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Marine Protected Areas: reserve effect or natural variability? The Patagonian octopus case

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Population characteristics can be influenced by specific factors of the habitat and the natural variability of populations can confuse the effect related to protected environments. This study compares the demographic characteristics of Octopus tehuelchus *in three coastal environments: two Marine Protected Areas (San Antonio Bay (SAB) and Islote Lobos (IL)) and a traditional fishing zone (El Fuerte (EF)). Weight–frequency distributions, sex-ratio and recruitment were monthly compared between the three intertidal zones.* Octopus tehuelchus *was smaller in IL, where fishing intensity is lower or null, and reached the largest sizes in the main fishing area of EF and within SAB (where there is no regulation and a mid–high fishing intensity). The sex proportion in SAB and EF was 1:1 all along the year. Although the proportion of mature females in IL was higher, the highest recruitment was observed in EF (the traditional fishing ground). These new data suggest that previous studies, which reported that Marine Protected Areas have positive effects for* O. tehuelchus *populations, can no longer be supported, and highlight the importance of understanding and quantifying the magnitude and range of natural variability in each environment when assessing the effectiveness of Marine Protected Areas.*

Keywords: Marine Protected Areas, population variability, *Octopus tehuelchus*, Patagonia

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INTRODUCTION

The population biology of any group of animals includes the quantitative aspects of their biology that allow understanding their changes in abundance and distribution (Begon *et al.*, 2006). The description of the population characteristics is essential to fully understand the relationship between the species and other components of the ecosystem, and to be able to determine the effects of human activities over these populations. Several studies have characterized some of the local responses of marine communities to protection from fisheries (García-Rubies & Zabala, 1990; Bennett & Attwood, 1991; Rakitin & Kramer, 1996; Babcock *et al.*, 1999; Pinnegar *et al.*, 2000; Guidetti & Sala, 2007; Stockwell *et al.*, 2009). Despite the growing literature about the expected responses of populations and communities to protection within Marine Protected Areas (MPAs) or no-take areas, most of the mechanisms that are supposed to work in marine reserves have not yet been empirically demonstrated (García-Charton & Perez-Ruzafa, 1999).

Coastal marine ecosystems are highly variable, and the biotic and abiotic factors inherent to these environments can affect the bio-ecological characteristics of cephalopod populations living within them (Boyle & Rodhouse, 2005). Density, spatial distribution, size–frequency and age structure can be influenced by specific factors of the habitat. In this respect, the natural variability of populations can confuse the effect of the protection of environments. Moreover, the natural forces that drive the spatial and temporal variation in the population structure can be both physical (habitat complexity, temperature and salinity) and biological (recruitment, predation, prey availability, etc.). Thus, the problem is in determining the relative importance of such processes in influencing the population structure characteristics (García-Charton & Perez-Ruzafa, 1999).

In San Matías Gulf (Patagonia), the presence and population features of the small octopus *Octopus tehuelchus* d'Orbigny (1934) seem to differ between several intertidal environments. Narvarte *et al.* (2006) compared sex-ratio and recruitment in two sites of the west coast of San Matías Gulf, one of which was a MPA. These authors reported that abundance and recruitment within the MPA was three times higher and that these differences may be explained by the establishment of the reserve and the decrease in fishery activities, which significantly decreased the catch of brooding females, thus allowing a higher egg survival. On the other hand, our previous studies have shown that *O. tehuelchus* has a strong variability and plasticity (evidenced by variation in the progression of maturity, growth, life-span and reproductive traits) in response to the environment in which each individual is developed (Storero *et al.*, 2010, 2012).

The main objective of this study was to describe and compare some demographic characteristics of *O. tehuelchus* in different coastal environments of San Matías Gulf, in order to establish differences and similarities between these populations, and discuss them in relation to their natural

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variability, the effectiveness of marine reserves and the importance of differentiating between the reserve effect and natural variability.

MATERIALS AND METHODS

Background of *Octopus tehuelchus*

The Patagonian octopus inhabits the intertidal and subtidal environments from South Brazil (30°S) to North Patagonia (45°S). In Patagonia (San Matías Gulf), the high abundances favour the exploitation by artisanal fishers who collect octopuses by hand with an iron-gaff or by turning over rocks. *Octopus tehuelchus* is a small octopus (up to 150 g), which lays 40–80 large eggs (approximately 9–12 mm long × 3–5 mm wide) during the end of the summer and autumn. Eggs are laid in holes in the rocks or in empty shells. Embryonic development occurs in winter, with four months of parental care. Hatchlings emerge in spring/summer (dorsal mantle length: 4–6 mm; total length: 10–14 mm; and total weight: 0.052–0.139 g, approximately) and the benthic young have habits similar to those of adults. The lifespan is two/three years and growth is seasonal, with slow growth rates during winter. Size at maturity is approximately 40 mm of dorsal mantle length. *Octopus tehuelchus* is an opportunistic predator that feeds on molluscs and crustaceans (Pujals, 1986; Iribarne, 1990, 1991a, b; Ré & Gómez Simes, 1992; Narvarte *et al.*, 2006; Storero *et al.*, 2010, 2012).

Study sites

San Antonio Bay (SAB: Figure 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 semi-diurnal tides between 6 and 9 m in range, channels, and sandy–pebbly bottoms. Because SAB is characterized by a high species richness and biological diversity, it was declared a MPA in 1993. Despite the conservation status of the area, there are a few conservation actions to protect migratory birds that feed, rest or reproduce in the bay, without considering the other components of the ecosystem. Low tides expose large muddy intertidal flats, where people from the surrounding urban areas collect octopuses from artificial shelters (usually bottles, pipes, pots, etc.). There is no management plan that considers this artisanal octopus fishery, and particular management measures only regulate the pot–longline fishery in the subtidal zone. Furthermore, the existence of strong oceanographic patterns in SAB originates particular adaptations of the *O. tehuelchus* population (i.e. extended maturation and sub-annual cohorts (Storero *et al.*, 2010)).

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 (Figure 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 rodriguezii* and *Perumytilus purpuratus* as the dominant species, and the presence of various algae, crabs and gastropods (Narvarte *et al.*, 2006). During spring/summer months, the area is regularly visited 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, also used to be a traditional fishing ground until it was declared a MPA in 1977 (Figure 1). It is composed of six islands connected to land during low tide, is characterized by rocky shores, and inhabited by small mussels, crabs and snails. Although it became a protected area for the conservation of marine mammals and birds that inhabited the islands, and although there is no regulation of the fishery in this reserve, the fishing effort on octopuses has diminished (Narvarte *et al.*, 2006). In this sense, the characteristics of

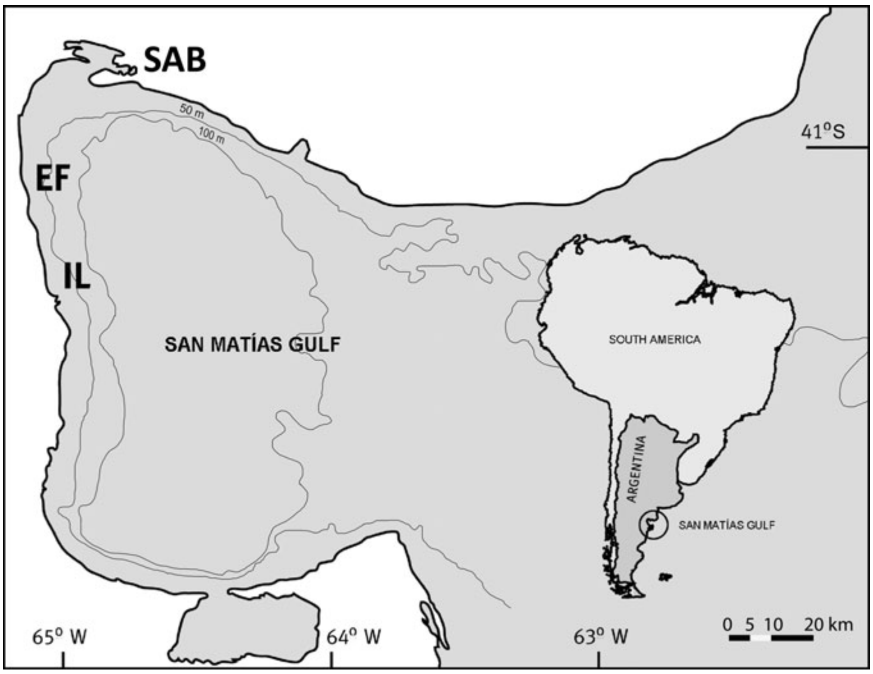


Fig. 1. Study area and sampling sites: SAB, San Antonio Bay; EF, El Fuerte; IL, Islote Lobos.

the area (i.e. located away from urban areas, inaccessible to vehicles, etc.) favours the very low/null fishing intensity.

Biological sampling and data analysis

Octopuses were monthly collected by an expert fisherman in the intertidal zone of SAB, EF and IL from October 2005 to September 2007. Between 6 and 26 transects (300 m^2, 100 m long × 3 m wide) were monthly carried out depending on the weather conditions and the tide height. Samples were taken to the laboratory and frozen, and then defrosted and processed. Dorsal mantle length (DML, in mm), total body weight (BW, in g) and sex were recorded for each individual. Due to the characteristics of artisanal fishery (i.e. seasonality and low incomes to fishers) after recording the data, the catch was returned to the fisherman for sale.

To characterize the demographic structure in each study site, size–frequency distributions (weight) and their progression were analysed along the study period. Weight–frequency distributions were compared between sites and sexes with the Kolmogorov–Smirnov test. Also, individual BW was compared between sexes and sites with analysis of variance (ANOVA), and Tukey's test was used for *a posteriori* comparisons.

Sex-ratios were compared between months and sites and the Chi-square test was used to test differences in the proportion of sexes. When differences in sex-ratios were detected, an additional test was performed to explore whether the different proportion was due to gender differential survival or birth. Three groups (with individuals seasonally grouped) were considered: juveniles (≤27 mm DML, immature), adults (>27 mm DML, maturing or mature gonads with large volume: Pujals, 1986) and post-spawning adults (>27 mm DML, flaccid gonads with grey-violet coloration: Pujals, 1986).

Recruitment was monthly analysed in each study site using the number of juveniles (immature octopuses) fished by transect in relation to the number of mature females. The number of octopuses (juveniles or mature) by transect was seasonally averaged with the aim to identify the main recruitment season in each site. The number of juveniles by transect was compared for the main recruitment season, between years and sites with ANOVA. Also, the juvenile per mature female ratio was calculated for the seasons of maximum recruitment. To calculate these ratios, mature females from the same year were used because the study period did not allow us to use the mature females that originated each cohort (Storero *et al.*, 2010). Taking into account the cohorts previously detected in Storero *et al.* (2010), different individuals were used to calculate the ratios. For summer recruits (in SAB): summer juveniles/spring mature females; for spring recruits (in the three study sites): spring juveniles/autumn mature females.

RESULTS

Weight–frequency distributions

Monthly weight–frequency distributions showed significant differences between sites along the study period (Kolmogorov–Smirnov test, $P < 0.05$) with heavier octopuses in EF, except for October and November, when the heavier octopuses were observed in SAB (Figure 2). Weight–frequency distributions were similar between sexes for every month in SAB and EF (Kolmogorov–Smirnov test, $P > 0.05$). In contrast, the distributions in IL were significantly different between sexes, with females showing higher weights than males (Kolmogorov–Smirnov test, $P < 0.05$).

Comparisons of individual total BW between sexes and sites, showed a significant interaction because males from EF and females from IL showed similar body weights. Females were heavier than males in the three study sites. Also, octopuses from SAB were heavier than those from EF, which, in turn, were heavier than those from IL (ANOVA: Table 1; Figure 3).

Sex-ratios

A different pattern was observed in the sex-ratios between sites. In general, SAB and EF showed a similar proportion 1:1 (female to male), with a few months where the ratio favoured either sex. In contrast, IL showed a higher proportion of females along the entire study period (Chi-square test, $P < 0.05$: Figure 4).

The analysis of sex-ratio by sizes in IL showed that adult and post-spawning females outnumbered males in most of the seasons (Chi-square test, $P < 0.05$). The sex-ratio for juveniles was 1:1 along the year (there was only one exception in spring 2005).

Recruitment

The mean number of juveniles caught along transects varied between seasons, being spring (September–November) the main recruitment season for the three study sites (Figure 5).

In general, the highest number of mature females was observed in IL during autumn. Although the abundance of mature females in SAB was also high, the number of juveniles caught by transect for the entire period was on average five times higher in EF (in average SAB 0.16 juveniles $transect^{-1}$; EF 0.92 juveniles $transect^{-1}$). IL also had a high abundance of juveniles (in average 0.66 juveniles $transect^{-1}$) but variable between the springs analysed. EF showed the most successful recruitment in the three springs analysed, whereas SAB showed the least successful (ANOVA: Table 2; Figure 5). SAB and IL showed the presence of juveniles in the population (in lower proportion) during the summer months (December–February). The highest juvenile per mature female ratio was observed in EF followed by IL and SAB (Table 3).

DISCUSSION

This study showed differences in the population characteristics of the Patagonian octopus in three coastal environments of San Matías Gulf. Although the weight–frequency distributions during some months were similar among sites, it is not possible to establish a unique and general pattern of size–frequencies for the populations of *O. tehuelchus* in the three sites studied. Boyle & Boletzky (1996) mentioned that life history characteristics inherent to cephalopods (short lifespan, fast growth and early reproduction) exaggerate the difficulties to establish useful generalizations on cephalopod populations. In our study in contrast to that observed in EF

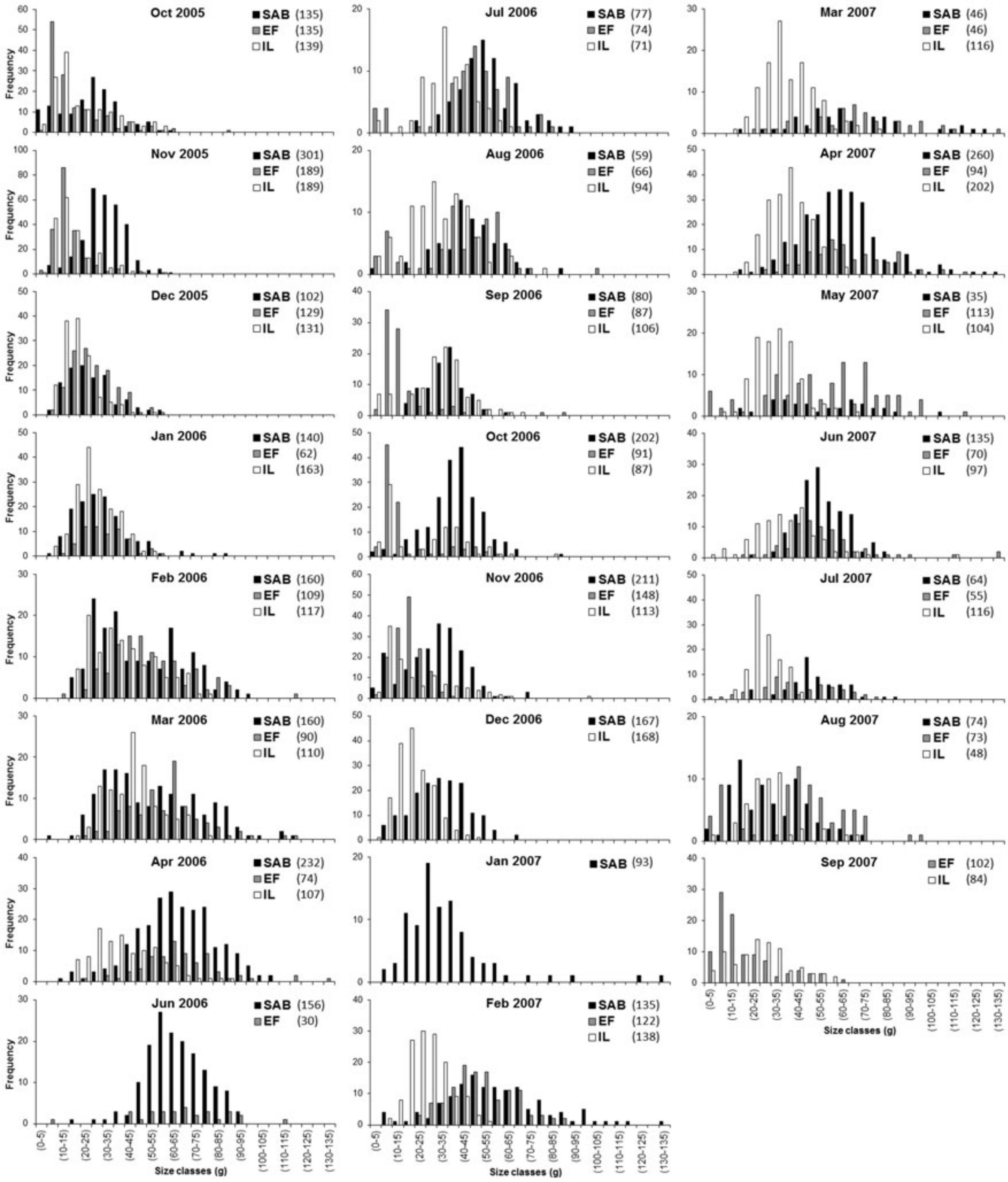


Fig. 2. Monthly weight – frequency distributions in the three study sites: SAB, San Antonio Bay; EF, El Fuerte; IL, Islote Lobos. Total number of octopuses is shown in parentheses.

and SAB, IL showed significant differences in the weight distributions of males and females. The comparison of the mean weight showed that females were heavier than males, and that octopuses from SAB were heavier than those from EF and IL. Several studies carried out in cephalopods have shown that these organisms are able to show a wide variation in size depending on the environments in which they develop their ontogeny (Belcari *et al.*, 2002; Boyle & Rodhouse, 2005; Lefkaditou *et al.*, 2008). Moreover, our previous studies have shown that the growth pattern, lifespan and the reproductive traits of *O. tehuelchus* also varies in different environments, probably influenced by the oceanographic characteristics in each site (Storero *et al.*, 2010, 2012). This means that phenotypic plasticity may be one of the main features of octopus populations and this should be taken into account when evaluating the effects of MPAs.

Table 1. Result of the two-way analysis of variance to test for differences in total weight between sampling sites and sexes.

Source of variation	df	MS	F	*P* value
Site	2	203403.70	509.61	<0.0001
Sex	1	64343.89	161.21	<0.0001
Site*sex	2	2424.74	6.07	0.0023
Error	7652	399.14		
Total	7657			

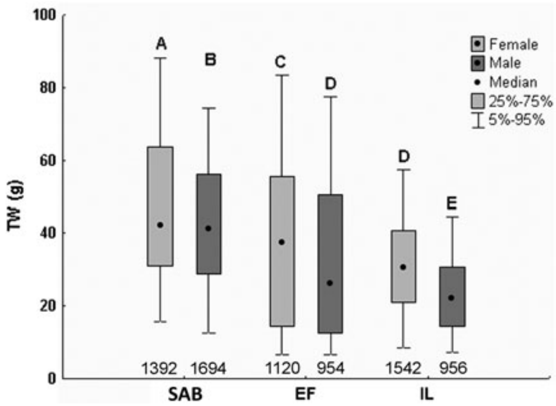
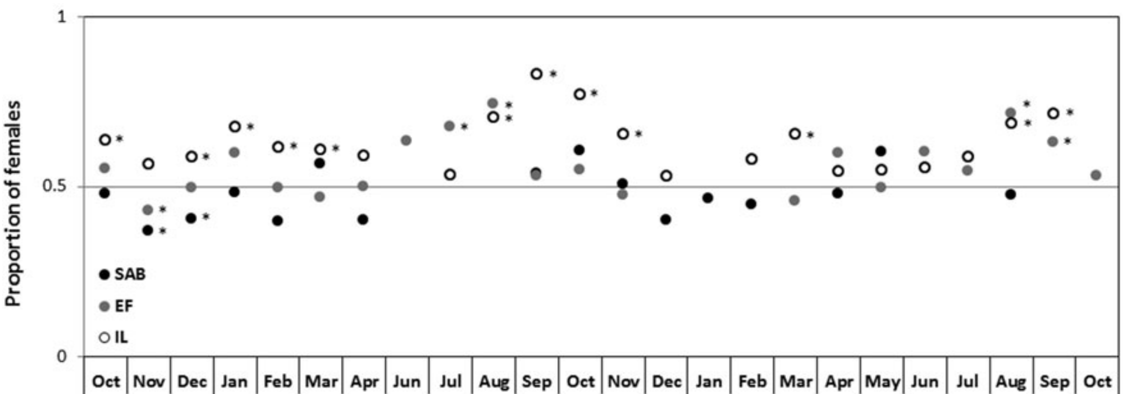


Fig. 3. Box-plot for male and female total weight (g): SAB, San Antonio Bay; EF, El Fuerte; IL, Islote Lobos. Different letters indicate significant differences (analysis of variance, Tukey's test $P < 0.05$). Values below each box indicate total number of octopuses analysed by sex and site.

The sex-ratio in the intertidal of SAB and EF was 1:1 throughout the year. The slight tendency favouring females in EF during some winter months (July–August) may be related to increased vulnerability to fishing of brooding females, which never leave the shelter while brooding. In contrast, females of IL outnumbered males throughout the year. The analysis of sex-ratios by sizes showed that the different proportions could be due to differential survival between males and females, since the sex-ratio of juveniles ($\leq$27 mm DML) was 1:1. Also, post-spawning females outnumbered males, which may be related to the fact that they remain in the shelter during brooding months and are therefore more vulnerable to the sampling method or fishing. Additionally, differences in sex-ratios of adult and post-spawning octopuses in IL may be due to the higher mobility of males, which forces them to be more exposed to predation. Voight (1992) mentioned that males become more mobile at senescence to search sexually receptive females. So, as octopuses reach senescence, the cost of predation is less than the cost of not reproducing and therefore mature males are the most mobile individuals of the population and mature females the least mobile ones. In IL, predation pressure may be higher due to the presence of marine mammals and birds that are not present in the other study sites. Moreover, the populations of some marine birds (e.g. Magellanic penguin *Spheniscus magellanicus* and cormorants *Phalacrocorax* spp.) and mammals (e.g. southern sea lion *Otaria flavescens*), which are commonly cited as active predators of *O. tehuelchus* (Malacalza *et al.*, 1994; Koen Alonso *et al.*, 2000), have increased in recent decades due to protection (Dans *et al.*, 2004). Thus, the increased exposure to predators of adult and post-spawning males and the high predation pressure may originate a differential survival of females, causing an imbalance of the sex-ratio in IL.

Although the main recruitment season was spring (September–November), there was also some recruitment of juveniles (in a lower proportion) during the summer and winter months. Two authors of this paper have previously reported that recruitment during the 1990s was three times higher in IL (the MPA) than in EF, and that this may be due to a higher survival of embryos, which is a consequence of the decrease in fishing and low removal of brooding females during the brooding season (Narvarte *et al.*, 2006). Our new data collected over two years showed rather different results, and demonstrate that the idea that MPAs have positive effects for *O. tehuelchus* populations can no longer be supported.

Although a higher proportion of mature females was observed in IL (some months twice higher than in EF), the highest recruitment was observed in the fishing ground of EF. Indeed, taking into account the annual catches of *O. tehuelchus* in EF (30 t approximately: Millán, 2007), fishing does not seem to be the main factor affecting the pattern and intensity of recruitment. Our results highlight the importance of understanding and quantifying the magnitude and range of natural variability in each environment at the moment of assessing the effect of MPAs, as it seems to occur in IL or SAB. García-Charton *et al.* (2000) mentioned that the ability to detect and predict the responses of marine populations and communities to the establishment of MPAs



	2005			2006											2007									
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
N_{SAB}	113	57	102	96	83	99	45	-	-	-	26	73	115	95	93	135	-	69	35	-	-	38	-	-
N_{EF}	134	189	129	62	109	90	74	30	74	66	87	91	148	-	-	132	46	94	111	70	55	73	102	119
N_{IL}	138	189	131	163	117	110	107	-	71	94	106	87	113	168	-	138	115	202	104	97	116	48	84	-

Fig. 4. Monthly proportion of females: SAB, San Antonio Bay; EF, El Fuerte; IL, Islote Lobos. *, significant differences (Chi-square test, $P < 0.05$); N, total number of octopuses (males and females) analysed by month and site. When N was lower than 30, the Chi-square test was not performed.

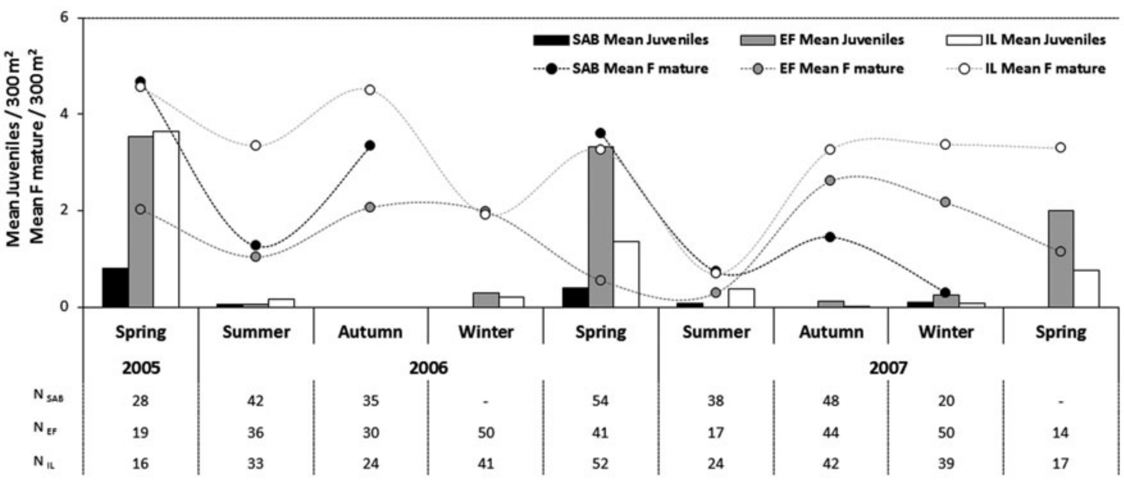


Fig. 5. Mean number of juveniles and mature females caught by transect (300 m^2). Standard deviations are not displayed to facilitate graph interpretation. SAB, San Antonio Bay; EF, El Fuerte; IL, Islote Lobos; N, number of transects (300 m^2) carried out by site and season.

depends on the ability to distinguish between the influences due to management and the natural variability due to natural factors (such as natural mortality, migration, survival and recruitment). Most studies on the effect of MPAs point out that size, density and/or recruitment are higher within the reserves than within fishing areas; however, our results show an opposite tendency. *Octopus tehuelchus* was smaller in the marine reserve of IL (where the fishing intensity is low or null) and reached larger sizes in the main fishing area of EF and within the MPA of SAB (where there is no regulation and there is a mid–high fishing intensity). The highest recruitment was observed in the traditional fishing area, and since *O. tehuelchus* has no larval stage (i.e. the early-born individuals have habits similar to those of the adults) density should be strongly related to recruitment success.

Halpern (2003) analysed the impact of MPAs on different organisms and remarked that density, biomass, size and diversity are significantly higher inside reserves than outside them (or after reserve establishment versus before). However, he also found that invertebrates did not follow this pattern, probably due to their exploitation level and its position in the food chain or to the main goals of reserves, which usually are not designed to protect invertebrates. In our study, the MPA of SAB was established to protect migratory birds that feed, rest or reproduce in the bay, not taking any particular conservation action on other components of the ecosystem. With this respect, there is no management plan that considers the octopus fishery, and particular management measures only regulate the artisanal pot–longline fishery in the subtidal zone. Also, the existence of strong oceanographic patterns in SAB originates particular adaptations of the *O. tehuelchus* population (i.e. higher weights, extended maturation, sub-annual cohorts and sex-specific size at maturity: Storero *et al.*, 2010, 2012).

Finally, most studies on MPAs compare size, abundance, biomass and species richness inside and outside reserves without considering the complexity of each site. Leite *et al.* (2009) observed higher abundance of *Octopus insularis* within a fishery area than inside a national park, mentioning that open areas should be related to the availability of suitable habitats (particularly with dens). Also, Guidetti & Sala (2007) remarked that the non-linearity in the community-wide effect of reserves suggests that caution is needed in treating reserves and unprotected areas as two experimental treatments in ecological studies.

Table 2. Result of the two-way analysis of variance to test for differences in the number of juveniles caught by transect for the main recruitment season (spring), between years and sites.

Source of variation	df	MS	F	*P* value
Year	2	1.60	2.90	0.1127
Site	2	9.06	16.43	0.0015
Year*site	3	1.12	2.04	0.1871
Error	8	0.55		
Total	15			

Table 3. Juvenile per mature female ratio in the main recruitment season (spring). SAB, San Antonio Bay; EF, El Fuerte; IL, Islote Lobos.

	SAB	EF	IL
Summer 2006	0.02		
Spring 2006	0.12	1.61	0.30
Summer 2007	0.02		
Spring 2007		0.76	0.23

As shown for other octopuses, several factors like refuge and prey availability (Iribarne, 1990; Katsanevakis & Verriopoulus, 2004a; Leite *et al.*, 2009), seasonality (Pierce *et al.*, 2008) and/or temperature (Sobrino *et al.*, 2002; Katsanevakis & Verriopoulus, 2004b) may be interacting and regulating the population dynamics of *O. tehuelchus*. Future studies should focus on elucidating which are the main factors that could be playing an important role, influencing the populations of the Patagonian coast.

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