

Spatial and temporal patterns in size and maturation of *Loligo plei* and *Loligo sanpaulensis* (Cephalopoda: Loliginidae) in southeastern Brazilian waters, between 23°S and 27°S

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SUMMARY: Patterns of population dynamics of *Loligo plei* and *Loligo sanpaulensis* in southeastern Brazil were investigated with samples obtained from commercial catches and research cruises from 1999 to 2000 and from 2002 to 2003. Size and maturity structure of the two species varied according to depth and season. Body size decreased with depth for *L. plei*, whereas for *L. sanpaulensis* size increased with depth up to 100 m and decreased again in deeper areas. GSI and incidence of mature animals decreased with depth in both species. *L. plei* females matured at a larger size in summer, while size at maturity in *L. sanpaulensis* was greater in autumn. For *L. plei*, reproductive events occurred in the late winter and spring, in depths up to 40 m, and during summer in inshore waters. *L. sanpaulensis* increased reproductive activity in summer, winter and spring between depths of 30 and 80 m. The presence of high proportions of immature squid offshore suggests that juveniles might develop in these areas and, upon maturation, migrate back to inshore waters to spawn, particularly in spring and summer. However, differences found in aggregation patterns in different depth strata, as well as the seasonal differences found in the size structure of *L. plei* and *L. sanpaulensis*, could ultimately be due to changes in the water column related to food availability. Considering that *L. plei* and *L. sanpaulensis* are both caught as by-catch by shrimp trawlers throughout the year, we also discuss hypotheses on the life cycle of the species and its implications for fishery management. We recommend measures to protect squid spawning grounds by creating spring and summer protected areas where trawling would be prohibited until 60 m depth, i.e. in the area and time of year when mature individuals concentrate.

Keywords: *Loligo*, squid, cephalopod, spatial and temporal patterns, fisheries, Brazil.

RESUMEN: PATRONES ESPACIALES Y TEMPORALES EN TALLA Y MADURACIÓN DE *LOLIGO PLEI* Y *LOLIGO SANPAULENSIS* (CEPHALOPODA: LOLIGINIDAE) EN AGUAS DEL SURESTE DE BRASIL, ENTRE 23°S Y 27°S. – Se investigó la dinámica poblacional de *Loligo plei* y *Loligo sanpaulensis* en el sureste de Brasil, a partir de muestras obtenidas de capturas comerciales y campañas de investigación desde 1999 a 2000 y de 2002 a 2003. La estructura de tallas y de maduración de ambas especies varió de acuerdo con la profundidad y la estación. La talla disminuyó con la profundidad en *L. plei*, mientras que en *L. sanpaulensis* se incrementó hasta los 100 m y disminuyó de nuevo en áreas más profundas. El índice gonadosomático y la incidencia de animales maduros disminuyó con la profundidad en ambas especies. Las hembras de *L. plei* maduraron a una talla mayor en verano, mientras que la talla de madurez de *L. sanpaulensis* fue mayor en otoño. Para *L. plei*, la reproducción se produjo a final del invierno, a profundidades de hasta 40 m, y durante el verano, en aguas costeras. Para *L. sanpaulensis*, se identificó un incremento en la actividad reproductiva en verano, invierno y primavera entre las profundidades de 30 a 80 m. La presencia de altas proporciones de calamares inmaduros en mar abierto sugiere que los juveniles podrían desarrollarse en esas aguas y, con la maduración, migrar a las aguas costeras para frezar, particularmente en primavera y verano. No obstante, las diferencias en patrones de agregación observadas en diferentes estratos de profundidad, así como las diferencias estacionales encontradas en la estructura de tallas de *L. plei* y *L. sanpaulensis*, podría ser función de cambios en la columna de agua relacionados con la disponibilidad de alimento. Considerando que *L. plei* y *L. sanpaulensis* se capturan como *by catch* de los arrastros de camarón a lo largo del año, se discuten las hipótesis de ciclos de vida específicos y sus implicaciones en la gestión de la pesquería. Recomendamos medidas para proteger las áreas de puesta del calamar mediante la creación de áreas protegidas, donde el arrastre esté prohibido hasta 60 m, en primavera y verano, área y periodo en que los individuos maduros se concentran.

Palabras clave: *Loligo*, calamar, cefalópodos, patrones espaciales y temporales, pesquerías, Brasil.

INTRODUCTION

Loliginid squid play a significant economic and ecological role in coastal marine ecosystems worldwide as many species are fishery resources and represent a key link in marine food webs (Pierce and Guerra, 1994; Santos and Haimovici, 2002; Boyle and Rodhouse, 2005; Pierrepont *et al.*, 2005; Rodhouse, 2005; Staudinger, 2006). Along the southern Brazilian coast, *Loligo plei* (Blainville, 1823) and *Loligo sanpaulensis* (Brakonieccki, 1984) are the most abundant species of Loliginidae, and are fishery resources of local interest (Perez *et al.*, 2005; Gasalla *et al.*, 2005a,b).

Loligo plei is commercially caught from Cape Frio (22°S) to Cape Santa Marta Grande (28°S), and is the most important Loliginid species in the fisheries of the Brazilian states of São Paulo and Santa Catarina. In these areas, *L. plei* is mainly fished as a by-catch of the pink-shrimp fishing trawlers (Perez *et al.*, 2005) and seasonally by coastal hand jigging (Gasalla, 2004; Gasalla *et al.*, 2005b; Martins *et al.*, 2006). Catches by all gears peak in summer. However, *Loligo sanpaulensis* is of secondary importance in commercial fishing in the southeastern Brazilian states of São Paulo and Santa Catarina, but is the main fished loliginid squid species in the states of Rio de Janeiro and Rio Grande do Sul (Gasalla *et al.*, 2005a).

In Brazil, studies of the two species began during the 1970s through sampling undertaken in the FAUNEC survey, conducted by the University of São Paulo (Juanicó, 1979). Later, studies concentrated mainly on the *L. sanpaulensis* population along the coasts of Rio Grande do Sul and Cape Frio (Haimovici and Andriquetto, 1986; Costa and Fernandes, 1993; Andriquetto and Haimovici, 1996; Santos and Haimovici, 1998). In the mid 1990s, studies on squid population dynamics were initiated in Santa Catarina and São Paulo based on commercial fisheries, and since then studies have focused on *Loligo plei* (i.e. Perez and Pezzutto, 1998; Perez, 2002; Perez *et al.*, 2002; Gasalla *et al.*, 2005a,b).

In summary, previous knowledge has shown that both *Loligo* species have short life cycles and are semelparous. Males have a broader size range distribution and larger maximum sizes than females and their length-frequency distribution is approximately log-normal, while female lengths usually show normal distributions. In addition, some hypotheses on spatial patterns in size of maturation

in relation to season, depth ranges and inshore-offshore migration have been proposed (Juanicó, 1979; Andriquetto and Haimovici, 1991, 1996; Perez, 2002). One hypothesis suggests that there might be more than one population of *L. sanpaulensis* in Brazilian waters (Gasalla *et al.*, 2005a). This hypothesis refers specifically to work carried out by Juanicó (1979) that showed four distinct groups with different morphological characteristics within *L. sanpaulensis* samples caught between Rio de Janeiro (22°S) and Rio Grande (32°S). The northern-most and southern-most groups seem to be much alike, and are separated spatially by the intermediate Santa Catarina (27°S) group (Juanicó, 1979), which tends to suggest that the differences could be environmentally driven.

Considering that knowledge of the life history and population structure of a species is crucial for fishery management, this paper presents results of a study on spatial and temporal variation in size and maturation of *L. plei* and *L. sanpaulensis* along the southeastern coast of Brazil.

MATERIALS AND METHODS

The study area is located in the South Brazil Bight (SBB), spanning southern Rio de Janeiro state (23°S) to Itajaí, in Santa Catarina state (27°S). From August 1999 to December 2000, and between August 2002 and July 2003, *L. plei* and *L. sanpaulensis* were obtained as by-catch of pink-shrimp (*Farfantepenaeus* spp) trawl fishing, at depths of 30 to 100 m. Monthly or, when possible, weekly samples were collected at the ports of Santos and Guarujá. Size-stratified random subsamples (Sparre and Venema, 1998) were collected and, when catches were very small, all landed squids were sampled. Skippers were interviewed to obtain information about the fishery, such as location and depth of capture. In some cases, complementary information was obtained from landing records held in the Instituto de Pesca "ProPesq®" fishery database. Complementary data were obtained from demersal fish surveys of the REVIZEE National Research Program. In this case, specimens of *L. sanpaulensis* were collected with the bottom-trawler "Soloncy Moura" at depths ranging from 100 to 150 m in February, April and June 2002.

Mantle length (ML, mm) and total body weight (BW, g) were recorded in the laboratory. Sex and

maturity stages were identified according to a scale proposed by Juanicó (1983) and adapted by Perez *et al.* (2002): (I) immature, (II) in maturation, (III) mature and (IV) spawners. Individuals that could not be sexed were classified as “juvenile”.

Length–weight relationships (LWR) were calculated using the expression:

$$BW = aML^b,$$

the parameters a (intercept) and b (slope) were estimated by non-linear regression. Analysis of covariance (ANCOVA) was used to test differences between the slopes of the LWR obtained for each sex. In view of the supposed existence of more than one population of *L. sanpaulensis* in Brazilian waters, the LWR was also calculated for two separate groups: (a) individuals caught between Santos (24°S) and Itajaí (27°S), and (b) those captured in the northern part of the studied area (between 23°50'S and 23°00'S).

Gonad weight (GW) and accessory reproductive organ weight (AOW) (spermatophoric Complex + Needham's sac + penis, for males, and oviduct + nidamental glands + oviducal gland, for females) were obtained. Appropriate standard indices of maturity and reproductive activity were tested before adopting the gonadosomatic index (GSI) (*sensu* Macy, 1982; Raya *et al.*, 1999; Perez *et al.*, 2002), which is defined here as:

$$GSI = 100 \times \frac{GW + AOW}{BW}$$

Commercial trawl data were used to describe the seasonality of the maturation process, expressed by the bimonthly variation in GSI values for males and females. The sex ratio was calculated monthly for the different depth zones, and significant deviations from 1:1 were tested using Chi-squared (χ^2) tests (Zar, 1996).

Maturity ogives were estimated from the proportion of mature squids for each sex per size class, with a logistic curve

$$P = \frac{1}{1 + e^{-b(ML - ML_{50\%})}} \quad (\text{King, 1996}).$$

The mean length at which 50% of the individuals are mature was calculated as $ML_{50\%} = -a/b$, where “ a ” and “ b ” are the intercept and the slope of the plot between mean length and proportion of mature individuals.

Data from commercially trawled and survey samples were used to investigate the spatial and temporal distribution of population strata of *L. plei* and *L. sanpaulensis*. Mean values of ML and GSI of males and females, and the proportion of each maturity stage, were analyzed (a) throughout the year, and (b) from four different depth zones (A1: 30 to 39 m; A2: 40 to 60 m; A3: 61 to 80 m; and A4: 100 to 150 m).

Since not all length distributions displayed a normal distribution, a maximum likelihood estimate (Haddon, 2001) was used to test for differences in mean lengths throughout the year, and between four different depth zones. The “normal” likelihood function

$$f(x) = \frac{1}{\sqrt{2\pi\sigma}} \exp\left[-\frac{(x-\mu)^2}{2\sigma^2}\right]$$

was adopted for females, and a “log-normal” function

$$f(x) = \frac{1}{x\sqrt{2\pi\sigma^2}} \exp\left[-\frac{(\ln(x) - \ln(\mu))^2}{2\sigma^2}\right]$$

was used for males, based on observed length frequency distribution characteristics, where x is observed ML and μ is the mean value (expected ML).

Likelihood profiles were constructed to evaluate statistical differences between mean ML values (Hilborn and Mangel, 1997), where overlapping distributions indicate similar average ML values.

RESULTS

Size structure

A total of 1584 *L. plei* specimens were analyzed (Table 1), of which, complete depth and latitude data were available for 1341 individuals. Males ranged from 40 to 300 mm in mantle length, and reached greater sizes than females, whose length was between 30 and 180 mm. The overall length-frequency distribution for females was approximately normal whereas that for males was approximately log-normal (Fig. 1).

A total of 938 *L. sanpaulensis* individuals were analyzed, of which, 623 came from the fishery and 315 from fish research surveys (Table 2). Mantle length frequencies showed unimodal distributions for both sexes. Males reached larger sizes than females, and they varied from 25 to 163 mm and from 29 to 111 mm respectively (Fig. 1).

TABLE 1. – Numbers of *Loligo plei* measured for each class, sex and maturity stage from samples taken by commercial shrimp trawlers in 1999-2000 and 2002-2003. ML = mantle length.

ML (mm)	Juvenile	Females				Total	Males				Total	
		Stage I	Stage II	Stage III	Stage IV		Stage I	Stage II	Stage III	Stage IV		
30		1				1						
40		1				1	2					2
50	4	2	1	2	1	6	8	1				9
60	10	6	1	7		14	10	1	1			12
70	11	8	2	4		14	17	3	7			27
80	20	22	10	3		35	32	17	9			58
90	19	37	10	26		73	28	24	13			65
100	3	29	27	36		92	19	58	23			100
110		25	25	52	1	103	14	44	34			92
120	1	7	29	52		88	4	36	35	2		77
130		5	27	64	1	97	2	25	31	2		60
140			7	64		71		29	26	5		60
150		1	1	28		30	1	15	35	5		56
160				18		18		15	32	1		48
170				8		8		6	26	1		33
180			1	2		3		4	29	2		35
190								1	28	3		32
200									14	1		14
210									17			17
220									16			16
230									12	1		13
240									7			7
250									6			6
260									6			6
270									3	2		5
280									4	1		5
290									4			4
300									1	1		2
Total	68	144	141	366	3	654	137	279	419	27		862

TABLE 2. – Numbers of *Loligo sanpaulensis* measured for each class, sex and maturity stage from samples taken by commercial shrimp trawlers in 1999-2000 and 2002-2003 and ground fish cruises of the REVIZEE program. ML = mantle length.

ML (mm)	Juvenile	Female				Total	Male				Total	
		Stage I	Stage II	Stage III	Stage IV		Stage I	Stage II	Stage III	Stage IV		
10	3											
20	39	1				1	1					1
30	43	3				3	19		1			20
40	28	14		3		17	24	4	2			30
50	9	11	9	4		24	19	9	13			41
60	2	11	10	15		36	13	9	17			39
70		5	22	84	2	113	4	16	24			44
80		3	11	82		96		7	45			52
90		2	3	27		32		2	47	1		50
100				1		1		1	69			70
110				1		1			37			37
120									38			38
130									25			25
140			1	1		2			25			25
150							1		7	1		9
160									2			2
170								1	1			2
180									1			1
190								1				1
200												
210												
220												
230									1			1
Total	124	50	56	218	2	326	81	50	355	2		488

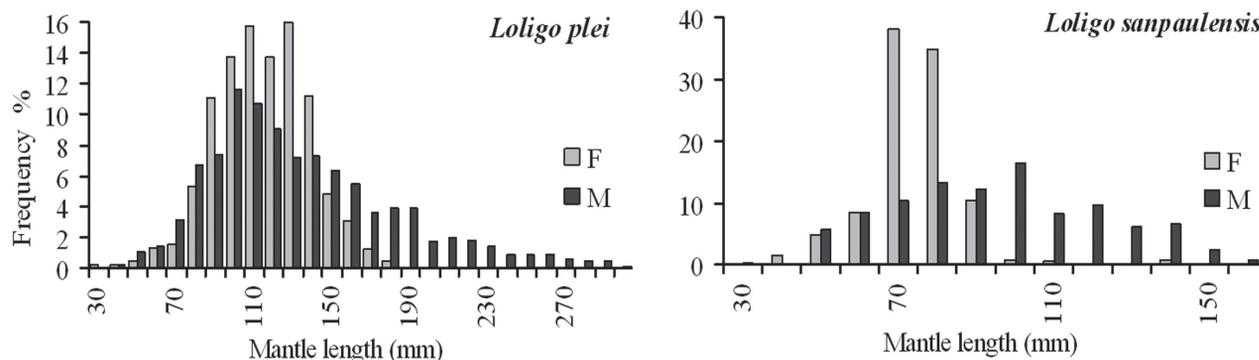


FIG. 1. – Mantle length frequency distribution of *L. plei* (1584 individuals) and *L. sanpaulensis* (938 individuals) caught by trawl fishing landings between 1999-2000 and 2002-2003. Black bars represent males and grey bars represent females.

Length-weight relationships

The relationships between mantle length and body weight of male and female *Loligo plei* were $BW = 0.00828ML^{1.765}$ ($r^2 = 0.92$, $n = 862$) and $BW = 0.00349ML^{1.963}$ ($r^2 = 0.84$, $n = 654$) respectively. The slopes (“b”) of the LWR differed significantly between the sexes (ANCOVA; $F = 6.055$, $df = 1$, $P = 0.014$) and the females were heavier at a given length than males.

The LWR calculated using all females of *L. sanpaulensis* showed a low coefficient of determination ($r^2 = 0.28$), which indicates that the regression did not fit the data perfectly. This was due to the fact that length and weight ranges varied, mainly in females, between squids caught between Santos and Itajaí, which showed larger sizes, and those captured in the northern portion, which were smaller. Thus, data were separated into two different sets, which resulted in higher r^2 values. Then, the length-weight relationships for males and females for individuals caught between Santos and Itajaí were $BW = 0.00409ML^{1.954}$ ($r^2 = 0.877$, $n = 114$) and $BW = 0.00117ML^{2.289}$ ($r^2 = 0.739$, $n = 138$). For individuals caught in the northern area the relationships were $BW = 0.00377ML^{1.980}$ ($r^2 = 0.867$, $n = 236$) and $BW = 0.00312ML^{2.039}$ ($r^2 = 0.524$, $n = 111$) respectively.

Differences between sexes in the slopes of length-weight relationships were significant in both areas (Santos and Itajaí, $F = 249.7$, $df = 1$, $P < 0.0001$; northern area, $F = 52.3$, $df = 1$, $P < 0.0001$).

Seasonal variation in length and length-at-maturity

Seasonal differences in mean ML of *Loligo plei* were observed; the smallest immature males and fe-

males (stage I) were found during summer months, and the largest individuals were present during winter. Winter mature individuals (stage III and IV) were also smaller than those captured in summer. Mean lengths of immature and mature females showed strong differences between summer and winter, as shown by likelihood profiles, but these differences were not consistent among the males (Fig. 2). Females of *L. plei* matured at a larger size in summer ($ML_{50\%} = 139$ mm) while males showed similar size at maturity in summer ($ML_{50\%} = 160$ mm), autumn ($ML_{50\%} = 155$ mm) and winter ($ML_{50\%} = 154$ mm) (Fig. 3).

Mean ML in *Loligo sanpaulensis* was significantly different at different periods of the year, but only for mature individuals (Fig. 2). The largest immature males and females were found during winter, and in the case of mature individuals both sexes showed larger sizes during autumn. Immature and mature individuals showed lower mean ML during autumn and spring respectively (Fig. 2). Size at maturity in *L. sanpaulensis* was greater in autumn for both sexes: $ML_{50\%}$ was 82 mm and 119 mm respectively (Fig. 3).

Reproductive index, maturation and sex ratio

A clear pattern of size and maturation in relation to depth was found for *L. plei*, as both the mean ML and mean GSI decreased with increasing depth (Fig. 4). This fact was confirmed by likelihood estimates that demonstrated similarities in body size only between depth classes A3 and A4 (80 to 150 m) for both sexes (Fig. 5). Two groups of mature individuals could be distinguished, one abundant and represented by larger individuals located inshore, and another, less abundant and with smaller speci-

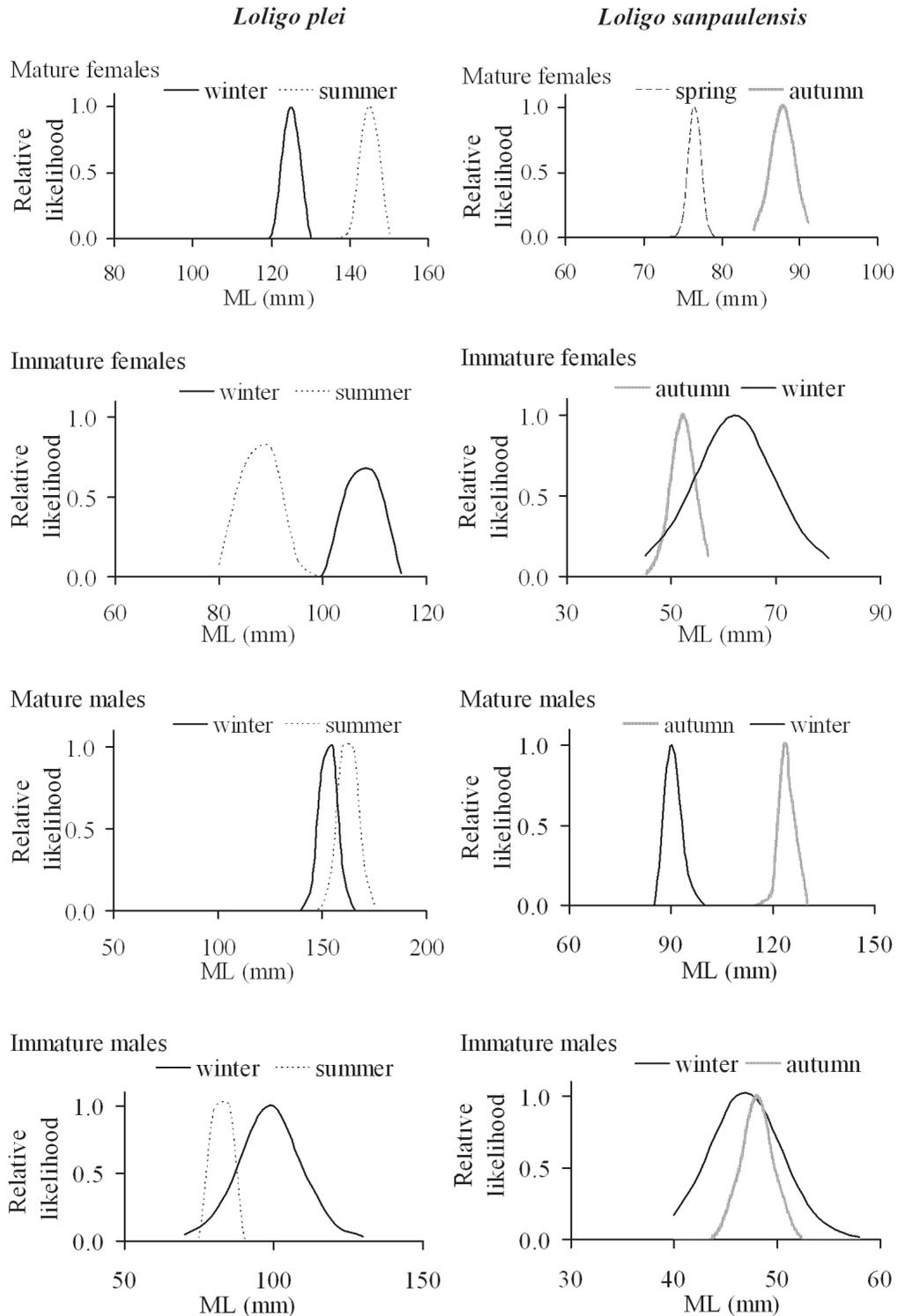


FIG. 2. – Likelihood profiles showing seasonal differences in mean mantle length (mm) for mature and immature males and females of *L. plei* and *L. sanpaulensis*.

mens, located offshore in depths between 61 and 150 m (Fig. 6). Significant variation in length in relation to depth was also confirmed by ANOVA ($P < 0.001$). The frequencies of occurrence of immatures and juveniles were highest in inshore areas, concentrated

between 61 and 100 m, and during autumn and summer (Figs. 6 and 7).

Mature *L. plei* individuals were found throughout the year (Fig. 7), with maturation peaks for both sexes between September/October and January/February.

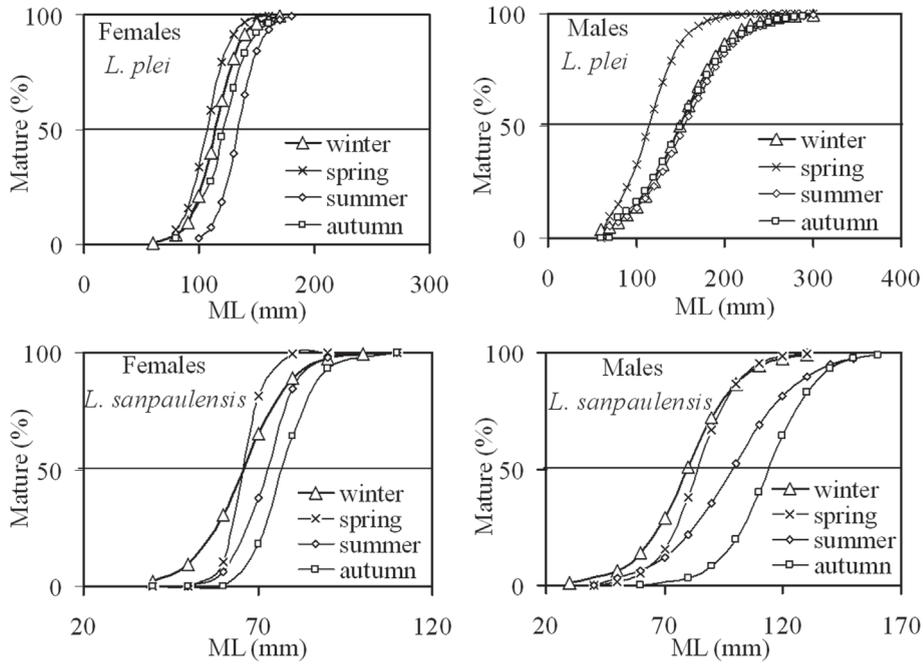


FIG. 3. – Seasonal maturity ogives for males and females of *L. plei* and *L. sanpaulensis*.

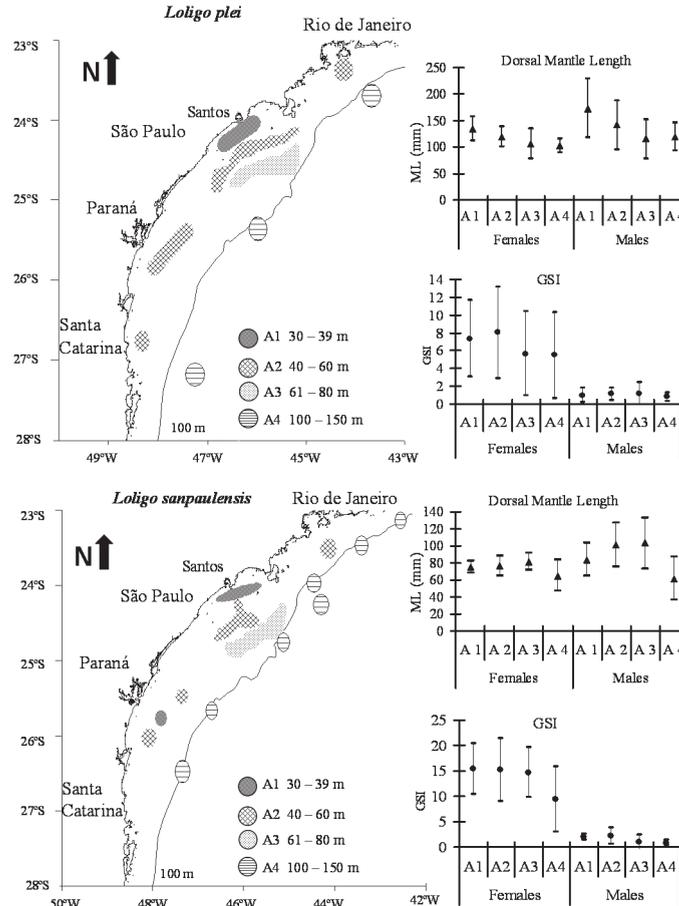


FIG. 4. – Cross-hatched areas represent the catch location of *L. plei* and *L. sanpaulensis* by depth strata (A1: 30-39 m, A2: 40-60 m, A3: 61-80 m and A4: 100-150 m). On the right, mean and standard deviation of mantle length (mm) and gonado-somatic index (GSI) are shown for each depth stratum and sex.

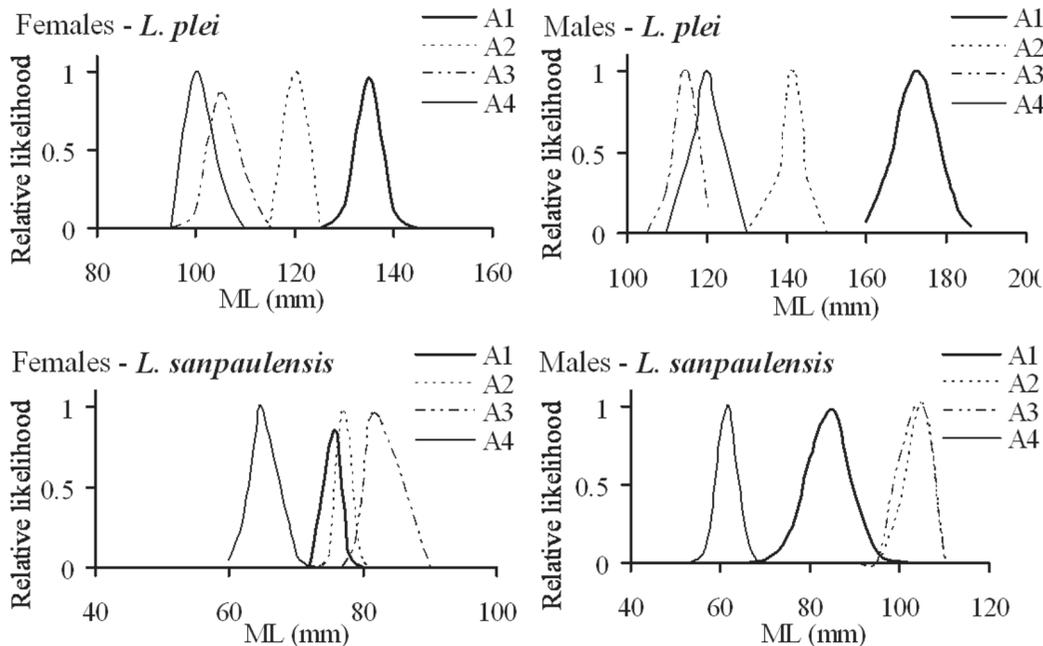


FIG. 5. – Likelihood profiles showing differences between mean mantle length (mm) at different depth strata (A1, A2, A3 and A4) for males and females of *L. plei* and *L. sanpaulensis*. Depth strata are those presented in Fig. 4.

TABLE 3. – Results of the ANOVA test for differences in GSI between months for *L. plei* and *L. sanpaulensis* data sets.

Species	Sex	n	df	MS	F	P-value
<i>Loligo plei</i>	M	672	20	4.58	3.843	0.00000
<i>Loligo plei</i>	F	424	20	224.03	12.538	0.00000
<i>Loligo sanpaulensis</i>	M	318	13	6.51	3.628	0.00002
<i>Loligo sanpaulensis</i>	F	225	13	97.48	3.556	0.00005

n: number of squid sampled; *df*: degrees of freedom; MS: mean square

ruary (Fig. 8). An ANOVA for monthly mean GSI values (Table 3) showed highly significant differences ($P < 0.001$) in all cases. For males, little variation was observed in GSI, except in July/August 1999, January/February 2000 and 2003, and September/October 2002. Females showed a strong GSI peak between September/October 2000 (late winter and spring) and a secondary peak in January/February 2000 (summer).

There were significantly more males than females ($P < 0.05$) in the total sample. The predominance of males was significant in depths between 40 and 60 m ($\chi^2 = 10$; $P < 0.05$) and 61 and 80 m ($\chi^2 = 23$; $P < 0.05$). In months with GSI peaks the sex ratio was 1:1 (Fig. 8 and 9), followed by a trend of mature male predominance just after the peak (Fig. 9).

The ML and GSI of *L. sanpaulensis* increased with depth up to depths of 100 m, and decreased again with depths greater than 100 m (Fig. 4). Likelihood

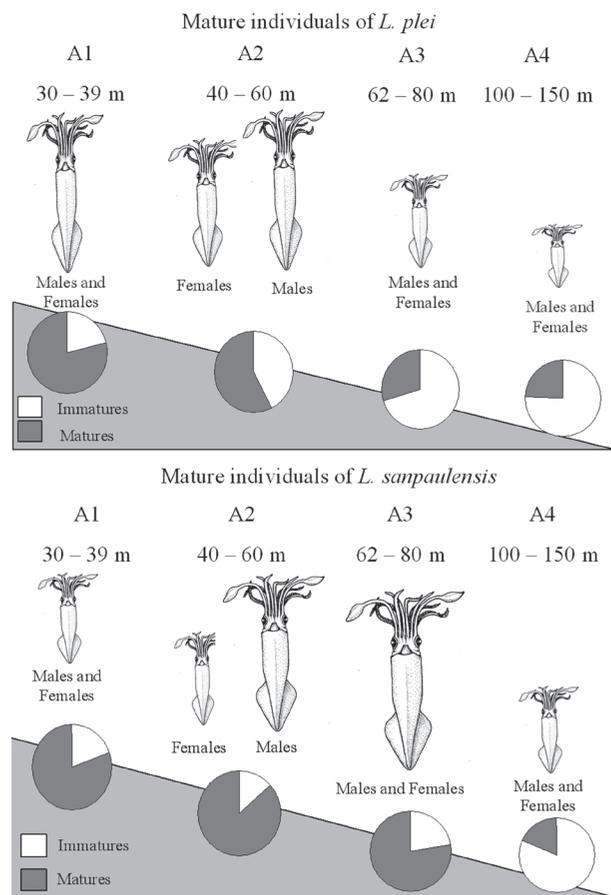


FIG. 6. – Schematic representation of differences in size of mature squids and frequency of mature and immature individuals by depth strata in *L. plei* and *L. sanpaulensis*.

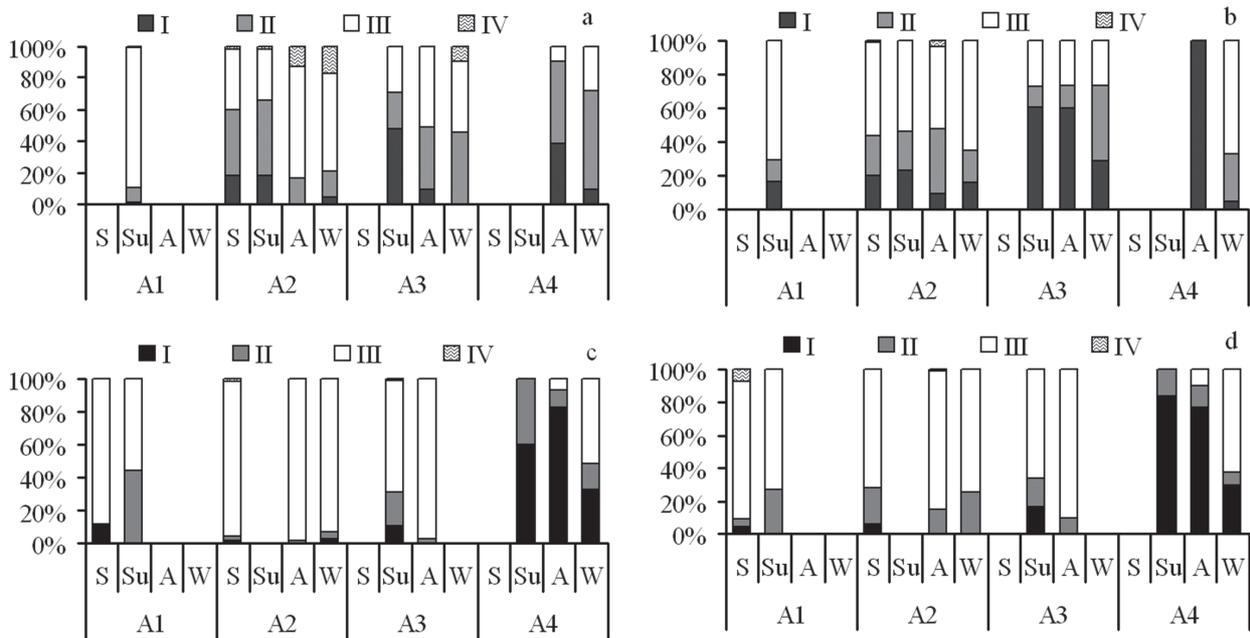


FIG. 7. – Importance of maturity stages of *L. plei* by depth strata (A1, A2, A3 and A4) in (S) spring, (Su) summer, (A) autumn and (W) winter. (a) males and (b) females of *L. plei* and (c) males and (d) females of *L. sanpaulensis*. Depth strata are those presented in Fig. 4.

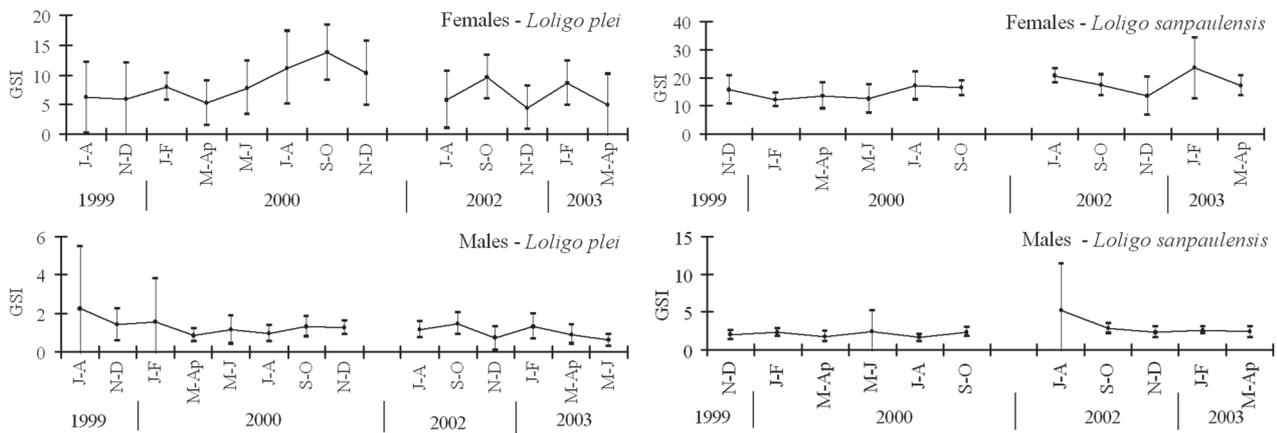


FIG. 8. – Bimonthly variation of the mean GSI with standard deviation for females and males of *L. plei* and *L. sanpaulensis*.

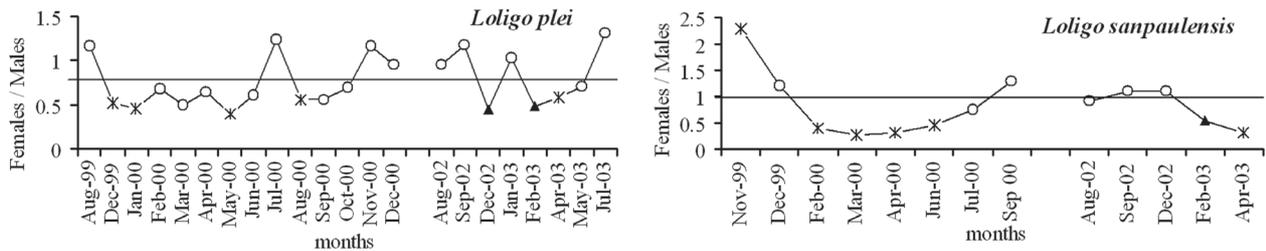


FIG. 9. – Monthly variation of the sex-ratio in samples of (a) *L. plei* and (b) *L. sanpaulensis*. (○) sex-ratio 1:1; (*) mature predominance (> 60%) and (▲) immature predominance (> 60%).

estimates did not confirm differences in mean ML between depth strata A1 and A2 in females or between A2 and A3 in males (Fig. 5). The same pattern was

observed for the mean length of mature individuals (Fig. 6). The highest percentages of matures were found at depths of 30 to 80 m, and immatures (stage I

and II) at depths greater than 100 m, especially during summer and autumn (Figs. 6 and 7).

Mature individuals of *L. sanpaulensis* were present throughout the year in high frequencies (Fig. 7). There was limited variation in GSI data, mainly for males, but the GSI peaked in summer and winter for both sexes (Fig. 8). Highly significant differences (ANOVA; $P < 0.001$) were recorded between months in all GSI data (Table 3)

Males were significantly predominant over females in areas deeper than 40 m (A2, $\chi^2 = 5.9$; A3, $\chi^2 = 35$; A4, $\chi^2 = 12$; $P < 0.05$), and in almost the entire sample ($\chi^2 = 32$; $P < 0.05$). Seasonally, females showed predominance over males only in November 1999 ($P < 0.05$), while males predominated just after the breeding peak in November/December 1999 and January/February 2003. The 1:1 sex ratio proportion was observed after the breeding peak in July/August 2002 (Fig. 9).

DISCUSSION

Sexual dimorphism in size is well known in loliginids, and males of many species show larger maximum sizes than females (Moreno *et al.*, 1994; Pierce *et al.*, 1994; Raya *et al.*, 1999; Rocha and Guerra, 1999; Perez *et al.*, 2002). This was clearly seen in the present study for both *Loligo* species. In addition, the slopes of the length-weight relationship and the weight per unit length were greater in females than in males, possibly because females invest more in the reproductive organs than in somatic growth (Forsythe and Van Heukelem, 1987).

Better fits in the *L. sanpaulensis* length-weight relationship were found when data were sorted into two different areas, which may be related to the occurrence of different stocks in the studied area, as already suggested by Juanicó (1979) and Gasalla *et al.* (2005a).

Our study showed that mature squids are caught as a by-catch of the pink-shrimp commercial trawling throughout the year, which suggests that spawning occurs in the fishing area all year round, with increases in reproductive activity in some seasons. The variation range of mean GSI values was narrow for *L. sanpaulensis* and for males of *L. plei*, but seems to be comparable with other studies (i.e. see Δ IGS in Guerra and Rocha (1994) for *L. vulgaris* and *L. forbesi*; Perez *et al.* (2002) for *L. plei*, and Olyott *et al.* (2006) for *L. vulgaris*). Keeping this in mind, *L.*

plei showed slightly more reproductive activity during late winter and spring (September/October) as well as summer (January/February). Despite a gap in data for *L. sanpaulensis*, the periods of increased spawning activity for this species appear to be in summer and winter, which is also consistent with previous observations by Andriguetto and Haimovici (1996).

The 1:1 sex ratio observed in and around reproductive seasons suggests aggregation for mating in the studied area, similar to other cases (i.e. Barón and Ré, 2002). There are indications of higher post-mating female mortality or migration as mature males predominated just after some reproductive seasons, which was also found by Augustyn (1990) and Perez *et al.* (2002). There was also a higher incidence of spawner males than females throughout the study period, which could be explained by the hypothesis of greater longevity of males, as suggested for *L. sanpaulensis* by Aguiar (2006) and for *L. plei* by Jackson and Forsythe (2002).

Temperature seasonality and food availability are the main factors that typically influence the growth of cephalopods (Boyle and Rodhouse, 2005). The seasonal variation and the segregation patterns of maturity, mean length and size-at-maturity in deeper areas found for *L. plei* and *L. sanpaulensis* in this study could be associated with seasonal differences in temperature and food availability observed along the southeastern coast of Brazil, due to a complex and dynamic hydrographic variation (Campos *et al.*, 1995; Borzone *et al.*, 1999). The influence of South Atlantic Central Water (SACW) is frequently detected in the continental shelf at the end of spring and summer, which causes changes in the water column temperature due to an influx of colder (less than 18°C), less saline waters (Campos *et al.*, 1995; Castro and Miranda, 1998). Due to the coastal upwelling of this nutrient-rich water mass, the primary productivity is higher, and this is reflected in higher trophic levels. During autumn and winter the SACW moves back to the upper slope, and in this period, the water column is homogenized on the shelf and a decline in biological production is observed (Campos *et al.*, 2000).

Thus, seasonal environmental changes and food availability can be important factors that shape *Loligo* spp aggregation patterns, as previously noted for other loliginids worldwide (Hatfield and Cadrin, 2002 for *L. pealeii*; Arkhipkin *et al.*, 2004 for *L. gahi*; Olyott *et al.*, 2006 for *L. vulgaris*). Moreno

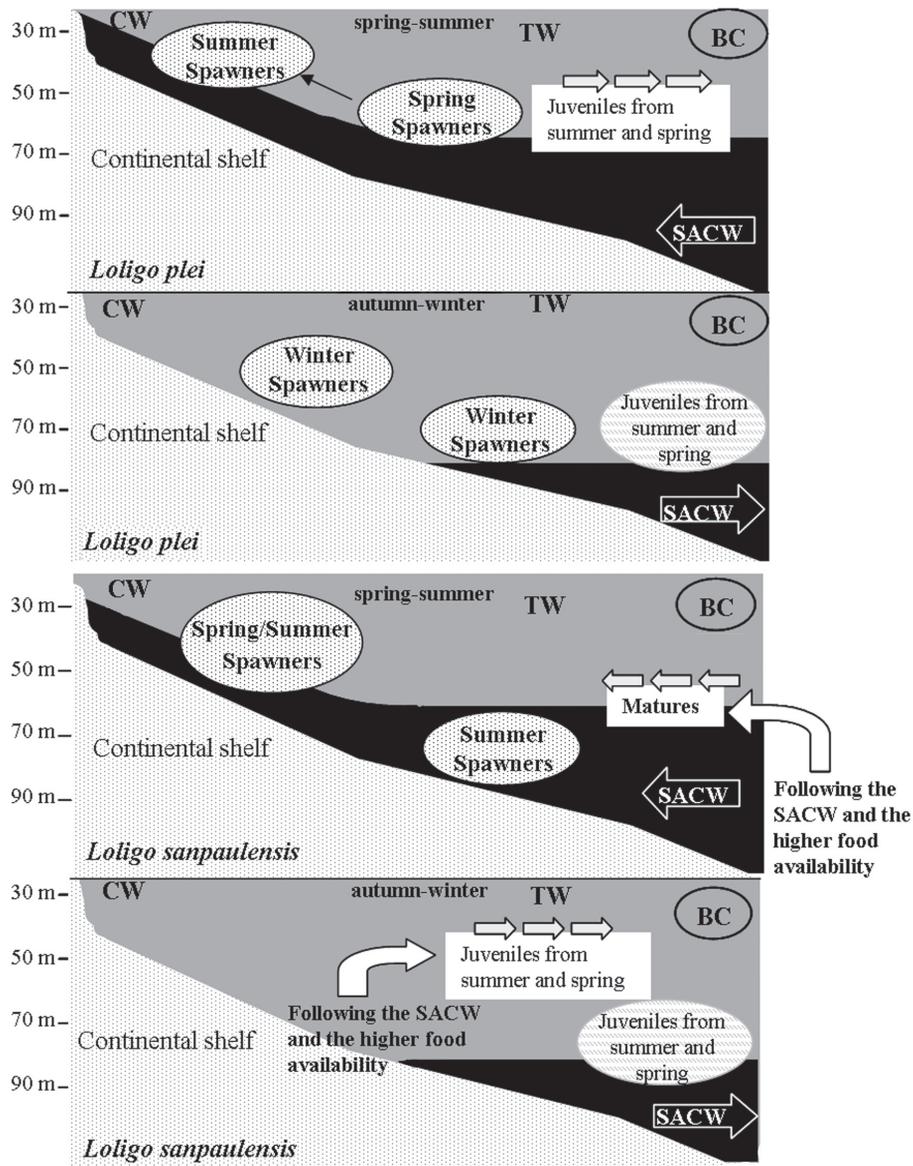


FIG. 10. – Schematic diagrams of population displacement in different strata during spring-summer and autumn-winter of *L. plei* and *L. sanpaulensis* in the studied area. The dark zone indicates the intrusion and retreat of the South Atlantic Central Water (SACW). BC is the core of the Brazil Current; TW, Tropical Water and CW, Coastal Water.

et al. (2005) show that immature individuals of *L. vulgaris* exposed to more favourable environmental conditions (more available food and/or warmer temperatures) grow faster and these individuals attain the minimum size for maturity earlier. In individuals exposed to colder waters and lower food availability in the first life stages, maturity may be delayed and investment in growth prolonged, which would result in maturation at larger sizes.

Considering the hypothesis raised by Perez *et al.* (2006) that *L. plei* off southern Brazil might live up to around 9 months of age, it is possible that larger summer (January/February) spawners found in the

present study could have been the progenitors of the smaller winter-spring (September/October) matures. Due to the possibly greater growth rates that immature individuals show during spring and summer (Perez, pers. comm.), it is likely that our late winter (September) spawners were the parents of larger mature individuals responsible for the reproductive event in summer.

Figure 10 summarizes the main hypotheses raised on displacement and life cycles of *L. plei* and *L. sanpaulensis*. *L. plei* showed aggregation for reproduction in shallow waters during the summer, and in greater depths during the spring and winter. In *L. san-*

paulensis, reproductive events of summer were concentrated between depths of 30 and 80 m. The results suggest that juveniles of both species arising from spring and summer spawning migrate from inshore nursery grounds to deeper waters (between 100 and 150 m) in the northern zone of the studied area.

Thus, the segregation patterns of size and maturity of *L. plei* show that larger-sized individuals and mature individuals concentrate closer to the coast, and smaller sized and immature squid concentrate in deeper areas. High concentrations of mature *L. plei* individuals inshore during summer might take advantage of the high temperature and high food availability associated with the SACW intrusion. However, since mature *L. plei* are caught throughout the year, some portion of the population may not always find these favourable conditions and still might be competent to breed. Such life cycle plasticity due to the combination of variable reproductive characters in individuals is the key to cephalopod survival in variable environments (Boyle and Rodhouse, 2005), and their life cycle is probably timed to take advantage of good conditions.

Compared with *L. plei*, an opposite size segregation pattern seems to occur for *L. sanpaulensis*, as the size of individuals and predominance of mature individuals increase with depth and decrease again in depths greater than 100 m. This has also been suggested by other authors in different sub-regions, such as Juanicó (1979) and Andriquetto and Haimovici (1991) based on oceanographic surveys off Rio Grande do Sul (southern Brazil) and Costa and Fernandes (1993) in Cape Frio (northern-most southeast Brazilian shelf). According to Barón and Ré (2002), immature *L. sanpaulensis* individuals in the north eastern coast of Patagonia (Argentina), migrate offshore during certain periods of the year, and return inshore when mature.

It should be emphasized that age determination is still necessary to confirm interpretations of the relationships between hatching season and the differences in length and size-at-maturity of seasonal groups, as found in temperate ecosystems (e.g. Boyle *et al.*, 1995; Moreno *et al.*, 2005).

Nevertheless, our results seem to suggest important sustainable management implications for squid populations. Firstly, considering that *L. plei* and *L. sanpaulensis* are caught as by-catch by pink-shrimp trawlers, broader strategies rather than single target-species management would be beneficial (i.e. multi-species approaches). However, in view of the costs

of ecosystem management in the short term, simpler, focused measures could be more reliable. One possible suggestion for protecting squid spawning grounds would be to implement spring and summer protected areas where trawling would be prohibited until 60 m depths, i.e. in the area and time of year when mature individuals concentrate. Regulating trawling activities and broadening previously established seasonal closures for the shrimp fleet may allow potential squid spawners to escape, shrimp to recruit (mainly pink-shrimp), and other by-catch fishery stocks to recuperate.

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REFERENCES

- Aguiar, D.C. – 2006. *Idade e crescimento da lula Loligo sanpaulensis Brakoniecki, 1984 (Cephalopoda: Myopsida) do sudeste - sul do Brasil*. Master dissertation, Inst. Oceanog., Univ. São Paulo, São Paulo.
- Andriquetto, J.M. and M. Haimovici. – 1991. Abundance and distribution of *Loligo sanpaulensis* Brakoniecki, 1984 (Cephalopoda: Loliginidae) in Southern Brazil. *Sci. Mar.*, 55(4): 611-618.
- Andriquetto, J.M. and M. Haimovici. – 1996. Reproductive cycle of *Loligo sanpaulensis* Brakoniecki, 1984 (Cephalopoda: Loliginidae) in southern Brazil. *Sci. Mar.*, 60(4): 443-450.
- Arkhipkin, A.I., R. Grzebielec, A.M. Sirota, A.V. Remeslo, I.A. Polishchuk and D.A.J. Middleton. – 2004. The influence of seasonal environmental changes on ontogenetic migrations of the squid *Loligo gahi* on the Falkland shelf. *Fish. Oceanogr.*, 13(1): 1-9.
- Augustyn, C.J. – 1990. Biological studies on the chokker squid *Loligo vulgaris reynaudii* (Cephalopoda: Myopsida) on spawning grounds off the south-east coast of South Africa. *S. Afr. J. mar. Sci.*, 9: 11-26.
- Barón, P.J. and M.E. Ré. – 2002. Reproductive cycle and population structure of *Loligo sanpaulensis* of the northeastern coast of Patagonia. *Bull. Mar. Sci.*, 71(1): 175-186.
- Borzzone, C.A., P.R. Pezzuto and E. Marone. – 1999. Oceanographic characteristics of a multi-specific fishing ground of the Central South Brazil Bight. *Mar. Ecol.*, 20(2): 131-146.
- Boyle, P.R., Pierce, G.J. and Hastie, L.C. – 1995. Flexible reproductive strategies in the squid *Loligo forbesi*. *Mar. Biol.*, 121: 501-508.
- Boyle, P.R. and P. Rodhouse. – 2005. *Cephalopods: ecology and*

- fisheries. Blackwell Science, Ames.
- Campos, E.J.D., J.E. Gonçalves and Y. Ikeda. – 1995. Water mass characteristics and geostrophic circulation in the South Brazil Bight: Summer of 1991. *J. Geophys. Res.*, 100(C9): 18537-18550.
- Campos, E.J.D., D. Velhote and I.C.A. Silveira. – 2000. Shelf break upwelling driven by Brazil Current cyclonic meanders. *Geophys. Res. Lett.*, 27(6): 751-754.
- Castro, B.M and L.B. Miranda – 1998. Physical oceanography of the western Atlantic continental shelf located between 4°N and 34°S. In: R. Robison, K.H. Brink (eds.), *The sea*, pp. 209-251. John Wiley and Sons.
- Costa, P.A.S. and F.C. Fernandes. – 1993. Reproductive cycle of *Loligo sanpaulensis* (Cephalopoda: Loliginidae) in the Cabo Frio region, Brazil. *Mar. Ecol. Prog. Ser.*, 101: 91-97.
- Forsythe, J.W. and W.F. Van Heukelem. – 1987. Growth. In: P.R. Boyle (ed.), *Cephalopod Life Cycles. Vol. II. Comparative Review*, pp. 135-156. Academic Press, London.
- Gasalla, M.A. – 2004. Women on the water? The participation of women in seagoing fishing off Southeastern Brazil. In: Williams, S.B., A.M. Hochet-Kibongui and C.E. Nauen (eds.), *Gender, fisheries and aquaculture: Social capital and knowledge for the transition towards sustainable use of aquatic ecosystem. ACP-EU Fish. Res. Rep.*, 16. (also in ftp://ftp.cordis.europa.eu/pub/inco2/docs/08gasalla_brazil.pdf)
- Gasalla, M.A., J.A.A. Perez, C.A. Marques, A.R.G. Tomás, D.C. Aguiar and U.C. Oliveira. – 2005a. *Loligo sanpaulensis*. In: M.C. Cergole, A.O. Ávila-da-Silva, and C.L.B. Rossi-Wongtschowski, (eds.), *Análise das principais pescarias comerciais da região Sudeste-Sul do Brasil: dinâmica populacional das espécies em exploração*, pp. 62-68. Série documentos REVIZEE, Instituto Oceanográfico da Univ. de São Paulo, São Paulo.
- Gasalla, M.A., F.A. Postuma and A.R.G. Tomás – 2005b. Captura de lulas (Mollusca: Cephalopoda) pela pesca industrial desembarcada em Santos: Comparação após 4 décadas. *Braz. J. Aquat. Sci. Technol.*, 9(2): 5-8.
- Guerra, A. and F. Rocha – 1994. The life history of *Loligo vulgaris* and *Loligo forbesi* (Cephalopoda: Loliginidae) in Galician waters (NW Spain). *Fish. Res.*, 21: 43-69.
- Haddon, M. – 2001. *Modelling and Quantitative Methods in Fisheries*. Chapman and Hall, London.
- Haimovici, M. and J.M. Andriquetto. – 1986. Cefalópodes costeiros capturados na pesca de arrasto do litoral sul do Brasil. *Arq. Biol. Technol.*, 29(3): 473-495.
- Hatfield, E.M.C. and S.X. Cadrin. – 2002. Geographic and temporal patterns in size and maturity of the longfin inshore squid (*Loligo pealeii*) off the northeastern United States. *Fish. Bull.*, 100(2): 200-213.
- Hilborn, R. and M. Mangel. – 1997. *The ecological detective: confronting models with data*. New Jersey, Princeton Univ. Press.
- Jackson, G.D. and J.W. Forsythe – 2002. Statolith age validation and growth of *Loligo plei* (Cephalopoda: Loliginidae) in the north-west Gulf of Mexico during spring/summer. *J. Mar. Biol. Ass. U.K.*, 82: 677-678
- Juanicó, M. – 1979. *Contribuição ao estudo da biologia de Cephalopoda Loliginidae do Atlântico Sul Ocidental entre Rio de Janeiro e Mar del Plata*. Ph.D. thesis, Univ. de São Paulo, São Paulo.
- Juanicó, M. – 1983. Squid maturity scales for population analysis. In: J.F. Caddy (ed.), *Advances in assessment of world cephalopod resource. FAO Fish. Tech. Pap.*, 231: 341-378.
- King, M. – 1996. *Fisheries biology, assessment and management*. Blackwell Science, United Kingdom.
- Macy, W.K. – 1982. Development and application of an objective method for classifying long-finned squid, *Loligo pealeii*, into sexual maturity stages. *Fish. Bull.*, 80(3): 449-459.
- Martins, R.S., J.A.A. Perez and C.A.F. Schettini – 2006. The squid *Loligo plei* around Santa Catarina Island, southern Brazil: ecology and interactions with the coastal oceanographic environment. *J. Coast. Res.* 39: 1285-1290.
- Moreno A., M.M. Cunha and J.M.F. Pereira – 1994. Population biology of veined squid (*Loligo forbesi*) and European squid (*Loligo vulgaris*) from the Portuguese coast. *Fish. Res.*, 21: 71-86
- Moreno, A., J. Pereira and M. Cunha – 2005. Environmental influences on age and size at maturity of *Loligo vulgaris*. *Aquat. Living Resour.*, 18: 377-384.
- Olyott, L.J.H., W.H.H Sauer and A.J. Booth. – 2006. Spatio-temporal patterns in maturation of the chokka squid (*Loligo vulgaris reynaudii*) off the coast of South Africa. *ICES J. Mar. Sci.*, 63: 1649-1664.
- Perez, J.A.A. – 2002. Biomass dynamics of the squid *Loligo plei* and the development of a small-scale seasonal fishery off southern Brazil. *Bull. Mar. Sci.*, 71(2): 633-651.
- Perez, J.A.A. and P.R. Pezzutto. – 1998. Valuable shellfish species in the by-catch of shrimp fisheries in southern Brazil: spatial and temporal patterns. *J. Shell. Res.*, 1(17): 303-309.
- Perez, J.A.A., D.C. Aguiar and U.C. Oliveira. – 2002. Biology and population dynamics of the long-finned squid *Loligo plei* (Cephalopoda: Loliginidae) in southern Brazilian waters. *Fish. Res.*, 58: 267-279.
- Perez, J.A.A., M.A. Gasalla, D.C. Aguiar, U.C. Oliveira, C.A. Marques and A.R.G. Tomás – 2005. *Loligo plei*. In: M.C. Cergole, A.O. Ávila-da-Silva, and C.L.B. Rossi-Wongtschowski, (eds.), *Análise das principais pescarias comerciais da região Sudeste-Sul do Brasil: dinâmica populacional das espécies em exploração*, pp. 62-68. Série documentos REVIZEE, Instituto Oceanográfico da Univ. de São Paulo, São Paulo.
- Perez, J.A.A., D.C. Aguiar and J.A.T. Santos – 2006. Gladius and statolith as tools for age and growth studies of the squid *Loligo plei* (Teuthida: Loliginidae) off southern Brazil. *Braz. Arch. Biol. Technol.*, 49(5): 747-755.
- Pierce, G.J. and A. Guerra – 1994. Stock assessment methods used for cephalopod fisheries. *Fish. Res.*, 21: 255-285.
- Pierce, G.J., P.R. Boyle, L.C. Hastie and L. Key. – 1994. The life history of *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish waters. *Fish. Res.*, 21: 17-41.
- Pierrepont, J.F., B. Dubois, S. Desormonts, M.B. Santos and J.P. Robin. – 2005. Stomach contents of English Channel cetaceans stranded on the coast of Normandy. *J. Mar. Biol. Ass. U. K.*, 85: 1539-1546.
- Raya, C.P., E. Balguerías, M.M. Fernández-Nuñez and G.J. Pierce. – 1999. On reproduction and age of the squid *Loligo vulgaris* from the Saharan Bank (north-west African coast). *J. Mar. Biol. Ass. U. K.*, 79: 111-120.
- Rocha, F. and A. Guerra. – 1999. Age and growth of *Loligo vulgaris* and *Loligo forbesi*, in Galician waters (north-west Spain). *J. Mar. Biol. Ass. U. K.*, 79: 697-707.
- Rodhouse, P.G. – 2005. World Squid Resources. In: *Review of the state of world marine fishery resources. FAO Fish. Tech. Pap.*, 457: 175-187.
- Santos, R.A. and M. Haimovici. – 1998. Trophic relationships of the long-finned squid *Loligo sanpaulensis* on the Southern Brazilian Shelf. *S. Afr. J. Mar. Sci.*, 20: 81-91.
- Santos, R.A. and M. Haimovici. – 2002. Cephalopods in the trophic relations off southern Brazil. *Bull. Mar. Sci.*, 71(2): 753-770.
- Sparre, P. and S.C. Venema. – 1998. Introduction to tropical fish stock assessment. Part 1: Manual. *FAO Fish. Tech. Pap.*, 306/1.
- Staudinger, M.D. – 2006. Seasonal and size-based predation on two species of squid by four fish predators on the Northwest Atlantic continental shelf. *Fish. Bull.*, 104: 605-615.
- Zar, J.H. – 1996. *Biostatistical Analysis*. Prentice Hall, New Jersey.

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