



Revision of the population structuring of *Illex argentinus* (Castellanos, 1960) and a new interpretation based on modelling the spatio-temporal environmental suitability for spawning and nursery

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ABSTRACT

During the last 30 years, interpretation of the population structuring of *Illex argentinus* evolved from a single to a six-stock model, in which stocks are characterized by having distinct spawning seasons, areas and migration patterns. It is assumed that major spawning activity occurs in discrete pulses along the outer-shelf/slope off Argentina/southern Brazil during late-fall/winter and that early life stages develop near the Brazil-Malvinas Confluence (BMC). Nevertheless, there are inconsistencies in the delimitation of stocks and the interpretation of their life histories. Here, we developed a model based on records of seawater temperature and chlorophyll-*a* concentration to establish the quality of different areas of the species' geographic distribution as spawning and nursery grounds. Whereas the outer-shelf/slope domain south of 37°S presents marked seasonal restrictions for embryonic development and breeding, coastal areas within 44°–28°S are highly suitable most of the year. Squid in pre-spawning aggregations at the outer-shelf/slope south of 41°S would invest less energy to reach equally suitable spawning areas at the coast than at the BMC. Findings of paralarvae, stranded juveniles and mature squid in coastal areas off northern Patagonia support the predictions of the model. Based on these results, the population structuring and reproductive–migration patterns are reviewed and a new interpretation is proposed: *Illex argentinus* spawns not only in discrete seasons and areas on the slope and mid/outer shelf,

but also conducts quasi-permanent spawning migrations to coastal areas, resulting in a more continuous pattern of recruitment than previously considered and in weak stock differentiation.

Key words: *Illex argentinus*, nursery grounds, population structuring, reproductive migration, spawning areas

INTRODUCTION

The Argentinean short-fin squid *Illex argentinus* (Castellanos, 1960) sustained the world's most important cephalopod fishery in volume of landings during the last decade (FAO, 2010). According to the prevailing interpretation, several distinct spawning groups segregate spatio-temporally along the shelf and slope off South America from 24° to 54°S, forming more or less discrete population sub-units. Although these have been referred to as 'spawning stocks' (Brunetti *et al.*, 1998; Haimovici *et al.*, 1998) or 'spawning groups' (Arkhipkin, 2000; Crespi-Abril *et al.*, 2008; Alvarez Perez *et al.*, 2009), the use of the latter term seems more appropriate as it does not necessarily imply genotypic or phenotypic differentiation (Hare, 2005). However, to be consistent with the most widely employed denominations, here we use the term stock for the originally defined group names (Brunetti, 1988; Haimovici *et al.*, 1998). Although it was initially considered that *I. argentinus* formed a single population (Sato and Hatanaka, 1983; Csirke, 1987), this was later divided in a major winter-spawning and a minor summer-spawning stock (SSS) (Hatanaka *et al.*, 1985; Hatanaka, 1988). The winter-spawning stock was subdivided into the Bonaerensis-North Patagonian Stock (BNS, spawning in winter) and South Patagonian Stock (SPS, spawning in fall), partly decoupled through a latitudinal cline along the outer shelf and slope off Argentina and Uruguay (Brunetti, 1988). Also, based on data collected on the shelf between 39° and 41°S, Brunetti (1988) and Nigmatullin (1989) postulated the existence of a Spring Spawning Stock (SpSS) concentrated between the 60

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and 150-m isobaths. Concurrently, a group of fully mature *I. argentinus* was observed in waters of San Matías Gulf (41°–42°S, northern Patagonia), presumably forming part of the same spawning stock (Morsan and González, 1996). Later on, Crespi-Abril *et al.* (2008, 2010) confirmed the presence of both SpSS and SSS in coastal waters off northern Patagonia and also detected mated and fully mature females in winter, revealing that the species has a complex reproductive schedule in coastal waters. For Brazilian waters, Haimovici *et al.* (1998) proposed the existence of the Southern Brazil Stock (SBS) distributed within 27°–34°S, and recently Alvarez Perez *et al.* (2009) distinguished another group formed by small-sized individuals attaining maturity year-round on the shelf-break and upper slope (bottom depths: 170–400 m), hereafter referred to Central Brazil Stock (CBS).

Although the six-spawning-group model of *I. argentinus* agrees with structuring patterns described for other ommastrephids (Boyle and Rodhouse, 2005), some inconsistencies arise. First, spawning peaks of the outer shelf/slope stocks (SPS, BNS, SBS) temporarily overlap (June–August), making discrimination ambiguous. Secondly, the location of the spawning ground of the SPS is still uncertain. It has been suggested that this could be either: (i) the Brazil Current (27°–36°S) and its confluence with Malvinas Current (37°–38°S) on the slope (Hatanaka *et al.*, 1985; Arkhipkin, 2000), in which case it coincides with those of the BNS and the SBS (Brunetti and Pérez Comas, 1989; Haimovici *et al.*, 1998), or (ii) the Malvinas Current, with northward transport of egg masses towards the BMC (Brunetti and Ivanovic, 1992; Rodhouse *et al.*, 1992; Waluda *et al.*, 1999, 2001). However, as incubation of embryos at different experimental conditions has shown that development can not complete below a temperature threshold of approximately 10°C (Sakai *et al.*, 1999), the last situation seems improbable due to limits imposed by low seawater temperatures typical of this current (Piola and Matano, 2001). Thirdly, the separation between the BNS and SBS has been questioned, and interpretation based on the available data leads to two possible scenarios: (i) the SBS is an extension of the BNS (Brunetti, 1988) or (ii) the BNS forms part of the major SBS (Santos and Haimovici, 1997). Fourthly, it has been postulated that the SpSS may actually be a delayed portion of the BNS due to the lack of a robust body of information on the aggregations of mature individuals and presence of paralarvae in the proposed spawning ground (Carvalho and Nigmatullin, 1998; Laptikhovskiy *et al.*, 2001). Lastly, although genetic studies have been conducted to validate this popula-

tion subdivision, conclusions obtained so far have been contradictory and insufficient to resolve the identity of the hypothetical spawning stocks (Carvalho *et al.*, 1992; Adcock *et al.*, 1999; Martínez *et al.*, 2005; Jerez, 2007). As presently recognized spawning groups of *I. argentinus* have been defined based on surveys conducted on the mid- and outer-shelf and slope (Haimovici *et al.*, 1998), the role of coastal waters as spawning and nursery grounds has been neglected to date. Thus, the above-mentioned inconsistencies may reflect the spatial incompleteness of the information used to interpret the population structuring.

In this work, we evaluate the suitability of different marine regions off southern South America for spawning and nurseries of *I. argentinus* by examining the surface seawater temperature (SST) and primary productivity conditions in the region, and by presenting direct evidence obtained in field samplings. Based on these analyses, we confront the prevailing interpretations on the spatio-temporal location of spawning and nursery grounds of *I. argentinus* to an alternative one staying that *I. argentinus* also uses highly productive coastal fronts off Patagonia for these life-history events, and we propose a new population structuring scheme for the species.

METHODOLOGY

Early life stage spatio-temporal survival modeling

In this study it was considered that the embryonic development of *I. argentinus* is possible within a restricted temperature range, approximately from within 11.4–13.0°C to some high temperature threshold value higher than 23.2°C according to Sakai *et al.* (1998), and that the probability of successful hatching varies with seawater temperature experienced during the embryogenesis according to the function developed from additional experimental data reported by Sakai *et al.* (1999):

$$\begin{aligned} \text{If } r_1 < X < r_2 & \quad S = a(X - r_1)(X - r_2)/100 \\ \text{If } X \leq r_1 \text{ or } X \geq r_2 & \quad S = 0 \end{aligned} \quad (1)$$

where S is the probability of embryonic survival, X is the seawater temperature in degrees Celsius, $a = -1.15$, $r_1 = 9.6$ and $r_2 = 27.1$. As egg masses of ommastrephid squids are laid and drift above the pycnocline (Sakurai *et al.*, 2000), it can be assumed that thermal history experienced by embryos during development is well reflected by SST. Therefore, the annual SST regime was analyzed for the complete range of geographic distribution of *I. argentinus* and used to spatio-temporally model its embryonic survival. A 9-year (2000–2008) SST data series

(AVHRR Pathfinder 5) was obtained from NASA JPL Physical Oceanography DAAC (<http://earthdata.nasa.gov/data/data-centers/po-daac>) for the area located between 24 and 54°S and 44°W to the coast. As the embryonic development of this squid lasts only a fraction of a month (e.g., 19 days at 10°C and 4 days at 26°C; Sakai *et al.*, 1998), data with a temporal resolution of 1 month were considered appropriate to develop the model. Also, taking into account the extension of the geographic distribution of the species, a 1°-latitude × 1°-longitude spatial resolution was used. For each spatial unit, the SST temporal data series was fitted by least-square nonlinear regression to the function:

$$\text{SST}(t) = T_0 + T_1 \cos[w(t - t_0)] \quad (2)$$

where $\text{SST}(t)$ is the estimated mean SST for month 't', T_0 is the annual mean temperature, T_1 is the amplitude of the seasonal cycle, $w = 2\pi/12 \text{ month}^{-1}$, t is the month (starting from January) and t_0 is the phase that coincides with the month of the year in which temperature is maximum (Rivas, 1994; Cinti *et al.*, 2004). Embryonic survival in each month of the year at each spatial unit was then estimated based on the function of Sakai *et al.* (1999) and the mean SST estimated by the regression model.

Once a squid hatchling emerges from the egg mass, several factors (e.g., predation pressure, intra-specific competition) may condition its survival; however, food availability is essential to continue its existence. Particularly for *I. argentinus* paralarvae, microalgae, along with bacteria and protozoans, not only constitute the first food during the rhynchoteuthion phase (Vidal and Haimovici, 1998) but also give trophic support to the meso-zooplankton that is preyed upon during the rest of the planktonic phase. Taking this into consideration, and as no relationship has been established between paralarvae survival and food availability, we assumed that a positive linear relationship exists between primary productivity, as a measure of food availability, and paralarvae survival. Therefore, remote sensor estimations of chlorophyll-*a* concentration (Chl-*a*, in mg m^{-3}) (OBPG SeaWiFS) were acquired from the GES-DISC Interactive Online Visualization ANd aNalysis Infrastructure (Giovanni) made available by NASA's Goddard Earth Sciences (GES) Data and Information Services Center (DISC) (<http://reason.gsfc.nasa.gov/OPS/Giovanni/ocean.swf8D.shtml>). Monthly mean Chl-*a* in each 0.1°-latitude × 0.1°-longitude unit was averaged for the period 2000–2008 as in the analysis of embryonic survival.

Spawning and nursery areas of *I. argentinus* must have both suitable seawater temperature and primary productivity conditions to ensure survival of early

life stages. Therefore, an *I. argentinus* early development suitability index (SI) for each month of the year at each 0.1°-latitude × 0.1°-longitude unit was calculated as the product of S and Chl-*a* in that unit. For visualization purposes the values of S, Chl-*a* and SI were interpolated using the 'ordinary kriging method' (Stein, 1999) and mapped for each month and for the whole area of geographic distribution of the species.

Once mapping of monthly SI was complete, the currently accepted hypothesis about the spatio-temporal location of spawning and nursery areas was compared with an alternative one. For this, the time required for a squid to reach a suitable spatial unit for spawning and nursery, departing from known aggregations of mature individuals, was estimated based on actual sustained speed of tracked *Illex* squid (0.3 m s^{-1}) (O'Dor, 2002), applying no correction for current transport. Also, as squids from the SPS and BNS could use maximum-speed surface jets from Malvinas Current, flowing northwards/northeastwards off the slope at approximately 0.5 m s^{-1} (Palma *et al.*, 2008), to reduce the time spent in their reproductive migration, an extreme scenario in which these only favor migration to the BMC was considered.

Paralarvae and juvenile sampling and processing

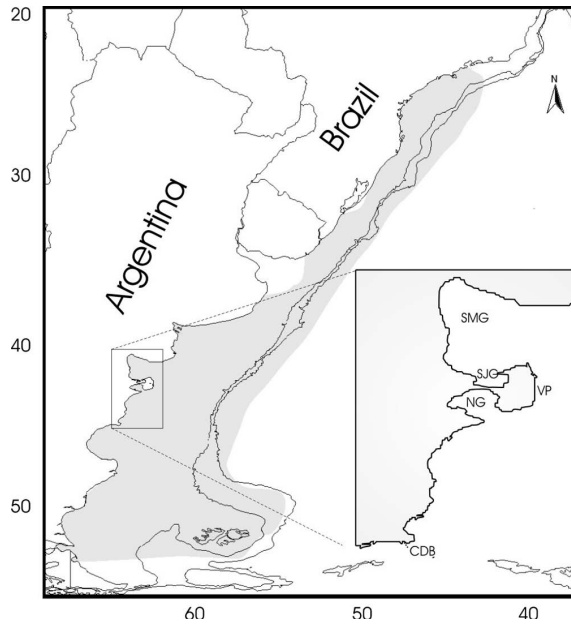
Five coastal regions off northern and central Patagonia, characterized by the presence of quasi-permanent productivity fronts, were surveyed to determine the presence and abundance of *I. argentinus* paralarvae: San Matías Gulf, Valdés Peninsula coastal area, San José Gulf, Nuevo Gulf, and Cape Dos Bahías (Fig. 1, Table 1). In spring (October–December) and summer (January–March) these tidal fronts form a quasi-continuous major frontal system that supports a large concentration of top predators (e.g., marine mammals, sea birds) and highly productive fisheries (Acha *et al.*, 2004). For all regions, plankton samples were obtained with a 295- μm mesh size Hensen net, 50-cm mouth diameter, equipped with a flowmeter. All of the hauls were conducted at speeds ranging between 2.5 and 4 knots. All of the specimens were included in the catalog of the marine invertebrate collection of the Commercial Fish and Shellfish Laboratory of the National Patagonian Center (LAPEMAR-CENPAT) and are available for further examination.

RESULTS

Early life stage spatio-temporal survival modeling

From January to April a broad region of high embryonic survival (S) is observed between 35° and 46°S,

Figure 1. Geographic distribution of *Illex argentinus* and reference locations on the coastline of Southern South America. San Matías (SMG), San José (SJG), Nuevo (NG) gulfs, Valdés Peninsula coastal area (VP), and Cape Dos Bahías (CDB). Continuous lines represent the 200 and 1000 m isobaths.



from the oceanic waters beyond the slope to the coast, with decreasing values further north and further south, and with a northward bending over the outer shelf/

slope (Fig. 2). At any given latitude south of 41°S and north of 35°S, embryonic survival is higher on the inner shelf and coastal waters than on the outer shelf/slope (Fig. 2). From May to July areas with the highest *S* are sequentially located further north (Fig. 2). *S* spatially retracts on the outer shelf/slope, declining to zero south of 45°S in May and south of 38°S in July (Fig. 2). Although *S* from the mid-shelf to the coast is much higher during this period, its spatial extension sequentially decreases south to north (Fig. 2). In July and August, *S* is zero on the entire Argentinean shelf and slope, except for San Matías and Nuevo gulfs (Fig. 2). From October to December the inner shelf and coastal areas show increasing *S*, both in magnitude and extension (Fig. 2).

Analysis of the estimated Chl-*a* revealed that in January the highest productivity areas are found in coastal waters within 31°–38°S and 39°–41°S, on the inner shelf southeast from the Valdés Peninsula coastal area (42.5°–44°S), and on the mid-shelf between 50° and 52°S, and that a large region with Chl-*a* estimates ranging within 1–2 mg m⁻³ extends both on the inner and outer shelf between 45° and 52°S (Fig. 3). From February to April Chl-*a* decreases in magnitude and spatial extension throughout the whole region, but 1–3 mg m⁻³ concentration areas remain both along the coast and on large patches on the mid-shelf (Fig. 3). From May to September the Chl-*a* is the lowest of the year, but reduced areas with 1–3 mg m⁻³ persist along the coast (Fig. 3). From October to December a large area of high

Table 1. Chlorophyll-*a* concentrations typical of coastal areas off Patagonia and summary of plankton tows conducted in the present study.

Area	Chlorophyll- <i>a</i> concentration (mg m ⁻³)	Sampling regime	Relevant references of oceanographic characteristics of each area
San Matías Gulf	0.30–2.00	14 H-Ss, 14 O (November 2009)	Lusquiños, 1977; Carreto <i>et al.</i> , 1974; Gagliardini and Rivas, 2004; Romero <i>et al.</i> , 2006; Moreira <i>et al.</i> , 2009; Romero <i>et al.</i> , 2006
Valdés Península coastal area	1.00–2.50	3 H-Ss, 3 O (November 2009)	
San José Gulf	0.5–2 (with peaks of up to 11.6)	2 H-Ss, 2 O (November 2009)	Charpy and Charpy-Roubaud, 1980; Rivas, 1990; Amoroso and Gagliardini, 2010
Nuevo Gulf	0.20–4.20	9 H-Ss, 15 O, 46 H-St (January, April, July and August 2005 and April 2006) Hand collection of stranded juveniles (September 2007)	Rivas and Ripa, 1989; Gil, 2001
Cape Dos Bahías	0.20–8.00	42 H-Ss (February and December 2009, March, July and September 2010)	Akselman, 1996; Acha <i>et al.</i> , 2004; Bogazzi <i>et al.</i> , 2005; Rivas <i>et al.</i> , 2006; Romero <i>et al.</i> , 2006

H-Ss, horizontal sub-surface tow; H-St, horizontal stratified tow; O, oblique tow.

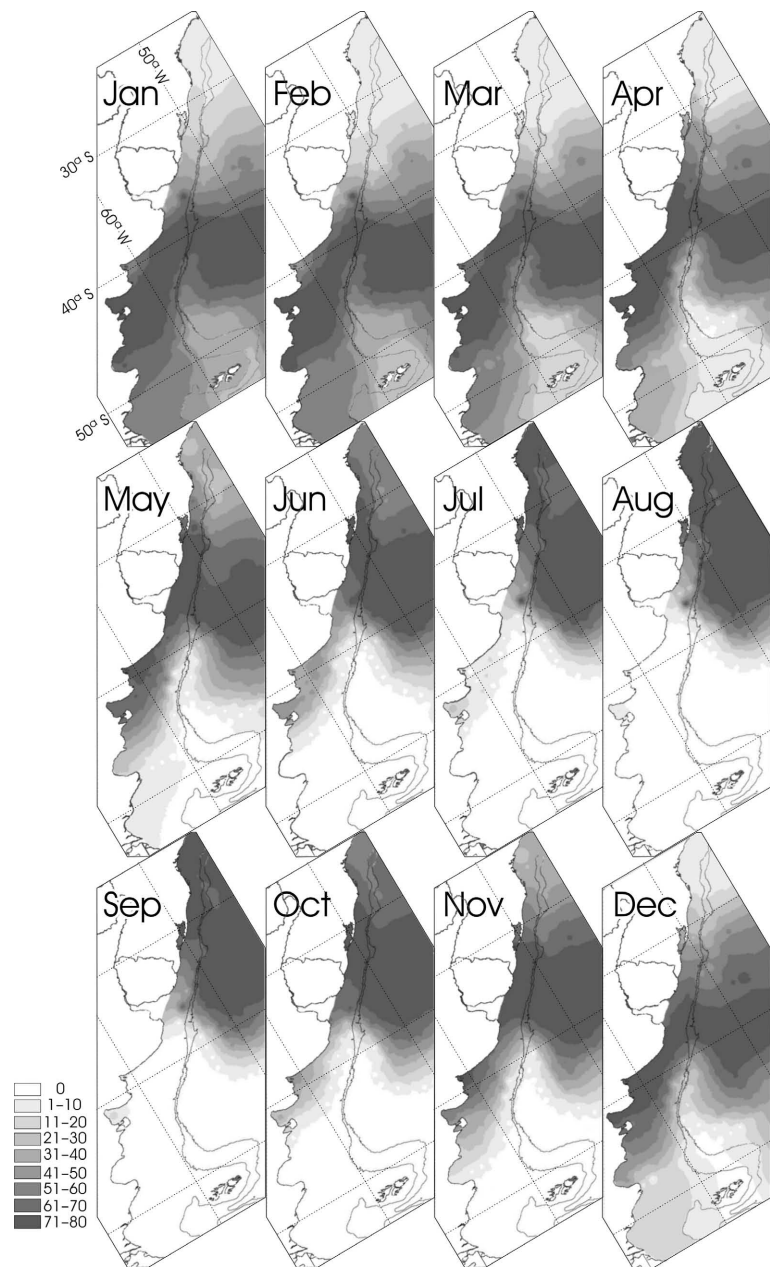


Figure 2. Monthly variation of the probability of the embryonic survival of *Illex argentinus* estimated from the 9-year mean SST (NOAA-AVHRR). Probability is expressed in percentage. Continuous lines represent the 200 and 1000-m isobaths.

Chl-*a* develops on the mid- (32°–46°S) and outer shelf/slope (39°–51°S), while 1–3 mg m⁻³ Chl-*a* is sustained along the coast (Fig. 3).

In January, the areas with the highest values of SI are located in coastal waters between 38° and 46°S. A large region with moderate values of early life stage development suitability extends on the inner shelf and slope between 45° and 52°S (Fig. 4). From February to April, SI decreases in magnitude and extension, and areas with the highest values are observed near the coast (Fig. 4). From May to July, SI is zero on the shelf south of 47°S, and progressively becomes zero on the

outer shelf/slope south of 37°S (Fig. 4). In August and September there are no suitable areas over the Argentinean shelf except for the waters of the San Matías and Nuevo gulfs (Fig. 4). From October to December, SI increases in magnitude and extension on the inner and mid-shelf (Fig. 4). Coastal waters off Uruguay and Southern Brazil show high values of SI during all seasons except summer (Fig. 4).

Time required for squid from the pre-reproductive aggregation of the SPS to reach similarly suitable areas for early life stage development at the coast/inner shelf and at the BMC was estimated to be 20–23 and

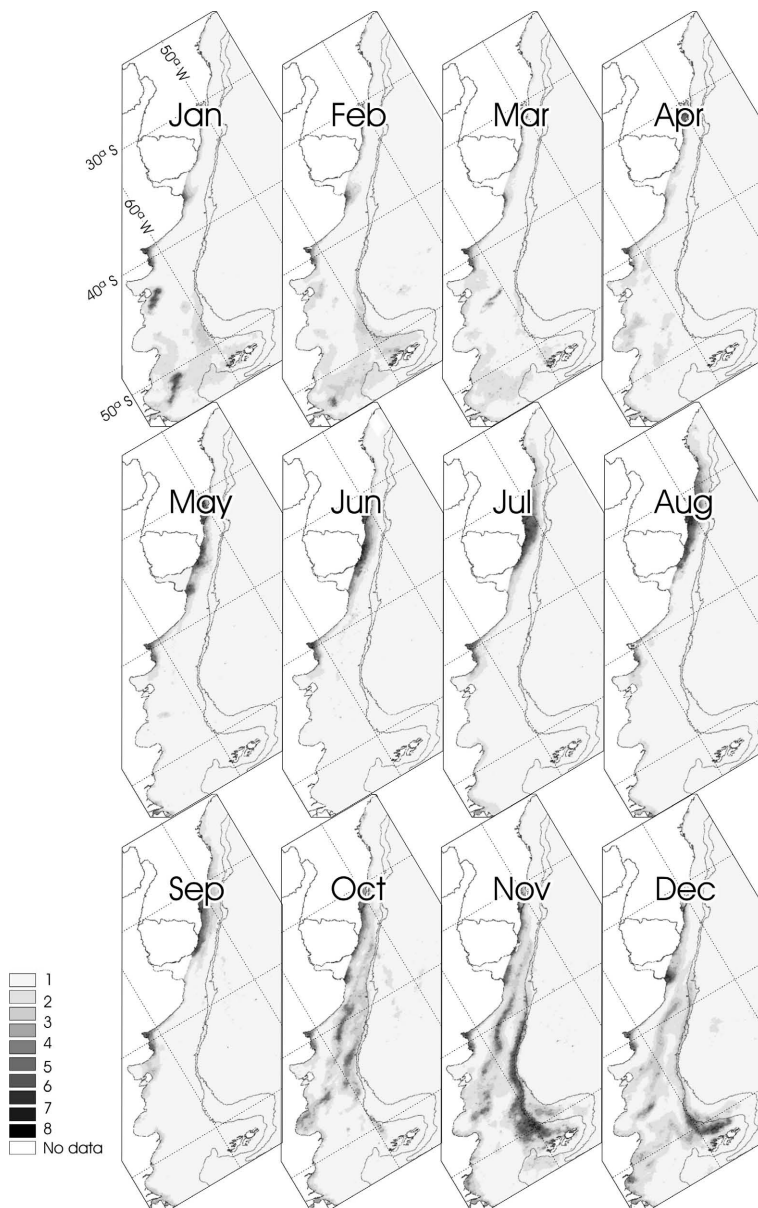


Figure 3. Nine-year average of mean monthly chlorophyll-*a* concentration (mg m^{-3}) (OBPG SeaWiFS). Continuous lines represent the 200 and 1000-m isobaths.

45 days, respectively, if no current transport is considered. In contrast, if transport by maximum-speed surface jets of Malvinas Current is taken into account, the time spent by a squid to reach the BMC would be 20 days (Fig. 5). As the pre-reproductive aggregation of *I. argentinus* corresponding to the BNS occupies more than 4° of latitude, the southern and northern portions were considered separately. A squid aggregation in a central location of the southern portion would require 6 days to reach suitable areas at coast/inner shelf or 37 days to reach equally suitable areas in the BMC (13 days if current transport is considered). In July a squid located at the northern part would require 10 or 5 days (2 days considering

Malvinas Current transport) to reach the coast/inner shelf or BMC regions, respectively, whereas in August it would take 37 or 7 days (3 days considering Malvinas Current transport; Fig. 5). Individuals from the SpSS concentrated at the inner shelf between 39° and 41°S are located at a highly suitable area, so it would take them no time to stay or 20 days to reach a similar value of suitability at the BMC (Fig. 6). A similar pattern is observed for individuals from the same stock located close to the mouth of San Matías Gulf, for whom it would take no time to spawn at the same location or 44 days to reach equally suitable areas for spawning at the BMC. Squid from the SSS, aggregated from January to February on the inner shelf near

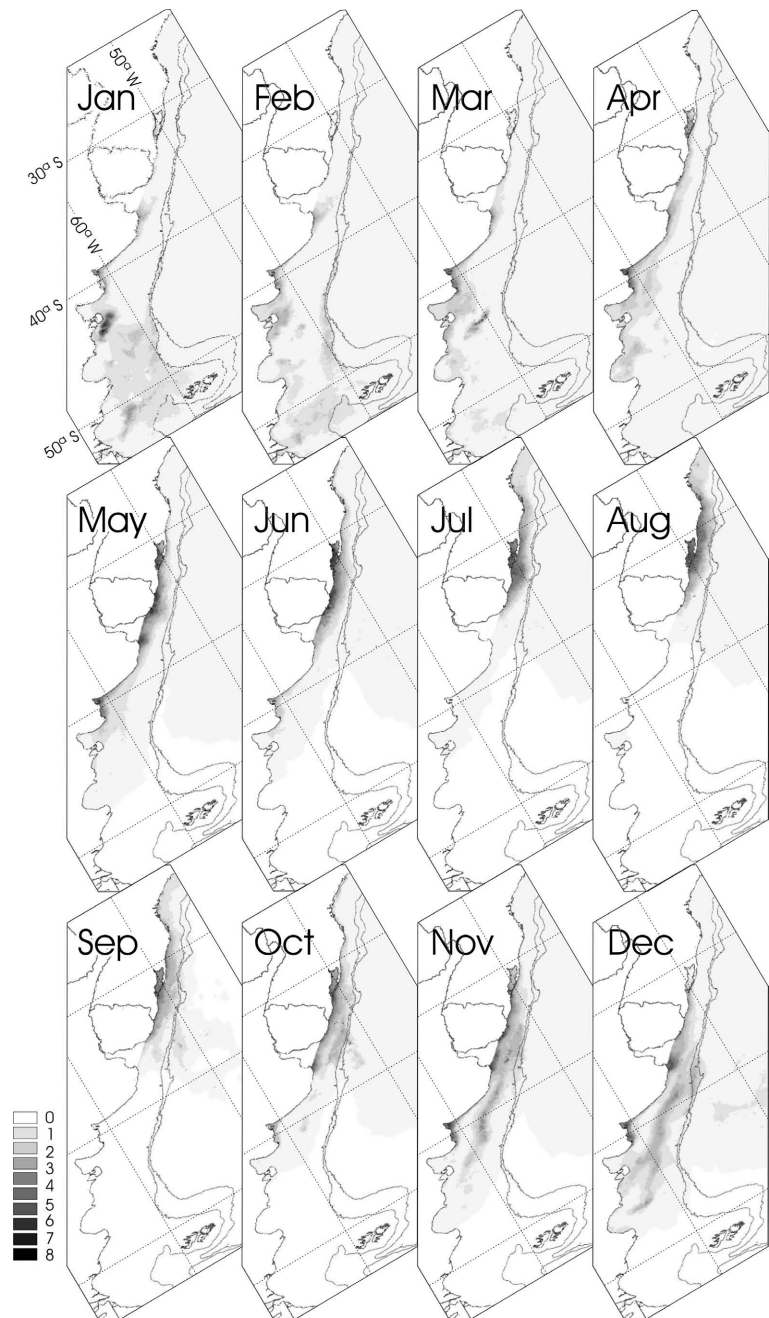


Figure 4. Monthly variation of the early life stage survival and development suitability index estimated as the product of embryonic survival and chlorophyll-*a* concentration (mg m^{-3}). Continuous lines represent the 200 and 1000-m isobaths.

Valdés Peninsula coastal area, are located at the region with the highest values of SI over the whole range of the species' distribution (Fig. 5). Specimens from the SBS and CBS, respectively concentrating on southern (winter) and northern (year round) portions of the range between 24° and 34°S on the slope and outer shelf, are found at highly suitable areas, so they would find a suitable environment, although no migration takes place. In contrast, it would take them <10 days to reach equally suitable areas on the coast/inner shelf.

Early life stage findings

A total of $29\,851\text{ m}^3$ of seawater was filtered in 150 tows performed (available as Supporting Information). *Illex argentinus* paralarvae were found in San Matías and Nuevo gulfs, and Cape Dos Bahías (Fig. 7). In San Matías Gulf, four *I. argentinus* (mean mantle length: 4.7 mm) paralarvae were caught in five (three horizontal/two oblique) of 28 tows (14 horizontal/14 oblique) (6430 m^3 of seawater filtered) in spring of

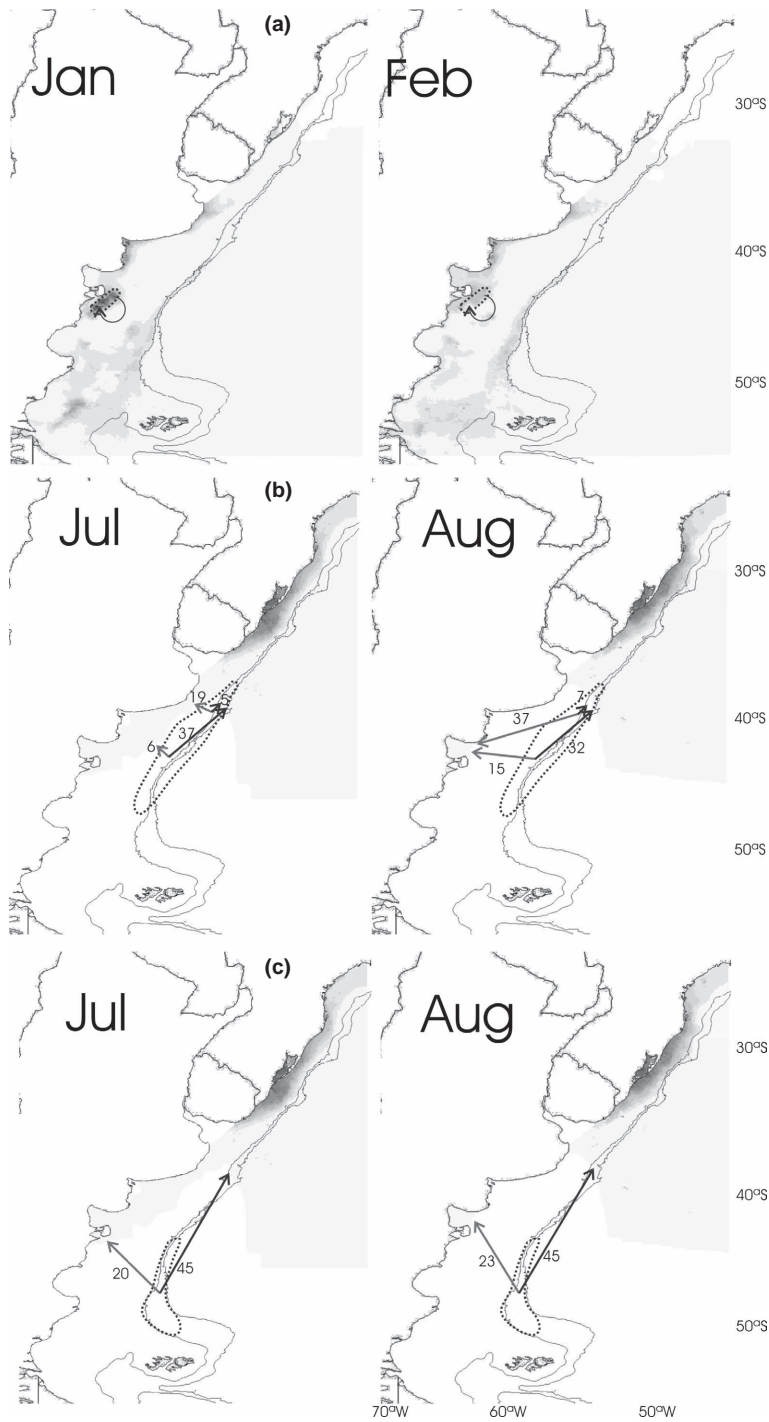


Figure 5. Probable reproductive migration pattern for *Illex argentinus* individuals from the Summer Spawning Stock (a), and comparison of two alternative reproductive migration patterns for *Illex argentinus* individuals from the Bonaerensis Northpatagonian Stock (b), and from the South Patagonian Stock (c) considering two areas with similar suitability index as spawning destination. The dashed line encloses the area of the pre-reproductive concentration of mature individuals (Haimovici *et al.*, 1998), straight arrows show the migration route to the coast (gray), to the confluence of the Brazil-Malvinas currents (black), and curved arrow indicate that squid stay at the pre-reproductive aggregation area. Numbers not in parentheses indicate the days required for a squid to reach each destination considering that no current transport takes place. Numbers in parentheses indicate the estimated time required for migration to the BMC considering Malvinas Current transport.

2009, representing estimated mean densities of 0.07 paralarvae per 100 m³ (SE = 0.28 paralarvae per 100 m³). In Nuevo Gulf, five paralarvae of *Illex argentinus* (mean mantle length: 7.6 mm) were obtained in two of 70 (horizontal) tows (9674 m⁻³ of seawater filtered) in fall (April–June) in two consecutive years (2005 and 2006). The mean density in this gulf was

0.14 paralarvae per 100 m³ (SE = 0.87 paralarvae per 100 m³). Additionally, in September of 2007, 10 stranded juveniles (mean mantle length: 36.2 mm) were collected on a beach located at the western margin of Nuevo Gulf (Fig. 7). In Cape Dos Bahías two paralarvae (mean mantle length: 3.2 mm) were found in one of 42 tows (7567 m⁻³ of seawater

Figure 6. Comparison of two alternative reproductive migration patterns for an *Illex argentinus* individual from the Spring Spawning Stock moving to alternative areas with similar suitability index. The dashed line encloses the area of the pre-reproductive concentration of mature individuals (Haimovici *et al.*, 1998), arrows indicate the migration route. A gray \blacktriangle arrow implies that a squid remains in the pre-reproductive aggregation area and black arrow indicates that the squid migrates to the confluence of the Brazil-Malvinas currents (black arrow). Numbers indicate the days required for a squid to reach each destination.

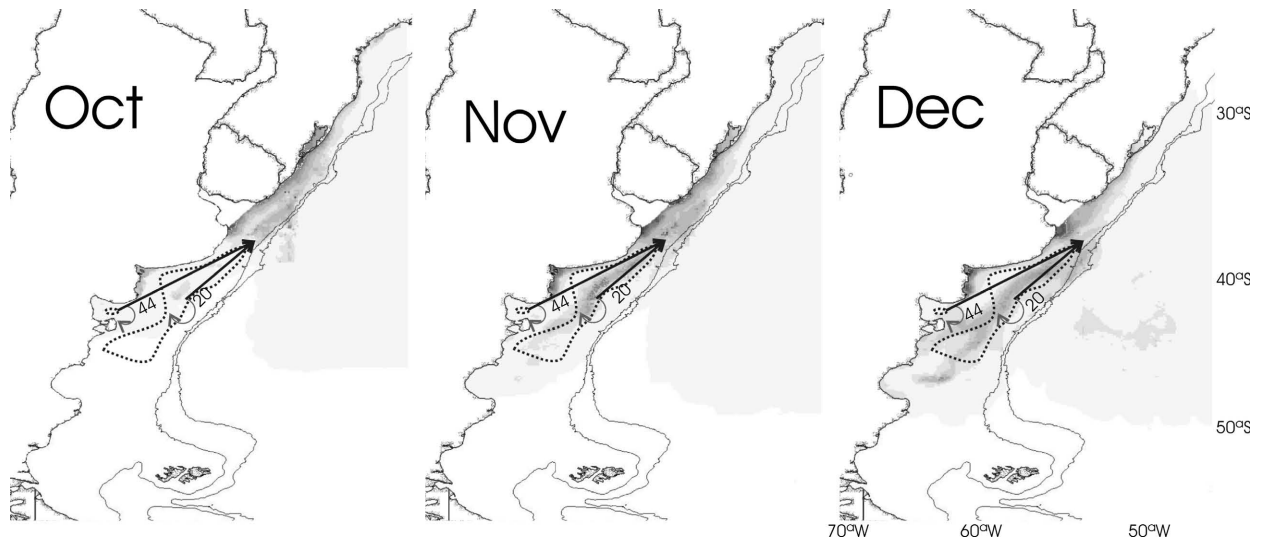
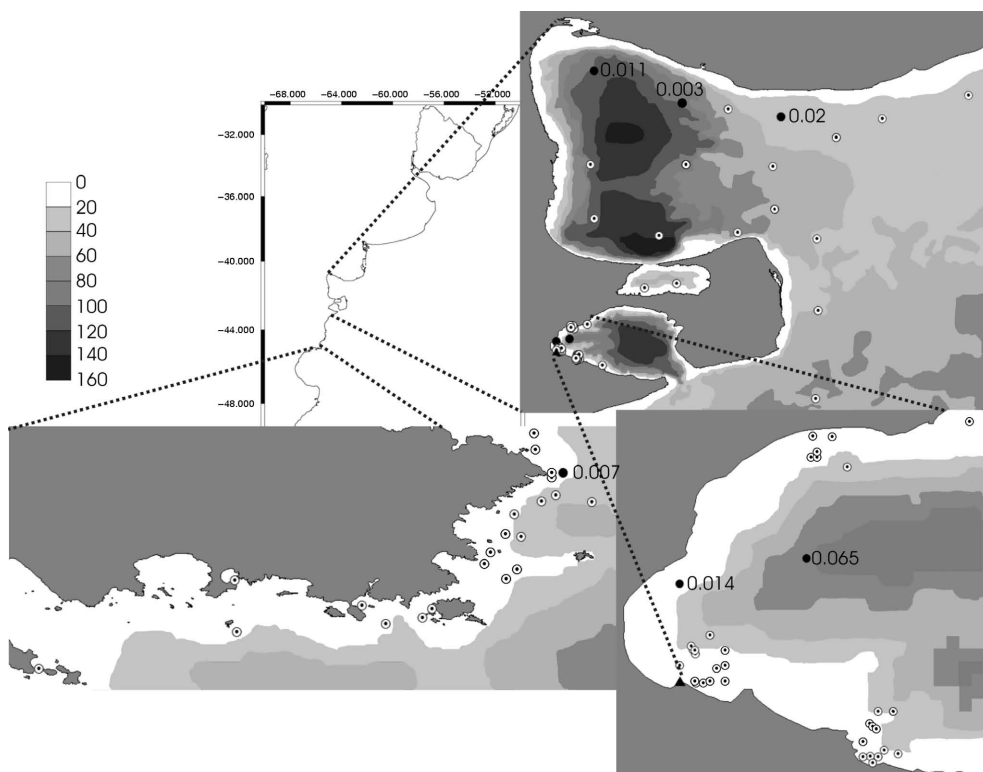


Figure 7. Location of zooplankton Hensen net tows conducted in this study. White circles with black dot indicate stations with no paralarvae. Black circles indicate stations with *Illex argentinus* paralarvae. Black triangle shows the location of stranded juveniles. Numbers indicate paralarvae density as individuals per 100 m^3 . Bathymetry scale in meters.



filtered) in summer of 2009. The mean estimated density in this region was 0.03 paralarvae per 100 m³ (SE = 0.15 paralarvae per 100 m³).

The spatio-temporal location of paralarvae sampled during this and previous work where this was made explicit (Brunetti and Ivanovic, 1992; Leta, 1992; Parfeniuk *et al.*, 1992; Haimovici *et al.*, 1995; Barón, 2003; Vidal *et al.*, 2010) were all associated with SI values over the median for all of the model units (range: quantiles 0.51–0.97).

DISCUSSION

This study provides an advance over the present *I. argentinus* population structuring interpretations, by providing a model accounting for embryonic and paralarvae development suitability over its complete geographic distribution, considering both thermal conditions and food availability. Nevertheless, due to the nature of data sources available, some assumptions had to be made. As remote sensor seawater temperature monitoring only reflects conditions at the sea surface, estimations of embryonic survival based on this source could be biased. However, there is strong evidence that ommastrephid squids spawn above the pycnocline (Sakurai *et al.*, 2000), where seawater is almost thermally homogeneous, and that it is difficult to obtain *in situ* measurements of this variable over the whole spatio-temporal distribution of any species, the use of remotely sensed SST represents a valid option. Furthermore, this approach has been widely used in previous studies to explain the relationship between environmental conditions and CPUE patterns in the fisheries (Waluda *et al.*, 1999, 2001; Sakurai *et al.*, 2000). The experimental function of embryonic survival probability of *I. argentinus* on seawater temperature (Sakai *et al.*, 1999) was based on the response of embryos from a few SSS specimens to different thermal treatments and therefore may not reflect the complete thermal adaptability of the species. However, in a previous study, Sakai *et al.* (1998) established thermal thresholds for embryonic survival from progenitors belonging to both the BNS and SPS that did not differ significantly from those reported on Sakai *et al.* (1999). Therefore, it can be assumed that their function gives an acceptable approach to estimate the embryonic survival of *I. argentinus* along its latitudinal range of distribution. Regarding the assumptions made in order to use remotely sensed Chl-*a* as a measure of food availability, there are two relevant issues to consider. On one hand, although data from OBPG-SeaWiFS provides estimates of Chl-*a* from the sea surface, the relationship between surface

Chl-*a* and zooplankton abundance has been tested (Strömberg *et al.*, 2009) and can be reasonably assumed. On the other hand, this study assumes that a linear relationship exists between primary and secondary productivity, as this has been observed in many environments (Begon *et al.*, 2006). Furthermore, the direct relationship between paralarvae abundance (implicitly their survival) and Chl-*a* has been tested already (Rocha *et al.*, 1999; Roberts and van den Berg, 2002; Vidal *et al.*, 2010).

Captures of *I. argentinus* in zooplankton net tows are highly variable. For example, Parfeniuk *et al.* (1992) reported that *I. argentinus* paralarvae were present in only two of 376 tows performed on the slope and rise off the Argentinean shelf, whereas Haimovici *et al.* (1995) obtained an exceptionally high frequency of positive hauls (55 of a total of 80) off southern Brazil. Some of the possible causes of this variability are the net avoidance and patchy distribution of these organisms (Wormuth and Roper, 1983; Haimovici *et al.*, 2002). Considering the last cause, in the present study both oblique and vertically stratified horizontal tows were conducted to increase the chances of catching paralarvae. Estimated density values (0.3–6.5 paralarvae per 10³ m³) were comparable to those reported in previous studies for *I. argentinus* (0.07–80 paralarvae per 10³ m³; Haimovici *et al.*, 1995, 1998; Vidal *et al.*, 2010) and other ommastrephids (10–52 *Todarodes pacificus* paralarvae per 10³ m³; Shimura *et al.*, 2005).

All of the *I. argentinus* paralarvae and juveniles found in this and other studies were caught in areas with values of SI over the median, supporting our model. However, as most of the available data are limited to specific areas or seasons, it is not possible fully to test the prediction power of the model with an appropriate level of statistical robustness.

At present, it is assumed that the major spawning areas of *I. argentinus* are located on the outer shelf and slope and in oceanic waters along the latitudinal range of distribution of the species off southern South America (Haimovici *et al.*, 1998). Considering the above-mentioned inconsistencies, it is necessary to reconsider the interpretations on the spatio-temporal location of spawning activity and the associated population structuring. Based on available information (Hatanaka *et al.*, 1985; Hatanaka, 1988; Haimovici *et al.*, 1998; Arkhipkin, 2000; Alvarez Perez *et al.*, 2009), outcomes from the predictive model developed in this study and new evidence on the presence of *I. argentinus* paralarvae in coastal waters, an alternative interpretation on *I. argentinus* population structuring is presented below.

Two different locations of the fall/winter spawning ground of the SPS (Haimovici *et al.*, 1998) are considered at present: (i) the outer shelf/slope south of 44°S and (ii) the Brazil Current over the shelf/slope between 27° and 36°S, north of the BMC. The outcomes of our model revealed that embryonic development is not possible on the outer shelf/slope from June to October south of 37°S due to prevailing low SST; thus only the second location is viable. In this context, the SPS and BNS should be considered a single spawning group, as the main difference between them is the location of the spawning area. However, alternative spawning and nursery grounds have never been considered, such as coastal regions characterized by high values of SI. If Malvinas Current transport is not considered, comparisons show that pre-spawning individuals concentrated on the outer shelf/slope south of 44°S would reach suitable habitats to spawn near the coast in a shorter period of time, and at lower energetic expense, than near the BMC. In an extreme scenario, if current transport is considered to exclusively favor migration to the BMC, the duration of migrations to either of both destinations would be similar. However, squid migrating to suitable coastal areas could also take advantage of the current transport to approach their destination, at least in part of their route. Several pieces of evidence support the existence of reproductive migration of *I. argentinus* to coastal environments. First, there is the presence of mature and mated females in coastal waters of San Matías Gulf year-round, with peaks in winter, spring and summer (Crespi-Abril *et al.*, 2008). Secondly, there is the finding of stranded juveniles in September on the coast of Nuevo Gulf reported in the present study, whose estimated hatching time based on mantle lengths and the size-at-age curve published by Brunetti *et al.* (1998) is late fall (May/June). Lastly, there is the occurrence of persistent events of massive adult strandings on the coast of Northern Patagonia from May to September for a period of at least 15 years (1970–1985), previous to the development of the industrial fishery in the South-West Atlantic (Crespi-Abril, 2011).

The suggested winter-spawning ground of the BNS comprises a large geographic area on the slope and oceanic waters between 35° and 45°S (Haimovici *et al.*, 1998). The outcome of the model shows that for mature individuals concentrated in July and August at the northern part of this area, it is more economic, in terms of energy expense, to perform a spawning migration to the BMC instead of the coast, whether considering the Malvinas Current transport or not. In contrast, for individuals located at the southern part of that area, it is more convenient (or equally economical if current

transport is considered) to migrate to coastal or mid-shelf waters off Argentina to spawn than the displacement to the BMC. As mentioned above for the SPS, there is direct evidence showing that from fall to winter squid use waters north of BMC (Santos and Haimovici, 1997; Alvarez Perez *et al.*, 2009; Vidal *et al.*, 2010) and Nuevo and San Matías gulfs as spawning and breeding grounds (Crespi-Abril *et al.*, 2008, 2010).

According to Brunetti (1988), the *I. argentinus* SpSS spawns on the mid-shelf between 35° and 45°S, and in San Matías Gulf. The lack of further published information on the presence of spawners or paralarvae in that area led some researchers to question the existence of this spawning group (Carvalho and Nigmatullin, 1998; Laptikhovsky *et al.*, 2001). However, recent work has provided evidence on the occurrence of a persistent peak of reproductive activity of the species in spring in waters from San Matías Gulf, corroborating its existence (Crespi-Abril *et al.*, 2008). The results of the model developed in this study give additional support to this conclusion by showing that coastal areas north of 42°S, including San Matías Gulf, are suitable and warrant the reproductive success of the species during the spring months. Furthermore, findings of *I. argentinus* rhynchoteuthion paralarvae in the region in November provide the necessary evidence to conclude that the SpSS effectively exists and that its members use San Matías Gulf and neighboring continental shelf waters as spawning and breeding areas.

The existence of an *I. argentinus* group spawning in summer on the mid-shelf between 42° and 44°S (SSS) is widely accepted (Brunetti, 1988; Haimovici *et al.*, 1998). However, it has been pointed out that this group represents only a small fraction of the population (less than 5%) (Hatanaka *et al.*, 1985; Hatanaka, 1988; Haimovici *et al.*, 1998). Crespi-Abril *et al.* (2008, 2010) reported the presence of mature individuals from the SSS in San Matías Gulf during the summer months which were clearly distinguishable from the SpSS based on their size frequency distributions and size-at-maturity curves. During the summer months, waters off most of the Argentinean coast and the inner shelf between 42° and 45°S are highly suitable for spawning and breeding. Furthermore, the finding of paralarvae in summer zooplankton samples taken off Cape Dos Bahías and Nuevo Gulf demonstrate that *I. argentinus* spawns not only on the mid-shelf but also in coastal waters off the Patagonian region.

Two spawning groups have been identified off southern/central Brazil between 27°S and 34°S; one formed by large-sized squids forming winter-spawning

concentrations on the outer-shelf and slope (400–700 m deep) between 26° and 29°S, which corresponds to the SBS, and another one (identified here as CBS) characterized by small-sized individuals aggregating year-round on the outer shelf (<400 m deep) north of 28°S to spawn (Alvarez Perez *et al.*, 2009). The outcomes of our model show that the suitability of that region for spawning and breeding is high year-round. Findings of rhynchoteuthions, advanced paralarvae and juveniles in shelf and coastal waters between 28° and 30°S in late spring demonstrate the existence of an extended spawning period in that region and the use of coastal waters for reproduction (Vidal *et al.*, 2010).

Considering the available numerical simulations of water circulation on the Southwestern Atlantic Shelf (Palma *et al.*, 2008), *I. argentinus* egg masses spawned

in coastal waters are expected to be transported in different directions, depending on their vertical location in the water column. Those placed near the sea surface most probably would be transported offshore over the continental shelf, whereas those released near the bottom would be carried inshore. However, as it is known that the egg masses of ommastrephids generally drift near the pycnocline (Sakurai *et al.*, 2000), their average transport should result in an intermediate pattern between those mentioned above.

In Argentina, coastal areas from the continent to 12 nautical miles offshore, and the gulfs are under provincial jurisdiction. Except for San Matías Gulf, no specific fishing licensing or research effort has been focused on *I. argentinus* by the provinces. Thus, neither the spatial distribution of fishing effort associated with licenses provided to the fleet to exclusively

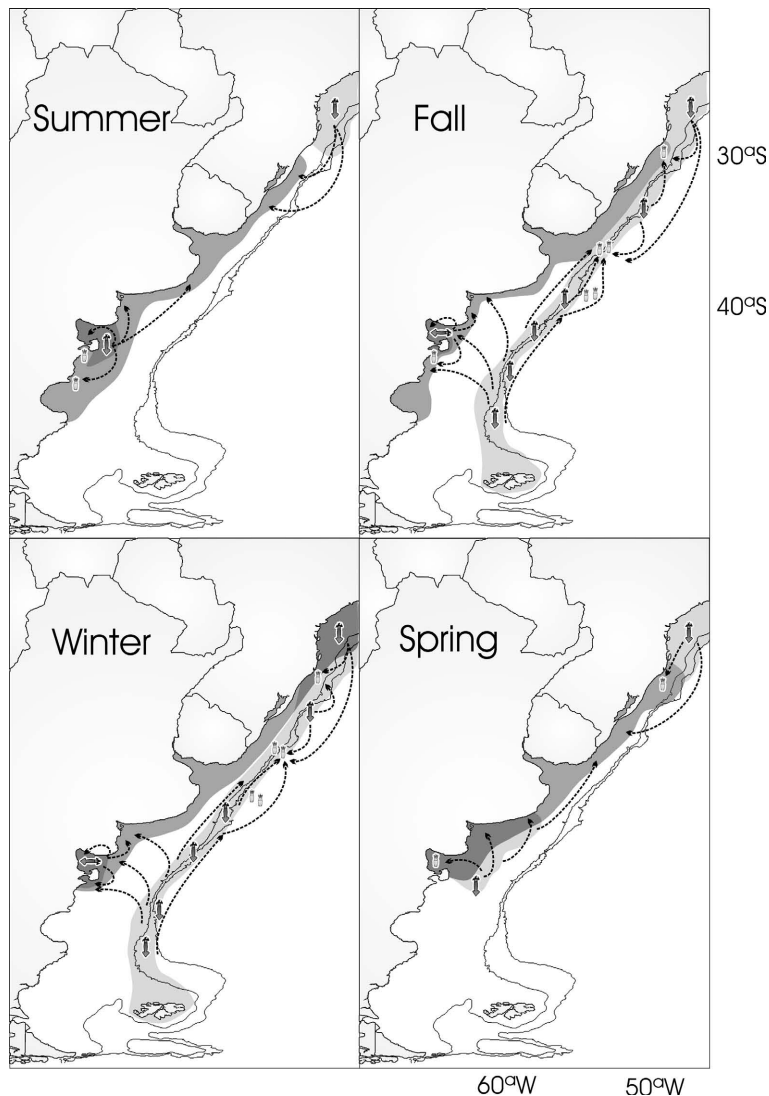


Figure 8. Schematic representation of the inferred reproductive migration patterns of *Illex argentinus* by season. Light-gray areas represent major pre-reproductive concentrations of mature squid reported in the literature. Dark-gray areas correspond to coastal regions suitable for spawning and breeding as estimated in the present study. Paralarvae and adult figures show the location of these life stages according to published data and findings in the present study. Dashed arrows indicate the migration patterns of mature squids from pre-reproductive concentrations to coastal spawning and breeding grounds.

operate in federal jurisdiction nor the federal research programs conducted by the National Institute of Fishing Research and Development (INIDEP) cover the entire geographic distribution of the species. The omission of coastal regions surveyed for the presence of different life stages of *I. argentinus* may bias the interpretation of its population structuring and life cycle. The only exceptions in the last 30-year period have been the studies conducted on the species in Nuevo and San Matías gulfs (Morsan and González, 1996; Crespi-Abril *et al.*, 2008, 2009, 2010). The new evidence provided by our model and the finding of paralarvae and juveniles demonstrate that the coastal region is being used by the species for spawning and breeding. A similar conclusion has been obtained in the last years for other important species of ommastrephid squids (Sakurai *et al.*, 2000; Gilly *et al.*, 2006; Staaf *et al.*, 2008; Kidokoro *et al.*, 2010). It can therefore be concluded that *I. argentinus* can spawn year-round in coastal areas off southern South America, with seasonal peaks coupled with primary productivity pulses and seasonal retractions on the southern portion of the spawning grounds due to seawater temperature limitations. In this context, the population may not be subdivided into discrete spawning groups but there would be quasi-permanent migrations to coastal spawning grounds and a return of part of the recruited individuals to the shelf and slope in the course of the life cycle (Fig. 8). This viewpoint could explain the abundance and age-composition patterns reported by Arkhipkin (1993), who pointed out that four short-span (monthly) generations respectively born in June, July, August and September were usually detected in waves of abundance in the fishery at three different latitudinal ranges (nominal latitudes: 52°, 46° and 42°S) on the outer shelf/slope between April and June by the Russian fleet. Furthermore, the interpretation presented here would explain the lack of significant genetic and morphometric differences between individuals corresponding to the presumed spawning stocks of *I. argentinus* (Adcock *et al.*, 1999; Martínez *et al.*, 2005; Jerez, 2007; Crespi-Abril *et al.*, 2009). Continuous spawning activity with seasonal peaks has been observed in several species of ommastrephid squids. For example, using back-calculated hatching dates, Arkhipkin (2000) demonstrated that spawning of *Illex coindetti* from the Strait of Sicily occurs throughout the year. For *Illex illecebrosus*, O'Dor & Dawe (1998) suggested that spawning occurs throughout the year, with a primary peak in winter and a secondary one in summer. Likewise, Quetglas & Morales-Nin (2004) observed that hatching of *Todarodes sagittatus* in the

Mediterranean Sea occurs throughout the year with a clear peak in November. Therefore, year-round continuous spawning in *I. argentinus* rather than discrete seasonal spatio-temporally segregated spawning would not represent an exceptional case among the members of the group.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Position and date of the plankton tows conducted in coastal areas off northern Patagonia indicating the presence (*r*) and absence of paralarvae (*n*) of *Illex argentinus*.