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SUBSURFACE PELAGIC *SARGASSUM*[1]

BY

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ABSTRACT

Observations are given which indicate that the presence of *Sargassum* below the sea surface is associated with lines of convergence of surface waters and with wind speeds in excess of about 4 m sec^{-1}. It is suggested that descending currents under the convergence lines carry the plants down.

Measurements of compression and of rates of rise of *S. natans* of various densities were made at Bermuda. Results of these measurements indicate that these plants may be carried down by descending currents in excess of 4.5 to 7.2 cm sec^{-1}, and that the plants can maintain positive buoyancy, for short periods of time at least, under pressures equal to 100 m of sea water.

The pressure of the gases in the spherical bladders on *S. natans* was found to change diurnally.

INTRODUCTION

The author has often noted that *Sargassum* tends to spread out close to the sea surface during light winds and calm, whereas the plants float deeper in the water with fewer leaves thrust through the surface during winds of force 3 or greater. This phenomenon seems to indicate that descending currents, occurring during higher winds, maintain a sustained drag on the plants, thus reducing their apparent buoyancy below that of plants which are not influenced by vertical currents. During higher winds the author has seen a great many *Sargassum* plants at various depths beneath the sea surface; on one occasion more than ten per cent of the plants seen were below the surface.

The purpose of this paper is to present some observations which indicate that subsurface *Sargassum* is carried downward by descending currents under lines of convergence of surface waters. The presence of these phenomena in surface waters of a lake and ocean has been shown by Langmuir (1938) and Woodcock (1944). It is suggested that plants may remain below for a time and then return to the surface as the speed of the converging and descending currents diminishes. Also presented are data showing the compression and rates of rise of *Sargassum* of varying densities. These measurements were made in order to estimate the depths at which water pressure would cause a

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[1] Contribution No. 489 of the Woods Hole Oceanographic Institution, and Contribution No. 152 of the Bermuda Biological Station for Research.

plant to lose all positive buoyancy[2] and to estimate the speeds of currents necessary to draw plants downward. Pressure changes in the gas bladders supporting the plants were also measured, because, as suggested by Parr (1939: 9), such changes might modify the rates of rise, assuming some elasticity of bladder walls. A diurnal cycle of gas pressure was found in these bladders.

Previously questions concerning pelagic *Sargassum* beneath the surface of the North Atlantic have been given scant attention. Murray and Hjort (1912: 336) suggested that these plants have a negative buoyancy due to fragmentation by wave action. Winge (1923: 11) stated that subsurface *Sargassum* is probably burdened with an excess growth of epizoans, or that it has too few floats to maintain positive buoyancy. Parr (1939: 9) made net tows for a distance of 24 nautical miles, using five *Sargassum* nets simultaneously at different levels from the surface downward. The results of this tow and of direct observations from the deck of the ship led him to doubt that the sinking of whole plants takes place in "quantitatively significant" amounts.

SOME PHYSICAL CONDITIONS UNDER WHICH *SARGASSUM* IS SEEN BENEATH THE SEA SURFACE

Sargassum below the sea surface is almost always beneath floating plants which are formed into lines (see Fig. 1) that lie approximately parallel to the wind direction at the time of observation. Winge (1923: 11) attributed this alignment to a differential sailing which caused slower plants to be drawn into the wake of those that were more exposed to wind drag. Langmuir (1938) explained the weed lines as "wind induced" zones of convergence of surface waters which are parts of systems of left and right helical vortex pairs lying with their long axis parallel with the wind (see Fig. 2). Measurements among similar lines on Lake George (Langmuir, 1938) showed water descending (2 to 3 cm sec^{-1}) under the convergence lines and ascending in the divergent regions. Later Woodcock (1944) showed that drift bottles having a positive buoyancy of one gram, when placed 2 m apart on the sea surface and in a line normal to the wind, always reformed into lines lying parallel with the wind. This indicated that the convergence of surface waters into lines parallel with the wind also occurs on the open sea.

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[2] The terms "positive buoyancy" and "negative buoyancy" refer to the sign of the buoyant force, which is the weight of the water displaced minus the weight of the immersed plant.

In view of the work cited above, it is reasonable to assume that plants seen in lines are carried there by converging surface waters and that those under these lines are carried down by converging and descending waters. However, no direct measurements have been made of descending currents under lines of *Sargassum*.

The observations in Fig. 3 suggest that the presence of *Sargassum* beneath the sea surface under lines of convergence is related to wind speed. Records were made of the occurrence and nonoccurrence of subsurface plants together with attending wind and thermal conditions.[3] The plus signs denote a period of observation (from the ship's bow or mast) of ten minutes or more when *Sargassum* was plentiful and when it was seen on the surface only.[4] The circle indicates a similar period during which surface plants were plentiful and during

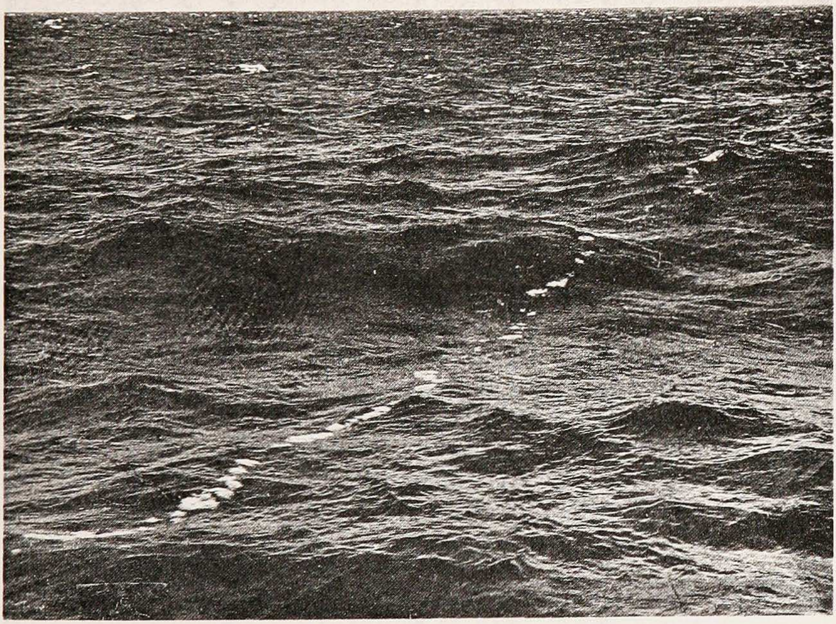

Figure 1. A photograph of a line of *Sargassum* on the sea surface.

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[3] These observations were all made in Central Atlantic waters within a few hundred miles of Bermuda and over a period of several years.

[4] Only those plants free from the influence of the ship's hull were included in these data.

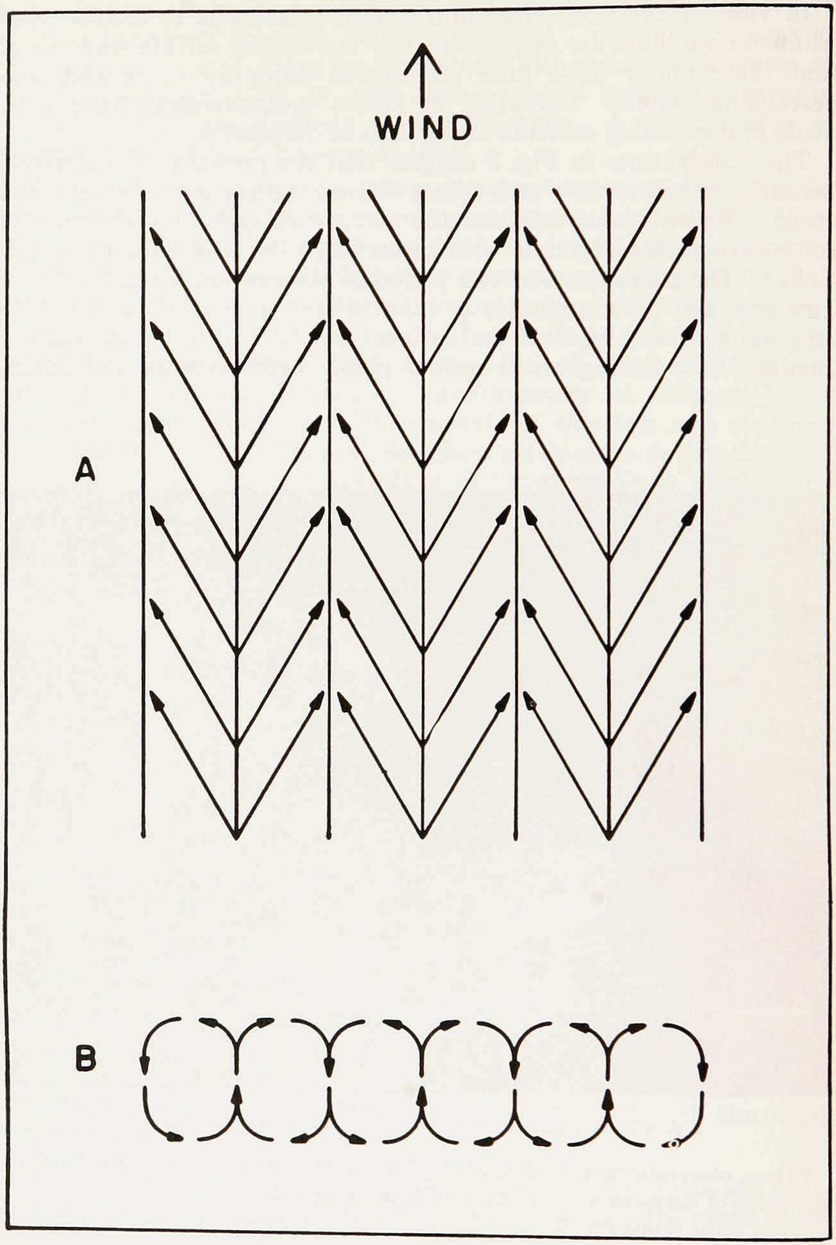

Figure 2. Idealized drawing of (A) the assumed horizontal motions of surface waters and (B) the assumed motions in a vertical section normal to the axis of the vortices.

which they were seen at an estimated depth of a meter or more below the surface. In Fig. 3 these symbols are plotted against wind speed and $e_s - e_3$ values.[5] This was done because these variables are, under average oceanic conditions, among the major factors determining changes in the rate of heat and water loss from surface waters (Montgomery, 1941: 19). During higher winds and higher values for $e_s - e_3$, more rapid descending motions would be expected because greater volumes of relatively heavy water are being produced by evaporation and cooling at the surface. The locations of the circles in Fig. 3 show that no *Sargassum* is seen beneath the surface at wind speeds less than 4 m sec^{-1}. There is no indication in these data that evaporation, as expressed by $e_s - e_3$, has any effect on the occurrence of subsurface plants.

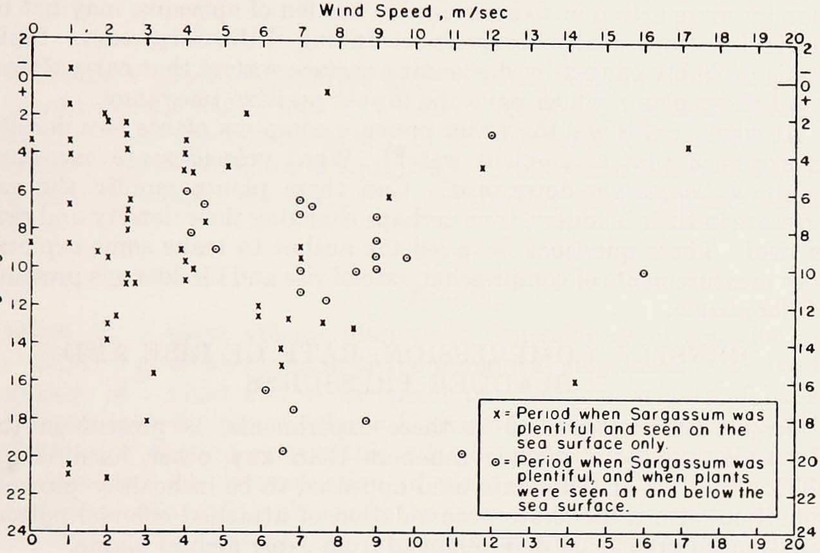

Figure 3. Showing symbols representing the occurrence and nonoccurrence of subsurface *Sargassum* at various wind speeds and at various values of $e_s - e_3$.

During many observation periods with higher winds, no subsurface plants were visible (see x symbols at wind speeds above 4 m/sec in Fig. 3). It is assumed that at such times stronger vertical currents

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[5] e_s = the saturation pressure of aqueous vapor over sea water at sea surface temperatures. e_3 = partial pressure of aqueous vapor at a height of about 3 meters above the sea.

had carried the subsurface plants to depths at which they were not visible.

Fig. 3 and the remarks about wind-induced vortices in surface waters suggest that the *Sargassum* seen below the sea surface is drawn down by local descending currents which are associated with higher winds.[6] Thus, decreasing positive buoyancy, due to fragmentation by wave action or to an excessive burden of epizoans, may not be the factor which finally brings about sinking of the *Sargassum*. Sinking is probably caused by descending surface waters that carry downward those plants which have the lowest positive buoyancy.

At what depths will the water pressure compress plants to a density in excess of that of ambient water? What velocities are necessary to draw *Sargassum* downward? Can these plants modify the gas pressure in their bladders, thus perhaps changing their density and rate of rise? These questions have led the author to make some exploratory measurements of compression, rate of rise and bladder gas pressure of *Sargassum*.

DENSITY, COMPRESSION, RATE OF RISE AND BLADDER PRESSURES

Sargassum natans, used in these experiments, is present in the Bermuda region in greater numbers than any other form (Parr, 1939: 65). All of the plants used appeared to be in healthy growing condition with a moderate accumulation of attached colonial epizoa. Unattached organisms were removed from experimental plants.

Density. This portion of the study was performed in order to obtain an approximation of the pressure required to compress a plant to the sinking point in sea water. As was expected, this pressure increased with decreasing initial plant density. The method used to determine density will be discussed first.

The damp-dry plants were weighed and placed in sea water and ballasted with brass weights until the addition of a final 2 to 5 mg

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[6] It is of interest to note that Parr's subsurface tow of *Sargassum* nets was made at a time when the average wind was force 2 (1 to 2 m sec^{-1}, see ATLANTIS log for Feb. 9, 1935, on file at the Woods Hole Oceanographic Institution, Woods Hole, Mass.). The nets caught no subsurface plants, and Parr (1939: 10) suggested that this fact indicated the absence of quantitatively significant amounts of subsurface *Sargassum*. However, at these wind speeds no subsurface weed has been seen by the author (see Fig. 3).

It should not be judged that these observations indicate serious errors in Parr's quantitative studies of the distribution of *Sargassum*, which were based upon surface collections. The observations indicate the possibility of error in surface collections during winds of 4 m sec^{-1} or more.

weight caused sinking. Thus the combined weights of the immersed plants plus the ballast were brought to a weight very nearly equal to the weight of the displaced sea water. Density (S_d) was then derived in the following manner:

$$S_d = \frac{S_w}{\dfrac{S_w + b}{d_t} - b_v}, \tag{1}$$

where S_w = plant weight in air (g), b = ballast weight (g), d_t = density of ambient sea water, and b_v = ballast volume at sea water temperature. When the volume of a plant is determined, as shown by the term in the denominator of equation (1), plant density can be modified a known amount by adding or subtracting small ballast weights. Thus,

$$S_d = \frac{S_w + b}{S_v + b_v}, \tag{2}$$

where S_v = plant volume [derived in denominator of equation (1)].

Table I gives an example of the numerical steps used to derive the density of a plant and of the plant plus various weights of ballast. The figure at the top of column E gives the density of the unballasted *Sargassum;* the accuracy of this value depends in major part upon the accuracy of the determination of plant weight. The figure at the bottom of column E is obviously the same as the density of the ambient sea water. In this case the *Sargassum* was experimentally ballasted until the weight of the plant plus the brass was equal to the weight of the displaced water (within 2 to 5 mg).

The damp-dry condition of the plants for weighing was achieved by spreading them between layers of absorbent diaper cloth which had been dampened with sea water, after which the cloth was pressed gently on all sides for about three minutes in order to bring most of the plant surfaces into contact with the cloth. Plant weighing errors were not determined. Lowndes (1942) found up to 8% error in the weighing of live marine organisms. A positive error of 8% in the weighing of the plant would cause an error of about + 0.0075 in the computed unballasted plant density given in Table I (cf., top figures of columns E and F). Since this error approaches zero as ballast is added, and since the density of plant plus ballast approaches that of the ambient water (see column F), the densities derived here are to be regarded as carefully determined approximations, the accuracy becoming greater as the density approaches that of sea water. These densities serve the desired purpose of indicating the general nature of the relationship between plant density, compression, and rate of rise.

TABLE I.—AN EXAMPLE OF THE METHOD USED TO DERIVE THE DENSITY OF A *Sargassum* PLANT AND THE ATTACHED BALLAST. THE WEIGHT OF THIS PLANT WAS 177.8 GRAMS; AMBIENT SEA WATER TEMPERATURE 22.2–22.5° C; SALINITY 36.40 °/oo; DENSITY 1.0252; PRESSURE, ABOUT ONE ATMOSPHERE

A	*B*	*C*	*D*	*E*	*F*
Ballast weight	Sargassum *weight plus ballast weight**	*Ballast volume*	*Volume of* Sargassum *plus ballast*	*Density of* Sargassum *plus ballast*	*Column E corrected for 8% positive weighing error*
b	$S_w + b$	b_v	$S_v + b_v$	$\frac{S_w + b}{S_v + b_v}$	$\frac{S_w - (S_w .08) + b}{S_v - \left(\frac{S_w .08}{1.0252}\right) + b_v}$
grams	grams	cm^3	cm^3	g cm^{-3}	g cm^{-3}
0.0	177.8	0	191.342†	0.9292	0.9217
8.05	185.85	0.95	192.296	0.9665	0.9619
12.05	189.85	1.43	192.773	0.9848	0.9817
15.05	192.85	1.79	193.131	0.9986	0.9965
17.05	194.85	2.03	193.369	1.0077	1.0063
18.55	196.35	2.21	193.547	1.0145	1.0136
19.05	196.85	2.27	193.607	1.0168	1.0161
19.55	197.35	2.33	193.668	1.0190	1.0185
20.05	197.85	2.38	193.726	1.0213	1.0210
20.55	198.35	2.44	193.785	1.0236	1.0235
20.92	198.72	2.49	193.835	1.0252‡	1.0252

* Buoyancy corrections in air were not made.

† This volume is determined as shown by the term in the denominator of equation (1); all volume and density values in this table are based upon this value.

‡ This density is empirically established by ballasting the plant to neutral buoyancy in sea water of this density. The maximum error (5 mg) in this ballasting produces an insignificant weighing error of about 2 x 10^{-5} grams per gram.

Compression. Ballasted and unballasted plants, their densities established as described previously, were tested for compression in a pressure chamber which was large enough to test a whole plant and which had a lucite viewing port at the top. Plants were placed in sea water, after which the top of the chamber was sealed. By forcing more sea water into the chamber, the internal pressure was slowly increased until the enclosed plant was observed to sink slowly, at which point the water pressure was read from a gauge of known error. Compression of these plants was then expressed as the change in density with pressure, this change in density being approximately equal to the density of the ambient sea water[7] minus the initial density of the plant.

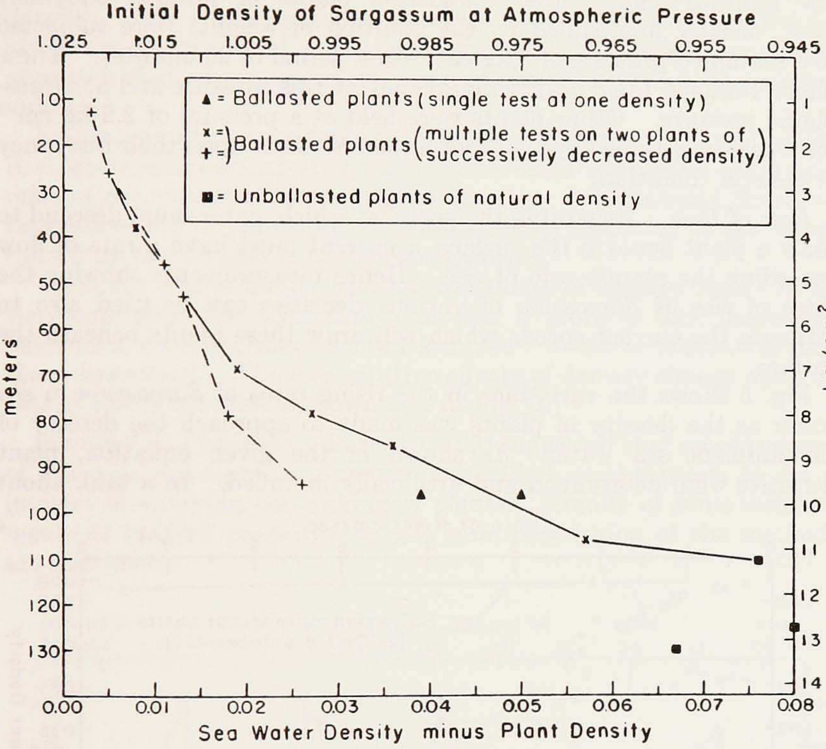

Figure 4. The effects of increasing hydrostatic pressure on the indicated initial densities of ballasted and unballasted *Sargassum*. The symbols indicate the sinking points of plants.

Fig. 4 gives the results of numerous compression tests on *Sargassum* of various initial densities and shows the effect of pressure in increasing these densities. The symbols represent the pressures or depths at which the plants of known initial density (top scale) were so compressed that they sank very slowly in sea water. The lower scale shows the approximate increase in plant density due to compression. The general trend of the points suggests a marked change in the rate of compression of the plants as the pressure is increased above

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[7] Sea water densities were taken from Knudsen's (1901) tables. Salinities were determined by titration of chlorides with silver nitrate [the Oxner (1920) method].

about 7 kg cm^{-2}. This change in rate is attributed to the beginning of the implosion of the gas-filled bladders.

Plants represented in Fig. 4 were held at the higher pressures for a few minutes only. Other *Sargassum* plants of natural buoyancy (i. e., density unmodified by the addition of weight) were subjected to a sustained pressure of 5 kg cm^{-2} for a period of 90 minutes. These plants retained their positive buoyancy at this pressure and at atmospheric pressure. Other plants were held at a pressure of 2.2 kg cm^{-2} for a period of three days without apparent effect upon their buoyancy or general condition.

Rate of Rise. Regarding the speed at which water must descend to draw a plant beneath the surface, a current must have a rate of flow exceeding the plant's rate of rise. Hence measurements showing the rates of rise of *Sargassum* of various densities can be used also to estimate the current speeds which will draw these plants beneath the surface.

Fig. 5 shows the variations in the rising rates of *Sargassum* in sea water as the density of plants was made to approach the density of the ambient sea water. As shown in the given equation, plant densities were determined and artificially modified. In a tank about

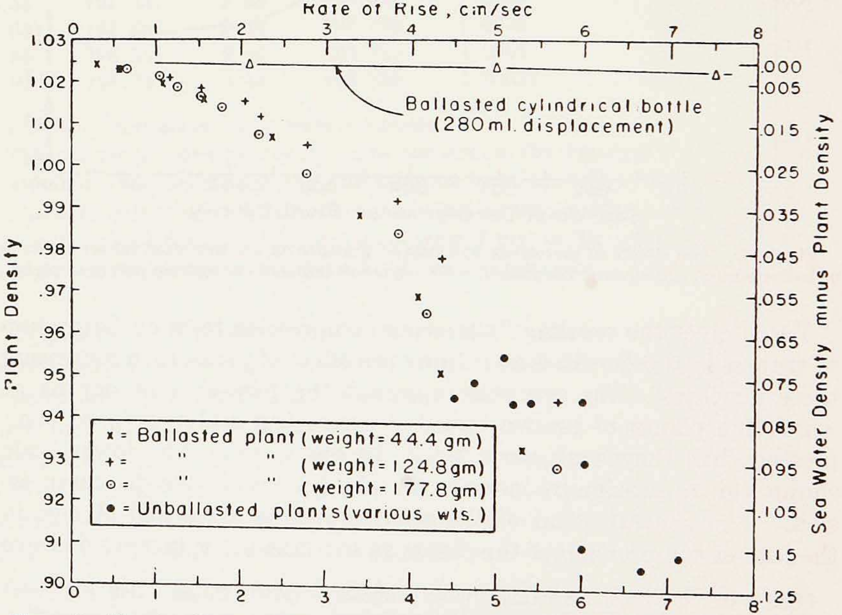

Figure 5. Showing the rates of rise of *Sargassum* of various natural and modified densities.

one meter square with a large window in one side, plants were released in sea water at an average depth of 80 cm and their rates of rise were timed after they reached terminal velocity. The black dots in Fig. 5 represent the densities and rates of rise of *Sargassum* of natural density. The other symbols represent three plants whose weights are shown in the legend. As the density of these plants was caused to approach that of sea water, the rate of rise decreased in the manner indicated.

Varying numbers of attached organisms on the experimental plants (i. e., gooseneck barnacles, bryozoa, etc.) seemed to have no effect upon rates of rise, except as they modified density. It is assumed, therefore, that the effect of ballasting on plant density is similar to the effects caused by the weights of attached organisms.

Thus, for plants having the natural range of density found in the Bermuda area, the data shown in Fig. 5 indicate that descending currents in excess of about 4.5 to 7.2 cm sec^{-1} would be required to draw them downward. The comparative effects of density change upon the rate of rise of a bottle is shown also in Fig. 5.

Bladder Gas Pressures. Parr (1939: 9) suggested that measurements of the gas pressures in *Sargassum* bladders might prove to be of interest in studying the sinking of plants. Results of some measurements of bladder pressures, with a brief description of the methods, are now given.

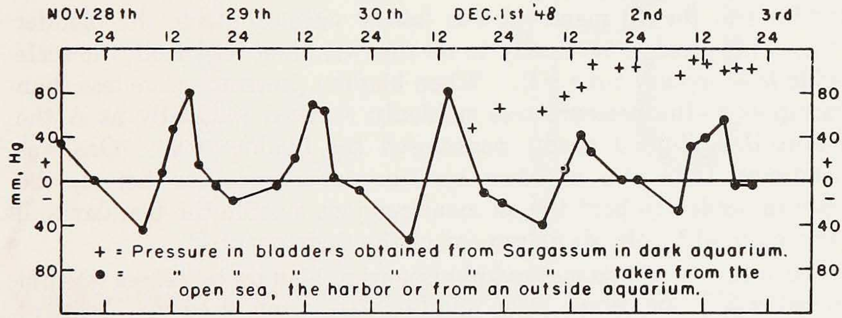

Figure 6. Variations with time of the gas pressure in *Sargassum* bladders.

Fig. 6 shows the pressures in bladders of *S. natans* during five days. Each point represents the average pressure of from 5 to 15 bladders taken from several plants. For each observation period fresh plants were taken from the sea, harbor or open-air aquarium. Pressures shown in Fig. 6 have been corrected for the effects of small water temperature variations and atmospheric pressure changes. (During the five-day period, sea-water temperature varied between 20° and 22.6° C, and atmospheric pressure varied from 760 to 768 mm.) *S. natans* shows a diurnal pressure cycle similar to, but of greater amplitude than, that found by Frye (1915) in kelp bladders. From the results of Damant (1937) with rockweed (*Ascophyllum nodosum*) bladders, it is supposed that the *Sargassum* was secreting oxygen inside the bladders, thus increasing the gas pressure during the day. However, continuous darkness in an aquarium caused an increase in and a maintenance of a positive pressure in *Sargassum* bladders. The plus symbols in Fig. 6 show the pressures in bladders from these plants, and a marked variation from the usual diurnal pressure cycle is evident. Positive pressure is constant in an environment of continuous darkness whereas alternating positive and negative pressures occur with day and night alternations. Thus *Sargassum* should be added to the list of marine algae whose bladder gases show diurnal pressure fluctuations.

Fig. 7 shows the simple apparatus used to measure the pressures. Bladders were taken from plants immersed in sea water and were placed upon the glass micropipette (B in Fig. 7). The penetration of the micropipette tip[8] through the bladder wall, which could be felt readily, coincided with the sudden movement of bladder gas displacing the liquid (mineral oil) in the glass micropipette. Pressure was then applied on the syringe (A) until the gases were forced back into the bladder and the oil meniscus was barely visible outside the bladder wall. The pressure necessary to do this was then read from the scale beside the mercury tube (C). When bladder pressures were less than atmospheric, the pressure was suddenly reduced manually at A the instant the oil-filled needle penetrated the bladder wall. Gas was withdrawn from the bladders by this technique. As before, the pressure needed to hold the oil meniscus just outside the bladder wall was measured by the displacement of the mercury at C.

The accuracy of this method of measuring bladder pressures was not determined. The same basic method has been used by Damant (1937), by Robert Chambers (personal communication) and others. The author has found no evidence to indicate that the pressures are seriously in error. The sign of the pressures was shown to be correct by inserting the tips of glass micropipettes partly filled with water into bladders and noting whether this water flowed into or out of the

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[8] Methods used in making micropipettes are described by Chambers and Grant in the 1948 edition of Encyclopaedia Britannica, under the title "Micromanipulation."

bladders. This was done with average pressures of − 20 mm and + 50 mm of mercury.

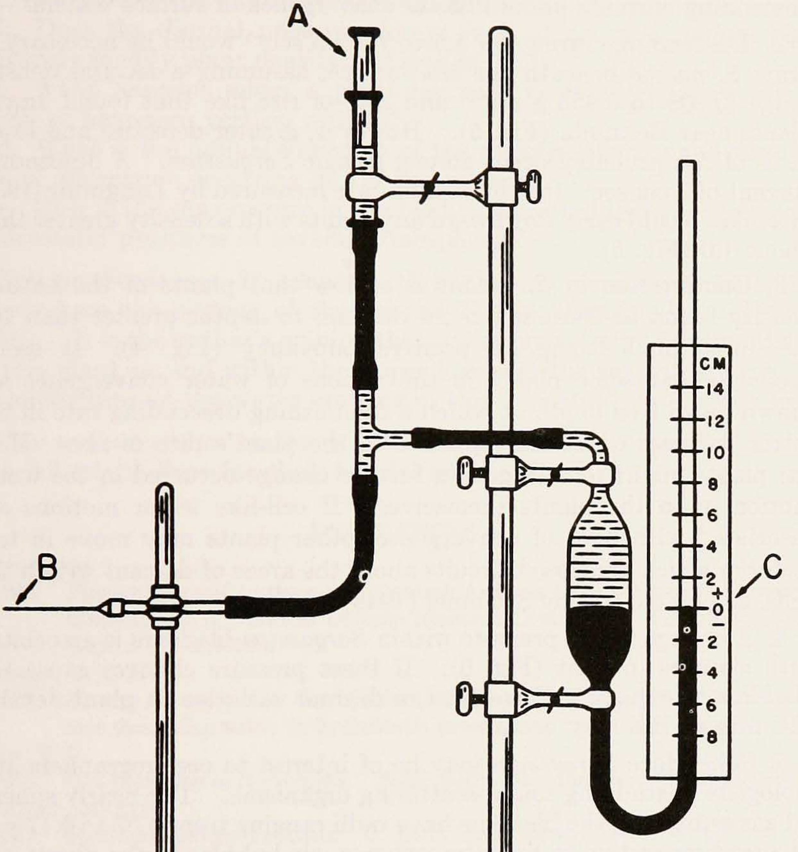

Figure 7. Diagramatic sketch of the apparatus used to determine the gas pressures in the bladders of *Sargassum*.

SUMMARY AND REMARKS

A beginning having been made in answering some of the questions about subsurface *Sargassum*, the following summary and remarks seem pertinent at this stage in the study.

1. The presence of *Sargassum* beneath the sea surface is associated with higher winds. These plants are probably drawn downward by descending currents under lines of convergence of surface waters.

2. Descending currents of 4.5 to 7.2 cm sec^{-1} would be necessary to draw *S. natans* beneath the sea surface, assuming a natural density range (0.905 to 0.955 g ml^{-1}) and rate of rise like that found among plants near Bermuda (Fig. 5). However, greater densities and lower rates of rise probably occur among pelagic *Sargassum.* A descending current of 3 cm sec^{-1} (the maximum rate measured by Langmuir [1938] in a lake) would carry downward any plants with a density greater than about 1.0 (Fig. 5).

3. Compression in *S. natans* is so low that plants of the natural density found at Bermuda could descend to depths greater than 100 meters without losing all positive buoyancy (Fig. 4). It seems probable that some plants in the regions of water convergence are drawn down to a depth at which a diminishing descending rate in the water becomes equal and opposite to the plant's rate of rise. Here the plants might remain until a further change occurred in the water motion or in the plants themselves. If cell-like water motions are associated with lines of convergence, other plants may move in trajectories which are closed circuits about the areas of descent within the cells, as pointed out by Stommel (1949).

4. A change in gas pressure within *Sargassum* bladders is associated with changes in light (Fig. 6). If these pressure changes cause the bladders to expand and contract, a diurnal variation in plant density and rate of rise may occur.

5. Subsurface *Sargassum* may be of interest to oceanographers and biologists in studying sound-scattering organisms. The nearly spherical gas bubbles in the bladders have radii ranging from 0.02 to 0.17 cm. At pressures of two to five atmospheres, air bubbles in the above size range are resonant to sound frequencies of 5 to 20 kilocycles (Anon., 1946: 463). There are several hundred of these bladders on an average plant.[9] Near atmospheric pressure the plants have been found to scatter sound markedly at a frequency of 26 kc (Smith, personal communication).

Suggestions for further study of subsurface Sargassum

In view of the foregoing measurements and observations, we may ask:

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[9] It should be noted, however, that effects of the bladder walls upon resonance of the enclosed bubble are unknown.

a. What is the rate of rise and density of plants actually present under convergence lines at sea? How do these quantities vary in plants collected during different wind speeds?

b. Does the diurnal pressure change in bladders of *S. natans* significantly modify plant density and rate of rise?

c. What happens when a plant becomes neutrally buoyant at a depth of near-zero vertical motion?

d. What is the annual variation of the average density and rate of rise of *Sargassum* occurring on the sea surface?

e. How is the gas pressure in the bladders affected by long sustained hydrostatic pressures of several atmospheres?

Pelagic *Sargassum* is adapted, through long periods of time, to survival on the surface of the central North Atlantic Ocean (Parr, 1939). It is the author's opinion that a thorough study of the motions of this plant on and within the upper layers of the sea will add to an understanding of the water motions in this important part of the sea.

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