

REPRODUCTIVE BIOLOGY OF THE SHORT-FINNED SQUID *ILLEX COINDETII* (CEPHALOPODA, OMMASTREPHIDAE) OF THE NORTHEASTERN ATLANTIC

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SARSIA



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For the purposes of this study, 5 311 post recruit of *Illex coindetii* were collected from the fishery on the Galician shelf, with sizes ranging from 32 to 379 mm dorsal mantle length (ML). Samples were taken monthly from November, 1991 to October, 1992. Sexual maturation, spawning season and population structure of *Illex coindetii* were analyzed. The spawning season extended throughout the year reaching a peak in July-August, with size at first maturity in males, 128 mm ML and in females, 184 mm ML. Males mature at a smaller size and attain lower size (279 mm ML) than females (379 mm ML). The sex ratio of the whole population sampled was slightly biased towards males, nevertheless monthly variations observed and the ratio obtained (1.09 : 1) does not suggest that there is spatial segregation by sexes in the fishing ground. From the total sample, 185 males and 281 females, covering the whole range of ML's, were randomly separated out to calculate maturation indices. A correlation between the subjective scales and the values of these indices was established in both sexes. The nidamental gland length proved to be a reliable parameter for distinguishing between stages of maturity in females. The fecundity of the species varied between 3 500 and 285 000 oocytes, (the most frequent range being from 30 000 and 200 000 oocytes) in the ovary and the oviducts. The principal axis of the vitellogenic oocytes and eggs varied between 0.8 and 1.2 mm. It was estimated that 1 g of eggs in the oviduct contained $2\,331 \pm 912$ eggs. The number of spermatophores in the spermatophoric sac varied between 81 and 1 555, and it was observed that the number and the length of the spermatophores tended to increase with size of the males. *Illex coindetii* may be considered as an intermittent spawner.

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KEYWORDS: *Illex coindetii*; squid; sexual maturation; fecundity; reproductive pattern.

INTRODUCTION

Illex coindetii VÉRANY, 1839, extends across the Mediterranean, eastern Atlantic from the British Isles to Namibia and Gulf of Mexico and Caribbean waters in the western Atlantic (ROPER & al. 1969; SANCHEZ 1981a; ROPER & al. 1984; NESIS 1987; GUERRA 1992). From 1992 to date this species is commercially exploited in Galician waters (NW of the Iberian Peninsula), yielding 500-1 000 tonnes per year (GONZALEZ & al. 1994). Although there are studies on the reproductive habits of the species in the Mediterranean (MANGOLD 1963; BOLETZKY & al. 1973; SANCHEZ 1981b) and off the African coast (LAPTIKHOVSKY & NIGMATULLIN 1993), to date there are no studies on the Northeastern Atlantic. This paper presents the first detailed study of the reproductive biology of *Illex coindetii* in this area. There are, however, relatively abundant data on this subject for squids of the other species of the genus

Illex. For the study of sexual maturation process in *Illex* species, scales of maturity have been proposed on the basis of various viewpoints: (a) histological analysis complemented by gonadosomatic and gonadal indices (SCHULDT 1979; BRUNETTI 1990); (b) differences in external and internal morphology of the animals and changes occurring in the gonads during the ontogenesis of the species (LIPINSKI 1979); (c) by combining different indices (DURWARD & al. 1978; SANCHEZ 1981b; BURUKOVSKY & al. 1984; NIGMATULLIN & al. 1984). There are also data on egg number in the female oviducts (MANGOLD 1963; SCHULDT 1979; BRUNETTI & al. 1991), on egg number in egg masses (BOLETZKY & al. 1973; DURWARD & al. 1979; O' DOR & al. 1980), and calculated the numbers of vitellogenic oocytes found in the ovary and eggs in the oviducts (MANGOLD 1963; DURWARD & al. 1978; SANCHEZ 1981b; RODHOUSE & HATFIELD 1990). Total realised fecundity has also been estimated taking into account the difference between the

total number of oocytes in prespawning and spent females (NIGMATULLIN & LAPTIKHOVSKY 1990; LAPTIKHOVSKY & NIGMATULLIN 1992, 1993).

It is important to study the reproductive biology of cephalopods because it has been shown that these molluscs exhibit a full range of reproductive modes from semelparity to non-seasonal iteroparity (MANGOLD & al. 1993). However, reproductive biology has been studied in very few cephalopod species. All *Illex* species are considered to exhibit intermittent spawning (LAPTIKHOVSKY & NIGMATULLIN 1993).

This paper deals with size at first maturity, spawning season, variation in maturation indices with maturity in both sexes, sex ratio, fecundity and variation in number and size of mature spermatophores.

MATERIAL AND METHODS

The sampling plan designed to study maturity, spawning season and sex ratio of *Illex coindetii* involved the random collection of 500 specimens monthly, covering the widest range of sizes possible. From November, 1991 to October, 1992, 5311 post-recruits were examined from catches by the Galician trawler fleet, fishing between 100-350 m depth on the Galician shelf. The squids were acquired at the fish markets in Burela, Celeiro and Riveira, from where they were immediately transported to a coldstore at 4° C. In the laboratory, the animals were frozen (-20° C). Once defrosted at tap water temperature, total body weight (BW) and dorsal mantle length (ML) of each specimen was recorded. The size range of specimens varied from 32 to 379 mm ML. Specimens were dissected, sexed and assigned a maturity stage according to a modification of the scale proposed by LIPINSKI (1979). Five stages were used for males: Juvenile (I), immature (II), preparatory (III), mature (IV) and spent (V); and six for females: Juvenile (I), immature (II), preparatory (III), maturing (IV), mature (V) and spent (VI). For data analysis, stages IV and V of females and IV of males were considered as mature.

A subsample of 185 males ranged from 68 to 279 mm ML and 281 females with sizes varying between 77 and 379 mm ML were examined, and the nidamental gland length (NGL) were measured to the nearest mm. The following weights in g were noted: spermatophoric complex (SCW) in males and nidamental glands (NGW), ovary (OW), oviducts (OVW) and oviductal glands (OGW) in females. The following indices were calculated: spermatophoric complex index for males (SI), nidamental gland index for females (NGI), and ovarian index (OI):

$$SI = (SCW/BW) \cdot 100$$

$$NGI = (NGL/ML) \cdot 100$$

$$OI = (OW/(BW - OW)) \cdot 100$$

To estimate fecundity of *Illex coindetii*, 115 mature females with sizes ranging from 106 to 379 mm ML were used. In a preliminary study, 43 females from monthly subsamples were examined, having been frozen for a month. However, it was not possible to estimate

the fecundity of these females since it proved impossible to separate the oocytes from the ovaries without fragmenting them. In view of the difficulties derived from working with frozen individuals, 72 mature females totally fresh were used. One sample from the central part of the ovary and a further sample from the oviduct, with weights ranging from 0.1 and 0.25 g, were removed. Both samples were fixed in fresh 'Gilson' fluid. Once in the fixing agent, they were shaken vigorously until the oocytes separated from the surrounding tissues. After keeping the sample in the fixing agent two days, the hardened oocytes were separated out, one by one, under an illuminated magnifying glass. All the oocytes of the sample were counted and forty mature randomly selected oocytes between 0.8 and 1.2 mm were measured. Finally, the number of oocytes in the ovary and the oviducts contained in the weight of the samples was extrapolated to the total ovary and oviduct weights, respectively. Although the correct use of fecundity is the total number of eggs spawned throughout the spawning period, in order to do not introduce new terminology, this term is defined in this paper as the total number of estimated vitellogenic oocytes in the ovary and the eggs in the oviducts. The number of vitellogenic and eggs per g of gonad (ovary + oviducts), per g of oviduct and per g of female were calculated.

The spermatophoric complex of 68 mature males was stored in 96 % ethanol. Fixing time was for a minimum of two days, after which spermatophores were separated out and counted under a illuminated magnifying glass. Subsamples of 40 spermatophores per spermatophoric complex were measured using vernier calipers. A Chi square test (SOKAL & RHOHLF 1969) was applied to calculate the significance between the monthly and the overall of sex ratio. Statistical procedures were performed using the SPSS statistical package (ETXEBERRIA & al. 1990).

RESULTS

Maturity by size class

Out of the 5 311 *Illex coindetii* individuals examined, 227 were juveniles of indeterminate sex, 2 652 males and 2 432 females. The mantle length range varied between 32 and 126 mm for juveniles of indeterminate sex, between 45 and 279 mm for males and between 48 and 379 mm for females.

The first important observation to note is the lack of spent male (stage V) *Illex coindetii* during the sampling period (Table 1A). Furthermore, the small proportion of preparatory males (stage III) is also worth noting as it suggests that the transition from immature to mature must be very fast.

The results obtained indicated the existence of one size mode at maturity, which is shown by the increase in the percentage of mature individuals as the size increases (Fig. 1). The size range of the mature males studied was very wide, varying between 93 and 279 mm. The most common sizes of mature males ranged from 120 to 200 mm ML. The size at which 50 % of the animals were mature (size mode at maturity) was 128 mm ML (Fig. 1).

Female *Illex coindetii* have one size mode at maturity, as do males. The size mode at maturity was 184 mm ML

(Fig. 1). The size range for mature females was very wide, varying between 103 and 380 mm ML. However, it was not frequent to find smaller sized mature females. Also, an increase in maturity of females was observed with growth (Table 1B, Fig. 1).

A small proportion of spent females (stage VI) was found. The ovary of these animals lacked vitellogenic oocytes. Rachis and its filamentous ramifications were only observed in remains of immature oocytes. The oviducts were also empty although, occasionally, remains of oocytes were found inside. The nidamental glands and oviductal glands lacked consistency.

These results indicated that males mature at a lesser mantle length and attain a smaller size than females. It was also observed that small mature males and females (80-120 mm ML) and large sized immature males and females (> 180 mm ML) represent a small proportion of the population sampled.

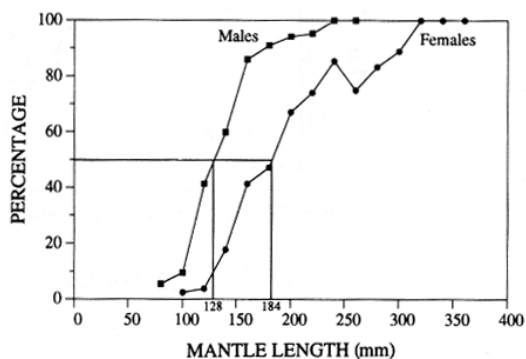


Fig. 1. Percentage of *Illex coindetii* mature male and female for each mantle length class.

Table 1. Percentages of males (A) and females (B) *Illex coindetii* for each maturity stage and 20 mm mantle length (ML) classes.

A.	ML	I	II	III	IV	V	n
	40-59	100					21
	60-79	100					88
	80-99	85.8	5.4	3.3	5.4		138
	100-119	71.5	12.5	6.6	9.4		415
	120-139	25.0	19.3	14.3	41.4		691
	140-159	6.8	14.2	19.1	59.9		664
	160-179	1.3	4.5	8.2	86.0		455
	180-199	1.8	0.9	6.3	91.0		110
	200-219	2.9		2.9	94.2		35
	220-239			4.8	95.2		21
	240-259				100		10
	260-279				100		4

B.	ML	I	II	III	IV	V	VI	n
	40-59	100.0						4
	60-79	100.0						44
	80-99	95.5	4.5					84
	100-119	94.7	2.0	1.0	1.4	1.0		280
	120-139	84.3	8.8	3.1	1.3	2.5		391
	140-159	55.7	22.1	4.3	11.6	6.1	0.2	432
	160-179	17.9	27.4	13.6	24.7	16.4		455
	180-199	7.1	29.4	16.3	21.8	23.9	1.5	321
	200-219	1.0	15.7	16.2	24.5	36.5	6.1	198
	220-239		7.3	18.6	15.3	56.4	2.4	124
	240-259		4.2	10.4	27.1	52.1	6.2	48
	260-279			25.1	58.3	8.3	8.3	14
	280-299			16.7	16.7	58.3	8.3	12
	300-319			11.1	11.1	66.7	11.1	9
	320-339				28.6	57.2	14.2	7
	340-359				60.0	20.0	20.0	5
	360-379					50.0	50.0	4

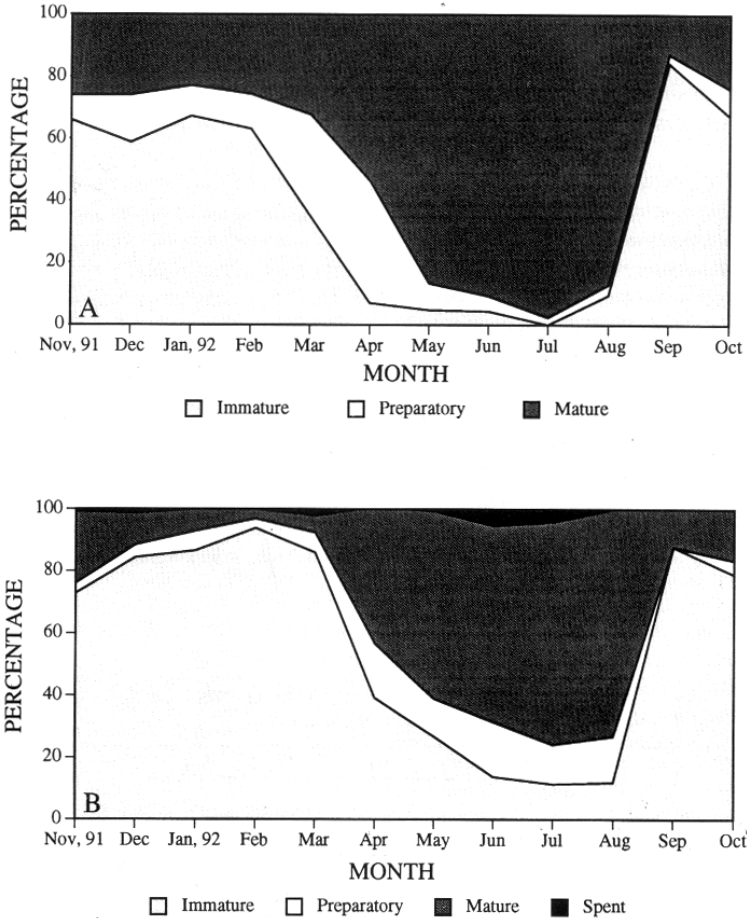


Fig. 2. Monthly distribution of the maturity percentages for male (A) and female (B) *Illex coindetii*.

Monthly variation of maturity and spawning season

Mature males were observed throughout the sampling period. Between April and August 1992, over 50 % of individuals were completely mature (Fig. 2A). Also, except in August, immature males were found throughout the year.

These results indicate the existence of reproductive activity throughout the year, reaching a peak in maturity in July.

The monthly distribution of the maturity percentages in female *Illex coindetii* follows the same pattern as in males (Fig. 2B). During the sampling period, two different

Table 2. Spermatophoric complex index (A) and nidamental gland index (B) for each maturity stage in *Illex coindetii*.

A.	SI	n	B.	NGI	n
Stage I	0.52 ± 0.48	29	Stage I	13.0 ± 2.3	52
Stage II	1.89 ± 0.80	18	Stage II	20.3 ± 8.1	43
Stage III	3.55 ± 1.09	27	Stage III	29.4 ± 9.6	18
Stage IV	5.10 ± 1.04	102	Stage IV	44.6 ± 6.3	52
Stage V	–	0	Stage V	47.1 ± 7.2	93
			Stage VI	24.3 ± 3.0	6

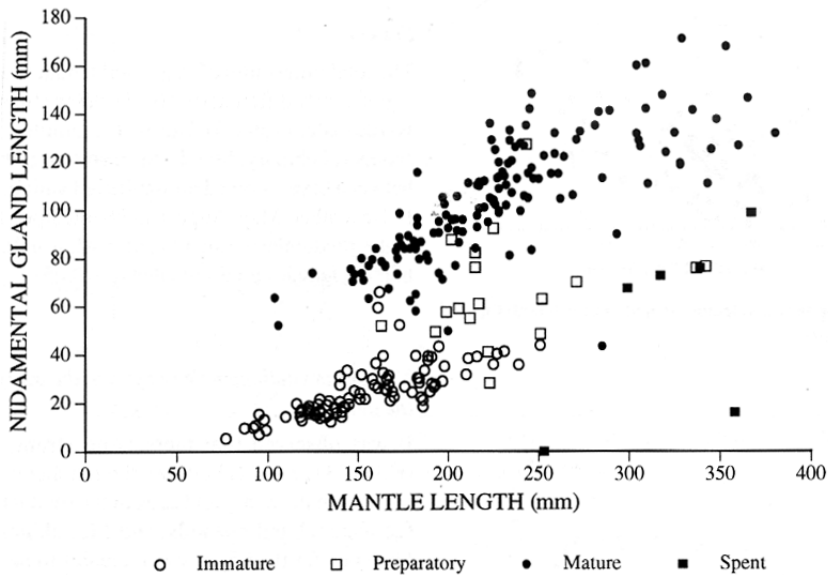


Fig. 3. Relationship between nidamental gland length and mantle length for each maturity stage of female *Illex coindetii*.

periods may be defined: (a) in autumn-winter, when the percentage of immature females was higher than that of mature females; (b) in spring-summer, when an increase in the percentage of mature females was observed. A small proportion of spent females was observed, the majority of which were found in June and July, which coincides with the observed peak in maturity.

The male *Illex coindetii* accommodate spermatophores in the paleal cavity of the females. Spermatophores were observed fixed to the internal mantle wall in bunches of between 25 and 100 spermatophores located, either, close to the base of the left or right gill. A total of 73 % of the mature females have one or more bunches of spermatophores fixed, which indicated that the majority had copulated more than once. These females were observed throughout the sampling period, their sizes ranging from 106 to 379 mm ML. No female was found to have copulated at the immature stage (I, II) or preparatory stage (III).

It was observed that spermatophores are split, with time, on the apical part. Sometimes, mature females with two or more spermatophore bunches were found, each bunch with a different morphology: totally/partially split or whole. This seems to indicate that there is a time interval between copulation.

In September, a sudden increase in the percentage of immature juveniles (60-100 mm ML) was observed (Fig. 2), which indicates the existence of a significant recruitment of juveniles to the fishery towards the end of

summer. This recruitment was maintained until March, decreasing gradually during the months of spring and summer. Although the number of mature individuals decreased in autumn and winter, reproductive activity was also observed during this season, which was verified by the existence of copulated females.

These data suggest an extended spawning period covering the whole year, with greater reproductive activity during spring and summer. The reproductive peak in females coincides with that of males in July and August.

Equivalence between the subjective maturity scale and the maturation indices

The spermatophoric complex index in males increased with the sexual maturation of the animal (Table 2A).

Based on the nidamental gland index, it was also possible to differentiate between the stages of sexual maturity in female *Illex coindetii* (Table 2B). Fig. 3 show that nidamental gland length allows to distinguish roughly between three physiological conditions (immature, preparatory and mature) using a quantitative data, increasing the accuracy when comparing with identification based on subjective criteria. Although this parameter isolated cannot be used to differentiate maturity stages, it is interesting in Fishery Science when large and quick samplings should be done frequently by inexperienced samplers.

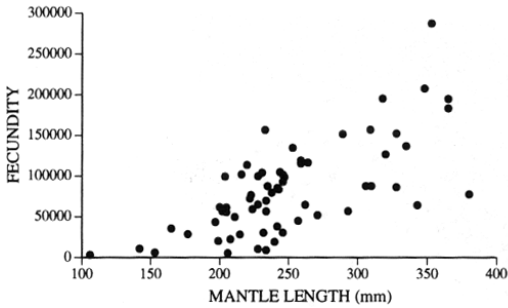


Fig. 4. Relationship between fecundity and mantle length for female *Illex coindetii*.

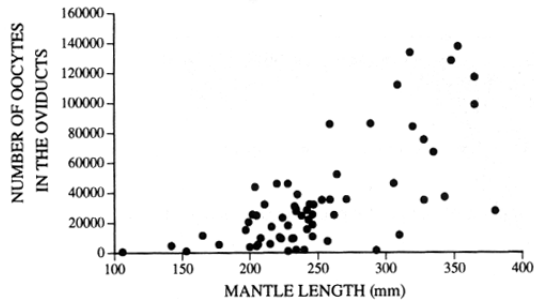


Fig. 5. Relationship between number of eggs in the oviducts and mantle length for female *Illex coindetii*.

Both in males and females there was a slight overlapping of index values between the stages of maturity. This overlapping is caused by the continuity of the sexual maturation process. Nevertheless, the results indicated that the stages of maturity may be differentiated using the maturation indices.

Sex ratio

The total proportion of males and females calculated was significantly different ($p < 0.05$), being slightly biased towards males (Table 3). During the months of November, January, February, March, April and June, the proportion between sexes showed no significant variation ($p > 0.05$). In December, May, August and September, however, the males predominated significantly, while in June and October, the females predominated ($p < 0.05$).

Number of vitellogenic oocytes in the ovary and eggs in the oviducts

It was observed that there is no strong relationship ($r^2 = 0.431$; $n = 72$) between the number of vitellogenic oocytes in the ovary and eggs in the oviducts (fecundity; see material and methods) and ML, although there is a tendency for the larger sized females to be more fecund than the smaller ones (Fig. 4). The number of vitellogenic oocytes and eggs varied between 3 500 and 287 000, although the most common fecundity was between 30 000 and 200 000 oocytes. The fecundity in the small sized females (100-180 mm) was low, being 3 500 oocytes for a 106 mm ML copulated female.

The number of eggs in the oviducts varied considerably between the mature females of all sizes (Fig. 5). The relationship between the number of oocytes and ML was weak ($r^2 = 0.479$; $n = 72$).

Based on the fecundity and the number of eggs in the oviducts, the amount of oocytes per g of gonad ($1\ 891 \pm 738$); the number of eggs per g in the oviduct ($2\ 331 \pm 912$) and the number of vitellogenic oocytes per g in females (182 ± 88) were calculated.

Table 3. Monthly and total sex ratio of *Illex coindetii*. M = males; F = females; J = unsexed juveniles; T = significance of T- test.

	M	% M	F	% F	J	% J	T
Nov 91	150	32.7	151	32.8	158	34.4	$p > 0.05$
Dec 91	288	54.8	224	42.6	14	2.6	$p < 0.05$
Jan 92	279	52.2	254	47.6	1	0.2	$p > 0.05$
Feb 92	241	48.6	255	51.4	0	0	$p > 0.05$
Mar 92	263	52.6	236	47.2	1	0.2	$p > 0.05$
Apr 92	242	50.0	242	50.0	0	0	$p > 0.05$
May 92	246	60.0	164	40.0	0	0	$p < 0.05$
Jun 92	231	44.9	284	55.1	0	0	$p < 0.05$
Jul 92	175	54.0	149	46.0	0	0	$p > 0.05$
Aug 92	148	59.4	101	40.6	0	0	$p < 0.05$
Sep 92	172	53.9	107	33.5	40	12.6	$p < 0.05$
Oct 92	217	44.0	265	53.8	11	2.2	$p < 0.05$
Total	2652	49.9	2432	45.8	227	4.3	$p < 0.05$

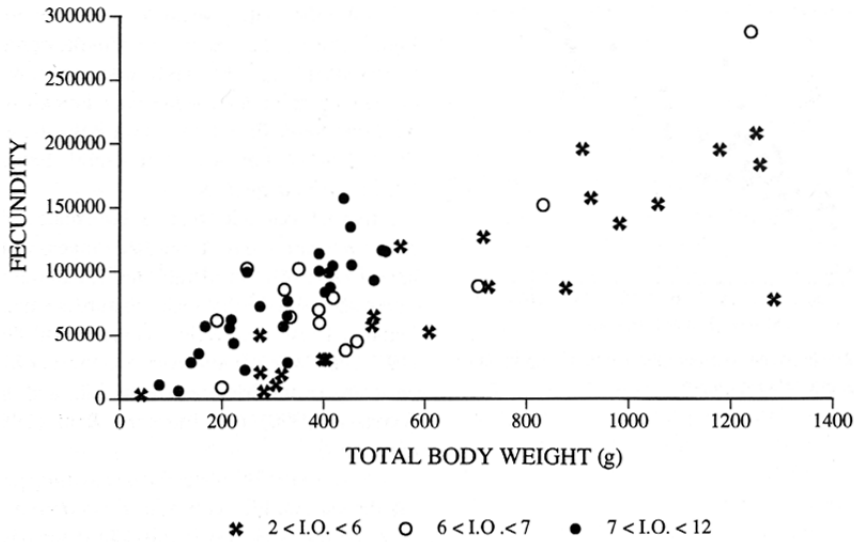


Fig. 6. Relationship between fecundity and total body weight in accordance with ovarian index for female *Illex coindetii*.

Females weighing below 600 g had high (7-12), average (6-7) and low (2-6) ovarian indices, while females weighing above 600 g only had average or low ovarian indices (Fig. 6).

The range of major axis of eggs in the oviducts and in the vitellogenic oocytes in the ovary was similar, varying between 0.8 and 1.2 mm. The average length of eggs in the oviduct was 0.922 ± 0.061 mm, and the average length of the vitellogenic oocytes in the ovary was 1.002 ± 0.058 mm. In the ovary, smaller sized oocytes were also observed (0.1-0.7 mm). However, due to the difficulty involved in separating them from the extremely fragile stroma without causing breakage, it was impossible to estimate their abundance in the samples.

Spermatophores

The number of spermatophores counted in the spermatophoric complex varied between 81 in one male with a ML of 107 mm, and 1 555 in one male with a ML of 242 mm. Although the number of spermatophores tended to increase with the animal size (Fig. 7), a weak relationship between the two variables was observed ($r^2 = 0.403$; $n = 68$).

In mature male *Illex coindetii*, an increase in the spermatophore mean length was observed with size (Fig. 8). The average length of spermatophores (ALS) varied between 11.1 in a male measuring 107 mm and 37.7 mm in a male measuring 245 mm. The best fit linear regression was: $ALS = -4.056 + 0.155 ML$ ($r^2 = 0.831$; $n = 68$).

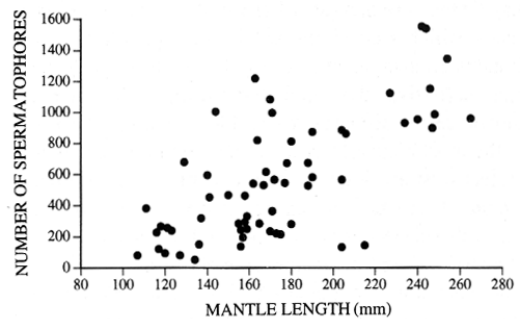


Fig. 7. Relationship between number of spermatophores and mantle length for male *Illex coindetii*.

DISCUSSION

Despite there being large sized mature males with a spermatophoric complex full of spermatophores, copulated females and spent females, no spent male has been caught in the fishing area. Observations of male *Illex coindetii* off the coast of Galicia coincide with observations by SCHULDT (1979) on *Illex argentinus*, DURWARD & al. (1979) on *Illex illecebrosus*, and RODHOUSE & al. (1988) on *Alloteuthis subulata* which indicated that the males of certain species continue producing spermatophores after reaching maturity and copulation, in which case, no authentic post-spawning stage would exist. So, in large sized

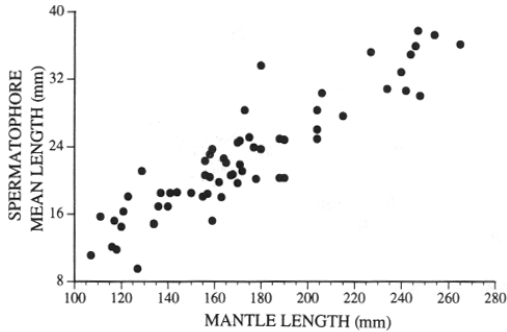


Fig. 8. Relationship between spermatophore mean length and mantle length for male *Illex coindetii*.

mature male *Illex coindetii* (200–260 mm ML), no decrease in the size of testes or spermatophores was noted, which indicates that spermatophores are still produced. However, it seems very rare for these animals to die without making use of the large amount of genetic material. Therefore, it may be the case that (a) fishermen throw away the spent males, which seems improbable since spent females are found in the samples and during visits on board the fishing vessels; (b) that after copulation, the males, for some unknown reason, become inaccessible to fishing, which may be the most plausible explanation; and c) males are less subject to spawning and post-spawning morphological changes due to the lesser expenses on reproduction. Spent males also die in relatively good condition and can hardly be distinguished from mature animals. Furthermore, there is no regeneration of gonads, this is inferred among other reasons, because the large sized males, from 12 to 15 months old, are at the limit of their estimated life span (GONZALEZ & al., in press).

The low percentage of males at the preparatory stage suggests that the transition from immaturity to maturity occurs in a short period of time. This coincides with descriptions by DURWARD & al. (1979) in studies in the aquarium of *Illex illecebrosus* and ARKHIPKIN & LAPTIKHOVSKY (1994) for *Illex argentinus*.

Also, the percentage increase of mature males with size indicates the existence of one single maturation size, which contrasts with observations made by BRUNETTI (1981) who found two gonadal maturation sizes in male *Illex argentinus*. The size of first sexual maturation for male *Illex coindetii*, estimated at 128 mm ML is below the sizes calculated by BRUNETTI & al. (1991) for males in summer spawning subpopulations of *Illex argentinus*. O'DOR (1983) also found a higher value in first sexual maturity size in male *Illex illecebrosus*.

Unlike the males, spent female *Illex coindetii* were found. Observations coincide with the description made by BRUNETTI & al. (1991) and LAPTIKHOVSKY & NIGMATULLIN (1992) regarding *Illex argentinus*. Female *Illex coindetii* have one single first size mode at maturity, which was estimated at 184 mm ML, a size slightly below that calculated for *Illex argentinus*.

It may be concluded that: (a) both male and female *Illex coindetii* mature over large size ranges, which points to the existence of a considerable individual variation in maturation size; and (b) that males mature at smaller sizes than females. These observations coincide with DURWARD & al. (1979) for *Illex illecebrosus*, SANCHEZ (1981b) for *Illex coindetii* in the Mediterranean Sea, and RODHOUSE & HATFIELD (1990), and BRUNETTI & al. (1991) for *Illex argentinus*.

SANCHEZ (1981b) observed a spawning period extending throughout the year in *Illex coindetii* in the Western Mediterranean. However, this author noted two spawning peaks. Observations of other *Illex* species show different spawning seasons (BRUNETTI 1981; NIGMATULLIN 1989; LANGE & SISSEWINE 1981; HATANAKA & al. 1982; COELHO & O'DOR 1993). This indicates that the spawning season and the reproductive peaks for the *Illex* genus are very flexible and probably very closely linked to environmental conditions, as suggested by RASERO (1994) for *Todaropsis eblanae* off Galician coast.

The presence of several spermatophore bunches with varying morphology in the same female suggests that males copulate several times with different females, which means, that mating is promiscuous, as suggested by NIGMATULLIN (1989) and LAPTIKHOVSKY & NIGMATULLIN (1992) for *Illex argentinus*.

No spermatophore bunches were found in immature female *Illex coindetii*, and so it seems that the presence of mature females is the factor which starts off copulation, as indicated by DURWARD & al. (1979) in studies in aquarium on *Illex illecebrosus*. The number of spermatophores per bunch fixed in female *Illex coindetii* in the NE Atlantic coincides with the range observed by LAPTIKHOVSKY & NIGMATULLIN (1992) in *Illex argentinus*.

Likewise, in various copulated female *Illex coindetii*, it was also observed that several spermatophore bunches were present with a different morphology: totally or partially sectioned (spent), and whole (fresh). Taking into account that: (a) several spermatophore bunches were found in differing situations (fresh and spent) in the same female and (b) that the gonadal gland secretions during egg-laying may be the inducing factor for the release of spermatozooids (DURWARD & al. 1979), it may be concluded that females spawn several times during any given spawning period.

The maximum estimated value of the spermatophoric index for *Illex coindetii* is slightly higher than that calculated by NIGMATULLIN (1989) for *Illex argentinus*, who

estimated a maximum of five. This higher value for *Illex coindetii* does not cause an increase in the number or size of spermatophores, which are similar in both species (NIGMATULLIN, 1989; LAPTIKHOVSKY & NIGMATULLIN, 1992).

It was observed that the gonadal indices in female *Illex coindetii* off the coast of Galicia are higher than those observed in other species of the *Illex* genus (BURUKOVSKY & al. 1984; DURWARD & al. 1979). One of the reasons which may explain this is the large size of the individuals, which have the largest ML observed in this species. Other reason could be the absence of fully mature females during the studies mentioned above.

It is important to underline that it is not possible to use frozen samples for preservation of gonads, aimed to the estimation of fecundity, for avoid of receiving of doubtful results. The fecundity of *Illex coindetii* off the Galician coast estimated in this work includes that given by SANCHEZ (1981b) in animals of the same species in the Western Mediterranean. These estimations are similar to those observed by RODHOUSE & HATFIELD (1990) in studies of *Illex argentinus* in nature. Observations in aquarium by Boletzky & al. (1973) for *Illex coindetii*, DURWARD & al. (1979) and O'DOR & al. (1982) for *Illex illecebrosus* show fecundity rates which are close to those found in *Illex coindetii* in the NE Atlantic. These estimations of the fecundity of *Illex coindetii* contrast with those made by MANGOLD (1963), who indicated that females produced between 5 000 and 10 000 eggs during their life cycle. Studies by NIGMATULLIN & LAPTIKHOVSKY (1990) and LAPTIKHOVSKY & NIGMATULLIN (1992, 1993) on *Illex argentinus* calculated the fecundity rate of this species to between 75 000 and 1 200 000 oocytes. These estimations for *Illex argentinus* are clearly above those made by other authors since the latter calculate the fecundity considering the pre-vitellogenic and vitellogenic oocytes, whereas the above cited authors only considered the vitellogenic ones. Observations of spent females of *Illex coindetii* showed that some portion of pre-vitellogenic oocytes remains in the ovary after spawn. Taking into account these results and observations of egg-laying in the *Illex* genus in aquarium (BOLETZKY & al. 1973; DURWARD & al. 1979; O'DOR & BALCH 1985), estimations by NIGMATULLIN & LAPTIKHOVSKY appear to overestimate the fecundity of *Illex argentinus*. The calculations of fecundity rate which are nearest to those calculated for animals spawning in captivity seem to be those made counting vitellogenic oocytes in the ovary and eggs in the oviducts. On the other hand, the number of eggs per g of oviduct in *Illex coindetii* was near to the calculations by BRUNETTI & al. (1991) for *Illex argentinus*.

SANCHEZ (1981b) for *Illex coindetii* in the Mediterranean; NIGMATULLIN & LAPTIKHOVSKY (1990) and BRUNETTI & al. (1991) for *Illex argentinus*, and O'DOR (1983) for *Illex illecebrosus*, indicated ranges of major axis for eggs

included in those described for *Illex coindetii* in Galician waters. This shows that the size of oocytes are similar for the genus *Illex*.

Based on the two interpretations of fecundity outlined above and the wide size range of oocytes in mature female ovaries, two questions are raised: a) Do all the oocytes produced in the female ovary reach maturity? It would appear not since during the sampling period, remains of immature oocytes in certain spent female ovaries were observed. These observations support indications by LAPTIKHOVSKY & NIGMATULLIN (1992, 1993) for *Illex argentinus* who pointed out that a female spawned between 70-75 % of the total number of oocytes; b) What spawning pattern do female *Illex coindetii* adopt? Due to the lack of observations in nature, it is only possible to work on a hypothesis. So, with regard to *Illex illecebrosus*, MESNIL (1977); DURWARD & al. (1979); O'DOR (1983); MANGOLD (1987) among others, noted a simultaneous, complete spawning, followed by a final egg-laying and post-spawning death; whereas AMARATUNGA & al. (1978) argued that all that refers to this aspect of the life cycle of this species continues to be conjecture. In this paper, it is indicated that *Illex coindetii* spawns intermittently throughout the spawning period. This type of spawning has already been proposed by NIGMATULLIN & LAPTIKHOVSKY (1990) and LAPTIKHOVSKY & NIGMATULLIN (1992, 1993) for *Illex argentinus*. Four indices support the hypothesis of the existence of intermittent spawning in *Illex coindetii*:

1. The existence of spermatophore bunches with different morphology in certain mature females and their relationship with the spawn, an aspect covered earlier in this paper.

2. Only weak relationships between the fecundity and the ML, and between the number of eggs in the oviduct and the ML. In the Galician trawl fishery, the range of sizes of mature female *Illex coindetii* was very wide, varying between 106 and 379 mm ML. No immature females of over 260 mm were found, and therefore a considerable growth in mature females was noted. In this way, if the females increase in size once maturity is attained and there is an important variation in the fecundity of females of the same size, this seems to suggest that these females spawn intermittently. HARMAN & al. (1989) indicated similar results for *Sthenoteuthis oualaniensis* to those observed for *Illex coindetii*.

3. The third indication of intermittent spawning is related to the ovarian index in mature females. The weight of mature female *Illex coindetii* varied between 50 and 1 250 g. Within this range, two situations were observed: a) in females weighing between approximately 50 and 600 g, and (b) in females from 600 g and above. In the first weight range, females were found in one of three states (Fig. 6): a) Type A females: with a low ovarian index and low fecundity; b) Type B females: with an average OI and average

fecundity; c) Type C females: with a high OI and high fecundity. An explanation for these three states is that the Type C females have still not spawned, the Type B females have spawned at some time and that the Type A females have laid several times, which is a sign of intermittent spawning.

In the second weight range of mature females (600-1 250 g), only females with a low or average ovaric index and high fecundity (Fig. 6) were found. This may be explained if these females had matured at high body weights. If this is the case, then in the sampling performed in 1991-92, it should have been possible to detect large immature females, which did not occur. Nevertheless, in the sampling performed in February and March, 1993, 23 immature females, 16 in preparatory stage and nine mature females ranging from 600-1 250 g BW were found. These results indicate the existence of large sized immature females in the population. The explanation for not having caught large sized immature females during the sampling in 1991-92 is that these animals live in areas off the Galician coast where there is no trawl fishery, and the vessels which perform this type of fishing chiefly operate in rocky areas which are inaccessible to trawlers. The gillnet gear was not sampled in 1991-92 for several reasons: (a) it is not a regular fishery which is mainly fished during the winter months; (b) sampling is not certain since there are no regular landings at the ports; and (c) cephalopods are hardly fished with this gear since this fishery is primarily for hake.

According to the above, two maturation situations were observed: (a) females maturing at a small size (50-600 g); and (b) females maturing at a large size (600-1,200 g). This suggests the existence of two maturation groups for *Illex coindetii* in the Galician fishery, as occurs with other cephalopods in the same area, e.g. *Loligo forbesi* and *Loligo vulgaris* (GUERRA & ROCHA 1994). Observations by BRUNETTI (1981) on *Illex argentinus* also indicated two maturity groups.

4. The final indication of intermittent spawning is based on observations of pre-vitellogenic and vitellogenic oocytes in the ovary. Although it was not possible to analyze the size frequencies of the smallest oocytes (0.1-0.7 mm) since they are too fragile to be separated from the stroma without being damaged, they exist in the ovary and are abundant. If all the oocytes are not going to be spawned since immature oocytes were observed in the ovaries of the post-spawning female, it seems that the 0.7 mm sized oocytes are able to enter the oviducts. In the studies by NIGMATULLIN & LAPTIKHOVSKY (1990) and LAPTIKHOVSKY & NIGMATULLIN (1992) on *Illex argentinus*, and by HARMAN & al. (1989) on *Sthenoteuthis oualaniensis*, both species supposedly have intermittent spawning, and the existence of different sized oocytes in the ovary was also indicated. Nevertheless, this indication is more related to the type of ovulation present in

Illex coindetii, since in the case of the copulated mature females, all sizes of oocytes were found.

Although there was an increase in the number of spermatophores with size, the linear relationship between the variables was weak. This was interpreted as an indication that the male *Illex coindetii* copulates more than once, which coincides with observations by NIGMATULLIN (1989) and LAPTIKHOVSKY & NIGMATULLIN (1992) in *Illex argentinus*. The number of spermatophores in male *Illex coindetii* in the Galician fishery is higher than that observed in animals of the same species inhabiting other geographical areas (SANCHEZ 1981b; SANCHEZ & al. in press). Nevertheless, NIGMATULLIN (1989) found a similar number of spermatophores in *Illex argentinus*. Also, in studies of *Illex illecebrosus* kept in aquarium, DURWARD & al. (1979) counted between 200 and 700 spermatophores in animals which had already copulated; a clear sign that male *Illex* copulate more than once. NIGMATULLIN & al. (1984) also examined male *Illex illecebrosus*, and found a slightly lower range of spermatophores than that found in males off the coast of Galicia.

On the whole, *Illex coindetii* experiences a partial ovulation of oocytes at the time of spawning and its spawn occurs intermittently involving new oocyte maturation between spawning events.

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REFERENCES

- Amaratunga, T., M. Roberge & L. Wood 1978. An outline of the fishery and biology of the short-finned squid *Illex illecebrosus* in eastern Canada. – *Technical Report of Fisheries Marine Series of Canada* 833(2):1-17.
- Arkhipkin, A. & Laptikhovsky, V 1994. Seasonal and interannual variability in growth and maturation of winter-spawning *Illex argentinus* (Cephalopoda, Ommastrephidae) in the Southwest Atlantic. – *Aquatic Living Resources* 7:221-232.
- Boletzky, S. V., L. Rowe & L. Aroles 1973. Spawning and development of the eggs, in the laboratory, of *Illex coindetii* (Mollusca: Cephalopoda). *Veliger* 15:257-258.
- Brunetti, N. E. 1981. Distribución de tallas y biología reproductiva del calamar (*Illex argentinus*) en el Mar Argentino.

- Campanias de Investigación Pesquera realizadas en el Mar Argentino por los B/I 'Shinkai Maru' y 'Wather Herwig' y el B/P 'Marburg'. Años 1978 y 1979. – *Resultados de la parte Argentina. Abril 1981*. Contribución no 383:119-127.
- Brunetti, N. E. 1990. Escala para la identificación de estados de madurez sexual del calamar (*Illex argentinus*). – *Frente Marítimo* 7A:73-84.
- Brunetti, N. E., M. L. Ivanovic, E. Louge & H. E. Christiansen 1991. Estudio de la biología reproductiva y de la fecundidad de dos subpoblaciones del calamar (*Illex argentinus*). – *Frente Marítimo* 8A:73-84.
- Burukovsky, R. N., Y. M. Froerman & Ch. M. Nigmatullin 1984. Reproductive biology and scale of maturity stage of reproductive system of female squid (*Illex illecebrosus*). *NAFO Scientific Research Documents* 84/IX/120.
- Coelho, M. L. & R. K. O'Dor 1993. Maturation, spawning patterns and mean size at maturity in the short-finned squid *Illex illecebrosus*. Pp. 81-91 in: Okutani T., R. K. O'Dor & T. Kubodera (eds) *The Recent Advances in Cephalopod Fisheries Biology*. Tokyo. Tokai University Press.
- Durward, R. D., T. Amaratunga & R. K. O'Dor 1978. Maturation index and fecundity for female *Illex illecebrosus* (LeSueur, 1821). – *ICNAF Research Documents* 78/II/1.
- Durward, R. D., E. Vessey, R. K. O'Dor & T. Amaratunga 1979. Aspects of maturation, mating, and larval development of *Illex illecebrosus* relevant to field studies. – *ICNAF Research Documents* 79/II/13.
- Etxeberria, J., L. Joaristi, & L. Lizasoain 1990. Programación y análisis estadísticos básicos con SPSS-PC (+). – Pp. 1-310 in: Parainfo, Madrid.
- González, A. F., M. Rasero & A. Guerra 1994. Preliminary study of *Illex coindetii* and *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in northern Spanish Atlantic Waters. – *Fisheries Research* 21:115-126.
- González, A. F., B. G. Castro & A. Guerra, in press. Age and growth in the short-finned squid *Illex coindetii* off Galician waters based on statolith analysis. – *ICES Journal of marine Science*.
- Guerra, A. 1992. Mollusca, Cephalopoda. – Pp. 1-327 in: Ramos, M. A. (ed.) *Fauna Ibérica* 1. Museo Nacional de Ciencias Naturales. CSIC. Madrid.
- Guerra, A., & F. Rocha 1994. The life history of *Loligo vulgaris* and *Loligo forbesi* (Cephalopoda: Loliginidae) in Galician waters (NW Spain). – *Fisheries Research* 21:43-69.
- Harman, R. F., R. E. Young, S. B. Reid, K. M. Mangold, T. Suzuki & R. F. Hixon 1989. Evidence for multiple spawning in the tropical oceanic squid *Stenoteuthis oualaniensis* (Teuthoidea: Ommastrephidae). – *Marine Biology* 101:513-519.
- Hatanaka, H., T. Kawakami, E. Fujii, K. Tamai, T. Amaratunga, J. Young, D. Chaisson, T. McLane, A. Lange, L. Palmer, J. Prezioso & M. Sweeney 1982. Aspects on the spawning season and ground. Distribution and migration of short-finned squid (*Illex illecebrosus*) in larval and juvenile stages in the Northwest Atlantic. – *NAFO Scientific Research Documents* 82/VI/32.
- Lange, A. M. T. & M. P. Sissenwine 1981. Evidence of summer spawning of *Illex illecebrosus* (LeSueur) off the Northeastern United States. – *NAFO Scientific Research Documents* 81/VI/33.
- Laptikhovsky, V. V. & Ch. M. Nigmatullin 1992. Características reproductivas de machos y hembras del calamar (*Illex argentinus*). – *Frente Marítimo* 12A:23-37.
- Laptikhovsky, V. V. & Ch. M. Nigmatullin 1993. Egg size, fecundity and spawning in females of the genus *Illex*. – *ICES Journal of marine Science* 50:393-403.
- Lipinski, M. R. 1979. Universal maturity scale for the commercially important squids (Cephalopoda: Teuthoidea). The results of maturity classification of *Illex illecebrosus* (Le Sueur, 1821) populations for the years 1973-1977. – *ICNAF Research Documents* 79/II/38.
- Mangold, K. 1963. Biologie des céphalopodes bentiques et nectoniques de la Mer Catalane. – *Vie et Milieu* 13 (Suppl.) 285 pp.
- Mangold, K. 1987. Reproduction. – Pp 157-200 in: Boyle, P. R. (ed.) *Cephalopod Life Cycles*, vol. 2. London. Academic Press.
- Mangold, K., R. E. Young & M. Nixon 1993. Growth versus maturation in cephalopods. Pages 679-704 in T. Okutani, R. K. O'Dor & T. Kubodera (eds) *The Recent Advances in Cephalopod Fisheries Biology*. Tokyo. Tokai University Press.
- Mesnil, B. 1977. Biological characteristics and biomass estimates of squid, *Loligo pealei* and *Illex illecebrosus*, on mid Atlantic and Southern New England shelves. – *ICNAF Research Documents* 77/IV/4.
- Nesis, K. N. 1987. Keys to the Cephalopods of the world. – Pp. 223-237 in: Burgess, L. A. (ed.) *Cephalopods of the world*. Berkshire. T. F. H. Publications.
- Nigmatullin, Ch. M. 1989. Las especies de calamar más abundantes del Atlántico Sudoeste y sinopsis sobre la ecología del calamar (*Illex argentinus*). – *Frente Marítimo* 5A:71-81.
- Nigmatullin, Ch. M. & V. V. Laptikhovsky 1990. Fecundity of females of the squid *Illex argentinus* (Castellanos 1960): the formation and peculiarities of utilisation in ontogenesis. – Pp. 89-90 in: *5th All-Union conference on the commercial invertebrates*. Thesis of the reports. Minsk (Naroch). Moscow. UNIRO.
- Nigmatullin, Ch. M., R. M. Savirov & Y. M. Froerman 1984. Reproductive biology and scale of maturity stages of the reproductive system of male squid (*Illex illecebrosus*). – *NAFO Scientific Research Documents* 84/IX/119.
- O'Dor, R. K. 1983. *Illex illecebrosus*. – Pp. 175-199 in: Boyle, P. R. (ed.) *Cephalopod Life Cycles*, vol. 2. London. Academic Press.
- O'Dor, R. K. & N. Balch 1985. Properties of *Illex illecebrosus* egg masses potentially influencing larval oceanographic distribution. *NAFO Scientific Council Studies* 9:69-76.
- O'Dor, R. K., N. Balch & T. Amaratunga 1982. Laboratory observation of midwater spawning by *Illex illecebrosus*. – *NAFO Scientific Research Documents* 82/VI/5.
- Rasero, M. 1994. Relationships between abundance and upwelling: the case of *Todaropsis eblanae* (Cephalopoda, Ommastrephidae) in Galician waters (NW Spain). – *ICES Council Meetings*/K.20.
- Rodhouse, P. G. & E. M. C. Hatfield 1990. Dynamics of growth and maturation in the cephalopod *Illex argentinus* Castellanos 1960 (Teuthoidea: Ommastrephidae). – *Philosophical Transactions Royal Society London*, B 329:229-241.

- Rodhouse, P. G., R. C. Swinfen & A. W. A. Murray 1988. Life cycle, demography and reproductive investment in the myopsid squid *Alloteuthis subulata*. – *Marine Ecology Progress Series* 45:245-253.
- Roper, C. F. E., C. C. Lu & K. Mangold 1969. A new species of *Illex* for the Western Atlantic and distributional aspects of other *Illex* species. – *Proceedings of the Biological Society of Washington* 82:295-322
- Roper, C. F. E., M. J. Sweeney & C. E. Nauen 1984. FAO Species Catalogue. *Cephalopods of the World*. An annotated and illustrated catalogue of species of interest to fisheries. – *FAO Fisheries Synopsis* 3 (125), 277 pp.
- Sánchez, P. 1981a. Cefalópodos capturados durante la campaña 'Benguela I' en el SO africano. – *Resultados Expediciones Científicas* 9:29-37.
- Sánchez, P. 1981b. *Características bioecológicas de Illex coindetii (Vérany, 1839) en el Mar Catalán*. – Tesis Doctoral. Universidad de Barcelona. 219 pp.
- Sánchez, P., A. F. González, P. Jereb, V. V. Laptikhovsky, K. Mangold, Ch. M. Nigmatullin, S. Ragonese & C.F.E. Roper in press. Population/species summary by geographic region. I. *Illex coindetii*. in E. Dawe, R. K. O'Dor and P. G. Rodhouse, eds. *A review of Recruitment dynamics in the squid genus Illex*. – *FAO Fisheries Technical Paper*.
- Schuldt, M. 1979. *Contribución al conocimiento del ciclo reproductivo de Illex argentinus*. – Monografías 10, La Plata. Comisión de Investigaciones Científicas de la Provincia de Buenos Aires (Argentina). 110 pp.
- Sokal, R.R. & F. J. Rohlf 1969. *Biometry*. – W.H. San Francisco: Freeman and Co. 766 pp.

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