SPAWNING PATTERN AND FECUNDITY OF THE OMMASTREPHID SQUID *Todaropsis eblanae* IN NORTHEASTERN ATLANTIC WATERS

Mario Rasero, Angel F.González and Angel Guerra

Instituto de Investigaciones Marinas (I.I.M. - CSIC), Eduardo Cabello, 6

36208 Vigo, Spain

ABSTRACT

Eight maturing, 94 mature and 6 spent females of *Todaropsis eblanae* collected from commercial trawlers fishing off Galician waters (NW Spain) were examined. Potential and Residual Fecundity of the species were calculated. From these estimations, a Real Fecundity of about 120,000 eggs was estimated.

Several signs of multiple spawning were detected, the 4 more important being: i) Real Fecundity was four times higher than the maximum number of mature oocytes observed in the oviducts; ii) No correlation between the number of oocytes in the ovary and the number of oocytes in the oviducts was found in mature mated females; iii) Oocyte sizes in the ovary of mature females ranged from 0.1 to 1.2 mm, with a modal length of 0.3 mm. Mature oocytes in the oviducts ranged from 1.2 to 1.8 mm; and iv) Thickness of nidamental glands was highly correlalated with oviduct fullness.

According to these results, it can be concluded that *T. eblanae* is a standard multiple spawner with relatively low fecundity. The increase of recent evidences of multiple spawning among the ommastrephids seems to indicate that this reproductive pattern is widely extended in the family, and also perhaps in the whole Cephalopoda Class.

INTRODUCTION

Reproduction is the essential fact in the life cycle of any species, since it is the process by which genetic material is transmitted from one generation to the next, thus ensuring the continuity of the species in time.

Because the reproductive biology of the genus *Nautilus* is very different from that of the rest of the class Cephalopoda (Saunders, 1984; Mangold, 1989; Mangold et al., 1993), to introduce the reproduction in cephalopods, it would be suitable focusing this subject on the subclass Coleoidea. It may be considered that all coleoid cephalopods share certain general reproductive characteristics: they are fast growing dioecious animals with a short life span (6 months - 4 years), they reproduce towards the end of life with no gonadal regeneration, and die after reproduction (Mangold et al., 1993). The hormone of the optic glands seems to control this process of growth, reproduction and death, the speed and duration of the process depending on the intrinsic characteristics of the species, and on several environmental factors such as food, light and temperature (Mangold, 1987, 1989).

Following the discovery of the optical gland system and its function (Wells and Wells, 1959), and in view of evidences of massive mortalities after reproductive concentrations in some species (e.g. *Loligo opalescens*; Fields, 1965), the notion spread that it was characteristic of cephalopods to perform a final spawning, which was closely followed by death. In other words, it was considered that cephalopods were typical "semelparous" organisms, despite the difficulty in adequately defining this term (Kirkendall and Stenseth, 1985). In 1975, Boletzky published the first observations of prolonged and intermitent spawning in *Sepia officinalis*. Since then, new indications and evidences of multiple spawning in several cephalopods have been published, to such an extent that nowadays, it appears that the existence of a "reproductive holocaust" (O'Dor and Wells, 1987) is, by no means, a standard characteristic of the cephalopods, but rather a particular mechanism of a few species in particular (Mangold et al., 1993).

As regards nektonic cephalopods, or "squids" (Order Teuthoidea), the reproductive pattern of several species is relatively well known, particularly among the loliginids and ommastrephids. In all known cases, spawning is terminal, ocurring over a relatively short period of time, towards the end of the animal's life. But two basic types may be defined, as follows:

a) Simultaneous terminal spawning or "simultaneous spawning": one single or several spawnings occur, but always within a very short period of time and with no maturation of oocytes between them. This pattern could be considered as strict semelparity. *Loligo opalescens* (Hixon, 1983) is one of the examples of this typology, and also the ommastrephids *Illex illecebrosus* (O'Dor, 1983) and *Todarodes pacificus* (Ikeda et al., 1993).

b) Multiple terminal spawning or "multiple spawning: the term "multiple spawning" was defined by Harman et al. (1989) as the reproductive mechanism characterized by the continuous maturation of oocytes during the reproductive period, the eggs being intermittently hatched by the female during this period. *Thysanoteuthis rhombus* (Nigmatullin et al., 1991), *Loligo vulgaris* and *L. forbesi* (Rocha, 1994; Boyle et al, 1995), and the ommastrephids *Sthenoteuthis oualaniensis* (Harman et al., 1989), *Illex argentinus* (Laptikhovski and Nigmatullin, 1993) and *Illex coindetii* (González, 1994) can be considered multiple spawners.

As mentioned above, some species of the family Ommastrephidae have a simultaneous terminal spawning, and others a multiple spawning. Nevertheless, and although knowledge of the reproductive biology of certain species in this family is practically non-existent, it may be considered that all the ommastrephids share certain basic characteristics:

- Fecundity is relatively high, ranging from 75,000 oocytes in small sized *Illex illecebrosus* (Laptikhovsky and Nigmatullin, 1993), to over six million in *Dosidicus gigas* (Ehrhardt et al., 1983).

- Mature oocytes are small in size, measuring a minimum of 0.7 mm in the genus *Illex* (Laptikhovsky and Nigmatullin, 1993), and a maximum of 2.5 mm in *T. eblanae* (Hastie et al., 1994).

- The nidamental glands produce a gelatinous substance which covers the eggs during

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spawning, forming the egg mass. These masses are transparent, very delicate, unorganized, and large in volume. They are only known for a limited number of species, i.e. *Illex illecebrosus, Todarodes pacificus* and *Illex coindetii*, and are found on extremely rare ocassions in the open seas (Clarke, 1966; Boletzky et al., 1973; Durward et al., 1980; O'Dor et al., 1982; Okutani, 1983; O'Dor and Balch, 1985).

- Fertilization generally occurs (except in species belonging to the genus *Illex*) in the buccal membrane, where sperm is transferred from the spermatophores to a buccal pouch (Mangold, 1987).

Very little is known to date of the reproductive characteristics of *Todaropsis eblanae*. (Ball, 1841) There are only two published papers on this subject (Mangold-Wirz, 1963 and Hastie et al., 1994), which offer a useful, although incomplete, overview of reproduction in this species.

This paper is an attempt to deepen present day knowledge of reproduction in *T. eblanae*, as regards fecundity and type of spawning. The paper shows a small part of the results of an extensive study on the biology of ommastrephids in the Northeast Atlantic, particularly in Galician waters (NW Spain, see Fig.1)

MATERIALS AND METHODS

1. Maturity scale:

The maturity scale for the present study was based on the "universal" scale by Lipinski (1979), and those by Nigmatullin et al. (1984) and Burukovsky et al. (1984) for *Illex illecebrosus*, although adapted to the specific characteristics of *Todaropsis eblanae*. Five stages of maturity were considered. Stages I and II were grouped together as "IMMATURE".

I) The ovary is barely observable as a filament. The nidamental glands are two thin translucent laminae. The oviducts and oviductal glands are invisible.

II) The ovary is enlarged and its structure is plain to see. The nidamental glands are still not fused but are thicker than in "I" and slightly white in colour. The oviducts are easily observed, and the oviducal glands appear as 2 small translucent dots.

III) MATURING: the ovary is large, and maturing oocytes can be observed by eye naked. The nidamental glands are bright white, fused together and large in size. The structure of the oviducts is clearly visible and the oviducal glands are thick and bright white in colour.

IV) MATURE: this stage is characterized by the presence of mature, orange coloured oocytes in the oviducts. The degree of filling of the oviducts is highly variable. The nidamental glands are very big, measuring about 70% of the dorsal mantle length (DML), and generally projecting out from the mantle cavity. Their consistency is usually somewhat softer than in the previous stage. Maturing oocytes are observed - yellowish in colour - in the ovary. In some areas of the ovary no maturing oocytes are visible, but rather only the ovaric structure, an indication that the oocytes in this zone have already passed to the oviducts. Generally,

discharged spermatophores and remains of sperm appear in the ventral part of the buccal membrane, indicating that the female has been mated. Although not considered in this study, it would be advisable for future work on *T. eblanae* to consider two different categories of mature females (stages IVa and IVb), which would be distinguished by the presence or absence of discarded spermatophores in the buccal membrane. The non-mated females, although already mature, have still not initiated spawning, whereas the mated females have most probably done so. This distinction can be of great importance when performing studies on fecundity.

(V) SPENT: the animal has a poor aspect, the body has a very soft consistency and usually presents wounds or breakages. The nidamental glands have almost liquid consistency, being very small, or even having practically disappeared. The oviducts are empty or with a few mature oocytes. The ovary is very small, normally covered of a mucose substance. Either few or no oocytes are observed in the ovary. The digestive gland may be very small and the gills blackened.

2. Fecundity and reproductive pattern:

Four samples were taken at the fish markets of Burela and Celeiro (Fig.1) from March to June, 1993. The vessels from these ports are small bottom trawlers fishing on the nearby shelf and slope (100-500 m depth), returning to port daily. A total of 94 mature female *T. eblanae* were collected: 4 in March, 26 in April, 33 in May and 29 in June. Eigth maturing and six spent females were also collected. The samples were transported on ice to the laboratory, where they were immediately processed fresh.

Unless indicated otherwise, this study was performed on the 108 females collected during 1993 sampling. For some of the analyses, data from mature females sampled in 1992 under the same conditions, time and ports were considered. The following data were obtained for all the females:

- Size: DML was measured to the nearest millimeter, with a metal ichthyometer.

- Weight: total body weight (W) was obtained with 1 g precision, using a Mettler Toledo PB8001 balance.

- State of sexual maturity was performed as mentioned above.

- Weight of both oviducts, both nidamental glands, and ovary was measured using a Mettler PE 200 balance with 0.01 g precision.

- Nidamental glands size of 45 mature females: the longest nidamental gland was measured with a 1 mm precision calliper.

- The presence or absence of discharged spermatophores in the ventral zone of the buccal membrane was noted.

To estimate the number of mature oocytes in the oviducts, a sample was extracted (sample weights between 0.2 and 0.6 g) from the central zone of one of both oviducts. The sample was fixed in 4% formalin after a slight shaking. Approximately one month later,

ovocytes were counted on a Petri dish under binoculars (10 x). On the basis of this countings, the number of oocytes present in the oviducts was estimated.

To estimate the number of oocytes in the ovary, a sample was extracted (sample weights between 0.05 and 0.15 g) from the central zone of the ovary. The sample was fixed in 4% formalin after a slight shaking. One or several months later, the sample was placed in a Bogorov capsule and the oocytes were individualized with the help of two dissection needles under binoculars (10 to 40 x). The smaller oocytes, which could not be individualized without risk of damage, were left on the remains of the connective tissue. Later, all the oocytes present in the sample were counted. On the basis of this count, the number of oocytes present in the ovary was estimated.

To obtain size distributions of the mature oocytes present in the oviducts, samples were extracted from the oviducts of 6 mature females. The diameters of 40 spherical oocytes were measured in each of the six samples. Measurement was performed a few minutes after obtaining the sample, on a Petri dish with seawater, under binoculars (30 x) equipped with a micrometric eyepiece.

To obtain the size distribution of the oocytes in the ovary, the smaller diameters of more than 100 oocytes ($108<n<127$) were measured from the ovaries of 6 mature females. The measured oocytes were randomly selected from the sample used to calculate fecundity. They were measured in a Bogorov capsule under binocular microscope (30 to 40 x) equipped with a micrometric eyepiece.

The following parameters related to fecundity were defined:

Oviductal Load (OL): number of mature oocytes present in the oviducts of a mature female.

Ovarian Load (VL): number of oocytes (all sizes) present in the ovary of a female at any stage of maturity.

Potential Fecundity (PF): total number of oocytes present in a female which has still not initiated spawning, but has already initiated yolk production (female III or IVa). As indicated by Laptikhovski and Nigmatullin (1992) for species of the genus *Illex*, these females have already finished the production of oocytes. In the case of a non-mated mature female (IVa), potential fecundity would be OL + VL. In the case of a maturing (III) female (which were the only ones used to estimate the PF in this study), the potential fecundity would be the same as the OL.

Total Load (TL): OL+OV in a mated mature female (IVb).

Residual Load (RL): ovarian load of a spent (V) female. It is considered that these oocytes will no longer participate in any spawning, and that there has been no reabsorption of oocytes, since this phenomenon has not been described, to date, in cephalopods.

Real Approximate Fecundity (RAF): it is impossible to calculate the real fecundity of an individual (total number of eggs comprising its spawning or spawnings), except where spawning occurs under controlled conditions. For this reason, an approximate value (RAF) was calculated for the species. RAF is the result of the difference between the average PF and the average RL.

An index of the nidamental glands thickness (NGT) was calculated using the following formula: NGT = (NGW x 100) / NGL; where NGW is the weight of both nidamental glands, and NGL is the length of the longest one.

RESULTS

Table 1 shows the average, the standard deviation and the range of the estimations of PF, RL and RAF.

Figure 2 shows the relationship (OW=0.667+0.000937 OL; r^2 = 0.95) between the oviductal load (OL) and the weight of the oviducts in g (OW). An average of 994 mature oocytes per gramme of oviduct was calculated, with a standard deviation of 148. The average number of oocytes in the oviducts was 12,167, with a standard deviation of 7,848.

The size distribution of mature oocytes in the oviducts is shown in Figure 3. The presence of oocytes between 1.3 and 2 mm diameter was observed, being the most common 1.5-1.6 mm.

Figure 4 shows the relationship between the oviductal load and the ovarian load. A low correlation between both parameters was observed.

Figure 5 shows the total load relative to DML. A low correlation was observed between both parameters.

Figure 6 shows the size distribution of oocytes found in the ovaries of six mature females. The presence of oocytes of all sizes was noted, although the frequency progressively decreases from the 0.3 mm class, stabilizing at between 0.7 and 1 mm, the large ones rarely reaching more than 1.1 mm.

High correlation (r = 0.80; p<0.01) was found between the index of nidamental gland thickness (ING) and the weight of the oviducts (Figure 7). In this figure, data on the mature females from the 1992 sampling were also included (see Material and Methods).

The percentage in weight of the nidamental glands in mature females (100 x weight of the glands / total body weight) ranged from 6.69 to 16.42%. The percentage in weight for the oviducts (100 x weight of the two oviducts / total body weight) varied between 0.20 and 7.21%, and for the ovary (100 x weight of the ovary / total body weight) varied between 1.43 and 8.61%. The percentage in weight of the whole reproductive apparatus (100 x [nidamental g.+ oviducal g.+ ovary + oviducts] / total body weight) ranged from 6.83 to 30.04%, averaging 18.90 ± 4.17%.

The 86.1% of the mature females collected in the sampling were mated. No signs of mating were found in any immature or in maturation female (unpublished data).

DISCUSSION

The reproductive pattern of cephalopod females has been focused on far more than that of males. Nevertheless, with the exception of the studies by Mangold-Wirz (1963) and Hastie et

al. (1994), little else is known on the mechanism and characteristics of the reproduction of *T. eblanae*. Actually, it is currently considered that multiple spawning, i.e. the existence of several spawnings with oocyte maturation between them (Harman et al., 1989), is a relatively common mechanism among teuthoid cephalopods. Indications or evidences of multiple spawning are known in several species of ommastrephids. Other species of this family seem to perform simultaneous terminal spawning, which is followed by the death of the female (see Introduction). Therefore, it is interesting to know if spawning of *T. eblanae* belongs to the simultaneous type or if, on the contrary, it follows the multiple spawning model.

Regarding fecundity, on the basis of data in Table 1, the RAF was estimated at 122,129 ± 18,271.5 oocytes. As it was previously indicated, this fecundity is only an orientative value. Nevertheless, the relatively small variation observed in the PF and RF estimates leads one to consider, despite the small number of females used in the estimates, that the RAF is a good approximation to the real average fecundity of this species.

The RAF value obtained in this study is far higher than the existing fecundity estimates for this species, which fluctuate between 5,000 and 10,000 oocytes (Mangold-Wirz. 1963), or between 5,000 and 30,000 (Hastie et al., 1994). The size of mature female *T. eblanae* collected in these two mentioned studies are only slightly lower than those observed in Galician waters. Thus it is not expected that the differences in size can be the cause of such a great divergency in estimated fecundities. The weights of the ovaries of mature females from Scottish waters were notable lower (from 1 to 20 g, but mainly between 2 and 15 g, Hastie et al., 1994) to those observed in Galician waters (from 5 to 30 g, but mainly from 15 to 25 g). This may be one of the causes for the difference in fecundity estimates. It would be difficult to establish the reasons for such a variation in the ovary weight for females of the same species and similar size. This variation may be linked to the methodology used in fixing and preserving the samples, although the explanation may also lie in ecological reasons (food intake of the species, oceanographic conditions such as temperature, etc). Likewise, it appears possible that the females used to calculate fecundity in Scottish waters had already begun to spawn. Nor is it beyond doubt that an infraestimate of fecundity ocurred in the results by Mangold-Wirz (1963) and Hastie et al., (1994), due to failing to count all the sizes of oocytes present in the ovary (including the smallest ones measuring 0.1 to 0.3 mm), which is not the case in this study.

Considering the RAF estimated in this paper, *T. eblanae* is probably the ommastrephid which presents the lowest fecundity. Potential fecundities - increasing with size - of 75,000 to 1,200,000 oocytes have been estimated in *Illex argentinus*, of 80,000 to 800,000 oocytes in *Illex coindetii*, and of 200,000 to 630,000 in *Illex illecebrosus*, it being considered that the real fecundity of these species may fluctuate around 60 to 70% of the values indicated (Laptikhovski and Nigmatullin, 1993). Fecundity of 1.10^6 to 6.10^6 oocytes was estimated for *Dosidicus gigas* (Ehrhardt et al., 1983). In *Sthenoteuthis oualaniensis*, a total of 1,643,000 oocytes were estimated in the ovary of a mature female (Harman et al., 1989). The fecundity of *Todarodes pacificus* has been calculated at 320,000-470,000 eggs (Soeda, 1956, fide Okutani, 1983). Other estimates consulted are not comparable with those presented here, as they were

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exclusively taken on the basis of the count of mature oocytes, or on the basis of the count of oocytes bigger than a given size.

The size of the mature oocytes of *T. eblanae* (1.3-2 mm, chiefly 1.5-1.6 mm) is greater than that observed in *Illex coindetii* from Galician waters (0.8-1.2 mm, González, 1994), and in species of oceanic ommastrephids of the genera *Dosidicus*, *Ommastrephes*, *Stenoteuthis* and others (0.75-0.85 mm, Laptikhovski and Nigmatullin, 1993). It is, however, similar to that of other ommastrephids living on the shelf and slope, such as *Todarodes*, *Martialia* and *Nototodarus* (1.2-1.6 mm, Laptikhovski and Nigmatullin, 1993), and to that observed in *T. eblanae* from Scottish waters (1.2-2 mm, Hastie et al., 1994).

The relatively small size, and the scarce muscular development of *T. eblanae* , leads one to consider that this species is not given to much swimming, and does not perform big migrations. This conclusion may be also inferred from the constant presence in the sampling area, throughout the year, of individuals at all stages of maturity (unpublished data). This fact, linked with the preference of this species for the bottom of shelves and slopes (Roper et al., 1984), besides the previously highlighted combination of large sized eggs and low fecundity, indicates that the life strategy of *T. eblanae* lies far from that of the oceanic ommastrephids and, to a certain extent, has similarities with the life strategy of some loliginids.

Little can be said about the variation in the fecundity of *T. eblanae* in relation to size, since there are not enough data available. Nevertheless, the range of sizes of mature female *T. eblanae* is relatively small (unpublished data), and the PF estimated is quite constant within the range of sizes considered (Table 1). Thus, a large variation in the individual fecundity does not appear to be likely.

Regarding on the type of spawning, enough signs of multiple spawning have been found, as to be able to consider that this is the spawning mechanism of *T. eblanae* in the study area. These multiple spawning signs are as follows:

1) Comparing the RAF with the average number of mature oocytes found in the oviducts (or even with the maximum number, see Fig.2), it may be deduced that a female should perform several loading and unloading cycles of the oviducts, i.e. several spawnings, to spawn all the oocytes produced.

2) Considering Figure 4, the low correlation between the oviductal and the ovarian load indicates that there is no continuous accumulation of mature oocytes in the oviducts as they leave the ovary. In accordance with the observations by Laptikhovski and Nigmatullin (1992) in ten species of ommastrephidae, those indicated by Coelho (1990) in *Illex illecebrosus*, by Hung Baeg et al. (1993) in *Loligo bleekeri*, and the preliminary observations in *T. eblanae* by the authors (unpublished data), oogenesis halts either prior to or at the same time as the start of vitellogenesis. Therefore, before female reaches active sexual maturity, the oocyte production halts. Thus, if only one terminal spawning occurs, the mature oocytes produced by the ovary should accumulate in the oviducts until spawning is performed. During this process, the ovarian load decreases due to the lack of production of new oocytes. In this case, the correlation between oviductal load and ovarian load would be quite high. Therefore, the low

correlation found between both parameters is another indication of the existence of several spawnings.

3) An important indication is related with the sizes of oocytes present in the ovary and oviducts of mature females (Figure 3 & 6). Oocytes of all sizes have been found in the ovaries of these females (Fig. 6). The relatively small oocytes, which have still not finished vitellogenesis, were particularly abundant. The size distribution in Figure 6 is perfectly in accordance with the observations by Harman et al., (1989) in females of *S. oualaniensis*, and is also comparable to oocyte sizes found by Hastie et al. (1994) in the ovary of a mature female *T. eblanae*. Nevertheless, only mature oocytes were found in the oviducts, with relatively homogeneous sizes (Fig. 3). This diference in oocyte sizes between ovary and oviducts indicates that maturation of oocytes may occur between spawnings. If no inter-spawning maturation occurs, most of the oocytes present in the ovary of a mature female would be large sized mature oocytes (or RF would be much higher than the observed). Therefore, it can be concluded that this species performs several spawnings with maturation of oocytes between them, this process perfectly adjusting to the mechanism defined by Harman et al., (1989) as a multiple spawning.

4) Comparing Figure 5 with the RAF estimations, it may be deduced that most of the females represented in that figure (all of them mated, females IVb) had previously released part of their oocytes, while still preserving another fraction of them. This is another sign of multiple spawning.

5) Figure 7 shows the index of thickness of the nidamental gland in relation to oviduct weight. The high correlation observed appear to suggest that the thickness of the nidamental glands depends on the weight of the oviducts or, in other words (see Figure 2), that it depends on the number of mature oocytes in the oviducts. The nidamental glands are responsible for producing the gelatinous mass surrounding the eggs during spawning (Arnold and Arnold, 1977; Guerra, 1987). Therefore, it may be expected that these glands will be subjected to cycles of loading and unloading at the same time as those of the oviducts. A very similar phenomenon was observed by Young and Nixon (fide Mangold, 1987) when they found a high positive correlation between the volume of oocytes in the oviducts and the volume of nidamental glands of *Sthenoteuthis oualiensis*. Apparently, in that study, the nidamental glands increased their mass while the oviducts were filling up, and decreased after producing the egg mass, i.e. the same phenomenon as Figure 7 appears to imply. This would be a further indication of multiple spawning.

To complete the picture of the type of spawning of *T. eblanae*, although it appears to be clear that it is multiple, little more can be said as to the number of spawnings (except that there must be a minimum of four, according to what may be implied from dividing the RAF by the maximum load observed in the oviducts), and nothing may be added as to the frequency of the spawnings, the number of oocytes comprising each spawning, or the length of the period of functional maturity.

The percentage of body weight represented by the nidamental glands (6.69 to 16.42%) is

below that calculated by Hastie et al. (1994) in female *T. eblanae* from Scottish waters (7.5 to 27.7%). Despite this difference, and in accordance with Hastie et al. (1994), it may be considered that *T. eblanae* has the largest nidamental glands (in relative terms) of all the ommastrephidae. In other species of the same family, weight percentages for nidamental glands have been indicated of below 3.5% in *Stenoteuthis oualaniensis* (Harman et al., 1989), below 10% in *Illex argentinus* (Rodhouse and Hatfield, 1990), and around 4% in *Todarodes sagittatus* (Joy, 1990). As previously indicated, the fecundity of *T. eblanae* is possibly the lowest of all the ommastrephidae. So, it may be considered that these big nidamental glands are a "response" to the low number of eggs, ensuring them a greater protection than that of other ommastrephids, which release far greater number of eggs, although having much smaller nidamental glands.

Female *T. eblanae* are mated in the buccal membrane, preferably in the ventral area, where a variable number of spermatophores is fixed. Sperm is transferred to buccal pouches (6-8), which are also located in the ventral part of the buccal membrane (Mangold, 1987; Joy, 1989; author's observations). Nothing is known about the existence of courtship prior to copulation, nor of how mating occurs. Mature male *T. eblanae*, apart from having the distal part of the 4th right arm hectocotylized (with lamellae), have several hard and dark structures (7-9 in each arm) in the proximal portion of both 4th arms, in the shape of nails or spurs, called "cirrated lappets" (Naef, 1923; Adam, 1952; Roper et al., 1984; Guerra, 1992). *T. eblanae* is the only cephalopod having these "lappets" and, although it may be assumed that they have some function during courtship and mating, their concrete function is unknown.

Since the results obtained in this study indicate that females perform several spawnings (and the males of this species are also able to copulate several times, unpublished data), it may be assumed that each spawning of an egg mass is followed by a new copulation, as indicated by Laptikhovski and Nigmatullin (1992) for *Illex argentinus*.

Among the ommastrephidae, there appear to exist two distinct patterns as regards the time when mating occurs.

1) In *Todarodes pacificus*, as observed by Ikeda et al., (1993), the males copulate with immature females, and is the mating which gives rise to maturation (start of vitelogenesis) in the females.

2) In the genus *Illex*, as observed by Durward et al. (1980) for *Illex illecebrosus*, Laptikhovski and Nigmatullin (1992) for *I. argentinus* and González (1994) for *I. coindetii*, males only copulate with mature females, i.e. females with mature oocytes in their oviducts. In this case, it is the maturation of the females which gives rise to copulation, unlike in the previous case.

In *T. eblanae* from Galician waters, evidences of mating have only been found in mature females (unpublished data), and not all mature females were mated (86.1%). In waters off the coasts of Scotland, it was even rare to find evidences of mating in the mature females of *T. eblanae* (Hastie et al., 1994). Therefore, it may be concluded that this species follows the second pattern, the one typical of *Illex*, to whose subfamily (Illicinae) it belongs (Guerra,

1994). To discover whether is the female which accepts copulation when mature, or whether is the male which perceives that the female is mature and is available for copulation, or if both phenomena occur, would require direct observations in the natural environment or experiments in aquarium. These observations and experiments would also answer questions which still remain unsolved regarding several aspects of the reproductive strategy of this species. These include the existence of courting, the copulation, the fecundation of mature oocytes, the formation of the egg masses, the frequency and number of spawnings and copulations, the amount of oocytes in each spawning, the embryonic development, and the morphology, ecology and behaviour of the paralarvae.

ACKNOWLEDGEMENTS

LITERATURE CITED

ADAM, W., 1952. Résultats scientifiques des expéditions océanographiques belges dans les eaux côtières africaines de l'Atlantique Sud (1948-1949), Céphalopodes. *Bulletin du Musée royal d'Histoire naturelle de Belgique*, 3(3): 142 pp.

ARNOLD, J.M. & WILLIAMS-ARNOLD, L.D., 1977. Cephalopoda: Decapoda. In: *Reproduction of marine invertebrates* (Eds.: Giese, A.C. & Pearse, J.S.,), 4: 243-290. Academic Press, New York.

BOLETZKY, S.W., 1975. The reproductive cycle of Sepiolidae (Mollusca: Cephalopoda). *Pubbl. Staz. zool. Napoli*, 39: 84-95.

BOLETZKY, S.v., ROWE, L. & AROLES, L., 1973. Spawning and development of the eggs, in the laboratory, of *Illex coindetii* (Mollusca: Cephalopoda). *The Veliger*, 15: 257-258.

BOYLE, P.R., PIERCE, G.J. & HASTIE, L.C. 1995. Flexible reproductive strategies in the squid *Loligo forbesi*. *Mar. Biol.*, 121: 501-508.

BURUKOVSKY, R.N., FROERMAN, Yu. M. & NIGMATULLIN, Ch. M., 1984. Reproductive biology and scale of maturity stage of the reproductive system of female squid (*Illex illecebrosus*). *NAFO SCR Doc.*, 84/IX/120.

CLARKE, M., 1966. A review of the systematics and ecology of oceanic squids. *Adv. Mar. Biol.*, 4 : 91-300.

COELHO, M.L., 1990. Gametogenesis in the squid *Illex illecebrosus*. *Journal of Cephalopod Biology*, 1(2): 75-99.

DURWARD, R.D., VESSEY, E., O'DOR, R.K. & AMARATUNGA, T., 1980. Reproduction in the squid, *Illex illecebrosus*: first observations in captivity and implications for the life cycle. *ICNAF Sel. Papers*, 6: 7-13

EHRHARDT, N.M., JACQUEMIN, P.S., GARCIA, B.F., GONZALES, D., LOPEZ, J.M., ORTIZ, C. & SOLIS, N., 1983. On the fishery and biology of the giant squid *Dosidicus gigas* in the gulf of California, Mexico. In: *Advances in Assessment of World Cephalopod Resources* (Ed.: J.F. Caddy). FAO Fisheries Technical Papers, 231: 306-340. FAO Fisheries Department.

FIELDS, W.G., 1965. The structure, development, food relations, reproduction and life history of the squid *Loligo opalescens* Berry. *Calif. Dept. Fish & Game, Fish. Bull.*, 131: 1-108.

GONZALEZ, A.F., 1994. *Bioecología de* Illex coindetii *(Verany, 1839) (Cephalopoda: Ommastrephidae) de las aguas de Galicia* . Tesis Doctoral. Universidad de Vigo. 237 pp.

GUERRA, A., 1987. La reproducción en los moluscos cefalópodos. In: *Reproducción en acuicultura* (Eds.: Espinosa de los Monteros, J. & Labarta, U.): 185-216. Plan de formación de técnicos superiores en acuicultura (FEUGA), Madrid.

GUERRA, A., 1992. Mollusca, Cephalopoda. In: *Fauna Ibérica* (Ed: Ramos, M.A.), Vol. 1. Museo Nacional de Ciencias Naturales (CSIC), Madrid.

HARMAN, R.F., YOUNG, R.E., REID, S.B., MANGOLD, K.M., SUZUKI, T. & HIXON R.F., 1989. Evidence for multiple spawning in the tropical oceanic squid *Stenoteuthis oualaniensis* (Teuthoidea: Ommastrephidae). *Mar. Biol.*, 101: 513-519.

HASTIE, L.C., JOY, J.B., PIERCE, G.J. & YAU, C., 1994. Reproductive biology of *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in Scottish waters. *J. mar. biol. ass. U.K.*, 74, 367-382.

HIXON, R.F., 1983. Loligo opalescens. In: *Cephalopod life cycles* (Ed.: P.R. Boyle), 1: 95-114. Academic Press, London.

HUN BAEG, G., SAKURAI, Y. & SHIMAZAKI, K., 1993. Maturation processes in female *Loligo bleekeri* Keferstein (Mollusca: Cephalopoda). *The Veliger*, 36(3): 228-235.

IKEDA, Y., SAKURAI, Y. & SHIMAZAKI, K., 1993. Maturation process of the japanese common squid *Todarodes pacificus* in captivity. In: *Recent advances in cephalopod fisheries biology* (Eds.: Okutani, T., O'Dor, R.K. & Kubodera, T.): 179-187. Tokay University press, Tokyo.

JOY, J.B., 1989. *The fishery biology of ommastrephid squids in Shetland waters*. Master Thesis. Univ. of Aberdeen. 118 pp.

JOY, J.B., 1990. The fishery biology of Todarodes sagitattus in Shetland waters. *Journal of cephalopod biology*, 1(2): 1-19.

KIRKENDALL, L.R. & STENSETH, N.C., 1985. On defining "breeding once". *Amer. Nat.*, 125: 189-204.

LAPTIKHOVSKI, V.V. & NIGMATULLIN, CH. M., 1992. Características reproductivas de machos y hembras del calamar (*Illex argentinus*). *Frente marítimo*, **12** (A): 23-37.

LAPTIKHOVSKI, V.V. & NIGMATULLIN CH.M., 1993. Egg size, fecundity and spawning in females of the genus *Illex* (Cephalopoda: Ommastrephidae). *ICES J. Mar. Sci.*, **50**: 393-403.

LIPINSKI, M., 1979. Universal maturity scale for the commercially important squids (Cephalopoda: Teuthoidea). The results of maturity classification of the *Illex illecebrosus* (LeSueur, 1821) populations for the years 1973-1977. *ICNAF Res. Doc.*, **79/II/38**.

MANGOLD-WIRZ, K., 1963. Biologie des céphalopodes benthiques et nectoniques de la Mer Catalane. *Vie Milieu*, Supplement **13**, 285 pp.

MANGOLD, K.M., 1987. Reproduction. In: *Cephalopod life cycles* (Ed.: P.R. Boyle), **2**: 157-200.

MANGOLD, K.M., 1989. Reproduction, croissance et durée de vie. In: Traité de zoologie (Grassé, P.P., Ed.). Vol. V(4). *Céphalopodes* (Mangold, K.,.Ed.): 493-552. Masson, Paris.

MANGOLD, K.M., YOUNG, R.E. & NIXON, M., 1993. Growth versus maturation in cephalopods. In: *Recent advances in cephalopod fisheries biology* (Eds: Okutani,T., O'Dor, R.K. & Kubodera, T.): 697-703. Tokai University press, Tokyo.

NAEF, A., 1923. Die Cephalopoden. Fauna e Flora del Golfo di Napoli, **35**(1) 2: 313-863.

NIGMATULLIN, Ch. M, SABIROV, R.M. & FROERMAN, Yu. M., 1984. Reproductive biology and scale of maturity stage of the reproductive system of male squid (*Illex illecebrosus*). *NAFO SCR. Doc.*, **84/IX/119**.

NIGMATULLIN, CH.M., ARKHIPKIN, A. I. & SABIROV, R.M., 1991. Structure of the reproductive system of the squid *Thysanoteuthis rhombus* (Cephalopoda: Oegopsida). *J. Zool. London*, **224**: 271-283.

O'DOR, R.K., 1983. Illex illecebrosus. In: *Cephalopod life cycles* (Ed.: P.R. Boyle), **1**: 175-199. Academic Press, London.

O'DOR, R.K., BALCH, N. & AMARATUNGA, T., 1982. Laboratory observations of midwater spawning by *Illex illecebrosus* . *NAFO SCR Doc* **82/VI/5**: 7 pp.

O'DOR, R., K. & BALCH,N., 1985. Properties of *Illex illecebrosus* egg masses potentially influencing larval oceanographic distribution. *NAFO Sci. Coun. Studies*, **9**: 69-76.

O'DOR, R.K. & WELLS, M.J., 1987. Energy and nutrient flow in cephalopods. In: *Cephalopod life cycles* (Ed.: P. R. Boyle), **2**: 109 -133. Academic Press, London.

OKUTANI, T., 1983. Todarodes pacificus. In: *Cephalopod life cycles* (Ed.: P.R. Boyle), **1**: 201-214. Academic Press, London.

ROCHA, F., 1994. *Aspectos biológicos y ecológicos de* loligo vulgaris *y* Loligo forbesi *(Cephalopoda, Loliginidae) en las costas de Galicia (NW de España)*. Tesis doctoral. Universidad de Oviedo. 240 pp.

RODHOUSE, P.G. & HATFIELD, E.M.C., 1990. Dynamics of growth and maturation in the cephalopod *Illex argentinus* de Castellanos, 1960 (Teuthoidea: Ommastrephidae).

Phylosophycal transactions of the Royal Society of London (B), **329**: 229-241.

ROPER, C.F.E., SWEENEY, M.J. & NAUEN, C.E., 1984. FAO species catalogue. Vol. 3. *Cephalopods of the world*. An annotated and illustrated catalogue of species of interest to fisheries. *FAO Fish. Synop.*, **125**(3): 277 pp.

SAUNDERS, B.W., 1984. *Nautilus* growth and longevity: evidence from marked and recaptured animals. *Science*, **224**: 990-992.

SOEDA, J., 1956. Studies on the ecology and the breeding habits of the squid, *Ommastrephes sloani pacificus* (Steenstrup). *Bull. Hokkaido Reg. Fish. Res. Lab.*, **14**: 1-24.

WELLS, M.J. & WELLS, J., 1959. Hormonal control of sexual maturity in *Octopus* . *J. Exp. Biol.*, **36**: 1-33.

Figure 1: Map of the area sampled
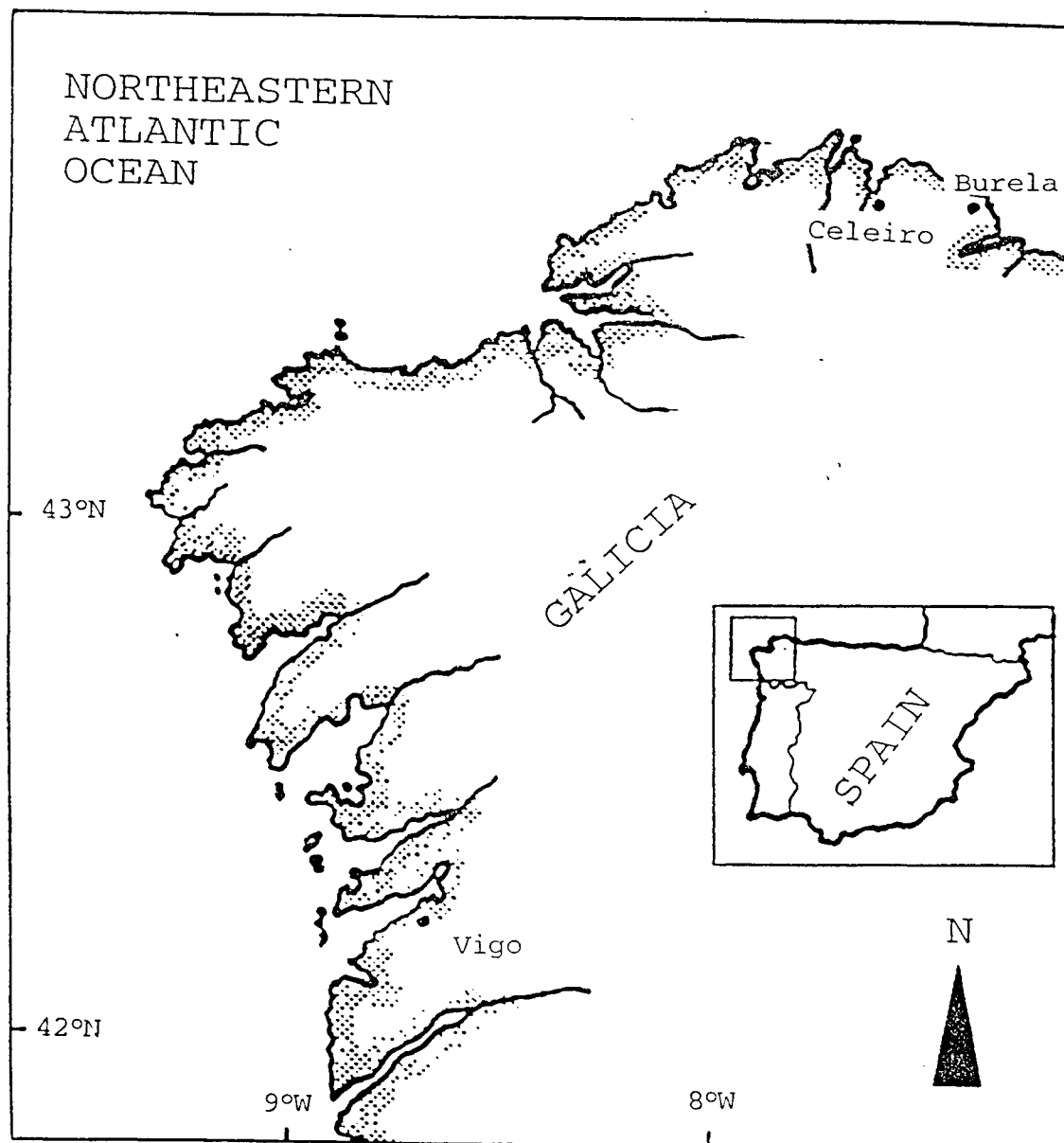
Table 1: Estimates of potential fecundity, residual load and real approximate fecundity (RAF). Sd= standard deviation. n = Number of females used in the estimates.

	Average	Sd	Range	n	DML Range (mm)
Potential fecundity	124,397	18,069.4	99,979] 143,792	8	131-196
Residual load	2,268	2,710.1	0-6,968	6	141-198
RAF	122,129	18,271.5			

Figure 2: Mature females: oviductal load in relation to the weight of both oviducts.
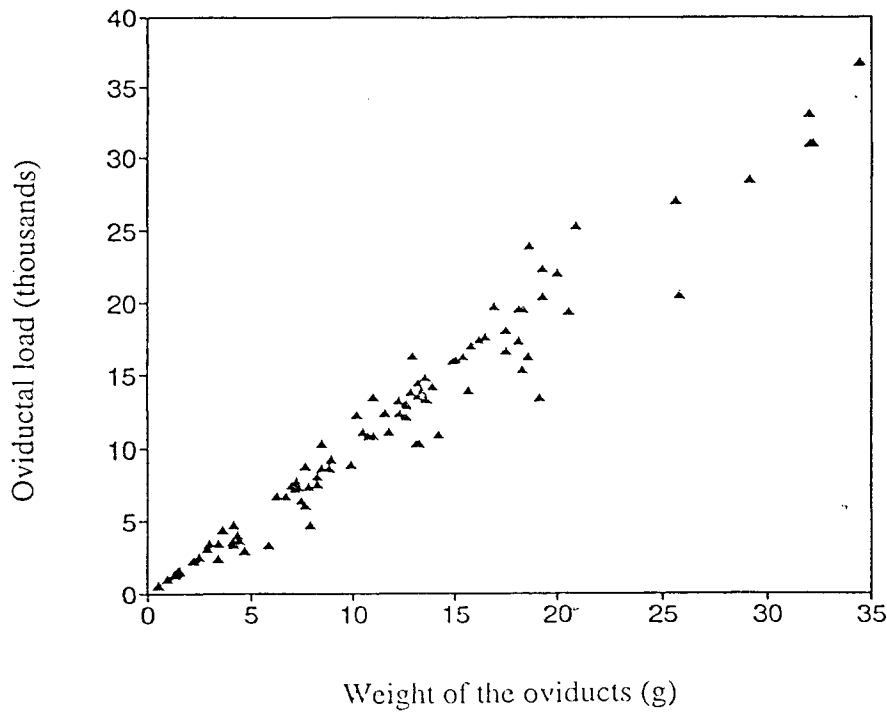
FIGURE 3: Size distribution of mature oocytes found in the oviduct samples of 6 mature females. The number of oocytes measured in each sample was 40. Each of the sections in each column represents the size distribution (as a percentage) in each of the six samples.
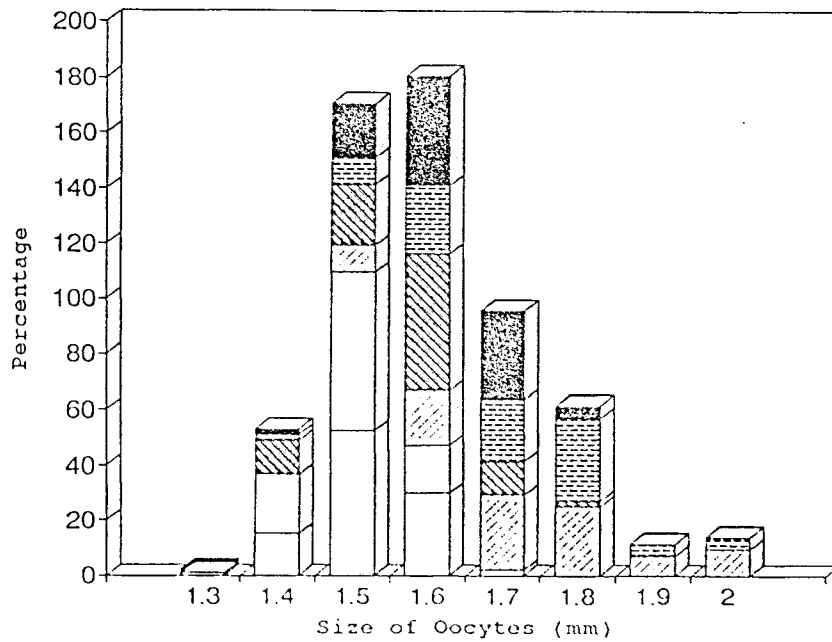
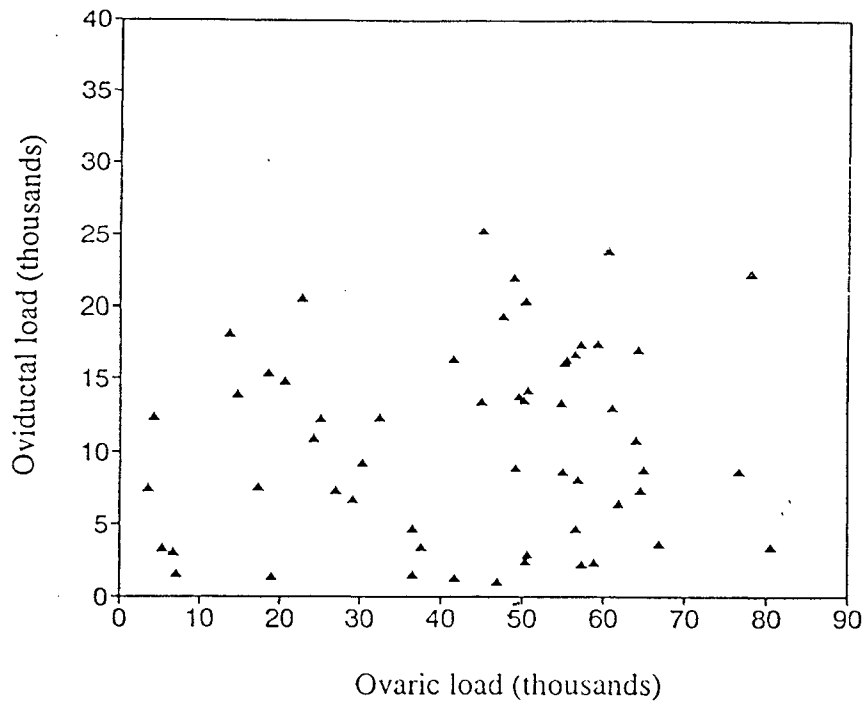Figure 4: Illustration of the oviductal load in relation to the ovarian load of mature females.

Figure 5: Illustration of the total load in relation to the DML in mature females.
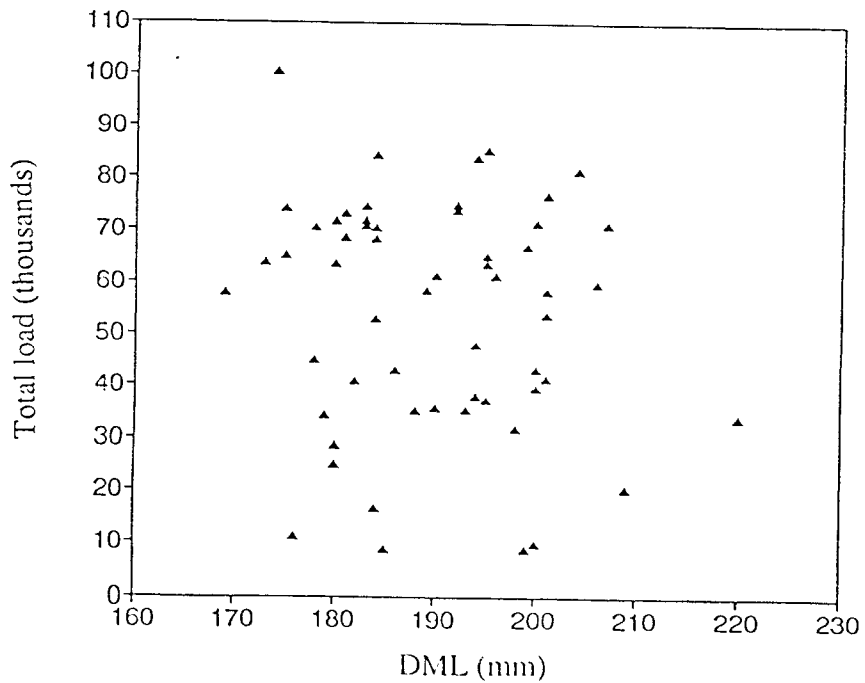
FIGURE 6: Size distribution of oocytes found in the ovary samples of six mature females. The number of oocytes measured in each sample ranged from 108 to 127. Each of the sections in each column represents the size distribution (as a percentage) in each of the six samples.
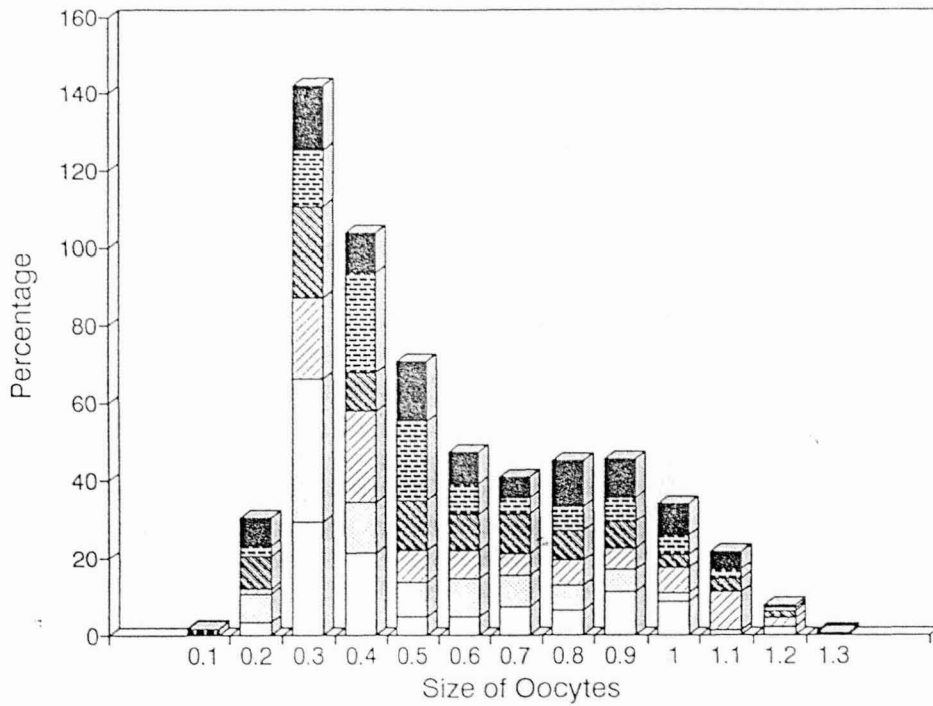

FIGURE 7: Illustration of the index of nidamental gland thickness (NGT) in relation to the weight of the oviducts.