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QUANTITATIVE OBSERVATIONS ON THE PELAGIC SARGASSUM VEGETATION OF THE WESTERN NORTH ATLANTIC

WITH PRELIMINARY DISCUSSION OF MORPHOLOGY AND RELATIONSHIPS

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CONTENTS

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[1] Joint contribution from Woods Hole Oceanographic Institution (No. 234) and Bingham Oceanographic Foundation.

INTRODUCTION

Since the days of Columbus, the enormous amounts of floating weeds drifting about in the so-called Sargasso Sea have excited the interest of scientists and of laymen as well; and in laymen's minds the most exaggerated myths have grown around the phenomenon, not always without scientific pretense. Since the earlier investigations and theories have already been fully reviewed by Krümmel (1891) and by Winge (1923), it will not be necessary in this report to give any detailed account of the past history of the sargasso weed problems in the scientific literature. Suffice it to say that in spite of the widespread interest most of the earlier studies have been largely speculative and purely incidental, apart only from the investigations of Krümmel, of Antze, his successor in this work, and of Winge. In the works of Krümmel and Winge, we see the first two organized attempts at a semi-quantitative approach along widely different lines. In both cases, however, the quantitative aspect was only arrived at by deduction from, and statistical treatment of, data which were not in themselves truly representative in a quantitative sense.

The basis for Krümmel's investigations was provided by the records of floating weeds observed from German ships crossing the North Atlantic and entered in their log-books as required by the "Deutsche Seewarte" over a period of many years. From these data the frequency of observation per geographical coordinate unit (1° square)[1] were calculated and plotted to show the boundaries of the Sargasso Sea, and its subdivisions into more or less concentric regions of various degrees of frequency of the floating weeds. Although of very great interest and value, the figures thus obtained obviously remain only purely numerical with no indication of their quantitative significance in terms of weights or volumes (see page 70).

Winge's material, on the other hand, was of an entirely different kind, consisting of the actual samples collected by various Danish research and merchant ships. These samples obtained a semi-quantitative significance from the fact that they were not dipped up separately but were brought in as part of the material collected in plankton-net hauls near the surface. Since, however, it is not feasible to estimate the surface area taken in by such a tow, with a circular net which does not operate strictly and uniformly at the surface, it would be quite impossible to try to convert the values obtained from such samples into quantitative figures per unit area even if the log distances of the hauls were known (this is not mentioned by Winge, who merely states their usual duration to have been about half an hour). Nor is any such attempt made by Winge, who confines his presentation of the semi-quantitative aspects of his material to indications of the size of the samples by the size of the dots by which they are represented on his distribution chart (Winge, 1923, fig. 22, p. 14) without any numerical tabulations or citations in the text. The quantitative significance of Winge's material is thus purely relative, with no suggestion of absolute values. It may further be stated on the basis of the experience gained during the present investigation, that even the extensive series of samples studied by Winge, which was undoubtedly by far the largest material purposely collected for a special investigation up to that time, can hardly have been adequate to give a reliable picture even of relative distributions and abundances.[1] Winge accordingly very properly confines his treatment of gross distribution to a mere fixation of the outer boundary for the regular occurrence of the typical drifting weeds, that is generally speaking simply the boundary between their presence in any amounts at all, and their absolute absence under normal circumstances.

In connection with a series of hydrographic cruises to the Central American Seas on the research ship "Atlantis," sponsored jointly by the Woods Hole Oceanographic Institution and by Yale University (under the auspices of the Bingham Oceanographic Foundation) an opportunity offered to carry further the work of Krümmel, Antze, and Winge in the western portion of the Sargasso Sea, and to attempt to put the problems on an absolute quantitative basis. For this purpose a very simple surface scoop-net, to be towed by the ship while under way between stations, was designed especially for the collecting of drifting weeds. In the course of the work so far this net has been in

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[1] Not, of course, a true unit of area except for squares in identical latitude.

[1] Winge's chart (loc. cit. fig. 2) shows a total of 185 samples (positive hauls) and 209 negative hauls for the entire North Atlantic over a period of 12 years (1911–1922), of which 173 positive and 44 negative hauls fall within the boundary of the about 8 million square kilometers of the Sargasso Sea as indicated by Winge. With the extremely unequal distribution of the weeds even in the regions of their greatest abundance, and with the very important annual fluctuations in the total amounts present, observed in the course of the investigation here reported upon, the wisdom of Winge's commendable restraint in the quantitative treatment of his material is obvious.

actual operation in the surface of the sea over a cumulative distance of seven thousand (6998) nautical miles, with a total of nearly five thousand (4759) pounds of pelagic weeds brought on board for sorting and weighing. It is the data and material thus gathered which form the basis of this first, and in various respects preliminary, report on these *Sargassum* investigations.

In the present paper we are exclusively concerned with the plants themselves, chiefly with their quantitative distribution only, and with the conclusions which the quantitative data may enable us to draw with regard to the question of maintenance of the pelagic vegetation.

To establish the necessary definitions, the weeds themselves will be described and illustrated in considerable detail, but their taxonomy can only be dealt with in a purely tentative manner. The problems of the ecology of the animal life associated with the *Sargassum* weed flora will be reported upon separately by M. D. Burkenroad and will not be considered in this paper.

METHOD

The collector shown in the accompanying figure 1 was towed at the normal cruising speed of the ship from the head of the hydrographic boom, which was kept swung out over the side so as to bring the net beyond the disturbing influences in the wake of the hull itself. The distortion of the quantitative results which might arise from the artificial concentration of weeds immediately along the side of the ship, where the surface water is being displaced by its passage, was thus avoided. It was, on the other hand, not practicable to bring the collector beyond the influence of the rapidly spreading bow wave under the conditions of work on board.[1] There was no observable indication, however, that the bow wave might have any appreciable effect upon the *amount* of weeds entering the collector, except possibly in very rough weather. While the bow wave will, of course, change the position of individual plants to a slight extent, so that other specimens may reach the net than those which would have been caught in the absence of the wave, the bow wave did not, away from the immediate path of the hull itself, cause any noticeable change in the *density* of weed distribution and therefore not in the *quantity* but only in the identity of the individual plants obtained in the collector. Significant changes in the density of weeds seem entirely limited to the wake of the ship and its immediate boundaries on the two sides, which were avoided. The author is therefore confident that the net has normally been so placed as to obtain a truly representative catch, within the limits of its efficiency (see below), at least in a sufficiently close approximation for all purposes of this investigation.

It has been found that the net can be operated successfully under favorable conditions at cruising speeds up to 10 knots, but in a rough sea 7–8 knots would seem to be the maximum. The length of the towing wire must, of course, be so adjusted as to keep the upper horizontal bar of the collector opening above surface at all times. With a fairly high attachment of the wire, so that a relatively great length is required, this adjustment can be very easily accomplished and maintained even in quite rough weather. Low attachment with a short length is disadvantageous and makes the control difficult. With suitable adjustments and reasonably favorable conditions the collector hardly ever skips the surface, and only rarely submerges the top of its frame on a heavy roll of the ship. Skipping and diving, however, are the factors which limit the usability of the gear in rough weather, and under such circumstances collecting has always been abandoned until conditions have improved. Even when not skipping

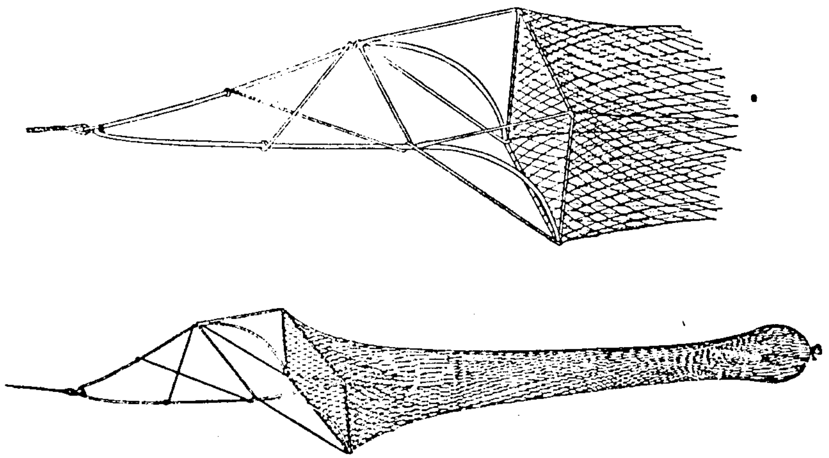

Figure 1. Pelagic weed collector. Detail of frame, *above* (see text); entire net, *below*.

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[1] This might also be easily accomplished by a simple arrangement on the otter-board principle; but would entail more labor than the other purposes of these cruises would permit.

and diving, the collector will, of course, not maintain an absolutely constant level in the sea and will occasionally rise high enough to permit some floating plants to escape below.[1] This, in the author's opinion, is the main and probably the only significant source of error in the approximative value of the quantitative results. While our figures therefore give only minimum values, innumerably repeated observations of the collector in operation[2] have convinced the author that this error can on the average probably not exceed 10 per cent, and is certainly less than 25 per cent of the true value, this error being, of course, entirely negative so that the recorded catches represent minimum values for the true abundance of the weeds.

The square metal frame for the opening of the net is exactly 2 feet wide inside and 20¼ inches high. The median length from the top horizontal cross-bar to the forward end of the bridle part of the framework is 5 feet. The main parts, i. e. the arched bridle irons and bottom cross-bar, were made of ⅝″ round steel, the braces and the remaining framework for the square opening of the net of ⅜″ steel.

The net itself is cylindrical, 11 feet long and of uniform width, 8 feet in circumference. The posterior end is simply closed and lashed tight with a short rope when the net is made ready for a haul. The first 3 feet have 1½ inch stretched mesh (¾″ square) of 18-thread medium twine; the following 3 feet 1 inch stretched mesh (½″ square) of 15-thread medium twine; and the last 5 feet ½ inch stretched mesh (¼″ square) of 6-thread medium twine.

It is important to have the forward bridle portion of the collector frame, by which it is attached to the wire, curve slightly upward as shown in our figure as it was found experimentally that this is necessary to keep the collector from turning over too easily. With the proper curvature its position in the water is very stable, and it is only rarely upset by a wave.

It was found very convenient to have the collector attached both to the hydrographic wire, letting this remain slack while towing, and to a

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[1] Deepening the opening would probably not remove this factor, since the collector rises to reach an equilibrium between the oblique strain due to its friction in the water and the vertical gravitational forces, and would therefore only rise higher to reduce the strain to the same point. Weighting of the frame would patently be disadvantageous under normal conditions (causing shortening of wire and increased tendency to dive).

[2] Since the collector is usually parallel with the stern of the ship, it can be easily and directly observed from deck.

heavier towing wire which carries the strain while the net is in the water, the hydrographic winch and wire being used only for lifting and setting the gear (without reducing the ship's speed), for which its strength is more than adequate.

The duration of each haul was made dependent upon the ship's and the staff's convenience, except when weeds were very abundant, in which case the collector must always be lifted as soon as the load in the net reaches a reasonable size, which can easily be judged by observations from the deck of the ship. The length of each haul has been determined by recording the reading of the ship's log at the beginning and at the end. This also gives a very convenient method of determining its geographical location by reference to the log reading at the noon position of the ship.

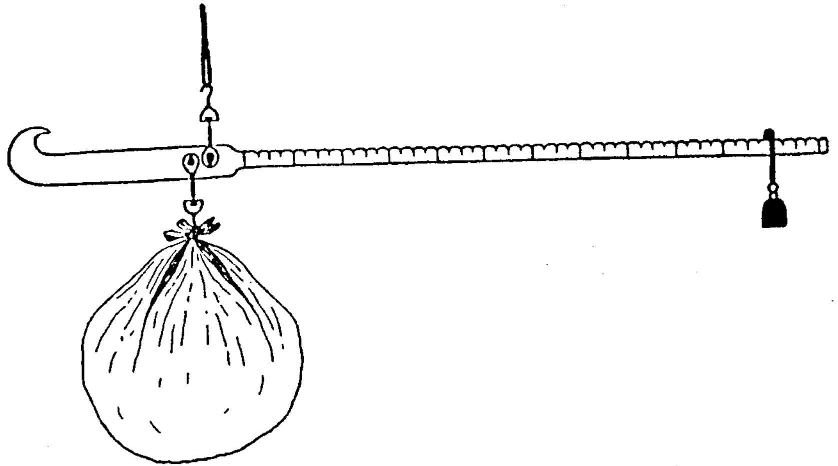

Figure 2. Scales used for weighing weeds on shipboard.

After the haul has been sorted the various species of weeds have been weighed separately in a fresh condition (wet, not desiccated) in cheesecloth bundles of suitable size by the use of an old-fashioned beam scale with a movable weight, swinging free from a strap above, as indicated in the accompanying diagram. It may be worth mentioning from practical experience that this type of beam scale would seem to be the only equipment fully suitable for such weighings on shipboard. Spring scales of any type are impractical at sea for the obvious reason that they will reflect the rise and fall of the ship in a bobbing up and down of their readings and of the object to be weighed. This difficulty is avoided in scales working on the principle of equal momentums balanced against each other, since both sides are then affected in the same manner by the movements of the ship, but it is further necessary also to avoid even beam scales which do not swing free in all directions so that no frictional or momentum differences may develop by an inclination of the instrument in accordance with the varying inclinations of the ship. The simplest equipment to fulfill these requirements is undoubtedly the instrument here used.

Weights have been read to nearest ¼ pound. Total hauls less than one pound of all species combined, or less than ¼ pound of a single species have merely been recorded by the presence of the various forms of *Sargassum* found therein.

After weighing, generous samples of all varieties present have been preserved in cheesecloth bundles kept in 10 per cent neutralized formalin in 30–50 gallon oak barrels. Samples of these samples have subsequently been pressed and mounted on herbarium sheets in the Bingham Laboratory. As a practical suggestion, perhaps already familiar to the botanists, one might mention that it has been found advantageous in the case of stiff and recalcitrant specimens first to put them under press between blotters for 12–24 hours, and thereafter soak them again in water, after which treatment they readily yield to the desired arrangement of leaves and branches. No thinning out of the specimens has been undertaken in preparing them for the herbarium, since the total habitus of the plant is an important feature in investigations of the kind here undertaken.

VERTICAL DISPERSAL OF FLOATING WEEDS

One may sometimes hear or see the statement made by travelers that they have observed pelagic weeds drifting by quite deep down in the water. Apart from occurrences in the turmoil of the wake or in the leeway of a ship, these assertions are quite contrary to the author's own experience in so far as any at all quantitatively significant frequency is concerned. It is also contrary to mechanical probability that the weeds should be able to drift at any significant distance below the surface for a sufficient length of time to produce a vertical dispersal of sufficient importance to require consideration in a quantitative investigation, for the reason that when a weed becomes accidentally

submerged it will rapidly be losing buoyancy by compression of the gases in its bladders, and if it gets beyond the point at which it will continue to sink indefinitely its further descent will for this reason be an accelerated movement.[1] Inversely, the ascent of plants which have not reached the sinking point will also be an accelerated movement due to the expansion of their bladders as the pressure is again reduced. This will also hold true even if the plants should have a certain ability to regulate the gas contents of their bladders according to requirements (this is a point well worth investigating), unless their power of regulation should be able to function with great rapidity, which seems extremely unlikely in any case. With both ascent and descent from a submerged level thus being accelerated motions, the likelihood of a plant accidentally maintaining equilibrium for any length of time at a subsurface level is, or course, extremely slight; the more so since it is normally only likely to become submerged under conditions of great turbulence.

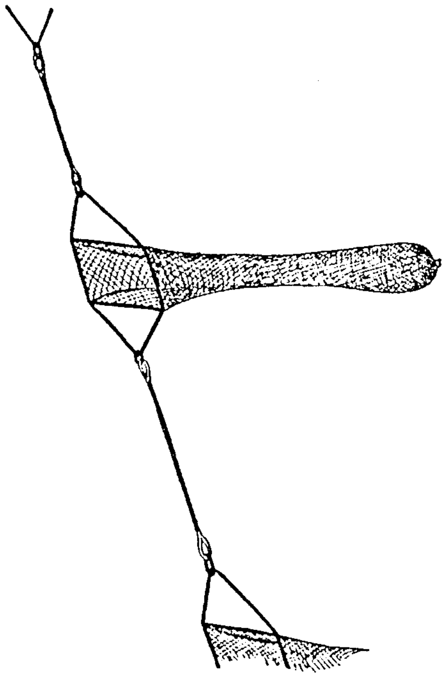

Figure 3. Collecting net frames used for study of vertical dispersal. Note that wire crossing opening of nets to block entrance of weeds has been avoided.

To substantiate by direct evidence our assumption that pelagic weeds under normal conditions occur in quantitatively significant amounts only at the very surface itself, a 24.3 mile haul (No. 151) was made with 5 nets suspended below each other along the same wire,

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[1] It is not impossible that violent storms may cause a certain loss of entire plants by forcing them down below the sinking point through mechanical turbulence, although this loss will probably be slight.

using a different type of frame as illustrated in our figure 3. The results were the following:

Net 1. Normal position at surface, but with more diving than usual, due to less favorable wire angle required for the operation of the entire set. Quantities therefore minimum values:

37.5 lb.	*S. natans I* (1.54 lb. per mile)
9.0 "	*S. fluitans III* (0. 37 lb. per mile)
4.0 "	*S. fluitans X* (0.17 lb. per mile)
1.5 "	*S. natans II* (0.06 lb. per mile)
52.0 lb.	Total Weeds

Net. 2. Top horizontal bar averaging about 1.5 meters vertical depth. Catching at surface while net No. 1 was being attached (unavoidable).
0.45 lb. Total Weeds. Probably mostly caught at surface.

Net 3. Top horizontal bar averaging avout 5–6 meters vertical depth. A couple of plants observed entering at surface.
2 small plants (taken at surface).

Net 4. Top horizontal bar averaging about 15–18 meters vertical depth. One small plant observed entering at surface.
1 small plant (taken at surface).

Net 5. Top horizontal bar averaging about 35–40 meters vertical depth.
Empty.

In other words, not even No. 2 net, operating only 1.5 meters below the surface, gave a quantitatively significant catch in proportion to the catch made at the surface, the weeds actually collected at the depth at which No. 2 net was intended to operate weighing less than 1/100 of the total weight of weeds obtained in the surface net. Furthermore, nothing was obtained in any of the deeper nets from their proper level. In quantitative investigations of the floating *Sargassum* vegetation collecting at the surface alone will therefore give an adequate picture of abundance in absolute terms with only the reservations already made on page 6.

TAXONOMIC DISCUSSION

An inspection of the available literature on the genus *Sargassum* cannot fail to impress one very strongly with the prevailing state of uncertainty in regard to the classification and nomenclature of many, if not most, of its members in the western Atlantic. In any given area it generally seems fairly easy to differentiate the local *Sargassum* flora into a comparatively few (say 2–5) locally distinct benthonic forms, plus the usual two pelagic "species" found drifted ashore. But in a comparison between descriptions or material from different regions it frequently becomes very difficult to speak with any assurance of absolute taxonomic identities or distinctions. Compared over their entire range of distribution many of the forms show a distressing tendency towards more or less complete intergradations and the question arises as to whether these intergradations are real or apparent, that is whether they are the result of parallel modifications of phylogenetically distinct strains, or actually express a systematic continuity through local variations.

Unquestionably the genus *Sargassum* thus offers great inherent obstacles to a clear understanding of its taxonomy, and different possibilities suggest themselves in explanation of this situation① It is possible that the genus may comprise a great number of actually independent taxonomic units covering, in the aggregate, a very wide range of morphological differences, but being so closely intergraded within this range as to defy clear definition and reliable recognition of each unit separately② It is also possible that there may in reality be only a very few truly independent forms of such great morphological instability under varying environmental conditions that the thread of their taxonomic affinities is very hard to follow through the maze of their phenotypic diversities③ It may finally also be that we have a few quite stable and well differentiated forms combined with other systematic units of extreme morphological instability which serve to obscure the nomenclature and classification of the entire genus. In the author's opinion, the latter possibility is most likely to offer the true explanation of the inherent difficulties of *Sargassum* taxonomy. From the material so far studied it would for instance appear as though *Sargassum hystrix* might safely be regarded as a relatively quite stable form not subject to significant local modifications of its essential specific characteristics. This is apparently also true in a lesser degree of *S. polyceratium* and *S. platycarpum*. On the other hand, there can be no question of the great individual as well as geographical variability within the *S. vulgare—S. pteropleuron* group.

While the preceding remarks are applicable both to the benthonic and to the pelagic weeds, the classification of the latter offers further special difficulties of its own, arising from the fact that it has not as yet proved possible to establish definite specific affinities between the pelagic weeds and the sessile relatives from which they must be, or have been, derived. The question of whether the derivation of the floating forms is entirely a matter of past evolution or whether it also continues actively today, and whether the pelagic weeds should accordingly be dealt with as independent systematic (genotypic) units or merely as phenotypic variations of sessile species, directly induced by the changed conditions of the drifting stage, is therefore still unanswered. So long as this state of affairs remained unaltered, it was patently impossible to establish a definitive classification and nomenclature for the pelagic forms. This has been very strongly felt by Winge in his resort to numerical designations instead of binominal nomenclature; and it is only through samples discovered in the material here reported upon that the difficulty has finally been overcome for the first time in the case of one of the dominant floating weeds, heretofore known only in the sterile pelagic form.

While material is being gathered for a collateral investigation of the taxonomy and classification also of the benthonic species of *Sargassum*, with a view to elucidating the probable derivation and relationships of the pelagic weeds, this phase of the work has not yet reached a stage where it is possible to draw any definite conclusions. Nor is it necessary for the purposes of the present report on the quantitative observations made to date to enter into a discussion of the sessile relatives of the drifting forms to which our figures exclusively pertain. We shall therefore in the following confine ourselves to the description and discussion of those weeds which in the course of these investigations have been found to form part of the pelagic *Sargassum* flora.

For a convenient instrument for the identification of the benthonic species of the Western Atlantic, the reader may be referred to Howe's brief synopsis of the Bahaman flora (Howe, 1920), which, when supplemented by Collins and Hervey's key and descriptions of the *Sargassa* of Bermuda (Collins and Hervey, 1918, pp. 80–84), has been found most useful for a preliminary orientation of the shore collections examined by the writer. More extensive descriptions, but unfortunately only of a more limited number of species may also be found in Börgesen (1914 a, b) and Taylor (1928). It is clear, however, that much of the nomenclature and classification used by these various authors must still be considered to be of a purely tentative character.

In regard to the pelagic weeds, the most useful and most comprehensive account available to date is that given in Winge's report (Winge, 1923, pp. 21–29), and it has been particularly fortunate in the field work connected with these investigations to be able to refer constantly to Winge's text and illustrations in the task of sorting on board nearly five thousand pounds of floating plants and of correlating the zoological with the botanical observations made in that connection.

In Winge's account, however, the nomenclatural problems have been left entirely as they were and the prevailing uncertainties are emphasized by a resort to simple numerical designations instead of a binominal terminology. The probable relations between the various floating forms, as indicated by their morphological similarities or distinctions, are likewise given only scant consideration.

Although the results of the present investigation are as yet far from having eliminated all the difficulties which have hampered the discussions of the pelagic weeds in the past, they nevertheless lead forward along three different lines towards a better understanding of the taxonomic problems of the floating *Sargassa*.

On one hand the existing information concerning the diversity of morphological forms observable in the pelagic state is confirmed, and is further increased by the discovery of an additional variety (*S. natans, IX*) in one of the series or "species," tending to be dominant within its own domain, and of a dimorphic condition in another "species," (neither of which is mentioned in Winge's descriptions of the floating weeds). On the other hand, the extensive collections now available clearly show by their intergradations that at least three of the varieties tentatively treated as equivalent units in Winge's report,[1] plus the additional variety above mentioned, arrange themselves quite naturally into a single series, which may thus be treated as a taxonomic unit, tentatively given the rank of a species, and to which a binominal designation (*Sargassum natans*) can therefore be applied with full recognition of its possibly composite systematic character.

[1] Winge (1923, p. 28) is of the opinion "that the 8 species enumerated by [him] are «good species»." Of these only 6 are here considered under separate species headings.

Finally, the discovery of a fertile specimen of the other one of the two dominant pelagic weeds (*S. fluitans*), attached to a small piece of driftwood, has served to show that the sterile and unattached pelagic form of this species at least is not morphologically modified from the fertile and sessile type of plant in so far as vegetative parts are concerned, the modifications being, in other words, entirely confined to the loss of fertility alone. While this discovery has no direct bearing upon the question of the average duration of the pelagic state, or in other words, the average age afloat of the specimens constituting the oceanic *Sargassum* flora, it does enable us from now on to make definite search for benthonic fields of a known type of sessile *Sargassum* weed from which the recruiting of the pelagic population of *S. fluitans* may still be going on today, with the knowledge that evolutionary modifications calling for an *a priori* assumption that this recruiting must be entirely a matter of past history are at least not involved in the case of this particular one of the two dominant members of the floating *Sargassum* flora. ?

Before proceeding further with the discussion of the variations, relationships and distributions of each of the various forms of floating *Sargassum* with which we are here concerned, it is perhaps best first to give a brief synopsis of the definitions on which we have based the identifications and nomenclature, or numerical designations, to be used in this report. In this synopsis we shall only include the pelagically important forms, that is the forms found only in a pelagic state and those of the normally benthonic varieties which are apparently capable of maintaining a pelagic existence, without obvious degeneration or essential morphological modification, for a sufficient length of time to become significant members of the oceanic *Sargassum* flora. The synopsis thus covers all forms of *Sargassum* observed in *open ocean* in the course of this investigation, which can safely be taken to mean all forms at all likely to be found afloat at least in the western half of the Sargasso Sea proper. Only near shore, in the neritic margins of the pelagic domain, will holo-benthonic forms not defined in this key be likely to occur adrift at the surface, and for the identification of such weeds reference has already been made to Howe's work on the Bahaman forms (Howe, 1920) and to the synopsis of the Bermudian species given by Collins and Hervey (1917). To avoid duplication and confusion, Winge's numerical designations have been retained whenever it has been found impossible or inadvisable as yet to replace them with a binominal nomenclature, and new numerical designations have been introduced in sequence with Winge's, regardless of the fact that the resulting numerical sequence is in most instances without any relation to the writer's views on the probable relationships of the forms so designated.

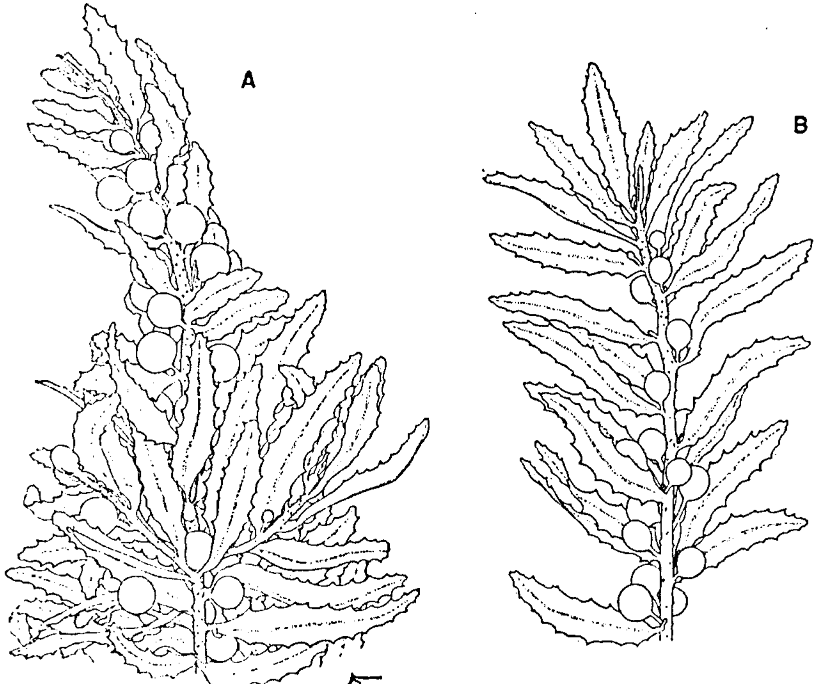

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Figure 4. *Sargassum fluitans* (*X*). *A*. Part of plant. *B*. Single branch. Drawn from formalin specimens by D. T. Pitcher. × 6/7.

ARTIFICIAL KEY TO THE WEEDS FOUND IN PELAGIC COLLECTIONS

A. Dwarf form, size of plant usually only about 1 inch. Bladders small, very numerous. Stems thickly beset with long thorns. Leaves rare, very small when present. . . . . *Sargassum V*, Winge 1923.

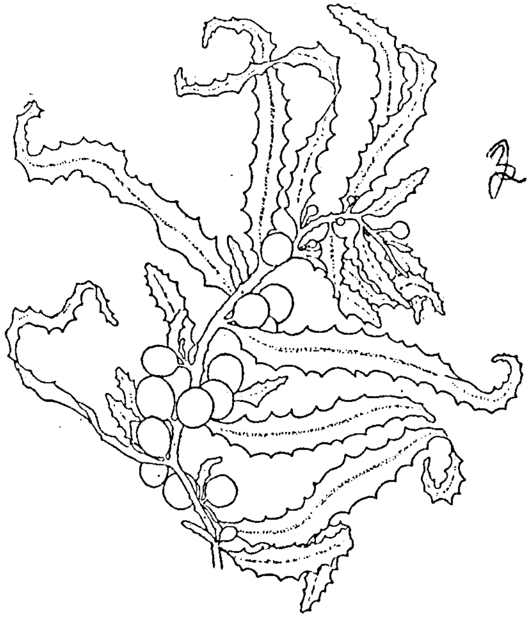
B. Not dwarfed. Leaves present, usually abundant.

  I. Stems thorny, especially on distal parts.

    a. Leaves linguiform to ovate, usually flaccid when caught pelagically. Plants normally fertile, with receptacles (fruitleaves) present. Not a pelagic weed. . . . . . *S. polyceratium* Montagne. ? *Sargassum IV* Winge, 1923.

b. Leaves lanceolate; edges dentate or serrate; midrib not very prominent, never winged or dentate. Always sterile, without receptacles. . . . . *S. fluitans* Börgesen 1914b.

1. Many subequal, close-set, short branches without distinct differentiation of main branches or stems. Entire plant typically of a dense, globular, or short cylindrical habitus. Branches of third and higher orders normally very short and obscured by the foliage. Foliation very dense, fully developed bladders usually greatly outnumbered by leaves. Leaves in fresh condition thicker and stiffer than in III. Color dark olive. . . . . *S. fluitans* (*X*), Parr.
   Basal shoot form of *S. fluitans*.
2. Usually only one or two long main branches, with relatively few, long, wide-set branches of the second and of higher orders, giving entire plant a loose, open and stringy habitus. Foliation less dense than in X. Fully-developed bladders usually more numerous than leaves.
   S. fluitans (*III*).
   Sargassum III, Winge 1923.
   Distal shoot form of *S. fluitans*.



S fluitans

Figure 5. *Sargassum fluitans* (*III*). Part of branch. Drawn from formalin specimen by D. T. Pitcher. × 6/7.

c. Leaves linear to lanceolate. Plants normally fertile with receptacles present. Not pelagic weeds.
S. pteropleuron Grunow.
S. vulgare Agardh.

II. Stems smooth throughout.

a. Leaves thick, linguiform to ovate, bluntly rounded at their distal end, their margins subentire, entire or vaguely dentate. Habitus open and loose with very long and very wide-set branches of second order, with branches of third order generally *abruptly* smaller; or very dense, subcylindrical, with extremely short, profusely foliate branches of second order. Foliation always very dense, hiding the structural features of the entire plant, or at least on the distal portions of the secondary branches in the long-branched form. Color tending to dark tobacco-brown. Often fertile. *S. hystrix* Agardh.
? *Sargassum VI* Winge, 1923.[1]

b. Leaves thinner, narrowly to broadly lanceolate, or linguiform, always conspicuously dentate. Habitus always bushy, with generally *gradual* reduction in the size of the branches of higher order (not abrupt as in *S. hystrix*). Foliation always quite open and relatively sparse,[2] never obscuring the structural features of the plant. Color yellowish to brown. Never fertile.
S. natans Linneus, *sensu lato*.

1. Bladders with a shorter or longer spike at their distal end, sometimes developed into a narrow, leaf-like appendage. Leaves linear to narrowly lanceolate; when fully developed typically about 30–40 mm. long, .5–1 mm. wide, their width contained about 30–50 times in their length.[3] Habitus finer than in any of the following forms. *Average* distance between origins of branches[4] usually 6–8 mm., only rarely as little as 5 mm. Number of bladders actually

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[1] In his key Winge (1923, p. 29) defines *Sargassum VI* as having stems without thorns, which agrees with *S. hystrix*, although Winge's illustration of *S. VI* (*loc. cit.* fig. 10, p. 25) otherwise shows rather more resemblance with our *S. fluitans X*.

[2] True also of *S. natans* (*IX*) in comparison with *S. hystrix*. *S. n.* (*IX*) can also be distinguished from *S. hystrix* by its narrowly lanceolate, strongly dentate leaves. Broad leaves in the *natans* series occur only in the very openly-growing (*VIII*).

[3] The broad-leaved variety, referred to *S. natans* (*I*) on the basis of the presence of bladder spikes, may have leaf-widths up to 3 mm., contained as little as 12 times only in their length.

[4] Excluding distal parts still actively growing.

present at any time usually only about half the number of leaves.................................*S. natans* (*I*).

Sargassum I, Winge 1923.

S. natans var. *ciliata* Börgesen 1914a.

2. Bladders quite smooth, without distal appendage of any sort.

x. Very open growth. *Average* distance between origins of branches typically 7–8 mm., very rarely as little as 5 mm. Number of bladders actually present at any time usually considerably less than number of leaves.[1]

o. Leaves (linear to) narrowly lanceolate, when fully developed typically about 40–60 mm. long and 1.5–3 mm. wide, their width contained 15–30 times in their length. Habitus coarser and more open than in (*I*).

S. natans (*II*).

S. natans var. *typica* Börgesen 1914a.

Sargassum II, Winge 1923.

oo. Leaves lanceolate to broadly lanceolate, when fully developed typically about (25) 30–50 mm. long and 5–6 mm. wide, their width being contained about 5–10, typically 7–8 times in their length.[1] Habitus still coarser and more open than that of (*II*).

S. natans (*VIII*).

Sargassum VIII, Winge 1923.

xx. Denser growth. *Average* distance between origins of branches generally less than 5 mm. Number of bladders actually present at any time usually about equal to or greater than number of leaves. Leaves lanceolate, strongly dentate, when fully developed about 30–40 mm. long and 1.5–2.5 mm. wide, their width being contained about 15–25 times in their length....................*S. natans* (*IX*), Parr.

S natans

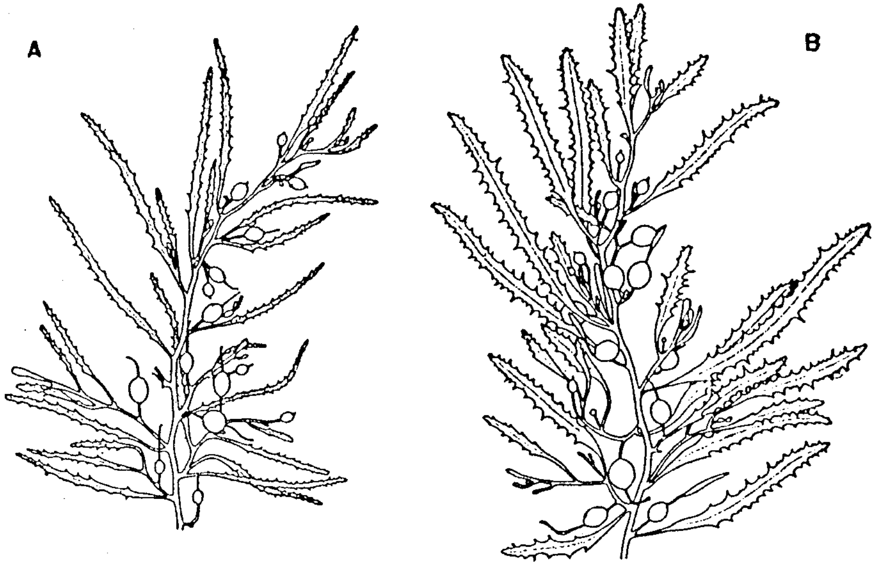


Figure 6. *Sargassum natans* (*I*). *A*. Narrow leaved. *B*. Broadleaved plant. Drawn from herbarium specimens by D. T. Pitcher. × 6/7.

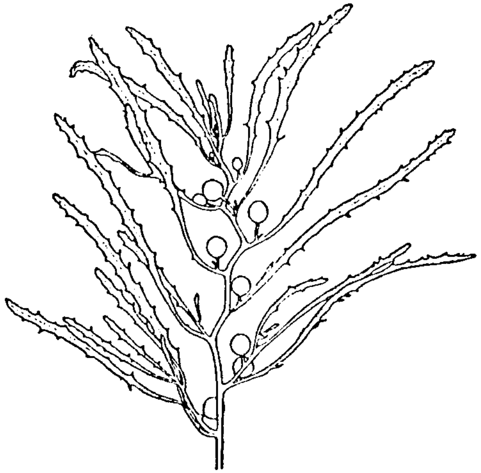


Figure 7. *Sargassum natans* (*II*). **Drawn from herbarium specimen by D. T. Pitcher. × 6/7.**

& NO spikes on bladder

---

[1] When counting the number of branches arising over a given distance from the stem under examination one must, of course, always be careful to exclude the apical portion in which the stem is still actively growing.

[1] In the typical floating form the absolute width of the leaf (ab. 5 mm.) is surprisingly constant regardless of variations in its length. Narrower leaves, of widths down to 2.5 mm. contained up to 15 times in their lengths, occur in atypical forms pointing in one form towards (*II*), in another form towards a benthonic origin.

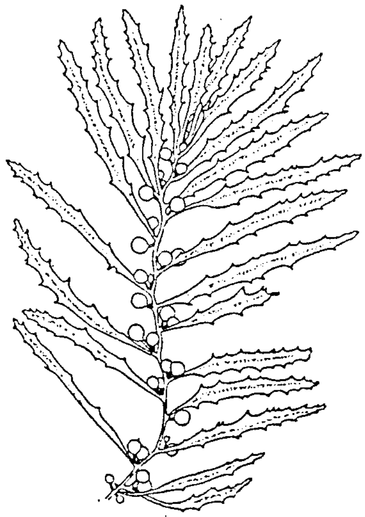


Figure 8. *Sargassum natans* (*IX*). Drawn from herbarium specimen by D. T. Pitcher. × 6/7.

no spike
natans
(middle)

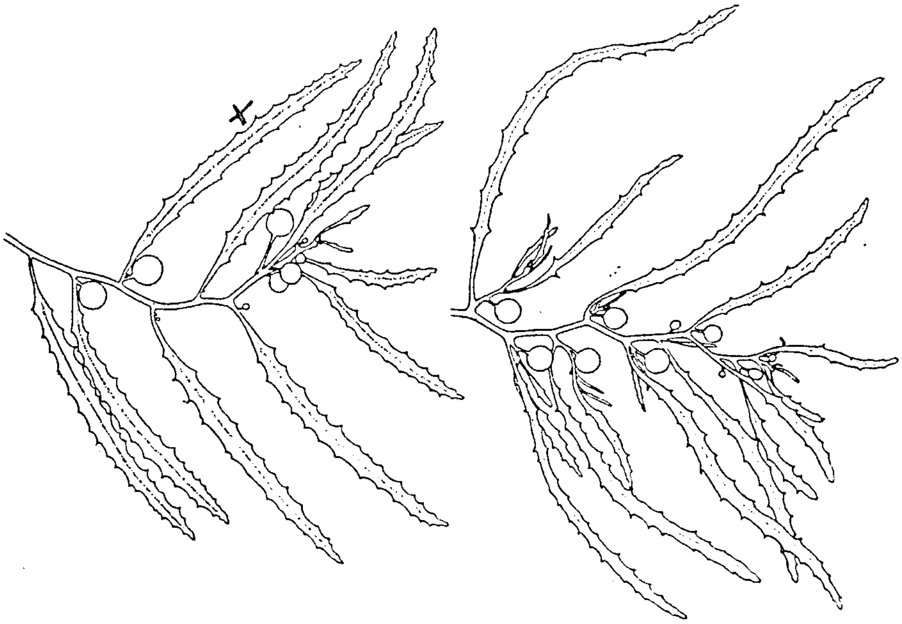
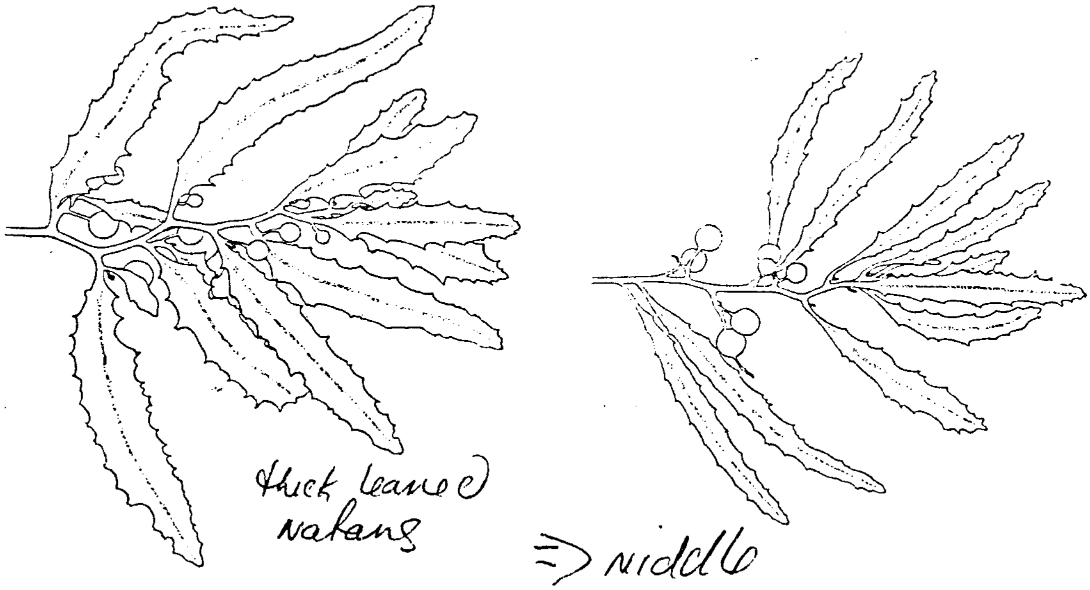


Figure 9. *Sargassum natans*. Transitions between (*II*) and (*VIII*). Drawn from herbarium specimens by D. T. Pitcher. × 6/7.



thick leaved
natans

=> middle

Figure 10. *Sargassum natans* (*VIII*). Branches of plants with medium and with broad leaves. Drawn from herbarium specimens by D. T. Pitcher. × 6/7.

ECOLOGICAL CLASSIFICATION

On an ecological basis, two or three different classes of floating weeds may be distinguished according to the roles they play in the pelagic flora and the role and duration of the pelagic stage in the ecology of the individual species. In one class we have the eupelagic weeds, that is the species or varieties of *Sargassum* which in a quantitative sense have their main occurrence in the pelagic condition or which are as yet only known at all in a floating stage. In this class we have the species or series of forms included under the designations of *S. natans* and *S. fluitans*. These eupelagic forms, of course, contribute by far the largest quantity of vegetation to the drifting community as were to be expected from their definition. In the second class, the quasipelagic forms, typically represented by *S. hystrix* and perhaps comprising no other form among those here considered, we might group the weeds which are normally benthonic and sessile, but which, when they are torn loose from the bottom, are able to survive in the pelagic condition, without significant morphological changes, for a sufficient length of time for them to contribute a quantitatively significant element to the floating flora in the peripheral parts of the Sargasso Sea without being able to maintain a significant representation in its central area, among the weeds of longer pelagic existence (see page 68). Finally, the third class may be made to comprise the holo-benthonic forms which are only accidentally found drifting at the surface, where they either rapidly perish (*S. polyceratium* and others) or rapidly become modified into a holopelagic form in which the identity with the benthonic type becomes unrecognizable (it is still not impossible that *S. natans* may be a derivation *with* morphological modifications from a benthonic form with which it can not as yet be identified). The forms of the holo-benthonic class are, of course, normally only encountered in the neritic boundaries of the Sargasso Sea proper, and it is only a very few of the holo-benthonic forms which have so far been found in pelagic collections at all, outside of the narrowest and most turbulent straits and coastal waters. Clearly the likelihood of finding a holo-benthonic form even accidentally present in a pelagic collection is determined (1) by the ease with which it is torn loose from its sessile condition which again will be dependent (a) upon the tensile strength of its stems, (b) upon the nature of the substratum generally selected for attachment (e. g., forms growing mainly on rocks and pilings are less likely to be found adrift than forms growing on smaller objects), and (c) upon the degree of exposure, generally correlated with depth, of their benthonic zone of distribution (the fact that *S. filipendula* seems so rare at the surface even in such a locality as the Straits of Florida is undoubtedly correlated with its generally relatively deep benthonic habitat in southern waters). It is further determined (2) by the degree and durability of the buoyancy of the weed when loosened. In the great amount of pelagic collections sorted in the course of this investigation only 3 holo-benthonic forms have been found to occur with sufficient frequency at the surface in the neritic margins to warrant their inclusion in our key on page 15.

While Winge does not explicitly classify the 8 varieties of floating weeds, described by him according to the relative importance of their pelagic as compared with their benthonic occurrence the implicit statements made in his text are quite in accordance with the grouping of the various "species" here suggested.

DESCRIPTIVE ATLAS OF EUPELAGIC WEEDS

The synopsis given in the preceding differentiates only the typical representatives of each of the various forms encountered in the course of these investigations. Actually, however, the eupelagic forms show every possible type of intergradation, even to intergradations (at least in superficial descriptive features) between the *S. fluitans* and *S. natans* series. It therefore seems desirable that the descriptive account of these variable and intergrading series should be further elaborated for future use in comparisons between collections. Since we are chiefly concerned with the eupelagic weeds only, we shall in the following confine our attention to the two series identified as *S. natans* and *S. fluitans*. In the hope that this may prove the most useful and practical method of presentation, the account will be given in the form of an annotated descriptive atlas of photographic herbarium silhouettes.

In this connection it should also be mentioned that the epizoan fauna inhabiting the weeds often provides valuable guidance for the classification of the weeds themselves, due to the specificity of certain dominant forms. The writer is indebted to M. D. Burkenroad for the following statement of these relationships and their probable interpretation.

> "Almost every individual plant of eupelagic *Sargassum* is overgrown by some one of a limited number of species of colonial epizoan which, upon the outer and younger portions of the plant at least, dominates the attached fauna. Each of these dominant species of epizoan is limited, not geographically or seasonally, but rather to certain forms of plant. Upon *S. I* of the *natans* series the dominant is almost without exception the sulphur-yellow Campanularian hydroid *Clytia noliformis*. Upon *S. natans II* the same *Clytia* is usually the dominant, and this hydroid occasionally occupies what appear to be plants of *S. VIII* and *S. IX* of the *natans* series. *S. natans IX* is, however, much more usually overgrown with the yellow Sertularian hydroid *Sertularia mayeri* or with the black species *S. flowersi*, which infrequently occupy what appears to be *S. II*. Upon *S. natans VIII* the dominant form is usually the white Plumularian hydroid *Aglaophenia minuta*. In the *fluitans* series, the usual dominant of *S. III* is the same species as in *S. natans VIII*, *Aglaophenia minuta*; on occasion, however, a plant of *S. fluitans III* may be overgrown by *Sertularia flowersi*, *S. mayeri*, the white branching *S. versluysi*, the white unbranched *S. brevicyathus*, the tan-colored Sertularian *Pasythea quadridentata*, or the delicate white Plumularian *Monotheca margaretta*. *S. X* of the *fluitans* series may have as its dominant hydroid *Clytia noliformis*, *Sertularia mayeri*, or *S. flowersi*, but frequently lacks a clear dominant; it is almost invariably occupied by a Chilostomatid bryozoan which never occurs upon any other form of holopelagic *Sargassum*. Finally, the dominant hydroid of *Sargassum V* is either of two species of Tubularian hydroid one of which resembles *Clava*, the other *Syncoryne*.
>
> A difference in hydroid fauna between broad-leaved and narrow-leaved forms of

> pelagic *Sargassum* taken in the same locality was noted by Hentschel, 1920; and was remarked by Winge, 1923, as a supplement to the distinctions between *S. natans I* and *S. fluitans III*. The use of the faunal distinction for separation of intergradient or nearly resembling forms of *Sargassum*, as *S. natans II* and *S. natans VIII* or *IX*, *S. fluitans III* and *S. fluitans X*, is however complicated by the impossibility of determining whether a doubtful plant bears an unusual dominant, or whether it is an atypical plant with the usual dominant. Thus, typical *S. natans VIII* almost always bears *Aglaophenia*, and the plants occupied by *Clytia* or *Sertularia* are often of less characteristic form and might perhaps represent *S. natans II*. Further, according to what seems at present the most satisfactory hypothesis relative to the mechanics of distribution of the epizoa of pelagic *Sargassum*, the limitation of given epizoans to given forms of plant has more the quality of a succession phenomenon than that of, say, host-parasite specificity. Therefore, unusual combinations are to be expected, *especially upon plants of atypical form;* and the definition of boundaries between plant forms according to their epizoan associates would be an arbitrary procedure. The following facts and assumptions lead to the hypothesis in question:
>
> In addition to the dominant colonial epizoans, each plant of pelagic *Sargassum* bears what may be termed a subfauna of hydroids (*Gemmaria*, *Halecium nanum*, *Plumularia setaceoides*, *P. catharina*, *Obelia*, *Clytia bicophora*, and others) and the very abundant bryozoan *Membranipora tuberculata* which (in sharp contrast to the dominant hydroids, more than one species of which is only infrequently found growing upon a single plant) may occur all together or in any combination, and in association with any dominant epizoan. The subfaunal epizoa, although more frequent upon some forms of *Sargassum* (*S. fluitans III*) than upon others (*S. natans I*), occur in much the same proportion one to another upon any form of plant. This nonspecific subfauna is most frequent, in contrast to the dominant epizoans, upon the older and inner parts of the plants; and its components often occur in small discrete patches, rather than as continuous extensive colonies. The subfauna is as a whole distinguished from the dominant forms by a much greater frequency of sexual reproduction or of the development of long transfer stolons.
>
> The evidence seems irrefutable that floating *Sargassum* grows actively, that its older parts gradually break off and sink, and that its numerical abundance is maintained chiefly by division of the stock. It is therefore clear that a sterile dominant epizoan must keep pace with the extension of the plant upon which it grows, in order to avoid being lost with the older portions of the plant. On the other hand, the subfauna, reproducing sexually or with other special means of facilitating transfer from plant to plant, need not overgrow the entire plant to assure the maintenance of its stock; and its adjustment to the dynamic peculiarities of the substratum therefore need not be so close as in the case of the dominant epizoans.
>
> Experiments made at the Bermuda Biological Station in 1936 suggest that the specificity and the exclusiveness of the dominant hydroids is not an immediate effect either of the substratum (successful transfers of *Aglaophenia* to *S. natans I*, etc.; ready growth of all forms on glass) or of the epizoan association (culture in mixed stands of the various dominant forms). Thus, for example, the limitation in nature of *Aglaophenia* to *S. fluitans III* and *S. natans VIII* is not a matter of direct and immediate dependence upon these specific plant substrata or of a directly deleterious effect of the tissue of *S. natans I;* and further, the lack in nature of any examples of *S. fluitans III* dominated by a mixture of *Aglaophenia* and *Pasythea* is not the result of a direct incompatability of one of these hydroids with the other. It therefore seems more likely that the apparent selectiveness exhibited by the dominant epizoans is the result either of a difference in the history of the plants or of some indirect, quantitative process, than that it is the result of a qualitative restriction.
>
> Transfer of epizoans both dominant and subfaunal from one plant to another occurs without special means on the high sea to some extent, when the plants are massed together during protracted periods of calm, or are bound together by the silken tubes constructed by the nereid worm or by the amphipod *Sunamphithoë*, or by the egg-strands of flying-fishes. Such transfer seems to occur with sufficient, although a low, frequency to have produced a complete mixture of originally separate dominant faunas, given the long period of pelagic existence of the plants for which the evidence seems clear. It therefore appears that the assumption of an originally distinct geographical derivation of *S. natans I* and *S. fluitans III*, or of the plants of *S. fluitans III* with *Aglaophenia* from those with *Pasythea*, can not serve to account for the observed distinctions in dominant fauna.
>
> The simplest explanation of the peculiarities of distribution of the dominant epizoans might in part at least be supplied by an assumed relation of their individual rates of growth to that of the different plants and of each other. *S. natans I* never bears other dominant than *Clytia noliformis*. It might be assumed that this plant has a rate of growth and of disintegration higher than that of the other forms of holopelagic *Sargassum*, and that the *Clytia* is the only dominant able to keep pace with it. *S. natans II*, which occasionally is occupied by *Sertularia*, might be supposed to have a somewhat slower rate of growth and death; *S. fluitans X* and *S. natans IX*, which are often occupied by *Sertularia* or *Pasithea*, a still slower rate; *S. fluitans III* and *S. natans VIII*, which generally bear *Aglaophenia*, the slowest rate of all. Since *Clytia* appears to be able to utilize larger planktonts as food than can the Sertularian and Plumularian hydroids, the availability of these more motile organisms to *Clytia* might perhaps be assumed to be more reduced by the presence among the *Clytia* of close, repellant stands of Plumularians and Sertularians than would the availability of smaller organisms to the latter by the Campanularian. Such an effect might account for the infrequency with which *Clytia* dominates plants assumed to have a growth rate slow enough for the maintenance of *Sertularia* or *Aglaophenia*. The more efficient seive created by the growth-form of *Aglaophenia* might be considered to account for the more usual occurrence of this than of the Sertularians upon plants of growth rate sufficiently slow to permit the maintenance of *Aglaophenia*. Since the plankton of the Sargasso seas which can be utilized by hydroids is relatively sparse, it might further be assumed that a competition for food between intergrown colonies of different hydroids might occur, which would, other things being equal, favor the originally larger colony, in much the same way as a single shop has difficulty in meeting the competition of one which is a member of a chain. This initial difficulty in the replacement of an established by an invading form might reinforce infrequency of transfer in minimizing the occurrence of mixtures of dominant forms upon a single plant.
>
> Direct evidence for the hypothetical relation between plant and epizoan tentatively outlined above is exceedingly difficult to obtain. Experiments at Bermuda suggested that *Clytia* may have a higher rate of linear extension than do the Sertularians and Plumularians, but were inconclusive. No clear indication of effective food competition in mixed stands of hydroids was obtained, but was perhaps hardly to be expected in the fertile neritic waters where the relatively few and short experiments were made. Nothing is directly known of the growth-rates of the different forms of pelagic *Sargassum*. The fact that the subfauna is more abundant on *S. fluitans III* than on *S. natans I* seems consistent with the assumption of a slower rate of growth and of disintegration in the former, since the subfauna seems clearly to depend for maintenance of its stock on the dissemination of new colonies rather than on continuous growth. It also seems consistent that the order of frequency and of thinness of habitus of the plants is more or less in direct ratio to their hypothetical rate of growth and disintegration. Various objections to the hypothesis, and numerous accessory points requiring explanation, which are not mentioned above, will it is expected be considered in detail in future essays on the remarkably complex animal community of pelagic *Sargassum*."
>
> M. D. BURKENROAD, *in lit.*

In favor of Burkenroad's suggestion that dominance among the epizoans may be determined by the relationship between their rates of growth and the linear rate of growth of the plants, it may be pointed out that, even if we assume an equal volume or weight rate of growth for all forms of weed, e. g., in grams per week per kilogram, the absolute linear rates of growth (e. g., mm. increase in length per stem per week) would vary from one weed form to another approximately as assumed by Burkenroad as an explanation of epizoan dominance. Since it has the finest stems and leaves, *S. natans* (*I*) would have to add greater linear increases to its plant to give the same increase in weight per unit weight than would the somewhat coarser, *S. natans* (*II*). Still less linear increase would be required of the dense *S. natans* (*IX*) and least of all of the coarse *S. natans* (*VIII*) and of the *S. fluitans* series.

S. Natans SERIES

To give a general definition of the entire *S. natans* series seems a virtual impossibility. In difficult cases, especially when dealing with incomplete plants of certain forms of the *S. natans VIII* type, the complete absence of thorns on the stems becomes the sole determining feature by which the specimen can be assigned to the *S. natans* as distinct from the *S. fluitans* series. It might actually be said that every morphological feature shared in common by all members of the *S. natans* series are of purely negative character as indicated in the following diagnosis.

Receptacles absent. All branches of same general type. Cryptostomata absent or extremely scarce. Branches smooth, without thorns. Leaves simple, never forked, relatively straight, without conspicuous morphological twist, their costae distinct but without conspicuous ridge. Edges of leaves usually distinctly to strongly serrate.

It is evident that the preceding diagnosis is almost worthless apart from the elimination of forms which by the possession of characters *not* found in the *S. natans* series can be excluded from the latter, while it does not form a sound basis for positive identifications. With regard to all positive features such as leaf-size and form, and all characteristics of general habitus capable of expression in counts or measurements, the variations within the series are so great as to defy any attempt at giving a generalized definition for the whole series.

It might be stated that the leaves are generally very firm in comparison with leaves of similar width and thickness in benthonic forms, notably in comparison with *S. filipendula*, but also in comparison with most other benthonic species which have come to the writer's attention, except the more robust types of *S. pteropleuron*. But even this relative rigidity of foliage is not without exceptions, particularly among the more broad-leaved representatives of *S. natans* (*VIII*).

In view of this generally negative character of the common diagnosis of the entire group, it will be necessary for positive identification to make comparisons individually with every form comprised within its series. For this purpose the accompanying atlas has been arranged in descriptive sequence from the most narrow-leaved to the most broad-leaved specimens found in the available collections.

Abnormally produced leaves, not corresponding to the descriptions of typical plants given in the following, occasionally occur particularly in the basal portions of larger specimens, and are illustrated by an example of *S. natans* (*II*) given in figure 18 on page 38.

Silhouette 1 (figure 11) shows a typical, slender, fine-leaved specimen of *S. natans* (*I*), of moderate size (ab. 21 cm.), with distal spikes on every bladder, many of the spikes being narrowly foliate with a few serrations. Leaves 30–35 mm. long, about 1 mm. wide, sharply dentate. Bladders 2–2.5 mm. diameter, their pedicels 2–5 mm. long.

Silhouette 2 (figure 11) shows a small sprig of a broader-leaved variety of *S. natans* (*I*). Note the fully developed leaf arising from one of the bladders. Leaves 35–40 mm. long, 1.5–2.0 mm. wide, sharply dentate. Bladders 2–2.5 mm. diameter, their pedicels 2–4 mm. long.

Silhouette 3 (figure 11) shows a fragment of a still more broad-leaved specimen of *S. natans* (*I*), in which distal spikes are only present on a small minority of the bladders. Leaves 30–50 mm. long, 1.5–2.5 mm. wide, sharply dentate. Bladders about 3 mm. diameter, their pedicels short, only about 2 mm. or less.

Silhouette 4 (figure 11) finally shows a large (36 cm.) robust specimen of *S. natans* (*I*), in which many bladders completely lack distal spikes, and the spikes present on others are generally thin, simple and short. Leaves 35–45 mm. long, 1.5 (–2.0) mm. wide, sharply dentate. Bladders 3.0–4.0 mm. diameter, their pedicels 3–5 mm. long. It is evident that this specimen leads without any abrupt transition to:

Silhouette 5 (figure 11) which is a slender and narrow-leaved representative of *S. natans* (*II*), entirely free from bladderspikes and quite typical of numerous other representatives of the finer varieties of this form. Leaves 50–60 mm. long, sharply dentate, 1–1.5 mm. wide. Bladders about 3 mm. diameter, their pedicels about 2 mm. or less.

Silhouette 6 (figure 12) shows a slightly more luxuriant representative of *S. natans* (*II*) than that shown in silhouette 5. Leaves 50–70 mm. long, 1.5–2.0 mm. wide, sharply dentate. Bladders 3–4 mm. diameter, their pedicels 1–3 mm. long.

Since *S. natans* forms a continuous series of intergradations so far as leaf and plant form is concerned, one might, on the basis of the plants alone, be inclined to extend the range of modifications covered by the designation *S. natans* (*II*) to include also several of the relatively narrow-leaved forms shown in the following silhouettes. But, on the basis of the epizoans as identified by Burkenroad, the typical dominants of *S. natans* (*VIII*) (*Aglaophenia*) are present already on the specimens shown in silhouettes 8, 9, and the following figures. Taking epizoans into consideration, we therefore restrict *S. natans* (*II*) to the narrow range shown by silhouettes 5 and 6 (epizoan: *Clytia*), and this is the form, only slightly coarser than *S. natans* (*I*), in which the weeds without bladderspikes most commonly occur in the open Atlantic.

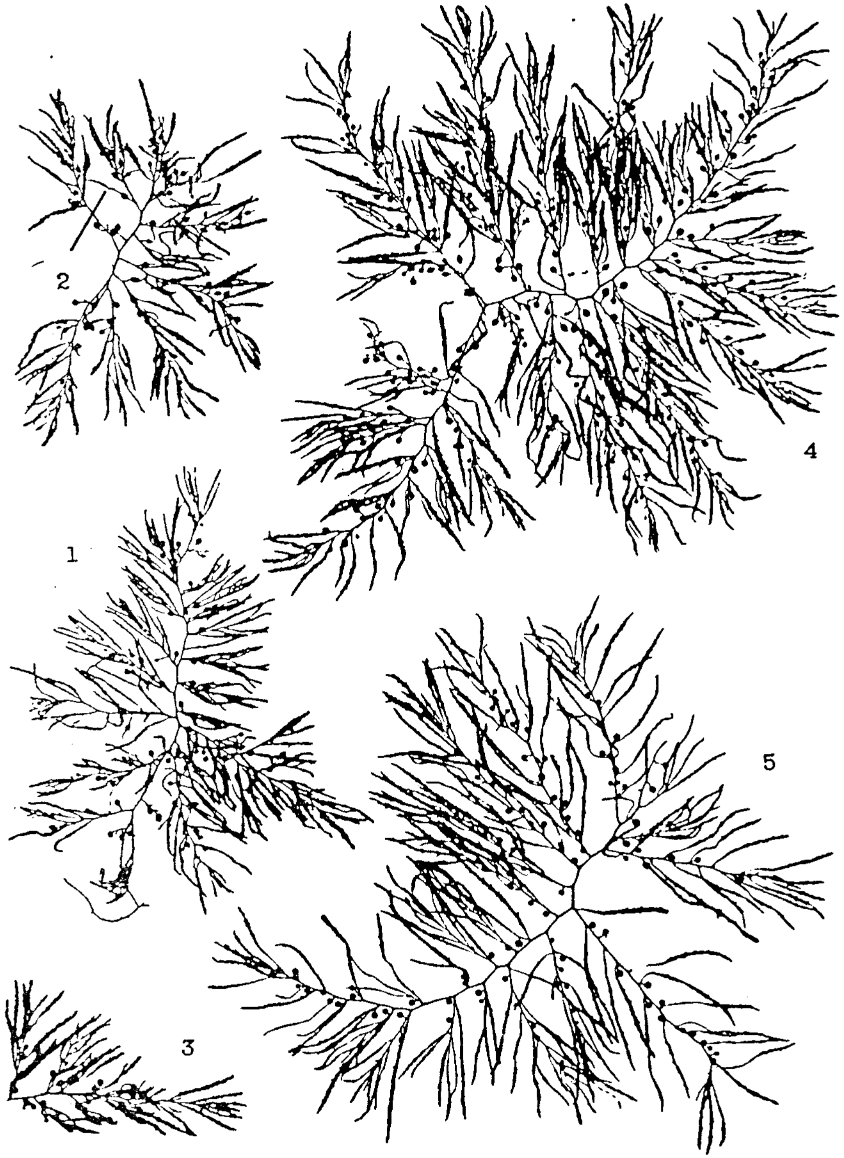


Figure 11. Silhouettes 1–4: *Sargassum natans* (*I*). Silhouette 5: *S. natans* (*II*), slender variety. Scale see figure 12.

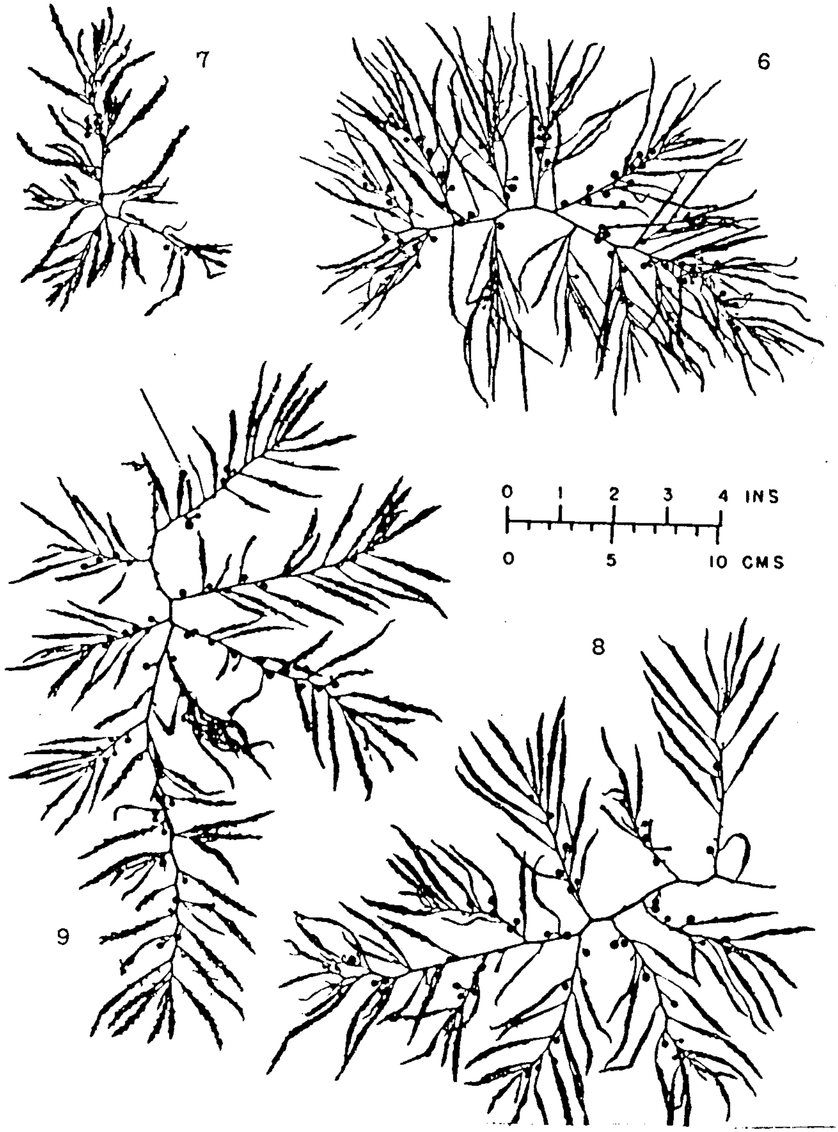


Figure 12. Silhouettes 6–7: *Sargassum natans* (II). Silhouettes 8–9: *S. natans* (VIII). See text.

Silhouette 7 (figure 12) shows a similar variation towards broader and softer foliage in *S. natans* (*II*) as that shown by silhouette 3 in *S. natans* (*I*). Leaves 40–50 mm. long, 2.5–3 mm. wide, sharply dentate. Bladders about 3.0 mm. diameter, their pedicels 2 mm. long or less. This specimen has also been found by Burkenroad to have an atypical epizoan fauna dominated by *Sertularia*.

A somewhat divergent, more densely foliate variety of *S. natans* (*II*), with extremely sharply dentate, but quite narrow leaves and relatively numerously retained bladders is shown in silhouette 22 (figure 16, p. 34) for comparison with *S. natans* (*IX*).

Silhouettes 8 and 9 (figure 12) represent very narrow-leaved specimens of *S. natans VIII*, so designated on the basis of their epizoan fauna (dominant: *Aglaophenia*). Leaves 50–60 mm. long, 3–3.5 mm. wide, sharply dentate (9) or rather weakly serrate (8). Bladders about 4 mm. diameter, pedicels about 2 mm. Silhouette 9 shows a bladder in a terminal position on a leaf or foliate pedicel 17 mm. long.

Since epizoan fauna could not regularly be taken into consideration in mass sorting on shipboard, it is evident from subsequent determinations on preserved material that many of these narrow-leaved *S. natans VIII* have been entered in the field records as *S. natans II*. This discrepancy between field records and final determinations mainly affects the data from the waters near the coast of the West Indian Islands and within the Central American Seas but is not significant for the open Atlantic, in which the bulk of the weeds without bladderspikes of the *S. natans* series occurs in the typical form of *S. natans II* shown in silhouettes 5 and 6.

In silhouette 10 (figure 13) an increase in leaf width and coarseness is noted. Leaves 40–55 (65) mm. long, 3.5–4.0 mm. wide, moderately dentate. Bladders 3–4 mm. diameter, their pedicels 1–2.5 mm. long, except when alate or foliate, when they may be as much as 20 mm. long. Silhouette 10 shows several narrowly alate pedicels, and one broadly foliate with dentate margin and with the terminal vesicle carrying a long, slightly foliate distal spike.

Silhouettes 11–13 show further variations of *S. natans VIII* with moderate leaves. In silhouette specimen 11 the leaves are fairly short and blunt, 40–50 mm. long, 3.5–5.0 mm. wide, and sharply dentate. Bladders small, 2.5–3.0 mm. diameter, on 1–3 mm. pedicels. In specimen 12 the leaves are longer and more pointed, 50–60 mm. long, 3.5–4.0 mm. wide. Bladders 3.5–4.0 mm. diameter, on 2–4 mm. pedicels.

Silhouette 14 (figure 14) represents a very vigorous specimen of *S. natans* (*VIII*), in which the comparatively narrow and pointed leaves still point towards the intergradation with *S. natans* (*II*). Leaves 40–50 mm. long, 3.5–4.5 mm. wide. Bladders 4 mm. diameter on 1–3 mm. pedicels.

Silhouettes 15–17 (figure 14) show an assortment of moderately robust but quite typical *S. natans* (*VIII*) with relatively short and broad leaves, which

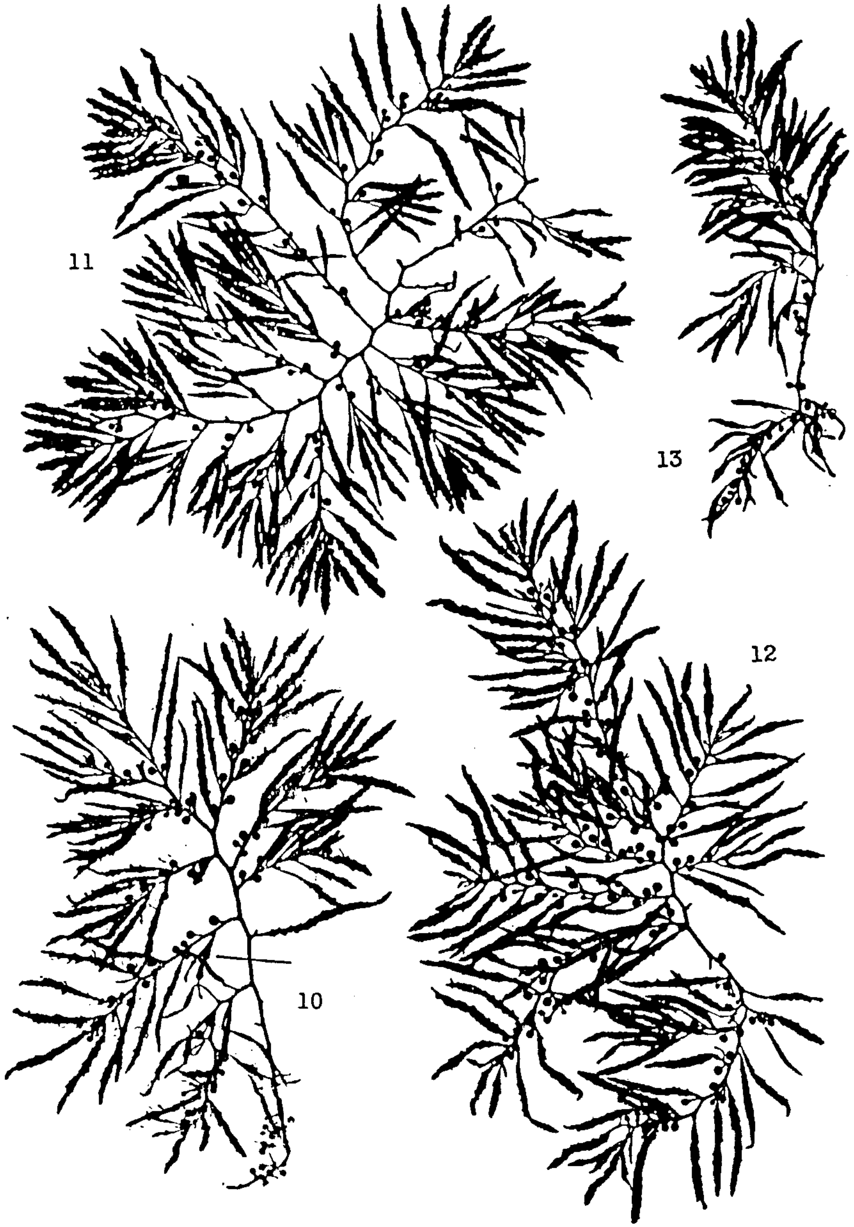


Figure 13. Silhouettes 10–13: *Sargassum natans* (VIII). See text. Scale, see figure 16.

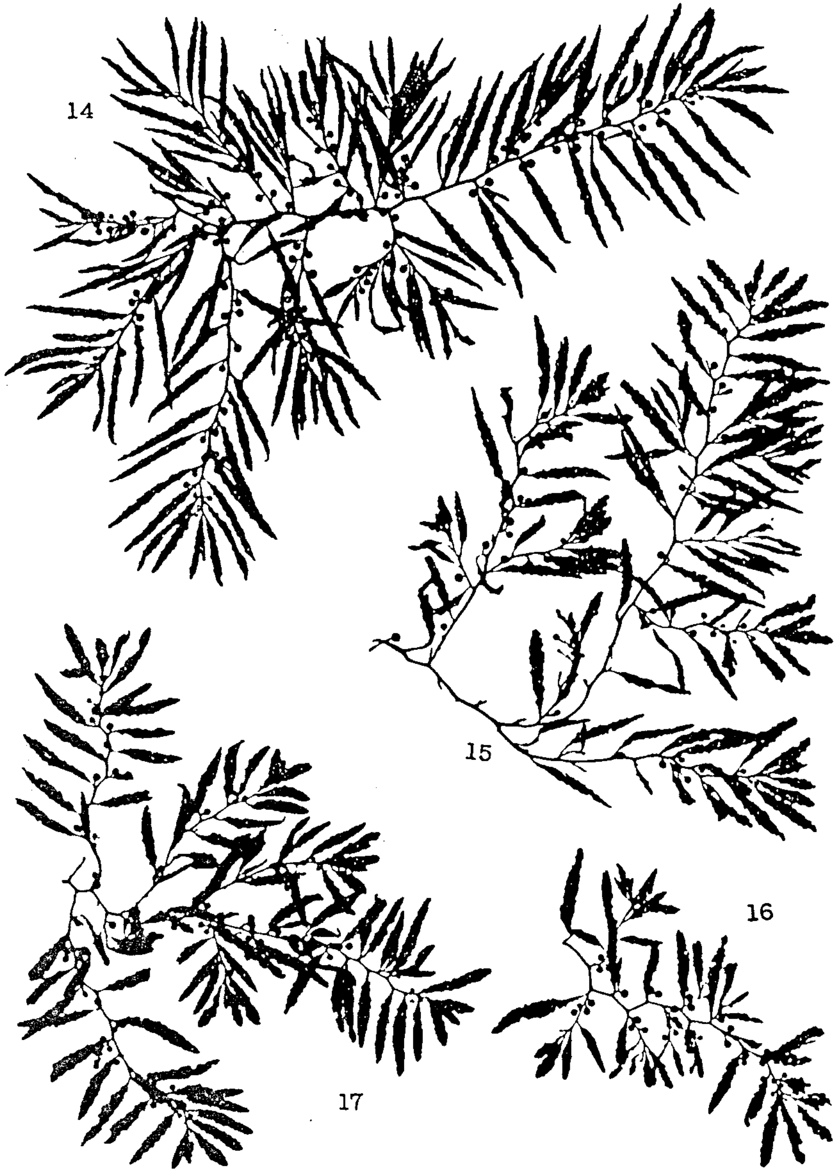


Figure 14. Silhouettes 14–17: *Sargassum natans* (*VIII*)). Scale see figure 16.

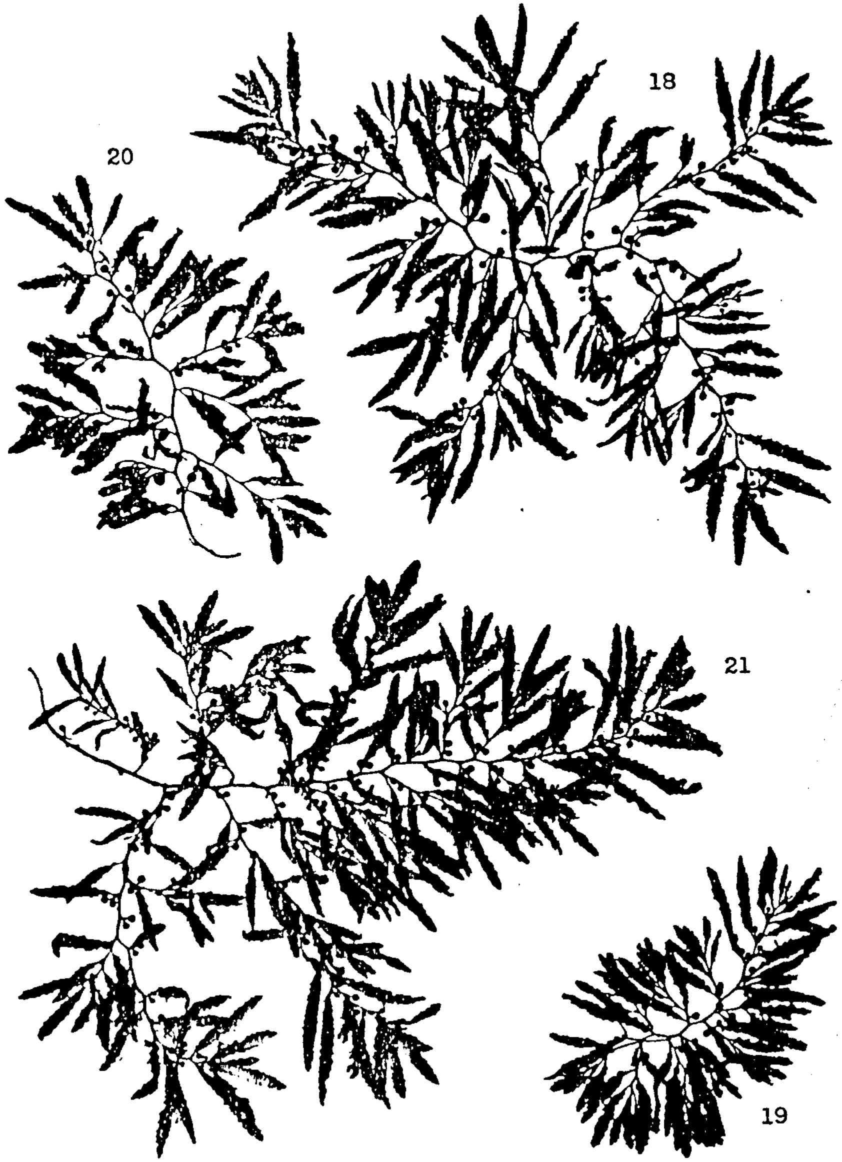


Figure 15. Silhouettes 18–21: Typical, broad-leaved *Sargassum natans* (*VIII*). Scale see figure 16.

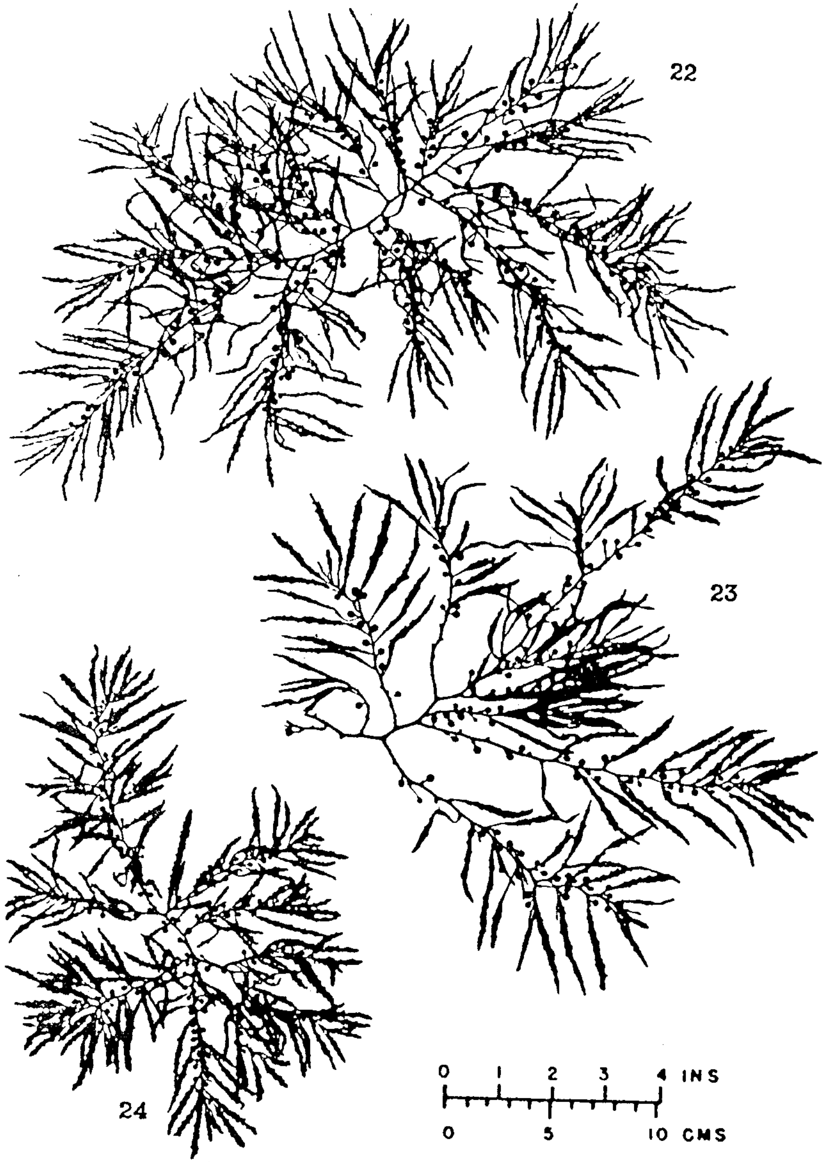


Figure 16. Silhouette 22: *Sargassum natans* (II) and silhouette 23: *S. natans* (VIII), for comparison with silhouette 24: *S. natans* (IX).

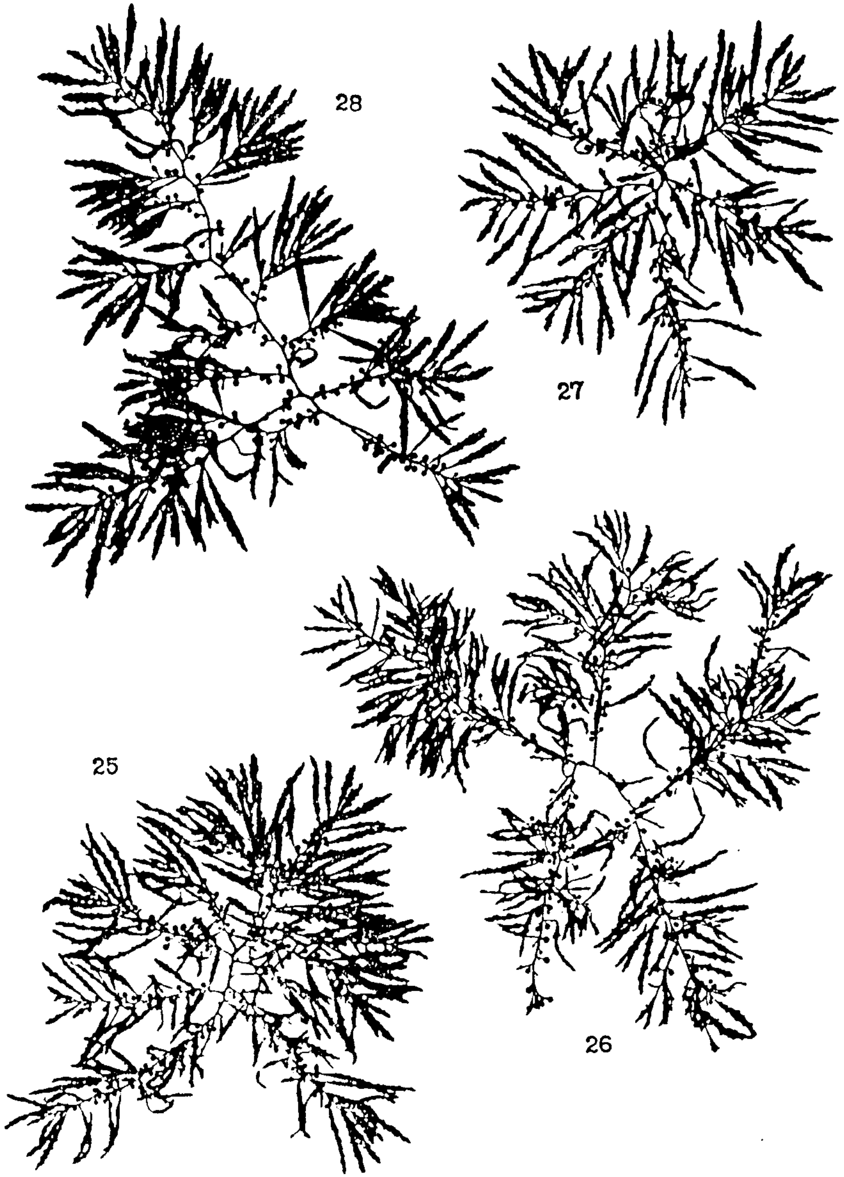


Figure 17. Silhouettes 25-27: *Sargassum natans (IX)*. Silhouette 28: Transition from *S. natans (IX)* to *S. natans (VIII)*. Scale see figure 16.

integrate with *S. natans* (*II*) through such intermediates as that shown in silhouette 11 (figure 13). Leaves 40–45 mm. long, 5–6 mm. wide (Nos. 15 and 17), 6–7 mm. wide (No. 16). Bladders 3–4 mm. diameter, on 1–2 mm. pedicels.

Silhouettes 18–21 (figure 15) finally illustrate various examples of luxuriant *S. natans* (*VIII*) at the end of this series. Leaves 35–45 mm. long (Nos. 18–20), 45–55 mm. long (No. 21), 5–6 mm. wide (Nos. 18–20), 6–7 mm. wide (No. 21). Bladders 3–4 mm. diameter, on 1–2 mm. pedicel. No. 18 with one slightly alate pedicel 4 mm. long with one denticulation.

Silhouette 22 (figure 16) shows a comparatively densely foliate variety of *S. natans* (*II*), with moderate, narrow, sharply dentate leaves and comparatively numerously retained bladders, pointing towards *S. natans* (*IX*). Leaves 45 mm. long, 1–1.5 mm. wide. Bladders 2.5–3 mm. diameter, on pedicels 1–3 mm. long.

Silhouette 23 (figure 16) shows a robust specimen of *S. natans* (*VIII*) of the same general type as that shown in silhouette 9 (figure 12), but with more numerous bladders. Apart from the latter feature, silhouette 23 is here given for its contrast with rather than its resemblance to *S. natans* (*IX*). Leaves 50–55 mm. long, 2.5–4 mm. wide. Bladders 3–3.5 mm. diameter, on pedicels 1–3 (7) mm. long.

Silhouettes 24–27 (figures 16–17) give typical examples of *S. natans* (*IX*), with its small, sharply dentate leaves, dense growth, numerous bladders, etc., which clearly show the actual distinctness of this form from all other members of the *S. natans* series illustrated in this report. Leaves 30–40 mm. long, 2–3 mm. wide. Bladders 1.5–2.5 mm. diameter, on pedicels 1–2 mm. long.

In silhouette 28 (figure 17), we have a specimen caught in the same haul as the others shown in figure 17 which combines the profuse foliation and numerous small bladders of *S. natans* (*IX*), with a leaf-size and form pointing clearly towards such representatives of *S. natans* (*VIII*) as that shown in silhouette 11 (figure 13, page 31) while its relations are still further complicated by the presence of long, foliate, distal spikes on several of its bladders. Leaves 40–45 mm. long, 2–4 mm. wide. Bladders small, 2–2.5 mm. diameter, on 1–2 (4) mm. pedicels.

S. Fluitans SERIES

The group here referred to under the taxonomic designation of *S. fluitans* Börgesen seems much simpler than the *S. natans* series in the sense that its variations, apart from the dimorphism to be described below, seem to be individual rather than serial and systematic. The entire range of individual variations with reference to leaf form, etc. in *S. fluitans* is also narrower than the range of serial variations in *S. natans*. It is therefore possible to give the general definition of the *S. fluitans* series a more positive form than that given in the diagnosis of *S. natans*, as follows:

Receptacles absent. Branches with thorns, frequently extending to the pedicels of the bladders, but sometimes quite scarce and mainly observable only

near the actively growing distal ends of the branches. Leaves[1] typically 4–5 mm. apart, usually simple, very rarely forked, their width usually 3–5 mm., normally contained about 5–12 times in their length, which usually varies between 20 and 60 mm.[2] Cryptostomata almost always present at least on some of the leaves, sometimes on all, but always small, inconspicuous and irregularly arranged. Costae distinct, but without conspicuous ridge. Edges of leaves vaguely dentate to strongly serrate.

The separate plants of *S. fluitans* occur chiefly in two typically quite distinct forms, of which we shall here begin with the description of the form designated as *S. fluitans* (*X*).

In its typical form *S. fluitans* (*X*) is most conspicuously characterized by its general habitus which is that of a dense, globular or oblong cluster, of quasi-radially arranged, short, subequal, richly foliate, branches. The overall length of such plants is usually only about 20 cm. or less and rarely exceeds 30 cm. in any direction. The branches on the *average* originate less than 6 mm. apart. The leaves are relatively short, usually less than 50 mm. long,[3] and typically only about 30 mm. or less, although average leaf lengths approaching 50 mm. is occasionally characteristic of specimens with a general habitus entirely typical of *S. fluitans* (*X*). The leaves are thick, comparatively very firm, and relatively straight and flat, without conspicuous morphological twist. In fresh material they also differ from the leaves of *S. fluitans* (*III*), in being of a dark olivaceous green color, instead of yellowish brown. Cryptostomata seem to be always present, and indeed fairly numerous, although inconspicuous and irregularly arranged. The edges of the leaves are typically less sharply serrate than in *S. fluitans* (*III*), although the serrations are extremely variable and always distinct. While most of the bladders are smooth at the distal end, typical specimens often show a number of aristate vesicles with the apical point sometimes continued into a fully formed leaf up to 20 mm. length. The pedicels of the bladders also frequently show an unusual length (up to 9 mm., at least), although their length is normally only about 2–5 mm. In this *variability* of the vesicles, their pedicels and apical appendages rather than in their usual form *S. fluitans* (*X*) seems to differ from *S. fluitans* (*III*), as it also does by its typically much more abundant cryptostomes and by the other features mentioned in the preceding. An epizoan species occurring exclusively on *S. fluitans* (*X*) is mentioned by Burkenroad on page 23.

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[1] Only leaves sufficiently far below the distal end of the branch to be considered fully developed are taken into account in this description.

[2] As also in the *S. natans* series, exceptionally long leaves exceeding 80 mm. length are occasionally found in the basal portions of the plant (see figure 18). These exceptional leaves would appear to have had an increased growth in length only and therefore show a very high ratio between width and length (1 : 20 or more). But since there are rarely more than a single or a couple of these long leaves present on any single specimen, they do not contribute significantly to its general appearance.

[3] Leaves of exceptional length occur also in this form.

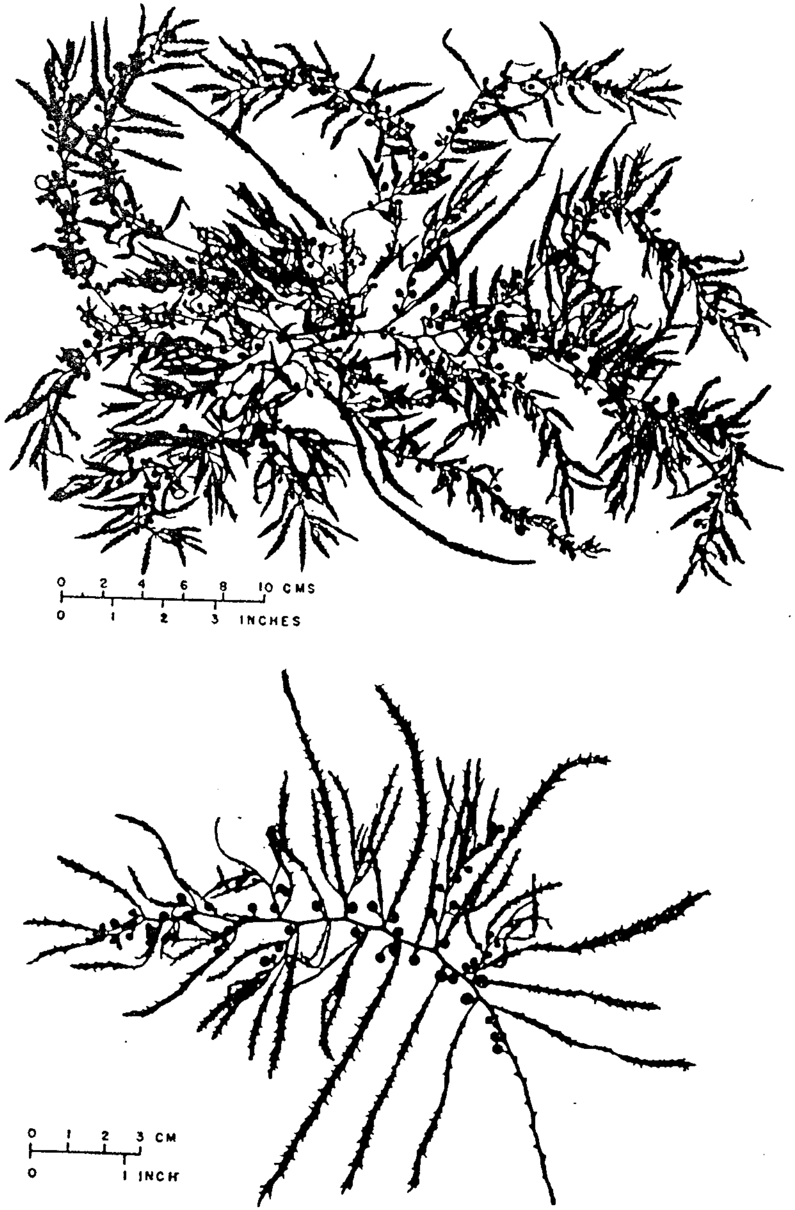

Figure 18. Herbarium silhouettes showing abnormally produced leaves in *Sargassum fluitans* (*III*), above; and in *S. natans* (*II*), below.

From its more typical form described in the preceding and illustrated in fig. 4, *S. fluitans* (*X*) shows numerous individual variations illustrated in figs. 19–20.

Figure 19 shows various specimens of typical *S. fluitans* (*X*) of more or less circular or slightly oblong[1] shape without differentiation of major (main) and minor stems or primary branches. Considerable variation of leaf form and size may be noted even within this relatively homogeneous group. Silhouette 29, overall length 37 cm.; leaves 25–40 mm. long, 3–4.5 mm. wide. Bladders 4–6 mm. diameter, circular or ovate, a few with small distal spikes, one with distal spike broadly foliate. Silhouette 30, 15 cm. overall, leaves and bladders as in No. 29. Silhouette 31, length 20 cm., represents a variety with slightly more slender growth. Leaves usually not over 4 mm. wide, 30–40 mm. long, with more distinct midrib than in the forms with blunter leaves. Silhouette 32, 30 cm. overall, has generally smaller leaves than the other specimens shown in figure 19, the length of the leaves being predominantly less than 25 mm., although a few reach 35 mm., their width predominantly 2–2.5 mm., exceptionally 4 mm. Silhouette 33, on the other hand, shows a long-leaved variety of *S. fluitans* (*X*), with leaves 45–60 mm. long but only 2–2.5 mm. wide.

Figure 20 shows various examples of *S. fluitans* (*X*) of looser growth, pointing towards *S. fluitans* (*III*). These specimens all have naturally fairly flat, straight and thick leaves and would all, on the basis of fresh material, without hesitation be sorted with *S. fluitans* (*X*). Silhouette 34 shows the large, strongly ovate bladders (up to 6 mm. largest axis) which seem particularly common on the more luxuriant plants of *S. fluitans* (*X*). The leaves are 35–50 mm. long, 3.0–4.5 mm. wide, with not very strongly serrate margins. A bifurcated leaf is conspicuously shown. Silhouette 35 agrees with 36 in foliage, etc., differing only in its general habitus. Silhouette 36 shows a rather aberrant form with straight, narrow, only weakly serrate leaves, 35–40 mm. long and 2–2.5 mm. wide. The type of growth is also unusual, and the cryptostomata slightly less inconspicuous and more regularly arranged than normal for *S. fluitans* (*X*). It is not without hesitation that this plant is included in the *S. fluitans* (*X*)? series, not as part of its intergradations but rather as a divergent extreme variety.

Silhouette 37 shows a nearly isodiametric, fairly typical, though rather loosely grown, plant of *S. fluitans* (*X*) in which one single branch has been produced to assume the appearance of *S. fluitans* (*III*). With regard to general habitus, the "basal" part of No. 37 compares with such specimens as No. 35. With regard to leaf size, form and texture it is in perfect agreement with No. 31. Leaves 25–35 mm. long, 25–35 (40) mm. wide. While the produced branch if

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[1] The oblong shape of the two larger specimens is due to a selection of plants of this form to fit the herbarium sheet rather than to a normal preponderance of elongate over iso-diametric form with larger size.

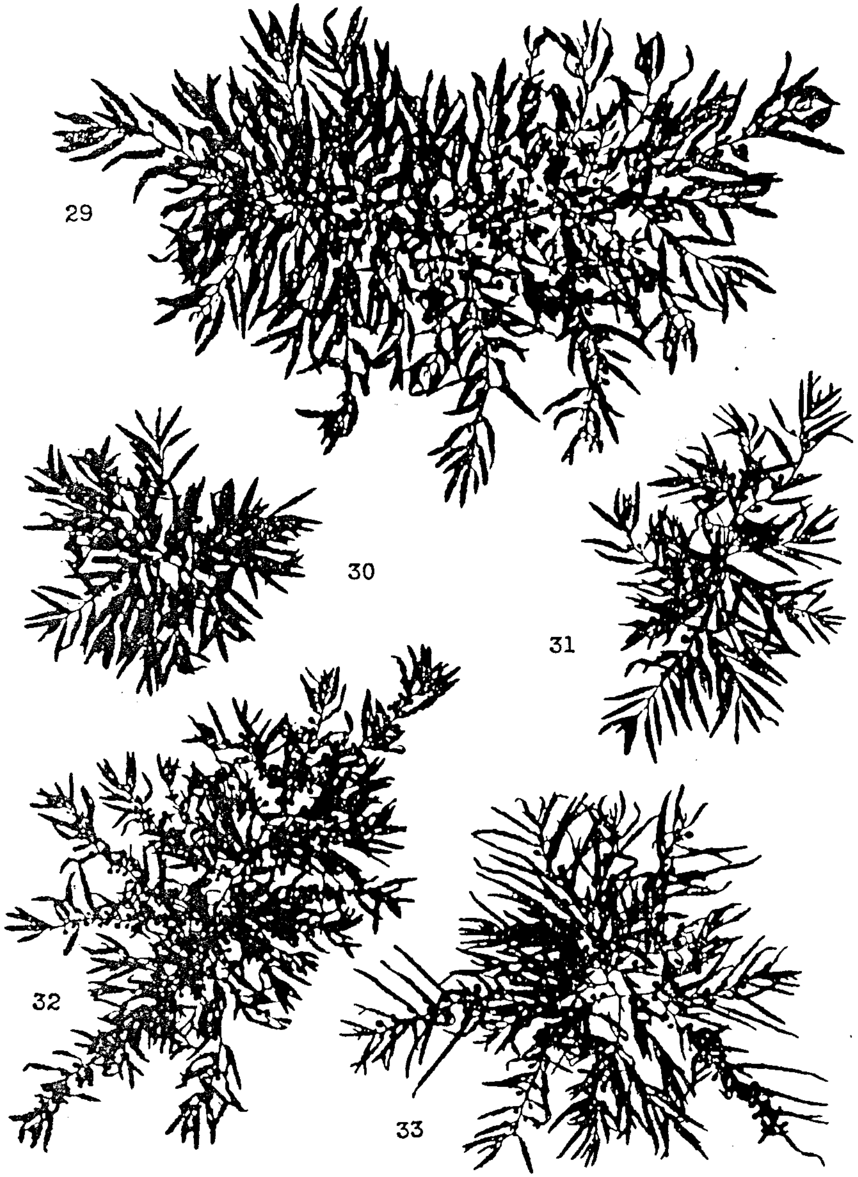

Figure 19. Silhouettes 29–33: *Sargassum fluitans* (*X*). Typical dense growth. Scale see figure 21.

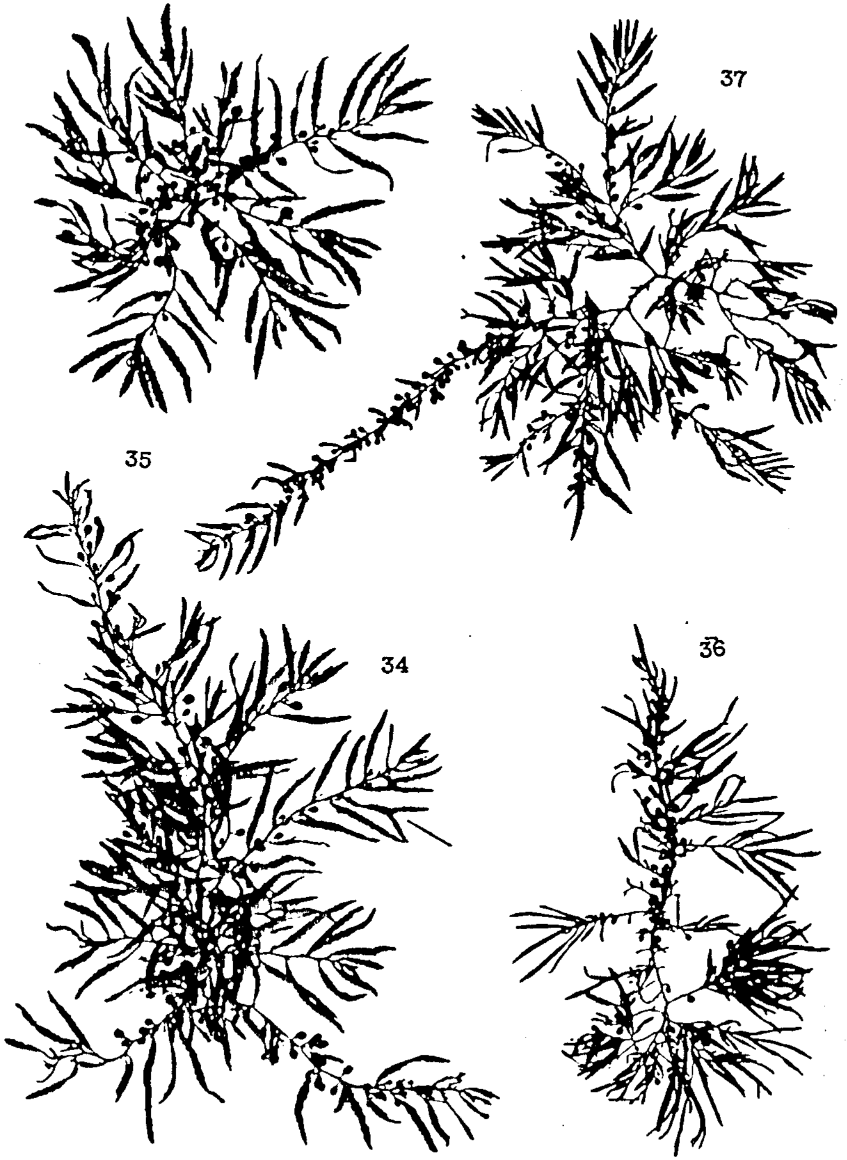

Figure 20. Silhouettes 34–36: *Sargassum fluitans* (*X*). Looser growth. Silhouette 37: *S. fluitans* (*X*) and *S. fluitans* (*III*) on same plant. See text. Scale see figure 21.

separated from the basal branches would unhesitatingly have been classified as a fragment of some such typical representative of *S. fluitans* (*III*) as that shown in silhouette 43.

Several larger examples (too large for herbarium preservation) in which still more fully developed and branched stems of *S. fluitans* (*III*) are organically connected with still more typical, dense clusters of *S. fluitans* (*X*) are available in liquid preservation.

S. fluitans (*III*) is typically very easily distinguished from *S. fluitans* (*X*) by its loose, open and stringy general habitus, dominated by one or several long main branches sharply differentiated from the much shorter and subordinate secondary branches which generally originate *on the average* more than 6 mm., typically around 7 mm., apart. The plants may reach an overall length between ends of main branches approaching 1 meter and usually occur in sizes of 30 cm. or more in any region of vigorous growth. The leaves are usually longer than in *S. fluitans* (*X*), generally more than 30 mm., typically 40–60 mm. long in well-developed specimens, with the width (typically 4–5 mm.) usually contained 8–12 times in their length. The leaves are crisp and firm but not so thick as in *S. fluitans* (*X*), typically conspicuously twisted and curled, the twisting and curling being more pronounced the more luxuriant the general appearance of the plant. Color in fresh plants yellowish brown (light tobacco brown). Cryptostomata often absent from single leaves but very rarely absent from all leaves on a plant of reasonable size. They also commonly occur throughout the foliage but are usually much fewer on each leaf than in typical representatives of *S. fluitans* (*X*). Edges of leaves usually sharply serrate. Bladders without spikes, smoothly rounded at apical end, on short pedicels, normally less than 3 mm. long.

The specimens classified as *S. fluitans* (*III*) also show a considerable diversity of individual variations particularly with regard to general appearance of foliage and abundance of thorns on the stems.

Figure 21 shows various luxuriant examples of typical *S. fluitans* (*III*). Leaves 45–60 mm. long (35–45 mm. in No. 40), and 4–5 mm. wide.

Figure 22 illustrates the intergradations toward smaller and narrower leaves, and variations in general habitus. In No. 42 leaves are 35–45 mm. long, and about 4 mm. wide. In No. 43, 35–40 mm. long, and 3–3.5 mm. wide. On No. 44 about 35 mm. long, and 2.5–3 mm. wide.

Figure 23 shows several examples of the finer-leaved forms of *S. fluitans* (*III*) (Nos. 45–48) and compares these with specimens of the *S. natans* series of the same general appearance. No. 45 is a densely foliate branch of *S. fluitans* (*III*), with leaves 30–40 mm. long, 2.5–3.5 mm. wide. No. 46 is a quite common, slender and rather sparsely foliate type with leaves about 35 mm. long, 2–3 mm. wide. The actual specimen represented in silhouette 47 is in some respects intermediate between *S. fluitans* (*III*) and *S. fluitans* (*X*) with regard to foliage

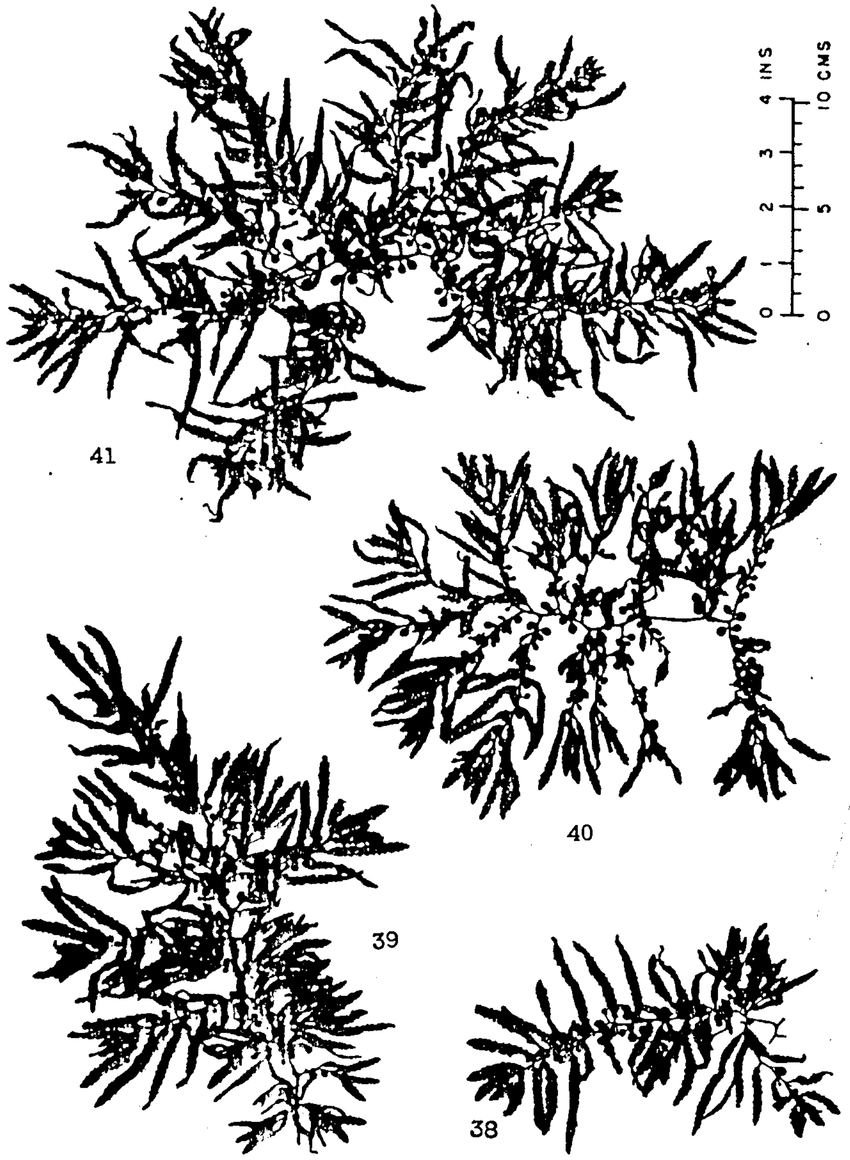

Figure 21. Silhouettes 38–41: *Sargassum fluitans* (*III*). Luxuriant, broad-leaved specimens.

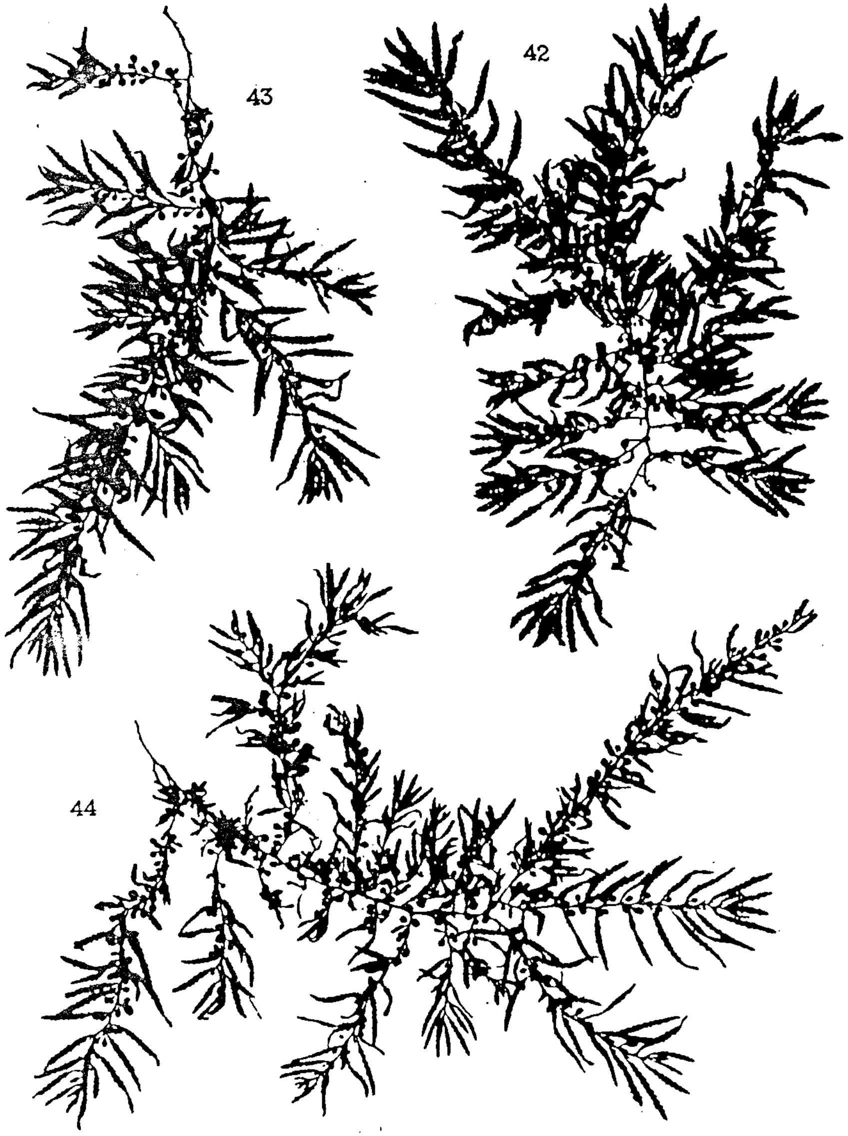

Figure 22. Silhouettes 42–44: *Sargassum fluitans* (*III*). Slender, narrow-leaved specimens. Scale see figure 21.

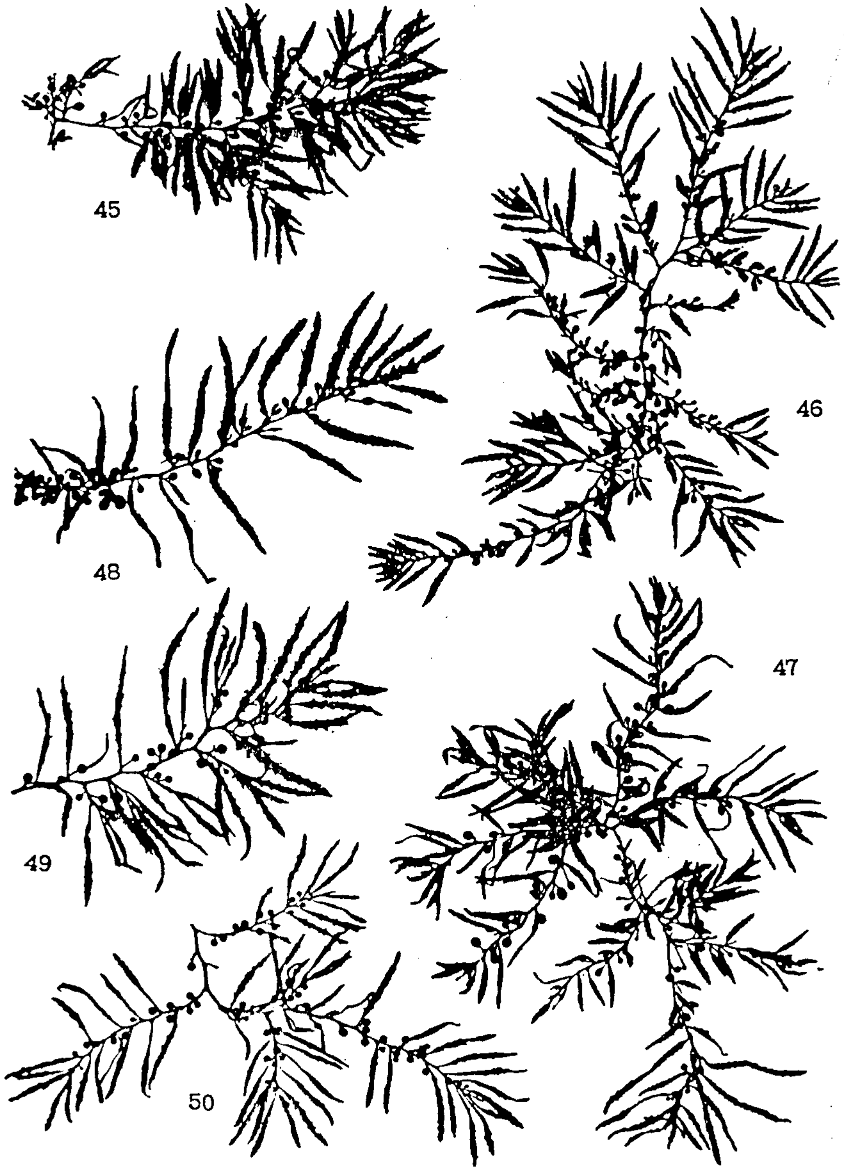

Figure 23. Silhouettes 45–47: Slender specimens of *Sargassum fluitans* (*III*) for comparison with similar specimens of *S. natans* (*II–VIII*) shown in silhouettes 49–50. Scale see figure 21.

and general type of growth. Leaves 35–50 mm. long, 2–2.5 mm. wide. No. 48 is a single stem of a very long-leaved *S. fluitans* (*III*), presented for comparison with a long-leaved branch from the *S. natans* series shown in silhouette 49. Leaves (of No. 48) 50–60 mm. long, 3.5–4.5 mm. wide.

Silhouettes 49–50 belong to the *S. natans* series (narrow-leaved (*VIII*), or broad-leaved (*II*)). In No. 49 leaves are 50–65 mm. long, 3–4 mm. wide. In No. 50 leaves are about 35 mm. long and 2.5–3 mm. wide. Comparisons of No. 50 with Nos. 46 and 47, and between Nos. 48 and 49 will probably sufficiently illustrate how even the differentiation between *S. fluitans* and *S. natans* may come to seem quite arbitrary for specimens of *S. fluitans* in which only a few minute thorns may be discovered on their stems by close examination. It seems characteristic, particularly of the slender varieties of *S. fluitans* similar to that shown in silhouette 46 (although not true of this particular specimen), that the thorns on stems and branches may not uncommonly be greatly reduced both as to numbers and sizes. This tendency towards a relative smoothness of stems seems associated with a reduced apparent vigorousness of the entire plant, so that a close inspection of each specimen to differentiate between *S. fluitans* and similar members of the *S. natans* series is much more often required in the marginal zones of the pelagic vegetation (as, for instance, in the Gulf of Mexico during the cold season) than in the Sargasso Sea proper, and in the Cayman and Caribbean seas.

PRELIMINARY DISCUSSION OF RELATIONSHIPS

In the preceding we have described how the *S. natans* group forms a single continuous series of intergradations in the manner indicated in our figure. While the derivation of such a series might have occurred from either direction, *S. natans* (*VIII*) is, in the author's opinion, the form most suggestive of benthonic origin both from the point of view of its geographical distribution (p. 66) and its morphological character, which frequently recalls the irregular growth of sessile plants to a much higher degree than does any of the other extremely regular pelagic forms of the *S. natans* series. In this statement the author has in mind the commonly observed lack of equivalence in *S. natans* (*VIII*) between branches of the same order originating near each other from a common stem. Occasionally this lack of equivalence extends beyond a mere difference in size and general appearance between such branches, to a perceptible difference in the form of their leaves. This lack of equivalence between branches of the same order also quite frequently expresses itself very conspicuously in the general appearance of the entire plant by a complete disruption of the pattern of fairly regular and quite gradual decrease in the size of the branches originating along the main stem from its basal to its distal end. In all other forms of *S. natans* adjacent branches from the main stem will usually be found to be of approximately the same general size and appearance and their size will show a gradual decrease towards the tip of the main stem. While this is, of course, also frequently true of *S. natans* (*VIII*), it seems definitely impossible to claim that this is any general rule for that form in anything like the extent to which it is true of the others. Under otherwise equal circumstances such irregularities should suggest orientation in three dimensions rather than to a linear axis in one dimension only.

Without pretending to claim that it amounts to much more than a personal guess, the writer would therefore be inclined to look for the derivation of the entire *S. natans* series through *S. natans* (*VIII*).

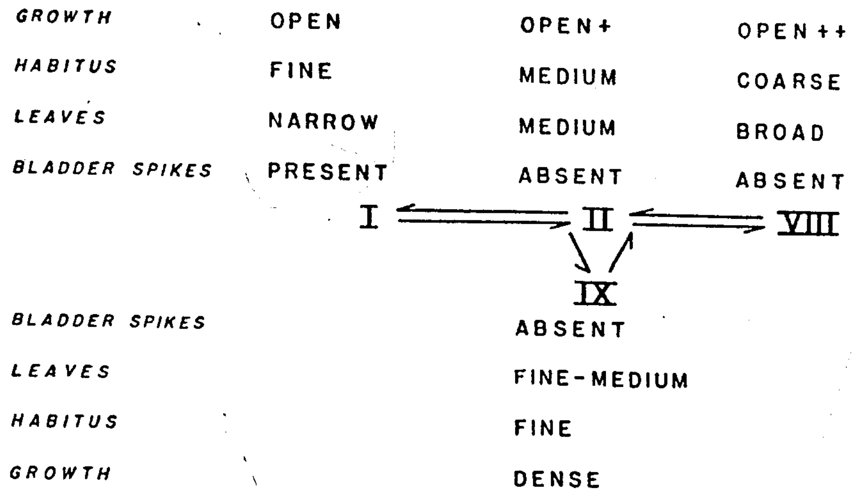

Figure 24. Table illustrating apparent intergradations in *Sargassum natans*. Features given are those of typical representatives of each form.

In the preceding description we have already mentioned that there are cases in which the differentiation between a relatively robust but narrow-leaved *S. natans* (*VIII*) and a slender and nearly smooth-stemmed *S. fluitans* (*III*) also seems to become quite arbitrary. It is probably unlikely that the true *S. natans* (*VIII*) could actually have been derived from *S. fluitans*, and the author merely wishes to state that he has not been able to satisfy himself that this possibility can be entirely excluded on a morphological basis, and that confusions may occasionally arise in the identification, particularly of smaller specimens or fragments, on the borderline between *S. natans* (*VIII*) and *S. fluitans* in general appearance.

In the *S. fluitans* group we also find a considerable variation in general appearance which has been sufficiently described in the preceding and only two features remain for discussion here, namely, the interesting dimorphism shown by this species in its floating state and the single fertile specimen which apparently can be referred to this form without serious hesitation.

The dimorphism between *S. fluitans* (*III*) and (*X*) may seem insignificant when described in words and pictures only, but in the fresh material the difference is typically so striking that the two forms were without difficulty segregated for weighing in the routine sorting of the hauls from the beginning of the investigation long before the proper status of *S. fluitans* (*X*) had been established by a more critical examination of long series of samples. Among the healthy weeds in the Sargasso Sea proper, *S. fluitans* (*X*) could, as a matter of fact, undoubtedly have been sorted from the rest blindfolded, by a mere feeling of its form and the characteristic stiffness or crispness of touch by which it differs from the thinner leaves and more flexible form of *S. fluitans* (*III*). The general differences between *S. fluitans* (*III*) and (*X*) have been sufficiently described on p. 37. Occasionally we find a perfectly typical branch of *S. fluitans* (*III*) with its thinner, larger and more twisted leaves, its looser growth and more open foliation, dangling from an otherwise quite typical *S. fluitans* (*X*), with its dense globular growth of short, stiff branches, densely foliate with stiffer and less twisted leaves than those of *S. fluitans* (*III*), and closer examination of this stem of *S. fluitans* (*III*) reveals that it is actually a true branch from the clump of *S. fluitans* (*X*). An only moderately well developed example of this sort is shown in herbarium silhouette No. 37, fig. 20. Other examples in which the branch of *S. fluitans III* is larger and still more completely characteristic of this form, while the basal clump of *S. fluitans* (*X*) is also denser and more typical of its own kind are available in liquid preservation. In view of the scarcity with which these two forms of *S. fluitans* are thus found in organic continuity with each other, it is evident that when an *S. fluitans* (*III*) branch is formed it must break off very early and easily from the *S. fluitans* (*X*) clump. It also seems probable, in view of the generally 5–20 times greater amount of *S. fluitans* (*III*) found in the Sargasso Sea, that this form, once it has separated from *S. fluitans* (*X*), continues to grow and to multiply by fragmentation true to its own type.

If we consider the relationship between the long branches of *S. fluitans* (*III*) type and the short, crowded branches of *S. fluitans* (*X*) form in the plants in which both occur together, the situation obviously offers great similarities with the relationship between the long distal shoots and the ring of short basal branches so commonly observed in various forms of sessile *Sargassum*, particularly among the more robust species.

It therefore seems fairly reasonable to see a certain parallelism between the dimorphism of the pelagic *Sargassum fluitans* and the dimorphism between distal and basal shoots within a single specimen among the sessile species. If this parallelism is more than a figure of speech, it patently requires some explanation. While the writer is not able to suggest any definite theory bearing upon this problem, he feels that reference might be made to the fact that once the long distal branches have split off from the basal clump, the latter will, as it rolls around in the turbulent motions of the sea, only be able to maintain a radial orientation with reference to some point in its middle which becomes its average center of rotation; while the long distal branches (*S. fluitans* (*III*)) must tend to rotate around the *axes* of their main stems, and if they also have long lateral branches flattening out at the surface due to the buoyancy of their bladders, they should indeed tend to become relatively stable with reference to their position relative to the sea surface. If the ability to maintain a fairly steady axial orientation with reference to light, gravity, etc. favors growth of the *S. fluitans* (*III*) (distal shoot) type, and the complete lack of this ability favors the development of the basal shoot habitus of *S. fluitans* (*X*), we shall therefore be able to understand why either form tends to become self-perpetuating within its own type of growth after the plant has become pelagic and the two types of branches have become separated from each other by fragmentation.

FERTILE ATTACHED SPECIMEN OF *S. Fluitans*

A complete plant with fertile branches and a basal holdfast attached to what would appear to be a rather weathered piece of root (mangrove-root ?) was obtained in haul No. 133, on August 27–28, 1934, in average latitude 37° 50′ N. and longitude 69° 25′ W. The sterile parts of this plant fall completely within the usual range of variation in pelagic representatives of *S. fluitans*, with regard to all features of leaves, bladders, thorniness of stems, etc., even to the great paucity, irregularity, and inconspicuousness of the cryptostomata. The sterile branches, if collected separately, would therefore unhesitatingly have been referred to this species, and there is accordingly little reason to hesitate about identifying the entire plant in the same manner. It is, on the other hand, not possible to obtain an at all satisfactory agreement with any description of the currently recognized benthonic species of Sargassum from the Atlantic, and the name of *S. fluitans* Börgesen is therefore retained. While the general character of the plant points towards an affinity with the *Sargassum vulgare* group, the writer has, at least tentatively, come to the conclusion that this group in itself probably constitutes a very heterogeneous assembly of forms among which several taxonomically distinct units will probably become recognizable when more adequate collections are obtained. A diagnostic description of the specimen in hand follows:

Stems rather coarsely muriculate, with thorns extending on to the bases of some of the larger leaves and also occurring between the receptacles on a few of the ultimate receptacular branchlets. Leaves on ordinary branches, or on short spur branches of second or third order; subsessile, conspicuously assymetric at the base; fully developed leaves about 30–35 mm. long and about one-fifth as

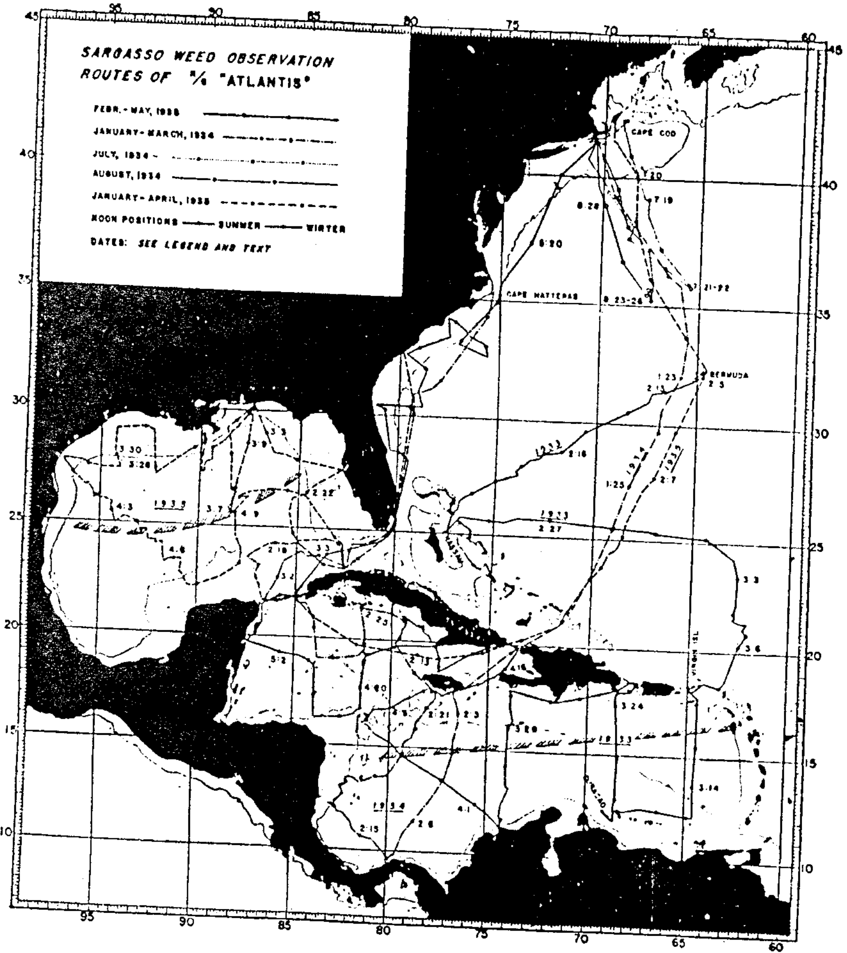

Figure 26. "Atlantis" routes over which Sargassum weed collections have been made. Dots mark noon positions with dates given at intervals (e. g. 3: 14 to be read: March 14).

DOMINANT FORMS

Among the eupelagic forms which altogether constitute more than 99 per cent of the total pelagic vegetation of the investigated portion of the Sargasso Sea proper, *Sargassum natans* (*I*) (*S. natans ciliata* Börgesen) and *S. fluitans* (*III*) far outweigh all other varieties in quantitative significance, comprising together between 89 and 99 per cent of the total. *S. fluitans* (*X*) and *S. natans* (*II*) (*S. natans typica* Börgesen) are next in importance in the order mentioned, the former occasionally, the latter only very rarely occurring even on the same order of magnitude of abundance in single hauls as the two varieties first named. Certain gross features of distribution would seem to be shared in common by all forms of the *S. fluitans* and *S. natans* series, except *S. natans* (*VIII*). These (see figure 26) consist of a common southern boundary of occurrence within the Caribbean along a line drawn from about 16°–17° northern latitude at the eastern end to about 14° in the west; in a very sharply marked change in abundance from the scarcity of the Caribbean region inside of the Antillean chain of islands to the relative richness of the Sargasso Sea proper outside; and in the occurrence of a secondary maximum in the inner portions of the Gulf of Mexico.

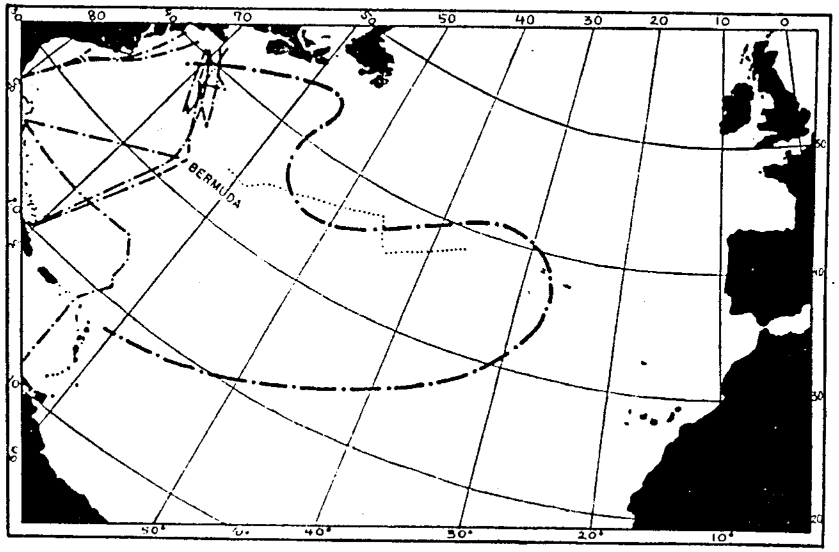

Figure 27. "Atlantis" routes (dot and dash) inserted in the contour line of the Sargasso Sea boundary drawn according to Winge (1923, Fig. 2). Dotted line indicates course over which weed was collected with dipnet by Mr. D. Spencer Berger during the summer of 1934.

CARRIBBEAN AND CAYMAN SEAS

The location of the southern boundary of significant occurrence of pelagic weeds within the Caribbean has been determined by visual observation over about 900 route miles on four crossings of the empty area in 1933 (see figure 26), and by 648.6 towing miles with net empty[1] of eupelagic weeds (except *S. natans* (*VIII*)) over about 800 route miles in 1934.

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[1] Within the first 100 miles south of the boundary marked on figure 26 isolated small sprigs of eupelagic weeds too scarce for quantitative measurements are occasionally obtained, but still farther south even such rare fragments are totally absent from all hauls (except *S. natans* (*VIII*)). That scattered weeds must occasionally spread beyond the normal boundary of pelagic vegetation is of course obvious.

Between this southern boundary of weed occurrence and the Yucatan Channel the Caribbean area includes about 375,000 square nautical miles.

The failure of the pelagic vegetation to penetrate southward into the Caribbean Sea is in excellent agreement with the findings of Nielsen (1925) and of Parr (1937, p. 85), showing that the surface water of the Caribbean is mainly or entirely of southeastern origin, while the Sargasso Sea water only penetrates into the Central American basins at intermediate depths in the maximum salinity layer.

The change in abundance of pelagic weeds per mile from the Sargasso Sea proper to the Caribbean, which occurs abruptly at the various passages between the Antillean Islands, is not a mere matter of differences in precise amounts but one of differences in the order of magnitude of weed abundance, the average quantities per mile found inside of the Caribbean region north of the southern boundary of weed distribution (91.7 towing miles in 1933; 911.6 towing miles in 1934; 540.7 towing miles in 1935) being for both of the dominant pelagic forms (*S. natans* (*I*) and *S. fluitans* (*III*)) less than one-tenth of the averages obtained in the Sargasso Sea proper (see table on page 59). From the records for 1934 it would appear that the relative difference between Caribbean and Sargasso Sea abundance in that year at least was even much greater in the case of *S. natans* (*I*) (ratio 50 : 1) than in the case of *S. fluitans* (*III*) (ratio about 15 : 1). The explanation of this geographical difference in *relative* distributions of the 2 species in 1934 is not clear, but it is evident from our observations of the great variations in local abundance over short distances within the Sargasso Sea proper, as shown by the fluctuations in pounds per mile in successive hauls, that chance distribution of the pelagic weeds in the regions near the various entrances to the Caribbean, and chance variations in winds and currents as well, must play a very important part in the quantitative relationship between Caribbean and Sargasso Sea vegetation, and that this relationship can therefore not be expected to show any great degree of constancy from time to time.

"The pelagic weeds of the Caribbean and Cayman Seas are generally fresh, healthy and vigorous looking, with no evidence of significant mortality anywhere. Nor do epizoan incrustations, although on the average somewhat more abundant than in the Sargasso Sea, ever seem to reach an intensity which would constitute a threat to the buoyancy and the survival of the weeds."

GULF OF MEXICO

In the secondary region of abundance in the inner portions of the Gulf of Mexico (see figure 26) the quantities of weeds per mile (696.9 towing miles, March–April, 1935) reach or approach the order of magnitude of the quantities observed in the Sargasso Sea proper, without reaching quite to the same average amounts. As we may see from the table on page 59 *S. natans* (*I*) accounts for 87 per cent of the eupelagic weeds, and among the remaining 13 per cent, *S. natans* (*VIII*) and *S. fluitans* occur in about equal quantities. Holobenthonic weeds are surprisingly rare in comparison with their occurrence in the Caribbean and the Straits of Florida in similar semi-neritic waters, being far too scarce for quantitative recording.

As shown on our map the secondary region of abundance includes about 90 thousand square nautical miles; with an average of about 1 ton per square mile (see table, p. 59) its total floating vegetation at the time of observation may therefore be estimated in rough approximation at about 90,000 tons wet weight.

That there should be an accumulation of floating weeds in the inner portions of the Gulf is natural to expect when we remember that the transportation of these plants must be as much, if not more, influenced by winds as by ocean currents, and that the winds over the Gulf of Mexico and adjacent waters have a prevailing easterly component at all times of the year. There would thus be a general tendency for weeds floating in through the Yucatan Channel to be driven into the Gulf in a westerly or northwesterly direction, and to accumulate there in the northwesterly portion, even though the waters of the Caribbean current turn sharply to the right and flow directly out through the Straits of Florida (Parr 1935).

The secondary maximum in the Gulf of Mexico is entirely separated from the Sargasso Sea proper without any continuity of abundance through the intervening region (660.8 towing miles in the southwestern part of the Gulf and in the Straits of Florida, April 1935). This complete segregation of the two communities of abundant pelagic vegetation is further confirmed by other evidence from the character of the weeds themselves and their epizoan fauna, as we shall immediately see.

Compared with the vegetation of the Caribbean and the Sargasso Sea proper, the eupelagic weeds of the secondary maximum in the Gulf of Mexico were, at least at the time of sampling (March–April, 1935), of a relatively unhealthy appearance throughout. Of the three varieties above mentioned, *S. fluitans* shows the effects of the presumably adverse conditions in the Gulf even more strongly and more generally than the other two, being present chiefly in the form of small, chopped fragments of only a few inches length, while complete plants are relatively very scarce. In the case of *S. natans* (*VIII*) larger plants are much more frequent than in *S. fluitans*, but small fragments also abound, and a majority of the larger pieces bear evidence of a more or less extensive loss of leaves, bladders and branches. Of the three eupelagic forms *S. natans* (*I*) may perhaps appear to be the variety most, or longest, able to withstand the adverse circumstances, although this distinction is very difficult to draw. Except in the northwestern boundary zone, this form is usually comparatively fresh in its most distal portions, while the proximal parts generally show strong evidence of degeneration and decay to an extent only rarely seen in other waters. The prevailing size of plant also differs less from the normal in the case of *S. natans* (*I*) than in the case of the other two varieties just discussed.

Towards the northwestern boundary of the secondary maximum, however, all three varieties seem to reach an apparently dying state together in which *S. natans* (*I*) also breaks up, loses the remnants of its distal freshness, and suffers extensive losses of leaves and bladders along with the other two forms. It may be mentioned at this point that perhaps due to mechanical rather than physiological strength, the largest and least mutilated pieces found at the extreme northwestern boundary generally belong to *S. natans* (*VIII*).

Parallel with the deterioration of the plant itself, we find a greatly increased epizoan infestation of the floating weeds in the secondary maximum, unequalled anywhere else except in isolated instances. This infestation also reaches a maximum at the northwestern boundary particularly in regard to heavy incrustations by such forms as *Membranipora* and it is evident that the weight of these incrustations here very frequently must cause the plants or plant fragments to sink from the surface and may perhaps occasionally do so throughout the secondary maximum, contrary to what we have found in the Caribbean and the Sargasso Sea proper.

Taken all together the features of the pelagic vegetation in the secondary maximum are so distinct that a random sample could never be mistaken for a sample from any other region studied in the course of these investigations. Geographically the occurrence of vegetation of this type is sharply limited to the inner portion of the Gulf of Mexico with no evidence of a dispersal towards the southeastern region of the Straits from which it might spread to other waters via the Florida current and the Caribbean counter-current following the Yucatan coast to the southward.

The complete segregation of the secondary maximum is moreover suggested by Burkenroad's findings that the epizoan communities associated with the weeds of the secondary maximum are to some extent different from those of any other region, both in their composition in regard to dominant forms and by the presence of various endemic species, including even a separate species of *Sargassum* crab (*Portunus*).

This segregation also confirms the author's earlier conclusion from hydrographic data (Parr, 1935) that there is no significant outward flow of the surface waters from the inner Gulf of Mexico to the Straits of Florida (at least during the winter season). If such outflow did occur at a significant rate with reference to the accumulation of floating weeds, every period of calm (or absence of easterly winds) would see a dispersal towards the Straits of Florida, and it would scarcely be conceivable that such a well-defined maximum could accumulate and maintain its position, if its existence were based upon a precarious balance in a conflict between direct wind drift to the northwest and an underlying permanent tendency for steady currents in the opposite direction.

It is evident from the foregoing that the secondary maximum in the Gulf of Mexico can hardly represent an essentially self-sustaining unit of vegetation similar to that of the Sargasso Sea proper (see pp. 68–84), but is rather to be regarded as a comparatively stagnant accumulation of slowly perishing weeds deflected from the surface drift of the Caribbean current on its passage from the Yucatan Channel to the Straits of Florida (see Parr, 1935). A relatively high mortality is apparent from the character of the weeds themselves, particularly in the northwestern portion of the maximum during the period of sampling, and can further be deduced from the fact that the strict confinement of the weeds and their characteristic epizoan fauna to the inner portions of the Gulf clearly shows that this secondary maximum of pelagic vegetation has no significant outlet to adjacent regions and that its mortality must therefore on the average compensate for the additions received from Caribbean waters.

It should be mentioned at this point that *S. natans* (*I*), constituting as we have seen more than 85 per cent of the floating weeds of the secondary maximum, shows no more morphological evidence of recent derivation from the bottom in this region than it does in the middle of the Sargasso Sea proper. On the contrary, it does as a rule, when reasonably well preserved with fresh distal portions, show an even more general lack of plane or axial orientation (see page 46) than the average in the Sargasso Sea, being usually of a quite regularly globular habitus. On general appearance one would therefore without much hesitation or doubt judge it to be an old pelagic weed, and the author is quite confident that the possibility of significant local sources may be completely disregarded. In regard to the other two relatively insignificant weeds, it is more difficult to have a definite opinion on this point, partly due to their poor condition in the secondary maximum (*S. fluitans*) and partly for other reasons connected with their general distribution.

Although we have thus come to consider the secondary maximum as a chance aggregation of moribund plants, the fact that an accumulation does occur and that a special epizoan fauna can develop in connection with it and can reach an abundance not seen elsewhere, clearly shows that the process of destruction must even here require on the average a very considerable time. How long must for the present remain an open question.

That the presumably high mortality of weeds in the secondary maximum will probably not be equally distributed over all seasons of the year goes without saying. Undoubtedly the mortality must reach its maximum during the period of minimum temperatures (air and water, see page 81–82) and must then in all probability be even greater than indicated in our material which was all collected after the spring equinox (apart only from a few samples in the presumably healthier southeast corner of the secondary maximum).

Although the loss by mortality (including sinking of overloaded living plants) must be sufficiently in excess of growth increment to balance the addition of drifting plants from the Caribbean, since otherwise the accumulation would become infinite, there is nevertheless every indication in the appearance of the apical points of the weeds in better condition that some slight growth may have been occurring even at the time of sampling, and this growth should be expected to increase during the warm season. It must, on the other hand, probably be during the relatively unproductive winter months with their high mortality that the pelagic vegetation makes its greatest contribution to the layers below. The quantitative importance of the pelagic Sargassa in the total metabolism of the sea must, however, be quite as insignificant in the Gulf of Mexico as in the Sargasso Sea proper for the reasons explained on pages 67–68.

It is probable that the secondary maximum in the Gulf of Mexico may change its location from time to time according to changes in meteorological and hydrographic conditions, but it might be worth mentioning that the Gulf of Campeche, i. e., the southwestern part of the Gulf of Mexico west of the Campeche Bank was found to be free of floating weeds also when visited by the Mabel Taylor expedition in April, 1932.

SARGASSO SEA

Figures 28 and 29 shows the poundage per mile of *Sargassum fluitans (III)* and *S. natans (I)* in the Sargasso Sea proper, i. e. in the region between Bermuda and the Antilles, plotted against the distances traveled, and the length of the individual hauls represented by the width of each column. By the ratio between the blank distances and the distances covered by the black histograms the figures thus also give an impression of the extent to which the region has been sampled with the collector actually operating in the surface. The total towing mileage within the Sargasso Sea proper (south of Bermuda) adds up to 1316 nautical miles distributed on the individual years in the following manner: *1933:* 268 miles; *1934:* 526 miles; *1935:* 522 miles. From these hauls a total of 3090 pounds of pelagic weeds (*1933:* 689.5 pounds; *1934:* 1635.5 pounds; *1935:* 765.5 pounds) were obtained, weighed, sorted and examined.

From the records for 1934 it looked as though there might be a center of abundance of floating weeds in the approximate geographical center of the area investigated, but the figures obtained in 1935 show this feature of distribution to have been only of a transitory character subject to very great changes with time. It is quite evident from our figures that it would be absolutely impossible from the data for 1934 and 1935 combined to attempt to determine zones of various degrees of abundance within the Sargasso Sea proper; but this may in itself be regarded as a very useful and important addition to our knowledge of the pelagic vegetation, since it shows very clearly an extremely high degree of variability in the distribution of weeds from time to time, and enables us to avoid premature conclusions on the assumption of more stable conditions. Considering the scale on which the sampling was undertaken, a discussion of zones of abundance might reasonably have been considered justified on the basis of the data from 1934, in the absence of the records for 1935. As it is, such detailed considerations will have to be postponed until we can begin to work

with averages of observations many times repeated over the same routes. At the present stage we must confine ourselves to a discussion of the gross averages for each year over the entire length of the routes falling with the Sargasso Sea proper. These averages distribute themselves in the manner shown in the table given on the next page.

In the region of the Western Sargasso Sea north of 35° northern latitude (see figure 30, p. 62) we are in the marginal zone of the pelagic weed community. Seasonal fluctuations in the location of the northern limits of survival and other variable factors of the environment in this region obviously make it unwise to attempt any generalizations and computations of averages until much more information may become available than that which is now at hand. The records from this northwestern area are therefore simply presented without further comment in the route-histograms given in figure 30.

AVERAGE AMOUNTS OF EUPELAGIC WEEDS ESTIMATED IN KILOGRAMS PER SQUARE NAUTICAL MILE

	Nassau to Virgin Is.	Bermuda to Turks Is.	
SARGASSO SEA:	1933	1934	1935
S. natans(I)............	2,019	4,863	1,117
S. fluitans (III).........	1,445	458	652
All others...............	85	46	228
Totals, Sargasso Sea:.....	3,549	5,367	1,997
NORTHERN CARIBBEAN:	1933	1934	
S. natans (I)............	68	94	
S. fluitans (III).........	46	30	
All others...............	—	3	
Totals, Caribbean:	114	127	
CAYMAN SEA:			1935
S. natans (I)............			24
S. natans (VIII).........			11
S. fluitans...............			36
Total, Cayman Sea:			71
SECONDARY MAXIMUM, GULF OF MEXICO:			1935
S. natans (I)............			884
S. natans (VIII)........			66
S. fluitans..............			67
Total, Secondary Maximum:			1,017

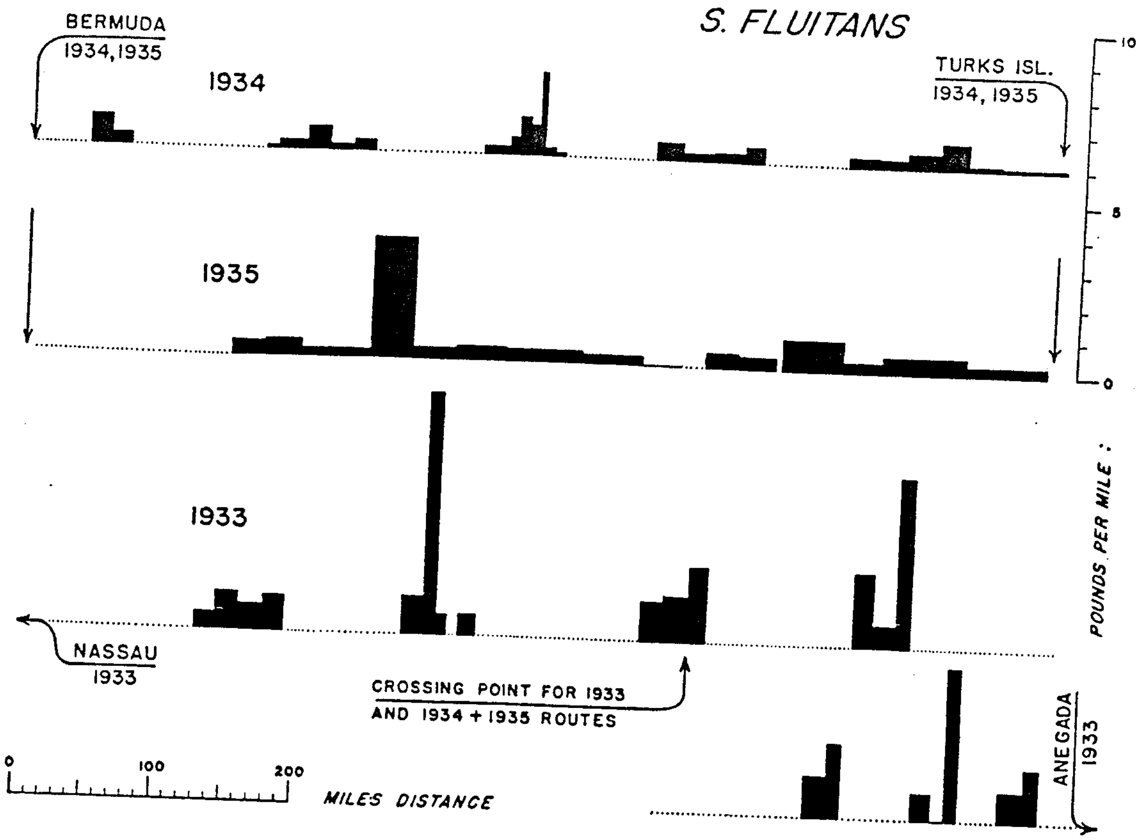

Figure 28. Route histograms showing abundance of *Sargassum fluitans* (*III*) in the Sargasso Sea. See legend of figure 29. Note that scale of pounds per nautical mile is five times as large as that used in figure 29.

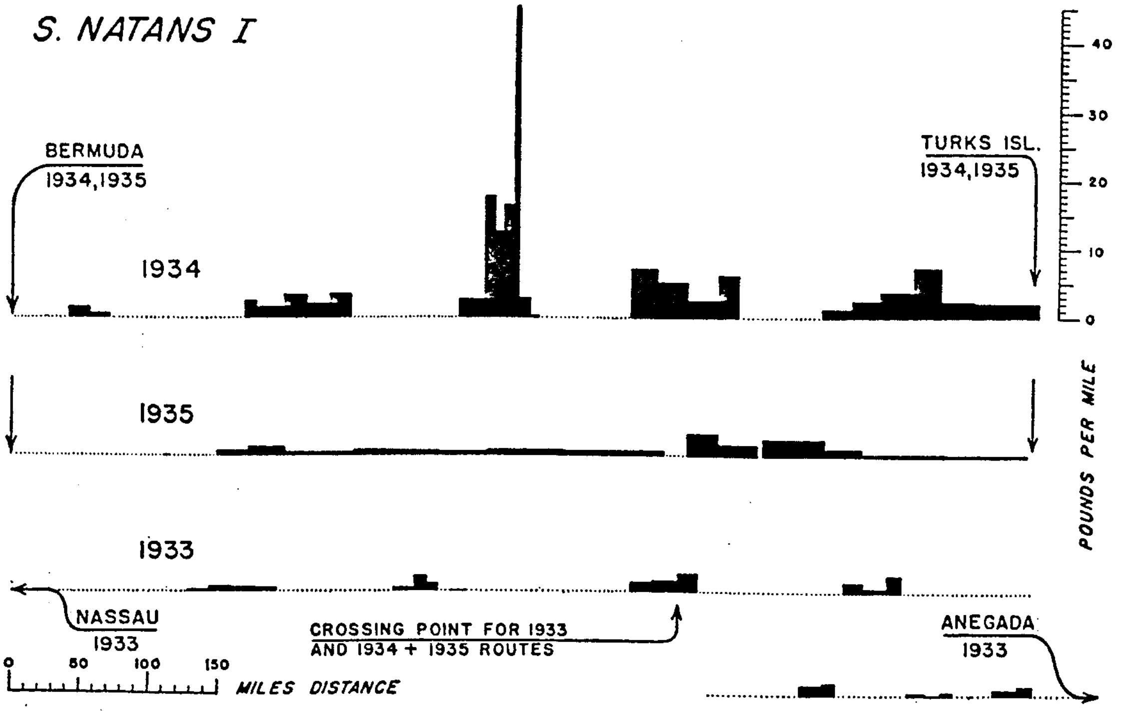

Figure 29. Route histograms for *Sargassum natans* (*I*). Quantity in pounds per nautical mile shown by the heights, length and location of the hauls by the widths and positions of the columns. The 1934 and 1935 routes are virtually identical, while the 1933 route crosses their tracks nearly at right angles at the point shown by arrow. See figure 26.

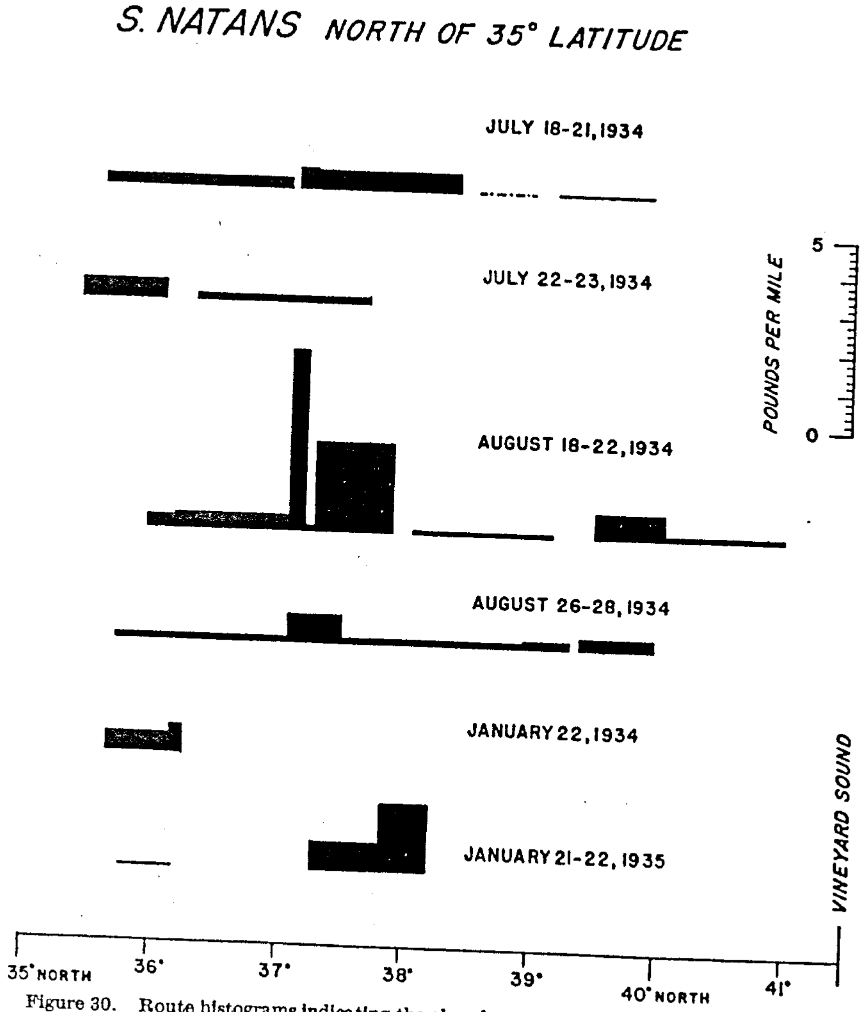

Figure 30. Route histograms indicating the abundance of *Sargassum natans* (*I*) at various times of observation north of 35° northern latitude. Base of histograms measured by latitude instead of route miles.

ANNUAL FLUCTUATIONS

From the table on page 59 we see that the variations observed from year to year are not merely variations in distribution but also variations in the ratio of almost 1 : 3 in the total abundance of weeds over the routes traveled, which were virtually identical in 1934 and 1935. The greatest ratio of variation (almost 1 : 5) is observed in the quantities of *S. natans* (*I*), although this remains by far the most abundant weed in all three years. That these annual variations do not merely appear fortuitously in our records due to inadequate sampling but actually express a real difference in the abundance of pelagic weeds between January 1934 and February 1935 may safely be taken for granted when we consider that the cumulative towing mileage in each year covered a little more than two-thirds of the total distance between Bermuda and Windward Passage. There is, according to the statements of the guard at Fort St. Catherine beach,

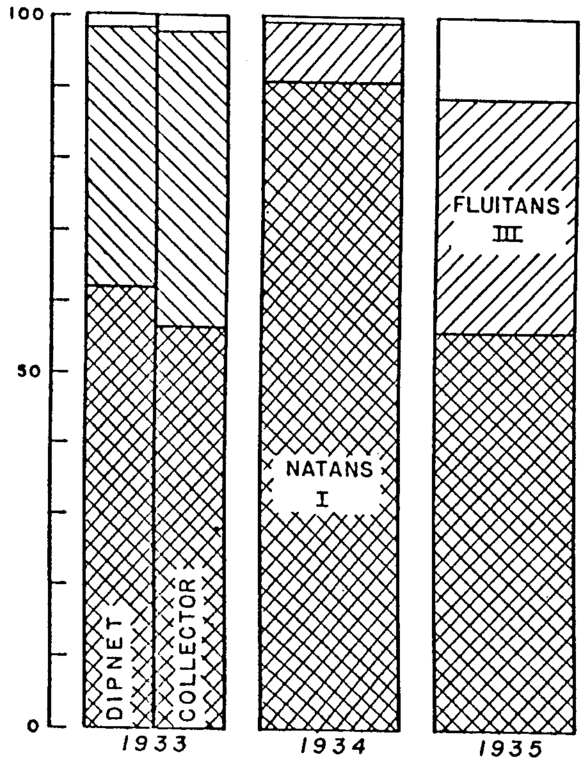

Figure 31. Variations in average relative abundance by weight of *Sargassum natans* (*I*) and *Sargassum fluitans* (*III*) in the Sargasso Sea, south of Bermuda, in 1933, 1934, and 1935.

also corroborative evidence for this conclusion in the fact that much less weed drifted into the beaches of Bermuda in 1935 than in 1934, as judged by the amount of work required to keep the beaches clean during these two years.

So long as no quantitative data are available from other parts of the Sargasso Sea, it is, of course, an open question whether this difference in abundance over the Bermuda-Windward Passage route expresses an annual difference in the total amount of pelagic vegetation in the entire domain of the drifting weeds, or merely indicates a change in their distribution, the centre of abundance being located farther to the eastward in 1935. There is, however, in the author's opinion, no *a priori* reason to assume that such annual changes in abundance might not affect the total vegetation of the entire Sargasso Sea, the combination of growth conditions and loss in the marginal zones being more favorable in some years than in others.

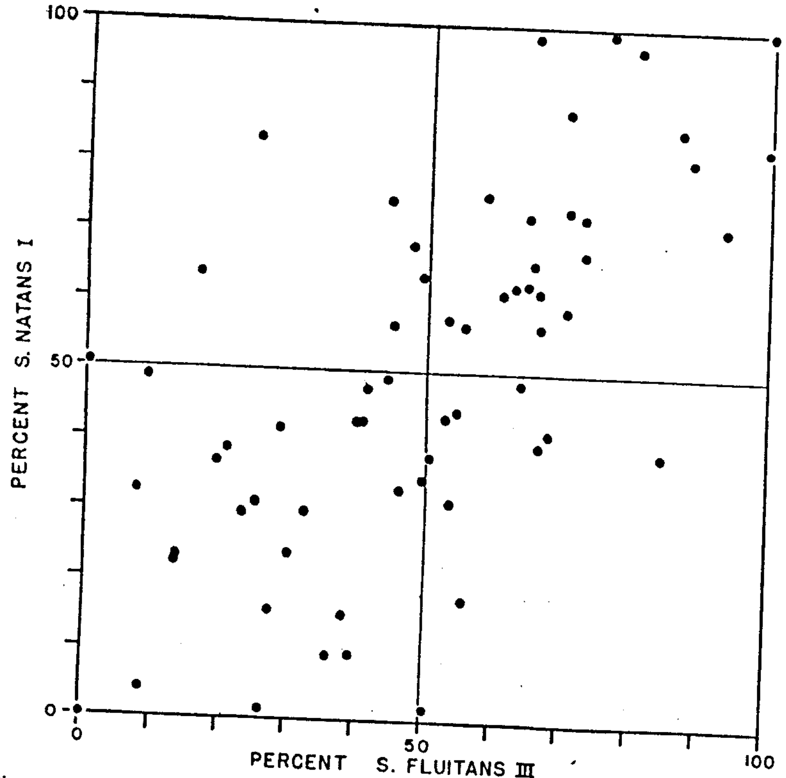

Figure 32. Correlated variations in amount of *Sargassum natans* (*I*) and *S. fluitans* (*III*) on successive hauls. Amount per haul expressed in per cent of the sum of the quantities obtained of each species in the haul considered and in the haul immediately preceding. See text.

CORRELATED VARIATIONS IN WEED DISTRIBUTION

It is perhaps a purely fortuitous circumstance that the year of maximum abundance of *S. natans* (*I*) is the year of minimum abundance of the other pelagic forms over the routes traveled. On this point a comparison might also be made with the relative quantities obtained on the route from Bermuda to Nassau, Bahamas, by random sampling with a dip net (see page 51).

Frequencies of Pelagic Weeds in Per Cent of Total

	1933		1934	1935
	Nassau to Virgin Isl.	Bermuda to Nassau	Bermuda to Turks Isl.	
S. natans (*I*)	56.3%	62.0%	90.7%	55.9%
S. fluitans (*III*)	41.3%	36.4%	8.2%	32.6%
All others	2.4%	1.6%	.9%	11.4%

If we consider the variations in the amounts of the different weeds obtained in the single hauls, we generally find a very definite positive correlation between the quantities of *S. natans* (*I*) and *S. fluitans* (*III*), showing that these forms, as were to be expected, follow the same general laws of local dispersal or aggregation under the influence of winds and currents and do not normally show any tendency to alternate in their occurrence over short distances. This positive correlation in the variations of single catches is shown in our figure 33 where the amount per haul of the two varieties above mentioned is expressed in per cent of the sum of the quantity in the haul considered and that in the preceding haul so that values from 50% to 100% express an increase, and values below 50% a decrease from the preceding catch. This positive correlation between the variations in the quantities of the two species in succeeding single catches refers only, of course, to local variations in distribution and has absolutely no direct bearing upon the problem of possible fundamental differences in their distribution of abundance over larger areas or in point of longer time intervals.

DISTRIBUTION OF LESS ABUNDANT FORMS

In view of the great predominance of *S. natans* (*I*) and *S. fluitans* (*III*) in the pelagic material the preceding discussion of the general quantitative distribution of floating weeds also constitutes a specific discussion of the distribution of these two forms. For the less abundant varieties the quantitative data are not adequate for a discussion of distributions in numerical terms.

In general, *S. natans* (*II*) and *S. fluitans* (*X*) show the same distribution pattern as *S. natans* (*I*) and *S. fluitans* (*III*), being most frequent where the latter are most abundant.

S. natans (*IX*) can, on the other hand, almost be described as endemic of the Cayman Sea east of the main Caribbean current, where it may even exceed the typical *S. natans* (*I*) in single hauls (No. 162). *S. natans* (*IX*) is also occasionally seen downstream as far as the Straits of Florida, but we have no specimens which we would refer to this form from any region beyond the Straits. Its morphological intergradations with the *S. natans* (*I–II–VIII*) series would make it seem very unreasonable to regard *S. natans* (*IX*) as anything but a phenotypic modification. In its typical, and predominant form, it can nevertheless be quite as easily differentiated from the other forms of the *S. natans* series as these can be differentiated among themselves, and it seems somewhat surprising to find such a distinct variety with so limited distribution. Since such specimens can obviously not change their appearance very rapidly, and since, moreover, *S. natans* (*IX*) is characterized by a greater relative abundance of bladders than that observed in the other forms, which would prevent it from sinking at a more rapid rate than these, it seems implied that the absorption of surface drift from the eastern Cayman Sea into the main Caribbean current must be rather slight.

The distribution of *S. natans* (*VIII*) is in various essential features entirely different from that of *S. natans* (*I*), *S. fluitans* (*III*) and all the other pelagic forms. Although *S. natans* (*VIII*) occurs with the others also in the open Sargasso Sea, it is definitely rare in that region, and has its main distribution *within* the Central American seas where the other forms occur only secondarily and in lesser abundance than in the Atlantic. We have mentioned already that, although rare, as are all pelagic weeds, south of the southern boundary of normal occurrence in the Caribbean, *S. natans* (*VIII*) constitutes the *majority* of the scattered sprigs occasionally encountered in southern Caribbean waters, while it is in very rare minority in the Atlantic. In one instance 1.2 pounds of this form were collected in the S-W bight of the Caribbean near the southern end of Mesquito Bank, with no other pelagic weeds but with four pounds of benthonic weeds present. *The S. natans VIII* flora is thus the only one which would be capable of entering the Caribbean Current from the left, while *S. fluitans* and *S. natans I–II* impinge upon its flow from the right-hand side. In the Northeastern Cayman Sea *S. natans* (*VIII*) is quite common and the 1935 records show a couple of hauls between Cuba and the Cayman Islands in which this was the most abundant form, although the weight per mile did not exceed 1/30 of a pound. In the Gulf of Mexico *S. natans* (*VIII*) reaches its greatest absolute abundance, frequently exceeding one-tenth of a pound per mile (1935), but the secondary maximum, with reference particularly to the distribution of *S. natans* (*I*) in this region, causes the indicated relative abundance of *S. natans* (*VIII*) to be less in the Gulf than in the Cayman Sea. If it should otherwise prove possible and reasonable to attempt to derive the *S. natans* series from a broad-leaved, rather than a narrow-leaved, benthonic relative via *S. natans* (*VIII*), the geographical distribution of this form with its maximum abundance within the Central American seas instead of in the open Atlantic, would lend support to this interpretation to which the author is also otherwise inclined.

The peculiar dwarf form, Winge's *Sargassum V*, seems generally distributed in the western Sargasso Sea and also occurs in Central American waters, but is everywhere so scarce that no discussion of relative variations in abundance seems possible. Our material entirely confirms Winge's observations on the peculiarly high frequency of this otherwise scarce weed in the bundles of floating *Sargassum* of which the flying fish form their nests.

TOTAL QUANTITY OF PELAGIC VEGETATION

In spite of the great differences in the average quantities obtained from year to year, it will be seen from our table on page 59 that all our records for the Sargasso Sea proper remain within the same order of magnitude and it is probably safe to assume that this therefore expresses at least the order of magnitude of the abundance of pelagic weeds for the entire Sargasso Sea. As outlined by Krümmel and by Winge, the region of the Sargasso Sea includes about two million square miles. From our table on page 59, we see that the total quantity of floating weeds per square mile is to be reckoned in tons, the total vegetation of the entire Sargasso Sea must therefore be on the order of magnitude of millions of tons. Specifically our records for the various years applied to the entire region would give a total estimate of about 4 million tons on the basis of the 1935 data, 7 million tons on the basis of the 1933 observations, and 11 million tons according to the records of 1934. Other things being equal it is, of course, most likely that the true value should be within the range of those above estimated, and until further data become available, we may accept this probability with proper reservation as a working hypothesis. Regardless of the still very tentative character of this assumption as to the limitations within which the exact value is likely to fall, there is no valid reason to doubt that at least the correct order of magnitude is indicated in our figures as already above mentioned and to that extent we shall in the following discussions consider them valid without further reservations.

A floating vegetation of millions of tons of pelagic *Sargassum* seems very impressive at first thought, and has already tempted such eminent investigators as Hjort (in Murray and Hjort, 1912, p. 718) to refer to the presence of these floating weeds at the surface in explanation of an increased abundance of animal life at the deeper levels of the Sargasso Sea. But a comparison with the estimates of total oceanic productivity now available immediately shows that the drifting Sargassa can only be a quantitatively very insignificant element in the general metabolism of the sea, even within the region of their maximum abundance.

Atkins (1923) and Cooper (1933, 1934) have calculated the total annual phytoplankton production in the British Channel to be around 1.4 kilograms wet weight per square meter of surface, corresponding to nearly 5000 tons per square nautical mile, and Seiwell (1935) has given reasons for assuming that the productivity of the tropical North Atlantic must be at least on the same general order of magnitude as that of more northern waters. Comparing with our own observations of average abundance of pelagic *Sargassum* (2–5½ tons per square nautical mile) we thus find that the standing crop of floating vegetation even within the Sargasso Sea proper is only on the order of magnitude of thousandths of the probable total annual (plant) production of these waters. While we do not have any definite information as yet as to the actual rate of growth of pelagic *Sargassum*, it is undoubtedly safe to assume that they do not produce in excess of ten times their own weight per year, and it seems most likely that their actual growth will only be a fraction of this amount. Taking a ten times turnover as our maximum figure, we see that the floating vegetation will, at a very liberal maximum, only be able to account for hundredths or less of the probable total annual production of the Sargasso Sea.

DURATION AND NATURE OF THE PELAGIC PHASE OF THE FLOATING SARGASSA

One of the most debated questions in marine biology is the problem of whether the population of floating weeds occupying the so-called "Sargasso Sea" is merely a chance aggregation of slowly perishing individuals unable to maintain a prolonged existence when torn away from their "normal" benthonic habitat, or whether it is an essentially self-sustaining community of plants to which the pelagic existence has become secondarily normal, and which are able to maintain and multiply themselves indefinitely by mere vegetative growth, mechanical fragmentation, and irregular partition of the individuals through disintegration from the basal end.

Reviewing the history of the problem it is perhaps fair to say that the more direct the method of approach and the more adequate and accurate the material and observations, the more definite have the various investigators been in their acceptance of the latter theory, while the opposing viewpoint has been mainly based upon circumstantial and indirect reasoning with frequent resort to unsubstantiated specific assumptions from general knowledge.

In Winge's report the various arguments for or against the theory of an essentially self-sustained pelagic *Sargassum* population have been so fully set forth and critically analyzed that no detailed account of the entire discussion is necessary at this time, and we shall therefore merely confine ourselves to a brief restatement of the main points brought out by previous workers, in so far as they have withstood criticism and remain to be considered today.

In favor of the theory of an enduring pelagic existence the following three arguments already advanced in the previous literature would seem to have the greatest significance.

1) It was calculated by Krümmel (1891, p. 140) that it would on the average take the benthonic weeds detached from the shores of the Bahaman region at least about half a year (5¾ months) to drift around to the eastern part of the Sargasso Sea (that the possibility of eastern sources of weeds derived from the bottom is without quantitative significance has long been recognized) and a much longer time would of course be required for them to be spread over the entire oceanic domain of the pelagic *Sargassum*. Krümmel accordingly postulates that the weeds must at least be able to endure a pelagic existence for several years since their oceanic distribution otherwise becomes quite inexplicable. It is difficult to see how any valid objections might be raised against this argument, and its general import has also been accepted by Winge (1923). On this point one may also now claim definite support from the results of the Danish eel investigations[1] which show that the pelagic larvae of the European eels, hatched in the southwestern part of the Sargasso Sea, take 2–2½ years to reach the coastal waters of Europe, towards which they are being carried by the North Atlantic Current system which is also responsible for the distribution of the pelagic *Sargassum*.

2) Although direct observational evidence is as yet lacking, the vigorous appearance of the entire vegetation in the central area of the Sargasso Sea speaks very convincingly of plants in active growth, a fact which was first commented upon by von Humboldt,[2] and has been repeatedly confirmed by independent observations of numerous later investigators,[3] most recently by Ostenfeld, who states (in Winge 1923, p. 19) that "there is no doubt that *Sargassum*-shoots grow rapidly while drifting." Disregarding the problematical question of the *speed* of growth, which can be definitely settled only by direct experimental observations, the present writer entirely fails to see how any doubts could ever be entertained in regard to the universal occurrence of growth as such by anybody who has had opportunity to observe the living, pelagic weeds at sea, with the healthily-colored budding leaves, branches and vesicles on their distal portions and their vigorous older parts.

3) From Krümmel's and Antze's figures Winge (1923, pp. 17 and 20) has also claimed to be able to extract definite statistical evidence of growth among the pelagic weeds by showing that their frequency is subject to a simultaneous increase in all regions of the Sargasso Sea from summer to fall, a phenomenon which would be inexplicable on the assumption that all increases of the floating population must be due to the detachment of new contingents of weeds from

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[1] For a summary see Johs. Schmidt (1932).

[2] Through this observation von Humboldt was led to conclude that a bank of benthonic *Sargassum* ("*Fucus* Bank") would have to be found to the west of the Azores and another to the South-West of Bermuda (see Winge 1923, p. 5), assumptions which have since been thoroughly refuted by the development of our knowledge of the geography of the Atlantic Ocean.

[3] Meyen, Thunberg, Harvey, Leps, Martens, Perrier, Schütt, Hentschel (see Winge 1923, pp. 6–7).

benthonic fields, since these, in so far as they exist, can only be located along the Western boundaries of the Sargasso Sea. While fully accepting the fact of pelagic growth, as already above mentioned, the author is inclined to look for a modified interpretation of the change in statistical frequency pointed out by Winge. When dealing with frequencies one must always keep in mind that a frequency is only a purely numerical index without quantitative significance in terms of weights or volumes (see page 2). The fact that the recorded frequency of weeds is increased from summer to fall therefore merely means that a greater number of individual observations of floating vegetation have been made in the fall, but does not necessarily imply that the greatest increase in the total bulk of the population has occurred during this period. It is undoubtedly reasonable to assume, as Winge does, that the warm season must be the most propitious season for pelagic *Sargassum* growth. As it happens, the warm season is also generally the calmest season in the Sargasso Sea. From spring to early fall the weeds will therefore not only have their best growth, but will also perform this growth with relatively little partition of the plants, and the increase in bulk will therefore not be fully reflected in a corresponding increase in frequency. At the onset of the stormier season, the individual plants should therefore be expected to be of the greatest average size and therefore most likely to break down under the force of external disturbances which are undoubtedly a major factor in the process of their partition. Once the breakdown has occurred the resistance of the now smaller plants to further disrupting influences has thereby been increased so that continued disturbances will only have a greatly reduced effect upon their multiplication by fragmentation, in comparison with the effectiveness of the first onset of the disturbances in the fall. Following this period of maximum multiplication in the fall we can then safely assume that there must be a period of maximum loss of entire plants during the cold season when the marginal danger-zone of low temperatures along the entire northern boundary (see page 81) advances into the territory of previously favorable conditions, at the same time as the increasing strength of the easterly trade winds at lower latitudes must cause an increased amount of pelagic weeds to be thrown ashore on the Antillean and Bahaman coasts in the South-West. Within the statistical pattern of a self-sustained pelagic vegetation, growing slowly in bulk throughout the warm season, it is therefore possible to expect a relatively sudden increase in frequency, i. e., in number of plants in the fall, followed by a slow decline both in frequency and bulk during the winter, and with the decline in *frequency* quite likely to continue through the season of active increase in total bulk, in the absence of adequate external disturbances to cause the mechanical multiplication of the growing plants, while loss of entire plants in the marginal zones goes on all year round to a greater or less extent. With full recognition of these possibilities, however, the author is strongly inclined to doubt that even they are sufficient to explain the annual cycle in the frequency with which drifting weeds are encountered by passing ships, particularly on the point last mentioned in the preceding, i. e. with regard to the surprisingly high rate at which the decline in the frequency of the weeds is continued up to midsummer, as shown by the following relative frequencies for the entire Sargasso Sea taken from Winge (1923, p. 16).[1]

Spring	*Summer*	*Autumn*	*Winter*
159.5	148.9	189.6	177.2

It now becomes necessary to call to mind again the fact that these figures are only a cumulative expression of the frequency with which drifting weeds have been observed within each 1° coördinate unit, regardless of amount of weeds observed on each occasion. It is evident, of course, that the aggregation of the drifting weeds in relatively large rafts or floes with wide stretches of empty water between will serve to reduce the numerical frequency with which floating vegetation would be encountered, and will therefore serve to reduce the number of entries in records of the sort upon which Krümmel's and Antze's figures are based. It is also obvious that periods of relatively calm weather will favor the concentration of the drifting weeds into larger and larger aggregations, reducing the *frequency* of the rafts as their average size increases, and that the onset of greater surface disturbances in the fall will serve to break up and disperse the larger rafts even more than it affects the partitioning of the individual plants.[2] In the author's opinion, the continued decline in the frequency of pelagic *Sargassum* observations during the warm season until the sudden increase occurs in the fall is probably largely to be explained in this manner as an expression of the annual cycle in the number and average size of the weed-patches, and is only to a much lesser extent due to fluctuations in the number of individual plants, while it is not at all *directly* connected with seasonal variations in the total bulk of the floating vegetation.

It might also be mentioned at this point that such variations in degree of dispersal or aggregation of the floating weeds will, of course, have a geographical as well as a seasonal aspect and may perhaps serve to explain some of the irregularities in the geographical distribution of the Krümmel-Antze frequency values.

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[1] The figures represent the sums of the Krümmel-Antze frequency percentages per 5° geographical coördinate unit, 45 such units being included in the entire Sargasso Sea area.

[2] The concentration of the weeds during calm weather into large, more or less circular rafts, offering the least statistical chance of intercept with the course of a ship, and their dispersal by the wind into thinner and thinner stripes and single plants or small tufts, has been fully described by Winge himself (1923, pp. 11–12) and his observations are entirely in accordance with our own.

4) The proponents of the theory of an enduring pelagic existence have with perfect justification pointed to the inability to find any benthonic fields of the pelagic weeds of an extent and abundance which would be at all adequate to account for the large amount of floating plants on the assumption that their pelagic existence was of a short duration and this we shall attempt to elaborate further in the following pages. One weakness in this line of reasoning has been the uncertainty as to the identity of the benthonic forms from which the pelagic weeds might be derived. As a result of the present investigation, this problem has now been solved for one of the two floating species which make up the bulk of the pelagic flora, but the discovery of its benthonic counterpart has merely served to strengthen the argument concerning the inadequacy of the benthonic flora to explain the pelagic one, since this benthonic form is certainly not a common variety even among the generally apparently rather scanty sessile *Sargassa*.

In regard to the arguments which have been raised against the theory of an essentially self-sustained pelagic *Sargassum* community it seems sufficient to say that these have all been so adequately refuted by Winge and others whose work he reviews and refers to, and in whose reasoning the author entirely concurs, that no valid specific objection based upon actual facts really remains to be disposed of today.[1] The criticism which still has to be met is mainly that of a purely negative skepticism, healthy in any field of research, springing in this case from an unwillingness to entertain the possibility of an indefinitely protracted pelagic existence of a sterile vegetation which evidently never resorts to reproductive processes of multiplication. And even this attitude of skepticism can scarcely be said to be entirely in accordance with all general knowledge since life apparently indefinitely sustained and multiplied by vegetative processes, only, is certainly not unknown in botany from many examples other than the Sargassa, even among higher plants.

That the eupelagic weeds always lack organs of fructification in their floating existence was first observed by Meyen (1884) and has been fully confirmed by every subsequent investigator, except Küntze (1881), whose claims to have found fertile pelagic specimens in his collections have already been discredited by Winge (1923, p. 20). To add our own experience to the cumulative evidence from the experience of others, we may say that among the thousands of eupelagic weeds sorted in the course of the investigations here reported upon we have not seen one single *unattached* fertile plant, and only in the one instance of a specimen of *S. fluitans* floating attached to a piece of mangrove root (?) in the marginal zone of the Sargasso Sea were organs of fructification found to be present (see p. 49).

It is interesting to note that Meyen, who first observed the sterility of the floating weeds, was nevertheless also the first writer to suggest that the pelagic plants may continue to live, grow, and multiply by partition indefinitely (for thousands of years), carrying the theory so far in fact as to assume that the quantity of weeds in the Sargasso Sea must be constantly increasing.

Perhaps a few simple mathematical considerations may serve to clarify the problem and make the conclusions arrived at more acceptable on the basis of general knowledge.

If we assume that there is a constant annual recruitment, *a*, torn off from the bottom to form the pelagic community, and that the floating vegetation suffers a constant annual loss, *d*, by mortality in excess of growth increment, *d* being expressed as a fraction of the vegetation present at the beginning of each year (fraction of 1), then the size of the total pelagic population, *P*, when it has reached equilibrium between annual recruitment and annual net loss will obviously be expressed by the equation:

$$(1) \qquad P = a + a\,(1-d) + a\,(1-d)^2 \ldots\ldots\ldots + a\,(1-d)^n$$

in which $a\,(1-d)^n$ expresses the reduced size of a given annual recruitment from the bottom after n years afloat. To get the average age in the pelagic state, D, of the entire drifting vegetation we must therefore weight (multiply) each term (remnant of an annual recruitment) on the right side of equation (1) by its age afloat and divide the expression thus obtained by the entire size of the pelagic population as given in (1), thus:

$$(2) \qquad D = \frac{0.a + 1.a\,(1-d) + 2.a\,(1-d)^2 \ldots\ldots\ldots + n.a\,(1-d)^n}{a + a\,(1-d) + a\,(1-d)^2 \ldots\ldots\ldots\ldots\ldots + a\,(1-d)^n}$$

Substituting $k = 1 - d$ and eliminating a we get

$$(2a) \qquad D = \frac{k + 2k^2 \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots + nk^n}{1 + k + k^2 \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots + k^n}$$

adding 1 and treating it as an infinite series we obtain

$$(2b) \qquad D + 1 = \frac{1 + 2k + 3k^2 \ldots\ldots\ldots\ldots\ldots\ldots}{1 + k + k^2 \ldots\ldots\ldots\ldots\ldots\ldots}$$

or, since the enumerator in (2b) is simply the second power of the denominator

$$(2c) \qquad D + 1 = 1 + k + k^2 \ldots\ldots\ldots\ldots\ldots\ldots\ldots$$

and, since the expression on the right side of equation (2c) for an infinite series

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[1] The tendency for refuted contentions to survive in the general literature is unfortunately fairly universal. Thus Küntze's unfortunate claim to have disproved the existence of any Sargasso Sea at all reappears as a statement disposing of the entire phenomenon in a work as recently published as J. E. Tilden's "The Algae and their life relations," University of Minnesota, 1935 (page 334).

approaches the limiting value of $\frac{1}{1-k}$*, this gives:

$$D + 1 = \frac{1}{1-k} \quad \text{or} \quad D = \frac{1}{1-k} - 1$$

Introducing again $d = 1 - k$ we thus have

$$D = \frac{1}{d} - 1 \tag{3}$$

If we now go back to equation (1), substitute $k = 1 - d$, and introduce the limiting value $\frac{1}{k-1}$ for the series $1 + k + k^2 \ldots\ldots\ldots\ldots + k^n$ we obtain

$$P = a\left(\frac{1}{1-k}\right)$$

Substituting again $d = 1 - k$ and solving for d this gives

$$d = \frac{a}{P}$$

Substituting for d in (3) we have

$$D = \frac{P}{a} - 1 \tag{4}$$

From this equation it is evident that if the average duration of the pelagic phase should be one year only, the annual recruitment must equal one half of the entire floating vegetation. A six months average duration would require an annual recruitment equal to two-thirds of the total vegetation. Conversely an annual recruitment of one-tenth of the floating vegetation corresponds to an average lifetime afloat of 9 years.

Having tentatively established in the preceding chapter that the total pelagic *Sargassum* vegetation is apparently on the order of magnitude of 5–10 million metric tons, wet weight, we may now proceed to discuss whether it is at all conceivable that the annual recruitment could be in a proportion to this total amount which would indicate a short average duration of the pelagic phase according to equation (4).

(A) Considering first the possible sources of benthonic weeds, we immediately find these to be very restricted both in extent and in richness of flora from which the pelagic forms may be derived. The coastal areas in the Eastern Atlantic, limited under any circumstances to the outlying islands of the Azores, Madeira

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* K being only a fraction of 1.

and the Canaries have already been eliminated from discussion in the previous literature due not only to their insignificant extent but also to the fact that they do not actually fall within the Sargasso Sea proper, but are barely touched by its extreme boundary in the case of the Azores and fall entirely outside of the region of the floating weeds in the case of the other islands. We can therefore confine ourselves to the question of possible benthonic sources in the Western Atlantic.

The fact that the Caribbean area south of Jamaica and Honduras is empty of floating weeds excludes the coasts of the Lesser Antilles and the South American continent from quantitative consideration. There remains then in the East only the coasts of the Greater Antilles, the Bahamas, Florida, the Gulf of Mexico and Bermuda, and the banks between Jamaica and Honduras.

(B) Within these coastal belts algae of the type of *Sargassum* can, of course, only occupy a relatively shallow belt. The literature does not seem to contain any unquestionable records of sessile *Sargassum* from depths over 50 meters and it does, at all events, on the basis of present knowledge, seem extremely unlikely that there can be any quantitatively significant *Sargassum* flora below this depth, but for the sake of the argument we may consider the entire zone down to 100 meters depth as being potentially inhabitable by benthonic *Sargassa*. From the available hydrographic charts the total area of this zone along the coasts and on the banks mentioned above has been estimated as somewhat less than 220,000 square miles. Inclusion of all areas down to 200 meters depth would not change this amount in any significant manner, due to the prevailing shape of the bottom contours, nor would exclusion of all areas below 50 meters depth change its order of magnitude, although it would result in a more appreciable reduction in the amount. Taking all factors and allowances into consideration, the author is inclined to believe that the estimate above given cannot be much less than twice the actual potential area of vegetation. It might furthermore be pointed out that quite probably several large areas here included, such as the northern bank in the Gulf of Mexico should actually have been excluded from consideration in relation to the pelagic flora for hydrographic or other reasons. However, we may let the estimate stand as a maximum figure of potential vegetation area, with reference to depth, in the order of magnitude of hundreds of thousands of square miles, or more precisely about 200,000 square miles.

(C) But this large area is far from being uniformly covered with a blanket of *Sargassum* vegetation. Quite to the contrary, the local fields of sessile *Sargassa* have to be patiently and diligently searched for in most regions. In the first place at least half of the total area included in the figure arrived at under point (B) consists of *large continuous stretches* of fine sands and muds entirely unsuitable as a substratum for sessile *Sargassum*, and in the stretches defined as "shell and sand" or "coral and sand," which constitute by far the greater portion of

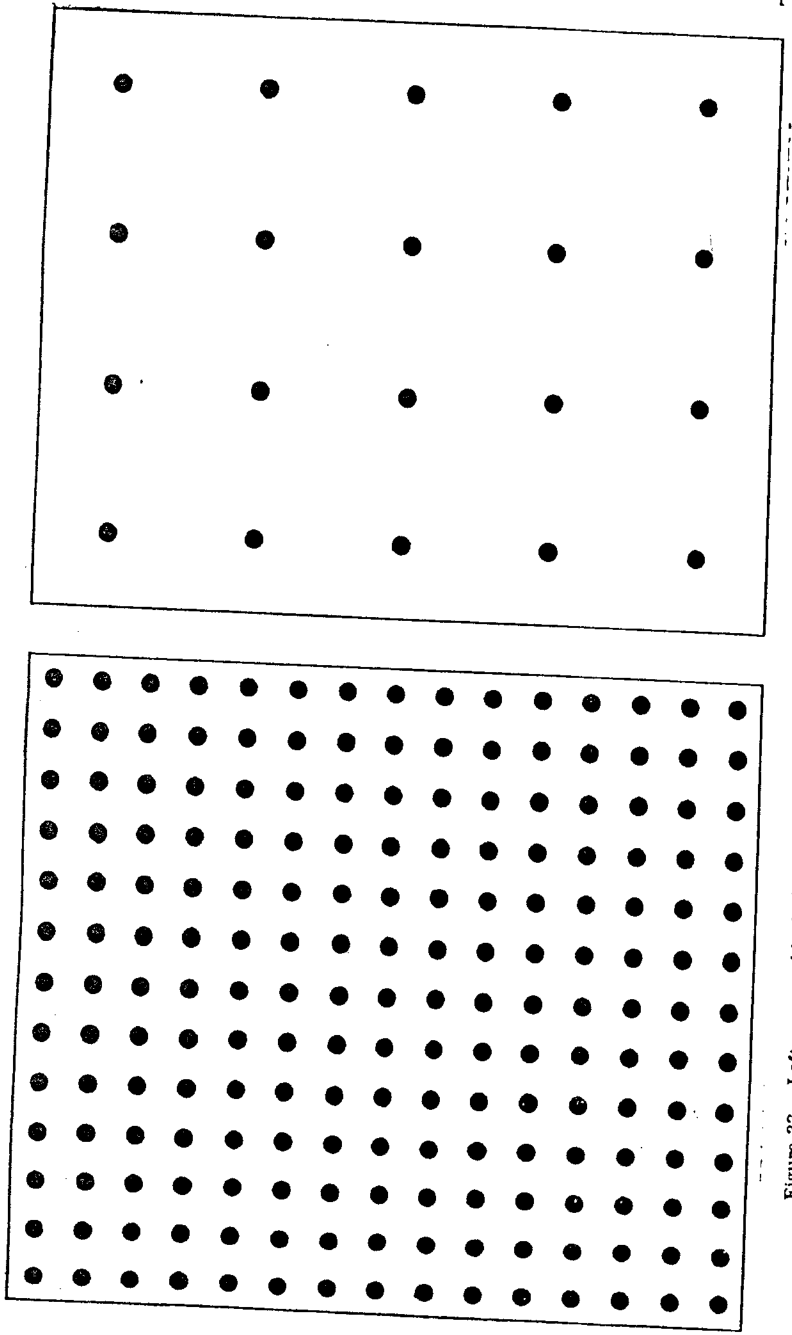

Figure 33. Left square: black dots covering about 1/10 of area. Right square: black dots covering about 1/100 of area.

the other half, fine sand undoubtedly covers by far the largest part of the actual area. The 200,000 square miles above the 100 meter contour line can thus, extremely conservatively, be reduced to about 50,000 square nautical miles potentially inhabitable by benthonic *Sargassa*. If, further, the author's experience in shallow-water collecting in the regions here considered is any index of the frequency of the weeds, even those portions of the total area from shore to 100 meters which may be considered in a general way, i. e., spotwise, inhabitable by *Sargassum* are actually covered only to an extent to be reckoned in hundredths of their total area. Since quantitative data are not available, and are probably impossible to obtain at any time in view of the character of the bottoms with which we are here dealing, a simple visual presentation of 1/10 and 1/100 as coverage given in figure 33 may perhaps help the reader in evaluating his own impressions. If the coverage should be on the order of magnitude of tenths of the area, the reader's impression of the average density of *Sargassum* inhabitation on suitable bottom throughout the Central American region must correspond at least to the density shown in the right part of our diagram, or to a multiple of this density. If the reader's impression is of a density intermediate between those shown in the left and in the right part of our figure, then a coverage to be reckoned in hundredths of the area is implied. For the purpose of our discussion, we shall merely assume that the average density throughout the inhabitable half of the bottoms of the coastal belts here considered does not exceed *twice* that shown at the right of our figure, or one-fifth coverage, which, in the writer's opinion is probably nearly 10 times the actual coverage. By this generous allowance for coverage, which the author is convinced will be more than acceptable to anybody experienced in shallow-water collecting in these waters, combined with our reduction of potentially inhabitable area to 50,000 square miles, or less, the order of magnitude of the possible area actually covered by benthonic *Sargassum* vegetation has now become reduced from hundreds of thousands to tens of thousands of square miles, more precisely to about 10,000 square miles, or less. And it seems most probable that we have at this point left a margin of safety for our further calculations on the order of the ratio of 10 : 1.

(D) But as already pointed out by others, and abundantly confirmed by the collections of benthonic *Sargassa* available to the writer, the benthonic forms from which the pelagic weeds *may* be derived are not those which occur most abundantly where a sessile flora is found. On the contrary, so far as present knowledge indicates, the benthonic form from which we now know that the pelagic *S. fluitans* (see page 49) may be recruited must certainly be very limited in its occurrence in the sessile fields so far investigated, and we have no definite knowledge as yet of any form at all being taken on bottom which may with any assurance be considered the "parental" form of the pelagic *S. natans*. The species (or varieties) constituting the overwhelming majority of all available records and collections of the benthonic flora so far as known today are particularly *S. filipendula*, *S. polyceratium*, *S. pteropleuron*, *S. hystrix* and to a lesser extent those forms of *S. vulgare*, which can be definitely ruled out as contemporary sources of the pelagic weeds. On the basis of today's knowledge, at least, we may thus safely assume that weeds from which the pelagic forms may possibly be recruited comprise less than one-tenth of the entire benthonic flora; in other words they occupy less than 1/10 of the area of vegetation already limited by previous reasoning to less than 10,000 square miles, i. e., the possible source of floating weeds must cover an area of an order of magnitude of only one thousand square miles, *or less*.

(E) But if an area of benthonic vegetation[1] reckoned only in thousands of square miles should make an annual contribution to the pelagic flora reckoned in millions of tons, as required if the average duration of the pelagic phase is only to be reckoned in years (not tens of years) (see (4) page 74) it would have to surrender an annual yield on the same order of magnitude as the total average crop of a terrestrial vegetation, or the total annual phytoplankton production in the upper 70 meters in such a productive region as the British Channel,[2] that is a yield on the order of magnitude of thousands of tons per square mile. It seems very unlikely, of course, that the total production of a sessile algal flora can ever remotely approach the production of total phytoplankton, or a total terrestrial vegetation, but for the sake of the argument we may at this point assume that it might possibly at least be on the same order of magnitude.

(F) But allowing for the possibility of this extremely improbable, high order of productivity of the benthonic vegetation, we would also have to assume a 100 per cent effective harvesting of this production by storms and wave action to make the yield available to the pelagic flora, and also that this harvesting was the only significant source of loss to the benthonic vegetation. Both assumptions would be patently absurd. Although the violent hurricanes of the West Indian region may unquestionably be very effective in tearing loose sessile vegetation, they undoubtedly are not on the average 100 per cent effective even in their direct path, although they might achieve this efficiency in certain places. If they were, the maintenance of the benthonic flora would become a problem even more disturbing than that of the pelagic vegetation. The paths of the hurricanes in an average year will, moreover, only cover a fraction of the entire coastal area with which we are here concerned. Storms of lesser intensity cover wider areas, of course, but also with less efficiency. A very considerable amount of the weeds torn loose from the bottom will further be removed from our consideration by being immediately thrown ashore to destruction. At this point one should bear in mind that the most effective wave-action, or one might perhaps even say the only effective wave-action in the shallow-water belt, will be obtained from a wind direction with an on-shore component, which, *ipso facto*, should be expected to deposit the better part of its harvest directly upon the adjacent shores. Taking all things into consideration, it certainly seems very improbable that wave-action should be able to *harvest and successfully bring into* the pelagic population more than at most 1/10 of the total annual production of the benthonic vegetation. But now we are down to an annual contribution from benthonic fields to the pelagic phase on an order of magnitude of tenths of the total pelagic population, even assuming a *benthonic* productivity at least on the same order of magnitude as the productivity of terrestrial vegetation or the total productivity in the British Channel.

In other words, it would be beyond all reason to assume that there are sources of benthonic vegetation adjacent to the Sargasso Sea which could make an annual contribution to the pelagic population on an order of magnitude greater than one-tenth of the order of magnitude of the pelagic population itself; and that therefore in accordance with equation (4) (page 74) it seems inconceivable that the average duration of the pelagic existence should have to be reckoned in less than tens of years (at least 10), probably in hundreds or thousands.

There is also another approach to the determination of at least the order of magnitude of the average duration of the pelagic existence through an approximate evaluation of the size of the annual contribution *a* to the pelagic flora from direct observational records. It is obvious, of course, that weeds torn loose from the bottom will retain, in a recognizable form, various features of general habitus, characteristic of their sessile phase, for a certain length of time after they have entered their pelagic existence. These features are particularly associated with polarity of growth, which in the sessile form is a polarity of the entire plant with reference to a single plane, the horizontal, or the solid substratum, but in the pelagic weeds of long standing is merely a ploarity of parts (branches, etc.) with reference to an axis, or a system of axes, represented by stems and branches. There are also other characters more difficult of definition but easily recognized on actual specimens. Since the change from benthonic to pelagic habitus can only be accomplished through growth, it probably requires a very considerable period of time (see Winge 1923, p. 20). Certainly those who are willing to doubt the ability of the floating weeds to form a self-sustaining population by vegetative growth must also be more than willing to grant this point. If we assume then that the floating weeds will retain recognizable evidence of their recent derivation from the bottom for 1/10 of a year, the weeds in our pelagic collections thus recognized should represent approximately 1/10 of the annual contribution from the benthonic vegetation to the pelagic flora. But in the case of the *S. natans* series of floating weeds, the total amount of plants observed with any indication of an at all recent derivation from the bottom is less than one-thousandths (1/1000) of the total amount collected,

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[1] Of forms which might form the source of the pelagic weeds.

[2] The estimates given by Atkins (1923) indicate a production of somewhat less than 5000 tons per square nautical mile.

when we allow for the possibility that this entire series might be derived via the form of *S. natans VIII*, described on page 46. If *S. natans I*, constituting more than 9/10 of the pelagic volume of this series should not be derived in this manner, the indicated contribution from bottom for 1/10 of a year is even less than 1/1000, in fact it is absolute 0. For the *S. natans* series the value of the annual recruitment a in our equation (4) (page 74) thus seem to be less than 10/1000 or 1/100 of the floating population P, and the average duration of the pelagic existence for these weeds D should consequently be at least one hundred years, or more.

In the case of the *S. fluitans* series, the problem becomes somewhat complicated by the question of the extent to which the form *S. fluitans X* as a whole should be considered as showing evidence of recent derivation from a benthonic existence. By far the greater portion of *S. fluitans X*, however, has already lost its benthonic and developed a pelagic polarity, and if we include, with generous allowance, only those plants of *S. fluitans X* and *III* which definitely show the kind of evidence of recent benthonic derivation mentioned above, we are also in this case down to an order of magnitude for the 1/10 annual contribution of thousandths, only, of the total pelagic stock,[1] *i. e.* to an amount to be reckoned only in fractions of hundredths, putting the entire annual contribution a at fractions of 1/10 of the population P, and the average duration D of the pelagic life of *S. fluitans* at least at multiples of 10 years, approaching 100 years or more.

From an entirely different set of premises we thus again arrive at the conclusion that the average duration of the pelagic existence must probably be at least multiples of 10 years for *S. fluitans*, and 100 or a multiple of 100 years for *S. natans*, and it does not seem as though any reasonable allowance for seasonal variations (our data being mostly gathered during the early spring) or other possible errors in our second method of approach could bring this minimum value down to less than 10 years for either group of eupelagic weeds, certainly not under any circumstance in the case of *S. natans*.

In the preceding discussion we have dealt with the possible total cumulative loss by mortality[2] in excess of increment by vegetative growth, d, suffered by the entire pelagic population over its entire area of distribution, having for convenience assumed this loss to affect equally all pelagic year-classes, *i. e.*, all annual contingents from the benthonic vegetation regardless of the past duration of their pelagic existence. It now becomes necessary to look into the nature of this loss by mortality and in particular to inquire into the extent to which it may prove to be geographically limited or at least a geographical variable. The author's conclusions on this point may be very briefly stated. In all the collecting on which this report is based no evidence suggestive of any mortality of entire plants was noted among the eupelagic weeds in their oceanic domain, south and east of the so-called "Gulf Stream," *at sea* between Bermuda and the Antilles. That is, we have never, in the Sargasso Sea proper, seen any evident degeneration of the plants themselves, such as that observed in other waters, nor any over-incrustation which might threaten to submerge an entire weed. The observations recorded on page 10, showing how strictly their buoyancy confines the floating eupelagic *Sargassa* to the very surface alone, might also be referred to at this point since they also, within their limitations, serve to show the absence of plants approaching equilibrium with the specific gravity of sea water as an initial step towards their destruction by sinking. In other words, the assumption of a heavy mortality in the Sargasso Sea proper seems purely speculative and quite discordant with any observable evidence. That some loss will occur in the form of the sinking of basal fragments of a plant which may become severed from their connections with the buoyant distal portions, when the weed "multiplies" by a mechanical breakup is evident, but there is no reason whatsoever to assume that this loss is not adequately compensated for by the growth of the younger distal parts which remain afloat. The more so since we can only assume that it is mainly through the increased size of the entire plant due to this distal growth that the stress on its stems in the action of the waves reaches the point where fragmentation is likely to occur. In the author's opinion it is essentially only through the chance of their drifting away from the central area into the marginal zone, and even onto the shores, that death of the entire plants threatens the weeds which have once arrived in the Sargasso Sea proper.

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[1] But not to *less* than 1/1000 as in the case of *S. natans*.

[2] Sinking due to loss of buoyancy or excess weight of epizoan fauna is, of course, included as a form of death in our use of the term mortality throughout these pages.

The marginal zones of mortality during mid-winter and the very early spring apparently include at least the northern half of the Gulf of Mexico, the entire Gulf Stream north of Florida, in particular the expanse between Bermuda and Cape Cod, and the northern boundary of the Sargasso Sea in general; and in these waters obvious degeneration of the entire plants can be abundantly observed also among the eupelagic weeds still floating on the high seas. The plants commonly appear dark brown and battered, seem to suffer considerable losses of leaves and bladders, and give little or no indication of fresh distal growth.[1] It seems most probable, of course, that low temperatures must be the main causative factor of this degeneration. Winge (1923, p. 18) makes the statement that [pelagic] *Sargassum* apparently cannot thrive in a temperature lower than 18° C., but in the author's opinion it is insufficient to look for an explanation of their distribution in the seawater temperatures alone, for the reason that the weeds through their buoyancy are actually always in part above the surface of the water directly exposed to the air, although only by a very small fraction of

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[1] This description, of course, applies only to the plants which are presumably dying. The marginal zones above mentioned are by no means entirely free from healthy-appearing weeds even in mid-winter.

their mass at a time. In this manner portions of a plant may have been exposed to a chilling from the cold winter storms frequent in the Gulf of Mexico and in the other marginal zones above mentioned, of which we would find no adequate indication in the surface temperatures of the sea. The parts which would first be exposed to these detrimental effects would naturally be the most buoyant, which are normally the most distal ones in which the potentiality of future growth is also located. If the parts thus exposed are killed and disintegrate or fall off, other buoyant parts would then turn towards the suface to be similarly destroyed, the basal or central parts of the weed, with the least buoyancy, always remaining the longest, until the buoyancy of the entire plant has become reduced to the point where the final remnant ultimately sinks to its destruction. Probably this process of gradual, rotating killing of distal parts by exposure to air temperatures and chilling winds is the explanation of the ball-like degenerating weeds consisting chiefly or entirely of proximal parts only, with relatively few leaves and bladders left, which we have often observed in the Gulf of Mexico.

Weeds which have been washed ashore and washed off again before their decay had been completed, and which therefore continue their degeneration at sea will, of course, also have to be reckoned with in the marginal zones.

During summer the Gulf of Mexico can probably be eliminated as a region of temperature-death in open sea, and the lethal zone will be shifted farther to the West of the Gulf Stream boundary and to the North and East of Bermuda, but the fact remains that the western boundary of this current and the area towards which its main flow is directed will all year round represent the main regions of mortality for the pelagic flora, since these are the regions in which the floating weeds will be most rapidly, and in greatest bulk, brought into contact with unfavorable temperature conditions. That a very considerable amount of weeds is actually carried into these lethal regions is amply shown by our own collecting in the cross-section between Cape Cod and Bermuda, both in the summer (healthy weeds at this point) and in the winter (many unhealthy specimens among healthier ones) and the further transportation to the North-West into still more dangerous waters is clearly indicated by the tongue-like extension of the boundaries of pelagic *Sargassum* occurrence to the NW of Bermuda, shown in Winge's map (Winge, 1923, fig. 2).

It is evident that the weeds most likely to be carried by the Gulf Stream into these areas of dangerous temperatures are those which have just started their pelagic existence within the very waters of current system with which we are dealing, that is, the fresh annual contingent from the benthonic flora of the Antillean, Central American and Southern North American coasts; while the likelihood of the plants which have already safely reached the central regions of the Sargasso Sea being returned to its Gulf Stream boundary is, of course, considerably less, although still significant. The recently detached benthonic

recruits to the pelagic flora which have escaped the danger of being immediately washed ashore, therefore still have to survive the hazards of the northward flow in which they find themselves, and through which they undoubtedly must suffer a considerable reduction in numbers, before they can actually be said to have become definitely a part of the pelagic population. For observational confirmation of this speculative deduction, we may refer to the fact that the occurrence of all the rapidly perishing holobenthonic weeds, and also of the relatively long-lived quasi-pelagic *S. hystrix* is strictly confined to the region of the Gulf Stream system (Winge 1923, as well as our own observations), thus showing no evidence of a significant direct translation across the current into the central region of the Sargasso Sea proper. We may further point out that all the specimens of eupelagic weeds showing any possible indication whatsoever of a fairly recent derivation from bottom have also been found exclusively in the region of the Gulf Stream system.[1] It therefore seems possible to state with a fair amount of assurance that a large part if not the bulk of the presumptive annual contribution from benthonic vegetation to pelagic flora will be forced to traverse the dangerous region North and East of Bermuda before actually becoming incorporated in the population of the Sargasso Sea proper. It is therefore probable that only a very much reduced contingent finally achieves this goal, or in other words that the loss by mortality in excess of vegetative growth is not equally distributed on all pelagic year classes but affects chiefly the new contingent or O-class, and that the average expectancy of duration of the pelagic existence for the older contingents which have once successfully escaped the hazards of the Gulf Stream drift and arrived in the Sargasso Sea proper is therefore very much *i. e.*, probably many times, greater than indicated in our estimates of minimum possible average duration for the entire pelagic population including the O-class still floating in the marginal zone.

For the assumption that a relatively heavy mortality does occur in the region North and East of Bermuda, particularly North of 40° latitude, we have our own observations of an increasing frequency of unhealthy-looking weeds north of Bermuda during winter, and we may also refer to Krümmel's observation (Krümmel, 1891, p. 138) that pelagic weeds are found north of 45° latitude only in late summer and fall, but not during the rest of the year. Krümmel interpreted this as evidence of a periodic (seasonal) contribution from the benthonic vegetation farther south which in the normal course of events would reach these higher latitudes at that time, but Winge (1923, pp. 15–16) has shown the lack of necessity for resorting to this assumption in explanation of this particular phenomenon, and has in general proved the incorrectness of Krümmel's theory.

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[1] We here include in this term the entire territory of the Central American Seas, including also the outer coastal waters of the Bahamas and Antilles, swept by the Antilles Current which joins with the Florida Current before Cape Hatteras to form the so-called "Gulf Stream."

Winge instead refers the disappearance of the pelagic weeds from the higher latitudes during late fall and winter to the onset of the North and Northwesterly winds of the cold season. While it is quite possible that these winds might drive some surviving weeds back to lower latitudes, it is also evident that they would at the same time provide a most effective chilling mechanism for the destruction of the weeds under their influence. With some allowance for the factor of regressive transportation in terms of latitude the author therefore sees in Krümmel's observations mainly the effect of a shifting southward of the lethal zone during the cold season. Finally, one may *a priori* submit that if a relatively high degree of mortality is not to be found at the northern cold boundary of the Sargasso Sea towards which a major portion of the new contingents from the benthonic fields are driven, it would be preposterous to assume the existence of any significant mortality contrary to all appearances in the central area of the Sargasso Sea proper. Arguments against the assumptions on this particular point would therefore be arguments in favor of the main conclusion in regard to the longevity of the sterile floating weeds, in which the author joins such previous investigators as Krümmel and Winge themselves, Meyen, Hentschel and others.

While it thus seems evident that the annual contingent actually received in the Sargasso Sea proper is certainly very small in proportion to its entire pelagic *Sargassum* population, it is on the other hand also obvious that such a contribution from benthonic vegetation, however small, if it actually does exist[1] must serve to increase the total floating population until a balance is reached where it compensates for the loss by mortality in excess of the vegetative increment and multiplication of the entire pelagic stock. And it would be unreasonable to assume that the pelagic population has not been in existence for a sufficiently long time to have reached this equilibrium between loss and recruitment today.

Through the reasoning explained in the preceeding we therefore arrive at the conclusion that the pelagic *Sargassum* population of the so-called Sargasso Sea, apart from its marginal zones, is probably an essentially self-sustaining unit with a potentially infinite longevity and a very long normal expectancy of life for its individual plants, receiving (*at most*) only a very slight annual contribution from benthonic vegetation merely sufficient to compensate for its own loss by a slight excess of mortality over vegetative growth increment, suffered mainly through a continually occurring chance return of some of its members to the dangerous marginal zones from which a corresponding recruitment of freshly detached plants which have escaped its hazards are received in exchange.

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[1] The author is as yet inclined to consider it in terms of a possibility only, at least insofar as *Sargassum natans* is concerned.

LIST OF HAULS MADE WITH PELAGIC WEED COLLECTOR

The following list is a definitive account with regard to the amounts of the dominant forms of pelagic weeds obtained in the individual hauls. That is to say, it presents the final figures and notes concerning the presence and abundance, or the absence, of *S. natans* (*I*) and *S. fluitans* (*III*), or of *S. fluitans* as a whole (*III* + *X*) where no distinction has been made between the two forms in which this species may occur. The list is also final with regard to the abundance of any other type of *pelagic Sargassum*, wherever such other forms were obtained in sufficient quantity to be recorded by weight. In addition to these definitive *quantitative* figures one will also find entries of all notes so far made, whether on shipboard or during the subsequent examination of the preserved material, concerning the mere presence of the rarer forms in amounts too small to be weighed. These non-quantitative records of the mere presence of a form cannot, however, be guaranteed to be entirely complete, in view of the vast amounts of weeds which had to be sorted on board, and thereafter discarded, and of the likewise very large amount preserved. It is quite likely that the reexamination of the preserved material alone, planned in connection with the final systematic analysis after sufficient benthonic collections have also been obtained, will increase the number of records of rarer weeds present in individual hauls.

There is also considerable variation in the details given in the field-records of each haul. When made under instructions in the absence of the writer[1] the standard entries are simply the weights of "fine-leafed" (*I*) and of "coarse-leafed" (*III*) weeds, which, together with a total preservation of all unusual-looking weeds, and a random sample of the dominant ones, provides ample information for the purposes of this investigation.

When a small catch was preserved in its entirety, the weight of the separate forms was subsequently determined, after sorting in the laboratory, as the wet weight in formalin, which will not differ significantly from the wet weight of the fresh material. The weight of such small samples determined in the laboratory could naturally be recorded in more accurate figures than those used in the weighing of large samples on board (usually nearest ¼ pound). In other instances, when difficulties in sorting arose on board in the absence of the writer, the total weight of the descriptive category "coarse-leafed" or "large-leafed," was taken on board and entered in the field-record, with a specially large random sample preserved, from which the relative amounts of the forms combined in this category were subsequently determined in the laboratory. In the case of the hauls made in the Gulf of Mexico during 1935 (Nos. 172–188), *S. natans VIII* and *S. fluitans* were commonly combined in the field-records under the heading of "broad-leaved" weeds, and the weight recorded under this head-

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[1] Hauls Nos. 1–113 and 141–172 were all made and sorted under the supervision of the writer with the assistance of the ship's company.

ing has only subsequently been divided according to the relative abundance of the two forms in the large random samples. In the Gulf of Mexico the true *S. fluitans* generally occurred only in such fragmentary (although not quantitatively insignificant) material that it was not found practical to attempt to distinguish between its two forms. The discovery of the actual identity between *S. fluitans III* and *X* (on 1934 winter-cruise material) also lessened the emphasis upon a separate sorting of these two forms. In the 1935 records *X* has therefore only been entered as a notation of its presence in the quantitative record of *S. fluitans* given under *III* (the always predominant form) when some well-developed plants of the *X* form were conspicuous in the catch.

The following example may serve as an interpretation of the entries used in the records of the individual hauls.

Example:

#51. 1/27. 23°23.5′ N. 69°57.5′ W. 19.0 Mi. 44.00 I. 5.00 III. II. V. X.

Read:

Haul No. 51. January 27. Median latitude 23°23.5′ N. Median longitude 69°57.5′ W. Length of haul through the water (log-distance) 19.0 nautical miles.[1] 44.00 pounds of *S. natans* (*I*) (wet weight). 5.00 pounds of *S. fluitans* (*III*). *Sargassum II*, *V*, and *X* present in small amounts.

1933

SOUTH OF BERMUDA.

#1. 2/13.	31°25.5′ N.	66°45′. W.	3.0 Mi.	.50 I.	2.00 III.		
#2. 2/13.	31°24′ N.	66°52.5′ W.	8.0 Mi.	2.75 I.	9.75 III.		
#3. 2/13.	31°22′. N.	67° 3′. W.	10.0 Mi.	3.75 I.	13.50 III.		

SARGASSO SEA. NASSAU TO ANEGADA PASSAGE.

#4. 2/26.	25°38′ N.	75°16′ W.	14.1 Mi.	4.00 I.	6.50 III.	II.	X.
#5. 2/26.	25°36′ N.	75° 0′ W.	15.9 Mi.	12.00 I.	16.50 III.	2.00 X.	II.
#6. 2/26.	25°34′ N.	74°41.5′ W.	16.5 Mi.	12.25 I.	12.75 III.	1.25 X.	
#7. 2/26.	25°36.5′ N.	74°23′ W.	14.3 Mi.	8.50 I.	15.00 III.		
#8. 2/27.	25°46′ N.	72°35′ W.	14.4 Mi.	5.25 I.	15.50 III.	1.25 X.	II.
#9. 2/27.	25°46′ N.	72°23′ W.	8.0 Mi.	10.25 I.	56.00 III.	2.00 X.	
#10. 2/27.	25°45.5′ N.	72°15′ W.	6.7 Mi.	7.00 I.	4.00 III.		
#11. 2/27.	25°44.5′ N.	71°57′ W.	13.0 Mi.	.25 I.	8.00 III.		
#12. 2/28.	25°31.5′ N.	69°23′ W.	15.2 Mi.	21.00 I.	17.50 III.	2.50 X.	
#13. 2/28.	25°30′ N.	69° 5′ W.	17.0 Mi.	28.50 I.	22.00 III.	1.75 X.	.25 II
#14. 2/28.	25°29′ N.	68°40′ W.	13.0 Mi.	36.00 I.	28.50 III.	3.50 X.	
#15. 3/1 .	25°17.5′ N.	66°41.5′ W.	14.1 Mi.	19.75 I.	30.25 III.	.50 X.	
#16. 3/1.	25°17′ N.	66°23′ W.	17.2 Mi.	9.50 I.	10.50 III.	.50 X.	
#17. 3/1.	25°16′ N.	66° 7.5′ W.	7.1 Mi.	17.75 I.	35.00 III.	1.00 X.	
#18. 3/3.	23°19′ N.	62°30′ W.	16.7 Mi.	24.50 I.	20.25 III.	.25 X.	
#19. 3/3.	23° 5′ N.	62°40′ W.	9.4 Mi.	17.00 I.	20.50 III.	VIII.	
#20. 3/4.	22° 2.5′ N.	62°43′ W.	12.7 Mi.	4.50 I.	10.50 III.		
#21. 3/4.	21°51′ N.	62°46′ W.	9.2 Mi.	Less than 1 lb. total haul			
#22. 3/4.	21°42.5′ N.	62°44′ W.	6.7 Mi.	3.50 I.	30.00 III.		
#23. 3/5.	21° 8′ N.	62°13′ W.	18.0 Mi.	16.50 I.	16.25 III.		
#24. 3/5.	20°56′ N.	62° 8′ W.	10.7 Mi.	13.75 I.	16.75 III.		

1933

CARIBBEAN.

#25. 3/13.	10° 1′ N.	64°28.5′ W.	14.0 Mi.	No weed			
#26. 3/27.	17°25′ N.	71°40′ W.	21.4 Mi.	1.00 I.	1.00 III.		
#27. 3/27.	17°30′ N.	72° 6′ W.	31.5 Mi.	1.00 I.	1.00 III.		

CAYMAN SEA NEAR WINDWARD PASSAGE.

#28. 4/18.	20° 0′ N.	74°19′ W.	11.0 Mi.	.50 I.	.50 III.		
#29. 4/18.	19°51′ N.	74°30′ W.	27.8 Mi.	2.00 I.	.50 III.		

1934

CAPE COD TO BERMUDA.

#30. 1/22.	36°21′ N.	66°39′ W.	5.9 Mi.	.70 I.	2.40 III.	V.		
#31. 1/22.	36°18′ N.	66°21′ W.	36.8 Mi.	.50 I.	11.00 III.			

SARGASSO SEA. BERMUDA TO TURKS ISLAND.

#32. 1/23.	31°57′ N.	65°52′ W.	14.5 Mi.	21.50 I.	12.50 III.	X.		
#33. 1/23.	31°44′ N.	66° 2′ W.	14.0 Mi.	6.50 I.	5.25 III.			
#34. 1/24.	30° 9′ N.	66°51′ W.	8.0 Mi.	18.50 I.	1.00 III.			
#35. 1/24.	29°06′ N.	66°53′ W.	19.7 Mi.	30.00 I.	5.00 III.	II.		
#36. 1/24.	29°38′ N.	67° 0′ W.	14.8 Mi.	46.50 I.	10.00 III.	II.		
#37. 1/24.	29°26′ N.	67° 9′ W.	16.8 Mi.	33.25 I.	3.00 III.	1.00 II.		
#38. 1/24.	29°11′ N.	67°17′ W.	15.2 Mi.	51.00 I.	5.00 III.	II.	X.	
#39. 1/25.	27°46′ N.	68° 0′ W.	19.4 Mi.	49.00 I.	4.25 III.	.50 II.	X.	
#40. 1/25.	27°33′ N.	68°10′ W.	5.8 Mi.	103.00 I.	3.00 III.	2.50 II.	X.	
#41. 1/25.	27°28.5′ N.	68°13′ W.	5.7 Mi.	71.00 I.	6.25 III.	1.00 II.	X.	
#42. 1/25.	27°21.5′ N.	68°16′ W.	7.5 Mi.	123.00 I.	6.75 III.	2.25 II.	VIII.	
#43. 1/25.	27°18′ N.	68°18′ W.	2.6 Mi.	118.00 I.	6.25 III.	2.50 II.	V.	
#44. 1/25.	27°13′ N.	68°20′ W.	7.7 Mi.	16.00 I.	1.75 III.	II.	V.	X.
#45. 1/25.	27° 5.5′ N.	68°23′ W.	5.8 Mi.	1.25 I.	.75 III.			
#46. 1/26.	25°50.5′ N.	68°56′ W.	18.0 Mi.	127.00 I.	9.50 III.	.60 II. V.	.80 X. VIII.	
#47. 1/26.	25°33′ N.	68° 2′ W.	19.7 Mi.	100.00 I.	4.25 III.	1.50 II.	.90 X. VIII.	
#48. 1/26.	25°12.5′ N.	69°12′ W.	20.0 Mi.	46.00 I.	5.00 III.	1.10 II.	V.	X
#49. 1/26.	24°56.5′ N.	69°19′ W.	13.0 Mi.	79.00 I.	6.00 III.	.90 II.	.60 X.	
#50. 1/27.	23°48′ N.	69°46′ W.	30.5 Mi.	33.00 I.	8.75 III.	II.	V.	X.
#51. 1/27.	23°23.5′ N.	69°57.5′ W.	19.0 Mi.	44.00 I.	5.00 III.	II.	V.	X.
#52. 1/27.	23° 5′ N.	70° 8′ W.	24.3 Mi.	89.00 I.	10.00 III.	II.	V.	X.
#53. 1/27.	22°46′ N.	70°20′ W.	18.2 Mi.	128.00 I.	14.00 III.	II.	V.	X.
#54. 1/27.	22°28′ N.	70°32′ W.	23.5 Mi.	50.00 I.	3.00 III.	II.	V.	X.
#55. 1/27–28.	21°58′ N.	70°52′ W.	46.0 Mi.	94.00 I.	4.00 III.	II.	V.	X.

TURKS ISLAND TO WINDWARD PASSAGE.

#56. 1/28.	21°37′ N.	71° 9′ W.	7.0 Mi.	3.00 I.	.80 III.		
#57. 1/28.	21°27′ N.	71°15′ W.	14.6 Mi.	16.00 I.	1.10 III.		
#58. 1/28.	21°13′ N.	71°21′ W.	18.4 Mi.	72.00 I.	2.25 III.	II-VIII.	X.
#59. 1/28.	20°56′ N.	71°38′ W.	32.4 Mi.	120.00 I.	7.00 III.	II.	
#60. 1/28.	20°42′ N.	72° 4′ W.	19.1 Mi.	1.00 I.	1.50 III.	VIII.	

CARIBBEAN I. WINDWARD PASSAGE TO PANAMA.

#61. 1/29.	19°53′ N.	73°27′ W.	43.3 Mi.	12.00 I.	4.00 III.	II.	V.	
#62. 1/29.	19°24′ N.	74°10′ W.	69.2 Mi.	3.00 I.	.80 III.	VIII.		
#63. 1/29.	18°57.5′ N.	74°44′ W.	17.6 Mi.	1.00 I.	.20 III.	II.		
#64. 1/29–30.	18°26.5′ N.	75°23′ W.	70.0 Mi.	10.00 I.	2.00 III.			
#65. 1/30.	17°52′ N.	76°16′ W.	46.3 Mi.	3.50 I.	Few sprigs III.			
#66. 2/2.	17°35′ N.	76°39′ W.	17.4 Mi.	2.40 I.	.30 III.	.20 II.	X.	
#67. 2/2(–3).	17°20′ N.	76°36′ W.	15.0 Mi.	2.50 I.	.40 III.	II.	VIII.	X.

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[1] Not necessarily identical with the geographical length of the haul in the presence of significant currents.

1934

CARIBBEAN I. WINDWARD PASSAGE TO PANAMA.—*Cont.*

#68.	2/3.	17° 3′	N.	76°30′	W.	16.7 Mi.	3.00 I. 2.00 III.
#69.	2/3.	16°33′	N.	76°27′	W.	43.6 Mi.	.24 I. .16 III. IX?
#70.	2/3(–4).	15°53′	N.	76°30′	W.	40.3 Mi.	1.20 I. 1.10 III.
#71.	2/4.	15° 2′	N.	76°39′	W.	35.7 Mi.	.10 I.
#72.	2/4–5.	14°12′	N.	76°50′	W.	67.1 Mi.	One sprig I.
#73.	2/5.	13°14′	N.	77°50′	W.	40.3 Mi.	One sprig I.
#74.	2/5.	12°50′	N.	77° 3′	W.	16.8 Mi.	.30 I. II.
#75.	2/5–6.	12° 2.5	N.	78°10′	W.	66.0 Mi.	I.
#76.	2/6.	11°17′	N.	78°45′	W.	41.5 Mi.	VIII.
#77.	2/6.	10°43′	N.	79° 6′	W.	37.1 Mi.	Fragment I.
#78.	2/7.	10°13′	N.	79°21′	W.	27.8 Mi.	No weed.

CARIBBEAN II. PANAMA TO EAST POINT OF JAMAICA.

#79.	2/14.	9°35′	N.	79°57′	W.	9.6 Mi.	One sprig III.
#80.	2/14.	9°44′	N.	80° 1′	W.	12.5 Mi.	No weed.
#81.	2/14.	10° 1′	N.	80°16′	W.	34.0 Mi.	VIII.
#82.	2/15.	10°34′	N.	80°48′	W.	56.1 Mi.	4.00 VIII.
#83.	2/15.	10°55′	N.	81°34′	W.	45.1 Mi.	.70 VIII.
#84.	2/16.	11°55′	N.	82°35′	W.	18.2 Mi.	Empty
#85.	2/16.	12° 9′	N.	82°50′	W.	11.0 Mi.	Empty
#86.	2/17.	13°23′	N.	82° 9′	W.	7.0 Mi.	Empty
#87.	2/17.	13°26′	N.	82° 0′	W.	16.4 Mi.	Empty
#88.	2/17.	13°21′	N.	81°38′	W.	26.2 Mi.	No *Sargassum.*
#89.	2/18.	13°22′	N.	81° 5′	W.	24.5 Mi.	No *Sargassum.*
#90.	2/18.	13°36′	N.	80° 8′	W.	31.0 Mi.	I. III.
#91.	2/18–19.	13°59′	N.	79°47′	W.	33.9 Mi.	Empty
#92.	2/19.	14°27′	N.	79°28′	W.	37.8 Mi.	3.75 I. .25 III. II. VIII.
#93.	2/19.	14°55′	N.	79°16′	W.	25.0 Mi.	2.10 I. .80 III. II.
#94.	2/20.	15°40′	N.	78°50′	W.	36.5 Mi.	5.50 I. .25 III. II. VIII.
#95.	2/20.	16° 8′	N.	78°39′	W.	17.8 Mi.	6.00 I. .50 III. VIII.
#96.	2/20.	16°24′	N.	78°27′	W.	20.0 Mi.	I. II.
#97.	2/21.	17° 1′	N.	78° 0′	W.	35.8 Mi.	1.50 I. 1.30 III. II. VIII.
#98.	2/21–22.	17°53′	N.	78° 0′	W.	60.5 Mi.	9.00 I. 1.60 III. II. V. VIII. IX.

CAYMAN SEA. EAST POINT OF JAMAICA TO YUCATAN CHANNEL.

#99.	2/22.	18°28′	N.	78°40′	W.	38.8 Mi.	2.00 I. 1.70 III. II. V. VIII.
#100.	2/22–23.	19°19′	N.	79°21′	W.	74.8 Mi.	2.70 I. 1.20 III. II. V. VIII.
#101.	2/23.	19°55′	N.	79°41′	W.	16.5 Mi.	1.10 I. .40 III. II. V. VIII.
#102.	2/23.	20°11′	N.	79°31′	W.	19.5 Mi.	.40 I. .40 III. II. VIII.
#103.	2/23.	20°28′	N.	79°23′	W.	19.4 Mi.	1.30 I. 2.20 III.
#104.	2/24–25.	21°15′	N.	80° 9′	W.	111.8 Mi.	I. II. III.
#105.	2/26.	19°22′	N.	81°31′	W.	19.0 Mi.	.80 I. II. III. VIII.
#106.	2/26–27.	19°11′	N.	82° 0′	W.	39.0 Mi.	7.50 I. 2.50 III. II. V. VIII.
#107.	2/27.	19° 5′	N.	82°42′	W.	28.9 Mi.	2.20 I. II. III. VIII.
#108.	2/27.	19° 2′	N.	83°20′	W.	40.6 Mi.	2.50 I. 1.50 III.
#109.	2/27–28.	19°20′	N.	83°52′	W.	29.5 Mi.	1.50 I. III.
#110.	2/28.	20° 2′	N.	83°56′	W.	39.5 Mi.	.50 I. II. III. VIII.
#111.	2/28.	21°21′	N.	84°18′	W.	42.2 Mi.	2.40 I. 1.40 III.

GULF STREAM NORTH OF MIAMI, FLORIDA.

#112.	3/8–9.	27°40′	N.	79°41′	W.	174.0*Mi.	60.00 I. 13.00 III. II. V. VIII. X.
#113.	3/9.	30° 5′	N.	79°12.5′	W.	52.4 Mi.	64.00 I. 8.20 III. 1.00 X.

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* Geograph. length 240

1934

BETWEEN CAPE COD AND BERMUDA.

#114.	7/18–19.	39°47′	N.	68° 7′	W.	48.2 Mi.	1.20 I. .55 III.
#115.	7/19.	38°59′	N.	67°47′	W.	30.5 Mi.	Only 2 small plants altogether.
#116.	7/19–20.	37°59′	N.	67°24′	W.	75.2 Mi.	46.50 I. 3.00 III.
#117.	7/20.	37°33′	N.	67° 9′	W.	18.7 Mi.	
#118.	7/20.	37°19′	N.	67° 2′	W.	8.0 Mi.	4.25 I.
#119.	7/20.	36°58′	N.	66°42′	W.	38.8 Mi.	23.75 I. III.
#120.	7/20–21.	36°21′	N.	65°58′	W.	62.1 Mi.	
#121.	7/22–23.	36° 3′	N.	65°52′	W.	53.5 Mi.	25.00 I.
#122.	7/23–24.	37° 0′	N.	67°30′	W.	102.9 Mi.	15.75 I. 4.00 III.
#123.	8/18.	40°21′	N.	69°47′	W.	59.4 Mi.	5.50 I. 2.25 III.
#124.	8/18.	39°38′	N.	69°20′	W.	43.8 Mi.	28.75 I. 6.25 III.
#125.	8/21.	38°20′	N.	68°54′	W.	71.6 Mi.	4.00 I. 1.50 III. VIII.
#126.	8/21–22.	37°33′	N.	67°56′	W.	44.7 Mi.	105.00 I. 20.25 III.
#127.	8/22.	37°17′	N.	67°31′	W.	7.2 Mi.	1.00 I. .25 III.
#128.	8/22.	37° 9′	N.	67°37′	W.	9.0 Mi.	43.00 I. 3.75 III.
#129.	8/22.	36°34′	N.	67°29′	W.	61.3 Mi.	24.50 I. 2.25 III.
#130.	8/22–23.	35°56′	N.	67°21′	W.	15.5 Mi.	5.00 I. .25 III.
#131.	8/26–27.	36° 4′	N.	68°12′	W.	92.3 Mi.	13.25 I. .75 III.
#132.	8/27.	36°53′	N.	68°58′	W.	20.1 Mi.	21.50 I. 4.25 III.
#133.	8/27–28.	37°50′	N.	69°25′	W.	94.5 Mi.	14.50 I. 4.50 III.
#134.	8/28.	38°16′	N.	69°49′	W.	27.6 Mi.	5.25 I. 2.25 III.
#135.	8/28.	39°18′	N.	70° 4′	W.	41.9 Mi.	12.50 I. 9.00 III.

1935

CAPE COD TO BERMUDA.

#136.	1/21.	38° 2.5′	N.	68°10′	W.	24.8 Mi.	1.75 I. 1.25 III. X.
#137.	1/21–22.	37°33′	N.	68° 0′	W.	35.9 Mi.	.75 I. 1.25 III.
#138.	1/22.	35°53′	N.	67°17′	W.	28.8 Mi.	1.75 III.
#139.	1/23.	33°42′	N.	65°31′	W.	30.9 Mi.	1.75 I. 6.50 III.
#140.	1/23.	33° 7.5′	N.	65° 2.5′	W.	49.9 Mi.	4.75 I. 14.50 III. II.

SARGASSO SEA. BERMUDA TO TURKS ISLAND.

#141.	2/6.	29°56′	N.	65°55′	W.	17.65 Mi.	13.75 I. 7.25 III. 1.00 II. VIII. X.
#142.	2/6.	29°38′	N.	66° 4′	W.	21.5 Mi.	22.00 I. 11.00 III. 4.00 II-VIII. V. 1.00 X.
#143.	2/6.	29° 6′	N.	66°23′	W.	44.8 Mi.	12.00 I. 11.00 III. 1.50 II. 2.00 X. VIII.
#144.	2/7.	28°30′	N.	66°41′	W.	25.0 Mi.	16.50 I. 87.20 III. II. 1.50 X. VIII.
#145.	2/7.	28° 3′	N.	66°56′	W.	28.6 Mi.	18.00 I. 10.00 III. 1.50 X. 1.50II. VIII. V.
#146.	2/7.	27°35′	N.	67°17′	W.	33.1 Mi.	16.00 I. 12.00 III. 3.50 II. 5.50 X. VIII.
#147.	2/7.	26°57′	N.	67°44′	W.	55.5 Mi.	47.00 I. 21.00 III. 5.00 II. 6.50 X.
#148.	2/8.	26°11′	N.	68°10′	W.	46.0 Mi.	29.00 I. 12.00 III. 3.50 II. 3.50 X.
#149.	2/8.	25°37′	N.	68°25′	W.	29.4 Mi.	19.00 I. 2.50 X. II.
#150.	2/8.	24°55′	N.	68°42′	W.	17.3 Mi.	54.00 I. 7.5 III. 2.25 II. 6.00 X. IX.
#151.*	2/8–9.	24°35′	N.	68°54′	W.	24.3 Mi.	37.50 I. 9.00 III. 1.50 II. 4.00 X.
#152.	2/9.	23°58.5′	N.	69°27′	W.	39.5 Mi.	88.00 I. 35.00 III. 3.00 II. 17.50 X. VIII. IX?
#153.	2/9.	23°31.5′	N.	69°45′	W.	23.3 Mi.	23.00 I. 7.00 III. 2.00 II. 1.50 X. VIII.
#154.	2/9.	22°56′	N.	70°13′	W.	58.4 Mi.	17.00 I. 2.75 III. 1.25 II. 1.50 X.
#155.	2/10.	22° 4′	N.	70°40′	W.	57.9 Mi.	10.50 I. 15.00 III. 2.00 X. II. VIII.

TURKS ISLAND TO WINDWARD PASSAGE.

#156.	2/10.	21°17.5′	N.	71°15′	W.	49.4 Mi.	8.25 I. 2.50 III. 1.25 X.
#157.	2/10–11.	20°30′	N.	72°46.5′	W.	92.3 Mi.	14.00 I. 4.00 III. II. VIII. X.

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* For account of subsurface nets used at this station see page 10.

1935

CAYMAN SEA. WINDWARD PASSAGE TO YUCATAN CHANNEL.

#158.	2/11–12.	19°57′ N.	74°14′ W.	69.3 Mi.	4.25 I. III. II. VIII. IX. X.
#159.	2/12–13.	19°24′ N.	76°30′ W.	172.6 Mi.	1.72 I. 4.20 III + X. .28 VIII. II.
#160.	2/13.	19°20′ N.	78°37′ W.	47.3 Mi.	1.10 I. 3.60 III + X. .62 VIII. .15 II. .30 IX.
#161.	2/13–14.	19°34′ N.	80°11′ W.	116.1 Mi.	1.70 I. 4.00 III + X. .40 VIII. II.
#162.	2/14.	19°53′ N.	81°54′ W.	67.9 Mi.	.80 I. 2.20 III + X. 2.20 VIII. II. 1.32 IX.
#163.	2/14–15.	20°27′ N.	83° 2′ W.	78.5 Mi.	2.00 lb. Total haul. Details not available.
#164.	2/15.	21°12.5′ N.	84°20′ W.	89.0 Mi.	.38 I. .81 III. 1.10 VIII. IX.

GULF OF MEXICO I. SOUTHEASTERN REGION BETWEEN YUCATAN BANK AND STRAITS OF FLORIDA.

#165.	2/16–17.	22°15′ N.	86°52′ W.	73.3 Mi.	No pelagic weeds.
#166.	2/18.	24°15′ N.	85°51′ W.	24.4 Mi.	.20 I. .75 III. .10 VIII. II.
#167.	2/18–19.	23°49′ N.	84°16′ W.	143.5 Mi.	.40 I. 1.30 III. .20 VIII.

GULF OF MEXICO II. NORTHERN GULF.

#168.	3/5–6.	27°32′ N.	88°21′ W.	50.4 Mi.	4.50 I + III + VIII.
#169.	3/6.	26°55′ N.	88°21′ W.	40.9 Mi.	4.00 I + III + VIII.
#170.	3/6.	26°23′ N.	88°12′ W.	48.7 Mi.	33.50 I. Fragments III. VIII.
#171.	3/6.	25°54.5′ N.	88°18′ W.	1.4 Mi.	I. VIII.
#172.	3/7.	25°43′ N.	88°23′ W.	10.9 Mi.	17.25 I. III. .50 VIII.
#173.	3/25.	28° 8′ N.	89°24′ W.	68.9 Mi.	45.25 I. 1.85 III. 1.90 VIII.
#174.	3/25–26.	27°30′ N.	89°47′ W.	35.5 Mi.	26.50 I. .95 III. 2.80 VIII.
#175.	3/26.	27°33′ N.	89°53′ W.	18.4 Mi.	17.00 I. 1.40 III. .35 VIII.
#176.	3/26.	27°57.5′ N.	89°53′ W.	21.9 Mi.	14.50 I. .50 III. .50 VIII.
#177.	3/26.	28°22.5′ N.	89°50′ W.	21.3 Mi.	12.25 I. .25 III. .50 VIII.
#178.	3/27.	c.28°45′ N.	c.89°50′ W.	42.3 Mi.	60.75 I. 4.50 III. 4.50 VIII.
#179.	3/27.	28°21′ N.	90°18′ W.	41.9 Mi.	33.75 I. 3.00 III. 3.00 VIII.
#180.	3/27–28.	27°40′ N.	91°24′ W.	92.3 Mi.	64.00 I. 11.75 III. + VIII.
#181.	3/28.	27°25′ N.	92°12′ W.	30.5 Mi.	11.00 I. .75 III. 1.00 VIII.
#182.	3/29.	c.29° 7′ N.	92°41′ W.	27.6 Mi.	30.50 I. 2.75 III. 3.25 VIII.
#183.	3/29.	29° 7′ N.	93°19′ W.	40.2 Mi.	18.75 I. 4.90 III. 1.00 VIII. X.
#184.	3/31–4/1.	27°41′ N.	96°26′ W.	54.2 Mi.	27.50 I. 4.50 III. 3.00 VIII. X.
#185.	4/1.	27°15′ N.	96°30′ W.	14.4 Mi.	6.75 I. 2.00 III. .25 VIII.
#186.	4/2–3.	25°57′ N.	94°44′ W.	62.4 Mi.	13.00 I. 1.20 III. 4.80 VIII.
#187.	4/3–4.	c.25°12′ N.	c.94°6′ W.	64.1 Mi.	13.50 I. .80 III. 1.20 VIII.

GULF OF MEXICO III. YUCATAN BANK.

#188.	4/8–9.	24° 5′ N.	87°57′ W.	58.8 Mi.	I. VIII.

GULF OF MEXICO IV. FLORIDA BANK.

#189.	4/11–12.	25°48′ N.	84° 5′ W.	86.4 Mi.	5.25 I. .60 III. .40 VIII. II.
#190.	4/12.	24°36′ N.	83° 2′ W.	40.0 Mi.	4.25 I. 1.30 III. .45 VIII.

STRAITS OF FLORIDA.

#191.	4/13.	23°41′ N.	81°52′ W.	77.7 Mi.	1.25 I. 1.75 III. II. VIII.
#192.	4/13–14.	24°42′ N.	80°33′ W.	59.4 Mi.	1.00 I. III. II. VIII.

GULF STREAM NORTH OF MIAMI, FLORIDA.

#193.	4/19–20.	28°10′ N.	79°42.5′ W.	135.3 Mi.	7.50 I. 0.50 III. + VIII.
#194.	4/20.	30°24′ N.	79°25′ W.	51.5 Mi.	3.75 I. 3.25 III. 1.00 VIII. X.

SUMMARY

The frame and net of a collecting apparatus specially designed to gather floating weeds from the sea surface on a quantitative basis is described, and the method of operation discussed (pp. 4–8).

It is pointed out that this collector has been in actual operation in the surface of the Sargasso Sea and of the Central American Seas for a total cumulative towing length of nearly 7,000 nautical miles, and that as a result of this towing more than 4,700 pounds of pelagic weeds have been sorted and weighed on board (pp. 3–4).

An account is given of experiments confirming the lack of vertical dispersal of pelagic *Sargassum* weeds (pp. 8–10).

The taxonomy of the pelagic *Sargassum* weeds is discussed in a preliminary fashion, with a practical key for their identification, and a descriptive atlas of herbarium silhouettes. A non-binominal, purely descriptive classification of the dominant forms is used as a basis for comparisons and discussions of distributions. The opinion is expressed that the fixed, more or less distinct external forms in which the truly pelagic weeds occur, probably represent only phenotypic variations of not more than two separate species, *S. natans* and *S. fluitans*. It is further pointed out that even the distinctness of these two species, although apparently most probable, cannot as yet be considered to be established entirely beyond all doubt (pp. 11–51).

A fertile plant attached to a drifting piece of wood (mangroove root ?), but otherwise indistinguishable from sterile representatives of the pelagic *S. fluitans*, is described (pp. 49–51).

The quantitative distribution of the dominant pelagic weeds is described (pp. 51–68). It is pointed out that the floating vegetation in the Caribbean and Cayman Seas is always very sparse, and that it is virtually completely absent from the entire southern half of the Caribbean itself. In the northwestern region of the Gulf of Mexico, however, a secondary accumulation of apparently deteriorating weeds in considerable abundance was observed over a wide area. At least during the winter period in which observations were made these weeds were obviously in a very poor condition and on the average extremely heavily overgrown by epizoan incrustations (pp. 54–58).

The main region of occurrence of thriving pelagic weeds was found to be entirely outside the Central American Seas in that part of the open North Atlantic designated as the Sargasso Sea. Observations in the western Sargasso Sea during three separate cruises with a total towing-length of over 1300 nautical miles indicate an abundance of pelagic weeds, varying in the records for the three years between about two and somewhat more than five metric tons wet weight per square nautical mile. If these figures are representative of the entire Sargasso Sea, the total pelagic vegetation might be estimated at four to ten million metric tons. It is suggested that this may be accepted as a usable statement of the order of magnitude of the total pelagic *Sargassum* vegetation of the North Atlantic (pp. 54–58).

Annual fluctuations in the relative frequencies of the two predominant types of pelagic weeds, *S. natans I* and *S. fluitans III*, are pointed out (pp. 59–64), and the distribution of the less abundant pelagic forms is discussed separately (pp. 65–67). It is shown that the distribution of the broadleaved *S. natans VIII* differs fundamentally from that of all other pelagic *Sargassa* in that it has its maximum abundance within the Central American Seas and not in the open Atlantic (p. 66).

By a process of elimination on the principle of *reductio ad absurdum*, it is concluded that there is no conceivable source and process of annual renewal of pelagic *Sargassum* vegetation from benthonic flora which could possibly maintain the floating vegetation in its observed abundance with an average duration of the pelagic state of the individual plants to be reckoned in less than decades (pp. 68–84).

The distribution of the pelagic *Sargassum* weeds confirms previous hydrographic conclusions on two points. 1) The failure of the drifting flora to penetrate southward across the Caribbean agrees with the assumption that the Caribbean surface water is mainly derived from the SE *via* the North Equatorial Current and not from the Sargasso Sea itself (p. 54). 2) The accumulation of floating weeds in the northwestern part of the Gulf of Mexico must be interpreted as a result of pure wind drift, due to prevailing easterly winds, moving the weeds in relation to the water, and this accumulation could scarcely take place in the presence of a significant tendency to outward movement of the surface water itself towards the Straits of Florida (p. 56).

MAIN SOURCES TO WHICH REFERENCE HAS BEEN MADE IN THIS REPORT

Since it does not seem necessary in this connection to print the entire bibliography of the earlier literature already reviewed by Winge (1923), only the sources which have been of main usefulness for direct reference in the preparation of this report are listed herewith for the reader's convenience, together with such references as did not come within the scope of Winge's discussion. The latter should be consulted for any author or title not mentioned in the following.

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