

Seasonal and interannual variability in growth and maturation of winter-spawning *Illex argentinus* (Cephalopoda, Ommastrephidae) in the Southwest Atlantic

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Abstract

An investigation was carried out during the *Illex argentinus* trawl fishery (January-July) in the fishery regions of 42°S and 45-47°S off the Exclusive Economic Zone of Argentina between 1985 and 1990. Statoliths of 5,232 squid were sampled and processed to study age and growth patterns in squid, hatched in different months. Among squid of similar ages (within an age interval from 180 to 300 days), the May-hatched squid were the smallest while the September-hatched were largest. Growth rates of squid of the same hatching-months were significantly different according to year, but these differences were considerably smaller than those observed between various hatching-months within one year. The largest individuals at a given age were captured in 1990, and the smallest in 1985. Males and females became mature at age 220-320 and 210-360 days respectively. The maturation period lasts 1.5-2.5 months in males and 1 month in females. Early and late-maturing groups were observed within each hatching-month. The peak of spawning was in July of 1984, 1986, 1987, in June of 1985 and in August of 1989.

Keywords: Squid, Oegopsida, *Illex*, statoliths, growth, maturation, spawning, Atlantic.

Variabilité saisonnière et interannuelle de la croissance et de la maturation d'Illex argentinus (Cephalopoda, Ommastrephidae) de ponte hivernale, dans l'Atlantique Sud-Ouest.

Résumé

Les recherches ont été effectuées lors de la période de pêche chalutière d'*Illex argentinus* de janvier à juillet, dans les zones de pêche entre 42°S et 45-47°S au-delà de la zone économique exclusive de l'Argentine, de 1985 à 1990. Il a été échantillonné et traité 5 232 statolithes pour l'étude de l'âge et de la croissance de calmars dont l'éclosion s'est produite à différents mois de l'année. Parmi les calmars d'âge similaire (entre 180 et 300 jours), les calmars éclos en mai étaient les plus petits, tandis que ceux éclos en septembre étaient les plus grands. La vitesse de croissance de calmars du même mois d'éclosion diffère considérablement suivant les années, cependant ces variations sont moindres, comparées à celles observées chez les représentants de différents mois d'éclosion au cours d'une année. Les individus les plus grands, d'un âge donné, ont été capturés en 1990, et les plus petits en 1985. La maturité sexuelle est atteinte à l'âge de 220-320 jours pour les mâles et 210-360 jours pour les femelles. Les pontes les plus abondantes ont été enregistrées au mois de juillet 1984, 1986, 1987 ainsi qu'au mois de juin 1985 et au mois d'août 1989.

Mots-clés : Calmar, Céphalopode, Oegopsida, *Illex*, statolithes, croissance, maturation, Atlantique Sud-Ouest.

INTRODUCTION

The Argentine short-finned squid *Illex argentinus* (Castellanos, 1960) is one of the most important commercial resources in the southwest Atlantic. It inhabits shelf and slope waters from southern Brazil to the Burdwood Bank and the Falkland Islands, and open waters of the Argentine Basin. Mantle length (ML) of mature males ranges from 140-320 mm, whereas that of mature females ranges 150-420 mm (Nesis, 1987). *I. argentinus* has a one-year life-cycle and year-round spawning with a pronounced winter spawning peak. Recently, different aspects of age and growth, population structure and reproductive biology of *I. argentinus* have been studied (Hatanaka, 1986; Nigmatullin, 1989; Arkhipkin, 1990; Rodhouse and Hatfield, 1990; Arkhipkin and Scherbich, 1991; Brunetti *et al.*, 1991; Arkhipkin, 1993). However, little is known about seasonal and interannual variability in rates of growth and maturation.

Interannual aspects of squid growth rates have been poorly studied, because the method of age determination is highly labour intensive. Such an investigation needs a continuous monitoring of a population over several years. Until now, only Villanueva (1992) has demonstrated annual variation in the growth rate of *Todarodes angolensis* (Ommastrephidae) from Namibian waters over three consecutive years based on statolith analysis. Squid grew faster in 1987 (which was a cold year) than in the relatively warm years of 1988 and 1989.

The duration of maturity stages in squid has been practically unknown, with one exception: Mangold *et al.* (1975) reported that a female of *I. illecebrosus* matured in 17 days under total food deprivation. It was revealed that early maturation in cephalopods reared in captivity might be due to: abundant food during early growth followed by restricted food intake during late phases of ontogenesis; short day length; low light intensity and high water temperature (Mangold, 1987).

This study reports on seasonal and interannual variability in growth rates and maturation of *I. argentinus*, based on extensive squid age and growth studies by statolith analysis.

MATERIAL AND METHODS

Sampling was carried out during January-July in the fishery regions of 42°S and 45-47°S off the exclusive Economic Zone of Argentina between 1985 and 1990. *I. argentinus* were collected from catches of Soviet research and fishing vessels. Mantle length (ML) was measured within 1 mm and body weight (BW) to within 1 g. Maturity stages were identified after Nigmatullin (1989) including:

– *Immature animals* (stages 1 and 2): males have no sperm in testis, females have no oocytes with follicular folds.

– *Physiologically maturing animals* (stages 3 and 4): males have sperm in the testis, but no fully developed spermatophores in the Needham sac; females have oocytes with follicular folds in the ovary, but no ripe eggs in oviducts.

– *Physiologically mature* (substages 5-1 and 5-2) *and functionally mature* (substage 5-3) *animals*: males have normal spermatophores in the Needham sac, females have ripe eggs in oviducts. – Substage 5-1: in males, less than 20% of the Needham sac volume is filled by spermatophores; in females, ripe eggs occupy < 10% of the total volume of oviducts. – Substage 5-2: in males, 20-50% of the Needham sac volume is filled by spermatophores, testis does not reduce; in females, ripe egg volume ranged from 10 to 60% of total volume of ovary and oviducts. – Substage 5-3: in males, 50-100% of the Needham sac volume is filled by spermatophores, testis reduces and becomes grey; in females, ripe egg volume is about 60-80% of the total volume of ovary and oviducts, ovary reduces in size.

– *Spawning animals* (stage 6): reproductive system reduces, body tissues and inner organs degenerate, gills of females with numerous attached spermatophores.

– *Spent animals* (stage 7): reproductive system completely destroys.

Statoliths from 5,232 specimens (table 1) were removed at sea according to Dawe and Natsukari (1991) and stored in 96% ethanol. Further analyses of statoliths were made in the laboratory using statolith ageing techniques elaborated by one of the authors

Table 1. – Numbers of statoliths sampled from different monthly cohorts of *Illex argentinus* in various years males/(females).

		May	June	July	August	September	Total
1985	♂	8	22	62	31	1	124
	♀	17	60	93	50	7	227
1986	♂	41	97	88	4	0	230
	♀	131	224	146	11	1	513
1987	♂	13	99	202	127	48	489
	♀	67	289	373	206	81	1,016
1988	♂	49	143	239	141	87	659
	♀	131	259	359	300	205	1,254
1990	♂	0	11	68	102	39	220
	♀	3	56	163	210	68	500
Total		460	1,260	1,793	1,182	537	5,232

(A. A.) (Dawe and Natsukari, 1991). Growth in increments in the ground statolith were counted twice from the nucleus to the margin of the dorsal dome under transmitted light ($\times 400$). Daily periodicity in statolith growth increments has been validated in *I. illecebrosus* (Hurley *et al.*, 1985). We therefore consider that the total number of growth increments in sibling species *I. argentinus* likely represents squid

age in days. Hatching dates were backcalculated from the dates of capture. Hatching-months were defined by grouping of squid over month of hatching (e.g. squid hatched from 1 to 30 June were regarded as the June-hatched squid etc.).

In the present study, we did not attempt to fit an ontogenetic growth model for each hatching month of squid mainly because of the fact that we sampled squid only during the second part of their life (age range from 150 to 360 days) and therefore had no information on patterns of their larval and juvenile growth. Our main purpose of group growth-curve construction was to compare average sizes of squid belonging to various hatching months at successive ages and calculate growth rates at each given age interval. Growth curves of mantle length and body weight (BW) for males and females of each hatching-month in different years were constructed using means from representative hatching months or years (Ricker, 1958) with an assumption that mortality rates were similar among same-aged squid of the ontogenetic period studied. The data (ages) were divided into 30-day increment classes (e.g. 240 increment class represents from 225-254 increments (days), 270 increment class from 255-284 increments (days) etc.). Mean ML and BW were calculated for each increment class for group growth curve construction. Differences between age-specific means of ML and BW due to each sex or hatching-month at the same age was estimated by the two-sample analysis with null hypothesis test (differences = 0 at $\alpha = 0.05$). Instantaneous relative growth rates (G) were calculated from mean values of ML and BW for each 30-day interval after Forsythe and Van Heukelem (1987). Growth rates were compared for all size classes of all hatching-months, but statistical analysis was applied to one representative group, the 240 increment class (tables 2 and 3).

Duration of maturity stages was estimated according to the following assumptions. It is well-known that squid are monocyclic animals with a continuous asynchrony in gonad development (Nesis, 1987), i.e. each individual passes through a given maturity stage only once during ontogenesis. For estimation of the duration of different maturity stages, we assumed that specimens which achieve a given stage earlier (at a younger age) than most others, would have attained the next stage earlier (later), respectively. Hence, the difference in the minimum ages between two successive maturity stages (e.g. 3 and 4) was taken to represent the duration of stage 3 in early maturing animals; the difference in the maximum ages corresponds to duration of stage 4 in late maturing squids. For statistical comparisons of maturation in different hatching-months, we used the mean ages of squid at each maturity stage. The method of probability paper (Harding, 1949) was used for separation and estimation of ML means of groups from bimodal distributions of maturity stages versus age.

RESULTS

Hatching time

It was possible to determine spawning time or, more exactly, peak of survival of hatched larvae and juveniles of *I. argentinus* sampled in different years by backcalculating hatching dates. Samples were taken regularly throughout the fishery period in 1987, 1988 and 1990. Most squid were sampled during summer (January-February) in 1986, and in autumn (March-April) in 1985 (fig. 1).

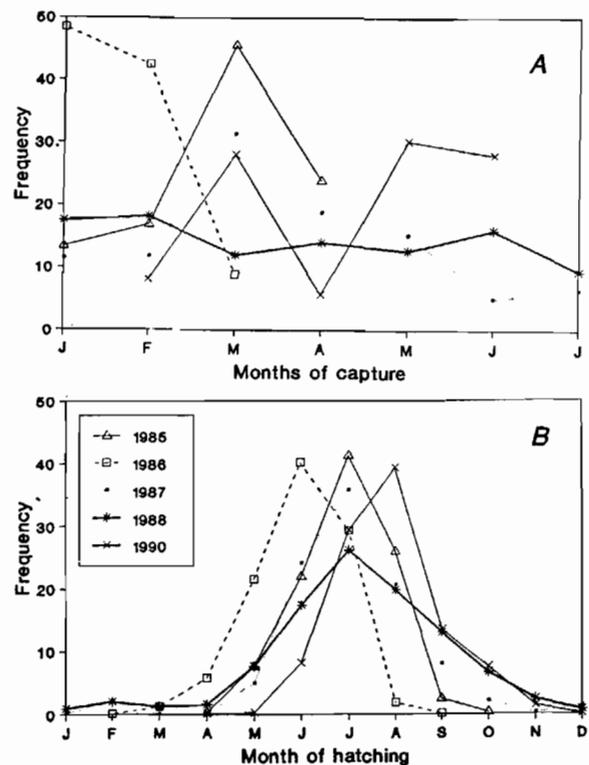


Figure 1. - *Illex argentinus*: distribution of sampling dates (A) by year of sampling and hatching dates, in the previous year (B).

The distribution of hatching dates of squid within any year was unimodal with a well-defined peak in July of the previous year for squid sampled in 1985, 1987 and 1988. For 1986, the hatching peak was in June and for 1990, the hatching peak was in August of the previous year. The most prominent peak of hatching was observed for squid captured in July of 1985 (40%), the lowest for July 1988 (27%). In 1988 and 1990, there was a high proportion of spring-hatched squid (September-October) (fig. 1).

Table 2. – Mantle lengths (ML, mm) and body weights (BW, g) (range, mean and standard deviation) and statistical difference (*t*-criteria) among the samples of squid at age 240 days of different hatching-months (data pooled over years for each hatching-month). Values of *t*-criteria lower than corresponding to $p=0.95$ (differences are not significant) are indicated by asterisk.

	May	June	July	August	September
	N	N	N	N	N
MALES					
Mantle length	162-244 (202.5) SD = 18.7 49	165-286 (213.7) SD = 25.0 123	178-270 (228.2) SD = 18.4 140	200-300 (238.5) SD = 17.9 61	210-310 (261.5) SD = 22.3 33
Body weight	115-270 (191.2) 27	95-520 (225.0) SD = 87.4 90	150-490 (277.3) SD = 71.7 120	160-940 (343.9) 53	220-780 (490.5) 33
	<i>t</i> -criteria:	June	July	August	September
May					
ML		2.892	8.385	10.252	12.965
BW		1.935*	5.971	5.723	11.500
June					
ML			5.416	6.911	9.977
BW			4.753	6.399	13.036
July					
ML				3.656	8.961
BW				4.231	12.459
August					
ML					5.447
BW					4.995
FEMALES					
Mantle length	160-273 (221.9) SD = 18.8 162	170-294 (234.1) SD = 24.8 261	200-320 (251.7) SD = 24.4 276	212-335 (262.0) SD = 20.1 126	245-365 (292.5) SD = 29.4 57
Body weight	60-460 (200.9) SD = 63.7 97	87-540 (254.2) SD = 94.8 147	150-930 (342.2) SD = 126 217	160-1040 (397.0) SD = 120.3 101	370-1175 (597.3) SD = 183.2 56
	<i>t</i> -criteria:	June	July	August	September
May					
ML		5.348	13.369	17.410	20.808
BW		4.857	10.450	14.265	19.418
June					
ML			8.276	10.999	15.549
BW			7.198	10.455	17.439
July					
ML				4.168	11.112
BW				3.678	12.194
August					
ML					8.179
BW					8.237

Seasonal and ontogenetic variability

Original data for seasonal differences in size-at-age distributions of both sexes are shown in *figures 2* and *3*. An effect of sex on growth in mantle length was observed at age >180 days (*fig. 4*) when the instantaneous relative growth rate (G) of females became greater than that of males. At age 270-300 days, female ML for any hatching-months was 30-50 mm greater than that of males. At age 180-

240 days, males were heavier (despite being shorter) than females; at age 240 days, BW of males and females became similar and at age >240 days females were heavier than males (*fig. 5*).

Differences in size-at-age and growth rates of different hatching-months within one year were shown for squid hatched in winter 1987 and captured during the fishery in 1988. Within the age range studied (150-360 days) and at any age, the May-hatched squid were the smallest in both ML (*fig. 4*) and

Table 3. – Mantle lengths (ML, mm) and body weights (BW, g) (range, mean and standard deviation) and statistical differences (*t*-criteria) among the August-hatched squid at age 240 days born in different years. Values of *t*-criteria lower than corresponding to $p = 0.95$ (differences are not significant) are indicated by asterisk (N = number of squid sampled).

	1987 range (\bar{x})	N	1988 range (x)	N	1990 range (x)	N
MALES						
Mantle length	213-265 (230.9)	20	210-300 (266.3)	32	210-300 (261.8)	11
	SD = 11.2		SD = 18.3		SD = 28.0	
Body weight	210-940 (335.3)	15	200-685 (357.4)	29	250-790 (522.2)	11
	SD = 184.4		SD = 114.5		SD = 178.9	
	<i>t</i> -criteria:		1988		1990	
1987						
ML			30.23		4.388	
BW			0.489*		2.586	
1988						
ML					2.325	
BW					3.463	
FEMALES						
Mantle length	224-335 (260.9)	58	230-330 (266.3)	54	240-340 (289.7)	16
	SD = 19.0		SD = 19.1		SD = 32.6	
Body weight	210-1040 (385.2)	37	240-1085 (427.6)	50	310-1100 (601.3)	16
	SD = 129.4		SD = 102.9		SD = 240.3	
	<i>t</i> -criteria:		1988		1990	
1987						
ML			1.489*		4.513	
BW			1.701*		4.252	
1988						
ML					3.612	
BW					4.109	

BW (fig. 5). ML and BW, at any age increased with month of hatching from May to September. All hatching-months differed significantly from each other (table 2). The minimum difference due to month of hatching in length-at-age and weight-at-age for both sexes were observed between the May and June-hatched squid, the maximum between the May and September-hatched squid. In contrast, the G of ML and BW showed a reverse pattern in squid at age > 180 days: the May-hatched squid usually had the highest G and the September-hatched squid the lowest G (fig. 4 and 5). Due to considerable differences in sizes between those two hatching-months at age 180-210 days, the relatively small May-hatched squid did not attain the sizes of large September-hatched squid, despite the fact that they had higher relative growth rates.

Interannual variability

To demonstrate interannual variation in size-at-age and growth rates, the August-hatched squid were chosen (fig. 6). Size differed significantly among years in both sexes at the same age, but yearly effects were

small (table 3) compared to hatching-month effects within any year. Generally, the August-hatched squid were largest in 1990 and smallest in 1985.

Maturation

Males

Males became physiologically mature (stages 3-4) over a wide age range; from 142 to 299 days (table 4). Bimodal distribution in age-at-maturity was evident for all hatching-months, with early-maturing and late-maturing males starting to mature at ages 160-210 days and 200-230 days, respectively (fig. 7). The proportion of early-maturing males decreased from 85-90% for the June and July-hatched squid to 65-70% for the August-hatched squid and 40% for the September-hatched squid. From the data pooled over years for each hatching month, mean age at the beginning of maturation also decreased with month of hatching: the August and September-hatched males started maturing (stages 3 and 4) at 10-15 days younger than males hatched in June and a month younger than males hatched in May (table 4). Early-maturing

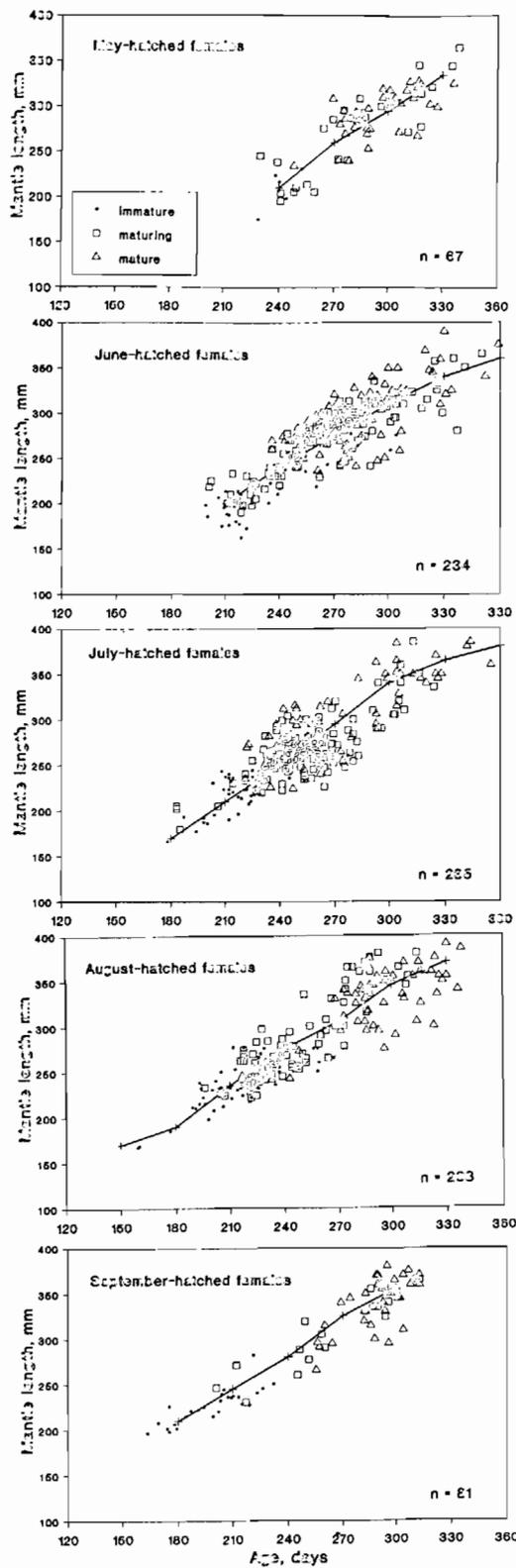


Figure 2. — *I. argentinus*: size-at age of females of different hatching months in 1987.

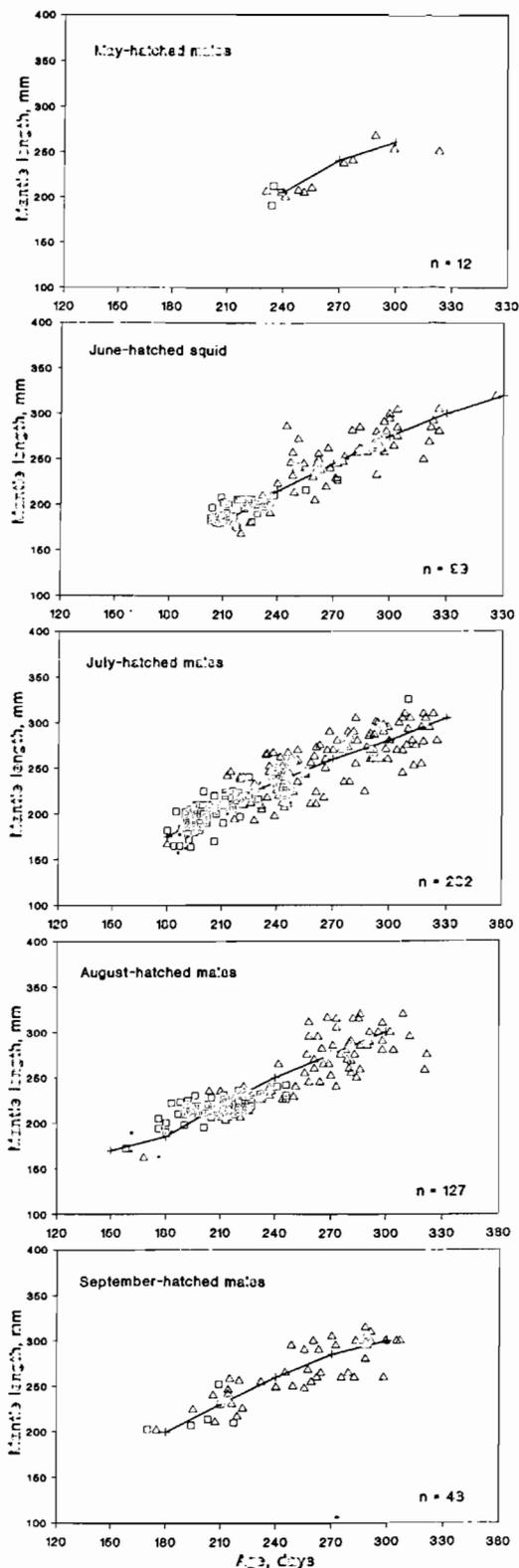


Figure 3. — *I. argentinus*: size-at age of males of different hatching months in 1987. Symbols are the same as in figure 2.

Table 4. - Mean age, 95% confidence intervals (in parentheses) and ranges of age in days at different maturity in males of *Illex argentinus* (squid of the same monthly cohorts in different years were combined).

Month of hatching	Maturity Stages							
	3 and 4 (combined)		5-1		5-2		5-3	
	Age	N	Age	N	Age	N	Age	N
May \bar{x}	238.5 (24.2)		241.4 (18.9)		268.5 (6.2)		261.7 (20.2)	
range	232-255	7	206-290	17	221-323	65	220-276	9
June \bar{x}	215.5 (7.6)		231.9 (5.6)		256.4 (4.6)		259.8 (13.4)	
range	167-299	64	196-290	67	191-356	182	218-335	19
July \bar{x}	205.6 (3.2)		223.1 (5.1)		253.6 (3.7)		270.3 (10.7)	
range	173-245	112	174-310	97	180-326	287	220-317	24
August \bar{x}	189.3 (4.9)		224.7 (7.2)		251.3 (5.7)		271.5 (22.5)	
range	142-245	66	190-272	46	193-207	75	222-331	10
September \bar{x}	180.7 (18.2)		232.2 (10.6)		255.0 (5.6)		270 and 288	
range	154-232	9	161-271	28	175-307	89		2
Total \bar{x}	203.9 (3.1)		227.9 (2.9)		254.5 (2.7)		266.4 (5.6)	
range	142-253	258	161-310	255	175-356	701	218-335	64

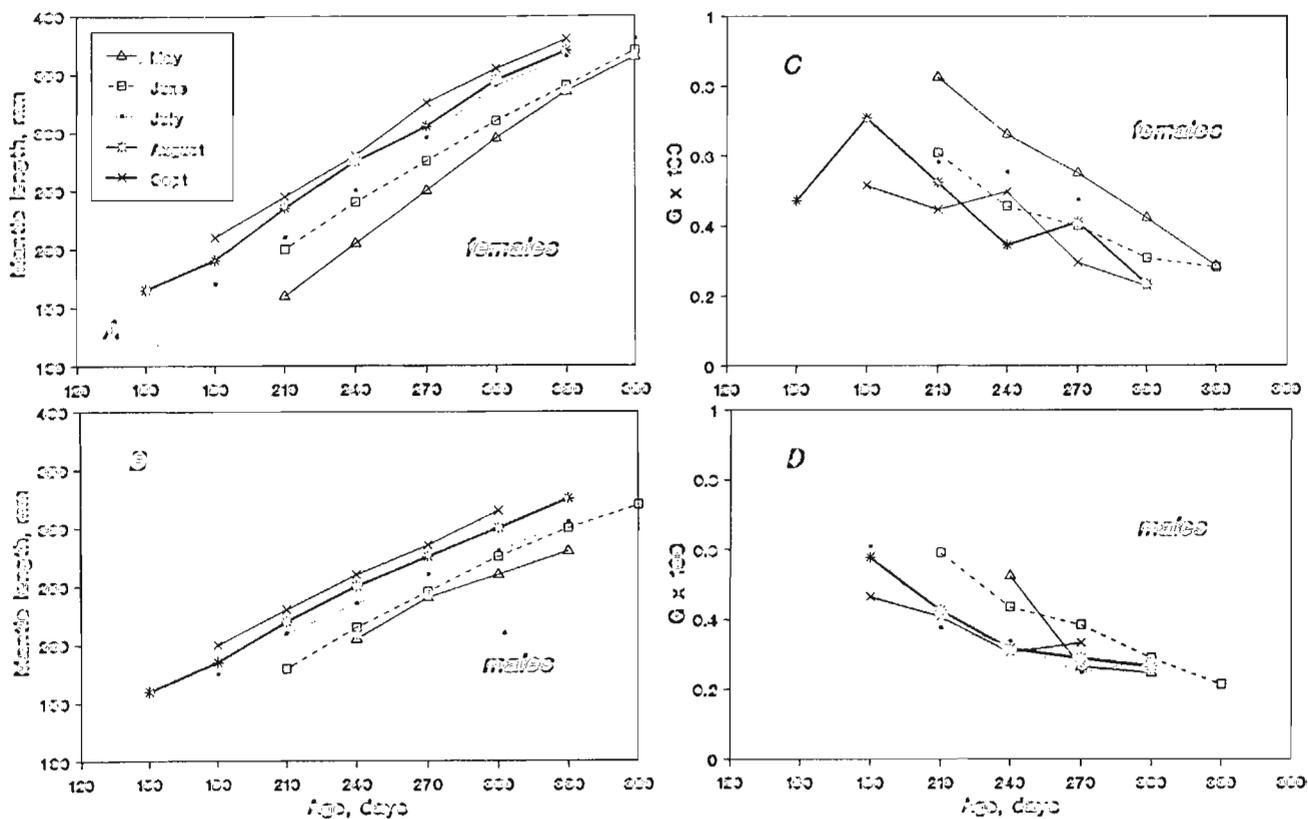


Figure 4. - *I. argentinus*: A-B. Composite graphs of group growth curves and C-D. Instantaneous daily growth rates (G, x 100) of mantle length in males and females of different hatching months in 1937.

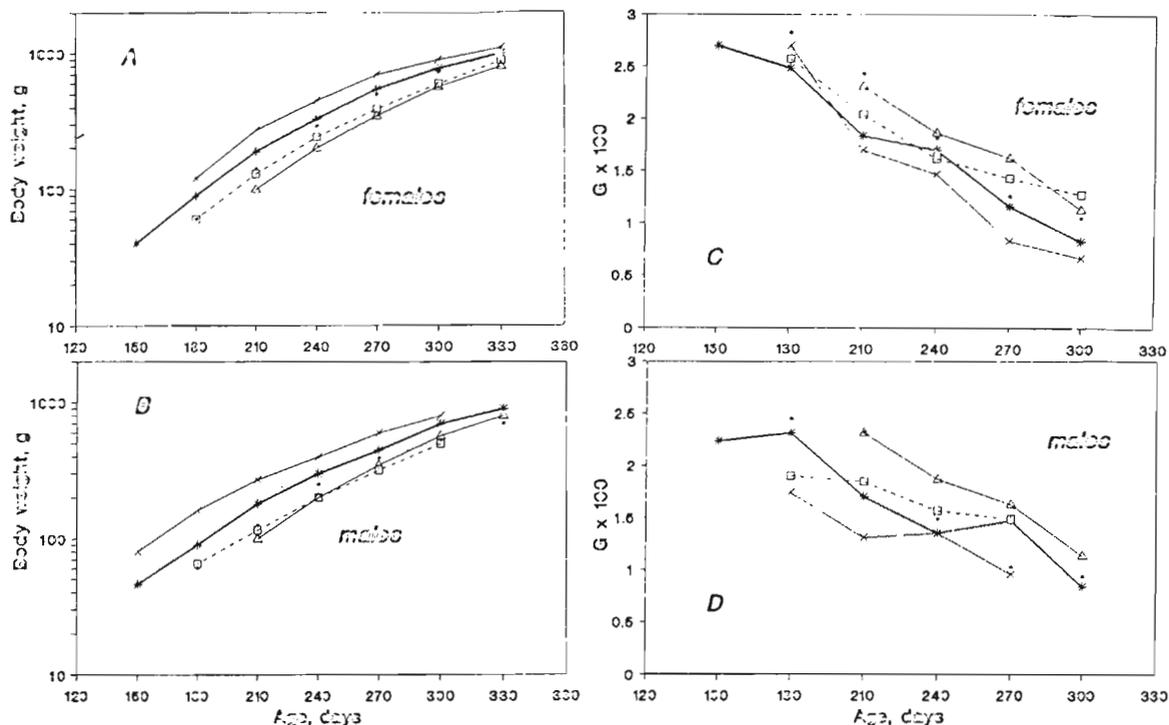


Figure 5. - *I. argentinus*: A-B. Composite graphs of group growth curves and C-D. Instantaneous daily growth rates (G, $\times 100$) of body weight in males and females of different hatching months in 1987. Symbols are the same as in figure 4.

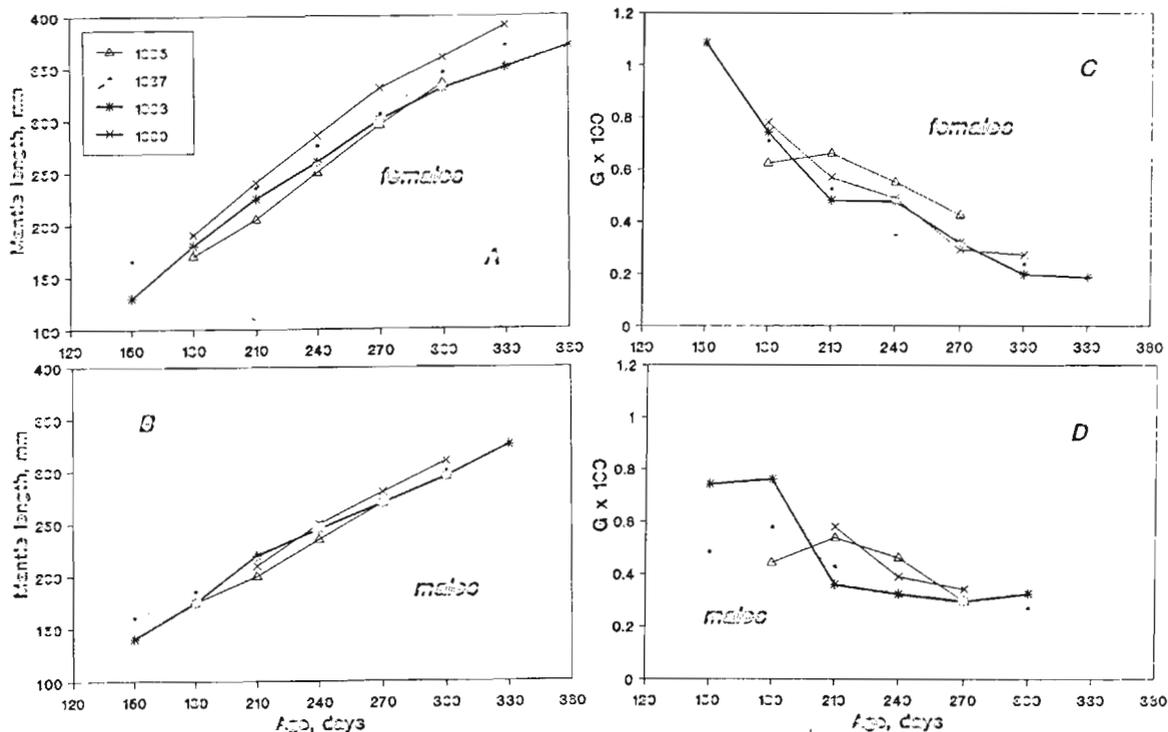


Figure 6. - *I. argentinus*: A-B. Composite graphs of group growth curves and C-D. Instantaneous daily growth rates (G, $\times 100$) of mantle length in males and females of August-hatched squid in different years.

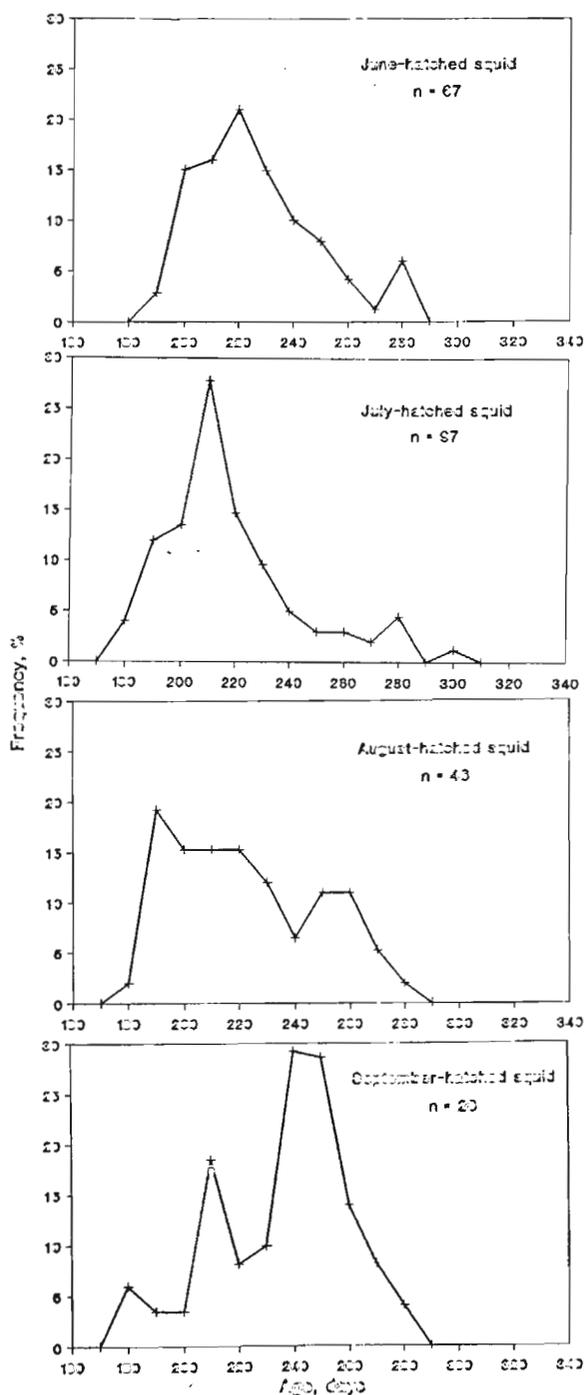


Figure 7. - *I. argentinus*: age frequency distribution of maturing males (maturity stage 3 and 4 pooled) of different hatching months.

males usually attain maturity (5-3 stage) at age 220-250 days, late-maturing males at age 260-310 days. Thus, maturation requires about 1.5-2 months in the early-maturing males and 2-2.5 months in late-maturing males in each hatching-month.

Maturity stages 3 and 4 were transitory and lasted several days, regarding squid of approximately similar

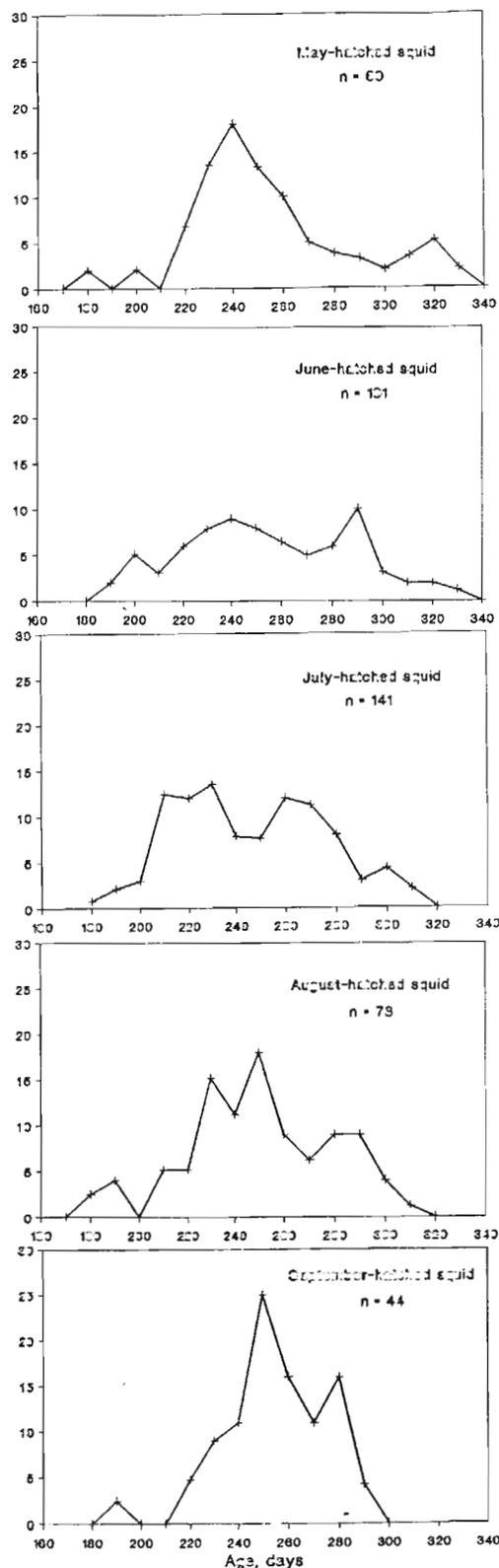


Figure 8. - *I. argentinus*: age frequency distribution of maturing (maturity stage 4) females of different hatching months.

Table 5. – Mean age, 95% confidence interval (in parentheses) and range of age in days, in females of *Illex argentinus* at different maturity stages (squid of the same monthly cohorts from different years were combined).

Month of hatching	Maturity Stages									
	3		4		5-1		5-2		5-3	
	Age	N	Age	N	Age	N	Age	N	Age	N
May \bar{x}	251.8 (6.2)		253.4 (8.2)		259.8 (9.0)		265.9 (5.3)		263.9 (13.7)	
range	218-312	41	187-324	60	218-339	43	221-336	104	227-327	17
June \bar{x}	233.7 (4.3)		258.8 (7.0)		265.8 (6.5)		270.9 (4.3)		260.3 (20.9)	
range	194-293	70	193-350	101	195-341	116	198-363	187	213-340	16
July \bar{x}	242.5 (13.0)		250.3 (5.0)		273.6 (5.2)		267.6 (4.4)		275.0 (7.2)	
range	181-328	179	190-316	141	197-324	124	202-355	193	219-332	48
August \bar{x}	245.2 (6.1)		254.2 (6.6)		270.2 (5.5)		280.3 (5.4)		281.7 (10.6)	
range	180-304	91	183-313	78	195-314	83	197-338	143	233-336	21
September \bar{x}	251.2 (7.3)		260.5 (6.0)		269.2 (5.3)		280.4 (4.3)		276.6 (10.0)	
range	185-315	29	195-310	44	198-317	70	202-348	91	225-342	16
Total \bar{x}	243.1 (2.8)		254.5 (3.0)		268.8 (2.8)		272.4 (2.7)		274.0 (4.5)	
range	180-328	410	183-350	424	195-341	436	197-363	718	213-340	141

age at these stages in hatching-months studied and considering the rare occurrence of animals at these stages in catches throughout the year. It seems that mean age of males at the maturity substage 5-1 had been slightly overestimated, as it was difficult for collectors at sea to correctly identify the beginning of the substage due to poor visibility of the first 10-20 spermatophores in the Needham sac. According to our estimates (table 4), the substage 5-1 lasted from 10-15 to 20 days; the 5-2 and 5-3 substages lasted together about 40-50 days in early-maturing squid and 50-70 days in late-maturing males.

Throughout maturity stage 5, late-maturing males produced and accumulated about 1,000-1,200 (up to 1,400) spermatophores including about 150-200 spermatophores produced at substage 5-1 (Laptikhovskiy and Nigmatullin, 1992). It was therefore possible to estimate the daily production of spermatophores (*i.e.* 10-15 spermatophores at substage 5-1 and 15-20 spermatophores at the substages 5-2 and 5-3).

Females

Females started maturing (stage 3) at age 180-328 days (table 5). As with males, there were both early-maturing and late-maturing individuals (fig. 8). However, in contrast to males, mean age at maturation was bimodal for all the hatching-months, with maturation beginning at about 190-250 days in early-maturing and about 260-300 days in late-maturing females, respectively. The ratio between early- and late-maturing females was rather uniform in relation to hatching-month (again in contrast to males); early-maturing animals constituted about 60-80% of the total catch. Mean age of the early-maturing females at maturity stage 4 was 225 days, at substage 5-1 - 230 days, at substage 5-2 - 235 days; in late-maturing

females, the mean age was 297 days, 304 days and 310 days, respectively. The duration of the maturation period in both forms lasted no more than one month. The period of initial egg accumulation (5-1 and 5-2 maturity substages) lasted 10-15 days in both forms. The duration of the functional maturity (5-3 maturity substage) and spawning period could not be determined in the present study due to lack of spent specimens.

Full oviducts of large females from the autumn and winter groups (about 280-350 mm ML) contain 150-200 thousand eggs (Shuldt, 1979; Laptikhovskiy and Nigmatullin, 1992, 1993). Therefore, daily egg production during the initial egg accumulation was estimated to be approximately 10,000 eggs with total weight 4-5 g (0.5-0.8% of BW).

DISCUSSION

Differences in body size in squid of similar age, belonging to different hatching-months, was mainly due to different growth rates in juveniles younger than 150 days. The winter-hatched juveniles (especially those of the August and September-hatched squid) foraged in the most favourable period and conditions (the end of spring and summer) and attained 170-180 mm ML at age about 180 days. The May-hatched juveniles (<150 days) foraged in colder and less productive seasons (winter and the beginning of spring) and at an age of 6 months they had attained only 130-140 mm ML. Furthermore, despite having the highest relative growth rates in summer (at age >180 days), May-hatched squid could not achieve the size of August and September-hatched individuals which grew slowly more in the relatively cold autumn: the initial differences in body size at age

180 days were too great to compensate for. The same phenomenon of increasing growth performance with hatching month was revealed in winter-hatched *I. argentinus* foraging around the Falkland Islands in March-beginning of June (Rodhouse and Hatfield, 1990) and in spring-hatched congeneric *Illex illecebrosus* migrating to Newfoundland waters in summer-autumn (Dawe and Beck, 1992).

A greater decrease in relative instantaneous growth rates (G in ML) at age >180 days, for males than females (Arkhipkin, 1990), may be explained by the earlier maturation of males as well as by changes in allometric growth of the head and arms, which become enlarged in mature males (Koronkiewicz, 1980). A slower growth in weight of males than that of females took place from age 240 days onward.

Size-at-age of squid of the same hatching-months differed significantly over the years, but yearly effects were not as pronounced as seasonal (hatching-month) effects. Probably, at age >150 days, when the squid of genus *Illex* become active nektonic swimmers (Froerman, 1985), they can select the most favourable environment with best food availability. However, in cold 1986 and 1990 individuals were somewhat larger than in warm 1985 (our data). Similar results were observed in *T. angolensis*, whose growth rates were highest in 1987 (Villanueva, 1992) when the climate in the Benguela system was unusually cool.

The two groups which could be distinguished by age at maturity within each hatching-month may have corresponded to the two types of juvenile foraging groups; in Patagonian Shelf (early-maturing squid) and in open waters of north Argentina Basin (late-maturing squid) (Arkhipkin, 1993).

Earlier start of maturation in males than females is well-known for *I. argentinus* (Arkhipkin, 1989, 1990; Rodhouse and Hatfield, 1990). However, despite the earlier beginning of maturation in males than females, both sexes attained functional maturity simultaneously. It is apparent that the simultaneous achievement of

functional maturity is adaptive because of the absence of seminal receptacles in *Illex*, which precludes early copulation and sperm storage by not fully mature females until the beginning of spawning. In squid species whose females feature seminal receptacles in the buccal membrane (*Sthenoteuthis pteropus*), males attain functional maturity earlier than females and usually copulate with functionally maturing females, so the male life cycle is shorter (Arkhipkin and Mikheev, 1992).

The daily egg production in *I. argentinus* (0.5-0.8% of BW) is considerably lower than that of relatively sessile gastropods, in which it may reach 17% of BW under similar or even longer duration of spawning. Thus, in gastropods, the ratio between generative production versus somatic production during spawning period is >0.3-0.5 (Roshchin *et al.*, 1989; Haramaty, 1991). In *I. argentinus* females, relative growth rate of the whole reproductive system was 0.6-1.6% of BW (V.L., unpubl.). Daily growth rates in BW of mature females of *I. argentinus* at age >300 days were 0.7-1.9% of BW (Arkhipkin, 1990) so during egg accumulation a major share of the daily BW increment is utilized for reproductive growth. Full oviducts of large females from the autumn and winter groups (about 280-350 mm ML) contain 150-200 thousand eggs (Schuldt, 1979; Laptikhovskiy and Nigmatullin, 1992, 1993).

Results of the present paper confirmed earlier suggestions (Hatanaka, 1986; Nigmatullin, 1989 and others) of the predominance of winter spawned squid *I. argentinus* in the fishery regions 42 and 45-47°S off the Exclusive Economic Zone of Argentina and are consistent with those obtained in the southern part of the Patagonian shelf, 47°21'-52°S (Rodhouse and Hatfield, 1990). The proportion of winter spawning squid in catches was estimated to be about 75-85%. The relative stability of the spawning peak (usually in July) suggests the relative temporal stability of spawning biotopes.

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REFERENCES

- Arkhipkin A. I., 1989. Age and growth of squids of the family Ommastrephidae. Ph. D. Thesis, Shirshov Institute of Oceanography, Moscow, 132 p.
- Arkhipkin A. I., 1990. Edad y crecimiento del calamar (*Illex argentinus*). *Frente Marit.*, **6 A**, 25-35.
- Arkhipkin A. I., 1993. Age, growth, stock structure and migratory rate of prespawning short-finned squid *Illex argentinus* based on statolith ageing investigations. *Fish. Res.*, **16**, 313-338.
- Arkhipkin A., A. Mikeev, 1992. Age and growth of the squid *Sthenoteuthis pteropus* (Oegopsida: Ommastrephidae) from the Central-East Atlantic. *J. Exp. Mar. Biol. Ecol.*, **163**, 261-276.
- Arkhipkin A. I., Z. N. Scherbich, 1991. Crecimiento y estructura intraspecifica del calamar, *Illex argentinus* (Castellanos, 1960) (Ommastrephidae) en invierno y primavera en el Atlantico Sudoccidental. *Scient. Mar.*, **55**, 4, 619-627.
- Brunetti N. E., M. L. Ivanovich, E. Louge, H. E. Christiansen, 1991. Estudio de la biología reproductiva y de la fecundidad en dos sub poblaciones del calamar (*Illex argentinus*). *Frente Marit.*, **8 A**, 73-84.
- Dawe E. G., Y. Natsukari, 1991. Light microscopy. In: Squid age determination using statoliths. P. Jereb, S. Ragonese, S. von Boletzky, eds., Mazara del Vallo, N.T.R.-I.T.P.P. Spec. Publ., **1**, 83-96.
- Dawe E. G., P. C. Beck, 1992. Population structure, growth, and sexual maturation of short-finned squid at Newfoundland, Canada, based on statolith analysis. *Int. Counc. Explor. Sea, C.M.*, 1992/K: **33**, 23 p.
- Forsythe J. W., W. F. Van Heukelem, 1987. Cephalopod growth. In: Cephalopod life cycles, P. R. Boyle, ed., London, Academic Press, 135-155.
- Froerman Yu. M., 1985. Ecology and mechanism of abundance dynamics of the short-finned squid *Illex illecebrosus*. Ph. D. Thesis Abstract, Shirshov Institute of Oceanography, Moscow, 24 p.
- Haramaty L., 1991. Reproductive effort in the nudibranch *Phestella sibogae*: Calorimetric analysis of food and eggs. *Pacif. Sci.*, **45**, 257-262.
- Harding J. P., 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. *J. Mar. Biol. Assoc. U.K.*, **28**, 141-153.
- Hatamaka H., 1986. Growth and life span of short-finned squid *Illex argentinus* in the waters off Argentina. *Bull. Jpn. Soc. Sci. Fish.*, **52**, 1, 11-17.
- Hurley G. V., P. Odense, R. K. O'Dor, E. G. Dawe, 1985. Strontium labelling for verifying daily growth increments in the statoliths of the short-finned squid (*Illex illecebrosus*). *Can. J. Fish. Aquat. Sci.*, **42**, 380-383.
- Koronkiewicz A., 1980. Size, maturity, growth and food of squid, *Illex argentinus* (Castellanos, 1960). *Int. Counc. Explor. Sea, C.M.* 1980/K: **18**, 27 p.
- Laptikhovsky V. V., Ch. M. Nigmatullin, 1992. Características reproductivas de machos y hembras del calamar (*Illex argentinus*). *Frente Marit.*, **12 A**, 23-37.
- Laptikhovsky V. V., Ch. M. Nigmatullin, 1993. Egg size, fecundity, and spawning in females of the genus *Illex* (Cephalopoda: Ommastrephidae). *ICES J. Mar. Sci.*, **50**, 393-403.
- Mangold K., D. Froesh, R. Boucher-Rodoni, V. L. Rowe, 1975. Factors affecting sexual maturation in cephalopods. *Pubbl. Staz. Zool. Napoli.*, **39**, Suppl. 259-266.
- Mangold K., 1987. Cephalopod reproduction. In: Cephalopod life cycles, P. R. Boyle, ed. London Academic Press, 187-200.
- Nesis K. N., 1987. Cephalopods of the world. Neptune city, T.F.H. Publ., 351 p.
- Nigmatullin Ch. M., 1989. Las especies del calamar mas abundantes del Atlantico sudoeste y siniopsis sobre ecología del (*Illex argentinus*). *Frente Marit.*, **5 A**, 71-81.
- Ricker W. E., 1958. Handbook of computations for biological statistics of fish populations. *Fish. Res. Board Can.*, **119**, 300 p.
- Rodhouse P. G., E. M. C. Hatfield, 1990. Dynamics of growth and maturation in the cephalopod *Illex argentinus* de Castellanos, 1960 (Teuthoidea; Ommastrephidae). *Phil. Trans. R. Soc. London*, **B**, **329**, 229-241.
- Roschchin V. E., L. L. Nagorskaya, A. P. Golubev, A. E. Plenin, 1989. Ecological and physiological bases of different quality of growth and reproduction in the mussel *Physella integra* (Gastropoda, Pulmonata). *Ecologiya*, **4**, 63-68.
- Schuldt M., 1979. Contribucion al conocimiento del ciclo reproductor de *Illex argentinus* (Cephalopoda, Ommastrephidae), *Monogr. Com. Invest. Sci. Prov. Buenos Aires, La Plata*, **10**, 110 p.
- Villanueva R., 1992. Interannual growth differences in the oceanic squid *Todarodes angolensis* Adam in the northern Benguela upwelling system, based on statolith growth increment analysis. *J. Exp. Mar. Biol. Ecol.*, **159**, 157-177.