

REPRODUCTIVE CYCLE AND POPULATION STRUCTURE OF *LOLIGO SANPAULENSIS* OF THE NORTHEASTERN COAST OF PATAGONIA

Pedro José Barón and María Edith Ré

ABSTRACT

The squid *Loligo sanpaulensis* is distributed from southern Brazil to northern Patagonia. Previous studies have been conducted on the reproduction of this species in northern and central areas of its distribution. In northern Patagonia, lower and more variable temperatures were expected to cause sharper patterns in the temperature-regulated aspects of the reproduction. Periodic sampling was conducted from December 1996 to July 1999, and main biological characters and maturity stages were registered. Average mantle length (ML) was 55.1 mm ($n = 1455$). Large specimens were most abundant in November–March and small specimens were found in April–July. Sex ratio was significantly different from 1:1 (10 females:7 males). Mean ML at maturity was 65.3 mm in males and 77.6 mm in females. Mature specimens and recruits were found in summer. During fall, the largest size classes disappeared and juveniles were abundant. Throughout winter, juveniles progressively disappeared, and recruits were present. In late spring mature specimens entered the sampling area. A single spawning season from late spring to summer was observed. The disappearance of the largest size classes occurred three to four months later than that reported for Mar del Plata (38°S).

Studies on the reproductive cycle of cephalopods have shown that semelparity is a generalized pattern within the group and that death follows spawning (Mangold, 1987). However, there are particular aspects of reproduction that have been associated with each species and its environment, such as the extent of the reproductive season with or without peaks of activity (Mangold, 1987; Boyle and Pierce, 1994), the presence of multiple modes of recruitment (Hatfield, 1996), the location and extension of spawning grounds (Roberts and Sauer, 1994), the fecundity (O’Dor, 1998) and rate of paralarval survival (Okutani and Watanabe, 1983).

Loligo sanpaulensis is distributed along the Atlantic coast of South America from 20°S to 46°S (Castellanos, 1967; Roper et al., 1984). Water temperatures decrease and show wider seasonal fluctuations as latitude increases along this latitudinal range of distribution, forming an environmental gradient. As in other cephalopod populations (Mangold, 1987), populations of *L. sanpaulensis* from higher latitudes are expected to have shorter spawning seasons than those from lower latitudes. Northern populations of *L. sanpaulensis* have been reported to have long or year-round spawning seasons with two annual peaks of activity. At 23°S (Cabo Frio, Brazil) these spawning peaks were observed in winter (June–August) and summer (January–February) (Costa and Fernandes, 1993), and between 28°–34°S (southern Brazil), peaks were found in winter/spring and summer (Andrighetto and Haimovici, 1996). At 38°S (Mar del Plata, Argentina), it was observed that the spawning season encompassed the spring–fall period, with highest activity in late spring–summer in some years and that it started earlier (winter) in other years (Vigliano, 1985). Temporal changes in the size structure of *L. sanpaulensis* populations have been analyzed from 23°S to 38°S (Juanicó, 1979; Vigliano, 1985; Costa and Fernandes, 1993; Andrighetto and Haimovici, 1991; Pineda et al., 1998).

The present study, conducted in the southern part of the species distribution (43°–44°S, Northern Patagonia, Argentina), completes this series of works on the species reproduction and population structure by observing the patterns imposed by the extreme conditions of the environmental gradient affecting the species.

MATERIALS AND METHODS

Sampling of *L. sanpaulensis* Brakoniecki, 1984 population was conducted in 28 fishing trips from December 1996 to July 1999 on board of the fishing vessels STELLA MARIS (19.8 m, 240 Hp) and MARTA ESTHER (7.8 m, 40 Hp) registered in the port of Rawson (43°20'S, 64°04'W). In 26 fishing trips, *L. sanpaulensis* was fished as by-catch of the shrimp (*Pleoticus mülleri*) and the prawn (*Artemesia longinaris*). The fishing gears consisted of an otter trawl (STELLA MARIS) with a net of 60 mm mesh size and a beam trawl (MARTA ESTHER) with a net of 50 mm mesh size. Sampling with these fishing gears was normally in Engaño Bay (43°20'S–64°04'W, depths 5–10 m) except for one fishing trip to 'El Pozón' (43°14'S–64°46'W, depth 50–55 m) and another one to Escondida Island (43°43'S–65°17'W, depth 40–50 m). Since navigation in the Port of Rawson is restricted to high tides, vessels fishing in Engaño Bay and 'El Pozón' operate during 4–5 h per fishing trip, independently of the gear and vessel type. The overall catch of *L. sanpaulensis* per fishing trip was similar for beam and otter trawls, all the fishing trips to Engaño Bay and El Pozón were considered to represent the same fishing effort for the purpose of relative abundance estimation. Additional information was obtained in two fishing trips to Escondida Island (43°43'S–65°17'W, depth 40–50 m), using an otter trawl with a net of 120 mm mesh size to target on hake (*Merluccius hubbsi*), and in two samplings with coastal seine net (15 mm mesh size) (Yatch Club Beach and Doradillo Beach, February 1999) and another one with jigs (Pier Storni, March 1998) in Nuevo Gulf (42°46' S, 65°02' W). Due to the variety of gears employed, these data are not included in comparisons of abundance. In every case, the sample constituted the total catch of *L. sanpaulensis* for the trip, except for the sample of December 1998 (Escondida Island) which consisted of one third of the capture.

The mantle length (ML) of each individual was measured to the nearest millimeter with a digital caliper following Roper et al. (1984), and weighted (TW) with a Delta Range electronic scale (precision: 0.01 g). Sex and stage of maturity were determined for the whole catch, including individuals of less than 10 mm ML, using the scale of Lipinski and Underhill (1995). Methylene blue staining was used to detect the sexual organs of the smaller squids.

To determine the size at maturity (ML 50%) the proportions of mature males and females was calculated at 10 mm size classes for all the individuals from which sex was recorded (850 females and 592 males). Individuals at maturity stages 4, 5 and 6 (Lipinski and Underhill, 1995) were considered 'mature'. In both sexes, a logistic curve of maturity was fitted by regression to the proportions of mature individuals in the size classes using the least squares method and the formula $P_i = 1 / (1 + e^{-(a + b \cdot L_i)})$, where P_i and L_i are respectively the proportion of mature individuals and the midpoint of the size class i , and a and b are the estimated constants. Size at maturity was then calculated as $ML\ 50\% = -a/b$.

The length of testes (TL) and nidamental glands (NiL) were measured in all the males and females. Measurements were done with a digital caliper to the nearest millimeter or, in the smaller individuals, with a micrometer mounted in a Wild dissecting microscope. Weights were recorded to the nearest 0.01 g with a Mettler PC 440 - Delta Range scale. The nidamental glands index (NGI = NiL / ML) and testes index (TI = TL / ML) were then calculated as suggested by Costa and Fernandes (1993) and Andriquetto and Haimovici (1996) for the species.

RESULTS

SIZE STRUCTURE OF THE POPULATION.—The total catch of *L. sanpaulensis* consisted of 1,470 individuals, with a mean ML of 55.1 mm (SD = 27.4, n = 1455) and an average TW of 11.7 g (SD = 18.3, n = 1450). *L. sanpaulensis* was captured in all months in which sampling was accomplished, except September 1998 (Table 1). The samples of December 1996, November 1997 and December 1998 contained relatively large individuals (Fig. 1), and were only captured in the fishing area of Escondida Island (Table 1). The size frequency distributions (Fig. 1) revealed the presence of squids of sizes larger than 90 mm ML during the end of spring to summer (November–March) and the absence of these classes during the rest of the year. Recruits of sizes smaller than 20 mm ML were caught in April 1997, February–March and May–July 1998, and April 1999. Intermediate

Table 1. Summary of the fishing trips and catches of *Loligo sanpaulensis*. SM = Stella Maris, ME = Marta Esther, OT (120 mm) = Otter trawl with a net of 120 mm mesh size, OT (60 mm) = Otter trawl with a net of 60 mm mesh size, BT = Beam trawl with a net of 50 mm mesh size, SN = Seine net of 15 mm mesh size.

Date	Locality	Depth (m)	Vessel	Fishing gear	Catch (numbers)
10-Dec-96	Escondida Island	40-50	SM	OT (120 mm)	16
8-Apr-97	Engaño Bay	2-6	SM	OT (60 mm)	51
12-Nov-97	Escondida Island	40-50	SM	OT (120 mm)	6
30-Dec-97	Engaño Bay	5-10	SM	OT (60 mm)	138
30-Jan-98	Engaño Bay	5-10	SM	OT (60 mm)	18
5-Feb-98	Engaño Bay	5-10	SM	OT (60 mm)	7
13-Feb-98	Engaño Bay	5-10	SM	OT (60 mm)	21
3-Mar-98	El Pozón	53	SM	OT (60 mm)	182
19-Mar-98	Pier Stormi	15		jigs	4
6-Apr-98	Engaño Bay	5-10	SM	OT (60 mm)	28
7-May-98	Engaño Bay	5-10	SM	OT (60 mm)	240
5-Jun-98	Engaño Bay	5-10	SM	OT (60 mm)	154
25-Jul-98	Engaño Bay	5-10	SM	OT (60 mm)	16
28-Jul-98	Engaño Bay	5-10	SM	OT (60 mm)	39
26-Aug-98	Engaño Bay	0	SM	OT (60 mm)	0
28-Aug-98	Engaño Bay	5-10	SM	OT (60 mm)	5
22-Sep-98	Engaño Bay	5-10	SM	OT (60 mm)	0
24-Sep-98	Engaño Bay	5-10	SM	OT (60 mm)	0
19-Oct-98	Engaño Bay	5	ME	BT	63
30-Oct-98	Engaño Bay	5	ME	BT	10
12-Nov-98	Engaño Bay	10	ME	BT	75
16-Dec-98	Escondida Island	40-50	SM	OT (60 mm)	91
28-Jan-99	Engaño Bay	6	SM	OT (60 mm)	38
29-Jan-99	Engaño Bay	5	ME	BT	7
11-Feb-99	Engaño Bay	5	SM	OT (60 mm)	57
19-Feb-99	Yatch Club Beach	5		SN	10
21-Feb-99	Doradillo Beach	5		SN	0
25-Mar-99	Engaño Bay	5	ME	BT	9
30-Apr-99	Engaño Bay	5	SM	OT (60 mm)	24
15-May-99	Engaño Bay	5	ME	BT	138
25-Jul-99	Engaño Bay	5	ME	BT	23
Total					1470

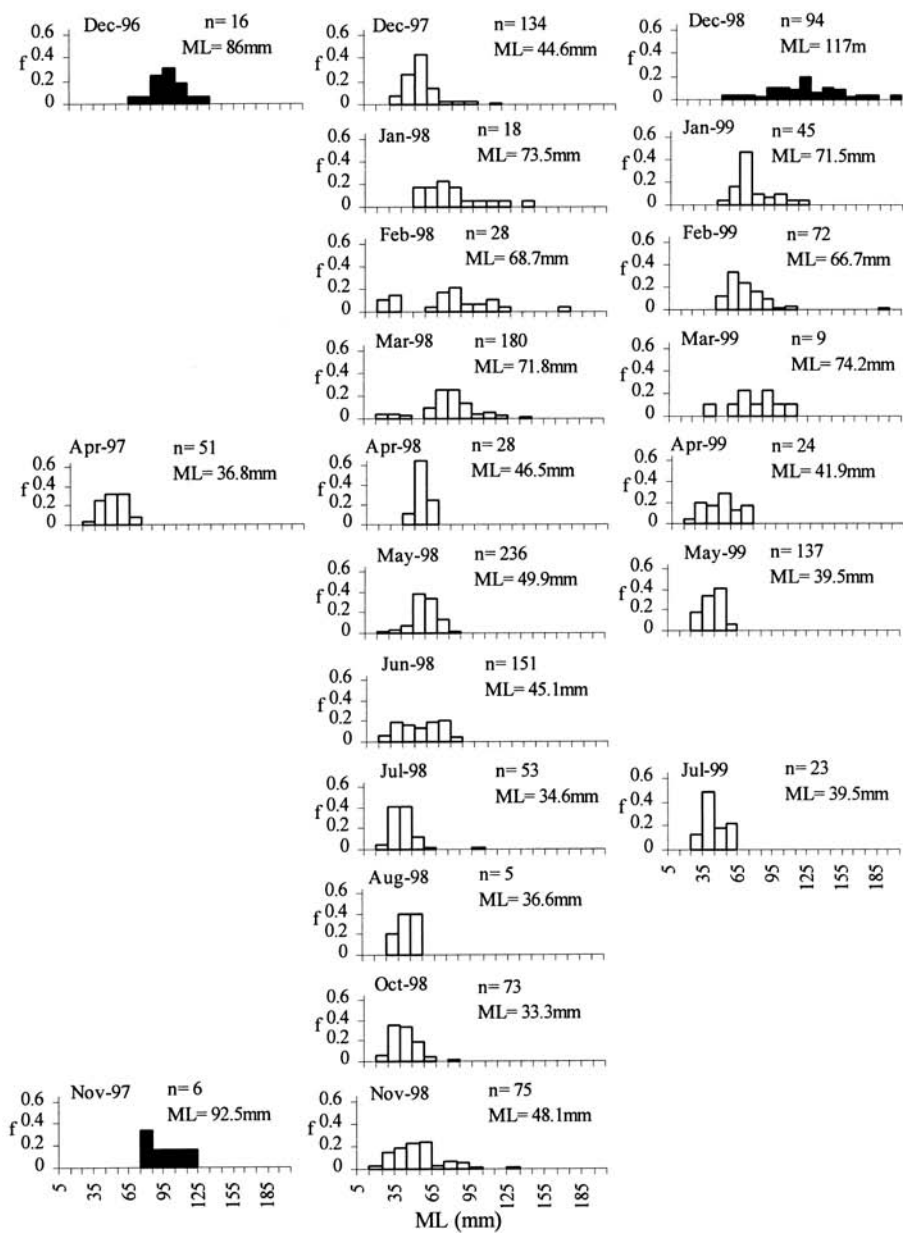


Figure 1. Monthly size frequency (f) distributions of *Loligo sanpaulensis* sampled from northern Patagonia. Shaded areas indicate samples from Escondida Island. ML indicates the mean mantle length of the individuals captured during each month.

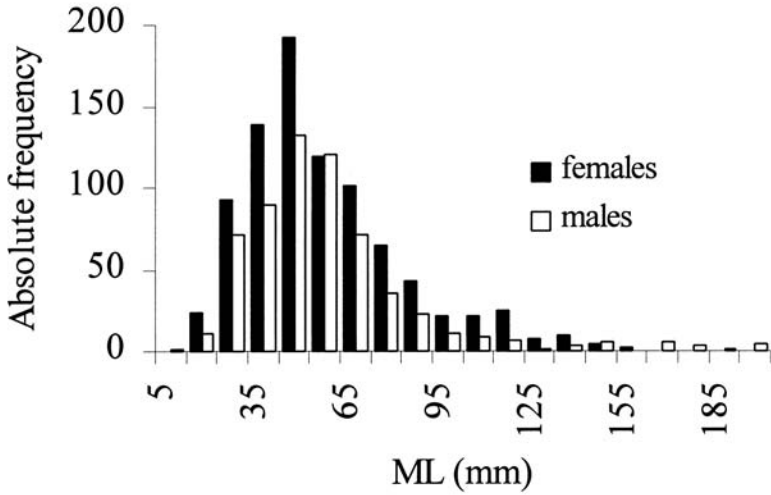


Figure 2. Frequency distributions of sexes of *Loligo sanpaulensis* per size class (pooled data for all catches).

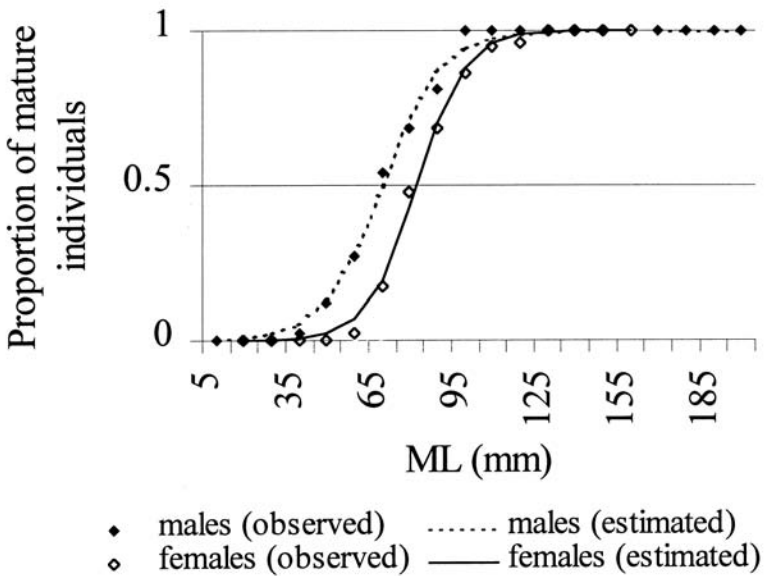


Figure 3. Proportion of mature individuals of *Loligo sanpaulensis* per 10 mm size class and maturity curves fitted by regressions.

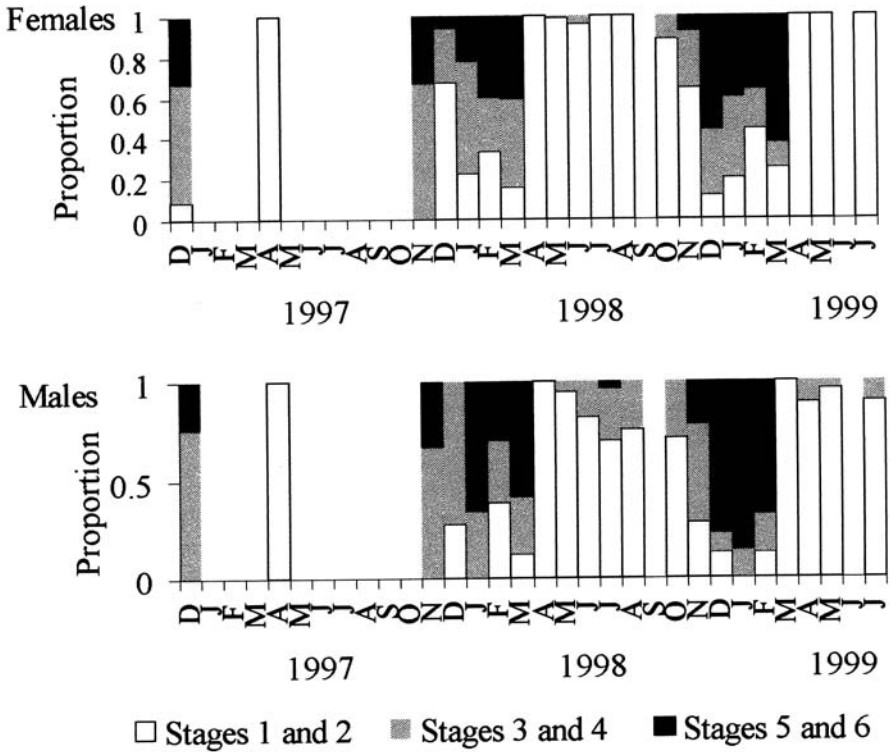


Figure 4. Monthly distribution of the proportion of *Loligo sanpaulensis* at different stages of maturity.

size classes became noticeable from April to June and disappeared from the fishing area in July. Catches were scarce during the end of winter (Table 1) and became more abundant at the beginning of spring. Throughout the sampling, the largest squids were caught in Escondida Island (Fig. 1). In Engaño Bay the largest animals were caught during the summer months (Fig. 1). A squid of a record size for the species of 200 mm ML was captured with jigs in Nuevo Gulf in March 1998. The most abundant catches per trip were obtained in December of 1997, March, May and June of 1998, and May 1999 (Table 1).

REPRODUCTIVE CYCLE.—The observed sex ratio (870 females:594 males) showed highly significant differences from 1:1 (Chi-square, $P < 0.01$). Sex ratio showed an annual cyclic variation, with higher female abundance in summer 1997/1998 (Chi square, $P < 0.05$) and fall 1998 and 1999 ($P < 0.01$), and equal proportions of males and females during winter and spring. Females outnumbered males in almost all the size classes except those greater than 160 mm (Fig. 2).

The curves of maturity obtained by regression were $P_i = 1/(1 + \exp^{-(6.2 + 0.09L_i)})$ ($n = 19$, $r^2 = 0.996$) for males and $P_i = 1/(1 + \exp^{-(8.9 + 0.12L_i)})$ ($n = 15$, $r^2 = 0.998$) for females, where P_i is the proportion of mature animals in the ML class i , and L_i is the midpoint of the ML class i (Fig. 3). The sizes at maturity (ML 50%) estimated from these equations were 65 mm ML for males and 78 mm ML for females.

An annual cyclic pattern was found in the frequencies of individuals at different stages of maturity. In Figure 4 individuals at the six stages of maturity of the scale of Lipinski

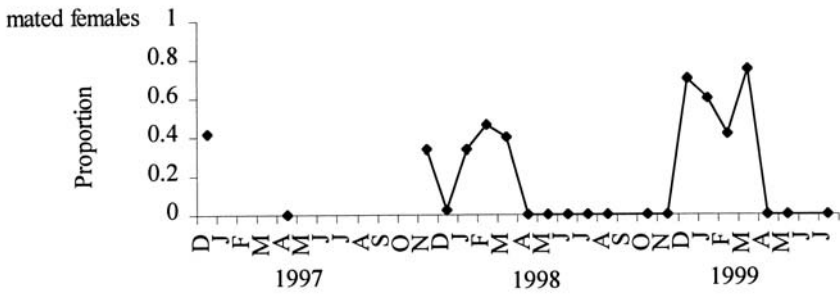


Figure 5. Monthly distribution of the proportion of *Loligo sanpaulensis* mated females.

and Underhill (1995) are grouped into 3 classes (stages 1 and 2: early immature and immature, stages 3 and 4: maturation and advanced maturation, stages 5 and 6: maximum maturation with spawning and terminal spawning) to allow for an easy interpretation of this pattern. It was observed that stage 1 and 2 individuals prevailed from April to November/December, individuals at stages 3 and 4 were present from October/November to March/April and squids at stages 5 and 6 were abundant from November/December to March/April (Fig. 4). A slight delay was observed in the maturation of females compared to males (Fig. 4). Females with spermatophores attached to the mantle, the mouth pouch, or both, were found only from November/December to March (Fig. 5).

The bimonthly variation of the nidamental glands (NGI) and testes (TI) indices show annual cyclic patterns (Fig. 6). NGI showed lower values from April/May to August/September, raised abruptly in February/March in 1997 and in December/January in 1998, maintaining high values during the summer months and falling to the lowest values in April/May. TI presented a similar pattern but in contrast to NGI it progressively raised from June/July 1998 to December/January 1999 (Fig. 6).

DISCUSSION

L. sanpaulensis is caught as by catch in coastal waters of northern Patagonia. Even though various types of fishing gear were employed to obtain samples during this study, most of the animals were caught with an otter trawl with a net of 60 mm mesh size on board of the vessel *Stella Maris* (78%) (Table 1). Also, most catches were obtained in Engaño Bay (79%) (Table 1). Another loliginid present in the captures was *Loligo gahi*, but this species was present in low numbers compared to *L. sanpaulensis*.

Considering the temporal variation of the size structure and reproductive cycle of the population in coastal waters of northern Patagonia, it can be interpreted that during the summer spawning individuals and recruits probably hatched at the beginning of the spawning season (spring) are present in the coastal area. In autumn, the largest individuals die after spawning and juveniles are abundant. In winter, these juveniles reach a critical size and migrate to deeper waters and only the individuals that hatched in mid-fall (from the last egg masses deposited during the spawning season) remain in the area. This scheme is completed in mid-spring with the return of mature and maturing animals to coastal waters to reproduce. Similar life cycles have been observed in *L. sanpaulensis* (Costa and Fernandes, 1993) and other Loliginidae (Mangold, 1987; Hatfield et al., 1990; Augustyn et al., 1992).

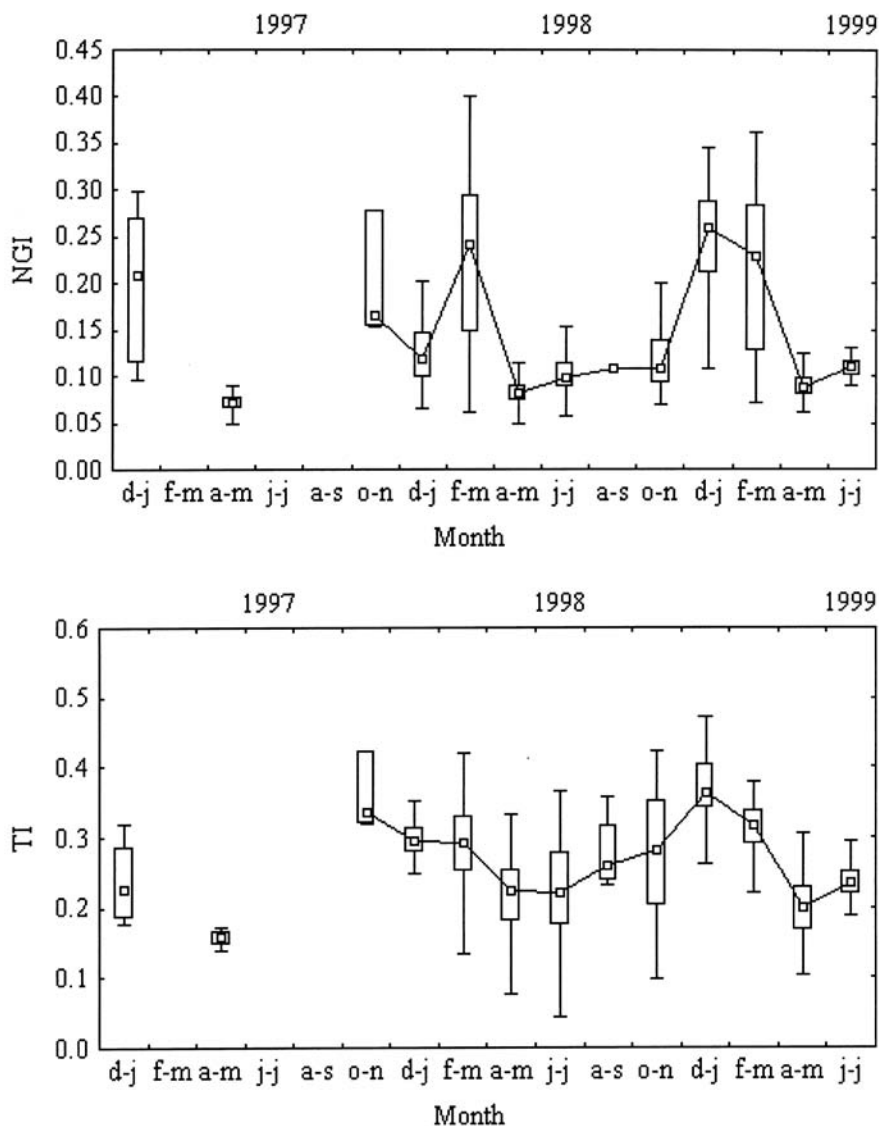


Figure 6. Bimonthly distribution of the maturity indexes. Top: Nidamental glands index (NGI), Bottom: Testes index. Mark = Median, Box height = Interquartile range ($IQR = Q_3 - Q_1$), Bars = range of values within $(Q_1 - IQR) - (Q_3 + IQR)$.

In northern Patagonia, after the cool season (winter), water temperatures high enough for spawning could be reached later during the year than in more northern areas of the range. This would result in differences in the timing of life-cycle events that would be reflected in the size structures of the populations. The size frequency distributions found in this study and those reported by Vigliano (1985) for the fishing area of Mar del Plata did not show many similarities when compared month to month. However, Vigliano (1985) found recruits smaller than 20 mm in January and he identified the sudden disappearance of individuals of size classes larger than 70 mm in November–December 1982, followed

by months of high recruitment (November, December and January); in other words, he found the same pattern reported in the present study but occurring three-four calendar months in advance. Also, the size frequency histograms presented by Pineda et al. (1998) for the fishing area of Mar del Plata revealed that the disappearance of the largest individuals occurs a few months earlier in Mar del Plata than in northern Patagonia. These authors found few individuals larger than 60 mm in February, large individuals entering the fishing area in July (females) and August (males) and a growing abundance of these size classes between September and November (Pineda et al. 1998). A similar situation was reported for *Loligo opalescens* populations from southern California (low latitude, winter/spring spawning) (Hixon, 1983) and from mid and northern California (high latitude, late spring/fall spawning) (Spratt, 1978).

The 200 mm male found in this study constitutes the size record for the species. The maximum size reported in the FAO's cephalopod species catalog (Roper et al. 1984) is 160 mm. Squids of up to 190 mm were found by Vigliano (1985), Andriquetto and Haimovici (1991) and Pineda et al. (1998).

The overall sex ratio found in this study differs from that observed by Vigliano (1985) (1321 males: 1210 females), Costa and Fernandes (1993) (340 males:365 females) and Andriquetto and Haimovici (1996) (918 males:875 females), who detected no significant differences in the sexes proportion. This difference could be the result of the use of different methodologies; squids of smaller size classes were not sexed in previous studies, being classified as 'juveniles' or 'undetermined' (Vigliano, 1985; Costa and Fernandes, 1993; Andriquetto and Haimovici, 1996). However, if the smaller size classes of squids from this study were not included in the analysis of sex ratio, the sample would be still biased towards predominance of females. Differences from the 1:1 sex ratio have been found in several cephalopod species, and can be attributable to different habitat selection by males and females or to fishing gear selectivity (Mangold, 1963). Hatfield (1992) found that the male:female sex ratio decreased with increasing depth in the *L. gahi* population. Boyle and Pierce (1994) found increased proportions of female *Loligo forbesi* in Scottish waters during the reproductive season, and equal proportions during the periods of recruitment. In the present study, the female:male sex ratio was significantly greater than 1:1 during the summer 1997/1998 and autumns of 1998 and 1999. It could be interpreted that the equal proportions of females and males during spring were associated with the mating activities and that the greater proportions of females in the summer samples were related to the spawning season. The expected migration of juvenile males from the sampling area during autumn, followed by juvenile females in late autumn-early winter could explain the significantly greater proportions of females found during this season. During the winter, males and females that did not reach the critical size to migrate would remain in the sampling area, resulting in a slightly greater proportion of females than males being present in the fishing area.

It is suggested that elevated temperatures lead to faster growth (Hatfield, 2000) and faster development of the gonads of cephalopods (Richard, 1966; Van Heukelem, 1976). As expected, the sizes at maturity observed in this study in male (65 mm ML) and female (78 mm ML) *L. sanpaulensis* were greater than those reported by Costa and Fernandes (1993) (50–55 mm ML in males, 55–60 mm ML in females) at the northern limit of the species distribution. Nevertheless, this comparison must be considered carefully given that these authors did not use the same maturity scale as in this study for their estimations.

Based on the results of the present work it can be concluded that in northern Patagonia there exists a single annual spawning period extending from November/December to March. The finding of *L. sanpaulensis* eggs masses (Barón, 2001) coincided with the capture of spawned males (stage 6) and mature females with spermatophores with jigs (March 1998, Nuevo Gulf). Throughout an extended survey, the egg masses of *L. sanpaulensis* have been found only from February to May (only embryos in advanced stages of maturity in May) (Barón, 2001). These findings are in agreement with the scheme of a reproductive cycle with a single annual spawning season for *L. sanpaulensis* in coastal waters of northern Patagonia.

At the latitude of the study area (43°S, Port of Rawson), monthly mean SST varies between approximately 9.6°C (August) and 17.2°C (February), while in the northern part of *L. sanpaulensis* distribution (23°S, Cabo Frio), the same parameter varies between approximately 22°C (August) and 26.5°C (March-April) (data from satellite images, AVHRR Oceans Pathfinder – NOAA/NASA). Preliminary data from laboratory experiments with the embryos of *L. sanpaulensis* (Barón, in prep.) show that the embryonic development is arrested below approximately 12°C and above 23°C. It seems reasonable to hypothesize that the reproductive cycle of *L. sanpaulensis* is constrained by high temperatures at the northern limits of the species distribution and by low temperatures in the southern limits, and that spawning at these areas is limited to a brief period of the year. However, animals inhabiting warm environments at low latitude coastal waters would be able to migrate to deeper (cooler) waters to spawn during the warmest months, extending their breeding season. This could be the case for the *L. sanpaulensis* population from the Cabo Frio region, in which the mean SST are higher than 23°C for most of the year and the highest concentrations of mature individuals are found in waters deeper than 45 m (Costa and Fernandes, 1993). Other aspects of the reproductive cycle pattern found by these authors may be the result of the combined effects of several environmental factors (Van Heukelem, 1979; Mangold, 1987). In northern Patagonia, low water temperatures restrict spawning to the late spring-summer period and probably to shallow (warm water) bottoms. This lack of choice results in a clearly defined breeding season, delimited by a concise annual peak of temperature. A similar situation as been reported for the *L. pealei* populations from the Gulf of Mexico (low latitude, extended breeding season) (Hixon, 1980) and from the Northwest Atlantic (high latitude, seasonal breeding season) (Summers, 1983).

ACKNOWLEDGMENTS

The authors are grateful to the captains of the vessels STELLA MARIS and MARTA ESTHER, O. Nicanoff and O. Valetti, and their crew and to J. Berón and E. Humaña for their assistance with the sampling tasks and commitment with this study. The comments of two anonymous reviewers have improved the quality of this paper.

LITERATURE CITED

- Andrighetto, J. M. and M. Haimovici. 1991. Abundance and distribution of *Loligo sanpaulensis* Brakoniecki, 1984 (Cephalopoda, Loliginidae) in southern Brazil. *Sci. Mar. Barc.* 55(4): 611–618.
- _____ and _____. 1996. Reproductive cycle of *Loligo sanpaulensis* Brakoniecki, 1984 (Cephalopoda; Loliginidae) in southern Brazil. *Sci. Mar.* 60(4): 443–450.

- Augustyn, C. J., M. R. Lipinski and W. H. H. Sauer. 1992. Can the *Loligo* squid fishery be managed effectively?. A synthesis of research on *Loligo vulgaris reynaudii*. S. African J. Mar. Sci. 12: 903–918.
- Barón, P. J. 2001. First description and survey of the layings of *Loligo gahi* D'Orbigny, 1835, and *Loligo sanpaulensis* Brakonieccki, 1984, from coastal waters of Patagonia. J. Shellfish Res. 20(1).
- Boyle, P. R. and G. J. Pierce. 1994. Fishery biology of northeast Atlantic squid: an overview. Fish. Res., 21(1–2): 1–16.
- Castellanos, Z. 1967. Contribución al estudio biológico de *Loligo brasiliensis* Bl. Bol. Inst. Biol. Mar. 14: 15–35.
- 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(1–2): 91–97.
- Hatfield, E. M. C., P. G. Rodhouse and J. Porebski. 1990. Demography and distribution of the Patagonian squid (*Loligo gahi*, d'Orbigny) during the austral winter. J. Cons. Int. Explor. Mer. 46: 306–312.
- _____. 1992. Recruitment, demography and growth of the patagonian squid *Loligo gahi* (D'Orbigny, 1835) in Falkland Island waters. Ph.D. Thesis. Brithish Antarctic Survey, Nat. Environ. Res. Council, Cambridge, U.K.
- _____. 1996. Towards resolving multiple recruitment into loliginid fisheries: *Loligo gahi* in the Falkland Islands fishery. ICES J. Mar. Sci. 53: 565–575.
- _____. 2000. Do some like it hot? Temperature as a possible determinant of variability in the growth of the Patagonian squid, *Loligo gahi* (Cephalopoda: Loliginidae). Fish. Res. 47: 27–40.
- Hixon, R. F. 1980. Growth, reproductive biology, distribution and abundance of three species of loliginid squid (Myopsida: Cephalopoda) in the northwest Gulf of Mexico. Ph.D. Thesis, Univ. Miami, Coral Gables, Florida.
- _____. 1983. *Loligo opalescens*. Pages 95–114 in P. R. Boyle, ed. Cephalopod life cycles, vol. 1. Species accounts. Academic Press, London.
- Juanicó, M. 1979. Contribuição ao estudo da biologia dos Cephalopoda Loliginidae do Atlântico sul ocidental, entre Rio de Janeiro e Mar del Plata. Doctoral Tese. Instituto Oceanográfico da Univ. São Paulo. 102 p.
- Lipinski, M. R. and L. G. Underhill. 1995. Sexual Maturation in squid: quantum or continuum?. S. Afr. J. mar. Sci. 15: 207–223.
- Mangold, K. 1963. Biologie des Céphalopodes benthiques et nectoniques de la Mer Catalane. Vie et Milieu, Supplément no. 13. 290 p.
- _____. 1987. Reproduction. Pages 157–200 in P.R. Boyle, ed. Cephalopod life cycles, vol. II. Academic Press, London.
- O'Dor, R.K. 1998. Squid life-history strategies. Pages 236–250 in P. G. Rodhouse, E. G. Dawe and R. K. O'Dor, eds. Squid recruitment dynamics: The genus *Illex* as a model, the commercial *Illex* species and influences on variability. FAO Fish. Tech. Pap. 376.
- Okutani, T. and T. Watanabe. 1983. Stock assessment by larval surveys of the winter population of *Todarodes pacificus* Steenstrup (Cephalopoda: Ommastrephidae), with a review on early works. Biol. Oceanog. 2: 401–431.
- Pineda, S. E., N. E. Brunetti and N. Scarlato, 1998. Los loliginidos. Pages 13–36 in E. E. Boschi, ed. El mar Argentino y sus recursos pesqueros, vol. 2. INIDEP, Mar del Plata.
- Richard, A. 1966. La température facteur externe essential da croissance pour de Cephalopoda *Sepia officinalis* L. C.r. hebd. Séanc. Acad. Sci. Paris, Ser. D. 267: 2360–2363.
- Roberts, M. and W. H. H. Sauer. 1994. Environment: the key to understanding the South African chokka squid (*Loligo vulgaris reynaudii*) life cycle and fishery? Antarctic Sci. 6: 249–258.
- Roper, C. F. E., M. J. Sweeney and C. E. Nauen. 1984. Cephalopods of the world, vol.3: An annotated and illustrated catalogue of species of interest to fisheries. FAO Fish. Synop. no. 125. FAO, Rome. 277 p.

- Spratt, J. D. 1978. Age and growth of the market squid *Loligo opalescens* Berry, in Monterey Bay. Calif. Dept. Fish. Game Fish. Bull. 169: 35–44.
- Summers, W.C. 1983. *Loligo pealei*. Pages 115–142 in P. R. Boyle, ed. Cephalopod life cycles, vol. 1. Species accounts. Academic Press, London.
- Van Heukelem, W. F. 1979. Environmental control of reproduction and life span in *Octopus*: An Hypothesis. In S. E. Stancyk, ed. Reproductive ecology of marine invertebrates. Univ. South Carolina Press. 11 p.
- Vigliano, P. H. 1985. Contribución al conocimiento de la biología de *Loligo brasiliensis* Blainville 1823 (Mollusca, Cephalopoda) en aguas argentinas. Tesis Doctoral, Facultad de Ciencias Naturales. Univ. Nac. de La Plata. 183 p.

ADDRESS: Centro Nacional Patagónico, Consejo Nacional de Investigaciones Científicas y Técnicas, Boulevard Brown s/n, Puerto Madryn (9120), Chubut, Argentina. E-mail: (P.J.B.) <baron@cenpat.edu.ar>, (M.E.R.) <re@cenpat.edu.ar>.