Studies in the Dictyotaceae.

III. The Periodicity of the Sexual Cells in *Dictyota dichotoma*.

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With six Diagrams in the Text.

WHILE studying the development of the sexual cells in *Dictyota* the interesting discovery was made that the process was practically simultaneous, not only for a given plant, but for all the plants of the locality; that the crop so produced took but little time to mature and become liberated, and that a succession of many of these crops were produced during the course of the fruiting season. A closer study enabled one to see that each crop was initiated, matured, and discharged all within a fortnight, and that a general liberation of the oospheres and antherozoids of the locality took place on a certain day, or sometimes two or three days, immediately after the highest spring tide.

Although the main facts were put beyond any doubt at an early period of the inquiry, there were slight variations in the times of maturation of some of the crops, and of particular sori, as well as of occasional plants. These deviations from the general rule took a longer time and more careful study to account for. Records have been systematically kept of the details relating to these crops from 1897 to the present year, and these enable us to come to a definite conclusion with regard to the factors concerned in bringing about the periodicity, as well as in producing local departures from the normal course of events.

In order to understand the facts, a general description of the sexual plant will be useful. *Dictyota* is an annual. Germlings, and, in all probability, small vegetative shoots from the preceding autumn which have remained dormant during the winter and spring, commence to elongate during May, and here and there fruiting plants may be met with about the end of June, but reproduction is not by any means common until the end of July. During August and September the process is general and perfectly

regular in its periodicity, but towards the end of October it becomes slower, finally ceasing about the middle or end of November. In very mild and bright winters new sori may be produced even at Christmas ; this, however, is exceptional, and the sori sometimes seen on the plants in mid-winter are in most cases arrested ones from October.

The proximal portion of the thallus as well as the edges are always free of sori ; and when a plant is in its earliest crops and still actively elongating, the distal parts are also without reproductive cells. The remaining portions have on both surfaces numerous sori, which are all of the same age, except a few at the distal end of the reproductive area, which are always younger. The reason for the latter fact is evident : this portion of the thallus being younger and only just removed from the meristematic condition, arrives at the stage capable of bearing sori a few days later than the general initiation of the crop.

The gametangia arrive at maturity about the highest spring tide, and, as will be explained in detail in another section, they are liberated during a very short period of time soon afterwards.

At the period of liberation, or a few tides after, the faint rudiments of the sori of the new crop begin to make their appearance. They are not localized on any definite region as are the tetrasporangia of *Padina*, but are scattered over the parts occupied by the preceding crop together with a short distal extension of it. With each successive crop the clear distal area becomes smaller and smaller, apical elongation becoming gradually slower, until at last the reproductive area reaches close to the apical cell itself.

In a very short time after the escape of the gametes the walls of the gametangia degenerate and disappear, but, as already described¹, the position of the liberated sorus is always indicated by the old basal cells, which are continuous with the cortex or limiting layer of the thallus, but rendered conspicuous by their increased size and different colour. At first they are much paler, owing to the small number and size of the chloroplasts and the paucity of colouring matter in them. They gradually acquire a deeper colour, still the scars of the two last crops can always be distinguished from each other. In the case of the male plants the raised borders of sterile cells is a further indication of the position of the old sori. These basal cells are incapable of giving rise to new gametangia, and when the whole or nearly the whole surface has been used up in this manner the plant dies, the process being hastened in some localities by the attacks of endo- and epi-phytes as well as of various animals.

The following examples illustrate some of the above points a little more clearly :—

1. A male plant 12 in. long and $\frac{1}{4}$ in. wide below the first dichotomy. The distal $\frac{1}{2}$ in. was quite clear of sori, and the current crop reached $1\frac{1}{2}$ in.

¹ Ann. of Bot., xviii, 1904, p. 184.

beyond the scars of the last crop. Thus the elongation during the last fortnight was only one-third of that for the preceding fortnight.

2. Female plant in its third crop. The proximal clear area was $1\frac{1}{2}$ cm. long, that occupied by the scars of the first crop 3 cm., the second crop 7 cm., and the current crop 13.5 cm., while the remaining 3 cm. at the distal end had not started reproduction. There is in most cases a progressive increase in the extension of the reproductive area in the case of the first three or four periods.

Vigorous plants produce such a number of sori that they soon exhaust themselves and decay. Many plants that start fruiting early are found in this condition by the end of September, and the first violent gale sweeps many of them away. The fact that we find many young plants in their first crop in early October proves that they must be the offspring of tetrasporic plants of the current season. There is thus a continuous succession of young plants commencing the process of reproduction from the end of June to mid-October.

THE HISTORY OF A SINGLE CROP OF SEXUAL CELLS.

In order to understand the course of events, it will be convenient to follow in detail the development of a single crop from the first appearance of the rudiments to the discharge of the mature gametes. Diagram I shows the results of observations at the Swillies in the Menai Straits during the early part of August, 1901, plotted down in such a manner as to show the relation borne by the various stages in the development of the crop to the heights of the tides. The vertical columns represent the days of the month, while the curve in the upper part shows the hours of high water and the heights of the tides in feet. The lower part of the diagram is utilized to denote the stage of division of the antheridium as seen in surface view. Thus, a small cross placed on the lowermost line indicates an undivided rudiment, and a similar one on the sixth line shows that there are sixty-four cells in surface view. After the final division of the antheridium a short time elapses before maturation is completed and liberation sets in, and during this interval the only division that occurs in the oogonium rudiment—that which separates the stalk-cell—is accomplished. In the diagram this is indicated by means of the dotted line. Finally, the stage at which liberation of gametes takes place is denoted by inserting the marks above the tenth line.

The first observations were made on the sixth of the month, when most of the antheridial rudiments were found to be undivided; a few were two-celled and a very small number four-celled. On the eighth and tenth the plants gathered showed hardly any advance, but by the twelfth the great majority of the antheridia were in the two- or four-celled stage. By the fifteenth many were apparently mature, and

some which were taken into the laboratory and kept in a damp chamber overnight and immersed in sea-water the following morning yielded motile antherozoids. On the seventeenth there was a general liberation of gametes in the Straits. In order to obtain abundance of swarming antherozoids it was not necessary on this occasion to place the male plants in a damp chamber overnight. By the evening of this day most of the female plants could be seen even with the naked eye to be clear of oogonia excepting for a few at the distal ends. By the eighteenth at least three-fourths of the crop had been cleared off: on the nineteenth only a few sori were left—most of these were the distal belated ones, others had been arrested just before maturity. On this day the first faint and undivided rudiments of the succeeding crop made their appearance. By the twentieth the whole plant was clear of the old crop, and the new antheridia, though still undivided, were more prominent in size and colour than before.

In this particular case, general liberation took place about three tides after the highest spring. If in the diagram we connect this and the middle of the line of average development for each day, we get a curve which we may call the *optimum of development*. This we may safely regard as expressing the time of development of a single sorus, and the great majority of the sori in the locality coincide with it in their times of initiation and rate of development.

In the case of this crop the diagram further shows that although some of the rudiments appear eight or nine tides before the lowest neap, and others as late as one tide after it, the majority are initiated about four tides before the lowest neap. The life of an average sorus from its first appearance to its discharge would be about nineteen tides (ten days); the width of the 'crop-band' is from eight to ten tides, and the whole time taken by the crop from the appearance of the earliest of the rudiments to the liberation of the latest is about twenty-eight tides. The presence of younger sori on the distal part of the reproductive area of certain plants has already been explained, and it is clear that such cases should be excluded from the diagrams, for in the case of plants which have ceased to elongate, and where the reproductive area reaches to the very apex, all the sori are practically in the same stage. It should be observed, however, that most of the distal sori thus belated in their initiation accelerate their development to such an extent that their liberation is not much behind the others, so that even including them the periodicity is still well marked. There are other circumstances which sometimes interfere with the periodicity—these will be dealt with further on—but they do no more than slightly modify the normal process.

COMPARISON OF DIFFERENT CROPS.

If now we study the crop for late August and early September, 1902, and compare the results, as represented in Diagram II, with those just described, we find that although there is general agreement between the two, there are several differences in matters of detail. We first observe that general liberation is delayed until about the fifth tide after the highest spring. Now as maturation and liberation are so evidently dependent on the spring tides, one would naturally expect the process to be accelerated directly as the height of the spring tides. Here, however, although all the spring tides in the second series are higher than those of the first, liberation, instead of being earlier, is actually later. This state of things occurred so frequently that it was at first conjectured that the increase in the amount of exposure during low water of the higher spring tides subjected the plants to more than their optimum of light or of heat, and in that way brought about their retardation. Though it is quite true that the plants are very sensitive to light, and possibly to variations of temperature, we now know that the above suggestion is not the correct one.

There are other variations also which appear in the tabulated results of the observations. The length of the optimum line may be nineteen tides, as in the diagram quoted, or any number up to twenty-five tides. The width of the crop-band may vary from five tides to about ten, while the whole time occupied by a crop may range from twenty-four to thirty-four tides.

In order to explain these variations it was natural to look for their causes in the fluctuations of the amounts of light and heat. Consequently careful records were kept of the state of the weather, especially as to amount of sunlight and the temperature of the sea. It is now found that the influence of these factors is quite secondary. Thus the liberation of the crop of September 23, 1899, took place five tides after the highest spring tide, the weather being very dull, cold, and stormy during the whole period. The crop of August 25 in the same year was liberated exactly at the same interval after the highest spring, though the weather during this period had been continuously bright and warm. Particulars relating to the weather are consequently omitted from the tables, and only such data are included as have been found to have an influence in deciding these variations. At the same time it must be remembered that extremes of illumination or of temperature may assist other causes in producing acceleration or retardation.

When all attempts to explain these variations on meteorological grounds had thus proved abortive, the solution was sought for in the fluctuations of the tides themselves. Now, although the main fact of

periodicity is clearly dependent upon the difference between spring and neap tides, it was not anticipated that the slight differences between one spring tide and another would be reflected in variations in the time of appearance of the different stages of the crops. But, unlikely as it may seem, it is here that we must look for the primary causes of the differences, while meteorological phenomena of various kinds may occasionally either restrain or intensify them. When looked at from this standpoint the results are so simple and consistent that it may be of some interest to state that all the data for the North Wales coasts had been collected and tabulated in chronological order before the right clue to their meaning was discovered. This makes the record more valuable than if the explanation had been in one's mind while studying the facts.

The tidal peculiarities here referred to are either differences of rise between successive spring tides, or differences in the intervals of time separating them from each other.

1. There is generally a fairly regular alternation of higher and lower spring tides. Sometimes the higher ones occur at the New Moon, and the lower at the Full: at other times the reverse is the case. It is but rarely that the two spring tides occurring in a month are the same height. During the fruiting period of *Dictyota*, this inequality always obtains, and there is the further consideration that the equinoctial tides, which occur about this time, are higher than ordinary spring tides. Thus, to take two examples from the year 1899:—

	The spring tide on August 9 was 18 ft. 4 in.			
	"	"	"	25 " 21 ft. 8 in.
Again	„	„	„	October 12 " 18 ft. 11 in.
While	„	„	„	27 " 21 ft. 7 in.

In the following discussion the spring tides will be designated simply 'lower' or 'higher' springs, as the case may be, whether they are ordinary or equinoctial.

2. The interval between two highest spring tides, corresponding to and very nearly coinciding with the interval between New and Full Moon (or between Full and New Moon), and technically called a 'semilunation,' varies in length. In the tables it is sometimes as low as twenty-five tides, while at other times it is as high as thirty-one tides.

Tables I and II give the most important of the data relating to these two groups of tides. The records of the other tides are fragmentary, but as far as they go they are in complete harmony with the results here quoted.

The following are some of the most obvious deductions from the tabulated results.

1. In the case of the higher spring tides of either August or September

TABLE I. CROPS LIBERATED DURING THE HIGHER SPRING TIDES IN AUGUST AND SEPTEMBER. (MENAI STRAITS.)

	Date of liberation of crop.									
	1		2		3	4	5	6	7	8
	Height of highest spring tide.		Height of lowest preceding neap tide.		Number of tides from the highest spring tide of the last series to the highest of this.	Length of crop optimum, i.e. the number of tides taken to develop a single sorus.	Ratio of crop optimum to tidal period (col. 3), the latter taken as 100.	Time of maximum liberation, in tides after the highest spring tide.	Breadth of 'crop-band' in tides.	Number of tides from the earliest liberation to final clearance of crop.
	ft.	in.	ft.	in.						
1	21	8	11	8	27					
2	21	9	11	4	28	21	75	5	6.8	24
3	21	4	11	3	29	22	76	5	10	
4	21	1	10	10	31	24	77	5	6-7	32-34
5	20	4	13	0	27	20	74	4-5	10	
6	20	5	12	11	25	19	76	5	5-6	
7	20	10	12	4	27	20	74	5	10	27

TABLE II. CROPS LIBERATED DURING THE LOWER SPRING TIDES IN AUGUST AND SEPTEMBER.

	18	11	10	6	30	22	73	3	8-10	30
8	August 20, 1898									
9	August 9, 1899	18	4	11	11			2		
10	August 28, 1900	18	8	12	1	21	78	3	10-12	28-30
11	August 17, 1901	19	3	12	11	19	76	3-4	8-10	29
12	August 23, 1902	19	3	11	0	25	81	3	10-12	32-34
13	August 3, 1903	18	1	12	2	22	76	3	10	

TABLE III. CROPS LIBERATED DURING OCTOBER AND NOVEMBER.

	21	6	10	9	31	22	76	7	7-8	
14	October 3, 1901									
15	October 12, 1899	18	11	10	5	29		12		
16	October 27, 1899	21	7	12	3	27	74	14	6	27
17	November 3, 1901	21	5	11	6	29		12		

liberation of gametes nearly always takes place about five tides after the highest, while in the case of the lower springs there is an apparent acceleration, and it occurs about *three* tides after the highest.

2. The above rule for the time of liberation is quite independent of the length of the interval from one spring tide to another. Thus in the table of higher tides, whether the semilunation includes twenty-five, twenty-seven, twenty-nine, or thirty-one tides, maximum liberation is effected about the *fifth* tide after the highest, and, excepting in the case of No. 12, there is the same uniformity in Table II.

3. Though the length of the interval between two highest spring tides does not determine the exact time of liberation, it has a direct influence upon the length of the period taken by an average sorus to develop; in other words, the length of the optimum line varies directly as the number of tides included in the semilunation. Thus in No. 6 the interval between the spring tides is twenty-five tides, while in No. 4 it is thirty-one. In the former case the optimum line is nineteen, while in the latter it is twenty-four. In Col. 5, where this relation is shown in percentages, this is seen more clearly. Out of thirteen recorded cases, nine are either 74 or 75 %, the average of the whole being 76 or, excluding No. 12, 75.4.

This confirms in a striking way the conclusion arrived at from other facts—that the development of the crops is chiefly dependent on the spring tides, and that the process goes on but slowly during neaps.

4. In the following table the crops are arranged according to the number of tides in the semilunation.

	<i>Date of crop.</i>	<i>Length of semi-lunation.</i>	<i>Height of lowest neap.</i>		<i>Length of crop optimum.</i>
			ft.	in.	
1	September 6, 1902	25	12	11	19
2	August 17, 1901	25	12	11	19
3	August 8, 1902	27	13	0	20
4	August 27, 1903	27	12	4	20
5	August 28, 1900	27	12	1	21
6	September 23, 1899	28	11	4	21
7	August 15, 1900	29	11	3	22
8	August 20, 1898	30	10	6	22
9	September 3, 1901	31	10	10	24
10	August 23, 1902	31	11	0	25

While it confirms what has been said before, it also brings out another fact which must have some influence upon the length of the optimum or the rate of development. As a general rule, the longer the interval the poorer will be the neap tides, and in consequence the activity of reproduction will be correspondingly diminished.

5. It was at first thought possible that just as the spring tides were advantageous for maturation, so there might be some special virtue in *neap*

tides for initiation and the earlier stages. The above shows this idea to be erroneous. The earliest rudiments are generally formed while the liberation of the preceding crop is still going on; hence there is a slight but distinct overlap. The optimum of initiation takes place generally from four to two tides before the lowest neap. It seems then that as soon as the old crop has ceased its demands upon the plant, the 'reproductive energy' becomes directed to the formation of new sori; these make their appearance immediately. At first their progress is fairly rapid, but with the gradual lowering of the tides at neap, development becomes somewhat slower, to be once more greatly accelerated as the spring tides come on. Hence, if the optimum line were drawn with absolute accuracy, it would show a slight curve towards the vertical at each end, while the middle portion would be very nearly horizontal. This cannot be well shown in the diagrams, as the data are not sufficiently full.

6. We have taken the divisions in the antheridium as indications of the rate of development of the crop. As already explained, there is only one division in the oogonium rudiment—the one which separates the stalk-cell. In the case of the tetrasporangium this division takes place at a very early stage; here it is delayed until a few tides before the highest.

7. In most of the cases which are fully recorded there is a fairly close and significant correspondence between the semilunation and the number of tides occupied by the whole crop from the very earliest initiation to the final clearance. In Tables I–III this is seen when columns 3 and 8 are compared for the crops numbered 4, 7, 8, 10, 12, and 16. Thus, although any given sorus takes much less than a semilunation for its development, the whole crop occupies practically the whole of the interval from a given tide to the corresponding one in the next series.

8. Initiation and liberation during the earlier crops each occupies about ten to twelve tides. Later, in September and October, there is far greater uniformity as to stages of development, and the width of the crop-band is reduced to from six to eight tides, sometimes even fewer. This can be well seen by comparing Diagrams I and II. The principal reason for this is probably the cessation of growth, for elongation, as has already been shown, exercises a slightly disturbing influence on the regularity of the process. It is possible also that the recurrence of the crop-periods impresses the rhythm more distinctly upon the individual; this can be conceived of as possible whether we regard the periodicity as inherited or merely induced during ontogeny.

9. Reverting to a point already mentioned, the existence on the distal portion of an elongating plant of sori very much younger than on the remainder of the thallus naturally suggests an inquiry as to their subsequent fate. Do they mature and liberate with the current crop, or remain until the succeeding one? Very careful observation of a large

number of cases makes it certain that the great majority mature very soon after the others. In some cases, particularly when the conditions are unfavourable, they are arrested shortly before maturity, degenerate *in situ*, and very soon fall off. In very exceptional cases, more especially when very late in starting, they may remain on the plant till the succeeding crop. It is evident that in the first case there must be considerable acceleration as compared with the crop-optimum. This is probably due to the greater vigour of the part. Now, if younger sori can be started in the manner just described, at the 'wrong period,' so to speak, why could similar ones not be interpolated among the older sori on the other parts of the thallus? The probable answer is that the formative reproductive material or energy is diverted into the adjacent sori, which being already started form centres of reproductive metabolism for the neighbouring cells. When a plant gets old it frequently happens that the distal sori, instead of being later, actually liberate before the others. The reason for this would probably be found in the senility of the older parts and the greater metabolic activity of the distal portions, which have not as yet produced many crops.

10. In most cases the crop-band, if accurately plotted, would show a greater width at the initiation end than at the other; hence there must be acceleration of the later among the ordinary sori. (Here the exceptional distal sori discussed in paragraph 9 are excluded.) This is clearly shown in Diagram I, where the difference amounts to as many as four tides.

In Diagrams III and IV the optima of the two sets of crops above discussed are compared. The interval between the highest spring tide and the discharge of the gametes in the two cases is well shown, and the agreement between the crops in the respective groups is most striking. The diagrams also show the variation in length of the optima, but it does not indicate the corresponding variation in the length of the tidal periods.

In the above discussion the crops of October and early November are left out of consideration. In view of the regularity of the August and September crops those of the later months disclose a very remarkable retardation, which progressively increases until initiation coincides with the rising spring tides, and liberation is effected at, or just before, the lowest neaps, thus almost reversing their usual tidal relations. It would only be natural to expect a retardation towards the close of the season when so many unfavourable conditions supervene; the remarkable thing, however, is that *the optimum is not lengthened by a single tide*. This is well shown in Table III, where the percentages in column 5 are 76 and 74. Here, then, although there is great retardation, the periodicity is as clearly marked as ever.

In the second paper of this series I suggested that it would be interesting to find out whether the periodicity, which up to that time

had only been verified for the coasts of North Wales, obtained also in other districts, or was merely a phenomenon induced by circumstances peculiar to the locality. A number of short visits had been paid to Weymouth, Torquay, Sidmouth, and other places, and the sexual plants observed on these occasions clearly suggested periodicity. During the summer of last year, as well as of this, I spent five weeks at the Marine Biological Laboratory in Plymouth, and while there I was able to follow out the whole course of development of a number of crops. The periodicity is as well marked here as in the Menai Straits, but the liberation of the crops is delayed several tides beyond the time when it occurs on the North Wales coasts. This is exceedingly significant, and the reason for it will be discussed later on.

Furthermore, a careful examination of the plants in the herbaria of the Natural History Museum and of Kew shows clearly that periodicity occurs on the coasts of other countries, especially on those of France and Spain, and even in various parts of the Indian Ocean and Australasia. Besides, there are unmistakable indications of its obtaining in the case of several foreign species of *Dictyota*. At the same time specimens were seen where sori of different ages were mixed up together. It would not be wise to generalize too much from herbarium specimens, but we may safely conclude that periodicity obtains generally in the case of several species of *Dictyota* in seas where the rise and fall of the tide is fairly well marked.

PROBABLE CAUSE OF PERIODICITY.

Whatever factor be suggested as the cause of this phenomenon, it must of necessity be one which varies with the tides and which produces its most potent effect during or soon after the spring tides. There are several which seem to satisfy these requirements to some extent, such as variations in the degree of aeration and of pressure, and particularly differences of temperature and of illumination.

The amount of aeration may possibly have some influence on the form and on the size of the plants, but it is most unlikely that it has anything to do with determining the periodicity of reproduction, for the great difference in amount of aeration between deep-growing plants never exposed, and those which are habitually emergent during low water of spring tides, is not reflected in any way in the condition of the sexual crops.

The alternation of pressure may have a much greater influence as a stimulus than we generally give it credit for, but actual observation of the widely different kinds of habitats in which *Dictyota* flourishes—in rock-pools at half-tide level as well as in deep channels, some never exposed and others left bare by the majority of spring tides—persuade us that this factor does not satisfactorily explain the phenomenon.

As for temperature, though it is a fact that exposure to a very high degree of heat brings about irregularities in the development of the gametangia, or otherwise causes injury to the plants, it is extremely improbable that the particular fluctuations of temperature to which the plants are subjected as a direct consequence of the alternation of neap and spring tides, are the effective causes of the regular succession of crops. If we take the Menai Straits, for instance, the difference between the temperature of the water in the channels where the current is nearly always flowing, and that of the shallow bays and eddies, or the pools left by the retreating tide, is enormous. A few inches below the surface the temperature in the current is fairly constant, showing a mean of about 13° C. in June, 14.5° in July, and 15.5° in August. When plants are left in shallow rock-pools they may in a short time experience a temperature of 21° C. or more; and as for the plants that are left quite uncovered, they will be subject to extremes of temperature that are greater still. It is important to remember that the most luxuriant plants and those which display the greatest regularity in the development of their crops are those which grow in the deep channels, where the temperature shows the least amount of fluctuation.

The lowering of temperature during October and November may have something to do with the retardation of the crops, but only as a secondary cause, as will be shown below.

I have been definitely forced to the conclusion that the stimulus which incites the plants to produce their fortnightly crops of gametes is the periodic change in the amount of light received by them, as a direct result of the alternation of neap and spring tides.

The time and mode in which the rhythmic variation of light takes place varies in different localities according to the time of the tides. Thus in the Swillies (Menai Straits) low water of the highest spring tides always takes place about six o'clock, morning and evening, while that of the lowest neap tides takes place about noon. The result is that during low water of neaps a considerable depth of water covers the plants, and this intercepts much of the light (Diagram V). It would be instructive to measure the amount of light obtained by a plant at various times; hitherto there has been no opportunity of doing this. During low water of spring tides many of the plants are actually emergent, and the others are so near the surface that they suffer but little loss of light. This is shown in Diagram VI. But this is not all, for during neap tides only one low water period occurs during daylight, the other taking place about midnight, whereas in the spring tide periods there are two exposures to the maximum of light—one at six in the morning, the other about the same hour in the evening. If, as is here contended, light be the determining factor in bringing about this rhythmic succession of crops, then it is perfectly evident that in the

Menai Straits we have ideal conditions for securing to the plants a high degree of illumination which at no time is in danger of being excessive. Partly as a result of this, *Dictyota* grows far more luxuriantly and fruits more freely and with greater regularity in the Straits than in any other locality where I have studied it.

If the above hypothesis be true, a locality where the times of the tides are the reverse of those obtaining at Bangor ought to yield different results. At Plymouth, for instance, the low water of springs always takes place about midday, thus giving only one period of strong illumination during the day. Of the three crops which I have most closely followed at Plymouth, two were developed during the higher spring tides of early August—one last year and the other at the corresponding period of the present year. In both cases general liberation did not take place until seven tides after the highest. In the third case, which was a low tide one, the crop was still later; initiation did not take place until after the lowest neap, and the crop was not discharged until at least twelve tides after the highest spring. The temperature was lower and the light poorer during this period than it was during the two preceding ones, so that some portion of the retardation may be due to this cause. Even after allowing for this, it is clear that all the crops are later at Plymouth than they are in the Menai Straits, a result which fits in admirably with the 'light' hypothesis. It may be suggested that inasmuch as the times of the tides are the reverse of those in the Menai Straits, giving two daylight periods of low water at neaps and only one during springs, that the times of initiation and liberation should also be exactly reversed. It must be borne in mind, however, that at the spring low water the plants are very much more exposed to the light than during the neap ebbs, and, what is still more important, that the light at noon is far more intense than at six o'clock. When collecting in the vicinity of Plymouth I observed that luxuriant fruiting plants were never found excepting where they were shaded from the direct rays of the noonday sun during the spring ebbs. The various forms of *Dictyota* are very abundant on the south coast, but when they are compared with those growing on the North Wales coasts one is at once struck with the smaller size of the plants and the greater difficulty of finding well-fruited specimens. The luxuriance of the Menai Straits plants may be partly due to the greater range of the tides and to the continuous circulation of clean sea-water; but it is highly probable that much of the success of the plants there, as compared with those of the south coast, depends on the fact that the total illumination obtained by them in the Straits is greater than that experienced by the Plymouth plants, and at the same time that maximum illumination occurs at a time of the day when there is far less danger of excessive insolation.

It has been pointed out in a preceding section that after the higher

springs the crops in the Menai Straits are later in their liberation by at least two tides than after low springs. The idea that this apparent retardation is due to excessive illumination, or to exposure to the air during the extraordinary low water of these tides cannot be correct, for it obtains in deep channels and in well-shaded rock-pools just as in more exposed habitats. The explanation is to be sought for at the other end of the crop period. A low spring crop liberates early simply because it had a good start during the higher springs of the preceding series, and the comparative lateness of the high spring crop is due to the less favourable light conditions prevailing during its early stages.

In the case of Plymouth it is highly probable that the above relations are reversed. The two higher springs recorded agreed in having the liberation seven tides after the highest, while the low spring crop took as many as twelve tides before the plants were cleared. When the records are so few it is unsafe to generalize, but if the above relation be correct it will be seen that this also harmonizes perfectly with the hypothesis. In these cases the crop periods lie wholly within the respective spring tide periods. It is only natural then that a high spring crop should mature early. It is in accordance with this also that we find the optimum length in the latter shorter than in the lower springs.

The remarkable retardation of the crops in the Menai Straits during October can also be easily explained in the same way. That this reversal of the time is not due to very unfavourable circumstances is shown by the fact that the optimum length of the crop is not increased. As the day shortens, the light during both morning and evening of spring tide ebbs becomes gradually poorer, until at last the midday light of neaps is actually better than morning and evening light of springs. The result is that the crop periods very nearly correspond to those obtaining at Plymouth.

A very striking instance of this is also seen in Cardigan Bay, where low water of spring tides takes place about three o'clock. Here, during August and September, sexual plants are far more liable to injury by excessive insolation than are the Straits plants, while later in the season the light during the early morning hours is missing altogether. These two peculiarities combine to bring the fruiting period of the plant to a close much earlier than in the Straits.

In August and September there is an overlap of the crops amounting frequently to two or five tides. During October, however, there is a gradually widening interval between the clearance of one crop and the first appearance of the succeeding one. A very remarkable circumstance, however, is that in spite of the retardation in the time of initiation there is no lengthening of the whole crop period. This seems to show that the rhythmic influence is so fixed in the plant that when conditions of light (and of temperature) change, the new crop is delayed until there is a sufficient

accumulation of reproductive energy and the necessary amount of light stimulus to start the 'wave' of activity.

By mid-November it generally happens that the antheridial sori become very small, and only a few of the cells in the centre of the sorus divide up to form antherozoids. This is chiefly due to senility (aided, of course, by unfavourable conditions), for one finds even at this time vigorous young plants in their first or second crop where this does not occur, and female plants with very few unshed oospheres. This shows the importance when studying the periodicity of these crops to take into account the age and vigour of the individual plant. In the earliest records also there was another slight error arising from the fact that when plants whose crops are nearly mature are brought into the laboratory, the liberation of gametes may be accelerated. In this way one has frequently succeeded in getting antherozoids to swarm in the laboratory five tides before liberation has started in the sea. How this acceleration is brought about—whether by increase of light, a higher temperature, or increased oxygenation—has not yet been made out, though several attempts have been made to solve the question by direct experiment.

It has been shown in the case of several plants, particularly of *Algae*, that a mere change of environmental conditions suffices to stimulate them to reproductive activity, or to a change in their mode of reproduction. It is a point deserving of consideration, whether the alternation of extreme conditions experienced during the ebb and flow of the spring tides does not in some way have an effect upon sexual reproduction in *Dictyota*. If it has any influence it clearly can be nothing more than a stimulus, and the evidences in favour of light being the effective agent in controlling periodicity appear overwhelming. In the Menai Straits, where there are two periods of full illumination during the day, liberation takes place very soon after the highest spring tide; at Plymouth, where there is only one such period, liberation is retarded. In the Straits, when the periods of maximum light change owing to the shortening of the day, the whole crop period is correspondingly shifted without incurring any alteration in its length or any other respect. On the North Wales coasts the liberations after low spring tides are earlier than those after high springs, whereas at Plymouth the contrary seems to be the rule. In all these cases the peculiarities are easily correlated with the times of springs and neaps and the consequent effect upon the light.

I have spoken above of light as *controlling* the periodicity of gamete production, and not as causing it. This is because it is shown in the next section that the phenomenon may occur in the total absence of tides and of any fluctuation in light besides the usual diurnal one.

IS PERIODICITY AN HEREDITARY CHARACTER?

The question which naturally arises at this point is—to what extent is the phenomenon of periodicity in *Dictyota* due to heredity? There are two possibilities which may be considered. We may conceive in the first place, of sensitiveness to a light stimulus being transmitted to the sexual generation in such a way that in all cases where there is a rhythmic fluctuation of light there will also be a corresponding periodicity in the production of gametes. Thus the *tendency* would always be present, only requiring the appropriate stimulus to manifest itself. In localities where there are no perceptible tides this stimulus would be absent, and consequently there would be no periodicity of crops. In the alternative case we may conceive of the character being so firmly fixed upon the sexual generation, that periodicity would manifest itself under any conditions, whether there would be any corresponding fluctuation of light or not. Should this supposition be the correct one, then the rôle of the light is merely to control the periodicity by fixing the periods of initiation and liberation, but not in any way to originate it.

At first the facts seemed to point to an ideal case of direct induction of a character by environmental conditions during the ontogeny of the plant. Thus the crops of June and early July appeared very vague and indistinct in their periodicity, for on the same plant would be found sori of several different ages. One might naturally suppose this to be due to the plants being as yet too young to have acquired the rhythm. Following this came the more and more distinctly marked periodicity of August and September, succeeded in October and November by retardation and irregularity, as the conditions became altered. The whole hypothesis seemed to fit the facts in a most admirable manner, but it was soon shown to be illusory. If only the portions of the July plants already mature be considered, the crops are found to be perfectly normal in their time of development, and in the case of the October crops the retardation really follows the changed light arrangements, and the finding of old and young stages together late in the season is chiefly due to the failure of many of the sori to become quite mature. Thus the periodicity is perfectly regular throughout, and there are no evidences of its being induced.

It would be very interesting to ascertain what happens in those seas where there are no appreciable tides; still more instructive would it be to cultivate the sexual plants from tetraspores. This is a most difficult undertaking, but it is to be hoped that some means will be found of getting plants under culture to thrive as in the sea. The history of one of the experiments tried by me is very curious and is exceedingly important in this connexion.

It has already been explained that the plant never fruits in the sea before June, and also that a fruiting plant transferred into a culture vessel in the laboratory may complete and liberate the current crop, but it is very unusual indeed for it to mature another. In October of last year two plants of *Dictyota*, one male, the other female, were placed in a glass dish about eight inches in diameter and containing about an inch of water. The dish was then closed with a lid and left absolutely undisturbed; the lid was not raised until the beginning of April in the following year. When examined the bottom of the dish was covered with what appeared to be brown dirt, but which on closer examination turned out to be a multitude of healthy little germlings, evidently the result of normal sexual fusion and not of parthenogenesis. The parent plants themselves had disappeared, with the exception of a number of little tips of branches, not more than $\frac{1}{4}$ inch long. When these were examined every piece was found to bear young sori, and *these were all in the same stage of development*. Two days afterwards the oogonia were apparently mature, and in two days more they all were liberated, while on the succeeding day the oospores had completed their first segmentation. In the same manner two more crops were developed. The first and second *took about the usual time* to pass through the various stages, but the last of the three was a weak one: many of the gametangia failed to mature, and after that the little branch-tips died, partly from exhaustion, but partly, it is to be feared, as a result of the interference of the experimenter.

Judging from the fate of numerous other cultures, the following was probably the course of events. The two plants when first transferred into the dish suddenly stopped the production of crops for a considerable period. After a time, however, they were able to adapt themselves to their changed environment, and when the necessary metabolic processes had been going on (very slowly, it is true), there came at last a time when the slow accumulation of reproductive energy caused the simultaneous initiation of sexual cells over the whole plants without the intervention of any kind of external stimulus. Gradually the older, basal portions became exhausted, died and decayed, leaving the bigger branches beyond the first dichotomy free. Still later, the smaller branches became separated in the same way, but each separate branch, however small, continued its rhythmic production of gametes, and on all the separate little pieces *the process was carried on simultaneously*.

After labouring to demonstrate the complete dependence of the periodicity upon the tide-table, it is startling to come upon a case like the above, where there cannot possibly be any circumstance external to the plant to suggest any rhythm in reproduction. It may be argued that inasmuch as these individual plants had been subjected to tidal influence when growing in the sea, they may have acquired the periodicity in such

a way as to 'remember' it, so to speak, after a period of quiescence, and under circumstances when the original stimuli were no longer present, where the temperature was fairly uniform, and when there was no fluctuation in the amount of daylight. This may have some amount of truth in it, but it seems to me far easier to believe that the periodicity is hereditary: that it arose in some ancestor of *Dictyota dichotoma*, and that it was afterwards modelled and fixed by the alternation of neap and spring tides until it became what we now see it. Even should this explanation be correct, it is difficult, however, to see how the crops in the dish should maintain the same optimum length as before, and especially how the small fragments should synchronize so remarkably after their separation from each other.

Briefly stated, then, the conclusion we come to is, that the periodicity of the sexual cells is a hereditary character, and consequently may be expected to manifest itself in seas and habitats where there are no tides. At the same time the sexual cells are so responsive to changes in the amount of illumination that the time of their development in seas where there are tides is regulated by the increased illumination obtained during the low water of spring tides.

LOCAL CONDITIONS AND THEIR EFFECT UPON THE CROPS.

The most favourable conditions for the production of regular crops of gametes are the following:—

(1) Ample light for their needs, without exposure to much direct sunlight at low water.

(2) A plentiful circulation of pure, clean water. As the plants are easily torn away or otherwise injured, the currents or waves must not be violent.

(3) Freedom from epiphytes and from dirt.

A few examples will show how the crops are affected when these conditions are not fulfilled.

Near the Menai Bridge a very shallow pool, four feet above low-water level, had well-grown sexual plants of *Dictyota*, whose sori were very unequal in development, and many of which failed to mature. In the channel below, growing on *Halidrys*, were luxuriant clean plants whose sori were all in the same stage, and of which none failed to mature. Immediately below these, but growing on the bottom of the channel, were other plants which were generally white with mud. At spring tide such plants often showed many sori near maturity, but with oogonia near their edges, which had been arrested and were degenerating, numerous whole sori which had ceased developing, sori that were fairly young, together with a large number of germlings growing *in situ*.

In the first example the irregularity and failure were due to excessive insolation and a high temperature, caused by the high level of the pool and consequent long exposure. In the case of the bottom plants, the same result is brought about by the continual settling of dirt on the surface of the thallus. Most of this foreign matter rests upon the hair clusters of the plant, and any sharp movement of the plant suffices to shake it off. The irregularities caused by the dirt are far greater in the lower portion of the thallus, where movement caused by currents is less felt. It must be kept in mind that even in these cases the periodicity is still sharply marked.

At Gallows Point, near Beaumaris, there are a number of muddy pools where *Dictyota* grows well. When these are covered at the flow, there is an eddy which prevents the current being much felt. The result is that the plants are to a great extent deprived of light by the mud suspended in the water, and especially by that which settles on the surface of the plants, making them appear hoary white. As this dirt is mostly kept from actual contact with the surface cells of the thallus by the hairs, the injury from mechanical irritation must be very slight compared with that caused by loss of light. On the same plant might be found, in addition to the normal condition, a large number of arrested gametangia, others that were decayed, oogonia which had reverted to the vegetative condition and segmented in the manner described in my last paper, and still others apparently mature—probably belated ones from the preceding crop. In addition to this, we find that the plants here are later in starting their reproduction by a fortnight or a month, and that they are slower in maturing their crops, than the cleaner plants of the Swillies.

In several places on the coast of Anglesea and Carnarvon, as well as in the English Channel, there are quiet sheltered bays where, during ordinary springs, there is a sufficient depth of water to protect the plants from excessive insolation. During the extraordinarily low water of the equinoctial springs, however, the plants are nearly or quite exposed; and as in many of these localities the exposure to maximum light takes place at midday or early in the afternoon, the result is that the plants suffer injury, the thallus becomes pale, and the gametangia are killed. The antheridia are fully divided and appear quite mature, but the antherozoids passively float out. It is probable that one reason for the failure of algologists to recognize the motility of the male gametes was that the specimens they studied had been injuriously affected in this way.

Another circumstance that affects the crops unfavourably is the presence of other plants within or upon the thallus, and it is in situations like the above that this is most apt to be troublesome. Endophytes generally grow between the cells, and in some cases their presence is

not so prejudicial to the plant as is that of epiphytes. Spores of small Algae are apt to be caught by the projecting edges of the sori, and if their growth is very rapid they deprive the surface cells of much of the light they would otherwise obtain. At Plymouth a small green Alga particularly affected the antheridial sori, the surfaces of which it covered with branching, creeping filaments before they managed to liberate their contents. When the hair clusters are eaten off the thallus by marine animals, as they frequently are, the access of foreign spores is greatly facilitated. When the plant becomes infested in this way with epiphytes the result is immediately observable in a diminished production of gametangia, a greater inequality in the ages of the sori, and some amount of delay in their maturation. In this connexion the general ecology of the habitats becomes important. In some localities most of the Algae reproduce in winter or spring, while in others the majority are summer- or autumn-fruiting plants. It is clear that *Dictyota* in the former habitats will be freer of epiphytes than in the latter, and their own reproduction will be correspondingly more successful.

During two visits paid to Meadfoot (Torquay) this August, most of the sexual sori were found to be several stages later than the Plymouth plants. The plants were apparently free from epiphytic growth, but on examining them microscopically they were found to be completely covered with exceedingly fine, nearly colourless, filaments, seemingly of a cyanophyceous nature, and it was probably this growth that caused the marked retardation of the crop.

It has been proved above that changes in the meteorological conditions do not determine the main facts of periodicity for any locality, but that they may, and frequently do, bring about slight modifications in the time of development by either accelerating or retarding it. One striking result of continuously favourable weather conditions is to make the development of the sori more uniform. In the diagrams this is visible in the narrowness of the crop-bands. When, on the other hand, unfavourable weather prevails, the sori are less uniform and the crop-band becomes wider.

If meteorological observations were kept, in order to test the effect of weather on the crops, mere daily records of the total amount of sunshine, mean temperature, &c., would not be satisfactory, for the state of the weather during low water of spring tides is manifestly of greater importance to the plant than during any other time. This applies to the amount of sunshine, the temperature of the air and of surface water (in the case of exposed or nearly exposed plants), and also the force of the wind. The effect of the latter on plants in the lower zones is much greater at low than at high water. If the wind is moderate the movement of the waves is beneficial to the plants in causing effective

aeration, and in keeping their surfaces clean ; if, on the other hand, the wind is violent, the waves tear the plants away or injure them by abrasion of the surface cells, causing various kinds of adventitious growths. When *Dictyota* grows on surf-beaten rocks it is generally dwarf, and in female plants most of the oogonia fail to mature, but divide vegetatively until the whole surface becomes thickened with parenchymatous growth.

Why oogonia, when arrested, should sometimes degenerate and ultimately fall off, while at other times they revert to the vegetative condition and form multicellular growths which remain permanently on the thallus, we cannot decide, nor do we know exactly under what particular conditions this takes place, except that it is apt to occur late in the season, and also in laboratory cultures. It is highly probable that in the second case the arrest takes place at an earlier stage than in the first.

Having described habitats where unfavourable conditions prevail, it would not be amiss to describe the one where I have found the sexual plants to flourish best. This is in the Swillies, a part of the Menai Straits already alluded to, where there are deep channels with clean sandy bottoms, through which there are continuous steady currents of clear water. Immense tufts of *Halidrys* grow down in the lowest zone, and on these tufts an abundance of luxuriant *Dictyota* plants flourish which, in consequence of the clearness of the water, and the currents, aided by the continual swaying movement of the long *Halidrys* on which they are borne, are kept perfectly free of both dirt and epiphytes. These plants are of a large size, healthy in appearance, and of a rich deep colour, while their crops are most abundant and regular in their development. On the south coast the habitat most nearly resembling this that has come under my observation is in some deep channels to the landward side of the Mewstone (Plymouth), where clean and luxuriant *Dictyotas* grow, not upon *Halidrys* in this case, but upon *Cystoseira*.

It has been pointed out that one of the results of unfavourable conditions is the arrest and sterilization of gametangia. It is interesting to note that these are nearly always located at the outer edges of the sori. In this way the normally borderless sori of oogonia acquire borders of sterile cells, and in extreme cases all the gametangia are arrested, or only a few in the very centre arrive at maturity. Even in the case of plants where there has been no sterilization the same thing is observable, in the fact that liberation generally starts in the middle of the sorus. This localization of the reproductive energy is interesting. First there seems a 'flow,' as it were, into definite areas which change with each crop ; then we have greater vigour in the centre of such an area, as shown in the more frequent failure of the peripheral cells.

While studying the periodicity of *Dictyota* this summer at Plymouth,

I gathered between Penlee and Rame Head a unique specimen. Though I have examined many thousands of plants in different parts of the coast, I have never come across one similar to this. It was apparently a male plant with the antheridia mature, but in the lower part the sori had very numerous oogonia as well. All the sori on the distal third of the plant were male. On the remainder of the plant the number of oogonia progressively increased towards the base, so that they were most numerous on the weakest part of the plant. Some of the sori had a few oogonia at one end or close to the periphery: in a few curious cases the borders of the male sori had been converted into oogonia. Some sori were wholly female and devoid of borders, and in cases where there were a few antheridia these were squeezed up in the centre between the swelling oogonia. Besides the general appearance of the plant, another circumstance pointed to its being a male which had developed female cells, and that was that in a great many cases the oogonia were derived from half-antheridia: that is to say, the antheridium rudiment divided once, or even twice, and then the two, three, or four resulting cells became oogonia. This, of course, resulted in very great inequality of size in the oospheres. While examining the specimen many of the eggs could be seen emerging from the oogonia. Three pieces of the plant were placed in as many culture-vessels, to see if the eggs would be fertilized; and as a control experiment, pieces of ordinary male and female plants were placed in a fourth. The antherozoids were not attracted by the oospheres. Sometimes wandering sperms would approach an egg, stop an instant above its surface and then proceed on their way—a fact which is of some significance in view of recent attempts to prove that there is no attraction in external fertilization. When the cultures were examined a few days afterwards the eggs in the control-culture had become normal germlings in an advanced stage of segmentation, but in the three other cultures a few eggs had divided parthenogenetically (a further proof that the bodies were eggs, and not gigantic sperms), while the rest remained undivided. At the time of writing the control-germlings are growing well, the other three sets died. An examination of the older scars shows conclusively that the previous crops were similarly anomalous.

PERIODICITY IN HALISERIS.

During the two past summers strenuous attempts have been made to work out the history of sexual reproduction in the remaining British genera of the Dictyotaceae—as yet, however, with but indifferent success. Though abundance of *Taonia* and *Padina* have been obtained, not a single sexual plant of the former, and but very few of the latter, have been collected. *Haliseris* is a more uncommon plant, but there is not the same disproportion between the numbers of the sexual and asexual individuals. At Plymouth

the plant is only obtainable by dredging, and even then it is so scarce that it is very difficult to hit upon. Though excellent tetrasporic specimens had been obtained, it was not till August 22 that sexual plants were brought up. The gametangia in these specimens showed such uniformity that periodicity was irresistibly suggested. All the antheridia were half-developed, showing 16-32 cells in surface view, and there were no rudiments. Scars of one previous crop were disposed in close proximity to the midrib, while the current crop area extended laterally outwards, and in a proximal as well as distal direction.

The next successful dredging was on August 29. All the antheridial sori were mature, and there were no rudiments. The female plants had numerous mature oogonia, and no young stages; but the numerous empty oogonia with the covers still undissolved indicated very recent liberation.

On September 1 some more plants were dredged. Of these the male plants had all the antheridia completely discharged, and there were no fresh sori, while the female plants had the mature oogonia liberated, but showed numerous very faint rudiments. The evidence in favour of periodicity is very strong, but without additional data it is impossible to decide to what extent it conforms with the periodicity of *Dictyota*.

While studying *Haliseris* two additional facts were ascertained, which, though not bearing directly on the subject of this paper, are of sufficient interest to justify their inclusion:—

(1) The antherozoids, as surmised by Johnson¹, are ciliated, and their activity is quite as great as that of the antherozoids of *Dictyota*.

(2) The liberated oospheres of *Haliseris*, when not fertilized, segmented a few times parthenogenetically and then died, exactly in the same manner as the unfertilized eggs of *Dictyota* do.

SUMMARY.

1. The reproductive period of *Dictyota dichotoma* in this country begins about the end of June or the beginning of July, and continues till the end of October or mid-November, the most active months being August and September. The antheridia and oogonia are produced in fortnightly crops which synchronize with the spring tides. In any given locality the great majority of gametangia on all healthy, mature plants are initiated at the same time; they pass through the several stages of development simultaneously, and general liberation and fertilization take place on a particular day, at a fixed interval after the highest spring tide.

2. In the Menai Straits the rudiments appear a few tides before neap, and the mature gametes are liberated from three to five tides (i. e. on the second or third day) after the highest succeeding spring. At Plymouth the crops are later, and liberation does not take place till from seven to twelve

¹ Johnson ('91), Lin. Soc. Journ., xxvii.

tides after the highest. The October crops in the Menai Straits are retarded until the original times of initiation and liberation are almost reversed.

3. Whether liberation in the Menai Straits takes place three tides after the highest, or whether it is delayed till the fifth tide, depends primarily not upon meteorological conditions, but upon the heights of the spring tides. Of the two sets of springs which occur during a month, one is generally higher than the other. This alternation of higher and lower springs is fairly regular, and, during the fruiting period of *Dictyota*, is very well marked, owing to the exceptional equinoctial tides, the difference in some cases amounting to three feet. In the Straits the crop matured during the higher springs is liberated about the fifth tide after the highest, whereas in the succeeding lower springs the crop is liberated about the third tide after the highest. At Plymouth the reverse is the case, the shorter interval (seven tides) coinciding with the higher springs, and the longer (ten to twelve tides) with the lower spring tides.

4. The 'optimum of development' (= the time taken by an average sorus to develop) is variable in length. In the Menai Straits it may be from nineteen to twenty-five tides. This inequality is due not to meteorological conditions, but to the variable length of the 'semilunation,' or the interval between new and full moon, and consequently between the springs. Sometimes this is as low as twenty-five tides, while at others it is as many as thirty-one. The length of this interval does not affect the actual period of liberation, but it determines the length of the 'optimum of development,' the average ratio of the latter to the semilunation being 76 : 100.

At Plymouth it is probable that the length of the 'optimum of development' is directly dependent on the height of the spring tides, and not upon the length of the semilunation.

5. In the Menai Straits, where the crop is started during the waning of one set of springs and matured during the succeeding set, development is at first fairly rapid; it then becomes slower during neap tides, finally being accelerated again with the increasing 'rise' of the spring tides. At Plymouth, where the crop starts at or soon after neap, development is at first slow, but becomes progressively more rapid towards the close of the period. Thus all the facts go to show that development is determined by the time and height of the spring tides, and that progress is very slow during neaps.

6. Owing to this acceleration of development at maturation, the late-starting sori at the distal ends of growing plants are not much behind the rest of the crop in their liberation, and the 'crop-band' is consequently several tides narrower at the liberation than at the maturation end."

7. As the season progresses the crops show greater uniformity in the ages of the gametangia, so that the 'crop-bands,' which at first were ten to twelve tides wide, become narrowed to six tides or fewer.

8. Of the various factors (temperature, pressure, aeration, &c.) which fluctuate with the alternation of neap and spring tides, the one which seems to account most satisfactorily for the facts of periodicity is the increased illumination experienced by the plant during low water of spring tides; and the striking difference between the details of periodicity at Plymouth and in the Menai Straits are due to the difference in the time of day at which low water of spring tides occurs in the two places.

In the Menai Straits (east end) this always takes place between five and six, morning and evening, so that there are two periods of maximum illumination every twenty-four hours, whereas low water of neaps occurs about twelve o'clock. Here there is only one ebb during daylight, and the illumination then is much poorer than during low water of springs. At Plymouth the reverse is the case, low water of spring tides occurring at noon and at midnight; thus the total amount of light obtained during springs is less, and the difference between neap- and spring-tide illumination is not so great as in the Straits. The result is that at Plymouth the plants are poorer, and the crops several tides later in their development.

9. Other peculiarities in the times of the crops may be explained in the same way, e. g. the retardation of the October crops in the Menai Straits is due to the loss of morning and evening illumination owing to the shortening of the day. (This retardation is not accompanied by a lengthening of the crop period.) The earlier liberation after low springs in the Straits is due to the better start obtained by the crops during the preceding higher springs. At Plymouth, where each crop, starting about neap, coincides with a single set of spring tides, the time of liberation (and probably also the length of the crop period) is directly dependent on the height of the tides.

10. The times of initiation and liberation thus fixed primarily by the time and height of the spring tides may be slightly accelerated or retarded by exceptional meteorological conditions. Winds may cause a difference of two to three feet in the height of the water, and a rise of one inch in the barometer may result in a depression of six or seven inches in the tide, while extreme fluctuations of temperature or light may directly influence the rate of development of the crop.

11. So intimate is the relation between the tides and the crops of sexual cells, that a study of the tidal almanac for any locality will enable us to predict the actual days during August or September in any given year on which general liberation and fertilization of gametes will occur; and even should exceptional conditions prevail, the resulting error will only be about a day earlier or later than the one predicted. It follows that in all places on our coasts where low water of springs occurs at the same hour (i. e. in places with the same 'establishment') maximum liberation will take place on the same day.

12. A study of herbarium specimens shows that periodicity in the case of *Dictyota dichotoma* obtains in other seas besides our own, in localities widely separated from each other and extending as far as Australasia, and in several other species of the genus. There is as yet no evidence to show that it occurs in seas where there are no appreciable tides.

13. In the case of the tetrasporic plants of all our British genera of Dictyotaceae there is no trace of periodicity. Throughout the season, and at every stage of the tides, sporangia of all ages may be found together on the thallus.

14. In a laboratory experiment fragments of plants collected in October and left undisturbed in a small glass dish produced a succession of crops the following April. All their stages were quite similar, the length of the crop period was exactly the same as if the plants had been in the sea, and liberation and fertilization took place in a perfectly normal manner. The natural inference is that periodicity is a hereditary character. At the same time the preceding observations show with equal clearness that in seas where there are tides the periods of the crops are directly regulated by the alternation of high and low tides, so as to secure for the crops the maximum advantage possible from the increased illumination during low water of spring tides.

15. The above observations apply to 'healthy' plants. Such plants require for their development:—

(1) Ample light, without exposure to much direct sunlight at low water.

(2) A continuous circulation of pure, clean water.

(3) Freedom from endophytes, epiphytes, and dirt.

Where these conditions are not secured the following results may ensue:—

(1) Delay in commencing the reproductive season.

(2) Retardation of the crop.

(3) Inequality in the ages of the sori.

(4) Reversion of half-developed gametangia to the vegetative condition.

(5) Degeneration of more advanced gametangia.

In quiet bays without much shelter the plants are apt to suffer from excessive insolation, especially if the weather happens to be very bright during low water of equinoctial tides: this is generally associated with the attacks of parasites, which are particularly abundant in such waters. In such cases the antherozoids are discharged from the mature sori in a passive condition.

The lower temperature and diminished light towards the close of the season result in smaller sori and a great increase in the number of aborted gametangia.

16. A solitary specimen of *Dictyota* was collected whose sori had both

oogonia and antheridia. Some of the oogonia were small, being equivalent to half- or quarter-antheridia. When liberated none of the oospheres attracted the antherozoids, but some of them divided parthenogenetically and then died.

17. *Haliseris* seems to have a similar periodicity in the development of the sexual cells, but the details of the process have not as yet been fully worked out. As surmised by Johnson, the antherozoids are ciliate. They are also very active, and the unfertilized eggs show the same parthenogenetic phenomena as do the eggs of *Dictyota*.

Having discovered a plant whose sexual reproduction shows such remarkable response to external stimuli, it is evidently desirable that observations such as have been here attempted should be made on other coasts, and at the same time be made much more detailed and accurate. My apology for the incompleteness of my own is that they were really only incidental to my cytological work on the group, and made under great difficulties in the short intervals obtained during professional work. If such work be taken up by other algologists, I hope this paper will be of some assistance in setting about the initial steps. To perform such a task successfully, it would be necessary to find a habitat such as the Swillies, where an abundance of clean and healthy plants could be obtained. Plants should be collected and examined at least every alternate day, records should be made from healthy mature plants only, and full particulars should be kept of the times and heights of the tides, and—a point which I omitted to mention in the body of the paper—the direction and force of the wind and the state of the barometer should be entered, for the two things frequently modify very materially the tides as given in the tidal almanac. In fact, the only method of dealing satisfactorily with the tides would be to have a self-recording tide-gauge: this would give an absolutely faithful record of the height of the water at any given moment. In addition to this it would be necessary to accurately measure the amount of light obtainable at different periods of the tide and the variations of temperature. Were this sort of accurate work done at a number of stations, it would form a valuable contribution to our knowledge of the response given to external stimuli by the reproductive process in this plant.

I gratefully beg to express my obligation to the Council of the Royal Society for giving me a grant of money to enable me to carry on my study of the Dictyotaceae on the South Coast, and also to the Royal Microscopical Society for nominating me to their table in the Marine Biological Laboratory at Plymouth. To Dr. Allen, the Director of the latter institution, and his assistant, Mr. Smith, I also wish to express my deep obligation for their unfailing courtesy and their readiness to place the resources of the establishment at my disposal. It is a matter of surprise that so few algologists take advantage of such a well-equipped and admirably conducted station.

DIAGRAM I. Maturation of crop during lower Spring tide (Menai Straits).

DIAGRAM II. Maturation of crop during higher Spring tide.

DIAGRAM III. Comparison of optima of crops liberated during higher Spring tides in August and September (Menai Straits).

DIAGRAM IV. Crops liberated during lower Spring tides. August and September (Menai Straits).

The numerals under the curves refer to tides in Diagrams I and II.

DIAGRAM V. Heights and hours of low water of neap tides during three days in August in the Swillies (Menai Straits).

DIAGRAM VI. Heights and hours of low water of Spring tides during three days in August in the same locality.

NOTE.—For Plymouth the times of the tides should be reversed so that in Diagram V low water would occur twice during daylight, and in Diagram VI low water would occur at midnight and midday. For October tides in the Straits if the 'darkness' band is extended, the advantage of the Spring tide low water is obliterated to a great extent.

Williams, J. Lloyd. 1905. "Studies in the Dictyotaceae." *Annals of botany* 19, 531–560. <https://doi.org/10.1093/oxfordjournals.aob.a089027>.

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