

R. Diekmann · U. Piatkowski

## Early life stages of cephalopods in the Sargasso Sea: distribution and diversity relative to hydrographic conditions

Received: 31 October 2001 / Accepted: 11 February 2002 / Published online: 10 April 2002  
© Springer-Verlag 2002

**Abstract** The distribution of early life stages of cephalopods was studied during a cruise of the German R.V. “Poseidon” to the Sargasso Sea in March 1993, covering an area south-east of Bermuda from 24°N to 31°N and 61°W to 65°W. Hydrographic measurements were carried out by conductivity, temperature and depth casts and/or expendable bathythermographs. The subtropical convergence zone was detected at a latitude of approximately 27°20′N and divided the Sargasso Sea into a northern and a southern area. Zooplankton sampling with a 6 m<sup>2</sup> Isaac–Kidd midwater trawl and Bongo nets yielded a total catch of 909 specimens of early life stages of cephalopods, representing at least 13 families and 20 mainly oceanic species. Multivariate statistical analyses were performed in order to compare the species composition and abundance of cephalopods. Two different assemblages were clearly identified, north and south of the front. According to the position of the front an analysis of similarity (ANOSIM) was applied, which confirmed the observed differences in species composition at a highly significant level. The Cranchiidae, mainly represented by the endemic species *Leachia lemur*, was the most abundant family, especially in the northern part of the Sargasso Sea, and was mainly responsible for the distinction between the cephalopod assemblages. In general, higher abundances of early life stages and a higher diversity was observed north of the subtropical convergence zone, which is assumed to form a faunal boundary.

### Introduction

Central oceanic regions such as the Sargasso Sea have traditionally been thought to be low productive areas and have been compared with terrestrial deserts (Ryther 1963). Recent studies have shown that this assumption is partially wrong. In historical data sets the primary production in the oligotrophic central gyres has been underestimated by a factor of 2–4 (Goericke and Welschmeyer 1998), though productivity and biomass are still relatively low. A contrasting view is that the Sargasso Sea is characterised by a dynamic phytoplankton community, with low biomass but high growth rates that are balanced by high rates of grazing (Jackson 1980; Goldman 1993). Compared to slope and shelf waters, however, the Sargasso Sea shows consistently lower biomass concentrations in zooplankton (Deevey 1971; Deevey and Brooks 1977; Ortner et al. 1978; Wiabe et al. 1985; Ashjian et al. 1994). The distribution is less patchy and the average mean depth of the biomass concentration is similar during both day and night (Ashjian et al. 1994).

The Sargasso Sea, however, is not a homogeneous oceanic region. It lies within the North Atlantic Subtropical Convergence Zone (STCZ), a transition zone between the prevailing westerlies and the easterly trades (Voorhis 1969; Halliwell et al. 1994). The convergence zone is characterised by enhanced meridional gradients of near-surface temperature and a decreasing depth of the upper (seasonal) thermocline from south to north (Halliwell et al. 1994). During winter and spring an extensive large-scale thermal front develops, which meanders in east–west direction (Voorhis and Hersey 1964; Voorhis 1969). The thermal gradient is only marginally detectable during summer (Halliwell et al. 1991b), but there is also some evidence that the front may be present throughout the year (Backus et al. 1969; Colton et al. 1975). It separates the central part of the Sargasso Sea into a cooler, more-productive northern part and a warmer, less-productive southern part. The enhanced

Communicated by O. Kinne, Oldendorf/Luhe

R. Diekmann (✉) · U. Piatkowski  
Institut für Meereskunde, Düsternbrooker Weg 20,  
24105 Kiel, GermanyE-mail: [rdiekmann@ifm.uni-kiel.de](mailto:rdiekmann@ifm.uni-kiel.de)  
Fax: +49-431-6001515

primary production north of the front, which may be up to ten-times higher than in the south, may be due to a deeper winter mixing compared with a stronger stratification of the water column south of it (Ryther and Menzel 1960). In correspondence with the differences in productivity, a general decline in abundance and differences in species composition has been observed in north–south direction, e.g. epipelagic copepods (Colton et al. 1975) and mesopelagic fishes (Backus et al. 1969).

Cephalopods have been frequently investigated in the western North Atlantic, but hardly any work has been performed in the Sargasso Sea. Expeditions at the beginning of the last century investigated the cephalopod fauna around Bermuda (e.g. Pfeffer 1912; Berry 1920; Peile 1926), but the number of hauls and the catchability of their nets were limited. The first intensive study was carried out by Voss (1960), who described the cephalopod fauna around the Bermudian islands. Catches with different net types yielded 21 cephalopod species, of which at that time only three had previously been reported from that area; however, detailed distribution patterns were not analysed. Since then the cephalopod fauna of the oceanic parts of the western North Atlantic have not been further studied. Investigations have concentrated rather on the Florida Current (Cairns 1976; Lea 1984) and the Gulf Stream system (Dawe and Stephen 1988).

In the present paper the cephalopod fauna of the Sargasso Sea is examined for the first time. In order to reduce avoidance effects and to ensure a nearly quantitative sampling (Piatkowski 1998), early life stages of cephalopods have been considered. The sampling was conducted with two different standard zooplankton nets (IKMT6, Bongo), essentially in north–south directions, and, thus, crossing the STCZ. Distribution patterns of oceanic cephalopods are described, and species assemblages are identified. Observed spatial differences in species composition are discussed with regard to hydrographic features of the region.

## Materials and methods

### Sampling

Data were collected in the Sargasso Sea during the R.V. “Poseidon” cruise 200/1 in March 1993, which had been initiated to detect spawning grounds of the European eel *Anguilla anguilla* (Schnack et al. 1994). Stations were located south-east of Bermuda, covering an area from 24°N to 31°N and 61°W to 65°W (Fig. 1). Early life stages of cephalopods were sampled using a Bongo net (500 µm mesh size, 27 hauls), essentially on a north–south transect at 62°W, and an Isaac–Kidd midwater trawl (IKMT6, 300 µm mesh size, 11 hauls at 9 stations). The Bongo net was towed for approximately 90 min at downward oblique hauls between 100 m depth and the surface. The IKMT6 was applied in different depths from 300 to 80 m; towing time was approximately 60 min. Ship speed during sampling was kept at 3 knots. Filtered water volumes were estimated using calibrated flowmeters, which were mounted in the centre of the net openings. All samples were initially preserved in 4% formalin, buffered with borax. Cephalopods were sorted and identified to the lowest taxonomic level possible. Cephalopod

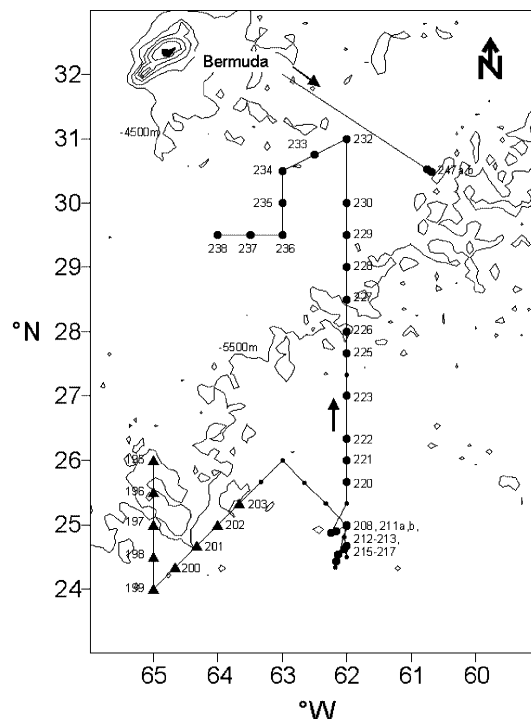


Fig. 1. R.V. “Poseidon” cruise 200/1, March 1993. Sampling area in the Sargasso Sea (bold points represent Bongo hauls; triangles IKMT6 hauls). CTD data were gathered at all marked stations

densities ( $N/1000\text{ m}^3$ ) were then estimated and used in the initial species–station table for the spatial analysis of cephalopod community structure.

Hydrographic data were collected using expendable bathythermographs (XBTs; 10 stations) and conductivity, temperature and depth casts (CTD, model ME OTS 1500; 38 stations). XBTs were only deployed on the northern part of the 65°W transect (not illustrated in Fig. 1). The CTD was launched at all other stations, always in advance of the zooplankton tows.

### Data analysis

Multivariate statistical analyses were performed to examine differences in species composition and abundances of early life stages of cephalopods. IKMT6 hauls were not included in these analyses, since only a few hauls in the southern Sargasso Sea were performed. Prior to analysis, the densities of cephalopod species ( $N/1000\text{ m}^3$ ) at each “Bongo station” were fourth-root transformed. The transformation reduced the weighting of dominant species and increased the importance of rare ones (Field et al. 1982). The similarity between stations was calculated by means of the Bray–Curtis measure (Bray and Curtis 1957; Field et al. 1982). Samples were classified by hierarchical agglomerative cluster analysis using the group-average linking method and ordinated using non-metric, multi-dimensional scaling techniques (MDS; Kruskal 1964).

According to the prevailing hydrographic regimes, the Sargasso Sea was separated into a northern and a southern region, divided by the position of the thermal front (see “Results”). The cephalopod catches in these two regions were compared using different subroutines of the Primer-E (5) computer program (Clarke and Warwick 2001). Analysis of similarities (ANOSIM; Clarke and Warwick 1994) was employed to test for differences in species composition between the two areas. In cases when the ANOSIM showed significant results, the similarity percentage routine (SIMPER; Clarke and Warwick 1994) was applied to examine

which cephalopod species were most responsible for contrasts in the community analysis. In addition various univariate indices, the Magalef's species richness index ( $D$ ), the Shannon–Wiener diversity index ( $H'$ ) and Pielou's evenness index ( $J$ ), were calculated for the samples north and south of the thermal front.

## Results

### Oceanographic conditions

Oceanographic data were measured on two transects in a north–south direction from 24°N to 31°N at a longitude of 65°W and 62°W, respectively. On both sections a sharp near-surface temperature gradient was detected, which demonstrated the location of the thermal front. South of the front the water was stratified, whereas northward the surface layer was mixed. In Fig. 2 the temperature profile at 62°W, the transect of intensive sampling, is illustrated. The temperature gradient was encountered at approximately 27°20'N. South of this front the 21°C isotherm was measured below 100 m water depth. To the north this isotherm reached the surface at approximately 29°30'N. The northern area was characterised by a mixed layer of approximately 50–100 m thickness. At 65°W the stratification in the southern area was slightly intensified, and the most pronounced temperature gradient was again found at approximately 27°20'N.

### Cephalopod families and major species

A total of 909 specimens of early life stages of cephalopods were caught in 11 IKMT6 and 27 Bongo hauls; 13 families and 20 species were identified (Table 1). Since many specimens could only be assigned to higher taxa, the number of families and species must be considered as minimal. All specimens belonged to the Oegopsida and the incirrate Octopoda. In the Bongo hauls the Cranchiidae were dominant (38.2%), mainly represented by the endemic species *Leachia lemur*. The Enoploteuthidae and the Onychoteuthidae were moderately abundant,

with 18.2% and 9.0%, respectively. In terms of density the most abundant species were *L. lemur* (0.72 per 1000 m<sup>3</sup>), followed by *Abraliopsis pfefferi* (0.38 per 1000 m<sup>3</sup>), *Onychoteuthis banksii* (0.26 per 1000 m<sup>3</sup>), *Megalocranchia* sp. (0.22 per 1000 m<sup>3</sup>) and *Selenoteuthis scintillans* (0.21 per 1000 m<sup>3</sup>).

Specimens sampled with the IKMT6 were generally larger compared to specimens from the Bongo catches. With the exception of *Thysanoteuthis rhombus*, which was only found in the IKMT6 samples, the same species were identified in the collections of both net types; however, the relative composition was different. Highest abundances in the IKMT6 samples were observed for the Enoploteuthidae and Onychoteuthidae, each comprising 21.6% of the total catch. Rhynchoteuthion stages of Ommastrephidae accounted for 15.7%. Cranchiidae were less abundant (9.9%) and were dominated by *Helicocranchia* sp., mainly identifiable as *H. papillata*. Species densities were not calculated because of inaccurate flowmeter readings.

Differences in the total abundance of early life stages in day- or night-time samples were not detected. Therefore, diel effects on the catchability of the two nets were not taken into consideration.

### Distribution of cephalopods in relation to the thermal front

The investigation of early life stages of cephalopods in the Bongo hauls revealed marked north–south differences in abundance. North of the thermal front, at 27°20'N densities of cephalopods increased from an average of 1.70 ind. per 1000 m<sup>3</sup> in the southern part of the Sargasso Sea to 4.03 ind. per 1000 m<sup>3</sup> in the north (Fig. 3). Highest abundances were encountered north of 29°N, with a maximum of 8.92 ind. per 1000 m<sup>3</sup>.

Classification of the cephalopod densities in the Bongo hauls separated the 27 samples at an arbitrary level of 65% dissimilarity into two large (I and II) and one small cluster (III) (Fig. 4). The first (I) and the third (III) cluster included all samples south of the subtropical convergence and three further stations north of it. The second cluster (II) comprised exclusively samples taken in the northern area of the Sargasso Sea. Ordination (MDS) of the same data confirmed this finding (Fig. 5): all samples from the northern Sargasso Sea were grouped to the right of a line drawn in a nearly vertical direction, whereas samples from the southern area were positioned to the left of this line. The sample from station 221, which formed a single cluster (III) in the classification, was slightly separated from the other samples in the MDS plot (Fig. 5).

In order to test the a priori hypotheses that there are differences in the species composition between the northern and the southern part of the Sargasso Sea, an ANOSIM was performed. It showed that the species compositions of both areas, separated by the STCZ, did significantly differ (global  $R=0.481$ ;  $P<0.001$ ) and,

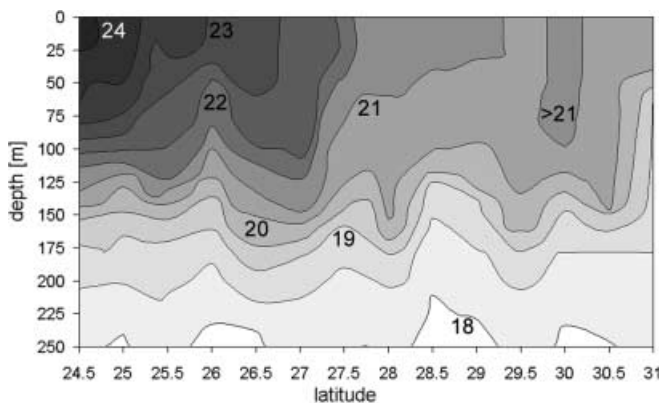


Fig. 2. R.V. "Poseidon" cruise 200/1, March 1993. North–south temperature section at 62°W from 250 m water depth to the surface

**Table 1.** Early life stages of cephalopods collected during the R.V. "Poseidon" cruise 200/1, March 1993. Numbers of higher taxa only include specimens that could not be further identified ( $N_{abs}$  total catch in numbers;  $Rel. N$  percentage of total catch according to gear type;  $N/1000 m^3$  mean species density, only Bongo net)

Order, family	Species	Bongo net			IKMT 6	
		$N_{abs}$	$Rel. N$ (%)	$N/1000 m^3$	$N_{abs}$	$Rel. N$ (%)
Order Teuthida						
Sub-O. Oegopsina	Oegopsina indet.	50	9.36	0.29	52	13.87
Family	<i>Ancistrocheirus lesueurii</i>	4	0.75	0.02	5	1.33
Family	<i>Brachioteuthis</i> sp.	8	1.50	0.05	2	0.53
Family	<i>Chiroteuthis</i> sp.	8	1.50	0.05	3	0.80
Family	<i>Ctenopteryx sicula</i>	3	0.56	0.02	5	1.33
Family Cranchiidae	Cranchiidae indet.	3	0.56	0.02		
Cranchiinae	<i>Leachia lemur</i>	126	23.60	0.72	6	1.60
Taoninae	Taoninae indet.				5	1.33
	<i>Helicocranchia papillata</i>	24	4.49	0.06	15	4.00
	<i>Helicocranchia</i> sp.	10	1.87	0.14	2	0.53
	<i>Taonius pavo</i>	3	0.56	0.02	1	0.27
	<i>Megalocranchia</i> sp.	38	7.12	0.22	8	2.13
Family	Enoploteuthidae indet.	27	5.06	0.15	51	13.60
Family	<i>Enoploteuthis leptura leptura</i>	3	0.56	0.02		
	<i>Abraliopsis pfefferi</i>	67	12.55	0.38	30	8.00
Family	<i>Selenoteuthis scintillans</i>	36	6.74	0.21	19	5.07
Family	Ommastrephidae indet.	13	2.43	0.07	25	6.67
Family	<i>Ommastrephes bartramii</i>	7	1.31	0.04	16	4.27
	<i>Hyaloteuthis pelagica</i>	6	1.12	0.03	18	4.80
Family	<i>Onychoteuthis banksii</i>	45	8.43	0.26	70	18.67
	<i>Onykia cariiboea</i>	3	0.56	0.02	11	2.93
Family	Pyroteuthidae indet.	4	0.75	0.02	7	1.87
Family	<i>Pyroteuthis margaritifera</i>	29	5.43	0.17	18	4.80
	<i>Pterygioteuthis giardi giardi</i>	8	1.50	0.05	1	0.27
Family	<i>Thysanoteuthis rhombus</i>				2	0.53
Family	Thysanoteuthidae					
Order Octopoda						
Family	<i>Argonauta argo</i>	6	1.12	0.03		
Family	Argonautidae					
Family	<i>Tremoctopus</i>	3	0.56	0.02	3	0.80
Family	<i>violaceus violaceus</i>					
Sum		534			375	

thus, supported the results from the classification and ordination. The following exploratory analysis (SIMPER) indicated which species contributed most to the differences between the samples from the northern and the southern stations (Table 2). The Cranchiidae dominated in the north; the family was mainly represented by *Leachia lemur*, *Megalocranchia* sp. and *Helicocranchia* sp., mostly identifiable as *Helicocranchia papillata*. Other characteristic species in the northern part of the sampling area based on absolute abundances, were *Abraliopsis pfefferi*, *Pyroteuthis margaritifera* and *Onychoteuthis banksii*. Samples south of the STCZ were characterised by relatively high abundances of *A. pfefferi*, rhynchoteuthion stages of Ommastrephidae, *O. banksii* and *Selenoteuthis scintillans*. The cephalopod fauna of the southern Sargasso Sea differed from that of the northern area by relatively higher abundances of *S. scintillans* and ommastrephid species as well as by low numbers of cranchiid species, especially *L. lemur*.

Taxa which exclusively occurred north of the subtropical convergence, though mostly in low abundances, were *Ancistrocheirus lesueurii*, *Ctenopteryx sicula*, *Brachioteuthis* sp., *Chiroteuthis* sp., *Helicocranchia papillata*, *Taonius pavo* and *Argonauta argo*.

The calculation of different dominance and diversity indices for the pooled species densities north and south of the front reflected the observed differences between the two areas (Table 3). A total of 18 different species, compared to 10 in the southern part of the Sargasso Sea, were identified in the north (Ommastrephidae were not included at the species level), and the density of early life stages of cephalopods was more than three-times higher. The Magalef index ( $D$ ) and Shannon's diversity index ( $H'$ ) showed higher values for the northern part of the Sargasso Sea, whereas Pielou's evenness index ( $J$ ) was slightly smaller. This was due to the dominance of just one species, *L. lemur*, in the northern area and the relatively even distribution of species abundances in the south.

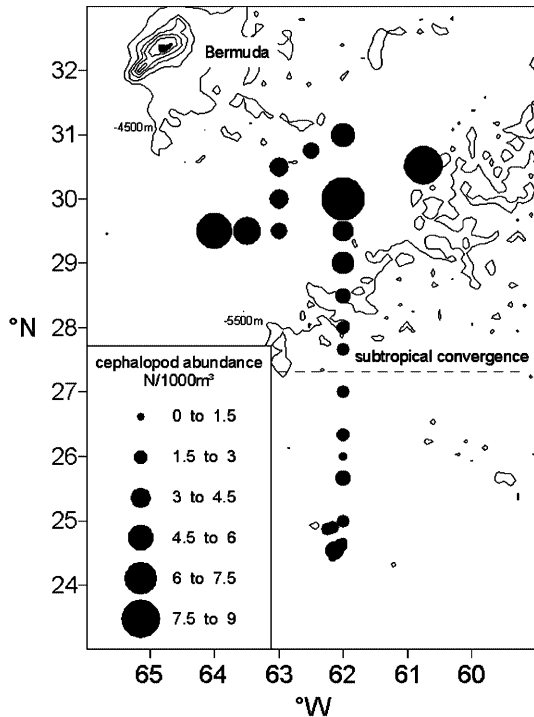


Fig. 3. R.V. "Poseidon" cruise 200/1, March 1993. Densities of cephalopod early life stages at each Bongo station ( $N/1000\text{ m}^3$ ). The horizontal line indicates the position of the thermal front

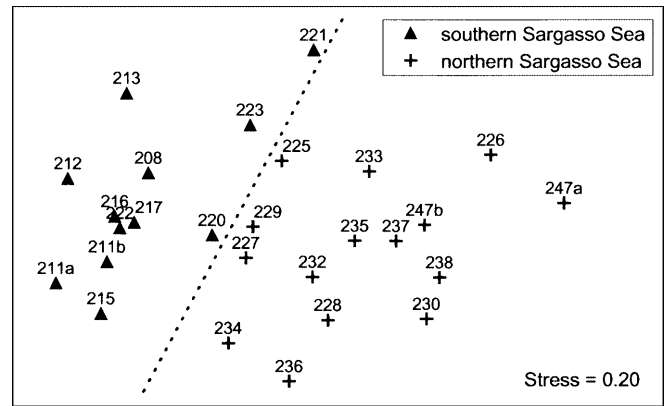


Fig. 5. Ordination of the 27 Bongo stations according to cephalopod assemblages. The dotted line separates samples north of the thermal front from samples south of it

small paralarvae, even of the muscular type, effectively (Roper 1977; Rodhouse et al. 1992). Limitations are caused by the seasonal occurrence of early life stages of those species, which do not spawn year round, making them susceptible to plankton sampling only shortly after spawning events. Furthermore, spawning areas are not always identical with the distributional range of the adults. Hence, the distribution patterns of the early life stages do not necessarily reflect those of the adults.

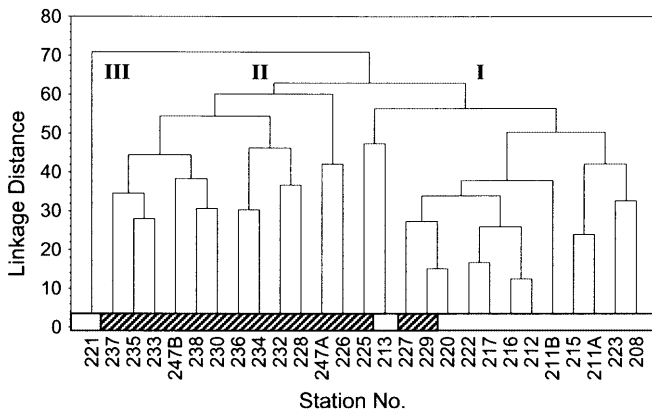


Fig. 4. Classification of the 27 Bongo stations according to cephalopod assemblages. Hatching indicates samples north of the thermal front

**Discussion**

**Sampling methods**

The collection of early life stages of cephalopods with zooplankton nets has advantages and limitations. Advantages are the considerably lower avoidance effects of young and small planktonic cephalopods in comparison to their rapidly swimming adults (Piatkowski et al. 1993; Piatkowski 1998). The sampling devices used in this study, Bongo net and IKMT6, are supposed to sample

**Cephalopod families and major species: Bongo and IKMT6 catches**

In this study cephalopod fauna was investigated for the first time in an extensive area of the Sargasso Sea. Mesopelagic cephalopods such as the Cranchiidae and Enoploteuthidae dominated the catches, because most of their hatchlings occur in near-surface waters before they exhibit a marked ontogenetic descent to develop into the juvenile and adult stages (Roper and Young 1975; Young 1978). In general, a typical oceanic cephalopod community was present. The species composition was similar to other collections of pelagic cephalopods in the subtropical western North Atlantic (Voss 1960; Gibbs and Roper 1970; Lu and Roper 1979; Lea 1984; Dawe and Stephen 1988), but was depauperate of shelf-associated species such as Myopsida and some Ommastrephidae (e.g. *Illex illecebrosus*) as well as early life stages of benthic Octopoda. The same families, Cranchiidae and Enoploteuthidae, dominated in our study and in earlier collections of a one-degree-square area south-east of Bermuda (Gibbs and Roper 1970). A comparison of the species composition between our study and the former study, which mainly collected juvenile to adult specimens, indicated that most of the cephalopod species seem to spawn in early spring or year round, respectively. For most oceanic cephalopods only scattered information about spawning periods exists. For instance, the peak spawning time of *Abrialiopsis pfefferi*, investigated at Deepwater Dumpsite 106 (Lu

**Table 2.** SIMPER analysis: discriminating species between the northern and the southern areas of the Sargasso Sea. Species are ordered according to decreasing contribution (%) to the total dissimilarity, up to 90% cumulative contribution

Species	Average abundance		Contribution (%)	Cumulative contribution (%)
	Southern Sargasso Sea	Northern Sargasso Sea		
<i>Leachia lemur</i>	0.04	1.14	17.86	17.86
<i>Selenoteuthis scintillans</i>	0.31	0.12	8.96	26.82
<i>Helicocranchia</i> sp.	0	0.36	8.24	35.05
Ommastrephidae	0.22	0.09	7.9	42.95
<i>Onychoteuthis banksii</i>	0.21	0.29	7.64	50.59
<i>Pyroteuthis margaritifera</i>	0.05	0.32	7.17	57.76
<i>Megalocranchia</i> sp.	0.08	0.29	7.03	64.79
<i>Abraliopsis pfefferi</i>	0.25	0.49	5.99	70.78
<i>Brachioteuthis</i> sp.	0	0.08	5.63	76.41
<i>Pterygioteuthis giardi</i>	0.03	0.06	4.03	80.43
<i>Chiroteuthis</i> sp.	0	0.07	3.08	83.51
<i>Ancistrocheirus lesueuri</i>	0	0.04	2.98	86.49
<i>Argonauta argo</i>	0	0.06	2.94	89.43

**Table 3.** Univariate indices of the northern and the southern Sargasso Sea regions. Rhynchoteuthion stages of the family Ommastrephidae were not included on the species level

	Southern Sargasso Sea	Northern Sargasso Sea
No. of species	10	18
Density ( $N/1000\text{ m}^3$ )	14.832	53.614
Magalef's species richness ( $D$ )	3.337	4.269
Pielou's evenness ( $J$ )	0.832	0.781
Shannon's diversity [ $H'(\log e)$ ]	1.917	2.257

and Roper 1979), was estimated to take place primarily in summer, though spawning females occurred already in spring. In the present collection early life stages of *A. pfefferi* represented the second most-abundant species. Therefore, spawning was likely to have started already in the early months of the year. From records of *Megalocranchia megalops* collected during their study, Lu and Roper (1979) concluded that this species spawns from winter to early spring. This agrees with the occurrence of recently hatched specimens in our study.

#### Distribution of cephalopods in relation to the thermal front

In the eastern North Atlantic Lu and Clarke (1975) observed an increase of cephalopod abundances and species number from north to south, from temperate to subtropical and tropical regions. This also seems to be true for the western North Atlantic. Dawe and Stephen (1988) considered the north wall of the Gulf Stream to be a boundary that restricts the distribution of tropical-subtropical cephalopod species to higher latitudes. Our sampling in the relatively small area of the Sargasso Sea south of the Gulf Stream core revealed reverse relationships: abundances and species diversity were significantly higher in the northern part of the investigated area. This pattern has also been demonstrated for small invertebrate zooplankton (Böttger 1982), epipelagic copepods (Colton et al. 1975) and mesopelagic fishes

(Backus et al. 1969). These studies related the differences to the position of the STCZ, characterised by a distinct thermal front.

In March 1993 the front was located at a latitude of approximately 27°20'N. This lies within the region of pronounced frontogenesis, which has been described in the latitude range of 22–32°N (Voorhis and Hersey 1964) or, in more recent studies, between 26°N and 32°N (Halliwell et al. 1991a,b, 1994). The front forms in the upper 200 m, where the colder water of the northern Sargasso Sea converges with the warmer mixed layer of the southern Sargasso Sea (Wegner 1982; Halliwell et al. 1991b). It is usually detectable by a temperature gradient of 1°C within a distance of 10 km (Voorhis and Hersey 1964). The most obvious feature during our cruise was the strong stratification of the water mass south of the STCZ, which limited the mixing of the surface layer. In the same season as our investigation, Ryther and Menzel (1960) measured distinct differences in primary production near Bermuda. South of 30°N they detected a rapid decline in productivity to approximately 10% of that found at stations at the northern end of their transect (35°N). This strong gradient of primary production, coinciding with the position of the front, is likely to have an influence on the distribution of zooplankton, as proposed by Backus et al. (1969). Cold core rings, separated from the Gulf Stream and enclosing cold and nutrient-rich slope water, possibly enhance this effect (Ortner et al. 1978). Niermann (1986) observed a decreasing abundance of species and individuals of *Sargassum natans* epibionts in the southern part of the Sargasso Sea. He attributed this decrease to lower primary production and, thus, a lack of suitable food in this region. In the waters north of the thermal front, Böttger (1982) measured a two- to three-times higher microzooplankton biomass than in the stratified waters south of it. This small size fraction of zooplankton is an important food resource for fish larvae (Arthur 1977) and likely sustains higher abundances of early life stages of cephalopods, supporting the remarkable increase in the cephalopod densities north of 29°N. Previous studies

have also noted north–south differences in the biota of the Sargasso Sea (Backus et al. 1969; Colton et al. 1975; Böttger 1982), with species diversity being higher in the northern area. This was also observed for the early life stages of cephalopods. Seven species/genera were exclusively found in the north. Furthermore, different species dominated the cephalopod assemblages. In the north the cranchiid *Leachia lemur* was by far the prevailing species. According to Voss et al. (1992) it is restricted to the North Atlantic Subtropical Region west of about 50°W and seems to be endemic to the northern and southern Sargasso Sea. The high abundance and the centre of distribution of *L. lemur* north of the STCZ is probably attributable to the putative higher productivity in that area. Although the genus *Leachia* is generally confined to low-productive subtropical waters, increased abundances of cranchiids always appear to be related to areas of intensified productivity (Voss 1988).

In comparison, *Selenoteuthis scintillans*, which besides *L. lemur* is mainly responsible for the north–south differences in species composition (SIMPER), was relatively scarce in the northern area. Its geographical distribution in the western North Atlantic extends from approximately 8–41°N (Voss and Stephen 1992), completely covering the investigated part of the Sargasso Sea. The conspicuous low abundances of *S. scintillans* found north of the STCZ correspond to the densities estimated by Lu and Roper (1979). Their results and our study indicate that the northern Sargasso Sea represents the northern boundary of distribution for this species. Supported by the observation that the occurrence of *S. scintillans* north of the Gulf Stream is restricted to warm core eddies (Voss and Stephen 1992), temperature seems to be the limiting factor.

In conclusion, the distribution patterns of early life stages of cephalopods confirm that the thermal front represents a distinct boundary, both in species composition and in abundance, with a considerable decrease from north to south (Backus et al. 1969; Colton et al. 1975; Böttger 1982; Lea 1984). The latitudinal decrease is not gradual, but pronounced at the front. Whether this is also true for adult cephalopods is still in question. As juvenile and adult squids are highly mobile and mesopelagic species inhabit completely different parts of the water column compared to their hatchlings, possible north–south differences are more difficult to detect. In order to understand the influence of the hydrography on the distribution patterns of oceanic cephalopods, it is necessary to achieve a better picture of the overall distribution of cephalopods in the western North Atlantic and to improve the knowledge about their biology, i.e. spawning periods, sites and feeding habits.

**Acknowledgements** We wish to thank Prof. D. Schnack, the initiator and chief scientist of the R.V. “Poseidon” cruise 200/1, for his encouragement and support. Thanks are given to Drs N. Rohlf and K. Wieland, who left the valuable cephalopod collection in our hands, and to Prof. N. Voss for fundamental taxonomic advice. This study was supported by grants from the Deutsche Forschungsgemeinschaft (Pi 203/6-1, Pi 203/6-2).

## References

- Arthur DK (1977) Distribution, size, and abundance of micropepods in the California Current system and their possible influence on survival of marine teleost larvae. *Fish Bull* (Wash DC) 75:601–611
- Ashjian CJ, Smith SL, Flagg CN, Mariano AJ, Behrens WJ, Lane PVZ (1994) The influence of a Gulf Stream meander on the distribution of zooplankton biomass in the Slope Water, the Gulf Stream, and the Sargasso Sea, described using a shipboard acoustic Doppler current profiler. *Deep-Sea Res* 41:23–50
- Backus RH, Craddock JE, Haedrich RL, Shores DL (1969) Mesopelagic fishes and thermal fronts in the western North Atlantic. *Mar Biol* 3:87–106
- Berry SS (1920) Preliminary diagnoses of new cephalopods from the western Atlantic. *Proc US Natl Mus* 58:293–300
- Böttger RC (1982) Studies on the small invertebrate plankton of the Sargasso Sea. *Helgol Meeresunters* 35:369–383
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol Monogr* 27:325–349
- Cairns SD (1976) Biological results of the University of Miami deep-sea expedition's 118 cephalopods collected in the Straits of Florida by the R/V Gerda. *Bull Mar Sci* 26:233–272
- Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Natural Environmental Research Council, UK
- Clarke KR, Warwick RM (2001) Primer-E (5) computer program 2001. Natural Environmental Research Council, UK
- Colton JB, Smith DE, Jossi JW (1975) Further observations on a thermal front in the Sargasso Sea. *Deep-Sea Res* 22:433–439
- Dawe EG, Stephen SJ (1988) The cephalopod assemblage of the Gulf Stream system east of 60 degree W. *Malacologia* 29:235–245
- Deevey GB (1971) The annual cycle in quantity and composition of the zooplankton of the Sargasso Sea off Bermuda. I. The upper 500 m. *Limnol Oceanogr* 16:219–240
- Deevey GB, Brooks AL (1977) Copepods of the Sargasso Sea off Bermuda: species composition and vertical and seasonal distribution between the surface and 2000 m. *Bull Mar Sci* 27:256–291
- Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analysing multispecies distribution patterns. *Mar Ecol Prog Ser* 8:37–52
- Gibbs RH, Roper CFE (1970) Ocean Acre preliminary report on vertical distribution of fishes and cephalopods. In: Farguhar GB (ed) Proceedings of an international symposium on biological sound scattering in the ocean. Maury Center Report 005, Department of Navy, Washington DC, pp 119–133
- Goericke R, Welschmeyer NA (1998) Response of Sargasso Sea phytoplankton biomass, growth rates and primary production to seasonally varying physical forcing. *J Plankton Res* 20:2233–2249
- Goldman DA (1993) Distribution of cephalopod paralarvae across the Florida Current front in the Florida Keys: preliminary results. *Rev Biol Trop* 41:31–34
- Halliwel GJ, Cornillon P, Brink KH, Pollard RT, Evans DL, Regier LA, Toole JM, Schmitt RW (1991a) Descriptive oceanography during the frontal air–sea interaction experiment: medium- to large-scale variability. *J Geophys Res* 96:8553–8567
- Halliwel GJ, Ro YJ, Cornillon P (1991b) Westward-propagating SST anomalies and baroclinic eddies in the Sargasso Sea. *J Phys Oceanogr* 21:1664–1680
- Halliwel GJ, Peng G, Olson DB (1994) Stability of the Sargasso Sea subtropical frontal zone. *J Phys Oceanogr* 24:1166–1183
- Jackson GA (1980) Phytoplankton growth and zooplankton grazing in oligotrophic oceans. *Nature* 284:441
- Kruskal JB (1964) Multidimensional scaling by optimising goodness of fit to a non-metric hypothesis. *Psychometrika* 29:1–27
- Lea CE (1984) Pelagic cephalopods of the Florida Current. Dissertation, Texas A&M University, College Station

- Lu CC, Clarke MR (1975) Vertical distribution of cephalopods at 40°N, 53°N and 60°N at 20°W in the North Atlantic. *J Mar Biol Assoc UK* 55:143–163
- Lu CC, Roper CFE (1979) Cephalopods from the Deepwater Dumpsite 106 (western Atlantic): vertical distribution and seasonal abundance. *Smithson Contrib Zool* 288:1–36
- Niermann U (1986) Distribution of *Sargassum natans* and some of its epibionts in the Sargasso Sea. *Helgol Meeresunters* 40:343–353
- Ortner PB, Wiebe PH, Haury L, Boyd S (1978) Variability in zooplankton biomass distribution in the northern Sargasso Sea: the contribution of Gulf Stream cold core rings. *Fish Bull (Wash DC)* 76:323–334
- Peile AJ (1926) The Mollusca of Bermuda. *Proc Malacol Soc Lond* 17:71–98
- Pfeffer G (1912) Die Cephalopoden der Planktonexpedition: Zugleich eine monographische Übersicht der Oegopsiden Cephalopoden. In: Hensen VAC (ed) *Ergebnisse der Plankton Expedition der Humboldtstiftung 2F(a)*. Lipsius and Tischler, Kiel, pp 1–815
- Piatkowski U (1998) Modern target sampling techniques provide new insights into the biology of early life stages of pelagic cephalopods. *Biol Mar Medit* 5:260–272
- Piatkowski U, Welsch W, Röpke A (1993) Distribution patterns of the early life stages of pelagic cephalopods in three geographically different regions of the Arabian Sea. In: Okutani T, O'Dor RK, Kubodera T (eds) *Recent advances in cephalopod fisheries biology*. Tokai University Press, Tokyo, pp 417–431
- Rodhouse PG, Symon C, Hatfield EMC (1992) Early life cycle of cephalopods in relation to the major oceanographic features of the Southwest Atlantic Ocean. *Mar Ecol Prog Ser* 89:183–195
- Roper CFE (1977) Comparative captures of pelagic cephalopods by midwater trawls. *Symp Zool Soc Lond* 38:61–87
- Roper CFE, Young RE (1975) Vertical distribution of pelagic cephalopods. *Smithson Contrib Zool* 209:1–48
- Ryther JH (1963) Geographical variations in productivity. In: Hill MN (ed) *The sea*. Wiley, New York, pp 347–380
- Ryther JH, Menzel DW (1960) The seasonal and geographic range of primary production in the western Sargasso Sea. *Deep-Sea Res* 6:235–238
- Schnack D, Piatkowski U, Wieland K (1994) *Fahrtbericht zur Aal-Expedition mit FS Poseidon (Reise 200/1) in die Sargasso See im Frühjahr 1993*. Ber Inst Meereskde Kiel 248:1–33
- Voorhis AD (1969) The horizontal extent and persistence of thermal fronts in the Sargasso Sea. *Deep-Sea Res* 16:331–337
- Voorhis AD, Hersey JB (1964) Oceanic thermal fronts in the Sargasso Sea. *J Geophys Res* 69:3809–3814
- Voss GL (1960) Bermudan cephalopods. *Fieldiana Zool* 39:419–446
- Voss GL, Stephen SJ (1992) Family Lycoteuthidae, Pfeffer, 1908. In: Sweeney MJ, Roper CFE, Mangold KM, Clarke MR, von Boletzky S (eds) *Larval and juvenile cephalopods: a manual for their identification*. *Smithson Contrib Zool* 513:67–71
- Voss NA (1988) Evolution of the cephalopod family Cranchiidae (Oegopsida). In: Clarke MR, Trueman ER (eds) *The Mollusca*, vol 12. Paleontology and neontology of cephalopods. Academic Press, London, pp 293–314
- Voss NA, Stephen SJ, Dong Zh (1992) Family Cranchiidae, Prosch, 1849. In: Sweeney MJ, Roper CFE, Mangold KM, Clarke MR, von Boletzky S (eds) *Larval and juvenile cephalopods: a manual for their identification*. *Smithson Contrib Zool* 513:187–210
- Wegner G (1982) Main hydrographic features of the Sargasso Sea in spring 1979. *Helgol Meeresunters* 35:385–400
- Wiebe PH, Flier GR, Davis CS, Barber V, Boyd SH (1985) Macrozooplankton biomass in Gulf Stream warm-core rings: spatial distribution and temporal changes. *J Geophys Res* 90:8885–8901
- Young RE (1978) Vertical distribution and photosensitive vesicles of pelagic cephalopods from Hawaiian waters. *Fish Bull (Wash DC)* 76:583–615