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REPRODUCTIVE BIOLOGY OF *ILLEX COINDETII* AND *TODAROPSIS EBLANAE* (CEPHALOPODA: OMMASTREPHIDAE) OFF NORTHWEST AFRICA (4°N, 35°N)

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ABSTRACT

From 1352 *Illex coindetii* and 713 *Todaropsis eblanae* obtained from the by-catches of trawlers fishing off Northwest Africa (4°03′N, 34°40′N), body size at sexual maturity and spawning seasons were estimated. An approximation to the potential reproductive output was estimated for female and male *Illex coindetii* and for male *Todaropsis eblanae*. For *Illex coindetii*, in both sexes, sexual maturity occurred at a wide range body size. However both, range and size at maturity for both sexes decreased from north to south. The maturing and spawning periods were extended to the whole year, although they seemed to take place with higher intensity during the spring-summer in the northern and central zones, but during autumn at the Gulf of Guinea. The difference in temperature between the different zones may be the main physical condition influencing the inter-zonal differences. Significant correlation between spermatophore mean size and DML was observed. The highest number of spermatophores was 1412. The potential fecundity in females was estimated to be over 729,000 oocytes. The maximal number of spermatangue groups was six, and the highest number of spermatangues observed was 1996. High genetic diversity should be expected in the progeny of one female *I. coindetii* after they mate with several males. For *T. eblanae*, sexual maturity in females occurred at a larger size than in males. The estimated sizes at maturity were 168 and 130 mm DML for females and males respectively. Two main spawning seasons were observed, the first in spring and the second in autumn-winter. The highest number of spermatophores was 269 (the mean number was 100). Mature males can be recognised by having as maximum 1 sucker, and no less than 4 ridges in the right row of the fourth right arm.

Among the ommastrephid species inhabiting at the central-eastern Atlantic, the broadtail short-finned squid, *Illex coindetii* (Verany, 1839) and the lesser flying squid, *Todaropsis eblanae*, Ball (1841) are the most frequently caught species on the shelf and slope (Hernández-García, 1991). They constitute an important by-catch species in some demersal fisheries of Spain, Portugal and at the central-eastern Atlantic (Rasero, 1994; Coelho, 1985; Roper et al., 1984). However, both species are not the object of a directed fishery along the African coast; although, seasonally large catches of these squids are obtained locally (1.5–2.5 mT per 5–6 hrs bottom trawl) but, the fishery regulations do not allow permission for landing these. Partly because of all this, there are still aspects of the biology and ecology which remain poorly described in this area (e.g., the reproductive biology). *T. eblanae* is one of the lesser known cephalopods from the central-eastern Atlantic, there being little knowledge about its biology and life history among the ommastrephid species (Laptikhovsky and Nigmatullin, 1999). Results on general biology were presented by Burukovsky et al. (1979); about depth distribution by Hernández-García (1991); on egg size and fecundity by Laptikhovsky and Nigmatullin (1999), and Nigmatullin and Laptikhovsky (1999); preliminary results on diet by Nigmatullin (1972) and Hernández-García (1992); and on reproduction by Hernández-García (1995). Detailed works, including reproduction, have been published for this species inhabiting northward latitudes (Hastie et al., 1994; Rasero, 1994). In relation to *I. coindetii*, a large knowledge of several biological and ecological aspects of the congeneric species *I. argentinus* and *I. illecebrosus* is now available concerning the reproductive biology (see among others: Durward et al., 1979; Nigmatullin, 1989; Nigmatullin and Laptikovsky, 1990; Haimovici and Álvarez-Pérez, 1990; Brunetti, 1991; Laptikovsky and Nigmatullin, 1993). This is also the situation for these and other exploited ommastrephid species in different areas (Sánchez, 1981; Jereb and Ragonese, 1995; Osako and Murata, 1983). More recently, they have also received special attention in zones where they are not the target species, i.e., *I. coindetii* in the waters off Galicia (González, 1994; González et al., 1994), and *T. eblanae* in the same zone (Rasero, 1994; González et al., 1994) and in North Atlantic waters (Hastie et al., 1994; Lordan et al., 1998). Knowledge about the reproductive aspects of *I. coindetii* from the central-eastern Atlantic is still limited; although some general data is available (Burukovsky et al., 1979) as well as a few studies of egg size and fecundity (Laptikovsky and Nigmatullin, 1993; Nigmatullin and Laptikovsky, 1994).

The present work on *I. coindetii* and *T. eblanae* aims to analyse and describe the important aspects of the reproductive biology (e.g., sex ratio, size at maturity, spawning period). For *I. coindetii*, the differences observed in length-weight and morphometric relationships (Hernández-García, 1995; Hernández-García and Castro, 1998) provided a good base for the study of the reproductive biology drawing distinctions between the different geographical zones along the African coast. The results will produce a better understanding of the species biology and ecology and could serve as a guide in future populational studies in this Atlantic area.

MATERIAL AND METHODS

The material for this study was collected from the by-catches of the bottom trawl fisheries taking place at the central-eastern Atlantic, between 4°03′N and 34°40′N. Squids (both species) were caught mainly during the years 1990 and 1991 (some specimens were caught during last months of 1989 and four *I. coindetii* on 13 January 1992). The description of the fishing methods and areas can be found in Hernández-García (1995) and Hernández-García and Castro (1998). *I. coindetii* was caught in depths ranging from 42.6 to 695.4 m. For this species, the area was divided in the same three zones as that in previous studies: northern zone (Morocco and Sahara coast), central zone (from Mauritania to Sierra Leone), and southern zone (from Sierra Leone to Liberia). To study the reproductive biology, a total of 1352 squids (656 females and 696 males) were considered. A total of 713 *T. eblanae* were obtained from the same area, in depths ranging from 38 to 787 m. From the total sample, a sub-sample of 486 squids (247 females and 239 males) was considered for the study of the reproductive biology. For 8 juveniles with DML ranging from 39–54 mm (mean 45 mm, SD = 8.62), sex could not be determined.

After capture, squids were frozen in individual plastic bags for each trawl. Later, at the laboratory, squids were thawed at room temperature. The dorsal mantle length (DML) was measured to the nearest 1 mm and the total weight (BW) weighed to the 0.01 g and sex was determined for each specimen. Sub-samples were taken for more detailed analysis (see below). For a sub-sample composed by 107 females and 95 males *I. coindetii* and 167 females and 157 males *T. eblanae*, a maturity stage (MS) (I, juvenile; II, immature; III, maturing; IV-V, mature; VI, spent) was assigned taking as a basis the appearance and relative size of their reproductive components (qualitative scale based on Lipinski's scale (1979)). Data on reproductive components were collected by weighing (to 0.01 g) the following components in females: ovary, oviducts, oviducal glands and nidamental glands; and in males: testis and the Needham's complex. The glands were separated from the ovary and the oviducts, and the Needham's complex from the testis, trying to completely eliminate the membranes and vascular conduits that cover each one of these elements. The moisture excess was eliminated by placing them on blotting paper. The weight of the spermatophoric sac was determined independently when it contained spermatophores. Paired organs (e.g., female glands) were weighed together. This data was then used to determine maturity indices (see below). Simultaneously, other qualitative and quantitative data were taken (e.g., data related to the presence of spermatangues in female). For males, in order to obtain a way to assess the maturity stage without the need to dissect the animal, for a sub-sample of *I. coindetii* males, the relationship between the indices and the length of the modified part of the hectocotylus (LmH) was analysed; and in *T. eblanae* males, the count of the ridges and suckers on the fourth pair arms was carried out and they were then related to the maturity indices.

STUDY OF THE MATURITY AND SPAWNING PERIOD.—In order to know the size or sizes at maturity, the percentage of mature specimens in each size class was determined, assembled in size classes of 1 cm and afterwords represented under the central mark of the size class. This was estimated, graphically, as that one in which 50% of the squids reached this stage (mature).

Maturity indices were calculated in order to show the maturation process for each squid through the evolution of their values, to discriminate between populational groups (Juanico, 1980, 1983; Mangold, 1987); and to confirm the qualitative scale which differentiated the stages of sexual maturity by adjusting each one of the stages to an interval of the indice values. The following indices of reproductive status were calculated: Gonadosomatic Index (GSI) and Reproductive system Index (RsI).

The data series (indices values) were analysed using Kruskal-Wallis' statistical test (Siegel, 1990) to determine the interval of values corresponding to each stage of the qualitative scale. For *I. coindetii*, for this purpose, a sample of 107 females and 95 males was considered for both indices; and for *T. eblanae* a sample constituting 167 females and 157 males for the RsI, and a sample of 104 females and 96 males for the GSI. The analysis was done for all possible comparisons among the groups of data corresponding to each stage. As null hypothesis (H_0) it was established that there is no difference among the F values associated for the MSs compared. The alternative hypothesis (H_1) stated that the MSs do not possess the same average values (F values are different). The α fixed was 0.05. The indices used had the following expressions:

a) *Gonadosomatic Index (GSI)*—The ratio between the mass of the reproductive system (RSW) and the total mass (BW) excluding the mass of the stomach, i.e.

$$\text{GSI} = \text{RSW} / (\text{BW} - \text{weight of the stomach})$$

b) *Reproductive system Index (RsI)*—Relationships among the masses of the components of the reproductive system. The equations are:

$$\text{RsI}_{(\text{female})} = (\text{OgW} + \text{NgW}) / \text{RSW})$$

$$\text{RsI}_{(\text{male})} = (\text{ScW} + \text{SsW}) / \text{RSW})$$

where OgW= Oviductal glands weight; NgW= Nidamental glands weight; ScW= Spermatophoric complex (Needham's complex) weight; SsW= Spermatophoric sac weight. The RSW includes the ovary and oviduct weight or the testis weight too. In order to find out the spawning season, the mean of the indices for each month was calculated.

POTENTIAL REPRODUCTIVE OUTPUT.—After weighing, the spermatophoric sac was preserved in alcohol (70%) or frozen. Spermatophores from 41 *I. coindetii* and 11 *T. eblanae* males were counted (total count), and lengths of random sub-samples of non-deformed spermatophores were measured from 37 and 10 males of each species respectively using a binocular microscope fitted with an eyepiece graticule.

The major axis length of ripe eggs was measured from random sub-samples. For *Illex coindetii* females the potential fecundity (PF) (total oocyte stock in ovary + oviduct) was estimated according to the methodology used by Laptikovsky and Nigmatullin (1993). Histological cuts of the ovary from females in different maturity stages were carried out in order to determine the proportion of egg sizes in each one. The presence of bunches of spermatangues in the females, their position and the number groups of them were recorded. Spermatangues bunches or groups were taken and the spermatangues in each group counted in 16 females. Lengths of random sub-samples of spermatangues were measured from 14 females, as it was done for the spermatophores.

RESULTS

ILLEX COINDETII

The sex ratio was not significantly different from 1:1 during the entire sampling period and the different zones ($P > 0.05$). Males (mean DML = 144 mm, range 55–214 mm) were smaller on average than females (mean DML = 178 mm, range 79–305 mm). No totally spent specimens were obtained, but some males with the testis near to exhaustion were found (this was considered on the basis of the yellow color of the testis, its reduced size and possessing a large spermatophoric sac plenty of spermatophores). A male was found (198 mm DML) having a testis weight of 1.75 g and a spermatophoric sac weight of 11.94 g.

MATURATION: GEOGRAPHICAL VARIATION AND DEPTH DISTRIBUTION.—Sexual maturity in females occurred at 137–305 mm, whereas in males it was evident over a shorter size range (97–214 mm). Thus, the size at maturity for female and male were 208 and 160 mm respectively over the whole area, but differences were observed between zones. In the northern zone (Morocco and Sahara coasts), some males of DML 190 mm had an empty spermatophoric sac, while no males with DML larger than 130 mm where found in the southern zone with an empty spermatophoric sac. This indicates that in the southern zone (Liberia, Gulf of Guinea) specimens reached sexual maturity at a smaller size. Thus, when analysing the data by zones, mature females were in the size ranges 162–305, 137–245 and 137–232 mm for the northern, central and southern zones respectively (Fig. 1A) whereas mature males were in size ranges 128–214, 125–185 and 93–173 mm from north to south respectively (Fig. 1B). Thus, the size at 50% maturity for both sexes decreased with the latitude; being, from northern to southern zones respectively, for the females 218, 196 and 172 mm (Fig. 1A) and 166, 153 and 127 mm for the males (Fig. 1B). Differences in size at maturity between sexes were about 50 mm independently of the zone. Mature females (Fig. 2A) and mature males (Fig. 2B) were found over the whole depth range (42–695 m).

MALES: MATURATION AND MATING.—In the case of the males, both indices, GSI and RsI were adequate to represent the male maturation pattern (Kruskal-Wallis; $P < 0.0001$ in all cases; Tables 1 and 2). GSI values close to 0.04 were found all year round (Fig. 3). Likewise, the RsI showed values higher than 0.4 yearly in the northern zone (Fig. 4). GSI and RsI took the mean lower values in April and autumn, just after they presented maximal values. For the southern zone, GSI and RsI had values over 0.04 and 0.4 respectively for all months with the data available (mean values remained over the corresponding values of the maturity stage IV (Figs. 3,4)). Males with spermatophoric sacs weighing more than 4 g were found all year round, with the exception of September. The correlation between the length of the modified part of the hectocotylus (LmH) and the GSI was not significant ($n = 211$, $P = 0.073$, $R^2 = 0.274$); but, a significant correlation was observed between this length and the RsI ($n = 224$, $P < 0.000$, $R^2 = 0.345$, $RsI = 0.1479 + 0.013*LmH$). Males having a LmH bigger than 20 mm are expected to be mature. The different degree of the

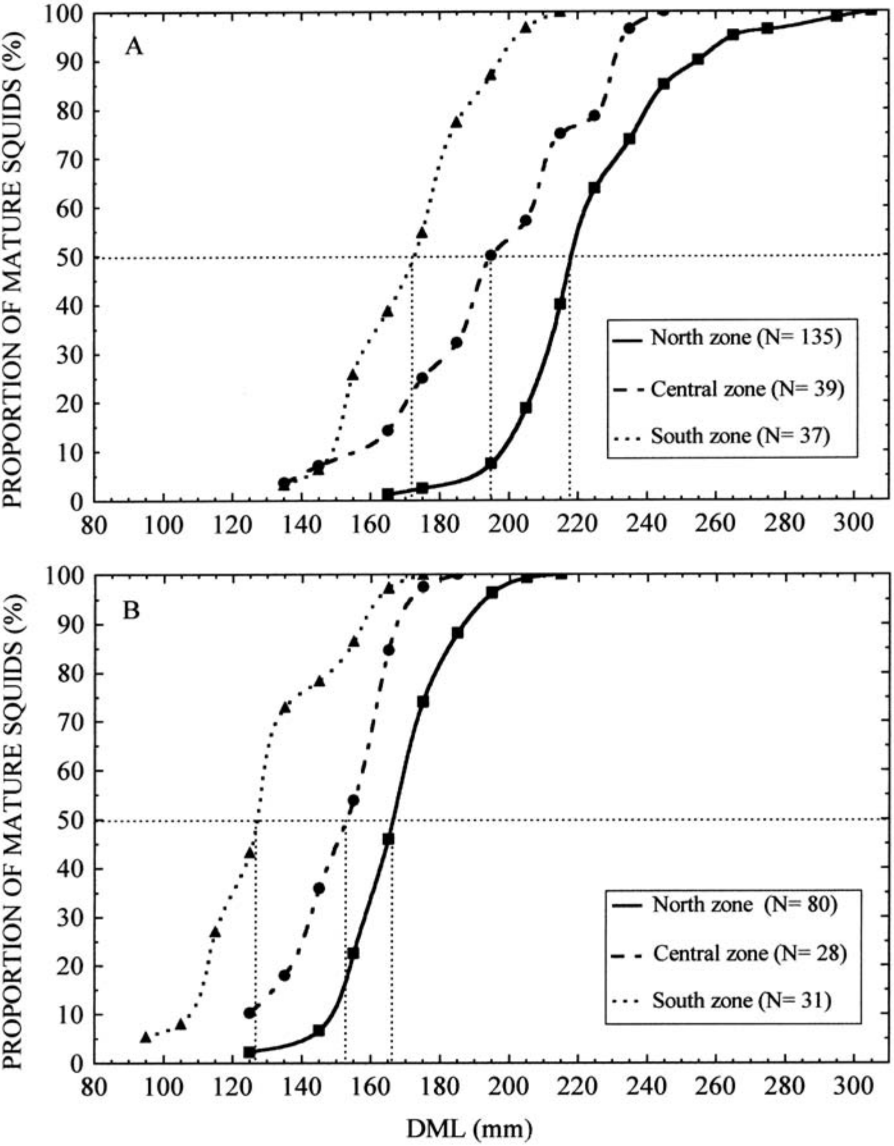

Figure 1. Size at maturity. Proportion of mature squids in 10 mm categories of dorsal mantle length (DML) classes for *Illex coindetii* females (A) and males (B).

muscle contraction between specimens, and probably that the samples had been frozen, could have affected in a significant way the length registered.

POTENTIAL PRODUCTION OF SPERMATOPHORES.—The mean number of spermatophores was 465 (n = 41, range = 25–1412, SD = 340). It was observed that the number of spermatophores increased according to the size of the animal, but the definition of this increase was not clear, as was shown by the R^2 values (0.244, 0.062 and 0.371 for the whole area, the northern-central and southern zones respectively) of the linear regressions. Larger squids had larger spermatophores (Mean spermatophore length = 4.57 + 0.134 DML, n =

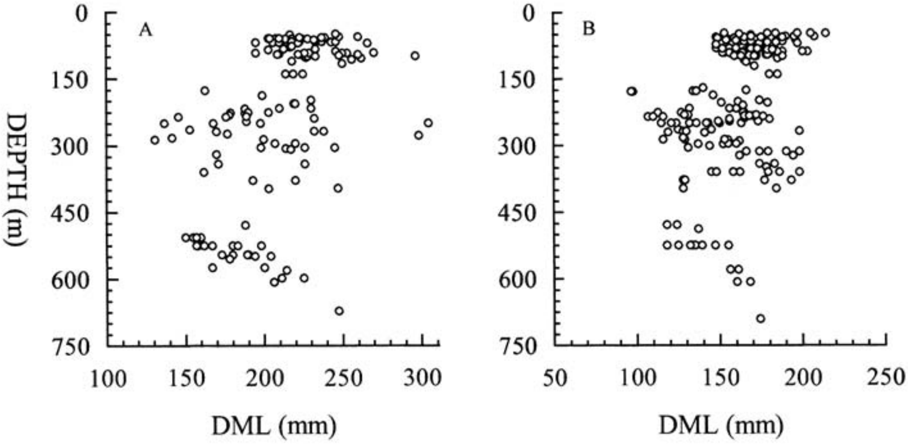

Figure 2. Bathymetric distribution of mature females (A) and mature males (B) *Illex coindetii* in northwest African coast.

37, $R^2 = 0.708$). The mean length of the spermatophores oscillated between 18.74–34.83 mm; but, they were homogeneous in size in each individual (n = 37, SD of the length of the spermatophores ranged between 0.38 and 5.15; but they were above 3.50 only in two cases).

FEMALES: MATURATION AND SPAWNING.—The GSI represented the different maturity stages better than RsI (all comparisons showed significant differences, Kruskal-Wallis; $P < 0.0004$ and lower; Table 3); on the contrary, RsI did not prove to be an useful index for females, since it just distinguished between juvenile and non juvenile individuals (H (4, n = 107) = 30.22623, $P < 0.0001$; Table 4). Therefore, it was considered more adequate to study the maturity based on the GSI. Monthly mean values in each zone and their dispersions were determined and, it was observed that mature females could be found all year round (GSI > 0.160) (Fig. 5). The higher GSI values were obtained during spring–summer, with a decrease in autumn in the northern and central zones. The highest percentage of mature females was found in spring (41.3%) in these zones, and the lowest was in autumn (6%). On the contrary, in the southern zone, the highest percentage of mature females was observed in autumn (52%). Ovaries whose weight represented more than 8% of the body weight were observed during the annual cycle whereas values over the mean were only found in spring and summer at the northern and central zones.

The latter coincides with the yearly distribution of females with spermatangues: 're- ceptive' females (with spermatangues) were found all year round, although it was spring

Table 1. Descriptive statistic values for GSI in each MS and Kruskal-Wallis test probabilities for comparisons between the GSI values (GSI = RSW / (BW – weight of the stomach)) associated to the different MS of male and female *Illex coindetii*. S = sex, m = male, f = female.

MS	n	Mean	SD	I-II-III-IV-V	II-III-IV-V	III-IV-V	IV-V
I	12	0.0008	0.0028	$P < 0.0001$			
II	12	0.0108	0.0051		$P < 0.0001$		
III	14	0.0292	0.0073			$P < 0.0001$	
IV	24	0.0420	0.0065				$P < 0.0001$
V	33	0.0572	0.0100				

Table 2. Descriptive statistic values for RsI in each MS and Kruskal-Wallis test probabilities for comparisons between the RsI values (RsI = (ScW + SsW) / RSW) associated to the different MS of male *Illex coindetii*.

MS	n	Mean	SD	I-II-III-IV-V	II-III-IV-V	III-IV-V	IV-V
I	12	0.0625	0.1217	P < 0.0001			
II	16	0.2900	0.0634		P < 0.0001		
III	9	0.2833	0.0250			P < 0.0001	
IV	21	0.4080	0.0622				P < 0.0001
V	37	0.5356	0.0969				

when receptive females attaining smaller sizes were observed (Fig. 6). Females in maturity stage III were already mated with small spermatangue groups in this season. These spermatangues were stuck to their disc in the mantle at the base of the gill, right and/or left, and close to the opening of the oviduct. They were more frequently attached on the right side (ventral view); and, this was considered to be a result of the slightly larger proportion (52%, total male number analysed = 593) of males with the IV left arm modified. The number of spermatangue groups oscillated between one and three. Some very big clusters were found at times, probably coming from multiple mating, since some of the spermatangues looked ‘worn-out’, as well as a great disk that seemed to be really formed by several disks partially leaning one against the others. Thus, it was estimated that a maximum of six clusters were present. Among the 16 females whose spermatangues were counted, one of them had a total of 1996 spermatangues. The average number of spermatangues per female was 484 (range = 150–1996, SD = 432); although, individual clusters with 8–25 spermatangues were found in females showing several clusters. Moreover, some spermatangue groups found in the same female showed a difference of about 7 mm in length. On the other hand, some females carried groups of ‘fresh’ spermatangues while other clusters barely contained the disk. The mean spermatangue length was 12.66 mm (n of females = 14, range = 6.10–15.00 mm, SD = 1.77).

Potential Fecundity.—Differences in maximal weight of each one of the reproductive components (ovary + oviduct, nidamental gland) between zones were found (maximal weight of the gonad (%) in northern, central and southern zones were 21.60, 18.71 and 14.00 respectively). The last, considering that the squid reached shorter sizes at the southern zone (Gulf of Guinea), indicate that in general the PF should be strongly reduced from north to south. The size range of the oocyte larger axis was 0.80–1.30 mm (mean = 1.07, SD = 0.13) and of the smaller axis was 0.55–0.90 mm (mean = 0.75, SD = 0.11). The PF was estimated for three females only, after considering that samples were not suitable for such purpose. This was estimated to be as a result of: firstly, samples were frozen for a long time in most of the cases, and then numerous oocytes were broken during the analysis and thus introduced error in the estimation; secondly, in the ovary of mature females, oocytes in all degrees of development (immature, maturing (with follicle ‘trabecules’), and mature ones) are present (determined by means of the histological cuts, Fig. 7). The results obtained were in the range of 54,000–171,500 oocytes for females with DML between 218 and 234 mm.

Todaropsis eblanae

The sex ratio was not significantly different from 1:1. Males (mean DML = 107.3 mm, range 43–164 mm, n = 348) were smaller on average size than females (mean DML =

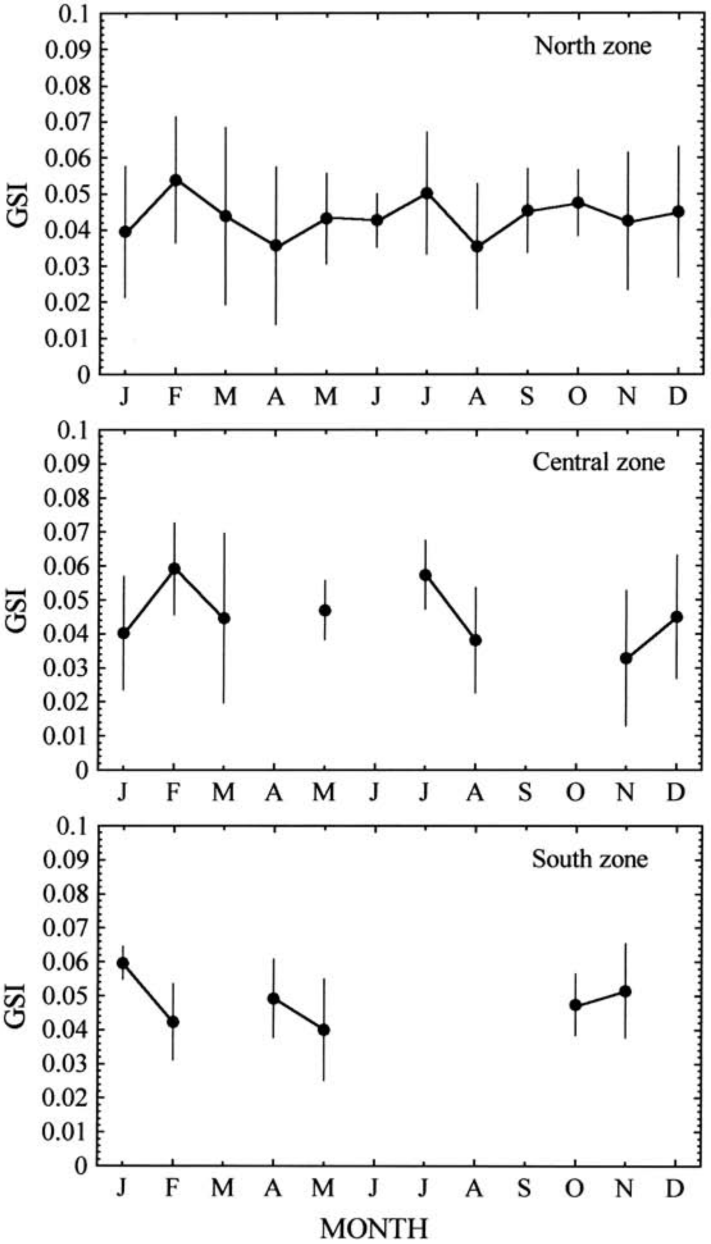

Figure 3. Monthly mean values and dispersions (SD) of the Gonadosomatic Index (GSI) of male *Illex coindetii* by zones.

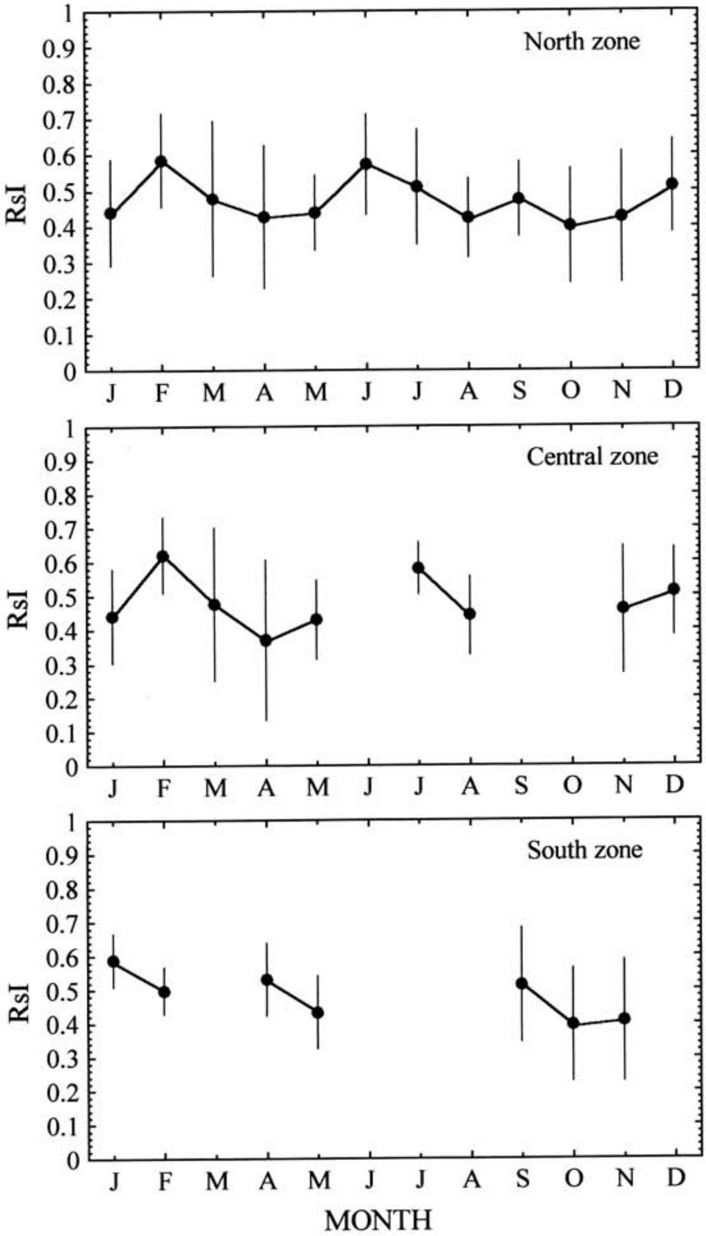

Figure 4. Monthly mean values and dispersions (SD) of the Maturity Index (RsI) of male *Illex coindetii* by zones.

Table 3. Descriptive statistic values for GSI in each MS and Kruskal-Wallis test probabilities for comparisons between the GSI values (GSI = RSW / (BW − weight of the stomach)) associated to the different MS of female *Illex coindetii*.

MS	n	Mean	SD	I-II-III-IV-V	II-III-IV-V	III-IV-V	IV-V
I	19	0.0005	0.0022	P < 0.0001			
II	16	0.0206	0.0156		P < 0.0001		
III	12	0.1050	0.0323			P < 0.0001	
IV	11	0.1600	0.0219				P = 0.0004
V	49	0.1971	0.0368				

126.2 mm, range = 44–215 mm, n = 357). Spent individuals were not found. On the other hand, it is remarkable that even on examining the samples, it was possible to notice a low proportion of males with spermatophores in the spermatophoric sac and of females with spermatangues stored into the buccal membrane receptacles (21 mated females were observed).

Maturity Size.—Sexual maturity in females started at a larger size than in males, in agreement with the sexual dimorphism observed. The nidamental gland reached very large sizes, weighing as much as 14.33% (maximal value observed) of the total weight (excluding the weight of the stomach). This value was slightly lower than the weight of the ovary and oviduct together, 17.41%. In several females, the nidamental glands were extended to the anterior border, slightly outside of the mantle.

T. eblanae mature females were distributed into a wide range size, 128–212 mm DML (Fig. 8). It was appreciated, independently of the size of the sample, that there were a low percentage of small and large size mature females. Although this was a mere reflection of the distribution of sizes in the sample, it was not in contradiction with the fact that the proportion of mature individuals increases with the size, which suggests a sole maturity size. The size at maturity estimated was 168 mm (Fig. 8). A similar situation was observed for males. The size range for mature males was 109–164 mm (Fig. 8). Low percentages of mature males were also observed for small and large size animals. Consequently, it was considered that males, like females, show a sole maturity size, which was estimated to be 130 mm (Fig. 8). Therefore, males matured at a smaller size than females, the difference being about 19 mm between the smallest mature males and females and of 38 mm between the sizes at maturity of both sexes.

Spawning Season.—In females, RsI proved to discriminate only between the immature and maturing-mature squids (Table 5). On the other hand, although the GSI represented satisfactorily the different qualitative phases, the difference between the stages IV and V was not significant (P = 0.1483; Table 6). For females and according to the GSI values,

Table 4. Descriptive statistic values for RsI in each MS and Kruskal-Wallis test probabilities for comparisons between the RsI values (RsI = (OgW + NgW) / RSW) associated to the different MS of female *Illex coindetii*.

MS	n	Mean	SD	I-II-III-IV-V	II-III-IV-V	III-IV-V	IV-V
I	18	0.2205	0.1496	P < 0.0001			
II	17	0.3629	0.0686		P = 0.4594		
III	11	0.3981	0.0362			P = 0.6689	
IV	15	0.3953	0.0299				P = 0.5014
V	46	0.3926	0.0459				

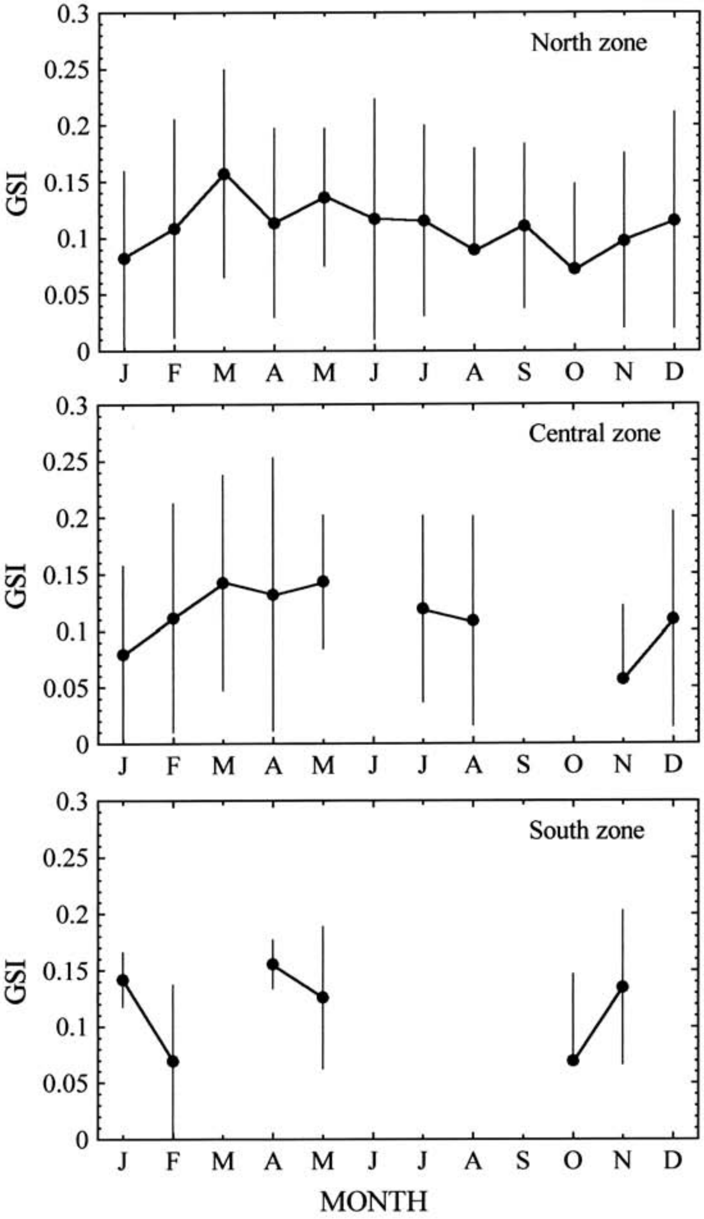

Figure 5. Monthly mean values and dispersions (SD) of the Gonadosomatic Index (GSI) of female *Illex coindetii* by zones.

although mature squid were present almost all year round, the period of reproductive activity was composed of two periods, spring (March and April) (GSI> 0.1660) and autumn (Fig. 9A). This phase could be prolonged until the winter if the RsI values were considered. It coincided with the distribution of mated females (the higher numbers were observed in autumn (6) and in winter (8)). The number of spermatangues per females was

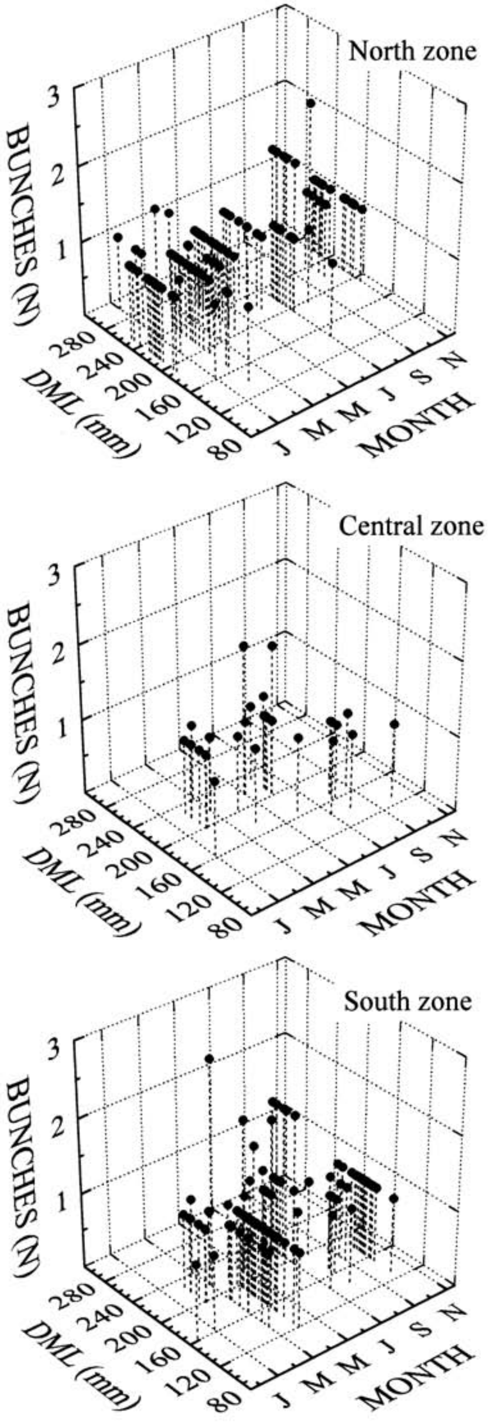

Figure 6. Monthly distribution of mated females *Illex coindetii* according to the number of main spermatangue bunches by zones.

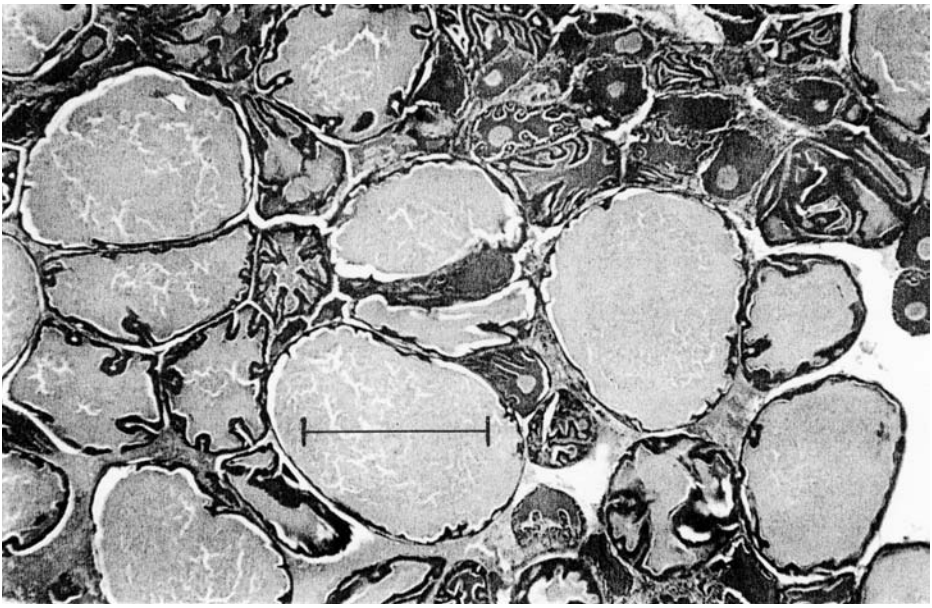

Figure 7. Histological cut (ovary) from a mature female *Illex coindetii*. Immature, maturing (with 'follicle trabecules') and mature 'eggs' are present at the same time. Scale bar = 1 mm.

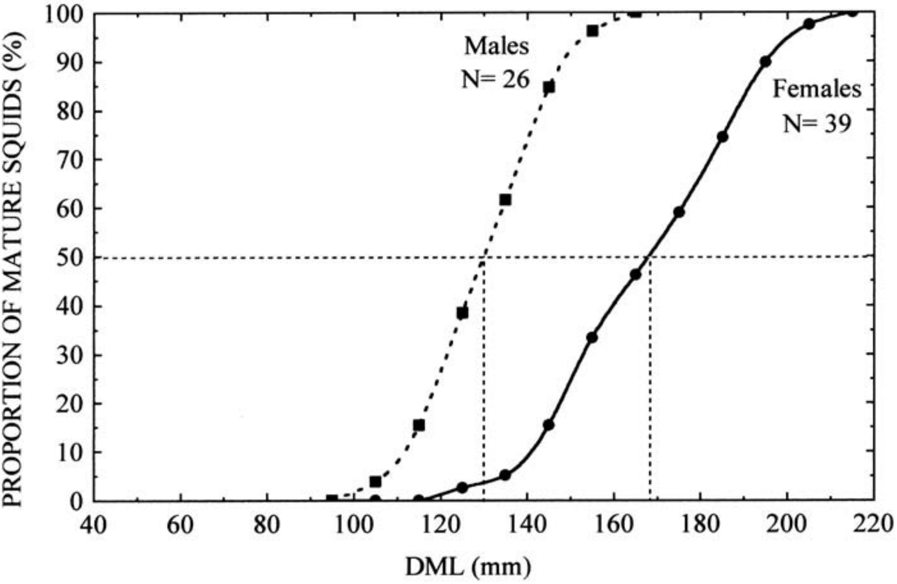

Figure 8. Size at maturity. Proportion of mature squids in 10 mm categories of dorsal mantle length (DML) classes for *Todaropsis eblanae*.

Table 5. Descriptive statistic values for RsI in each MS and Kruskal-Wallis test probabilities for comparisons between the RsI values (RsI = (OgW + NgW) / RSW)) associated to the different MS of female *Todaropsis eblanae*.

MS	n	Mean	SD	I-II-III-IV-V	II-III-IV-V	III-IV-V	IV-V
I	82	0.1752	0.1649	P < 0.0001			
II	40	0.2980	0.1241		P < 0.0001		
III	5	0.5120	0.0558			P < 0.5227	
IV	13	0.5146	0.0541				P = 0.3107
V	27	0.5003	0.0582				

variable; the size of these was approximately 5 mm, with a thickness of 1 mm at the base and thinner at the tip. The largest axis of mature eggs oscillated between 0.80 and 1.3 mm.

For males, RsI discerned better that the GSI between the qualitative maturity stages (Tables 7 and 8 respectively), although significant differences between the stages I-II, II-III and I-II-III were not found (H(1, n = 108) = 2.323852, P = 0.1274; H(1, n =81) = 3.495125, P = 0.0616; H(2, n = 136) = 3.808772, P = 0.1489 respectively). On the other hand, the distinction by mean of GSI between the first three stages was satisfactory (P<0.0001); but no significant differences were obtained for comparisons of the III-V stages (P>0.05). In general, males showed the highest values of the indices in autumn-spring (Fig. 9B,C), which was appreciated clearer in the case of the GSI when considering the squid size.

The mean number of spermatophores was 100 (n = 11, range = 11–269, SD = 70.17). Spermatophore lengths ranged from 20.72 to 27.35 mm, but showed little variation within individuals, the SD observed ranging between 0.77 and 1.90 mm (n =10). Significant correlations were observed between the variations of the number of suckers and ridges of the fourth right arm (ventral view) and the GSI (N of suckers (rr) = 3.52 – 51.85 × GSI, R^2 = 0.629; N of ridges (rr) = 2.28 + 27.82 × GSI, R^2 = 0.672 (right row both) and N of suckers (lr) = 11.84 – 164.25 × GSI, R2 = 0.685 for number of suckers of the left row (or internal)). The suckers disappear during the maturation process and the ridges are developed (increasing its number and size). According to the evolution of the sucker and ridge number, in mature males there are as maximum one sucker and no less than four ridges on the right row and as maximums two suckers on the left row.

Table 6. Descriptive statistic values for GSI in each MS and Kruskal-Wallis test probabilities for comparisons between the GSI values (GSI = RSW / (BW – weight of the stomach)) associated to the different MS of female *Todaropsis eblanae*.

MS	n	Mean	SD	I-II-III-IV-V	II-III-IV-V	III-IV-V	IV-V
I	59	0.0001	0.0013	P < 0.0001			
II	18	0.0100	0.0059		P = 0.0001		
III	3	0.0333	0.0208			P = 0.0012	
IV	8	0.1662	0.0717				P = 0.1483
V	16	0.2112	0.0393				

Table 7. Descriptive statistic values for RsI in each MS and Kruskal-Wallis test probabilities for comparisons between the RsI values (RsI = (ScW + SsW) / RSW)) associated to the different MS of male *Todaropsis eblanae*.

MS	n	Mean	SD	I-II-III-IV-V	II-III-IV-V	III-IV-V	IV-V
I	55	0.1820	0.1904	$P < 0.0001$			
II	53	0.2205	0.1143		$P < 0.0001$		
III	28	0.1792	0.1263			$P < 0.0001$	
IV	13	0.3984	0.2464				$P < 0.0646$
V	8	0.6012	0.2049				

DISCUSSION

It is necessary to bear in mind that the results come from the combination of two-year data. Therefore, they could be affected by inter-annual variations. For both species, males become mature at a smaller size than females, which is in accordance with other authors observations for ommastrephids (see Durward et al. (1979) for *I. illecebrosus* and Sánchez (1981) and González (1994) for *I. coindetii*). The wide size range of mature individuals, although it could be influenced by the large extension of the studied area, together with the sole size at maturity, show the existence of a great individual variability.

As far as females were concerned, the fact that the RsI was not behaving properly could be due to the stability in the proportions between the reproductive system components during the maturation process (Durward et al., 1979). Thus for *I. coindetii*, the relationships between the ovary weight and the nidamental and oviductal gland weights showed a significant correlation ($n = 446$, $P = 0.003$, $R^2 = 0.881$ for the nidamental gland, $n = 446$, $P = 0.002$, $R^2 = 0.869$ for the oviductal gland).

The analysis of the monthly variation of the maturity showed that spawning could take place all year round, as was suggested by Laptikhovsky and Nigmatullin (1993), Hernández-García (1995) and Arkhipkin (1996). But, the reproductive activity was more intense during spring-summer (seasons in which there was a higher frequency of mated females, and when the smallest mated females were observed). In the Mediterranean Sea, Sánchez (1981) observed the same situation although the author found the maximum activity in autumn. González (1994) observed similar results for waters off Galicia, with the maximum spawning activity at the end of the spring-summer period. The different seasonal reproductive peaks were more accentuated in northern and central zones (in spring-summer), while at the southern zone there was a higher intensity in autumn, but with no strong peak. The data available from the south zone did not cover the entire year, but seemed to indicate that at low latitudes, the spawning process could be almost con-

Table 8. Descriptive statistic values for GSI in each MS and Kruskal-Wallis test probabilities for comparisons between the GSI values (GSI = RSW / (BW – weight of the stomach)) associated to the different MS of male *Todaropsis eblanae*.

MS	n	Mean	SD	I-II-III-IV-V	II-III-IV-V	III-IV-V	IV-V
I	40	0.0001	0.0001	$P < 0.0001$			
II	26	0.0115	0.0083		$P < 0.0001$		
III	16	0.0506	0.0187			$P < 0.1287$	
IV	7	0.0642	0.0151				$P < 0.8451$
V	7	0.0685	0.0234				

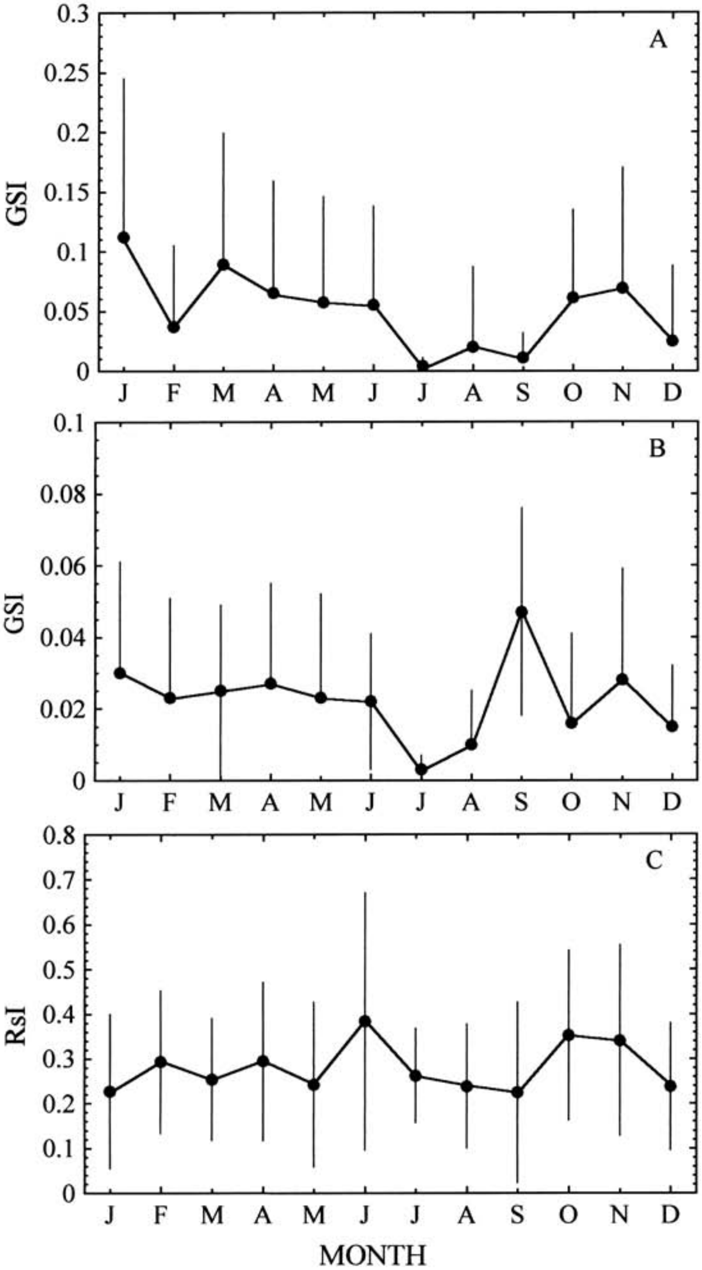

Figure 9. Monthly mean values and dispersions (SD) of the Gonadosomatic Index (GSI) of female (A) and male (B), and of the RsI for male (C) *Todaropsis eblanae*.

tinuous in intensity all year round. In the southern zone, the homogeneity of the temperature could facilitate a continuous spawning process, with no need for squids to live long (growing larger) to spawn. These considerations are consistent with the results on age obtained by Arkhipkin (1996). In general, no squids older than 6 months were found in

Sierra Leone waters. This could explain the existence of large mature females in the northern and central zones. The temperature in these zones is lower (18°–22°C) year round than in the Gulf of Guinea (26°–29°C) (Zuev et al., 1985; Picaut, 1984). Squids hatching in late spring and summer are not developed enough to mature during the next 6 mo, they will remain immature during winter and maturing and spawning processes will be during the following early spring, when they will be about 1 yr old.

The values of the oocyte larger axis obtained (0.80–1.30 mm) were close to those observed for this species by Sánchez (1981) (1.00–1.20 mm), González (1994) (0.80–1.20 mm) and Laptikhovsky and Nigmatullin (1993) (0.90–1.00 mm). Considering that the genus *Illex* has ripe egg dimensions close to the minimum for cephalopods (Mangold, 1987; Laptikhovsky and Nigmatullin, 1993), large differences cannot be expected between squids with different sizes. Therefore, if the PF is estimated for the female having the heaviest ovary-oviduct (ovary-oviduct weight = 112 g, a female 290 mm DML), a total of 729,900 oocytes is obtained as PF. This is a close value to the maximal (800,000 oocytes) estimated by Laptikhovsky and Nigmatullin (1993). Then, the experimental smaller values obtained (54,000 and 171,500 oocytes) could be very much influenced by the squid size (218 and 234 mm DML). Considering the reduction in ovary weight with latitude and that egg size should not vary strongly, the potential fecundity (PF) would possibly decrease when descending in latitude.

The existence of females with small spermatangue clusters (e.g., 25 spermatangues) could be indicative of young mature males (stage IV) already mating. The discovery of very big clusters, which sometimes in fact seemed to consist of small ones, proved that the maximal number oscillates between 4 and 6; therefore, these females would have carried out many separate matings. The latter was also suggested by Nigmatullin (1989) for *Illex argentinus*. Moreover, to support this, it can be considered the case of that female, in which 1996 spermatangues were counted, a larger value than the maximal number of spermatophores found in the male with the highest spermatophore amount, even larger than the maximum obtained by González (1994). Other elements that sustain the thesis of multiple mating are the presence of groups of spermatangues with different sizes and not 'worn-out' or the presence of fresh and worn-out groups in the same female. Moreover, the last also implies that these females had carried out at least a partial spawning. Therefore, it can be considered that *I. coindetii* females mate with several males, probably in a short time period, which will produce a high increase in the genetic diversity in the progeny of each individual. Nigmatullin and Laptikhovsky (1990) and Laptikhovsky and Nigmatullin (1993) proposed a reproductive model for the genus *Illex* characterized by the existence of multiple spawning, falling in intensity up to the death of the animal. The observations described above are consistent with that model.

Mature males (RsI > 0.4 and GSI > 0.04) were found during the whole year, as observed by Sánchez (1981) and González (1994) in Mediterranean and waters off Galicia respectively. The maximal number of spermatophores recorded in the Needham's sac (1412) was close to the one (1550) obtained by González (1994) but, significantly larger than the value 790 obtained by Sánchez et al. (1998) in waters off Africa. The range obtained in the present study (25–1412) was also wider than the one obtained by the latter authors (290–790) but, the mean lengths of the spermatophores observed (18.74–34.83 mm, for all individuals) coincide with the values obtained these authors for West African waters and with those obtained by Sánchez (1981) for the Catalan Sea (20–35 mm). They were bigger than those found by González (1994) for the Galician waters (11.1–37.7

mm). It could be that at higher latitudes, males produce a larger spermatophore number but with a smaller length. The maximal number of spermatophores counted cannot be considered the like maximal number that *I. coindetii* male is able to produce. It is possible, that the studied males have transferred part of the first genetic material to one or more females in early intercourses. This contributes also to the low R^2 values observed for the relation squid size (DML) – number of spermatophores.

In relation to *T. eblanae*, the results obtained are close to those observed by other authors in two different areas of the North Atlantic (González et al., 1994; Hastie et al., 1994), but they look different from the results reported by Burukovsky et al. (1979). These latter authors indicated that sexual maturity is attained at mantle lengths of 130–160 and over 150 mm for males and females respectively. These values are higher than those obtained in this work (the minimum sizes observed were 109 and 128 mm for male and female respectively). This difference could be due to inter-annual differences, or that those authors did not have a sample covering the entire size range (including small mature squids). On the contrary, González et al. (1994) and Hastie et al. (1994) observed smaller mature individuals of both sexes in waters off Galicia and the North Sea: mature females with size 110 mm, as well as mature males of 92 mm. It is necessary to consider that the maximal sizes observed at that latitude were smaller. Thus, the size range for male was 40–141 mm (Hastie et al., 1994). Both values, number and length of the spermatophores are larger than those observed by Hastie et al. (1994) for this species taken in Scottish coastal waters. The maximal number observed were 130 spermatophores and their maximal length was 18.1 mm. These lower values could be related with the shorter size reached by this species in northward latitudes.

The maturation process took place in both sexes at the same time, and they were close to the period in which mated females were observed. All this can be considered indicative that maturation and spawning is taking place in a very short time period. The latter could explain the low proportion of mature specimens and the scarce presence of mated females. Here, it is considered initially that sampling was not biased, since fishing took place between 23 and 1043 m, although the species was caught in a shorter depth range.

The maturation and spawning season was estimated to be in autumn-spring, which is close to the results obtained by Hastie et al. (1994). Mating and spawning take place during late summer and autumn in northward latitudes. On the contrary, Burukovsky et al. (1979) found that these processes were taking place from March till November. No clear explanations can be offered at present for such differences between the results presented here and the findings of the last authors. One possibility is that squid when they mature inhabit the water column, far away from the bottom and not available to the demersal fishery.

The low proportion of individuals at the maturity stage III observed for both species is remarkable. It suggests that the maturity process could be very fast. This coincides with results obtained by Durward et al. (1979) for *Illex illecebrosus* (a process that in females lasted about one month), by González (1994) for *I. coindetii* and by Hernández-García et al. (1998) for *Todarodes sagittatus*.

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