



Habitat of Argentine squid (*Illex argentinus*) paralarvae in the southwestern Atlantic

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ABSTRACT: *Illex argentinus* is one of Argentina's most important commercial species and sustains one of the most important cephalopod fisheries worldwide. Catches, and presumably population abundances, show strong interannual fluctuations, probably forced by processes which occur during the species' early life history. However, knowledge of paralarvae ecology and the influence of the environment on larval survival are fragmentary and limited. In this work, we describe the habitat of *I. argentinus* paralarvae caught in 4 research cruises between 34° and 42° S, taking into account information on seasonal transport of paralarvae by currents, chlorophyll a concentrations, characteristics of water masses and water column structure. Argentine squid paralarvae habitat is environmentally complex. Paralarvae occur in the plankton when the biological production in the area is relatively low but offshore transport is at a minimum, thus decreasing the chances of the paralarvae being exported to places unsuitable for survival. We discuss how the synchronization of the squid reproductive cycle relates to these environmental events and may improve paralarvae survival and recruitment.

KEY WORDS: Fisheries · Reproductive cycle · Rhynchoteuthion · Ommastrephidae · Shortfin squid

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1. INTRODUCTION

Ommastrephid squids are found in all oceans and their rapid growth and abundance make ommastrephid fisheries the most important cephalopod fisheries worldwide (Arkhipkin et al. 2015). These squid are important prey and predators, occupying a wide range of trophic levels in marine pelagic food webs throughout their lifespan (Ivanovic 2000, Boyle & Rodhouse 2005, Coll et al. 2013). The species belonging to this family are semelparous, with a lifespan of around a year; consequently, environmental variability strongly influences population abundance (Dawe & Brodziak 1998, Waluda et al. 2001, Torres Alberto et al. 2021). As is the case for most marine species with planktonic larvae, survival of squid paralarvae

is critical for recruitment and is highly influenced by environmental conditions (Boletzky 1994, Sakurai et al. 1996, Sakai et al. 1998, Yamamoto et al. 2002). Squid paralarvae must grow and develop while simultaneously avoiding predation. Recently hatched paralarvae have weak swimming capabilities, and eggs and paralarvae rely on currents to reach and stay in favorable conditions (in terms of temperature and food) for their development. Hatchlings of the Ommastrephidae family are among the smallest of the cephalopods and show a characteristic morphology, with the tentacles fused into a proboscis (Brunetti 1988, 1990, Fernández-Álvarez et al. 2017). These paralarvae are known as rhynchoteuthion. Despite increased knowledge of the subadult and adult biology of several species of ommastrephid, current

understanding of early life stages is fragmentary and limited, largely due to sampling difficulties.

The Argentine shortfin squid *Illex argentinus* is one of the most important commercial fisheries in Argentina (Haimovici et al. 1998). It inhabits the southwestern Atlantic between 22 and 54° S. Its range spans the continental shelf, the shelf break and adjacent oceanic areas, but is limited to the region influenced by temperate–cold waters of subantarctic origin (Brunetti 1988). On the continental shelf, 4 stocks (or subpopulations) of *I. argentinus* have been identified based on reproductive season and spawning ground location (Brunetti 1988, Haimovici et al. 1998). The south Patagonic stock (SPS) is the most abundant and the main support of regional fisheries (Brunetti et al. 1999). The SPS reproduces during autumn and winter along the Patagonian slope between 45 and 48° S, near or within the Malvinas Current (MC). Egg masses are then transported northward by currents to the northern part of the Argentine continental shelf and the Brazil–Malvinas confluence (BMC; 38° S), where eggs experience the thermal conditions necessary for hatching (Fig. 1) (Koronkiewicz 1986, Brunetti 1988, Brunetti & Ivanovic 1992, Torres Alberto et al. 2021). The abundance of the SPS shows strong interannual fluctuations, and the transport of eggs and paralarvae to inhospitable regions is postulated as the main cause of recruitment failure, thus modulating recruitment (Brunetti & Ivanovic 1992, Bakun & Csirke 1998, Torres Alberto et al. 2021).

Sakai et al. (1998) provided a detailed description of the early developmental stages of *I. argentinus* based on laboratory incubations and established the temperature range that favors development. Field studies have shown that *I. argentinus* paralarvae are found along the shelf and in adjacent oceanic waters off Uruguay and Argentina, in temperatures >12°C, throughout the year but particularly between May and August (Leta 1987, Brunetti 1988, 1990, Brunetti & Ivanovic 1992, Leta & Chiesa 1992, Rodhouse et al. 1992, Vidal 1994, Haimovici et al. 1995, 1998). Previous studies on paralarval habitat have not gone beyond establishing which water

masses paralarvae were found in. In this work, we revisit the current description of larval habitat and add information on seasonal transport by currents, on chlorophyll *a* (chl *a*) concentrations and other characteristics of the local water masses, and discuss how they relate to the synchronization of the squid reproductive cycle and affect paralarval survival.

2. MATERIALS AND METHODS

2.1. Study area

The sampled area included the continental shelf (depths <200 m) between 34° and 42° S off the coast of Argentina and Uruguay (Fig. 1). In this region, temperature shows a marked seasonal cycle, but salinity presents a similar pattern year-round (Guerero & Piola 1997). Waters are cold and vertically homogeneous during autumn and winter. The sea-

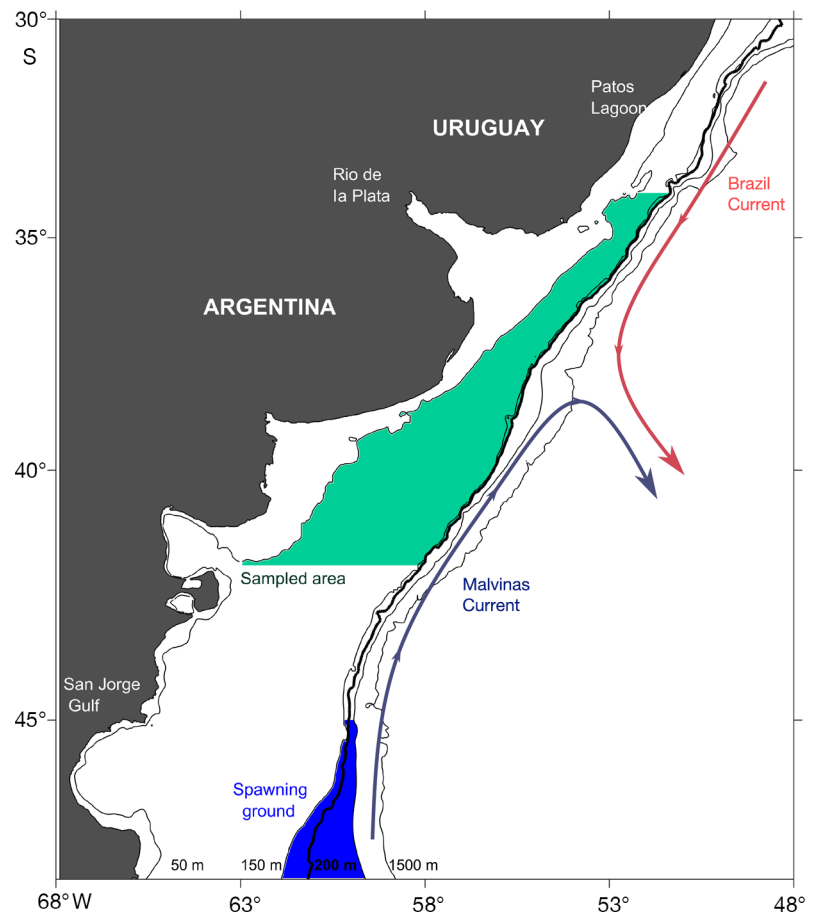


Fig. 1. Map showing the sampled area located between 34 and 42° S and the 50 and 200 m isobaths and the presumed spawning ground of the south Patagonic stock of *Illex argentinus* (blue). The colored arrows represent the Malvinas and Brazil currents. Black lines represent isobaths of 50, 150, 200 (bold line), 800 and 1500 m

sonal thermocline begins to form in spring, becoming stronger during summer (Martos & Piccolo 1988). The study area includes 2 regions (Piola et al. 2018): the Patagonian continental shelf (south of 38°S) and the central shelf of the southwestern Atlantic (from 38 to 28°S).

The Patagonian continental shelf is a wide plateau subject to intense westerly winds and high tidal amplitude. It is bounded offshore by the cold, nutrient-rich and relatively fresh waters of the MC, which flows northwards to about 38°S. The mean circulation over the shelf has a north-northeast orientation (Piola et al. 1997). Variations in circulation over the inner and mid-shelf are mainly driven by wind forcing, but the along-shore circulation over the outer continental shelf (~ 30 km in width) is modulated by variability in the MC (Lago et al. 2021). Over the continental shelf there are at least 3 water masses (Guerero & Piola 1997, Piola et al. 2018): coastal water (CW), central shelf water (SW) and Malvinas water (MW). MW is of subantarctic origin, is transported by the MC and has a relatively high salinity (33.8–34.2); CW is formed by water from the Strait of Magellan diluted by river discharges and generally has a salinity below 33.4; and SW is formed from a mix of MW and CW and has a salinity between 33.4 and 33.8.

Instead, the central shelf has a mean southward flow between 28°S and 38°S, which is largely controlled by the Brazil Current (BC). Moreover, this region is strongly influenced by the continental discharge of the Rio de la Plata and the Patos Lagoon, and by its proximity to the BMC, which bounds its offshore limit and promotes energetic exchange between shelf and deep ocean waters. In this region there are 2 water masses (Piola et al. 2018): subtropical water (STW) and the freshwater discharge from the Rio de la Plata (RdPW). The former has higher temperatures than the water masses further south and a relatively high salinity (>35) and the latter has the lowest salinity of the region's water masses (<31.8). There are also 2 fronts which bound the

BMC: the Subantarctic Front (SAF) to the south and the Subtropical Front (STF) to the north. The STF represents the southern limit of the BC, while the SAF constitutes the northern limit of the MC (Peterson & Whitworth 1989). Sources of variability in the location of these frontal zones are not fully understood and are subject to discussion (e.g. Combes & Matano 2014, Artana et al. 2019).

The plankton production cycle throughout the sampled area follows the timing and displacement of the shelf stratification, typical of temperate–cold seas. From spring to early summer, phytoplankton and subsequent zooplankton abundance peaks expand from coastal to offshore areas and from north to south. During autumn, a secondary peak of productivity is observed along the shelf break (Carreto et al. 1981, 2016).

2.2. Paralarvae

Rhynchoteuthion paralarvae were collected during 4 research cruises carried out by the RV 'Dr. Eduardo L. Holmberg' and the RV 'Dr. Víctor Angelescu', belonging to the National Institute for Fisheries Research and Development, Argentina (INIDEP). Research cruises took place during April, May and June (austral autumn) of 2004, 2009, 2012 and 2019 (Table 1). The sampled area spanned from 34 to 42°S between the 50 and 200 m isobaths along both the Argentine and Uruguayan continental shelf (Fig. 1). Sampling information for each research cruise is presented in Table 1. All samples were preserved onboard in 5% buffered formalin. Plankton samples were sorted and analyzed in the laboratory. *Illex argentinus* paralarvae were identified and measured following Brunetti (1990) and Sakai et al. (1998). During the 2019 research cruise, stratified sampling methods were employed to investigate the vertical distribution of paralarvae by size, by calculating the proportion of paralarvae smaller or larger

Table 1. Date range, geographic coverage, number of samples and sampling strategy of research cruises. EH: RV 'Dr. Eduardo L. Holmberg', VA: RV 'Dr. Víctor Angelescu'. Nets are named following Wiebe & Benfield (2003)

Research vessel/Yr	Dates	Latitudinal range	— Number of stations —		Sampling method		Max. depth (m)
			Total	With paralarvae	Net (mesh aperture, µm)	Towing type	
EH04/2004	April 5 to May 14	37–42°S	40	8 (20%)	Nackthai (300)	Oblique	163
EH04/2009	May 5 to June 2	35–40°S	30	10 (33.3%)	Bongo (300 and 500)	Oblique	192
EH04/2012	May 5 to June 1	34–39°S	40	10 (25%)	Bongo (300 and 500)	Oblique	205
VA05/2019	May 17 to June 7	34–40°S	35	10 (28.6%)	Multinet (300)	Stratified	150

than 2 mm ML in 3 layers: 0–30 m depth (upper), 30–100 m depth (middle), and >100 m depth (deep).

2.3. Oceanographic information

2.3.1. *In situ* data

CTD profiles (temperature and salinity) were obtained at each sampling station. These data were employed to study the vertical structure of paralarvae habitat and to plot paralarvae abundance in a temperature–salinity diagram to study the relationship between abundance and characteristics of water masses. In the case of oblique towing sampling methods, temperature and salinity were averaged for the sampled water column.

2.3.2. Satellite products

Egg masses of ommastrephid squid are known to drift within surface waters above the thermocline. Once hatched, hatchlings swim to the surface (Sakurai et al. 2000, Boyle & Rodhouse 2005, Puneeta et al. 2015, Ringvold et al. 2021). As *I. argentinus* hatchlings stay on the surface, we employed sea surface temperature (SST) to study thermal conditions in the area where squid paralarvae are expected to hatch. We also used satellite chl *a* concentration (CSAT) to expand our description of environmental conditions where squid paralarvae were caught. Both SST and CSAT were estimated from MODIS Aqua (<https://oceancolor.gsfc.nasa.gov/13/>). We downloaded L3 monthly composites of 4 km spatial resolution images and averaged April and May images for each cruise. We also computed the annual cycle using monthly climatology (2003–2020) and calculated the monthly mean and SD over the sampled area (green polygon in Fig. 1).

In addition, we calculated surface geostrophic velocity from sea surface height (SSH) to estimate surface currents that would transport paralarvae. To estimate SSH, we employed maps of absolute dynamic topography (ADT), a reprocessed product of multimission altimeter satellite gridded SSH of the global ocean for the whole time series (1993–2020) (<http://marine.copernicus.eu/>). Temporal resolution was daily and spatial resolution was $0.25^\circ \times 0.25^\circ$.

It is assumed that only a fraction of the paralarvae remain on the continental shelf each year, as most are exported to the oceanic realm by eastward energetic fluxes driven by the BMC. Once exported to the

open ocean, paralarvae cannot return to the continental shelf. Therefore, individuals trapped by the offshore flux are lost to the squid population (Brunetti & Ivanovic 1992, Bakun & Csirke 1998). Circulation variability (along with other factors) could determine interannual differential exportation of eggs and/or paralarvae to the ocean, defining recruitment strength (Torres Alberto et al. 2021). To quantify the variability associated with circulation that affects recruitment strength, we computed the zonal component of the velocity over the 200 m isobath between 34 and 41° S. Then, at every pixel along the isobath, we computed the percentage of days that had a geostrophic velocity component towards the west (towards the coast, which brings the egg masses or paralarvae over the continental shelf and is favorable for successful recruitment) over the entire time series. The daily data of the time series were filtered by calculating a moving average (every 5 d) and then we estimated the seasonal average.

2.3.3. Modeled trajectories and fate of squid paralarvae

We used modeled trajectories of squid egg masses and estimations of recruitment success from Torres Alberto et al. (2021) to identify the shelf break regions where paralarvae would enter the continental shelf ecosystem. The modeled trajectories are the result of a combination of geostrophic currents computed from satellite altimeter data and an algorithm that represents the advection process of the egg masses (regarded as neutrally buoyant particles). The particles were released in the spawning ground (between 45 and 48° S) and their trajectories were tracked along the Patagonian slope to the hatching ground (between 35 and 40° S, see their Fig. 1). We considered the latitude of entrance the point at which the particles entered the continental shelf ecosystem and counted the number of particles that entered at each point during the modelling exercise.

3. RESULTS

3.1. Paralarvae occurrence and surface conditions

Fig. 2 shows the numerical density of paralarvae at each station, the monthly average of SST during

April and May, and the mean position of the SAF for each sampling cruise. Paralarvae ML ranged from 1.15 to 4.60 mm. Almost all paralarvae were caught at temperatures $>11^{\circ}\text{C}$, which is the minimum thermal threshold for hatching and development of the species, as shown by laboratory experiments (Sakai et al. 1998). Moreover, large interannual variability of SST was observed (Fig. 2).

The position of the SAF represents the southern limit of the BMC, and is the principal conduit for exportation of paralarvae offshore from the continental shelf (Torres Alberto et al. 2021). Both SSH and SST reflect the high interannual variability in the position of the SAF (Fig. 2).

Mean CSAT was relatively low for the autumn months in the sampled area (Fig. 3). In May 2004 and

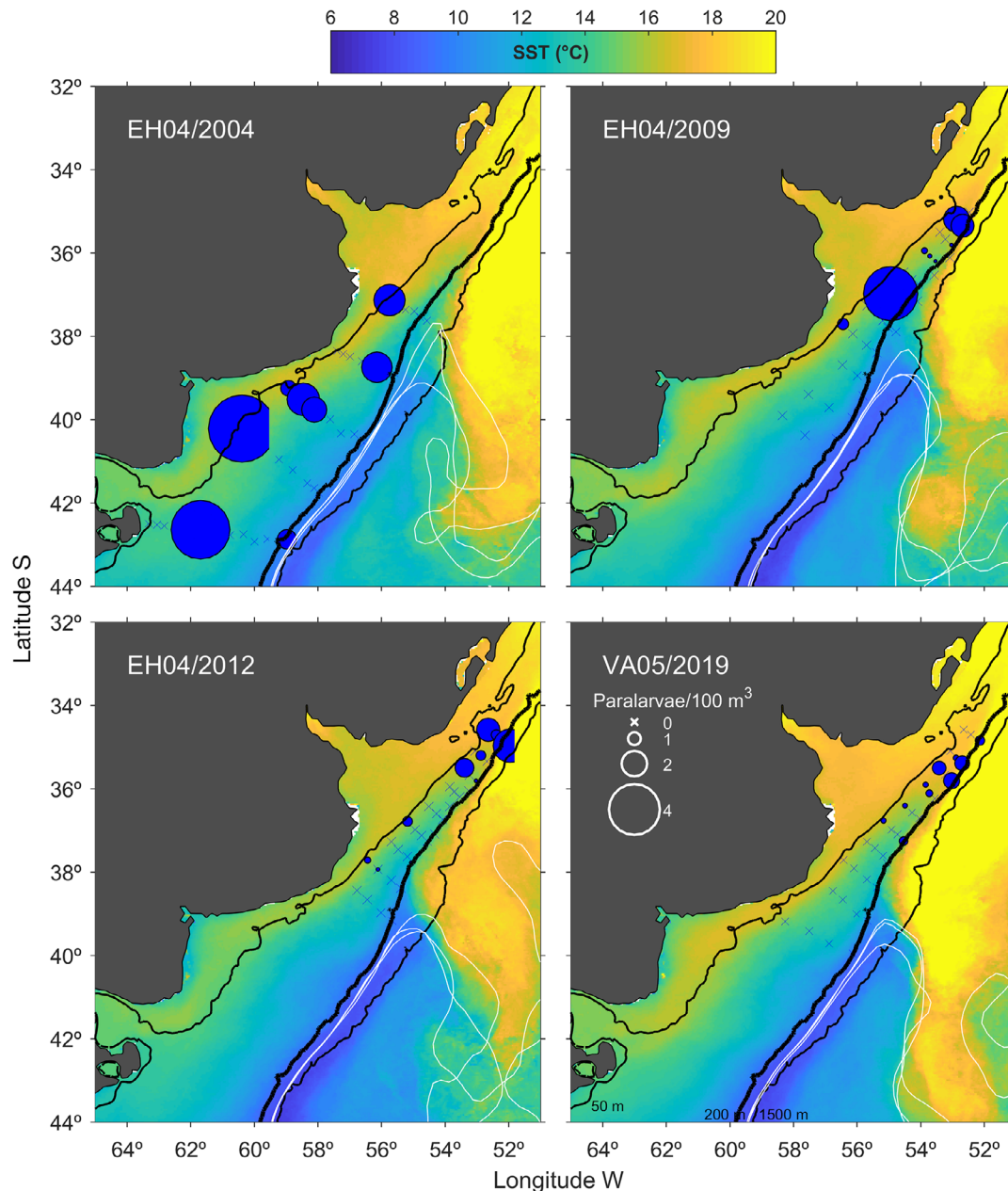


Fig. 2. Numerical density of paralarvae during cruises EH04/2004, EH04/2009, EH04/2012 and VA05/2019. Crosses represent sampling stations without paralarvae. The size of the circles is proportional to the number of paralarvae per 100 m^3 . Colors show the monthly averaged SST (April and May) for each cruise. White isolines correspond to 0.2 m of absolute dynamic topography that represents the position of the Subantarctic Front (the northern limit of the Brazil-Malvinas Confluence) during April and May. Black lines are the 50, 200 (bold line), and 1500 m isobaths

2009, CSAT ranged between 1 and 3 mg m^{-3} over the continental shelf, while in 2012 there were patches of higher concentration (3–6 mg m^{-3}) over the shelf break near 40°S. Most stations where paralarvae were caught were not associated with high concentrations of CSAT.

Fig. 4 shows the latitudinal range of entrance of squid egg masses onto the shelf, as modeled by Torres Alberto et al. (2021). Points correspond to entrance points of the egg masses flowing from the

Patagonian spawning grounds. There are 2 main regions of the shelf break where paralarvae enter the continental shelf area: between 37 and 37.5°S and between 39 and 39.5°S (Fig. 4).

More than 50% of days during the winter and spring were favorable for paralarvae entrance and retention on the continental shelf at the 2 shelf break regions identified in Fig. 4 (shaded areas in Fig. 5). Fig. 5 also shows that between 34.5 and 36.8°S, most of the water is advected to the deep ocean year-round.

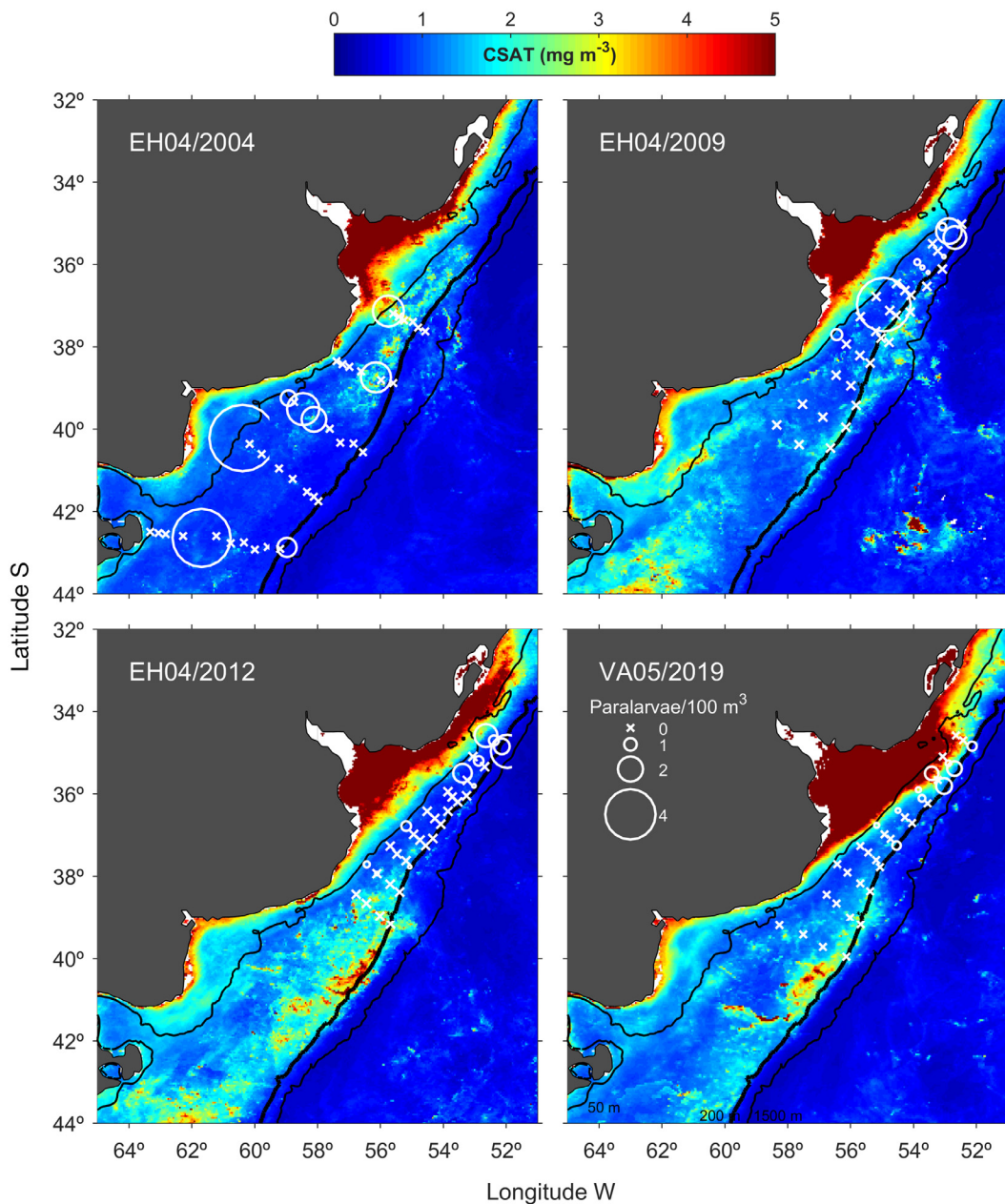


Fig. 3. Density of paralarvae during cruises EH04/2004, EH04/2009, EH04/2012 and VA05/2019. Crosses represent sampling stations without paralarvae. The size of the circles is proportional to the number of paralarvae per 100 m^3 . Colors represent the satellite chlorophyll a concentration (CSAT). Black lines are the 50, 200 (bold line), and 1500 m isobaths

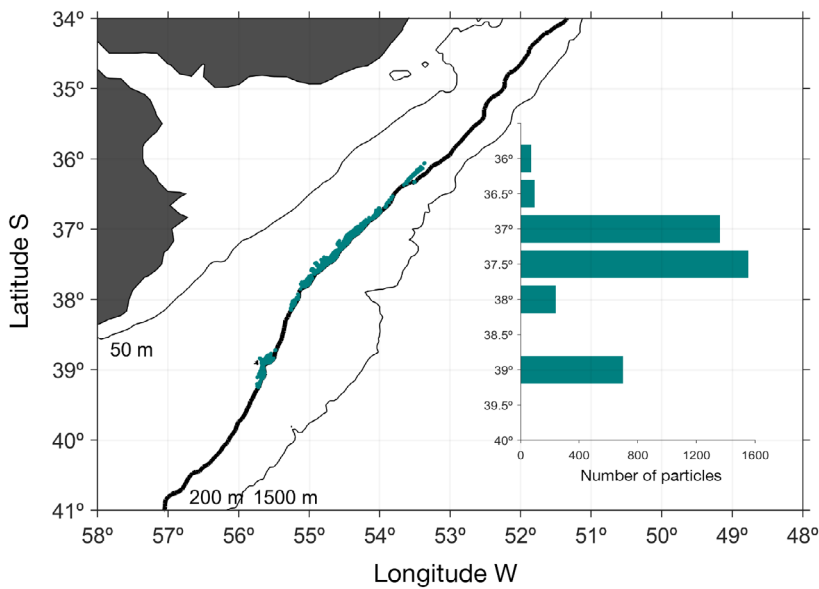


Fig. 4. Latitudinal range of entrance points to the continental shelf (green points over the bold line representing the 200 m isobath) of squid egg masses, as modeled by Torres Alberto et al. (2021). The bar graph shows the number of particles entering the shelf region at different latitudes during the modelling exercise

3.2. SST and CSAT annual cycles

The annual patterns of SST and CSAT in paralarvae habitat are shown in Fig. 6. SST shows a clear seasonal cycle, with a maximum in February and a minimum in August; CSAT also shows a seasonal pattern, with a maximum in October and a minimum

in March. Paralarvae occur in the plankton at a time when the water is cooling quickly and mean chl *a* concentrations are relatively low.

3.3. Paralarvae and water masses

The highest densities of paralarvae occurred in SW (41.5%) and MW (24.4%), in a thermohaline range of 4–20°C and 33.4–34.2 salinity (Fig. 7). Lower paralarvae densities were found in CW (7.3%) and RdPW (2.4%), with a thermohaline range of 14–19°C and <33 salinity. STW hosted 14.6% of the paralarvae, with temperatures >18°C and salinities >35.2. One station, with medium paralarvae density, had temperatures <12°C and salinities >34, denoting the influence of MW transported by the MC.

3.4. Water column vertical structure

During EH04/2004, the stations with paralarvae presented 2 main patterns: those in shallow waters (<50 m depth) showed a homogenous water column and those in deep water (>80 m) showed

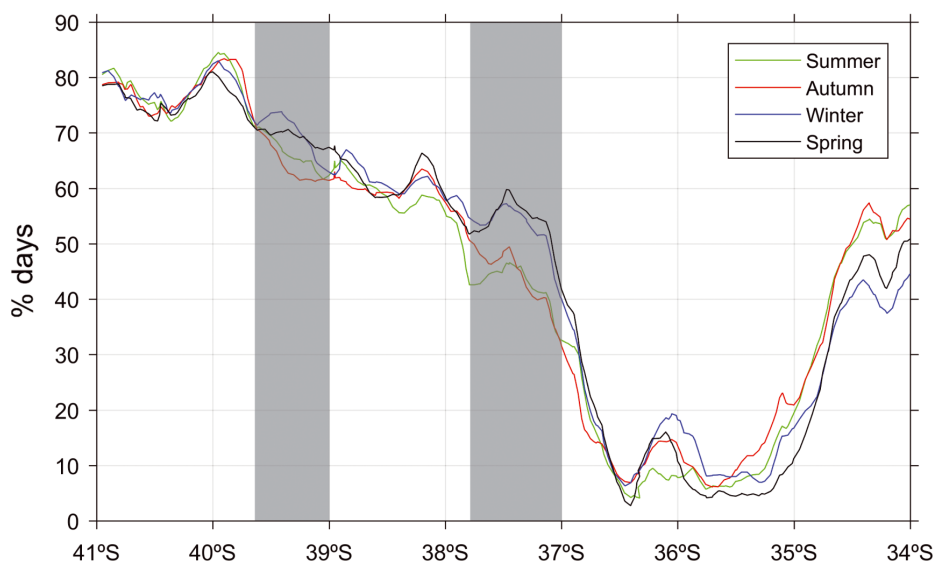


Fig. 5. Percentage of days in each season in which the zonal velocity component of the geostrophic velocities along the 200 m isobath is towards the coast (westward) between 41° and 34° S. The shaded bars show where paralarvae principally enter the continental shelf, following Fig. 4

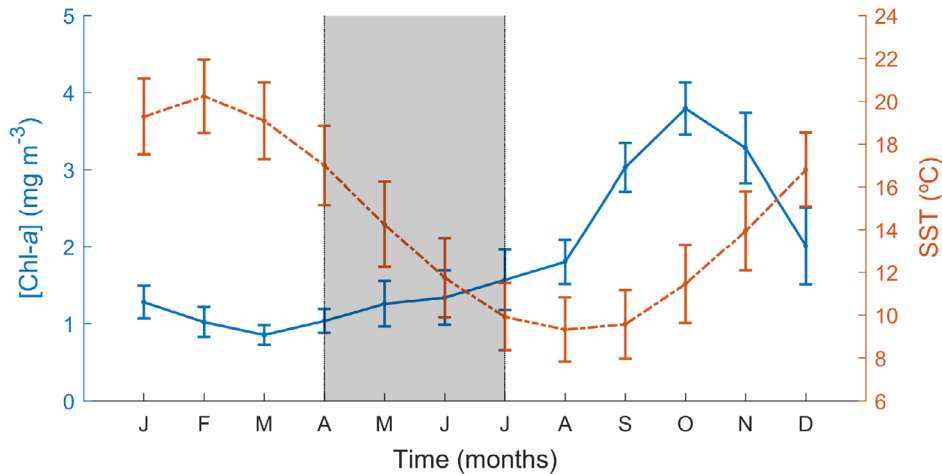


Fig. 6. Monthly average chlorophyll *a* concentration and mean SST in paralarvae habitat for the period between 2003 and 2020. The gray area (April–July) indicates when paralarvae occur in the plankton. Error bars represent SD

a sharp thermocline near 50 m. This situation is typical for the end of the summer on the Patagonian shelf: the seasonal thermocline is absent in shallower waters and persists in deeper waters at about 50 m (Piola et al. 2018). As autumn progress, the water column becomes homogeneous everywhere on the Patagonian shelf. Indeed, during EH04/2009 and EH04/2012, all the stations showed weaker stratification than during EH04/2004, possibly because these stations were sampled a month later than stations were sampled during EH04/2004. During VA05/2019, plankton samples were collected at different depths and paralarvae were caught in different strata. Results show that paralarvae were found above and below the thermocline and also at stations where the water column was homogenous (Fig. 8). The vertical distribution of paralarvae as a function of their ML sizes shows that 60% of those larger than 2mm were found between 0 and 30 m depth, while more than 70% of the paralarvae smaller than 2 mm were found between 30 and 100 m depth. The mean (\pm SD) ML at each depth layer was 2.52 ± 1.17 mm at 0–30 m and 1.79 ± 0.66 mm at 30–100 m. Only one paralarva (ML = 2.25 mm) was found at depths greater than 100 m.

4. DISCUSSION AND CONCLUSIONS

4.1. Horizontal and vertical distribution of paralarvae

Our data show the presence of early-stage paralarvae recently hatched on the shelf waters off Uruguay and northern Argentina with a size range of 1.15 to 4.60 mm ML; paralarvae are reported to hatch

at 1 mm ML (Brunetti 1990, Haimovici et al. 1998, Sakai et al. 1998). Paralarvae habitat is complex in terms of oceanographic processes, influenced by Río de la Plata discharge, the currents near the BMC, the transition between shelf water of various origins, and MC waters (Signorini et al. 2006). Paralarvae occurred in different water masses, but highest densities were found in the mixing waters of SW and MW (over 65.9%, see Fig. 7). Paralarvae were caught in patches distributed throughout the sampled area, which agrees with previous reports for autumn (Leta 1987, Brunetti & Ivanovic 1992, Haimovici et al. 1998). The SPS is by far the largest stock of *I. argentinus* (>80% of all catches in the southwest Atlantic derive from this stock). Based on the correlation between the SPS spawning season and the time when paralarvae were caught, we could expect that most of the paralarvae belonged to this stock, but it is possible that a small proportion belonged to the Bonaerensis-north Patagonian stock (BNPS), which spawns on the shelf break between 36° and 37°30' S close to the BMC (Haimovici et al. 1998) during winter (Brunetti 1988, Brunetti et al. 1998). Both stocks spawn in different areas and seasons, but their hatchlings may simultaneously converge on the same hatching area.

The vertical structure of the water column is complex in paralarvae habitat. The influence of the Río de la Plata discharge at shallower stations and the intrusion of MW at deeper stations create a highly structured habitat, with some stations showing thermal and/or salinity stratification (Fig. 8). Data obtained with a multinet allowed us to study paralarval vertical distribution. Although few individuals were caught per station, data show that paralarvae occur above and below the thermocline and not only near the surface (between 0 and 30 m) as reported by other au-

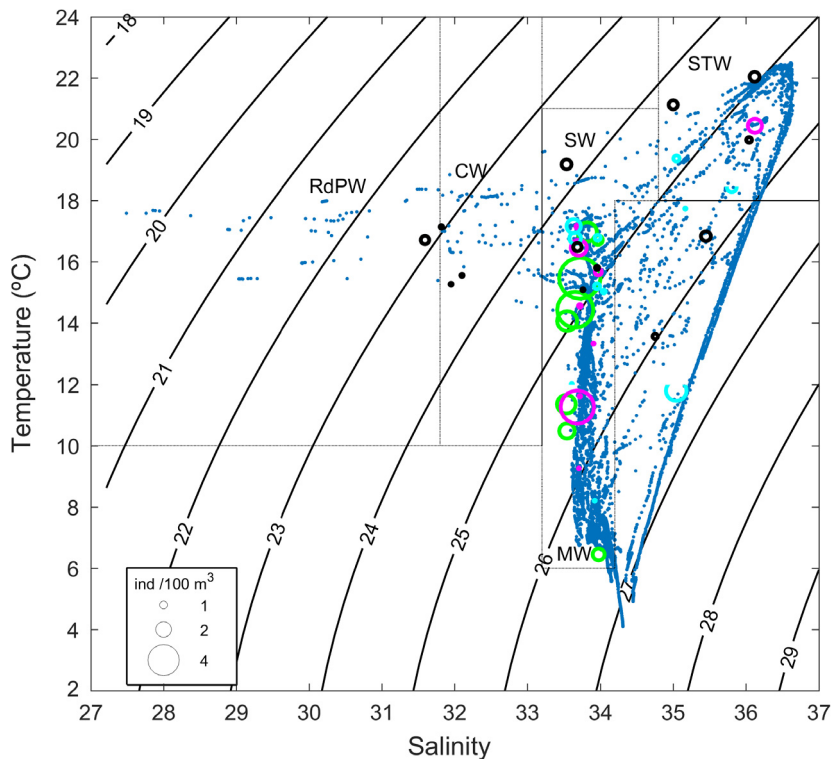


Fig. 7. Temperature–salinity diagram of *in situ* data (blue dots) obtained during the 4 research cruises. Paralarvae density (circles) is shown on the diagram according to the temperature and salinity values obtained from the CTD at each station. Circle sizes are proportional to the number of paralarvae per 100 m³, and colors correspond to the different research cruises: green, magenta, cyan and black correspond to EH04/2004, EH04/2009, EH04/2012 and VA05/2019, respectively. Letters indicate the water masses, and are delineated by light gray lines (for more detail see Section 2.1): Rio de la Plata water (RdPW), coastal water (CW), central shelf water (SW), Malvinas water (MW) and subtropical water (STW)

thors (e.g. Brunetti & Ivanovic 1992). Our finding could be the result of mixing and not only of increased paralarval swimming capability gained with development. Although ommastrephid paralarvae show no large diel vertical migrations, Yamamoto et al. (2002, 2007) showed an increase of *T. pacificus* paralarvae size with depth: the hatching sized paralarvae occurred near the surface, and as size of paralarvae increased, they gradually descended in the water column so variability in depth increased with ontogeny. The scarcity of paralarvae caught in the cruise where the stratified sampling was performed (total $n = 17$) does not allow us to make any conclusions regarding size-related depth distribution (Fig. 8).

4.2. Environmental conditions of paralarvae habitat

Many studies emphasize the importance of environmental conditions for survival of squid early stages, as they influence embryonic development as well as

paralarval and juvenile growth, and ultimately modulate cephalopod distribution and abundance (Pierce et al. 2008, Moreno et al. 2012, Villanueva et al. 2016). Environmental conditions during austral autumn do not seem to be optimal but still meet the minimum requirements for hatchling survival.

4.2.1. Temperature

Bakun & Csirke (1998) suggested that temperature determines the embryonic development rate of squid early stages: as temperature increases, the duration of embryonic development decreases, producing smaller hatchlings. Conversely, at lower temperatures, embryonic development takes longer, but resultant hatchlings are larger. Larger size could provide an advantage over potential predators, improving survival chances (Pecl et al. 2004).

Sakai et al. (1998) experimentally determined a minimum thermal threshold between 11.4 and 13.0°C for *I. argentinus* hatching; in agreement with this, Haimovici et al. (1998) reported that paralarvae of this species caught in the field occurred at temperatures between 12 and 22°C. Most of the paralarvae

analyzed in our study were caught in continental shelf and/or subantarctic waters, in a thermohaline range of 10.5 to 20.47°C and 33.5 to 34.19 salinity (Fig. 7). Monthly mean values of SST for the region show that paralarvae habitat got colder as the season progressed, but temperatures remained near or above the thermal threshold (Fig. 6). Once paralarvae have hatched, subsequent low temperatures during development could result in larger specimens (Pecl et al. 2004), improving survival during early life. These advantages could explain, at least partially, why individuals of the SPS are the largest and occur with the greatest abundance in the fishery (Arkhipkin & Laptikhovskiy 1994).

4.2.2. Chl *a* horizontal distribution and seasonal cycle

Chl *a* concentration was low during austral autumn months; however, some relatively high abundance patches occur at the shelf break front. High values

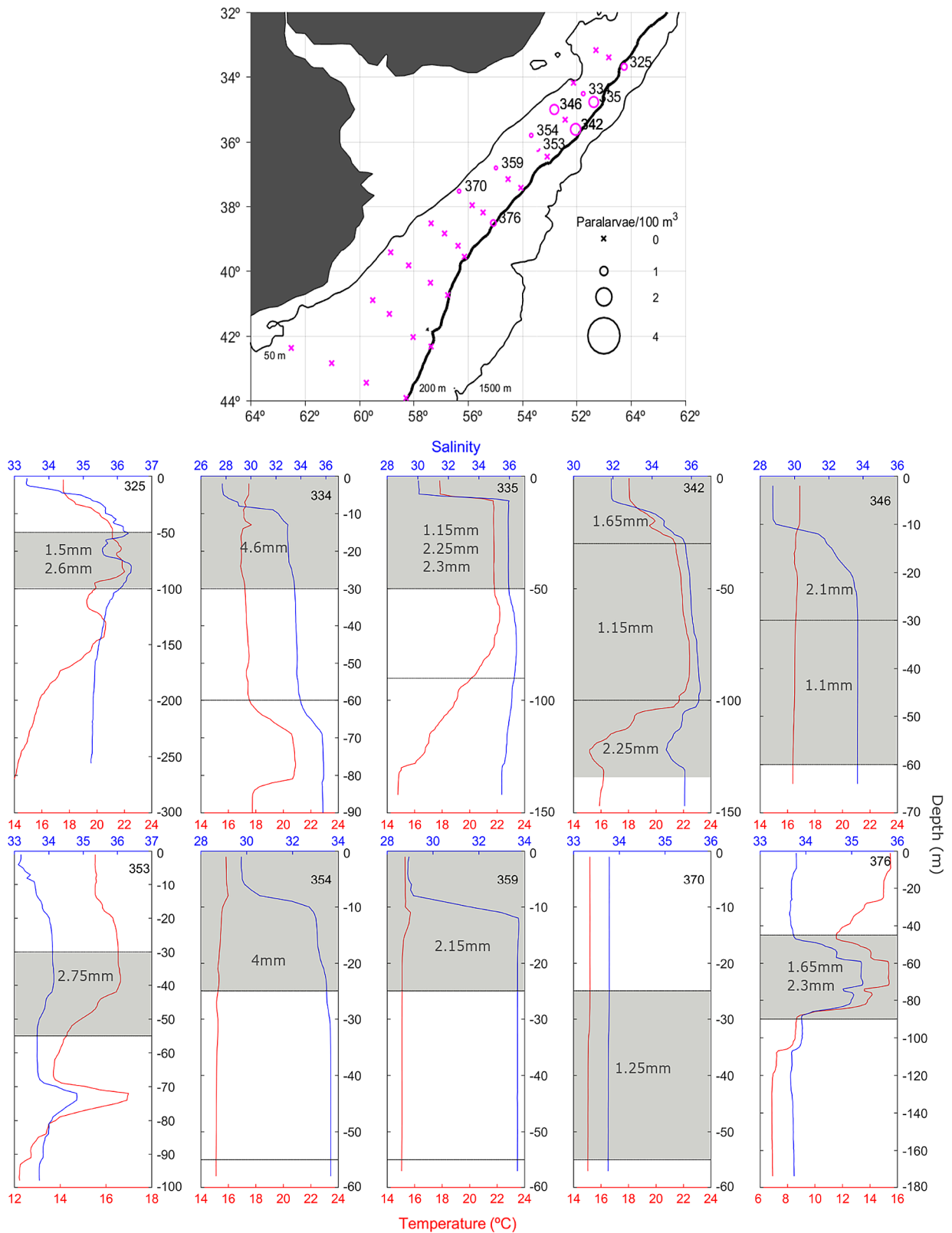


Fig. 8. Map indicating density of paralarvae caught during research cruise VA05/2019 and CTD profiles for stations where paralarvae were caught, showing temperature and salinity as a function of depth (m). The station numbers on the map correspond to those on the plotted CTD profiles. Horizontal lines in CTD profiles mark the layers sampled (multinet) at each station and the gray shading represents the layer where paralarvae were caught. Numbers in the shaded area are the mantle lengths of the paralarvae caught in that layer

associated with the Rio de la Plata plume and shallow coastal areas could be an artifact arising from turbid waters. Regardless, paralarvae occurrence does not seem related to the relatively high CSAT patches (Fig. 3).

The seasonal cycle of CSAT over the sampling region shows just one peak, occurring during spring; however, *in situ* measurements along a transect at 38°S also showed a smaller peak during autumn, after the breakdown of the thermocline (Carreto et al. 1995). Satellite data presented here (averaged over the sampled area) show a slight increase in chl *a* concentrations the autumn months, when paralarvae occur in the plankton, but it is by no means a peak (Fig. 6). Thus, paralarvae occur when chl *a* concentrations are relatively low. The link between chl *a* and paralarvae has been investigated for other ommastrephids (Van Noord & Dorval 2017, Martins et al. 2020), and no direct relationships were found. While knowledge of the diet of *I. argentinus* rhyctoteuthion is very scarce, some authors have established that Ommastrephid paralarvae are detritivores during the early stages of the life cycle (Vidal et al. 2010, Fernández-Álvarez et al. 2018). A change in feeding behavior is observed when the proboscis begins to divide and the arms are developed, between 2.5 and 4.0 mm ML (Vidal 1994); fragments of copepods and mucus were found in the digestive tracts of paralarvae between 3.7 and 5.0 mm ML. All this could indicate that chl *a* abundance is not critical at the earliest stages of paralarval development, when individuals feed on detritus and/or dissolved organic matter (DOM), and therefore it would not be expected that the life cycle be timed such that hatching happens during the phytoplankton bloom. However, at larger sizes (ML >2.5 mm, Vidal 1994), when individuals begin to feed on copepods, biological production could be an important aspect of paralarvae habitat.

4.2.3. Circulation

Another important factor in the ommastrephid life cycle is variability of the circulation of the large current systems with which the species is associated (Hatanaka et al. 1985, O'Dor 1992, Coelho et al. 1994, Bakun & Csirke 1998). Circulation over the outer continental shelf and slope could be an important control factor for early life stages to be retained on the continental shelf, improving individuals' survival

chances. Paralarvae that cannot remain on the continental shelf are exported to the oceanic realm, from where there are no mechanisms allowing their return to the shelf ecosystem; those paralarvae can be considered lost to the population (e.g. Brunetti & Rossi 1990, Torres Alberto et al. 2021).

Our results (based on the modelling exercise by Torres Alberto et al. 2021) indicate that egg masses spawned in southern Patagonia and transported northwards have the highest chances of entering the shelf ecosystem in 2 relatively narrow regions: between 37 and 37.5°S and between 39 and 39.5°S (Fig. 4). Moreover, winter and spring are the seasons when the chances that paralarvae will be exported offshore are lower. All these results are in agreement with the model-derived volume balances by Matano et al. (2014) and with the geostrophic velocities estimated from satellite altimetry (Strub et al. 2015, Ruiz Etcheverry et al. 2016). Those authors show that seasonal variation in off-shelf transport is relatively small and out of phase with variation of the southern mass flux, and that it decreases during winter and increases during summer (Matano et al. 2014). Considering the seasonal differences of percentage of days with zonal geostrophic velocities south of 37°S (Fig. 5), the onshore component is dominant in winter and spring, which translates into more chances for paralarvae to enter and remain over the continental shelf during those seasons. Northward of this gateway to the shelf ecosystem, the region between 34.5 and 36.8°S constitutes a kind of funnel, where most of the water is strongly advected to the deep ocean, in agreement with the results by Torres Alberto et al. (2021).

Paralarvae abundance distribution for each research cruise (Figs. 2 & 3) is, in general, consistent with previous modelling work (Torres Alberto et al. 2021). Most paralarvae occur over the shelf between the latitude range of entrance or north, in accord with the mean northward circulation pattern forced by winds during the winter months (Piola et al. 1997, 2018). However, although most paralarvae distribution data collected in 2004 were consistent with this overall pattern, there was a patch of high abundance at 42°S, probably due to interannual variability in surface circulation.

4.3. Synchronization of the life cycle

Despite the importance of paralarval ecology in understanding stock fluctuations of commercial species, direct studies investigating the response of

paralarvae to oceanographic variation are scarce (Boletzky 2003, Roura et al. 2016), mainly due to the low number of paralarvae usually captured in zooplankton surveys (Vecchione 1987, Olmos Pérez et al. 2017). SPS recruitment variability is mainly controlled by oceanographic fluctuations related to the northward transport of egg masses, their retention on the continental shelf, and the attainment of the thermal habitat required for egg hatching (Torres Alberto et al. 2021). Once in the 'right place', paralarvae need to feed, and in general terms, it is expected that synchronization of spawning time with planktonic food peaks would improve their chances of survival (Olmos Pérez et al. 2017). In the case of the SPS, however, the seasonal pattern of chl *a* concentrations shows that paralarvae occur in the plankton when biological production is relatively low (though as noted in Section 4.2.2, paralarvae may feed on detritus and/or DOM). The food supply at this time must be sufficient for the survival of paralarvae of this stock, which sustains one of the largest squid fisheries in the world, but the lack of synchronization between the SPS life cycle and peak food availability is intriguing. Why not spawn so that paralarvae hatch near the peak of plankton production on their nursery grounds? Paralarvae occur in the plankton when offshore transport is at a minimum in the sampled area (winter–spring in Fig. 5), decreasing their chances of being exported to the oceanic realm. Because such exportation is the main cause of recruitment failure (Brunetti & Ivanovic 1992, Bakun & Csirke 1998), minimizing paralarvae drift to the deep ocean is likely imperative for this stock. If this is the case, the risk of being exported offshore is a more important factor than starvation for recruitment success.

A second hypothesis, focused on adult females instead of paralarvae, can be proposed. The squid life cycle is a morphological cycle superimposed over a spatial cycle (Sinclair 1988). The cycle seems to be synchronized in such a way that paralarvae drift and then juveniles migrate, grow and develop to reach their feeding grounds in southern Patagonia as adults during the abundance peak of the amphipod *Themisto gaudichaudii* between 49 and 52° S (summer–early autumn) (Sabatini & Colombo 2001). Female squid feed heavily on this crustacean (Ivanovic & Brunetti 1994, Ivanovic 2000, 2010) just before crossing the shelf to spawn near the shelf break (Brunetti 1988, Brunetti et al. 1998). Ommastrephid squids take energy for egg production directly from food, rather than from reserves (i.e. income breeding, Rocha et al. 2001, Rosa et al. 2005). The high lipid

content of the amphipods (e.g. Mayzaud & Boutoute 2015) would constitute a rich source of energy to maximize fecundity and/or egg quality.

These hypotheses are not mutually exclusive. The SPS life cycle results in both a lower exportation risk for paralarvae and the exploitation of a highly energetic food source by females just before spawning.

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