 when only 2,616 ton were landed, but since the year 2000 it has reached annual catches larger than 27,000 ton; it reached a maximum annual landing of 78,798 ton in 2001, representing an export value of around U$S 375,000,000 (SAGPyA, 2001). The largest catches of this species come from San Jorge Gulf and adjacent waters, constituting 79% of the total catch reported for the Patagonian area during 1991-2004 (Bertuche *et al*., 2005). In the coastal waters off Buenos Aires province (38º-40ºS) there is also a small scale fishery with annual landings under 30 ton (Bertuche *et al*., 2000).

The distribution of *Pleoticus muelleri* is restricted to the western Atlantic, from Rio de Janeiro, Brazil (23ºS) to Santa Cruz, Argentina (50ºS). In Brazil (Sao Paulo coast) and Uruguay (Punta del Diablo) an incipient artisanal fishery of this crustacean is also developed, with catches lower than 34 ton (Costa *et al*., 2004; Castilho *et al*., 2008a; Segura *et al*., 2008).

This demersal benthic species remains in the marine environment throughout its relatively short life cycle. In Argentina, for fishery management, this resource is considered annual (Boschi, 1989, 1997; Bertuche *et al*., 2000, 2005).

Pleoticus muelleri shows different reproductive behaviours along its distributional area, being the reproduction a continuous process in tropical areas and seasonal in higher latitudes (Boschi, 1997; Costa *et al*., 2004; Castilho *et al*., 2008a).

In the Patagonian coast, reproduction occurs between 42-47ºS during springtime and summertime. Mature and inseminated females are found in a depth range of 23 to 100 m, at temperatures ranging from 7.5º to 15.5ºC, and salinities between 32.85 and 34.26 psu (Macchi *et al*., 1998; Fernández *et al*., 2011).

The species is a determinate annual fecundity spawner. This implies that mature females have a stock of vitellogenic oocytes when the reproductive season begins, which is partially or totally spawned during the breeding period without recruitment of new oocytes during this season (Macchi *et al.*, 1992, 1998). Total fecundity estimated for January 2007 ranged between 39,981 and 674,811 oocytes for a size range of 90-222 mm total length (Fernández *et al*., 2011).

The knowledge of the reproductive process in a short life cycle species subjected to intense fishing pressure needs constant attention for its fishery management. In this study, certain aspects of the reproductive dynamics of *Pleoticus muelleri,* distributed between 42-47°S, were analyzed in order to determine spatial and temporal variations in the onset and duration of the reproductive season.

MATERIALS AND METHODS

Size structure and frequency distribution of macroscopic maturity stages of adult females

Study site and sampling

Samples and data were obtained from trawling done during 24 research cruises organized by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) between 2000 and 2010, and 59 commercial fishing fleet trips performed during 1998-2010; only vessels with main engine power greater than 800 HP were considered. The study area is located between 42-47°S and 62ºW-coastline (Fig. 1).

A conventional shrimp trawl net of approximately 35.0 m long, 1.5 m vertical opening and 45 to 50 mm mesh size was used. Trawling operations were 15-30 min long at a mean speed of 3.5 knots during the research cruises and from 15 min to 3 h 40 min at 2.7-4.1 knots during the commercial trips (Fernández, 2006; Roux, *et al*., 2007). Detailed descriptions of the sampling procedures are available in Angelescu &

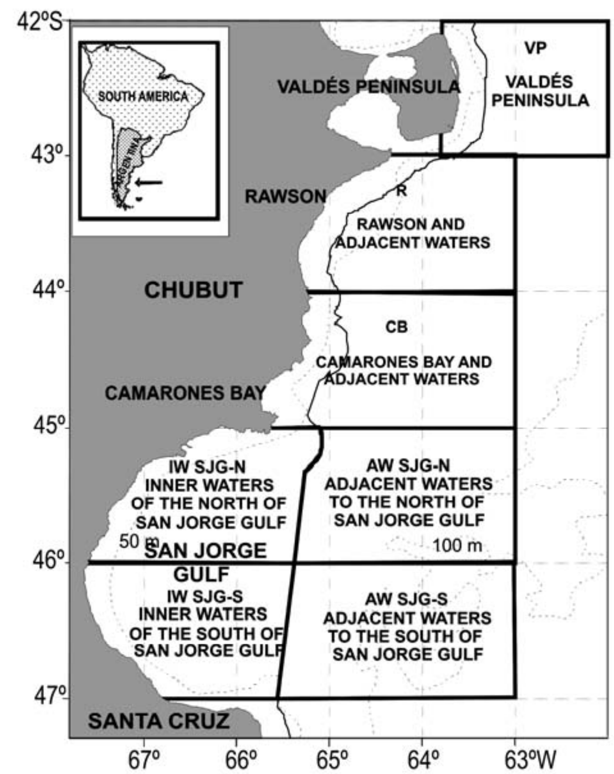

Figure 1. Definition of sectors within the study area. The line parallel to the coast indicates the boundary between the national and the provincial jurisdiction.

Figura 1. Sectores definidos dentro del área de estudio. La línea entera paralela a la costa indica el límite entre la jurisdicción provincial y nacional.

Boschi (1959). The shrimp were sexed and measured. Carapace length (CL), defined as the distance from the orbital angle to the posterior margin, was measured to nearest mm. The reproductive condition of females was determined by macroscopic observation of the ovarian development through the caparace (color and size of the gonads) according to the scale of Boschi (1989). This scale includes three stages: 1) immature (IMMF), ovaries with no apparent coloration, 2) mature (MF), ovary is green, it can reach the last segment of the abdomen, and 3) inseminated (IF), ovary as stage 2 with a spermatophore attached ventrally to the cephalothorax. According to Iorio *et al*. (2000), the macroscopic stages of mature and inseminated females correspond to advanced stages of ovarian development histologically determined (yolked oocytes and yolked oocytes with peripheral vesicles). Therefore, as spawning occurs within 2-9 days from the formation of peripheral vesicles (Macchi *et al*., 1992, 1998), the presence of spermatophores in mature females is an appropriate indicator to identify spawning grounds and reproductive seasons.

Biological data recorded during research cruises and commercial fishing fleet trips were processed using the Datofox software (Hansen & Buono, 2000). A total of 3,917 samples were standardized (catch per one hour trawl) in order to group and average them by month and sector of study. An interannual treatment was not possible because the available information during our study period was very irregular; then, each month-sector sample was the result of pool data of available years. The considered sectors were: The Valdés Peninsula (42-43ºS, 62ºW-coastline) (VP), Rawson and adjacent waters (43-44ºS, 63ºW-coastline) (R); Camarones Bay and adjacent waters (44-45ºS, 63ºW-coastline) (CB); inner waters of the San Jorge Gulf (45-47ºS, limit of provincial jurisdiction-coastline), which is subdivided north (IW SJG-N) and south (IW SJG-S) of 46ºS, and adjacent waters to the San Jorge Gulf (45-47ºS, 63ºW-limit of provincial jurisdiction), which is also subdivided at 46ºS (AW SJG-N and AW SJG-S) (Fig. 1).

Samples of different sources were not mixed. Those collected from research cruises were used to describe IW SJG-S (January to September and November), and R and BC (January, February and November), and samples taken from commercial trips were utilised for IW SJG-S (October and December), R (September, October and December) and for the remaining sectors and months.

Statistical analyses

The size-frequency distributions (intervals of 1 mm of CL) of mature and inseminated females resulting from the pooled available data for R, CB, IW SJG-N and IW SJG-S (August to February) and AW SJG-N and AW GSJ-S (June to November) were represented.

A cluster analysis using the squared Euclidean distance combined with Ward's method to analyze the size-frequency distributions of mature and insemi-nated females between sectors and months, was performed. This combination determines that the groups obtained at each level of similarity are the most homogeneous internally and the most heterogeneous among them (Diday *et al*., 1982).

To analyze the macroscopic maturity stages, the frequency of IMF, MF and IF in relation to the total number of adult females was considered. Adut females are those with lengths equal or larger than the size of first maturity. Iorio *et al*. (2000) determined the carapace length of 31 mm as the size of first gonadal maturity for females, and 28 mm for males.

In order to have a better visualization of the reproductive process, monthly percentage distributions of immature, mature and inseminated females per sectors were graphed from August to July.

The frequency of sexual maturity stages of adult females between sectors and months were analyzed. According to the available information the following comparations were possible: 1) R, CB, IW SJG-N, IW SJG-S, AW SJG-N and AW SJG-S from August to November, 2) R, CB, IW SJG-N and IW SJG-S from August to February, and 3) IW SJG-N and IW SJG-S from August to April. A Multivariate Scaling (Mardia *et al*., 1979) considering the Euclidean distance was applied to visualize similarities and differences in the structure of the frequency distributions. A cluster analysis (Johnson & Wichern, 1998) between months for each sector (Euclidean distance and average linkage) was also accomplished to determine graphically the similarities.

Maps of seasonal distribution of mature and inseminated females were elaborated with the Graphic software 'Surfer', version 7.

Microscopic examination of ovarian maturity stages

For the microscopic examination of ovaries, specimens were collected from 12 INIDEP research cruises, and 28 commercial fishing fleet trips from August 1994 to July 1998 exclusively from inner waters of San Jorge Gulf. The samples were collected every 15 days, totaling 121 samples. At each trawl station, 40-50 adult females were taken at random. The selected females (n = 2981) were preserved in 10% formalin. The carapace length, body weight and gonad weight of each female were recorded. A small portion of ovarian tissue was removed from the middle part of the ovary and processed through routine histological techniques: dehydrated in ethanol, cleared in xylol and embedded in paraffin. Sections were cut at 5-µm thickness and stained with Harris's hematoxylin followed by eosin counterstain. Microscopic observation allows the definition of five maturity stages (Macchi *et al.*, 1992): immature (ovaries with oocytes undergoing a primary growth), early maturing (ovaries with oocytes at the beginning of vitellogenesis), advanced maturing (ovaries with yolked oocytes), ripe (yolked oocytes with peripheral vesicles) and post spawning (ovaries with primary growth oocytes, with follicular mobilization and/or yolked oocytes in atresia). The results of ovarian staging were grouped monthly and the relative frequency of each stage was estimated; the number of females per month ranged between 17 and 185.

RESULTS

Size structure

The size-frequency distributions of pooled data for each sector are shown in Figure 2. The mean size of MF in R, CB, IW SJG-N and IW GSJ-S were estimated at 43.3 ± 4.4, 47.6 ± 3.2, 42.6 ± 3.3 and 40.2 ± 2.9 mm CL, respectively. For IF, the mean sizes were 43.6 ± 3.4 mm CL in R, 44.3 ± 2.4 mm CL in CB, 43.1 ± 3.3 mm CL in IW SJG-N and 41.0 ± 2.8 mm CL in IW SJG-S sector. For AW SJG-N and AW GSJ-S, MF mean sizes of 44.0 ± 4.0 mm CL and 48.2 ± 4.0 mm LC were estimated, respectively. In these sectors IF were not observed.

The analysis of the size-frequency distributions obtained for MF and IF via a cluster analysis (Fig. 3) indicated different groups. From the MF dendrogram (Fig. 3a), two groups were detected. Group 1 was composed mainly by the size structures of AW SJG-N and AW SJG-S (June to September), R (August to December), CB (July to November) and IW SJG-N (August, September, March and April). In group 2, a cluster constituted by the size structures of IW SJG-S (October to March), IW SJG-N (October to February), CB (December to February) and R (January and February) was observed. The size structure of AW SJG-N from October and November were also integrated to this cluster. Regarding the size structures of AW SJG-S (October and November), IW SJG-S (September) and AW SJG-S (July), they were excluded from the groups because of their high degree of dissimilarity**.** Mean sizes of groups 1 and 2 were 46.1 ± 3.6 mm CL and 41.4 ± 3.6 mm CL, respectively.

For IF, two groups were observed (Fig. 3b). Group 1 was comprised by the size structures of IW SJG-S (February and March), R (January and February) and CB (February); while group 2 included the size structures of CB (October to January), R (November and December), IW SJG-N (October to April) and IW SJG-S (November to January). Mean sizes of groups 1 and 2 were 39.8 ± 3.0 mm CL and 44.0 ± 3.0 mm CL, respectively.

Spatial-temporal distribution of the macroscopic maturity stages of females

Based on the samples obtained from 1998 to 2010, MF were observed more often in a much wider area than IF (Figs. 4 and 5) and the presence of the latter appeared limited to coastal areas and for a shorter period (October to April).

MF were registered from July to February in CB and from August to February in R. In IW SJG-N and IW SJG-S, the only sectors where complete monthly information were available, MF were registered from August to April in the north and from September to March in the south (Fig. 6). In adjacent waters to the San Jorge Gulf, MF occured from June (0.2-0.3%) onwards, increasing up to 31% during November in AW SJG-N; in AW SJG-S, the highest percentages (3.0%) were observed from September to November. In all sectors (except in AW SJG-N and AW SJG-S), the period between November and February was characterized with the highest percentages of MF and IF; mean values of total mature females (MF+IF) were 78.7% for R, 65.8% for CB, 66.4% for IW SJG-N and 18.7% for IW GSJG-S. From August to October, mean values were lower than 10% for all sectors. In March and April in IW SJG-N the percentages of total mature females were 27.5% and 15.3%, respectively, and 5.1% in March IW SJG-S.

As regards IF, they were observed from October to February in R and CB, between October and April in the north of the gulf (inner waters) and between November and March in the south. The highest percentages of IF were registered in December in R and in January in CB, IW SJG-N and IW SJG-S (Fig. 6).

In the Valdés Peninsula, where an occasional data was colleted in November 2001, the percentage of total mature females was 77.2%, of which 54.4% were inseminated.

Comparative analysis of the monthly frequency of sexual maturity stages of adult females between sectors: R, CB, IW SJG-N, IW SJG-S, AW SJG-N and AW SJG-S (August to November), R, CB, IW SJG-N and IW SJG-S (August to February), and IW SJG-N

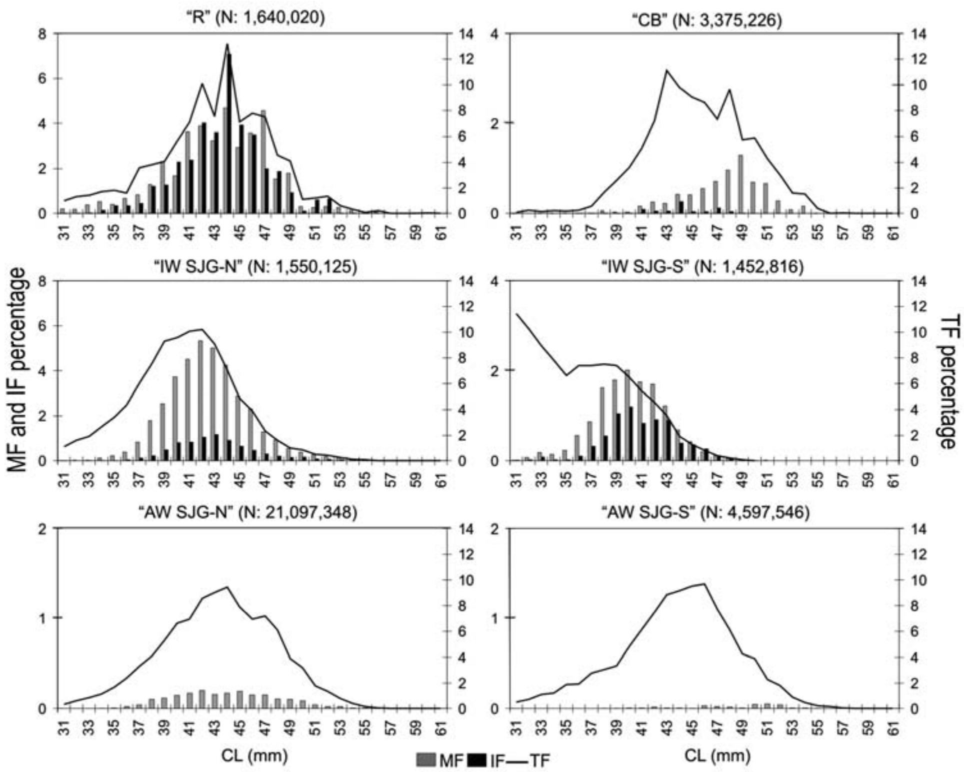

Figure 2. Size-frequency distributions of mature (MF) and inseminated females (IF) in relation to total adult females (TF) for each study sector (1998-2010).

Figura 2. Distribución porcentual de tallas de hembras maduras (MF) e impregnadas (IF) en función del total de hembras adultas (TF), de cada sector de estudio (1998-2010).

and IW SJG-S (August to April) (Fig. 7), differentiated two groups, which correspond to those described in the above paragraph. Group 1 constituted by August, September and October which showed a homogeneous behaviour (Figs. 7a-7c). Group 2 was composed by the remaining months: November (Fig.7a), November, December, January and February (Fig. 7b) and November, December, January, February and March (Fig. 7c), with heterogeneous characteristics between months and sectors. The highest homogeneity of IW SJG-S in relation to the other sectors was observed (Figs. 7a-7c), as well as the integration of April IW SJG-N and IW SJG-S, and November IW SJG-S, to the first group of months (Fig. 7c).

The cluster analysis per sector (Fig. 8) showed that the groups 1 and 2 defined in the Multivariate Scaling analysis were differentiated at higher dissimilarity levels in R, CB, IW SJG-N, AW SJG-N and AW SJG-S (above 20%) than in IW SJG-S. This analysis also revealed that November, within months of group 2, differentiated from December, January and February in R, while November and December were separated from February and January in CB. In IW SGJ-S, December, January and February were also grouped, while November was integrated to the first group. August, March and April in IW SJG-N and IW SJG-S were also integrated to group 1.

In relation to the adjacent waters to the San Jorge gulf, it was observed that November (group 2) was clearly differentiated from August, September and October (group 1) in AW SJG-N, while November and October (group 2) were separated from August and September (group 1) in AW SJG-S.

Temporal analysis of microscopic ovarian maturity stages in the San Jorge Gulf

Ovarian maturity stages in samples of *P. muelleri* from the San Jorge Gulf, as determined by histology, varied considerably according to the sampling month and sector (Fig. 9). A noticeable predominance of immature females was observed in IW SJG-S from autumn (May) to the beginning of springtime (October) (Fig. 9a). In August, an incipient beginning of the vitellogenesis (1.39%) was observed. Then, this stage increased to reach a value close to 20% in

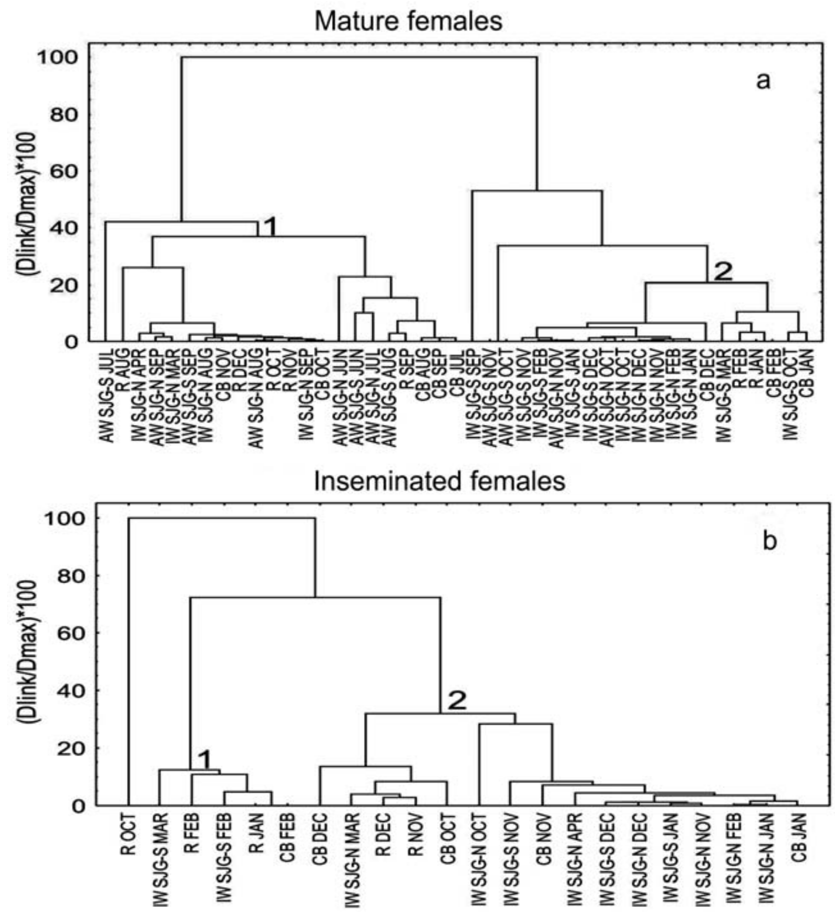

Figure 3. a) Dendrograms of similarity of monthly size structure of sectors R, CB, IW SJG-N, IW SJG-S, AW SJG-N and AW SJG-S for mature females, and b) R, CB, IW SJG-N and IW SJG-S for inseminated females.

Figura 3. a) Agrupamientos jerárquicos de las estructuras de tallas mensuales de los sectores R, CB, IW SJG-N, IW SJG-S, AW SJG-N y AW SJG-S para hembras maduras, y b) R, CB, IW SJG-N y IW SJG-S para hembras impregnadas.

November. There was no information from December, but the stages of advanced maturing and ripe predominated in January. In this month first signs of post spawning (2.25%) were also observed. The presence of mature females remained at lower rates in February and March than in January, increasing the post spawning phase towards the end of summertime and early autumn.

In IW SJG-N (Fig. 9b), the ovarian maturation process also began in August, but unlike the south, the oocyte growth progressed faster in September, with the presence of females in advanced maturing stage (7.49%) from this month onward. This stage persisted in the following months as well as the ripe stage but with different intensity, the former reaching values of around 50% between December and February. The first post spawning specimens in the samples were observed in October. There was no information for April, but all the females analyzed in May were in post spawning or immature stages.

DISCUSSION

The spatial-temporal analysis of reproductive activity of red shrimp *Pleoticus muelleri* adult females carried out gathering all the scattered information collected between 1994 and 2010, have increased our knowledge on the reproductive dynamics of this species in the San Jorge Gulf and adjacent waters, areas from which the largest reported landings of the fishery come from.

Mature and inseminated females, according to De la Garza *et al*. (2008) are at least one year old. *P. muelleri* can reach a theoretical maximum age of 3.5 years old that corresponds to L_∞ of 57.0 mm CL in the case of females.

In *P. muelleri* from Patagonian coast, reproduction takes place mainly during springtime and summertime between 42 and 47ºS. Macroscopic observation of adult females at different stages of maturity indicates that the reproductive activity of this species has

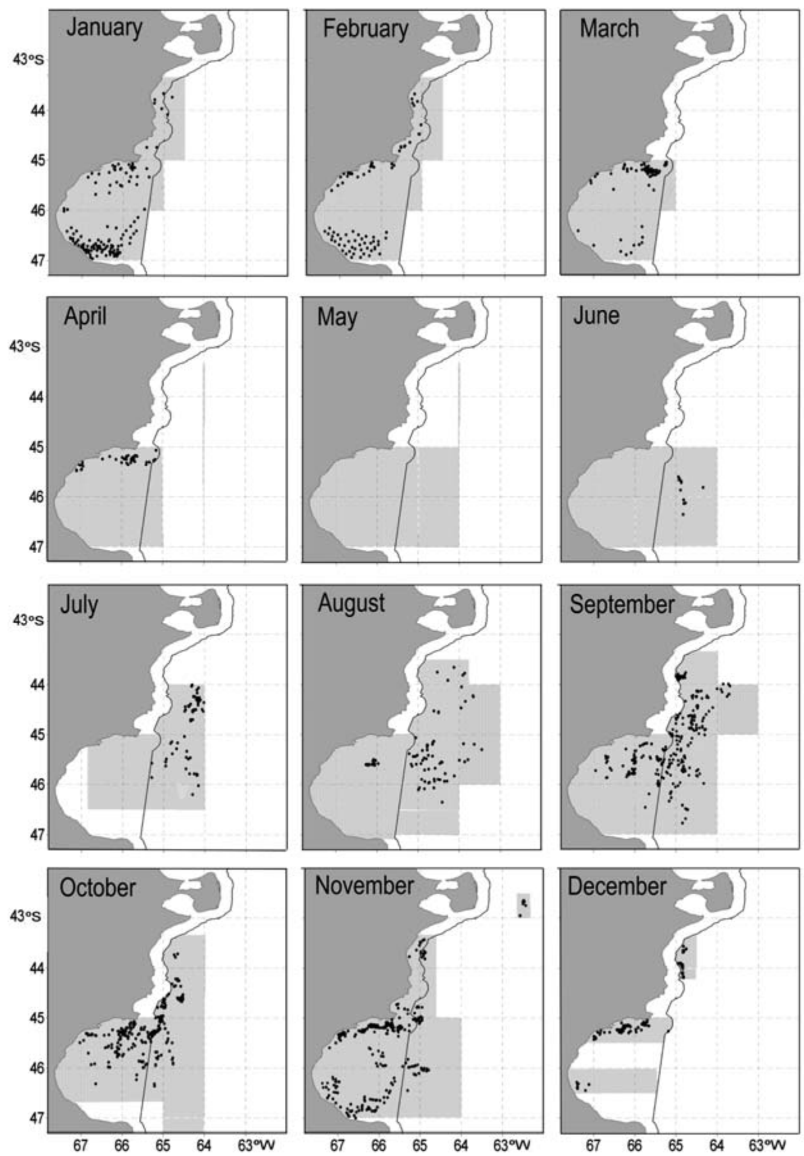

Figure 4. Spatial-temporal distribution of shrimp mature females (1998-2010). Light grey indicates areas sampled during research cruises and by the commercial fishing fleet.

Figura 4. Distribución espacio-temporal de las hembras maduras de langostino (1998-2010). Las áreas grises son las zonas de procedencia de la información, considerando tanto las campañas de investigación como las mareas de la flota comercial langostinera.

latitudinal variations as well as temporal heterogeneity in all surveyed sectors. This coincides with the results of Castilho *et al*. (2008b) for *Pleoticus muelleri* of the coast of São Paulo, Brazil, and those reported by Crocos & Van der Velde (1995) and Crocos & Coman (1997) for other penaeids (*e.g. Penaeus semisulcatus*, *P. longistylus* and *P. latisulcatus*) from Carpentaria Gulf, Australia. Castilho *et al*. (2008b) indicated seasonal variations in the frequency of mature females related to bottom water temperature. Crocos & Van der Velde (1995) observed a seasonal and interannual variability in reproductive patterns for *P. semisulcatus*, both in the adult female abundance and in proportion of mature females as in the beginning and intensity of spawning. These authors indicated that penaeids have complex seasonal patterns of reproduction, especially associated with the variability of environmental conditions.

In R, CB and IW SJG-N sectors, where the highest proportions of MF and IF were recorded between November and February, estimations of mean abundance of total mature females for this period were

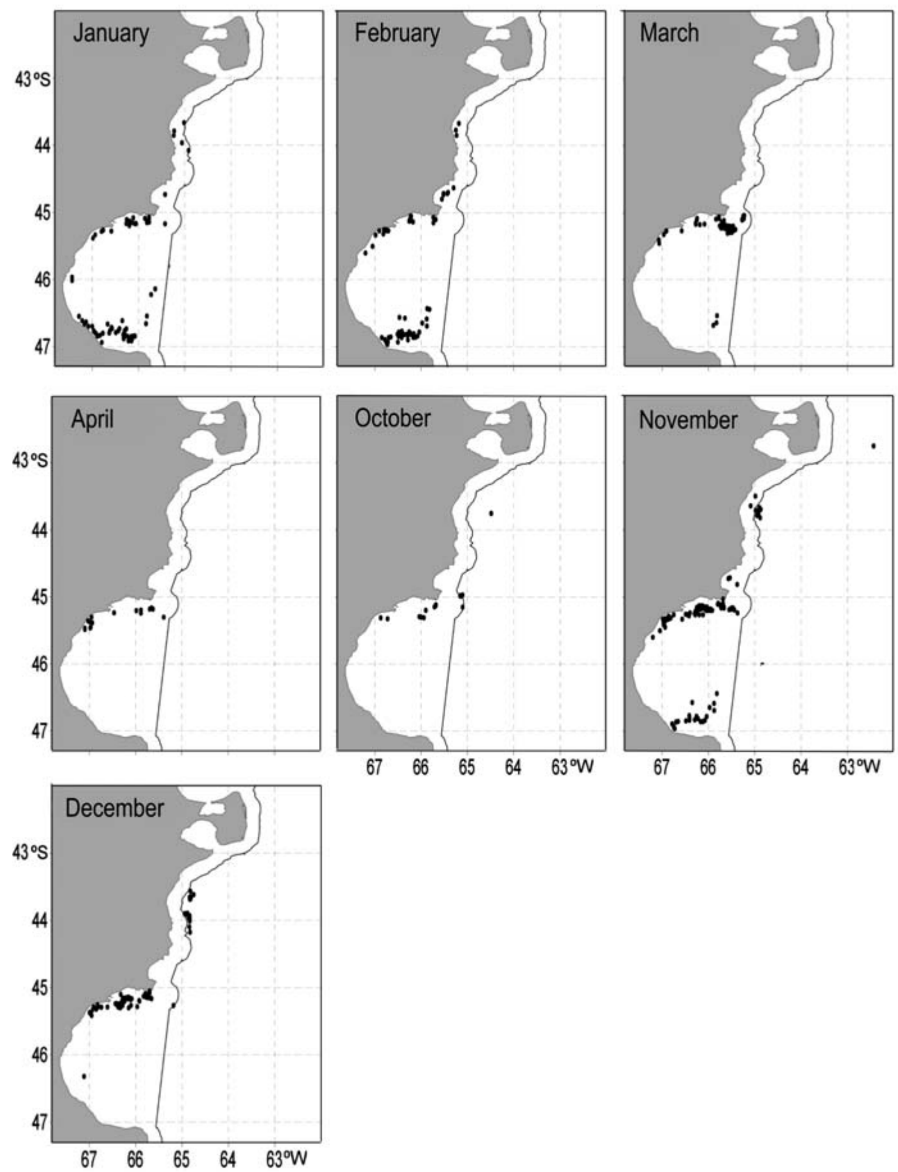

Figure 5. Spatial-temporal distribution of shrimp inseminated females (1998-2010).
Figura 5. Distribución espacio-temporal de las hembras impregnadas de langostino (1998-2010).

also greater than IW SJG-S, according to Fernández & Hernández (*pers. comm.*). Mean abundance of total mature females in number of individuals per hour trawl (data of the commercial fleet from 2006-2010) were 1,343 ind h^{-1} in R, 1,810 ind h^{-1} in CB and 5,224 ind h^{-1} en IW SJG-N, while in IW SJG-S it was estimated in 240 ind h^{-1}. Proportions of MF and IF recorded in the Valdés Peninsula coast in November are similar to that registered in Rawson sector. The low percentages of MF and IF observed in the southern gulf sector could be underestimated due to occurrence of some inaccessible areas for trawling where shrimps could be located.

Histological and macroscopic studies performed for San Jorge Gulf, showed that ovary maturation starts in August, both north and south, while spawning begins in early springtime (October) in the northern sector and in late springtime (November-December) in the south as mentioned by Fernández & Macchi (2010). The presence of IF (close to spawning) in coastal waters until early autumn, April in the north and March in the south, as well as the observation of eggs and larvae from December to April in the northern gulf sector by Boschi (1989) and from November to March in both the north and south of the gulf by De la Garza *et al*. (2008), support these findings.

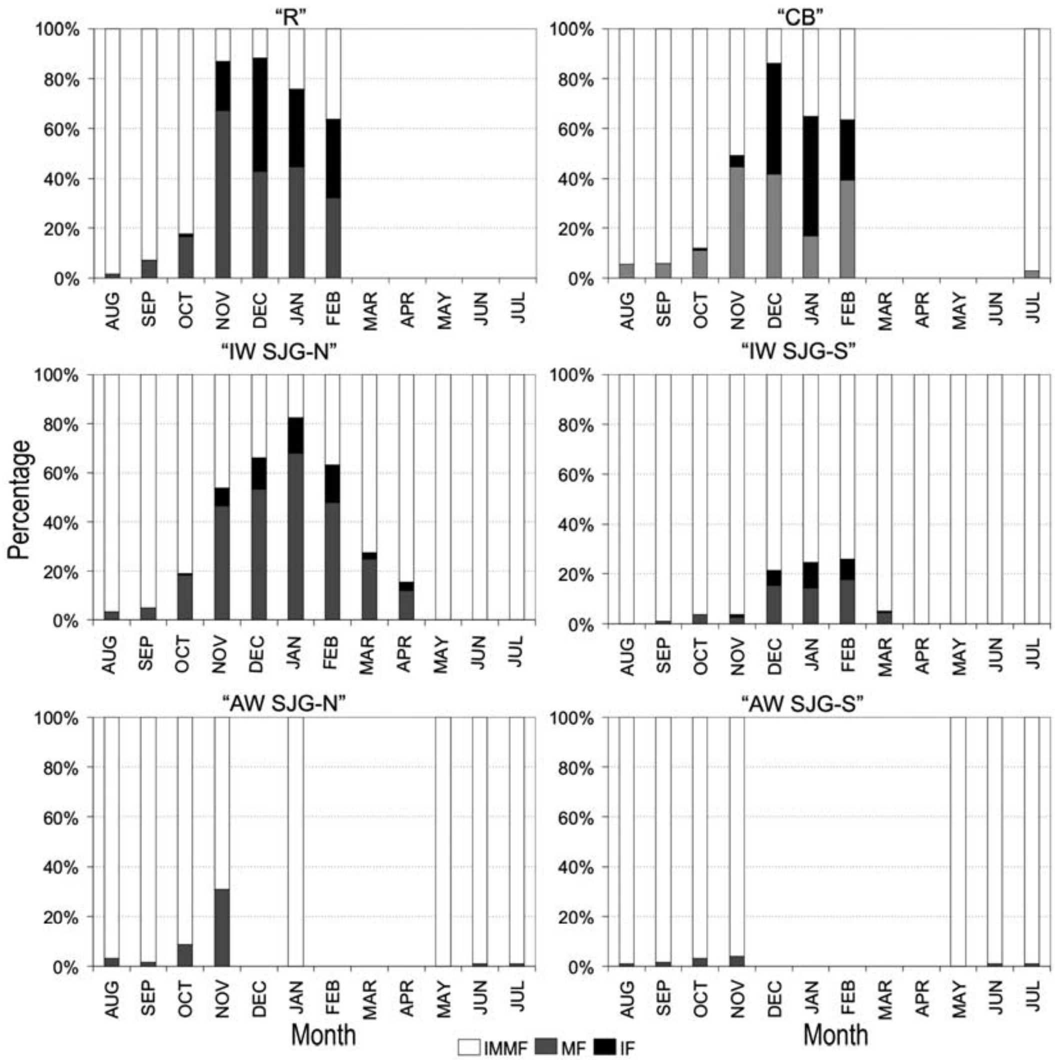

Figure 6. Monthly percentage distribution of immature, mature and inseminated females of shrimp from each study sector (1998-2010).

Figura 6. Distribución porcentual mensual de hembras inmaduras, maduras e impregnadas de langostino para los sectores de estudio considerados (1998-2010).

Regarding the end the reproductive process in R and CB, where we had no available data from March to June, Ruiz & Mendia (2008) found in R that it finishes by the end of March, as all sampled females were immature in April.

The observation of MF in adjacent waters to the San Jorge Gulf and Camarones Bay during wintertime in low abundance (mean value of 67 ind h^{-1}, 0.1% of the catch) according to Fernández & Hernández (*pers. comm.*), could be related to the migration pattern of this species. In agreement with migration studies of *P. muelleri* done by De la Garza *et al*. (2008), the MF observed during June and July in adjacent waters to the San Jorge Gulf and in the area between 44-45ºS (CB) would come from inner waters of the gulf; they could be a remaining fraction of the summertime ovarian maturation. De la Garza *et al.* (2008) suggested a migration of the shrimps from inside the gulf towards the east-northeast waters (adjacent waters); where this species is frequently captured between June and July. In early springtime, the shrimp moves towards CB and R in search of better environmental conditions related with food availability and reproduction.

The space-time analysis of size structures of MF showed that the largest sizes were found in the adjacent waters to the San Jorge Gulf as well as in Rawson and Camarones Bay in springtime. This agrees with the results of Boschi (1989) and De la Garza (2008), describe a clear increase of the mean

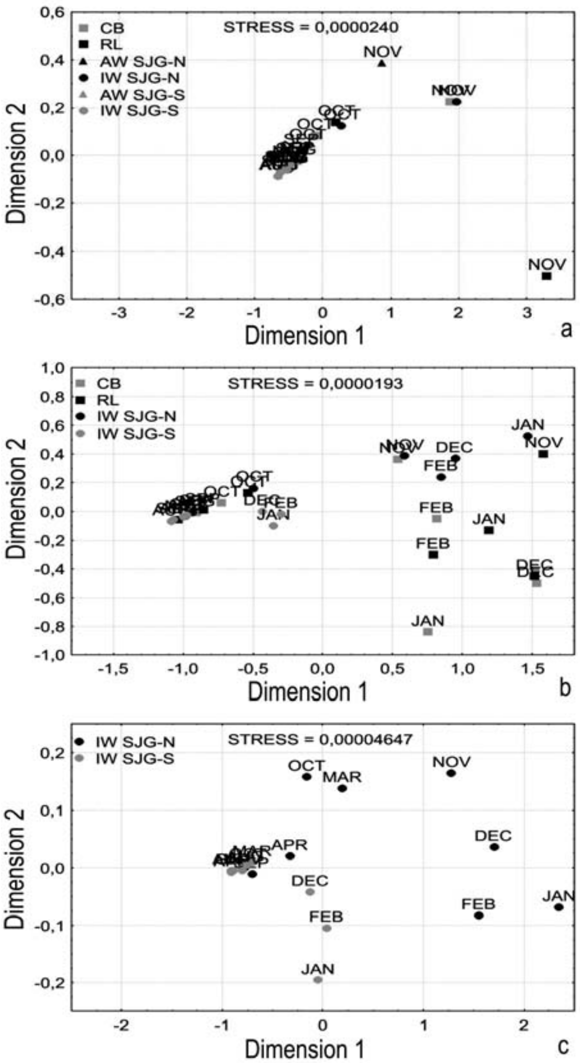

Figure 7. Multivariate Scaling of the monthly frequency of sexual maturity stages of adult females among sectors. a) Sectors: R, CB, IW SJG-N, IW SJG-S, AW SGJ-N and AW SJG-S (August to November), b) sectors: R, CB, IW SJG-N and IW SJG-S (August to February), and c) sectors: IW SJG-N and IW SJG-S (August to April), 1998-2010 period.

Figura 7. Escalamiento multivariado de las frecuencias mensuales de los estadios de madurez de hembras adultas entre sectores. a) Sectores R, CB, IW SJG-N, IW SJG-S, AW SGJ-N y AW SJG-S (agosto a noviembre), b) sectores R, CB, IW SJG-N y IW SJG-S (agosto a febrero), y c) sectores IW SJG-N y IW SJG-S (agosto a abril), período 1998-2010.

and modal sizes from the south of San Jorge gulf to Rawson, through the mouth of the gulf. According to De la Garza *et al.* (2008) in the second half of the year, individuals with sizes larger than 37 mm CL for males and 44 mm CL for females are located towards the north-northeast and in adjacent waters to the San Jorge Gulf. Sizes smaller than 36 and 43 mm CL for males and females, respectively, are observed in the inner waters of the gulf. From November onward, sizes larger than 43 mm CL are also observed north of 45º10'S, suggesting a migration of adult shrimps from the gulf towards north. Such a clear spatial-temporal pattern was not observed for the IF sizes.

The space-time variability of the reproductive process would be related to the development of environmental processes, especially with the change of water temperature and light period (Macchi *et al*., 1998; Fernández *et al*., 2011). In our study area a bottom water temperature gradient from north to south of 1.5-2ºC is observed during all seasons. According to Louge *et al*. (2009, 2011) during wintertime, the mean values of bottom water temperature ranged between 8.5-9.5ºC in 43-45ºS, while in the north and south of San Jorge Gulf they ranged between 8.0-8.5ºC and 7.0-7.5ºC, respectively. In summertime, mean values were between 12.0-15.0ºC in 43-45ºS, and in the gulf they ranged between 11.0-12.0ºC in coastal waters and 8.0-9.0ºC in the inner area. Regarding the importance of water temperature in the reproductive process, the effect of its increase to induce maturation and spawning has been widely studied (Macchi *et al*. 1998, Fernández *et al.*, 2011). Fernández *et al*. (2011), linked the spatial distribution of abundance of mature and inseminated females with depth and bottom water temperature and salinity, noting a direct relationship between abundance and bottom temperature. The authors also detected a higher temperature range preference for inseminated females than for the mature ones.

The shoreward movement of ripe females, evidenced by the restricted occurrence of IF in coastal waters, where reproduction takes place, would be related to the search of suitable spawning and nursery grounds (Boschi, 1989; Fernández *et al*., 2007; De la Garza *et al.*, 2008). These environments are characterized by warm temperatures and the development of frontal systems (Boschi, 1989; Bogazzi *et al*., 2005, De la Garza *et al.*, 2008). These fronts have high primary and secondary productivity that would ensure the best opportunities for larval survival. In addition, these environments are areas of low depth and scarce hydrodynamics suitable for development of juveniles (Fernández, 2006; Fernández *et al*., 2007). Crocos *et al*. (1995) indicate that the migration of spawners of *Penaeus semisulcatus* in the gulf of Carpentaria, from deep to coastal areas, was related to the development of the thermocline and a certain hydrographic regime which would facilitate larval advection to nursery grounds. Reproductive migrations have been descrybed for several species of prawns and shrimps of the

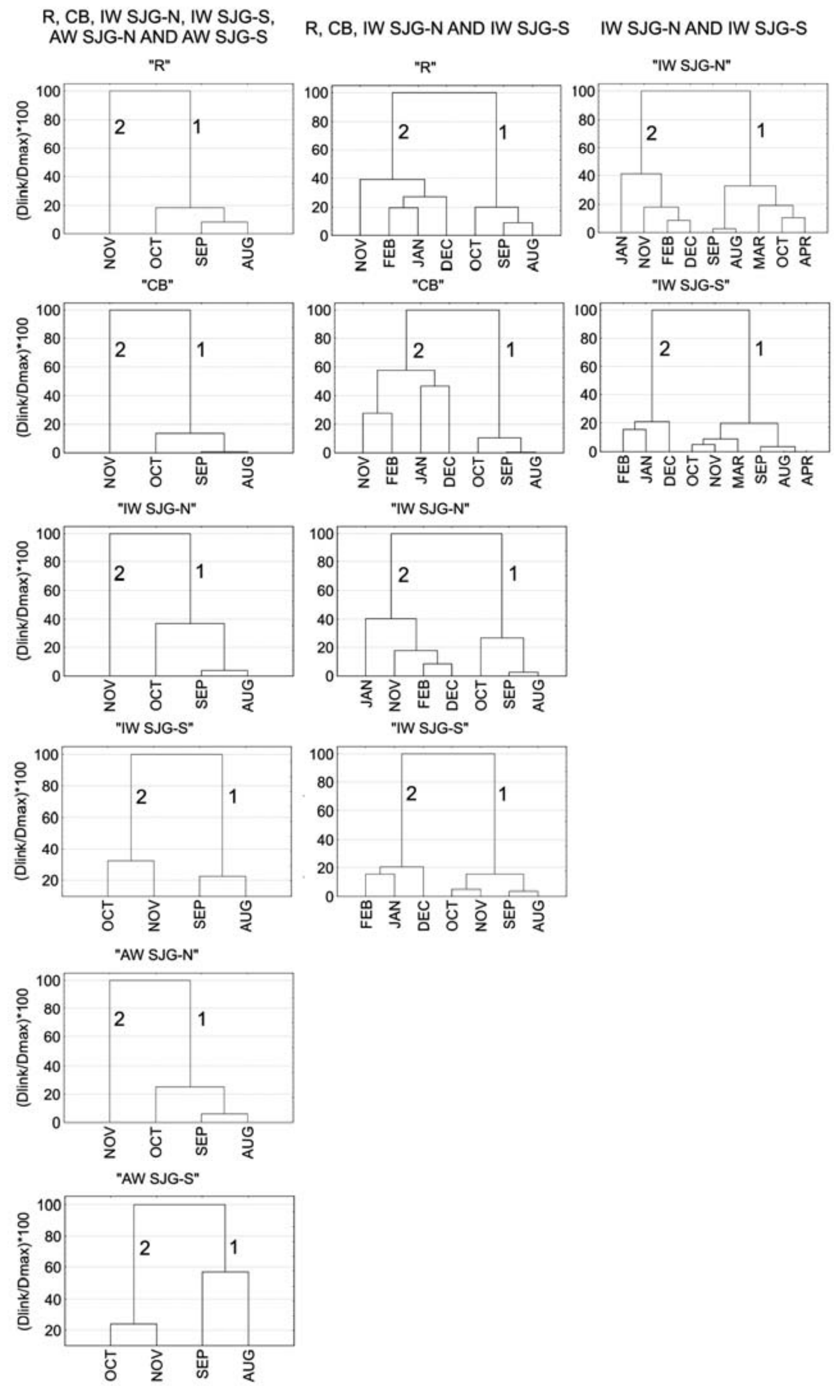

Figure 8. Similarity dendrograms monthly frequencies of sexual maturity stages of adult females per sector. Sectors: R, CB, IW SJG-N, IW SJG-S, AW SGJ-N and AW SJG-S; R, CB, IW SJG-N and IW SJG-S; and IW SJG-N and IW SJG-S, 1998-2010 period.

Figura 8. Agrupamientos jerárquicos de las frecuencias mensuales de los estadios de madurez de hembras adultas por sector. Sectores: R, CB, IW SJG-N, IW SJG-S, AW SGJ-N y AW SJG-S; R, CB, IW SJG-N y IW SJG-S; y IW SJG-N y IW SJG-S, período 1998-2010.

Solenoceridae and Penaeidae families. Baelde (1992) describes for *Haliporoides sibogae*, a deep water solenocerid from southeast Australia, a movement along the coast from south to north searching grounds to spawn. Dall *et al.* (1990) indicate that the spawning migrations are part of the biological cycle for most

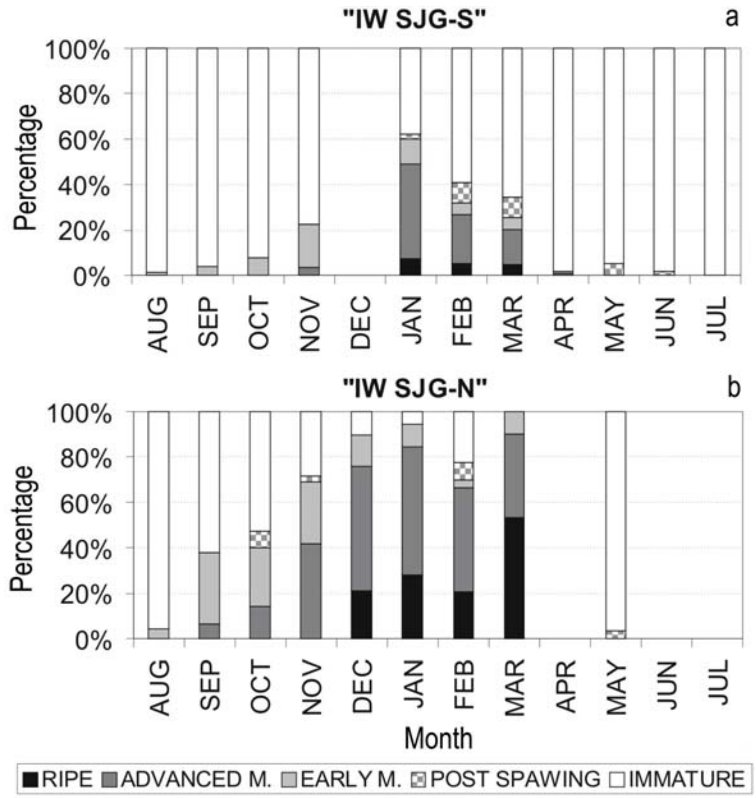

Figure 9. Stages of ovarian development in adult females from inner waters of San Jorge Gulf, a) IW SJG-S and b) IW SJG-N, 1994-1998 period.

Figura 9. Estadios de desarrollo ovárico en hembras adultas en aguas interiores del golfo San Jorge, a) IW SJG-S y b) IW SJG-N, período 1994-1998.

littoral prawns and shrimps, and that migrations occur both towards offshore deeper and inshore shallower waters.

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