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Spatial distribution of cephalopod paralarvae in San José Gulf (Northern Patagonia, Argentina): The role of tidal circulation in larval dispersal

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ABSTRACT

The spatial distribution of cephalopod paralarvae was studied in waters of San José Gulf (SJG), a shallow basin connected to a larger gulf (San Matías, SMG) through a narrow mouth located on its northwestern margin. The gulf is characterized by a remarkable tidal circulation pattern providing contrasting hydrodynamic conditions between the western and eastern domains. Zooplankton net tows ($n = 104$) and depth-temperature profiling ($n = 70$) were conducted on a monthly basis at fixed stations forming a regular grid from October (mid spring) 2011 to March (late summer) 2012. Temperature-depth profiles showed that while the western domain seawater column remains well mixed by tidal currents during the whole period, stratification develops from November to March on the eastern domain. Positive zooplankton net tows were sporadic for early-life stages of *Semirossia tenera* ($n = 1$) and *Robsonella fontaniana* ($n = 3$), and more frequent for those of *Doryteuthis sanpaulensis* ($n = 9$) and *Illex argentinus* ($n = 9$). The latter were found almost exclusively in the western domain whereas those from *D. sanpaulensis* were mainly sampled in the eastern domain. Low abundance of *I. argentinus* paralarvae in the eastern domain suggests that buoyant egg masses of this squid are not released in SJG; instead they, or the hatching paralarvae emerging from them, could be sequentially advected from and expelled to SMG by tidal currents. On the other hand, the spatial distribution of *D. sanpaulensis* paralarvae suggests that those hatching on the shallow marginal bottoms of the eastern domain are retained in this region while those hatching at the western domain are flushed out to SMG by tidal currents.

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1. Introduction

Cephalopod early-life stages are good swimmers capable of performing significant vertical migrations, but they cannot move against major water currents (Yamamoto et al., 2007). Thus, horizontal larval transport is influenced mainly by the seasonality and patterns of oceanic circulation (Roberts, 2005). Horizontal larval transport has long been recognized as a key process determining the recruitment dynamics of several cephalopod populations (Bakun and Csirke, 1998; Zeidberg and Hamner, 2002; Roberts and van den Berg, 2005). This kind of transport is species-dependent since it can be affected by the duration of the planktonic life phase, estimated in days for most ommastrephids and weeks for several loliginids (Yang et al., 1980; Arkhipkin and Perez, 1998). Also, since it is well known that early-life stages from different species occupy different strata of the water column (Bower and Takagi, 2004), depth-specific patterns of water mass horizontal circulation can differentially affect their distribution.

Understanding the effects of oceanographic processes on the spatial distribution of early-life stages is essential for a better understanding of cephalopod life cycles and spatio-temporal structuring of their populations (Crespi-Abril and Barón, 2012). Early-life stages can be concentrated and retained within frontal systems (Rodhouse et al., 1992; Piatkowski et al., 1993; Röpke et al., 1993; González et al., 2005), where biophysical characteristics would determine early life-stage survival, growth and recruitment success (Waluda et al., 2001; Jackson and Domeier, 2003; Otero et al., 2008). Frontal systems present intrinsic variations in primary production magnitude and in their spatio-temporal location due to the

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complex oceanographic processes that generate them (Bakun, 1996). These variations modify early-life stages survival and recruitment success producing marked fluctuation on stock abundance, with the consequent variation in fisheries yields (Waluda et al., 1999; Dawe et al., 2000; Sakurai et al., 2000).

Patagonian coastal waters and the adjacent shelf are characterized by the presence of highly productive areas generated by mesoscale oceanographic processes (i.e., tidal and thermo-haline frontal systems) (Acha et al., 2004). These regions, particularly the Northern Patagonian gulfs (Nuevo, San José and San Matías) and the shelf off Valdés Peninsula, are used by several cephalopod species as feeding and spawning grounds (Barón, 2001, 2003; Barón and Ré, 2002; Ortíz, 2009; Storero, 2010; Crespi-Abril and Barón, 2012). Nevertheless, little information is available on the spatial distribution and abundance of early-life stages and juvenile cephalopods in this region (Barón, 2003; Crespi-Abril et al., 2010; Crespi-Abril and Barón, 2012), either because of their patchy distribution and their ability to avoid plankton nets (Vecchione, 1987) or due to poor sampling effort conduced in the region during the past.

In this study we analyze the spatio-temporal distribution of cephalopod early-life stages in San José Gulf, a small-sized basin with a marked frontal system formed by tidal circulation and coastal topography (Amoroso and Gagliardini, 2010), representing a unique scenario to propose alternative hypothesis about the mechanism of larval transport on a fine spatial scale.

2. Materials and methods

2.1. Study area

San José Gulf (SJG) (Fig. 1) is a small basin (surface: 817 km^2; mean depth: 40 m; maximum depth: 80 m) located on the northern margin of Valdés Peninsula. It opens to a larger and deeper gulf (San Matías, SMG) through a 6.9-km wide mouth located on its northwestern margin. The tidal regime is semidiurnal, with an average amplitude of 6 m (Servicio de Hidrografía Naval, 1983) generating strong tidal currents through its mouth and producing large superficial gyres on its western domain, while the eastern one seems to be less affected, as it has been evident by examination of satellite imagery (Amoroso and Gagliardini, 2010). Esteves et al. (1986) detected higher concentration of nutrients in the western domain ($N—NO_3$ = 4.0 μmol l^{-1} in winter and 1.0 μmol l^{-1} in summer) than in the eastern domain ($N—NO_3$ = 2.0 μmol l^{-1} in winter and 0.5 μmol l^{-1} in summer) throughout the year. Although no information has been published yet on how tidal circulation affects the vertical structure of the water column, differences in nutrient concentration in both domains suggest that in the western one it is permanently mixed (Esteves et al., 1986; Pizarro, 1975).

2.2. Thermal structure of the water column and early-life stages sampling

Five monthly oceanographic surveys were conducted from October 2011 to March 2012 in SJG (Fig. 2 and Table 1). In each of them, a 300 μm-mesh size Hensen net (70 cm mouth diameter) equipped with a flowmeter (Fig. 2) was towed at oceanographic stations forming a regular grid within SJG; nine stations (1–9) were located in the western domain, twelve (15–26) in the eastern domain, and five (10–14) in the transition zone between them (Fig. 2). From a total of 104 zooplankton net tows performed (33,200 cubic meters of filtered seawater), those conducted at stations with bottom-depths larger than 30 m were oblique, maximum depth of tows varying as a function of bottom depth, and those conducted at shallower stations were horizontal (Table 1). In all cases, tow velocity was two knots approximately.

Early-life stages present in the zooplankton samples were preserved in 5% formalin solution in seawater for further determination under dissecting microscope. Specific keys and reference material were used to determine the taxonomic status of cephalopods in the samples (Brunetti, 1990; Barón, 2003; Ré et al., 2003; Ortíz, 2009; Ortiz and Ré, 2011). Mantle length (ML) was measured on all individuals using the micrometric scale of the dissecting microscope under 60× magnification. Relative abundance of each species was estimated as the number of individuals per 100-m^3 of filtered seawater. Because normality assumptions could not be checked with the data available for *Doryteuthis sanpaulensis* (a total of nine abundance values were obtained in spring and summer), differences in median abundance of this species between seasons (see Section 3.2) were evaluated by a Monte Carlo permutation test (n = 5000) (Manly, 1991). Abundance values were randomly permutated with respect to season under the null hypotheses of no differences between spring and summer. Calculations were done using an *ad-hoc* code programmed in R language (version 2.7.1, R Development Core Team, 2008), available from the authors upon request.

Temperature-depth (TD) profiles were obtained during each zooplankton tow using a bathythermograph with data logger attached to the net mouth, built and calibrated for this purpose at the Centro Nacional Patagónico (Eng. J. Dignani, Electronics Lab). Temperature and depth resolution of the sensors were 0.06 °C and 0.05 m respectively. The frequency of data recording was set at 3 s. To obtain a smooth vertical TD profile in each station, temperature records were pooled and used to estimate a mean temperature value for each 2-m stratum. Only data for depths >2 m were analyzed to avoid error caused by the operation of the plankton net during and immediately after deployment. Temperature and depth data are not available for surveys conducted in November 2011 in the western domain, and in December 2011 in the entire gulf.

3. Results

3.1. Vertical structure of San José Gulf seawater column

Data recorded between October and March allowed characterizing the thermal structure of the water column at different stations in SJG during the austral spring (October to December) and summer (February and March). Patterns observed on the TD profiles from different seasons and oceanographic stations allowed confirming that the water column of the western domain of SJG (stations 1–9) are permanently mixed by tidal circulation, while at the eastern domain (stations 15–25) it stratifies from November to March. Among the well mixed western and the stratified eastern domains, a transition zone was detected (stations 10–14), showing intermediate patterns on the TD profiles (Fig. 3). In October, TD profiles were similar for all stations showing that in this month, when surface seawater temperature is almost at its annual minimum, the thermal structure of the gulf is rather homogeneous (Fig. 3). Temperature of the seawater column ranged between 10.4 °C and 10.9 °C in the transition zone, between 10.7 °C and 11.8 °C in the western domain, and between 10.7 and 12.4 °C in the eastern domain. In November, as seawater temperature increased (12.3–12.9 °C and 12.1–14.9 °C for the transition zone and the eastern domain respectively), the eastern domain started to stratify, more markedly at the deeper stations, and the thermocline started to develop approximately at 10 m below the surface. In February, the temperature was higher than during the spring; the overall temperature range for SJG was 15.7–18.2 °C. The eastern domain was markedly stratified and the thermocline was obvious at 20 m below the surface; in contrast temperature of the seawater column at stations from the western domain and the transition zone remained vertically homogeneous

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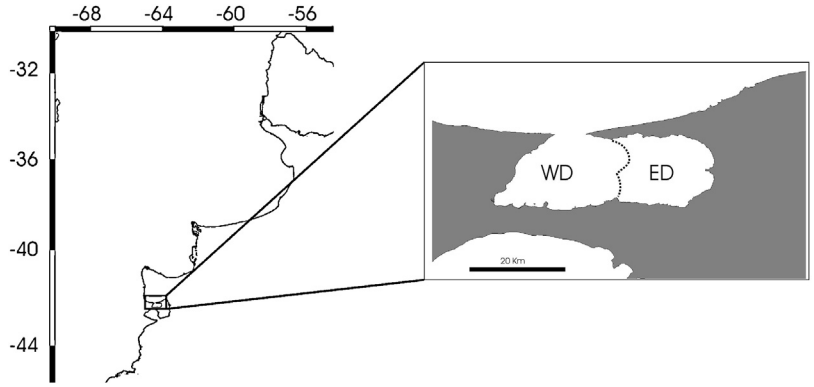

Fig. 1. Location of San José Gulf, northern Patagonia, Argentina. The dotted line indicates a schematic division between western (WD) and eastern (ED) domains derived from Amoroso and Gagliardini (2010).

(Fig. 3). During this month, differences in maximum surface temperature between domains reached 1.0 °C, the eastern one being warmer than the western and transition zone. TD profiles stabilized below the thermocline at approximately 35 m below the surface, ranging between 15.8 and 16.1 °C, 15.8 and 16.4 °C and 15.9 and 16.4 °C for the western domain, the transition zone, and the eastern region respectively. In March, stratification of the eastern domain started to vanish while maximum surface seawater temperature dropped to 17.3 °C. The difference in maximum surface temperature between domains decreased to 0.5 °C during this month (excluding the station 9, in which the maximum registered temperature also reached 17.3 °C on 12 March 2012).

3.2. Temporal and spatial distribution of early-life stages

Four cephalopod species were identified in the plankton samples: *Dorytheutis sanpaulensis*, *Illex argentinus*, *Semirossia tenera* and *Robsonella fontaniana* (Table 1). The most frequent were *D. sanpaulensis* and *I. argentinus*; both found in nine stations in abundances ranging between 0.2 and 99.5 paralarvae 100^{-1} m^{-3} and 0.5 and 191.0 paralarvae 100^{-1} m^{-3}, respectively (Table 1 and Fig. 4). Paralarvae of *D. sanpaulensis* ranging between 1.1 and 5.9 mm ML were captured from November to March, but were more abundant in the summer months (February and March) (Monte Carlo Permutation one-tailed Test P [difference between median

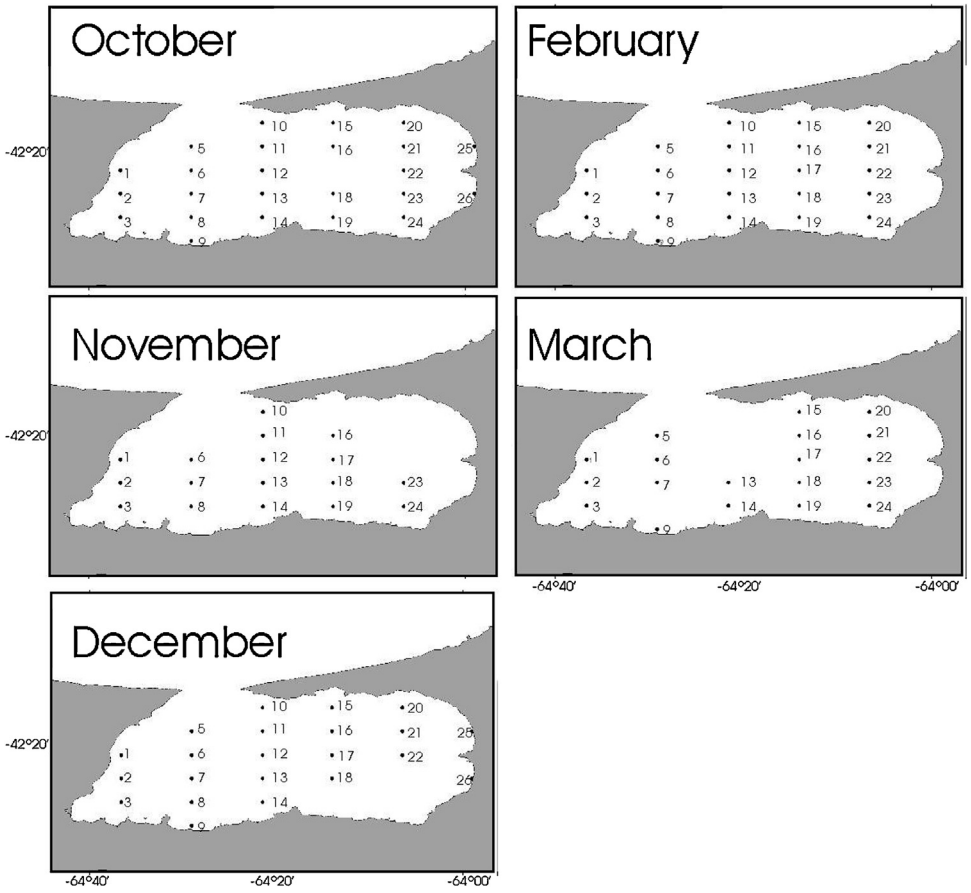

Fig. 2. Spatial distribution of the stations sampled in San José Gulf, northern Patagonia, Argentina, on each month.

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Table 1
Cephalopods captured in plankton samples from San José Gulf, northern Patagonia, Argentina.

Species	Date	Station	Gulf domain	Number of individuals/ abundance (100^{-1} m^{-3})	Maximum depth sampled (m)	Bottom depth (m)
Illex argentinus	1 February 2012	6	W	1/3.9	41	80
		7		1/1.7	42	66
		8		1/14.1	21	36
		9		2/54.8	–	6
	8 February 2012	19	E	1/191.0	23	31
	15 February 2012	2	W	2/–	22	31
		3		2/19.6	13	22
	14 March 2012	13	T	1/0.7	30	63
		24	E	1/0.5	16	29
Dorytheutis sanpaulensis	11 November 2011	16	E	1/0.2	22	58
	26 November 2011	10	T	2/0.7	27	69
	30 November 2011	3	W	1/0.5	–	32
	19 December 2011	10	T	1/0.4	–	30
	08 February 2012	16	E	1/99.5	42	58
	15 February 2012	11	T	1/1.7	42	72
	14 March 2012	15	E	5/3.4	21	37
		20		1/1.6	17	26
		21		1/0.5	34	55
Robsonella fontaniana	13 October 2011	11	T	1/0.2	36	73
	11 November 2011	17	E	1/–	20	67
	1 February 2012	9	T	1/27.4	–	6
Semirossia tenera	26 November 2011	18	E	1/1.71	30	59

abundances $\leq 0] = 0.04$). In contrast, paralarvae of *I. argentinus* ranging between 2 and 6 mm in ML were captured only in the summer months (February and March).

Records for *R. fontaniana* and *S. tenera* were more sporadic (Table 1). Individuals of *R. fontaniana* ranging between 3 and 6 mm in ML were captured in October, November and February, while the only one belonging to *S. tenera* was 3.2 mm in ML and was captured in November.

A marked spatial segregation was observed between the paralarvae of *D. sanpaulensis* and *I. argentinus* (Fig. 5). The highest

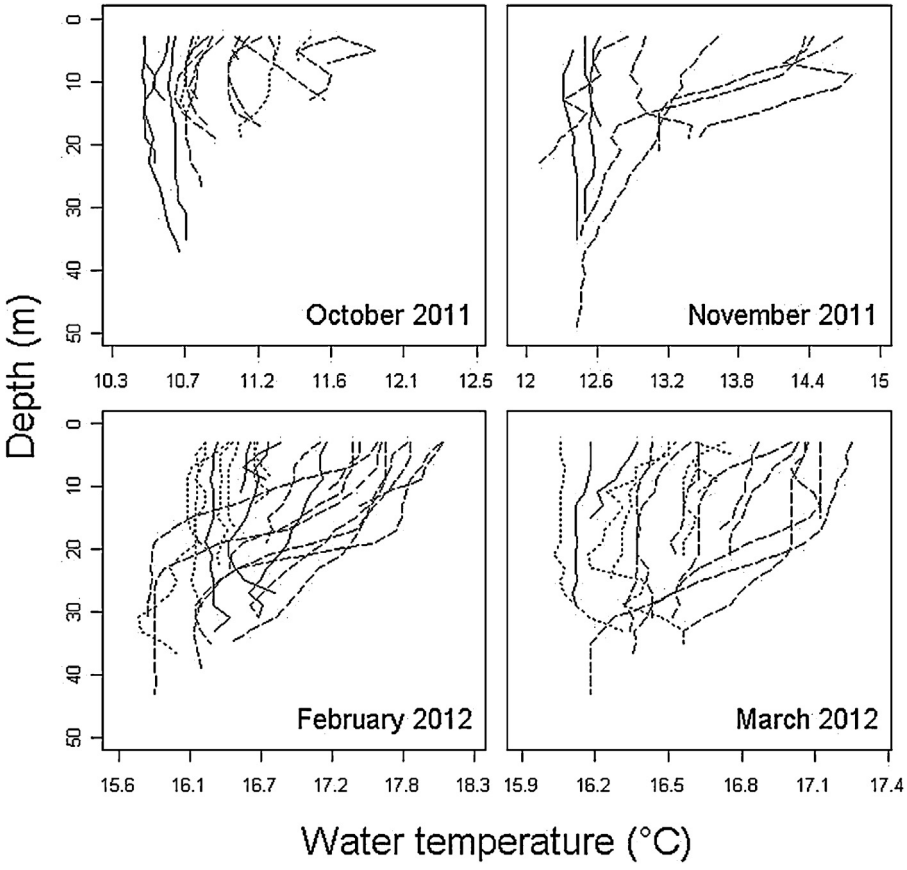

Fig. 3. Vertical sea water temperature profiles within San José Gulf, northern Patagonia, Argentina, between October 2011 and March 2012. Dotted line: West domain; solid line: transition zone; dashed line: East domain.

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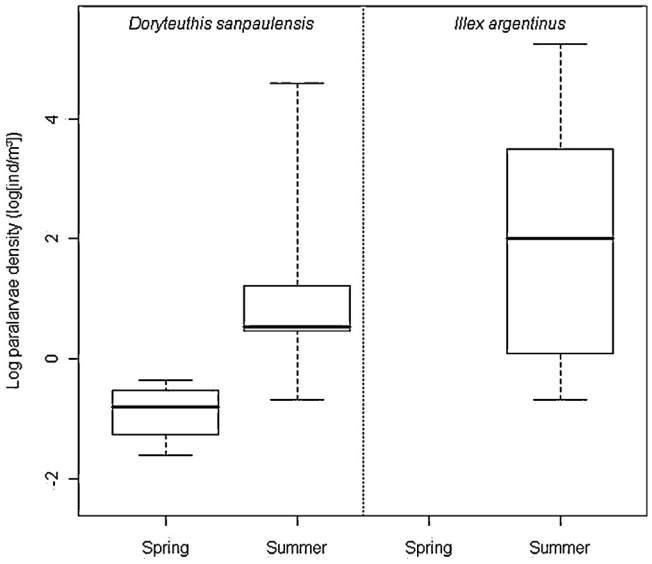

Fig. 4. Boxplots showing relative abundance of *Illex argentinus* and *Doryteuthis sanpaulensis* paralarvae within San José Gulf, northern Patagonia, Argentina, in summer and spring. The black line represents the median; superior and inferior limits of the box represent 0.25 and 0.75 quantiles respectively, and upper and lower limits represent maximum and minimum values.

relative abundances of *D. sanpaulensis* paralarvae were found mainly in the north of the eastern domain of SJG. Conversely, most samples containing *I. argentinus* were found in the south of the western domain. *R. fontaniana* was found both at stations belonging to the eastern (station 17) and western domain (station 9) and in the transition zone (station 11) (Table 1), while *S. tenera* was found in the eastern domain (station 18).

Seawater temperature at stations in which paralarvae of *D. sanpaulensis* were captured ranged between 12.5 °C and 17 °C. The highest relative abundances were obtained where sea water temperature was higher (Fig. 6). Seawater temperature at stations where paralarvae of *I. argentinus* were captured was constrained

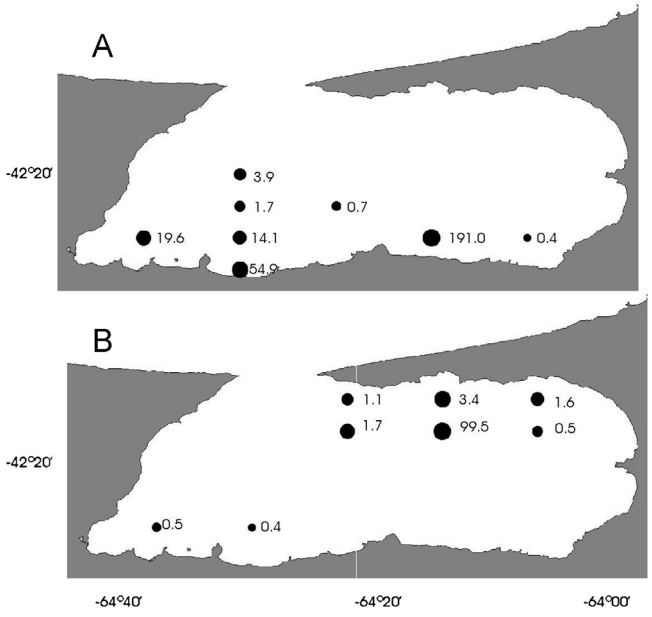

Fig. 5. Spatial distribution of *Illex argentinus* (A) and *Doryteuthis sanpaulensis* (B) paralarvae in San José Gulf, northern Patagonia, Argentina. Relative abundance is expressed as number of individuals 100^{-1} m^3.

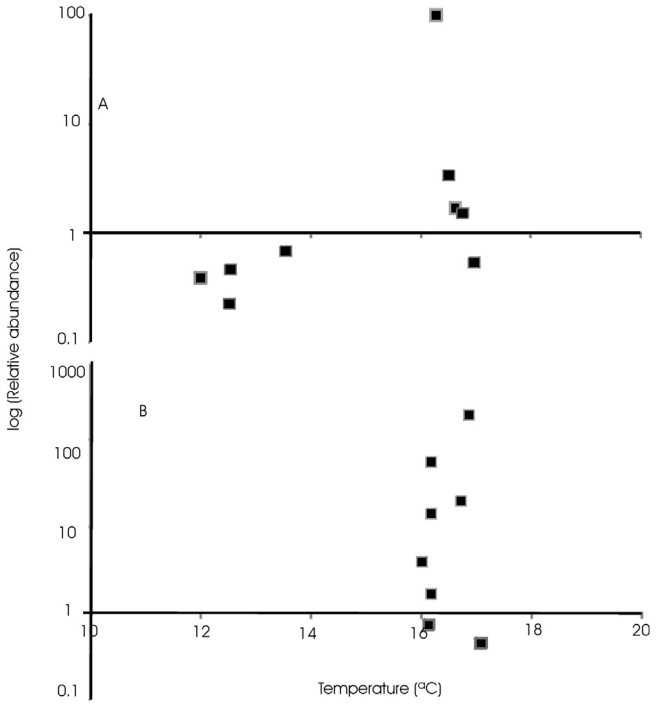

Fig. 6. Relative abundance of cephalopod early-life stages (paralarvae 100^{-1} m^3) versus sea water temperature in San José Gulf, northern Patagonia, Argentina: *Doryteuthis sanpaulensis* (A) and *Illex argentinus* (B).

to a narrower temperature range (16–17 °C). The relation between relative paralarvae abundance and sea water temperature did not present a clear pattern for this species (Fig. 6). Water temperature ranged between 10.6 °C and 13 °C in stations where *R. fontaniana* was caught, and it was 13.1 °C in the station where *S. tenera* occurred.

4. Discussion

Tidal circulation has a major role on the hydrodynamic structure of SJG. As shown by satellite imagery (Amoroso and Gagliardini, 2010; Amoroso et al., 2011), cold bottom water from the Valdés Peninsula tidal front, circulating westwards by the southern margin of SMG, is injected during rising tides into SJG by its narrow mouth, generating a highly turbulent flux on its western domain. During ebb tides seawater is expelled through the mouth to SMG, forming eddies moving northwards for up to 100 km, reaching the center of SMG (Amoroso and Gagliardini, 2010). Considering that the mean tidal amplitude of SJG is 6 m and that the mean depth of the gulf is 40 m, the volume of seawater flowing through the mouth in every rising and ebb tide represents approximately 15% of its total volume (Rivas, 1990). Furthermore, since the process is asymmetrical between domains, this figure must be even higher for the western domain, explaining the homogeneous structure of the water column in it. In contrast, the eastern domain remains stratified from mid-spring (November) to late summer (March), suggesting that the vertical structure of the water column in this domain is poorly affected by tidal circulation. In the transition zone between both domains, a thermal front is formed at the surface (Amoroso and Gagliardini, 2010).

Considering this contrasting hydrodynamic scenarios, it is expected that the western domain acts as a high-speed conveyor belt transporting in and out of SJG mouths' section large amounts of planktonic organisms per time unit, and that the front between domains acts as a retention area, concentrating part of plankters

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carried by currents at the western domain in its boundary and delivering them to the eastern domain where water flow to SMG is low.

Cephalopod early-life stages are frequently associated with highly productive areas (e.g., upwellings areas, frontal systems) since these regions provide the necessary food supply for growth and development (Rodhouse et al., 1992; Piatkowski et al., 1993; Röpke et al., 1993; González et al., 2005). Thus, annual or decadal changes in the extension of these areas have been used to explain fluctuations in cephalopods stocks abundances (Waluda et al., 1999; Sakurai et al., 2000; Roberts and van den Berg, 2005). Several highly productive frontal systems have been characterized along the coastal waters and inner shelf off Argentina (Acha et al., 2004; Bogazzi et al., 2005). It is known that these areas provide the necessary food for early-life stages of several species of fishes, bivalves and crustaceans that sustain important fisheries (Acha et al., 2004). However, although several commercially valued cephalopods species are present in coastal waters and the inner shelf off these regions (Iribarne, 1990; Barón and Ré, 2002; Crespi-Abril et al., 2008; Ortíz, 2009; Storero, 2010; Crespi-Abril and Barón, 2012), knowledge about their role in regulating cephalopod population dynamics is still poor.

Adults and early-life stages of the four species of cephalopods found in the zooplankton samples have been reported to present contrasting behaviors. The sepioid *S. tenera* is a small, muddy-bottom dweller with a wide Western Atlantic distribution, ranging from the Gulf of Maine to Argentina (Reid and Jereb, 2005). Although this coastal species is present in SJG (Ré et al., 2003), its occurrence in the zooplankton samples was sporadic. Individuals from this sepiolid have been captured in neritic waters from the coast to the outer shelf in the northwestern Atlantic Ocean (Vecchione et al., 2001), mainly associated to bottom waters. Furthermore, Boletzky (1977) has reported that benthic sepioids like this species produce benthic hatchlings. Therefore, their comparatively low abundance (<5% of all paralarvae) could be due to their low probability of being captured in oblique and horizontal subsurface tows performed in our study. *R. fontaniana* is a small benthic octopus present in the southeastern Pacific Ocean, from Peru (6°S) to Tierra del Fuego (55°S), and in the southwestern Atlantic Ocean, from SMG to the south, with a bathymetric distribution ranging from littoral coastal areas up to 225 m depth (Adam, 1938; Pickford, 1955; Castellanos, 1967; Castellanos & Menni, 1969; Nesis, 1987; Ré, 1989, 1998; Ibáñez et al., 2008). Spawning grounds of this species are unknown but it has been suggested that females spawn in coastal shallow waters within the northern Patagonian gulfs of Argentina (41°S–43°S, Ortiz and Ré, 2011). Although *R. fontaniana* has planktonic hatchlings (Ortiz and Ré, 2011), these were comparatively rare in our samples (<10% of all paralarvae). However, despite infrequent in samples, *R. fontaniana* was particularly abundant (27.4 individuals 100 m^{-3}) in the shallowest station (6 m depth) reflecting that its presence in SJG is not sporadic.

I. argentinus is distributed from the southern Brazil (22°S) to Malvinas Islands (54°S) over the Argentinean shelf and slope (Haimovici et al., 1998). Recent research studies have addressed the relevance of coastal water frontal systems off northern Patagonia on the reproduction and recruitment of this species (Crespi-Abril et al., 2008, 2010; Crespi-Abril and Barón, 2012). This study not only reinforces this viewpoint but also provide insights on its fine scale patterns of paralarval transport. Paralarvae of this species presented a marked spatial segregation in SJG, being present almost exclusively in the southern region of the western domain during a limited period of time (mainly in February). The abundance of paralarvae in the present study ranged between 0.5 and 191 paralarvae 100 m^{-3}, in agreement with previous observations reported for the species in outer shelf and slope (0.1–80 paralarvae 100^{-1} m^{-3}; Haimovici et al., 1998; Vidal et al., 2010) and in coastal waters (0.3–6.5 paralarvae 100^{-1} m^{-3}, Crespi-Abril and Barón, 2012). Their presence in SJG could be explained either by the spawning activity of females in this basin or by the influx of egg masses/paralarvae through its mouth carried by waters from the neighboring Valdés Peninsula Frontal System. The first alternative seems unlikely since egg masses laid on the western domain would not be retained until hatching take place due to the high rate of water exchange caused by tidal circulation. In this context, the second explanation seems the most likely since there are several evidences that support it. Recently, Crespi-Abril and Barón (2012) suggested that Valdés Peninsula Frontal System is one of the regions with the highest suitability for spawning and early life-stage survival during the summer. This observation was derived from a model that considered the sea surface temperature (SST) and chlorophyll-a (Chl-a) concentration estimates over the distribution area of *I. argentinus*. This approach has some restrictions since it is constrained only to two relevant environmental variables and it does not consider interaction with other species (i.e., predation, competition); therefore, the conclusions derived should be considered with caution. However, empirical observations such as the presence of paralarvae and important aggregations of mature individuals (Haimovici et al., 1998) provided evidences that Valdés Peninsula Frontal System is actually a spawning ground for *I. argentinus*. Circulation patterns observed in satellite imagery (Amoroso and Gagliardini, 2010; Amoroso et al., 2011) also give a strong support to the second alternative. However, although SJG may be acting as a pathway of egg masses and paralarvae, it cannot be completely discarded that the species uses its waters as a spawning ground. In either case, the observations presented in this work evidence that summer spawning groups fished in the northern part of SMG (Crespi-Abril et al., 2008) and those aggregating in the Valdés Peninsula Frontal System (Haimovici et al., 1998) are interconnected not only by migration of adult squids, but also by passive transport of egg masses and paralarvae.

D. sanpaulensis presents a wide geographical distribution from Brazil (20°S) to Argentina (~46°S) (Jereb et al., 2010). It has been reported that the species spawns in northern Patagonian waters (Barón, 2001, 2003; Barón and Ré, 2002), but the information on the abundance and distribution of their paralarvae is scarce. It is worthwhile to mention that *D. sanpaulensis* paralarvae were caught during most of the sampling period. In the northeastern region off the coast of northern Patagonia egg masses of the species occur almost exclusively from November to March, with no marked peak of occurrence (Barón, 2001). This last point agrees with the protracted spawning period (several months) reported for the species (Barón and Ré, 2002; Barón, 2003). On the other hand, paralarvae from this species were found almost exclusively in the northern region within the eastern domain of SJG. Hatchlings emerging from egg masses laid by this species on the bottoms of the eastern domain of SJG are probably locally retained in this low-circulation area.

In this study, spatially-representative plankton sampling of SJG provided novel information on the distribution of cephalopod paralarvae and allowed to propose different hypothesis on the patterns of distribution of these organisms. Since it is known that rhythmic larval migrations synchronic with tidal or daily variations in circulation patterns often results in transport patterns of meroplanktonic larval stages different from those predicted based on average circulation (Queiroga and Blanton, 2004), knowledge on the vertical distribution and migrations of paralarvae from Patagonian cephalopod species is essential to understand transport mechanisms (Queiroga and Blanton, 2004). Further studies should be designed and conducted to fulfill this gap of knowledge.

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Authors' contributions

Crespi-Abril was contributed in laboratory work, data analysis and writing. Villanueva Gomila was contributed in field and laboratory work and data analysis. Venerus and Barón were contributed in data analysis and writing.

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References

Acha, E.M., Mianzan, H.W., Guerrero, R.A., Favero, M., Bava, J., 2004. Marine fronts at the continental shelves of austral South America Physical and ecological processes. J. Mar. Syst. 44, 83–105.
Adam, V.W., 1938. Robsonella nom. nov. für Joubinia Robson, 1929 (*Cephalopoda Octopoda*). Zool. Anz. 121, 223–224.
Amoroso, R.O., Gagliardini, D.A., 2010. Inferring complex hydrographic processes using remote-sensed images: turbulent fluxes in the patagonian gulfs and implications for scallop metapopulation dynamics. J. Coast. Res. 6, 320–332.
Amoroso, R., Parma, A.M., Orensanz, J.M., Gagliardini, D.A., 2011. Zooming the macroscope: medium-resolution remote sensing as a framework for the assessment of a small-scale fishery. ICES J. Mar. Sci. 68 (4), 696–706.
Arkhipkin, A., Perez, J.A.A., 1998. Life-history reconstruction, in: Rodhouse, P., Dawe, E., O'Dor, R. (Eds.), Squid recruitment dynamics. The Genus Illex as a Model, the Commercial Illex Species and Influences on Variability. FAO Fisheries Technical Papers 376, Rome, pp. 157–180.
Bakun, A., 1996. Patterns in the Ocean. Ocean Processes and Marine Population Dynamics. California Sea Grant, National Oceanic and Atmospheric Administration and Centro de Investigaciones Biológicas del Noroeste, La Paz.
Bakun, A., Csirke, J., 1998. Environmental processes and recruitment variability, in: Rodhouse, P.G., Dawe E.G., O'Dor R.K. (Eds.), Squid Recruitment Dynamics, FAO Fisheries Technical Paper, Rome, pp. 105–124.
Barón, P.J., 2001. First description and survey of the egg masses of *Loligo gahi* and *Loligo sanpaulensis* from the Patagonian coastal waters. J. Shellfish Res. 20 (1), 289–295.
Barón, P.J., 2003. The paralarvae of two South American sympatric squid: *Loligo gahi* and *Loligo sanpaulensis*. J. Plankton Res. 25 (11), 1347–1358.
Barón, P.J., Ré, M.E., 2002. Reproductive cycle and population structure of *Loligo sanpaulensis* of the northeastern coast of Patagonia. Bull. Mar. Sci. 71, 175–186.
Bogazzi, E., Baldoni, A., Rivas, A., Martos, P., Reta, R., Orensanz, J.M., Lasta, M., Dell'Arciprete, P., Werner, F., 2005. Spatial correspondence between areas of concentration of Patagonian scallop (*Zygochlamys patagonica*) and frontal systems in the southwestern Atlantic. Fish. Oceanogr. 14 (5), 359–376.
Boletzky, S.V., 1977. Post-hatching behavior and mode of life in cephalopods. Symp. Zool. Soc. Lond. 38, 557–567.
Bower, J.R., Takagi, S., 2004. Summer vertical distribution of paralarval gonatid squids in the northeast Pacific. J. Plankton Res. 26 (8), 851–857.
Brunetti, N., 1990. Description of rhynchoteuthion larvae of *Illex argentinus* from summer spawning population. J. Plankton Res. 12, 1045–1057.
de Castellanos, Z.A., 1967. Catálogo de los moluscos marinos bonaerenses. Anal. Comisión Investig. Cient. Provincia Buenos Aires 8, 9–365.
Castellanos, Z.A., Menni, R.C., 1969. Sobre dos pulpos costeros de la Argentina. Neotrópica 15, 89–94.
Crespi-Abril, A.C., Morsan, E.M., Barón, P.J., 2008. Contribution to understanding the population structure and maturation of *Illex argentinus* (Castellanos, 1960): the case of the inner-shelf spawning groups in San Matías Gulf (Patagonia, Argentina). J. Shellfish Res. 27, 1225–1231.
Crespi-Abril, A.C., Dellatorre, F., Barón, P.J., 2010. On the presence of *Illex argentinus* (Castellanos, 1960) (Cephalopoda: Ommastrephidae), paralarvae and juveniles in near-shore waters of Nuevo Gulf, Argentina. Lat. Am. J. Aquat. Res. 38 (2), 297–301.
Crespi-Abril, A.C., Barón, P.J., 2012. 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. Fish. Oceanogr. 21 (2–3), 199–214, http://dx.doi.org/10.1111/j.1365-2419.2012.00615.x.
Dawe, E.G., Colbourne, E.B., Drinkwater, K.F., 2000. Environmental effects on recruitment of short-finned squid (*Illex illecebrosus*). ICES J. Mar. Sci. 57, 1002–1013.
Esteves, J.L., Solis, M., Cejas, J., Vera, R., 1986. Golfo San José: resultados de las campañas oceanográficas 1984/1985. Technical Report. Chubut Province Administration, Chubut, Argentina (in Spanish).
González, A.F., Otero, J., Guerra, A., Prego, R., Rocha, F.J., Dale, A.W., 2005. The influence of the oceanographic regime on the planktonic phase of *Octopus vulgaris and Loligo vulgaris* in a seasonal upwelling region. J. Plankton Res. 27, 271–277.
Haimovici, M., Brunetti, N., Rodhouse, P., Csirke, J., Leta, R., 1998. *Illex argentinus*, in: Rodhouse, P., Dawe, E., O'Dor, R. (Eds.), Squid Recruitment Dynamics. The Genus Illex as a Model, the Commercial Illex Species and Influences on Variability. FAO Fisheries Technical Papers 376, Rome, pp. 27–58.
Ibáñez, C.M., Sepúlveda, R.D., Guerrero, J., Chong, J., 2008. Redescription of *Robsonella fontaniana* (Cephalopoda: Octopodidae). J. Mar. Biol. Assoc. UK 88, 617–624.
Iribarne, O., 1990. Use of shelter by the small Patagonian octopus *Octopus tehuelchus*: availability, selection and effects on fecundity. Mar. Ecol. Prog. Ser. 66, 251–258.
Jackson, G.D., Domeier, M.L., 2003. The effects of an extraordinary El Niño/La Niña event on the size and growth of the squid *Loligo opalescens* off southern California. Mar. Biol. 142, 925–935.
Jereb, P., Vecchione, M., Roper, C.F.E., 2010. Family *Loliginidae*. In: Jereb, P., Roper, C.F.E. (Eds.), Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Vol. 2. Myopsid and Oegopsid Squids. FAO Species Catalogue for Fishery Purposes, 4(2), Rome, pp. 38–117.
Manly, B.F.J., 1991. Randomization and Monte Carlo Methods in Biology. Chapman and Hall, London.
Nesis, K.N., 1987. Cephalopods of the World. Squid, Cuttlefishes, Octopuses and Allies. TFH Publications Inc., Neptune City, NJ.
Ortíz, N., 2009. Biología poblacional del pulpo colorado Enteroctopus magalocyathus en la costa Patagónica Norte y Central y sus implicancias en el manejo pesquero. Universidad de Buenos Aires, Buenos Aires (Ph.D. thesis).
Ortiz, N., Ré, M.E., 2011. The eggs and hatchlings of the octopus *Robsonella fontaniana* (Cephalopoda: Octopodidae). J. Mar. Biol. Assoc. UK 91 (03), 705–713.
Otero, J., Salgado, X.A., González, A.F., Groom, S.B., Miranda, A., Cabanas, J.M., Guerra, A., 2008. Bottom-up and top-down controls of common octopus (*Octopus vulgaris*) in a wind-driven upwelling area (Galicia, NE Atlantic). Mar. Ecol. Prog. Ser. 362, 181–192.
Piatkowski, U., Welsch, W., Röpke, A., 1993. Distribution patterns of the early life stages of pelagic cephalopods in three geographically different regions of the Arabian Sea. In: Okutani, T., O'Dor, R.K., Kubodera, T. (Eds.), Recent Advances in Cephalopod Fisheries Biology. Tokai University Press, Tokyo, pp. 417–431.
Pickford, G.E., 1955. Revision of Octopodidae in the British Museum. Part II. A re-examination of the specimens of *Robsonella fontaniana* in the collections of the British Museum. Bull. Br. Mus. (Nat. Hist.) Zool. 3, 163–167.
Pizarro, M.J., 1975. Análisis de los resultados de la primera campaña oceanográfica en el golfo San José. Technical Report. Centro Nacional Patagónico, Puerto Madryn, Argentina, 19 p. (in Spanish).
Queiroga, H., Blanton, J., 2004. Interactions between behaviour and physical forcing in the control of horizontal transport of Decapod Crustacean Larvae. Adv. Mar. Biol. 47, 107–214.
R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, ISBN 3-900051-07-0. Available from: http://www.r-project.org
Ré, M.E., 1989. Estudios ecológicos sobre el crecimiento y la alimentación de *Octopus tehuelchus* d'Orbigny en Puerto Lobos, Golfo San Matías. Universidad Nacional de La Plata, Buenos Aires, Argentina (Doctoral thesis).
Ré, M.E., 1998. Pulpos Octopódidos (Cephalopoda: Octopodidae). In: Boschi, E.E. (Ed.), El Mar Argentino y sus Recursos Pesqueros. Tomo 2: Los moluscos de interés pesquero. Cultivos y estrategias reproductivas de bivalvos y equinoideos. Publicaciones especiales INIDEP, Mar del Plata, Argentina, pp. 69–98.
Ré, M.E., Kuba, L., Díaz, M.A., 2003. Primera descripción de puestas del globito tierno *Semirossia tenera* (Verrill, 1880) (Cephalopoda, Sepiolidae). Abstract. In: V Jornadas Nacionales de Ciencias de Mar, Mar del Plata, (in Spanish).
Reid, A., Jereb, P., 2005. Family Sepiolidae, in: Jereb, P., Roper, C.F.E. (Eds.), Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Vol. 1. Chambered Nautiluses and Sepioids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae). FAO Species Catalogue for Fishery Purposes, 4(1), Rome, pp. 153–203.
Rivas, A.L., 1990. Heat balance and annual variation of mean temperature in the north-Patagonian gulfs. Acta Oceanol. 13 (3), 256–272.
Roberts, M.J., 2005. Chokka squid (*Loligo vulgaris reynaudii*) abundance linked to changesin South Africa's Agulhas Bank ecosystem during spawning and the early life cycle. ICES J. Mar. Sci. 62, 33–55.
Roberts, M.J., van den Berg, M., 2005. Currents along the Tsitsikamma coast, South Africa, and potential transport of squid paralarvae and ichthyoplankton. Afr. J. Mar. Sci. 27 (2), 375–388.
Rodhouse, P.G., Symon, C., Hatfield, E.C., 1992. Early life cycles of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. Mar. Ecol. Prog. Ser. 89, 183–195.
Röpke, A., Nellen, W., Piatkowski, U., 1993. A comparative study on the influence of the pycnocline on the vertical distribution of fish larvae and cephalopod paralarvae in three ecologically different areas of the Arabian Sea. Deep-Sea Res. 40, 801–819.
Sakurai, Y., Kiyofuji, H., Saitoh, S., Goto, T., Hiyama, Y., 2000. Changes in inferred spawning areas of *Todarodes pacificus* (Cephalopoda: Ommastrephidae) due to changing environmental conditions. ICES J. Mar. Sci. 57, 24–30.
Servicio de Hidrografía Naval Argentino, 1983. Carta Golfo San José H-277, Argentina, 1:20,000.

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Storero, L.P., 2010. Características ecológicas del pulpito Octopus tehuelchus en tres ambientes del Golfo San Matías. Universidad Nacional de Córdoba, Córdoba (Ph.D. thesis).

Vecchione, M., 1987. Juvenile ecology. In: Boyle, P.R. (Ed.), Cephalopod Life Cycles. 2. Comparative Reviews. Academic Press, London, pp. 61–84.

Vecchione, M., Roper, C.F.E., Sweeney, M.J., Lu, C.C., 2001. Distribution, Relative Abundance and Developmental Morphology of Paralarval Cephalopods in the Western North Atlantic Ocean. NOAA Technical Report NMFS 152, 58 pp.

Vidal, E.A., Haimovici, M., Hackbart, C.S., 2010. Distribution of paralarvae and small juveniles to primary production in an upwelling area off southern Brasil. ICES J. Mar. Sci. 67, 1346–1352.

Waluda, C.M., Trathan, P.N., Rodhouse, P.G., 1999. Influences of oceanographic variability on the recruitment in the *Illex argentinus* (Cephalopoda: Ommastrephidae) fishery in the South Atlantic. Mar. Ecol. Prog. Ser. 183, 159–167.

Waluda, C.M., Rodhouse, P.G., Podestá, G.P., Trathan, P.N., Pierce, G.J., 2001. Surface oceanography of the inferred hatching grounds of *Illex argentinus* (Cephalopoda: Ommastrephidae) and influences on recruitment variability. Mar. Biol. 139, 671–679.

Yamamoto, J., Shimura, T., Uji, R., Masuda, S., Watanabe, S., Sakurai, Y., 2007. Vertical distribution of *Todarodes pacificus* (Cephalopoda: Ommastrephidae) paralarvae near the Oki Islands, southwestern Sea of Japan. Mar. Biol. 153, 7–13.

Yang, W.T., Hanlon, R.T., Krejci, M.E., Hixon, R.F., Hulet, W.H., 1980. Culture of California market squid from hatching – first rearing of *Loligo* to subdult stage. Aquabiology 2 (6), 312–318.

Zeidberg, L.D., Hamner, W.M., 2002. Distribution of squid paralarvae, *Loligo opalescens* (Cephalopoda: Myopsida), in the Southern California Bight in the three years following the 1997–1998 El Niño. Mar. Biol. 141, 111–122.

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