Reproductive biology of *Octopus tehuelchus* d'Orbigny, 1834 (Cephalopoda: Octopodidae) in southern Brazil

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ABSTRACT

Octopus tehuelchus is a small octopus endemic to subtropical and temperate waters of the southwestern Atlantic continental shelf. Its reproductive biology was studied by examining 319 individuals, measuring 20 to 79 mm mantle length (ML), collected between 1979 and 2009 along the coast of southern Brazil. Females are more numerous in shallower waters and attain larger size than males. Fully mature males and females were observed in all seasons and mean mantle length at maturity was 46 mm for females and 27 mm for males. The number of intraovaric oocytes of maturing females ranged from 20 to 448 and was positively correlated with female size. In mature females, a wide range of intraovaric oocytes diameters was observed, in some cases with a bimodal distribution. The number of eggs in the four layings ranged from 86 to 237, the diameters ranged from 8.2 to 14.5 mm and no bimodality was observed. Digestive gland grew proportionally to body weight along maturation in females but not in males, suggesting accumulation of reserves for spawning and parental care in females and priority for sexual maturation over growth in males. The comparison of the reproductive cycle of *O. tehuelchus* in southern Brazil with populations from northern Patagonia shows that the species has the potential for year round spawning, but ecological constrains only allows it to express this potential in the lower latitudes of its distribution.

Additional keywords: Mollusca, Reproductive cycle, sexual maturation, fecundity, southwestern Atlantic

INTRODUCTION

Cephalopods have developed a wide array of reproductive strategies, which enable them to occupy all marine habitats (Rocha et al., 2001). Particularly, the family Octopodidae has experienced an intense speciation, occupying coastal benthic environments from the tropics to temperate regions (Norman, 2003). In this family, a range of reproductive strategies occurs, from species with wide distribution, large body size, small eggs, high fecundity and pelagic hatchlings, such as *Octopus vulgaris* (Guerra, 1975; Mangold, 1987; Rocha et al., 2001; Otero et al., 2007; Villanueva and Norman, 2008) to more narrowly distributed species, with small body size, larger eggs, low fecundity and benthic development, such as *Octopus tehuelchus* (Pujals, 1982; Iribarne, 1991; Ré, 1998). This last species occurs from subtropical southeastern Brazil (20° S) (Haimovici and Perez, 1991) to the temperate habitats of San Jorge Gulf, in northern Patagonia, Argentina (43°S) (Ré and Simes, 1992; Ré, 1998).

In southern Brazil, *Octopus tehuelchus* occurs over the continental shelf, as deep as 100 m depth and usually associated with gastropod shells (Haimovici and Andriguetto, 1986). Due its low abundance in commercial landings, its life cycle and biology are poorly known in Brazil. However, the species is frequently found in stomach contents of demersal teleosts and marine mammals from this region (Santos and Haimovici, 2002). In the Patagonian gulfs, the species is commercially exploited as small artisanal fishery (Storero, 2010).

Most information on the growth and reproductive biology of the species comes from studies conducted in Patagonia, in an environment predominantly that includes rocky bottoms, discharge of freshwater creeks and channels, high tidal range (up to 9 m), and large seasonal variation of temperature and luminosity (Pollero and Iribarne, 1988; Iribarne, 1991; Navarte et al., 2006; Klaich et al., 2008; Storero et al., 2010). This environment contrasts with that of southern Brazil, which presents sandy and muddy bottoms, small tidal range and, due to its more northerly distribution, temperature rarely below 12°C, even in the cold months (Haimovici et al., 1996) and lower variation in luminosity between winter and summer (Bakun and Parrish, 1990).

The aim of this work is to study the reproductive biology of *Octopus tehuelchus* in the subtropical environment of the continental shelf in southern Brazil, which will allow for a better understanding of the reproductive strategy along the species distribution.

MATERIALS AND METHODS

Data Collection: Specimens of *Octopus tehuelchus* were collected from bottom trawl surveys by the R/V

ATLÂNTICO SUL and from commercial trawling along southern Brazil in the 28° S to 34° S range at depth from 15 to 100 m, between 1979 and 2009. Specimens were fixed in 10% formalin and preserved in 70% ethanol.

All preserved individuals, 125 males and 194 females, had their total length (TL), dorsal mantle length (ML), total body weight (BW), and digestive gland weight (DGW) recorded. Females had their ovary weight (OW), oviducts weight (including the oviducal glands) (OvW), and maximum diameter of oviducal glands recorded. Maximum diameters of oocytes (MDO) were measured with a caliper to the nearest 0.1 mm. All developing intraovaric oocytes over 4 mm were counted. Four egg clutches were collected on gastropod shells, spawned eggs were measured and recently hatched individuals, without the yolk sac, were measured and weighed. In males, testis weight (TW) and spermatophoric sac (including the glandular system) weight (SSW) were weighed within 0.01 g precision. Spermatophores in the Needham's sac were counted and measured at the nearest 0.1 mm on a micrometric scale.

The reproductive cycle was analyzed by a combination of the monthly frequencies of males and females in each maturity stage and the monthly variations of the maturity and gonadosomatic indices.

A maturity index (MI) was calculated as MI = SSW/ (TW + SSW) for males and MI = OvW/ (OW + OvW) for females (Hayashi, 1970). The gonadosomatic index (GSI) was calculated as GSI = (SSW/ (BW − SSW)) × 100 for males and GSI = (OW/ (BW − OW)) × 100 for females (Otero et al., 2007). Digestive gland index (DGI) was calculated as DGI = (DGW/ (BW − DGW)) × 100, similar to the one used for *Octopus vulgaris* (Otero et al., 2007).

The maturity scale was modified from Guerra (1975), Pujals (1982), and Perez and Haimovici (1991). For females, five stages were defined based on the size, color and transparency of the oviducts and oviducal glands in preserved specimens as well as the mean diameter of the developing oocytes: *Immature (I):* translucent oviducts, oviducal glands little differentiated, with diameter usually smaller than 2 mm; *Initial maturity (II):* whitish oviducal glands between 2 and 3 mm in diameter and developing oocytes 2 to 4 mm long; *Intermediate maturity(III):* oviducal glands brown/black, 3 to 4.5 mm in diameter, most oocytes between 4 and 7.5 mm long; *Advanced maturity (IV):* enlarged oviducts, sometimes with oocytes being released, mean diameter of the larger oocytes over 7.5 mm; *Post-spawning (V):* ovary clearly flaccid with reduced size and few eggs in it, oviducts dilated and small oviducal glands.

The maturity scale for males included four stages: *Immature (I):* small and whitish testis, glandular system slightly differentiated and absence of spermatophores in the Needham's sac; *Initial maturity (II):* testis under development, usually heavier than the glandular system and Needham's sac with few (<20) spermatophores; *Advanced maturity (III):* testicle weight lighter than glandular system and Needham's sac full; *Post-liberation of spermatophores (IV):* glandular system still bulky,

Needham's sac partially or totally empty, with spermatophores being released and testicle relatively small, striped and usually less heavy than the glandular system.

Potential fecundity was defined as the number of developing oocytes with diameters over 4 mm in ovaries of stages III and IV females. The few smaller ones, which were probably atresic, were discarded.

Data Analyses: Reproductive indices were compared with the non-parametric Kruskal-Wallis test for multiple comparisons, because assumptions for normality and homogeneity of variance were not satisfied.

The sex ratio was calculated for the categories "month", "mantle length", and "depth". To allow for comparable numbers of specimens, ML was grouped in four 15 mm classes and depth in three classes: under 30 m, from 30 to 59 m, and 60 m and over. Significant deviations from the 1:1 proportion were tested using the χ^2 test, adjusted to Yates correction (Zar, 1984).

Length-weight relationships were estimated for the total sample and according to sex. Data were adjusted to power model ($y = ax^b$), where y = BW; x = ML; a = the y-intercept; and b = the slope. The goodness of fit was expressed by r^2 and the analysis of covariance (ANCOVA) (Zar, 1984) was used to test for differences in the slope of log-transformed relationships.

The mean mantle length at maturity (ML50%) was estimated starting from the proportion (Pi) of stages III and IV individuals, grouped in 6 mm ML classes, adjusted to the logistic model: Pi = 1–{1/ 1 + exp [− (α + βMLi)]}

The Bhattacharya method (Bhattacharya, 1967; King, 2007) was used to discriminate normal components in the diameter frequency distribution of intraovaric oocytes.

RESULTS

Sex Ratio: Females were significantly more abundant that males (174:125), however the sex ratio did not differ significantly when grouped monthly (Table 1). The proportion of females was significantly higher among the specimens larger than 45 mm ML (χ^2 = 13.89 and 5.18; p <0.05) (Table 2), suggesting that females grow larger than males. The number of females was higher in all depth ranges, however, the differences between sexes was only significant at depths shallower than 30 m (χ^2 = 4.17; (p <0.05) (Table 3).

Length-Weight Relationships: Females *O. tehuelchus* ranged from 21 to 79 mm ML (mean 47.2) and from 8.3 to 228.5 g BW (mean 69.5) and males ranged from 20 to 76 mm ML (mean 42.6) and 4.7 to 125.1 g BW (mean 46.0). The dorsal mantle length/total body weight relationships (ML/BW) were calculated only for individuals caught in 2009 (n = 64), which were less affected by the dehydration observed in specimens preserved in alcohol for long periods. Relationships were best described by the power equations (Table 4): females: BW = 0.0211×

Table 1. Monthly variation in sex ratio of *Octopus tehuelchus* in southern Brazil.

Month	Number	Females	Males	χ^2
Jan	49	59%	41%	1.67
Mar	5	40%	60%	0.40
Apr	14	50%	50%	0.07
May	18	67%	33%	2.00
Jun	43	51%	49%	0.05
Aug	14	64%	36%	1.21
Sep	44	64%	36%	3.30
Oct	14	57%	43%	0.36
Nov	56	63%	38%	3.52
Dec	30	40%	60%	1.23

Table 2. Sex ratio variation of *Octopus tehuelchus* according to ML 15 mm classes in southern Brazil (*significant χ^2 departures from the 1:1 sex ratio $p < 0.05$).

ML Classes range (mm)	Number	Females	Males	χ^2
15 – 29.9	17	35%	65%	1.53
30 – 44.9	140	51%	49%	0.04
45 – 59.9	104	68%	32%	13.89*
> 60	38	68%	32%	5.18*

Table 3. Sex ratio variation of *Octopus tehuelchus* according to 30 m depth classes in southern Brazil (*significant χ^2 departures from the 1:1 sex ratio $p < 0.05$).

Depth range (m)	Number	Mean females ML (mm)	Females	Males	χ^2
< 30	24	45	71%	29%	4.21*
30 – 59	171	45,0	56%	44%	2.58
> 60	58	47,8	60%	40%	2.50

$ML^{2.2098}$, males: $BW = 0.0113 \times ML^{2.3337}$ and both sexes combined: $BW = 0.0072 \times ML^{2.4772}$. Slope comparisons did not show heterogeneity between sexes (ANCOVA, $p = 0.634$). However, these results should be considered with care due to the low number of individuals, particularly of males (Table 4).

Maturation and Size-at-Maturity: Fully mature males and females were observed in all seasons. Therefore, the mean size and weight at maturity were calculated including specimens collected year round.

Females in stages I and II (n = 76) were observed in all size ranges including seven females over 60 mm ML (Figure 1). Females in stages III and IV (n = 95)

measured over 24 mm ML and weighed over 30 g. Despite the small variation, the mean ML increased significantly with maturation ($p < 0.05$) (Table 5). The maturity curve of females showed a good fit to the logistic model ($r^2 = 0.980$) and $ML_{50\%}$ calculated was 45.9 mm (Figure 2).

Males in stages I and II (n = 58) were observed in all sizes including five individuals over 60 mm (Figure 1). All males in stages III and IV (n = 65) were over 30 mm ML and 15 g BW. The $ML_{50\%}$ was 27.4 mm, however, the maturity curve of males did not show a good fit to the logistic model ($r^2 = 0.129$) (Figure 2).

Seasonality: Females in stages I or II were observed in all months sampled. Stage III individuals were caught more frequently in April, June, and November and stage IV individuals were caught in all months sampled, mainly in January, August, and September (Figure 3). A single stage V female with an egg clutch was observed in July. Three other egg clutches without the spawned female were found in the same month and a fourth was observed in November. Reproductive indices were not homogeneous throughout all months ($p < 0.05$) (Fig 4). Higher (GSI) and lower (MI) associated to sexual maturity were observed in January (summer) and June, August, and September (late autumn to late winter).

Immature and initial maturity males (stages I and II) occurred year round, but more frequently in April, June and December. Stages III and IV also occurred in all sampled months, more frequently in January (summer), September, October, and November (late winter and early spring) (Figure 3). There were no significant differences in the monthly means of IM and GSI ($p > 0.05$), indicating mature males in all seasons (Figure 4).

In both sexes, maturity stages and reproductive indices support a year-round sexual maturation cycle.

Pre-spawning Oocytes and Spermatophores: The mean number of oocytes in the ovaries of 67 maturing females (stages III and IV) was 246.8 (range from 20 to 448). The diameter of the oocytes ranged from 1.8 to 13.9 mm (Table 5). A wide range of oocyte diameters was observed within the ovaries of every individual, in some cases with a bimodal distribution. The number of oocytes (ON) increased significantly with female ML (ON=1.4889×(ML) 1.3094; $r=0.524$ n=67) (Figure 5). Immature and initial maturity females (stages I and II, n = 68) had 185 oocytes in average (50 to 514), most with diameters under 4 mm (Table 5).

In stages III and IV males (n = 67), the number of stored spermatophores in Needham's sac ranged from 1

Table 4. Range of mantle length (ML) and total body weight (BW) and power regression parameters of length/weight relationships for females and males of *Octopus tehuelchus* caught in southern Brazil in 2009.

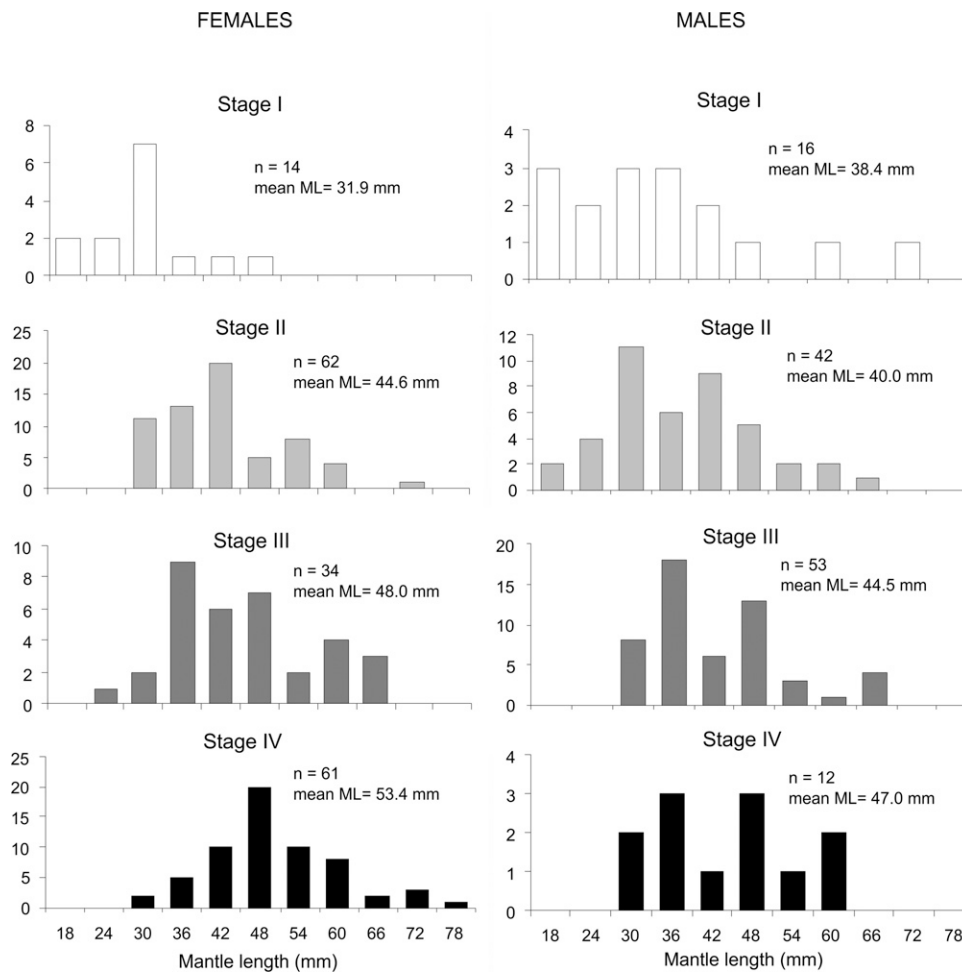|	n	min-max (mean) ML	min-max (mean) BW	A	B	r^2
Females	47	30–65 (49.9) mm	21.9–228.5 (123.4) g	0.0211	2.2098	0.7240
Males	17	28–52 (40.1) mm	32.5–119.4 (65.1) g	0.0113	2.3337	0.8290
Both sexes	64			0.0072	2.4772	0.8347

Figure 1.   Frequency of mantle length (ML) classes in each maturity stage of females and males of *Octopus tehuelchus* in southern Brazil.

Table 5.   Variation in the number and maximum diameter (MDO) of intraovaric oocytes in females of *Octopus tehuelchus* in different maturation stage (Stages I, II, III and IV) in southern Brazil.

	Stage I	Stage II	Stage III	Stage IV
Number of females	12	56	22	45
Mean female ML ($\pm$ SD) (mm)	32.8 $\pm$ 7.4	43.9 $\pm$ 9.5	46.6 $\pm$ 9.1	48.5 $\pm$ 8.4
Range oocytes number	50 to 350	65 to 514	20 to 410	112 to 448
Mean oocytes number ($\pm$ SD)	139.7 $\pm$ 76.6	226.9 $\pm$ 108.0	205.1 $\pm$ 93.3	267.1 $\pm$ 83.5
Range MDO (mm)	0.2 to 3.0	1.0 to 7.4	1.8 to 10.8	1.5 to 13.9
Mean MDO ($\pm$ SD) (mm)	1.4 $\pm$ 0.7	3.1 $\pm$ 0.8	5.5 $\pm$ 1.8	8.0 $\pm$ 2.2

to 62 (21.2 $\pm$ 12.3), with maximum length ranging from 1.7 to 57.4 mm (21.2 $\pm$ 8.9). Non-significant correlation was found between the number of spermatophores and the ML (r = 0.086) (Figure 5) nor between the length of the spermatophores and the ML (r = 0.03).

Spawning and Hatchlings: All the egg clutches were observed in gastropod shells of *Tonna galea* and *Adelomenon brasiliana*. The number of eggs attached to the shells ranged from 86 to 237 (165.2 $\pm$ 60.5; n = 4).

The maximum diameter of these eggs ranged from 8.1 to 14.4 mm and their diameter distribution were unimodal.

Recently hatched octopuses (n = 16) resembled small adults, and measured from 5.0 to 6.40 mm ML and from 10.5 to 15.0 mm TL and weighed from 0.07 to 0.12 g (Table 6). During one of the cruises, a spawned female with her eggs stuck to a gastropod shell was placed inside a recipient with sea water and some eggs hatched. Recently hatched octopus did not show any swimming behavior, remaining near the bottom of the recipient.
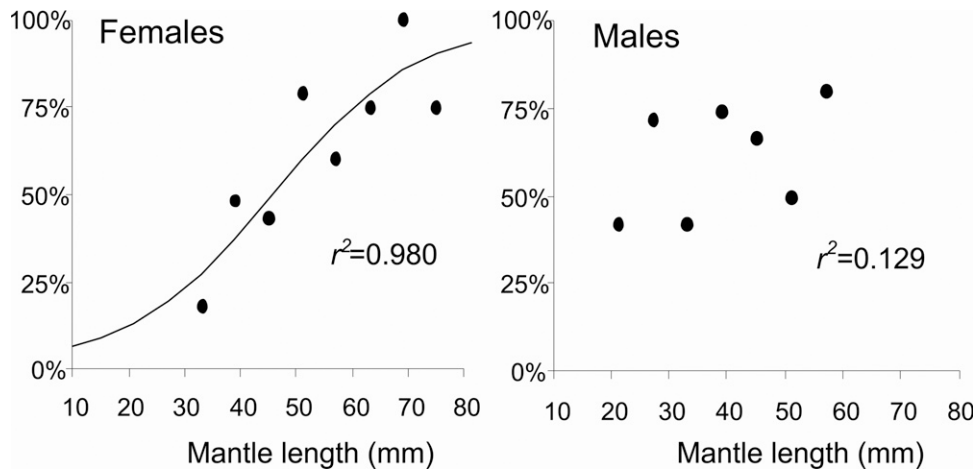
Figure 2. Relative frequency curve of mature individuals by mantle length (ML) classes (mm), of females and males of *Octopus tehuelchus* in southern Brazil adjusted to a logistic model.
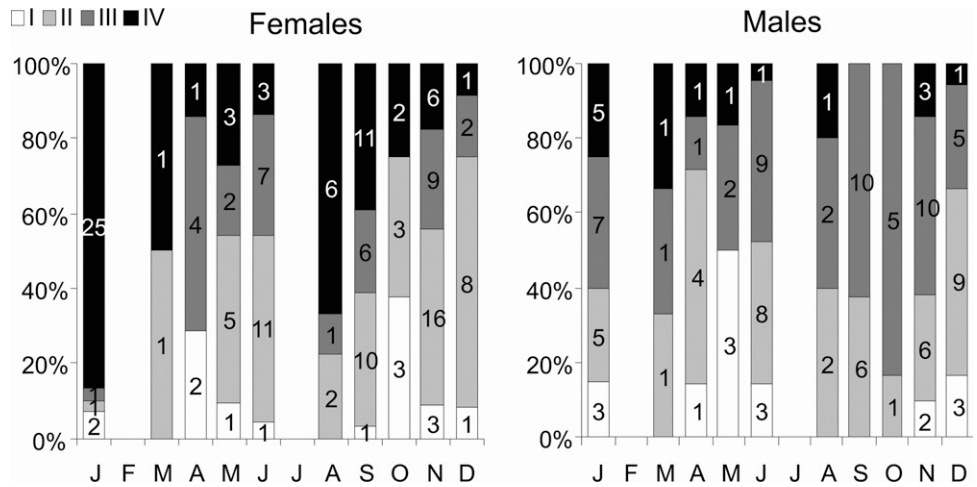

Figure 3. Monthly frequency (%) of the maturity stages of *Octopus tehuelchus* females and males in southern Brazil (values in the bars indicate the number in each stage).

Digestive Gland Index and Reproductive Investment: The digestive gland weight (DGW) of females increased significantly with sexual maturation ($p < 0.05$). The digestive gland index (DGI) was significantly lower in stage I ($p < 0.05$), and remained constant in the others stages (Figure 6). Monthly DGI of females did not follow a seasonal pattern: the lowest values were observed in April and May and the highest ones, in January, March, August, and December (Figure 7).

Digestive gland weight and index of males did not show significant changes along maturation ($p > 0.05$), although small decrease in DGI means along maturation was observed (Figure 6). Seasonally, higher DGI values were observed in spring (Figure 7).

DISCUSSION

Octopus tehuelchus is a small species with large eggs and low fecundity, endemic to the subtropical and temperate waters of the southwestern Atlantic continental shelf (Haimovici and Perez, 1991; Ré, 1998). This study shows that its reproductive biology can adapt to both environments, with seasonal spawning in temperate waters and year round spawning in subtropical environments. Temperature, light intensity and daily photoperiod can influence growth and reproduction in cephalopods (Mangold, 1987). However, these factors may influence particular species or populations in different ways (Boyle and Rodhouse, 2005). Temperature an photoperiod differ between northern Patagonia (40° to 42° S), where daylight ranges from 9 to 15 h and air temperatures along the San Antonio Bay coast range between 6° C and 24° C (Iribarne, 1991) and southern Brazil (32° S), where daylight ranges from 10 to 14 h (Bakum and Parrish, 1990) and bottom temperatures on the continental shelf range between 12° C and 24° C (Haimovici et al., 1996). Although not discriminating the effects of each factor, Iribarne (1991) observed that high intensity of light
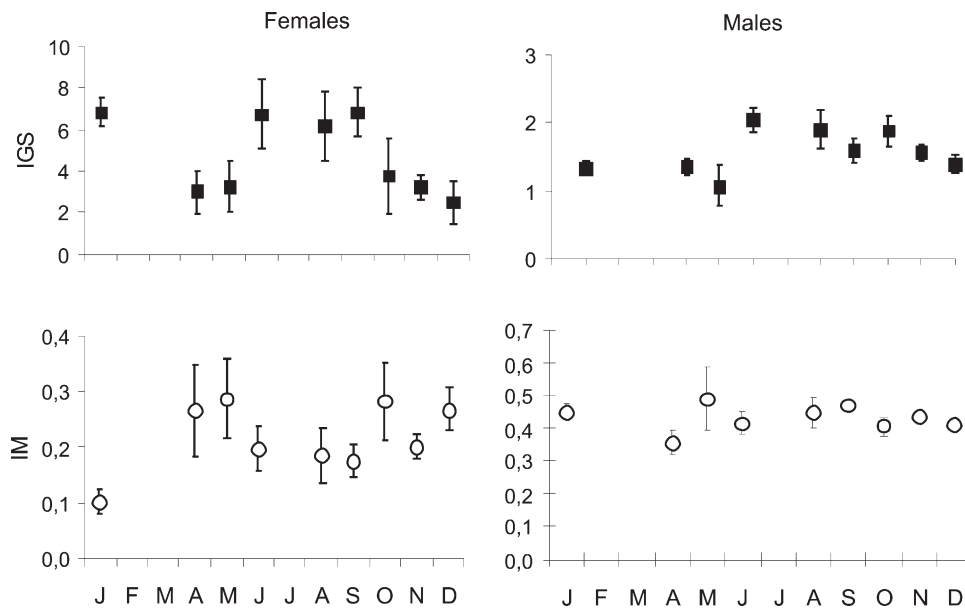
Figure 4. Monthly trends of mean (±SE) values of the gonadosomatic index (GSI) and the maturity index (MI) of *Octopus tehuelchus* females and males in southern Brazil.
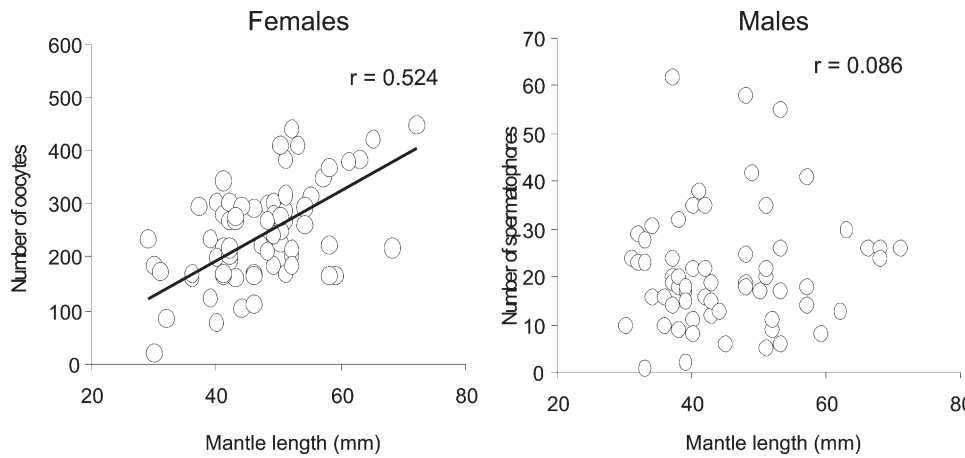

Figure 5. Relationship between mantle length (ML) and potential fecundity (number of developing oocytes and spermatophores) of mature females and males of *Octopus tehuelchus* in southern Brazil.

Table 6. Variation in the number and maximum diameter of eggs (MDE) and in the mantle length (ML), total length (TL) and total body weight (BW) of hatchling on four egg clutches of *Octopus tehuelchus* in southern Brazil compared to northern Patagonia. (Iribarne, 1991; Ré, 1998).

	Southern Brazil	Northern Patagonia
Maximum of eggs per clutch	237	227
Mean egg clutch fecundity (± SD)	165.15 ± 60.84	No data
Range MDE (mm)	8.13 to 14.44	9.0 to 12.0
Mean MDE (± SD) (mm)	10.33 ± 1.09	9.87 ± 0.61
Measured hatchling	16	280
Mean hatchling ML (± SD) (mm)	5.77 ± 0.46	6.64 ± 0.38
Mean hatchling TL (± SD) (mm)	12.06 ± 1.06	14.23 ± 0.83
Mean hatchling BW (± SD) (mg)	0.095 ± 0.014	0.139 ± 0.019

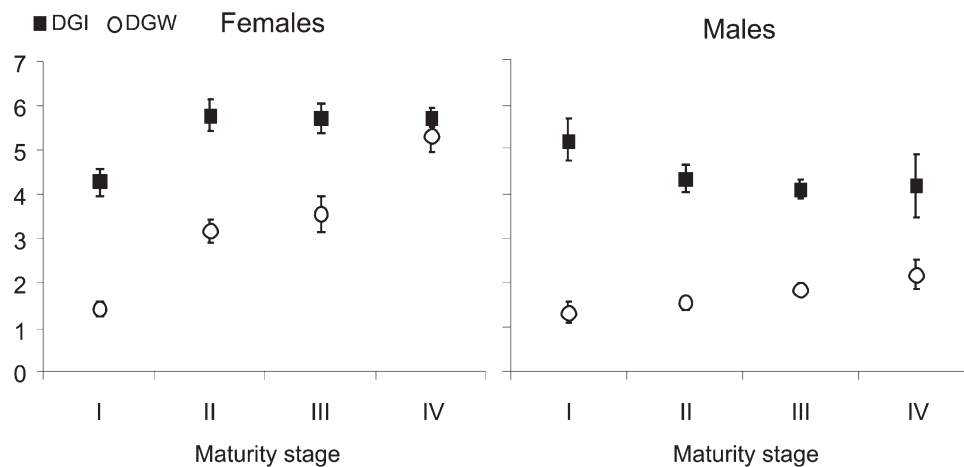**Figure 6.** Mean (±SE) of digestive gland weight (DGW) and digestive gland index (DGI) in each maturity stages of *Octopus tehuelchus* females and males in southern Brazil.
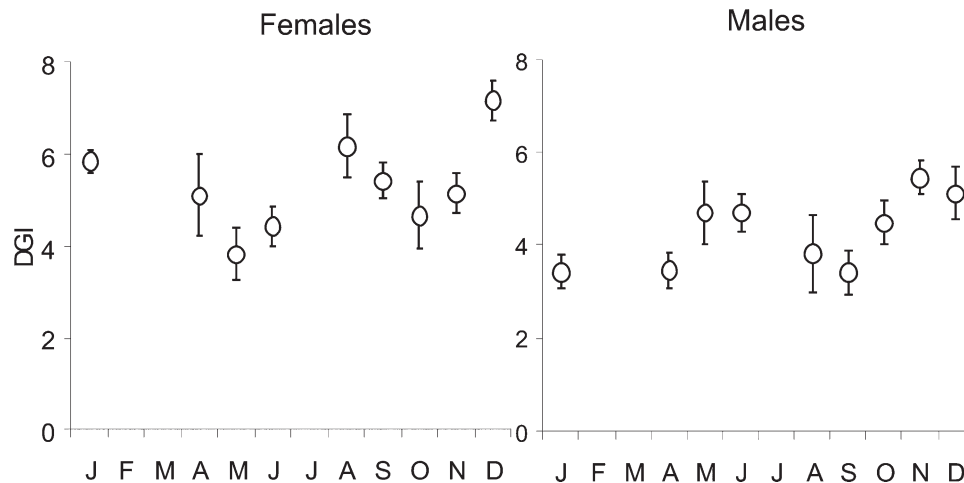

Figure 7. Monthly trends of mean (±SE) values of the digestive gland index (DGI) of *Octopus tehuelchus* females and males in southern Brazil.

and temperature were associated to the intensification of growth and sexual maturation of *Octopus tehuelchus* in northern Patagonia, where sexual maturation occurs between December and May and spawning occurs from June to November (Pujals, 1982; Ré 1989). More recently, Storero et al. (2010) observed two distinct sub-annual cohorts in the mantle length distributions within San Antonio Bay, suggesting that *O. tehuelchus* can have a more extended spawning season even in the higher latitudes of its distribution. In contrast, in southern Brazil, mature males and females were observed year-round and egg broods were sampled both in cold and warm months.

Octopus tehuelchus uses a wide variety of bottoms types to deposit eggs. On the rocky bottoms of San Matias Gulf (41° to 42° S), the eggs are attached directly to the substrata (Ré, 1998). On the sandy bottoms of the San Antonio Bay (40°40′ S), the eggs are attached to shelters, mainly bivalve shells of *Ostrea puelchana,*

Ammiantis purpurata, Mytilus edulis platensis, Chlamys tehuelchus, and *Pitar rostratus* or gastropod shells of *Buccinanops gradatum, Odontocymbiola subnodosa,* and *Zidona dufresnei* (Iribarne, 1990). Although most of these mollusks also occur in southern Brazil (Rios, 2009), egg laying of *Octopus tehuelchus* in this region was found only inside shells of large sized gastropods *Tonna galea* and *Adelomenon brasiliana.* Iribarne (1990) notes that the abundance of small shells in San Antonio Bay could favor the selection of smaller octopuses. However, the availability of larger shells in southern Brazil does not seem to have favored larger individuals in this region.

In southern Brazil, a wide range of sizes of developing intraovaric oocytes and of egg sizes in the egg clutches (Figure 8) were observed. In northern Patagonia, some females also showed oocytes at different stages of development (Pujals, 1982). These wide ranges in oocytes size may decrease competition among siblings. However, there are differences in the evolution of the
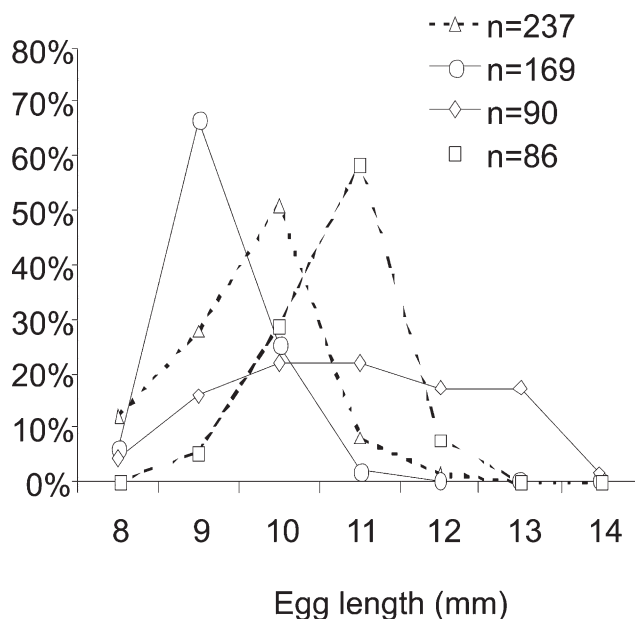
Figure 8. Frequency of spawning eggs size in four egg clutches of *Octopus tehuelchus* in southern Brazil.

DGI between regions, that suggest that the individual spawning period may be longer in southern Brazil: in northern Patagonia, the DGI decreases along sexual maturation and can be associated to intense reserve mobilization along a short spawning season (Pujals, 1982; Iribarne, 1991); in southern Brazil, the DGI remains high along maturation, suggesting accumulation of reserves for a longer period of spawning and parental care of the eggs. However, it is not consensual that the digestive gland has an important role in energy storage in cephalopods, as many authors also consider the reserves in the muscle and gonads (Moltchaniwskyj and Semmens, 2000; Rosa et al., 2004; Semmens et al., 2004).

In males, the DGI decreases in both regions, characterizing a larger mobilization of energy reserves for the reproduction and anticipation of sexual maturation rather than growth (Iribarne, 1991). Moreover, males mature at smaller sizes than females in both areas (Ré, 1989). In the San Matias Gulf, females mature up to three months after males. After copulation, the sperm is stored in the oviducal glands of females (Ré, 1998).

The lack of seasonality in the spawning in southern Brazil may be associated to year-round availability of food for hatchlings. Productivity on the inner shelf of southern Brazil is relatively high (Ciotti et al., 1995), mostly as a consequence of the nutrient-rich runoff from the La Plata River and Patos Lagoon (Piola et al., 2005). In this region, other neritic cephalopods such as *Doryteuthis(Loligo) sanpaulensis* spawn year-round (Andriguetto and Haimovici, 1991; Haimovici, 1998a) and many bony fishes are multiple spawners (Haimovici, 1998b). In the Patagonian gulfs, productivity is dependent on tidal fronts and shows a strong seasonal variation, where higher productivity rates are concentrated in spring and summer (Acha et al., 2004). In temperate environments, such as the northern Patagonian gulfs, seasonality in productivity limits food availability and consequent survival and growth for young octopus in the cold season more difficult. Furthermore, according to Klaich et al. (2006), food intake, growth, and food conversion of *O. tehuelchus* in experimental conditions were lower at 10°C when compared to 15°C.

Based on our data, we have concluded that *O. tehuelchus* has the potential for year round spawning, but ecological constrains such as temperature, which influences metabolism, and photoperiod, which influences productivity, enables the species to express this potential only in the lowest latitudes of its distribution range.

ACKNOWLEDGMENTS

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