

PHOTOSYNTHESIS AND PHOTOTAXIS IN *ULVA LACTUCA* GAMETES¹

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During reproduction many multicellular algae form fertile areas which differ in color from the vegetative portions and from which are ultimately shed diversely pigmented gametes. These color differences may involve large changes in the ratios of the chlorophylls, carotenoids or phycobilins present in vegetative cells, making such algal material useful for studies concerned with the physiological functions of plastid pigments (Carter, Cross, Heilbron and Jones, 1948; Strain, 1951; Haxo and Blinks, 1950).

The physiology of algal gametes themselves is incompletely understood. For example, few observations have been reported concerning the phototaxis and respiratory activity of these specialized cells and the extent to which they have retained the capacity for photosynthesis. In *Fucus vesiculosus*, Whitaker (1931) reported that the olive-green, non-motile eggs are photosynthetically active, whereas the motile, orange antherozoids are inactive, or at best only very slightly active in this respect, but display a very high rate of oxygen consumption (about 5 times that of the unfertilized egg and about 13 times that of the vegetative tissue). Carter, Cross, Heilbron and Jones (1948 and personal communication, 1952) observed that beta-carotene is the predominating pigment of the orange antherozoids in three species of *Fucus* and in *Ascophyllum nodosum*; chlorophyll was not present in *Fucus vesiculosus* in sufficient amount to be either isolated or identified.

In various members of the Ulvales, the physiological and biochemical changes associated with gametogenesis and sporogenesis can be followed in the intact thallus and such studies can subsequently be extended to the free-swimming gametes. In the sea-lettuce, *Ulva lactuca*, the thallus in both diploid and haploid generations is a broad sheet of rather uniform thickness, composed of two layers of cells embedded in a gelatinous matrix. The gametophyte is heterothallic and during reproduction the vegetative cells give rise progressively to "chlamydomonad-type" gametes along the otherwise undifferentiated thallus margins (Schiller, 1907; Carter, 1926; Smith, 1947). It has been reported that division of the vegetative protoplast takes place at night, resulting in the formation of eight biflagellate gametes which are shed early in the morning (Schiller, 1907; Carter, 1926). After fusion of the isogamous gametes, there is a reversal of the light response, the zygotes being negatively phototactic.

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The color differences associated with gamete formation in *U. lactuca* are apparently similar to, but not always as marked as, those reported by Smith (1947) for *U. lobata* found on the coast of California. In the latter species, the fertile portions of the female thalli are olive-green, and the corresponding portions of the male thalli are tan in color. Strain (1951) has attributed the color changes in the *U. lobata* to variations in the proportions of the chlorophylls and carotenes, the fertile portions of the thalli containing five times as much carotene as the grass-green portions. Smith (1947, 1951) reported that *U. lobata* shows a definite fortnightly periodicity in gamete formation and liberation which is correlated with tidal succession. At Woods Hole, Mass., during the summer months fertile *U. lactuca* can usually be found only at intervals at any one location, suggesting a periodic reproduction; however, the extent to which reproduction in this species is under environmental control is not known.

The present investigation is concerned with studies of photosynthesis, respiration, phototaxis, and pigmentation in free-swimming gametes of *U. lactuca*, as well as some corresponding observations on vegetative thalli and fruiting thallus margins.

MATERIALS AND METHODS

Fronds of *Ulva lactuca* L. var. *rigida* Le Jolis (cf. Taylor, 1937) which, by the characteristic opacity and color of the thallus margins, showed evidence of incipient reproduction were collected every few days at low tide in the vicinity of Woods Hole during July and August, 1951. They were maintained in individual pans of sea water in the laboratory until the reproductive cells were shed. Not infrequently a fair percentage of the thalli treated in this manner failed to release either gametes or zoospores. Most fronds which did shed were found to be gametophytic, a distinction which could not be made in the field since the fruiting margins of both female gametophytes and sporophytes are similar in color. The gametes were concentrated by phototaxis, collected with an eye-dropper, and in some cases tested for sex according to the method employed by Smith (1947). The gametes were transferred to centrifuge tubes for measurement of packed cell volume.

Comparison of the rates of photosynthesis and respiration of vegetative thalli and unshed fruiting margins were made on freshly cut discs and strips of thallus. Manometric measurements were made at 25° C. in artificial or natural sea water containing 0.016 *M* carbonate-bicarbonate and having an initial pH of 8.5 (Clendenning and Haxo, unpublished). The light source was a 1000 watt air-cooled projection lamp which provided a maximum light intensity of 5400 f.c. at the manometer vessel. The light was filtered through eighteen inches of water. Polarographic measurements of oxygen production were made in saturating light at about 25° C. by the procedure described by Haxo and Blinks (1950).

Phototactic movement was measured in a cylindrical absorption cell (thickness 1.0 cm., diameter 2.5 cm.) provided externally with a vertical cross hair. By alternate illumination of opposite sides of the cuvette, the gametes which had been introduced as a dilute suspension were first collected as a very thin and uniform layer on the glass wall, and then made to cross the cuvette as a sharply defined wave. The time taken for the wave of gametes to move 5 mm. to the midpoint of the cuvette, as determined visually, was taken as a measure of the motility rate. Rate of movement in different spectral regions of equal intensity was measured

with the aid of an Eppley thermopile and Farrand interference filters having peak transmissions at about 440, 560, 620, 680 and 700 m μ . White light intensities were measured with a Weston Sunlight Illumination Meter.

The chloroplast pigments were extracted by one-minute exposure to hot water followed by repeated extractions with methanol. Extraction with absolute methanol was continued until the samples were colorless. The extracted pigments were transferred to ethyl ether by the addition of concentrated sodium chloride solution. Water was removed from the ether by chilling and subsequent drying with anhydrous sodium sulfate. The chlorophyll was estimated spectrophotometrically (Model B Beckman) on an aliquot of the total pigment solution, using Comar's equations (1942). The carotenoids were separated from the chlorophyll by saponifying the total pigment extract with 10–20% KOH. Carotenes and xanthophylls were separated by partition of the petroleum ether solution over 90% methanol and were estimated spectrophotometrically in petroleum ether. Total carotenoids were also estimated from extinction measurements made at 445 m μ on the total pigment extract after correcting for chlorophyll absorption at this wave-length. The total carotenoid values obtained in this way were in close agreement with the sums of the separately determined carotenes and xanthophyll contents. The carotenes from the male gametes were fractionated chromatographically on a column of powdered magnesium oxide and identified on the basis of their characteristic absorption spectra in hexane. For purposes of standardization, alpha- and beta-carotene were isolated from carrots and their absorption curves determined with the spectrophotometer employed in this investigation.

RESULTS

The photosynthetic and respiratory activities of equal areas (1.77 cm.²) of vegetative and fruiting portions of *Ulva* thallus which were observed manometrically are shown in Figure 1. Rectangular Warburg vessels containing 7 ml. of bicarbonate-enriched sea water (0.016 *M*) were employed in this experiment. This volume of liquid provided a large reservoir of bicarbonate, but the associated diffusion lag obscured the details of the transitions. Rates calculated from these data refer to the steady state (Table I). Respiration was much higher in the fruiting thallus margins than in the green vegetative tissue, whereas both net and total photosynthesis was lower. The photosynthetic and respiratory activities are expressed in different terms in Table I, which allow comparisons with the data for free-swimming gametes presented in Table III.

The early time course of photosynthesis in vegetative *Ulva* and other aquatic plants has been previously characterized polarographically by Blinks and Skow (1938), the essential features being an initial oxygen gush, followed by an induction period before the main trend of oxygen evolution resumes. In the present experiments fruiting thallus margins consistently exhibited a longer induction period and lower final rates of O₂ production than vegetative parts of the same thallus after identical pre-treatments. In a typical experiment the tissue was held tightly against the electrode with cellophane as in earlier applications, a condition which would magnify the effects of a high respiration rate on photosynthetic induction, and was maintained in dim light for one hour prior to illumination with saturating light. Oxygen production by the fruiting thallus was sluggish and

detectable only in the third minute of illumination. Successive light exposures reduced, but did not abolish, the induction period (Fig. 2a, b, c, d) and no suggestion of an oxygen gush was observed. In the vegetative tissue, however, the oxygen gush and induction period were complete within the first 30 seconds and, upon successive exposures to strong light, oxygen production proceeded at its full rate almost instantaneously, in agreement with the earlier findings of Blinks and Skow (1938, Fig. 5; cf. Haxo and Blinks, 1950, Fig. 6).

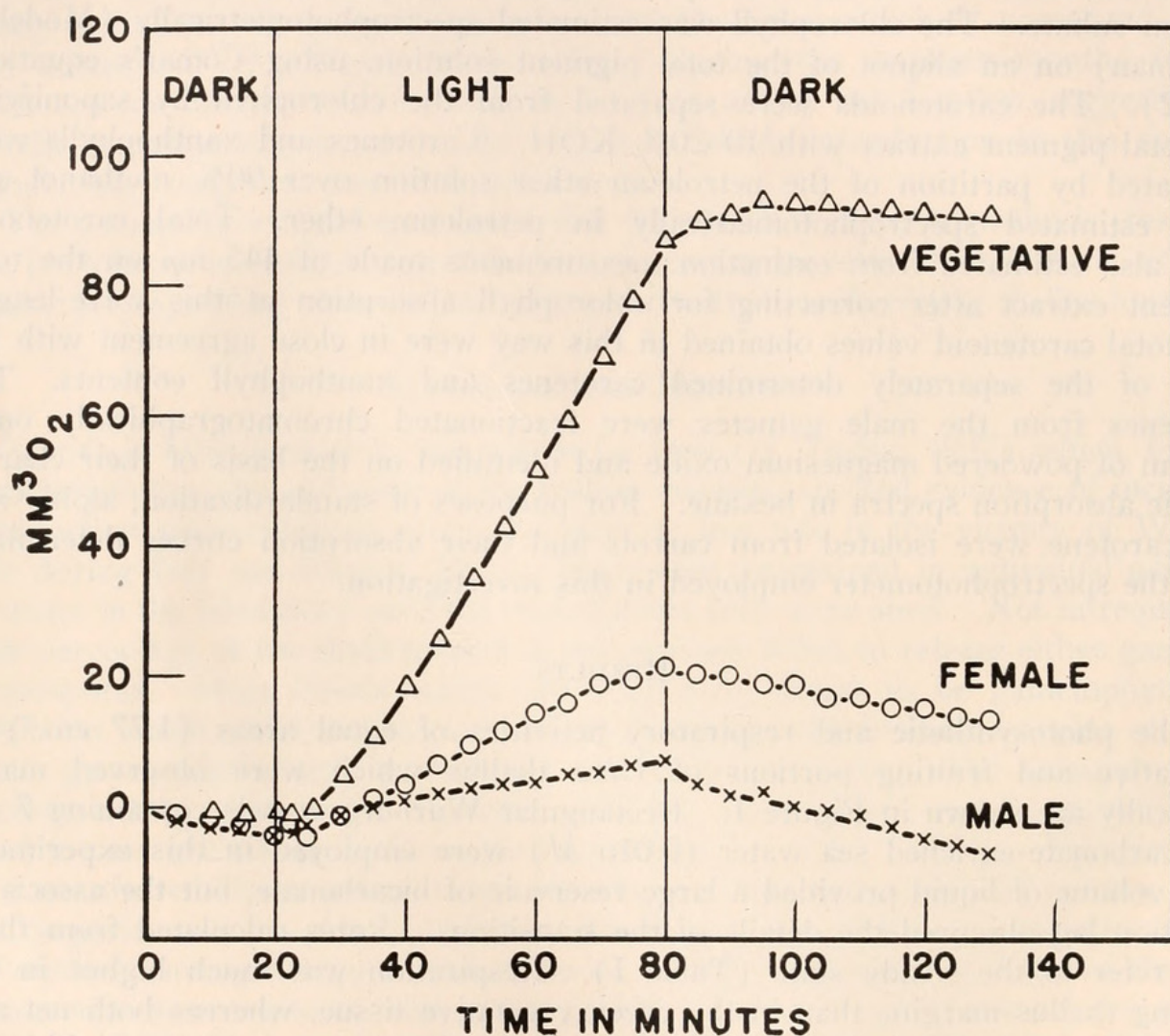


FIGURE 1. Photosynthesis and respiration of vegetative tissue and fruiting thallus margins in carbonate-enriched sea water at 25° C. Area of thallus disc, 1.77 cm².

The tissues employed in the foregoing manometric experiment were analyzed for solids, chlorophyll and carotenoids (Table II). The yellowish or male fruiting thallus margin showed the lowest chlorophyll content. The olive-green fruiting margins (in all probability female, but mating responses were not determined in this instance) contained about the same chlorophyll concentration as the vegetative thallus. The carotene contents of both types of fruiting thallus margins were about three times higher than that of the vegetative thallus. The xanthophyll contents of all three samples were essentially the same, so that there was more xanthophyll than carotene in the vegetative tissue, and less xanthophyll than carotene in the reproductive thallus margins. The pigment analyses for the vegetative thalli are

TABLE I

Photosynthetic and respiratory activity of vegetative thallus and fruiting thallus margins of Ulva lactuca

Gas exchange	Fruiting thallus margin		Vegetative thallus
	Male	Female	
Photosynthesis (corrected)			
mm. ³ O ₂ /hr./dm. ²	1290	2100	5980
mm. ³ O ₂ /hr./gm. fresh wt.	1620	3070	6180
mm. ³ O ₂ /hr./gm./solids	7110	12,300	25,400
mm. ³ O ₂ /hr./mg. chlorophyll	1320	1720	3490
Respiration			
mm. ³ O ₂ /hr./dm. ²	755	605	270
mm. ³ O ₂ /hr./gm. fresh wt.	950	885	280
mm. ³ O ₂ /hr./gm. solids	4180	3530	1180
mm. ³ O ₂ /hr./mg. chlorophyll	775	499	160

in reasonable agreement with those reported previously for *U. lactuca* by Seybold and Egle (1938). These authors gave the following values (when expressed as mg./gm. solids): chlorophyll-a, 3.3; chlorophyll-b, 1.5; total chlorophyll, 4.8; carotene, 0.16; xanthophyll, 0.77; total carotenoid, 0.93.

Expressed on a solids basis, the free-swimming female gametes contain twice as much chlorophyll and half as much carotene as the male gametes; the xanthophyll content was the same in both cases (Table III). Comparisons cannot readily be made on the same basis between the pigment content of the free-swimming gametes and that of the vegetative thalli (Table II). It is interesting to note, however, that the ratio of chlorophyll:carotenoid has changed from 8.3 in the vegetative tissue to 2.7 in the female gametes and 1.1 in the male gametes. Strain (1951) has reported that in *U. lobata* a large portion of the increased carotene content of the sexually differentiated margins is due to the gamma-carotene isomer, only a little of which occurs in vegetative thalli. A similar change appears to occur in *U. lactuca*.

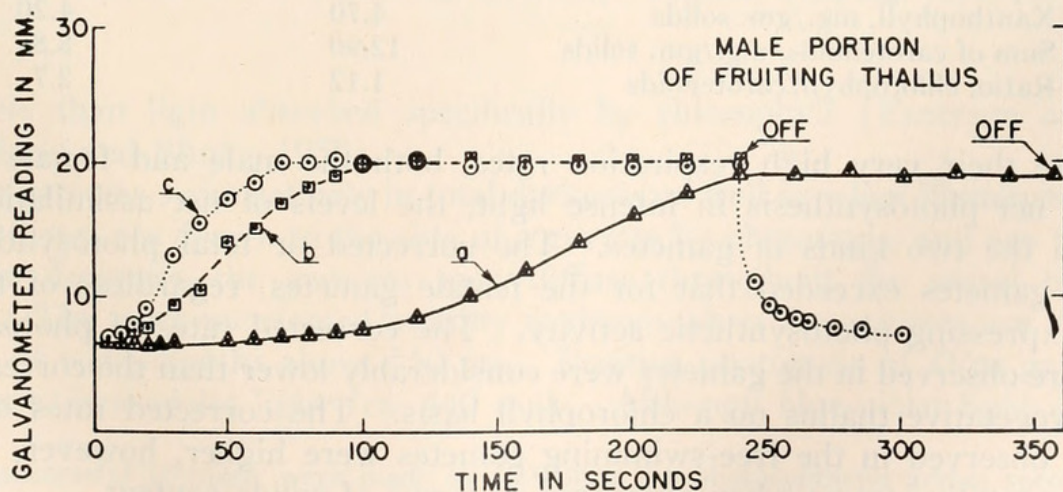


FIGURE 2. Initial time course of oxygen evolution which was observed polarographically on a strip of male fruiting thallus margins at ca. 25° C., after a pre-treatment of one hour in dim light.

TABLE II

Chlorophyll, carotenoid and solids data for vegetative and reproductive thallus margins of Ulva lactuca

Constituents	Fruiting thallus margins		Vegetative thallus
	Yellowish	Greenish	
Fresh wt., mg./dm. ²	797	683	967
Solids, mg./dm. ²	181	171	230
Chlorophyll, mg./gm. solids	5.41	7.15	7.29
Carotene, mg./gm. solids	1.35	1.49	0.34
Xanthophyll, mg./gm. solids	0.68	0.64	0.54
Sum of carotenoids, mg./gm. solids	2.03	2.13	0.88
Ratio, chlorophyll/carotenoids	2.7	3.4	8.3

Chromatographic and spectral analyses of the abundant carotene fraction present in the male gametes indicated the following composition: 43% gamma-carotene, 32% beta-carotene, 3% alpha-carotene, and 22% unidentified carotene.

The green (♀) and yellow (♂) gametes, whose photosynthesis and respiration are reported in Figure 3 and in Table IV, were actively phototactic at the time, and also showed the normal clumping reaction of opposite sexes on admixture. Respiration of the male gametes exceeded that of the female,² and respiration of both types exceeded that of the unshed fruiting margin as well as of the vegetative thallus. Expressed on a solids basis, the respiration of the male gametes was almost thirty times greater than that of the vegetative thallus, and was about fourteen times greater in terms of chlorophyll content.

TABLE III

Chlorophyll, carotenoid and solids data for Ulva lactuca gametes

Constituents	Male gametes	Female gametes
Dry wt., mg./ml. packed cells	96	105
Chlorophyll, mg./gm. solids	14.42	24.0
Carotene, mg./gm. solids	8.20	4.68
Xanthophyll, mg./gm. solids	4.70	4.20
Sum of carotenoids, mg./gm. solids	12.90	8.88
Ratio, chlorophyll/carotenoids	1.12	2.7

Despite their very high respiration rates, both the male and female gametes exhibited net photosynthesis in intense light, the levels of net assimilation being similar in the two kinds of gametes. The corrected or total photosynthesis for the male gametes exceeded that for the female gametes, regardless of the basis used in expressing photosynthetic activity. The corrected rates of photosynthesis which were observed in the gametes were considerably lower than the corresponding rate for vegetative thallus on a chlorophyll basis. The corrected rates of photosynthesis observed in the free-swimming gametes were higher, however, than the rate for vegetative tissue when expressed in terms of solids content.

² The present data are insufficient to establish whether the isogamous male and female gametes of *U. lactuca* differ significantly in this respect.

Photosynthesis by the gametes has been compared manometrically in red and white light (Fig. 4). The rate of oxygen evolution obtained with saturating white light was identical to that observed on exposure of the gametes to the component red light. In contrast to their phototaxis, photosynthesis by the gametes was effectively sensitized by light absorbed specifically by chlorophylls. Their photosynthetic mechanism could be completely saturated by red light which was entirely ineffective in orienting the swimming motion. This experiment does not establish the relative effectiveness of chlorophylls and carotenoids as sensitizers of photosynthesis in the gametes of green algae.³ However, all earlier studies of vegetative green algae have indicated that light absorbed by the carotenoids is utilized less

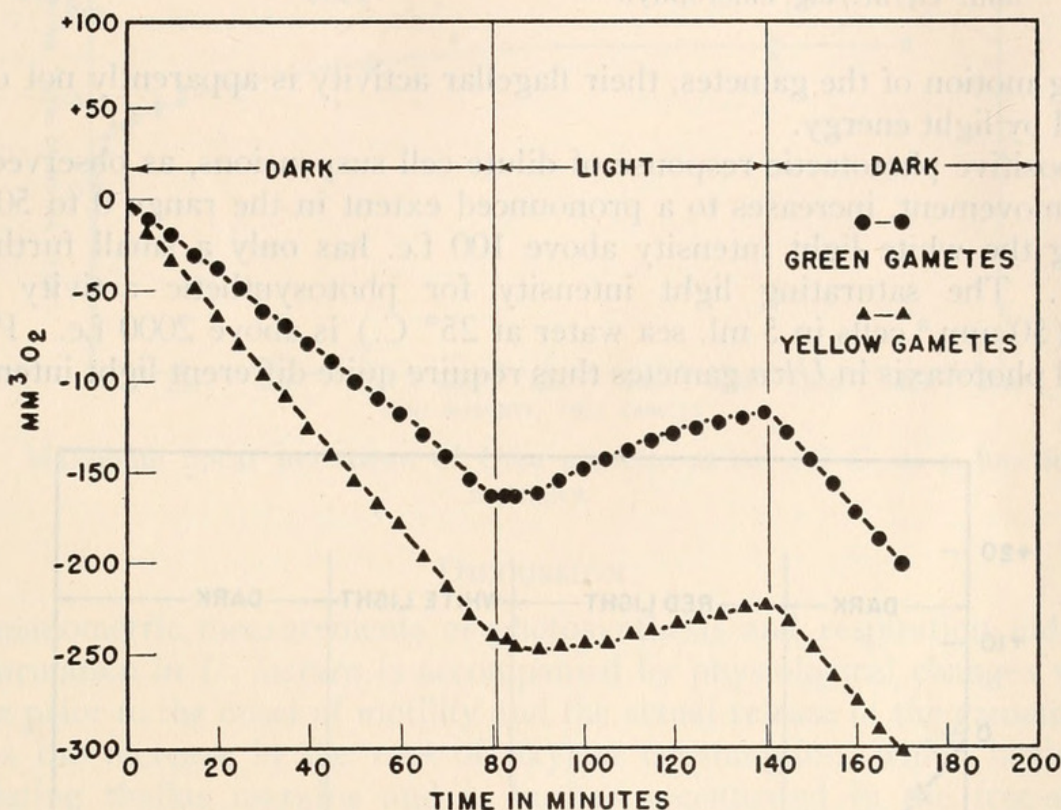


FIGURE 3. Photosynthesis and respiration in male and female *Ulva* gametes in carbonate-enriched sea water at 25° C.; 0.0815 mg. chlorophyll in male, 0.161 mg. chlorophyll in female gametes.

effectively than light absorbed specifically by chlorophyll (Emerson and Lewis, 1943; Haxo and Blinks, 1950).

Ulva gametes swim actively in total darkness as well as when illuminated. Thus when gametes are drawn to the side of a cuvette by phototaxis, and are then maintained in darkness, the gametes soon diffuse throughout the vessel by random motion. The same unoriented motility is shown when the gametes are illuminated by light of wave-lengths above 550 m μ . Positive phototaxis of *Ulva* gametes is a response to blue-violet light (ca. 440 m μ). Although blue-violet light orients the

³ Unsuccessful attempts were made to determine the photosynthetic action spectra of male margins, employing the available polarographic apparatus which did not permit estimation of the large respiration correction. Upon illumination of this tissue at low and moderate light intensities, either no change in oxygen concentration at the electrode or an actual uptake of oxygen was noted.

TABLE IV

Photosynthetic and respiratory activity of Ulva lactuca gametes

Gas exchange	Male gametes	Female gametes
Photosynthesis (corrected)		
mm. O ₂ /hr./ml. packed cells	3960	3550
mm. O ₂ /hr./gm. solids	41,200	33,800
mm. O ₂ /hr./mg. chlorophyll	2570	1410
Respiration		
mm. ³ O ₂ /hr./ml. packed cells	3380	2750
mm. ³ O ₂ /hr./gm. solids	35,200	26,200
mm. ³ O ₂ /hr./mg. chlorophyll	2200	1090

swimming motion of the gametes, their flagellar activity is apparently not otherwise controlled by light energy.

The positive phototactic response of dilute cell suspensions, as observed by rate of linear movement, increases to a pronounced extent in the range 0 to 50 f.c., but increasing the white light intensity above 100 f.c. has only a small further effect (Fig. 5). The saturating light intensity for photosynthetic activity in *Ulva* gametes (50 mm.³ cells in 5 ml. sea water at 25° C.) is above 2000 f.c. Photosynthesis and phototaxis in *Ulva* gametes thus require quite different light intensities for

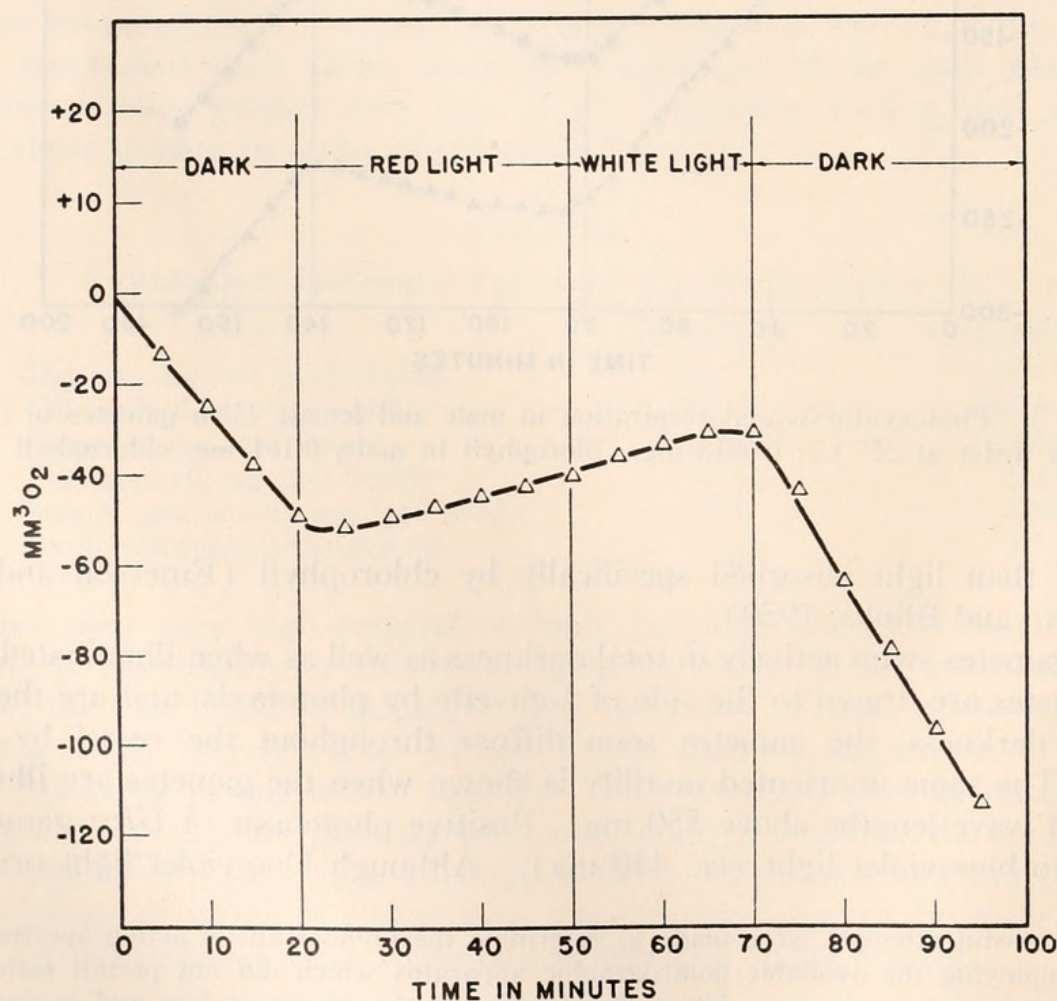


FIGURE 4. Photosynthesis and respiration in female *Ulva* gametes in red and white light, approximately 50 mm.³ gametes in 7 ml. carbonate-enriched sea water at 25° C.

saturation, and also have very different wave-length specificities. Red light is highly effective in sensitizing their photosynthesis although it plays no part in inducing the phototactic response.

The fastest rate at which *Ulva* gametes have been observed to swim towards a strong light source is *ca.* 18 mm. per minute (Fig. 4). The size of the gametes, exclusive of flagella, is *ca.* 7.6 by 3.6 μ (length 6.9–8.3 μ , width 3.5–3.8 μ). From the observed rates of phototactic movement and size of the cells, it is apparent that *Ulva* gametes swim more than two thousand times their body length in one minute.

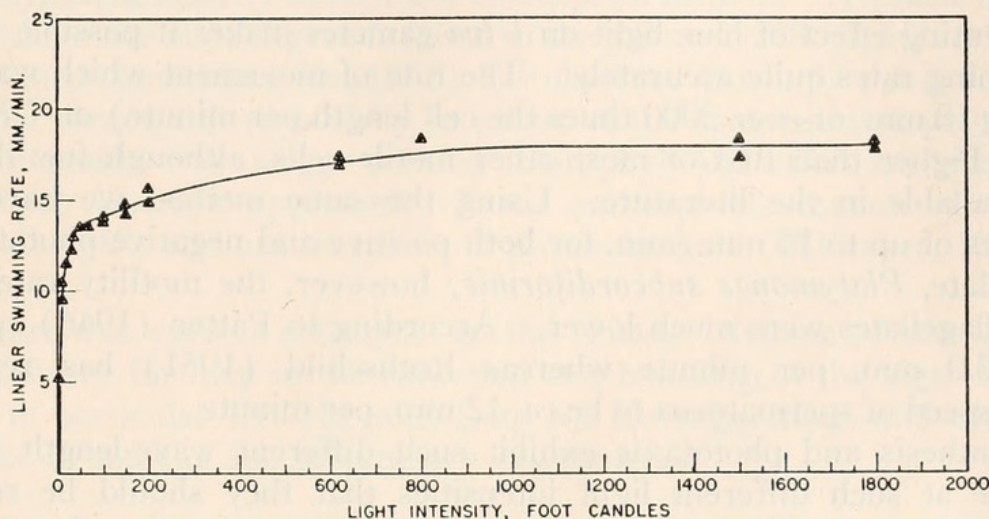


FIGURE 5. Maximum linear movement of *Ulva* gametes at *ca.* 25° C. as a function of light intensity.

DISCUSSION

The manometric measurements of photosynthesis and respiration indicate that gamete formation in *U. lactuca* is accompanied by physiological changes which are detectable prior to the onset of motility and the actual release of the gametes. Most notable is the increase in the rate of oxygen consumption, which begins in the differentiating thallus margins and is further accentuated in the free-swimming gametes. It would be of interest to ascertain whether this increase in metabolic activity is gradual or abrupt, and whether it is associated with specific stages in gametogenesis. Although the entire vegetative thallus of the *Ulva* gametophyte may ultimately give rise to gametes, at any one time gametogenesis is normally restricted to the peripheral margins of the thallus. Fruiting specimens have been collected, however, in which the thallus has been torn internally, leaving the periphery intact. The vegetative area bordering the cut surfaces occasionally has been observed to have undergone color differentiation and ultimately to release gametes. Experimental studies might reveal more fully the conditions under which gamete formation is initiated and maturation of the gametes proceeds.

The pronounced induction period which was observed polarographically in the fruiting thallus margin is attributed to oxygen deficit resulting from the high respiration rate of this tissue, as well as its relative inaccessibility to oxygen while pressed tightly against the platinum electrode. Blinks and Skow (1938) had earlier found for vegetative *Ulva* and other aquatic plants that the induction loss is magnified by lengthy dark anaerobic periods, and may be eliminated by adequate aeration in the dark or by successive exposures to bright light.

The respiration of free-swimming *Ulva* gametes is very much higher than has been observed previously in photosynthetically active cells, and is about 50% higher than that reported by Whitaker for the non-photosynthetic *Fucus* antherozoids. The compensation point of *Ulva* gametes has not yet been determined accurately over a range of temperature and cell densities, but with 50 mm.³ cells in 5 ml. sea water at 25° C., the compensating white light intensity was above 1500 f.c. Because of their high respiration rate, the compensation point for *Ulva* gametes is much higher than any of the values which were recently assembled by Rabinowitch (1951).

The orienting effect of blue light on *Ulva* gametes makes it possible to measure their swimming rates quite accurately. The rate of movement which was observed in this way (18 mm. or over 2000 times the cell length per minute) on *Ulva* gametes is probably higher than that of most other motile cells, although few data of this sort are available in the literature. Using the same method we have observed motility rates of up to 16 mm./min. for both positive and negative phototaxis in the green flagellate, *Platymonas subcordiformis*; however, the motility rates observed for several flagellates were much lower. According to Patten (1946) spermatozoa travel 1.5–3.0 mm. per minute whereas Rothschild (1951) has reported the translatory speed of spermatozoa to be ca. 12 mm. per minute.

Photosynthesis and phototaxis exhibit such different wave-length specificities and saturate at such different light intensities that they should be regarded as unrelated processes in *Ulva* gametes. This probably represents the situation for flagellated algae in general, since phototaxis in, for example, *Euglena* and *Chlamydomonas* (Mast, 1917), *Volvox* (Laurens and Hooker, 1920), and in the green and red phenotypes of *Dunaliella salina* (Blum and Fox, 1933) has been shown to be limited to the blue end of the spectrum. *Rhodospirillum rubrum* presents a special case since Thomas and Nijenhuis (1950) have reported that the action spectra, saturating light intensities and responses to cyanide and ethyl urethane were the same for photosynthesis and phototaxis in this organism.

Both male and female fertile portions of *U. lactuca* thalli contained more carotene than did vegetative portions of the thallus, being apparently similar in this respect to *U. lobata* (Strain, 1951). In the free-swimming gametes the carotene content of the male gametes was about twice that of the female reproductive cells. High carotenoid concentrations are generally characteristic of male gametes, whereas there is a greater retention of chlorophyll in the female gametes (Karrer *et al.*, 1943; Carter *et al.*, 1948; Strain, 1951). The widespread accumulation of carotenoids in reproductive cells and tissues suggests that carotenoids may play a role in sexual reproduction (Emerson and Fox, 1940; Cook, 1945; Goodwin, 1950), in addition to their probable role as sensitizers of phototaxis (Wald, 1943). Whatever the role of carotenoids in sexuality may be, it seems evident that the abundant accumulation sometimes observed in gametes is in considerable excess of the requirements for this function and may not be related to it. *Allomyces* species accumulate abundant stores of gamma-carotene in the male gametes (Emerson and Fox, 1940); however, Turian (1952) has inhibited the visible production of pigment without apparently altering the capacity for mating. The apparently normal sexual reproduction of albino strains of *Neurospora* (Hungate, 1945) is another case in point.

Photosynthetically active cells always contain at least traces of chlorophyll but the minimal chlorophyll requirements for photosynthesis have not been established with certainty (*cf.* Rabinowitch, 1945, 1951). In investigations of this question, advantages are presented by algal gametes, in that the cells are in a healthy state of high metabolic activity irrespective of their chlorophyll content. Furthermore, by use of several species it might be possible to obtain for study a series containing successively smaller amounts of chlorophyll. In *U. lactuca* the chlorophyll content of the female gametes was almost twice that of the male gametes and yet showed a lower photosynthetic activity in terms of chlorophyll content. A visible color differentiation of about the same degree is found in the gametes of *Bryopsis corticulans* but Blinks (personal communication, 1952) has observed that only the green (female) gametes show photosynthetic activity in excess of the compensation point. As was indicated previously, *Fucus* eggs contain chlorophyll and effect net photosynthesis in strong light, whereas, apparently, *Fucus* antherozoids contain no chlorophyll (Carter *et al.*, 1948) and are incapable of photosynthesis (Whitaker, 1931).

Thanks are due various colleagues in the Botany Division of the Marine Biological Laboratory for help in the collection and handling of the algae used in this study; and in particular Dr. Maxwell Doty for his suggestions and Shirley Trefz for assistance in some of the preliminary experiments.

SUMMARY

1. Fruiting margins of *Ulva lactuca* thallus are characterized by a higher content of carotenoids, as well as by higher respiratory and lower photosynthetic activity, than the corresponding vegetative thallus. Photosynthesis in the male margin was also characterized by a longer induction period than was observed in the vegetative thallus by the polarographic method.

2. The changes in pigment composition observed in *Ulva lactuca* during reproduction are similar to those reported for *Ulva lobata*. The male gametes of *Ulva lactuca* contained twice as much carotene and half as much chlorophyll as the female gametes. The male carotene fraction contained 43% gamma-carotene, 32% beta-carotene, 3% alpha-carotene and 22% unidentified carotene. The xanthophyll contents of the male and female gametes were similar. The chlorophyll/carotenoid ratio was 8.3 in the vegetative thallus, 2.7 in the female gametes and 1.1 in the male gametes.

3. The respiration of the male gametes exceeded that of the female gametes, was almost thirty times greater than that of the vegetative thallus on a solids basis, and was about twelve times greater in terms of chlorophyll content.

4. Both male and female gametes exhibited net photosynthesis in intense white light, but a very high light intensity was required to compensate their respiration, which is the highest that has been reported for cells possessing photosynthetic activity.

5. Positive phototaxis of *Ulva* gametes is a response to blue-violet light, which orients their swimming but does not otherwise control their flagellar activity. Their maximum rate of linear movement is attained at moderate light intensity (*ca.* 100 f.c.). The gametes swim 2500 times their own body length each minute.

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