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Reproductive biology of winter-spring spawners of *Illex argentinus* (Cephalopoda: Ommastrephidae) off southern Brazil*

R.A. SANTOS¹ and M. HAIMOVICI

Departamento de Oceanografia, Universidade do Rio Grande,
Cx.P. 474, Rio Grande-RS 96201-900, Brazil.

¹Curso de Pós-Graduação em Oceanografia Biológica, E-mail: posras@super.furg.br

SUMMARY: The reproduction and fecundity of winter-spring spawners of the shortfin squid *Illex argentinus* off southern Brazil (27°S-34°S) were studied in samples from bottom trawl surveys on the outer shelf and upper slope from 1986 to 1992. The mantle length-total weight relationships were for males: $TW = 0.00002456 ML^{2.974}$ for females: $TW = 0.00004265 ML^{2.842}$ and pooled: $TW = 0.00005376 ML^{2.809}$. Males were heavier than females at the same ML. Fully mature squids were found from July to October. Mantle length and total weight of fully mature males ranged from 188 to 296 mm (mean 252.2 mm) and 195.5 to 611 g (mean 382.7 g) and for females from 225 to 356 mm (mean 307.4 mm) and 234 to 772 g (mean 558.4 g). Total weight was maximum at full maturity and decreased in the subsequent stages of both sexes. Mean weight and mean major axis length of ripe oocytes in the oviducts were 0.48 mg (sd= 0.10 mg) and 1.27 mm (sd= 0.08 mm), respectively. Total and oviduct mean fecundities, in thousands of oocytes larger than 0.4 mm, in ten fully mature females (294-336 mm ML) were 177.2 (93.0 to 294.3) and 118.4 (51.5 to 233.9), respectively. Spawning season in this region seems to be more protracted than in higher latitudes. Our results suggest that a northward migration could take place prior to spawning and that in winter and spring, southern Brazil may be a major spawning ground of *Illex argentinus* that contributes to the local and to the Uruguay and northeastern Argentina recruitment.

Key words: *Illex argentinus*, squids, Brazil, reproduction, populational groups.

RESUMEN: BIOLOGÍA REPRODUCTIVA DE CALAMARES (*ILLEX ARGENTINUS*) DESOVANTES DE INVIERNO Y PRIMAVERA EN EL SUR DE BRASIL. — El ciclo reproductivo y la fecundidad de calamares *Illex argentinus* desovantes de invierno y primavera en el sur de Brasil (27°-34° S) fue estudiado a partir de muestras obtenidas con redes de arrastre de fondo en la plataforma externa y el talud superior, entre 1986 y 1992. Las relaciones de longitud dorsal del manto (LM, mm)-peso total (PT, g) fueron para los machos: $PT=0.00002456 LM^{2.974}$, para las hembras: $PT= 0.00004265 LM^{2.842}$ y para ambos sexos: $PT = 0.00005376 LM^{2.809}$. Los machos fueron más pesados que las hembras del mismo LM. Calamares maduros ocurrieron desde julio hasta fines de octubre. Los LM y PT de los machos maduros variaron entre 188 y 296 mm (media: 252.2 mm) y de 195.6 a 611.0 g (media: 382.7 g); y de las hembras maduras variaron entre 225 y 356 mm (media: 310.1 mm) y 234 a 772 g (media: 558.4 g). Los pesos totales disminuyeron en los estadios de desove parcial y total. El eje mayor medio de los ovocitos maduros en los oviductos fue de 1.27 mm (ds = 0.08 mm) y el peso medio de 0.48 mg (ds = 0.10 mg). La fecundidad media, en miles de ovocitos mayores a 0.4 mm, de 10 hembras maduras (294-336 mm LM) fue en los oviductos 118.4 (51.5 a 233.9) y la total 177.2 (93.0 a 294.3). La época del desove en el sur de Brasil parece ser más prolongada que la de regiones más meridionales. Diversas consideraciones presentadas en la discusión llevan a pensar que desovantes de invierno y primavera en la región migran desde mayores latitudes y que el sur de Brasil es un importante área de desove que contribuye al reclutamiento local, así como de Uruguay y de la región norte de Argentina.

Palabras clave: *Illex argentinus*, calamares, Brasil, reproducción, grupos poblacionales.

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INTRODUCTION

The Argentinean shortfin squid, *Illex argentinus* (Castellanos, 1960), has been recorded on the continental shelf and slope of the Southwestern Atlantic Ocean from 22°S to 54°S (Hatanaka, 1986; Haimovici and Perez, 1991) and sustains a large fishery in the southern range of its distribution (Csirke, 1987). Its life cycle is closely associated with the subtropical convergence formed by the Brazil and Malvinas currents. The shortfin squid fishery potential in southern Brazil is unknown as it is not regularly fished. However, there is evidence of its ecological importance from bottom trawl surveys (Haimovici and Perez, 1990), stomach contents of predators (Santos, 1992) and larval surveys (Haimovici *et al.*, 1995).

The life cycle of *I. argentinus* is approximately one year (Hatanaka, 1988; Rodhouse and Hatfield, 1990; Arkhipkin, 1990). Several spawning groups have been reported with different reproductive seasons and adult sizes. Hatanaka *et al.* (1985) and Hatanaka (1988) concluded that there is a minor summer north-Patagonic spawning population and a major south-Patagonic winter spawning population that leaves the feeding grounds over the Southern Patagonian shelf and migrates northward, probably towards warm waters influenced by the Brazil Current, to spawn. Nigmatullin (1989), Arkhipkin (1990) and Arkhipkin and Scherbich (1991) refer to four seasonal cohorts off Argentina. Brunetti (1988) distinguished three main spawning stocks that she designated as "Summer Spawning Stock" (SSS), "South Patagonic Stock" (SPS) and "Bonaerensis north-Patagonic Stock" (BNPS), the last extending to southern Brazil. Haimovici and Perez (1990) found mature, mated and spawning females in winter off southern Brazil and designated this Southern Brazil Stock (SBS). Additional signs of spawners off southern Brazil include the occurrence of recently hatched rynchoteuthion paralarvae of *I. argentinus* in the region (Haimovici *et al.*, 1995). However the question of number and identity of the populational groups of this species is, by no means, a closed issue.

In this paper, the reproductive biology of the winter and spring spawners of *Illex argentinus* off southern Brazil is described. Since the squid matures off northern Argentina and Uruguay in winter and spring, and no geographic barriers are evident to the north of De la Plata River, arguments in favour of the hypothesis proposed by Hatanaka *et al.* (1985) and Haimovici *et al.* (1990, 1995) of a northward migration in winter and spring to spawn off southern Brazil, are tested by a comparison of aspects of the reproduction in different regions.

MATERIAL AND METHODS

Specimens of *Illex argentinus* obtained from research cruises with bottom trawl nets by the R/V "Atlântico Sul" during July and September 1986, September-October 1991 and October 1992, were examined for sex (n=512) and maturity (n=326). The samples were collected along the continental outer shelf and slope between 27°S and 34°S, at depths ranging from 100 to 533 m (Fig. 1).

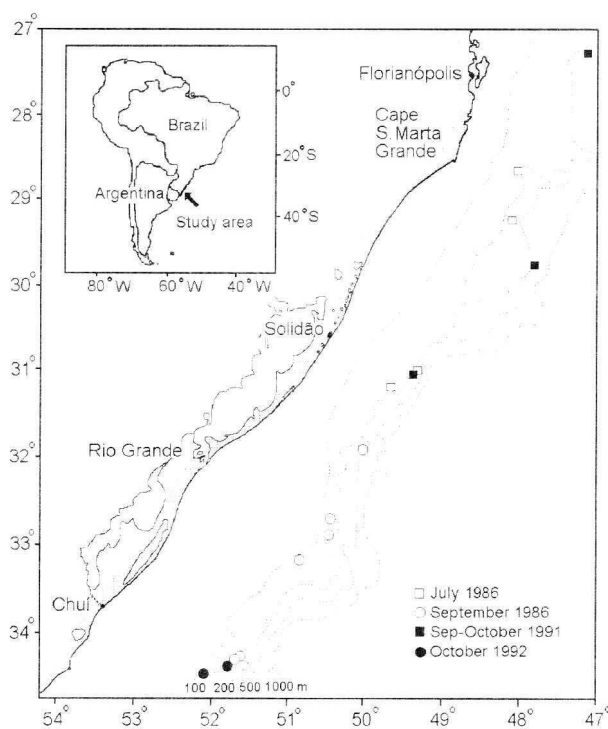


FIG. 1. – *Illex argentinus* winter and spring sites of sampling off southern Brazil.

Most squid larger than 150 mm mantle length were frozen for further dissection ashore. Smaller specimens were usually fixed in 10% formal saline solution neutralised with borax, and preserved in 70% ethylic alcohol after landing. The dorsal mantle length (ML) was measured to the nearest mm. Total (TW) and somatic weight (TW less the weight of the reproductive organs) were determined to 0.1 g. Maturity stages were assigned following Brunetti (1990). In the text females are said to be "immature" at stages I and II, "maturing" at stages III-IV, "fully mature" at stage V, "mated" at stage VI, "partly spawned" at stage VII and "spent" at stage VIII. The males are said to be "immature" at stages I and II, "maturing" at stages III-IV, "fully mature" at stage V, "partly spent" at stage VI and "spent" at stage VII.

The nidamental gland weight (NGW), ovary weight (OW), oviduct weight (OdW), oviducal gland weight (OGW), testis weight (TeW), spermatophoric complex weight (SCW) (including sperm duct, spermatophoric organ, spermatophoric duct, spermatophoric sac and penis) were determined to 0.1 g. The nidamental gland length (NGL), the hectocotylyzed arm length (HAL between the first sucker and the tip) and the length of the hectocotylyzed section (HL) were measured to 0.1 mm.

To characterise reproductive status, the hectocotylus index (HI = HL/HAL), the nidamental gland index (NGI = NGL/ML) and the gonadosomatic indices of females (GSI = (OW + OdW + OGW + NGW) / TW) and males (GSI = (SCW + TeW) / TW) were calculated.

The length of the major axis (OL) of approximately 50 oocytes from the anterior and posterior sections of unfrozen fresh ovaries and oviducts of 15 mature to spent females (maturity stages V to VIII) were measured under a stereoscopic microscope. Measurements were made prior to fixation, because changes in the shape of the oocytes from oval to an irregular polygonal form occurs during the fixing process.

For fecundity estimates oocytes larger than 0.4 mm OL were counted in sub-samples of approximately 200 mg from the anterior, central and posterior sections of the ovaries and the anterior and posterior sections of the oviducts of 12 females at maturity stages V to VII. Ovaries and oviducts were fixed in 5% formol saline solution before counting. Oocyte counts per g of ovary from the anterior, central and posterior sections of the ovaries did not differ significantly ($P > 0.05$) nor between the anterior and posterior sections of the oviducts ($P > 0.05$). Ovary and oviduct oocyte counts were therefore pooled from the different sections (Table 1).

TABLE 1. – Oocyte counts per gram of ovary and oviduct in their different sections for *Illex argentinus* in maturity stages V to VII.

Organ	Section	Mean	sd	Range	n
Ovary	Anterior	1694.8	657.82	669-2596	12
	Central	1566.3	522.94	857-2311	11
	Posterior	1590.4	857.97	732-2272	12
Oviduct	Anterior	2178.3	396.45	1307-2631	12
	Posterior	2145.9	438.50	1413-2627	12

Total fecundities and relative fecundities (number of oocytes per g of total and somatic weight) were estimated for the oviducts and ovary and them summed.

Analysis of variance and covariance were carried out for comparisons of variables (weight, length, counts, indices) between categories (sex, stages, size groups), employing the STATGRAPHICS Statistical Package (1991 STSC, Inc.). Proportions were compared with Chi-square test (Zar, 1994).

RESULTS

Sex ratios

The proportion of males and females was calculated for different size groups from the pooled samples (Table 2). This proportion did not differ significantly from 1:1 ratio for juveniles and maturing squids, under 200 mm ML ($P > 0.05$). Over 200 mm ML, including mature and spawning specimens, the proportion of females was a slightly higher (54.8%) than males ($P < 0.05$).

TABLE 2. – Sex percentages (%) of *Illex argentinus* in winter-spring samples off southern Brazil.

Mantle length (mm)	n	Unsexed	Males	Females
<100	25	40.0	28.0	32.0
100-200	71	5.6	49.3	45.1
>200	416	-	45.2	54.8 *

*Chi-square significantly different from 1:1 ratio ($\alpha=0.05$)

Mantle length composition and sex ratios of mature to spawning squid were recorded in the three larger sample groups (Fig. 2). The first off Solidão (31° S; 14/15 Sep. 1986), where the proportion of females was 39.4% and 34.6% of them were mated. The second was from off Florianópolis (27° S, 29/30 Sep. 1991) and the proportion of females was 81.9% and 85.3% of them were mated. In the third, from off Chuí (34° S, 30 Oct. 1992), the proportion of females was 64.7% and 92.3% of them were mated. The sex ratio was significantly different from 1:1 in all three samples ($P < 0.05$).

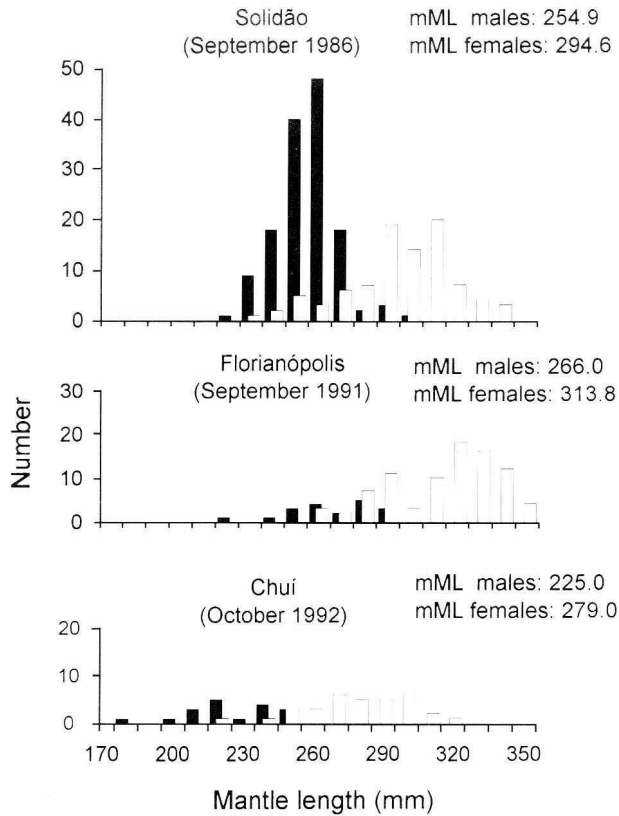


FIG. 2. – Mantle length distributions of fully mature *Illex argentinus* in three major samples (in black: males and in white: females), mML: mean mantle length (mm).

Mantle length-total body weight relationships

Power relationships between mantle length (mm) and total weight in (g) were calculated for 81 males (61-296 mm ML) and 166 females (63-356 mm ML) (Fig. 3):

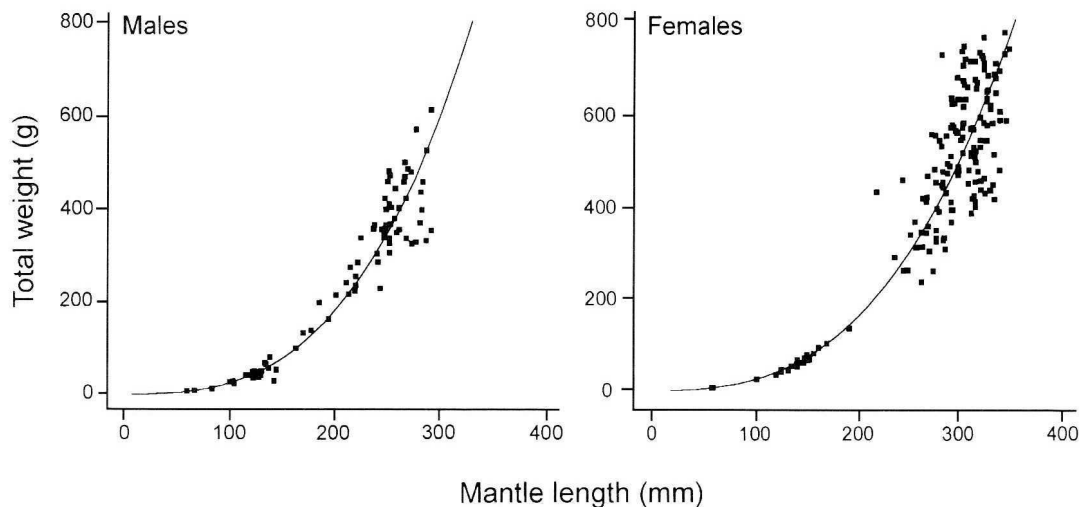


FIG. 3. – Mantle length and total weight relationships of *Illex argentinus* sampled in southern Brazil in winter and spring.

TABLE 3. – Number of *Illex argentinus* sampled in different months, per maturity stage.

	Males						Females							
	Maturity stage						Maturity stage							
	I-II	III	IV	V	VI	VII	I-II	III	IV	V	VI	VII	VIII	
July	1	9	5	7			3	8	3	2	5	1		
September	7	14	2	15	14	6	11	13	1	19	46	32	3	
October	3			1	15	5	1		1	6	16	14	5	

Males: $TW = 2.456 \times 10^{-5} ML^{2.974}$ ($r^2 = 0.97$)

Females: $TW = 4.265 \times 10^{-5} ML^{2.842}$ ($r^2 = 0.95$)

Pooled: $TW = 5.376 \times 10^{-5} ML^{2.809}$ ($r^2 = 0.96$)

Males were generally relatively heavier than females ($P < 0.01$).

Reproductive cycle of males

Fully mature males were found from July to October and partly spent males from September to October (Table 3).

Maximum length was attained at full maturity. Total weight and somatic weight also were maximum at maturity but decreased in partly spent and spent males (Fig. 4). Larger mantle length was attained at stage V (188-296 mm, mean ML for stages V to VII was 252.2 mm). Greatest total weight was attained at stage V (195.5-611.0 g, mean 382.7 g) and it then decreased significantly at more advanced stages ($P < 0.01$), on average by 14.3% in partly spent and 26.9% in spent males. Somatic body weight also attained the highest values at stage V and decreased by 31.7% in partly and spent males.

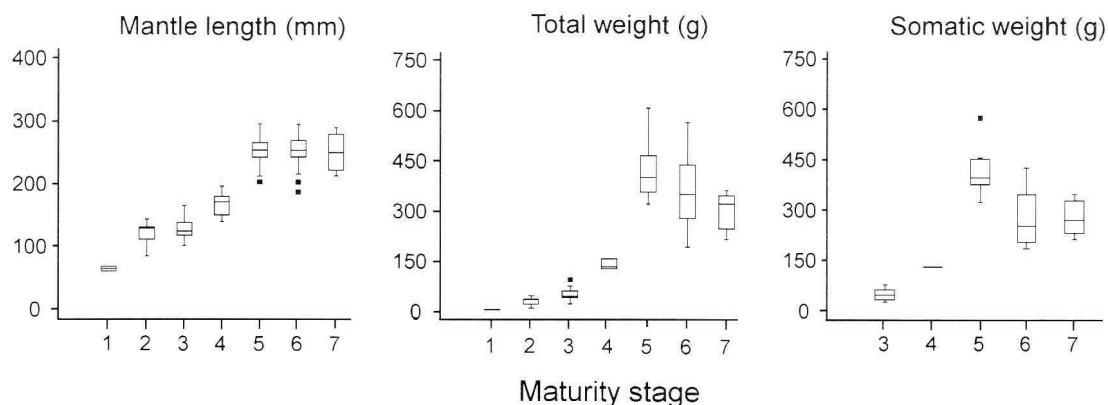


FIG. 4. – Mantle length, total and somatic weight at different maturity stages of males of *Illex argentinus* sampled in southern Brazil in winter and spring.

The proportion of hectocotylization on the left or right fourth arm among 140 males did not differ significantly from 1:1 ($P > 0.05$). Two specimens had both IV arms hectocotylized. The hectocotylus index (HI) increased with maturation (Fig. 5). It was significantly higher in spent compared to mature males ($P < 0.05$). Maximum HI was 0.69 in a spent male. HI over 0.5 indicated maturity in 93.9% ($n = 49$) of the males, but 34.3% ($n = 38$) of mature specimens had HI under 0.5.

By comparison with HI, the gonadosomatic index (GSI) attained its maximum at stage V ranging from 0.050 to 0.081 (mean GSI 0.060) and decreased in partly spent and spent males (Fig. 5).

Reproductive cycle of females

Fully mature and partly spawned females were found from July to October (Table 3). Maximum length was attained at full maturity, total and somatic weight also were maximum at maturity and decreased in partly spawned and spent females (Fig. 6).

Larger mantle length was attained at stage V (225-356 mm, mean ML for stages V to VIII was 307.4 mm). Total weight was also maximum at stage V (234.0-772.0 g, mean TW for stages V to VIII was 558.4 g) and was significantly lower at subsequent stages ($P < 0.01$). Maximum somatic weight was attained at stage V and decreased in later stages. Total weight and somatic weight decreased 15.8% and 14.1% respectively from mature to spent females.

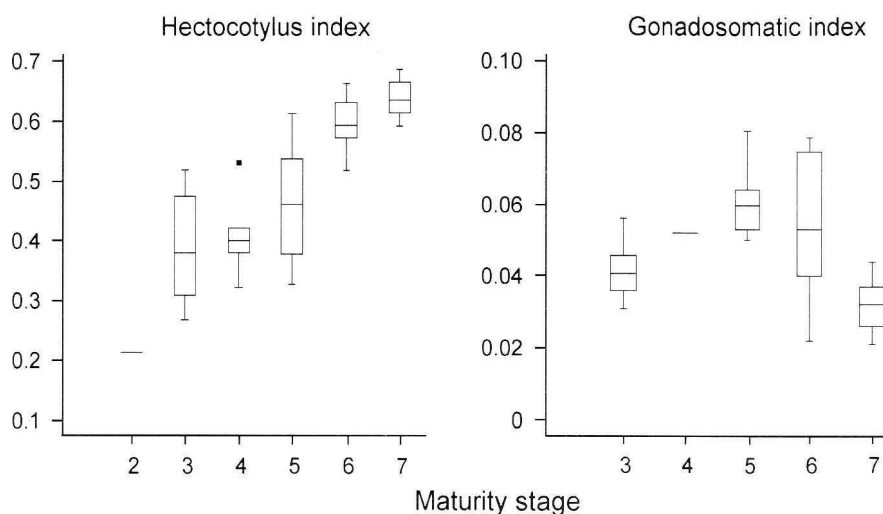


FIG. 5. – Hectocotylus Index and Gonadosomatic Index at different maturity stages of males of *Illex argentinus* sampled in southern Brazil in winter and spring.

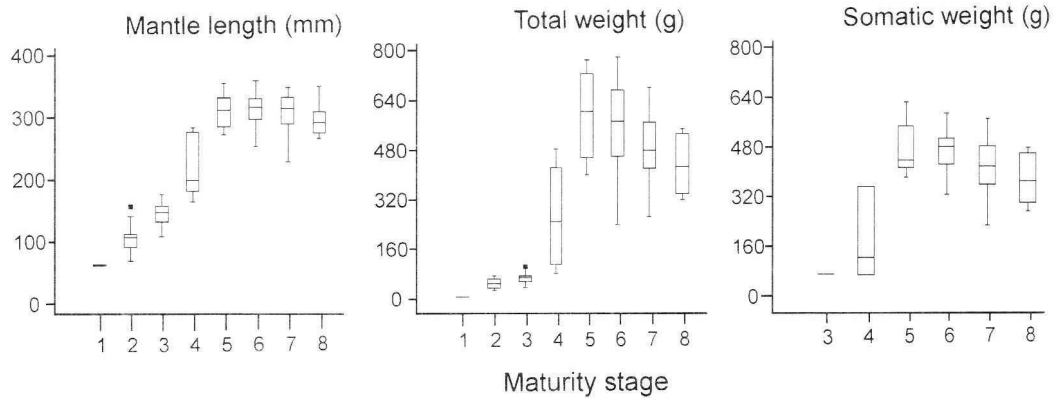


FIG. 6. – Mantle length, total and somatic weight at different maturity stages of females of *Illex argentinus* sampled in southern Brazil in winter and spring.

The smallest female with spermatophores attached (inside the mantle cavity, near the oviducal glands), was caught in July. It measured 197 mm and was apparently in stage IV of gonadal development, with a large ovary and a few oocytes in the oviducts. The largest non-mated female measured (311 mm ML) was also in stage IV and was caught in July.

The nidamental gland index (NGI) increased abruptly between stages III and IV and after stage V, with ratios between 0.4 and 0.7 (mean NGI for stages V to VIII was 0.47) (Fig. 7). GSI of females increased up to maturity (stages V and VI) ranging from 0.13 to 0.35 (mean 0.22) and decreased significantly in the subsequent stages ($P < 0.05$) (Fig. 7).

Oocyte size and numbers

The major axis length of the measured oocytes (OL) of 15 mature to spent females varied in the ovaries from 0.4 to 1.6 mm and in the oviducts from 0.9 to 1.6 mm (Fig. 8). The mean OL in anterior and posterior ovary and oviduct sections in different maturity stages (V-VIII) were calculated (Table 4). An ANOVA showed that the mean OL in the anterior section of the ovaries was slightly, but significantly smaller than in the posterior section ($P < 0.01$). Oocytes were significantly larger in the oviducts ($P < 0.01$) but no difference was found between the anterior and posterior sections (Fig. 9).

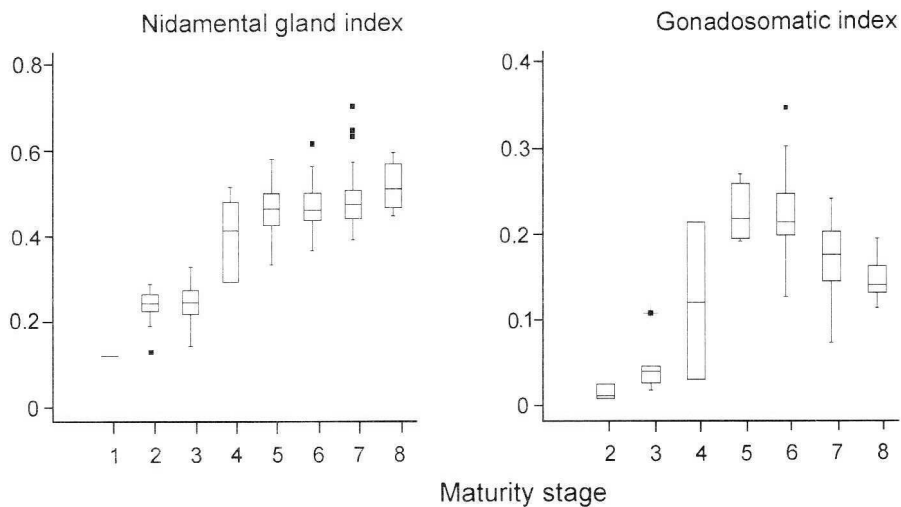


FIG. 7. – Nidamental Gland Index and Gonadosomatic Index at different maturity stages of females of *Illex argentinus* sampled in southern Brazil in winter and spring

TABLE 4. – Mean oocyte majoraxis length (mm) of *Illex argentinus* in southern Brazil from different parts of ovaries and oviducts. Parentheses indicate range.

	Maturity stage							
	V	n	VI	n	VII	n	VIII	n
ML (mm)	275-300	2	294-311	2	(242-313)	9	269-270	2
Ovary								
anterior	1.02(0.4-1.6)	109	1.10(0.5-1.5)	113	1.06(0.4-1.6)	488	0.98(0.4-1.6)	104
posterior	1.08(0.4-1.6)	112	0.92(0.4-1.4)	109	1.11(0.4-1.6)	485	1.16(0.6-1.5)	108
Oviducts								
anterior	1.25(0.9-1.5)	116	1.24(1.1-1.5)	111	1.28(1.0-1.6)	508	1.25(0.8-1.5)	109
posterior	1.29(1.0-1.6)	115	1.28(1.0-1.4)	102	1.28(0.9-1.6)	512	1.23(1.0-1.4)	113

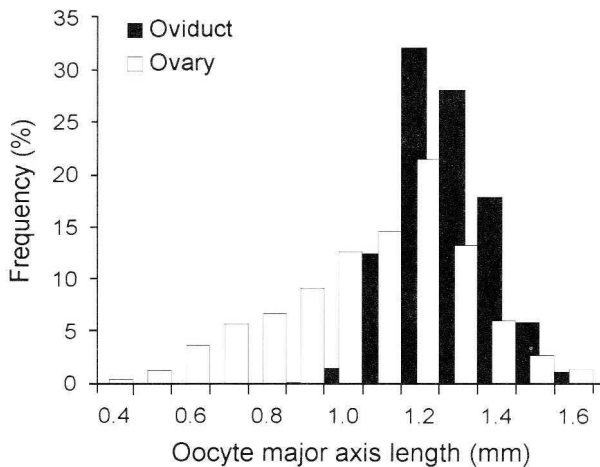


FIG. 8. – Oocyte major axis length from ovaries and oviducts of mature females *Illex argentinus* sampled in southern Brazil in winter and spring.

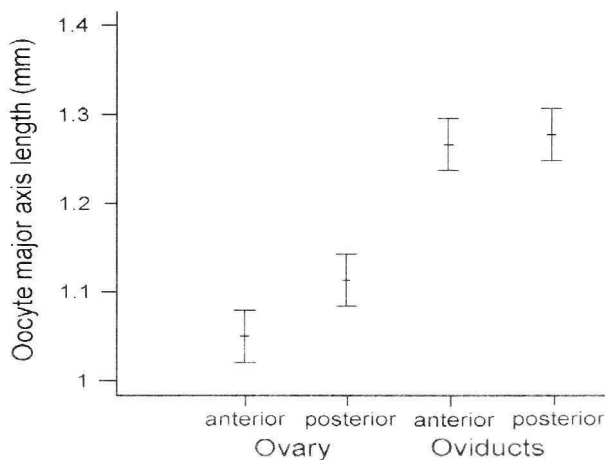


FIG. 9. – Oocyte major axis length mean and 95% confidence intervals in the different sections of ovary and oviducts of mature females *Illex argentinus* sampled in southern Brazil in winter and spring.

The mean major axis of fresh unfrozen ripe oocytes of oviducts was 1.27 mm (sd= 0.08 mm). The mean weight of ripe oocytes in fixed oviducts of 12 mature females was 0.48 mg (sd= 0.10 mg).

Fecundity

Total and relative fecundities of twelve females between stages V to VII was estimated (Table 5). Fully mature and mated females had greater ovary and oviduct fecundities than partly spawned females, but in the later, the number of oocytes in the ovary was still considerable. For the mature females (stages V-VI, n: 10, ML: 294-336 mm) the mean and range of the fecundities, in thousands of oocytes larger than 0.4 mm, were for ovary: 58.7 (36.3 to 105.7); oviduct: 118.4 (51.5 to 233.9) and total: 177.2 (93.0 to 294.3). Relative fecundities were greater in the fully mature mated females (Table 5).

DISCUSSION

Clear evidence of winter and spring spawning in southern Brazil has been provided by the occurrence of paralarvae and juveniles (Haimovici and Perez, 1990; Haimovici *et al.*, 1995) and by the presence of a high proportion of fully mature, partly spawned and spent squids in samples from a wide range of latitudes (27°S-34°S). In fact the only other evidence of *Illex argentinus* spawning is off the northern Patagonian shelf in summer (Table 6).

Several aspects of the life history and reproduction of *Illex argentinus* along its distribution range were compared to discuss the geographical continuity of the populations and the relative importance

TABLE 5. – Total and relative fecundity mean estimates, for oocytes larger than 0.4 mm, and maturity indices for *Illex argentinus* in southern Brazil. Parentheses indicate range.

Maturity stage	V	VI	VII
Mantle length (mm)	(300-336)	(294-332)	328-347
Total body weight (g)	(514-680)	(562-726)	538-541
n	4	6	2
Nidamental Gland Index (NGI)	(0.42-0.58)	(0.45-0.56)	0.45-0.46
Gonadosomatic Index (GSI)	(0.21-0.25)	(0.20-0.35)	0.14-0.19
ovary oocytes (x1000)	44.5 (36.3-55.1)	68.1 (47.2-105.7)	51.6-63.5
oviduct oocytes (x1000)	97.1 (51.5-122.0)	132.7 (87.1-234.0)	32.5-56.5
total oocytes (x1000)	141.7 (93.0-177.2)	200.9 (137.5-294.3)	84.0-119.9
total oocytes/g total weight	244 (162-311)	309 (199-424)	155-206
total oocytes/g somatic weight	317 (213-414)	424 (251-607)	181-255
ovary oocytes/g total weight	77 (67-97)	104 (79-149)	95-109
ovary oocytes/g somatic weight	100 (85-129)	140 (100-185)	111-135
oviduct oocytes/g total weight	167 (90-214)	205 (120-337)	60-97
oviduct oocytes/g somatic weight	217 (118-285)	283 (151-483)	70-120

of southern Brazil as spawning ground for the species. For this, comparisons were made on available information on length-weight relationships, parasites, paralarval distribution, spawning and hatchery grounds, ranges of sizes at full maturity, maturity indices and mature oocyte counts from different nominal stocks. Mantle length-total weight curves of males and females from southern Brazil and other fishing areas (Leta, 1981; Koronkiewicz, 1986; Brunetti, 1988; Rodhouse and Hatfield, 1990), are shown in Figure 10. Although it was not possible to make statistical comparisons, length-weight relations suggest that *Illex argentinus* is relatively heavier in the south of its range. Note that differences would be larger if, instead of total weight, only somatic weight was considered, because squid in southern Brazil were more mature than those in other regions. As also observed by the other authors (Leta, 1981; Brunetti, 1988; Rodhouse and Hatfield 1990;), males were relatively heavier than females, probably because of the greater development of their head and arms.

Hectocotylization and nidamental gland indices for sexually mature males and females from different regions are shown in Table 6. Schuldt (1979) and Brunetti (1990) stated that hectocotylization of over 45% of the arm characterised mature males. Our data showed that there was a great individual variability of HI among the maturing, mature and spent males, as also observed by Coelho *et al.* (1985) for *Illex illecebrosus*. Caution is therefore recommended in the utilisation of HI to characterise maturity. On the other hand, the NGI was well correlated with maturity stages of females and the mean

values attained at maturity were similar to those observed in other latitudes by Brunetti (1990), Rodhouse and Hatfield (1990), and Hatfield and Rodhouse (1992). For females off southern Brazil, the GSI showed that at maturity, up to 35% of the total body weight was gonads and accessory organs, compared to 8% in males. These values did not differ much from those observed by Rodhouse and Hatfield (1992) and Laptikhovsky and Nigmatullin (1992).

The means of major axis length (OL) and weight (OW) of ripe oocytes in the oviduct have been measured by several authors (Table 6). OL in this study was larger than the observed by Schuldt (1979), Brunetti *et al.* (1991) and Laptikhovsky and Nigmatullin (1992), and smaller than the observed in a single female by Rodhouse and Hatfield (1990). In contrast, OW in southern Brazil was comparable with those found by Rodhouse and Hatfield (1990) and Laptikhovsky and Nigmatullin (1992). It was concluded that differences in the size of ripe oocytes may have been due to fixation and preservation by different authors and make OL comparisons of little use.

The total fecundity in fully mature squids was similar to that observed by Rodhouse and Hatfield (1990) but lower than that estimated by Laptikhovsky and Nigmatullin (1992) who found up to 750,000 oocytes larger than 0.05 mm, for winter spawners up to 370 mm ML, on the Patagonian shelf (Table 6). The females available in our analysis were smaller than those considered by these authors and only oocytes larger than 0.4 mm were counted. This leads to substantially different estimates because

TABLE 6. – Summary of selected characteristics of the four main spawning stocks of *Illex argentinus*. (ML: mantle length; m: males; f: females). Parentheses indicate range.

Stocks	Summer Spawning (SSS)	South Patagonic (SPS)	Bonaerensis Northpatagonic (BNPS)	Southern Brazil (SBS)
Spawning seasons and grounds	December to February (summer) Intermediate shelf, 42°S-47°S [1]	April to August (late autumn and winter) Slope, north of 44°S under the Malvinas or the Brazil Currents [1] [2] [3]	July to September (winter to spring) Slope, north of 38°S under the Malvinas or Brazil Currents [1] [4]	July to November (winter and spring). Slope, between 27°S and 34°S, under the Brazil Current. [5] [6] [12]
Hatchery grounds	Northpatagonian shelf Evidence: paralarvae, spawning and spent adults [7]	Probably along the slope in the Malvinas Current. Evidence: maturing specimens [8]	Probably along the slope near the subtropical convergence. Evidence: mature and fecundate females [7]	Southern Brazilian shelf and slope. Evidence: paralarvae, spawning and spent adults [5] [6] [12]
Range of ML(mm) at full maturity	m: 140-220 f: 150-250 [9]	m: 190-320 f: 250-410 [2] [10] [9]	m: 180-320 f: 230-370 [1]	m: 188-296 f: 240-356 [5] [12]
Oviduct oocyte major axis (mm)	1.19 (1.00-1.30) [1]	1.00-1.70 [2]	1.19 (1.00-1.30) [1]	1.27 (0.9-1.6) [12]
Ripe oocyte weight (mg)	0.38 (0.32-0.46) [11]	0.43 [2] 0.32-0.52 [11]		0.48 (0.38-0.59) [12]
Oviduct oocyte counts (x1000) and ML range (mm)	18.5 (1.5-47.4) ML:190-255 [1] 20.0 [10]	90.1 mean ML: 279 [2]	59.6 (14.6-137.8) ML: 210-350 [1] 20.0-200.0 ML: 220-340 [4]	118.4 (51.5-233.9) ML: 294-336 [12]
Total oocyte counts (x1000) and ML range (mm)	101(82-148) ML: 173-192 [10]	202.7 mean ML: 279 [2] 600-750 ML:330-370 [10]		177.2 (93.0-294.3) ML: 294-336 [12]
Nidamental gland index at maturity	0.48 [7]	0.40-0.55 [2]	0.44 [7]	0.47 (0.40-0.70) [12]
Hectocotylus Index at maturity	over 45% [7]		over 45% [4] [7]	56% (33-69%) [12]

[1] Brunetti *et al.*, 1991; [2] Rodhouse and Hatfield, 1990; [3] Koronkiewicz, 1986; [4] Schuldt, 1979; [5] Haimovici and Perez, 1990; [6] Haimovici *et al.*, 1995; [7] Brunetti, 1990; [8] Haimovici, *et al.*, in press; [9] Nigmatullin, 1989; [10] Laptikhovskiy and Nigmatullin, 1992; [11] Laptikhovskiy and Nigmatullin, 1993; [12] This paper.

Schuldt (1979) observed, in histological slides, that the proportion of oocytes below 0.4 mm was still large in females in advanced maturation, although some of them are probably not released (Laptikhovskiy and Nigmatullin, 1993). The oviduct fecundities of fully mature females were similar to those observed by Schuldt (1979), Rodhouse and Hatfield (1990) and Brunetti *et al.* (1991) (Table 6).

But, if the Argentinean shortfin squid spawn in batches, with an asynchronous vitellogenesis, as proposed by Laptikhovskiy and Nigmatullin (1993), oviduct oocyte counts would not be a good estimator of the total number of oocytes released. Despite the difficulties in the estimation of the proportion of ovary oocytes that should complete maturation, total fecundity is preferable for comparisons.

The importance of southern Brazil as a spawning ground for *Illex argentinus* is still not fully understood. In part this is because the abundance of the species in the region has been only indirectly assessed from bottom trawl surveys (Haimovici and Perez, 1991), studies of trophic relations (Santos, 1992) and paralarval surveys (Haimovici *et al.*, 1995) but not from fishing, as there is no commercial fishery for this species in southern Brazil.

Brunetti (1988) suggests that southern Brazil is a continuation of the Bonaerensis north-Patagonic Stock (BNPS) and that an offshore migration of mature specimens occurs off northern Argentina and Uruguay. Our results suggest that a northward spawning migration of maturing *Illex argentinus* associated with the Brazil and Malvinas Currents system is more likely. There is no direct evidence, such as from marking experiments, but several indirect signs support the hypothesis that southern Brazil may be a major spawning ground for *Illex argentinus* and egg masses or paralarvae could be carried southward and recruit to the Uruguayan and Argentinean shelf. These are:

In contrast to southern Brazil, maturing specimens off Uruguay and northern Argentina were found but in winter and spring mature, partly spawned and spent squids were rare or absent (Schuldt, 1979; Brunetti, 1990; Brunetti *et al.*, 1991).

Size at maturity did not differ from those found off northern Argentina and Uruguay and southern Brazil (Table 6).

Illex argentinus had a higher relative importance in the diet of fish caught on the outer shelf and slope of southern Brazil in the cold part of the year (Zavala-Camin, 1981; Santos, 1992). This suggests that migrants from northern Argentina arrive in winter and spring.

Didymozoids, typical of the digestive tract helminth fauna of tropical and subtropical squids (Hocheberg, 1983), were absent in mature *Illex argentinus* caught in winter and spring, while they were present in the group caught in summer and fall and in juveniles caught year round (Santos, 1992). The absence of didymozoids in the spring spawners would be expected if juveniles and subadults developed in colder waters. In fact, didymozoids were not found in the southern distribution of *Illex argentinus* (Nigmatullin, 1989; Nigmatullin and Shukgálter, 1990; Sardella *et al.*, 1990).

Spawning takes place under the core of the Brazil current, where hatchlings have been found (Haimovici *et al.*, 1995) and paralarvae and egg masses could be transported southward by this current.

A review of paralarval surveys showed that most *Illex argentinus* paralarvae have been collected off Uruguay and southern Brazilian waters (Haimovici *et al.*, in press).

Squids caught in southern Brazil had relative lighter body weights than those sampled further south (Fig. 10). If southern Brazil spawners grew off Uruguay and Argentina, the difference may be associated with the energetic cost of a longer northward reproductive migration. Alternatively a larger supply of food for the winter and spring spawners from the more productive southern region, may provide an explanation for this observation. The spawning season in southern Brazil appears to be more protracted than in higher latitudes, extending at least to October. Individuals spawning over longer periods might benefit from feeding during and after maturity, as observed by Santos (1992) and Ivanovic and Brunetti (1994). The difference in body weight between mature, partly spawned and spent females was in the order of 15% (Fig. 6) less than off Argentina, where according Laptikhovsky and Nigmatullin (1993), individual females spawned over one month and differences were around 40%.

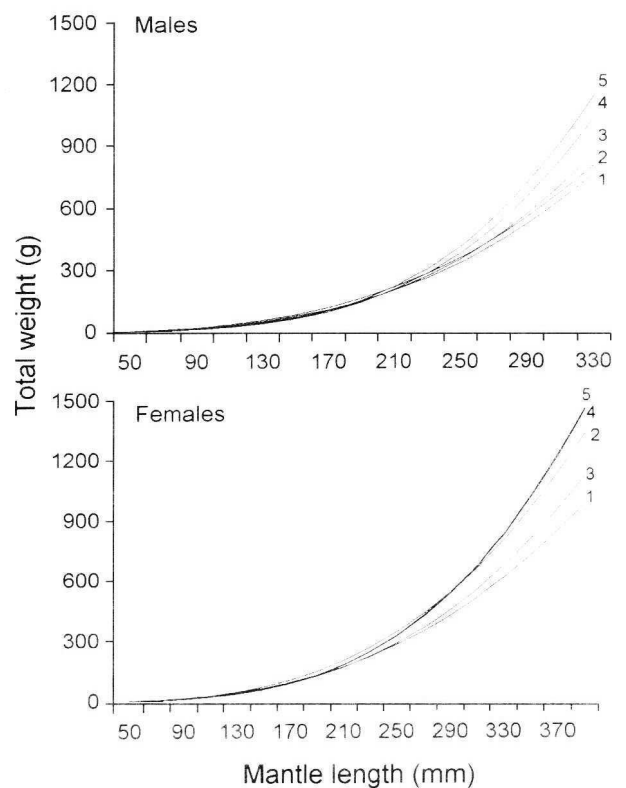


FIG. 10. – Mantle length and total weight relationships of *Illex argentinus* from different regions: 1, southern Brazil; 2, off Uruguay (Leta, 1981); 3, northern Argentina (Brunetti, 1988); 4, around Malvinas Islands (Koronkiewicz, 1986); and 5, southern Argentina (Rodhouse and Hatfield, 1990).

The association between squid migrations and currents has been reported by Hatanaka, *et al.* (1985), Coelho (1985) and O'Dor (1992). Hatanaka *et al.* (1985) suggest there is a relatively short northward migration of maturing *Illex argentinus* and that planktonic juveniles are transported by the Brazil Current to the south. Brunetti (1988: Fig.20) has shown that maturing and mature shortfin squid leave the northern Argentinean and Uruguayan shelf in winter and early spring and move offshore and Leta (1992) suggested that the winter spawning grounds extend up to southern Brazilian waters. Both authors concluded that southern Brazil is a minor spawning ground for *Illex argentinus*. Our results suggest that longer migrations could take place and that in winter and spring, southern Brazil may be a major spawning ground that sustains local recruitment and contributes to the recruitment to Uruguayan and Argentinean waters.

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