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Seasonal distribution of the cephalopod *Alloteuthis subulata* in the central and southern North Sea

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Alloteuthis subulata was monitored in the waters of the central and southern North Sea from 1991 to 1998 as part of the International Bottom Trawl Surveys. More than 90% of all cephalopods encountered belonged to *A. subulata*, which species thus should be considered the dominant cephalopod in the southern North Sea. Migration patterns appeared to be entirely determined by water temperatures. During autumn and early winter, juvenile animals migrated from the cooling southeastern coastal waters to the deeper, in winter relatively warmer, waters of the central North Sea. In spring, the young adults migrated back to the warming shallow coastal waters along the Danish, German, Dutch, Belgian and southeastern British shores. After spawning in these waters, most of the adults died. The life cycle of *A. subulata* proved to be largely or entirely confined to the central and southern North Sea, and the species should therefore be considered a permanent inhabitant of these waters.

Key words: Cephalopoda, Loliginidae, *Alloteuthis subulata*, biology, life cycle, migration patterns, water temperature, North Sea.

INTRODUCTION

Alloteuthis subulata (Lamarck, 1798), a small squid belonging to the Loliginidae (fig. 1), is considered the most common cephalopod species living in the North Sea. During parts of the year, *A. subulata* probably is the most important source of food for many fish species (Kristensen, 1966). The maximum mantle length of male and female animals is considered to be 20 cm and 12 cm, respectively. However, in the North Sea animals generally do not exceed lengths of 14 cm for males and 10 cm for females.

The ecology of *A. subulata* is partially understood. Poppe & Goto (1993) consider this a necto-benthic species that prefers the upper sublittoral zone. Also Roper et al. (1984), following Grimpe (1925) and Ten Broek (1941), consider *A. subulata* a species that swims close to the sea bottom, no deeper than 200 m (the continental shelf). Both sexes appear early in summer for spawning in the southern North Sea. Some adults migrate to coastal waters for egg deposition in September, and most of them die soon after. Juveniles can be observed till the end of November, when they have attained a mantle length of 3 cm.

The supposed migration patterns during winter are more controversial. According to some authors, the juveniles subsequently disappear from the North Sea (Roper et al., 1984), to return later on from the north (Grimpe, 1925; Ten Broek, 1941) or both from

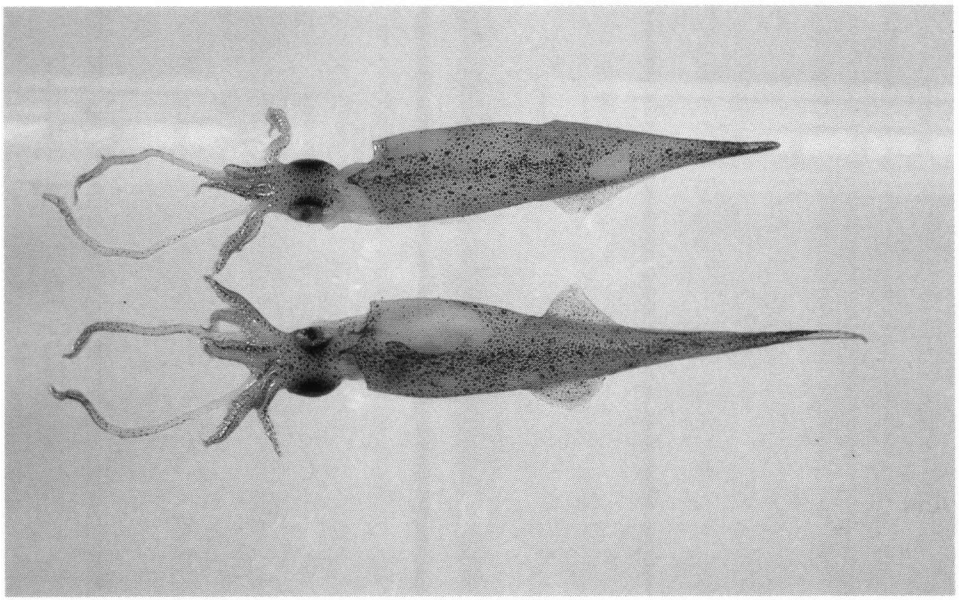

Fig. 1. *Alloteuthis subulata* (Lamarck, 1798), male (below) and female (above).

the north and the south (Kristensen, 1966). Grimpe (1925) and Ten Broek (1941) mention that the returning animals are observed earlier in the German Bight than along the Dutch southwestern coast, indicating a southward migration. At variance with these authors, De Heij (1997) considers *A. subulata* to be a permanent inhabitant of the central and southern North Sea, living in the northwestern parts during winter and migrating to the shallow coastal waters in spring.

Migration patterns were also noticed by Moreno (1993) and Rodhouse et al. (1988) at the Portuguese and English Channel coasts. Adult animals migrated inshore for spawning, followed after a while by offshore migration of the juveniles. Such migration patterns may well be due to seasonal changes in water temperature, an aspect that has not been studied as yet for *A. subulata*. Average water temperatures in the North Sea during the year have been described by Heessen & Daan (1994). The present study presents a systematic analysis of seasonal migration of *A. subulata* in the central and southern North Sea, in conjunction with seasonal changes in water temperature.

MATERIAL AND METHODS

From 1991 to 1998, the Netherlands Institute for Fisheries Research (RIVO-DLO) in IJmuiden, The Netherlands, participated in the International Bottom Trawl Survey in the central and southern North Sea (51 ° — 57°30′ N). Fishing was done with a trawl with a 20 m horizontal × 5 m vertical opening, and 2 cm meshes. For the inventory, the North Sea was divided into rectangles of one degree longitude by half a degree latitude, equalling about 30 × 30 nautical miles. During each survey, about 50 out of

the 110 rectangles were sampled during 30 minutes of fishing. At the same time, water temperature and salinity were monitored at 5 m depth as well as at the bottom. Fishing was restricted to rectangles in open sea up to six miles from the shore. Surveys were carried out four times a year (in February, May, August, and November) up to 1995, once (February) in 1996, twice (February and November) in 1997, and once (February) in 1998. In this study, only data are used from 1993 and consecutive years, because data on *Alloteuthis subulata* from the first two survey years were not yet reliable. Numbers of *A. subulata* out of total numbers of cephalopod catches were analysed, and mantle length was measured for all individual animals. For some years, the data were extended with data from other research programmes of RIVO-DLO. *A. subulata* and other cephalopods were identified using Roper et al. (1984).

RESULTS

Cephalopod catches consisted mainly (> 90%) of *A. subulata* (table 1). Other cephalopods found were *Loligo forbesi* Steenstrup, 1856, *L. vulgaris* Lamarck, 1798, *Sepiola atlantica* Orbigny, 1840, *Sepia officinalis* Linnaeus, 1758, *Eledone cirrhosa* (Lamarck, 1798), and *Todaropsis eblanae* (Ball, 1841). In the first two years of the survey (1993 and 1994), catches were largest in November, while in 1995 larger numbers were encountered in May rather than in November. Analysis of the mantle length frequencies revealed that from February to August, most of the animals were in the range of 3–7 cm mantle length. Sex identification (although difficult for the smaller specimes, of which the hectocotylus was often damaged) revealed that most of these were females. At a dorsal mantle length of 8 cm, 23% of all animals were males; at 9 cm length, 52%, at 10 cm length, 74%, and above 10 cm, 100% of all animals were males. Only in November, mainly juveniles were encountered with dorsal mantle lengths in the range of 2–4 cm. Due to the 2 cm mesh used for fishing, smaller animals, if at all present, escaped from observation. Combining the data from tables 1 and 2, it is evident that most of the adult animals disappear at the end of the summer. In November, only 0.5% of all animals caught exceeds 5 cm in length (table 2).

Occurrence of *A. subulata* was not linked to water salinity (table 3). In the central and southern North Sea, salinity normally varies from 34–35‰ in open sea, down to 30‰ close to river mouths. Among 534 hauls, 81 hauls had a salinity of 35‰, 363 hauls a salinity of 34‰, 37 hauls a salinity of 33‰, and 53 hauls a salinity between 32‰ and 30‰. *A. subulata* was encountered in the entire salinity range, although it was only present at lower salinities in spring and summer during spawning close to the coast (not shown).

Year	Hauls	Cephalopods	Percentage *A. subulata*	Percentage *A. subulata* per season			
				February	May	August	November
1993	273	25434	98	<1	14	2	83
1994	192	31753	98	18	14	<1	66
1995	134	10087	92	1	77	2	20

Table 1. Cephalopod and *Alloteuthis subulata* catches in the Dutch hauls for the International Bottom Trawl Surveys in the central and southern North Sea from 1993 through 1995.

Mantle length (cm)	February (n = 990)	May (n = 529)	August (n = 373)	November (n = 1946)
1	0.0	0.0	0.0	0.0
2	0.1	0.0	1.9	38.5
3	10.0	10.2	9.9	39.8
4	21.1	27.0	21.2	21.2
5	26.2	21.4	16.1	0.0
6	22.2	16.3	13.9	0.0[1]
7	13.8	12.3	15.8	0.0[1]
8	4.5	6.0	13.4	0.0[1]
9	0.4	4.7	6.2	0.0[1]
10	0.8	1.7	1.1	0.0[1]
11	0.4	0.2	0.3	0.0[1]
12	0.4	0.0	0.3	0.0
13	0.0	0.0	0.0	0.0
14	0.0	0.2	0.0	0.0

[1] Together, these six values add up to 0.5

Table 2. Relative distribution of mantle lengths of *Alloteuthis subulata* during the year. Pooled data from samples from 1994 (February, May, August, November), 1995 (February, May, August, November), 1996 (February), 1997 (February and November), and 1998 (February).

Allotheutis subulata was encountered at all depths investigated, from 15 m close to the Dutch and Danish coast, to 105 m in the northwestern parts of the surveyed area (table 4). Preference for a specific depth was not apparent. However, *A. subulata* was encountered largely at greater depths during winter (November to February) than in spring and summer (May to August). This is likely due to a preference of *A. subulata* for higher water temperatures. Animals were caught from hauls covering the entire range of temperatures, from 2°C to 20°C, although only exceptionally from temperatures below 5°C

Water salinity	Hauls	Percentage of hauls with *A. subulata*
35‰	81	51
34‰	363	44
33‰	37	23
32‰ — 30‰	53	29

Table 3. Numbers of hauls in different water salinity classes, and percentages of the salinity class hauls in which *Alloteuthis subulata* was caught. Pooled data from 1993 to 1995 (all four seasons), and from 1996 to 1998 (February).

Fishing depth	February		May		August		November	
	Fraction[1]	Average	Fraction	Average	Fraction	Average	Fraction	Average
< 20 m	0 / 7		2 / 7	15	4 / 4	13	4 / 29	51
25 m	10 / 54	1	25 / 32	282	6 / 12	4	25 / 60	162
35 m	23 / 56	5	16 / 25	212	14 / 31	15	13 / 45	49
45 m	13 / 43	5	17 / 30	98	13 / 35	17	23 / 51	715
55 m	10 / 18	21	7 / 11	83	1 / 11	<1	2 / 5	266
65 m	6 / 9	193	7 / 21	45	0 / 9		1 / 1	810
75 m	16 / 20	708	8 / 16	31	0 / 12		2 / 5	266
> 80 m	22 / 26	641	9 / 22	258	0 / 27		1 / 1	1234
Total	100 / 233		91 / 164		38 / 141		71 / 197	

[1] (Number of hauls with *A. subulata*) / (Total number of hauls)

Table 4. Fraction of hauls with *Alloteuthis subulata* at various depths throughout the year, and average number of *A. subulata* caught in these hauls in 30 min. Pooled data from 1993 to 1995 (February, May, August, November) and from 1996 to 1998 (February).

(table 5). However, when analysed within the seasons, larger average numbers of *A. subulata* were generally caught at higher temperatures than at lower ones (table 5). Statistical analysis of the average water temperature at fishing depth and fishing depth throughout the season in the years 1993 to 1998 for hauls in which *A. subulata* was present, versus those in which it was absent, revealed that successful hauls mostly were from depths which had a higher water temperature (table 6). In February, such higher temperatures occurred at great depth only, and catches were mainly from greater depths. In May, water temperatures at lower and greater depths were similar in most years, due to a warming up of the sea in spring, and except for 1993 catches were not influenced by fishing depth. In August, water temperature profiles had reversed, and hauls from shallow warmer waters yielded more *A. subulata* than hauls from deeper waters. In November, shallow and deep waters again had similar temperatures, and fishing depth did not influence *A. subulata* catches (table 6).

Migration of *A. subulata* within the year 1994 is shown in fig. 2a-d. Evidently, the animals migrate throughout the seasons to depths in which they find higher water temperatures. In summer, temperatures are higher in shallow waters close to the shores, explaining why the animals spawn close to the shore. In winter, the animals do not disappear from the central and southern North Sea but migrate to the deeper parts of the North Sea, where temperatures are relatively higher than in shallower waters. In May and November, intermediate distribution patterns are observed. Migration may also vary from year to year, dependent on climatic differences affecting water temperature. While in a severe winter (1997) *A. subulata* was only found at great depths in the northwestern central part of the North Sea (fig. 3a), in a mild winter (1998) many animals may still be found close to the Dutch coast (fig. 3b). Similarly, migration during spring to shallower waters may be retarded when a mild winter is followed by a cold springtime (fig. 3c).

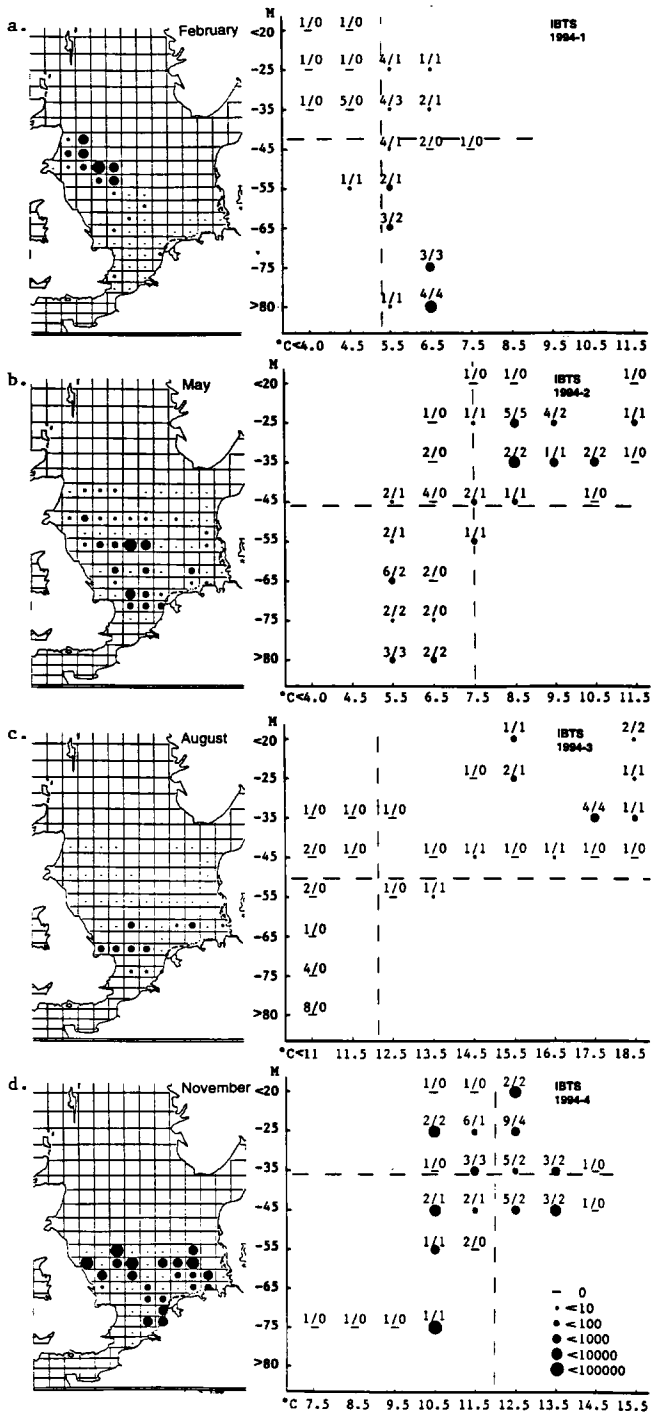

Fig. 2. Occurrence of *Alloteuthis subulata* in the southern North Sea at various depths and water temperatures during the year 1994.

Water temperature class	February		May		August		November	
	Fraction[1]	Average	Fraction	Average	Fraction	Average	Fraction	Average
< 4 °C	1 / 31	<1	0 / 0	–	0 / 0	–	0 / 0	–
4.5 °C	6 / 42	1	0 / 0	–	0 / 0	–	0 / 0	–
5.5 °C	23 / 64	18	9 / 17	3	0 / 0	–	0 / 0	–
6.5 °C	40 / 63	154	19 / 54	130	0 / 24	–	0 / 0	–
7.5 °C	26 / 29	778	24 / 42	110	0 / 14	–	0 / 1	–
8.5 °C	3 / 3	12	21 / 24	427	0 / 11	–	2 / 6	368
9.5 °C	1 / 1	2	13 / 18	179	0 / 6	–	0 / 5	–
10.5 °C	0 / 0	–	4 / 6	34	1 / 10	1	12 / 28	523
11.5 °C	0 / 0	–	1 / 2	12	1 / 6	<1	17 / 50	213
12.5 °C	0 / 0	–	0 / 1	–	1 / 6	<1	25 / 66	179
13.5 °C	0 / 0	–	0 / 0	–	1 / 3	2	14 / 33	462
14.5 °C	0 / 0	–	0 / 0	–	4 / 10	13	1 / 6	20
15.5 °C	0 / 0	–	0 / 0	–	6 / 16	9	0 / 1	–
16.5 °C	0 / 0	–	0 / 0	–	10 / 16	39	0 / 0	–
17.5 °C	0 / 0	–	0 / 0	–	6 / 10	21	0 / 0	–
18.5 °C	0 / 0	–	0 / 0	–	5 / 6	6	0 / 0	–
19.5 °C	0 / 0	–	0 / 0	–	3 / 3	3	0 / 0	–
Total	100 / 233		91 / 164		38 / 141		71 / 196	

[1] (Number of hauls with *A. subulata*) / (Total number of hauls)

Table 5. Fraction of hauls with *Alloteuthis subulata* at various water temperatures throughout the year, and average number of *A. subulata* caught in these hauls in 30 min. Pooled data from 1993 to 1995 (February, May, August, November) and from 1996 to 1998 (February).

Year	*A. subulata* present or absent in hauls	February		May		August		November	
		T (°C)	D (m)	T (°C)	D (m)	T (°C)	D (m)	T (°C)	D (m)
1993	present	6.3*	67.5*	8.3*	38.6*	16.3*	37.0*	11.6	32.6
	absent	5.6*	36.7*	6.8*	56.7*	11.4*	57.0*	11.6	35.6
1994	present	6.0*	59.3*	7.6	49.4	16.9*	33.8*	12.1	33.6
	absent	4.9*	34.2*	7.4	43.4	10.0*	59.6*	11.8	38.4
1995	present	7.1*	43.7*	7.2	46.4	15.7*	35.4*	13.0	32.8
	absent	6.0*	36.9*	7.5	53.7	8.7*	63.4*	12.9	29.0
1996	present	5.6*	65.1*	...	...	...	...	...	...
	absent	3.0*	34.1*	...	...	...	...	...	...
1997	present	6.6*	80.9*	...	...	...	...	11.7	33.6
	absent	4.4*	39.9*	...	...	...	...	11.5	34.7
1998	present	6.9	50.0*	...	...	...	...	...	...
	absent	5.9	39.4*	...	...	...	...	...	...

Table 6. Average water temperature (T) and fishing depth (D) throughout the season in the years 1993 to 1998 for hauls in which *Alloteuthis subulata* was or was not caught. Incomplete data for 1996 to 1998, in which years surveys were carried out in February only (1996 and 1998) or also in November (1997). Per year and season, pairs of values followed by an asterisk are significantly different at P = 0.05 (Student's t-test).

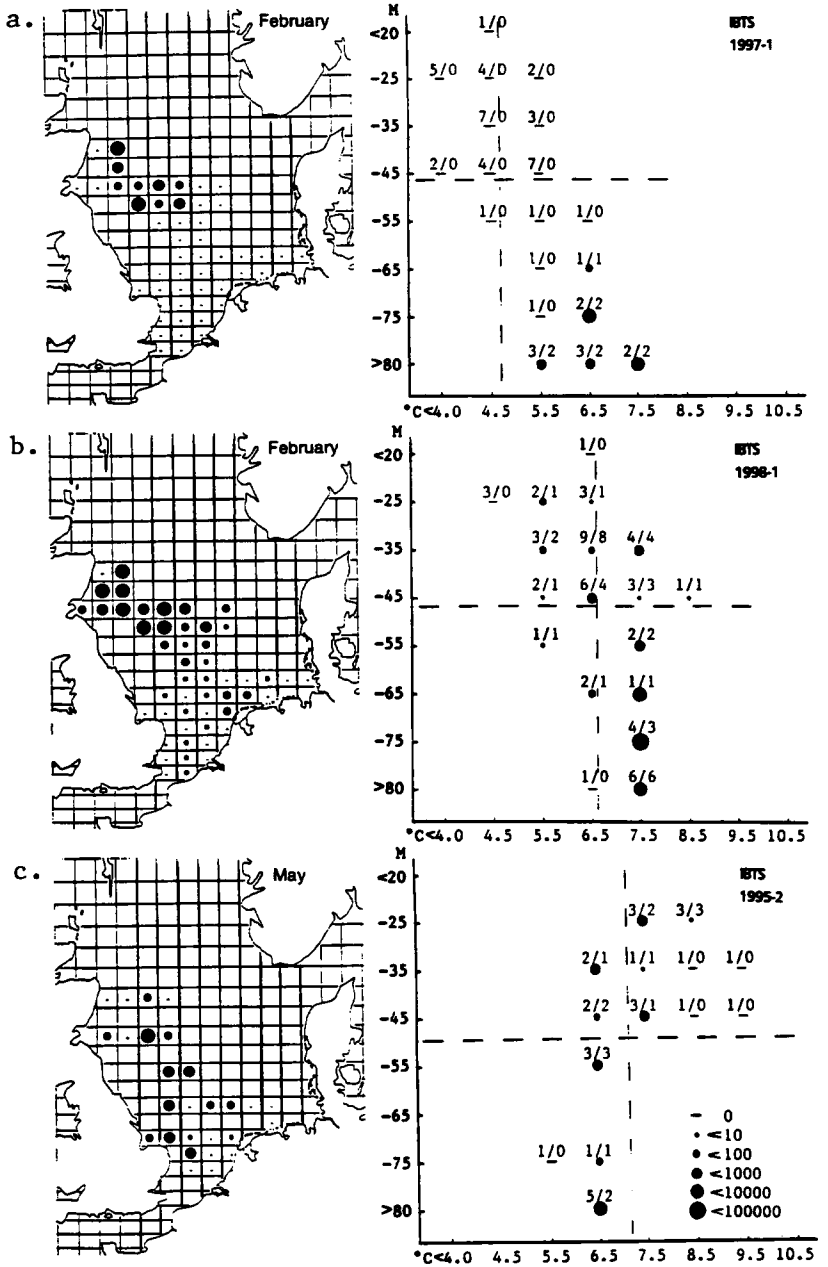

Fig. 3. Occurrence of *Alloteuthis subulata* in the southern North Sea at various depths and water temperatures. a, Severe winter (February 1997); b, mild winter (February 1998); c, cold springtime following a mild winter (May 1995).

DISCUSSION

This study confirms that *A. subulata* is the dominant cephalopod in the central and southern North Sea. More than 90% of all cephalopods found belong to this species. Numbers were lowest in August, representing not more than 2% of yearly catches. This is likely due to general death of the adults after spawning, as also indicated by the fact that later in the year (November) virtually only juveniles were found. During winter, *A. subulata* juveniles grow from 3 cm mantle length (November) to 5 cm (February). On average, growth does not continue thereafter: animals caught in May still have an average mantle length of 5 cm, and probably use their energy supplies for producing eggs and sperm. It is unknown from which length *A. subulata* is able to reproduce in the North Sea. For the English Channel, Rodhouse et al. (1988) report a dorsal mantle length of 5-18 cm and 6-14 cm for fertile male and female animals, respectively. For Portuguese waters, Moreno (1993) reports mantle lengths of 4-18.5 cm and 5.5-10.5 cm, respectively. If this is true, nearly 37% of the animals caught in the North Sea in surveys in May were still too young for reproduction (see table 2).

Migration patterns of *A. subulata* appearing from this study are as follows. During winter, most animals are found in the deep waters in the northern and northwestern parts of the North Sea, north of the Dogger Bank. In spring, the population migrates to the shallower coastal waters of the German and the Southern Bight, where spawning occurs during summertime. Most of the adults die after spawning, but those remaining as well as the juveniles migrate back to the northwestern deep waters in autumn and early winter. Migration patterns are largely determined by water temperatures. The animals continuously seem to move to warmer waters, both within and between seasons. For the same reasons, a mild winter followed by a cold spring resulted in considerable retardation of migration to warmer coastal waters.

Migration in response to temperature changes has been reported for several fish species on the northeast continental shelf of the USA (Mountain & Murawski, 1992). For North Sea cod, an overall age-dependent relationship between cod density and temperature has been reported, but not a temperature-dependent migration (Heessen & Daan, 1994), possibly because the distance over which cod migrates is restricted (Daan, 1978). Our results indicate that migration in *A. subulata* is much more pronounced.

The present findings show that *A. subulata* is a permanent inhabitant of the central and southern North Sea. Since very few animals were found in the Channel mouth, it is unlikely that much genetic exchange occurs with the population living in the English Channel waters (Rodhouse et al., 1988). This also means that the southern North Sea population does not migrate into the English Channel during winter, as previously suggested (Kristensen, 1966). In how far exchange with and migration to the Atlantic Ocean occurs (Grimpe, 1925; Ten Broek, 1941) cannot be judged, since no data are available on the presence of *A. subulata* in the latter region. In conclusion, the life cycle of *A. subulata* is largely or entirely confined to the central and southern North Sea, and the species should therefore be considered a permanent inhabitant of these waters.

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