Some notes on Todarodes sagittatus (Lamarck) with a description of the hectocotylus

by
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In one of his "Notes sur les Céphalopodes" ADAM (1960) gives a survey of what is hitherto known about the so-called "hectocotylus" in the family Ommatostrephidae. The hectocotylus exists only in males and is used in mating, when the spermatophores are removed from the mantle-cavity of the male into that of the female. At first sight it is a rather amorphous organ, developed from the top of the ventral arm, without affecting its general shape. It can reach down to half-way the length of the arm (see below). From ADAM's paper it appears that in *Todarodes sagittatus* (Lamarck) this organ is still almost unknown. As, moreover, the position of the hectocotylus had proved to vary within this group, as in some species it is constantly found either at the right or at the left side, in other species it occurs variably at the right or at the left side, while in again other species it may be present on both sides, it seemed worth while to study the material of *Todarodes sagittatus* present in Dutch museums.

In the present account an enumeration of the specimens in the collections of the Rijksmuseum van Natuurlijke Historie (Leiden) and the Zoölogisch Museum (Amsterdam) is given and remarks are made especially about the characters differing in the two sexes. Moreover a compilation of what is known about the occurrence and the biology is given.

The name *"Ommatostrephes sagittatus"* was used by many authors (e.g. PFEFFER (1912), JAECKEL (1958), MUUS (1959)), but according to ADAM (1939, 1960) this name is not correct and the species should be placed in the genus *Todarodes*. The work of JAECKEL (1958) dealing with all aspects of the group contains a good key to the species of Cephalopoda in the North Sea. Good drawings of the female are given by POSSELT (1891), PFEFFER (1908, 1912), JAECKEL (1958), and by MUUS (1959).

From the data in the literature results that male specimens of *Todarodes sagittatus* are fairly rare and only scantily known. POSSELT (1891) already mentions the lack of males in his anatomical study of the species. In the present list comprising 49 specimens there are

ANNOTATED LIST OF SPECIMENS

All measurements in cm, except for the suckers, of which they are given in mm. Only the lengths of the fourth (ventral) and third arm are given; roughly they are as long as the first (dorsal) and second arm, respectively.

Sex	Date	Locality	Total length of animal including tentacle	Length of mantle (ventral)	Length of fin (ventral)	Outline of mantle at insertion of fin	Outline of mantle (widest part)	Length of right arm IV	Length of right arm III	Length of right tentacle	diameter of largest sucker on right tentacle	M = mature	L = Museum Leiden A = Museum Amsterdam
♀	?	?	103	39	19	22	34	25.5	29.5	50	-	M	L
♀	6-6-1930	Noordwijk	97.5	48.5	22.5	24	31.5	24.5	28.5	41	10	M	L
♀	Easter 1934	Egmond	96	45	20	26	28	23	27.3	40	-	-	A
♀	15-3-1938	Katwijk	95.5	46.5	22	26.5	34.5	25	26	40	-	-	L
♀	1950	?	95	43	21	22.5	30	24	27	41	-	-	A
♀	20-5-1928	Wassenaar	94	43	19.5	19.5	29.5	24	29	42	-	-	A
♀	27-3-1933	Noordwijk	93.5	42.5	21	27.5	34	23	29	42	-	-	L
♀	11-1936	North Sea	93	44	20	23	31	22	27.5	39.5	-	M	A
♀	6-5-1928	Noordwijk/Zandvoort	88	41	19	21	32	23	28	41	9.5	M	L
♀	15-3-1938	Katwijk	86.5	42.5	20	24.5	31	20.5	24.5	35.5	9	M	L
♀	?	?	86	39	17	23.5	35.5	20.5	23.5	35	-	M	A
♀	?	North Sea	85	41	19	20	29	23	25	35	-	M	A
♀	?	N. North Sea	84.5	39.5	21.5	19	28.5	20	25	34	-	M	A
♀	?	N. Sea near Iceland	81.5	38	20	20	27.5	20	24.5	35.5	-	M	A
♀	24-3-1930	's-Gravenzande	81	40.5	20	21.5	28.5	20.5	24	32.5	9	M	L
♀	6-4-1938	Domburg	77	40.5	19	18	26	17.5	20	29.5	-	M	A
♀	11-1961	Zandvoort	75	34	16	18	25.5	17.5	21	33	-	M	A
♀	31-3-1946	Callantsoog	75	35	16.5	17.5	24	17.5	21	33	-	-	A
♀	18-11-1931	Zandvoort	75	32.5	16	23	27.5	19.2	23	36	8	M	L
♀	Autumn 1956	Ijmuiden	74.5	34	16.5	22	27	21	24.5	34	8.5	M	L

♀	7-6-1939	? Skirk	73.5	31	14.5	18	20.5	17	20.	-	-	-	A
♀	21-4-1928	Cocksdorp	71.5	33	16	17	22	16	19.5	29	7.5	-	L
♀	22-2 or 11-4 1939	Huisduinen	70.5	36	17.5	16	21	16.5	19	27.5	9	M	L
♀	?	?	70.5	32	16.5	16.5	23	16.5	20	30	-	-	A
♀	29-4-1951	's-Gravenzande	70	32.5	15.4	16	23.5	19	21.5	30	-	-	L
♀	3-1958	Vere	70	33	16	21	26	17.5	23	30	8	-	L
♀	23-2-1930	Scheveningen/Kijkduin	69.5	32.5	15.5	17	23.5	17	19.5	24.7	7	-	L
♀	2-2-1885	Scheveningen	68.5	36.5	18.5	23	28	18	20	25	8.5	M	L
♀	?	Arctic	68	33	16.5	16.5	19	16	19.5	29	-	-	A
♀	?	Noordwijk	67	32.5	16	14	20.5	16.5	19	28	-	-	L
♀	1880	Scheveningen	67	27	16	22	30	17	22	31	-	-	A
♀	29-4-1936	Noordwijk	65	33	15.7	20	23.5	16	20	27	7.5	-	L
♀	30-4-1928	Terschelling	65	29	12.5	17	22	15.5	18.5	28	-	-	A
♀	? 2-5- 1937	Petten	65	27.5	14.5	13.5	20	15	18	29.3	-	-	L
♀	4-1866	Katwijk	64.5	28	14	15.5	21.5	14.5	17.5	28	7.5	-	L
♀	16-5-1929	Renesse	64.5	28	14	17	21	14	17.5	29.5	7.5	-	L
♀	11-1884	Noordwijk	64	33	15.5	19	24	16	16	23.5	8	M	L
♀	1862	Katwijk	60	27	13.5	18	20.5	16	18.5	27	7.5	-	L
♀	17-4-1955	Noordwijk	59	30	13.5	13	19	12.5	15.5	22.5	-	-	L
♀	12-4-1939	Zandvoort	55	32.5	14.5	14.5	20.5	15.5	17.5	17[2]	-	-	L
♀	?	Domburg	51.5	25	13.5	11.5	16	12	-[1]	18	-	M	A
♀	22-2 or 11-4 1939	Huisduinen	51	27.5	13.5	11.5	16	11.2	11.5	19	8	-	L
♀	?	Mediterranean ?	47	24	12	12.5	19.5	12	14	18.5	-	-	A
♀	11-1961	Zandvoort	-	34	-	-	-	-	-	-	-	-	A
♂	2-5-1937	Castricum	73.5	34.5	16.5	17.5	26.5	15.8	21	31	7	M	A
♂	?	Mediterranean ?	62	31	15.5	16	27	14.1	19	24	7	-	A
♂	6-7-1937	Westgat, Rode Boei	58.7	31	13.5	11.5	22	16	18.5	20	3.5	M	L
♂	10-4-1952	Ameland	53	25	10.5	11	19.5	10[3]	14	22	6	-	A
♂	28-4-1928	Ter Heyden	48	24.5	11	12	16.5	11	13.5	18.5	4.5	-	L

[1]) Organ damaged. [2]) Length of left tentacle 17 cm, of right tentacle 13.5 cm. Both tentacles seem regenerated; there are only two rows of suckers. [3]) Hectocotylus broken off.

five males, this means that females are about nine times more frequent than males. Most of the specimens available were washed ashore on the Dutch coast, only in some cases they were captured in the North Sea. GRIMPE (1925) mentions observations of thousands of specimens of various sizes in the early autumn along the coasts of both northern seas and the Mediterranean. Only rarely sexually mature animals occurred, while there were hardly any males. According to this author the animals did not seem to have had the intention to spawn. In this respect he refers to SARS (1878) and VERRILL (1880), who report that the animals preyed upon herring-shoals and often stranded in large numbers. GRIMPE states the presence of animals washed ashore — which seemed to have gone astray from larger groups — only during the months of August to February along the North Sea shores of N. Germany. In the mating season they seem not to take any food and therefore he assumes later spawning, in the spring or early summer. Spawning would take place in off-shore waters and consequently one would find the larvae there. In contrast with the statements of GRIMPE, KAAS & TEN BROEK (1940) record the occurrence of the species along the Dutch coast throughout the whole year; rarely in summer, most frequent in April. BRUUN (1945) gives data concerning hundreds of animals washed ashore on Iceland in September, 1932, and October, 1939. All his measured specimens were, in contrast to the statements of GRIMPE, of the same age and apparently in their first year. The species would be quite common in late summer and autumn in that region. He also mentions predation on fishes. In June, RUSTAD (1952) observed a large quantity of these squids in a bay near Bergen (Norway), of which he states that many were washed ashore afterwards. About the sex ratio and the state of sexual maturity neither BRUUN nor RUSTAD give any information. Finally JAECKEL (1958) published a lot of interesting facts about the species, next to statements similar to those of the authors mentioned above. He states the occurrence of large groups along the Norwegian coast (e.g., Bergen), mostly in winter (November to March), only single specimens in July and August. Near Scotland they are most frequent in February, along the Dutch coast in April, but here they also occur in May and in winter. He states the absence of the species in the North Sea (Belgium, Holland, N. Germany) in summer, except for some rare, mostly large, specimens. Off the East coast of England the species is common throughout the whole year. He also mentions fluctuating occurrence of the species on the coast of Yorkshire (E. England), the animals being of greatly variable sizes. Penetration into the North Sea would occur both from northern and southern directions. Here they live in depths from 0 to 170 m;

at night they often come to the surface. In other localities they have been captured at depths of up to 1000 m. Spawning was ascertained to occur N.E. of Scotland in July and August. The pear-shaped egg-capsules (30 × 8 mm), containing 12-14 eggs (0.8-1 mm), are pelagical. Larvae are supposed to have been found West of Scotland. Sometimes animals are found as stomach-contents of various fishes. Their age is estimated as up to circa two years. He gives a maximum total length of 150 cm, but POSSELT (1891) and PFEFFER (1912) mention observations of VÉRANY of up to 165.5 cm, by a weight of 12-15 kg.
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As KAAS & TEN BROEK (1940) stated already — and as is shown in the present list — the species occurs along our coast during the whole year. Among the material at hand, there are a fair number of females (17) with well developed ovaries and nidamental glands (serving to envelop the eggs). According to POSSELT (1891) fully developed ovaries and nidamental glands are indicative of sexual maturity. Of ten of these mature specimens the dates of collecting are known; these are in the months of February (1), March (2), April (1), May (1), June (1), November (4). In my opinion these data do not point to a distinct mating season, though this was suggested by many authors for this species and was really ascertained in various related groups. Of some species, however, spawning in different periods is known (cf. JAECKEL, 1958). It seems of interest to mention that in April, the month in which the bulk of our specimens has been collected, there was only one sexually mature female. In males testes and spermatophores are also well developed in the mating season only (cf. BROCK 1882, in *Sepia officinalis* L.). Two of the five males at my disposal possess a well developed spermatophore-sac with spermatophores, which measure 23-25 (—30) × 1 mm; they were collected in May and July. The sexually mature females measure 25-48.5 cm in length of mantle, the males 34.5 and 31 cm.

The species ranges in the N.E. Atlantic Ocean; from Iceland and the White Sea to Madeira and the Azores, and into the Mediterranean. (cf. SARS, 1878; PFEFFER, 1912; GRIMPE, 1925; KAAS & TEN BROEK, 1940; BRUUN, 1945; RUSTAD, 1952; JAECKEL, 1958; MUUS, 1959).

As already mentioned the males are sharply distinguished from the females by having a hectocotylised arm. During my investigations it seemed of interest to search for more external differences between males and females. These appeared, however, to be rather few. Generally in adult animals there is a marked difference in the size of the

sexes. The total length of the females may be up to twice as long as that of the males. The mantles of the females show a widening above the finned portion, which is probably due to the nidamental glands. This widening is less distinct in males (fig. 1). Checking of characters such as the ratio between linear measurements of various body parts (e.g., finned portion in length of mantle), the number of rows of suckers on tentacles and arms, the number of small teeth in the suckers, etc., did not yield satisfactory results. In some cases I found females that were of the same size as males, with suckers up to twice as large in diameter than in the males, never the reverse.

Of the hectocotylised arm of *Todarodes sagittatus*, as far as I know only JATTA (1896) and PFEFFER (1912) give descriptions. JATTA gives an indistinct drawing of the hectocotylus, accompanied by a short description in which he says that the hectocotylisation occurs on the tip of the right ventral arm, so that one-fifth of it undergoes the transformation. According to PFEFFER also the right ventral arm is transformed, in this case one-fourth. The male specimen, of which he gave an ample description, was in a bad condition, accordingly he did not give an illustration of it. The poor statements of KAAS & TEN BROEK (1939) do obviously not refer to a hectocotylised arm (see also ADAM, 1960). In my opinion they studied a female. In all our five specimens, and in those mentioned in the literature, the right ventral arm is hectocotylised. One of our males has the hectocotylus broken off, so it is not included in the following remarks nor in the description. The transformed part covers one-fifth (cf. JATTA) to almost half the length of the arm. In our material the total lengths of the hectocotyli are 3.5, 5.8, 7, and 7.3 cm, taking 31.8, 41.1, 43,7, and 46.2 per cent, respectively, of the total lengths of the hectocotylised arms. This means that the longer the hectocotylus is, the more the percentage of hectocotylisation increases. There is, however, neither a distinct linear relation to the total length of the arm, nor to the total length of the whole animal, nor between these two measurements, as may be seen in the following table. The sexually mature specimens are indicated with M; the lengths are given in cm.

		M		M
length of animal (including tentacle)	48	58.7	62	73.5
length of mantle	24.5	31	31	34.5
length of hectocotylised arm	11	16	14.1	15.8
length of hectocotylus	3.5	7	5.8	7.3
percentage of hectocotylisation	31.8	43.7	41.1	46.2

On the unchanged lower part of the arm there are 12 to 16 pairs of normal suckers, normally inserted on the semiglobular elevations. The suckers slightly decrease in size towards the hectocotylus. On the hectocotylus they are absent, only in one case I found a very reduced

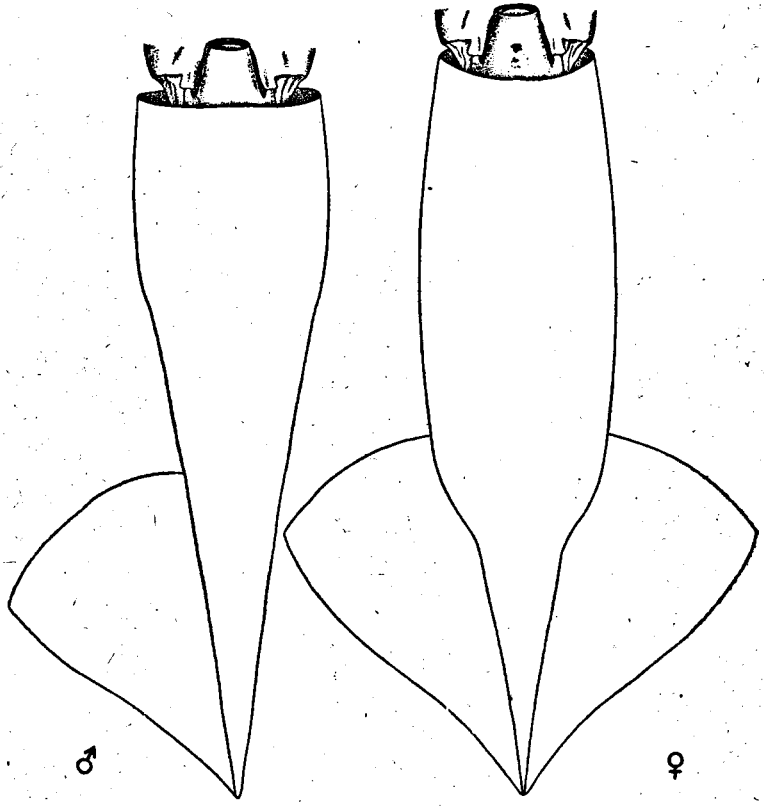

Fig. 1. Differences in outline in the mantles of a male and a female specimen (± 1/3 ×). Diagrammatic after R.M.N.H. Nr. 2699 and 415 (males) and Nr. 585 and 948 (females).

sucker inside the ventral lamella. The spherical elevations on the dorsal side of the arm (R in fig. 2) change into a range of tapering projections, which gradually decrease in size towards the top. These projections are connected by a skin fold, except for their uppermost part. The spherical elevations on the ventral side of the arm (L in fig. 2) continue as un upright longitudinal lamella, with an undulating upper

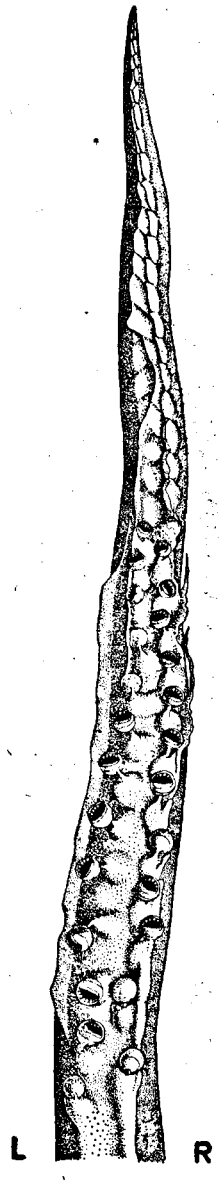

Fig. 2. Hectocotylised arm. (1 ×). After R.M.N.H. No. 2699. L, ventral; R, dorsal side.

edge. This lamella, also tapering towards the top of the arm, is about twice as high as the ridge of projections on the dorsal side. Mainly on the inner region there are transversal thickenings, which are obviously homologous to the elevations below the suckers, since a small rudiment of the sucker remains visible as a very minute tubercle (not visible in the figure). Between this lamella on the ventral side of the arm and the ridge on the dorsal side a zigzag furrow is visible.

Finally I wish to express my gratitude to Mrs. W. S. S. VAN DER FEEN-VAN BENTHEM JUTTING, who offered me hospitality in the Zoölogisch Museum, Amsterdam, and to Dr. C. O. VAN REGTEREN ALTENA (Rijksmuseum van Natuurlijke Historie, Leiden), for various kinds of help.

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SAMENVATTING

De hectocotylus van de inktvis *Todarodes sagittatus* (Lamarck) was tot nu toe vrijwel onbekend, als gevolg van de relatieve zeldzaamheid der mannetjes. Onder de 49 onderzochte exemplaren uit de collecties van Leiden en Amsterdam bevinden zich 5 mannetjes (zie tabel p. 74/75). De hectocotylus, die zich steeds aan de rechter ventrale arm bevindt, is beschreven (fig. 2). Tevens is een overzicht gegeven over het voorkomen van de soort in de Noordzee en werden enkele opmerkingen over de biologie gemaakt. Tenslotte is vastgesteld, dat de uitwendige verschillen tussen de sexen, behoudens de aanwezigheid van de hectocotylus bij de mannetjes, slechts gering zijn (fig. 1).