REPRODUCTIVE BIOLOGY OF RED SQUID (*Ommastrephes bartramii*) IN THE SOUTHWEST ATLANTIC*

by

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RESUMEN

Biología reproductiva del calamar rojo (*Ommastrephes bartramii*) en el Atlántico Sudoccidental. Se analizaron muestras de calamar rojo (*Ommastrephes bartramii*) obtenidas durante seis cruceros de investigación realizados en la región del Atlántico Sudoccidental adyacente a la plataforma de la Argentina y del Uruguay (33° S-42° S; 43° W-55° W) durante el verano-otoño del período 1997-2002. Las campañas se desarrollaron a bordo del BI japonés "Shinko Maru N° 3" equipado con máquinas poteras en el marco del Programa de Investigación conjunto entre Japón y la Argentina. Los rangos de tallas de los calamares analizados fueron 10-40 cm de largo del manto (LM) para los machos y 12-49 cm LM para las hembras. Se identificaron dos grupos de calamares: mayores y menores de 20 cm LM. El grupo de calamares menores de 20 cm LM se caracterizó por la presencia de individuos inmaduros y la proporción de sexos alrededor de 1:1 en toda el área investigada. Los calamares cuyas tallas superaron los 20 cm LM incluyeron ejemplares inmaduros y maduros, con un aumento de la proporción de machos y de individuos maduros, y de la talla media hacia el norte. Solo se capturaron ejemplares maduros al norte de los 39° S. Las tallas y los pesos del 50% de los ejemplares que estaban maduros fueron estimados en 30,48 cm LM y 852,95 g de peso total (PT) para los machos y en 42,30 cm LM y 2.287,18 g PT para las hembras. El crecimiento en peso del aparato reproductor (PAR) de ambos sexos fue muy lento hasta el comienzo de la maduración (machos: 27-32 cm LM; hembras: 37-45 cm LM). Los índices cuantitativos de madurez basados en mediciones gravimétricas de las estructuras que conforman el aparato reproductor mostraron que al comienzo de la maduración sexual el peso total del mismo representa menos del 1% del PT en ambos sexos. Luego, el crecimiento del aparato reproductor se acelera hasta que el PAR representa el 5% y 8% del PT en los machos y hembras maduros, respectivamente.

SUMMARY

Red squid (*Ommastrephes bartramii*) samples were collected during six exploratory cruises carried out in the Southwest Atlantic region off Argentina and Uruguay (33° S-42° S; 43° W-55° W) during summer-autumn of the period 1997-2002 on board the japanese jigger "Shinko Maru N° 3" under a joint research programme approved by Japan and Argentina. Size ranges of the squids analyzed were 10-40 cm mantle length (ML) for males and 12-49 cm ML for females. Two groups of squids were identified: smaller and larger than 20 cm ML. The group under 20 cm ML was characterized by the presence of immature squids and a sex ratio of around 1:1 in the whole study area. The squids of more than 20 cm ML included from immature to mature individuals. The mean sizes, proportion of mature individuals and proportion of males within this group increased northwards. Mature individuals were captured north of 39°S. The size and weight at 50% maturity were estimated at 30.48 cm ML and 852.95 g body weight (BW) for

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males and 42.30 cm ML and 2,287.18 g BW for females. The growth in weight of the reproductive system in both sexes was slow until the onset of maturity (males: 27-32 cm LM; females: 37-45 cm LM). The quantitative indices of maturity based on gravimetric measurements of the reproductive system structures showed that in both sexes the reproductive system total weight (RSW) represented less than 1% of BW by the onset of maturity. Then, the growth of the reproductive system accelerated, with RSW reaching 5% of male BW and 8% of female BW by the end of maturity.

Key words: *Ommastrephes bartramii*, cephalopod fisheries, size distribution, sexual maturity, Southwest Atlantic.
Palabras clave: *Ommastrephes bartramii*, pesquería de cefalópodos, distribución de tallas, madurez sexual, Atlántico Sudoccidental.

INTRODUCTION

This contibution concludes a series of papers on the distribution, abundance and food of the red squid *Ommastrephes bartramii* (LeSueur, 1821) based on data collected during six exploratory cruises carried out in the Southwest Atlantic region off Argentina and Uruguay between 1997 and 2002 (Brunetti and Ivanovic, 2003; Ivanovic and Brunetti, 2003). Results include some aspects of the reproductive biology of the species such as sex ratio and maturity stages per latitude, size/weight at maturity and maturity indices in order explain the summer-autumn migration pattern of the red squid in the area. The results are compared to those reported for the North and Southwest Pacific regions.

MATERIALS AND METHODS

Samples were taken from six exploratory cruises carried out by the Japanese jigging vessel "Shinko Maru N° 3" under the Japan-Argentina joint research programme developed from 1997 through 2002. The area off Argentina and Uruguay between 33° S and 42° S was investigated in order to obtain information on the distribution and relative abundance of *O. bartramii* from late summer through autumn (Figure 1, Table 1; Brunetti and Ivanovic, 2003).

A total of 8,929 individuals collected in 94 stations were sampled on board for dorsal mantle length (ML, nearest 1 mm), sex (S) and maturity stage (MS) according to the classification of Brunetti (1990) for *Illex argentinus,* with the exclusion of stage VI of females (mated mature

Table 1. Date and number of stations performed in the jigging cruises carried out by RV "Shinko Maru N° 3" in the Southwest Atlantic Ocean, and total number of sampled red squids per sex (N), with their mean mantle length (ML) and variances (S^2), and number of red squids sampled for the analysis of the reproductive system (NR).

Tabla 1. Fecha y número de estaciones efectuadas en los cruceros de pesca exploratoria realizados por el BI "Shinko Maru N° 3" en el Atlántico Sudoccidental; número total de calamares analizados de cada sexo (N), con sus largos de manto promedio (ML) y sus varianzas (S^2), y número de individuos examinados para el análisis del aparato reproductor (NR).

			Males				Females			
Year	Date	N° of station	ML	S^2	N	NR	ML	S^2	N	NR
1997	1-9 March	10	21.05	47.30	986	172	17.98	21.25	513	139
1998	2-11 March	10	23.56	11.65	466	80	25.65	18.47	622	91
1999	27 Feb-10 Mar	12	24.23	33.26	850	98	23.65	41.29	543	102
2000	26 Feb-7 Mar	10	26.26	37.54	863	59	25.97	48.62	552	131
2001	6-16 April	20	26.44	29.68	876	58	29.19	47.84	855	219
2002	16 May-1 Jun	32	24.88	22.28	680	232	29.92	55.12	1,123	278
Total		94			4,721	699			4,208	960

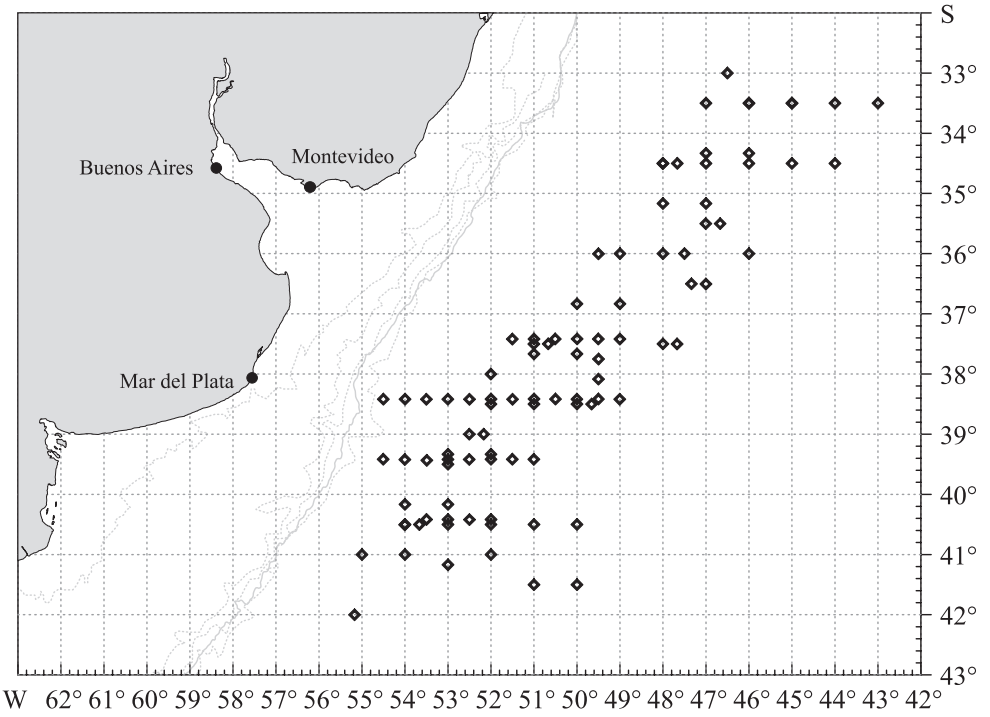

Figure 1. Location of the fishing stations occupied during the six annual exploratory jigging cruises for red squid carried out by the RV "Shinko Maru N° 3" in the period 1997-2002 in the Southwest Atlantic.

Figura 1. Localización de las estaciones de pesca efectuadas durante los seis cruceros anuales de pesca exploratoria de calamar rojo con poteras realizados por el BI "Shinko Maru N° 3" en el período 1997-2002 en el Atlántico Sudoccidental.

inidividuals). Instead, the presence of mated females, with spermatangia attached to the buccal membrane was noted, independently of their gonadal development.

Total body weight (BW; to the nearest 1 g) was measured for 3,041 individuals and its relation to ML was fitted to a power function by linear regression using the logarithmic transformation of BW and ML.

The estimation of the maturity ogive of mature individuals (MS IV and V) was based on fitting of the logistic curve. The equation used is:

$$pm = \frac{1}{1 + e^{-c(ML - ML_{50\%})}} + \varepsilon_{ML}$$

where *pm* is the mean proportion of mature individuals, *ML* is the mantle length and ε_{ML} is an error term with binomial distribution. The coefficient $ML_{50\%}$ is the mantle length at which 50% of individuals are mature, and *c* is a coefficient related to the steepness of the logistic curve. The logistic curve was fitted by maximum likelihood method. Confidence intervals of the coefficients were estimated using the asymptotic property of the estimators with $\alpha = 0.05$. The maturity range (MR) was defined as the difference between $ML_{75\%}$ and $ML_{25\%}$ to establish the size range in which the percentage of mature squids varied between 25% and 75%. The same procedure was applied to total weight (BW) as the independent variable.

For the analysis of the reproductive system, 1,659 squids were sampled (NR in Table 1) and measurements were made to the nearest 0.01 g or 1 mm. For males, testis weight (TW), spermatophoric complex weight (SCW = spermatophoric gland + vas deferens + Needham's

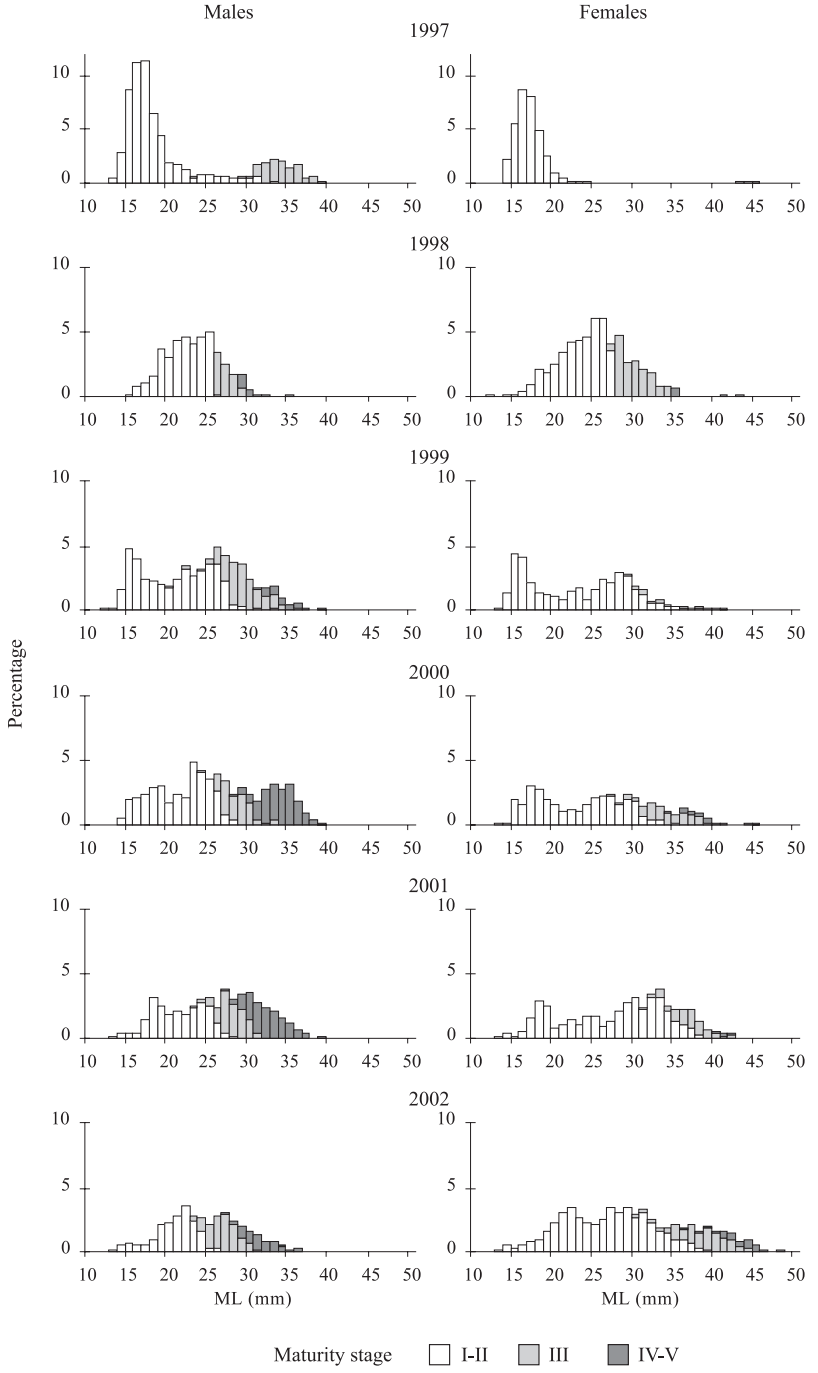

Figure 2. Percentual distribution of sizes (ML) and maturity stages per size, sex and year of the red squid caught during the six surveys of the RV "Shinko Maru N° 3" in the Southwest Atlantic.

Figura 2. Distribución porcentual de tallas (ML) y de estadios de madurez por talla, sexo y año del calamar rojo capturado durante los seis cruceros realizados por el BI "Shinko Maru N° 3" en el Atlántico Sudoccidental.

sac), hectocotylized arm length (HAL) and hectocotylus length (HL) were measured. For females, ovary weight (OW), oviduct + oviducal gland weight (ODW) and nidamental gland weight (NGW) and length (NGL) were registered. Reproductive system weight (RSW) of each sex was estimated as the sum of the weights of all component structures. A total of 30 oocytes taken from the oviducts of a full mature female were measured along their long and short axis using an ocular micrometer with a precision of 0.01 units and then transformed to mm. Indices for each sex were calculated as follows:

-Males
Testis weight index:
TWI = 100 * (TW / (BW - TW))
Spermatophoric complex weight index:
SCWI = 100 * (SCW / (BW - SCW))
Reproductive system weight index:
RSWI = 100 * ((TW + SCW) / (BW - TW – SCW))
Hectocotylization index:
HI = 100 * (HL / HAL)
-Females
Ovary weight index:
OWI = 100 * (OW / (BW - OW))
Oviduct + oviducal gland weight index:
ODWI = 100 * (ODW / (BW - ODW))
Reproductive system weight index:
RSWI = 100 * ((OW+ODW+NGW) / (BW-OW-ODW- NGW))
Nidamental gland length index:
NGLI = 100 * NGL / ML

RESULTS

Size distribution, sex ratio and maturity stages

Pooled individual sizes over the 6-year period analyzed ranged from 10 to 40 cm ML for males, and from 12 to 49 cm ML for females, with the modal size of females larger than that of males (Figure 2). Two groups of squids were clearly identified within both sexes: individuals smaller and larger than 20 cm ML. The specimens smaller than 20 cm ML were always immature (98% MS I), while those larger than 20 cm ML were found to include from immature to mature individuals (MS I to V). Spent individuals were not observed. A detailed analysis of each cruise was presented by Brunetti and Ivanovic (2003).

A shift of the 1:1 sex ratio was observed in both groups of squids when they were analyzed on a latitudinal basis (Figure 3). The proportion of males decreased with increasing latitude but the degree of change was different between both size groups. Within the "small-size" group, the sex ratio ranged from a minimum of 0.55:1 to a maximum of 1.57:1 and the trend of decreasing male proportion with increasing latitudes was less evident. On the other hand, within the "large-size" group, the trend of decreasing male proportion with increasing latitudes was extremely marked with a sex ratio of 11.79:1 at 33° S and a sex ratio of 0.41:1 at 41° S.

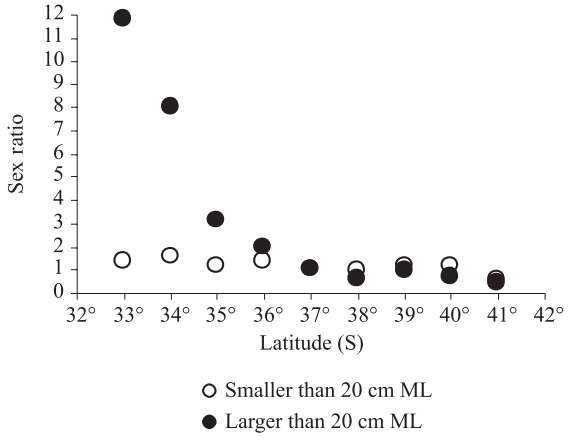

Figure 3. Sex ratios (males/females) per latitude of capture for Southwest Atlantic red squids smaller and larger than 20 cm mantle length (ML).

Fig*ura 3. Proporción de sexos (machos/hembras) por latitud de captura del calamar rojo del Atlántico Sudoccidental menor y mayor de 20 cm de largo de manto (ML).*

Among squids larger than 20 cm ML, the proportion of mature individuals was low, particularly between females, of which 80% were immature (MS I and II), 16% maturing (MS III), 3% early mature (MS IV) and, only four animals (1%) were found fully mature (MS V, Figure 4). Regarding mating, five females were found with spermatophores attached to the buccal membrane. Four of them were caught in the north area (33°-35°S) and their MS were IV and V. The fifth specimen was an immature female (MS II) caught at 36°30' S. The maturity development of males was more advanced, with 48% of immature, 27% of maturing and 24% of mature individuals. For any latitude, the size range of females was wider than that of males. The highest proportion of mature individuals was observed to the north of 36° S. From there, the immaturity ratio increased southwards, together with a decrease of the mean sizes of both sexes.

Body weight and mantle length relationship

The relationship between BW and ML per sex is shown in Figure 5. As a practical tool, the relationship calculated considering both sexes together is also presented. Females attained heavier weights than males. The maximum body weights recorded were 2,040 g, for a male of 408 mm ML, and 3,300 g, for a female of 488 mm ML. Both animals were fully mature.

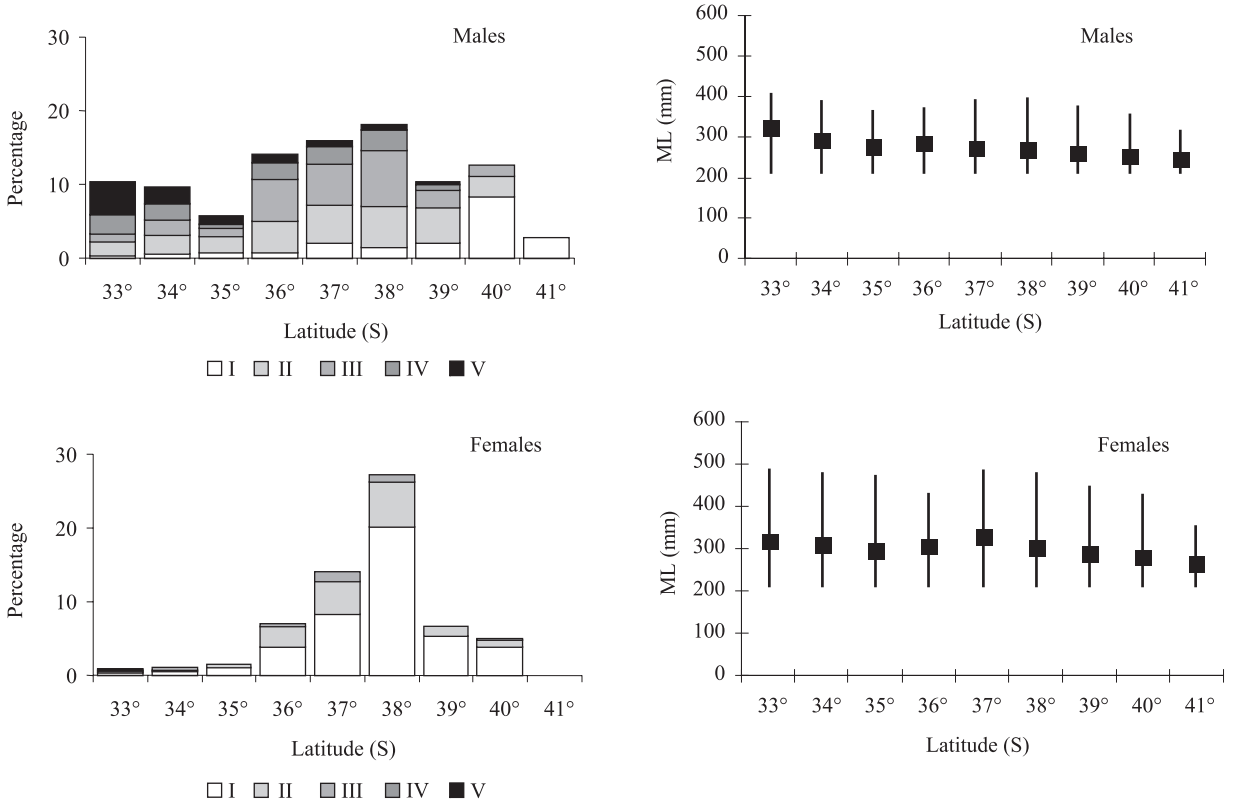

Figure 4. Percentual distribution of maturity stages, size range and mean size (ML) per latitude of capture and per sex of the red squid larger than 20 cm ML caught during the six cruises of the RV "Shinko Maru N° 3" in the Southwest Atlantic.

Figura 4. Distribución porcentual de estadios de madurez, rango de tallas y tallas medias (ML) por latitud de captura y por sexo del calamar rojo mayor de 20 cm LM capturado durante los seis cruceros realizados por el BI "Shinko Maru N° 3" en el Atlántico Sudoccidental.

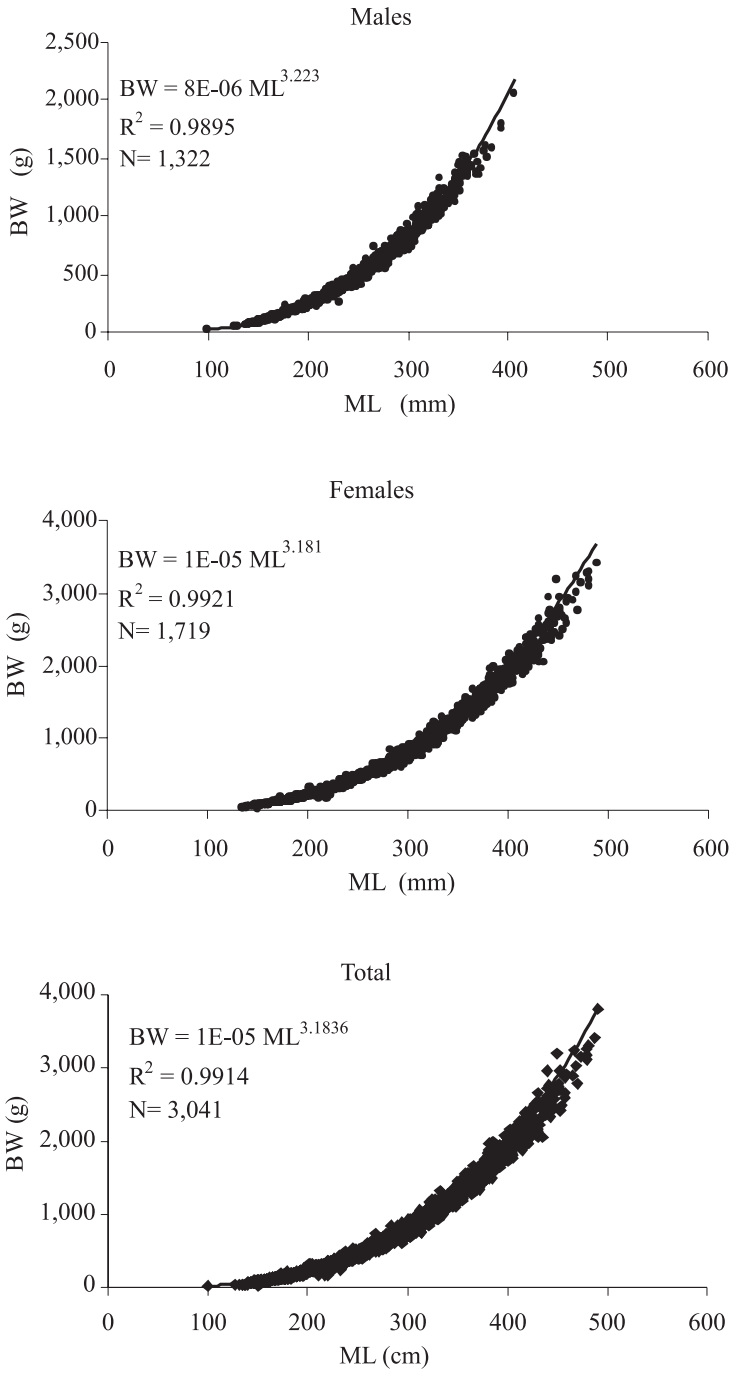

Figure 5. Observed (circles) and estimated (line) relationships between body weight (BW) and mantle length (ML) for the male, female and total (male+female) red squids caught during the six surveys of RV "Shinko Maru N° 3" in the Southwest Atlantic.

Figura 5. Relaciones observadas (círculos) y estimadas (línea) entre el peso del cuerpo (BW) y el largo del manto (ML) de los machos, hembras y ambos sexos sumados (total) del calamar rojo capturado durante los seis cruceros realizados por el BI "Shinko Maru N° 3" en el Atlántico Sudoccidental.

Size and weight at maturity

The size at 50% maturity was estimated at 30.48 cm ML for males and 42.30 cm ML for females (Figure 6, Table 2). The MR of males (2.210 cm) was shorter than that of females (3.769 cm), showing that the maturation process involved a shorter size range. It is worth mentioning that sizes over 45 cm ML among females were poorly represented since at most four animals were available per size class.

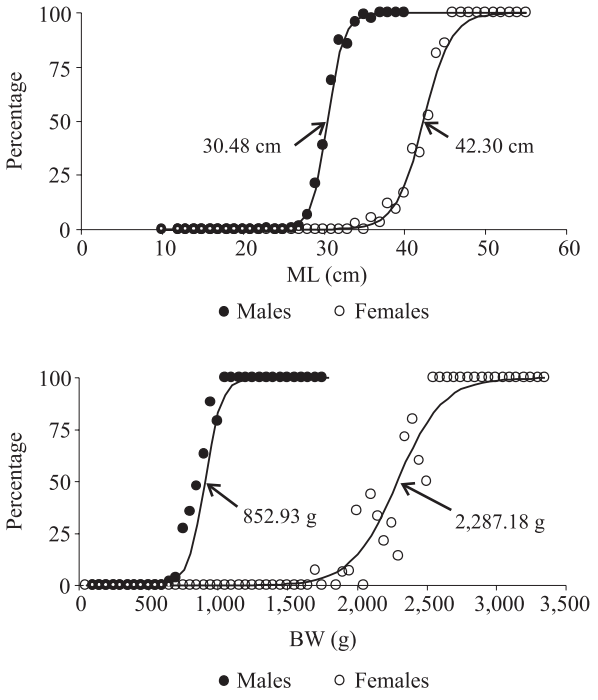

Figure 6. Observed (circles) and estimated (line) relationships between the percentage of male and female mature red squids and mantle length (ML), and between the percentage of male and female mature red squids and body weight (BW). Arrows indicate the $ML_{50\%}$ and $BW_{50\%}$ estimated values.

Figura 6. Relaciones observadas (círculos) y estimadas (línea) entre el porcentaje de machos y hembras maduros de calamar rojo y el largo del manto (ML), y entre el porcentaje de machos y hembras maduros de calamar rojo y el peso del cuerpo (BW). Las flechas indican los valores estimados de $ML_{50\%}$ y $BW_{50\%}$.

In terms of body weight, $BW_{50\%}$ values were 852.95 and 2,287.18 g for males and females, respectively. Again, the MR of males was the lowest.

When analyzing $ML_{50\%}$ and $BW_{50\%}$ in BW/ML relationship, they corresponded to the moment when the increment in length slowed down while the increment in weight accelerated (Figure 5).

Reproductive system development and maturity indices

The study of the development of the reproductive system of males showed that their reproductive systems weighted less than 1% of BW during immaturity (MS I and II), when squids had mean sizes less than 244 mm ML and mean BW less than 443 g (Figure 7, Table 3). For the same maturity stages TWI and SCWI showed values lower than 0.6% and 0.25%, respectively. When the maturation process started, in animals at MS III, the testis weight increased notably, reaching a mean TWI of 1.6%. The development of the structures of the spermatophoric complex was indicated by the doubling of the SCWI that reached a mean value of 0.45%. In early mature animals (MS IV) over 300 mm ML, testis growth continued, showing a mean TWI of 2.4%, while the storage of the first spermatophores inside the Needham's sac produced an increment of the mean SCWI to 1.18%. In fully mature squids, the testis weight reached a maximum, and the mean SCWI reached almost the same value as the TWI, around 2.5%, because of the filling of the Needham's sac with spermatophores. At this maturity stage, the whole reproductive system represents in average 5.3% of the body weight. The highest testis weight was 45.8 g, observed in a squid of 371 mm ML, and the highest spermatophoric complex weight was 79 g, in a specimen of 354 mm ML.

The hectocotylization process was observed in MS-I animals larger than 200 mm ML where the mean HI was 10.4% (Table 3). In MS-II squids, the HI ranged from 11.2% to 22.0%. On the other

Table 2. Estimated parameters (C, $ML_{50\%}$ and $BW_{50\%}$) of the maturity ogives by mantle length and body weight of Southwest Atlantic male and female red squid, with their 95% confidence intervals between parenthesis, and estimated mantle lengths and body weights at 25% ($ML_{25\%}$ and $BW_{25\%}$) and 75% maturity ($ML_{75\%}$ and $BW_{75\%}$) and their difference (MR).

Tabla 2. Parámetros estimados (C, $ML_{50\%}$ y $BW_{50\%}$) de las ojivas de madurez en largo del manto y peso total para ambos sexos del calamar rojo del Atlántico Sudoccidental, con los intervalos de confianza del 95% entre paréntesis, y largos del manto y pesos totales estimados cuando el 25% ($ML_{25\%}$ y $BW_{25\%}$) y el 75% ($ML_{75\%}$ y $BW_{75\%}$) de los calamares están maduros y su diferencia (MR).

	Males	Females
Mantle length (cm)		
C	0.994 (+/-0.084)	0.583 (+/-0.089)
$ML_{50\%}$	30.479 (+/-2.534)	42.299 (+/-6.120)
$ML_{25\%}$	29.374	40.414
$ML_{75\%}$	31.584	44.183
MR	2.210	3.769
Body weight (g)		
C	0.016 (+/-0.003)	0.006 (+/-0.001)
$BW_{50\%}$	852.926 (+/-143.968)	2287.183 (+/-475.064)
$BW_{25\%}$	786.129	2107.746
$BW_{75\%}$	919.723	2466.620
MR	133.594	358.874

Table 3. Analysis of the reproductive system of Southwest Atlantic red squid males per maturity stage (MS). Mean size (ML) and weight (BW) of the squids sampled. Minimum, mean and maximum values and number of individuals sampled for spermatophoric complex and testis weight. Mean values of the following indices: spermatophoric complex weight index (SCWI), testis weight index (TWI), reproductive system weight index (RSWI) and hectocotylization index (HI).

Tabla 3. Análisis del aparato reproductor de los machos de calamar rojo del Atlántico Sudoccidental por estadio de madurez (MS). Talla (ML) y peso (BW) medio de los calamares de la muestra. Valores mínimos, medios y máximos de los pesos del complejo espermatofórico y del testículo y número de individuos analizados. Valores medios de los siguientes índices: índice en peso del complejo espermatofórico (SCWI), índice en peso del testículo (TWI), índice en peso del aparato reproductor (RSWI) e índice de hectocotilización (HI).

			Spermatophoric complex weight (g)				Testis weight (g)				Mean indices (%)			
MS	ML (mm)	BW (g)	Min.	Mean	Max.	N	Min.	Mean	Max.	N	SCWI	TWI	RSWI	HI
I	200	240	0.1	0.4	1.3	119	0.1	0.5	2.0	187	0.15	0.2	0.3	10.4
II	244	443	0.4	1.1	6.0	166	0.3	2.9	14.9	176	0.22	0.6	0.8	15.2
III	284	691	0.5	3.3	8.9	142	2.5	11.0	24.0	146	0.45	1.6	2.1	28.9
IV	328	1037	4.5	12.4	37.2	99	14.5	24.3	37.9	98	1.18	2.4	3.6	41.0
V	358	1354	13.0	34.0	79.0	66	24.2	34.0	45.8	66	2.56	2.6	5.3	45.3

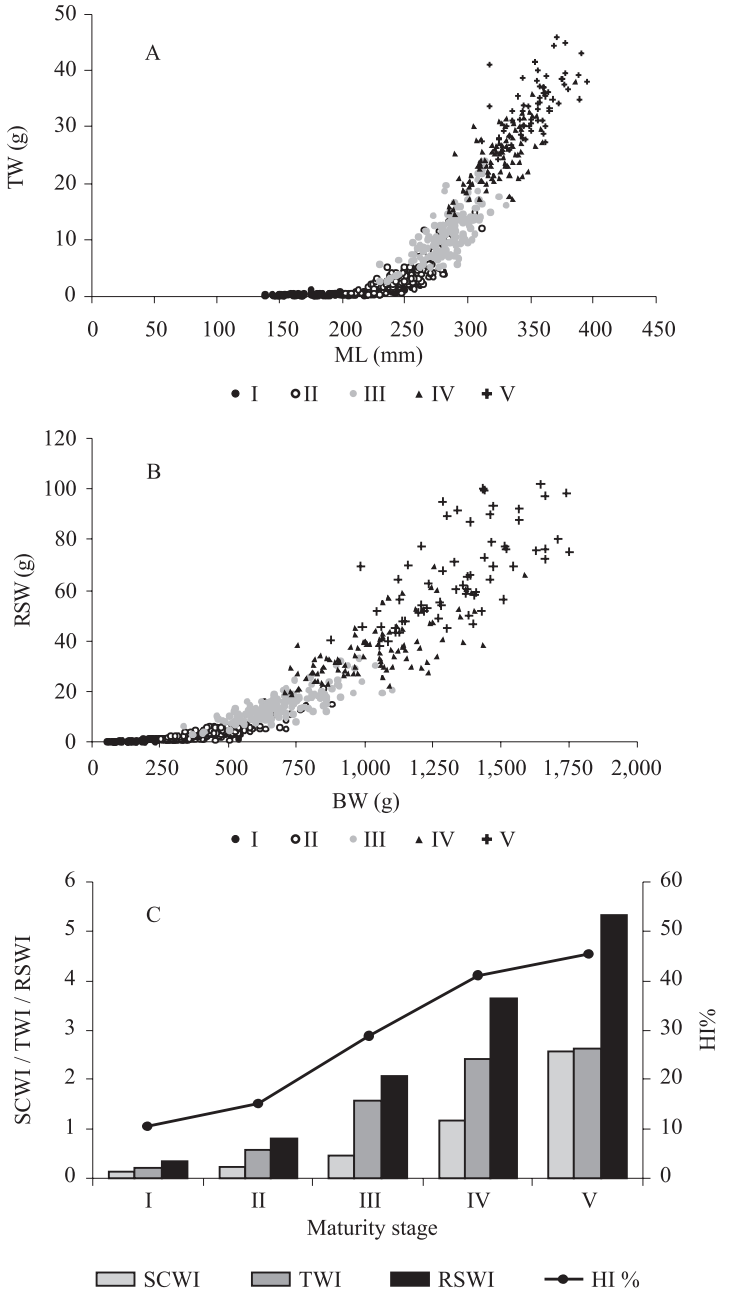

Figure 7. *O. bartramii* males. A) Relationship between testis weight (TW) and mantle length (ML) per maturity stage. B) Relationship between reproductive system weight (RSW) and body weight (BW) per maturity stage. C) Mean values of the spermatophoric complex weight index (SCWI), testis weight index (TWI) and reproductive system weight index (RSWI) on the left axis and mean hectocotylization index (HI) on the right axis, per maturity stage.

Figura 7. Machos de O. bartramii. A) Relación entre el peso del testículo (TW) y el largo del manto (ML) por estadio de madurez. B) Relación entre el peso del aparato reproductor (RSW) y el peso del cuerpo (BW) por estadio de madurez. C) Valores medios del índice en peso del complejo espermatofórico (SCWI), del índice en peso del testículo (TWI) y del índice en peso del aparato reproductor (RSWI) sobre el eje izquierdo y del índice de hectocotilización (HI) sobre el eje derecho, por estadio de madurez.

hand, among mature individuals, the HI ranged between 37% and 45% in MS-IV squids, and between 40% and 53% in MS-V specimens.

The female reproductive system suggested a very slow growth as indicated by the small ovary and oviduct weights in individuals with mantle lengths smaller or equal than 450 mm (Figure 8, Table 4). An "explosive" increment in the weight of the female reproductive organs appeared to have occurred at MS V, as suggested by their indices. As a whole, the RSWI grew from 0.47% in MS I to 1.07% in MS IV, to increase then seven times (8.13%) at MS V. The NGL showed a similar developmental pattern, with a first phase of small weights for individuals with mantle lengths ranging from 120 to 450 mm, followed by a notable increase in weight within a relatively short ML range (450-500 mm). The maximum ODW (130 g) and NGL (195 mm) were observed in a squid of 491 mm ML, 3,800 g BW and 140 g OW.

A sample of 30 oocytes was extracted from the oviducts of a full mature female. They were oval in shape and showed a mean length of the long axis of 1.27 mm ($S^2 = 0.0091$) whereas that of the short axis was 0.89 mm ($S^2 = 0.0071$).

Table 4. Analysis of the reproductive system of Southwest Atlantic red squid females per maturity stage (MS). Mean size (ML) and weight (BW) of the squids sampled. Minimum, mean and maximum values and number of individuals sampled for oviduct and ovary weight and nidamental gland length. Mean values of the following indices: oviduct weight index (ODWI), ovary weight index (OWI), reproductive system weight index (RSWI), nidamental gland weight index (NGWI) and nidamental gland length index (NGLI).

Tabla 4. Análisis del aparato reproductor de las hembras de calamar rojo del Atlántico Sudoccidental por estadio de madurez (MS). Talla (ML) y peso (BW) medio de los calamares de la muestra. Valores mínimos, medios y máximos de los pesos del oviducto y ovario y del largo de la glándula nidamental y número de individuos analizados. Valores medios de los siguientes índices: índice en peso del oviducto (ODWI), índice en peso del ovario (OWI), índice en peso del aparato reproductor (RSWI), índice en peso de la glándula nidamental (NGWI) e índice en largo de la glándula nidamental (NGLI).

			Oviduct weight (g)				Ovary weight (g)				Nidamental gland length (mm)			
MS	ML (mm)	BW (g)	Min.	Mean	Max.	N	Min.	Mean	Max.	N	Min.	Mean	Max.	N
I	194	212	0.01	0.10	0.60	379	0.03	0.84	3.80	438	6	12.90	22	398
II	288	742	0.05	0.49	3.80	330	0.55	3.94	11.50	362	14	26.51	48	353
III	384	1713	0.20	1.21	4.60	104	4.30	10.67	22.60	124	28	48.83	80	125
IV	427	2372	1.00	4.03	10.40	22	6.70	20.62	78.00	28	47	73.31	148	29
V	468	3060	25.00	85.50	130.00	4	115.00	147.75	205.00	4	165	180.25	195	4

	Mean indices (%)				
MS	ODWI	OWI	RSWI	NGWI	NGLI
I	0.06	0.38	0.47	0.20	6.63
II	0.08	0.53	0.67	0.31	9.06
III	0.07	0.62	0.71	0.39	12.64
IV	0.16	0.83	1.07	0.46	17.06
V	2.71	5.12	8.13	3.46	38.56

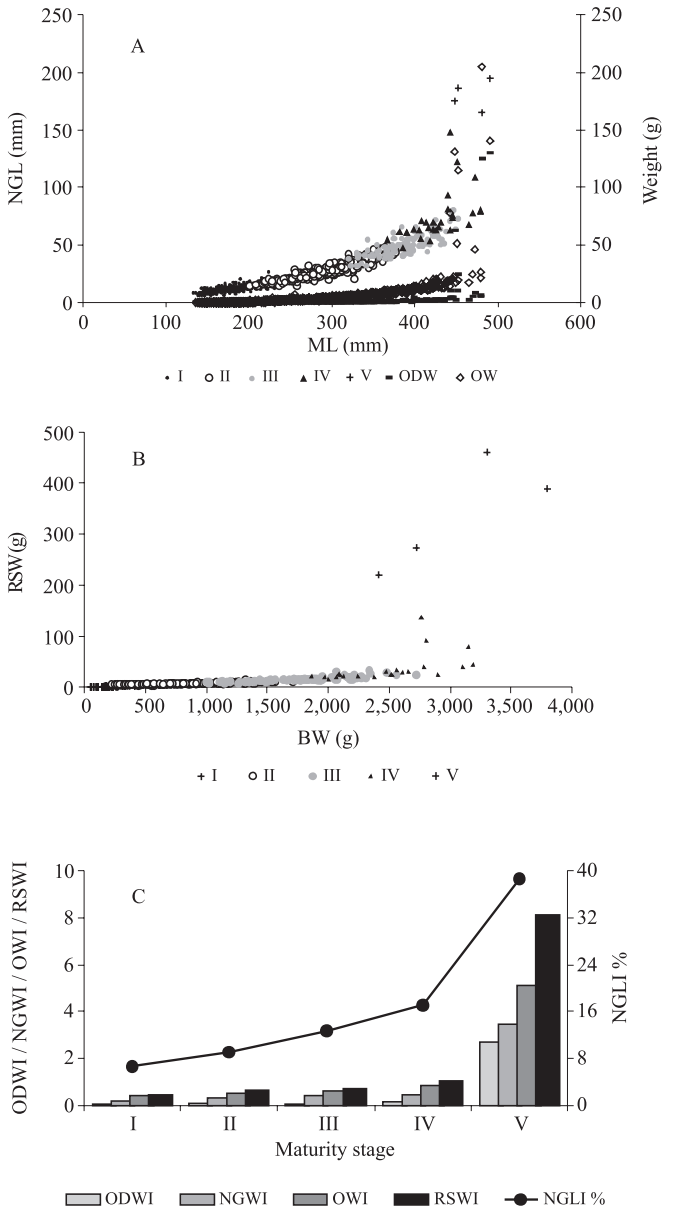

Figure 8. *O. bartramii* females. A) Relationships between oviduct (ODW) and ovary weight (OW) with mantle length (ML) and nidamental gland length (NGL) per maturity stage with ML. B) Relationship between reproductive system weight (RSW) and body weight (BW) per maturity stage. C) Mean values of oviduct weight index (ODWI), nidamental gland weight index (NGWI), ovary weight index (TWI) and reproductive system weight index (RSWI), on the left axis, and nidamental gland length index (HI), on the right axis, per maturity stage.

Figura 8. Hembras de O. bartramii. A) Relación entre el peso del oviducto (ODW) y del ovario (OW) con el largo del manto (ML) y del largo de la glándula nidamental (NGL) por estadio de madurez con ML. B) Relación entre el peso del aparato reproductor (RSW) y el peso del cuerpo (BW) por estadio de madurez. C) Valores medios del índice en peso del oviducto (ODWI), del índice en peso de la glándula nidamental (NGWI), del índice en peso del ovario (OWI) y del índice en peso del aparato reproductor (RSWI), sobre el eje izquierdo, y del índice en largo de la glándula nidamental (NGLI), sobre el eje derecho, por estadio de madurez.

DISCUSSION

This research covers only three months of the year (March-May) and a small portion, restricted to the southern limit, of the whole distributional area of *O. bartramii* in the Southwest Atlantic region. Few studies had been conducted to investigate this area, most of them by Russian expeditions during the 60's and 70's (Dunning, 1998) and Uruguayan cruises during the 80's (Leta, 1986, 1989).
The observed size and weight ranges were coincident with those reported in Russian, Uruguayan and other investigations (Dudnik *et al.,* 1973 –cited in Dunning, 1998–; Maxim, 1979 and 1983; Leta, 1986 and 1989; Lipinski and Linkowski, 1988). However, Nigmatullin (1989, cited in Dunning, 1998) reported the catch of larger squids in this area, males up to 42 cm ML and 2.2 kg BW and females up to 80 cm ML and 20-25 kg BW.

Multi-cohort seems to be a recurrent pattern of red squid populations that has been observed in the Pacific and Southwest Atlantic regions (Leta, 1986; 1989; Murata, 1990; Dunning, 1993; 1998; Yatsu *et al*. 1998). Two cohorts were detected during this study. The first includes small immature squids up to 20 cm ML with sex ratio around 1:1 and equally distributed in the whole study area. The second cohort comprises immature-to-mature animals larger than 20 cm ML that exhibit an increase in mean size, degree of maturity and proportion of males towards northern latitudes. Mature males were captured north of 39° S and mature females north of 35° S.

Males appear to mature earlier than females. The size at 50% maturity and maturity ranges estimated for both sexes were consistent with those summarized in Dunning (1998) for the same region, and also for the North and Southwest Pacific (Yatsu *et al*., 1998). In all studied regions, males begin to reach maturity at 27-32 cm ML and females at 37-45 cm ML. A second group of large females, maturing at sizes over 50 cm ML in the North Pacific (Nakamura and Siriraksophon, 1992; Yatsu *et al*., 1998) and over 60 cm ML in the Southwest Atlantic and Southwest Pacific (summarized in Dunning, 1998), was not captured during "Shinko Maru" cruises.

Evidences suggest great similarities between the life spans and migratory patterns of red squid of the Southwest Atlantic and those of the North and South Pacific regions (Sinclair, 1991; Dunning, 1993; Murata and Hayase, 1993). During summer and autumn, squids occupy the vicinity of the Subarctic (36° N-46° N) and Subantarctic frontal regions (36° S-42° S), which are highly productive areas that provide the appropiate environment to feed and grow (Seki, 1993; Watanabe *et al.*, 2004). At the end of autumn, they start their migration to the spawning grounds in subtropical waters (25° N-27° N; Hayase, 1995). In the study area, the sexual segregation of the squids over 20 cm ML north of 36° S, with males outnumbering females and a large proportion of mature individuals, very much resembled the pattern reported by Dunning (1993) for the Tasman Sea region during summer and autumn. The pattern is explained as an early migration of maturing males towards northern warmer waters, with females remaining in the cooler southern waters to continue feeding and growing. In the Southwest Atlantic region, it is probable that the spawning and nursery areas are placed off the Brazilian shelf between 25° S and 29° S, where surface water temperatures (24-26 °C) are similar to those of similar latitudes in the North and South Pacific. Support for a northern location of the Southwest Atlantic red squid spawning and nursery areas is provided by Maxim (1979) and by Leta (1989). Maxim (1979) found only 22 out of 921 females examined at MS IV and none fully mature individual south of 30° S during January-April, and Leta (1989) found no mature females south of 34° S during August-September. Besides, juveniles ranging 3-9 cm ML were found in the stomach contents of yellowfin tuna captured in Southern Brazil (28° S-35° S) during winter-spring (Vaske and Castello, 1998).

Although all the structures of the reproductive system of both sexes were conspicuous within the analyzed size range, the growth of the reproductive organs appears to have been notably slow until MS III was reached (13-27 cm ML in males and 12-37 cm ML in females). At this maturity stage the whole reproductive system weighted less than 1% of BW. Then, the reproductive system growth appears to have progressed rapidly, attaining maximal weights representing 5% and 8% of the body weight of males and females, respectively. A similar developmental pattern of the reproductive system has been already reported for the North and Southwest Pacific (Murata *et al.*, 1988; Dunning, 1993; Yatsu *et al.*, 1998).

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