BASTERIA, 69: 91-119, 2005

Seasonal distribution of cephalopod species living in the central and southern North Sea

A. DE HEIJ

Celebesstraat 5, NL 6707 ED Wageningen, The Netherlands; atedeheij@yahoo.com

&

R. P. BAAYEN

Gijsbrecht van Amstellaan 18, NL 3703 BD Zeist, The Netherlands; baayen@tiscali.nl

During the International Bottom Trawl Surveys and International Beam Trawl Surveys from 1996 to 2003, ten cephalopod species were encountered in the central and southern North Sea in six families: Loliginidae (*Alloteuthis subulata, Loligo forbesi, Loligo vulgaris*), Sepiolidae (*Sepiola atlantica, Rossia macrosoma, Sepietta oweniana*), Sepiidae (*Sepia officinalis*), Ommastrephidae (*Todaropsis eblanae*), Onychoteuthidae (*Onychoteuthis banksii*), and Octopodidae (*Eledone cirrhosa*). Apart from *A. subulata*, none of the species lived in the investigated area in large numbers. In general, the central and southern North Sea is not a favourable habitat for cephalopods due to the shallowness of the water. The occurrence of individual species is further restricted by water temperature or salinity requirements, as shown by their seasonal migration patterns. These parameters depend on sea depth, time of the year, and influx of water from outside. Inside the central and southern North Sea, deep waters are relatively cool in summer but relatively warm in winter, while the shallow coastal waters of Belgium and The Netherlands are warm in summer and cold in winter. This explains the seasonal migration of *Alloteuthis subulata*, a species indigenous to the North Sea that prefers relatively warm waters. It migrates northwestwards before winter and southeastwards in late spring. A similar migration pattern exists for the two other species in the Loliginidae, *Loligo forbesi* and *L. vulgaris*. Temperature requirements of *Eledone cirrhosa* differ, and so does its migration pattern. For other cephalopods, water salinity rather than temperature is critical. *Rossia macrosoma* is restricted to the northern range of the central North Sea because it requires high salinities. Moderate salinities are endured by *Todaropsis eblanae*, a species that occurs in moderate numbers in the western part of the central North Sea. Low salinities are endured by *Sepia officinalis* and *Sepiola atlantica*, which spend part of their life in the estuaries and may even survive in water with a salinity of only 27‰. While *Sepiola atlantica* lives in the entire central and southern North Sea, *Sepia officinalis* is restricted to the coastal waters and estuaries. Numerous other cephalopod species occur in the deeper waters of the Atlantic and the Channel. Incidental findings of unusual cephalopod species in the central and southern North Sea, such as those of *Onychoteuthis banksii* in the present study, are likely due to animals being taken along with the invading currents of the Gulf Stream.

Key words: Cephalopoda, North Sea, life cycle, migration patterns, seasonal distribution, water salinity, water temperature.

INTRODUCTION

Under auspices of the International Council for the Exploration of the Sea (ICES), a number of European countries perform surveys of the marine fauna of the North Sea. Fishery surveys of the central and southern North Sea are conducted by the Netherlands Institute for Fisheries Research (RIVO), IJmuiden, as part of the International Bottom Trawl Survey (IBTS) and of the International Beam Trawl Survey (BTS). The main focus of the surveys is to collect data on a number of commercial fish populations for annual fisheries management advice. Biodiversity studies are also carried out. In this study, the occurrence and seasonal distribution of cephalopod species in the central and southern North Sea was examined between 1996 and 2003.

The average depth of the central and southern North Sea, part of the continental shelf (51°-58° N), is 45 m. Locally, close to Scotland, depths of more than 100 m exist. The bottom of the central and southern North Sea consists of sand with banks of shingle or clay. The cephalopod species living in this part of the North Sea therefore are mainly neritic species, favouring shallow waters, and living either on (benthic species) or just above the bottom (demersal species). Eighteen species have so far been reported from the central and southern North Sea (Tesch, 1908; Grimpe, 1925; Stevenson, 1935; Kaas, 1939; Jaeckel, 1958; Kristensen, 1962; Muus, 1963; Lacourt & Huwae, 1981). The dominant cephalopod species (> 90% of all catches) in the North Sea is *Alloteuthis subulata* (Lamarck, 1798), a small squid belonging to the Loliginidae. *A. subulata* is a permanent inhabitant of these waters. Migration patterns of *A. subulata* within the central and southern North Sea were studied by De Heij & Baayen (1999). During autumn and early winter, juvenile animals migrate from the cooling southeastern coastal waters to the deeper, in winter relatively warmer, waters of the central North Sea. In spring, the young adults return to the warming shallow waters along the Danish, German, Dutch, Belgian, and southeastern British coasts. After spawning, most of the adults die (De Heij & Baayen, 1999).

The present study considers all cephalopod species encountered between 1996 and 2003 in the central and southern North Sea. Data are provided on their occurrence and migration in relation to water temperature and salinity. Aim of the study was to elucidate in how far the cephalopod species living in the central and southern North Sea differ in ecological niche and seasonal migration patterns.

MATERIAL AND METHODS

Since the 1960s, the Netherlands Institute for Fisheries Research (RIVO) participated in the International Bottom Trawl Survey in the central and southern North Sea. The research area covered ICES fisheries areas and divisions IVb and IVc, and small parts of IVa and VIId. From 1991 to 1995 these surveys were carried out four times a year, in February, May, August, and November. A standard bottom trawl (GOV-trawl) was used as the survey gear. From 1996, the bottom trawl survey was only carried out in February, while a beam trawl survey was carried out from mid-August to mid-September. In this study, data were used from 1996 to 2003, and, as a supplement, data from other surveys from 1994 to 1996.

For the sampling grid of these surveys, the North Sea was divided into rectangles of one degree longitude by half a degree latitude, equalling about 30 × 30 nautical miles. In every rectangle one or more 30 minutes hauls were made. For each haul the actual sea depth was recorded. Also, water temperature and salinity were recorded at 5 m depth as well as at the bottom. Data on temperature and salinity are not available for all hauls (for

details, see tables). In this study, we used temperature and salinity at fishing depth. Fishing was restricted to rectangles in open sea up to six miles from the shore. In February, about 50 out of the 110 rectangles were sampled with the fisheries research vessel "Tridens" (length 73 m), using a GOV-trawl. This is a bottom trawl with a high vertical net-opening of 5 to 6 m and a horizontal opening of approximately 20 m. The cod-end has a mesh size of 20 mm (stretched mesh). The GOV-trawl is especially used for sampling gadoids and herring.

In August-September 85-90 rectangles were sampled, by "Tridens" and by "Isis" (length 27 m). "Isis" mainly covered the south-eastern North Sea with two to four hauls per rectangle. The remaining parts of the central and southern North Sea were covered by "Tridens" (one haul per rectangle). In the summer survey both ships used two 8 m beam trawls with a 60 cm high net-opening and 4 cm mesh-size in the cod-end. Beam trawls are used especially designed for catching flatfish. Due to the relatively low vertical net-opening, they are suboptimal for pelagic cephalopods. Nevertheless, an indication of cephalopod occurrence was thus obtained, thanks to the shallowness of the North Sea, the tendency of many species to stay close to the bottom at daytime and swim upwards during the night, and the large numbers of hauls per year. Only catches from the starboard nets of both ships were fully analysed. On board of "Tridens", cephalopod catches from starboard and rare cephalopod species from port side were collected and frozen for further examination in the laboratory. Cephalopods caught by "Isis" were not collected due to staff and time shortage.

Cephalopods were identified according to Roper et al. (1984). For all species found, numbers of animals caught per rectangle per 30 minutes were analysed. In case of animals brought ashore, sex was identified in so far as possible, and mantle length was measured for all individuals.

RESULTS

Eight cephalopod species were encountered in the February surveys between 1996 and 2003 (table 1): *Alloteuthis subulata* (Lamarck, 1798), *Eledone cirrhosa* (Lamarck, 1798), *Loligo forbesi* Streenstrup, 1856, *L. vulgaris* Lamarck, 1798, *Onychoteuthis banksii* (Leach, 1817), *Sepia officinalis* Linnaeus, 1758, *Sepiola atlantica* d'Orbigny, 1840, and *Todaropsis eblanae* (Ball, 1841). High but fluctuating numbers of *A. subulata* were encountered in this time of the year, from a total of 1233 animals in 1996 to 20,590 animals in 1998 (approximately 60,000 animals in total over the 8-year survey period). The number of specimens of the other species was low, from a mere 395 animals of *S. atlantica* caught in the 8-year survey period down to 2 animals of *O. banksii* caught in 1999 but not encountered in any other year. Using data on the number of hauls, haul depth, salinity and temperature (table 2), frequency distributions were calculated for each species according to depth, temperature and salinity (table 3).

Nine cephalopod species were encountered in August - September surveys by "Tridens" between 1996 and 2003 in deep water: *A. subulata, E. cirrhosa, L. forbesi, L. vulgaris, Rossia macrosoma* (Delle Chiaje, 1829), *S. officinalis, Sepietta oweniana* (d'Orbigny, 1840), *S. atlantica,* and *T. eblanae* (table 4). The number of animals per species was low (*A. subulata, E. cirrhosa, L. forbesi, S. atlantica*) to extremely low (*L. vulgaris, R. macrosoma, S. officinalis, S. oweniana, T. eblanae*). Five of these species were also encountered in the catches of "Isis" in shallower water: *A. subulata, E. cirrhosa, Loligo* spec., *S. officinalis,* and *S. atlantica.* In these shallower waters, higher numbers of *A. subulata* and *S. officinalis* were encountered than in deeper waters, while very low numbers or none at all were encoun-

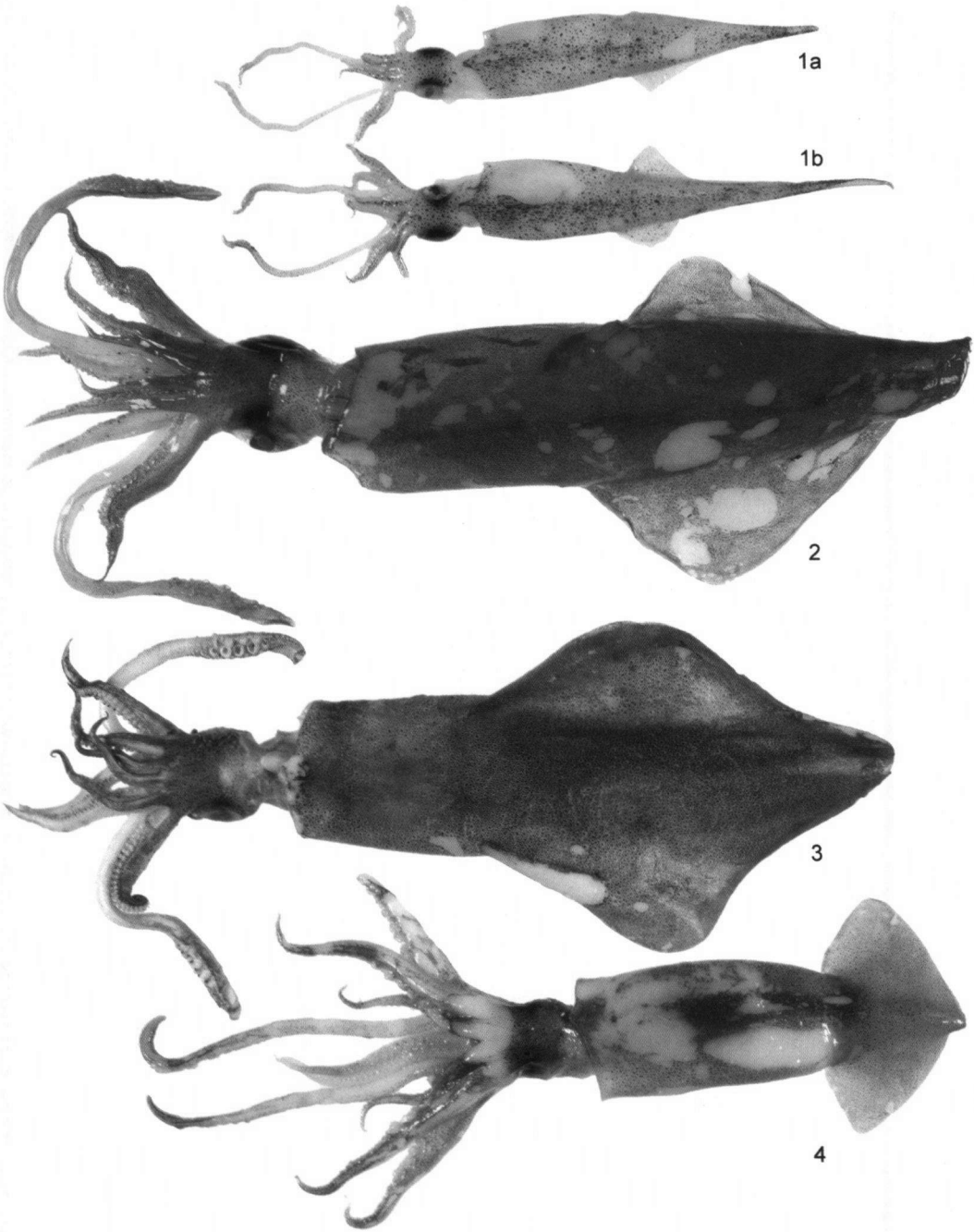

Plate 1. North Sea cephalopods collected during the RIVO surveys. **1**, *Alloteuthis subulata* (Lamarck, 1798), **a** female, **b** male. **2**, *Loligo forbesi* Steenstrup, 1856. **3**, *Loligo vulgaris* Lamarck, 1798. **4**, *Todaropsis eblanae* (Ball, 1840).

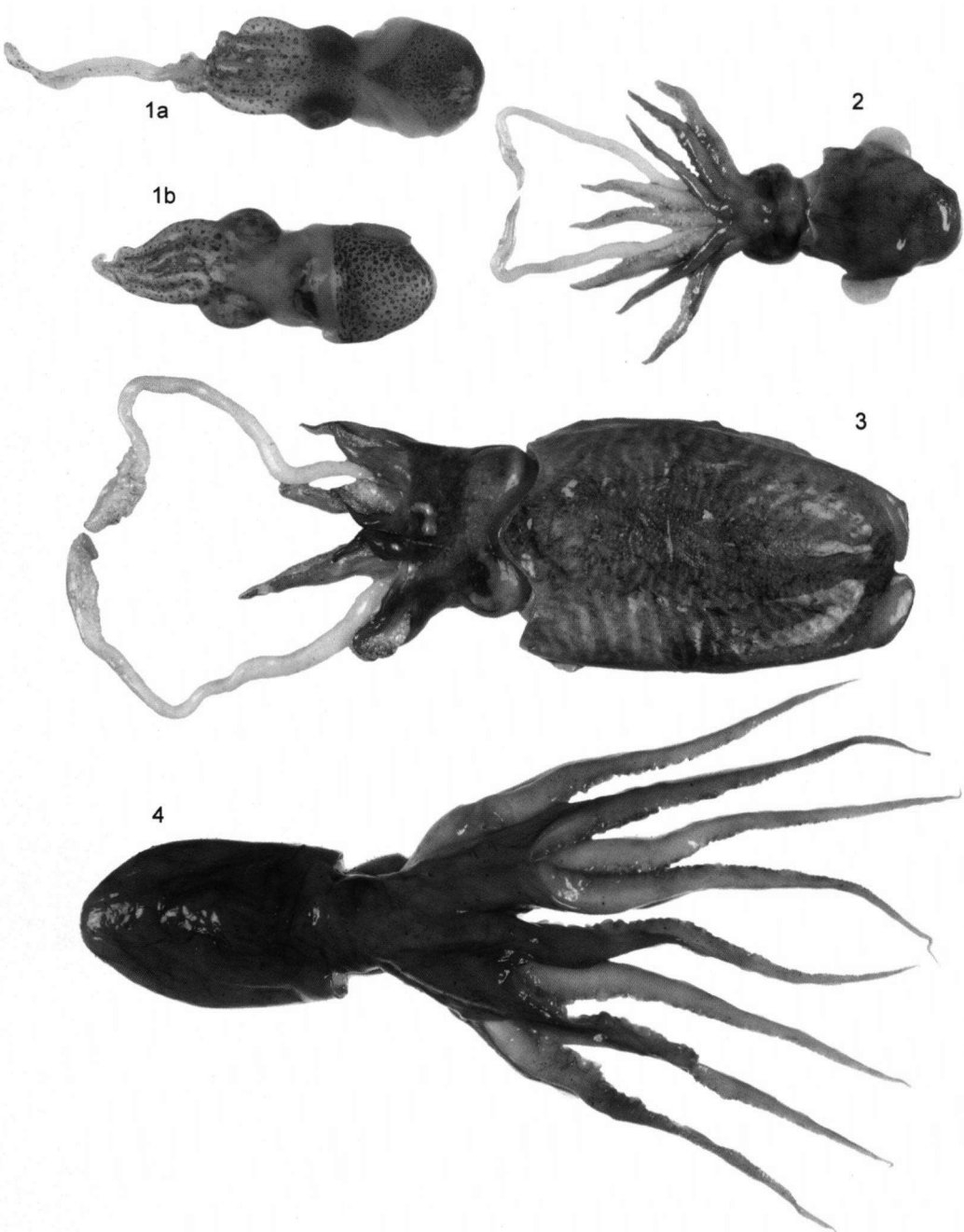

Plate 2. North Sea cephalopods collected during the RIVO surveys. **1**, *Sepiola atlantica* d'Orbigny, 1840, **a** dorsal, **b** ventral. **2**, *Rossia macrosoma* (Delle Chiaje, 1829). **3**, *Sepia officinalis* Linné, 1758. **4**, *Eledone cirrhosa* (Lamarck, 1798).

tered for *E. cirrhosa, R. macrosoma, S. oweniana,* and *T. eblanae.* Total numbers of animals for the nine species caught in August and September by "Tridens" and "Isis" revealed very low numbers of *A. subulata* in September compared with February (table 1). Numbers of *E. cirrhosa, R. macrosoma,* and *S. officinalis* were higher in September than in February. Using data on the number of hauls, haul depth, salinity and temperature (table 5), frequency distributions were calculated for each species according to haul depth, temperature and salinity (table 6).

Ecological and seasonal distribution patterns for the ten species encountered in this study are as follows. In the February surveys, *A. subulata, E. cirrhosa, L. forbesi,* and *T. eblanae* were mainly or exclusively (*E. cirrhosa*) present in deeper water (depth class 80 m). In this time of the year, *L. vulgaris* and *S. atlantica* preferred more shallow waters (depth classes from 23 to 60 m). The species also differed in temperature preference. *A. subulata, L. forbesi,* and *T. eblanae* preferred water temperatures of 8 °C. *L. vulgaris* and *S. atlantica* preferred waters of 8-9.5 °C, while *E. cirrhosa* preferred relatively cool waters (68 °C). Most species were found at high salinities (35.2 ‰), except for *S. atlantica,* which was found at salinities of between 34.4 and 34.8 ‰. *T. eblanae* was almost exclusively found at the highest salinity (35.2 ‰). In the August and September surveys, *A. subulata* was mainly present in shallow water (23 m and 40 m depth classes) at 15-18 °C. A similar preference was found for *L. forbesi* and *L. vulgaris,* species that were found at moderate salinities (34.4-34.8 ‰). *E. cirrhosa, R. macrosoma, S. atlantica,* and *T. eblanae* preferred deep waters (80 m and 100 m depth classes) with a temperature of 6-12 °C and a salinity of 34.8-35.2 ‰.

LOLIGINIDAE Steenstrup, 1861

Alloteuthis subulata (Lamarck, 1798) (Plate 1 fig. 1a, b)

In February, large numbers of *A. subulata* were found in deep water (depth class 80 m) in the central North Sea and close to Scotland, at temperatures around 8 °C and a high salinity (35.2 ‰) (tables 1, 3; fig. 1). Specimens caught in February were relatively young (mantle length 2-14 cm, mostly 4-6 cm). Sex identification, based on the morphology of the hectocotylus, is possible for animals of 6 cm and larger. Males generally were larger than females; at 8 cm dorsal mantle length, females were dominant, while at 11-14 cm dorsal mantle length nearly only males were found (table 7). In August-September, low numbers of *A. subulata* were encountered, mainly in shallow water (23 m and 40 m depth classes) at 15-18 °C and 34.4 ‰ salinity (tables 4, 6).

Loligo forbesi Steenstrup, 1856, and *L. vulgaris* Lamarck, 1798 (Plate 1 figs 2, 3)

In February, moderate numbers of *L. forbesi* and *L. vulgaris* were caught, part of which were incomplete and could not be identified (table 1). *L. forbesi* was found at 80 m depth, 8.0 °C and 35.2 ‰ salinity (table 3), at similar places as *A. subulata* (fig. 2). *L. vulgaris* was found at a slightly wider range of conditions (table 3), in the southern North Sea rather than close to Scotland as for *L. forbesi* (fig. 3). Specimens of *L. forbesi* were slightly larger (11-43 cm) than those of *L. vulgaris* (7-34 cm); in both species, males were slightly larger than females (table 7). In September, both species were found at 23-40 m depth, at temperatures of 15-18 °C and salinities of 34.4-34.8 ‰ (table 6), in similar numbers as in

February. Animals caught in winter were mostly adult (table 7). Animals caught in August-September were mostly juveniles, with the exception of a few specimens of *Loligo forbesi* (coexistence of two generations). In August-September, most animals were caught in the coastal waters of The Netherlands, Germany and Denmark by "Isis" but could unfortunately not be taken ashore for identification at species level (fig. 4, table 4). In general, the ecological preference of both species was similar to that of *A. subulata* (tables 3, 6), but in winter *L. forbesi* finds the preferred conditions in the north-western part of the central North Sea, while *L. vulgaris* additionally occurs in the English Channel (figs 2, 3).

SEPIOLIDAE Leach, 1817

Sepiola atlantica d'Orbigny, 1840 (Plate 2 fig. 1a, b)

In all years of the study, moderate numbers were caught in February (table 1). Animals were found at all depths, temperatures and salinities, although warmer waters (9.5 °C) were favoured as well as moderate salinities (34.4-34.8 ‰) (table 3). *S. atlantica* was found in the entire central and southern North Sea, particularly close to Scotland and in the Channel, but not in the colder waters to the north of the Wadden Sea (fig. 5). In August-September, similar numbers of animals as in February were caught in some years, while in other years very few animals were caught or none at all (table 4). This species was encountered again over the full range of depth, temperature and salinity conditions (table 6), with a preference for deeper waters (100 m) as present close to Scotland (fig. 5). In February, size ranged from 1.0 to 2.5 cm, in August-September from 1.0 to 3.1 cm. Males and females were equally sized and present in equal proportions (table 8). Frequency distributions for temperature and salinity classes in August-September suggested that two populations may be involved, one consisting of larger animals (on average 2.5 cm) preferring colder waters (9.0-12.0 °C), the other consisting of smaller ones (on average 1.9 cm) preferring higher temperatures (21.0 °C), and both living at 34.7-34.9 ‰ average salinity (table 6).

Rossia macrosoma (Delle Chiaje, 1829) (Plate 2 fig. 2)

R. macrosoma was not encountered in February. In August-September, animals were caught incidentally in deeper (100 m) and colder (6.0-12.0 °C) waters with a high salinity (34.8-35.2 ‰) (tables 4, 6). The animals were in the size-range of 3-7 cm and consisted mainly of females (table 8). Differences in size between males and females were not observed. *R. macrosoma* was only found in the northern part of the survey area (fig. 6), in the rectangles fished in August-September but not in February.

Sepietta oweniana (d'Orbigny, 1840)

S. oweniana was not encountered in February. Four females sized 3.5-4.0 cm were caught in August-September 1999, close to the southern coast of Norway, in 60 m deep waters at 6.0-9.0 °C (tables 4, 6 and 8). *S. oweniana* was only found in the northern range of the survey area (fig. 7). Since these rectangles were not fished in February, no conclusions can be drawn on seasonal differences in distribution. For these catches no information on salinity is available.

SEPIIDAE Keferstein, 1866

Sepia officinalis Linnaeus, 1758 (Plate 2 fig. 3)

In February, four incidental females of *S. officinalis* sized 11-23 cm were found at various locations and conditions (tables 1, 3; fig. 8). *S. officinalis* was more regularly caught in August-September, in shallow (23-40 m depth) and warm (18.0-21.0 °C) coastal waters and in the Channel (tables 4, 6; fig. 8). The distribution over the size classes (table 7; including data from "Isis" from 1995) revealed the presence in August-September of two generations: large numbers of juveniles (2-8 cm; too small for sex identification), and low numbers of adults (11-20 cm, both males and females). *S. officinalis* inhabits warmer southern waters during winter, and migrates to shallow, warm coastal waters during summer.

OMMASTREPHIDAE Steenstrup,1857

Todaropsis eblanae (Ball, 1840) (Plate 1 fig. 4)

In February, *T. eblanae* was incidentally found, except for an invasion of animals in 1998 (table 1). The animals (5-11 cm long; too small for sex identification) lived in deeper waters (60-80 m) of the northwestern part of the central North Sea (fig. 9), mainly at 8.0 °C and 35.2 ‰ salinity (table 3). In August-September, low numbers of *T. eblanae* were found in most years; invasions were not observed (table 4). The animals lived in slightly deeper waters (80-100 m) in the same region and at similar temperatures and salinities as in February (table 6; fig. 9). Females were more abundant and slightly larger than males (table 7).

ONYCHOTEUTHIDAE Cray, 1849

Onychoteuthis banksii (Leach,1817)

The single findings of *O. banksii* were made in February 1999. One animal of 11.5 cm (sex unidentifiable) was caught in the central North Sea at 84 m depth in water of 7°C and 35.0 ‰ at 56°07' N 2°8' E. A second, female of 17.0 cm was caught in the entrance of the Channel at 37 m depth in water of 7.4°C and 35.2 ‰ salinity at 51°25' N 23' E (fig. 10).

OCTOPODIDAE d'Orbigny, 1845

Eledone cirrhosa (Lamarck, 1798) (Plate 2 fig. 4)

In February, *E. cirrhosa* was incidentally encountered close to Scotland, at 80 m depth, 6.0-8.0 °C and salinities of 34.8-35.2 ‰ (tables 1, 3; fig. 11). In September, considerably larger numbers were encountered in the same area and deeper south and east in the North Sea, in waters with similar depth (60-100 m), temperature (6.0-12.0 °C) and salinity (34.8-35.2 ‰) as in February (tables 4, 6; fig. 11). The small catches in February are likely due to the use of a bottom trawl that touches the sea bottom much more lightly than the beam trawls used in August-September, thus allowing animals to escape. The seasonal distribution pattern suggested temporary southward migration of *E. cirrhosa* from the northern

North Sea into the northern part of the central North Sea during spring and summer. The animals caught in August-September were mainly females. Twenty of the 22 males found over all years were caught in a single year (2000), despite similar total catches of *E. cirrhosa* in autumn of 1998, 1999 and 2000 (table 4). The animals mainly had a dorsal mantle length of 5-8 cm, incidentally up to 14 cm. Individual weight was also recorded, because of difficulties to measure the dorsal mantle length accurately. Animal weight increased considerably with size (table 7).

DISCUSSION

Ten cephalopod species were encountered in the central and southern North Sea in the IBTS and BTS surveys from 1996 to 2003. These species belonged to six families: Loliginidae (*Alloteuthis subulata, Loligo forbesi, L. vulgaris*), Sepiolidae (*Sepiola atlantica, Rossia macrosoma, Sepietta oweniana*), Sepiidae (*Sepia officinalis*), Ommastrephidae (*Todaropsis eblanae*), Onychoteuthidae (*Onychoteuthis banksii*), and Octopodidae (*Eledone cirrhosa*). Of these ten species, *R. macrosoma* was encountered only at the northernmost part of the investigated area, while *O. banksii* and *S. oweniana* were very rare and seemed to have entered the central and southern North Sea accidentally. Despite 459 hauls in February 1996-2003 (equalling 230 fishing hours) and 1114 hauls (557 fishing hours) in August-September 1996-2003, no more than 2 and 4 animals, respectively, were caught of the latter two species. The remaining species (*A. subulata, L. forbesi, L. vulgaris, S. atlantica, S. officinalis, T. eblanae, E. cirrhosa*) may be considered inhabitants of the central and southern North Sea. Of these, only *A. subulata* lives in the investigated area in large numbers. The same seven species were also considered regularly present in the "southern North Sea" (= the central and southern North Sea of the present study) by Muus (1963). The latter author considered *Octopus vulgaris* Lamarck, 1798 to also inhabit this area, as recalled by later authors (Janssen, 1975; Lacourt & Huwae, 1991). Grimpe (1925) reported the species only from coastal waters in Belgium and The Netherlands. Kristensen (1966) believed that *O. vulgaris* was a rare invader of the southern North Sea. *O. vulgaris* seems to have disappeared from the central and southern North Sea around 1965 (Boer, 1971) and was not recorded in the present study.

The central and southern North Sea forms a very shallow part of the European continental shelf. The cephalopod species living there are mainly neritic, and often benthic or demersal, species. Of the 11 orders, 50 families, 154 genera and approximately 718 species in recent Cephalopoda (Nesis, 2003), 7 families (2 partially), 42 genera and 371 species are considered neritic or partly neritic. Five of the 7 neritic families inhabit the central and southern North Sea (neritic: Loliginidae, Sepiolidae, Sepiidae; partially neritic: Ommastrephidae, Octopodidae). The Onychoteuthidae, represented in our study by two isolated findings of *Onychoteuthis banksii*, are oceanic (Nesis, 2003). The Ommastrephidae are partially neritic and include several very large species believed to belong to the Dutch fauna (Janssen, 1975; Lacourt & Huwae, 1981) but not encountered in this study. All reported findings of such large animals pertain to aged animals washed ashore, possibly after spawning. Such animals have likely entered the waters of the central and southern North Sea accidentally (Jansen, 1975).

The cephalopod species inhabiting the central and southern North Sea (*A. subulata, L. forbesi, L. vulgaris, S. atlantica, R. macrosoma, S. officinalis, T. eblanae, E. cirrhosa*) cover a mere 1% of all cephalopod species and no more than 2.5% of the neritic cephalopod species. The central and southern North Sea apparently are not a favourable habitat for cephalopods: only one species (*A. subulata*) occurs in large numbers, the others occur in relatively low

numbers. The quantities of squid caught by commercial fisheries in the northern North Sea and northwest of Scotland are far higher than those caught in the central and southern North Sea; still larger quantities of squid and also cuttlefish are landed from the English Channel (Pierce et al., 2002). Landings of *E. cirrhosa* and *O. vulgaris* from the central and southern North Sea are nearly zero. In contrast, 35 species of cephalopods have been reported by Muus (1963) from the coastal area of the northeastern Atlantic Ocean. Ecological constraints are the shallowness of the water, salinity, temperature and depth. Many cephalopods live in deep waters, and the shallow waters of the investigated parts of the North Sea do not seem to offer favourable conditions. According to some authors, animals may encounter problems with the mud on the sea bottom coming from the rivers and settling in shallow waters (Jaeckel, 1957). Remarkably, the Myopsida [including Loliginidae and Sepiidae (Jaeckel, 1957)], with protective eye lids, dominate in these waters. A similar protective, moveable eye lid (Jaeckel, 1957) is present in *E. cirrhosa*, the single member of the Octopodidae encountered in this study. Waters with higher temperatures (such as the Mediterranean Sea) or greater depths (such as the Atlantic Ocean) are inhabited by far higher numbers of cephalopod species (Muus, 1963; Collins et al., 2001).

The occurrence, seasonal distribution, ecological niche and migration patterns of the ten species encountered in this study are discussed below.

Alloteuthis subulata

A. subulata is a neritic, demersal species associated with sandy and hard bottoms (Roper et al., 1984). Jaeckel (1958) considers it an necto-pelagic species, living to a depth of 200 m and preferring sandy, muddy or hard sea bottoms. Stevenson (1935) considered *A. subulata* to be the commonest cephalopod in the deep waters [40 fathoms (=72 m) or more] under the Yorkshire coast in winter and early spring. This agrees with data from the present (fig. 1) and a previous study (De Heij & Baayen, 1999). Large numbers of young animals were caught in February, while moderate numbers of full-grown animals were encountered in August-September, in accordance with Grimpe (1925). Most animals caught in winter had probably died by August-September, after spawning in May or June. Juvenile animals hatched from the eggs were too small in August-September to be caught; they are found from November onwards (De Heij & Baayen, 1999). During autumn and early winter, the juveniles migrate from the cooling southeastern coastal waters to feeding grounds in the deeper, in winter relatively warmer, waters of the central North Sea and east of Scotland (De Heij & Baayen, 1999). In spring, the young adults return to the warming shallow coastal waters along the Danish, German, Dutch, Belgian and southeastern British coasts for spawning. Ecological niche and seasonal migration in relation to water temperature have been discussed in detail by De Heij & Baayen (1999). *A. subulata* is fully adapted to the ecological conditions present in the central and southern North Sea and completes its life cycle in these waters.

Loligo forbesi

L. forbesi is a necto-benthic species that prefers deeper waters (to 400 m or more) than *L. vulgaris* (Jaeckel, 1958). Grimpe (1925) considered it to inhabit the entire North Sea, except close to the coast of the Netherlands. On the other hand, Kristensen (1966) reported that *L. forbesi* migrates in spring from northern waters towards the coastal waters of the Netherlands to depths of 30 m or, when water salinity is sufficiently high, closer to the

shore. The present study does not offer any conclusive evidence on the occurrence of *L. forbesi* in coastal waters of the Netherlands. However, it is unlikely that *L. forbesi* occurs close to the Dutch coast: Vooys et al. (1993) report no findings from 1931 to 1990 within 60-65 km from Den Helder (in the northwest of the Netherlands). In the present study, *L. forbesi* was abundant particularly close to the Scottish coast (Aberdeen) in February. *L. forbesi* is a common target of commercial fisheries from Aberdeen (Pierce et al., 1998). Along the eastern Scottish coast and more to the north, outside of the area investigated in the present study, *L. forbesi* is also fished upon but catches fluctuate from year to year. By-catch of *L. vulgaris* here is exceptional (Pierce et al., 1998; Bellino et al., 2001). In the Channel, *L. forbesi* is abundant and is also subject to a directed fishery (Pierce et al., 2002). Near Calais, *L. vulgaris* is frequently caught along with *L. forbesi* (Royer et al., 2002). Total squid landings in Aberdeen and British harbours along the Channel are nevertheless low, indicating that the central and southern North Sea are a marginal area for *L. forbesi*. The central and southern North Sea are probably merely used for feeding: during the spawning season (December to February), the Scottish population mainly inhabits the waters to the north and north-west of Scotland (Bellino et al., 2001), and the Channel population inhabits the western part of the English Channel (Royer et al., 2002).

Loligo vulgaris

L. vulgaris is a necto-benthic species favouring shallow waters, exceptionally up to a depth of 250 m (Jaeckel, 1958). Roper et al. (1984) consider it a neritic semi-pelagic species. It is considered to inhabit the waters along the eastern coast of the North Sea to the waters opposing the German and Danish Wadden Islands (the German Bight) (Grimpe, 1925; Tinbergen & Verwey, 1945). In the present study, *L. vulgaris* was encountered in February close to Aberdeen as well as in the Southern Bight (fig. 3). It is abundant in the eastern Channel in winter (Royer et al., 2002). *L. vulgaris* enters the southern North Sea in spring for spawning (Kristensen, 1966; Tinbergen & Verwey, 1945). The egg masses used to be known among Dutch coastal fishermen as "Grondkwal" (Bottom Jellyfish) (Boer, 1971). The distribution map for August - September (fig. 3) shows a gap along the coast of the Netherlands due to unidentified *Loligo* specimens that were not sampled for later identification. Vooys et al. (1993) report abundant presence of *L. vulgaris* close (60-65 km) to Den Helder from 1931 to 1990. Most *Loligo* sp. caught close to the coast of the Netherlands in August-September likely belong to *L. vulgaris*. During autumn, *L. vulgaris* returns to the south. Some of the animals seem to get mixed up with groups of *L. forbesi*: both species are often caught together. A comparison of the two distribution maps nevertheless shows that *L. vulgaris* is a distinctly more southern species than *L. forbesi*.

Sepiola atlantica

According to Jaeckel (1958), *S. atlantica* is a benthic species living mainly on sandy sea bottoms. Yau & Boyle (1996) consider *S. atlantica* to be a nectobenthic species. *S. atlantica* is endemic for the European Atlantic coast and its bays and coves (Jaeckel, 1958). It is not uncommon in the North Sea, where it is found during summer very close to the shore in the sea arms and estuaries and during winter in more deep water (Tesch, 1908; Grimpe, 1925; Stevenson, 1935; Van Moorsel, 2004). In the present study, adults were encountered both in February and in August-September. With an estimated life of six to eight months, this indicates that several generations may be produced annually. The figures of Yau &

Boyle (1996) and remarks made by Jaeckel (1958) support this conclusion. In the present study, two populations seemed to occur, the individuals of one of which are considerably larger (24-31 mm) than regular *S. atlantica* (maximally 23 mm). Investiga-tions are currently being carried out at the National Museum of Natural History and Leiden University to check whether both populations differ in DNA sequences (J. Goud and E. Gittenberger, personal communication).

Rossia macrosoma

R. macrosoma is a demersal species of shallow to medium deep waters (30-600 m). It inhabits the deep waters (> 100 m) of the northern North Sea along the Norwegian coast to the Skagerrak and along the Scottish coast to about 55°30′ N (Grimpe, 1925; Jaeckel, 1958). *R. macrosoma* occurs exceptionally in the eastern part of the Channel (Muus, 1963). No reports are available from the southern North Sea. During the eight years of the present study, merely three animals were caught south of 57°30′ N (fig. 6). Only when the fishing area was extended northward to 58°N, in 1998, considerably more animals were caught. Since the only specimens caught came from the northernmost rectangles that were surveyed exclusively in August-September, no conclusions on seasonal changes in distribution may be drawn from the present study. According to Roper et al. (1984), *R. macrosoma* migrates between deeper (winter) offshore waters and shallow (summer) coastal waters. Our data suggest that water salinity, rather than depth, may be the critical factor (table 6). Findings were made in saline waters, whatever the depth or temperature, but never in less saline waters (compare also fig. 6 with figs 12 and 14). In the central and southern North Sea, high salinities are limited to the cold, deep waters in the north and the deep-water Channel just off the Belgian coast (figs 12, 14). The common occurrence of *R. macrosoma* in the northern North Sea but not in the eastern Channel explains why it reaches the northern part of the central North Sea but not the southern North Sea.

Sepietta oweniana

S. oweniana is a small nectobenthic species that is found on the continental shelf and slope of the northeast Atlantic and adjoining seas (Bergström and Summers, 1983). In the northeastern Atlantic Ocean it is mostly found at 50-100 m (range: 50-600 m) (Roper et al., 1984). Quetglas et al. (2000) reported *S. oweniana* from the Baleares from greater depths (100 m to 600 m), with a preference for depths greater than 200 m. Collins et al. (2001) reported *S. oweniana* from the deep waters on the break of the continental slope, to the south-west of Ireland. The preferred salinity, 34 to 35 ‰ (Bergström and Summers, 1983), would not seem to be a limiting factor for geographic distribution. In this study, *S. oweniana* was incidentally found to have invaded the central and southern North Sea. Reports from the Westerscheldt (Tesch, 1908, cited by many authors without further proof) are questionable.

Sepia officinalis

S. officinalis is a neritic, demersal species preferring sandy and muddy bottoms of shallow, warm coastal waters (Roper et al., 1984; table 6). The animals reproduce in inland river arms and waters and even occur in coastal lagoons in waters with a very low salini-

ty (27‰) (Von Boletzky, 1983). Annual counts of animals in the Easterscheldt in the south of the Netherlands are presented by Gittenberger & Schrieken (2004). In spring, *S. officinalis* enters the southern North Sea from the Channel (Kristensen, 1966) and migrates along the eastern shores of the North Sea up to the Skagerrak (Grimpe, 1925; Jaeckel, 1958). It is rarely found along the Yorkshire coast (Stevenson, 1935). *S. officinalis* is found in the Easterscheldt from May to November (Gittenberger & Schrieken, 2004). In years with a strong influx of Atlantic water in the north-western North Sea, animals have incidentally been found in January or February in Scottish waters (Stephen, 1944). Findings in the present study follow the same patterns.

Todaropsis eblanae

T. eblanae is a demersal species of the deeper shelf and continental slope, usually associated with sandy and muddy bottoms (Wormuth, 1998). In spite of its occurrence in deeper waters than loliginids (20-700 m), *T. eblanae* is believed to have a life history and behaviour more similar to neritic squids than to oceanic ones like the rest of the Ommastrephidae (citation of Clarke, 1996 in Robin et al., 2002). Grimpe (1925) and Jaeckel (1958) consider the species to occur exceptionally in the northern North Sea. Along the eastern Scottish coast, invasions of *T. eblanae* have been observed (Hastie et al., 1994). These invasions have been attributed to either an enhanced water salinity resulting from increased influx of Atlantic water from the north-west, or higher water temperatures, coinciding with increased numbers of southern species such as *Loligo vulgaris* and *Sepia officinalis*. In the present study, *T. eblanae* was caught mainly in the north-western part of the central and southern North Sea, with an invasion in February 1998 (table 1). Water salinity may be the limiting factor (tables 3, 6). In the present study, mainly juvenile animals were caught in February, as judged from the dorsal mantle length. During summer, adult males but no adult females were encountered. Animals are considered adult and fertile at a dorsal mantle length of 11 cm (males) and 16 cm (females) (Gonzales, 1994; Wormuth, 1998; Arkhipin & Laptikhovsky, 2000).

Onychoteuthis banksii

O. banksii is an oceanic nectonic squid (Arkhipin & Nigmatullin, 1997) living in warm and temperate oceanic waters at an average depth of 150 m (range: 0-800 m). Especially from January to March, it may enter the northeastern part of the Atlantic Ocean from tropical and subtropical waters, with the warm waters of the Gulf Stream (Roper, 1984). Grimpe (1925) considers *O. banksii* to be almost cosmopolitan and reports findings from the northern part of the North Sea to the Skagerrak and the Kattegat. It is incidentally found in the central and southern North Sea.

Eledone cirrhosa

E. cirrhosa is a benthic species living from the coastline down to about 500 m depth. Females lives between 30-80 m depth, males below 100 m. The species is believed to be rather stationary (Roper et al., 1984). Grimpe (1925) reported *E. cirrhosa* from the central and northern North Sea, with a few observations from the southern North Sea. Below 30 fathoms (54 m), *E. cirrhosa* was frequently caught close to the Yorkshire coast (Stevenson,

1935; Pierce et al., 2002). Kristensen (1966) reported low numbers of *E. cirrhosa* from the southern North Sea, especially close to the coast of the Netherlands in years with high water salinity. In this area the numbers of *E. cirrhosa* increased from 1931 to 1970, to decrease again from 1981 to 1990 (Vooys et al., 1993) and eventually disappear entirely. In the present study, carried out between 1996 and 2003, only a single *E. cirrhosa* was caught in this area by "Isis" off the Belgian coast (fig. 11). According to their size (Boyle & Knoblock, 1982), animals caught in the present study were not more than one year old. *E. cirrhosa* has a life cycle of 2-3 years (Roper et al., 1984). We have no explanation for the large number of males of *E. cirrhosa* in 2000 (tables 4, 7). *E. cirrhosa* prefers a water temperature of 12°C, survives in cooler waters, but does not live in waters of 15°C or higher.

CONCLUSIONS

Ten cephalopod species were encountered in the central and southern North Sea in six families (Loliginidae, Sepiolidae, Sepiidae, Ommastrephidae, Onychoteuthidae, and Octopodidae). Apart from *Alloteuthis subulata,* none of the species lived in the investigated area in large numbers. Far higher numbers of the same species, even of *A. subulata,* occur in adjacent waters (Muus, 1963; Pierce et al., 2002). In general, the central and southern North Sea are not a favourable habitat for cephalopods due to the shallowness of the water. The species occurring in the central and southern North Sea are neritic, benthic or demersal, and as such adapted to the specific conditions of these waters.

The seasonal distribution of the cephalopods occurring in the central and southern North Sea depends largely on temperature and salinity. These parameters depend on sea depth, time of the year, and influx of Atlantic water (figs 12-14).

In the central and southern North Sea, deeper water is relatively cool in summer and relatively warm in winter, while the shallow coastal waters of Belgium and The Netherlands are warm in summer and cold in winter. This explains the seasonal migration of *A. subulata,* a species indigenous to the North Sea that prefers relatively warm waters. It migrates northwestwards before winter and southeastwards in late spring (De Heij & Baayen, 1999). A similar migration pattern exists for the two other species of the Loliginidae, *Loligo forbesi* and *L. vulgaris.* Additional to that pattern, the occurrence of the latter two species is also influenced by the influx of relatively warm Atlantic water from the Gulf Stream into the southern North Sea through the Channel (where *L. vulgaris* is abundant), and into the northern part of the central North Sea from the north, along Scotland (where *L. forbesi* is abundant). The seasonal distribution of *Eledone cirrhosa* similarly depends on water temperature. *E. cirrhosa* prefers a temperature of about 12°C, survives in cooler waters, but does not live in waters of 15°C or higher. As a consequence, its migration pattern differs from that in the Loliginidae.

For other cephalopods, salinity rather than temperature is critical. *Rossia macrosoma* and *Todaropsis eblanae* require high salinities. This seems to be fairly critical for *R. macrosoma* which lives in the northern range of the central North Sea, but less so for *T. eblanae,* a species that occurs in moderate numbers in the western part of the central North Sea. In contrast, low salinities are endured by *Sepia officinalis* and *Sepiola atlantica.* Both species spend part of their life in the estuaries and may even survive in water with a salinity as low as 27‰ (Von Boletzky, 1983). While *S. atlantica* lives in the entire central and southern North Sea, *S. officinalis* is restricted to coastal waters and estuaries. Since the survey did only include part of these waters, the numbers of *S. officinalis* are necessarily underestimated in the present study.

Differing from the previously discussed species, *Sepietta oweniana* preferentially

inhabits deep waters (Bergström & Summers, 1983; Collins et al., 2001; Quetglas et al., 2000).

Numerous other cephalopod species occur in the deeper waters of the Atlantic and the Channel. Incidental findings of unusual cephalopod species in the central and southern North Sea, such as those of *Onychoteuthis banksii* and *Sepietta oweniana* in the present study, are generally made either in the northern part of the investigated area or in the south. Such findings are probably due to animals being taken along during periods with a strong influx of Atlantic waters. This also explains the findings along the shores of the North Sea of large and spectacular animals of exotic species (Stevenson, 1935; Jansen, 1975; Lacourt & Huwae, 1981).

ACKNOWLEDGEMENTS

This study was made possible by the help of RIVO, IJmuiden, The Netherlands, that provided us with survey data and frozen animals from the surveys. Thanks are particularly due to Dr H. J. L. Heessen, who helped us in many ways and whose comments on the manuscript were highly valuable, and to the crew of the research vessels "Tridens" and "Isis". The authors wish to thank Ing. Leo Poleij for indispensable help with the computer maps of the North Sea.

Year	*Alloteuthis subulata*	*Loligo forbesi*	*Loligo vulgaris*	*Loligo* sp.[1]	*Sepiola atlantica*	*Sepia officinalis*	*Todaropsis eblanae*	*Onychoteuthis banksii*	*Eledone cirrhosa*	Total (n)
1996	1233	0	51	0	37	0	0	0	1	1322
1997	5767	2	0	0	41	0	1	0	0	5811
1998	20590	21	11	22	91	1	26	0	1	20763
1999	3782	21	15	0	43	0	2	2	0	3865
2000	3488	7	13	1	31	0	0	0	2	3542
2001	7867	11	33	1	45	1	0	0	0	7958
2002	9879	2	19	57	31	0	1	0	0	9989
2003	7329	59	33	1	76	1	4	0	1	7504
Total (n)	59935	123	175	82	395	3	34	2	5	60754

[1]) Unidentifiable animals belonging to either *L. forbesi* or *L. vulgaris*.

Table 1. Cephalopod catches in February in the IBTS surveys in the central and southern North Sea with "Tridens" from 1996 to 2003. n = number of specimens.

Year	Number of hauls	Depth	Temperature	Salinity
1996	45	46 (17-90) m	4.0 (-1.3-7.8) °C	34.3 (31.1-35.2) ‰
1997	51	47 (18-94) m	5.2 (1.9-7.2) °C	34.4 (31.6-35.0) ‰
1998	54	47 (18-87) m	6.6 (4.3-8.0) °C	34.5 (31.4-35.4) ‰
1999	53	48 (19-86) m	5.2 (2.9-9.1) °C	34.4 (31.2-35.3) ‰
2000	55	49 (16-93) m	6.2 (5.0-7.8) °C	34.3 (30.4-35.2) ‰
2001	72	46 (18-96) m	6.1 (3.5-8.3) °C	34.2 (30.0-35.1) ‰
2002	61	47 (19-97) m	7.0 (5.4-9.4) °C	34.1 (28.4-34.9) ‰
2003	68	42 (15-84) m	5.9 (3.7-7.4) °C	34.2 (30.7-35.5) ‰

Table 2. Number of hauls in February in the IBTS surveys in the central and southern North Sea with "Tridens", average haul depth, and average water temperature and salinity at that depth from 1996 to 2003. Ranges are given between brackets.

	Number of hauls	*Alloteuthis subulata*	*Loligo forbesi*	*Loligo vulgaris*	*Loligo* sp.[1]	*Sepiola atlantica*	*Sepia officinalis*	*Todaropsis eblanae*	*Onychoteuthis banksii*	*Eledone cirrhosa*
Depth class										
23 m	101	< 1 %	0%	7%	1%	23%	63%	0%	0%	0%
40 m	188	2%	7%	55%	16%	25%	31%	0%	32%	0%
60 m	51	20%	23%	9%	83%	38%	0%	15%	0%	0%
80 m	87	78%	70%	29%	0%	14%	6%	85%	68%	100%
Temperature class										
3.5 °C	75	< 1 %	0%	0%	0%	8%	12%	0%	0%	0%
6.0 °C	261	12%	14%	6%	< 1 %	20%	88%	8%	0%	60%
8.0 °C	88	87%	86%	52%	2%	11%	0%	92%	100%	40%
9.5 °C	3	1%	0%	42%	98%	60%	0%	0%	0%	0%
Salinity class										
34.0 ‰	102	2%	2%	1%	2%	9%	33%	0%	0%	0%
34.4 ‰	78	3%	4%	7%	2%	39%	0%	0%	0%	0%
34.8 ‰	184	20%	27%	63%	33%	37%	16%	< 1 %	25%	80%
35.2 ‰	63	75%	67%	29%	63%	15%	51%	100%	75%	20%
Total (n)	427	57710	112	153	57	391	3	33	2	4

[1]) Unidentifiable animals belonging to either *L. forbesi* or *L. vulgaris*.

Table 3. Number of hauls and frequency distribution of cephalopods in February according to haul depth classes, corrected for the number of hauls, in the IBTS surveys in the central and southern North Sea with "Tridens" from 1996 to 2003. n = number of hauls or number of specimens.

	Alloteuthis subulata			*Loligo forbesi*			*Loligo vulgaris*			*Loligo spec.*[1]			*Sepiola atlantica*			*Rossia macrosoma*			*Sepietta oweniana*			*Sepia officinalis*			*Todaropsis eblanae*			*Eledone cirrhosa*			Total
Year	TRI	IS	TOT	TRI	IS	TOT	TRI	IS	TOT	TRI	IS	TOT	TRI	IS	TOT	TRI	IS	TOT	TRI	IS	TOT	TRI	IS	TOT	TRI	IS	TOT	TRI	IS	TOT	
1996	0	0	0	1	0	1	12	0	12	0	7	7	0	0	0	0	0	0	0	0	0	0	10	10	0	0	0	3	0	3	33
1997	19	20	39	3	0	3	0	0	0	0	2	2	1	64	65	0	0	0	0	0	0	0	2	2	1	0	1	14	0	14	126
1998	128	27	155	7	0	7	0	0	0	0	56	56	18	64	82	1	0	1	0	0	0	0	0	0	9	0	9	47	0	47	357
1999	44	72	116	5	0	5	0	0	0	0	0	0	3	1	4	13	0	13	4	0	4	0	4	4	4	0	4	53	0	53	203
2000	35	277	312	11	0	11	0	0	0	0	12	12	2	1	3	8	0	8	0	0	0	0	26	26	5	0	5	56	0	56	433
2001	24	246	270	1	0	1	0	0	0	0	2	2	9	6	15	9	0	9	0	0	0	0	3	3	5	0	5	18	0	18	323
2002	93	76	169	21	0	21	1	0	1	0	9	9	69	2	71	8	0	8	0	0	0	0	11	11	9	0	9	14	0	14	313
2003	110	536	646	72	0	72	4	0	4	4	55	59	76	2	78	3	0	3	0	0	0	1	0	1	4	0	4	60	2	62	925
Total	453	1254	1707	121	0	121	17	0	17	4	143	147	178	140	318	42	0	42	4	0	4	1	56	57	37	0	37	265	2	267	2713

[1]) Unidentifiable animals belonging to either *L. forbesi* or *L. vulgaris*.

Table 4. Cephalopod catches in August-September in the BTS surveys in the central and southern North Sea with "Tridens" (TRI) and "Isis" (IS) from 1996 to 2003. TOT = total number of specimens.

Year	Number of hauls		Depth		Temperature		Salinity	
	Tridens	Isis	Tridens	Isis	Tridens	Isis	Tridens	Isis
1996	44	89	55 (18-102) m	32 (16-47) m	9.3 (4.0-16.8) °C	NA	34.7 (33.9-34.7) ‰	NA
1997	43	84	60 (24-101) m	31 (14-49) m	9.9 (6.6-17.7) °C	18.2 (11.2-21.9) °C	34.6 (34.0-35.1) ‰	NA
1998	51	70	59 (24-116) m	30 (15-50) m	11.6 (7.5-17.3) °C	NA	34.8 (34.0-35.2) ‰	NA
1999	61	94	61 (26-115) m	32 (15-50) m	10.5 (7.0-18.0) °C	17.1 (9.4-19.7) °C	34.8 (34.1-35.2) ‰	NA
2000	63	91	59 (23-113) m	33 (15-48) m	10.3 (6.9-17.2) °C	NA	34.9 (33.4-35.8) ‰	NA
2001	65	70	60 (24-111) m	31 (13-49) m	10.6 (6.1-18.6) °C	17.3 (14.4-20.1) °C	NA	NA
2002	62	73	62 (22-114) m	32 (13-47) m	10.9 (7.4-18.4) °C	17.6 (12.3-22.2) °C	35.0 (32.1-35.8) ‰	NA
2003	68	86	61 (29-122) m	31 (15-52) m	11.9 (7.2-18.5) °C	18.6 (17.6-21.4) °C	34.9 (34.3-35.4) ‰	NA

Table 5. Number of hauls in August-September in the BTS surveys in the central and southern North Sea with "Tridens" and "Isis", average haul depth, and average water temperature and salinity at that depth from 1996 to 2003. Ranges are given between brackets. NA = not available.

	Number of hauls			*Alloteuthis subulata*	*Loligo forbesi*	*Loligo vulgaris*	*Loligo spec.* 1)	*Sepiola atlantica*	*Rossia macrosoma*	*Sepietta oweniana*	*Sepia officinalis*	*Todaropsis eblanae*	*Eledone cirrhosa*
	Tridens	Isis	Total	Tridens + Isis	Tridens	Tridens	Isis	Tridens + Isis	Tridens	Tridens	Isis	Tridens	Tridens
Depth class													
23 m	32	209	241	30%	46%	88%	50%	8%	0%	0%	62%	0%	0%
40 m	92	168	260	63%	35%	0%	50%	< 1 %	1%	0%	38%	2%	2%
60 m	96	11	107	3%	17%	10%	0%	18%	0%	100%	0%	9%	34%
80 m	100	0	100	4%	0%	2%	0%	15%	6%	0%	0%	28%	28%
100 m	31	0	31	0%	1%	0%	0%	59%	93%	0%	0%	61%	36%
Temperature class				Tridens + Isis				Tridens + Isis					
6.0 °C	99	0	99	< 1 %	1%	0%	0%	1%	31%	31%	0%	34%	12%
9.0 °C	113	5	118	2%	2%	2%	0%	15%	33%	69%	0%	48%	29%
12.0 °C	66	28	94	4%	18%	0%	0%	31%	36%	0%	0%	18%	59%
15.0 °C	50	68	118	31%	53%	57%	30%	2%	0%	0%	0%	0%	0%
18.0 °C	23	244	267	51%	26%	41%	12%	3%	0%	0%	69%	0%	0%
21.0 °C	0	43	43	13%	0%	0%	58%	18%	0%	0%	31%	0%	0%
Salinity class				Tridens 2)				Tridens 3)					
34.0 ‰	15	NA	NA	20%	0%	0%	NA	44%	0%	NA	NA	0%	6%
34.4 ‰	63	NA	NA	64%	47%	0%	NA	7%	0%	NA	NA	18%	6%
34.8 ‰	169	NA	NA	14%	47%	100%	NA	43%	12%	NA	NA	34%	47%
35.2 ‰	104	NA	NA	2%	6%	0%	NA	6%	88%	NA	NA	48%	41%
Total (n)	351	388	739	1214	104	17	120	229	27	4	15	33	142

1) Unidentifiable animals belonging to either *L. forbesi* or *L. vulgaris*.

2) Data from "Tridens" only (275 specimens of *A. subulata*)

3) Data from "Tridens" only (110 specimens of *S. atlantica*)

Table 6. Number of hauls and frequency distribution of cephalopods in August-September according to haul depth classes, corrected for the number of hauls, in the BTS surveys in the central and southern North Sea with "Tridens" and "Isis" from 1996 to 2003. NA = not available.

Dorsal mantle length class (cm)	*Alloteuthis subulata*				*Loligo forbesi*				*Loligo vulgaris*				*Sepia officinalis*				*Todaropsis eblanae*				*Eledone cirrhosa*					
	February		August - September		February		August - September		February		August - September		February		August - September		February		August - September		February		August - September			
	ns	nm	ns	nm	ns	nm	ns	nm	ns	nm	ns	nm	ns	nm	ns	nm	ns	nm	ns	nm	ns	nm	mw	ns	nm	mw
2	145	?	16	?	0		0		0		0		0		2	?	0		0		0			5	?	20
5	1349	9	43	?	0		3	?	0		27	?	0		331	?	14	?	0		1	0	50	81	6	70
8	386	87	138	23	0		27	?	2	0	34	?	0		11	1?	9	?	4	?	1	0	183	75	13	211
11	40	36	44	20	2	1	35	6	12	6	5	0	1	0	2	0	1	0	29	14	1	0	365	21	3	512
14	3	3	4	4	6	4	22	8	24	14	0		0		15	3	0		22	2	1	0	618	3	0	676
17	0		0		17	11	15	9	30	8	0		0		17	10	0		0		0			0		
20	0		0		25	9	14	8	22	13	0		2	0	2	2	0		0		0			0		
23	0		0		13	3	6	6	10	6	0		1	0	0		0		0		0			0		
26	0		0		11	5	0		8	6	0		0		0		0		0		0			0		
29	0		0		8	7	1	1	4	3	0		0		0		0		0		0			0		
32	0		0		4	3	1	1	1	0	0		0		0		0		0		0			0		
35	0		0		8	7	2	2	0		0		0		0		0		0		0			0		
38	0		0		3	2	0		0		0		0		0		0		0		0			0		
41	0		0		1	1	0		0		0		0		0		0		0		0			0		
T	1923	135	245	47	98	53	126	41	113	56	66		4	0	380	16	24	0	55	16	4	0	1216	185	22	1490

Table 7. Frequency distribution for *A. subulata, L. forbesi, L. vulgaris, S. officinalis, T. eblanae,* and *E. cirrhosa* of dorsal mantle length classes in February and in August-September. Data for *S. officinalis* include those from the "Isis" survey in 1995. For *E. cirrhosa,* animal weight is also given. Question marks indicate animal sizes that were too small for sex identification. Numbers followed by a question mark indicate animals identified as males, but not excluding the presence of other males. ns = number of specimens, nm = number of males, mw = mean weight per specimen (g), T = totals.

	Sepiola atlantica				*Rossia macrosoma*			*Sepietta oweniana*		
	February		August - September		August - September			August - September		
Dorsal mantle length class	ns	nm	ns	nm	Dorsal mantle mantle length	ns	nm	Dorsal mantle length class (cm)	ns	nm
1.0	12	2?	1	1	1.0	0		1.0	0	
1.3	31	12	0		2.0	0		2.0	0	
1.6	82	45	3	3	3.0	13	?	3.0	2	0
1.9	55	23	10	1	4.0	12	2	4.0	2	0
2.2	10	3	7	3	5.0	5	1	5.0	0	
2.5	2	0	14	7	6.0	9	1	6.0	0	
2.8	0		4	1	7.0	3	0	7.0	0	
3.1	0		3	0	8.0	0		8.0	0	

Table 8. Frequency distribution for *S. atlantica, R. macrosoma,* and *S. oweniana* of dorsal mantle length classes in February and in August-September. Question marks indicate specimen sizes that were too small for sex identification. Numbers followed by a question mark indicate animals identified as males, but not excluding the presence of other males.

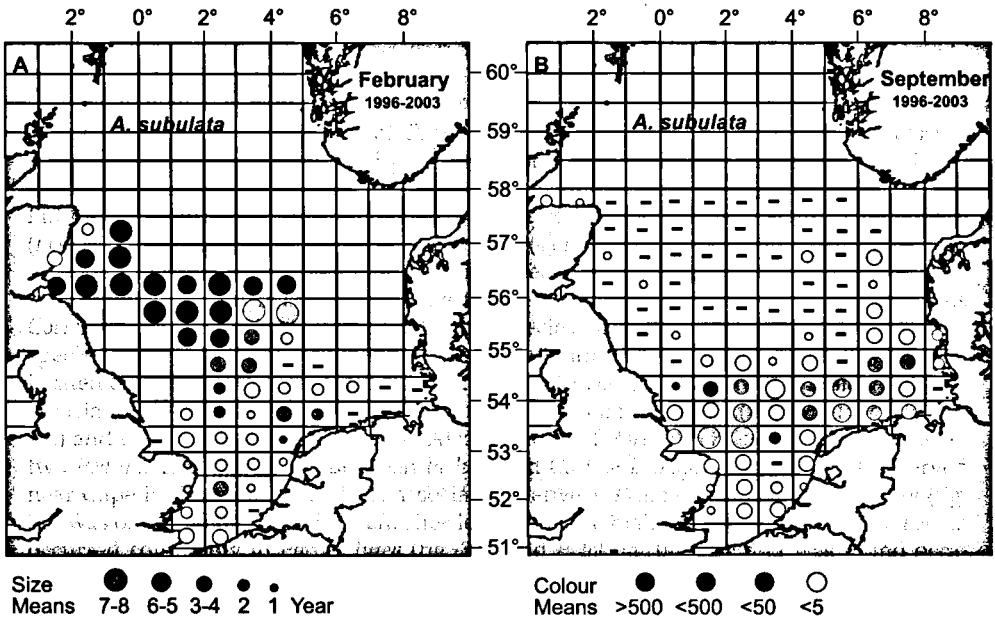

Fig. 1. Geographic distribution of *Alloteuthis subulata* in February and in August-September. The maximum number of animals caught in a single rectangle in February and in August-September was 1370 and 218, respectively.

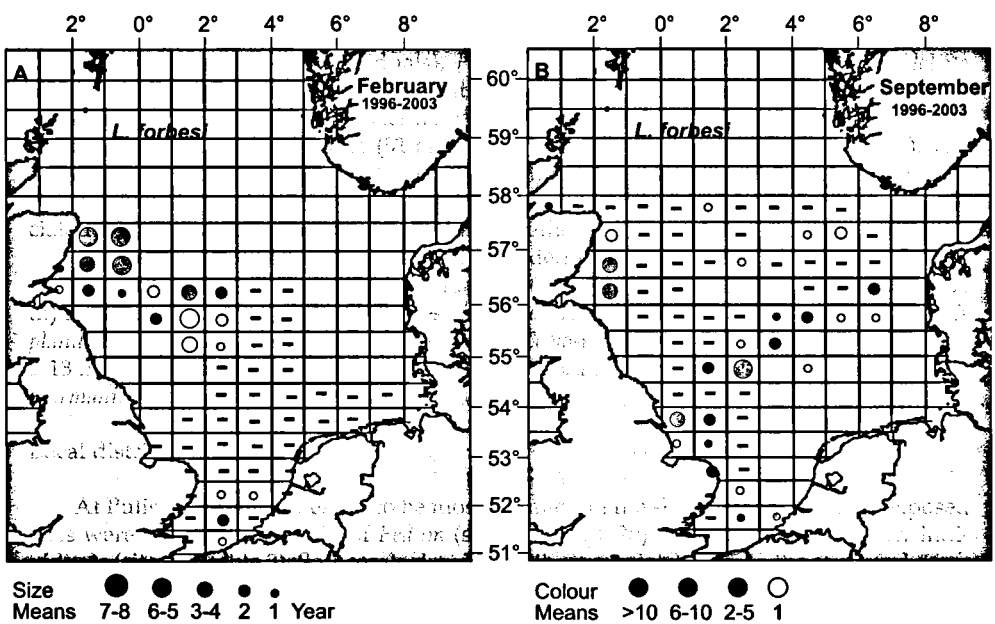

Fig. 2. Geographic distribution of *Loligo forbesi* in February and in August-September. The maximum number of animals caught in a single rectangle in February and in August-September was 6 and 23, respectively.

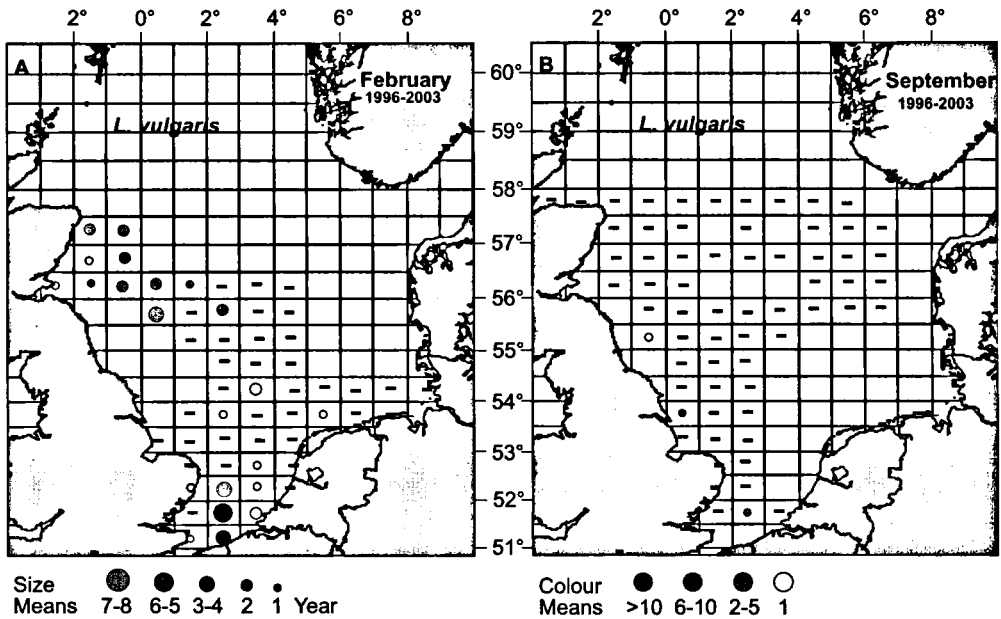

Fig. 3. Geographic distribution of *Loligo vulgaris* in February and in August-September. The maximum number of animals caught in a single rectangle in February and in August-September was 12 and 12, respectively.

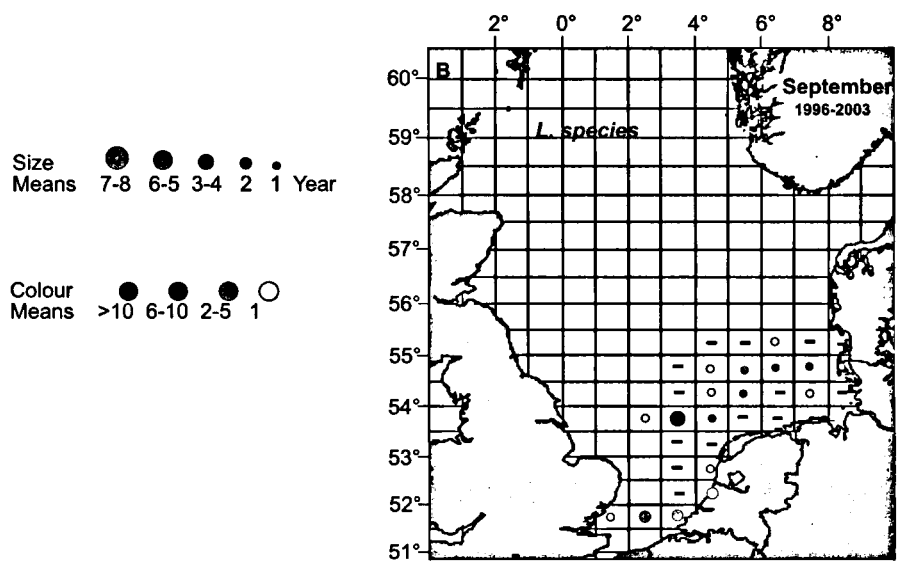

Fig. 4. Geographic distribution of *Loligo* spp. (unidentifiable whether *Loligo forbesi* or *L. vulgaris*) in August-September. The maximum number of animals caught in a single rectangle was 8.

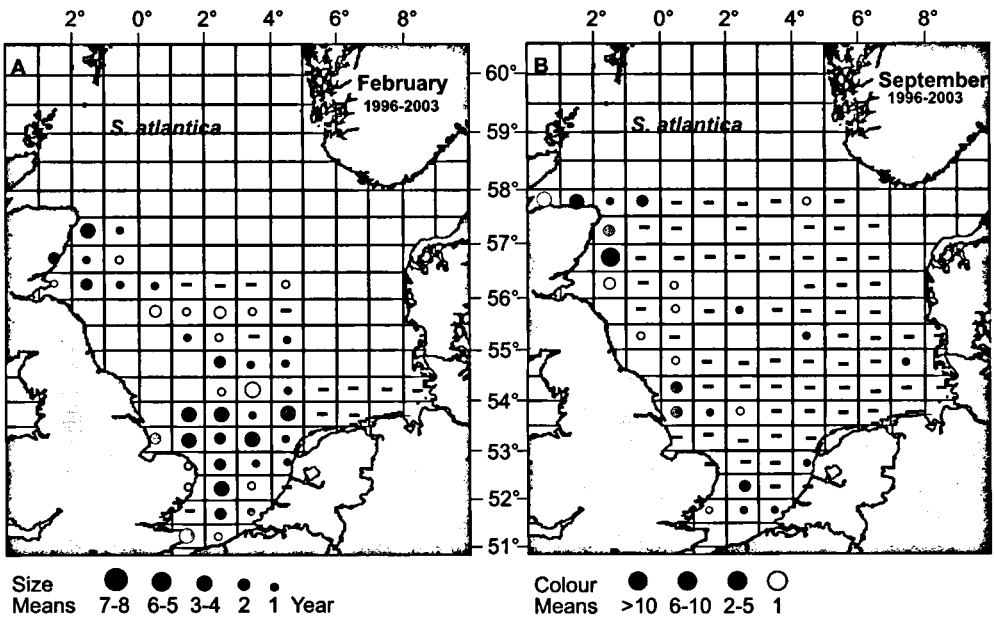

Fig. 5. Geographic distribution of *Sepiola atlantica* in February and in August-September. The maximum number of animals caught in a single rectangle in February and in August-September was 23 and 64, respectively.

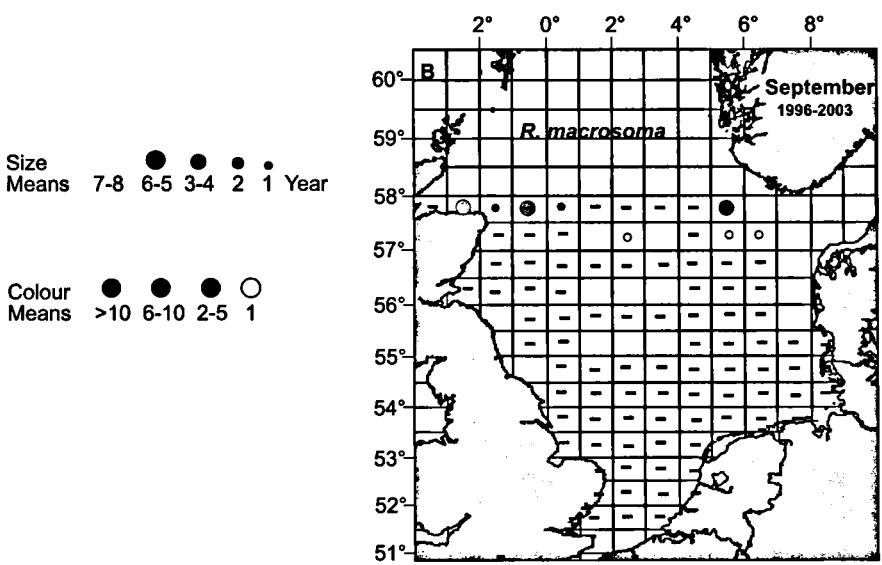

Fig. 6. Geographic distribution of *Rossia macrosoma* in August-September. The maximum number of animals caught in a single rectangle was 6.

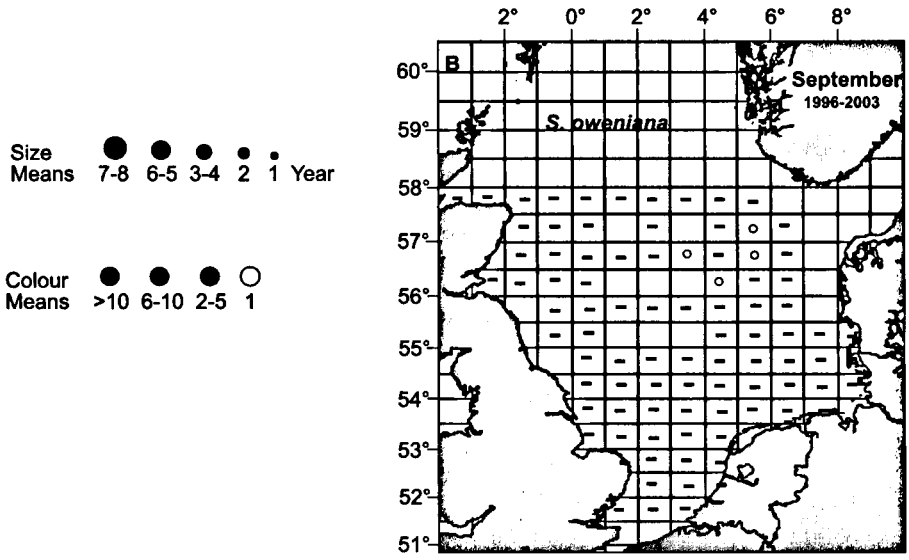

Fig. 7. Geographic distribution of *Sepietta oweniana* in August-September. The maximum number of animals caught in a single rectangle was 1.

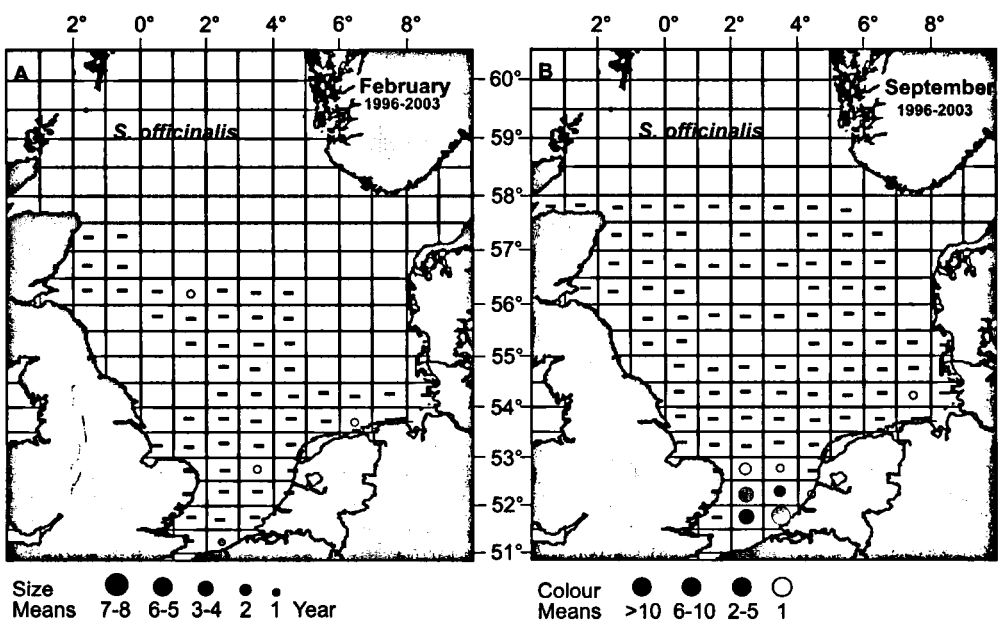

Fig. 8. Geographic distribution of *Sepia officinalis* in February and in August-September. The maximum number of animals caught in a single rectangle in February and in August-September was 1 and 10, respectively.

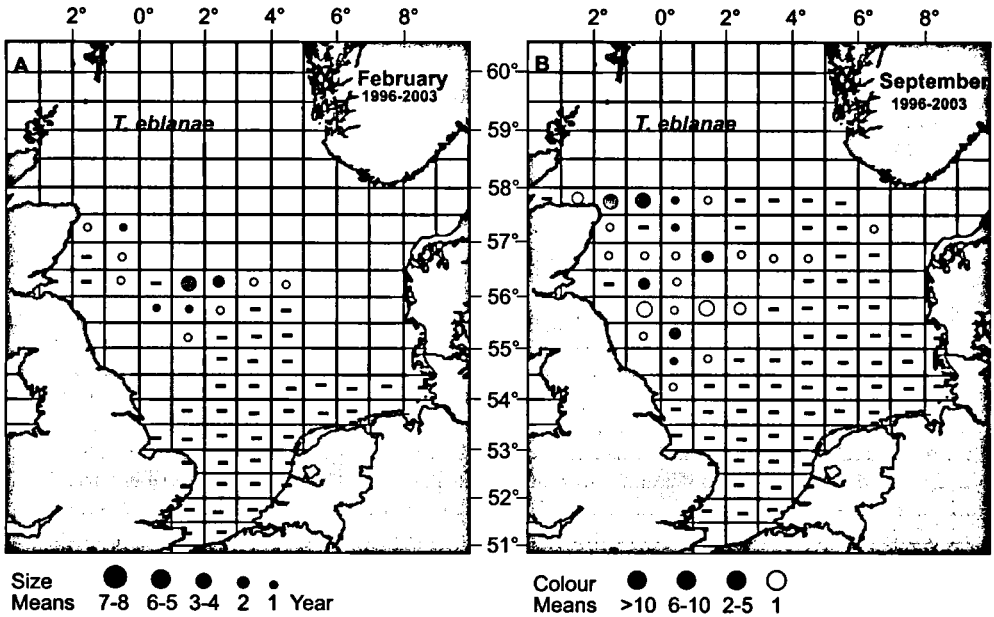

Fig. 9. Geographic distribution of *Todaropsis eblanae* in February and in August-September. The maximum number of animals caught in a single rectangle in February and in August-September was 8 and 4, respectively.

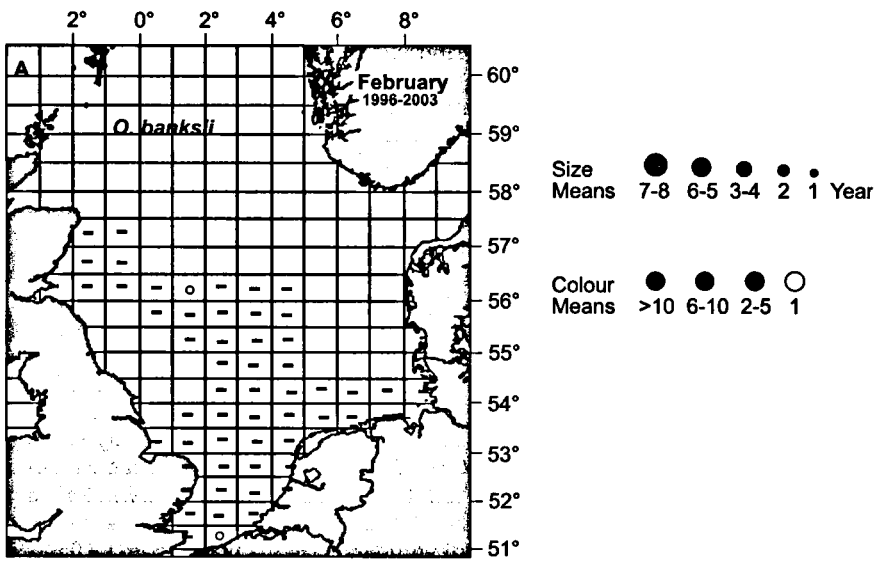

Fig. 10. Geographic distribution of *Onychoteuthis banksii* in February and in August-September. The maximum number of animals caught in a single rectangle in February and in August-September was 1 and 7, respectively.

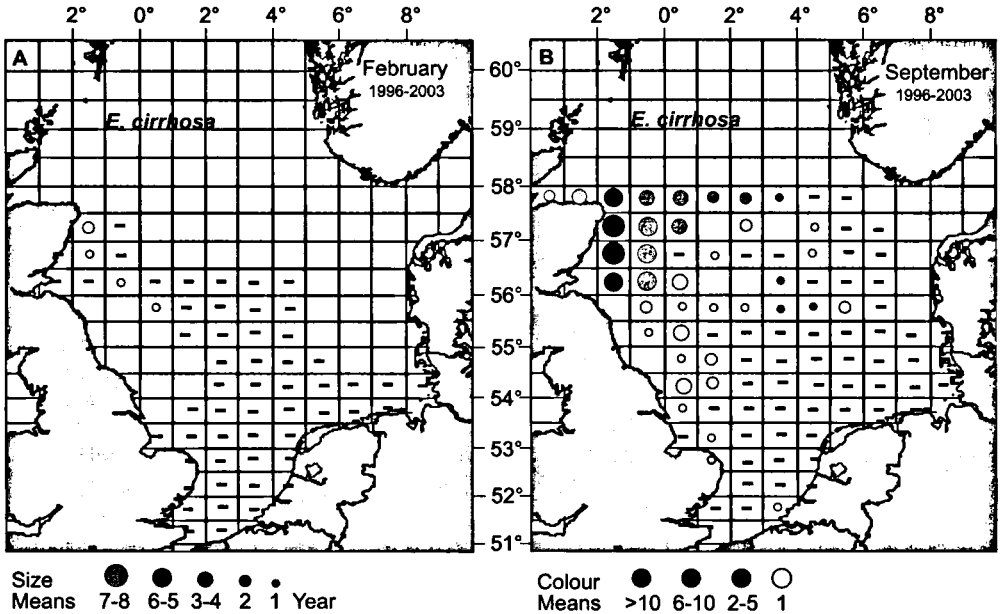

Fig. 11. Geographic distribution of *Eledone cirrhosa* in February and in August-September. The maximum number of animals caught in a single rectangle in February and in August-September was 1 and 7, respectively.

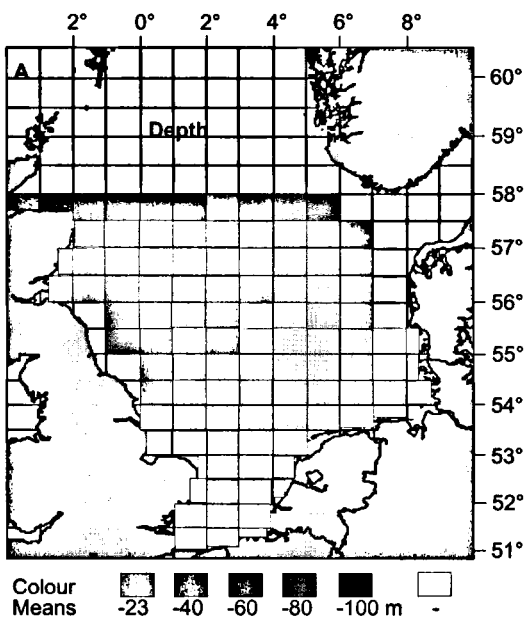

Fig. 12. Depth of the central and southern North Sea. Averages from measurements available for each of the rectangles.

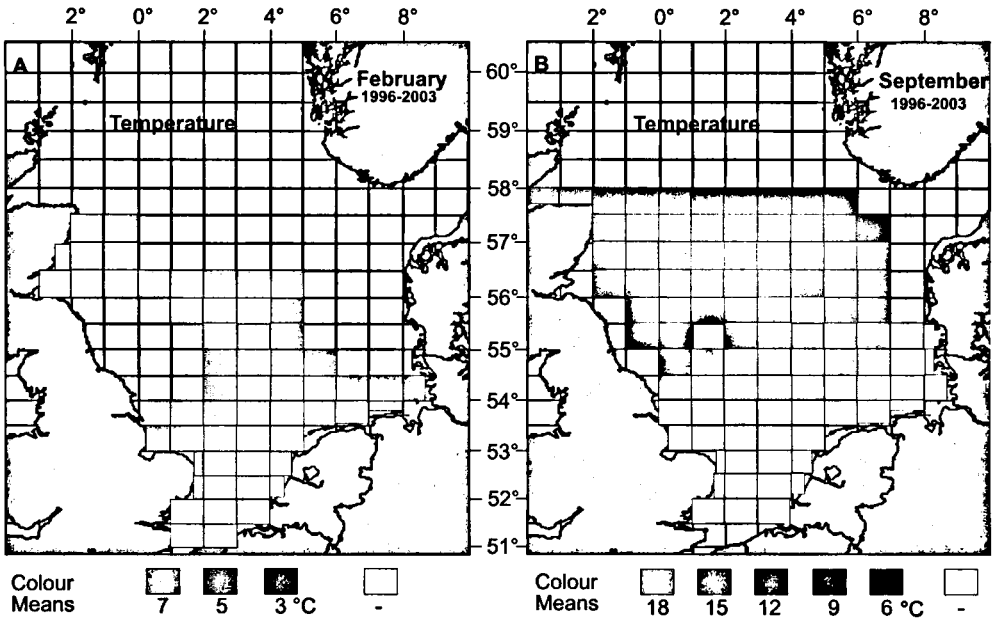

Fig. 13. Water temperature of the central and southern North Sea in February (a) and in August-September (b). Averages from measurements available for each of the rectangles.

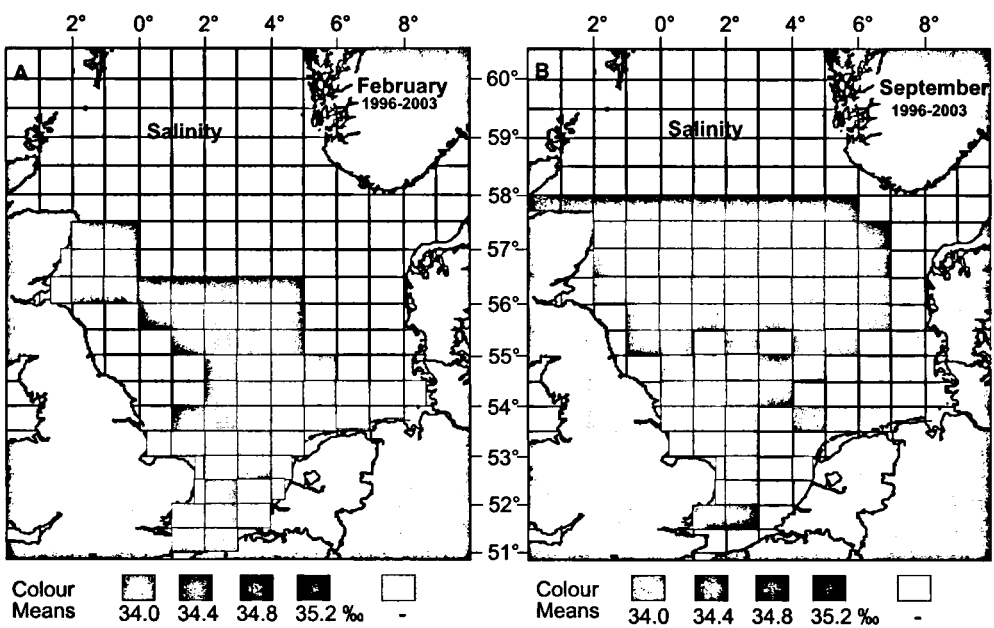

Fig. 14. Water salinity of the central and southern North Sea in February (a) and in August-September (b). Averages from measurements available for each of the rectangles.

REFERENCES

ARKHIPKIN, A.J., & V. W. LAPTIKHOVSKY, 2000. Age and growth of the squid *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) on the northwest Africa shelf. – Journal of the Marine Biological Association of the United Kingdom 80: 747-748.

ARKHIPKIN, A.J., & C.M. NIGMATULLIN, 1997. Ecology of the oceanic squid *Onychoteuthis banksii* and the relationship between the genera *Onychoteuthis* and *Chaunoteuthis* (Cephalopoda: Onychoteuthidae). – Journal of the Marine Biological Association of the United Kingdom 77: 839-869.

BELLINO, J.M., G.J. PIERCE & J. WANG, 2001. Modelling intraannual variation in abundance of squid *Loligo forbesi* in Scottish waters using generalised additive models. – Fisheries Research 52: 23-39.

BERGSTRÖM, B.I., & W.C. SUMMERS, 1983. *Sepietta oweniana.* In: BOYLE P.R., ed., Cephalopod life cycles. I, Species accounts: 75-91.

BOER, P., 1971. Het voorkomen van inktvissen langs de Nederlandse kust. – Het Zeepaard 31: 65-77.

BOLETZKY, S. VON, 1983. *Sepia officinalis.* In: BOYLE, P.R., ed., Cephalopod life cycles. I, Species accounts: 31-52.

COLLINS, M., C. YAU, L. ALLCOCK & M.H. THURSTON, 2001. Distribution of deep-water benthic and bentho-pelagic cephalopods from the north-east Atlantic. – Journal of the Marine Biological Association of the United Kingdom 81: 105-117.

GITTENBERGER, A., & N. SCHRIEKEN, 2004. Octopuses, squids and cuttlefish (Cephalopoda) in the Netherlands. – Vita Malacologica 2: 33-38.

GONZÁLEZ, A.F., M. RASERO & A. GUERRA, 1994. Preliminary study of *Illex coindetti* and *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in northern Spanish Atlantic waters. – Fisheries Research 21: 115-126.

GRIMPE, G., 1925. Zur Kenntnis der Cephalopodenfauna der Nordsee. – Wissenschaftliche Meeresuntersuchungen herausgegeben von der Kommission zur wissenschaftlichen Untersuchung der deutschen Meere in Kiel und der Biologischen Anstalt auf Helgoland. Neue Folge 16 (1, 3): 1-124.

HASTIE, L. C., J. B. JOY, G. J. PIERCE & C. YAU, 1994. Reproductive biology of *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in Scottish waters. – Journal of the Marine Biological Association of the United Kingdom 74: 367-382.

HEIJ, A. DE, & R.P. BAAYEN, 1999. Seasonal distribution of the cephalopod *Alloteuthis subulata* in the central and southern North Sea. – Basteria 63: 129-138.

HOLME, N. A., 1974. The biology of *Loligo forbesi* Steenstrup (Molluca: Cephalopoda) in the Plymouth area. – Journal of the Marine Biological Association of the United Kingdom 54: 65-77.

JAECKEL, G. A., 1958. Cephalopoden. In: GRIMPE, G., & E. WAGNER, eds, Die Tierwelt der Nord- und Ostsee 9 (b3): 480-723.

JAECKEL, S. H., 1957. Kopffüsser (Tintenfische). Die Neue Brehm-Bücherei: 1-81. A. Ziemsen Verlag, Wittenberg / Lutherstadt.

JANSSEN, A. W., 1975. Systematische lijst van Nederlandse recente en fossiele mollusken. – Mededelingen van de Werkgroep Tertiaire en Kwartaire Geologie 12: 115-170.

KAAS, P., 1939. Teuthologische aanteekeningen I. – Basteria 4: 34-45.

KRISTENSEN, J., 1966. De inktvissen langs de Nederlandse kust. – Correspondentieblad van de Nederlandse Malacologische Vereniging 118: 1240-1243.

LACOURT, A.W., & P.H.M. HUWAE, 1981. De inktvissen (Cephalopoda) van de Nederlandse kust. Wetenschappelijke Mededelingen van de Koninklijke Nederlandse Natuurhistorische Vereniging 145: 1-32.

MOORSEL, G. VAN, 2004. Dwerginktvissen (Sepiolidae) in Nederland. – Het Zeepaard 64: 78-91.

MUUS, B.J., 1963. Index des fiches d' identification du zooplancton. Cephalopoda in the North Atlantic. Conseil International pour l'Exploration de la Mer, sheet 94-98.

NESIS, K.N., 2003. Distribution of recent Cephalopoda and implications for Plio-Pleistocene events. Berliner Palaeobiologische Abhandlungen 3: 199-224.

PIERCE, G. J., N. BAILEY, Y. STRATOUDOKIS & A. NEWTON, 1998. Distribution and abundance of the fished population of *Loligo forbesi* in Scottish waters: analysis of research cruise data. – ICES journal of Marine Science 55: 14-33.

PIERCE, G., I. YOUNG & J. WANG, 2002. An overview of cephalopods relevant to the SEA 2 and SEA 3 areas. University of Aberdeen, Report TR 009: pp 42.

QUETGLAS, A., A. CARBONELL & P. SÁNCHEZ, 2000. Demersal continental shelf and upper slope cephalopod assemblages from the Balearic Sea (North western Mediterranean). Biological aspects of some deep-sea species. – Estuarine, Coastal and Shelf Science 50: 739-749.

ROBIN, J.P., V. DENIS, J. ROYER & L. CHALLIER, 2002. Recruitment, growth and reproduction in *Todaropsis eblanae* Ball, 1941), in the area fished by French Atlantic trawlers. – Bulletin of Marine Science 71: 711-724.

ROPER, C.F.E., M.J. SWEENEY & C.E. NAUEN, 1984. Cepholopods of the world. – FAO Fisheries Synopsis 125 (3): 1-277.

ROYER, J., P. PÉRIÈS & J.P. ROBIN, 2002. Stock assessment of English Channel loliginid squids: updated depletion methods and new analytical methods. – ICES Journal of Marine Science 59: 445-457.

STEVENSON, J.A., 1935. The cephalopods of the Yorkshire coast. – Journal of Conchology 20: 102-116.

TESCH, J.J., 1908. Bijdrage tot de fauna der Zuidelijke Noordzee III. Cephalopoda. Ten deele verzameld met de "Wodan". – Jaarboek van het Rijks-Instituut voor het Onderzoek der Zee -1908: 3-24.

TINBERGEN, L., & J. VERWEY, 1945. Zur Biologie von *Loligo vulgaris* Lam. – Tijdschrift der Nederlandsche Dierkundige Vereeniging 7: 213-286.

VOOYS, C.G.N. DE, J.IJ. WITTE, R. DAPPER, J. VAN DER MEER & H.W. VAN DER VEER, 1993. Lange termijn veranderingen op het Nederlandse continentale plat van de Noordzee: Trends in everte-braten van 1931-1990. – Netherlands Institute for Sea Research Report 1993-17: pp 68.

WORMUTH, J.H., 1998. Workshop deliberations on the Ommastrephidae: a brief history of their systematics, and a review of the systematics, distribution, and biology of the genera *Martialia* Rochebrune and Mabille, 1889, *Todaropsis* Girard, 1890, *Dosidicus* Steenstrup, 1857, *Hyaloteuthis* Gray, 1849, and *Eucleoteuthis* Berry, 1916. In: VOSS, N.A., M. VECCHIONE, R.B. TOLL & M.J. SWEENEY, eds, Systematics and biogeography of cephalopods, Volume II. Smithsonian Contributions to Zoology 586: 373-384.

YAU, C., & P.R. BOYLE, 1996. Ecology of *Sepiola atlantica* (Mollusca: Cephalopoda) in the shallow sublittoral zone. – Journal of the Marine Biological Association of the United Kingdom 80: 747-748.