

SUMMER DISTRIBUTION, ABUNDANCE AND POPULATION STRUCTURE OF *ILLEX ARGENTINUS* ON THE ARGENTINE SHELF IN RELATION TO ENVIRONMENTAL FEATURES

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The distribution, abundance and population structure of *Illex argentinus* in relation to oceanographic conditions during summer 1996 were analysed following a research cruise to the Argentine shelf (39°–51°30'S). Squid were distributed over the whole area, but the main concentrations were on the intermediate and outer Patagonian shelf (44°30'–47°30'S), where there was a thermal front (12–15°C). Three squid groups were detected through study of the distributional area, size, maturity stage, age and hatching month. North of 41°S, there were immature individuals of 14–21 cm mantle length (*ML*) that had hatched mostly in June. Small mature, spawning and spent squid (males 14–22 cm *ML*, females 18–26 cm *ML*) were found on the inner and intermediate shelf between 40°30' and 46°30'S. They had hatched from January to April, with a clear peak in March. South of 45°S, males of 17–25 cm *ML* and females of 17–29 cm *ML* were found over the intermediate and outer shelf; most males were mature whereas the majority of the females were immature. They had hatched from May to July, with a peak in June. The relationship between statolith increment and size showed that the growth rates of the later-hatched individuals were faster than those of individuals hatched earlier. The squid preyed almost exclusively on zooplankton (87%), mostly the hyperiid amphipod *Themisto gaudichaudii* (79%).

During summer 1996 the Japan Marine Fishery Resources Research Centre (JAMARC) and the National Institute for Fisheries Research and Development of Argentina (INIDEP) conducted a joint survey in Argentine waters, the main aim being to obtain information on the distribution, migration and population structure of the Argentine short-finned squid *Illex argentinus*.

Illex argentinus is common over the Argentine shelf from 34 to 52°S, where it sustains one of the most important fisheries of the South-West Atlantic (Castellanos 1964, Otero *et al.* 1981, Brunetti 1990a). In summer, concentrations are densest over the Patagonian shelf (43–55°S), where spawning concentrations of small squid (14–25 cm mantle length *ML*) are encountered in the north (43–46°S) and pre-reproductive concentrations of larger animals (17–29 cm *ML*) between 46 and 51°S. These groups are known traditionally as the Summer Spawning Stock (SSS) and the South Patagonic Stock (SPS) respectively (Brunetti 1988, Brunetti and Pérez Comas 1989a). On the Bonaerensis-North Patagonian shelf (34–43°S), there are scattered concentrations of immature animals, identified as the Bonaerensis-North Patagonic Stock (BNPS, Brunetti 1988, Brunetti and Pérez Comas 1989b).

Information on the summer distribution, abundance and stock structure in relation to concurrent oceanographic

conditions obtained during the cruise is presented in this paper.

MATERIAL AND METHODS

A research cruise was carried out by the JAMARC R.V. *Shinko Maru N° 3* in waters of the Argentine shelf, between 39° and 51°30'S, during summer 1996. The cruise programme consisted of two legs, conducted from 2 to 20 January (Stations 1–30) and from 22 January to 26 February (Stations 31–61). Oceanographic observations (water temperature, conductivity and salinity) were made to a depth of 450 m at 61 stations using CTD, and squid were jigged 48 times. The jigging gear consisted of 25 single and 32 double machines. Stations were placed along nine transects (I–IX) to facilitate analysis of the results in relation to latitude and depth (Fig. 1).

Abundance is expressed as catch per unit effort (*cpue*), calculated as

$$cpue = \text{catch (kg)} / [\text{hours} * \text{line}]$$

In all, 4 809 squid were sampled (up to 150 individuals at each station) for mantle length (*ML*, mm), sex and maturity stage (eight-point scale, Brunetti 1990b).

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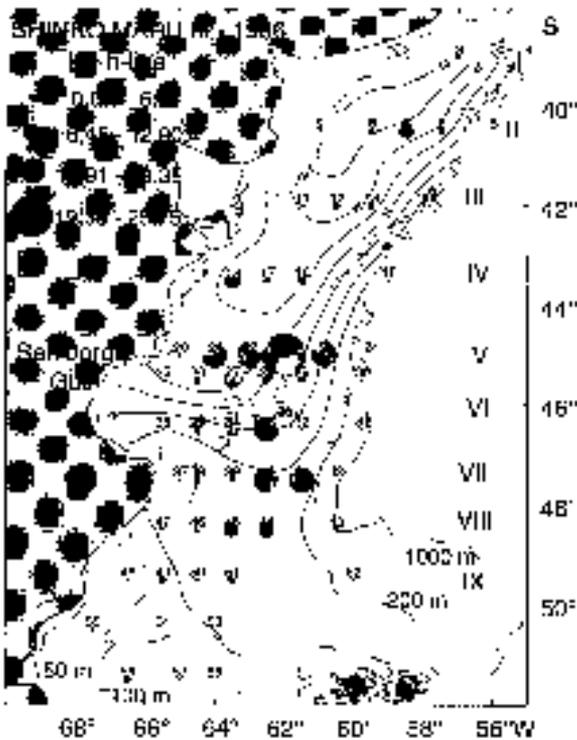


Fig. 1: Location of stations (1–61) and transects (I–IX), abundance of *Illex argentinus* and surface temperature (°C) in the surveyed area

The stomach contents of 280 animals caught at 31 fishing stations were examined under a binocular microscope, and food items were identified to species level where possible.

The statoliths of 648 animals were processed for age determination studies. They were extracted from the first 20 squid in each sample and stored in liquid paraffin. To process them, they were first immersed in 96% ethanol to dissolve the paraffin and then in 7% sodium hypochlorite to remove the organic membrane that remained attached to the statolith surface. Then they were washed in distilled water and placed on glass slides to dry. Once dry, they were dipped in a fresh drop of "Protexx", with the convex surface uppermost, then ground by hand using different grades of waterproof sandpaper. Throughout the grinding process, progress was continually checked by microscopic examination until the nucleus could be seen clearly. Before counting the increments, a drop of xylene was placed on each statolith to help clear it. Increments were counted on a Sony colour monitor

image produced by a Nikon Labophot-2 light microscope, equipped with a video camera, at a magnification of 400×. The increments were counted according to the method described by Morris and Aldrich (1985) along the main axis of statolith growth, beginning from the first visible ring outside the nucleus and continuing to the dorsal edge of the dome.

Growth rates for each age-class of 10 days (m_i) represented within each hatching month and a mean growth rate for the month (m) were estimated as follows:

$$m_i = (ML_{t_2} - ML_{t_1}) / (t_2 - t_1)$$

$$m = \sum m_i / N$$

where ML is the mean mantle length at age t ; $t_2 - t_1 = 10$, and N is the number of 10-day age-classes within each month.

The age-size data of wild paralarvae ($n = 70$) and juveniles ($n = 68$) hatched during the months January–March of previous years were added to fit a growth model for the summer-hatched group. The following logistic model, fitted by Newton's method (Dennis and Schnabel 1983), was applied:

$$ML_x = ML_\infty / (1 + \exp[-G(x - x_0)])$$

where G is the instantaneous growth rate at the origin ($ML = 0$; Campana and Jones 1992) and x_0 is the age at the inflection point of the curve and the age of maximum absolute growth rate.

The absolute growth rate at age x (g_x) was calculated from:

$$g_x = G ML_x (ML_\infty - ML_x) / ML_\infty$$

RESULTS AND DISCUSSION

Oceanographic conditions

The continental shelf of the South-West Atlantic between 35 and 56°S is one of the largest in the world. It covers 2×10^6 km² and extends along 2 400 km of coastline between the La Plata River and Cape Horn (Mouzo 1981). Three main water masses, mostly of subantarctic origin, are encountered on the continental shelf and slope: Slope/Malvinas waters, with high salinity and low temperature; midshelf waters, characterized by a minimum in salinity; and coastal waters, defined as a vertically homogeneous water column with low or high salinity depending on the salt budget attributable to run-off or the influence of the coastal gulf concentration basis (Scasso and Piola 1988, Rivas

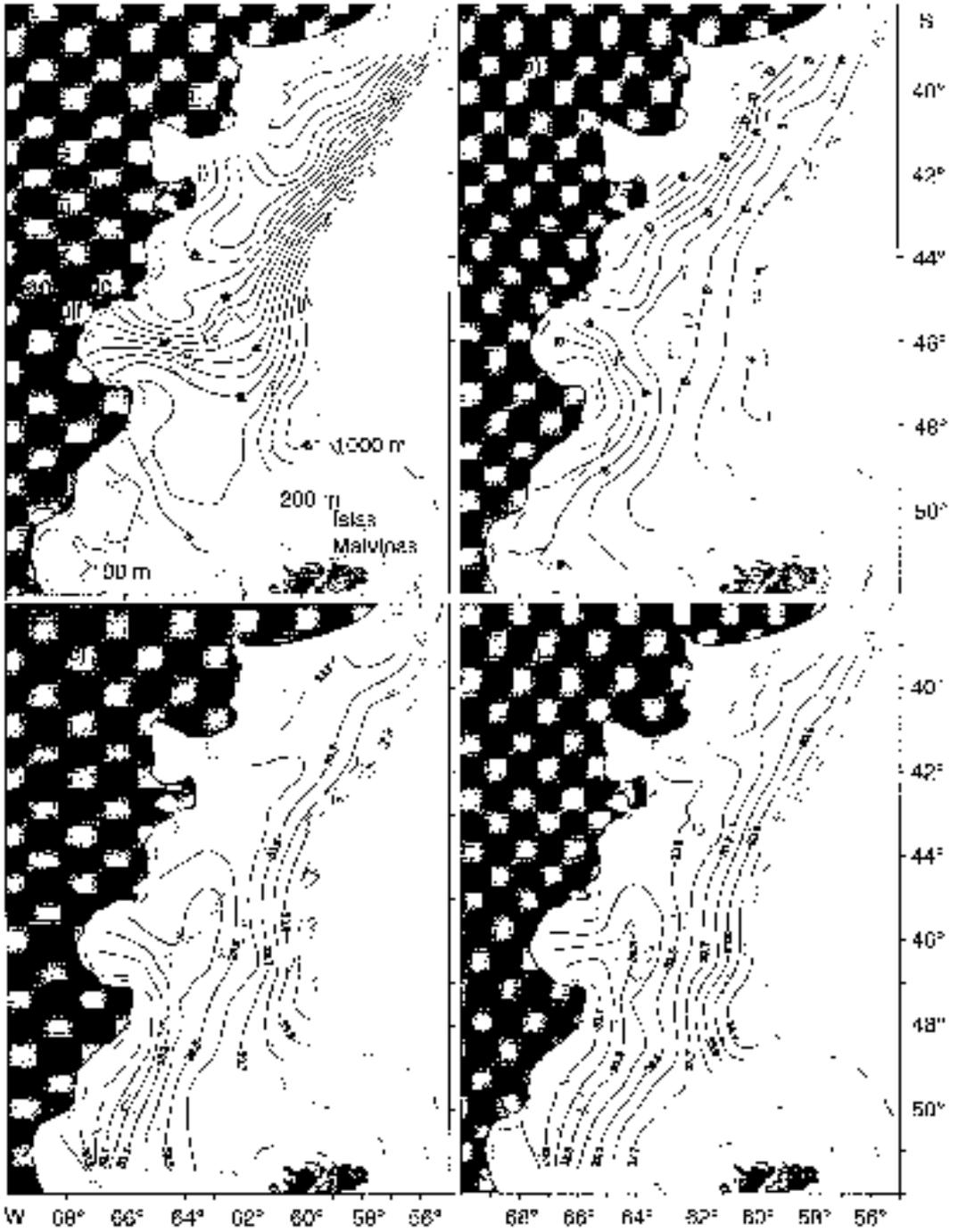


Fig. 2: Distribution of (a) surface and (b) bottom temperature ($^{\circ}\text{C}$) and (c) surface and (d) bottom salinity ($\times 10^{-3}$) in the surveyed area

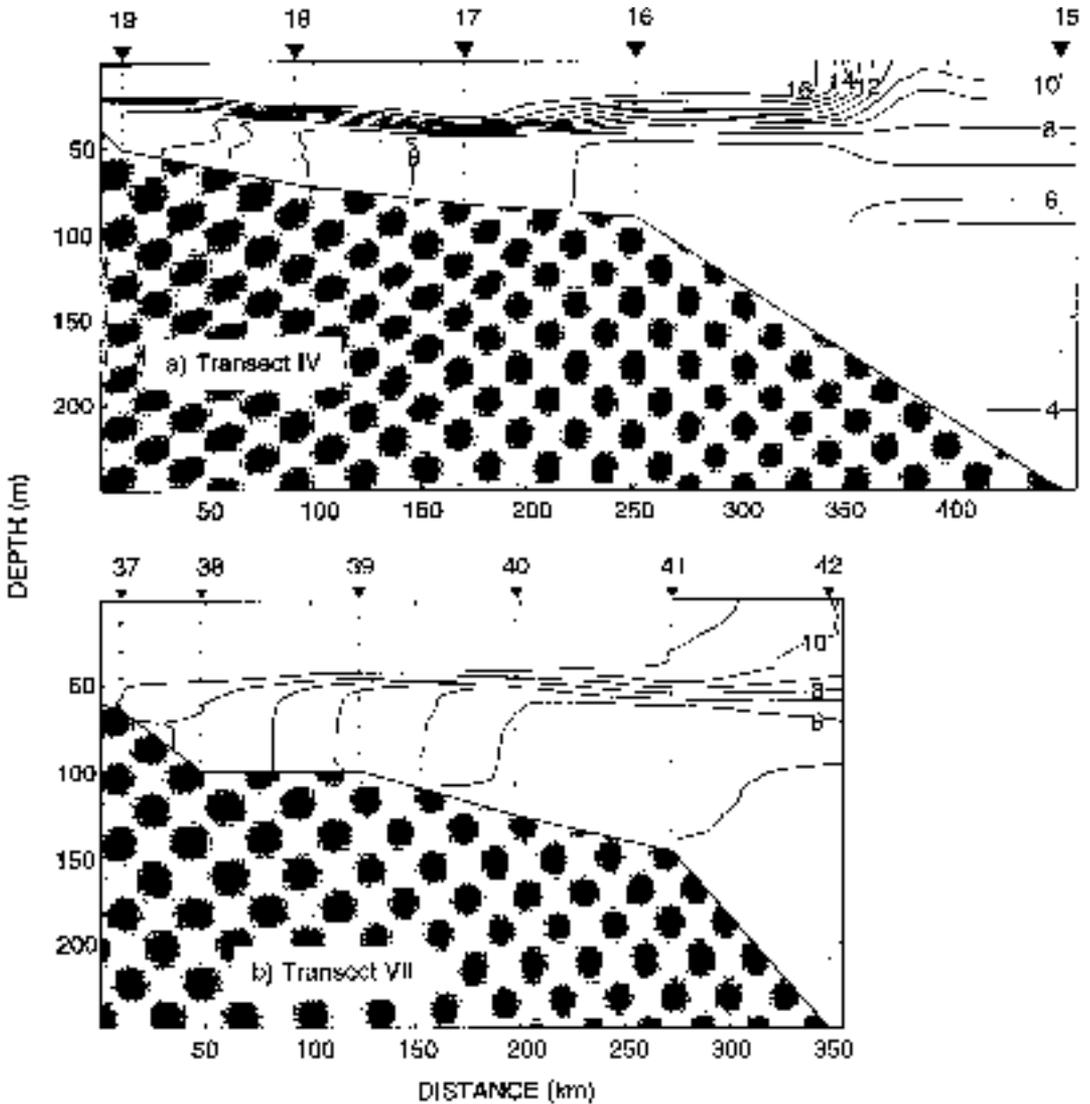


Fig. 3: Vertical distribution of temperature ($^{\circ}\text{C}$) along (a) Transect IV (Bonaerensis-North Patagonian Shelf System) and (b) Transect VII (Southern Patagonian Shelf System)

and Beier 1990, Guerrero and Piola 1997).

The sea surface temperature in the survey area revealed two main thermal systems (Fig. 2a), a northern one ($39\text{--}45^{\circ}\text{S}$), situated on the Bonaerensis-North Patagonian shelf, characterized by a warm surface core with temperatures $>15^{\circ}\text{C}$ as a result of the differential heating of the sun, and a southern, cooler one ($47\text{--}52^{\circ}\text{S}$), with surface temperatures $<12^{\circ}\text{C}$, over the

South Patagonian shelf. A wide frontal zone ($120\text{--}150\text{ km}$), with a well-defined horizontal gradient of temperature ($12\text{--}15^{\circ}\text{C}$), represented the boundary between the two systems. This thermal front extended across the shelf from the San Jorge Gulf out to the 100 m isobath and then to the north between the 100- and 200-m isobaths. Bottom temperatures (Fig. 2b) were characterized by a decreasing gradient from the shall-

Table I: Location, surface temperature, surface-bottom temperature difference, thermocline depth, mean bottom depth and mean wind speed (January–February mean values from statistical wind speed at coastal meteorological stations corresponding to the latitude of each transect) for the nine transects

Transect	Latitude (S)	Surface temperature (°C)	Surface-bottom temperature difference (°C)	Thermocline depth (m)	Mean bottom depth (m)	Mean wind speed (knots, 1971–1980)
I	39°00′	19.0	11.0	25	65	25.01
II	40°20′	18.0	11.5	25	65	18.94
III	42°00′	17.0	9.0	25	75	18.94
IV	43°00′	16.0	8.0	30	70	25.72
V	45°00′	15.0	8.0	40	105	31.02
VI	46°00′	12.5	6.0	45	100	32.07
VII	47°20′	11.0	4.0	45	120	30.71
VIII	48°30′	11.0	4.0	45	115	30.71
IX	49°30′	11.0	4.5	45	120	38.64

low warmer waters near the coast to the deep cooler waters off the continental shelf, where the influence of water from the Malvinas Current was clear.

The surface and bottom salinity distributions (Fig. 2c, d) showed N-S gradients where the sea bed was shallower than 100 m, and E-W gradients in deeper water. The first area, between the coast and the 100 m isobath, was associated with the northern system as defined by surface temperature. There, salinity values ranged from 33.4×10^{-3} in the north of the San Jorge Gulf to 33.7×10^{-3} at 39°S (33.8×10^{-3} at the bottom). A lateral mixing between shelf and coastal waters accounted for the gradient regime observed over the South Patagonian shelf. The salinity ranged from values as low as 32.8×10^{-3} (33.0×10^{-3} at the bottom) at the most south-westerly station to values $>34.0 \times 10^{-3}$ (34.1×10^{-3} at the bottom) at the south-easterly station.

There was a two-layer vertical stratification along all nine transects of the surveyed area. Transects I through IV corresponded to the Bonaerensis-North Patagonian Shelf System (<100 m deep), whereas Transects VI–IX (>100 m deep) were located in the South Patagonian Shelf System. Transects IV and VII have been chosen to characterize each system (Fig. 3). Transect V is defined as the zone of transition. The typical summer pattern expected for the area, i.e. a surface warm mixed layer over a cool bottom advective layer, was observed (JAMARC 1996). The surface mixed layer results from heat exchange with the atmosphere (spring-summer warming) and down-mixing by wind stress. The bottom layer, isolated from the atmosphere, is maintained by advection of water from the south and lateral mixing with Malvinas water along the slope and with coastal water at its western edge.

In order to explain changes in physical conditions and their relation to forcing between the two systems, three oceanographic parameters were estimated for each transect: mean temperature of the mixed layer,

temperature difference between surface and bottom, and mean depth of the thermocline (Table I). These parameters were compared against mean bottom depth and mean statistical wind speed from the nearest coastal station (period 1971–1980; Servicio Meteorológico Nacional 1982). Some general trends could be recognized as latitude increased:

- (i) a decrease in sea surface temperature;
- (ii) a decrease in the surface-bottom temperature difference;
- (iii) an increase of the bottom depth;
- (iv) a deepening of the thermocline;
- (v) an increase in wind speed.

The increased thickness of the mixed layer and the deepening of the thermocline over the South Patagonian shelf resulted from an increase in the strength of the mean wind field and, to a lesser extent, from the increase in bottom depth.

Distribution and population structure

Illex argentinus were captured at 39 jigging stations over the shelf, from 39° to 51°30′S and 50 to 150 m deep (Fig. 1). A wide distribution of *cpue* (0.01 – 25.75 kg·h·line⁻¹) was observed. Largest catch rates were limited to the intermediate and outer shelf between 44°30′ and 47°30′S, in the thermal front (12–15°C).

The length frequency distributions by sex and maturity stage (Fig. 4) and the age and hatching months of the squid sampled (Fig. 5) show that at least three squid groups were present in the area surveyed.

Squid were scarce between 39° and 40°30′S (<12.90 kg·h·line⁻¹). Most were small and immature (14–21 cm *ML*), with no appreciable difference in size distribution between the sexes. They were 192–218

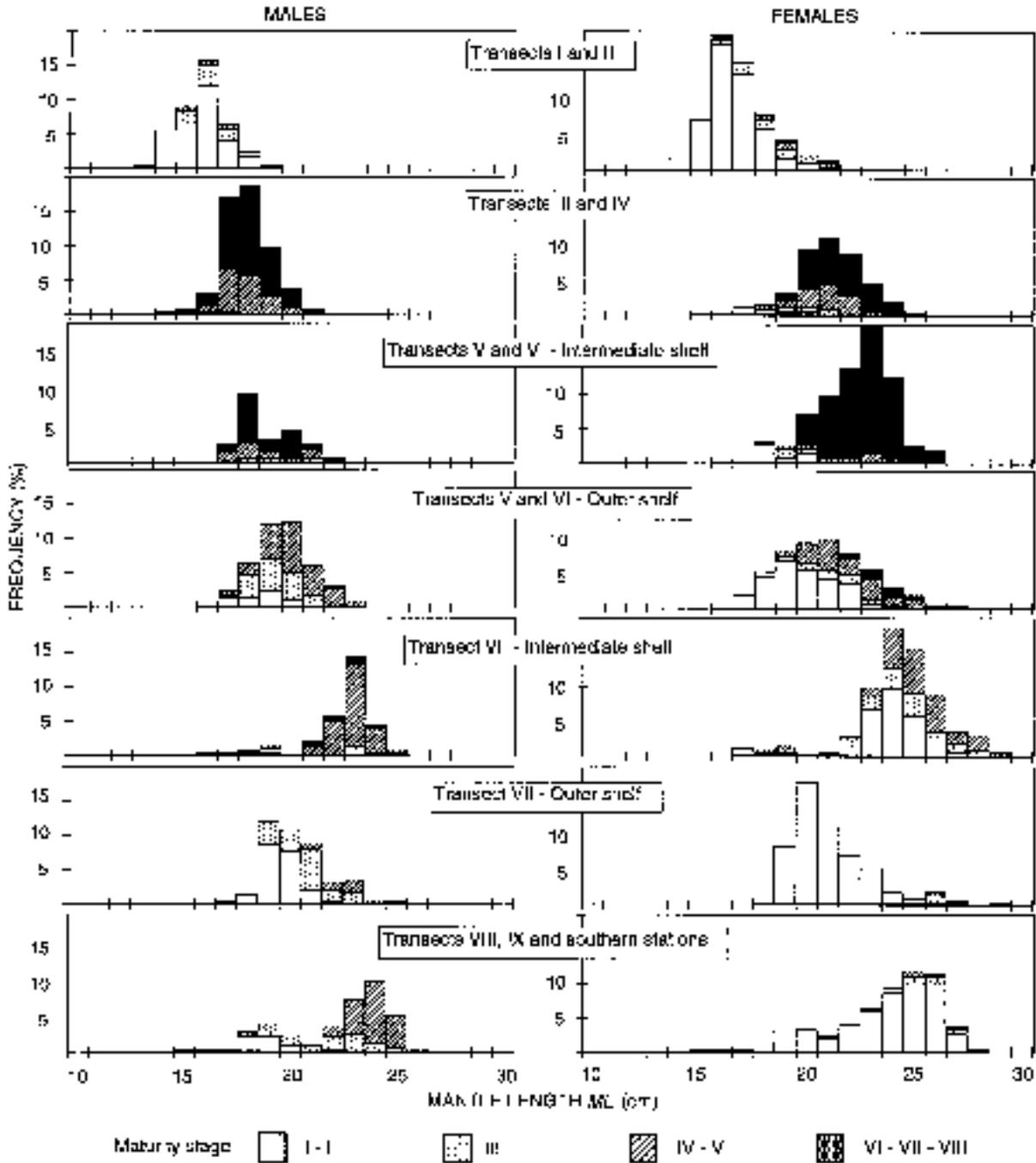


Fig. 4: Length frequency distribution and maturity stages by size of both sexes of squid sampled by transect (I-IX)

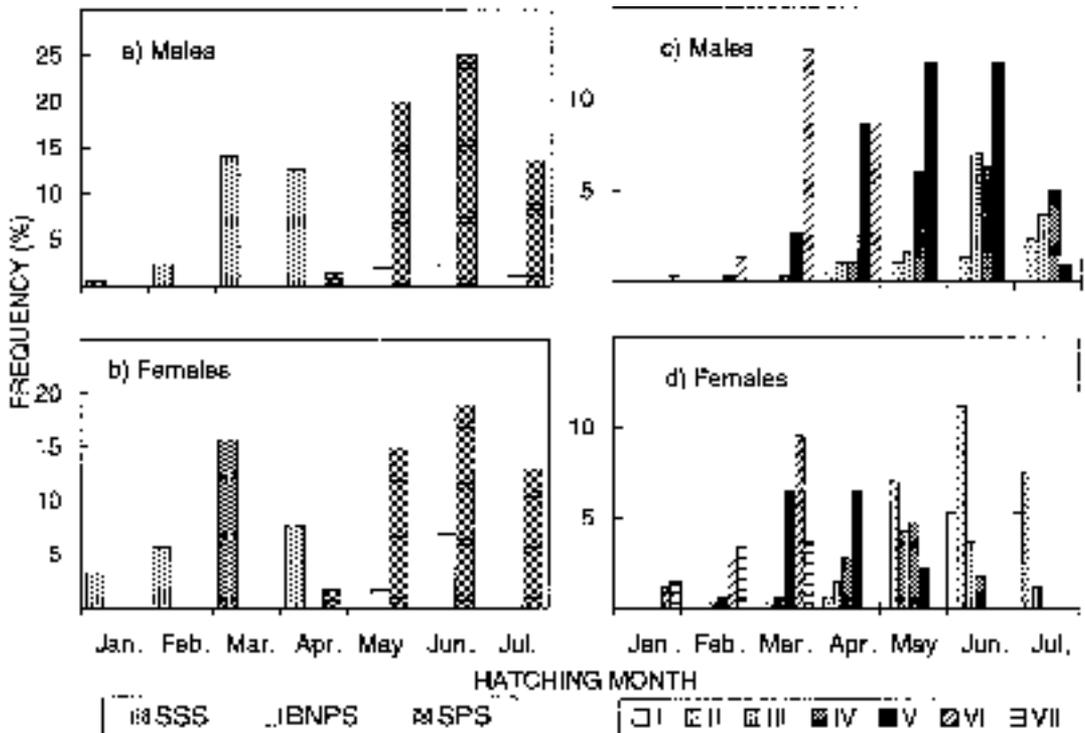


Fig. 5: (a) and (b) Hatching month frequency distribution of the three squid stocks (SSS = Summer Spawning Stock, BNPS = Bonaerensis North Patagonic Stock, SPS = South Patagonic Stock); (c) and (d) maturity stage frequency distribution by hatching month

days old (hatching months: May–July) and they could be identified as belonging to the BNPS.

Over the intermediate shelf between $40^{\circ}30'$ and $46^{\circ}30'S$, there was a second group of squid (250–360 days old), with males (14–22 cm *ML*) smaller than females (18–26 cm *ML*). They were mature (Stage V) or spawning-spent (Stages VI, VII and VIII) and were clearly members of the SSS that spawn in the area between December and March (Brunetti and Pérez Comas 1989a). They had hatched during summer (January–April), with a clear peak in March. The greatest concentrations ($6.45\text{--}25.75\text{ kg}\cdot\text{h}\cdot\text{line}^{-1}$), mostly of spawning and spent squid, were on the warmer side of the thermal front (Stations 21, 22 and 23).

The third group, identified as belonging to the SPS, was detected from the outer shelf of Transects V and VI to the south. It was represented by squid 190–280 days old hatched between April and July, with a peak in June. In this group there were differences in maturity and size distribution between males and females. The

frequency of immature classes increased with latitude but, for the same sizes, the maturity of males (III–IV) was considerably more advanced than that of females (I–II). The main concentrations ($6.45\text{--}19.34\text{ kg}\cdot\text{h}\cdot\text{line}^{-1}$) were found along the cooler side ($11\text{--}13^{\circ}\text{C}$) of the thermal front, between 45° and $47^{\circ}30'S$.

Squid (14–21 cm *ML*) born in August and September, that had not been detected during previous cruises, were found in very low abundance on Stations 46 and 49 (Figs 1, 4).

Age and growth

Six morphological stages are recognized during the statolith development to adulthood for *Illex argentinus* (Brunetti and Ivanovic 1991), in contrast to the five stages defined for other ommastrephids (Morris and Aldrich 1984, Arkhipkin 1990). Three regions are

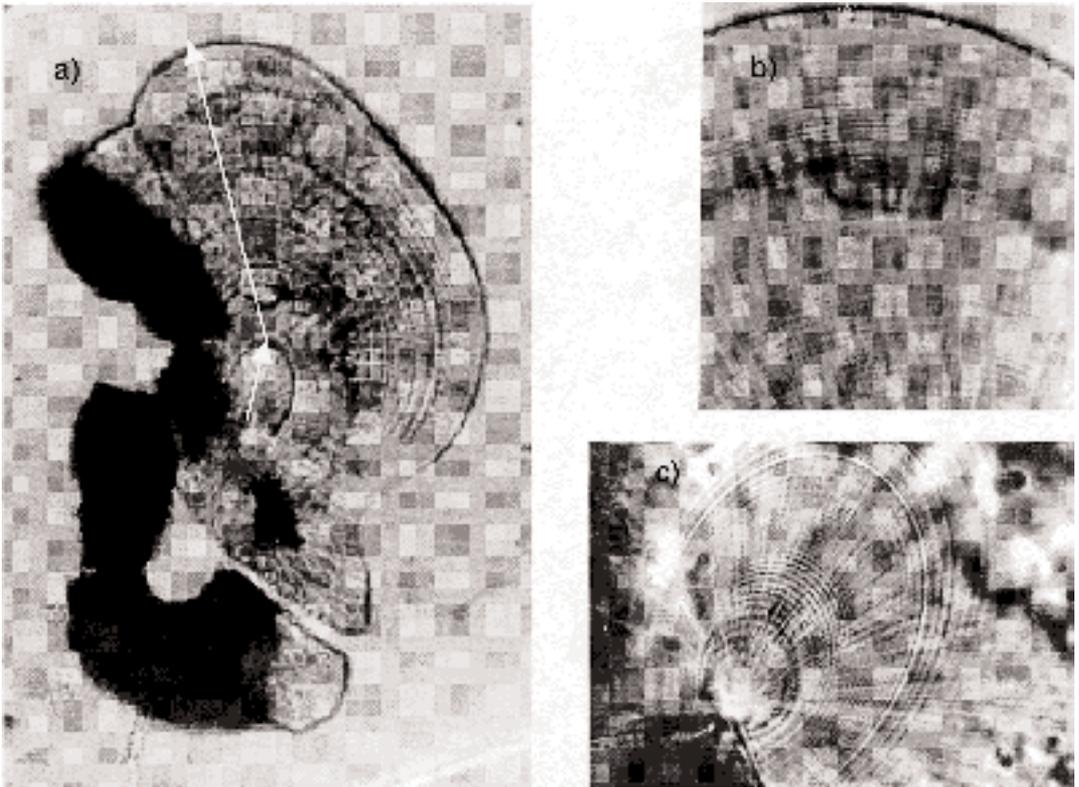


Fig. 6: (a) Posterior view of a polished statolith of an *Illex argentinus* adult (female, $ML = 248$ mm, statolith total length = 1.01 mm). Arrows indicate the counting axis. (b) View of the dark zone. (c) View of the nucleus and postnuclear zone

recognizable outside the nucleus in the ground statoliths of the adults (Fig. 6), as previously described by Arkhipkin (1990) for the same species and Morris and Aldrich (1985) for *Illex illecebrosus*.

The translucent and rounded nucleus (25–35 μm diameter, 18–22 μm radius) contained the focus (10 μm diameter), and no rings were observed inside. The increments outside the focus were therefore counted as the number of days after hatching. The first region (postnuclear; Fig. 6c) was oval in shape and translucent under transmitted light, and it contained relatively narrow increments ($x = 1.31$ μm ; $SD = 0.11$; $n = 25$). The main growth axis extended from the focus to the margin of this region (120–140 μm), where it changed its direction (45°) towards the dorsal dome as the second zone (dark) developed. The dark zone was the largest zone within the statolith, opaque in nature and with wide increments ($x = 3.1$ μm ; $SD = 0.39$; $n = 25$). In the area between these two zones, there were crystals

arranged irregularly, occluding the increments, as seen by Morris and Aldrich (1985). The third zone (peripheral) was translucent and contained narrow increments ($x = 1.43$ μm ; $SD = 0.15$; $n = 25$). This was also the area where counting was most difficult, probably as a result of the effects of the convex nature of the statolith margin.

The nucleus of the statolith has been shown to be formed during the last embryonic stages (28–30, Sakai *et al.* in prep.), and it shows the same dimensions, at hatching, as observed in this study, which also agree with those recorded from wild paralarvae. Similar diameters of the nucleus were cited by Arkhipkin (1990) for the same species (20–32 μm), Morris and Aldrich (1985) for *Illex illecebrosus* (15–21 μm) and Arkhipkin (1996) for *Illex coindetii* (20–24 μm).

The postnuclear zone starts to develop immediately after hatching, and corresponds to the paralarval stage, because the statoliths of the largest paralarvae

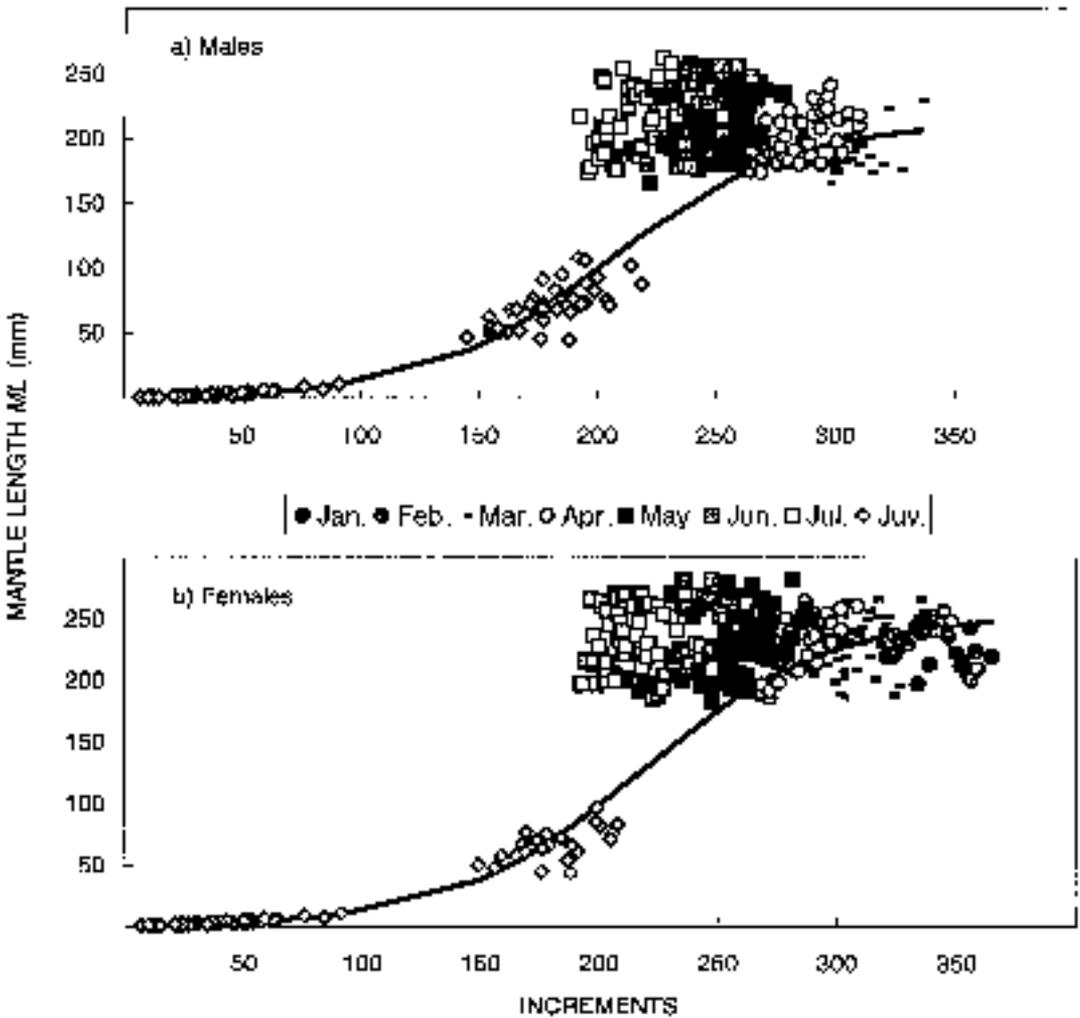


Fig. 7: Relationship between mantle length and number of increments by hatching month (Summer Spawning Stock, January–April; South Patagonic Stock, May–July) and sex and the logistic model fitted for the Summer Spawning Stock (Juv. = paralarvae and juveniles)

only have this zone present. The stage corresponds to the first 70–80 days of the life cycle, from 1.1 to 7–8 mm *ML*. The transitional phase, defined as the period from splitting of the proboscis, occurs when they are between 60 and 80 days old and 5–8 mm *ML*. The dark zone can be detected clearly in the squid from 20 mm *ML*, coincident with the development of the statolith domes.

The number of increments counted in the postnuclear zone is the largest yet cited, implying the longest paralarval stage yet reported. Arkhipkin (1990) also

considered the zone as corresponding to the paralarval stage, but he counted between 32 and 50 increments (1.5–3.0 μm width), whereas Morris and Aldrich (1985) registered between 31 and 51 increments (2.5–3.5 μm) for *Illex illecebrosus*.

Differences in size-at-age and mean growth rates (*m*) during various hatching months for the SSS (January–April) and SPS (May–July) squid are shown in Table II and Figure 7. The sizes ranged from 160 to 260–290 mm *ML* (males and females respectively). The age in days ranged from 188 to 365, but most in-

Table II: Age-classes, mean size (*ML*) ranges and growth rates (*m* and *g*) for both sexes of the SSS (January–April) and SPS (May–July) *Illex argentinus*

Hatching month	Males				Females			
	Age-class (10 days' range)	Mean <i>ML</i> range (mm)	<i>m</i> (mm·day ⁻¹)	<i>g</i> (mm·day ⁻¹)	Age-class (10 days' range)	Mean <i>ML</i> range (mm)	<i>m</i> (mm·day ⁻¹)	<i>g</i> (mm·day ⁻¹)
January					340–360	214–219	0.075	0.19
February	310–330	179–173*		0.22	320–350	224–217*	0.338	0.28
March	280–330	197–219	0.210	0.40	280–330	213–258	0.635	0.56
April	250–300	187–206	0.634	0.60	250–300	225–253	1.004	0.87
May	230–270	196–236	0.853		230–280	200–255	1.291	
June	200–260	188–248	1.147		200–260	207–263	1.307	
July	190–230	191–254	1.153		190–230	226–241	0.906	

* The mean length of the older age-class is smaller than the mean length of the younger age-class

dividuals of both sexes were between 200 and 320 days old. Males were smaller than females at the same age, and there were no males older than 336 days, although females reached 365 days old. This suggests a shorter lifespan for males than females. The SPS squid were between 190 and 280 days old and had a faster growth rate than those of the SSS, which were between 250 and 360 days old. Within each stock the youngest squid had the fastest growth rates. A similar observation regarding growth rate has been made by Rodhouse and Hatfield (1990) and Arkhipkin (1993) for the winter-hatched squid (May–August).

Even though data for the whole life cycle of the SSS were not available, age ranges 100–150 and 220–260 days being lacking, the growth pattern fitted a logistic model:

$$\text{Male} - ML_x = 212.84 / (1 + \exp[-0.0263(x - 205.06)])$$

$$(r^2 = 0.9711, n = 212);$$

$$\text{Female} - ML_x = 253.03 / (1 + \exp[-0.0254(x - 217.68)])$$

$$(r^2 = 0.9597, n = 223).$$

The mean of the absolute growth rates (g_x) for the same age ranges of the SSS adults are compared with m in Table II. The absolute growth rates of both sexes were similar up to approximately 180 days old, after which the female growth rate was faster. Uozumi and Shiba (1993) proposed the same model for the March–May group, suggesting a long paralarval stage of 70–80 days, which agrees with the current observations.

Feeding

The main food of the squid sampled was zooplankton (87.19%), of which the hyperiid amphipod *Themisto*

gaudichaudii was the most common item (78.89%). The remaining 8.30% consisted of euphausiids. Fish accounted for 8.65% of the total, but more than half could not be identified because no otoliths or identifiable scales were found. The remainder consisted of two species, *Engraulis anchoita* and *Merluccius hubbsi*, in a ratio of 3:1. Squid were poorly represented in the diet (4.15%) and were identified on all occasions as *Loligo* sp.

Diet was analysed separately for the Bonaerensis–North Patagonian shelf (B) and the South Patagonian shelf (P) squid. Two zones were considered in the first case: north and south of 40°30'S (B–I and B–II respectively). Consumption of *Themisto gaudichaudii* increased with increasing latitude, representing 47.62% of the total food consumed in B–I, 81.66% in B–II and 89.61% in P. In contrast, the percentage of euphausiids in the diet decreased (B–I: 47.62%, B–II: 2.96%, P: 0%). The proportion of fish (B–II: 10.06%, P: 7.79%) and squid (B–II: 5.33%, P: 2.6%) eaten in the two southern areas was low and similar, whereas in the northern zone, very few fish (4.76%) and no squid were consumed. Analysis of squid diet by size showed no clear trends in prey preference. Even though the largest squid ate the most fish in B–II, the opposite was observed in P.

For the three main categories of food listed (zooplankton, fish and squid), 97.14% of squid examined had only one type of prey in the stomach, 2.50% had two types and 0.36% had eaten the three types simultaneously.

The results of prey analysis agree with those of Ivanovic and Brunetti (1994), which showed that, over the South Patagonian shelf during summer, the diet is composed almost exclusively of *Themisto gaudichaudii*. However, a situation observed here and not previously reported is that, even in low pro-

portion, the smallest squid were found preying on fish.

CONCLUDING REMARKS

The distribution, main concentration areas and population structure found during this cruise agreed with those described for previous research cruises covering the same geographical area (Brunetti 1981, Otero *et al.* 1981, Hatanaka 1986, 1988). On the basis of age, hatching month distribution, size and maturity stage, three squid groups were present in the surveyed area:

- SSS – distributed in the southern area (40°30'–46°30'S) of the Bonaerensis-North Patagonian Shelf System, age-range 250–360 days, adults of small size (males smaller than females), mature and spawning/spent animals, hatching months January–April;
- SPS – distributed in the South Patagonian Shelf System (46°30'–51°30'S), age-range 190–280 days, males smaller than females, immature/maturing animals, hatching months May–July;
- BNPS – distributed in the northern area (39°–40°30'S) of the Bonaerensis-North Patagonian Shelf System, age-range 192–218 days, no appreciable difference in size between the sexes, immature animals, hatching months May–July.

There is strong evidence, through the presence of spawning/spent individuals together with newly hatched paralarvae (Brunetti 1990c, Brunetti and Ivanovic 1992), that the intermediate shelf between 41°30'S and 45°S is the site of annual summer spawning. There, a frontal system between well-mixed coastal waters and stratified shelf waters develops during summer (Glorioso 1987), so providing the appropriate thermal conditions (>13°C) for embryonic development. During the cool season, when thermal conditions and food availability are disadvantageous, summer spawners exhibit slow rates of growth and small sizes at maturity.

Autumn-winter spawners (SPS and BNPS) time their reproductive activity to take advantage of the plankton production cycle, which follows the typical development of the seasonal stratification of cold-temperate waters. The squid match the phytoplankton and the following zooplankton peaks, i.e. from spring to early summer, shifting from the coast to offshore and from 38°S to the south (Carreto *et al.* 1981). This availability of food, together with the lower temperatures found during their migration, would provide the conditions for attaining large size at maturity, as proposed by Van Heukelem (1979). The SPS squid found

during the cruise were associated with the areas of greatest zooplankton concentration (Santos 1994), where they preyed mainly on amphipods.

The results of the cruise show the situation at the beginning of the fishing season, when squid from the SSS and SPS groups are available to be fished over the Patagonian shelf. In February and March the fishery is centred around the SSS reproductive aggregations, whose lifespan finishes around March, and on the SPS feeding schools. The fishery on the SPS group continues until the end of June, following its displacement over the shelf to the reproductive grounds in deep water. During May the fishery moves to the Bonaerensis-North Patagonian shelf, where the BNPS is caught until September.

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