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# Physiology of benthic algae in tide pools I. Photosynthesis-temperature relationships in summer*

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Nine species of seaweeds were collected from tide pools or subtidal zone in summer, and their photosynthesis- and respiration-temperature curves were simultaneously determined in the range from 15°C or 20°C to 40°C. The optimum temperature for photosynthesis was apparently higher in the algae from tide pools than in those from subtidal zone. There were also remarkable differences in heat-resistibility among the algae collected from different levels. The highest temperature recorded in the tide pools, that is 40°C or more, is conidered to be severe even for the algae living there because their photosynthetic activities were decreased during an experiment at 40°C for one hour or less. Their activities were, however, recovered up to the initial level by culturing at 25°C for 18 hours or less. There were also remarkable differences in photosynthesis-temperature relationships between the samples of the same species collected from the upper level and the lower level.

The patterns of photosynthesis-temperature curve in *Ulva pertusa* implied existences of at least two enzyme systems, one of which was heat-susceptible and the other heat-resistible, participating in the photosynthetic process of this alga.

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The water temperature in tide pools sometimes rises up to 40°C or above in summer at Shimoda. It is surprising to find out some seaweeds living in such hot water. One of the present authors reported a characteristic phototsynthesis-temperature curve showing large heat-resistibility for an alga collected from a tide pool in summer (YOKOHAMA 1973a).

In this paper photosynthesis-temperature relationships in several algae collected from tide pools will be reported in comparison with those of algae from subtidal zone.

## Materials and Methods

The algae were collected from tide pools or subtidal zone at the shore near the Shimoda Marine Research Center, Shimoda (34°40′N 138°57′E), Izu Peninsula.

The collections were made in the morning. The collected algae were soaked in a large volume of sea water and carried to the laboratory of the Marine Research Center, where they were then kept in running sea water before use. This work was made in the summer of 1977.

*Gracilaria verrucosa*, *Gymnogongrus flabelliformis*, *Sargassum thunbergii*, *Enteromorpha crinita* and *Ulva pertusa* were collected from tide pools at higher intertidal zone where water temperature sometimes rised up to 40°C or above. *Corallina pilulifera* and another sample of *Gymnogongrus flabelliformis* were collected from pools at middle intertidal zone where the highest temperature recorded was about 35°C. On the other hand the algae collected from

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subtidal zone are considered to have been growing at almost constant temperature lower than 25°C.

Photosynthetic production and respiratory consumption of oxygen by the algae were measured with differential gas-volumeters (YOKOHAMA and ICHIMURA 1969). The vessels of the gas-volumeters were of 15 m*l* in capacity. When measuring photsynthetic oxygen evolution by algal material, a piece of 2-3 $cm^2$ or comparable size obtained from the young pasrt of a thallus was placed in the reaction vessel with 5 m*l* of filtered sea water. The light source used was an incandescent lamp mounted in a lantern slide projector. At the position of the reaction vessel the light intensity was 40 klux which was considered to be intense enough to saturate the photosynthesis in most seaweeds judging from the data in the previous papers (YOKOHAMA 1973b, 1973c, KAGEYAMA and YOKOHAMA 1974). When measuring respiratory oxygen consumption by algal material in the dark, the vessel used had a side arm containing a few drops of 20% potassium hydroxide solution to absorb carbon dioxide. The quantity of algal material in the reaction vessel was three- to fourhold that used in measuring the photosynthesis.

The same piece of tissue was used throughout a series of measurements at different temperatures, begun at 15°C or 20°C and ended at 40°C. A photosynthesis- or respiration curve was made up from the data of the three to six series of measurents.

## Results

Fig. 1-3 show the photosynthesis- and respiration-temperature curves obtained in five species of Rhodophyceae. The curves in Fig. 1 are in two species of Corallinaceae, one of which was *Corallina pilulifera* collected from a tide pool at middle intertidal zone and the other was *Serraticardia maxima* from low water mark. Those in Fig. 2 are in two *Gracilaria* species *G. verrucosa* from a tide pool at higher intertidal zone and *G. textorii* from low water mark. Those in Fig. 3 are in *Gymnogongrus flabelliformis* from a tide pool at higher intertidal zone and from that at middle intertidal zone. As can be seen, in the algae from the tide pools the optimum temperature for photosynthesis was 30°C or above and a rate close to the optimum level was maintained at 35°C, while in the algae from subtidal zone the optmum temperature was lower than 30°C, and the activity was almost lost at 35°C. There was also a remarkable difference in photosynthesis-temperature relationships between the individuals of *Gymnogongrus flabelliformis* collected from

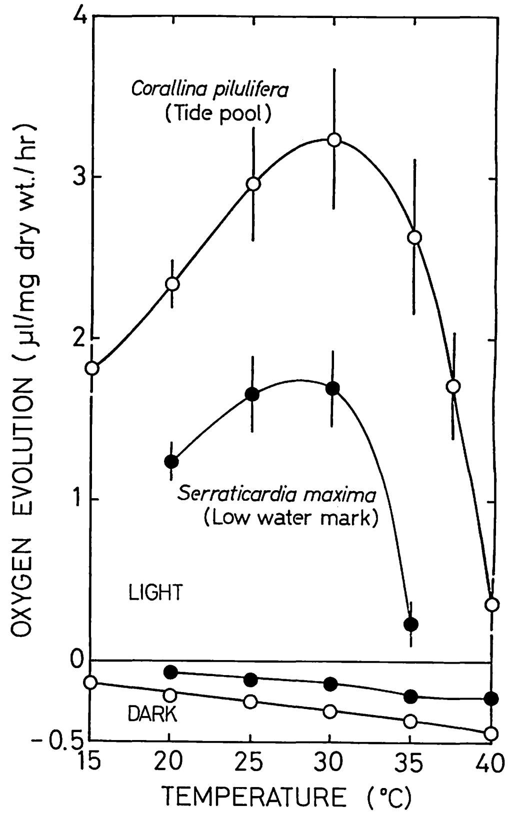


Fig. 1. Photosythesis- and respiration-temperature relationships in the two species of Corallinaceae, one of which was *Corallina pilulifera* collected from a tide pool at middle intertidal zone and the other *Serraticardia maxima* from subtidal zone (low water mark). Mean values of measurements repeated three to six times are plotted with the standard deviations. Light intensity was 40 klux.

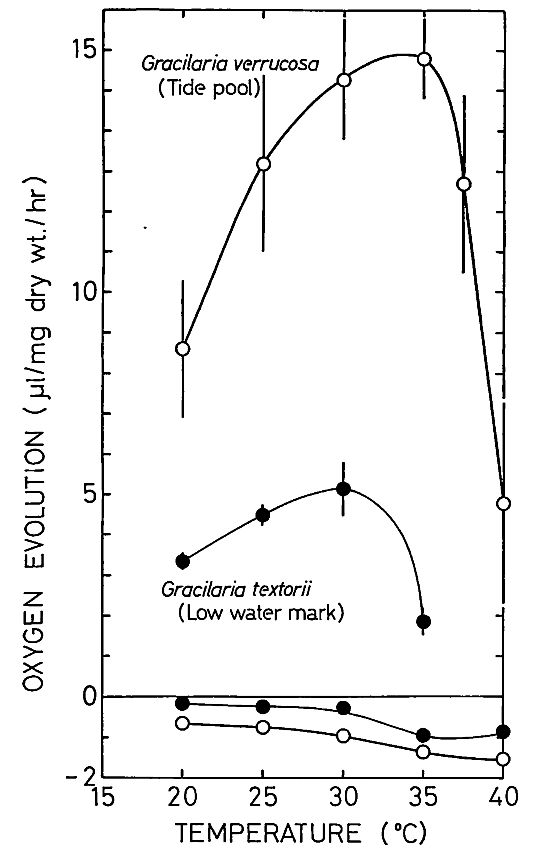


Fig. 2. Photosynthesis- and respiration-temperature relationships in *Gracilaria verrucosa* from a tide pool at higher intertidal zone and *G. textorii* from subtidal zone (low water mark).

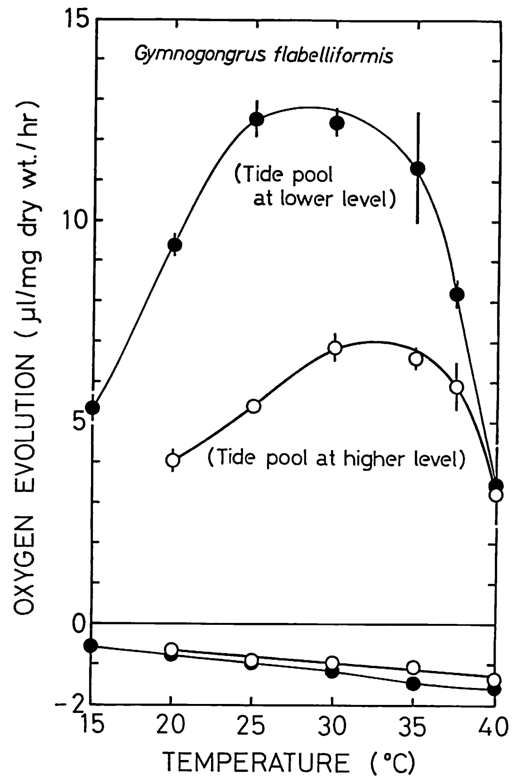


Fig. 3. Photosynthesis- and respiration-temperature relationships in *Gymnogongrus flabelliformis* from a tide pool at higher intertidal zone and from that at middle intertidal zone.

the tide pool at higher intertidal zone and from that at middle intertidal zone as can be seen in Fig. 3.

The difference in photosynthesis-temperature relationships is also remakable between a brown alga *Sargassum thunbergii* from a tide pool and a subtidal brown alga *S. ringgoldianum* as can be seen in Fig. 4. As for the respiration, the rate in the latter alga rapidly increased with increase in temperature especially in the higher range.

The curves of the chlorophycean algae are shown in Fig. 5 and 6. As can be seen, the phtosynthesis-temperature relationships in *Ulva pertusa* varied with the depth of collection. The optimum temperature in the sample from a tide pool at higher intertidal zone was about 30°C, while that in the sample from low water mark was 25°C. The curve of the latter has an apparent shoulder at around 35°C, which implies that the photosynthesis in this alga was participated not only by the enzyme system with the optimum at 25°C but also by another system with the optimum at around 35°C.

*Enteromorpha crinita* was collected from a tide pool at the highest level of intertidal zone. As can be seen in Fig. 6, it had an extreme heatresistibility.

The photosynthetic mechanisms of all the algae collected seemed more or less injured at 40°C. Soon after the measurement at 40°C for one hour or less the photosynthetic rate in each sample was measured again at 25°C and compared with that measured at the same temperature before the experiment at 40°C. The ratio of the rate after 40°C

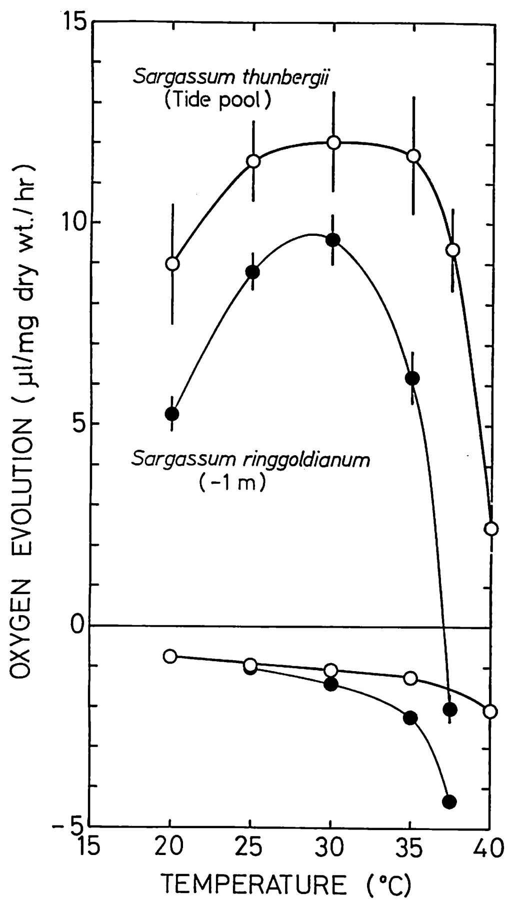


Fig. 4. Photosynthesis- and respiration-temperature relationships in *Sargassum thunbergii* from a tide pool at higher intertidal zone and *S. ringgoldianum* from subtidal zone (depth of 1 m).

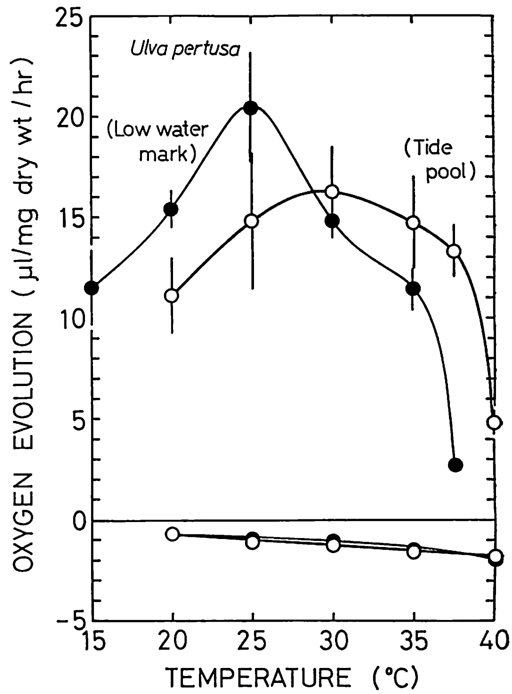


Fig. 5. Photosynthesis- and respiration-temperature relationships in *Ulva pertusa* from a tide pool at higher intertidal zone and from subtidal zone (low water mark).

to that before 40°C was 0.5 to 0.85 in the algae from the tide pools at higher intertidal zone as shown in Fig. 7. The ratio was about 0.2 in *Corallina pilulifera* from the tide pool at middle intertidal zone. The ratios in the algae from subtidal zone were extremely low or negative. The photosynthetic activities of the former group of algae were recovered up to the initial level during incubation at 25°C for 18 hours or less. The activities of the latter group were never recovered in the same condition.

## Discussion

There were remarkable differences in photosynthesis-temperature relationships between the algae collected from the tide pools and those from subtidal zone. The patterns of the photosynthesis-temperature curves in the former algae are adaptive to the special condition of the tide pools. However, the highest temperature recorded in the tide pools, that is 40°C or above, was considerably higher than the optimum temperature for photosynthesis in those algae and seems severe for them. In general cases the environmental temperature never exceeded the optimum temperature for photosynthesis in aquatic plants (ARUGR 1965a, 1965b, YOKOHAMA 1971, 1973a, HEALEY 1972, HATA and YOKOHAMA 1976). During the low tide on a sunny day in summer the photosynthetic activities of the algae living in the tide pools at higher intertidal zone are considered to be more or less decreased since their activities were remarkably decreased with an artificial exposure to 40°C for one hour or less. The activities would be, however, re-

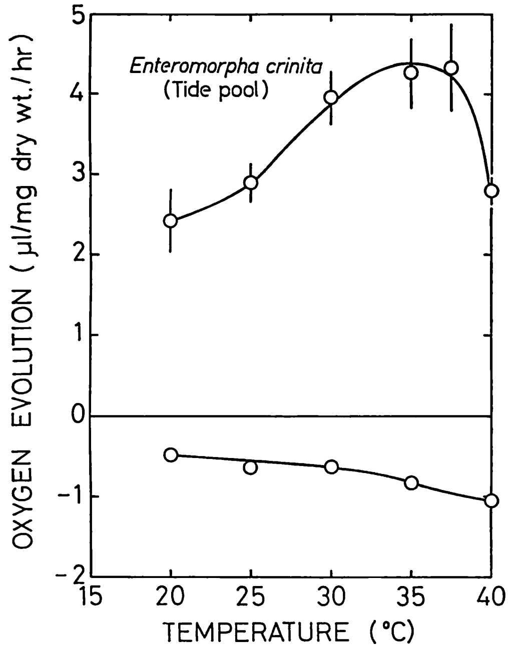


Fig. 6. Photosynthesis- and respiration-temperature relationships in *Enteromorpha crinita* from a tide pool at the highest level of intertidal zone.

covered up to their initial levels by the next morning since they were experimentally recovered at 25°C for 18 hours or less.

There were also remarkable differences in photosynthesis-temperature relationships between the samples of the same species collected from the upper level and the lower level. The shift of the optimum temperature between the different samples of *Ulva pertusa* is considered to have resulted from change in ratio between the two enzyme systems paticipating in the photosynthesis, one of which is heat-susceptible and the other heatresistible, since the peak at 25°C and the shoulder at around 35°C of the photosynthesis-temperature curve in the sample from subtidal zone imply existences of both the enzyme systems.

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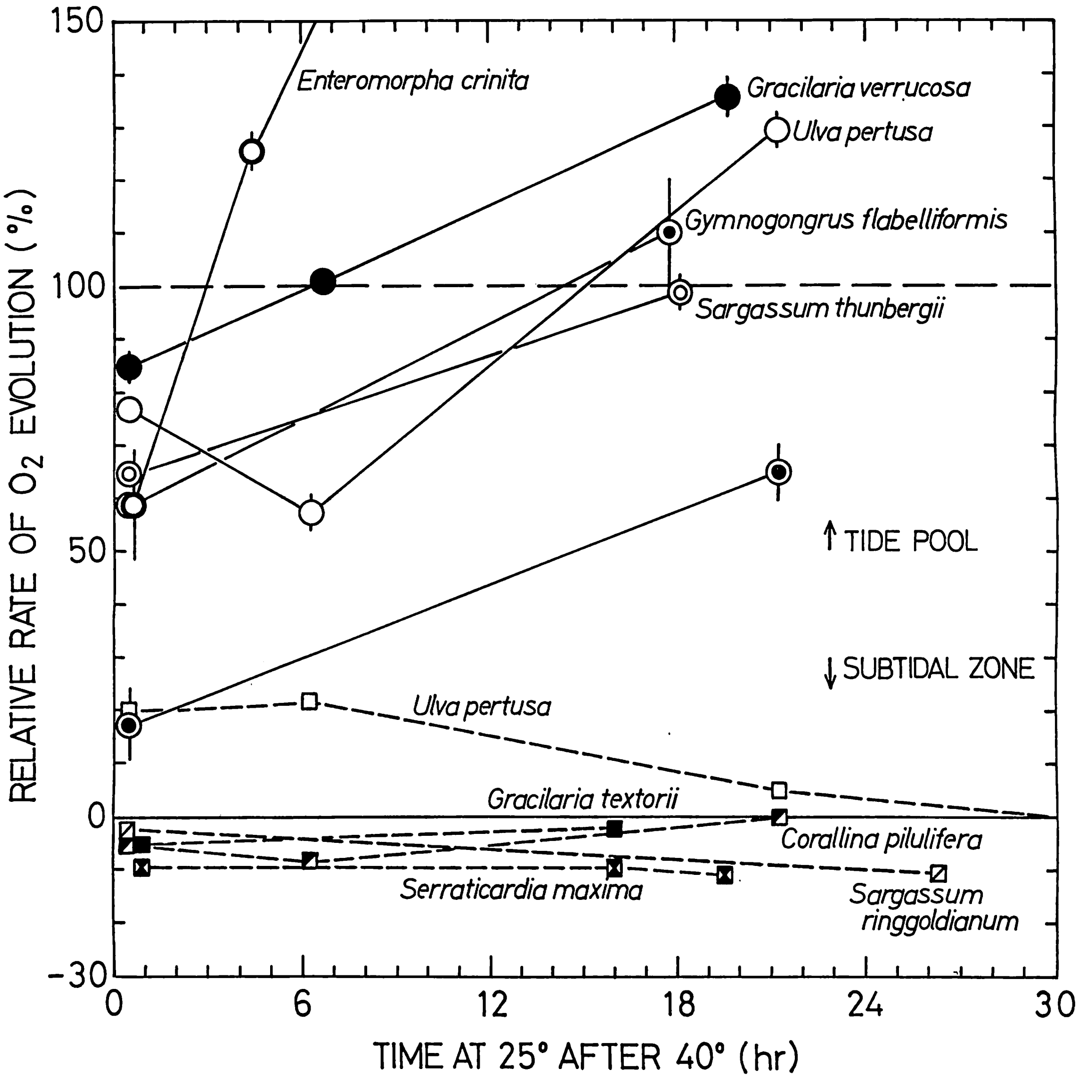


Fig. 7. The time courses of recovery of photosynthetic activity at 25°C in the algae from the tide pools and from subtidal zone after exposure to 40°C for about one hour. A relative rate means the percentage of a photosynthetic rate measured at 25°C after the exposure to 40°C per that measured at the same temperature before the exposure to 40°C.

**水沢政雄*・影山明美**・横浜康継**：タイドプール性海藻の生理 I. 夏季の光合成―温度特性**

伊豆下田では夏季には潮間帯上部のタイドプールの水温が 40°C 前後になることが多い。このようなタイドプールと漸深帯とから数種づつ海藻を採って，光合成―温度特性を比較したところ，前者から得たものは後者からのものに較べて光合成の至適温度が高く耐熱性も優れていた。それらも 40°C に 1 時間近く置くと光合成活性がかなり低下したが，その後の 25°C 中で18時間以内に完全に復活した。漸深帯からのものは 40°C でほとんど失活し，復活もしない。アナアオサは両環境から得たが，この種では環境により，低温型・高温型酵素系間の関与の比率が異なることを暗示する光合成―温度曲線が得られた。(*168 東京都杉並区久我山 4 -29-23，立教女学院短期大学. **415 静岡県下田市 5 -10- 1，筑波大学下田臨海実験センター)