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CONTRIBUTION TO UNDERSTANDING THE POPULATION STRUCTURE AND MATURATION OF *ILLEX ARGENTINUS* (CASTELLANOS, 1960): THE CASE OF THE INNER-SHELF SPAWNING GROUPS IN SAN MATIAS GULF (PATAGONIA, ARGENTINA)

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ABSTRACT *Illex argentinus* is known for spatiotemporally segregating into reproductive aggregations on the mid-continental shelf and slope off southern South America. In this study we found that the species also mates and spawns in San Matías Gulf, a coastal basin off northeastern Patagonia. Basing on the analysis of size and maturity structure of squids caught over a 28-month period in waters of the gulf, distinct demographic pulses were identified in the samples each year. Two of them were more consistent, one comprising small-sized individuals reaching full maturity in January to February (summer) and the other including larger individuals maturing between September and October/December (spring). Also, a less conspicuous group of mature individuals was observed in June/July (winter) of the last sampling year. So far, differences in the parameters of the size-at-maturity curves of these population components allow considering at least two stocks for management of *I. argentinus* in the gulf.

KEY WORDS: squid, population structure, *Illex argentinus*, maturity process, spring spawning, summer spawning

INTRODUCTION

Many authors have stressed the importance of studying the structure and biology of fish and shellfish populations for an accurate assessment and management of fisheries operating upon them (Hilborn & Walters 1992, Walters & Martell 2004, Hoggarth et al. 2006, Hibberd & Pecl 2007). For ommastrephids, a group of oceanic squids well known for segregating into discrete "stocks" with different sizes at maturity, chronology of maturation, morphological characteristics, and growth patterns, this has been shown to be particularly relevant (O'Dor & Lipinski 1998, Arkhipkin et al. 2000, Argüelles et al. 2001, Martínez et al. 2002, Chen & Chiu 2003). As pointed out by Hare (2005), stocks can either be "genotypic" or "phenotypic." Genotypic stocks, have been defined as "randomly interbreeding members of a species whose genetic integrity persists whether they remain spatially and temporally isolated as a group or segregate for breeding and otherwise mix freely with other genotypic stocks" Kutkuhn (1981). Phenotypic stocks, on the other hand, are "intraspecific groups that differ in the expression of certain characters owning to environmental or genetic effects" (Hare 2005). Microcohorts, as depicted by Caddy (1991), "distinct components of recruitment within a single year class population," could represent a particular case of a phenotypic stock generated by environmental effects if they result from pulses of recruitment of individuals hatching at different times of an extended reproductive season experiencing different conditions (i.e., food availability or seawater temperature) reflected in the acquisition of particular biological parameters (i.e., growth rates, sexual maturation rates).

The Argentinean short-fin squid, *Illex argentinus* (Castellanos, 1960), a neritic-oceanic squid from the South West Atlantic, follows the general pattern observed in the ommastrephids. Several populational units from a single year-class, with particular spawning seasons and areas, have been recognized on the Argentinean shelf and slope. These include the South Patagonian Stock (SPS) inhabiting the outer shelf and slope south of 44°S and spawning on the slope between 45° to 48°S in the winter months; the Bonaerensis-North Patagonian Stock (BNPS), distributed north of 43°S up to the Malvinas (Falkland)/Brazil currents convergence, presumably spawning in late winter on the western side of the convergence; the Summer Spawning Stock (SSS) living and spawning on the mid and outer shelf between 42° and 46°S from December to February; and the Spring Spawning Stock (SpSS) found in mid-inner shelf between 38° and 41°S (Brunetti 1988, Nigmatullin 1989, Brunetti et al. 1998, Haimovici et al. 1998) (Fig. 1). Also, the existence of a fifth stock has been reported for Brazilian waters (Haimovici et al. 1998). However, only the BNPS and SPS have been studied in detail because of their catch volume (Arkhipkin & Laptikhovsky 1994, Brunetti et al. 1998, Haimovici et al. 1998, Arkhipkin 2000, Walluda et al. 2005, Agnew et al. 2005, Madureira et al. 2005, Martínez et al. 2005). The other two stocks, distributed on the Argentinean inner shelf, have not been studied as intensively as the former. Furthermore, it has been pointed out that the information on the SpSS is scanty and contradictory (Carvalho & Nigmatullin 1998) and that it might be an extension of the BNPS (Laptikhovsky et al. 2001).

Fishery landings of *I. argentinus* fell down from more than 1.1 million tons in 1999 to less than 0.3 million tons in 2005 (FAO 2007), probably reflecting changes of abundance in the fishing grounds (Basson et al. 1996, Walluda et al. 2001, Walluda et al. 2001, Nigmatullin et al. 2004). Although it is difficult to quantify the effects of exploitation, environmental regulation (i.e., failure in recruitment because of suboptimal temperatures, particular hydro-dynamic conditions or low food availability) and the combination of both on the changing abundance of this resource, it is broadly accepted that the species has been under high fishing pressure (Nigmatullin et al. 2004, FAO 2007). Theoretical and empirical evidences have shown that intense fishing may cause artificial selection pressures generating rapid evolutionary effects in *Illex* species, readily recognizable

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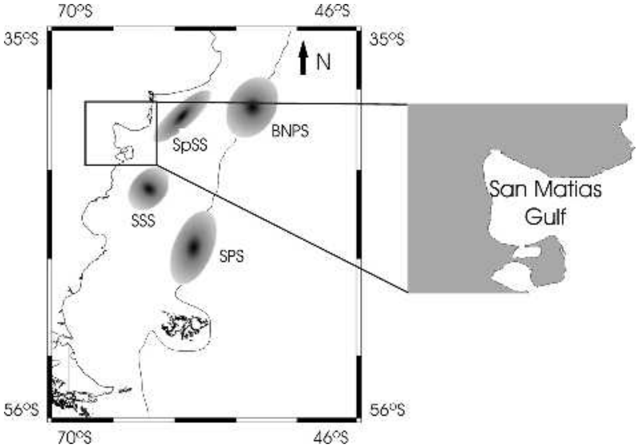

Figure 1. San Matías Gulf and spawning areas suggested in previous studies (Haimovici et al. 1998) for the different stocks of *Illex aregentinus* on the Argentinean shelf and slope. BNPS: Bonaerensis-Northpatagonian Stock; SPS: South Patagonian Stock; SpSS: Spring Spawning Stock; SSS: Summer Spawning Stock.

in their population structures (Rodhouse et al. 1998, Murphy & Rodhouse 1999). Because squids have short lifespan coupled with high growth and early reproduction, studying their population structure and dynamics may provide "little framework of predictive theory" (Boyle & Boletzky 1996, Boyle & Rodhouse 2005). Thus, although many works have been published on the population structure and dynamics of *I. argentinus*, it is necessary to update the information available and to improve their comprehension.

In San Matías Gulf (Northern Patagonia, 41° to 42°S, 63° to 65°W, Fig. 1), *I. argentinus* is fished throughout the year as by-catch in the Argentinean hake *Merluccius hubbsi* bottom trawl fishery; being more abundant during winter and spring, with peaks generally occurring in August. Since 1994, a small fleet of jiggers has been allowed to exploit this resource from June to September each year; but catches have been widely variable (Millan 2006). Studying the size structure of *I. argentinus* samples landed in 1991 at the San Antonio Oeste port, Morsan and González (1996) recognized a modal progression of large-sized individuals (20–30 cm ML for males and 25–35 cm ML for females) from fall to early summer. These attained full maturity in August to November (spring), being absent from the samples afterwards. In the following months (November to December of 1991), a modal size class composed of smaller individuals in maturing condition became apparent in the samples. Based on these observations, Morsan and González (1996) hypothesized that two different stocks, probably the SSS and SpSS, could be present in waters of San Matías Gulf. However, the characteristics of the information available did not allow them to prove this hypothesis.

In this paper, we analyze the size structure and chronology of maturation, mating and spawning of *I. argentinus* in San Matías Gulf from June 2005 to November 2007, providing the first estimations of size at maturity for males and females. Based on our results, we discuss the importance of alternative processes driving the population structuring of the species in the area.

MATERIAL AND METHODS

Samples of *I. argentinus* were obtained on a bimonthly basis from June 2005 to November 2007 on board of 25-m long bottom trawlers operating in San Matías Gulf, from hauls conducted with 120 mm mesh-size nets. The specimens were stored in sealed plastic bags and preserved in ice-chillers until examination in the laboratory. To determine temporal changes in size frequency distributions (SFD) of squid samples, dorsal mantle length (ML) of each individual was measured to the nearest centimeter using an ichthyometer. To describe the temporal patterns of maturation, squids were staged following the scale proposed by Nigmatullin (1989). This scale categorizes the process of maturation in 7 stages; stages I, II, and III correspond to immature individuals with progressive formation of gonads, stage IV consist of specimens in physiological maturation, stages V and VI comprise animals in functional maturation (capable to mate), and stage VII include fully spawned individuals. Also, total weight was registered using a digital scale (Mettler PC440) and dimensions of different reproductive organs were recorded, including weights of the nidamental glands (NiW), ovary (OvW), and oviducts (OdW) in females and weights of the testes (TeW) and spermatophoric complex (ECoW) in males. Also, the presence of spermatophores attached to the inner part of the mantle of females was registered to determine the seasonality of mating. Maturity (MI) index was estimated as:

$$\mathrm{MI} = \frac{(\mathrm{OvW} + \mathrm{OdW} + \mathrm{NiW}) * 100}{\mathrm{TW}} \quad \text{for females, and}$$

$$\mathrm{MI} = \frac{(\mathrm{TeW} + \mathrm{ECoW}) * 100}{\mathrm{TW}} \quad \text{for males.}$$

The proportions of mature males and females in 1-cm ML classes were calculated to determine size at maturity (ML 50%). For this analysis, individuals at maturity stages IV to VII were considered mature. For both sexes and for each year, a logistic curve of maturity was fitted by regression to the proportion of mature individuals in the size classes using the least square method and the relationship:

$$P_i = \frac{1}{1+e^{-(a+b*\mathrm{ML}_i)}}$$

where P_i and ML_i are respectively the proportion of mature individuals and the mantle length at size class "*i*", and *a* and *b* are constants. Size at maturity was calculated as $\mathrm{ML50\%} = -a/b$, and goodness of fit of the model was tested with a generalized linear model (GLM) assuming a binomial distribution of the data and using a logit link function (McCullagh & Nelder 1998). Additionally, females were examined to determine the presence of spermatophores attached to the inner surface of the mantle. The size at which 50% of females had spermatophores (MLsp50%) was estimated using the same relationship, but considering that P_i was the proportion of females with spermatophores at size class "*i*". Goodness of fit of the model was obtained using the same method as in the analysis of size at maturity.

RESULTS

Size Structure and Maturity Temporal Progression

A total of 3,812 individuals (1,630 females and 2,182 males) were collected through the study period. Two recruitment pulses of immature squids (stages I and II) were observed each year, the first one in late fall to early winter and the second one in spring to early summer (Fig. 2). After each pulse, there was a progressive

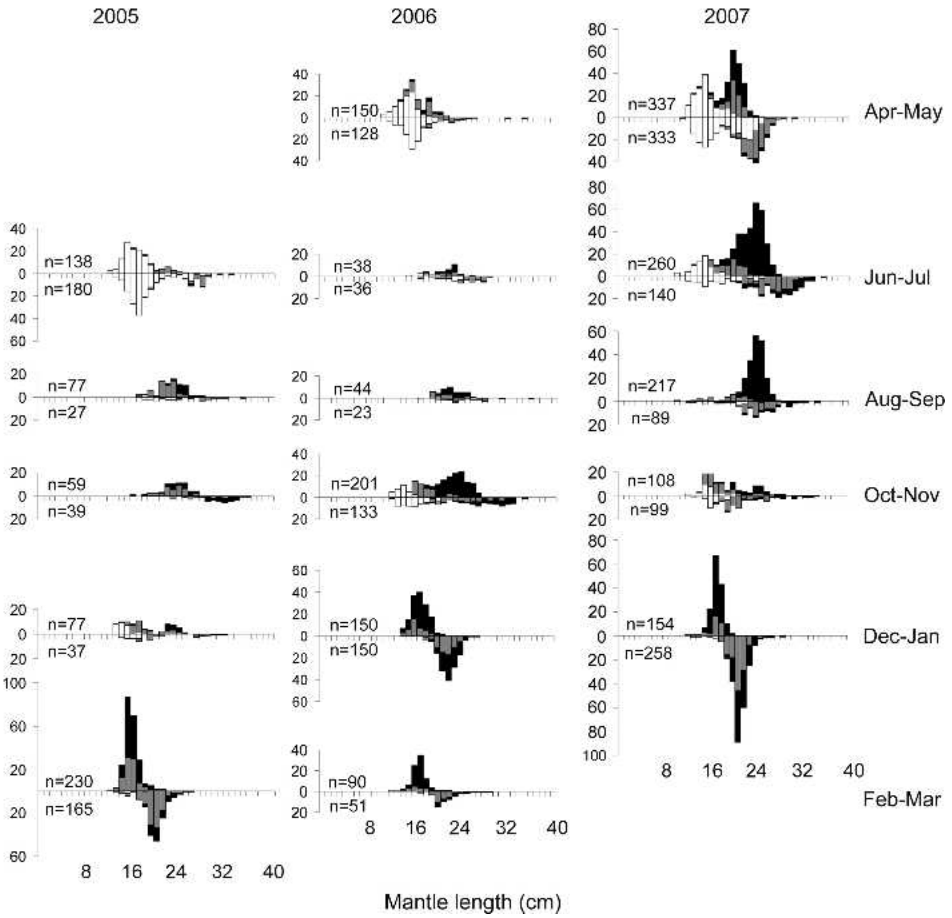

Figure 2. Size frequency distributions and maturity condition of each bimonthly sampling of *Illex argentinus* caught in the San Matias Gulf. Immature individuals (stages I and II) are represented in white; maturing individuals (stages III and IV) in grey; and mature individuals (stages V and VI) in black.

increase in squid size, especially conspicuous in females and a sequential passage to more advanced stages of maturity, both in males and females (Fig. 2). Mature (stages V and VI) and maturing (stages III and IV) individuals were present in all samples analyzed (Fig. 2), but highest proportions of mature ones were found in late winter to spring of 2005, late summer and mid-spring of 2006, and summer and winter of 2007. Mated females were observed year round, but highest proportions occurred in spring (October to November of 2005 and 2006), summer (February to March of 2006 and December 2006 to January of 2007) and winter (June to July of 2007) (Fig. 3). Largest mature and mated females observed in these periods were absent in the immediate forthcoming samples (Fig. 2 and Fig. 3). Mature individuals caught in summer were smaller-sized than those sampled in other seasons, being easily recognizable as distinct modal components in the SFDs of all mature individuals (Fig. 4).

During the sampling period, minima of the female maturity index (MI) were observed in fall and winter months, and maxima occurred in spring and summer (Fig. 5). In males, MI presented minima in fall to mid winter and maxima from late winter to summer (Fig. 5).

Size at Maturity

ML50% estimations obtained from the proportion of mature males and females at size-class were respectively 16.39 cm and 23.65 cm. However, because mature individuals caught in summer were markedly smaller than the rest, the proportion of mature individuals at size-class deviated from the expected logistic pattern (Fig. 4). To determine if ML50% of individuals caught in summer differed from that of individuals caught during the rest of the year, two distinct generalized linear models were fitted to data (one for each sex) using the season of capture as a covariate. Also, to test interannual variations in the ML50%, the sampling year (2005, 2006, and 2007) was incorporated as a covariate in the GLMs (Fig. 4). The results were similar in the models fitted for males and females. There were significant effects of season of capture (Wald F test, $P < 0.001$, df $= 1$), but no effects of sampling year (Wald F test, $P > 0.05$, df $=1$) (Fig. 4). The goodness of fit of the models was tested using the maximum likelihood estimator (scaled deviance) for both sexes. The estimated proportion of mature individuals did not differ significantly from the observed data (Males: Scaled deviance $=$ 32.04, df $= 67$, $P > 0.05$; Females: Scaled deviance $= 93.3$, df $=$ 95, $P > 0.05$). Therefore, ML50% was estimated separately for mature individuals caught in summer and in the rest of the year. Estimations of ML50% were respectively 18.92 and 13.92 cm ML for males and females caught in summer and 21.15 and 26.91 cm ML for those captured during the rest of the year (Fig. 4).

In the analysis of the proportion of mated females at size-class the results were similar to those obtained for the proportion of mature individuals: significant differences between

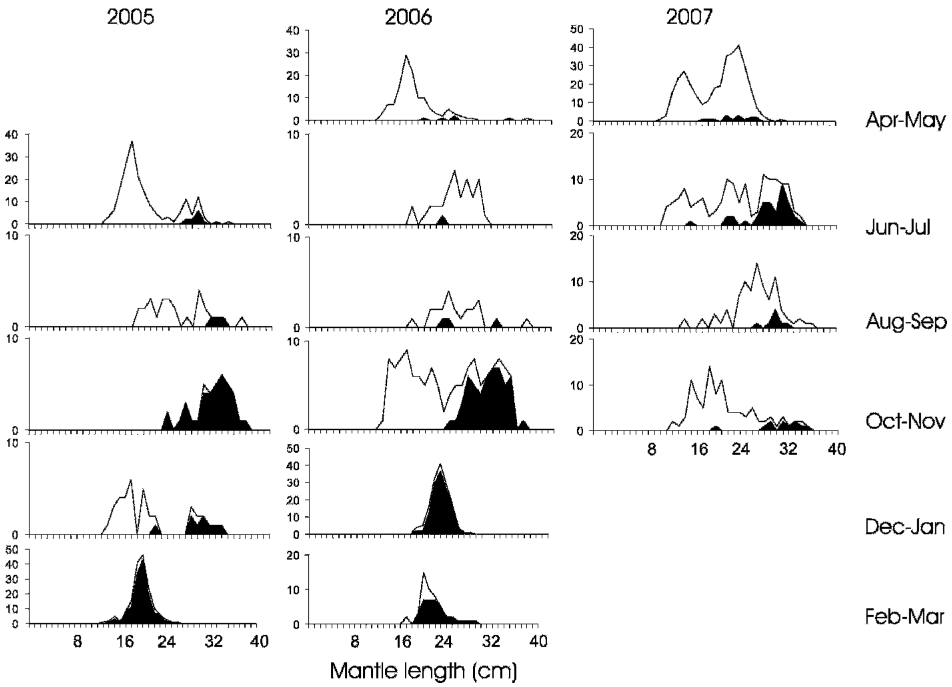

Figure 3. Size frequency distribution of mated (black bars) and unmated (white bars) *Illex argentinus* females caught in the San Matias Gulf.

season of capture (Wald F test, $P < 0.001$, df = 1) and no significant differences between sampling years (Wald F test, $P > 0.05$, df = 1). The model fitted properly the data observed (Scaled deviance = 46.48, df = 40, $P > 0.05$). For females caught in summer and in the rest of the year, MLsp50% estimations were respectively 27.36 and 17.11 cm ML. In both groups, more than 85% of females at maturity stages IV and V showed spermatophores attached to their inner mantle.

DISCUSSION

Several squid species have the potential to segregate into different stocks with particular spawning seasons and areas (O'Dor & Lipinski 1998). Multimodal patterns of SFDs in squid samples can reflect the presence of individuals from more than one spawning group temporarily inhabiting a common area (Collins et al. 1999, Arkhipkin et al. 2000) or can also be attributable to other factors like ontogenetic migration and differential mortality of some components of the population (Boyle & Boletzky 1996, Boyle & Rodhouse 2005). The combination of multiple stocks in a fishing area and the intrinsic variability in the SFD of each stock can result in complex population structures difficult to elucidate. Yet, understanding the structural characteristics of exploited populations is crucial for their assessment and management (Carvalho & Nigmatullin

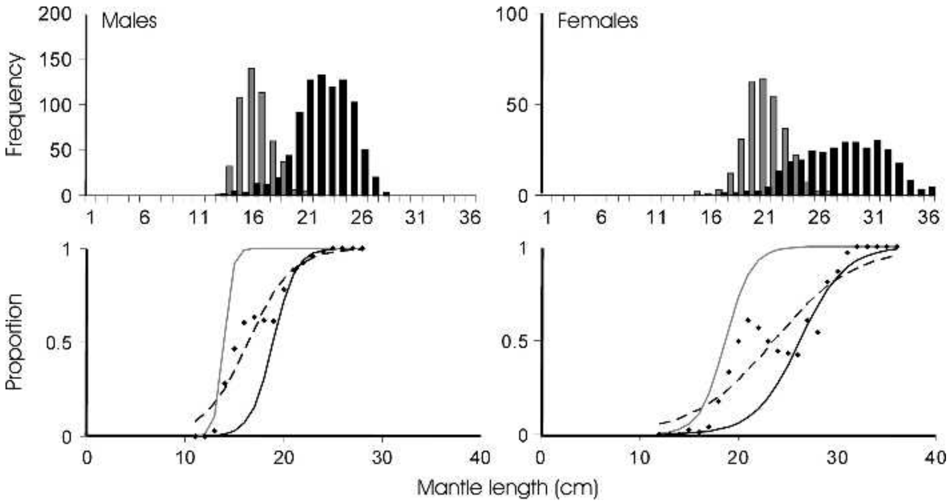

Figure 4. Size frequency distributions of mature male and female *Illex argentinus* (top) and maturity curves fitted by regression to the proportion of mature individuals at size class (bottom). Mature individuals caught in January and February are shown in gray and those captured between June and December are shown in black.

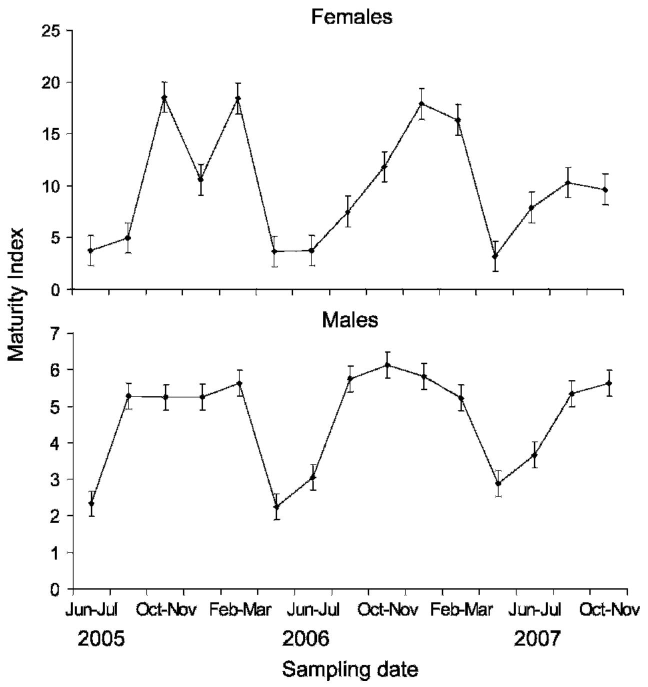

Figure 5. Temporal variation of the maturity index (MI) of male and female *Illex argentinus* sampled in San Matías Gulf during the study.

1998, Walters & Martell 2004, Hammer & Zimmerman, 2005, Hoggarth et al. 2006, Hibberd & Pecl 2007).

Although, the population units of *I. argentinus* have been profusely investigated (Sato & Hatanaka 1983, Brunetti 1988, Nigmatullin 1989, Haimovici et al. 1998, Brunetti et al. 1998, Arkhipkin 2000), their identification and the characterization of their structure and dynamics are far from being concluded. In our analysis of SFDs and maturity stages of *I. argentinus* from San Matías Gulf, two different pulses of immature individuals were identified each year in the samples, one recruiting in April to July and the other in October to November. In the months after their recruitment, squids in the samples presented a gradual maturation. Mating peaks observed in spring of 2005 and 2006, winter of 2007, and summer of 2006 and 2007 matched the periods of higher proportion of mature females and were followed by the disappearance of these individuals in the forthcoming samples, suggesting the occurrence of spawning and subsequent massive death. The presence of two modal components in the SFDs of males and females and the proportions of their maturity stages indicate that at least two groups of individuals with different sizes and maturity conditions coexist in San Matías Gulf during most part of the year. As reported for this and other squid species, MI showed that males mature earlier in than females, ensuring that most females have enough mates available previous to spawning (Haimovici et al. 1998, Barón & Ré 2002).

Our results, not only show evidence for the presence of at least two spawning groups in San Matias Gulf, but also allow confirming that these differ in some population parameters. The estimation of ML50% showed that the group of females spawning during the summer months had marked differences in their sizes-at-maturity relative to the group of squids maturing in other seasons of the year. Furthermore, the absence of significant interannual differences in ML50% and MLsp50% estimations for both groups demonstrate that these parameters were persistent throughout the study period. Therefore, for management purposes the spawning groups characterized in this study should be considered as different "stocks."

In this work, we show that two pulses of immature individuals and at least two peaks of mature and mated individuals occur yearly in waters of the San Matias Gulf, typically in spring and summer. However, in winter (June to July) of 2007 mature mated individuals poorly represented in winter of previous years were found in the samples. Also, in spring (October to November) of 2007 some large mated and mature females were present. Whether these individuals belong to a unique group spawning through an extended season or to two independent spawning groups is difficult to determine with the data available so far. In any case, because mature individuals and mated females were present year-round, gene flow is likely between these groups, reducing the chances for a genetic structuring caused by reproductive isolation.

So far, spawning grounds of *I. argentinus* have been reported only for the slope and continental shelf of southern South America (Haimovici et al. 1998). In this work we provide evidence supporting that the species also spawn in coastal basins off Patagonia. The presence of a nutrient-rich oceanographic frontal system in the northeastern portion of the gulf and another two in adjacent inner shelf waters, respectively known as the "San Matías," "El Rincón" and "Valdes Penninsula" frontal systems (Glorioso 1987, Glorioso & Simpson 1994, Guerrero & Piola 1997, Bogazzi et al. 2005) may provide the potential to support high plankton and nekton densities required by paralarvae and juveniles of this species to feed.

Many uncertainties are still to be resolved regarding the population structure of the inner shelf and coastal stocks of *I. argentinus*. Further studies should include the analysis of growth and age from mark readings on statolith sections, sampling of paralarvae and juveniles, population genetics analysis, as well as a continuous monitoring of catch samples obtained by the commercial fleet. Because of its particular oceanographic conditions, San Matias Gulf may provide an appropriate scenario to study these stocks and to increase the knowledge of the complex *I. argentinus* population structure.

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