ORIGINAL ARTICLE

Reproductive traits of the small Patagonian octopus *Octopus tehuelchus*

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Abstract This study evaluated the reproductive features of *Octopus tehuelchus* in three coastal environments of San Matías Gulf (Patagonia). Monthly samples of *O. tehuelchus* were used to estimate size at maturity, compare seasonal changes in oocyte size frequency distributions between sites as well as oocyte number and size between female maturity stage and sites. Females in Islote Lobos had a smaller size at maturity than females in San Antonio Bay and El Fuerte, probably as a consequence of a generally smaller body size. Males in San Antonio Bay were smaller at maturity than females. *O. tehuelchus* is a simultaneous terminal spawner. Fecundity (expressed as number of vitellogenic oocytes in ovary) was lower in Islote Lobos, and an increase in oocyte number in relation to female total weight was found. Females in San Antonio Bay had the largest oocytes, which may indicate higher energy reserves for the embryo and therefore higher juvenile survival. There was a close relationship between reproduction, growth and condition, represented as size at maturity, number and size of vitellogenic oocytes and period of maturity and spawning. Given the local variation in some reproductive features of *O. tehuelchus*, studies should focus on the environmental factors, which bring about this variation, and on how it affects the dynamics of local populations.

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Introduction

To ensure the sustainable development of fisheries, data on life cycle variables (growth and reproductive traits such as maturation, age and size at maturity, fecundity, site and time of spawning) are required, which allow for an understanding of the dynamics, and their environmental variation, of the exploited populations.

Fecundity is one of the variables that determines reproductive success and is defined as the number of eggs or descendants produced by an individual during its lifetime (Begon et al. 2006). In octopodids, fecundity is generally estimated by the number of oocytes in the ovary. However, this merely represents a potential fecundity, which may differ from the real value since not all eggs in the ovary will mature, be fertilized and spawned (Barratt et al. 2007). Moreover, it is rather difficult to compare oogenesis among cephalopods species, because oocytes have been measured and described not in the same way (Laptikhovsky and Nigmatullin 1992; Laptikhovsky and Arkhipkin 2001).

Environmental plasticity seems to be characteristic of cephalopods. Different aspects of their life cycle (e.g. growth, reproduction and life span) have been found to vary even among seemingly similar areas of close proximity (Boletzky 1986; Forsythe et al. 2001; Jackson and Moltschaniwskyj 2002; Carvalho and Sousa Reis 2003; Storero et al. 2010). Thus, understanding the variations in the reproductive features of commercially important species in different environments is essential for the sustainable management of their populations.

The small Patagonian octopus *Octopus tehuelchus* has been an important fishery resource in various coastal environments of San Matías Gulf (Patagonia) for at least six decades. Our recent studies have shown that this octopus has a high environmental plasticity in growth, period of maturity and life span (Storero et al. 2010). This suggests that there may also be variations in the species' reproductive traits, such as patterns of oocyte maturation and fecundity.

The main goal of this study was to evaluate and compare the reproductive pattern and fecundity of *O. tehuelchus* in three coastal environments of San Matías Gulf. The specific objectives were the following: (1) to determine size at maturity in each site, (2) to analyse monthly oocyte growth, (3) to evaluate the differences in oocyte number and size in relation to maturity stage and site and (4) to analyse the relationship between oocyte number and body weight in each site.

Materials and methods

Study area

San Antonio Bay (SAB, Fig. 1) is located in the north-west sector of San Matías Gulf (40°42′S–40°50′S/64°43′W–65°07′W). It is an estuarine shallow water system with semidiurnal tides ranging between 6 and 9 m, channels and sandy–pebbly bottoms. SAB was declared Marine Protected Area in 1993 owing to its high biological diversity. Low tides expose large muddy intertidal flats, where people from the surrounding urban areas collect octopuses using artificial shelters (usually bottles, pipes, bricks, pots, etc.).

The north-west region of San Matías Gulf shows extended rocky intertidal shores. El Fuerte (EF, 41°14′S/65°08′W), located 55 km southward of SAB (Fig. 1), has been a traditional fishing area for the last 60 years. This rocky intertidal zone is characterized by tidal pools with the small mussels *Brachidontes rodriguezi* and *Perumytilus purpuratus* as the dominant species, and the presence of various algae, crabs and gastropods (Narvarte et al. 2006). The area is regularly visited during spring/summer months by fishermen who collect octopuses using a 40-cm-long iron gaff, or by turning over rocks (Iribarne 1991a).

Islote Lobos (IL, 41°26′S/65°03′W), located 45 km southward of EF and constituted by six islands connected to land during low tide, has also been a traditional fishing ground until it was declared Marine Protected Area in 1977 (Fig. 1). It is characterized by rocky shores, inhabited by small mussels, crabs and snails. Since it was pronounced protected area for the conservation of marine mammals and birds, the fishing effort on octopuses has diminished (Narvarte et al. 2006), although there is no regulation of the fishery in this reserve.

Biological sampling and data analysis

Samples from the intertidal zones of SAB, EF and IL were collected monthly from October 2005 to July 2007. Size at maturity (dorsal mantle length at which 50 % of the individuals is mature) was estimated with the logistic model

$$M(L) = 1 \left/ \left(1 + e^{(-c^*(L-L_{50}))}\right)\right.,$$

where $M(L)$ is the proportion of mature octopuses at length L, c the curve intensity and L_{50} the length at which 50 % of individuals is mature. Maximum likelihood was used for parameter estimation (Wileman et al. 1996; Aubone and Wöhler 2000), and the asymptotic test was carried out to compare the coefficients (Kendall and Stuart 1979). Females at stages M2, M3 and M4 (maturing, mature and post-spawning, according to Pujals 1986), and males with macroscopically visible spermatophores within the spermatophoric complex were considered mature.

To evaluate oocyte growth, ovaries of a number of females were analysed. A monthly subsample ($N = 30$) was preserved in formaldehyde (5 %) and then transferred to alcohol (70 %). Four ovaries of each maturity stage (M0, M1, M2, M3, M4; Pujals 1986) were studied under a stereomicroscope. Vitellogenic oocytes (i.e. >0.344 mm; Pujals 1986) in the ovary were counted (excluding damaged ones) and measured (longest axis in mm). Monthly oocyte size frequency distributions were analysed and compared with Kolmogorov–Smirnov test ($\alpha = 0.05$).

For each site, the number of vitellogenic oocytes was compared between maturity stages with one-way ANOVA ($\alpha = 0.05$). Their number and size for mature females (M2 and M3) were compared between sites with one-way ANOVA ($\alpha = 0.05$). Tukey's test was used for a posteriori comparisons, and when necessary, data were log-transformed to meet the ANOVA assumptions. The relationship between the number of vitellogenic oocytes and female total weight was evaluated and compared with ANCOVA ($\alpha = 0.05$). Fecundity was calculated by counting the number of vitellogenic oocytes in the ovary of mature females (M2 and M3). Small previtellogenic oocytes (<0.344 mm; Pujals 1986) were not considered, thus underestimating potential fecundity (Laptikhovsky and Nigmatullin 1992). Nevertheless, counting vitellogenic oocytes allowed for an easy approximation of the actual fecundity.

To assess whether females continue spawning when brooded eggs get lost, experiments with medium-size females that were brooding eggs (in different developmental stages) were carried out in the laboratory. Developing eggs were carefully removed from the shelter at the beginning of the experiment. Females were fed ad libitum with prey collected from the natural environment (the crab

Fig. 1 San Matías Gulf and study sites. *SAB* San Antonio Bay, *EF* El Fuerte, *IL* Islote Lobos
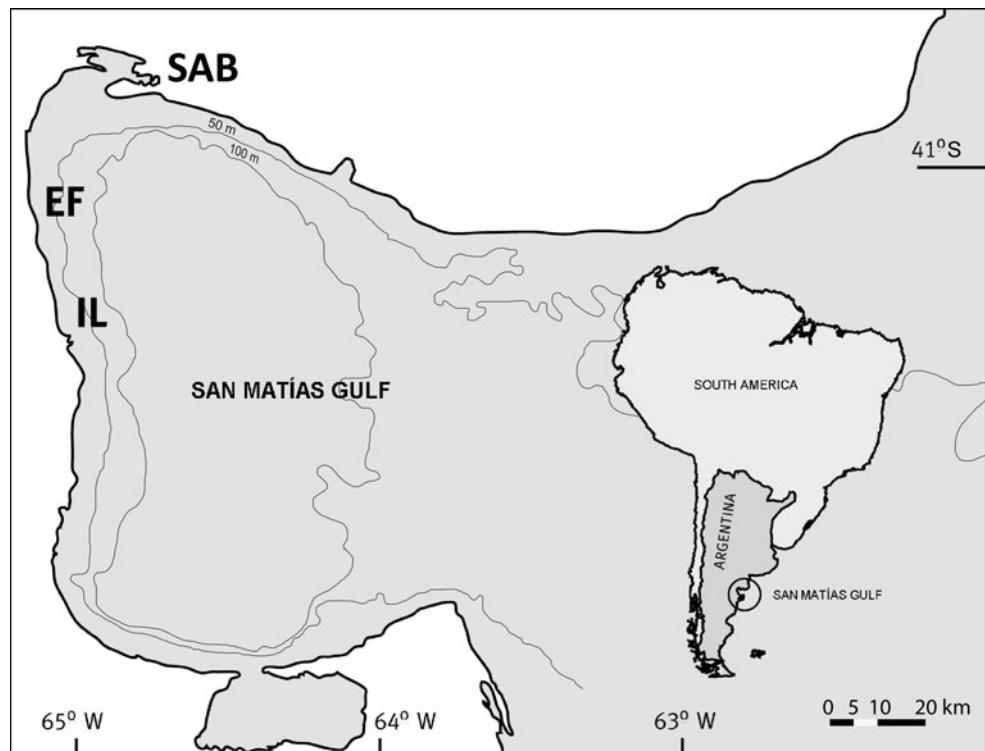
Neohelice granulata) and their behaviour was monitored daily. Salinity, temperature and photoperiod were kept similar to the natural conditions (33 ppm, 18–19 °C, LD 14:10). After 15–20 days, females were removed from the experimental tank and killed. The number of eggs laid during the experiment was recorded. Dorsal mantle length (DML, mm) and total body weight (TW, g) were recorded, and the ovary was examined macroscopically for the development of the oocytes left. The experiment was repeated eight times, and eight females with eggs not removed were kept as controls under similar conditions.

Results

Size at maturity

In SAB, the estimated size at maturity of females was higher than that of males, but in EF and IL, both sexes had similar size at maturity (Tables 1, 2). Females had the smallest size at maturity in IL, with no significant differences between SAB and EF (Tables 1, 2; Fig. 2). In contrast, males showed the highest size at maturity in EF, and no differences were found between SAB and IL (Tables 1, 2; Fig. 3).

Oocyte size frequency distributions

The ovaries of *O. tehuelchus* showed almost simultaneous growth of vitellogenic oocytes with a gradual increase in their modal size. In general, during spring months (September–November), we observed small oocytes that increased in number and size towards the summer (December–February). During autumn (March–May), ovaries were full of large vitellogenic oocytes that were beginning to be released. Post-spawning ovaries, with medium-size vitellogenic oocytes, were observed during winter (June–August).

Monthly growth of vitellogenic oocytes showed significant differences between sites (Fig. 4), particularly between SAB and the other sites (Table 3). For example, spring distributions in SAB showed still large vitellogenic oocytes, while in EF and IL, these had been released completely during autumn–winter (Fig. 4). In a few months, distributions were significantly different between EF and IL (Table 3).

Number and size of vitellogenic oocytes

Between 14 and 506, vitellogenic oocytes were recorded in the ovaries. Their number varied significantly both between maturity stages and study sites. Considering maturity stages (ANOVA$_{SAB}$ $F_{(4,227)} = 25.95$, $P < 0.0001$; ANOVA$_{EF}$ $F_{(4,230)} = 44.60$, $P < 0.0001$; ANOVA$_{IL}$ $F_{(4,216)} = 26.51$, $P < 0.0001$; Fig. 5) Tukey's test showed that immature females (M0 and M1) had fewer vitellogenic oocytes in the three study sites than mature females (M2 and M3). No difference was found between post-spawning females (M4) and mature females.

Table 1 Estimated parameters of the logistic curves for the proportion of mature females and males as a function of body size

	SAB		EF		IL	
	Female	Male	Female	Male	Female	Male
c	0.192	0.159	0.150	0.261	0.129	0.218
	(0.17–0.22)	(0.14–0.18)	(0.13–0.17)	(0.23–0.29)	(0.11–0.15)	(0.19–0.25)
L_{50}	43.681	37.001	44.537	41.843	36.078	36.799
	(37.50–49.86)	(31.50–42.50)	(38.75–50.32)	(36.53–47.16)	(30.24–41.92)	(31.68–41.91)
N	1,123	1,659	977	953	1,221	957

Confidence intervals in brackets

Table 2 Asymptotic test to compare the coefficients of the estimated logistic curves using maximum likelihood to the proportion of mature females and males

	$H_0: L_{50,1} = L_{50,2}; c_1 = c_2$	$H_0: c_1 = c_2$	$H_0: L_{50,1} = L_{50,2}$
SAB–EF			
Female	$P = 0.079$	$P = 0.45$	$P = 0.075$
Male	$P < 0.0001$ (**)	$P = 0.0002$ (**)	$P = 0.0001$ (**)
SAB–IL			
Female	$P < 0.0001$ (**)	$P < 0.0001$ (**)	$P = 0.006$ (**)
Male	$P = 0.025$ (*)	$P = 0.024$ (*)	$P = 0.861$
EF–IL			
Female	$P < 0.0001$ (**)	$P = 0.302$	$P = 0.0001$ (**)
Male	$P < 0.0001$ (**)	$P = 0.184$	$P < 0.0001$ (**)

* Significant differences
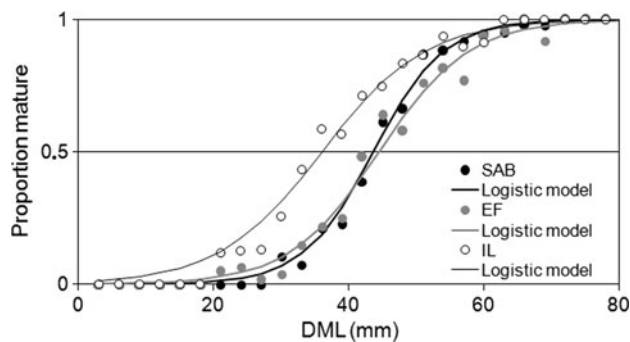
Fig. 2 Logistic curves fitted to the proportion of mature females by size (dorsal mantle length) to estimate size at maturity (L_{50}) using maximum likelihood. *SAB* San Antonio Bay, *EF* El Fuerte, *IL* Islote Lobos
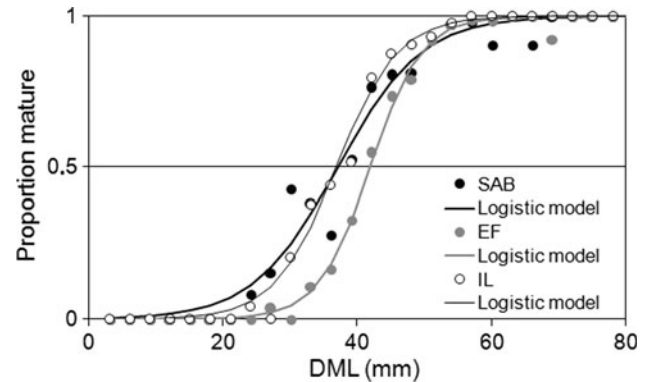
Fig. 3 Logistic curves fitted to the proportion of mature males by size (dorsal mantle length) to estimate size at maturity (L_{50}) using maximum likelihood. *SAB* San Antonio Bay, *EF* El Fuerte, *IL* Islote Lobos

Oocyte number and female total weight

Mature octopuses (M2 and M3) from IL had fewer vitellogenic oocytes than octopuses from EF and SAB (ANOVA$_\text{sites}$ $F_{(2,283)} = 18.55$, $P < 0.0001$; Fig. 5). Fecundity expressed as the number ($M \pm$ SD) of vitellogenic oocytes of mature females (M2 and M3) was 231.49 ± 69.94 (SAB), 246.28 ± 84.48 (EF) and 179.4 ± 49.45 (IL), respectively.

Ovaries showed a wide variability in the size of vitellogenic oocytes. Mature females (M2 and M3) from SAB had the largest oocytes followed by IL and EF (ANOVA$_\text{sites}$ $F_{(2,63144)} = 113.01$, $P < 0.0001$; Fig. 6).

There was a strong correlation between the log number of vitellogenic oocytes and the log total weight of females (Fig. 7). In the three sites, the increase in the number of vitellogenic oocytes was explained (more than 55 %) by total weight through a power relationship, and the highest increase was found in EF.

Laboratory experiments

After removal of brooded eggs, 37 % of females in captivity continued spawning (Table 4). The weight of these
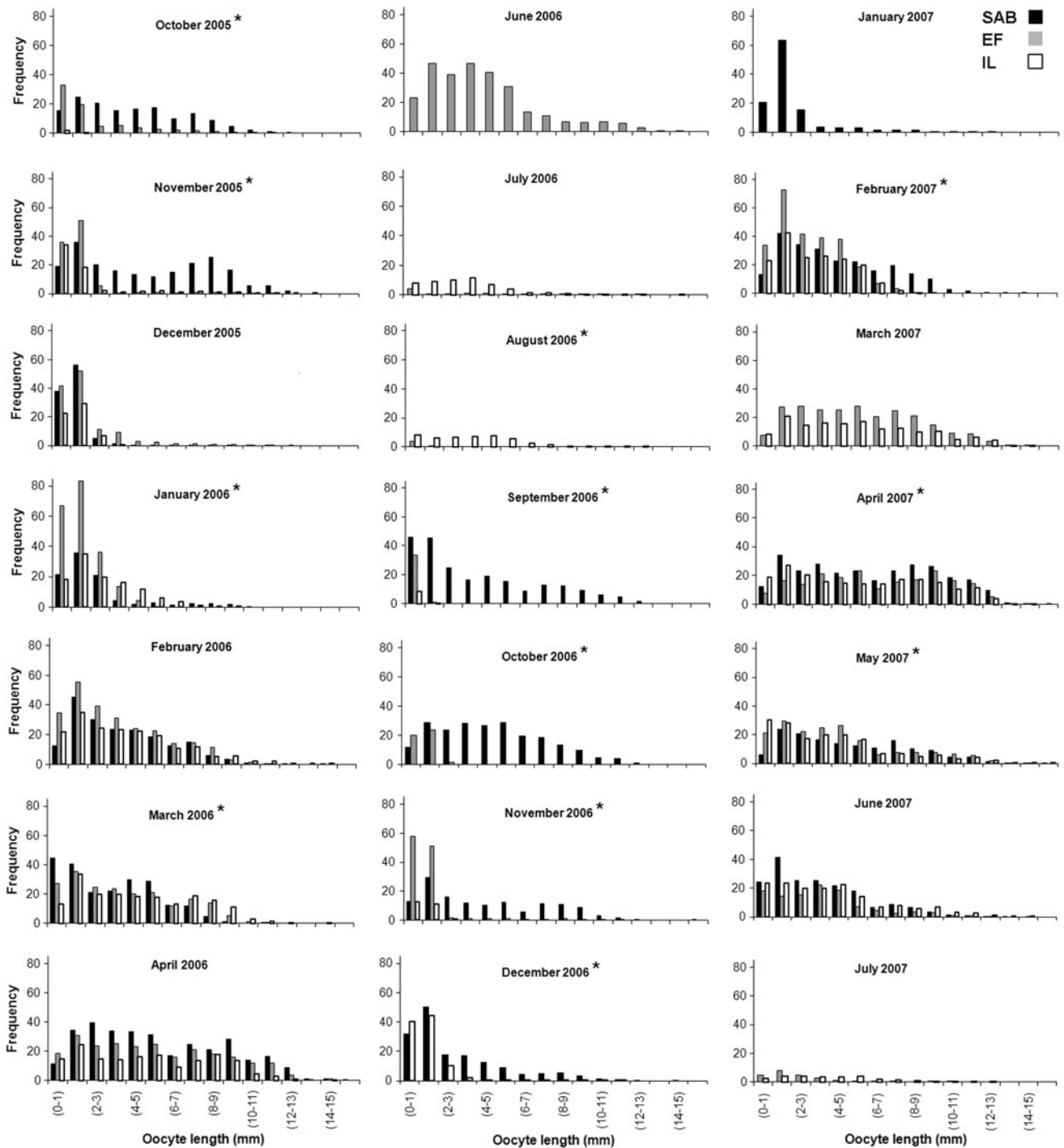
Fig. 4 Monthly oocyte size frequency distributions in the three study sites. *Asterisk* indicates the months with significant differences between sites (Kolmogorov–Smirnov test, $P < 0.05$)

females was 48.72 ± 7.56 g, and the developmental state of their clutches at the time of removal was recent. In contrast, the weight of females that did not continue spawning was 33.84 ± 7.70 g, and their clutches when removed were in a medium-advanced developmental stage. The weight of control females was 42.04 ± 10.7 g; they survived the experimental period, and in one case, hatchlings emerged from the eggs during the experiment.

Table 3 Comparisons of the monthly size frequency distributions between study sites

	SAB–EF	SAB–IL	EF–IL
2005			
Oct	*	NS	NS
Nov	*	*	NS
Dec	NS	NS	NS
2006			
Jan	NS	NS	*
Feb	NS	NS	NS
Mar	NS	*	NS
Apr	NS	NS	NS
May	–	–	–
June	–	–	–
July	–	–	NS
Aug	–	–	*
Sep	*	*	NS
Oct	*	–	–
Nov	*	*	NS
Dec	–	*	–
2007			
Jan	–	–	–
Feb	*	*	NS
Mar	–	–	NS
Apr	NS	NS	*
May	NS	*	NS
June	–	–	NS
July	–	–	NS

Kolmogorov–Smirnov test ($\alpha = 0.05$)

NS non-significant, * significant, – no data

Fig. 5 Mean number of vitellogenic oocytes ($\pm$SD) by maturity stage and study site. *Different letters* indicate significant differences (Tukey's test $\alpha = 0.05$). *Boxes* indicate comparison of mature females (M2 and M3) between sites. *SAB* San Antonio Bay, *EF* El Fuerte, *IL* Islote Lobos

Discussion

This study contributes to an understanding of the variations in reproductive pattern of *O. tehuelchus* in different coastal sites of San Matías Gulf. In Islote Lobos, female size at maturity was 18 % smaller (8 mm DML) than in the other sites studied. This may be a direct consequence of the fact that these individuals never reached the size of the individuals in El Fuerte or San Antonio Bay (Storero et al. 2010).

In El Fuerte and Islote Lobos, males and females had a similar size at maturity, whereas in San Antonio Bay, males were smaller at maturity than females. This early maturation of males in San Antonio Bay may be related to the extended period of maturity of females in this site (Storero et al. 2010), while males mature quickly when having reached a minimum size. As mentioned by several authors for cephalopods in general (Guerra and Castro 1994; Jackson and Wadley 1998; Leporati et al. 2008) and as it seems to be for *O. tehuelchus*, maturation should be more related to body size than age, suggesting that certain physiological threshold associated with size has to be reached before maturation can take place.

Sex-specific size at maturity has been observed in different cephalopod species (Alvarez Perez and Haimovici 1991; Moreno et al. 2005; Rodríguez-Rúa et al. 2005; Leporati et al. 2008). Otero et al. (2007) mentioned that, in *O. vulgaris*, the delayed reproductive development of females and the larger size at maturity compared to males may be associated with the fact that a higher proportion of body mass is involved in female reproductive development. Our previous studies on age and growth in *O. tehuelchus* (Storero et al. 2010) suggest that there is a complex set of factors affecting the growth pattern and maturity in the different environments of San Matías Gulf. Thus, during the spawning season, octopuses that have reached the size threshold will either begin the maturation process or else delay maturation and continue growing until the next spawning season. Indeed, if there is a specific minimal size for maturation to take place, differences in size at maturity are expected to occur between groups, which, under distinct environmental condition, differ in growth rate (Moreno et al. 2005). Estimates of size at maturity for *O. tehuelchus* in Brazil were similar to our results with respect to females but not to males (Alves and Haimovici 2011). In accordance with our observations, geographic size differences can be attributed to the spatial differences in environmental variables such as temperature, light and/or food availability.

Numerous studies have suggested that counts of vitellogenic oocytes underestimate the actual fecundity and that due to the asynchronous development and maturation of oocytes, fecundity estimates should be based on counts of the total number of oocytes (potential fecundity) (Laptikhovsky and Nigmatullin 1992; Laptikhovsky and Arkhipkin 2001). Although in the present study only vitellogenic

Fig. 6 Box-plot of the size of
vitellogenic oocytes by maturity
stage and study site. *Horizontal
line* median; *bar* 25–75 %,
vertical line 5–95 %. *SAB* San
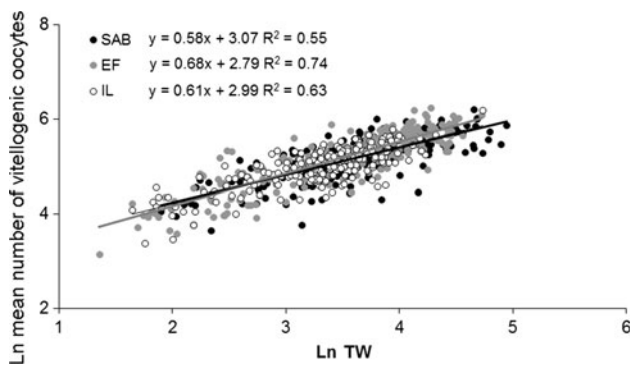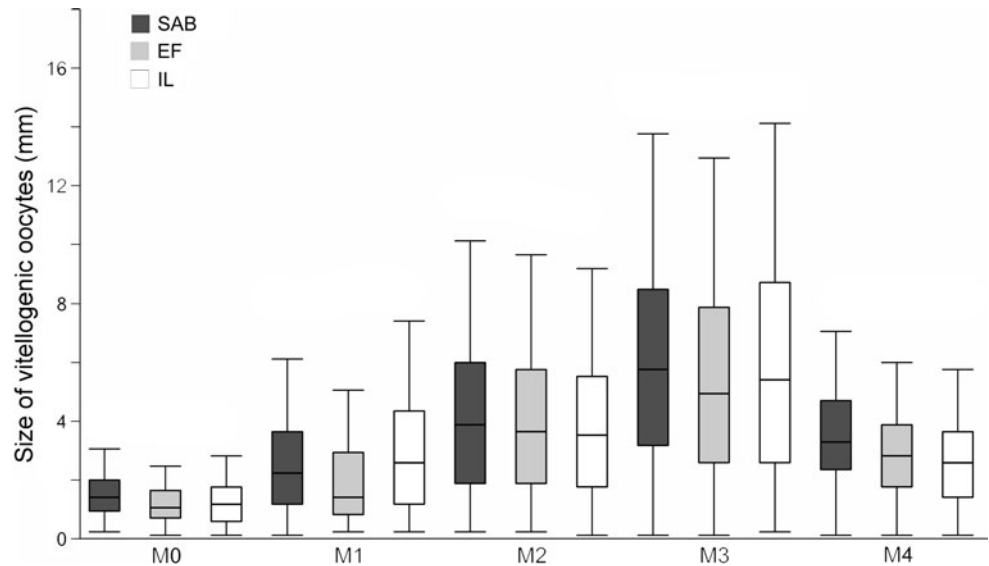Antonio Bay, *EF* El Fuerte,
IL Islote Lobos

Fig. 7 Relationships between ln mean number of vitellogenic
oocytes and ln female total weight in the three study sites. *SAB* San
Antonio Bay, *EF* El Fuerte, *IL* Islote Lobos

oocytes were measured and counted, this allowed for an
approximation of the actual fecundity of *O. tehuelchus* and
a comparison of animals from the three study sites.

Differences in oocyte size frequency distributions
between sites confirm the species' extended reproductive
period in San Antonio Bay, where octopuses showed
ovaries with large mature oocytes over several months.
This extended reproductive period in the bay favours the
existence of subannual cohorts with different growth pat-
terns depending on the environmental conditions (Storero
et al. 2010). On the other hand, in Islote Lobos, the mat-
uration seems to be a bit delayed compared to El Fuerte.
This delay in maturation time results in larger specimens,
and skilled fishermen take advantage of this by moving
from one fishing ground to another to collect larger indi-
viduals and extend the fishing season (pers. obs.).

Size distributions of vitellogenic oocytes showed a sin-
gle cohort that grew in size and number when approaching

the maturation and spawning season in the three study sites.
According to this synchronous ovulation pattern and the
existence of a single spawning event, *O. tehuelchus* should
be considered a simultaneous terminal spawner. Our results
agree with histological observations (Pujals 1986), which
showed groups of oocytes in similar stage and with similar
pattern of yolk accumulation. Although this seems to be the
most likely strategy for the individuals in San Antonio Bay,
it is interesting to note that the extended spawning season
may be a consequence of batch spawning and/or lack of
synchronization during the spawning and breeding period
in the population (Boyle et al. 1995; Boletzky 2003). Such
a high individual flexibility in reproductive strategies has
been shown in other cephalopods, where within the same
population, some females lay just one egg mass and die,
while some others may spawn intermittently over a long
period of time (Boletzky 1986, 1988; Gabel-Deickert
1995). Also, the extended spawning period in San Antonio
Bay may be a way to increase fecundity or may be related
to environmental differences (e.g. in temperature or food
availability), which in turn may affect yolk deposition and
the synchronous development of oocytes. The wide size
range of oocyte in mature females and the preliminary
laboratory experiments indicate that females may spawn
over several days or even weeks (at least over 20 days,
according to the laboratory data), which would generate
groups of eggs in different developmental stages within a
clutch and, which may, in turn, favour hatchling survival.

The differences in number and mean size of vitellogenic
oocytes between study sites may be due to respective dif-
ferences in body size. Octopuses from Islote Lobos were
smaller than those in the other sites (Storero et al. 2010)
and this may directly relate to lower fecundity (fewer
vitellogenic oocytes in the ovary) and smaller size at

Table 4 Laboratory data on spawning pattern

No.	TW (g)	OW (g)	DW (g)	Eggs_ini	Eggs_final	Development
1	42.8	4.2	3.8	27	36	Recent
2	57.2	0.75	2.17	97	4	Recent
3	46.1	0.91	1.62	106	16	Recent
4	41.4	0.4	1.33	75	0	Medium
5	28	0.93	0.61	16	0	Medium
6	32.4	0.34	1.22	84	0	Medium-advanced
7	45.4	1.03	1.29	95	0	Medium-advanced
8	28.6	0.66	0.72	13	0	Advanced
9	62	3.08	2.72	53	53	Recent
10	33.6	2.3	2.48	47	47	Recent
11	46.3	0.31	1.62	69	69	Medium-advanced
12	46.8	0.51	1.87	74	74	Medium-advanced
13	50.9	0.74	1.97	116	116	Medium-advanced
14	34.7	0.72	0.82	17	17	Advanced
15	42.7	0.46	1.1	65	65	Advanced
16	27.8	0.36	0.62	24	16 (8)	Hatched

TW total weight (g), *OW* ovary weight (g), *DW* digestive gland weight (g), *Eggs_ini* number of eggs in the shelter at the beginning of the experiment, *Eggs_final* number of eggs in the shelter at the end of the experiment. Octopuses 9–16 are controls. Hatched juveniles in brackets

maturity. Fecundity, expressed as number of vitellogenic oocytes in the ovary of mature females, was higher in El Fuerte and San Antonio Bay. Our results are consistent with the data given by other authors (Pujals 1986; Iribarne 1991b) and for similar small octopuses (e.g. *Octopus joubini* with 50–200 eggs; Forsythe 1984). In Brazil, the mean number of oocytes recorded in ovaries of maturing females of *O. tehuelchus* was 246.8 (range 20–448) (Alves and Haimovici 2011). As this conforms to our results for vitellogenic oocytes, these authors probably also did not evaluate potential fecundity (i.e. total number of oocytes in ovary) but only counted vitellogenic eggs.

Assuming that the Patagonian octopus is a simultaneous terminal spawner and that the number of vitellogenic oocytes is a good indicator of fecundity, larger octopuses are likely to contribute more to the next generation. As observed for other octopodids as well, our results showed an increase in oocyte number with female total weight (Laptikhovsky 2001; Oosthuizen and Smale 2003; Carvalho and Sousa Reis 2003; Otero et al. 2007; Alves and Haimovici 2011; Ortiz et al. 2011).

Interestingly, the number of oocytes in post-spawning females (M4) was similar to that in mature females (M2 and M3). This may indicate that the small Patagonian octopus has large eggs and very low actual fecundity when compared to potential fecundity. The number of eggs laid by different octopus species is influenced by several factors such as substrate availability, quality of shelter and/or reabsorption within the ovary (Iribarne 1990; Anderson 1997; Melo and Sauer 1998). *O. tehuelchus* ovaries did not

show large numbers of atretic oocytes, and shelter quality and availability was not a limiting factor (pers. obs.).

Females in San Antonio Bay showed the largest oocytes. Thus, embryos are provided with higher energy reserves and this should be reflected in a higher survival rate of the benthic hatchlings.

The present study shows a close relationship between reproduction, growth and condition, represented as size at maturity, number and size of vitellogenic oocytes within the ovary, and the period of maturity and spawning. Future research should focus on indexes describing potential fecundity (Laptikhovsky and Nigmatullin 1992). This would allow comparing data of *O. tehuelchus* with those from other large-egged octopus species.

Finally, the demonstrated variations in some reproductive traits as well as data of our previous studies on growth and life history (Storero et al. 2010) highlight a distinct environmental plasticity of the small Patagonian octopus. It remains to be elucidated which factors (e.g. oceanographic, physical, biological and human) bring about these variations and how they affect the dynamics of the coastal populations.

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