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Water density pathways for shelf/slope migrations of squid *Illex argentinus* in the Southwest Atlantic

Alexander I. Arkhipkin*, Michaël Gras, Alex Blake

Fisheries Department, Falkland Islands Government, P.O. Box 598, Stanley, FIQQ 1ZZ, Falkland Islands

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ABSTRACT

Argentine shortfin squid *Illex argentinus* (Ommastrephidae) is one of the most abundant cephalopods in the Southwest Atlantic, with total annual catch exceeding 1 mln t in some years. During its annual life cycle, *I. argentinus* perform long distance migrations, from their subtropical spawning grounds in Uruguay and southern Brazil to temperate feeding grounds on the Patagonian Shelf and back. Oceanography and squid distribution were studied during a research survey carried out in the south-eastern part of the Patagonian Shelf to reveal environmental cues that determine pathways of shelf to continental slope pre-spawning migrations. It was found that the outflows of less dense Patagonian Shelf Waters (PSW) over the slope may act as proxies determining the locations of *I. argentinus* migrations from the shelf to the slope. During maturation *I. argentinus* did not significantly change their buoyancy with females becoming slightly more buoyant with depth. Subsequent movement of mature *I. argentinus* to denser Sub-Antarctic Superficial waters (SASW) located at deeper depths (600–700 m) enable them to approach near-neutral buoyancy and therefore facilitate the distant pre-spawning migrations.

1. Introduction

Nektonic squid of the family Ommastrephidae are highly migratory animals. During their short (mostly annual) life cycle, these squid are able to move thousands of kilometres between their spawning and feeding grounds often located in different temperate zones of the world's oceans (Arkhipkin, 2013). One of the typical representatives of these migrants is the Argentine short-finned squid *Illex argentinus*. This squid is one of the most abundant cephalopods in the world, inhabiting shelf and slope waters between 22°S and 54°S of the Southwest Atlantic (Jereb and Roper, 2010). *I. argentinus* is also an important commercial resource with total annual catch attaining 1 mln t in some years (Rodhouse et al., 2013).

Population structure of *I. argentinus* is complicated and consists of several spatial and temporal distinct populations/stocks (Hatanaka, 1986). During their annual life cycle, squid of the winter-spawning South Patagonian Stock undertake the longest ontogenetic migration among all *I. argentinus* stocks (Arkhipkin, 2013). They migrate from their supposed subtropical spawning grounds over the continental shelf of southern Brazil and Uruguay in August–September (Haimovici et al., 1998; Leta, 1987) and arrive to their feeding grounds on the Patagonian Shelf in February (Brunetti et al., 1998; Arkhipkin, 2013). In March, squid reach the southernmost periphery of their species range at 54°S, feeding upon abundant planktonic resources (Sabatini and Alvarez Colombo, 2001). Squid start to mature in April, and then begin to shift to the shelf edge off Argentina and the Falkland Islands. In May–June, they descend to 600–800 m depths and migrate along the continental slope with the Falkland Current back to their spawning grounds (Hatanaka, 1988; Arkhipkin, 1993).

I. argentinus, like all other muscular ommastrephid squid, are slightly heavier than water and therefore have slight negative buoyancy (Wells and O'Dor, 1991). During their active migrations, squid utilise a physiologically effective climb-and-glide cycle consisting of alternating jet propulsion expels during the climb and fin movements and spread to facilitate the downward glide (O'Dor, 1988). The buoyancy of *I. argentinus* adults has not yet been estimated despite its importance in assessing the efficacy and reasons for their deepwater pre-spawning migrations along the slope rather than shallow water migrations on the shelf.

Interestingly, migrations of the South Patagonian Stock of *I. argentinus* from the shelf to deep waters take place in a relatively small area of the continental slope between 50°S and 47°S, as revealed by the movements of the squid fishing fleet (trawlers and jiggers) in the Argentinean EEZ, Falkland Islands Conservation

* Corresponding author.
E-mail address: aarkhipkin@fisheries.gov.fk (A.I. Arkhipkin).

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Zones and high seas in May–June (Arkhipkin, 1993; Rodhouse et al., 2013). This area is characterized by highly dynamic oceanography (Zyrjanov and Severov, 1979), with the warm outflow of less dense shelf waters coming from the northwest and cold meander of denser waters of the Falkland Current spreading onto the shelf from the southeast. Until now, the environmental cues that might determine the routes of pre-spawning migrations of squid from the shelf to slope are unknown.

The Fisheries Department of the Falkland Islands (FIFD) closely monitored the shelf/slope pre-spawning migrations of *I. argentinus* by analysing the movement and catches of a numerous licensed jigging fleet in the eastern part of the Patagonian Shelf and Slope in April and May 2014. Once the squid started to disappear from catches on the shelf and move to deeper waters where they became inaccessible for the jigging fleet, the FIFD carried out an oceanographic and biological survey in order to reveal environmental factors influencing the distribution and movement of squid during their pre-spawning migrations. Additionally, the buoyancy of different sexes and maturity stages of *I. argentinus* was investigated for comparison with ambient water density as one of the potential oceanographic cues to identify the migratory habitat and depth.

2. Material and methods

2.1. Sample collection

The timing and area of the survey (Fig. 1) was determined by an analysis of the distribution and amount of catch of the licensed jigging fleet that fished on the shelf and shelf edge of the eastern part of the Patagonian Shelf in April–May 2014. It is a license requirement of the FIFD that any vessel fishing within the Falkland Interim Conservation and Management Zone (FICZ) and Falkland Outer Conservation and Management Zone (FOCZ) send daily information about their fishing activities including the geographical location, amount and composition of catch. The jigging fleet followed the pre-spawning movement of *I. argentinus* aggregations on the shelf of FICZ/FOCZ that shifted eastwards and northwards to the continental slope at the end of April (Fig. 2A and B). Near the shelf edge, squid schools moved to deeper waters to carry on their pre-spawning migrations along the Patagonian slope, and became inaccessible to the jigging fleet that usually fish for squid no deeper than 350 m water depth (Rodhouse et al., 2013). In 2014, the deepwater migrations were observed in the first half of May, with subsequent disappearance of the jigging fleet from that area (Fig. 2C and D). The survey comprised of a total of 49 complex oceanographic and biological stations was carried out exactly at that time (between 3 and 17 May 2014) in the north-eastern part of the Patagonian Shelf and continental slope (Fig. 1).

The CTD profiler Seabird SBE 25 was deployed to collect profiles of temperature and salinity immediately prior to or straight after each trawl. The data were collected from the surface to approximately 5 m above the bottom with the deployment speed of 1 m/sec. Temperature, conductivity and pressure data were collected at a rate of 8 records per second. Temperature was recorded directly from the temperature sensor, whereas salinity and density (as σ-t) were calculated using SeaSoft software. Vertical transects and spatial surfaces of temperature, salinity and density were obtained using Ocean Data View version 4.5.4 (Schlitzer, 2013). All oceanographic sensors were calibrated once a year in the premises of Seabird Inc (Bellevue, WA, USA).

Trawl hauls were performed near the bottom using an Engel semi-pelagic trawl (40.2 m headline and a 38.7 m footrope) equipped with rockhopper gear and Super-V trawl doors. Net monitor sensors have been attached to the upper panel of the trawl to monitor the vertical opening over the bottom (7–12 m). Mesh size in the trawl codend was 95 mm and trawling speed ranged between 4 and 4.5 knots (7.4–8.3 km/hr). Trawl duration was between 1 and 2 h fishing at the bottom depending on bottom condition during trawling.

Catch was sorted by species and weighed using an electronic marine adjusted balance *Marel* (Gardabaer, Iceland). A random sample of 100 specimens of *I. argentinus* (or total catch if less than that) was taken from each trawl catch for biological analysis. The dorsal mantle length was measured to the nearest 0.5 cm using electronic measuring boards *Fishmeter 100* and *Fishmeter 50* (Scantrol, Bergen, Norway). Sex and maturity stage were identified using a six-stage scale by Lipinski (1979). Length frequency histograms were made for each sex separately for two regions, north and south of 48°S. A total of 374 females and 394 males were sampled in the northern area, whereas 927 females and 923 males were sampled in the southern area. Sex-ratios were tested using χ^2 tests.

2.2. Data independence

Spatial auto–correlations of CPUE (catch per unit effort, in kgs per hour) and oceanographic data (water density, in g/cm^3; see Section 2.3 for more details about the choice of variables) were explored using geostatistical methods (Rivoirard et al., 2000; Zuur et al., 2007; Zuur et al., 2009). Geographical coordinates collected at each station of the research cruise in World Geodetic System of 1984 (WGS84) were first projected in World Mercator projection using the proj4 package (Urbanek, 2012) of R statistical software (R Core Team, 2014). The projected coordinates and function “variogram” of R package gstat (Pebesma, 2004) were then used to plot the experimental variograms ($\hat{\gamma}(h)$) of water density at 50 m deep and log transformed non null CPUE (see Section 2.3 for more details about removal of null values) using the following formula

$$\hat{\gamma}(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z(x_i + h) - z(x_i)]^2$$

where $N(h)$ is the number of pair points separated by the vector distance h in the summation, $z(x_i)$ is the value of the response variable at point x_i (i.e., sea water density at 50 m or log transformed non null CPUE). The spatial correlation was found for water density data. According to the shape of the curve observed, the exponential model (Rivoirard et al., 2000; Zuur et al., 2007, 2009) was fitted as:

$$\hat{\gamma}(h) = C\left[1 - \exp\frac{(-|h|)}{a}\right]$$

where C is the sill (limit of the variogram, i.e., variance of the dataset) and a the range (distance when the semi-variance reaches 95% of the sill, i.e. distance where data are considered independent).

2.3. Modelling water density and I. argentinus CPUE

Water temperatures, salinities and densities at the sea surface, 50, 100, 150, 200 m depths as well as at sea bottom were used as independent variables in linear and mixed effects models to explain the CPUE considered as the dependent variable. This exploration revealed that *I. argentinus* abundance was significantly correlated to the sea water density measured at 50 m depth using the depth class of the station as a random variable. Depth classes of stations were defined every 100 m. However, one trawl performed at 148 m was included in the first class and the 2 deepest classes were combined as only 2 trawls were undertaken between 550 and 612 m. According to Zuur et al. (2009), the best way of processing such data is to use a mixed effect model for nested data where *I. argentinus* abundance is the dependent variable explained by water density at 50 m and using depth class as a random variable. Both random