Fisheries Research 110 (2011) 217–223

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Short communication

The reproductive cycle of the red octopus *Enteroctopus megalocyathus* in fishing areas of Northern Patagonian coast

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ARTICLE INFO

Article history:
Received 31 December 2010
Received in revised form 16 February 2011
Accepted 24 March 2011

Keywords:
Atlantic Ocean
Cephalopods
Enteroctopus megalocyathus
Fishery
Reproductive biology

ABSTRACT

The reproductive cycle of *Enteroctopus megalocyathus* was studied based on monthly diving surveys carried out between July 2004 and June 2007 over fishing areas at San José and Nuevo gulfs (Northern Patagonian coast, Argentine). Spermatophore production and storage and ovary-weight increase followed the trend in sea bottom temperatures, and reached maximum values at the beginning of summer. Mature males were found from mid winter onwards, while a low proportion of females showed spermatangia attached to the distal oviducts from mid spring to mid summer when they attained advanced maturity stages. A low frequency of spawning activity was observed during summer and winter months. There were no significant seasonal differences in the sex ratio. Total body weight (BW) and dorsal mantle length (ML) at 50% maturity were estimated at 1072 g and 135.4 mm for males and at 1613 g and 158.5 mm for females. Potential fecundity ranged from 1429 to 6427 oocytes and the number of fully developed spermatophores storage ranged from 1 to 13. Both, potential fecundity and number of spermatophores were significantly correlated with BW and ML. Although mating and breeding can occur in fishing areas, our results suggest that they are most likely to take place in sites deeper than the fishing grounds. This pattern is discussed considering the temperature-regulated aspects of cephalopods reproduction and the local oceanographic processes occurring in the gulfs.

1. Introduction

Most cephalopods are seasonal breeders, semelparous and short lived organisms, for which environmental variability plays an important part in their life cycles. Because migratory movements appear to be relatively synchronized to their reproductive cycle, the period of maturation has an intrinsic role influencing the population size and location, which in turn determine their availability to fisheries (Boyle and Boletzky, 1996; Semmens et al., 2007). In this context, reliable knowledge of fished cephalopods reproductive biology is essential to the understanding of their life history and dynamics to assist assessment and management (Leporati et al., 2008; Guerra et al., 2010).

The red octopus, *Enteroctopus megalocyathus* (Gould, 1852), is a cold water adapted species of sub-Antarctic distribution. In the southwest Atlantic Ocean, it has been found from the San Matías Gulf (41°30′S 64°40′W) to the Beagle Channel (54°53′S 67°50′W), Falkland (Malvinas) Islands (51°50′S 59°40′W) and Burdwood Bank (56°10′S 54°20′W), with a bathymetric distribution ranging from intertidal areas up to 170 m deep. In the southeast Pacific Ocean (Chilean coast), geographic range comprise from 42° to 56°S, and up to 240 m depth (Ré, 1984, 1998a,b; Osorio et al., 2006; Villanueva and Norman, 2008; Ibáñez et al., 2009; Ortiz, 2009).

Understanding the life history of *E. megalocyathus* is particularly important because commercial fishing for this species is developing. In Argentina, the red octopus is harvested by small-scale fisheries that operate by diving in shallow waters or by extracting the animals from rocky intertidal shores located along the Patagonian coast. In the north Patagonian Atlantic coast (San José and Nuevo gulfs) (Fig. 1), the species is harvested mainly by diving using an iron-hook from holes and crevices located in isolated rocky outcrops or in submerged abrasion limestone platforms (Ré, 1998b; Ortiz et al., 2006). The fishing period is restricted from March to November, when octopus abundance in shallow waters is highest (Ré, 1998a,b). Although fisheries of *E. megalocyathus* are unregulated and there are no official statistics of their landings, Ré (1998b) estimated captures from 10 to 15 tons per year for this area, while Cinti et al. (2003) estimated around 9–10 tons for intertidal harvesting in Camarones Bay (44°42′S 65°54′W) and its surrounding areas. Landings are unknown for the southern fishing grounds in the Atlantic Ocean. In contrast, captures of *E. megalocyathus* are approximately 500 tons per year in the Chilean coast (Ibáñez and Chong, 2008).

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doi:10.1016/j.fishres.2011.03.016

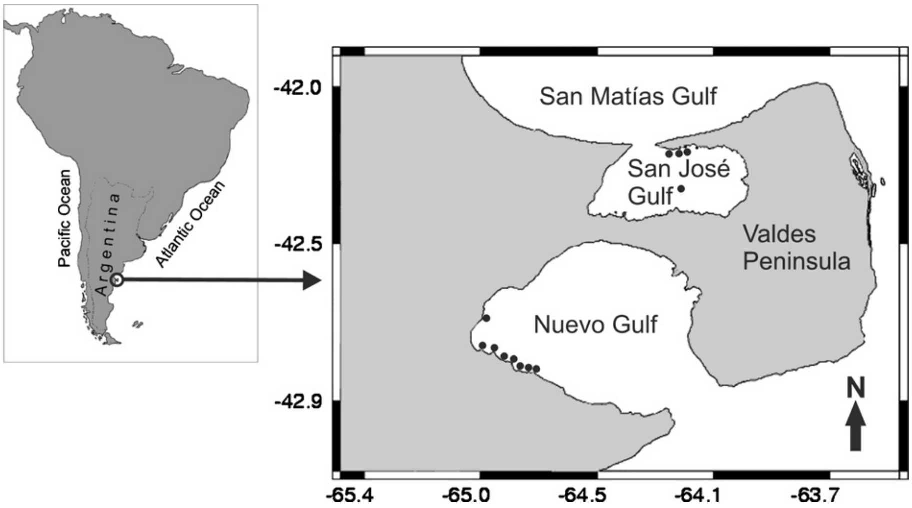

Fig. 1. Study area. Dots indicate sampling sites in the two northern Patagonian gulfs.

E. megalocyathus is a relatively large benthic species which can reach 1 m total length and 4 kg total weight (Ré, 1998a; Chong Lay-Son et al., 2001). In subtidal areas, females have been seen to attach egg strings to the roofs of holes and crevices on a few occasions, providing parental care to their embryos until they hatch. This species has large eggs which give rise to the largest planktonic hatchling octopus reported (mean total length: 18.3 mm) (Ortiz et al., 2006; Villanueva and Norman, 2008). Males have large spermatophores which can reach up to 390 mm length depending on male body size (Ré, 1984). Previous studies in the Atlantic and the Pacific Oceans seem to indicate a maximum reproductive activity during spring and summer (Ré, 1984; Chong Lay-Son et al., 2001). However, many basic aspects of their reproductive biology and population dynamics are poorly known or remain to be investigated. In this context, the objectives of this paper included the determination of the main reproductive parameters of *E. megalocyathus* such as the fecundity, the sex ratio, the size at maturity, and the study of the timing of mating and spawning in San José and Nuevo gulfs.

2. Materials and methods

2.1. Sampling sites and data collection

Specimens were collected during monthly sampling trips carried out between 2004 and 2007 in Nuevo Gulf and 2004 and 2005 in San José Gulf (Fig. 1). Octopuses were caught at depths ranging from 3 to 25 m, by free or scuba diving, and with a hook used to capture red octopus. After capture, each den was examined for egg masses of *E. megalocyathus*. When found, the egg clutches were removed using the hook and assigned to an approximate stage of embryonic development according to Naef (1928). The egg masses found in San José Gulf have already been reported elsewhere (Ortiz et al., 2006). Sea water temperature was registered at depth of the fishing sites at each date of sampling, using a water multianalyzer.

After capture a total sample of 1171 red octopuses was sexed on the basis of the presence of the hectocotylus. However, all the other observations and measurements were performed in 1045 animals which did not present damaged tissue (i.e. torn mantles or reproductive systems) as a consequence of the fishing process.

In fresh animals dorsal mantle length (ML) and total body weight (BW) were measured to the nearest 1 mm and 1 g respectively. Additionally, each female was examined for the presence of spermatophores or spermatangia (i.e. evaginated spermatophores) (Perez et al., 1990) attached to the distal oviducts. Visceral masses were preserved in 10% formaldehyde solution and then reexamined and assigned to a maturity stage according to a macroscopic maturity scale developed for *E. megalocyathus* (Tables 1 and 2) (Ortiz, 2009). Male scale does not include the spent stage because it was not observed in samples. In each individual, the whole reproductive system (RS) was weighed. Besides, the weight of the ovary (OV), distal oviducts and oviducal glands (DO) in the female, and the testis (TE), spermatophoric sac and terminal organ (SS) in the male were recorded to the nearest 0.01 g.

Potential fecundity (PF) was estimated in females belonging to the advanced maturity stage (Table 1) by counting the number of striated and vitellogenic oocytes in two subsamples of approximately 5–6% each, taken from the dorsal and from the mid area of the gonad and scaling this to total ovary weight. Relative fecundity

Table 1
Macroscopic maturity stages for females of *Enteroctopus megalocyathus*.

Maturity stages of females	Macroscopic characteristics
I. Virgin	Difficult to determine sex with the eye naked Hard to differentiate reproductive system from the rest of the internal organs
II. Immature	Small-sized, white ovary filled with liquid. The reproductive system differentiates itself from the rest of the internal organs, but its size is still small compared to them. Distal oviducts narrow with respect to oviducal glands. White oviducal glands. Proximal oviducts are distended and easily visualized
III. Juvenile	Medium-sized ovary and from white to ivory in color. Ivory oviducal glands. Distal oviducts slightly swollen. Proximal oviducts not easily visualized. A few, small and longitudinally striped oocytes become evident through the ovary wall. Slightly distinguishable rings in the proximal oviducts
IV. Advanced maturity	Maximum-sized, ivory ovary of a firm consistence. Reproductive system of similar size to the rest of the visceral mass. Oviducal glands with two distinct bands: one narrow and ivory band and one broad and dark band. Distal oviducts very swollen, widened and filled with liquid. Medium-sized oocytes, with longitudinally striped appearance recognizable through ovary wall. Ring-like structures in the proximal oviducts clearly distinguishable
V. Mature-spawning	Pink ovary lacking in firmness. Oviducal glands with ivory and dark bands. Unexpanded distal oviducts. Mature (smooth) oocytes in the proximal oviducts and free in the ovary lumen
VI. Spent	Pink and flaccid ovary, with a few or no eggs inside. Post-ovulatory follicles distinguishable through the ovary wall. Thick and unexpanded distal oviducts. Widened proximal oviducts

Table 2
Macroscopic maturity stages for males of *Enteroctopus megalocyathus*.

Maturity stages of males	Macroscopic characteristics
I. Virgin	Difficult to determine sex and recognize terminal organ with the eye naked. Hard to differentiate genital bag from the rest of the internal organs
II. Immature	White testicle bigger than spermatophoric complex. Terminal organ easy to recognize. Well defined reproductive system. Genital bag of smaller-size appearance than the rest of visceral mass
III. Advanced maturity	Large, yellowish testicle, of bigger size appearance than spermatophoric complex. Ducts of the spermatophoric complex slightly swollen with shreds of spermatophores in formation inside. Eventually, small fragments of an outer tunic without inner content can be found in the spermatophoric sac. The reproductive system has a similar size than the rest of the viscera
IV. Mature-spawning	Turgescent spermatophoric complex of a size appearance similar or bigger than testicle with wide duct lumen. Mature spermatophores stored in the spermatophoric sac and/or the terminal organ. Maximum-sized reproductive system (often bigger than the rest of visceral mass)

(RF) in females was estimated as the ratio of PF to BW. Three egg clutches could be completely extracted. Because they were found along with brooding females having an empty ovary, eggs were counted to obtain the real fecundity. In mature-spawning males (Table 2), PF was calculated by counting the number of ripe spermatophores stored in the spermatophoric sac (Otero et al., 2007) and terminal organ of each individual.

2.2. Data analysis

Several gravimetric indices were calculated as: organ weight × 100/(body weight – organ weight). This formula was used to compute RSI, TEI, SSI, OVI, and ODI. The relative frequencies of each sexual maturity stage, the seasonal trend of indices values, and results of finding of egg clutches in the field were analyzed to describe the reproductive cycle. For both sexes, Persons correlation coefficient (r) was used for evaluating the covariation between PF and ML or BW. The sex ratio was calculated over the total sample and by seasons. Deviations from the expected 1:1 ratio were tested using the χ^2 test and Yates correction was applied for those periods with <25 animals (Sokal and Rohlf, 1979; Zar, 1996).

To determine size at maturity ($BW_{50\%}$ and $ML_{50\%}$), males at maturity stage IV and females at IV and V stages were considered ‘mature’. Because *E. megalocyathus* females in spent condition undergo a significant reduction of size and weight (Fig. 2), stage VI was not considered in this analysis. $BW_{50\%}$ and $ML_{50\%}$ were calculated after fitting the proportion of mature individuals grouped at 150 g and 15 mm classes respectively to a logistic model as in Crespi-Abril et al. (2008). Goodness of fit of the model was tested according to the same authors.

3. Results

3.1. Seasonality of maturation

A delay from 3–4 months was observed in the increase of the RSI of the females compared to the males, and maximum RSI values coincided in both sexes, one or two months later than the maximum seawater temperature was registered. Nevertheless, spermatophore production and storage and ovary-weight increase represented by SSI and OVI, followed the trend in sea bottom temperatures (Fig. 3).

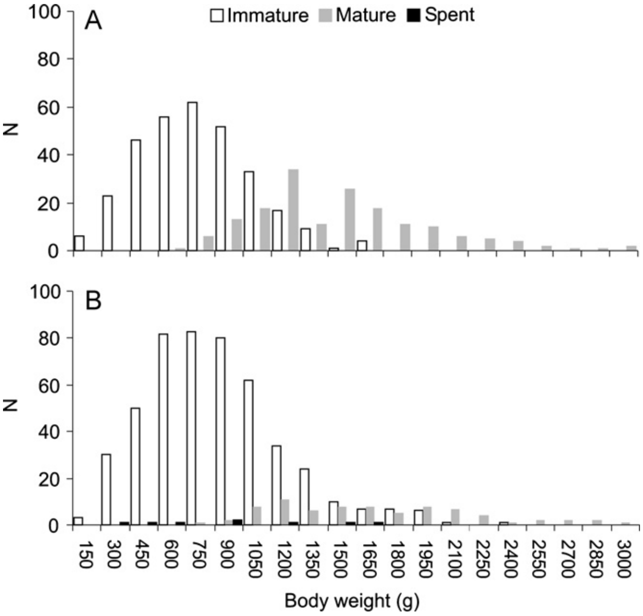

Fig. 2. Weight-frequency distribution and maturity condition of males (A) and females (B) of *Enteroctopus megalocyathus* caught in Nuevo and San José gulfs. Specimens are grouped into immature (stages I, II and III of both sexes), mature (males at stage IV, and females at stages IV and V) and spent (females at stage VI).

3.1.1. Males

The ML of males (n = 478) ranged from 48 mm to 220 mm and the BW ranged from 40 to 2950 g (Fig. 2). From mid-end of summer to the end of autumn, indices values remained low maturing males prevailing (Figs. 3 and 4). In winter, TEI began to increase, while SSI remained relatively unchanged owing to the low frequencies of males with spermatophore storage. The maximum frequencies of animals having spermatophores storage only in spermatophoric sac were observed in mid winter. From this period, this proportion decreased while frequency of specimens with spermatophores also in terminal organ increased. TEI peaked in November of the three years, but as a consequence of sperm release from testis and spermatophore storage in spermatophoric sac and terminal organ TEI started to decreased, and SSI reached maximum values one or two months later, coinciding with the peak of RSI values (Fig. 3). Accordingly, almost all males were mature-spawning (stage IV) by these months (Fig. 4).

3.1.2. Females

Females analyzed (n = 567) ranged from 58 mm to 220 mm ML and 115 to 2918 g BW (Fig. 2). The lowest indices values were registered from the end of summer to early winter. At the mid of spring, females in stage IV began to be caught. As a result, a marked increase of RSI was registered, primarily due to an increase in ovary weight. Highest OVI and RSI were observed in January 2005, December 2005 and December 2006. Similar results were obtained when ODI was taken into consideration (Figs. 3 and 4). Mature-spawning (stage V) and spent (stage VI) females were rarely obtained over the fishing areas. They were mostly caught from late spring to early autumn, but also appeared in winter (Fig. 4).

3.2. Mating and spawning activity

Spermatangia attached to distal oviducts were observed in five stage-IV females, collected in November 2004 (one animal), January

Table 3
Results of the survey on egg clutches of *Enteroctopus megalocyathus* in the fishing areas of the north Patagonian Atlantic coast.

Date of collection	Sampling site	Approximate stages of embryonic development at time of egg collection	Number of eggs in the clutch
1-Mar-2005	SJG[a]	I–VI	–
3-Mar-2005	SJG[a]	I–VI	1469
3-Mar-2005	SJG[a]	I–VI	–
22-Apr-2005	SJG[a]	XIV–XVI	–
18-Ago-2005	SJG[a]	XX (at hatching)	–
18-Ago-2005	SJG[a]	I–VI	–
23-Dec 2005	GN	I–VI	–
28-Feb-2006	GN	I–III	964
16-Mar 2006	GN	VII–IX	1532

[a] From Ortiz et al. (2006). GN, Nuevo Gulf; SJG, San José Gulf. Stages of embryonic development according to Naef (1928).

2005 (two animals), December 2005 (one animal) and February 2007 (one animal). Through the whole sampling period, nine egg clutches were found. Those at early stages of embryonic development (between I and VI stage) were obtained in summer and winter, at intermediate stages in autumn (between XIV and XVI) and at advanced stages in winter (Table 3).

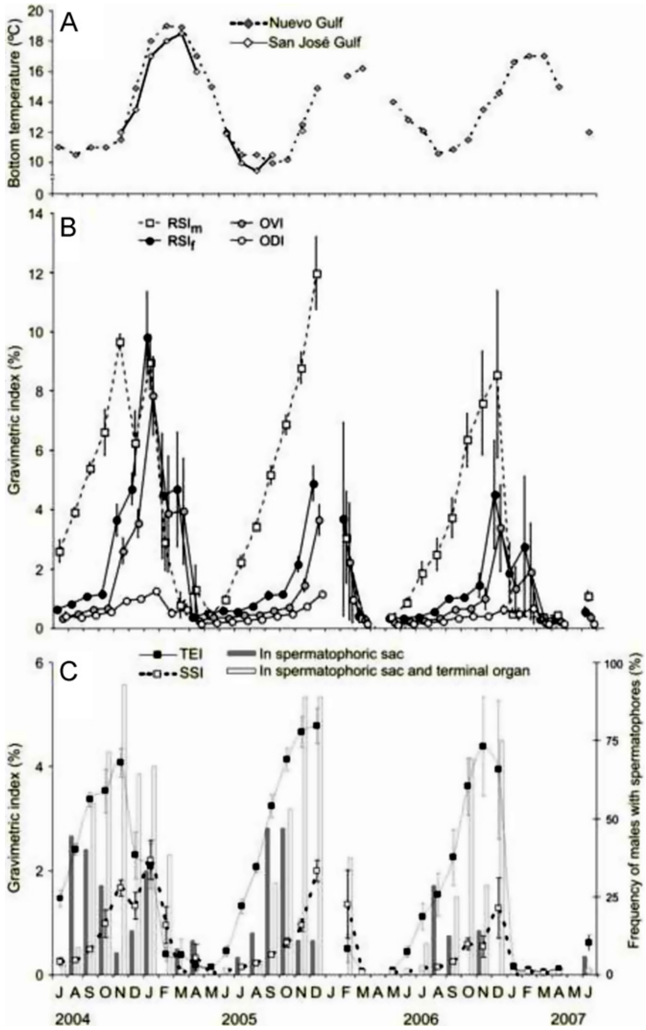

Fig. 3. *Enteroctopus megalocyathus*. (A) Monthly variation of the sea bottom temperature registered in sampling sites, (B) mean (±S.E.) values of the gravimetric index of the reproductive system of males (RSI$_m$) and females (RSI$_f$), of the ovary (OVI), and of the distal oviducts and oviducal glands (ODI), (C) mean (±S.E.) values of the gravimetric index of the testis (TEI), of the spermatophoric sac and terminal organ (SSI) and monthly frequency of spermatophore localizations in the reproductive system of males.

3.3. *Reproductive output*

Males PF ranged from 1 to 13 spermatophores (mean ± SD = 3.1 ± 2.3). Females PF ranged from 1429 to 6427 (mean ± SD = 3729 ± 1443) oocytes (Fig. 5). Both sexes showed significant positive correlations between PF and BW ($P < 0.001$) (males: $r = 0.52$, $n = 137$; females: $r = 0.81$, $n = 30$), and ML ($P < 0.001$) (males: $r = 0.55$, $n = 137$; females: $r = 0.73$, $n = 30$). Females RF ranged from 1.2 to 3.2 oocytes/g BW (2.2 ± 0.56) and it was neither dependent on female BW nor ML ($P > 0.05$). The mean number of eggs per clutch was 1321.6 eggs (Table 3).

3.4. *Sex ratio*

Of the individuals examined in the total sample, 546 were males and 625 were females. The overall ratio of males to females was 0.87:1 and the proportion of females was significantly higher than males ($\chi^2 = 5.329$; $P < 0.05$). However, there were no significant deviations from 1:1 when compared by seasons ($0.1 < P < 0.8$).

3.5. *Size at maturity*

The smallest mature male sampled was 528 g BW and 102 mm ML (Fig. 2). The smallest advanced mature female was 659 g BW (Fig. 2) and 105 mm ML. The BW$_{50\%}$ and ML$_{50\%}$ were 1072 g and 135.4 mm for males and 1613 g and 158.5 mm for females respectively. The goodness of fit of the models, tested by using the maximum likelihood estimator (scaled deviance, SCD), did not show significant differences between the estimated proportion of mature individuals and the observed data ($P > 0.05$) (BW of males: SCD = 327.4, df = 476; ML of males: SCD = 351.4, df = 476; BW of females: SCD = 276.1, df = 565; ML of females: SCD = 262, df = 565).

4. Discussion

There is a trade-off between egg size and fecundity in cephalopods (Mangold, 1983; Boyle and Rodhouse, 2005). According to Mangold (1987) low fecundity is expected in small species with large eggs, high fecundity in animals of large adult size and small eggs, and relatively high fecundity in those having large eggs and considerable adult size. Since *E. megalocyathus* has a relatively large adult size, large-sized eggs (10.7 mm length) (Ortiz et al., 2006), and PF of 1429–6427 oocytes (Subsection 3.3), it seems to belong to the third category. Although only three complete egg clutches were obtained in the field, the mean number of eggs per clutch was closely related to PF range. Besides, in agreement with our results, Ré (1998a) estimated 2500 and 2900 oocytes for advanced maturity females of 815 and 1400 g weight respectively. However, even when our PF estimations were in the range of the PF estimated from females with similar BW captured in the Chilean coast (PF: 1000–17,000 oocytes, female BW: 1500–3000 g approxi-

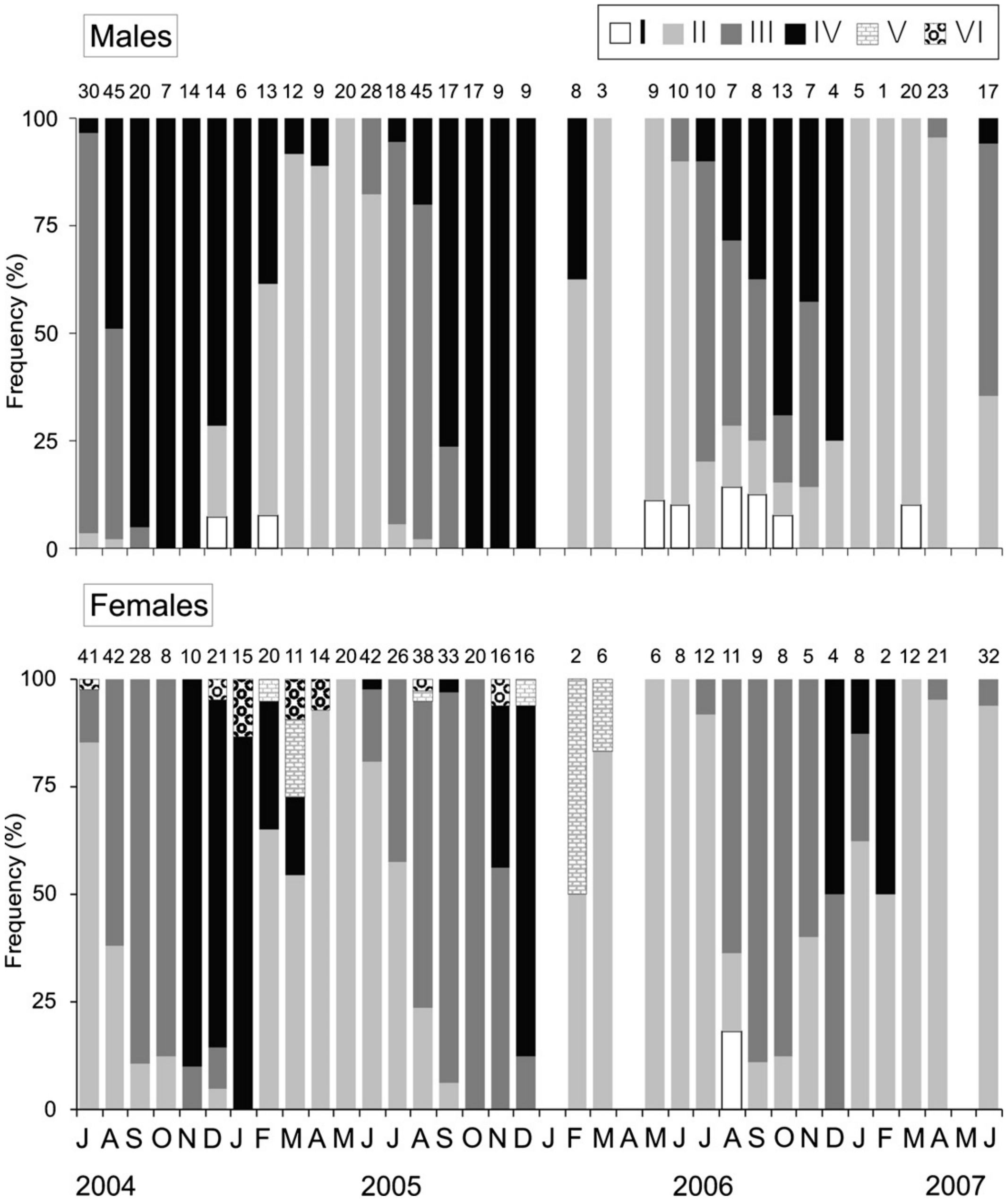

Fig. 4. Monthly variation of the percentage of *Enteroctopus megalocyathus* males (A) and females (B) at different stages of maturity. Figures on top of the bars represent number of individuals in each sample.

mately) (Chong Lay-Son et al., 2001), the upper limit of our PF range was lower. In the case of male cephalopods, once they reach maturity the production and storage of spermatophores is an on-going process (Nigmatullin et al., 2003) and this would allow males to mate several times. Thus, PF estimations in males would depend upon the timing of catch and could be a reason for a mismatch between number of spermatophores and BW in *E. megalocyathus*. Compared with other species, male fecundity would be similar to *O. maorum*, which has up to 13 ripe spermatophores of 105–228 mm length (Grubert and Wadley, 2000). However, female fecundity could be compared with *O. maya* which has eggs of 11 mm length, and which can spawn 300–5000 eggs depending on the size of female (Solís Ramírez, 1967; Van Heukelem, 1983).

Our results showed that males reach maturity earlier in the year and at smaller size than females (Fig. 4 and Subsection 3.5). Size at maturity estimations were similar to those reported by Chong Lay-Son et al. (2001) in the Pacific coast (149 mm $ML_{50\%}$ for both sexes). Besides, as a tangible proof that mating can occur in the fishing areas, spermatangia in distal oviducts were recognized from mid spring to mid summer in a small number of advanced maturity females. However, in the following months, SSI decreased as result of the recruitment of immature-stage males to the fishing areas, rather than the presence of spent ones (Figs. 4 and 5). This maturity pattern suggests that a peak of mating and the subsequent death of males (as is expected in cephalopod populations) (Boyle and Rodhouse, 2005) would be reached outside the fishing grounds in the following months.

For the north Patagonian Atlantic coast, Ortiz et al. (2006) suggested a breeding season extended from late summer to late winter. The present results indicate the occurrence of spawning activity during summer though in a low proportion of individuals. In addition, a low frequency of juvenile-stage females in March and

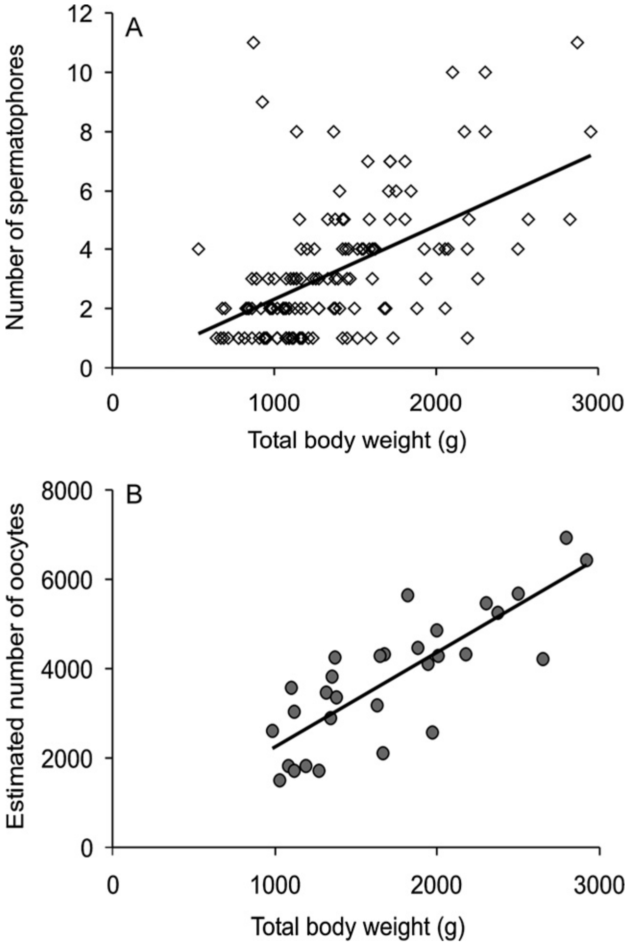

Fig. 5. *Enteroctopus megalocyathus*. Relationship between total body weight and potential fecundity in males (A), $y = 0.025x + 0.1559$; and females (B), $y = 2.1116x + 152.72$.

April, of females at advanced maturity stages in July, and of newly spawned eggs in August (Fig. 4 and Table 3), suggests a weaker spawning period in winter. Therefore, taking into account the spawning periods of summer and winter, and a time of embryogenesis which took nearly six months at 12 ± 0.7 °C from eggs at early stages of embryonic development (Ortiz, 2009), the breeding season in the north Patagonian Atlantic coast is likely to encompass nearly all year around.

Environmental factors, primarily temperature, have been shown to contribute to the seasonality of sexual maturation and reproduction of cephalopod species. These factors, associated to local oceanographic processes, would serve to lead population movements of different spatial scales (Boyle and Boletzky, 1996; Semmens et al., 2007). Moreover, spawning regions have been shown to be linked to specific temperature zones, possibly because changes in temperature during embryonic development directly influence the developmental rate and success of hatching (Boletzky, 1987; Ortiz and Ré, 2011). During winter, in San José and Nuevo gulfs the water column is well mixed, keeping a nearly isothermal condition. During summer the water column stratifies thermally and develops a thermocline (which is stronger in Nuevo Gulf) between 20 and 40 m depth, below which temperature is more stable and range from 12.4 to 14 °C (Rivas, 1990; Rivas and Ripa, 1989; Rivas and Beier, 1990). In this season, we suggest a bathymetric migration of most brooding females out of the study area and towards deeper and thermally stable sites suitable for spawning. This could explain the drop in the number of individuals at advanced maturity stages approaching shallow waters during summer, the low frequency of mating, and the low number of egg clutches, mature-spawning, and spent stages of females found throughout the sampling period. Moreover, temperature has been shown to control the rate at which sexual maturity runs (Van Heukelem, 1976). Thus, temperature increase from middle spring might favor sexual maturation, while temperature values reached in summer would lead to migrations to deeper waters. As it was observed, this pattern seems to give rise to a reproductive cycle with a strong seasonal scheme. In addition, seasonal sex ratios were close to 1:1, suggesting that both sexes would move from near shore to offshore areas and vice versa nearly at the same time.

In Nuevo and San José gulfs, *E. megalocyathus* is harvested up to nearly 25 m depth. The localized migration to deeper waters inferred for *E. megalocyathus* would determine spatiotemporal scales relevant to population dynamics which in turn would have implications for fishermen and for the biological sustainability of the resource. On the one hand, during the reproductive season of summer, available biomass decreases and most divers stop fishing (Ré, 1984). On the other hand, summer population movements towards deep spawning sites would permit the escape from the fishing pressure of a fraction of mature-spawning males and most mature-spawning and spent females. These patterns might be crucial for the hatching success of *E. megalocyathus* when considering the extended period of parental behavioral care.

Cephalopod populations dynamics seem to be influenced mainly by phenotypic plasticity in response to environmental variability (Mangold, 1987; Boyle and Boletzky, 1996). Our study sites were located at the northern boundary in the Atlantic Ocean of the red octopus distribution. If temperature controls sexual maturation leading to migratory movements, reproductive cycle and population dynamics could be different in fishing grounds with narrow seasonal temperature variations. Therefore, for future management initiatives, assessments of the state of sexual maturity may be necessary in fishing areas at higher latitudes, or if fishing methods not constrained by the depth (i.e. pots or traps) were to be implemented in the gulfs of the north Patagonian Atlantic coast.

Acknowledgements

We express our gratitude to Miguel A. Díaz, Ricardo B. Vera, Julio C. Rúa, Augusto Cesar Crespi-Abril and Alejo Irigoyen for their help with fieldwork, and to Luisa Kuba, Gastón Trobbiani, Clara Rosas, and Marianela Beltrán for their help during sampling processing. We also thank two anonymous reviewers for their comments. This study was carried out within the framework of the project PICT 2002 No. 12737, provided by Agencia Nacional de Promoción Científica y Tecnológica.

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