ON THE WIND-INDUCED SINKING OF *SARGASSUM*[1]

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Abstract: *Sargassum* has been photographed on the sea floor at depths of 5000 m. *Sargassum* was subjected to various pressures to simulate the effect of it being carried down in Langmuir circulation. The time-depth relation for *Sargassum* to become negatively buoyant was measured; the plant can become negatively buoyant at pressures of only 30 db if left at this pressure for ≈ 5 h. Both the higher critical pressure for the failure of gas vesicles and the longer resistance to subcritical pressure of pelagic *Sargassum*, compared with the benthonic varieties, suggest an evolutionary adaptation to an open ocean existence. Once negatively buoyant, *Sargassum* will sink to the sea floor in about 40 h. The measurements are consistent with large scale sinking of *Sargassum* given the conditions of strong winds and a deep mixed layer both of which exist in winter months in the Sargasso Sea.

INTRODUCTION

Holopelagic *Sargassum* with its associated floral and faunal assemblage is found in substantial quantities in the Sargasso Sea, Caribbean Sea, and Gulf of Mexico (Winge, 1923; Parr, 1939; Deacon, 1942). It is also known from areas of the central Pacific Ocean (Vozzhinskaya, 1965). It is normally positively buoyant and hence confined to the upper portion of the water column. Woodcock (1950) showed that for short periods pelagic *Sargassum* could maintain positive buoyancy at pressures equivalent to 100 m of sea water. Howard & Menzies (1969) have shown that in the upper meter of the ocean, where it occurs, pelagic *Sargassum* may account for up to 60 % of the net primary productivity. Because of its proximity to the air–sea interface and the dominant nature of its rôle in carbon fixation and metabolism there, the *Sargassum* community may represent an important, though geographically limited, pathway for the incorporation of oceanic pollutants into the marine biosphere. This is particularly true for atmospherically derived materials (*e.g.*, the volatile heavy metals; Pb, Hg, Se, As, Sb, and Cd) and for those compounds such as hydrocarbons and pesticide residues which tend to concentrate at the sea surface.

The presence of relatively large clumps of *Sargassum* in photographs of the sea floor, as reported by Schoener & Rowe (1970), is clear evidence that it is directly

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involved in the vertical transport of organic carbon and trace constituents from the sea surface to the ocean floor where it is available for metabolism by the benthos. The means by which *Sargassum* sinks is not completely known. Possibly the fragmentation of weed clumps due to wave action with the subsequent sinking of the older more heavily encrusted (higher density) portions of the algae is one mechanism. Small pieces of *Sargassum* from the Gulf of Mexico so encrusted with *Membranipora* sp. and *Lepas* sp. as to be just barely positively buoyant have occasionally been observed (N. J. Blake, pers. comm.). Similarly, diseased *Sargassum* may lose its buoyancy. It seemed to us, however, that the entrainment of *Sargassum* clumps in the zones of convergence and downwelling associated with Langmuir circulation cells (as suggested by Woodcock, 1950) may be an equally important mechanism. Such a process could sink larger clumps of weed with lower density than could fragmentation alone.

We give here the results of experiments which evaluate the time-dependence of the loss of buoyancy by pelagic *Sargassum* under different pressures, some observations on the mechanism of gas vesicle failure, and the behavior of *Sargassum fluitans* Børgesen and *S. natans* (Linnaeus) J. Meyen in simple model Langmuir circulation regimes. These data, when combined with the as yet undetermined velocity fields within Langmuir circulation cells, will eventually allow estimates of the flux of *Sargassum* to the ocean floor to be calculated.

MATERIALS AND METHODS

Clumps of *S. natans* and *S. fluitans* 7 to 15 cm in diameter were dip-netted for the experiments on cruise TR-146 of *R. V. Trident* in January 1974 and on a cruise of the *USNS Lynch* in September 1974 – both to the western Sargasso Sea. All *Sargassum* samples for pressure experiments were judged to be relatively young and healthy as evidenced by their yellow-green appearance and lack of significant encrustation by *Membranipora* sp. and other epibionts. Samples of weed clumps were used within 6 h of collection. Three varieties of *Sargassum* were studied in the pressure experiments namely *S. natans* with gas vesicle of outside diameter of 2–4 mm; *S. fluitans*, 2–4 mm diameter; and *S. fluitans*, 4–7 mm diameter. Experiments were made in sea water at ambient temperatures of 22–25 °C. Steel pressure chambers $\approx$ 15 cm in diameter and 50 cm deep (one was an adaptation of a Fyre Fyter® fire extinguisher) with Plexiglass® viewing parts afixed to the ends were used. Hydrostatic pressure was applied using a hand operated hydraulic pump with a pressure gauge calibrated against a standard. The time for a plant clump to become negatively buoyant was determined by stopwatch and visual observation through the viewing port.

Observations on the failure of individual *Sargassum* gas vesicles under hydrostatic pressure were made in a 25 × 150 mm test tube, connected to the ship's sea water system. By using the sea-water pressure system, a monitoring gauge, and bypass valves, we could vary the pressure in the test tube at will and simulate compression at depths

of up to 65 m. The rounded end of the test tube served to magnify the vesicle affording an excellent view of the details of the mechanism and sequence of failure.

Additional observations on the failure of 'old' (red-brown) compared with 'young' (yellow-green) gas vesicles and on the loss of buoyancy of vesicles as a function of time were made by enclosing the samples in plastic bags and sending them down to various depths on the ship's hydrowire. Loss of buoyancy was estimated by measuring the velocity at which the gas vesicles rose, at atmospheric pressure, before and after subjection to the pressure regime. This was done by pushing the vesicles (with a glass tube) to a depth of 30 cm in sea water contained in a vertical cylinder and measuring the time of rise with a stopwatch after release.

Data on the rate at which whole weed clumps (up to 25 cm in diameter) rise at atmospheric pressure were also obtained on this October 1971 cruise of *R. V. Trident*. Measurements were made in a 70 cm deep 75 l garbage can by pushing the plants to the bottom and timing their rise with a stopwatch. Each determination was the average of three or more observations.

Several *Sargassum* samples were collected in the Eastern Gulf of Mexico, near The Dry Tortugas, on a cruise of the *R. V. Bellows* in October 1974. These were used to study the rate of rising of clumps as a function of plant 'density' (weight of the whole plant divided by the weight of the water displaced by the plant when fully submerged). To simulate increasing algal density, the gas vesicles were sequentially removed during the measurements.

Observations were made as in the previous experiments and measurements continued until the plants became negatively buoyant.

RESULTS AND DISCUSSION

PRESSURE EXPERIMENTS

Seventy-three whole-plant *Sargassum* samples were individually subjected to various constant hydrostatic pressures ($<$ 5 sec pump-up time) and the time to become negatively buoyant at the specific pressure was observed. Fig. 1 shows the results of these experiments. Pressure is expressed as meters of sea water. A semi-log plot of the data showed an apparently linear relationship of the variables: the hypothesis of linearity was tested and accepted. The regression line was calculated as:

$$\hat{z} = 102(\pm 4) - 23(\pm 3) \log t \tag{1}$$

where $\hat{z}$ is pressure (db) and t is time (min) and the values in the parentheses are the standard error of the slope and intercept.

The data were remarkably consistent considering that different varieties of weed were collected at different times of the year on two cruises covering a wide geographic area. There appear to be no differences in behavior towards a constant pressure regime between the two species of *Sargassum* tested. Similarly, there was no apparently con-
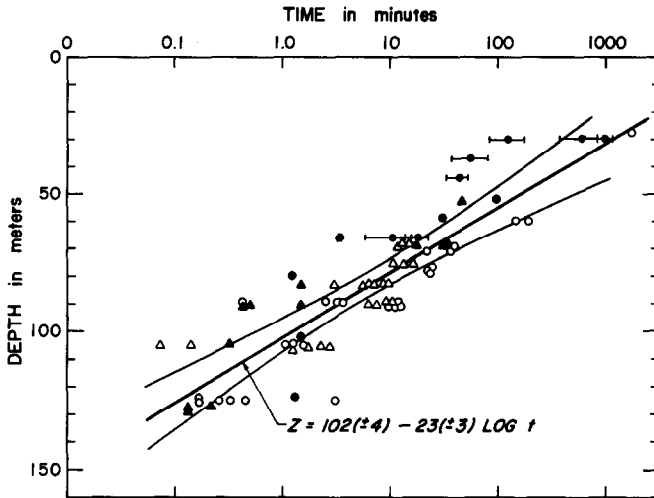
Fig. 1. Time for a *Sargassum* clump to become negatively buoyant when it was held at a constant depth (pressure): ●, *S. natans*, 2–4 mm, Sept. 1974; ○, *S. fluitans*, 2–4 mm, Jan. 1974; ▲, *S. fluitans*, 4–7 mm, Jan. 1974; △, *S. natans*, 2–4 mm, Jan. 1974; bars indicate uncertainty in the time measurements.

sistent difference between varieties of *Sargassum* with 'small' (2–4 mm) or with 'large' (4–7 mm) gas vesicles.

The main result which we wish to stress is the marked time-dependence of the loss of algal clump buoyancy as a function of pressure. While the pressures we used ranged from 30 to 130 db, the time to neutral buoyancy of the *Sargassum* changed by a factor of 10^4. The results clearly show that *Sargassum* becomes negatively buoyant at very shallow depths if held there long enough. At a pressure of 30 db, for example, *S. natans* lost its ability to float over a range of 2 to 17 h. Although it is unlikely that *Sargassum* would be held at constant depth in the ocean for long periods, it could be repeatedly carried down in Langmuir cells and subjected to cycling pressures whose average is equal to those used here. At pressures of 120 to 130 db, *Sargassum* clumps began to sink within a few seconds. In several tests Woodcock (1950) also found there was a loss of buoyancy at a depth of 110 to 130 m.

A similar time-dependence for the loss of flotation ability has been noted for a benthonic variety, *S. leptopodum* (Hurka, 1971). The pelagic species have, however, a much greater 'critical' pressure for immediate failure ($\approx$ 130 db as compared with $\approx$ 40 db) as well as greater resistance to 'sub-critical' pressure. This suggests an evolutionary adaptation by the pelagic species to the rigors of an open ocean existence.

Sargassum, which is positively buoyant at the sea surface, could be carried downward in the ocean if the velocity of the downwelling water were greater than the still-water rate of rise of the plant clumps. In this situation the algae would be subjected to a varying pressure regime. The vertical advection of *Sargassum* in the ocean at velocities of 0.5 cm/sec to over 50 cm/sec relative to the sea surface, was simulated in a
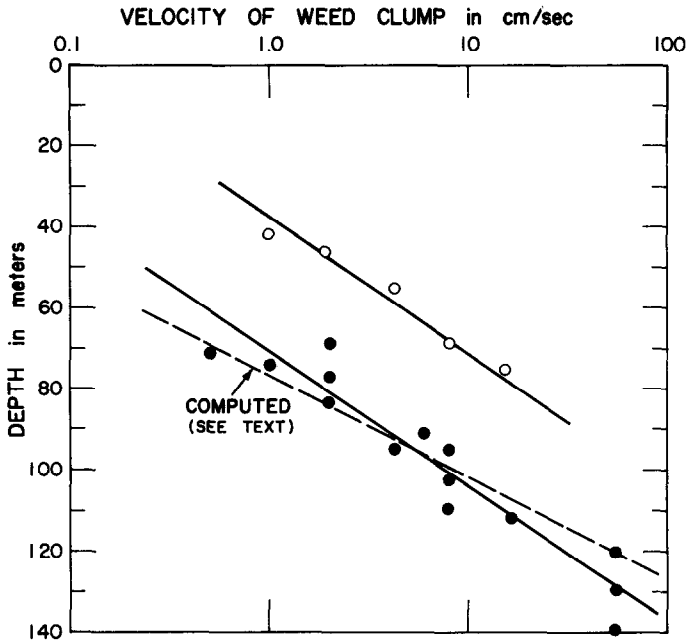
Fig. 2. Depth of neutral buoyancy of *Sargassum* as a function of its downward velocity in the ocean as simulated in a pressure cell: solid lines experimental observations, dashed line calculated: ○, *S. fluitans*, 4–7 mm; ●, *S. natans*, 2–4 mm; both Sept. 1974.

separate series of pressure experiments by increasing the pressure in the test chamber with increasing time until the algae was observed to become negatively buoyant. Fig. 2 shows the results of tests with *S. fluitans* (4–7 mm) and *S. natans* (2–4 mm). The results fall closely along two straight lines on the semi-log plot with *S. fluitans* being displaced ≈ 35 m shallower than *S. natans*. For slow vertical advection velocities *Sargassum* becomes negatively buoyant at approximately half the depth of fast speeds. For example, *S. natans* became negatively buoyant at a pressure of 130 db at 55 cm/sec but at only 70 db at 0.5 cm/sec. This further indicates that the time-dependence of 'critical' depth is very important. We consider that the 35 m displacement between the two response curves in Fig. 2 is not due to a difference between the species, but is related rather to the size of the gas vesicles (see below).

FAILURE OF *SARGASSUM* FLOTATION VESICLES

The gas vesicles of *Sargassum* are almost spherical thin-walled gas vesicles. A typical wall thickness is 0.2 mm and diameter 4.0 mm. They are capable of withstanding pressures up to 130 db for short periods of time. The 'failure' of numerous gas vesicles took place in the following sequence. As pressure was increased the gas vesicles first became flattened and then a dimple appeared in their wall. Eventually, a crease

was formed in the wall and this frequently extended over one-third of the circumference. When the pressure was applied slowly, equivalent to a vertical speed of 1.0 cm/sec, the wall was slowly squeezed in; but when the increase of pressure was more rapid, 10 cm/sec, the gas vesicles were observed suddenly to form a crease and this was accompanied by a popping sound clearly audible from outside the tank. Large gas vesicles (4–7 mm) began to crease (with some popping) at depths of only 35 m and smaller vesicles (2–4 mm) at 100 m to 135 m. When the pressure was cycled after the crease appeared, small air bubbles were seen to escape from the gas vesicles and water was found inside the wall indicating a rupture.

The rupture of the wall appears to be related to the ratio of wall thickness (t) to the
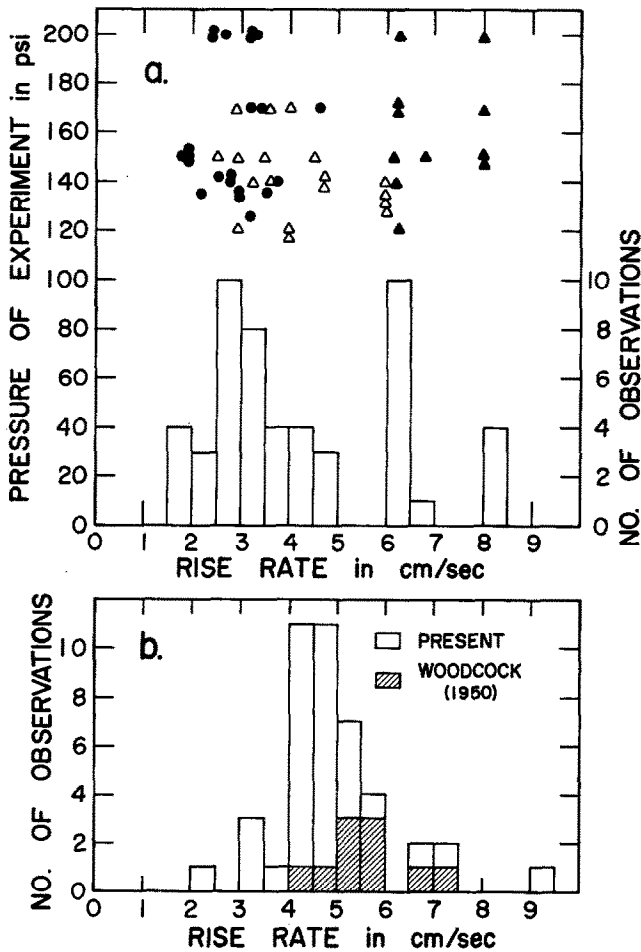

Fig. 3. a, histogram of the rate of rise of *Sargassum* clumps at surface pressures after pressure experiments: individual results shown as a function of the pressure of the experiment: Jan. 1974; *S. fluitans*, 2–4 mm; *S. natans*, 2–4 mm; *S. fluitans*, 4–7 mm; symbols as in Fig. 1. b, rate of rise of *Sargassum* at surface pressures using data of Woodcock (1950), and that of present work: Oct. 1971.

overall diameter (d). For thin-walled spheres ($t \ll d$) the pressure differential (ΔP) that gas vesicles can support can be approximated by $\Delta P = 4P_c(t/d)$; P_c is a critical wall pressure. For small t/d (large gas vesicles) the wall supports a smaller pressure differential than for larger t/d (the smaller vesicles). It may be seen from the data in Fig. 2, that under some regimes large gas vesicles 'fail' at lower pressure, but the larger diameter vesicles (4–7 mm) appear to recover more quickly since their rate of rise was largely unchanged after the pressure experiments (Fig. 3a, upper part). This suggests that loss of buoyancy, *i.e.*, 'failure', for the larger vesicles results from collapse and loss of volume without breaking the gas vesicle wall. The smaller gas vesicles are more subject to irreversible rupture than are the large ones.

Older gas vesicles (red-brown, covered with calcareous encrustations) appear to be more brittle than younger ones (yellow-green, no encrustations) and tend to rupture more readily. In an experiment with 423 'old' and 'young' gas vesicles sent down to 500 m on a hydrowire and returned to the surface, over 1/4 of the bladders had lost positive buoyancy, while 52 % of the 'old' gas vesicles had ruptured compared with only 10 % of the 'young' ones.

SARGASSUM AND LANGMUIR CIRCULATION

Langmuir (1938) reported sighting long lines of *Sargassum* in the Atlantic which were oriented in the direction of the wind. He suggested that such windrows are a result of a clockwise and counterclockwise helical water flow progressing slowly downwind, and this motion has become known as Langmuir circulation. Downwelling speeds of 3 to 6 cm/sec have been observed in Langmuir cells under windrows with wind speeds of 3–9 m/sec (Scott, Myer, Stewart & Walther, 1969). The downwelling speeds appear to be directly proportional to the windspeed over the range of conditions so far examined. One would expect higher downwelling speeds associated with higher wind velocities. Woodcock (1950) observed *Sargassum* to be carried down by the descending water under the lines of convergence.

Near the surface, where *Sargassum* is normally found, it is positively buoyant and has rates of rise of 2–9 cm/sec with an average speed of 5 cm/sec (Fig. 3b, lower part). Since pressure changes the buoyancy it also changes the rate of rise of *Sargassum* through the water. The change in plant velocity with pressure and time was modelled as follows. First, it was assumed that the downwelling of the water in a Langmuir regime is at a constant velocity. Since the velocity field associated with Langmuir circulation in the oceans has not been well described, this seems a reasonable first estimate. Secondly, it was assumed that *Sargassum* loses positive buoyancy linearly with time at a specific depth and becomes negatively buoyant according to the time-depth relation given by Equation (1). To a first approximation this is true for the gas vesicles alone and our results suggest that it is justified for whole clumps. Fig. 4 gives the vertical velocity of gas vesicles after they had been held at a depth of 50 m for various times. The loss of buoyancy was calculated using the mean experimental ver-
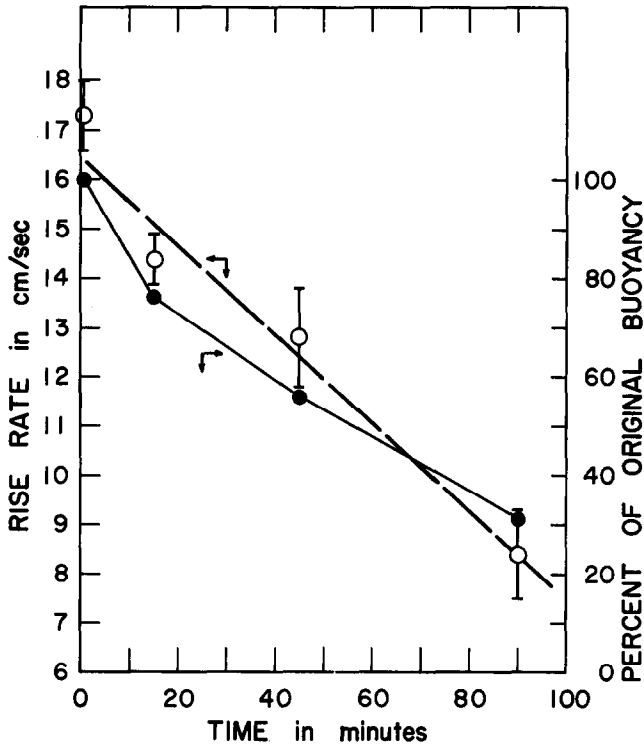
Fig. 4. Loss of rate of rise and buoyancy of individual *Sargassum* gas vesicles when held at a pressure of 50 db (50 m): mean and s.e. (bars) of rate of rise of 40 pneumatocysts; calculated buoyancy based on upward velocities.

tical velocities, assuming the bladders were spherical (5 mm diameter), and by the graph given by Schlichting (1968) to determine the drag coefficients.

To simulate the loss in buoyancy-rate of rise relationship for whole plants, the rate of rise of weed clumps was measured while the gas vesicles were removed. The bladder removal and rate measurements were continued until the plant became negatively buoyant. Since the five specimens used in this experiment had different initial numbers of gas vesicles, the loss of buoyancy (vesicle removal) was adjusted by considering it to be 100 % when the plant became negatively buoyant. Loss of *Sargassum* clump buoyancy, expressed as the percentage of vesicles removed, was plotted against the rate of rise adjusted to an initial rise rate of 5.0 cm/sec. The results are shown in Fig. 5. The values lie relatively close to the assumed linear loss of rise rate as a function of buoyancy loss. The slight upward curve may possibly be explained by the non-linear drag-velocity relationship together with the artificiality of the simulation. The removal of gas vesicles would have a tendency to decrease the drag of the whole weed clump.

The validity of using the time-depth relationship of Equation (1) and the assumption
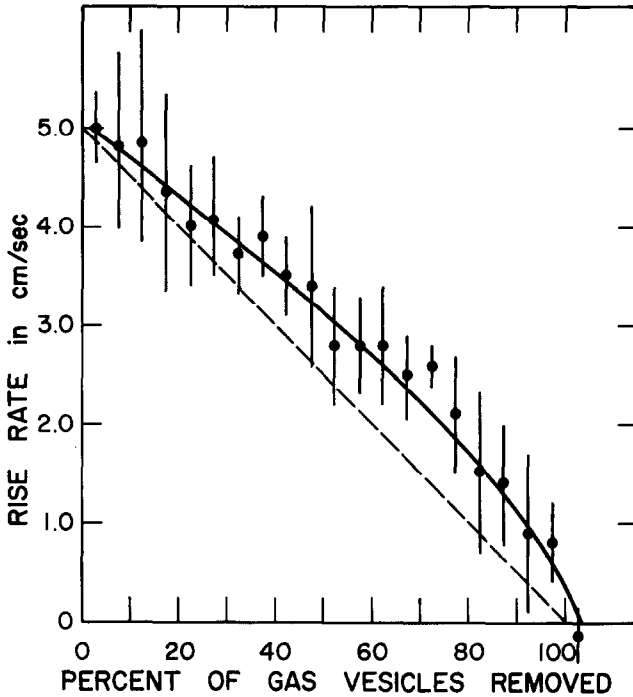
Fig. 5. Rate of rise of *Sargassum* plants as a function of loss of buoyancy (vesicle removal): composite of five experiments adjusted to 5 cm/sec rate for comparison: dashed line indicates linear loss of rate as a function of loss of buoyancy.

of a linear loss of rise rate for *Sargassum* clumps at a given depth is supported by the data of Fig. 2. We calculated the depth of neutral buoyancy as a function of the downward velocity of *Sargassum* under constant downwelling velocities and constant clump rates of rise. The calculated depth of neutral buoyancy lies within 10 m or less of the observed depth for *S. natans* (2–4 mm). To obtain the calculated time-depth relationship for neutral buoyancy, one further assumption is needed, namely, that the linear loss of positive buoyancy extends over all depths and that as *Sargassum* is transported into deeper water the loss of buoyancy could be integrated. This assumption seems justified from the data of Fig. 2.

We know that as *Sargassum* loses buoyancy, its rate of rise, or velocity relative to the water, changes. To take this into consideration a more refined calculation was carried out based on the above assumptions. The calculations were made by an iterative method in which the downwelling speed was assumed to be constant with depth, and that plants with an initial upward velocity of 5 cm/sec relative to the sea surface were carried down. As a plant is carried down, it looses buoyancy, velocity relative to the water decreases and its net downward velocity is increased. The results are shown in Fig. 6 for two cases. For Curve a, we assumed that constant downwelling velocities extended to depths greater than the *Sargassum* 'critical depth' and calculated
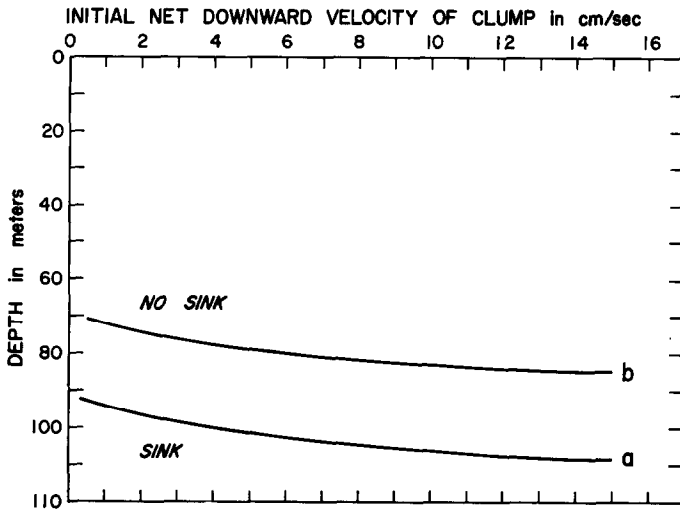
Fig. 6. a, depth of loss of buoyancy calculated for different initial downward velocities of *Sargassum* clumps: loss of buoyancy as a function of time and pressure included: b, characteristic size of a Langmuir cell required to cause loss of buoyancy of young, healthy plants: a square cell with constant water velocity around its perimeter is assumed.

the depth at which it became negatively buoyant. For Curve b, we assumed a Langmuir cell with a square cross section and constant velocities (equal to the downwelling velocity) all the way around the perimeter of the cross section: we also assumed that if a plant reached the bottom of the downwelling limb of the cell before it was negatively buoyant it would then be carried horizontally across the bottom of the cell. We assumed that the plant would not rise vertically out of this horizontal velocity field and that it would be carried horizontally at velocities equal to the downwelling water velocity. Calculations using this model were made by adjusting the dimensions of the Langmuir cell so that a plant would become negatively buoyant after its horizontal trip across the bottom of the cell and before it became entrained in the upwelling limb. That is, 1) a plant is carried downward by water of constant downwelling velocity; 2) the velocity of the plant relative to the water changes as the plant loses buoyancy; 3) at some point it 'turns the corner' and travels across the bottom of the cell at a velocity equal to the downwelling velocity of the water; 4) during this part of its transit it loses buoyancy with time according to the simple relationship in Equation (1); and 5) a plant caught in the upwelling limb will be returned to the surface and a plant which becomes negatively buoyant before reaching the upwelling limb will sink out of the velocity field. By adjusting the dimensions of the cell so that a plant just becomes negatively buoyant at the end of its horizontal travel on the bottom of the cell, we calculate the 'characteristic' size of Langmuir cells required to sink *Sargassum*. These calculations were made for a variety of plant 'initial downward velocity' (downwelling water velocity minus stillwater rate of rise of plant). The

results are shown in Fig. 6, curve b. It should be emphasized that this refers to the net initial downward velocity of young, healthy *Sargassum* clumps. It is based on the data from Fig. 1 and since it does not take into account factors of age, *etc.*, it represents a maximum cell size necessary to sink *Sargassum*. Furthermore, the plant clumps could be repeatedly caught by Langmuir cells and the repeated pressure cycling could cause loss of buoyancy at depths shallower than those shown here (characteristic cell size). Limited experiments were conducted in which pressure was cycled in time, and shallower 'critical' depths were measured.

NECESSARY CONDITIONS FOR THE WIND-INDUCED SINKING OF *SARGASSUM*

   In order for *Sargassum* to be transported from the sea surface to the ocean floor by Langmuir circulation it must be caught in zones of convergence and downwelling, be carried below its critical depth, and be kept at depth long enough for it to sink out of the mixed layer. Once below the mixed layer the plant can sink to the sea floor in one to two days. (A *Sargassum* clump which had been sent to 5000 m by hydrowire had a vertical sinking rate of 3.5 cm/sec when it was brought to the surface.) The down welling speed in the Langmuir circulation must be greater than the rise rate of *Sargassum* (average 5 cm/sec) and it must penetrate deeper than the critical depth, $\approx$ 100 m. Data presented by Scott, Myer, Stewart & Walther (1969) suggest sustained winds
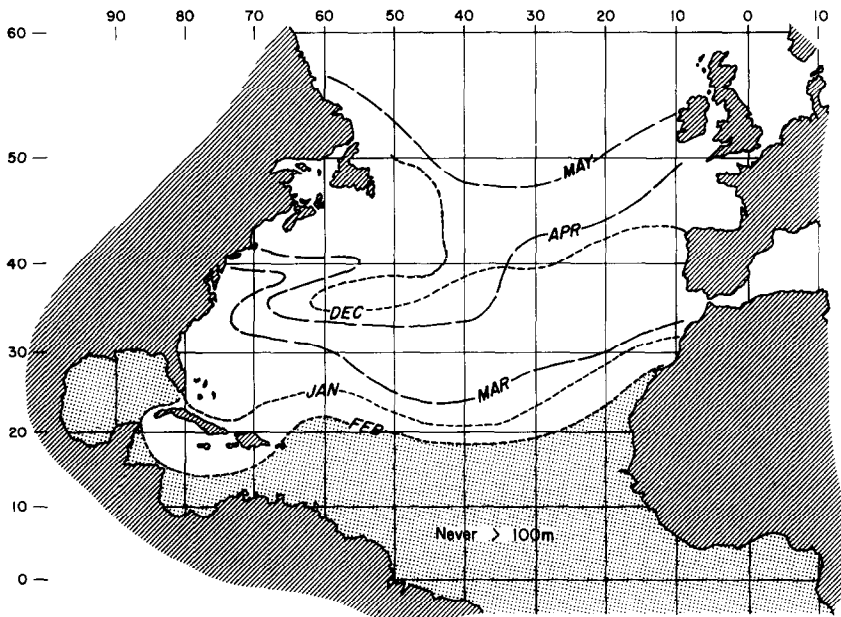

Fig. 7. Southern limits of a 100 m thick mixed layer in the North Atlantic as a function of time of year (after Fuglister, 1949).

of 25 kt (12 m/s) can produce downwelling speeds of 10 cm/sec in Langmuir circulation. Both high winds (> 25 kt) and a deep mixed layer (> 100 m) are found in the Sargasso Sea in winter months (Fuglister, 1949; U.S. Navy, 1955), as shown in Fig. 7. The deepest layers and strongest winds are found in January, February, and March in the vicinity of the region of the formation of 18 °C water (Worthington, 1959) in the northwestern Sargasso Sea. The photographs which show *Sargassum* on the sea floor (Schoener & Rowe, 1970) were taken near this area. The Gulf Stream which carries warmer water from the south, may transport *Sargassum* from milder conditions in the Caribbean and southern Sargasso Sea, where the plant can remain in the surface layer, northward into a region where conditions will sink *Sargassum*. One would expect the least *Sargassum* to be lost in midsummer (June July, and August) with the shallowest mixed layer (15–30 m) and lowest wind speeds.

We do not suggest that all *Sargassum* caught by Langmuir circulation (> 5 cm/sec, > 100 m) will be lost from the surface. Langmuir circulation consists of a hierarchy of cell sizes; only the largest is equivalent to the mixed layer depth (Assaf, Gerard & Gordon, 1971). Some plants could be caught by smaller sized cells and never reach their critical depths. They would eventually be re-circulated to the surface. Some plants caught in the larger cells could be mixed out of the downwelling region and also be re-circulated to the surface. The conditions described here apply to healthy, low density plants. Older plants with more brittle gas vesicles, plants with a higher density due to encrustations of epibonts, or plants whose gas vesicles have been 'weakened' by exposure to sub-critical Langmuir circulation regimes, can be expected to sink in less extreme conditions.

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