

## Proceedings of the Iowa Academy of Science

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Volume 62 | Annual Issue

Article 80

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1955

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### Recommended Citation

Lynch, William F. (1955) "Phototropic Responses of Bugula Larvae in the Presence of Stimulating and Anaesthetic Agents," *Proceedings of the Iowa Academy of Science*: Vol. 62: No. 1 , Article 80.  
Available at: <https://scholarworks.uni.edu/pias/vol62/iss1/80>

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## Phototropic Responses of Bugula Larvae in the Presence of Stimulating and Anaesthetic Agents\*

By WILLIAM F. LYNCH

### INTRODUCTION

Observations on phototropic responses of the larvae of *Bugula neritina* and of *B. flabellata* in the presence of stimulating and anaesthetic agents indicate that the light reactions of these organisms may have a diagnostic value for predicting acceleration or retardation of the rate of metamorphosis. Experiments on *B. neritina* were conducted at the Bureau of Fisheries, Beaufort, North Carolina; those on *B. flabellata*, and less extensive observations on *B. turrita*, were made at the Marine Biological Laboratory, Woods Hole, Massachusetts.

Northern and southern species of *Bugula* larvae show many similarities in their pre-fixational behavior, but they also exhibit certain differences. Thus, the natatory period of the southern species, *B. neritina*, is much briefer than that of the two northern species, *B. flabellata* and *B. turrita*. *B. neritina* has a free-swimming period ranging from about fifteen minutes to four hours, but occasionally it endures for as long as six or even eight hours under laboratory conditions. By the end of an hour, however, the mean number of unmetamorphosed larvae was found to be 7.7 per cent with a standard deviation of 6.2% in a series of nine observations made on larvae in sea water at a temperature of 27 to 29°C. and having a density of 1.016 to 1.018 gr./cc. inclusive. (The lowest salinity of twenty-five samples of sea water taken near the laboratory equalled a specific gravity of 1.016 and the highest equalled a density of 1.022 gr./cc.). The northern species both have a much longer period of pre-fixational swimming, and the length of the natatory phase appears to depend on several factors, one of which will be considered in the discussion. The northern and southern species also show similarities and differences in their phototropic reactions.

That the photic reactions of the larvae are associated in some way with their physiological condition is evidenced by the pre-fixational reactions of the organisms. Both *B. flabellata* and *B. turrita* have an intensely photopositive phase immediately after their release from ovicells of the parental colonies, and this is followed by a photonegative response to light. As described by Grave (1930), the photopositive phase usually lasts about three or four hours.

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\*Part of the observations made in this paper were made possible by a grant from the National Science Foundation, 1954.

The transition from positive to negative phase is a gradual one, and during this period larvae can be seen swimming back and forth from the side of the dish nearest the source of diffuse daylight to the side farthest away from the window. These larvae retain their photonegative response until the time of fixation. At the time of metamorphosis the larvae are generally as strongly photonegative as they were formerly photopositive after their release from the parental ovicells. The larvae of *B. neritina*, on the other hand, remain photopositive in normal sea water and under conditions of diffuse daylight from the time of their release from the parental colonies until they are ready to undergo fixation. Just before attachment, however, the larvae become somewhat indifferent to light, so that setting frequently occurs in a random fashion; but the period is so brief that it can be easily overlooked. At the time of fixation these organisms do not show the intense negative reaction to light that is so characteristic of the northern species. Indeed, they seem to go only as far as the transitional stage of the northern species; then their reactions to light are abruptly ended by fixation. Under experimental conditions, however, larvae of the southern species can be forced to resemble the behavioral patterns of the northern species in their pre-fixational activities. Thus, when the salinity of sea water is reduced to a specific gravity of 1.010 by the addition of distilled water, the larvae of *B. neritina* not only prolong their natatory period extensively but they also generally show a distinctly photonegative phase before attachment.

#### OBSERVATIONS

**Intensity of phototropic reaction.** A correlation between the light reactions of the larvae and their time of setting was first observed in 1944. At that time numerous experiments on *B. neritina* were being carried out in order to determine the effect of salinity on the rate of metamorphosis (Lynch, 1947). At that time it was noted that metamorphosis was greatly inhibited by a reduction of salinity to a value at which the density of sea water was 1.010 gr./cc. Simultaneously the larvae exhibited a photopositive reaction that was judged to be stronger than that of organisms in sea water at higher salinities, having specific gravities of 1.016 to 1.022. This correlation between swimming time and the intensity of the photic responses of the larvae, albeit an imperfect one, is shown in Table I. The following may be noted: (1) At thirty and at sixty minutes after release of the organisms from the ovicells the intensity of the photopositive reaction of larvae in sea water having a specific gravity of 1.010 gives some indication that the organisms will not metamorphose as rapidly as those exposed to normal conditions of salinity, i.e., the surrounding medium having densities varying from 1.016 to 1.022 gr./cc. (2) The prolonged

Table 1

Phototropic responses and the rate of metamorphosis of the larvae of *B. neritina* at various salinities expressed as specific gravities or as densities in grams/cc.

Specific gravity	No. of observations	Temperature of sea water	Percentage of unmetamorphosed larvae in minutes		Phototropism at minutes after release from ovicells		Phototropism at time of attachment
			30	60	30	60	
1.010	1	28.8	100	100	+	+	+
	2	28.0	100	89	+	+	—
	3	28.0	100	89	+	+	+
	4	28.5	100	100	+	+	0
	5	26.5	100	97			—
	6	26.5	100	97			—
	7	26.5	100				—
	8	26.5	100	100			—
1.016	1	28.8	15	7	±	0	0
	2	29.0	50	5	+	±	0
	3	27.0	0	0	0	0	0
	4	28.5	81	35	+	+	+
1.018	1	28.0	14	1	+	+	+
	2	29.0	50	6	+	+	0
	3	27.5	22	14	+	0	0
	4	28.5	14	4	0	0	0
1.020	1	28.5	21	14	0	0	0
	2	29.0	17	5	+	0	0
	3	27.0	66	11	0	0	0
	4	25.0	2	2	θ	θ	θ
1.022	1	28.5	15	5	θ	—	—
	2	29.0	21	7	+	0	0
	3	27.0	83	0	+	+	+
	4	25.0	0	0	0	0	0

Legend: + + = strongly positive  
 + = positive  
 ± = weakly positive  
 — — = strongly negative  
 — = negative  
 θ = weakly negative  
 0 = indifferent

Note: The indifferent phase, marked (0), of *B. neritina* may represent the transitional phase of *B. flabellata* and *B. turrita*

natant phase of larvae in sea water having a specific gravity of 1.010 eventually causes the organisms to become photonegative by the time of attachment. (3) If one looks at the column indicating the phototropism of the organisms at the end of sixty minutes, it may be noted that there are more cases of larvae indifferent to light in sea water at normal salinities (density = 1.016 to 1.022 gr./cc.) than there are in media diluted to a specific gravity of 1.010, there being only four cases out of sixteen in which the larvae was photopositive at the end of an hour. This evidence alone, however, might prove unconvincing were it not for other indications of a similar trend that were found when various physical and chemical inductors of metamorphosis were used.

### Reversal of phototropism and loss of light reactions.

1. *The effect of inhibitors of metamorphosis.* Table II shows a positive correlation between a loss of light reactions and a subsequent inhibition of metamorphosis. An absence of photic response, following subjection of the larvae to various anaesthetic agents, seems to have considerable diagnostic value for predicting a subsequent inhibition of metamorphosis. Whether there is a direct causal relationship between loss of light reactions and inhibition of metamorphosis cannot be stated definitively; but the frequent occurrence of the two events suggests that the phenomenon may be more than merely coincidental. Of the nine factors listed in Table II (A), only the last one has produced questionable results. Mixtures of 80 cc. of sea water/20 cc. of N CaCl<sub>2</sub> had produced inhibition of metamorphosis, as reported in a former paper (Lynch, 1949 a). But subsequent trials with the same proportions of sea water and isotonic CaCl<sub>2</sub> failed to show a statistically significant difference between experimental larvae and the controls (Lynch, 1952). Apparently the only other factor that would retard the rate of metamorphosis would be a drop in pH; and experiments with mixtures of isotonic CaCl<sub>2</sub> and sea water gave no indication of an increased hydronium ion concentration. The cause of the discrepancy in the observations made with normal and with isotonic solutions still remains obscure.

2. *The effect of inductors of metamorphosis.* In the presence of stimulating agents which induce precocious metamorphosis, larvae change from a positive to a negative phototropism sooner than the controls, as indicated in Table II. The first four agents which effect a precocious reversal of phototropism in the larvae of *B. flabellata* are also good inductors of metamorphosis. Neutral red, *the most potent of the dyes used*, not only produces a more rapid

Table 2

Factors causing a loss of photic responses (A) and those which induce a premature reversal of phototropism (B). All observations were made on *B. flabellata*, except those on the effects of intense light; the latter were made on *B. neritina*.

A	B
<p>Factors causing a loss of light reactions, the larvae being neither positive nor negative and gathering in the center of the container. Factors marked (*) inhibit metamorphosis; those marked (**) prevent it.</p>	<p>Factors causing a precocious change in phototropism from positive to negative. Factors marked (*) are inductors of metamorphosis. The number of asterisks being roughly proportional to the effectiveness of the factors.</p>
<p>1. ** Excess of magnesium (80 cc. MgCl<sub>2</sub>/20 cc. sea water) at a pH of 8.0. (NaOH added).</p>	<p>1. *** CuCl<sub>2</sub> added to sea water 5 mg/1. Change within 30 min., and negative reaction intense.</p>
<p>2. ** Excess of potassium in sea water in same proportions as magnesium and in lower concentrations. The pH = 7.8.</p>	<p>2. *** Neutral red in sea water in concentr. of 1:100,000. Larvae change within 30 min. and become intensely negative.</p>
<p>3. ** Three ion media (Mg. K. Na; Mg, K. Ca; Mg. Na Ca), except those in which Mg is the ion omitted.</p>	<p>3. ** Methylene blue (1:100,000). Change occurs later than in neutral red and the reaction is less intense.</p>
<p>4. ** Acidified sea water at a pH of 5.7 (acetate buffer) or 6.0 (Mc Ilvaine buffer).</p>	<p>4. * Eosin (1:50,000 and 1:100,000). Larvae intensely negative by one hour.</p>
<p>5. ** KCN in sea water. Concentration = 0.001 M; pH = 7.8.</p>	<p>5. ? Intense light from 100 watt bulb (and also sunlight). Change within one hr. and negative action very intense.</p>
<p>6. ** Alcohol, a 3-3.3% solution in sea water. The addition of neutral red (1:300,000) allows metamorphosis, but larvae show considerable inhibition.</p>	<p>6. ? Sea water at 9.0 (NaOH) and at 9.6 (borate buffer). Change is immediate with borate buffer. Some change with glycine buffer (7.8).</p>
<p>7. ** Ca-free van't Hoff's beta solution.</p>	<p>7. ? Sea water diluted 50%. Change within one hr. and negative reaction very intense.</p>
<p>8. ** Sea water reduced to a temperature of 5°C. with or without neutral red (1:100,000).</p>	<p>8. Sea water acidified by HCl to 5.7 or 7.3. Negative reaction intense after pH rises from 5.7 to 6.8. Metamorphosis inhibited.</p>
<p>9. Slight excess of isotonic CaCl<sub>2</sub> (20:80: :CaCl<sub>2</sub>:sea water.</p>	

change in phototropism than that caused by methylene blue, a weaker metamorphogenic agent, but the negative reaction is also more intense, when both dyes have a concentration of 1:100,000 (pH = 7.8). Eosin, the weakest of the three dyes in terms of inductive potency, poses some difficulties. In one trial with eosin at a concentration of 1:100,000 (pH = 7.8) the larvae were violently photonegative at the end of an hour, but there was little evidence,

if any, of precocious metamorphosis. In another trial the larvae were also strongly photonegative by two hours, but in this case all the larvae eventually became photopositive at the time of setting. This is a very unusual phenomenon! When the concentration of eosin was doubled (2:100,000), the negative response was very strong by two hours, and the larvae metamorphosed at a somewhat more rapid rate than they did in the lower concentration. For some unknown reason there were enormous numbers of geonegative settings following treatment with eosin; in this respect the larvae were notably different from those in sea water containing neutral red dye, for the latter gave somewhat fewer attachments to the surface films than to the bottoms of the containers. Copper chloride, like neutral red, reversed the phototropism of the larvae within thirty minutes, when the amount added to sea water was 5 mg./liter (Lynch, 1949 b). Finally, larvae immersed in sea water at 5°C. first lost their reactions to light and then became photonegative, as the temperature was lowered to -2°C. At this temperature precocious metamorphosis was induced (unpublished data). Since only a single observation on the light reactions of the larvae was made, the phototropic effect of sea water at zero and below has not been included in Table II. One must be cautious in forming generalizations concerning phototropism in *Bugula* larvae, for their light reactions are less constant than their metamorphic responses to physical and chemical agents. For the first four factors listed above, then, there is rather good correlation between the light reactions of the larvae and their subsequent rate of metamorphosis.

On the other hand, correlations between a reversal of phototropism and a precociously induced metamorphosis are less convincing for the remaining four factors listed in Table II. The last of these, sea water acidified by HCl (no. 8), inhibits metamorphosis, and a removal of larvae from sea water acidified by HCl would presumably give negative results comparable to those reported for larvae transferred from sea water acidified by glacial acetic acid (Lynch, 1955). Definite information is wanting for the other three factors causing a premature reversal of phototropism from positive to negative. Thus, it is not known what effect either intense artificial illumination or strong sunlight have on the rate of metamorphosis (Cf. Lynch, 1947, for methods). Presumably intense illumination might hasten the rate of metamorphosis, since light acts synergistically with neutral red dye (Lynch, 1955). Likewise, there is no definite information available at the present time concerning the effect that alkalinity has on the metamorphic rate. In some experiments with sea water raised to a pH of 8.8 by NaOH all the larvae underwent cytolysis; in others, the larvae metamorphosed normally. The few observations made on the effects of removing larvae from sea water at a pH of 8.8 (and higher) to their

normal medium yielded negative results. This problem, therefore, has not been studied thoroughly. The fact that a high pH can cause both cytolysis and a reversal of phototropism would seem to indicate that alkalinity under proper conditions might prove to be an accelerator of the rate of metamorphosis. Finally, the seventh factor listed in Table II, a reduction in salinity, remains one of the most puzzling so far encountered by the writer. Many experiments were performed on the larvae of *B. flabellata* with sea water diluted 50% by distilled water in an attempt to cause them to duplicate the behavior of the southern species. So far all experiments have given negative results.

Nevertheless, observations concerning the effects of diluted sea water have yielded some pertinent information. At a dilution of 50%, cytolysis frequently followed a natatory period of apparently normal duration. In other instances normal metamorphosis took place after exposure to this dilution of sea water. When the amount of distilled water was increased to 60%, precocious fixation began, but the completion of metamorphosis was interfered with to such an extent that normal zooids did not form. At dilutions of 70%, cytolysis was still more inevitable, unless the larvae were removed to their normal medium immediately after metamorphosis had begun. In distilled water alone ejection of the holdfast was accompanied by immediate cytolysis. Indeed, these and other experiments indicate that cytolysis and metamorphosis have much in common. Possibly, then, the change in phototropism from positive to negative that can be observed in the larvae of *B. flabellata* in diluted sea water indicates that an incipient cytolysis has begun. Rescuing the larvae soon enough from this unfavorable environmental condition can result in a normal metamorphosis, such as that which occurs when larvae are transferred to their normal medium from sea water diluted by 50% (Lynch, 1952).

There appear to be two possible explanations of the difference in response of northern and southern species to diluted sea water. First, the southern species, which lives under estuarine conditions at Beaufort, may have acquired an adaptation that would prevent larvae from attaching during low tide and under conditions of reduced salinity. This seems possible, since McDougall (1943) observed that colonies grow more luxuriantly near the surface than they do when submerged a few feet below mean low water mark. This may indicate that attachment during high tide would favor subsequent growth of the colonies. Secondly, the conditions of salinity prevailing at Beaufort may not have been duplicated exactly, since a sensitive hydrometer was not available at Woods Hole. The great similarities in behavior of the northern and southern species lead the writer to believe more strongly, as experimental evidence increases in volume, that differences which appear



to be specific in nature are caused more generally by environmental variables than by genetic constitution. Even larvae of sessile organisms of different phyla show remarkable similarities in their prefixational behavior. Thus, larvae of the ascidians (Grave, 1935), of the bryozoans and of the worm *Spirorbis* (Knight-Jones, 1951) exhibit striking similarities in their reactions to light and darkness, to various chemical agents and to attached organisms of the same species.

#### DISCUSSION

From the above data there appears to be a positive correlation between loss of photic reactions and a subsequent inhibition of metamorphosis. On the other hand, the evidence just reviewed is more indicative of trends than it is compelling for the formulation of a hypothesis that inductors of precocious metamorphosis invariably cause a premature reversal of phototropism or that the future rate of metamorphosis can be predicted from the intensity of a phototropic reaction, either positive or negative. It had been asked whether all agents which cause a premature reversal of phototropism in *Bugula* larvae also induce precocious metamorphosis, and it was found that definite information concerning some of these factors is not available. The question might be asked whether all inductors of precocious metamorphosis so far encountered reverse prematurely the light reactions of the larvae.

Both hypertonic sea water and an excess of  $\text{CaCl}_2$  are good inductors of metamorphosis. The latter is immediately effective in proportions of 80 cc. of isotonic  $\text{CaCl}_2$ /20 cc. of sea water at a pH of 8.0. Hypertonic sea water generally does not have a pronounced effect on the rate of metamorphosis unless the freezing point depression is -2.73 or lower (Lynch, 1952). Neither of these inductors of metamorphosis, however, cause a notable reversal of phototropism. But in both cases larval activity is greatly reduced, apparently because both these solutions have a deleterious effect on ciliary action. And a reduction in activity, whether followed by inhibition of fixation or acceleration of the metamorphic rate, invariably causes a loss of oriented swimming movements. Larvae react neither positively nor negatively; they do not even gather in the center of the container, as do those described as having lost their light reactions. Strong phototropic responses, either positive or negative, require much activity on the part of bryozoan larvae. This is not true, however, of all organisms, for Holmes (1905, p. 317), after observing the reactions of *Ranatra*, stated, "The causes that produce the negative reaction to light are, as a rule, those which lead to diminished activity and excitement. Cold, exposure to darkness, and the quieting effect of contact stimuli lead to a condition of lessened excitability and, perhaps as a result

of this, to a negative reaction to light." In bryozoan larvae the effects of various agents on ciliary movements must be taken into account in considering possible correlations between changes of light reactions and subsequent inhibition or acceleration of metamorphosis.

Since much of this paper has concerned comparisons of the behavior of northern and southern species of *Bugula* larvae certain environmental factors characteristics of the experimental conditions attending these observations should be mentioned. These concern the normal duration of the natatory period.

During one of the summers prior to 1954, experiments on *B. flabellata* were carried out in a comparatively cool basement room of the Marine Biological Laboratory. In twelve observations involving 686 larvae it was found that  $77\% \pm 16\%$  had metamorphosed by twelve hours, and 23% were still unattached. During other summers prior to 1954, however, experiments were performed in a somewhat warmer room on the second floor of "the brick building". During one of these summers the natatory period of *B. flabellata* was determined by a series of eighteen observations. These were afterwards reported by the writer (Lynch. 1949 a). If the results of the last seven, involving comparatively short natatory periods, can be attributed to an increased osmotic pressure due to evaporation of the medium, as appears obvious, the other eleven show only two cases in which 25-35% of the larvae were unmetamorphosed by twelve hours and two instances in which 5-10% remained unattached. In seven of the eleven observations less than 3% were unaffixed at twelve hours. During the summer of 1954, observations were carried out on the second floor of the "Old Lecture Hall", where the temperature during the afternoon became unpleasantly hot, generally ranging from 24-27°C. and often reaching 29°C. During this summer the photonegative phase of the larvae set in earlier than it did in any prior observations, sometimes within an hour or two after release of the organisms from the ovicells, and the rate of metamorphosis was also accelerated. During that summer one set of seven experiments gave an unusually high mean rate of metamorphosis at the end of an hour, being  $63.0 \pm 19.2\%$ . Another set of eighteen experiments, performed at temperatures averaging about two degrees lower than the above, gave a mean of  $50 \pm 23\%$ , and another set of eight gave  $40 \pm 20\%$  as the mean at one hour. These rates of metamorphosis appear to be unusually high for the northern species.

Experiments on *B. neritina*, during the summers of 1944 and 1945, were performed at still higher temperatures, that of the room ranging from 30-32°C. and that of the sea water varying generally from 27 to 29°C. In these cases the rate of metamorphosis was found to be  $96 \pm 4.7\%$  at the end of an hour for larvae in sea water having a specific gravity of 1.022 to 1.023. With increasing

temperatures, then, the normal duration of the natatory period seems to decrease progressively. Furthermore, heating sea water containing *B. flabellata*, induces an unusually rapid rate of metamorphosis (Lynch, 1949 b). These observations pose an interesting question. What differences in the duration of the natant period of northern and southern species can be assessed to genetic constitution and what variables can be attributed to environmental factors?

In 1948, before the writer was aware of the effects that increasing temperatures appear to have on the duration of the natatory period of *B. flabellata*, an attempt was made to solve the problem of the notable difference in natatory periods of northern and southern species. At that time the writer considered that the much briefer natant phase of *B. neritina* might be due to the copper content of Beaufort sea water, assuming it to be higher than that prevailing at Woods Hole, since the former lies at the mouth of the Newport river, which would presumably bring copper into the sea. This assumption was later verified by Glaser and Anslow (1949), who found the copper content of Beaufort sea water to be as high as  $1 \times 10^{-6} M$ , whereas that of Woods Hole was only  $2.5 \times 10^{-7} M$ . (These authors note that their estimations of copper content of Beaufort sea water may have been affected by errors due to contamination.) Larvae of the northern species, *B. flabellata*, were placed in sea water taken at low tide and shipped to Woods Hole from Beaufort. But no observable abbreviation of the natatory period could be observed by using this sea water. Unfortunately, however, the temperature had not been raised to that prevailing at Beaufort. Conceivably, had both the copper content and the temperature characteristic of Beaufort been duplicated at the time the experiments were performed, the natatory period of the northern species might have closely approximated that of *B. neritina*.

#### SUMMARY AND CONCLUSIONS

The observations just reviewed concerning the apparent effects of increasing temperatures by no means warrant a conclusion that the notably briefer free-swimming period of the southern species can be attributed solely to temperature or to a combination of higher temperature and greater copper content of the sea water. But they are suggestions of possible correlations. Bryozoan larvae are extremely sensitive to even delicate changes in environment. This is shown by the fact that the larvae of *B. flabellata* are extremely inhibited in artificial sea water but undergo fixation at a rate almost equal to that of the controls when as little as 0.02 mg. of  $\text{CuCl}_2$  is added per liter of artificial media.\* There appear to be environmental factors tending to induce metamorphosis that are

\*Evidence, obtained after this paper went to press, indicates that factors other than copper may have been involved in these experiments.

delicately balanced by those which inhabit fixation. Changes in extrinsic factors, almost unperceptible to the observer, can alter both the rate of metamorphosis and the reactions of the larvae to light and gravity. Temperature, the amount and intensity of light received, darkness, the *milieu* of ions surrounding the larvae, and perhaps the length of time the eggs are held within the ovicells before hatching—all these factors profoundly affect the physiological condition of the organisms and their concomitant phototropic reactions as well as the length of the natatory period.

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