SCIENTIA MARINA

Some aspects of the biology of *Todarodes sagittatus* (Cephalopoda: Ommastrephidae) from the Balearic Sea (Western Mediterranean)*

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SUMMARY: A total of 346 individuals (152 males and 194 females) of *Todarodes sagittatus* caught by commercial trawlers working down to 800 m in the Balearic Sea (Western Mediterranean) was studied. Data are presented on size frequency distributions, length-weight relationships, and relationships between mantle length and various measurements of the beak. Some aspects of the reproductive biology (maturity and gonad development) were also determined. Reproductive period could be situated in the second half of the year, since the number of mature individuals was maximum from July to October for males and from September to December for females. The sex ratio was found to be significantly different from 1:1 only outside this second semester. No individual appeared in hauls performed below 100 m depth and the greatest frequency of appearance was between depths of 400 and 800 m. All mature females were caught deeper than 500 m, indicating that spawning could take place from this depth. The mean mantle length increased with depth, suggesting a possible ontogenic migration.

Key words: Cephalopods, *Todarodes sagittatus,* morphometric relationships, reproductive biology, bathymetric distribution, Western Mediterranean.

RESUMEN: ALGUNOS ASPECTOS DE LA BIOLOGÍA DE *TODARODES SAGITTATUS* (CEPHALOPODA: OMMASTREPHIDAE) EN EL MAR BALEAR (MEDITERRÁNEO OCCIDENTAL). – Se han estudiado un total de 346 individuos (152 machos y 194 hembras) de *Todarodes sagittatus* procedentes de barcos arrastreros que faenan hasta 800 m de profundidad en el Mar Balear (Mediterráneo occidental). Han sido analizadas las distribuciones de talla, la relación talla-peso y las relaciones de varias medidas del pico respecto a la longitud total del manto. Se han determinado también algunos aspectos de la biología reproductiva, como la madurez y el desarrollo gonadal. El período reproductor podría situarse en el segundo semestre del año, ya que el número de individuos maduros fue máximo de julio a octubre para los machos y de septiembre a diciembre para las hembras. Solamente fuera de este segundo semestre la proporción de sexos difirió significativamente de 1:1. No apareció ningún individuo en los lances efectuados por encima de los 100 m, y la mayor frecuencia de aparición se encontró entre los 400 y 800 m de profundidad. La totalidad de las hembras maduras fueron capturadas por debajo de los 500 m, lo cual parece indicar que la puesta tiene lugar a partir de esta profundidad. Se ha observado que la talla media del manto aumenta con la profundidad, indicando una posible migración ontogénica.

Palabras clave: Cefalópodos, *Todarodes sagittatus,* relaciones morfométricas, biología reproductiva, distribución batimétrica, Mediterráneo occidental.

INTRODUCTION

The European flying squid *Todarodes sagittatus* (Lamarck, 1798), is an oceanic species broadly distributed throughout the north and north-east Atlantic, in an area stretching from the Barents Sea to Iceland and south to the Bermuda Islands (Nesis, 1987). The species extends east to Madeira and the Canary Islands, and from there along the north-west African coast to latitude 16º-18º N. It also inhabits the Mediterranean Sea (Nesis, 1987). As a result of this vast distribution area, geographic variations have been found between populations of the Atlantic Ocean (Borges 1990, 1995).

The majority of studies concerning *T. sagittaus* have been carried out in waters of the north Atlantic, mainly in Norway and in the Shetland Islands. Thus, Clarke (1966), Wiborg (1972, 1978, 1980, 1981), Wiborg and Gjøsæter (1981), Wiborg and Fossum (1982), Wiborg and Beck (1984), Sennikov and Bliznichenko (1985), Sundet (1985), Joy (1989), Shimko (1989), Borges (1990), Hernández-García (1991, 1995) and Borges and Wallace (1993) analysed the biology and distribution of this species. The diet was studied by Breiby and Jobling (1985) and Hernández-García (1992). Rosenberg *et al.* (1980) and Shimko (1984) determined the age from statoliths. Morphometric variations between populations were analysed by Borges (1990, 1995). The oxygen-binding properties of the blood of *T. sagittatus* and other cephalopod species were studied by Brix *et al.* (1989). Finally, the study of the beak of this species was included in the work of Pérez-Gándaras (1983).

T. sagittatus has been taken for centuries as a by catch in southern European trawl fisheries and exploited in specific jigging fisheries of some northern countries, specially in Norway (Borges and Wallace, 1993). However, the presence of this species in the north-east Atlantic is very irregular, since it invades these waters only during some years (Borges, 1990). In this way, in Norway the more important landings occurred in the early 1980s and, after a dramatic decrease since 1985 and a practical absence since 1990, *T. sagittatus* appeared again in the fishery statistics in 1995 (ICES, 1996).

Although some authors have commented on certain aspects of the biology of *T. sagittatus* in the Mediterranean (Morales, 1958; Mangold-Wirz, 1963), there is not a single specific work concerning its biology in this Sea. Thus, this study is a first attempt to address the lack of knowledge of this
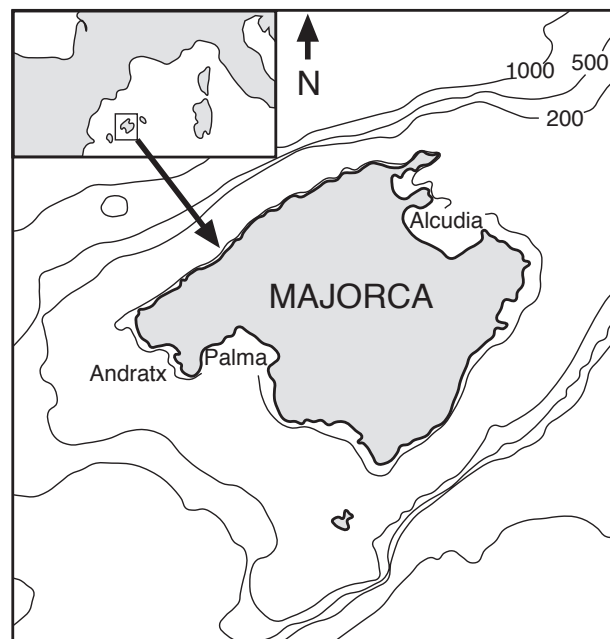

Fig. 1. – Area of study in the present work: the Balearic Sea (Western Mediterranean).

species in Mediterranean waters. For this purpose, length frequency distributions, morphometric relationships, reproductive biology and bathymetric distribution of specimens caught off the Island of Majorca (Balearic Sea, Western Mediterranean) are analysed.

MATERIAL AND METHODS

All the individuals sampled were fished by commercial trawlers off the ports of Andratx, Alcúdia and Palma (Fig. 1). Monthly samples were taken from August 1995 to August 1996.

On board, haul data (date, position, duration, depth and course) were recorded. All the hauls were performed during daytime hours (from 8 a.m. to 4 p.m., approximately). All squids caught in each haul were taken to the laboratory, and the following measurements were noted: mantle length (ML, to the nearest mm), total weight (TW, to the nearest 0.1 g), sex and maturity stage. The beak was also extracted from each individual and it was measured at once.

The parameters of the length-weight relationships were calculated with the power formula $TW = aML^b$. Calculations were made for males and females separately and also by pooling both sexes.

To determine sexual maturity, a three stage scale was used as follows [adapted from Borges and Wallace (1993) and Villanueva and Sánchez (1989)]:

Immature (I): In females that had a very small ovary and thin, transparent nidamental glands. In males with translucent sexual organs and an empty spermatophoric sac.

Maturing (II): In females that had an ovary with a granulate structure and enlarged nidamental glands. In males with a whitish spermatophoric organ and no spermatophores in the spermatophoric sac.

Mature (III): In females with an oviduct full of eggs and very large nidamental glands. In males with the spermatophores present in the Needham's sac.

In order to define a maturity index for females the criterion applied in Durward *et al.* (1979), modified according to Villanueva and Sánchez (1989), was used. In addition to this index (defined as M=(NGL/ML)100) the absolute relationship between mantle length and nidamental gland length was obtained.

To determine the evolution of the sexual organs in the development of the individuals, the nidamental gland length (NGL) for females and the weight of the testis (TestW) and the spermatophoric complex (SC) for males, were also measured.

For males, two methods were used. In the first one, the linear regression relationship between testis weight and total body weight was calculated. In the second one, the following index was used (Brunetti, 1990):

$$\text{gonadal index} = [(\text{TestW}+\text{SC})/(\text{TW}-(\text{TestW}+\text{SC}))]100$$

The normality of this index was tested by the Kolmogorov-Smirnov test and, since it revealed normal distribution (p>0.05), the Student's t-test was used to analyse differences between successive maturity stages. In all the statistical tests applied in this study a significance level (α) of 0.05 was considered.

The length at first maturity (L_{50}) was calculated for both sexes using the Lionor08 programme (J. Lleonart, Institut de Ciències del Mar-Barcelona, unpublished).

The frequency of appearance, defined as the number of samples in which the species was caught in relation to the number of samples taken at each depth, was also calculated.

The linear relationship between mantle length and two beak measurements, upper rostral length (URL) and lower rostral length (LRL) (Clarke, 1986), were obtained for males and females separately. A vernier calliper was used to determine the measurements of the beak to the nearest 0.1 mm.

Finally, in order to follow the evolution of *T. sagittatus* landings, monthly statistics from the total Majorcan fleet were collected from the central fish auction wharf of Majorca.

RESULTS

Size-frequency distributions and length-weigh relationships

A total of 346 individuals (152 males, 194 females) were analysed (Table 1), ranging from 8.1 to 30.7 cm ML in males, and from 11.8 to 41.8 cm ML in females.

Size-frequency distributions of the specimens caught during the period sampled are shown in Figure 2. Although the number of individuals in each

TABLE 1. – Number and weight of individuals of *T. sagittatus* analysed in all the hauls carried out during the year of sampling.

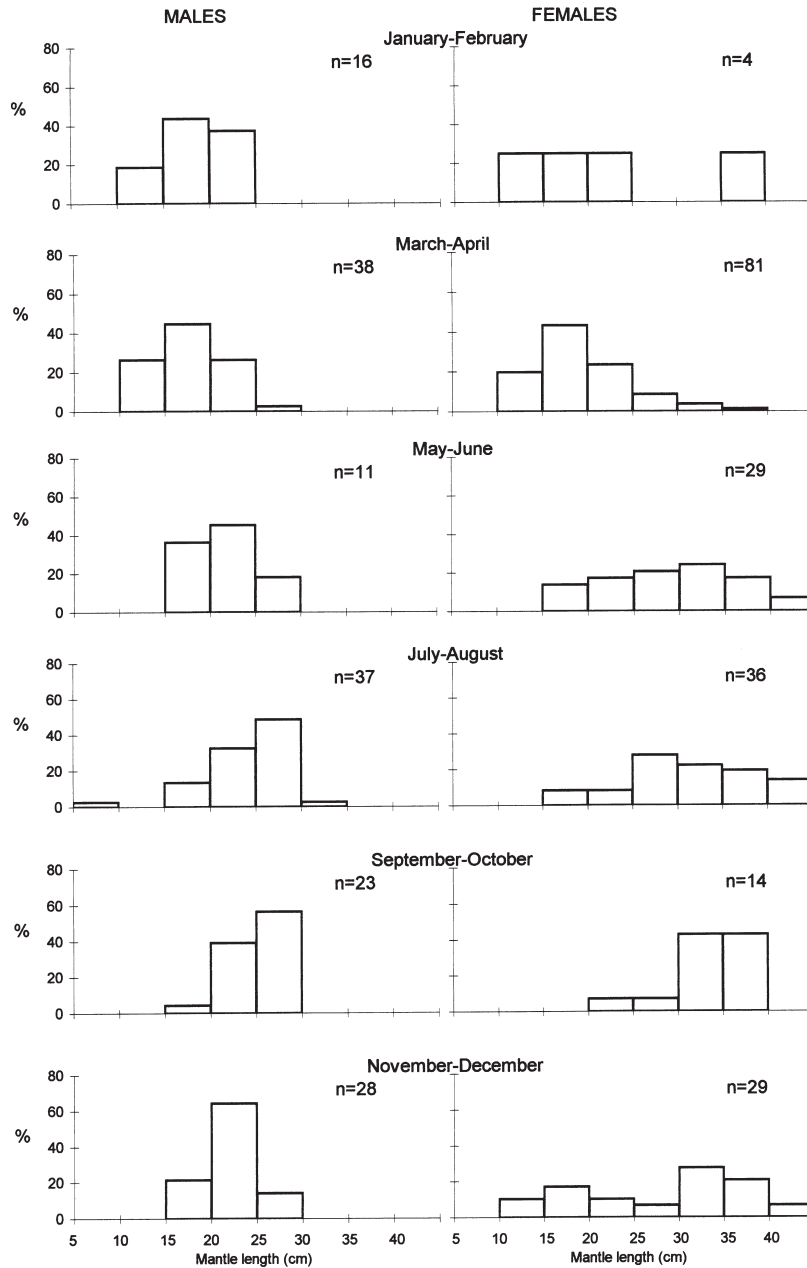| Depth range (m)	Number of hauls	Frequency of appearance (%)	Hours of trawling	Number of specimens	Weight of specimens (g)	Specimens sampled
<100	26	0	48.77	0	0	0
100-200	20	60.0	73.81	38	6327.6	38
200-400	9	55.5	29.00	72	15390.0	72
400-600	14	92.9	105.84	126	83068.5	126
600-800	27	92.6	182.46	110	70266.0	110
Total	96		439.88	346	175052.1	346

MALES   FEMALES

FIG. 2. – Bimonthly size-frequency distributions for both sexes of *T. sagittatus*.

bimonthly period was rather small, some general features were observed. The modal progression of the males could be followed from March-April (15-19 cm ML) to July-August (25-29 cm ML), when they reached their largest size. In the following bimonthly periods (September-October and November-December) size did not increase. For females there was a broad range of sizes during the main part of the year, and thus their modal progression was more difficult to follow. However, it could be noticed that small and medium sized females occurred in the first

half of the year, while the larger ones predominated in the second half (but with the incorporation of small ones in November-December).

The parameters of the relationship between mantle length and total weight for males, females and both sexes together are shown in Table 2. The slopes and the intercepts for each sex were compared (Zar, 1984) and significant differences were observed in both parameters ($p < 0.001$). These differences indicated that females increased in weight faster than males.

TABLE 2. – Parameters of the power relationship, TW=aML^b, between mantle length (ML) and total weight (TW) for males, females and both sexes together of *T. sagittatus*.

Sex	a	b	n	r
Males	0.011	3.282	152	0.987
Females	0.009	3.334	194	0.996
Both	0.010	3.313	346	0.994

The growth in weight was found to be allometrically positive in all three cases. The p-values of the Student's t-test were $0.02 < p < 0.05$ for males and $p < 0.001$ for females and both sexes together.

Sex ratio, maturation and reproduction

The bimonthly variation of the sex ratio is shown in Figure 3. It was found that in January-February males were significantly more abundant than females (Chi-square test, $0.010 < p < 0.025$), while the females predominated in March-April ($p < 0.001$) and in May-June ($0.010 < p < 0.025$). In all other periods, the sex ratio was not significantly different from 1:1 ($0.90 < p < 0.95$ in July-August, $0.10 < p < 0.25$ in September-October and $0.75 < p < 0.90$ in November-December).
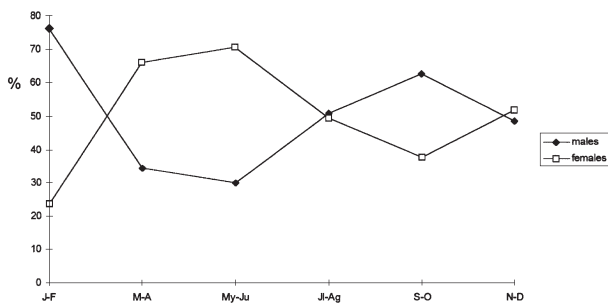
FIG. 3. – Bimonthly variations of the sex ratio of *T. sagittatus*.

In order to determine the evolution of maturity stages throughout the year, the data were analysed bimonthly. The results are shown in Figure 4, for males and females separately. Although mature individuals were present all the year round, the maximum was from July to October for males and from
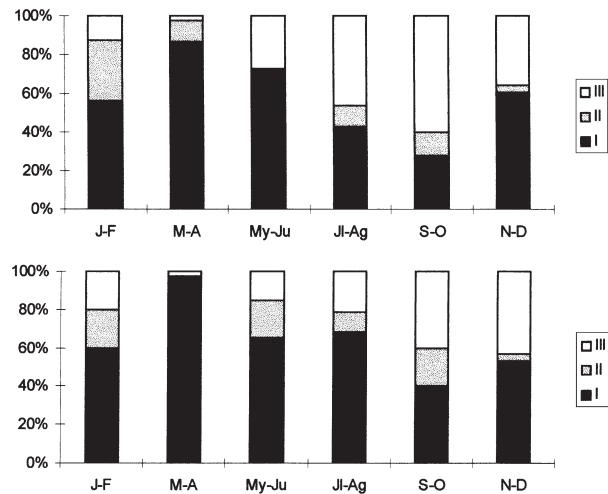
FIG. 4. – Evolution of maturity stages throughout the year for males (A) and females (B) of *T. sagittatus*.
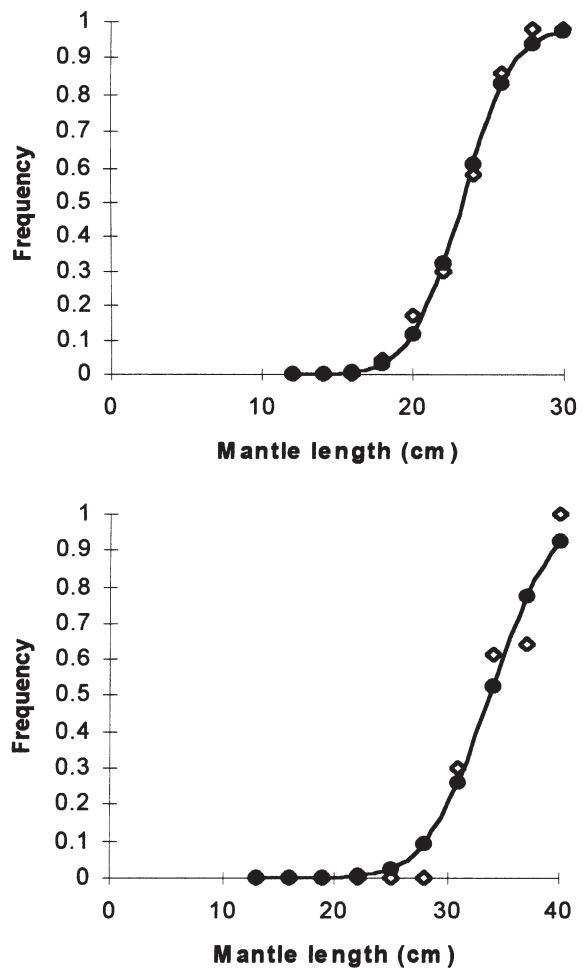
FIG. 5. – Frequency of mature individuals in relation to mantle length for males (A) and females (B) of *T. sagittatus*.

TABLE 3. – Absolute relationship between mantle length (ML) and nidamental gland length (NGL), maturity index (M) (Durward *et al.*, 1979) and size range for the three female maturity stages of *T. sagittatus*.

Maturity stage	ML/NGL	M	Size range (cm)
I	>5.5	<190	11.8-34.5
II	3.0-5.5	190-350	32.1-38.4
III	<3.0	>350	31.8-41.8

FIG. 7. – Relationship between male gonadal index (Brunetti, 1990) and total weght for each of three maturity stages of *T. sagittatus*.

September to December for females. A minimum existed in March-April for both sexes.

The smallest mature male and female analysed were 19.6 and 31.8 cm ML, respectively, whereas the length at first maturity was 23.2 cm ML for males and 33.7 cm ML for females (Fig. 5).

Table 3 shows the results of the absolute relationship between mantle length (ML) and nidamental gland length (NGL), the maturity index (M) described above and the size range for the three female maturity stages.

TABLE 4. – Mean, standard deviation and p-values of the Student's t-test between successive maturity stages for the male gonadal index of *T. sagittatus* (Brunetti, 1990).

Maturity stage	Mean	Standard deviation	p
I	1.582	1.007	
			<0.0001
II	2.900	1.190	
			<0.0001
III	4.704	0.974	

The results of the relationship between the gonadal index and total body weight is shown in Figure 7. The mean, standard deviation and p-value of the Student's t-test between successive maturity stages of this index are shown in Table 4. As can be seen, significant differences were found for each pair of successive stages.

Bathymetric distribution

The depth range was divided in accordance with the bathymetric distribution of the fishing grounds in which the trawlers were working. Thus, five strata could be obtained: <100 m, 100-200 m, 200-400 m, 400-600 m and 600-800 m. The frequency of appearance is recorded in Table 1 and, as can be seen, the greatest frequency occurred between 400 and 800 m.

The mean and standard deviation of the mantle length in relation to the stratum sampled are shown in Figure 8, for males and females separately. An increment in size of individuals as depth increased was observed for both sexes. Although small sized
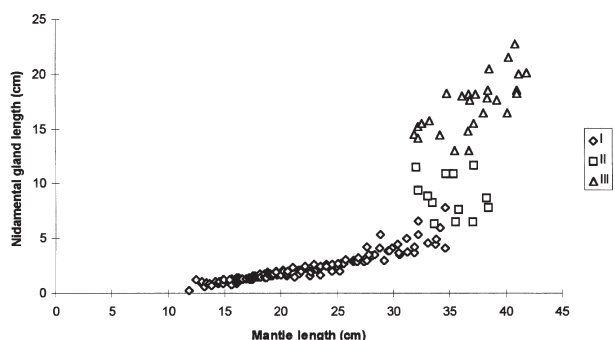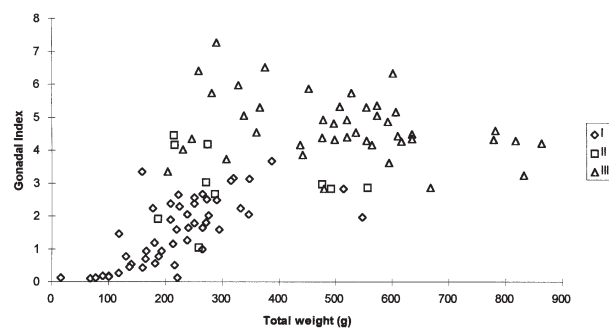

FIG. 6. – Relationship between nidamental gland length and mantle length for each of three maturity stages of *T. sagittatus*.

In immature females the ML/NGL relationship was always higher than 5.5, while in mature female it never exceeded 3.0. For maturing individuals the relationship fell between these values.

Figure 6 shows the relationship between nidamental gland length and mantle length.

For males, the relationship between testis weight and total body weight gave these parameters:

$$\text{TestW} = -1.210 + 0.021\text{TW};$$
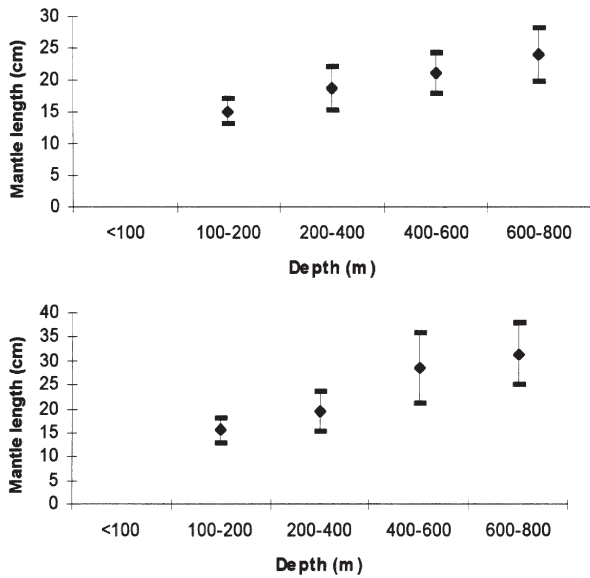$$\text{with } n = 122 \text{ and } r = 0.923$$

FIG. 8. – Mean and standard deviation of mantle length for each stratum sampled for males (A) and females (B) of *T. sagittatus*.

TABLE 5. – Size range for the mantle length of males and females of *T. sagittatus* in each stratum sampled.

Depth range (m)	Males	Females
100-200	12.3-19.0	11.8-22.5
200-400	13.3-25.1	12.4-32.1
400-600	11.0-27.8	15.4-41.0
600-800	8.1-30.7	15.4-41.8

specimens were caught in hauls carried out at the deeper strata, no large sized individuals appeared in the shallower depths, which could explain the increase of standard deviation with depth mainly in the case of females. In order to validate this fact, the largest and smallest sized specimens caught in each depth range are reported (Table 5).

Mantle length-beak measurement relationship

The linear regression relationships between mantle length and upper and lower rostrum length (URL and LRL, respectively) were analysed for each sex separately. The intercepts and slopes of each pair of measurements were compared between sexes and, although no significant differences were observed between elevations ($0.20<p<0.50$ for URL and

TABLE 6. – Parameters of the relationship between two beak measurements (URL and LRL) and mantle length (ML) for males, females and both sexes together of *T. sagittatus*. (URL = a + bML and LRL = a + bML).

Beak measurement	Sex	a	b	n	r
URL	Males	-0.904	0.033	100	0.971
	Females	-1.393	0.034	140	0.984
	Both	-1.244	0.034	240	0.982
LRL	Males	-0.918	0.031	100	0.965
	Females	-1.323	0.032	140	0.985
	Both	-1.205	0.032	240	0.982

$0.10<p<0.20$ for LRL), the slopes differed significantly ($0.01<p<0.02$ for URL and $0.005<p<0.01$ for LRL).

The parameters of the relationships were calculated separately for each sex (Table 6) and the relationship of both sexes together is also given for the cases when a specimen could not be sexed (e.g. stomach contents studies).

Fishery

At the central fish auction wharf of Majorca statistics of *T. sagittatus* were not available until June 1993, before which all squid species were
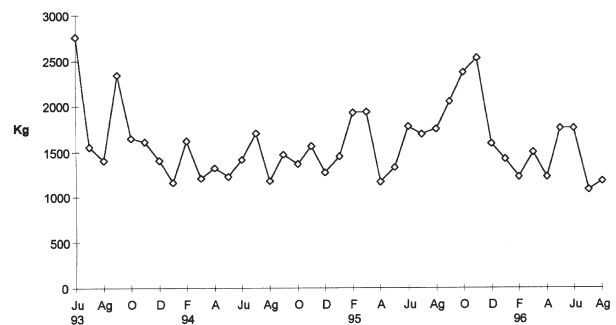

FIG. 9. – Monthly landings of *T. sagittatus* of the Majorcan trawl fleet from June 1993 to August 1996.

pooled together in the 'Squids' category. Monthly statistics for the total landings of the Majorcan trawl fleet are shown in Figure 9. As can be observed, there was no monthly fluctuations throughout the period considered. On the other hand, and owing to the short period available, it was not possible to determine if there were yearly variations in the catches.

DISCUSSION

In the Mediterranean Sea the ommastrephid squid *Todarodes sagittatus* is caught as a by-catch by trawlers working on the continental slope, usually between 200 to 800 m. Catches of the squid are more important in Italian and Grecian waters than in the Spanish waters (Mangold and Boletzky, 1987). In the Balearic Sea this species is mainly fished by those ships of the trawl fleet which target the red shrimp (*Aristeus antennatus*) and the Norway lobster (*Nephrops norvegicus*). The results obtained in this study concerning the abundance of this squid in the Mediterranean are in accordance with Mangold-Wirz (1963). Although this species is caught all the year round, the number of individuals in each haul is usually very low (Table 1). However, a shoal containing an important number of specimens can be fished in some cases. As an example, a haul with fifty-four squids was fished on one occasion. In this case, a shoal of *Lepidopus caudatus* was also taken and the stomach contents of the squids revealed that they were hunting the fishes (Quetglas, pers. obs.). As can be observed from these results, *T. sagittatus* usually seems to live in groups of very few individuals, even alone (Moiseev, 1991), rarely forming shoals containing important numbers of individuals. However, it could also be argued that trawling was not a good gear for fishing this species. In this way, the scarcity in trawl catches lead Joy (1989) to suggest that *T. sagittatus* would be caught off the bottom. The observations of this squid 2-10 m above the bottom (Moiseev, 1991) seems to emphasize this suggestion. Consequently, the number of individuals caught would be underestimated, as a result of the sampling method.

Like other ommastrephid squids (Lipinski and Wrzesinski, 1980; Laptikhovskii, 1989) *T. sagittatus* carry out vertical migrations, swimming towards the surface at night (Morales, 1958; Mangold-Wirz, 1963; Moiseev, 1991). However, this last author hypothesized that not the whole population rose to the surface. He could observe that squid were caught on the surface at night and they were simultaneously present in the catches of bottom trawls landed from the depths of 1040-1200 m.

In the Mediterranean Sea *T. sagittatus* could live off the continental shelf, as indicated by the fact that no individual was caught in the hauls undertaken above a depth of 100 m. The greatest frequency of individuals was distributed between 400 to 800 m, since the appearance frequency at this depth was greater than 90%. However, nothing could be indicated about its deepest limit because trawlers do not usually work below 800 m. In the north-western Mediterranean, Villanueva (1992b) did not find this species in samples taken at depths between 1000 and 2000 m. The studies carried out in Norwegian waters indicated that *T. sagittatus* occurs in coastal and bank areas (80-200 m) and even more superficially (20-100 m), as indicated by Wiborg and Gjøsæter (1981). In the North Atlantic Ridge it was observed at a depth of 1947 m (Moiseev, 1991).

As can be seen from Figure 8, the bathymetric distribution of this species is related to size in the Mediterranean, since the mean mantle length of both sexes increases with depth. This situation would be clearer if it was possible to prove that small individuals caught during hauls carried out at great depths were taken while the net was being lifted, as suggested by Villanueva and Sánchez (1989) for *T. angolensis*. This idea would be supported by Laptikhovskii (1989) and Roeleveld (1989), who found out that juveniles of this species inhabited the upper mesopelagic levels, while adults and subadults were associated with the bottom of the continental slope and deeper mesopelagic levels. It can be observed from the results of the present work, that immature individuals inhabit shallower waters and they displace downward during maturation, indicating a possible ontogenic migration. This kind of migration was also observed in *T. angolensis* and seems to be related to the onset of sexual maturity, changes in diet and lower relative growth rates with high individual variation (Villanueva, 1992a).

Very little information exists about the depth of spawing of *Todarodes* species. Clarke (1966) suggests that spawning possibly takes place on the continental slope. Nigmatullin and Laptikhovsky (1994) included *Todarodinae* species in the offshore reproductive strategy, whose spawning occurs usually in the offshore side of western and eastern boundary currents, near the bottom of the shelf and continental slope. Spawning of *T. angolensis* would occur at depths of more than 300 m (Nigmatullin, 1989; Laptikhovskii and Zorikova, 1992). Since in present study all mature females were caught deeper than 500 m, spawning could take place from this depth. These results are in accordance with Shimko (1984), who found three pre-spawning females of *T. sagittatus* at 560 m depth in north-east the Atlantic.

In all the preceeding studies concerning *T. sagittatus,* females were always more abundant than males. Thus, Mangold-Wirz (1963) states that "there is total agreement with all the authors that males are infinitely rarer than females". In all the studies made

in the Northeast Atlantic, males were always scarce, or sometimes totally absent (Wiborg and Gjøsæter, 1981; Wiborg and Fossum, 1982; Wiborg and Beck, 1984; Sundet, 1985; Borges, 1990). In this case, however, a feeding migration occurs from spawning areas, and it is possible that most males do not take part in it (Wiborg and Gjøsæter, 1981). Our results from the Mediterranean Sea showed that, coinciding with the spawning period (from July to December), the sex ratio was always 1:1. This fact would be expected in these months, since aggregation of both sexes would take place. From May to June females were significantly more abundant than males, with males only being predominate over females in January-February. However, the January-February data should be treated with caution because the number of individuals in this period was rather low. These results seem to show that outside the reproductive period males and females live in different habitats. Males probably inhabit waters where trawlers generally do not work, but further studies would be needed to take this possibility into account. In this way, the results obtained by Joy (1989) for *Todaropsis eblanae* could be quoted. This author found significant differences between the sex ratio in trawl and seine net samples, with the male:female ratio of 1:1.38 and 1:0.87 respectively.

Although *T. sagittatus* has a fairly protracted spawning period in the Northeast Atlantic, two main peaks have been found. However, there is no good agreement between authors (Rosenberg *et al.,* 1981; Wiborg, 1981; Wiborg and Gjøsæter, 1981; Sundet, 1985) for the months of spawning, and thus these peaks occur during the winter-spring and summer-autumn periods. Mangold-Wirz (1963) suggests that spawning in the Mediterranean could take place in autumn (September-November). From the results of the present study it can be observed that, despite mature females appearing throughout the year, the reproductive period could begin in June and last until January, although it occurred mainly from September to December. Mature males were also found all the year round, but the greatest frequency began in July-August and lasted until December. Thus, males seem to begin maturation one month before females. The delay in maturation for females is very common in cephalopods. In *T. pacificus,* for example, sexual maturity of males takes place 3-6 months earlier than females (Hamabe, 1962). This delay allows maked females to store spermatangs on the buccal membrane where they remain until the eggs are mature (Mangold-Wirz, 1963).

The smallest mature male and female analysed were 19.6 and 31.8 cm ML, respectively, whereas the length at first maturity was 23.2 cm ML for males and 33.7 cm ML for females.The results for the maturity index of females were similar to those obtained by Villanueva and Sánchez (1989) for *T. angolensis* since, despite overlapping of the mantle length between successive maturity stages, mature females were never smaller than 30 cm ML and immature ones never exceeded 35 cm ML.

The results of the relationship between nidamental gland length and mantle length were also analogous to those obtained by Villanueva and Sánchez (1989). A sudden increase was observed in this relationship when females reached 30-35 cm ML suggested the onset of sexual maturity.

ACKNOWLEDGEMENTS

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