

ON THE BIOLOGY OF THE EUROPEAN FLYING SQUID *TODARODES SAGITTATUS* (LAMARCK, 1798) (CEPHALOPODA, OMMASTREPHIDAE) IN THE CENTRAL EASTERN ATLANTIC

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A total of 206 specimens of the ommastrephid squid *Todarodes sagittatus*, obtained from three areas of the central eastern Atlantic (Canary Islands/African coast, Madeira, and the Gettysburg Bank area south of Portugal) were examined. New information on size, mass, length-mass relationships, reproductive biology, and diet of the squid from a hitherto not very well studied area is supplied. Females dominated the samples (78%) and attained larger size and mass than males. Dorsal mantle lengths of *T. sagittatus* in the Canary Islands/African coast samples and in the Madeira region were similar, 167–348 mm for females and 175–269 mm for males. From the Gettysburg Bank all specimens were immature, females ranging between 71 and 276 mm and males from 98 to 233 mm. Mature females were found mainly during winter and mature males nearly year-round, indicating that they mature earlier than females and at a smaller size. Prey consisted mainly of fish (54.9%), decapods (18.8%) and cephalopods (12.1%). Otoliths and fish bones identified from stomach contents suggest that myctophids were the most common and diverse prey.

The European flying squid *Todarodes sagittatus* (Lamarck, 1798) (Cephalopoda, Ommastrephidae) is one of the most abundant oceanic cephalopods in the Atlantic Ocean and the adjacent Mediterranean Sea (Clarke 1966). It is found from the polar seas in the north to the equator in the south, living in the open ocean and near the coasts, at the surface and near the bottom at depths down to 2 500 m (Nesis 1987). Although its spawning areas are not known precisely, *T. sagittatus* is thought to make extensive spawning and feeding migrations within the whole northern Atlantic (Shimko 1989, Borges and Wallace 1993).

An intense jigging fishery for the species took place periodically during the early 1980s, particularly near the Norwegian coast, when large schools appeared off the coast and in the fjords between June and December (Wiborg and Beck 1984, Sundet 1985). It was also a fairly important bycatch of the redfish fishery near Iceland (Jónsson 1980). In winter, *T. sagittatus* migrates into deeper offshore waters; spawning is thought to take place on the continental slope (Clarke 1966).

In the north of its distributional range, studies have been carried out on the species' biology (Borges and Wallace 1993), morphometrics (Borges 1995), growth (Rosenberg *et al.* 1980) and diet (Breiby and Jobling 1985). However, knowledge of its biology and life cycle is still very poor. This is particularly true for the southern part of its distribution, for which few biological data have been collected. Recently, exploitation rates of oceanic squid species have

increased as beliefs about the large size of some of the resources have developed. However, considerably more scientific information is required before the fishery potential of *T. sagittatus* in the eastern Atlantic can be ascertained with some confidence.

In the present paper, new information on various aspects of the general biology of *T. sagittatus* from 206 specimens collected in several areas of the central eastern Atlantic is documented. Until now most information on *T. sagittatus* in the region has been gleaned from examination of animals taken from its most important predators, such as swordfish (Hernández-García 1995a) and short-finned pilot whales (Hernández-García and Martín 1994). The data considerably expand knowledge of the life cycle of the species in the southern range of its North Atlantic distribution; particular attention is paid to aspects of its reproductive biology because information on that subject is notably scarce.

MATERIAL AND METHODS

The specimens examined were collected in the northern zone of the CECAF (Commission for the Eastern Central Atlantic Fisheries) area (between 37°04' and 14°14' N, Fig. 1). In all, 206 squid, 45 from the Gettysburg Bank/southern Portugal region, 130 from the Canary Islands/African coast and 31

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Fig. 1: Locations of *Todarodes sagittatus* sampling areas (hatched) in the central eastern Atlantic

from Madeira, were studied. According to their origin and the way they were caught, they were grouped into three categories. The first group comprised those taken from 13 catches made with a pelagic Engels trawl (308 mesh, 10-mm mesh in the codend) during a research cruise of the F.R.V. *Poseidon* near the Gettysburg Bank and south of Portugal in June 1994. The second group were animals caught near Madeira by hand-jigging; they were obtained from market samples in July and August 1959. The last group consisted of animals taken as bycatch in the commercial fishery along the coasts of Morocco and Senegal. They were trawled along with the directed catch of benthic cephalopods (*Octopus* and *Sepia*) and crustaceans. A few extra squid caught around the Canary Islands by artisanal fishing are also included in this group. Capture dates of this group were May 1989 – January 1992.

In the total sample were 153 females, 37 males, 12 unsexed specimens and four animals which, owing to

damage to the mantle, arm crown and internal organs, could not be measured in full so were excluded. Dorsal mantle length (*DML* in mm) was recorded for 195 animals, total mass (*TM* in g), eviscerated mass and mantle mass for 193. Stomach contents, beaks and statoliths were extracted and preserved for later examination. The sex of the animals was determined wherever possible and the stage of sexual maturity recorded according to Lipiński's universal scale (Lipiński 1979). The mass of the different organs of the reproductive system (ovary, nidamental glands, oviducal glands, oviducts, testis, etc.) was also recorded. Finally, it was noted when females possessed spermatangia on the buccal membrane.

The following indices were calculated:

- Gonadosomatic index (*GI*) – the ratio between the mass of the reproductive system and the total mass, excluding the mass of the stomach, i.e.

$$GI = \text{mass of reproductive system} / (TM - \text{mass of stomach})$$
- Maturity index (*MI*) – relationships between the masses of the components of the reproductive system. The equations are

$$MI^{(TM)} = (NidG + OvG) / S, \text{ and}$$

$$MI^{(\zeta)} = (Nc + Ss) / S,$$

where *S* includes the mass of the ovary, oviducts, oviducal glands (*OvG*) and nidamental glands (*NidG*) for females; and that of the testis, Needham's complex (*Nc*) and spermatophoric sac (*Ss*) for males.

To study the diet, all food items in the stomach were placed on filter paper to remove the moisture and thereafter weighed. Prey items were identified to the lowest possible taxon. For each stomach examined, counts were made of the number of prey items per category/taxonomic group. An index of the prey's numerical importance *IN* (Castro 1993) was calculated as $\% \text{ importance} = (\% \text{ number} \times \% \text{ occurrence})^{1/2} \times 100$, i.e. the percentage relationship between the number of individuals of each prey category recorded for all stomachs and the total number of individuals of all prey categories.

All regression equations and statistical tests were performed with the software package CSS STATISTICA.

RESULTS

Size and mass

Data on number, sex, size and mass of *Todarodes sagittatus* collected from each of the three areas stud-

Table I: Number, sex (M = male, F = female), mean, standard deviation (SD) and range of dorsal mantle length *DML* (mm) and total mass *TM* (g) of *Todarodes sagittatus* caught in various regions of the central eastern Atlantic

Region	Number	Sex	Variable	Mean	SD	Range
Gettysburg Bank and south off Portugal 34°59'–37°04'N, 8°18'–13°01'W June 1994	14	M	<i>DML</i>	176	41.6	98–233
	14	M	<i>TM</i>	123	73.6	23–241
	19	F	<i>DML</i>	177	56.3	71–276
	19	F	<i>TM</i>	146	127.6	11–468
Madeira 32°30'–33°30'N, 16°00'–18°00'W July – August 1959	9	M	<i>DML</i>	199	15.9	175–220
	9	M	<i>TM</i>	160	29.5	120–205
	13	F	<i>DML</i>	211	32.4	168–263
	13	F	<i>TM</i>	201	84.9	95–335
Canary Islands/African coast 14°14'–27°50'N, 16°47'–17°50'W May 1989 – January 1992	8	M	<i>DML</i>	231	32.1	186–269
	8	M	<i>TM</i>	318	146.2	125–493
	121	F	<i>DML</i>	278	39.7	167–348
	120	F	<i>TM</i>	541	233.9	107–1 156
Whole region 14°14'–37°04'N, 8°18'–18°00'W	31	M	<i>DML</i>	197	39.6	98–269
	31	M	<i>TM</i>	184	119.5	23–493
	153	F	<i>DML</i>	260	54.9	71–348
	152	F	<i>TM</i>	462	262.6	11–1 156
	11	Unsexed	<i>DML</i>	183	35.4	96–225
	10	Unsexed	<i>TM</i>	131	42.9	65–195

ied are summarized in Table I. The largest animals were caught along the coasts of Morocco/Senegal, mainly over the continental slope. Smallest animals were found in oceanic waters near the Gettysburg Bank and south of Portugal. Specimens caught near the Canary Islands during May and June and off Madeira during July and August were similar in size (172–223 mm and 168–263 mm respectively). Males were smaller than females and seemingly more abundant around islands than over the shelf abutting the main land mass.

Sex ratio

Males were always scarce (Table I). Most samples contained female squid (78%), males constituting only 16% of the total number sampled; 6% of the animals remained unsexed due to damage of the internal organs. Near the Gettysburg Bank and south of Portugal, the percentage of males (42%) was much higher than in the other regions.

Length-mass relationships

Pooling the data from all areas, dorsal mantle length *DML* ranged between 71 and 348 mm for females and between 98 and 269 mm for males; total mass *TM* ranged between 11 and 1 156 g for females and between

23 and 493 g for males (Table I). Regression equations for the relationship $TM = a DML^b$ for females and males separately are given in Figure 2. The regression coefficients for the two sexes were similar (Table II). The correlation coefficient β was greater than 0.98 for both sexes, so more than 98% ($r^2 \times 100$) of the variation in mass was explained by the fitted curve.

The masses of the ovary and the nidamental glands increase during maturation. Therefore, specific length-mass relationships for immature ($DML < 250$ mm) and maturing/mature females ($DML > 250$ mm) were also calculated (Table II). The slope coefficient of the curve was greater for maturing/mature than for immature females. The maximum ovary mass was 8.73% of *TM* (Fig. 3a). A similar calculation was not performed for males because the maximum testis mass found was only 1.6% of *TM* (Fig. 3b).

Table II: Equation parameters of the length-mass relationships of *Todarodes sagittatus* (a and b are regression coefficients, β = correlation coefficient)

Sex	Number examined	a	b	β
Males	31	0.0000134	3.086	0.982
Females	152	0.0000120	3.116	0.987
Females <i>DML</i> < 250mm	50	0.0000651	2.787	0.988
Females <i>DML</i> > 250mm	102	0.0000008	3.595	0.915
All specimens	193	0.0000089	3.167	0.987

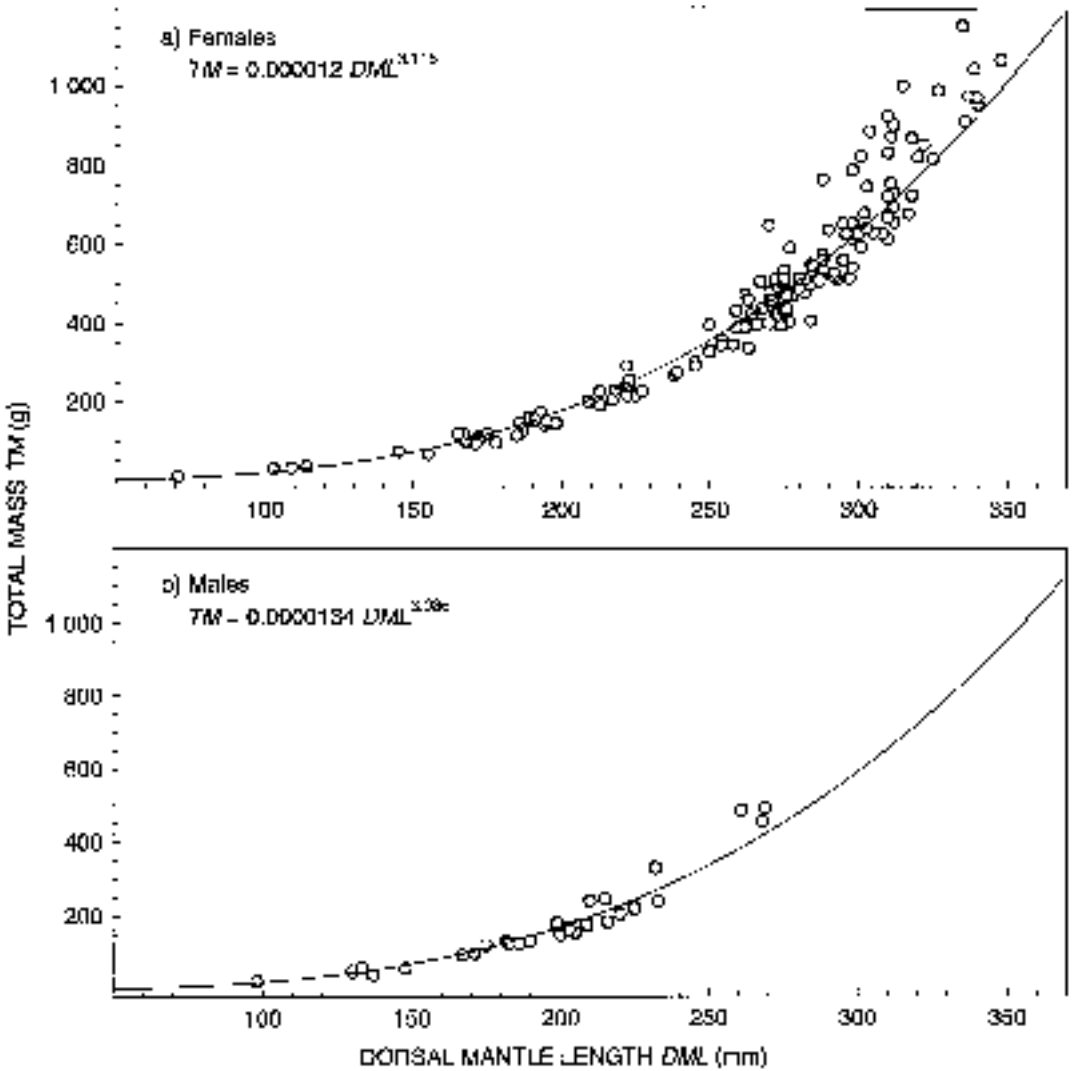


Fig. 2: Length-mass relationships for (a) female and (b) male *Todarodes sagittatus*

Reproductive biology

Although the results are based on a relatively small sample, the following observations can be made. The sex ratio revealed a clear dominance of females (78%). The maturation process in females begins at a DML of c. 220 mm, indicated by the increasing maturity index at that size (Fig. 4a). At a DML of c. 250 mm, the ovary mass starts to increase rapidly (Fig. 3a). The largest ovary mass recorded was 75.7 g. Mature females were more common during winter (Fig. 4a, b). In summer, the maturation process seems to be delayed,

because only very large mature/maturing females with increased ovary mass and a high gonadosomatic index are found (Figs 3a, 4b). Furthermore, mated females were only recorded in winter catches (Fig. 5), and only one spent female, its ovary with a few residual oocytes, its liver small and its mantle loose, thin and shrunk, was recorded near the African coast.

From the rather small sample of males obtained (Table I), it seems that mature males with advanced maturity and high gonadosomatic indices can be caught nearly year-round (Figs 6a, b). The conclusion is that males mature earlier than females, and at a smaller size.

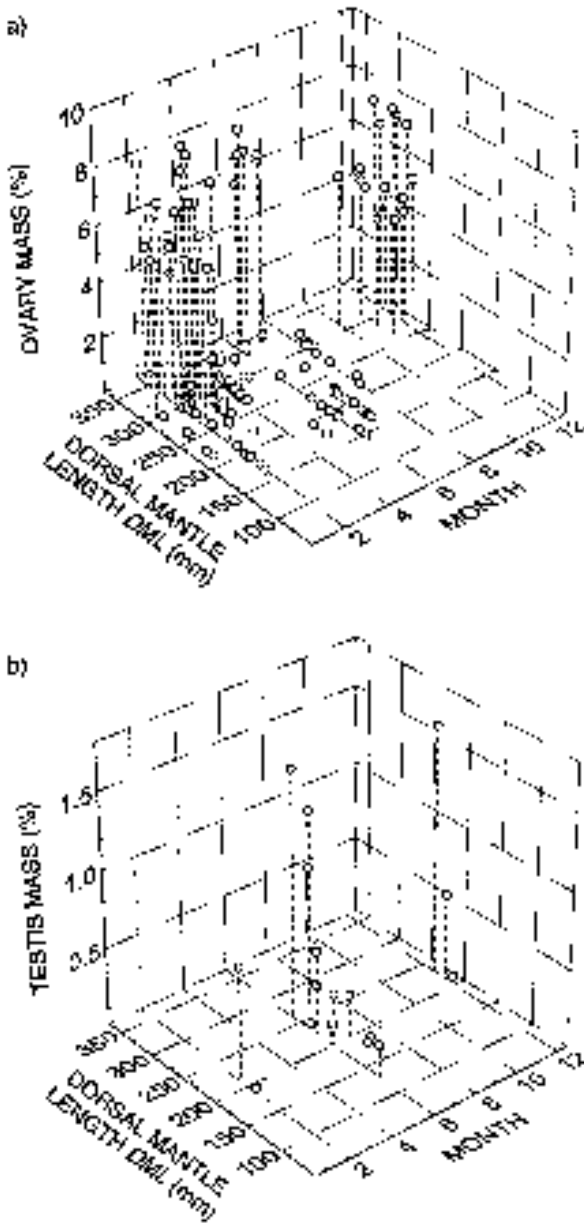


Fig. 3: (a) Ovary and (b) testis mass as percentages of total body mass (excluding stomach mass) in relation to time (month) and dorsal mantle length of *Todarodes sagittatus*

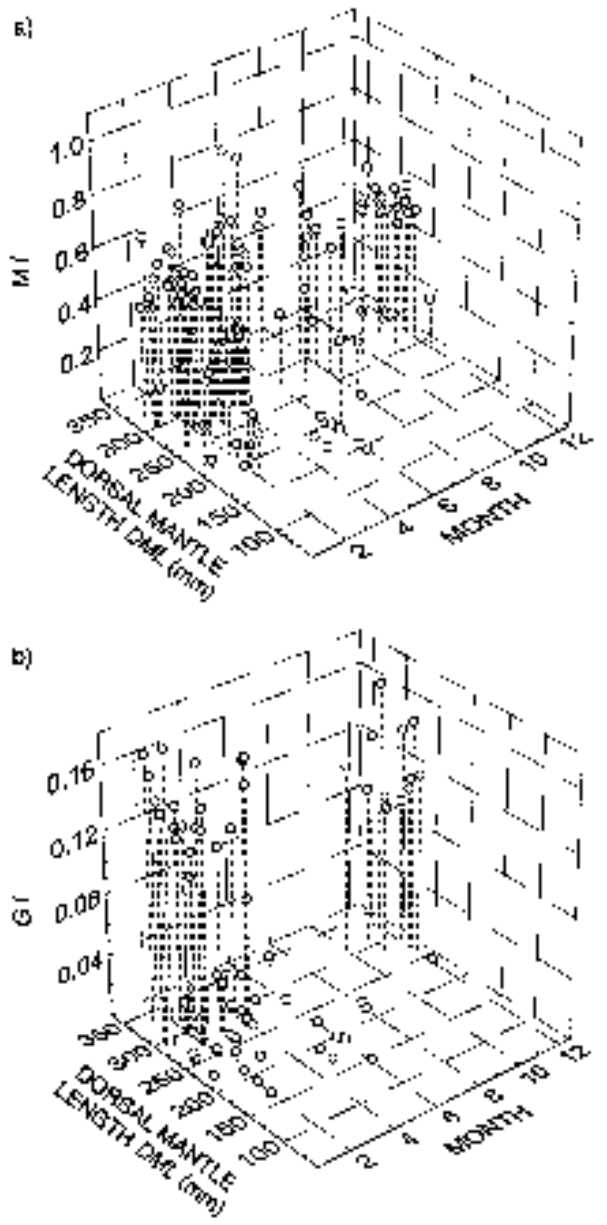


Fig. 4: (a) Maturity index MI and (b) gonadosomatic index GI in relation to time (month) and dorsal mantle length of female *Todarodes sagittatus*

Diet

Identified prey items in the diet of *Todarodes sagittatus* from the Canary Islands/African coast and the

Gettysburg Bank region are summarized in Table III. There are six main taxonomic groups, fish being the most abundant prey ($IN = 54.9\%$), followed by decapod crustaceans (18.8%), cephalopods (12.9%) and euphau-

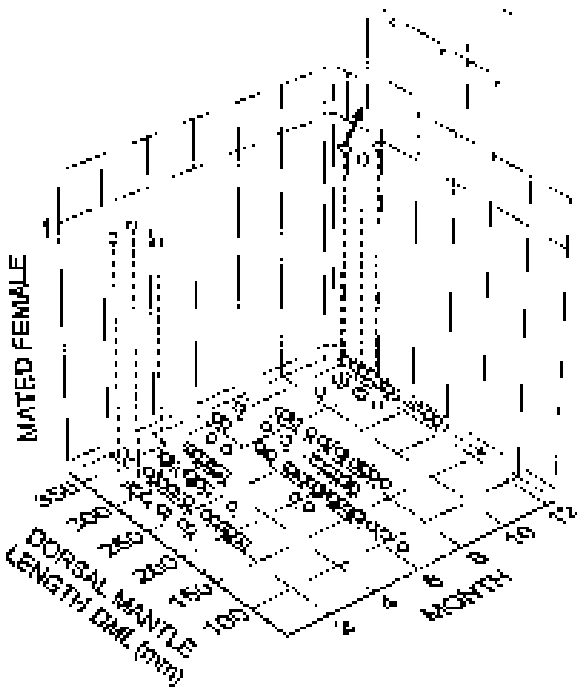


Fig. 5: Time of occurrence (month) and dorsal mantle length of mated female *Todarodes sagittatus*, compared with those of unmated females

siids (12.1%). Isopods and amphipods were of minor importance, both accounting for <1%. A striking observation was the high percentage of euphausiids in the prey of the Gettysburg Bank samples, where *IN* reached nearly 40%. They consisted of at least two species, one belonging to the genus *Thysanopoda*, the other to the genus *Euphausia* (*E. krohni*?). Euphausiids were totally absent from the squid prey around the Canary Islands and off the African coast.

Fish were also the most diverse prey. Otoliths and fish bones identified suggest that myctophids dominated. This family is complex, so prey proved almost impossible to identify to species or even to genus. However, of those identified, *Diaphus* was the most abundant genus (6.8%, Table III). The genus *Lampanyctus* was also found, and, given its known geographic distribution, the species in the stomachs was most probably *L. festivus*. Other unidentified myctophids summarized under the heading Myctophidae indet. in Table III were probably *Ceratoscopelus maderensis*, *Electrona carlsbergi*, *Myctophum* (*M. punctatum*?) and *Symbolophorus* sp., all of which are common in the study area. The subfamily Macrourinae was identified from scales and some otoliths; the genus *Nezumia*

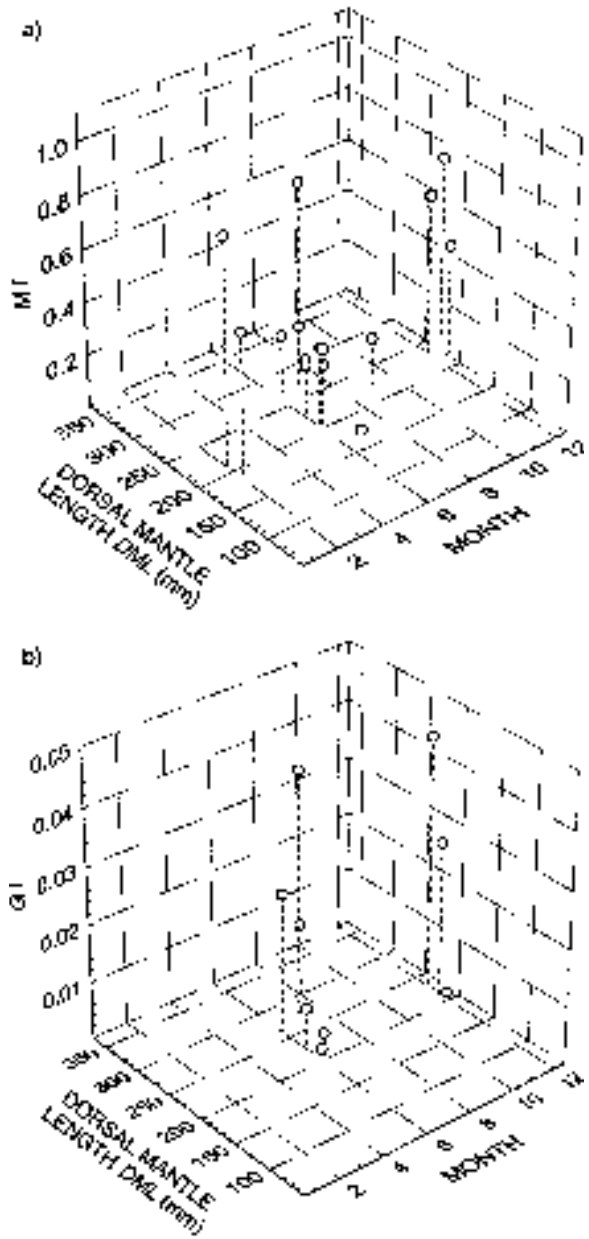


Fig. 6: (a) Maturity index *MI* and (b) gonadosomatic index *GI* in relation to time (month) and dorsal mantle length of male *Todarodes sagittatus*

is thought to have been the taxon found.

Decapod crustaceans belonged to the genus *Plesionika* (represented by three species: *P. martia*, *P. heterocarpus* and *P. edwardsii*). Other decapods in the stom-

Table III: Prey of *Todarodes sagittatus* from the central eastern Atlantic

Prey	Index of numerical importance <i>IN</i> (%)		
	Canary Islands and African coast (<i>n</i> = 74)	Gettysburg Bank (<i>n</i> = 22)	Both regions (<i>n</i> = 96)
Pisces	59.29	45.38	54.87
<i>Diaphus dumerilii</i>	0.84	—	0.57
<i>Diaphus</i> spp.	6.15	7.28	6.20
<i>Lampanyctus</i> sp.	0.84	—	0.57
<i>Hygophum</i> sp.	—	6.30	1.99
Myctophidae indet.	2.51	9.97	5.07
Macrourinae indet.	7.10	—	4.87
<i>Capros aper</i>	1.63	—	1.15
<i>Epigonus telescopus</i>	3.13	—	2.15
<i>Microchirus boscanion</i>	1.67	—	1.15
Teleostei indet.	35.38	21.83	31.16
Euphausiacea	—	38.25	12.06
Isopoda	1.18	—	0.81
Amphipoda	—	1.82	0.57
Decapod crustaceans	22.32	10.92	18.79
<i>Plesionika</i> spp.	1.67	—	1.15
Sergestidae indet.	2.38	—	1.62
Galatheidae indet.	2.51	—	1.72
Decapod crustaceans indet.	15.82	10.92	14.30
Cephalopoda	17.14	3.64	12.90
<i>Sepia</i> sp.	0.84	—	0.57
? <i>Abralia veranyi</i>	—	1.82	0.57
<i>Brachioteuthis</i> sp. 0.84	—	0.57	—
<i>Todaropsis eblanae</i>	0.84	—	0.57
Ommastrephidae indet.	5.86	—	4.02
Cranchiidae indet.	1.67	—	1.15
Oegopsida indet.	7.10	1.82	5.44

achs represented the families Processidae, Palaemonidae (subfamily Palaemoninae) and Pandalidae.

Cephalopods were identified mainly from beaks. Only the ommastrephid *Todaropsis eblanae* could be identified to species, but the genera *Sepia* and *Brachioteuthis* and, in the family Cranchiidae, *Helicocranchia* and *Leachia* were identified.

DISCUSSION

Todarodes sagittatus is a robust ommastrephid of medium size growing as large as 750 mm dorsal mantle length. Clarke (1966) stated that males attain larger size (640 mm *DML*) than females (490 mm *DML*). Wiborg and Beck (1984) found that maturing animals in Norwegian waters are larger (males 360–400 mm, females 370–470 mm *DML*) than maturing animals from the central eastern Atlantic (Figs 4a, 6b), perhaps indicating the existence of different populations. The possible existence of more than one population in the North-East Atlantic was debated by Shimko (1989) and Borges and Wallace (1993), but more recently, Borges (1995), by applying discriminant function analysis to the morphometrics of *T. sagittatus* caught

off Norway, Scotland and Portugal, also suggested the possible presence of different populations in the same area. Samples from the southern range of the species' distribution south of Portugal, however, were not considered in the analysis.

The current data suggest that maturation of female *T. sagittatus* starts at a *DML* of c. 220 mm (Fig. 4a) and that ovary mass increases rapidly from a *DML* of c. 250 mm (Fig. 3a). These values are close to those recorded for *Todarodes angolensis*, the southern congener of *T. sagittatus* which is abundant in Namibian waters, by Villanueva and Sánchez (1989). As in the current data set, those authors found a larger percentage of adult females in their sample. This pronounced difference in the numbers of females and males, females always being more abundant than males, is probably related to the reproductive biology of the species. The present data show that maturity of females peaks in winter, that males reach maturity before females, and that males (though scarce) are found year-round. The hypothesis would therefore be that males spend a considerable part of their life in different habitats from the females. Females can store spermatophores on the buccal membrane for a long time before they reach full maturity and are ready to spawn. This enables them to be fairly independent of

the need for extensive co-occurrence with mature males. The presence of mated females in the samples from the slope off Africa (Fig. 5) indicates spawning areas there. It cannot be excluded, however, that mating itself took place farther offshore and that females migrated inshore thereafter.

Season is suggested to have a strong influence on the maturation process. During summer mature females were not abundant, and mated females were totally absent. These findings agree with those of Wiborg and Beck (1984) and Shimko (1989), who found highly mature animals in the Norwegian Sea mainly in winter. In the present study, young *T. sagittatus* were recorded around the Canary Islands at the beginning of April and around the Gettysburg Bank in June, probably derived from winter spawners. On the other hand, fresh *T. sagittatus* with oviducts full of eggs were sampled from the stomach contents of a short-finned pilot whale found floating dead south-west of Tenerife, Canary Islands, in February 1992 (Hernández-García and Martín 1994). That record suggests that spawning might also take place in early spring.

The results presented here emphasize the fact that reproduction of *T. sagittatus* is not restricted to an area in the central Atlantic over the Mid-Atlantic Ridge and around the Azores, as suggested by Shimko (1989). Mature males and females as well as mated females and one spent female were found along the African coast, south of the Canary Islands, which indicates a spawning population there. Histological evidence of protracted spawning by *T. sagittatus* was not found.

Most of the studies on the feeding biology of *T. sagittatus* have been carried out along the Norwegian coast and around the Shetland Islands (Wiborg and Beck 1984, Breiby and Jobling 1985, Sundet 1985, Joy 1990). They all considered pelagic species to be the main prey. Fish, mostly herring and young gadoids, were most important in those studies, followed by decapod crustaceans, euphausiids and molluscs. Those findings are in accord with the present results. Predominantly benthic feeding was only found in larger squid in the current samples, the fish *Microchirus boscanion* and the cephalopod *Sepia* sp. occurring in stomach contents of squid collected near the African coast. These benthic species are more important in the prey of the ommastrephid squid *Illex coindetii*, which is known to be an active benthic predator along the west coast of Africa (Castro and Hernández-García 1995, Hernández-García 1995b). However, the proportion of benthic prey in squid stomachs is probably much underestimated, because it consists of a high percentage of soft-bodied animals which are not detectable in squid stomach contents.

As squid grow they change their prey spectrum,

something clearly shown in the current samples. The smaller specimens from the Gettysburg Bank took a high proportion of euphausiids, a macroplanktonic crustacean group which was not detected in the squid samples from the Canary Islands/African coast region. Similar results were obtained by Sánchez (1982), who reported that young *Todarodes sagittatus* took more small pelagic prey than the more advanced adult stages. Juvenile and immature squid prey mainly on euphausiids, particularly when these crustaceans form dense concentrations in the surface layers during the night (Rubiés 1976). As squid grow rapidly, they track across a wide range of prey organisms and their diet shifts from small planktonic organisms to larger nektonic animals consisting of myctophids, herring-like fish and young gadoids. To achieve this, the relative size of the squid's brachial crown changes rapidly (Rodhouse and Piatkowski 1995). Similarly the morphology and the relative size of the beaks, which are very efficient tools that can adapt to a changing feeding mode, also change (Hernández-García *et al.* 1998).

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