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Cretan subspecies of
***Metafruticicola nicosiana***
Neubert & Hirschfelder
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# The distribution of Sepiolidae (Cephalopoda) in the Northeast Atlantic Ocean

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A comprehensive survey of the distribution of the Family Sepiolidae of the Continental Shelf of the North Atlantic Ocean was performed, from the Portuguese-Spanish border to Bergen, Norway (42°N to 62,50°N, respectively). Eleven species in six genera were caught: *Sepiola atlantica, S. pfefferi, S. ligulata, S. tridens, Rondeletiola minor, Sepietta neglecta, Sepietta oweniana, Rossia macrosoma, R. palpebrosa, Neorossia caroli and Stoloteuthis leucoptera.* The geographic distribution of each of these species is presented in maps based on sea areas divided into ICES station rectangles of half a degree latitude and one degree longitude. The horizontal distribution and depth preferences of each species were analysed. To aid identification, a brief morphological redescription of each species is provided.

Key words: *Sepiola, Sepietta, Rondeletiola, Rossia, Neorossia, Stoloteuthis*, distribution, NE Atlantic Ocean.

## Introduction

Under the responsibility of the International Council for the Exploration of the Sea (ICES, Copenhagen), fish stocks are surveyed once a year (or twice a year in the Irish Sea and North Sea) in order to assess the population sizes of the different fish species in the Northeast Atlantic Ocean. From 2009 to 2015, specimens of the Sepiolidae encountered during these surveys were included as an official ICES side-catch project. Identifications were performed by the first two authors in Naturalis (Leiden) shortly after the samples had been preserved on board in ethanol 70%. Vouchers of the different species from all ICES rectangles are kept in the Naturalis collection.

The Sepiolidae Leach, 1817, or bobtail squids, are small cephalopods with a dorsal mantle length (DML) up to 80 mm and a sac-shaped body bearing a pair of rounded fins, which are longer than their attachment to the mantle. Most species are of limited commercial use. The best known species is the coastal *Sepiola atlantica* d'Orbigny, 1842 (Fig. 1), which has been the subject of many morphological, anatomical and ecological studies (Yau, 1994; Oesterwind, 2010). An overview of the Northeast Atlantic Ocean sepiolids is given in Table 2.

A first general review of the world's cephalopod resources was prepared for the FAO (Food and Agriculture Organization of the United Nations) by G.L. Voss in 1973. A follow up of a more comprehensive and revised compilation was published in 1984: The FAO Species Catalogue (Vol. 3) *Cephalopods of the World* by Roper et al. It includes 173 cephalopod species of actual or potential fishery interest. Sepiolidae Leach, 1817 were at that time arranged under Sepioidea Neaf, 1912 with 16 species of sepiolids listed worldwide and four of them occurring in the NE Atlantic Ocean.

**Fig. 1.** *Sepiola atlantica* d'Orbigny, 1842.

A revised FAO Species Catalogue (No. 4) was published in three volumes by Jereb & Roper (eds) in 2005-2016, in which the Sepiolidae were reviewed by Reid & Jereb (2005: 153-203). Twenty-eight species of current interest to worldwide fisheries are listed and described; for the NE Atlantic 12 species, each more or less of current fisheries interest: *Sepiola atlantica*, *S. ligulata* (with a question mark), *S. aurantiaca*, *S. pfefferi*, *S. rondeletii*, *Rondeletiola minor*, *Sepietta neglecta*, *S. oweniana*, *Rossia macrosoma*, *Neorossia caroli*, *Heteroteuthis dispar* and *Stoloteuthis leucoptera*.

Hastie et al. (2009: 138-141) listed the cephalopod species of the North-Eastern Atlantic with references to their biogeography, ecology, exploitation and conservation. They listed 8 sepiolid species: *Neorossia caroli, Rossia macrosoma, R. glaucopsis, Rondeletiola minor, Sepietta neglecta, S. oweniana, Sepiola atlantica* and *S. aurantiaca.* Most sepiolid distribution data were previously published by Collins et al. (2001).

Since 2005 we have been involved in sepiolid studies of the North Sea. De Heij & Baayen (2005) reported in their inventory of the North Sea cephalopods: *Sepiola atlantica*, *Sepietta oweniana* and *Rossia macrosoma*. Groenenberg et al. (2009) produced an initial molecular phylogeny of Sepiolidae in the North Sea and reviewed the literature. Oesterwind et al. (2010) reported *Sepiola atlantica* from the northern North Sea, of which all the samples turned out to be *Sepiola tridens* De Heij & Goud, 2010. Goud & de Heij (2011) rediscovered *Rondeletiola minor* from the North Sea (Hoek, 1893). Goud & de Heij (2012) separated *Sepiola pfefferi* (type-locality North Sea) from *Sepiola aurantiaca* (Mediterranean). De Heij & Goud (2013) reviewed the occurrences of *Sepiola atlantica*, *S. tridens*, *S. pfefferi*, *Sepietta neglecta*, *S. oweniana* and *Rondeletiola minor* in the Netherlands and the neighbouring North Sea. Goud & de Heij (2014) reported on the EVHOE (2012, leg. 1) results, in which they listed *Sepiola atlantica*, *S. tridens*, *S. ligulata*, *Sepietta oweniana*, *S. neglecta*, *Rondeletiola minor*, *Rossia macrosoma*, *Neorossia caroli* and *Stoloteuthis leucoptera* from the Bay of Biscay.



| Country | Survey acronyms | Time of the year | Years | Area |
|---|---|---|---|---|
| Denmark | NS-IBTS | half of January - end of February | 2012 - 2014 | North Sea |
| France | NS-IBTS | half of January - end of February | 2009 - 2014 | Eastern part English Channel, North Sea |
| Germany | NS-IBTS | half of January - end of February | 2010 | North Sea |
| Netherlands | NS-IBTS | half of January - end of February | 2009 - 2014 | Eastern part English Channel, North Sea |
| Norway | NS-IBTS | half of January - end of February, 2014 August | 2013 - 2015 | North Sea |
| Scotland | NS-IBTS | half of January - end of February | 2009 - 2010 | North Sea |
| Sweden | NS-IBTS | half of January - end of February | 2010 , 2012 | North Sea |
| Netherlands | BTS | end of august - end of September | 2009 - 2013 | North Sea |
| France | EVHOE | half October - end of November | 2010 - 2014 | Bay of Biscay, Celtic Sea |
| Ireland | IGFS, 2009 IBTS | half October - half of December, 2009 February | 2009 - 2014 | Celtic Sea, Atlantic Ocean West and North of Ireland |
| Spain | POR | September | 2009 - 2011 | Atlantic Ocean, Porcupine Bank |
| Spain | DEM | October | 2009, 2011-2013 | Atlantic Ocean around NW Spain, Bay of Biscay |
| North Ireland | CO1 , CO4 | March , October | 2010 - 2014 | Irish Sea |

**Table 1.** List of the participating countries, the survey's acronym, and time of the year and area of the survey. All the technical collecting data and eco-data such as bottom temperature and bottom salinity are available via the ICES web-site https://datras.ices.dk.

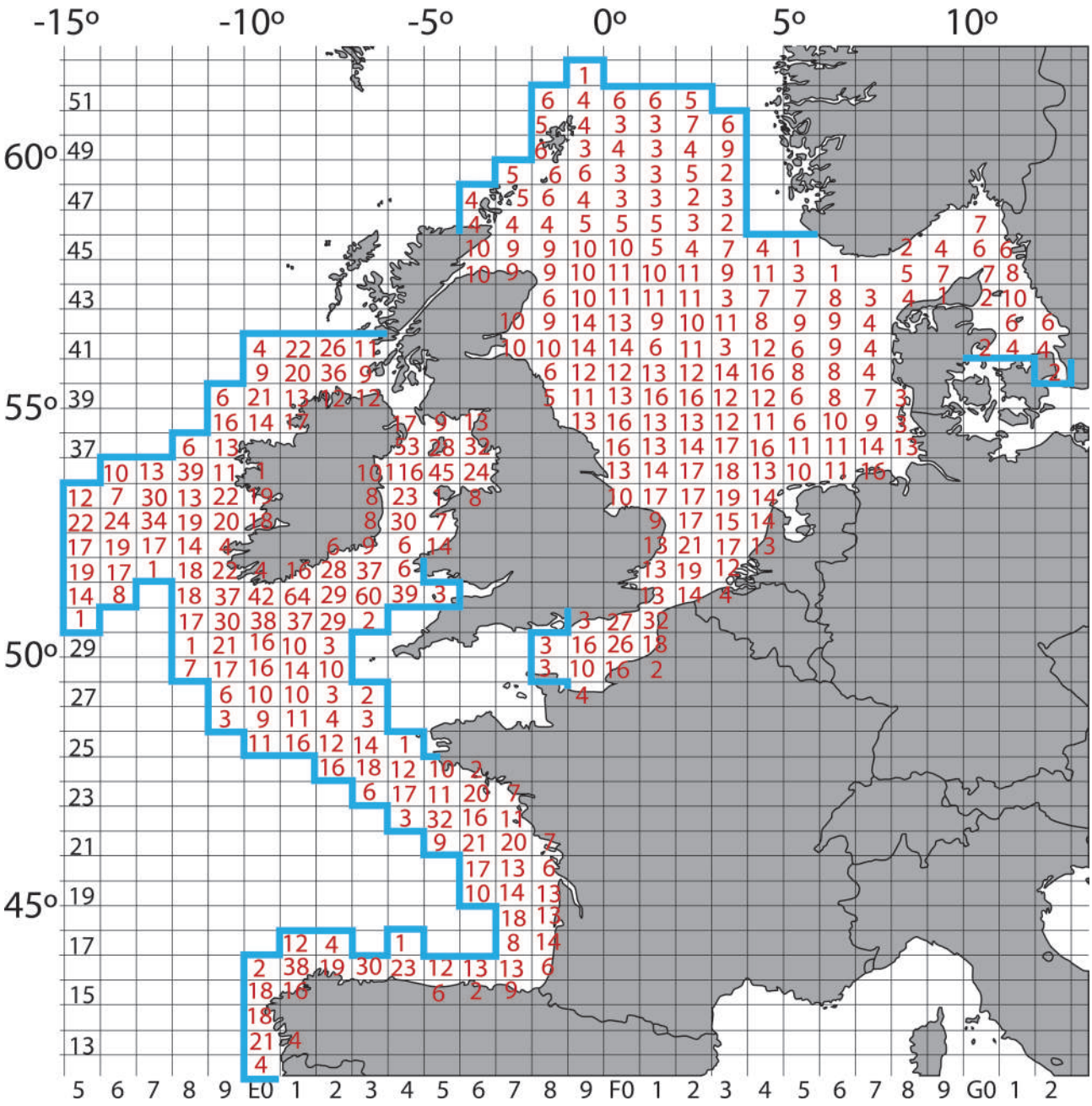



**Fig. 2.** The ICES rectangles on the Northeast continental flat of the North Atlantic Ocean, each with the total number of hauls included in this study, based on surveys between 2009 and 2015.

## Methods

For the inventory, the area of the NE Atlantic Ocean is divided into rectangles of half a degree latitude and one degree longitude, equalling about 30 x 30 nautical miles. Standardized sampling is carried out in every ICES rectangle by trawling with a standard ground net (GOV) for half an hour at an average speed of 3-4 nautical miles per hour; this corresponds to a distance of about 3.4 to 3.8 km. The standard net for bottom-trawling is 45-50 m wide and 5 m high; the cod-end mesh is 2.0 cm. The net has a rolling rubber chain-bar along the foot rope, which closely follows the bottom. Trawl samples were taken at depth between 15 and 800 m on the continental shelf from the Portuguese-Spanish border to Bergen, Norway, 42°N to 62,50°N; and in the west from the edge of the continental shelf to the Skagerrak (15°W to 10°E). There are no data available from the western part of the English Channel (Fig. 2).

Identification to species on board is impractical, so samples were fixed and preserved in 70% ethanol, ideally replaced after two weeks.

| Subfamily | Genus | Species | total | male | female | juv. |
|---|---|---|---|---|---|---|
| Sepiolinae Leach, 1817 | *Sepiola* Leach, 1817 | *Sepiola atlantica* d'Orbigny, 1842 | 1499 | 835 | 659 | 5 |
| | | *Sepiola ligulata* Neaf, 1912 | 459 | 235 | 884 | 0 |
| | | *Sepiola pfefferi* Grimpe, 1921 | 1877 | 992 | 884 | 1 |
| | | *Sepiola tridens* De Heij & Goud, 2010 | 7678 | 5281 | 2365 | 12 |
| | *Rondeletiola* Naef, 1921 | *Rondeletiola minor* (Neaf, 1912) | 4646 | 2303 | 2224 | 9 |
| | *Sepietta* Naef, 1912 | *Sepietta neglecta* Naef, 1916 | 338 | 132 | 204 | 2 |
| | | *Sepietta oweniana* (d'Orbigny, 1841) | 2124 | 777 | 1179 | 158 |
| Rossiinae Appellöf, 1898 | *Rossia* Owen, 1835 | *Rossia macrosoma* (Delle Chiaie, 1830) | 665 | 49 | 62 | 554 |
| | | *Rossia palpebrosa* Owen, 1835 | 14 | 3 | 10 | 10 |
| | *Neorossia* Boletzky, 1971 | *Neorossia caroli* (Joubin, 1902) | 8 | 8 | 2 | 3 |
| Heteroteuthinae Appellöf, 1898 | *Stoloteuthis* Verrill, 1881 | *Stoloteuthis leucoptera* (Verrill, 1878) | 10 | 7 | 3 | 0 |

**Table 2.** Overview of the Sepiolidae Leach, 1817, of the Northeast Atlantic Ocean, with the number of specimens caught per species.

## Results

A summary of the Sepiolidae received between January 2009 and March 2015, is given in Table 2. Most specimens received were preserved in good condition.

### Geographical distributions

A total of 19476 specimens of Sepiolidae were obtained from 4291 hauls between 2009 and the spring of 2015. They were identified as 11 species belonging to

| Depth in | Hauls* | *S. atlantica* | *S. ligulata* | *S. pfefferi* | *S. tridens* | Hauls* | *R. minor* | *S. neglecta* | *S. oweniana* | *R. macrosoma* | *R. palpebrosa* | *N. caroli* | *S. leucoptera* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| meters | No. | % | % | % | % | No. | % | % | % | % | N | N | N |
| <26 | 153 | 17.99 | 0 | 0.93 | 0.12 | 153 | 0.02 | 0 | 0.07 | 0 | 0 | 0 | 0 |
| 26-50 | 845 | 40.63 | 0.11 | 3.91 | 0.48 | 842 | 0.02 | 1.48 | 0.47 | 0.16 | 0 | 0 | 0 |
| 51-75 | 545 | 25.19 | 1.06 | 13.57 | 3.94 | 535 | 0.21 | 9.35 | 3.09 | 0.41 | 0 | 0 | 0 |
| 76-100 | 543 | 14.72 | 10.57 | 27.21 | 9.39 | 520 | 1.01 | 13.40 | 4.03 | 4.15 | 0 | 0 | 0 |
| 101-125 | 508 | 1.47 | 47.29 | 29.12 | 49.07 | 482 | 11.63 | 18.61 | 13.44 | 10.00 | 1 | 0 | 0 |
| 126-150 | 511 | 0 | 18.66 | 23.84 | 20.57 | 461 | 6.28 | 8.66 | 7.15 | 5.31 | 0 | 1 | 0 |
| 151-175 | 303 | | 3.42 | 0.37 | 5.68 | 258 | 2.28 | 8.88 | 6.00 | 3.49 | 2 | 0 | 0 |
| 176-200 | 130 | | 5.23 | 0 | 1.47 | 114 | 1.14 | 0.86 | 8.92 | 3.20 | 2 | 1 | 2 |
| 201-250 | 158 | | 3.58 | 0 | 1.67 | 133 | 2.94 | 1.44 | 9.93 | 9.86 | 0 | 0 | 0 |
| 251-300 | 124 | | 3.80 | 0.23 | 4.25 | 100 | 7.70 | 22.90 | 17.95 | 17.21 | 2 | 1 | 0 |
| 301-350 | 92 | | 6.28 | 0 | 0.80 | 87 | 13.08 | 3.37 | 13.71 | 27.32 | 0 | 0 | 0 |
| 351-400 | 70 | | 0 | 0.83 | 1.67 | 65 | 24.46 | 3.03 | 9.82 | 9.54 | 0 | 3 | 0 |
| 401-500 | 107 | | | 0 | 0 | 95 | 20.74 | 8.04 | 2.06 | 4.60 | 6 | 0 | 4 |
| 501-600 | 67 | | | | 0.89 | 44 | 6.16 | 0 | 1.64 | 3.73 | 1 | 1 | 4 |
| 601-700 | 44 | | | | 0 | 38 | 0.83 | | 0 | 0 | | | |
| 701-800 | 15 | | | | | 14 | 1.51 | | 0.74 | | | | |
| 801-824 | 3 | | | | | 1 | 0 | | 0 | | | | |
| Totals | 4218 | 1499 | 458 | 1877 | 7678 | 3942 | 4623 | 338 | 2123 | 662 | 14 | 7 | 10 |

**Table 3.** Mean percentage per species per depth zone. For *R. palpebrosa*, *N. caroli* and *S. leucoptera* are given the total number of specimens (N). Totals: The total number of caught specimens per species that were used for the depth analyses. During DEM 2012 and 2013 only *Sepiola* species were collected. The blue zone indicates the general depth with the average highest sepiolid percentage of numbers. In green the highest percentage of numbers per species is highlighted.

six genera (Table 2). Fig. 2 shows the whole sampling area with the number of performed hauls in each rectangle of 0.5° latitude and 1° longitude. Details of the distribution of each species are illustrated in Figs 3-10 by symbols corresponding to the mean number of specimens obtained per haul for each ICES rectangle. Three species (*Rossia palpebrosa*, *Neorossia caroli* and *Stoloteuthis leucoptera*) were obtained only rarely; their samples are represented on a single distribution map, Fig. 11, using actual numbers of specimens obtained.

## Depth distributions

For depth analyses, 19289 specimens were used from 4218 hauls. In Table 3 the depths are divided in zones of 25 m down to 200 m depth, in zones of 50 m between 201 m and 400 m depth and in zones of 100 m between 401 m and 800 m. In the second column the total number of hauls in each zone is given. For the different species the mean percentages of specimens per depth zone are recorded. The total number of specimens is given only for *R. palpebrosa*, *N. caroli* and *S. leucoptera*. In this table, the differences in depth preference are shown among the species. There were sufficient data to show the difference in distribution behaviour of *Sepiola atlantica* in winter and summer only in the Irish Sea (Table 4).
The male : female ratio of the species is analysed and the dorsal mantle length (DML) of all males and females was measured. In the descriptions of the species below, these aspects are described in more detail.

| Depth | Spring 2010, 2012-2014 Hauls | % | Autumn 2012-2014 Hauls | % |
|---|---|---|---|---|
| <25 | 6 | 3,5 | 8 | 7,4 |
| 26-50 | 100 | 7,1 | 75 | 28,5 |
| 51-75 | 63 | 11,7 | 43 | 32,7 |
| 76-100 | 59 | 44,5 | 47 | 21,5 |
| 101-120 | 6 | 33,3 | 4 | 9,9 |

**Table 4.** Irish Sea, *Sepiola atlantica*, differences in depth preference in spring and autumn.

## Identification and distribution of each species

### *Sepiola atlantica* d'Orbigny, 1842
(Figs 1, 3, 12a, Table 4)

Description. — Total length (without tentacles) < 45 mm, DML < 22 mm. Sex ratio (males : females) of captured specimens 4 : 3 (Table 2). Mantle fused with head dorsally. Two kidney-shaped light organs on ventral side of ink sac, visible near opening of mantle cavity. Tentacular club length > 7 mm, width > 1.9 mm with 8 rows of small suckers. All arms with 2 rows of suckers. Arms IV with a distal part of markedly smaller suckers arranged in 6 to 8 rows.

Male hectocotylus (first arm left, Fig. 12a) bearing (proximal to distal): 3 suckers on base; a bi-lobed papilla directed towards the first arm right; a crest with 3-4 large suckers; 2-3 small suckers; a main crest with 3-4 large suckers; 9-12 pairs of small suckers at arm tip (De Heij & Goud, 2010: 57, fig. 5b). Hectocotylus discernible in specimens of DML > 8 mm.

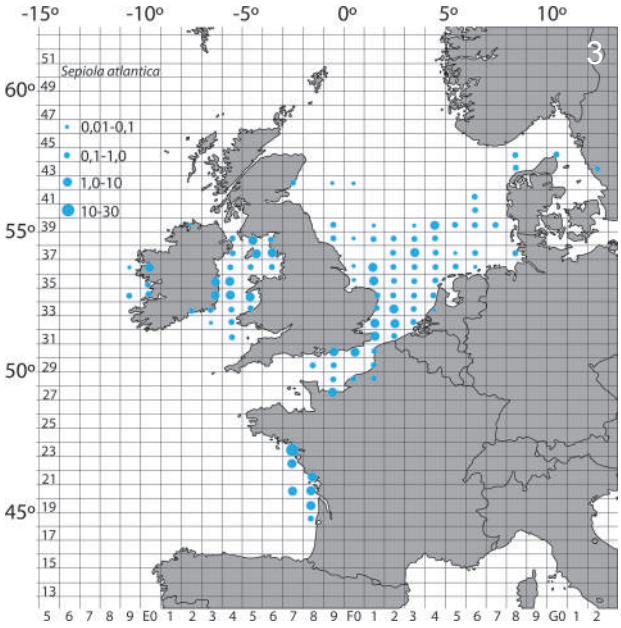
Distribution. — Of 1499 specimens of *Sepiola atlantica* captured, 98 % were caught between 10 and 100 m (Table 3). Its distribution is therefore limited to shallow coastal waters, from just outside the Bassin d'Arcachon, the estuary of the Gironde, along the coast of the Vendee and south coast of Brittany to Lorient (France), Irish Sea, some bays on the west coast of Ireland, the English Channel and the southern part of the North Sea to the Skagerak (Fig. 3). *S. atlantica* has also been reported from the estuary of Ria de Vigo (Rodrigues et al. 2009, 2010, 2011). In our samples from just outside the Ria de Vigo we did not identify any *S. atlantica* (Fig. 3). However, inspection of a specimen of the *Sepiola* population studied by Rodrigues et al. sent to us confirmed the presence of *Sepiola atlantica* at this locality, demonstrating that it is a truly coastal and estuarine species. The data for the Irish Sea show a difference in depth preference between March-April and September; in March-April, specimens were caught in deeper water than in September (Table 4).

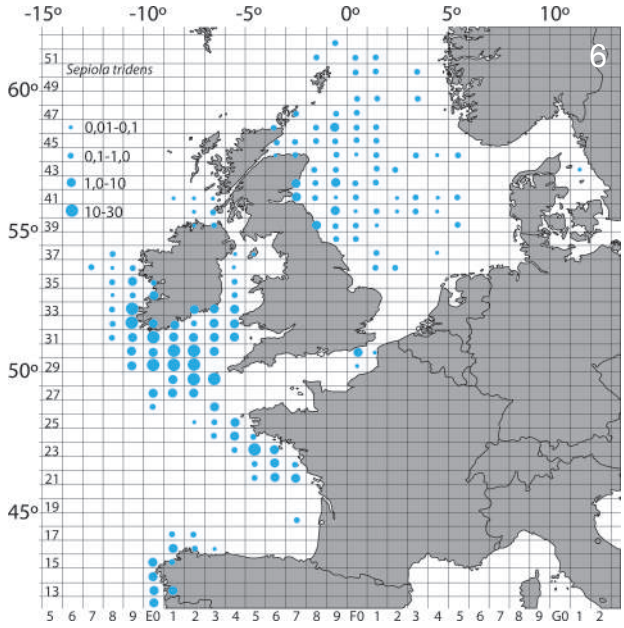
D'Orbigny (1839-1842) described (in Férussac and d'Orbigny, 1835-1848) *Sepiola atlantica* from the estuary of the Gironde, France. Fig. 3 shows that *S. atlantica* is still living in the area of the type locality.

Remarks. — *Sepiola atlantica* is often found alone or sometimes together with *S. pfefferi* and occasionally with *Rondeletiola minor* (Gironde estuary, 2012).

### *Sepiola ligulata* Naef, 1912 (Figs 4, 12b)

Description. — Total length (without tentacles) < 40 mm, DML < 20 mm. Average DML of males is 13 mm, of females is 14 mm. Sex ratio (males : females) of captured specimens approximately 1 : 1 (Table 2). Mantle fused with head dorsally. The ventral mantle edge has a median indentation, but not as deep as in *S. pfefferi*. Two kidney-shaped light organs on ventral side of ink sac, visible near opening of mantle cavity. All arms with two rows of suckers. Bursa copulatrix (females) positioned in left side of mantle cavity, ex-


Sepiola atlantica
3
0,01-0,1
0,1-1,0
1,0-10
10-30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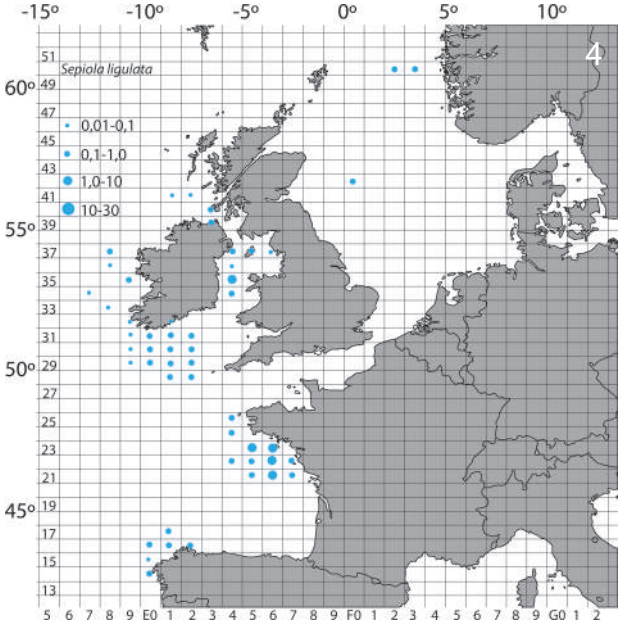
6
0,01-0,1
0,1-1,0
1,0-10
10-30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4
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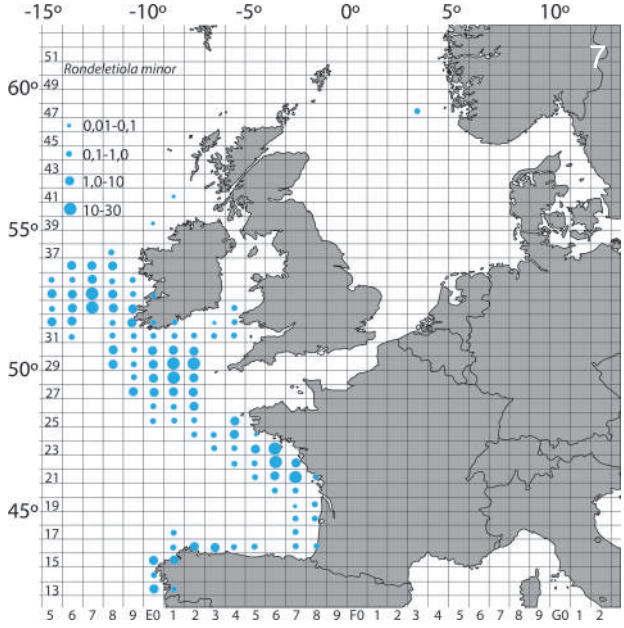
1,0-10
10-30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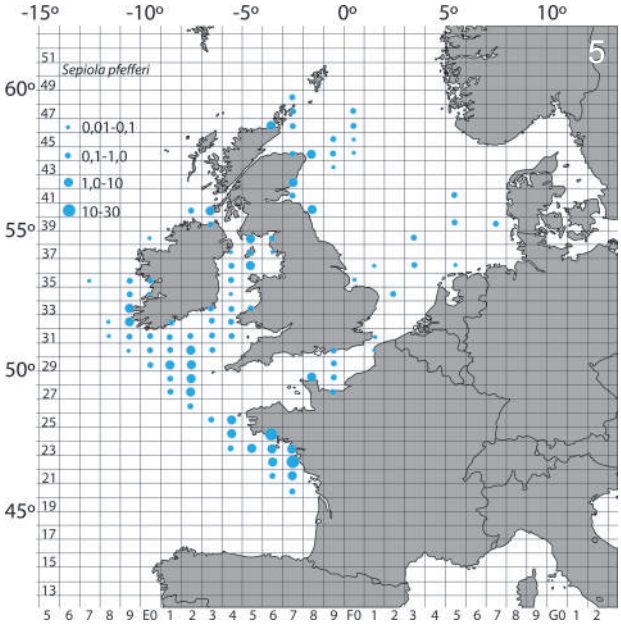
7
0,01-0,1
0,1-1,0
1,0-10
10-30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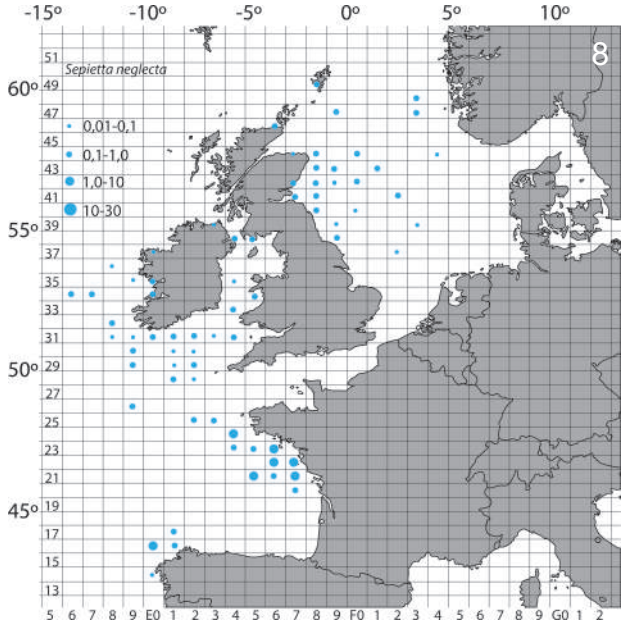
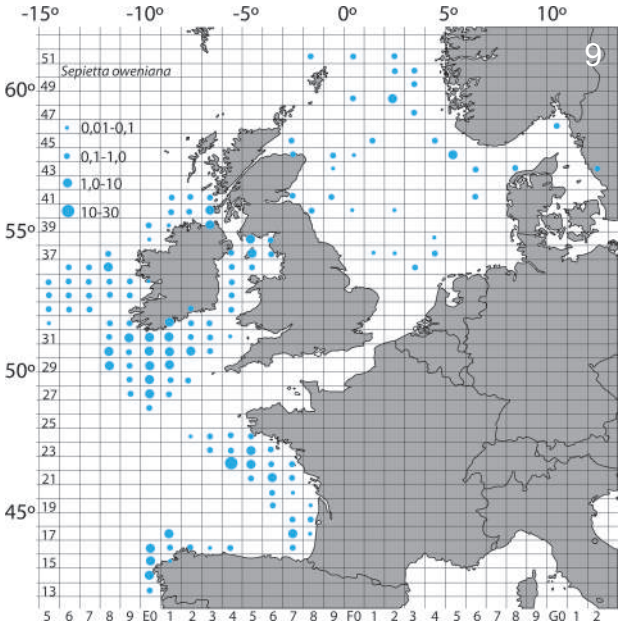
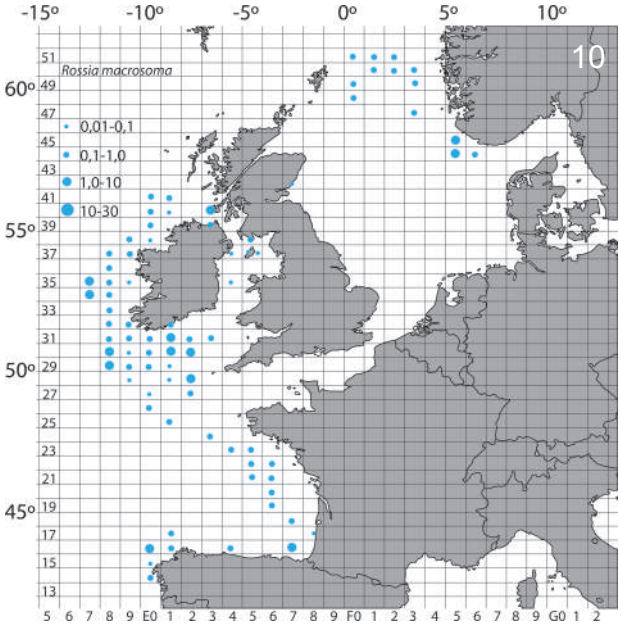
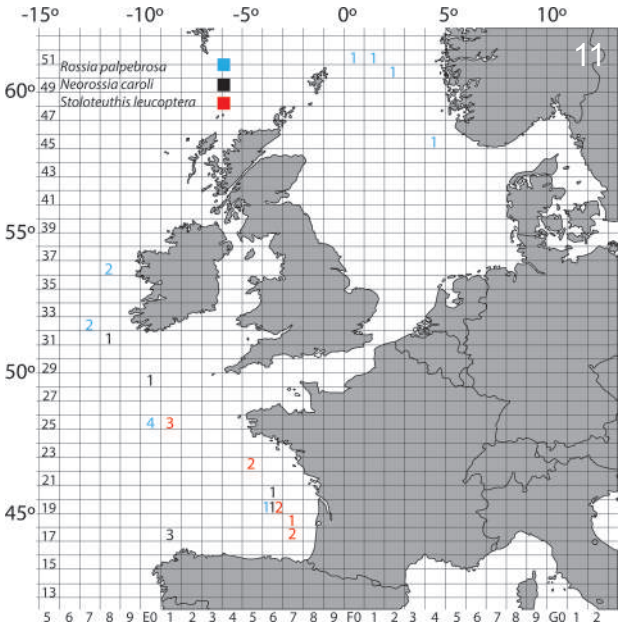
5
0,01-0,1
0,1-1,0
1,0-10
10-30


Sepietta neglecta
8
0,01-0,1
0,1-1,0
1,0-10
10-30




tends through the median septum into the right side of the mantle cavity.

Male hectocotylus (first arm left, Fig. 12b) bearing (proximal to distal): 3 small suckers on base; 2 large lobes (1 more or less T-shaped on the left side); hectocotylus widened, with 2 rows of 16-18 suckers. Hectocotylus discernible in specimens of DML > 7 mm.

Distribution. — Approximately 77 % of 458 *Sepiola ligulata* specimens were caught between 75 and 150 m depth with a maximum between 101 and 125 m (Table 3), but approximately 24 % of the specimens are caught deeper than 150 m.

*Sepiola ligulata* is found around the north west point of Spain, in the northern part of the Bay of Biscay, and in low numbers in the Celtic Sea, west of Ireland to the west coast of Scotland, Irish Sea and sporadically in the northern part of the North Sea, in depths to 190 m, along the Norwegian south west coast (Fig. 4). *Sepiola ligulata* is rare everywhere, except in the 100 - 150 m depth layer in the northern part of the Bay of Biscay.

Remarks. — *Sepiola ligulata* is often found together with *S. tridens, Rondeletiola minor* and *S. pfefferi*.

*Sepiola pfefferi* Grimpe, 1921 (Figs 5, 12c)

Description. — Total length (without tentacles) < 35 mm, DML < 18 mm. Average DML of males is 12 mm, of females is 13 mm. Sex ratio (males : females) of captured specimens 9 : 8 (Table 2). Mantle fused with head dorsally. The ventral mantle edge has two lobes towards the head with a rather deep median caudal curve in between (in preserved specimens sometimes difficult to see). Two kidney-shaped light organs on ventral side of ink sac, visible near opening of mantle cavity. All arms with two rows of suckers. Bursa copulatrix (females) positioned in left side of mantle cavity. Male hectocotylus (first arm left, Fig.12c) bearing (proximal to distal): 2 pairs of suckers on base; a thin sharp pointed lobe and 2 little finger-like lobes directed towards the 2nd arm left; 2 pairs of small suckers; 2-3 pairs of large suckers; 8-10 pairs of small



**Figs 3-11.** Distribution maps of Sepiolidae species on the Northeast continental shelf of the North Atlantic Ocean; symbols refer to the mean number of specimens obtained per haul. **3,** *Sepiola atlantica*. **4,** *Sepiola pfefferi*. **5,** *Sepiola ligulata*. **6,** *Sepiola tridens*. **7,** *Rondeletiola minor*. **8,** *Sepietta neglecta*. **9,** *Sepietta oweniana*. **10,** *Rossia macrosoma*.
**11,** *Neorossia caroli, Rossia palpebrosa* and *Stoloteuthis leucoptera* on the Northeast Atlantic Ocean. Symbols refer to the total number of specimens obtained per ICES rectangle.

suckers at arm tip (Grimpe, 1921: 9, fig. 5). Hectocotylus discernible in specimens of DML > 6 mm.

Distribution. — Approximately 80 % of 1877 *Sepiola pfefferi* specimens were caught between 75 and 150 m depth with a maximum between 101 and 125 m (Table 3); only 1,5 % of the population deeper than 150 m and 18% more shallow as 75 m.

*Sepiola pfefferi* has been caught in the northern part of the Bay of Biscay, Celtic Sea, west of Ireland to the west coast of Scotland, Irish Sea, eastern part of the English Channel, north west part of the North Sea and sporadically in the southern North Sea (Fig. 5).

Grimpe (1921) described *Sepiola pfefferi* from 53°53'N 00°32'E, the type locality. There is a recent population of *S. pfefferi* in that area, which is 80 m deep whereas the surrounding sea has a maximum depth of only 40 m.

Remarks. — *Sepiola pfefferi* is often found together with *S. tridens* and *S. ligulata,* but also with *S. atlantica.*

*Sepiola tridens* De Heij & Goud, 2010 (Figs 6, 12d)

Description. — Total length (without tentacles) < 40 mm, DML < 20 mm. Sex ratio (males : females) of captured specimens is very extreme 2 : 1 (Table 2). Average DML of males is 14 mm, of females is 15 mm. Mantle fused with head dorsally. Two kidney-shaped light organs on ventral side of ink sac, visible near opening of mantle cavity. Tentacular club length > 7 mm, width > 1.7 mm with 8 rows of small suckers. All arms with 2 rows of suckers. Arms IV with a distal part of markedly smaller suckers arranged in 6 to 8 rows. A character which it has in common with *S. atlantica.*

Male hectocotylus (first arm left, Fig. 12d) bearing (proximal to distal): 3 suckers on base; a bi-lobed papilla directed towards the first arm right; a crest with 3-4 large suckers; 2-3 small suckers; a main crest with 5-8 large suckers; 9-12 pairs of small suckers at arm tip (De Heij & Goud, 2010: 57, fig. 5b). Hectocotylus discernible in specimens of DML > 7 mm.

Distribution. — Approximately 79 % of 7678 *Sepiola tridens* specimens are caught between 75 and 150 m depth with a maximum between 101 and 125 m (49%, table 3), just below the depth of *S. atlantica*; 16 % of the rest occur at greater depth than 150 m down to 600 m (Table 3). There were only a few hauls that contained both species.

*Sepiola tridens* is found in low numbers around the northwest point of Spain; the northern part of the Bay of Biscay; in high numbers in the Celtic Sea, west of Ireland to the west coast of Scotland; in low numbers in the deeper part of the Irish Sea and in the northern part of the North Sea (Fig. 6). *Sepiola tridens* is the most common sepiolid in the NE Atlantic Ocean.

In the description of *S. tridens* (de Heij & Goud, 2010: 54-55) it seems to be a dominant species of the northern North Sea, but in fact, the highest numbers of *S. tridens* are found in the Celtic Sea and the northern part of the Bay of Biscay.

Remarks. — *Sepiola tridens* is often found together with *Rondeletiola minor*, *Sepietta oweniana*, *Sepiola pfefferi* and *S. ligulata.*

*Rondeletiola minor* (Naef, 1912) (Figs 7, 12e)

Description. — Total length (without tentacles) < 44 mm, DML < 21 mm. Sex ratio (males : females) of captured specimens approximately 1 : 1 (Table 2) . Average DML of males is 14 mm, of females is 15 mm. Mantle fused with head dorsally. Head with relatively long arms, is narrower than the width of the mantle sack. The light organ on the ventral side of the ink sac is round with a pore on both sides of the median septum, visible near opening of mantle cavity. All arms with 2 rows of suckers.

Male hectocotylus (first arm left, Fig.12e) bearing (proximal to distal): 3 suckers on base; a big papilla with left a half curl to the right; above the papilla the arm widened slightly; right (dorsal) side 20-22, left side 18-20 in large dicline suckers. Hectocotylus discernible in specimens of DML > 8 mm.

Distribution. — With a total of 4646 specimens *Rondeletiola minor* is the second commonest species after *Sepiola tridens* in the Northeast Atlantic area.

*Rondeletiola minor* is caught from less than 25 m to 800 m depth (the widest range of all species); 18 % of the population occurs between 101 and 150 m and 58 % between 301 and 500 m (Table 3). The population structure of these two depth populations doesn't seem different; they have the same DML average and the same male : female ratio.

*Rondeletolia minor* appears on the continental shelf of the northwest coast of Spain, Bay of Biscay, Celtic Sea, west of Ireland and Porcupine Bank, some single observations west of Scotland, Irish Sea and in the deep trough (to 190 m) along the Norwegian southwest coast (Fig. 7).

Remarks. — *Rondeletiola minor* is often found together with *Sepiola tridens* and *Sepietta oweniana*. On the Porcupine Bank they occur only together with *S. oweniana.*

*Sepietta neglecta* Naef, 1916 (Figs 8, 12f)

Description. — Total length (without tentacles) < 55 mm, DML < 24 mm. Sex ratio (males : females) of cap-

tured specimens 2 : 3 (Table 2). Average DML of males and females is 17 mm. Mantle fused with head dorsally. No light organs on ventral side of ink sac. Tentacular club length > 10 mm, with 11-13 rows of small suckers (Grimpe, 1925: 17). All arms with 2 rows of suckers. Male hectocotylus (first arm left, Fig.12f) bearing (proximal to distal): 4 suckers on base; a tri-lobed papilla; above the papilla the arm widened slightly; right (dorsal) row 4 large suckers; 13-14 small suckers; left row 17-18 small suckers to the tip.

Distribution. — *Sepietta neglecta* (338 specimens) seems to be a species of more shallow waters (approximately 42 % of the catches are between 50 and 125 m), but the data also show a population (23 % of the catches) between 251 and 300 m (Table 3).

*Sepietta neglecta* has been found around the northwest corner of Spain, the northern part of the Bay of Biscay, Celtic Sea, west of Ireland, Irish Sea, middle and northern part of the North Sea and Skagerak, but never in great numbers (Fig. 8).

Remarks. — *Sepietta neglecta* is often found together with *Sepiola tridens* and *S. pfefferi*, but also with S*epietta oweniana.*

*Sepietta oweniana* (d'Orbigny, 1839–1841)
(Figs 9, 12g)

Description. — Total length (without tentacles) < 95 mm, DML < 40 mm. Sex ratio (males : females) of captured specimens 2 : 3 (Table 2). Approximately 7.5 % of the specimens were juveniles of less than 16 mm DML.

Average DML of males is 25 mm, of females is 27 mm. Mantle fused with head dorsally. No light organs on ventral side of ink sac. Tentacular club length at least 10 mm (by a DML of 19 mm) with 20-24 or more rows of very small suckers (Grimpe, 1925: 17). All arms with two rows of suckers. Male hectocotylus (first arm left, 12g) bearing (proximal to distal): 4 suckers on base; a bi-lobed papilla with left a hook-like, inwardly curved, horn; on the right side of the widened hectocotylus 3 large suckers; 2-3 small suckers; 2-3 large suckers; 12-13 pairs of small suckers at arm tip. Hectocotylus discernible in specimens of DML > 16 mm.

Distribution. — *Sepietta oweniana* (2124 specimens) is caught between 25 and 600 m depth with a small peak in the populations between 101 and 125 m (13 %) and a maximum between 251 and 350 m (32 %) (Table 3).

*Sepietta oweniana* is distributed from around the northwest point of Spain, Bay of Biscay, Celtic Sea, west of Ireland to the west coast of Scotland, Porcupine Bank, the Irish Sea and in the middle and northern parts of the North Sea (Fig. 9).

Remarks. — *Sepietta oweniana* is often found with *Sepiola tridens* and *Rondeletiola minor* (Porcupine Bank), but also with *Sepietta neglecta* (Bay of Biscay, Celtic Sea).

*Rossia macrosoma* (Delle Chiaie, 1830) (Fig. 10)

Description. — Total length (without tentacles) < 160 mm, DML < 85 mm. It isn't possible to say anything about the male : female ratio; 83% of the specimens were juvenile. Mantle is not fused with head dorsally. No light organs on ventral side of ink sac. Basal parts of the arms with 2 rows of suckers; middle part 4 rows; towards the top 3 to 2 rows of suckers.

Male hectocotylus (both dorsal arms) with small basal suckers wide apart. Males are easily recognised by the enlarged suckers spread over the arm-pairs II, III and some over IV.

Distribution. — *Rossia macrosoma* is a species of deeper waters, but all the juveniles show a broad range between 26 and 600 m with a small peak between 101 and 125 m (11 %) and approximately 45 % of the population between 251 and 350 m (Table 3).

*Rossia macrosoma* is distributed from around the northwest point of Spain, Bay of Biscay, Celtic Sea, west and north of Ireland, some in the Irish Sea, some east of Scotland and in the northern part of the North Sea (Fig. 10).

Remarks. — *Rossia macrosoma* has been trapped often together with *Sepietta oweniana, Sepiola tridens* and *Rondeletiola minor.*

*Rossia palpebrosa* Owen, 1834
(Fig. 11, numbers in blue)

Description. — Total length (without tentacles) < 100 mm, DML < 45 mm (Reid & Jereb, 2005: 197). For sex ratio to less specimens (Total 14) . Mantle is not fused with head dorsally. No light organs on ventral side of ink sac. All arms with two rows of suckers. Males are easily to recognise by the enlarged suckers spread over the arm-pairs 2 and 3.

Distribution. — Nine of the 14 *Rossia palpebrosa* are found along the edge of the continental shelf from the Bay of Biscay, Celtic Sea and west of Ireland, between 401 and 500 m depth. Five of *R. palpebrosa* are from the deep trough (to 190 m) along the Norwegian southwest coast (Table 3).

Remarks. — *Rossia palpebrosa* seems to be mainly an arctic species (Gardiner & Dick, 2010: 212).

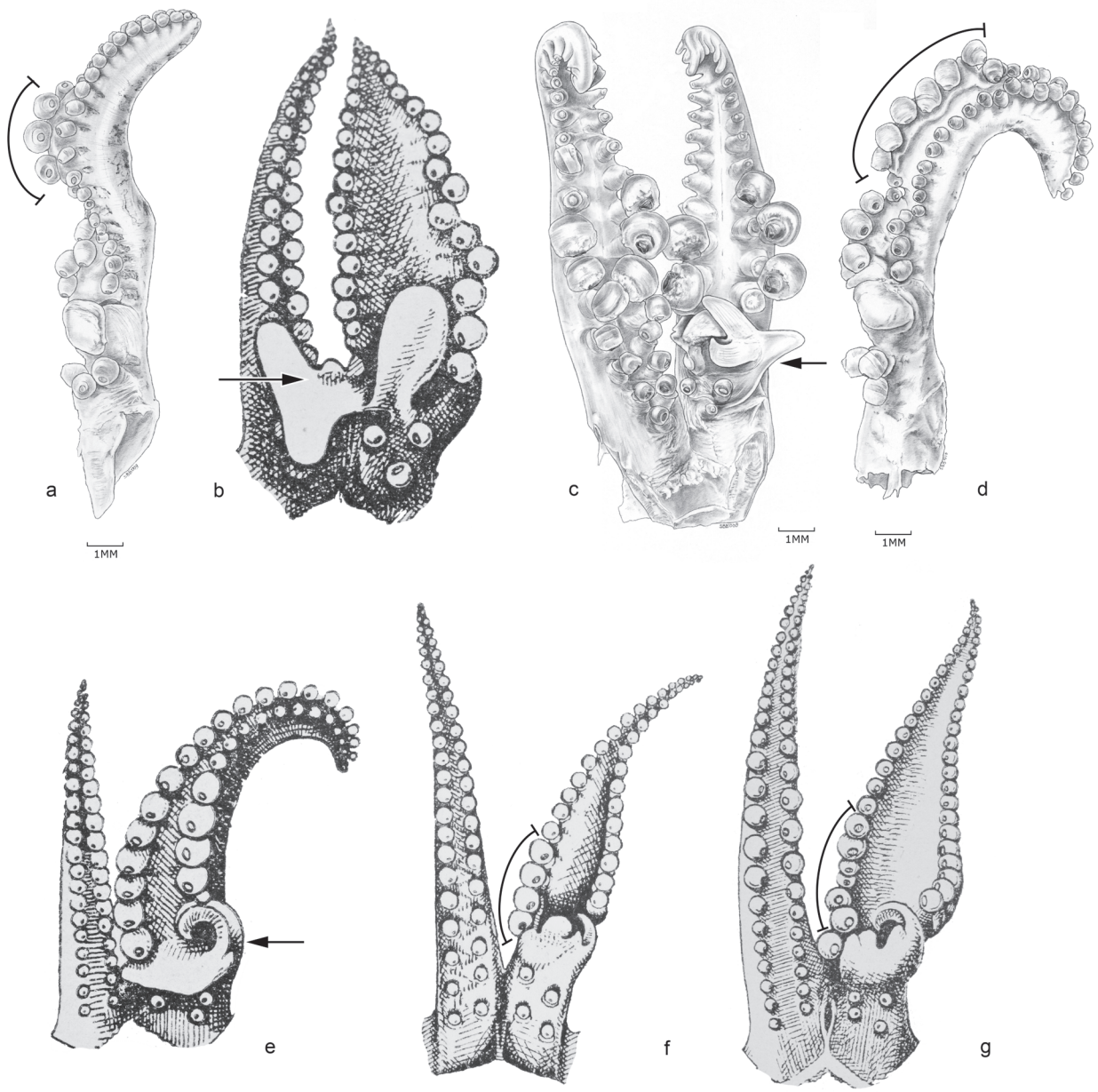





**Fig. 12.** The hectocotyli of the Sepiolinae in the Northeast Atlantic Ocean. **a.** *Sepiola atlantica* after De Heij & Goud, 2010: fig. 5B. **b.** *Sepiola ligulata* after Naef, 1912: fig. 1g. **c.** *Sepiola pfefferi* after Goud & De Heij, 2012: fig. 12. **d.** *Sepiola tridens* after De Heij & Goud, 2010: fig. 5A. **e.** *Rondeletiola minor* after Naef, 1912: fig. 1i. **f.** *Sepietta neglecta* after Naef, 1916: fig. 2b. **g.** *Sepietta oweniana* after Naef, 1912: fig. 1e. Figs **a**, **c**, **d**: Bas Blankevoort del.

*Neorossia caroli* (Joubin, 1902)
(Fig. 11, numbers in black)

Description. — Total length (without tentacles) < 200 mm, DML < 83 mm (Reid & Jereb, 2005: 190). Sex ratio not determined because of small sample size (total 7). Mantle is not fused with head dorsally. Mantel edge is somewhat wide V- shaped along the middle of the dorsal side. Head wider than width of mantle sack No light organs on ventral side of ink sac. All arms with 2 rows of suckers. Hectocotylus present in both dorsal arms.

Distribution. — Seven specimens of *Neorossia caroli* were trapped: 2 males (24 and 26 mm), 1 female (34 mm) and 3 juveniles (16, 17 and 23 mm DML). Four specimens were caught between 351 and 600 m depth (Table 3) on the edge of the continental shelf, from northwest Spain and the Bay of Biscay (Fig. 11).

Remarks. — *Neorossia caroli* is a deep water species (Collins et al., 2001: 106).

*Stoloteuthis leucoptera* (Verrill, 1878)
(Fig. 11, numbers in red)

Description. — Total length (without tentacles) < 30 mm, DML < 18 mm (Reid & Jereb, 2005: 190). For sex ratio too few specimens are available (7 males, 3 females). Mantle fused with head dorsally.

Dorsal mantle length is less than ventral mantle length. On ventral side the mantle margin reaches up to the level of the eyes. Ventral mantle is broadly flattened as a dark shield-like structure. All arms with 2 rows of suckers. Between arm pairs I to IV a broad web extends up to 60 % of the length of the arms. No hectocotylus, but the suckers of arm pairs 2 and 3 are enlarged, especially the dorsal sucker on the 2$^{end}$ arm pair at the margin of the web is a large one. Inside the mantle cavity lays a large round light organ (with two small dark pores in the bottom of the organ) on the ventral side of the ink sac.

Distribution. — *Stoloteuthis leucoptera* is a rare species of deeper water, living along the edge of the continental shelf in the Bay of Biscay (Table 3) between 400 – 600 m (8 specimens) and 2 between 175-200 m. In five years we saw only 10 specimens, 6 of them in the year 2012.

## Discussion

Geographic distributions. — Reid & Jereb (2005) summarized knowledge on geographic distributions of Sepiolidae. On the basis of the recent surveys some distributions are extended, whereas others can be questioned. They recorded 5 species of *Sepiola* in the Northeast Atlantic Ocean: *S. atlantica* (p. 159), *S. aurantiaca* Jatta 1896 (p. 180), *S. ligulata* (p. 164, with a ?), *S. pfefferi* (p. 180) and *S. rondeleti* Leach, 1834 (p. 167). The surveys in the present study recorded only 4 species: *Sepiola atlantica, S. ligulata, S. pfefferi* and *S. tridens. Sepiola aurantiaca* and *S. rondeleti* were not encountered. Goud & de Heij (2012) showed, that *S. aurantiaca* is a Mediterranean species. *S. rondeleti* is probably also limited to the Mediterranean Sea. There are no published records of *S. rondeleti* for the NE Atlantic Ocean, as far as we can ascertain.

The NE Atlantic *S. atlantica* populations were shown to belong to two different species (de Heij & Goud, 2010): *Sepiola atlantica* inhabits shallow coastal waters, also in the most southern part of its distribution (Rodrigues et al. 2009, 2010, 2011) and *S. tridens* lives somewhat deeper. The overlap in depth distribution between *S. atlantica* and *S. tridens* is very limited (Table 3). Their combined distributions (Figs 3 and 6) match the area indicated on the map for *S. atlantica* in Reid & Jereb (2005: 160).

The ? in the map of *Sepiola ligulata* in front of the Bay of Biscay in Reid & Jereb (2005: 164), questioning the Atlantic distribution, isn't necessary. *Sepiola ligulata* was found in many ICES survey rectangles of the NE Atlantic (Fig. 4). Guerra (1986: 181) reported it from the estuary of the Ria de Vigo. There is no older report of the occurrence of *S. ligulata* in the Northeast Atlantic.

Reid and Jereb (2005: 180) described the geographical distribution of *Sepiola pfefferi*: Faroe Islands and southern Norway to Brittany, France. Continental shelf. The recent surveys confirm these data and widen its distribution towards the Celtic Sea, Irish Sea and north of Ireland (Fig. 5).

The Atlantic distribution of *Rondeletiola minor* is indicated by Reid & Jereb (2005: 175) only along the Spanish and Portuguese coast. The occurrence of a population of *R. minor* along the northwest coast of Spain was reported by Guerra (1982: 300). Collins et al. (2001: 106) reported the catch of *R. minor* in the Porcupine Seabight. During the ICES surveys *R. minor* turned out to be a very numerous species from west of Ireland including the Porcupine Bank, towards the Celtic Sea and the Bay of Biscay (Fig. 7). It is the second most important sepiolid in the NE Atlantic area (Table 3).



Reid & Jereb (2005: 176) reported *Sepietta neglecta* from the continental shelf along the Portuguese and Spanish coast, the Bay of Biscay as far as the southern part of the Celtic Sea, the English Channel and from the North Sea into the Skagerrak. ICES surveys found *S. neglecta* in most of the Celtic Sea and west of Ireland and in southern parts of the Irish Sea, but not in the eastern part of the English Channel and the southern North Sea (Fig. 8).

Reid & Jereb (2005: 179) reported *Sepietta oweniana* from the continental shelf along the Portuguese and Spanish coast, the Bay of Biscay to the northern part of Norway and in the Skagerrak. ICES surveys did not find *S. oweniana* in the eastern part of the English Channel and only occasionally in the southern North Sea (Fig. 9).

Females of *Sepietta oweniana* and *S. neglecta* are probably often misidentified, because many of the specimens in the surveys samples had lost their tentacles. A useful discriminating character is the number of sucker rows on the tentacular club; 20-24 rows on the clubs of *S. oweniana* versus 11-13 rows on the clubs of *S. neglecta*. The males however also show a clear difference in hectocotylus (Figs 12f-g); the females show no difference in the bursa copulatrix.

Reid & Jereb (2005), in their key to subfamilies

and genera in the family Sepiolidae, show a (poor) drawing (p. 157, fig. 226) of a hectocotylus of *S. oweniana*, whereas on page 178 a hectocotylus of *S. neglecta* is erroneously figured as of *S. oweniana*. A clear difference between the hectocotyli of these two species can be found in the sucker composition. The right-hand row of suckers of the widened hectocotylus (figured from the ventral side, infect the row shown on the left) of *S. neglecta* has 4 clearly larger suckers after the papilla, followed by smaller suckers towards the end. *S. oweniana* has 3 larger suckers followed by 2-3 smaller and again 2-3 larger suckers, also followed by many smaller suckers towards the end (Fig. 12g).

Cuccu et al (2009: 189-193) describe the variability of the hectocotylus of *S. oweniana* from Sardinian seas (central western Mediterranean), of which they also show several anomalous hectocotyli. All hectocotyli have small suckers or a gap between the 2 sections with enlarged suckers along the right-hand side.

Females of *S. neglecta* are usually recognized in association with the males (in the same sample) identified by their hectocotylus. The skin colour of both males and females is comparable within the same species: typically more pronounced with higher contrasts in *S. neglecta*, similar to *Rondeletiola minor*. Skin colour patterns in *S. oweniana* are more uniform. We do realize that these skin characteristics are somewhat vague and that in the case of *Sepietta*, differentiation between females, based on DNA analysis does solve this issue better (Groenenberg et al., 2009: 366).



The data of *Rossia macrosoma* largely match the distribution given by Reid & Jereb (2005: 184). Only in the eastern part of the English Channel and the Porcupine Bank no specimens were found. They are well known from the Porcupine Seabight as indicated by Collins et al. (2001: 107) (Fig. 10).

*Rossia palpebrosa* is an amphi-North Atlantic species and is for the NE Atlantic mentioned by Reid & Jereb (2005: 197) from Iceland to the North Sea and west of Ireland till 51°N. We have seen 4 specimens from the southern Celtic Sea at 48.25°N 9.5°W and in the Bay of Biscay 5 specimens, the most southern one from 44.25°N 3.5°W (Fig. 11, numbers in blue), all at depths between 400 and 500 m. In accordance with Reid & Jereb (2005: 196-197) the name *Rossia palpebrosa* has been used instead of *R. glaucopsis.* Reid & Jereb (2005: 196-197) use the name *R. glaucopsis* for a species in the southern Pacific, Chile and the name *R. palpebrosa* for the species living along the coasts of the North western- and the North eastern Atlantic Ocean between 75 and 549 m depth. We are not aware of a taxonomic study that solves this issue more permanently.

*Neorossia caroli* is according to Reid & Jereb (2005: 191) distributed throughout the Eastern Atlantic and the Mediterranean Sea. During the NE Atlantic surveys (2009-2015) we found 2 specimens in the Celtic Sea (125-200 m), 3 in the Bay of Biscay (146-499 m) and 2 northwest of Spain (600-700 m): 1 specimen at 51.25°N 11.5°W, 1 specimen at 49.75°N 9.5°W, 1 specimen at 45.75°N 3.5°W, 1 specimen at 45°25N 3.5°W, and 3 specimens at 44.25°N 8.5°W (Fig. 11, numbers in black)

Degner (1925: 76) described the catch of one specimen of *Stoloteuthis leucoptera* 170 km southwest of Cap St. Mathieu (France) between the English Channel and the Bay of Biscay. This is the only observation of *S. leucoptera* from the NE Atlantic area that we found in the literature. The very thin red line in the map of Reid & Jereb (2005: 200) on the edge of the continental shelf in the Bay of Biscay matches the distribution shown in Fig. 11. *S. leucoptera* is an amphi-Atlantic species known from depth between 160 to 700 m. We encountered 10 specimens in the Bay of Biscay and NW of Spain, 2 at 46.75°N 4.5°W (between 175 and 200 m), 1 at 45.75°N 2.5°W (400-500 m), 2 at 45.25°N 3.5°W (400-500 m), 2 at 44.25°N 2.5°W (400-600 m), 3 at 48.25°N 8.5°W (400-600 m) (Fig. 11, numbers in red).

Depth distributions. — All species have distinctive depth ranges (Table 3). For each species, the depth with the highest percentage of specimens is indicated in green. The part of the depth range between 100 and 125 m is indicated in blue. At that depth the sepiolids, *Sepiola pfefferi*, *S. ligulata* and *S. tridens*, have their maximum abundance. Even the deep water species, *Rondeletiola minor*, *Sepietta oweniana* and *Rossia macrosoma*, have a small peak between 100 and 125 m. *Sepietta neglecta* is a midwater species with its main distribution between 75 and 125 m and a smaller peak at 251-300 m. In all species, there is no difference in the average DML between the different depth zones. There are no differences in depth among age classes.

There is an overall maximum abundance of sepioloids between 100 and 125 m for all shelf species. *Sepiola atlantica* is the only species living in shallow water; it does not occur in the zone between 100 and 125 m or deeper.

Differences in sex ratios. — The differences between the species in the sex ratio are remarkable (Table 2). There are three patterns:

1) The male : female ratio is more or less 1 : 1 in *Sepiola ligulata, S. pfefferi* and *Rondeletiola minor* (all with slightly more males).

2) More males than females in *Sepiola atlantica* (4 : 3) and *S. tridens* (2 : 1).

3) More females than males in *Sepietta* species in both *S. neglecta* and *S. oweniana (*2 : 3).

The most extreme difference in sex ratio in one haul was observed in *Sepiola tridens*: 80 males and 2 females, on 13th of November 2013 (IGFS survey, haul number: 113), 51.172° latitude and -8.922° longitude, depth 112 m.

Czudaj et al. (2013: 803) found for *Rondeletiola minor* along the Portuguese coast more males (n=218) than females (n=169) in their catches. We observed in the NE Atlantic surveys more or less equal numbers in a total of 2302 males and 2224 females.

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