J. mar. biol. Ass. U.K. (1959) 38, 153–167
Printed in Great Britain

EXPERIMENTS ON SOME EFFECTS OF CERTAIN ENVIRONMENTAL FACTORS ON *GRACILARIA VERRUCOSA* (HUDSON) PAPENFUSS

By W. Eifion Jones

Marine Biology Station, Menai Bridge, Anglesey

(Text-figs. 1–3)

At an early stage of an autecological study of *Gracilaria verrucosa* (Hudson) Papenfuss it seemed possible that the best growth of the plants occurred in places, such as the Achill Sound and the Church Island Channel in the Menai Straits, where, in the absence of heavy wave action, strong currents flowed over the plants. Experiments were carried out, in the sea, to investigate the effect of currents on the growth rate; the apparatus used and described here would probably be suitable for the investigation of current effects on other sedentary marine organisms.

These experiments also led to some observations on the effects of illumination on the pigmentation and growth rate of the plants which were supplemented by laboratory experiments. High intensity illumination in the laboratory also demonstrated positive phototropism in the plant.

FIELD EXPERIMENTS

Apparatus

The raft shown in Fig. 1 was designed and constructed in timber. Two of the four parallel compartments (*W* and *Y*) were open at the ends, top and bottom. The other two (*X* and *Z*) had pointed bow and stern sections closing them to the current and also perforated wooden bottoms which were shown, by trials, to be necessary to prevent turbulent upwelling when the raft was moored in a rapid current. The raft was moored astern of an anchored barge in the Menai Straits, both being free to swing with the tidal stream so that the raft faced constantly into the current. The tidal current in this part of the Straits reaches about 3 knots. To prevent the entry of floating weed and other debris, the open compartments were protected at both ends and bottom by ½ in. mesh wire netting. Shrimp netting of ⅜ in. mesh was lashed over the top to prevent floating matter being washed into the compartments by waves. The net also had the effect of shading the interior to some extent.

When first launched the raft floated with 10–12 cm freeboard; waterlogging of the wood later reduced this and eventually net floats had to be attached to maintain a freeboard of 5–8 cm. Water entered rapidly through the perforated bottoms of the closed compartments. The accumulation of waterborne silt in these compartments demonstrated the movement of water in and out of them and that stagnation need not be feared.

In each compartment longitudinal battens were arranged to support four 'Tufnol' plastic bars. Two specimens plants were tied to each bar; thin nylon

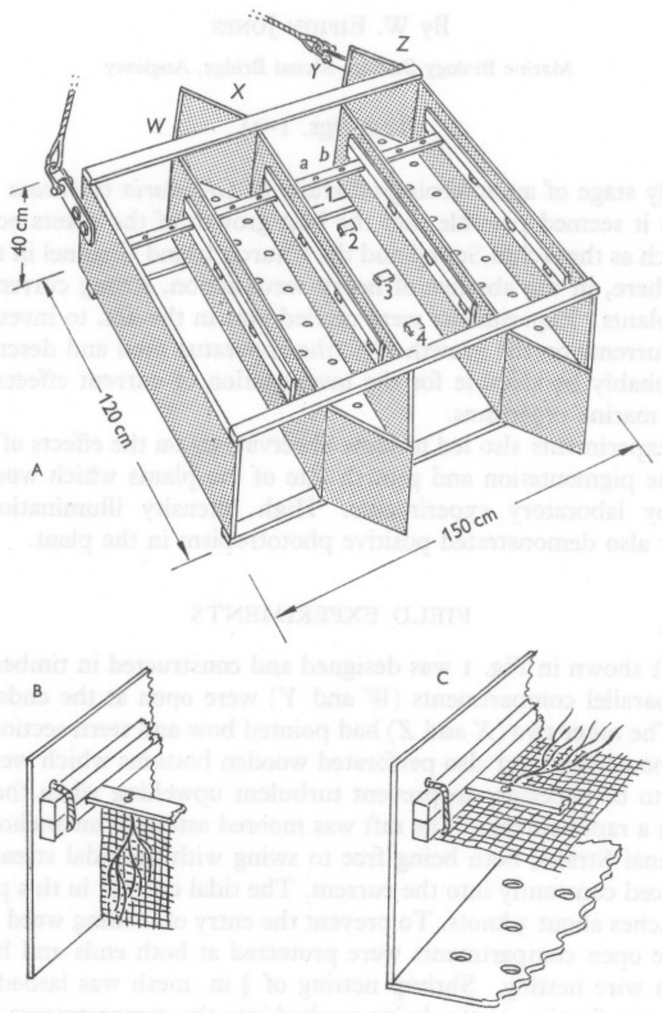

Fig. 1. A, raft used in experiments on the growth of *Gracilaria verrucosa*. Some structural members are omitted for clarity. The four compartments are lettered as shown for reference; the positions of the 'Tufnol' bars bearing the plants are shown in compartment *Y* and were similar in the others. B and C, modifications to compartments *W* and *Z* respectively as described in the text.

fishing gut proved to be the most satisfactory material for this purpose. The bars with the plants attached were removed periodically for examination.

The raft was used in this form during the first season's experiments.

Recording

The specimens used consisted either of a single branched axis with its individual holdfast or else a suitably sized clump of axes arising from part of an expanded holdfast of several seasons' growth. For convenience these specimens are hereafter referred to as 'plants'. The plants were weighed at the start of the experiment and subsequently at intervals of about 10 days. During the first season they were also photographed against a background ruled in 2 cm squares to investigate form changes.

Weighing was carried out with the plants suspended from the arm of a 0–1 g torsion balance so as to be completely submerged in sea water. This method avoided the uncertainty involved if the superficial moisture had to be removed before the plant was weighed in air and also reduced the risk of damage by desiccation during weighing. Although the weight measured was small, owing to the density of the plants being only a little greater than that of sea water, this method was found to be quick and reliable, provided care was taken to ensure that the plants did not touch the sides of the containing vessel or the water surface during weighing and that no air bubbles were trapped amongst the branches.

Results of the first season's experiments

The comparative increases in the fresh weight of a set of thirty-two plants, collected at Criccieth and grown on the raft from 25 June to 6 July 1954, are shown in Table 1. Fig. 1A shows the arrangement of the raft compartments and plant positions. It will be seen that while plants in the open compartments *W* and *Y* increased by about 62%, those in the closed compartments increased by only about 36%. These differences are statistically highly significant. Results in succeeding periods were similar, except where loss of plants or damage occurred.

Conclusions from the first season

It was obvious that growth was more rapid in those compartments open to the current, but it became evident that this was not necessarily due to the direct effect of the current itself. It was observed that the plants in the compartments open to the current lost their original dark red colour, changing to a light straw, while those in the still water compartments were not greatly changed. It is generally accepted that this loss of colour results from strong sunlight and occurs in many red algae in summer. The difference in pigmentation in the current and still water compartments presumably resulted from

TABLE 1. COMPARATIVE INCREASE IN WET WEIGHT OF PLANTS ON RAFT DURING PERIOD 25 JUNE–6 JULY 1954

The values given for the weights are the torsion balance scale deflexions. These are almost exactly one-third of the fresh weight in g.

		Weight			
	Plant	25. vi.	6. vii.	Gain	% gain
W. Open	1*a*	0·57	0·90	0·33	57·89
	b	0·46	0·81	0·35	76·09
	2*a*	0·77	1·51	0·74	96·10
	b	0·27	0·52	0·25	92·59
	3*a*	0·37	0·60	0·23	62·16
	b	0·30	0·03*	—	—
	4*a*	0·96	1·22	0·26	27·08
	b	0·79	0·97	0·18	22·70
		Mean gain 62·09 %			
X. Closed	5*a*	1·91	2·74	0·83	43·45
	b	0·13	0·24	0·11	86·61
	6*a*	2·43	2·86	0·43	17·69
	b	0·26	0·30	0·04	15·38
	7*a*	1·76	2·33	0·57	32·38
	b	0·47	0·68	0·21	44·68
	8*a*	2·28	2·81	0·53	23·45
	b	0·80	1·02	0·22	27·50
		Mean gain 36·14 %			
Y. Open	9*a*	0·50	0·90	0·40	80·00
	b	0·19	0·32	0·13	68·42
	10*a*	1·30	2·12	0·82	63·07
	b	0·25	0·45	0·20	80·00
	11*a*	0·89	1·40	0·51	57·30
	b	0·17	0·30	0·13	76·57
	12*a*	1·88	2·78	0·90	47·87
	b	0·36	0·44	0·08	22·22
		Mean gain 61·93 %			
Z. Closed	13*a*	2·02	2·88	0·86	42·57
	b	0·42	0·48	0·06	14·29
	14*a*	1·20	1·65	0·45	37·50
	b	0·57	0·77	0·20	35·09
	15*a*	0·77	1·02	0·25	32·47
	b	0·29	0·40	0·11	37·93
	16*a*	0·40	0·65	0·25	62·50
	b	0·19	0·25	0·06	31·57
		Mean gain 36·74 %			

Analysis of variance

Source of variation	Degree of freedom	Sum square	Mean square	Variance ratio	Probability
Current	1	5229·83	5229·83	11·3	1·0–0·1 %
Pairs of compartments	2	1·53	0·77	·0017	> 20 %
Replication	27	12532·81	464·17	1·0	> 20 %
Total	30				

* Plant damaged: in calculation this value taken as equal to mean of remaining plants in block I.

differences in illumination. The shading by the partitions caused some reduction in the amount of light reaching the lower parts of each compartment. Thus, where the current was flowing, the plants were trailed out horizontally, level with the tufnol bars, less than 10 cm below the water surface and so received all the light available at that level. In the closed compartments, on the other hand, the plants hung downwards most of the time and therefore received less light because of the shade cast by the partitions and the mutual shadow of their own fronds. Thus the results obtained might be due primarily to differences in illumination rather than conditions of current or still water. In the following season the experiment was redesigned to investigate this.

Modification of the apparatus

One closed compartment (*X*) was left unchanged. In the other (*Z*) a net was arranged horizontally below the tufnol bars so that the plants were held permanently spread level with them (Fig. 1 C). One open compartment (*Y*) was not altered; in the other (*W*) a series of nets was fitted, one behind each bar so as to prevent the plants being swept out horizontally by the current which, instead, kept them pressed against the nets in the hanging position (Fig. 1 B). As the currents flowed for only part of the day (on the flood and ebb) and as some movement of the free plants occurred in all but a flat calm, the new conditions meant that plants in compartment *Z* would obtain the most light and those in *W* the least.

Recording was carried out as before except that the plants were not regularly photographed and that a note was kept of the changes in their colour.

Results

Table 2 gives the results of these experiments. As the periods between successive weighings were not all of equal length, the weight increases are divided by the length of the period and presented as percentage increases in weight per day. The table includes the changes made in the position of the groups of plants after the first growth period (24 May–8 June), when those in the current compartments were exchanged with those in still water, and also shows the observed colour changes in the plants.

During the first growth period the plants in compartment *Z* (held horizontal in still water) and those in *Y* (free in current) showed an average daily increase in weight of 5·33 and 4·39% respectively. Those in compartment *X* (free in still water) and in *W* (held vertically in current) showed, respectively, 2·75 and 2·82% increase per day. Statistical analysis showed that the differences resulting from conditions of still water and current were not significant, but that the difference between the increase in the plants which received most light (in *Z* and *X*) and those which were shaded was highly significant.

TABLE 2. GROWTH OF *GRACILARIA VERRUCOSA* SHOWN AS PERCENTAGE INCREASE IN FRESH WEIGHT PER DAY IN CONDITIONS OF CURRENT AND STILL WATER, FULL LIGHT AND SHADE ON A RAFT DURING 1955

(1) Condition of plants on 24 May	(2) Compartment occupied 24 May–8 June	(3) % gain per day 24 May–8 June	(4) Condition of plants on 8 June	(5) Compartment to which transferred 8 June	(6) % gain per day 8 June–21 June	(7) Condition of plants on 21 June	(8) % gain per day 21 June–5 July	(9) Condition of plants on 5 July	(10) Condition of compartment on 5 July and treatment	(11) % gain per day 5 July–27 July	(12) Conditions of plants on 27 July
Fully pigmented	*Z* (held horizontal in still water)	5·86	All red colour lost	*W*	0·58	Some red colour regained	2·57	Red colour almost fully regained	Many filaments of algae on nets. Cleared 5 July	2·18	Fully pigmented
		1·91*			0·78		3·16			1·64	
		4·91			1·57		0·92			3·95	
		5·80			0·57		0·82			—	
		4·79			1·14		0·09*			—	
		4·86			—		3·18†			4·54	
		5·15			1·26		1·46			0·24*	
		6·20			1·21		1·56			—	
	Mean	5·33			1·01		2·02			3·08	
Fully pigmented	*Y* (free in current)	5·00	Red colour much reduced	*X*	3·00	Most red colour lost	2·10	Most red colour lost		—	Most red colour lost
		4·42			4·37		2·36			3·54	
		—			3·54†		2·35			—	
		—			4·95†		4·13			2·97	
		—			5·45†		3·31			2·98	
		—			4·00†		1·93			3·26	
		4·85			2·31		0·74			3·72	
		4·29			3·42		2·40			—	
	Mean	4·39			3·92		2·41			3·29	
Fully pigmented	*X* (free in still water)	3·85	Red colour slightly reduced	*Y*	2·97	Red colour greatly reduced	1·86	Red colour largely restored	Heavy growth of filamentous algae. Cleared 5 July	2·86	Red colour much reduced
		1·35			4·28		—			4·86	
		1·67			2·35		2·33			—	
		—			3·48		3·28			—	
		3·84			2·15		2·72			6·18	
		4·34			4·85		0·82			1·69	
		1·47			2·53		2·71			6·05	
		2·64			4·96		1·86			4·77	
	Mean	2·75			3·42		2·23			4·40	
Fully pigmented	*W* (held vertical in current)	4·10	Colour unaffected	*Z*	3·15	All red colour lost	2·55	All red colour lost		4·14	All red colour lost
		3·55			4·77		2·46			1·46	
		1·69			5·02		1·93			0·24*	
		1·33			4·58		2·26			2·82	
		2·56			5·04		2·29			2·52	
		3·66			4·86		2·85			2·55	
		0·46*			2·30		1·63			—	
		—			2·76†		4·86			1·82	
	Mean	2·82			4·06		2·60			2·71	

Notes. Each horizontal row concerns the same plants throughout the experiment.

* Damaged plants: not included in calculations.

† New plants introduced to replace casualties.

Conclusions

It appears from these results that the effect observed in the earlier experiment was only secondarily due to current and resulted from the better illumination received by the plants spread out by the flow of water. Later experiments were made in the laboratory on the direct effect of current.

The plants in compartment *Z*, being constantly in a horizontal position, probably received more light than those in *Y*, which were horizontal only when the tidal currents flowed. The growth rate in *Z* did appear, from its mean value of 5·33%, to be higher than that in *Y* (4·39%), but statistical analysis did not show the difference to be significant.

Causey, Prytherch, McCaskill, Humm & Wolf (1946) showed that unshaded *Gracilaria* reached its maximum growth rate at 60 cm below the surface without improvement at lesser depths. In the present experiment pronounced differences in growth occurred in plants within the upper 35 cm of water but, owing to shading, plants nearer the surface received very much more light than the lower ones. Measurement of the light reaching the plants with the raft afloat and the nets in position was not practicable. A Weston meter showed that when the raft was out of the water the shading effect of its sides reduced illumination at the bottom of the compartments to about one-eighth of that at the level of the tufnol bars. Thus, if plants at the latter level were receiving 25% of the incident light owing to loss at the water surface (Sverdrup, Johnson & Fleming, 1942), then, after allowing for the difference shown by the meter, the lower parts might receive about 3%.

Bleaching effects

During the first growth period (24 May–8 June) the plants in the two well-illuminated compartments changed colour from their original dark red to a light straw colour as the photolabile phycoerythrin was lost. The colour of the plants in the two shaded compartments was virtually unaltered.

After weighing at the end of the period (on 8 June) the plants were replaced in different compartments for the remainder of the experiment. These changes are shown in Table 2. They involved interchange of the plants from compartment *W* (current and shade) with those from *Z* (still water and good illumination) and a similar interchange between compartments *X* (plants hanging in still water) and *Y* (plants free in current).

In the next period (8–21 June) bleached plants in the 'shaded' compartment *W* showed a much lower growth rate than unbleached plants in the same compartment in the previous period, while the unbleached plants in the 'light' compartment *Z* showed a high rate comparable to that of the first period. During this and subsequent periods the plants in *W* regained their colour while, at the same time, their growth rate increased, the successive average values for the daily rise in fresh weight being 1·01, 2·02 and 3·08%.

The latter value was rather higher than that for unbleached plants in the same compartment during the first growth period but may have been erroneously high as damage and loss had reduced the numbers of plants in the compartment and adversely affected the replication. At the same time, in compartment *Z*, the plants became bleached while growing rapidly (4·06% per day) in the 8–21 June period and, in the subsequent periods, grew at lower rates of 2·60% and 2·71% per day. This rate was similar, incidentally, to that of fully pigmented plants in the shaded compartments.

Meanwhile, settlement of the raft as its timbers became waterlogged and the loss of the attached floats frequently resulted in its being virtually awash and this, while not greatly affecting plants in *W* and *Z*, greatly reduced the shading effect in compartment *X* owing to the plants in it being swayed by movements of the raft and the shipping of water. In fact a reverse shading effect occurred between compartments *X* and *Y* owing to the rapid growth of filamentous algae in the latter (open to current) which shaded the *Gracilaria* plants and slowed their growth. At the same time, the plants in *Y* regained their colour and when, on 5 July, the shading weed was removed, a period of rapid growth followed comparable to that during the first period (24 May–8 June) and in both cases resulting, presumably, from the full illumination of unbleached plants.

Before considering the final conclusions to be drawn from these results it is proposed to describe supplementary experiments carried out in the laboratory.

LABORATORY EXPERIMENTS

EXPERIMENTS ON THE EFFECTS OF WATER CURRENTS ON GROWTH RATE

As a check on the current/still water experiment plants were grown in 3 cm. diameter Pyrex glass tubes. Four tubes were used and supplied with sea water from the laboratory system via a constant head device. The outflow from each tube was controlled by means of a screw clip closing a rubber tube. The rate of flow from each tube was found by timing the collection of a measured volume from the outlet. To prevent any rise in temperature the tubes rested in a tray and tap water was directed on to each. A thermometer was placed in each tube and showed that no temperature differences occurred.

Weighed portions of a single plant, divided at its expanded basal holdfast, were placed in the tubes. They were grown for 9 days under constant, even illumination of 600 lux from daylight type fluorescent tubes and then weighed again.

Results

Table 3 gives the results obtained.

TABLE 3

Approx. rate of flow (ml./h)	Increase in fresh weight (%)
22	7·7
1,500	14·9
7,200	20·4
36,000	20·2

Conclusions

It appears that the growth rate increases with increasing flow up to about 7 l./h, after which, under the conditions of light and temperature prevailing here, further increase in the flow rate does not induce faster growth. These results must, of course, be treated with great caution owing to the lack of replication and the shortcomings of the apparatus, in which it was difficult to maintain a steady flow. However, a flow rate of 7 l./h is equivalent to a current of about 1 m/h through the tube, so that it seems that currents cannot be expected to have a direct effect on the growth rate in the field, even allowing for the higher light intensity which the plants would receive for part of the time under natural conditions. More movement of water would occur even in the calmest conditions and, in fact, it seems that current becomes a limiting factor only when the water moves so slowly as to be almost stagnant. This is in agreement with the observations of Gessner (1940) who showed that respiration and assimilation rates in *Fucus* spp. were retarded up to 50% in stagnant water, compared with water in a shaken vessel.

EXPERIMENTS ON EFFECTS OF HIGH INTENSITIES OF ILLUMINATION

The bleaching effect observed on the shore and in the raft experiments occurred under conditions of intense summer illumination. Confirmatory experiments in the laboratory therefore require the provision of light of the same order of intensity.

Apparatus

In these experiments, two Strand Electric pattern 23 N theatre spotlights were used. These employ 500 W projector bulbs in highly efficient spherical reflectors and have a lens system concentrating the light in an 11° cone. They were set up so as to shine on to a mirror, inclined at 45° to the horizontal, which deflected their beams downwards. (This was to allow the lamp filaments to burn in the correct vertical position.) At a total distance of 65 cm from the front lenses the light from both lamps coincided on an area about 20 cm in diameter and here there was placed a white enamel dish 5 cm deep, through which a constant stream of sea water was passed, without causing ripples on the surface. Although the lamps produced considerable heat it was found possible to prevent the temperature of the water in the dish rising above its original level (that of the laboratory supply) by suitably adjusting the rate of flow.

The light intensity was not uniform over the whole of the illuminated area; in the brightest, central area the intensity of illumination was about 56,000 lux, as measured by a Weston meter with Invercone calibrated from a standard source. This value fell off away from the centre of the illuminated area and was of the order of 30,000–35,000 lux at the periphery. It must be borne in mind that the spectrum of the light from tungsten filaments is very different from normal daylight. The former is deficient in the ultra-violet and the shorter wavelengths of the visible spectrum. Thus, although in these experiments the measured intensities are comparable and the results similar, no quantitative correspondence should necessarily be expected between the results of the laboratory and field experiments.

Methods

Both mature plants and sporelings of *Gracilaria verrucosa* have been used. With the former it was intended to test the effect of increasing daily periods of intense illumination and at the same time to observe whether any phototropic response occurred. The latter phenomenon seemed likely from the observation of some forms assumed by the plant in the field. To prevent confusion of the results by the reflexion of the light upwards from the bottom of the dish and to hold the plants in a fixed position, they were attached by nylon thread to perforated 'Tufnol' plastic plates, each about 23 × 7 cm. so that no branches projected beyond the edges. When not under the bright light, the plants received constant illumination of about 500 lux from fluorescent lamps. In the first experiment three 'plants' were used, all parts of the same tetrasporic clump. The fresh weight of each was recorded before the experiment began and their colour checked against an arbitrary standard designed to show the change from complete bleaching to full pigmentation in eight numbered steps.

One of the plants was left in the dish under a constant illumination of 500 lux all the time to serve as a control, the others were given additional daily periods under the bright lights of 30 min and 1 h respectively for the first run of 12 days, these periods being increased in subsequent runs.

As only two plants could be accommodated under the lamps at once and as daily periods of 8 h were envisaged in the later stages, replication of this experiment was not practicable and this must detract from the reliability of the results.

Phototropism

At the end of the first run of 12 days the form of the control plant was unchanged. The branches of the other two, which had received respectively 6 and 12 h of strong illumination, were turned upwards towards the light

(Fig. 2), except where they were secured to the tufnol plates. After each weighing between runs these plants were turned over before being tied again to the plate; in each case the upward curvature was quickly re-established. Although appreciable growth of the control took place during the experiment, no upturning of its branches occurred. It may therefore be concluded: (i) The upturning is not due to gravity, since this factor affected all plants, including the control, equally. (ii) There is a pronounced positive phototropism in response to bright light of the order of full daylight but not, apparently, in response to lower intensities. As the lower intensities are sufficient to promote growth, it seems possible that the upturning is not so much the result of an auxin migration (its usual explanation in higher plants), which might be expected to occur under all intensities, but is a direct effect of the high light intensity, perhaps by speeding up growth of the more shaded and therefore less bleached lower side (see below). (iii) The response has been observed after as little as 3 h total intense illumination.

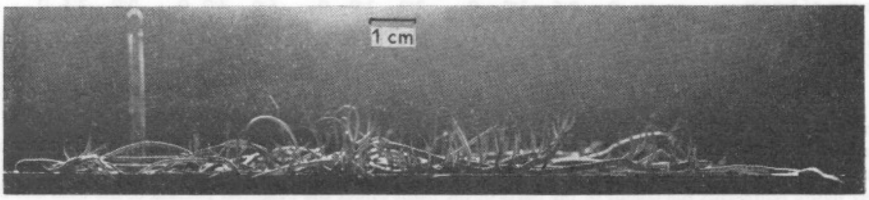

Fig. 2. Plant of *Gracilaria verrucosa* showing response to unidirectional illumination. Those branches which are not secured to the 'Tufnol' plate are turned upwards towards the incident light. The hooking over of the extreme tips of the branches was caused by desiccation during their photography. The scale line is 1 cm.

Changes in pigmentation and growth

The main changes observed and the length of the daily high light period in successive runs are shown in Table 4.

Pigmentation changes became noticeable during the second run, the parts of the plants under the brightest area of the field becoming lighter in colour, while the remainder in the less intense light lost less of their pigments. It was also noticed that the loss of pigment was, at this stage, restricted to the sides of the fronds facing the light, while the sides in contact with the tufnol plates were less affected. As the daily light period was increased, the bleaching effect became more marked until almost all the plant was bleached in each case. Little change in pigmentation occurred in the control. The temperature in both dishes throughout the experiment was maintained between 12·5° and 14·5° C.

During one run the control plant was placed on the white bottom of the dish and not on the tufnol plate. During this period a fourfold increase in the growth rate occurred in the control compared with that in other periods, which may be attributed to the increased light obtained by reflexion upwards from the bottom of the dish and internal reflexion between this and the water surface. Normally most of the light passing the plant would be absorbed by the tufnol plate.

The effect of increasing daily illumination is shown in Fig. 3, which also indicates the state of pigmentation. It will be seen that there appears to be a direct relationship between the daily illumination and the increase in fresh weight as long as pigmentation is not greatly affected, but that after bleaching occurs the growth rate, so far as can be judged from the data available, does not rise very much with further increases in the period of illumination and falls

TABLE 4. GROWTH OF *GRACILARIA VERRUCOSA* WHEN SUBJECTED TO HIGH-INTENSITY ILLUMINATION

Duration of run...				17–29 May			29 May–9 June			9–18 June			18–29 June			29 June–9 July		
Plant...	*a*	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*
Daily hours of bright light	—	—	—	0	0·5	1·0	0	2·0	3·0	0	5·0	4·0	0	6·0	2·5	0	8·0	8·0
% gain in fresh weight at end of run*	—	—	—	2·0	6·5	10·1	31·4†	20·1	29·0	7·7	25·9	23·6	8·8	33·3	15·5	3·0	19·8	20·3
Colour at‡ end of run	(17 May) 6	6	6	6	6	6	6	3–5	2–5	6	1–4	2–4	5–6	1–2	2–4	5–6	1–2	1–2

* Corrected to give equivalent for 12 days.

† Plant '*a*' not on tufnol plate during run 29 May–9 June—received better illumination than in other runs.

‡ Values given are according to arbitrary standard where 1 = bleached, 8 = very dark. Where two values are given the lower figure represents the colour of the parts of the plant under the brightest portion of the field and the higher one the remaining darker parts.

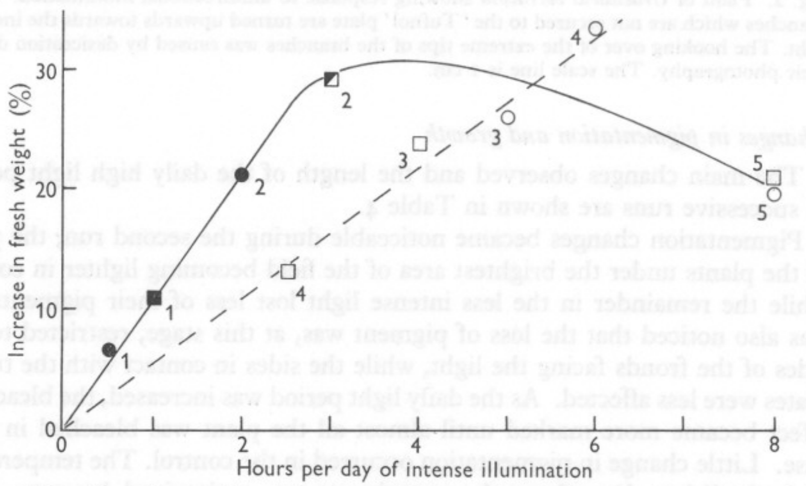

Fig. 3. The effect of increasing daily dosage of intense illumination on the growth and pigmentation of *Gracilaria verrucosa*. The numerals alongside each symbol indicate the consecutive periods of illumination. The vertical scale represents percentage increase in fresh weight in 12 days. Symbols: ●, 1st plant; ■, 2nd plant. Pigmentation: ■, fully pigmented; ◩, half bleached; □, fully bleached; — □ —, growth in fully bleached condition.

appreciably when the daily dosage is raised to 8 h. The growth of plant '*c*' during the fourth run (18–29 June), when in the bleached condition, was only about half that obtainable in an equal period of illumination when unbleached. In fact the values of the percentage increases in weight of the plants in the bleached state, for periods of illumination up to 6 h, fall on a straight line whose slope is approximately half (actually 1:1·9) that for the unbleached plants, a value which agrees with the results of the raft experiments.

When the same lighting system was used in experiments on sporelings the results were very different. Sporelings at an early stage of development, up to 1 week old, grown from carpospores shed in the laboratory, were illuminated by the light for periods of up to 1·5 h daily. Although there was a slight initial increase in growth rate, the loss of phycoerythrin was very rapid and development ceased after a total of 4–5 h illumination. The sporelings did not recover from this treatment. Controls which received constant illumination of 400 lux grew normally and retained their colour.

GENERAL CONCLUSIONS AND DISCUSSION

The following conclusions may be drawn from the results of the experiments described here, bearing in mind that additional, more refined, experiments would be required to place them on a more exact quantitative basis.

(i) Phycoerythrin in living *Gracilaria verrucosa* disappears under the action of light intensities of the order of full daylight.

(ii) When the light is reduced, phycoerythrin is regenerated. In shade where the light intensity is approximately 12% of that just below the sea's surface, considerable regeneration occurs in ten days.

(iii) The bleaching effect does not appear to depend on unusually high temperature. In the laboratory it occurred at under 14·5° C and in the field the temperature was substantially the same (rising from 10° to 14° C), while both regeneration of pigments and their bleaching proceeded.

(iv) The growth rate of the plant, under all lighthing conditions so far observed, is lower in the bleached condition than when fully pigmented. At the low intensities under which phycoerythrin is regenerated unbleached plants grow from twice to three times as fast as bleached ones; at intensities high enough to cause bleaching, unbleached plants grow from 1·5 times to twice as fast as bleached plants.

The slower growth of bleached plants points to phycoerythrin being directly useful to the plant in its growth processes. This reinforces, in terms of the growth rate, what has been demonstrated by several workers in the measurement of assimilation rates in the Rhodophyceae. Wurmser & Ducleaux (1921) showed that the assimilation rates of *Rhodymenia* and *Chondrus* when red were twice as great as when green (i.e. bleached, presumably), a value which fits in well with the present results.

Although the loss of phycoerythrin reduces the growth rate of the plant this does not appear to be a serious difficulty in nature since bleaching is caused by the high summer illumination, and at these intensities the growth, even of bleached plants, is rapid. On open shores with clear water bleaching begins to be noticeable in late spring and early summer and it is at this time, when the light intensity is high but before the plants lose all their phycoerythrin, that growth is fastest. Later bleaching becomes more pronounced and the growth rate falls but the maximum size is reached in late summer when the plants are fully bleached.

The reduction in the growth rate of plants which have been intensely illuminated for a long daily period is also in agreement with previous work: Meyers & Burr (1940) showed that, in *Chlorella*, high light intensities (above 15,000 lux) reduced the rate of photosynthesis. The plants recovered from this high illumination, recovery being slower the longer the period of illumination and the higher the intensity, but at very high intensities permanent injury took place. In the case of sporeling material of *Gracilaria*, injury from which the sporelings do not recover occurs under intensities of the order of full daylight when this is received for 4–5 h. This can explain why plants of *Gracilaria* are not found in upshore pools where intensities of this order may be received for considerable periods every day in summer.

This work was carried out at the suggestion of Prof. L. Newton, whose encouragement and helpful comments I should like to acknowledge.

SUMMARY

A raft is described which permits experiments on the effect of current and still water on marine organisms. This has been used in experiments on *Gracilaria verrucosa* which, supplemented by laboratory experiments, show that, while there is no direct current effect on the growth, there is an indirect effect. This is an increase in the growth rate due to the better illumination of plants spread out by the current.

The bleaching of the thalli when illuminated by light of high intensity has been observed on the raft and demonstrated under tungsten spotlamps in the laboratory. It has been shown that the colour is regained when the light is reduced and that growth is from one and a half to three times as fast in unbleached plants as in those from which the phycoerythrin has gone. This difference between bleached and unbleached plants is less marked at high light intensities.

Positive phototropism of the branches of the plant has been demonstrated.

High light intensities have been found to have an adverse effect on mature plants only after prolonged illumination but to be quickly harmful to sporelings. It is suggested that this may limit the upshore distribution in pools.

REFERENCES

CAUSEY, N. B., PRYTHERCH, J. P., McCASKILL, J., HUMM, H. J. & WOLF, F. A., 1946. Influence of environmental factors upon the growth of *Gracilaria confervoides*. *Bull. Duke Univ. Mar. Sta.* No. 3, pp. 19–24.

GESSNER, F., 1940. Die Bedeutung der Wasserbewebung für die Atmung und Assimilation der Meersalgen. *Jb. wiss. Bot.*, Bd. 89, pp. 1–12.

MEYERS, J. & BURR, G. O., 1940 Studies on Photosynthesis: some effects of high light intensities on *Chlorella*. *J. gen. Physiol.*, Vol. 24, pp. 45–67.

SVERDRUP, H. V., JOHNSON, M. W. & FLEMING, R. H., 1942. *The Oceans, their Physics, Chemistry and General Biology*. New York.

WURMSER, R. & DUCLEAUX, J., 1921. Sur la photosynthèse chez les Algues Floridées. *C.R. Acad. Sci., Paris*, T. 171, pp. 1231–1233.