THE RELATIONSHIP OF LIGHT DURATION TO OXYGEN CONSUMPTION IN THE GREEN, FRESHWATER SPONGE SPONGILLA LACUSTRIS

ERNEST J. SZUCH, EUGENE H. STUDIER and ROGER B. SULLIVAN, JR. Department of Biology, University of Michigan-Flint, Flint, Michigan 48503, U.S.A.

(Received 5 July 1977)

Abstract—1. Oxygen consumption of green Spongilla lacustris in the light is lower than that in the dark.

2. The relationship between oxygen consumption (OC in μ l O₂/mg dry wt/hr) and hours of continuous light (HL) is:

$OC = 1.207 - 0.0143 (HL)^2$.

3. For light durations greater than 9 hr. symbiotic zoochlorellae produce photosynthetically derived oxygen in excess of the needs of the symbiotic complex.

INTRODUCTION

The occurrence of symbiotic algae is quite widespread in the invertebrate phyla. They have been reported in the Phyla Protozoa, Porifera, Coelenterata, Ctenophora, Rotatoria, Platyhelminthes, Annelida, Mollusca and Echinodermata (McLaughlin & Zahl, 1966). Although, in many instances, the exact nature of these algal-invertebrate associations has not been determined, possible advantages to the algal symbiont and the animal host have been pointed out. Symbionts may receive protection, carbon dioxide and other inorganic nutrients while the host may derive oxygen, some form of nutriment and an automatic removal of wastes.

Spongilla lacustris, a freshwater sponge common to cold-temperate regions of the northern hemisphere (Penney & Racek, 1968), is usually drab to bright green due to the presence of presumably intracellular symbiotic zoochlorellae. This association has been described as protocooperation-a non-obligatory association from which both members derive benefit (Miller, 1964). Few studies have dealt specifically with aspects of this symbiosis. Miller (1964), using symbiotic and aposymbiotic organisms, studied the effect of symbiotic algae on sponge growth. It appears that the only previous study of oxygen production and consumption in a freshwater algal-sponge association is that of Gilbert & Allen (1973) on S. lacustris. Most investigations have been primarily concerned with the animal component of the symbiotic complex (Simpson & Gilbert, 1973, 1974; Gilbert, 1974; Gilbert et al., 1975; Brauer, 1975; Frost, 1976).

It is of interest to know if oxygen produced by the endocellular algae during photosynthesis might fulfill part or all of the host's oxygen requirements. In this paper rate of oxygen production and consumption of symbiotic *S. lacustris* is assessed under various periods of light duration. to 6 July, 1976 from Hoisington Lake, Livingston County, Michigan. Sponges emerge from the predominantly sandy bottom at a water depth of 1-2 m. Chemical analysis of water collected from the area of the sponge population, determined using Hach prepackaged chemical methods (Hach Chemical Co., Ames, Iowa, 50010), showed the following: alkalinity, 120.3 mg/l CaCO₃; calcium hardness, 101.7 mg/l CaCO₃; total hardness, 187.1 mg/l CaCO₃; silica, 27.5 mg/l SiO₂; pH 8.3; no detectable nitrogen or phosphate. Osmotic pressure, measured with an Advanced Instruments Wide Range Osmometer (Model 3W), was 2.2 mOsm/l. Temperature of the lake water was 16°C. Sponges were hand-picked and immediately transported to the laboratory. Specimens were used as soon as possible after collection, usually within 4 hr.

Sponges were tested at 0, 2, 4, 6, 8 and 12 hr of light/24 hr, with each light cycle ending at 0400 hr. A different piece of sponge was used in each test. All of the tests were conducted in an environmental chamber (Sherer-Gillett, Model No. CEL-5123-7) operated at the chosen light cycle at a temperature of $16 \pm 1^{\circ}$ C and light intensity of 41 W/m^2 (range $37-44 \text{ W/m}^2$) as measured with a YSI-Kettering Radiometer (Model 65A).

For each test a section of non-gemmulating sponge 2-5 cm in length was placed in each of 6 glass-stoppered 250 ml Erlenmeyer flasks. Flasks were filled with freshly collected lake water with care taken to minimally aerate this water during transfer. Two flasks with no sponges wcrc also filled with lake water to be incubated along with those containing the sponges to determine plankton productivity and respiration. Flasks were stoppered, making sure there were no trapped air bubbles, and sealed with petrolatum. Exact volumes of each flask were determined by differential weighing of the emply flask and the flask filled with water, with the proper corrections for the density of water.

Oxygen concentrations at the beginning and end of each 24-hr incubation period were determined by the Winkler method, as described by Hoar & Hickman (1967), using a Gilmont 2.0 ml Micrometer Buret.

Dry weights were determined with a Mettler Type H6 Analytical balance after air-drying sponge pieces until constant weight was achieved.

RESULTS AND DISCUSSION

MATERIALS AND METHODS

Sponges used in this study were collected from 21 June

Corrections for plankton metabolism were made in calculating oxygen consumption of the sponges. Vari-

ation in the hours of continuous light per day resulted in changes in oxygen consumption of *S. lacustris*. The relationship between oxygen consumption (OC in μ l O₂/mg dry wt/hr) and hours of continuous light per day (HL) is:

$$OC = 1.207 - 0.0143 (HL)^2 (+0.029)(+0.0007)$$

where values in parentheses are standard errors for the intercept and slope (F = 393.7, df 1 and 33, $P \le 0.0005$ and $r^2 = 0.92$).

Oxygen consumption of *S. lacustri* in the light is lower than that of organisms in the dark (Fig. 1). This difference could be the result of inhibition of the sponge's respiration by light but is more likely the result of algal photosynthesis. Oxygen produced by the endocellular algae is used by the host's cells. thus reducing the need for removal of oxygen from the environment. Hence the rate of oxygen uptake is depressed in the light even though the algal-sponge complex continues its respiratory processes.

Given the experimental condition, 9.19 hr of continuous light result in no net oxygen consumption for the symbiotic complex on a 24-hr basis. For days of continuous light greater than 9.19 hr, algae supply oxygen in excess of its needs and those of the sponge combined for the entire 24-hr period. The temperature and light intensity to which the organisms were exposed fall well within the range of the natural situation. Thus, the 14 15 hr days encountered by the organisms in their environment during the summer months is sufficient to produce enough photosynthetically derived oxygen to supply the total oxygen demands of the symbiotic system. This suggests independence from a continuous exogenous supply of oxygen.

In the only previous study of oxygen utilization by *S. lacustris*, Gilbert & Allen (1973) measured oxygen production of the organism during a 2.3-hr incubation period under natural conditions. Their values can be converted to units comparable to ours by using the weight relationship determined in their study as follows: the mean ratio of ash-free dry weight to dry weight is 0.78. In this way, a limited number of comparisons with their data are possible.

> LI M D M M D

Fig. 1. The relation of oxygen consumption (positive values) or production (negative values) of green *Spongilla lacustris* in μ l/mg dry wt/hr to hours of continuous light per day.

Gilbert & Allen (1973) found that on 3 August 1970, from 1140 to 1400 hr, the amount of oxygen consumed as a result of respiration of the symbiotic complex was 8.16 µl O₂/mg dry wt/hr. Our value for respiration, determined for a 24-hr incubation period in the dark, is 1.207 μ l O₂/mg dry wt/hr. Some of this difference is assumed to be a result of different experimental temperature (24 and 16 C, respectively). However, compensating for the temperature effect by assuming a Q10 of 3 still makes their value more than twice ours. We must agree with these investigators that their value for basal respiration is elevated. Gilbert & Allen (1973) also estimate that the oxygen consumed by the symbiotic complex over a 24-hr period is more than that produced by the algae. This is in direct contradiction to our data. On the date of their measurements, the symbiotic complex was exposed to approximately 14.5 hr of light (List, 1968) at a measured light intensity 2.3 times that used in our study and should therefore produce oxygen in excess of its needs. Again, elevated temperature may explain part of this contradiction.

As pointed out by Miller (1964) for *S. lacustris* and Pardy & Dieckmann (1975) for *Hydra viridis*, the oxygen relations discussed above are probably secondary consequences of both species' symbiotic relationships with their zoochlorellae. The major role of the algae for both of the above host species is most likely nutritional supplementation (Miller, 1964; Pardy & Dieckmann, 1975). For *S. lacustris*, however, it seems clear that the algae, by virtue of their photosynthetic production of free oxygen. must be useful to the sponge and result in some degree of improvement in the life situation of the host.

Acknowledgements We thank Drs G. L. Pace and R. W. Dapson for their critical reviews of this manuscript.

REFERENCES

- BRAUER E. B. (1975) Osmoregulation in the fresh water sponge, Spongilla lacustris. J. exp. Zool. 192, 181-192.
- FROST T. M. (1976) Investigations of the Aufwuchs of freshwater sponges. I. A quantitative comparison between the surfaces of *Spongilla lacustris* and three aquatic macrophytes. *Hydrobiologia* 50, 145-149.
- GILBERT J. J. (1974) Field experiments on sexuality in the freshwater sponge Spongilla lacustris. The control of oocyte production and the fate of unfertilized oocytes. J. exp. Zool. 188, 165–178.
- GILBERT J. J. & ALLEN H. L. (1973) Chlorophyll and primary productivity of some green, freshwater sponges. Int. Revue ges. Hydrobiol. 58, 633–658.
- GILBERT J. J., SIMPSON T. L. & DE NAGY G. S. (1975) Field experiments on egg production in the fresh-water sponge Spongilla lacustris. Hydrobiologia **46**, 17-27.
- HOAR W. S. & HICKMANN C. P. JR (1967) A Laboratory Companion for General and Comparative Physiology. Prentice-Hall, Englewood Cliffs.
- LIST R. J. ed. (1968) Smithsonian Meteorological Tables. Smithsonian Press, Washington.
- MCLAUGHLIN J. J. A. & ZAHL P. A. (1966) Endozoic algae. In Symbiosis (Edited by HENRY S. M.), Vol. I. Academic Press, New York.
- MILLER S. A. (1964) The effect of symbiotic algae on the growth of *Spongilla lacustris*. Masters Thesis, University of Washington.





- PARDY R. L. & DIECKMANN C. (1975) Oxygen consumption in the symbiotic hydra Hydra viridis. J. exp. Zool. 194, 373-378.
- PENNEY J. T. & RACEK A. A. (1968) Comprehensive Revision of a Worldwide Collection of Freshwater Sponges (Porifera: Spongillidae). Smithsonian Press, Washington.
- SIMPSON T. L. & GILBERT J. J. (1973) Gemmulation, gemmule hatching. and sexual reproduction in fresh-water

sponges. I. The life cycle of Spongilla lacustris and Tubella pennsylvanica. Trans. Am. microsc. Soc. 92. 422-433.

SIMPSON T. L. & GILBERT J. J. (1974) Gemmulation, gemmulc hatching, and sexual reproduction in fresh-water sponges. II. Life cycle events in young, larva-produced sponges of Spongilla lacustris and an unidentified species. Trans. Am. microsc. Soc. 93, 39-45.