Distribution of *Sargassum natans* and some of its epibionts in the Sargasso Sea

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Abstract: *Sargassum* was collected during the Sargasso Sea Eel Expedition in Spring 1979. On average, the morphological form type *Sargassum natans* (I) made up 85 % of the total wet weight of the samples. South of the thermal front, larger amounts of weeds were observed. Here, the bladder size of *S. natans* (I) was significantly smaller (surface 47 ± 7 mm²) than in the northern part (surface: 64 ± 15 mm²), while phylloids showed no differences. The composition and density of some epibionts were examined. *Membranipora tuberculata* (Bryozoa), *Clytia noliformis* (Hydrozoa) and the calcarious algae *"Melobesia* sp.*"* (Rhodophyta) were studied quantitatively according to different features at 17 stations. *M. tuberculata* was the most abundant epibiont followed by *C. noliformis*. Compared with these species, *"Melobesia* sp.*"* occurred in considerably lower quantities. *M. tuberculata* showed a preference for bladders rather than phylloids; *C. noliformis* was found more frequently on phylloids than on bladders. *"Melobesia* sp.*"* did not show any preference. Frequency and abundance of these epibionts were higher north of the thermal front than south of this front. North of the front *S. natans* (I) was less abundant but bladders were larger.

INTRODUCTION

Floating *Sargassum* (Family Fucaceae) is found in the western North Atlantic and is also known from the western and central parts of the Pacific Ocean (Yoshida, 1963; Vozzhinskaja, 1965). In the Atlantic, the Sargasso Sea is one of the main distribution areas of the so-called gulf-weed. Here, it forms a holopelagic population and maintains itself by vegetative growth only.

Origin and distribution of these weeds have been discussed by Winge (1923) and Parr (1939). Butler et al. (1983) reviewed the quantity and distribution of *Sargassum* as estimated by various authors.

The attached fauna of *Sargassum* has been described in several publications. Many authors have reported on the temporal and geographical variation of the mobile fauna (Timmermann, 1932; Fine, 1970; Butler et al., 1983; Stoner & Greening, 1984) but regarding the sessile fauna and flora mainly qualitative descriptions are available (Hentschel, 1922; Prat, 1935; Burkenroad, 1939; Weis, 1968; Morris & Mogelberg, 1973; Woelkerling, 1975; Butler et al., 1983). Quantitative analyses have been carried out in relation to settlement and succession of epibionts by Conover & Sieburth (1964) and Ryland (1974). Semiquantitative examinations of geographical distribution were carried out by Timmermann (1932). This paper examines whether the biogeographical differences north and south of the north aquatorial subtropical convergence confirmed by many authors are reflected by some epibionts of *Sargassum natans*.

The present study concentrates on the quantitative aspects of the relationship between *Membranipora tuberculata* (Bryozoa), *Clytia noliformis* (Hydrozoa) and *"Melobesia* sp.*"* (Rhodophyta) in order to ascertain possible differences in the density of the epibionts of *Sargassum natans* (I) with respect to parts of the thallus and geographical regions. In contrast to the *Sargassum* material collected by Hentschel (1922) and Timmermann (1932), which was in part very sparse and obtained during different seasons of several years, the material presented here is more homogenous, since it was collected at a comparatively great number of stations and during a shorter period of sampling.

MATERIAL AND METHODS

The *Sargassum* material was gathered during the 92nd journey of the F.R.V. "Anton Dohrn" from 1 March to 6 May 1979 (Tesch, 1982). The floating gulfweed was collected using a Neuston net (David, 1965) at 207 stations (Tesch, 1982). Details of methods of sampling surface plankton have been published by John (1982).

The samples were preserved in a 4 % formaldehyde-seawater solution buffered with hexamethylene tetramine. The morphological forms of *Sargassum* were determined according to Winge (1923), Parr (1939), and Woelkerling (1975). The morphological form type *Sargassum natans* (I) was used for examining the epibionts because this was the species occurring most frequently in the samples. In addition, its epibiontic variety is not so high as that of the species *S. fluitans.* This makes it easier to determine the quantitative differences in the abundance of the epibionts.

The epibionts were identified and a quantitative analysis was made of the most frequent species *Membranipora tuberculata, Clytia noliformis* and *"Melobesia* sp.*".* A quantification of the Spirorbides (Polychaeta) was omitted because in a large number of sampling vessels the individuals had fallen off the weed bunches.

First, the intensity of encrustment by bryozoans and by calcareous algae of all *Sargassum* weed from all stations was roughly divided into weak, medium and heavy encrustment. Then, the material from 17 stations (Fig. 1), 9 in the northern and 8 in the southern Sargasso Sea, was examined in the following manner: All bunches of *Sargassum natans* (I) without branches were set aside. If samples contained more than 15 bunches a subsample was taken; otherwise the whole sample was examined. The age of the bunches was estimated according to the colour and condition of stem bladders and phylloids (Niermann, 1982). These estimations were based on the criteria of Hentschel (1922) and Rhyland (1974). In order to guarantee comparability, only the phylloids and the bladders of the main axis were examined because of their regular arrangement in pairs. The examination of the main axis itself was omitted, because here the large colonies of Bryozoa were often considerably damaged and had to some extent fallen off. If the main axis had broken off, the examination was continued on the upper side branch.

The surface area and the length of the leaflets were determined using a planimeter. For this purpose, they were inbedded in glycerolgelatine between two thin sheets of glass. The surface area of the ball-like bladders was determined with the help of the measured length and width.

The epibionts of both phylloids and bladders were determined according to the criteria listed in Table 1.

A comparison of points (1) and (2) demonstrates how the processing of the main axis

Table 1. Mean values ($\overline{m}$) and standard deviations ($s_{\overline{m}}$) of the examined epibionts in the northern and southern Sargasso Sea. Geographical differences were tested by the U-Test (Wilcoxon & Cox, cf. Sachs, 1973). Differences in distribution of the epibionts on bladders and phylloids were tested with the Sign-Test (Dixon & Mood, cf. Sachs, 1973). For these results see text. P = likehood of a true H_o. N.S. = not significant

Criteria for examination		Northern stations		Southern stations		
		$\overline{m}$	$s_{\overline{m}}$	$\overline{m}$	$s_{\overline{m}}$	P
For the whole bunch						
(1) Percentage of bladders of which more than 75 % of the surface area was overgrown with *Membranipora tuberculata* (%).	: bladders	22 ±	12	4 ±	2	0.025
For the main axis only						
(2) Percentage of bladders of which more than 75 % of the surface area was overgrown with *Membranipora tuberculata* (%).	: bladders	38 ±	26	10 ±	5	0.025
(3) Percentage of bladders and phylloids covered with						
a. epibionts in general	: bladders	93 ±	6	57 ±	11	0.01
(%)	: phylloids	81 ±	9	43 ±	15	0.01
b. *Membranipora tuberculata*	: bladders	74 ±	16	41 ±	7	0.001
(%)	: phylloids	40 ±	23	15 ±	11	0.025
c. *Clytia noliformis*	: bladders	32 ±	24	21 ±	11	N.S.
(%)	: phylloids	47 ±	23	30 ±	14	N.S.
d. "*Melobesia* sp."	: bladders	25 ±	22	1.8 ±	1.3	0.01
(%)	: phylloids	30 ±	24	4.3 ±	2.0	0.05
(4) Intensity of the coverings on bladders and phylloids.						
Membranipora tuberculata						
a. Number of colonies	: bladders	163 ±	45	110 ±	32	0.025
($n \cdot dm^{-2}$)	: phylloids	87 ±	55	34 ±	26	0.025
b. Number of colonies with up to 10 zooids	: bladders	64 ±	33	34 ±	19	0.05
($n \cdot dm^{-2}$)	: phylloids	47 ±	44	12 ±	13	0.025
c. Percentage of surface area covered (%)	: bladders	54 ±	39	21 ±	9	0.05
	: phylloids	7 ±	9	2 ±	2	N.S.
Clytia noliformis						
d. number of hydroids	: bladders	550 ±	400	270 ±	160	N.S.
($n \cdot dm^{-2}$)	: phylloids	1180 ±	800	460 ±	250	0.025
"*Melobesia* sp."						
e. Intensity of encrustation	: bladders	33 ±	36	1.7 ±	1.7	Not tested
(expressed in degrees)	: phylloids	57 ±	50	3.5 ±	2.6	Not tested

is representative for the encrustation of the whole bunch. For the whole examination an amount of 139 bunches, averaging 17 bladders and 15 phylloids per bunch were used.

RESULTS

The north equatorial subtropical convergence defined by the thermal front (Wegner, 1982) was used as the border between the northern and the southern Sargasso Sea. In this paper the convergence is characterized by the 21 °C surface isotherm.

Distribution of *Sargassum*

Figure 1 shows the distribution of the gulf weed collected with the neuston net. For the sake of clarity, neighbouring stations were combined. A detailed quantitative distribution of the gulf weeds in Spring 1979 was given by Niermann et al. (1985). *S. natans* (I) could be found in almost all samples at an average rate of 80–90 % (wet weight). *S. fluitans* (III) amounted to 15 to 23 %. The morphological forms *S. natans* (II) and *Sargassum* (V) occurred sporadically (sometimes up to 2–5 %). Two hauls, betweeen 40° and 50° W, contained fragments of *Ascophyllum*. The highest abundance of the gulfweed was between 22° and 28° N, decreasing seemingly towards the north and south.

A difference in size of the bladders of *S. natans* (I) could be found by comparing the stations north and south of the thermal front. For this comparison the surface of all bladders (total: N = 987 north; n = 1516 south of the thermal front) were combined per bunch (n = 56 north and n = 83 south). The mean values per station tested by the U-test
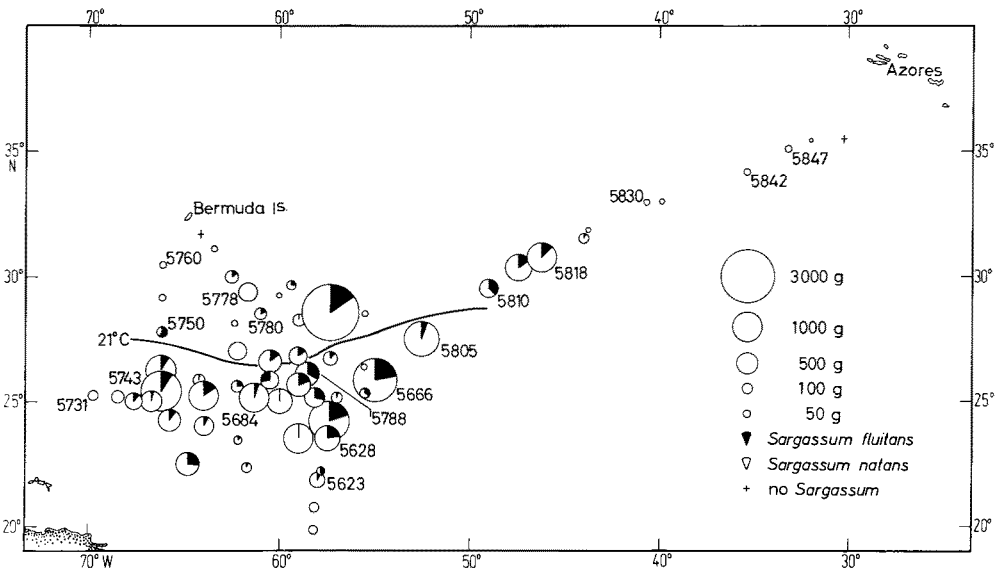

Fig. 1. Distribution of *Sargassum* (wet weight; g · 10^{-3} m^{-2}). The quantity of *Sargassum* per station is characterized by the width of the circles. Station numbers indicate stations where epibionts were examined

(Wilcoxon & Cox, cf. Sachs, 1973) were significantly higher at stations north of the thermal front (north: A = 64 ± 15, n = 9; south: A = 47 ± 7, n = 10; p = 0.005). The biggest bladders were found at the most northern stations.

No differences regarding surface area and length could be observed between phylloids north and south of the thermal front. Similarly, no appreciable differences in age were ascertained in the weeds examined at the 17 stations in the northern and southern Sargasso Sea.

Epibionts

Distribution on bladders and phylloids

Membranipora tuberculata, *Clytia noliformis* and *"Melobesia* sp." were observed at all stations. *C. noliformis* was found more frequently on bunches than on torn-off bladders floating separately from the bunches. Spirorbids were present at almost all stations. However, they had often fallen off the weeds, especially off the drifting bladders. Cypris larvae and *Lepas pectinaria* occurred mainly on loose bladders; Cypris larvae were partly encrusted with *M. tuberculata*. On weed bunches, spirorbids, lepadides and Cypris larvae seemed to be more frequent on bladders than on leaflets. The hydroids *Obelia dichotoma* and *Zanclea costata* were very often found on old bladders. They frequently settle on dead bryozoan colonies. *O. dichotoma* was detected at stations north of the convergence, while *Zanclea costata* was represented at only 2 stations in the northern and two stations in the southern Sargasso Sea.

The distribution of *M. tuberculata*, *C. noliformis* and *"Melobesia* sp." on leaflets and bladders was tested using the "Sign test" (Dixon & Mood, cf. Sachs, 1973). The percent amount of leaflets encrusted with *"Melobesia* sp." did not differ significantly from the portion of encrusted bladders (Table 1: 3d). However, the intensity of encrustation on leaflets was higher than on bladders (Table 1: 4e).

The settlement of *C. noliformis* and *Membranipora tuberculata* on phylloids differed significantly from that on bladders: *Clytia* was found more often an phylloids than on bladders (Table 1: 3c, 4d), while bladders were more densely populated than the phylloids by *Membranipora* (Table 1: 4a–4c); this was especially obvious in small colonies of up to 10 zooids: 62 % (58 % north; 74 % south of the thermal front) of the small colonies were observed on bladders. Ryland (1974) found nearly the same relation (60 % on bladders; 40 % on phylloids) but without significant preference. The difference in colonisation is also evident with regard to the share (average of all stations) of the bladders (m = 68 %) and phylloids (m = 32 %) of the main axes encrusted with *Membranipora* (Table 1: 3b). Similarly, the percentage of surface area of *Sargassum* encrusted with *Membranipora* is about 8 times higher on bladders than on phylloids (Table 1: 4c). However, it has to be taken into consideration that, in general, more bladders than leaflets had been found at the lower, strongly encrusted part of the thallus so that the values of the leaflet-encrustation might be lower for this reason.

Geographical differences

Figure 2 shows the distribution of *Sargassum natans* with different degrees of encrustation by *Membranipora* and *"Melobesia"*. At each station, the estimated values

of the encrustment of individual bunches were averaged. The stations with medium encrustation were not taken into consideration in order to obtain a better selectivity. The comparison of temperature and encrustation shows that the gulf weeds in the colder parts of the northern Sargasso Sea are more strongly encrusted with *Membranipora* than the weeds in the southern parts. The intensity of encrustation of the bunches changes distinctly in the region of the thermal front.

Table 1 reflects the average values of the different criteria used in the examination of epibionts at the stations north and south of the thermal front. The standard deviation of the mean results on the *Sargassum* bunches is very high, especially with regard to the distribution of *Clytia noliformis*. The values of the criteria from all stations north and south of the thermal front were tested by the U-test (Wilcoxon & Cox, cf. Sachs, 1973).
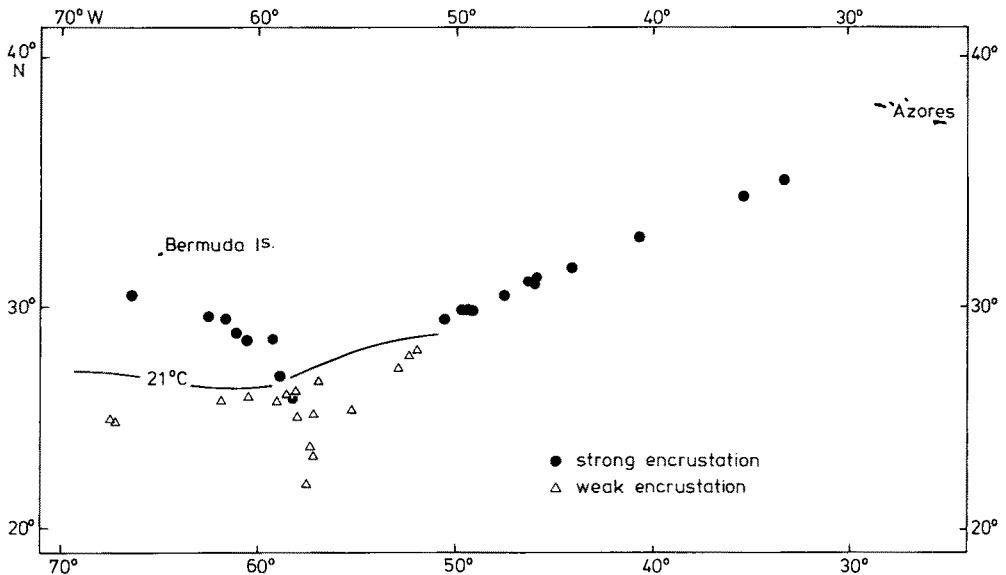

Fig. 2. Distribution of stations with high and low degrees of encrustation

With regard to *Membranipora* and *"Melobesia"* all examination results could be confirmed to a level of at least 5 %. One exception is the criterion "percentage of the surface area of phylloids covered with *Membranipora"* (Table 1: 4c).

A remarkable difference between north and south was noted with regard to the distribution of the small *Membranipora* colonies with up to 10 individuals. In the northern Sargasso Sea, the number of these young colonies per surface area of bladders and phylloids was more than twice as high as in the southern part (Table 1: 4b).

With regard to the criteria of the distribution of *Clytia*, no significant differences, with one exception, could be confirmed between the stations to the north and those to the south of the thermal front (Table 1: 3c; 4d).

Remarks on methods

A comparison of the two criteria "percentage of the bladders with more than 75 % *Membranipora* encrustation" on the whole bunch and on the main axis (Table 1: Point 1 and 2) shows that the exclusive processing of the main axis reflects very well the proportions of the encrustation of the whole bunch (Table 1: 1; 2). At every station, the values of the whole bunches are proportionally lower than those of the main axes (n = 16; r = 0.9; p = 0.001; rank correlation of Spearman, cf. Sachs, 1973).

Table 1 shows that differences between the stations are similarly reflected by the differing results on the epibionts on bladders and leaflets. The simple and quickly determinable criteria, i.e. "Percentage of bladders with more than 75 % encrustation" (Table 1: 1; 2); "percentage of bladders or phylloids covered with epibionts" (Table 1: 3a–3d), show a greater difference between the northern and southern stations. The criteria needing lengthy processing (Table 1: 4a–4d), i.e. "surface area encrusted with *Membranipora*", "number of colonies", show a greater variation between the bunches than the points mentioned above and, therefore, fail to reflect very clearly the differences between stations. In addition there is a strong variation between the leaflets, possibly due to the fact that heavily encrusted leaflets have often fallen off. Therefore, results depend strongly on their random presence.

DISCUSSION

The distribution and composition of *Sargassum* species as estimated by Parr (1939) and some other authors is reviewed by Butler et al. (1983). The composition of *Sargassum* species varies according to geographical regions and shows annual fluctuations (Parr, 1939). *S. natans* (I) usually amounts to up to more than half of all *Sargassum* species. *S. fluitans* (III) is represented by about 10–35 %. The portion of other *Sargassum* species is low, mostly lower than 2 %, seldom higher than 10 %. So our findings are in the range found by Parr (1939) in the years 1934 and 1935 for this region.

Several authors have observed that there is no area of continued high abundance of *Sargassum* weed, but that the distribution changes according to season and due to the mesoscale circulation of the Sargasso Sea (Butler et al., 1983). Our findings of high amounts of *Sargassum* south of the thermal front might be attributed to the heavier mixing in the northern Sargasso Sea during winter; old and fresh parts of the weeds sink down by way of the Langmuir-circulation to a depth where they lose their positive buoyancy (Johnson, 1977; Assaf et al., 1971). In addition, the low air and water temperatures of the winter months may lead to a decrease in quantity of weeds in the northern Sargasso Sea (Winge, 1923; Parr, 1939).

The higher temperature of the water could explain why most *Sargassum* is found south of the thermal front. In this connection, the difference in bladder size at stations north and south of the thermal front should be mentioned. Due to the better temperature conditions, the weeds of the southern Sargasso Sea display faster growth, develop more bladders, have therefore, on average, a higher number of younger and smaller bladders and leaflets than the weeds in the northern region, where the older and bigger bladders predominate.

The distribution of the examined epibionts on different parts of *Sargassum natans* (I) is shown in Table 1. *Membranipora tuberculata* is more abundant on bladders than on

phylloids. The settling place is chosen by its Cyphonautes larvae. The settling behaviour of the larvae is immediately expressed by the distribution of the small colonies on the weed bunches. It seems that Cyphonautes larvae prefer to settle on bladders. One explanation for this preference could be differences between bladders and phylloids in the qualities of substrate. The "tannin effect" (Sieburth & Conover, 1965) could be another explanation. The tannin occurring in the growing tips of the weeds inhibits the establishment of a surface microflora. This factor might influence the settlement of the larvae (Ryland, 1974). The bladders are formed at a later stage and therefore they show no "tannin effect".

The settlement of the Cyphonautes larvae on the bladders, which form a harder substrate than the quickly deformable leaflets, are advantageous for the establishment of later colonies. Phylloids are more vulnerable than the sturdier bladders to mechanic influences, and are more likely to fall off after becoming dry from drifting on the water surface in calm seas (Woodcock, 1950). Old leaflets were more frequently damaged or rotted quicker than older bladders. Thus, the phylloids have a higher dropping rate. Another reason for their falling off could be the encrustation by Bryozoa, which reduces the photosynthesis rate in the leaflets. Apart from this, it is conceivable that the phylloids, due to their stiff encrustation with bryozoa, are no longer able to adapt to the movements of the waves, and thus break off.

The frequent occurrence of hydroids on leaflets may be caused by differences in form between phylloids and bladders. In contrast to Membranipora, which grows in encrustments, the spreading of Clytia is mainly linear. The extended leaflets are more favourable to the growth of the latter than the bladders: due to the length of its edge zone a phylloid offers more space to the hydroids than bladders with comparable surface area (Hentschel, 1922).

In this examination, a difference in abundance of Membranipora tuberculata, "Melobesia sp." and Clytia noliformis has been found between the north and south of the Sargasso Sea. The density of these epibionts expressed in frequency per dm^{-2} and percentage encrusting of phylloids and bladders is more intensive north of the thermal front. With Clytia noliformis, the north-south difference could only be verified with regard to the criterion "number of hydroids" on the leaflets. However, all the other examined criteria have the same tendency (Table 1: 3c; 4d). The results of Timmermann (1932) showed similar differences in the abundance of Membranipora and Clytia between the stations north and south of the thermal front. Despite the different sampling months, the findings of Timmermann (1932) and the present study are remarkably similar (Table 2).

The distribution of Cyphonautes larvae in the Sargasso Sea as observed by Lohmann (1904) may be taken as another proof of the higher intensities of bryozoan encrustation in the northern Sargasso Sea. At 16 stations north of the subtropical convergence, he found on average 116 larvae whereas at the 12 southern stations he found only 12 per station.

Many other authors have shown that there are bio-geographical differences between the northern and southern Sargasso Sea. They all noted a decline in the variety and abundance of species in the southern Sargasso Sea: Hulbert (1964) for phytoplankton; Böttger (1982) for small invertebrate plankton; Backhus et al. (1969) for mesopelagic fishes; Lohmann (1904) for Doliolida; Cifelli & Sachs (1966) for Foraminifera; Colton et al. (1975) for epipelagic copepods; John (1984) for fish larvae.

Table 2. Percentage of bladders covered with *Membranipora* and *Clytia*
(Criterion No. 3 in Table 1)

Area	North Sargasso Sea		South Sargasso Sea	
Reference	Timmermann (1932)	Niermann (1986)	Timmermann (1932)	Niermann (1986)
Station No. (month)	2; 11 (XII) 19; 20 (I)	see Fig. 1 (IV)	1–10 (VIII–XII) 23–26 (I)	see Fig. 1 (IV)
Bladders covered with *Membranipora* (%)	76	74 ± 16	36	41 ± 7
Bladders covered with *Clytia* (%)	35	32 ± 24	29	21 ± 11

The changes from the north to the south are not gradual but abrupt, coinciding in most cases with the course of the North Atlantic subtropical convergence, also called the "thermal front". The position of the thermal front changes according to the seasons. It is often located in the region between 27° and 28° N (Backus et al., 1969). Despite the not fully established thermal front during the cruise in Spring 1979 (Wegner, 1982), the variation in settling intensity of the epibionts north and south of the convergence was obvious.

The decreasing frequency of species and individuals in the southern part of the Sargasso Sea can be attributed to the pronounced stratification of the water column in this region. Here, the upper layers of the water are cut off from the supply of nutrients, which has an immediate effect on the primary production (Menzel & Ryther, 1960; Hulbert, 1964; Backus, 1969). Examination of the stomach contents of *Membranipora tuberculata* and *Clytia noliformis* have shown that their nutrition consists mainly of nannoplankton such as Diatomea, Coccolithophorida and Peridinea (Hentschel, 1922; Burkenroad, 1939). So the decrease in *M. tuberculata* and *C. noliformis* in the southern part could probably be attributed to the lack of food in this region.

The strongly decreased occurrence of the calcareous alga "*Melobesia*" in the southern Sargasso Sea may be immediately linked with the nutrients or with a smaller amount of some trace elements in this region. According to Carpenter & Cox (1974), the distribution pattern of the *Sargassum* epiphytes can be directly correlated with differences in concentration of nutrients in the Sargasso Sea. Menzel et al. (1963) and Menzel & Ryther (1960) have shown that low iron content limits the production of phytoplankton in the southern Sargasso Sea. The distribution pattern of the nitrogen-fixing *Dichotrix*, which occurs as an epiphyte on *Sargassum*, is linked with the available iron in this region (Carpenter & Cox, 1974).

In this way, beside the temperature effect mentioned above, the here confirmed stronger development of the *S. natans* (I) bladder in the northern Sargasso Sea could also be attributed to the higher concentration of nutrients in this region.

Likewise it has to be taken into consideration that due to the higher growing rates of *Sargassum* in the southern Sargasso Sea, conditioned by temperature as mentioned above, and in combination with the "tannin effect" (Sieburth & Conover, 1965), the expansion of the epibionts relative to the surface area of the weeds is smaller than at the

northern stations. Also, one can expect that due to the slower growth of the northern weeds the average age of their bladders and phylloids is higher than that of the southern population, and hence the average density of epibionts could be greater.

On the other hand the age of the weeds was determined according to the criteria of Ryland (1974) and no appreciable difference was ascertained in the north and south of the thermal front. At all examined stations (except St. 176 with old bunches) both old and young thalli were represented in equal manner. That means that bladder size and density of epibionts are influenced more by nutrients than by temperature, if not by other factors.

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